

Palaeobiological implications of the bone microstructure of South American traversodontids (Therapsida: Cynodontia)

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We document the bone microstructure of traversodontids from Argentina and Brazil and make detailed comparisons of the bone microstructure of these cynodonts with that of other traversodontids, nonmammaliaform therapsids (including cynodonts), and Mesozoic mammalian taxa. Our analysis provides information on traversodontid ontogenetic age, growth patterns and life-style adaptations. The osteohistological data derived from the current study, as well as data on other nonmammaliaform cynodonts, provide an understanding of the evolution of life-history patterns among the therapsids. We show that many of the nonmammaliaform cynodonts (including some traversodontids) formed bone at rapid rates but retained flexible developmental growth patterns. In addition, although we observe a trend of increasingly rapid osteogenesis among the traversodontids, our findings do not discern a particular bone tissue type as a synapomorphy of the clade. This reinforces earlier hypotheses that the microscopic structure of bone is influenced by several intrinsic and extrinsic factors, and is not constrained by phylogeny alone.

Introduction

Over the past several years, there has been a growing interest in using bone microstructure to interpret aspects of the biology of extinct animals.¹⁻⁴ Although investigations of the bone microstructure of nonmammaliaform therapsids began fairly early,⁵⁻⁹ in recent years there has been a surge of such studies on nonmammaliaform therapsids from the Karoo Basin of South Africa (dicynodonts,¹⁰⁻¹² cynodonts,¹³⁻¹⁶ and gorgonopsians and therecephalians¹⁶). Even more recently, studies of fossil bone microstructure have been undertaken in five Mesozoic mammaliaform taxa.¹⁷ However, it is noteworthy that except for an earlier study by De Ricqlès,⁸ the bone microstructure of traversodontid cynodonts, which are the most diverse group of nonmammaliaform cynodonts, has been poorly sampled.

The study reported here documents the bone microstructure of three South American traversodontid cynodonts from Argen-

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tina (Table 1): *Andescynodon mendozensis* Bonaparte;¹⁸ *Massetognathus pascuali* Romer;¹⁹ and *Exaeretodon frenguelli* Cabrera.²⁰ Material of *Exaeretodon riograndensis* Abdala, Barberena and Dornelles²¹ from Brazil was also prepared for this study, but unfortunately the material was diagenetically altered during fossilization, and its histological details were obliterated. Detailed comparisons of our study material are made with earlier osteohistological findings of nonmammalian therapsids, including other traversodontids,⁸ as well as with that of Mesozoic mammaliaform taxa.¹⁷ Thus, the current study of these three species expands our understanding of nonmammaliaform cynodont biology, and provides valuable palaeobiological insight into the Traversodontidae.

Materials and methods

Each of the traversodontid taxa studied is described separately below, and a description of the histological method follows thereafter.

Andescynodon mendozensis Bonaparte, 1969

Andescynodon is the most abundant taxon from the Cerro de las Cabras Formation.²² The largest skulls of *Andescynodon* range from 80 to 90 mm and its body length was probably between 400 and 500 mm. On the basis of its dental morphology, *Andescynodon* is considered to be an omnivorous cynodont.^{23,24} The femur (PVL 3836, Table 1) is the smallest femur known of this taxon and was associated with a skull of *A. mendozensis* that had a basal skull length of 65 mm (Table 2). Considering its skull length, the individual that we studied is estimated to be about 72% of adult body size, and therefore of subadult ontogenetic status. Indeed, the *Andescynodon* femur studied here is 80% of the length of the largest traversodontid femur known from Cerro de las Cabras Formation (since this bone was not associated with a skull, however, it could be either from *Andescynodon* or another traversodontid, such as *Rusconiodon*, which is also known from these deposits).

Massetognathus pascuali Romer, 1967

Abundant remains of *Massetognathus* are known from the Chañares Formation of Argentina.^{19,25,26} The maximum skull length of this taxon is about 205 mm and its estimated body length is 1.3 m.²⁵ The femur included in this study (PVL 4613, Table 1) is part of a skeleton of a diagnostic *Massetognathus* specimen. The estimated length of PVL 4613 (see Table 2) is 66% of the largest femur known, and it is similar in size to that of MCZ 3691 R, which is a virtually complete and articulated skeleton of *Massetognathus* that Abdala and Giannini²⁵ have proposed is subadult in age.

