# ASPECTS OF THE CRANIAL MORPHOLOGY OF THE THEROCEPHALIAN *Moschorhinus* (REPTILIA: THERAPSIDA)

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## ERRATA

| | | |
|---|---|---|
| p iii, line 11 | : | For "alhough" read "although". |
| p 11 | : | "The dorsal part of the pterygoid contacts the foot of the epipterygoid dorsally" should read "The dorsal part of the pterygoid contacts the ventral surface of the foot of the epipterygoid". |
| pp 6, 7 | : | "within the jugal arch" should read "medial to the jugal arch". |
| pp 6, 25, 26, 32, 129 | : | "temporal fossa" should read "temporal *fenestra*". |
| p 82 | : | "ventro-lateral flange of the parietal" should read "latero-ventral flange of the parietal". |
| pp 9, 62, 63, 65, 105, 150, 151, 172 | : | "processus ascendens of the epipterygoid" should read "processus ascendens". |
| pp 123, 124, 128, 130, 131 | : | "Jollie (1962)" should read "Jollie (1973)". |
| pp 103, 161 | : | "Nopsca" should read "Nopcsa". |
| Add to References | : | BOONSTRA, L.D. 1938. On a South African mammal-like reptile Beuria cynops. Palaeobiologica 6 : 164-183. |
| | : | OWEN, R. 1876. Description of the Reptilia of South Africa in the collection of the British Museum". 1-2 London : British Museum. |

## ABSTRACT

A sound understanding of the morphology of the Therocephalia is essential to our understanding of the reptile-mammal transition. In this thesis the anatomy of the posterior half of the Moschorhinus skull is described in detail. This study revealed many aspects overlooked or misinterpreted by other authors.

Two Moschorhinus skulls were studied externally. Several misinterpretations concerning the anatomy of the skull were discovered in the literature. It was therefore deemed necessary to redescribe the external morphology of the skull of Moschorhinus.

The skulls were subsequently sectioned with a rock-cutting saw and the matrix filling the endocranium of each was prepared out in order to study the interiors. This study yielded vital information concerning the morphology of the endocranium of Moschorhinus which was previously unknown. Moreover, this is the first detailed description of the complete braincase of a therocephalian.

The position of certain cartilaginous and membranous structures, which would have been present in life, is discussed. This new information also made it possible for the first time to reconstruct the unossified side-wall of the endocranium and to determine the lateral limits of the brain and associated features of a therocephalian. Endocasts of the braincases were made and with the help of these, the morphology of the inner ear and certain

parts of the brain as well as the position of certain cranial nerves and bloodvessels could be determined. These features are described and compared with those of other therapsids. The morphology of the inner ear is compared to that of gorgonopsians and cynodonts. The probable morphology of the side wall of the endocranium, brain and associated structures are compared with those of extant reptiles. The position of the cranial bloodvessels is compared with that of cynodonts and extant reptiles and a new theory concerning the evolutionary development of these bloodvessels from the primitive reptile level to the cynodont level is proposed. It was found that alhough many mammal-like features are present in the therocephalian skull, the morphology of the braincase, cranial bloodvessels, brain and associated structures were essentially typically reptilian.

In the light of this new information concerning the anatomy of the posterior half of the skull and associated soft structures of Moschorhinus, the taxonomic position of this genus relative to the other Therocephalia is discussed.

## DECLARATION

I declare that this thesis is my own unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

(Name of Candidate)

30th day of October, 1989.

## ACKNOWLEDGEMENTS

I wish to thank Dr C.E. Gow and Prof J.W. Kitching for their advice and guidance. I would also like to thank my family and especially my wife, Juanita, for their continuous support and patience. I am also grateful for the Wits University Senior Bursary received in 1985 and 1986.

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# CHAPTER 1: INTRODUCTION

The interrelationships of the Therocephalia and their relationship with the Cynodontia are not known well enough. Certain authors such as Broom (1938), Brink (1951), Hopson & Crompton (1969) and Kemp (1972) are of the opinion that the cynodonts had a therocephalian ancestor, while others such as Romer (1969), Kermack & Kermack (1984) and Hopson & Barghusen (1986) argue that the cynodonts arose independently of Therocephalia from a more primitive ancestor. Most of the former authors accept scaloposaurid ancestry for the cynodonts while Kemp (1972, 1982) has argued that the cynodont ancestor was closely related to the whaitsiids.

To unravel therapsid phylogeny it is essential to know more about therocephalian morphology. The present study attempts to broaden our knowledge of Moschorhinus kitchingi, which is an interesting therocephalian with a mixture of primitive and advanced characters.

The skull of Moschorhinus has been described by Broom (1920), Boonstra (1934b), Brink (1958) and Mendrez (1974a). The elements forming the anterior half of the skull are well known from these descriptions. However, due to the poorly preserved braincases in most Moschorhinus specimens, or insufficient preparation thereof, certain misconceptions arose concerning the relations of the elements constituting the posterior half of the skull.

Two Moschorhinus skulls were selected for this study. Although these skulls are somewhat damaged and distorted, the pos-

terior parts of the skulls are in such a condition that with careful preparation it was possible to discover a wealth of information that added to our knowledge of the Moschorhinus skull. The elements constituting the posterior half of the skull and their interrelationships are described in Chapter 3.

Our knowledge of the therocephalian endocranium is based on the work of authors such as Haughton (1918), Boonstra (1934b), Broom (1936), Olson (1938b), Crompton (1955) and Boonstra (1968). Aforementioned descriptions were done mostly on scaloposaurids and pristerognathids, and until now nothing has been known about the moschorhinid endocranium.

The abovementioned Moschorhinus skulls were sectioned, the one sagitally, the other horizontally and the matrix was removed, thereby exposing the walls of the endocranium. The elements forming the posterior part of the endocranium and their interrelationships are described in Chapter 4.

Certain aspects of the Moschorhinus skull are compared to those of other therapsids and the relationships of the brain, bloodvessels and nerves to the surrounding bony elements are discussed in Chapter 5.

## CHAPTER 2: MATERIAL AND METHODS

Two previously undescribed specimens were selected for this study, Moschorhinus kitchingi (Broom) BP/1/2788 and BP/1/4636. BP/1/2788 was found by J.W. Kitching at Stoffelton, Ai eel Native Trust (now part of Kwa Zulu), near Bulwer, Natal in the Daptocephalus zone (Kitching 1977) (Dicynodon lacerticeps - Theriognathus Assemblage-zone, S.A.C.S. 1980). BP/1/4636 was found by J.W. Kitching on the farm Fairydale in the Bethulie district, Orange Free State in the Lystrosaurus zone (Kitching 1977) (Lystrosaurus - Thrinaxodon Assemblage - zone, S.A.C.S. 1980).

Moschorhinus kitchingi BP/1/2788 (Plates 1, 2, 3)

Most of the matrix surrounding this skull had been removed with a hammer and chisel prior to this study. The matrix within the temporal cavities had not been removed. This vertically distorted specimen is 21,5 cm long. The major parts of the skull roof and occiput are missing, exposing the dorsal part of the natural endocast of the braincase and nasal capsule. The jugal and postorbital arches are damaged. Teeth are present in the damaged and distorted mandible. Aspects of this specimen's teeth and mandible were used in the reconstruction of the lateral view of the skull (Fig. 3).

Moschorhinus kitchingi BP/1/4636 (Plates 4 - 9)

The whole skull was prepared by means of an air-hammer and

engraving tool for this study. This distorted skull is 25 cm long. Parts of its jugal and postorbital arches are missing and the occiput is damaged. Although this skull is severely damaged, it yielded vital information. The descriptions and reconstructions (Figs. 1 - 12) of the posterior part of the skull and the dental formula are based on this specimen.

The skulls were coated with Glyptal cement to prevent the flaking off of brittle parts. After the external morphology of the skulls was extensively studied, photographed and illustrated, each was cast in a block of plaster of Paris.

Moschorhinus kitchingi BP/1/2788 (Plates 13, 14)

The exposed dorsal part of the natural endocast of this specimen was covered with a layer of epoxy resin prior to the abovementioned step in order to preserve the original shape of the endocast after the matrix was removed. The block containing this specimen was sectioned horizontally with a Highland-Park rock-cutting saw with a 40,64 cm (16 inch) diameter diamond-edged circular blade. The matrix filling the endocranium was carefully removed with an air-hammer and engraving tool, thereby exposing the endocranial roof and floor. The reconstructions of the endocranial roof (Fig. 8) and floor (Fig. 9) are partly based on this specimen.

Moschorhinus kitchingi BP/1/4636 (Plates 10 - 12)

The block containing the posterior part of this specimen was sectioned sagittally with the abovementioned saw. The matrix filling the endocranium was also removed with the air-hammer and

engraving tool. Although the skull is damaged externally, the endocranium though compressed, is in good condition. Most of the information used to describe and reconstruct the endocranium was acquired from this specimen (Figs. 1 - 12).

Endocasts of silicone rubber were made of the posterior parts of the cleaned endocrania of these specimens (Plates 15 - 17). Silicone rubber is a substance commonly used today in the making of moulds. Because of its resistance to temperature changes, distortion and shrinkage, it is ideally suited to this purpose. Endocasts could only be made of the posterior part of the endocrania because the lateral walls in the orbitotemporal regions are unossified.

## CHAPTER 3: EXTERNAL MORPHOLOGY OF THE SKULL

The posterior half of the Moschorhinus skull consists of the following endochondral elements : the epipterygoid, prootic, opisthotic, quadrate, supraoccipital, exoccipital and basioccipital and the following dermal elements : the squamosal, quadratojugal, jugal, interparietal, parietal, postorbital, tabular and pterygoid. The parasphenoid and basisphenoid are of dermal and endochondral origin.

The lateral wall of the braincase can be seen within the jugal arch (Fig. 4). The large parietals form the sharp-crested roof of the braincase and the dorsal borders of the temporal fossae. The posterior wall of the temporal fossa is largely formed by the squamosal. The medial wall of the temporal fossa is formed by the epipterygoid, the prootic, the ventro-lateral part of the pterygoid, the lateral part of the opisthotic, and anterior parts of the supraoccipital and interparietal. Several features relating to bloodvessels and nerves can be seen within the temporal fossa.

The posterior surfaces of the parietal, interparietal and supraoccipital form the medial surface of the occiput, dorsal to the foramen magnum (Fig. 6). These elements are flanked by the tabulars which cover part of the squamosal posteriorly. The lateral part of the occiput is formed by the posterior parts of the squamosal and the opisthotic. The foramen magnum is flanked by the exoccipitals. The ventro-medial border of the occiput is marked by the basioccipital. Two of the most salient features of

the occiput are the large post-temporal fenestra and the parocci-pital fossa.

The elements exposed within the jugal arches and those form-ing the occiput are described in detail below.

EPIPTERYGOID (Figs. 1 - 4)

In lateral view (Figs. 3, 4) the flattened, bladelike epipte-rygoid can be seen. It contacts the parietal, supraoccipital and prootic dorsally and the pterygoid, prootic and squamosal ventral-ly. The upper part of the processus ascendens (dorsal lamina, Mendrez 1972, 1974a, 1974b) expands anteriorly to form an antero-dorsal process and posteriorly to form a postero-dorsal process. The basal part of the epipterygoid expands anteriorly to form an antero-ventral process and posteriorly to form a postero-ventral process (Mendrez 1972, 1974a, 1974b). A small posterior apophysis is present on the posterior edge of the processus ascendens, which probably made sutural contact with the lateral part of the base of the antero-dorsal process of the prootic (it is unfortunately damaged in all Moschorhinus examined). The ventro-medial part of the postero-dorsal process of the epipterygoid contacts the ante-rr lateral part of the antero-dorsal process of the prootic just above the contact of the posterior apophysis with the prootic, thus forming a circular foramen - the posterior foramen of the epipterygoid ("foramen veineux", Mendrez 1974a) (see Fig. 4). There is a shallow funnel-like indentation surrounding the foramen on the lateral surface of the epipterygoid. A low ridge runs diagonally across the lateral surface of the epipterygoid from the

tip of the postero-dorsal process, passes anterior to the foramen and terminates in the middle of the ventral part of the epipterygoid as a small tuberosity. This posterior foramen of the epipterygoid should not be confused with the dorsal venous foramen (see discussion). The dorsal border of the epipterygoid fits in snugly under the parietal. The central part of the dorsal border of the epipterygoid is overlapped laterally by the ventro-lateral descending flange of the parietal. The tip of the postero-dorsal process curves slightly downwards, away from the parietal, exposing the interparietal upon which the dorsal part of the postero-dorsal process lies.

The antero-ventral process of the epipterygoid is quite small in relation to the postero-ventral process. It originates antero-ventrally from the base of the processus ascendens. The antero-ventral process terminates anteriorly to the dorso-lateral ridge of the pterygoid and is in confluence with the posterior corner of this ridge. The term antero-ventral process of the epipterygoid is preferred to the "pterygoid process of the epipterygoid" (Crompton 1955) since the whole of the ventral border of the epipterygoid contacts the pterygoid. The foot of the epip erygoid covers the dorsal surface of the antero-lateral third of the quadrate ramus of the pterygoid (see Ch. 4; Fig. 4).

The postero-ventral process of the epipterygoid originates at the base of the processus ascendens from where it flares out postero-laterally as an elongated, horizontal fan overlying the middle third of the quadrate ramus of the pterygoid. These two processes are confluent laterally and posteriorly but not medially and anteriorly. The postero-ventral process is slightly raised medially along its whole length, producing a medially facing

groove which originates under the vertically inclined anterior part of the postero-ventral process. The groove tapers off as it approaches the posterior border of the postero-ventral process. The term postero-ventral process of the epipterygoid is preferred to the "quadrate process of the epipterygoid" (Crompton 1955) since it is doubtful whether the epipterygoid actually did contact the quadrate in Moschorhinus.

The posterior part of the postero-ventral process of the epipterygoid is fan shaped. The lateral half of the posterior border stretches across the dorsal surface of the quadrate ramus of the pterygoid. The posterior border contacts the anterior border of the antero-ventral process of the squamosal medially, the contact being visible in dorsal and ventral views. This region of the epipterygoid forms part of the antero-lateral corner of the pterygo-parocciptal foramen (Figs. 1, 2, 4).

In lateral view (Fig. 4), the ventral suture of the epipterygoid runs in the middle of the lateral side of the structure formed with the quadrate ramus of the pterygoid. The suture dips anteriorly and then curves upwards delimiting the border of the antero-ventral process. Posteriorly the suture runs diagonally upwards in a straight line delimiting the ventral border of the postero-ventral process laterally on the dorsal side of the quadrate ramus of the pterygoid.

The processus ascendens of the epipterygoid juts upwards and slightly inwards. The middle part of the processus ascendens is relatively constricted in comparison with the dorsal and ventral parts, giving the epipterygoid an hour-glass shape in lateral view. The ventral part of the epipterygoid is directed outwards posteriorly and inwards anteriorly. This closely reflects the

orientation of the quadrate ramus of the pterygoid, while the dorsal part of the epipterygoid is more parasagittally inclined.

A very distinct and large cavum epiptericum is present, bordered medially by the antero-ventral process of the prootic and laterally by the epipterygoid. Certain nerves and veins traverse the cavum epiptericum (see discussion).

PTERYGOID (Figs. 1, 2, 4, 5)

The pterygoids are complex bones which form a ventral bridge between the nasal capsule anteriorly and the braincase posteriorly.

The pterygoids are fused antero-medially. Contrary to the descriptions of Brink (1958) and Mendrez (1974a) no suture could be detected between them in ventral view (Fig. 2). There is however, a spindle-shaped ventral keel, here called the interpterygoid keel, where the bones meet. The posterior part of this keel projects dorso-medially into the interpterygoid vacuity. The central part of each pterygoid contacts the vomer and the palatine anteriorly. The sutures between these elements can be seen in ventral view (Fig. 2). A big robust anterior process projects laterally from the central part of the pterygoid. This process, the transverse process of the pterygoid, contacts the ectopterygoid antero-laterally. This suture can be seen in dorsal, ventral and lateral views (Figs. 1, 2, 4).

The central part of the pterygoid can be subdivided into a dorsal component with approximately horizontal dorsal and ventral surfaces and a ventro-medial, parasagittally vertical flange. The

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The central part of the pterygoid can be subdivided into a dorsal component with approximately horizontal dorsal and ventral surfaces and a ventro-medial, parasagittally vertical flange. The

dorsal part of the pterygoid contributes largely to the part of the basicranium anterior to the crista sellaris and posterior to the nasal capsule (see Ch. 4). The quadrate ramus of the pterygoid flares out postero-laterally from this part of the pterygoid. The well-developed vertical, lateral surface of the dorsal part of the pterygoid is marked by two sharp-edged ridges, a dorsal one called here the dorso-lateral ridge of the pterygoid and a ventral one called here the ventro-lateral ridge of the pterygoid. Both these ridges can be seen in lateral view (Fig. 4). The dorso-lateral ridge originates on the pronounced dorso-medial part of the transverse process. It curves postero-medially at first and then runs parasagittally up to the antero-medial part of the quadrate ramus. From this point it curves postero-laterally following the curvature of the anterior border of the quadrate ramus, and finally terminates antero-medially to the antero-ventral process of the epipterygoid. The ventro-lateral ridge originates on the medial part of the posterior surface of the transverse process as a very faint ridge, gradually becoming more pronounced as it runs posteriorly. It also follows the curvature of the dorso-lateral part of the pterygoid, curving first postero-medially, then running parasagittally and finally postero-laterally to mark the ventro-lateral border of the quadrate ramus. These lateral ridges are situated far apart anteriorly but converge posteriorly as the lateral surface between these ridges tapers down. The dorsal part of the pterygoid contacts the foot of the epipterygoid dorsally (see Fig. 9; Ch. 4).

The ventro-medial flange of the pterygoid can be seen in ventral and lateral views (Figs. 2, 4). Its dorsal part slopes ventro-medially from the ventro-medial surfaces of the quadrate

ramus of the pterygoid and the dorsal part of the pterygoid. These essentially parasagittally orientated flanges of the pterygoids jut ventrally and slightly medially but their ventral limits do not contact one another, thereby leaving a medial cavity, the interpterygoid vacuity. Each flange becomes thinner in transverse section as it progresses ventrally. The thin postero-ventral parts of these flanges cover the lateral surfaces of the anterior part of the parasphenoid keel. The ventral apertures of the parabasal canals lie on either side of the parasphenoid keel, anterior to the basisphenoid. Each is formed by the postero-ventral part of the ventro-medial flange anteriorly and by the ventro-medial part of the basisphenoid process of the pterygoid laterally. The suture-line separating each flange from the parasphenoid keel emerges from the interpterygoid vacuity anteriorly, runs in a posterior and slightly lateral direction between the ventral surfaces of the pterygoids (Fig. 2) and then curves dorsally on the lateral surface of the keel and plunges into the parabasal canal on its antero-medial wall (Fig. 4). The ventro-medial flange is confluent posteriorly with the basisphenoid process of the pterygoid (Figs. 2, 4).

The basisphenoid process juts posteriorly and slightly laterally from the ventro-medial flange. Its medial surface covers the antero-lateral surface of the posterior part of the basisphenoid. The suture between these two elements runs in a lateral direction on the ventral surface of the basisphenoid, from the postero-lateral margin of the ventral aperture of the parabasal canal to the convex ventro-lateral part of the basisphenoid (Fig. 2). The suture runs from here in an antero-dorsal direction on the lateral surface of the basisphenoid to the medial corner of

the posterior rim formed by the basipterygoid process of the basisphenoid and the quadrate ramus of the pterygoid (Fig. 5).

Seen from dorsal and ventral views (Figs. 1, 2) the quadrate ramus of the pterygoid juts postero-laterally at an angle of approximately 45° from the central part of the pterygoid. In lateral view (Fig. 4) the quadrate ramus dips slightly ventro-laterally from its origin antero-medially. The quadrate ramus contacts the opisthotic postero-laterally thereby closing off a space between it and the braincase. This is the cranioquadrate passage (see Romer 1956).

The quadrate ramus has a well-developed vertical antero-lateral surface. This surface is bordered by the dorso-lateral ridge of the pterygoid antero-dorsally and by the ventral limit of the epipterygoid postero-dorsally. It is bordered ventrally by the ventro-lateral ridge of the pterygoid. The antero-medial part of the quadrate ramus is triangular in transverse section because the dorsal surface runs approximately horizontally and the ventral surface is concave. This has the result that the quadrate ramus tapers down postero-medially to form a thin, blade-like postero-medial edge. The antero-lateral surface of the quadrate ramus gradually becomes smaller distally causing the postero-lateral part of the quadrate ramus to be flat in cross-section.

The postero-ventral edge of the quadrate ramus covers the antero-lateral two-thirds of the quadrate process of the opisthotic dorsally. Part of the suture between these two elements can be seen in lateral view (Fig. 4). The postero-medial edge of the quadrate ramus contacts the antero-lateral border of the antero-ventral process of the squamosal (Figs. 1, 4). This suture runs postero-laterally from the contact formed between these two ele-

ments and the posterior part of the postero-ventral process of the epipterygoid and terminates at the contact formed between these two elements and the opisthotic. The antero-medial two thirds of the quadrate ramus is covered dorsally by the epipterygoid. The suture between these two elements has been described above. The postero-medial part of the quadrate ramus covers the ventral part of the basipterygoid process of the basisphenoid proximally. The suture between these two elements cannot be seen in ventral view, as it runs on the thin anterior rim of the craniquadrate passage (see Ch. 4; Fig. 9).

The proximal part of the quadrate ramus is very broad but it gradually becomes narrower as it progresses postero-laterally. It is at its narrowest ventral to the postero-ventral process of the epipterygoid. Postero-lateral to this process it gradually widens again up to its postero-lateral border (Figs. 1, 2). This broad, concave, postero-lateral part forms the anterior part of the quadrate recess and is in confluence with the concave antero-ventral process of the squamosal which forms the posterior part of the quadrate recess (Fig. 4).

PROOTIC (Figs. 1 - 6)

The prootic and opisthotic are two separate elements. The sutures between these bones will be discussed later.

The prootic is a complex bone with five major processes. The terminology used by Mendrez (1972) to describe these processes will be followed here. The prootic meets the basisphenoid ventrally, the squamosal and opisthotic postero-laterally, the epi-

pterygoid antero-laterally and the supraoccipital dorsally.

In lateral view (Fig. 4) two distinct ridges can be seen running diagonally across the prootic, more or less parallel to each other. The ridge running from the central process to the antero-dorsal process is here called the central ridge of the prootic (the "delicate rising crest" of Mendrez 1972, p. 205). The ridge running from the lip of the fenestra ovalis to the antero-ventral process of the prootic, is here called the ventral ridge of the prootic (the "sharp crest", Mendrez 1972, p. 203 and the "strong crest", Mendrez 1972, p. 205; 1974b, p. 76).

In lateral view it can be seen that the prootic has two distinct anterior processes directed diagonally antero-dorsally, viz: the antero-dorsal process above and antero-ventral process below. These two processes are separated by the incisura prootica. Olson (1944), Crompton (1955), Mendrez (1972) and others used these terms to describe the anterior part of the prootic.

The anterior part of the antero-dorsal process makes contact with the medial surface of the epipterygoid, while the antero-ventral process passes medially to the epipterygoid forming a large vacuity between it and the epipterygoid - the cavum epiptericum, which will be discussed later. The antero-dorsal process runs more or less parallel to the sagittal plane, whereas the antero-ventral process points inwards.

The antero-dorsal process of the prootic (processus anterior superior, Siebenrock 1893; posterior pro-otic process, Boonstra 1934b) is a flattened, broad, projection which originates more or less in the middle of the prootic. Its dorsal border is in continuation with the dorsal border of the rest of the prootic, and its

ventral border is a continuation of the central ridge of the prootic. The antero-dorsal process is rather broad posteriorly but tapers anteriorly, the thinnest part being its anterior edge which contacts the postero-medial edge of the epipterygoid laterally. This region is damaged in the specimen described by Mendrez (1974). The antero-ventral edge of the antero-dorsal process forms the posterior border of the posterior foramen of the epipterygoid. There is a slight lateral protrusion on the posterior part of the ventral border of the antero-dorsal process causing a ventro-laterally directed prominence in the central ridge of the prootic. This part of the prootic most probably made contact with the posterior apophysis of the epipterygoid, because of its inclination towards, and proximity to, the apophysis.

Bordering the antero-dorsal process of the prootic dorsally and meeting the antero-dorsal process of the epipterygoid is the flat, fingerlike antero-lateral process of the supraoccipital. The suture between the supraoccipital and prootic is not continuous. Posteriorly to the ventral edge of the postero-dorsal process of the epipterygoid a small triangular gap is formed between the supraoccipital and prootic. This is the dorsal venous foramen commonly found in many therapsids (see discussion).

The plane of the antero-dorsal process is diagonally inclined in cross-section. The ventral border flares out laterally while the dorsal border is medially inclined, reflecting the orientation of the epipterygoid.

The antero-ventral process of the prootic (processus anterior inferior, Siebenrock 1893; anterior pro-otic process, Boonstra 1934b) originates below the point of articulation between the posterior apophysis of the epipterygoid and the antero-dorsal

process. This process is the ossified pila antotica (pleurosphenoid) (De Beer 193"; Olson 1944; Säve-Söderbergh 1947; Crompton 1955). The dorsal border of the antero-ventral process curves upwards in a crescent shape. The antero-ventral process is vertically inclined in cross section and curves inwards anteriorly. The antero-ventral process is traversed anteriorly by a horizontal groove. Above this shallow indentation, a low ridge runs from the posterior border of the incisura prootica anteriorly. This low ridge flares out anteriorly, forming two small, anteriorly jutting projections.

The incisura prootica is wide and deep. It is bordered ventrally by the concave dorsal border of the antero-ventral process and dorsally by the straight ventral border of the antero-dorsal process.

The foramen for the facial nerve (VII) is situated between the central and ventral ridges of the prootic. This foramen is nearer the former ridge and on the same level as the ventral border of the antero-ventral process of the prootic anterior to it, and the central process of the prootic posterior to it.

There is a small ventral notch between the ventral border of the antero-ventral process and the braincase floor. Its posterior border is formed by the anterior border of the basal region of the prootic. The ventral border is formed by the basisphenoid. This is the same as the notch described by Crompton (1955) for the Scalaposauridae though here it is more open anteriorly.

The prootic has three prominent lateral processes of approximately the same length. The central process of the prootic (lateral process of the prootic, Kemp 1972) can be seen in lateral (Fig. 4), dorsal, ventral and occipital views. It juts out late-

rally and slightly postero-ventrally towards the squamosal. Its antero-lateral corner contacts the postero-medial corner of the postero-ventral process of the epipterygoid. The medial part of the antero-ventral process of the squamosal (prootic process of the squamosal, Mendrez 1974b) contacts this central process in a complex manner: the distal part of the central process forms two flanges, one antero-dorsally, the other postero-ventrally, between which the thin medial blade of the antero-ventral process of the squamosal is wedged. These two elements form an antero-dorsally curving bar which forms the anterior border of the pterygo-paroccipital foramen. The dorsal crest-like border of this bar is a continuation of the central ridge of the prootic, while the antero-ventral border forms a sharp concave crest running from the dorsal lip of the fenestra ovalis medially to the postero-medial corner of the postero-ventral process of the epipterygoid laterally. The distal part of the central process is spindle-shaped in cross section. The base of the central process, however, is triangular in cross section because of a short, sharp crest which forms the postero-medial corner of the process. This crest originates on the postero-medial part of the central process, curves postero-medially and terminates on the anterior surface of the postero-ventral process of the prootic.

Behind the central process of the prootic a more posteriorly inclined, flattened process, the postero-ventral process of the prootic, originates. This process can be seen in occipital view. It contacts the opisthotic ventro-laterally. This unified structure forms the posterior wall of the pterygo-paroccipital foramen, the ventral border of the post-temporal fenestra and the anterior wall of the paroccipital fossa. The postero-ventral process forms

only the dorso-medial quarter of the posterior wall of the ptery-go-paroccipital foramen, and the medial half of the ventral border of the post-temporal fenestra.

