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DICYNODONT (THERAPSIDA) BONE HISTOLOGY: PHYLOGENETIC AND PHYSIOLOGICAL IMPLICATIONS

by

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ABSTRACT

The bone histology of humeri of a number of taxonomically well established and easily definable dicynodont genera is described and compared. The bone of *Aulacephalodon, Cistecephalus, Dicynodon, Endothiodon, Lystrosaurus, Kannemeyeria* and *Oudenodon* consists of alternating fibro-lamellar and lamellated bone tissue, while that of *Diictodon* consists only of fibro-lamellar tissue. The presence of fibro-lamellar bone in all the genera studied, indicates that the bone was deposited rapidly, but the occurrence of lamellated bone tissue suggests that all the genera except *Diictodon*, also had intermittent periods of slow growth. This is the first time that a comparative study of bone histology of different dicynodont genera has been attempted by using one particular bone element to standardise intergeneric comparisons.

KEY WORDS: Therapsida, Dicynodontia, bone histology.

INTRODUCTION

The Anomodontia were a large group of herbivorous therapsids that arose during the late Permian and, by the end of the period, were the dominant herbivorous element of the vertebrate fauna. Only a few representatives survived into the Triassic. The subgroup Venjukovioidea, are the most primitive of the Anomodontia and are known only from the Permian deposits of the Russian zones I and II, as well as the lowermost 3 biozones of the Beaufort Group (Brinkman 1981; Rubidge and Hopson 1990). The other subgroup, the Dicynodontia (*sensu* Rubidge and Hopson 1990) are better known and are represented by a relative abundance of specimens.

The presence of dicynodonts through the complete stratigraphic range of the Beaufort Group in South Africa has led to their extensive use in the biostratigraphic subdivision of the rocks of the Beaufort Group in South Africa (Keyser and Smith 1978; Kitching 1977; Rubidge 1990), and they have been successfully employed in taphonomic and palaeoenvironmental studies (Smith 1980; Smith 1990a).

As a group the dicynodonts have been well studied phylogenetically (e.g. Cluver and King 1983; Cox and Li 1983; Keyser and Cruickshank 1979; King 1988), taxonomically and morphologically (e.g. Cluver 1971; Cluver and Hotton 1981; Cluver and King 1983, King 1981), and some functional aspects of the skulls and skeletons have been addressed (Cluver 1971; Crompton and Hotton 1967; King 1981; King, Oelofsen and Rubidge 1989). With the relatively recent discovery of burrows in the rocks of the Beaufort Group, more avenues of research have been opened up and speculations regarding their mode of life have been made (Groenewald 1991; Smith 1987).

In the past, histological descriptions of the bone tissues of members of the Dicynodontia have been given by Gross (1934) and Ricqlès (1974, 1976). Gross's study dealt with only one species of the group whilst that by Ricqlès was concerned with bone tissues of therapsids as a whole – not specifically of the dicynodonts as is the case in the present study.

METHODS

Since bone tissue structure varies from one bone element to another (even in the same animal), this study considered only the humeri of different well established and easily identifiable dicynodont genera (*sensu* Cluver and King 1983; Keyser and Cruickshank 1979; King 1988). The present study provides a good basis for comparison of the histological tissue types of the different dicynodont genera since it compares the bone tissue structure of homologous bones, as well as homologous regions of the specified bone. This is significantly different from previous studies which examined various isolated bones. Notable too is the fact that the humeri were selected from adult animals so that ontogenetic differences in the bone structure should not interfere with comparisons between the various genera.

The genera were chosen so that at least one representative genus of each dicynodont subfamily, as indicated by the branches of the published cladograms (Cluver and King 1983; Keyser and Cruickshank 1979; King 1988), was studied (Figure 1); the only exceptions

were *Eodicynodon*, *Kingoria* and *Pristerodon*, owing to a lack of suitable material.

