The Permian mammal-like herbivore *Diictodon*, the oldest known example of sexually dimorphic armament

Corwin Sullivan¹, Robert R. Reisz^{2*} and Roger M. H. Smith³

¹Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

²Department of Biology, University of Toronto at Mississauga, Mississauga, Ontario L5L 1C6, Canada

³Earth Sciences Division, South African Museum, P.O. Box 61, Cape Town 8000, South Africa

Dicynodonts, a highly successful group of Palaeozoic tetrapods, were herbivores with keratinous beaks, and were frequently equipped with large, neomorphic tusks. *Diictodon* is a particularly abundant dicynodont genus, allowing statistical investigation of its palaeobiology. Anatomical, morphometric and distributional analyses provide evidence of sexual dimorphism, based on the presence or absence of formidable tusks. Tusk occurrence is also correlated with the presence of a cranial boss on the skull roof and, possibly, with greater cranial size. This earliest well-documented example of dimorphic armament suggests that sexual dimorphism, and the complex social behaviour that accompanies it, have long been characteristic of the synapsid lineage.

Keywords: sexual dimorphism; vertebrates; Palaeozoic; amniote; herbivorous synapsid; dicynodont

1. INTRODUCTION

Among the most significant evolutionary events in the history of life on land was the development of the modern ecological structure in which terrestrial plants support a large population of herbivores, which in turn support relatively few predators. This trophic organization was not fully developed until the Late Permian (259–251 Myr ago) of the Palaeozoic, when the vertebrate primary consumer base was largely formed by a group of therapsid synapsids ('mammal-like reptiles'), the dicynodonts (see King 1990; Sues & Reisz 1998). The fossil record indicates that herbivorous dicynodonts were not only taxonomically diverse, extraordinarily abundant and globally distributed, but also extended from the Late Permian to the Late Triassic, across the Permo-Triassic boundary (King 1988).

Although comparatively distant relatives of mammals, dicynodonts independently acquired numerous mammal-like features (Hopson & Barghusen 1986; Hopson 1995; Sidor 2000), including a secondary palate, mammal-like skull architecture in the temporal region and reduced phalangeal formula, at least 50 Myr before the advent of mammals. However, numerous dicynodonts replaced the primitive dentition with a strong keratinous beak, so that advanced forms were toothless apart from the frequent presence of formidable tusks. Although these striking structures are completely absent in some genera (e.g. *Oudenodon*), and always present in others (e.g. *Dicynodon*), the most intriguing condition is their variable presence in genera such as the highly abundant *Diictodon*, because it raises the question of whether tusked and tuskless individuals represent opposite sexes (Toerien 1953), different age classes (Barry 1957) or different species.

2. THE GENUS *DIICTODON*

King (1993) recently carried out a taxonomic revision of the small and widespread dicynodont *Diictodon*, and recommended recognition of only a single species, *D. galeops* Broom 1913. However, this conclusion supposes that the variable presence of tusks reflects intraspecific variation in the form of either dimorphism or ontogeny. This supposition can be tested by examining the patterns of distribution of the tusked and tuskless morphotypes in time and space, and the nature of the anatomical differences between them; *Diictodon* is particularly suitable for such a study because of the large sample sizes available. The extraordinary abundance of *Diictodon* partly reflects its wide geographical range, incorporating numerous sites in the Karoo basin as well as occurrences in China (Sun 1973) and Tanzania (Maisch 1995), and its persistence over a stratigraphic interval that incorporates four of the five recognized Permian Karoo biozones and may represent up to 10 Myr (King 1993).

Although *Diictodon* lacks the fossorial specializations of the cistecephalid dicynodonts (Cluver 1974), it has been associated with helical burrows of characteristic architecture that occur in floodplain deposits near ancient fluvial channels (Smith 1987), and a few specimens have been found entombed in terminal chambers. The infilled burrows are widely scattered, perhaps because of sporadic preservation, and show a degree of similarity to Tertiary burrows attributed to the beaver *Palaeocastor* (Smith 1987). However, the spiral burrowing of *Diictodon* remains unique among non-mammalian vertebrates. Like the cistecephalids, *Diictodon* is near the lower end of the dicynodont size range (average skull length ca. 9 cm), and most other dicynodonts were presumably too large for effective burrowing. *Diictodon* also differs from other dicynodonts histologically, in that appendicular skeletal elements studied by Chinsamy & Rubidge (1993) display uniform rather than periodically (perhaps seasonally) retarded growth.

* Author for correspondence (rreisz@utm.utoronto.ca).

The most characteristic osteological feature of *Düctodon*, a sharp angle between the descending caniniform process and the maxillary rim, is shared only with *Robertia* among described dicynodont genera and hints at a distinctive diet and feeding mechanism (Cluver 1970; Cox 1998).

