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A DETAILED DESCRIPTION OF THE INTERNAL STRUCTURE OF THE SKULL OF *EMYDOPS* (THERAPSIDA: DICYNODONTIA)

by

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ABSTRACT

A detailed morphological study of two skulls of *Emydops* was undertaken by using the serial grinding technique. Graphic 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*, *Cistecephalus* and *Diictodon*. *Emydops* and *Cistecephalus* show more advanced features in common with each other than with other dicynodonts. 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* differs from other dicynodonts in that the parasphenoid has a definite suture with the pterygoid anterior to the pterygoid-basisphenoid suture, instead of passing between the pterygoids without contacting them, as reported by Olson (1944).

KEY WORDS: Therapsida, Dicynodontia, *Emydops*.

INTRODUCTION

Eodicynodon (Barry 1974), *Dicynodon leoniceps* (Sollas and Sollas 1913), *Diictodon* (Agnew 1958), *Cistecephalus* (Keyser 1973), *Lystrosaurus* (Cluver 1971), *Pristerodon* (Barry 1967) and *Emydops* (partially, Olson 1944), are the only dicynodont genera in which the internal structures have been described by using the serial grinding technique. *Emydops* is interesting because of its mix of characters, some plesiomorphic e.g. palatines extend medially and become incorporated into the rear of the secondary palate, and some apomorphic e.g. palatal exposure of palatine a flat, horizontal plate with a concave posterior border (King 1990).

Sollas and Sollas (1913) used the serial grinding technique to reveal internal structures such as the 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. Their discovery marked the beginning of the quest to understand the inner structures of the fossil skull. Olson (1944) studied the inner ear, occipital region and basicranial axis of *Emydops*. Hopson (1964) used Olson's sections to describe the mode of tooth replacement.

For the purpose of the current study two *Emydops* skulls were serially ground in order to describe the internal cranial structures.

MATERIALS AND METHODS

Materials

Two specimens from the BPI collections were identified as *Emydops* on the criteria given by King (1988). Specimen BP/1/4386 is from the farm Klein Bloukop, Richmond (31° 32'S 23° 34'E) and specimen BP/1/1619 is from the farm Dunedin, Beaufort West (31° 57'S 22° 25'E). Both specimens are from the *Cistecephalus-Aulacephalodon* assemblage zone.

Methods

The two specimens were serially ground with a Croft parallel grinder (Croft 1950). 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.

Photographs and drawings of the specimen before grinding was begun supplied an adequate permanent record. Prior to grinding both specimens were cast, measured, drawn and photographed and encased in plaster of Paris. When dry the cylindrical block of plaster containing the specimen was attached to the micrometer footplate with warm dental modelling wax. This was left to cool and set before grinding was undertaken.

The section interval decided on was 0.25mm as this interval gives the best results in small specimens (Sollas 1903). Every section was either etched with 3% acetic acid or stained with Alizarine Red S depending on the contrast between bone and matrix. Photographs of each section were taken and in addition to that each section was traced with the aid of an epidiascope. 200 sections were obtained for BP/1/4386 and 260 for BP/1/1619.

The tracings were used to reconstruct both specimens on graph paper according to the method of Pusey (1939).

RESULTS

The features of the skull roof do not differ from the usual dicynodont pattern. This paper will mainly concentrate on the internal structures as they have not been described in *Emydops* before.

Lachrymal

The lachrymal (Figure 1A) forms part of the wall of the naso-lachrymal duct. Almost at a point where the jugal and lachrymal meet, the maxilla forms the outer wall of the naso-lachrymal duct. This duct runs the whole length of the lachrymal and opens directly into the nasal cavity.

Septomaxilla

The septomaxilla (Figure 1B) is situated posterior to the premaxilla and is sutured to the maxilla ventrally and laterally in the posterior wall of the external naris; it has a triangular shape with a medial canal which runs anteroposteriorly for the whole length of the septomaxilla. The medial canal opens medially into the nasal cavity for a short distance. Posteriorly the septomaxilla 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 Jacobson's organ. A longitudinal groove is present on the dorsal side of the septomaxilla, marking an interdigitating contact with the maxilla.

