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CYCLICAL GROWTH IN THE LONG LIMB BONES OF A SAUROPOD DINOSAUR

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Structures indicative of cyclical growth are described for the first time in a long limb bone of a half-grown sauropod dinosaur. This provides a mean by which age and growth rate are tentatively assessed. The significance of the findings in terms of sauropod physiology is discussed and it is concluded that the data are accordant with an imperfect mass homeothermy and incipient (mass) endothermy as a model of sauropod physiology.

Key words: bone histology, growth, paleophysiology, Dinosauria, Sauropoda.

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INTRODUCTION

When they are not remodeled by Haversian substitution, the long limb bones of sauropods, like those of the other dinosaurs, are generally described in the literature as formed by densely vascularized laminar and/or plexiform primary bone tissues, lacking obvious "rings" of cyclical growth (Currey 1962; Enlow and Brown 1957; Enlow 1969; Ricqlès 1968*a*, *b*, 1974, 1975, 1976, 1976—77, 1980). However, in the course of a general survey of the literature on dinosaur bone histology, some indications that cyclical growth rings might indeed exist in dinosaur bones were found, but the available data were far from unequivocal and convincing (see discussion in Ricqlès 1980 and references therein).

In view of the potential importance of the histophysiological interpretation of bone tissue with respect to patterns of growth in dinosaurs, and of inference from growth patterns about physiology, it was considered advisable to search for new evidence regarding this problem. An onto-histogenetical study of growth in a sauropod dinosaur, the results of which will be published elsewhere, has yielded clear instances of cyclical growth patterns in the long bones of a half-grown individual. These findings are briefly reported here and some of the consequences discussed.

While this paper was beeing prepared for publication, similar findings have been reported by Reid (1981), who describes obvious "growth rings" in the pelvic bones of another sauropod. This stress the possibility that such structures may be indeed much more common in the bones of sauropods, and perhaps in other dinosaurs too, than was previously recognized. If so, it would be interesting to understand why such structures have remained generally unnoticed so far.

MATERIALS AND METHODS

The material consists of an incomplete growth series of the Mid--Jurassic sauropod *Bothriospondylus* from northwestern Madagascar (Malagasy Republic). Several anatomical (Thevenin 1907; Lapparent 1943; Lavocat 1955; Ogier 1975) and histological (Ricqlès 1968*a*, *b*) studies of this sauropod are available as a background for the onto-histogenetical study currently in progress.

Thin sections best suited for detailed histological descriptions with the compound microscope are not well suited for the recognition of cyclical growth in the long bones of sauropods (pl. 7). This may in part account for the late recognition of the cyclical growth rings in these bones. Indeed, good histological sections of the petrographic type are usually rather thin (less than 80 µm) and the mounting medium further tends to reduce the optical contrast between successive growth cycles, while observation at high magnifications makes the recognition of overall cycles and patterns difficult. However, polished transverse sections of whole bones, or fairly thick unmounted sections, observed with the naked eye or at low magnifications under the binocular dissection microscope, in some instances reveal obvious growth cycles.

RESULTS

The cross section of the proximal diaphysis of a humerus (MAA 214) about 60 cm long, therefore of a roughly half-grown individual (maximum recorded humeral length for the species is 155.5 cm: Ogier 1975), is 85×50 mm at the level of the origin of the delto-pectoral crest (pl. 8). The bone cortex varies in thickness from 5 mm on the anterior, concave face of the bone, to 12.5 mm on the postero-medial and 15 mm on the postero-external faces of the bone. Most parts of the cortex are formed by the general "fibro-lamellar" pattern of primary (periosteal) bone (Ricqlès 1974, 1975, 1976—77). It varies from typical plexiform tissue to reticular tissue, or tissue with only parallel longitudinal primary osteons, from place in the section. Haversian substitution is already extensive and plentiful in the deep half of the cortex, and even spreads into the external cortex of the internal tuberosity, as well as into the cortex of the delto-pectoral crest.

