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Author(s): John R. Horner, Kevin Padian, Armand de Ricqles

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Comparative osteohistology of some embryonic and perinatal archosaurs: developmental and behavioral implications for dinosaurs

John R. Horner, Kevin Padian, and Armand de Ricqlès

Abstract.—Histologic studies of embryonic and perinatal longbones of living birds, non-avian dinosaurs, and other reptiles show a strong phylogenetic signal in the distribution of tissues and patterns of vascularization in both the shafts and the bone ends. The embryonic bones of basal archosaurs and other reptiles have thin-walled cortices and large marrow cavities that are sometimes subdivided by erosion rooms in early stages of growth. The cortices of basal reptiles are poorly vascularized, and osteocyte lacunae are common but randomly organized. Additionally, there is no evidence of fibrolamellar tissue organization around the vascular spaces. Compared with turtles, basal archosaurs show an increase in vascularization, better organized osteocytes, and some fibrolamellar tissue organization. In dinosaurs, including birds, vascularization is greater than in basal archosaurs, as is cortical thickness, and the osteocyte lacunae are more abundant and less randomly organized. Fibrolamellar tissues are evident around vascular canals and form organized primary osteons in older perinates and juveniles.

Metaphyseal (“epiphyseal”) morphology varies with the acquisition of new features in derived groups. The cartilage cone, persistent through the Reptilia (crown-group reptiles, including birds), is completely calcified in ornithischian dinosaurs before it is eroded by marrow processes; cartilage canals, absent in basal archosaurs, are present in Dinosauria; a thickened calcified hypertrophy zone in Dinosauria indicates an acceleration of longitudinal bone growth.

Variations in this set of histological synapomorphies overlap between birds and non-avian dinosaurs. In birds, these variations are strongly correlated with life-history strategies. This overlap, plus independent evidence from nesting sites, reinforces the hypothesis that variations in bone growth strategies in Mesozoic dinosaurs reflect different life-history strategies, including nesting behavior of neonates and parental care.

John R. Horner. *Museum of the Rockies, Montana State University, Bozeman, Montana 59717-0040.*

E-mail: jhorner@montana.edu

Kevin Padian. *Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, California 94720-3140*

Armand de Ricqlès. *Équipe Formations Squelettiques, URA CNRS 11 37, Université Paris VII, 75251 Paris cedex 05, France, and Collège de France, Paris, France*

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Introduction

Over the past two decades, data derived from studies of dinosaur bone histology have been used in discussions of physiology (Chinsamy 1990, 1993b; Reid 1984a, 1984b, 1987, 1997b; Ricqlès 1980, 1983, 1992; Horner et al. 1999), and to infer ontogenetic patterns and rates of growth of specific taxa (Chinsamy 1990, 1993a, 1995; Varricchio 1993; Reid 1993; Ricqlès et al. 1997, 1998; Curry 1999; Horner et al. 1997, 2000). Although some features of bone growth and tissue patterns remain open to interpretation, these studies show that the cortical tissue patterns of subadult and adult non-avian dinosaurs and pterosaurs (Ricqlès et al. 2000) are for the most part different from those of living non-avian reptiles. Diaphyses

in the longbones of most adult dinosaurs have a highly vascularized compacta with fibrolamellar tissue, often replaced by dense Haversian systems. This is similar to the diaphyseal compacta found in large birds and mammals. Additionally, in most dinosaur taxa the cortex is interrupted by lines of arrested growth (LAGs) similar to those in many living non-avian reptiles and a few living mammals. The preserved “epiphyseal” regions of dinosaur longbones (see Reid 1997a) reveal structures described by some researchers as most similar to those of birds (Barreto et al. 1993), and by others as primitive, similar to those of turtles and crocodylians (Geist and Jones 1996; Reid 1996).

In an attempt to clarify the identities of cer-

tain observed histological structures, and to provide new histological data to help test previous hypotheses of dinosaur growth dynamics and behavior (Horner and Weishampel 1988), we compared the histological patterns of young dinosaurs with those of young living reptiles—specifically, the embryonic and perinatal histological structures (of both periosteal and endochondral origin) in five non-avian dinosaurs as well as a turtle, a crocodylian, and three birds. We quantified percentages of porosity as a proxy for vascular space within the diaphyses, and we derived an index for the thickness of the calcified hypertrophied cartilage in the metaphyses. From these data we derived relative growth rates (Ricqlès 1980; Breur et al. 1991; Chinsamy 1993b; Barreto and Wilsman 1994). These rates can be compared with similar parameters in extant birds, and can be correlated to life-history strategies (Starck and Ricklefs 1998b).

Materials and Methods

Histological specimens were taken from the ornithomimid dinosaurs *Orodromeus makelai*, *Maiasaura peeblesorum*, *Hypacrosaurus stebingeri*, and an unidentified lambeosaurine, and from the theropod dinosaur *Troodon* cf. *formosus*. Embryonic remains were extracted from fossilized eggs (Horner 1999), and perinatal remains were found either in postulated nests or on nesting horizons as isolated elements (Horner 1994). Preliminary studies of the comparative cortical histology of adult hadrosaurian dinosaur skeletons suggest that the tibia and femur undergo the least amount of remodeling during ontogeny (Horner et al. 1997, 2000; Ricqlès et al. 1998) and are therefore most useful in comparative growth studies. All specimens used in this study are in the histology collection of the Museum of the Rockies (MOR), Montana State University.

Diaphyses were thin-sectioned transversely at or near the fourth trochanter of the femur or at midshaft of the tibia, or were serially sectioned through the entire diaphysis (Fig. 1A). "Epiphyses" were cut both longitudinally and transversely (serial sections) through the entire metaphysis (see Francillon-Vieillot et al. 1990), and deep into the diaphysis (Fig. 1A).

Femora and tibiotarsi or tibiae of embryonic

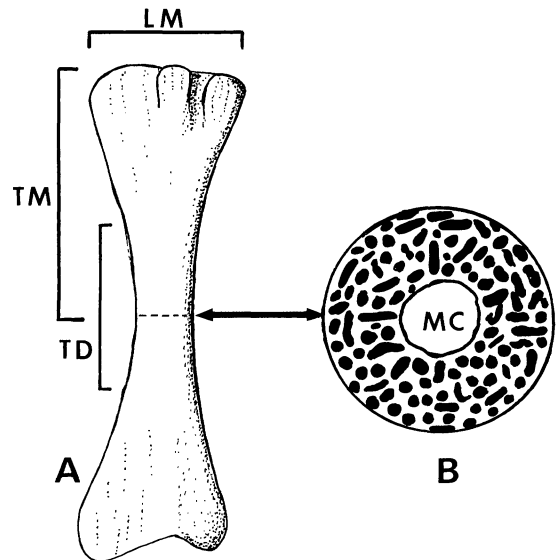


FIGURE 1. Methodology. A, Femur showing positions of thin-sections. Transverse sections were usually taken along the entire lengths of bones, or for metaphyseal studies, through the proximal half (TM), whereas specimens for diaphyseal studies were taken throughout the diaphysis and into the bases of the metaphyses (TD). Longitudinal sections, used for metaphyseal study (LM) were serial-sectioned across the entire element. B, Typical transverse section used for determining percentage of porosity. Image analysis program gives percentage of porous space (black) in relationship to cortical bone (see Table 1), irrespective of the marrow cavity (MC).

and neonatal archosaurs, including three birds—ostrich (*Struthio camelus*), emu (*Dromaius novaehollandiae*), meadowlark (*Sturnella* sp.)—and a crocodylian (*Alligator mississippiensis*), were sectioned like those of the dinosaurs listed above. Additionally, the femora and tibiae of a 55-day embryo of the snapping turtle (*Chelydra* sp.) were sectioned because turtles, an outgroup to archosaurs, are reported to share some histological structures with crocodylians and birds (Haines 1938, 1942, 1969).

Paleontological specimens were drawn, photographed, and molded before thin-sectioning. Specimens were embedded under vacuum in polyester resin, then cut on a low-speed diamond saw. Embedded specimens were preground on the mounting surface with 600-grit silicon carbide paper to increase adhesion. Specimens were mounted on glass slides using two-ton epoxy. Mounted sections were ground and polished using the same procedures as for paleontological specimens,

TABLE 1. Vascularization percentages of cortical tissues of various reptilian embryonic and neonatal skeletal elements. The vascularity index is a dimensionless ratio between the length of the element and the percentage of vascularity.

