

## BONE HISTOLOGY AND GROWTH PATTERNS OF SOME NONMAMMALIAN THERAPSID

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**ABSTRACT**—The bone histology of gorgonopsian, therocephalian and cynodont genera, ranging from the Late Permian to Early Jurassic, was examined. The analysis reveals a predominance of cortical fibrolamellar bone tissue in most skeletal elements. The high prevalence of fibrolamellar bone tissue suggests an overall rapid osteogenesis, but interruptions in the form of annuli and/or LAGs do occur. Inter-elemental histovariation within individuals, such as primary tissue type, cortical porosity, LAGs and annuli, extent of secondary reconstruction and endosteal bone deposition, is observed. In general, propodials were found to have grown faster than epipodials. Distinct growth patterns were identified for each of the genera studied. These growth patterns vary from a cyclical growth pattern in the Late Permian gorgonopsian, *Scylacops* to fast, sustained growth in the Early Jurassic cynodont, *Tritylodon*. Growth patterns of contemporaneous genera are also noted and discussed. A possible trend towards fast growth, and an independent decrease or eventual loss of developmental plasticity within the therapsids, is proposed.

### INTRODUCTION

During the Late Paleozoic–Mesozoic eras, the nonmammalian therapsids dominated the terrestrial ecosystems. Of these, the anomodonts, gorgonopsians, therocephalians and cynodonts (the neotherapsids, sensu Hopson, 1999) have been studied in considerable detail and their taxonomy, osteology, and functional morphology are well established (e.g., Boonstra 1964; Kemp, 1969, 1982; Jenkins, 1971; Hopson and Barghusen 1986; Rowe, 1988; King, 1988; Sigogneau-Russell, 1989; Allin and Hopson, 1992; Crompton, 1995; Sidor and Hopson, 1998; Ray, 2000; Blob 2001). However, their life history strategies or growth patterns are poorly understood.

Bone histology is used to obtain valuable biological information from the bones of fossil animals, as it generally remains intact after fossilization. Previous work on osteohistology has contributed significantly to understanding various aspects of the biology of dinosaurs and other archosaurs (e.g., Reid, 1984; Ricqlès, 1983; Chinsamy, 1993a, b; Varricchio, 1993; Curry, 1999; Horner et al. 2000, 2001; Chinsamy and Elzanowski, 2001). Studies on several synapsid taxa by Gross (1934), Enlow (1969) and Ricqlès (1969, 1972, 1974, 1975, 1976) have shown that the bone microstructure is composed of various primary tissue types ranging from lamellar zonal tissue to fibrolamellar bone with primary osteons arranged in longitudinal, laminar and radial patterns. Other features include dense vascularization and limited secondary reconstruction in the deeper cortex. Ricqlès (1969, 1976) noted a marked distinction between gorgonopsian, therocephalian and dicynodont bone microstructure, although several of the specimens studied were of unidentified long bones, which frequently could not be positively identified to genus level due to bad preservation of the material. More recent work on dicynodonts (Chinsamy and Rubidge, 1993; Ray and Chinsamy, 2004) and nonmammalian cynodonts (Botha and Chinsamy, 2000) has shown a wide range of histological characteristics, which appear to be dependent on a variety of factors such as ontogeny, environment and biomechanics.

The current study documents the bone histology, inter-elemental histovariability and evolutionary trends in the growth

patterns of several neotherapsid genera encompassing its three main clades (sensu Rubidge and Sidor, 2001). These include the gorgonopsians *Aelurognathus* and *Scylacops*, the therocephalian *Pristerognathus* and the cynodonts *Procynosuchus* and *Tritylodon*. All the genera examined here are taxonomically valid (Jenkins, 1971; Kemp, 1979, 1980; van den Heever, 1980; Sigogneau-Russell, 1989; King, 1993; Ray and Chinsamy, 2003) and well documented in the various Assemblage Zones of the highly fossiliferous Beaufort Group of South Africa (Kitching and Raath, 1984; Rubidge, 1995).

The genera *Aelurognathus* and *Pristerognathus* have been previously examined using isolated skeletal elements (Ricqlès, 1969). Ricqlès (1969) found that an *Aelurognathus* femur showed a well-vascularised sub-plexiform to reticular network and that a *Pristerognathus* femur exhibited a well-vascularised bone tissue with longitudinally oriented primary osteons.

Detailed comparisons are also made with the dicynodont *Diictodon* (Ray and Chinsamy, 2004) and the cynodonts *Diademodon* and *Cynognathus* (Botha and Chinsamy, 2000).

### MATERIAL AND METHODS

#### Material

The gorgonopsians, *Scylacops* (SAM-PK-10188) and *Aelurognathus* (SAM-PK-K10000) were examined from multiple limb bones and ribs (Table 1). The therocephalian *Pristerognathus* was studied from various skeletal elements of the specimens SAM-PK-5018 and SAM-PK-11557. Several skeletal elements of the basal cynodont *Procynosuchus* and the more derived cynodont *Tritylodon* were studied (Table 1). Apart from a *Procynosuchus* rib (TSK 34), which is from the Late Permian Madumabisa Mudstones of the Luangwa valley, Zambia, all the specimens were recovered from stratigraphic horizons of the Beaufort Group, Karoo SuperGroup, South Africa. All the skeletal elements examined were selected from positively identified genera.

The bone histology and growth pattern of *Diictodon* was based on various skeletal elements from an ontogenetic series of 13 individuals, which were recovered from the Late Permian *Tropidostoma* and *Cistecephalus* Assemblage Zones of the Beaufort Group, South Africa (Ray and Chinsamy, 2004). Histological information on the cynodonts, *Diademodon* and *Cynognathus* is derived from Botha and Chinsamy (2000) and involved a detailed analysis of various limb bones, recovered from the Early

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TABLE 1. Locality, horizon and skeletal elements examined of each specimen. Total length of the elements used for histological analysis is given in mm, except for those marked with asterisks

Taxon	Specimen number	Locality	Elements used	Length (mm)
<b>GORGONOPSIA</b>				
<i>Cistecephalus</i>	Assemblage Zone, Late Permian			
<i>Scylacops</i>	SAM-PK-10188	Dunedin	Humerus	100
			Radius	83.25
			Ulna	99
			Femur	174.8
			Fibula	96.67
			Partial rib	—
<i>Tropidostoma</i>	Assemblage Zone, Late Permian			
<i>Aelurognathus</i>	SAM-PK-K10000	Leeukloof	Humerus	110.75
			Femur	163.63
			Tibia	94.37
<b>THEROCEPHALIA</b>				
<i>Priesterognathus</i>	Assemblage Zone, Late Permian			
<i>Priesterognathus</i>	SAM-PK-5018	Abrahamskraal	Humerus	125.3
			Radius	37.07*
			Ulna	45.23*
			Femur	174.72
			Tibia	42.92
			Fibula	18.59**
	SAM-PK-11557	Die Cypher	Fibula	24.29**
			Rib	18.78**
<b>CYNODONTIA</b>				
<i>Cistecephalus</i>	Assemblage Zone, Late Permian			
<i>Procynosuchus</i>	B/P/1/3747	New Bethesda	Radius	8.24**
	SAM-PK-8511	Fraserburg	Clavicle	3.29**
	TSK 34	Luangwa valley, Zambia	Rib	3.02**
<i>Jurassic Massospondylus</i>	Range Zone, Elliot Formation, South Africa			
<i>Tritylodon</i>	B/P/1/5160	Ladybrand	Humerus	55.07
	B/P/1/5089	Ladybrand	Humerus	55.77
	B/P/1/4785	Fouriesburg	Humerus	52.77
			Radius	—
			Ulna	—
			Rib	—
	B/P/1/5671	Clarens	Humerus	82.35
	B/P/1/5167	Bethlehem	Radius	34.9

\*proximal diameter, \*\*midshaft diameter. **Institutional abbreviations:** **B/P/1/**, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; **NMQR**, Bloemfontein National Museum, Bloemfontein, South Africa; **SAM**, South African Museum, Cape Town, South Africa; **TSK**, Oxford University, Oxford, England, **UCMZ**, University of Cambridge, Museum of Zoology, Cambridge, England.

Triassic *Cynognathus* Assemblage Zone of the Beaufort Group, South Africa.

## Methods

A comprehensive histological analysis of a taxon would ideally involve the examination of multiple skeletal elements of individuals at different ontogenetic stages. This would permit an assessment of histovariability in individuals, as well as through ontogeny. However, the fossil record rarely preserves complete skeletons and the destructive nature of histological analysis makes it virtually impossible to obtain an ideal sample (Chinsamy, 1995). In the present study, we focused on multiple skeletal elements (see Table 1), especially on the long limb bones as these are least remodeled (Enlow, 1963; Chinsamy and Dodson, 1995; Sander, 2000). To eliminate variation due to ontogeny, documentation of the inter-elemental histovariability was restricted mainly to the adult individuals. Relative size, muscle scars and well-finished bone surfaces were used to identify adult individuals a priori. All the specimens were photographed, morphological variations noted and standard measurements re-

corded. Complete specimens in the collection were measured to estimate the length of the partial/incomplete elements examined for histology. Thin sections were prepared following the techniques outlined by Chinsamy and Raath (1992). Wherever possible several serial sections (transverse and longitudinal) from the same element were processed. In fragmentary elements, the mid-diaphyseal regions were selected for thin sectioning and if not available, the more proximal or distal regions were sectioned. Mid-diaphyseal regions are ideal as they are the least remodeled regions within a limb bone, however, not all the study elements were complete.

The thin sections of the fossil bones were studied using a petrographic polarizing microscope. Histological terminology and definitions generally follow that of Francillon-Vieillot et al. (1990) and Reid (1996). The porosity of the cortex is calculated at the mid-cortical region following the procedures outlined by Chinsamy (1993a). Only elements with available, well-preserved mid-diaphyseal regions were used in this analysis. The porosity is quantified as a percentage of total cortical area using the image analysis software Jandel Sigma Scan Pro, version 4.0. The procedure was repeated for every third field of view at a magnification of 10 $\times$  and approximately 8–10 fields were examined per slide. The term ‘growth ring’ is used to refer to any stratification produced by cyclical growth, namely zones, annuli and lines of arrested growth (LAGs). The cortical or relative bone wall thickness (RBT) is calculated as the ratio of the cross sectional bone wall thickness to the cross sectional diameter of the bone and expressed as a percentage (Bühler, 1986; Chinsamy, 1993b). RBT was calculated from the thin sections at 2 $\times$  magnification. For incomplete specimens, where it was not possible to measure RBT, an average thickness of the cortex is given. Such measurements (RBT and cortical porosity) were standardized in the diaphyseal sections of each bone.

