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NOTES ON A SPECIMEN OF *DIADEMODON* PREVIOUSLY REFERRED TO *CYCLOGOMPHODON*

by

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ABSTRACT

The anterior portion of the cranium of a medium-sized cynodont is described. The specimen was previously described briefly by Brink and Kitching (1953), who assigned it to the genus *Cyclogomphodon* Broom, and it was upon this specimen that they based their rediagnosis of that genus. The detailed study of this specimen has revealed that the supposed features which they considered to be generically distinctive for *Cyclogomphodon* either do not exist or that their validity falls away when this specimen is considered, in an ontogenetic context, as a not yet fully grown individual. It is concluded that this fossil represents a medium-sized, "juvenile", individual of *Diademodon*.

INTRODUCTION

During an investigation of the evidence for salt glands in Triassic theriodonts, a specimen of a cynodont skull was sectioned serially in the coronal plane (Grine, in preparation). It consisted of the reasonably well-preserved front portion of the cranium, that is, a nearly complete snout and most of the orbital region, of a medium-sized animal. This fossil was from the collection of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, catalogued as Field Number 1171, Museum Number 319. It was figured and described briefly by Brink and Kitching (1953), who assigned it to the genus *Cyclogomphodon.*

They noted that this fossil and a second, less well-preserved specimen of the anterior part of a skull (BPI.FN. 2519, MN. 320) were

> ". . . of a type closely allied to *Diademodon*, but much smaller and, judging from general appearance alone, we immediately established that they belong to a different genus. After careful consideration we came to the conclusion that they represent Broom's genus *Cyclogomphodon*" (1953, p. 42).

Indeed, they rediagnosed that genus on the strength of several characteristics which were evinced, primarily, by the first specimen, as the second was rather poorly preserved.

The specimen (BPI.FN. 1171) was collected by J. W. Kitching from *Cynognathus* Zone sediments on the slopes of the Matyantya feature in the middle of the Matyantya basin south-west of Lady Frere, Cape Province. The locality has been illustrated by Brink and Kitching (1953, fig. 32).

The purpose of this paper is to describe in detail this fossil, and to discuss the validity of *Cyclogomphodon* as it was rediagnosed by Brink and Kitching (1953).

DESCRIPTION

BPI.FN. 1171 consists of the front portion of the cranium of a medium-sized animal. The snout is very nearly complete and has been separated from the rest of the skull along an uneven plane which transects the posterior third of the orbital region. The matrix, which fills the nasal cavity and is adherent to the back of the specimen is a grey coloured, fine-grained sand or mudstone.

The rostrum is reasonably well preserved, having suffered some slight distortion in the orbital region. The dentition is very poorly preserved. The dorsal interorbital surface has been pushed ventrolaterally to the right, and thus the right orbit appears to be somewhat reduced in height and of a more ellipsoid shape than the left. The anterior part of the snout is relatively free from distortion except that on the right side the anterior rostral expansion has been flattened slightly, and the intact portion of the right alveolar margin has been crushed medially.

The bone on the dorsal and lateral aspects is free from matrix: but this is still adherent to the medial and inferior walls of both orbits, the back of the specimen and the anterior portion of the hard palate. Numerous fine cracks are present and many of these, which appear to be sun-cracks, have widened slightly and are filled with matrix. The right side of the snout, that is, the face of the maxilla, has suffered considerably more from surface damage than has the left.

Vertical Aspect

Viewed from the dorsal aspect (fig. 1, a and b) the snout evinces a lyriform shape, a characteristic feature of *Diademodon.* The orbits appear to have been ovoid in shape and orientated such that they faced anterolaterally before distortion affected this region. The maxillary depressions are well-preserved and

