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ASSESSING THE BIOLOGY OF FOSSIL VERTEBRATES THROUGH BONE HISTOLOGY

by

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ABSTRACT

Soon after death and burial of an animal, the organic components of bone generally decay. The closely associated inorganic components (mainly apatite) are more resilient and even after millions of years of burial, preserve the spatial organisation of the collagen fibres and hence the structure of the bone. In the past fossil bone histology has been the subject of substantial research. Such studies have included a wide array of extinct vertebrates including fishes, amphibians, pelycosaurs, therapsids, ichthyosaurs, pterosaurs, and dinosaurs.

The relative rate of bone formation is indicated by the texture of the fibrillar matrix, while the overall nature of the primary compact bone provides a direct assessment of whether bone deposition was continuous or interrupted. The amount of secondary bone formation depicts the extent of primary bone resorption and subsequent redeposition. In addition, the internal organisation of bone indicates remodelling and relocation processes of growth, including functional adaptations of the bone morphology. Thus, osteohistology reflects ontogeny, growth dynamics, biomechanical adaptations, as well as various events that punctuate the life history of an animal.

KEYWORDS: Bone histology, bone microstructure, osteohistology, vertebrates, fossils.

INTRODUCTION

Fossilization subjects a bone to a variety of diagenetic processes resulting in substantial changes in the composition of the bone. Notable among these are an increase in apatite crystallinity, loss of organic matter, and the uptake or loss of minor elements. The amount of diagenesis that occurs is variable and depends on a variety of factors including biological and chemical ones. Occasionally the microscopic structure of a fossil bone is affected by microbial action, but it is more usual for the integrity of the histology to be preserved. Even after millions of years of burial some of the earliest vertebrates have the histological structure of their bones intact.

Early studies in fossil bone microstructure (e.g. Hasse 1878; Quekett 1849; Seitz 1907), laid the foundation for further research into comparative osteohistology. As early as 1923, Moodie reported pathologies in fossil bones and in 1933, Nopsca & Heidsieck used bone microstructure to distinguish ontogenetic status of half grown and immature trachodont dinosaurs. Further research (e.g. Enlow 1969; Enlow & Brown 1956, 1957, 1958; Gross 1934; Peabody 1961) provided a better understanding of histological patterns among major vertebrate groups, from fishes to mammals, including both fossil and recent samples. More recently workers such as Ricqlès (e.g. 1974, 1976, 1980) and Reid (e.g. 1984a, 1984b, 1987, 1990) advanced the field of palaeo-osteohistology substantially by documenting bone structure among a variety of tetrapods, and particularly provided more insight into the nature of dinosaurian bone. My own work has dealt with the histological changes through ontogeny among various species of dinosaurs (Chinsamy 1990, 1993, 1995b). I have also considered both modern and fossil reptiles (Chinsamy 1991; 1994; Chinsamy & Rubidge 1993) and birds (Chinsamy 1995a; Chinsamy *et al.* 1994, 1995).

The physiological meaning of dinosaur bone has been the subject of much debate (e.g. Bakker 1986; Reid 1987; Ricqlès 1980). In this short paper, I present some of the characteristics of bone microstructure and an interpretation of their implications. It was presented to a general audience at the 50th Anniversary Celebrations of the Bernard Price Institute for Palaeontological Research, Johannesburg. For a more comprehensive analysis of bone microstructure, the referenced papers should be consulted.

WHAT DOES BONE MICROSTRUCTURE *ACTUALLY* REVEAL?

Macroscopic examination of a section of bone immediately reveals the amount of compact bone making up the bone wall, the size and shape of the medullary cavity (if present), and whether or not cancellous bone is present. When a thin section is prepared (Chinsamy & Raath 1992) and examined under a light microscope, microstructural details are revealed. Several aspects of the biology and overall growth of an animal can be deduced on the basis of histological characteristics present in the bone. Notable among these are the following:

Rate of osteogenesis

By examining a thin section of fossil bone under crossed polarisers, the organisation of the fibrillar matrix can be assessed. When bone formation is rapid, the

matrix is random and disorganised, resulting in woven bone tissue. When this tissue is formed numerous blood vessels are typically enclosed. Lamellar bone is later deposited around the vessels to form primary osteons, and the tissue is then termed fibro-lamellar bone (Figure 1). When bone deposition is slow, the matrix is more organised and lamellar bone tissue results (Amprino 1947) (Figure 2). Both these tissue types, and variants thereof, can be observed in a single section of bone. Thus, the rate at which an animal grows is directly reflected by the rate at which bone is deposited and the nature of the fibrillar matrix (Amprino 1947).