Taxa	Element	Length (in mm)	Slide ID	% Vascularity	Vascular index
Turtle	Tibia	5	97-1-T, Fi-1	12	0.33
Alligator	Femur	17	98-4-FE-6	14	1.21
Alligator	Femur	110	95-9-F2-3	4	27.5
Meadowlark	Tibia	18	97-1-T+9	29	0.62
Emu	Tibia	60	98-5-T/F-2	32	1.88
Ostrich	Tibia	82	96.1-T-1	30	2.73
<i>Troodon</i>	Femur	35	96-15-F-2	26	1.35
<i>Orodromeus</i>	Femur	15	96-9-o-f-3	20	0.75
<i>Maiasaura</i>	Tibia	55	96-11-T1-24	34	1.62
<i>Maiasaura</i>	Femur	125	90-18-400F-2	26	4.8
<i>Maiasaura</i>	Tibia	430	JvTIB-005-1	10	4.3
<i>Hypacrosaurus</i>	Femur	85	96-13-F1-9	35	2.43
Lambeosaurine	Femur	50	98-8-T1-22	36	1.39
Lambeosaurine	Femur	130	96-13-F-10-F-3	30	4.33

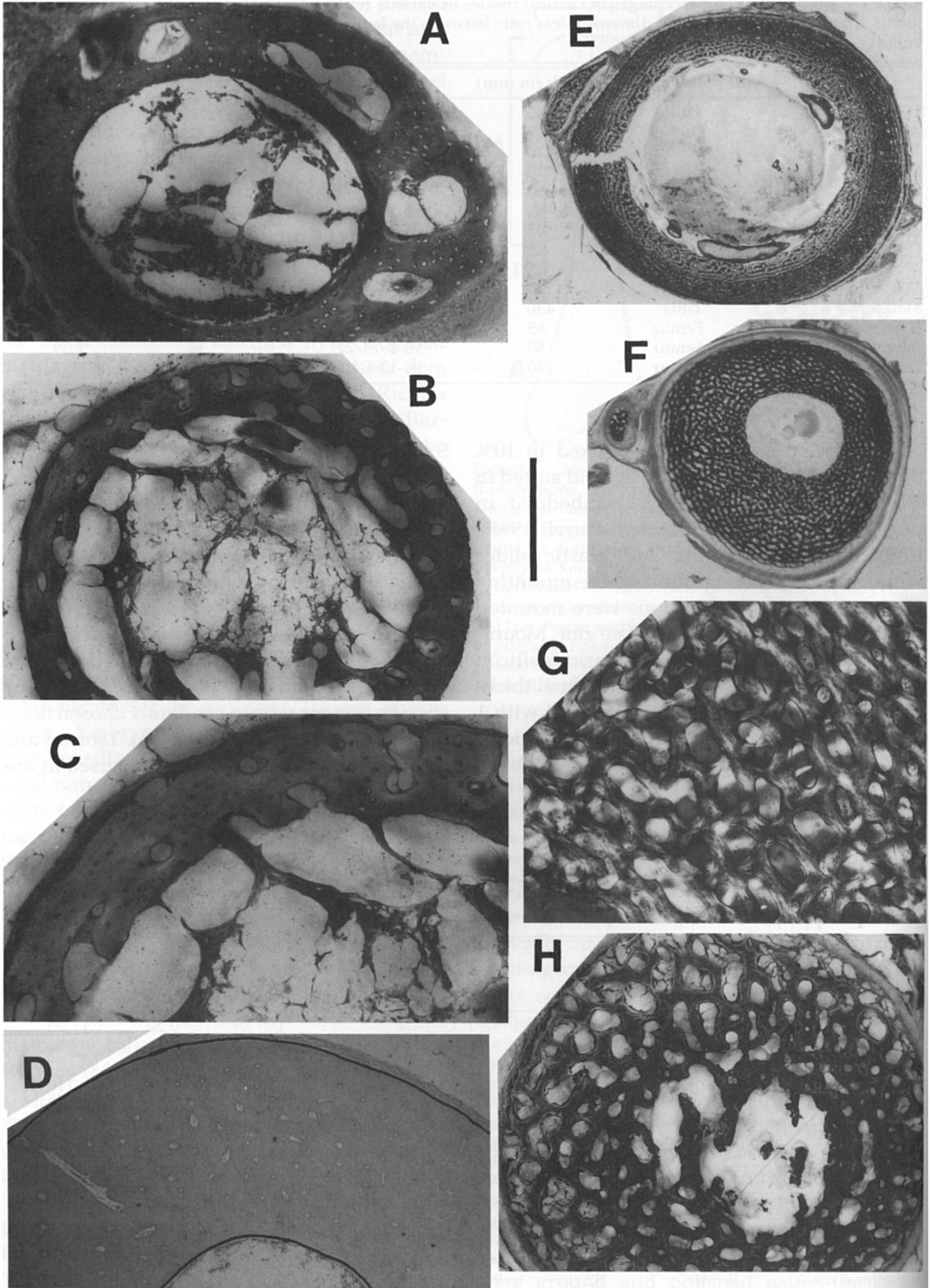
above. Recent specimens were fixed in 10% buffered formalin for two weeks and stored in 70% ethanol. The bone was embedded in poly/methacrylate (Sterchi and Eurell 1995). Embedded thin-sections and plastic slides were both lightly preground on the mounting surface, and the thin-sections were mounted using low-viscosity cyanoacrylate glue. Mounted sections were ground using various silicon carbide paper grits (60-P4000) to a final thickness of 100 μm –400 μm , and polished with 1 μm aluminum oxide solution using a microcloth. Slides were stained according to Diane

S's Microwave T-blue (Toluidine) method (Eurell and Sterchi 1994).

Percentage of porosity (a proxy for vascular space) within the cortex (Table 1) was determined using a Buehler Omnimet image analysis system. The overall area of total vascular space was calculated (Fig. 1B), independent of cortical thickness. Because the transverse sections are very small in embryonic bones, the entire surface area was measured, rather than specific regions within randomly chosen fields as detailed by Chinsamy (1993b). Tables 1 and 2 provide dimensions of the bones used in this

TABLE 2. Thickness of the calcified hypertrophic cartilage (CHC) zone of various reptilian embryonic and neonatal skeletal elements based on measurements made from longitudinal sections. P is proximal and D is distal with reference to which end the CHC thickness measurements was made. The CHC index is a dimensionless ratio between the length of the element and the thickness of the CHC. The CHC thickens with length increases in dinosaurs, but much less or not significantly in non-dinosaurian reptiles.

Taxon	Element	Length (in mm)	Slide ID		CHC thickness (in mm)	CHC index
Turtle	Tibia	5	97-1-T, Fi-L4	P	0.20	25
Turtle	Femur	5	97-1-F, P-L1	P	0.40	12.5
Alligator	Femur	17	98-4-FE-L-3	P	0.80	0.21
Alligator	Femur	110	95-9-G1-L2	D	1	110
Meadowlark	Tibia	21	97-1-T-L1	P	4.2	5.0
Ostrich	Tibia	105	96-1-J-L1	P	25	4.2
Emu	Tibia	60	98-5-T/F-L3	D	8	7.5
Emu	Tibia	60	98-5-T/F-L3	P	19	3.2
<i>Troodon</i>	Femur	35	96-15-F-L1	P	5	7
<i>Orodromeus</i>	Femur	15	96-9-o-f-L5	P	1.5	10
<i>Maiasaura</i>	Femur	70	90-18-FEM-432-1	D	13	5.4
<i>Maiasaura</i>	Tibia	55	96-11-T1	P	19	2.89
<i>Maiasaura</i>	Tibia	120	90-18-T-L1	P	18	6.67
<i>Hypacrosaurus</i>	Femur	82	96-13-F3-L1	D	12	6.83
Lambeosaurine	Femur	60	95-12-H-F-L1	P	18	3.33



study. When discussing vascularity and porosity in extinct animals, as per paleobiological custom, we use "vascularity" in an anatomical sense (referring to structures or spaces that were formerly filled by vascular tissues), and we use "porosity" simply as an index of space within the bone tissue, because soft tissues other than vascular canals originally filled it.

The thicknesses of the zones of hypertrophic calcified cartilage (Table 2) were measured in all taxa identified in the extant animals using the T-blue staining method mentioned above.

In this work, we restrict the term "neonate" to living forms. Because we cannot measure the exact time of hatching and identify the "neonate" ("newborn") in extinct forms, we use the term "perinate" ("around birth"). Embryos of the Recent taxa are full-term, and the non-avian dinosaur embryos are hypothesized, on the basis of known egg volumes (Horner 1999), to be either near-term (hadrosaur embryos) or midterm (*Troodon*). Although multiple sections of various bones were surveyed for all fossil taxa, only single sections are used as indices here: first, because the sections in question are representative of the developmental stages through which these animals pass, and second, because it is difficult to determine which stages of growth are directly "comparable" among widely separated lineages.

Results

Diaphyseal Histology.—The mid-diaphyses of the embryonic and neonate non-dinosaurian leg bones have similar histological structures but varying porosity (Table 1). The cortex from the mid-diaphysis of the tibia of the embryonic snapping turtle has a few enlarged vascular spaces on one side of the element, but is devoid of vascularization on the opposite

side (Fig. 2A). Porous space, most of which housed vascular canals, occupies about 12% of this section, but the fibula has no porous space. The endosteal surface of the tibia is distinct and smooth, and the element has a large marrow cavity. Osteocytes are common but have no organization associated with the vascular spaces. There is also no evidence of fibrolamellar tissue in any area of the sections.

The mid-diaphysis of the tibia of a full-term embryonic alligator is similar to that of the turtle in having a thin-walled cortex and a large marrow cavity (Fig. 2B). Vascular canals are spread evenly throughout the section and the porosity index is about 14% of the total area. Osteocyte lacunae are common and show organization around some vascular canals (Fig. 2C). At the periphery of some vascular canals is evidence of initial fibrolamellar development. In larger juvenile (less than one year old) alligators (Fig. 2D), the porosity has decreased to 4% (Table 1) and there has been only minor osteonal development. In both the turtle and alligator, the vascular spaces are for the most part round in transverse section, and therefore longitudinally oriented within the element.

