Palaeont. afr., **32**, 75-82 (1995)

DENTITION AND FEEDING NICHE OF *ENDOTHIODON* (SYNAPSIDA; ANOMODONTIA).

by

E. M. Latimer, C. E. Gow and B. S. Rubidge

BPI Palaeontology, University of the Witwatersrand, Johannesburg, Private Bag 3, Wits 2050, South Africa

ABSTRACT

The cranial morphology and extensive dentition of the dicynodont therapsid *Endothiodon* are different from those of any other dicynodont and it clearly had a different feeding niche. Recently prepared material from Mozambique which has relatively well preserved dentition has revealed that the mode of tooth replacement of *Endothiodon* differs in the upper and lower jaws. The very high and narrow vaulted palate with a close fitting, pointed lower jaw indicates that *Endothiodon* had a small mouth with muscular cheeks and extensive cheek pouches, suggesting a browsing feeding niche.

KEYWORDS: Therapsida, Dicynodontia, *Endothiodon*

INTRODUCTION

The anomodont genus *Endothiodon* is known from South Africa, Zambia, Tanganyika (Cox 1964), India (Kutty 1972), and Brazil (Keyser 1981). However, because most of the skull material is fragmentary, relatively little is known about the cranial anatomy of this atypical dicynodont. Several specimens collected in Mozambique in 1956 which are housed in the collections of the Bernard Price Institute for Palaeontological Research have recently been prepared. Comparison of this material with specimens from the Beaufort Group of South Africa reveals important new information on the dentition and possible mode of feeding of *Endothiodon*.

In South Africa, where the majority of *Endothiodon* specimens have been found, the stratigraphic range of the genus extends from the *Pristerognathus* Assemblage Zone to the upper regions of the *Cistecephalus* Assemblage Zone (Smith & Keyser In Press a & b). Because its stratigraphic range is relatively limited the genus has been used as a zone fossil in previous biostratigaphic subdivisions of the Beaufort Group in South Africa (Broom 1906, 1907, 1909; von Huene 1925; Watson 1914 a,b).

The Mozambiquean material was sent to Dr S H Haughton, then director of the Bernard Price Institute, in 1957, by Dr F Mouta, who had collected it in the Lugno area of Niassa Province in 1956.

Cox (1964), in revising the taxonomy of *Endothiodon*, used the palate and dentition to reduce nine species to three. He also speculated that the animal may have fed by grubbing vegetable matter out of swampy ground. In contrast, our research suggests that *Endothiodon* was a specialised browser. The genus is unique among anomodonts in having premaxillary teeth and also has differing modes of tooth replacement in upper and lower jaws.

MATERIAL AND METHODS

The Mozambiquean material consists of several fragmentary skull pieces, of which two snouts are the most complete, and several incomplete jaws consisting of the symphyseal region and considerable portions of one or both tooth rows. All have suffered postmortem damage, including total or partial loss of teeth, but some crowns functional at time of death remain. As this is a surface collection which required no excavating, exposed bone has been weathered but freshly exposed bone is very well preserved.

Most preparation was undertaken mechanically using an air scribe, but as the bone is not adversely affected by acid the carbonate rich matrix was speedily removed in 5% formic acid, the bone being strengthened during preparation with a dilute, penetrating solution of Glyptal Cement.

DESCRIPTION

Lower Jaw

Although the purpose of this paper is to describe the dentition of *Endothiodon*, as the lower jaw of this genus has not been described in detail it is here described briefly as far as preservation of the material permits. In the collection studied only the anterior portions of the jaw rami are preserved and the surangular, prearticular and articular bones are missing.

In the symphyseal region the dentaries are curved upwards into a sharply pointed and narrow beak which fits closely into the highly vaulted palate of the upper jaw. A broad groove is present on the dorsal surface of the dentary lateral to the teeth.

A lateral dentary shelf is absent in *Endothiodon* (Cluver & King 1983), but in all specimens examined a bulbous swelling of the dentary is present on the ventrolateral side of the jaw (Fig. 1 A&D) anterior to

