

LONG BONE HISTOLOGY OF THE HADROSAURID DINOSAUR *MAIASAURA PEBBLESORUM*: GROWTH DYNAMICS AND PHYSIOLOGY BASED ON AN ONTOGENETIC SERIES OF SKELETAL ELEMENTS

JOHN R. HORNER¹, ARMAND DE RICQLÈS² and KEVIN PADIAN³

¹Museum of the Rockies, Montana State University, Bozeman, Montana 59717-0040;

²Équipe Formations Squelettiques, URA CNRS 11 37, Université Paris VII, 75251 Paris cedex 05, France
and Collège de France, Paris, France;

³Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, California 94720-3140

ABSTRACT—Ontogenetic changes in the bone histology of *Maiasaura pebblesorum* are revealed by six relatively distinct but gradational growth stages: early and late nestling, early and late juvenile, sub-adult, and adult. These stages are distinguished not only by relative size but by changes in the histological patterns of bones at each stage. In general, the earliest stages are marked by spongy bone matrix with large vascular canals. Through growth, the cortical bone differentiates into fibro-lamellar tissue that tends to become more regularly layered in the outer cortex. By the sub-adult stage, lines of arrested growth (LAGs) begin to appear regularly. Resorption lines and substantial Haversian substitution in many long bones also begin to appear at this stage, and the external cortex has a lamellar-zonal structure in some bones that indicates imminent cessation of growth.

Judging by the rates of apposition of similar bone tissues in living amniotes, and by the number and placement of LAGs, these patterns suggest that young *Maiasaura* nestlings grew at very high rates, and at high and moderately high rates during later nestling, juvenile, and sub-adult stages, slowing to low and very low growth rates in adults (7–9 m total length). The nesting period would have lasted one to two months, late juvenile size (3.5 meters) would have been reached in one or two years, and adult size in six to eight years, depending on the basis for extrapolating bone growth rates.

The histological tissues, patterns, and inferred growth rates of the bones of *Maiasaura* are completely different from those of living non-avian reptiles, generally similar to those of most other dinosaurs and pterosaurs for which data are available, and much like those of extant birds and mammals. No living reptiles (except birds) grow to adult size at these rates, nor do they show these histological patterns. We conclude that *Maiasaura* did not grow at all like living non-avian reptiles, which cannot be considered informative models for most aspects of dinosaurian growth (or physiology, to the extent that growth rates reflect metabolism). The use of lines of arrested growth (LAGs) to infer dinosaurian physiology has never been tested and is not supported by independent lines of evidence; their use in calculating age is also more complex than previously suggested and should not be based on single bones.

INTRODUCTION

The hard tissue histology of dinosaurs has been studied since the mid-1800s (e.g., Owen, 1840; Quekett, 1855; reviews in Ricqlès, 1980; Reid, 1990; Ricqlès et al., 1991), and after a long period in which few studies were done, experienced a minor renaissance with the work of Enlow and Brown (1956, 1957, 1958) and Enlow (1969). Since the 1960s, comparative histological studies of fossil bone, especially of dinosaurs, were spurred to a large extent by the popular controversy over “hot-” versus “cold-blooded” physiology. This debate was rooted from the beginning in paleohistological data (Ricqlès, 1980). The emphasis (sometimes overemphasis) on relatively tenuous implications of the paleohistological evidence available at the time is understandable, but it may have overshadowed other less debatable and equally interesting aspects of comparative paleohistology (Ricqlès, 1989). Virtually all gross comparative paleohistological data from studies to date have come from opportunistic observations of more or less scrappy bone material over a wide and fairly unconstrained taxonomic range. Nonetheless, these studies have provided useful data and raised important issues. For obvious practical reasons, this “opportunistic” approach has so far been the most readily available. However, it is important to acknowledge that the lack of comprehensive, comparative paleohistological studies places limitations on the potential value of paleophysiological inferences and conclusions that have been based on necessarily limited samples. In order to use bone histology to test some of the

hypotheses that have recently been proposed about growth, physiology, behavior, and ecology in extinct vertebrates, investigators need to study as many parts of the skeleton as practical, through as many growth stages as possible. Such studies can also build on and profit from precise, detailed studies of bone histology in living vertebrates (e.g., Enlow, 1969).

We begin with the generalization that four principal factors determine the type and form of hard tissues that are deposited in the skeletons of vertebrates at any given time. These factors are phylogeny, ontogeny, mechanical, and environmental. There are, of course, other factors (e.g., chance, injury, illness, starvation, and individual differences) that can affect the formation of bone in specific regions of a skeleton at any particular stage of growth, but they are less universal than the four we list here. The support for this generalization, which probably will not appear controversial to those familiar with the evidence, comes from patterns seen in living vertebrates (e.g., Enlow, 1969), and need not be detailed extensively here. By describing the developmental bone histology of skeletons of various taxa, it will eventually be possible to compare histological patterns that are rooted in a phylogeny established on the basis of independent character evidence. This approach can provide the controls that will permit the testing of hypotheses about mechanical and environmental factors that are thought to contribute to histological patterns.

The discovery of an unprecedented abundance of skeletons of the ornithomimid dinosaur *Maiasaura pebblesorum* (Horner and Makela, 1979; Horner, 1983, 1984; Horner and Weisham-

TABLE 1. Dimensions and museum catalog numbers of the specimens examined in this study for each ontogenetic stage. **Abbreviations:** BWT, bone wall thickness; MOR, Museum of the Rockies; YPM-PU, Princeton University collections now curated at the Yale Peabody Museum.

Growth stage	Museum no.	Femur length/BWT	Approx. body length	LAGs
Early Nestling	YPM-PU 22432	7 cm/2.5 mm	45 cm	0
Late Nestling	YPM-PU 22400	12 cm/2–4 mm	90 cm	0
Early Juvenile	YPM-PU-22472	18 cm/3–7 mm	120 cm	0
Late Juvenile	MOR-005JV	50 cm/10–15 mm	3.5 meters	0–1
Subadult	MOR-005SA	68 cm/11–22 mm	4.7 meters	1–5
Adult	MOR-005A	100 cm/13–22 mm	7.0 meters	2–6

pel, 1988; Schmitt et al., 1998) has allowed us to sample size classes of individuals ranging from embryos in eggs to adults that have not clearly stopped growing, even at femur lengths of well over a meter. The aims of our work (e.g., Horner et al., 1997, 1999, in press; Padian et al., 1999; Ricqlès et al., 1997, 1999) are, first, to describe the histological diversity linked to anatomical and ontogenetic factors (Ricqlès, 1976); second, given the known relationship between growth dynamics and histological patterns and processes among living tetrapods, to assess the growth dynamics in this dinosaur; and third, to assess the relevance of such data and interpretations to the problems of dinosaurian metabolic, thermal, and growth physiologies (e.g., Dunham et al., 1989; Ricqlès, 1980, 1992; Reid, 1990, 1997a, b).

MATERIALS AND METHODS

The specimens used in this study were derived from nesting grounds, bonebeds, and isolated skeletons, all from the upper middle part of the Two Medicine Formation (mid-Campanian) of Montana. The histological samples were derived from bones collected by Princeton University and Montana State University field crews over a period that extended from 1978 through 1995. The specimens at stages that we designate adult, subadult, and late juvenile all came from a single catastrophic bone bed in the Willow Creek Anticline of Montana. They were of discrete, non-overlapping size classes, and so can be said to represent age-classes of a single population (Schmitt et al., 1998). The division into age classes is further supported by the presence of a consistent number of lines of arrested growth in bones of a given size class (discussed below), whether or not these are annual lines.

A variety of bones including vertebrae, ribs, limb girdles, and long bones of the limbs were sectioned from six ontogenetic stages, totaling about 200 sections from over 50 different elements. Transverse sections were cut in the diaphyseal regions of all long bones at mid-shaft, and longitudinal sections were cut in the epiphyseal regions (see Appendix 1). Selected sections are illustrated in Figures 2–4. Bone wall thicknesses were not always uniform along a single bone's circumference; average, representative values are given in Table 1. The selected bones were processed according to current techniques, including plastic embedding in polyester resin, sawing with a diamond powder disk on a precision saw, grinding on a lap wheel, and polishing after the desired optical contrast (and not a given thickness) was reached (e.g., Ricqlès and Bolt, 1983; Wilson, 1994).

Fossil bone can record all the structures, either calcified (calcified cartilage) or ossified (bone), that were present as mineralized living tissue. It can also preserve records of the orientation of once-present collagen fibrils, mineralized *in vivo* by tiny crystals of hydroxyapatite; small, usually dark spaces where bone cells were once located (lacunae); and the tiny canals (canaliculi) that linked them to each other, as well as vascular canals that once contained blood vessels (Pawlicki, 1984; Chinsamy and Dodson, 1995). Alterations to the bone, such as

infiltration of sediment solute, often causes color changes in the bone; local invasion by bacteria when the bone was fresh can obscure or destroy original tissue structures; and local diagenetic factors can alter the bone so that its original structures cannot be distinguished. For histological purposes, most fossil bone, however, is relatively unaltered from its original state, other than possibly having been permineralized.

Nomenclature and definitions of structures used in this paper are derived from Francillon-Vieillot et al. (1990). For basic surveys of bone histology, see Ricqlès (1975), Reid (1996, 1997a), and other works cited here.

HISTOLOGICAL DESCRIPTION

General Trends in Histological Changes with Growth

Six growth stages have been recognized for this study, namely small nestlings, large nestlings, early juveniles, late juveniles, sub-adults, and adults (Fig. 1). These stages were recognized on the basis of both relative size of the bones and also on patterns of histological differences that emerged during the course of the study. The first two stages are relatively well marked in the material, both by size and by shapes and proportions. The small nestlings are about 45 cm in total length, and the large nestlings reach about 90 cm. The early juveniles are about 120 cm in total length, the late juveniles around 3.5 meters, the sub-adults nearly 5 meters, and the adults used in this study (but not necessarily fully grown) are about 7 meters in length. The first three stages are represented by non-overlapping size classes. The latter three stages are more arbitrarily delineated from each other, mainly on the basis of overall size. This is because at these latter stages, most bone proportions maintain a constant allometric growth relationship (isometric in the hind limb) to each other as size increases (Dilkes, 1993). It is not known whether the growth (and presumably age) stages would match (possibly yearly) age cohorts, and we have not tried to divide them in that way *a priori*.

Small Nestlings—The bone tissue that forms the shafts of the longer limb bones at this stage (Fig. 2A) is typically much like the embryonic bone tissue observed in advanced fetal stages of large mammals and in hatchling birds. This bone is composed of vascular canals surrounded by an undifferentiated mineralized bone matrix (Francillon-Vieillot et al., 1990). The cortex is relatively thick because the marrow cavity has barely begun to develop or differentiate. The cortical bone tissue is rather spongy, and is composed of a network of bone trabeculae separated by large vascular canals. In cross section, these canals are roughly circular or oval and somewhat flattened parallel to the external surface of the bone; or they are radially elongated, depending on the section and region of the bone cortex. Radially arranged canals can be seen in the bone cortex, especially in a cross-section of the femur that incorporates the fourth trochanter (Fig. 2A). Some of the canals partially merge, giving a more spongy texture to the local tissue. At this stage of ontogeny, there is hardly any centripetal deposition of primary osteonal material at the periphery of the canals.