The internal (medial) face of the bone has a cortex which thickens from 6 mm anteriorly to 12.5 mm posteriorly. To the naked eye it characteristically shows 6—8 faint superimposed cycles in its whole thickness. Each cycle comprises a narrow band, darker in reflected light, and a wide band, lighter colored and apparently more vascularized. While the narrow bands maintain a more or less constant thickness, the clearer bands widen according to the overall thickness of the cortex. In the thicker parts of the cortex, the optical contrast between narrow and wide bands tends to fade entirely. Cyclical patterns of bone deposition are not evident in the other parts of the cortex, except in the thin concave anterior cortex close to the delto-pectoral crest.

Histological examination (pl. 9) with the compound microscope of the regions just described shows it to be formed of fibro-lamellar tissues. Numerous primary osteons, organized around longitudinal and circular vascular canals, are embedded in woven periosteal bone tissue. Each cycle contains from 2 to 12 primary osteons, counted in a radial direction, depending on the overall thickness of the local cortex. The closely packed osteons form the bulk of the wide, lighter bands seen with the naked eye. The limit between two successive cycles appears formed by a denser and thicker condensation of fibrous bone, and corresponds to the thin, darker bands seen with the naked eye. This bone is coarsely bundled with most fibers running longitudinally. In some places, this layer of dense fibrous bone is underlined by a rest line (cementing line) and even, in the thinnest parts of the cortex, by a thin sheet of lamellar surface bone *sensu* Smith 1960.

DISCUSSION

Histological significance

The regularity and consistency of the cyclical bone patterns reported here preclude the possibility that they are artifacts due to fossilization. The structure also makes it unlikely that we are dealing with non-cyclical accretion of surface bone within the fibro-lamellar bone pattern (Ricqlès 1974, 1975, 1976—77) due to local remodeling sequences. Neither can the pattern in this case be attributed to cyclical phenomena of subperiosteal erosion ("tide lines") due to the local drifting-modelling sequence linked to overall growth (Enlow 1963; Ricqlès 1980). Clearly we are dealing here with successive cyclical bursts of deposition in a fibro-lamellar pattern of bone tissue. Fibro-lamellar bone tissues are generally considered, from their systematic and topographic distribution among living vertebrates, to be associated with fast, continous, non-cyclical deposition (Ricqlès 1975, 1976—77). However, judging from its structure, the bone pattern described here seems clearly indicative of some sort of cyclical deposition. Indeed, the local variations in structure of the growth "rings" allow a precise functional interpretation. In the thinnest regions of the cortex, a temporary lowering (deposition of a circumferential thin sheet of lamellar surface bone) and even arrest of bone deposition (rest line), followed directly by a resumed growth at ordinary, higher rate, (fibrous bone and primary osteons) seems indicated. In the regions with an overall higher growth rate, hence where the thickness of cortex deposited per unit time is larger, temporary lowering of the rate of deposition is marked only by a poorer vascularization of the fibrous cortex. Finally, in the thickest parts of the cortex, with the highest rates of bone deposition, the growth cycles become inconspicuous, as the bone turns into typical, homogeneous laminar of plexiform tissue. To sum up, in the regions of overall slower deposition, a lesser thickness of bone is deposited per time unit and the optical and structural contrast between various phases of the successive cycles is well-marked. On the other hand, in most other regions, where rate of deposition was relatively higher, the contrast between the various phases of the cycles is less obvious or disappears entirely.

The various patterns of periosteal bone, classified as "lamellar-zonal" and "fibro-lamellar" tissues, should be understood as a continuum (Ricqlès 1975, 1976—77) rather than as mutually exclusive and sharply contrasted categories. Here, we have an example of an overall rapidly-deposited bone tissue, which nevertheless shows a cyclical deposition in some localized parts of the tissue, while other regions in the same bone are indicative of a continuous, rather than cyclical, bone apposition. Because different parts of a bone are submitted to varying conditions of growth, they routinely show extensive differences in bone histology (Enlow 1963). It is very likely that other parts of the skeleton of this sauropod, because they were under different conditions of growth for local morphogenetical reasons, would be expected to show other, perhaps even more contrasting, histological differences indicative of cyclical and continuous growth respectively. This is exactly, in fact what has been demonstrated recently by Reid's findings who describes, in the pelvic bones of a sauropod, bone growth marks which are more obvious than those reported here in a limb bone. It is possible that, for local morphogenetical reasons, the shape of some bones forming the pelvic girdle of sauropods are better suited for the recording of obvious growth cycles than are the long bones of the limbs of the same animal.