Institutional abbreviations: MCN-PV, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; PVL, Colección Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina.

Table 1. Material studied.

Specimen number	Taxon	Formation	Age	Skeletal element	Thin sections*
PVL 3836	<i>Andescynodon mendozensis</i>	Cerro de las Cabras Formation, Argentina	Anisian	Femur	2 X.S mid-diaphyseal 1 L.S
PVL 4613	<i>Massetognathus pascuali</i>	Chañares Formation, Argentina	Ladinian	Femur	4 X.S 2 L.S
PVL 2162	<i>Exaeretodon frenguelli</i>	Ischigualasto Formation, Argentina	Carnian	Distal fibula	4 X.S 2 L.S
MCNPV 10001	<i>Exaeretodon riograndensis</i>	Santa Maria Formation, Brazil	Carnian	Tibia	3 X.S 2 L.S

*X.S, cross section; L.S, longitudinal section.

Table 2. Measurements of femora length in *Andescynodon* and *Massetognathus*.

	Femur length (cm)
<i>Andescynodon</i>	
PVL 3836	3.7 (80%)
PVL 3894	4.3
PVL 4430	4.4
PVL 3890 [†]	4.6
<i>Massetognathus</i>	
MCZ 3691 R	5.3
PVL 4613	5.5* (66%)
PVL 5444	5.6
MCZ 3812	8.3
MCZ 3813	8.3

*Estimated length. Materials indicated in bold are those sectioned in this study. Percentage of the bone length sectioned in relation with the largest bone of the sample (assumed to be that of an adult of the taxon) is indicated in brackets.

[†]Material not associated with skull remains and therefore tentatively assigned to the taxon.

Exaeretodon frenguelli Cabrera, 1943

Exaeretodon is one of the best representatives of the Traversodontidae, and one of the common forms in the Ischigualasto Formation.²⁷ The species is well known and it has been well-studied anatomically.^{28–30} The skull length of the species reaches 400 mm and an estimated body length of 2.5 m. *Exaeretodon* were omnivores, showing the expanded upper postcanines with a high and sharp sectorial crest. A distal portion of the fibula was included in the analysis (PVL 2162, Table 1). Considering the size of the element, the specimen is probably from an adult.

Exaeretodon riograndensis Abdala, Barberena and Dornelles 2002

Exaeretodon riograndensis is represented by a few specimens recovered from the Santa Maria Formation in southern Brazil.²¹ A complete tibia (MCNPV 10001, Table 1) was included in the current histological analysis.

Histological methods

As a consequence of limited diagnostic material available for histological analyses, we were unable to study the same skeletal element for each taxon. However, since several studies have found that long bones (such femora, tibiae and humeri) are especially well suited for histological analysis as they reliably preserve the histological record of growth processes,^{3,4} we limited this analysis by selecting representative long bones of each taxon. The sampled traversodontid bones were embedded in a clear epoxy resin and thin sections were prepared according to the method outlined in Chinsamy and Raath.³¹ Transverse sections were made in the diaphyseal regions of all the sampled bones, and in addition we were able to make longitudinal sections of the femora of *Andescynodon*, *Massetognathus*, and the tibia of *Exaeretodon riograndensis*. The thin sections were examined under ordinary light and polarized microscopes. Image analysis and measurements were conducted using NIS-Elements (version 2.2).

Results

Andescynodon mendozensis

Transverse sections of the femur show a central medullary cavity that is surrounded by a fairly thick compact bone wall that measures on average about 1239 μm (Fig. 1). Although the bone is somewhat fragmented, the bone wall thickness is deducible and is about 29% of the diameter. A large number of radially organized blood vessels are visible in the compacta (Fig. 1).

