A Detailed Description of the Skull of *Emydops* (Therapsida: Dicynodontia).

Heidi Fourie

A Dissertation submitted to the Faculty of Science
University of the Witwatersrand, Johannesburg
for the Degree of Master of Science.
Johannesburg 1991

ABSTRACT

A detailed morphological study of two skulls of *Emydops* was undertaken by using the serial grinding technique. Graphical, wax model and computer-3D reconstructions of various aspects of the skulls were made. The internal structures are described in detail and compared to other small dicynodonts such as *Eodicynodon*, *Pristerodon*, *Tropidostoma*, *Cistecephalus* and *Diictodon*. The structure of the skull of *Emydops* conforms within the limits of variation known for this genus, to descriptions given in the literature. It was found that *Emydops* is different from other dicynodonts in that the parasphenoid has a definite suture with the pterygoid anterior to the pterygoid-basisphenoid suture, which is not noticed and mentioned for other dicynodonts, except for *Emydops* (Olson, 1944).

DECLARATION

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

13th day of January, 19[illegible].

ACKNOWLEDGEMENTS

I am indebted to the following people;
Dr. C.E. Gow for his supervision and encouragement.
Dr. J.W. Kitching for critical reading of the manuscript.
Dr. G.M. King for her advice and valuable discussions.
Dr. B.S. Rubidge for his time and advice.
Prof. B. Kramer, General Anatomy (Wits University) for the use of the departments computer programme and equipment, and Dr. H.P. Brunhübner for his assistance with the Image Analyser.
The Hillbrow Hospital staff and Dr. Francis Thackeray for the CAT scans.
Last but not least, my husband W.J. Visser for his love and support. Also all my friends at BPI Palaeontology.

CONTENTS

LIST OF FIGURES

List of Figures:

1. INTRODUCTION

Dicynodonts lived during the late Permian and Early Triassic and are found abundantly in the lower (*Eodicynodon*-*Tapinocaninus*, *Tapinocephalus*-*Bradysaurus*, *Pristerognathus*-*Diictodon*, *Tropidostoma*-*Endothiodon*, *Cistecephalus*-*Aulacephalodon* and *Dicynodon*-*Theriognathus* assemblage zones) and middle (*Lystrosaurus*-*Procolophon* assemblage zone) part of the Beaufort Group, and to a lesser extent in the upper (*Cynognathus*-*Diademodon* assemblage zone) (Rubidge, in preparation) part. The group has been extensively studied, because they contain the most primitive mammal-like reptiles found in South Africa and went extinct by the end of the Triassic and because of their abundance, but only six workers have produced serial sections in order to study the cranial detail of dicynodonts. Dicynodonts studied in this way have been:- *Dicynodon* *leoniceps* (Sollas and Sollas, 1913), *Emydops* sp. (Olson, 1944), *Diictodon* (*Dicynodon*) *grimbeeki* (Agnew, 1958), *Pristerodon* *buffaloensis* (Barry, 1967), *Cistecephalus* *microrhinus* (Keyser, 1973a), and *Oudenodon* *baini* (Keyser, 1975).

1.1 *Emydops*

The internal skull morphology of *Emydops* has never been described in detail. Sollas and Sollas (1913) discovered, by applying the serial sectioning technique to the genus *Dicynodon*, the presence of a grooved vomer, the well-marked floccular recess, the existence of an ectopterygoid, the maxillary antrum as an inter-osseal space, and the septomaxilla in the Dicynodontia for the first time. This marked the beginning of the quest to understand the inner structures of the fossil skull. In 1944 Olson tentatively referred his serially sectioned dicynodont specimen to the genus Emydops, but studied only the inner ear, occipital region and basicranial axis. Hopson (1964) used Olson's (1944) sections of the Emydops specimen to describe the mode of tooth replacement. Crompton and Hotton (1967) described the functional morphology of dicynodonts using BP/1/2642, but incorrectly identified their specimen as Emydops; subsequently research has shown this specimen rather to belong to the genus Pristerodon (pers. observation). The sphenethmoid, inner ear, blood vessels and nerves, tooth replacement and palatoquadrate complex of most dicynodonts have not been described as yet. For the purpose of this study two Emydops skulls were serially ground to describe the internal skull structures which will add to the descriptions of the fossil skull morphology of dicynodonts. Emydops was chosen because of its plesiomorphic (palatines extend medially and become incorporated into the rear of the secondary palate) and synapomorphic (palatal exposure of palatine a flat, horizontal plate with a concave posterior border (King, 1990)) characters.

Broom (1913) described three species of Emydops, E. minor,

E. arctatus (Cistecephalus arctatus)(Owen, 1876) and E. longiceps. He described Emydops as having a greater parietal width than Dicynodon and as differing from Pristerodon in having no posterior serrations on the postcanine teeth.

In his "Mammal-like Reptiles of South Africa", Broom, (1932) illustrates the various Emydops species described at that date. Toerien (1953) added E. murraysburgensis and E. kitchingi to this list.

Haughton and Brink (1954) recognised eleven species of Emydops, namely: E. arctatus, E. kitchingi, E. longiceps, E. longus, E. microdon, E. minimus, E. minor, E. murraysburgensis, E. parvus, E. platyceps, and E. trigoniceps. Cluver and King (1983) only recognised E. longiceps, E. longus, E. minor and E. platyceps. King (1988) accepted all the species listed by Haughton and Brink (1954).

1.2 Techniques to study the internal structure of fossil skulls

In order to accomplish a greater understanding of the fossil skull, techniques designed to reveal more detail than mechanical or acid preparation and the cutting of thick sections are necessary. The major difficulty with mechanical preparation is to dissect out fine detail of the internal skull morphology and some specimens may disintegrate with acid treatment (Crompton, 1955). The identification and homologies of the components of the interorbital septum (sphenethmoid) are not well described in dicynodonts. Serial grinding is one method which can effectively reveal fine details of the internal anatomy, at least in refractory fossil material such as that offered by the Karoo reptiles. A disadvantage is that serial grinding, because it is a destructive process, should not be practised on types or other particularly valuable specimens. However the amount of information to be gained by serial grinding more than out-weighs this disadvantage, and in many instances photographs of the ground surface can provide a permanent record, and are extremely useful for reference purposes (Agnew, 1958).

Furthermore, many symmetrical specimens, even though rare, could legitimately be divided into halves, one side be used for sectioning and the other for surface morphology and permanent record (Simpson, 1933).

Cranial characters, such as the tooth replacement, sutures, foramina, grooves, inner ear, interorbital septum, and the basicranium are described in more detail and it allows the examination of the path of bloodvessels and nerves. Serial grinding has the advantage over non-sectioning methods, in that it indicates the presence of even the smallest embryonic teeth if they have begun to calcify (Hopson, 1964).

The serial grinding technique therefore gives a satisfactory picture of the relationships of the skull bones as well as information about the internal structures which are not readily available from other methods of preparation. Four methods of reconstruction were used, because each method emphasised different features (see below).

1.2.1 Graphic Reconstruction

This method takes the minimum of effort and can be done quickly at any time. It is however required that a base line exists to pile the drawings i.e. the sections must have reference marks and in this study three guideholes were used. Separate structures can be reconstructed on separate pieces of paper as well as contour drawings to show the anterior and posterior views (Pusey, 1939).

1.2.2 Wax Model

With this method of reconstruction each bone can be cut out of the wax individually and it permits the representation of different bones in wax of various colours. The only problem is that the wax increases in thickness around the margins as the required shapes are cut from it, it is therefore necessary to check at regular intervals to ascertain what this increase is and correct it in the model (Brink, 1960).

The model can assist in shading the drawings.

1.2.3 Image Analysis

Image analysing is a fairly new computer method employed in neontology and palaeontology to obtain three-dimensional images from consecutive drawings obtained by serial grinding or serial sectioning of anatomical material. Image analysis is used quite extensively in dentistry and the other medical sciences.

Three-dimensional reconstruction of serially sectioned organs and tissues aids in the visualization of their spatial arrangement, relationships of component elements and quantification of structures (Ongaro et al, 1991). The Kontron Image Analysis programme used here is just one of many used for 3D-reconstructions. It consists of the computer hardware, including a digitizing pad, and a software package.

1.2.4 CAT Scanning

Computer aided tomography is used in many hospitals to provide cross-sectional images which represent the X-ray attenuation coefficient of the tissues or bone in the imaged plane. A 3D-image is reconstructed by a computer from X-ray transmission data obtained during the scan (Zonneveld et al, 1985). This technique is very expensive and not often used for Karoo fossils as the matrix is too dense.

2. MATERIALS AND METHODS

2.1 Materials

The specimens selected for the study are housed in the collections of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand. They were all collected from rocks of the Lower Beaufort Group (*Dicynodon*-*Theriognathus*, *Cistecephalus*-*Aulacephalodon*, *Tropidostoma*-*Endothiodon*, *Pristerognathus*-*Diictodon* and *Tapinocephalus*-*Bradysaurus* assemblage zones)(Rubidge, in preparation). As there are quite a number of *Emydops* specimens it was possible to serially grind two specimens. The least distorted, best preserved, specimens in a reasonable size range were chosen as finer detail are difficult to observe on a small specimen and sutures may be fused in big specimens. A further 73 specimens (Appendix C) had been prepared by the preparators of the Bernard Price Institute for Palaeontological Research and were available for comparative purposes.

2.1.1 Specimens used for serial grinding

The specimens were identified as *Emydops* on the following criteria (King, 1988); Small dicynodonts with broad intertemporal region and wide parietal exposure on the skull roof. Palatine meets posterior border of premaxilla and is transversely enlarged into a horizontal plate with a concave posterior border. Anterior trough-like extension of the interpterygoid vacuity on to vomerine septum short or absent. Embayment in palatal rim anterior to canniniform process. Interpterygoidal crest weak, not continued on to ventral surface of anterior pterygoid ramus. Dentary shelf prominent. Anterior symphysial region of dentary drawn up into a sharp cutting edge. Shallow groove on dorsal edge of dentary behind symphysis.

Specimen BPI/1/4386

This specimen is from the farm Klein Bloukop, Richmond (31° 32'S 23° 34'E). The biostratigraphical horizon is the Cistecephalus-Aulacephalodon assemblage zone. The lower jaw is present in position. Distortion is very slight. For cranial measurements see Appendix D

Specimen BP/1/1619

This specimen is from the farm Dunedin, Beaufort West (31° 57'S 22° 25'E), and was identified as Emydops on the criteria given by King, (1988). The biostratigraphical horizon is the Cistecephalus-Aulacephalodon assemblage zone. It is slightly distorted. A crack runs through the temporal opening on the right side of the skull, but does not damage any of the internal structures. For cranial measurements see Appendix D.

2.1.2 Reference material used

The following type specimens were examined:

Emydops minimus (Broom, 1935). Skull in the Transvaal Museum, Pretoria (Cat. No. 242) from the farm Kookfontein, Victoria West. Horizon: *Cistecephalus*-*Aulacephalodon* assemblage zone.

Emydops microdon (Broom, 1936). Skull in the Transvaal Museum, Pretoria (Cat. No. 269) from the farm Leeuwkloof, Beaufort West. Horizon: *Cistecephalus*-*Aulacephalodon* assemblage zone.

Emydops murraysburgensis Toerien, 1953. Skull in the Bernard Price Institute (Cat. No. 609) from the farm Blaauwpoort, Murraysburg. Horizon: *Cistecephalus*-*Aulacephalodon* assemblage zone.

Emydops kitchingi Toerien, 1953. Skull in the Bernard Price Institute (Cat. No 625) from the farm Blaauwpoort, Murraysburg. Horizon: *Cistecephalus*-*Aulacephalodon* assemblage zone.

2.2 Methods

The two *Emydops* skulls (BP/1/4386 and BP/1/1619) were serially ground using a Croft parallel grinder. This process is tedious and time consuming, but it is the only method in which the finer details of the inner structures can be studied.

Various machines and modifications have been used for serial sectioning and serial grinding in the past 47 years. Sollas (1903) first described the serial sectioning method using a grinding apparatus. Sollas and Sollas (1913) using an improved machine applied the technique on a specimen of Dicynodon leoniceps.

Sollas and Sollas (1916) described an unknown dicynodont species. Olson (1944) looked at the inner ear and neurocranium of six anomodonts (one being assigned to the genus Emydops), four theriodonts, two specimens of Captorhinus, one specimen of Diadectes, and two specimens of Dimetrodon. He retained a permanent record of each section by the use of nitrocellulose peels. Nitrocellulose peels were not used in the present study as the photographs and drawings supplied an adequate permanent record.

Olson and Whitmore (1944) described the apparatus used by them for serial grinding and the making of nitrocellulose peels. Croft (1950) described the Croft parallel grinder. This instrument proved to be the best for studying the internal structures of the fossil skull. The Croft parallel grinder is a combination of a large micrometer and a tripod method. The micrometer is used to determine the grinding interval. The Croft parallel grinder differs from earlier apparatus by using steel balls as rolling supports for the tripod. In this way free movement is obtained over the grinding plate, negligible abrasion of the supports, exceptional precision in the determination of the grinding interval, a fairly wide range in the size of specimens which can be accommodated, and easy conversion to automated grinding.

Crompton (1955) described the method of serial grinding with a Croft parallel grinder and gave advice on how the drawings can be done with the help of an epidiascope.

Agnew (1958) studied the sphenethmoid region and cranial kinesis of *Diictodon grimbeeki* (=*Dicynodon grimbeeki*) with the aid of a Croft grinder while Brink (1960) gave advice on the Croft parallel grinding method and referred to problems, such as sectioning up to the last trace of bone. Barry (1963) used the parallel grinding technique to serially grind *Pristerodon buffaloensis* and other therapsids to study the ear region. Hopson (1964) used Olson's (1944) specimens to describe tooth replacement. Barry (1965) used the drawings and photographs of *Pristerodon buffaloensis* for his studies on the epipterygoid-alisphenoid region, and later (1967) described the skull of *Pristerodon buffaloensis* in full detail.

Boonstra (1968) described another method of cutting thin slabs with a diamond-studded circular saw, but this can only be done with large specimens. Cluver (1971) using the same method as Boonstra (1968) gave a detailed description of the anomodont genus Lystrosaurus.

2.2.1 Procedure

2.2.1.a Casting of specimen

Prior to grinding both specimens used in this study were measured, drawn and photographed before they were encased in plaster of Paris. The best way of preserving the original specimen is to produce a silicon rubber or latex mould and then to cast it with epoxy-resin and fibre glass for a permanent record. The two resulting casts are stored at the Bernard Price Institute for Palaeontological research, University of the Witwatersrand.

Each specimens was placed in a vertical orientation with its snout facing downwards on the micrometer disc. A cardboard cylinder was placed around the specimen and plaster of Paris was poured into the cylinder. The plaster of Paris must be quick drying and non-absorbent, because the grinding is done in a wet grinding medium. The specimens were left to harden for approximately 15min, before the cardboard cylinders were removed and the positions of the ventral and dorsal sides of the skulls marked. They were then left for the plaster to dryout completely. The cylindrical block of plaster containing the specimen was then attached to the micrometer footplate with warm dental modelling wax. This was left to cool and set before grinding was begun.

As the length of the micrometer cylinder is limited (only a 100mm) it is not always possible to include an extra block of plaster between the specimen and the supporting disc so that grinding could proceed to the rear of the squamosals. In order to achieve this an additional layer of plaster was added later; however, it is preferable to make the block longer before grinding if the specimen is small enough, as it obviates errors of orientation.

2.2.1.b Setting up of micrometer

The Croft parallel grinder was set up next to a tap and basin for a ready supply of water. The retaining rings for the ball-bearings were fixed onto the zinc grinding plate with plasticine.

The embedded fossil on the footplate was screwed into the micrometer cylinder and the scale was set. The reading on the micrometer was noted. The cylinder is calibrated for 100mm. The section interval decided on was 0.25mm as this interval gives the best results in small specimens. Two grades of carborundum powder were used, first a coarser powder (400 grit) for grinding and then the finer powder (600 grit) for polishing. Every section was either bleached with 3% acetic acid or stained with Alizarine Red S (Sodium

Alizarin - Sulphonate) depending on the contrast between bone and matrix. Photographs of each section were taken with the aid of a photomicroscope. Then each section was traced with the aid of an epidiascope so as to obtain a permanent record. Three set markers or guideholes on the drawing board were transferred to each tracing for later orientation during the reconstructing phase. Two hundred sections were obtained for BP/1/4386 and two hundred and sixty for BP/1/1619.

2.2.2 Reconstructions (See 1.2.1, 1.2.2 and 1.2.3)

The tracings were used to reconstruct both specimens on graph paper according to the method of Pusey (1939). Five views were drawn; dorsal, ventral, lateral, occipital and medial. The Kontron Image Analysis programme was used to obtain a three dimensional image of each specimen. Part of the lower jaw of BP/1/4386 was reconstructed with dental modelling wax to confirm the short dorsal dentary groove and the tooth arrangement.

The Kontron Image Analysis division KAT 286 programme was used. Using the Image Analyser a drawing of each section was traced with a digitizer and then stacked on the previous section. The thickness of the sections was determined by the grinding intervals and was measured in pixels. In this way a 3D-image of the whole skull could be obtained, and by using the computer programme it was possible to project any plane through the skull onto the screen. These images could then be photographed.

Markers were put on every drawing traced with the aid of an epidiascope to make graphic reconstruction and image analysis easier. These markers were transferred to the drawing pad of the analyser. It is important not to use the digitizing pen as it damages the digitizing sheet, but rather the digitizing mouse. The Kontron Image analysis programme has eight channels which are colour-coded and individual bones can be allocated to different channels. As the skull has more than eight bones, this was found to be a major shortcoming as they cannot all be differentially colour coded in one run. Three to four less important bones, such as the skull roof bones were assigned to one channel and by doing this the sutures were lost. It was done as follows (Figure 22 and 24);

BP/1/4386	Channel 1	Premaxilla, vomer.
	Channel 2	Maxilla, jugal.
	Channel 3	Lower jaw, quadrate, quadratojugal.
	Channel 4	Skull roof bones.
	Channel 5	Postcanine, dentary teeth sphenethmoid, epipterygoid.
	Channel 6	Palatine, pterygoid, ectopterygoid, opisthotic, basisphenoid.
	Channel 7	Basioccipital, squamosal, tabular.

BP/1/1619 Channel 1 Premaxilla, vomer.
Channel 2 Maxilla.
Channel 3 Skull roof bones, jugal, squamosal.
Channel 4 Sphenethmoid, epipterygoid.
Channel 5 Palatine, pterygoid, ectopterygoid, basisphenoid.
Channel 6 Quadrate, quadratojugal, periotic, basioccipital.
Channel 7 Tabular.

The sutures could, however, be recovered in the framework (Figure 27) mode or by running the programme again coding for different bones. Different combinations will give different features (Figure 23).

Five menus are available in the directory; editing, moving, scanning, printing and inserting. The markers were set first, then a suitable channel was chosen and the drawings were stacked in append mode. If a mistake was made the whole section could be deleted and the corrected section could be inserted. To obtain the 3D-image the elevation, rotation and tilt angles were manipulated. Before tracing, the elevation, rotation and tilt angles must be checked, as for tracing and stacking they must be on set values (for example E - 0,00, R - 0,00, T - 70,00) throughout the skull. When plotting or photographing certain channels could be deleted, or a framework function could be chosen. There was also a zoom function for close-up views. Sections were saved automatically on the hard disk, or on back-up high density floppies.

The CAT scan of the type specimen of Emydops minimus (Figure 28) was examined to see if there is a possibility of using this method instead of the serial grinding technique. However in this process the image was blurred and transverse sutures were lost. The scanning interval of 1mm was too thick for this 5cm long specimen. Most of the longitudinal sutures were visible such as the frontal suture, as well as some of the dentary teeth. The interparietal to parietal suture was quite clear. It was also evident that the right side of the skull was not well preserved. The greatest advantage of CAT scanning is that it is one method of determining if a specimen is well enough preserved for serial grinding, and can thus be a useful tool for the study of fossils.

The advantage of CAT scanning is that it is less time consuming than Image analysis. A 5cm specimen took only 45min to scan. Back-up diskettes were made by the hospital staff and kept in the hospital and from these further sets of X-rays can be obtained.

The specimen was scanned in contiguous 1mm transaxial slices. The scan parameters included 46 projections, 7 second scans, 125kV, and 0,52 amp-seconds with high-resolution imaging at doubled windows of 2700/3500 Hounsfield Units and centres of 600/[illegible]00 HU (Figure 29).

3 RESULTS

3.1 Description

3.3.1 *Emydops* Specimen no. BP/1/4386

Snout and Skull Roof (Figure 1, 2, 3 & 4).

The features of the skull roof do not differ from the usual dicynodont pattern, except for the fact that the intertemporal region is wider than the interorbital region.

Premaxilla.

The premaxilla is quite thick in transverse section and has a posteromedial contact with the nasal. The anteriormost tip of the snout is thin in comparison with the rest of the premaxilla. The skull roof region of the premaxilla tapers posteriorly between the nasals in an interdigitating suture. The premaxillae form the internasal septum.

Septomaxilla.

The septomaxilla is not well preserved, see BP/1/1619 for the description.

Nasal.

A nasal boss is present (Figure 1). The interdigitating suture of the nasal with the frontal is unclear. The internasal suture is slightly open suggesting that this is a young specimen. The nasal borders onto the maxilla and prefrontal laterally. The nasal bone is very thin posteriorly and thickens anteriorly. The dorsal exposure of the nasal bone is thicker than the lateral sides where the nasal bone can be seen in section on the inner surface of the maxilla.

Maxilla.

The maxilla is the largest bone in the snout region. The maxilla is in contact with the lachrymal laterally, the prefrontal dorsally, and sutures with the jugal posteriorly. The lateral portion of the maxilla is thicker than the ventral palatal exposure. It forms the greater part of the floor of the nasal cavity. In section it can be seen that the maxilla has a ventral (palatal exposure) and a lateral part with a channel between them that opens into the nasal cavity.

Prefrontal.

The prefrontal meets the frontal posterodorsally and borders the orbit posteriorly. It is in contact with the lachrymal laterally. The nasal overlies the prefrontal at their suture.

Lachrymal.