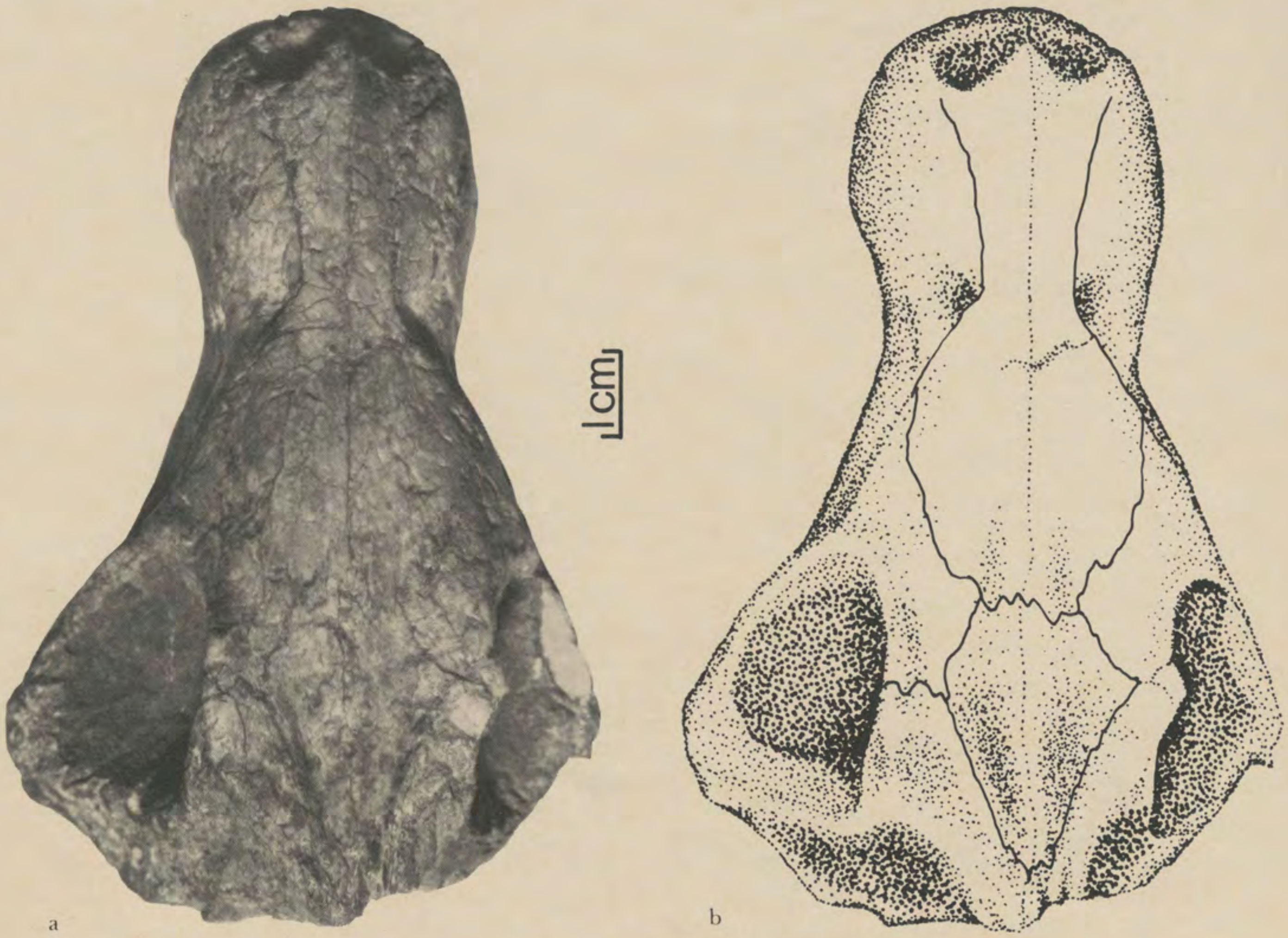

Figure 1. BPI.FN. 1171 in vertical aspect. All scales in centimetres. a, photograph; b, drawing.

are relatively deep, well-delineated excavations; the pit on the left side is situated very slightly forward in relation to the one on the right. The maxillae broaden laterally below the depressions before the bones turn ventrally to reach the alveolar borders. Brink and Kitching (1953) considered these depressions to be "very small, unlike the average condition in *Diademodon*" (p. 43). Also, as mentioned above, they felt that this fossil was "of a type closely allied to *Diademodon*, but much smaller" (p. 42). However, when this specimen is considered in the context of an ontogenetic growth series (Grine and Hahn, 1978; Grine, Hahn and Gow, 1978), it is apparent that it is certainly not too small to be a *Diademodon*, nor are the glandular depressions "very small" relative to the size of the snout.

The anterior margins of the nasal bones have been damaged, and the anteriorly projecting premaxillary keel is missing. Also, the external faces of both premaxillae have suffered from bone loss and the damaged roots of the incisors are exposed. It is evident that there were four incisors on each side. The lateral walls of the external nasal aperture show damage, but on the right side the very posterior part of the septomaxilla-maxillary suture is evident. On both sides, the ventromedially directed processes of the septomaxillae have been broken away.