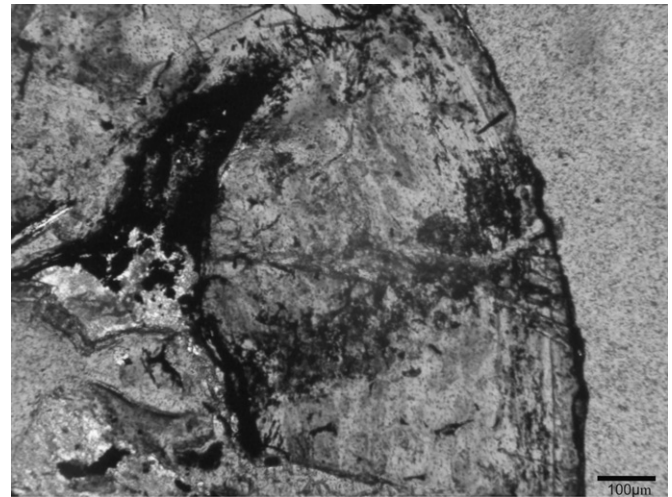


Fig. 1. *Andescynodon mendozensis*, femur, PVL 3836, Anisian, Cerro de las Cabras Formation. Transverse section showing a thick compact bone wall that surrounds the medullary cavity. Note the presence of radially orientated channels that house blood vessels, and the single line of arrested growth near the peripheral edge of the bone wall.

These tend to be simple blood vessels, without any osteonal development around them. The overall bone tissue has a lamellar texture. In the peripheral region, one line of arrested growth (LAG) is visible. In longitudinal sections of the bone, columns of calcified cartilage are present at the distal ends, and islands of calcified cartilage are present in some bony struts.

Massetognathus pascuali

Transverse sections of the femur reveals a fairly thick bone wall (980 μm), of which about 47% consists of compacted coarse cancellous bone tissue (Fig. 2A). The periosteal bone tissue comprises parallel-fibred bone with a predominance of simple blood vessels that are mainly longitudinally arranged. Some circumferentially orientated blood vessels occur. A large number of erosion cavities are present around the medullary cavity (Fig. 2A). Compacted coarse cancellous bone is present in more distally located sections (Fig. 2A). Longitudinal thin sections of the femur showed struts of endochondral bone, and a narrow layer of calcified cartilage at the 'articular' end of the bone (Fig. 2B).

Exaeretodon riograndensis

Unfortunately, even though the gross morphology of the tibia is well preserved, the thin sections of the bone reveal that the bone has been diagenetically altered,³ and no histological detail is preserved.

Exaeretodon frenguelli

Thin sections of the fibula revealed that although the bone wall is quite fragmented, the histology is still discernible. The bone wall is fairly thick and consists of a compact bone region (measures about 880 μm), which is well vascularized by predominantly longitudinally orientated vascular canals (Fig. 3). Under polarized light, the osteonal structure around the vascular channels is clearly visible. There appear to be 1–2 rather faint growth rings visible, but these cannot be followed around the entire compacta. Bone around the medullary cavity comprises fibrolamellar bone tissue, whereas bone nearer the periosteal surface is more lamellar in structure. More distally located sections have much more cancellous bone present. A large number of erosion cavities are present around the medullary cavity, but few show secondary deposits of bone.