The lachrymal forms part of the wall of the naso-lachrymal duct (Figure 9B), almost at a point where the jugal and lachrymal meet, the maxilla forms the other wall of the naso-lachrymal duct. This duct runs from the anterior of

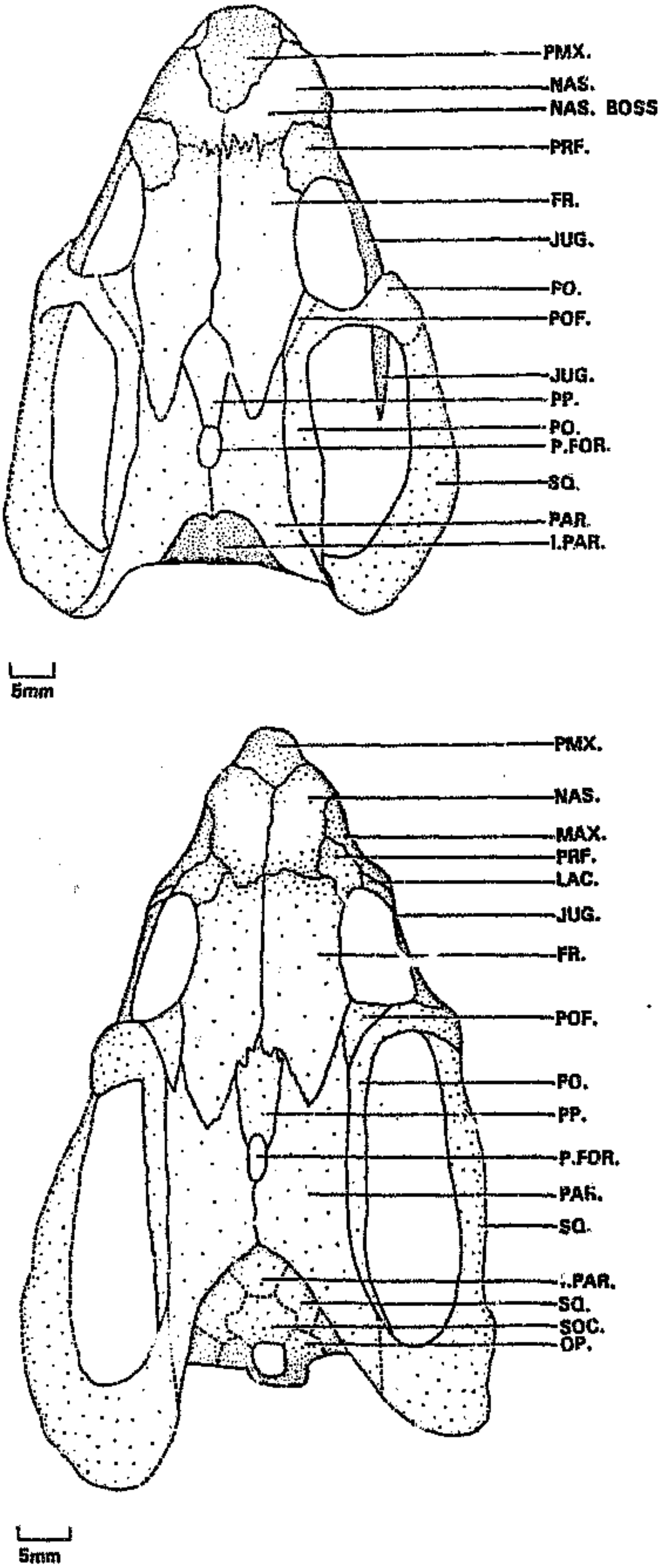


Figure 1: Emydops. Specimen BP/1/4386 (top) and specimen BP/1/1619 (bottom), dorsal views prior to grinding. All abbreviations in Appendix A.

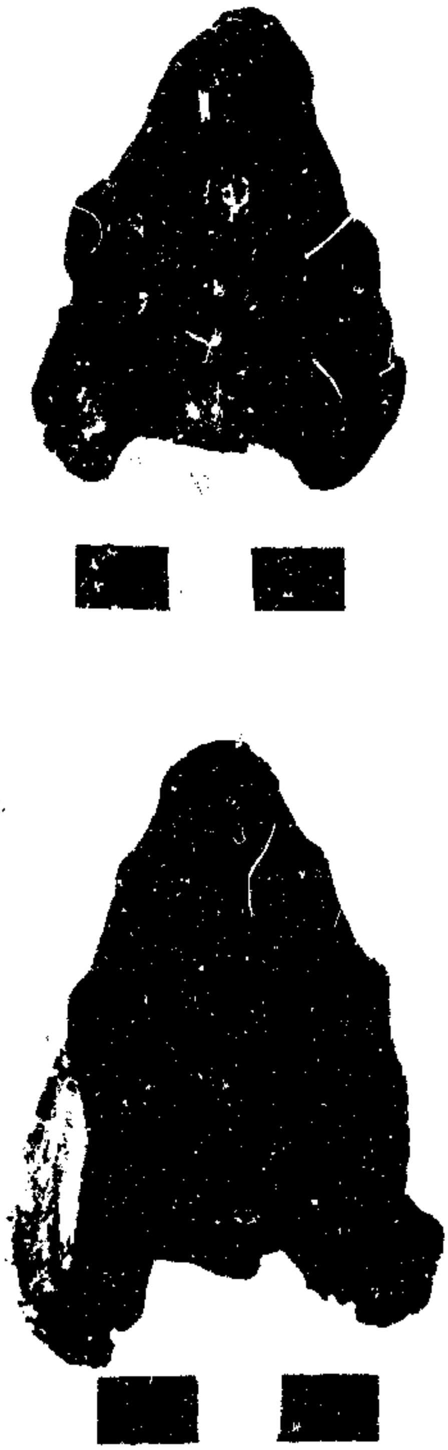


Figure 2: Photographs of dorsal views of BP/1/4386 (top) and BP/1/1619 (bottom). Scale on all photographs 3cm.

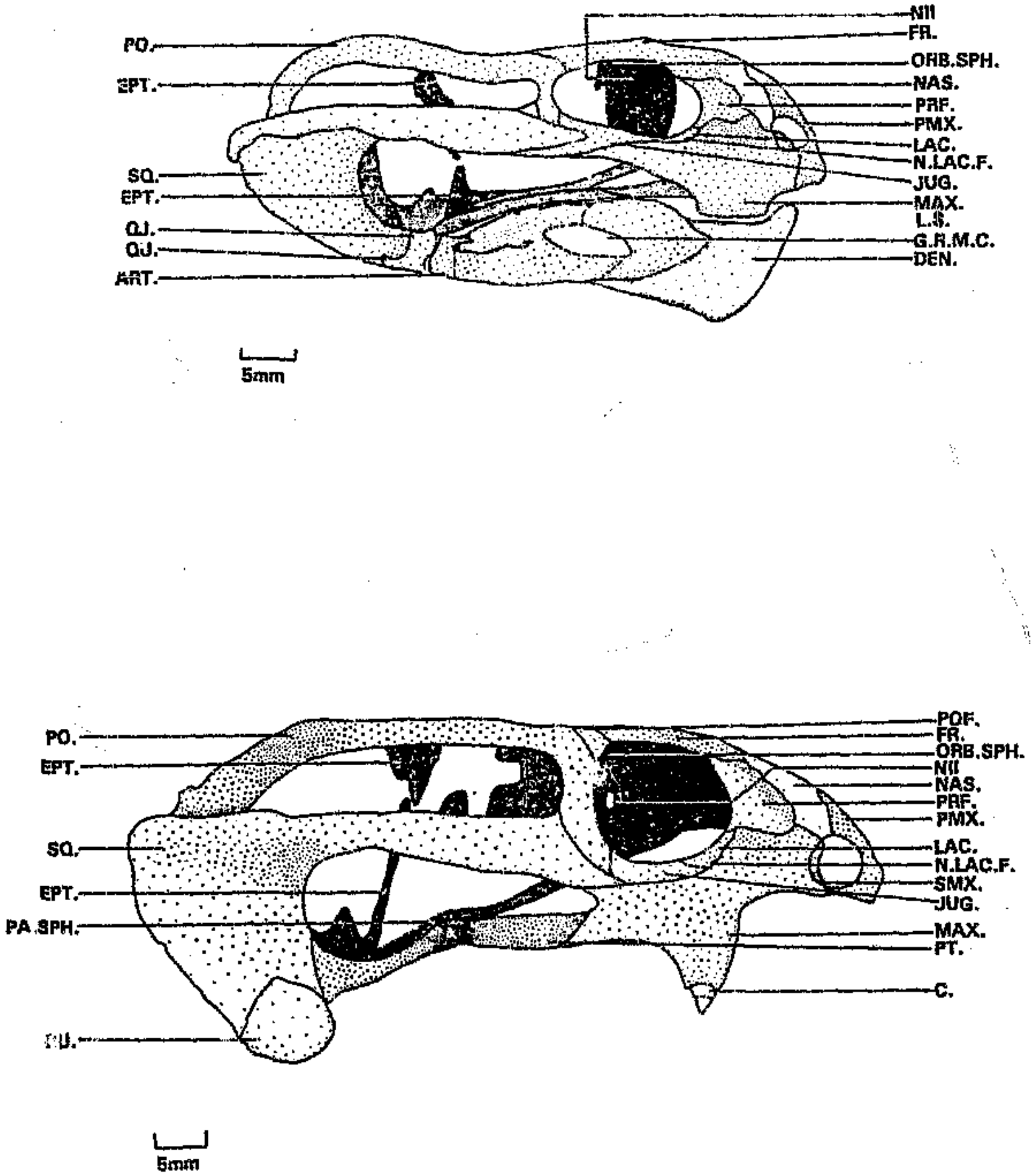


Figure 3: <u>Emydops</u>. Graphic reconstruction of specimen BP/1/4386 (top) and specimen BP/1/1619 (bottom), lateral views.

the lachrymal to the lachrymal-maxilla suture and opens directly into the nasal cavity. The lachrymal forms part of the anterior border of the orbit. It partly underlies the frontal and underlies the maxilla so that it is on the inner surface of the maxilla. The transverse sections show the lachrymal on the inner surface of the prefrontal extending downwards to meet the maxilla and jugal laterally.

Frontal.

The frontal meets the parietal posteriorly, and is in contact with the preparietal posteromedially and with the orbit and postfrontal laterally. Both the postorbital and postfrontal are overlain by the frontal dorsally. In section, the anterolateral portions of the frontals are cupped ventrally to surround the olfactory canals which run longitudinally towards the nasal region (Figure 19).

Postfrontal.

The postfrontal is an almost triangular shaped bone forming the posterodorsal border of the orbit. It meets the postorbital laterally and the parietal posteriorly. In section it can be seen that the postfrontal is overlain by the frontal and also forms part of the cupping of the olfactory canals.

Postorbital.

The medial side of the postorbital is in contact with the parietal, and it forms the anterior and medial borders of the temporal fenestra. In section it can be seen that the parietal overlies the postorbital dorsally. The postorbital has a posterior hook-shaped contact with the squamosal, as well as laterally overlapping the jugal and squamosal. The postorbital, jugal and squamosal meet on the zygomatic arch, with the postorbital dorsally, the jugal ventrally and the squamosal is laterally. Exact contacts and sutures are not clear.

Preparietal.

The preparietal extends anteriorly as far as a point in line with the anterior limit of the temporal fenestra, and borders onto the pineal foramen posteriorly and the parietal laterally. It is a superficial bone. In section the sutures of the preparietal are indistinguishable so that it can be deduced that these sutures do not run through into the braincase, but they are only visible on the skull roof.

Parietal.

The parietals form the posterodorsal roof of the skull and include the pineal foramen. Each is in contact with the supraoccipital behind the pineal foramen, but the suture is only visible in section. The interparietal meets the posterior border of the parietal. The medial parietal lamina extends downwards from the parietal behind the posterior border of the pineal foramen and suture with the

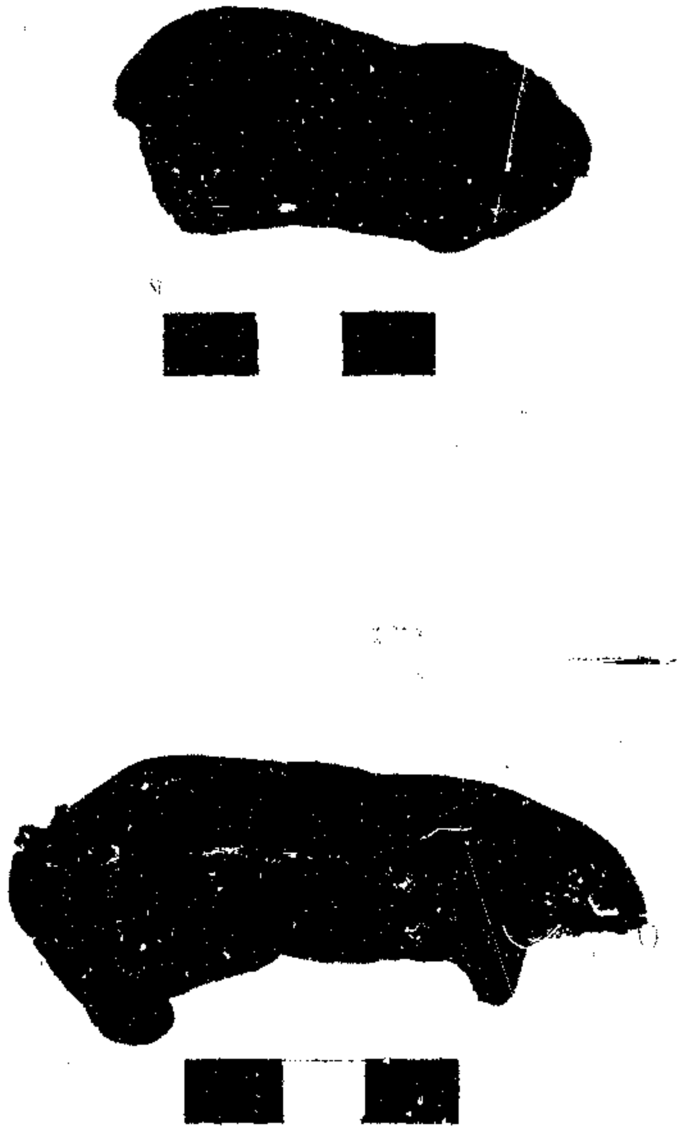


Figure 4: Photographs of lateral views of BP/1/4386 (top) and BP/1/1619 (bottom).

epipterygoid ventrally on its inner surface. In section the parietal laminae form an inverted U (Figure 5A).

Jugal:

The jugal, palatine and ectopterygoid can be seen meeting in section (Figure 9C). The jugal is a fairly big bone. The jugal and squamosal have an S-shaped contact as seen in section. The jugal extends anteriorly as far as the anterior of the orbit and the posterior of the maxillary antrum. The ventral part of the jugal rests on the maxilla and a groove is present between them. In section it can be seen that the jugal and maxilla suture laterally. The squamosal overlies the jugal at their suture.

Squamosal.

The squamosal forms the posterior and lateral borders of the temporal fenestra and overlies the jugal anteriorly where the jugal margins the orbit ventrally.

Sphenethmoid Region. (Figure 5A & 25).

The presphenoid is displaced to the left side in this skull. A displaced bone with a medial foramen is present dorsally of the presphenoid, and could be the mesethmoid and should have occupied part of the space anterior of the orbitosphenoids. There are no signs of the orbitosphenoid due to this region not being well preserved.

The presphenoid is a large and fairly thick bone showing the spongy internal nature of the bone in section and it is flat ventrally and rounded anterodorsally. The rostroparasphenoid is not attached to the vomer ventrally, but lies on top of the vomer. The rostroparasphenoid is grooved dorsally from its tip to just anterior of the parasphenoid-pterygoid suture. The parasphenoid sutures with the pterygoid posteriorly immediately anterior to the level of the pterygoid-basisphenoid suture (Figure 6B). The parasphenoid bone is visible through the interpterygoid vacuity and is V-shaped in section. Both the vomer and parasphenoid rostrum are grooved anteriorly as if they housed a cartilaginous structure or contained a groove between them (Figure 10, section 78). Just posterior of the septosphenoid is a separate presphenoid, it has separated from the parasphenoid and is situated medial to the postorbital and may have been connected to the septosphenoid with cartilage as it is grooved ventrally (Figure 5A).

The Palate. (Figure 7 & 8).

Premaxilla.

On the palatal surface of the skull the premaxilla borders onto the maxilla laterally and has a very small contact with the palatine posteromedially. The premaxilla-maxilla suture is interdigitating and extends posteriorly as far as the anterior of the premaxilla-vomer suture. The premaxilla overlies the vomer on the ventral side for a short distance.

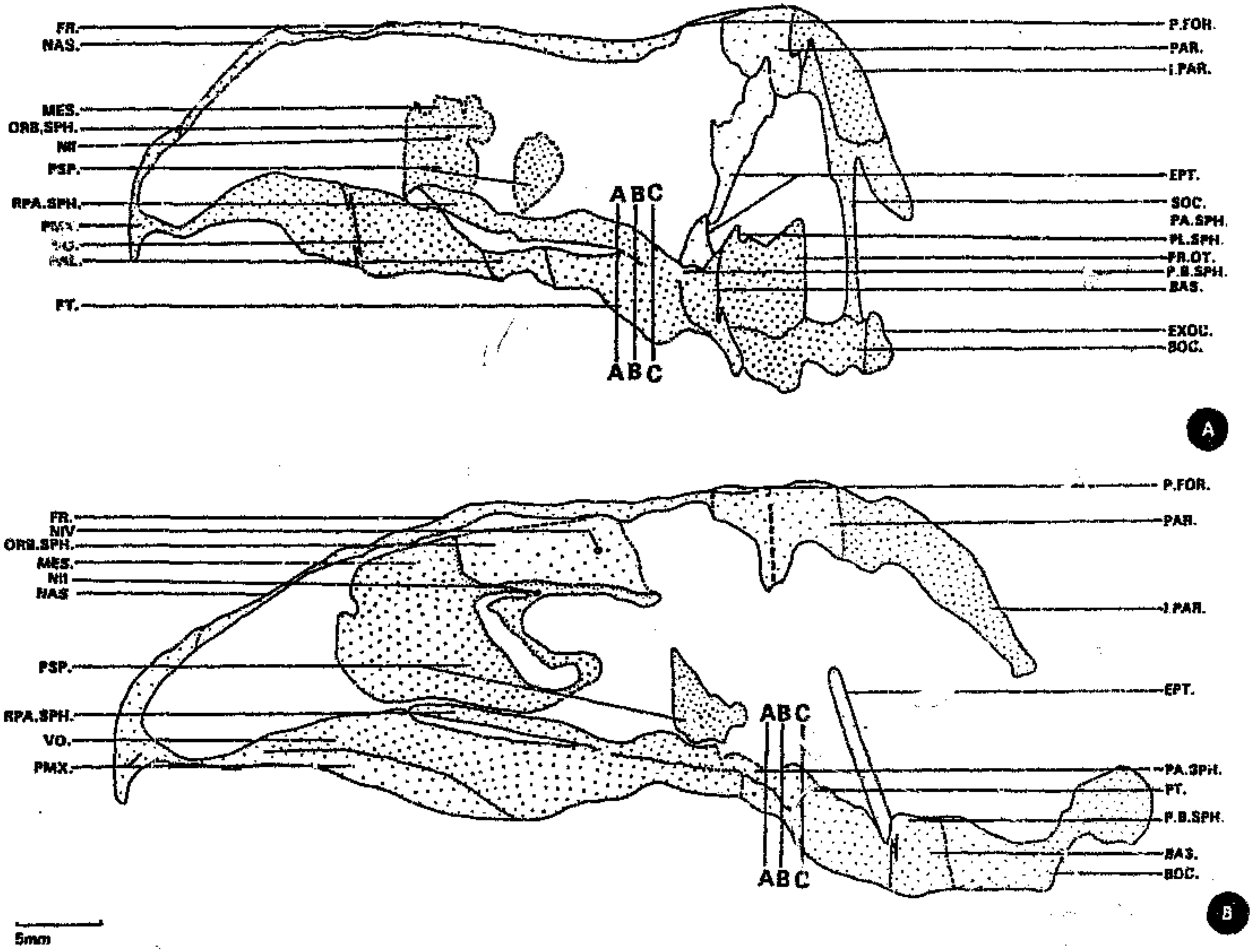


Figure 5: Graphic reconstruction of medial views of sphenethmoid and palatoquadrate complexes of A: BP/1/4386, and B: BP/1/1619.

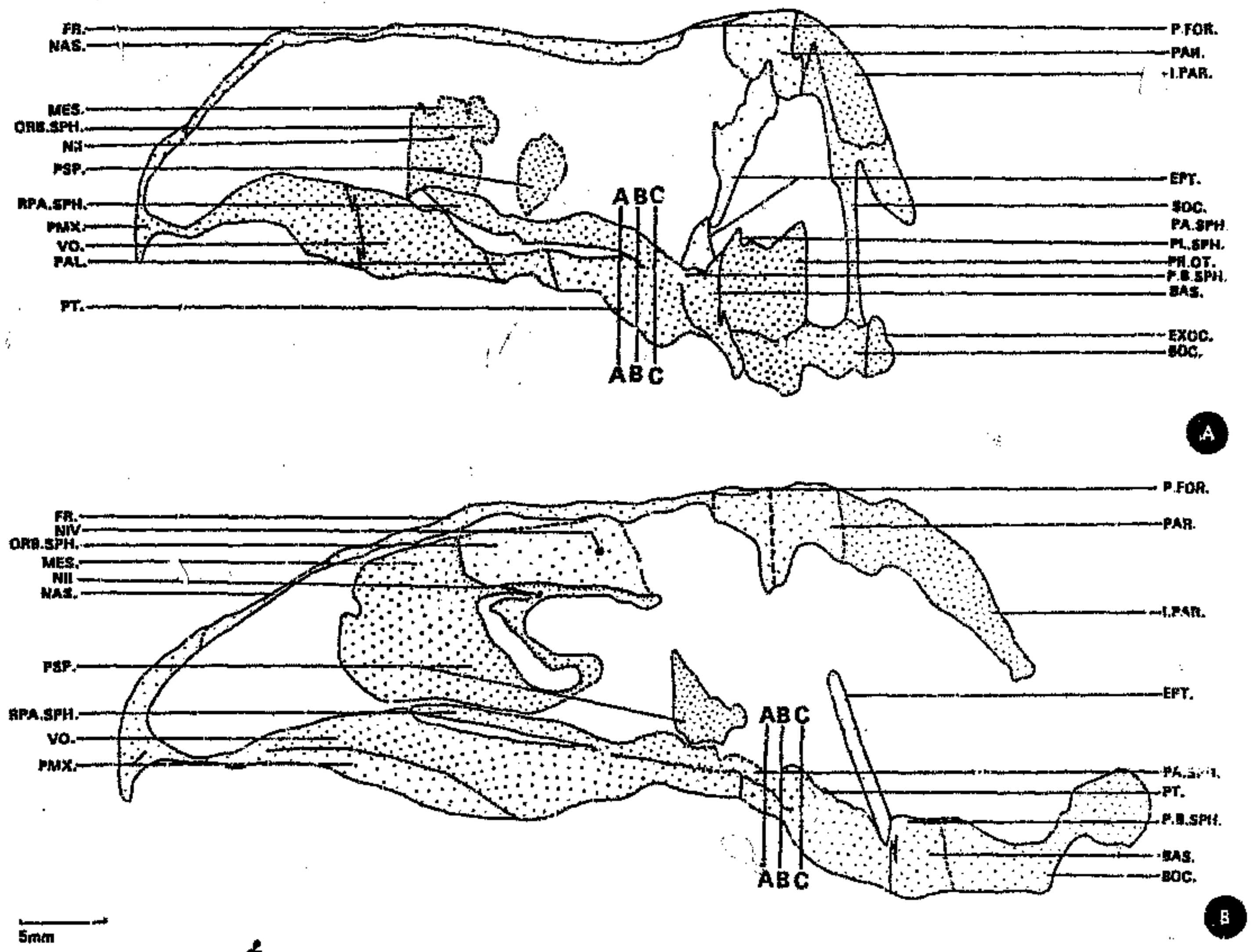


Figure 5: Graphic reconstruction of medial views of sphenethmoid and palatoquadrate complexes of A: BP/1/4386, and B: BP/1/1619.

