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NOTES ON SOME NEW *DIADEMODON* SPECIMENS IN THE COLLECTION OF THE BERNARD PRICE INSTITUTE

By A. S. Brink

ABSTRACT

Seven *Diademodon* specimens are dealt with and all are reasonably adequately figured. These comprise a large *D.mastacus* specimen already featured in publication; a complete skull of *D. grossarthi*; an interesting snout of *D.haughtoni*; and four immature *D.browni* specimens of various ages and sizes. The latter form part of about eight similar individuals found in an area some two yards square and could be the litter of a single *Diademodon* family. Attention is focussed on the snouts and the peculiar nature of the external nares.

INTRODUCTION

Since an interesting large *Diademodon mastacus* specimen was last featured in description in 1956 (Brink)*, several specimens of this genus have been added to the collection of the Bernard Price Institutue. These comprise a wide variety, though few in number, and they exhibit some features worth recording. One of these is a new species, *D. rhodesiensis*, described in a paper (Brink: Two cynodonts from the Ntawere Formation in the Luangwa valley of Northern Rhodesia) which appears (p.77) in this issue of Palaeontologia Africana. It is not further dealt with in this paper.

The *D. mastacus* referred to above is a sagittal half of a skull, excellently preserved, and a photograph of the left side of the anterior half of the skull was published (Brink, 1956)*. A diagrammatic palatal view was also featured, based on this specimen, but since it was thought that the narrowness of the palate is the result of distortion, it was broadened in the figure. In view of the condition in the new specimens it is clear that the palate of *Diademodon* is indeed extremely narrow and the postcanine rows of teeth form very conspicuous arcs. The published figure was intended as diagrammatic to illustrate a particular argument, but it is nevertheless unfortunate that an incorrect impression of the actual shape was conveyed.

The specimen (Cat. No. 314) is now figured (figures 16, 18 and 20) more accurately and more comprehensively according to the specimen as it is preserved. It is not noticeably distorted. The missing right half is restored from the left side and the basicranial region is restored from the *D. grossarthi* specimen also described

* Palaeont. Afric. IV, p. 77.

in this paper. Certain structural details not clearly visible in one or the other of these two specimens could almost invariably be confirmed by its fellow.

The specimen of *D. grossarthi* is most excellent. It lacks the premaxillaries and there is some damage along the left occipital crest and external auditory meatus fold, but otherwise it is prefectly preserved, especially the superficial bone texture, and it could be cleaned quite completely, leaving matrix only within the nasal cavity and brain case.

Another excellent specimen is, unfortunately, only the preorbital half of a very large skull of *D. haughtoni*. This specimen is particularly good from the point of view of its bone surface preservation. The external nares are in good condition and it is this specimen which focused attention not only on the peculiar arrangement in this region but also on the considerable measure of individual and specific variation.

This paper deals further with four of some eight immature *D. browni* specimens discovered in an area about two yards square (Kitching: Notes on some fossil pockets and bone beds etc., p. 113 of this issue of *Palaeont.Afric.*). These four specimens are complete skulls, the smaller two with lower jaws, but they are somewhat crushed. The larger two are not distorted and, while they lack lower jaws, their palates could be cleaned rather well. The balance of the specimens are fragmentary portions of skulls and are not yet prepared. The four specimens featured have skeletal bones associated, enough to indicate that they had been buried separately, but the skeletons are very incomplete and distorted. Few individual bones are in a good enough condition for description.

There can be little doubt that these specimens form the young of perhaps a single *Diademodon* family. The number and the differences in size may suggest that more than one litter, or even more than one family, is involved. Whatever the case, their close association points at intimate family life although successive perishing in mud at a drinking place could be an alternative explanation, especially in view of the fact that a *Bauria* and two other cynodonts are equally intimately associated. Successive perishing may account for the differences in ages. It would nevertheless appear that the period of time involved had been less than a season.

MATERIAL

DIADEMODON MASTACUS Seeley, 1894.

1*st Specimen:* Sagittal half of large skull (M314/F2522), perfectly preserved, from *Cynognathus*-zone beds on the farm Luiperdskop, Burghersdorp district.

DIADEMODON GROSSARTHI Broili and Schröder, 1935.

2*nd Specimen:* Complete, large, well preserved skull (M359/F3754) from *Cynognathus*-zone beds on the Lady Frere Commonage.

DIADEMODON HAUGHTONI Broili and Schröder, 1935.

3rd Specimen: Preorbital half of a very large skull (M360/3757) from *Cynognathus*-zone beds on the Lady Frere Commonage.

DIADEMODON BROWNI Seeley, 1894.

4th Specimen: Immature skull, without lower jaw, rather complete and well preserved, with some skeletal bones associated (M361/F3772) from a fossil pocket in middle *Cynognathus*-zone beds on the farm Cragievar about a mile south of Burghersdorp.

5th Specimen: Immature skull, without lower jaw, rather complete and well preserved, smaller than the previous specimen (M362/F3773) from exactly the same locality.

6th Specimen: Immature skull and lower jaw, somewhat crushed (M362/F3769), slightly smaller than the 5th specimen, from exactly the same locality.

7th Specimen: Immature skull and lower jaw, with some additional skeletal bones, partially distorted (M364/F3771), smaller than the 6th specimen and from exactly the same locality.

In the accompanying table of measurements and where convenient in the text, specimens are referred to by numbers in accordance with the above list.