In addition, at least one dicynodont genus was chosen for each successive vertebrate biozone of the Beaufort Group (Rubidge *in press*), except the *Eodicynodon-Tapinocaninus* Assemblage Zone because of the paucity of material from this zone. This was done in an effort to ensure that "trends" or changes in the nature of the humeral histology of the dicynodonts from the Permian to the Triassic would be recognised.

TABLE 1:
Specimens examined in this study

GENUS	SPECIMEN NUMBER
Kannemeyeria	BP/1/1660
Lystrosaurus	BP/1/3236
Dicynodon	SAMK7893
Cistecephalus	BP/1/4086
Aulacephalodon	BP/1/4490
Oudenodon	BP/1/3963
Diictodon	SAMK6821
	SAMK7015
	SAMK6717
Endothiodon	BP/1/268/56
	BP/1/129/56
	SAM6618

Each humerus was photographed and standard measurements of each were recorded. Thin sections were prepared of the mid-shaft region according to the technique described by Chinsamy and Raath (1992). Examination of the bone tissue structure was conducted using light microscopy.

RESULTS

Cross sections of the humeri of the various genera of dicynodonts revealed similarities and differences between the various genera. *Lystrosaurus, Dicynodon, Aulacephalodon, Oudenodon, Endothiodon, Cistecephalus* and *Kannemeyeria* showed similarities in their bone tissue structure. The bone tissue structure of *Diictodon* differed from all the other dicynodont genera studied.

Among all the genera the compacta surrounding the medullary cavity is of variable thickness. A large amount of cancellous bone occupies the medullary cavity. The spongy bone encroaches on the compact bone and in some cases the compact bone is merely a thin lining around the cancellous bone tissue.

In the case of *Lystrosaurus, Dicynodon, Aulacephalodon, Oudenodon, Endothiodon, Cistecephalus* and *Kannemeyeria*, histological examination of the microstructure of the compact bone indicated that it consisted of laminar bone tissue of the fibro-lamellar complex. However the continuous deposition of this woven bone tissue is interrupted by the

