

GROWTH PATTERNS OF *THRINAXODON LIORHINUS*, A NON-MAMMALIAN CYNODONT FROM THE LOWER TRIASSIC OF SOUTH AFRICA

by JENNIFER BOTHA *and* ANUSUYA CHINSAMY

Zoology Department, University of Cape Town, Private Bag, Rondebosch, 7701 Cape Town, South Africa; current address: Karoo Palaeontology, National Museum, PO Box 266, Bloemfontein 9300, South Africa; e-mail: jbotha@nasmus.co.za

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Abstract: The growth dynamics of the Early Triassic non-mammalian cynodont *Thrinaxodon liorhinus* were assessed through bone histology. Several limb bones of various sizes were examined, revealing a rapidly deposited, uninterrupted, fibro-lamellar bone tissue. A region of slowly deposited parallel-fibred bone occurs peripherally in most skeletal elements studied, becoming more extensively developed in the larger limb bones. On the basis of the bone histology, it is proposed that *Thrinaxodon liorhinus* grew rapidly during early ontogeny, and at a slower rate with

increasing age, possibly once sexual maturity was reached. Variation in bone tissue patterns at different stages of ontogeny is noted and discussed. Given that growth rings are generally absent from the skeletal elements studied, and that the environment was seasonal, it appears that *Thrinaxodon liorhinus* growth was unaffected by environmental fluctuations.

Key words: growth patterns, bone histology, non-mammalian cynodont, *Thrinaxodon*.

THRINAXODON LIORHINUS was a small, short-limbed, carnivorous non-mammalian cynodont whose remains have been recovered from Early Triassic strata in South Africa and Antarctica (Brink 1954; Colbert and Kitching 1977; Hammer 1990; Rubidge 1995). It represents the next stage in non-mammalian cynodont evolution after the basal Late Permian non-mammalian cynodont, *Procynosuchus* (Kemp 1982; Rubidge and Sidor 2001). The genus is thought to have played a particularly significant role in synapsid evolution and several authors have suggested that mammals evolved from a *Thrinaxodon*-type ancestor as it combines several basal features with more derived ones (Fourie 1974; Kemp 1982; Battail 1991).

Morphological studies have shown that *Thrinaxodon* had a basic alternating tooth-replacement pattern similar to that of extant crocodylians and lizards (Estes 1961; Crompton 1963; Fourie 1974). However, more derived characteristics such as a complete bony secondary palate (Watson 1920; Parrington 1933) and a double occipital condyle (Hopson 1964; Grine *et al.* 1979; Kemp 1982) are also present. Furthermore, anterolateral ridges have been documented in *Thrinaxodon* nasal cavities, which may indicate the presence of respiratory turbinates and may imply that *Thrinaxodon* had expanded ventilation rates and aerobic capacities compared with that of extant crocodylians and lizards (Brink 1955; Hillenius 1992).

The most notable morphological postcranial development in *Thrinaxodon* is an expansion of the inner part of

the rib shaft to form a series of closely interlocking plates. Several functional implications of these intercostal plates have been proposed, including musculature control (Gregory and Camp 1918), strengthening of the vertebral column (Jenkins 1971), the prevention of lateral bending (Kemp 1982) as well as rib cage support during possible diaphragm contractions (Gregory and Camp 1918; Brink 1956, 1958).

These studies have used traditional morphological and anatomical methods to study the palaeobiology of *Thrinaxodon*, which has helped improve our understanding of the morphological changes that occurred during the 'reptile to mammal' transition. In the current study, a detailed analysis of the bone microstructure of multiple, different sized *Thrinaxodon* limb bones will provide further information about the biology of this genus. It is well recognized that when the bone microstructure (histology) of an extinct animal is well preserved, it provides a host of information about the ontogeny, individual age, lifestyle habits and growth patterns of the animal (Chinsamy and Dodson 1995). Various aspects of its physiology can be indirectly deduced as well (Chinsamy and Rubidge 1993; Chinsamy and Dodson 1995).

MATERIAL AND METHODS

The study material was excavated from the Early Triassic *Lystrosaurus* Assemblage Zone, Katberg Formation,

Beaufort Group, Karoo Supergroup of South Africa (Groenewald and Kitching 1995) (Text-fig. 1). Based on sedimentary facies, the environment is thought to have been warm and temperate, with seasonal rainfall and floods (Tucker and Benton 1982; Smith *et al.* 1993; Rubidge 1995; Smith 1995).