Aging the dinosaur

The total number of cycles observed in the cortex and adjacent spongiosa is at most 10. In view of the spacing trend between each cycle and of the diameter of the inner cancellous bone, it is possible to draw a rough estimation of the number of previous cycles first deposited in the younger cortex and ultimately eroded away when this juvenile cortex was changed into the cancellous bone of the inner spongiosa (Castanet et Cheylan 1979). This suggests that at most 16 cycles and at least 8 cycles were eroded away by endosteal and Haversian substitution. Now, assuming that the cycles are annual (an assumption for which there is admittedly no direct evidence, because the structure of the growth rings described here is rather different from the growth marks demonstrated to be annual in the bones of living reptiles: Castanet et Cheylan 1979; Buffrenil 1980), this would mean that this sauropod would have needed at least 18 and at most about 26 years to reach a little less than half its maximal adult size. This assumes that *Bothriospondylus* humeral proportions did not experience extensive allometric changes relative to body size during growth, which is likely (Ogier 1975). If we accept the more conservative, longer age estimate (26 years) as more reasonable and also assume, for the sake of simplicity, a linear relation of growth with age during the main phase of growth preceding maturity, this would indicate an age roughly 43 years for an individual with a humerus length of 103.4 cm, at the 2/3 of its maximum recorded adult size (maximum recorded humeral length is 155.5 cm: Ogier 1975). This fits well with Case's estimate of 40 years for the beginning of sexual maturity of the sauropod *Hypselosaurus* (a smaller genus from the upper-Cretaceous of France) at 2/3 of its maximum adult size (Case 1978).

Growth rates and sauropod physiology

Now the question is to know exactly what growth rates are indicated by the various patterns of fibro-lamellar (i.e. plexiform) tissues and whether it is reasonable to assume that these rates could be reached and maintained by animals with a typically reptilian physiology. Young farm-grown crocodilians, kept under optimal growth conditions, can during early life sustain growth rates probably at least twice as high as wild specimens of the same species under natural circumstances. Indeed, these farm-kept specimens show obvious fibro-lamellar bone tissues in their long bones, deposited during their early, active, phase of growth (Buffrenil 1980; Kappelman 1979). Thus, assuming that sauropods could have been able to maintain, for several tens of years, the highest growth rates now known among young farm-grown crocodiles, they could have deposited fibro-lamellar bone tissues during all their active growth phase and reached sexual maturity in a few decades at most (Ricqlès 1974).

Finally, as K strategists with large sizes and high individual longevities (Richmond 1965; Ricqlès 1979), they would have progressively changed their primary bone into dense Haversian bone during their long subsequent adult life.

Some paleoecological data (Russell, Beland and McIntosch 1980) as well as the study of brain-body size relationships (Hopson 1977, 1980) suggested that adult sauropod dinosaurs had a cellular metabolism geared to "reptilian" levels, or at most somewhere "half way" between typical reptilian (i.e. ectothermic) and bird or mammalian (i.e. endothermic) levels. On the other hand, the available evidence so far derived from bone histology suggested growth rates roughly similar to those of large living endotherms (Ricqlès 1974, 1976), and hence a probably endothermic level of metabolism as well. Now, the discovery of growth marks in sauropod long bones perhaps brings these various lines of evidence in accordance. It suggests that sauropods probably had mass homeothermy (a system of "passive" thermoregulation damping daily variations in body temperature, but unable to damp seasonal (yearly) variations). Because of the great mass of the sauropods, this was probably associated with an incipient or mass endothermy, a consequence of the slow dissipation of the large amounts of heat endogeneously produced, even at relatively low metabolic rates (McNab 1978).

