GROWTH PATTERNS DEDUCED FROM THE BONE HISTOLOGY OF THE CYNODONTS *DIADEMODON* AND *CYNOGNATHUS*

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ABSTRACT—*Diademodon* and *Cynognathus* were contemporary cynodonts that lived during the Early to Middle Triassic. Their fossilized remains are found in the same deposits and, in the absence of diagnostic cranial material, the postcranial skeletons of these animals are considered indistinguishable from one another. In this study the bone histology of *Diademodon* and *Cynognathus* was examined, using thin sections of several long bone elements. Distinctive histological patterns were recognized for each genus: the cortex of *Diademodon* is zonal, consisting of alternating bands of fibro-lamellar and lamellar bone tissue, whereas that of *Cynognathus* consists of uninterrupted fibro-lamellar bone tissue. The bone histology indicates that *Diademodon* had a cyclical growth strategy whereas *Cynognathus* grew continually, at a constant, rapid rate throughout the year. Quantification of the vascularization of the compacta using image analysis, has shown that the bone tissue of *Cynognathus* is significantly more vascularized than that of *Diademodon*. The marked differences in their bone histology and vascularization, have permitted the generic identification and distinction of postcranial material (limb bones) previously categorized as either *Cynognathus* or *Diademodon*. This study of *Diademodon* and *Cynognathus* is the first detailed examination of the bone histology of representatives of the Triassic Cynodontia. The characteristic patterns of bone histology in *Diademodon* and *Cynognathus* have directly revealed information about their growth strategies and has demonstrated the use of bone histology to distinguish between the genera when associated cranial material is absent.

INTRODUCTION

The radiation of the Cynodontia is generally regarded as one of the most significant events in therapsid history because it includes the ancestry of the mammals. *Diademodon* and *Cynognathus* are cynodonts that lived during the Early to Middle Triassic (Scythian to Early Anisian; Kitching, 1995), their remains being well represented in the *Cynognathus* Assemblage Zone in the Beaufort Group of Southern Africa. *Diademodon*, an omnivore, and *Cynognathus*, a carnivore, have very distinctive cranial and dental morphologies. Yet, their postcranial skeletons appear to be indistinguishable (Brink, 1955; Jenkins, 1971) except for slight differences, such as those in the neural spines and centra of the vertebral column (Brink, 1955). Because these animals were contemporaries, their remains are frequently found in the same fossil assemblages, which poses difficulty in distinguishing their postcrania when no associated cranial material is preserved.

The gross skeletal morphology of *Diademodon* (Seeley, 1894; Watson, 1911; Brink, 1955; Hopson, 1971; Grine, 1977; Grine et al., 1978) and *Cynognathus* (Seeley, 1908; Broom, 1911, 1913; Gregory and Camp, 1918) is reasonably well studied (Brink, 1955; Jenkins, 1971; Kemp, 1982), though very little is known about their biology. This study documents the bone histology and the histological variation within each genus, as well as ontogenetic changes in the bone. Bone histology has become increasingly significant in paleobiological studies of extinct vertebrates. Assessments regarding ontogeny, growth and various other aspects of the life history of animals can be directly deduced from the bone (Chinsamy and Dodson, 1995). Comparative studies of the bone histology of extinct and extant animals (e.g., Enlow and Brown, 1956; Ricqlès, 1969, 1976; Peabody, 1961; Castanet et al., 1988; Chinsamy 1991) have provided a wealth of information regarding the ontogeny, individual age, growth and, indirectly, the physiology of fossil animals.

This study represents the first detailed account of Triassic cynodont bone histology and provides a direct assessment of the growth strategies of *Diademodon* and *Cynognathus.*

MATERIALS AND METHODS

Long bones (humeri, femora, tibiae, fibulae) were used in this study as they are not extensively remodeled (particularly in the mid-shaft region) and therefore permit a reasonable assessment of an animal's ontogenetic growth pattern (Chinsamy and Dodson, 1995). In addition, Horner et al. (1999) found that LAG (lines of arrested growth) counts were more readily observed due to better preservation.

All thirteen skeletal elements examined in the study were excavated from the *Cynognathus* Assemblage Zone, Beaufort Group, South Africa (Table 1). Only postcranial material directly associated with cranial elements permitting identification of the particular genus were used in this study. Ten diagnostic *Diademodon* limb elements were collected from locations at Lady Frere, Burgersdorp, Aliwal North, and Rouxville, South Africa. Three diagnostic limb elements of *Cynognathus* were collected from Aliwal North, South Africa.

The specimens were photographed and the total length and mid-shaft diameters were measured (Table 1). The width of the proximal and distal regions were also measured for comparison between incomplete and complete specimens (Table 1). Thin sections were prepared according to the methodology of Chinsamy and Raath (1992) and were examined using a petrographic microscope. Image analysis, according to the method of Chinsamy (1993), was used to quantify the degree of vascularization of each section. Vascularization was quantified in the different skeletal elements of each genus, as well as between them. In addition, vascularity was quantified in juveniles and adults of *Diademodon.* Such measurements were standardized in the mid-cortical region of mid-shaft sections of each bone.

