

# Growth increments in teeth of *Diictodon* (Therapsida)

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Growth increments *circa* 0.02 mm in width have been observed in sectioned tusks of *Diictodon* from the Late Permian lower Beaufort succession of the South African Karoo, dated between about 260 and 245 million years ago. Mean growth increments show a decline from relatively high values in the *Tropidostoma/Endothiodon* Assemblage Zone, to lower values in the *Aulacephalodon/Cistecephalus* zone, declining still further in the *Dicynodon lacerticeps/Whaitsia* zone at the end of the Permian. These changes coincide with gradual changes in carbon isotope ratios measured from *Diictodon* tooth apatite. It is suggested that the decline in growth increments is related to environmental changes associated with a decline in primary production which contributed to the decline in abundance and ultimate extinction of *Diictodon*.

Key words: Permian, mammal-like reptiles, dentition, extinctions, palaeoclimate.

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## Introduction

A remarkable diversity of fauna can be seen today in the national parks of southern Africa. However, visitors to the Karoo National Park near Beaufort West can appreciate the fact that a totally different diversity is represented by fossils of mammal-like reptiles (Therapsida) which lived in the area more than 200 million years ago, before the break-up of Gondwanaland. Notably, mammal-like reptiles belonging to the dicynodont genus *Diictodon* (Figs 1 and 2) are relatively common in the Late Permian Lower Beaufort succession of the South African Karoo, dated between about 260 and 245 million years ago.

Although *Diictodon* has a wide stratigraphic range covering all of the biozones of the Lower Beaufort, it declines in abundance towards the top of the succession, coinciding with a general decline in dicynodont diversity (King 1990a). Reasons for the decline are not fully understood, but it has been suggested that environmental change contributed to a gradual rather than sudden decline in abundance and ultimate extinction of *Diictodon* and other dicynodonts (King 1990a and

1990b). Chemical analysis of *Diictodon* teeth has in fact shown a gradual decline in stable carbon isotope ratios ( $^{13}\text{C}/^{12}\text{C}$ ) towards the end of the Permian (Thackeray *et al.* 1990). These changes are comparable in scale and direction to shifts in stable carbon isotope

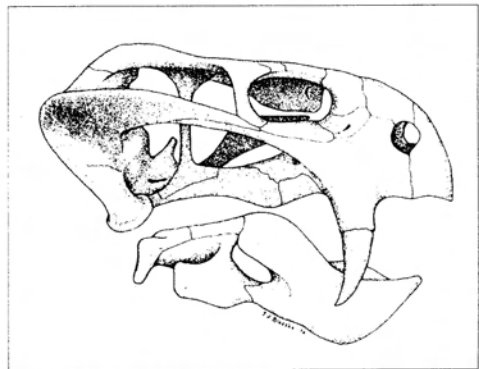


Fig. 1. Cranium of *Diictodon*, showing tusk-like canine. *Diictodon* is a mammal-like reptile that is well represented in the Late Permian Lower Beaufort succession of the South African Karoo (260 - 245 million years ago). Drawn by J. Blaeske, South African Museum.



Fig. 2. Reconstruction of *Diictodon*. Drawn by I. Chesselet, Transvaal Museum, Pretoria.

ratios in marine carbonates from Eurasia, suggesting that the carbon isotope ratios reflect global changes in Late Permian palaeoenvironments (Baud *et al.* 1989; Holser & Magaritz 1987; Holser *et al.* 1989; Magaritz *et al.* 1988). Although the exact nature of environmental change during the Late Permian is not known, a detailed analysis of growth increments in sectioned dicynodont teeth may serve to throw light on the impact that environmental changes may have had on *Diictodon* and other taxa during this period.

A method of measuring growth increments in dicynodont teeth is described in this exploratory study, and the following specific questions are addressed:

- What is the mean growth increment in teeth of *Diictodon* in different Vertebrate Assemblage zones in the Late Permian Lower Beaufort succession of the South Africa Karoo?
- Are there significant differences in the mean growth increment between zones?
- Is there any trend in the changes in mean growth increment, and does this coincide with a decline in carbon isotope ratios that could reflect a decline in primary production?

