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Chinsamy, Anusuya

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Bernard Price Institute for Palaeontological Research
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PHYSIOLOGICAL IMPLICATIONS OF THE BONE HISTOLOGY OF *SYNTARSUS RHODESIENSIS* (SAURISCHIA: THEROPODA)

by

Anusuya Chinsamy

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg

ABSTRACT

Femora of *Syntarsus rhodesiensis* specimens of differing ontogenetic stages were sectioned and prepared for histological study. Features such as the structure of the cortical bone tissue, the degree of vascularisation and haversian substitution, and the general pattern of bone deposition through ontogeny, are described. The question of the bearing of bone histology on interpretation of the probable physiology of *Syntarsus* is also discussed.

INTRODUCTION

Interpretations of the physiological patterns of extinct animals have long fascinated palaeontologists who have sought to understand the fossils as once living organisms. Anatomical features such as locomotor apparatus (Bakker, 1971, 1972, 1980), brain size (Hopson, 1978/79), predator prey ratios (Bakker, 1971, 1972, 1980), and bone histology (De Ricqlès, 1974, 1976, 1980) are examples of what has been studied to try to gain insight into the type of physiology that extinct animals once experienced. It has become increasingly clear that the histological structure of fossil bone can provide better clues to physiology than most other methods (Bennett & Ruben, 1986).

Work on fossil bone histology began relatively early in the nineteenth century (Nopcsa & Heidsieck, 1933), and subsequently interest in the field has developed considerably (e.g. Enlow & Brown, 1956, 1957, 1958; Peabody, 1961; Enlow, 1963, 1969; Currey, 1962). Palaeohistology is still considered a relatively new field of study, but it has now broadened its horizons from being initially mainly comparative and descriptive to include considerations of functions and physiology (De Ricqlès, 1974, 1976, 1980; Reid, 1984, 1987; Buffrénil, Farlow, and De Ricqlès, 1986). There is still much debate over the physiological meaning of different tissue types (Reid, 1984, 1987; Bouvier, 1977 ; De Ricqlès, 1976, 1980, 1983), but the general consensus is that bone histology may provide some clues as to the animal's growth rate, metabolic rate, activity levels, and hence some indications concerning its heat production and thermoregulatory ability.

In this study an attempt was made to deduce aspects of the possible physiology that *Syntarsus* once experienced, as reflected in its bone histology. The general bone histology is described initially and thereafter follow speculations on the animal's thermoregulatory ability, possible evidence for sexual dimorphism, and also the probable growth strategy it employed.

MATERIALS AND METHODS

Femora of the early Jurassic theropod dinosaur, *Syntarsus rhodesiensis*, were obtained from the collections of the Natural History Museum of Zimbabwe. Gross femoral dimensions were used to assign the femora to approximate "age-classes" following Raath (1977). The femora were also sorted on the basis of trochanteric development into two variants, robust and gracile, which Raath (1977) thought reflected sexual dimorphism. He suggested that the robust femora may belong to females.

Specimens were embedded in Epofix cold mounting resin which was prepared according to the manufacturer's specifications. The specimens were sectioned below the 4th trochanter and further along the shaft . Thin sections were subsequently prepared using a "Micro-Trim" section-cutting machine. The sections were then ground on a Buehler Ecomet III grinder using 400, 600 and 1000 grit carborundum paper discs, until judged to be of acceptable thinness. Aluminium oxide powder sprinkled onto a cloth-covered lap-wheel was used for final polishing. Water was used as a coolant.

Gross examination of prepared slides was carried out under a Zeiss Stereomicroscope. More detailed examination was carried out under a Zeiss Photomicroscope 2.

RESULTS

Bone Histology of *Syntarsus rhodesiensis*.

The bone of *S. rhodesiensis* comprises a distinctive cortical region enclosing a large central medullary cavity. It seems that the medullary cavity was devoid of trabeculae, since no traces of trabeculae have been observed in bone from either young or old animals. The cortex is stratified into distinct types of bone signifying what is interpreted as periods of slowed and fast growth (fig. 1A).