Cyclical versus non-cyclical growth

The overall structure of the primary compact bone provides a direct assessment of whether bone deposition was continuous or interrupted. A cyclical rate of bone deposition is evident when the compacta is stratified into

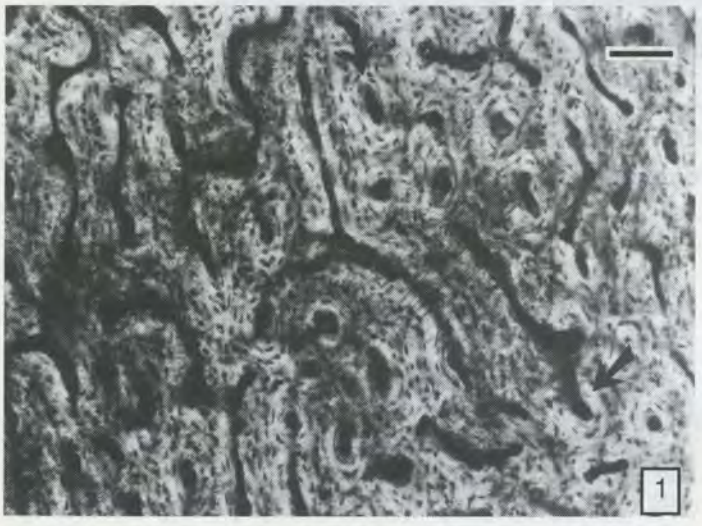


Figure 1: Cross section of a juvenile *Massospondylus* femur (BP/1/ 5253) from the Early Jurassic of South Africa, showing fibro-lamellar bone with numerous primary osteons (arrows) embedded in the woven bone matrix. Scale bar = 76 microns.

distinct growth rings or alternating bands of tissue types. This type of tissue is termed lamellar-zonal and the resulting bands of tissue are the zones and annuli. The zones tend to be more vascularised and represent periods of fast growth, while the poorly vascularised annuli signal periods of slower growth. Pauses in osteogenesis are marked by distinct lines of arrested growth (LAGs).

Among extant reptiles, it is generally found that a single zone and annulus are formed per year. Experiments with fluorochrome dyes have verified that this pattern of bone deposition is seasonally related, with zones formed during the warmer months and annuli resulting during unfavourable periods. Thus, the stratification of the compacta into zones and annuli allows an animal to be aged on the basis of its bones. This study is termed skeletochronology (Castanet & Smirina 1990; Patnaik & Behera 1981). Double or accessory lines can sometimes occur: e.g., Caetano (1990) has demonstrated bi-annual cycles of activity in *Triturus marmoratus* living at high altitudes. These are readily discernible and are known to be linked to bi-annual cycles of activity. It should be noted that there are no reports of only one LAG formed every two years, which supports the deductions that LAGs in fossil vertebrates are more than likely annual (e.g., Chinsamy 1990, 1993; Sander 1990; Varricchio 1993).

In a study of nine mammalian orders Klevezal & Kleinenberg (1969) reported growth lines occurring in the bones of animals from cold regions, and marine habitats, as well as in mandibles of small lagomorphs and rodents. More recently Leahy (1991) reported growth lines in the bones of a kangaroo, while Chinsamy has found growth lines in a polar bear (Chinsamy & Dodson 1995). It is therefore apparent that growth lines are not restricted to reptiles. More research is required to ascertain what triggers the switch from uninterrupted fibro-lamellar bone to an interrupted type (Farlow *et al.* 1995).

Sustained, uninterrupted bone formation results in the lack of zonation in the compacta. The tissue comprising the compacta can be wholly of fibro-lamellar bone or can grade into a pseudo-lamellar or lamellar type of tissue.

Fibro-lamellar bone is common among mammals and birds, and is known to be formed by rapid osteogenesis (e.g. Amprino 1947; Reid 1990) (Figure 1). The frequent occurrence of this tissue in the bones of dinosaurs has led to assertions that dinosaurs were endotherms (e.g. Bakker 1986). However, fibro-lamellar bone is known from bones of juvenile crocodiles (Buffrénil 1980), pelycosaurs (Enlow & Brown 1957), captorhinids (Enlow & Brown 1957), gorgonopsians (Ricqlès 1976) and dicynodonts (Chinsamy & Rubidge 1993; Gross 1934; Ricqlès 1972). Thus the occurrence of fibro-lamellar bone in these reptiles, which are generally considered to be ectotherms, fails to support a correlation between fibro-lamellar bone and endothermy. It therefore appears that a sustained rate of fibro-lamellar bone formation indicates that bone deposition was rapid. However, exactly how fast deposition has to be to form fibro-lamellar type of tissue is uncertain, and requires further research.

Several dinosaur species appear to have an interrupted pattern of bone deposition (Chinsamy 1994; Reid 1990). This usually takes the form of alternating fibro-lamellar bone and LAGs, with or without annuli, thus switching from rapid to slow deposition periodically, and possibly annually (Figure 3). The trigger for this alternating rate of bone deposition is unknown, but could be seasonal as in modern reptiles. This ability to vary the rate and trajectory of growth is possibly a result of variable metabolic rates, which would have enabled the animal to survive periodically stressful periods.

