

https://dspace.org/

Cranio-osteologlcal studies in Dicynodon grimbeeki with special reference to the sphenethmoid region and cranial kinesis

Agnew, John David

1959-07-01
Bernard Price Institute for Palaeontological Research
http://hdl.handle.net/10539/16094
None

Downloaded from a DSpace repository. https://dspace.org/

CRANIO-OSTEOLOGICAL STUDIES IN DICYNODON GRIMBEEKI WITH SPECIAL REFERENCE TO THE SPHENETHMOID REGION AND CRANIAL KINESIS

By John David Agnew*

Abstract

The skull structure of *Dicynodon grimbeeki* has been studied by means of serial sections. It was found that *D. grimbeeki* is akinetic and that, although several mammal-like characteristics are present, *Dicynodon* occupies a specialized side-branch of therapsid evolution — a view which has been advocated by many authors. The sphenethmoid region in anomodonts is discussed, and it is concluded that the basicranial axis in *Dicynodon* is comparable with that of mammals.

Introduction

The general structure of the skull of *Dicynodon* is now rather well known, although the variations encountered in the anomodonts as a group are enormous. Certain points, however, still require further attention. The identification and homologies of the components of the interorbital septum, i.e. the so-called sphenethmoid (septosphenoid or prebasisphenoid) complex, are not well understood. Furthermore the possibility of cranial kinesis in anomodonts has not been adequately discussed, even where specimens have been studied by means of serial sectioning. Special attention is given to these two problems.

The technique of serial sectioning, employed on the specimens here described, is laborious and time-consuming, but the only one which can effectively reveal fine details of the internal anatomy, at least in refractory fossil material such as that offered by the Karroo reptiles. A disadvantage is that the specimen is entirely destroyed, so that this method cannot be practised on types or other particularly valuable specimens. But the amount of information to be gained by serial sectioning more than out-balances this disadvantage, and in any case photographs of the ground surfaces can provide a permanent record, and are extremely useful for reference purposes. In fact, for accurate work they are essential.

A full description of the technique of sectioning is given by Olsen and Whitmore (1944) and Croft (1950). Various improvements to this technique were introduced by Crompton (1955 a) who also explains the use of a "base-line", essential when graphic reconstructions are to be made.

Three skulls (see below) were used in this investigation. These were supplied with base-lines and imbedded in blocks of Calistone Plaster of Paris, due regard being paid to the proper orientation of each skull in the block. Sectioning was carried

* Department of Zoology, University of Pretoria.

out with a Croft Parallel Grinder. All three were transversely sectioned from front to back. Enlarged tracings of the projected surfaces were then made, and these were used in drawing the graphic reconstructions according to the method of Pusey (1939).

Descriptions are based almost entirely on Specimen A, since it is almost perfect and has undergone a minimum of distortion. This was an unidentified skull from the Bernard Price Institute, but proved on sectioning to fit the description of *Dicynodon grimbeeki* Broom very well. Where doubtful structures were encountered, use was made of a second series of sections (Specimen B) of *D. grimbeeki,* one of the specimens examined by Toerien (1953). Occasional reference is also made to a third series of sections (Specimen C). In this skull systematic photographing of the sections was carried out. As is pointed out below, Specimen C cannot strictly speaking be considered a *Dicynodon.* It is nevertheless structurally very similar to the other two specimens.

Specimen A: Bernard Price Institute Museum No. 294. *Dicynodon sp.* cf. *grimbeeki* Broom 1935. From Rosary, Beaufort West. The farm Rosary adjoins the farm Dunedin, previously known as Quaggasfontein. Stratigraphic position: *Endothiodon* zone. Skull without lower jaw. Both stapes missing. Snout region slightly distorted, parts of the zygomatic arches missing, but otherwise perfect. Judging from the sutures it was a mature animal, and had two well-developed canines, both broken off at the points of exit from the sockets. It was transversely sectioned from front to back at intervals of 150 mu. There were 368 sections, each enlarged 6.66 x for the tracings.

Specimen B: Transvaal Museum Number 381. Topotype of *Dicynodon grimbeeki* Broom 1935. From Leeuwkloof, Beaufort West. Most of the fossil specimens collected on the farm Leeuwkloof come from the Harpuisberge on the farm. Stratigraphic position: Top of *Endothiodon* zone. Skull without lower jaw, imperfect in several respects, distorted and crushed in certain regions. No canines are present, but canine buds were observed. (See Barry 1958). Also transversely sectioned from front to back, at intervals of 250 mu. There were 401 sections, each enlarged 4 x for the tracings.

Speecimen C: Transvaal Museum Number 390. Identification uncertain. Originally identified as *Dicynodon sollasi* Broom 1921, being a topotype (?) of this species. Sectioning has revealed that several small post-canines are present (see Fig. 33). It is therefore, sensu stricto, not even a *Dicynodon,* but a member of the Endothiodontidae. From *Biesjiespoort,* Victoria West. The locality Biesjiespoort is often mentioned in the literature, but it should be noted that Biesjiespoort is a Railway station, and that specimens referred to this locality can come from any of the following four farms: Nobelsfontein, Houdenbeck, Highlands, Modderfontein. Stratigraphic position: Top of *Endothiodon* zone. Skull without lower jaw, distorted in parts, zygomatic arches and skull roof damaged. Both stapes and part of right quadrate missing. Transversely sectioned from anterior to posterior at intervals of 250 mu. There were 338 sections, each enlarged 4 x for the tracings.

Description and Discussion

As mentioned above, the descriptive parts of this section are confined to Specimen A, with reference to Specimen B for the sake of completeness. Only in the section dealing with the sphenethmoid complex are all three specimens utilized.

1. Craniometry

In studying skull variation in *Dicynodon sollasi* and *Dicynodon grimbeeki*, Toerien (1953) selected fifteen measurements and indices for comparative purposes. The same method is used here in order to compare Specimen A with those described by Toerien, and to give additional information on the measurements of *D. grimbeeki*.

TABLE I

(*Table of Measurements and Indices, Specimen A*)

Measurement or Index	*Value*
(1) Skull Length	58.6 mm.[1]
(2) Basal Length	53.2 mm.[1]
(3) Skull Width	46.6 mm.
(4) Interorbital Width	15.5 mm.
(5) Intertemporal Width	16.5 mm.
(6) Snout Length	18.6 mm.[1]
(7) Snout Length plus Orbital Length	27.3 mm.[1]
(8) Tip of Snout to Pineal Length	34.4 mm.[1]
(9) $\frac{(3)}{(1)} \times 100$	79.5[1]
(10) $\frac{(4)}{(5)} \times 100$	94.0
(11) $\frac{(4)}{(3)} \times 100$	33.3
(12) $\frac{(5)}{(3)} \times 100$	35.4
(13) $\frac{(6)}{(1)} \times 100$	31.7[1]
(14) $\frac{(7)}{(1)} \times 100$	46.6[1]
(15) $\frac{(8)}{(1)} \times 100$	58.7[1]

[1] Measurements and indices marked thus are approximate; a small error is possible.

In Fig. 31 these measurements and indices are plotted against the corresponding ranges of seventeen specimens of *D. grimbeeki* examined by Toerien. It will be seen that the specimen under discussion falls below the range in five cases, and above it in three. The remaining seven values fall within the described ranges. It is perhaps significant that Index No. 10 (Interorbital Width expressed as a percentage of the Intertemporal Width), which Toerien regards as the "nearest approach to a constant proportion", falls within the known range. The palatal structure is typically that of *D. grimbeeki* as described by Toerien. Furthermore the skull was found in *Endothiodon* zone beds, which stratigraphically represent the level of origin of *D. grimbeeki*. The skull has therefore been referred to *Dicynodon grimbeeki* Broom 1935.

In Fig. 32, Index No. 13 (Snout Length expressed as a percentage of Skull Length) is plotted against two graphs, taken from Toerien (1953), which show the relationship of snout length to skull length in tusked and tuskless specimens of *D. grimbeeki*. The position of Index No. 13 deviates widely from Toerien's graphs, which in the case of tusked specimens of *D. grimbeeki* was based on five points only, one of them doubtfully a "male" (tusked specimen). This suggests a modification, shown in Fig. 32 by the dotted line, to accommodate Specimen A and to eliminate the doubtful male. Statistically these three graphs are analysed in the table below, which gives the coefficent of correlation for each graph, and the 95 per cent confidence limits of the population coefficient of correlation (p).

	Sample Size	*Coeff. of Correlation (r)*	*95% Conf. Limits of p*
(1) "Males"	5	0.98	0.60 — 0.99
(2) "Females"	8	0.65	—0.10 — 0.92
(3) Mod. Graph	5	0.24	—0.73 — 0.87

When a level of significance of 0.05 is used, the null hypothesis that no correlation exists in case (1) above cannot be rejected. In other words there is almost certainly a definite correlation between the two variables. In the other two cases, judgment is reserved, since the samples are too small, and there may or may not be a definite correlation. To a large extent the argument pivots around Toerien's Specimen No. T.M. 298, which, he writes ". . . has no tusks and is probably a female, but it could also be a young male in which the tusks had not yet erupted." (Toerien 1953, p. 59).

The significance of the modified graph for tusked specimens lies in the fact that it then parallels the graph for tuskless specimens, and that in both cases a positive heterogonic (or allometric) coefficient of 1.27 is obtained. It should be noted that the allometry coefficient is here calculated, using skull size as a basis, and not the usual body size. Nevertheless, this is a legitimate usage if the finding of Olson (1944), that "within major therapsid groups skull length shows a markedly constant change with change in body size" (p. 9), is accepted.

Since there is a "frequent relation between heterogony of a character and its

restriction to one sex" (Huxley 1932), this would seem to suggest that snout growth, and therefore the presence or absence of canines which largely affect it (Toerien 1953), is not an expression of sexual dimorphism. In other cases of heterogony it is

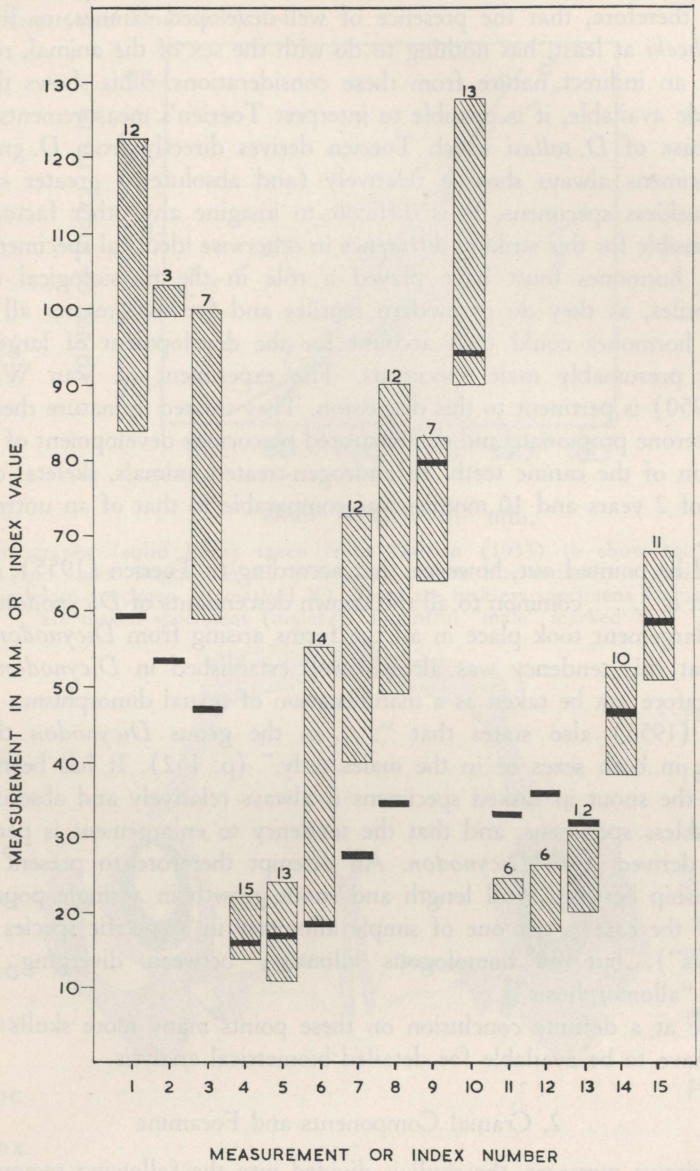

Fig. 31—Range in measurements and index values for 17 specimens of D. grimbeeki. Data from Toerien (1953). Ranges indicated by means of shaded blocks, values for Specimen A by black lines. Number above each block is the number of items used in compiling the block.

sometimes found that the heterogonic organ is only mildly so in one sex, and much more strongly heterogonic in the other.