The sutures which delineate the frontals and nasals are clearly visible, and on the left side the short suture which separates the prefrontal from the postorbital is discernible. Although the extraorbital limits of the lachrymal bones are indicated in Brink's illustrations of the specimen (1953, figs. 36 and 38), these sutures are not evident on the original specimen.

The nasal bones are somewhat hour-glass shaped; they show a moderate spread just behind the nasal aperture, a constriction at about mid-length in the region of the glandular depressions, and a marked posterior expansion. The nasals achieve their greatest width approximately midway between the orbits and the maxillary depressions, from which point the sutures converge posteriorly. The nasofrontal suture appears as a jagged transverse line.

The frontals form a rough diamond shape. From the nasofrontal, the fronto-prefrontal sutures diverge to reach their widest points at what is judged to be approximately mid-orbital length. On the left side, at least, this point corresponds closely to the position of the transversely orientated prefrontal-postorbital suture. From here the fronto-postorbital sutures converge posteriorly to meet in the midline. Along the interfrontal suture the bone is raised up into a low, narrow, median sagittal ridge. The postorbitals rise upwards from the frontals in lateral and posterior directions, and thus the frontal bones are situated in a shallow depression. This concavity in the posterior interorbital region is encountered also in *Diademodon* crania, and generally appears to be more deeply excavated in the Type Two cranial morphotype (Grine *et al.*, 1978).

Lateral aspect

The left side of the snout (fig. 2a and b) is better preserved than the right (fig. 2c), which has suffered from crushing and surface damage. Viewed from the lateral aspect, the dorsum of the snout (the nasal bones) slopes gently downwards from the orbits to the back of the nasal aperture. The alveolar margin has been broken away along almost all of its length; thus, the apparent height of the snout is reduced by as much as two to three millimetres in some places. Brink and Kitching (1953) noted "the extremely low snout, which alone contrasts so to the general *Diademodon* condition that it is a difference of more than specific nature" (p. 43). The snout of this specimen is rather low even if several millimetres are added to the alveolar margin; but relative to its length, the height of the snout is well within the limits encountered in *Diademodon*. A low rostral profile has been recognised as one of a suite of characteristics shown by *Diademodon* crania of the Type Two morphotype (Grine *et al.*, 1978).

