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POSTCANINE TOOTH FUNCTION AND JAW MOVEMENT IN THE GOMPHODONT CYNODONT *DIADEMODON* (REPTILIA; THERAPSIDA)

by

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ABSTRACT

The postcanine dentition of *Diademodon* was well adapted, in both morphology and pattern of replacement, to exercising and maintaining precise occlusion. These teeth may be grouped into three morphological classes, consisting of conical, gomphodont and sectorial teeth. The anterior conicals may have acted as gripping teeth, and the posterior sectorials may have been utilized as food "tenderizers" or shredders, while the intermediate gomphodont teeth were utilized in the mastication of food items. The gomphodont teeth, which show evidence of heavy wear, were examined in the scanning electron microscope (SEM), in order to attempt a reconstruction of the masticatory jaw movements in this animal, based on the morphology and orientation of the occlusal wear facets. The occlusal surfaces of the gomphodont teeth are pitted. The pitted occlusal surface texture is an indication of either abrasion or attrition, resulting from direct pounding of the lower teeth against their maxillary antagonists. It is concluded that masticatory jaw movements in *Diademodon* were wholly orthal. There is no dental evidence to support the contention that this reptile exercised either propalinal (Hopson, 1971) or ectental chewing movements. The jaw closing action in *Diademodon* appears to have been equivalent to the masticatory power stroke.

CONTENTS

	Page
INTRODUCTION	123
Toothmorphology	124
Tooth replacement	125
MATERIALS AND METHODS	126
TOOTH WEAR AND OCCLUSION	126
DISCUSSION	131
SUMMARY	134
ACKNOWLEDGEMENT	134
REFERENCES	134

INTRODUCTION

The Triassic cynodonts represent an advanced stage in the trend towards the development of a mammal-like masticatory apparatus. This trend involved, among other things, the enlargement of the dentary, the expansion of a dorsally directed coronoid process, the appearance of a prominent angular process and, in the omnivorous-herbivorous forms, the development of precise occlusion between opposing postcanine teeth (Barghusen, 1968; Crompton, 1972). Concomitant with these osteological and dental developments, the pattern of jaw adductor musculature appears also to have undergone changes from that of a typical reptilian organization to a condition approaching the mammalian pattern (Barghusen, 1968). *Diademodon* (fig. 1) was one of the earliest of the mammal-like reptiles to exhibit the combination of a mammal-like jaw adductor musculature and precise postcanine occlusion (Crompton, 1972). The postcanine dentition of *Diademodon* was well adapted, in both morphology and pattern of replacement, to exercising and maintaining occlusion.

Numerous workers have shown, for various genera of reptiles and mammals (extant as well as extinct), the correlation between the position and orientation of the wear facets on the teeth and the jaw movements during chewing which produced these facets (Mills, 1966; Every, 1970; Crompton and Hiiemae, 1970; Crompton, 1972; Hiiemae and Kay, 1973; Kay and Hiiemae, 1974a and b). The postcanine dentition of *Diademodon* was examined in order to attempt a reconstruction of the masticatory jaw movements in this animal, based on the morphology and orientation of the occlusal wear surfaces.

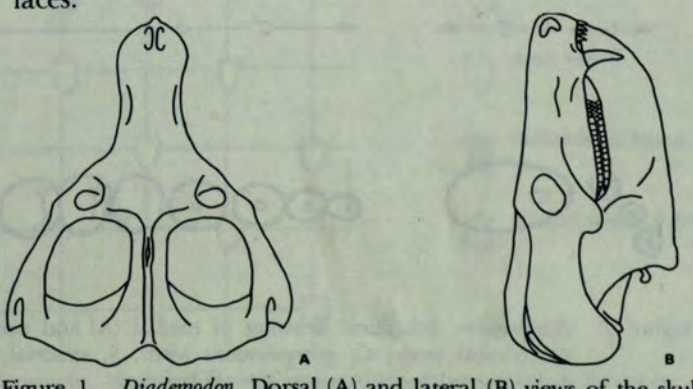


Figure 1. *Diademodon*. Dorsal (A) and lateral (B) views of the skull.

A moderately advanced cynodont, *Diademodon* is well known from the *Cynognathus* zone sediments of the Orange Free State and Cape Province, South Africa (Kitching, 1972). The fossil remains of this reptile have been recovered also from the Ntawere Formation, Upper Luangwa Valley, Zambia (Kitching, 1963; Brink, 1963a), and more recently from the Omingonde Mudstone Formation (Lower Etjo Beds) of South West Africa (Keyser, 1973). Thus *Diademodon* appears to have been late Early Triassic to early Middle Triassic in age (Du Toit, 1954; Cox, 1967; Keyser, 1973).

Tooth Morphology

The postcanine teeth of *Diademodon* may be grouped into three morphological classes (fig. 2). Conical teeth occupy the anterior end of the tooth row; behind these is a series of gomphodont teeth, and multicuspidate (sectorial) teeth constitute the posterior end of the tooth row.

The homodont, conical teeth are usually three to four in number. These teeth have been considered as "premolars" by several authors (e.g. Broom, 1905, 1913; Brink, 1955) by analogy with mammalian dentitions; but, in view of more recent work (Hopson, 1971) on the replacement of these teeth, it would appear that their classification as "premolars" is unwarranted. These homodont teeth do, however, appear to represent a morphological and morphogenetic class distinct from the gomphodont teeth; thus their classification as a discrete group, i.e. conical teeth, appears to be justified.

Like the conical teeth, the sectorial teeth at the back of the tooth row are also usually three to four in number. Each sectorial tooth is multicuspidate and elongated mesio-distally. The crown is dominated by a large, somewhat recurved buccal cusp, and this is surrounded lingually by a well developed cingulum, which generally supports from five to seven small cuspules. In overall morphology these teeth resemble the cheek teeth of the galesaurid *Thrinaxodon*. Fourie (1963) classified the sectorial teeth of *Diademodon* into two types — "sectorial" at the very back of the series (fig. 2, c and d) and, just anterior to these, "large sectorial" (fig. 2, b). From the most posterior to the most anterior tooth, however, this group of teeth exhibits an almost continuous morphological gradient, any one tooth being nearly indistinguishable from its immediate neighbour. It is unlikely, therefore, that these posterior teeth represent more than one morphological class or "tooth family". They are, however, morphologically distinct from the gomphodont series; thus their classification as a distinct rather homogeneous group, i.e. sectorial teeth, appears to be warranted.

The gomphodont teeth, the so-called "molars" of *Diademodon,* are fairly constant in general crown form or gestalt. The maxillary gomphodont teeth are consistently larger bucco-lingually than mesio-distally, i.e. they are broader than long; and unworn teeth possess a larger buccal cusp and a smaller lingual cusp, connected by a transverse crest. There are usually three to five small mesio-lingual, and three to five small disto-lingual accessory cuspules surrounding the perimeter of the crown. These cuspules were quickly obliterated by wear. The lower gomphodont crowns are generally circular in outline; the bucco-lingual dimension is usually slightly greater than the mesio-distal, but these two dimensions may be equal or, in some instances, the mesio-distal may exceed the bucco-lingual dimension. As