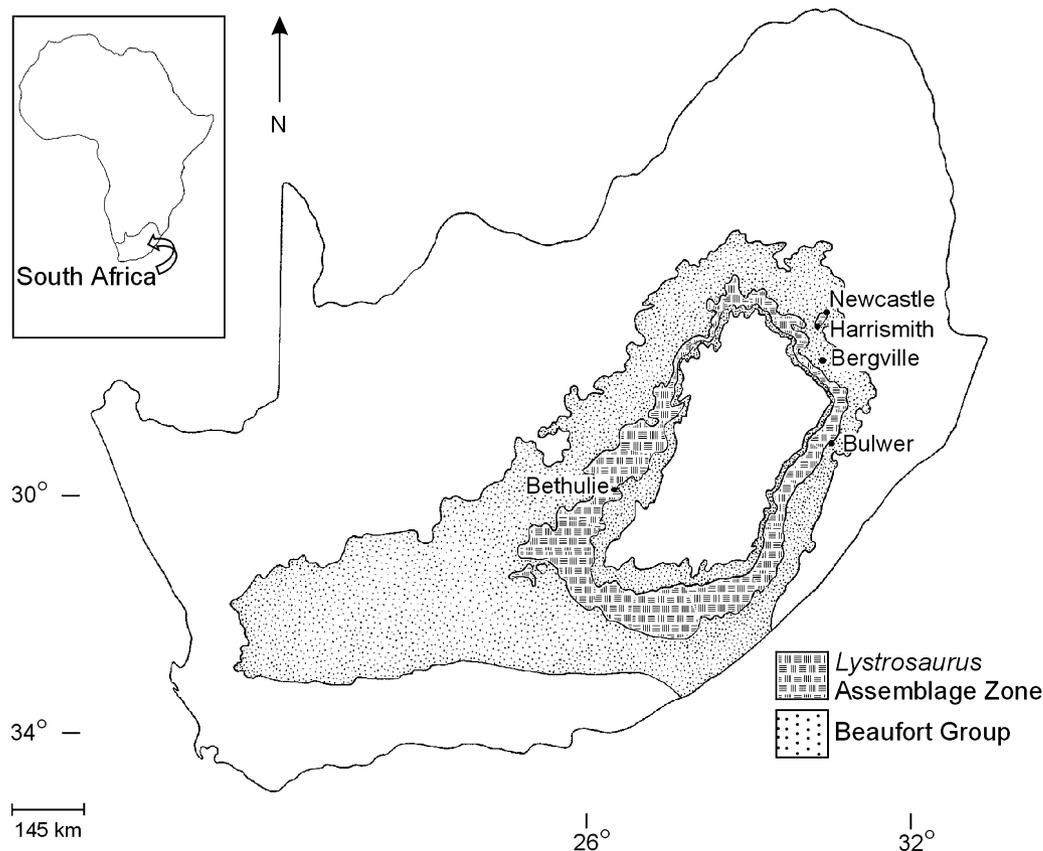
Ten positively identified *Thrinaxodon* limb bones (identified on the basis of associated cranial material) comprising humeri, radii, ulnae and femora were selected for histological analysis (Table 1). Limb bones were specifically chosen as they are usually more frequently preserved and therefore more readily available for study. They also permit a reasonable assessment of the ontogenetic growth of an animal as they do not experience extensive secondary remodelling in the midshaft regions (Chinsamy 1990, 1991; Francillon-Vieillot *et al.* 1990a; Horner *et al.* 1999).

The total lengths, midshaft diameter and proximal widths of the limb bones were measured. Measurements of the complete specimens were used to estimate the total lengths of the incomplete elements and the percentage adult size of each element was estimated. Specimen BP/1/1730 is the largest complete specimen in the study and on the basis of the size and well-finished bone

surfaces, is considered to be a mature individual. Using this specification, the ratio of diameter to length for the radius, humerus, ulna and femur was calculated. These ratios were then used to determine the total lengths of the incomplete elements in the study. The estimated total length of each incomplete element was then divided by the total length of the respective complete element from specimen BP/1/1730 and a percentage of adult size was thus obtained.

Thin sections were prepared using a similar method to that used by Chinsamy and Raath (1992). As far as possible, elements were serially sectioned so that intra-elemental histovariability as well as inter-elemental histovariability could be documented.

The channels in fossil bone represent the area where lymph, nerves and vascular canals traverse the bone tissue when the animal was alive (McKenzie and Klein 2000). Although the organic components are destroyed during fossilization, the channels themselves usually remain intact, allowing the area they occupied in a given cross-section of bone to be quantified. As these channels would have included lymph and nerves as well as vascular canals when the animal was alive, it is recognized that the



TEXT-FIG. 1. Map of South Africa showing the *Lystrosaurus* Assemblage Zone in the Katberg Formation, Beaufort Group, Karoo Supergroup of South Africa. The *Thrinaxodon* specimens used in this study were recovered from localities near the towns Bergville, Bethulie, Bulwer, Harrismith and Newcastle. Map compiled from the Reader's Digest (1994) and Groenewald and Kitching (1995).