It is difficult to draw any definite conclusions as far as the relationship between sex and size of canines is concerned, merely from these measurements. Much more data will have to be available on these points to be at all conclusive. Barry's (1958) contention therefore, that the presence of well-developed canines, or their absence, in *D. grimbeeki* at least, has nothing to do with the sex of the animal, receives some support of an indirect nature from these considerations. This shows that as more data is made available, it is possible to interpret Toerien's measurements differently.

In the case of *D. sollasi* which Toerien derives directly from *D. grimbeeki,* the tusked specimens always show a relatively (and absolutely) greater snout length than the tuskless specimens. It is difficult to imagine any other factor except sex to be responsible for this striking difference in otherwise identical specimens. Certainly androgenic hormones must have played a rôle in the physiological economy of Karroo reptiles, as they do in modern reptiles and for that matter all vertebrates. These sex hormones could then account for the development of large canines in what were presumably male specimens. The experiment of Van Wagenen and Hurme (1950) is pertinent to this discussion. They treated immature rhesus monkeys with testosterone propionate and demonstrated precocious development of the skeleton and eruption of the canine teeth. In androgen-treated animals, skeletal development at an age of 2 years and 10 months was comparable to that of an untreated 7 year old control.

It should be pointed out, however, that according to Toerien (1955), enlargement of the snout is ". . . common to all the known descendants of *Dicynodon*". (p. 155). As this enlargement took place in all the forms arising from *Dicynodon,* it is quite possible that this tendency was already well established in *Dicynodon* itself, and should therefore not be taken as a manifestation of sexual dimorphism.

Toerien (1955) also states that ". . . in the genus *Dicynodon* there appear to be tusks in both sexes or in the males only." (p. 152). It has been mentioned above that the snout in tusked specimens is always relatively and absolutely greater than in tuskless specimens, and that the tendency to enlargement is perpetuated in the forms derived from *Dicynodon.* An attempt therefore to present graphically the relationship between skull length and snout growth in a single population may be futile, if the case is not one of simple allometry in a specific species (Simpson's "heterauxesis"), but of homologous allometry between diverging populations (Simpson's "allomorphosis").

To arrive at a definite conclusion on these points many more skulls of *D. grimbeeki* will have to be available for detailed biometrical analysis.

2. Cranial Components and Foramina

For descriptive purposes, the skull is divided into the following regions:

(a) The Snout and Skull Roof
(b) The Palate
(c) The Sphenethmoid Region

(d) The Occipital and Basicranial Regions
(e) The Periotic
(f) The Lower Jaw.

(a) *The Snout and Skull Roof.*

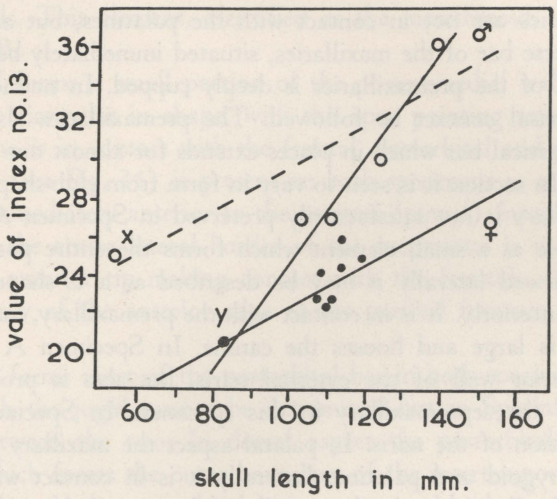

Fig. 32—Two graphs (solid lines) taken from Toerien (1953) to show the relationship between skull and snout lengths, in *D. grimbeeki*. Broken line indicates a possible modification to accommodate Specimen A (marked X). Dots are tuskless specimens (females?), circles are tusked specimens (males?). Doubtful "male" marked Y.

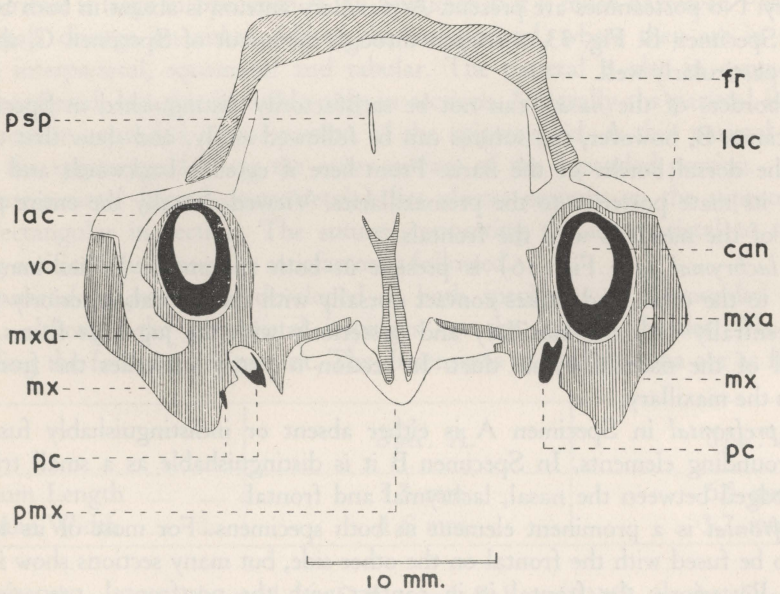

Fig. 33—Specimen C: A transverse section through the roots of the canines, just anterior to the orbits and immediately behind the ductus nasolacrimalis, to show the postcanines (pc). Can, canine; fr. frontal; lac, lachrymal; mxa, maxillary antrum; mx, maxillary; pc, postcanine; pmx, premaxillary; psp, presphenoid; vo, vomer.

The *premaxillaries* (see Fig. 35) are completely fused; no median suture is visible. In palatal aspect they are seen to be in contact with the maxillaries for approximately one third of the skull length. Posteriorly a single median process is in contact with the vomer.

The premaxillaries are not in contact with the palatines, but are separated from them by a transverse bar of the maxillaries, situated immediately behind the choanae. The anterior half of the premaxillaries is deeply cupped. In neither specimen could the premaxillary-nasal contact be followed. The premaxillaries also form the internasal septum, a vertical bar which in places extends for almost one third the distance to the skull roof. In section it is seen to vary in form from club-shaped to rectangular.

The *septomaxillary* is not satisfactorily preserved in Specimen A. In Specimen B it is distinguishable as a small element which forms the entire posterior wall of the external naris. Viewed laterally it may be described as a U-shaped bone, with the concavity facing anteriorly. It is in contact with the premaxillary, maxillary and nasal.

The *maxillary* is large and houses the canine. In Specimen A it seems to form part of the posterior wall of the external naris, but this is probably due to the accidental loss of the septomaxillary in this specimen. In Specimen B it takes no part in the formation of the naris. In palatal aspect the maxillary is in contact with the jugal, ectopterygoid and palatine. Laterally it is in contact with the lachrymal, nasal and jugal. In Specimen A, the maxillaries bear a single pair of large canines, the roots of which are enormous, curving backward slightly and projecting into the anterior portion of the orbits. Here each root is capped by a thin lamina of the maxillary. No postcanines are present. A maxillary antrum is absent in both Specimen A and Specimen B. Fig. 33, a section through the snout of Specimen C, shows the antrum particularly well.

The borders of the *nasals* can not be satisfactorily distinguished in Specimen A. In Specimen B, however, the sutures can be followed easily, and show that the bone forms the dorsal border of the naris. From here it extends backwards and dorsally to meet its mate posterior to the premaxillaries. Viewed dorsally the entire posterior contact of the nasals is with the frontals.

The *lachrymal* (see Fig. 36) is present in both specimens. It lies immediately anterior to the orbit, and makes contact dorsally with the frontal, anteriorly with the nasal, ventrally with the maxillary and posteriorly with the jugal. It forms part of the wall of the naso-lachrymal duct. In section it partly underlies the frontal and overlaps the maxillary.

The *prefrontal* in Specimen A is either absent or indistinguishably fused with the surrounding elements. In Specimen B it is distinguishable as a small triangular bone wedged between the nasal, lachrymal and frontal.

The *frontal* is a prominent element in both specimens. For most of its length it seems to be fused with the frontal on the other side, but many sections show irregular sutures. Posteriorly the frontal is in contact with the postfrontal, preparietal and parietal. It also fills most of the area between the orbits. In section, the anterior portions of the frontals are cupped ventrally to surround partially the olfactory canals,

which run longitudinally towards the nasal region. (See Fig. 38). For almost the entire posterior two-thirds of its length the frontal is in contact with the ventrally situated orbitosphenoid. Small recesses in the frontals house these wing-shaped elements. The frontals are also in contact with a small median element lying between the orbitosphenoids. This element, identified as the mesethmoid, is present in both Specimens A and B.

The *postfrontal* forms a small portion of the posteromedial wall of the orbit. In Specimen A it is triangular in shape, with the apex pointing towards the foramen magnum. The bone is in contact with the frontal, postorbital and parietal.

The *preparietal* (see Fig. 34) is present on both specimens as a median diamond-shaped element, immediately anterior to the parietal (pineal) foramen. In Specimens A and B, almost the entire lateral border of the preparietal is in contact with the parietal, only the anterior tip making contact with the frontals. In both specimens a small portion only of the anterior edge of the parietal foramen is formed by the preparietal.

The *postorbital* forms most of the postorbital bar in both specimens. In Specimen B the contact with the jugal cannot be determined but in Specimen A there is an oblique suture between the two. In dorsal aspect the postorbital shows as a thin elongated bone which forms the outer boundary of the intertemporal skull roof. For almost its entire length the postorbital is in contact with the parietal. Posteriorly, however, its contacts are obscure, and the relation with the squamosal is indistinct in both specimens.

The *parietal* is large in Specimen A. In Specimen B it is much narrower. Posteriorly the parietals diverge on either side of the interparietal, where they are in contact with the interparietal, squamosal and tabular. The parietal is also in contact with the supraoccipital, but this is visible only in sections. Ventrally the parietal is joined with the entire expanded dorsal portion of the epipterygoid. A thin parietal lamina overlaps the epipterygoid along the outer surface of the expanded portion.

The *interparietal* (fused postparietals) lies almost entirely on the supraoccipital and is rectangular in section. The sutures connecting the interparietal to the surrounding ossifications cannot be satisfactorily followed.