TABLE OF MEASUREMENTS

	1st	2nd	3rd	4th	5th	6th	7th
Total length of skull	333	313		158	125	106	97
Length to occipital condyles	293	276		147	119	99	90
Length to parietal notch	291	273		135	108	94	84
From snout tip to pineal—	206	197		106	88	78	69
to anterior borders of temporal vacuities	190	177		91	76	67	59
to anterior borders of orbits	134	126	165	63	51	43	39
to pterygoid processes	188	172		98	77	62	
to posterior border of secondary palate	119	112	137	61	48		
Maximum width of snout	68	62	74	30	27	23	19
Minimum width of snout	46	47	55	26	23	20	18
Interorbital width	60	60	65	28	25	22	23
Maximum width of skull	227	254		115	94	79	71

DISCUSSION

The first three specimens

These three specimens (*D.mastacus*, *D.grossarthi* and *D.haughtoni*) do not warrant separate comprehensive and detailed analyses. It is felt that the figures are adequate. Only certain aspects of interest and significant variations will be dealt with on a comparative basis.

The 3rd specimen (*D. haughtoni*) is more than four times the size of the smallest 7th specimen (*D. browni*). This should not be evaluated in terms of a growth

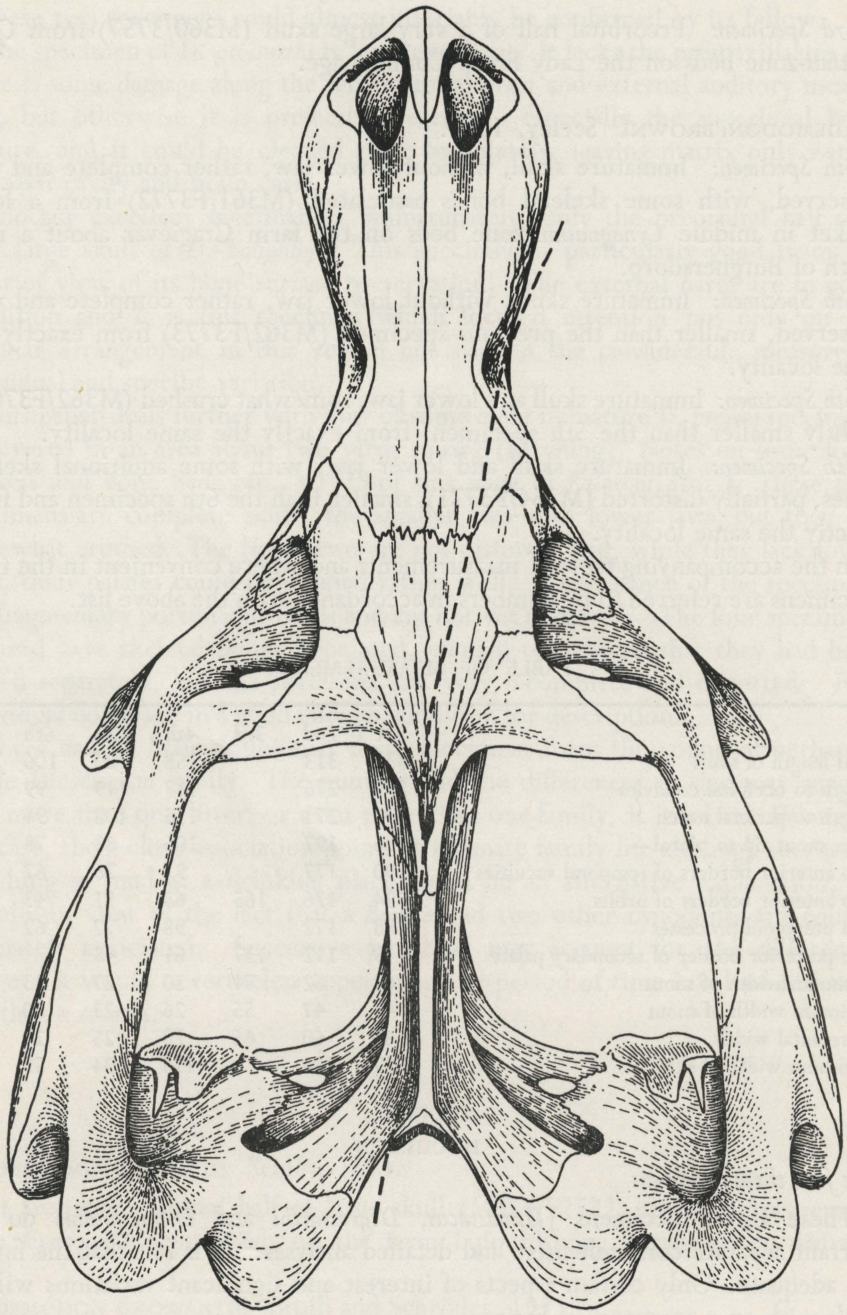


Fig. 16—Dorsal view of the 1st specimen, *Diademodon mastacus*, $\frac{1}{2}$ natural size.