All three taxa of birds have relatively thick, spongy diaphyses with highly vascularized compacta (Fig. 2E–H), each with some degree of osteonal development. Porosity ranges from approximately 29% to 32%. In the ratite tibiotarsi (Fig. 2E,F) the marrow cavities are much more clearly defined than in the meadowlark tibiotarsus (Fig. 2H). Osteocyte lacunae are abundant throughout the compacta of each taxon and are organized around the vascular canals. Vascular spaces vary considerably in shape, and vascularity patterns may be characterized as either laminar or reticular (Enlow and Brown 1956, 1957; Ricqlès 1968) depending on location (although more canals run longitudinally than in other directions).

←

FIGURE 2. Transverse mid-diaphyseal sections of extant tibiae. A, Tibia of 55-day embryonic snapping turtle (*Chelydra* sp.). B, Tibia of full-term embryonic *Alligator mississippiensis*. C, Enlarged view of tibia showing osteocytes. D, Tibia of neonate (less than one year of age) *Alligator mississippiensis* showing vascularity. E, Tibia and fibula (upper left) of full-term ostrich (*Struthio camelus*). F, Tibia and fibula (left) of full-term emu (*Dromaius novaehollandiae*). G, Enlarged view of emu tibia showing fibrolamellar organization around vascular canals. H, Tibia of? hatching meadowlark (*Sturnella* sp.). Scale for A, B, G, and H, 0.4 mm; C, 0.2 mm; D, 1 mm; E and F, 4 mm.

Fibrolamellar bone is developed around most of the vascular spaces (Fig. 2G) and continues to develop throughout ontogeny. The fibulae of the birds lack marrow cavities but are highly vascularized.

Embryonic non-avian dinosaurs have porosity percentages ranging from 20% (*Orodromeus*) to 36% (*Hypacrosaurus*; see Table 1). The longbones of each of the embryonic dinosaurs have a highly vascularized, thick cortex and a poorly developed marrow cavity (Fig. 3A–F). Fibrolamellar tissue organization and osteonal development have begun in all taxa, and most osteocyte lacunae are organized around the vascular canals (Fig. 3E). Like the degree of vascularity, the vascular patterns themselves also vary among taxa. The *Orodromeus* femur (Fig. 3A) has vascular canals that are primarily longitudinal, whereas *Troodon* (Fig. 3B) has a combination of longitudinal and circular canals. The hadrosaur bones (Fig. 3C–F) have a reticular pattern with vascular spaces running in all directions. Fibrolamellar deposition and osteonal development continue through ontogeny, constricting the vascular spaces and in turn decreasing the porosity percentages (see *Maiasaura*, Table 1). As a result, larger perinate and juvenile specimens of each of the dinosaur taxa have more compact, laminar to subplexiform bone (Varicchio 1993; Horner and Currie 1994; Horner et al. 2000).

“Epiphyseal” Histology.—The preserved ends of extinct dinosaur bones are not identical to the epiphyses of living vertebrates; rather, they represent those portions of the growth zone where the hypertrophied cartilage has been calcified in vivo (Ricqlès 1972, 1975; Reid 1984a, 1996, 1997a; Rimblot-Baly et al. 1995; Barreto 1997). The articular cartilage, the zone of proliferating chondrocytes, and the zone of noncalcified hypertrophy are not preserved, and this fact must be considered when comparing the dinosaur “epiphyses” with those of extant taxa, and this is why we place the word in quotation marks. Haines (1938, 1942, 1969) and Fell (1925) provided excellent descriptions of the early process of calcification and ossification in nonmammalian tetrapods. The following description complements and em-

phasizes many of their points concerning turtles, crocodylians, and birds.

The longbones of the full-term embryonic snapping turtle have massive cartilage cones that extend from the cartilaginous epiphysis deep into the diaphysis (Fig. 4A). This cone is composed of uncalcified hypertrophied chondrocytes, even where it meets the marrow cavity (Haines 1938). Calcification is found locally, primarily near the *encoche d’ossification* (see Francillon-Vieillot et al. 1990), the region where the periosteal bony collar abuts against the cartilage epiphysis (Fig. 4B). Here, accessory erosion rooms are formed adjacent to the metaphyseal walls by canals that penetrate the metaphyseal cortex, rather than being derived from the primary marrow cavity. Thin plates of endochondral bone are evidently deposited on the calcified cartilage walls of these accessory marrow cavities (Haines 1938), but in this specimen there is no evidence of bone deposition at the base of the cartilage cone where it meets the marrow cavity (Fig. 4A).

The longbones of the full-term alligator embryo are similar to the turtle only in that they also have cartilage cones that persist well into the diaphyses (Fig. 4C). The cartilage first calcifies and then ossifies along the periphery of the cartilage cone, adjacent to the periosteal cortex (Fig. 4D). This process occurs within marrow cavities that clearly originate from the diaphyseal marrow cavity, rather than as accessory metaphyseal cavities as in the turtle. In transverse section, short marrow tubes, formed at the base of the cartilage cone, are round with scalloped borders (Fig. 4E). They are apparently eroded by chondroclastic activity, as Haines (1938) comprehensively described and illustrated them in *Crocodylus niloticus*. (Haines was not able to identify a cartilage cone, perhaps because it had been replaced ontogenetically in his specimen, but we have been able to confirm its presence in our less mature specimens.) Calcification is highly localized at the base of the cone, and as a result, endochondral bone deposition is also highly localized. Calcification, concurrent erosion of the cartilage cone, and endochondral bone deposition occur primarily from the cone’s periphery (Haines 1938) within elongated tubelike structures.

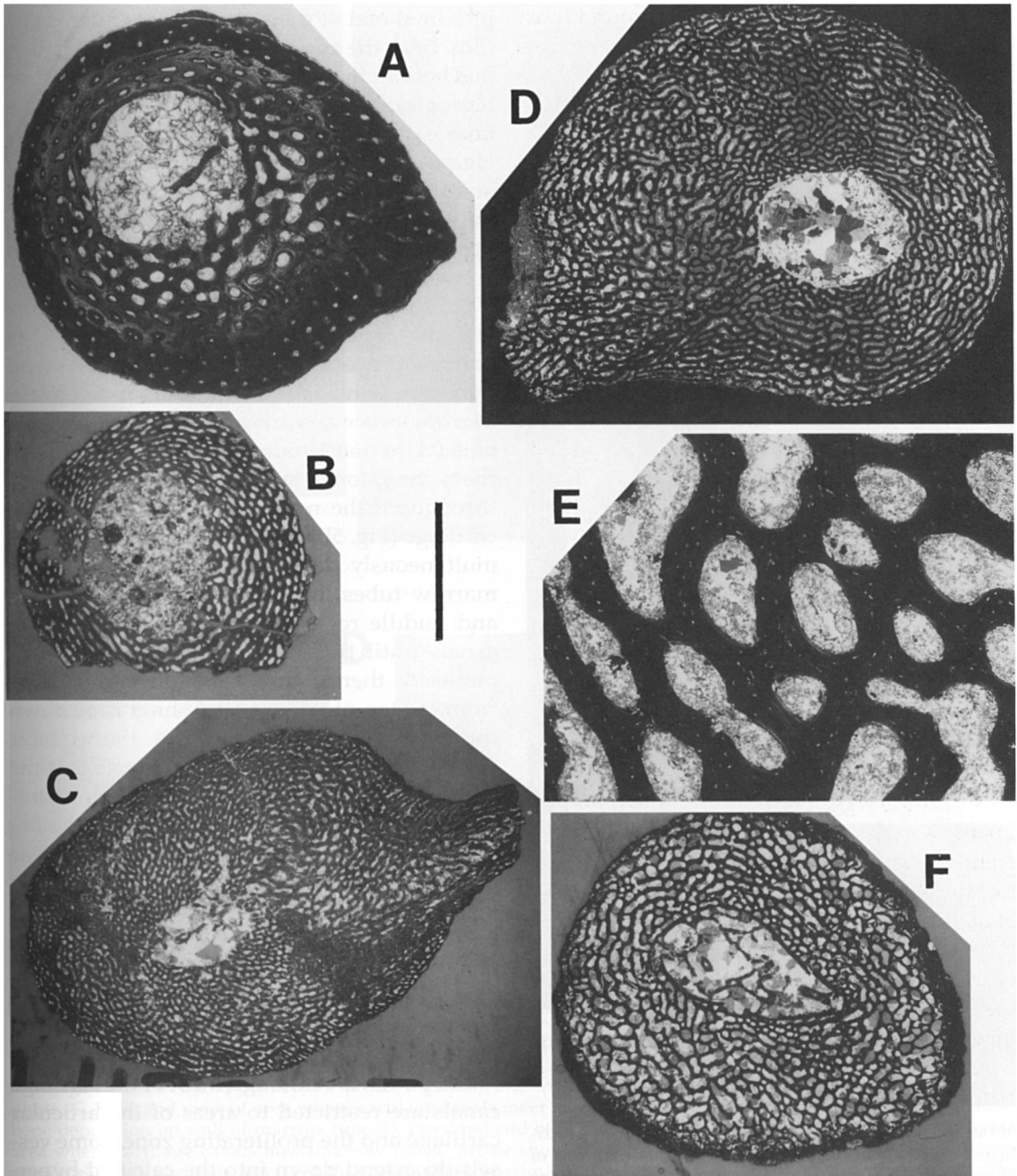


FIGURE 3. Transverse mid-diaphyseal sections of extinct Dinosauria. A, Femur of embryonic *Orodromeus* cf. *makelai*. B, Femur of embryonic *Troodon* cf. *formosus*. C, Femur of embryonic cf. *Maiasaura peeblesorum*. D, Femur of embryonic cf. *Hypacrosaurus stebingeri*. E, Enlarged view of *Hypacrosaurus* femur showing organized osteocytes and initial deposition of fibrolamellar tissue (wispy lines in bone matrix). F, Tibia of embryonic lambeosaurine. Scale for A, 1 mm; B, C, D, and F, 4 mm; E, 0.4 mm.

