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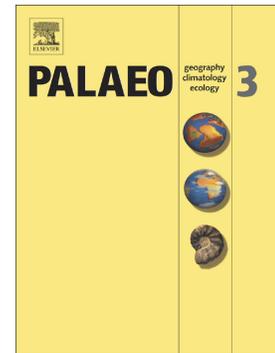
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Stable isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) give new perspective on the ecology and diet of *Endothiodon bathystoma* (Therapsida, Dicynodontia) from the late Permian of the South African Karoo Basin.

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Abstract

The late Permian dicynodont *Endothiodon* is characterised by its specialised feeding system, most notably manifested in its long rows of post-canine teeth and corresponding keratinous

surfaces. This specialisation has fuelled discussion of not only the masticatory biomechanics in *Endothiodon* but also of its diet and ecology. To shed light on the latter two, we compared the oxygen ($\delta^{18}\text{O}_p$) and carbon ($\delta^{13}\text{C}_c$) stable isotope compositions of *Endothiodon* tooth and bone apatite with those of the co-occurring dicynodont *Tropidostoma*, another late Permian dicynodont of similar size. Preliminary results indicate that *Endothiodon* had significantly lower ratios for stable isotopes of both oxygen and carbon. The $\delta^{18}\text{O}_p$ values from *Endothiodon* suggest that its lifestyle was more water-dependent (i.e. obligate drinker) than *Tropidostoma*, pointing to the possibility of a semi-aquatic ecology, whereas $\delta^{13}\text{C}_c$ values suggest that *Endothiodon* had a diet primarily comprising riverine vegetation, with the possibility that juveniles consumed terrestrial insects. The data suggest a negligible role for roots, seeds, or algae in the diet of *Endothiodon*.

Keywords: late Permian, stable isotopes, Poortjie Member, Hoedemaker Member, herbivory, insectivory.

1. Introduction

Dicynodonts were a highly successful clade of therapsids that formed a major part of the herbivore guild in tetrapod communities from the mid-Permian to the mid-Triassic. One reason for their success was likely their development of keratinous sheaths on the palate and lower jaw, combined with greatly expanded adductor jaw musculature (Kemp, 2012). All dicynodonts possess a keratinous beak in lieu of precanine teeth but in more derived forms the post-canine teeth are entirely lost, though most retain a pair of canine tusks. Of the earliest-diverging taxa, *Endothiodon* is peculiar in that it is characterized by relatively long upper and lower tooth rows on the dentary, premaxilla and maxilla (Ray, 2000). Teeth were replaced in waves in the dentary resulting in the appearance of multiple tooth rows (Macungo et al.,

2020). In adult individuals, the teeth are pear-shaped, posterolaterally compressed, and serrated, whereas in juveniles, they are small and conical (Ray, 2000).

This peculiar tooth pattern and other unique features of the skull and jaw have raised questions about the feeding biomechanics of *Endothiodon*, most recently discussed by Cox and Angielczyk (2015). A corollary question to this that remains poorly understood is to which diet was this specialized feeding apparatus adapted. Cox (1964) suggested that *Endothiodon* used its beak to grub vegetable matter out of the ground, such as roots and tubers, whereas Latimer et al. (1995) postulated that *Endothiodon* was a specialised browser that subsisted on dense riparian vegetation. Cox (1998) proposed an even more specialised feeding niche based on the unusual vaulted palate, interpreting it as an adaptation to processing conifer cones to extract the seeds. The difference between juvenile and adult teeth has also been taken to reflect a change of diet during ontogeny (Parks, 1969; cf. Demar and Bolt, 1981), whereby juveniles subsisted on a more generalised diet comprising vegetation and possibly invertebrates that transitioned into more specialized herbivory in adults (Ray, 2000).

The specialized feeding system and diet of *Endothiodon* are of particular interest because in Gondwanan basins for which biostratigraphic resolution is sufficiently good, this taxon appears to be the first large herbivore to appear after the extinction of dinocephalian therapsids (Angielczyk et al., 2014; Day et al., 2015b; Day and Smith, in press). In the southwestern part of the Main Karoo Basin of South Africa, this extinction occurs at or slightly above the base of the Poortjie Member of the Teekloof Formation (Day et al., 2015a, 2018). *Endothiodon* has its lowest occurrence in the mid-Poortjie Member (*Priesterognathus* Assemblage Zone=lower *Endothiodon* Assemblage Zone), and ranges up into the overlying

Hoedemaker Member (*Tropidostoma* Assemblage Zone =upper *Endothiodon* Assemblage Zone) and Oukloof Member (*Cistecephalus* Assemblage Zone).

The disappearance of dinocephalians has been linked to the Capitanian mass extinction (Day et al., 2015b; Schneider et al., 2019) and *Endothiodon* is thus an important part of the tetrapod recovery, having its greatest relative abundance soon after its initial appearance (Day and Smith in press). As noted by Cox and Angielczyk (2015; p. 22), 'if *Endothiodon* was a dietary specialist, its broad geographic distribution indicates that its preferred food source must have been widespread', which suggests that the food sources were especially common after extinction event, or were more resilient to any environmental changes that had contributed to it. The palaeobotanical record for the tetrapod-bearing sequences at this time is, however, very poor. Nevertheless, a better understanding of the diet and lifestyle (i.e. water dependence) of *Endothiodon* could provide useful information about the environmental and floral changes associated with the early recovery of terrestrial ecosystems after the Capitanian mass extinction.

Stable carbon and oxygen isotope studies of bone and tooth apatite offer the possibility to better identify both the diet and the lifestyle of vertebrates. Indeed, the $\delta^{18}\text{O}$ value of apatite is correlated to both body temperature and to the oxygen isotope composition of vertebrate body water ($\delta^{18}\text{O}_{\text{bw}}$) which is mostly derived from the consumption of either meteoric water or plant water, or a combination of both (D'Angela and Longinelli, 1990; Kohn, 1996). Water oxygen input and output between the environment and the animal's body differ between terrestrial and aquatic species. This is expressed by a difference of magnitude of ^{18}O -enrichment of body water relative to drinking water, caused mostly by transcutaneous evaporation, urine or faeces (Luz and Kolodny, 1985; Bryant and Froelich, 1995; Amiot et al.,

2007, 2010). Extant mammals consuming large quantities of water, or spending time in it have lower $\delta^{18}\text{O}_{\text{bw}}$ values than those with a terrestrial ecology (Bocherens et al., 1996; Kohn et al., 1996; Cerling et al., 2008). For instance, the $\delta^{18}\text{O}$ value recorded in apatite of hippopotamuses is lower than that of other terrestrial mammals. Depending on the water-dependence of the terrestrial species, $\delta^{18}\text{O}$ values of hippopotamus are about 3‰ lower than those of water-dependent animals and the difference can be as high as 7‰ when compared with water-independent species (Bocherens et al., 1996; Cerling et al., 2008; Clementz et al., 2008). Therefore, by comparing the apatite $\delta^{18}\text{O}$ values of various co-existing vertebrates with different lifestyles, it should be possible to interpret the ecology of extinct taxa.

