

Biological aspects of the Permian dicynodont *Oudenodon* (Therapsida: Dicynodontia) deduced from bone histology and cross-sectional geometry

Jennifer Botha

South African Museum, Iziko Museums of Cape Town, P.O. Box 61, Cape Town, 8000 South Africa.
E-mail: jbotha@iziko.org.za

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Bone histology and cross-sectional geometry were used to examine the growth patterns and lifestyle habits of the Late Permian dicynodont, *Oudenodon*. Several limb bones were analysed, revealing rapidly deposited fibro-lamellar bone, interrupted by annuli or sometimes Lines of Arrested Growth. Peripheral slowly deposited parallel-fibred bone was observed in several elements. It is suggested that the initial growth of *Oudenodon* was rapid during the favourable growing season, but decreased or sometimes ceased completely during the unfavourable season. Growth was cyclical and may have been sensitive to environmental fluctuations. The slowly forming parallel-fibred bone towards the sub-periosteal surface in several elements indicates a permanent transition to slow growth and may reflect the onset of sexual maturity. Bone cross-sectional geometry results reveal a markedly thick cortex, indicating a possible modification for digging. These cross-sectional geometry values, in conjunction with the limb morphology, suggest that *Oudenodon* was fossorial.

Keywords: Therapsida, *Oudenodon*, bone histology, growth patterns.

INTRODUCTION

The Dicynodontia are recognized as the most successful herbivorous therapsid group of the Late Permian (King 1990). They radiated into several, varied ecological niches and became the most numerous herbivorous tetrapods by the end of this period (Hotton 1986; King 1990). As a result of the highly varied and widespread nature of this group, the dicynodonts have received much attention in the literature, both systematically and morphologically (e.g. Angielczyk 2001; Cluver & Hotton 1983; Cluver & King 1983; Hotton 1986; Keyser 1975; Keyser & Cruickshank 1979; Rubidge & Sidor 2001). The focus of previous studies has been on cranial descriptions, locomotory modifications and masticatory systems (e.g. Cluver 1971; Cluver & Hotton 1983; Cluver & King 1983; Cox 1998; Kemp 1982; Keyser 1975; King 1996; King *et al.* 1989), while other biological traits, such as growth patterns and lifestyle habits, have been less extensively studied.

A few studies, such as those of Chinsamy & Rubidge (1993), Enlow and Brown (1957) and Ricqlès (1972, 1976, 1991), have used bone histology to deduce the growth patterns of several dicynodont genera. However, these studies were not comprehensive examinations and thus provided limited information. In addition, only one type of element was usually examined, making it difficult to deduce generic patterns of growth.

The lifestyle habits of a few dicynodonts such as *Lystrosaurus* (Brink 1951; Broom 1903; Groenewald 1991; King 1991; King & Cluver 1991), *Cistecephalus* (Cluver 1978) and *Diictodon* (Ray & Chinsamy 2003; Smith 1987) have been examined using burrow casts and functional anatomy to suggest specific modes of life.

Oudenodon was a medium-sized dicynodont (skull length from 100–300 mm) whose skeletal remains have been excavated from Late Permian deposits in South

Africa (Cluver & Hotton 1983). The morphology of the skull has been described in detail (Broom 1912; Cluver & Hotton 1983; Cluver & King 1983; Keyser 1975; Owen 1860) and distinctive features include a lack of teeth in both the upper and lower jaws, a deep and relatively narrow secondary palate, a sharp maxillary crest behind the caniniform process, the absence of maxillary tusks and narrow dentary tables on the dentaries (Cluver & Hotton 1983; Cluver & King 1983).

Although the cranial morphology of *Oudenodon* (Cluver & Hotton 1983; Cluver & King 1983; Keyser 1975;) and to a lesser extent the postcranial skeleton (Broom 1901), have been examined, little pertaining to the biology of this genus has been discussed. Thus, there is inadequate information regarding the growth patterns and lifestyle habits of *Oudenodon* for deducing its overall biology.