The premaxilla is clasped by the dorsally extended vomer medially at their suture. A prominent premaxillary ridge is present on the ventral exposure. There are four equally spaced anterior foramina visible in the premaxilla in crossection (Figure 9A). The two lateral foramina are first seen as four foramina that unite posteriorly to form two foramina, and then continue for some distance posteriorly and are situated in ventral triangular protrusions of the premaxilla, these protrusions form the anterior palatal ridges. This part of the premaxilla is se circular in transverse section.

Maxilla.

The maxilla meets the ectopterygoid posteromedially, jugal and palatine posteriorly. The most posterior part of the maxilla is overlain by parts of the ectopterygoid dorsally when viewed in section. Small foramina are present in the maxilla. The maxilla and premaxilla form a dorsomedial groove posteriorly.

Maxillary antrum.

The maxillary antrum forms an inter-osseal maxillary space surrounded by the maxilla, jugal and lachrymal. The maxillary antrum is the bony socket sheathing the root of the canine. The posterior wall of the antrum consists of the jugal and maxilla laterally and lachrymal dorsally, and is excavated to form the labial fossa. This fossa housed

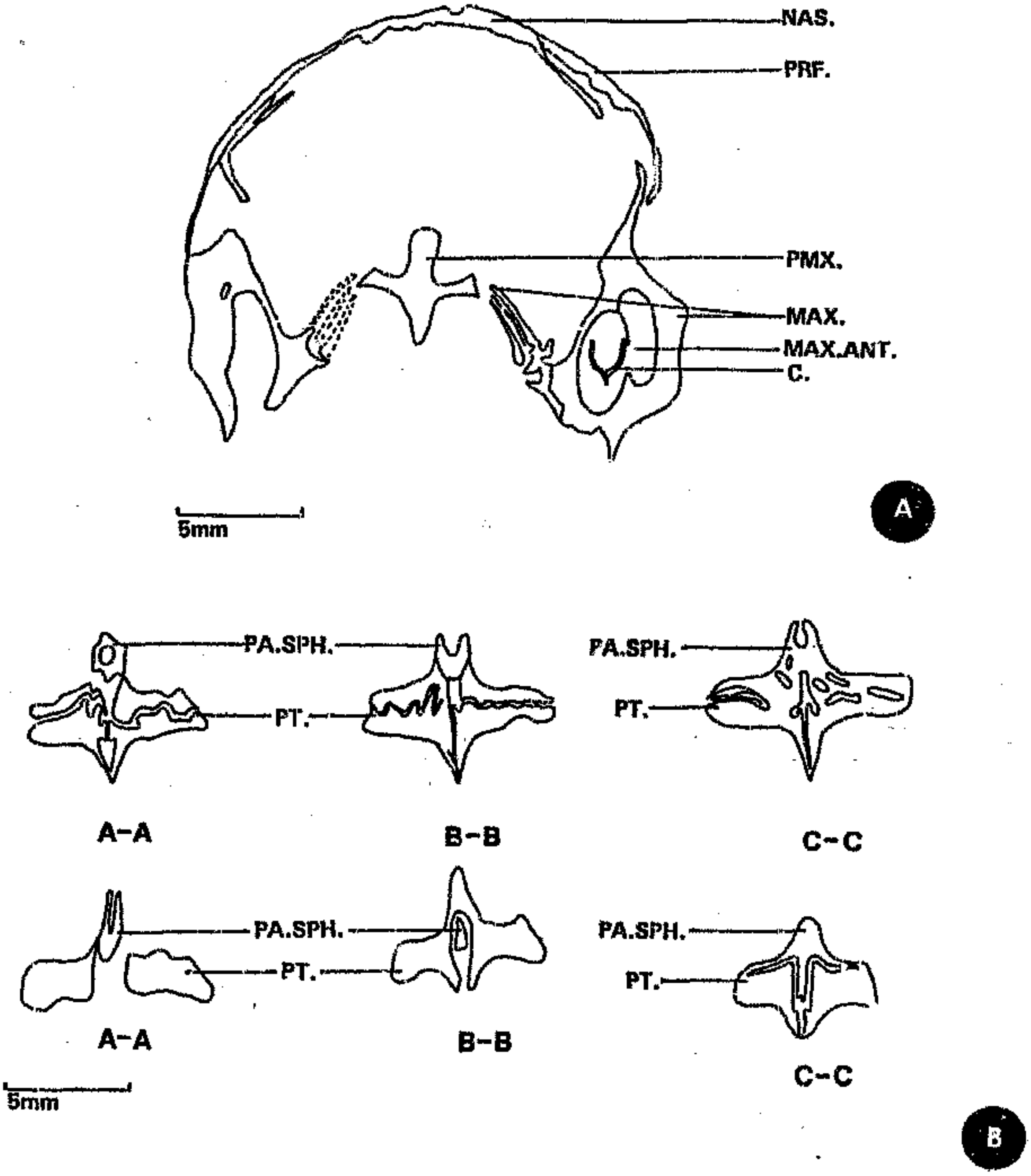


Figure 6: Transverse sections to show,
A: maxillary entrum consisting of two compartments.
B: the parasphenoid-pterygoid suture in BP/1/4386 (top, sections 115, 117 & 119) and BP/1/1619 (bottom, sections 160, 164 & 168).

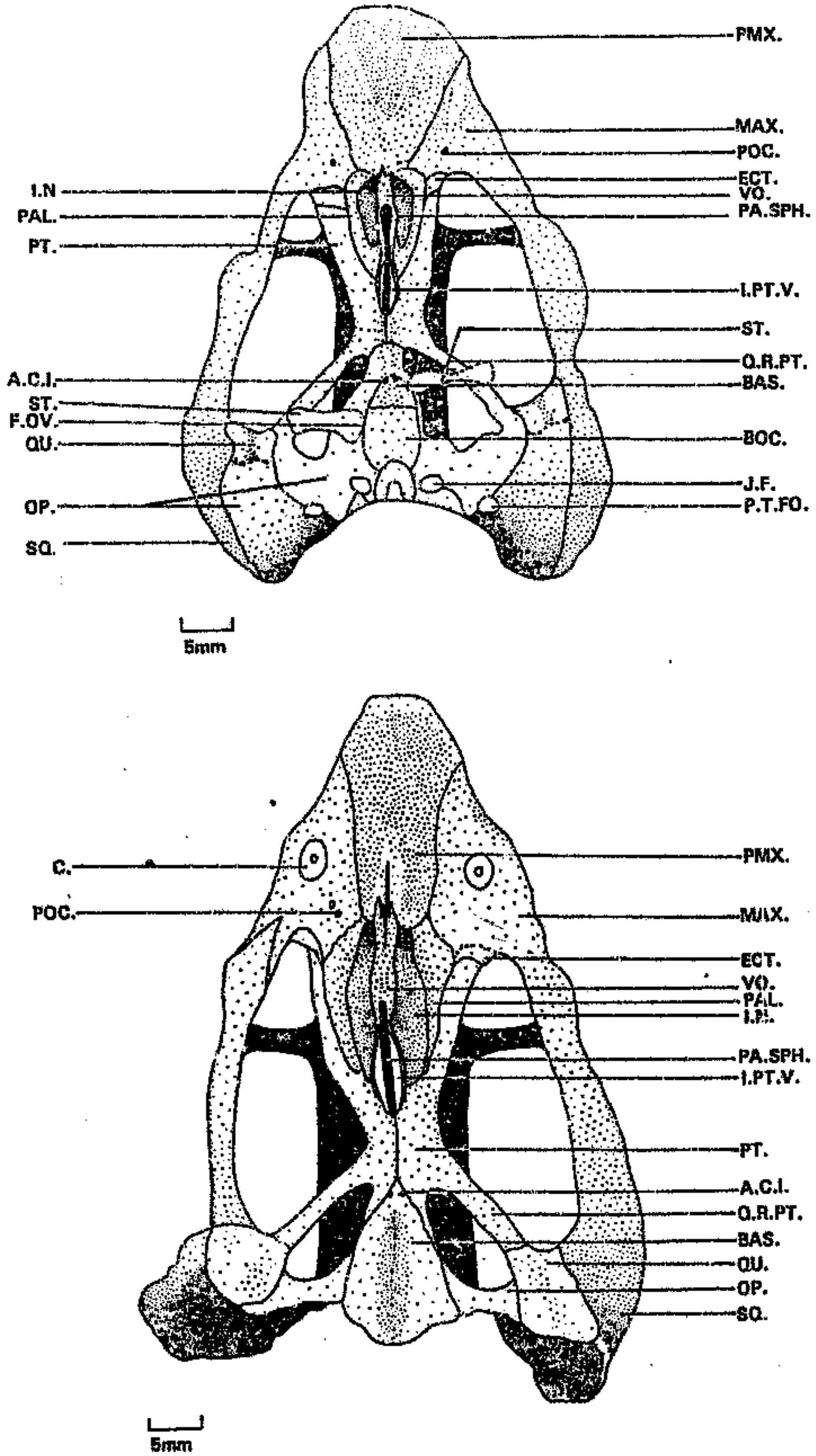


Figure 7: Emydops. Graphic reconstruction of specimen BP/1/4386 (top) and specimen BP/1/1619 (bottom), palatal views.

the maxillary branch of the trigeminal nerve (Ewer, 1961). The antrum consists of two compartments, and the unerupted canine is situated in the compartment nearest to the midline. This compartment opens into the palatal surface anteriorly (Figure 6A).

Dentition:

Right Upper Jaw (Figure 18).

All the postcanine teeth are situated in sockets and only the first tooth is fully erupted. An unerupted canine is present in the maxillary antrum. The first postcanine lies posteroventrally of the canine, and is the biggest. The second postcanine is situated posterodorsally of postcanine one. Replacement postcanine teeth are not visible as the teeth are young, erupting from the front to the back.

Left Upper Jaw (Figure 18).

The canine is situated in the maxillary antrum and had not erupted at this stage. The first postcanine is fully erupted and is situated ventrally of the canine. Postcanine two is situated next to the first, right on the edge of the maxillary rim: it is smaller than the first postcanine. As they are very small teeth, they are probably young erupting teeth.

Vomer (Figure 10).

The vomer borders on the interpterygoid vacuity posteriorly

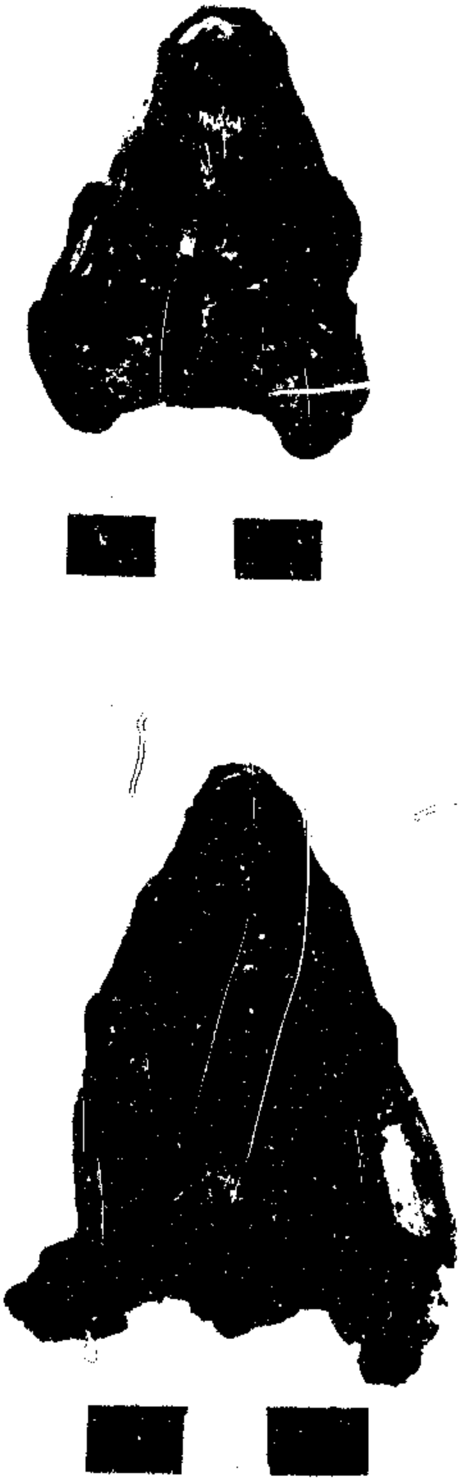


Figure 8: Photographs of palatal views of BP/1/4386 (top) and BP/1/1619 (bottom).

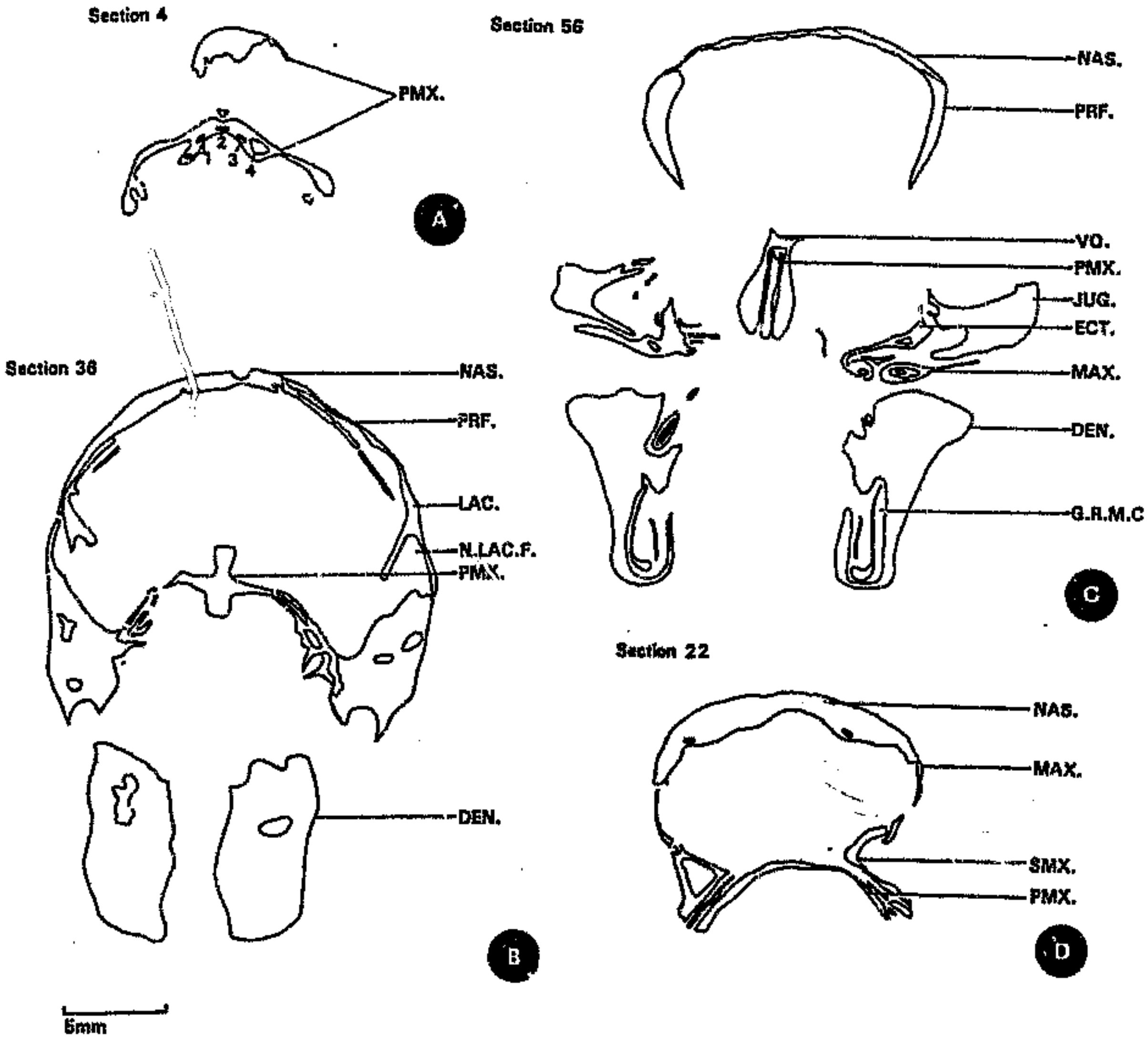


Figure 9: Transverse sections through the snout of sectioned specimens,
A: premaxilla pierced by foramina (BP/1/4386),
B: shape of premaxilla (BP/1/4386) and naso-lachrymal foramen (BP/1/4386),
C: ectopterygoid (BP/1/4386), and
D: septomaxilla (BP/1/1619).

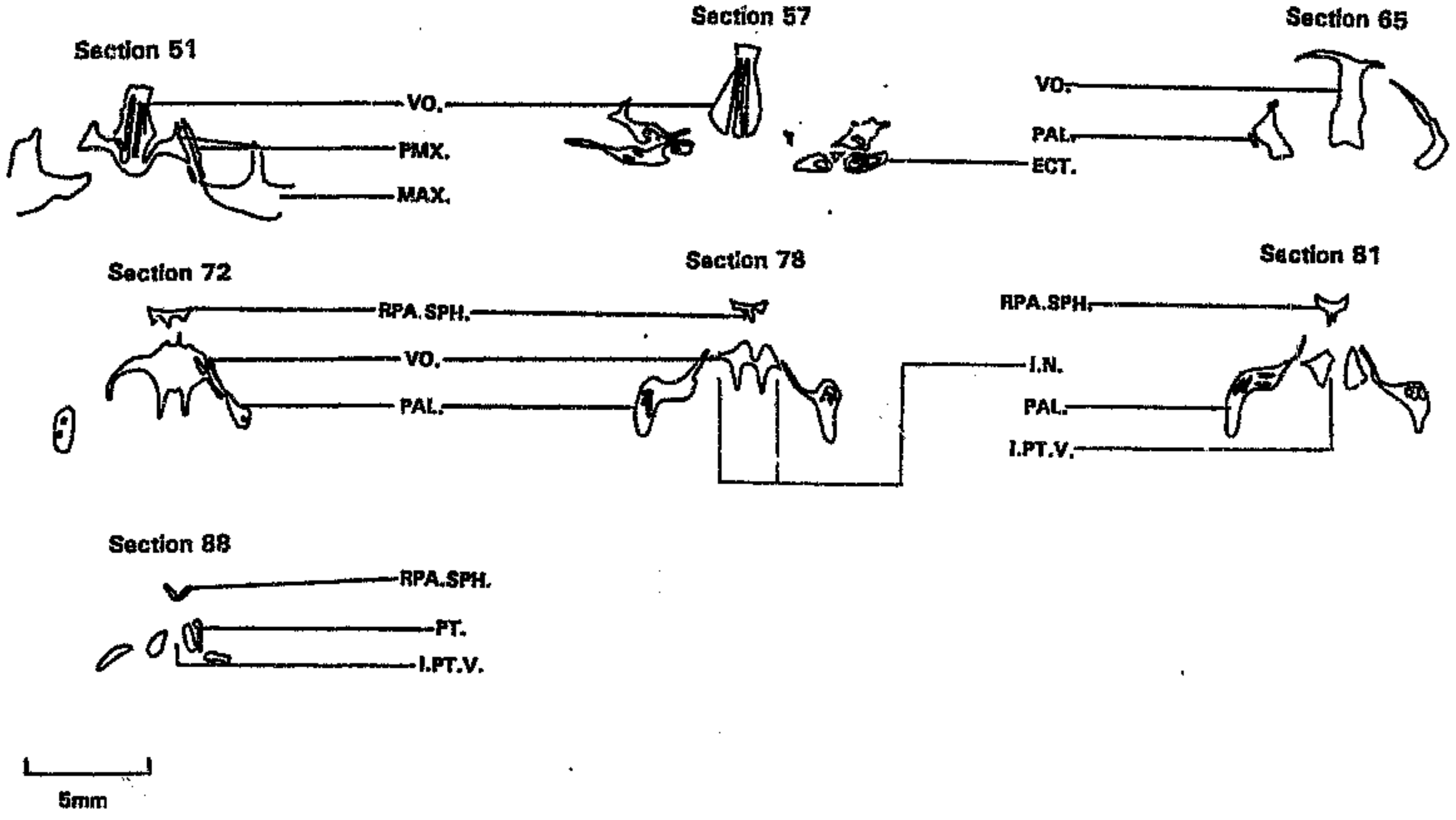


Figure 10: *Emydops*. Specimen BP/1/4386. Transverse sections through the vomer.

and laterally for a short distance. The vomer sutures with the premaxilla anteriorly (section 51) in a long medial suture. The two anterior wings (section 57) form the extensions of the premaxilla and do not continue posteriorly. The vomer is characterised by two dorsolateral wings and one ventral rounded protrusion. At approximately two thirds of its length from the anterior end, the vomer divides into two dorsolaterally projecting flanges (section 65), each of which attaches laterally to the palatine (section 72) and posteriorly to the pterygoid (section 88) to border with the internal nares (section 78). The ventral surface is deeply grooved marking the anterior of the interpterygoid vacuity (section 81). The dorsal surface of the vomer is also grooved (section 72), housing the anterior portion of the parasphenoid rostrum in a loose fit. Posteriorly at the closure of the internal nares the vomers are triangular shaped bones, separated by a medial groove. This medial groove closes off dorsally to form the anterior of the interpterygoid vacuity ventrally.

Palatine.