## BONE HISTOLOGY

In the following section, an overview of the bone microstructure of each genus precedes the more detailed description of individual skeletal elements, especially where multiple elements from the same individual were studied.

### *Scylacops* (Gorgonopsia)

**General Description**—Various skeletal elements from a single individual of *Scylacops* (SAM-PK-10188) were examined for histological analysis (Table 1). In general, the cortical bone is zonal in all the elements studied and contains wide zones separated by annuli and LAGs (Fig. 1). The wide zones are composed of a primary woven-fibered bone matrix with mainly longitudinally oriented channels, with osteonal deposits forming primary osteons and fibrolamellar bone tissue. The outer cortical periphery is irregular with few channels opening subperiosteally. The longitudinally oriented channels in this region show few osteonal deposits and are larger than the well-developed primary osteons. The organization of the primary osteons varies depending on the element and even locally within the same section. The medullary cavity in all the elements are lined by endosteally lamellated bone, the extent of which varies depending on the position and type of element. Secondary reconstruction is prevalent in the inner cortex resulting in erosively enlarged resorption cavities. Secondary osteons are occasionally visible.

**Humerus**—Although the proximal metaphyseal region of the humerus was studied, the narrow cortex shows at least three LAGs. The large medullary cavity contains bony trabeculae. Few resorption cavities are present in the perimedullary region. Secondary osteons are absent.

**Ulna**—(Fig. 1A). A distinct, but narrow cortex (RBT = 16.02%) characterizes the mid-diaphysis of the ulna. The cortex

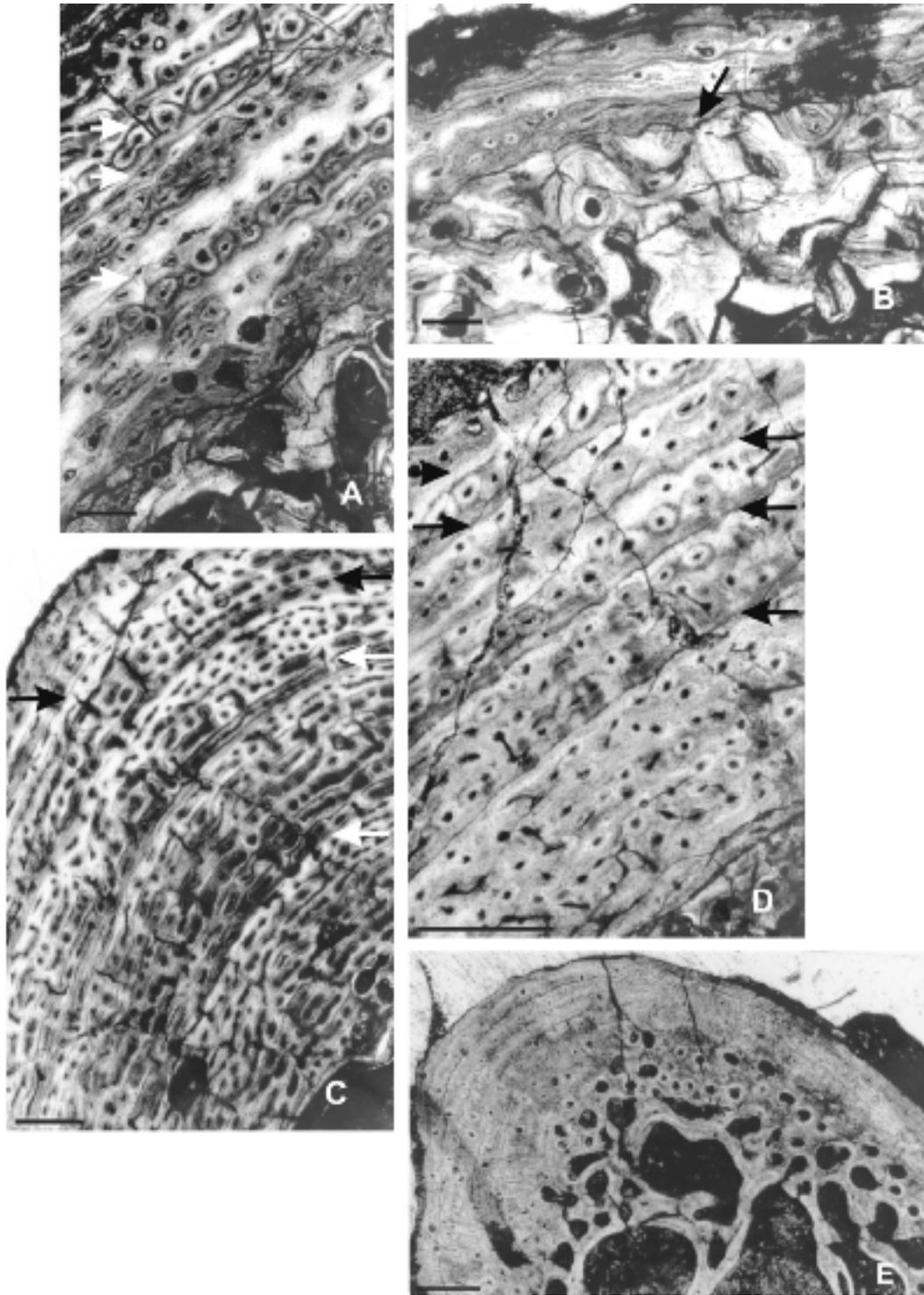


FIGURE 1. Transverse sections of *Scylacops* (SAM-PK-10188) showing **A**, ulna with zones of fibrolamellar bone tissue separated by annuli and LAGs (arrows); **B**, radius showing a distinct reversal line (arrow) separating periosteal and endosteal deposition; **C**, femur showing zonal fibrolamellar tissue with primary osteons in a lamina-subplexiform pattern and separated by distinct LAGs; **D**, fibula showing essentially longitudinally oriented primary osteons, interrupted by annuli and LAGs and **E**, rib showing primary osteons with occasional radial anastomoses. Note the irregular subperiosteal periphery in the bones. Arrows indicate LAGs. A and B scale bars equal 200  $\mu\text{m}$ ; C, D, and E scale bars equal 400  $\mu\text{m}$ .

is composed of wide zones separated by five annuli and LAGs. The zones contain fibrolamellar bone tissue and mostly longitudinally oriented primary osteons with occasional circumferential anastomoses. In the deeper cortex, the primary osteons often

occur in bundles. The cortical porosity is approximately 3.8%. In the perimedullary region, erosionally enlarged resorption cavities and a few secondary osteons are visible. Internal to this region, is a zone of compacted coarse cancellous bone. The med-

ullary cavity contains endosteal bony trabeculae. A prominent reversal line separates endosteal and periosteal growth.

**Radius**—(Fig. 1B). The diaphyseal transverse section of the radius (SAM-PK-K10188) shows a thick, zonal cortex (RBT = 24.30%), containing six annuli and LAGs. Each annulus is followed by a LAG. The primary osteons of the zones show radial and circumferential anastomoses. The cortical porosity is low (2.53%) possibly because of the essentially avascular annuli and LAGs. The medullary cavity is surrounded by compacted coarse cancellous bone tissue, which is separated from the periosteal cortex by a prominent reversal line (Fig. 1B). The distinctive feature of the radius is the extensive secondary reconstruction though it is confined to the perimedullary and inner cortical region. This includes erosionally enlarged canals and a few secondary osteons.

In the radial metaphyseal sections, the medullary cavity is surrounded by compacted coarse cancellous bone tissue and a distinct reversal line separates it from the narrow primary cortex. The latter, composed of fibrolamellar bone tissue, has a low cortical porosity and the primary osteons are mainly longitudinally oriented.

**Femur**—(Fig. 1C). The diaphyseal transverse section of the femur shows a large free medullary cavity surrounded by a thick cortex (average thickness is approximately 2.6 mm). There are five LAGs in the cortex, separating zones composed of fibrolamellar bone tissue. The arrangement of the primary osteons is markedly different from that of the other limb bones and mainly consists of a laminar to subplexiform pattern. The cortical porosity is slightly higher than that of the epipodials (4.33%). The perimedullary region of the femur shows similar secondary reconstruction as in the other bones examined and contains resorption cavities with centripetally deposited lamellated bone tissue, few forming well developed secondary osteons. A thin layer of endosteal lamellated bone deposition is seen at the resorptive medullary margin.

**Fibula**—(Fig. 1D). The mid-diaphyseal transverse section of the *Scylacops* fibula shows a thick zonal cortex and a small medullary cavity. The primary osteons of the cortical fibrolamellar bone tissue are mostly longitudinally oriented and a few show radial and circumferential anastomoses (Fig. 1D). The cortical porosity is approximately 3.6%. There are at least six LAGs including a prominent annulus (approximately 30  $\mu$ m in thickness) in the deep cortex. The LAGs usually undulate around the primary osteons and are roughly parallel to the peripheral margin. Near the subperiosteal margin, the channels show few osteonal deposits.

A narrow zone of secondary reconstruction is present at the perimedullary region, which shows resorption cavities and a few secondary osteons. The irregular margin of the medullary cavity shows endosteal lamellated bone deposition. This is especially visible in the metaphyseal sections. The peripheral margin of the medullary cavity is irregular and resorptive towards the medial edge, whereas compacted coarse cancellous bone is present on the other side to compensate for bone resorption. A distinct reversal line separates the endosteal and periosteal growth.

