Original article

On the bone histology of some Triassic pseudosuchian archosaurs and related taxa

L'histologie osseuse de quelques archosauriens pseudosuchiens triasiques et formes apparentées

Armand J. de Ricqlès [a,b,*], Kevin Padian [c], John R. Horner [d]

[a] *Équipe formations squelettiques, URA CNRS 8570, Université Paris-7, 75251 Paris cedex 05, France*
[b] *Collège de France, Paris, France*
[c] *Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, CA 94720-3140, USA*
[d] *Museum of the Rockies, Montana State University, Bozeman, MT 59717, USA*

Abstract

The long bone histology of some major groups of extinct Triassic crocodile relatives (phytosaurs, aetosaurs, poposaurs) is generally similar to that of living and fossil crocodylomorphs. Early deposition of more or less fibro-lamellar, fast-growing tissue gives way to cycles of deposition of a layer of less well-vascularized, predominantly parallel-fibered bone, followed by an annulus of nearly avascular bone and a line of arrested growth (LAG). These cycles, forming the so-called lamellar-zonal pattern of bone tissue suggesting slow growth, differ from the situation in most ornithosuchians (pterosaurs and dinosaurs), in which the pattern is generally that of fast-growing fibro-lamellar tissue throughout, that may become less vascular and eventually avascular only as full size is reached. LAGs are common, but annuli are not. Although the pseudosuchian pattern is presumed primitive for archosaurs, erythrosuchians (non-archosaurian Archosauriformes) apparently grew much like dinosaurs did, so the pseudosuchian pattern may not necessarily be primitive for Archosauriformes. Moreover, the histological patterns of the basal crocodylomorph *Terrestrisuchus* suggest elevated growth rates compared to typical crocodiles, though not as high as those of dinosaurs and pterosaurs. In general, there is a clear difference in histological tissue types, and hence in growth regimes and rates, between pseudosuchians and ornithosuchians, which extends back to the separation of these two archosaurian lineages at least by the Middle Triassic.

* Corresponding author.
E-mail address: ricqles@ccr.jussieu.fr (A.J. de Ricqlès).

Résumé

L'histologie des os longs de groupes importants de pseudosuchiens triasiques (phytosaures, aetosaures, poposaures) est assez semblable à celle des crocodylomorphes éteints et actuels. À de premiers dépôts de tissus d'apposition rapide (complexe fibro-lamellaire) succèdent progressivement des dépôts osseux cycliques s'effectuant à des vitesses modérées. Chaque cycle comprend typiquement une zone épaisse d'os vascularisé, alternant avec un mince *annulus* d'os avasculaire, complété par une ligne d'arrêt de croissance (L.A.C.). Ces cycles, caractéristiques du patron « lamellaire-zonaire » de dépôt osseux relativement lent, contrastent avec la disposition histologique dominante chez les ornithosuchiens (ptérosaures, dinosaures), où le mode de croissance est caractérisé par de l'os à dépôt rapide (complexe fibro-lamellaire) qui ne cesse d'être déposé qu'à l'extrême fin de la croissance, pour être alors complété par de l'os peu vascularisé à dépôt lent. Les lignes d'arrêt de croissance sont présentes chez les ornithosuchiens mais paraissent rarement associées à des annuli typiques. Bien que le modèle observé chez les pseudosuchiens puisse être considéré comme « primitif » pour les archosaures, le fait que les Erythrosuchidés (des Archosauriformes non archosauriens du trias inférieur) aient déjà un patron histologique indiquant une croissance rapide du type dinosaurien suggère que le patron pseudosuchien ne représenterait pas la véritable condition plésiomorphe pour les archosauriformes. De plus, les structures histologiques du crocodylomorphe primitif *Terrestrisuchus* suggèrent des vitesses de croissance plus élevées que celles des crocodyliens « typiques » post-triasiques, sans atteindre, peut être, celles des grands dinosaures et ptérosaures. L'histologie osseuse indique une nette différence entre les modes de croissance généralement suivis par les pseudosuchiens et les ornithosuchiens au moins depuis le trias moyen.

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1. Introduction

In the 1970s, dinosaur bone histology re-emerged as an active field of research, in part because it was linked to the issue of thermo-metabolic regimes (e.g., de Ricqlès, 1976; Thomas and Olson, 1980). Recently, this interest has been re-kindled, because the increasingly accepted hypothesis that birds evolved from small coelurosaurian dinosaurs has obvious implications for the evolution of endothermy in birds (e.g., de Ricqlès, 2000; de Ricqlès et al., 2001; Erickson et al., 2001; Schweitzer and Marshall, 2001; Padian and Horner, 2002; Prum, 2002). Completely apart from this question, however, studies of bone histology are most valuable in providing baseline data for relative and absolute rates of growth in individual bones, bone tissues, and taxa. These data in turn may bear decisively on issues of growth and life history strategies (Chinsamy, 1993, 1994; Curry, 1999; Reid, 1997a,b; Horner et al., 2000; de Ricqlès, 2000; Sander, 2000).

To understand the potential contribution of bone histology to the issue of the evolution of metabolic regimes in archosaurs, we have taken a comparative approach that puts the histological characteristics of bone into ontogenetic and phylogenetic perspectives (e.g., de Ricqlès et al., 2001; Horner et al., 2000, 2001; Padian et al., 2001). Here, we extend our studies to a preliminary consideration of pseudosuchians, the sister lineage to ornithosu-
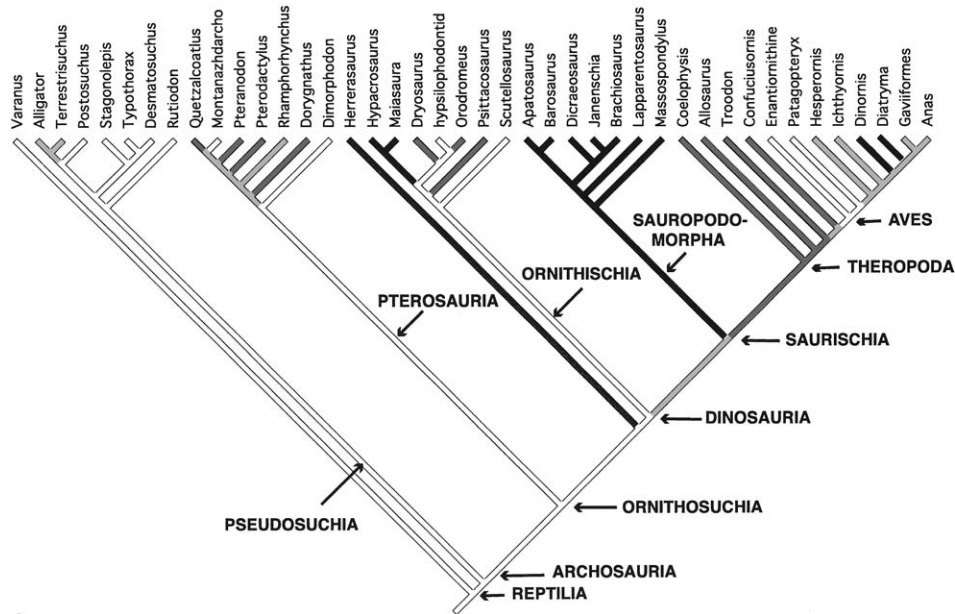
Fig. 1. Cladogram of the major taxa of Archosauria, emphasizing taxa that have been studied histologically. Adapted from Padian et al. (2001).
Fig. 1. Cladogramme général des archosauriens mettant l'accent sur les taxons ayant fait l'objet d'une analyse histologique.

chians within Archosauria (Gauthier, 1984, 1986). We question whether the patterns of tissue type and deposition seen in the bones of living crocodiles are more broadly distributed among their archosaurian relatives, and at what point the patterns seen in dinosaurs and their relatives diverged from those of other archosaurs. This brings us to consider whether crocodiles really represent "basal" archosaurs and their relatives in patterns of growth and its underlying metabolism, or whether the rather different general patterns of ornithosuchian bone growth are just as likely to be the primitive condition.

Fig. 1 shows a general consensus of recent trees that reflect archosaurian relationships. Archosauria is defined as a crown group with birds and crocodiles as terminal sister taxa, following Gauthier (1984, 1986). Gauthier was the first to situate the major lineages of archosaurs in a cladistic framework (see also Gauthier and Padian, 1985). His results placed Proterochampsidae, Erythrosuchidae, and Proterosuchidae as successive outgroups to the Archosauria, and he included all these taxa in the node group Archosauriformes. Later work (e.g., Benton and Clark, 1988; Sereno, 1991; Sereno and Arcucci, 1990; Arcucci, 1986, 1987; Parrish, 1993; Benton, 1999) has generally tended to confirm Gauthier's original phylogeny, with some amendations. Sereno and Arcucci (1990), for example, found that Ornithosuchidae belonged within the Pseudosuchia; Sereno (1991) placed *Euparkeria* outside Archosauria; Parrish (1993) separated Poposauridae, Rauisuchidae, and Prestosuchidae, often placed in one clade, into three lineages; Arcucci's (1986, 1987) work on *Lagerpeton* and *Pseudolagosuchus* clarified their placement within Dinosauromorpha. These changes have been generally incorporated by later studies. A few works

(e.g., Juul, 1994; Welman, 1995) produced considerably different general results, but these have not been supported by other studies (e.g., Benton, 1999; Sumida and Brochu, 2000). Some studies have found quite different results for individual taxa; for example, Bennett (1996) and Peters (1997) both placed pterosaurs well outside archosaurs. Merely for present purposes, however, we concentrate on results duplicated by several studies, and on taxa that have been assessed histologically. These taxa are highlighted in Fig. 1.

The structures and physiology of crocodiles have historically been key factors in trying to understand dinosaurian growth regimes and metabolic levels (Regal and Gans, 1980; Spotila, 1980; Paladino and Spotila, 1994; Ruben, 1991, 1995). As the only extant archosaurs apart from birds, crocodiles are considered more or less typical ectotherms that exemplify the classical "reptilian" physiological condition assumed to be plesiomorphic for basal archosaurs. Understandably, such characteristics have sometimes been extended to Mesozoic dinosaurs and even basal birds (Thomas and Olson, 1980; Ruben, 1991). However, the last common ancestor of birds and crocodiles lived during the Middle Triassic, about 225 million years ago (dating from the first appearance of taxa representing the crocodile-bird divergence), leaving time for extensive modifications in each clade since their separation. Because living birds and crocodiles are so different in their growth strategies and metabolic regimes, it cannot be assumed that any extant members of crocodiles and birds retain physiological characteristics that were present at the time of their divergence (Schweitzer and Marshall, 2001). Any physiological characteristics shared by crocodiles and birds (such as multicamerate lungs and a four-chambered heart) can be hypothesized to have been inherited from their common ancestor. But without the test of distribution in other archosaurs (all of which are extinct), we cannot rule out the hypothesis that such characteristics merely evolved convergently.

In order to bring new data to such questions, we surveyed the bone histology of the major groups of Triassic archosaurs. Our sample of Pseudosuchia comprised the early and unusual crocodylomorph *Terrestrisuchus* and several fossil crocodilians not figured here, including a captive alligator raised under optimal conditions for growth (see Padian et al., submitted for publication). The full history of Crocodylomorpha was not extensively sampled for this study; for detailed information see Enlow and Brown (1957); de Buffrénil (1980); Hutton (1986); and Hua and de Buffrénil (1996). We principally sampled representatives of some extinct Triassic pseudosuchian clades, including phytosaurs, aetosaurs, and poposaurs. We asked whether the patterns of bone growth and tissue deposition were similar among living crocodilians and extinct pseudosuchians, and at what points in the evolution of these groups these histological patterns appeared.

In contrast to these pseudosuchians, we also surveyed some basal ornithosuchians from the Triassic. General phylogenetic patterns of ornithosuchian bone histology have been reported by Padian et al. (submitted for publication). The bone histology of pterosaurs, particularly more derived forms, is discussed elsewhere (de Ricqlès et al., 2000; Jenkins et al., 2001), and further treatment of basal pterosaurs is in progress. Regrettably, no material is yet available from some important basal dinosauromorph ornithosuchians, such as *Lagosuchus*/*Marasuchus*, *Lagerpeton*, and *Lewisuchus*, all from the early Late Triassic of Argentina (e.g., Arcucci, 1986, 1987; Sereno, 1991; Sereno and Arcucci, 1990). We did sample *Herrerasaurus*, classified variously as a theropod, a basal saurischian, or a dinosauriform very close to true dinosaurs (Sereno, 1999; Holtz and Padian, 1995). Undisputed

theropods are represented here by the Triassic *Coelophysis*. We leave aside basal Sauropodomorpha, which have already received some histological survey (e.g., Chinsamy, 1993) and are consistent with the patterns seen in their sister group, the Theropoda. Triassic Ornithischia are almost unknown from reasonable skeletal material; we have sampled the Early Jurassic *Scutellosaurus*, an ornithischian basal to the Thyreophora (stegosaurs, ankylosaurs, and their relatives), and these results are reported elsewhere (Padian et al., submitted for publication).

2. Historical overview

Early histological descriptions of "thecodontian" (basal archosaurian and archosauriform) bones were provided by Seitz (1907), Gross (1934), and Enlow and Brown (1956-1958), and summarized by de Ricqlès (1976). Most early work was based on the Parasuchia or phytosaurs, Late Triassic forms with a crocodile-like morphology and amphibious ecology. According to Seitz (1907), *Phytosaurus* and *Termatosaurus* had cortical bones tissues much like those of fossil and extant crocodiles, with extensive evidence of protracted cyclical growth. Thick vascularized zones (see de Ricqlès et al. (1991) for definitions of histological structures, and Castanet et al. (1993) for ontogenetic context of these structures) alternate with narrow avascular annuli made of lamellar or parallel-fibered bone tissues of periosteal origin. In the zones, vascular canals run into longitudinally oriented primary osteons that are embedded either in circumferential coarse bone lamellae of periosteal origin or in woven periosteal bone. Haversian reconstruction is rather extensive in the deep cortex and in the endosteal margin. The marrow cavity may contain numerous trabeculae of remodeled, finely bundled endosteal bone tissue.