### Method and materials

Twelve *Diictodon* teeth from the Karoo fossil collections of the South African Museum (Cape Town) and the Geological Survey of South Africa (Pretoria) were used for purposes of this exploratory study. These are some of the specimens that were also used for isotopic analysis (Thackeray *et al.* 1990). The teeth were cut in cross-section by means of a diamond-tipped saw and polished by using carborundum paper and diamond paste. Under 100 x magnification and an appropriate angle of polarisation, concentric growth increments could be seen in most specimens. These are generally distinguishable as fine dark lines separated by broader light bands (Fig. 3). Such growth lines resemble tree rings in appearance. The distance between fine dark lines here constitutes a single "growth increment". From transverse sections of *Diictodon* teeth, it is apparent that the concentric rings seen in cross-section represent part of a series of cones of growth, tapering towards the tip of a tusk.



Fig. 3. Growth increments in a sectioned, polished tooth of *Diictodon*. Scale in intervals of hundredths of a millimetre. Specimen K6737 (UCT 3030) from the *Tropidostoma/Endothiodon* Assemblage Zone.

Measurements of growth increment width were obtained by means of a graticule divided into intervals of hundredths of a millimetre. Distances between successive growth lines in any particular section tended to be similar, but no attempt was made to measure the distance between any two adjacent growth lines. Instead, the distance between several growth lines was measured across part of a sectioned tooth, and a mean growth increment (MGI) calculated for that region. For example, if five growth lines were clearly visible in one region, covering a distance of .10 mm (ten divisions of a graticule divided into hundredths of a millimetre), the mean growth increment for that part of the tooth was calculated as 0.02 mm. Growth lines were not always continuously distinct in cross-sectioned teeth, but mean growth increments were calculated for parts of sectioned teeth where such lines were clearly visible. At least five MGI values were calculated per specimen. Means and standard deviations were obtained for sets of MGI values obtained for teeth from particular assemblage zones in the Late Permian succession of the South African

Karoo. These results can be compared with mean values for stable carbon isotope ratios obtained from *Diictodon* teeth from the corresponding assemblage zones.

On account of the conical nature of growth, any attempt to measure width of growth lines in cross-sectioned teeth will depend to some extent on the position where such teeth are sectioned. In this study, where possible, teeth were sectioned at a position where a canine was between about four and five mm in diameter, thus providing some degree of control over variability associated with the position where measurements are taken. Growth increments in a sectioned tooth of a modern crocodile, *Crocodylus niloticus*, were examined for purposes of comparison with *Diictodon* teeth.

## Results

Results obtained for *Diictodon* teeth from different Assemblage Zones are presented in Table 1. A mean MGI value of  $0,020 \pm 0,004$  mm is based on 124 measurements from all of the *Diictodon* teeth included in this analysis. The mean MGI values for teeth from different zones in the Late Permian sequence show a decline from relatively high values in the *Tropidostoma/Endothiodon* Assemblage Zone, to lower values in the *Aulacephalodon/Cistecephalus* zone, declining still further in the *Dicynodon lacerticeps/Whaitsia* zone at the end of the Permian. Tests for differences in mean MGI values were performed using Student's t-tests. At  $P=0,05$ , the mean MGI value of  $0,022 (\pm 0,002 \text{ mm}, n=44)$  obtained for the *Tropidostoma/Endothiodon* Assemblage Zone is significantly higher than that obtained for the *Dicynodon lacerti-*

*ceps/Whaitsia* zone ( $\text{MGI} = 0,016 \pm 0,002 \text{ mm}, n = 25$ ) at the end of the Permian sequence, but is not significantly different from the mean MGI value of  $0,020 (\pm 0,004 \text{ mm}, n=35)$  calculated for the intermediate (*Aulacephalodon/Cistecephalus*) zone. The mean value for the latter is not significantly different from the mean MGI of  $0,019 \pm 0,002 \text{ mm} (n = 20)$  obtained for the Dinocephalian zone at the base of the Late Permian. The pattern of changes in mean growth increments appears to be similar to that found from a study of stable carbon isotope ratios measured in *Diictodon* teeth (Thackeray *et al.* 1990). Notably, the most positive isotope ratios in the Late Permian Karoo sequence were obtained from the *Tropidostoma/Endothiodon* Assemblage Zone, declining progressively in the upper zones. Isotope ratios for teeth from the Dinocephalian Assemblage Zone are similar to values obtained for the *Aulacephalodon/Cistecephalus* zone, comparable to the situation in which MGI values for the Dinocephalian zone are not significantly different from MGI values calculated for teeth from the *Aulacephalodon/Cistecephalus* zone.