.. third process. the postero-dorsal process of the prootic, contacts the intermediate process of the squamosal dorsally. It can be seen in lateral view (Fig. 4). The postero-dorsal process forms most of the antero-dorsal rim of the post-temporal fenestra. This process tapers off from a relatively broad base medially to a point jutting laterally, terminating in the lateral part of the roof of the post-temporal fen stra. This process protrudes from under the intermediate process of the squamosal antero-medially, but more laterally it is covered anteriorly by the intermediate process of the squamosal. Its postero-medial half is covered by the postero-dorsal process of the opisthotic.

The suture between the basal region of the prootic and the basisphenoid can be seen in lateral (Figs. 4, 5) and ventral 2(Fig. 2) views. The lateral suture runs diagonally from the floor of the braincase antero-dorsally to the fenestra ovalis postero-ventrally. The antero-dorsal part of the lip surrounding the fenestra ovalis is formed by the basal region of the prootic (Fig. 5).

As Mendrez (1972, 1974) has remarked, the opisthotic and prootic are two quite separate bones. A clearly distinguishable suture divides them. The postero-dorsal process of the opisthotic does not make contact with the lateral border of the postero-dorsal process of the prootic, nor is it visible in anterior view as Mendrez (1974a) stated to be the case. The postero-dorsal process of the opisthotic covers the postero-medial half of the postero-dorsal process of the prootic posteriorly. In occipital

view one can observe within the post-temporal fenestra a part of the suture between the postero-dorsal processes of the prootic and the opisthotic. This suture runs vertically for a short distance, skirting the lateral border of the postero-dorsal process of the opisthotic, and then curves medially along its ventral border to where the postero-medial borders of the postero-ventral and postero-dorsal processes of the prootic originate. Laterally to this, the suture runs between the medial lip formed by the postero-ventral process of the prootic and the postero-ventral flange of the paroccipital process of the opisthotic. Ventrally to this medial lip the suture which divides the postero-ventral process of the prootic and the antero-dorsal flange of the opisthotic runs laterally. It can be traced posteriorly in the paroccipital fossa (Mendrez 1972, p. 203) and anteriorly between the antero-dorsal flange of the paroccipital process of the opisthotic and the postero-ventral process of the prootic. The suture curves first ventrally then medially along the border of the postero-ventral process of the prootic. It then skirts the base of the central process of the prootic antero-ventrally and the posterior corner of the dorsal lip of the fenestra ovalis, before it enters the roof of the fenestra ovalis medially (Fig. 5).

The concave, dorsal border of the prootic can be seen in lateral view curving postero-dorsally to meet the medial border of the intermediate process of the squamosal. The central part of the dorsal border of the prootic (dorsal limit of the "lame dorsale" of the prootic, Mendrez 1974a) forms sutural contact with the supraoccipital. The largest part of the ventral border of the lateral-supraoccipital fossa is formed by the dorsal border of the prootic (this fossa is discussed below).

OPISTHOTIC (Figs. 1 - 6)

The opisthotic contacts the exoccipital and basioccipital postero-medially, the prootic antero-medially, the tabular, supra-occipital and squamosal dorsally, the squamosal, pterygoid and quadrate laterally, and the stapes ventrally.

The opisthotic consists of a robust transverse bar - the paroccipital process, a T-shaped ventro-medial tuberosity - the internal process, and a small, flattened dorso-medial projection - the postero-dorsal process (Mendrez 1972, 1974a, 1974b).

The paroccipital process of the opisthotic is V-shaped in parasagittal section. This V-shaped process is formed by two flanges joined antero-ventrally. The postero-ventral flange is more massive than the antero-dorsal flange. The cavity formed by these two flanges is the paroccipital fossa of the opisthotic and is V-shaped in longitudinal section. This fossa can be seen in dorsal and occipital views (Mendrez 1972, 1974a, 1974b).

The paroccipital process is laterally subdivided into two processes which can be distinguished in ventral view, viz: posteriorly - the mastoid process of the opisthotic and anteriorly - the quadrate process of the opisthotic (see Fig. 13).

The mastoid process is marked by a ventral ridge originating approximately in the middle of the paroccipital process and terminating near the bulbous lateral end of the mastoid process. This ventro-laterally curving ventral ridge adds to the robustness of the mastoid process. The mastoid process is thickest near its distal end where the ventral ridge terminates. The posterior margin of the mastoid process marks the postero-ventral border of the paroccipital fossa. The postero-lateral part of the mastoid

process articulates with the squamosal laterally while its antero-lateral part is free. A shallow indentation separates the mastoid and quadrate processes of the opisthotic, and forms the so-called roof of the middle ear ("toit de l'oreille moyenne", Mendrez 1974a). The quadrate process of the opisthotic, which juts outwards antero-laterally, is thinner, broader and longer than the mastoid process. It becomes broader laterally, similarly to the mastoid process, to form a bulbous lateral end. The quadrate process projects further laterally than the mastoid process. The posterior third of the dorso-lateral surface of the quadrate process of the opisthotic contacts the quadrate process of the squamosal and the anterior two thirds contacts the posterior part of the quadrate ramus of the pterygoid. This can be seen in lateral (Fig. 4) and dorsal (Fig. 1) views. The lateral surface of the quadrate process of the opisthotic loosely articulates with the quadrate and its antero-ventral surface loosely contacts the stapes.

The antero-dorsal flange of the paroccipital process (anterior wall of the paroccipital process, Mendrez 1972) contacts the postero-ventral process of the prootic medially. This combined structure forms the posterior wall of the pterygo-paroccipital foramen (seen in dorsal view), the ventral border of the post-temporal fenestra and the antero-dorsal border of the paroccipital fossa (both seen in occipital view). The anterior ridge of the paroccipital process, marking the anterior border of the opisthotic, originates at the antero-lateral edge of the quadrate process of the opisthotic and terminates near the dorsal lip of the fenestra ovalis. The base of the central process of the prootic and the dorsal lip of the fenestra ovalis (also formed by the prootic)

contact the antero-medial part of the opisthotic (Fig. 5). The suture between the prootic and opisthotic has already been described.

The opisthotic forms the posterior third of the fenestra ovalis. The suture between the opisthotic and the basioccipital can be seen in ventral and occipital view. It emerges from the postero-ventral corner of the fenestra ovalis and then turns medially across the ventral surface of the lip of the fenestra ovalis (Fig. 5). The suture then curves postero-medially behind the tuberculum spheno-occipitale, runs around the internal process of the opisthotic and then curves laterally after passing medially to the jugular foramen. On reaching the postero-ventral lip of the jugular foramen, the suture extends into the jugular foramen in an antero-dorsal direction.

The internal process of the opisthotic can be seen in ventral and occipital views. It is formed by a ridge originating on the ventro-medial part of the paroccipital process, curving and expanding ventro-medially and terminating as a ventro-medial tuberosity between the jugular foramen and fenestra ovalis. From this tuberosity a thin antero-lateral and thicker, blunter postero-medial extension project. The central tuberosity protrudes further ventrally than its extensions. The posterior extension forms the ventral lip of the jugular foramen and the anterior extension forms the postero-ventral corner of the lip of the fenestra ovalis (Fig. 5). There is a small groove separating the anterior extension from the medial part of the opisthotic which forms the posterior border of the fenestra ovalis. Similarly the posterior extension is separated ventrally from that part of the opisthotic which forms the anterior part of the roof of the jugular foramen

by a shallow groove (Fig. 2). This groove runs from inside the jugular foramen antero-medially, more or less parallel to the ventro-lateral suture of the exoccipital, and terminates on the postero-medial surface of the paroccipital process. The part of the opisthotic which the posterior extension of the internal process overlies, projects into the jugular foramen and forms with the exoccipital posteriorly, the roof of the jugular foramen. A short groove is present on the posterior face of the ridge and tuberosity, ventral to the groove at the jugular foramen (Figs. 2, 6).

In occipital view the suture between the antero-lateral part of the exoccipital and the postero-medial surface of the opisthotic can be seen. This suture runs from inside the jugular foramen, around the exoccipital ventro-laterally and then dorso-medially. Also visible in occipital view is the suture between the medial corner of the postero-dorsal process of the opisthotic and the ventro-lateral corner of the supraccipital. It originates half-way along the dorsal border of the exoccipital.

The postero-dorsal process of the opisthotic (visible in occipital view) originates medially to the paroccipital fossa and the lip (formed by the postero-ventral process of the prootic and the postero-ventral flange of the paroccipital process) covering the dorso-medial part of the paroccipital fossa. The postero-dorsal process of the opisthotic is a flat projection which curves dorso-laterally. It forms the postero-medial surface of the post-temporal fenestra. Its lateral border stretches as far medially as the lip covering the dorso-medial part of the paroccipital fossa (a medial indentation separates these two structures). The postero-dorsal process of the opisthotic makes sutural contact

along its dorso-medial border with the supraoccipital. This suture continues in a dorso-lateral direction as it follows the dorsal border of the postero-dorsal process. The suture between the supraoccipital and tabular originates halfway along this border. Part of the dorsal border of the postero-dorsal process contacts the ventral border of the tabular. The lateral border of the postero-dorsal process contacts the postero-ventral part of the intermediate process of the squamosal. The short ventral border of the postero-dorsal process of the opisthotic contacts the posterior part of the postero-dorsal process of the prootic. The postero-dorsal process of the opisthotic is not visible in anterior view as Mendrez (1974a) has observed in Moschorhinus kitchingi, S.A.M. K.118. It rather resembles the condition found by Mendrez (1974b) in Promoschorhynchus platyrhinus RC. 116, where the postero-dorsal process is completely covered anteriorly by the intermediate process of the squamosal and the antero-dorsal process of the prootic.

SQUAMOSAL (Figs. 1 - 4, 6)

The squamosal is a large, complex bone with several processes. The terminology used by Mendrez (1972) will be used to describe these processes. The squamosal makes contact with the parietal, interparietal, supraoccipital, prootic, opisthotic and tabular medially, the pterygoid and epipterygoid anteriorly and with the jugal and quadrate laterally.

The major part of the posterior wall of the temporal fossa is formed by the three large medial processes of the squamosal. The

laterally sloping dorsal border of the squamosal forms the postero-dorsal border of the temporal fossa and anterior part of the lambdoid crest. The three medial processes occur one above the other (Fig. 4). The antero-ventral process (third squamosal process, Crompton 1955) is separated from the intermediate process (second squamosal process, Crompton) by the post-temporal fenestra. The intermediate and dorsal processes (first squamosal process, Crompton) are separated by the posterior fold forming part of the lateral-supraoccipital fossa.

The medial part of the broad dorsal process of the squamosal covers the postero-lateral part of the parietal (Fig. 1). The lateral surface of the dorsal process is confluent with that of the parietal as are their dorsal and ventral borders. The dorsal process of the squamosal is fused to the tabular along most of its posterior surface. Its ventral border is marked by the fold forming the posterior part of the lateral-supraoccipital fossa (Fig. 4). Part of this fold is occupied by the anterior extension of the interparietal which contacts the ventral border of the dorsal process postero-dorsally.

In lateral view it can be seen that the dorsal border of the intermediate process of the squamosal forms the ventral border of the abovementioned fold and contacts the postero-ventral area of the part of the interparietal which is laterally exposed. The anterior part of the intermediate process makes sutural contact with the antero-lateral process of the supraoccipital dorsally and with the prootic ventrally. The medial part of the ventral border of the intermediate process of the squamosal forms a V-shaped notch in which the postero-dorsal process of the prootic is wedged. This fused structure forms the dorso-medial part of the

roof of the post-temporal fenestra while the dorso-lateral part of the roof is formed by the lateral part of the ventral border of the intermediate process.

In occipital view it can be seen that the medial part of the intermediate process makes sutural contact with the ventro-lateral part of the tabular, and with the dorso-lateral part of the postero-dorsal process of the opisthotic ventro-medially.

In lateral view the ventral border of the intermediate process can be seen. It curves ventro-laterally in a cresent-shape, delimiting the dorso-lateral rim of the post-temporal fenestra, until it becomes the dorsal border of the antero-ventral process of the squamosal. The dorsal border of the antero-ventral process forms the lateral part of the pterygo-paroccipital foramen. The medial blade of the antero-ventral process of the squamosal (the prootic process of the squamosal, Mendrez 1974b) is wedged into a V-shaped notch formed by the lateral part of the central process of the prootic. The postero-medial border of the postero-ventral process of the epipterygoid contacts the antero-ventral process of the squamosal antero-medially. The whole antero-lateral border of the antero-ventral process of the squamosal, except for its distal end, contacts the postero-medial edge of the quadrate ramus of the pterygoid. This suture has been described previously.

The laterally directed flange of the squamosal overlies most of the opisthotic, but these elements are in contact where their distal borders meet (Fig. 6). The ventro-lateral part of the antero-ventral process of the squamosal contacts the dorsal part of the postero-lateral tip of the quadrate process of the opisthotic posterior to the squamosal-pterygoid contact (Fig. 4). This suture is visible anteriorly to the quadrate notch in the squamo-

sal (this notch is described below). The ventro-lateral part of the squamosal seen in occipital view is the mastoid process of the squamosal. The suture between the dorsolateral border of the mastoid process of the opisthotic and the ventromedial border of the mastoid process of the squamosal is visible in occipital and ventral views. Except for these two abovementioned distal sutures and the suture with the postero-dorsal process of the opisthotic, the rest of the squamosal overlies, but does not contact, the opisthotic. It thus forms the lateral parts of the roof of the pterygo-paroccipital foramen and the roof of the paroccipital fossa.

A deep dorsally-directed quadrate notch is present anteriorly in the distal part of the squamosal for housing the dorsal part of the quadrate (Fig. 4). This notch is surrounded by the jugal laterally, the postero-lateral part of the anteroventral process of the squamosal (which covers the quadrate process of the opisthotic) antero-ventrally and the thick lip formed by the jugal process of the squamosal dorsally. A shallow depression is present in the squamosal ventro-laterally to this notch and lateral to the quadrate process of the opisthotic. This indentation, the quadrate recess of the squamosal, is probably synonymous with that described by Kemp (1969) and with the squamosal recess ("recessus squamosal") of Mendrez (1972a). The posterior part of the quadrate fits into this recess. The quadrates are lost in most of the Moschorhinus specimens because they were loosely articulating bones with no sutural connections.

In occipital view the following features can also be seen: the postero-ventral border of the intermediate process of the squamosal curves ventro-laterally, forming the postero-lateral

border of the post-temporal fenestra and part of the postero-lateral border of the paroccipital fossa. A ridge runs in a dorso-ventral plane on the mastoid process of the squamosal laterally to its contact with the opisthotic. A postero-ventral facing indentation on the mastoid process of the squamosal borders this ridge laterally. Ventrally to this indentation and ridge, and medially to the posterior part of the quadrate, a notch is situated posteriorly between the two lateral processes of the opisthotic.

The dorso-lateral part of the squamosal (the jugal process) curves anteriorly to join the posterior end of the jugal. Unfortunately the jugal arch is either lost or damaged to such a degree in those specimens studied, that a detailed description is impossible.

SUPRAOCCIPITAL AND INTERPARIETAL (Figs. 3, 6)

Both the supraoccipital and the interparietal are visible in occipital and lateral view. In occipital view, the broad supraoccipital contacts the interparietal dorsally, the tabulars dorso-laterally, the postero-dorsal processes of the opisthotics ventro-laterally and the exoccipitals ventrally. The exoccipitals cover the ventro-medial part of the supraoccipital except for a narrow gap between the exoccipitals where the supraoccipital forms the dorso-medial part of the roof of the foramen magnum. The suture between the tabular and supraoccipital runs diagonally in a dorso-medial direction from its origin at the junction of the ventral borders of the tabular and supraoccipital, to the dorsal border of the supraoccipital. The suture between the ventral border of the

interparietal and the dorsal border of the supraoccipital is horizontal and short. A large, deep occipital indentation is present in the region of the interparietal. Two smaller, ventral indentations, forming part of the larger indentation are present on the dorsal part of the supraoccipital. These flank a short ridge originating in the middle of the dorsal part of the supraoccipital and continued dorsally on the interparietal.

In occipital view the interparietal is a small, laterally ovate bone, bordered ventrally by the supraoccipital, laterally by the tabulars and dorsally by the parietal.

The aforementioned occipital indentation causes the interparietal, parietal, medial part of the tabular and the dorsal part of the supraoccipital to be set deeper than the rest of the surrounding elements. This indentation was for the attachment of certain neck muscles.

In lateral view, ventral to the postero-medial angle of the temporal foramen (Mendrez 1974a, p. 80) is the lateral-supraoccipital fossa, a large, oval indentation bordered dorsally by the parietal whose ventral border forms a concave overhang. The ventral border of this fossa is formed by the concave dorsal edge of the antero-dorsal process of the prootic and the anterior border by the antero-ventrally curving posterior edge of the postero-dorsal process of the epipterygoid. The fossa tapers off posteriorly into a short, horizontal fold. The antero-medial part of the intermediate process of the squamosal forms the posterior border of the fossa and the ventral part of its posterior fold. The dorsal border of the fold is formed by the ventral borders of the parietal and the dorsal process of the squamosal. The dorsal venous foramen lies in the antero-ventral region of this fossa.

The anterior extensions of the supraoccipital and interparietal are visible within the lateral-supraoccipital fossa. The antero-lateral process of the supraoccipital lies at a more medial level than any of the surrounding elements, forming the medial wall of the lateral-supraoccipital fossa. The antero-lateral process of the supraoccipital contacts the parietal dorsally, the postero-dorsal process of the epipterygoid anteriorly, the antero-dorsal process of the prootic ventrally, the intermediate process of the squamosal postero-ventrally and the anterior extension of the interparietal postero-dorsally. The dorsal venous foramen is visible ventral to the epipterygoid-supraoccipital contact and anteriorly to the prootic-supraoccipital contact.

The anterior extension of the interparietal fills the postero-dorsal corner of the lateral-supraoccipital fossa. The interparietal is triangularly shaped and contacts the antero-lateral process of the supraoccipital antero-ventrally, the dorsal border of the intermediate process of the squamosal postero-ventrally, the ventral border of the parietal antero-dorsally and the ventral border of the dorsal process of the squamosal postero-dorsally.

PARIETAL (Figs. 1, 3, 4, 6)

The parietals are fused into a single element. The parietal element forms the postero-dorsal part of the skull. It contacts the squamosal and tabular postero-ventrally, the prootic and epipterygoid ventro-laterally, the postorbital antero-laterally and the frontal anteriorly.

In occipital view the parietal is situated between the dorso-

medial borders of the tabulars and the dorsal border of the interparietal. Its dorsal border is in confluence with those of the tabular and squamosal. These borders form the ventro-laterally curving, dorsal border of the occiput.

The parietal element has a pronounced sagittal crest. The antero-dorsal rim of the temporal fossa is formed by an acute curving ridge on the postero-dorsal and dorso-lateral surface of the postorbital (Fig. 1). These postorbital ridges bow posteriorly and are continued on the dorso-medial surface to produce the sagittal crest. The sagittal crest is widest at its origin anterior to the parietal foramen. Posteriorly it becomes narrower and splits into the two postero-laterally flaring lambdoid crests, which form the dorso-medial border of the occiput posteriorly and part of the postero-dorsal rim of the temporal fossa laterally.

The parietal, in dorsal view, has an hour-glass shape. Broad and robust anteriorly, it is constricted in the middle above the epipterygoids and forms two postero-laterally flaring flanges which form the anterior parts of the lambdoid crests.

The broad anterior part of the parietal contacts the frontal and postorbitals (Figs. 1, 3, 4). In dorsal view it can be seen that the suture between the postero-dorsal border of the frontal and the antero-dorsal border of the parietal has a zig-zag arrangement. The antero-ventrally sloping area between the anterior border of the parietal and the parietal foramen, i.e. the broad origin of the sagittal crest, is corrugated. In BP/1/4636, four small but distinct parasagittal ridges are present in this region. The two medial ridges join up with the sagittal ridge of the frontal anterior to them. This sagittal ridge runs on the dorsal surface of the skull from the middle of the nasals, over the

frontals and joins the medial ridges of the parietal which terminate on the slope anterior to the parietal foramen.

The postero-medial flange of the postorbital and the antero-lateral part of the parietal are separated by a suture which can be seen in dorsal and lateral view.

The parietal foramen for the pineal body is situated in the anterior part of the sagittal crest on the same level as the posterior border of the postero-medial flange of the postorbital (Fig. 1). The external opening of the parietal foramen is a narrow spindle-shaped slit, similar to the condition in the Moschorhinus specimens described by Brink (1958) and Mendrez (1974a).

In lateral view the vertically curving suture between the dorsal process of the squamosal and the posterior flange of the parietal can be seen. This suture matches the occipital suture between the parietal, interparietal and the tabular. The ventral border of the parietal forms the roof of the brain-case. The anterior third of the ventral border of the parietal does not make sutural contact with any bony elements since this part of the brain-case was unossified. The middle part of the parietal is triangular in cross-section. The lateral edges of the ventral border of this triangle contact the dorsal border of the epipterygoid and the dorsal part of the antero-lateral process of the supraoccipital on each side. The short ventro-lateral descending flange of the parietal overlaps the anterior two thirds of the dorsal border of the epipterygoid. The posterior part of the ventral area of the parietal contacts the dorsal border of the interparietal. The ventro-lateral edge of the parietal, posterior to its suture with the epipterygoid, forms the dorsal border of

the lateral-supraoccipital fossa.

EXOCCIPITAL (Figs. 1, 2, 5, 6)

In occipital view it can be seen that the exoccipital contacts the postero-ventral part of the supraoccipital dorsally, the postero-medial part of the opisthotic laterally and the posterior part of the basioccipital ventro-laterally. The concave medial side of the exoccipital forms the lateral wall of the foramen magnum.

The exoccipital is divided externally into a flat antero-dorsal part and a postero-ventral projection. The ventro-lateral half of the antero-dorsal part overlaps the postero-medial part of the opisthotic and the dorso-lateral half meets postero-ventral part of the supraoccipital. The antero-dor. part has two pronounced, acute rims, a medial one forming the dorso-lateral lip of the foramen magnum, and a ventral one forming a ridge demarcating the postero-dorsal lip of the jugular foramen.

The postero-ventral projections of the exoccipitals form, together with the posterior part of the basioccipital, the occipital condyle. The exoccipitals form the dorso-lateral parts of the occipital condyle and the basioccipital the ventral third. The occipital condyle in RP/1/4636 has a central indentation on its articular surface not described before in Moschorhinus (Figs. 1, 6). This indentation involves the postero-dorsal part of the basioccipital third of the condyle and the postero-medial parts of the exoccipitals. The indentation and the associated lateral bosses hint at a double condyle condition. The suture between the

exoccipital and the basioccipital runs parasagittally from dorso-medially inside the foramen magnum (Fig. 1), over the dorsal rim of the occipital condyle diagonally to a point ventro-laterally on the convex ventral rim of the occipital condyle. From here the suture runs anteriorly for a short distance on the ventral surface of the occipital condyle and then curves dorso-laterally, over the ventro-medial lip of the jugular foramen, from whence it plunges into the jugular foramen in an antero-dorsal direction. The dorso-medial side of the postero-ventral projection of the exoccipital forms the posterior part of the ventro-lateral wall of the foramen magnum (and the concave dorso-medial border of the occipital condyle) and its postero-dorsal rim demarcates the posterior border of the foramen magnum. The ventro-lateral side of the postero-ventral projection forms the ventro-lateral border of the occipital condyle, and the anterior border of the ventro-lateral side forms the posterior lip of the jugular foramen (Fig. 2). The lateral wall of the postero-ventral projection is penetrated by two small foramina near the mouth of the jugular foramen for the hypoglossal nerve (XII).

BASIOCCIPITAL (Figs. 1, 2, 4, 5, 6)

The basioccipital forms the posterior part of the basicranium and the ventral part of the occiput. In ventral view the basioccipital contacts the basisphenoid anteriorly, the opisthotic laterally and the exoccipitals postero-laterally.

The antero-ventral part of the basioccipital and the postero-ventral part of the basisphenoid form the two spheno-occipital

tubercles. The suture between the anterior border of the basioccipital and posterior border of the basisphenoid can be seen in ventral view. It dips diagonally in an antero-ventral direction from the ventral lip of the fenestra ovalis, curves medially and surrounds the posterior part of the spheno-occipital tubercle. The suture in the indentation between the two tubercles is set further posteriorly than those parts of it which bisect the tubercles.

Postero-laterally to each spheno-occipital tubercle occurs the small laterally directed process of the basioccipital which forms part of the ventral lip of the fenestra ovalis (Fig. 5). This small process is wedged between the postero-lateral corner of the basisphenoid anteriorly and the anterior border of the internal process of the opisthotic posteriorly.

The suture between the internal process of the opisthotic and the basioccipital has a roughly diagonal, antero-lateral, postero-medial orientation. Seen in ventral view, it emerges from the fenestra ovalis and runs medially across its ventral suface for a short distance. The suture turns postero-medially and skirts the antero-lateral extension of the internal process of the opisthotic, before curving slightly postero-laterally around the ventro-medial tuberosity and the postero-medial extension of the internal process of the opisthotic.

Between the posterior border of the internal process of the opisthotic and the postero-ventral edge of the occipital condyle, a short parasagittal flange separates the ventro-lateral border of the basioccipital and the ventro-medial border of the occipital projection of the exoccipital. This suture can be seen in ventral view.

The posterior part of the basioccipital has a rugose ventral surface. This rectangular part of the basioccipital, situated posteriorly to the level of the jugal foramina, forms the convex base of the occipital condyle.

In dorsal view the posterior part of the basioccipital which participates in the formation of the occipital condyle is visible as a thin strip flanked by the postero-ventral projections of the exoccipitals. The basioccipital is wedge-shaped in occipital view, the broad concave base of the wedge being formed by the ventral surface of the basioccipital. The suture between the basioccipital and exoccipital has been described above.

*BASISPHENOID AND PARASPHENOID* (Figs. 2, 4, 5)

The basisphenoid and parasphenoid are commonly fused in therapsids (Haughton 1918; Olson 1944; Parrington 1946, 1955; Crompton 1955; Watson & Romer 1956; Boonstra 1968; Cluver 1971). Most of these authors therefore refer to the combined structure as the para-basisphenoid complex. Although these two elements are fused ventrally in Moschorhinus, a suture dividing the dorsal parts can be seen in lateral view (Fig. 4). In this description therefore, the basisphenoid and parasphenoid are regarded as two separate elements.

The basisphenoid contacts the parasphenoid antero-ventrally, the prootic postero-dorsally, the basioccipital posteriorly and the pterygoid antero-laterally.

Running dorso-medially, forming part of the floor of the endocranium, is the antero-dorsal process of the basisphenoid.

Lateral to it lie the two laterally projecting basipterygoid processes of the basisphenoid (Fig. 9). The dorsal parts of the basisphenoid are described in detail in Chapter 4.

The posterior part of the basisphenoid is broad and robust and is pear-shaped in transverse section. It has a deep ventral indentation originating anteriorly posterior to the parasphenoid keel. This indentation divides the ventral part of the basisphenoid into two broad postero-laterally running prominences each forming the anterior part of the spheno-occipital tubercle. The lateral walls of the basisphenoid slope dorso-medially from these ventral bulges to the narrow dorsal part of the basisphenoid. The basisphenoid meets the prootic postero-dorsally, the lateral part of this suture (Fig. 5) has been described previously. The basisphenoid contacts the basioccipital posteriorly (see above; Figs. 2, 5). The basisphenoid-prootic suture and the basisphenoid-basioccipital suture meet at the antero-ventral margin of the fenestra ovalis (Fig. 5) and the basisphenoid forms only a small sector of the lip surrounding the fenestra ovalis. The anterolateral surfaces of the posterior part of the basisphenoid are covered by a thin basisphenoid process on either side. The sutures between these elements can be seen in lateral and ventral views (Figs. 2, 5) and have been described previously.