Parietal

The medial parietal lamina of BP/1/4386 (Figure 2A) extends downwards from the parietal behind the posterior border of the pineal foramen and is sutured to

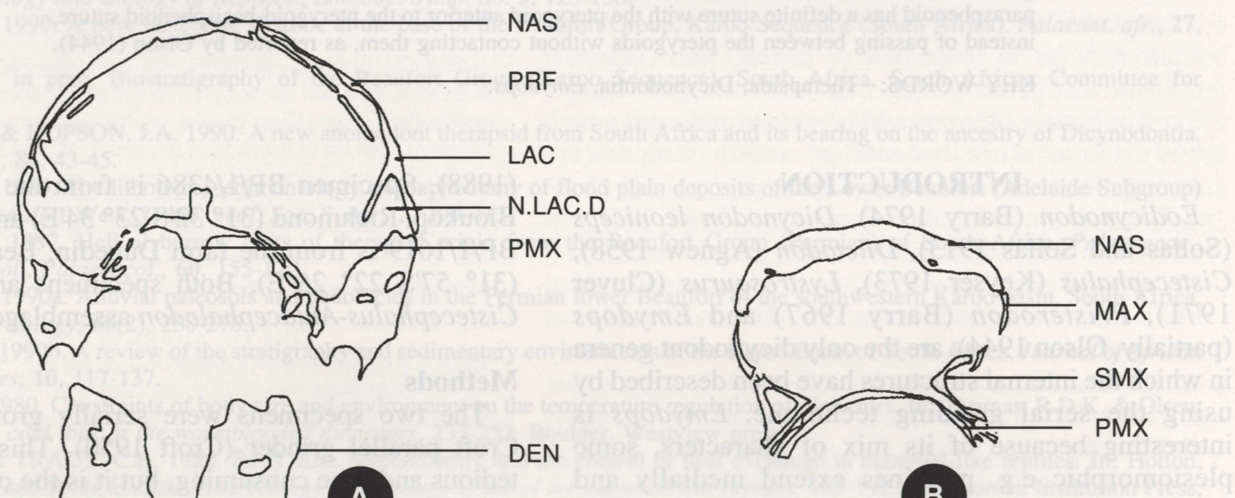

Figure 1: Composite figure of transverse sections to show, A: naso-lachrymal duct (BP/1/4386), B: septomaxilla (BP/1/1619), C: maxillary antrum consisting of two compartments, and D: graphic reconstruction of lateral view of left inner ear of BP/1/4386.