Because *Robertia* is rare and has not been extensively studied, it is not clear whether it also shared the burrowing capability and mode of bone growth seen in *Düctodon*. However, these characteristics imply that *Düctodon* at least was physiologically and ecologically unusual among dicynodonts, and understanding the significance of the variable presence of tusks in this genus is critical to rounding out the emerging palaeobiological picture.

3. DISTRIBUTION OF TUSKED AND TUSKLESS SPECIMENS

We used field data on the occurrence of *D. galeops*, collected largely in the course of previous taphonomic studies (Smith 1989, 1993), to investigate the stratigraphic and regional distribution of tusked and tuskless specimens. Counts of *Düctodon* specimens from several successive stratigraphic levels at a single Karoo locality (Leeukloof 43), and from several different outcrops on the Dunedin farm, Beaufort West (figure 1) show that tusked and tuskless specimens invariably occur together in productive horizons, usually in comparable, if not exactly equal, numbers. Homogeneity χ^2 -analysis (Zar 1999) indicates that the ratio of tusked to tuskless specimens is not heterogeneous and does not deviate significantly from 1:1 either within the stratigraphic section sampled at Leeukloof (heterogeneity $\chi^2_{12} = 11.3$, $p = 0.50$; pooled $\chi^2_1 = 0.232$, $p = 0.63$) or among the various localities sampled on the farm Dunedin (heterogeneity $\chi^2_{16} = 16.1$, $p = 0.45$; pooled $\chi^2_1 = 0.883$, $p = 0.35$). Although these detailed occurrence data are stratigraphically and geographically restricted, there is no reason to believe that they are not representative of *Düctodon* in the Karoo basin.

The preservational association between the two morphotypes is so close and consistent as to leave little doubt that it results from cohabitation during life rather than post-mortem accumulation. Such association would be almost inexplicable if the two morphotypes represented separate species: it seems implausible that they would show such a pattern of unvarying co-occurrence, especially given that their similar size and morphology would make them natural competitors. However, consistent association would be expected of either opposite sexes or members of different age classes within a single species, and the lack of significant deviation from a 1:1 ratio is particularly compatible with the hypothesis of sexual dimorphism (Fisher 1930).

4. ANATOMICAL CHARACTERISTICS OF TUSKED AND TUSKLESS SPECIMENS

We analysed a sample of 28 well-preserved *Düctodon* crania using principal components analysis, applied to the variance-covariance matrix of seven log-transformed measurements on the skull (figure 2). This method mathematically combines the original variables to create a new set of quantities, the principal components, which are automatically uncorrelated with one another and defined

Figure 1. Occurrence of tusked (open bars) and tuskless (filled bars) *Düctodon* specimens (a) at various stratigraphic levels at the locality Leeukloof 43, Beaufort West, South Africa, and (b) at various field localities on the Dunedin farm, South Africa. Tusked and tuskless specimens almost invariably occur together when *Düctodon* is found in substantial numbers.

to express as much of the variability within the dataset as possible (Shea 1985). The analysis was done using the computer program NTSYS-pc (Rohlf 1990).

The sample is quite morphometrically homogeneous, as the first principal component alone accounts for the vast majority (83.5%) of the variation in the dataset (table 1) and subsequent components may be regarded as statistically insignificant because the percentage of variation they explain is less than the reciprocal of the number of starting variables (Zelditch *et al.* 1989). The first component is positively correlated with all of the original variables, as is typical for morphometric analyses, and clearly reflects the three-dimensional size of the skull. Tusked specimens have a higher average score on this component ($t_{26} = 2.30$, $p = 0.30$), indicating slightly greater average size, and the Mann-Whitney *U*-test confirms that the two morphotypes can be distinguished based on the tendency of tusked specimens to score higher ($t_s = 2.18$, $p = 0.029$).

Figure 2. (a) Plot showing the first two principal components obtained in a morphometric analysis of *Diictodon*, using the seven cranial measurements shown in (b). Tusked specimens (open circles) tend to score higher than tuskless specimens (filled circles) on the first principal component, indicating larger average body size, but there is no apparent clustering of the specimens into morphometrically distinct groupings.

Table 1. Principal components obtained in a morphometric analysis of the skull of *Diictodon*.

principal component	% variance explained	mean value	
		tusked specimens	tuskless specimens
1	83.5	0.035	-0.046
2	6.8	-0.002	0.003
3	5.1	-0.009	0.012

However, there is a degree of overlap between tusked and tuskless specimens, and the magnitude of the difference in means is extremely small (table 1; average skull length, an intuitively clear albeit one-dimensional measure of size, is 7.89 cm in tuskless specimens and 9.51 cm in tusked ones). This renders implausible Barry's suggestion that the tuskless individuals should be interpreted as young juven-

Table 2. Qualitative characters tested for correlated occurrence in the skull of *Diictodon*.