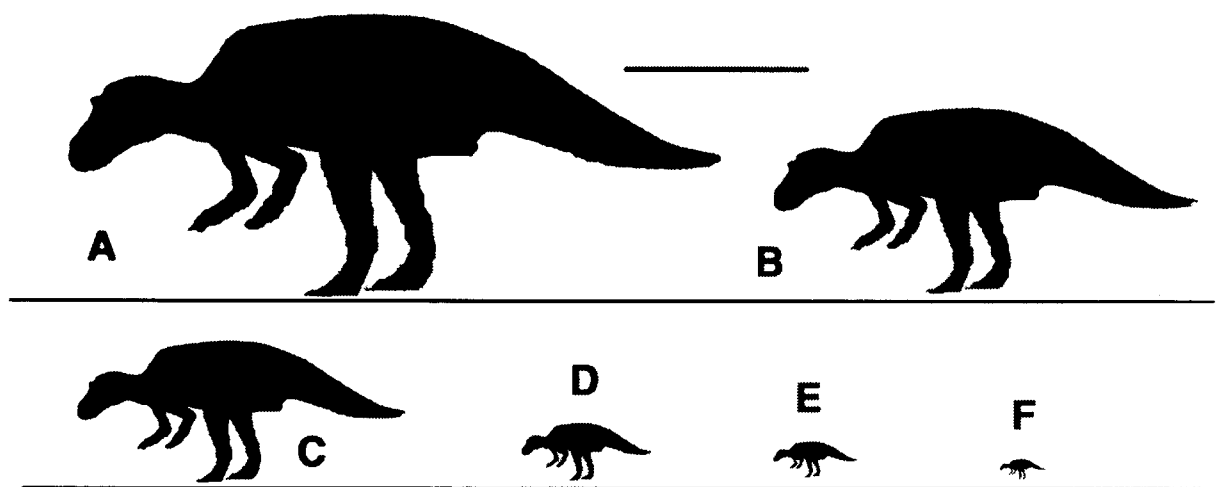


FIGURE 1. Approximate body sizes of six gradational growth stages of *Maiasaura peeblesorum*, based on size and osteohistologic features. A, adult; B, subadult; C, large juvenile; D, small juvenile; E, large nestling; F, small nestling. Scale bar equals 2 meters.

The fine bone trabeculae of periosteal origin are isotropic under crossed nicols, which is characteristic of embryonic bone because its fibrous structure is oriented at random. These trabeculae contain very numerous osteocytic lacunae (Fig. 2B), and form a more or less regular fine meshwork, the shape and structure of which vary from bone to bone and from place to place in a section. Many of the outermost vascular canals open at the surface of this kind of bone, as Bennett (1993) observed in juvenile individuals of the pterosaur *Pteranodon*.

The central marrow cavity, when present, is very small and poorly defined (Fig. 2A), and it has an irregular periphery that shows evidence of clastic activity. In fact, the periphery of the marrow cavity is lined by partially resorbed trabeculae of the inner periosteal bone. In addition, irregular bone trabeculae or bone islands in the marrow cavity itself may contain some calcified cartilage (Reid, 1984:645, 1997a). These are the remains of early endochondral ossification that occurred in the diaphysis after the cartilaginous shaft was initially invaded by clastic cells, which began to form the medullary cavity.

At this stage, no evidence of secondary bone deposition can be observed, and no Sharpey's fibers (which record the orientation of muscle fibers attaching to the bone) are clearly developed, but some characteristic features of bone morphology (e.g., the fourth trochanter of the femur) can already be distinguished.

The epiphyses in *Maiasaura*, as in all fossil animals, differ from those of living animals because although they are cartilaginous, the terminal surfaces are not true articular surfaces. Rather, they represent the interface between the lost uncalcified cartilage and the underlying calcified cartilage (Ricqlès, 1992; Reid, 1996). Hence the "true" epiphysis is almost entirely lost in fossil vertebrates, and our use of the term "epiphyses" for fossil animals reflects this. The epiphyses at this stage (Fig. 2C) are formed by extremely thick pads of calcified cartilage that occupy nearly the entire metaphyseal region, and extend into the diaphyseal region. The calcified cartilage contains numerous transphyseal canals oriented mostly longitudinally in the epiphyses (Figs. 2F, G, 4A) and irregularly in the metaphyses (Horner et al., in press).

The thin periosteal cortex lines the metaphyseal regions externally as far distally as the *encoche d'ossification*, the "notch" or "slot" that forms the boundary between the cortex and the epiphysis (Fig. 2D). It contains up to six or seven elongated vascular clefts, depending on the region. These are lon-

gitudinally and obliquely oriented, and they match in structure those observed on cross sections of diaphyses. No Sharpey's fibers were observed in these regions, and no endosteal compaction of the periosteal cortex apparently took place in the metaphyses at this stage of development.

Large Nestlings—This ontogenic stage is very distinct histologically from the preceding one. In cross section, the shafts of the long bones (and similar parts from the girdles and dermal bones) generally have a cortex that is well differentiated from the marrow cavity (Fig. 2E). The cortex is typically formed of primary (periosteal) bone tissue, very densely vascularized and loosely woven. The bone tissue corresponds to the general fibro-lamellar pattern seen in young birds and mammals (Ricqlès, 1980; Castanet et al., 1996), as well as in other dinosaurs and pterosaurs (e.g., Varricchio, 1993; Ricqlès et al., in press). At this stage, we begin to see an organization of finely fibered lamellar bone deposited centripetally that becomes the primary osteons.

The amount of deposition of osteonal bone (and hence the diameter of vascular canals) varies locally, as does the precise pattern of bone vascularization (Fig. 4B). Depending on the bone and on its position in the section, one can observe laminar, plexiform, or longitudinal parallel osteonal patterns in the dermal and endoskeletal bones. The outermost vascular canals are often larger in the subperiosteal space, and they retain a large diameter because osteonal deposition has only started to take place in this newly deposited bone tissue. New woven bone trabeculae of periosteal origin can form short spikes spreading outward.

The periphery of the marrow cavity is highly resorptive, often with an irregular shape. The innermost periosteal cortex is actively eroded to make room for the outwardly expanding medullary cavity. Endosteal bone trabeculae differentiate to form a moderately developed perimedullary spongiosa in some cases (Fig. 4C). A very modest amount of erosion-reconstruction has taken place in some bone elements in this region in large nestlings.

The characteristic shapes, differential growth rates, and local anatomical specializations of various bones are already clear at this stage of ontogeny (see next section). Numerous Sharpey's fibers are differentiated in regions of dense tendinous or ligamentous insertion. Local apophyses and trochanters show specific orientations and densities of the vascular network of their primary bone tissues.

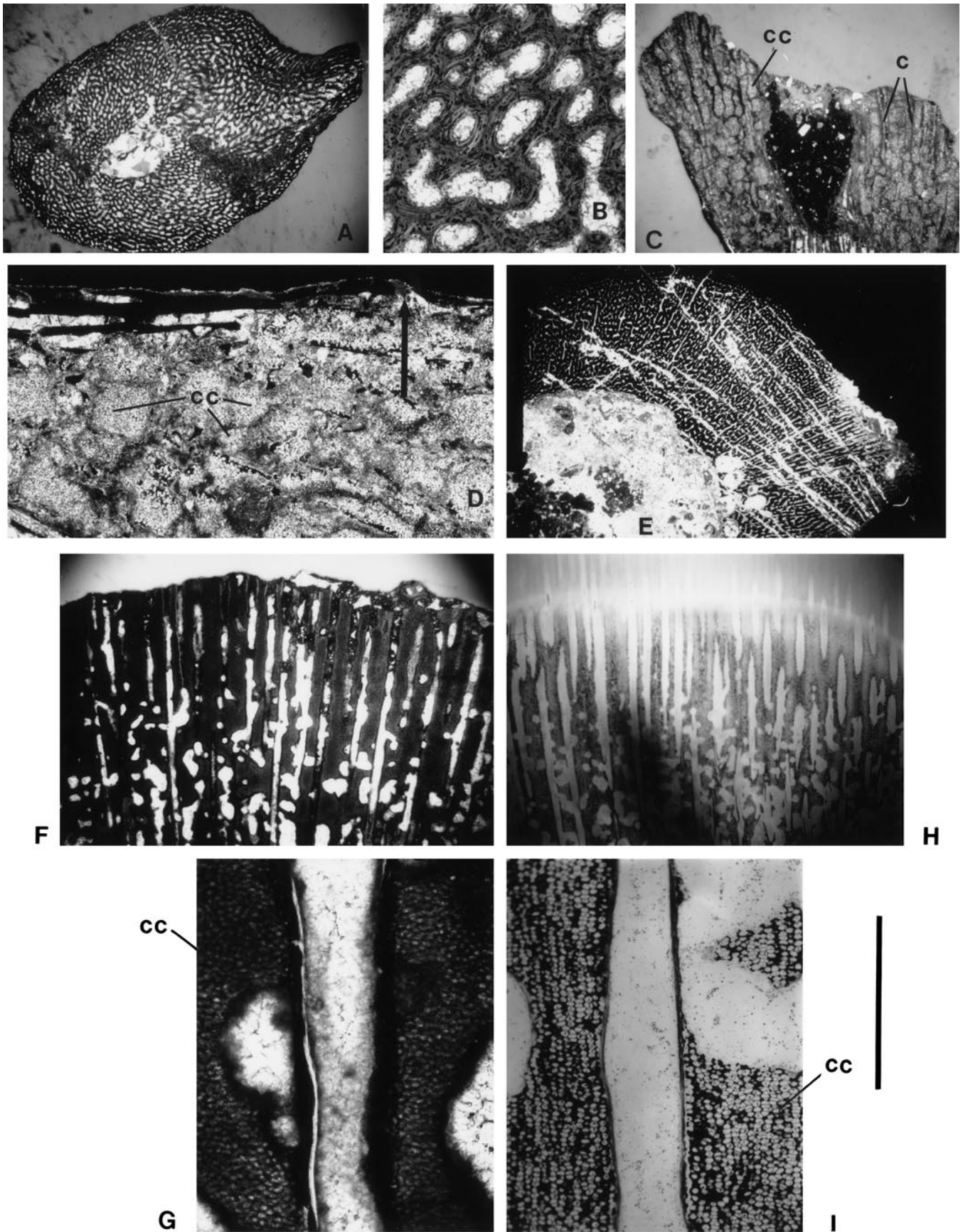


FIGURE 2. A–G, *Maiasaura peeblesorum*. A, cross-section through the femoral shaft of an early nestling, at the fourth trochanter, showing the small medullary space and the large vascular spaces in the spongy matrix; B, same section as previous, showing osteocyte lacunae (probably enlarged by bacterial erosion); C, longitudinal section in the lateromedial plane of the distal femur of an early nestling. Both distal condyles