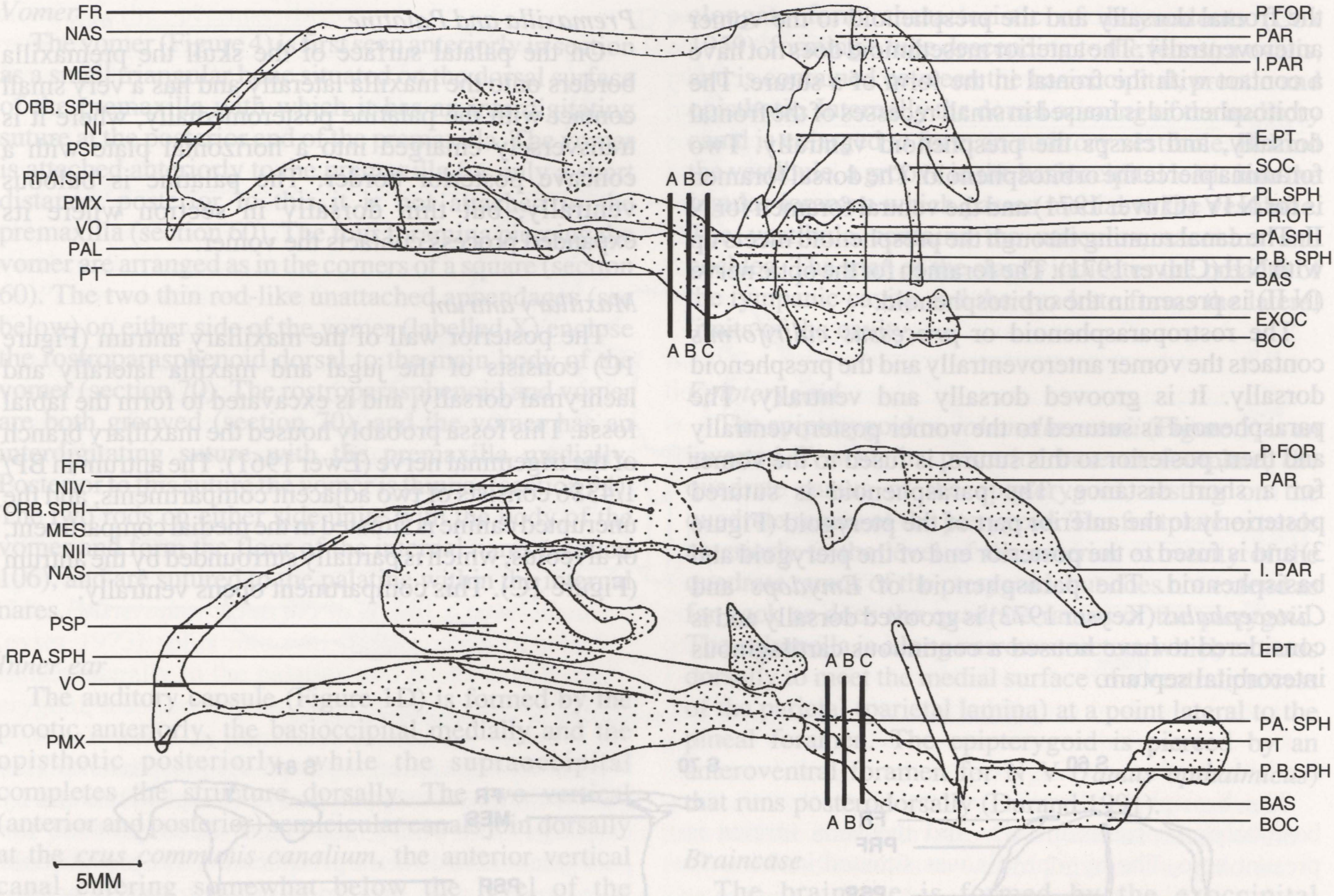

Figure 2: Graphic reconstruction of medial views of sphenethmoid complex: Top: BP/1/4386. Bottom: BP/1/1619. Section lines A-A, B-B and C-C are explained in Figure 3.

the epipterygoid ventrolaterally. In section the parietal laminae form an inverted U.

The parietal laminae of BP/1/1619 (Figure 2B) extend downward from the anterior border of the pineal foramen to form a channel for the pineal body or nerve which is completed by the ascending rami of the epipterygoids that are sutured to the inner surface of the parietal laminae.

Sphenethmoid region

The septosphenoid (orbitosphenoid and mesethmoid) is roughly rectangular in lateral view with a large median cavity posteriorly and a small median notch anteriorly (Figure 2B). The presphenoid is wider posteriorly and has a posterior extension situated loosely on the parasphenoid. The orbitosphenoid is sutured to