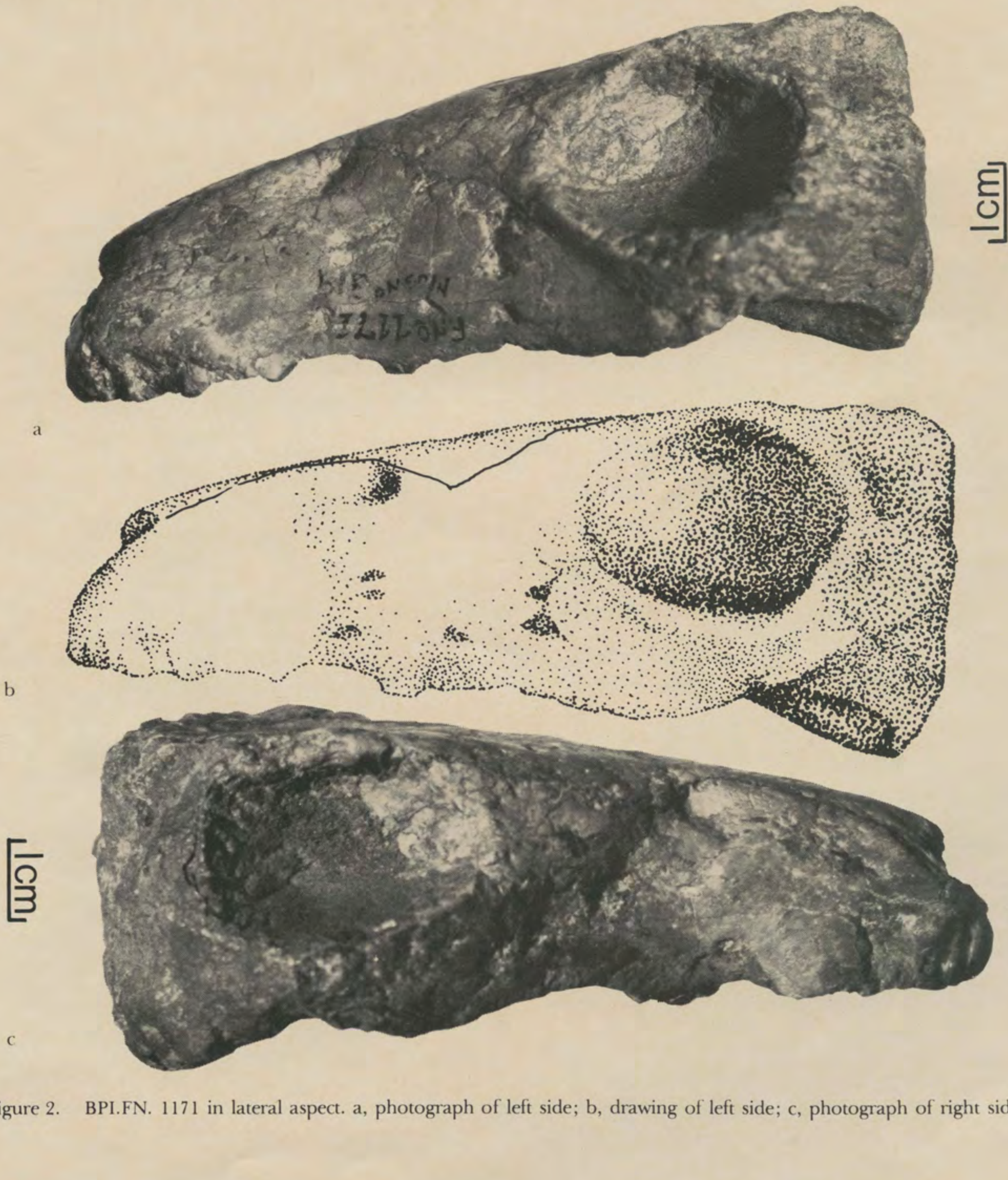

Figure 2. BPI.FN. 1171 in lateral aspect. a, photograph of left side; b, drawing of left side; c, photograph of right side.

There is a slight bulbous expansion of the maxilla anterior to the orbit. This feature appears as a superolaterally directed convexity which imparts a faintly inflated appearance to the snout in this region; and it is encountered, in various degrees of development (dependent upon the size of the individual), in a number of *Diademodon* crania, especially those which have a Type Two morphotype (Grine, in preparation).

The glandular depressions are lodged entirely within the confines of the maxillae. The inferior half of the maxilla on the left side (this region on the right has been damaged) possesses some six foramina (fig. 2b), which are interpreted here as the openings of neurovascular canals. Anteriorly, the maxillae become bulbous and inflated from just behind the canine sockets forward to the premaxillae, which are expanded similarly. The surface of the bone in this region is smooth and shows no trace of the grooves which, in other diademodontine specimens, course over this area, from the glandular depressions to the external nares. The nasal aperture extends back to a level just posterior to the distal side of the fourth incisor.

Due to the multitude of "sun-cracks" covering the surface, neither the maxillolachrymal nor the maxillojugal sutures on either side is discernible. Two matrix-filled cracks on the left side, however, correspond rather closely to Brink's illustrations of the lachrymal bone's outline (1953, figs. 36 and 38); but as a number of similar cracks cover the surface it is impossible to determine accurately the outline of this bone. Also, a rather large crack runs vertically from the anterior margin of the left orbit to the alveolar border, but it does not correspond at all to the position which Brink indicated for the maxillojugal suture. Similarly, it is not possible to determine whether this crack does, in fact, even represent a suture.

Basal Aspect

The ventral surface of the specimen (fig. 3a and b) is rather poorly preserved, and also it has suffered from the preparator's grinding wheel. The dentition is represented solely by badly broken roots and ground-down cross-sections of sockets; but it is apparent that the dental arcade was lyriform in shape, with the postcanine tooth rows diverging posteriorly. The general shape of the dental arcade is typ-