1	canine tusks: present versus absent
2	pineal boss: present versus absent
3	nasal boss: laterally subdued versus laterally elevated
4	boss posteromedial to caniniform process: present versus absent
5	coverage of parietal flanges by postorbitals: partial versus nearly complete
6	parietal flanges: widely separated versus close together
7	labial fossa: shallow versus deeply excavated
8	postparietal: associated with intertemporal bar versus associated with occipital surface versus intermediate
9	splenials: fused at symphysis versus separated by a vertical suture line
10	ridge above post-temporal fenestra: present versus absent

iles, especially considering that most tuskless individuals lack characteristically 'juvenile' features, such as open suture lines and smooth, minimally rugose bone surfaces (Barry 1957). The one (tuskless) specimen that shows these features is very small, and appears on a bivariate plot of the first two principal components (figure 2) as an extreme outlier. It may well represent a juvenile, and its removal from the analysis reduces the variation accounted for by the first principal component to 75.6%, though other components remain insignificant. The size distinction between tusked and tuskless skulls now barely fails to satisfy the usual $\alpha = 0.05$ criterion of statistical significance (t -test: $t_{25} = 1.88$, $p = 0.071$; Mann-Whitney: $t_s = 1.83$, $p = 0.068$), indicating that the difference in cranial size becomes equivocal when only definite adults are considered.

Figure 2 shows that tusked and tuskless specimens are interspersed on the plot without forming discrete clusters, and are therefore broadly similar in their cranial proportions. This morphometric homogeneity is consistent with the view that *Diictodon* is monospecific, at least with regard to its occurrence in the Karoo basin, as argued by King (1993) and Sullivan (2000). Neither of these authors had the opportunity to examine material from China or Tanzania.

In addition to the possible size discrepancy, tusked and tuskless specimens of *Diictodon* differ in the occurrence of certain qualitative skull features. χ^2 -tests of the mutual independence of several skull characters (table 2; full analysis in Sullivan (2000)) show that tusked specimens (figure 3) are more likely to have the postparietal bone positioned on the occipital surface rather than within the intertemporal bar ($\chi^2_2 = 6.83$, $p = 0.033$), and are more likely to have a bony boss surrounding the pineal opening on the skull roof ($\chi^2_1 = 6.39$, $p = 0.012$). The existence of this complex of correlated features implies that the tusked and tuskless morphotypes indeed represent biologically important categories. The association between the presence of tusks and the presence of a pineal boss is particularly intriguing, as nasal and supraorbital bosses have previously been suggested as sexually dimorphic structures in the dicynodonts *Aulacephalodon* (Tollman *et al.* 1980) and *Lystrosaurus* (Thackeray *et al.* 1998).

Figure 3. Skull reconstructions of (a) tuskless (presumably female) and (b) tusked (presumably male) *Diictodon* in lateral view. Numbered arrows (i)–(iii) indicate the positions of the three thin sections from the right side of the snout and lower jaw from the presumed female and male. (c)(i) Transverse section through the snout showing a strong caniniform process on the presumed female, even though there is no evidence of any tooth or any tooth germ (Royal Ontario Museum, ROM 52623). In addition, there is no trace of a socket on the maxillary shelf where a tooth could have developed on the maxillary bone of the presumed female. (ii) Cross-section through the tusk of a large, almost adult specimen (ROM 52624), showing growth occurring in the pulp region, with new dentine being deposited medial to the older dentine, filling in the pulp cavity in the root portion of the tusk. (iii) Transverse section through the snout resulting in a longitudinal section through a massive tusk in the area of the maxillary bone also showing new dentine being deposited in the pulp cavity (ROM 52624). Abbreviations: d, dentine; lj, lower jaw; m, maxilla; nd, secondary dentine; pc, pulp cavity. Scale bar, 1 cm.

This argument rests, in large part, on the observation that cranial bosses appear well suited for use in intraspecific antagonistic interactions, suggesting a strong analogy to the many living tetrapods in which males develop specialized armament in association with intense competition over either territories or females (Shine 1989; Andersson 1994). The horns, antlers, tusks, bosses, spines and other structures that serve this purpose in various species may be largely symbolic, in that contests between males are frequently decided by highly ritualized combat or even threatening displays rather than serious fighting. However, the term ‘armament’ seems appropriate for any structure that could plausibly have an offensive or defensive role in combat, whether it is used to actually attack rivals or merely to threaten them.