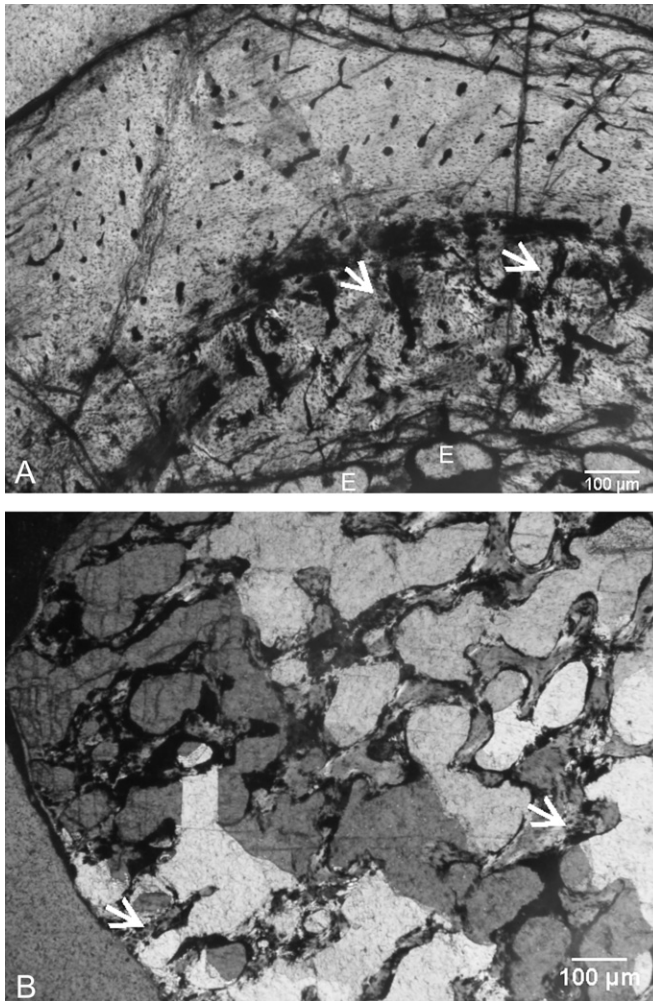


Fig. 2. *Massetognathus pascuali*, femur, PVL 4613, Ladinian, Chañares Formation. **A.** Transverse section showing the overall nature of the compact bone wall. Arrows indicate the compact coarse cancellous bone surrounding the medullary cavity, and internal to this lie a few enlarged erosion cavities (E). **B.** Longitudinal section. Arrows indicate calcified cartilage near the articular end of the bone.

Discussion

The microscopic structure of the fossilized bone (bone histology/osteohistology) provides a host of information about various aspects of the life history of extinct animals.^{1-4,16} For example, deductions about an ontogenetic age, developmental patterns and growth strategies can be assessed directly from the histology of fossil bones. More specifically, different types of bone tissue permit deductions about the relative rate at which the bone was formed.³² Thus, a fast rate of bone formation results in fibro-lamellar bone tissue in which the collagen fibres are haphazardly arranged and form a woven bone matrix wherein numerous primary osteons occur.¹⁻³ A slower rate of bone formation results in a more lamellar type of bone tissue with a more organized arrangement of collagen fibres, and distinctly flattened osteocytes. Intermediates between these two bone tissue types occur and result in different, easily distinguishable types of tissues.¹⁻³ In recent years, bone depositional rates of different tissue types have been quantified using fluorochrome staining techniques in a variety of modern vertebrates.³³⁻³⁵ From these analyses it appears that bone depositional rates of particular tissue types are quite variable and depend on several factors, including ontogeny, location in the skeleton, and environment. As a result, extrapolating actual bone depositional rates directly from modern vertebrates to extinct animals is questionable.^{3,4,34} In the current study of traversodontid osteohistology, therefore, we

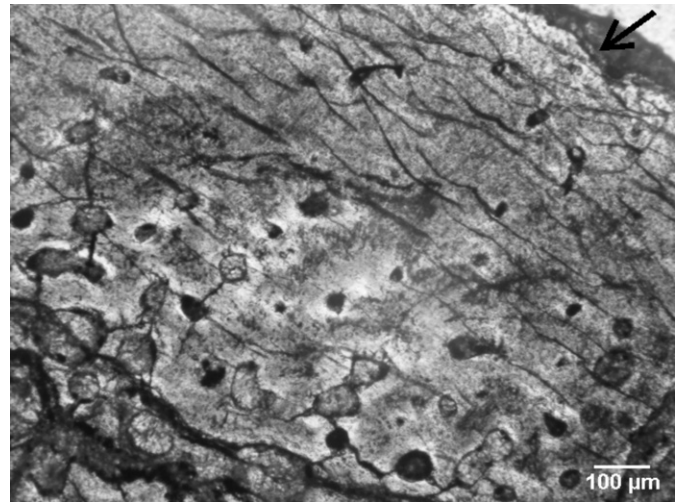


Fig. 3. *Exaeretodon frenguelli*, fibula, PVL 2162, Carnian, Ischigualasto Formation. Arrow indicates the peripheral edge of the bone wall. Note the presence of enlarged channels in the peri-medullary region of the bone.

use qualitative, relative rates of bone deposition for comparisons between the taxa.