This unique physiological situation, perhaps a form of heterothermy (Ricqlès 1980), optimized by the warm, equable climatic conditions of the Mesozoic, may thus account for the peculiarities of growth among sauropods. Given also the problems of feeding time and efficiency, and energy budgets already discussed by many (e.g. McGowan 1979; McFarland *et al.* 1979; Thomas and Olson (eds.) 1980) it is thus not necessary to assume endothermic (i.e. at avian or mammalian levels) energetics to account for growth patterns in sauropods.

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EXPLANATION OF THE PLATES 7—9

Plate 7

Bothriospondylus madagascariensis. Cross section of long bone diaphysis from a halfgrown individual. See also de Ricqlès 1968*a*, 1975. „Traditional" view of sauropod bone histology

1. Plexiform bone tissue formed by periosteal apposition of woven bone (*w.b.*) and by centripetal apposition of lamellar bone (*l.b.*) forming primary osteons around the circular (*c.v.cl.*), radial (*r.v.cl.*) and longitudinal (*l.v.cl.*) vascular canals. Average magnification, as used here for current histological observations, is not conductive to an easy recognition of overall growth cycles.
2. Higher magnification of plexiform tissue. The vascular canals form a dense three-dimensional meshwork.

Plate 8

Bothriospondylus madagascariensis. Same material

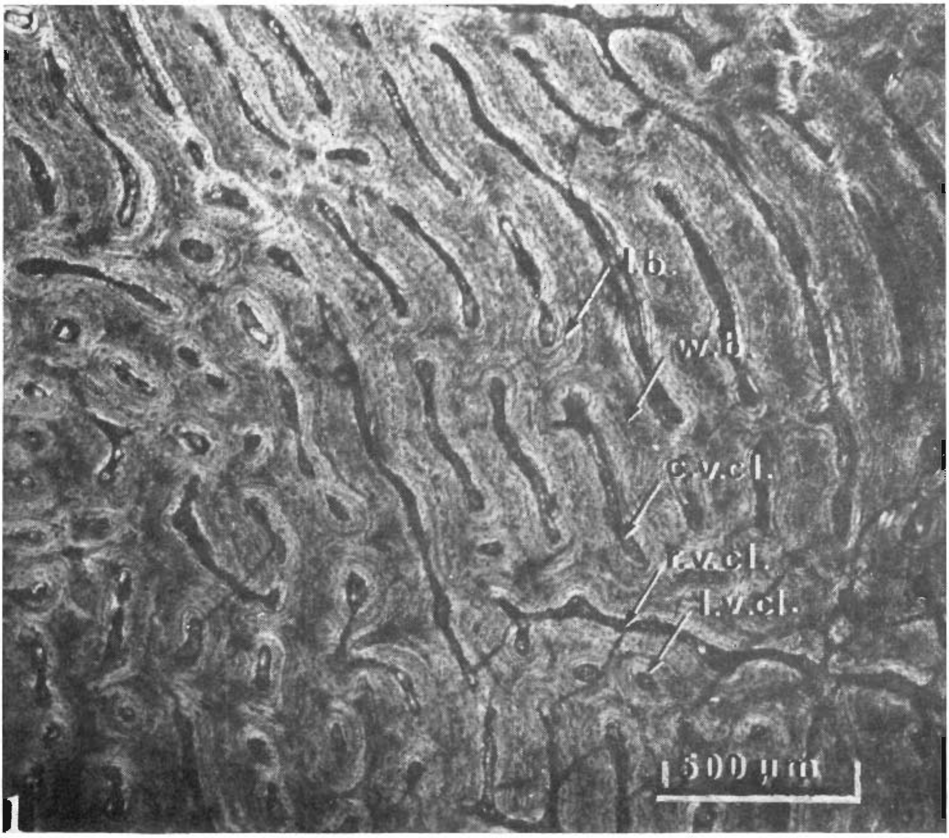
1. Schematic cross section of the humeral diaphysis of a growing individual showing the various regions discussed in the text.
2. Low magnification of the anterior cortex close to the deltopectoral crest delineated above, showing about nine increment cycles. Each arrow indicates the slowest phase of an (annual?) growth cycle.