The region of rapid growth consists of highly vascular fibro-lamellar bone. Primary osteons that occur are mainly longitudinal in form, but circumferential vessels are also found. The blood vessels tend to anastomose

and form a reticular arrangement (fig. 1B). Secondary osteons occur in the region nearest the medullary cavity, especially in the bone of adult animals. The osteocytes are highly branched, particularly those around the lumen of each vascular canal.

The region of slowed growth is comparatively much narrower and is relatively poorly vascularised, if at all. In the smallest, and therefore presumably youngest, bones that have been examined, at least one growth ring has been observed. In the bone from progressively larger, and therefore presumably older specimens, the number of such concentric growth lines increases (Table 1). The number of growth rings is not a true reflection of the age of the animal since the first growth rings are obliterated due to reconstruction in the peri-medullary region.

Rest lines, indicating a slowing down in growth or pauses in growth, have been observed in the peripheral region of the bone from adult animals (fig. 1C).

Perimedullar erosion cavities occur in the cortex of the bones of the robust forms but not in those of the gracile forms. The cavities are formed by the erosion of surrounding bone, resulting in enlarged cavities in the cortical bone. Haversian reconstruction of these cavities occurs at a later stage, as is seen by the centripetal redeposition of bone within them. Thus in the cortex one may see a range of cavities of different sizes as well as a range in stages of reconstruction (Figure 1D).

Table 1.

Specimen Number	Number of Growth Rings
QG 713	3
QG 715	3
QG 174A	2
QG 727	4
QG 716	5
QG 753	6
QG 726	5
QG 725	6
QG 731	6
QG 760	5
QG 45	1
QG 744	3
QCT6Q	4

DISCUSSION

The physiological implications of bone histology has been the focus of much debate and controversy. Bakker (1972, 1975, 1980) was amongst the earliest to declare that dinosaurs were endotherms because their bone histology resembled that of extant endotherms and also because of the high vascularity of their bone. De Ricqlès (1983) has recently changed his standpoint that dinosaurs are endotherms (1974, 1976) to one that dinosaurs occupied an intermediate position on the continuum from ectothermy to endothermy. I believe that to a certain extent bone does have physiological implications but one has to be extremely careful of generalisations and simplistic arguments. I endorse Reid's (1987) view that bone tissue should not be used by itself to identify ectothermy and endothermy, since no particular type of tissue is characteristic of one or the other physiological state.

Fibro-lamellar bone tissue has previously been used as a criterion for endothermy (Bakker, 1972, 1975), but Reid (1987), and Enlow & Brown (1956, 1957, 1958) have shown that it occurs in a wide range of animals which includes both endotherms and ectotherms. It is however interesting to note that such tissue is usually taken to indicate a sustained rapid rate of bone deposition and the implication is that only a high basal metabolic rate would result in this type of deposition. Reid (1987) has argued that the occurrence of fibro-lamellar bone in therapsids such as deinocephalians, and in juvenile crocodiles from crocodile farms (Buffrenil & Buffetaut, 1981), shows that an animal need not be endothermic to have such a bone tissue pattern, and that they were probably inertial homeotherms that managed to maintain a high body temperature because of high ambient temperature. I basically agree with this view, but I think it necessary to emphasise that a high body temperature would be associated with an elevated metabolic rate irrespective of whether this is achieved by internal physiological regulation or is due to high ambient temperature.

Haversian bone tissue is formed by the resorption of bone surrounding a vascular canal and subsequent filling of the resulting enlarged cavity by centripetal deposition of new lamellar bone. The cause of haversian bone formation is a point of much contention. Many ideas have been proposed why haversian bone forms: e.g. in response to biomechanical adaptation to physical strain (Ostrom, 1980); as a result of physical necrosis of the osteocytes (Enlow, 1962), etc. However, Meister's (1951) research on the bone of Canada Geese during moult seems to support the idea of Amprino (1967) that bone functions partly as a store of phosphates and calcium, in which and from which such salts can be fixed or freed as the animal requires them. Dense haversian bone tissue has been found to occur in the bones of mammals, birds and in some reptiles such as turtles (Order Cryptodira). The unifying factor amongst all these different animals is the fact that they are able to maintain high activity levels resulting in elevated body temperature, which again implies that they were capable of high metabolic rates.