The basisphenoid contacts the narrow antero-dorsally projecting parasphenoid antero-ventrally. These elements are fused ventrally and no suture could be distinguished between them. It can be assumed that the spindle-shaped ventral keel, which is the ventral part of the process forming the parasphenoid rostrum, is also of parasphenoid origin.

The ventral apertures of the parabasal canals can be seen in

ventral and lateral views (Figs. 2, 5). These [illegible] lay on either side of the parasphenoid keel and [illegible] ventral to the posterior part of the basisphenoid. Each is bordered laterally by a basisphenoid process of the pterygoid [illegible] anteriorly by a ventro-medial flange of the pterygoid. The postero-medial corner of each ventro-medial flange of the pterygoid covers the lateral surface of the narrow anterior part of the parasphenoid keel on either side. The suture between them can be seen in ventral and lateral views (Figs. 2, 4) and has been described previously.

## CHAPTER 4 : ENDOCRANIUM

The endocranium is defined as the inner surface of the dermal and endochondral elements of the skull which enclose the endocranial cavity. The endocranium is arbitrarily divided into three parts, firstly the nasal capsule, secondly the braincase (the area housing the brain) and thirdly the dorsal surface of the central part of the basicranium anterior to the crista sellaris and posterior to the nasal capsule. It is necessary to make a distinction between the braincase and the dorsal region of the central part of the basicranium because nervous tissue made contact only with a small medial strip of the latter. Other (mainly vascular and muscular) structures covered the rest of the dorsal surface of the ventral part of the basicranium. The braincase and the dorsal region of the central part of the basicranium are described here.

Moschorhinus has an elongated, narrow braincase with a high roof as is common in therapsids (see Haughton 1918; Watson 1921; Broom 1932; Olson 1944; Boonstra 1968). The area on either side dorsal to the basicranium and ventral to the roof of the endocranium, anterior to the level of the parietal foramen, is unossified. No trace of an orbitosphenoid or an interorbital septum could be found, in contrast to the situation in the gorgonopsians and whaitsiids (see Kemp 1969, 1972). The absence of these structures leaves the endocranium between the epipterygoid and snout wide open. In life this area would have been filled by membranes and cartilaginous bars, as in extant reptiles, which did not fossilize.

The roof of the braincase is formed by the ventro-medial surfaces of the frontals, fused parietals, supraoccipital and the dorso-medial parts of the exoccipitals. The posterior part of the sidewall of the braincase is formed by the medial surfaces of the following elements: the dorsal part of the epipterygoid, the lateral part of the supraoccipital and the prootic, opisthotic and exoccipital. The anterior part of the sidewall of the braincase was formed by the aforementioned membranes and cartilaginous bars. These structures will be discussed later. The sella turcica, which is situated in part of the dorsal surface of the basisphenoid, represents the anterior part of the floor of the braincase. The floor of the braincase posterior to the crista sellaris is formed by the dorsal surfaces of the following elements: the ventro-medial parts of the exoccipitals, the dorso-medial strip of the basioccipital and the ventro-medial flanges of the prootics The cochlear recess and auditory canal lie within the opisthotic, prootic and basioccipital. The vestibule lies in the prootic and opisthotic.

Several interesting features are found in the braincase. These are, briefly, the depressions and foramina for veins on the roof and sidewall of the braincase, the notch for the trigeminal nerve (V), foramen for the facial nerve (VII) and the floccular fossa in each prootic. There are two foramina for the hypoglossal nerve in each exoccipital, the pituitary fossa in the basisphenoid and the parietal foramen in the parietal. Also present are the jugular foramen, the vestibule and foramen ovale on each side and the foramen magnum. The probable positions of the cranial nerves and bloodvessels are discussed in the next chapter.

The elements forming the medial surface of the braincase and

]the medial strip of the part of the basicranium anterior to the crista sellaris and their positions relative to each other are described. The probable morphology of the non-osseous part of the braincase will be discussed in the next chapter.

PARIETAL (Figs. 7, 8)

The ventral surface of the fused parietals forms the roof of the central part of the braincase. In ventral view (Fig. 8) the parietal element contacts the frontals antero-medially, the postorbitals antero-laterally the epipterygoid ventro-laterally and the supraoccipital postero-ventrally.

In sagittal section it can be seen that the parietal canal (Boonstra 1968) penetrates the parietal element at the level of the antero-dorsal border of the epipterygoid. Although the parietal canal has a narrow, spindle-shaped dorsal aperture in the sagittal crest, it has a large, oval aperture ventrally, situated in the centre of a funnel-shaped indentation in the parietal. These apertures are here referred to as the dorsal parietal foramen and ventral parietal foramen respectively. A broad, well-defined ridge, the ventro-medial ridge of the parietal, runs from the parietal foramen anteriorly to the supraoccipital posteriorly. The pronounced lateral borders of the ridge originate posteriorly at the suture between the parietal and supraoccipital. As the borders run anteriorly from their origin, they curve initially sharply in a medial direction, then gradually laterally, skirting the funnel-shaped indentation in which the ventral parietal foramen lies.

The ventro-medial ridge is flanked on either side by a wide gutter, here called the ventro-lateral gutters of the parietals. This is similar to the condition Olson (1937) found in Cynosaurus longiceps. Each lateral wall of the ventro-medial ridge forms the medial wall of a ventro-lateral gutter. The depth of the ventro-lateral gutter varies: it is deepest posteriorly, immediately anterior to the parietal-supraoccipital suture and then gradually becomes shallower as it meanders in an anterior direction. It finally tapers out just anterior to the level of the anterior border of the ventral parietal foramen. The postero-lateral corner of the gutter lies dorsal to the antero-medial part of the antero-lateral process of the supraoccipital. The lateral wall of the gutter is formed by the medial surfaces of the ventro-lateral descending flange of the parietal and that of the dorsal border of the anterior part of the epipterygoid. The anterior part of the lateral wall is formed by a low ridge on the lateral part of the ventral surface of the parietal. The medial and lateral walls of the gutter gradually become lower as the gutter continues anteriorly. At its anteriormost position the walls are reduced to mere ridges which meet anterior to the level of the anterior part of the ventral parietal foramen. A single ridge continues from this point antero-laterally along the whole length of the roof of the braincase. This ridge is here called the dorso-lateral ridge of the braincase. It crosses the anterior part of the parietal, runs along the length of the frontal and continues on the prefrontal where it becomes part of the ventral flange of the prefrontal which forms the antero-medial wall of the orbit (Figs. 4, 7, 8).

Anterior to the ventral parietal foramen, a cresent-shaped suture can be seen in ventral view (Fig. 8) separating the antero-

medial part of the parietal from the frontals. This suture continues in an antero-lateral direction for a short distance up to where the postero-medial flange of the postorbital covers the parietal. The suture skirting this flange of the postorbital (seen in lateral view, Fig. 4) runs from this point diagonally in a postero-dorsal direction up to a point level with the parietal canal. The suture-line then runs antero-dorsally and can be seen on the dorsal surface of the skull where it joins the dorsal suture separating the frontal and parietal (Fig. 1).

The ventro-lateral descending flange of the parietal contacts the antero-dorsal two-thirds of the epipterygoid. Part of the suture separating these two elements can be seen in medial and ventral views (Figs. 7, 8). It originates anteriorly at the tip of the antero-dorsal process of the epipterygoid at the level of the anterior border of the ventral parietal foramen. The suture meanders on the medial side of the epipterygoid firstly postero-medially, then postero-laterally, then postero-medially again. It finally joins the suture between the supraoccipital and the parietal.

A part of the suture between the parietal and supraoccipital can be seen in medial and ventral views (Figs. 7, 8) running along the small cresent-shaped fold at the highest point in the skull roof. It then plunges into the posterior part of the ventro-lateral gutter of the parietal. The suture can only be seen in oblique antero-medial view (not figured) since it runs lateral to the antero-lateral process of the supraoccipital. The suture now runs in an antero-ventral direction along the dorso-lateral border of the antero-lateral process of the supraoccipital within the gutter. The suture terminates at the postero-medial point of contact

between the epipterygoid and the ventro-lateral descending flange of the parietal.

FRONTAL (Figs. 7, 8)

The frontal forms the anterior part of the roof of the braincase (Fig. 8). It makes sutural contact with the parietal posteriorly, the postorbital postero-laterally, the prefrontal antero-laterally and the nasal anteriorly. The broad, central section of its ventral surface is essentially horizontally inclined but the concave, lateral process of the frontal flares dorso-laterally to form part of the dorso-medial wall of the orbit (see also Fig. 4).

Running between the central section and each lateral process of the frontal is the dorso-lateral ridge of the braincase. This low ridge originates, as was mentioned before, on the ventral surface of the parietal. It curves antero-laterally as it runs from the antero-lateral part of the ventral funnel-like indentation in the parietal. It then runs across the frontal onto the ventral flange of the prefrontal. This ridge marks the dorso-lateral limit of the braincase (see discussion).

The suture between the postorbital and the frontal originates posteriorly at the contact formed between these two elements and the parietal (Fig. 8). From this point the suture curves antero-laterally and dorsally, running along the dorso-medial wall of the orbit. The suture-line finally curves around the dorsal rim of the orbit to continue on the dorsal surface of the skull (see also Figs. 1, 4). The ventral surface of the frontal is covered antero-laterally by the postero-ventral processes of the nasal and the

prefrontal (Fig. 8). The suture between the prefrontal and frontal runs mainly on the anterior part of the dorso-medial wall of the orbit. The suture originates medially at the contact formed between these elements and the nasal. It then crosses the dorso-lateral ridge of the braincase as it runs in a zig-zag pattern postero-laterally and dorsally along the ventral third of the dorso-medial wall of the orbit. It then twists sharply and curves antero-laterally and dorsally along the remaining two-thirds of the dorso-medial wall. The suture finally curves around the dorsal rim of the orbit and continues on the dorsal surface of the skull (see also Figs. 1, 4).

A broad sagittal ridge is present on the roof of the nasal capsule, here named the sagittal ridge of the nasal capsule. It lies on the same level as the rest of the braincase posterior to it, and would not have been distinguishable if it were not for the two gently sloping, broad fossae flanking it (Fig. 8). The fossae (here named the dorsal fossae of the nasal capsule) and therefore also the ridge, terminate posterior to the level of the canines. The posterior limit of each fossa lies in the antero-ventral part of the central section of each frontal. The remainder of the fossa lies mostly in the nasal element.

The ventral suture between the frontal and nasal runs diagonally in an antero-medial direction from the contact formed between these two elements and the prefrontal, through the posterior part of the dorsal fossa of the nasal capsule (Fig. 8). It emerges from the medial limit of the fossa and curves more medially on the sagital ridge of the roof of the nasal capsule where it finally meets its counterpart on the midline.

SUPRAOCCIPITAL (Fig. 7, 8)

The supraoccipital forms the major part of the postero-dorsal wall of the braincase, but is represented by only a narrow strip in the roof of the posterior tubular section of the braincase which houses the medulla oblongata. In medial view (Fig. 7) it can be seen that the supraoccipital slopes postero-ventrally towards the dorso-lateral constriction in the braincase which marks the anterior border of the abovementioned tubular section. The constriction is formed by a short pronounced medial wall on each opisthotic and a slight ventrally projecting transverse ridge on the supraoccipital. In longitudinal section the narrow ventro-medial strip of the supraoccipital is deflected postero-dorsally posterior to this ridge.

As seen in ventral and medial views (Figs. 7, 8) the supra-occipital contacts the parietal and epipterygoid antero-dorsally, the prootic antero-ventrally and the opisthotic and exoccipital postero-ventrally.

The supraoccipital is concave in cross-section because of its two antero-laterally curving sides. The pointed anterior part of each side (here called the antero-lateral process of the supraoc-cipital) contacts the medial surface of the postero-dorsal border of the epipterygoid antero-ventrally and contacts the parietal dorso-laterally. The medial lip of this process overlies the posterior part of the ventro-lateral gutter of the parietal. The dorsal and medial surfaces of the antero-lateral process are in confluence with those of the dorso-medial flange of the epiptery-goid (Figs. 7, 8). The postero-dorsal margin of the dorsal venous foramen is formed by part of the antero-ventral border of the

supraoccipital posterior to the antero-lateral process.

The antero-ventral border of the supraoccipital contacts the postero-dorsal border of the prootic posterior to the dorsal venous foramen (Fig. 7). The suture runs postero-ventrally towards the floccular fossa. It then curves laterally along the roof of the floccular fossa where it meets the opisthotic (Fig. 8). The suture between the supraoccipital and opisthotic runs from its origin on the roof of the floccular fossa in a postero-medial direction and exits posteriorly from the fossa. It continues in a posterior direction and curves initially dorso-medially to skirt the anterior border of the wall formed by the medial surface of the opisthotic (Figs. 7, 8). It then curves over the dorsal part of the wall and meets the exoccipital posterior to the wall. The suture between the supraoccipital and exoccipital curves dorso-medially as it runs posteriorly along the roof of the tubular section which housed the medulla oblongata. This suture finally exits through the foramen magnum. A small, inconspicuous groove lies medial to the suture, anterior to the foramen magnum.

PROOTIC (Figs. 7, 8, 9)

The prootic is concave in cross-section. In medial view (Fig. 7) it can be seen that the lateral side forms part of the side-wall of the braincase, and in dorsal view (Fig. 9) that the ventro-medial side forms part of the floor of the braincase.

The prootic contacts the supraoccipital postero-dorsally, the epipterygoid antero-dorsally, the opisthotic posteriorly, the

exoccipital and basioccipital postero-ventrally and the basisphenoid antero-ventrally.

The big, postero-laterally plunging floccular fossa (subarcuate fossa, Olson 1944) lies medially against the supraoccipital, prootic and opisthotic (Figs. 7, 8, 9). The greater part of this fossa lies in the prootic which forms its lateral, antero-dorsal and ventral walls. The supraoccipital forms its dorso-medial wall and the opisthotic its posterior wall. The medial opening of the facial nerve (VII) can be seen mid-way between the floccular fossa and the incisura prootica (Fig 7). No foramen for the abducens nerve (VI) could be found (see Ch. 5).

The anterior half of the prootic consists of two antero-dorsally projecting processes: the antero-dorsal and antero-ventral processes (see Ch. 3; Fig. 7). The medial surface of the short, broad antero-dorsal process is slightly concave. Its concave dorsal corner forms the ventral margin of the dorsal venous foramen. The lateral surface of the antero-dorsal tip of the antero-dorsal process of the prootic lies upon the medial surface of the postero-ventral tip of the [illegible]rsal process of the epipterygoid. The antero-dorsal b[illegible] the antero-dorsal process of the prootic slopes in an antero-ventral direction from the anterior border of the dorsal venous foramen dorsally to the dorsal border of the posterior foramen of the epipterygoid ventrally. The antero-ventral part of the antero-dorsal process of the prootic forms the posterior border of the posterior foramen of the epipterygoid. As mentioned before, the incisura prootica lies between the antero-dorsal and antero-ventral processes of the prootic (see Ch. 3).

The antero-ventral process of the prootic (the ossified pila

antotica, is triangular in cross-section. It has a flat, vertically inclined lateral face (described in Ch. 3). On its medial face however it has a sharp, pronounced ridge. This ridge, the medial ridge of the antero-ventral process, runs from the antero-dorsal extremity of the process to the crista sellaris postero-ventrally (Fig. 7). The two medial ridges of the antero-ventral processes probably indicate the attachment of the membrane forming the floor of the braincase dorsal to the sella turcica (this aspect will be discussed later). The sloping face of the antero-ventral process dorsal to the medial ridge would therefore form part of the lateral wall of the braincase proper. The sloping face of the antero-ventral process, ventral to the medial ridge, would on the other hand form part of the roof over the sella turcica. The concave, sharp-edged postero-dorsal border of the antero-ventral process forms the antero-ventral border of the incisura prootica (Fig. 7). The equally sharp-edged, convex antero-ventral border of this process runs postero- ventrally and forms posteriorly the dorsal border of the ventral notch. It is also in confluence with the dorso-lateral flange of the basisphenoid which in turn forms the ventral border of the ventral notch.

The floor of the braincase, from the level of the internal auditory meatus to the crista sellaris is formed on either side by the dorsal surface of the ventro-medially projecting flange of the prootic (Fig. 9). The ventro-medial flange was named the basicranial process of the periotic by Olson (1938b). It is proposed however that this term be changed to the "basicranial process of the prootic" because it appears to be present exclusively in synapsids with separate prootics and opisthotics (see discussion). The two basicranial processes meet medially on the floor of the

braincase and thereby cover the anterior part of the basioccipital and the posterior part of the basisphenoid (Fig. 7). The basicranial process slopes ventro-medially from that part of the prootic which forms the side-wall of the braincase. Its anterior border runs postero-medially and is the extension of the medial ridge of the antero-ventral process of the prootic (Fig. 9). The anterior parts of the basicranial processes cover most of the postero-dorsal part of the basisphenoid. However, where the anterior borders of the two processes curve sharply postero-medially, just prior to meeting on the mid-line, the dorso-medial lip of the basisphenoid, which forms the crista sellaris, is exposed. The anterior border of the crista sellaris is in confluence with the two medial ridges of the antero-ventral processes of the prootics on either side. The anteriormost part of each basicranial process forms a small but distinct overhang over the postero-dorsal part of the sella turcica lateral to the dorsum sellae.

The antero-medial suture between the prootic and basisphenoid can be seen in medial view (Fig. 7). It runs posteriorly from the antero-ventral corner of the antero-ventral process of the prootic, posterior to the ventral notch, along the medial wall of the posterior part of the sella turcica. The suture curves dorso-medially as it runs posteriorly and emerges from the sella turcica lateral to the dorsum sellae from where it runs postero-medially on the floor of the braincase posterior to the crista sellaris. The suture between the two basicranial processes of the prootics can be seen in dorsal view (Fig. 9). It runs from just posterior to the crista sellaris along the mid-line and terminates at a small pit (function unknown) anterior to the dorso-medial surface of the basioccipital. The postero-medial corner of the basicra-

nial process skirts this foramen and contacts the antero-lateral corner of the antero-dorsal projection of the basioccipital.

The posterior border of the basicranial process contacts the anterior border of the basicranial process of the exoccipital medially and the antero-medial corner of the opisthotic on the floor of the braincase laterally (Fig. 9). This suture runs laterally and slightly posteriorly from the antero-dorsal projection of the basioccipital, through the depression on the floor of the braincase lateral to it. The suture then crosses the ventro-medial rim of the internal auditory meatus and plunges ventrally into it.

The internal auditory meatus of Moschorhinus opens widely into the cranial cavity as in other therapsids (Olson 1944). The concave ventral rim of the internal auditory meatus is raised above the surrounding floor of the braincase. This feature is accentuated by the depression in the floor of the braincase medial to it. The ventro-medial rim of the meatus is formed anteriorly by the prootic and posteriorly by the opisthotic. The cochlear recess lies ventral to the level of the floor of the braincase (Fig. 9). The prootic-opisthotic suture runs vertically on the medial wall of the cochlear recess and terminates in the ventral part of the recess. The postero-lateral border of the ventral part of the prootic contacts the dorso-lateral part of the basioccipital within the inner ear. This suture runs dorso-laterally and slightly anteriorly through the ventral part of the cochlear recess, then along the length of the auditory canal where it skirts the ventro-medial bulge in the canal anteriorly and exits finally through the fenestra ovalis.

The anterior half of the inner ear is situated in the pro-

otic. The prootic forms the anterior walls of the cochlear recess and the auditory canal. It also forms the anterior and greater parts of the dorsal and lateral walls of the vestibule. The vestibule (i.e. the dorsal part of the inner ear, Baird 1970) is separated from the floccular fossa by a horizontal medially-protruding ledge, here called the ventral ledge (Fig. 7). The dorsal surface of this ledge forms the ventro-medial border of the floccular fossa and the ventral surface forms the dorso-medial border of the vestibule. The medial rim of the ventral ledge can be considered as the dorsal border of the internal auditory meatus. The ventral ledge appears on the side-wall of the braincase at the level of the anterior part of the floccular fossa and it terminates just posterior to the floccular fossa, dorsal to the foramen in the opisthotic. The antero-medial rim of the internal auditory meatus curves dorso-laterally, following the curve of the braincase-wall, and joins the anterior part of the ventral ledge.

The lateral wall of the vestibule is formed anteriorly by the prootic and posteriorly by the opisthotic. The dorsal part of this wall has a groove running ventrally from the abovementioned foramen in the opisthotic, along the prootic-opisthotic suture (Fig. 7). This foramen and the groove were most probably for the crus communis (Olson 1944; Sigogneau 1974). At the level of the floor of the braincase there are two deep lateral depressions in the lateral wall of the vestibule. These depressions are the anterior and posterior ampullary recesses (Olson 1944). Only the anterior ampullary recess can be seen in medial view (Fig. 7) since the posterior ampullary recess lies below the level of the floor of the braincase. The dorsal borders of these recesses can be seen in ventral view (Fig. 8). The anterior ampullary recess

lies in the prootic and the posterior ampullary recess lies in the opisthotic and prootic. The medial aperture of the auditory canal opens into the vestibule ventral to the ampullary recesses and dorsal to the cochlear recess (Figs. 8, 9).

The suture between the prootic and the opisthotic originates dorsally on the roof of the floccular fossa at the junction between these two elements and the supraoccipital (Fig. 8). The suture runs from this point laterally and slightly posteriorly in the middle of the roof of the floccular fossa. The suture curves postero-ventrally on the lateral wall of the fossa and runs medially along the posterior part of the floor of the fossa (Fig. 9). The suture exits from the postero-ventral corner of the fossa, crosses the ventral ledge and runs within the depression for the crus communis (Fig. 7). Within the posterior ampullary recess the suture continues ventrally but now curves antero-laterally until it enters the auditory canal. From this point the suture runs laterally and slightly posteriorly on the roof of the auditory canal and exits dorsally through the fenestra ovalis (Fig. 8).

OPISTHOTIC (Figs. 7, 8, 9)

The opisthotic forms the posterior part of the floccular fossa, the posterior part of the inner ear and the anterior part of the jugular canal. It also forms a relatively small portion of the lateral wall and the floor of the braincase compared to the other bony elements (Figs. 7, 9). Most of its medial surface is occupied by a prominent, broad wall which separates the inner ear and the medial aperture of the jugular canal ("paroi médiale de

l'oreille interne", Sigogneau 1974). This wall is here referred to as the medial wall of the opisthotic. The foramen for the crus communis is situated anteriorly to this wall (Fig. 7). The opisthotic contacts the supraoccipital dorsally , the prootic anteriorly, the basioccipital antero-ventrally and the exoccipital postero-medially.

The medial wall of the opisthotic is an important landmark in the braincase Its antero-ventral surface, i.e. the portion from the foramen for the crus communis dorsally to the floor of the braincase ventrally, is the posterior border of the internal auditory meatus. The posterior border of the groove for the crus communis is formed by this part of the medial wall. The postero-medial surface of the medial wall slopes gently postero-laterally and ventrally into the jugular foramen. The medial walls of the opisthotics, the ventrally projecting transverse ridge of the supraoccipital and the basicranial ridges of the exoccipitals mark the anterior constriction of the posterior tubular section of the braincase which housed the medulla oblongata (see Ch. 5; Figs. 7, 8).

The sutures between the opisthotic and the prootic and supra-occipital have already been described. The opisthotic forms the posterior part of the vestibule and the posterior part of the auditory canal. The suture between the basioccipital and the antero-ventral part of the opisthotic can be seen within the inner ear (Fig. 9). The suture runs laterally along the posterior wall of the cochlear recess then along the postero-ventral part of the auditory canal and exits through the ventral part of the fenestra ovalis.

The jugular canal (jugular tube, Boonstra 1968) is formed

anteriorly by the opisthotic and posteriorly by the exoccipital. Two postero-laterally running sutures separate these two elements. The dorsal suture can be seen in ventral view (Fig. 8) running from the contact formed between the opisthotic, exoccipital and supraoccipital on the roof of the braincase. The suture initially runs ventrally posterior to the medial wall of the opisthotic and then curves postero- laterally into the medial aperture of the jugular canal. It continues postero-laterally within the jugular canal and exits dorsally through the jugular foramen. This suture is in the same position as the supraoccipital-prootic suture which according to Olson (1937) passes dorsally through the jugular foramen. This, and the fact that the hypoglossal nerve (XII) always penetrates the exoccipital and not the supraoccipital as Olson suggests proves that his identification of this element was incorrect. The ventral suture between the opisthotic and exoccipital can be seen in dorsal view (Fig. 9) running from the contact formed between them and the prootic on the floor of the braincase. This contact lies within the depression on the floor of the braincase between the inner ear and the antero-dorsal projection of the basioccipital. The depression is confluent with the ventral part of the jugular canal and together they form a postero-laterally running ventral trough. The ventral suture meanders in a postero-lateral direction within the ventral trough and exits through the postero-ventral part of the jugular foramen. The antero-medial corner of the ventral part of the opisthotic forms the antero-lateral part of the ventral trough and the posterior half of the rim forming the ventral border of the internal auditory meatus.

EXOCCIPITAL (Figs. 7, 8, 9)

Within the braincase the exoccipital contacts the prootic antero-ventrally, the basioccipital ventro-medially, the opisthotic antero-laterally and the supraoccipital dorso-medially. The exoccipital forms the posterior half of the jugular canal. Two foramina for the hypoglossal nerve (XII) penetrate the ventro-lateral part of each exoccipital. The medial apertures of these foramina lie posterior to the jugular canal, the dorsal aperture lies more posteriorly than the ventral aperture (Fig. 7). The lateral apertures open within the postero-lateral limit of the jugular foramen (Fig. 5).

The concave medial surfaces of the exoccipitals form the greatest part of the posterior tubular section of the braincase that housed the medulla oblongata. The exoccipitals cover the dorso-lateral parts of the posterior part of the supraoccipital. This means that only a small ventro-medial portion of the supraoccipital is left uncovered in the roof of this section of the braincase. Similarly only a small dorso-medial strip of the basioccipital is left uncovered on the floor of this section.

The posterior tubular section of the braincase runs from the constriction in the braincase posterior to the level of the internal auditory meatus anteriorly, to the *foramen magnum* posteriorly. As was mentioned previously, the constriction marking the anterior limit of this section is formed laterally by the medial walls of the opisthotics and dorsally by the transverse ridge on the ventral surface of the supraoccipital. Ventrally however, the constriction is marked by the paired, diagonally-running ridges on the floor of the braincase formed by the exoccipitals. These

ridges are here referred to as the basicranial ridges of the exoccipitals (Fig. 9). Each basicranial ridge slopes ventrally from the posterior part of the medial aperture of the jugular canal in an antero-medial direction on the floor of the braincase and terminates posteriorly to the antero-dorsal projection of the basioccipital. The antero-lateral surface of this ridge forms the postero-medial wall of the ventral depression on the floor of the braincase leading to the jugular canal. Postero-medial to this ridge lies an oval-shaped depression in the floor of the braincase leading to the ventral foramen of the hypoglossal nerve.

The ventral part of the exoccipital stretches from the anterior level of the internal auditory meatus anteriorly, to the posterior limit of the occipital condyle posteriorly (Fig. 9). The much shorter dorsal part of the exoccipital stretches from the medial wall of the opisthotic anteriorly to the dorsal border of the foramen magnum posteriorly (Figs. 7, 8). The sutures between the exoccipital and the supraoccipital, prootic and opisthotic have already been described. The suture between the exoccipital and basioccipital can be seen on the floor of the braincase (Fig. 9). This straight, parasagittal suture runs from the exoccipital, basioccipital and prootic contact anteriorly to the indentation in the occipital condyle posteriorly.

A small, medial tuberosity can be seen dorsal to the medial aperture of the jugular canal (Figs. 7, 8). A short groove on the medial face of the exoccipital, posterior to its suture with the opisthotic, separates this tuberosity and the medial wall of the opisthotic. This groove runs ventro-laterally and is confluent with the dorsal part of the medial aperture of the jugular canal (Figs. 7, 8).