The *parietal foramen,* well-developed in both specimens, is surrounded by the parietals, although the preparietal impinges on the anterior border. No bosses surrounding the foramen are present. The dimensions of the foramina are as follows:

	Spec. A.	*Spec. B.*
Maximum Length	3.3 mm.	6.5 mm.
Maximum Width	1.6 mm.	3.7 mm.

Sclerotic plates were observed by Sollas and Sollas (1916) in the *Dicynodon* they sectioned. These authors also mention that "Huxley noticed these in 1859 in *Dicynodon Murrayi.*" (p. 538). No trace of any sclerotics could be detected in

Specimen A. In Specimen B, four consecutive sections through the orbital region show small plates of bone, immediately above the jugal arch. These could possibly be sclerotics.

(b) *The Palate.*

The relationships of the elements constituting the palate conform to the description, given by Toerien (1953) of *D. grimbeeki*. Except for the median ridge, the palatal

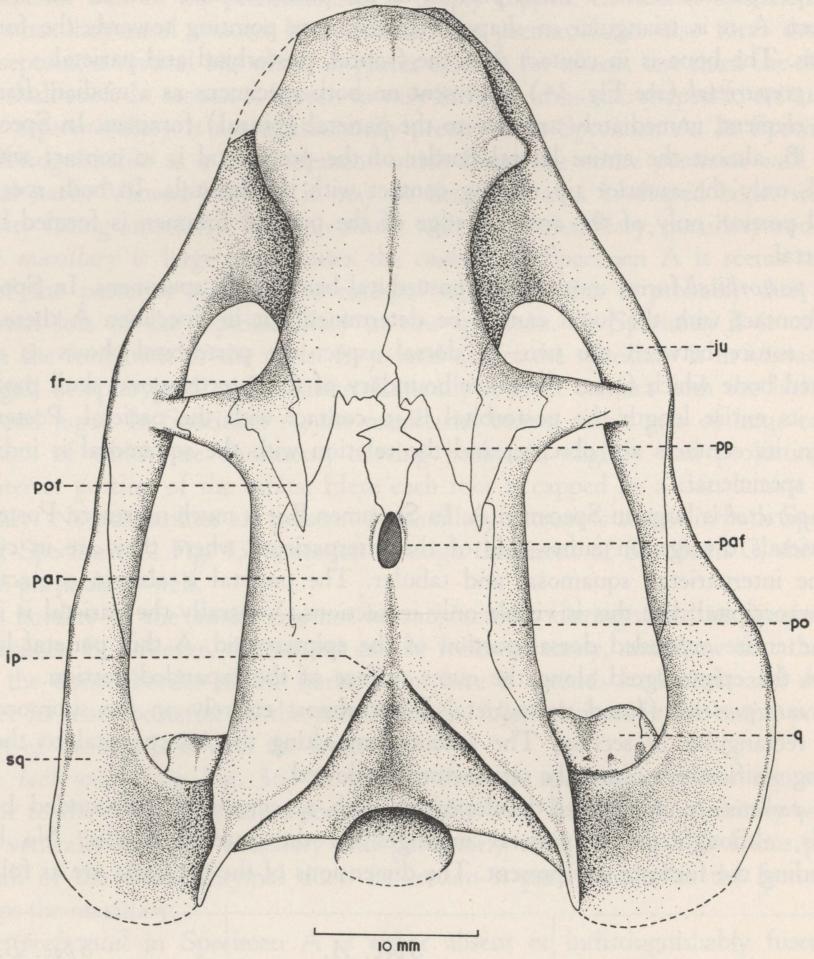

Fig. 34—Specimen A: A dorsal reconstruction of the skull. **fr,** frontal; **ip,** interparietal; **ju,** jugal; **paf,** parietal foramen; **par,** parietal; **po,** postorbital; **prof,** portfrontal; **pp,** preparietal; **q,** quadrate, **sq,** squamosal.

ridges of the premaxillary are not as well-developed in Specimen A as in Toerien's "type" of the palate.

The *palatine* is relatively larger than in the type palate. Anteriorly it is precluded from contact with the premaxillary by a narrow bar of the maxillary. The lateral

surface of the palatine is in contact, for equal distances, with the ectopterygoid anteriorly and the pterygoid posteriorly. The inner border of the palatine is joined, for its entire length, with the vomer. There is a distinct vacuity (just over 2 mm. long) between the palatine and the vomer posteriorly, on either side of the anterior tip of the interpterygoidal vacuity. The palatines, together with the vomer, form the posterior walls of the internal nares.

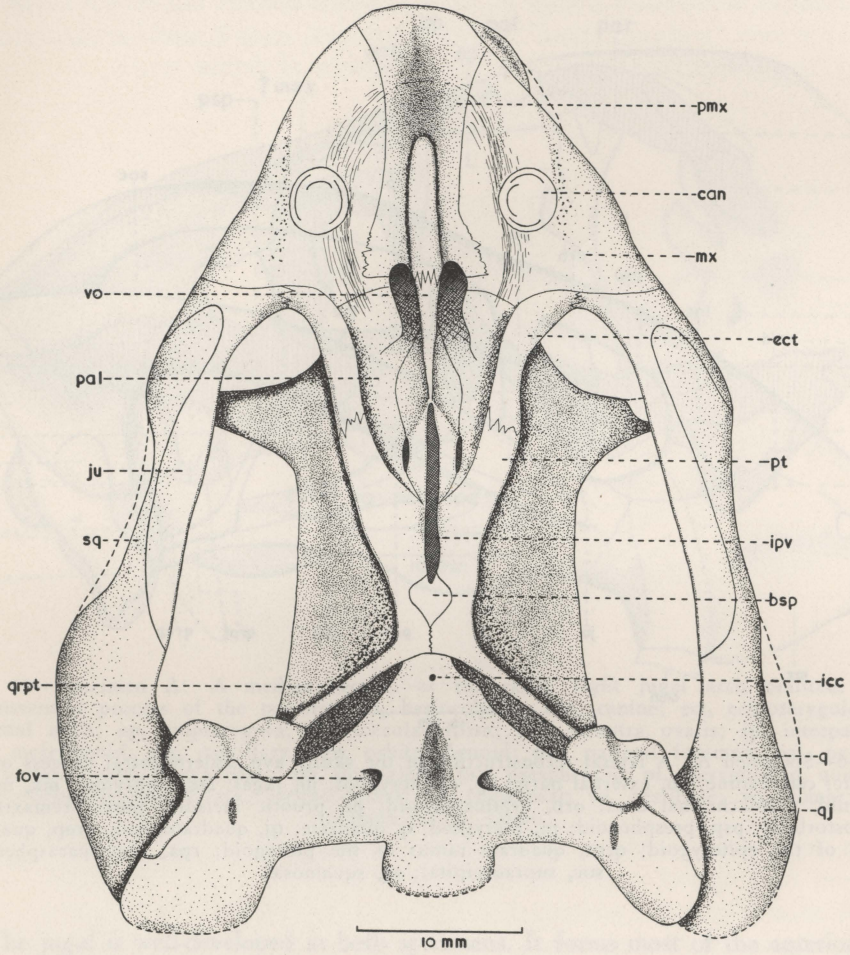

Fig. 35—Specimen A: A palatal reconstruction of the skull. **bsp,** basisphenoid; **can,** canine; **ect,** ectopterygoid; **fov,** fenestra ovalis: **icc,** internal carotid canal; **ipv.** interpterygoidal vacuity; **ju,** jugal; **mx,** maxillary; **pal,** palatine; **pmx,** premaxillary; **pt,** pterygoid; **q,** quadrate; **qj,** quadrato-jugal; **qrpt,** quadrate ramus of the pterygoid; **sq,** squamosal; **vo,** vomer.

The *ectopterygoid* (= transversum = transpalatine) is present in both Specimens A and B. In palatal aspect, it forms the anteromedial border of the opening between zygoma and basis cranii. Laterally it is in contact with the jugal, anteriorly with the maxillary, while the medial and posterior borders impinge on the palatine and

pterygoid respectively. The ectopterygoid develops a very intricate suture with the pterygoid; in section this shows as loose and interconnected islands of bone in the body of the pterygoid. The extreme anterior tip of the ectopterygoid is concealed in the maxillary, and can only be seen in sections. (See Fig. 38).

The *pterygoid* makes no contact with the vomer. Anteriorly it is in contact with

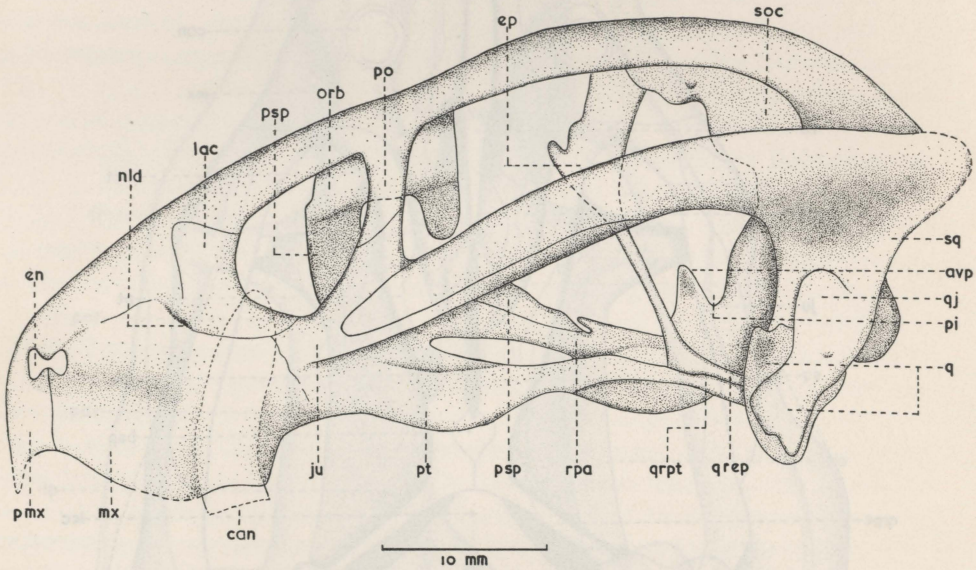

Fig. 36—Specimen A: A lateral reconstruction of the skull. **avp,** anteroventral process of the periotic; **can,** canine; **en,** external naris; **ep,** epipterygoid; **ju,** jugal; **lac,** lachrymal; **mx,** maxillary; **nld,** nasolachrymal duct; **orb,** orbitosphenoid; **pi,** proötic incisure; **pmx,** premaxillary; **po,** postorbital; **psp,** presphenoid; **pt,** pterygoid; **q,** quadrate; **qj,** quadratojugal; **qrep,** quadrate ramus of the epiterygoid; **qrpt,** quadrate ramus of the pterygoid; **rpa,** rostroparasphenoid; **soc,** supraoccipital; **sq,** squamosal.

the palatine and ectopterygoid; posteriorly it develops lateral contacts with the parabasisphenoid. An extensive interpterygoidal-intervomerine vacuity is present. The quadrate ramus of the pterygoid is a long thin bar of constant thickness which abuts against the pterygoid process of the quadrate.

The *vomer* is a median element which in places is grooved or bifid both dorsally and ventrally. Anteriorly it clasps the internasal septum in a complex suture, and

in the interorbital region supports the rostroparasphenoid. In palatal aspect it develops extensive relations with the palatine, and forms the bar separating the internal nares.