Extent of vascularisation

The amount and type of vascularisation is revealed by microscopic examination of thin sections of the bone. Depending on the rate of bone formation different forms of vascularisation can result. The orientation of the vascular canals depends on the form of the spaces that were initially enclosed. Ricqlès (1974; 1976) used the



Figure 2: Transverse section of a recent lizard femur showing lamellar-zonal bone tissue. Note the periodic LAGs indicated by the arrows. Simple, radially arranged blood vessels occur in the compacta. Scale bar = 192 microns.



Figure 3: Cross section of a metatarsal of the Late Cretaceous *Archaeornithomimus* from the Iren Dabasu Formation of the Peoples Republic of China, showing LAGs (arrowheads) interrupting the deposition of fibro-lamellar bone in the compacta. Scale bar = 192 microns.

arrangement of the vascular canals to define topological categories of tissues within the fibro-lamellar complex: e.g., reticular, plexiform, laminar etc.

Vascularity can be sparse or dense. Simple blood vessels, primary osteons and secondary osteons can be easily recognised in a bone section (Figures 1, 2, 3, 4). Simple blood vessels show no alteration in the bone around the vascular channel (Figure 2), while primary osteons show a lamellar type of tissue around the blood vessels (Figure 1, 3). Primary osteons are formed during rapid bone deposition, whereas secondary osteons (Figure 4) do not reflect rate of bone formation, but are produced by a process termed Haversian reconstruction. This involves the removal of bone around a primary vascular canal, followed by subsequent redeposition of bone in the erosion cavity. Primary and secondary cylindrical osteons usually contain single vascular canals whereas the irregular, circumferential and radial types commonly contain multiple canals.

Secondary osteons are easily identified due to the occurrence of a cement line or reversal line which marks the furthest extent of bone removal. Successive generations of secondary osteons can form in the same location, resulting in dense Haversian tissue, where even the interstitial bone between the secondary osteons is secondary in nature.

The time taken to form a secondary osteon can be assessed by addition of the time taken for resorption and that for redeposition (Lacroix 1971). I have used this formula to estimate the minimum age of a juvenile *Dryosaurus* which had just begun to undergo Haversian reconstruction in its bone (Chinsamy 1995b). It is also possible to multiply the number of generations of osteons by the number of days it takes to form a single osteon in order to estimate the minimum age of an animal. However, caution needs to be exercised when doing this since Haversian reconstruction can occur at different stages of ontogeny (e.g. Currey 1960), and also since

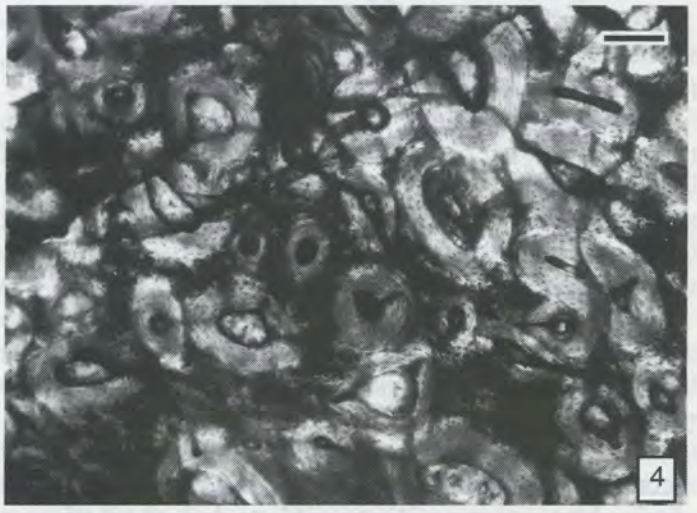


Figure 4: Secondary osteons in a sauropod bone fragment from the Early Cretaceous of Niger, Africa. Scale bar = 192 microns.

secondary osteons are not formed continuously, there is no way of determining the time lapse between each generation of osteons.

Numerous suggestions have been proposed regarding the biological significance of secondary osteon formation. These have included metabolic starvation resulting in damage to the vascular system (Currey 1960), physical necrosis of osteocytes (Enlow 1962), and biomechanical adaptation to physical strain. One of the arguments that has received the most support is that secondary osteons are the result of phosphocalcic metabolism (Amprino 1967). This argument was utilised by Bakker (e.g., 1986) to propose that the dense Haversian bone in dinosaur bone implies high metabolic rates, and hence endothermy in dinosaurs. It has however, now become increasingly clear that secondary osteons are not reliable indicators of metabolic rates. They are known to occur in bones of turtles (Enlow & Brown 1957), crocodiles (Chinsamy 1990) and tortoises (Reid 1987), but are absent in small mammals such as rodents and bats, as well as in passerine birds which are highly active (Bouvier 1977).