Institutional Abbreviations—BP/I/, Bernard Price Institute for Paleontological Research, Johannesburg, South Africa; **NMQR**, National Museum, Bloemfontein, South Africa; **SAM-**

TABLE 1. Estimated lengths (mm) based on measurements of diameter and condylar width.

| Genus | Specimen no. | Length (mm) estimation based on measurements of | | % adult |
		Diameter	Condylar width	
Diademodon				
humeri	SAM-PK-K8971	57.36		32.06
	UCMZ T492	70.41		39.35
	BP/I/3772	75.57		42.23
	SAM-PK-K-1332	77.7		43.48
femora	UCMZ T495		93.67	57.95
	UCMZ T503		103.09	63.77
	UCMZ T493		118.63	73.39
tibia	UCMZ T447	111.94		77.21
Cynognathus				
femora	SAM-PK-K-6235	190.13		68.40
	NMQR 3019	201.21		72.38
	NMQR 3019	277.98		100

Note: The *Diademodon* fibula (UCMZ T448) and mid-shaft (NMQR 2682) have been omitted from Table 1. No large fibula was available to calculate the % adult (but UCMZ T448 is at least 92.8 mm in length). The specimen NMQR 2682 could not be identified to a specific long bone element (due to weathering).

PK-K, South African Museum, Cape Town, South Africa; **UCMZ T**, Cambridge University, Cambridge, England.

RESULTS

Bone Histology of *Diademodon*

Diademodon humeri that are 32–40% of the adult length consist of a relatively narrow bone wall surrounding a small medullary cavity with a small amount of cancellous bone. The cortex consists of primary bone tissue, containing zones and annuli (Fig. 1). The zones are wide and comprise highly vascularized fibro-lamellar bone tissue. The osteocyte lacunae are globular and the canaliculi (fine spaces connecting osteocytes) are small and sparse. Longitudinal vascular canals are arranged in laminae and some have radial and circumferential anastomoses. The annuli are narrow and consist of avascularized, lamellar tissue, containing few, flattened osteocyte lacunae. A LAG is observed in one of the two humeri (SAM-PK-K8971) following an annulus. Peripheral rest lines and secondary osteons were not observed. Secondary reconstruction, in the medullary cavity region, appears to have just begun in one of the humeri (UCMZ T492).

Diademodon humeri and femora that are 42–73% of the adult length consist of a compacta surrounding a medullary cavity that contains a large amount of cancellous bone. The cortex mainly consists of primary bone tissue, although some secondary tissues are present (Fig. 2). The primary bone is zonal, consisting of alternating zones and annuli (Fig. 2A). Numerous globular osteocyte lacunae with small, sparse canaliculi are present in the zonal regions. The annuli consist of narrow regions of avascular lamellar tissue (with occasional radial blood vessels transgressing them) and contain few, flattened osteocyte lacunae. At least three LAGs are observed in the humerus BP/I/ 3772, each of which follows an annulus. In SAM-PK-K1332 and UCMZ T493, although several annuli are observed, only a single LAG is observed, following the outermost annulus. Peripheral rest lines are not observed in any of the specimens. Secondary reconstruction is evident by the presence of several enlarged erosion cavities in the medullary cavity region, some of which show redeposition of bone. Some isolated secondary osteons are also observed in the humeri in this region (Fig. 2B). Among the femora, all show resorption cavities, though secondary osteons are visible only in the femur UCMZ T493. Towards the metaphyseal regions of the humeri compact coarse cancellous bone tissue is observed in the region around the medullary cavity. This tissue was also observed in a distal thin section of a femur (UCMZ T493). Compact coarse cancellous bone is also more extensive in the deltopectoral crest region of the humeri, stretching from the medullary cavity all the way to the periphery of the bone.