BASIOCCIPITAL (Figs. 7, 9)

A very small portion of the dorsal surface of the basioccipital is exposed on the floor of the braincase. Within each inner ear a thin lateral-running strip can be seen and on the floor of the braincase a thin medial strip can be seen (Fig. 9).

Within the inner ear the basioccipital forms the postero-ventral part of the cochlear recess and the ventral part of the auditory canal. The basioccipital here meets the prootic anteriorly and the opisthotic posteriorly, as described earlier. The thin medial strip on the floor of the braincase formed by the basioccipital meets the exoccipital laterally and the prootic antero-laterally, as described above.

In sagittal section (Fig. 7) it can be seen that the dorso-medial surface of the basioccipital gradually slopes antero-dorsally from the posterior limit of the occipital condyle posteriorly to the level of the internal auditory meatus anteriorly. The dorso-medial exposure of the basioccipital terminates in the form of a small nodule named here the antero-dorsal projection of the basioccipital. This is similar to the situation found in the dinocephalians (Boonstra 1968). Anterior to this projection a small pit is situated in the floor of the braincase. The postero-ventral parts of the basicranial processes of the prootics cover the antero-dorsal part of the basioccipital anterior to the level of the internal auditory meatus and the dorsal projection. Ventral to the basicranial processes of the prootics, the anterior part of the basioccipital contacts the posterior part of the basisphenoid. In sagittal section, the suture runs ventrally for most of its length but curves postero-ventrally before reaching

the ventral surface of the skull.

EPIPTERYGOIL (Figs. 7, 8, 9)

The dorsal part of the medial surface of the epipterygoid forms part of the side-wall of the braincase. The ventral and biggest part of the medial surface on the other hand forms the lateral wall of the cavum epiptericum. The epipterygoid contacts not only the floor, but also the roof of the endocranium. The epipterygoid contacts the parietal and supraoccipital dorsally, the prootic posteriorly and the pterygoid ventrally.

The central section of the dorsal part of the epipterygoid is marked by a medially projecting bulge, called here the dorso-medial bulge of the epipterygoid. A prominent flange runs diagonally across the dorsal part of the epipterygoid postero-ventral to the abovementioned bulge, this flange is here termed the dorso-medial flange of the epipterygoid. Separating the abovementioned two structures is a shallow groove, here called the dorso-medial groove of the epipterygoid, which is confluent postero-dorsally with the ventro-lateral gutter of the parietal (Fig. 7). A similar groove has been described by Kemp (1979) in Procynosuchus.

The dorsal border of the epipterygoid contacts the ventro-lateral descending flange of the parietal. The dorso-medial suture between the epipterygoid and the parietal can be seen in medial and ventral views (Figs. 7, 8). It runs along the dorso-lateral border of the ventro-lateral gutter of the parietal. The course of this suture has already been described. The dorso-medial bulge of the epipterygoid lies immediately ventral to this

suture. The bulge forms the central part of the lateral wall of the ventro-lateral gutter of the parietal and the dorso-lateral wall of the dorso-medial groove of the epipterygoid.

The medial surface of the dorso-medial flange is in confluence with those of the antero-lateral process of the supraoccipital posteriorly and the postero-dorsal process of the epipterygoid ventrally. The dorsal surface of the dorso-medial flange is in confluence with that of the antero-lateral process of the supraoccipital. The dorso-medial groove of the epipterygoid therefore slopes antero-ventrally dorsal to the dorso-medial flange and postero-ventral to the dorso-medial bulge from the ventro-lateral gutter of the parietal with which it is in confluence posteriorly (Fig. 7).

The postero-dorsal process of the epipterygoid contacts the antero-lateral process of the supraoccipital. The suture originates laterally within the ventro-lateral gutter of the parietal where the parietal, supraoccipital and epipterygoid meet. The suture runs dorso-medially from here and emerges from the gutter onto the medial surface of the braincase. The suture now curves in a postero-ventral direction from the antero-dorsal lip formed by the antero-lateral process of the supraoccipital and the dorso-medial flange of the epipterygoid, and terminates in the dorsal corner of the dorsal venous foramen. The medial surface of the posterior dorsal process of the epipterygoid is concave, forming a shallow fossa, here called the dorso-medial fossa of the epipterygoid (Figs. 7, 8). This fossa is bordered postero-ventrally by the straight antero-dorsal border of the antero-dorsal process of the prootic which covers the postero-ventral edge of the postero-dorsal process of the epipterygoid medially. The suture between

these two elements can be seen in medial and ventral views (Figs. 7, 8). It runs in an antero-ventral direction from the anterior border of the dorsal venous foramen posteriorly, to the dorsal border of the posterior foramen of the epipterygoid anteriorly. The antero-dorsal limit of the dorso-medial fossa is formed by the ventro-lateral sloping medial surface of the dorso-medial flange of the epipterygoid. The fossa gradually deepens posteriorly, with the result that the postero-dorsal corner of the dorso-medial fossa lies more laterally than the antero-lateral process of the supraoccipital (the ventral border of which overlaps this fossa slightly). This dorsal venous foramen, which is formed dorsally by the antero-lateral process of the supraoccipital, ventrally by the antero-dorsal process of the prootic and anteriorly by the postero-dorsal process of the epipterygoid, therefore opens into the posterior part of the dorso-medial fossa. The posterior foramen of the epipterygoid lies directly ventral to this fossa (Figs. 7, 8).

The medial surface of the dorsal part of the epipterygoid forms part of the side-wall of the braincase. The medial surface of the rest of the processus ascendens of the epipterygoid, ventral to the level of the posterior foramen of the epipterygoid, forms the lateral wall of the cavum epiptericum. The processus ascendens juts dorso-medially from the foot of the epipterygoid which contacts the pterygoid ventrally. The medial surface of the processus ascendens is convex in horizontal cross-section. As described in Ch. 3 the ventral part of the epipterygoid expands antero-medially and postero-laterally to form the antero-ventral and postero-ventral processes of the epipterygoid respectively.

In dorsal view (Fig. 9) it can be seen that the foot of the

epipterygoid stretches out anteriorly and medially to the processus ascendens of the epipterygoid. It covers the dorsal surface of the antero-lateral third of the quadrate ramus of the pterygoid from the origin of the ramus proximally, to the origin of the postero-ventral process of the epipterygoid distally. The foot of the epipterygoid stretches out antero-medially to the antero-ventral process of the epipterygoid. The anterior part of the foot tapers off anteriorly and terminates where its lateral and medial borders meet at the level of the anterior limit of the antero-dorsal process of the basisphenoid.

The medial border of the foot of the epipterygoid runs approximately parallel to the dorso-medial ridge of the pterygoid (Fig. 9). This suture between the epipterygoid and pterygoid runs on the dorsal surface of the central part of the basicranium on a lower level than the lateral and medial ridges. In BP/1/2788 there is a deep furrow between these ridges through which this suture runs (see Plate 14). This furrow is relatively deep where it originates posteriorly on the dorsal surface of the central part of the basicranium, approximately 8 mm anterior to the level of the pituitary fossa. The furrow tapers off anteriorly, until it disappears just posterior to the anterior limit of the foot of the epipterygoid. This condition is not seen in BP/1/4636, where there is only a shallow indentation bordered postero-laterally by the postero-lateral bulge of the foot which is situated just anterior and medial to the base of the processus ascendens. This results in the central part of the foot of the epipterygoid being elevated above the level of the surrounding surface and the anterior and medial parts of the foot are on the same level as the surrounding surface.

The postero-medial border of the foot of the epipterygoid curves postero-laterally around the abovementioned bulge and runs parallel to the postero-medial edge of the quadrate ramus of the pterygoid, leaving a thin strip of the dorsal surface of the quadrate ramus uncovered, and terminates in the groove below the origin of the postero-ventral process of the epipterygoid (described in Ch. 3). From this point the suture between the quadrate ramus of the pterygoid and the postero-ventral process of the epipterygoid runs in a postero-lateral direction within the groove formed by these two elements. In ventral view (Fig. 2) this suture can be seen where it emerges medial to the quadrate ramus of the pterygoid, where the groove tapers off posteriorly.

PTERYGOID (Figs. 7, 9)

Although the pterygoid does not form part of the braincase, it plays an important role in the formation of the basicranium. The greatest part of the floor of the endocranium outside the braincase and nasal capsule is formed by the dorsal surface of the pterygoid.

In dorsal view (Fig. 9) it can be seen that the fused pterygoids contact the palatines and fused vomers anteriorly, the ectopterygoid antero-laterally, the parasphenoid medially, the basisphenoid postero-medially and the epipterygoids postero-dorsally.

The two pterygoids are fused anterior to the parasphenoid rostrum to such a degree that no suture can be distinguished between them. The parasphenoid juts antero-dorsally between the

two pterygoids and contacts the dorso-medial part of each dorsally. This dorsal suture between the parasphenoid and the pterygoid can be seen in dorsal view (Fig. 9). It runs within the ventral part of the gutter flanking the parasphenoid rostrum on either side. The gutter is bordered laterally by a steep, sloping wall formed by the dorso-medial surface of the pterygoid and medially by the concave, lateral surface of the parasphenoid rostrum. These gutters are named the basicranial gutters here. Each gutter originates posteriorly at the anterior level of the "processus ascendens" of the epipterygoid as a shallow indentation on the postero-medial contact between the basisphenoid and the pterygoid. The deepest part of the gutter lies lateral to the posterior part of the parasphenoid rostrum, gradually becoming shallower anteriorly. It meets its fellow anterior to the parasphenoid to form a broad, shallow depression. Anterior to this the medial depression is split into two by a thin, distinct medial ridge. This ridge is called here the antero-dorsal ridge of the basicranium and the parasagittal groove on either side is called the antero-dorsal groove of the pterygoid. The antero-dorsal grooves terminate abruptly posterior to the pterygoid-vomer suture. The antero-dorsal ridge originates half-way between the anterior limit of the parasphenoid rostrum and the pterygoid-vomer suture. This ridge runs in an anterior direction where the dorso-medial suture between the two pterygoids would have been. It then crosses the pterygoid-vomer suture and continues anteriorly forming the apex of their dorso-medial sloping surfaces where the dorso-medial suture between the fused vomers would have been. The dorso-medial ridges of the pterygoids join the antero-dorsal ridge of the basicranium anterior to the antero-dorsal grooves of the ptery-

goids. The dorsal ramifications of the parabasal canal open within the dorsal gutter of the basicranium on the pterygoid-parasphenoid suture-line. In BP/1/4636 there are two foramina in the gutter on the right hand side and three foramina in the gutter on the left hand side. The posterior pair of foramina lie lateral to the posterior part of the parasphenoid rostrum within the deepest part of the gutter. The anterior foramina lie lateral to the anterior part of the parasphenoid rostrum. The parasphenoid-pterygoid suture can be seen running between the posterior and anterior foramina. It is unfortunately impossible to follow the suture anterior to the anterior foramen because of the degree of ossification in the region anterior to the parasphenoid rostrum. *The dorso-lateral limits of the gutter and the antero-dorsal* groove of the pterygoid are marked by the distinct dorso-medial ridge of the pterygoid. This ridge originates anteriorly at the pterygoid vomer suture lateral to the antero-dorsal groove of the pterygoid. It continues posteriorly but grows less distinct as it approaches the posterior limit of the dorsal gutter.

The dorso-lateral limit of the central part of the pterygoid is marked by the distinct dorso-lateral ridge of the pterygoid. The posterior part of this ridge is, as was mentioned before, in confluence posteriorly with the antero-ventral process of the epipterygoid. The foot of the epipterygoid covers the postero-lateral part of the pterygoid dorsally, as described previously.

The region between the dorso-lateral ridge and dorso-medial ridge of the pterygoid is parasagittally concave. This concavity which involves the medial part of the foot of the epipterygoid and most of the dorsal surface of the central part of the pterygoid is shallow posteriorly but becomes more marked anteriorly. The

anterior part of the medial surface of this depression is elevated above the level of the rest of the dorsal surface of the central part of the pterygoid posterior and lateral to it. This is due to the fact that the dorso-medial ridge slopes in an antero-dorsal direction anterior to the parasphenoid rostrum, whereas the dorso-medial ridge runs approximately horizontally (Fig. 4). The aforementioned depression is confluent anteriorly with the deep cavity in the nasal capsule lateral to the vomer and anterior to the transverse process of the pterygoid. This is accentuated by the fact that the dorso-lateral ridge is confluent antero-laterally with the dorsal limit of the transverse process and the dorso-medial ridges which are confluent with the sharp antero-dorsal ridge of the basicranium.

The pterygoid contacts the vomer and palatine anteriorly. In dorsal view (Fig. 9) the suture between the pterygoid and vomer runs in a ventro-lateral direction on the medial wall of the cavity in the nasal capsule anterior to the transverse process of the pterygoid and lateral to the vomer. The suture originates on the antero-dorsal ridge of the basicranium medially and terminates laterally where the pterygoid and vomer meet the palatine. The dorsal suture between the transverse process of the pterygoid and postero-medial part of the palatine runs from this point first posteriorly and slightly laterally and then curves sharply laterally within the postero-medial part of abovementioned cavity. This suture passes ventrally through the suborbital vacuity on its medial lip to continue on the palate ventrally (Fig. 2).

The dorsal suture between the postero-medial border of the pterygoid and the antero-lateral border of the basipterygoid process of the basisphenoid runs on the floor of the endocranium

(Fig. 9). It originates within the posterior part of the basicranial gutter and leaves it by curving in a postero-lateral direction. The suture terminates posteriorly where the postero-medial border of the quadrate ramus of the pterygoid forms the anterior limit of the cranioquadrate passage.

In ventral view (Fig. 2) the basipterygoid process of the basisphenoid is obscured by the ventro-medial part of the quadrate ramus of the pterygoid, as in the Scaloposauridae described by Crompton (1955). However, the basipterygoid process of the basisphenoid is exposed in dorsal view (Fig. 9) on the floor of the endocranium. It seems likely therefore that the lateral part of the thin basipterygoid process of the basisphenoid is wedged between thin dorsal and ventral postero-medial flanges of the pterygoid. These two flanges apparently fuse postero-laterally to form the posterior part of the medial half of the quadrate ramus. To check this assumption it would be necessary to section this area transversely.

BASISPHENOID AND PARASPHENOID (Figs. 7, 9)

The dorsal part of the basisphenoid can be subdivided into the antero-dorsal process and the two basipterygoid processes flanking it. The antero-dorsal process is the medial part of the basisphenoid which is elevated above the surrounding dorsal surface of the basicranium formed by the dorsal surfaces of the pterygoids, epipterygoids, parasphenoid and basipterygoid processes of the basisphenoid. This long, narrow process lies antero-ventral to the part of the braincase floor formed by the basicra-

nial processes of the prootic (Figs. 4, 9). Its dorsal surface is concave and contains the pituitary fossa. The dorsal part of the process is therefore considered to be the anterior part of the floor of the braincase, namely the sella turcica.

The antero-dorsal process of the basisphenoid stretches from the crista sellaris posteriorly to the antero-dorsal portion of the parasphenoid rostrum anteriorly (Fig. 9). The antero-dorsal process terminates anteriorly as an angular tuberosity. This tuberosity is slightly narrower transversely than the rest of the antero-dorsal process. It has two transversely-running ridges, the one anteriorly forming the postero-dorsal rim of the spatula-shaped structure formed in conjunction with the parasphenoid. The other ridge marking the anterior limit of the sella turcica, lies dorsally where the antero-ventrally sloping and the postero-ventrally sloping surfaces of the tuberosity meet (Fig. 4). Two small, curving ridges run either side of its antero-ventral surface, and may have been the points of attachment of certain cartilaginous elements forming part of the side wall of the braincase (this aspect will be discussed later).

Situated posterior to the abovementioned anterior tuberosity is the trough-like dorsal area of the antero-dorsal process of the basisphenoid. The anterior part of this process has a smooth, concave surface, flanked by the thin, dorso-laterally projecting flanges of the basisphenoid (Fig. 9). The small, oval-shaped pituitary fossa lies within the posterior part of this trough-like structure anterior to the level of the posterior borders of the basipterygoid processes of the basisphenoid. In sagittal section (Fig. 7) it can be seen that the area situated anterior to the pituitary fossa lies more dorsally than the area between the

pituitary fossa and the dorsum sellae. This results in the pituitary fossa having a higher anterior than posterior wall. The areas surrounding the pituitary fossa slope towards it. A small depression lies in the floor of the sella turcica directly posterior to the pituitary fossa (Fig. 9). The dorso-lateral flanges of the basisphenoid gradually become thicker in cross-section as they progress posteriorly. They are best developed lateral to the pituitary fossa, but become lower and taper down to mere ridges posteriorly (Figs. 4, 7).

The dorsal surface of the basisphenoid posterior to the pituitary fossa and anterior to the dorsum sellae is also concave in transverse section (compare with Procynosuchus, Kemp 1979). This region is broader than the anterior part of the antero-dorsal process however, and also more open laterally because the dorso-lateral flanges are lower in this region. Stretching from the dorsum sellae posteriorly halfway to the pituitary fossa anteriorly, lies the postero-medial ridge of the sella turcica on the dorsal surface of the basisphenoid. In the posterior region of the floor of the sella turcica lie two shallow parasagittal indentations. Each indentation is walled medially by the postero-medial ridge of the sella turcica and antero-laterally by the dorso-lateral flange of the basisphenoid (Fig. 9). This indentation is called here the depression for the retractor bulbi muscle (see discussion). The dorso-lateral flange of the basisphenoid forms the ventral part of the ventral notch in this region.

The posterior wall of the sella turcica is formed by the antero-medial surface of the postero-dorsal portion of the basisphenoid. In sagittal section (Fig. 7) it can be seen that the basisphenoid contacts the basioccipital posteriorly, as was de-

scribed previously. The postero-dorsal part of the basisphenoid is covered dorso-medially by the basicranial process of the prootic and dorso-laterally by the postero-ventral process of the prootic. The antero-medial surface of its lateral part is in confluence with the ventro-medial surface of the antero-ventral process of the prootic, posterior to the ventral notch. The concave medial surface formed by the abovementioned two elements is also the postero-lateral wall of the depression for the retractor bulbi muscle (Fig. 7). As described above, the medial ridge of the antero-ventral process of the prootic forms the anterior limit of the basicranial process of the prootic ventro-medially. This portion of the prootic forms a small overhang dorso-lateral to the posterior part of the depression for the retractor bulbi muscle. The concave dorsum sellae is situated posterior to the postero-medial ridge of the sella turcica. It is not covered dorsally by the antero-medial parts of the basicranial processes of the prootics. It is situated slightly more anterior than the posterior limits of the depressions for the retractor bulbi muscles lateral to it. Its dorsal limit is in confluence with the medial ridges of the antero-ventral processes of the prootics on either side. The medial suture between the basisphenoid and prootic has already been described.

The horizontally-inclined basipterygoid processes of the basisphenoid jut laterally from the central part of the basisphenoid (Fig. 3). The ventro-medial limit of each process stretches from the basicranial gutter anteriorly, to the level of the ventral notch posteriorly, and seems to occupy the whole dorsal surface of the basisphenoid lateral to the dorso-lateral flanges. Its concave, postero-lateral border forms the antero-medial limit

of the cranioquadrate passage. The basipterygoid process lies on the same level as the surrounding floor of the endocranium and therefore on a more ventral level than the antero-dorsal process of the basisphenoid. The dorsal surface of each process slopes dorso-medially towards the lateral wall of the dorso-lateral flange proximally, thereby forming a concave parasagittal area between them, which leads towards the dorsal gutter of the basicranium anterior to it. This concave area becomes smaller posteriorly as the dorso-lateral flange and the postero-lateral rim of the basipterygoid process become less prominent in this region. The basipterygoid process is covered ventrally and to a degree dorso-laterally by the quadrate ramus of the pterygoid. The sutures between them have been described previously.

The thin parasphenoid juts from its keel ventrally in an antero-dorsal direction between the two pterygoids. It is exposed on the floor of the endocranium, wedged ventral to the antero-dorsal process of the basisphenoid. This dorsal part of the parasphenoid is here referred to as the parasphenoid rostrum (Fig. 4). The sides of the parasphenoid rostrum form the medial walls of the basicranial gutters. The parasphenoid meets the dorso-medial parts of the pterygoids lateral to it within the basicranial gutter. These sutures have been described previously. This contact between the pterygoid and parasphenoid closes the interpterygoid vacuity dorsally. The exact sagittal relations between the pterygoid, basisphenoid, parasphenoid, the ventral limit of the pituitary fossa and the dorsal limit of the interpterygoid vacuity are not known. The reason for this is that the central part of the basicranium was not sectioned sagittally in order to preserve the near-perfect sella turcica of this specimen.

The anterior-most part of the parasphenoid rostrum is not covered dorsally by the basisphenoid. The dorsal surface of this round anterior portion is horizontally flattened and forms together with the anterior-most tip of the basisphenoid a concave spatula-shaped structure (Fig. 9). This is also the widest part of the parasphenoid. The anterior margin of the parasphenoid rostrum curves postero-ventrally ventral to the spatula-shaped region (Fig. 4). The suture between the parasphenoid and basisphenoid runs antero-dorsally from the postero-medial limit of the basicranial gutter posteriorly to the spatula-shaped anterior part formed by these two elements anteriorly.

# CHAPTER 5 : DISCUSSION

## 5.1 EXTERIOR OF THE POSTERIOR HALF OF THE SKULL

### Prootic and Opisthotic

In his paper on the Scaloposauridae Crompton (1955) described a fused periotic and mentioned that Olson (1944) had not found any dividing suture in the periotic of those therocephalians he had studied either. The specimen known as "Therocephalian A" (Olson 1944) was discovered in the Tapinocephalus zone. Its locality (Boonstra 1969, Kitching 1977) and size indicate that it is most probably a pristerognathid. Olson (1938b) described this specimen as having a periotic, but Boonstra (1954) and Van den Heever (personal communication) found a prootic and opisthotic in the Pristerognathidae. It has been shown by Van den Heever & Hopson (1982) that "Therocephalian B" (Olson 1944) is actually a gorgonopsian. Olson (1944) described a periotic in this specimen as well as in the other gorgonopsians he studied. Authors such as Sigogneau (1970, 1974) describe a prootic and opisthotic in the Gorgonopsia. It is possible however that the suture between the prootic and opisthotic is difficult or impossible to detect in the region surrounding the fenestra ovalis in certain adult gorgonopsians and pristerognathids, but the co-ossification of these elements is not complete enough to consider these groups as having a periotic. The scaloposaurids also had an opisthotic and prootic as described by Mendrez (1972) and not a periotic as Crompton (1955) described. Neither the whaitsiids (personal observation)

nor the moschorhinids had periotics, and clearly distinguishable prootics and opisthotics are present instead. It seems quite clear that the therocephalians had a prootic and opisthotic and not a periotic.

Quadrate

The pterygoid process of the quadrate as it is described by Mendrez (1974a) is actually not part of the quadrate, but is the posterior end of the quadrate ramus of the pterygoid. The quadrates in the Moschorhinus kitchingi specimen described by Mendrez (1974a), and the specimens described here, have been lost. Of those specimens available for study only one specimen (BP/1/378) had a quadrate. The specimen is unfortunately badly damaged and distorted in this region with the result that only the shape of the quadrate can vaguely be seen.

Judging from the shape of the remains of the quadrate of the abovementioned specimen and that of the quadrate recess of the squamosal of other specimens, the quadrate was a relatively broad bone, approximately the same shape and size as that described by Mendrez (1974b) in Promoschorhynchus platyrhinus. Moschorhinus seems to have had a dorso-medial process which fitted into the quadrate notch of the squamosal. This process is probably synonymous with the "squamosal process of the quadrate" described by Mendrez (1974b) in Promoschorhynchus platyrhinus. This notch and slot arrangement allowed the quadrate to articulate with the squamosal in a hinge-like manner. The posterior part of the quadrate lay within the quadrate recess of the squamosal. The medial part of the quadrate made contact with the lateral tip of the quadrate process of the opisthotic which is not covered by the

squamosal or pterygoid.

The stapes may have been longer than Mendrez (1974a) indicated in Moschorhinus kitchingi, and would extend futher laterally to make contact with the quadrate. The lateral side of the quadrate would have contacted the medial part of the quadratojugal. Because of the absence of the stapes and quadratojugal it is not possible to describe the relations between these elements and the quadrate.

Pterygo-paroccipital foramen

The "pterygo-paroccipital" foramen is unique to certain therapsids. It is surrounded primarily by the prootic in the therocephalians and cynodonts. An anterior and posterior process of the prootic (central process and postero-ventral process of the prootic in Moschorhinus, Fig. 1) form the greatest part of the foramen. In therocephalians the squamosal and opisthotic close the lateral end of this foramen between the two prootic processes (see Ch. 3; Brink 1958; Mendrez 1974a, 1974b). In certain cynodonts the foramen is closed laterally by the quadrate ramus (postero-ventral process) of the epipterygoid (see Watson 1920; Simpson 1933; Brink 1955; Romer 1969) and not by the quadrate ramus of the pterygoid as Watson (1911) thought. In the abovementioned cynodonts the quadrate rami of the pterygoids end lateral to the cranioquadrate canals while the quadrate rami of the epipterygoids continue posteriorly.

The opisthotic and prootic of most cynodonts are fused to form a periotic (Olson 1944). It is important to keep in mind that the posterior wall of the pterygo-paroccipital foramen is formed by the prootic and opisthotic in the therocephalians (see

Ch. 3; Fig. 1 and Mendrez 1972). In Thrinaxodon the posterior prootic process has elongated laterally to meet the anterior prootic process (see Parrington 1946). The pterygo-paroccipital foramen of Thrinaxodon is therefore exclusively formed by the prootic since the opisthotic (and other elements) are excluded from this foramen. A similar condition is found in Diarthrognathus (Crompton 1958) except here the pterygo-paroccipital foramen is completely surrounded by two lateral flanges of the periotic. In advanced cynodonts with a periotic it may seem as if the posterior wall of the pterygo-paroccipital foramen is formed by the paroccipital process of the opisthotic. This is not the case however. It would seem, judging by abovementioned examples, that the posterior prootic process fused to the paroccipital process of the opisthotic in advanced cynodonts. An antero-ventral "step" in the so-called paroccipital process of Diarthrognathus (Crompton 1958) may indicate the position of fusion of the prootic and opisthotic elements. The fused product forms a robust, laterally projecting bar which resembles the primitive paroccipital process of the opisthotic, and is confused as such by most authors studying advanced cynodonts and primitive mammals. Several authors (eg. Crompton 1964; Hopson 1964; Romer 1969; Kemp 1979; Sun Ailing 1984) refer to a prootic and opisthotic in cynodonts while failing to describe the suture that would have been present if there were two elements. Cynodonts (with the possible exception of Procynosuchus, Kemp 1979) such as Oligokyphus (Crompton 1964), Bienotherium (Hopson 1964), Probelesodon (Romer 1969) and Bienotheroides (Sun Ailing 1984) should have a periotic as Kühne (1956) found in Oligokyphus, Crompton (1958) found in Diarthrognathus and Gow (1986) found in

Irirachodon, Diademodon and Tritylodon.

It would seem therefore that the "pterygo-paroccipital" foramen is formed primarily by the prootic (or embryonic prootic element in the case of a periotic) and not by the quadrate ramus of the pterygoid nor by the paroccipital process of the opisthotic, although these two elements and the squamosal play a lesser role in the formation of this foramen in certain therocephalians and cynodonts. It is suggested however that the term pterygo-paroccipital foramen be retained since it has become entrenched in the anatomist's vocabulary.

Dorsal venous foramen

In her paper on Moschorhinus Mendrez (1974a) referred to the opening dorsal to the posterior apophysis of the epipterygoid and the antero-dorsal process of the prootic as the "foramen veineux". It would seem that the dorsal part of the antero-dorsal process of the prootic is damaged in her specimen. The posterior foramen of the epipterygoid and dorsal venous foramen are separated by the antero-dorsal process of the prootic. This process is expanded dorsally to contact the supraoccipital and the postero-dorsal process of the epipterygoid. The term "dorsal venous foramen" is preferred to venous notch (Boonstra 1934b; Cox 1959), dorsal notch (Mendrez 1972) and venous foramen (Mendrez 1974b) because it is a foramen rather than a notch, being completely surrounded by bone, and because it distinguishes between the two abovementioned venous foramina.