Stable carbon isotope composition ($\delta^{13}\text{C}$) of vertebrate apatite can be used to estimate the diet of a species. Apatite-diet ^{13}C -enrichment varies between species, most probably as a result of different digestive patterns (DeNiro and Epstein, 1978; Quade et al., 1992; Passey et al., 2005). The apatite $\delta^{13}\text{C}$ values of herbivorous animals reflect those of their vegetarian diet, and those of carnivorous animals originate from the flesh of their prey. The flesh-plant ^{13}C -enrichment in herbivore tissue is about $1 \pm 1\text{‰}$ (Barnes et al., 2007), whereas the plant $\delta^{13}\text{C}$ value is controlled by its photosynthetic pathway (Ehleringer and Monson, 1993) and environmental conditions (Kohn, 2010). During the Permo-Triassic, plants used only the C3 pathway (Osborne and Beerling, 2006), and today C3 plants record $\delta^{13}\text{C}$ values between -35‰ and -22‰ (Smith and Epstein, 1971; O’Leary, 1981). This range of values results from the different environments in which the plants grow. An increase in openness of the environment, water-stress or sunlight will increase $\delta^{13}\text{C}$ values of the plants (reviewed in Ehleringer and Monson, 1993). As a result, the difference of $\delta^{13}\text{C}$ values between species could indicate a difference in diet and lifestyle. To determine whether *Endothiodon* had a different ecology and diet to that of the other dicynodonts, we compare stable oxygen ($\delta^{18}\text{O}_\text{p}$

and $\delta^{18}\text{O}_c$) and carbon ($\delta^{13}\text{C}_c$) isotope compositions of bone and teeth from specimens of *Endothiodon* with values from specimens of *Tropidostoma* from the same localities, although *Tropidostoma* first appears only in the Hoedemaker Member. These results are also compared to published values for *Diictodon* (Rey et al., 2018) from the same stratigraphic interval to distinguish differences between ecological and environmental factors.

2. Material and methods

2.1. Sample Collection

The bones of sixteen tetrapod fossils were sampled, of which three also had their teeth sampled. All samples were analysed for their stable oxygen and carbon isotope composition of apatite phosphate and carbonate. Sample sizes were limited by the availability of particular species from specific geological horizons and the presence of suitable specimens with appropriate stratigraphic and reliable taxonomic data bearing in mind the destructive nature of sampling for stable isotope analysis. The samples collected for this study included six *Endothiodon* sp., nine *Tropidostoma* sp., and one unidentified pareiasaur. These fossils were recovered from three localities in the Main Karoo Basin of South Africa which all cover the same stratigraphic interval and are geographically separated by less than a hundred kilometres, between 21.25° and 22.08° of latitude and -32.31 and -32.22° of longitude (Fig. 1; Supplementary Table 1). The lithostratigraphy at each of these localities is well defined and all sampled fossils can be stratigraphically positioned with a high degree of precision between the Poortjie Member and the Lower Hoedemaker Member. All specimens are curated at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg.

2.2. Analytical techniques

We isolated the phosphate ions using acid dissolution and anion-exchange resin in order to measure the oxygen isotope composition of the apatite phosphate group (Lécuyer, 2004). Once quantitatively precipitated in a thermostatic bath set at a temperature of 70 °C, the silver phosphate was filtered, washed with double deionized water, and dried at 50 °C. Oxygen isotope compositions of the Ag_3PO_4 crystals were measured using a high-temperature pyrolysis technique involving a VarioPYROcubeTM elemental analyzer (EA) interfaced in continuous flow (CF) mode to an IsoprimeTM isotopic ratio mass spectrometer (IRMS) (EA-Py-CF-IRMS technique) at the Laboratoire de Géologie de Lyon (UMR 5276, Université Claude Bernard Lyon 1). For each sample, 5 aliquots of 300 μg of Ag_3PO_4 were mixed with 300 μg of pure graphite powder and loaded in silver foil capsules. Pyrolysis was performed at 1450 °C. Measurements were calibrated against the NBS120c (natural Miocene phosphorite from Florida: $\delta^{18}\text{O} = 21.7\%$; Lécuyer et al., 1993) and the NBS127 (barium sulfate, BaSO_4 : $\delta^{18}\text{O} = 9.3\%$; Hut, 1987). Silver phosphate samples precipitated from standard NBS120c were repeatedly analysed ($\delta^{18}\text{O}_p = 21.7\%$; $1\sigma = 0.3$; $n = 8$) along with the silver phosphate samples derived from fossil bioapatites to ensure that no isotopic fractionation occurred during the wet chemistry. Data are reported as $\delta^{18}\text{O}_p$ values vs. V-SMOW in ‰ δ units.