The bone tissue of the *Diademodon* tibia (77% of the adult length) and fibula consists of a thick cortex surrounding a small medullary cavity that contains very few trabeculae. Bands of endosteally lamellated bone tissue surround the medullary cavity
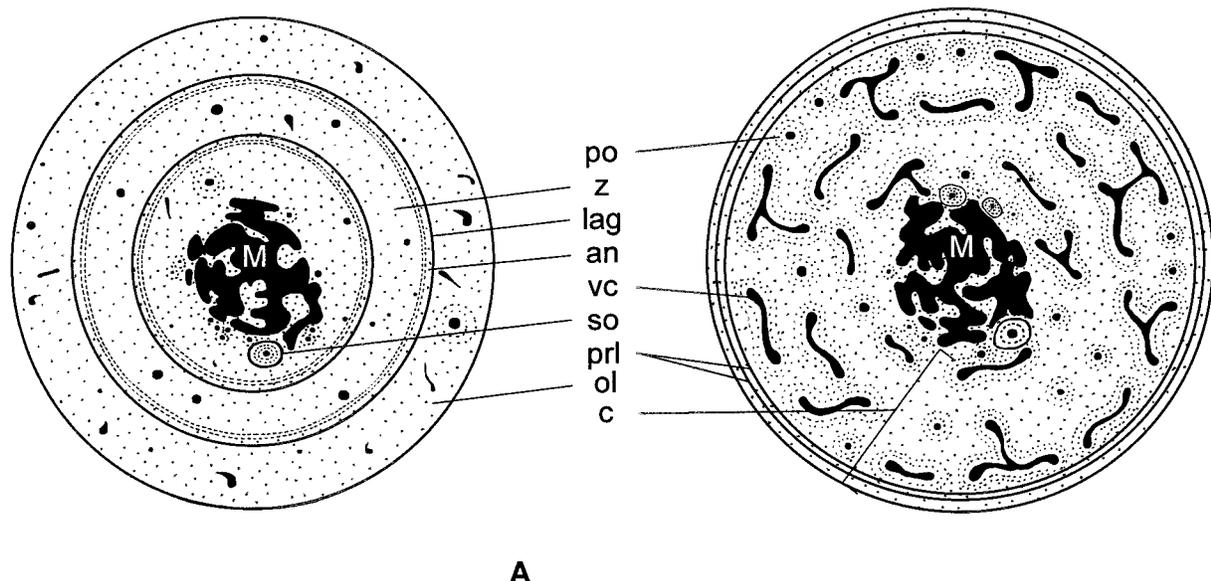

A

B

FIGURE 1. Schematic diagram representing transverse sections through the midshaft of a long bone, showing zonal bone (**A**) and azonal bone (**B**) respectively. **Abbreviations**: **an**, annulus; **c**, cortex; **lag**, line of arrested growth; **M**, medullary cavity; **ol**, osteocyte lacuna; **po**, primary osteon; **prl**, peripheral rest lines; **so**, secondary osteon; **vc**, vascular canal; **z**, zone.
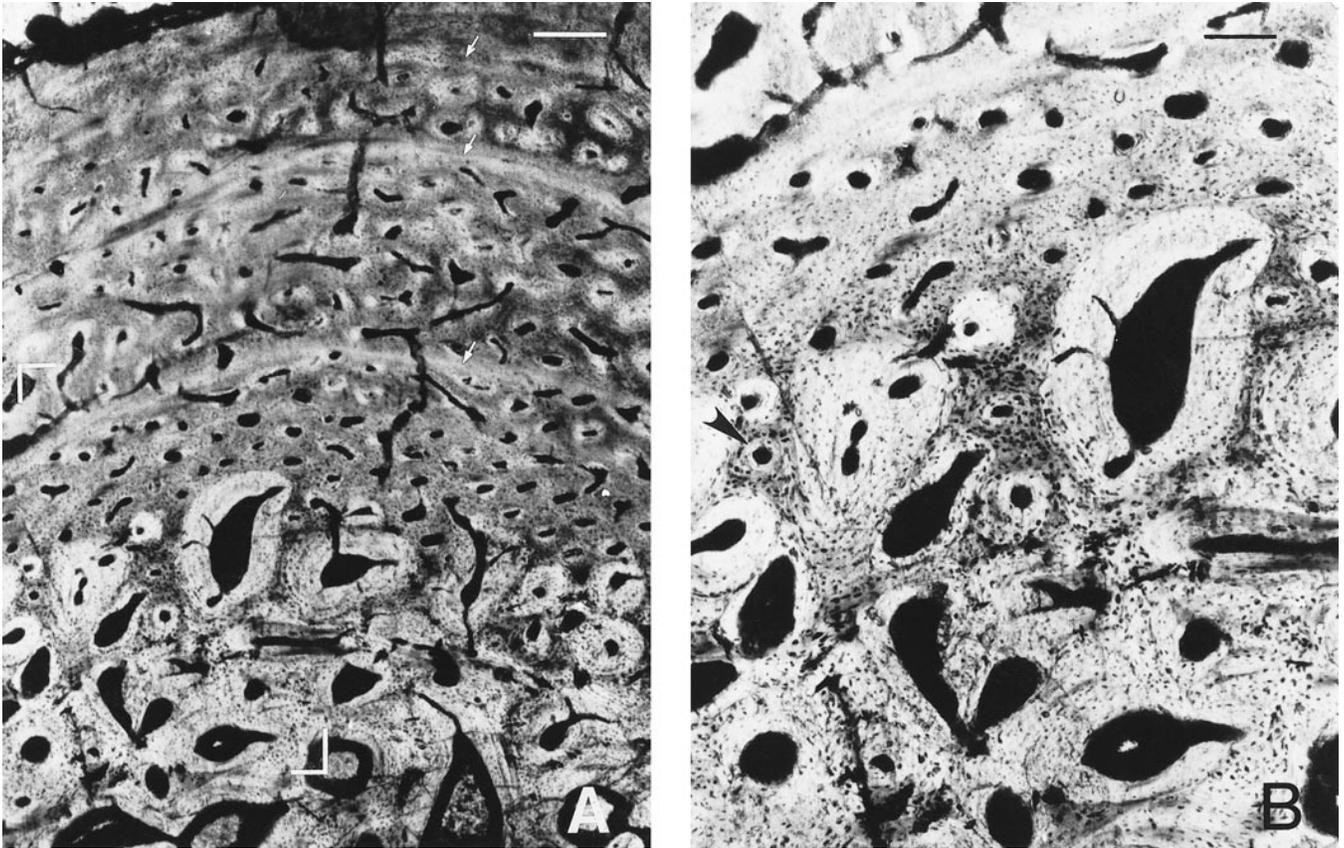
FIGURE 2. **A**, alternating zones and annuli (arrowheads) of a transverse section of a *Diademodon* humerus (BP/I/ 3772), distal to the midshaft. Note the secondary reconstruction in the medullary cavity region (see **2B**); **B**, higher magnification of the area framed above, showing secondary osteons (arrow head) and enlarged vascular cavities in the compacta. Scale bars equal 125 μm.