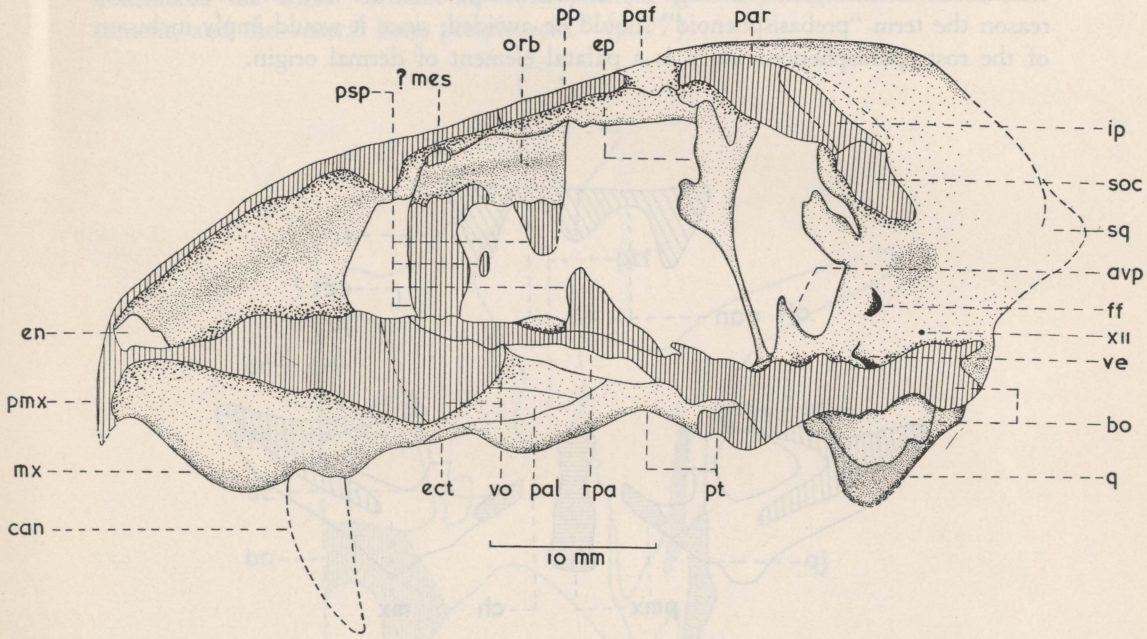

Fig. 37—Specimen A: A median section of the skull, right jugal arch omitted. **avp,** anteroventral process of the periotic; **bo,** basioccipital; **can,** canine; **ect,** ectopterygoid; **en,** external naris; **ep,** epipterygoid; **ff,** floccular fossa; **fov,** fenestra ovalis; **ip,** interparietal; **mes,** mesethmoid; **mx,** maxillary; **orb,** orbitosphenoid; **paf,** parietal foramen; **pal,** palatine; **par,** parietal; **pmx,** premaxillary; **pp,** preparietal; **psp,** presphenoid; **pt.** pterygoid; **q,** quadrate; **rpa,** rostroparasphenoid; **soc,** supraoccipital; **sq,** squamosal; **ve,** vestibule; **vo,** vomer; **XII,** foramen for N. vagus.

The *jugal* is well-developed in both specimens. It forms most of the anterior part of the jugal arch, where it develops a long suture with the squamosals. In palatal aspect, the jugal is in contact medially with the ectopterygoid and anteriorly with the maxillary. Viewed laterally it is in contact anteriorly with the lachrymal and maxillary. Together with the postorbital, the jugal forms the postorbital bar.

(c) *The Sphenethmoid Region.*

(The sphenethmoid, strictly speaking, forms part of the basis cranii, but it is here considered under a separate heading.)

The sphenethmoid (septosphenoid or prebasisphenoid) complex, which forms the bony interorbital septum in *D. grimbeeki* can be ideally studied in the anomodonts, as this group appears to have the most completely developed craniofacial axis of all reptiles. This region is of great importance, not only for a more complete understanding of the anomodont skull, but especially where comparisons with the conditions obtaining in mammals are desired. The complex itself arises wholly by ossification of embryonic cartilage — dermal components are not involved. For this reason the term "prebasisphenoid" should be avoided, since it would imply inclusion of the rostroparasphenoid which is a palatal element of dermal origin.

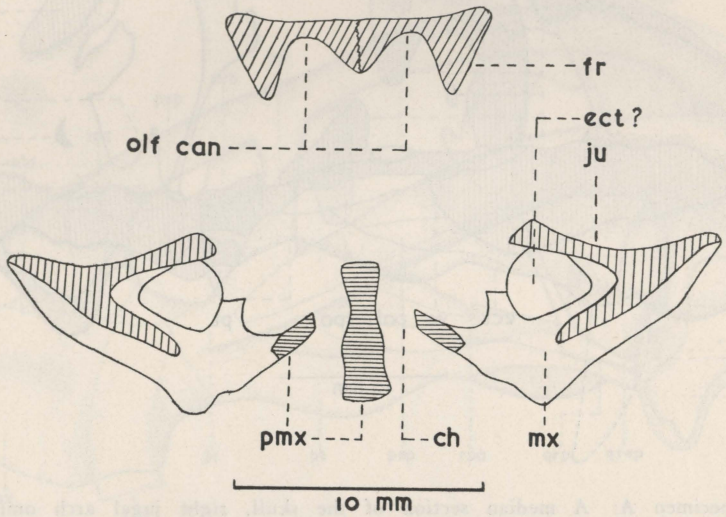

Fig. 38—Specimen A: A section through the choanae. **ch,** choana; **ect,** ectopterygoid; **fr.** frontal; **ju,** jugal; **mx,** maxillary; **olf can,** olfactory canal; **pmx,** premaxillary.

The origin and derivation of the structure in this region have up to the present not been fully agreed upon, with the result that a terminology has arisen which, instead of clarifying the position, has complicated it. Versluijs (1936) writes: "Es ist fraglich, ob diese Verknocherung eine Neubildung ist oder ob sie auf das Sphenethmoid (Gürtelbein) der Amphibien züruckgeführt werden muss". (p. 732). Nevertheless, Olson (1944) maintains that ". . . the condition of *Captorhinus* appears to have arisen from that of the primitive amphibian with relatively little change. The sphenethmoid of *Captorhinus* is not greatly different from that of the therapsid except that there is a ventral element in the latter." (p. 77).

Attempts to homologize the components of the bony interorbital septum with mammalian elements have similarly not been entirely satisfactory, nor have they

been universally accepted. Olson (1944) writes: "The principal problems of evolution of the sphenethmoid complex are to be found in the transition from therapsids to mammals. The situation is complicated by the lack of agreement upon the homologies of the elements involved. Seeley (1898) called the whole complex orbitosphenoid; Sollas and Sollas (1914, 1916) considered it all mesethmoid; Broom (1926, 1929, 1930, 1935) has concluded that the whole complex is presphenoid. The writer (1938) considered the dorsal element as orbitosphenoid with a possible mesethmoid component, and the ventral bone presphenoid." (p. 77).

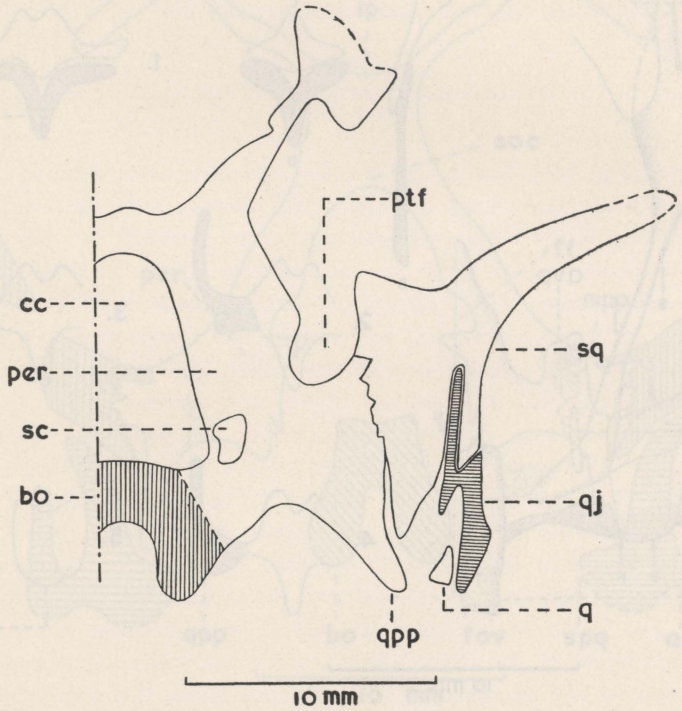

Fig. 39—Specimen A: A transverse section immediately posterior to the fenestra ovalis. **bo**, basioccipital; **cc**, cranial cavity; **per**, periotic; **ptf**, post-temporal fossa; **q**, quadrate; **qj**, quadratojugal; **qpp**, quadrate process of the periotic; **sc**, semicircular canal (?); **sq**, squamosal.

More recently, Camp (1956) has studied this region in a variety of anomodonts, and has proposed further terms to describe the various elements in this region. Camp uses the term "septosphenoid" because ". . . the interorbital septum arises in the anterior trabecular region, and the dorsal wings enclosing the forebrain must arise in the planum supraseptale. This evidently means that it cannot be exactly homologized with any of the bones of recent reptiles or mammals." (p. 315). Where sperate lateral wings occur, he calls them "frontosphenoids". This argument, however, is not necessarily valid, since Malan (1946) has found that ". . . the orbitosphenoid ossification, limited in Lacertilia to the pila metoptica, has in *Monopeltis*

invaded the planum supraseptale, the dorsal part of the interorbital septum, and the posterodorsal part of the nasal septum." (p. 113). In Specimen A, the whole posterior half of the orbitosphenoid ossifications lies behind the posterior margins of the orbits, so that at least part of the orbitosphenoid must have been derived from the pila metoptica. In *D. grimbeeki* this element does not seem to owe its

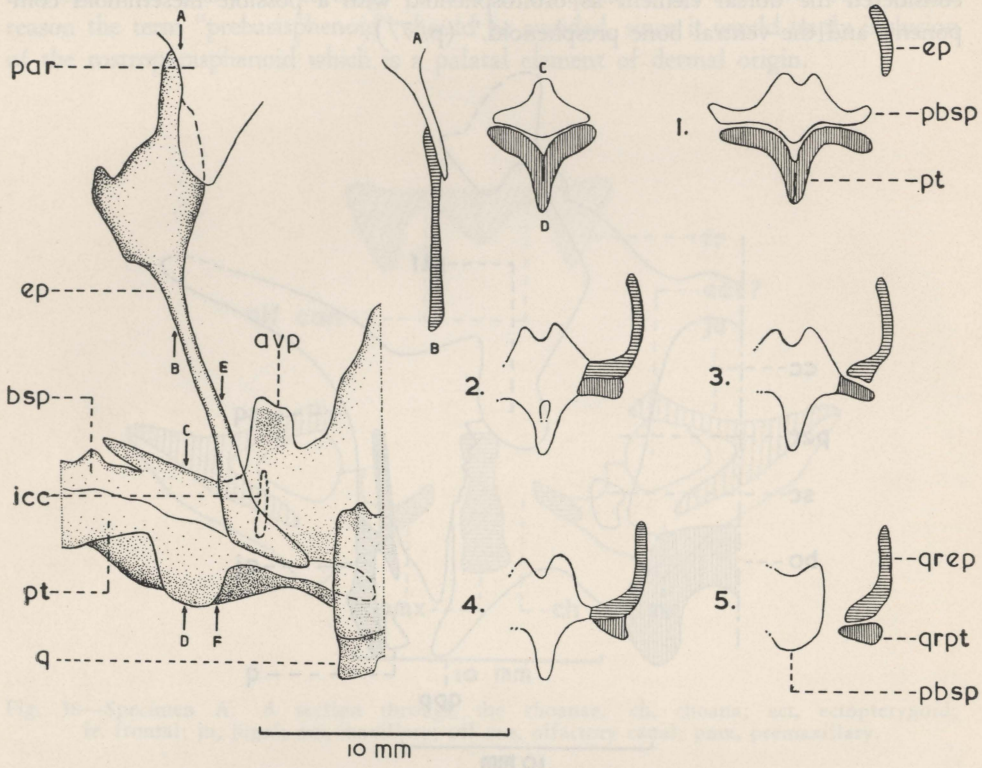

Fig. 40—Specimen A: Lateral reconstruction of left epipterygoid and palatobasicranial articulation. A-B, C-D, are sections at the indicated positions. 1 to 5: A series of consecutive sections, progressing in a posterior direction, beginning with No. 1 at E-F. **avp,** antero-ventral process of the periotic; **bsp,** basisphenoid; **ep,** epipterygoid; **icc,** internal carotid canal; **par,** parietal; **pbsp,** parabasisphenoid; **pt,** pterygoid; **q,** quadrate; **qrep,** quadrate ramus of the epipterygoid; **crpt, quadrate** ramus of the pterygoid.