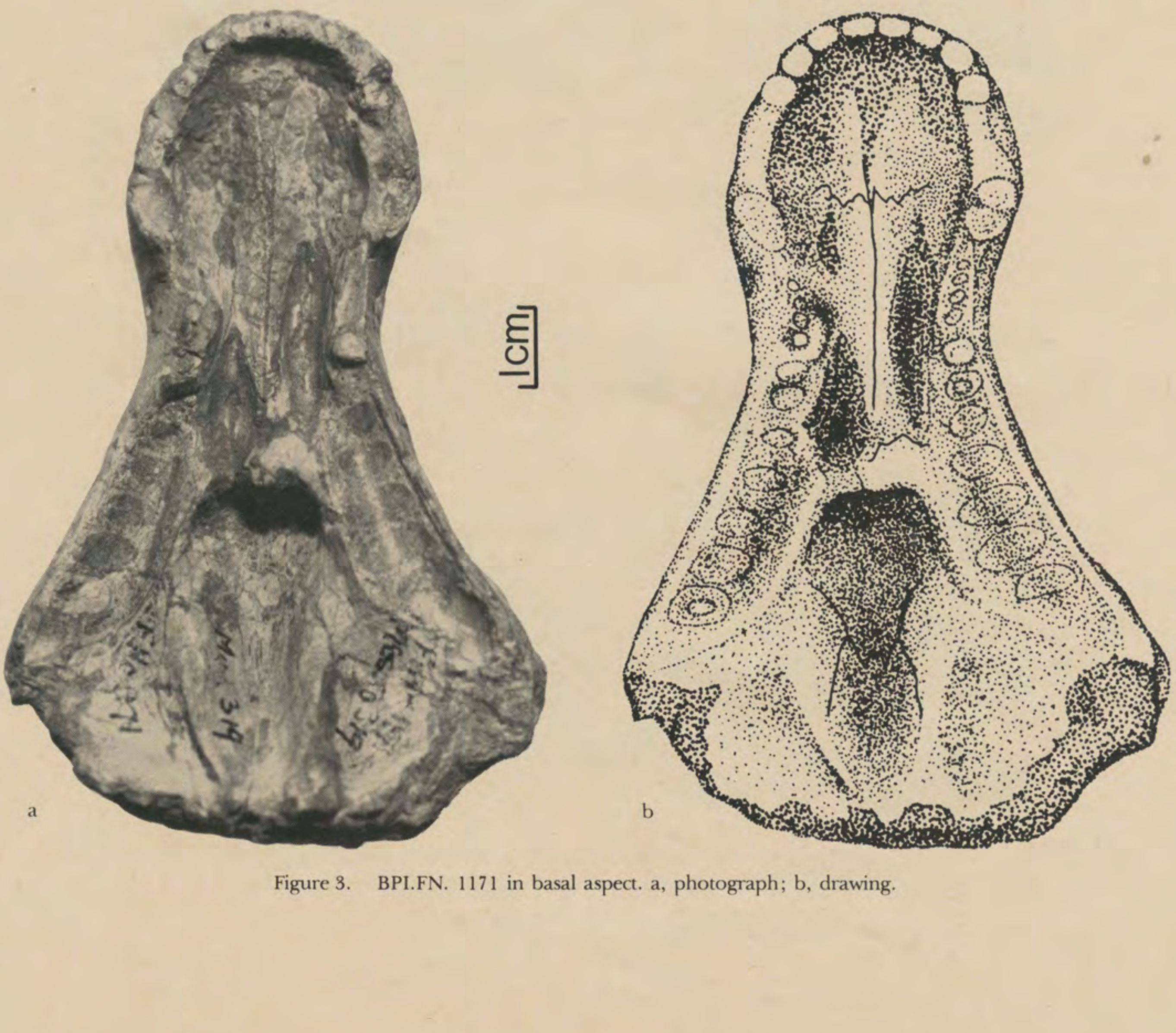

Figure 3. BPI.FN. 1171 in basal aspect. a, photograph; b, drawing.

ical of that encountered in *Diademodon.* The four incisors in each premaxilla are represented by damaged roots. There is a considerable diastema between the last incisor and the canine on each side.

Only fragmented and unclear alveolar cross-sections of the canines remain. As pointed out by Brink and Kitching (1953), the canines appear to be rather small and there is evidence of replacement on the left side. They considered the size of the canines in this specimen as both one of the features which warranted its being placed in a distinct genus as well as one of the diagnostic characteristics of *Cyclogomphodon.* If one considers this fossil in an ontogenetic context, however, the relatively small size of the canines can be appreciated. Whilst it is evident that the left canine is in the process of replacement, the apparently single right canine may represent either the apical end of the shedding tooth or possibly a section through the tip of the replacement tooth. Brink and Kitching (1953) recorded that the canines "measure in cross-section less than the largest molar" (p. 43). They do not state whether the diameter referred to is the mesiodistal or the buccolingual; but nevertheless, as it seems that the canines were replaced less frequently than the postcanines in the diademodontids, and as it has been shown both that the postcanine teeth were replaced fairly rapidly in juveniles (Hopson, 1971) and that the molariform teeth exhibit a posteriorly increasing size gradient (Grine, 1976, 1977), it would appear that in a juvenile animal the molariform teeth could have surpassed the canines in size. In this specimen it seems that this is the case, and that the situation was being altered at the time of death.