To measure the oxygen isotope composition of the apatite carbonate group, about 10 mg of tooth or bone powder was pre-treated (Koch et al., 1997). Powders were washed with a 2% NaOCl solution to remove organic matter and were then rinsed five times with double deionized water and air-dried at 40 °C for 24 hours. Potential secondary carbonate was removed by adding 0.1 M acetic acid to the powder and leaving overnight, after which the powder was rinsed five times with double deionized water and air-dried at 40 °C overnight. The powder/solution ratio was kept constant at 0.04 g mL⁻¹ for both treatments. Stable isotope ratios were determined using a Thermo Gasbench II at the Stable Light Isotope Laboratory of

the Archaeology Department of the University of Cape Town. For each sample, an aliquot of 2 mg of pre-treated apatite was reacted with 7 drops of supersaturated orthophosphoric acid at 72 °C for at least two hours under a He atmosphere before starting 9 measurement cycles of the isotopic composition of the CO₂ produced with a Thermo Finnigan Delta Plus XP continuous flow isotope ratio mass spectrometer. The measured carbon and oxygen isotopic compositions were normalized relative to the NBS-18, NBS-19 and an internal calcite standard 'Cavendish Marble' ($\delta^{13}\text{C} = 0.34\text{‰}$; $\delta^{18}\text{O} = -8.95\text{‰}$). Reproducibility for the carbon and oxygen isotopic compositions of apatite carbonate is better than $\pm 0.10\text{‰}$ and $\pm 0.15\text{‰}$, respectively. The carbon and oxygen isotopic compositions are expressed as δ values relative to V-PDB for both carbon and oxygen (in ‰ δ units). The oxygen values were converted from V-PDB to V-SMOW following the equation from Coplen et al. (1983).

2.3. Robustness of the stable isotope record

The enamel layer of Permian tetrapod teeth is so thin that only dentine and bones could be sampled for analysis. Both have more porous apatite than enamel, with smaller and less densely inter-grown crystals (Mills, 1967). As a result, secondary precipitation within or at the surface of the biogenic crystals, adsorption of ions on the surface of those crystals, or even the dissolution and recrystallization with isotopic exchange might have altered their original isotope compositions. To differentiate apatite altered by diagenesis, all samples were tested for primary preservation by comparing their $\delta^{18}\text{O}_p$ values against their $\delta^{18}\text{O}_c$ values.

In skeletal tissues of extant mammals, the $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ are positively correlated because of precipitation close to equilibrium with body water in both phosphate and carbonate. Re-equilibration of those compounds during diagenesis is not expected because

isotopic exchange rates between carbonate-water and phosphate-water are radically different. Therefore altered enamel should show isotopic shifts from the empirical $\delta^{18}\text{O}_p\text{-}\delta^{18}\text{O}_c$ line (Iacumin et al., 1996; Zazzo et al., 2004b). Accordingly, it is expected that the distribution of pristine $\delta^{18}\text{O}$ values should display a positive regression line with a slope close to unity. Also, at low temperature, inorganic alteration has little effect on the phosphate of the apatite, even in geological time (Tudge, 1960; Lécuyer et al., 1999), but the phosphate can be altered by microbially mediated diagenesis (Zazzo et al., 2004a). The inorganic alteration would result in a high overall carbonate content or a low discrepancy between carbonate $\delta^{18}\text{O}_c$ and phosphate $\delta^{18}\text{O}_p$ values, whereas organic alteration should show the opposite with a greater $\delta^{18}\text{O}_c\text{-}\delta^{18}\text{O}_p$ value. The carbonate content can be estimated from the mean magnitude of the current voltage (mV) measured during the analysis of the CO_2 by mass spectrometer (Supplementary Table 1).

In our dataset, most of the analysed samples yielded peaks for the mass 44 ions with a mean amplitude ranging from around 500 mV and 3100 mV, which is in accordance with the weight of the samples. However, four samples, 7267-B; 7570-B; 7618-B and 7624-B (with B standing for 'bone sample'), gave mean magnitudes greater than 3400 mV, even reaching more than 10000 mV, suggesting an excess of secondary precipitated carbonate in the apatite. Accordingly, their $\delta^{18}\text{O}_c$ and $\delta^{13}\text{C}$ values have been considered to not represent the original signal and were discarded.

Among the four discarded specimens, one (7267-B) has a tooth which had also been sampled. Comparison of the $\delta^{18}\text{O}_c$ values between teeth and bones of the same individuals (Fig. 2) shows that the values follow a slope close to unity except for sample 7267-B, confirming the altered status of the carbonate values for the bone sample of this individual.

In addition, comparison between $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ values (Fig. 3) shows that four specimens deviate from the theoretical line with a slope equal to one. Three of them (7267-B; 7570-B and 7618-B) have already been discarded for their $\delta^{18}\text{O}_c$ and $\delta^{13}\text{C}$ values, with even higher discrepancies between carbonate $\delta^{18}\text{O}_c$ and phosphate $\delta^{18}\text{O}_p$ values, based on their elevated mean magnitude. The fourth one, (7754-B), presents an expected mean magnitude of its signal, and therefore cannot be discarded based on its $\delta^{18}\text{O}_c$ values but rather on $\delta^{18}\text{O}_p$. One data point (7624-B) has a very high mean magnitude but does not fit with the other discarded values (Fig. 3). The possible reason is that its phosphate group has also been altered and thus the $\delta^{18}\text{O}_p$ value does not represent the original signal and should thus also be discarded. Finally, one data point (7753-B), which has an outlying $\delta^{13}\text{C}$ value compared to those of other samples of the same species and from the same stratigraphic horizon, had to be discarded for its carbon isotope value. In summary, two of the 19 values have been discarded due to their anomalous $\delta^{18}\text{O}_p$, four for their $\delta^{18}\text{O}_c$, and five for their $\delta^{13}\text{C}$.

3. Results

The $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ values of the sixteen non-altered samples range between 5.2‰ and 8.0‰ V-SMOW and between 11.2‰ and 16.6‰ V-SMOW, respectively. Non-altered samples have $\delta^{13}\text{C}_c$ values ranging from -10.8‰ to -7.8‰ V-PDB. The $\delta^{18}\text{O}_p$ and the $\delta^{13}\text{C}_c$ values are plotted against their stratigraphic position in Figures 4 and 5.

3.1. Oxygen isotopes

The five *Endothiodon* specimens from the Poortjie Member have $\delta^{18}\text{O}_p$ values that range from $5.4 \pm 0.1\%$ to $6.2 \pm 0.2\%$ V-SMOW. An unidentified pareiasaur from the middle

of this member has a higher value of $8.0 \pm 0.4\%$ V-SMOW. The eight *Tropidostoma* specimens from the overlying Hoedemaker Member yielded $\delta^{18}\text{O}_p$ values that range from $6.1 \pm 0.2\%$ to $7.5 \pm 0.1\%$ V-SMOW. A Wilcoxon Mann-Whitney test reveals a significant difference between the median value of the *Endothiodon* and *Tropidostoma* sample populations (p-value = 0.003).