Bone histology is a well-established technique for examining growth patterns and lifestyle habits of extinct animals (e.g. Enlow & Brown 1957; Reid 1996; Ricqlès 1976, 1980). The bone histology of *Oudenodon* has previously been described by Ricqlès (1972) and Chinsamy & Rubidge (1993). Ricqlès (1972) examined a humerus and a femur, whereas Chinsamy & Rubidge (1993) used a humerus to interpret the growth patterns of *Oudenodon*. Although informative, both descriptions were brief and neither study considered inter-elemental histovariability. Although, Ricqlès (1972) examined a humerus and a femur, histological variation between the two elements was not discussed. It is becoming increasingly evident that inter-elemental histovariability should be considered when deducing the overall growth patterns of a genus (Botha 2002; Curry 1999; Horner *et al.* 1999, 2000; Starck & Chinsamy 2002; Ray *et al.*, in press).

A technique known as bone cross-sectional geometry can be used in conjunction with bone histology analysis to

Table 1. *Oudenodon* specimens used in this study and their localities. All specimens were recovered from the *Dicynodon* Assemblage Zone, Teekloof Formation, Beaufort Group of South Africa. SAM-PK-K refers to South African Museum, Iziko Museums of Cape Town, South Africa. SAM-PK-K4807 and SAM-PK-10019 consist of several disarticulated elements representing several individuals.

Locality	Specimen number	Skeletal element	Region sectioned
Richmond	SAM-PK-K4807a	Femur	Midshaft, proximal
	SAM-PK-K4807b	Femur	Midshaft, proximal
	SAM-PK-K4807c	Femur	Proximal
	SAM-PK-K4807d	Fibula	Midshaft, proximal
	SAM-PK-10019a	Femur	Midshaft, proximal
	SAM-PK-10019b	Tibia	Proximal
	SAM-PK-10019c	Fibula	Midshaft, proximal
	SAM-PK-10019d	Humerus	Distal
	Murraysburg	SAM-PK-11141	Femur

provide information regarding an animal's lifestyle. Studies have shown that a direct relationship exists between an animal's lifestyle and the structural design of its bones (Bou *et al.* 1990; Fish 1993; Stein 1989; Wall 1983). For example, fossorial animals have thick, relatively short limb bones with a high force moment of their forelimb muscles for digging (Bou *et al.* 1990; Casinos *et al.* 1993). Equally, the bones of sirenians, cetaceans, crocodylians and certain aquatic birds have extremely high bone densities to counteract buoyancy (Buffr enil *et al.* 1990; Hua & Buffr enil 1996). Osteological modifications of an extinct animal can therefore provide valuable information for determining the type of habitat an animal occupied.

In a study conducted by Wall (1983), who examined the cortical thickness (bone wall) of 49 mammalian genera, it was found that most of the aquatic mammals studied had a significantly higher limb bone density than that of the terrestrial mammals. He proposed that if the compact bone wall exceeds 30% of the average diameter, the animal is aquatic or at least semi-aquatic, possibly as an adaptation to counteract buoyancy (Wall 1983).

Magwene (1993) studied the bone cross-sectional geometry of several crocodylian, lizard, non-mammalian therapsid and mammalian femora and found that, on average, non-mammalian therapsids and mammals have thinner bone walls compared to crocodylians and lizards. He argued that non-mammalian therapsids and mammals have lighter bones as a weight-saving modification because they are subject to greater bending and torsional stresses due to their higher activity levels. In contrast, crocodylian and lizard limb bones are more robust and stiff as they have less active lifestyles (Magwene 1993). Magwene examined each group collectively, but when the results are examined according to lifestyle, 75% of the semi-aquatic crocodylians and lizards and all of the arboreal/fossorial lizards studied had a cortical thickness of more than 30%. Similarly, 38% of the fossorial/arboreal mammals had a cortical thickness that exceeded 30%, while several of the other fossorial mammals had a cortical thickness that was at least 28%. Thus, Wall's '30%' threshold appears adequate for indicating the approximate minimum cortical thickness required for aquatic lifestyles, as well as for fossorial or arboreal lifestyles. Thus, bone cross-sectional geometry can be used to provide further information regarding the lifestyle habits of *Oudenodon*.

MATERIALS AND METHODS

The *Oudenodon* study elements, which were positively identified from associated cranial material, include several limb bones (humerus, femora, tibiae, fibulae). All specimens were recovered from the *Dicynodon* Assemblage Zone, Balfour/Teekloof Formation, Beaufort Group of South Africa (Rubidge 1995).