## Discussion

Since the pattern of changes in mean growth increments in *Diictodon* teeth corresponds to the pattern of variability in carbon isotope ratios measured from *Diictodon* tooth apatite in the corresponding zones, it is suggested that the decline in growth increment might be indirectly if not directly associated with envi-

Table 1

Mean growth increment values (MGI) and standard deviations obtained for *Diictodon* teeth from the Late Permian Lower Beaufort succession of the South African Karoo (260 - 245 million years ago). Sample size (n) refers to the number of MGI values used for calculating means and standard deviations. N refers to the number of teeth in each sample

| Assemblage Zones                      | Mean MGI (mm) | s.d.    | n       | N       |
|---------------------------------------|---------------|---------|---------|---------|
| <i>Dicynodon lacerticeps/Whaitsia</i> | 0,016         | .002    | 25      | 4       |
| <i>Aulacephalodon/Cistecephalus</i>   | 0,020         | .004    | 35      | 3       |
| <i>Tropidostoma/Endothiodon</i>       | 0,022         | .002    | 44      | 5       |
| <i>Pristerognathus/Diictodon</i>      | No data       | No data | No data | No data |
| Dinocephalian                         | 0,019         | .002    | 20      | 1       |

ronmental changes towards the end of the Permian.

What evidence is available to support this suggestion? Plants prefer to take up the lighter of the two stable carbon isotopes ( $^{12}\text{C}$  rather than  $^{13}\text{C}$ ) in the course of photosynthesis, and a general decline in  $^{13}\text{C}/^{12}\text{C}$  isotope ratios reflecting global changes in atmospheric  $\text{CO}_2$  could be interpreted in terms of declining primary production (Thackeray *et al.* 1990). Berner (1989) suggested that increased continental aridity was a primary factor in causing global changes in stable carbon isotope ratios in Late Permian palaeoenvironments. There is in fact evidence for increased aridity in the Late Permian in the South African Karoo (Keyser 1966; Smith 1990), and this would certainly have contributed to a decline in primary production. Since *Diictodon* was a herbivore (Hotton 1986), changes in carbon isotope ratios in its teeth could reflect global changes in the composition of atmospheric  $\text{CO}_2$  associated with possible changes in primary production and consequent changes in the isotopic composition of the plants on which *Diictodon* fed.

If the general decline in carbon isotope ratios of *Diictodon* teeth towards the end of the Permian is a reflection of a gradual decline in primary production, as suggested, one may ask how such a decline could have affected *Diictodon* and other dicynodonts. One possibility is that the relative abundance of *Diictodon* was limited by the biomass of plants on which it fed, and the probability of extinction would have increased.

At present it is not certain whether more than one species of the genus *Diictodon* is represented in the Late Permian sequence of the South African Karoo (G.M. King, *pers. comm.*). Despite this uncertainty, the gradual nature of change in both MGI and carbon isotope ratios, combined with evidence for gradual changes in the diversity in dicynodonts (King 1990a and 1990b), appears to

support the case that the extinction of dicynodonts was associated with gradual rather than sudden periodic changes of the kind which have been suggested from an analysis of marine invertebrates (Raup & Sepkoski 1984). The gradual changes observed in southern Africa is consistent with evidence for gradual changes in Late Permian palaeoenvironments elsewhere (Baud *et al.* 1989; Holser & Magaritz 1987; Holser *et al.* 1989; Magaritz *et al.* 1988).

Growth increments of the kind found in *Diictodon* teeth have also been observed in a sectioned tooth of a modern crocodile, *Crocodylus niloticus*. Remarkably, the mean growth increment of  $0.020 \pm 0.004$  mm calculated from all *Diictodon* tooth measurements included in this analysis is similar to the mean value calculated for the crocodile. It is too early to infer that this coincidence necessarily reflects physiological similarities between modern crocodiles and *Diictodon*. However, the similarities in growth increments suggest that detailed analysis of crocodile teeth could provide a useful model for purposes of interpreting growth increments in *Diictodon*.

The period of time associated with each concentric ring in *Diictodon* teeth is not known. However, *daily* increments are known from studies of growth structures in other organisms, including not only mammalian taxa (Dean 1987) but also corals (Wells 1963) and molluscs (Sire & Bonnet 1984). In primate teeth, incremental markings in dentine are known to grow at a rate of approximately 0.004 mm per day (Dean, 1987). Such increments are certainly associated at least in part with environmental variability (e.g. daily changes in temperature), although growth increments may also be influenced by variation in physiological processes. Notably, Vollrath *et al.* (1975) documented a seven-day cycle in the activity of the mammalian pineal gland, and it is perhaps not coincidental that a near-weekly (circumseptan) cycle is associated

with incremental structures known as parenchymata and lines of Retzius in mammalian teeth (Dean 1987). Analyses of growth increments in modern reptiles could provide an opportunity to determine whether or not such growth lines, similar if not identical to those found in *Diictodon* teeth, are circadian phenomena. It is just possible that a detailed analysis of *Diictodon* teeth may lead to a fuller understanding of the factors that contributed to the extinction of this genus and other dicynodonts.