Ontogenetic Status

Generally, surface texture and articular surfaces of a fossil bone can indicate ontogenetic status of the animal. However, occasionally one is faced with a specimen that cannot be readily distinguished as adult or juvenile purely on morphological grounds. An examination of the animal's bone microstructure will reveal its ontogenetic status since juvenile and adult bone have distinctive microscopic structure (e.g. Nopsca & Heidsieck 1933).

The bone tissue of juveniles appears more porous in structure. Rapid bone formation results in a woven bone matrix with osteocytes haphazardly arranged (Figure 5). With increasing development the porous spaces become infilled by lamellar bone tissue, and primary osteons result (Figure 6). (In more slowly growing animals, e.g., lizards, the juvenile tissue can consist of a parallel fibred or pseudo-lamellar tissue with simple blood vessels). With maturity, the animal may switch from an earlier more rapidly formed type of bone tissue, to a more slowly formed tissue. For example, an earlier fibro-lamellar bone tissue pattern may change to a lamellar, pseudo-lamellar or lamellated type.

Microscopic changes in bone structure have been documented by the examination of growth series of specific skeletal elements of individual dinosaur species. For example, Chinsamy has documented the histological changes in growth series of femora of *Syntarsus* (Chinsamy 1990), *Massospondylus* (Chinsamy 1993) and *Dryosaurus* (Chinsamy 1995b), while Varricchio (1993) reported on the bone microstructure of three metatarsals and two tibiae of different sized *Troodon formosus*.

Bone formed late in life typically shows a slow rate of accretion. Depending on the nature of the tissue deposited during late ontogeny, it is possible to deduce whether an animal experienced indeterminate or determinate growth. Lamellated late bone or a series of closely spaced peripheral rest lines have been reported in mammals and birds that experience terminal growth. Such lines have also been recorded in *Brachiosaurus* (Gross 1934) which has an earlier non-zonal pattern, while *Syntarsus* (Chinsamy 1990), an unidentified theropod (Reid 1993; probably *Sauronitholestes,* personal communication 1996), and *Rhabdodon* (Reid 1990) record rest lines

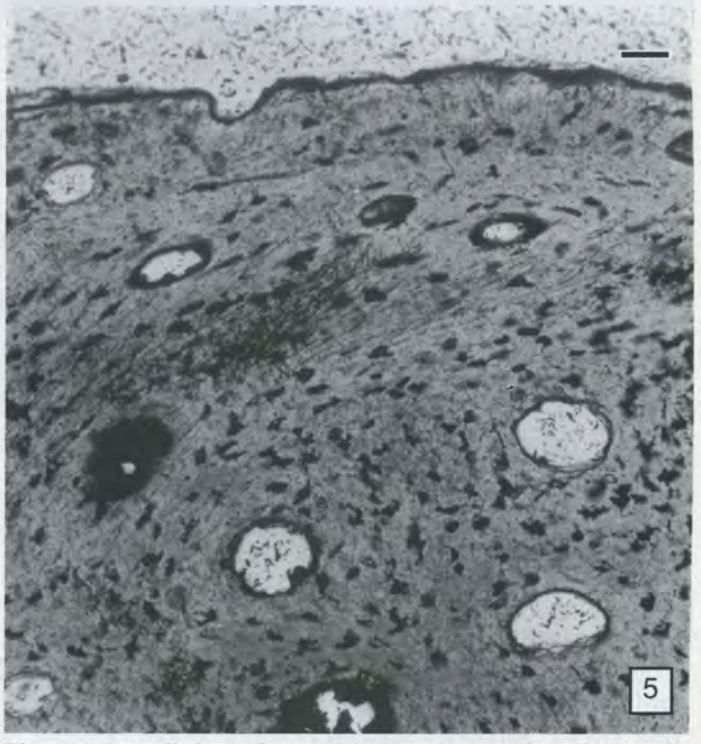


Figure 5: Juvenile bone tissues. A. Transverse section of a juvenile hadrosaur from the Late Cretaceous of Alberta showing rapid bone formation with several longitudinally orientated vascular channels. Scale bar = 46 microns.