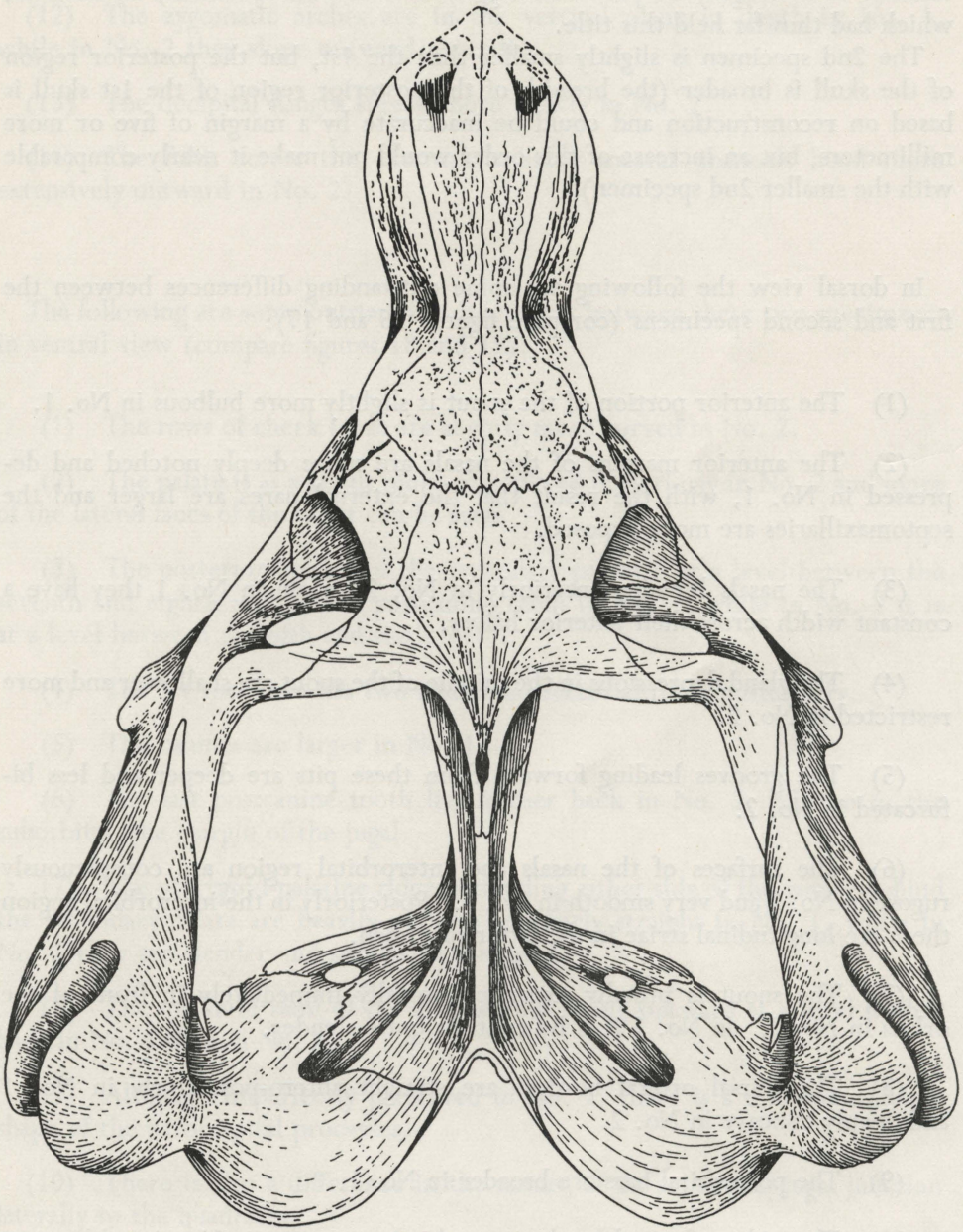


Fig. 17—Dorsal view of the 2nd specimen, *Diademodon grossarthi*, $\frac{1}{2}$ natural size.

series; an adult *D. browni* is apparently half the size of the present specimen of *D. haughtoni*, which can claim a record for size among all *Diademodon* specimens known. It is roughly 25 per cent. bigger than the 1st specimen, *D. mastacus*, which had thus far held this title.

The 2nd specimen is slightly smaller than the 1st, but the posterior region of the skull is broader (the breadth of the posterior region of the 1st skull is based on reconstruction and could be inaccurate by a margin of five or more millimeters, but an increase of this order would not make it nearly comparable with the smaller 2nd specimen).

In dorsal view the following are some outstanding differences between the first and second specimens (compare figures 16 and 17):

(1) The anterior portion of the snout is slightly more bulbous in No. 1.

(2) The anterior margins of the nasals are more deeply notched and depressed in No. 1, with the result that the external nares are larger and the septomaxillaries are more exposed.

(3) The nasals broaden anteriorly in No. 2, while in No. 1 they have a constant width across their anterior halves.

(4) The gland depressions in the middle of the snout are shallower and more restricted in No. 2.

(5) The grooves leading forward from these pits are deeper and less bifurcated in No. 2.

(6) The surfaces of the nasals and interorbital region are conspicuously rugose in No. 2 and very smooth in No. 1. Posteriorly in the interorbital region there are longitudinal striae in the latter specimen.

(7) The snout is broadly expanded dorsally immediately in front of the orbits in No. 2. In No. 1 it is by contrast quite slender.

(8) The dorsal orbital borders are straight antero-posteriorly in No. 1 and deeply concave in No. 2.

(9) The postorbital bars are broader in No. 1.

(10) The ridges formed by the postorbitals peter out in No. 1 and become sharper laterally while they remain on the borders of the temporal vacuities. In No. 2 they remain robust, increase in breadth and swing to the orbital borders.

(11) The squamosals penetrate with thinner wedges more deeply forward into the jugal folds on the zygomatic arches in No. 2.

(12) The zygomatic arches are in the vertical plane in depth in No. 1, while in No. 2 they slope outward ventrally.

(13) The occipital flanges spread more widely in No. 2.

(14) The folds across the external auditory meatus channels bend more extensively outward in No. 2.

The following are some outstanding differences between these two specimens, in ventral view (compare figures 18 and 19):

(1) The rows of cheek teeth are slightly more curved in No. 2.

(2) The palate is as a result more constricted posteriorly in No. 2 and more of the lateral faces of the snout can be seen.