The number of postcanine teeth in this specimen is difficult to ascertain. On the right side three broken stumps of what appear to have been conical teeth are present; anterior to the first stump there is the ground down cross-section of what may have been either the first functional conical or a "plugged" socket. Behind the last stump on this side the alveolar bone has been ground away by Brink and Kitching in the form of a deep longitudinal trough, in which the matrix filled alveoli of six and the sectioned root of a seventh molariform are visible. On the left side the alveolar bone behind the canines has been ground away. The matrix-filled sockets of four conical teeth are visible; here, too, it is possible that the first may represent a "plugged" socket. Behind this the broken stump and the sectioned root of what appear to have been the first two molariform teeth are preserved. Distal to these the bone has been ground away in a manner similar to that encountered on the opposite side: here the sockets of a further five molariform teeth are exposed. Brink illustrated another two teeth behind the eleventh postcanine socket on each side (Brink and Kitching, 1953, fig. 37); but the present author was unable to satisfy himself of the presence of these additional sockets.

If we presume, as did Brink and Kitching (1953), that the first postcanine socket on each side represents a functional conical tooth rather than a "plugged" socket, and that the broken stump on the left side and its antimere represent the first molariform teeth, then the postcanine dental formula of this specimen would be four conicals and seven molariforms. Although the sockets are not visible, there may have been at least one sectorial tooth behind the last molariform on each side.

The anterior of the palate is reasonably well-preserved, with patches of matrix still adherent on the left and right sides. On the right, the cross-sectioned tip of a lower incisor is embedded in the matrix medial and slightly distal to the fourth upper incisor. A rather large, wedge-shaped incisive canal separates the two premaxillae. The palatal fossae which receive the lower canines are shallow, but their depth is increased somewhat by the keel-like projection of the premaxillary bars which constitute the inner walls of these concavities. The medial portions of the transversely orientated sutures, which separate the premaxillae from the horizontal palatal processes of the maxillae, are visible on both sides; the lateral extent of these sutures is obscured by matrix. The longitudinal suture which separates the palatal processes of the maxillae is very evident. The palate on both sides has been abraded away by the preparator's grinding wheel, and this has imparted, artificially, a very well-developed longitudinal keel to the median part of the palate. On the right side the bone has been ground away from the level of the fourth postcanine through the palatine, and on the left from the level of the canine to the palatine bone. The horizontal plate of the palatine is present on the left side, and has been displaced from the maxillary portion of the palate at what appears to be the palatomaxillary suture.

Brink and Kitching (1953) considered the palate of this specimen to be shorter than in *Diademodon,* and regarded this feature as one of the distinguishing characteristics of *Cyclogomphodon.* In a study of cranial growth in *Diademodon* it has been found that the hard palate and the snout (the preorbital rostrum) elongate in a nearly isometric relationship, that is, the palate and snout grow at approximately the same rate (Grine, in preparation). Also, it has been noted that in *Diademodon* skulls, a coronal plane which passes through the snout tangent to the anterior margins of both orbits traverses the ventral surface of the cranium through the vomer a few millimetres behind the posterior margin of the palate (Grine, unpublished). The same relationship between the front of the orbits and the back of the palate exists also in this specimen. Thus, the palate of this fossil is most certainly not short, relative to the length of the snout.

Posteriorly, on the ventral surface, the suture which delineates the vomer is clearly visible. This bone is rather triangular in shape, with the apex directed posteriorly. The anterior, longitudinally directed limbs of the pterygopalatine suture are discernible as well. In his illustration of this specimen, Brink indicated the transverse limbs of the pterygopalatine suture, as well as the limits of the epipterygoid bone on each side (Brink and Kitching, 1953, fig. 37), but the present author was unable to find these sutures on the original specimen.