of both bones. The cortex of both the tibia and fibula consists of alternating vascular zones and avascular annuli, similar tissues to those present in the humeri and femora, except that very few radial and circumferential anastomoses occur. Six LAGs are observed in the tibia and multiple LAGs occur in the fibula. Peripheral rest lines were present in both elements (Fig. 3A, B). Secondary remodeling has occurred in both elements, though it is more extensively developed in the fibula. Few small secondary osteons surround the medullary cavity in both elements.

The most mature *Diademodon* specimen (NMQR 2682) is a shaft of an unidentified long bone. The peripheral part of the bone wall has been destroyed, but the diameter is assessed at approximately 21mm. The bone tissue consists of a thick cortex surrounding a large medullary cavity that contains a large amount of cancellous bone. The bone wall consists of a large amount of secondary tissues and contains a number of growth rings similar in character to those observed in the humeri and femora of the previous age category. Multiple LAGs are observed sometimes before and sometimes after each avascular annulus. Secondary osteons extend to the peripheral surface of the bone. Peripheral rest lines do not occur.

Skeletochronology of *Diademodon*

Because a zonal bone tissue characterizes *Diademodon* long bones, skeletochronology (Francillon-Vieillot et al., 1990) can be applied, i.e., the age of the individuals can be estimated by counting the number of growth rings present in the cortex (Table 2).

The mid-shaft NMQR 2682 has been omitted from this skeletochronological assessment because the peripheral part of the bone wall has not been preserved therefore preventing an accurate count of the number of growth rings present in the compacta. The humerus SAM-PK-K8971 shows no secondary remodeling and was used to estimate the total number of growth rings present in the older individuals. Because three of the humeri (UCMZ T492; BP/I/ 3772; SAM-PK-1332) show secondary remodeling around the medullary cavity, it is reasonable to assume that some of the earlier growth rings may have been resorbed. In these cases the total number of growth rings was estimated by measuring the distance between the growth rings in the smallest individual (SAM-PK-K8971) and using this measurement to estimate the number of growth rings that had been resorbed in the older individuals (Castanet and Cheylan, 1979). This number was added to the number of growth rings that were visible. By using the same method as above, the number of growth rings in the femur UCMZ T493, which also showed secondary remodeling, was estimated by using the actual number of growth rings present in the youngest femur. The rate of bone deposition was found to decrease with maturity, but this was not consistent and it must be stressed that the rate will appear to change depending on the morphology of the bone and from where the section was taken.