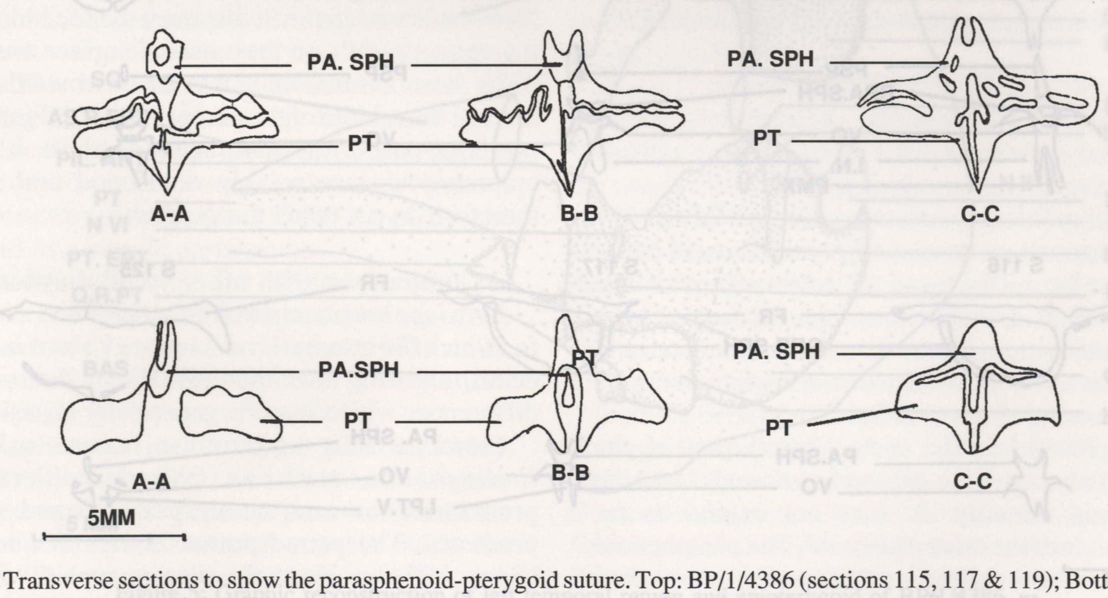

Figure 3: Transverse sections to show the parasphenoid-pterygoid suture. Top: BP/1/4386 (sections 115, 117 & 119); Bottom: BP/1/1619 (sections 160, 164 & 168).

the frontal dorsally and the presphenoid to 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. Two foramina pierce the orbitosphenoid. The dorsal foramen is for N IV (Cluver 1971) and the ventral foramen for N II. The canal running through the presphenoid meets up with N II (Cluver 1971). The foramen for the optic nerve (N II) is present in the orbitosphenoid.

The rostroparasphenoid or *processus cultriformis* contacts the vomer anteroventrally and the presphenoid dorsally. It is grooved dorsally and ventrally. The parasphenoid is sutured to the vomer posteroventrally and then, posterior to this suture, is fused to the vomer for a short distance. The parasphenoid is sutured posteriorly to the anterior part of the pterygoid (Figure 3) and is fused to the posterior end of the pterygoid and basisphenoid. The parasphenoid of *Emydops* and *Cistecephalus* (Keyser 1973) is grooved dorsally and is considered to have housed a continuous cartilaginous interorbital septum.

Premaxilla and Palatine

On the palatal surface of the skull the premaxilla borders onto the maxilla laterally and has a very small contact with the palatine posteromedially, where it is transversely enlarged into a horizontal plate with a concave posterior border. The palatine is bulbous ventrally, but thin dorsally in section where its expanded process contacts the vomer.

Maxillary antrum

The posterior wall of the maxillary antrum (Figure 1C) consists of the jugal and maxilla laterally and lachrymal dorsally, and is excavated to form the labial fossa. This fossa probably housed the maxillary branch of the trigeminal nerve (Ewer 1961). The antrum in BP/1/4386 consists of two adjacent compartments, and the unerupted canine is situated in the medial compartment, or alveolus, which is partially surrounded by the antrum (Figure 1C). This compartment opens ventrally.