Lateral supraoccipital fossa

In therocephalians a fossa is present on the lateral wall of

the otic capsule ventral to the parietal, whereas the dorsal venous groove is found in approximately the same region as in cynodonts. The parietal forms a marked concave lip overhanging this fossa (see Fig. 4, Boonstra 1938; Crompton 1955; Kemp 1972; Mendrez 1972, 1974a, 1974b). This fossa is called here the lateral-supraoccipital fossa in Moschorhinus, because as in Promoschorhinus (Mendrez 1974b) and in the scaloposaurids (Crompton 1955; Mendrez 1972) the biggest part of this fossa lies on the lateral face of the supraoccipital (Ch. 3). In Theriognathus (Owen 1876) on the other hand, this fossa lies on the dorsal part of the lateral face of the prootic (Kemp 1972) and in Bauria it lies on the lateral face of the interparietal and dorsal part of the prootic (Boonstra 1938). The supraoccipital is not exposed in the temporal region in these forms. The scaloposaurids differ from abovementioned therocephalians in that their lateral-supraoccipital fossa is less pronounced and they have a large dorsal venous notch instead of a dorsal venous foramen (see Crompton 1955; Mendrez 1972).

It would seem that, of the abovementioned therocephalians, the scaloposaurids have the more primitive condition regarding the morphology of this region. This region evidently became more ossified through therocephalian evolution. The antero-dorsal process of the prootic expanded from the primitive scaloposaurid condition where it is a very small, loose-standing projection, to the moschorhinid condition where it is a broad flange contacting the epipterygoid and forming a large part of the side-wall of the braincase. The diminishing in size and the closure of the dorsal venous foramen were directly influenced by the broadening of the antero-dorsal process.

## 5.2 ORBITOTEMPORAL REGION (Fig. 10)

Non-osseous part of the braincase

The non-osseous part of the braincase left many traces on the floor and roof of the bony endocranium of Moschorhinus. This is especially the case on the dorsal surface of the central part of the basicranium. To understand the significance of certain structures in the skull of Moschorhinus and by implication the morphology of certain non-osseous parts of the side-wall of the braincase it is necessary to study descriptions of this region in extant reptiles. Säve-Söderberg (1946, 1947) described this region in Sphenodon and the Lacertilia. The Sphenodon braincase (Säve-Söderbergh 1947) in particular seems to share certain similarities with that of Moschorhinus.

The side-wall of the braincase in the orbitotemporal region consists mainly of cartilaginous and membranous elements in rep-2tiles. Five cartilaginous parts which are of interest here are: the pila antotica, pila metoptica, taenia marginalis, solum supra-septale and the interorbital septum. The fenestrae present between these cartilaginous parts in embryos (De Beer 1937) are covered later in life by membranes which are named after the fenestrae (Säve-Söderbergh 1947). There are three membranes of interest here namely the fenestra optica, fenestra metoptica and the fenestra prootica. There are other membranes and cartilaginous bars present in extant reptiles besides the abovementioned but these are unfortunately isolated from the bony elements. It is therefore impossible to estimate their probable location in fossils such as Moschorhinus.

The taenia marginalis runs between the otic capsule and the

nasal capsule, ventral to the dermal bones which form that part of the endocranial roof. In Sphenodon lateral ridges are present on the ventral surface of the endocranial roof marking the position where the taenia marginales were attached to it (Siebenrock 1893; Säve-Söderbergh 1947). It is postulated that the posterior part of the so-called dorso-lateral ridges of the braincase present in Moschorhinus (Fig. 8) and those ridges described in the gorgonopsian Cynosaurus by Olson (1937) are homologous to those described in Sphenodon. These ridges seem to be a common occurrence in therapsids (eg. Broom 1914, 1936, 1938; Haughton 1918; Boonstra 1968; Fourie 1974). In certain therapsids (eg. Leontocephalus, Kemp 1969) the taenia marginalis even seems to have ossified in this region.

These ridges usually originate anterior to the epipterygoid. This however does not imply that the taenia marginalis was limited to this region. The taenia marginalis also runs medial to the epipterygoid and contacts the antero-lateral part of the supraoccipital (Säve-Söderbergh 1947). It seems as if the taenia marginalis did not have an effect on the epipterygoids in reptiles in which the epipterygoid is small and forms only superficial contact with the parietal. In Moschorhinus however, the dorsal part of the epipterygoid forms extensive sutural contact with the parietal and even contacts the supraoccipital and prootic exactly where these elements would contact the taenia marginalis. A similar situation is also found in the cynodonts (Brink 1955; Bonaparte 1966; Kemp 1969) and Theriognathus (Kemp 1972).

In Moschorhinus there are distinct ridges on the medial surface of the epipterygoid directly ventral to its dorsal limit. These ridges are called here the dorso-medial flange and the

dorso-medial bulge of the epipterygoid (Fig. 7). It is postulated that these ridges are the remnants of the taenia marginalis for the following reasons: Firstly because the dorso-medial bulge of the epipterygoid makes sutural contact with the medial part of the latero-ventral flange of the parietal which originally would have made contact with the taenia marginalis. Secondly, the bulge (and the antero-ventral process of the epipterygoid) lie in line with the dorso-lateral ridge of the braincase anterior to it. Thirdly, the dorso-medial flange of the epipterygoid contacts the antero-lateral process of the supraoccipital exactly where this element would have contacted the posterior part of the taenia marginalis. It seems likely therefore that the dorsal part of the epipterygoid of Moschorhinus, and possibly that of other advanced therapsids, ossified within the taenia marginalis element (Presley & Steel 1976). Kemp (1979) described a groove on the medial surface of the side-wall of the braincase running on the epipterygoid-parietal suture and argued that it marks the contact between these elements and the taenia marginalis. It seems more likely that the anterior cerebral vein ran in this groove en route to the transverse sinus (see Dendy 1909; O'Donoghue 1920). This vein may be homologous to that which ran in the dorso-medial groove of the epipterygoid in Moschorhinus.

The taenia marginalis contacts the solum supraseptale (planum supraseptale, De Beer 1937; Romer 1956) anteriorly (see Säve-Söderbergh 1947). This cartilaginous element is confluent with the taenia marginalis and also runs ventral to the dermal bones forming the endocranial roof. It forms part of the medial wall of the orbit ventral to the prefrontal element in Sphenodon. In Moschorhinus the dorso-lateral ridge of the braincase is con-

fluent anteriorly with the posterior margin of the ventral flange of the prefrontal (Figs. 7, 8). It seems therefore that the contact between the solum supraseptale and the frontal and prefrontal elements is marked by the anterior part of the ridge and posterior margin respectively.

The taenia marginalis contacts the pila metoptica and pila antotica ventrally via the pila accessoria and taenia parietalis media cartilages, thereby enclosing the fenestrae optica, metoptica and prootica (Gaupp 1900, Säve-Söderbergh 1947). It is well known that the antero-ventral process of the prootic of therapsids is the ossified pila antotica (eg. Olson 1944). The orientation of the antero-ventral process helps to confirm the suggestion that the dorso-medial flange of the epipterygoid is the remnant of the posterior part of the taenia marginalis. The antero-ventral process curves towards the dorso-medial flange and its blunt, flat antero-dorsal limit lies very close to the flange (Fig. 7). It is suggested that a short cartilaginous bar (the posterior part of the taenia parietalis media, Säve-Söderbergh 1947) ran between this limit of the antero-ventral process of the prootic and the antero-ventral part of the dorso-medial flange of the epipterygoid. The area thus enclosed between the dorso-medial flange of the epipterygoid and the antero-dorsal and antero-ventral processes of the prootic is the fenestra prootica. The fenestra prootica membrane was anchored to the sharp medial edge of the antero-ventral border of the antero-dorsal process postero-dorsally. The sharp postero-dorsal edge of the antero-ventral process marks the antero-ventral anchoring point. The membrane was anchored dorsally either to the anterior part of the dorso-medial flange of the epipterygoid thereby enclosing a pocket between it

and the postero-dorsal process of the epipterygoid which housed the transverse sinus (this sinus will be discussed later). Alternatively it could have been anchored to the ventral part of the postero-dorsal process, between the dorso-medial fossa and the posterior foramen of the epipterygoid.

The fenestra metoptica is bound by the pila accessoria and taenia parietalis media to the taenia marginalis dorsally. It is bound anteriorly by the pila metoptica, posteriorly by the pila antotica and ventrally by the trabecula cranii and the antero-dorsal part of the basisphenoid (Säve-Söderbergh 1947). The trabeculae cranii which are bound dorsal to the parasphenoid are in confluence with the antero-lateral parts of the basisphenoid posteriorly. The infundibulum and the pituitary body lie dorso-medial to these structures and medial to the metoptic membranes which are bound to their dorsal parts (Säve-Söderbergh 1946). The pituitary fossa of Moschorhinus lies within the posterior part of a smooth-surfaced trough walled laterally by the dorso-lateral flanges of the basisphenoid (Fig. 9). It is suggested that the ventral part of the infundibulum lay within the trough instead of the interorbital septum (see Kemp 1979) and that the thin dorso-lateral flanges are in fact the ossified trabeculae cranii. The ridges that slope postero-laterally from these flanges can be considered to be the cristae trabeculari.

The pilae metopticae, which form the anterior borders of the metoptic fenestrae, meet ventrally forming what Gaupp (1900) termed the subiculum infundibuli. The antero-ventral parts of the pilae metopticae are bound to the interorbital septum anteriorly and the trabeculae cranii ventrally (Säve-Söderbergh 1947). Two small parasagittal ridges are present on the anterior tuberosity

of the antero-dorsal process of the basisphenoid in Moschorhinus (Fig. 9). It is suggested that these ridges indicate the anchoring points of the ventral parts of the cartilaginous pilae metopticae and therefore also the position of the postero-dorsal part of the ossified subiculum infundibuli which seems to have fused to the trabeculae cranii postero-ventrally. In Moschorhinus therefore it would seem that the membrane covering the fenestra metoptica was anchored posteriorly to the sharp-edged antero-ventral border of the antero-ventral process of the prootic. The membrane was anchored anteriorly and dorsally to the cartilaginous pila metoptica and taenia marginalis respectively and ventrally to the thin dorsal border of the dorso-lateral flange of the basisphenoid (ossified trabecula cranii).

The anastomotic vein penetrates the antero-ventral corner of the fenestra metoptica membrane through the fissura supratrabecularis, anterior to the pituitary and ventral to the subiculum infundibuli. [illegible]henodon and certain Lacertilia (Säve-Söderbergh 1946, 1947). [illegible]chinus seems to have had a different arrangement however. The pituitary body and ventral part of the infundibulum seem to have been situated very close to the dorsal surface of the antero-dorsal process of the basisphenoid. It would be improbable therefore that the anastomotic vein could run transversely across this section of the basisphenoid flanked by the dorso-lateral processes (ossified trabeculae cranii). The shape of the parasphenoid rostrum suggests that the interorbital septum was not attached to its dorsal surface as in those reptiles described by Säve-Söderbergh (1947). It seems that the anastomotic vein ran transversly across the spatula-shaped part of the parasphenoid rostrum anterior to the antero-dorsal process of the

basisphenoid.

Säve-Söderbergh (1946, 1947) described the membranes surrounding the pituitary body in reptiles. The sella turcica is roofed by the crista sellaris posteriorly. A tough membrane stretches antero-dorsally from the sella turcica to the base of the cartilaginous structure confluent with the ossified pila antotica. The membrane stretches from this position anteriorly, ventral to the level of the roots of the oculomotor nerves (III) and attaches to the dorsal part of the subiculum infundibuli. This membrane is penetrated by the infundibulum and the internal carotid arteries. Evidence for a similar membrane can be found in Moschorhinus. A well-developed, sharp ridge runs along the medial face of the antero-ventral process of each prootic. These ridges are confluent with the sella turcica. It is quite clear that a membrane homologous to that described by Säve-Söderbergh (1946, 1947) was attached to these ridges and the sella turcica. There are two differences however between the situation in extant reptiles and that in Moschorhinus. Firstly, because a foramen for the abducens nerve (VI) is absent from the prootic in Moschorhinus, these nerves would have penetrated the membrane together with the internal carotid arteries. Secondly, the antero-ventral processes of Moschorhinus are more extensively developed than those of extant reptiles, and stretch almost to the roof of the endocranium. The medial ridge runs along the whole length of each process. It would seem improbable that the membrane could have run ventral to the cerebrum and attach to the subiculum infundibuli from this position. It is suggested therefore that this membrane terminated in the vicinity of the dorsal extremity of the antero-ventral process of the prootic. The membrane must have been concave

dorsally to accommodate the central part of the brain which passed medial to the dorsal parts of the antero-ventral processes. This membrane probably served as a floor for the anterior parts of the medulla oblongata and optic lobes and formed a roof over the posterior part of the infundibulum and pituitary body.

The pituitary body of extant reptiles is sheathed by the postero-ventral corners of the fenestra metoptica membranes (Säve-Söderbergh 1946). These membranes are fused together posterior to the pituitary body. This posterior membrane is attached postero-ventrally to the medial ridge between the fossae for the retractor muscles and dorsally to the tough membrane described previously. The posterior membrane is penetrated by the hypophysial vein. The situation in Moschorhinus seems to have been identical to that in extant reptiles. The dorso-lateral flanges of the basisphenoid which are the ossified trabeculae cranii, are strongly developed anterior to the level of the pituitary fossa. These flanges taper off lateral to the pituitary fossa however. It is suggested that the postero-ventral parts of the metoptic membranes were not attached to the cristae trabecularis as one might think, but rather left the dorso-lateral flanges lateral to the pituitary fossa and joined each other posterior to the fossa. The small pit immediately posterior to the fossa may indicate the anterior point of attachment of this fused membrane. There is no doubt however, that this membrane was attached postero-ventrally to the postero-medial ridge of the sella turcica.

The interorbital septum lies antero-ventrally to the braincase and is connected to it by certain bars and membranes. The interorbital septum is attached to the floor of the endocranium along the midline, anterior to the level of the pila metoptica

(Säve-Söderbergh 1947). In Moschorhinus this region of attachment is marked by the distinct antero-dorsal ridge of the basicranium which runs sagittally on the fused vomers and the anterior part of the fused pterygoids. The only difference between the interorbital septum of Moschorhinus and those of extant reptiles is that it seems as if the interorbital septum of Moschorhinus was not attached to the very short, broad anterior part of the parasphenoid rostrum. The possible origin of the interorbital septum was described by Olson (1944).

It is impossible to determine the exact positions of the fynestrae septi superior, optica and epioptica and the bars between them with certainty in Moschorhinus. The positions of these structures on the reconstruction of the non-osseous lateral wall of the orbitotemporal region (Fig. 10) are therefore only rough approximations.

Eye-muscles

There are several clues in the Moschorhinus endocranium as to where certain eye-muscles were attached. It seems that the arrangement of the eye-muscles in Moschorhinus closely matched that of Sphenodon (Säve-Söderbergh 1946, 1947).

The retractor musculature (bursalis and retractor bulbi muscles) of Sphenodon are enclosed in a membranous sac which stretches from the posterior part of the sella turcica to the eye (Säve-Söderbergh 1946). The bursalis muscle lies dorsal within this sac in relation to the retractor bulbi muscle. The retractor bulbi muscle originates in the retractor fossa while the bursalis muscle originates partly in the retractor fossa and partly on the tough membrane antero-dorsal to the crista sellaris. The sac

enclosing these muscles is attached postero-medially to the medial ridge between the retractor fossae together with the membrane posterior to the pituitary body. Anterior to this the medial side of the sac is attached to the fenestra metoptica membrane. Posteriorly the dorso-medial side of the sac is attached to the fenestra metoptica membrane. Posteriorly the dorso-medial side of the sac is attached to the tough membrane antero-dorsal to the crista sellaris. The dorso-lateral side of the sac is attached to the pila antotica.

The concave posterior part of the sella turcica in Moschorhinus was clearly divided into two pockets by a membrane which was attached to the medial ridge and the dorsum sellae (see previous section). The large depression for the retractor bulbi muscle forms the floor of each pocket (Fig. 9). The lateral part of the crista sellaris and the ventral part of the medial ridge of the antero-ventral process of the prootic, together with the membrane attached to them, formed a roof over this region. The posterior part of the bursalis muscle probably originated in the small postero-dorsally directed depression covered dorsally by abovementioned bony parts. The lateral wall of the pocket is formed by the medial surface of the antero-ventral process of the prootic and concave postero-dorsal part of the basisphenoid (Fig. 7). The sac containing the retractor muscles was evidently housed within this pocket and ran antero-laterally across the crista trabecularis. In its anterior course it passed lateral to the dorso-lateral flange of the basisphenoid (ossified trabecula cranii) and the fenesta metoptica membrane which was attached to the flange.

The rectus musculature (i.e. rectus anterior, inferior,

superior and posterior muscles) are attached to certain membranes and cartilages in the orbitotemporal region in reptiles (Säve-Söderbergh 1947). The rectus anterior muscle is attached to the postero-dorsal part of the interorbital septum and the rectus inferior muscle is attached to the cartilagio hypochiasmatica. The rectus superior muscle is attached to the subiculum infundibuli and part of the fenestra metoptica membrane. The small head of the rectus posterior muscle is attached to the posterior part of the subiculum infundibuli and the large head on the trabecula cranii and the fissura supratrabecularis.

The exact positions of attachment of the rectus anterior and rectus superior muscles are impossible to determine in Moschorhinus. There are however certain indentations on the dorso-lateral flange (ossified trabecula cranii) and the antero-dorsal tuberosity (ossified posterior part of the subiculum infundibuli) of the basisphenoid which would suggest sites of attachment for certain muscles. It is postulated firstly that the rectus posterior muscle was attached to the concave lateral face of the dorso-lateral flange (Fig. 3), and secondly, that part of the rectus superior muscle was attached to the lateral face of the antero-dorsal tuberosity of the basisphenoid which is placed more medially than the part of the basiphenoid ventral to it (Figs. 3, 9).

## 5.3 POSTERIOR PART OF THE ENDOCRANIUM

### Osseous braincase

The posterior part of the endocranium of Moschorhinus is larger than those of the gorgonopsians (Boonstra 1934a; Kemp 1969), pristerognathids (Boonstra 1968) and scaloposaurids (Crompton 1955; Mendrez 1972). The central part of the braincase (i.e. the region between the level of the internal auditory meatus and the level of the parietal canal) and the sella turcica of Moschorhinus are longer than those of the abovementioned therapsids. This results from the anterior extension of the prootic, epipterygoid and parasphenoid especially (Fig. 7). The foramen for the facial nerve (VII), the incisura prootica and the membrane between the anterolateral processes of the prootics of Moschorhinus are consequently situated more anteriorly than those of the above-mentioned therapsids. The same goes for the position of the internal carotid and palatine foramina and pituitary fossa in the sella turcica. Although it can be concluded from these adaptations that Moschorhinus had a relatively large brain for a therocephalian, Moschorhinus also has a number of primitive and unique features in the braincase which are discussed below.

The basicranial processes of the prootics meet on the floor of the braincase in Moschorhinus. This condition is also present in Dimetrodon (Olson 1936b); titanosuchians, dinocephalians (Boonstra 1958), gorgonopsians (Olson 1937; Broom 1948) and the pristerognathids (Broom 1936; Olson 1938b; Boonstra 1968). The prootics of scaloposaurids (Crompton 1955), whaitsiids (personal observation) and cynodonts (Olson 1944; Fourie 1974) have withdrawn from the floor of the braincase. The dorso-medial surface

of the posterior part of the basisphenoid and its contact with the basioccipital are thus exposed in the scaloposaurids, whaitsiids and cynodonts. In the case of Lystrosaurus, the unossified zone between these elements is exposed (Cluver 1971).

A structure resembling the dorsum sellae and crista sellaris is formed by the prominent antero-medial parts of the basicranial processes of the prootics in e.g. the gorgonopsians (Olson 1937, 1933a) and dinocephalians (Boonstra 1968). However, these processes are relatively smaller in pristerognathids (Boonstra 1968) and Moschorhinus (Figs. 7, 9) and do not replace or completely cover the true dorsum sellae and crista sellaris formed by the basisphenoid.

Not only the prootics, but also the exoccipitals of Moschorhinus contribute extensively to the formation of the endocranial floor. The postero-medial parts of the basicranial processes of the prootics contact the anterior parts of the exoccipitals on the endocranial floor. This condition seems to be unique to Moschorhinus. The endocranial floor consists almost exclusively of these elements, the basioccipital being reduced to a small medial strip and the opisthotics forming only a small portion of the floor. This too seems to be unique to Moschorhinus, since the basioccipital plays a major part in the formation of the endocranial floor in all other therapsids (e.g. Broom 1938; Olson 1944; Crompton 1955; Parrington 1955; Boonstra 1968). The postero-ventral parts of the prootics and the antero-ventral parts of the exoccipitals and the opisthotics cover the dorso-lateral parts of the basioccipital. The basioccipital is thus excluded from the endocranial floor between the medial strip of the basioccipital and the internal auditory meatus

(Fig. 9). The participation of the basioccipital in the inner ear is also greatly reduced in Moschorhinus compared to other therapsids (Olson 1938a, 1938b; Bonaparte 1966, Cluver 1971; Sigogneau 1974). This element is confined to the ventral part of the auditory canal and the postero-ventral part of the cochlear recess, where it forms a narrow strip stretching from the fenestra ovalis laterally, to the medial wall of the cochlear recess medially (Fig. 9).

A small pit is present anterior to the antero-dorsal projection of the basioccipital (Fig. 9). This pit is possibly in connection with a larger cavity homologous to the so-called unossified zone in the basicranium (Olson 1944; Boonstra 1968). It is not known whether an unossified zone is present in Moschorhinus because the section through the basicranium runs slightly to the right of the midline. The unossified zone, if present, would lie medially between the basioccipital and basisphenoid or between these elements and the basicranial processes of the prootics. It is possible that the section passed lateral to this cavity if the cavity is relatively narrow. (The sutures seen between the basioccipital, basisphenoid and prootic in Fig. 7 are those exposed in parasagittal section). In certain dinocephalians this unossified zone is covered dorsally by the medial parts of the basicranial processes of the prootics (Boonstra 1968). It is possible that this is the case in Moschorhinus as well.

The anterior processes of the prootic in Moschorhinus are enlarged compared to those of other therapsids. The antero-dorsal process especially, shows dorsal and anterior expansion compared to those of the scaloposaurids (Crompton 1955; Mendrez 1972), pristerognathids (Haughton 1918; Boonstra 1934b) and gorgonop-

sians (Watson 1921; Boonstra 1934a; Olson 1937). The antero-dorsal process in these animals is weakly developed, leaving open a wide gap between it and the parietal. In Moschorhinus as in certain cynodonts (Watson 1913; Brink 1955; Bonaparte 1966), this gap has been closed up due to the dorsal expansion of the antero-dorsal process, leaving a small foramen for the passage of the dorsal head vein. The anterior expansion of the antero-dorsal process of Moschorhinus brings it into contact with the posterior part of the epipterygoid. This is similar to the situation in Theriognathus (Kemp 1972) and the cynodonts (Brink 1955; Bonaparte 1966; Fourie 1974; Kemp 1979; Gow 1986). The prootic - epipterygoid contact of Moschorhinus differs from that of the abovementioned animals. The anterior margin of the antero-dorsal process of the prootic forms extensive sutural contact with the posterior margin of the epipterygoid in these animals. However, in Moschorhinus it can be seen that the antero-dorsal process of the prootic overlaps the postero-dorsal process of the epipterygoid medially. In Thrinaxodon (Fourie 1974) both conditions are found: a small process lies medial to the postero-dorsal part of the epipterygoid, ventral to the suture between the anterior limit of the dorsal part of the prootic and the posterior limit of the dorsal part of the epipterygoid. Since Romer (1956) stated that the prootic does not contact the epipterygoid in therocephalians, it can be assumed that he described the condition in scaloposaurids and pristerognathids.

The unossified zone commonly found in the endocranial roofs of the scaloposaurids (Crompton 1955), Theriognathus (personal observation) and cynodonts (Fourie 1974; Kemp 1979) is absent in Moschorhinus. The unossified zone lies between the parietal and

supraoccipital, opposite the interparietal. The interparietal is excluded from the endocranium by the antero-dorsal extension of the medial part of the supraoccipital which contacts the parietal in Moschorhinus (Fig. 7).

A progressive expansion o. dorsal part of the epipterygoid can be seen within the T. cephalia (Barry 1965). The dorsal part of the epipterygoid is relatively narrow in the pristerognathids (Boonstra 1934b, 1968) it being little wider than that of the gorgonopsians (Watson 1921; Kemp 1969). In the scaloposaurids however, expansion of the dorsal part is much more evident (Crompton 1955; Mendrez 1972). This broadening is even more pronounced in Moschorhinus (Figs. 3, 7) and Euchambersia (Boonstra 1934b). In the whaitsiids (Boonstra 1934b; Brink 1958) the expansion of the epipterygoid reaches its climax and resembles the condition found in certain cynodonts (e.g. Thrinaxodon, Fourie 1974 and Procynosuchus, Kemp 1979).

The degree of expansion of the epipterygoid is indicative of its involvement in the formation of the side-wall of the braincase. In the pristerognathids and the scaloposaurids only the dorsal tip of the epipterygoid is incorporated in the lateral wall of the braincase. The rest of the epipterygoid lies lateral to the anterior processes of the supraoccipital and prootic and the fenestra prootica membrane, as is the case in the Gorgonopsia. In whaitsiids on the other hand, the part of the epipterygoid dorsal to the level of the antero-ventral process of the prootic is incorporated in the side-wall of the braincase, as is the case in the Cynodontia. The part of the side-wall of the braincase which is formed by the fenestra prootica membrane in the gorgonopsians, pristerognathids and scaloposaurids is substituted for the dorsal

half of the epipterygoid in the whaitsiids and cynodonts. It seems that with the progressive involvement of the epipterygoid in the formation of the side-wall of the braincase, the fenestra prootica diminished in size so that finally the cynodonts have one or two trigeminal foramina posterior to the processus ascendens and a small antero-ventral process of the prootic. If a fenestra prootica membrane was present at all in cynodonts, it would only have served to isolate the trigeminal ganglion from the endocranium rather than have formed a substantial part of the lateral wall of the braincase.

In Moschorhinus an interesting combination of both abovementioned conditions is found. The antero-ventral process of the prootic is much larger than that of most therocephalians, barring the scaloposaurids (Crompton 1955; Mendrez 1972) and maybe Promoschorhynchus (Mendrez 1974b). The membrane covering the large fenestra prootica thus formed would form the side-wall of the braincase in that region (this aspect has been discussed previously). The enlarged dorsal third of the epipterygoid forms the part of the side-wall of the braincase dorsal to this membrane.

Endocast (Fig. 11; Plates 15, 16, 17)

Very little concerning the morphology of the brain could be learned form the endocasts made of the posterior part of the endocranium. This is due mainly to two factors: firstly, the side-wall of the braincase in the orbitotemporal region is unossified and secondly, the brain of Moschorhinus, as is the case in most reptiles, did not fill the endocranial cavity and therefore

left behind few traces on the bony endocranium (see Olson 1944; Jerison 1973; Hopson 1979).

The exact dimensions of the optic lobes, cerebrum and olfactory lobes of Moschorhinus are impossible to estimate because these structures were bound laterally by the non-osseous part of the side-wall of the braincase. This also applies to the position of the foramina for the optic, oculomotor, trochlear and abducens nerves and the lateral part of the infundibulum. In certain gorgonopsians (Watson 1921; Kemp 1969), Theriognathus (Kemp 1972) and cynodonts (Brink 1955) it is possible to determine the position and relative size of the olfactory lobes at least, because of the presence of an orbitosphenoid.