TABLE 1. *Thrinaxodon* specimens used in this study and the localities from which the specimens were recovered. All localities are situated in the *Lystrosaurus* Assemblage Zone, Katberg Formation, Beaufort Group, Karoo Supergroup of South Africa (Text-fig. 1). The radius BP/1/4282a and the ulna BP/1/4282b were taken from the same individual. The femora SAM-PK-K8004a and 8004b are the right (a) and left (b) femora of one individual.

District	Specimen no.	Skeletal element	No. of sections	Region sectioned
Bergville	BP/1/5208	humerus	11	complete
	BP/1/5018	ulna	11	complete
Bethulie	BP/1/4282a	radius	11	complete
	BP/1/4282b	ulna	12	complete
	SAM-PK-K8004a	femur	6	proximal/midshaft
	SAM-PK-K8004b	femur	8	complete
Bulwer	BP/1/2820	humerus	13	complete
Harrismith	SAM-PK-K1221	humerus	10	proximal/midshaft
Newcastle	BP/1/1730	radius	11	complete
Unknown	SAM-PK-K1395	femur	4	midshaft

vascular canals may not have occupied the entire channel area. For example, Starck and Chinsamy (2002) found that only 20 per cent of the channel area in Japanese quail bones contained vascular canals and that sometimes more than one vascular canal occupied a single channel space.

The area occupied by channels within selected cross-sections (referred to as channel area) was quantified in the *Thrinaxodon* limb bones to detect porosity differences between the different elements, as well as through ontogeny. This quantification of the channel area indicates the maximum possible area of the vascular canals when the animal was alive, giving an approximate vascularization value that can be compared between different elements.

The quantification method was standardized using transverse thin sections of the mid-diaphysis in the mid-cortical region of each bone. Asymetrix Digital Video Producer 3.0 (1994) was used to capture images at 10 \times magnification from a Nikon Alphaphot-2 YS2 petrographic microscope. The Jandel Scientific Sigma Scan/Image Analysis (Pro 41993) was used to analyse the images. After randomly selecting a field of view in the mid-cortex, every third field of view from that point was

examined. The sum of the surface area of all channels in each field of view was then calculated (in μm). Two thin sections in the mid-diaphyseal region of each bone were quantified and the mean of the two sections was calculated. This mean was converted into a percentage, representing the total area occupied by the channels in the given section.

Bone histology terminology follows that of Francillon-Vieillot *et al.* (1990b), Reid (1996) and Starck and Chinsamy (2002).

Institutional abbreviations. BP/1/, Bernard Price Institute for Palaeontological Research, Johannesburg; SAM-PK-K, Iziko: South African Museum, Cape Town.

RESULTS

The estimated percentage adult size of each element studied is shown in Table 2. The overall bone tissue of *Thrinaxodon* consists of fibro-lamellar bone, which generally becomes parallel-fibred towards the periphery. The globular osteocyte lacunae are abundant and radiate

TABLE 2. Gross measurements of the *Thrinaxodon* limb bones and a reflection of percentage adult size.

Specimen no.	Skeletal element	Diameter (mm)	Proximal width (mm)	Length (mm)	Per cent adult
SAM-PK-K8004a	femur	1.84	–	18.74	41.98
SAM-PK-K8004b	femur	–	2.28	18.74	41.98
SAM-PK-K1395	femur	3.83	11.03	34.53	77.35
BP/1/2820	humerus	4.77	12.94	30.37	75.85
SAM-PK-K1121	humerus	–	13	32.57	81.34
BP/1/5208	humerus	5.41	11.38	33.46	83.57
BP/1/4282a	radius	2.98	6.18	32.23	96.65
BP/1/1730	radius	3.54	7.02	33.34	100
BP/1/5018	ulna	6.09	10.67	31.87	93.12
BP/1/4282b	ulna	5.22	6.61	33.09	96.65

branched canaliculi. The vascular canals in the fibro-lamellar tissue are mostly longitudinally orientated primary osteons with radial anastomoses whereas the parallel-fibred region contains few simple vascular canals.

Femora

The femora, SAM-PK-K8004a and 8004b (both from a single individual, approximately 42 per cent adult size; see Table 2), do not contain a distinct parallel-fibred peripheral region, but the osteocyte lacunae become more organized and the tissue becomes less vascular towards the subperiosteal surface

(Text-fig. 2A). The bony trabeculae at the ends of the bones are sparse. Those that are present lie parallel to the long axis of the bone. Secondary osteons are absent.