The palaeobiological implications of the bone microstructure for each of the study animals are discussed separately below. This is followed by a general description of traversodontid bone microstructure considering both previously published material and specimens in the current study, and a then by comparison of traversodontid bone microstructure with nonmammaliaform cynodonts, and Mesozoic mammaliaforms.

Bone microstructure of the South American traversodontids

Andescynodon mendozensis. The *Andescynodon* femoral microstructure is distinctive from that of the other traversodontids studied in that it has the thickest bone wall (almost 30% of the cross-sectional diameter of the bone), and also in having a number of radially orientated 'vascular canals' in a lamellar matrix of bone. The latter characteristic suggests that bone formation occurred in this animal at a much slower rate when compared with the other traversodontids studied. Interestingly, thick bone walls in terrestrial animals have been documented in the nonmammaliaform cynodonts, *Thrinaxodon*¹⁵ and *Trirachodon*,¹⁴ and have been interpreted as suggesting a fossorial lifestyle – a deduction additionally supported by the fact that both these cynodonts have been found associated with burrows.^{36,37} Furthermore, modern burrowing vertebrates (e.g. the naked mole rat, *Heterocephalus glaber*, the porcupine, *Erethizon*; as well as burrowing or digging lizards: *Gerrhonotus grantis*, *Heloderma suspectum* and *Phrynosoma doublasi*) are also known to have thick bone walls.^{38,14,17} It is possible that *Andescynodon*, with its small body size, may also have been fossorial, but it should be noted that its skeletal remains have not been associated with burrows, and as in the majority of non-mammaliaform cynodonts (including possibly 'burrowing forms', *Trirachodon* and *Thrinaxodon*), there are no anatomical features in its skeleton suggestive of this type of lifestyle.

The columns of calcified cartilage near the articular surfaces, as well as islands of calcified cartilage within bony struts near the ends of the bone in the longitudinal sections of the femur, suggest that the specimen examined is an individual that was still growing at the time of its death, and agrees with the size-based deduction that it is a subadult individual.

Massetognathus pascuali. The *Massetognathus* femoral bone microstructure suggests a faster rate of osteogenesis than that of

Andescynodon, and a slower rate of bone formation compared with *Exaeretodon*. The large number of peri-medullary erosion cavities also suggests that secondary resorption of bone was well under way. Longitudinal sections of the femur revealed the presence of calcified cartilage nearest the 'articular surface' of the bone, which suggest that maximum skeletal size had not yet been attained. The sparse occurrence of calcified cartilage and its restriction to a narrow region at the ends of the bone suggests that the individual was not very young and, more likely, subadult in ontogenetic status. These histological findings support the assumption that PVL 4613, like MCZ 3691 R, is a subadult.²⁵

Exaeretodon frenguelli. The bone microstructure of the fibula of *Exaeretodon frenguelli* provides information regarding its growth dynamics. The initial deposition of a well-vascularized bone tissue in a woven bone matrix indicates a rapid growth phase, which was followed by a slower rate of growth as indicated by the parallel-fibred bone tissue. During the latter phase of growth, it is not certain but it seems that periodic pauses in the rate of bone deposition may have occurred. This type of growth pattern, with a rapid initial growth and subsequent slower growth, has been observed in several nonmammaliaform therapsids,¹⁶ as well as in mammaliaforms such as *Morganucodon* and the multituberculates *Kryptobaatar* and *Nemegtbaatar*.¹⁷ Resorption of bone is indicated by the presence of a large number of erosion cavities. The sparse occurrence of secondary osteons is indicative of a slower rate of re-deposition of bone in the erosion cavities.