Bone Histology of *Cynognathus*

The *Cynognathus* femora are all large (68.40%, 72.38%, and 100% of the adult length). The bone tissue consists of a thick
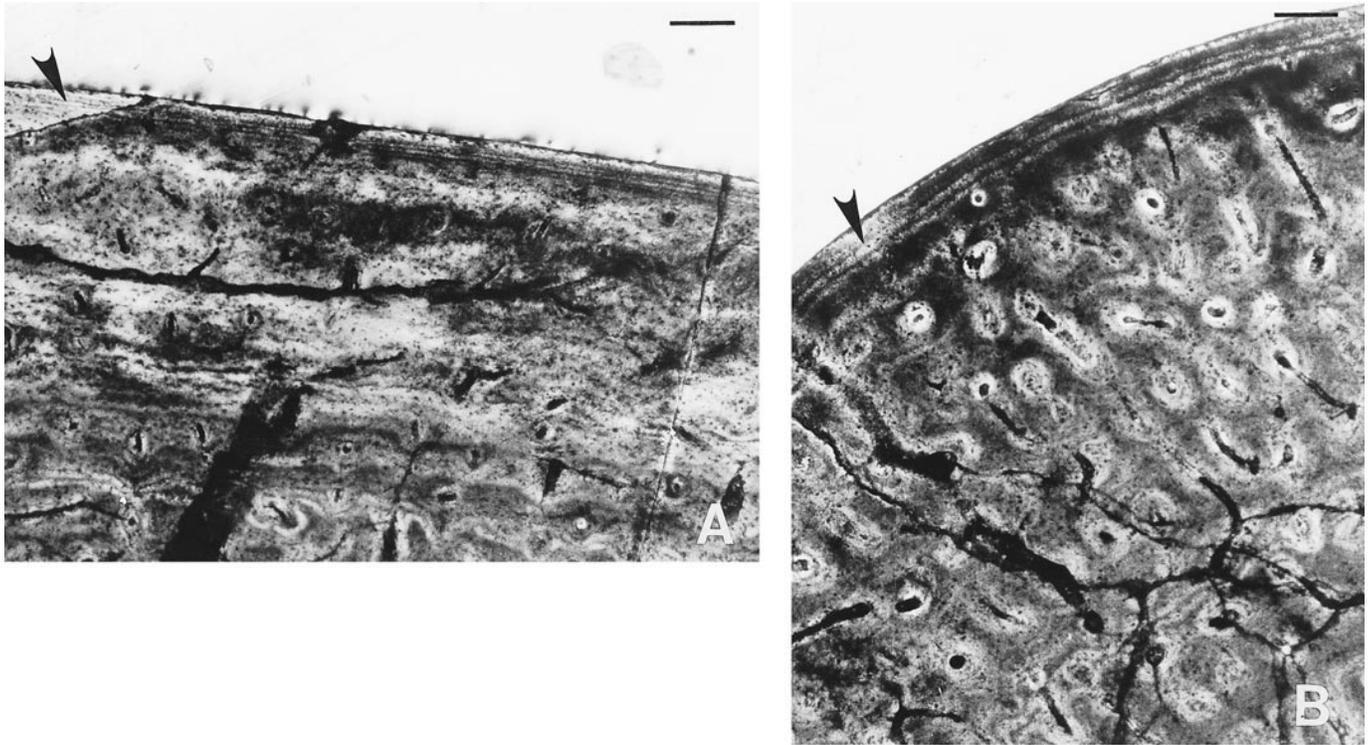
FIGURE 3. Peripheral rest lines (arrows) in *Diademodon*. **A**, mid-diaphyseal transverse section of a tibia (UCMZ T447); **B**, mid-diaphyseal transverse section of a fibula (UCMZ T448). Scale bars equal 125 μm.

cortex surrounding a medullary cavity that contains a large amount of cancellous bone. The cortex consists of uninterrupted fibro-lamellar bone tissue (Fig. 4), i.e., no zones, annuli or LAGs are present. The highly woven bone matrix contains abundant globular osteocyte lacunae that are haphazardly arranged. Longitudinal vascular canals anastomose radially to form a plexiform arrangement. There are a few small secondary osteons, situated in the vicinity of the medullary cavity (Fig. 4).

TABLE 2. Estimation of the number of growth rings for the *Diademodon* bone elements. NMQR 2682 has again been omitted for the reasons given in Table 1.

Specimen no.	No. growth rings observed	Total no. growth rings estimated
humeri		
SAM-PK-K8971	6	6
UCMZ T492		7
BP/I/3772	9	12
SAM-PK-K-1332	5	16
femora		
UCMZ T495	3	3
UCMZ T503	4	4
UCMZ T493	8	15
tibia		
UCMZ T447	6	
fibula		
UCMZ T448	5	

Quantification of Vascularity in *Diademodon* and *Cynognathus*

Using the Jandel Scientific Image Analysis program (Jandel Scientific, 1993), the percentage vascularity of the midcortical regions of the thin sections were calculated. Table 3 presents these results, and shows that *Cynognathus* bones are much more vascularized than those of *Diademodon.*

DISCUSSION

Bone Histology

The most obvious difference in bone histology between *Diademodon* and *Cynognathus* is the presence of growth rings in *Diademodon* and the absence of any interruptions in the rate of bone deposition in *Cynognathus.* Growth rings in *Diademodon* indicate that the bones experienced a cyclical rate of bone formation, whereas the absence of growth rings in the bone tissue of *Cynognathus* indicates that it grew continuously at a sustained rapid rate (Reid, 1987).

The cortex of *Diademodon* consists of alternating fibro-lamellar and lamellar bone tissue. Fibro-lamellar bone tissue is located within the zonal regions and suggests a rapid rate of bone deposition (Ricqlès, 1974, 1980). Fibro-lamellar bone tissue is widely recognized in extant mammals and birds. Though rarer in reptiles, it is known to occur within the zonal regions of *Alligator mississippiensis* (Reid, 1997), *Crocodylus porosus* (Reid, 1984), and *Crocodylus johnstoni* (Reid, pers. comm., 1999) living in the wild, as well as those grown on commercial crocodile farms (Chinsamy, 1995). Among extinct animals, it is also common in a number of non-avian dinosaurs (Ricqlès, 1980; Reid, 1990; Chinsamy, 1990, 1993) and in several dicynodont genera (Chinsamy and Rubidge, 1993).

TABLE 3. Percentage area occupied by vascular canals in the mid-cortical regions of the midshafts of *Diademodon* and *Cynognathus.* NMQR 2682 has been omitted for reasons given in Table 1.