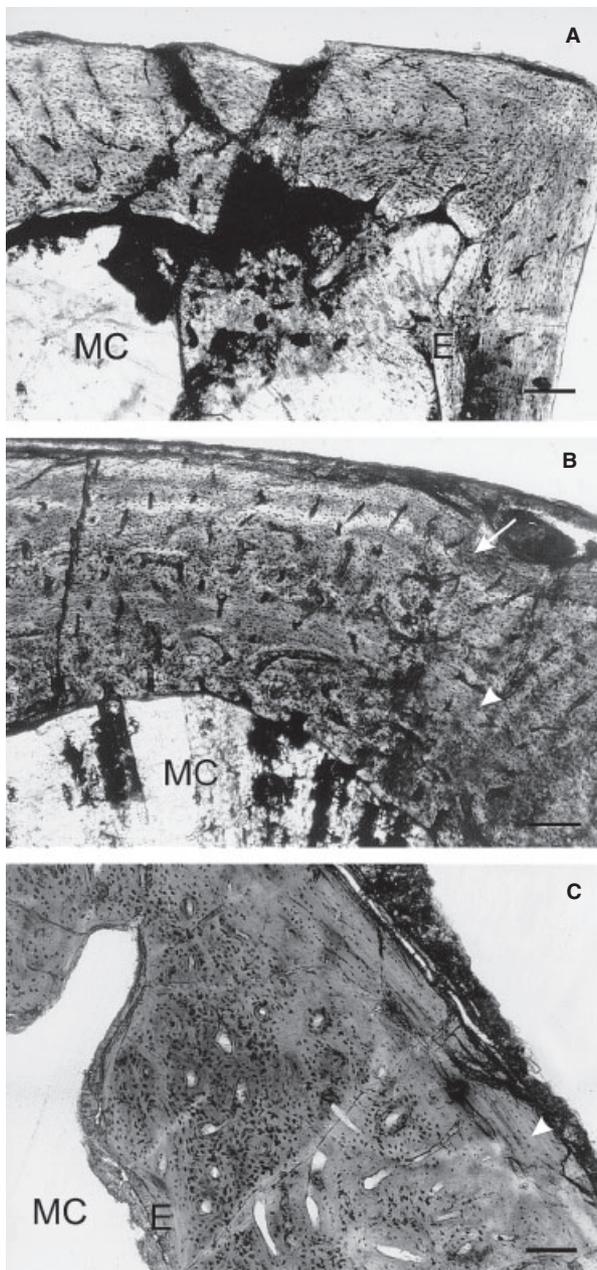
The femur, SAM-PK-K1395 (77 per cent adult size; see Table 2), exhibits an annulus of parallel-fibred bone in the mid-cortex, which contains flattened osteocyte lacunae (Text-fig. 2B, arrowhead). A narrow, poorly vascularized region at the subperiosteal surface contains osteocyte lacunae that appear more organized than the rest of the cortex. This may correspond to another annulus or the onset of parallel-fibred bone tissue (Text-fig. 2B, arrow). A few Sharpey's fibres are observed on the ventral side of the bone.

Humeri

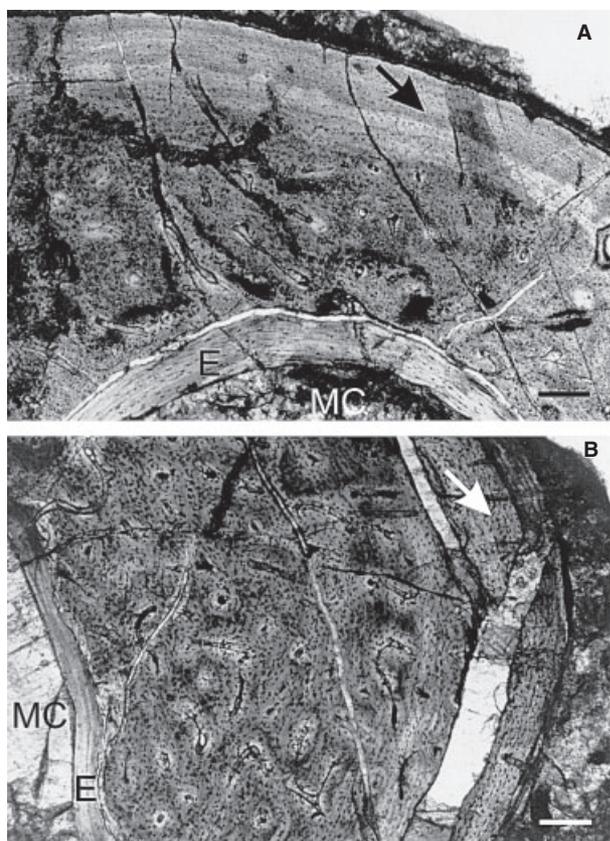
The three humeri examined fall between 75 and 84 per cent of the adult *Thrinaxodon* size. A thin layer of circumferential endosteal lamellar tissue, containing a mixture of globular and flattened osteocyte lacunae, surrounds the medullary cavity in the midshaft region of the humerus SAM-PK-K1121 (Text-fig. 2C). This layer disappears towards the metaphyses, where large cancellous spaces and bony trabeculae near the medullary cavity become more extensive. Secondary remodelling is most extensive on the dorsal side of all three humeri and resorption is generally more extensive in the largest humerus (BP/1/5208). Resorption cavities (resulting from bone drift) are extensive in the delto-pectoral crest regions and compacted coarse cancellous bone is observed towards the metaphyseal regions. Secondary osteons are absent from all three humeri. Thin bony trabeculae form a spacious network at the ends of the bones. A narrow region of parallel-fibred bone is visible at the outer margin of SAM-PK-K1121 (Text-fig. 2C, arrowhead), and a similar area of organized osteocyte lacunae is observed in BP/1/5208.