Traversodontid bone microstructure and developmental growth patterns

The analysis of diagnostic traversodontid taxa permits some overall deductions about traversodontid bone microstructure and developmental patterns. A distinctive feature of the bone microstructure of the traversodontid taxa is that they are comprised essentially of primary bone tissue. Some peri-medullary erosion cavities are evident in *Exaeretodon* and *Massetognathus*, but secondary osteons tend to be sparse. These findings with regard to the compact bone tissues are consistent with that described by De Ricqlès⁸ for *Gomphodontosuchus* and *Traversodon*, suggesting that calcium metabolism among the traversodontids was not intensive, and appears not to have imposed heavy demands on their skeletons.¹² In addition, because *Andescynodon* and *Massetognathus* appear to be subadults, we would not expect extensive development of secondary reconstructed bone (which tends to increase with increasing maturity). The *Exaeretodon* sample, on the other hand, is from an older individual—this is evident from the change in texture of the bone, that is, from a fibrolamellar tissue type to a lamellar type. Interestingly, in this individual, large peri-medullary erosion cavities occur, but secondary deposits therein have not yet formed.

The osteohistology of the traversodontids suggest that the different taxa experienced different growth strategies—*Andescynodon mendozensis* with its characteristic lamellar textured bone and the absence of osteonal development around the channels in the bone that housed blood vessels, suggests that bone formation and hence growth occurred at a slower rate than in both *Massetognathus pascuali* and *Exaeretodon frenguelli*. The compacta of *M. pascuali* tends to be uninterrupted, and consists of parallel-fibred bone tissue with simple blood vessels—these features suggest a faster rate of bone formation than in *A. mendozensis*. It is possible that an earlier, more rapid (and perhaps cyclical) phase of growth has been eroded away by

secondary reconstruction, but this cannot be ascertained from the material at hand. If additional juvenile samples become available for histological study, it would be worth verifying whether indeed this was the case. If the initial phase of rapid growth were absent, then it would appear that *Massetognathus* has the distinctive characteristic of intermediate, but sustained rate of bone formation (and hence growth). The presence of fibrolamellar bone and primary osteons in the compacta of *Exaeretodon frenguelli* suggests that it had the fastest rate of growth as compared with the traversodontids in this study. The initial fast rate of bone growth is followed by more slowly formed lamellar bone tissue (and as mentioned above, it is uncertain whether growth was interrupted). These histological features of *Exaeretodon* suggest that the individual had passed its rapid phase of growth, and that its growth was slowing down. The fact that closely spaced peripheral rest lines (indicative of the attainment of maximum body size)²⁻⁴ are not visible in the compacta imply that the *Exaeretodon* fibula had not yet reached its maximum size.

The longitudinal sections of the bones provided an assessment of growth in length, and permitted deductions regarding relative ages of individuals: the calcified cartilage in the *Andescynodon* and *Massetognathus* specimens examined suggests that they were still growing at the time of death, being more likely subadults. However, the more extensive development of the calcified cartilage at the extremity suggests that the *Andescynodon* femur was growing more rapidly in length than the *Massetognathus* specimen. This is particularly noteworthy as the *Andescynodon* femur is 80% as long as the largest femur from the deposit whereas the *Massetognathus* bone is 66% of the largest known. This raises the intriguing possibility that perhaps the largest traversodontid femur known from the Cerro de las Cabras Formation is not representative of the largest, adult size of *Andescynodon*, as the histological features in the femur studied clearly suggest that it was still rapidly growing in length.

Thus, our analysis of the bone microstructure of these Argentinian traversodontids showed that although *Andescynodon* and *Massetognathus* clearly passed their most rapid phases of growth, they had not yet reached skeletal maturity. The *Exaeretodon* fibula suggests that this individual was more mature, and appositional growth had visibly slowed. Curiously, it is also apparent that there seems to be a trend of increasing the rate at which bone is deposited, i.e. from the most basal traversodontid to the more derived forms such as *Exaeretodon* and *Gomphodontosuchus*.⁸ This seems to parallel the trend found among the more basal nonmammaliaform cynodonts.³⁹

It is also worth noting that palaeoenvironmental analyses suggest that both *Andescynodon* and *Exaeretodon* lived in humid, warm climates.^{40,41} However, the alluvial plain, with lakes, swamps and marshes interpreted for the Cerro de las Cabras Formation⁴⁰ from which *Andescynodon* was recovered, represents a more equable humid environment than the predominantly fluvial Ischigualasto Formation (from which *Exaeretodon* was obtained) that shows seasonal variations in water availability.^{26,41} Differences observed in the bone microstructure of these taxa, and hence bone growth, therefore possibly reflect innate biological differences between the taxa.