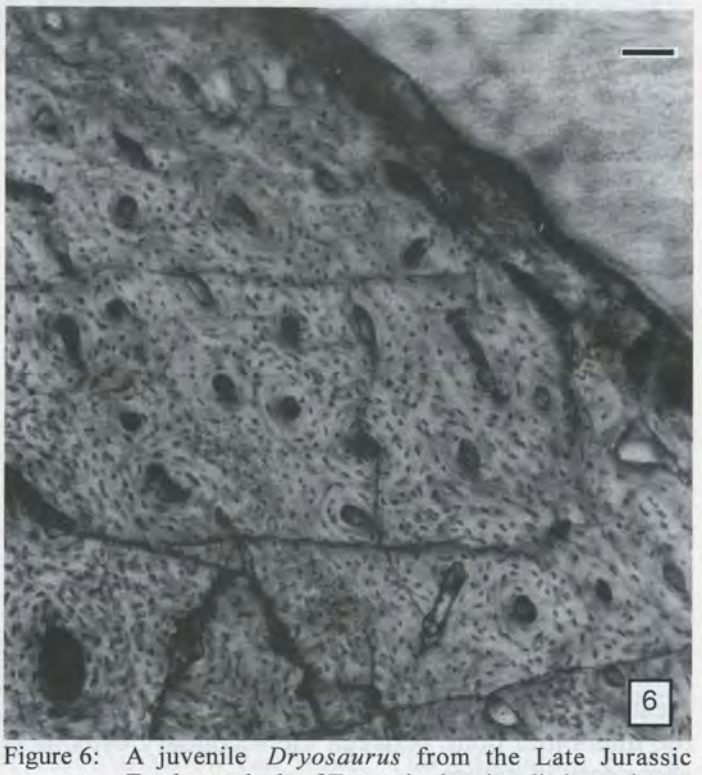


Figure 6: A juvenile *Dryosaurus* from the Late Jurassic Tendaguru beds of Tanzania showing distinct primary osteons in the woven bone matrix of the fibro-lamellar bone tissue. Scale bar = 50 microns

after a zonal pattern of bone deposition. Indeterminate growth is indicated by the absence of such lines, and the continuous formation of bone in the peripheral region e.g. in *Massospondylus* (Chinsamy 1993) and in *Dryosaurus* (Chinsamy 1995b).

Remodelling and Relocation

The internal microscopic texture of a bone bears testimony to the reshaping (remodelling) of the bone during its growth through ontogeny. As a bone grows in length and in diameter, various regions are relocated to new positions (Enlow 1969). Growth in length is attained by endochondral formation of bone, while growth in diameter occurs by subperiosteal or subendosteal deposits. The occurrence of different tissues signifies the occurrence of different events; e.g., the presence of compacted coarse cancellous bone tissue indicates that endosteal deposits of bone resulted in the compaction of a region that previously consisted of spongy bone (Figure 7). Reversal in the direction of growth from inward to outward (or vice versa) is indicated by the occurrence of reversal lines as well as differing tissue types. Thus, the stratified compacta of a bone represents the different types of tissue produced by different growth and remodeling activities that the bone experienced (Enlow 1969).

Biomechanical adaptations

It is generally accepted that the architecture of a bone is adapted to the weight of the animal, and to the mechanical properties of the bone itself (e.g. Rogers & Labarbera 1993). Various tensile and fatigue tests have shown that the different tissue types in the compacta exhibit different strengths. Thus, the tissue type, as well as its porosity and composition, results in a variation of the mechanical properties throughout the cortical thickness.

Bone is recognised as an adaptive tissue and remodels in response to changes in its mechanical environment. In a recent study, Heinrich *et al.* (1994) found that in a growth series of *Dryosaurus lettowvorbecki*, a distinctive change in the relative amount and distribution of the cortical bone occurred through ontogeny. They ascribed these changes in the cross sectional properties of the femora to increasing mechanical loads, and a caudal shift in the animals' centre of gravity as a result of a change in its preferred mode of locomotion (i.e., a shift from quadrupedality to bipedality).



Figure 7: Compacted coarse cancellous bone in the compacta of an adult *Dryosaurus* (GPIT 1713/103 distal) from the Tendaguru beds of Tanzania. Scale bar = 76 microns.

Bone wall thickness

A functional relationship exists between bone wall thickness, the habitat of the animal (Bühler 1986; Wall 1983) and the forces that act on the bone. It appears that long bones of animals are structures that have minimum mass which enables them to perform locomotory functions at minimum energy cost (Currey & Alexander 1985).

Examination of cross sectional architecture of femora of different species reveals distinct differences in bone wall thickness which appear to be related to the lifestyles of the animal. Some bones have thick walls and a small medullary cavity or sometimes none, whilst others have thin walls and large medullary cavities. Much research has been directed to quantify and ascertain why these differences occur (Bühler 1986; Currey & Alexander 1985; Wall 1983). Bühler (1986) quantified the observable differences in bone wall thickness by using a value termed the relative bone wall thickness (RBT) which is a ratio of the cross sectional bone wall thickness to the cross sectional diameter. Bühler (1986) calculated the RBT for a variety of birds, and deduced that long bones of birds are highly developed light weight structures, with large flying birds having much thinner bone walls than small to medium sized species.