Genus	Specimen no.	% vascularization
Diademodon		
humeri	SAM-PK-K8971	6.30
	UCMZ T492	8.81
	BP/I/3772	6.12
	SAM-PK-1332	3.96
femora	UCMZ T495	8.05
	UCMZ T503	4.96
	UCMZ T493	7.91
tibia	UCMZ T447	2.29
fibula	UCMZ T448	1.52
Cynognathus		
femora	SAM-PK-K6235	17.46
	NMQR 3019	15.50
	NMQR 3019	12.76

Experiments conducted on modern reptiles have shown that the growth rings present in their bones are annual, i.e., a zone is formed during the favorable growing season and an annulus is formed during the unfavorable season (Peabody, 1961; Castanet et al., 1988; Buffrenil and Buffetaut, 1981). Given that among extant animals such zonal tissue is an annual phenomenon, it is reasonable to conclude that they also reflect an annual cycle in *Diademodon.*

This deduction is reinforced by independent paleo-environmental reconstruction, which indicates that *Diademodon* lived in floodplains bordered by stable, flourishing riparian-type vegetation. These floodplains existed in a semi-arid climate, with a seasonal rainfall (Smith et al., 1993; Kitching, 1995). Given such a strong seasonal environment, it is likely that the growth rings within *Diademodon* are seasonally influenced. The bone histology directly indicates that *Diademodon* grew quickly during the favorable season and slowly, or even sometimes, not at all, during the unfavorable season.

In contrast, *Cynognathus* appears to have grown at a rapid and continuous rate. Evidence of this can be seen by the presence of uninterrupted fibro-lamellar bone tissue and the absence of any annuli or LAGs within the cortex. Fibro-lamellar bone tissue occurs within the zonal regions of *Diademodon* and was therefore deposited only periodically, whereas the fibro-lamellar bone within *Cynognathus* was formed continuously. The bone histology of *Cynognathus* suggests that it grew at a constant rate throughout the year and that its growth was independent of environmental conditions.

Because *Diademodon* and *Cynognathus* were contemporaries and their remains are often found together, it is reasonable to assume that they experienced the same climatic conditions. It is possible that *Diademodon's* food supply may have been seasonally influenced, whereas *Cynognathus,* a carnivore, would have depended on the same type of food throughout the year. The growth rate in *Diademodon* may have decreased during the unfavorable season because of food shortage or the presence of less nutritive food (Reid, pers. comm., 2000). It is however, also possible that these differences in their growth strategies of *Diademodon* and *Cynognathus* reflect inherent physiological differences. *Diademodon's* growth may have been dependant

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FIGURE 4. Mid-diaphyseal transverse section of a *Cynognathus* femur (SAM-PK-K6235), showing uninterrupted fibro-lamellar bone tissue. Scale bar equals 250 μm.

on changing environmental conditions, whereas *Cynognathus* may have been able to grow consistently, irrespective of seasonality.

Closely spaced rest lines in the periphery of the cortex are well known in mature mammals and in some dinosaurs (Chinsamy, 1990; Reid, 1997). They are interpreted as indicating a determinate growth strategy (Ricqlès, 1976; Chinsamy and Dodson, 1995) because they suggest a slowing down in the rate of growth. The presence of peripheral rest lines in the tibia and fibula of *Diademodon* indicate that these bones are from mature individuals whose overall growth had slowed down. The rest of the *Diademodon* specimens are probably from sub-adult individuals. The *Cynognathus* individuals are all possibly sub-adult, or alternatively, may have experienced an indeterminate growth strategy, i.e., they grew continuously throughout their lives, as is the case among many living reptiles (Ricqlès, 1976).

During bone growth, the metaphyseal diameter is reduced due to the inward, endosteal growth of the cortex, coupled with periosteal resorption (Enlow, 1963). By extending into areas already containing coarse-cancellous trabeculae, the process of endosteal growth directly converts cancellous bone tissue into compact bone tissue. (Enlow, 1963). The progressive resorption of the metaphyseal cortex and deposition of the new, larger diaphyseal cortex in the proximal and distal regions of the bone can be seen by the presence of compacted coarse cancellous bone in the deltopectoral crest of the humerus of *Diademodon*.

A number of secondary osteons were observed in two of the *Diademodon* humeri (BP/I/ 3772; SAM-PK-1332), in one of the femora (UCMZ T493), in the tibia (UCMZ T447) and fibula (UCMZ T448), and in the mid-shaft (NMQR 2682). In the humeri, femur, tibia, and fibula, the secondary osteons were situated around the medullary cavity and were not extensively developed. However, in the mid-shaft element studied (the most mature element from the *Diademodon* sample), the tissue was dominated by the presence of secondary osteons. This implies that the extensive development of secondary osteons was related to age (Ricqlès, 1980; Reid, 1987).

Secondary osteons were also present in all the *Cynognathus* femoral sections. Here, they were small, sparse, and generally situated near the medullary cavity margin. No secondary osteons extended through the cortex and dense Haversian bone tissue was absent.