The space between the endocranial roof and the brain in Moschorhinus would have been filled with certain non-neura tissues including venous sinuses which, while obscuring the dorsal part of the brain, left traces behind on the roof as in other reptiles (Hopson 1979). An endocast of the ventro-lateral gutters of the parietal, in the roof of the endocranium, shows two parasagittal ridges superficially resembling cerebral hemispheres (Plate 16). If, however, the cerebral hemispheres did contact the endocranial roof, gently sloping depressions would be expected in this region (as in Nythosaurus, Watson 1913; and Probainognathus, Quiroga 1980) rather than deep, steep-walled grooves as in Moschorhinus and Theriognathus. It is also unlikely that the cerebral hemispheres would be so far apart, diverge anteriorly or be situated this far posterior to the parietal foramen. An endocast of the dorso-medial fossa of the epipterygoid yields a bulge which is easily confused with the optic tectum (Plate 15). Hopson (1979) proved that it is far more likely that these ridges and

bulges were formed by the longitudinal and transverse venous sinuses respectively (these sinuses will be discussed in detail later). It is important to mention at this stage that the transverse sinus ran between the optic tectum and the cerebellum (Dendy 1909; Hopson 1979).

In contrast to the grooved ventral surface of the parietal and medial surface of the dorsal part of the epipterygoid, the concave antero-ventral surface of the supraoccipital is smooth. This was probably caused by the combined influence of the broad posterior part of the longitudinal sinus situated between the posterior part of the brain and the endocranial roof, and the particularly thick dural covering of the posterior part of the brain (Hopson 1979). The endolymphatic sacs which were apparently situated inside the cranial cavity on either side of the posterior part of the longitudinal sinus (Dendy 1909) probably also played a role.

The only trace left by neural tissue in the endocranial roof of Moschorhinus is the ventral parietal foramen and the surrounding funnel-shaped indentation. The ventral parietal foramen probably marks the junction between fore- and midbrain (Kemp 1969). Although the parietal canal seems extremely large in sagittal section (Fig. 7), one has to bear in mind that the canal becomes narrower transversely as it runs from the oval-shaped ventral parietal foramen (Fig. 8) to the slit-like dorsal parietal foramen (Fig. 1). This is also the case in Theriognathus (personal observation). Edinger (1955) discussed the relative sizes of the parietal eye and foramen and concluded that the size of the foramen parallels the size of the parietal eye. It is important to note however that the parietal foramen of reptiles with a thin

skull-roof differs radically from those with a thick skull roof in which a parietal canal (Boonstra 1968) is present. It is wrong to assume that because the parietal eye fills the foramen in extant animals, the same would be the case for those extinct forms with parietal canals. If this was the case, dinocephalians would have had parietal eyes only slightly smaller than the rest of their brains. It is possible that the typical parietal foramen of extant reptiles and the parietal canal of therapsids had different functions. It is postulated that the parietal eye filled only the dorsalmost part of the parietal canal and maybe not even all of it. In animals such as Moschorhinus and Theriognathus it would seem as if the parietal eyes must have been quite small judging by the size of the dorsal foramen. The ventral part of the canal and the ventral parietal foramen, which could not have been filled by the parietal eye, are large in comparison. This, and the fact that the indentation surrounding the ventral parietal foramen indicates the position of the pineal body (Roth & Roth 1989) suggests that the dorsal part of the pineal body occupied the ventral part of the canal. The parietal nerve which connects the parietal eye to the pineal body would then have passed through the central part of the canal. If it is assumed that the parietal organ had the same structure and function as those in extant reptiles then it is highly unlikely that the nerve would have filled the canal. It is suggested that the parietal nerve and possibly even the parietal and pineal bodies were enveloped in non-neural soft tissue.

In contrast to the anterior and dorsal parts of the brain of Moschorhinus, the ventral part of the brain seems to have been situated close to the bony surface of the endocranium (Olson

1944). This is reflected by the tubular part of the endocranium, the deep impressions in the endocranial floor, the deep floccular fossae, the pituitary fossa and the trough for the infundibulum. Nerve-impressions are absent from the endocranial side-walls, probably indicating that the brain was situated close to the nerve foramina.

An endocast of the posterior tubular section (Plates 15, 16, 17) yields a cylindrical structure which seems to be approximately the same size and shape as the medulla oblongata. The cast of the jugular canal juts postero-laterally from its anterior part. The position of the posterior cerebral vein appears as a laterally-running, irregular-shaped ridge on the dorsal part of the jugular canal cast (Plate 15). Posterior and ventral to the prominent jugular canal cast are two small twigs which are the casts of the foramina for the rami of the hypoglossal nerve. The basicranial ridge of the exoccipital which appears as a postero-lateral sloping groove on the endocast (Plate 17) indicates the anterior limit of the long floor of the tubular section. The oval-shaped depression in the endocranial floor, posterior to the basicranial ridge, seems to be an impression of a hypoglossal ganglion. It occurs on the endocast as a ventral bulge confluent postero-laterally with the anterior hypoglossal twig (Plate 17).

The medial wall of the opisthotic leaves a broad, concave depression on the endocast between the cast of the jugular foramen posteriorly and the casts of the inner ear and flocculus anteriorly. The endocranium suddenly becomes wider and higher anterior to the medial walls of the opisthotics and basicranial ridges of the exoccipitals.

On the endocranial floor, medial to each internal auditory

meatus and antero-lateral to each basicranial ridge of the exoccipital, lies a deep depression confluent postero-laterally with the jugular canal. These depressions appear in the form of a lobed structure on the ventral part of the endocast. The lobes are divided medially by a notch in the endocast formed by the antero-dorsal projection of the basioccipital (Plate 17). Olson (1944), Kemp (1979) and Kielan-Jaworowska (1963, 1986) argue that these depressions were formed by the pons but Hofer & Thenius (1960) and Edinger (1975) disagree.

Anterior to the medial wall of the opisthotic and dorsal to the inner ear, lies the large floccular fossa. This fossa is easily identifiable on the endocast (Plate 15). It seems to be similar in size to those in gorgonopsians (Olson 1944; Kemp 1969), Theriognathus (personal observation) and cynodonts (Watson 1913; Olson 1944; Quiroga 1980). The flocculus marks the posterior part of the cerebellum.

The position of the cochlea, common and posterior ampullary recesses, crus communis and auditory canal are easily identified on the cast of the [illegible] (Plates 15, 16, 17). The short, pyramid-shaped cast of the cochlea is separated from the cast of the pons-like structure by a crescent-shaped notch in the endocast, formed by the ventro-medial rim of the internal auditory meatus. The casts of the cochlea and the long, ventro-laterally sloping auditory canal are the most ventral structures on the endocast. Between the casts of the cochlea and the floccular fossa are three jutting processes on the cast of the inner ear (Plate 15). The larger process situated anterior to the cast of the floccular fossa is that of the common ampullary recess. The most medially situated process, of the two processes postero-

. to the cast of the floccular fossa, is the cast of the crus communis and the laterally situated process is the cast of the posterior ampullary recess.

The position of the facial nerve is indicated on the endocast by the long cylindrical projection situated between the cast of the inner ear and the triangular cast of the incisura prootica (Plates 15, 16, 17). The actual exit of the trigeminal nerve would have been much smaller than the cast of the incisura prootica because the incisura prootica would have been partially covered by the fenestra prootica membrane. The position of the root of the trigeminal nerve marks the anterior limit of the cerebellum (Kemp 1969). It is suggested that what Olson (1944) termed the foramen ovale (FOOV) in his endocast reconstructions should actually indicate the ventral portion of the incisura prootica. The inner ear is clearly situated in the proximity of the flocculus and not anterior to the facial nerve. The cranial nerves will be described later.

The pronounced flexure of the midbrain is marked by the medial ridges of the antero-ventral processes of the prootics. These ridges curve antero-dorsally and the membrane between them would form the floor of the midbrain. The dorso-lateral part of this membrane probably ran between the lateral parts of each optic tectum and cerebral hemisphere, due to their dorsal position. This membrane would have been penetrated medially by the central part of the brain including the infundibulum. The ventral of the infundibulum seems to have formed contact with the antero-dorsal process of the basisphenoid, judging by the smooth trough situated in its dorsal surface. This argument is strengthened by the presence of a small oval fossa within the trough which seems

to have contained the pituitary. The endocast of this region (Plates 15, 17) strongly suggests an infundibulum with a postero-ventrally situated pituitary. The pituitary of Moschorhinus was evidently quite small for such a big animal. Speculations on the actual size of the pituitary should be approached with caution in those therapsids without a clear medial fossa in the sella turcica. It is improbable that the pituitary was as massive or bilobed as was suggested by eg. Watson (1913), Nopsca (1926), Olson (1944) and Kielan-Jaworowska (1983). It does not seem as if the pituitary made contact with the sella turcica in those therapsids described by the abovementioned authors. It should be kept in mind that a large portion of the sella turcica was occupied by bloodvessels and eye-muscles (Hopson 1979). The cast of the posterior part of the sella turcica in Moschorhinus also yields a large, bilobed structure (Plate 17), but as was described previously, this region was occupied by eye-muscles. The optic chiasma would have been situated antero-dorsal to the subiculum infundibuli.

Using the abovementioned landmarks, the brain, inner ear and certain endocranial bloodvessels were reconstructed (Fig. 11). The position of the cerebrum, olfactory lobe, optic chiasma, posterior part of the infundibulum and the optic, oculomotor, trochlear and abducens nerves are of necessity only rough approximations in this reconstruction. The reconstruction is noticably higher than the endocast, it should be kept in mind however that the skull of Moschorhinus BP/1/4636 (therefore also the endocranium and the endocasts) is compressed dorso-ventrally.

## 5.4 CRANIAL NERVES

Optic (II), oculomotor (III) and trochlear (IV) nerves

Although it is impossible to determine the exact positions of the opticus, oculomotorius and trochlearis foramina with certainty, it is possible to give an approximate estimation of their positions in relation to certain structures in the basicranium.

The opticus foramen, through which the optic nerve (II) exits, lies within the fenestra optica which is situated anterior to the pila metoptica and dorsal to the posterior part of the interorbital septum (Säve-Söderbergh 1947). If the antero-dorsal tuberosity of the basisphenoid in Moschorhinus is indeed the ossified subiculum infundibuli, then the probable position of the fenestra optica would be slightly anterior to it and approximately half-way between it and the skull-roof (Fig. 10).

The oculomotorius and trochlearis foramina are situated in the fenestra metoptica (i.e. posterior to the pila metoptica). In the reptiles described by Säve-Söderbergh (1947) the trochlearis foramen is situated dorsal to the subiculum infundibuli, approximately halfway between it and the skull-roof. The oculomotorius foramen lies on a lower level than the abovementioned two foramina. It is situated further posteriorly than the trochlearis foramen and lies approximately dorsal to the position of the internal carotid foramen (Dendy 1909). This was most probably the situation in Moschorhinus too. The oculomotor nerve (III) runs between the sac which encloses the posterior part of the retractor musculature (bursalis and retractor bulbi muscles) and the fenestra metoptica membrane in those reptiles described by Säve-Söderbergh (1946). It innervates the bursalis, retractor

bulbi, superior rectus, inferior rectus, anterior rectus and inferior oblique muscles. The trochlear nerve (IV) innervates the superior oblique muscle (Jollie 1973).

Trigeminal nerve (V)

The root of the trigeminal nerve exits through the incisura prootica (Fig. 6) into the cavum epiptericum which housed the trigeminal ganglion (gasserian ganglion, Goodrich 1958; semilunar ganglion, Starck 1979). Starck (1979) mentions however that a single trigeminal ganglion is absent in most reptiles. There are two smaller ganglia present instead; the ophthalmic ganglion and the maxillo-mandibular ganglion. It would be difficult to decide which of the two possibilities would have been present in Moschorhinus because a single trigeminal ganglion is present in amphibians and mammals (Starck 1979).

The ramus ophthalmicus ran in an anterior direction and passed through the orbit into the nasal capsule. From the descriptions of O'Donoghue (1920) and Oelrich (1956) it is evident that certain branches of the ophthalmic ramus are accompanied by branches of the superior orbital artery and not by the primary head vein as depicted by Presley & Steel (1976). The ramus ophthalmicus passed mesial to the processus ascendens of the epipterygoid and lateral to the non-osseous side-wall of the braincase (Säve-Söderbergh 1947, Presley & Steel 1976). Romer (1956) mentioned that the ramus ophthalmicus runs close to the side-wall of the braincase. Säve-Söderbergh (1946, 1947) described in Sphenodon a horizontal groove on the lateral face of the anteroventral process of the prootic in which the posterior part of the ramus ophthalmicus runs. It seems that this was the case in

Moschorhinus as well. In Moschorhinus there is a distinct indentation present on the lateral face of the antero-ventral process of the prootic. This indentation runs anteriorly and slightly dorsally from the antero-ventral border of the incisura prootica (Fig. 5).

The ramus maxillaris and ramus mandibularis passed posterior to the processus ascendens into the temporal cavity (Presley & Steel 1976). Certain authors (Brink 1956; Mendrez 1972, 1974a, 1974b) argue that the posterior apophysis of the epipterygoid separated these two rami (see Fig. 4). Others (Watson 1920, Kemp 1972) argue that both rami emerged through the foramen dorsal to the posterior apophysis (the posterior foramen of the epipterygoid). Crompton (1955) proposes a third alternative, namely that both rami emerged ventral to the posterior apophysis. The greatest part of the cavum epiptericum (and therefore also the trigeminal ganglion) lies below the level of the posterior foramen of the epipterygoid. Since the ramus maxillaris must have been directed ventrally, as is the ramus mandibularis, it is unlikely that it would first be deflected dorsally from the ganglion to pass through the posterior foramen of the epipterygoid and then ventrally towards the maxilla. It is more feasible that the ramus maxillaris passed together with the ramus mandibularis ventral to the posterior apophysis, suggesting that the posterior foramen of the epipterygoid is not homologous to the cynodont trigeminal foramen (see Fig. 16).

In cynodonts the whole posterior edge of the epipterygoid contacts the antero-lateral part of the prootic, leaving only the trigeminal foramen between them for the exit of the maxillary and mandibular rami of the trigeminal nerve and a vein (Gow 1986).

This foramen always lies above the quadrate ramus (postero-ventral process) of the epipterygoid (Simpson 1933; Parrington 1946; Brink 1955; Hopson 1964; Romer 1969; Fourie 1974). In other reptiles (including therocephalians) the ossification of the side-wall of the braincase has not reached this stage and is therefore much more open. It would therefore be incorrect to refer to the region between the epipterygoid and the lateral face of the prootic, through which the trigeminal rami and the vena cerebralis media passed, as the trigeminal foramen. There is also a fundamental difference between the "trigeminus foramen" described by Säve-Söderbergh (1947) and the trigeminal foramen of cynodonts. The trigeminus foramen is situated in the ventral corner of the fenestra prootica membrane which spans the incisura prootica. This foramen through which the trigeminal root exits should be common to all reptiles with an incisura prootica (including cynodonts and therocephalians). The trigeminal foramen is seperated from the incisura prootica, which lies medial to it, by the dorsal part of the cavum epiptericum (see Gow 1986).

Abducens nerve (VI)

The root of the abducens nerve usually exits through a foramen in the base of the antero-ventral process of the prootic (ossified pila antotica) (see Haughton 1918, Goodrich 1958, Starck 1979). In Moschorhinus (own observation, Mendrez 1974a) and Promoschorhynchus (Mendrez 1974b) this foramen is absent. Olson (1938a) mentions that a foramen for the abducens nerve may be absent in certain gorgonopsians and VI would in this case pass anterior to the prootic (see Watson 1921; Boonstra 1934a). This seems to have been the case in Moschorhinus as well. The abducens

nerves therefore must have pierced the membrane between the two antero-ventral processes of the prootics. Each nerve then ran in an anterior direction lateral to the fenestra metoptica membrane to innervate the bursalis, retractor bulbi and posterior rectus muscles (Säve-Söderbergh 1946).

Facial nerve (VII)

The root of the facial nerve exits through its foramen between the central and ventral ridges of the prootic (Figs. 4, 5). No impression for the geniculate ganglion (gasserian ganglion, Mendrez 1972) could be found on the lateral surface of the prootic. The medial aperture of the foramen for the facial nerve is situated half-way between the internal auditory meatus and the incisura prootica (Fig. 7). There is no groove or any other connection between the foramen and the inner ear in contrast with the situation found in the gorgonopsians described by Olson (1937, 1938a) and Sigogneau (1974). The foramen is situated very close to the internal auditory meatus in the scaloposaurids (Crompton 1955), pristerognathids (Haughton 1918; Olson 1938b), whaitsiids (personal observation) and cynodonts (Watson 1913; Simpson 1933; Fourie 1974; Hopson 1964; Kemp 1979). In Theriognathus the ventral ledge (ventral to the floccular fossa) forms a small overhang commencing at the level of the foramen, forming a slight groove between the foramen and the internal auditory meatus.

The small palatine ramus of the facial nerve ran in an antero-ventral direction from the geniculate ganglion to pass through the parabasal canal, accompanied by the internal carotid artery (Fig. 16). As the parabasal canal splits into two, the palatine ramus ran through the anteriormost canal, here named the palatine

canal. The palatine ramus was accompanied by the palatine artery which branched off from the internal carotid artery. After exiting from the palatine foramen which is situated in the basicranial gutter, the palatine nerve probably ran dorsal to the palatine artery which ran in the antero-dorsal groove of the pterygoid on either side of the interorbital septum (Fig. 9). The large mandibular ramus of the facial nerve ran postero-ventrally from the geniculate ganglion towards the fenestra ovalis (Fig 16). From here it ran posteriorly, accompanied by the posterior part of the vena capitis lateralis, between the stapes and the paroccipital process of the opisthotic (Romer 1956).

Vestibulocochlear nerve (VIII)

The vestibulocochlear nerve (statoacoustic nerve, Starck 1979) of reptiles is split into two branches: the anterior vestibular branch and the posterior acoustic branch. The vestibular branch innervates the utriculus and the anterior and horizontal ampullae. The acoustic branch innervates the lagena, papillae neglecta and basilaris and the posterior ampulla. The sacculus is innervated by both branches (Starck 1979). The vestibulocochlear nerve runs ventro-laterally from the medulla and enters into the inner ear either through a single opening or double foramina in the side-wall of the braincase (Romer 1956). The latter seems to have been the case in the dicynodont Kingoria described by Cox (1959). A small foramen is situated in the side-wall of the braincase, directly anterior to the internal auditory meatus in this animal. Cox (1959) postulated that the anterior branch of VIII penetrated it. Olson (1938b) described a similar foramen in a pristerognathid but postulated that it was for the facial nerve. Since this

foramen enters into the vestibule it is suggested that it is homologous to the foramen described by Cox (1959). In Moschorhinus however, no foramen could be found between the foramen for the facial nerve and the internal auditory meatus (Fig. 7). It seems that both branches of the vestibulocochlear nerve passed through the membrane which spanned the internal auditory meatus directly into the medulla because of the proximity of these two structures and the fact that this nerve left no impression in the endocranial wall. This short nerve which would be hidden by the inner ear in lateral view is not shown in Fig. 11.

Glossopharyngeal (IX), vagoaccessor (X) and hypoglossal (XII) nerves

There is no separate glossopharyngeal foramen in Moschorhinus. The glossopharyngeal nerve exited through the large jugular canal together with the vagoaccessory nerve and posterior cerebral (jugular) vein (Figs. 2, 5, 7). This is a common feature in the therapsids (Watson 1911, Haughton 1918, Kemp 1979). The hypoglossal nerve of Moschorhinus was apparently divided into two rami, each of which ran in a long, narrow tunnel which penetrates through the lateral portion of the exoccipital (Figs. 4, 7, 9). These rami would have exited into the jugular canal through its medial wall, near its external aperture (Fig. 4).

## 5.5 INNER EAR (Figs. 12 - 14)

The cast of the inner ear is one of the most salient features of the endocast (Plates 15, 17). The casts of the auditory canal, common recess for the anterior and horizontal ampullae and recess for the posterior ampulla can be seen in lateral view (Plate 15) and the casts of the auditory canal and cochlear recess can be seen in ventral view (Plate 17). The smooth surface of the inner ear of Moschorhinus suggests that it was fully ossified contrary to that of Theriognathus (personal observation).

The inner ear is situated in the prootic, opisthotic, supraoccipital and basioccipital bones (Fig. 12). The sutures between these elements have been described in detail in Chapter 4. The morphology of the inner ear of Moschorhinus is remarkably similar to that of the Cynodontia and Gorgonopsia.

The vestibule lies ventro-laterally to the rest of the cranial cavity. The saccular recess, cochlear recess, auditory canal and fenestra ovalis lie below the floor of the cranial cavity. The posterior ampullary recess and fenestra rotunda lie on the same level as the floor of the cranial cavity and the anterior and lateral ampullary recesses, the utricular recess and the bony labyrinth lie above it (Fig. 12).

The primitive condition in which the vestibule is connected to the cranial cavity by an extremely large internal auditory meatus (as described by Romer & Price (1940) in the Pelycosauria) is present. In the living state the meatus would have been partly covered by a membrane. This is identical to the situation in the Cynodontia (Watson 1911 & 1913), in the Gorgonopsia (Olson 1938a), in the Dinocephalia (Boonstra 1968) and in the Anomodontia (Olson

1944). It thus seems to have been a common therapsid feature.

The concave antero-medial border of the internal auditory meatus is in the form of a rather pronounced lip projecting slightly above the floor of the cranial cavity. It is formed by the prootic anteriorly and by the opisthotic posteriorly (Fig. 9). Anteriorly and posteriorly the lip slopes ventro-medially following the concave curvature of the wall of the cranial cavity. The medial border of the meatus slopes in an antero-dorsal direction from its lowest point postero-medially, this closely follows the orientation of the floor of the cranial cavity in that region. The margins of the internal auditory meatus are smooth as described by Olson (1938a) for the Gorgonopsia and would indicate the absence of cartilage in that region. The vestibule is open to the cranial cavity dorsal to the internal auditory meatus. It is therefore impossible to know the exact limits and morphology of the dorso-medial part of the vestibule, namely the medial parts of the crus communis, the utriculus and the dorsal part of the sacculus (see Fig. 13). It is also impossible to tell exactly where the endolymphatic duct and vestibulocochlear nerve would exit through the medial wall of the internal auditory meatus.

Dorsal to the vestibule, the deep floccular fossa (subarcuate fossa, Watson 1913) is present in the side wall of the cranial cavity (Fig. 12). The ventral ledge separates the floccular fossa from the vestibule. Just posterior to the floccular fossa the entrance to the bony canal for the crus communis is visible in the antero-dorsal part of the medial surface of the opisthotic. The ledge forms a roof over this entrance, runs anteriorly and terminates at the level of the anterior border of the vestibule. The ventral surface of this ledge forms the dorsal border of the

vestibule.

The vestibule is separated from the jugular canal by the prominent medial wall of the opisthotic. The wall runs in a ventro-lateral and slightly anterior direction to terminate just above the level of the floor of the cranial cavity. The rounded anterior surface of this wall forms the posterior border of the vestibule and the internal auditory meatus. The ventral border of this wall slopes ventro-laterally and forms the dorsal border of the concave notch in the opisthotic which housed the fenestra rotunda. This is contrary to the statment made by Sigogneau (1974) that the jugular canal is separated from the labyrinthic cavity by a bony medial wall only in the gorgonopsians and Dimetrodon. This, however, seems to be the case in some pristerognathids (see Olson 1938b & 1944) and cynodonts (see Brink 1955) but it is by no means the rule in synapsids as a whole. In other pristerognathids (see Haughton 1918; Broom 1935 and Vyushkov 1955), cynodonts (see Watson 1911 and Kemp 1979) and anomodonts (see Cox 1959 and Cluver 1971) a distinct wall separates the jugular canal from the vestibule. The majority of these fossils have relatively thin medial walls compared to that of Moschorhinus. There is in all cases ventral to the wall a communicating notch or even a channel (as desribed by Estes (1961) in Thrinaxodon) between the vestibule and jugular canal indicating the position of the fenestra rotunda. It is interesting to note how this region varies in different therocephalians. In the pristerognathid desribed by Olson (1938b & 1944) the jugular canal seems to be confluent with the posterior ampullary recess, in Theriognathus the bony wall separating the jugular canal and vestibule is relatively thin (personal observation) as is the case

in most other therapsids, and in Moschorhinus it is robust.

The membrane which would have covered the meatus in life was most probably suspended between the medial wall of the opisthotic posteriorly, the ventral ledge dorsally and the lip forming the ventro-medial border of the internal auditory meatus ventrally.

The large fenestra ovalis (fenestra vestibularis - Baird 1960) lies ventro-laterally to the vestibule. The shape of the fenestra ovalis is neither irregular nor double neither is it left partly uncovered by the footplate of the stapes as mentioned by Olson (1938b) in "Therocephalian A", it is round (see Fig. 5) as Mendrez (1974b) has recorded in Promoschorhynchus and completely covered laterally by the stapes as Mendrez (1974a) has found in Moschorhinus (S.A.M. No. K118). The long auditory canal formed by the prootic, opisthotic and basioccipital, runs dorso-medially from the fenestra ovalis and enters into the ventro-lateral part of the vestibule. The moschorhinid auditory canal (Figs. 8, 9) is as long as those found in certain gorgonopsians (Haughton 1918) and anomodonts (Cluver 1971), it is much longer than that of the whaitsiids (personal observation), the pristerognathids (Olson 1938b) and certain cynodonts (Brink 1955; Fourie 1974 and Kemp 1979). The canal is approximately circular in section. There is a small bulge on the postero-ventral surface of the proximal half of the canal forming a constriction in the canal (see Fig. 9). Haughton (1918) described a similar constriction in the gorgonopsian Scymnognathus.

The vestibule is confluent with a funnel-like cavity situated in the prootic, opisthotic and basioccipital, ventral to it (Fig. 12). This cavity contained the cochlea and part of the sacculus as well as parts of the perilymphatic system (Figs. 13,

14). The medial wall of the cavity formed by the prootic and opisthotic reaches straight up to the ventro-medial lip of the internal auditory meatus. The ventral extremity of the cavity is in the form of a small, pyramidal depression within the prootic (Fig. 12). This steep-walled depression is the lagenar part of the cochlear recess (see Baird 1970). The basioccipital, prootic and opisthotic meet at the postero-medial part of the dorsal border of the lagenar recess (Fig. 9). Some authors (eg. Olson 1938a and Sigogneau 1974) synonymize the lagena (which housed the lagenar macula) and cochlea but this is rather confusing. Although the reptilian cochlea is a very simple structure compared to those of mammals it is considerably more complex than the situation found in fish and amphibians. In fish and amphibians the lagena is a small projection on the sacculus and in reptiles, birds and monotreme mammals it occupies the distal part of the cochlea (see Romer 1970). The use of the term recessus scala tympani by authors such as Olson (1938a&b) and Kemp (1969) is misleading (see Sigogneau 1974). The Crocodilia is the only known reptile group with a fully developed scala tympani (see Romer 1970). Crocodilians have a distal perilymphatic tube (scala tympani) that runs along the length of the long, straight, bird-like cochlear duct (scala media). A proximal perilymphatic tube runs along the other side of the scala media, this is the scala vestibuli. In the other reptile groups the perilymphatic sac is not this specialized, the short perilymphatic duct (helicotrema - Baird 1960) is associated with the basilar papilla instead. The duct runs perpendicular medially to the cochlea instead of parallel to it as the scala tympani and vestibuli do in crocodiles. The perilymphatic sac lies posterior to the cochlea sharing the

same recess with the duct and cochlea. Since the primitive vestibule in therapsids is open to the cranial cavity, neither the fenestra rotunda nor the perilymphatic sac are completely enclosed in bone as they are in other recent reptiles such as the iguanids (see Baird 1960 & 1970). It is therefore incorrect to refer to the space leading to, or anterior to (as is the case in Moschorhinus) the notch for the fenestra rotunda in the therapsids as the recessus scala tympani. It is possible that Olson (1938b) and Kemp (1969) mistook parts of the posterior ampullary recess for the "recessus scala tympani". The division between the saccular and cochlear recesses within the funnel-like cavity is obscure. This seems to be a common situation in therapsids, certain authors (eg. Olson 1944) refer to it as the sacculo-cochlear recess. The medial wall of the cavity enclosed the medial parts of both the sacculus and the cochlea but the much lower lateral wall probably only enclosed the lateral part of the cochlea and parts of the perilymphatic cistern. The region below and medial to the dorsal border of the lateral wall will be referred to as the cochlear recess and the region immediately above it and ventral to the level of the dorsal border of the medial wall as the saccular recess (Fig. 12).