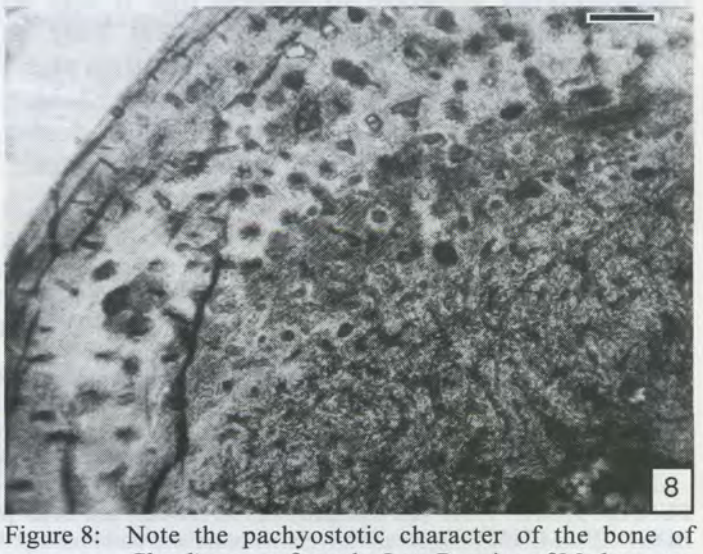


Figure 8: Note the pachyostotic character of the bone of *Claudiosaurus* from the Late Permian of Madagascar. Scale bar = 285 microns.

Wall (1983) measured the volume and weight of limb bones of terrestrial and aquatic mammals. He found that the limb bones of aquatic animals exhibited higher densities than terrestrial ones. Wall suggested that aquatic animals use an increase in compact bone mass to attain buoyancy in water, i.e. to counteract the buoyancy of the lungs.

Upon examination of the relative bone wall thickness (RBT) of adult *Syntarsus*, *Massospondylus*, *Crocodylus niloticus* and two species of birds (*Sagittarius serpentarius* and *Struthio camelus*) I found that the amphibious crocodile exhibited the highest bone wall thickness, while both birds had much lower RBT values than the dinosaurs, with *Sagittarius* having the lowest RBT (Chinsamy 1991). These findings correlate well with those of Wall (1983) and Bühler (1986).

Bone Microstructure of aquatic vertebrates

Besides the gross morphological adaptations that are evident in the skeletons of aquatic tetrapods, the internal organisation of the bone is also subjected to modifications. Depending on the particular type of adaptation of the animal, a very compacted, dense structure can result, termed pachyostosis, as in nothosaurs and sirenians (Buffrénil & Schoevaert 1989; Nopsca & Heidsieck 1933) or extreme cancellousness as in ichthyosaurs (Buffrénil & Mazin 1989), cetaceans (Buffrénil & Schoevaert 1988) and marine turtles (Rhodin *et al.* 1981) can occur. Buffrénil & Mazin (1989) used the pachyostotic nature of the compacta of *Claudiosaurus germaini* to suggest that it was an aquatic reptile (e.g. Figure 8). In a recent study on mosasaur rib microstructure, Sheldon & Bell (in press) deduced that *Clidastes* and *Tylosaurus*, which exhibited a reduced bone density inhabited deeper waters than *Platecarpus* which showed pachyostosis.

CONCLUSION

A fossilised skeleton of an animal provides a tremendous amount of information regarding its overall size and shape. Study of the microstructure of the bones provides an analysis of aspects of the biology and growth of the animal. In addition to phylogeny, bone tissue structure reflects ontogeny, and biomechanical function, as well as various other events that punctuate the life history of an individual.

The field of fossil bone microstructure is continually evolving. New research, particularly comparative and experimental studies of modern vertebrates, will allow deeper insight into the factors that influence bone deposition and bone biology as a whole. The outcome of such research, applied to fossil bone microstructure, will enhance our understanding of the biology and growth of extinct vertebrates.

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REFERENCES

AMPRINO, R. 1947. La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l'accroissement. *Archives de Biologie*, **58,** 315-330.

-------- 1967. Bone histophysiology. *Guys Hospital Report*, **116,** 51-69.

BAKKER, R.T. 1986. *The Dinosaur Heresies: New Theories Unlocking the Mystery of the Dinosaurs and their Extinction.* New York, William Morrow and Co. Inc.

BENNETT, S. C. 1993. The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology*, **19,** 92-106.

BOUVIER, M. 1977. Dinosaur haversian bone and endothermy. *Evolution,* **31,** 449-450.

BUFFRÉNIL, V. DE. 1980. Mise en evidence de l'incidence des conditions de milieu sur la croissance de *Crocodylus siamensis* (Schneider, 1801) et valeur des marques de croissance squelettiques pour l'évaluation de l'âge individuel. *Archives de Zoologie Expérimentale Générale,* **121,** 63-76.

-------- & MAZIN, J. M. 1989. Bone histology of *Claudiosaurus germaini* (Reptilia, Claudiosauridae) and the problem of pachyostosis in aquatic animals. *Historical Biology* **2,** 311-322.