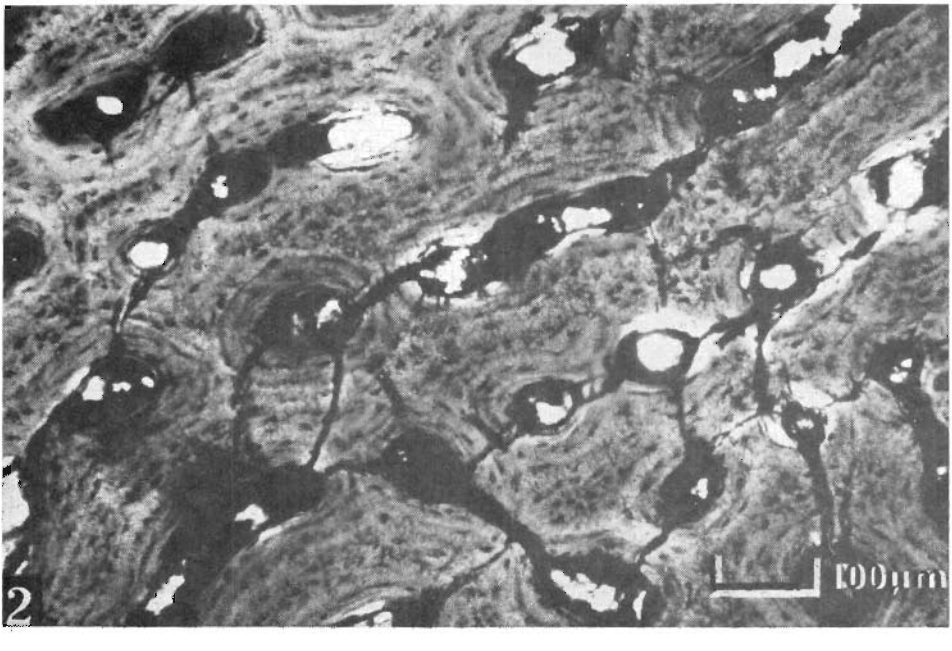
Plate 9

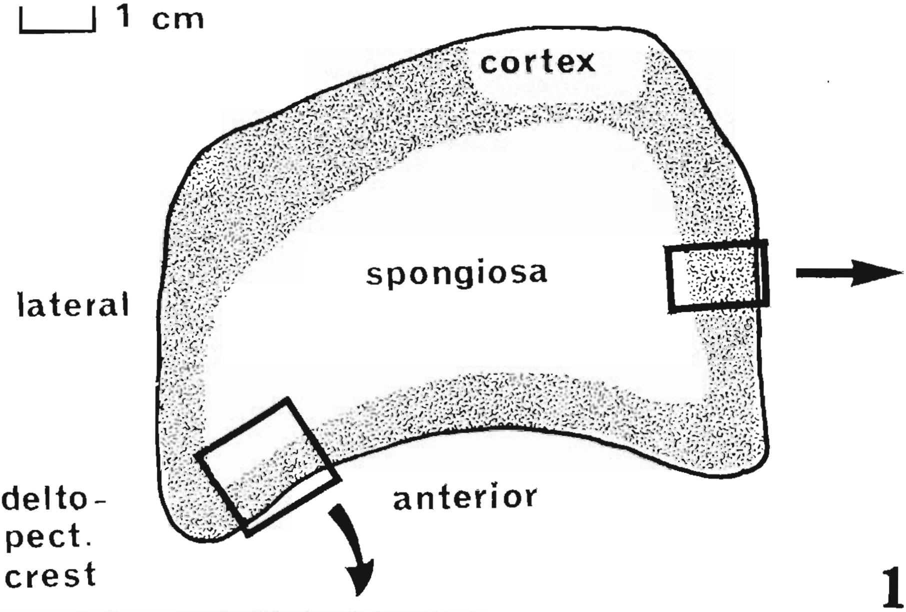
Bothriospondylus madagascariensis. Same material

1. Low magnification of the humeral cortex on the medial side of the bone, underlined on pl. 8. Low magnification makes the observation of overall growth patterns and cycles easier.
2. Magnification of the area delineated on the view above. The bone shows a subplexiform pattern of vascularisation. Although this magnification is still low for current histological observations, the recognition of growth cycles is already difficult.