The palatine meets the pterygoid posteriorly and laterally, the ectopterygoid anteriorly, and the interpterygoid vacuity and internal naris medially. The palatine-pterygoid suture is difficult to distinguish. The palatine is bulbous-shaped ventrally, but thin dorsally in section where its expanded process contacts the vomer. Ventral and dorsal grooves exist anteriorly on the palatine. The palatine meets the posterior border of the premaxilla and is transversely enlarged into a horizontal plate with a concave posterior border.

Ectopterygoid.

The ectopterygoid is seen in section as loose and interconnected islands of bone lying on the dorsal side of the palatine bone (Figure 9C). In section the ectopterygoid is seen to have a suture with the jugal. Both the palatine and ectopterygoid bones have cavities within them and are separated from one another by transverse channels or grooves.

Pterygoid.

The two anterior pterygoid processess enclosing the palatine and interpterygoid vacuity medially are thicker and rounder posteriorly where they fuse in the midline to mark the posterior extremity of the interpterygoid vacuity. This fusion takes place ventrally so that the resulting dorsal groove accommodates the parasphenoid rostrum. The pterygoid has a posterolaterally directed quadrate ramus which meets the quadrate. The pterygoid sutures with the basisphenoid posteriorly and anterior of this suture is the parasphenoid suture with the pterygoid. The two anterior bulbous processess unite to form the middle process of the pterygoid.

Basisphenoid.

The basisphenoid meets the pterygoid anteriorly and the basioccipital posteriorly. The pterygoid-basisphenoid suture is a very intricate suture and is situated on the anterior side of the pila antotica and just posterior of the quadrate ramus of the pterygoid. Anteriorly the basisphenoid is constituted of two parts with a groove or channel medially, then posteriorly the two parts fuse and only a shallow ventral groove remains. The paired carotid canals enter the basisphenoid ventrally, and dorsolaterally emerge together in the small fossa posterior to the vertical presphenoidal plate. The suture of the basisphenoid with the basioccipital is posterodorsally and the deep sella turcica is present here. The pineal body was situated in the sella turcica. The basisphenoid sutures with the prootic dorsolaterally. The basisphenoid forms the floor for the braincase. In section the basisphenoid meets the basioccipital dorsally and the prootics dorsolaterally with the basisphenoid continuing ventrally for a short distance.

Basioccipital.

The basioccipital sutures with the prootics dorsolaterally, and between these the long, ventrally directed auditory canal is contained (Figure 11A). The fenestra ovalis is situated between the basioccipital, stapes and paroccipital process, and the jugular foramen is present between the basioccipital and prootics. Posterolaterally the

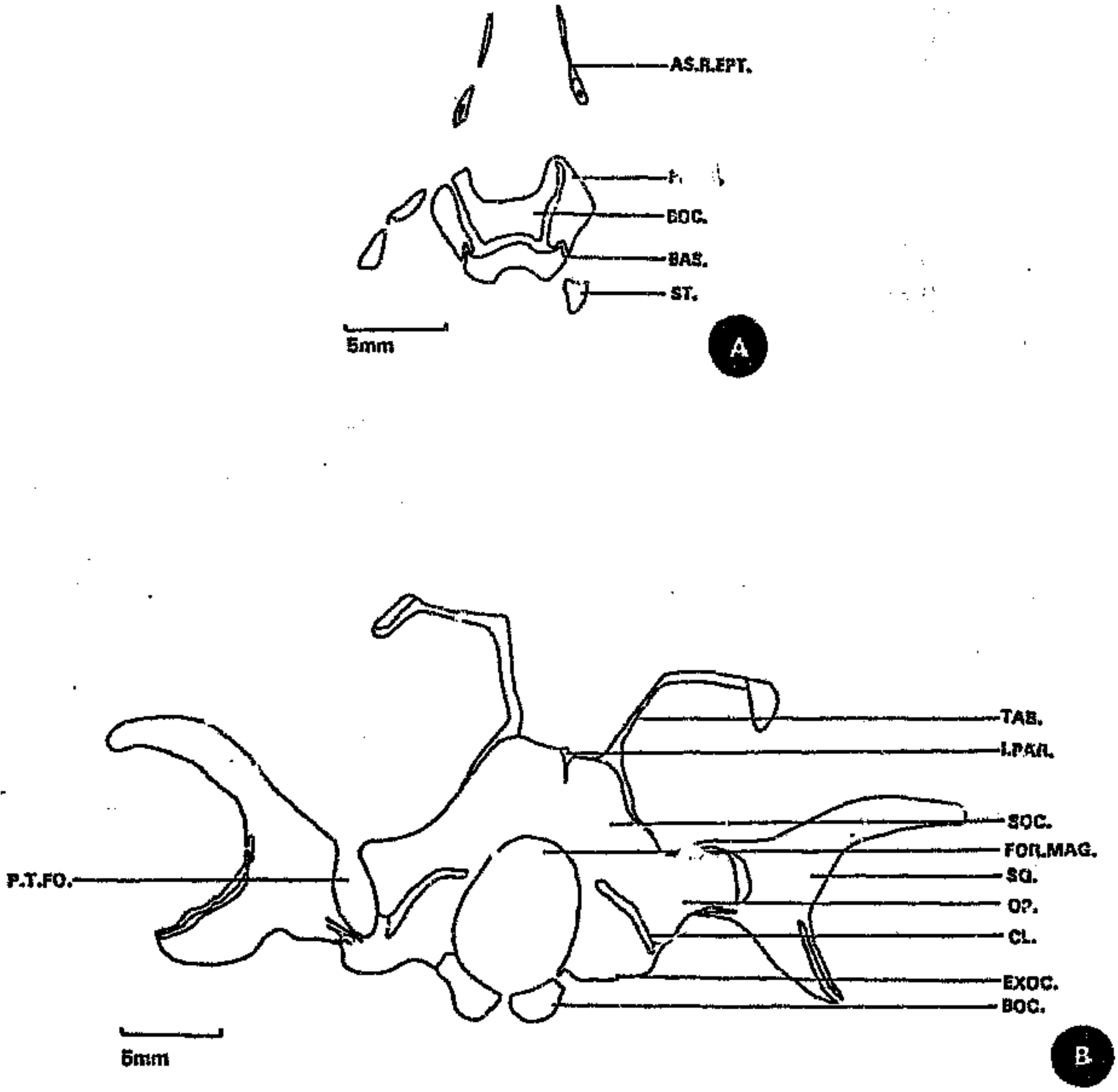


Figure 11: Transverse sections through,
A: basisphenoid-basioccipital suture showing the prootic suture (section 139)(BP/1/4386), and
B: cleft between supraoccipital, exoccipital and paroccipital of the opisthotic (section 179)(BP/1/4386).

basioccipital is fused to the opisthotic. The basioccipital and prootics unite posteriorly. The ventral surface of the basioccipital is marked by the development of the condyles. The basioccipital forms the ventral border of the foramen magnum.

Prootic.

The suture between the prootic and basisphenoid at the level of the pila antotica is clear. The prootics unite to form the slight dorsum sellae. The prootics extend dorsally and at the level of the dorsum sellae it is difficult to distinguish the prootic-basioccipital suture.

Stapes.

The stapes on the left side of the skull is displaced. The distal portion abuts against the quadrate. Half way along its length the stapes exhibits a slightly raised edge ventrally. This might have been the point of attachment of a cartilaginous process or a ligament (Barry, 1963). As in most anomodonts (Barry, 1963), with the exception of <u>Eodicynodon</u> (Rubidge, 1990a) and <u>Cistecephalus</u> (Keyser, 1973a) there is no stapedial foramen. The stapes viewed from the ventral side is broad and dumbbell shaped; in posterior view it is flat and L-shaped with the footplate forming the dorsal expansion. It overlaps the fenestra ovalis.

Inner ear (Figure 12).

The auditory capsule is formed by the prootic anteriorly, the basioccipital medially and the opisthotic posteriorly, while the supraoccipital completes the structure dorsally. The two vertical (anterior and posterior) semicircular canals join dorsally at the crus communis canalium, the anterior vertical canal entering somewhat below the level of the posterior canal. The horizontal semicircular canal joins the posterior vertical semicircular canal just above the posterior ampullary recess. The utriculus is present ventrally of the crus communis canalium. The sacculus has the elongate form characteristic of dicynodonts (Cox, 1959), forming a tube descending to the fenestra ovalis and is contained between the basioccipital, prootic and opisthotic. Internally the dorsal opening of the auditory canal is enlarged to form an auditory vestibule. Behind the vestibule, a groove in the basioccipital leads into the jugular foramen which passes medial to the vestibule. The vestibule contains the utriculus, sacculus and cochlea. The span of the stapes indicates the breadth of the tympanic cavity and the quadrate forms the lateral limits.

<u>The Palatoquadrate Complex</u> (Figure 5A, 16A & 22).

Epipterygoid.

The epipterygoid or columella cranii is T-shaped with its base or footplate (the quadrate ramus of the epipterygoid) resting on the quadrate ramus of the pterygoid. The

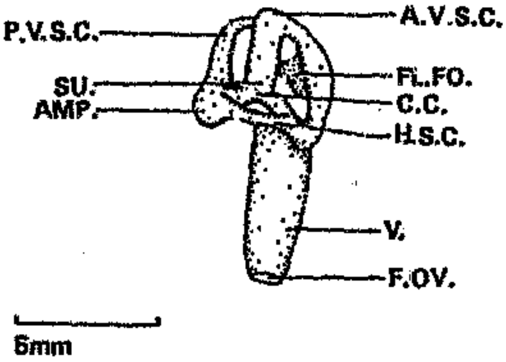


Figure 12: Graphic reconstruction of lateral view of left inner ear of BP/1/4386.

footplate extends anteriorly to the level of the anterior extremity of the quadrate ramus of the pterygoid, but does not extend as far backwards as the quadrate ramus of the pterygoid. The columella is a long narrow structure which extends dorsally to meet the medial surface of a ventral process of the parietal (parietal lamina) at a point lateral to the pineal foramen. The epipterygoid is pierced by an anteroventral foramen for N V (ramus opthalimicus) that runs posterodorsally (Durand, 1991) (Figure 16A).

Quadrate and quadratojugal.

The quadrate and quadratojugal are indistinguishably fused. The quadrate is in the shape of an inverted Y, thus forming sliding articular surfaces for the reception of the lower jaw. There is a distinct quadrate foramen between the quadrate and quadratojugal, possibly transmitting a nerve to the lower jaw (Cluver, 1971). The quadratojugal meets the squamosal dorsally and the quadrate meets the paroccipital process of the opisthotic medially as seen in section. The medial surface of the quadrate bears a smooth facet for the reception of the posterior end of the quadrate ramus of the pterygoid.

<u>Occipital and Otic Regions</u>. (Figure 14 & 15).

The braincase is formed by the exoccipital posteriorly and ventrally, the basioccipital and basisphenoid ventrally, the paroccipital process of the opisthotic and prootics

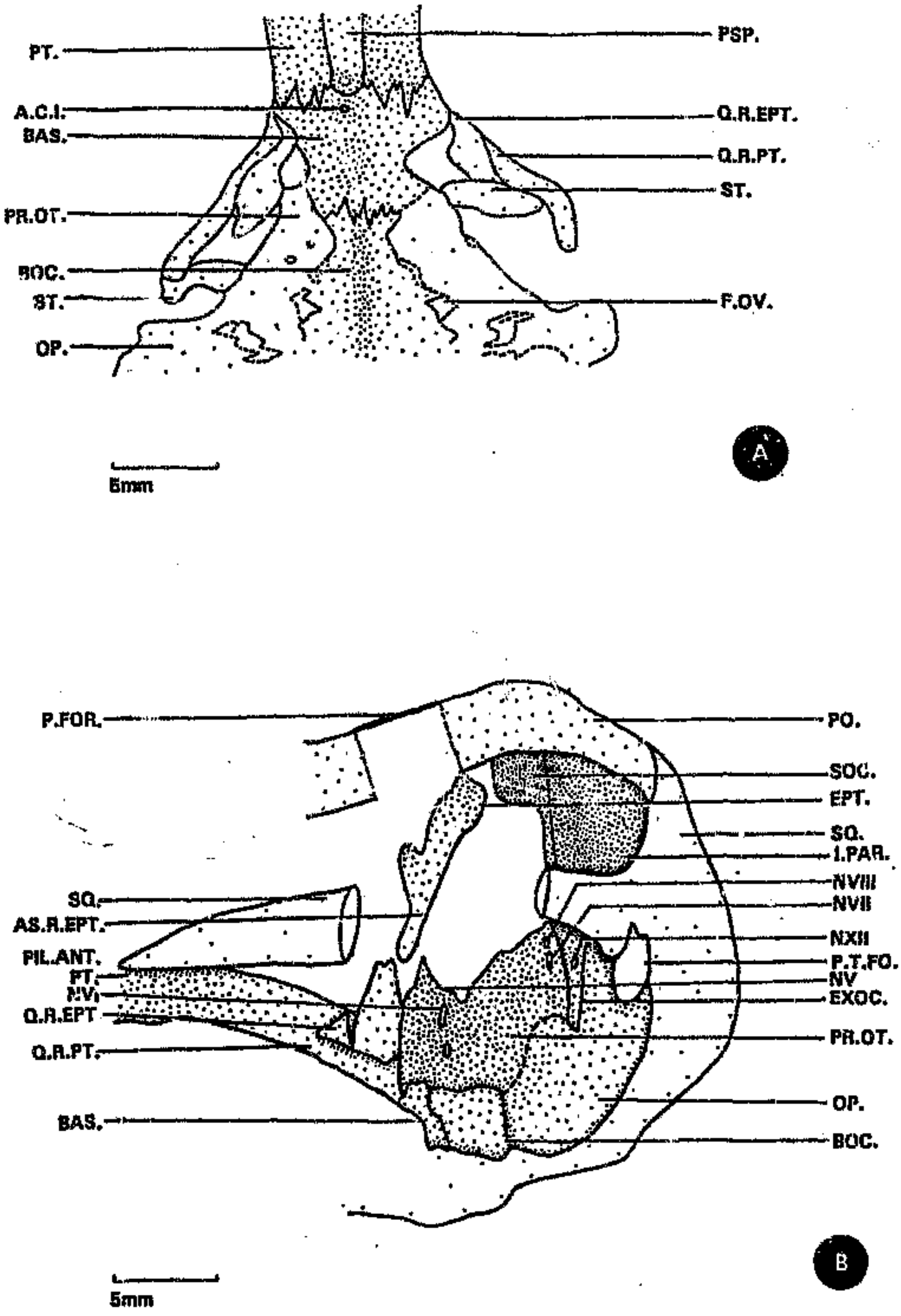


Figure 13: Graphic reconstruction of,
A: posteroventral view of neurocranium (BP/1/4386), and
B: left temporal region and epipterygoid of (BP/1/4386).

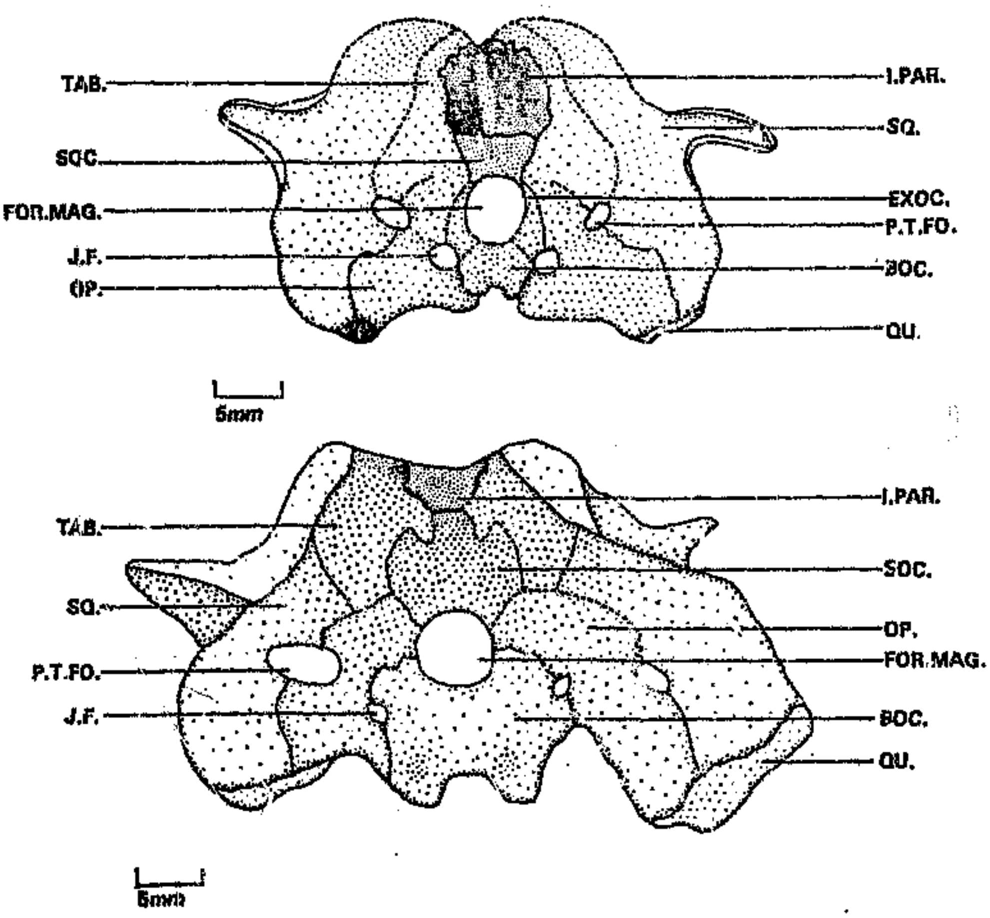


Figure 14: *Emydops*. Specimen BP/1/4386 (top) and specimen BP/1/2619 (bottom), occipital views prior to grinding.

laterally and the supraoccipital dorsally.

Interparietal.

The interparietal has a contact with the parietal dorsally, the tabular laterally, and ventrally with the supraoccipital. A transverse sinus is visible between the interparietal and supraoccipital (Figure 16B).

Exoccipital.

The exoccipital is visible in section and sutures with the basioccipital and opisthotic ventrally and laterally, and contacts the foramen magnum laterally. It is difficult to distinguish the contact between the prootic and exoccipital. Floccular recesses are visible on the medioventral side of the exoccipital. The dorsal contact of the exoccipital to the supraoccipital is not visible and it may be fused. The exoccipital is pierced by the mediodorsal hypoglossal foramen. The exoccipitals form the occipital condyle. Dorsally the exoccipital terminates on the occipital surface as a process for articulation with the proatlas. The exoccipital borders onto the jugular foramen dorsally and medioventrally.

Opisthotic and prootic.

Both the opisthotic and prootic are distinguishable. The large jugular canal (N IX,X,XI and jugular vein) lies between the exoccipital and opisthotic. The opisthotic

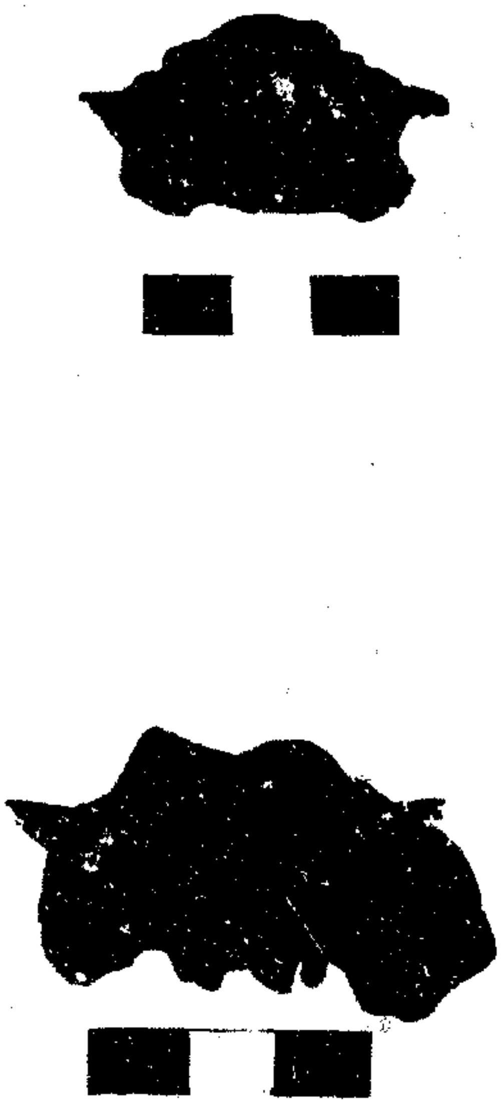


Figure 15: Photographs of occipital bones of BP/1/4386 (top) and BP/1/1619 (bottom).

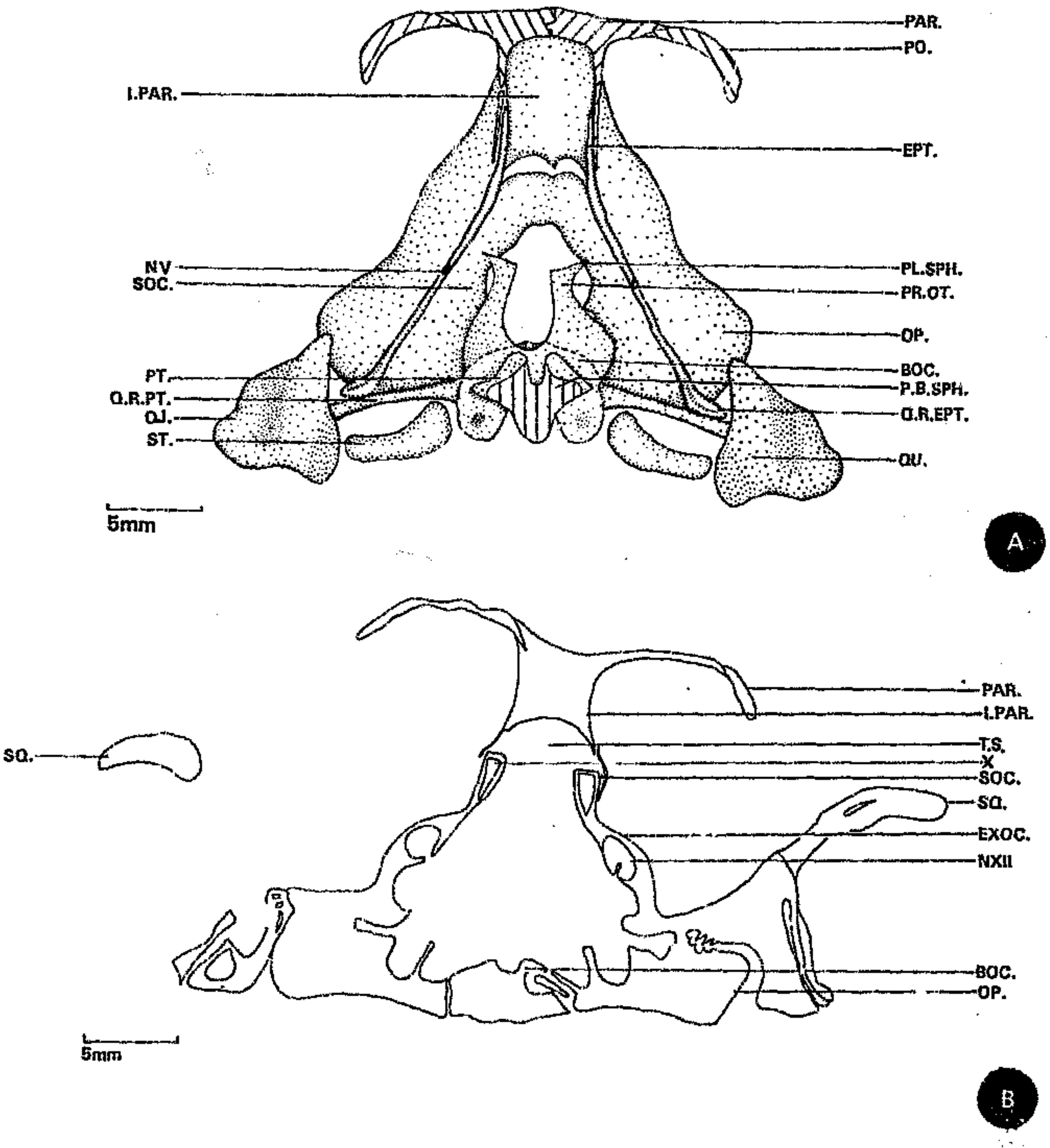


Figure 16: A: Graphic reconstruction of anterior view of palatoquadrate complex, and
B: transverse section 169 showing the supraoccipital cavity (labelled X) of BP/1/4386.

forms the medial and ventral borders of the post temporal fossa and meets the jugular foramen and exoccipital laterally, and abuts against the quadrate laterally. A cleft is present between the supraoccipital and the anterodorsal process of the prootic, and also between the supraoccipital, exoccipital and opisthotic (Figure 11B).