origin solely to the planum supraseptale, as Camp would suggest. Crompton (1958) who has recently studied *Diarthrognathus* (an Ictidosaur) maintains that "It is probable that an ossification of the orbital cartilage (planum supraseptale) forms the orbitosphenoid and an ossification of the remnants of the interorbital septum, the presphenoid". (p. 195). Furthermore, Roux (1947), in a detailed study of certain undoubtedly primitive mammals, stated that ". . . in all mammals, as

in the Therapsida, it (i.e. the basicranial axis) is composed essentially of three elements, viz. 1. The basioccipital . . . 2. the basisphenoid . . . and 3. the presphenoid (or mesethmoid) which . . . arises from an unpaired centre in the pars trabecularis." (p. 374).

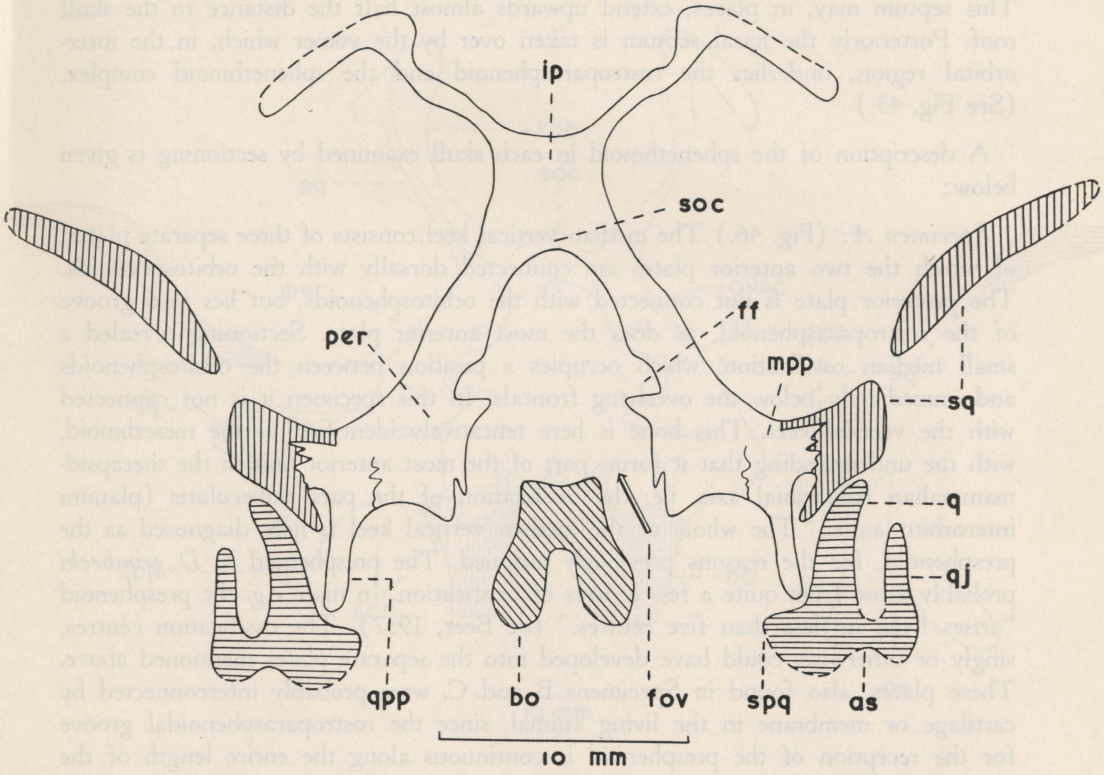

Fig. 41—Specimen A: A transverse section through the fenestra ovalis and vestibule. The quadrate foramen is visible as a deep cleft between the quadrate and quadratojugal. **as,** articular surface; **bo,** basioccipital; **ff,** floccular fossa; **fov,** fenestra ovalis; **ip,** interparietal; **mpp,** mastoid process of periotic; **per,** periotic; **q,** quadrate; **qj,** quadratojugal; **qpp,** quadrate process of periotic; **soc,** supraoccipital; **spq,** stapedial process of quadrate; **sq,** squamosal.

In naming the structures found in anomodonts, the terms presphenoid and orbitosphenoid can therefore be safely used. The term "mesethmoid" has been found by Roux (1947) to be partly homologous with the term presphenoid, the latter always connating that the orbitosphenoids have invaded the basicranial axis. This condition was also found to obtain in the specimens studied here. Furthermore, use of the mammalian terminology is merely a logical extension of the well-known

fact that during the evolution of the mammals, there was almost always a reduction or modification of existing elements. Witness, for example, the loss of the septomaxillaries, postfrontals, postorbitals, prearietal, etc., or the modification of the postdentary jaw elements in the elaboration of a more complex middle-ear region.

The sphenethmoid is situated immediately behind the nasal region which, in *D. grimbeeki,* is divided by a median vertical process of the fused premaxillaries. This septum may, in places, extend upwards almost half the distance to the skull roof. Posteriorly the nasal septum is taken over by the vomer which, in the interorbital region, underlies the rostroparasphenoid and the sphenethmoid complex. (See Fig. 43.)

A description of the sphenethmoid in each skull examined by sectioning is given below:

Specimen A: (Fig. 46.) The median vertical keel consists of three separate plates, of which the two anterior plates are connected dorsally with the orbitosphenoids. The posterior plate is not connected with the orbitosphenoids, but lies in a groove of the rostroparasphenoid, as does the most anterior plate. Sectioning revealed a small median ossification, which occupies a position between the orbitosphenoids and immediately below the overlying frontals. In this specimen it is not connected with the vertical keel. This bone is here tentatively identified as the mesethmoid, with the understanding that it forms part of the most anterior unit in the therapsid-mammalian basicranial axis, i.e. the ossification of the pars trabecularis (planum interorbitonasale). The whole of the median vertical keel is here diagnosed as the presphenoid, for the reasons previously outlined. The presphenoid in *D. grimbeeki* probably arose from quite a few centres of ossification. In man, e.g. the presphenoid "arises from no less than five centres." (de Beer, 1937). The ossification centres, singly or otherwise, could have developed into the separate plates mentioned above. These plates, also found in Specimens B and C, were probably interconnected by cartilage or membrane in the living animal, since the rostroparasphenoidal groove for the reception of the presphenoid is continuous along the entire length of the rostroparasphenoid. (See Fig. 46). The separate plates found in the fossilized skulls seem to represent "islands" of ossification in an extensive cartilaginous interorbital plate.

Specimen B: The condition here is basically the same as in Specimen A, but minor variations occur. The presphenoid consists of two plates, of which only the anterior one is invaded by the orbitosphenoids. Both lie in the usual position on the rostroparasphenoid. The mesethmoid is here continuous with the presphenoid for a length of 5.5 mm., and lies between the orbitosphenoids. In section, it is in the shape of a vertical bar, or thickened T, lying in close juxtaposition against the frontals. (See Fig. 45.)

Specimen C: The presphenoid, as in Specimen B, consists of two plates, of which only the anterior plate has relations with the orbitosphenoids. The mesethmoid

is very small, and is merely a nodule of bone, lying high up in the olfactory canals, against the skull roof. The orbitosphenoids have invaded the presphenoid to a much greater extent than in Specimens A or B. Laterally they extend downwards in places to half the height of the presphenoid. (See Figs. 43, 44).

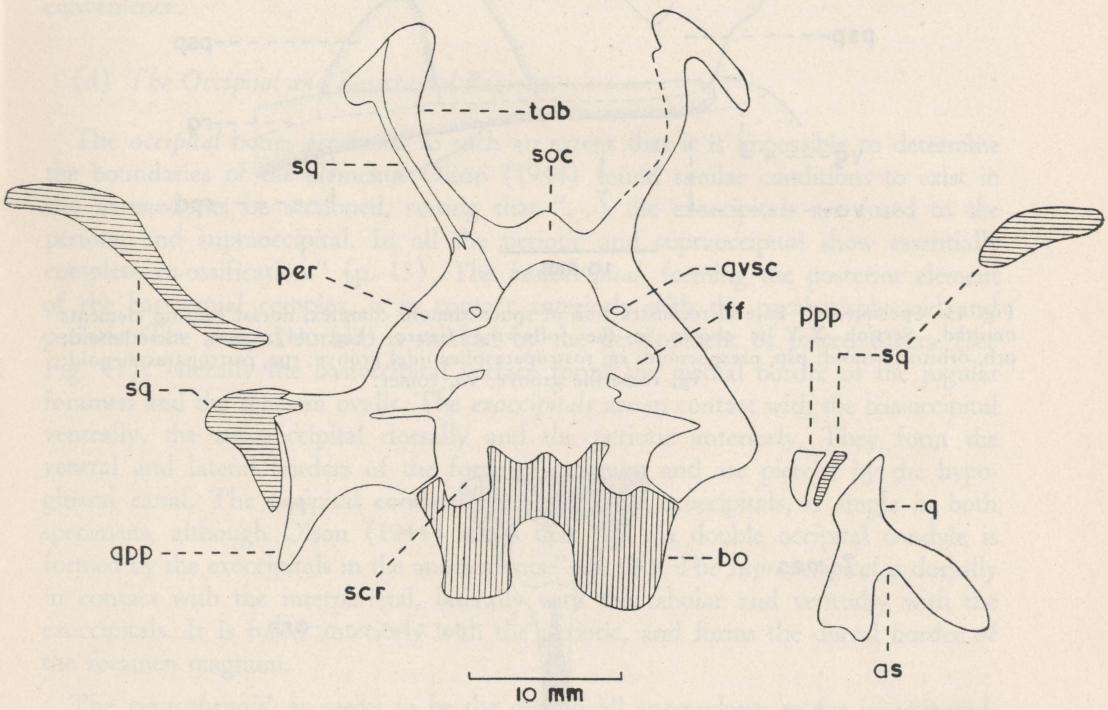

Fig. 42—Specimen C: A transverse section immediately anterior to the fenestra ovalis. **as,** articular surface; **avsc,** anterior vertical semi-circular canal; **bo,** basioccipital; **ff,** floccular fossa; **per,** periotic; **ppp,** paroccipital process of the periotic; **q,** quadrate; **qpp,** quadrate process of the paroccipital; **scr,** sacculo-cochlear recess; **soc,** supraoccipital; **sq,** squamosal; **tab,** tabular.

The interpretation of the facts and ideas presented in this investigation lends support to the view that the sphenethmoid can be traced right through vertebrate phylogeny as a constant unit representing the most anterior ossification of the basicranial axis, since, according to Roux (1947), the mammalian ethmoid "is commonly regarded as being homologous with the sphenethmoid of Amphibians and the sphenoid of Crossopterygia." (p. 378).