(3) The posterior border of the secondary palate is at a level between the seventh and eighth molariform postcanine teeth in No. 1, while in No. 2 it is at a level between the fifth and sixth teeth.

(4) The 1st specimen has two additional sectorial teeth posteriorly.

(5) The canines are larger in No. 1.

(6) The last postcanine tooth lies farther back in No. 2, relative to the suborbital free margin of the jugal.

(7) The pterygoid-palatine ridges extending either side of the vomer behind the secondary palate are heavily swollen and fairly straight in No. 1, while in No. 2 they are slender and somewhat S-shaped.

(8) The quadrate rami of the alisphenoids swing outward at a level farther back in No. 1 than in No. 2.

(9) Although imperfectly preserved in No. 1, there is a difference in the shape of the paroccipital processes.

(10) There is also a difference in the nature of the squamosal-jugal junction laterally to the quadrates.

(11) The quadratojugals cut inward into the squamosals in No. 2 and outward in No. 1.

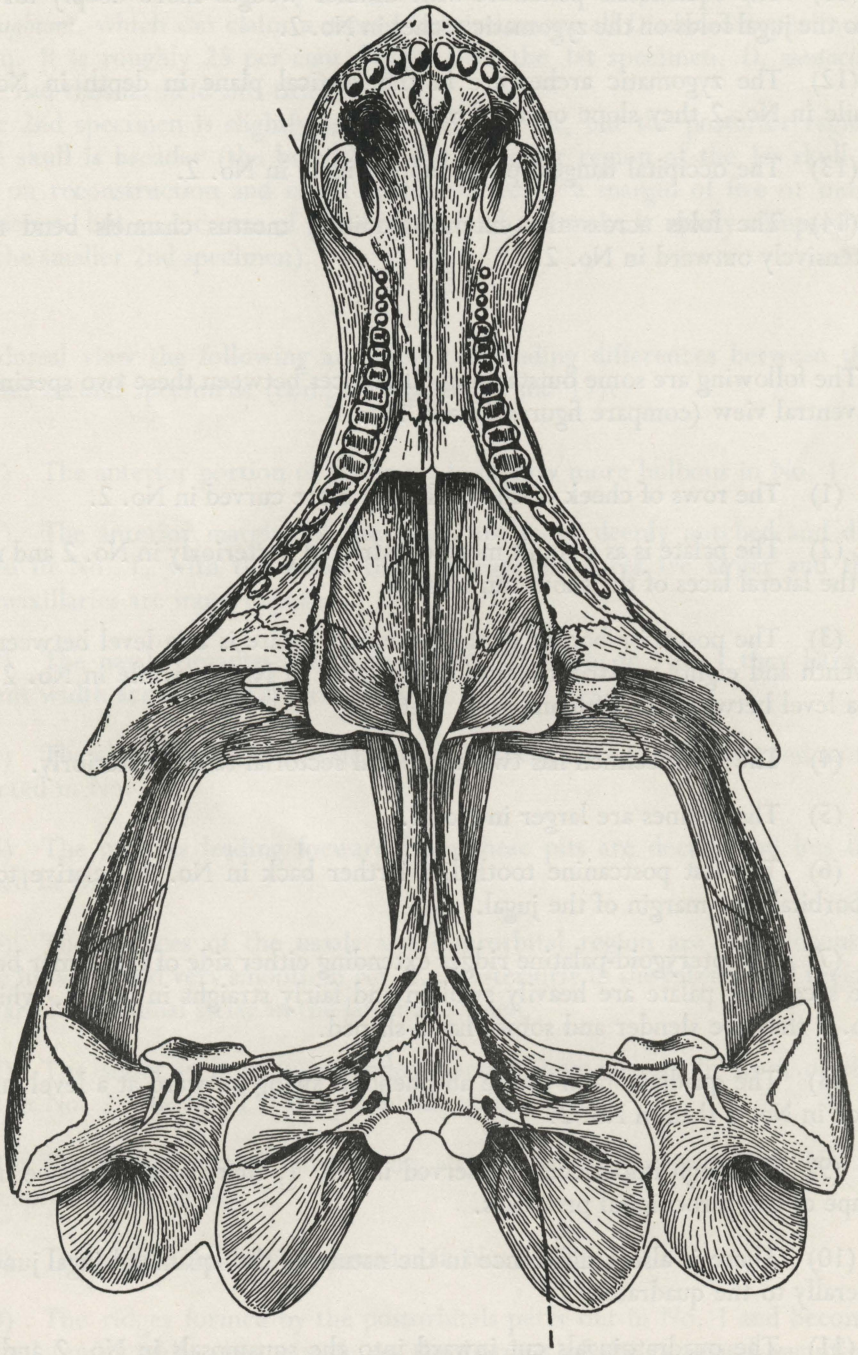


Fig. 18—Ventral view of the 1st specimen, *Diademodon mastacus*, ½ natural size.