Apart from these studies, little attention has been paid to pseudosuchian bone histology. Chinsamy (1994: p. 215) figured a cross-section of the femur of the poposaur *Postosuchus* as exemplifying "zonal bone". The external cortex in that specimen rather appears to be formed of a densely vascularized "fibro-lamellar complex" typical of dinosaurian bone tissue, associated with three lines of arrested growth. We analyze the bone tissues from two other specimens below.

An entirely distinct histological pattern was described by Gross (1934) in the large Early Triassic *Erythrosuchus* (from the *Cynognathus* Zone of the Beaufort Formation, South African Karoo) and confirmed by de Ricqlès (1976), based on additional material. In this large, quadrupedal, and presumably mostly terrestrial predator, the cortical tissue of the limb bones is already of the typical plexiform pattern, almost indistinguishable from those of large advanced dicynodonts (synapsids) and of many dinosaurs of various body sizes. This is particularly interesting because Erythrosuchidae are not archosaurs (i.e., within the divergence of common ancestry between crocodiles and birds), but more basal archosauriforms (they share with archosaurs such features as an antorbital fenestra and thecodont teeth).

Essentially on the basis of these and some additional data, de Ricqlès (1973, published 1978) developed an extended discussion of the possible origin and early evolution of thermo-metabolic physiologies in archosaurs. He took into account the available anatomical and histological data set in their stratigraphic context, and the contemporary discussions on the interrelationships of "thecodontians" (de Ricqlès, 1978, pp. 90-92; 94-96). One of

his main suggestions was that the "ectothermy" of post-Triassic and extant crocodilians might equally be a secondarily derived, rather than truly primitive, physiological condition (de Ricqlès, 1978, pp. 100-103). We revisit this issue in Section 5.

In this work, we treat basal dinosaurs and other ornithosuchians only briefly and for the sake of comparison. Considerable attention has been paid to the histological features of Triassic prosauropod dinosaurs such as *Plateosaurus* (e.g., Seitz, 1907; Gross, 1934; Enlow and Brown, 1957; also work in progress by Dr. Martin Sander: Sander and Klein, 2001a,b), which were recognized as similar to other dinosaurs in these respects. Other prosauropods from southern Africa have been assessed, although their ages are probably Early Jurassic in many cases. Currey (1960, 1962) first attempted to quantify vascularity in some unidentified prosauropod bones from southeastern Africa. He concluded that the vascular supply was as high as (or higher than) in extant artiodactyls, and explicitly raised the issue of its physiological significance. De Ricqlès (1968) described the bone histology of the large prosauropod *Euskelosaurus* from Maphutseng, Lesotho, and considered the possible significance of changes in histological patterns along an evolutionary series. Chinsamy (1993) studied *Massospondylus*, and used the extensive growth cycles recorded in its long bones to calibrate its growth trajectory. Among other Triassic dinosaurs, the theropod *Coelophysis* was figured and briefly discussed by Colbert (1995) and is discussed further here. Chinsamy (1990) provided considerable comparative data for the similar and closely related Early Jurassic theropod *Syntarsus*. No Triassic ornithischians have been studied histologically, partly because there is so little material; we have assessed the Early Jurassic basal thyreophoran *Scutellosaurus*, but in the interest of space we reserve detailed discussion elsewhere (see Padian et al., submitted for publication).

3. Materials and methods

We selected a sample of long limb bones, rib fragments, and dermal plates (scutes or osteoderms) from Triassic archosaurs and closely related taxa principally from the University of California Museum of Paleontology (UCMP) in Berkeley, mostly from the well-known Placerias Quarry (locality A269; Camp and Welles, 1956; Fiorillo and Padian, 1993) near St. Johns, AZ. Identifications of these bones were largely made by R.A. Long (see Long and Murry, 1995). Only the limb bones will be discussed here. Other specimens were kindly provided by curators of the Museum of Comparative Zoology, Harvard University (MCZ), the Virginia Museum of Natural History (VMNH) and the Museum of the Rockies, Montana University (MOR). Table 1 provides only a list of the specimens and osteological thin sections figured in this paper; these specimens are illustrated in Plates 1–9. These are a subset of a broader sample of specimens comprising approximately 20 taxa and 100 thin sections, plus a comparative range of archosaurian taxa described by Padian et al. (2001, Fig. 1).

Thin sectioning followed standard procedures. Typically, a fragment of shaft was taken from identified and labeled specimens and was cast. The cast was later restored in its anatomical position on the original bone. The fragment selected for the study was embedded in epoxy resin, allowed to polymerize slowly, and sawed on a low-speed diamond powder circular saw. Thin sections were processed on lap wheel machines according to

Table 1

Catalog of thin sections taken of the archosauromorph taxa used in this study

Liste des lames minces d'archosauromorphes utilisées pour cette étude

Taxon	Specimen number	Element	Thin section
Rutiodon sp.	UCMP 25921	Proximal femur	92-11–R1
Phytosauria indet.	UCMP 2186	Femur	92-11–2186-1
Desmatosuchus sp.	UCMP 32178	Proximal humerus	92-11 H, 1-3
Desmatosuchus sp.	UCMP28354	Proximal radius	92-11 D, 1-3
Stagonolepis sp.	UCMP 25914	Femoral shaft	92-11 FE 1, 1-2
Typothorax sp.	UCMP 25905	Proximal humerus	92-11 F1 L, 1-3
Typothorax sp.	UCMP 25905	Radial shaft	92-11 F 2, 1-2
Postosuchus sp.	UCMP 28353	Humerus shaft	92-11 H 1, 1-2
Postosuchus sp.	UCMP 25906	Tibia	92-11 T 1, 1-2
Terrestrisuchus sp.	VMNH 2274	Humerus	UCMP T 1-4
Alligator sp.	MOR, unnumbered	Humerus	95-4 HS 2
Herrerasaurus sp.	MCZ 7064	Humerus	99-22 H, 1-3
Herrerasaurus sp.	MCZ 7064	Tibia	99-22 T, 1-3
Coelophysis sp.	UCMP 129618	Right femur	88-24 F, 1-3

standard techniques (de Ricqlès and Bolt, 1983; Wilson, 1994) and observed and photographed with a compound microscope under ordinary or polarized light.

Most sections from long bone shafts are transverse, and taken at mid-shaft unless otherwise noted; a few longitudinal sections taken from epiphyseal regions are indicated as such. Sections taken from osteoderms are reported elsewhere (Main et al., MS).

## 4. Histological observations and inferences

Although the full taxonomic spectrum of Triassic archosaurs is still far from covered by this preliminary report, some clear patterns emerge, and we hope that our sample may help to sharpen future research questions and to provide some baseline data for considering problems of growth and metabolism in basal archosaurs.

Because our sample is limited, it cannot represent the range of tissues deposited through all parts of the skeleton at all stages of growth. Hence, in the course of describing histological structures, we offer hypotheses and interpretations of functional and ontogenetic factors that may explain the presence and development of these structures. These "first level" inferences require only simple uniformitarian assumptions. It seemed impracticable in the scope of the current work to separate these comments from pure description, because the descriptions would have been needlessly repeated later in an interpretative section. We trust that these descriptions and interpretations will be easily distinguished. Less direct, "second level" inferences are restricted to the Discussion.

4.1. Pseudosuchia: Parasuchia (Phytosauridae)

4.1.1. Rutiodon*: femur (Pl. 1(1), (2))*

This bone, sectioned near mid shaft, is oval in cross section, with a cortex 6-7 mm thick (Pl. 1(1)). The marrow cavity appears to be free, but cancellous tissues may not have been
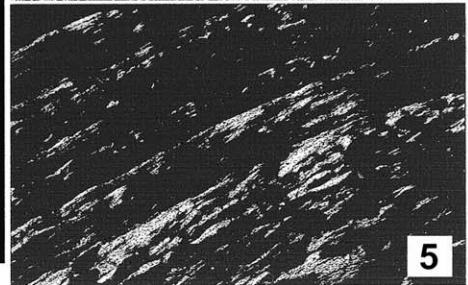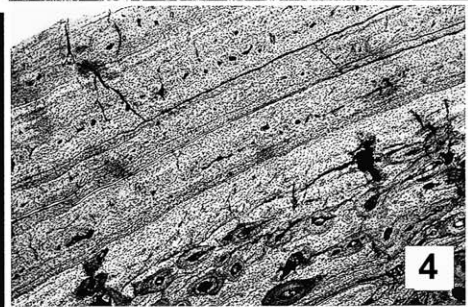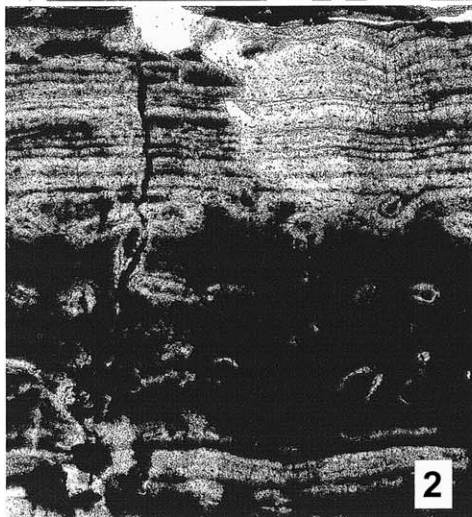
preserved. Locally, around the marrow cavity, a sheet of finely bundled, parallel fibered endosteal bone is associated with a poorly developed endosteal margin. This margin is marked by a few large, flattened erosion rooms that invade the deep cortex. It is striking that a few of the large erosion rooms are developed, rather than many of various diameters. These erosion rooms spread into the deep cortex, which is entirely of fibro-lamellar bone tissue of the sub-plexiform variety. In this tissue, most vascular canals are longitudinal, linked by circular canals in regular superposition to form a series of laminae; a few radial canals may locally unite successive laminae. This apparently fast-growing internal cortex forms about one-third to half of the overall cortical thickness. However, even here the woven component is not highly developed; this condition is, perhaps, a modification of the fibro-lamellar complex that shows high vascularization, although the fibrillar pattern is not completely typical. This has been described in the prosauropod *Euskelosaurus* (de Ricqlès, 1968; de Ricqlès et al., 1991) and other dinosaurs (Reid, 1996). This explains why the cortex appears lamellar under polarized light at low magnification, because this kind of tissue is not as woven as in typical dinosaurian fibro-lamellar bone tissues.

External to this fast-growing cortex is a conspicuous line of arrested growth (LAG) associated with an annulus. Growth resumes with a zone that has the same structure as the deep cortex, followed by another LAG and annulus and another zone of laminar tissue. External to this the bone becomes more lamellar-zonal in construction. It has a succession of annuli associated with LAGs that are intercalated with thinner zones that contain only

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Plate 1. Pseudosuchia: Parasuchia (Phytosauria). Scale = 0.5 mm for parts (1) and (3), 0.05 mm for part (2), and 0.25 mm for parts (4) and (5). (1) Femur of *Rutiodon* sp. (UCMP 25921, section 92-11 R1T), cross-section of the mid shaft cortex of a large individual. The innermost fibro-lamellar cortex becomes progressively overlain by successive irregular cycles of mostly lamellar-zonal tissues of periosteal origin. (2) Detail of previous section, the external cortex, taken near the upper left margin of (1). Strata of well vascularized fibro-lamellar tissue (dark bands) are intercalated between successive strata of coarsely lamellated periosteal bone, as the animal experiences a temporary burst of more active growth. (3) Femur of indeterminate phytosaur (UCMP 2186, section 2186-1T), cross-section of the mid shaft cortex of a large individual. The entire cortical thickness is dominated by cycles of lamellar-zonal deposition. Scattered Haversian replacement is more plentiful in the (older) perimedullar region, almost obliterating the primary tissues deposited earlier (toward bottom of figure). (4) Detail of previous section, slightly magnified, external cortex, taken near the upper center of (3). Poorly vascularized lamellar-zonal tissues, organized in successive depositional cycles, comprise the bulk of the cortex. (5) Same as (4), shown under polarized light. A large complement of circularly oriented lamellae is revealed by the optical anisotropy of the tissue.