Thus, although bone tissue cannot be used diagnostically to distinguish endotherms from ectotherms,

it can provide indications about the metabolic rate, as well as the rate and type of bone deposition that occurred. From this and other factors such as the environment, deductions regarding aspects of the possible physiology of the animal may be made.

The question then arises as to what physiological indications may be obtained from study of the bone histology of *Syntarsus*.

Three features worth considering in this connection are: a) the cortical stratification of the bone; b) perimedullar erosion cavities; and c) peripheral rest lines.

Cortical stratification

The most distinctive feature of *Syntarsus* bone histology is the stratification of the cortex into layers representing alternating periods of accelerated and slowed growth. The slowed growth is reflected by the poorly vascularised, lamellated annuli, while the periods of fast growth are represented by the highly vascularised zonal bone tissue. This cyclical nature of bone deposition resembles that found in many modern day ectotherms whose bone deposition is subjected to seasonal fluctuations (Enlow, 1969; Buffrénil & Buffetaut, 1981). *Syntarsus* bone structure differs from the "typical" reptilian pattern in that the zonal bone comprises fibro-lamellar bone tissue. This tissue is usually found in animals known to possess high metabolic rates, such as mammals and birds, and is considered to be the result of rapid bone deposition as a result of rapid growth. It may therefore be deduced that *Syntarsus* experienced alternating periods of lower and higher metabolic rates during its growth. This raises questions about the physiology of this animal which would produce this pattern of bone deposition.

Three alternative hypotheses may be considered, and these are outlined below:

1. *Syntarsus* as an ectotherm:

As mentioned earlier, the most obvious resemblance to ectotherms is the alternating periods of slowed and fast growth reflected in the cortical stratification of *Syntarsus* bone. The deposition of fibro-lamellar bone tissue during the period of active growth indicates accelerated metabolism. This type of bone tissue, although not common, is sometimes found in the bone tissue of ectotherms such as in the zonal region of young farm-raised crocodiles (Buffrénil & Buffetaut 1981; Chinsamy 1988), where optimal conditions for growth exist. Reid (1987) has also reported the presence of fibro-lamellar bone tissue in some primitive therapsids (e.g. Deinocephalia); these animals were possibly ectothermic, but their physiology is not known. Thus we see that fibro-lamellar bone cannot be ascribed only to endotherms because its presence has been observed in known ectotherms and in animals presumed to be ectotherms. The case of the farm-reared young crocodiles shows that, under favourable environmental conditions, normally slow-growing members of the archosaurian lineage are capable of responding with accelerated growth which can result in deposition of this kind of bone fibro-lamellar bone. The juvenile crocodiles probably did so by responding as homoiothermic ectotherms.

The implication in this hypothesis is that *Syntarsus* might have responded in a similar way i.e. that its body temperature was governed by ambient temperature, and it was unable to regulate body temperature endogenously. During favourable times, the high ambient temperature would produce high core body temperature, resulting in accelerated metabolism, accelerated growth, and the consequent deposition of fibro-lamellar bone in the highly vascularised zones; during times of low ambient temperature its core body temperature would drop, metabolism would slow, and a reduced rate of bone deposition would result in formation of the poorly vascularised annuli.

2. Possibility of *Syntarsus* having a thermo-physiological pattern intermediate between ectothermy and endothermy:

If endothermy was derived from ectothermy, then it stands to reason that animals with an intermediate thermoregulatory ability existed (indeed, many extant animals occupy intermediate positions on the continuum from classical heterothermic ectothermy to homoiothermic endothermy). *Syntarsus* might have been such an intermediate. McNab (1978) postulated that for endothermy to evolve from ectothermy would necessitate an initial increase in body size to attain inertial homoiothermy, followed by a decrease in body size with only a small drop in total rate of metabolism.