3.2. Carbon isotopes

For the carbon isotopes, we considered four *Endothiodon* specimens, the pareiasaur mentioned above, and seven of the *Tropidostoma* specimens to be unaltered. The *Endothiodon* $\delta^{13}\text{C}_c$ values range from $-10.8 \pm 0.1\%$ to $-9.5 \pm 0.1\%$ V-PDB, the pareiasaur has a slightly higher value of $-9.2 \pm 0.1\%$ V-PDB, and the *Tropidostoma* values range from $-9.5 \pm 0.1\%$ to $-7.8 \pm 0.0\%$ V-PDB. The median values for the *Endothiodon* and *Tropidostoma* sample populations also show significant differences when tested with a Wilcoxon Mann-Whitney (p-value = 0.017).

4. Discussion

4.1. Oxygen isotopes and the water dependence of *Endothiodon*

The significantly lower $\delta^{18}\text{O}_p$ values for *Endothiodon* relative to *Tropidostoma* (Fig. 4) suggest a difference of ecology; however, because the sampled specimens of each species come from different stratigraphic horizons there is the possibility that this reflects a difference in environmental isotopic values, which are variable over time. To account for this phenomenon we referred to a third dicynodont taxon, *Diictodon feliceps*, which at the Muggfontein locality has previously been sampled from both the Poortjie and Hoedemaker members (Rey et al., 2018; Fig. 4). This study demonstrated that $\delta^{18}\text{O}_p$ values of *Diictodon*

were consistent between the Poortjie and Hoedemaker members and led Rey et al. (2018) to conclude that there was no temperature change between the *Pristerognathus* and *Tropidostoma* Assemblage Zone. Consequently, we take the difference in the range of oxygen isotope composition between *Endothiodon* and *Tropidostoma* to be the result of a difference in water dependence.

As is the case in most dicynodonts (Nicolas and Rubidge, 2010), *Tropidostoma* was a terrestrial species (Botha and Angielczyk, 2007). The lower $\delta^{18}\text{O}_p$ values for *Endothiodon* indicate that this species had either a higher turnover of its body water as a result of more frequent drinking, or that it spent more time in water, similar to the lifestyle of extant hippopotamus (Clementz et al., 2008).

The sampled pareiasaur, which comes from the same stratigraphic horizon as the *Endothiodon* specimens, has an oxygen isotope composition almost 2‰ higher than the highest *Endothiodon* $\delta^{18}\text{O}_p$ value. As pareiasaurs have recently been shown to have been terrestrial rather than aquatic animals on the basis of their stable isotope compositions (Rey et al., 2020), the lower values for *Endothiodon* corroborate its closer relationship with water.

4.2. Carbon isotopes and the diet of *Endothiodon*

Stratigraphic separation is also a potential problem in the comparison between $\delta^{13}\text{C}_c$ values for *Endothiodon* and *Tropidostoma* in our sample. In this case $\delta^{13}\text{C}_c$ values derived from *Diictodon* tusks do show change between the Poortjie and Hoedemaker members, and have been interpreted as reflecting a shift from arid conditions to a more humid environment (Rey et al., 2018; Fig. 5). This interpretation comes from a decrease in $\delta^{13}\text{C}_c$ values for *Diictodon*, so we would expect that environmental influence on our sample led to a negative

shift in the sampled individuals from the Hoedemaker Member (*Tropidostoma*) relative to the same taxon if it were sampled from the lower Poortjie Member. Our results show that $\delta^{13}\text{C}_c$ values for *Tropidostoma* in the Hoedemaker Member are higher than those for *Endothiodon* in Poortjie Member so accounting for the negative environmental shift suggests an even greater disparity between the two taxa for this measurement.

The other explanation for the difference in $\delta^{13}\text{C}_c$ values between *Endothiodon* and *Tropidostoma* would be a difference of diet. Whereas *Endothiodon* has been interpreted to have very specialized feeding habits (Cox, 1964; Latimer et al., 1995; Cox, 1998; Ray, 2000), *Tropidostoma* was more likely a generalised browser (Sullivan and Benton, 2008) based on its similarity to *Oudenodon* (Botha and Angielczyk, 2007), which was interpreted as a browser using finite element analysis of its skull (Jasinski et al., 2009). By comparing our data to published results on carbon stable isotopes, we are in a position to evaluate some of the published interpretations on the diet of *Endothiodon*.

4.2.1. Diet based on insects

The hypothesis of an insectivorous diet originated from the conical shape of the juvenile dentition and may not be applicable to the adults which have a different tooth morphology (Ray, 2000). Tooth replacement in *Endothiodon* took place through successive waves (Latimer et al., 1995) with new teeth forming at the posterolingual end of the row and then moving to the anterolateral end as the tooth matured (Cox and Angielczyk, 2015). Because the replacement of teeth was steady and relatively fast (Latimer et al., 1995), and because we sampled the outer layer of bone, which is the most recently mineralized zone, our results should reflect a constrained period of time preceding the death of the sampled individuals. Amongst the six sampled *Endothiodon* specimens, three (BP/1/7267, BP/1/7570,

BP/1/7753) are of small size and are interpreted as juvenile or sub-adult, whereas two (BP/1/7564, BP/1/7754) are large (1.5 to two times the size of the smaller individuals) and are thus interpreted as adults. Another sampled specimen (BP/1/7356) is too fragmentary to estimate the age of the individual. No difference in the $\delta^{13}\text{C}$ values is evident between the presumed adults and juveniles, indicating either a similar diet throughout ontogeny or different diets with similar $\delta^{13}\text{C}$ values.

Insect $\delta^{13}\text{C}$ values reflect their food isotopic signature (Paetzel et al., 1979; Akamatsu et al., 2004). Depending on the area, the season of collection (Kato et al., 2004), and other factors such as the island size (Hyodo and Wardle, 2009) or the species studied, the isotopic relationship between terrestrial and the aquatic food network can vary. This is a result of the greater variability in the $\delta^{13}\text{C}$ of aquatic insects (Akamatsu et al., 2004; Kato et al., 2004; Paetzold et al., 2005). The reason for this is that terrestrial environments prior to the Miocene were dominated by C3-plants (Osborne and Beerling, 2006), which display a natural range of the $\delta^{13}\text{C}$ values between -35‰ and -21‰ (Kohn, 2010), but that are generally constant in a given environment. In aquatic ecosystems, herbivorous insects can feed on algae, allochthonous terrestrial detritus and microbial films in addition to aquatic plants, each having its own range of $\delta^{13}\text{C}$ values (Kato et al., 2004). The relatively narrow range of $\delta^{13}\text{C}_c$ values for *Endothiodon* would suggest a food source with a constant $\delta^{13}\text{C}$ value over time which leads us to reject aquatic insects as a food source.