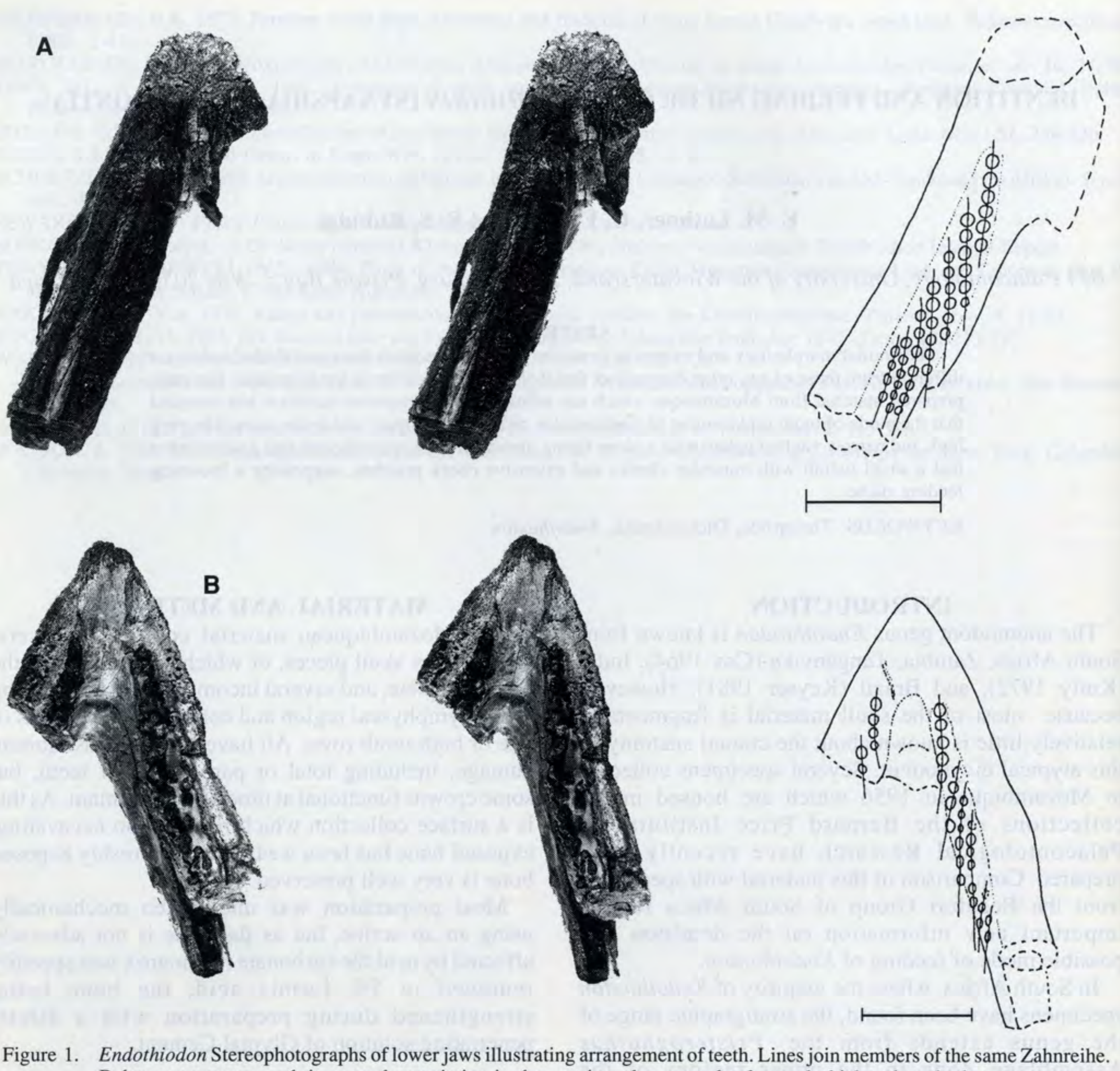


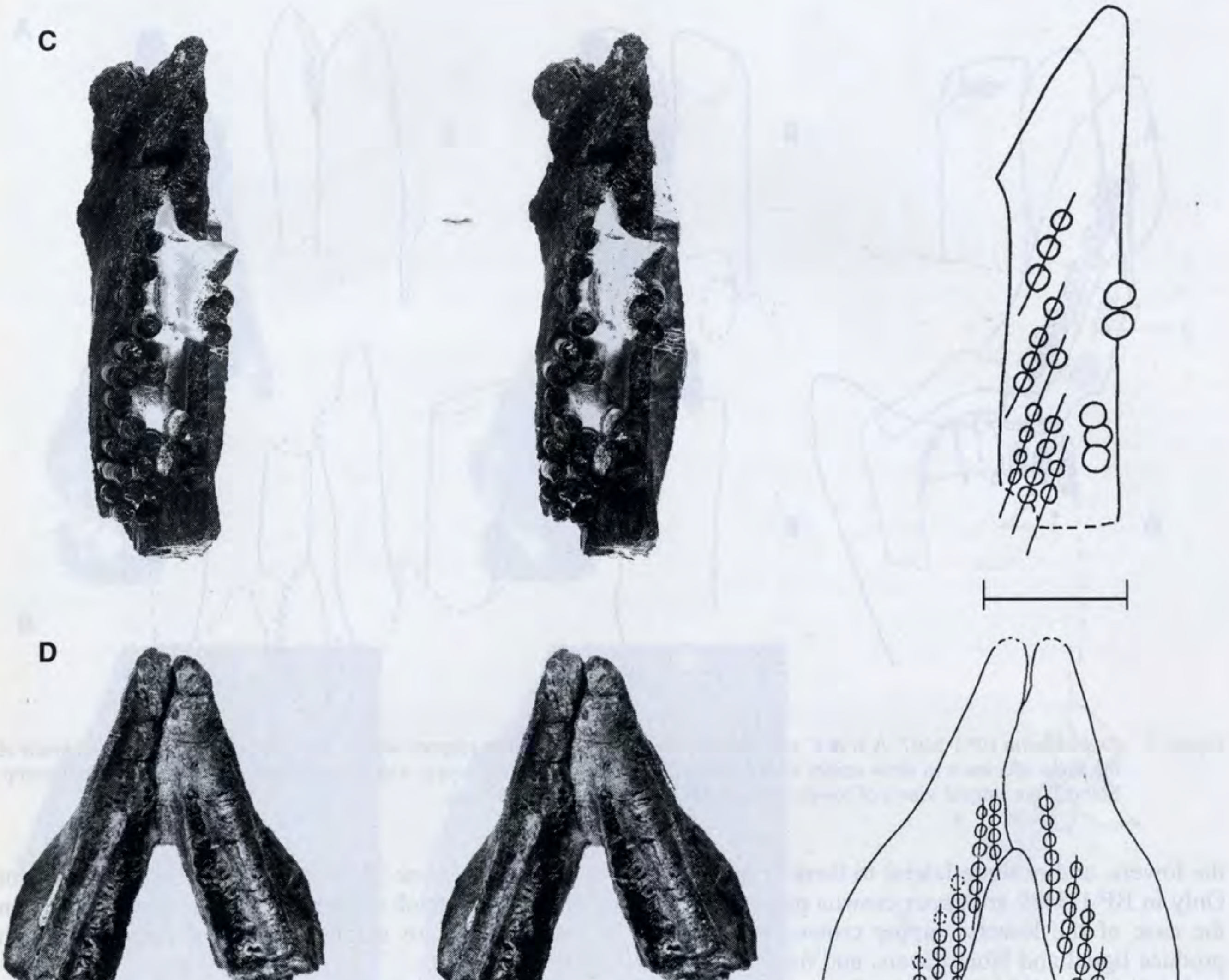
Figure 1. *Endothiodon* Stereophotographs of lower jaws illustrating arrangement of teeth. Lines join members of the same Zahnreihe. B has some upper teeth in natural association in the matrix – these are clearly much thicker than the lowers. A = BP\1\5494; B = BP\1\5492; C = BP\1\5489; D = BP\1\5491; Scales are 50mm.

the intramandibular fenestra. This swelling is not however the same as a lateral dentary shelf and the function is not yet understood.

The splenial is a relatively large bone and typically constitutes most of the ventral surface of the symphyseal region. The splenials form an anterodorsally oriented wedge between the dentaries, and in longitudinal section the splenial shows a distinct undulation within the symphysis at the anterodorsal part of the suture with the dentary. Posteriorly the splenial tapers to a point, low on the medial surface of the dentary.

The angular forms the largest portion of the ventral border of the lower jaw extending forwards as far as a point in line with the posteroventral border of the symphysis, where it forms a pointed contact between the dentary on the lateral side and the splenial on the medial side. None of the fragments have the posterior region of the angular preserved.

Cox(1964) considered that *Endothiodon* has three parallel rows of teeth in the dentary. However it is now apparent that it is not possible to group the teeth in parallel longitudinal rows, rather they fall into obliquely arranged Zahnreihen (Edmund 1969) or replacement waves (Figure 1). Zahnreihen are a series of consecutive replacement waves; each Zahnreihe is a row of teeth in which the