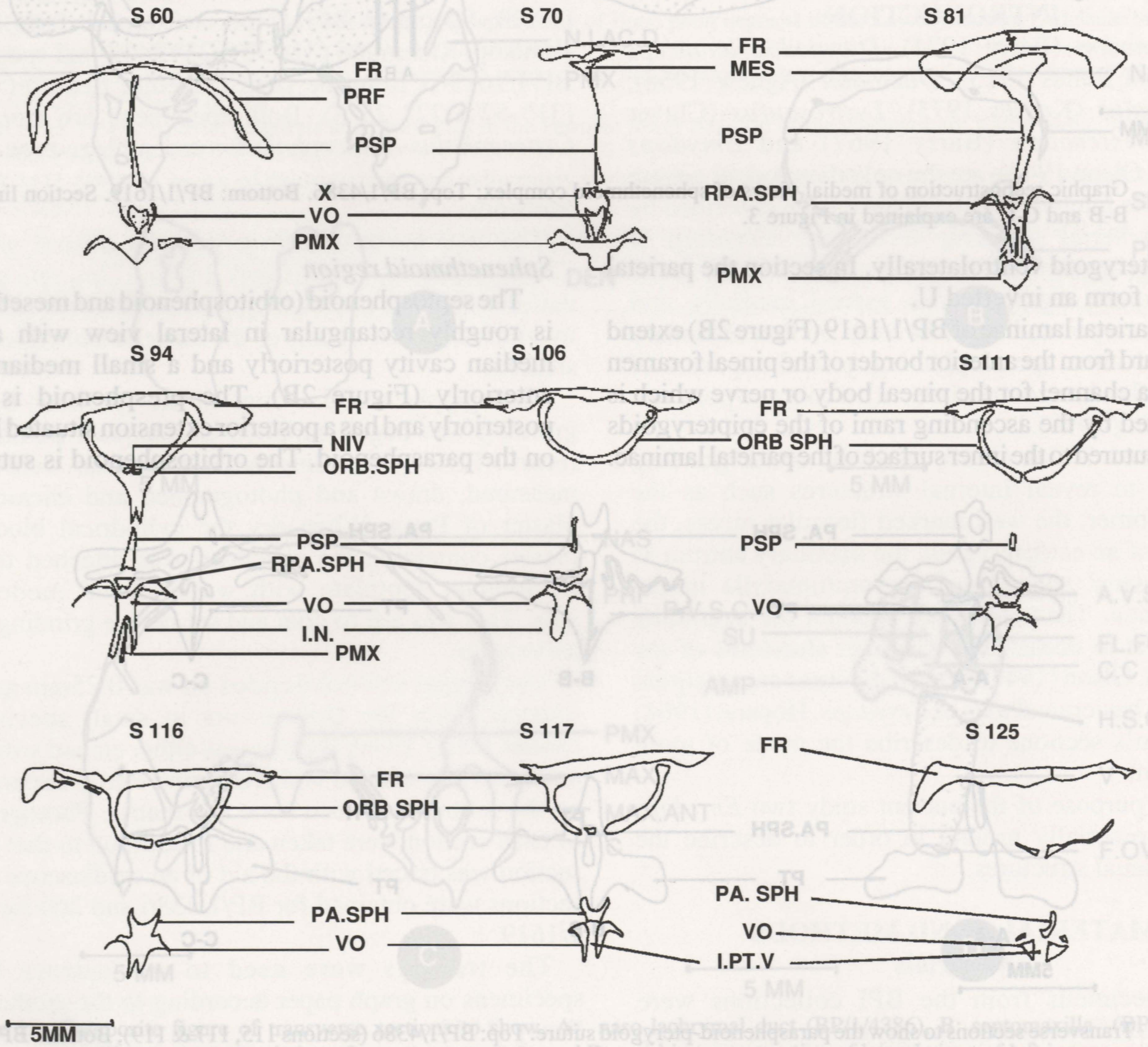

Figure 4: Transverse sections through the vomer and sphenethmoid regions of BP/1/1619.

Vomer

The vomer (Figure 4) 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, posterior to 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 (section 60). The two thin rod-like unattached appendages (see below) on either side of the vomer (labelled X) enclose the rostroparasphenoid dorsal to the main body of the vomer (section 70). The rostroparasphenoid and vomer are both grooved (section 70), and the vomer has an interdigitating suture with the premaxilla medially. Posterior to 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 are sutured to the palatine within the internal nares.

Inner ear

The auditory capsule (Figure 1D) 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) semicicular 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 ampullary recess. The utriculus is present ventrally of the *crus comminus 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 of the cavity.

Epipterygoid

The epipterygoid or *columella cranii* (Figure 5) is an inverted T, with its posterior base or footplate, the quadrate ramus of the epipterygoid, resting on the quadrate ramus of the pterygoid. The footplate extends anteriorly to the level of the anterior extremity of the quadrate ramus of the pterygoid, but does not extend as far back as does 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 opthalmicus*) that runs posterodorsally (Durand 1991).

Braincase

The braincase is formed by the exoccipital posteriorly and ventrally, the basioccipital and basisphenoid ventrally, the opisthotic and prootics laterally and the supraoccipital dorsally.