The pineal boss of *Diictodon* may be interpreted along such lines, as protection for the vulnerable pineal opening in shoving or head butting. The possible utility of the large tusks as weapons is obvious, particularly because of their considerable growth in both diameter and length (although post-mortem breakage is common) during the life of an individual, and additional deposition of dentine in the pulp cavity (figure 3c(ii)). The tusks become strongly ankylosed to the maxillae only in the largest known individuals, when growth has evidently stopped (figure 3c(iii)). An important role in feeding seems unlikely: the presumed females must have been able to eat despite lacking tusks, and there is no evidence of wear that would indicate activity of this kind. This is in contrast to the very extensive wear on the tusks of *Lystrosaurus*, in which tusks occur in all individuals (Cluver 1971). Similarly, the fact that a pineal boss occurs invariably rather than dimorphically in some dicynodonts, such as *Rhachiocephalus* (Keyser 1975), suggests that it may have served to protect the pineal opening against accidents or predator attack in these cases.

Under the proposition that the pineal boss and tusks functioned mainly in intraspecific conflict, the anatomical differences between the morphotypes (other than the placement of the postparietal bone) amount only to a discrepancy in armament and a probable discrepancy in size, at least of the cranium. *Diictodon* is therefore similar to the numerous extant tetrapods in which differences in size and armament are the characteristic pattern of sexual dimorphism; the most familiar examples occur among mammals, particularly artiodactyls, pinnipeds, elephants and primates (Ralls 1977). In some anuran species the male is larger and equipped with tusks or body spines (Shine 1979), and male galliform birds often have spurs or knobs on the legs or wings (Davison 1985). The fact that the morphological differences between the two morphotypes of *Diictodon* correspond to this common and phylogenetically widespread pattern, taken together with the co-occurrence of the two morphotypes noted above, is powerful evidence that the morphotypes are best interpreted as opposite sexes rather than different species or age classes.

5. DISCUSSION

The hypothesis of sexual dimorphism implies that behavioural and ecological patterns common to dimorphic living forms probably also apply to *Diictodon*. Among extant tetrapods, either sex may be larger, but differences in armament almost always involve the presence in the male of structures that are absent or weakly developed in the female. The correlation between such dimorphism and the occurrence of polygyny and male intrasexual conflict is particularly well established for various mammals (see Kinzey 1972; Jarman 1983; Wiig 1985), but male combat is also linked to dimorphism in anurans (Shine 1979) and galliform birds (Davison 1985). Even among reptiles, which rarely display dimorphism except in body size, the large heads and hypertrophied jaw muscles of a few male herbivorous lizards have been interpreted as weaponry developed under sexual selection pressure (Carothers 1984).

Although the relationship between a given species’ degree of sexual dimorphism and the structure of its mat-

ing system is complex and subject to confounding influences, especially in the fossil record (Plavcan 2000), the almost universal occurrence of some form of male aggression in species displaying strong dimorphism in armament is too obvious and well established to ignore. We therefore postulate that the tusked sex in *Diictodon* was almost certainly the male, and that the presence of dimorphism implies a relatively complex mating system characterized by antagonistic competition among males, however symbolically or ritualistically such competition may have been conducted.

Under this interpretation, the complex intraspecific interactions that must have accompanied dimorphism represent an intriguing aspect of the palaeobiology of *Diictodon*. Combined with the apparent ability of this animal to dig spiral burrows, as discussed above, they suggest a high level of behavioural sophistication. It remains to be determined whether such behavioural complexity was widespread in dicynodonts, as evidence of sexual dimorphism in other taxa such as *Aulacephalodon* and *Lystrosaurus* already suggests, or whether it was restricted to *Diictodon* and perhaps related to the specialized diet and continuous bone growth of this genus.

On a broader scale, the occurrence of strong dimorphism in armament in *Diictodon* is notable for being the oldest adequately documented example of its kind in the terrestrial vertebrate fossil record. Claims for dimorphism in older taxa (see Romer & Price 1940; Vaughn 1966) have been based on relatively minor morphological differences observed in a few specimens, and even if further sampling and study confirmed their validity, their magnitude would remain small compared with the striking distinction between tusked and tuskless specimens of *Diictodon*. The phylogenetic context of this prominent dimorphism is significant, in that the most ancient division within amniotes is the split between Synapsida (including mammals and their therapsid predecessors) and Sauropsida (including reptiles and birds), which dates back 315 Myr to the Carboniferous period (Laurin & Reisz 1995). As *Diictodon* represents the only well-documented Palaeozoic example of dimorphism in armament, it may be provisionally postulated that dimorphic armament, and the complex behaviours that must have accompanied it, first appeared in the synapsid rather than the sauropsid lineage, foreshadowing the widespread dimorphism and social complexity of extant mammals.

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