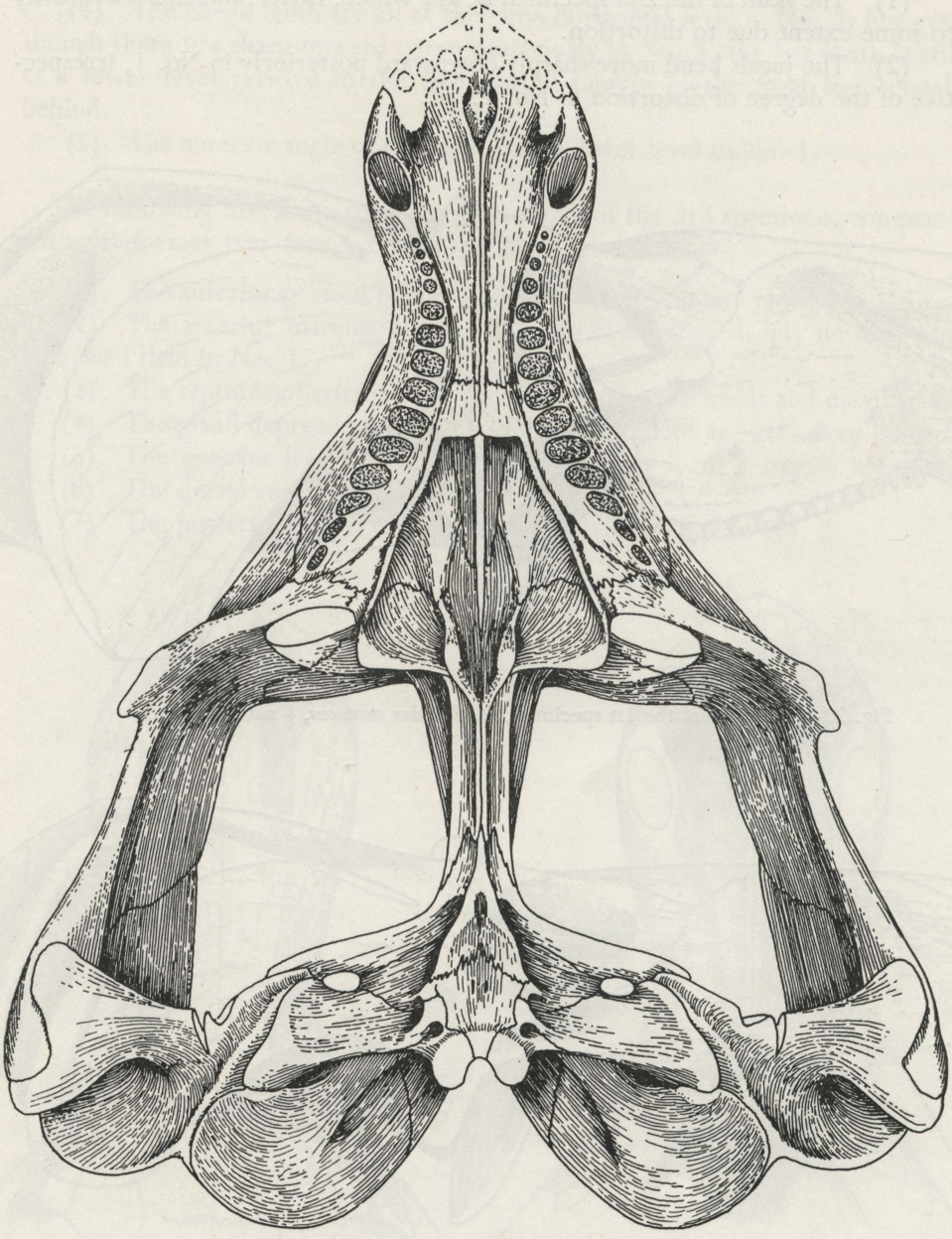


Fig. 19—Ventral view of the 2nd specimen, *Diademodon grossarthi*, $\frac{1}{2}$ natural size.

In side view the following are some differences between these two specimens (compare figures 20 and 21):

(1) The skull of the 2nd specimen is, as a whole, flatter, but this is evidently to some extent due to distortion.

(2) The jugals bend more sharply downward posteriorly in No. 1, irrespective of the degree of distortion in No. 2.

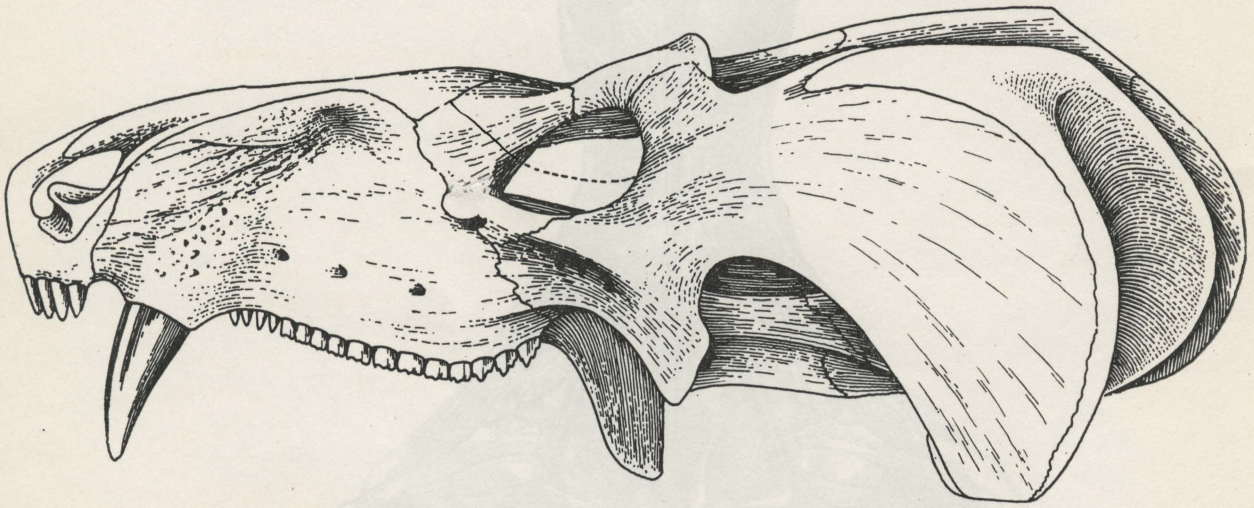


Fig. 20—Side view of the 1st specimen, *Diademodon mastacus*, ½ natural size.