Epiphyseal structures (Fig. 2F) are generally formed at this stage by thick pads of calcified cartilage that extend well into the metaphyses (Barreto et al., 1993). However, these extensions already vary considerably from one element to another. Transphyseal canals are still present at this ontogenetic stage. At some distance below the epiphyseal surface, the transphyseal canals meet the marrow tubes growing toward the epiphyses and these become more or less indistinguishable and confluent (Fig. 2F); along the wall of the marrow tubes, bone is deposited on the surface of the calcified cartilage (Fig. 2G), which becomes involved in the process of endochondral ossification. Its surface becomes coated by a thin film of endochondrally deposited, "primary" endosteal bone. Massive amounts of calcified cartilage are observed down into the metaphyses. Endochondral ossification produces a complex meshwork of bony trabeculae oriented longitudinally in the metaphyses, linked by short transverse trabeculae of endosteal bone. This cancellous tissue still contains large islands of hypertrophied calcified cartilage (Fig. 2F), even into the diaphyseal region, but the trabeculae are extensively remodeled by clastic erosion and secondary endosteal deposition. The inner tissues of the metaphyseal shafts, shown here in the proximal end of the tibia (Figs. 2F, G), are formed by thin endosteal coatings of bone laid down around the marrow tubes, which also seem to function as elongated 'erosion cavities' because cartilage erosion and endochondral ossification take place at their periphery. Figures 2F and 2G compare the metaphyseal structures of the proximal tibia of the large maiasaur nestlings to similar structures in the proximal tibia of a 7-day-old ostrich (Figs. 2H, I).

Juveniles—In our sample, "juveniles" are already animals of considerable size, judging by the standards of today's fauna. Nevertheless, bone histology shows that these individuals are still in an immature stage of development that is dominated by intensive growth. In early juveniles (Fig. 4D), the primary osteons are very well formed and much more distinct than at younger stages, and the centripetal lamellar deposits in the osteons are composed of a mature and well organized fine lamellar matrix. In contrast to later juveniles, there are no indications of secondary osteons near the endosteal surface.

In the long bone shafts of later juveniles, most of the cortex is primary and is formed of dense, thick (5 to 15 mm) deposits of regularly organized fibro-lamellar tissues (Fig. 3A). The primary osteons are organized as (often) parallel-longitudinal, laminar, plexiform, or (less often) reticular, or even (more rarely) radiating patterns, depending on the region of the bone and on its position in the skeleton. The outermost clefts of vascular canals are generally larger in diameter. Many canals are open subperiosteally, especially if they are oriented radially or obliquely. Systems of Sharpey's fibers are well developed locally in the external cortex.

Lines of discontinuity, such as "rest lines" or "growth lines," in the primary bone tissue are inconspicuous at this growth stage; in fact, we could locate only one true line of arrested growth (LAG) and then in only two specimens, a femur

and a fibula. In dense fibro-lamellar bone tissues, faint patterns in the superposition of the laminae are routinely present (Fig. 3A). These patterns can be traced to small differences in the mean diameters of primary osteons, vascular canals, overall color of bone, overall porosity, and other factors that run circumferentially in the cross sections of the shaft. For example, a group of laminae can have a denser appearance or generally larger vascular canals than the preceding (more internal) or succeeding (more external) ones. These patterns are difficult to observe, especially through the compound microscope, because their microanatomical details tend to disappear at high magnifications.

The marrow cavity is well developed. In most bones, bony trabeculae are present in the shafts, and the marrow cavity is subdivided by many reconstructed endosteal trabeculae that form a spongiosa. The endosteal margin is well developed, with large irregular bays of erosion that expand outward in the deep primary cortex and endosteal bone tissue that is deposited locally in the perimedullary cavities.

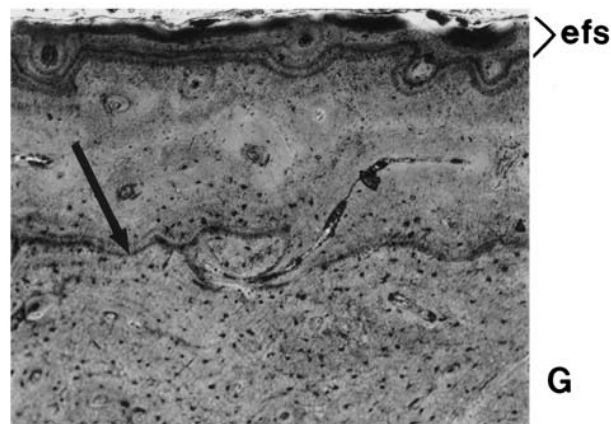
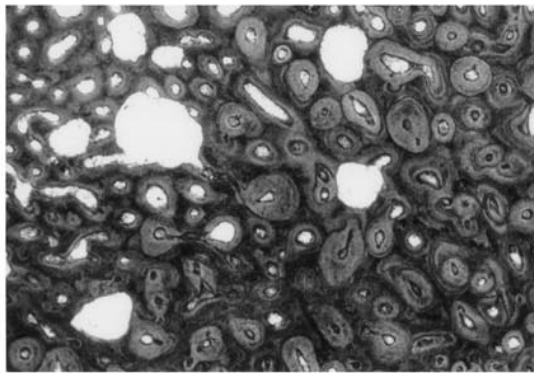
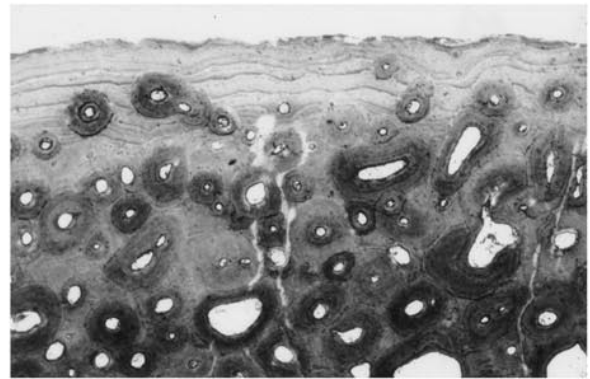
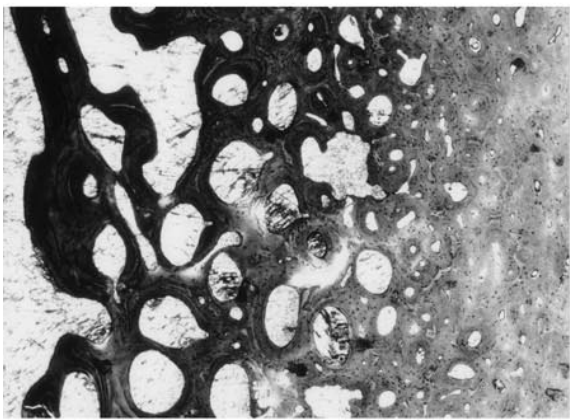
In most juvenile limb bones, typical Haversian reconstruction is already developed, but is somewhat scattered and limited to the deep cortex (Fig. 3B). However, Haversian tissue spreads in some local areas up to the external cortex, where it forms well-marked regions with extensive resorption and reconstruction by Haversian tissue, as in the metatarsals. These are frequently found at points of stress (e.g., the lateroventral corners of the metatarsals; Fig. 3C). Flat bones and long bones with a smaller overall radial growth (e.g., ribs, ischium, ulna) receive much more extensive Haversian substitution at this stage than do the longest bones of the skeleton (e.g., femur, tibia). No "external fundamental system" (e.g., Cormack, 1987) of subperiosteal lamellar bone is deposited, however (Fig. 3A), so despite the extensive Haversian reworking, the bone has not yet stopped or substantially slowed its growth.

Some epiphyses at this stage of development are still quite actively involved in longitudinal growth, according to their histological structure. Thick pads of calcified cartilage with longitudinally oriented cell spaces are crossed by longitudinally and transversely oriented shafts of endochondral bone throughout the metaphyseal regions (Fig. 3D). At the periphery of the metaphyses, the spongiosa (of endochondral origin) is endosteally compacted and it lines the periosteally deposited bone internally.

Sub-adults—These are already large animals with diaphyseal cross sections comparable in size to those of mature cows and horses. Dense cortical bone tissue can reach a thickness of over 20 mm (e.g., 5 mm for the neural spine; 10 mm for the rib; 15 mm, humerus; 12 mm, ulna; 9 mm, ischium; 22 mm, femur; 25 mm, tibia; 13 mm, fibula). In most long bone shafts, the dense cortex is still formed at this stage by a massive deposition of primary fibro-lamellar tissues (Fig. 3E). The vascular pattern varies according to its local position within a given section and from bone to bone, but a laminar to sub-plexiform organization of the fibro-lamellar tissue now clearly predomi-

←

surround an intercondylar space filled with matrix. The condyles mainly comprise calcified cartilage (cc) interrupted by dark longitudinal epiphyseal vessels or transphyseal canals (c) that together form thick pads of calcified cartilage. A section through the thin periosteal bone is visible at the bottom edge of the photo; **D**, distal end of femur, showing cleft that distinguishes the *encoche d'ossification* (*enc*). Two or three layers of primary trabecular bone of periosteal origin surround massive amounts of longitudinally oriented, hypertrophied calcified cartilage (cc); **E**, cross-section of the femur of a large nestling, taken at the base of the fourth trochanter, viewed under crossed nicols, showing well developed marrow cavity and the plexiform pattern of vascular canals; **F**, longitudinal section of the proximal tibia of a large nestling. Long marrow tubes apparently meet and subsume the transphyseal canals in this region. Between the marrow tubes are long columns of calcified cartilage on which the bone is being deposited by the marrow tubes deep in the metaphyses; **G**, detail of previous figure, showing marrow tube (center) depositing bone (long white line) on the surface of the surrounding calcified cartilage (note localized erosion of cartilage) **H**, **I** *Struthio camelus*, the ostrich. **H**, proximal tibia of the ostrich, viewed as in Figure 2F; **I**, detail of previous figure, viewed as in Figure 2G. Scale bar represents 5 mm for **A**, **C**, **E**, **F**, and **H**, and 500 μ (0.5 mm) for **B**, **D**, **G**, and **I**.



nates. The deep cortex is sometimes replaced by dense Haversian tissue. The marrow cavity is generally not free but contains an extensive system of secondarily endosteal bony trabeculae. The trabeculae vary in thickness and organization from long and thin to thick and short, and they often include irregular secondary osteons. All transitional stages are present, from a more or less dense spongiosa with thin trabeculae that encircle large, irregular marrow spaces to a denser spongiosa in which the trabeculae progressively attain the structure of very large secondary endosteal osteons, as previously described in saurpods (Rimblot-Baly et al., 1995). Some epiphyses are still involved in active longitudinal growth (Fig. 4G); the epiphyses are composed of hypertrophied calcified cartilage that is still spread through the metaphysis as elongated columns along which endochondral ossification proceeds, resulting in longitudinally oriented bone spongiosa. In sub-adult *Maiasaura*, it is difficult to ascertain the real size of the medullary sinuses in the marrow spaces because the cancellous bone structure is frequently crushed or collapsed. Surprisingly, this cancellous crushing is often seen in bones that otherwise seem to have suffered little crushing or deformation.