oldest is the anteriormost and the youngest the posteriormost, i.e. teeth have erupted sequencially from front to back. Most amniotes have single rows of marginal teeth; such retention of several Zahnreihen is an uncommon phenomenon.Teeth of more posterior Zahnreihen tend to be smaller, as is commonly the case in the marginal dentitions of amniotes generally. In all cases where the dentitions are sufficiently well preserved (BP\1\5489 to 5494 and 5497), it can be seen that new teeth were being added to even the most posterior Zahnreihen, showing that there was active, ongoing replacement throughout the tooth row.



Because of the persisting Zahnreihen the tooth bearing portion of the dentary is a broad zone in which the teeth are held in an area of spongy bone that is continually being remodelled. This area, which broadens posteriorly from the posterodorsal margin of the symphysis, extends medially from the medial margin of the dentary to the lingual edge of the lower jaw. The labial margin of this zone, where it is exposed by loss of teeth, displays deep, concave impressions of the roots (Figure 2D). The lingual margin (Figure 2D) bears a sequence of foramina within (behind) which developing, unerupted teeth can be seen. The margins of these crypts erode upwards as the new tooth grows (Figure 2F); the alveolar border then closes as the tooth moves labiad. As the majority of (especially fully functional) crowns are missing, it is not possible to work out the exact sequence of replacement. However it is apparent that there was no bilateral symmetry to the process (Figure 1). It is clear that replacement waves moved posteriad along the jaw, as shown by the relative maturity of new teeth.