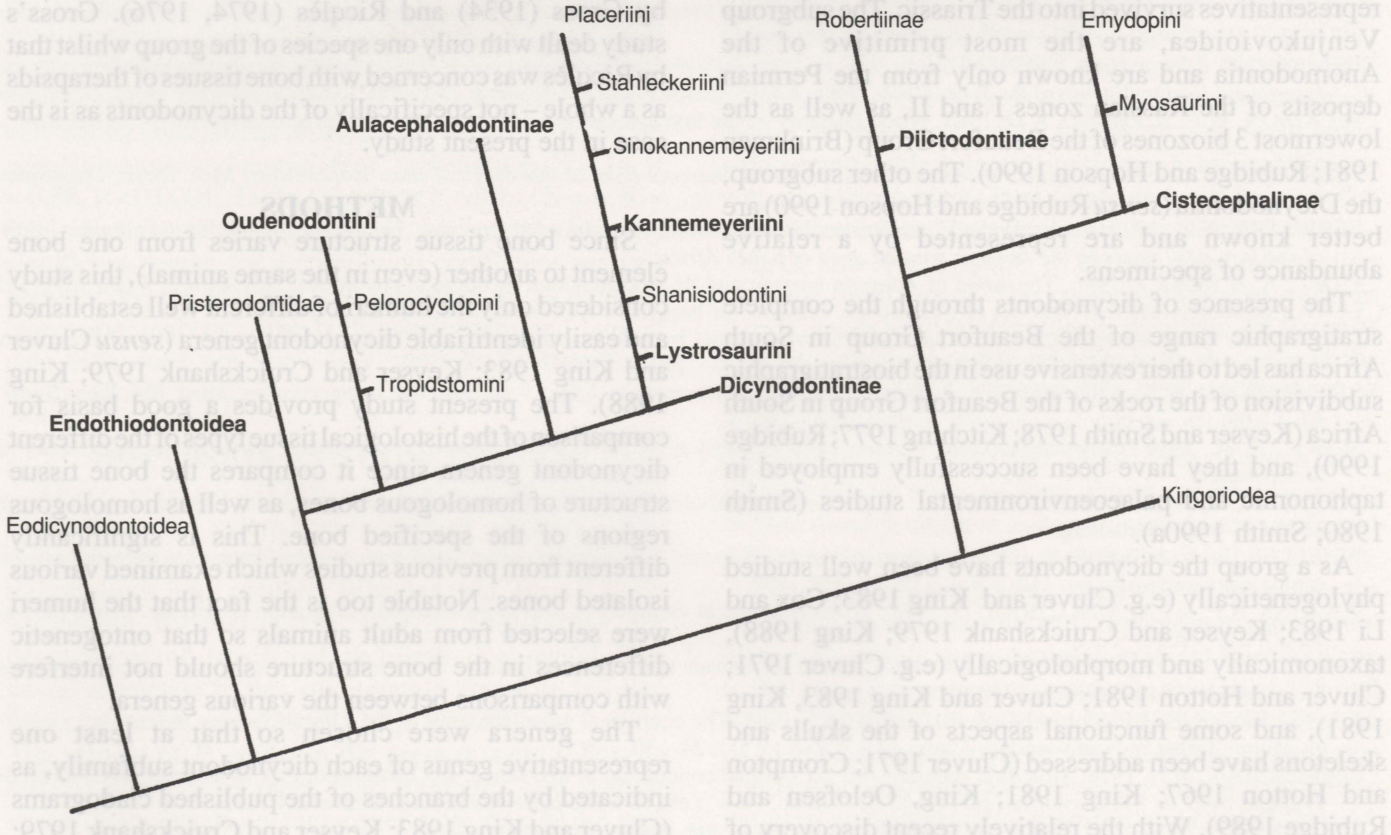

Figure 1: Cladogram of the dicynodonts (after King 1988). Bold indicates taxa sampled.