Syntarsus, as a medium sized coelurosaurian too small and inappropriately built to be an inertial homoiotherm, might represent a stage in which reduction of body size had occurred and that this, coupled with an elevated metabolic rate, allowed homoiothermy. It may have been capable of regulating its body temperature during the favourable season (perhaps when ambient temperatures were close to its optimum body temperature), resulting in rapid growth and deposition of fibro-lamellar bone in the zonal region. Inadequate ability to maintain optimal body temperature during the unfavourable season would result in arrested or slowed growth, which would account for the poorly vascularised annuli.

Many palaeontologists today accept that birds arose from the dinosaurs and that the most likely contenders for their ancestry are the small theropod (coelurosaurian) dinosaurs (e.g. Ostrom, 1973, 1975). Birds are undoubted endothermic animals, whereas there is much debate about the physiology of the dinosaurs. *Syntarsus* is a coelurosaurian dinosaur which shows evidence in its bone histology of an intermediate type of physiology between ectotherms and endotherms. If this is so, then already in the mid to late Mesozoic amongst the coelurosaurs there was a move towards endothermy. Birds might well have inherited this ability fully formed from their theropod ancestors in the Mesozoic.

3. *Syntarsus* as a heterothermic endotherm:

A third possibility, as far as the thermoregulatory

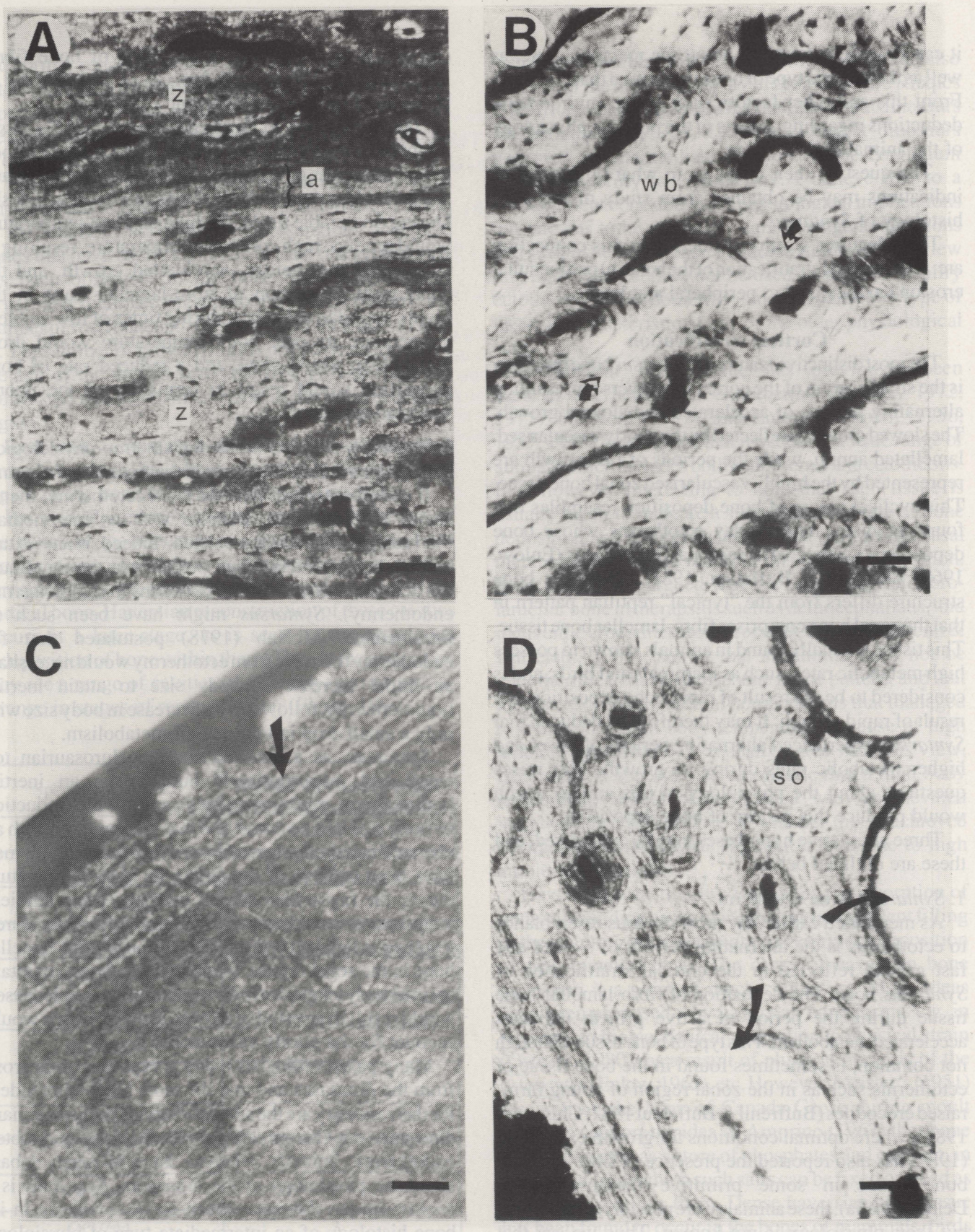


Figure 1 (A). *Syntarsus rhodesiensis* (Specimen number: 715a; BPI slide number 0100) femur. Transverse section. Note the well vascularised zones (z) alternating with the annulus (a). (scale: 10mm = 0.023 microns)

(B). *Syntarsus rhodesiensis* (Specimen number: 715a; BPI slide number 0100) femur. Transverse section. Primary osteons (arrows) embedded in a woven bone matrix (wb). (scale: 10mm = 0.046microns)

(C). *Syntarsus rhodesiensis* (Specimen number: 725e; BPI slide number 0022) femur. Transverse section. Note the presence of rest lines (arrow) in the peripheral region of the cortex. (scale: 10mm = 0.061 microns)