The crowns of unworn lower teeth are broad mesially, tapering towards the distal edge which bears sharp, posteriorly directed serrations extending almost to the tip (Figure 2 B,C,E & F). Roots are cylindrical. Only two undamaged crowns of teeth worn through use are present in the collection (Figure 2 A,B & C). These show that crowns became faceted on their lingual and labial sides. This could only be effected by contact with food. In all cases where they are preserved, the rounded tips of the teeth take on a high polish (like hard objects tumbled in a vegetable fibre medium). The crown facet on the labial side of the second tooth bears fine horizontal striations which are visible under a light microscope and were most probably caused by abrasive particles in the food.

Upper Jaw

Upper Dentition

The teeth of the upper jaw, which are roughly positioned in a single row, are considerably more robust, having at least twice the cross-sectional area of

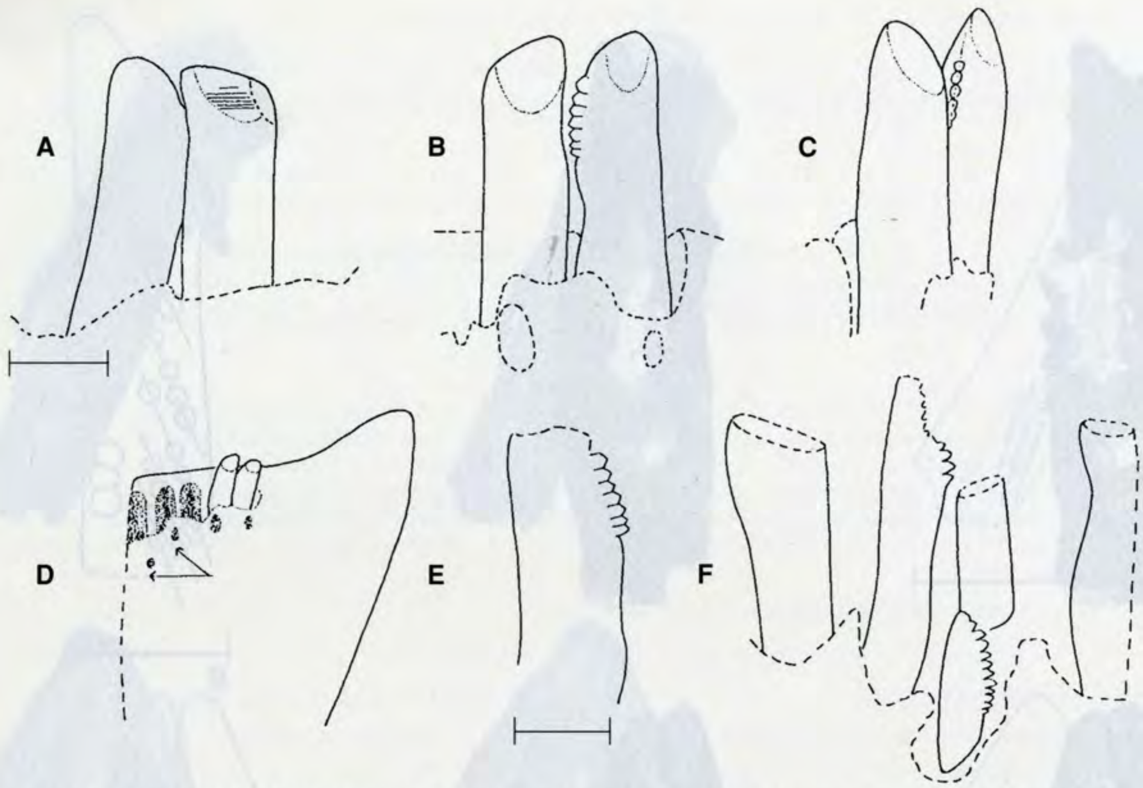


Figure 2. *Endothiodon* BP\1\5497. A,B & C are labial, lingual and distal views respectively of two left lower teeth. D is a sketch of the same specimen to show empty sockets behind these teeth, and the crypts within which new replacement teeth develop. E and F are lingual views of lower teeth of BP\1\5292. Scale bar: 50 mm.

the lowers, and occlude lateral to them (Figure 1 C). Only in BP\1\5489 are upper crowns preserved, as in the case of the lowers , upper crowns are worn to produce ligual and labial facets, and their tips have a high polish. Cox (1964) reported that the upper teeth of *Endothiodon* are serrated on their mesial edges.