Planche 1. Pseudosuchia : Parasuchia (Phytosauria). Échelle = 0,5 mm pour (1) et (3) ; 0,05 mm pour (2) ; et 0,25 mm pour (4) et (5). (1) *Rutiodon*, fémur, vue générale du cortex diaphysaire d'un grand individu. Le cortex le plus profond, de type fibro-lamellaire, se trouve progressivement surplombé par des cycles irréguliers de tissus lamellaires-zonaires d'origine périostique. (2) Détail du même. Le cortex externe comprend une couche de tissu osseux fibro-lamellaire (très sombre) bien vascularisé, intercalée au sein de couches successives de tissu lamellaire-zonaire formé de grossières lamelles d'os périostique. Cette structure correspond à une poussée temporairement plus active du dépôt osseux. (3) Phytosaure indéterminé. Section transversale de la diaphyse fémorale. La totalité de l'épaisseur du cortex, chez ce grand individu, est dominée par des cycles d'apposition successifs d'os lamellaire-zonaire. Le remplacement Haversien, assez dispersé, est plus dense dans le cortex profond périmédullaire, ontogénétiquement plus âgé, y masquant presque les tissus primaires d'apposition. (4) Même matériel, détail du cortex externe. Du tissu osseux lamellaire-zonaire faiblement vascularisé est organisé en cycles successifs formant la majeure partie de l'os déposé. (5) Même champ, lumière polarisée. L'anisotropie locale du tissu met en évidence l'important complément de lamelles orientées circulairement.
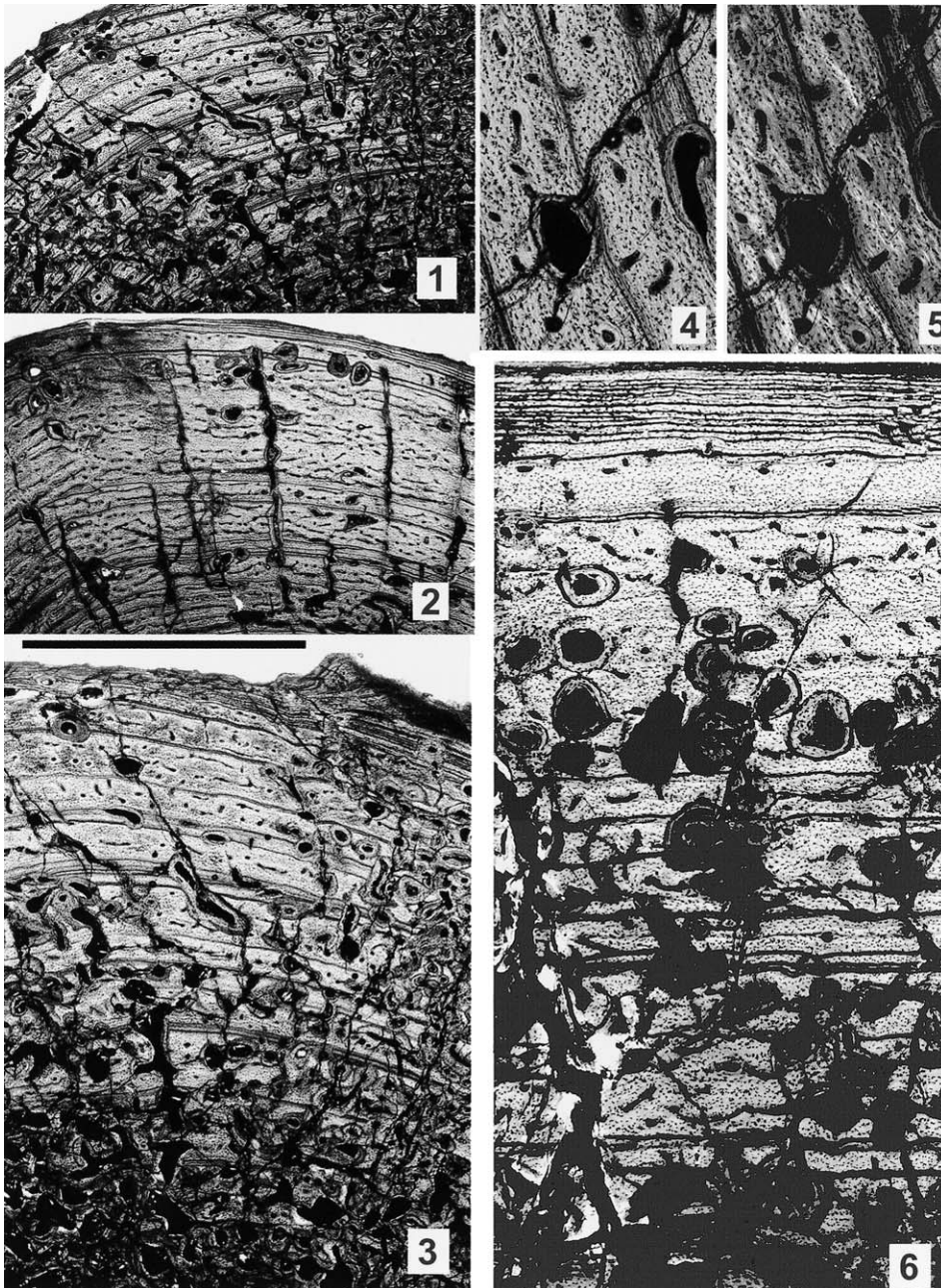
longitudinally oriented primary osteons. These tissues described so far are locally invested by scattered Haversian (secondary) osteons. The most external cortex is lamellar-zonal and contains many LAGs; the fine structure of the bone tissue becomes more parallel fibered externally, and the woven component of the fibro-lamellar tissue, described previously in more internal sections, is no longer in evidence. However, two of these external zones still contain a woven component (Pl. 1(2)).

The general growth pattern suggested by this section is of an individual that at first grew at a high rate and later turned to a slower and highly cyclical growth pattern, with highly protracted, probably indeterminate, growth. The primary cortex, except the most external part, preserves seven or eight cycles of growth. The most external cortex, which is avascular and translucent, preserves a high number of growth cycles reflected by six or seven LAGs that occur at progressively diminishing thickness as they approach the bone surface. This outermost cortex clearly implies a diminishing growth rate in later life.

4.1.2. Phytosaur: femur (Pl. 1(3))

This is a partial section from a large individual with a cortex thicker than 1 cm. It was probably prepared by Charles Camp or Frank Peabody in the 1950s. The bone shows no evidence of a marrow cavity, but this could have been destroyed during preparation. The internal cortex is formed by very large irregular secondary osteons with large Haversian canals, mixed with much smaller typical secondary osteons (Pl. 1(3)). The deep cortex is

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Plate 2. Pseudosuchia: Aetosauria (Stagonolepididae). Scale = 0.25 mm for parts (1)-(3), 0.05 mm for parts (4) and (5), and 0.1 mm for part (6). (1) Humerus of *Desmatosuchus* sp. (UCMP 32178, section 92-11 H-1T), general view of the cross-section of the cortex at mid-shaft. The lamellar-zonal cortex records numerous depositional cycles, with scattered Haversian reconstruction. (2) Another region in the previous section, which experiences a much higher growth rate that is maintained throughout the radial growth of the bone, probably for reasons related to local morphogenesis. The thick zones comprise fibro-lamellar organization. (3) Detail of a more slowly growing region, magnified from the middle portion of (1). The region of the surface, shown in the upper left of the figure, is rich in Sharpey's fibers, and it overlies an area in which Haversian tissue has spread densely outward. (4) Detail of the external cortex in the upper left corner of (3). Two zones lined by thin annuli and LAGs contain primary canals. (5) Same as (4), in partly polarized light. The lamellar-zonal organization is visible in the anisotropic appearance of the tissue, which also shows Haversian replacement. (6) Details of the outer cortex in another radial region of the same thin section. Haversian replacement has spread rather extensively outward. The most external cortex comprises numerous thin sheets of non-vascular bone that suggests the development of an external fundamental system.

Planche 2. Pseudosuchia : Aetosauria (Stagonolepididae). Échelle = 0,25 mm pour (1)–(3), 0,05 mm pour (4) et (5), et 1 mm pour (6). (1) *Desmatosuchus*. Humérus, aspect général du cortex diaphysaire. Le tissu lamellaire-zonaire exprime clairement de nombreux cycles de dépôt. Remaniement Haversien dispersé. (2) Même matériel, une autre région de la même section exprime par sa structure une vitesse de croissance radiale plus élevée pour des raisons de morphogenèse locale. Les zones épaisses atteignent une organisation fibro-lamellaire. (3) Même matériel, détail d'une région à croissance plus lente (voir aussi (1)). La crête superficielle riche en fibres de Sharpey à droite surmonte une région radiaire où un remaniement Haversien assez dense s'étend jusque dans le cortex externe. (4) Détail d'une région du cortex externe (voir (3)). Deux zones, séparées par un fin annulus complété d'une L.A.C., contiennent des canaux vasculaires. (5) Même champ, lumière partiellement polarisée. L'organisation lamellaire-zonaire se révèle par la relative anisotropie du tissu. Remaniement Haversien dispersé. (6) *Desmatosuchus*, humérus. Détail du cortex dans une autre direction radiaire. Le remaniement haversien dispersé gagne assez largement vers l'extérieur. Le cortex le plus externe comprend un grand nombre de couches minces non vascularisées évoquant un « système fondamental externe ».
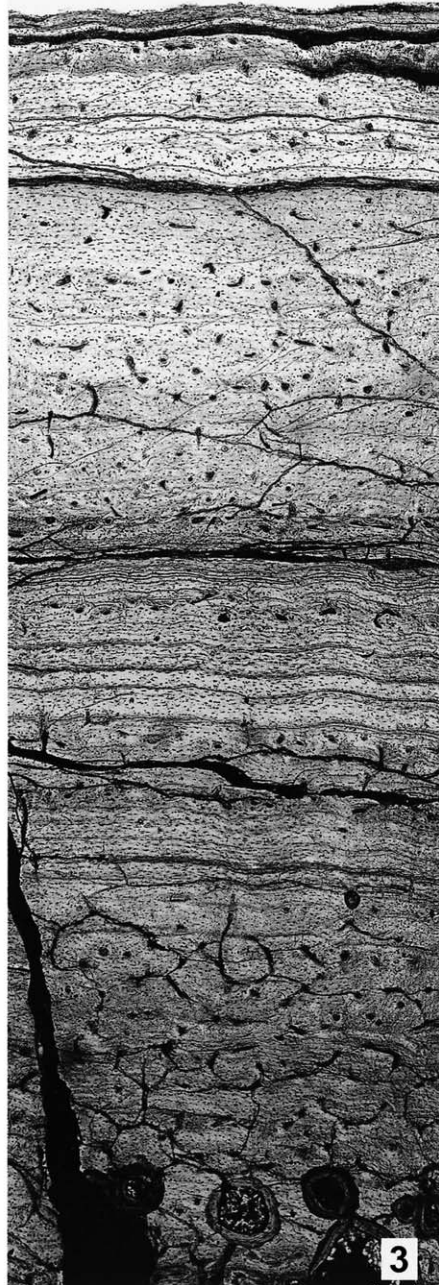
mostly formed by secondary osteons of average diameter that spread progressively into the external cortex. The external cortex as preserved is lamellar-zonal; about 10 cycles of growth can still be recognized. The deepest cycles in the cortex are obscured by scattered Haversian reconstruction. Lamellar tissue, as usual, is formed by a sequence of nearly avascular annuli associated with one to several LAGs. Polarized light shows that the fibers of the annuli are mostly circular (parallel-fibered) or form true lamellar tissue, depending on the region (Pl. 1(4) and (5)). The annuli are separated by thicker zones that contain rows of longitudinally oriented primary osteons, with very few anastomoses among them. These primary osteons are embedded in the coarsely lamellar periosteal tissue, but in some zones this coarsely lamellar tissue is replaced by woven bone. Localized regions show superposition of Sharpey's fibers from the surface to the deep cortex, and the usual extrusion of secondary osteons into the external cortex at those levels.

This bone appears to be mature, because there is extensive but diffuse Haversian substitution, and because the primary cortex records at least 10 cycles, with many more presumed to be destroyed in the deep cortex by Haversian substitution. The outer cortex preserves cyclical growth at moderate to low rates; no apparent changes in the pattern of bone deposition are signaled at its periphery.

4.2. Pseudosuchia: Aetosauria (Stagonolepididae)

4.2.1. Desmatosuchus: proximal humerus (Pl. 2)

This large section is irregularly oval in cross-section. Its marrow cavity is uncrushed, though imperfectly preserved, and contains a well-developed system of endosteal trabeculae. Near its periphery, a complex of nearly circular erosion rooms preserve some remnants of the deep cortex among them, and form a progressive transition into the cortex. From this endosteal margin, which is formed by irregular trabeculae, endosteal bone is deposited on the remaining islands of primary tissue. Scattered secondary osteons, representing Haversian reconstruction, spread externally into the cortex, especially in two opposite sections of the bone that may reflect tendinous insertions (Pl. 2(1) and (3)).

Plate 3. Pseudosuchia: Aetosauria (Stagonolepididae). Scale = 7 mm for part (1), 1 mm for (2), and 0.25 mm for (3). (1) Radius of *Desmatosuchus* sp. (UCMP 28354, section 92-11 D 2T), general view of cross-section of the shaft. An extensive inner region of compacted coarse cancellous bone, formed by sequential relocation of tissues of metaphyseal origin, is encircled by a lamellar-zonal cortex. (2) Detail of the same thin section as in (1), but from a different region. Successive zones of periosteal bone are well vascularized by longitudinal primary osteons. Annuli emphasize the growth cycles. (3) Femur of *Stagonolepis* sp. (UCMP 25914, section 92-11 FE 2T), general view of cross-section of the external cortex of the shaft. Vascularization is denser in the deeper zones. Numerous cycles of deposition have built up the cortex.