Two well-developed ridges run from the lateral walls of the internal nasal aperture (just behind the level of the posterior edge of the hard palate) in posterior, inferior and slightly medial directions. These structures have been referred to as the medial pterygoid ridges by Grine *et al.* (1978), who noted that they evince more relief and are more bulbous in their anterior aspects in the Type One than in the Type Two cranial morphotypes of *Diademodon*. Brink and Kitching (1953) maintained that these ridges,

> ". . . extending from near the midline over the pterygoids and palatines do not flatten out on the roof of the internal nares, as in *Diademodon*, but persist around the lateral margins to the posterior border of the secondary palate. The palatines extend backward along these ridges for rather a longer distance than in *Diademodon*" (p. 43).

The medial pterygoid ridges of this specimen are well-developed; but, as mentioned above, the development of these crests is variable in *Diademodon* and as such this specimen exhibits pterygoid development which is of a Type One morphology (Grine *et al.*, 1978). Also, as the transverse portions of the pterygopalatine suture could not be distinguished, even with the aid of a microscope, from the multitude of surface cracks, the validity of their second statement, that the palatine bones constitute a relatively long part of the medial pterygoid ridges, could not be tested.

The specimen has broken such that the pterygoid flanges on both the left and right are missing entirely. Brink and Kitching (1953) noted that:

> "The ridges that extend from the pterygoid processes [flanges] to the posterior border of the secondary palate in *Diademodon* are completely absent in this form" (p. 43).

Since these ridges are absent because the relevant part of the pterygoid on each side has been broken away, it is difficult to understand why they considered this feature as one of the diagnostic characters which validated the existence of *Cyclogomphodon* as a separate genus.

Metrical Features

Before the specimen was embedded for serial sectioning, a mould and a series of plastic casts were made of it. A number of measurements were taken on both the original and a plastic cast, in order to facilitate future comparisons of the cast with the original. The cast (and mould), as well as the series of coronal sections, are housed in the Bernard Price Institute for Palaeontological Research.

The measurements are recorded in Table 1, and the majority taken by the present author correspond to the measurements utilized by Grine and Hahn (1978) and Grine *et al.* (1978). Also included in Table

TABLE 1
Dimensions of BPI. FN. 1171, MN. 319 (in millimetres)

Measurement	Original Specimen		Cast
	This paper	Brink and Kitching (1953)	
Total length of specimen	105,8	—	102,6
(3)* pre-orbital length	66,0	65,0	64,4
(6) cranial masticatory length	77,9	—	76,0
(7) cranial postcanine masticatory length	57,0	—	56,0
(8) hard palate length	61,6	—	59,8
(20) interorbital width	31,1	33,0	29,9
(21) least snout width	30,0	30,0	28,5
(22) greatest snout width	36,8	37,0	35,6
(28) greatest breadth of maxillary tooth rows	49,8	—	49,0
(29) least breadth of maxillary tooth rows	24,2	—	23,5
(30) maxillary bicanine breadth	33,0	—	32,1
(38) maximum height of postorbital above maxillary base	36,2	—	34,6
(39) maximum height of maxilla	33,0	—	31,0
(43) orbital height	24,6†	—	23,6†
(47) mesiodistal diameter of maxillary canine (or socket)	11,5	—	10,5
posterior nasal breadth	—	28,0	—
middle nasal breadth	—	10,0	—
height of snout at level of canines	—	16,0	—
height of snout at level of glandular depressions	—	25,0	—
length of "molar" tooth row	33,2	43,0	—

* The numbers in parentheses refer to those measurements indicated in Grine and Hahn (1978) and Grine, Hahn and Gow (1978).
† indicates a mid-value of both sides.

1 are those dimensions recorded for this specimen by Brink and Kitching (1953). It is apparent from the table that in each instance the plastic cast is smaller than the original. Although this fossil was not included in the previous papers on allometric growth and variability in the diademodontines (Grine and Hahn, 1978; Grine *et al.*, 1978), it will be included in a future study (Grine, in preparation).

Internal Aspect

The snout was embedded in a block of Epofix resin and this was catalysed with Epofix hardener. It was then cut in serial coronal section from the tip of the rostrum, as preserved, to the back of the fossil; a series of 30 sections was obtained. The average thickness of each section is approximately 1,5 mm, and the distance between succeeding sections (the thickness of the saw blade) is 2,3 mm.

The vomer is represented in the sections through the nasal cavity; it rests in the median sagittal plane on the superior surfaces of the horizontal processes of the maxillae and forms a plate-like septum which runs upwards for about two-thirds of the height of the nasal cavity. The nasals form together an elongate arch; the horizontal superior portion (the medial half of each bone) curves downwards so that the lateral surface of the inferior part is covered by the maxilla (fig. 4).