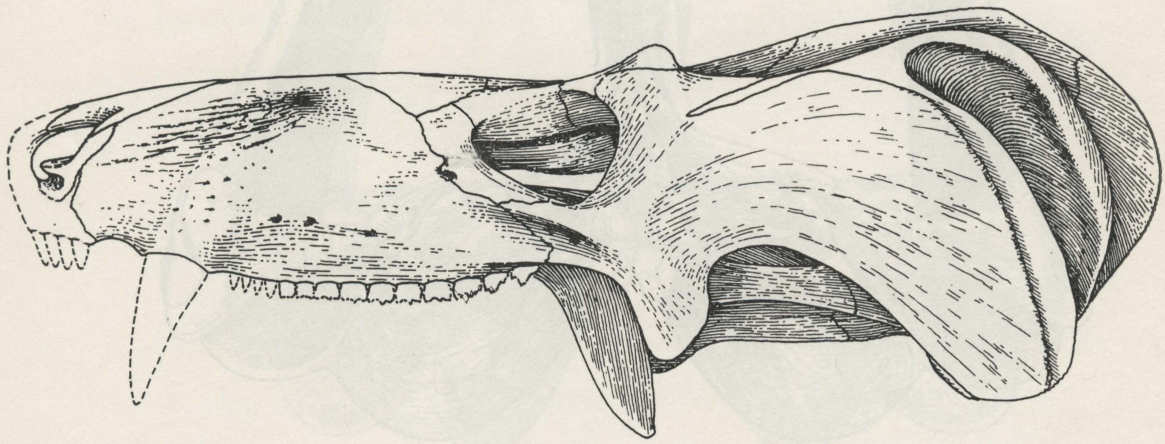


Fig. 21—Side view of the 2nd specimen, *Diademodon grossarthi*, ½ natural size.

(3) The external auditory meatus channels start farther forward dorsally on the zygomatic arches in No. 2. In No. 1 the channel is less curved and descends straight down, a rather conspicuous feature of this species.

(4) The cheek teeth are all at the same horizontal level in No. 2, but even though there is a sharp upward curve posteriorly in No. 1, the last tooth is still at a lower level relative to the free ventral margin of the jugal immediately behind.

(5) The anterior angle of the orbit is at a lower level in No. 1.

The following are some conspicuous features of the 3rd specimen, compared with the former two (see figure 22):

(1) The anterior portion of the snout is more robust and elongated.

(2) The anterior margins of the nasals are even more deeply notched and depressed than in No. 1.

(3) The septomaxillaries are not locked between the nasals and maxillaries.

(4) The gland depressions in the middle of the snout are very deep indeed.

(5) The grooves leading from these depressions form a rugose network.

(6) The dorsal surface of the snout is smooth.

(7) The posterior palate is even more constricted than in No. 2.

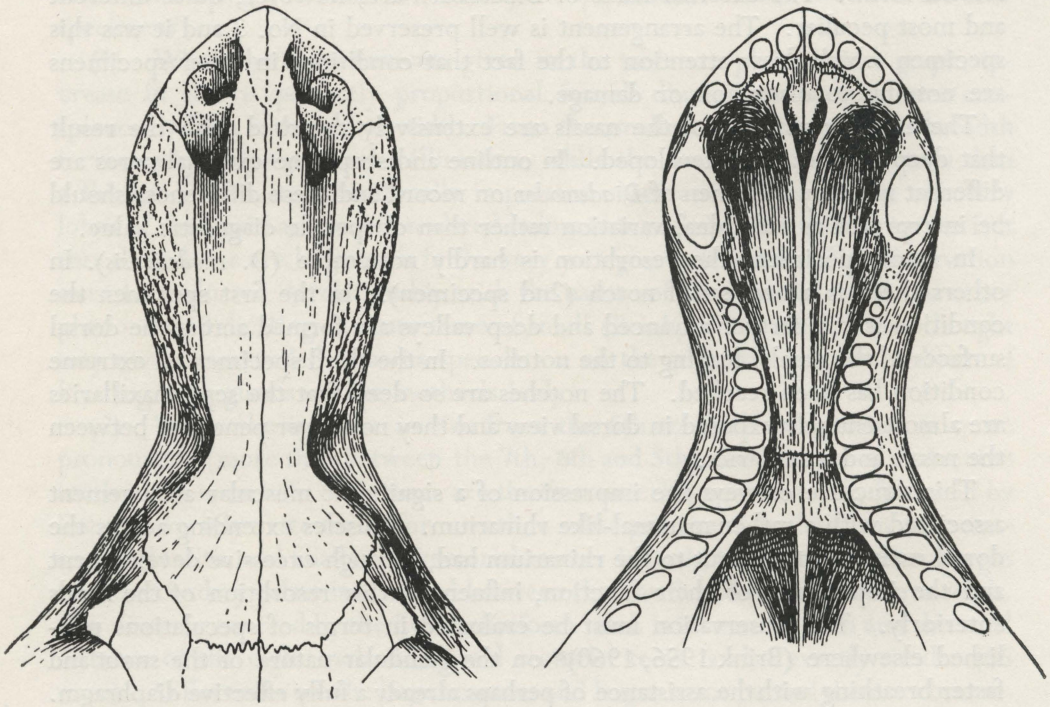


Fig. 22—A, Dorsal and B, Ventral views of the 3rd specimen, *Diademodon haughtoni*, $\frac{1}{2}$ natural size.

(8) The posterior border of the secondary palate is at the level of the middle of the seventh molariform postcanine.