Planche 3. Pseudosuchia : Aetosauria (Stagonolepididae). Échelle = 7 mm pour (1), 1 mm pour (2), et 0,25 mm pour (3). (1). *Desmatosuchus*, radius, vue générale, coupe transversale dans une partie proximale de la diaphyse. Une région interne bien développée correspond à du tissu spongieux rendu compact (du fait du repositionnement diaphysaire de tissus d'abord présents dans la métaphyse). Elle est entourée par de l'os d'origine périostique. (2) Même matériel, détail. Les zones successives de tissu osseux périostique sont bien vascularisées par des ostéones primaires longitudinaux. Des annuli soulignent les cycles de croissance. (3) *Stagonolepis*, fémur, section transversale dans la diaphyse. Vue générale du cortex externe. La vascularisation est plus dense dans les zones les plus profondes ; de nombreux cycles ont édifié le cortex.
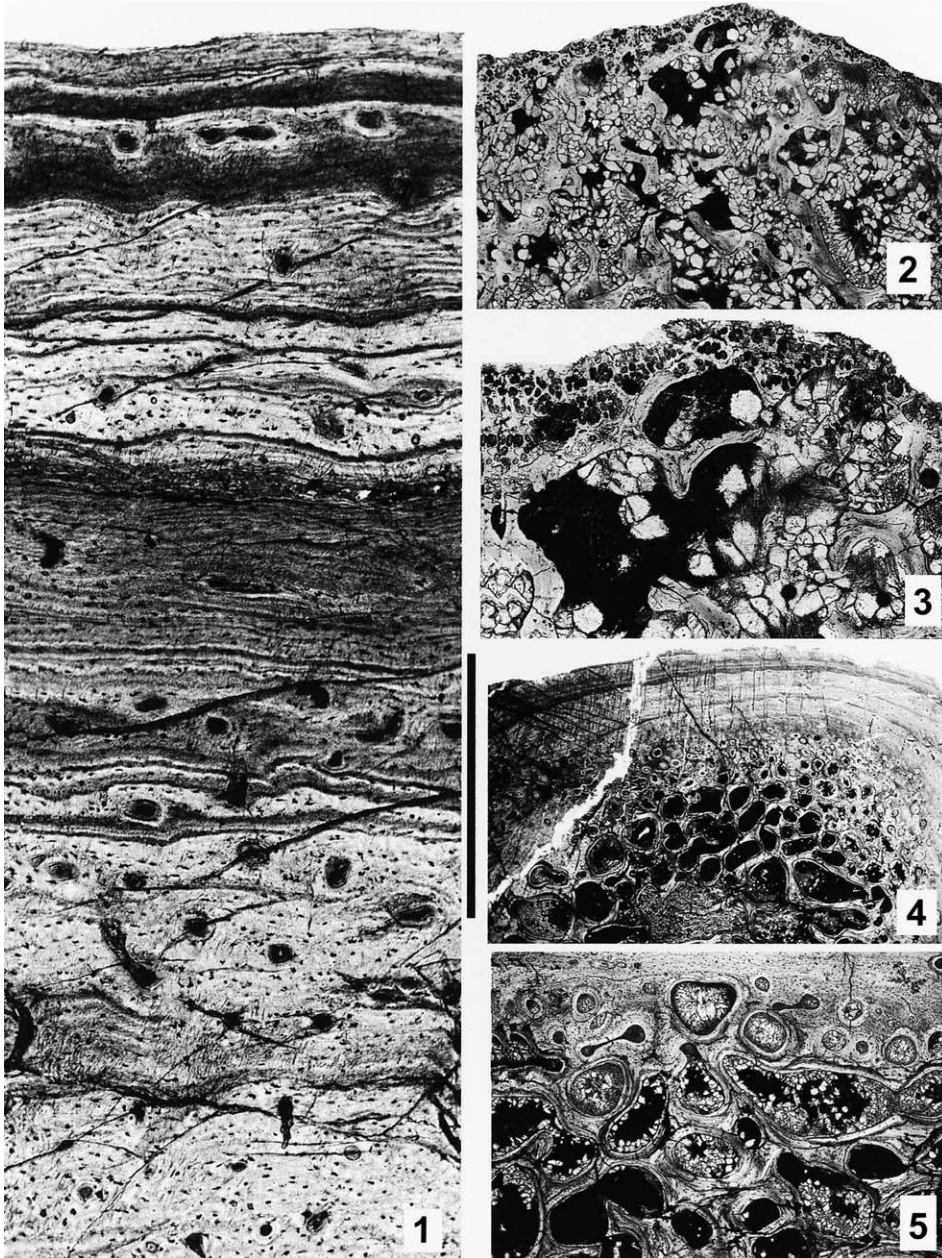
The cortex of periosteal origin does not have the same structure throughout. The inner, fastest-growing region has a series of about 10 cycles of growth that are clearly demarcated. The cycles include a zone formed of thick fibro-lamellar tissue with longitudinal primary osteons connected by circular vascular canals and, locally, a few short circular anastomoses, typical of much dinosaurian bone (Pl. 2(2)). However, in polarized light there is little distinction between the woven and the lamellar components of the complex, as in *Rutiodon*. The outer cycles are more lamellar than the inner cycles. Each zone is separated from the next by a distinct annulus of avascular bone associated with one or more LAGs. In this region, the most external cortex becomes lamellar and avascular and contains five or six LAGs. In the more slowly growing areas, the cortex, in contrast, has a more typical lamellar-zonal pattern of tissue deposition with about 10 growth cycles that are fairly distinct (Pl. 2(1) and (3)). Each zone in this region is formed by lamellar periosteal tissue that contains a few longitudinally oriented primary osteons (Pl. 2(4) and (5)). Each zone is separated from the next by avascular, lamellar annuli. The most external cortex is very thin and also contains many LAGs (Pl. 2(6)).

In sum, this bone shows striking local modifications of bone tissue deposition, which reflects the constraints of building local features of morphology that require more apposition of tissue in some directions than in others. This is why some tissues appear laminar on one side, graduating into less rapidly growing lamellar-zonal tissues on another face of the same section of bone. As noted previously, these tissue types are not phylogenetically determined, but are primarily influenced by functional needs. This section suggests that the animal grew initially at rather high rates that became more moderate, eventually slowing and reflecting high longevity.

Plate 4. Pseudosuchia: Aetosauria (Stagonolepididae). Scale = 0.25 for part (1), 1 mm for parts (2), (3), and (5), and 7 mm for part (4). (1) Femur of *Stagonolepis* sp. (UCMP 25914, section 92-11 FE 2T), as in Fig. 4(3), detail of lamellar-zonal tissue that forms the external cortex. Successive zones of lamellar periosteal bone are poorly vascularized by some primary osteons and are lined by thin, non-vascular annuli. Sharpey's fibers are locally abundant. (2) Proximal humerus of *Typothorax* sp. (UCMP 25905, section 92-11 F1 3L) in longitudinal section, a general view of a region on the proximal "epiphyseal" surface. A thin coating of calcified cartilage caps a system of bone trabeculae that are produced by endochondral ossification. (3) Detail of the top center of (2). The thin calcified cartilage comprises a few rows of hypertrophied chondrocyte lacunae that are poorly organized longitudinally. The bone trabeculae are also poorly organized in orientation. (4) Cross-section of the shaft of the radius of the same specimen (UCMP 25905, section 92-11 F2 2T). The extensive endosteal margin progressively merges with the periosteal cortex. (5) Detail of the endosteal margin of the same section, showing how the endosteal (secondary) osteons (large diameter) encroach upon the primary cortex outwardly.

Planche 4. Pseudosuchia : Aetosauria (Stagonolepididae). Échelle = 0,25 mm pour (1), 1 mm pour (2), (3) et (5), et 7 mm pour (4). (1) *Stagonolepis*, fémur. Détail du tissu lamellaire-zonaire formant le cortex externe (voir aussi Fig. 4(3)). Des couches successives d'os périostique lamellaire, délimitées par de minces annuli, sont faiblement vascularisées par quelques ostéones primaires longitudinaux et délimitées par de minces annuli. Des fibres de Sharpey abondent localement. (2) *Typothorax*. Section longitudinale dans la tête proximale de l'humérus. Vue générale d'une partie de la surface « épiphysaire » conservée. Des travées osseuses résultant de l'ossification enchondrale sont surmontées par une mince couche de cartilage calcifié. (3) Même matériel. Détail d'une région de la (2). Le cartilage calcifié comprend quelques rangées de logettes chondrocytaires hypertrophiées faiblement organisées longitudinalement. Les travées osseuses sont également peu orientées. (4) *Typothorax*, radius, vue générale d'une section transversale diaphysaire du même individu. Une marge endostéale bien développée forme une transition ménagée avec le cortex périostique. (5) Même matériel. Détail de la marge endostéale. Des ostéones secondaires endostéaux de grand diamètre pénètrent le cortex primaire.
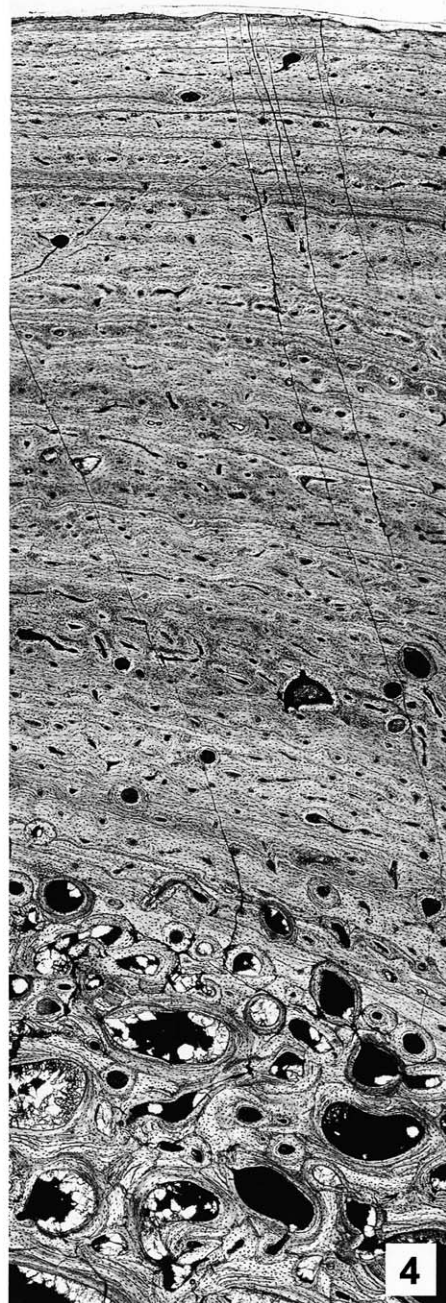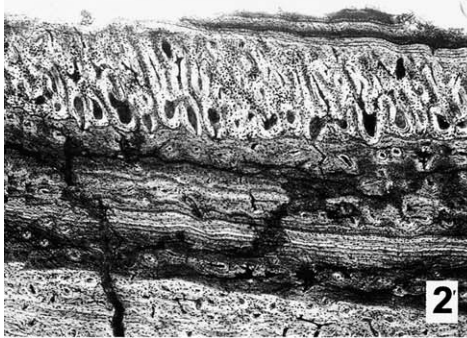
4.2.2. Desmatosuchus*: proximal radius (Pl. 3(1), (2))*

This uncrushed shaft has an irregular cross-section: one surface is flat and slightly concave, the other rounded and slightly convex (Pl. 3(1)). The cortical thickness is about 6 mm, and the marrow cavity is free of trabeculae and uncrushed. The marrow cavity is lined by convoluted sheets of endosteal bone that are clearly lamellar and vary extensively in thickness from one region to another. This endosteal coating, as usual, is associated in the deep cortex with a few large erosion rooms organized like large endosteal osteons.

The section was not taken exactly at the mid-shaft because it shows extensive evidence of sequential relocation. The deep cortex locally forms a kind of oval structure around the endosteal margin. Within this oval structure the tissue is a densely Haversian bone that locally merges with the regular periosteal cortex, again reflecting the histological consequences of secondary relocation (Enlow, 1963) (Pl. 3(2)). The more external cortex of periosteal origin is formed of tissues that vary locally and reflect asymmetrical growth in various diametral directions. This external cortex, in its most typical region, is characterized by a succession of zones and annuli. In the deepest cortex, each zone contains longitudinally oriented primary osteons set in a rather homogenous matrix that appears to contain mostly longitudinally oriented fibers and a few circularly oriented ones. These zones are separated by annuli that are thinner, avascular or nearly so, and associated with slightly convoluted LAGs (Pl. 3(2)). This structure is repeated in numerous cycles that form the external cortex, and its zones become progressively thinner toward the surface. The external cortex is almost avascular and has many LAGs. In one quadrant of the bone, where most of the thickness is composed of the dense Haversian tissue described previously, the external cortex is also almost avascular and has many LAGs. This region intergrades on either side into the more regularly organized tissue described previously. At least 10 superimposed cycles are visible in the cortex exclusive of the LAGs in the most external cortex, which are very numerous (Pl. 3(2)).

Plate 5. Pseudosuchia: Aetosauria (Stagonolepididae), Poposauria. Scale = 0.5 mm for part (1), 0.25 for parts (2) and (4), and 3 mm for part (3). (1) Radius of *Typothorax* sp. (UCMP 25905, section 92-11 F2 2T), as in Fig. 5(4), detail of the periosteal cortex. Typical lamellar-zonal tissue forms the entire cortex here. (2) In another part of the same thin section, sub-periosteal deposition has apparently resumed temporarily at a very high rate of growth, as shown by a hypervascularized zone of fibro-lamellar tissue with radially oriented canals. Note that growth at ordinarily low rates ultimately resumed locally in the outermost cortex. (3) Humerus of *Postosuchus* sp. (UCMP 28353, section 92-11 H1 2T), general view of a cross-section of the shaft. The inner part of the lamellar-zonal cortex shows diffuse perimedullar erosion. (4) Tibia of *Postosuchus* sp. (UCMP 28353, section 92-11 T1 2T), detail of the cortex in a radial direction that shows slower growth. Some inner zones are well vascularized by numerous primary osteons with short anastomoses.