The auditory canal enters into the vestibule dorsal to the lateral wall. The cochlear recess and auditory canal are separated by a wedge of bone and not confluent as in the pristerognathid described by Olson (1938b). The perilymphatic cistern must have filled the auditory canal to establish contact between the footplate of the stapes covering the fenestra ovalis laterally and the sacculus and cochlea medially. Moschorhinus would therefore have had a much larger cistern than therapsids with shorter

auditory canals. The cistern would have entered the vestibule at the level of the sacculus. It is probable that the cistern not only contacted the lateral part of the sacculus but also the dorso-lateral part of the cochlea. The cochlear recess widens considerably dorso-laterally and would therefore have been able to accommodate more than just the cochlea (see Fig. 12). The perilymphatic duct and the ventro-medial part of the cistern would have surrounded the cochlea in this region. The perilymphatic sac was situated more dorsally, anterior to the fenestra rotunda, and thus posteriorly to the sacculus in the saccular recess. The fenestra rotunda, which supported the secondary tympanic membrane, was situated, as mentioned previously, in the notch ventral to the medial wall of the opisthotic (Fig. 13).

The exact limits of the sacculus are obscured by the effect the surrounding perilymphatic system had on the bony walls of the cochlear recess. As in Lystrosaurus (see Cluver 1971) there is a ledge formed by the prootic and opisthotic on the lateral wall of the vestibule that might indicate the dorso-lateral limit of the sacculus (Fig. 12). In Moschorhinus the sharp-edge concave ledge is somewhat lower down than in Lystrosaurus. The ledge also forms the dorso-medial border of the auditory canal. The medial lip of the internal auditory meatus would mark the dorso-medial border of the saccular recess. The sacculus was situated below the level of the cranial floor as in Dimetrodon (see Romer & Price 1940). It was also situated below the level of the horizontal semicircular canal as described by Olson (1944) this is contrary to the situation found in Gorgonops by Sigogneau (1974) and certain extant reptiles eg. Squamata (see Baird 1970). The sacculus was situated opposite the opening of the auditory canal to facilitate contact

with the perilymphatic cistern and therefore its lateral limit is unknown (Fig. 14). The ventral limit of the sacculus is impossible to distinguish as was noted by Olson (1944).

Posterior to the floccular fossa on the lateral wall of the cranial cavity lies the foramen through which the crus communis passed (Fig. 12). Many authors eg. Watson (1913), Simpson (1933), Olson (1937 & 1938a) and Cox (1959) mistook it to be the foramen for the endolymphatic duct. Ventral to this foramen and the ventral border of the floccular fossa is a ventro-laterally sloping region whose ventral border forms the dorsal border of the internal auditory meatus. This strip has indentations which accommodates the lateral parts of the crus communis and utriculus. Ventral to the abovementioned foramen lies the well-defined groove for the ventro-lateral part of the crus communis. This groove gradually widens ventrally up to the ledge overhanging the posterior ampullary recess. The anterior surface of the ventral half of the wall separating the vestibule and jugular foramen forms the prominent posterior border of this groove. Ventral to the medially projecting lip forming the ventro-medial limit of the floccular fossa lies the shallow curved indentation on the prootic for the lateral surface of the utriculus. This indentation is confluent with the antero-ventrally widening groove of the crus communis on the opisthotic posteriorly and runs anteriorly up to the anterior limit of the anterior ampullary recess. From the positions of these two indentations relative to each other it is clear that the crus communis entered posteriorly into the utriculus as was found by Sigogneau (1974) in the gorgonopsids. The utriculus in turn would have communicated with the ampullae ventro-lateral to it (see Figs. 13, 14).

Ventral to the abovementioned region lie the large ampullary recesses which open widely into the vestibule. The posterior ampulla was situated within the posterior ampullary recess which projects postero-laterally into the opisthotic from the central vestibular area. The anterior and horizontal (exterior - Olson 1938a; external - Sigogneau 1974; lateral - Baird 1970) ampullary recesses are confluent and form a single large recess as was found by Cluver (1971) in the anomodonts and Kemp (1979) in the cynodonts. Olson (1938a & 1944) however, found separate recesses for the anterior and horizontal ampullae in the therapsids he studied. This common recess projects antero-dorsally from the central vestibular area into the prootic. It is much larger and projects further laterally than the posterior ampullary recess. It is also situated more dorsally than the latter recess. The antero-medial part of this common recess is closed off from the rest of the vestibule by a ventrally projecting lip formed by the prootic. The ledge marking the dorso-lateral limit of the sacculus also marks the ventral limit of the ampullary recesses. The ventral parts of the ampullary recesses are confluent dorsal to this rim. Two foramina lie in the dorso-lateral corner of the common ampullary recess. The antero-dorsal foramen is the entrance to the anterior semicircular canal and the postero-ventral foramen is the entrance to the horizontal semicircular canal. Two foramina are situated one above the other in the postero-lateral corner of the posterior ampullary recess. The dorsal foramen is the exit of the horizontal semicircular canal and the ventral foramen is the entrance to the posterior semicircular canal.

The anterior semicircular canal curves postero-dorsally within the prootic and supraoccipital from its anterior foramen in

the common ampullary recess for the anterior and horizontal ampullae, and encircles the flocculus antero-dorsally. Within the side-wall of the braincase it joins up with the posterior semicircular canal within the opisthotic to form the canal for the crus communis. The foramen through which the crus communis exited is situated posterior to the floccular fossa as was pointed out by Olson (1944). Contrary to the situation described by Sigogneau (1974) in Gorgonops, the anterior semicircular canal is not exposed in the roof of the floccular fossa in Moschorhinus but it runs very near its lateral surface (Figs. 8, 9). The shorter, less curved posterior semicircular canal runs from its foramen in the ventral corner of the posterior ampullary recess within the medial wall of the opisthotic. It runs for most of its length postero-dorsally, but curves anteriorly at its apex to join up with the anterior semicircular canal to form the canal for the crus communis. The horizontal semicircular canal curves posteriorly in a crescent from its anterior foramen in the common ampullary recess in the prootic to its posterior foramen in the dorsal corner of the posterior ampullary recess in the opisthotic. The medial wall of this canal is fully ossified, this is contrary to the situation in Theriognathus (personal observation), Gorgonops described by Sigogneau (1974) and the pristerognathid described by Olson (1938b). The semicircular ducts coursed through these canals from their origins at their ampullae (Fig. 13, 14). The anterior and posterior ducts formed the crus communis dorso-medially which was connected to the posterior part of the utriculus. The horizontal semi-circular duct would have passed through its posterior foramen situated in the posterior ampullary recess. It then ran dorsal to the posterior ampulla and

joined up with the postero-ventral part of the crus communis instead of entering the posterior ampulla as was stated by Sigogneau (1974).

No evidence of the position of the endolymphatic sac or duct (otic sac and duct - Baird 1960) could be found as mentioned by Olson (1944). The duct as well as the vestibulocochlear nerve would have passed through the massive internal auditory meatus without leaving a trace on the surrounding bone. The endolymphatic sac and duct would have been situated within the cranial cavity.

Olson (1938b) described a foramen in a pristerognathid within the prootic anterior to the internal auditory meatus that connected the common ampullary recess with the cranial cavity . He interpreted it as being the foramen by which the facial nerve (VII) exited from the vestibule. The facial nerve then ran anteriorly in the fallopian canal as in the case of a gorgonopsian and anomodont described by him (Olson 1938a&b) up to the foramen through which the vestibulocochlear nerve (VIII) exited laterally. The foramen leading from the vestibule to the cranial cavity may well be homologous to the one described by Cox (1959) in the dicynodont Kingoria. He described it as being the foramen for the anterior branch of VIII (see 5.4). In Moschorhinus however, this is not the case, the facial foramen is placed far anterior to the internal auditory meatus without anything resembling a fallopian canal connecting them. There is no trace of any association between the facial nerve (VII) and the vestibule.

## 5.6 CRANIAL BLOODVESSELS (Figs. 11, 15 - 19)

### Veins

There are structures such as grooves, fossae and foramina in the skull of Moschorhinus which indicate the courses of certain bloodvessels. The major veins especially have left many clues to their positions, because, as in extant reptiles, these veins ran close to the cranial walls. Many attempts have been made in the past to explain the probable courses for the bloodvessels of certain therapsids, the best known is that of Watson (1920).

Some confusion still exists concerning the identity and courses of certain head veins. The primary head vein (Presley & Steel 1976) (vena jugularis interna, Bruner 1907; main trunk, O'Donoghue 1920) is one of the major veins draining the reptilian skull. O'Donoghue 1920, quoting Grosser & Brezina (1895) and Salzer (1895) summarises the embriological origin of the primary head vein. The anterior part is the remnant of the vena capitis medialis and the posterior part is the remnant of the vena capitis lateralis. The vena capitis medialis drains the orbital sinus and lies on the base of the brain ventral to, and slightly mesial to, the primordia of the cranial nerves. The vena capitis lateralis runs from the level of the trigeminal ganglion in a posterior direction, lateral to the otic capsule, and passes under the paroccipital bone. Bruner (1907) and Romer (1956) make no distinction between the anterior and posterior parts of the primary head vein, Romer calls the whole vein the vena capitis lateralis and Bruner calls it the vena jugularis interna. Kermack et al (1981) call the vena capitis medialis the orbital branch of the vena capitis lateralis. O'Donoghue's definition for these veins

will be followed in this description although his depiction of the relationships between these veins and the surrounding bones is not above critisism.

It is unfortunate that O'Donoghue's (1920) commendable and often quoted description also contains several misinterpretations. He states quite correctly (p. 210) that the vena capitis medialis runs "near the mid-ventral line towards the orbital sinus" yet in his Plate 7, figure 2 it runs lateral to the epipterygoid. One can easily detect the irreconcilability of the vein on this drawing with that in his Text-figure 8. Goodrich (1958) and Presley & Steel (1976) have the vena capitis medialis in its correct position, namely mesial to the epipterygoid.

The position of the vena capitis lateralis is also wrong in Plate 7, figure 2 because here it runs through the post-temporal fenestra. The sectioned bone (no. 6) at the top of the skull is the parietal and the only opening ventral to the parietal in this area is the post-temporal fenestra (see Romer 1956, figure 59B). The vena capitis lateralis in O'Donoghue's drawing, accompanied by the mandibular branch of the facial nerve (VII) and the auricular artery, runs dorsal to sectioned bones (no. 19) named by him the squamosal and quadrate. Yet on p. 210 he states that the vena capitis lateralis and its companions run "through the foramen between the quadrate wing of the pterygoid bone and the otic capsule". This is quite correct and his statement on p. 209 corroborates this: the vena capitis lateralis "continues forwards under the paroccipital bone along the ventro-lateral wall of the auditory capsule", this is confirmed by Jollie (1962) and Presley & Steel (1976).

O'Donoghue made two other mistakes concerning the skull.

Firstly the sectioned bones (no. 19) in Plate 7, figure 2 are incorrectly named the squamosal and quadrate because these bones lie lateral to the post-temporal fenestra, opisthotic and prootic (see Romer 1956, figures 59B, 62C) and therefore also lateral and not ventral to the vena capitis medialis. The sectioned bones which form the ventral border of the post-temporal fenestra are in fact the prootic and opisthotic (see Ch. 3 and Romer 1956, figure 59B). Secondly O'Donoghue (p. 210) assumes that the foramen between the quadrate wing of the pterygoid and the otic capsule is homologous to the pterygo-paroccipital foramen of Watson (1911). This is where the misinterpretation of the cranial veins of the therapsids began. The pterygo-paroccipital foramen is situated in the prootic and is sometimes partially formed by parts of the squamosal or quadrate ramus of the epipterygoid. The pterygo-paroccipital foramen could therefore not be homologous to the opening between the quadrate wing of the pterygoid and the otic capsule which is in fact the cranioquadrate passage (see Romer 1956; Goodrich 1958; Jollie 1962).

Cynodonts often have a distinct groove which runs from the trigeminal foramen in a posterior direction across the lateral face of the periotic (or prootic in some cases). It finally runs ventrally through the pterygo-paroccipital foramen (see Watson 1911, 1920; Parrington 1946; Fourie 1974; Sun Ailing 1984; Gow 1986). This groove is called here the central venous groove to simplify matters. In therocephalians however, a ventro-laterally sloping shelf on the prootic can be seen dorsal to the central ridge. This shelf stretches from the incisura prootica anteriorly to the pterygo-paroccipital foramen posteriorly (see Ch. 3 and Fig. 4; Boonstra 1934b; Kemp 1972; Mendrez 1972, 1974b). It is

therefore probable that the same vein which ran along the central venous groove ran along the dorsal shelf.

Considering the previously mentioned inconsistencies in O'Donoghue's paper it becomes clear that the vena capitis lateralis did not run in the central venous groove (in cynodonts) or on the dorsal shelf (in therocephalians). Firstly, O'Donoghue (1920) and then Watson (1920) thought that the pterygo-paroccipital foramen of the therapsids is homologous to the cranioquadrate passage. This is wrong since not only are the bony elements forming these two passages different, but the therapsids, as all other reptiles, have a normal cranioquadrate passage between the quadrate ramus of the pterygoid and the otic capsule. Secondly, the reptilian vena capitis lateralis was accompanied by the mandibular ramus of the facial nerve (VII) (O'Donoghue 1920; Romer 1956; Goodrich 1958). If this vein ran in the central venous groove it would be impossible for it to accompany the mandibular ramus. The foramen for the facial nerve (VII) always lies ventral to the dorsal shelf and pterygo-paroccipital foramen in the therocephalians. The shelf and foramen for the facial nerve (VII) are separated by the pronounced central ridge of the prootic (see Fig. 4; Boonstra 1934b; Mendrez 1972, 1974b). In those specimens described by Boonstra (1934b) the foramen for the facial nerve (VII) lies quite a distance ventral to the dorsal shelf and much nearer to the groove ventral to the ventral ridge of the prootic leading to the ventral notch. In those specimens described by Mendrez (1972, 1974b) the foramen for the facial nerve lies between the central and ventral ridges as in Moschorhinus (Fig. 4). In the specimens described by Mendrez (1972, 1974b) the mandibular ramus would have to run almost vertically dorsally to

skirt the central process of the prootic, if it was to accompany a vein on the dorsal shelf. In all therocephalians the mandibular ramus would have to take the highly unlikely course of first projecting dorsally, crossing the central ridge of the prootic (which is more pronounced than the ventral ridge in most cases). It would then have to twist sharply posteriorly to run on the dorsal shelf accompanied by the vein. Reaching the central process of the prootic it would have to twist approximately at right angles to pass through the pterygo-paroccipital foramen. This elaborate course would bring the nerve just posterior (in some cases millimetres) from its starting point. In Promoschorhynchus (Mendrez 1974b) there is even a groove running postero-ventrally from the foramen for the facial nerve directly below the central process. This quite clearly indicates that the course of the mandibular ramus (and by implication the course of the vena capitis lateralis) was ventral to the central process, and therefore ventral to the pterygo-paroccipital foramen (Fig. 15). In cynodonts and primitive mammals the impossibility of a dorsal running vena capitis lateralis is even more apparent because the central venous groove lies on the lateral face of the prootic (or periotic), whereas the foramen for the facial nerve lies on the ventral surface of the skull in the cranioquadrate passage (lateral trough, Kermack (et al) 1981) (see Simpson 1933; Parrington 1946; Brink 1955; Romer 1969; Fourie 1974).

Thirdly, if the primary head vein entered the cranial cavity through the trigeminal foramen (of cynodonts) it would be too dorsal to run along the base of the brain and ventral and mesial to the roots of the cranial nerves as it should. Following Watson's (1920) argument, the primary head vein of Moschorhinus

would have exited from the cranial cavity through the posterior foramen of the epipterygoid which would put it at a level dorsal to the trigeminal ganglion. This foramen also seems too small for the primary head vein.

Finally if the vena capitis lateralis ran in the groove leading to the pterygo-paroccipital foramen, what happened to the vena cerebralis media? This aspect will be discussed later.

Evidently the primary head vein (vena cardinalis, Grosser & Brezina 1895) exited from the ventral region of the cavum epipterycum through the cranioquadrate passage, it then ran posteriorly towards the otic capsule. The vena capitis lateralis part ran along the lateral surface of the otic capsule and passed ventral to the paroccipital process of the opisthotic (O'Donoghue 1920; Romer 1956; Bonaparte 1966; Presley & Steel 1976; Kermack (et al) 1981). In Moschorhinus the course of the vena capitis lateralis is marked by the ventral groove running dorsal to the suture between the prootic and basisphenoid (Boonstra 1934b; Mendrez 1974b). This groove (groove for head vein, Säve-Söderbergh 1947; recessus vena jugularis, Oelrich 1956) is bordered dorsally by the ventral ridge of the prootic and runs from the ventral notch in a postero-ventral direction, it tapers off antero-ventral to the fenestra ovalis (Figs. 4, 5). The vena capitis lateralis left the lateral surface of the prootic at this point and ran postero-laterally to pass between the stapes and the concave ventral border of the paroccipital process of the opisthotic. This vein joins, posterior to the paroccipital process, the posterior cerebral (jugular) vein which exits through the jugular foramen (Fig. 15). It is this vein which runs within the cranioquadrate passage in cynodonts.

Many descriptions of the vascular system of the therapsid head are based upon Watson's (1920) interpretation of the Diademodon vascular system (eg. Cox 1959; Hopson 1964; Fourie 1974; Presley & Steel 1976; Sun Ailing 1984; Gow 1986). These authors maintain that the vena capitis lateralis of cynodonts exits through the trigeminal foramen, runs in the central venous groove and passes ventrally through the pterygo-paroccipital foramen. Notably the course of the vena cerebralis media proves to be a difficulty for abovementioned authors. Watson (1911, 1920), Fourie (1974), Presley & Steel (1976) and Sun Ailing (1984) ignore this vein. Hopson (1964) maintains that the vena cerebralis media emerged from the braincase through a foramen in the prootic. Cox (1959) and Kemp (1979) however, maintain that the vena cerebralis media joins the vena capitis lateralis inside the braincase before the latter exits through the trigeminal foramen. Bonaparte (1966) mistook what is probably the foramen for the facial nerve for a canal through which the vena cerebralis media exited.

The vena cerebralis media is a very important vein in extant reptiles according to the descriptions of Bruner (1907), Dendy (1909), O'Donoghue (1920), Säve-Söderbergh (1947), Romer (1956) and Jollie (1962) and it is therefore highly unlikely that it would have been absent in the therapsids. According to the above-mentioned authors the vena cerebralis media, after draining the transverse sinus, exits from the cranial cavity through the incisura prootica (together with the root of the trigeminal nerve). It continues laterally through the cavum epipterycum accompanied by the maxillary and mandibular rami of the trigeminal nerve, these elements then emerge posterior to the epipterygoid

and anterior to the otic capsule. The vena cerebralis media finally runs ventrally to join the vena capitis lateralis. In therapsids the vena cerebralis media would have emerged from the cranial cavity through the incisura prootica too (see Boonstra 1968; Hopson 1979). The incisura prootica of cynodonts lies medially to the so-called trigeminal foramen, it is clear that the trigeminal rami and a vein passed through it (see Gow 1986). In therocephalians however, the ossification of the sidewall of the braincase has not reached this stage, and excepting Moschorhinus and possibly Theriognathus there are no foramina bound by the epipterygoid and prootic, there is a big gap between these elements instead. The trigeminal rami and vein passed laterally through the cavum epipterycum directly into the temporal fossa. It is postulated that it was the vena cerebralis media which ran in the dorsal shelf in the therocephalians and the central venous groove in the cynodonts and not the vena capitis lateralis. The vena cerebralis media passed ventrally through the pterygo-paroccipital foramen to join the vena capitis lateralis which ran ventral to it (Fig. 15). Moschorhinus and whaitsiids are unique in that they are the only therocephalians with posterior epipterygoid foramina (see Fig. 4; Kemp 1972). In Moschorhinus this foramen is situated directly anterior to the dorsal shelf of the prootic. The posterior apophysis of the epipterygoid is in line with the central ridge of the prootic (see Ch. 3). It is postulated that the vena cerebralis media of Moschorhinus exited through this foramen after passing through the postero-dorsal part of the incisura prootica (Fig. 15).

The vena cerebralis media of therapsids with a pterygo-paroccipital foramen differs from that of other reptiles on two counts

if the abovementioned hypothesis is true. Firstly, the vena cerebralis media joined the vena capitis lateralis relatively posteriorly (just anterior to the fenestra ovalis) in the therapsids, while in other reptiles (O'Donoghue 1920; Säve-Söderbergh 1947; Romer 1956; Jollie 1962) it joins the vena capitis lateralis anterior to the otic capsule. Secondly, the vena capitis dorsalis joined the vena cerebralis media just as this vein enters the dorsal aperture of the pterygo-paroccipital foramen in therapsida whereas the vena capitis dorsalis does not form an extracranial junction with the vena cerebralis media in other reptiles (see O'Donoghue; Romer 1956; Jollie 1962).

Inside the cranial cavity of Moschorhinus a smooth, concave section can be seen on the medial face of the postero-dorsal process of the epipterygoid. The dorsal venous foramen enters the cranial cavity between the supraoccipital, epipterygoid and the prootic and is continuous with the abovementioned depression (Fig. 7; Ch. 4). The transverse sinus made contact with the cranial wall in this region (Dendy 1909; Hopson 1979; Kielan-Jaworowska 1986). This depression is called the dorso-medial fossa of the epipterygoid here, it lies just dorsal to the posterior foramen of the epipterygoid and anterior to the dorsal venous foramen. It is self-evident that the vena cerebralis media, which drains the transverse sinus, originated ventral to this fossa before it exited through the posterior foramen of the epipterygoid (Fig. 17). The separation of the vena cerebralis media from the trigeminal rami by the posterior apophysis of the epipterygoid seems to be unique to Moschorhinus and possibly whaitsiids (see Ch. 3; Brink 1956; Kemp 1972).

The dorso-medial groove of the epipterygoid is confluent

postero-dorsally with the ventro-lateral gutter of the parietal. It is probable that an endocranial vein ran in this groove to join the anterior part of the longitudinal sinus (fig.11). A similar groove, situated in the medial wall of the endocranium dorsal to the exit of the trigeminal nerve, is found in Theriognathus (personal observation) and has been described in cynodonts and primitive mammals (Hopson 1964, Kemp 1979, Kermack et al 1981). This feature is also detected as a ridge running approximately horizontally on the lateral surface of certain endocasts (Hopson 1979, Quiroga 1980, Kielan-Jaworowska 1986). Although this vein was situated posteriorly near to the transverse sinus it is doubtful whether it was the vena cerebralis media (Hopson 1964, 1979) because it would have been situated antero-dorsally relative to the transverse sinus and would have run anteriorly. The identity of this vein is obscure at present.

The anterior part of the primary head vein - the vena capitis medialis drains the orbital sinus (Grosser & Brezina 1895; Bruner 1907; O'Donoghue 1920; Romer 1956; Jollie 1962). In Moschorhinus there are two shallow parasagittal depressions on the floor of the cranial cavity, between the two dorsal ridges of the pterygoid, from the level of the orbit to the anterior level of the cavum epipterycum. This depression widens gradually anteriorly (Fig. 9; Ch. 4). It is postulated that the orbital sinus lay in the wider anterior part of the depression and that the vena capitis medialis ran from it along the narrower and shallower posterior part of the depression lateral to the dorsal gutter of the basicranial axis (see Fig. 18, Bonaparte 1966). In this position the vena capitis medialis would be near the base of the brain and mesial to the roots of the cranial nerves (Bruner 1907;

O'Donoghue 1920; Säve-Söderbergh 1946; Goodrich 1958) instead of halfway between the skull roof and floor as depicted by Presley & Steel (1976). These ventral depressions for the venae capitis mediales disappear in the anterior region of the floor of the cavum epipterycum. There is, however, on the medial part of the floor of the cavum epipterycum, a smooth parasagittal depression in the angle between the antero-dorsal process of the basisphenoid and the basispterygoid process of the basisphenoid lateral to the posterior part of the sella turcica (see Fig. 5; Säve-Söderbergh 1947). Bruner (1907) states that the vena capitis medialis runs straight from its origin at the orbital sinus, to the basisphenoid bone which it meets lateral to the hypophysis. It seems clear that the vena capitis medialis in Moschorhinus continued through the cavum epipterycum in this depression which is also, as is to be expected, in confluence with the ventral groove of the prootic (Fig. 5).

The vena capitis medialis joins the vena capitis lateralis anterior to the otic capsule, ventral to the level of the trigeminal ganglion. Certain authors describing these veins in extant reptiles suggest that the vena cerebralis media joins the primary head vein where the vena capitis lateralis begins, namely ventral to the trigeminal ganglion (O'Donoghue 1920; Romer 1956). While this may be true in extant reptiles, it is not the case in therapsids and should therefore not be considered as a diagnostic feature of these veins in reptiles as a whole. As was mentioned previously, the vena cerebralis media joins the vena capitis lateralis relatively posteriorly in therapsids.

The venae capitis mediales are connected by two short transverse veins namely the anastomotic vein (O'Donoghue 1920) ante-

riorly and the hypophysial vein (Bruner 1907) posteriorly.

The anastomotic vein has been discussed by Bruner (1907), O'Donoghue (1920), Säve-Söderbergh (1947) and Romer (1956). This vein forms a medial connection between the anteriormost parts of the venae capitis mediales where they expand into the orbital sinuses. The anastomotic vein penetrates the membranous fenestra metoptica through the canal in the fissura supratrabecularis. The fissura is situated between the interorbital septum and the region of the infundibulum, ventral to the subiculum infundibuli and dorsal to the trabecula cranii cartilage (Säve-Söderbergh 1947). The greatest part of the dorsal surface of the parasphenoid in Moschorhinus is covered by the antero-dorsal process of the basisphenoid which housed the ventral part of the infundibulum (Fig. 9; Ch. 4). The only probable position of the anastomotic vein would be dorsal to the short, spatula-shaped part of the parasphenoid rostrum, anterior to the antero-dorsal process of the basisphenoid. The parasphenoid rostrum lies in addition, next to the widening part of the depression on the floor of the braincase which indicates the junction of the vena capitis medialis and the orbital sinus (Fig. 18).

The hypophysial vein was described by Bruner (1907), Säve-Söderbergh (1947), Romer (1956) and Goodrich (1958). The hypophysial vein (vena pituitaria, Säve-Söderbergh 1947; pituitary vein, Romer 1956) joined the posterior parts of the venae capitis mediales close to their respective junctions with the venae capitis laterales. The hypophysial vein runs posterior to the pituitary body and anterior to the dorsum sellae and penetrated the posterior part of the fused fenestra metoptica membranes. The position of the hypophysial vein of Moschorhinus

seems to have been identical to those of extant reptiles. The vein passed through the ventral notch which is situated postero-laterally to the pituitary fossa and ventral to the antero-ventral process of the prootic (ossified pila antotica). The hypophysial vein joined the vena capitis medialis as this vein ran in the depression between the basipterygoid process and the dorso-lateral flange of the basisphenoid (Fig. 18). The postero-medial ridge of the sella turcica is flanked by a depression on either side for the retractor musculature (see Ch. 4). It seems therefore that the hypophysial vein had to pass between these muscles.