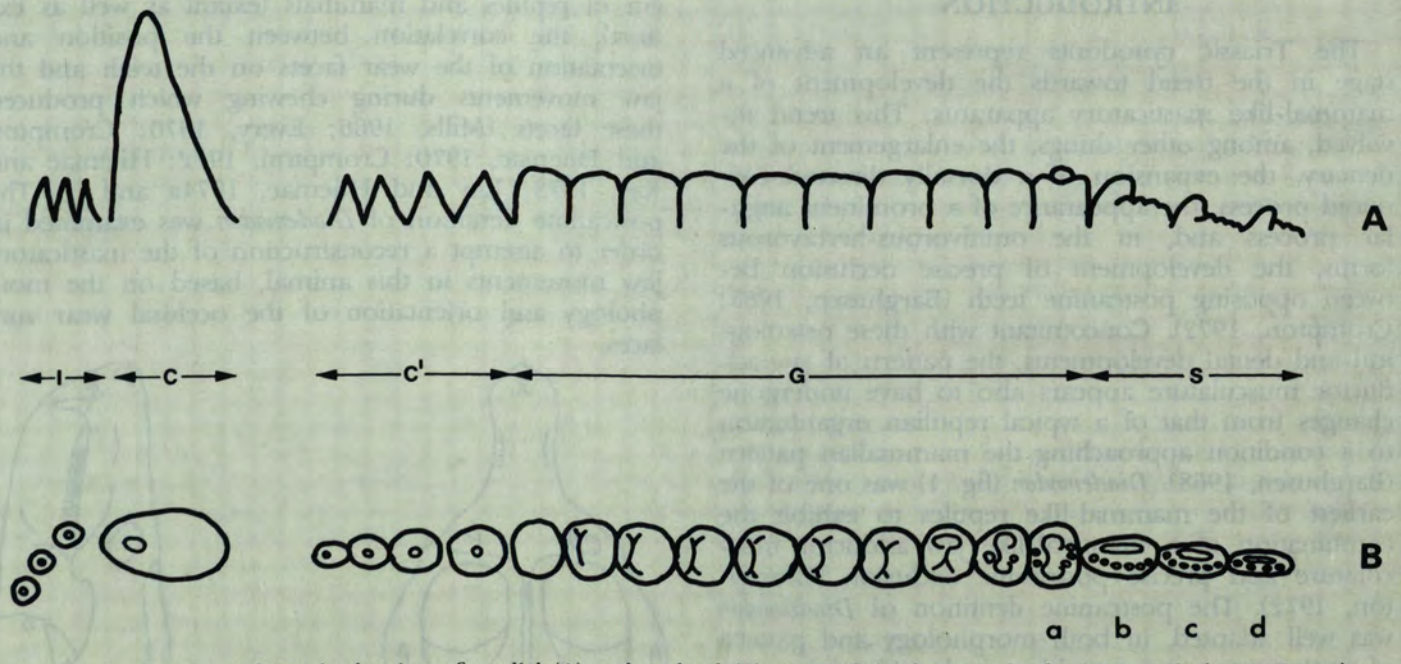


Figure 2. *Diademodon.* Schematic drawing of medial (A) and occlusal (B) views of the lower right dentition. I, incisors; C, canine; C^1, conical teeth; G, gomphodont teeth; S, sectorial teeth; a, intermediate gomphodont tooth; b, large sectorial tooth; c-d, sectorial teeth. See text for explanation.

in the upper gomphodont teeth, a moderately large buccal cusp and a subequal lingual cusp are present and connected by a low transverse ridge. A variable number of small peripheral cuspules are usually present. The variations in position, size and number of these cingular accessory cuspules on the gomphodont crown have been utilized by several authors (e.g. Seeley, 1894: Broom, 1932; Brink, 1955) as the foundation for numerous genera and species presently synonymized under *Diademodon tetragonus* (Hopson and Kitching, 1972). Fourie (1963) classified the most posterior teeth in the gomphodont series as "intermediate gomphodont". It appears that these "intermediate gomphodont" teeth are merely unworn, or very slightly worn, gomphodont teeth, the accessory cuspules of which have not been effaced by wear. Morphologically and, by the latest evidence on replacement, morphogenetically, the "intermediate gomphodont" teeth are inseparable from the rest of the gomphodont group; thus their inclusion in the latter appears to be justified. The number of gomphodont teeth in *Diademodon* may vary greatly, from five to eleven, dependent on the size of the animal. The smaller (ontogenetically younger?) specimens usually possess fewer gomphodont teeth than do the larger specimens.

Tooth Replacement

Tooth replacement in *Diademodon* has been scrutinized by numerous workers (Broom, 1913; Parrington, 1936; Crompton, 1955, 1963b; Fourie, 1963; Ziegler, 1969; Hopson, 1971; Osborn, 1974), resulting in varied conclusions concerning the detail and morphogenesis of the replacement pattern; but the gross pattern seems to be fairly well substantiated. Unlike the typical reptilian pattern of alternate replacement, *Diademoden* appears to have replaced teeth sequentially at the posterior end of each tooth class. The most anterior tooth of each class was shed and subsequently replaced by a tooth of the type in the preceding or immediately mesial class. Thus the most anterior sectorial tooth was shed and replaced by a gomphodont, and likewise, the most anterior gomphodont tooth was shed and replaced by a conical tooth. The most anterior conical tooth, however, was shed and was not replaced; rather, the vacated socket was "plugged" with bone (fig. 3). The conical and gomphodont tooth series both exhibit a size gradient, the most anterior tooth being considerably smaller than the most posterior tooth of each class (fig. 4). It seems reasonable to assume, therefore, that the conical and gomphodont teeth of each succeeding replacement generation were larger than those of the preceding generation (fig. 3). Thus, as replacement proceeded, the teeth became larger with each subsequent generation; in a teleological sense, the size of the teeth thus kept with the size of the animal possessing them.

As a result of this mode replacement, the more anterior teeth of each tooth class were exposed to the rigours of mastication for a longer period of time than those at the back of the series. This accounts for the often observed gradient of wear along

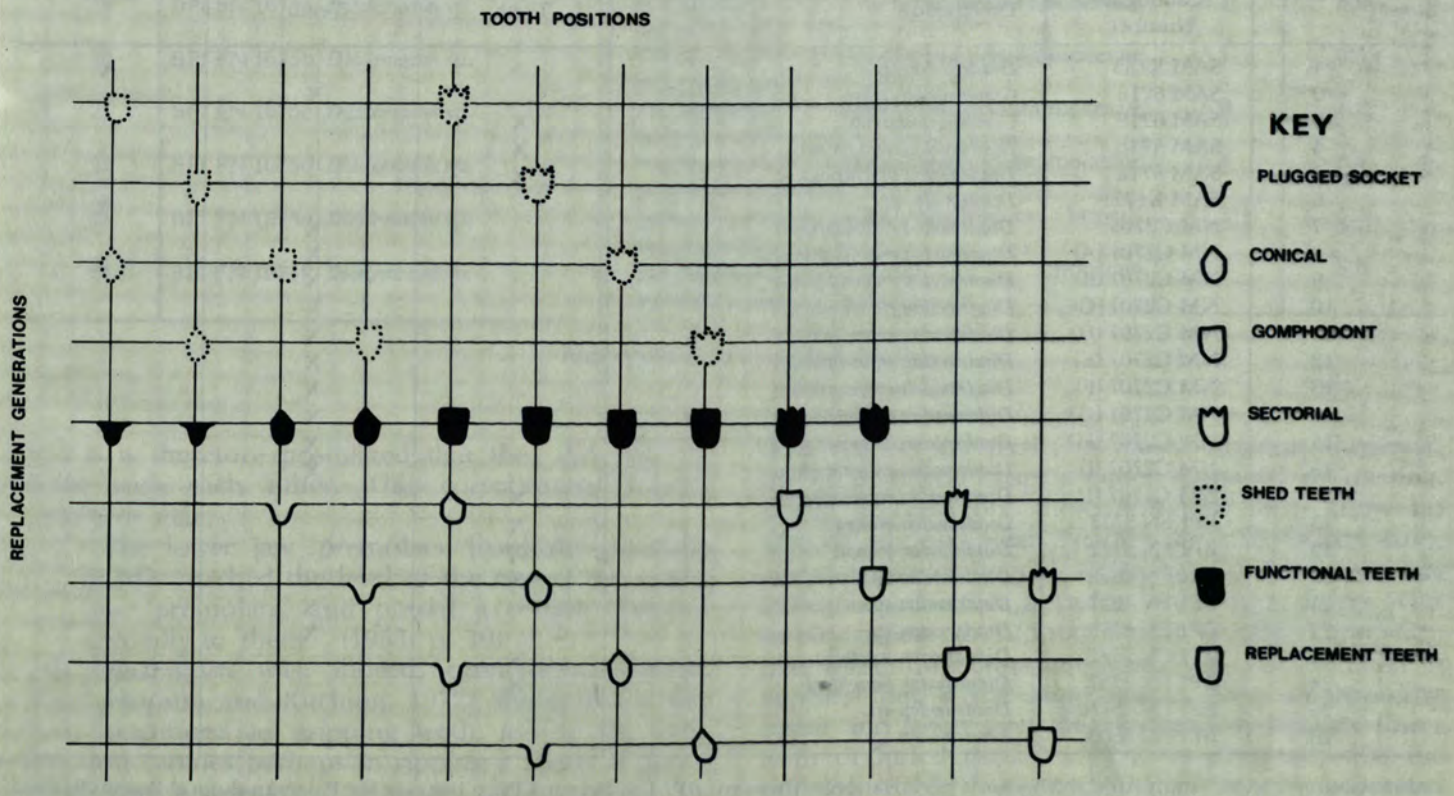


Figure 3. *Diademodon*. Schematic diagram of postcanine tooth replacement. Modified from Osborn, 1974. See text for explanation.

the gomphodont tooth row (fig. 4). Sequential replacement is a prerequisite for precise occlusion (Hopson, 1971). The relevance of sequential replacement to the mechanics of mastication in *Diademodon* will be discussed later.