Extant insectivorous mammals, such as the aardwolf or the bat-eared fox, present similar $\delta^{13}\text{C}_c$ values from carbonate enamel to those of carnivorous species (Codron et al., 2018). Between plants and muscular tissues of herbivores, ^{13}C -enrichment is about 1‰ (Barnes et al., 2007; Kelly, 2000), which is the same as that observed between plants and

insects (Petelle et al., 1979). The ingestion of muscular tissues and insects by predators creates a ^{13}C -enrichment in their bones and teeth, which is estimated to be 9-10‰ for both extant mammals (Koch, 2007) and reptiles (Stanton, 2006). The cumulating fractionations along the food chain culminate in a 10-11‰ ^{13}C -enrichment in the bones of carnivorous animals relative to plants.

Several studies have revealed variations in the apatite-plant isotopic fractionation of between 10‰ and 15‰ for herbivorous mammals (Lee-Thorp et al., 1989; Koch, 1998; Cerling and Harris, 1999; Passey et al., 2005), whereas it is 12‰ for herbivorous reptiles (Biasatti, 2004). Therefore, the $\delta^{13}\text{C}$ values of apatite of herbivorous animals should vary between -1‰ and +5‰. However this difference might be difficult to determine in ancient extinct species (Rey et al., 2020). The difference recorded between the $\delta^{13}\text{C}_c$ values of *Endothiodon* and *Tropidostoma* is within this range and possibly indicates a terrestrial insect diet for *Endothiodon*. It is also noteworthy that specialized detritivorous insects have higher $\delta^{13}\text{C}$ values (up to 3‰ higher than the food substrates) and reflect fungal development and humification processes in their diet (Hyodo, 2015). This is in agreement with our results and thus we cannot reject the possibility that detritivorous insects formed a significant part of the diet of juvenile *Endothiodon*.

4.2.2. Diet based on heterotrophic plant components

Leaves are not the only part of the plant which are available for foraging and some dicynodonts may have subsisted on roots or other hard plant material (King, 1993). Cox (1998) suggested that *Endothiodon* ate conifer cones, based on its vaulted palate that could have been used to hold cones while the lower beak extracted the seeds which were then macerated by the strange teeth present in this species. In extant C_3 plants, the heterotrophic

regions (stem, roots, seeds, and fruits) have relative ^{13}C -enrichment compared to the foliage (Damesin and Lelarge, 2003; Hobbie and Werner, 2004; Cernusak et al., 2009). Therefore, assuming that *Tropidostoma* was a leaf browser, the lower $\delta^{13}\text{C}$ values for *Endothiodon* suggest that this species did not feed extensively on roots or seeds.

4.2.3. Diet of riverine vegetation

Another possible food source for *Endothiodon* is algae. Only the C3 pathway was present in Permian plants (Osborne and Beerling, 2006) and the range of values recorded for extant members of this group is between -35‰ and -22‰ (Kohn, 2010). Extant algae have $\delta^{13}\text{C}$ values ranging from -23‰ to -12‰ (Smith and Epstein, 1971), which is higher than that of extant terrestrial C3 plants whose range of values is between -35‰ and -22‰ (Kohn, 2010). However, the lower $\delta^{13}\text{C}$ values compared to *Tropidostoma* are not consistent with a significant algal component in the diet of *Endothiodon*. A better explanation is that *Endothiodon* subsisted on plants growing on the banks of rivers, as proposed by Latimer et al., (1995) (See Discussion 4.1). $\delta^{13}\text{C}$ values in extant plants correlate with the humidity of the environment, whereby a mesic environment, such as found along the edge of watercourses, has a flora with more negative $\delta^{13}\text{C}$ values than that from a xeric environment (Garten and Taylor, 1992). Even in arid areas, a wet microhabitat can flourish along rivers or at springs. In these areas, plants have lower $\delta^{13}\text{C}$ values than those from the dry surrounding areas (Kohn, 2010). This is consistent with the data for *Endothiodon* relative to *Tropidostoma*, whereby the latter subsisted on vegetation growing in drier environments away from river banks.

4.3 Implications for the success of *Endothiodon*

Endothiodon represents one of the first new taxa to appear in the Karoo Basin as part of the recovery from the Capitanian mass extinction and it is tempting to believe that its

specialised feeding system was not coincidental. Retallack et al. (2006) reported an increase in the abundance and diversity of lycosid spores in the immediate aftermath of the Guadalupian (Capitanian) mass extinction, but the source of their data (Horowitz, 1990) sampled only uranium-bearing horizons of uncertain stratigraphic position in the southwestern Karoo and hence are of very limited use. More recently, Barbolini, (2014) and Barbolini et al. (2018) presented palynomorph occurrences within the tetrapod-bearing stratigraphic units of the Beaufort Group in the southwestern Karoo, which suggested a loss of species richness between the Abrahamskraal and Teekloof formations that was up to 75% of that observed at the Permo-Triassic boundary. This resulted from the extinction of short- and medium-ranging taxa of pteridophytes, algae, and acritarchs, all of which were likely water dependent (Barbolini pers. comm.). Origination of species in the Hoedemaker Member is very low but the two that do appear, *Michrhystridium stellatum* and *Protohaploxylinus sp.*, are also both water-dependent (Barbolini, 2014).

This is consistent with results of Rey et al. (2018) that suggested that aridification with relatively stable temperatures had attended the Capitanian extinction in the Main Karoo Basin, with a return towards wetter conditions occurring afterwards, in the upper Poortjie Member and into the lower Hoedemaker Member. The loss of large herbivores associated with the Capitanian mass extinction may therefore have been driven, at least in part, by the loss of riparian vegetation as well as the reduction in water availability directly. As humidity within the basin increased again, it is possible that *Endothiodon* may have followed belts of riparian vegetation as they re-established themselves along the watercourses. While *Endothiodon* clearly benefited from the opportunity presented by the Capitanian mass extinctions, the role of its unique feeding system in its success remains uncertain.