Growth patterns of the traversodontids within the context of the nonmammaliaform cynodonts and mammaliaforms

Earlier studies of the bone microstructure of nonmammaliaform cynodonts have shown that they have variable patterns of bone microstructure, ranging from a lamellar-zonal bone in *Procynosuchus*^{16,39} to zonal bone with fibrolamellar bone tissue

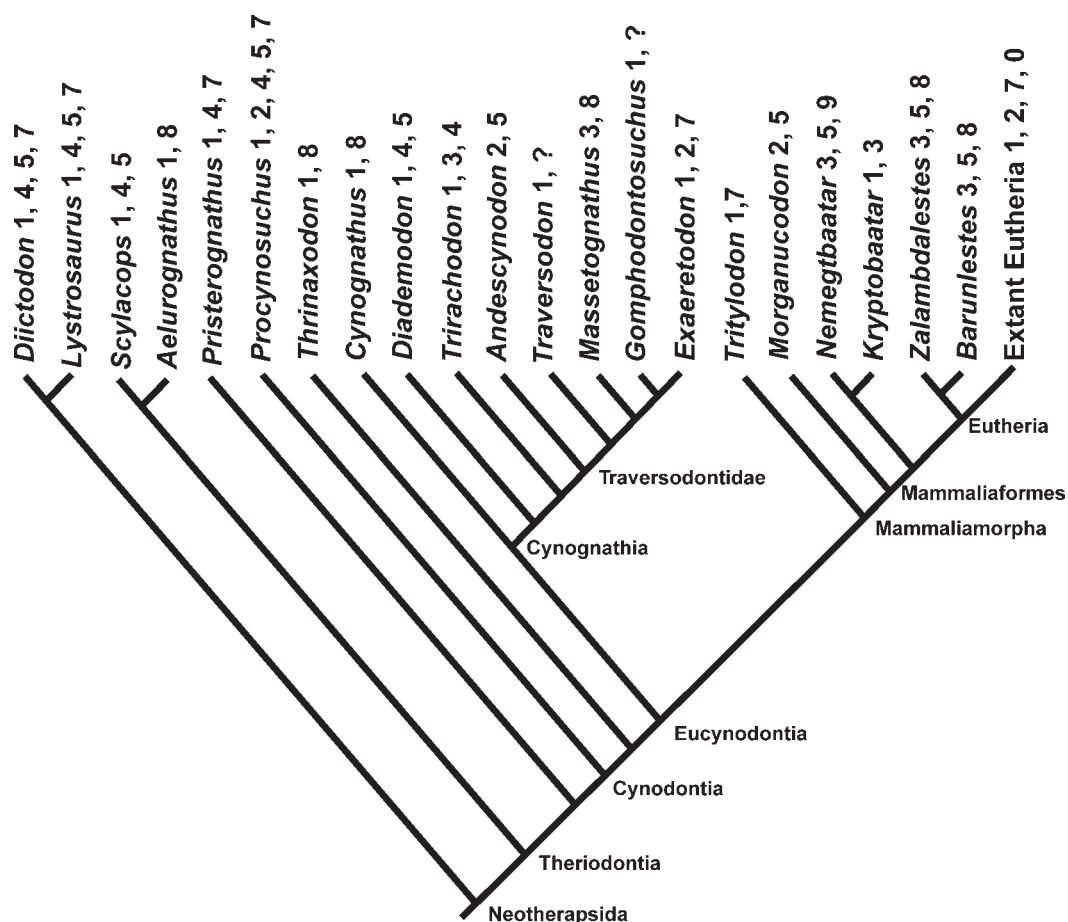


Fig. 4. Cladogram showing relationships of neotherapsida⁴³⁻⁴⁵ and associated histological features. 1, Fibro-lamellar bone; 2, lamellar bone tissue; 3, parallel-fibred bone tissue; 4, annuli; 5, lags; 6, lamellar-zonal bone tissue; 7, slowed later growth; 8, uninterrupted growth; 9, woven bone; 0, some eutherians (especially those in cold climates) can have interrupted growth patterns; ?, no further details are available.