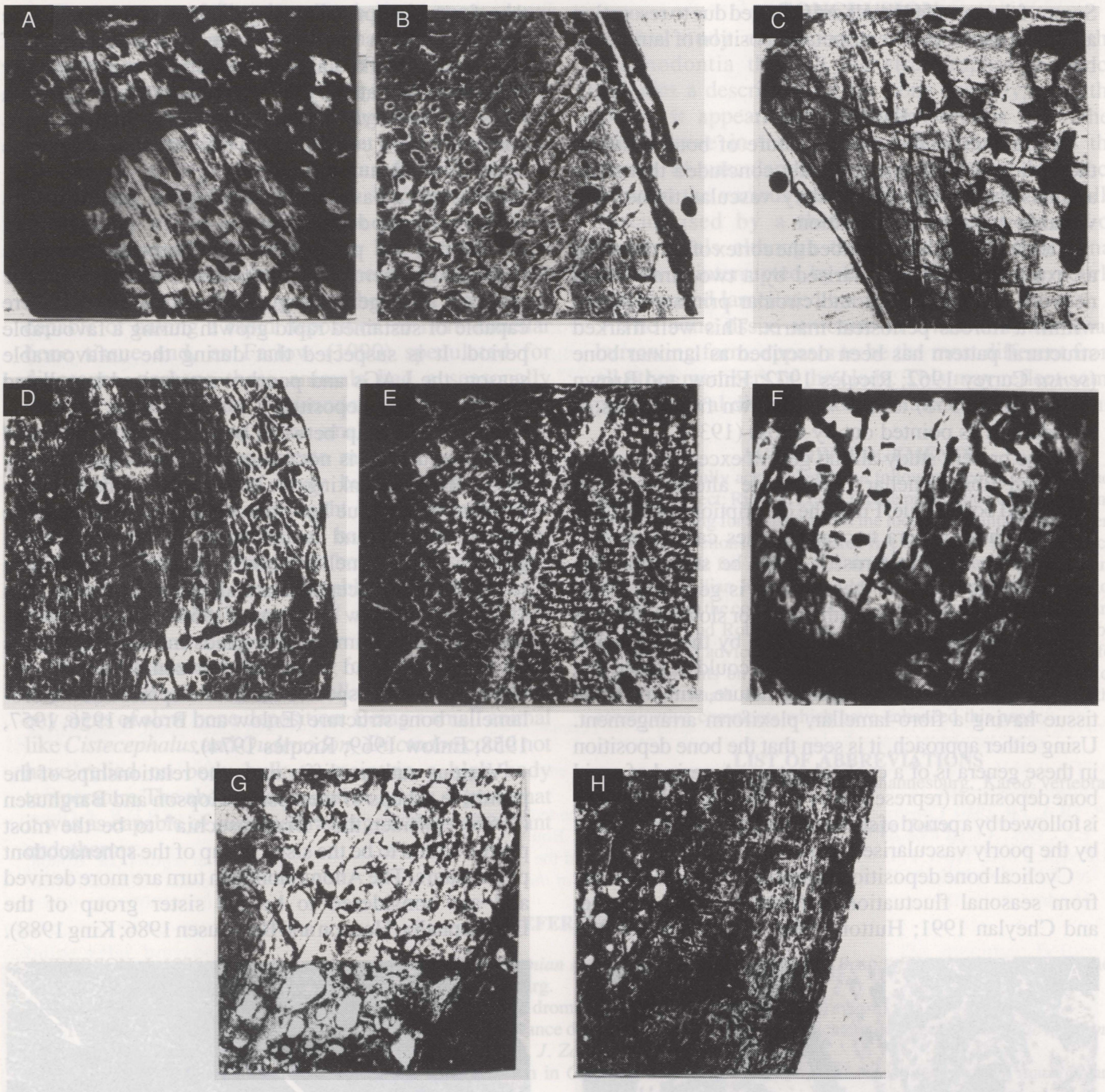

Figure 2: Transverse sections of humeri of various dicynodont genera showing the general nature of the compacta. Magnification 128X. *A. Endothiodon; B. Dicynodon; C. Cistecephalus; D. Oudenodon; E. Diictodon; F. Aulacephalodon; G. Kannemeyeria; H. Lystrosaurus.*

deposition of lines of arrested growth (LAG) and poorly vascularised, lamellated tissue (Figure 2, Figure 3A).

The degree of vascularisation of the bones of the different genera varies. The vascular canals are predominantly longitudinally orientated primary osteons, although many radial and circumferential anastomoses occur, resulting in a plexiform or sub-plexiform pattern in the tissue (Ricqlès 1974, 1976). Many of the perimedullary osteons showed enlarged resorption cavities, some having a layer of lamellated circumferential bone deposition, although completely formed secondary osteons were not commonly observed. Sharpey's fibres are present in the humeri of all the genera, although in *Aulacephalodon* these radially orientated fibres are more abundant and therefore highly conspicuous.

Diictodon is significantly different from all the other genera examined. In this case the compact bone of the humeri consisted only of fibro-lamellar bone tissue (Figure 2E). Numerous longitudinally arranged primary osteons embedded in a woven bone matrix occur (Figure 3B). Some radial and circumferential anastomoses occur, leading to a plexiform type of arrangement (Ricqlès 1974). There is no evidence of bone deposition slowing down or being interrupted by lines of arrested growth.

Some of the vascular canals are enlarged due to resorption and show the onset of centripetal deposition of lamellated bone.

DISCUSSION

In previous studies on the nature of bone tissue in therapsids, it has been generally concluded that these animals exhibited a moderately vascular tissue with variable structural organisation.

Ricqlès (1972) has described the cortex of dicynodonts as extremely well vascularised by a two-dimensional network of longitudinal and circular primary osteons within a fibrous periosteal matrix. This well marked structural pattern has been described as laminar bone (*sensu* Currey 1962; Ricqlès 1972; Enlow and Brown 1956, 1957, 1958) and is well known from bones of artiodactyls as pointed out by Gross (1934).