(D). *Syntarsus rhodesiensis* (Specimen number: 753b; BPI slide number 0032) femur. Transverse section. Secondary reconstruction in the perimedullary region of the cortex. Note the enlarged cavities (arrow) and the secondary osteons (so). (scale: 10mm = 0.035 microns)

ability of *Syntarsus* is concerned, is that it was an endotherm with a cyclical growth rate which was due to environmental stresses. From the aeolian sediments in which it was found, *Syntarsus* has been interpreted as having inhabited a hostile sandy desert during the late Triassic or early Jurassic (Raath 1977). Clear indications of periods of drought have been observed in the Elliot Formation by Kitching (pers. comm., 1989) as soil horizons interrupting the floodplain deposits.

Perhaps the annuli that are observed in *Syntarsus* bone tissue are reflections of physiological stress due to such droughts rather than to fluctuations in ambient temperature. Many advanced modern endotherms such as the poorwill (*Phalaenoptilus nuttalli*), and the Mojave squirrel (*Citellus mojavensis*), aestivate during prolonged periods of drought (Burton, 1970). Perhaps *Syntarsus* was as advanced as any modern day hibernating/aestivating mammal or bird, and aestivated to escape dehydration. During periods of aestivation its metabolism may have slowed sufficiently to produce the annuli.

From this hypothesis it might be speculated that the normal pattern of bone deposition in *Syntarsus* was fibro-lamellar, and that this pattern was only interrupted during periods of environmental stress such as the drought periods referred to above. In that case, the growth rings that have been observed might not necessarily reflect regular annual seasonal cycles of growth, but rather irregular periodicity. If, though, *Syntarsus* did aestivate, where would it have done so? The environment is considered to be a sand-dune desert (Raath 1977) with vegetation probably only around playa lakes and along major drainage courses. The animal has no obvious adaptations for burrowing, and also its size makes this an unlikely possibility. Migration out of the area in times of stress is a possibility, but the huge areal extent of the Gondwana desert makes that seem equally implausible.