Supraoccipital.

The supraoccipital is in contact with the upper half of the foramen magnum and is pierced by a dorsal cavity, probably for veins draining the deep structures of the head (Figure 16B). The tabular has a medial suture with the supraoccipital. The supraoccipital sutures with the opisthotic ventrally, and has a short contact with the parietal dorsally.

Tabular.

The tabular is very small and thin. The tabular sutures with the squamosal ventrally and laterally, but this is not clear on the occipital exposure.

Squamosal.

The squamosal is the biggest bone on the occiput. A ventral process of the squamosal forms a wedge between the anterolateral side of the quadrate and on the medial side of the paroccipital process. The squamosal meets the tabular, post temporal fenestra and opisthotic medially, and the quadratojugal ventrolaterally and the quadrate ventrally.

Lower Jaw. (Figure 17).

The lower jaw consists of the the dentary, angular, surangular, splenial, prearticular and articular bones.

Dentary.

Anteriorly the left and right dentary bones are fused at the symphysis. The dentary meets the surangular posteroventrally just behind the last dentary tooth. The dentary caps the anteriormost of the surangular for quite a distance before the surangular is visible on the dorsal surface of the jaw (Figure 17B). The dentary bone is very spongy and is the largest of the bones in the lower jaw, taking up more than half of the length of the lower jaw. It is pierced anteroventrally by a pair of canals probably nutrient foramina for bloodvessels to the horny beak. On the anterodorsal side of each ramus of the lower jaw, is a rounded depression, referred to as the dentary table. A short groove is present on the dentary labiad of the teeth which is also situated in a groove that runs parallel to the dentary groove. The dentary groove is short and extends the length of the postcanine row. The lateral dentary shelf is not very prominent.

Splenial.

The dentary meets the splenial posteroventrally and between

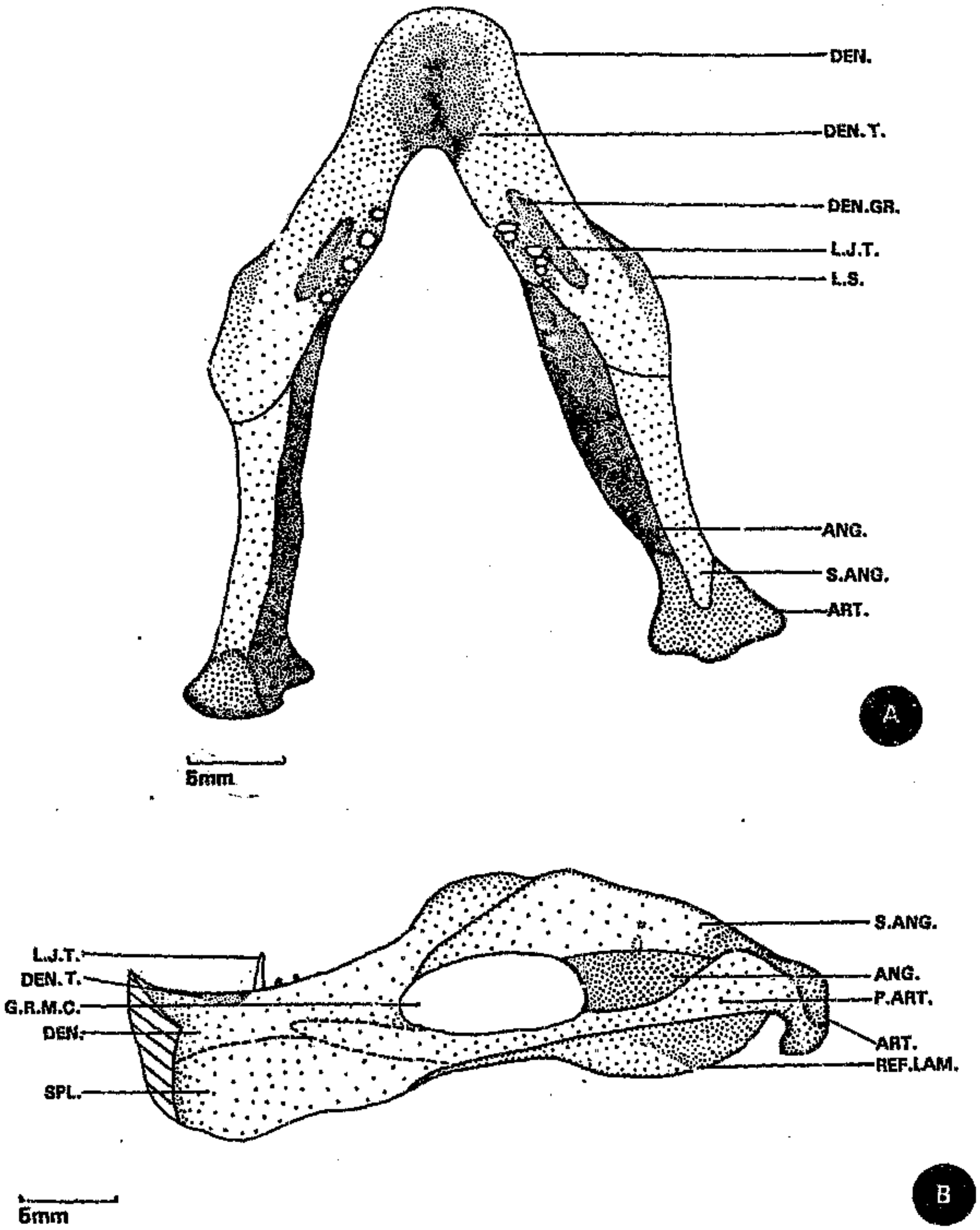


Figure 17: <u>Emydops</u>. Specimen BP/1/4386. Graphic reconstruction of,
A: dorsal view of lower jaw, and
B: medial view.

them the Meckelian groove is contained. The splenial overlies the angular posteroventrally and meets the prearticular posterodorsally.

Surangular.

The surangular, in section, is an almost circular bone. The surangular enlarges posteriorly and projects downwards on the medial side of the angular and lies along the lateral surface of the angular. The surangular is in contact with the prearticular on the ventrolateral and ventral sides. The surangular extends between the angular and prearticualar on the medial side of the jaw, but can only be seen in section. In section at the posterior articulating end of the lower jaw the surangular is present on the lateral side of the articular.

Angular.

The angular is a U-shaped bone anteriorly where it is attached to the dentary and W-shaped posteriorly. A process forming the angular notch is present lying on the outside leg of the W. The angular is situated on the lateral side of the lower jaw and forms the ventral and posterior borders of the mandibular fenestra and a lateral contact with the prearticular and is also fused to it at its base. The angular has a reflected lamina and a horizontal canal on its lateral side

Preearticular and articular.

The prearticular is indistinguishably fused to the articular. The Meckelian sulcus is present between the surangular, angular and prearticular. The articular contacts the quadrate of the upper jaw by two articulating facets. The prearticular becomes thinner as it extends posteriorly and extends anteriorly as a long thin medial bone to the level of the dentary teeth.

Dentition:

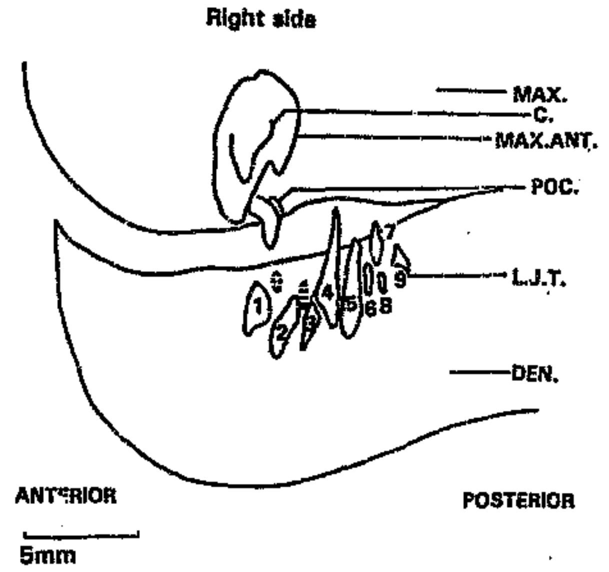
The teeth of most reptiles are not static, but are constantly being replaced. Hopson (1964) illustrated that dicynodonts have back to front waves of replacement in odd- and even-numbered tooth series. Resorbtion of an old root continues until its crown is shed and only a thin crescent of its root remains within the jaws. At this point, the young tooth is about to erupt. The upper teeth had a functional relationship with the lower jaw such as the lower teeth had with the palate (Crompton & Hotton, 1967). The lower jaw teeth are drawn backwards as the jaw closes on the food. Crompton and Hotton (1967) have described the dicynodont jaw adductor musculature in detail. See also King <u>et</u> <u>al</u>. (1989).

Right side (Figure 18)

Nine dentary teeth are visible in section. The first dentary tooth is not fully erupted and is situated lingually of the second. The second tooth is also not fully erupted and is situated lingually of three. Dentary tooth two is preceded by the partially resorbed roots of a tooth that previously occupied this position. Dentary tooth three is unerupted and is preceded by the partially resorbed roots of a tooth that previously occupied this position. Dentary teeth two and three are situated in very deep sockets. Dentary tooth four is fully erupted. Dentary tooth five is erupted. Dentary tooth six is not erupted. Dentary tooth seven is erupted. Dentary tooth eight is unerupted and separated from the unerupted small tooth nine by a bony partition.

Left side (Figure 18).

The first dentary tooth is small and unerupted and is situated in a deep socket. The second dentary tooth is not fully erupted and is situated more dorsally than one. There is an open socket between teeth two and four for dentary tooth three. Dentary tooth four is unerupted and it is situated lingually of five. Dentary tooth five is unerupted. Lingually to it are the remains of a resorbed tooth. Dentary tooth six is erupted and is situated next to the fully erupted seven which is situated lingually to eight. Dentary tooth eight is erupted. Dentary tooth nine is unerupted and is followed by an open socket for tooth ten. Eleven is the same size as tooth nine and is unerupted. Only tooth six has resorbed roots preceding it.



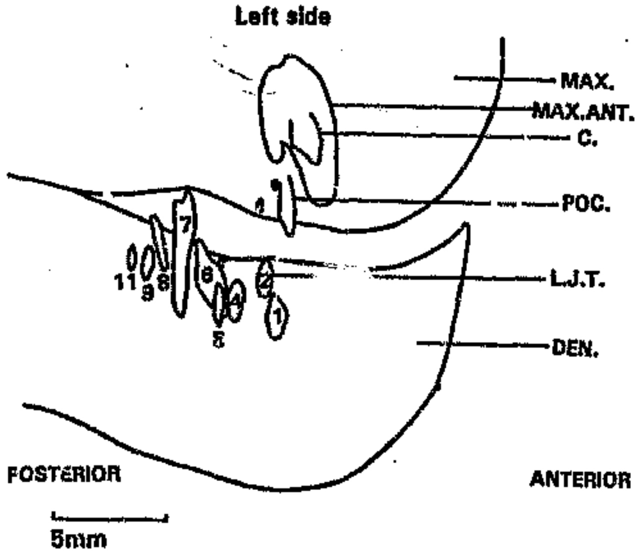


Figure 18: Graphic reconstruction of maxillary and mandibular dentitions of BP/1/4386.

The dentary teeth do not interact directly with the postcanine teeth of the upper jaw as they are situated further back than the upper postcanines to facilitate the sliding action of the jaw. The dentary teeth are situated in a groove in the dentary bone. Posterior serrations are not visible, but they should be present on the young teeth.

3.1.2 Emydops Specimen no. BP/1/1619

Only the features that differ from BP/1/4386 will be described here.

Snout and Skull Roof (Figure 1, 2, 3 & 4).

The septomaxilla has a dorsal exposure due to preparation damage on the nasals (Fig 9D). It is situated posterior of the the premaxilla and sutures with the maxilla ventrally and laterally in the posterior wall of the external naris; it has a triangular shape with a medial canal, running anteroposteriorly for the whole length of the septomaxilla. The medial canal opens into the nasal cavity medially for a short distance. The most anterior part of the septomaxilla contacts the premaxilla ventrally. Posteriorly it is separated from the premaxilla by a thin sheet of maxillary bone. The horizontal component of the septomaxilla presumably formed a roof for the anterior portion of the Jacobsons organ. A longitudinal groove is present on the dorsal side of the septomaxilla where the maxilla has an interdigitating contact with the septomaxilla.

The parietal laminae extend downwards from anterior to the pineal foramen to form a channel for the pineal body or nerve which is completed by the ascending rami of the epipterygoids that suture on the inner surface of the parietal laminae (Figure 5B).

Sphenethmoid Region (Figure 5B, 19, 20A & 26).

The septosphenoid (orbitosphenoid and mesethmoid) is roughly rectangular in lateral view with a large median cavity posteriorly and a small median notch anteriorly. The presphenoid is wider posteriorly and has a posterior extension situated loosely on the parasphenoid. The septosphenoid sutures with the frontal dorsally and the presphenoid with the vomer anteroventrally. The anterior mesethmoid does not have a contact with the frontal in the form of a suture. The orbitosphenoid is housed in small recesses of the frontal dorsally, and clasps the presphenoid ventrally. A pair of longitudinal foramina run anteroposteriorly through the orbitosphenoid. The dorsal foramen is for N II and the ventral foramen for N IV. The canal running through the presphenoid meets up with N II. The notch for the optic foramen (N II) is present on the orbitosphenoid. Foramina are also present on the presphenoid.

The rostroparasphenoid or processus cultriformis contacts the vomer anteroventrally and the presphenoid dorsally. It

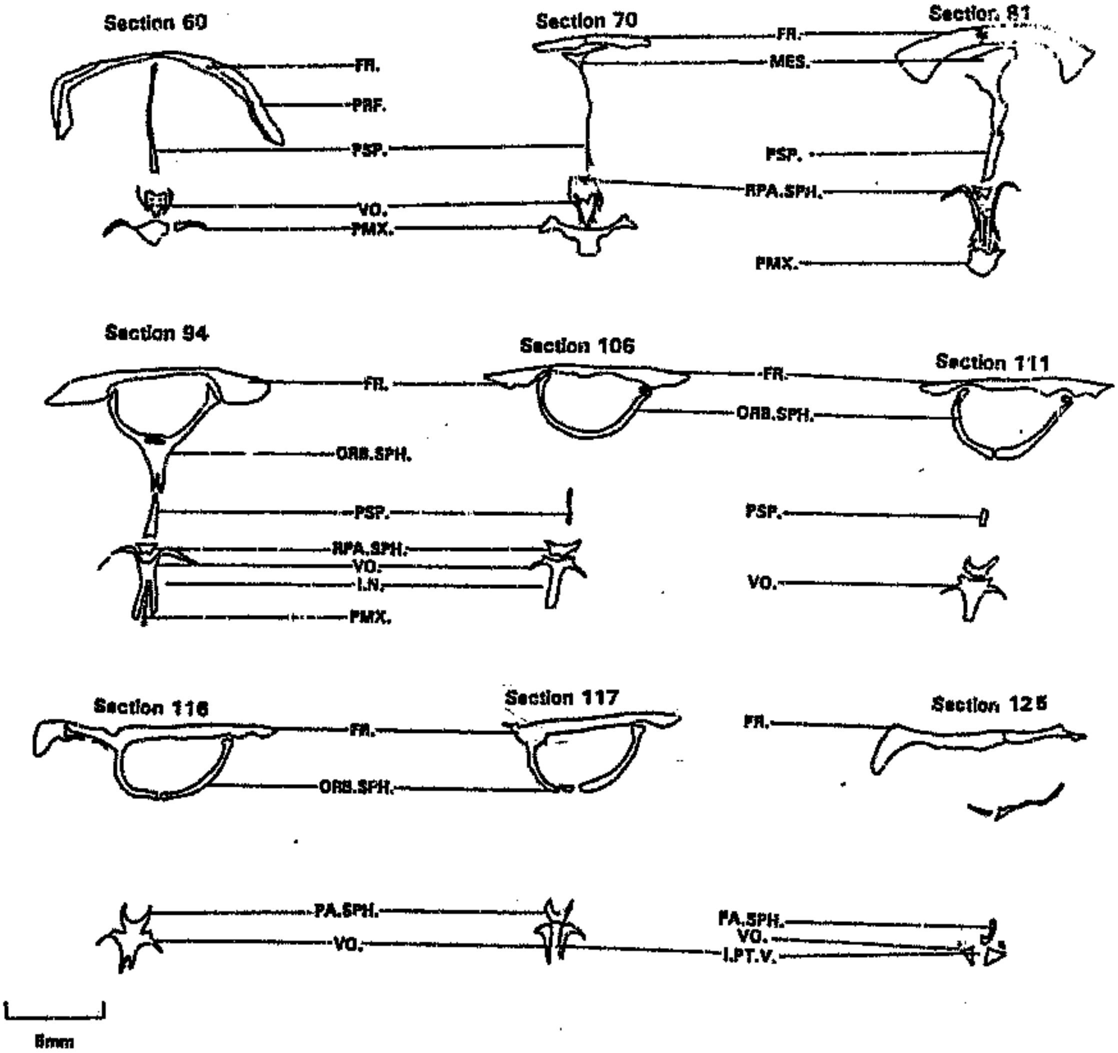


Figure 19: Transverse sections through the vomer and sphenethmoid regions of BP/1/1619.

is grooved dorsally and ventrally. The parasphenoid sutures with the vomer posteroventrally and is then posterior of this suture fused to it for a short distance. The parasphenoid sutures posteriorly with the anterior of the pterygoid (Figure 6B) and is fused to the posterior of the pterygoid and basisphenoid. The parasphenoid is grooved dorsally and is considered to have housed a continuous cartilaginous interorbital septum in Cistecephalus (Keyser, 1973a).

The Palate (Figure 7 & 8).

Anterior palatal ridges are absent and the premaxilla is grooved laterally of the median premaxillary ridge. The canine is at the erupting stage so that only the tip is visible, it fills the whole of the maxillary antrum to where the jugal sutures with the maxilla. Two not fully erupted postcanines are present. The first postcanine is larger and thus considered to be the elder.

Vomer.

The vomer (Figure 19) is first seen anteriorly in section as a small triangular bone situated on the dorsal surface of the premaxilla with which it has an interdigitating suture at the posterior end of the premaxilla. The vomer is attached anteriorly to the premaxilla for only a short distance and posteriorly of this it is not attached to the premaxilla (section 60). The four foramina piercing the vomer are arranged as in the corners of a square. There are two thin rod-like unattached bones (see below) on either side of the vomer which enclose the rostroparasphenoid dorsally of the main body of the vomer (section 70, Figure 20A, labelled X). The rostroparasphenoid and vomer are both grooved, the vomer dorsally and the rostroparasphenoid ventrally. Further posteriorly the vomer has an interdigitating suture with the premaxilla medially (section 81). Posteriorly of this suture the vomer is thinner (section 94). The two rods on either side unite with the body of the vomer and form the floor of the internal nares (section 106), and suture with the palatine on the inside of the internal nares.

Palatine.

The palatine sutures with the ectopterygoid dorsally as seen in section. The palatine meets the interpterygoid vacuity posteriorly and not laterally.

Pterygoid.