Embryonic and perinatal bird epiphyses differ in several respects from those of both turtles and alligators. At hatching, most altricial and precocial birds have little or no en-

dochondral bone in their longbones (Fell 1925; Starck 1989, 1994, 1996), but ossification progresses rapidly, especially in precocial taxa such as ratites (Reece and Butler 1984). In the

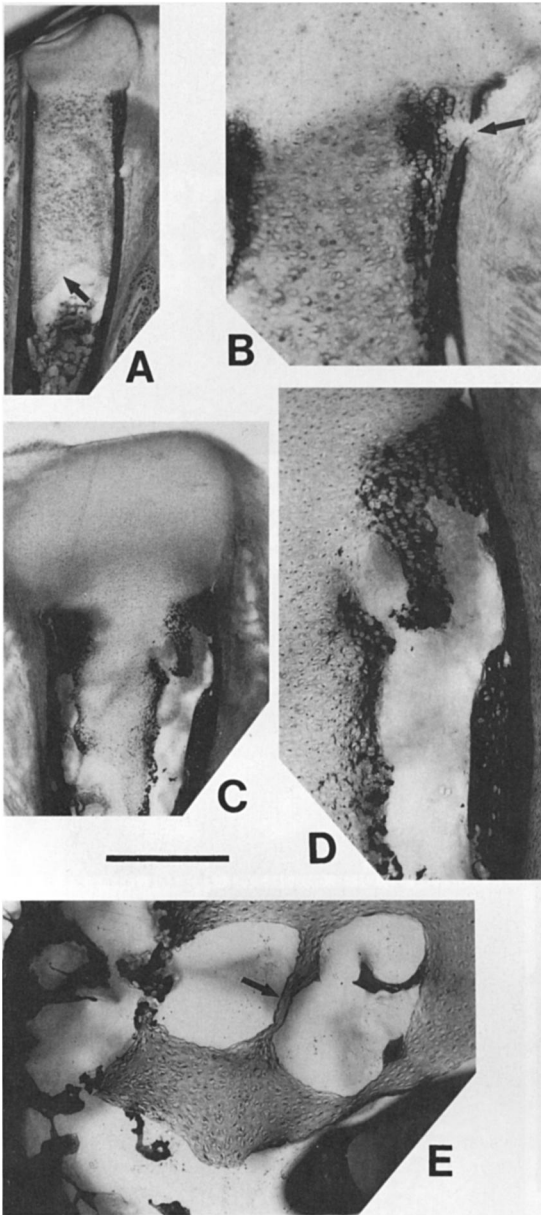


FIGURE 4. Longitudinal and transverse sections of turtle and crocodilian cartilage cones. A, Proximal tibia of embryonic *Chelydra* showing base (arrow) of cartilage cone. No erosion rooms evident. B, Proximal femur of embryonic *Chelydra* showing accessory erosion room pierced through periosteal collar (arrow) and calcified cartilage (dark spongy area between erosion room and cartilage cone). C, Proximal femur of embryonic *Alligator* showing cartilage cone. D, Enlarged view of *Alligator* femur showing marrow tubes extending from marrow cavity up along the periphery of the cartilage cone. E, Transverse section of the base of the cartilage cone from the proximal end of the *Alligator* tibia. Note the circular shape of the marrow tubes and the bone being deposited on their walls (arrow). Scale for A and C, 1 mm; B, D, and E, 0.4 mm.

proximal end of the prehatchling ostrich tibia (Fig. 5A), the cartilage cone contains numerous vessels that originate in the hyaline cartilage and extend into the cartilaginous metaphysis. These have been described as cartilage canals (Fell 1925; Haines 1942; Kuettner and Pauli 1983). These canals were apparently in place before the surrounding cartilage was deposited, and were thus trapped rather than eroded into the cartilage structure (Haines 1938; Ricqlès 1975). Very shortly after hatching, the hypertrophied cartilage calcifies, as marrow processes (with blood vessels) extend into peripheral regions of the cartilage cone. Marrow processes often meet the cartilage canals (Wise and Jennings 1973) and form with them very long, straight tubes that extend throughout the metaphyses and up into the cartilage (Fig. 5B–D). Endochondral bone is simultaneously deposited on the walls of the marrow tubes, primarily in their diaphyseal and middle regions, but not in the cartilage canals until the marrow processes have remodeled them. Transverse sections taken from the top of the hypertrophied zone down through the diaphyses reveal the circular structure of both the cartilage canals and the marrow vessels, and these can be distinguished from one another by their relationship with the surrounding cartilage. Because the cartilage canals were trapped during epiphyseal development, and not eroded into the cartilage matrix, the hypertrophic cartilage cells surrounding a cartilage canal appear to radiate out from the canal (Fig. 5E). Marrow tubes, on the other hand, have eroded into the cartilage matrix and cut through these radial patterns. Although most of the cartilage canals are restricted to areas of the articular cartilage and the proliferating zone, some vessels do extend down into the calcified hypertrophic zone in the metaphysis. Following a cartilage canal from the epiphyseal to the diaphyseal direction, the tube either joins a marrow tube or eventually terminates in a rounded point at its diaphyseal end (see Fig. 5D). The marrow processes conversely originate in the diaphysis and end in points near the epiphyseal end of the calcified zone.

The leg bones of both the perinatal *Orodromeus* (Fig. 6A) and the embryonic *Troodon* (Fig.

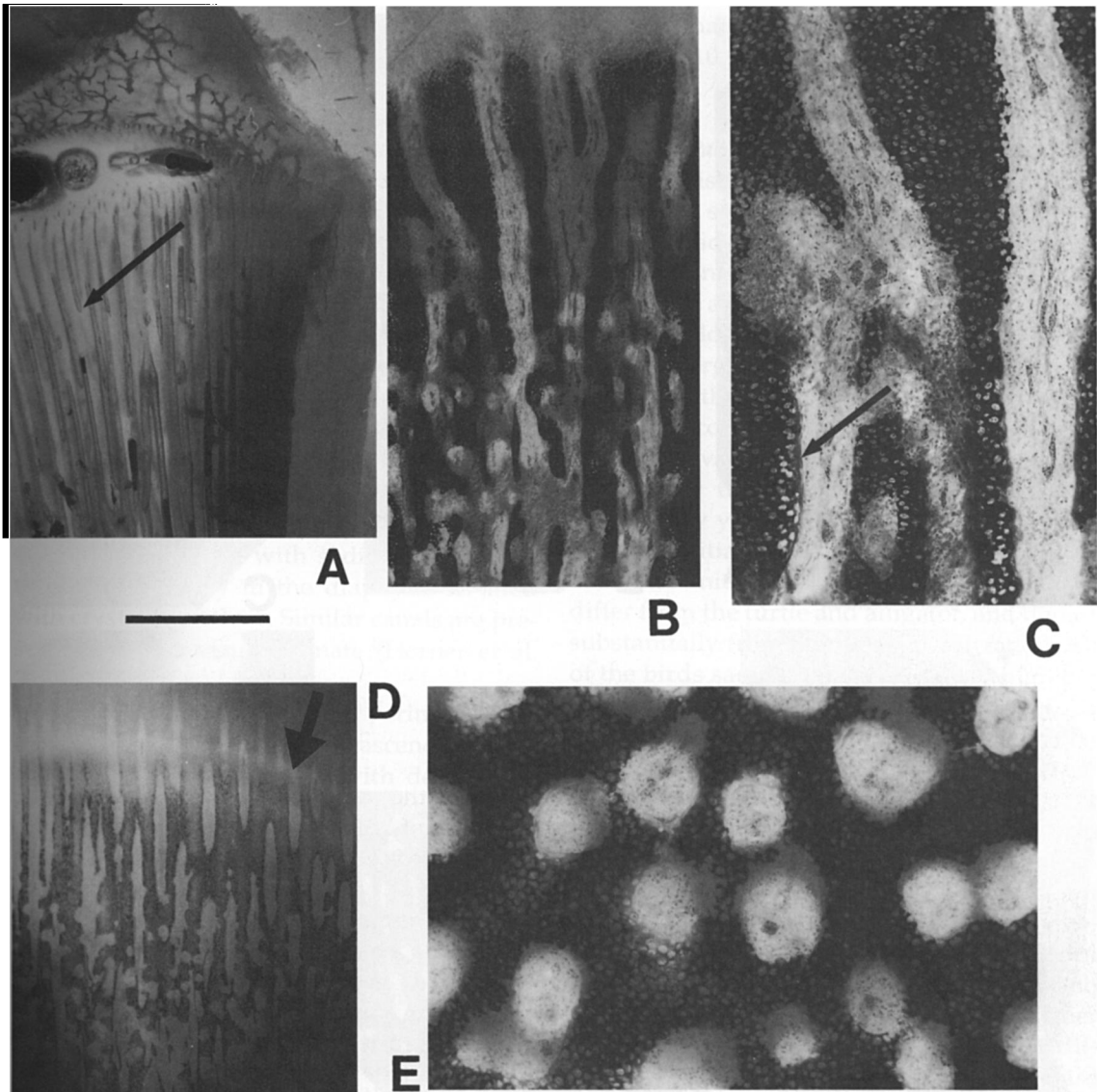


FIGURE 5. Longitudinal and transverse sections of bird metaphyses. **A,** Proximal tibia of embryonic ostrich (*Struthio camelus*) showing cartilage metaphysis with cartilage canals. Arrow shows the rounded end of a cartilage canal. **B,** Cartilage canals in the upper section of the? hatchling *Sturnella*, distal tibia with marrow tubes in lower portion of photo. **C,** Enlarged view of area where cartilage canals meet marrow tubes in the Meadowlark tibia. Arrow shows bone deposition on wall of marrow tube. **D,** Proximal end of ostrich (*Struthio camelus*) tibia showing metaphyseal area where cartilage canals meet marrow tubes. Arrow shows hypertrophied cartilage boundary. **E,** Transverse section through cartilage canals of the meadowlark proximal tibia showing absence of bone deposition on canal walls, and orientation of surrounding cartilage cells. Scale for A and D, 4 mm; B, 0.4 mm; C and D, 0.2 mm.