Limb bones were selected as they are the most readily preserved compared to other elements and they show the least secondary remodeling in the midshaft region (Francillon-Vieillot *et al.* 1990). Limb bones therefore provide the best record of the type of growth exhibited by the animal. Several different types of limb bones were included to ensure that inter-elemental histovariability was considered. The elements are from different individuals and represent various ontogenetic stages. Owing to their large size (approximate range between 90 and 160 mm in length) it is unlikely that any of the study elements represent juvenile individuals, they probably all represent subadult or adult individuals.

Most of the limb bones were transversely sectioned in the midshaft region. Proximal or distal regions were also sectioned where possible, depending on the particular element (Table 1). Each region of bone to be sectioned was embedded in the clear resin, Impset 21, to prevent the bone from disintegrating during the process. Once the resin had set, the area to be sectioned was cut using a Blanes diamond-tipped saw. The cut surface was polished until smooth using a Logitech LP50 lapping machine and then mounted onto a petrographic glass slide using the resin adhesive, Epotek. Pressure was then applied to the sections to eliminate any bubbles. A thin section, approximately 35 μm thick, was then cut using a Logitech CS10 cut-off diamond-tipped saw. The resulting thin sections were polished until smooth with the Logitech LP50 lapping machine and examined using a Leitz Laborlux K compound microscope. The bone histology was photographed using a Nikon FinePix S1 Pro digital camera.

Thin sections were also used to measure the cortical thickness of the midshaft region of each bone. The cortical thickness was measured in microns at four equidistant radial positions using an eyepiece micrometer in the Leitz Laborlux K compound microscope at $\times 40$ magnification. The mean of these four measurements was divided by the mean bone diameter and the final value expressed as a percentage.

RESULTS

Bone histology

A comprehensive analysis of the bone histology of the *Oudenodon* postcrania revealed moderately vascularized fibro-lamellar bone tissue, becoming parallel-fibred towards the periphery in some cases. Interruptions by annuli of lamellar bone or Lines of Arrested Growth (LAGs) were noted throughout the cortex in all elements. Some variation was noted between the different types of elements and will be described in detail below.

Femur. (SAM-PK-11141, SAM-PK-K4807a, SAM-PK-K4807b, SAM-PK-K4807c, SAM-PK-10019a). The femora contain small medullary cavities, which are surrounded by notably thick cortices. The primary bone tissue is fibro-lamellar bone with longitudinally oriented primary osteons (Fig. 1A), but a laminar network is present in SAM-PK K4807b and SAM-PK-10019a (Fig. 1B). Annuli of lamellar bone or LAGs interrupt the fibro-lamellar bone at intervals. The globular osteocyte lacunae in the fibro-lamellar bone become flattened in the annuli. They have branched canaliculi, which radiate out in all directions. Vascularization is generally moderate, decreasing towards the periphery in femora SAM-PK-11141, SAM-PK-K4807a and SAM-PK-K4807c where the overall bone tissue organization becomes parallel-fibred bone (Fig. 1C). In these regions of parallel-fibred bone, the sparse vascular canals become simple and the annuli are sometimes multiple (i.e. several annuli clustered together). Secondary remodeling with numerous secondary osteons is observed surrounding the medullary cavity of femur SAM-PK-K4807b (Fig. 1D). Sharpey's fibres are observed in femur SAM-PK-K4807a (Fig. 1E).

Tibia. (SAM-PK-10019b). The tibia consists of a markedly thick cortex and a free medullary cavity is absent. Trabeculae, lined with endosteal lamellar bone, fill the entire medullary cavity. The primary tissue consists of highly vascularized fibro-lamellar bone, which is interrupted by annuli (Fig. 2). Large, longitudinally oriented primary osteons, which form a laminar network in places, decrease in diameter towards the sub-periosteal surface.

Fibula. (SAM-PK-10019c, SAM-PK-K4807d). The medullary cavities are completely filled with bony trabeculae (Fig. 3A). Secondary remodeling, with large resorption cavities is extensive. The moderately vascularized fibro-lamellar bone tissue contains distinct annuli of lamellar bone tissue, but becomes poorly vascularized parallel-fibred bone at the periphery of SAM-PK-10019c (Fig. 3B). Longitudinally oriented primary osteons in the fibro-lamellar bone are replaced by small, simple vascular canals that are sparsely distributed in the parallel-fibred region. Distinct Sharpey's fibres are noted in SAM-PK-10019c (Fig. 3B) and SAM-PK-K4807d.