The presence of a groove on the dorsal surface of each pterygoid, which extends anteriorly from the front of the epipterygoid up to the pterygoid-ectopterygoid suture, is considered to have housed an anterior cartilaginous extension of the epipterygoid. This is based on the fact that the anterior and posterior edges of the footplate are sharply truncated (Cluver and King, 1983). The two

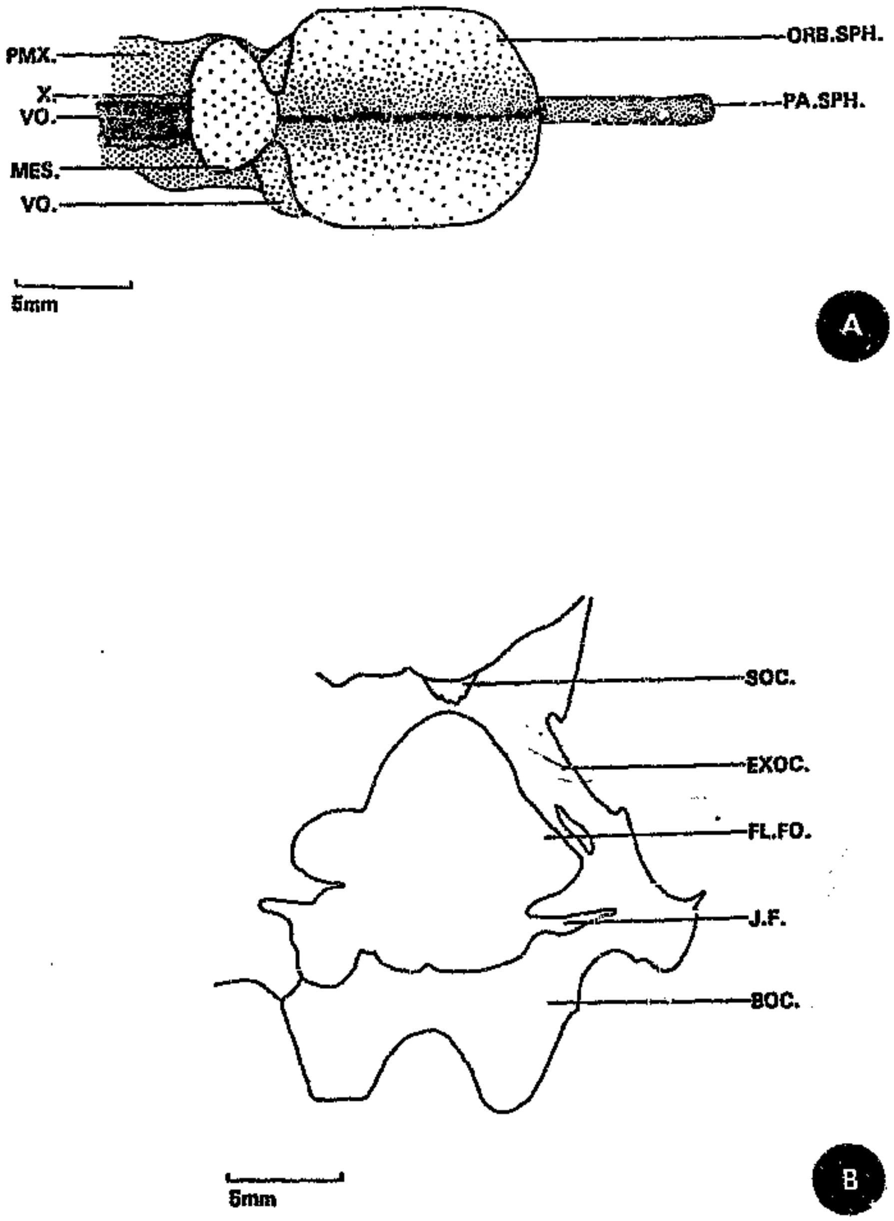


Figure 20: A: graphic reconstruction of dorsal view of sphenethmoid region, and
B: transverse section 213 to show the floccular fossa of BP/1/1619.

pterygoid bones at the posterior end of the interpterygoid vacuity has a median groove. It is here that the parasphenoid sutures with the pterygoid (Figure 6B) so that only a ventral groove is left. The pterygoid-basisphenoid suture is hardly noticeable.

Basisphenoid.

The basisphenoid sutures with the pterygoid anteriorly and with the basioccipital posteriorly; as this suture of the basisphenoid to the basioccipital is in a transverse plain it is difficult to distinguish in the sections.

Periotic and basioccipital.

The pleurosphenoid can be clearly seen on the pila antotica. The prootic is fused to the basisphenoid and basioccipital. The dorsum sellae and sella turcica are not distinct. A floccular fossa can be seen as a recess on the inside of the exoccipital (Figure 6B).

<u>The Palatoquadrate Complex</u> (Figure 3).

The suture of the epipterygoid with the downward extended process of the parietal lamina is visible anterior and dorsal to the suture of the footplate of the epipterygoid and the quadrate ramus of the pterygoid. The footplate is small and does not extend posteriorly beyond the pterygoid-basisphenoid suture. The quadratojugal is situated on the outside of the quadrate; it is much smaller. A ventral depression is formed where the quadrate and quadratojugal are fused and lateral to this are two ventral convexities, these form the facet for articulation with the articular of the lower jaw.

Occipital and Otic Regions (Figure 14 & 15).
A definite opisthotic-squamosal suture exists. The tabular does not seem to meet the post temporal fossa, but is bigger than in BP/1/4386. The exoccipital sutures are not easy to distinguish.

3.2 Bloodvessels and Nerves

Bloodvessels:
Some of the important foramina that could be traced are; The foramina present on the premaxilla, maxilla and around the root of the canine and on the dentary. They are thought to be nutrient foramina. These foramina are usually associated with the development of the horny beak, are thought to have the same function in dicynodonts as in Chelonia (Watson, 1960).

It is possible that the large septomaxillary foramen served to transmit bloodvessels and nerves into the nostril or housed a branch of the mucous gland that passed through to reach the Jacobsons organ (Wible *et al*, 1990).

The main supplier of blood to the brain are the anterodorsal internal carotid arteries and their foramina are visible in the basisphenoid (Figure 7). In the primitive reptilian pattern the internal carotids turn upwards into the braincase through paired foramina in the basisphenoid, they continue forward on to the underside of the sphenoid region and gives off palatine arteries. As there is no stapedial foramen the internal carotid artery would have passed forward just below the stapes as in modern reptiles (Romer, 1956). Just in front of the foramen for the internal carotid artery is another small foramen through which the palatine branch of nerve V II left the braincase.

The prootic incisure behind the pleurosphenoid served as a passageway for the root of the trigeminus nerve and the vena cerebralis media to exit into the cavum epiptericum, which housed the trigeminal ganglion (Durand, 1989). The vena cerebralis media joined the vena capitis lateralis beside the ganglionated root of the trigeminus (O'Donnoghue, 1920). The jugular foramen allows the posterior cerebral vein, the jugular vein as well as nerves IX, X and XI, to escape from the braincase.

The post temporal fenestra probably transmitted a branch of the vena capitis dorsalis from the occipital area through to the lateral supraoccipital fossa into the venous sinus between the interparietal and supraoccipital (Figure 16B). The vena capitis dorsalis probably formed a connection with the vena cerebralis media and the resulting vein passed through the pterygo-paroccipital foramen to join the vena capitis lateralis (Durand, 1991). There is a prominent groove leading down to the quadrate on the lateral side of the squamosal. This could be associated with the bloodflow of the post temporal fenestra (Cluver, 1971).

The lateral head vein (vena capitis lateralis) might have passed through a channel created between the stapes and the paroccipital process. The vena capitis lateralis passed back above the basipterygoid process, between the epipterygoid laterally and the pila antotica medially and through the pterygo-paroccipital foramen to leave the skull through the channel between the stapes and the paroccipital process, along with the hyomandibular branch of the facial nerve (Cluver, 1971). A foramen is also present between the quadrate and quadratojugal bones, and the mandibular vein may have left the skull through this foramen (King, 1990).

A cleft is present between the paroccipital process and the supraoccipital in <u>Emydops</u> (Olson, 1944) and <u>Diictodon</u> (Agnew, 1958) and it is believed that it was associated with the pineal circulation (Agnew, 1958). This cleft in BP/1/4386 is present between the supraoccipital, exoccipital and paroccipital process (Figure 11B).

Nerves:

The olfactory nerve (N I) is associated with the vomeronasal organ. It is impossible to determine the exact positions of the optic (N II), occulomotor (N III) and trochlearis (N IV) nerves. Both the oculomotor and trochlearis nerves are associated with the eye muscles, as well as the abduscens (N VI). The notch for the optic foramen (N II) is present on the orbitosphenoid as also the foramen for N IV (Figure 5).

The trigeminal nerve (N V) emerges from the braincase through the prootic incisure into the cavum epiptericum, which housed the trigeminal ganglion (Figure 13B). It has three major rami; the ramus opthalmicus ran through the epipterygoid foramen, the ramus maxillaris and ramus mandibularis passed posterior to the processus ascedens into the temporal cavity (Presley & Steel, 1976). The ramus mandibularis passed downward to enter the Meckelian fossa of the lower jaw and ran forward in the Meckelian canal. The ramus opthalmicus passed mesial to the processus ascedens of the epipterygoid into the orbit and the maxillaris emerged from the braincase, and together with the opthalmicus passed outward behind the epipterygoid, the maxillaris then ran along the upper jaw (Durand, 1991). In Emydops the epipterygoid is pierced by an anteroventral foramen for N V that runs posterodorsally (Figure 16A) and the labial fossa housed the maxillary branch of the trigeminal nerve.

The exit of the abduscens nerve (N VI) frequently pierces the lateral part of the dorsum sellae (Figure 13B)(Romer, 1956). The root of this nerve usually exits through a foramen in the base of the anteroventral process of the prootic (pila antotica). The fascialis nerve (N VII) gives off a small palatine ramus and also enters the Meckelian fossa in the middle ear region. Its root exits through its foramen between the central and ventral ridges of the prootic halfway between the internal auditory meatus and the incisura prootica (Figure 13B)(Romer, 1956).

The acoustic (or vestibulocochlear N VIII) (Durand, 1991) nerve enters into the inner ear through single or double foramina in the sidewall of the braincase (Romer, 1956). There is no separate foramen for the glossopharyngeal nerve (N IX) and both the vagus (N X) and accessorius (N XI) emerge through the jugular foramen. The hypoglossal (N XII) nerve has three roots which may emerge by two or three foramina through the exoccipital from the level of the floor of the braincase. In Emydops only one pair of these foramina was observed. The hypoglossal nerve would have exited into the jugular canal through its medial wall, near its external aperture (Durand, 1989).

4. DISCUSSION

The two serially ground specimens were compared to each other to emphasise their differences. They showed only minor morphological and sutural differences and none of these is generically important, but could be significant at the species level. Differences are mostly due to the state of preservation and skulls being of different sizes.

The sphenethmoid region and palatoquadrate complex of BP/1/4386 and BP/1/1619 have been described in 3.1.1 and 3.1.2 and are combined here to form a composite description of these features in Emydops.

A comparative study was undertaken to show that amongst dicynodonts there are differences which may be generically significant and the individual specimens were chosen because they were the only small dicynodonts in which the internal structures were described in enough detail for purposes of comparison.

The various features of BP/1/4386, BP/1/1619 and other small dicynodonts are summarised in Appendix B. The sutures mentioned are not very important as they are variable depending on the age and size of the specimen due to the closure of the sutures with age.

4.1 Comparison of the two serially ground specimens

The type specimens of Emydops were examined to become familiar with the genus. Features that both studied specimens (BP/1/4386 & BP/1/1619) have in common are: the palatine meets the posterior border of the premaxilla and is transversely enlarged into a horizontal plate with a concave posterior border. The anterior through-like extension of the interpterygoid vacuity on to the vomerine septum is short. The interpterygoidal crest is weak and not continued on to the ventral surface of the anterior pterygoid ramus.

The sphenethmoid region of specimen BP/1/4386 is not well preserved and the extent of the septosphenoid (mesethmoid, presphenoid and orbitosphenoid) cannot be determined with certainty. The mesethmoid and orbitosphenoid of BP/1/1619 show as a vertical plate with the mesethmoid lying anterior of the lateral wings of the orbitosphenoid. The foramina for N II and N IV can be seen in the orbitosphenoid (Figure 5).

The presphenoid is the most ventral part of the median vertical plate of the sphenethmoid and clasps the orbitosphenoid dorsally. It does not extend as far posteriorly as does the orbitosphenoid. The presphenoid consists of two parts and the second part lies unattached further posteriorly than the orbitosphenoid and is much smaller than the anterior part of the presphenoid. This part could have been attached to the sphenethmoid by cartilage, but could also have been part of the parasphenoid and not the presphenoid. The presphenoid is in contact with the rostroparasphenoid (processus cultriformis) anteroventrally. The parasphenoid is in turn in contact with the vomer ventrally and the pterygoid posteriorly in an extensive suture.

Both the vomer and rostroparasphenoid are grooved dorsally and ventrally as if cartilage was present to form a continuous interorbital septum as the parasphenoid is also grooved dorsally. At the premaxilla-vomer suture which is interdigitating, the premaxilla is clasped by the vomer.

Specimen BP/1/4386 displays the basisphenoid suture with the basioccipital posterodorsally and the basioccipital sutures with the prootic dorsolaterally. These sutures should be present in specimen BP/1/1619, but they are not distinguishable. The basisphenoid and parasphenoid are fused in both specimens. The sella turcica of BP/1/4386 is deep with a slight dorsum sellae and the pleurosphenoid of the pila antotica is indistinct. The sella turcica and dorsum sellae of specimen BP/1/1619 are not distinct and a well ossified pleurosphenoid is present on the pila antotica.

The prootic and opisthotic are apparently fused in

BP/1/1619, but in BP/1/4386 a distinct suture is present. A second notch lies dorsal to the prootic incisure, usually at the junction of the periotic and supraoccipital and it is believed to be associated with the venous system of the cranium (Olson, 1944). This could only be seen in BP/1/4386 and was not preserved in BP/1/1619.

The parietal laminae extend downward from the skull roof anterior of the pineal foramen to form the lateral laminae that meet the ascending rami of the epipterygoids on their mesial surface in BP/1/1619 and in BP/1/4386 these laminae only extend downwards from the level of the middle of the pineal foramen (Figure 5). The posterior part of the footplates of the epipterygoids are weakly developed and short and therefore do not reach the quadrate.

BP/1/1619 is larger (Appendix D) than BP/1/4386 and as expected the canine has erupted, where in BP/1/4386 the canine is still unerupted in the maxillary antrum. BP/1/1619 being the larger has two erupted postcanines and BP/1/4386 only one on each side.

The palates of the two specimens correspond except for the fact that the palatine in BP/1/1619 does not extend as far back as in BP/1/4386 and is excluded from meeting the interpterygoid vacuity by the vomer.

The dentary shelf is not very prominent. The anterior symphysial region of the dentary is drawn up in a sharp cutting edge and a shallow groove is present on the dorsal edge of the dentary behind the symphysis.

4.2 Comparison with other small dicynodonts

It is evident from the King (1990) cladogram, reproduced here as Figure 21 that the genera used for comparative purposes are in different families.

Eodicynodon is the most primitive, with paired vomers, paired premaxillaries and strongly developed pterygoid processes not found in any of the other genera. *Emydops* differs from *Eodicynodon* (Barry, 1974) in lacking these primitive features. The paired premaxillaries in *Eodicynodon* (Barry, 1974) point to the ancestral condition as is the condition in the primitive *Venyukovia* and *Otsheria*. The fusion of the premaxillaries in all other Beaufort Group Dicynodontia is a synapomorphic feature of Dicynodontia.

Pristerodon has a large and leaf-like palatine which receives the bite of the lower jaw teeth and the postcanines are arranged in a short row in a depression at an angle to the longitudinal axis of the palate. The postcanines of *Emydops* are reduced in number relative to more primitive dicynodonts and not situated in a depression.

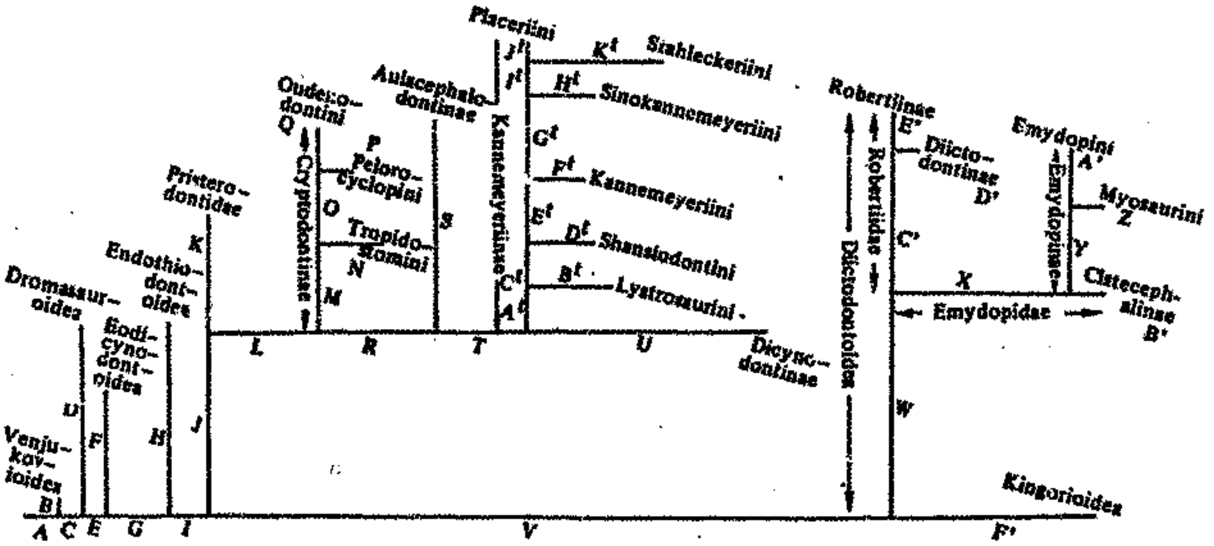


Figure 21: A cladogram expressing the relationships within the dicynodonts (King, 1990).

Tropidostoma (Keyser, 1973b) has been redescribed as *Cteniosaurus platyceps* (Cluver and King, 1983) and is not included on the cladogram. In King (1988) *Tropidostoma* and *Cteniosaurus* were placed in the same Tribe Tropidostomini as they were found to be related. *Tropidostoma* (Keyser, 1973b) lacks the narrow intertemporal region, where the parietal exposure lies within a groove. A postcaniniform crest is also present. It shows very advanced features such as a more extensive secondary palate and development of nasal bosses. *Tropidostoma* is included because of its more complete description. A narrow intertemporal region is only present in *Diictodon*.

Cistecephalus shows many advanced features such as the loss of the floccular fossa, and sella turcica, and interpterygoid vacuity. This can all be attributed to the shortening of the skull (Keyser, 1973a). The palate is advanced and there is a sutural contact between the epipterygoid and parietals.

Due to the pronounced overlap of the ventrolateral portion of the palatal surface of the premaxillary by the maxillary the palatal surface of the premaxillary is relatively narrow in *Eodicynodon* (Barry, 1974) and *Emydops* (this study). This relationship is reversed in *Pristerodon* (Barry, 1967).

Posteromedially the palatal portion of the maxillary participates in the formation of the lateral walls of the choana through the formation of a wedge which inserts between the premaxillary and the palatine of Pristerodon (Barry, 1967). This is absent in Emydops (present work), Tropidostoma (Keyser, 1973b) and Cistecephalus (Keyser, 1973a) and present in Eodicynodon (Rubidge, 1985) and Diictodon (Agnew, 1958).

Behind the premaxillary-vomer contact of Eodicynodon (Barry, 1974) the palatal surface of the anterior third of the vomers form a pair of relatively broad, rounded ridges. Immediately behind this region the vomers curve upward above the general palatal level and the ridges now become thin and blade-like with a V-shaped groove developing between them. In this way the vomers form the anterior and anterolateral borders of the interpterygoid vacuity as in most dicynodonts. Termed the intervomero-interpterygoidal vacuity by Barry (1974).

At approximately two-thirds posteriorly along its length the vomer in Eodicynodon (Barry, 1974), Emydops, Pristerodon (Barry, 1967) and Cistecephalus (Keyser, 1973a) splits into two flanges, each of which attaches laterally to the palatine and posteriorly to the pterygoid, thus forming the median and dorsal walls of the internal nares. In median section the vomer shows as a triangular bone with the apex of the triangle pointing ventrally in Pristerodon (Barry, 1967). From the apex to the point where the vomer splits, the ventral surface is deeply grooved as if it housed a cartilaginous structure. This is certainly also true for _Emydops_, _Pristerodon_ (Barry, 1967) and _Diictodon_ (Agnew, 1958). The dorsal surface of the plate-like median portion of the vomer is also grooved in most dicynodonts, housing the anterior portion of the parasphenoid rostrum in a close fit only in _Pristerodon_ and in a loose fit in the studied specimens.

The sphenethmoid complex consists of a median bony interorbital plate roughly rectangular in shape extending from the anterior rim of the orbit to the postorbital bar. The anterior part forms the septosphenoid (mesethmoid and presphenoid) and the posterior region the orbitosphenoid. The orbitosphenoid has two narrow, slightly convex wings that covered the olfactory lobes from above. This is standard for all dicynodonts, but various authors use different terminology. Broom (1926), Agnew (1958), Barry (1967) and Cluver (1971) explain the homology of the elements comprising the sphenethmoid complex and the terminology used by different authors in detail.

The wings of the orbitosphenoids of _Cistecephalus_ (Keyser, 1973a) extend as far back as the parietals and therefore cover a very much larger area relative to the size of the skull.

A short distance behind the interorbital plate of _Eodicynodon_ (Barry, 197 and _Emydops_ (BP/1/4386 & BP/1/1619) the dorsal portion of the parabasisphenoid bone ends abruptly as if it butted against an unossified portion of the interorbital plate, maybe a cartilage wall of the braincase. In the studied specimens this bone does not suture to the parasphenoid.

Barry (1967) found in _Pristerodon_ a suture dividing the parasphenoid rostrum horizontally and states that the shape of the posterior part of the rostrum lends support to the conclusion that it consists of two fused elements, the rostrum parasphenoidale ventrally and either a rostrum basisphenoidale or rostrum praesphenoidale dorsally. There is no sutural evidence for this in _Emydops_, but it can possibly not be ruled out for _Emydops_ and _Eodicynodon_ (Barry, 1974).

The parasphenoid in _Emydops_ (Olson, 1944), _Cistecephalus_ (Keyser, 1973a) and _Diictodon_ (Agnew, 1958) is fused to the basisphenoid posteriorly and the parabasisphenoid is in sutural contact with the basioccipital. The periotic overlies this complex and makes contact at the parabasisphenoid-basioccipital suture. The parasphenoid of the studied specimens is also fused to the basisphenoid, but sutures with the pterygoid just anteriorly to the quadrate ramus of the pterygoid. Olson (1944) also reported the fact that the rostral portion of the parasphenoid passed between the pterygoids and much of the junction must be between the pterygoid and parasphenoid. This may be a synapomorphic feature of Emydops as in all other dicynodonts the parasphenoid only passes between the pterygoids.

The epipterygoid of dicynodonts is T-shaped, with both the vertical and posteriorly directed horizontal limbs well developed. The vertical limb, or columella is relatively thin and extends upwards and slightly forwards towards the ventrally directed lamina extending from the ventral surface of the parietal.

The epipterygoid in Eodicynodon (Barry, 1974 and Rubidge, 1990a) is unusual in that its base is more expanded than in dicynodonts in general. The footplate extends from a point in line with the lateral flanges of the pterygoid to the root of the quadrate ramus of the pterygoid where it covers more than half the dorsal surface of the quadrate ramus of the pterygoid and extends to within 2mm of the quadrate. The region from the front of the epipterygoid up to the pterygoid-ectopterygoid suture, is considered to have housed an anterior cartilaginous extension of the epipterygoid (Cluver & King, 1983).