6B) have thickened pads of calcified cartilage near their "epiphyses," with intermittent marrow vessels, and a few inverted cone-shaped pits that appear to be the distal ends of cartilage canals. Endochondral bone is present on the walls of several marrow tubes and nearly reaches the proximal and distal surfaces of the

Troodon femur. The *Troodon* femur has large openings at either end, now filled with sediment (see Horner and Weishampel 1988), that extend into the marrow cavity of the diaphysis (Fig. 6B). These openings are hypothesized to have been filled in vivo by an uncalcified hypertrophied cartilage cone. Ossification of the

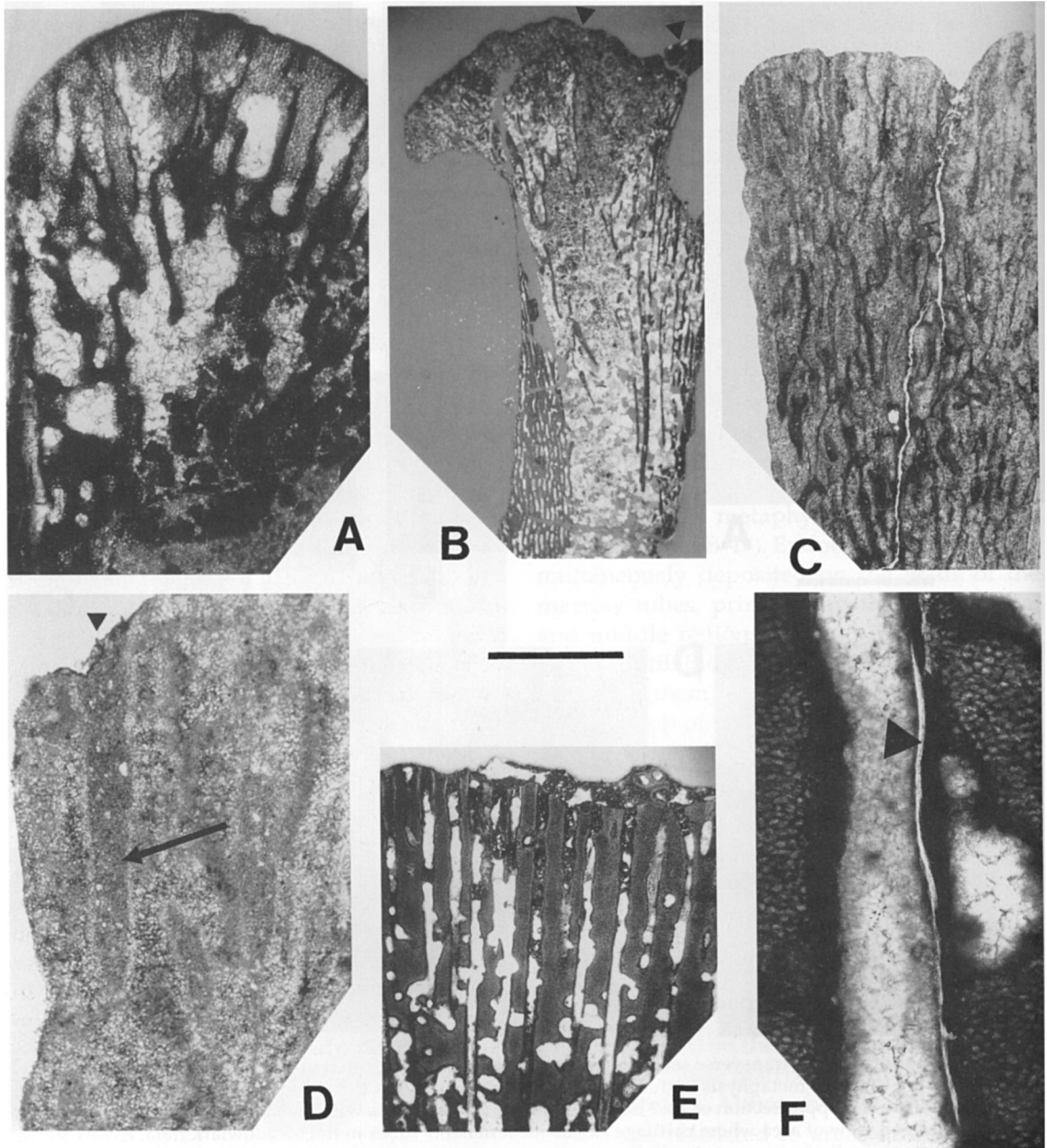


FIGURE 6. Longitudinal sections of dinosaur metaphyses. A, Proximal end of embryonic *Orodromeus* femur showing thin calcified cartilage zone penetrated by marrow tubes. Endochondral bone nearly reaches the proximal surface of the element. B, Proximal end of embryonic *Troodon* femur showing thin calcified cartilage zone penetrated by numerous marrow tubes. Arrows on dorsal surface show the limits of the sediment-filled "hole" hypothesized to have contained the cartilage cone. C, Proximal end of embryonic lambeosaurine femur showing massive calcified cartilage zone with no marrow tube penetration. D, Enlarged view of embryonic lambeosaurine proximal femur showing sediment-filled area (arrow) hypothesized to have been formed by a cartilage canal. Note its rounded lower end. E, Perinate *Maiasaura* proximal tibia showing region where cartilage canals meet marrow tubes. F, Enlarged view of *Maiasaura* proximal tibia showing bone deposition (arrow) on wall of marrow tube. Scale for A and D, 1 mm; B, C, and E, 4 mm; F, 0.4 mm.

Troodon femur occurred within marrow tubes (derived from the primary marrow cavity) around the periphery of the cone, as in extant archosaurs.

The embryonic and perinatal bones of the three hadrosaurs are composed of massive pads of calcified cartilage, extending through the metaphyses and into the diaphyses (Fig. 6C–F). In the lambeosaurine femur (Fig. 6C,D) there is no evidence of protruding marrow vessels within the “epiphysis” or distal metaphysis, but there are numerous structures at the “epiphyseal” surface that are interpreted to be remnants of cartilage canals. These structures are straight, tube-shaped canals that open to the “epiphyseal” surface and have round, pointed diaphyseal ends (Fig. 6D). They are filled with sediment, whereas the marrow cavity in the diaphysis is filled with crystalline calcite. Similar canals are present in the maiasaur perinate (Horner et al. 2000).

At the proximal end of the perinate (nestling) *Maiasaura* tibia (Fig. 6E), ascending marrow processes have united with descending cartilage canals to form long tubular structures that exit at the “epiphyseal” surface. Endochondral bone is laid down on the walls of these tubular structures (Fig. 6F). Transversely sectioned “epiphyseal”-metaphyseal regions show that these tubular structures (Fig. 7A–F) are identical to those seen in birds (Fig. 5E).

The calcified cartilage “cone” of the embryonic hadrosaurs retains the shape of the original embryonic cartilage model. Compare Figures 7A and 7D as an excellent example of the principle of “sequential relocation” (Enlow 1963; Ricqlès 1976, 1980), in which a given cross-section in the epiphysis becomes relocated into the metaphysis of the older bone. Serial sections TI-4 (Fig. 7A) through TI-8 (Fig. 7B) reveal the cross-sections of cartilage canals lacking endochondral bone, but showing a somewhat radial pattern in the surrounding cartilage (Fig. 7E). Sections TI-12 (Fig. 7C) through TI-16 (Fig. 7D) reveal cross-sections of marrow processes with endochondral deposition, and no evidence of a radial pattern surrounding them (Fig. 7 F). The cartilage ca-

nals and marrow processes meet near serial section TI-10.

Discussion

General Patterns of Neonate and Perinate Histology.—This brief survey of embryonic histology shows some clear correspondences with phylogenetic trends (Fig. 8). According to Enlow (1962), neonate compacta of most non-avian reptiles and Mammalia are composed of fine, cancellous, non-lamellar tissues with little or no organization of osteocytes. As the sections of the turtle and alligator show, both these taxa comply for the most part with Enlow’s observations, although there is some fibrolamellar tissue deposition in young alligators. Very young birds and other dinosaurs show an initial development of periosteal tissues and initial osteocyte organization that differ from the turtle and alligator, and depart substantially from Enlow’s generalization. All of the birds sampled have extremely high porosity percentages, with little variation among the sampled taxa, and a woven, highly cellular embryonic bone tissue. With the exception of *Orodromeus*, the non-avian dinosaur taxa have porosity percentages equal to or larger than those of the birds.