The endosteal margin is well developed at the periphery of the medullary region and can be quite extensive. Erosion cavities are more or less circular in cross section and they spread from the endosteal margin into the deep half of the cortex. This spread is evidently linked to the eventual development of Haversian tissue.

At the sub-adult stage of development, lines of arrested growth (LAGs) divide the fibro-lamellar cortex into a few thick superimposed strata of primary bone (Fig. 3E). For example, four to five LAGs can be observed in the humerus, two in the ulna, three in the ischium, one or two in the femur, two in the tibia, one in the fibula, and two in the metatarsal. These lines match the usual description of LAGs known in extant vertebrates and used for skeletochronological purposes (Peabody, 1961; Francillon-Vieillot et al., 1990; Reid, 1990; Castanet et al., 1993; Chinsamy, 1993a; Varricchio, 1993). They are extremely narrow, and are darker than the neighboring bone tissue. They undulate around the neighboring primary osteons and are roughly parallel to each other and to the cortex surface. They are often (but not always) spaced rather consistently: i.e., they are closer to each other toward the external surface of the cortex.

Some structures almost identical to LAGs, especially at low magnification, appear to be something quite different. Rather than “rest lines,” they would appear to be resorption lines, because the subjacent bone has previously experienced a phase of superficial (not periosteal) resorption (Enlow, 1963). This is demonstrated by the unconformity of the layered bone structure at these lines and by the highly scalloped surface of the lines that indicate osteoclastic erosion. Some bones at this growth stage are transformed into a mass of dense Haversian tissue; at

least three superimposed generations of secondary osteons may be developed in places.

The most external cortex has a lamellar-zonal structure, especially in smaller, highly reconstructed bones (Fig. 3G). In these thin external regions of the cortex, the bone tissue contains few or no primary osteons, and these are longitudinally oriented, embedded in a grossly lamellated periosteal tissue. When present, often in neighboring regions of the same bone, the primary osteons have small diameters and tend to form circular rows, alternating with non-vascular annuli (see Peabody, 1961). Sharpey’s fibers are locally numerous. Overall, this thin coating of bone, mostly formed of parallel-fibered periosteal tissue organized longitudinally, constitutes the beginnings of the “external fundamental system” at the surface of some bones at this stage. This system has been classically described among mammals as marking the development of the adult skeleton (e.g., Cormack, 1987), and has been observed in a variety of other dinosaurs (Chinsamy, 1990; Reid, 1984, 1993; Varricchio, 1993).

Adults—The large bones of adults have diaphyses in which the dense cortex reaches a thickness of 20 mm in the tibia, 13–22 mm in the femur, humerus, and metatarsal, 10 mm in the ribs and neural spines, and 7 mm in the ischium. These values are not significantly higher than in sub-adults, even though the adult bones are larger overall, including in diameter. This is because the medullary cavities expand at the adult stage, especially the perimedullary cavities at the endosteal margin. This margin becomes quite extensive and spreads diffusely into the deep cortex. As a result, the distinction between the compact cortex and the cancellous medullary cavity is not clear-cut.

In the largest long bones (femur, tibia, metatarsal, humerus), the dense external cortex is still basically formed of primary fibro-lamellar tissues (Fig. 4E). The tissue pattern is typically laminar, and several regions have a very regular series of laminations. An “external fundamental system,” already developed among sub-adults (Fig. 3H), tends to differentiate at the external surface in some regions of most bones (femur, metatarsal, humerus) but not in others (tibia). Lines of arrested growth (LAGs) are again observed in cross sections of the diaphyses: three in the humerus, up to five in the femur, four in the tibia (Fig. 4E), six in the metatarsal, two to five in the ischium, and at least four in the ribs (these numbers are minimal counts, and they are complicated by a series of such lines that often appear in the external fundamental system).

In smaller bones (rib, ischium, neural spine), which generally grow more slowly than the long bones, almost all the cortex is converted into dense Haversian tissue. Only a very thin sheet of primary bone is formed at the periphery by either a poorly developed laminar tissue or by a lamellar-zonal subperiosteal bone tissue. The internal (deep) cortex of the femur is extensively reconstructed, and dense Haversian bone is spread locally through almost the entire thickness of this bone. In the humerus,

←
FIGURE 3. *Maiasaura peeblesorum*. **A**, cross-section of the tibia of a late juvenile in the mid-shaft, showing the external cortex. Note the more open exterior vascular canals, and faint changes in bone color denoting irregularities in the otherwise regular laminar deposition; **B**, same cross section at higher magnification, taken through the deep cortex; the endosteal margin is at left. Note the large erosion cavities and endosteal trabeculae. Secondary osteons have invaded the deep cortex to the right; **C**, cross-section of the metatarsal of a late juvenile. Note the scattered Haversian tissue with extensive erosion cavities; **D**, longitudinal section of the proximal end of the fibula of a late juvenile. The epiphysis comprises thick rows of calcified cartilage perforated by marrow spaces associated with endochondral ossifications; **E**, external surface of the femur of a sub-adult, showing fibro-lamellar primary cortex interrupted by a LAG; **F**, sub-adult rib in cross-section, exterior surface of the cortex, showing LAGs packed at the surface, and Haversian systems in the inner cortex; **G**, external surface of the ulna in a sub-adult shows the beginnings of the “external fundamental system” (efs) characterized by a lamellar-zonal matrix with few primary osteons and relatively few osteocytes; **H**, the “external fundamental system” (efs) in the metatarsal of an adult; note LAGs in the external cortex, in which a few longitudinal vascular canals are scattered, and the outermost compact, nearly avascular bone. Scale bar represents 5 mm for **A**, **D**, and **E**, 800 μ for **B**, **C**, and **F**, and 500 μ for **G** and **H**.

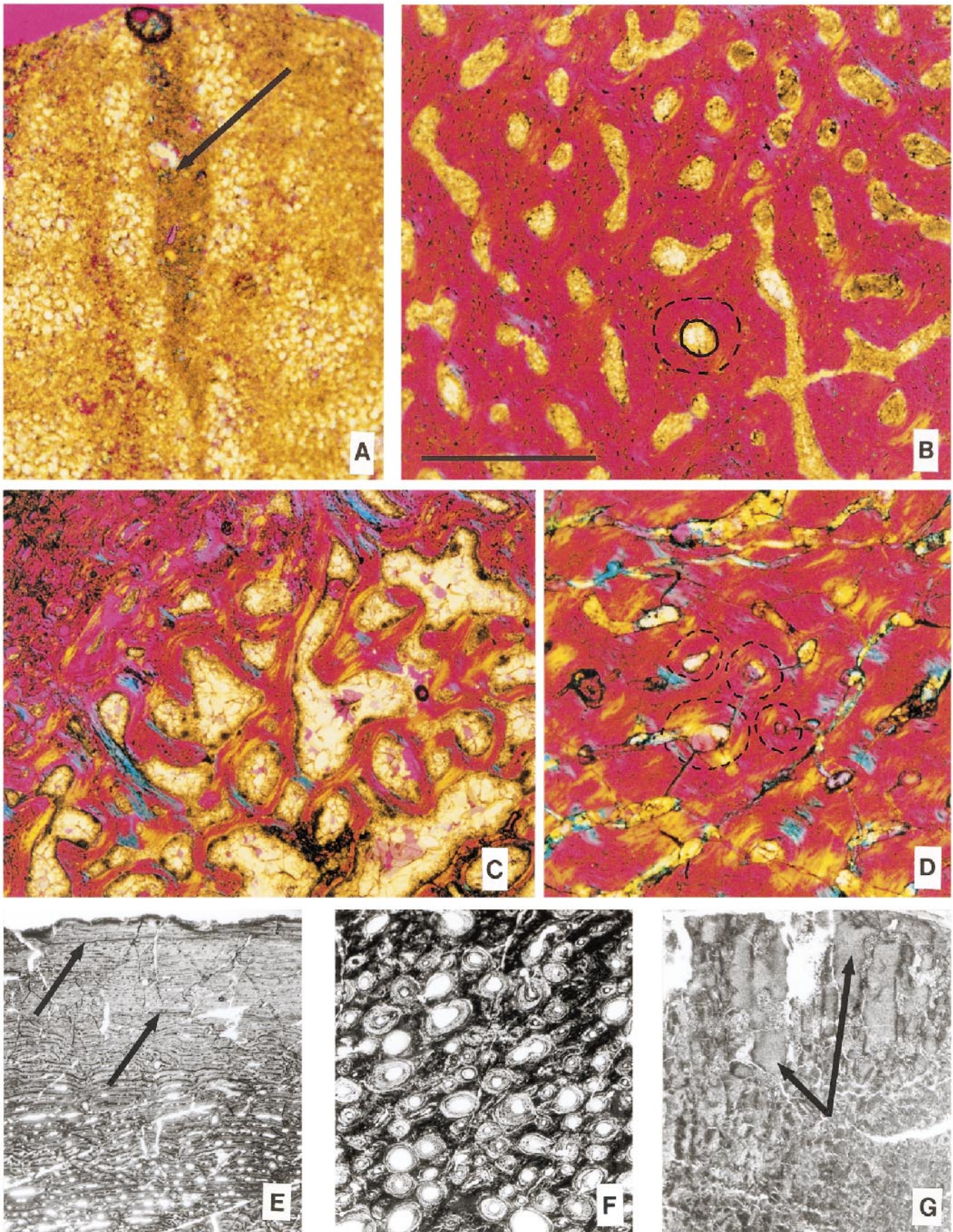


FIGURE 4. *Maiasaura peeblesorum*. **A**, detail of Figure 2C, showing transphyseal canals (center) in a matrix of hypertrophied calcified cartilage; **B**, detail of Figure 2E, emphasizing the numerous primary osteons with lamellar bone deposited centripetally within them. A single osteon is outlined in dashes, and its vascular canal in a solid circle; **C**, cross-section of the tibia of a larger nestling, taken at the distal diaphysis.

Haversian substitution is also dense in the internal cortex but it is spread rather diffusely and uniformly in most regions of the external cortex, rather than intensively in limited regions of the external cortex as in the femur. In the tibia, Haversian substitution is less extensive but it is spread locally throughout, as in the femur. In the metatarsal (Fig. 3H), Haversian substitution is spread extensively up to the external cortex, as in the humerus, but substitution is generally denser and less scattered (Fig. 4F). In all these bones, and in each region within each bone, the amount as well as the spread of Haversian substitution varies. It starts as a first generation of secondary osteons scattered over the primary tissues (in the external cortex), and ranges to dense Haversian bone with several superposed generations of secondary osteons (in the deep cortex). These differences also appear to be specific to individual bones and to regions within each bone. In the smaller bones (ischium, ribs, neural spines), three to four generations of secondary osteons are superimposed locally.