Ontogenetic Changes

Although the sizes of the four *Diademodon* humeri are similar, the amount of secondary remodeling and number of growth rings differ quite markedly between those that lie within the 30–40% of the adult length category and those in the 42–44% of the adult length category. Furthermore, the total number of growth rings in the cortex increase as secondary remodeling becomes more extensive (Table 2). Of the observed elements 30% did not contain LAGs, however all these elements were juvenile. This supports the above suggestion that secondary reconstruction is age related. The *Diademodon* humeri all appear to be at varying sub-adult stages of ontogeny. The 30–40% of the adult length category consists of individuals that are clearly not juveniles and are approaching the sub-adult stage, whereas the 42–44% of the adult length category consists of individuals that are even more mature, i.e., closer to the adult stage. Younger individuals show very little secondary remodeling. One LAG occurs after one of the annuli in a humerus (SAM-PK-K8971), whereas no LAGs were observed in the other humerus (UCMZ T492). This suggests that the growth of younger individuals usually slowed during the unfavorable season, but did not always cease completely. Secondary osteons and a greater number of LAGs can be seen in the older *Diademodon* indi-

viduals, suggesting that growth usually ceased during the unfavorable season.

Skeletochronology cannot be applied to the limb bones of *Cynognathus,* therefore individual ages cannot be estimated. However, the sizes of the elements and presence of secondary osteons around the medullary cavity suggest that these individuals were not juveniles and were probably near adult.

Image Analysis

Image analysis revealed that the bone tissue of *Diademodon* is poorly vascularized. Vascularization is similar in the *Diademodon* humeri (6.3%) and femora (6.97%) and is markedly greater than in the tibia (2.29%) and fibula (1.52%). The tibial and fibular values are similar to those obtained for adult crocodilian femora (1.85%; Chinsamy, 1993), whereas the ontogenetically younger humeri and femora compare well with juvenile crocodilian values (4.59%; Chinsamy, 1993). The low vascularization of *Diademodon* is probably due to the presence of annuli in the cortex, which are either very poorly vascularized or avascular, and which decrease the general vascularization of the compacta. In contrast, the percentage vascularity of the *Cynognathus* femora (15.24%) is considerably higher than that of *Diademodon*. The presence of uninterrupted fibro-lamellar bone tissue in *Cynognathus* results in a higher overall vascularization of the compacta. These vascularization differences between the similarly sized *Diademodon* and *Cynognathus* further suggest that during the favorable growing season the dietary requirements of *Diademodon* were still comparatively less than those of *Cynognathus*. Considering Ham's (1965) suggestion that osteocytes in bone tissue need to be situated close to blood vessels in order to transport nutrients and waste products effectively, the higher vascularization of *Cynognathus* bone could imply a more efficient system for assimilation of nutrition.

CONCLUSIONS

1. *Diademodon* experienced a cyclical growth pattern reflected by the presence of alternating zones and annuli. Zones consist of fibro-lamellar bone tissue and annuli consist of lamellar bone tissue.

2. *Cynognathus* experienced a sustained, rapid growth pattern reflected by the presence of uninterrupted fibro-lamellar bone tissue.

3. The number of secondary osteons increases with increasing age in *Diademodon*.

4. Peripheral rest lines in the compacta of the *Diademodon* tibia and fibula, suggest a determinate growth strategy.

5. The *Cynognathus* compacta is more extensively vascularized than that of *Diademodon*. This observation correlates with the bone histology observed and suggests a faster overall growth rate, and higher energy demands in *Cynognathus*.

6. The compacta in the younger *Diademodon* specimens is more vascularized than the sub-adult compacta, presumably due to higher energy demands during early ontogenetic growth.

7. Because *Diademodon* and *Cynognathus* were contemporary and experienced the same environmental conditions, it is suggested that the differences in bone histology are a reflection of different inherent physiological factors.

ACKNOWLEDGMENTS

LITERATURE CITED

Brink, A. S. 1955. A study on the skeleton of *Diademodon.* Palaeontologia Africana 3:3–39.

Broom, R. 1911. On the structure of the skull in cynodont reptiles. Proceedings of the Zoological Society of London 11:900–905.

——— 1913. On the shoulder girdle of *Cynognathus.* Annals of the South African Museum 7:283–284.

Buffrenil, V., and E. Buffetaut. 1981. Skeletal growth lines in an Eocene crocodilian skull from Wyoming as an indicator of ontogenetic age and paleoclimatic conditions. Journal of Vertebrate Paleontology 1:57–66.

Castanet, J., D. G. Newman, and H. Saint Girons. 1988. Skeletochronological data on the growth, age and population structure of the tuatara, *Sphenodon punctatus,* on Stephens and Lady Alice Islands, New Zealand. Herpetologica 44:25–37.

Chinsamy, A. 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia:Theropoda). Palaeontologia Africana 27:77–82.

——— 1991. The osteohistology of femoral growth within a clade: a comparison of the crocodile, *Crocodylus niloticus,* the dinosaurs, *Massospondylus* and *Syntarsus* and the birds, *Struthio* and *Sagittarius.* Ph.D. dissertation, University of the Witwatersrand, Johannesburg, 200 pp.

——— 1993. Image analysis and the physiological implications of the vascularization of femora in archosaurs. Modern Geology 19:101–108.