Humerus. (SAM-PK-10019d). The bone tissue consists of fibro-lamellar bone interrupted by annuli, similar to the rest of the study elements (Fig. 4). LAGs are absent. The tissue is highly vascularized near the medullary cavity, but becomes moderately vascularized towards the sub-periosteal surface. Longitudinal primary osteons characterize the fibro-lamellar bone. Secondary remodel-

ing is extensive and a free medullary cavity is absent, which may be due to the section being taken from a more distal region compared to the other elements.

Bone cross-sectional geometry

The femur SAM-PK-K4807a has a cortical thickness of 46% and the cortical thickness of both femora SAM-PK-K4807b and SAM-PK-10019a is 39%. A mid-diaphyseal region was not available for femur SAM-PK-K4807c. Although midshaft regions of the fibulae were available for study, the medullary cavities were completely filled with bony trabeculae, making it impossible to discern a distinct transition between trabeculae and compact bone. Thus, the midshaft cortical thickness of these elements was not measured. Similarly, a free medullary cavity was absent from tibia SAM-PK-10019b. The cortical thickness of the humerus SAM-PK-10019d was not measured as a midshaft region was unavailable.

DISCUSSION

Bone histology

Histological examination of the bones revealed rapidly deposited fibro-lamellar bone, indicating rapid growth. The primary bone tissue organization varied from laminar to longitudinally oriented primary osteons. Annuli of lamellar bone or LAGs were observed interrupting the fibro-lamellar bone, which indicates that growth slowed down or even ceased periodically. These observations agree with the findings of Ricqlès (1972) and Chinsamy & Rubidge (1993), although Ricqlès did not refer to any annuli or LAGs in the humerus. Ricqlès (1972) noted that the humerus used in his study was highly vascularized, which may indicate that this element was from a juvenile individual and growth may have been too rapid to exhibit growth rings.

Although the overall bone tissue pattern observed in this study agrees with the findings of Ricqlès (1972) and Chinsamy & Rubidge (1993) there are some variations not previously noted. The most marked and significant variation is the presence of slowly forming parallel-fibred bone at the periphery of several femora (SAM-PK-11141, SAM-PK-K4807a, SAM-PK-K4807c) and a fibula (SAM-PK-10019c). This bone tissue indicates a marked decrease in overall growth and represents a permanent transformation to slow growth. Ricqlès (1972) did not note parallel-fibred bone in his examination of the femur. A transition from rapidly to slowly forming bone tissue has been reported in the non-mammalian cynodonts *Procynosuchus* (Ray *et al.*, in press) and *Thrinaxodon* (Botha & Chinsamy, in press). Such a feature has been documented in extant animals as well and it is suggested that this transition represents the onset of sexual maturity (Castanet & Baez 1991; Reid 1996; Sander 2000; Botha & Chinsamy, in press; Ray *et al.*, in press). The parallel-fibred bone in *Oudenodon* may represent the onset of sexual maturity whereby growth continued after sexual maturity was reached, but at a much slower rate.

It is suggested from the bone histology that femora SAM-PK-11141, SAM-PK-K4807a and SAM-PK-K4807c