Cancellous tissues are not much different between adults and sub-adults, but they are generally more developed among adults. The cancellous spongiosa has the usual structure of highly reconstructed irregular endosteal trabeculae, lining medullary spaces of various shapes. In transverse sections, the dimensions of marrow sinuses can reach 3–4 mm by 1–3 mm or more, but they are much longer in longitudinal sections. Erosion cavities in the endosteal margin are sub-circular in cross section, from 300 μm to 1,000 μm in diameter. Some surfaces of the erosion cavities have no bone deposited on them, presumably because clastic cells were still destroying bone centrifugally (Fig. 4F). Other cavities, or regions of a given cavity, have a coating of secondary, finely fibered endosteal bone. These systems progressively turn into more typical secondary osteons in the deep cortex. Some erosion cavities located more externally can remain very large (>400 μm in diameter) and can maintain connections with the neighboring system of vascular canals in the primary laminar tissue. These large cavities also receive secondary centripetal bone deposition.

Summary of Histological Changes During Ontogeny

The two youngest stages of *Maiasaura*, which we identify as nestlings, have periosteal and endochondral structures that indicate extremely rapid growth. In growth stages ranging from 45 to 90 cm in body length, cortical bone in *Maiasaura* is composed of highly vascularized, fibrolamellar tissue with a plexiform pattern. In contrast to previous descriptions (Horner and Weishampel, 1988; Geist and Jones, 1996), the epiphyseal-metaphyseal complex at the long bone ends is composed almost entirely of hypertrophied calcified cartilage with intertwined transphyseal canals, but with only sparse bone tissue (Fig. 2C; not composed mostly of bone, *pace* Geist and Jones, 1996). These same tissue patterns, usually associated mainly with fast-growing young individuals, are also well expressed in the juveniles and sub-adults (Fig. 3D), although in a somewhat more mature form. They are even developed in the major bones of adults (Fig. 4G), which suggests that even young adults may have continued to grow at high rates. Some bones of the skeleton show more or less early shifts toward lower growth rates,

or even almost cessation of growth, compared to other bones. In the adult skeleton, such elements are invariably smaller than the faster and/or longer growing “major bones.” Hence, allometric differences in growth, as well as “allochronic” changes in growth events between bones, seem to be faithfully recorded by bone histology (Varricchio, 1993; Castanet et al., 1996).

Haversian substitution begins in the deep cortex early in ontogeny, at the early juvenile stage. It progressively becomes more important (Fig. 3C), especially in smaller bones (such as the metatarsals), in bones that do not grow so quickly (such as the ribs: Fig. 3F), and in regions of larger bones that are subjected to local biomechanical demands (Reid, 1984). Haversian substitution becomes more general in all compact bones as individuals age. The secondary bone tissues that form the cancellous spongiosa in the marrow cavity and the endosteal margin around it (Fig. 4F) grow just like dense Haversian bone does, starting at least by the early juvenile stage. The “external fundamental system” (Fig. 3H) also develops earlier in smaller bones, or locally in larger bones, perhaps in accordance with particular biomechanical demands. However, it is still poorly developed at the surface of some major bones in adults.

The epiphyseal structures are actively involved in longitudinal growth up to the adult stages (Fig. 4G). These epiphyseal features include (1) large pads of calcified cartilage with longitudinally oriented, hypertrophied cell lacunae and (2) interspersed, longitudinally oriented (rather than areolar) erosion cavities. Their functions in growth appear to vary considerably from one epiphysis to another, though no complete record of such differences has been gathered for the present study.

In summary, the ontogenetic changes in the primary compact bone clearly show that there were significant ontogenetic changes in growth rates in *Maiasaura*. From very high initial growth rates (nestlings), growth proceeded at high and moderately high growth rates (early and late juveniles) toward moderately high (subadults) and finally low to very low growth rates (among adults).

DISCUSSION

Growth Rates and Individual Age

Two independent lines of evidence from bone histology can help to quantify how growth rates change during the ontogeny of *Maiasaura*, and to reciprocally test inferences about correlated factors such as individual age at various growth stages.

One line of evidence is growth rates that have been experimentally determined for various bone tissue types in living animals, comparing bones of known diameter and similar histology. This approach assumes the actualistic hypothesis that similar bone tissue types among extant and extinct vertebrates form under similar conditions, and therefore at similar growth rates (e.g., Ricqlès, 1980). Unfortunately, reliable experimental values linking growth rates to specific bone tissue types among living animals are still scarce (Ricqlès et al., 1991; Castanet et al., 1996). Buffrénil and Pascal (1984) obtained growth rates for the mink (*Mustela vison*), but these applied to the mandible, which is completely reworked after the fourth month, so their comparative utility for dinosaur bones is probably limited.

←

Reconstructed endosteal trabeculae of the internal cortex replaces a denser outer cortex of fibrolamellar bone (top left); **D**, cross-section of the femur of an early juvenile, near the fourth trochanter, under crossed nicols. Well-formed mature primary osteons (dashed lines) surrounded by a woven periosteal matrix can be seen in the central region of the cortex; **E**, cross-section of the external cortex in an adult tibia, showing the laminar (fibrolamellar) tissue interrupted by LAGs (arrows); **F**, cross-section of the endosteal margin in an adult metatarsal, showing numerous large secondary endosteal osteons, and erosion cavities invading the deep primary cortex; **G**, longitudinal section of a sub-adult tibia showing large rows of calcified cartilage with longitudinally oriented, hypertrophied cell lacunae and interspersed, longitudinally oriented erosion cavities and endochondral ossifications. Scale bar represents 5 mm for **E** and **G**, 800 μm for **C** and **F**, and 500 μm for **A**, **B**, and **D**.

Moreover, it could be argued that values obtained from a small mammal would considerably underestimate the growth rate values to be used for dinosaurs, and that values derived from (e.g.) ratite birds would be more realistic, both for morphologic and phylogenetic reasons. (We address this point in the next section.)

The second line of evidence is to count lines of arrested growth (LAGs) in periosteal bone to assess age (and growth rates), under the working hypothesis that LAGs in dinosaurs have the same chronometric significance as they do in many extant chondrichthyans, actinopterygians, amphibians, reptiles, and mammals (see e.g., Peabody, 1961; Smirina, 1972; Castanet et al., 1993). However, because LAGs in *Maiasaura*, as in some other dinosaurs, are developed in fibro-lamellar tissues, they may not be entirely comparable to the LAGs known to be annual in the bone tissues of many living ectotherms (see also discussions in Ricqlès, 1980, 1983; Reid, 1990, 1996:34; Chinsamy, 1994). On the other hand, they are indistinguishable from the growth lines recorded in the long bones of the non-hibernating, non-hibernating, large endothermic mammal, the elk *Cervus* (Horner et al., 1999). LAGs with distinct annuli are found in some dinosaurs (e.g., Reid 1984), and also in the polar bear (Chinsamy et al., 1998).

Counting LAGs in *Maiasaura* bones, as in those of other dinosaurs, is practically difficult for several reasons. (1) Some LAGs actually turn out to be erosion lines. These are linked to local morphogenetic changes in growth regime caused by modeling and remodeling dynamics of the entire bones (see e.g., Enlow, 1963; Ricqlès, 1980). (2) Some LAGs may have been eroded away by perimedullary erosion of the deep cortex and by Haversian substitution within the cortex. These missing data have been extrapolated by "retrocalculations" that reconstruct the probable number of eroded LAGs (e.g., Chinsamy, 1990; Castanet et al., 1993, for review), taking into account the diameters and numbers of LAGs that have been counted in younger bones. (3) Counting LAGs in the diaphyses does not always guarantee that the actual number can be observed (or retrocalculated). Theoretically, the total record of diametral growth can only be accurately recorded in a cross section that includes the "neutral point" of the diaphysis (i.e., the cross section that retains a constant topological and morphogenetic position relative to the two oppositely growing epiphyses (see e.g., Lacroix, 1971). Recording the exact "neutral cross section" for each bone diaphysis was a task beyond the practical possibilities of the present study. Nevertheless, we draw attention to the potential danger incurred by relying on whatever section of fossil bone may be available to assess individual age by counting LAGs.

In our discussion of juvenile tissues, we noted the presence of faint patterns in the superposition of laminae in fibro-lamellar tissue. Their significance is not obvious, but they appear similar to those described by Ricqlès (1983:pl. 9) and Rimblot-Baly et al. (1995) as signs of growth cycles, and they appear to represent some degree of bone growth change or fluctuation. The process of deposition of discrete laminae is prone to produce faint irregularities in deposition that need not have a cyclical (i.e., regularly recurring) significance. These patterns can be caused by small local changes in the rate of bone deposition that recur for morphogenetic or biomechanical reasons; they do not necessarily imply a complete change in the actual tissue type deposited, nor an arrest of growth (of which there is no evidence here). More research is necessary to understand such modulations in extant and fossil bone tissues, but they should not be confused with (annual) growth lines or other lines of arrested growth.

The preceding points show that an uncorrected enumeration of LAGs in random cross sections of long bones can produce overestimates (e.g., counting reversal lines as LAGs), and more

probably underestimates (because of perimedullary resorption, etc.). For example, Chinsamy (1990) counted growth lines in a series of *Massospondylus* femora and correlated these lines among bones based on the relative positions of lines in the bones of comparable or successive thicknesses. Her results are certainly reasonable, though as she recognized, individuals may vary in the thicknesses of their bones at various ages. We have noticed that bones of the same thickness do not always have the same number of LAGs, and also that lines of resorption may make it difficult to correlate LAGs and to know exactly how much tissue was resorbed at each line. It is also not possible to know a priori how much time of arrested growth is represented by a given LAG.

Results from Experimentally Obtained Growth Rates—

Table 1 lists the values of bone growth (based on bone wall thickness, BWT) observed in various bone diaphyses of *Maiasaura* through ontogeny. If we assume a mean value of 15 μm per day for the radial deposition of laminar bone tissue of the fibro-lamellar complex (a conservative assumption: see Buffrénil and Pascal, 1984, Ricqlès et al., 1991; Castanet et al., 1996), this yields an estimated deposition of about 5.5 mm of new laminar bone per year. This value is consistent with the actual thickness of laminar tissue deposited between two consecutive LAGs in the external cortex of sub-adult and adult *Maiasaura* (see Table 1 for growth ranges). The thickest primary cortical deposits appear to be laid down in the diaphysis of the tibia in adult *Maiasaura* (25 mm). At the constant rate used above, it would thus have taken roughly 4.6 years for the deposition of this external cortex, which accounts for approximately two-thirds of the local bone radius. The inner third of the bone wall, now eroded, was deposited during early ontogeny, and it would have been laid down at a somewhat higher rate characteristic of juvenile and younger animals. This rate could have been even three to four times higher, depending on the bone, judging from rates of growth in the legs of birds (Latimer, 1927:36; Church and Johnson, 1961; Castanet et al., 1996). But even if the inner cortex had been deposited at the same rate as the outer cortex, we could estimate that it would have taken no more than 2.3 years to complete, and so the whole bone suggests that the adult stage could have been reached in seven years.