In this connection it is interesting to mention the fact that the anurans *Xenopus,*

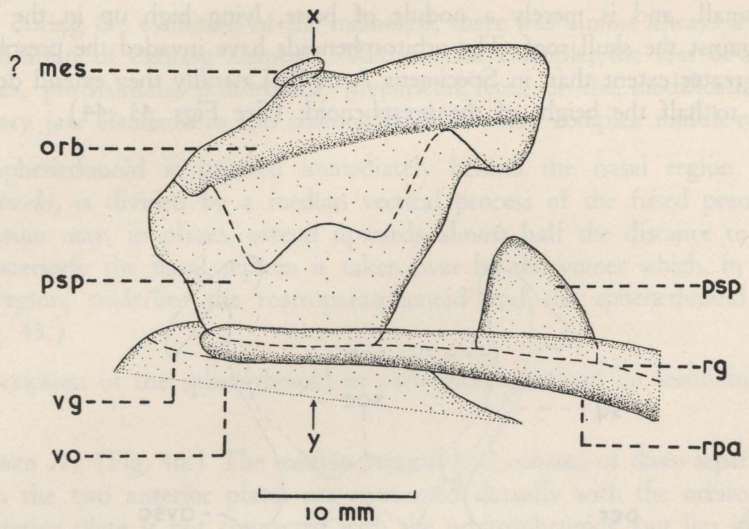

Fig. 43—Specimen C: Lateral reconstruction of sphenethmoid complex, dorsal roofing elements omitted. Section X-Y is shown in the following figure (Fig. 44). **mes,** mesethmoid; **orb,** orbitosphenoid; **psp,** presphenoid; **rg,** rostroparasphenoidal groove; **rpa,** rostroparasphenoid; **vg,** vomerine groove; **vo,** vomer.

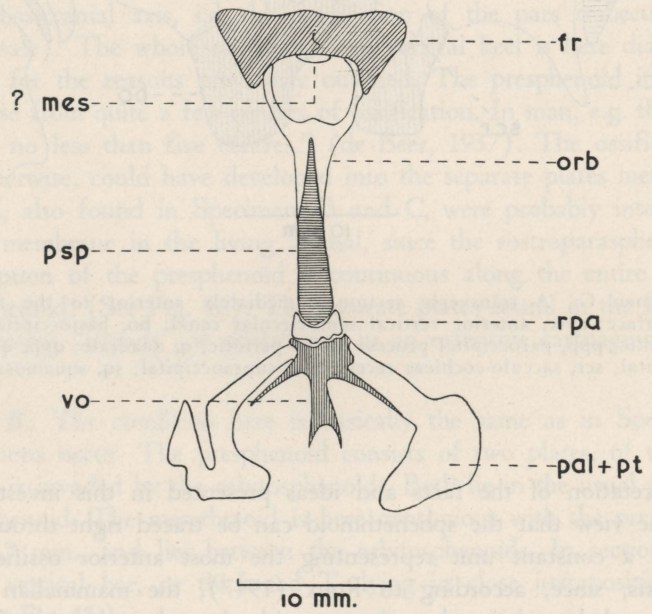

Fig. 44—Specimen C: Section X-Y shown in Fig. 43, but with dorsal and ventral elements included. **fr,** frontal; **mes,** mesethmoid; **orb,** orbitosphenoid; **pal,** palatine; **psp,** presphenoid; **pt,** pterygoid; **rpa,** rostroparasphenoid; **vo,** vomer.

Ascaphus and *Leiopelma* possess a pair of orbitosphenoid bones (see Sedra and Michael, 1957), whereas the majority of the Anura have a sphenethmoid bone. The sphenethmoid was then passed on to the therapsids and, via them, to the mammals. In these two groups, it became variously modified, especially by the development of lateral ossifications (orbitosphenoids). To describe these modified conditions of the sphenethmoid, the terms presphenoid and mesethmoid may be used, although, to a large extent, they are all equivalent. Their usage is dictated by custom and convenience.

(d) *The Occipital and Basicranial Regions.*

The *occipital* bones are fused to such an extent that it is impossible to determine the boundaries of the elements. Olson (1944) found similar conditions to exist in the anomodonts he sectioned, stating that ". . . the exoccipitals are fused to the periotic and supraoccipital. In all the periotic and supraoccipital show essentially complete co-ossification." (p. 13). The *basioccipital,* forming the posterior element of the basicranial complex, is in contact anteriorly with the parabasisphenoid and periotic. The ventral surface is marked by the development of paired tubera (see Fig. 41); laterally the basioccipital surface forms the medial border of the jugular foramen and the fenestra ovalis. The *exoccipitals* are in contact with the basioccipital ventrally, the supraoccipital dorsally and the periotic anteriorly. They form the ventral and lateral borders of the foramen magnum and are pierced by the hypoglossal canal. The occipital condyle, formed by the exoccipitals, is single in both specimens, although Olson (1944) states that ". . . a double occipital condyle is formed by the exoccipitals in the anomodonts." (p. 63). The *supraoccipital* is dorsally in contact with the interparietal, laterally with the tabular and ventrally with the exoccipitals. It is fused anteriorly with the periotic, and forms the dorsal border of the foramen magnum.

The *parasphenoid,* as seems to be the case in all anomodonts so far investigated, is completely fused to the basisphenoid. No sutures are visible to distinguish the two. The compound structure so formed is known as the parabasisphenoid. The rostrum of the parasphenoid (rostroparasphenoid = processus cultriformis) is prominent in both specimens. It is a thin process which curves upwards and forwards from just behind the interpterygoidal vacuity, and points towards the tip of the snout. The anterior half of the rostroparasphenoid lies in a shallow groove in the dorsal edge of the vomer; the posterior portion lies free of the underlying structures, the paired pterygoids. The dorsal edge of the rostroparasphenoid itself possesses an extensive longitudinal groove for the reception of the presphenoid ossifications. In section, the rostroparasphenoid is U- or V-shaped. In Specimen A the rostroparasphenoid is 15 mm. in length.

The *parabasisphenoid* has no posterior expansions which might represent the wings of the parasphenoid. The basipterygoid process, described in greater detail in the

section dealing with cranial kinesis, is small but distinct. The parabasisphenoid is pierced by a single internal carotid canal in both specimens. The canal runs almost vertically through the bone. Since most anomodonts investigated have paired carotid canals, this appears to be a variable feature in this group. The single canal found here probably represents a complete coalescence of the two. The sella turcica is situated immediately behind the carotid canal, and forms a depression in the dorsal surface of the basisphenoid. In both specimens the sella is merely a shallow depression, and a distinct dorsum sellae is absent. Posteriorly the parabasisphenoid makes contact with the basioccipital and periotic. In Specimen A, the parabasisphenoids are completely fused. In Specimen B, an unossified zone between the two marks the contact, but this zone is absent ventrally and no sutures can be seen. In palatal aspect, the parabasisphenoid is visible as a diamond-shaped area which borders on the posterior tip of the interpterygoidal vacuity. Behind this portion, the pterygoids meet for a short distance over the ventral surface of the parabasisphenoid. The internal carotid canal is medially situated behind the point of divergence of the two quadrate rami of the pterygoids.

The *epipterygoid* (columella cranii = alisphenoid) is well-developed in both specimens. It is perfectly preserved in Specimen A, but unfortunately parts of it are missing in Specimen B. The following four regions can be distinguished. (i) a dorsally expanded portion; (ii) a thin tubular shaft connecting this portion to (iii) a footplate which rests on the pterygoid and parabasisphenoid, and (iv) a quadrate ramus which extends towards the quadrate. The dorsal expansion is overlapped by a thin parietal lamina which in section is visible immediately after the parietal foramen has been traversed, sectioning from anterior to posterior. The shaft is approximately parallel to the median longitudinal plane, but is forwardly inclined, making a deviation of 20° from a plane normal to the horizontal cranial axis. The footplate of the epipterygoid has a very characteristic mode of attachment to the basipterygoid, being fused to this process and underlain by the pterygoid. The actual contact of the three bones is very small in extent and is usually visible in only 4 or 5 sections at the most — a distance in the region of 1 mm. The quadrate ramus of the epipterygoid is oval in section, and lies dorsal to the quadrate ramus of the pterygoid. The two rami are closely applied, but lie quite free from one another, and run outwards and backwards towards the quadrate. The epipterygoid ramus extends for only one half this distance. The epipterygoid does not make contact with the pleurosphenoid (= anteroventral process, see Fig. 37), as has been described in one anomodont by Olson (1944), so that the cranial cavity is open between these two elements. The epipterygoid is not pierced by foramina.

The *quadrate* and *quadratojugal* are fused at their base. Both elements are well-developed. The quadrate is not suturally connected with any of the other surrounding structures, and except for its connection with the quadratojugal, lies quite free in a concave area formed by the squamosal and paroccipital. In section the quadrate takes the form of an inverted Y, thus forming an articular surface for the reception

of the lower jaw. The pterygoid process is extremely small, and is represented by a slight ridge. Behind the pterygoid process, but more ventrally situated, is a stapedial process, which is quite distinct in both specimens (see Fig. 41). The quadratojugal is applied to the outer surface of the quadrate, but there is a distinct cleft or quadrate foramen between the two. The quadratojugal extends much farther posteriorly than the quadrate, and the dorsal part forms a characteristic "slotted" attachment to the squamosal (see Fig. 39).

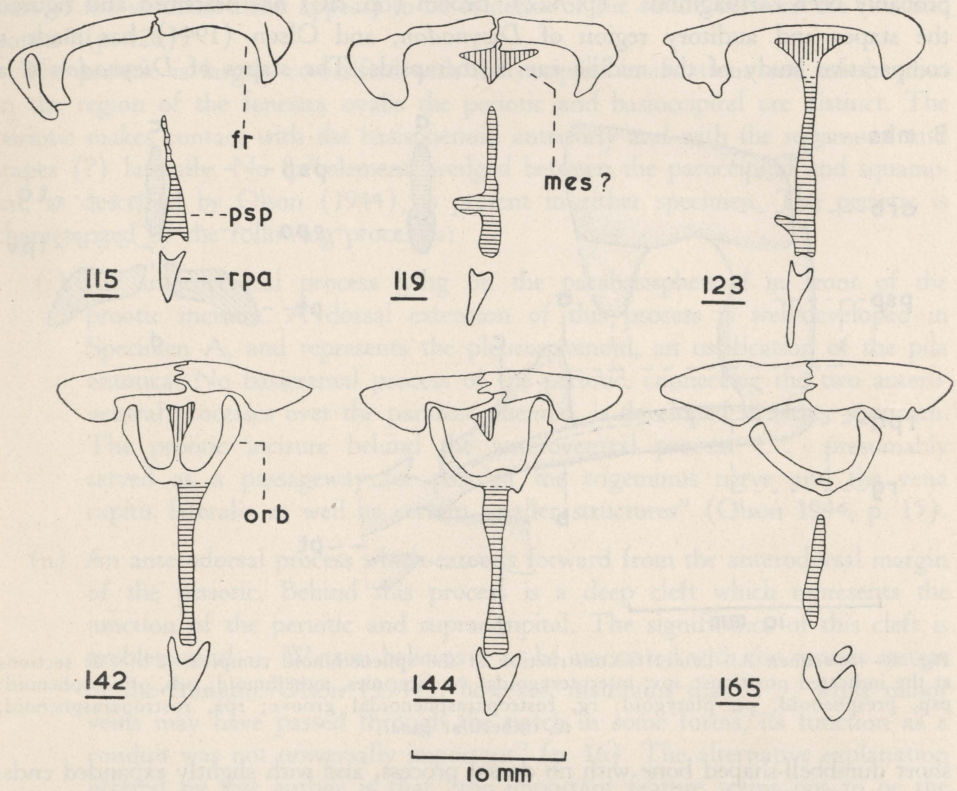

Fig. 45—Specimen B: Various transverse sections through the sphenethmoid (interorbital) region. Numbers are actual section numbers and progress in a posterior direction. Distance between two consecutive sections (e.g. 115-116) is 0.25 mm. **fr,** frontal; **mes,** mesethmoid; **orb,** orbitosphenoid; **psp,** presphenoid; **rpa,** rostroparasphenoid.