The vena capitis dorsalis of extant reptiles drains the occipital region and runs in an anterior direction through the post-temporal fenestra. From here it runs along the prootic and penetrates into the cranial cavity by means of an opening between the prootic and parietal to join the transverse sinus (Bruner 1907; Dendy 1909; O'Donoghue 1920; Romer 1956). It would seem as if this was essentially the same pattern followed by therapsids including Moschorhinus (Fig. 15). The occipital tributary of the vena capitis dorsalis ran in an anterior direction through the post-temporal fenestra. The function of the paroccipital fossa (Figs. 1, 6; Ch. 3) which occurs in certain therocephalians (Mendrez 1972, 1974a, 1974b) is obscure. This fossa lies directly ventral to the post-temporal fenestra. It is possible that this smooth-walled fossa contained a sinus which was associated with the occipital tributary of the vena capitis dorsalis. The dorsal aperture of the pterygo-paroccipital foramen and the anterior aperture of the post-temporal fenestra of therapsids lie very close to each other. In addition, the dorsal and central grooves (of cynodonts) for the vena capitis dorsalis and vena cerebralis

media respectively, meet in this region in certain therapsids (Watson 1920 Parrington 1946; Cox 1959; Fourie 1974; Kemp 1979). It seems therefore that the vena capitis dorsalis was confluent with the vena capitis media for a short distance anterior to the post-temporal fenestra (Fig. 15).

The vena capitis dorsalis of therapsids ran in the dorsal venous groove which is usually (but not always, eg. Procynosuchus, Kemp 1979) situated directly ventral to the parietal (Watson 1911, 1920; Parrington 1946; Kühne 1956; Cox 1959; Fourie 1974; Sun-Ailing 1984). The dorsal venous foramen of therapsids usually lies within the dorsal groove, this foramen has been described by eg. Watson (1920), Simpson (1933), Boonstra (1934b), Olson (1944), Cox (1959) and Bonaparte (1966). It is well-known from abovementioned descriptions that the vena capitis dorsalis of these therapsids ran antero-dorsally within the dorsal venous groove from the anterior opening of the post-temporal fenestra and entered into the cranial cavity through the dorsal venous foramen.

It is noticable that the dorsal venous foramen (or notch) of abovementioned therocephalians is situated quite a distance ventral to the depression directly ventral to the parietal where the cynodont counterpart is found. This is due to the fact that the therocephalian dorsal venous foramen lies between the antero-lateral process of the supraoccipital and the antero-dorsal process of the prootic while the cynodont counterpart lies between the parietal and prootic.

Judging by the size and the shape of the lateral-supraoccipital fossa, the fact that the dorsal venous foramen lies within this fossa and that the dorsal part of the fossa covers the original position of the dorsal venous groove, it seems clear that this

fossa contained a venous sinus (Fig. 15). It is suggested that the therocephalian vena capitis dorsalis expanded ventrally to form a venous sinus dorso-lateral to the otic capsule, and that the dorsal venous foramen was accordingly displaced ventrally. The vena capitis dorsalis of Moschorhinus, ran in a dorso-medial direction from its junction with the vena cerebralis media anterior to the post-temporal fenestra, to the posterior part of the lateral-supraoccipital fold. Here the vein expanded to form the lateral-supraoccipital sinus (Fig. 15). From the anterior part of this sinus a vein penetrated through the dorsal venous foramen into the cranial cavity. Here this very short vein, which can be considered to be the anterior part of the original vena capitis dorsalis, entered into the posterior part of the transverse sinus (Figs. 11, 17). It is suggested that a similar pattern was present in other therocephalians or [illegible] only difference between different groups would be the [illegible] lateral-supraoccipital sinus

Kielan-Jaworowska (1986) argues that the vessel which penetrates the post-temporal fenestra and which runs along the dorsal groove (and those vessels joining it) is an artery. The obvious venous nature of the abovementioned vessels and their association with venous sinuses renders her argument suspect.

The parietal vein joins the vena capitis dorsalis before the latter enters into the cranial cavity (see Bruner 1907; O'Donoghue 1920). Evidence for the parietal vein has been found in certain therapsids. The position of this vein is indicated by a groove usually running anterior to the venous foramen, this groove is also in confluence with the dorsal groove. In therocephalians no evidence for this vein has come to light until now

In Moschorhinus however, there is a short but distinct groove between the postero-dorsal process of the epipterygoid and the parietal, bordered medially by the supraoccipital, for the parietal vein (Fig. 4; Ch. 3). The position of this groove resembles those of Diademodon (Watson 1926; Brink 1955) and Thrinaxodon (Hopson 1964; Fourie 1974) where it also runs between the epipterygoid and parietal. The groove for the parietal vein of Moschorhinus differs from those of the abovementioned cynodonts in that it ends abruptly dorsal to the epipterygoid whereas in the others it runs anteriorly, past the epipterygoid into the orbital region. This might indicate that the parietal vein drained the orbital region in these cynodonts and that it drained the temporal fenestra in Moschorhinus (Fig. 15). In Moschorhinus the dorsal venous foramen lies relatively ventrally compared to the abovementioned cynodonts, this has the result that the groove for the parietal vein does not lie anterior to it. However, this groove is in confluence with the dorsal part of the lateral-supraoccipital fossa which is the original position of the vena capitis dorsalis

The longitudinal sinus has been described in extant reptiles by inter alia Bruner (1907), Dendy (1909) and O'Donoghue (1920). This vessel runs immediately beneath the cranial roof, along the mid-line from the olfactory lobes anteriorly to the foramen magnum posteriorly. The longitudinal sinus is connected on each side to the transverse sinus by a wide vessel named the torcular Herophili in front of the cerebellum. The torcular Herophili receives blood coming from the choroid plexus of the fourth ventricle (Dendy 1909). The longitudinal sinus is divided posteriorly into two posterior cerebral (jugular) veins each of which

passes through the jugular foramen (O'Donoghue 1920). It is known that the longitudinal sinus of certain reptiles loops around the pineal stalk (Dendy 1909) in others however, the longitudinal sinus forms two arms which surround the pineal stalk (Bruner 1907). It seems as if Moschorhinus resorted to the latter case. In Moschorhinus two parasagittal grooves are found in the roof of the endocranium, these are called the ventro-lateral gutters of the parietal (Figs. 7, 8; Ch. 4). This is also the case in Theriognathus (personal observation). It is suggested that the anterior part of the longitudinal sinus (i.e. the part anterior to the torcular Herophili, Dendy 1909) divided into two arms which ran in these gutters, surrounding the pineal stalk (Fig. 17). An endocast of this region yields two parasagittal ridges, superficially resembling cerebral lobes (Plate 16). All the evidence indicates however that these could not have been cerebral lobes (see 5.3). The only structure immediately below the skull roof is the longitudinal sinus (Dendy 1909; Romer 1956; Starck 1979; Hopson 1979). The posterior part of each groove on the roof of the endocranium is immediately dorsal to the fossa for the transverse sinus (see above), this is exactly where the anterior part of the longitudinal sinus is expected to originate. It is impossible to say whether the two arms of the anterior part of the longitudinal sinus met up again anterior to the pineal stalk because the gutters disappear anterior to the parietal foramen.

Very little can be said about the posterior part of the longitudinal sinus because it left no clues in the bone to indicate its course. It is suspected that it ran postero-medially along the smooth internal surface of the supraoccipital from the supraoccipital-parietal contact to the area dorso-medial to the

jugular foramina (Hopson 1979). It is likely that the highly vascular choroid plexus lay antero-ventral to this part of the supraoccipital and that the posterior part of the longitudinal sinus ran on its dorsal surface. Here the longitudinal sinus would be surrounded by other bloodvessels and the endolymphatic sacs (Dendy 1909). The posterior part of the longitudinal sinus of extant reptiles divides into the two posterior cerebral veins (posterior cephalic veins, Dendy 1909). Each posterior cerebral vein exits through a jugular foramen and joins the vena capitis lateralis ventro-laterally to it (Dendy 1909; O'Donoghue 1920; Säve-Söderbergh 1947). In certain reptiles an additional pair of posterior cerebral veins are present which exit through the foramen magnum (Bruner 1907; Romer 1956). The veins exiting through the jugular foramina are accompanied by the glossopharyngeal (IX), vagoaccessory (X) and hypoglossal (XII) nerves and are homologous to the avian and mammalian internal jugular vein (Dendy 1909; O'Donoghue 1920). According to Dendy (1909) each posterior cerebral vein "adheres closely to the inner surface of the cranial wall" and lies "just behind the projection of the auditory capsule". In Moschorhinus there is a distinct depression on the inner surface of the endocranium posterior to the medial wall of the opisthotic (Fig. 7; Ch. 4). This depression is confluent with the dorsal part of the internal opening of the jugular foramen. These depressions probably indicate the position of the proximal parts of the posterior cerebral veins.

The probable evolution of the major cranial veins from the primitive reptile level to cynodont level is diagramatically reconstructed in Fig. 19. The organization of the major cranial veins of primitive synapsids seems to have been similar to that of

Sphenodon and Lacertilia (see Fig. 19A). The presence of the pterygo-paroccipital foramen in both the therocephalians and cynodonts suggests that this foramen could already have been present in their common ancestor. It seems logical to assume that before the foramen was formed a prootic flange, homologous to the central process of the prootic in therocephalians, would have been present in the lineage leading to the therocephalians and cynodonts. This arrangement may have been very similar to that found in Procynosuchus (Kemp 1979). The vena cerebralis media would have been positioned posteriorly to this flange and antero-ventral to the post-temporal fenestra and the vena capitis dorsalis (see Fig. 19B).

During the closing of the pterygo-paroccipital foramen a junction seems to have been formed between the vena cerebralis media and the vena capitis dorsalis. This newly formed connection would have had an influence on the blood pressure and direction of flow of blood in this region resulting in the origin of two additional blood sinuses in this region in therocephalians (see Bruner (1907) for discussion on blood pressure and the presence of venous sinuses). It is assumed that some of the blood running from the transverse sinus via the anterior part of the vena cerebralis media would have entered the vena capitis dorsalis through their connection, thereby increasing the pressure in the vena capitis dorsalis. The paroccipital sinus could have been present to alleviate this pressure. Increased blood drainage through the parietal vein into the vena capitis dorsalis and the resulting rise in blood pressure could explain the presence of the lateral supraoccipital sinus. However, the direction of flow of the blood in the rest of the system seems to have been similar to that of

extant reptiles (Fig. 19C).

The diminished size of the post-temporal fenestra in cynodonts indicates that occipital portion of the vena capitis dorsalis diminished accordingly. The temporal part of the vena capitis dorsalis on the other hand increased in size and importance judging by the deep, broad gutter it occupied. This gutter continues anteriorly past the level of the dorsal venous foramen without diminishing in size in cynodonts such as Bienotherium and Thrinaxodon (Hopson 1964) and Diademodon (Brink 1955). The dorsal venous foramen seems to have been lost while a broad dorsal venous groove is present in Procynosuchus (Kemp 1979). This gutter continues also ventrally through the pterygo-paroccipital foramen in cynodonts such as Probelesodon (Romer 1969), Thrinaxodon (Hopson 1964) and Procynosuchus (Kemp 1979). It seems therefore that the parietal vein, temporal portion of the vena capitis dorsalis and the enlarged ventral part of the vena cerebralis media joined to form a continuous sirgle vein in cynodonts. The size of the groove for the vena cerebralis media in cynodonts such as Diademodon (Brink 1955) and Thrinaxodon (Hopson 1964) indicates that the anterior part of the vena cerebralis media diminished in size compared to that of therocephalians (the diameter of this vein in therocephalians can be estimated by looking at the size of the posterior foramen of the epipterygoid). It should be kept in mind that the vena cerebralis media proper passed through the pterygo-paroccipital foramen in therocephalians whereas abovementioned combined vein passed through this foramen in cynodonts. The appearance of this new vein indicates a change in function. It is proposed that the flow of blood reversed in the portion of this combined vein wich was derived from the temporal part of the

ancestral vena capitis lateralis. The function of the vena capitis lateralis is to drain the occipital area and that of the parietal vein is to drain the temporal area. This need not occur via the transverse sinus in the endocranium, especially not if the blood from this area can drain into the primary head vein via the ventral part of the vena cerebralis media which is a much shorter route (see Fig. 19D). This new drainage pathway would then also diminish the flow of blood through the dorsal venous foramen which may explain the reduced size of this foramen in cynodonts and even its absence in Procynosuchus (Kemp 1979). It is suggested that the posterior cerebral vein became more important during the evolution of the cynodonts to compensate for the diminished size of the anterior part of the vena cerebralis media. A certain percentage of the blood from the endocranium which would have been drained via the transverse sinus and vena cerebralis media in other reptiles would have been diverted through the posterior portion of the longitudinal sinus and posterior cerebral vein.

Arteries

Little can be said about the arteries of extinct reptiles, because unlike the veins, the arteries do not usually run close to the surface of the skull bones, and therefore leave few traces.

The reptilian internal carotid and its branches have been described by authors such as: Hofmann (1900), Dendy (1909), O'Donoghue (1920), Säve-Söderbergh (1947), Oelrich (1956) and Goodrich (1958). The arrangement of these arteries differs little from reptile to reptile and it seems as if Moschorhinus was no exception (see Fig. 16). The internal carotid runs in an anterior direction, ventro-laterally to the braincase. The stapedial

artery splits off from the internal carotid postero-ventral to the cranioquadrate passage. The internal carotid continues anteriorly and enters the parabasal canal together with the palatine ramus of the facial nerve. The entrance of this canal is situated between the basisphenoid, parasphenoid and pterygoid bones in Moschorhinus (Fig. 2). This canal runs dorsally between these elements and divides into two smaller canals each of which opens up on the floor of the endocranium. The exits of these two canals lie within the deep gutter alongside the parasphenoid rostrum and the antero-dorsal process of the basisphenoid (Fig. 9). The palatine artery seems to have split off from the internal carotid and passed together with the palatine nerve through the anterior canal (vidian canal, Säve-Söderbergh 1947; Oelrich 1956; Romer 1956). This canal is called the palatine canal here. The remainder of the internal carotid would have passed through the posterior canal, here called the internal carotid canal.

The course of the palatine artery of Moschorhinus seems to resemble that of the Lacertilia more closely than that of Sphenodon. The course of the palatine artery and nerve of Sphenodon has been described by O'Donoghue (1920) and Säve-Söderbergh (1946). Sphenodon has no palatine canal, in addition the palatine artery and nerve run ventro-medially to the base of the basipterygoid process of the basisphenoid bone. The internal carotid on the other hand penetrates the basisphenoid via the parabasal canal, which in this case does not split up, and is therefore equivalent to the internal carotid canal. The course of the iguanid palatine artery and nerve has been described by Säve-Söderbergh (1946) and Oelrich (1956). Iguanids differ from Sphenodon in that they have a palatine canal which penetrates the

basisphenoid. The palatine artery and nerve run in an anterior direction dorsal to the basipterygoid process of the basisphenoid and the transverse process of the pterygoid after exiting from this canal. The palatine artery gives off many branches, supplying blood to inter alia the pharyngeal membrane and pterygoid muscles. A ventral branch penetrates the suborbital fenestra and runs anteriorly to supply blood to the palate. The only major point of difference between the course of the iguanid palatine artery and that of Moschorhinus is that the exits of the palatine canals are situated relatively anteriorly in Moschorhinus because of the anterior extension of the basisphenoid. This means that the palatine artery and nerve exit from the palatine canal anterior to the level of the epipterygoid instead of in the sella turcica region as in Lacertilia. The palatine artery and nerve of Moschorhinus would also cross the pterygoid almost immediately in their anterior course over the floor of the endocranium instead of first crossing the basipterygoid process of the basisphenoid as in Lacertilia. In Moschorhinus there are two parasagittal grooves, here called the antero-dorsal grooves of the pterygoid, running anteriorly next to each other on the endocranial floor from the palatine foramina (Fig. 9; Ch. 4). It is probable that the palatine arteries ran along these grooves, ventral to the palatine nerves (see Fig. 18).

The internal carotid arteries enter into the cranial cavity via the internal carotid foramina on either side of the infundibulum. Each internal carotid artery divides into an anterior ramus cranialis and a posterior ramus caudalis (Hofmann 1900). The cranial ramus (opthalmic artery, Beddard 1905; anterior division of the internal carotid, Dendy 1909) runs anteriorly along the

base of the infundibulum and the optic chiasma. The caudal ramus (basilar artery, Beddard 1905; posterior division of the internal carotid, Deudy 1909) runs posteriorly medial to the oculomotor nerve (III) and the pila antotica. The two caudal rami meet ventro-medially to the brain to form the basilar artery which continues in a posterior direction on the floor of the braincase and eventually exits through the foramen magnum. There are several arteries branching off from the cranial and caudal rami to supply the brain with blood. Grooves indicating the courses of these branches of the internal carotid are absent in Moschorhinus. It is therefore difficult to interpret the exact course of these two arteries. It is possible however to make a close approximation of their courses by looking at the bones and other structures that would have surrounded them in real life. The internal carotid foramina of Moschorhinus open in the dorsal gutter of the basicranial axis, on either side of the antero-dorsal process of the basisphenoid dorsal to which the infundibulum was situated (Fig. 9; Ch. 4). The cranial ramus which ran anteriorly must have run dorsal to, and not within the gutter in order to pass over the palatine artery which probably did lie in the anterior part of the gutter. The caudal ramus which ran posteriorly must also have run dorsal to the gutter, firstly to pass over the vena capitis medialis which made contact with the basisphenoid posterior to the gutter (see above), secondly it had to run dorsal to the gutter to pass over the retractor bulbi muscle and hypophysial vein and thirdly this is the only position from which it could enter into the braincase between the two antero-ventral processes of the prootic. In its posterior course the caudal ramus would have run lateral to the dorso-lateral flange of the basisphenoid

anteriorly and the metoptic membrane posteriorly. The membrane which forms the roof over the sella turcica is situated between the two antero-ventral processes of the prootic. The two caudal rami would have entered into the ventral part of the braincase by piercing through this membrane close to the crista sellaris (see Säve-Söderbergh 1947). Whether the two caudal rami meet after entering the braincase antero-ventral to the trigeminal roots as in Sphenodon (Dendy 1909) or whether they meet posteriorly ventral to the medulla oblongata as in Testudo (Beddard 1905) is not known. The presence of the small antero-dorsal projection of the basioccipital (Fig. 9) suggests that the caudal rami probably were not joined, up to that level at least, and passed lateral to the projection (Fig. 18). It seems likely therefore that the caudal rami and basillar artery of Moschorhinus tended to the more primitive condition as in Testudo (see Dendy 1909 for argument on the primitive basillar artery).

The course of the stapedial artery in extant reptiles has been discussed by inter alia O'Donoghue 1920, Säve-Söderbergh 1947, Oelrich 1956, Romer 1956 and Goodrich 1958. The stapedial artery splits off from the internal carotid postero-ventral to the cranioquadrate passage. It penetrates the stapedial foramen of certain reptiles. In reptiles where this foramen is absent, the artery runs either dorsal or ventral to the stapes. The stapedial foramen is absent in Moschorhinus as in other therocephalians, but it is difficult to say whether the artery ran dorsal or ventral to the stapes. From this position the stapedial passes through the cranioquadrate passage and runs in an antero-dorsal direction lateral to the otic capsule. Here it splits into three branches: the occipital, temporal and mandibular arteries, each of which

ramify further. The temporal artery splits into the inferior orbital and superior orbital arteries which together with the mandibular artery are to a certain extent associated with the rami of the trigeminal nerve (V). This was doubtless the case in Moschorhinus too (Fig. 16), but is impossible to be sure of the exact courses of these arteries.

## CHAPTER 6 : CONCLUSIONS

Moschorhinus is in many respects a "typical therocephalian". It has large suborbital vacuities, a slit-like interpterygoid vacuity and large post-temporal fenestrae compared to the relatively smaller fenestrae of gorgonopsians and cynodonts. Moschorhinus also has large, *open* cranioquadrate passages between the long quadrate rami of the pterygoid and the braincase.

Superficially it seems as if Moschorhinus is an advanced therocephalian. Its braincase is enlarged compared to those of scaloposaurids and pristerognathids due to the expansion of the prootic and epipterygoid in the side-walls of the braincase. The antero-dorsal process of the prootic seems to be absent in the pristerognathids, while it is a small finger-like projection in the scaloposaurids. In Promoschorhynchus, Theriognathus and Bauria it is a little broader but it is still much smaller than that of Moschorhinus. The dorsal expansion of the antero-dorsal process of the prootic in Moschorhinus causes the closure of the dorsal venous notch found in the other therocephalians and gorgonopsians. As a result only a small foramen remains for the passing of the vena capitis dorsalis into the endocranium, resembling those found in cynodonts. The anterior expansion of the antero-dorsal process of the prootic brings it into contact with the epipterygoid, a condition found only in Theriognathus and cynodonts. The contact is however a primitive one in Moschorhinus because the antero-dorsal process merely lies on the medial surface of the epipterygoid, whereas in Theriognathus and cynodonts,

these elements makes sutural contact with each other forming confluent lateral and medial surfaces.

The expansion of the antero-dorsal process of the prootic in Moschorhinus would seem to be a relatively advanced characteristic, but the morphology of the antero-ventral process of the prootic indicates the reverse. The antero-ventral process of the prootic serves as a base of attachment for the fenestra prootica membrane. The elongation of this process (in comparison with those found in pristerognathids, scaloposaurids and whaitsiids) indicates that a large portion of the side-wall of the braincase of Moschorhinus was formed by this membrane. The antero-ventral processes of scaloposaurids and Bauria are much wider than those of Moschorhinus. The epipterygoid of Theriognathus, as in cynodonts, is extensively involved in the formation of the part of the side-wall of the braincase originally formed by the dorsal part of the fenestra prootica membrane. It can be concluded therefore that the scaloposaurids, Bauria and Theriognathus all have more ossified, and therefore more advanced, structures in this region of the braincase than Moschorhinus.

The expansion of the epipterygoid gives the impression that Moschorhinus was an intermediate in a succession of therocephalians which had undergone progressive ossification of the lateral wall of the braincase, with the pristerognathids and the scaloposaurids being the most primitive and the whaitsiids the most advanced.

The epipterygoid of Moschorhinus with its expanded dorsal part is evidently more advanced than those of pristerognathids and certain scaloposaurids, but a similar case can be seen in Regisaurus. The dorsal part of the epipterygoid of Regisaurus

forms, as in Moschorhinus, part of the lateral wall of the braincase dorsal to the fenestra prootica membrane. Regisaurus also has a posterior apophysis of the epipterygoid as in Moschorhinus, Promoschorhynchus and Theriognathus.

The expansion of the epipterygoid indicates its involvement in the formation of the side-wall of the braincase. The expanded dorsal portion of the epipterygoid in Moschorhinus seems small in comparison with the expanded processus ascendens in Theriognathus. It does not imply however that Theriognathus had a larger brain than Moschorhinus, a fact that can be confirmed by comparing their endocranial casts. What it does show is that the central part of the epipterygoid of Theriognathus took over the function of the dorsal part of the fenestra prootica membrane. It should also be noted that although the epipterygoid of Regisaurus shows a similar degree of expansion as that of Moschorhinus it is situated more posteriorly. The braincase of Regisaurus is therefore still smaller in relation to that of Moschorhinus.

The posteriorly situated processus ascendens of the epipterygoid forms a roof over the cranioquadrate passage in scaloposaurids. This should not be seen as an advanced characteristic however, because the cavum epiptericum is here situated directly dorsal to the cranioquadrate passage. Due to the anterior expansion of the proctic, the processus ascendens of the epipterygoid, and therefore the cavum epiptericum, are situated anterior to the cranioquadrate passage in Moschorhinus, Theriognathus and cynodonts. The cranioquadrate passage is roofed over partly by the postero-ventral process of the epipterygoid in cynodonts. The postero-ventral process of the epipterygoid in whaitsiids is much broadened and approaches the lateral face of the prootic. This

can be seen as the incipient formation of a roof over the cranio-quadrate passage. In Moschorhinus the passage is widely open dorsally.

The expansion of the epipterygoid and prootic implies that the brain of Moschorhinus was larger than those of the pristerognathids, scaloposaurids and gorgonopsians. The large sella turcica seems to bear this out too. It should be kept in mind however that Moschorhinus had a typical long, serially arranged reptilian brain which did not fill the endocranium. The presence of wide gutters in the endocranial roof and depressions in the medial surfaces of the epipterygoids indicate that Moschorhinus (and Theriognathus) had exceptionally large endocranial blood sinuses. The large sella turcica was partly occupied by eye-muscles and even though the infundibulum was sufficiently expanded to contact the sella turcica, the pituitary fossa is quite small.

The posterior apophysis of the epipterygoid closes the posterior foramen of the epipterygoid in Moschorhinus. This foramen can easily be confused with the cynodont trigeminal foramen. In therocephalians however, the posterior edge of the "processus ascendens" of the epipterygoid is situated far lateral to the lateral face of the prootic, leaving a gap between these elements through which the rami of the trigeminal nerve could exit. This gap is closed in cynodonts by the contact formed between the posterior edge of the epipterygoid and the lateral face of prootic, leaving one or two foramina between them for the exit of the trigeminal rami (and the vena cerebralis media). The posterior foramen of the epipterygoid is clearly not homologous with the cynodont trigeminal foramen but was used for the exit of the vena cerebralis media only. This vein probably ran dorsal to, and the

trigeminal rami ventral to, the posterior apophysis in Regisaurus and Promoschorhynchus.

Moschorhinus has many other primitive characteristics, some of which are shared with pristerognathids, scaloposaurids and even primitive therapsids. Moschorhinus has a gorgonopsid-like dentition, this is especially the case in BP/1/4636, because it lacks the precanine maxillary incisors which are present in all other known Moschorhinus specimens. The supraoccipital of Moschorhinus is exposed in the temporal region as in pristerognathids, scaloposaurids and gorgonopsians in contrast to Theriognathus, Bauria and the cynodonts. Moschorhinus has also a more robust skull than any other therocephalian.

The inner ear arrangement of Moschorhinus is primitive and does not differ from those of gorgonopsians and other therocephalians. It has a wide internal auditory meatus which opens into the ventral part of the endocranium. Moschorhinus also had a short, straight cochlea. The floccular fossa and foramen for the crus communis lie dorsal to the vestibule in contrast to the more posteriorly situated floccular fossa and foramen in cynodonts. The sacculus was situated below the level of the cranial floor as in Dimetrodon and below the level of the horizontal semicircular canal. Moschorhinus has a long auditory canal similar to those of gorgonopsians, anomodonts and dinocephalians.

The most important evidence for the primitiveness of the moschorhinid skull is found in the endocranium. The basicranial processes of the prootics contact each other on the floor of the endocranium. This feature is shared with the titanosuchians, dinocephalians, gorgonopsians and the pristerognathids and stands in stark contrast to the situation found in the scaloposaurs,

whaitsiids and the cynodonts. It must be added though that these processes of Moschorhinus are much thinner than those of the abovementioned groups and do not replace the crista sellaris either. The unossified zone in the endocranial roof found in scaloposaurids, whaitsiids and cynodonts is absent in Moschorhinus as in dinocephalians.

The relationship between the cranial nerves surrounding the inner ear in Moschorhinus differs radically from that of other therapsids. The jugular foramen of Moschorhinus is separated from the vestibule by the prominent medial wall of the opisthotic as in pelycosaurs and gorgonopsians. In the pristerognathids, scaloposaurids, whaitsiids and certain cynodonts on the other hand, the ventral part of the jugular canal opens into the vestibule. The medial foramen for the facial nerve lies far anterior to the internal auditory meatus in Moschorhinus, whereas this foramen lies close to the internal auditory meatus in gorgonopsians, pristerognathids, scaloposaurids, whaitsiids and cynodonts.

In spite of the fact that Moschorhinus has a larger braincase due to the expansion of the pterygoid and the proctic, it also has certain very primitive characteristics which would put its ancestor at a pre-pristerognathid level. Theriognathus, although very specialized in its own fashion, seems to share more characteristics with Moschorhinus than with pristerognathids or scaloposaurids. It is therefore suggested that the whaitsiids and moschorhinids arose from a common ancestor. Scaloposaurids seems to have their own set of primitive and derived characteristics and it is suggested that they arose independently from primitive therocephalian stock probably related to the pristerognathids.