MATERIALS AND METHODS

The maxillary and mandibular postcanine teeth of 26 different *Diademondon* specimens housed in the South African Museum, Cape Town, the National Museum, Bloemfontein and the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, were examined with either a hand lens or a binocular dissecting microscope under strong, oblique light (table 1). Neither the conical nor the sectorial teeth evinced any sign of occlusal wear, whereas the gomphodont teeth showed evidence of heavy masticatory use. Thus the gomphodont teeth were further scrutinized in the scanning electron microscope (SEM).

Fifty-one peels were made of the occlusal surfaces of both maxillary and mandibular gomphodont teeth, from 18 different *Diademodon* specimens. Peels were made of only those teeth which had been mechanically prepared and were entirely free of matrix. The peels were made using Xantopren impression material combined with Xantopren "soft" hardener catalyst. This material yields reliable results at magnifications up to 200x in the scanning electron microscope. Of these peels, some 22 were chosen for examination (table 2). The peels were trimmed, cleaned for 15 minutes in an ultrasonic bath of 95% ethanol, mounted and then coated with gold and palladium for examination.

Three isolated and broken gomphodont teeth from the collection in the Bernard Price Institute for Palaeontological Research (BPI FN 1675a, b and c) were chosen for direct examination in the SEM. Two of the specimens possessed fragmented, uneven root tips, and these ragged portions were cut-off and ground flat to facilitate mounting. The teeth were then cleaned in an ultrasonic bath of 95% ethanol for from one to two hours, mounted and subsequently coated with gold and palladium for examination. The peels and actual specimens were examined in the Cambridge S4 Stereoscan microscope at the University of the Witwatersrand.

The sample teeth were orientated in the microscope at low magnification (20x), and examined at magnifications up to 200x (peels) and 1 000x (actual specimens) for observation of occlusal wear.

TOOTH WEAR AND OCCLUSION

In the majority of specimens examined, the conical teeth are either damaged or, more often, missing as a result of post-mortem trauma. When present, however, these teeth evince no indication of wear;

Table 1

List of specimens examined with intact postcanine teeth.

Specimen	Institution Catalogue Number	Taxonomic Designation	Maxillary Teeth	Mandibular Teeth	Both
1	SAM K185	*Diademodon* sp.			X
2	SAM 6216	*Gomphognathus* sp.		X	
3	SAM 6219	*Gomphognathus* sp.	X		
4	SAM 571b	*Diademodon tetragonus*	X		
5	SAM 571a	*Diademodon brachytious*	X		
6	SAM K177	*Diademodon* sp.			X
7	NM C2705	*Diademodon entomophonus*		X	
8	NM C2707 (A)	*Diademodon entomophonus*		X	
9	NM C2707 (B)	*Diademodon entomophonus*		X	
10	NM C2707 (C)	*Diademodon entomophonus*		X	
11	NM C2707 (D)	*Diademodon entomophonus*		X	
12	NM C2707 (E)	*Diademodon entomophonus*		X	
13	NM C2707 (F)	*Diademodon entomophonus*		X	
14	NM C2707 (G)	*Diademodon entomophonus*		X	
15	NM C2707 (H)	*Diademodon entomophonus*		X	
16	NM C2707 (I)	*Diademodon entomophonus*		X	
17	NM C2707 (J)	*Diademodon entomophonus*	X		
18	BPI FN 3773	*Diademodon browni*	X		
19	BPI FN 3772	*Diademodon browni*	X		
20	BPI FN 4652	*Diademodon* sp.	X		
21	BPI FN 4647	*Diademodon* sp.		X	
22	BPI FN 1169	*Diademodon* sp.		X	
23	BPI FN 2522	*Diademodon mastacus*	X		
24	BPI FN 3757	*Diademodon haughtoni*	X		
25	BPI FN 1675a-f	*Diademodon* sp.			X
26	BPI FN 2665	*Diademodon* sp.		X	

Abbreviations: SAM, South African Museum; NM, National Museum; BPI FN, Bernard Price Institute for Palaeontological Research, Field Number.

Table 2

List of the specimens and teeth examined in the scanning electron microscope.

Specimen	Institution Catalogue Number	Taxonomic Designation	Locality	Tooth Type	Wear	M-D Diameter	B-L Diameter
1	SAM K185	*Diademodon* sp.	Beersheba, Burghersdorp	upper gomphodont	slight	6,4	9,3
2	SAM 6216	*Gomphognathus* sp.	Sesamondon spot, Aliwal North	lower gomphodont	heavy	6,6	(6,7)
3	SAM 6219	*Gomphognathus* sp.	Aliwal North	upper gomphodont	heavy	6,5	10,8
4	SAM 571b	*Diademodon tetragonus*	Wonderboom	upper gomphodont	absent	4,5	5,4
5	SAM 571b	*Diademodon tetragonus*	Wonderboom	upper gomphodont	absent	4,8	6,2
6	SAM 571a	*Diademodon brachytious*	Wonderboom	upper gomphodont	slight	4,1	6,0
7	SAM 571a	*Diademodon brachytious*	Wonderboom	upper gomphodont	slight	3,9	5,5
8	SAM K177	*Diademodon* sp.	Waterval, Burghersdorp	lower gomphodont	heavy	5,0	5,3
9	SAM K177	*Diademodon* sp.	Waterval, Burghersdorp	lower gomphodont	heavy	5,0	6,2
10	SAM K177	*Diademodon* sp.	Waterval, Burghersdorp	lower gomphodont	heavy	5,4	6,6
11	SAM K177	*Diademodon* sp.	Waterval, Burghersdorp	lower gomphodont	heavy	7,7	7,6
12	NM C2705	*Diademodon entomophonus*	Nooitgedacht, Burghersdorp	lower gomphodont	slight	6,8	7,5
13	NM C2705	*Diademodon entomophonus*	Nooitgedacht, Burghersdorp	lower gomphodont	slight	7,0	8,1
14	NM C2707(A)	*Diademodon entomophonus*	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	5,8	5,6
15	NM C2707(A)	*Diademodon entomophonus*	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	6,3	6,5
16	NM C2707(I)	*Diademodon entomophonus*	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	5,4	4,6
17	NM C2707(J)	*Diademodon entomophonus*	Nooitgedacht, Burghersdorp	upper gomphodont	heavy	5,0	5,9
18	NM C2707(J)	*Diademodon entomophonus*	Nooitgedacht, Burghersdorp	upper gomphodont	heavy	5,7	7,5
19	BPI FN 1675a	*Diademodon* sp.	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	6,1	5,8
20	BPI FN 1675b	*Diademodon* sp.	Nooitgedacht, Burghersdorp	upper gomphodont	moderate	(5,1)	6,5
21	BPI FN 1675c	*Diademodon* sp.	Nooitgedacht, Burghersdorp	upper gomphodont	moderate	6,0	8,8
22	BPI FN 1675d	*Diademodon* sp.	Nooitgedacht, Burghersdorp	lower gomphodont	moderate	5,4	5,5
23	BPI FN 1675e	*Diademodon* sp.	Nooitgedacht, Burghersdorp	lower gomphodont	heavy	(5,2)	5,3
24	BPI FN 1675f	*Diademodon* sp.	Nooitgedacht, Burghersdorp	(?)lower gomphodont	moderate	6,3	5,0

Abbreviations same as for Table 1.

and it is therefore postulated that they did not occlude with each other. This corroborates Brink's statement that:

> "The lower jaw 'premolars' [conicals] generally hardly reached the level of the tips of the upper jaw 'premolars' and passed a certain distance medially to them". (1955, p. 19)

If *Diademodon* was, indeed, omnivorous (Brink, 1955; Hopson and Kitching, 1972), the conicals may have functioned as gripping teeth, aiding the incisors and canines perhaps in ripping a piece of fleshy tissue from a carcass.