The replacement pattern of the upper teeth is not as easily determined as that of the lowers. Certainly it differs from the usual reptilian pattern of alternate replacement. Possibly because they are more robust, the upper teeth did not need replacement as frequently as the lowers. Specimen BP\1\338 (Figure 3 B), which is relatively well preserved, permitted some understanding of the mode of replacement of the upper teeth. In this specimen, as in all the specimens studied where this part of the skull is preserved, the first two teeth are borne by the premaxilla. The first position is occupied by a mature tooth. In the second position are two confluent alveoli, in the more lingual of these the tip of a replacement crown is just visible, while the more lateral cavity represents a tooth recently shed.

The first tooth position in the maxilla bears a mature tooth about to be shed. Resting against its lingual surface is a new tooth in an advanced state of eruption. The next two positions are occupied by the roots of mature teeth, the crowns of which are missing; labiad to these teeth are pits from which previous teeth had been shed. The next two positions are represented by empty, ovate sockets; the next by a mature tooth with an empty socket labiad to it, and the last position by a newly formed but badly damaged tooth.

Lines in Figure 3 B indicate that there is a consistent direction in which teeth migrate in the upper jaw, but in essence there are single, rather irregular rows of teeth in each maxilla.

Hopson has pointed out to us that there is a suggestion that the upper dentition, like the lower dentition, may be interpreted in terms of *Zahnreihen*. We agree, however, because we have mostly empty alveoli to deal with we are not confident to propose what the pattern might be.

FEEDING AND MASTICATORY FUNCTION

As Cox (1964) has suggested, upper teeth were probably opposed by a horny pad occupying the dentary sulcus labiad to the lower teeth (Figure 1); this is a fairly laterally restricted area into which to have to bite, which could just accommodate the degree of lateral drift which occured during the life of the teeth.

Lower teeth were not as restricted. As Cox(1964) pointed out these teeth occluded against the palatines, which presumably were also covered in life by horny pads. The palatine pads would have been shorter than the lower tooth rows: with the jaw fully occluded the pads would lie above the back of the tooth row. Thus for the front of the tooth row to be effective, the jaw would have to be drawn back. This would also allow opposing patterns of upper and lower tooth serrations to effectively slice up food in the mouth. This is excellent supporting evidence for the propalinal jaw movements envisaged for dicynodont anomodonts by Crompton and Hotton (1967) and King, Oelofsen & Rubidge (1989).