Planche 5. Pseudosuchia : Aetosauria (Stagonolepididae), Poposauria. Échelle = 0,5 mm pour (1), 0,25 mm pour (2) et (4), et 3 mm pour (3). (1) *Typothorax*, radius, section transversale diaphysaire. Détail du cortex périostique (voir aussi Fig. 5(4)). L'ensemble du cortex présente ici une organisation typiquement lamellaire-zonaire. (2) Même matériel. Dans une autre direction radiale, un dépôt périosté semble avoir temporairement repris à très grande vitesse, comme en témoigne une zone de tissu fibro-lamellaire hypervascularisé à canaux radiaires. On remarque que la croissance a finalement repris localement à une vitesse beaucoup plus faible. (3) *Postosuchus*, humérus, vue générale d'une section transversale de diaphyse. La portion profonde du cortex lamellaire-zonaire subit une érosion périmédullaire diffuse. (4) *Postosuchus*, tibia. Détail du cortex dans une région à faible croissance radiaire. Certaines zones en profondeur sont bien vascularisées par de nombreux ostéones primaires présentant de nombreuses anastomoses.
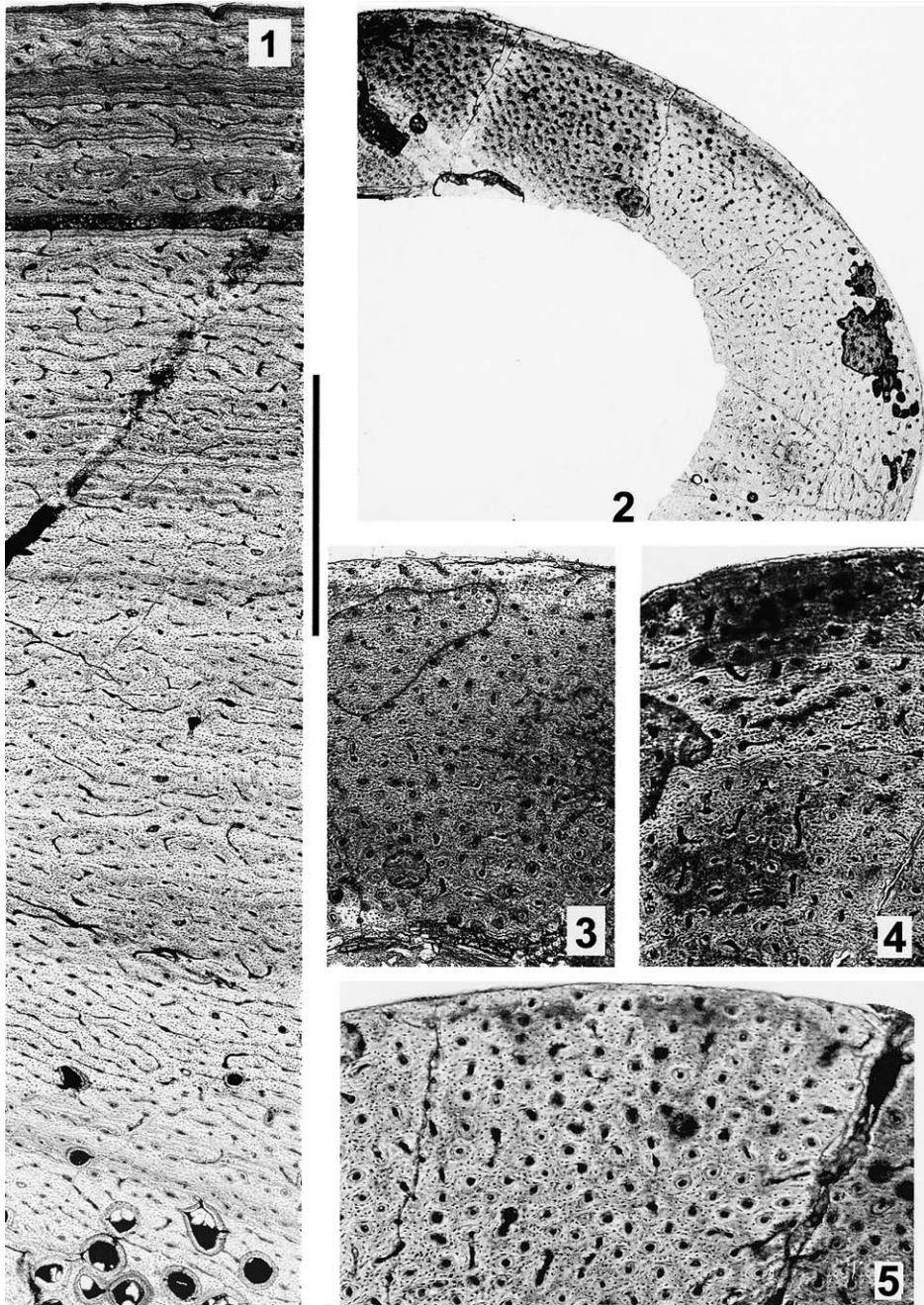
The patterns of bone tissue deposited in this section are clearly dominated by the morphogenetic constraints of the shape of the shaft in connection with problems of sequential relocation. Nevertheless, the general structure of the cortex is clearly decipherable and shows an indeterminate growth pattern at a rather low speed that might have been preceded earlier in ontogeny by more rapid growth, though there is hardly any record of such growth in this section.

4.2.3. Stagonolepis ("Calyptosuchus")*: femur (Pl. 3(3); Pl. 4(1))*

In this cross-section of the shaft, the cortex is often more than 1 cm thick (Pl. 3(3)). The marrow cavity is mostly free of trabeculae, but there is a distinct spongy endosteal margin around the marrow cavity that forms a transitional region into the deep cortex. This region is formed by large, irregular cancellae carved into the primary periosteal bone that forms the deepest cortex. These erosion rooms are lined along their periphery by a coating of secondary endosteal tissue, so they look like large unfinished secondary osteons. In some parts of this deep cortex, more typical, smaller secondary osteons spread into the innermost cortex outwardly, so the transition between spongy tissue and the cortex is progressive.

The deep cortex itself is fibro-lamellar and records early episodes of rapid growth; its vascular canals differentiate as primary osteons that are mostly oriented longitudinally, but have many radial and oblique (occasionally circular) anastomoses (Pl. 3(3)). The tissue in which these numerous vascular canals are laid down is not quite irregularly woven; polarized light reveals that most fibers run circularly. Hence, although the tissue is densely vascularized, it is not quite comparable to the fully differentiated fibro-lamellar complex seen in most dinosaurs and pterosaurs (Reid, 1996; de Ricqlès et al., 2000), as already noted above in *Rutiodon*.

Plate 6. Pseudosuchia: Poposauria, Crocodylomorpha: Sphenosuchia. Scale = 0.5 mm for part (1), 2 mm for part (2), and 0.25 mm for parts (3)-(5). (1) Tibia of *Postosuchus* sp. (UCMP 28353, section 92-11 T1 2T), detail of the cortex in a radial direction that shows more active growth. Most zones become thick regions of fibro-lamellar organization, set apart by thin, non-vascular annuli. The organization of the tissue almost attains a dinosaurian pattern here (see also Chinsamy, 1994, p. 215). (2) Humerus of *Terrestrisuchus* sp. (VMNH 2274, section UCMP T-2), general view of a cross-section of the cortex of the shaft. The primary cortex is relatively thin and entirely primary in structure. (3) The same specimen, section UCMP T-4, showing details of the cortex. The fibro-lamellar tissue is formed by numerous longitudinal primary osteons that are embedded in a woven matrix of periosteal origin. (4) A different region of the same section as the previous figure, in which the external cortex is divided by two LAGs, as in (2). (5) Same specimen, detail of the external cortex. The numerous small longitudinal primary osteons are well demarcated from the woven, densely cellular matrix of periosteal origin.

Planche 6. Pseudosuchia : Poposauria, Crocodylomorpha : Sphenosuchia. Échelle = 0,5 mm pour (1), 2 mm pour (2), et 0,25 mm pour (3)–(5). (1) *Postosuchus*, tibia, détail du cortex dans une région à croissance radiaire maximale. La plupart des zones deviennent plus épaisses et possèdent une organisation fibrolamellaires. Elles demeurent séparées par des annuli avasculaires. L'organisation du tissu atteint ici un patron pour ainsi dire dinosaurien (voir aussi Chinsamy, 1994). (2) *Terrestrisuchus*, humérus. Section transversale : vue générale du cortex diaphysaire. Le cortex est relativement mince et de structure entièrement primaire. (3) Même matériel. Détail du cortex. Le tissu fibro-lamellaire est formé par l'association de nombreux ostéones primaires longitudinaux enchâssés dans une matrice fibreuse d'origine périostique. (4) Même matériel. Dans une autre région, le cortex externe se subdivise du fait de la présence de deux L.A.C. (voir aussi (2)). (5) Même matériel. Détail du cortex externe. Les petits ostéones primaires longitudinaux sont nombreux et bien distincts de la matrice fibreuse périostique très riche en logettes périostéocytaires.
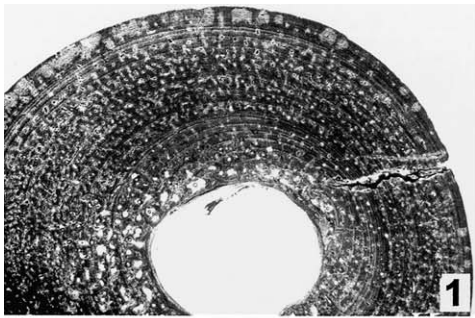
From the deep cortex toward the periphery, there is a sequence of depositional cycles in which the matrix just described is interrupted by a thick layer of almost non-vascular bone (annulus) formed by coarse circumferential lamellae. In this tissue, the bone fibers are highly organized into circular and longitudinal patterns, so the local structure of the bone appears truly lamellar. Each of the sequences of lamellar bone is associated with one or more LAGs, followed by the resumption of a sequence of apparently faster-growing bone, again alternating with a layer of slower-growing, nearly avascular bone. This alternation of faster- and slower-growing tissues (two layers of bone: zone and annulus and one LAG) is repeated into the outer cortex. The number of these cycles is difficult to assess objectively, and apparently varies with local thickness and complexity of the bone tissue, although careful observation shows that each cycle can be followed throughout the bone periphery. At least 10 cycles are recorded and there may be more that are more conspicuous in the thicker regions of the bone (Pl. 3(3); Pl. 4(1)).

The external cortex has fewer, thinner, and more poorly vascularized zones, so the predominance of the lamellae becomes greater. The most external cortex is lamellar and poorly vascularized, with several LAGs. It can be distinguished from what would be described as an external fundamental system (EFS: Cormack, 1987) in mammals, because there is no evidence of a demarcation of depositional rates that would reflect a definite cessation of growth. Locally, most of the cortical thickness may be permeated by radially oriented systems of Sharpey's fibers that were probably linked to tendinous or ligamentous insertions on the bone surface. Typically, in these regions, secondary osteons spread locally even through the outer cortex.

This bone shows an early growth at a relatively high rate, but perhaps not as fast as superficial observation might suggest. Although it is well vascularized, the pattern of orientation of the fibers is not quite typical of the fibro-lamellar condition. Later stages are organized along the typical cyclical lamellar-zonal pattern. Most of the adult cortex (at least

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Plate 7. Pseudosuchia: Crocodylomorpha; Ornithosuchia: Dinosauromorpha. Scale = 4 mm for part (1), 1 mm for parts (2) and (3), and 0.5 mm for part (4). (1) Cross-section of the shaft of the humerus of a specimen of *Alligator* sp. (MOR collections, section 95-4 HS 2T) from the Pleistocene of Florida. The thick lamellar-zonal cortex contains numerous growth cycles. (2) Detail of the top center portion of the previous figure. Scattered Haversian reconstruction spreads from the endosteal margin into the deep cortex. Primary vascular canals of the superimposed zones develop some short anastomoses. (3) Humerus of *Herrerasaurus* sp. (MCZ 7064, section 99-22 H 3T), general view of the external cortex of the shaft in cross-section. The typically plexiform fibro-lamellar tissue is homogenous throughout. (4) Same thin section as in (3), detail of the deep cortex. The endosteal margin is abruptly lined by a thin coating of endosteal bone that is unconformably laid down over the plexiform tissue. No other Haversian substitution has taken place.

Planche 7. Pseudosuchia : Crocodylomorpha ; Ornithosuchia : Dinosauromorpha. Échelle = 4 mm pour (1), 1 mm pour (2) et (3), et 0,5 mm pour (4). (1) *Alligator* sp. (Pléistocène de Floride), section transversale de la diaphyse humérale. Le cortex lamellaire-zonaire très épais montre de nombreux cycles de croissance. (2) Même matériel. Détail d'une région du cortex de (1). Un remaniement haversien dispersé se répand dans le cortex profond à partir de la région périmédullaire. Les canaux vasculaires primaires longitudinaux situés dans les zones successives développent quelques courtes anastomoses. (3) *Herrerasaurus*, humérus, région diaphysaire, vue générale du cortex externe. La région est entièrement constituée d'un dépôt homogène de tissu fibro-lamellaire plexiforme. (4) Même matériel, détail du cortex profond. La marge endostéale est abruptement délimitée par un mince dépôt endostéal transgressif sur le tissu primaire plexiforme. Il n'y a pas d'autre manifestation de phénomènes « Haversiens » d'érosion-reconstruction.
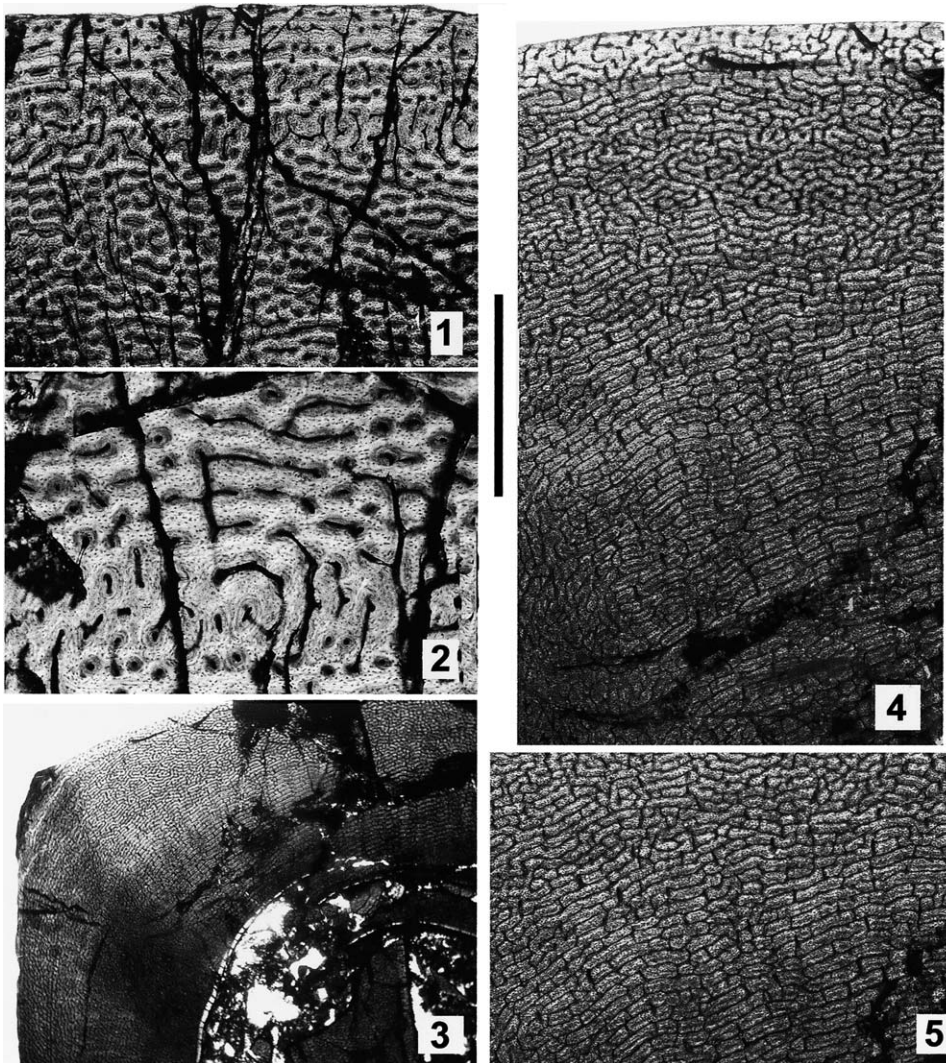
half) was laid down at fairly low to very low rates (perhaps 2 μm or less per day, based on Castanet et al., 1996), but with bursts of growth during the formation of successive zones.