**Rib**—(Fig. 1E). The transverse section of the rib shows a similarity with the limb bones in the cortical tissue type, endosteal bone deposition and secondary reconstruction. It has a thick cortex (RBT = 21.62%) and a small medullary cavity. As in the other bones, the cortex is zonal (Fig. 1E) and contains wide zones of fibrolamellar bone tissue separated by six LAGs. The longitudinally oriented channels have occasional radial anastomoses. A high prevalence of primary osteons occurs towards the medial side in comparison to the lateral side, which is probably related to the curvature of the rib. This resulted in a very low overall cortical porosity (2.24%). At places, LAGs are composed of multiple, narrow, closely spaced, but distinct lines. Resorption cavities in-filled by centripetally deposited lamellated bone and

secondary osteons are prevalent. Internal to this is a zone of cancellous spaces and endosteally deposited lamellated bone tissue. Several layers of deposition can be seen along the boundaries of the erosion cavities.

### *Aelurognathus* (*Gorgonopsia*)

**General Description**—The transverse sections of all the limb bones studied show a distinct, but narrow cortex and a large medullary cavity. The cortical thickness varies and is composed of fibrolamellar bone tissue with mostly longitudinal primary osteons, showing variable organization. The osteocyte lacunae are globular and distinct.

The subperiosteal periphery is irregular and shows subperiosteally open channels in the outer cortex. Near the periphery the canals are larger in comparison to those in the mid- and deep cortex and they show little osteonal deposition.

The medullary cavity on the other hand is composed entirely of endosteal bony trabeculae. There is a distinct reversal line between periosteal and endosteal growth. In the perimedullary region extensive compacted coarse cancellous bone is present.

**Humerus**—The incomplete nature of the diaphyseal cross section did not facilitate an RBT calculation, though its maximum thickness is approximately 2.6 mm. The cortex comprises fibrolamellar bone tissue with mainly longitudinally oriented primary osteons. The cortical porosity in a metaphyseal section is 4.68%. Secondary reconstruction in the form of enlarged resorption cavities and a few secondary osteons is visible on the ventral humeral surface. It shows variable deposition of endosteal lamellated bone, mainly at its dorsal medullary margin and a distinct reversal line between endosteal and periosteal growth (Fig. 2A). In the longitudinal epiphyseal sections, calcified cartilage is preserved at the epiphyseal ends along with profuse bony trabeculae.

**Femur**—The metaphyseal cortex is narrow and the RBT is only 5%. The channels within the cortex are mostly longitudinally oriented with few radial and circumferential anastomoses, forming an almost reticular pattern (Fig. 2B). The cortical porosity in the metaphyseal section is 8.32%. Growth rings are absent. Large cancellous spaces are present in the femoral perimedullary region. A similar presence of well vascularized fibrolamellar bone tissue was noted in the proximal end of a femur by Ricqlès (1969). The transverse section was further characterized by endosteal bone deposition with large erosion bays in the perimedullary region, profuse secondary osteons in the deeper cortex and the presence of a dense spongiosa in the medullary cavity.

**Tibia**—Longitudinal sections of the tibia show calcified cartilage at the articular ends (Fig. 2C). A narrow cortex, approximately 1 mm in thickness, is present around a large medullary cavity. The cortex is composed of fibrolamellar bone tissue. Radially oriented channels are especially abundant in the tibial cortex. Growth rings are absent. The perimedullary region contains large cancellous spaces and endosteal trabeculae.

### *Pristerognathus* (*Therocephalia*)

**General Description**—*Pristerognathus* was examined using multiple skeletal elements from two specimens. SAM-PK-5018 is relatively smaller than SAM-PK-11557 and is presumably the younger individual. Although most of the elements are badly preserved and a few show diagenetic alteration, the overall tissue organization is discernable. As in the gorgonopsians, the predominant extracellular matrix of the cortex in all the elements examined, is woven-fibered. The channels in the bone show centripetal osteonal deposits and constitute the fibrolamellar bone tissue (Fig. 3A–D). Most of the primary osteons are longitudinally oriented, but their arrangement changes in different skel-

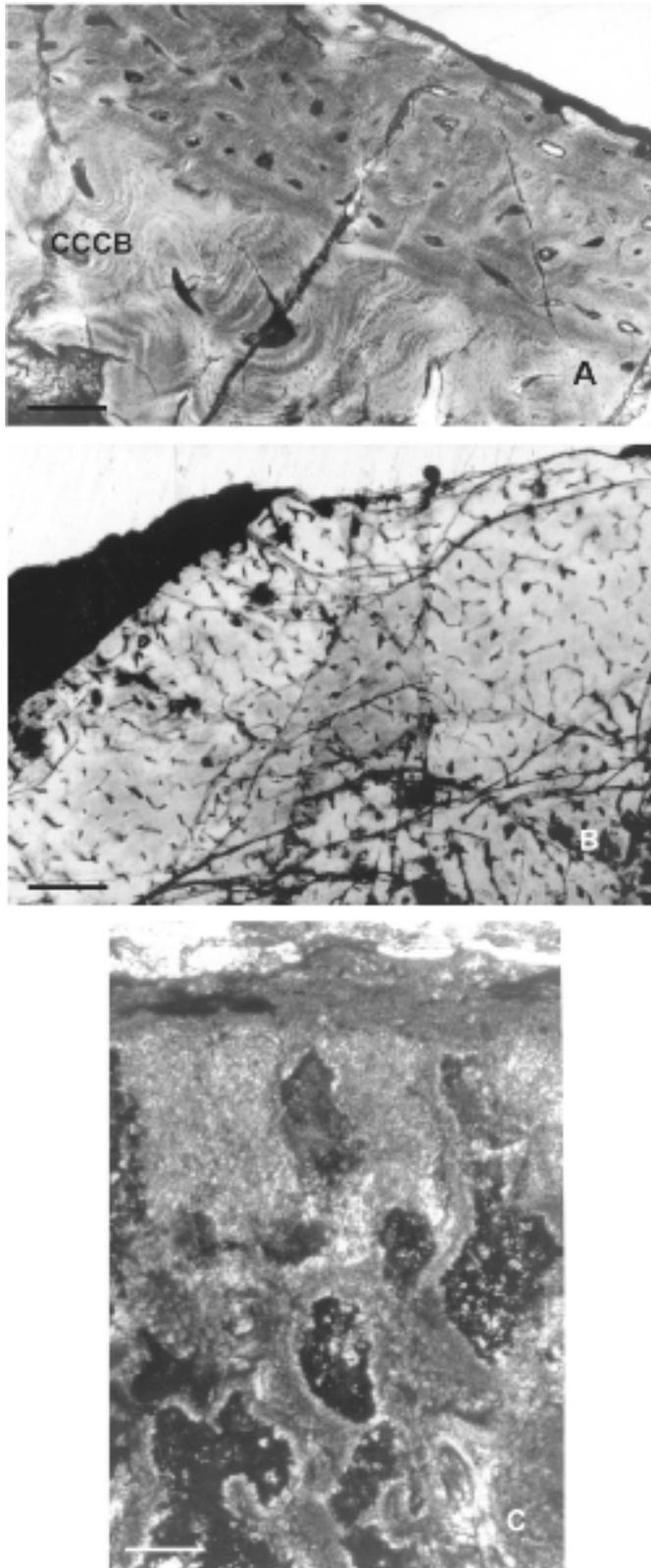


FIGURE 2. Transverse sections of *Aelurognathus* (SAM-PK-K10000) showing **A**, humerus revealing a distinct break between the primary fibrolamellar bone tissue and compacted coarse cancellous bone (CCCB); **B**, femur showing a reticular pattern of primary osteons and lack of growth rings; **C**, longitudinal section of the tibia showing epiphyseal calcified cartilage. Scale bars equal 400  $\mu\text{m}$ .

etal elements, position of the section along the bone shaft and even locally within the same section. In SAM-PK-5018, growth rings are absent, except for two narrow annuli in the tibia. The medullary cavity in general has a highly irregular periphery and shows deposition of endosteal lamellated bone. Secondly reconstructed resorption cavities, partially infilled by centripetal lamellated bone and a few well-formed secondary osteons are prevalent in all the elements. However, the extent of endosteal deposition and secondary reconstruction varies depending on the skeletal element and location of the section.

**Humerus**—The humeral diaphyseal section of SAM-PK-K5018 shows a thick distinct cortex (approximately 2.6 mm in thickness), which is composed of fibrolamellar bone tissue. The primary osteons are organized in a laminar-subplexiform pattern. In places a subreticular arrangement is visible. However, the primary osteons decrease towards the periphery. An irregular medullary margin and endosteal bony trabeculae characterize the medullary cavity. The perimedullary region contains compacted coarse cancellous bone tissue. Just external to this region, there are a few secondarily enlarged resorption cavities, though secondary osteons are absent.

**Radius and Ulna**—Metaphyseal sections of the radius and ulna were studied from the smaller specimen SAM-PK-K5018. The overall cortical bone is of the fibrolamellar complex. A thick radial cortex (RBT = 17.86%) surrounds the medullary cavity. It has a highly irregular medullary margin and the longitudinal axis shows drift towards the lateral edge. The longitudinally oriented primary osteons of the cortex show occasional radial anastomoses. Radially oriented channels are especially visible at the lateral and medial edges of the bone.

More towards the proximal end, the cortex of the radius decreases (RBT = 13.73%) and primary osteons show an almost reticular pattern in places. Extensive compacted coarse cancellous bone is seen in the perimedullary region, separated from periosteal growth by a distinct reversal line. A few resorption cavities are also visible, though secondary osteons are absent.

The most distinct feature of the ulna is the profusion of radially oriented channels in the bone, especially at the lateral and medial sides. In the perimedullary region, a few resorption cavities and secondary osteons are visible.

**Femur**—(Fig. 3A). The femoral diaphyseal section shows a thick cortex (RBT = 15.34%). As in the other elements, the cortex contains fibrolamellar bone tissue (Fig. 3A). The primary osteons are mostly longitudinally oriented, though radially oriented channels are also visible. In places a subreticular pattern of primary osteons are seen. The perimedullary region contains endosteal trabeculae. Few resorption cavities containing centripetally deposited lamellated bone tissue and secondary osteons are visible in the deep cortex.

The bone microstructure of the distal end of a femur reveals similar densely vascularized fibrolamellar bone tissue in the cortex, endosteal bone deposition in the deeper cortex resulting in a dense network of trabeculae, and large erosion bays (Ricqlès, 1969). Secondary reconstruction was however, nearly absent.