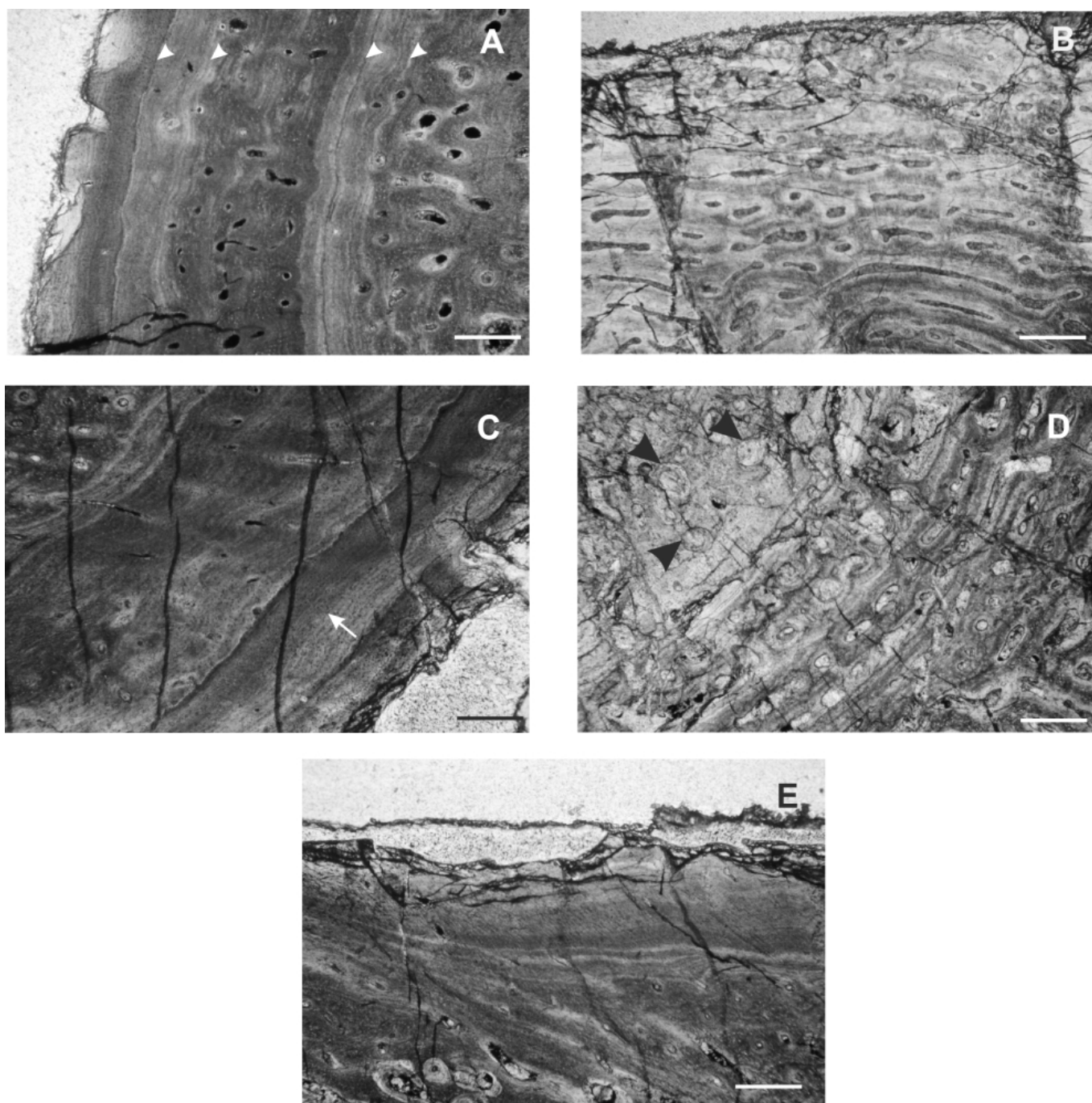


Figure 1. Bone histology of the *Oudenodon* femora. **A**, SAM-PK-K4807c, showing fibro-lamellar bone with longitudinally oriented primary osteons, interrupted by multiple annuli and LAGs (arrowheads). Parallel-fibred bone occurs at the periphery. Scale bar = 636 μm . **B**, SAM-PK-10019a, showing fibro-lamellar bone in a lamellar network. Scale bar = 636 μm . **C**, SAM-PK-K4807a, showing fibro-lamellar bone becoming poorly vascularized parallel-fibred bone towards the sub-periosteal surface (arrow). Scale bar = 610 μm . **D**, SAM-PK-K4807b, showing secondary osteons in the peri-medullary area (arrowheads). **E**, SAM-PK-K4807a, showing Sharpey's fibres. Scale bar = 635 μm .

represent adult individuals, whereas femora SAM-PK-K4807b and SAM-PK-10019a represent subadult individuals. Parallel-fibred bone is absent from the latter two femora and although the vascularization is moderate, there is no decrease in vascular density towards the periphery, thus indicating continued active growth at the time of death. The moderate vascularization and abundant secondary osteons suggest that these two femora do not represent juvenile individuals, but the absence of peripheral, slowly forming parallel-fibred bone indicates that overall growth had not yet begun to slow down.