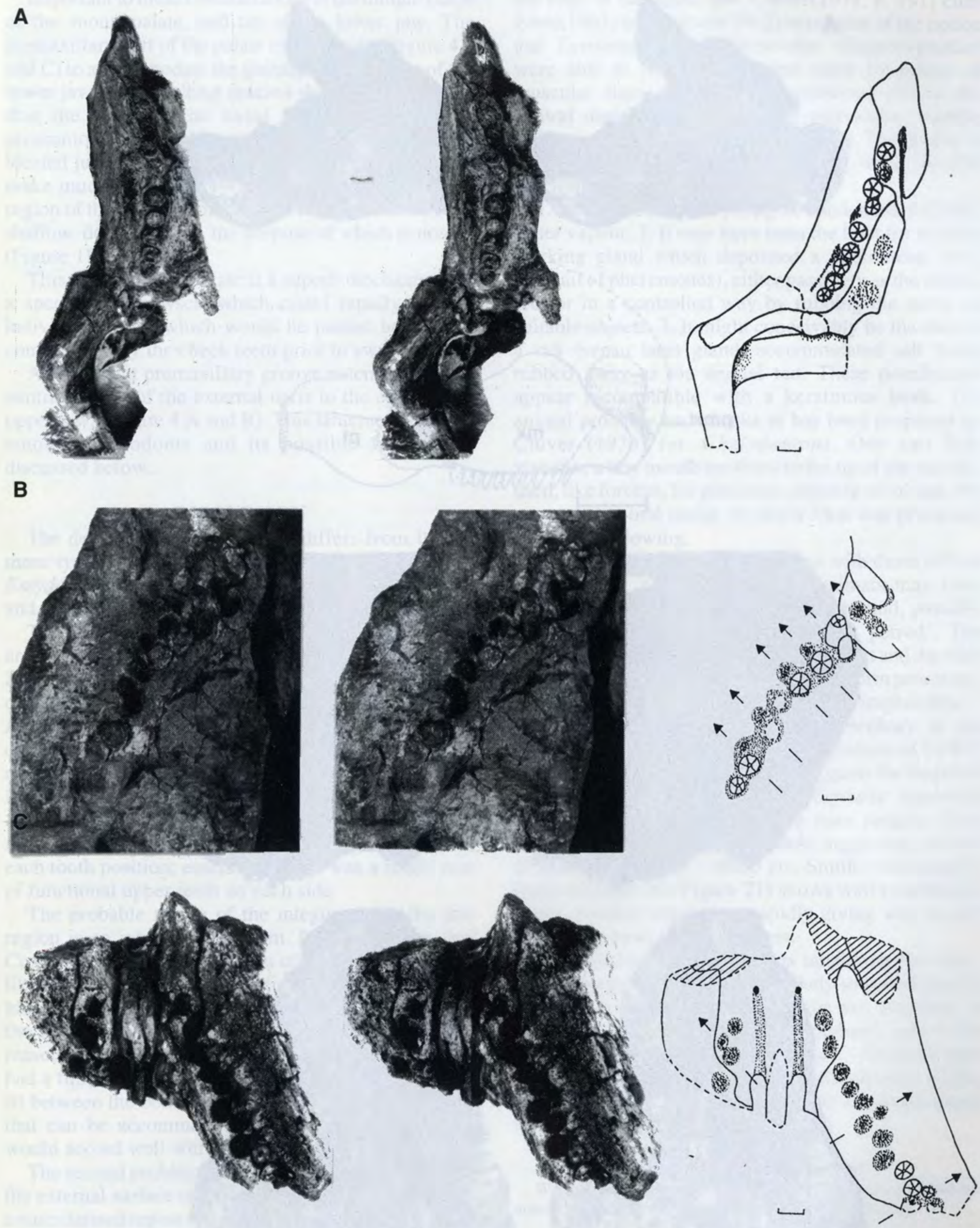


Figure 3. *Endothiodon* Stereophotographs of upper jaws, illustrating arrangement of teeth. Direction of movement of replacing teeth indicated by arrows. A. BP\1\5498 a small individual with a replacing second premaxillary tooth. B. BP\1\998. Right upper dentition. Lines indicate single tooth positions within the row. C. BP\1\5499. Upper dentition - interpretation only possible in the light of B. Scale bar: = 10mm

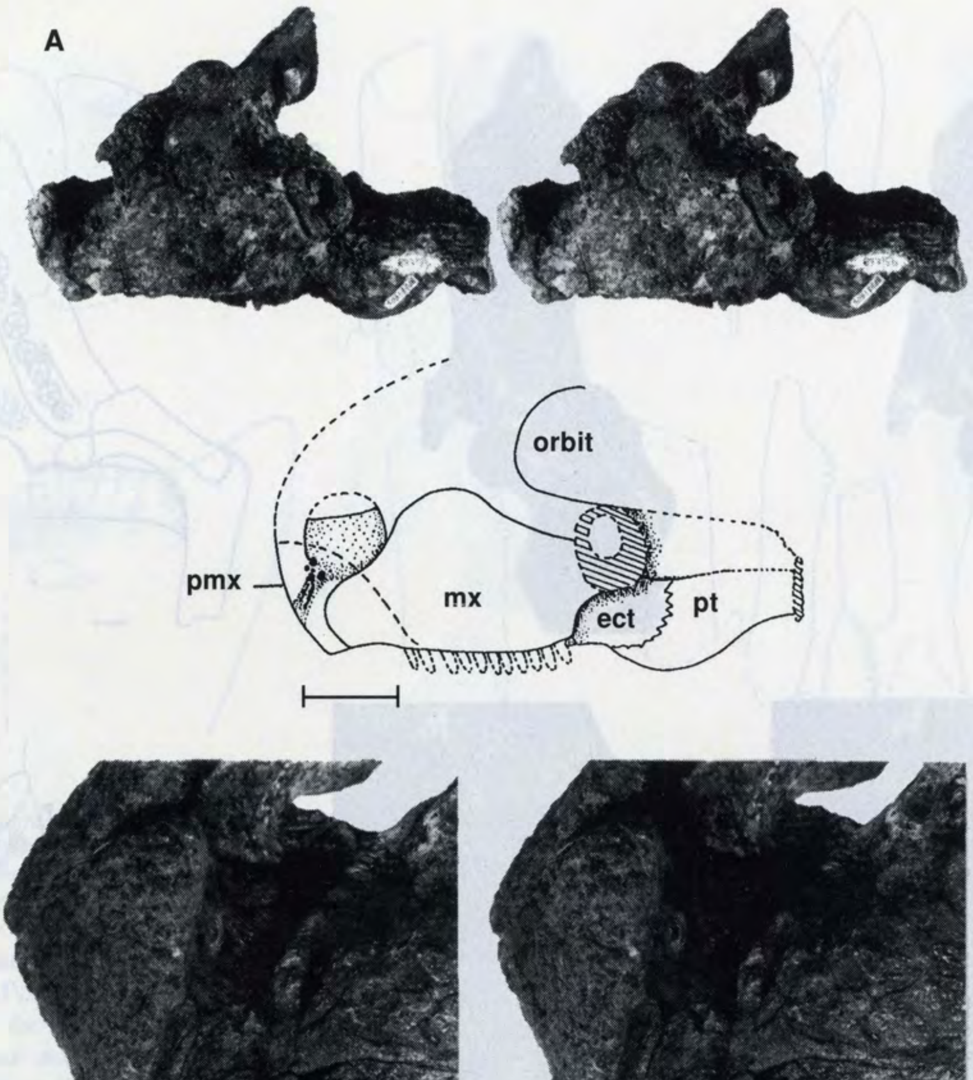


Figure 4. *Endothiodon* A and C Stereophotographs of the large snout BP\1\5505 (B is BP/1/5506).
A. Left lateral view photographs and drawings same scale. B. Snout detail to show ventrolateral groove in premaxilla. C.Palatal view. Scale bar = 50 mm