Generally, the sectorial teeth are better preserved than the conical teeth; in many instances, however, the large buccal cusp is either damaged or missing. Upon examination, these posterior teeth show no signs of occlusal wear. Neither the large buccal cusp, nor the smaller lingual accessory cuspules evince any indication of either abrasion or attrition facets. This would appear to support Fourie's (1963) contention that these multicuspidate teeth did not occlude. It appears that if the large buccal cusps of opposing upper and lower teeth did, in fact, overlap, the lower teeth occluded medial to the uppers, such that the occlusal surfaces of opposing teeth never contacted one another. The multicuspidate sectorial teeth

probably served to "tenderize" or perhaps shred a food bolus as it passed to the back of the jaw from the chewing battery of gomphodont cheek teeth.

The gomphodont series of teeth was responsible for the mastication of food items. As pointed out above, this series of cheek teeth exhibits a gradient of wear from the heavily worn most anterior teeth to the newly erupted, unworn, posterior gomphodonts (fig. 4).

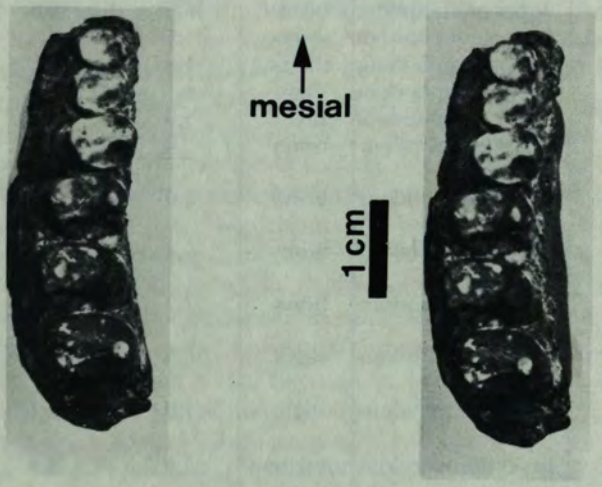


Figure 4. Stereophotograph of the left maxillary gomphodont teeth showing the heaviest wear on the lingual side of the crowns. NM C2707 J. Note the gradient of wear from the heavily worn anterior teeth to the slightly worn posterior teeth. The most anterior tooth is probably the first gomphodont; the erupting tooth at the posterior end of the row is a sectorial.

When the gomphodont teeth occluded, the upper overlapped the lowers both buccally and lingually; the lowers fitted into the embrasure formed between the transverse crests of adjacent upper teeth (Crompton, 1972) (fig. 5 A). This difference in size between the transversely broadened upper and circular lower crowns is perhaps significant, in as much as it may have permitted a rather liberal expression of mandibular adduction. That is, closing of the jaws could feasibly have brought the lower teeth into occlusion with their maxillary antagonists, several millimetres buccal (fig. 5 B) or lingual (fig. 5 C) to what might be termed the point of central occlusion, and an effective occlusal relationship still would have resulted. This situation may, perhaps, be correlated with the relative development (mass) and differentation of the various jaw adductor muscle groups. Possibly, the jaw adductor musculature of *Diademodon* was incapable of performing the complex, controlled movements which are characteristically expressed in mammalian mastication (Grine, in preparation).

Brink (1955) noted that:

> "the lower jaw 'molars' [gomphodont teeth] wear over the whole of their surfaces, while the upper jaw 'molars' wear only over the middle of the crowns". (p. 19)

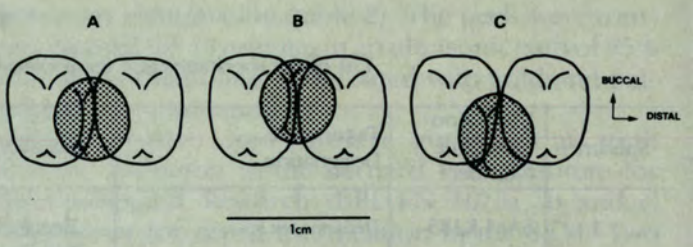


Figure 5. Dorsal view of the occlusal relationships between upper and lower gomphodont teeth. The lower tooth is shaded. A, "central" occlusal relationship; B, possible relationship with lower tooth occluding buccal of "central"; C, possible relationship with lower tooth occluding lingual of "central". See text for explanation.

Examination of *Diademodon* maxillae containing gomphodont teeth revealed, however, a number of specimens with teeth worn disproportionately on the buccal side (e.g. BPI FN 2522), and several specimens exhibiting heavier lingual wear on the gomphodont teeth (cf. fig. 4). It is not clear at present what, if any, taxonomic, ontogenetic or ecological significance these differences in gomphodont tooth wear among various specimens might indicate.

The occlusal surface relationships between unworn opposing upper and lower gomphodont teeth were not precisely matched. The cusps, crests and accessory cuspules did not exhibit the complex occlusal relationships which characterize the homologous structures of mammalian molar teeth. Rather, in *Diademodon* effective matching wear surfaces were produced only after considerable wear (Crompton, 1972); thus in those teeth exhibiting slight to moderate wear (fig. 6 B and C respectively), precise occlusion was manifested. The enamel covering the

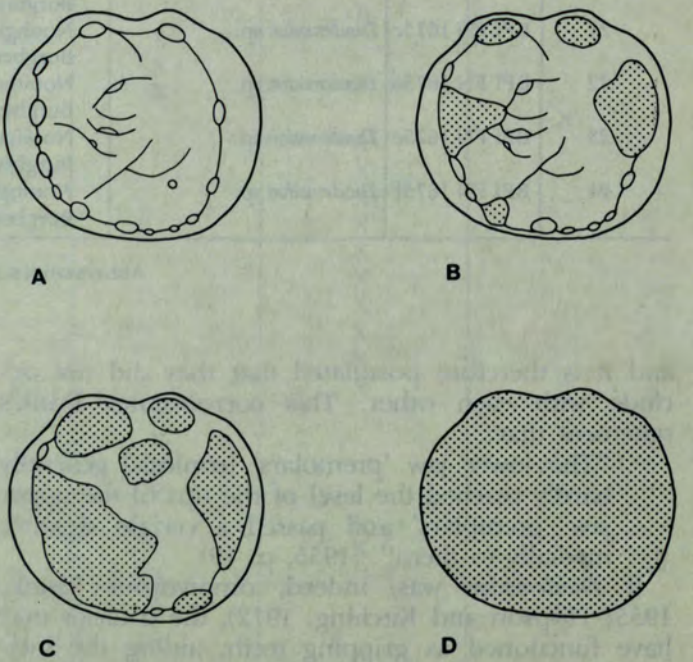


Figure 6. Lower gomphodont teeth in various stages of wear. A, unworn; B, slightly worn; C, moderately worn; D, heavily worn. Not to scale. Drawings by C. Gow.

gomphodont crown is thin, and probably non-prismatic (Poole, 1956; Moss, 1969), and as a result it was rapidly worn away; thus the occlusal surfaces of these teeth were quick to expose dentine. The main cusps and transverse crests of both upper and lower gomphodonts retained the thin enamel covering longer than the rest of the occlusal surface (fig. 7); however, continued wear rapidly obliterated all traces of occlusal surface morphology, resulting in featureless, flat-surfaced crowns pounding against one another. With time these teeth were shed sequentially, and replaced by conical teeth.

The occlusal surfaces of the gomphodont teeth, in various stages of wear (fig. 6), evince no indication of the presence of what might be called shearing surfaces (as indicated by wear facets possessing parallel striations or grooves). The only striations which are present are very short grooves running in a mesiodistal direction off the summit of the transverse crest in some slight to moderately worn teeth (fig. 8). These grooves are most likely an artefact of the imprecise matching of opposing occlusal faces in these teeth, and as such they can hardly be considered as representing an effective shearing surface (Crompton, 1972). The occlusal aspects of the gomphodont teeth characteristically reveal pitted, pock-marked surfaces (figs. 9; 10 A and C), an indication of either abrasion or attrition, resulting from direct pounding of the lower teeth against their maxillary antagonists. This corroborates Crompton's statement that the "external main cusp (actually the main buccal and lingual cusps and transverse crest) of the lowers pounded into the basin formed between two adjacent upper postcanines" (1972, p. 38); but no dental evidence exists to support his contention that vertical shearing planes were developed between the crests and cusps of the upper and lower gomphodont teeth.