In most dicynodonts the footplate is only weakly developed. In Cistecephalus (Keyser, 1973a) and Diictodon (Agnew, 1958) the footplate of the epipterygoid is continued backwards for almost half the length of the quadrate ramus of the epipterygoid. It is long in Pristerodon and Diictodon.

In the studied specimens (BP/1/4386 and BP/1/1619) the footplate of the epipterygoid does not extend anteriorly beyond the quadrate ramus of the pterygoid and does not cover it far posteriorly. In Tropidostoma the quadrate ramus of the epipterygoid does not extend along the quadrate ramus of the pterygoid and is short. In Tropidostoma the anterior extremity of the footplate of the epipterygoid is fused to the basisphenoid and the descending parietal plates are also fused to the expanded dorsal extremities of the epipterygoids. In Cistecephalus (Keyser, 1973a) the ventral plates of the parietals are split in order to clasp the broad dorsal expansions of the epipterygoids.

In Pristerodon and Diictodon the angle of the epipterygoid is connected to the basisphenoid by a short basipterygoid process. These are also described for Emydops (Olson, 1944) where the epipterygoid is believed to suture with these processes. The basipterygoid process could not be observed in Cistecephalus. It does look as if the epipterygoid touches the basisphenoid slightly at the pterygoid-basisphenoid suture in BP/1/4386 and there is a possibility that the basipterygoid process was present in BP/1/1619 but is not preserved.

As in *Pristerodon* (Barry, 1967) a well-demarcated groove is formed between the quadrate and quadratojugal, the latter being attached at its ventral and dorsal extremities in *Eodicynodon* (Barry, 1974). Barry (1965) postulated that there could have been a cartilaginous link between the quadrate and epipterygoid, as the posterior of the footplate almost reaches the quadrate. Barry (1967) believed that a great part of the stapes is suturally attached to the quadrate, but no evidence of this could be found in *Emydops* or other dicynodonts.

There is a prominent groove leading down to the quadrate on the lateral side of the squamosal on the occipital surface in *Emydops* (BP/1/1619) and *Cistecephalus* (Keyser, 1973a) and Keyser concludes that this groove was associated with the cervical musculature rather than with the function of hearing.

The basisphenoid of *Emydops* (Olson, 1944) contains the shallow sella turcica, comprises the indistinct dorsum sellae and basipterygoid processes, and is penetrated by the canals for the internal carotids. In *Diictodon* (Agnew, 1958) the sella turcica is merely a shallow depression situated immediately behind the carotid canal, and a distinct dorsum sellae is absent. The sella turcica is placed behind the anteroventral process of the periotics and is more posteriorly placed in *Cistecephalus* (Keyser, 1973) than in any other dicynodont.

Sutures between the opisthotic and prootic were not distinguishable in Tropidostoma (Keyser, 1973b), Cistecephalus (Keyser, 1973a), Diictodon (Agnew, 1958), Emydops (Olson, 1944) and BP/1/1619, the sutures were found in Eodicynodon (Barry, 1974), Pristerodon (Barry, 1967) and BP/1/4386.

As in Pristerodon the opisthotic in Eodicynodon carries a strongly developed ridge-like opisthotic process/tympanic process which laterally tapers into a posteriorly directed point. Present in most dicynodonts such as Emydops (studied specimens) and Tropidostoma.

Rubidge (1990a) postulated that the position of the post temporal foramen which is present on the medial side of the boundary between the supraoccipital and squamosal bones in line with a point about half way up the foramen magnum is "an extremely important" characteristic of Eodicynodon. In other dicynodonts the tabular and exoccipital take part in the formation of the side wall of the post temporal foramen, but it is also present in that position in Emydops (present work) and Pristerodon where the tabular and exoccipital take part in the side walls of the post temporal fossa, but can only be seen in section.

The interparietal of Eodicynodon (Barry, 1974) is not situated between the parietals as in Emydops and therefore the term postparietal is used. Barry (1974) described a medial postero-ventrally directed longitudinal ridge in Eodicynodon that divides the postparietal into bilateral concave elements. This is also present on the interparietal of Emydops (BP/1/4386), but it does not show a pronounced midline groove or cleft extending along the length of the bone, reflecting the ancestral paired condition as in Eodicynodon. There is however a median interparietal suture present in Emydops (BP/1/4386) and Cistecephalus (Keyser, 1973a), but it is not always visible on the occipital surface.

The groove in the dorsal side of the dentary of Pristerodon is more extensive than in Emydops (BP/1/4386). The shelf that projects laterally from the dorsal side of the surangular and merges posteriorly with the short retro-articular process of the articular of Eodicynodon (Rubidge, 1990b) is not present in Emydops.

The comparisons show that characters dependant on sutural patterns are not reliable to use on the cladogram, such as the dorsum sellae, sella turcica and the pleurosphenoid. These characters are also dependant on good preservation and the age of the specimen. A character that can be included in a cladistic analysis is the parasphenoid-pterygoid suture in Emydops.

5. CONCLUSION

The sphenethmoid and palatoquadrate complexes are described and do not differ much from the usual dicynodont pattern, except for slight morphological differences and the fact that the parasphenoid sutures with the pterygoid, before fusing to the basisphenoid in Emydops.

Courses of bloodvessels and nerves are proposed, but not all the relevant foramina are visible, nor the impressions these soft structures might leave on the surface of bones.

Both studied specimens conform to the generic diagnosis of Emydops (King, 1988). There are slight morphological differences between the two studied specimens which show the variation in one genus and skulls of different size. The positions and angles of the parietal laminae and epipterygoids differ and there is more variation in the basicrania (prootic and opisthotic) and palatoquadrate complexes than in the sphenethmoid region.

Comparisons with other genera are in agreement with the cladogram of King (1990). In all of the above mentioned specimens the vomer forms part of the anterior and part of the lateral sides of the interpterygoid vacuity. Eodicynodon and Cistecephalus retained the stapedial foramen. Eodicynodon has a coronoid process not found in the other genera and the epipterygoid footplate extends further back.

Diictodon, *Emydops* and *Cistecephalus* have reduced palatal exposures and the maxilla bears an embayment anterior to the caniniform process: this is not always preserved and is a cleft in *Eodicynodon*. *Emydops* and *Cistecephalus* share the short and narrow vomerine septum and the groove on either side of the median premaxillary ridge. Only *Emydops* has a palatal exposure of the palatine as a flat horizontal plate with a concave posterior border.

The dorsally grooved vomer in *Pristerodon* has a suture with the parasphenoid. The orbitosphenoid in *Cistecephalus* extends further back than in other dicynodonts. The basicranium (basisphenoid, basioccipital and opisthotic) of BP/1/1619 and BP/1/4386 have slight morphological differences, but are very similar to *Pristerodon*.

Appendix A: Abreviations.

A.C.I. - Arteria carotis interna.
AMP. - Ampulla.
ANG. - Angular.
ART. - Articular.
AS.R.EPT. - Ascending ramus of the epipterygoid.
ATLAS - Atlas.
A.V.S.C. - Anteroventral semicircular canal.
BAS. - Basisphenoid.
BOC.- Basioccipital.
C. - Canine.
C.C. - Crus canalium.
CL. - Cleft.
DEN. - Dentary.
DEN.GR. - Dentary groove.
DEN.T. - Dentary table.
ECT. - Ectopterygoid.
EPT. - Epipterygoid.
EXOC. - Exoccipital.
FL.FO. - Floccular fossa.
FOR.MAG. - Foramen magnum.
F.OV. - Fenestra ovalis.
FR. - Frontal.
G.R.M.C.- Groove for Meckel's cartilage.
H.S.C. - Horizontal semicircular canal.
I.N. - Internal naris.
I.PAR. - Interparietal.
I.PT.V. - Interpterygoid vacuity.
J.F. - Jugular foramen.
JUG. - Jugal.
LAC. - Lachrymal.
L.J.T. - Lower jaw teeth.
L.S. - Lateral dentary shelf.
MAX. - Maxilla.
MAX.ANT. - Maxillary antrum.

MES. - Mesethmoid.
NAS. - Nasal.
NAS. BOSS - Nasal boss.
N.LAC.F. - Naso-lachrymal foramen.
OP. - Opisthotic.
ORB.SPH. - Orbitosphenoid.
PAL. - Palatine.
PAR. - Parietal.
P.ART. - Prearticular.
PA.SPH. - Parasphenoid.
P.B.SPH. - Parabasisphenoid.
PIL.ANT. - Pila antotica.
P.FOR. - Pineal foramen.
PMX. - Premaxilla.
PL.SPH. - Pleurosphenoid.
POC. - Postcanine.
POF. - Postfrontal.
PO. - Postorbital.
PSP. - Presphenoid.
PRF. - Prefrontal.
PR.OT. - Prootic.
PP. - Preparietal.
PT. - Pterygoid.
P.T.FO. - Posttemporal fossa.
P.V.S.C. - Posteroventral semicircular canal.
QJ. - Quadratojugal.
Q.R.EPT. - Quadrate ramus of the epipterygoid.
Q.R.PT. - Quadrate ramus of the pterygoid.
QU.- Quadrate.
REF.LAM. - Reflected lamina of the angular.
RPA.SPH - Rostroparasphenoid.
S.ANG. - Surangular.
SMX. - Septomaxilla.
SOC. - Supraoccipital.
SPL. - Splenial.
SQ - Squamosal.

ST. - Stapes.
SU. - Sinus utricularis.
T.S. - Transverse sinus.
TAB. - Tabular.
V. - Vestibule.
VO. - Vomer.

NII - Foramen for the optic nerve.
NIV - Foramen for the trochlearis nerve.
NV - Foramen for the trigeminal nerve.
NVI - Foramen for the abduscens nerve.
NVII - Foramen for the facial nerve.
NVIII - Foramen for the acoustic nerve.
NXII - Foramen for the hypoglossal nerve.

BP - Bernard Price Institute for Palaeontological Research.

X - Figure 16, supraoccipital cavity.
X - Figure 20A, rod-like unattached bones.

	Rubidge,1990 Eodicynodon	Olson,1944 Emydops	BP/1/1619 Emydops	BP/1/4386 Emydops	Barry, 1967 Pristerodon	Keyser, 1973 Tropidostoma
Locality	Prince Albert	Murraysburg	Dunedin BW	Klein Bloukop R	Kirkvors M	Leeukloof BW
Zone	Eodicynodon	Cistecephalus	Cistecephalus	Cistecephalus	Cistecephalus	Cistecephalus
Septomax. within nostril	*	*	+	+	+	+
Jacobsons organ	*	*	+	+	−	*
Anterior palatal ridges	+	*	−	+	−	+
Fused premaxillaries	−	+	+	+	+	+
Paired vomers	+	−	−	−	−	−
Premax−pal contact	−	+	+	+	−	+
Maxillary antrum	+	*	+	+	+	+
Caniniform process	−	*	+	+	+	+
Teeth in depression	−	−	−	−	+	−
Max. embayment ant to c.	+	+	+	+	−	+
Pila antotica	+	+	+	+	+	*
Pleurosphenoid	+	+	+	+	+	*
Sella turcica	*	+	+	+	+	*
Distinct dorsum sellae	*	+	+	+	+	*
Sphenethmoid=orb+mes	+	+	+	+	+	+
Parabasisphenoid	+	+	+	+	+	+
Prootic incisure	*	+	+	+	+	*
Pineal on boss	+	−	−	−	−	−
Opisthotic/Tymp. process	+	+	+	+	+	+
Par. plate meet ept.	+	*	+	+	+	+
Ant ept meet bas.	+	+	−	−	−	+
Ept. meet qr.pt.	+	−	+	+	+	+
Stapedial foramen	+	*	*	−	−	−
Vestibule	*	+	+	+	+	*
Stapes preserved	+	*	−	+	+	+
Short dorsal groove on den.	*	*	*	+	−	*
Lateral dentary shelf	+	*	*	+	+	*
Coronoid process	+	*	*	−	−	*

Legend:
+ − present
− − absent
* − unrecorded

Appendix C: List of specimens referred to in the BPI collections.

Spec. No	Locality	Description
BP/1/262	Bakens klip M.	Indef.
BP/1/343	Biesjiespoort VW.	Diictodon
BP/1/366	Biesjiespoort VW.	D. sollasi
BP/1/515	Suurplaas GR.	Indef.
BP/1/609	Blaauwpoort M.	E. murraysburgensis (Type)
BP/1/625	Blaauwpoort M.	E. kitchingi (Type)
BP/1/687	Aasvogelskrans M.	Emydops
BP/1/688	Aasvogelskrans M.	Parringtoniella (Type)
BP/1/693	Aasvogelskrans M.	Indef.
BP/1/778	Ferndale GR.	Indef.
BP/1/821	Poortjie GR.	Emydops
BP/1/839	Houdconstant GR.	Emydops
BP/1/842	Doornplaas GR.	Emydops
BP/1/846	Doornplaas GR.	Indef.
BP/1/1209	Hoeksplaas M.	Emydops
BP/1/1307	Driehoeksfontein M.	Indef.
BP/1/1312	Driehoeksfontein M.	Pristerodon
BP/1/1491	Brookfield M.	Pristerodon
BP/1/1580	De Bad Fr. road	Indef.
BP/1/1610	Rosary BW.	Pristerodon
BP/1/1619	Dunedin BW.	Emydops
BP/1/1630	Dunedin BW.	Pristerodon with lower jaw
BP/1/1648	Dunedin BW.	Indef.
BP/1/1656	Dunedin BW.	Pristerodon
BP/1/1794	Kuilspoort BW.	Emydops
BP/1/1795	Kuilspoort BW.	Pristerodon
BP/1/1862	Leeukloof BW.	Emydops with lower jaw
BP/1/1872	Leeukloof BW.	Emydops
BP/1/1878	Leeukloof BW.	Emydops
BP/1/1890	Leeukloof BW.	Only lower jaw,Pristerodon
BP/1/1906	Leeukloof BW.	Emydops, lower jaw
BP/1/1917	Rosery BW.	Pristerodon
BP/1/1918	Rosary BW.	Juvenile, lower jaw.
BP/1/1919	Rosary BW.	With lower jaw, Pristerodon
BP/1/1941	Nobelsfontein VW.	With lower jaw, Pristerodon
BP/1/1947	Nobelsfontein VW.	Emydops
BP/1/1952	Nobelsfontein VW.	Pristerodon
BP/1/1962	Nobelsfontein VW.	Emydops
BP/1/1963	Nobelsfontein VW.	Emydops
BP/1/1964	Nobelsfontein VW.	Emydops
BP/1/1967	Nobelsfontein VW.	With lower jaw, Pristerodon
BP/1/2126	Kraaifontein M.	Pristerodon
BP/1/2127	Kraaifontein M.	Pristerodon
BP/1/2134	Kraaifontein M.	Pristerodon, lower jaw
BP/1/2299	BW. Commonage	Indef.
BP/1/2304	Leeukloof BW.	Pristerodon
BP/1/2366	Leeukloof BW.	Emydops
BP/1/2375	Leeukloof BW.	Emydops
BP/1/2390	Dunedin BW.	Pristerodon
BP/1/2393	Dunedin BW.	With lower jaw, Pristerodon
BP/1/2402	Dunedin BW.	Pristerodon
BP/1/2410	Dunedin BW.	Indef.
BP/1/2412	Dunedin BW.	Pristerodon
BP/1/2413	Dunedin BW.	With lower jaw, Emydops
BP/1/2545	Houdenbek VW.	Indef.
BP/1/2568	Kirkvors M.	Pristerodon
BP/1/2642	De Rust Ab.	Pristerodon
BP/1/2796	Stoffelton ANTBN.	With lower jaw, Emydops
BP/1/3005	Driehoeksfontein M.	Emydops, lower jaw.
BP/1/3013	Driehoeksfontein M.	Pristerodon
BP/1/3024	Driehoeksfontein M.	With lower jaw, Pristerodon

Spec. No	Locality	Description
BP/1/3053	Richmond riverbed	With lower jaw, Pristerodon
BP/1/3132	Driehoeksfontein M.	Pristerodon
BP/1/3159	Driehoeksfontein M.	Indef.
BP/1/3386	U Luangwa Valley 4	Pristerodon
BP/1/3399	U Luangwa Valley 4	Lower jaw, indef.
BP/1/3410	U Luangwa Valley 4	Pristerodon
BP/1/3601	U Luangwa Valley 4	Indef.
BP/1/3961	Middelwater H.	Pristerodon
BP/1/4185	Wynandsfontein VW.	Emydops, lower jaw.
BP/1/4187	Bulthoudersfontein VW.	Pristerodon
BP/1/4188	Bulthoudersfontein VW.	Pristerodon, lower jaw
BP/1/4386	Klein Bloukop RC.	Emydops, lower jaw

Ab.	=Aberdeen
ANTBN.	=Afdeel Native Trust Bulwer, Natal
BW.	=Beaufort West
Fr.	=Frazerburg
GR.	=Graaf Reinet
H.	=Hanover
M.	=Murraysburg
NF.	=Nieuwefontein
R.CP.	=Richmond CP
VW.	=Victoria West
D.	=Dicynodon
E.	=Emydops

Appendix D. Cranial measurements in mm of the two serially ground specimens.

	BP/1/4386	BP/1/1619
Skull length	55.0	67.2
Skull width	43.0	44.3
Width/length	78.0	65.0
Basal length	51.5	62.0
Interorbital w.	13.5	14.2
Intertemporal w.	19.5	20.6
Interorb/intertemp	69.0	69.0
Snout length	13.5	15.5
Snout/skull l.	25.0	23.0
Snout + orbital l.	21.0	26.7
Snout to pineal l.	35.5	37.0
Interorb/skull w.	31.0	32.0
Intertemp/ skull w.	45.0	46.5
Snout + orb/skull l.	38.0	39.7
Snout - pineal/sk l.	65.0	55.1

Appendix E: Photographs and drawings of image obtained on Image Analyser and Positive of CAT scan.

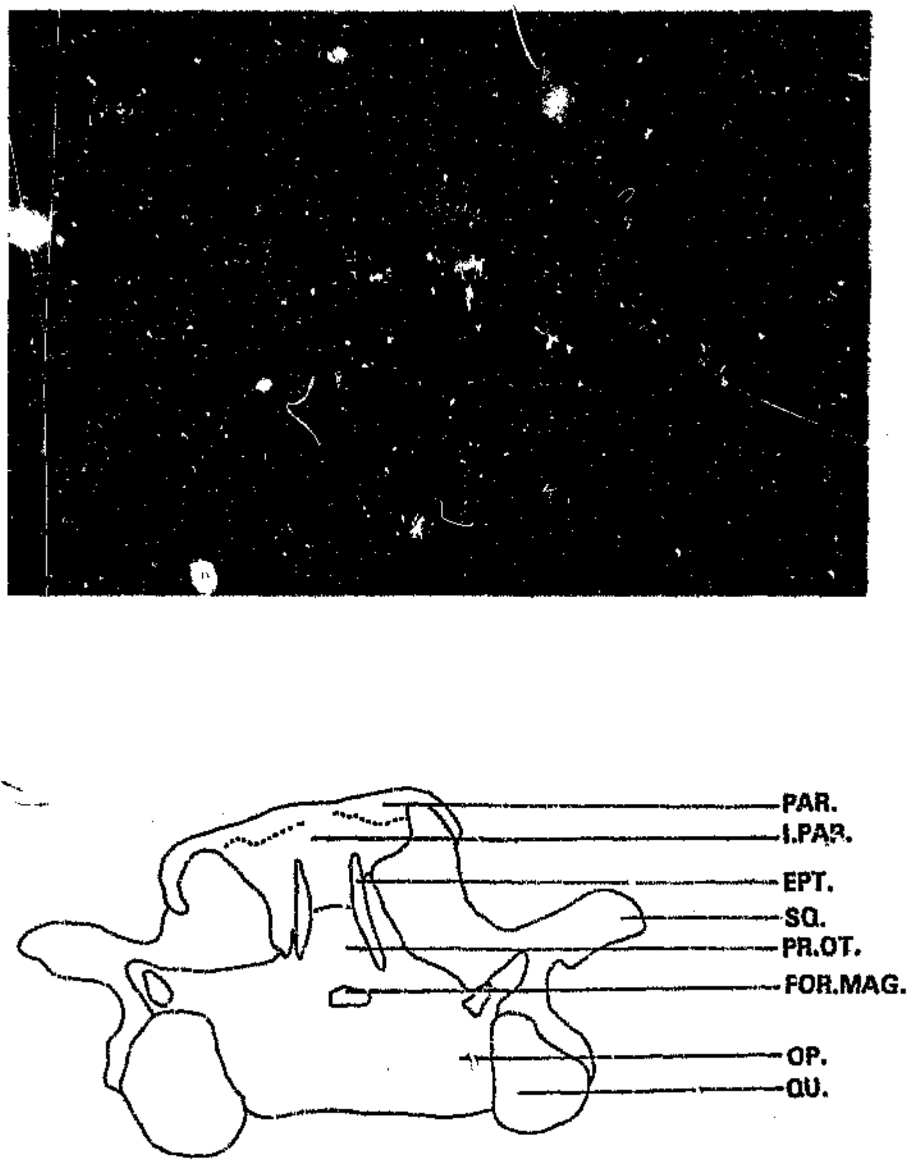


Figure 22: Posterior view of stacking with the image analysis programme. Specimen BP/1/4386 showing the ascending rami of the epipterygoids (Scale: Photograph magn. X1.64).