In the present study all the genera except *Diictodon*, exhibited fibro-lamellar bone tissue alternating with lamellated bone tissue. From the descriptions of the bone tissue of these genera two approaches can be used to describe the bone patterns: it could be stated that the humeral bone tissue of these genera is generally fibro-lamellar plexiform tissue with pauses or slowing down in the bone deposition rate represented by the LAGs and lamellated tissue. On the other hand it could be stated that the bone tissue is lamellar-zonal in nature, with the zonal tissue having a fibro-lamellar, plexiform arrangement. Using either approach, it is seen that the bone deposition in these genera is of a cyclical nature. A period of rapid bone deposition (represented by the fibro-lamellar tissue), is followed by a period of slow bone deposition (represented by the poorly vascularised annuli).

Cyclical bone deposition in reptiles is known to result from seasonal fluctuations (Castanet 1979; Castanet and Cheylan 1991; Hutton 1986; Ricqlès 1976). It is therefore appropriate to suggest that the bone tissue pattern found in the dicynodonts is also the result of seasonality. Marked alternating periods of wet and dry have been indicated by the presence of distinct growth rings in *Dadoxylon* (Anderson 1976; Snyman pers. comm. 1992), a conifer which occurs commonly in the rocks of the Beaufort Group.

Although a basic cyclic histological pattern occurs in the dicynodont humeri, as in present day ectotherms, the presence of the fibro-lamellar bone tissue and numerous primary osteons in a woven bone matrix in some genera suggests that these animals were capable of sustained rapid growth during a favourable period. It is suspected that during the unfavourable season, the LAGs and poorly vascularised lamellated bone tissue was deposited.

The relationship between bone tissue structure and thermoregulation is not a direct one and consequently any discussion linking the two is speculative. Fibro-lamellar bone tissue has often been considered a tissue formed rapidly and is indicative of rapid sustained growth. Fibro-lamellar bone in therapsids has been recognised in dinocephalians and eotheriodonts (Ricqlès 1974, 1976; Enlow and Brown 1956). These are of the oldest and most primitive therapsids known. Pelycosaurs on the other hand have lamellar-zonal bone tissue, although in some species the neural spines show fibro-lamellar bone structure (Enlow and Brown 1956, 1957, 1958; Enlow 1969; Ricqlès 1974).

Various authors differ as to the relationships of the primitive groups of therapsids. Hopson and Barghusen (1986) consider the "Biarmosuchia" to be the most primitive and to be the sister group of the sphenacodont pelycosaurs. The Anomodontia in turn are more derived and are considered to be the sister group of the Dinocephalia (Hopson and Barghusen 1986; King 1988).