Examination of the occlusal surfaces of worn gomphodont teeth in the SEM at high magnification (1 000x) yields pictures of surface textures which superficially resemble those encountered on aeolian sand grains (fig. 10 B and D). Neither the remnanat enamel on the occlusal surfaces (fig. 7), nor the enamel on the sides of the tooth crowns (figs. 11 and 12), exhibited surface textures like that evinced by the dentine. Likewise, the cementum surfaces of the exposed roots of isolated gomphodont teeth, although showing more textural relief than the enamel surfaces, do not show the same rugged, pitted surfaces which characterize the occlusal dentine surfaces of the same teeth (fig. 12). Thus neither the enamel nor the cementum surfaces evince the same textural morphology as is found on the occlusal dentine surfaces of the selfsame teeth. It therefore seems reasonable to conclude that the dentine surface texture encountered on the worn gomphodont teeth is a result, primarily, of masticatory rigours, and is not an artefact of secondary, post-mortem processes such as sand-blasting, traction or freeze-fracturing.

Clearly then, the function of the gomphodont teeth was the preparation of food items for deglutition. The occlusal surfaces of these teeth indicate that the lower pounded against the uppers, thus crushing or pulverizing the food during mastication; and that the jaw movements which brought

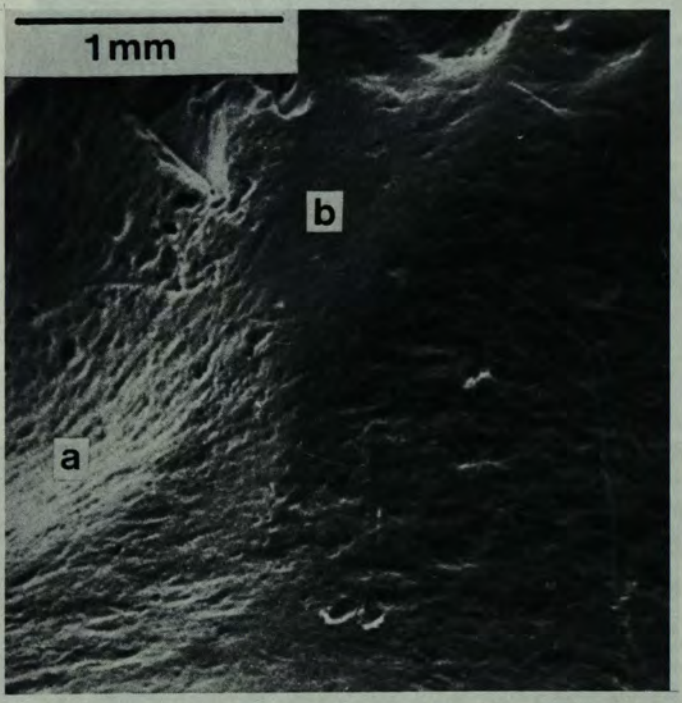


Figure 7. Scanning electron micrograph of the occlusal surface of a (? right) upper gomphodont tooth. The figure shows the pitted dentine surface, a, and the remnant of enamel covering the lingual cusp, b. Note the difference in surface textures. BPI FN 1675b. Oblique angle of 40 ° from the buccal side.

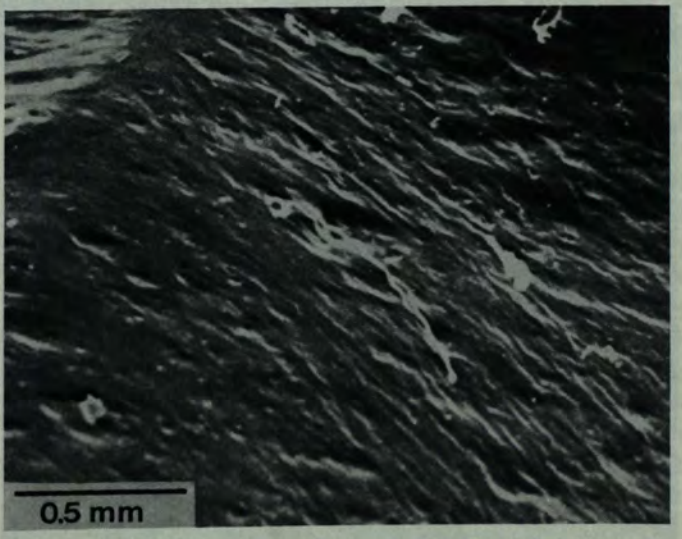


Figure 8. Scanning electron micrograph of a peel from the occlusal surface of a (? right) lower "intermediate" gomphodont tooth, exhibiting moderate wear. Note the grooves running off the summit of the transverse crest and the relatively smooth surface of the ridge. Note also that no grooves cross the summit of the crest. Oblique angle of 37 °, taken from lingual side. BPI FN 1675f. Picture inverted in order to show surface in positive relief.

these teeth into occlusion were wholly orthal (that is, directly up and down). There is no dental evidence to support the contention that *Diademodon* exhibited propalinal (fore and aft) masticatory movements (Parrington, 1934, 1936; Hopson, 1971); nor is there any dental evidence to support the statement that a "postero-dorsally directed power stroke may have been initiated in *Diademodon*" (Crompton, 1972). By the same token, the teeth evince no indication that this reptile exercised ectental (side to side) chewing movements, corroborating Brink's contention that "there could have been little lateral movement of the lower jaw when the jaw was closed" (1955, p. 19).