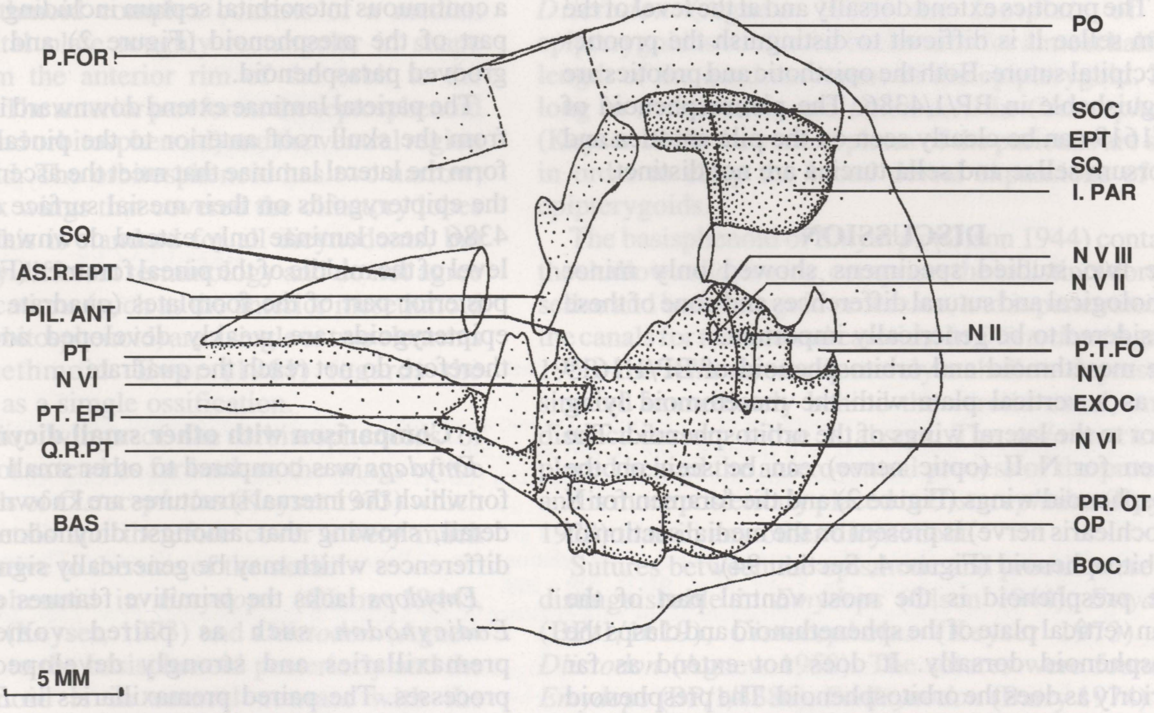

Figure 5: Graphic reconstruction of left temporal region and epipterygoid of BP/1/4386.

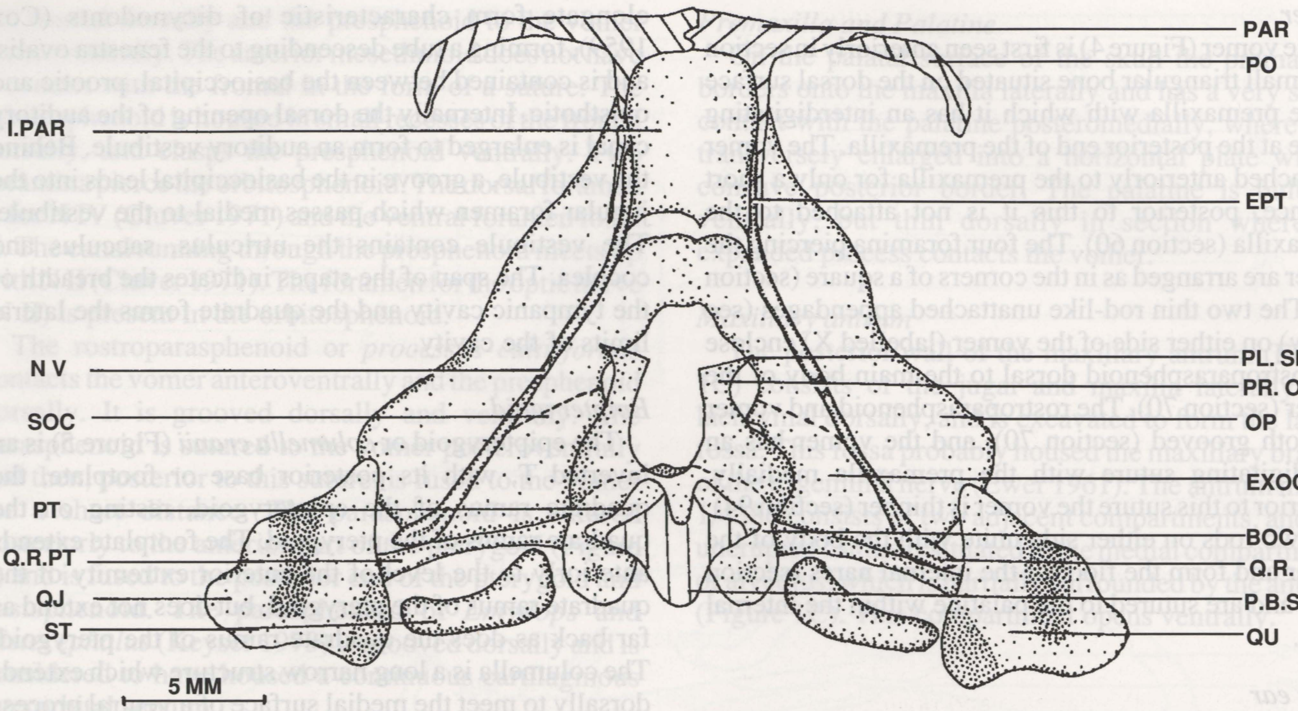

Figure 6: Graphic reconstruction of anterior view of palatoquadrate complex.