(9) The number of cheek teeth corresponds with that of No. 2, but the last sectorial tooth is twice as far forward of the suborbital free margin of the jugal as in No. 1.

(10) In side view there is a stronger resemblance with No. 1.

There are some structural details brought out by these specimens which, although not entirely new or contrary to previous interpretations, are rather well displayed. Specimen No. 1 portrays the quadrate-quadratojugal arrangement rather well. The figures are substantially clear and an elaborate description would be superfluous. The second specimen demonstrates rather clearly the deep penetration of the squamosal between the paroccipital and the alisphenoid (ventral view). There is no contact between the paroccipital and the quadrate or alisphenoid. When this region of the skull, as figured in the two specimens, is compared with a similar figure of *D. rhodesiensis* (see article earlier in this issue of *Palaeont. Afric.*) a great number of interesting variations will be noticed.

These specimens do portray a peculiar arrangement not previously recorded. Most *Diademodon* specimens have the region of the external nares so inadequately preserved that interpretations have often been guided by conditions in other related forms. The external nares of *Diademodon* are, however, quite different and most peculiar. The arrangement is well preserved in No. 3 and it was this specimen which drew attention to the fact that conditions in other specimens are not due to distortion or damage.

The anterior margins of the nasals are extensively resorbed with the result that deep notches have developed. In outline and shape the external nares are different in every specimen of *Diademodon* on record and these differences should be interpreted as individual variation rather than of specific diagnostic value.

In some specimens the resorbtion is hardly noticeable (*D. rhodesiensis*). In others there is a neat small notch (2nd specimen). In the first specimen the condition is still farther advanced and deep valleys are formed across the dorsal surfaces of the nasals, leading to the notches. In the third specimen an extreme condition has been reached. The notches are so deep that the septomaxillaries are almost entirely exposed in dorsal view and they no longer penetrate between the nasals and maxillaries.

This structure conveys the impression of a significant muscular arrangement associated with a rather mammal-like rhinarium. Muscles extending across the dorsal surface of the snout to the rhinarium had, through excessive development and the importance of their function, influenced this resorbtion of the nasals anteriorly. This observation must be evaluated in terms of speculations published elsewhere (Brink 1956, 1960)* on the glandular nature of the snout and faster breathing with the assistance of perhaps already a fully effective diaphragm.

* Palaeont Afric., IV, p. 77; VII, p. 155

The latter four specimens

These (Nos. 4, 5, 6 and 7; see figure 23) are the four better preserved and more complete specimens in a group of at least eight individuals recovered from a fossil pocket on the farm Cragievar some five miles south of Burghersdorp. All these specimens are immature individuals of the same species, *D. browni*, but they are all of different sizes. Although there is some individual variation which could partly be accounted for in terms of growth, it would appear that they are members of a single family group which lived intimately together and that they perished at the same time. If they were the young of a single mother, they obviously perished at various intervals, but still within a particular season.

None of the specimens could be cleaned to an extent where structural detail could be better displayed than in other existing specimens. All the specimens are encased in very hard matrix as well consolidated nodules, but the bone is relatively soft and brittle. Preparation could not be carried as far as the figures suggest; the figures have been prepared by superimposing ventral and dorsal view. The two larger specimens are undistorted, while distortion has been corrected in the two smaller specimens.

While none of the skulls is particularly attractive for detailed description and while the skull of this genus is satisfactorily known, it is sufficient to list merely some interesting observations. Firstly comparisons are made between the four specimens:

(1) When the measurements given in the table are plotted on a graph, increase in size is perfectly proportional for all dimensions except, most conspicuously, the interorbital width. From the smallest to the largest this breadth increases by only some five millimeters, while the overall increase is more than a third. This is an exceptionally important observation, because the olfactory lobes of the brain are accommodated below this region and it points to the fact that these lobes are large even in the very youngest individuals. This observation must be evaluated in relationship with the nature of the external nares and other phenomena indicating an acute sense of smell (Brink, 1956, 1960)*.This thought may even be extended to some speculation on the adaptation to the problem of locating milk glands on the mother's body.

(2) While the increase in size from the 5th to the 4th specimen is quite pronounced (more than between the 7th, 6th and 5th), the number of postcanine teeth is the same. In both there are the four anterior conical teeth, followed by five transversely ovate molariform teeth, a subsequent semi-molariform and semi-sectorial tooth, and finally two sectorial teeth. In both, too, the posterior margin of the secondary palate is at a level between the fourth and fifth molariform teeth. The distance covered by the five molariform teeth is 20 mm. in both and the total distance of the eight molariform and sectorial teeth is also exactly similar (35 mm.). Differences are the larger canines and larger space behind them accommo-

*Palaeont Afric., IV, p.77; VII, p.155.