Radii

The fibro-lamellar tissue of the radii is less vascular and the peripheral parallel-fibred region is thicker and more distinct than that of the humeri and femora (Text-fig. 3A). Multiple layers of



TEXT-FIG. 2. Transverse sections of *Thrinaxodon* femora and humeri. A, femur (SAM-PK-K8004b, 42% adult size), showing rapidly forming, fibro-lamellar bone. A thin layer of circumferential endosteal lamellar bone can be seen surrounding the medullary cavity; note the less haphazard arrangement of osteocyte lacunae towards the periphery. B, femur (SAM-PK-K1395, 77% adult size), showing fibro-lamellar bone interrupted by an annulus (arrowhead) and a similar, slowly forming region at the subperiosteal surface (arrow), which may indicate another annulus or an overall decrease in growth rate. C, humerus SAM-PK-K1121, again showing rapidly forming fibro-lamellar bone. A thin layer of circumferential endosteal lamellar bone surrounds the medullary cavity and the arrowhead at the periphery indicates a transition to parallel-fibred bone. MC, medullary cavity; E, circumferential endosteal lamellar bone. Scale bars represent 250 μm , apart from that in C, which is 125 μm .



TEXT-FIG. 3. Transverse sections of a *Thrinaxodon* radius and ulna. A, radius (BP/1/4282a, 97% adult size) and B, ulna (BP/1/4282b, 97% adult size), showing distinct parallel-fibred zones at the subperiosteal surfaces (arrows) and layers of circumferential endosteal lamellar bone around the medullary cavities. MC, medullary cavity; E, circumferential endosteal lamellar bone. Scale bars represent 125 μm .

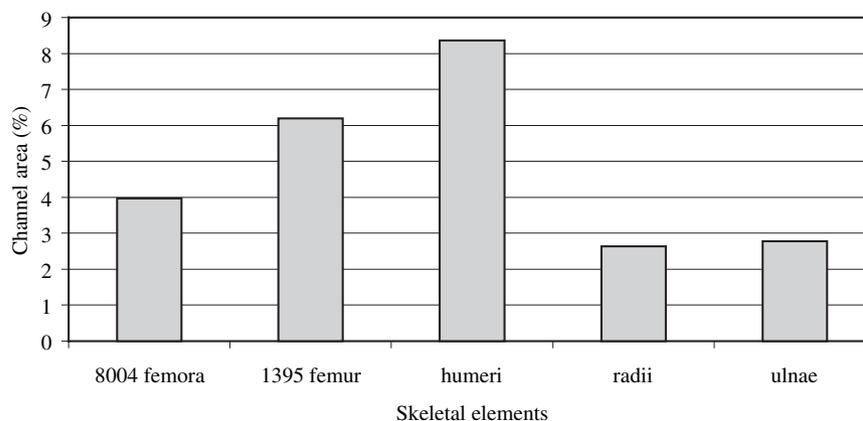
very poorly vascularized endosteal lamellar tissue surround the medullary cavities in the diaphyseal region of both elements (Text-fig. 3A). These layers disappear towards the metaphyses where large cancellous spaces near the medullary cavity become prominent. Compacted coarse cancellous tissue becomes progressively more extensive towards the metaphyses, where the primary compact tissue becomes almost non-existent. The resorption cavities are also more extensive on the anterior side of the bone. Sharpey's fibres are observed on the posteromedial side of the bone. An intricate network of thin bony trabeculae, sometimes forming isolated islets, is present towards the epiphyses of both radii.