**Tibia**—The tibial mid-diaphyseal transverse section (SAM-PK-K5018) shows a thick cortex (RBT = 24.54%) and a relatively small medullary cavity (average diameter = 408  $\mu\text{m}$ ). The cortical fibrolamellar bone tissue has a high porosity. There are abundant radially oriented channels, especially in the outer cortex, whereas the primary osteons show a variable arrangement in the deeper cortex, ranging between subplexiform to subreticular. There are two narrow annuli, one almost at the cortical periphery and the other in the outer cortex. The periphery of the medullary cavity is uneven and resorptive on one side. However, it shows deposition of avascular endosteal lamellated bone on the other side, suggesting a lateral shift of the tibial longitudinal axis. Whether the channels in the bone are secondarily reconstructed or not cannot be discerned due to bad preservation.

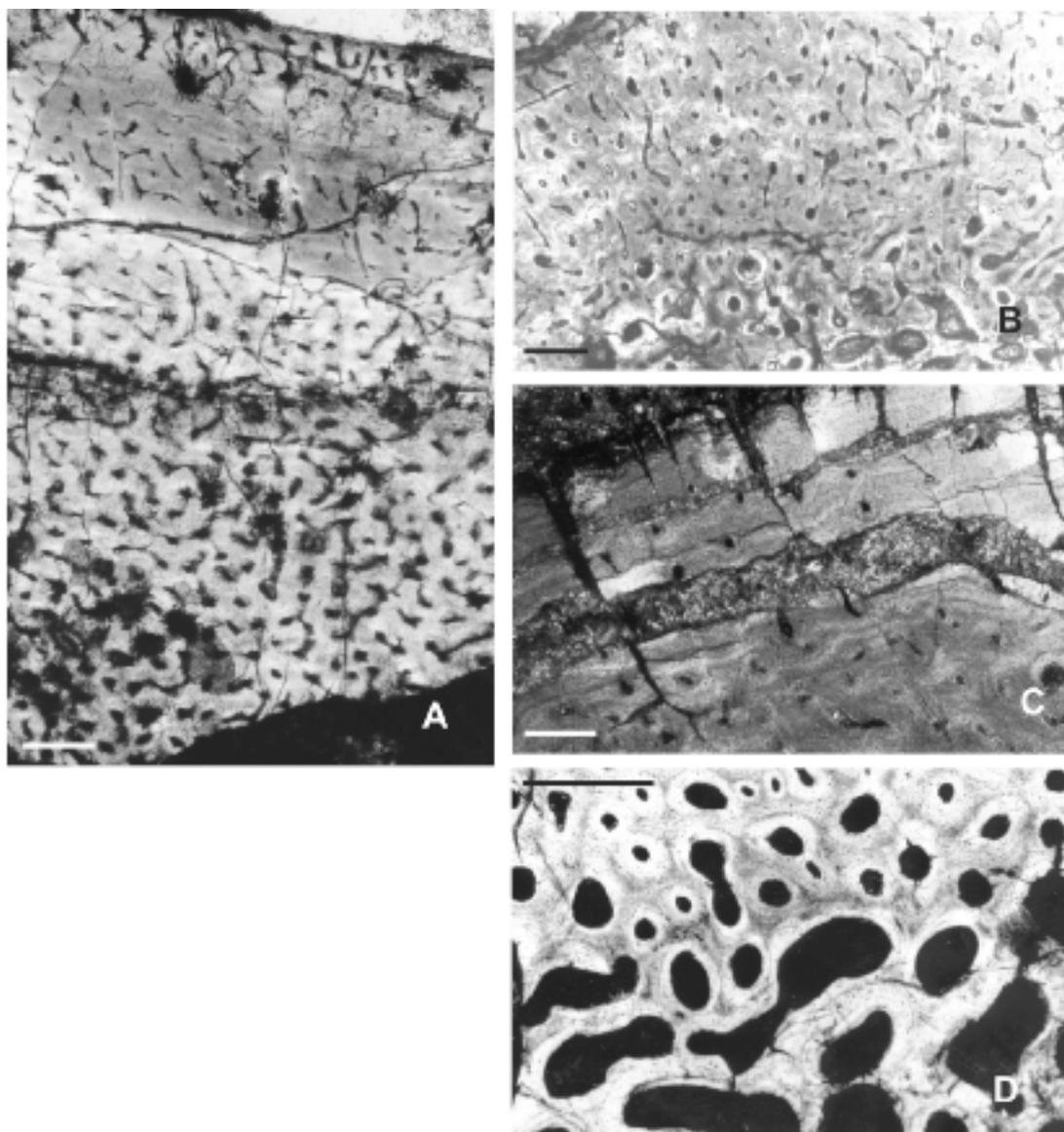


FIGURE 3. Transverse sections of *Pristerognathus* (SAM-PK-11557) showing **A**, femur consisting of uninterrupted fibro-lamellar bone with longitudinally oriented primary osteons and radial anastomoses; **B**, fibula with fibrolamellar bone tissue and longitudinally oriented primary osteons with radial anastomoses; **C**, outer cortex of the fibula showing closely spaced multiple annuli; **D**, perimedullary region of the rib showing cancellous pore spaces. Scale bars equal 400  $\mu\text{m}$ .

**Fibula**—(Fig. 3B). Two fibulae were examined from the specimens, SAM-PK-K5018 and the larger SAM-PK-11557. Diaphyseal sections of SAM-PK-11557 show a small free medullary cavity surrounded by a thick cortex (RBT = 25.11%). The essentially longitudinal primary osteons show radial and circumferential anastomoses and form almost a subreticular pattern in the deep cortex, but become sparse and small towards the periphery. The cortical porosity is 4.05%. Although SAM-PK-K5018 does not exhibit any growth rings, SAM-PK-11557 shows multiple, closely spaced, narrow annuli at the periphery (Fig. 3C). Another distinct feature of the fibula (SAM-PK-11557) is the extensive secondary reconstruction at the perimedullary region, which almost reaches the midcortex. It consists of resorption cavities and a few secondary osteons. Internal to this region, is a zone of cancellous bone and endosteally deposited avascular lamellated bone.

In the metaphyseal section of the fibula, SAM-PK-K5018, a narrow cortex surrounds a large medullary cavity. The medullary cavity contains endosteal trabeculae, especially at the periphery where convoluted compacted coarse cancellous bone is visible. The partially preserved cortex contains fibrolamellar bone tissue with longitudinal primary osteons. In the perimedullary region, a few secondarily enlarged channels and secondary osteons are present.

**Rib**—(Fig. 3D). Several rib fragments were studied from SAM-PK-11557. The transverse sections show a narrow cortex surrounding a large medullary cavity. The cortex is zonal and contains wide zones separated by two LAGs. The zones contain fibrolamellar bone tissue with essentially longitudinal primary osteons. However, arrangements of the primary osteons vary locally from subreticular to subplexiform. The medullary cavity has an uneven margin and contains endosteal trabeculae especially in the proximal sections.

### *Procynosuchus* (Cynodontia)

**General Description**—Three different skeletal elements from three different individuals were examined to reveal that the bone microstructure of *Procynosuchus* is distinct from that of the gorgonopsians and therocephalians. *Procynosuchus* is characterized by the predominance of lamellar-zonal bone tissue, which is particularly prominent in the clavicle and rib.

**Radius**—(Fig. 4A). The diaphyseal transverse sections of the radius (B/P/1/3747) are characterized by a thick cortex (RBT = 30.4%) and small medullary cavity. Approximately 80% of the inner cortex is composed of fibrolamellar bone with few longitudinally oriented primary osteons, which alternates with narrow annuli composed of lamellar bone. In contrast, the outer cortex or the peripheral 20% is composed of lamellar-zonal bone tissue and contains simple radially and longitudinally oriented canals. In this region the osteocyte lacunae show an almost linear arrangement. The cortex has a low porosity of 1.37%.

Few secondary osteons are present in the perimedullary region. Large cancellous spaces and an extensive network of bony trabeculae indicate endosteal deposition within the medullary cavity, which is considerably larger in the metaphyseal sections. Locally developed Sharpey's fibers are also visible in these metaphyseal sections, especially on the cranial and caudomedial surface of the radius.

**Clavicle**—The cortex of the clavicle (SAM-PK-K8511) consists entirely of lamellar-zonal tissue (Fig. 4B) with longitudinally oriented channels and extremely low cortical porosity (0.9%). Several LAGs are visible in the cortex and they become closely spaced towards the periphery. These LAGs are often multiple, narrow and closely spaced. Secondary osteons are observed in the perimedullary region. Large cancellous spaces and endosteal lamellar bone are prominent towards the ventral and medial ends of the clavicle. Sharpey's fibers are present on the cranial and dorsal sides.

**Rib**—An examination of the transverse sections of the rib (TSK 34) also reveals lamellar-zonal bone in the cortex. Extensive secondary remodeling is visible around the medullary cavity. The perimedullary region and deeper cortex contains abundant secondary and primary osteons, but shows a marked decrease towards the cortical periphery. Very few primary osteons and simple longitudinally oriented channels are present in the outer cortical area.

### *Tritylodon* (Cynodontia)

**General Description**—Five *Tritylodon* specimens were examined, the details of which are given in Table 1. Four humeri, ranging from 64% to 100% of the adult size, were examined. Although the average humeral RBT or the cortical thickness is 35%, it is found to vary greatly from 25–44% depending on the size of the humerus measured.

**Humerus**—(Fig. 5A). The thick cortex of the humerus is composed of fibrolamellar bone tissue and shows globular osteocyte lacunae with radiating canaliculi. The primary osteons vary from a radial to longitudinal orientation. There are no growth rings. The cortical porosity is approximately 5.26% in B/P/1/4785 (64% of the adult size). Secondary osteons are present in the perimedullary region. The circumferential endosteal lamellar bone tissue surrounds the medullary cavity in the mid-diaphyseal sections (B/P/1/5160), whereas a lateral shift of the longitudinal axis can be seen in the proximal metaphyseal sections of B/P/1/4785. The distal metaphyseal sections of B/P/1/5671 show extensive compacted coarse cancellous bone tissue at the medullary cavity, especially in the deltopectoral crest.