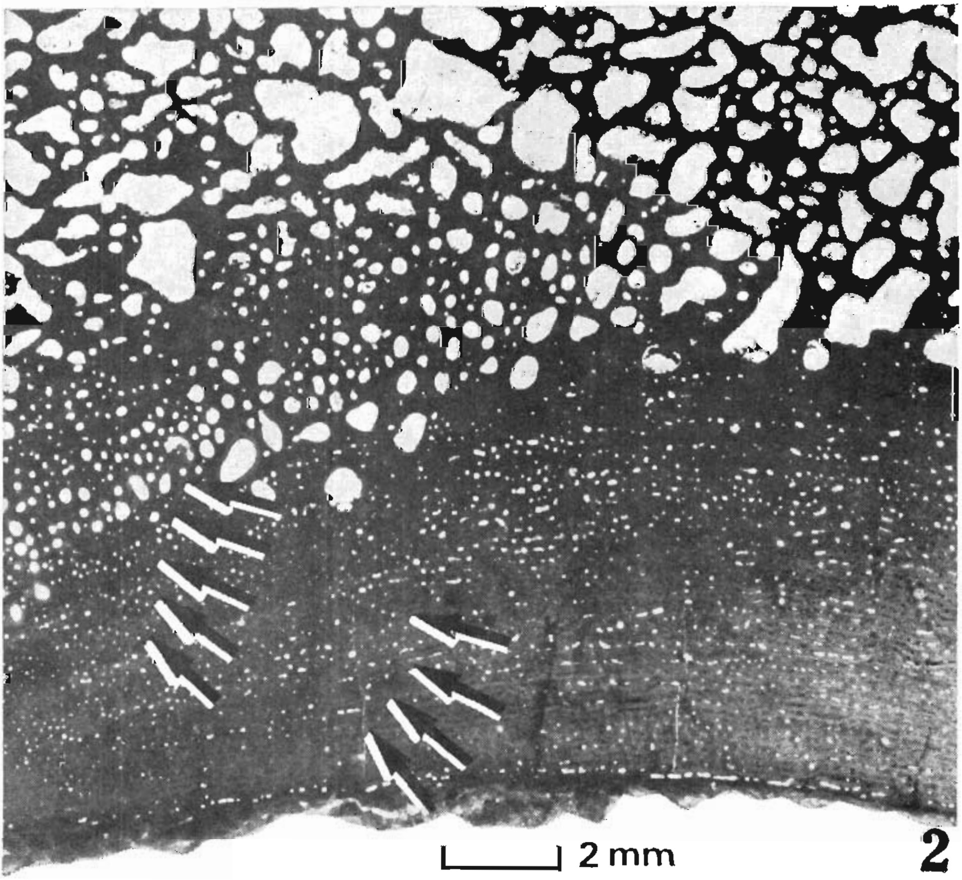
Arrows as for pl. 8:2


1
l.b.
w.b.
c.v.cl.
r.v.cl.
l.v.cl.
500 μm

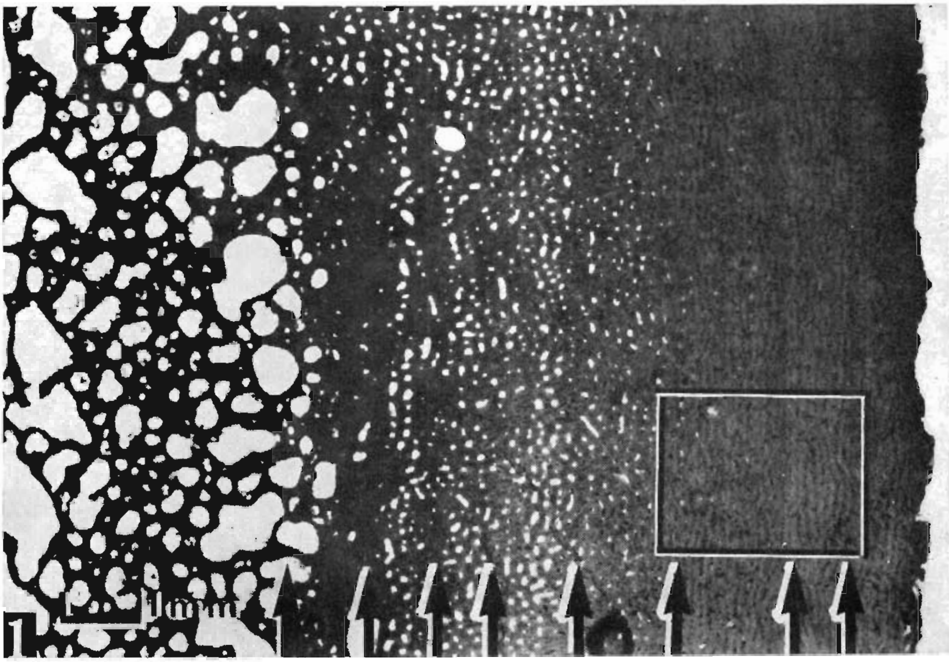