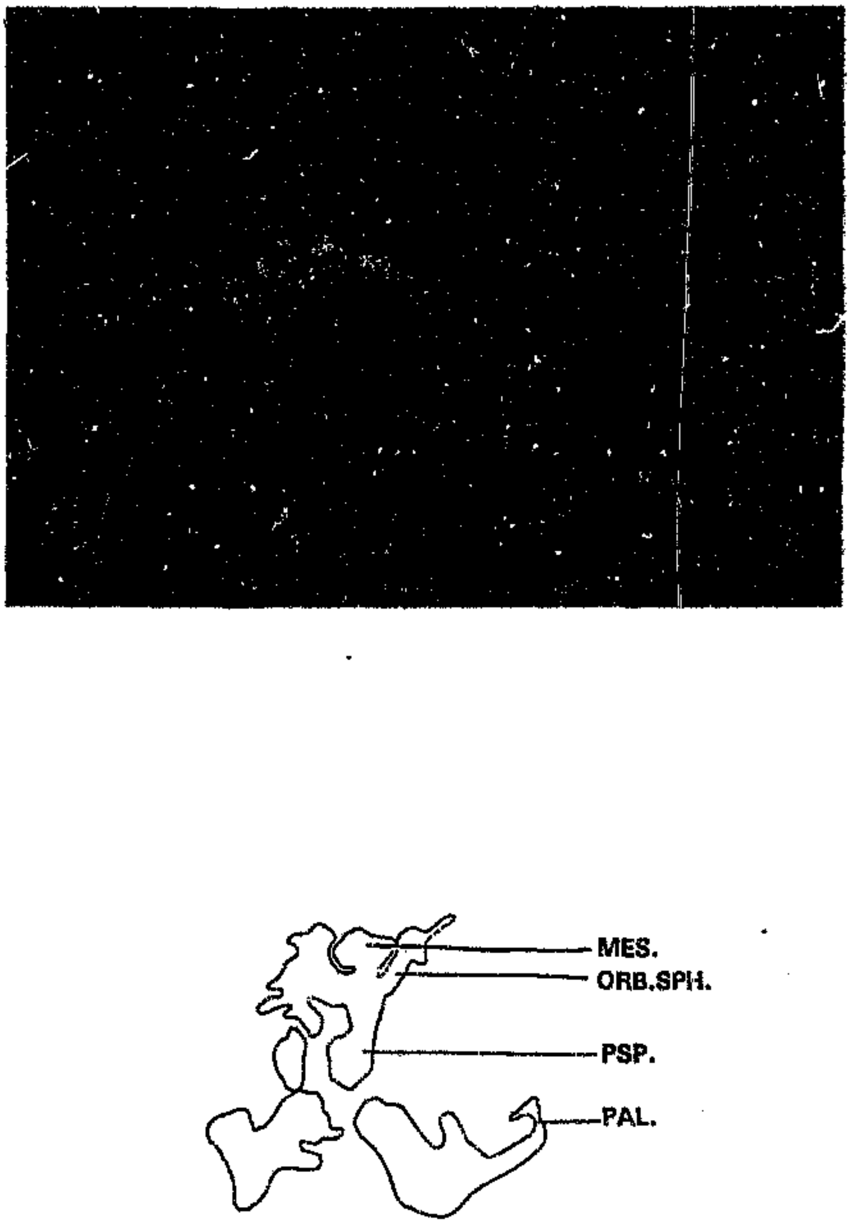


Figure 23: Photograph showing only two of the eight channels. Specimen BP/1/1619 showing the sphenethmoid region in three-dimensions.

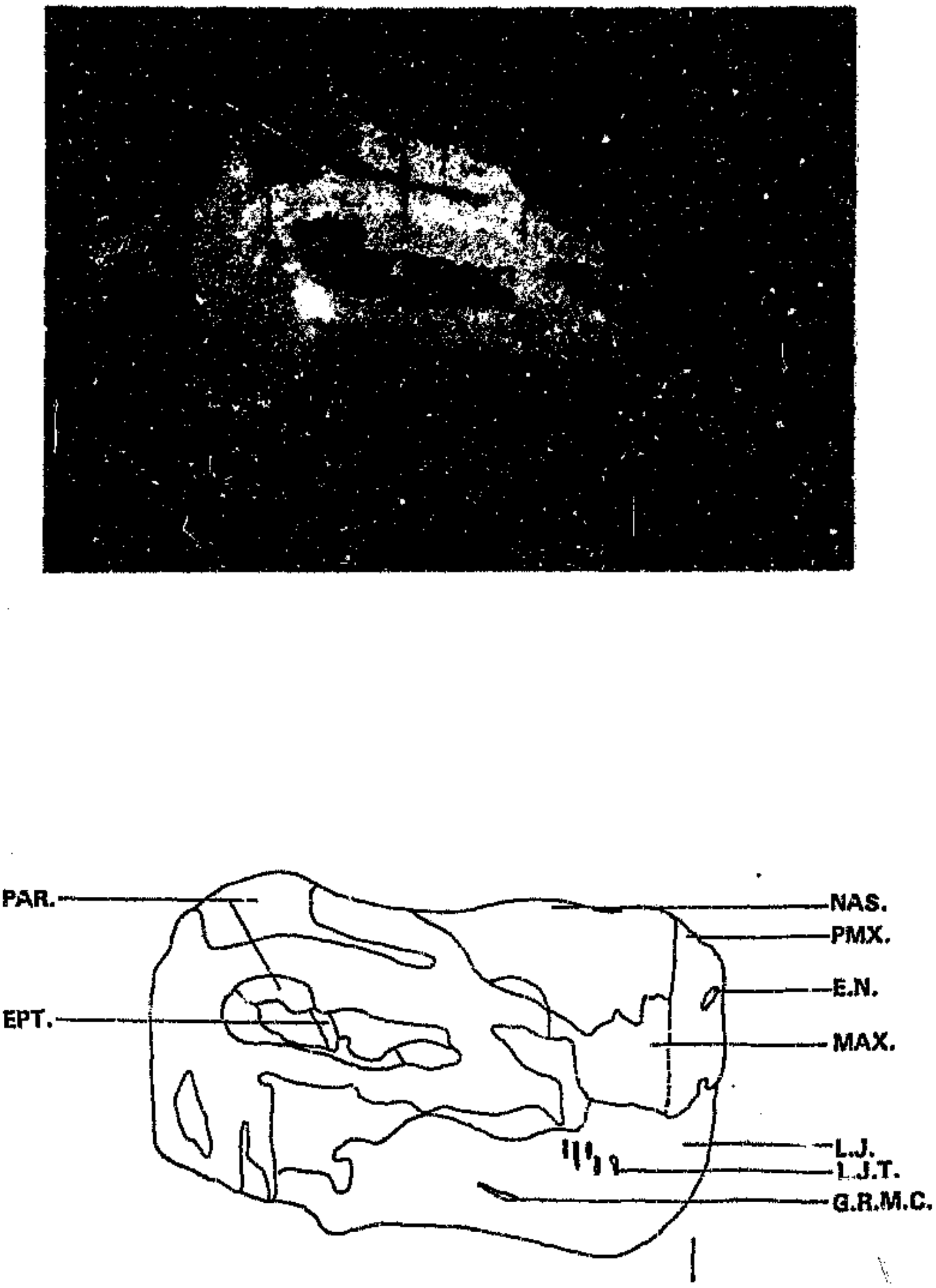


Figure 24: Photograph showing stacking in progress. Specimen BP/1/4356 lateral view with lower jaw.

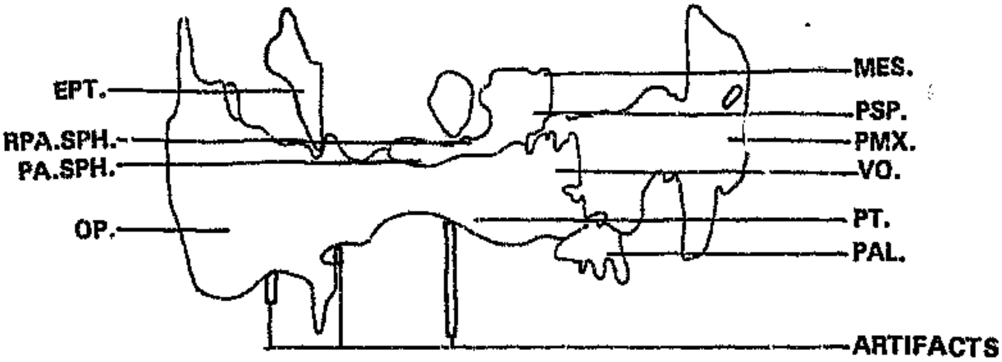


Figure 25· Medial view using the cutmode and deletion of some channels to highlight the inner structures of BP/1/4386.

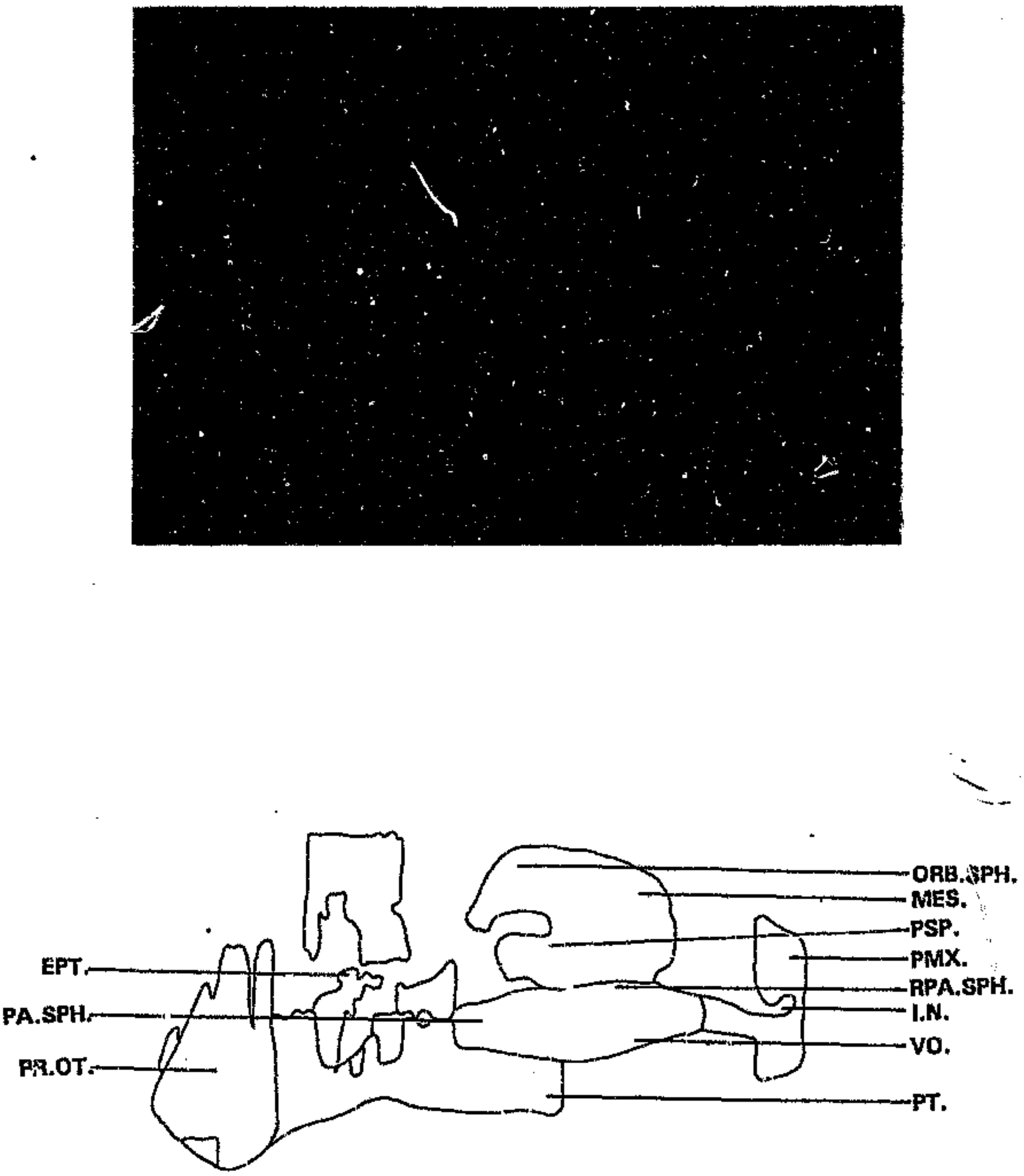


Figure 26: Medial view using the cutmode and deletion of some channels to highlight the inner structures of BP/1/1619.

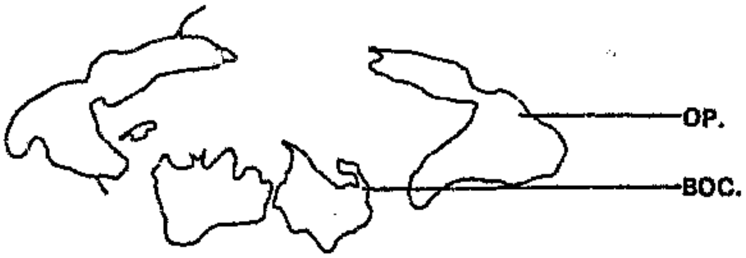


Figure 27: Occipital view in framework mode. Specimen BP/1/1619.

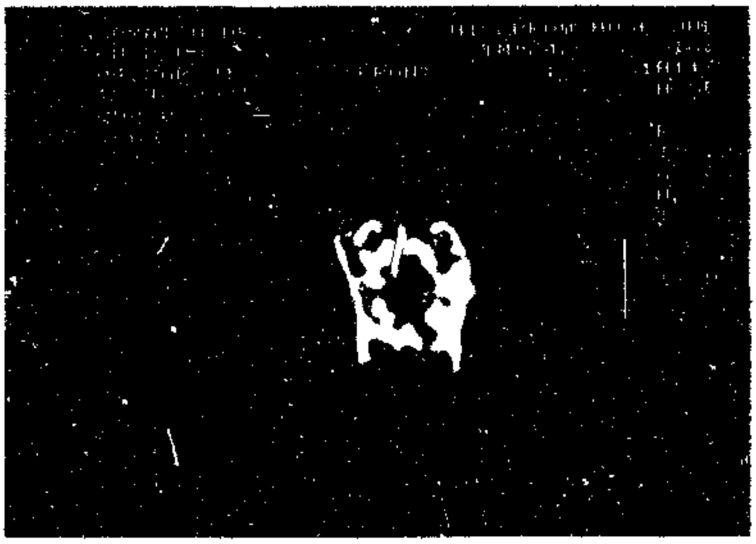


Figure 28: Photograph of CAT scan no. 39 of the type specimen of Emydops minimus Transvaal Museum (Cat no. 242).

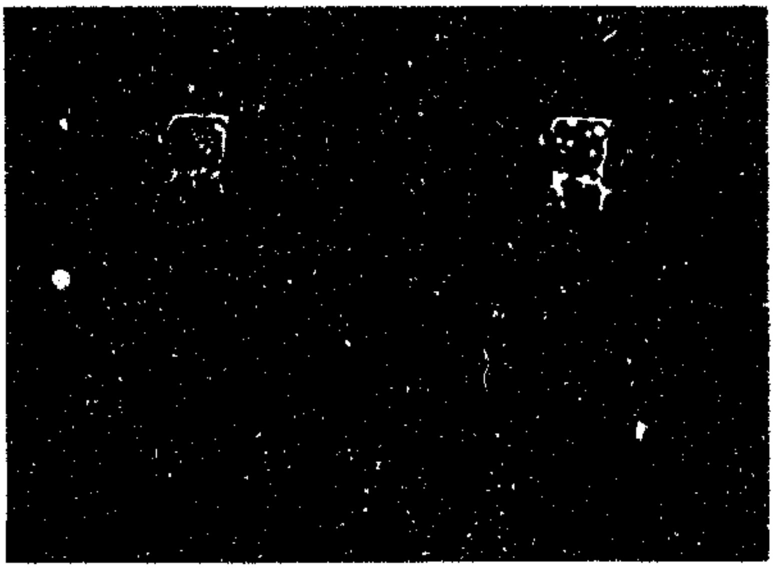


Figure 29: Composite photograph of four CAT scans (nos. 29, 30, 31 & 31).

REFERENCES

Agnew, J.D. 1958. Cranio-osteological studies in Dicynodon grimbeeki with special reference to the sphenethmoid region and cranial kinesis. Palaeont. afr. 6: 77 - 107.

Barry, T.H. 1963. On the variable occurrence of the tympanum in recent and fossil tetrapods. S. Afr. J. Sci. 59, (5): 160 - 175.

Barry, T.H. 1965. On the epipterygoid - alisphenoid transition in Therapsida. Ann. S. Afr. Mus. 48(17): 399 - 426.

Barry, T.H. 1967. The cranial morphology of the Permo - Triassic anomodont Pristerodon buffaloensis with special reference to the neural endocranium and visceral arch skeleton. Ann. S. Afr. Mus. 50(7): 131 - 161.

Barry, T.H. 1974. A new dicynodont ancestor from the upper Ecca (Lower Middle Permian) of South Africa. Ann. S. Afr. Mus. 64: 117 - 136.

Boonstra, L.D. 1968. The braincase, basicranial axis and median septum in the Dinocephalia. Ann. S. Afr. Mus. 50(10): 198-199.

Brink, A.S. 1960. A new type of primitive cynodont. Palaeont. afr. 7: 120 - 123.

Broom, R. 1913. On some new genera and species of dicynodont reptiles, with notes on a few others. Bull. Amer. Mus. Nat. Hist. 32: 441-

457.

Broom, R. 1926. On the mammalian presphenoid and mesethmoid bones. Proc. Zool. Soc. Lond. 1: 257 - 264.

Broom, R. 1932. The Mammal-like Reptiles of South Africa and the Origin of Mammals, Wetherby, London.

Broom, R. 1935. On some new genera and species of Karroo fossil reptiles. Ann. Tvl. Mus. 18: 382.

Broom, R. 1936. On some new genera and species of Karroo fossil reptiles. Ann. Tvl. Mus. 18(1): 68-69.

Cluver, M.A. 1971. The cranial morphology of the dicynodont genus Lystrosaurus. Ann. S. Afr. Mus. 56(3): 155-274.

Cluver, M.A. & King, G.M. 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. Ann. S. Afr. Mus., 91(3): 209 - 268.

Cox, C.B. 1959. On the anatomy of a dicynodont genus with evidence of the position of the tympanum. Proc. Zool. Soc. Lond. 132(3): 321-367.

Croft, W.N. 1950. A parallel grinding instrument for the investigation of fossils by serial sections. J. Paleont. 24(6): 693-698.

Crompton, A.W. 1955. Techniques for the study of Permo - Triassic fossils of South Africa. SAMAB 6 (3): 57-60.

Crompton A.W. & Hotton, N. III 1967. A functional study of the masticatory apparatus of dicynodonts. Postilla 109:7-11.

Durand, J.F. 1989. Aspects of the cranial morphology of the Therocephalian Moschorhinus (Reptilia: Therapsida). Ph.D Thesis, University of the Witwatersrand.

Durand, J.F. 1991. A revised description of the skull of Moschorhinus (Therapsida: Therocephalia). Ann. S. Afr. Mus. 99(11): 381-412.

Ewer, R.F. 1961. The anatomy of the Anomodont Daptocephalus leoniceps (Owen). Proc. Zool. Soc. Lond. 136(3): 375-402.

Haughton, S.H. & Brink, A.S. 1954. A bibliographical list of Reptilia from the Karroo beds of Africa. Palaeont. afr. 2:56 - 71.

Hopson, J.A. 1964. Tooth replacement in cynodont, dicynodont and therocephalian reptiles. Proc. Zool. Soc. Lond. 142(4): 629-633.

Keyser, A.W. 1973a. A preliminary study of the type area of the Cistecephalus zone of the Beaufort Series, and a revision of the anomodont family Cistecephalidae. Geol. Surv. Memoir 62: 33-34.

Keyser, A.W. 1973b. A re-evaluation of the genus Tropidostoma Seeley. Palaeont. afr. 16: 25-35.

Keyser, A.W. 1975. A re-evaluation of the cranial morphology and systematics of some tuskless Anomodontia. Geol. Surv. Memoir 67: 10.

King, G.M. 1988. Anomodontia. Encyclopedia of Palaeoherpetology. Part 17C. pp. 1-174 (Ed. P. Wellnhofer) München. Gustav Fisher Verlag Stuttgart.

King, G.M. 1990. The Dicynodonts: A study in Palaeobiology. Chapman and Hall. London.

King, G.M., Oelofsen, B.W. & Rubidge, B.S. 1989. The evolution of the dicynodont feeding system. Zool. J. Linn. Soc. 96(2): 185-211.

O'Donoghue, C.H. 1920. The blood vascular system of the tuatara, Sphenodon punctatus. Phil. Trans. R. Soc. (B) 210 (377): 175-252.

Olson, E.C. 1944. Origin of mammals based upon cranial morphology of the therapsid suborders. Geol. Soc. Amer. Special paper 55: 1 - 136.

Olson, F.R. & Whitmore, F.C. 1944. Machine for serial sectioning of fossils. J. Palaeont. 18, (2) pp. 210-215.

Ongaro, I., Sperber, G.H., Machin, G.A. & Murdoch, C.A. 1991. Fiducial points for Three-Dimensional Computer-assisted reconstruction of serial light microscopic sections of umbilical cord. The Anatonomical Record 229: 285-289.

Presley, R. & Steel, F.L.D. 1976. On the homology of the alisphenoid. J. Anat. 121 (3): 441-459.

Pusey, H.K. 1939. Methods of reconstruction from microscopic sections. J.L.R. microsc. Soc. 59: 232 - 244.

Romer, A.S. 1956. Osteology of the Reptiles. The University of Chicago press. Chicago.

Rubidge, B.S. 1985. The first record of a complete snout of the primitive dicynodont Eodicynodon Barry (Therapsida, Dicynodontia), Palaeont. navors. nas. Mus. Bloemfontein, 4, 501-512.

Rubidge, B.S. 1990a. Redescription of the cranial morphology of Eodicynodon oosthuizeni (Therapsida: Dicynodontia). Palaeont. navors. nas. Mus. Bloemfontein, 7(1): 1-25.

Rubidge, B.S. 1990b. The cranial morphology of a new species of the genus Eodicynodon (Therapsida: Dicynodontia). Palaeont. navors. nas. Mus. Bloemfontein, 7(2): 30-41.

Rubidge, B.S. (in preparation) (Ed.) South African Committee for Stratigraphy (SACS). Pretoria.

Simpson, G.G. 1933. A simplified serial sectioning technique for the study of fossils. Amer. Mus. Novit. 634: 1-60.

Sollas, W.J. 1903. A method for the investigation of fossils by serial sections. Phil. Trans. R. Soc. (B) 196: 259-265.

Sollas, I.B.J. & Sollas, W.J. 1913. A study of the skull of a Dicynodon by means of serial sections. Phil. Trans. R. Soc. Lond. (B) 204: 201-225.

Sollas, I.B.J. & Sollas, W.J. 1916. On the structure of the dicynodont skull. Phil. Trans. R. Soc. Lond. (B) 207: 531-539.

Toerien, M.J. 1953. The evolution of the palate in South African Anomodontia and its classifactory significance. Palaeont. afr. 1:49 - 115.

Watson, D.M.S. 1960. The anomodont skeleton. Trans. Zool. Soc. Lond. 29(3):144 - 148.

Wible, J.R., Miao, D. & Hopson, J.A. 1990. The septomaxilla of fossil and recent synapsids and the problem of the septomaxilla of monotremes and armadillos. Zool. J. Lin. Soc. 98: 203-228.

Zonneveld, F.W. & Wind, J. 1985. High-resolution computed tomography of fossil hominid skulls: A new method and some results. In: Hominid Evolution: Past, present and future (Ed. P.V. Tobias) pp 427-436. Alan R. Liss, Inc., New York.

Author: Fourie H
Name of thesis: A detailed description of the skull of emydops