Basisphenoid

The basisphenoid makes sutural contact with the basioccipital posterodorsally and the sella turcica is present here. The hypophysis was situated in the *sella turcica*.

Prootic and Opisthotic

The suture between the prootic and basisphenoid at the level of the pila antotica is clear (Figure 5). The prootics unite to form the slight dorsum sellae in BP/1/4386. The prootics extend dorsally and at the level of the dorsum sellae it is difficult to distinguish the prootic-basioccipital suture. Both the opisthotic and prootics are distinguishable in BP/1/4386. The pleurosphenoid of BP/1/1619 can be clearly seen on the pila antotica and the dorsum sellae and sella turcica are not distinct.

DISCUSSION

The two studied specimens showed only minor morphological and sutural differences and none of these is considered to be generically important.

The mesethmoid and orbitosphenoid of BP/1/1619 show as a vertical plate with the mesethmoid lying anterior to the lateral wings of the orbitosphenoid. The foramen for N II (optic nerve) can be seen on the orbitosphenoid wings (Figure 2) and the foramen for N IV (trochlearis nerve) is present on the medial section of the orbitosphenoid (Figure 4, Section 94).

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 *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 including the posterior part of the presphenoid (Figure 2) and the dorsally grooved parasphenoid.

The parietal laminae extend downward in BP/1/1619 from the skull roof anterior to the pineal foramen to form the lateral laminae that meet the ascending rami of the epipterygoids on their mesial surface and in BP/1/4386 these laminae only extend downwards from the level of the middle of the pineal foramen (Figure 2). The posterior part of the footplates (quadrate rami) of the epipterygoids are weakly developed and short and therefore do not reach the quadrate.

Comparison with other small dicynodonts

Emydops was compared to other small dicynodonts for which the internal structures are known in sufficient detail, showing that amongst dicynodonts there are differences which may be generically significant.

Emydops lacks the primitive features exhibited by *Eodicynodon* such as paired vomers, paired premaxillaries and strongly developed pterygoid processes. The paired premaxillaries in *Eodicynodon* (Barry 1974) point to the plesiomorphic condition as seen in the primitive *Venyukovia* and *Otsheria*. The fusion of the premaxillaries in *Emydops* is a synapomorphy shared with all other Dicynodontia (Cluver and King 1983).

Emydops does not show derived features such as the loss of the floccular fossa, *sella turcica*, and interpterygoid vacuity, which in *Cistecephalus* can all be attributed to the shortening of the skull (Keyser 1973). In *Emydops* the palate is derived and there is a sutural contact between the epipterygoid and parietals.

In *Pristerodon* (Barry 1967), *Eodicynodon* (Rubidge 1990) and *Diictodon* (Agnew 1958), the palatal portion of the maxilla participates posteromedially in the formation of the lateral walls of the choana through the formation of a wedge which inserts between the premaxilla and the palatine. This is not the case in *Emydops* (present work) and *Cistecephalus* (Keyser 1973).

At approximately two-thirds posteriorly along its length the vomer in *Emydops*, *Eodicynodon* (Barry 1974), *Pristerodon* (Barry 1967) and *Cistecephalus* (Keyser 1973) 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 transverse section the vomer is 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 true for *Emydops*, *Pristerodon* (Barry 1967) and *Diictodon* (Agnew 1958). The dorsal surface of the plate-like median portion of the parasphenoid rostrum is a loose fit in *Emydops* and a close fit in *Pristerodon*, the only two genera in which this is noted.

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 orbitosphenoid) and the ventral region the presphenoid. The orbitosphenoid has two narrow, slightly convex wings that covered the olfactory lobes from above. This is standard for all dicynodonts, but authors employ different terminology and do not agree whether ossifications (such as the anterior mesethmoid and posterior orbitosphenoid) are a single or two elements in the sphenethmoid. Ewer (1961) regards the sphenethmoid as a simgle ossification.