The age of nestlings can be estimated in another way. The diameters of the major bones (humerus, femur, tibia) are respectively 5, 10, and 8 mm at hatching (45 cm body length) and respectively 8, 15, and 13 mm for large nestlings (90 cm body length), reaching 19, 37, and 38 mm for late juveniles (3.5 m body length). This implies a diametral increase of 3–5 mm between the first two stages, and 11–25 mm between the second two stages. Dividing these diametral values in half to obtain radial growth increases, and assuming a conservative growth rate of 30 μm per day (cf. trabecular bone tissue values in Buffrénil and Pascal, 1984) for radial growth between hatching and the large nestling stage, the nestlings could reach maximum size in anywhere from 50 to 83 days (roughly 2.8 months at most). Similarly, assuming a constant (mean) growth rate of 17 μm per day (intermediate between those of "typical" fibro-lamellar tissues and primary trabecular tissues, according to Buffrénil and Pascal, 1984), this would allow between 1.1 and 2.4 years from hatching to reach what we call late juvenile size. If we add the higher of these two latter figures to the 4.6 years previously estimated to account for growth to the sub-adult and adult stages, the age to adult size is closer to seven years. (Note that we are using intermediate growth rates and taking the higher numbers from each calculated range of depositional duration, so we are erring conservatively.)

These results suggest that the one-year-old age cohort (intermediate between nestlings and specimens defined as late juveniles) is missing in our sample. (The early juvenile stage, re-

corded from a single femur, lacks LAGs and so either it died before reaching its first birthday, or a LAG was not recorded in the first year; see below.) An alternative model would hypothesize that the one-year cohort is not missing, and that the late juveniles are yearlings. This is consistent with the observation that no growth rings appear until the sub-adult stage, where there are already two, suggesting that these animals are in the two-year cohort (though they could be older if no LAG was recorded in the first year). The increase in bone diameter between these two morphological stages is 14, 27, and 30 mm respectively for the humerus, femur, and tibia, so the faster-growing bones would deposit 14–15 mm of radial bone thickness in a year (a quotient of as much as 40 μm daily). This rate is high compared to average growth rates in the seven-week-old mallard (<4 μm daily in the tibiotarsus, 7.5 in the femur, >16 in the coracoid, and 24 in the humerus (Castanet et al., 1996), although the earlier daily growth of the humerus approached 40 μm . But growth in the mallard may not be comparable to that of large dinosaurs for several reasons. As Castanet et al. (1996) point out, its histogenesis generally proceeds from laminar and subplexiform to plexiform and reticular, before finally becoming avascular (rather than the classic reticular to plexiform to laminar sequence seen in other amniotes; Ricqlès et al., 1991). More importantly, its degree of vascularization, including the size, frequency, and orientation of osteons, is only a fraction of what is seen in *Maiasaura* at comparable ontogenetic stages, and degree of vascularization is a better indicator of growth rate than particular variations in tissue type within the fibro-lamellar complex (Chinsamy, 1993b).

From these considerations, according to this alternative model, it can be hypothesized that *Maiasaura* yearlings (late juveniles) reached 3.5 meters in length, as bone wall thickness of the long bones increased at a rate of about 40 μm daily. From this stage, if growth slowed to (an average of) 15 μm daily, the diameter of the tibia expanded from 38 mm (late juvenile stage) to 110 mm (adult stage) in 4 years and 9 months, yielding an estimate of about six years to reach the beginning of what we regard as an adult stage (body length of about 7 meters).

To sum up, this line of evidence suggests high rates of bone deposition and rapid initial growth, but at rates that are not extraordinarily high during early life. Later, the rate of deposition tapers, with some irregularities in the rate of decrease, depending on the bone and on its local position in the section. Mammalian and avian growth rates known to be associated with the types of bone histology observed in *Maiasaura* (Buffrénil and Pascal, 1984; Castanet et al., 1996) suggest that this dinosaur could have reached adult size in six to seven years.

It may also be pointed out here that our study of a range of nestling bones in *Maiasaura* show that the epiphyseal and metaphyseal regions at these stages contained only a few struts of ossified bone, deep in the metaphysis, and a predominance of calcified cartilage. This suggests that the mobility of the animals at these stages would have been very limited. The occurrence of small juveniles with poorly ossified metaphyses in a nest-like structure (Horner and Makela, 1979) remains compelling evidence for the hypothesis that *Maiasaura* adults must have cared for their young, which were in the confines of nest-like structures.

Results from Counting Lines of Arrested Growth—In most bones in which LAGs could be observed and counted, the counting procedure described above produces a pattern consistent with the hypothesis that the number of LAGs increases regularly with the animal's size and presumably age (Chinsamy, 1990, 1993a). LAGs are absent in the bones of nestlings, and very rare even in late juveniles. This probably discounts the possibility that many LAGs were once present at these stages, but were later eroded away by Haversian substitution and expansion of the marrow cavity in the deep cortex. The numbers

of LAGs observed in the bones of sub-adults and adults may be regarded as a complete or nearly complete record at those stages. Furthermore, the absolute spacing and the trend in decreasing spacings of the lines through growth in the primary cortex are consistent with the inference that they record yearly growth cycles in bone that grows more and more slowly (Chinsamy, 1993a).

The discovery of relatively numerous examples of typical “growth marks” of various histological types in dinosaur bone (Reid, 1981, 1990; Ricqlès, 1983) does not discount the possibility that such dinosaurs grew quickly and did not need extended lifespans to reach adult size. In fact, the actual number of “growth lines” may be remarkably low for the dimensions and thicknesses of the bones (Reid 1990), compared to the bones of living non-avian reptiles. This discovery, if dinosaur LAGs are indeed annual, would support rather than falsify the hypothesis that dinosaurs were fast-growing animals, because rates of diametral expansion are never as great in the bones of non-ornithodiran reptiles as they are in the bones of birds, other dinosaurs, and pterosaurs (Ricqlès et al., in press), or in synapsids.

LAGs in the External Fundamental System—As noted in the descriptive section, several LAG-like lines can often be observed in the grossly woven, longitudinally fibered periosteal bone that, when present, forms the “fundamental external system” at the outer margins of adult bones. In some cases, these LAGs correspond directly to LAGs present elsewhere in the section as the most external LAGs of the fibro-lamellar complex. They are thus most probably isochronous LAGs that are simply embedded in different tissues. In other cases, the innermost line of the “external fundamental system” turns out to be a resorption line, without obvious temporal significance. More recently deposited external LAGs are quite similar to some LAGs that are deposited yearly in extant slow-growing bone tissues, in ectotherms as well as in mammals (Castanet et al., 1993; Chinsamy and Dodson, 1995) and birds (Klevezal, 1972; Chinsamy et al., 1995). If they were deposited for similar reasons in dinosaurs, they would indicate that the “adult” specimens of our sample are a few years older than other indicators suggest. At this stage, diametral growth took place at a very low rate, presumably after mature size (and probably sexual maturity) had been reached.

Variation in LAG Number Within a Skeleton—At a given ontogenetic stage, as recognized by size-classes (and presumably age-classes) within a large sample, the number of LAGs systematically and significantly differs from bone to bone. For example, most sub-adult bones of our sample showed two or three LAGs distributed through the primary cortex, but there was considerable variation: four to five LAGs in the humerus, two in the ulna, and one in the fibula. Although these three bones did not come from a single individual, the result is not anomalous in dinosaurs: the adult, holotype specimen of the hadrosaurid *Hypacrosaurus stebingeri* (MOR 549) showed 5–7 LAGs in the radius and fibula, 5–6 LAGs in a rib, and 7–8 LAGs in the tibia, but none in the metacarpal (Horner et al., 1999). Reid (1990:29; 1996:34) has recorded non-cyclic LAGs from *Allosaurus*, in one case seemingly with an interval of four years between them. This raises questions about the interpretation of LAGs from single elements. For example, if LAGs measured from (e.g.) femora are counted as indicators of annual growth cycles (Chinsamy, 1990, 1993a, 1994)—which we have no reason to support or deny on the basis of the evidence from *Maiasaura*—then the question emerges why a femur would suggest an age of three years for an individual while its rib would suggest nine or its tibia five.

Chinsamy (1993a), in an extensive comparative study of femora in the sauropodomorph *Massospondylus*, determined that the first LAG seen in the skeleton probably marked the com-

pletion of the first season of growth, and used successive LAGs to mark later annual increments. Using this reasoning, because the first LAG in the bones of *Maiasaura* does not appear until (what we recognize on the basis of size and histological grounds as) the sub-adult stage, we would conclude that it grew to a length of 3.5 meters in the first year. (This rate is plausible on other grounds, noted above.) However, as Chinsamy (1995) discovered, femora of the ornithomimid *Dryosaurus* show no growth lines at all, even in adults (see also Chinsamy et al., 1998), so the absence of LAGs even into large size may have no significance at all for chronometry. Furthermore, given the intraskeletal variation in the number of LAGs, it is not known a priori or on the basis of actualistic studies why one bone should be a reliable or consistent determinant of age, and others must accordingly be unreliable or inconsistent.

We know of no normal mechanism but an annual hiatus in growth that regularly produces LAGs in the long bones of any extant tetrapod. It is reasonable to assume on actualistic grounds that LAGs in extinct tetrapods were similarly annual, even though this assumption remains untested by direct means. On the other hand, an indirect test that LAGs were annual in these dinosaurs is provided by the agreement of the occurrence of LAGs with the thicknesses of given types of bone tissues deposited at normal rates (based on living animals) between successive LAGs (see above). However, LAGs are clearly not deposited each year in each bone of *Maiasaura*; and in some "hypsilophodontids" (generally recognized as a paraphyletic group) they do not seem to be present at all. Some bones evidently grow too quickly (or too slowly) to register a LAG each year. Therefore caution must be exercised in order to attempt the calculation of age based on LAGs, and they should not be based on single bones. A range of bones in the skeleton must be sampled through ontogeny. To our knowledge, no other studies have done this to date on extinct material.

Why LAGs are of Untested Significance in Physiological Inference

As noted above, most studies of dinosaur bone histology until very recent years tended to be opportunistic: specimens, often scrappy ones, were allowed to be cut and thin-sectioned usually because they came from very partial or taxonomically indeterminate specimens (e.g., Enlow and Brown, 1956–1958; Ricqlès, 1980). As a result of this history, no skeletally comprehensive, systematic understanding of the patterns of bone histology in extinct tetrapods has been developed to date. It is not surprising, therefore, that LAGs were not widely recognized in extinct taxa, partly because no thorough studies of skeletal patterns were carried out. But now, after several years of concentrated study, LAGs are known in nearly every extinct ornithomimid archosaur that has been studied histologically (e.g., Reid, 1981, 1990; Ricqlès, 1983; Ricqlès et al., in press; Chinsamy, 1990, 1993a; Chinsamy et al., 1995, 1998; Varricchio, 1993; Padian et al., 1995; etc.). However, these studies have also shown that the number and occurrence of LAGs vary among taxa as much as do tissue histology, ontogeny, and size.