4.2.4. Typothorax: *proximal humerus (Pl. 4(2), (3))*

Longitudinal sections of this humerus were taken to determine the growth stage of the bone, given that the size of the bone is that of a typical adult. The head itself is slightly offset ventrally. The articular surface is flat, with some superficial undulations (Pl. 4(2) and (3)). These undulations may coincide with funnel-like structures that may represent transphyseal canals, which penetrate deeply into the bone to meet the marrow spaces (Horner et al., 2001). The bone surface is lined superficially by a thin coating of hypertrophied calcified cartilage that shows a few cell spaces organized in longitudinal rows (Pl. 4(2)). Most of the bone is formed by secondary bone trabeculae that are endosteal in origin and highly remodeled. The spatial organization of these trabeculae is roughly longitudinal but with many areolar bays and irregular marrow spaces.

The preserved epiphyseal surface itself is formed by a very thin coat of hypertrophied calcified cartilage, which is lined by endosteal bone trabeculae that do not form a continuous sub-chondral bone plate. The cartilage also covers the surface of a few deep cone-shaped pits that punctuate the preserved epiphyseal surface (Pl. 4(3)). Directly within or below the cartilage, the marrow spaces lined by this bone are circular or areolar rather than longitudinal. In some places, not far from the cartilaginous surface, a few islands of calcified cartilage are found within the bony trabeculae, a consequence of endochondral

Plate 8. Ornithosuchia: Dinosauromorpha, Theropoda. Scale = 0.5 mm for part (1), 0.25 mm for part (2), 3 mm for part (3), and 1 mm for parts (4) and (5). (1) Tibia of *Herrerasaurus* sp. (MCZ 7064, section 99-22 T 1T), general view of the external cortex of the shaft in cross-section. The plexiform cortex is homogenous throughout, but some stratification, possibly associated with LAGs, shows in the most superficial layers. (2) Detail of the plexiform tissue of the same section. The organization of the woven (lighter) and osteonal (darker) components of the fibro-lamellar complex are readily visible. (3) Femur of *Coelophysis* sp. (UCMP 129618, section 88-24 CF 3T), general view of a cross-section of the cortex, which is formed entirely of regular plexiform tissue, with an abrupt endosteal margin that is lined by a thin coat of endosteal bone. (4) Same thin section under higher magnification. A possible LAG near the top of the photograph marks the superficial cortex. Faint, superimposed "modulations" in the density and color of the plexiform tissue can be followed at several levels in the deeper regions of the cortex. These features disappear under higher magnification. (5) Same thin section, detail of the primary cortex. Numerous radial anastomoses between successive laminae define the plexiform organization. One of the faint "modulations" in the density and color of the tissue can still be observed.

Planche 8. Ornithosuchia : Dinosauromorpha, Theropoda. Échelle = 0,5 mm pour (1), 0,25 mm pour (2), 3 mm pour (3), et 1 mm pour (4) et (5). (1) *Herrerasaurus*, tibia, section transversale de diaphyse. Le cortex fibro-lamellaire plexiforme est homogène mais une tendance à la stratification, peut être soulignée par des L.A.C., se manifeste dans sa partie tout à fait superficielle. (2) Même matériel. Détail du tissu plexiforme. L'organisation des composants fibro- (plus clairs) et osteonaux (plus foncés) du complexe fibro-lamellaire apparaît clairement. (3) *Coelophysis* fémur. Vue générale du cortex fémoral, section transversale de diaphyse. Le cortex est entièrement constitué d'un tissu plexiforme régulier, abruptement délimité en profondeur par un mince dépôt endostéal périmédullaire. (4) Même matériel. Une possible L.A.C. s'inscrit dans le cortex superficiel tandis que de subtiles « modulations » superposées intéressant la densité et la couleur du cortex profond par ailleurs homogène peuvent être distinguées à ce faible grossissement. (5) Même matériel, détail du cortex primaire. De nombreuses anastomoses radiaires entre laminae successives définissent l'organisation plexiforme du réseau vasculaire. On peut encore observer à ce plus fort grossissement l'une des discrètes « modulations » de la couleur et de la densité osseuse.

ossification. These small islands of calcified cartilage tend to disappear in older trabeculae, deposited deeper in the metaphysis.

The surface of the ventral condyle has a thicker layer of calcified cartilage that has a somewhat different organization than just the preserved epiphysis. There are fewer cells of hypertrophied calcified cartilage, and they are not organized in longitudinal rows, but are scattered within the globular cartilage. Other globular structures around some cell spaces of the calcified cartilage form hollow spheres. These resemble the *globuli ossei*, found during early endochondral ossification, that represent the lining by new bone of globular spaces previously occupied by cartilage cells (de Ricqlès et al., in press).

Below the ventral condyle is the region of undercutting (Haines, 1942), where bone trabeculae of the spongiosa become eroded away below the periosteum. This allows for the epiphyseal surface to be shaped. From this region toward the metaphysis, endosteal trabeculae become compacted by further endosteal deposition (Enlow, 1963) and form the cortical surface. Still further toward the diaphysis, this coarse compacted bone is covered by periosteal bone tissue of the *encoche d'ossification*. This periosteal bone is finely lamellar, with longitudinally oriented fibers, and it becomes thicker toward the diaphysis.

In sum, these features suggest a somewhat mature epiphyseal system that can still grow longitudinally at moderate rates.

4.2.5. Typothorax: *distal shaft of radius (Pl. 4(4), (5); Pl. 5(1), (2))*

This transverse section is from the distal half of the shaft of a radius; it has an oval shape and is about 2.5 cm in diameter. The cortex is up to 7 mm thick. In the marrow cavity, endosteal trabeculae merge at the periphery of the deep cortex to form an endosteal margin that is not uniformly developed (Pl. 4(4)). The margin has mostly circular erosion rooms interrupted by scattered secondary osteons that sometimes spread into the deep cortex (Pl. 4(5)). The cortex is of the general lamellar-zonal type, not densely vascularized. The primary osteons are mostly oriented longitudinally. Most of the fibers are oriented longitudinally within the bone, and the tissue appears to be coarsely lamellated. There are obvious cycles of growth, a few of them quite conspicuous, that divide the cortex into four or five successive regions; however, observed more precisely, the number of LAGs can be as many as 10 or 12 (Pl. 5(1)). Some growth cycles have been accentuated by post-mortem invasion by extraneous mineral matrix along some LAGs, making them more conspicuous.

The most external cortex is unusual. Although the section is not complete circumferentially, the preserved external surface along two of its quadrants is lamellar and poorly vascularized, with extensive evidence of LAGs. Along the intervening quadrants, a sheet of fibro-lamellar bone with many longitudinally and radially oriented primary osteons has apparently been deposited very quickly (Pl. 5(2)). Locally, this tissue appears to form the most superficial part of the cortex itself, but elsewhere it is covered by ordinary layers of the slow-growing external cortex. Sharpey's fibers are also locally present. These features suggest a burst of growth that slowed later along most of the surface, when the bone resumed growth at low rates. This type of tissue may simply reflect sequential relocation, i.e., the histogenetic constraints of reshaping the local bone morphology into a larger, different shape at a given bone level, while retaining the same general morphology at larger size through ontogeny (Enlow, 1963). An alternative interpretation is that this peculiar bone region may be pathological. In fact, Campbell (1966) described in an ornithopod dinosaur,

a localized bone lesion that resembles the tissue observed here. In any case, the section overall reflects protracted, indefinite growth at low rates, characterized by repeated cycles of deposition.

4.3. Pseudosuchia: Poposauridae

4.3.1. Postosuchus kirkpatricki: humerus (Pl. 5(3))

This thin section is from a slightly crushed, large bone with a cortex 7-9 mm thick. The marrow cavity is almost crushed flat, but seems to have lacked bony trabeculae. Around the marrow cavity (Pl. 5(3)), is a nearly continuous coating of endosteal tissue of variable thickness. Along opposite regions of the deep cortex are crescent-shaped deposits of dense Haversian tissues with new erosion rooms that indicate active reworking of bone deposited earlier. One of these regions appears to be well separated from the periosteal cortex, whereas the other gently merges into the deep periosteal cortex. This pattern suggests sequential relocation through development, as if these highly remodeled tissues had been closer to the epiphysis in younger, smaller bone, and were formed by compacted coarse cancellous tissue of the metaphysis.

The deep cortex is not substantially different from the more external cortex: it is lamellar and moderately well vascularized by longitudinal primary osteons. It is progressively eroded by circular erosion rooms. Some of these are active, and others have endosteal bone secondarily laid down along their periphery. The primary osteons of the periosteal cortex are more or less regularly arranged into circular rows that can be followed around the bone. The periosteal tissue is coarsely lamellar throughout, with extensive cycles of deposition. Rows of primary osteons are embedded within zones that are separated by thick annuli of nearly avascular bone, followed by LAGs that line the thick annuli. A trend to progressively less vascularization approaching the surface suggests progressively slower growth. Nearly 20 depositional cycles seem to be recorded in the cortex, but the complexity of the structures and the erosion and redeposition of bone inhibit an accurate count. The most external part of the cortex superficially resembles an EFS, but it is simply a continuation without differentiation from the more internal, progressively slower-growing cortex. This bone structure suggests a long-lived animal with protracted cyclical and indeterminate growth.

4.3.2. Postosuchus kirkpatricki: tibia (Pl. 5(4); Pl. 6(1))

A cross-section of a very large bone is taken in which the cortex is thicker than a centimeter. The shaft has been crushed, obscuring the marrow cavity, which appears to have been more or less free of cancellous trabeculae. The endosteal margin is very well developed and is lined by a more or less continuous coating of endosteal bone tissue. The endosteal margin (Pl. 5(4)) is a transitional region of cancellous tissue of endosteal origin, with many cycles of erosion and deposition. The cancellae are often flattened and elongate in cross-section. In other regions, they are more or less circular or irregularly shaped. This cancellous region is locally associated with a crescent-shaped island of dense Haversian bone, which suggests a sequence of secondary relocation of one side of the endosteal margin (as opposed to two in the humerus).

The cortex is mostly composed of typically lamellar-zonal tissue. The inner cortex is invaded by scattered secondary osteons and erosion rooms. The innermost cortex preserved locally is fairly well vascularized and was probably fibro-lamellar in construction, but only a small amount of this tissue is preserved at this ontogenetic stage. The rest of the cortex is formed by a succession of well-vascularized zones that alternate with thick, poorly defined annuli. These regions are fairly typical of the tissues described for other pseudosuchians. However, some zones (Pl. 6(1)) show fibro-lamellar organization containing mostly longitudinal primary osteons, with some circular and a few oblique anastomoses among the primary osteons. These well vascularized zones, which may reflect locally rapid deposition associated with cortical drift and remodeling of the bone, become thinner and less vascularized toward the external cortex. Between each zone is an annulus that is less vascularized and contains a few longitudinal primary osteons. These annuli are conspicuously associated with apparent LAGs, but these LAGs can also be observed within zones and are very numerous. The annuli are intercalated with the zones up to the most external cortex, where the bone becomes almost avascular and contains many LAGs. The cycles are difficult to quantify precisely, but they number at least 15 and may be much more numerous.

Polarized light shows that the fibrillar orientation of the deepest part of the cortex and some other areas is fibro-lamellar, whereas in most of the annuli and some of the most external zones that form most of the external cortex, there is a prevalence of circularly oriented fibers. This is a characteristic pattern of lamellar-zonal tissue. There is generally much anisotropy in regions close to the LAGs, which are conspicuous in polarized light. There is almost no Haversian tissue in the external cortex. The relief of the external surface of the bone, as usual, is linked with the insertion of Sharpey's fibers, which are associated with the proliferation of secondary osteons in the outer cortex.

In sum, this bone is very crocodilian in general features and suggests indeterminate growth, probably protracted longevity, and cyclical patterns of growth that appear typical of pseudosuchians.

4.4. Pseudosuchia: Crocodylomorpha: Sphenosuchia

4.4.1. Terrestrisuchus*: humerus (Pl. 6(2–5))*

The cross-section of the shaft is circular (Pl. 6(2)); the cortex is quite homogenous, with an abrupt distinction between the cortex and the marrow cavity, which is free of cancellous bone trabeculae. At the periphery of the marrow cavity, there is a very thin coating of endosteal bone that is very finely lamellar. The boundary of the marrow cavity is formed in some areas by the deep cortex, suggesting that it was experiencing local resorption (Pl. 6(3)). Some opposite regions of the cortex are distinctly thicker than others, ranging to half again as thick as the other. The homogenous cortex is formed of a periosteal matrix with little spatial organization of the fibers, and it is isotropic in polarized light. Nevertheless, toward the periphery, the cortex becomes more organized. Many fibers are organized circularly and there are one or two LAGs toward the periphery (Pl. 6(4)). Another section preserves the suggestion of another LAG set deeper in the cortex, perhaps a third of the distance from the surface.

The inner cortex is highly vascularized for a crocodilian, but the outer cortex is slightly less well vascularized. There are comparatively many osteocytes distributed throughout the

cortex, compared to typical crocodiles (Pl. 6(5)). The canals are only longitudinal, with few or no short anastomoses among them; hence there are no well-defined circular or radial canals. The primary osteons surrounding the canals are very small in diameter, but well defined under polarized light. There appear to be few cells lacunae in the lamellae of the primary osteons, but the lacunae of the tissue in which the osteons are embedded are rather plump. Many canaliculi radiate from these lacunae in all directions, but perhaps more toward the periphery. The organization of this bone tissue appears to be a simple form of the fibro-lamellar complex, in which the vascular channels are longitudinally arranged. Only in the outermost quarter of the preserved cortex, which is otherwise homogenous, is there any evidence that growth has slowed, because the fibers of the bone matrix appear to run more circularly in this region, the cell spaces are slightly more flattened, the canaliculi run preferentially toward the periphery, and two LAGs are present in this outermost cortex (Pl. 6(4) and (5)). There is no evidence of an EFS.

The histological features suggest a growth regime that is mostly continuous and relatively rapid for pseudosuchians, perhaps of the order of 6-7 µm/d, judging by rates derived from the mallard (Castanet et al., 1996). Growth appears to become more cyclical later in life, but was apparently continuing at the periphery of the cortex. This pattern, and the absence of secondary osteons in the deep cortex, suggests that growth was not complete and that the individual was still relatively young. The tubular architecture of the bone, and the absence of spongiosa in the shaft, is consistent with a fully terrestrial (rather than amphibious) habit (Crush, 1984).