The posterior wings of the orbitosphenoids of *Emydops* do not extend as far back as the wings of the orbitosphenoids of *Cistecephalus* (Keyser 1973) which reach the parietals and therefore cover a very much larger area relative to the size of the skull.

The parasphenoid in *Emydops* (Olson 1944), *Cistecephalus* (Keyser, 1973) and *Diictodon* (Agnew 1958) is fused to the basisphenoid posteriorly and the parabasisphenoid is in sutural contact with the basioccipital. The prootic overlies this complex and makes contact at the parabasisphenoid-basioccipital suture. The parasphenoid of the studied specimens is also fused to the basisphenoid, but is sutured to the pterygoid just anteriorly to the quadrate ramus of the pterygoid (Figure 3). Olson (1944) also reported 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 an autapomorphic feature of *Emydops* as in all other dicynodonts the parasphenoid passes between, and does not make contact with 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 of the parietal.

The footplate of the epipterygoid in *Emydops* (present study) 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 epipterygoid in *Eodicynodon* (Barry 1974; Rubidge 1990) 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 and King 1983).

In most dicynodonts the footplate is only weakly developed. In *Cistecephalus* (Keyser 1973) 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 *Cistecephalus* (Keyser 1973) the ventral plates of the parietals are split in order to clasp the broad dorsal expansions of the epipterygoids.

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 prootics and is more posteriorly placed in *Cistecephalus* (Keyser 1973) than in any other dicynodont.

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

A median interparietal suture is present in *Emydops*

(BP/1/4386) and *Cistecephalus* (Keyser 1973), but it is not always visible on the occipital surface.

CONCLUSION

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. In *Emydops* the sphenethmoid complex does not differ much from the usual dicynodont pattern, except that the parasphenoid sutures with the pterygoid, before fusing to the basisphenoid.

The positions and angles of the parietal laminae and epipterygoids differ and there is more variation in the prootic, opisthotic, basioccipital, basisphenoid and palatoquadrate complexes than in the sphenethmoid region of the Dicynodontia.

Emydops and *Cistecephalus* show more advanced features in common with each other than with other dicynodonts. These features include the absence of a maxillary wedge between the premaxilla and palatine and consequent reduced palatal exposure of the maxilla, the embayment on the maxilla anterior to the caniniform process, and the short and narrow vomerine septum, and the groove on either side of the median premaxillary ridge.

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LIST OF ABBREVIATIONS

AMP	Ampulla.
AS.R.EPT	Ascending ramus of the epipterygoid.
A.V.S.C	Anteroventral semicircular canal.
BP	Bernard Price Institute for Palaeontological Research.
BAS	Basisphenoid.
BOC	Basioccipital.
C	Canine.
C.C	Crus canalium.
DEN	Dentary.
EPT	Epipterygoid.
EXOC	Exoccipital.
FL.FO	Floccular fossa.
F.OV	Fenestra ovalis.
FR	Frontal.
H.S.C	Horizontal semicircular canal.
I.N	Internal naris.
I.PAR	Interparietal.
LAC	Lachrymal.
MAX	Maxilla.
MAX.ANT	Maxillary antrum.
MES	Mesethmoid.
N II	Foramen for the optic nerve.
N IV	Foramen for the trochlearis nerve.
N V	Foramen for the trigeminal nerve.
N VI	Foramen for the abducens nerve.
N VII	Foramen for the facial nerve.
N VIII	Foramen for the acoustic nerve.
NAS	Nasal.
N.LAC.D	Naso-lachrymal duct.
OP	Opisthotic.
ORB.SPH	Orbitosphenoid.
PAL	Palatine.
PAR	Parietal.
PA.SPH	Parasphenoid.
P.B.SPH	Parabasisphenoid.
PIL.ANT	Pila antotica.
P.FOR	Pineal foramen.
PMX	Premaxilla.
PL.SPH	Pleurosphenoid.
PO	Postorbital.
PSP	Presphenoid.
PRF	Prefrontal.
PR.OT	Prootic.
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.
RPA.SPH	Rostroparasphenoid.
SMX	Septomaxilla.
SOC	Supraoccipital.
SQ	Squamosal.
ST	Stapes.
SU	Sinus utricularis.
PT.EPT	Pterygoid ramus of the epipterygoid.
V	Vestibule.
VO	Vomer.

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