The hypothesis that high local vascularity of periosteal bone corresponds to high basal metabolism of the whole organism has not been adequately tested (Chinsamy 1993b), but no conclusive evidence contradicts it. On the other hand, some evidence suggests that actively differentiating bone tissues in the periosteum use more nutrients (through very dense vascularization) than do less physiologically active, slowly growing tissues. A clear relationship has recently been shown to exist in birds between the degree of vascularization of periosteal bone tissue and its rate of deposition (Castanet et al. 1996). Full-term embryonic and early neonates, ranging from the Struthioniformes (e.g., emu and ostrich) to the Passeriformes (e.g., meadowlark), have highly vascularized, woven bone tissues and high basal metabolic rates. It would appear to follow from simple actualistic comparison that non-avian dinosaurs, which have woven tissues and porosity percentages equivalent to those of birds, could also have had high basal metabolic rates on

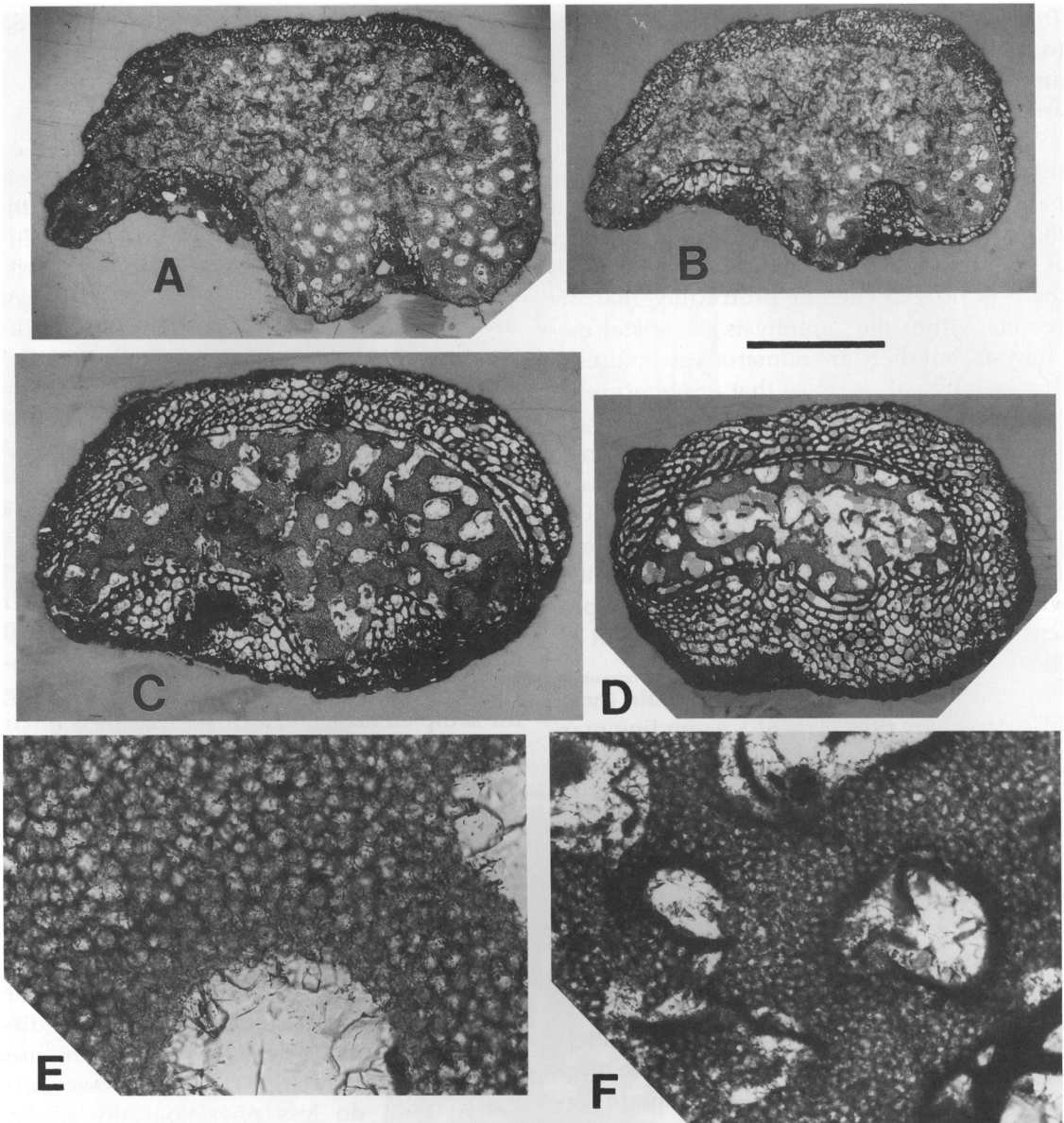


FIGURE 7. Transverse sections of proximal cf. *Maiasaura* tibia. A, Section TI-4 showing cut through cartilage canals. B, Section TI-8 showing cut through lower ends of cartilage canals. C, Section TI-12 showing cut through upper ends of marrow tubes with bone apposition on tube walls. D, Section TI-16 showing cut through lower end of marrow tubes near marrow cavity. E, Enlarged view of section (TI-4) through cartilage canals showing absence of bone on canal walls, and the organization of surrounding cells. F, Enlarged view of section (TI-14) through marrow tubes showing bone apposition of marrow tube walls. Scale for A and B, 4 mm; C and D = 3.75 mm; E and F, 0.2 mm.

that basis alone. Because these tiny dinosaurs represent embryonic or near-eclosion perinates, it is unlikely that the high vascularization of their bone could be explained by exercise or other biomechanical stresses. To the contrary, it is most probable that the high vascularization

of these young bones is correlated with a very rapid growth rate that was provided by high sustained metabolic rates. These features, shared by birds and non-avian dinosaurs (Fig. 8), are most parsimoniously interpreted as inherited from a common ancestor.

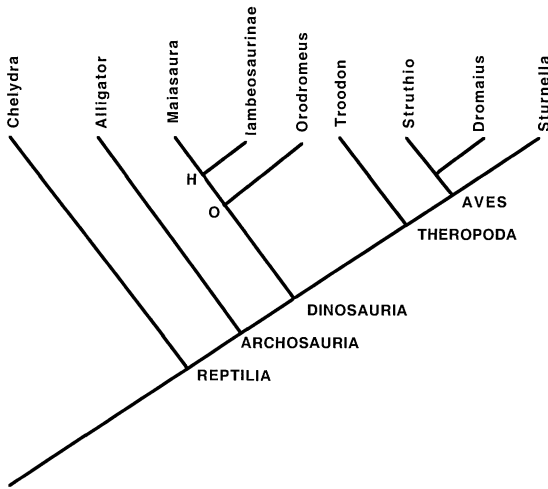


FIGURE 8. Cladogram of described taxa based on previous morphological data (Currie and Padian 1997) on which histological data are mapped. Characteristics of nodes are as follows. Reptilia: erosion rooms around periphery of cartilage cone; vascularized cortex. Archosauria: erosion rooms formed by marrow processes originating from marrow cavity; increase in vascularization; fibrolamellar deposition around vascular canals; organization of osteocytes. Dinosauria: cartilage canals; calcified hypertrophy zone elongated; increase in vascularization; increase in fibrolamellar deposition; increase in osteocyte organization. O, Ornithischia: simultaneous calcification of entire cartilage cone. H, Hadrosauridae: extreme elongation of calcified hypertrophy zone; increase in vascularization; reticular to plexiform vascularization pattern. Theropoda: increase in vascularization. Aves: retention of cartilage metaphysis until hatching.

The effects of body size could potentially be important here, because most small birds grow differently than large birds in developing compact laminar bone with low vascularization. Ostriches, turkey vultures, and other large birds, however, grow like the non-avian dinosaurs illustrated here, in depositing well-developed fibrolamellar bone, a pattern that is manifestly primitive for birds because it is typical of their theropod outgroups (Ricqlès et al. in press).

Significance of Histological Similarities and Differences.—As Haines (1938, 1942) clearly pointed out, epiphyseal (including metaphyseal) structures are generally similar in turtles, crocodylians, and birds, in that they all have a cartilage cone that is eroded by cellular activity associated with either accessory or primary marrow erosion bays. Whether by accessory marrow sprouts or processes extend-

ing from the primary marrow cavity, initial erosion and endochondral ossification occurred around the periphery of the long cartilage cones. In the non-avian dinosaurs studied, the only suggestion of an uncalcified cartilage cone occurs in the femur and tibia of *Troodon*, where large, sediment-filled holes extend from the "epiphyseal" surfaces deep into the metaphyses (Fig. 6B). Because these holes are now filled with matrix, and there is no evidence that they were once occupied by either calcified cartilage or bone, it is likely that they were filled with a nonmineralized tissue, most probably uncalcified hypertrophied cartilage not preserved by fossilization. In contrast, ornithischian dinosaurs had extremely thick pads or cones of calcified cartilage that formed an extensive calcified cone. Calcification of the cartilage preceded both erosion and osteogenesis (Caplan and Boyan 1994), but the cartilage was eventually eroded by marrow processes and replaced by endochondral bone trabeculae. As in birds, there is no evidence of erosion of the endosteal bone at the surface of the marrow cavity during late embryonic life (Romanoff 1960) in *Troodon* or the ornithischians.