4.5. Pseudosuchia: Crocodylomorpha: Crocodylia: Alligatoridae

4.5.1. Alligator *sp.: humerus (Pl. 7(1), (2))*

The bone histology of crocodiles is well known (e.g., de Buffrénil, 1980; Hua and de Buffrénil, 1996), and needs little detail here. This specimen is taken from the mid-shaft of the humerus of a Pleistocene alligator from Florida (USA) in the MOR collections (Pl. 7(1) and (2)). In the cross-section, the bone is slightly ovoid; the free marrow cavity is small compared to the thickness of the cortex, and is slightly offset from the center of the bone by lateral drift during early growth. In all respects, this is a typical crocodile long bone. Endosteal bone lines the marrow cavity. The cortex is lamellar-zonal throughout, with at least 12 depositional cycles in the typical alternation of annuli and zones. Poorly scattered cycles of erosion and deposition are evident, but there is not much Haversian reworking in the deep cortex. Some erosion has opened cavities that have not yet received secondary deposition of bone.

The primary cortex is vascularized mainly by primary osteons that are oriented longitudinally, with scattered short anastomoses that link two or three canals at most, usually in an irregular, radial, or circumferential direction. The most external cortex is less well vascularized than the internal cortex. This bone reflects highly cyclical, protracted growth at moderate rates.

4.6. Ornithosuchia: Dinosauromorpha

The patterns of long bone histology in nearly all the pseudosuchians we studied are virtually stereotypical. For contrast, we briefly discuss two basal dinosauromorph ornitho-

suchians, *Herrerasaurus* and *Coelophysis*. As for other basal ornithosuchians, literature on the histology of other basal dinosaurs was discussed above (see also Padian et al., submitted for publication); pterosaur histology was discussed by de Ricqlès et al. (2000) and Jenkins et al. (2001).

4.6.1. Herrerasaurus*: humerus (Pl. 7(3), (4))*

The humerus (Pl. 7(3) and (4)) is very similar to the tibia, and is entirely composed of homogenous plexiform to sub plexiform fibro-lamellar tissues. One side of the bone has a region of more circumferentially oriented canals. Vascularization is very high, with canals radiating in all directions, especially circumferentially. On the endosteal surface of the marrow cavity is a thin avascular bone layer (Pl. 7(4), bottom), slightly thicker than the one found on the tibia. At the periosteal surface is a very thin avascular layer that looks similar to an EFS, but has no internal LAGS.

4.6.2. Herrerasaurus*: tibia (Pl. 8(1), (2))*

The tibia cortex (Pl. 8(1) and (2)) is highly vascularized, and composed entirely of plexiform, fibro-lamellar tissue. Most vascular spaces are oriented in a circumferential pattern. Osteocytes are very well organized in the osteons around the vascular spaces. Again, a thin layer of avascular endosteal bone surrounds the marrow cavity. Close to the periosteal surface are very thin avascular layers suggestive of some cyclical modulations of bone deposition dynamics. There is no evidence of secondary osteonal development in any area of the element.

4.7. Ornithosuchia: Dinosauria: Theropoda

4.7.1. Coelophysis*: femur (Pl. 8(3–5))*

Most of the cortex (Pl. 8(3) and (4)) is made of homogenous fibro-lamellar tissue with a typical plexiform vascularization (Colbert, 1995). In some places, the plexiform pattern (Pl. 8(4) and (5)) is less regular and has fewer radial canals (sub-plexiform). In other places, the canals are more disorganized and have defined lozenge-shaped islands of bone between them: here the vascular pattern becomes reticular, but these various patterns continually intergrade from region to region. There are almost no secondary osteons in the deep cortex. A thin layer of endosteal bone surrounds the free marrow cavity; the canals of the deep cortex of primary bone cross the endosteal tissue to open into the marrow cavity. There is no evidence of an EFS; a faint LAG may be seen at a depth of approximately four laminae from the external surface. In parts of the section, there is evidence for three dark circumferential lines in the external cortex that might suggest LAGs, but appear to be merely artificial cracks. Observation at low power of the whole cortex (Pl. 8(3) and (4)) reveals slight overall changes in an otherwise homogenous tissue structure, suggesting some commensurate minor modulations in radial growth dynamics, as discussed in the hadrosaur *Maiasaura* (Horner et al., 2000).

The cortex comprises a typically fast-growing tissue deposited continually. This tissue resembles tissues found in large birds and other dinosaurs (Horner et al., 2000; Reid, 1996). In extant birds, such tissues can grow at rates between 10 and 50 μm/d or more (Castanet et al., 1996, 2000).

5. Discussion

5.1. Histology and bone growth patterns in Pseudosuchia

The pseudosuchian taxa we sampled were phytosaurs, aetosaurs, poposaurs, and crocodylomorphs—the best-known North American pseudosuchians of the Late Triassic (and Early Jurassic, in the case of crocodylomorphs). First, we wished to question whether their histological features, and hence bone growth patterns, were similar to those of living crocodilians. We found some decisive general similarities in the sequence of deposition of bone from the internal cortex to the outermost periosteal cortex. In the long bones of all these taxa, it appears that an early period of relatively rapid growth (common to vertebrates in general) is characterized by the deposition of fibro-lamellar bone, in which, in contrast to dinosaurs and pterosaurs, the bone fibers themselves retain a more or less parallel orientation (as opposed to woven). After this initial stage, the bone growth generally seems to settle into a typical pattern of lamellar-zonal cycles. In each cycle, a burst of moderately well-vascularized bone, in which most osteons are longitudinally oriented, is followed by a layer of avascular bone, and capped by a LAG. This cycle, which is repeated throughout most of the rest of growth, characterizes most of the histological ontogeny of the long bones in these taxa. As the animal reaches adult size, the thickness of these cyclical intervals progressively decreases. Finally, in at least some taxa, an EFS is deposited, in which the bone is entirely avascular and homogenous, and in which a number of LAGs may be preserved. The EFS represents growth that occurs more or less after the animal achieves adult size; but in some taxa that lack an EFS, it is not obvious that growth is complete or even determinate, and there is no evidence that the LAGs in the EFS are annual (Horner et al., 1999, 2000). A layer of endosteal bone of varied thickness may surround the marrow cavity, especially as growth nears completion. Secondary erosion rooms usually appear in the internal cortex, and often mature into systems of Haversian osteons that may be preferentially developed along certain radial axes of the bone. These areas are especially rich in Sharpey's fibers, and are likely linked to ligamentous or tendinous insertions.

The general ontogeny of long bone growth in extinct pseudosuchians is ostensibly similar to the situation in extant crocodiles. The bone of embryonic crocodiles shows features of rapid growth (Horner et al., 2001), and in immature crocodiles, growth rates can be very high, depending on ambient conditions and food supply. Generally, however, extant and extinct crocodiles settled into a growth trajectory that gently slowed until adult size was reached; even the largest known crocodiles simply enlarged the arc of this growth curve without changing its shape (Erickson and Brochu, 1999). The embryonic and hatchling stages of extinct pseudosuchians were not available; our inferences were based on the inner cortex of sub adult bones, when they were not too remodeled. This pseudosuchian pattern is in marked contrast to the situation in dinosaurs and pterosaurs, in which initial rapid growth was sustained and only slowed markedly as adult size was reached in large species (Curry, 1999; Horner et al., 2000, 2001; Padian et al., 2001, Sander, 2000). The "dinosaurian" pattern is clearly expressed here by *Herrerasaurus* and *Coelophysis*.

5.2. Phylogenetic patterns of bone histology and growth rates in archosaurs

If the general features of pseudosuchian and ornithosuchian bone histology, as far as known from published studies, were plotted on a cladogram (Fig. 1), they can test the

hypotheses on the evolution of histological patterns and form the basis for further studies and hypotheses (Padian et al., 2001).

On the pseudosuchian side, as noted above, the bone histology of extant crocodilians is reasonably well characterized (Enlow and Brown, 1957; Enlow, 1969; de Buffrénil, 1980; Hua and de Buffrénil, 1996). The sections from the major pseudosuchian outgroups to crocodiles, namely poposaurs, aetosaurs, and phytosaurs are added to this. All of these taxa, with the exception of *Terrestrisuchus*, show a typical pattern of relatively rapid early growth, followed by the cycles of lamellar-zonal bone separated by distinct LAGs, as in extant crocodiles. Reid (1997b) reported even more active growth in a living wild-caught crocodilian; his observations are exceedingly intriguing and deserve further description, because they reflect anomalously high growth rates among reported crocodilians, even captive-bred ones.

On the ornithosuchian side, dinosaurs and pterosaurs that reach large size show the same predominance of fibro-lamellar tissue that is seen in larger birds and mammals today (e.g., de Ricqlès et al., 2000; Horner et al., 2000). Hence, one hypothesis could postulate that the patterns seen in pseudosuchians and ornithosuchians originated at the bases of these stem-groups and have persisted to the present. Pseudosuchians have always been characterized by relatively slow and cyclical growth patterns; ornithosuchians have always been characterized by relatively rapid growth patterns that only diminish in rate as adult size is reached, but are somewhat slower in smaller species. These would explain the general differences in rates expressed in Fig. 1.

The situation becomes a little more ambiguous when an attempt is made to polarize these patterns more generally. Considering only other extant reptilian clades outside archosaurs, it could be inferred that the relatively slow growth rates seen in lepidosauromorphs (de Buffrénil and Castanet, 2000) and turtles are basal to archosaurs. Hence, pseudosuchians might simply retain these growth patterns; *Terrestrisuchus* may represent somewhat higher growth rates within crocodiles, although the specimen we studied appears not to be full-grown. Ornithosuchians would depart from the basic reptilian pattern by evolving (perhaps in quantum fashion) a fibro-lamellar complex of tissues that reflect rapid growth. What makes the picture more complex is that *Erythrosuchus*, an archosauriform, shows a type of fibro-lamellar pattern throughout its growth that is normally associated with the aforementioned large mammals, large birds and large dinosaurs (Gross, 1934, de Ricqlès, 1976). If the histological patterns of ornithosuchians were present in the immediate outgroups of archosaurs, it cannot be assumed that other, more distantly related, reptiles provide a reliable signal about histological patterns basal to Archosauria. It also cannot be assumed that pseudosuchians display the basal archosaurian pattern. An alternate hypothesis, therefore, could be that these histological patterns, and the modes of growth that they represent, evolved in archosauriforms and were carried on (and elaborated) in ornithosuchians; pseudosuchians secondarily reverted to a less well vascularized matrix, and a less determinate, more cyclical pattern of growth that persists in crocodiles today (de Ricqlès, 1978; Schweitzer and Marshall, 2001). *Terrestrisuchus* could represent a further reversion to more basal, rapid rates of growth, perhaps connected with a rapid evolution to small size like that hypothesized for the origin of birds (Padian et al., 2001; de Ricqlès et al., in press). Based on the multiple outgroup hypothesis of Maddison et al. (1984), the situation in erythrosuchians appears anomalous, not indicative of a change in polarity at these nodes.

Only histological analysis of more taxa among ornithosuchians, pseudosuchians, and archosauriforms will be able to test these alternative hypotheses further.

Generalizing from these results, it is uncontroversial that species with large body size grow more quickly than related species of smaller body size (Case, 1978). This alone, however, does not explain the difference in growth rates reflected in the bone tissues of pseudosuchians and ornithosuchians. Based on actualistic rates of bone growth for living pseudosuchians (crocodiles: de Buffrénil, 1980) and ornithosuchians (birds: Castanet et al., 1996, 2000), clear distinctions of growth rates among tissues can be assigned, and dinosaurs, which fall with the birds, are clearly different from the pseudosuchians. We have seen some relatively high rates of growth in young crocodiles, in *Terrestrisuchus*, and in Reid's (1997b) report of a wild-caught extant crocodile. On the other hand, we have seen anomalously low rates of growth in the small ornithischian *Scutellosaurus* which, based on inferred rates of growth in its immediate basal dinosaurian outgroups, is clearly secondarily derived (Padian et al., submitted for publication). It is difficult not to conclude that the two major branches of the archosaurs had markedly different basal metabolic rates beginning early in the history of their separation. This inference accords with other data regarding their posture and gait, functional morphology, biochemistry, and behavior (Thomas and Olson, 1980; Currie and Padian, 1998; Schweitzer and Marshall, 2001).

6. Conclusions

- Phytosaurs, aetosaurs, and poposaurs show typical histological patterns seen in the long bones of living crocodiles, and evidently grew much like them. Certainly they grew much more like crocodiles than like ornithosuchians (birds, other dinosaurs, and pterosaurs), which seem to have grown at sustained higher rates.
- What little is currently known of the growth patterns of the immediate outgroups to crown-group archosaurs raises the possibility that crocodiles and other pseudosuchians may not necessarily retain the basal archosauriform patterns of histological tissue deposition and growth. Growth rates in erythrosuchian archosauriforms may have been higher than those of most pseudosuchians, but this question requires further investigation. Hence, the evolutionary polarity of growth rates in basal archosaurs is not straightforward. Within archosaurs, however, pseudosuchians could occasionally revert to more rapid growth rates (e.g., *Terrestrisuchus*).
- Crocodiles cannot be assumed to represent the plesiomorphic condition for archosaurs in general or for dinosaurs in particular in the features of patterns of tissue deposition, rates and strategies of growth, and thermo-metabolic regimes. Mesozoic dinosaurs were probably not exactly like living birds in these respects, but what is known of them shows that they were much more like birds than like crocodiles (Horner et al., 2000; Padian and Horner, 2002, 2003). A split in metabolic regimes probably can be traced to the base of the pseudosuchian-ornithosuchian divergence.

References

Arcucci, A.B., 1986. Nuevos materiales y reinterpretacion de *Lagerpeton chanarensis* Romer (Thecodontia, Lagerpetonidae nov.) del Triasico Medio de La Rioja, Argentina. Ameghiniana 23, 233–242.

Arcucci, A.B., 1987. Un nuevo Lagosuchidae (Thecodontia - Pseudosuchia) de la fauna de Los Chanares (Edad Reptil Chanarense, Triasico Medio), La Rioja, Argentina. Ameghiniana 24, 89–94.