Reid (1981, 1984a, b, 1987, 1990, 1997a, b) was the first to recognize just how widespread LAGs are in dinosaur bones. He has used these insights to advance the question of dinosaurian "endothermy vs. ectothermy," long seen as a false dichotomy by other workers (Ricqlès, 1980; *pace* Bakker, 1968), toward a more complex formulation of the problem. Reid (1990) pointed to the prevalence of fibro-lamellar bone, otherwise unknown in other extinct reptiles (except pterosaurs: Enlow and Brown, 1957; Padian et al., 1995; Ricqlès et al., in press), and the prevalence of growth lines as the two major keys to understanding dinosaurian paleophysiology. Reid (1997b) sees dinosaurs as physiologically different from all other reptiles, with higher

basal metabolic rates and growth rates, and probably with a double-pump cardiovascular system. However, for him, the lack in many specimens of evidence of active growth ceasing before death points to a retention of the ability to grow throughout the lifespan of an individual, because they were still physiologically close enough to typical reptiles to do so.

These conclusions are reasonable on the basis of the available evidence, and as everyone recognizes, most questions of dinosaurian paleophysiology can never be experimentally settled, so many possibilities remain untested but viable (Rimblot-Baly et al., 1995). In the context of the present study, and other recent ones, it must be asked whether the differences in the presence and number of LAGs—which seem to be the primary evidence on which Reid, Chinsamy, Dodson, and others have rejected a metabolic regime for dinosaurs that is more fully comparable to birds and mammals than to reptiles—should have any bearing on further discussions of the problem. Chinsamy's (1995) discovery that *Dryosaurus*, a Late Jurassic hypsilophodont ornithomimid, lacked LAGs (see also Chinsamy et al., 1998) was interpreted as an indication that dinosaurs may have "varied" in physiological strategy; but this is a weaker conclusion than the obvious inference that, lacking any gross histologic difference between birds and mammals, *Dryosaurus* might well have had a metabolism closely commensurate with mammalian and avian levels. We do not particularly advocate that view. We simply observe that when dinosaurs have been observed to have LAGs in their bones, there seems to have been little hesitation to grant them metabolic restrictions that tie them to "typical" reptiles; whereas when they lack such LAGs, the converse has not been readily proposed. Although LAGs occur in a dozen orders of mammals (Klevezal and Kleinenberg, 1969; Klevezal, 1996)—and not only in small or aquatic ones—these mammals (such as the elk: Horner et al., 1999) have never been regarded as ectotherms, as far as we know. The presence of LAGs is a plesiomorphic state for vertebrates, tetrapods, amniotes, reptiles, archosaurs, and dinosaurs. Initially, judging from extant tetrapods, LAGs signaled annual growth cycles that were mediated by environmental cycles or stresses. However, as their persistence in mammals and birds shows, LAGs can no longer be interpreted as a sign that the animal cannot cope with its environment throughout the year, and so must shut down growth. These LAGs can be equally seen as a habit of phylogenetic legacy that, like deciduousness in warm temperate angiosperms that physiologically do not "need" to shut down growth for the winter, form in response to environmental cues more than to environmental stresses. LAGs in many Mesozoic dinosaurs, as in extant mammals and birds, may represent no more than the ghost of past physiologies (Ricqlès et al., 1999). The inference that their presence indicates a metabolism more like those of living reptiles must be tested independently (Ricqlès, 1980; Rimblot-Baly et al., 1995; Reid, 1997a, b). Ultimately, we suspect, evaluations of dinosaurian physiology will not depend on the presence or absence of LAGs.

We observe that the effects of phylogeny, mechanics, and environmental factors on the presence of LAGs in bone have never been tested by independent lines of evidence, especially on fossils. As we have seen, examination of comparative ontogeny has failed so far to produce any consistent patterns among dinosaurs, regardless of other factors. We agree with Reid (1990:46) that "dinosaurian physiology should be pictured as neither 'reptilian' nor 'avian,' but as simply dinosaurian, and as having no true modern counterpart." It is evident from the differences in ontogenetic histological patterns in various dinosaurs, as well as their obvious differences in size and ecological strategies, that dinosaurs can no more be characterized by a single simplistic physiological characterization than living birds or mammals can. *Maiasaura* is generally similar in its

histological features to other dinosaurs such as *Hypacrosaurus*, theropods, and sauropodomorphs, as well as to large pterosaurs. Studies of other taxa, however, may produce different results that will require interpretation in the contexts of ontogenetic, phylogenetic, mechanical, and environmental factors.

CONCLUSIONS

1. Growth rates in *Maiasaura* varied ontogenetically. The growth rates of juveniles were extremely high, and the prevalence of calcified cartilage in the metaphyses of even late juvenile stages suggests a sustained rapid growth. More or less lamellarly organized (fibro-lamellar) bone is not predominant until the sub-adult stage.

2. When growth rates are estimated using LAGs in the femur, if the onset of rest lines is assumed to mark the end of the first season, *Maiasaura* may have reached a length of over three meters in its first year. These estimates are commensurate with rates observed in living ratites. Furthermore, if the ontogenetic changes in bone tissue types are considered in comparison to these changes in living birds and mammals, it can be seen that *Maiasaura* did not settle into a pattern of deposition of regularly laminar bone until it was some five meters long (sub-adult stage, by our size calibrations). Even if these growth rate estimates were in error by as much as a factor of two, they could not be brought within the typical ranges of growth rates of living reptiles, though those grown under optimal conditions for a few months early in ontogeny often show unusually high rates of growth, and Reid (1997b:463) provides extraordinary evidence of well vascularized (though not lamellated) fibro-lamellar bone in a wild crocodile from North Carolina.

3. The use of ontogenetic series of a single bone, compared across individuals taken from the same populations or different populations of the same species, has limited value in constructing paleobiological generalizations. A single bone does not accurately describe the life history of the animal; it only reflects the ontogenetic history of that bone, with its attendant environmental and mechanical influences. Instead, full osteohistological profiles of the skeletal elements through growth are needed to provide a comprehensive picture of skeletal growth and events. Although we have focused on long bones in this paper, we have also studied other skeletal tissues; however, because their ontogenies and growth schedules add even more complexity to the picture, we have not emphasized them here.

4. The significance of lines of arrested growth (LAGs) in dinosaurs must be regarded as entirely inconclusive at this time. Although some independent evidence is consistent with annual rates of deposition of LAGs in some dinosaurs at some stages of growth, LAGs by themselves cannot be said to determine with confidence an animal's ontogenetic status, metabolic regime, or environmental tolerance.

ACKNOWLEDGMENTS

We thank Jill Peterson Rife, Karen Chin, Allison Gentry, and Ellen Lamm for histological preparations, David Varricchio, Greg Erickson and John Hutchinson for helpful discussions, and Bruce Selyem for photographic assistance. We are extremely grateful to Jacques Castanet, Anusuya Chinsamy, Robin Reid and David Elliott for their reviews and suggestions. This work was supported by NSF Grant EAR-9219035 to JRH, the Merck Family Fund, Jim and Bea Taylor, The Charlotte and Walter Kohler Charitable Trust, The Museum of the Rockies, the University of California Museum of Paleontology, and the Committee on Research of the University of California, Berkeley. This is UCMP Contribution No. 1678.

LITERATURE CITED

- Bakker, R. T. 1968. The superiority of dinosaurs. *Discovery*, Peabody Museum, Yale University 3(1):11–22.
- Barreto, C., R. M. Albrecht, D. E. Bjorling, J. R. Horner, and N. J. Wilsman. 1993. Evidence of the growth plate and the growth of long bones in juvenile dinosaurs. *Science* 262:2020–2023.
- Bennett, S. C. 1993. The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology* 19:92–106.
- Buffrénil, V. de, and B. Pascal. 1984. Croissance et morphogénèse post-natales de la mandibule du vison *Mustela vison*, Schreiber: données sur la dynamique et l'interprétation fonctionnelle des dépôts osseux mandibulaires. *Canadian Journal of Zoology* 62:2026–2037.
- Castanet, J., A. Grandin, A. Abourachid, and A. de Ricqlès. 1996. Expression de la dynamique de croissance dans la structure de l'os périostique chez *Anas platyrhynchos*. *Comptes Rendus à l'Académie des Sciences, Paris (Sciences de la vie)* 319:301–308.
- , H. Francillon-Vieillot, F. J. Meunier, and A. de Ricqlès. 1993. Bone and individual aging; pp. 245–283 in B. K. Hall (ed.), *Bone*, Vol. 7: *Bone Growth*. CRC Press, London.
- Chinsamy, A. 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). *Paleontologia africana* 27:77–82.
- 1993a. Bone histology and growth trajectory of the prosauropod dinosaur *Massospondylus carinatus* Owen. *Modern Geology* 18: 319–329.
- 1993b. Image analysis and the physiological implications of the vascularization of femora in archosaurs. *Modern Geology* 19:101–108.
- 1994. Dinosaur bone histology: implications and inferences; pp. 213–227 in G. D. Rosenberg and D. L. Wolberg (eds.), *DinoFest*. Paleontological Society Special Publication 7.
- 1995. Ontogenetic changes in the bone histology of the Late Jurassic ornithomimid *Dryosaurus lettowvorbecki*. *Journal of Vertebrate Paleontology* 15(1):96–104.
- , L. M. Chiappe, and P. Dodson. 1995. Mesozoic avian bone microstructure: physiological implications. *Paleobiology* 21(4): 561–574.
- , and P. Dodson. 1995. Inside a dinosaur bone. *American Scientist* 83:174–180.
- , T. Rich, and P. Vickers-Rich. 1998. Polar dinosaur bone histology. *Journal of Vertebrate Paleontology* 18:385–390.
- Church, L. E., and L. C. Johnson. 1961. Growth of long bones in the chicken. *American Journal of Anatomy* 114:521–538.
- Cormack, D. 1987. *Ham's Histology*. Lippincott, New York, 732 pp.
- Dilkes, D. W. 1993. Growth and locomotion in the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Upper Cretaceous of Montana. Ph.D. dissertation, University of Toronto, Ontario, Canada, 411 pp.
- Dunham, A. E., K. L. Overall, W. P. Porter, and C. A. Forster. 1989. Implications of ecological energetics and biophysical and developmental constraints for life-history variation in dinosaurs. *Geological Society of America Special Paper* 238:1–19.
- Enlow, D. H. 1963. Principles of bone remodeling. Charles C. Thomas, Springfield, Ill, 131 pp.
- 1969. The bone of reptiles; pp. 45–80 in C. Gans, (ed.), *Biology of the Reptilia*. Academic Press, London.
- Enlow, D. H., and S. O. Brown. 1956. A comparative histological study of fossil and recent bone tissues. Part I. *Texas Journal of Science* 8:403–443.
- 1957. A comparative histological study of fossil and recent bone tissues. Part II. *Texas Journal of Science* 9:185–214.
- 1958. A comparative histological study of fossil and recent bone tissues. Part III. *Texas Journal of Science* 10:187–230.
- Francillon-Vieillot, H., V. de Buffrénil, J. Castanet, J. Géraudie, F. J. Meunier, J. Y. Sire, L. Zylberberg, and A. de Ricqlès. 1990. Microstructure and mineralization of vertebrate skeletal tissues; pp. 471–530 in J. G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends*, Vol. 1. Van Nostrand Reinhold, New York.
- Geist, N. R., and T. D. Jones. 1996. Juvenile skeletal structure and the reproductive habits of dinosaurs. *Science* 272:712–714.
- Haines, R. W. 1942. The evolution of epiphyses and of endochondral bone. *Biological Reviews (Cambridge)* 174:267–292.