**Radius**—The radii (B/P/1/4785, 64% adult size, and B/P/1/5167, fragmentary) reveal distinct cortices, predominantly composed of fibrolamellar bone tissue. The cortex consists of a mixture of longitudinally oriented simple channels and primary os-

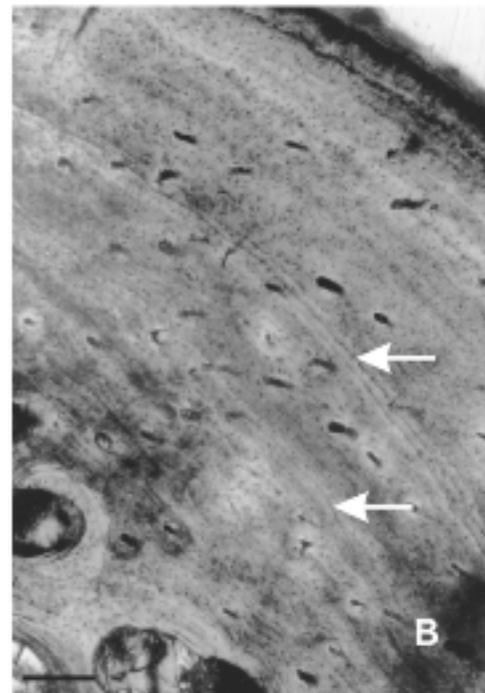
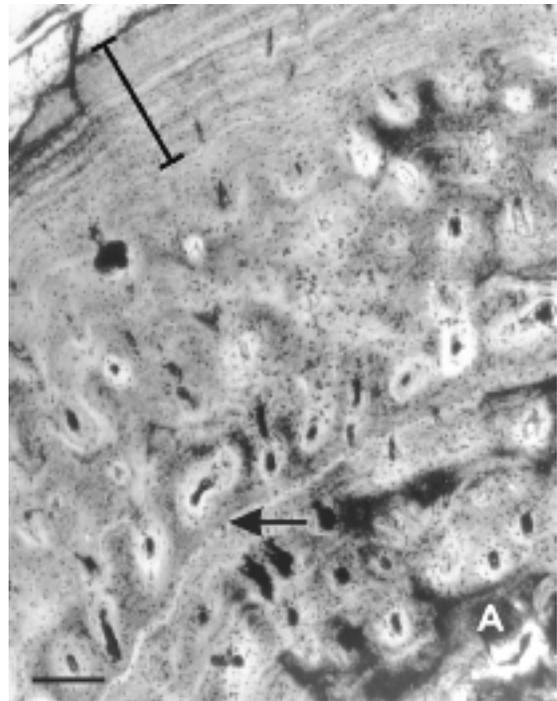


FIGURE 4. Transverse sections of *Procynosuchus* showing **A**, radius (B/P/1/3747) with the cortex composed of fibrolamellar bone tissue interrupted by annuli (arrow) and peripheral lamellar zonal bone (bracket). **B**, clavicle (SAM-PK-K8511) showing lamellar-zonal bone with LAGs (arrows) in the cortex. Scale bars equal 400  $\mu$ m.

teons. A slight change in tissue organization occurs at the subperiosteal periphery, where osteocyte lacunae are sparse and linearly arranged. This suggests a zone of parallel-fibered bone may be present, but this cannot be confirmed due to the poor preservation of the bone at the periphery. The cortical porosity of the radius, B/P/1/4785, is 3.15% and does not decrease towards

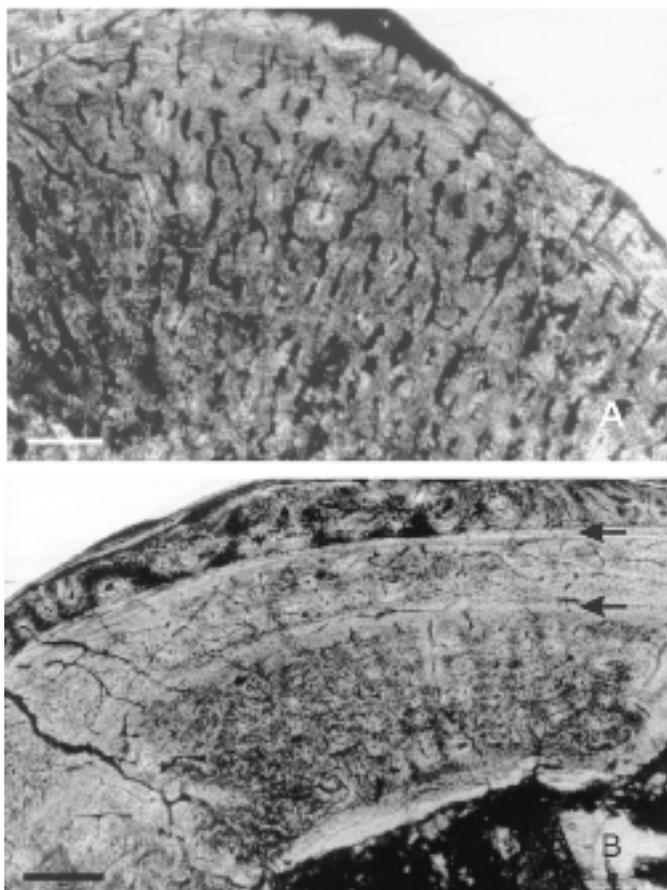


FIGURE 5. Transverse sections of *Tritylodon* showing **A**, fibrolamellar bone of the humerus (B/P/1/4785) and **B**, radius (B/P/1/5167) showing fibrolamellar bone tissue interrupted by two annuli. Scale bars equal 400  $\mu\text{m}$ .

the periphery. Although growth rings are absent in B/P/1/4785, two annuli were observed near the subperiosteal surface of B/P/1/5167 (Fig. 5B). There is extensive deposition of endosteal bone at the medullary margin, which is more pronounced in the metaphyseal region. The cortical porosity of B/P/1/5167 is 4.67%.

**Ulna**—The ulna, examined from specimen B/P/1/4785, consists of longitudinally oriented simple channels in a woven-fibered bone matrix. It has a moderate cortical porosity. Growth rings are absent and there is very little deposition of endosteal bone.

**Rib**—As in the other elements, the cortex of the rib is composed of fibrolamellar bone tissue. The primary osteons are longitudinally oriented. Dense osteocyte lacunae with radiating canaliculi and absence of growth rings characterize the cortical region. Few secondary osteons are present.

## DISCUSSION

### Growth Patterns

**Gorgonopsia: *Scylacops***—The most distinctive feature of *Scylacops* bone histology is the stratification of the cortex (Fig. 1). The zones consist of fibrolamellar bone tissue and are separated by narrow, but prominent, almost avascular lamellated annuli and/or LAGs. The presence of fibrolamellar bone tissue suggests rapid osteogenesis and hence fast growth, which was interrupted periodically by slow growth or complete cessation of growth as indicated by the annuli and LAGs (Amprino, 1947;

Ricqlès, et al. 1991; Chinsamy, 1997). In the Late Permian Karoo Basin the climate was hot and semi-arid with strongly seasonal rainfall (Keyser, 1966; Smith, 1993) and it is probable that *Scylacops* grew quickly during the favorable season and slowly or not at all during the unfavorable season.

SAM-PK-10188 was a large individual (skull length [SL] approximately 18 cm), with well-finished bone surfaces, suggesting that it was probably an adult or mature individual. However, the irregular cortical periphery and absence of peripheral rest lines imply that *Scylacops* was still growing. It possibly had an indeterminate growth strategy, similar to that of extant nonavian sauropsids.

**Gorgonopsia: *Aelurognathus***—Although few skeletal elements (humerus, femur, tibia) of SAM-PK-K10000 were available for study, *Aelurognathus* shows a marked difference in tissue organization to that of *Scylacops*, especially in the absence of cortical stratification. The predominant cortical bone is highly porous fibrolamellar bone tissue (Fig. 2A, B), similar to that observed by Ricqlès (1969). This bone tissue organization suggests rapid osteogenesis and fast growth. Growth rings are generally absent, suggesting sustained growth. The uneven subperiosteal peripheral cortical margin and absence of peripheral rest lines suggest that the individual (SAM-PK-K10000) was still growing. The preservation of calcified cartilage (Fig. 2C) in the epiphyseo-metaphyseal sections of the limb bones indicates that the epiphyseal structure was still actively involved in longitudinal growth (Haines, 1969). This suggests that SAM-PK-K10000 had not reached its full adult size, and was probably a sub-adult.

**Terocephalia: *Pristerognathus***—The predominant cortical bone in the various elements is fibrolamellar bone tissue with a high cortical porosity. This agrees with observations by Ricqlès (1969) on a *Pristerognathus* femur. These characteristics suggest rapid growth. The absence of LAGs and annuli from most of the elements (except the tibia) of the smaller individual (SAM-PK-5018) suggests that *Pristerognathus* experienced fast, uninterrupted growth early in ontogeny. Annuli were only present in the tibia of SAM-PK-5018, which may indicate inter-elemental histovariability or that the tibia grew more slowly than the other elements in general. The fast, sustained growth probably changed to relatively interrupted growth in the later stages as indicated by the subsequent occurrence of LAGs and annuli in the other skeletal elements (fibula and rib) of the larger specimen (SAM-PK-11557). The presence of closely spaced annuli at the periphery of the cortex of the SAM-PK-K11557 elements suggests that its overall growth decreased appreciably. It is proposed that *Pristerognathus* had a fast, sustained growth early in ontogeny, which became relatively slow and interrupted with age.

**Cynodontia: *Procynosuchus***—Due to the small sample size and fragmentary nature of the *Procynosuchus* material, the percentage adult size could not be calculated. The cortical bone of *Procynosuchus* in all the elements examined is zonal, consisting of either fibrolamellar tissue interrupted by annuli of lamellar-zonal tissue and/or LAGs, or solely lamellar-zonal bone (Fig. 4). The lamellar-zonal bone suggests a relatively slow rate of bone formation and hence a slow growth (Amprino, 1947; Ricqlès et al., 1991). The appearance of lamellar-zonal tissue at the radial periphery and its predominance in the clavicle and rib, very low cortical porosity and occurrence of more closely spaced annuli and LAGs near the periphery of the radius and clavicle suggest that these elements belong to adult/mature individuals.