The highly vascularized primary tissue with abundant primary osteons and absence of parallel-fibred bone in tibia SAM-PK-10019b suggests that this element is representative of an early subadult. The fibulae exhibit extensive secondary remodeling and are moderately vascularized. Fibula SAM-PK-10019c exhibits peripheral parallel-fibred bone, indicating that the overall growth rate had begun to slow down. These characteristics suggest that this element represents an adult individual. As parallel-fibred bone is absent from fibula SAM-PK-K4807d, it is probably a subadult. There is a slight decrease in

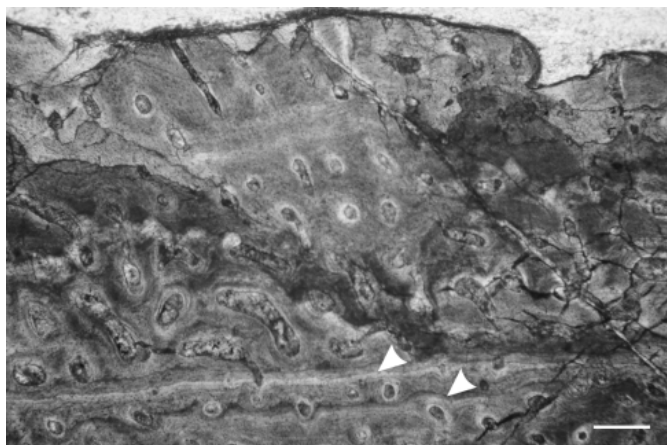


Figure 2. *Oudenodon* tibia SAM-PK-10019b, showing highly vascularized fibro-lamellar bone alternating with annuli of lamellar bone (arrowheads). Scale bar = 454 μm .

vascularization towards the sub-periosteal surface in humerus SAM-PK-10019d, but LAGs and parallel-fibred bone are absent. The presence of annuli and absence of LAGs indicates that growth slowed down periodically, but did not cease. These characteristics suggest that the humerus represents a subadult.

Sharpey's fibres were observed in several of the femora and fibulae. Chinsamy & Rubidge (1993) also noted Sharpey's fibres in the *Oudenodon* humerus in their study. It is possible that the bones of *Oudenodon* had an unusually large proportion of Sharpey's fibres. As Sharpey's fibres represent areas of muscle insertion (Leeson & Leeson 1981), it is possible that *Oudenodon* had well-developed muscles to cope with digging. However, Chinsamy & Rubidge (1993) also noted Sharpey's fibres in all the dicynodont humeri in their study. Thus, it is also possible that distinct Sharpey's fibres are a common feature of dicynodont bone histology and most dicynodonts may have had particularly well-developed musculature to cope with their semi-erect posture. Such prominent Sharpey's fibres have not yet been noted in non-mammalian cynodonts (Botha 2002) or gorgonopsians and therocephalians (Ray *et al.*, in press). It is also possible that the larger dicynodonts in Chinsamy & Rubidge's (1993) study had substantial muscles and thus distinct Sharpey's fibres to cope with their large size. More studies on dicynodont bone histology, including multiple element analyses, are required to deduce whether this is the case.

Inter-elemental histovariability

It is becoming increasingly apparent, particularly from more recent studies including different types of elements, that inter-elemental histovariability has a significant effect on interpreting generic patterns of growth (Botha 2002; Curry 1999; Horner *et al.* 1999, 2000; Starck & Chinsamy 2002; Ray *et al.*, in press). It is therefore essential to include several different types of elements in a bone histological study, although it is recognized that this may prove difficult at times when fossil preservation is poor.