Ulnae

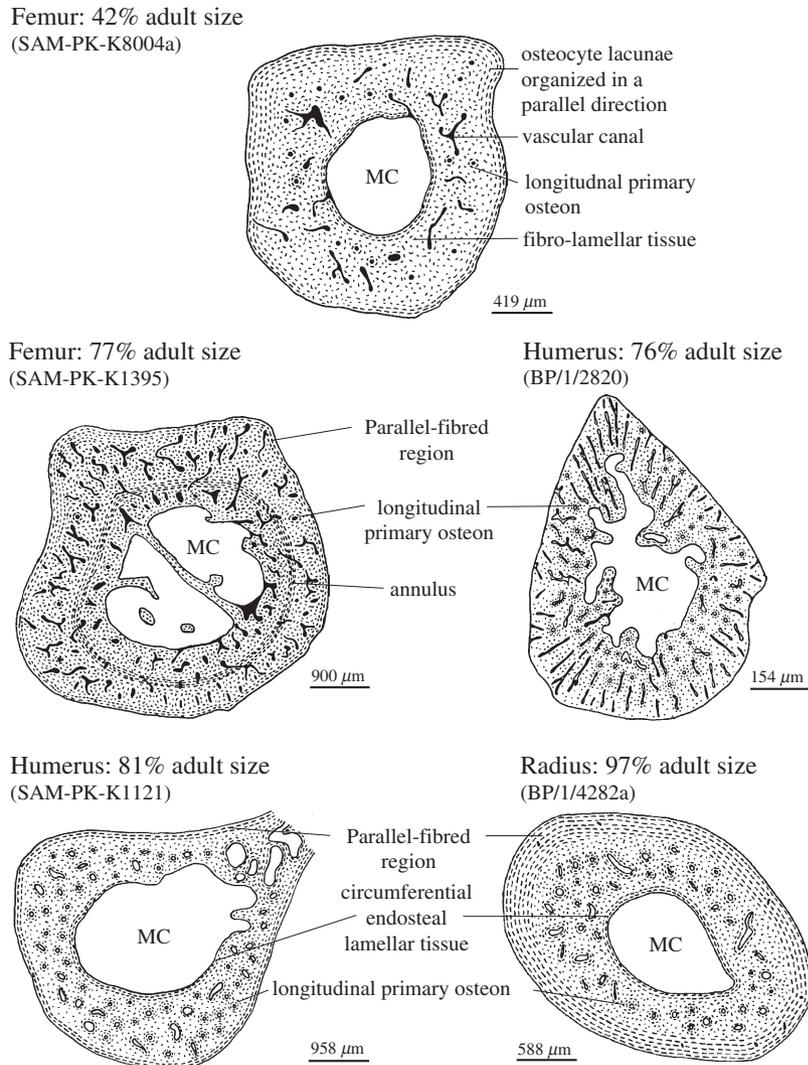
The tissue of the ulnae, BP/1/5018 (93.12 per cent adult length; see Table 2) and BP/1/4282b (96.65 per cent adult length; see Table 2), is similar to that of the radii (Text-fig. 3B). A few small secondary osteons are observed scattered throughout the cortex of BP/1/5018, and multiple layers of endosteal lamellar tissue surround the medullary cavities in the midshaft regions of both bones. Resorption cavities are more extensive in the metaphyses, especially on the anterior side of the bone. Both elements exhibit a few Sharpey's fibres in the ulna crest regions. A loose network of thin bony trabeculae is present at the ends of the bones.

Channel area

The channel area was quantified for all the elements in the midshaft regions in order to compare the extent of vascularization between each element (Text-fig. 4). A one-way ANOVA revealed a significant difference in midshaft percentage channel area between the different element types ($F = 22.26903$; $P < 0.05$), except between the radii and ulnae. Independent t -tests (one-



TEXT-FIG. 4. Midshaft percentage channel area of the *Thrinaxodon* skeletal elements. The values of the femora that are 42 per cent of the adult size (SAM-PK-K8004) as well as the femur that is 77 per cent of the adult size (SAM-PK-K1395) are notably different and, therefore, plotted separately. The channel area of the humerus SAM-PK-K1121 was not quantified owing to poor preservation.



TEXT-FIG. 5. Schematic histology comparing the histological variation between the *Thrinaxodon* elements at various ages.

tailed) showed that the differences lie between the humeri and femora ($t_s = 4.243$; d.f. = 7; $P < 0.05$); the humeri and radii ($t_s = 5.63$; d.f. = 4; $P < 0.05$); the humeri and ulnae ($t_s = 7.792$; d.f. = 6; $P < 0.05$) and between the femora and ulnae ($t_s = 2.776$; d.f. = 7; $P < 0.05$), but not between the radii and ulnae or radii and femora. The humeri have a significantly higher percentage channel area compared with any of the other elements, including the smallest and presumably youngest femora in the study.

The ontogenetic variation in percentage channel area and tissue organization within the *Thrinaxodon* limb bones has been summarized in Text-figure 5. The percentage channel area in the femora that is 42 per cent of the adult size is low and increases in the elements that are 75–84 per cent of the adult size. The percentage channel area then decreases again in the elements that are more than 90 per cent of the adult size. The vascular canals become longitudinally orientated and the parallel-fibred region also increases in the larger individuals.

DISCUSSION

All the *Thrinaxodon* limb bones exhibit fibro-lamellar bone to varying degrees, which indicates that this animal deposited bone at a relatively rapid rate. However, the parallel-fibred peripheral tissue in the larger and presumably ontogenetically older elements suggests that overall growth slowed down with age.