The shift to an overall slowly growing lamellar-zonal tissue, from the rapidly growing fibrolamellar bone and closely spaced LAGs towards the periphery of the radius, suggest an overall slowing down in growth. This does not mean that growth ceased after the attainment of maximum size, as a considerable amount of lamellar-zonal bone at the radial subperiosteal periphery suggests continued growth, merely at a slower rate. The transition

may instead indicate the onset of sexual maturity (Castanet and Baez, 1991; Reid, 1996; Sander, 2000). The presence of intermittent interruptions in growth as indicated by the annuli and LAGs points towards a cyclical growth strategy, which was probably seasonally influenced. As *Procynosuchus* was an insectivore (Kemp, 1979, 1980), it probably grew rapidly during the warm or wet season, when insects were abundant and more slowly or not at all during the cold or dry season. Hence, its overall growth strategy is of an initial fast growth followed by slow interrupted growth (possibly after attaining sexual maturity) and a dependence on environmental fluctuations. This growth pattern is very similar to that of the Nile crocodile described by Reid (1996), which also exhibits similar fibrolamellar tissue in its limb bones early in ontogeny, which later becomes lamellar-zonal bone (Reid, 1996, 1997). The low cortical porosity of *Procynosuchus* is also similar to that of adult *Crocodylus niloticus* (femoral cortical porosity of 1.85%, Chinsamy, 1991).

**Cynodontia: *Tritylodon***—The bone histology of *Tritylodon* reveals fibrolamellar bone tissue (Fig. 5) suggesting rapid growth similar to the cynodont, *Cynognathus* (Fig. 6). An abundance of longitudinal primary osteons and lack of growth rings (apart from one radius) characterizes *Tritylodon* histology. The growth rings in the radius, B/P1/5167 suggest that the animal experienced a particularly stressful growing season, but probably does not reflect the overall growth strategy of the genus as all the rest of the elements lack any interruptions in growth.

#### Inter-elemental Histological Variation

The noteworthy feature in the gorgonopsians, *Scylacops* and *Aelurognathus*, the therocephalian *Pristerognathus*, and the cynodonts *Procynosuchus* and *Tritylodon* is the inter-elemental histovariability, which is particularly evident where multiple elements of the same individual were examined. Table 2 documents these variations based on the organization of the primary osteons, which even varies locally within the same section, RBT, cortical porosity, incidence of annuli and LAGs, extent of secondary reconstruction and endosteal bone deposition. In *Scylacops* (SAM-PK-10188), the femur exhibits a tightly packed laminar to subplexiform pattern of the primary osteons and relatively high cortical porosity (4.33%) whereas the other limb bones have mainly longitudinally oriented canals and a cortical porosity of less than 4% (Fig. 7). Although the number of annuli and LAGs vary between five and six, relatively greater incidences are noted in the epipodials. Inter-elemental histovariation within the same individual is also observed in *Aelurognathus*, *Pristerognathus* and *Tritylodon* (Table 2). Although it was not possible to study such variation in *Procynosuchus* due to the small sample size and lack of multiple elements from a single individual, a marked difference in the tissue type between the radius and non-limb bones was observed. The tissue type changed from a fibrolamellar complex to lamellar-zonal bone in the radius, whereas the clavicle and rib exhibit only lamellar-zonal bone. Distinct histovariability is also seen between the limb bones of the same individual in the dicynodont *Diictodon* (Ray and Chinsamy, 2004).

The cortices of all the skeletal elements examined exhibit various arrangements of the primary osteons and differing cortical porosity. A recent study on the mallards by Margerie et al. (2002) shows that in the four major bone tissue types such as fibrolamellar bone tissue, lamellar-zonal, etc., (sensu Margerie et al. 2002) a correlation exists between the primary osteon diameter and growth rate. Larger primary osteons suggest fast growth and fibrolamellar bone tissue has the fastest growth rate compared to that of other major tissue types. However, caution should be exercised when inferring deposition rates from differing primary osteon patterns within fibrolamellar bone tissue (e.g., Castanet et al., 2000). Starck and Chinsamy (2002) have

shown that the rate of deposition of one type of fibrolamellar bone in the Japanese quail overlaps the full range of bone deposition rates associated with other types of fibrolamellar bone tissue described by Castanet et al. (2000).

Variations in the histology of the skeletal elements of the same individual have been observed in several individuals in the current study. This has also been observed in the dinosaurs, *Apatosaurus* (Curry, 1999) and *Maiasaura* (Horner et al., 2000). Since bone histology is affected by a variety of factors, including phylogenetic, ontogenetic, functional and biomechanical constraints (Ricqlès et al., 1991; Reid, 1996; Curry, 1999; Starck and Chinsamy, 2002), such variation within a single skeleton is not unexpected. Indeed, Starck and Chinsamy (2002) have documented bone deposition rates in the skeleton of Japanese quail and have reported variable rates in the skeleton, with the radius growing the slowest.

It is evident from Table 2 that the epipodials generally have a relatively low cortical porosity and more annuli and LAGs compared to the propodials within the same individual. This suggests not only variable appositional growth in the limb bones, but also that the epipodials probably had a slow growth relative to the propodials. In addition, other skeletal elements such as the ribs and clavicle, having extremely low cortical porosity and distinct annuli and LAGs, probably grew more slowly compared to the limb bones. This is especially apparent in *Procynosuchus*, where the cortices of the rib and clavicle are composed entirely of the slow growing lamellar-zonal bone tissue in contrast to that of the radius. These differences in the bone microstructure of the skeletal elements suggest, among other factors, variable responses of the individual element to environmental conditions (Starck and Chinsamy, 2002) including differing functional constraints.

#### Growth Patterns Within the Nonmammalian Therapsids

An osteohistological comparison between representative taxa spanning the major clades, including additional genera such as *Diictodon* (Ray and Chinsamy, 2004), *Diademodon* and *Cynognathus* (Botha and Chinsamy, 2000), reveal distinctly differing bone microstructure and growth patterns among the nonmammalian therapsids as summarized in Table 3. The dominant primary bone tissue type of all the genera studied is fibrolamellar bone (Fig. 8). This finding agrees with earlier observations by Ricqlès (1969, 1972). However, unlike Ricqlès, we have found that although fibrolamellar bone dominates, it is generally interrupted by LAGs and annuli (except in *Cynognathus* and *Tritylodon*).

The presence of fibrolamellar tissue even in the adult individuals suggests a periodic fast rate of bone deposition that (Amprino, 1947; Margerie et al., 2002), except for *Cynognathus* and *Tritylodon*, alternated with slower periods of growth or a complete cessation in growth (as suggested by the annuli and/or LAGs). Such interrupted, but fast growth is most pronounced in the adults. In the large Late Permian carnivorous *Scylacops*, the strongly cyclical growth is evident from the prominent, more or less equidistant five to six annuli and LAGs present in all the elements examined (Fig. 1). The annuli are composed of relatively avascular lamellated bone, suggesting an initial slowing down followed by the complete cessation of growth for a brief period as suggested by the LAGs. These interruptions represent changes in the rate of deposition and were probably temperature induced. The cyclical growth of *Scylacops* is markedly different from that of *Aelurognathus*, another contemporary, but small carnivore (SL = 14 cm). The latter had a fast, sustained growth early in ontogeny, which probably became interrupted later in ontogeny.

This relatively fast growth of *Aelurognathus* is comparable with that of the contemporaneous, similar sized (SL = 13 cm), but herbivorous dicynodont *Diictodon*. The latter shows indeter-

TABLE 2. Inter-elemental histovariability within a single individual. **A**, *Scylacops* (SAM-PK-10188); **B**, *Aelurognathus* (SAM-PK-K10000), **C**, *Pristerognathus* (SAM-PK-5018) and **D**, *Tritylodon* (B/P/1/4785).

Taxon		Humerus	Radius	Ulna	Femur	Tibia	Fibula
<b>A. <i>Scylacops</i></b>	<b>1</b>	longitudinal	longitudinal, with radial and circumferential anastomoses	longitudinal, occasional circumferential anastomoses	laminar-subplexiform	—	longitudinal
	<b>2</b>	3 LAGs	6 LAGs + annuli	5 LAGs + annuli	5 LAGs	—	6 LAGs + annulus
	<b>3</b>		2.53%	3.80%	4.33%	—	3.60%
	<b>4</b>	endosteal trabeculae	CCCB	CCCB	endosteal trabeculae	—	endosteal lamellated bone
	<b>5</b>	resorption cavities, secondary osteons	extensive, resorption cavities, secondary osteons	few secondary osteons, resorption cavities	resorption cavities, secondary osteons	—	resorption cavities, secondary osteons
<b>B. <i>Aelurognathus</i></b>	<b>1</b>	longitudinal	—	—	longitudinal, radial and circumferential anastomoses	longitudinal, radial and circumferential anastomoses	—
	<b>2</b>	2 LAGs	—	—	none	none	—
	<b>3</b>	high (4.68%)	—	—	8.32%	moderate	—
	<b>4</b>	CCCB	—	—	endosteal trabeculae	—	—
	<b>5</b>	resorption cavities, secondary osteons	—	—	—	—	—
<b>C. <i>Pristerognathus</i></b>	<b>1</b>	laminar-subplexiform	longitudinal, radial anastomoses	profusion of radial channels	longitudinal and radial bone channels	longitudinal and radial bone channels	longitudinal and radial bone channels
	<b>2</b>	none	none	none	none	2 annuli moderate	annulus high (4.05%)
	<b>3</b>	high	—	—	—	—	—
	<b>4</b>	CCCB	extensive CCCB	lamellated bone at perimedullary region	endosteal trabeculae	avascular endosteal lamellated bone	CCCB, layers of avascular lamellated bone tissue
	<b>5</b>	resorption cavities	resorption cavities	secondary osteons, resorption cavities	resorption cavities, secondary osteons	cannot be discerned	extensive, secondary osteons
<b>D. <i>Tritylodon</i>*</b>	<b>1</b>	longitudinal	primary osteons and simple longitudinal channels	longitudinal	—	—	—
	<b>2</b>	none	2 annuli	none	—	—	—
	<b>3</b>	high (5.26%)	moderate (3.15%)	moderate	—	—	—
	<b>4</b>	circumferential endosteal bone, CCCB	extensive	endosteal bone	—	—	—
	<b>5</b>	secondary osteons	—	—	—	—	—

1, organization of the primary osteons; 2, annuli and LAGs, 3, cortical porosity (quantified where possible); 4, endosteal bone deposition; 5, secondary reconstruction. **CCCB**, Compacted coarse cancellous bone; **LAG**, line of arrested growth; \*fibrolamellar bone tissue and lamellar-zonal bone tissue.

minate, but fast growth as suggested by the fibrolamellar bone tissue (Fig. 6A) and high cortical porosity that ranges from 6–8% even in the adults (Ray and Chinsamy, 2004). Growth was uninterrupted during the juvenile stage and was only periodically interrupted during adulthood, when environmental stress possibly resulted in estivation in deep helical burrows (Ray and Chinsamy, 2004).