Differing from both the turtles and the crocodylians is the presence in birds of cartilage canals that, as Haines (1933, 1942) suggested, might indicate that primitive birds or bird ancestors had secondary centers of ossification. All other taxa that have cartilage canals, including mammals and most lizards, also have secondary centers of ossification in their limb elements (Haines 1933, 1942). In that regard, the peculiar structure observed in the proximal end of the tibiotarsus of birds has sometimes been considered an independent epiphysis retained by birds (Haines 1938, 1942; Haines and Mohuiddin 1968). Whatever it may be, the remnants of cartilage canals in extinct dinosaurs with no evidence of secondary centers of ossification suggest that the function of the cartilage canals was probably the same for dinosaurs as it is for living birds: the canals provided nutrition and removed metabolites from the rapidly growing cartilaginous growth plates (Fyfe 1964; Wilsman and Van Sickle 1972; Kuettner and Pauli 1983; Thorpe 1988).

It is interesting to note that the "epiphyseal" regions of both the perinate *Orodromeus* and the embryonic *Troodon* limb elements are more completely ossified than any of the bones of the hadrosaurs. The zones of calcified cartilage, lacking ossified bone, are much thicker in the perinate *Maiasaura* and young perinate lambeosaurines than in either the embryonic *Troodon* or *Orodromeus*, and as a result endochondral ossification close to the "epiphyseal" surface is more extensive in *Troodon* and *Orodromeus* than in the hadrosaurs, which retained more cartilaginous material longer in ontogeny. Endochondral ossification progressed toward the "epiphyseal" surfaces as the hadrosaur perinates aged, varying considerably among elements by the time the perinates doubled in size from hatching. Variation in epiphyseal structures, notably the longitudinal orientation of hypertrophied cartilage cells, the organization of erosion bays, and the concomitant orientation of endochondral bone trabeculae, seems to record the actual activity in longitudinal growth of a given epiphysis (Ricqlès 1979), rather than other (e.g., phylogenetic) characteristics. This is evident from posthatchling *Maiasaura*, in which histological differences in the epiphyseal structures of the same bone are perfectly correlated to their respective involvement in longitudinal growth, as recorded by localization of the "neutral zone" (see Lacroix 1971) in complete sections of longbones.

Evidence for Cartilage Canals in Dinosaurs.— Given that only the mineralized in vivo portion of the epiphysis is preserved in fossil material, the identification of canals observed in the epiphyseal-metaphyseal complex of fossil bones can be problematic. Tubules that open through the preserved "articular" surface and extend into the metaphysis could potentially represent (a) cartilage canals, (b) termini of marrow tubules that are exposed by loss of the least mineralized calcified cartilage, (c) marrow tubules that extend through the calcified zone, or both (a) and (c). Hypotheses (b) and (c) can be combined because both interpret the tubules as outgrowths of the marrow, so the problem lies in distinguishing between (a) and (c) in the absence of in vivo tissues. Several lines of evidence are available.

First, there are extensive similarities between non-avian dinosaurs and birds, which are known to have cartilage canals (compare Figs. 5 and 6). Second, details of preservation often help to differentiate between what we recognize as marrow tubules and cartilage canals. In our dinosaur material, the latter are generally filled in by brown sandy-silty sediment similar to the surrounding matrix. Conversely, the marrow cavity is generally filled by crystalline calcite, which is also seen in the erosive processes that ascend from the marrow cavity. Canals filled with sediment clearly originated from the epiphyseal surface of the elements, whereas those filled with calcite apparently had no communication with the epiphyseal surface. Third, the formation and fate of marrow tubules and cartilage canals differ with respect to the composition of their walls and their relationship to other local tissues, cartilage, and early endochondral bone.

Cartilage canals (in birds, for example) differentiate in situ within regions of noncalcified cartilage of the epiphysis. Their trophic functions and the intussusceptual growth capacity of the cartilage in these regions demonstrate that the canals are developmentally related to this cartilage and that they develop at the same time. Marking this synchrony, the cartilage cells radiate centrifugally around the canals, and this pattern is accentuated later in the hypertrophic region (Haines 1969: Fig. 23B). The radial organization is retained when the cartilage matrix is calcified, and this is why it can still be observed in the calcified cartilage of fossil bones, especially in the active epiphysial regions of subadults that have thick pads of hypertrophied cartilage (Ricqlès 1975: Fig. 11).

In contrast, the tubules or processes that ascend from the marrow cavity have an entirely different histogenetic relationship to the cartilage. They are merely highly active outgrowths of the erosion front that lines the marrow cavity, carved into the surrounding tissue by chondroclastic activity and later finished by osteoblastic activity. Thus there are no precise morphogenetic relationships between these tubules and the cartilage, because the arrangement of the canals entirely results

from resorption processes (Haines 1938: Fig. 8).

Cartilage canals and marrow tubules also differ in the ontogeny of their diameters. Cartilage (or perforating) canals grow into the metaphyseal cartilaginous cone, and their diameters decrease toward the diaphysis. This constriction is sometimes thought to result from expansion of the hypertrophic cartilage, which shrinks the canals. This may be true for their initial constriction in the hypertrophic cartilage, but it cannot be true for calcified cartilage, which can no longer expand. The constriction in diameter, instead, may simply be a consequence of their relocation during growth. The canals originate from the epiphysis itself, which is set progressively farther from the diaphysis as longitudinal growth proceeds as a result of proliferation in the metaphysis. Accordingly, the cartilage canals, located in what is now the medullary cone, represent the oldest part of the canal system, which once developed toward the diaphysis in a smaller, less mature version of the epiphysis. Their smaller diameter in this region is commensurate with the smaller size of the femur in its previous growth stages.

It has been proposed that cartilage canals shrink and become a sort of pathway along which the erosive marrow canals may form. This may be true but is difficult to demonstrate, especially in fossils. If true, however, it would be evidence of the actual occurrence of cartilage canals. As it happens, sooner or later cartilage canals are involved in erosional action from chondroclasts, and by the endochondral bone deposition that follows. This process can take place along the generalized erosive front of the marrow cavity, and much earlier (i.e., closer to the epiphysis) if the canals ascending from the marrow cavity happen to merge with the cartilage canals. In the latter case, the periphery of the cartilage canals experiences localized chondroclastic erosion, eventually associated with bone deposition that involves the *globuli ossei* and other features of early endochondral bone deposition (see Haines 1938: Fig. 8). At this point the cartilage canals become structurally indistinguishable from the marrow tubules, but there is still a clear difference with respect to their

relationship to the cartilage. As Haines (1938: Fig. 8) clearly shows, as erosion rooms (which are transverse sections of ascending marrow processes) invade the hypertrophied cartilage, they show no regular spatial relationship to the cartilage cells, which thus appear to be randomly organized. However, around the periphery of a genuine cartilage canal that experiences initial erosion and early endochondral deposition, the characteristic radial organization of the chondrocytes is always retained (contrast our Figs. 7E and 7F) (see also Rimblot-Baly et al. 1995: Fig. 6d). Once the cartilage is massively eroded and extensive secondary endochondral bone trabeculae are deposited, it is no longer possible or even relevant to maintain the distinction between marrow tubules and cartilage canals.

Because the structures that we describe here as cartilage canals meet at least some of the distinguishing criteria detailed above, we feel justified in identifying them in some dinosaurs at some growth stages.

Calcification, Growth Rates, and Life-History Strategies.—According to Starck (1998), the growth rate of a bird skeleton should be predictable from the thickness of the proliferation zone (Kember and Kirkwood 1991), and yet, because this zone is not present in non-avian dinosaurs, it might follow that growth rates in non-avian dinosaurs cannot be estimated precisely on the basis of bone histology alone. However, the correspondence between the thickness of the proliferation zone and the development of the rows of calcified cartilage in birds strongly suggests that these factors are not independent. If so, the extreme similarity of the hypertrophied calcified cartilage region of the ostriches to those preserved in *Maiasaura* and the lambeosaurs at least strongly suggests commensurate growth rates.

Geist and Jones (1996) raised several hypotheses that countered previous work by Horner and Weishampel (1988), Horner and Currie (1994), Horner and Makela (1979), and Norell et al. (1995) concerning the interpretation of the tissues found in embryonic and perinatal non-avian dinosaurian bone, and the associated behaviors of adult and juvenile non-avian dinosaurs. However, comparative evidence falsifies each of their hypotheses.

Horner and Weishampel (1988) had contrasted the relative maturity of embryonic hindlimb bones among dinosaurian taxa, showing substantial variation in the degree of ossification of the epiphyseal region in perinates. They correlated this with altricial and precocial life-history strategies in birds, suggesting necessary differences in the degree of parental care after birth. Geist and Jones (1996) maintained that the condyles of *Orodromeus* could not be formed of calcified cartilage because this is not found in any living perinatal archosaur. The observations provided in the preceding sections of this paper (see also Figs. 5 and 6), however, confirm that some dinosaur neonates passed through a stage where the entire metaphyses were calcified but not ossified. There is considerable and overlapping variation among both birds and non-avian dinosaurs in the morphology of the cartilage cone and the extent of calcification and timing of ossification of various bones, but in all respects these taxa are far more similar to each other than to any other reptiles.