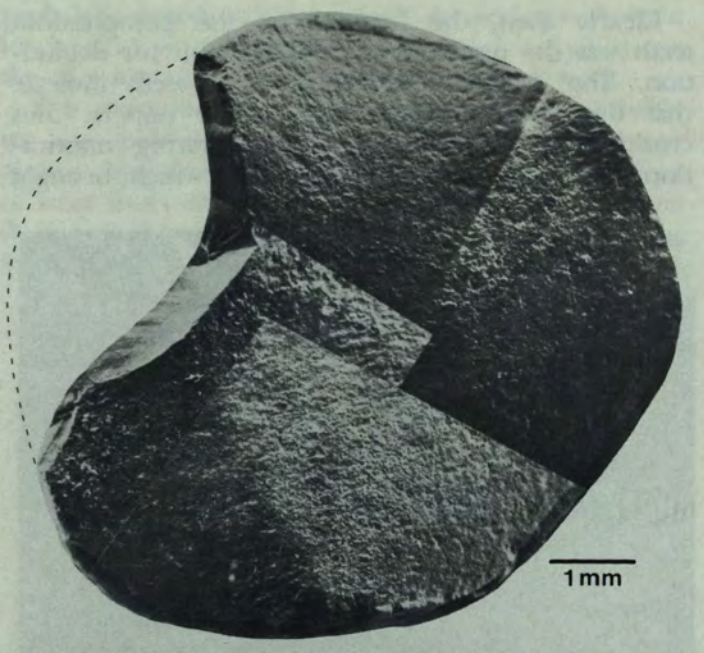
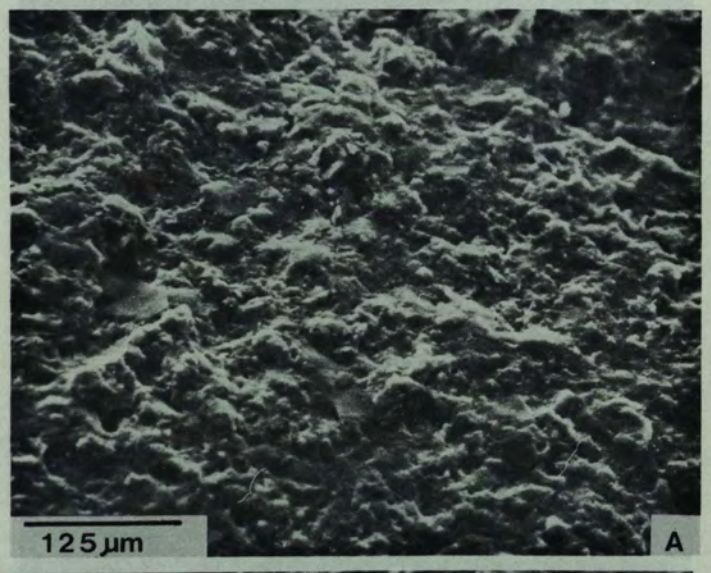
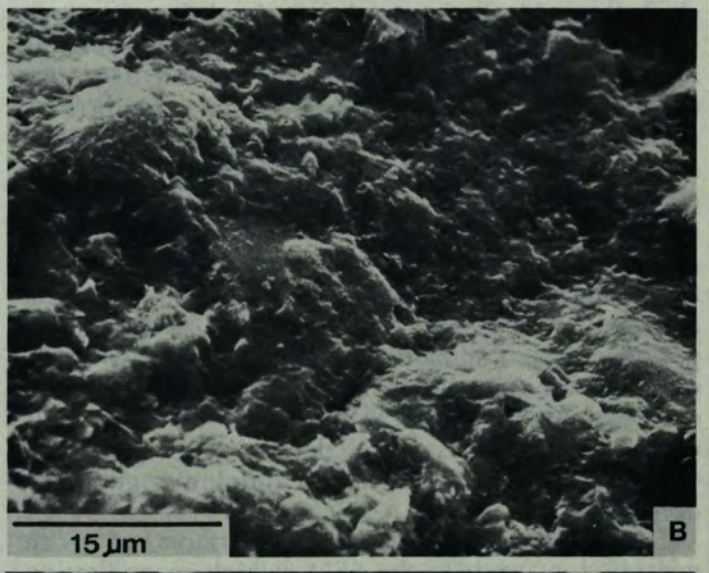
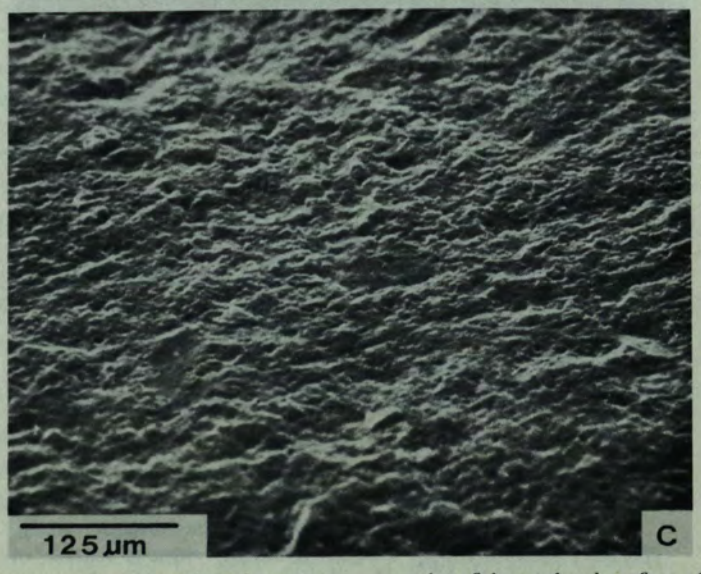


Figure 9. Composite scanning electron micrograph of the occlusal surface of a heavily worn (? right) lower gomphodont tooth. The outlined broken area represents post-mortem damage. Note the pitted surface texture of the dentine over the entire occlusal surface. BPI FN 1675a. Direct occlusal views.







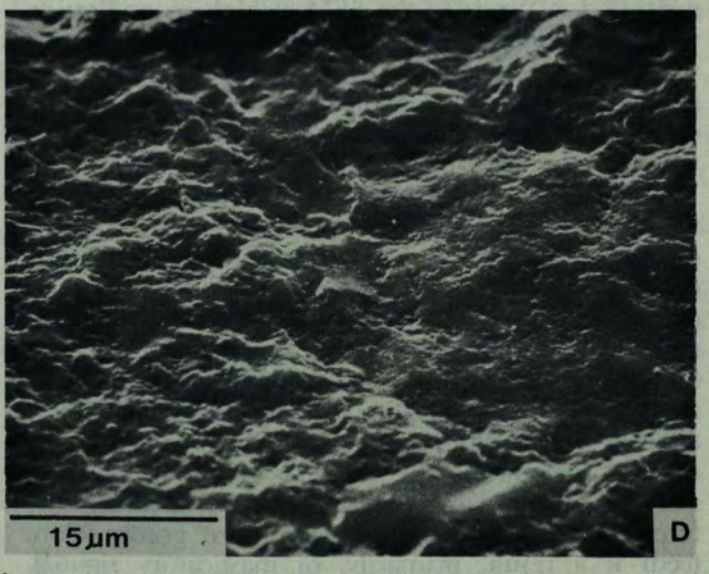


Figure 10. Scanning electron micrographs of the occlusal surface of the same tooth pictured in Figure 9. BPI FN 1675a. A, enlargement of area on the buccal (?) side of the tooth (see fig. 9), tilt angle of 25°; B, enlargement of the same area, tilt angle of 25°; C, enlargement of area on lingual (?) side of tooth, just distal to remnant of transverse crest, tilt angle of 25°; D, enlargement of the same area as shown in C, tilt angle of 25°.

The gomphodont teeth exhibited precise occlusion, in as much as the lower and upper teeth possessed matching wear faces; and the sequential replacement of these teeth permitted the maintenance of this type of occlusion. Furthermore, the shapes of the opposing upper and lower crowns, coupled with their mode of alternate occlusion (see fig. 5 A), may have served to retain their functional crown shapes for as long as possible under conditions of heavy, pounding wear. A similar mechanical design characterized the molariform teeth of the cotylosaur *Procolophon trigoniceps* (Gow, 1977).

DISCUSSION

The foregoing analysis of the occlusal surfaces of the postcanine dentition of *Diademodon* lends itself to the conclusion that masticatory jaw movements in this mammal-like reptile were wholly orthal. The pitted occlusal surfaces of the worn gomphodont teeth attest to an orthal movement of the lower jaw during chewing. The evidence against propalinal and ectental masticatory jaw movements in *Diademodon,* as gleaned from the dentition is, however, negative evidence. Several features of the cranium and lower jaw of *Diademodon,* however, do appear to provide further evidence against any significant propalinal or ectental jaw movements having been manifested in this animal during chewing.

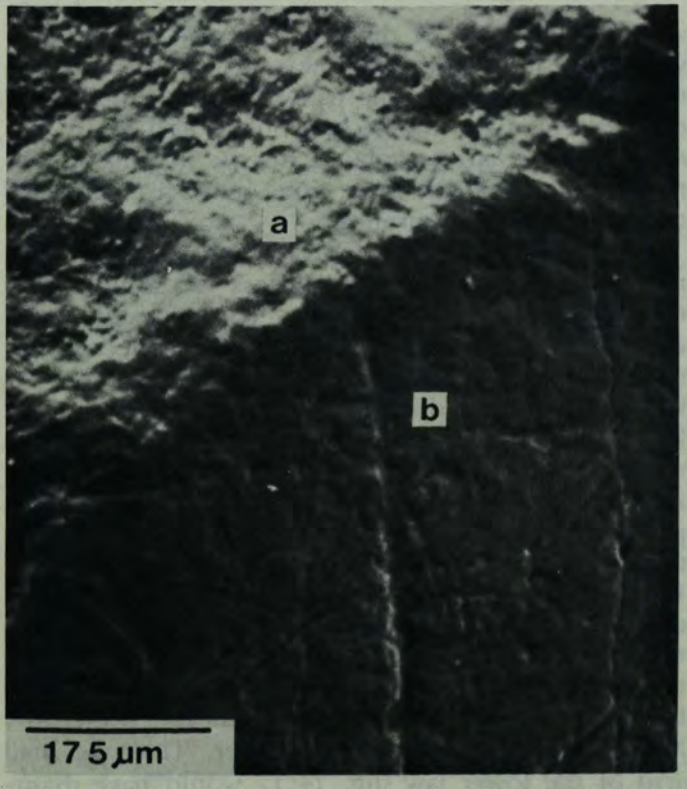


Figure 11. Scanning electron micrograph of an upper gomphodont tooth, showing the differences in surface textures between the occlusal dentine surface, a; and the non-occlusal enamel surface, b. BPI FN 1675c. Tilt angle of 51 °, oblique from buccal.