Similar growth patterns to that of *Aelurognathus* and *Diictodon* are also evident in the therocephalian, *Pristerognathus*, a large Late Permian carnivore (SL = 22 cm). It had a sustained fast growth as a juvenile, but growth became interrupted later in ontogeny. Several closely spaced peripheral annuli in the fibula suggest a marked slowing of growth in older individuals.

The nonmammalian cynodont genera show markedly differing growth patterns (Table 3, Fig. 8) with the early form, *Procynosuchus* (SL = 10 cm), showing rapid cyclical growth early in ontogeny and a considerable decrease in overall growth rate once adulthood was reached. Its overall growth, as suggested by the presence of lamellar-zonal bone in the limbs, is slow in comparison to that of the other taxa examined and is more similar to that of extant crocodylians. In contrast, the more derived, large Triassic genera, *Diademodon* and *Cynognathus*, show distinctly different growth strategies as noted by Botha and Chinsamy (2000). *Diademodon* an omnivore/herbivore experienced cyclical growth as indicated by the presence of fibrolamellar bone tissue interrupted by narrow annuli (Fig. 6B). The carnivorous *Cynognathus* had a sustained fast growth strategy as seen by the

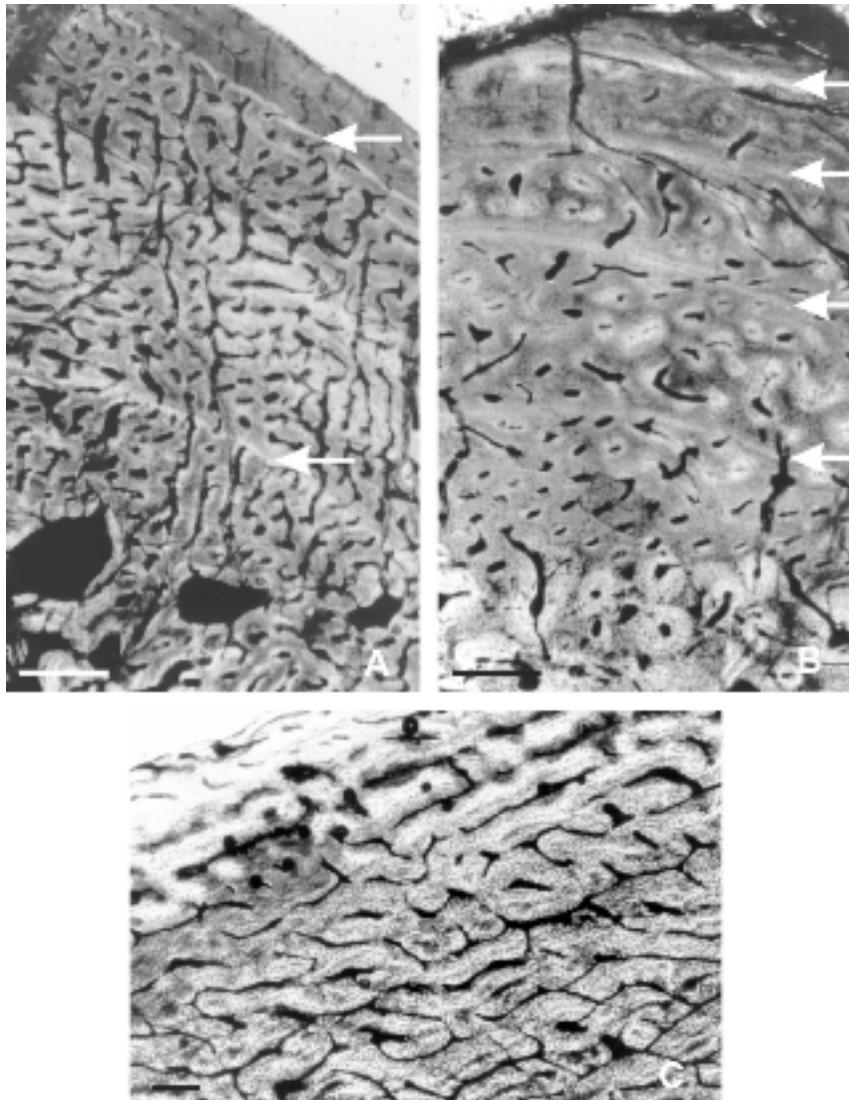


FIGURE 6. Diaphyseal transverse sections of adult limb bones containing fibrolamellar bone tissue in **A**, *Diictodon* (SAM-PK-K6716a) femur showing plexiform-subreticular pattern and two annuli. **B**, *Diademodon* (B/P/1/3772) humerus showing longitudinal primary osteons with few radial anastomoses and four annuli. **C**, *Cynognathus* ulna (NMQR3019) showing a subplexiform vascular arrangement and no annuli or LAGs. Arrows indicate LAGs. Scale bars equal 400  $\mu\text{m}$ .

presence of fibrolamellar bone tissue and absence of annuli or LAGs (Fig. 6C). As these two genera were contemporaneous and their remains are often found together in the same deposits, it is reasonable to assume that they experienced similar climatic conditions, which was semi-arid, with seasonal rainfall (Smith et al., 1993). The differences in their growth strategies have been attributed to either contrasting food requirements or inherent physiological differences (Botha and Chinsamy, 2000). The bone microstructure and growth strategy of *Tritylodon*, an Early Jurassic form and most closely related to the early mammals, suggests a fast, sustained growth that probably slowed down after attaining adult size. The bone histology of *Tritylodon* is similar to that of other tritylodontids such as *Bienotherium* and *Oligokyphus* (Ricqlès, 1969) and suggests that this family had undergone a progression towards overall rapid growth.

In summary, the dominance of fibro-lamellar bone indicates that these animals grew quickly, but the presence of annuli and/or LAGs indicates periodic arrests in growth. The most growth would therefore have occurred during the favorable season.

Similar LAGs have been observed in some rodents during hibernation (Klevezal, 1996), whereas Chinsamy et al. (1998) have shown that polar bears develop LAGs during extreme conditions. Starck and Chinsamy (2002) have suggested that LAGs are an expression of a high degree of developmental plasticity in animals, which is the ability to respond to changes in the environment by evoking different developmental regimes (Smith-Gill, 1983). This ability to stop growth and development during adverse environmental conditions is considered to be a highly functional trait that allows an individual to adjust to external conditions (Starck and Chinsamy, 2002). The variable incidence of annuli and LAGs in the genera examined could thus be interpreted as variable responses to environmental conditions. The growth pattern of *Scylacops* suggests a strong influence of seasonality on growth and a high degree of developmental plasticity, whereas the absence of LAGs suggests a loss of developmental plasticity, which is evident in *Cynognathus* and possibly *Tritylodon*. The growth strategy of *Tritylodon* is very similar to that of the extant mammals, which grow along comparatively inflexible

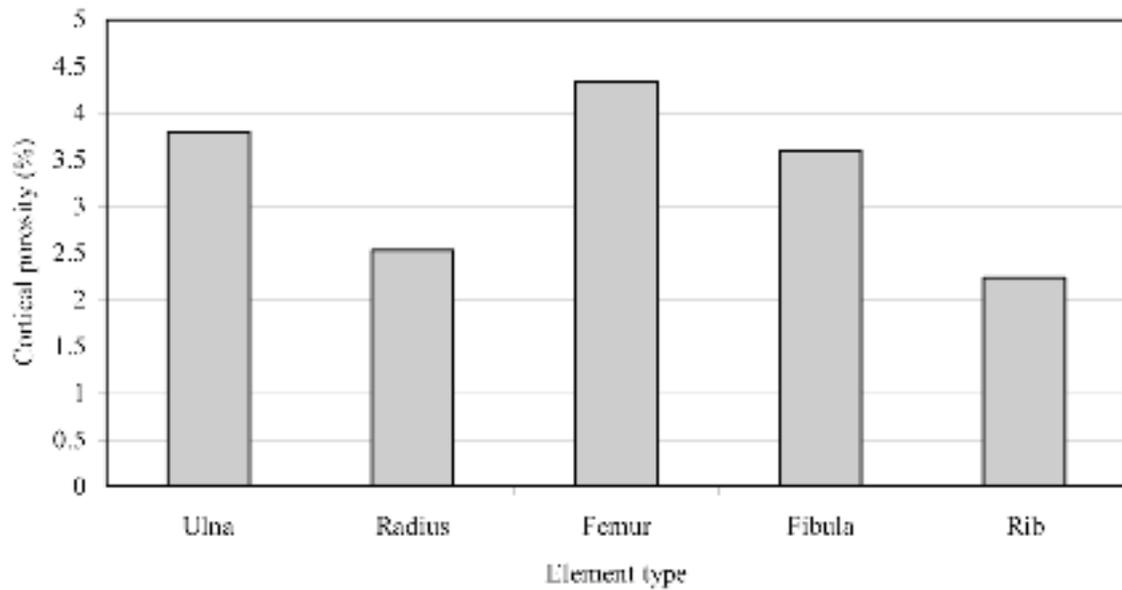


FIGURE 7. Cortical porosity of the various *Scylacops* elements. When comparing these elements, the femur has the highest cortical porosity of 4.33% and the rest of the limb bones and rib have a cortical porosity of less than 4%.