The fibro-lamellar tissue in the SAM-PK-K8004 femora indicates a rapid rate of bone deposition (Francillon-Vieillot *et al.* 1990b; Reid 1996). However, the increased organization and lower vascularization towards the periphery (Text-fig. 2A) suggest a lower bone deposition rate and hence growth rate, as vascular density is thought to correlate positively with growth rate in osseous tissues (Ricqlès 1983; Erickson and Tumanova 2000).

The SAM-PK-K8004 femora are 42 per cent of the adult size and are likely to have come from young individuals. When comparing the SAM-PK-K8004 femora with the older SAM-PK-K1395 femur (77% adult size) and humeri (75–84% adult size), the latter elements exhibit more extensive fibro-lamellar tissue and a higher overall vascularization, suggesting that they grew faster than the femora that are only 42 per cent of the adult size. Immature individuals usually have highly vascular tissues as a result of the large energy requirement of rapid growth (Withers 1992; Chinsamy 1993). It is therefore expected that the smaller femora (from individual SAM-PK-K8004) have a higher vascularization than the larger elements, but this is not the case. It is possible that individual SAM-PK-K8004 experienced different environmental conditions, causing differences in growth, compared with the other specimens in the study.

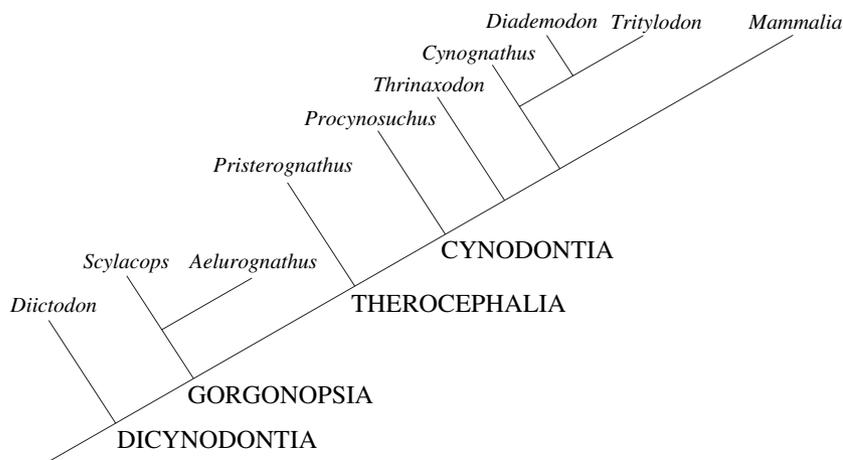
Apart from the femur, SAM-PK-K1395 (77% adult size), which contains an annulus in the mid-cortex (Text-fig. 2B), growth rings are absent from all elements. The annulus in this femur may represent an individual response to a particularly stressful, unfavourable environmental stimulus during which growth slowed down. The presence of fibro-lamellar tissue after the annulus indicates that the slowed growth occurred for a limited time period and that, thereafter, growth resumed at a rapid rate. The consistent lack of growth rings in the rest of the elements studied, however, suggests that *Thrinaxodon* experienced sustained growth and was possibly less susceptible to environmental fluctuations compared with other non-mammalian therapsids. For example, the Late Permian gorgonopsian *Scylacops*, non-mammalian cynodont *Procynosuchus* and the Early–Middle Triassic non-mammalian cynodont *Diademodon* (see Text-fig. 6 for phylogenetic relationships) exhibit cyclical growth throughout ontogeny

(Botha and Chinsamy 2000; Ray *et al.* 2004). The Late Permian dicynodont *Diictodon*, therocephalian *Pristerognathus* and gorgonopsian *Aelurognathus* show rapid, sustained growth early in ontogeny, only becoming interrupted by annuli and lines of arrested growth at a later stage (Ray *et al.* 2004). The environment was seasonal during both the Late Permian and the Triassic (Tucker and Benton 1982; Smith *et al.* 1993; Smith 1995; Ward *et al.* 2000) and it has been suggested that these cyclical growth patterns were in response to the fluctuating environment (Botha and Chinsamy 2000; Ray *et al.* 2004).

In contrast, the Early–Middle Triassic non-mammalian cynodonts *Cynognathus* and Early Jurassic *Tritylodon* exhibit rapid, sustained growth (Botha and Chinsamy 2000; Ray *et al.* 2004). These animals show similar uninterrupted fibro-lamellar bone to that of *Thrinaxodon* early in ontogeny and appear to have been less susceptible to environmental fluctuations.

Lifestyle may also have had an effect on the bone histology of *Thrinaxodon*. Recent evidence indicates that *Thrinaxodon* was a burrowing animal (Damiani *et al.* 2003). It is possible that *Thrinaxodon* burrowed to escape harsh environmental conditions and, thus, growth rings may have failed to materialize in the bone tissue.