Although the overall bone tissue organization is similar between the different types of *Oudenodon* elements in this study, some inter-elemental histological variation was

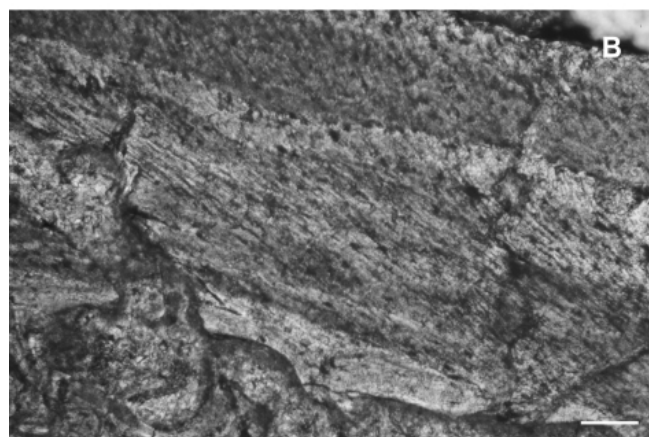
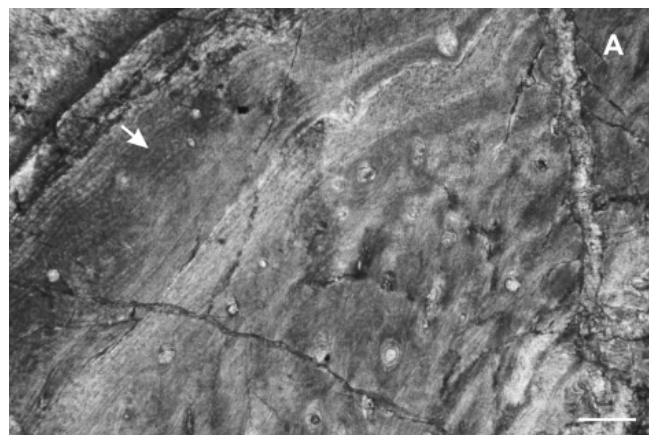


Figure 3. Bone tissue patterns of the *Oudenodon* fibulae. **A**, SAM-PK-10019c, fibro-lamellar bone with longitudinally oriented primary osteons, becoming parallel-fibred bone with simple vascular canals towards the periphery. Scale bar = 434 μm . **B**, High magnification, showing prominent Sharpey's fibres. Scale bar = 163 μm .

noted. For example, parallel-fibred bone was not observed in the humerus SAM-PK-10019d, but a midshaft region was not available for study and only the distal metaphyseal region could be examined. It is possible that the midshaft region, which would have exhibited more primary tissue, contained parallel-fibred bone. This is unlikely however, as the parallel-fibred bone occurs at the periphery, a region which could be observed in the humerus. Furthermore, Ricqlès (1972) did not document



Figure 4. Bone histology of the *Oudenodon* humerus SAM-PK-10019d, showing high vascularization in the inner and mid cortex, which decreases slightly at the sub-periosteal surface. Two annuli (arrowheads) can be seen interrupting the fibro-lamellar bone. Scale bar = 515 μm .

Table 2. Cortical thickness of the *Oudenodon* elements compared with other non-mammalian therapsids (represented as a percentage). *Scylacops* and *Pristerognathus* values were taken from Ray *et al.* (in press) and the *Aelurognathus* value was taken from Magwene (1993). Note that the *Pristerognathus* and *Aelurognathus* femora have a markedly lower cortical thickness compared to the *Oudenodon* femora. *Scylacops*, *Pristerognathus* and *Aelurognathus* were designated as adults (Magwene 1993; Ray *et al.*, in press).

Genus	Specimen number	Skeletal element	Cortical thickness (%)
<i>Oudenodon</i>	SAM-PK-10019a	Femur	39
	SAM-PK-K4807a	Femur	45
	SAM-PK-K4807b	Femur	39
<i>Scylacops</i>	SAM-PK-10188	Ulna	16
		Radius	24
<i>Pristerognathus</i>	SAM-PK-1157	Radius	18
		Femur	15
		Tibia	25
		Fibula	25
<i>Aelurognathus</i>		Femur	21

any parallel-fibred bone in the *Oudenodon* humerus in his study, neither was it noted in the study conducted by Chinsamy & Rubidge (1993). It is possible that both these elements as well as the humerus in this study were ontogenetically too young and thus depositing bone too fast to exhibit slowly forming parallel-fibred bone tissue. It is also possible that this may be an example of differential rates of bone growth between the various limb bones of a skeleton. It was noted in previous studies on non-mammalian cynodonts that proximal limb bones (i.e. humerus, femur) grew more quickly than distal limb bones (radius, ulna, tibia, fibula) (Botha 2002; Ray *et al.*, in press). Distal limb bones were less vascularized and annuli and/or LAGs were more numerous and distinct compared to those in the proximal limb bones. These characteristics indicate that the distal limb bones were growing more slowly than the proximal limb bones. Similarly, Starck & Chinsamy (2002), in a study on extant Japanese quail (*Coturnix japonica*), found that the mid-diaphyseal regions of the humerus and femur increased in cross-sectional thickness faster than the radius, ulna or tarsometatarsus. The humerus of *Oudenodon* may be the last limb bone within an individual to exhibit parallel-fibred bone.