TABLE 3. Histological characteristics and growth patterns of the nonmammalian therapsids studied. Sources of information for *Diictodon*, Ray and Chinsamy (2004); *Cynognathus* and *Diademodon*, Botha and Chinsamy (2000), Botha (2002). SL = skull length.

Taxon	Age	Lifestyle, size	Histological characteristics	Growth marks	Growth patterns
<i>Diictodon</i>	Late Permian, <i>Tropidostoma</i> and <i>Cistecephalus</i> Assemblage Zone	small fossorial herbivore, SL 13 cm	fibrolamellar bone tissue (FL), profuse radial channels, subplexiform-reticular pattern, high cortical porosity, resorption cavities, very few secondary osteons	variable incidences of narrow annuli and LAGs	sustained fast growth as juveniles; periodic interruption only in adults; indeterminate growth strategy
<i>Scylacops</i>	Late Permian, <i>Cistecephalus</i> Assemblage Zone	large carnivore, SL 18 cm	zonal FL, longitudinal primary osteons, moderate-low cortical porosity, endosteal lamellated bone, distinct reversal line, secondary reconstruction, few secondary osteons	pronounced LAGs and annuli	cyclical and indeterminate-growth strongly affected by environment
<i>Aelurognathus</i>	Late Permian, <i>Tropidostoma</i> Assemblage Zone	small carnivore, SL 14 cm	FL, longitudinal primary osteons, high cortical porosity, endosteal bone, distinct reversal line	none	possibly sustained, fast growth
<i>Pristerognathus</i>	Late Permian, <i>Pristerognathus</i> Assemblage Zone	large carnivore, SL 22 cm	FL, longitudinal and radial channels, high cortical porosity, few secondary osteons, endosteal bone deposition	annuli in tibia and fibula	sustained fast growth as juveniles; cyclical later in ontogeny, growth rate possibly decreased as adults
<i>Procynosuchus</i>	Late Permian, <i>Cistecephalus</i> Assemblage Zone	small insectivore SL c. 10 cm	zonal, FL and peripheral lamellar bone tissue, radial and longitudinal channels, very low cortical porosity, few secondary osteons	annuli and LAGs	relatively fast cyclical growth as juveniles; decreases markedly later in ontogeny to become overall slow growth
<i>Cynognathus</i>	Triassic, <i>Cynognathus</i> Assemblage Zone	large carnivore, SL 28 cm	azonal FL, plexiform arrangement, high cortical porosity, few secondary osteons	none	sustained rapid growth; indeterminate growth strategy
<i>Diademodon</i>	Triassic <i>Cynognathus</i> Assemblage Zone	large herbivore/ omnivore SL 21 cm	zonal, FL, longitudinal primary osteons with radial and circumferential anastomoses, moderate-low cortical porosity, extensive secondary reconstruction	annuli and LAGs	cyclical fast growth and periodic decrease/cessation in growth rate
<i>Tritylodon</i>	Early Jurassic, <i>Massospondylus</i> Range Zone	small herbivore, SL c. 8 cm	azonal FL, peripheral decrease in growth, longitudinal primary osteons, high cortical porosity, few secondary osteons	generally none	uninterrupted rapid growth, possibly decreased later in ontogeny

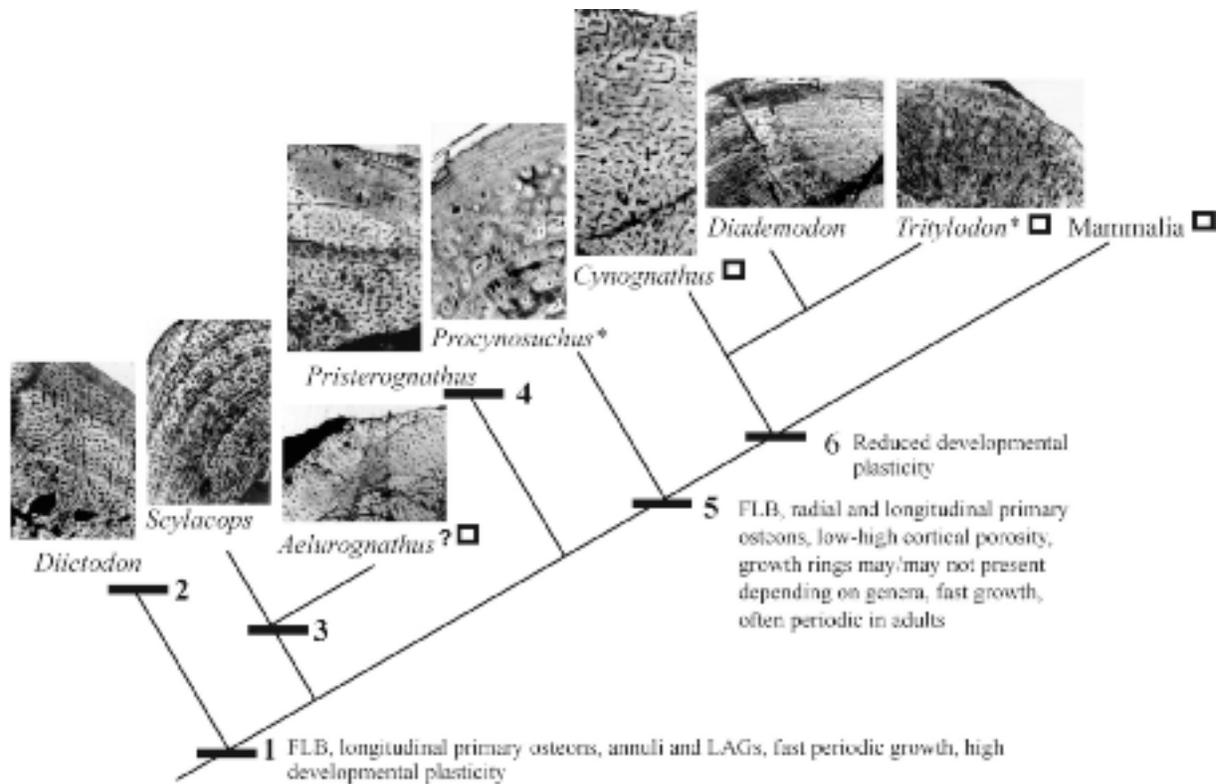


FIGURE 8. The cladogram (modified from Rubidge and Sidor, 2001) shows the evolution of growth strategies as revealed by bone histology. Transverse diaphyseal sections of the femora [\*except for *Procynosuchus* (radius) and *Tritylodon* (humerus)] show the changes in cortical tissue between the genera examined. The synapomorphies are as follows. 1, Neotherapsida—fibrolamellar bone tissue (FLB), longitudinal primary osteons, annuli and LAGs, fast but interrupted growth, high developmental plasticity; 2, Dicotylia (*Diictodon*)—Zonal FLB, laminar-plexiform pattern, high cortical porosity, fast cyclical growth; 3, Gorgonopsia (*Scylacops* and *Aelurognathus?*)—Zonal FLB, low-moderate cortical porosity, growth often affected by environment; 4, Therocephalia (*Pristerognathus*)—FLB, longitudinal primary osteons, high cortical porosity, fast sustained growth, periodic slowing down in adults; 5, Cynodontia (including mammals)—FLB, radial and longitudinal primary osteons, low-high cortical porosity, growth rings may/may not be present depending on genera, fast growth, often interrupted in adults. 6, Reduced developmental plasticity. Square (□) indicates sustained fast growth.

developmental trajectories (Starck and Chinsamy, 2002). Although the number of taxa studied here is too small to give any definite result, a preliminary investigation involving the mapping of optimized discrete and continuous data (Smith, 1994) reveals possible independent and parallel acquisitions of sustained fast growth in different nonmammalian therapsid lineages, especially in the nonmammalian cynodonts. The ability to form LAGs, and developmental plasticity were probably reduced in the stem groups.

### CONCLUSIONS

- In all the nonmammalian therapsids examined, the limb bone cortices contain fibrolamellar bone tissue, which qualitatively suggests rapid osteogenesis and fast growth. The presence of growth rings, however, indicates that this rapid growth was periodic. The organization of the primary osteons, cortical porosity, incidences of annuli and LAGs, extent of secondary reconstruction and endosteal bone deposition varies greatly within these study taxa suggesting distinct growth patterns.
- The Late Permian gorgonopsian, *Scylacops*, had distinctly cyclical, indeterminate growth, where periods of fast growth were interrupted by periods of slow growth or complete cessation of growth. This growth pattern differs from that of another gorgonopsian *Aelurognathus*, which probably had sustained fast growth early in ontogeny and interrupted growth only at a later stage.
- The growth pattern of the therocephalian *Pristerognathus* is very similar to that of *Aelurognathus*. In addition, growth slowed down markedly later in ontogeny as suggested by the presence of multiple, closely spaced annuli and LAGs near the subperiosteal periphery of the fibula.
- The cynodonts, *Procynosuchus* and *Tritylodon* show distinctly different bone microstructure and growth patterns. The former shows lamellar-zonal bone as primary cortical bone in the ribs and clavicle, whereas the radial cortex comprises an internal zone of fibrolamellar bone tissue surrounded by lamellar-zonal bone tissue. The overall tissue organization, annuli and LAGs and low cortical porosity suggest that *Procynosuchus* experienced an interrupted, but fast growth early in ontogeny, which slowed down appreciably once adulthood was reached. In contrast, the more derived, Early Jurassic *Tritylodon* had fast, sustained growth throughout ontogeny.
- Variations in the bone microstructure such as organization of the primary osteons, incidence of annuli and LAGs, cortical porosity, extent of secondary reconstruction and endosteal bone deposition was observed between the skeletal elements of the same individual in all the taxa studied. These variations have been attributed to the variable growth rate of different elements. It was found that the propodials usually grew faster than the epipodials, whereas the limb bones grew relatively faster than other skeletal elements such as the rib and clavicle.
- A phylogenetic assessment of the growth patterns of the study

taxa (including *Diictodon*, *Cynognathus* and *Diademodon*) suggests possible independent and parallel acquisitions of sustained fast growth in different neotherapsid lineages, especially in the nonmammalian cynodonts.

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