Important to these considerations is the unique shape of the snout, palate, and tip of the lower jaw. The premaxillary part of the palate rises steeply (Figure 4A and C) to accommodate the pointed, upturned tip of the lower jaw. This vaulting reaches so high (Figure 4A) that the floor of the nasal cavity slopes up to accommodate it and the anterior tip of the upper jaw is located just in front of the external nares. This would make mud grubbing very awkward. The symphyseal region of the sharply pointed lower jaw bears a narrow, shallow, dorsal groove, the purpose of which is unsure (Figure 1B).

This forceps-like muzzle is a superb mechanism for a specialised browser, which could rapidly nip off individual leaves which would be passed back to be comminuted by the cheek teeth prior to swallowing.

A prominent premaxillary groove extends from the ventral border of the external naris to the edge of the upper jaw, (Figure 4 A and B). This structure is unique among anomodonts and its possible function is discussed below.

DISCUSSION

The dentition of *Endothiodon* differs from that in more typical reptiles, including the dicynodont genus *Emydops* (Hopson 1964), in which replacement is rapid and alternate.

The multiple rows of dentary teeth in *Endothiodon* are the result of retention of several members of each Zahnreihe, and it appears that tooth replacement continued throughout the animal's life. Although *Endothiodon* is the only dicynodont to exhibit such a dentition in the lower jaw, similar arrangements are recorded in (for example) *Captorhinus* (Bolt and DeMar 1975), and some procolophonids (Gow 1977).

Replacement in the upper jaw was more usual, with never more than two teeth (of different ages) present at each tooth position; essentially there was a single row of functional upper teeth on each side.

The probable nature of the integument in the jaw region is an intriguing problem. It is interesting that Cox (1964) makes no mention of an extensive turtle-like horny beak as is usual for dicynodonts; he confines himself to proposing horny pads on the palatines and in the lateral dentary groove. There are essentially two reasons why it is difficult to conceive that the animals had a full, turtle-like beak. One is the incredibly close fit between the bones of the upper and lower jaws: all that can be accommodated here is tough skin (this would accord well with a browsing habit).

The second problem is the presence of the groove in the external surface of the premaxilla which runs from a vascularised region at the ventral border of the naris to the edge of the upper jaw. Cluver(1971, p. 191) cites Ewer(1961) and Watson(1912) in support of the notion that *Lystrosaurus* and *Dicynodon* (*Daptocephalus*) were able to close the external nares by means of muscular flaps attached to vascularised pits in the ventral narial border, involving premaxilla, maxilla and septomaxilla, but this is speculative. The groove in *Endothiodon* is clearly quite different; three possible functions suggest themselves.

1.It permitted the recycling of condensed, exhaled, water vapour. 2. It may have been the tract for a scent-marking gland which deposited a pheromone (or a cocktail of pheromones), either passively as the animal fed, or in a controlled way by rubbing the snout on suitable objects. 3. It might conceivably be the duct of a salt (sensu lato) gland, accummulated salt being rubbed away as the animal fed. These possibilities appear incompatible with a keratinous beak. The animal probably had cheeks as has been proposed by Cluver (1975) for *Chelydontops*. One can thus visualise a tiny mouth confined to the tip of the muzzle, used, like forceps, for precision cropping of foliage, but an extensive oral cavity in which food was processed prior to swallowing.

These suggestions are at variance with those of Cox (1964, p.18), who suggested the animals may have 'grubbed vegetable matter out of the ground, possibly in the extensive mud swamps of the period'. The closeness of the nares to the tip of the snout and the total lack of enlarged canines, or even caniniform processes, are additional reasons why we find this implausible.

Modern perceptions of the palaeoecology of the lower Beaufort differ from that of Plumstead (1963) cited by Cox (1964). Smith (1993) regards the Beaufort as consisting of predominantly fluvially deposited rocks, with floodplain accretion rates ranging from 0.4-5.5mm\yr, but with palaeosols suggesting periods of stasis from 5000 – 10000 yrs. Smith's taphonomic reconstruction (his Figure 21) shows well established, dense, riverine vegetation, rapidly giving way to arid conditions away from the rivers.