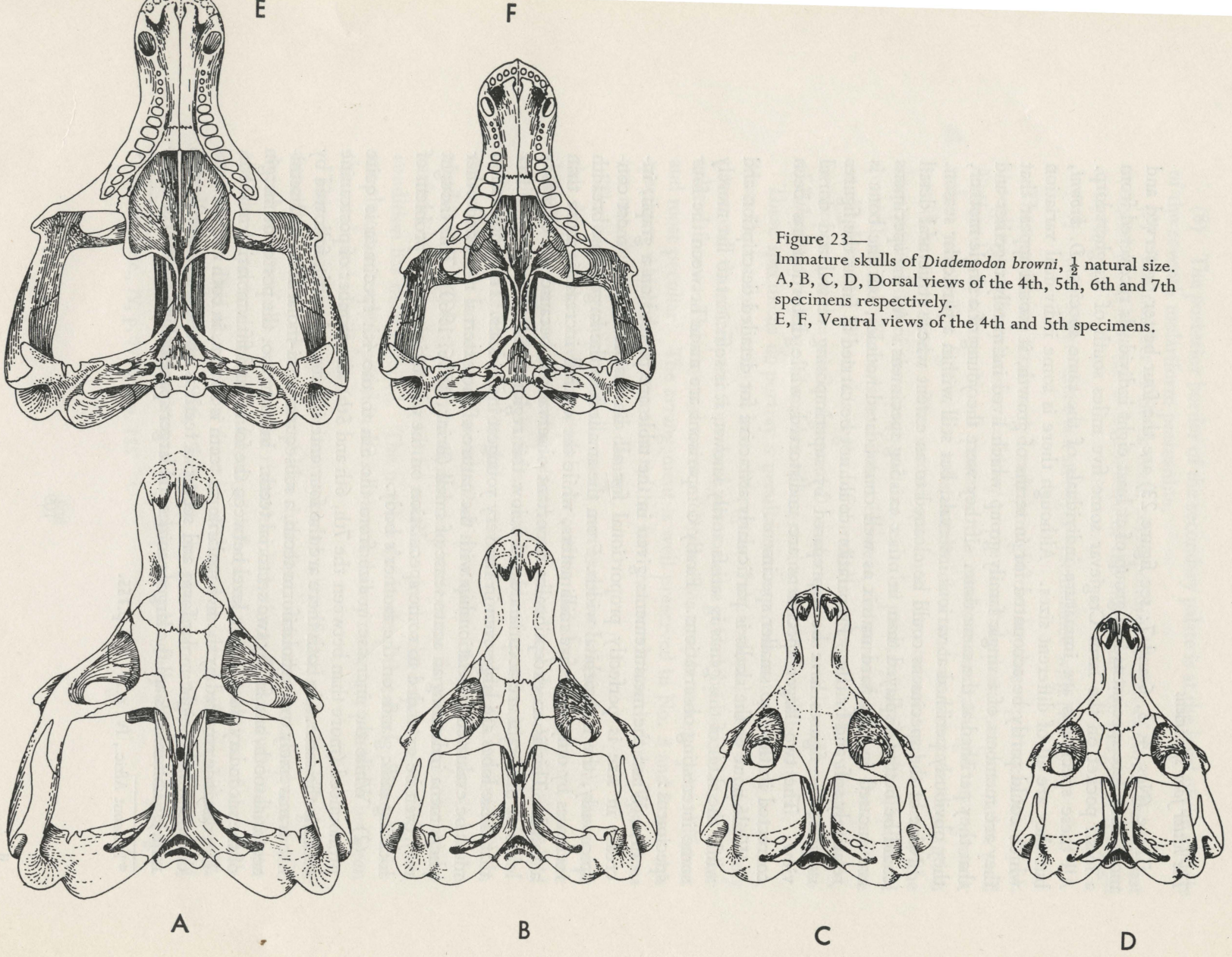


Figure 23—
Immature skulls of *Diademodon browni*, ½ natural size.
A, B, C, D, Dorsal views of the 4th, 5th, 6th and 7th specimens respectively.
E, F, Ventral views of the 4th and 5th specimens.

dating the four conical teeth in No. 4, and the last sectorial tooth lies a greater distance forward of the suborbital free margin of the jugal than in No. 5.

(3) In No. 4 the transverse bone is highly reduced, as is typical for the genus, but in No. 5 it is large and extends inward as is more typical of primitive forms.

(4) The shape of the squamosal projections which wedge into the jugals on the zygomatic arches displays a measure of individual variation.

Secondly, these four specimens are compared with adults as represented by the former three specimens. While these observations may have certain taxonomic value, they are listed only for their possible significance in terms of growth.

(1) In specimen 5 the quadrates are preserved and these demonstrate that in the immature state the quadrates and quadratojugals are distinguishable. The quadratojugals do not contribute to the articulation surface, a feature also noted in *Leavachia* (Brink: *Leavachia duvenhagei* Broom, p. 57 of this issue of *Palaeont. Afric.*) and this is apparently a characteristic feature of most Cynodonts.

(2) When the dentitions are compared it would appear that all transversely ovate molariform teeth are preceded by a semi molariform—semi sectorial tooth. This tooth is distinctly sectorial laterally and serves as a cutting tooth initially after eruption, but on further eruption an inner molariform platform appears, giving the same tooth now a triangular appearance. This may explain why in the younger specimens the triangular tooth is the 6th in the molariform series while in adults it is the eighth. No *Diademodon* is known in which the ninth tooth turns molariform on further eruption, even though the series may extend by two or three additional teeth. It would appear, therefore, that all the molariform teeth are preceded once by a semi-molariform tooth up to the seventh; the eighth is not replaced and subsequent teeth, also not replaced, are more typically sectorial. *Diademodon* may start its life immediately after "birth" with perhaps no molariform teeth, the first tooth after the four conical teeth still being the semi molariform "milk" tooth.

(3) In the young specimens the jugal processes are level with the orbits, but in the older forms they are more at the level of the postorbital bars. This should not be interpreted as a specific variation. These processes lean backward and supported muscles which extended posteriorly. so that with increase in size such a transposition is possible within any individual growth series.

(4) The snout is relatively delicate in the younger forms while in adults it becomes progressively bulbous and robust.

(5) The peculiar nature of the external nares and the notched anterior margins of the nasals noted in the adult specimens are equally conspicuous in the young specimens. This is, therefore, not a development which accompanies adulthood or old age and, whatever the olfactory significance, it was as significant to the newly "born" as to the most aged individual.