(e.g. *Diademodon*¹³ and *Trirachodon*¹⁴) and to uninterrupted fibrolamellar bone tissue (e.g. *Cynognathus*¹³ and the tritylodontids, *Tritylodon*,¹⁶ *Bienotherium* and *Oligokyphus*).⁸ These findings suggest an increasing trend towards more rapid growth as reflected by uninterrupted fibrolamellar bone tissues. However, it is noteworthy that the ability to form fibrolamellar bone (albeit periodically) seems to have been an early innovation among the nonmammaliaform therapsids, and is already present in *Scylacops*, a Late Permian gorgonopsian,¹⁶ as well as among the dicynodonts¹⁰⁻¹² (Fig. 4).

Our results on the bone microstructure of the traversodontids *Exaeretodon frenguellii*, *Massetognathus pascuali* and *Andescynodon mendozensis*, as well as those of *Gomphodontosuchus brasiliensis* and *Traversodon stahleckeri*, previously studied by De Ricqlès,⁸ show heterogeneous patterns of bone microstructure. This concurs with findings in several other nonmammaliaform cynodonts and therapsids,^{11-16,39} and appears to be a trend also in the basal mammaliaforms¹⁷ (Fig. 4).

Conclusions

Examined within a phylogenetic framework, the osteohistological data of traversodontids derived from the current study, as well as those of other nonmammaliaform cynodonts provided by previous contributions,^{8,13-16} permits comparisons of growth dynamics within these clades and provides an understanding of the evolution of life-history patterns among the therapsids. As a result of these studies, it appears that the ability to grow rapidly evolved fairly early in the Therapsida. Indeed, the widespread occurrence of fibrolamellar bone in Permian dicynodonts^{10,11} and

gorgonopsians¹⁶ suggests that this ‘innovation’ extends deep into the therapsid lineage.

However, it appears that many of the nonmammalian cynodonts (including some traversodontids), although having the ability to form bone at rapid rates, retained flexible growth trajectories (developmental plasticity), which may have been dictated by prevailing environmental conditions. This plasticity also appears to have been present among some Mesozoic eutherians (*Barunlestes* and *Zalambdalestes*¹⁷). Although most modern mammals grow rapidly without periodic interruptions, some living mammals that experience stressful environments such as harsh seasonal conditions (e.g. polar bears and small rodents), can have periodic interruptions in bone growth.^{3,42}

Thus, although there appears to be an increase in the rate of bone formation from basal nonmammaliaform cynodonts to more derived forms,^{16,39} and also among the traversodontids studied here, the plesiomorphic pattern of bone microstructure among the Therapsida is one of developmental plasticity.^{16,34} Within this general pattern, however, there are variations in the rate at which bone is deposited within the zonal region (i.e. whether fibrolamellar bone or lamellar bone forms) and whether the growth cycles are marked by abrupt pauses (indicated by lines of arrested growth) or simply a decrease in the rate of bone formation. It is also apparent that some therapsids (and particularly some nonmammaliaform cynodonts) have independently acquired the ability to grow along inflexible growth trajectories.^{13,16} Given the variability that occurs in the Cynodontia where the bone histology is known, it is apparent that there is not one particular type of bone tissue that can be

regarded as a synapomorphy for the clade. Thus, the microscopic structure of bone appears to be highly variable even among closely related forms, and therefore not constrained by phylogeny alone. On the contrary, the overall texture and nature of bone appears to be dependent on a host of extrinsic and intrinsic factors.^{3,4}

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