This paper serves as an example of the kind of research that can be undertaken on fossil specimens from the South African Karoo. Although the Karoo National Park is particularly concerned with the conservation of modern fauna and flora, it has another role, namely that of protecting palaeontological sites which are known to have fossilised remains of mammal-like reptiles that inhabited Gondwanaland some 250 million years ago. In addition, the park plays a useful educational role by displaying fossil specimens from the area, drawing attention to the kind of information that can be learnt from careful analysis of these interesting fossils.

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### References

BAUD, A., M. MAGARITZ and W.T. HOLSER. 1989. Permian-Triassic of the Tethys: Carbon isotope studies. *Geologische Rundschau* 78: 649-677.

BERNER, R.A. 1989. Drying, O<sub>2</sub>, and mass extinction. *Nature* 340: 603-604.

DEAN, M.C. 1987. Growth layers and incremental markings in hard tissue: a review of the literature and some preliminary observations about enamel

structure in *Paranthropus boisei*. *Journal of Human Evolution* 16: 157-172.

HOTTON, N. 1986. Dicynodonts and their role as primary consumers. Pp. 71-82. In: HOTTON, N., P.D. MACLEAN, J.J. ROTH, and E.C. ROTH (eds). *The Ecology and Biology of Mammal-like-reptiles*. Washington: Smithsonian Institution Press.

HOLSER, W.T. and M. MAGARITZ. 1987. Events near the Permian-Triassic boundary. *Modern Geology* 11: 155-80.

HOLSER, W.T., H-P. SCHONLAUB, M. ATTREP, K. BOECKELMAN, P. KLEIN, M. MARGARITZ, C.J. ORTH, A. FENNINGER, C. JENNY, M. KRALIK, H. MAURITSCH, E. PAK, J-M. SCHRAMM, K. STATTEGGER and R. SCHMOLLER. 1989. A unique geochemical record at the Permian-Triassic boundary. *Nature* 337: 39-44.

KEYSER, A.W. 1966. Some indications of arid climate during the deposition of the Beaufort Series. *Annals of the South African Geological Survey* 5: 77-79.

KING, G.M. 1990a. Life and death in the Permian-Triassic: The fortunes of the dicynodont mammal-like reptiles. *Sidney Haughton Memorial Lecture 3*. Cape Town: South African Museum.

KING, G. 1990b. Dicynodonts and the end-Permian event. *Palaeontologia Africana* 27: 31-39.

MAGARITZ, M, R. BAR, A. BAUD and W.T. HOLSER. 1988. The carbon-isotope shift at the Permian/Triassic Boundary in the southern Alps is gradual. *Nature* 331: 337-339.

RAUP, D.M. and J.J. SEPKOSKI. 1984. Periodicity of extinctions in the geologic past. *Proceedings of the National Academy of Sciences, U.S.A.* 81: 801-805.

SIRE, J.-Y. and P. BONNET. 1984. Croissance et structure de l'opercule calcifié du gasteropode polynésien *Turbo setosus* (Prosobranchia: Turbinidae): détermination de l'âge individuel. *Marine Biology* 79: 75-87.

SMITH, R.M.H. 1990. Alluvial palaeosols and pedofacies sequences in the Permian Lower Beaufort of the southwestern Karoo basin, South Africa. *Journal of Sedimentary Petrology* 60: 258-276.

THACKERAY, J.F., N.J. VAN DER MERWE, J.A. LEE-THORP, A. SILLEN, J.L. LANHAM, R.M.H. SMITH, A. KEYSER and P.M.S. MONTEIRO. 1990. Changes in carbon isotope ratios in tooth apatite of Late Permian therapsids. *Nature* 347: 751-753.

VOLLRATH, L., A. KANTARJIAN and C. HOWE. 1975. Mammalian pineal gland: 7 day rhythmic activity? *Experientia* 31: 458-460.

WELLS, J.W. 1963. Coral growth and geochronometry. *Nature* 197: 948-950.