Bone cross-sectional geometry

Based on a specimen found in a terminal burrow, previous studies have suggested that *Oudenodon* was fossorial. However, the suggestion was made on the basis of a juvenile specimen that had been recovered from a burrow at the base of the *Tropidostoma* Assemblage Zone, Teekloof Formation, Beaufort Group, South Africa (Smith 1987). The identification of this juvenile specimen is uncertain and *Oudenodon* is as yet, unknown from the *Tropidostoma* Assemblage Zone.

The bone cross-sectional geometry results in this study reveal a relatively thick cortex and may indicate a fossorial lifestyle. All the femoral cortical thickness values exceed 30%. Although the cortical thickness of the tibia and fibulae could not be quantified, the profusion of bony trabeculae within the medullary cavities would have provided extra strength and support to these elements. When comparing these results with other non-mammalian therapsids, *Oudenodon* exhibits a notably thick bone

wall (Table 2). Few cortical thickness values have been documented in the literature, which makes comparison difficult, but it can be seen from Table 2 that the cortical thickness of the *Oudenodon* femora is notably higher than that of the *Pristerognathus* (Ray *et al.*, in press) or *Aelurognathus* (Magwene 1993) femora. Although only ulna and radial values are available for the gorgonopsian *Scylacops*, neither value exceeds 30%. These results indicate that *Oudenodon* exhibits a particularly thick bone wall, possibly for a specific mode of life. If these results are examined in conjunction with the morphological modifications described by Broom (1901), they suggest that *Oudenodon* was fossorial. Broom (1901) described the postcranial skeleton of *Oudenodon* and it appears to exhibit modifications for a digging or fossorial lifestyle. The robust humerus has a well-developed delto-pectoral crest, the olecranon process on the ulna is greatly elongated and the radius and ulna are distally flattened. Furthermore, the broad, flat manus forms a large, flattened surface area and the phalanges end in large, distinct claws (Broom 1901). These morphological characteristics are typical of an animal that digs or burrows (Bargo *et al.* 2000; Yalden 1966). A positively identified specimen in a burrow complex could confirm this suggestion.

Implications for *Oudenodon* biology

The alternating bone tissue organization between rapidly deposited fibro-lamellar bone and slowly deposited lamellar bone within the annuli indicates that the growth of *Oudenodon* was cyclical. This bone tissue pattern is similar to those of *Dicynodon*, *Aulacephalodon*, *Endothiodon*, *Cistecephalus* and *Kannemeyeria* (Chinsamy & Rubidge 1993) as well as *Diictodon* (Ray & Chinsamy, in press). Experiments have revealed that seasonal fluctuations cause cyclical growth in extant reptiles (e.g. Castanet *et al.* 1993; Hutton 1986) and it is suggested that the cyclical growth patterns observed in these dicynodonts is due to a sensitivity to environmental fluctuations (Chinsamy & Rubidge 1993; Ray & Chinsamy, in press). As *Oudenodon* experienced a semi-arid climate with seasonal rainfall (Smith *et al.* 1993), it is possible that growth was influenced by seasonal fluctuations whereby the growth rate decreased or ceased during the unfavourable growing season. If *Oudenodon* was in fact fossorial, it may have

burrowed to escape harsh environmental conditions.

However, the peripheral parallel-fibred bone has not been noted previously in any dicynodont genus. Either this feature is unique to *Oudenodon* or it is generally found only in certain types of elements and will be revealed in other dicynodonts in future studies. It is also possible that previous studies have not examined elements that have been ontogenetically old enough to exhibit slowly forming parallel-fibred bone. Peripheral rest lines were not observed in any of the *Oudenodon* study elements, which suggests that growth continued throughout life, but at a much slower rate once sexual maturity was reached.

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