5. Conclusions

This work is a preliminary comparative study using stable oxygen and carbon isotope compositions of phosphate apatite of teeth and bones of the dicynodonts *Endothiodon* and *Tropidostoma* to determine their ecologies. Geochemical proxies were used to test the different ecologies proposed for *Endothiodon* characterized by its unique masticatory system among therapsids. Our results show significantly lower values of both $\delta^{18}\text{O}_p$ and $\delta^{13}\text{C}_c$ for *Endothiodon* when compared with those of *Tropidostoma*. Stable oxygen isotopes suggest that *Endothiodon* was more water-dependent than *Tropidostoma*, with a possibility that it was even semi-aquatic. Stable carbon isotopes suggest that the diet of *Endothiodon* did not include a substantial amount of roots, seeds or algae but rather that *Endothiodon* subsisted on a plant diet dominated by the mesic vegetation along water courses, although juveniles possibly fed on terrestrial insects. *Tropidostoma*, by contrast, may have lived on vegetation growing in drier environments back away from river courses. Although the reasons for the success of *Endothiodon* in the aftermath of the Carnian mass extinction remain unclear, these results suggest that it could be linked to riparian vegetation.

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Figure and table captions

Figure 1: Map showing the localities studied (black stars) near Beaufort West, South Africa. Light green: Abrahamskraal Formation; Dark green: Middleton Formation.

Figure 2: Bone values (b) are plotted against tooth values (t) of the same individual and compared to a line with a slope of 1, for their $\delta^{18}\text{O}_p$ values (A), $\delta^{18}\text{O}_c$ values (B) and $\delta^{13}\text{C}_c$ values (C). The circled $\delta^{18}\text{O}_c$ value corresponds to the sample 7267-B considered as altered (see text).

Figure 3: Phosphate $\delta^{18}\text{O}_p$ values plotted against corresponding carbonate $\delta^{18}\text{O}_c$ values, together with the empirical isotopic equilibrium line (Iacumin et al., 1996) with a slope close to unity (bold line). The altered samples are within the circle. The reduced major axis regression lines are represented for all samples (dash line) except unaltered ones (full line).

Figure 4: $\delta^{18}\text{O}_p$ values of each individual plotted against their stratigraphic position. The base of the stratigraphy (0m) corresponds to the base of the Poortjie Member. The bold horizontal line separates the Poortjie Member (below) and the Hoedemaker Member (above). Values from *Diictodon* are from Rey et al. (2018). Skull figures are from Day and Smith (2020) and Day and Rubidge (2020), published with permission from the Geological Society of South Africa. All scale bars represents 10 cm.

Figure 5: $\delta^{13}\text{C}_c$ values of each individual plotted against their stratigraphic position. The base of the stratigraphy (0 m) corresponds to the base of the Poortjie Member. The bold horizontal

line separates the Poortjie Member (below) and the Hoedemaker Member (above). Values from *Diictodon* are from Rey et al. (2018). Skull figures are from Day and Smith (2020) and Day and Rubidge (2020), published with permission from the Geological Society of South Africa. All scale bars represents 10 cm.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Highlights:

- Stable isotopes allow understanding palaeobiology and lifestyle of Permian tetrapods.
- Oxygen stable isotopes indicate *Endothiodon* was more water-dependent than *Tropidostoma*.
- Carbon Stable isotopes reveal dicynodont *Endothiodon* fed on riverine vegetation.
- Stable carbon isotopes show diet of juvenile *Endothiodon* probably included insects.