2
100μm

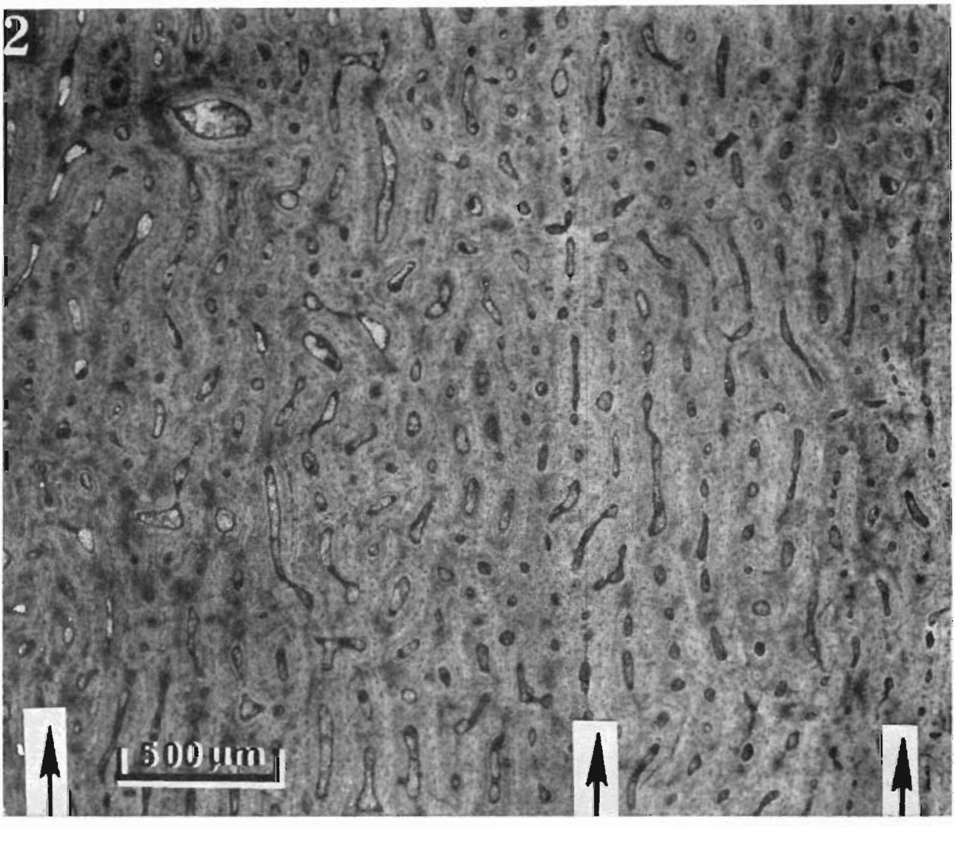

1 cm
cortex
spongiosa
lateral
delto-pect. crest
anterior

1


2 mm

2


1
1mm


2
500 µm