-------- & SHOEVAER T, D. 1988. On how the delphinid humerus becomes cancellous: ontogeny of a histological specialization. *J. Morphol.*, **198,** 149-164.

-------- 1989. Données quantitatives et observations histologiques sur la "pachyostose" du squellette du Dugong, *Dugong dugon* (Müller) (Sirenia, Dugongidae). *Canadian Journal of Zoology,* **67,** 2107-2119.

BÜHLER, P. 1986 Das Vogelskelett – hochentwickelter Knochen-leichtbau. *Arcus,* **5,** 221-228.

CAETANO, M. H. 1990. Use and results of skeletochronology in some urodeles (*Triturus marmoratus*, Latreille 1800 and *Triturus boscai*, Lataste 1879). *Annales des Sciences Naturelles, Zoologie*, **11,** 197-199.

CASTANET, J. & SMIRINA, E. 1990. Introduction to the skeletochronological method in amphibians and reptiles. *Annales des Sciences Naturelles, Zoologie*, **11,** 191-196.

CHINSAMY, A. 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). *Palaeontologia africana*, **27,** 77-82.

-------- 1991. *The osteohistology of femoral growth within a clade: A comparison of the crocodile,* Crocodylus niloticus, *the dinosaurs,* Massospondylus *and* Syntarsus *and the birds,* Struthio *and* Sagittarius. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

-------- 1993. Bone histology and growth trajectory of the prosauropod. dinosaur *Massospondylus carinatus* (Owen). *Modern Geology,* **18,** 319-329.

-------- 1994. Dinosaur bone histology: implications and inferences. **In:** G. D. Rosenberg, & Wolberg, D., Eds, *Dino Fest*, Paleontological Society, Special Publication no. 7, 213-227. Knoxville, University of Tennessee.