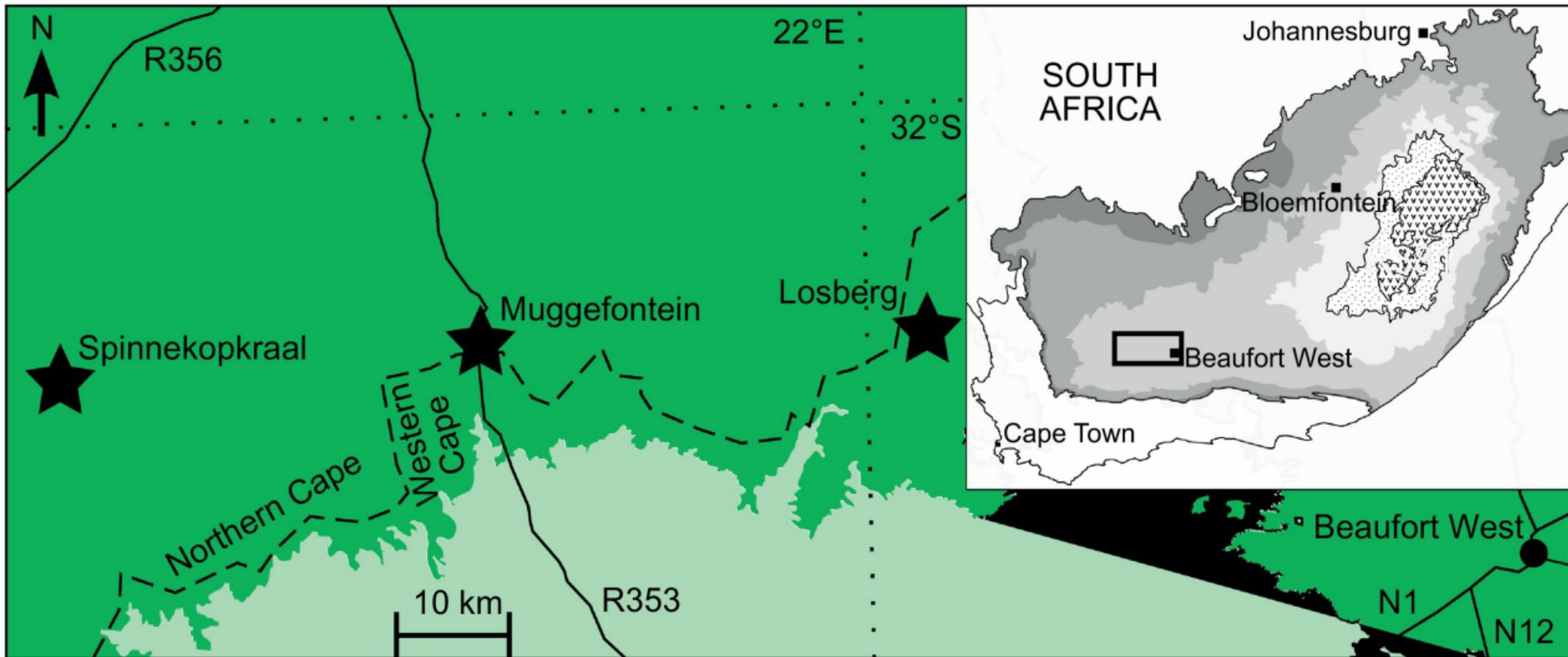


Figure 1

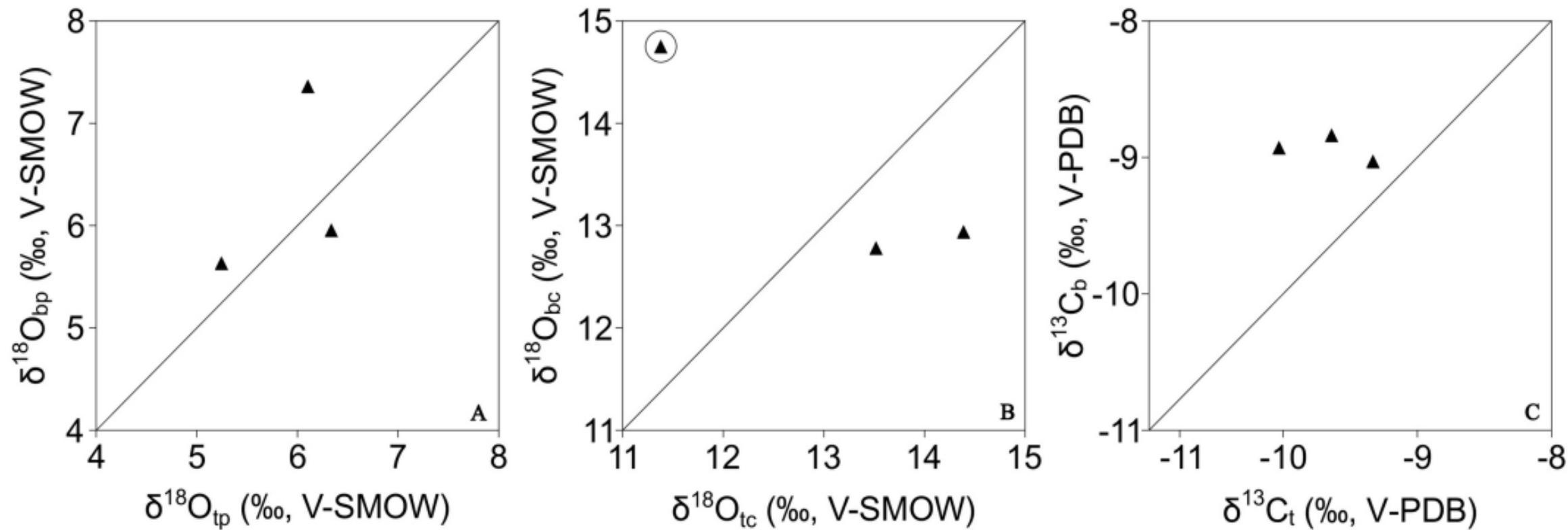


Figure 2

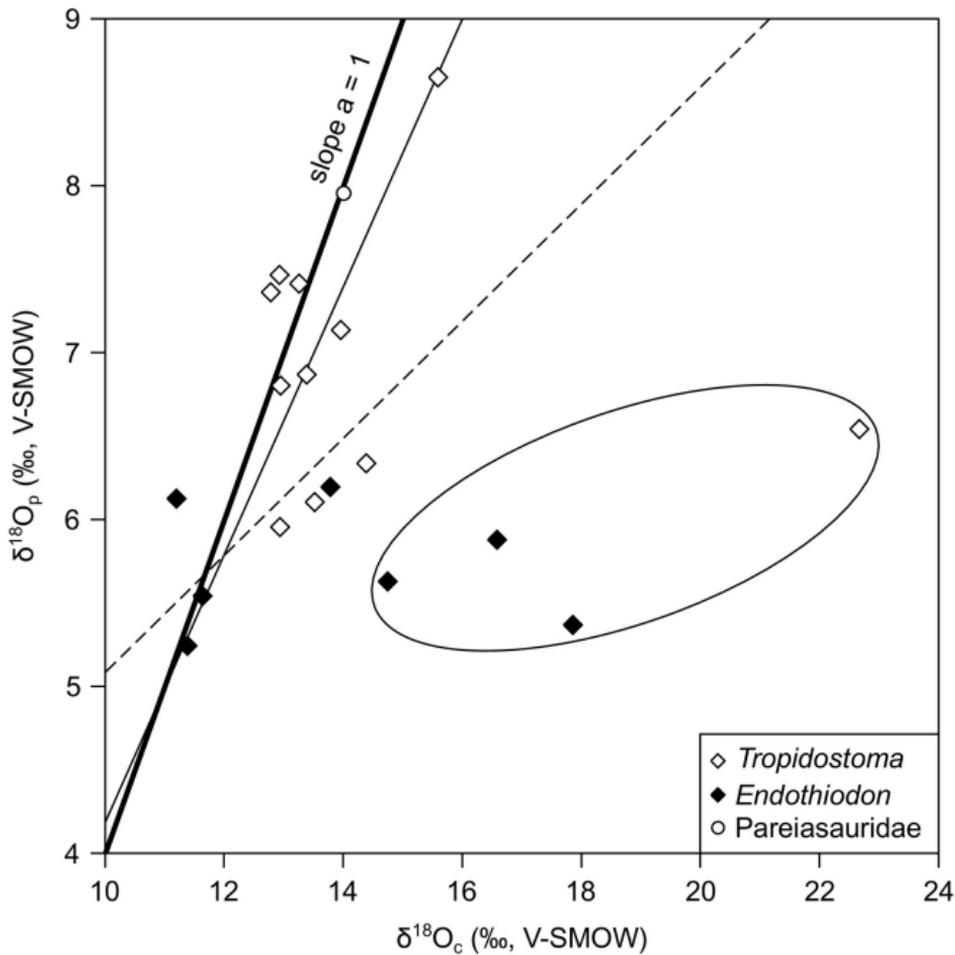