No indication of the grooves which Watson (1913) and Brink (1955, 1956) considered as evidence of the existence of ethmoturbinals was found on the inner aspect of the nasal bones of this specimen.

The sections revealed evidence of tooth replacement in this individual. The problem of tooth replacement in this and other diademodontine specimens will be dealt with fully in another paper

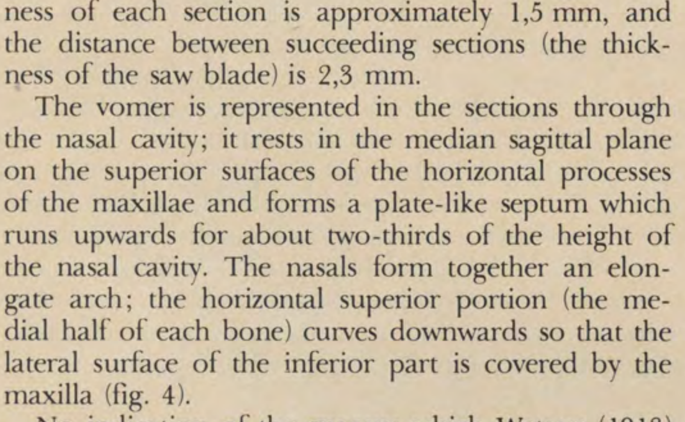

Figure 4. Coronal section through the region of the glandular depressions of BPI.FN. 1171. Section No. 10, viewed from the back.
GD, glandular depression;
M, maxilla;
N, nasal;
S, matrix filled socket;
TG, replacement tooth germ;
V, vomer.
Note the horizontal palatal processes of the maxillae have been ground away.

(Grine, in preparation). A number of tooth germs were found to be present in the alveoli, arranged so that at least one complete replacement would have occurred had this individual lived. The fact indicates the "juvenile" status of this specimen, thus the validity of a number of the features described above, which Brink and Kitching considered to be diagnostic of *Cyclogomphodon*, is brought into question. The majority of these are simply characteristic of a not yet fully-grown individual of *Diademodon*.

SUMMARY AND CONCLUSIONS

The anterior portion of the cranium of a medium-sized cynodont has been redescribed. The specimen, BPI.FN. 1171, MN. 1319, was previously figured and described briefly by Brink and Kitching (1953), who assigned it to the genus *Cyclogomphodon*, and utilized it, primarily, in their rediagnosis of that taxon. They considered it to be generically distinct from *Diademodon* on the basis of the following: (1) its small size, (2) the low snout, (3) the small size of its canines, (4) the short secondary palate, (5) the development of the medial pterygoid ridges, and (6) the absence of ridges from the pterygoid flanges to the alveolar border. A detailed study of this specimen has revealed that the supposed features which they considered to be generically distinctive either do not exist or their validity falls away when this specimen is considered, in an ontogenetic context, as a "juvenile" individual. It is concluded that this fossil represents a medium-sized, "juvenile", individual of *Diademodon*.

This specimen is of further interest by virtue of its inconsistent display of the cranial features detailed by Grine *et al.* (1978) for the Type One and Two morphotypes evinced by specimens of *Diademodon*. Whilst this snout shows several Type One features (e.g. the very well-developed medial pterygoid ridges, and the apparently ovoid-shaped and anterolaterally directed orbits), it also exhibits a number of Type Two characteristics (e.g. the low snout, and the bulbous expansion of the maxillae anterior to the orbits). The second specimen (BPI.FN. 2519) which Brink and Kitching (1953) included in *Cyclogomphodon* is poorly-preserved, but appears also to display a combination of morphotype characters (in their preliminary study, however, Grine *et al.* (1978) considered that this fossil possibly evinced a Type One morph). A recent examination of a large number of *Diademodon* crania has revealed that not a few specimens exhibit a similar mixing of features of the two morphotypes, and this in an apparently random manner, so that no single suite of characteristics can be determined to be either "primitive" or derived (Grine, in preparation).

The apparently random mixing of morphotypic characters in a number of *Diademodon* crania may lend further evidence to the notion that the Type One and Type Two morphs are not separable at anything above either a sexual or perhaps subspecific level. Thus, those specimens which display completely those features of one morphotype or the other (e.g. BPI.FN. 990, 2522, 3639, 4669, 3754, 3758, 3773) may represent the extremes of two broadly overlapping ranges.

ACKNOWLEDGEMENTS

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