We visualise *Endothiodon* as inhabiting the dense riverine vegetation (as the most likely source of quality browse), occupying a trophic niche not available to smaller, more fully terrestrial dicynodonts, and would therefore predict that articulated *Endothiodon* skeletons, i.e. those which have fossilised *in situ*, would most likely be found close to fossilised major river courses.

ACKNOWLEDGEMENTS

We thank Kevin Padian and James Hopson who refereed the manuscript and offered many constructive suggestions.

REFERENCES

BOLT, J.R. & R. DEMAR. 1975. An explanatory model of the evolution of multiple rows of teeth in *Captorhinus aguti*. *J. Paleont*. **49,** 814-832.

BROOM, R. 1906. The classification of the Karroo beds of South Africa. *Geological Magazine New Series Decade* **5,** 36.

BROOM, R. 1907. On the geological horizons of the vertebrate genera of the Karroo formation. *Rec. Albany Mus*. **2,** 156-163.

BROOM, R. 1909. An attempt to determine the horizons of the fossil vertebrates of the Karroo. *Ann. S. Afr. Mus*. **7,** 285-289.

CLUVER, M.A 1971. The cranial morphology of the dicynodont genus *Lystrosaurus*. *Ann. S. Afr. Mus*. **56**(5), 155-274.

CLUVER, M.A. 1975. A new dicynodont reptile from the *Tapinocephalus* Zone (Karoo System, Beaufort Series) of South Africa, with evidence of the jaw adductor musculature. *Ann. S. Afr. Mus*. **67**(2), 7-23.

CLUVER, M.A. & King, G.M. 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia: Therapsida) and a new classification of dicynodonts. *Ann. S. Afr. Mus*., **91,** 195-273.

COX, C.B. 1964. On the palate, dentition, and classification of the fossil reptile *Endothiodon* and related genera. *Amer. Mus. Novit*. No. **2171,** 25pp.

CROMPTON, A.W. and N. Hotton III. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). *Postilla*, **109,** 1-51

EDMUND, A.G. 1969. Dentition; pp. 117-200 in Gans, A. C, ed. Biology of the Reptilia Vol. 1 Morphology.

EWER, R.F.1961. The anatomy of the anomodont *Daptocephalus leoniceps* (Owen). *Proc. zool. Soc. Lond*. **136,** 375-402.

GOW, C.E. 1977. New procolophonids from the Triassic Cynognathus zone of South Africa. *Ann. S. Afr. Mus*. **72**(6),109-124.

HOPSON, J.A. 1964. Tooth replacement in cynodont, dicynodont and therocephalian reptiles. *Proc. Zool. Soc. Lond*. **142**(4), 629-633.

KEYSER, A.W. 1981. The stratigraphic distribution of the Dicynodontia of Africa reviewed in a Gondwana context. **In:** Cresswell M.M. & Vella P. Eds, *Gondwana Five*, 61-64. Rotterdam, A.A. Balkema.

KING, G.M., OELOFSEN, B.W. AND B.S.RUBIDGE, 1989. The evolution of the dicynodont feeding system. *Zool. J. Linn. Soc*. **96,** 185-211.

KUTTY. T.S. 1972. Permian reptilian fauna from India. *Nature*, **237,** 462-463.

PLUMSTEAD, E.P. 1963. The influence of plants and environment on the developing animal life of Karroo times. *S. Afr. J. Sci*. **59,** 147-152.

SMITH, R.M.H., 1993. Vertebrate taphonomy of Late Permian flood plain deposits in the South Western Karoo Basin of South Africa. *Palaios*, **8,** 45-67.

SMITH, R.M.H. & KEYSER, A.W. In press a. Biostratigraphy of the *Cistecephalus* Assemblage Zone. **In:** Rubidge, B.S. Ed. *Biostratigraphy of the Beaufort Group (Karoo Supergroup), South Africa*. Pretoria, South African Committee for Stratigraphy.

SMITH, R.M.H. & KEYSER, A.W. In press b. Biostratigraphy of the *Dicynodon* Assemblage Zone. **In:** Rubidge, B.S. Ed. *Biostratigraphy of the Beaufort Group (Karoo Supergroup), South Africa*. Pretoria, South African Committee for Stratigraphy.

VON HUENE, F. 1925. *Die sudafrikanische Karroo-Formation als geologisches und faunisches Lebensbild*. Berlin, Verlag van Gebruder Borntraeger.

WATSON, D.M.S. 1912. The skeleton of *Lystrosaurus*. *Rec. Albany Mus*.**2,** 287-295.

WATSON, D.M.S. 1914a. The zones of the Beaufort Beds of the Karoo System in South Africa. *Geological Magazine New Series Decade* **6**(1), 203-208.

WATSON, D.M.S. 1914b. On the nomenclature of the South African Pareiasaurians. *Annals Magazine Natural History*, **14,** 98-102.