The *squamosal* forms the greater part of the zygomatic arch. It develops an extensive contact with the jugal, very similar to the condition found in mammals. In section, the two are smoothly cupped together. Posteriorly the squamosal makes contact with the quadratojugal, periotic, the tabular and the occipital ossifications. It forms a major part of the border of the post-temporal fossa. On the occipital surface, the squamosal is overlain by the tabular.

The *tabular* is present in both specimens. It is a flat sheet of bone closely applied to the squamosal, and forming a portion of the occipital surface. Although the boundaries are indistinct, it makes contact with the interparietal, supraoccipital, and periotic, but does not contribute to the border of the post-temporal fossa.

The *stapes* is not present in Specimen A. In Specimen B, only the proximal portion of the left stapes is preserved. This lies in close apposition to the fenestra ovalis. There is no indication that the stapes was cartilaginous here, as Broom (1912) reported for *Oudenodon kolbei*: "A considerable part of the inner end has probably been cartilaginous." (p. 422). Broom (op. cit.) has described and figured the stapes and auditory region of *Dicynodon,* and Olson (1944) has made a comparative study of the middle ear in therapsids. The stapes of *Dicynodon* is a

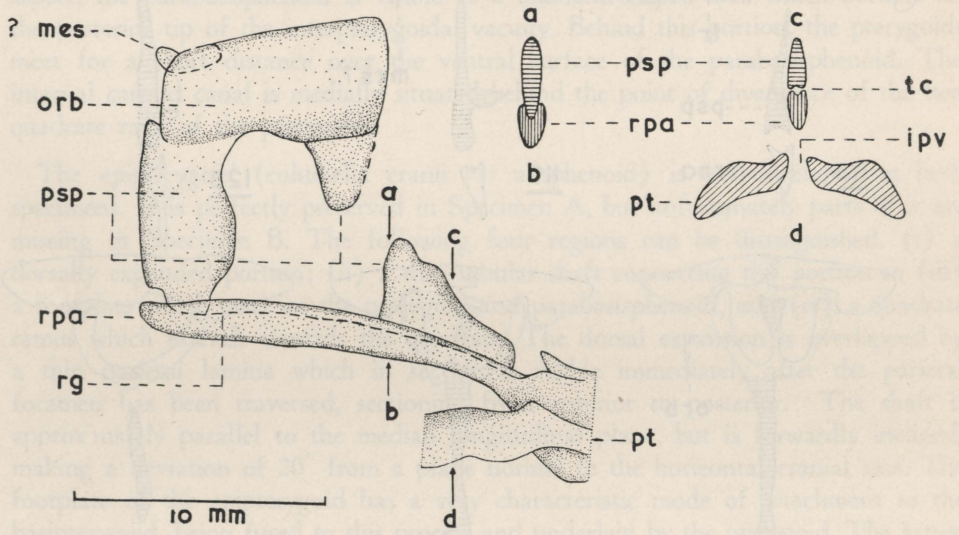

Fig. 46—Specimen A: Lateral reconstruction of the sphenethmoid complex, a-b; c-d: sections at the indicated positions. **ipv,** interpterygoidal vacuity; **mes,** mesethmoid; **orb,** orbitosphenoid; **psp,** presphenoid; **pt,** pterygoid; **rg,** rostroparasphenoidal groove; **rpa,** rostroparasphenoid; **tc,** trabecular canal.

short dumbbell-shaped bone with no dorsal process, and with slightly expanded ends. No stapedial foramen has been reported. Proximally the stapedial foot overlaps the margins of the fenestra ovalis, and engages a flat circular area on the lateral surface of the basioccipital tuber. Distally it articulates with the quadrate. There seems to have been no extrastapes. Camp (1948) has inferred the presence of a cartilaginous extrastapes in the American dicynodont *Placerias.* If present in *Dicynodon,* it is unlikely that it would have remained preserved, so that it is impossible to know whether one was present or not.

(e) *The Periotic.*

The *periotic* is a major component of the cranial wall. According to Olson (1944) about 80 per cent of the cranial wall in anomodonts consists of the periotic. He states

that "In the anomodonts, most of the cranial wall is formed by the periotic regardless of the size of the individual." (p. 104). Furthermore he found no division of the otic capsule. "In none of the specimens . . . is there any evidence of a suture separating the ossification of the otic capsule into two elements." (p. 11). In Specimens A and B the periotic is undivided; in only one section of Specimen A was a small incipient suture observed which might represent the division between proötic and opisthotic (see Fig. 41). This suture is not in the same position as the one found by Broom (1912) in a *Dicynodon*. He states: "Down the descending part of the vestibule there appears to be evidence of the suture between the two otic bones." (p. 420).

The periotic is largely co-ossified with the occipital ossifications and tabular, but in the region of the fenestra ovalis the periotic and basioccipital are distinct. The periotic makes contact with the basisphenoid anteriorly and with the squamosal and stapes (?) laterally. No "x"-element, wedged between the paroccipital and squamosal, as described by Olson (1944), is present in either specimen. The periotic is characterized by the following processes:

(i) An anteroventral process lying on the parabasisphenoid in front of the proötic incisure. A dorsal extension of this process is well-developed in Specimen A, and represents the pleurosphenoid, an ossification of the pila antotica. No basicranial process of the periotic, connecting the two anteroventral processes over the parabasisphenoid, is developed in either specimen. The proötic incisure behind the anteroventral process ". . . presumably served as a passageway for part of the trigeminus nerve and the vena capitis lateralis as well as certain smaller structures" (Olson 1944, p. 15).

(ii) An anterodorsal process which extends forward from the anterodorsal margin of the periotic. Behind this process is a deep cleft which represents the junction of the periotic and supraoccipital. The significance of this cleft is problematical — Watson believes it to be associated with the venous system of the cranium. Olson (1944), however, maintains that ". . . while minor veins may have passed through the notch in some forms, its function as a conduit was not universally important" (p. 16). The alternative explanation offered by this author is that "the important feature seems not to be the notch but the processes above and below which have resulted in its formation" (p. 16). He then homologizes the anterodorsal process of therapsids with the cartilage base for the "orbitosphenoid" cartilage in *Iguana,* and explains the presence of the cleft by the statement that "pronounced variation in the degree of ossification might be expected" (p. 16). The orbitosphenoid of *Dicynodon* lies far forward, in the interorbital region, so that it is unlikely that Olson's homology is correct. Watson's interpretation seems to be the more likely, i.e. the cleft is associated with the cranial vascular system, probably the pineal circulation. Steyn (1958) has recently demonstrated an abundant blood supply to the pineal

complex in certain Lacertilia. It was hitherto believed that the pineal eye had no demonstrable blood supply. The cleft could have housed the dorsal longitudinal sinus which collected the venous drainage from the pineal organ.

(iii) A paroccipital process which projects laterally and which, if the conditions found in these forms be homologized with those in living reptiles, probably represents a portion of the opisthotic. The paroccipital process itself consists of two subdivisions: a mastoid process which in both specimens makes a close sutural connection with the squamosal (see Fig. 41), and a quadrate process. The latter is a gently curved finger-like process which approximates the quadrate but lies quite free of it.

The important foramina of the brain-case are the following:

The fenestra ovalis which is large in Specimen A and which seems to represent the coalescence of both the fenestra ovalis and the jugular foramen. The medial border of the fenestra is formed by the basioccipital, and the outer edge by the periotic. The vestibule is widely open to the brain-case and lies a few sections posterior to the sacculo-cochlear recess. A distinct floccular fossa is present in both specimens and is visible in certain sections through the fenestra ovalis, or just anterior to the fenestra (see Figs. 41, 42).

No foramen for the nervus facialis can be observed in the periotic. This foramen has been figured many times in the literature, and is stated to occupy a position low down on the cranial wall, in front of the inner ear structure and usually above the unossified zone. In both specimens sectioned the foramen might possibly be blocked by matrix indistinguishable in colour from that of the surrounding bone.

A hypoglossal canal, for the nervus hypoglossus, is present and pierces the exoccipital.

(f) *The Lower Jaw*

Unfortunately in both of the *D. grimbeeki* specimens studied the lower jaw was missing. The jaw of *D. grimbeeki* has recently been described by Camp (1956) who found it to be a relatively massive structure in which both dentary and splenial form the symphysis. The lower jaw consists of the following elements: dentary, splenial, angular, surangular, prearticular and articular. The angular has a reflected lamina, and a Meckelian sulcus is present between surangular, angular and prearticular. Viewed laterally, this sulcus has in its middle a complete gap between dentary and surangular.

3. Cranial Kinesis

Kinetism is well known in certain modern reptiles and birds, but it has received scant attention in the therapsids. Olson (1944), who sectioned representative therocephalians, cynodonts, gorgonopsians and anomodonts, made no mention of kinetism at all. Recently Crompton (1955 (b)) has shown that in certain scalopo-saurids, which he sectioned, kinetic movement was possible. It is therefore instructive

to consider the problem in anomodonts, since kinetism of various types seems to have been independently evolved in several sub-mammalian groups. There are different types of kinetic movement that can be distinguished, and although there seems to be a correlation between kinetism and diet (or feeding habits), it is not a very exact one. This avenue of research has not been followed up to the point where generalizations are permissible.

Versluijs (1912), the pioneer student of kinetism, considered all therapsids to have akinetic skulls. He pointed out, however, that the pelycosaurian skull had a typical metakinetic build, but maintained that no movement was possible. In a later paper (1936) he concluded that "Die primitiven Cotylosauria müssen einen metakinetischen Schädel gehabt haben" (p. 747).

The mechanics of kinetism require that two segments of the skull should be able to slide along certain surfaces relative to one another. These are the occipital segment, consisting of the occipital ossifications, periotic and parabasisphenoid, and the maxillary segment, composed of the remaining cranial moiety. According to Crompton (1955 (b)) the tabular in *Ictidosuchops* (a theriodont) forms part of the occipital and not of the maxillary segment. These two segments should be able to change their position relative to one another. If the occipital segment be regarded as fixed, then when the jaws are maximally distended and kinesis is called into play the maxillary segment will rotate in such a way as to increase the effective gap between the jaws. The extra movement actuated by kinesis need not be great. Apparently in the case described by Crompton (1955 (b)) the function is not to allow of a wider gap but to absorb shock when vigorous biting takes place.

The crucial points are therefore to be found wherever these two segments are in contact. Crompton lists eight such points of contact, in *Ictidosuchops*. He also maintains that in the anomodonts the sphenethmoid complex firmly unites the basisphenoid to the skull roofing, and that this would rule out the type of kinetism proposed for *Ictidosuchops*. The serial sectioning of *D. grimbeeki* has revealed that the orbitosphenoids fit into smooth grooves along the ventral surfaces of the frontals, but it is difficult to say whether movement here is at all possible. Certainly the contact between the two is very smooth and they are by no means fused. The median presphenoid supporting the orbitosphenoids was presumably cartilaginous. Here again it is difficult to say whether movement along the groove was possible. It is unlikely, however, because the posterior region of this groove also housed the trabecular canal, which carries a branch of the internal carotid artery and the ramus palatinus of VII in their forward extensions. (Camp 1956).