Perimedullar erosion cavities

An interesting feature of the bone histology of *Syntarsus* is the occurrence of large perimedullary cavities in the bone compacta of the robust forms. If one accepts that bone acts as a store of phosphates and calcium, releasing them as required by the bioenergetic demands of animal (e.g. Meister, 1951; Amprino, 1967), then it suggests that the robust forms of *Syntarsus* experienced particular bioenergetic stresses which resulted in the formation of large erosion cavities in the bone where the minerals were withdrawn. Although it can be found in both males and females amongst mammals (especially in older individuals), this condition of osteoporosis is more commonly a feature amongst pregnant female mammals. It therefore seems to be linked in these cases to an increased need for phosphates and calcium during reproduction. During egg-laying, birds experience a loss in weight of their compact bone and also a resorption of the spongy bone that was deposited in the medulla of the long bones during ovulation (Meister, 1951). It has been suggested that the large erosion cavities found in the long bones of *Syntarsus* are osteoporotic cavities formed during egg-laying when the animal experienced an elevated need for calcium and phosphates (Raath 1977). Thus, from a histological perspective, Raath's (1977) postulation that the robust forms are females, is supported.

Peripheral rest lines

The presence of distinct rest lines in the periphery of the cortex suggests a determinate growth pattern in *Syntarsus*. Such rest lines are known to occur in the bones of mammals once adult size has been attained and growth as such has ceased. Amongst ectotherms, growth continues until the animal's death, although the rate of growth declines. Thus although it may seem that *Syntarsus* resembles "typical" ectotherms in general overall cortical structure, the resemblance is superficial, differing in the type of bone that is found in the zones and also in that the animal evidently has determinate growth.

CONCLUSION

Syntarsus bone histology has provided several indicators as to its possible physiological state. The presence of fibro-lamellar bone and primary osteons in the zones permits the deduction that this bone was laid down rapidly. This would require and thus implies a high metabolic rate. The presence of extensive "osteoporotic" resorption cavities in the perimedullary region of the bone of the robust forms suggests particular energetic demands in that form which are not shared by the gracile form. The fact that these animals show a determinate growth strategy allies them strongly with known endotherms.

The question of the thermoregulatory ability of *Syntarsus rhodesiensis* is highly debatable. From the pattern of the bone histology it appears that these animals were physiologically more advanced than any known modern day ectotherm, and were possibly as advanced as modern endotherms or, more likely, were tending strongly towards the endothermic condition. The final answer, though, still eludes us.

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REFERENCES

AMPRINO, R. 1967. Bone histophysiology. *Guys Hospital Report*, **2**: 51-69.

BAKKER, R. T. 1971. Dinosaur physiology and the origin of mammals. *Evolution*, **25** (4): 636-658.

------ 972. Anatomical and ecological evidence of endothermy in dinosaurs. *Nature*, **238**: 81-85.

------ 1975. Dinosaur renaissance. *Scient. Amer.*, **232** (4): 58-78.

------ 1980. Dinosaur heresy, dinosaur renaissance. In: THOMAS, R.D.K. and OLSON, E.C. (eds.), *A Cold Look at the Warm Blooded Dinosaurs*. AAS Selected Sympos. no. 28: 15-54., Westview Press, Boulder.

BENNETT, A. F. & RUBEN, J. A. 1986. The metabolic and thermoregulatory status of therapsids. In: Hotton, N, Maclean, P.D., Roth, J.J. & Roth, E.C. *The Ecology and Biology of Mammal-like Reptiles*. Smithsonian Institution Press, London.

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

BUFFRÉNIL, V. De and BUFFETAUT, E. 1981. Skeletal growth lines in an Eocene crocodile skull from Wyoming as an indicator of ontogenic age and paleoclimatic conditions. *J. Vert. Pal.*, **1** (1): 57-66.