Geist and Jones (1996) proposed that the pelvis was a better indicator than the long-bones of an animal's locomotory ability at hatching, and contrasted crocodiles and precocial bird neonates with altricial bird neonates. The degree of ossification of the pelvis is indeed important, but without concomitant ossification of the hindlimb, locomotory ability is no further advanced. They stated (p. 712) that "even altricial juveniles become active within the nest in a matter of days after hatching, and postnatal ossification of the pelvic girdle is relatively rapid." This is not true for species that are nest-bound and reliant on parental feeding for long periods. In every case the timing of ossification and behavioral factors are both determinant, but these can only be assessed indirectly in extinct forms. And regardless of the exact timing, if the bones of just-hatched dinosaurs were too frail for efficient locomotion, it is difficult to see how they could have survived predators without parental intervention.

Geist and Jones (1996: p. 714) stated that "[d]ata from extant specimens indicate that there are no qualitative differences in the development of longbone epiphyseal structure

in archosaurs, whether altricial or precocial." By "qualitative differences," Geist and Jones meant that the bones begin to ossify in the same order in all birds, as previously described by Starck (1989, 1993). However, it is not the order of ossification that is important in differentiating across the altricial-precocial spectrum, but the rate at which ossification proceeds. The bones ossify more quickly in some birds than in others, so that at hatching the skeletons of some birds are substantially better ossified (as measured by the proportions of endochondral bone to various forms of cartilage [Starck 1989, 1993, 1994]). The embryonic skeletal elements of both *Troodon* and *Orodromeus* have a much greater proportion of endochondral bone than do any of the posthatching, perinatal hadrosaurs. And this quantitative difference, cited by Starck (1994) as indicative of altricial-precocial differentiation among most birds (but see Starck and Ricklefs 1998b), supports the hypothesis for some variation of altriciality among the hadrosaurs. The greatly thickened calcified cartilage zones, indicative of equivalently thick proliferation zones, of the hadrosaurs indicate both high rates of growth and minimal mechanical strength, characteristics common to altricial birds.

Finally, Geist and Jones (1996: p. 714) disparaged "the discovery of eggs in close association with an adult *Oviraptor*" as evidence of birdlike parental behavior, noting that "nest-attending and brooding behavior is widely distributed" among extant reptiles and amphibians. Geist and Jones (p. 714) supported their views by noting that female crocodiles "often rest their lower throat or thorax directly on the nest for the duration of the 90-day incubation period." The observation is true, but this is not at all what *Oviraptor* was doing. It was sitting with its eggs beneath its abdomen, exactly as birds do, and as no other reptiles do; so it is important in evolutionary terms to distinguish one end of the nesting animal from the other. Further examples of this nesting behavior are given by Dong and Currie (1996), Norell et al. (1996), and Varricchio et al. (1997). Nesting behavior does not by itself say anything about altriciality or precociality in neonates. In this case it indicates that

certain behaviors and, as shown above, growth patterns were shared by birds and some Cretaceous non-avian dinosaurs. It is not unreasonable to expect other associated behaviors, such as a spectrum of altricial and precocial behaviors, to have been possible and even probable.

Conclusions

1. *In their embryonic and perinatal bone histology, non-avian dinosaurs are more similar to birds than to either turtles or crocodylians, but some non-avian dinosaurs differ from birds as well (Fig. 8). Degree of vascularization (as shown by porosity percentages) in non-avian dinosaurs is much closer to that of birds than to that of other reptiles. These percentages reflect higher nutrient supply, which allows higher growth rates and, by implication, correspondingly higher basal metabolic rates. Additionally, the apparent presence of cartilage canals, together with the extremely thick zones of calcified cartilage, also suggests high rates of growth (Ricqlès 1979; Thorpe 1988). Different from birds is the calcification of the entire (or nearly so) cartilage model in the ornithischians. In birds, the epiphyseal cartilage does not become calcified at the stage of hypertrophy, but remains unmineralized. It eventually gives rise to the cartilage cone after the marrow cavity and its peripheral metaphyseal processes form. Overly thickened physes (growth plates) occur in birds on occasion but are the result of abnormalities such as ricketts (Thorpe 1988). Because all embryonic and small perinatal hadrosaurian dinosaur bones that have been sectioned have enormous volumes of organized longitudinal rows of calcified cartilage, it is presumed that this condition is normal for them.*

The differentiation and persistence of cartilage cones has recently been described as a basal sauropsid character resulting from both phylogenetic and mechanical factors that favored a more rapid perichondral apposition than endochondral ossification (Carter et al. 1998). Characteristics of the cones—whether they are calcified or uncalcified, are eroded by primary or secondary marrow processes, have or lack cartilage canals—appear to depend on relative rates of deposition of endochondral

bone. Because embryonic turtles and crocodylians both retain uncalcified cartilage cones, it would appear that “epiphyseal” and metaphyseal growth was different in dinosaurs than in those taxa. The difference may lie in the region responsible for active longitudinal growth, i.e., in the growth zone of epiphyseal cartilage. The extensive intrinsic canal system in the cartilage of birds and other dinosaurs evidently reflects very active longitudinal growth at rates higher than in crocodiles and turtles. The specialized erosion of the cartilaginous cone by subperiosteal erosion bays (as seen in crocodiles and birds) may be a derived feature of archosaurs; in a further derived state, seen in non-avian dinosaurs and birds, the erosion is carried out through the fusion of medullary canals with the cartilage canals. The massive zones of calcified cartilage seen in the hadrosaurs probably represent mechanisms that aided in expeditious growth.

2. *If patterns of bone histology are correlated with rates of growth and development, dinosaurs might have had a range of these patterns similar to those of extant birds. Dinosaurs (including birds) departed substantially from the basic histologic patterns of growth in basal reptiles, as crocodiles also do to some extent (Fig. 8). At perinatal stages, growth is generally more rapid, vascularity higher, and tissue structures better organized. Vascular connections between the “epiphysis” and diaphysis suggest higher rates of longitudinal bone growth. Second, neither birds nor non-avian dinosaurs are uniform in their growth strategies; there may be some correlation to size or phylogenetic relationships, but in living birds the strongest correlation is to life-history strategy (Starck and Ricklefs 1998b). Finally, evidence from nesting sites further suggests that non-avian dinosaurs varied in the duration of time that neonates spent in the nest. Differential growth strategies among non-avian dinosaurs are correlated with life-history strategies that may be analogized from this evidence (Horner 1999, 2000). Regardless of this variation, the embryonic features of non-avian dinosaur skeletons were much more like those of birds in nearly every respect than like those of other living reptiles, which make poor models for*

growth rates and physiological parameters of extinct dinosaurs.

3. *Paleontological evidence supports inferences of nest guarding and extended nesting time; therefore, some non-avian dinosaur hatchlings could have been semiprecocial, semialtricial, or even altricial.* Whether bone histology is of any use in attempting to determine whether extinct dinosaurs were attended and fed by their parents is controversial (Geist and Jones 1996; Starck and Ricklefs 1998a,b), and yet there are distinct histological differences among the dinosaurian taxa examined in our study. The leg bones of both the embryonic *Troodon* and the hypothesized near-hatchling *Orodromeus* have "epiphyseal" regions that are clearly more mature than the "epiphyseal" regions of any of the hadrosaurs, regardless of whether the hadrosaurs are embryonic or posthatchling perinates. The massive metaphyseal pads of calcified cartilage present in the hadrosaurs, with only minor initial invasion by marrow erosion bays, suggest that the proliferation zone must have been extensive and that these dinosaurs were growing much faster than *Troodon* or *Orodromeus*. The difference in growth rates may well correspond to the relative sizes of these animals; *Orodromeus* and *Troodon* adults were relatively small compared with adult hadrosaurs.

The somewhat mature "epiphyses" and the moderate degrees of vascularization found in both the *Troodon* and *Orodromeus* leg bones may reflect a strategy represented by moderate growth of the neonates, afforded by some variation of a precocial life style. Coarse compacted cancellous tissue that originated endochondrally in *Orodromeus* and *Troodon* also suggests a completely functional bone architecture for small juveniles in these taxa. Additionally, the hatched eggs of *Troodon* are found only partially broken, suggesting that the hatchlings left the nest upon hatching (Horner 1984; Horner and Weishampel 1988, 1996).

Maiasaura perinates twice the reconstructed size of hatchlings (based on known volumes of eggs [Horner 1999]) have been found within the boundaries of hypothesized nests (Horner and Makela 1979). The simplest explanation for the presence of the juveniles in hypothe-

sized nests, and for the fact that longbones of these animals had enormous pads of calcified cartilage and little endochondral bone, has been to hypothesize a period of parental care while the neonates remained within the nest (Horner and Makela 1979; Horner 1984, 1996, 2000). Taphonomic data derived from the nesting horizons of these dinosaurs (Horner 1982) indicate that the occupants of the nesting ground were no larger than 2.5 times the reconstructed size of the predicted hatchlings (Horner 1994, 1999). This would suggest that care in the nest may have been limited to a rather short period of time after hatching, a period that may have simply allowed the young to reach a size at which they could keep up with adults. Following Nice (1962) or Starck (1993), the hadrosaurian dinosaurs would be classified as some variation of semi-altricial. Again, these features are not at all commensurate with patterns observed in living reptiles, which appear to be poor models for dinosaurian parental behavior, as well as for dinosaurian growth strategies and metabolic rates.

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