The assertion that the sphenethmoid complex firmly unites the basicranial axis to the dorsal roofing elements has not been conclusively proved. Even a very limited amount of movement in this region, in *D. grimbeeki* for example, would suffice to warrant inclusion in the kinetic category, provided of course that there is nothing else to prevent it from being operative.

Of the other possible regions where movement could take place, the dorsal occipital area is difficult to interpret in transverse sections since kinetic surfaces, if they are

present, are more or less vertically disposed, i.e. they are steeply inclined to the longitudinal cranial axis when this is orientated horizontally. Furthermore, fusion has occurred between various components of the occipital region. But kinetism of the type described in scaloposaurids is impossible for the following reasons:

(i) The palatobasicranial articulation allows of no sliding of the pterygoids and epipterygoids along the basipterygoid. (see Fig. 40). The relationships here are clearly revealed by sectioning. The elements participating are the basipterygoid, pterygoid and the footplate of the epipterygoid. Immediately anterior to the junction of the three, the pterygoids underlie the parabasisphenoid and are connected by a median longitudinal suture approximately 2 mm. in length. Movement in this region seems quite possible as the sections show a very smooth clear zone separating the two. Just posterior to this region the footplate of the epipterygoid lies on the pterygoid, and both are fused to the basipterygoid. This is visible in only a few sections, but it nevertheless conclusively shows that no movement is possible here. Farther backwards the quadrate rami of the pterygoid and epipterygoid extend outward at an angle of approximately 45° and run in a posterior direction toward the quadrate. The two rami lie closely applied to one another but are not united. The pterygoid ramus runs the full distance to make a loose contact with the small pterygoid process of the quadrate. These two were probably syndesmotically (or synchondrotically) connected in life, since the quadrate in therapsids is not firmly fixed to the skull, showing that it could perhaps move to a certain extent. The epipterygoid ramus extends for only half the distance towards the quadrate.

(ii) The paroccipital is fused to the squamosal. In *Ictidosuchops* Crompton finds an articulation between the mastoid process of the paroccipital and the squamosal. The two here are connected by means of an interdigitated suture. (See Fig. 39.) There is no possibility of movement.

As has been mentioned above, the question of sliding surfaces in the dorsal occipital region is difficult to assess. The sutures here are not easy to follow because considerable fusion between the occipital ossifications, the periotic and the basisphenoid has occurred. Olson (1944) has reported extensive fusion in the occipital region of the anomodonts he sectioned, and this may be a general condition in this group. Until more evidence is forthcoming, the question as to whether kinetic movement is possible in this region must be left as undecided.

The conclusion arising from these considerations is therefore that in the specimens studied, kinetism of the metakinetic type as described in *Ictidosuchops* is absent.

Mention must be made of two other types of "kinetism" which have been discussed in anomodonts. Camp (1956), in his study of the American dicynodont *Placerias,* indicated that in this form a degree of movement

might be permissible between the premaxillaries and the remainder of the skull. However that may be in *Placerias,* it is extremely unlikely in *Dicynodon.* The palatine process of the premaxillaries is tightly wedged between the maxillaries, and it has a complex suture with the vomer, which clasps the posterior limit. In addition, the nasals in *Dicynodon* overlap the premaxillaries, as Camp has indicated in his interpretation.

The other type to be considered arises from Crompton's view that ". . . Parrington . . . has a great deal of evidence to support the contention that kinetism is present in at least some of the gorgons, anomodonts and cynodonts. (He) does not find an articulation between the basisphenoid and the pterygoid, but rather between the basisphenoid and basioccipital below the unossified zone" (p. 171). Of the specimens studied, Specimen A has no unossified zone. Specimen B has an incipient unossified zone which extends only third of the distance in a ventral direction at the junction of the basisphenoid and basioccipital. The unossified zone in anomodonts (if present) generally marks this junction, although in both specimens no sutures are developed. The two (i.e. basisphenoid and basioccipital) are completely fused, so that any movement between them is out of the question.

The absence of kinetism can be regarded as a probable result of the herbivorous specializations adopted by *Dicynodon* and for that matter all advanced anomodonts. The skull is a solid, partially fused unit which housed powerful masticatory muscles and so enabled the animal to cope with hard plant material.

Summary and Conclusions

(i) The skull of *Dicynodon grimbeeki* has been studied by means of the serial sectioning technique. For this purpose two skulls were completely sectioned, and graphical reconstructions of various aspects of the skulls were made.

(ii) The structure of the skull roof and palate conforms, within the limits of variation known for this species, to descriptions given in the literature.

(iii) The periotic and the occipital ossifications are to a large extent fused. No division of the otic capsule could be observed.

(iv) In discussing the skull measurements, some evidence is advanced to support the contention of Barry (1958) that the presence or absence of canines in this species is not an expression of sexual dimorphism.

(v) In addition to the two skulls of *D. grimbeeki,* a third skull (that of an unidentified anomodont) was completely sectioned. A comparative study of the sphenethmoid region of all three skulls was made, and a terminology of the elements of the interorbital septum was investigated. It is concluded that the basicranial axis of *Dicynodon* is comparable to that of mammals, in that it consists of the same units and the same terminology is permissible.

In this connection the terms "septosphenoid" and "frontosphenoid", used to describe elements in the dicynodont interorbital septum, should be abandoned.

(vi) The presence of a floccular recess (or fossa), denied by Schepers (1937) in *Dicynodon dutoiti,* is confirmed in all three specimens studied.

(vii) It is suggested that the cleft between the supraoccipital and anterodorsal process of the periotic was associated with the vascular system of the pineal organ.

(viii) The problem of kinetism in *D. grimbeeki* is investigated. It was found that this species is akinetic, and that the loss of kinetism from presumably kinetic ancestors should be regarded as an adaptation to herbivorous feeding habits.

Acknowledgements

I wish to thank Dr. T. H. Barry for his constant help and encouragement. Also the staff of the Bernard Price Institute for Palaeontological Research in Johannesburg, for one of the specimens used in this study, and for many other kindnesses; the Director of the Transvaal Museum and Dr. J. T. Robinson for additional material; Prof. C. L. Camp, of the University of California, for a gift of literature.

References

(1) BARRY, T. H., 1958. On the significance of tuskless specimens of *Dicynodon grimbeeki* Broom. *Palaeont. Afric.*, V, 57-66.

(2) BROOM, R., 1912. On the structure of the internal ear and the relations of the basicranial nerves in *Dicynodon,* and on the homology of the mammalian auditory ossicles. *Proc. Zool. Soc., Lond.*, 419-425.

(3) BROOM, R., 1926. On the mammalian presphenoid and mesethmoid bones. *Proc. Zool. Soc., Lond.*, 257-264.

(4) CAMP, C. L., 1948. The Dicynodont ear. R. Broom Comm. Vol. Roy. Soc., S. Afr., 1948, 109-111.

(5) CAMP, C. L. and WELLES, S. P., 1956. Triassic dicynodont reptiles. *Mem. Univ. Calif.* Vol. 13, No. 4, 255-348.

(6) CROFT, W. N., 1950. A parallel grinding instrument for the investigation of fossils by serial sections. *J. Palaeont.* Vol. 24, No. 6, 693-698.

(7) CROMPTON, A. W., 1955 (a). Techniques for the study of Permo-Triassic fossils of South Africa. *S. Afr. Mus. Bull.* Vol. 6, No. 3. 57-60.

(8) CROMPTON, A. W., 1955 (b). A revision of the Scaloposauridae with special reference to kinetism in this family. *Res. Nat. Mus.*, Bloemfontein, Vol. 1, Part 7, 149-183.

(9) CROMPTON, A. W., 1958. The cranial morphology of a new genus and species of Ictidosaurian. *Proc. Zool. Soc., Lond.*, Vol. 130, Part 2, 138-216.

(10) DE BEER, G. R., 1937. The development of the Vertebrate skull. Oxford: Clarendon Press.

(11) HAUGHTON, S. H. and BRINK, A. S., 1954. A bibliographic list of reptilia from the Karroo beds of Africa. *Palaeont. Afric.* Vol. II.

(12) HUXLEY, J. S., 1932. Problems of relative growth. Methuen and Co., London.

(13) MALAN, M. E., 1946. Contributions to the Comparative anatomy of the nasal capsule and the organ of Jacobson of the Lacertilia. *Ann. Univ. Stell.* Vol. XXIV, Sect. A, No. 4.

(14) OLSON, E. R. and WHITMORE, F. C. Jr., 1944. Machine for serial sectioning of fossils. *J. Palaeont.*, Vol. 18, No. 2, 210-215.

(15) OLSON, E. C., 1944. Origin of mammals based upon cranial morphology of therapsid suborders. *Geol. Soc. Amer.* Spec. Paper No. 55.

(16) PUSEY, H. K., 1939. Methods of reconstruction from microscopic sections. *J. Roy. Microsc. Soc.* Vol. LIX, 232-244.

(17) ROUX, G. H., 1947. The cranial development of certain Ethiopian "Insectivores" and its bearing on the mutual affinities of the group. *Acta Zool.* XXVIII, 165-397.

(18) SEDRA, S. N. and MICHAEL, M. I., 1957. The Development of the Skull, Visceral Arches. Larynx and Visceral Muscles of the South African Clawed Toad, *Xenopus laevis* (Daudin) during the Process of Metamorphosis (from Stage 55 to Stage 66). *Verh. Koninkl. Nederl. Akad. Wetensch.* Afd. Nat. Tweede Reeks, Deel 61, No. 4.

(19) SCHEPERS, G. W. H., 1937. The endocranial cast of *Dicynodon dutoiti* sp. nov. *S. Afr. J. Sci.* Vol. XXXIII, 731-749.

(20) SOLLAS, I. B. J. and SOLLAS, W. J., 1914. A study of the skull of a *Dicynodon* by means of serial sections. *Phil. Trans. Roy. Soc.*, Lond. Series B, Vol. 204, 201-226.

(21) SOLLAS, I. B. J. and SOLLAS, W. J., 1916. On the structure of the dicynodont skull. *Phil. Trans. Roy. Soc.*, Lond. Series B, Vol. 207, 531-539.

(22) STEYN, W., 1958. The Pineal Circulation in Some Lizards. *S. Afr. J. Sci.* Vol. 54, No. 6, 143-147.

(23) TOERIEN, M. J., 1953. The evolution of the palate in South African Anomodontia and its classificatory significance. *Palaeont. Afric.*, Vol. I, 47-117.

(24) TOERIEN, M. J., 1955. Convergent trends in Anomodontia. Evolution. 9: 152-156.

(25) VERSLUIJS, J., 1912. Das Streptostylie-Problem und die Bewegungen im Schädel bei Sauropsiden. *Zool. Jb.* Suppl. 15, 2: 545.

(26) VERSLUIJS, J., 1936. Kranium und Visceralskelett der Sauropsiden. Handbuch der Vergl. Anat. der Wirbeltiere.

(27) VAN WAGENEN, G. and HURME, V. O., 1950, *Proc. Soc. Expt. Biol. Med.* 73: 296.

(28) WATSON, D. M. S., 1948. *Dicynodon* and its allies. *Proc. Zool. Soc., Lond.*, Vol. 118, 823-877.

(29) WATSON, D. M. S. and ROMER, A. S., 1956. A classification of therapsid reptiles. *Bull, Mus. Comp. Zool.* Vol. 114, No. 2.