-------- 1995a. Histological perspectives on growth in the birds *Struthio camelus* and *Sagittarius serpentarius*. **In:** Peters, S. Ed., *3rd symposium of the Society of Avian Paleontology and Evolution, 1992. Courier Forschungsinstitut Senckenberg*, **181,** 317-323.
-------- 1995b. Ontogenetic changes in the bone histology of the Late Jurassic ornithopod *Dryosaurus lettowvorbecki*. *Journal of Vertebrate Paleontology*, **15**(3), 96-104.
-------- & RAATH, M. A. 1992. Preparation of bone for histological study. *Palaeontologia africana*, **29**,39-44.
-------- & RUBIDGE, B. 1993. Dicynodont (Therapsida) bone histology: phylogenetic and physiological implications. *Palaeontologia africana,* **30,** 97-102.
-------- & DODSON, P. 1995. Inside a dinosaur bone. *American Scientist,* **83,** 174-180.
--------, CHIAPPE, L., & DODSON, P. 1994 Growth rings in Mesozoic avian bones: physiological implications for basal birds. *Nature,* **368,** 196-197.
-------- 1995. The bone microstructure of *Patagopteryx* and Enantiornithines. *Paleobiology* **21,** 561-574.
CURREY, J. D. 1960. Differences in the blood supply of bone of different histological types. *Quarterly Journal of Microscopical Science*, **101,** 351-370.
-------- & ALEXANDER 1985. The thickness of the walls of tubular bone. *Journal of the Zoological Society of London,* **206,** 453-468.
ENLOW, D. H. 1969. The bone of reptiles. **In:** Gans, C. & Bellairs, A. d'A., Eds., *Biology of the Reptilia. Morphology A*, 45-77. London, Academic Press.
-------- & BROWN, S.O. 1956. A comparative histological study of fossil and recent bone tissue. Part 1. *Texas Journal of Science*, **8** (4), 405-443.
-------- & ---------- 1957. A comparative histological study of fossil and recent bone tissue. Part 2. *Texas Journal of Science*, **9,** 186-214.
-------- & ---------- 1958. A comparative histological study of fossil and recent bone tissue. Part 3. *Texas Journal of Science*, **10**(2), 187-230.
FARLOW, J. O., DODSON, P., & CHINSAMY, A. 1995. Dinosaur biology. *Annual review of Ecology and Systematics,* **26,** 445-471.
GROSS, W. 1934. Die Typen des mikroskopischen Knochenbaues bei fossilen Stegocephalen und Reptilien. *Zeitschrift für Anatomie,* **103,** 731-764.
HASSE, C. 1878. Die fossilen Wirbel. Morphologische Studien. Die Histologie fossiler reptilwirbel. *Morph. Jb.* **4,** 480-502.
HEINRICH, R. E., RUFF, C. B. & WEISHAMPEL, D. B. 1993. Femoral ontogeny and locomotor biomechanics of *Dryosaurus lettowvorbecki* (Dinosauria, Iguanodontia). *Zoological Journal of the Linnean Society,* **108,** 176-196.
KLEVEZAL, G. A., & KLEINENBERG, S. E. 1969. Age Determination of Mammals from Annual Layers in Teeth and Bones. Translated from Russian by J. Salkind. Jerusalem, Israel Program for Scientific Translations Press.
LACROIX, P. 1971. The internal remodeling of bones. **In:** Bourne, G. H., Eds., *The Biochemistry and Physiology of Bone,* **3,** 119-144. New York, Academic Press.
LEAHY, G. D. 1991. Lamellar-zonal bone in fossil mammals: implications for dinosaur and therapsid paleophysiology. *Journal of Vertebrate Paleontology*, **11,**42A.
MOODIE, R. L. 1923. *Palaeopathology*. Urbana, University of Illinois Press.
NOPSCA, F.& HEIDSIECK, E. 1933. On the bone histology of the ribs in immature and half-grown trachodont dinosaurs. *Proceedings of the Royal Zoological Society* **1,** 221-223.
PATNAIK, B. K. & BEHERA, M. N. 1981. Age determination in the tropical agamid lizard, *Calotes versicolor* (Daudin) based on bone histology. *Experimental Gerontology,* **16,** 295-308.
PEABODY, F. E. 1961. Annual growth zones in vertebrates (living and fossil). *Journal of Morphology,* **108,** 11-62.
QUEKETT, J. 1849. On the intimate structure of bone, as comprising the skeleton in the four main classes of animals, viz., mammals, birds, reptiles and fishes, with some remarks on the great value of the knowledge of such structure in determining the affinities of minute fragments of organic remains. *Transactions of the Microscopical Society of London*, **2,** 46-58.
REID, R. E. H. 1984a. The histology of dinosaurian bone, and its possible bearing on dinosaurian physiology. *Symposium of the Zoological Society of London,* **52,** 629-663.
-------- 1984b. Primary bone and dinosaurian physiology. *Geological Magazine,* **121,** 589-598.
-------- 1987. Bone and dinosaurian "endothermy". *Modern Geology,* **11,** 133-154.
-------- 1990. Zonal "growth rings" in dinosaurs. *Modern Geology,* **15,** 19-48.
-------- 1993. Apparent zonation and slowed growth in a small Cretaceous theropod. *Modern Geology,* **18:** 39-406.
RHODIN, A.G., J. OGDEN, J. A. & CONLOGUE, G. J. 1981. Chondro-osseous morphology of *Dermochelys coriacea*, a marine reptile with mammalian skeletal features. *Nature*, **290,** 244-246.
RICQLÈS, A. DE. 1972. Recherches paléohistologiques sur les os longs de tétrapodes. III – Titanosuchiens, Dinocéphales et Dicynodontes. *Annales de Paléontologie,* **58:** 1-60.
-------- 1974. Evolution of endothermy: histological evidence. *Evolutionary Theory,* **1,** 51.
-------- 1976. On bone histology of fossil and living reptiles, with comments on its functional and evolutionary significance. **In:** Bellairs, A. d'A. & Cox, C. B., Eds, *Morphology and Biology of Reptiles,* 123-150. London, Academic Press.
-------- 1980. Tissue structure of dinosaur bone: functional significance and possible relation to dinosaur physiology. **In:** Thomas, R. D K. & Olson, E. C., Eds., *A Cold Look at the Warm Blooded Dinosaurs,* 103-139. Boulder, Westview Press.
-------- 1992. Paleoherpetology now: a point of view **In:** Adler, K., Ed., *Herpetology: Current Research on the Biology of Amphibians and Reptiles. – Proceedings of the First World Congress of Herpetology,* 97-120. Society for the Study of Amphibians and Reptiles, Oxford, Ohio.
ROGERS, R. R. & LABARBERA, M. 1993. Contribution of internal bony trabeculae to the mechanical properties of the humerus of the pigeon (*Columba livia*). *Journal of Zoology, London*, **230,** 433-441.
SANDER, P. M. 1990. Skeletochronology in the small Triassic reptile *Neusticosaurus. Annales des Sciences Naturelles, Zoologie,* 13 serie, **11,** 213-217.
SEITZ, A. 1907. Vergleichende Studien über den mikroskopischen Knochenbau fossiler und rezenter Reptilien und dessen Bedeutung für das Wachstum und Umbildung des Knochengewebes in allgemeinen. *Nova Acta Abhandlungen der Kaiserlichen Leopold-Carolignischen deutschen Akademie der Naturforscher,* **87,** 230-270.
SHELDON, A. & BELL, G. L. In press. Ecological implications of mosasaur bone microstructure. **In:** Calloway, J. M. & Nicholes, E. L. Eds., *Ancient Marine Reptiles.*
VARRICCHIO, D. J. 1993. Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology,* **13,**99-104.
WALL W. P. 1983. The correlation between limb-bone density and aquatic habits in recent mammals. *Journal of Paleontology,* **57**(2), 197-207.