Figure 3

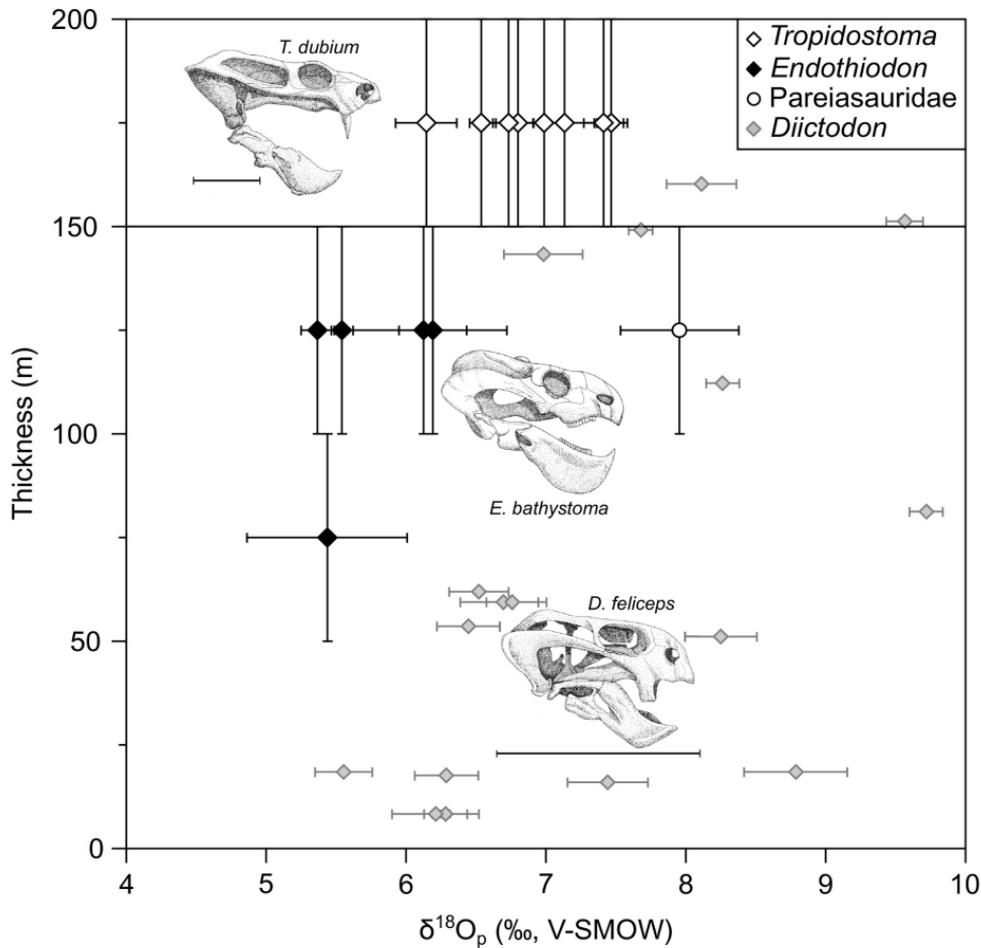


Figure 4

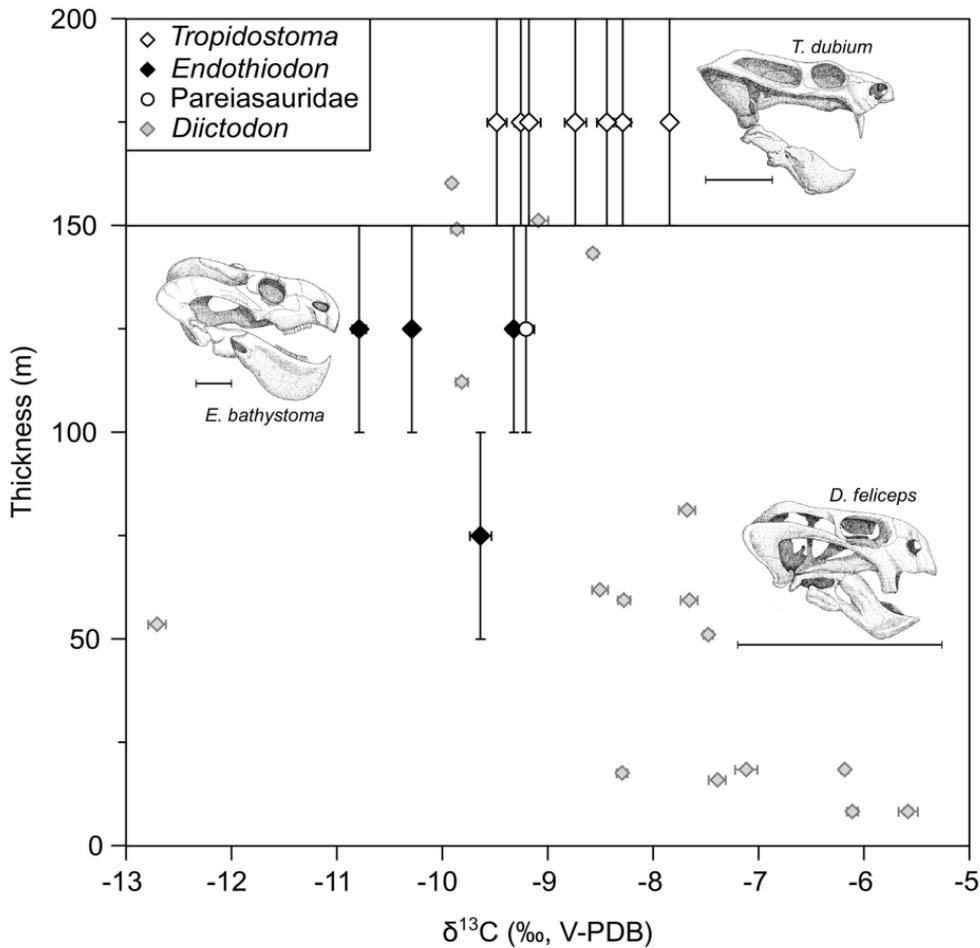


Figure 5