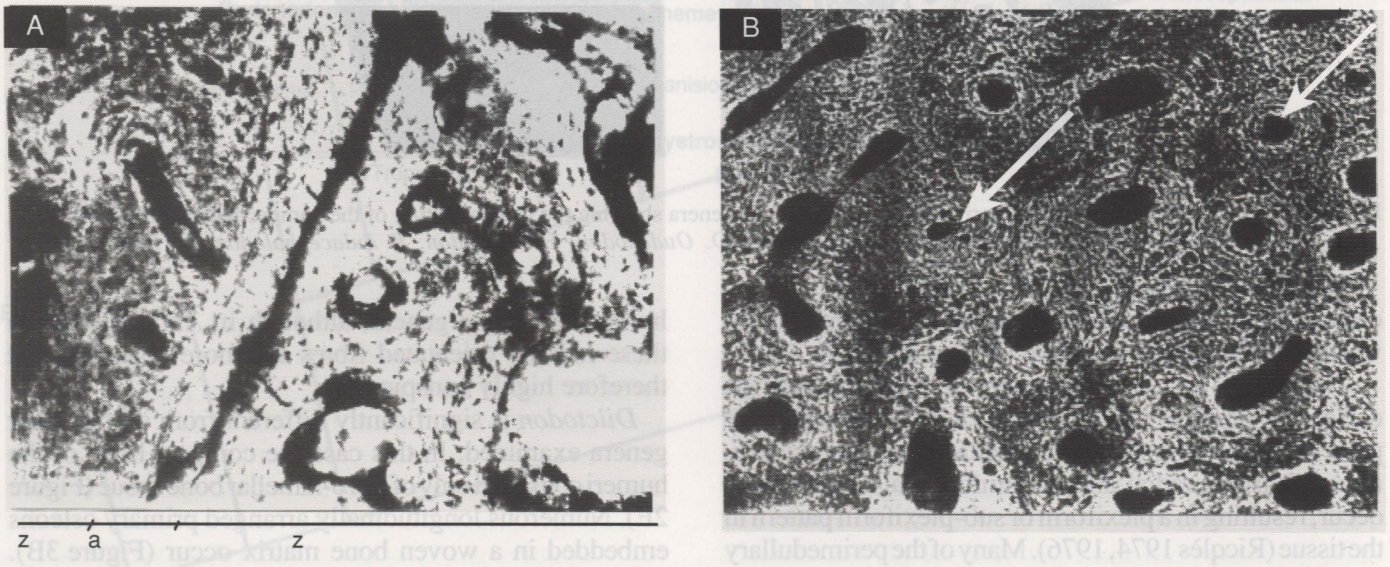

Figure 3: A. Transverse section of the humerus of *Kannemeyeria*. Labels indicate an annulus (a) and zones (z) of the compacta. Magnification 410X.
B. Transverse section of the humerus of *Diictodon*. Arrows indicate primary osteons embedded in the woven bone matrix. Magnification 410X.

The presence of fibro-lamellar bone in anomodonts suggests that they are capable of having rapid growth periodically. Mathematically derived models of the energy budgets (Spotila 1980; Tracy and Turner 1986) and thermoregulatory studies of large reptiles (McNab and Auffenberg 1976) suggest that under favourable conditions, a large body size can be effective in maintaining a faily constant high body temperature. Perhaps *Lystrosaurus, Dicynodon, Aulacephalodon, Endothiodon*, and *Kannemeyeria,* being fairly large animals themselves, behaved as inertial homeotherms during the favourable season. They were therefore capable of having a rapid deposition of fibro-lamellar bone tissue and, as Farlow (1990) speculated for dinosaurs, perhaps these animals had a seasonally variable metabolic rate. *Oudenodon* and *Cistecephalus* on the other hand tend to be smaller genera and it is unlikely that they were able to maintain a high body temperature because of body bulk. Smith (1990b) suggested that *Oudenodon* might have burrowed, and *Cistecephalus* is suspected of having been fossorial (Cluver 1978). Assuming that both of these animals lived in burrows they would be able to maintain a high body temperature because of stable temperature underground.

Diictodon, a known burrowing form (Smith 1987), on the other hand exhibits fibro-lamellar bone tissue without any signs of slow bone deposition. Being a small animal like *Cistecephalus* and *Oudenodon, Diictodon* could not have relied on body bulk to maintain a high body temperature.The absence of annuli or LAGs suggest that it was as capable of sustained rapid growth as are extant endotherms.

CONCLUSION

This study of the bone tissue structure of the Dicynodontia through the stratigraphic sequence provides a description of the bone tissue types in the group. It appears that the Dicynodontia are rather conservative in their bone tissue structure with the degree of vascularisation being the main difference between the various genera. Their bones are typically vascularised by a three dimensional network of bloodvessels although this rapid bone depositional pattern is interrupted by the deposition of the poorly vascularised lamellated bone tissue.

The bone tissue structure of *Diictodon*, the small burrowing form, appears to be the most different from all other members of the clade. This may reflect some physiological difference or specialisation of the genus.

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LIST OF ABBREVIATIONS

BP/I/ Bernard Price Institute, Johannesburg, Karoo vertebrate collection
SAM South African Museum, Cape Town.

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