Bennett, S.C., 1996. The phylogenetic position of the Pterosauria within the Archosauromorpha. Zoological Journal of the Linnean Society 118, 261–308.

Benton, M.J., 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. Philosophical Transactions Royal Society of London B 354, 1423–1446.

Benton, M.J., Clark, J.M., 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: Benton, M.J (Ed.), Phylogeny and Classification of the Tetrapods, vol. 1. Oxford University Press, Oxford, pp. 295–338.

de Buffrénil, V., 1980. Mise en évidence 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 individu. Archives de Zoologie Experimentale et Génerale 121, 63–76.

de Buffrénil, V., Castanet, J., 2000. Age estimation by skeletochronology in the Nile Monitor (*Varanus niloticus*), a highly exploited species. Journal of Herpetology 34, 414–424.

Camp, C.L., Welles, S.P., 1956. The North American genus *Placerias*. Memoir of the University of California 13 (4), 255–304.

Campbell, J.G., 1966. A dinosaur bone lesion resembling avian osteopetrosis and some remarks on the mode of development of the lesion. Journal of the Royal Microscopical Society 85 (2), 167–174.

Case, T.J., 1978. Speculations on the growth rates and reproduction of some dinosaurs. Paleobiology 4, 320–328.

Castanet, J., Francillon-Vieillot, H., Meunier, F.J., de Ricqlès, A., 1993. Bone and individual aging. In: Hall, B.K (Ed.), Bone Growth. Bone, vol. 7. CRC Press, London, pp. 245–283.

Castanet, J., Grandin, A., Abourachid, A., de Ricqlès, A., 1996. Expression de la dynamique de croissance dans la structure de l'os périostique chez *Anas platyrhynchos*. Comptes Rendus de l'Académie des Sciences, Paris (Sciences de la Vie) 319, 301–308.

Castanet, J., Curry Rogers, K., Cubo, J., Boisard, J.-J., 2000. Periosteal bone growth rates in extant ratites (ostrich and emu). Implications for assessing growth in dinosaurs. Comptes Rendus de l'Académie des Sciences, Paris 323 (3a), 543–550.

Chinsamy, A., 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). Paleontologia Africana 27, 77–82.

Chinsamy, A., 1993. Bone histology and growth trajectory of the prosauropod dinosaur *Massospondylus carinatus* Owen. Modern Geology 18, 319–329.

Chinsamy, A., 1994. Dinosaur bone histology: implications and inferences. Palaeontological Society 7, 213–228 (Special Publication).

Colbert, E.H., 1995. Little Dinosaurs of Ghost Ranch. Columbia University Press, New York.

Cormack, D., 1987. Ham's Histology. Lippincott, New York.

Crush, P.J., 1984. A late Upper Triassic sphenosuchid crocodilian from Wales. Palaeontology 27, 131–157.

Currey, J.D., 1960. Differences in the blood supply of bone of different histological types. Quarterly Journal of Microscopical Science 101, 351–370.

Currey, J.D., 1962. The histology of the bone of a prosauropod dinosaur. Paleontology 5 (2), 238–246.

Currie, P.J., Padian, K, 1998. The Encyclopedia of Dinosaurs. Academic Press, San Diego, CA.

Curry, K.A., 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria, Sauropoda): new insights on growth rates and longevity. Journal of Vertebrate Paleontology 19, 654–665.

de Ricqlès, A., 1968. Recherches paléohistogiques sur les os longs des Tétrapodes. I. Origine du tissu osseux plexiforme chez les dinosauriens sauropodes. Annales de Paléontologie 54 (2), 133–145.

de Ricqlès, A., 1976. On bone histology of fossil and living Reptiles, with comments on its functional and evolutionary significance. In: Cox, B., Bellairs, A. (Eds.), Morphology and Biology of Reptiles. Liun. Soc. Sympos. 3. Academic Press, London and N.Y., pp. 123–150.

de Ricqlès, A., 1978. Sur la classification, la signification fonctionnelle et l'histoire des tissus osseux des tétrapodes. Troisième partie: évolution. Annales de Paléontologie 64 (1), 85–111.

de Ricqlès, A., 2000. L'origine dinosaurienne des oiseaux et de l'endothermie avienne : les arguments histologiques. Annales de Biologie 39, 69–100.

de Ricqlès, A., Bolt, J., 1983. Jaw growth and tooth replacement in *Captorhinus aguti* (Reptilia, Captorhinomorpha): a morphological and histological analysis. Journal of Vertebrate Paleontology 3, 7–24.

de Ricqlès, A., Meunier, F.J., Castanet, J., Francillon-Vieillot, H., 1991. Comparative microstructure of bone. In: Hall, B.K (Ed.), Bone Matrix and Bone Specific Products. Bone, vol. 3. CRC Press, Boca Raton, FL, pp. 1–78.

de Ricqlès, A., Padian, K., Horner, J.R., Francillon-Viellot, H., 2000. Paleohistology of the bones of pterosaurs (Reptilia: Archosauria) : anatomy, ontogeny, and biomechanical implications. Zoological Journal of the Linnean Society 129, 349–385.

de Ricqlès, A., Padian, K., Horner, J.R., 2001. The bone histology of basal birds in phylogenetic and ontogenetic perspectives. In: Gauthier, J.A., Gall, L.M (Eds.), New Perspectives on the Origin and Early Evolution of Birds. Yale University Press, New Haven, CT, pp. 411–426.

de Ricqlès, A., Padian, K., Horner, J.R., Lamm, E.-T.H., Myhrvold, N., 2003. Osteohistology of *Confuciusornis sanctus* (Theropoda: Aves). Journal of Vertebrate Paleontology (in press).

Enlow, D.H., 1963. Principles of Bone Remodeling. Charles C. Thomas, Springfield, IL.

Enlow, D.H., 1969. The bone of reptiles. In: Gans, C., Bellairs, A. d'A., Parsons, T.S (Eds.), Morphology A. Biology of the Reptilia, vol. 1. Academic Press, New York, pp. 45–78.

Enlow, D.H., Brown, S.O., 1956. A comparative histological study of fossil and recent bone tissues. Texas Journal Science 8, 403–443 Part I.

Enlow, D.H., Brown, S.O., 1957. A comparative histological study of fossil and recent bone tissues. Texas Journal Science 9, 185–214 Part II.

Enlow, D.H., Brown, S.O., 1958. A comparative histological study of fossil and recent bone tissues. Texas Journal Science 10, 187–230 Part III.

Erickson, G.M., Brochu, C.A., 1999. How the "terror crocodile" grew so big. Nature 398, 205–206.

Erickson, G.M., Rogers, K.C., Yearby, S.A., 2001. Dinosaurian growth patterns and rapid avian growth rates. Nature 412, 429–433.

Fiorillo, A.R., Padian, K., 1993. Taphonomy of the Late Triassic *Placerias* Quarry (Petrified Forest Member, Chinle Formation) of eastern Arizona. Bulletin of the New Mexico Museum of Natural History and Science 3, 133–134.

Gauthier, J.A., 1984. A phylogenetic analysis of the higher categories of Diapsida (Reptilia). Ph.D. Thesis. University of California, Berkeley Department of Paleontology.

Gauthier, J.A., 1986. Saurischian monophyly and the origin of birds. Memoirs of the California Academy Science 8, 1–55.

Gauthier, J.A., Padian, K., 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In: Hecht, M.K., Ostrom, J.H., Viohl, G., Wellnhofer, P (Eds.), The Beginnings of Birds: Proceedings of the International Archaeopteryx Conference, Eichstatt. Freunde des Jura-Museums, Eichstatt, pp. 185–197 1984 Germany.

Gross, W., 1934. Die Typen des mikroskopischen Knochenbaues bei fossilen Stegocephalen und Reptilien. Zeitschrift für Anatomie 103, 731–764.

Haines, R.W., 1942. The evolution of epiphyses and of endochondral bone. Biological Reviews 174, 267–292.

Holtz, T.R., Padian, K., 1995. Definition and diagnosis of Theropoda and related taxa. Journal of Vertebrate Paleontology 15 (Suppl. 3), 35A.

Horner, J.R., de Ricqlès, A.J., Padian, K., 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. Paleobiology 25, 295–304.

Horner, J.R., de Ricqlès, A.J., Padian, K., 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. Journal of Vertebrate Paleontology 20, 115–129.

Horner, J.R., de Ricqlès, A.J., Padian, K., 2001. Comparative osteohistology of some embryonic and neonatal archosaurs: implications developmental and behavioral implications for dinosaurs. Paleobiology 27, 39–58.

Hua, S., de Buffrénil, V., 1996. Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). Journal of Vertebrate Paleontology 16 (4), 703–717.

Hutton, J.M., 1986. Age determination of living Nile crocodiles from the cortical stratification of bone. Copeia, 332–341.

Jenkins Jr., F.A., Shubin, N.H., Gatesy, S.M., Padian, K., 2001. A diminutive pterosaur (Pterosauria: Eudimorphodontidae) from the Greenlandic Triassic. Bulletin of the Museum of Comparative Zoology, Harvard University 155, 487–506.

Juul, L., 1994. The phylogeny of basal archosaurs. Paleontologia Africana 31, 1–38.

Long, R.A., Murry, P.A., 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. Bulletin of the New Mexico Museum of Natural History and Science 4, 1–254.

Maddison, W.P., Donoghue, M.J., Maddison, D.R., 1984. Outgroup analysis and parsimony. Systematic Zoology 33, 83–103.

Padian, K., Horner, J.R., 2002. Typology and transformationism in the origin of birds. Trends in Ecology and Evolution 17, 120–123.

Padian, K., Horner, J.R., 2003. Dinosaur physiology. second ed. In: Weishampel, D.B., Dodson, P., Osmolska, H (Eds.), The Dinosauria. University of California Press, Berkeley.

Padian, K., de Ricqlès, A., Horner, J.R., 2001. Dinosaurian growth rates and bird origins. Nature 412, 405–408.

Padian, K., Horner, J.R., de Ricqlès, A., 2003. Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies. submitted for publication.

Paladino, F.V., Spotila, J.S., 1994. Does the physiology of large living reptiles provide insights into the evolution of endothermy and paleophysiology of extinct dinosaurs? Palaeontological Society 7, 261–274 (Special Publication).

Parrish, J.M., 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. Journal of Vertebrate Paleontology 13, 287–308.

Peters, D., 1997. A new phylogeny for the Pterosauria. Journal of Vertebrate Paleontology 17 (Suppl. 3), 69A.

Prum, R.O., 2002. Why ornithologists should care about the dinosaurian origin of birds. Auk 119, 1–17.

Regal, P.J., Gans, C., 1980. The revolution in thermal physiology: implications for dinosaurs. In: Thomas, R.D.K., Olson, E.C (Eds.), A Cold Look at the Warm-Blooded Dinosaurs. AAAS Symposium . Westview Press, Boulder, CO, pp. 167–188.

Reid, R.E.H., 1996. Bone histology of the Cleveland-Lloyd dinosaurs and of dinosaurs in general, Part I: Introduction: introduction to bone tissues. Geology 41, 25–72 Brigham Young University Research Studies.

Reid, R.E.H., 1997a. How dinosaurs grew. In: Farlow, J.O., Brett-Surman, M.K (Eds.), The Complete Dinosaur. Indiana University Press, Bloomington, pp. 403–413.

Reid, R.E.H., 1997b. Dinosaurian physiology: the case for "intermediate" dinosaurs. In: Farlow, J.O., Brett-Surman, M.K (Eds.), The Complete Dinosaur. Indiana University Press, Bloomington, pp. 449–473.

Ruben, J.A., 1991. Reptilian physiology and the flight capacity of *Archaeopteryx*. Evolution 45, 1–17.

Ruben, J.A., 1995. The evolution of endothermy in mammals and birds: from physiology to fossils. Annual Review of Physiology 57, 69–95.

Sander, P.M., 2000. Long bone histology of the Tendaguru Sauropods: implication for growth and biology. Paleobiology 26, 466–488.

Sander, P.M., Klein, N., 2001. Heterochrony in Sauropodomorph dinosaur evolution as deduced from bone histology. Sixth International Congress of Morphology, Iena. Journal of Morphology, 248, pp. 279 (Abstract).

Sander, P.M., Klein, N., 2001. Life history studies on Sauropodomorph dinosaurs facilitated by controlled paleohistologic sampling of growth series. Journal of Vertebrate Paleontology 21, 96A (Abstract).

Schweitzer, M.H., Marshall, C.L., 2001. A molecular model for the evolution of endothermy in the dinosaur-bird lineage. Journal of Experimental Zoology 291, 317–338 (Molecular Development and Evolution).

Seitz, A.L., 1907. Vergleichende Studien uber den mikroskopischen Knochenbau Fossiler und rezenter Reptilien. Nova Acta Leopoldina Abhandlungen der Deutschen Akademie der Naturforscher 37, 230–370.

Sereno, P.C., 1991. Basal archosaurs: phylogenetic relationships and functional implications. Memoir of the Society of Vertebrate Paleontology 2, 1–53.

Sereno, P.C., 1999. The evolution of dinosaurs. Science 284 (5423), 2137–2147.

Sereno, P.C., Arcucci, A.B., 1990. The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 180, 21–52.

Spotila, J.R., 1980. Constraints of body size and environment on the temperature regulation of dinosaurs. In: Thomas, R.D.K., Olson, E.C (Eds.), A Cold Look at the Warm-Blooded Dinosaurs. AAAS Symposium. Westview Press, Boulder, CO, pp. 233–253.

Sumida, S.S., Brochu, C.A., 2000. Phylogenetic context for the origin of feathers. American Zoologist 40, 486–503.

Thomas, R.D.K., Olson, E.C, 1980. A Cold Look at the Warm-Blooded Dinosaurs. AAAS Sel. Symposium 28. Westview Press, Boulder, CO.

Welman, J., 1995. *Euparkeria* and the origin of birds. South African Journal of Science 91, 533–537.

Wilson, J.W., 1994. Histological techniques. In: Leiggi, P., May, P (Eds.), Vertebrate Paleontological Techniques, vol. 1. Cambridge University Press, New York, pp. 205–234.