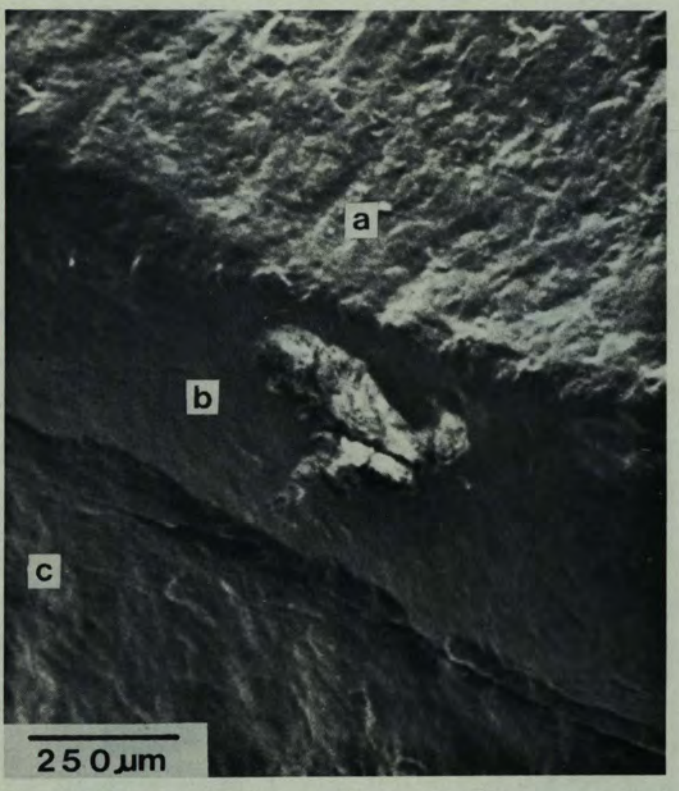


Figure 12. Scanning electron micrograph of an upper gomphodont tooth, showing the differences in surface textures between the occlusal dentine surface, a; the non-occlusal enamel surface, b; and the cementum surface, c. BPI FN 1675b. Tilt angle of 140 °, oblique from buccal.

The anterior region of the hard palate possesses two fossae which housed the crowns of the lower canines when the jaws were closed. These excavations are located antero-medial to the maxillary canines, and postero-lateral to the incisive canal. The premaxilla contributes the anterior wall of each fossa, while the medial, lateral and posterior walls are formed by the maxilla (Brink, 1955, and personal observation). When the jaws are closed, such that the gomphodont teeth were in occlusion, much of the lower canine crowns would have been "locked" into these fossae. Although these palatal excavations are rather large, they would have been lined with oral epithelium, thus decreasing their diameters. The amount of movement that the lower canines would have enjoyed, once lodged in these fossae, would probably have been negligible; but it is debatable whether this "locking" of the lower canines would have effectively restricted either lateral or fore-aft masticatory movements.

The pterygoids support long, robust, ventrally directed flanges. These processes are situated just medial to the inner border of the lower jaw, and in life would have been covered with soft tissue (as would the inner border of the mandible), thereby placing the flanges in even closer juxtaposition with the medial sides of the lower jaw. Thus, the pterygoid flanges may have been situated close enough to the

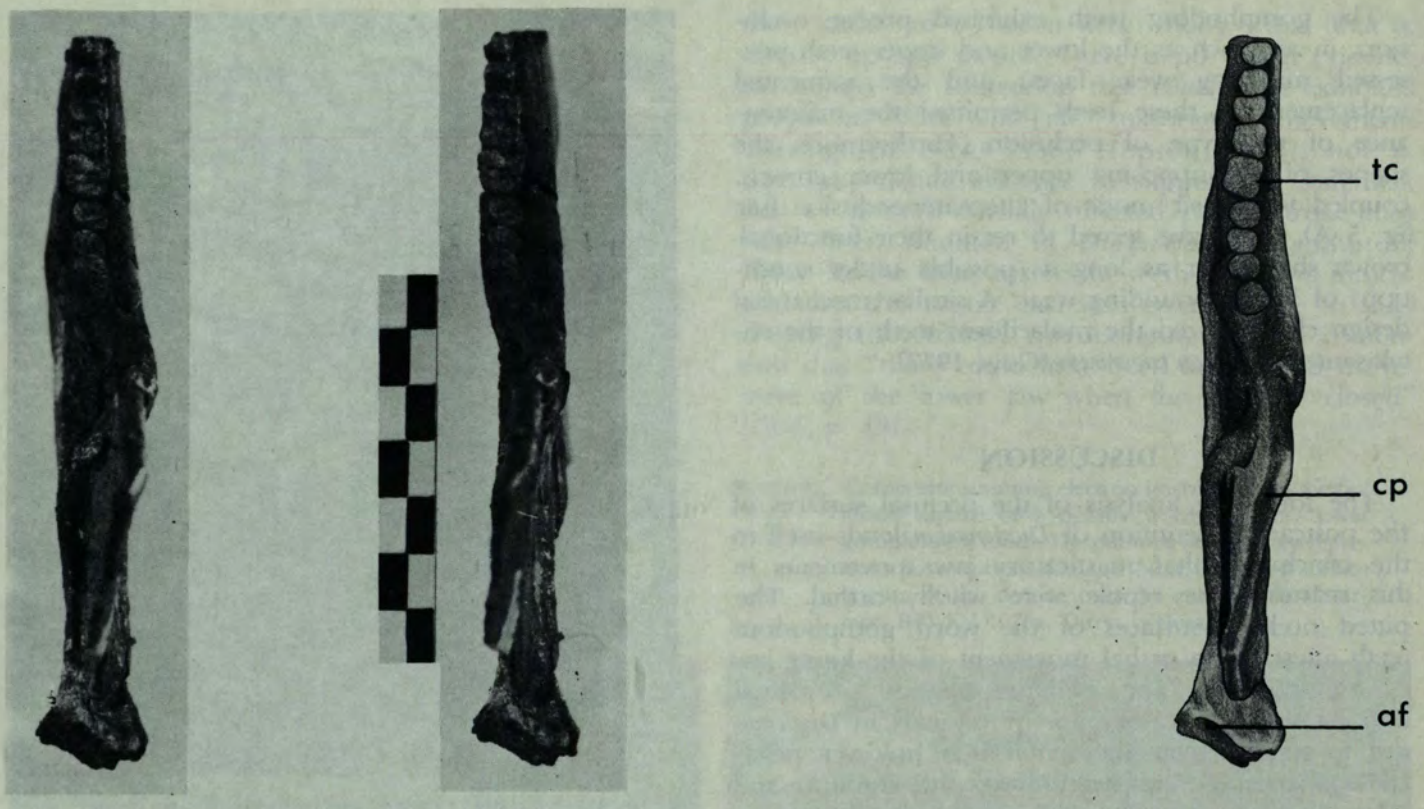


Figure 13. *Diademodon.* Left, stereophotograph of the right lower jaw; Right, drawing of same. Note the depth and orientation of the articular fossa; tc, tooth crown; cp, coronoid process; af, articular fossa. SAM K177. Scale in cm. Drawing by C. Richards.

inner sides of the lower jaw to have restricted effectively any gross lateral movement on the part of the mandible.

Finally, the jaw articulation in *Diademodon* is small compared to the size of the dentary. The articular bone possesses a divided, or double, glenoid fossa, consisting of a concave lateral fossa and a nearly flat medial fossa (Crompton, 1963b). The lateral fossa is elongated medio-laterally and convex from top to bottom; it is obliquely orientated, with the medial side higher and more anterior than the lateral side (fig. 13). It appears that only the lateral fossa articulated with the quadrate, and this articulation was probably rather weak (Crompton, 1963b). The structure and orientation of the lateral articular fossae are such that any lateral movement of the lower jaw (which possesses a very strongly fused symphysis) would have necessitated the dislocation of one of the joints. Similarly, in order to have effected propalinal jaw movement, both of the articular joints would have had to be dislocated. It appears, therefore, that the articular-quadrate joint in *Diademodon* was not constructed (adapted) so as to withstand either the movements or the resulting forces of lateral translation and rotation. Rather, the joint, by its construction and orientation, acted as a hinge (turning moment) for the lower jaw (fig. 14).