- , and A. Mohuiddin. 1968. Metaplastic bone. *Journal of Anatomy* 103:527–538.
- Horner, J. R. 1984. The nesting behavior of dinosaurs. *Scientific American* 250:130–137.
- , and R. Makela. 1979. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* 282:296–298.
- , K. Padian, and A. J. de Ricqlès. 1999. Osteohistology of some embryonic and perinatal archosaurs: phylogenetic and behavioral implications for dinosaurs. *Journal of Vertebrate Paleontology* 19(3, suppl.):53A.
- , ———, and ———. In press. Comparative osteohistology of some embryonic and neonatal archosaurs: implications for variable life histories among dinosaurs. *Paleobiology*.
- , A. de Ricqlès, and K. Padian. 1997. Histological analysis of a dinosaur skeleton: evidence of skeletal growth variation. *Journal of Morphology* 232(3):267.
- , ———, and ———. 1999. Variation in skeletochronological indicators of the hadrosaurid dinosaur *Hypacrosaurus*: implications for age assessment of dinosaurs. *Paleobiology* 25(3):49–78.
- , and D. B. Weishampel. 1988. A comparative embryological study of two ornithischian dinosaurs. *Nature (London)* 332:256–257.
- Klevezal, G. A. 1972. Determination of age in birds by layers in the periosteal zone. *Zoological Zhurnal* 57:917–922.
- . 1996. Recording structures of mammals. Determination of age and reconstruction of life history. A. A. Balkema/Rotterdam/Brookfield, 274 pp.
- , and S. E. Kleinenberg. 1969. Age Determination of Mammals from Layered Structures in Teeth and Bone. Israel Program for Scientific Translations, Jerusalem, 128 pp.
- Lacroix, P. 1971. The internal remodeling of bones; pp. 119–142 in G. H. Bourne (ed.), *The Biochemistry and Physiology of Bone*. Academic Press, New York.
- Latimer, H. B. 1927. Postnatal growth of the chicken skeleton. *American Journal of Anatomy* 40:1–57.
- Owen, R. 1840–45. *Odontography, a treatise on the comparative anatomy of teeth, etc.* H. Baillière, London, 655 pp.
- Padian, K., J. R. Horner, and A. de Ricqlès. 1999. Dinosaurian growth rates and the evolution of life history strategies. *Journal of Vertebrate Paleontology* 19(3, suppl.):67–68A.
- , A. de Ricqlès, and J. R. Horner. 1995. Bone histology determines identification of a new fossil taxon of pterosaur (Reptilia: Archosauria). *Comptes Rendus à l'Académie des Sciences, Paris (Sciences de la vie)* 320 (IIa):77–84.
- Pawlicki, R. 1984. Metabolic pathways of the fossil dinosaur bones. III and IV. *Folia Histochemica et Cytobiologica* 22:91–98; 99–104.
- Peabody, F. E. 1961. Annual growth zones in vertebrates (living and fossil). *Journal of Morphology* 108:11–62.
- Quekett, J. T. 1855. Descriptive and illustrated catalogue of the histological series contained in the Museum of the Royal College of Surgeons of England. Vol. 2. London, 320 pp.
- Reid, R. E. H. 1981. Lamellar-zonal bone with zones and annuli in the pelvis of a sauropod dinosaur. *Nature* 292:49–51.
- . 1984. The histology of dinosaur bone, and its possible bearing on Dinosaurian physiology; pp. 629–663 in M. W. J. Ferguson (ed.), *Structure, Development and Evolution of Reptiles*. Symposium of the Zoological Society of London No. 52. Academic Press, London.
- . 1984b. Primary bone and dinosaurian physiology. *Geological Magazine* 121:589–598.
- . 1990. Zonal “growth rings” in dinosaurs. *Modern Geology* 15:19–48.
- . 1993. Apparent zonation and slowed late growth in a small Cretaceous theropod. *Modern Geology* 18:391–406.
- . 1996. Bone histology of the Cleveland-Lloyd dinosaurs and of dinosaurs in general, Part I: Introduction: Introduction to bone tissues. *Brigham Young University Geology Studies* 41:25–72.
- . 1997a. How dinosaurs grew; pp. 403–413 in J. O. Farlow and M. K. Brett-Surman (eds.), *The Complete Dinosaur*. Indiana University Press, Bloomington and Indianapolis.
- . 1997b. Dinosaurian physiology: the case for “intermediate” dinosaurs; pp. 449–473 in J. O. Farlow and M. K. Brett-Surman (eds.), *The Complete Dinosaur*. Indiana University Press, Bloomington and Indianapolis.
- Ricqlès, A. de. 1972. Nature et signification des “surfaces épiphysaires” chez les Tétrapodes fossiles. *Comptes Rendus de l'Académie des Sciences, Paris* 274:3527–3530.
- . 1975. On bone histology of fossil and living reptiles, with comments on its functional and evolutionary significance; pp. 123–150 in A. d'A. Bellairs and C. B. Cox (eds.), *Morphology and Biology of Reptiles*. Linnean Society Symposium, Series 3.
- . 1976. Recherches paléohistologiques sur les os longs des Tétrapodes. VII. Sur la classification, la signification fonctionnelle et l'histoire des tissus osseux des Tétrapodes. 2ème partie: fonctions. *Annales de Paléontologie* 62: 71–126.
- . 1980. Tissue structures of dinosaur bone: functional significance and possible relation to dinosaur physiology; pp. 103–139 in R. D. Thomas and E. C. Olson (eds.), *A Cold Look at the Warm-Blooded Dinosaurs*. AAAS Selected Symposium 28. Westview Press, Boulder, Colorado.
- . 1983. Cyclical growth in the long limb bones of a sauropod dinosaur. *Acta Palaeontologica Polonica* 28:225–232.
- . 1989. Les mécanismes hétérochroniques dans le retour des tétrapodes au milieu aquatique. *Geobios, mémoire spécial* 12:337–348.
- . 1992. Paleoherpetology now: a point of view; pp. 97–120 in K. Adler and D. Costello (eds.), *Herpetology: Current research on the Biology of Amphibians and Reptiles*. Proceedings of the First World Congress of Herpetology (Canterbury, U.K.). Society for the Study of Amphibians and Reptiles. Oxford, Ohio.
- , and J. Bolt. 1983. Jaw growth and tooth replacement in *Captorhinus aguti* (Reptilia, Captorhinomorpha): a morphological and histological analysis. *Journal of Vertebrate Paleontology* 3: 7–24.
- , F. J. Meunier, J. Castanet, and H. Francillon-Vieillot. 1991. Comparative microstructure of bone; pp. 1–78 in B. K. Hall (ed.), *Bone*. Vol. 3: Bone Matrix and Bone Specific Products. CRC Press, Boca Raton, Florida.
- , K. Padian, and J. R. Horner. 1997. Comparative biology and the bone histology of extinct tetrapods: what does it tell us? Proceedings, Fifth International Congress of Vertebrate Morphology. *Journal of Morphology* 232 (3):246.
- , ———, and ———. 1999. The bone histology of basal birds in phylogenetic and ontogenetic perspectives. *Journal of Vertebrate Paleontology* 19 (3, suppl.):70–71A.
- , ———, ———, and H. Francillon-Vieillot. In press. Paleohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications. *Zoological Journal of the Linnean Society*.
- Rimblot-Baly, F., A. de Ricqlès, and L. Zylberberg. 1995. Analyse paléohistologique d'une série de croissance partielle chez *Lapparentosaurus madagascariensis* (Jurassique moyen): essai sur la dynamique de croissance d'un dinosaure sauropode. *Annales de Paléontologie* 81:49–86.
- Schmitt, J. G., J. R. Horner, R. R. Laws, and F. Jackson. 1998. Debris-flow deposition of a hadrosaur-bearing bone bed, Upper Cretaceous Two Medicine Formation, northwest Montana. *Journal of Vertebrate Paleontology* 18 (3, suppl.):76A.
- Smirina, E. M. 1972. Annual layers in bones of *Rana temporaria*. *Zoological Zhurnal* 51:1529–1534.
- Varricchio, D. J. 1993. Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology* 13(1):99–104.
- Wilson, J. W. 1994. Histological techniques; pp. 205–234 in P. Leiggi and P. May (eds.), *Vertebrate Paleontological Techniques*, Volume 1. Cambridge University Press, New York.

Received 18 November 1998; accepted 24 September 1999.

APPENDIX 1. Over 50 elements, represented by some 200 thin-sections, formed the basis for this study. Early nestlings: coronoid process of jaw, caudal vertebra, scapula, humerus, ulna, femur, tibia, fibula. Late nestlings: dentary, coronoid process, dorsal vertebra, sacral vertebra, rib, ossified tendon, scapula, humerus, ulna, ilium, femur, tibia, metatarsal, phalanges. Early juveniles: femur. Late juveniles: caudal vertebra, rib, scapula, humerus, ulna, ischium, femur, tibia, fibula, metatarsal. Subadults: rib, scapula, humerus, ulna, ischium, femur, tibia, fibula, metatarsal. Adults: rib, scapula, humerus, ulna, radius, ischium, femur, tibia, metatarsal. These six gradational stages, from early nestling (EN) to adult (AD), are provided with the labels of specific thin sections, the view (transverse or longitudinal), the skeletal element from which they were taken, and the figures in which they appear.

Stage	Thin-section label	View	Element	Figures
EN	FEM 432-5	T	femur	1A, 1B
	FEM 435-1	L	femur	1C, 1D, 3A
LN	GS 400-F-3	T	femur	1E, 3B
	TIB 400-E-1	L	tibia	1F, 1G
	TIB 400-5	T	tibia	3C
EJ	FEM 472-F-4	T	femur	3D
LJ	TIB-005-1	T	tibia	2A, 2B
	MET-005-7	T	metatarsal	2C
	FIB 005-B-1	L	fibula	2D
SA	SBA-FEM-005-C1	T	femur	2E
	RIB 005-1	T	rib	2F
	SBA-U-005-3	T	ulna	2G
	TIB-005-E1	L	tibia	3G
AD	MET-005-B3	T	metatarsal	2H
	TIB 005-A3	T	tibia	3E
	MET 005-A3	T	metatarsal	3F