BUFFRÉNIL, V. De, FARLOW, J. O. and RICQLÈS, A. De. 1986. Growth and function of *Stegosaurus* plates: evidence from bone histology. *Paleobiology*, **12** (4): 459-473.

BURTON, M. 1970. *Wanderers of Prairie and Desert*. Orbis Publishing, London.

CHINSAMY, A. 1988. *Comparative bone histology of a crocodilian, a theropod dinosaur and a bird*. Unpublished MSc dissertation, University of the Witwatersrand, Johannesburg.

CURREY, J.D. 1962. The histology of the bone of a prosauropod dinosaur. *Paleobiology*, **5** (2): 238-246.

ENLOW, D.H. 1962. A study of the post-natal growth and remodeling of bone. *Am. J. Anat.*, **110** (2): 79-101.

------ 1963. *Principles of Bone Remodeling*. Charles C. Thomas, Springfield, U.S.A.

------ 1969. The bone of reptiles. In: Gans, C. et al. (eds.), 1969. *Biology of the Reptilia*. Morphology A. volume 1: 45-77, Academic Press,London.

------ & BROWN, S. O. 1956. A comparative histological study of fossil and Recent bone tissue. Part 1. *Texas J. Sci.*, **8** (4): 405-443.

------ & BROWN, S. O. 1957. A comparative histological study of fossil and Recent bone tissue. Part 2. *Texas J. Sci.*, **9** (2): 186-214.

------ & BROWN, S. O. 1958. A comparative histological study of fossil and Recent bone tissue. Part 3. *Texas J. Sci.*, **10** (2): 187-230.

HOPSON, J.A. 1979. Were the dinosaurs warm-blooded? Translation of "Waren die Dinosaurier Warm-bluter" *Mannheimer Forum* 78/79: 123-184.

McNAB, B.K.1978. The evolution of endothermy in the phylogeny of mammals. *Am. Naturalist*, **112** (983): 1-21.

MEISTER, W. 1951. Changes in histological structure of the long bones of birds during the molt. *Anat. Rec.*, **3** (1): 1-21.

NOPCSA, F. B. & HEIDSIECK, E. 1933. On the histology of the ribs in immature and half-grown trachodont dinosaurs. *Proc. Zool. Soc. Lond.*, **1**: 221-226.

OSTROM, J. H. 1973. The ancestry of birds. *Nature*, **242**: 136.

------ 1975. The origin of birds. *Ann. Rev. Earth and Planetary Science*, **3**: 55-77.

------ 1980. The evidence for endothermy in dinosaurs. In: Thomas, R.D.K. & Olson, E.C. (ed.), *A Cold Look at the Warm Blooded Dinosaurs*. AAS Selected Sympos. no. 28: 15-54., Westview Press, Boulder.

PEABODY, F. E. 1961. Annual growth zones in living and fossil vertebrates. *J. Morph.*, **108** (1): 11-62.

RAATH, M.A. 1977. *The anatomy of the Triassic theropod Syntarsus rhodesiensis (Saurischia: Podokesauridae) and a consideration of its biology*. Unpublished PhD Thesis, Rhodes University, Grahamstown.

REID, R.E.H. 1984. Primary bone and dinosaurian physiology. *Geol. Mag.*, **121** (6): 589-598.

------ 1987. Bone and dinosaurian "endothermy". *Mod. Geol.*, **11**: 133-154.

RICQLÈS, A. J. De 1974. Evolution of endothermy: histological evidence. *Evol. Theory*, **1**: 51.

------ 1976. On bone histology of fossil and living reptiles with comments on its functional significance. In: Bellairs, A.d'A & Cox, C.B. (eds.) *Morphology and Biology of Reptiles*., Linn. Soc. Symp., no. 3: 123-150.

------ 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*. AAS Selected Sympos. no. 28: 103-139, Westview Press, Boulder.

------ 1983. Cyclical growth in the long limb bones of a sauropod dinosaur. *Acta Palaeont. Pol.*, **28** (1-2): 225.