The mechanics of mandibular adduction in *Diademodon,* as determined by the relative development and differentiation of the jaw adductor musculature, were such that little strain was placed on the relatively weak jaw joint. The pattern of sequential tooth replacement may have contributed also to a lessening of the stresses placed on the articular-quadrate joint and, at the same time, may have increased the efficiency of mastication.

Replacement at the posterior end of the tooth row, coupled with sequential loss of gomphodont teeth and their replacement by conical teeth at the anterior end of the row, perhaps served effectively to move the tooth row posteriorly, concomitantly with the growth of the dentary, thus maintaining younger (that is, relatively unworn) gomphodont teeth in the region of greatest occlusal pressure (fig. 14). Assuming the "bite point", or centre of greatest occlusal pressure, to be located near (probably slightly posterior to) the middle of the gomphodont series (fig. 14 BP), this point would have been moved posteriorly one tooth position with each replacement of sectorial teeth by gomphodont teeth. Owing to continuous, and possibly fairly rapid replacement, the bite point would have effectively moved posteriorly as the jaws grew larger and longer. Thus the load arm of the lower jaw (fig. 14 L) would have maintained a fairly constant length even as the tooth-bearing portion of the dentary enlarged. By the same token, it is possible that the pressure exerted at the bite point may have been increased as this point

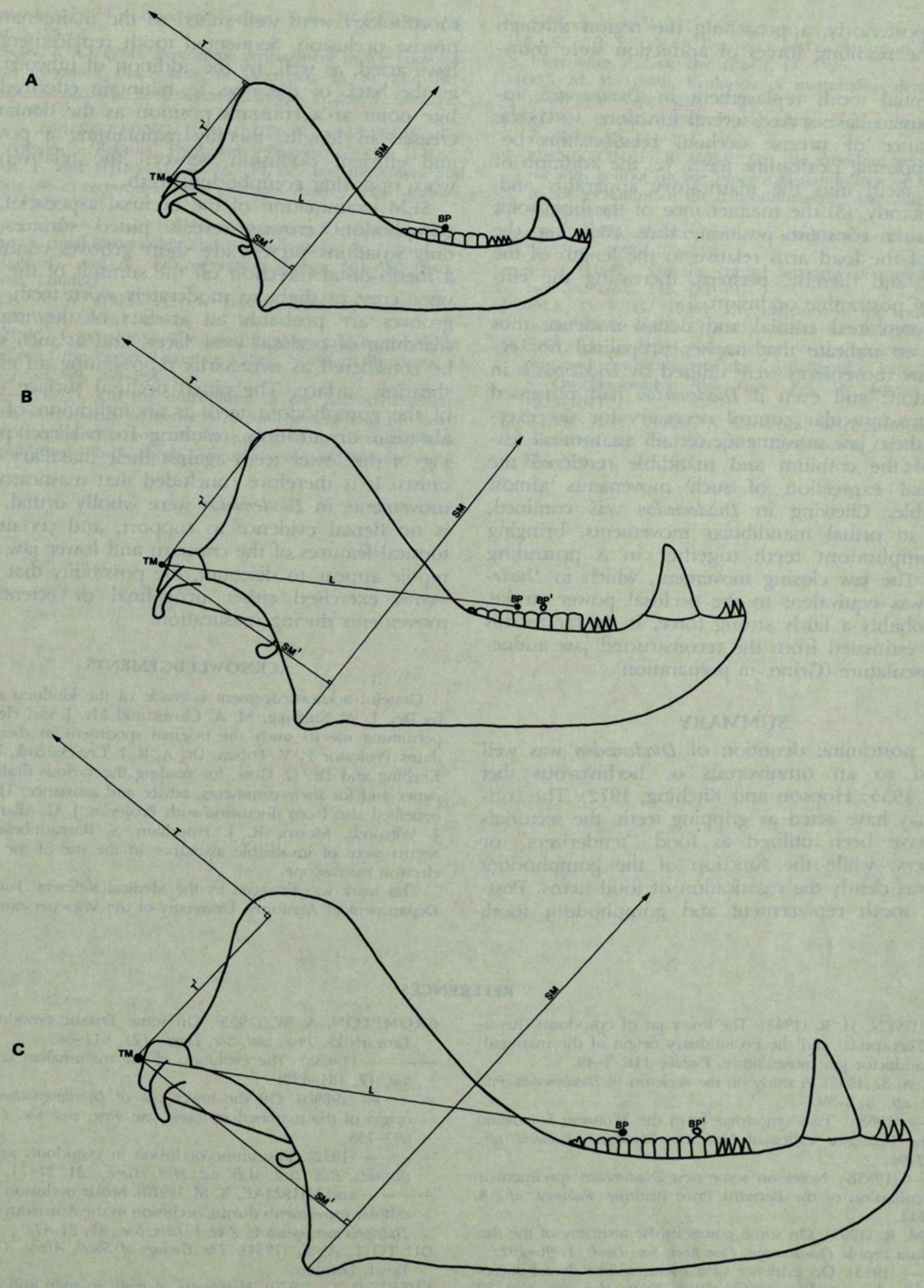


Figure 14. *Diademodon*. The correlation between sequential tooth replacement and jaw growth. A, hypothetical lower jaw of a young individual; B. lower jaw of an individual 1,33x larger, indicating the relative positions of the "static" bite point, BP¹ and the "actual" (moved) bite point BP; C, lower jaw of an individual 1,33x larger, indicating the relationships between the two bite points. BP, "actual" bite point; BP¹ "static" bite point; L, load arm of the jaw to bite point; SM, moment arm of M. masseter superficialis; SM¹, power arm of SM; T, moment arm of M. temporalis; T¹, power arm of T; TM, turning moment of the lower jaw. Lower jaw from Crompton (1963b). See text for explanation.

moved posteriorly, approaching the region through which the resulting forces of adduction were translated.

Sequential tooth replacement in *Diademodon* appears thus to have served several functions — (1) the maintenance of precise occlusal relationships between opposing postcanine teeth, (2) the addition of unworn teeth into the masticatory apparatus and, concomitantly, (3) the maintenance of the bite point at a fairly constant position, thus reducing the length of the load arm relative to the length of the dentary, and thereby, perhaps, increasing the efficiency of postcanine occlusion.

The combined cranial and dental evidence thus appears to indicate that neither propalinal nor ectental jaw movements were utilized by *Diademodon* in mastication; and even if *Diademodon* had possessed the neuro-muscular control necessary for the exercise of these jaw movements, certain anatomical features of the cranium and mandible rendered the functional expression of such movements almost impossible. Chewing in *Diademodon* was confined, rather, to orthal mandibular movements, bringing the gomphodont teeth together in a pounding action. The jaw closing movement, which in *Diademodon* was equivalent to the occlusal power stroke, was probably a fairly strong force, in so far as this can be estimated from the reconstructed jaw adductor musculature (Grine, in preparation).

SUMMARY

The postcanine dentition of *Diademodon* was well adapted to an omnivorous or herbivorous diet (Brink, 1955; Hopson and Kitching, 1972). The conicals may have acted as gripping teeth, the sectorials may have been utilized as food "tenderizers" or shredders; while the function of the gomphodont teeth was clearly the mastication of food items. Postcanine tooth replacement and gomphodont tooth morphology were well suited to the maintenance of precise occlusion. Sequential tooth replacement may have acted, as well, by the addition of unworn teeth at the back of the row, to maintain effectively the bite point at a constant position as the dentary increased in length, thereby maintaining a powerful and efficient occlusion between the relatively unworn opposing gomphodont teeth.

SEM examination of the occlusal aspects of worn gomphodont crowns reveals pitted surfaces. The only striations present are short grooves running in a mesio-distal direction off the summit of the transverse crest in slight to moderately worn teeth. These grooves are probably an artefact of the imprecise matching of occlusal wear faces, and as such cannot be considered as necessarily representing an effective shearing surface. The pitted occlusal surface texture of the gomphodont teeth is an indication of either abrasion or attrition, resulting from direct pounding of the lower teeth against their maxillary antagonists. It is therefore concluded that masticatory jaw movements in *Diademodon* were wholly orthal. There is no dental evidence to support, and certain anatomical features of the cranium and lower jaw of this reptile appear to discount, the possibility that *Diademodon* exercised either propalinal or ectental jaw movements during mastication.

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