The appearance of an increasingly organized arrangement of osteocyte lacunae at the periphery of the femora and humeri suggests the start of an overall slowing down in growth. The radii and ulnae exhibit this change in bone deposition more clearly as parallel-fibred bone (Text-fig. 3A–B), which consists of highly organized, poorly vascularized tissue. The only other study to examine the bone histology of *Thrinaxodon* was conducted by Ricqlès (1969). He examined the proximal end of an ulna and found that the number of vascular canals decreased



TEXT-FIG. 6. Cladogram showing the phylogenetic relationships of the therapsid genera that are compared with *Thrinaxodon* in this paper (modified from Rubidge and Sidor 2001 and Ray *et al.* 2004).

towards the periphery and that the osteocyte lacunae were orientated more parallel towards each other at the periosteal surface. The results in this study support the findings of Ricqlès (1969).

As the radii and ulnae in this study are more than 90 per cent of the adult size, it is reasonable to assume that they are adult individuals. Maximum size had probably not been reached, however, as the large amount of parallel-fibred tissue suggests that growth continued, but at a slower rate. The difference in bone tissue between the radii and ulnae and the rest of the limb bones may be due to histovariability within the skeleton whereby the radii and ulnae grew more slowly than the other elements. However, as the radii and ulnae are from ontogenetically older individuals, it is more likely that the presence of the extensive parallel-fibred bone is a result of a decrease in growth rate with an increase in age. The transition from fibro-lamellar to parallel-fibred bone may indicate the onset of sexual maturity (Castanet and Baez 1991; Reid 1996). Such a change in the rate of bone deposition, signifying a specific life history event, has also been observed in the extant walrus *Odobenus rosmarus* (Klevezal 1996), the African elephant *Loxodonta africana* (Jarman 1983) and in the longbones of Tendaguru sauropods (Sander 2000).

Thrinaxodon liorhinus was a fairly small animal (c. 50 cm in length: Brink 1954; Carroll 1988) and the relatively high growth rate, reflected by the fibro-lamellar bone tissue, may indicate that *Thrinaxodon* grew rapidly in order to attain adult size as quickly as possible. It is possible that the absence of growth rings in the fibro-lamellar bone is because this bone tissue was deposited within one season. Alternatively, the fibro-lamellar bone may have taken longer than one season to be deposited, but if the bone tissue was not affected by seasonality, growth rings would not have appeared.

Some intra-elemental histological variation was observed in the limb bones studied. The bone drift observed throughout the delto-pectoral crest regions of the humeri is possibly due to the presence of the deltoid musculature, namely *M. pectoralis* and *M. brachialis* (cf. Jenkins 1971). Bone drift occurs in the delto-pectoral crest regions of humeri due to the relocation of the protuberance along the bone shaft during growth. Sharpey's fibres observed in the distal metaphysis of the SAM-PK-K1395 femur may indicate the origin of the *M. femoro-tibialis* (cf. Jenkins 1971) as Sharpey's fibres occur in areas of muscle insertion (Leeson and Leeson 1981). Sharpey's fibres also observed on the posteromedial side of the radii may indicate the insertion of the biceps. Resorption cavities were found to be more prominent in the region of the ulna crest, which runs distally down the anteromedial side of the bone. Sharpey's fibres were also present in this region, indicating the possible

origin for the insertion of a radio-ulnar interbone ligament (cf. Jenkins 1971).

The inter- and intra-elemental histological variations were considered when interpreting the overall bone histology patterns of the *Thrinaxodon* limb bones. The general pattern suggests that *Thrinaxodon* growth was relatively rapid and uninterrupted early in ontogeny. The growth rate then decreased markedly, possibly when sexual maturity was reached. Thereafter, growth continued at a relatively slow rate.

CONCLUSIONS

Although the environment during the Early Triassic was seasonal, the bone histology of *Thrinaxodon* indicates that it grew in a rapid, sustained manner. This contrasts starkly with the periodically interrupted growth of other Triassic non-mammalian cynodonts such as *Diademodon*, and suggests that the biology of *Thrinaxodon* differed from this genus. Instead, the early growth of *Thrinaxodon* may have been more similar to the Early–Middle Triassic *Cynognathus*, which also exhibits uninterrupted, rapid growth. However, the abrupt change to slowly forming, parallel-fibred bone towards the periphery differs markedly from both *Diademodon* and *Cynognathus*. Moreover, the growth patterns observed in *Thrinaxodon* differ from all of the other Permian or Triassic therapsids that have been studied to date.

Considering that several *Thrinaxodon* individuals, from various localities, all showed an abrupt decrease in growth rate, it is reasonable to deduce that this is the result of inherent biological factors rather than environmental fluctuations.

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