——— 1995. Ontogenetic changes in the bone histology of the Late Jurassic ornithopod *Dryosaurus lettowvorbecki.* Journal of Vertebrate Paleontology 15:96–104.

———, and P. Dodson. 1995. Inside a dinosaur bone. American Scientist 83:174–180.

———, and M. A. Raath. 1992. Preparation of fossil bone for histological examination. Palaeontologia Africana 29:39–44.

———, and B. S. Rubidge. 1993. Dicynodont (Therapsida) bone histology: phylogenetic and physiological implications. Palaeontologia Africana 30:97–102.

Enlow, D. H. 1963. Principles of bone remodeling. Charles C. Thomas, Springfield, Illinois, 131 pp.

———, and S. O. Brown. 1956. A comparative histological study of fossil and recent bone tissues. Part 1. Texas Journal of Science 8:405–443.

Francillon-Vieillot, H., V. de Buffrénil, J. Castanet, J. Géraudie, F. J. Meunier, J. Sire, L. Zylberberg, and A. de Ricqlés. 1990. Microstructure and mineralization of vertebrate skeletal tissues; pp. 471–547. in J. G. Carter (ed.), Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Van Nostrand Reinhold, New York.

Gregory, W. K., and C. L. Camp. 1918. A reconstruction of the skeleton of *Cynognathus.* Part 5. Bulletin American Museum of Natural History 38:538–544.

Grine, F. E. 1977. Postcanine tooth function and jaw movement in the gomphodont cynodont *Diademodon* (Reptilia:Therapsida). Palaeontologia Africana 20:123–135.

———, B. D. Hahn, and C. E. Gow. 1978. Aspects of relative growth and variability in *Diademodon* (Reptilia:Therapsida). South African Journal of Science 74:50–58.

Ham, A. W. 1965. Histology. J. B. Lippincott Company, Philadelphia, 371 pp.

Hopson, J. A. 1971. Postcanine replacement in the gomphodont cynodont *Diademodon.* Zoological Journal of the Linnean Society 50:1–20.

Horner, J. R., A de Ricqlès, and K. Padian. 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. Paleobiology 25:295–304.

Jandel Scientific. 1993. Sigma Scan/Image. Measurement Software for Windows. Jandel Scientific, San Rafael, California, 200 pp.

Jenkins, F. A. 1971. The postcranial skeleton of African cynodonts. Peabody Museum of Natural History, Bulletin 36, Yale University, 216 pp.

Kemp, T. S. 1982. Mammal-like Reptiles and the Origin of Mammals. Academic Press, London, 363 pp.

Kitching, J. W. 1995. Biostratigraphy of the *Cynognathus* Assemblage Zone; pp. 40–45 in B. S. Rubidge (eds.), Biostratigraphy of the Beaufort Group (Karoo Supergroup). Series 1. South African Committee for Stratigraphy, Pretoria.

Peabody, F. E. 1961. Annual growth zones in living and fossil vertebrates. Journal of Morphology 108:11–62.

Reid, R. E. H. 1984. Primary bone and dinosaurian physiology. Geological Magazine 121:580–598.

——— 1987. Bone and dinosaurian ''endothermy.'' Modern Geology 11:133–154.

——— 1990. Zonal ''growth rings'' in dinosaurs. Modern Geology 15:19–48.

——— 1997. How dinosaurs grew; pp. 403–413 in J. O. Farlow and M. K. Brett-Surman (eds.), The Complete Dinosaur. Indiana University Press, Indiana.

Ricqlès, A. de 1969. Recherches paléohistologiques sur les os longs des tétrapodes II.—quelques observations sur la structure des os longs des thériodontes. Annales de paléontologie 55:3–52.

——— 1974. Evolution of Endothermy: Histological Evidence. Evolutionary Theory 1:51–80.

——— 1976. On bone histology of fossil and living reptiles, with comments on its functional and evolutionary significance; pp. 123–150 in A. d'A. Bellairs and C. B. Cox (eds.), Morphology and Biology of Reptiles. Linnaean Society 3.

——— 1980. Tissue structures of dinosaur bone. Functional significance and possible relation to dinosaur physiology; pp. 103–140 in D. K. Thomas and E. C. Olson (eds.), A Cold Look at the Warm-blooded Dinosaurs. Westview Press, Boulder.

Seeley, H. G. 1894. Researches on the structure, organization and classification of the fossil Reptilia. Section 3. On *Diademodon,* Philosophical Transactions of the Royal Society 185:1029–1041.

——— 1908. On the dentition of the palate in the South African fossil reptile genus *Cynognathus.* Geological Magazine 5:486–491.

Smith, R. M. H., P. G. Eriksson, and W. J. Botha. 1993. A review of the stratigraphy and sedimentary environments of the Karoo-aged basins of Southern Africa. Journal of African Earth Sciences 16:143–169.

Watson, D. M. S. 1911. The skull of *Diademodon,* with notes on those of some other cynodonts. Series 8. Annals and Magazine of Natural History 45:293–330.