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GROWTH IN SMALL DINOSAURS AND PTEROSAURS: THE EVOLUTION OF ARCHOSAURIAN GROWTH STRATEGIES

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ABSTRACT—Histological evidence of the bones of pterosaurs and dinosaurs indicates that the typically large forms of these groups grew at rates more comparable to those of birds and mammals than to those of other living reptiles. However, *Scutellosaurus*, a small, bipedal, basal thyreophoran ornithischian dinosaur of the Early Jurassic, shows histological features in its skeletal tissues that suggest relatively lower growth rates than in those of larger dinosaurs. In these respects *Scutellosaurus*, like other small dinosaurs such as *Orodromeus* and some basal birds, is more like young, rapidly growing crocodiles than larger, more derived ornithischians (hadrosaurs) and all saurischians (sauropods and theropods). Similar patterns can be seen in small, mostly basal pterosaurs such as *Eudimorphodon* and *Rhamphorhynchus*. However, superficial similarities to crocodile bone growth belie some important differences, which are most usefully interpreted in phylogenetic and ontogenetic contexts. Large size evolved secondarily in several dinosaurian and pterosaurian lineages. We hypothesize that this larger size was made possible by rapid growth strategies that are reflected by characteristic highly vascularized fibro-lamellar bone tissues that comprise most of the cortex. Dinosaurs and pterosaurs, like other tetrapods, generally grew more quickly in early stages and more slowly as growth neared completion. As in other vertebrate groups, taxa of small adult size may have grown at lower rates or for shorter durations than larger taxa did. Phylogenetic patterns suggest that by themselves, the low vascularity and inferred low growth rates seen in small dinosaurs and pterosaurs are not good indicators of thermometabolic regime, because they are correlated so strongly with size. They may reflect mechanical exigencies of small size rather than especially lower growth rates, tied to the process of deposition of particular kinds of bone tissues. The evolution of life history strategies in dinosaurs and pterosaurs, as they relate to rates of growth and adult body sizes, will be better understood as more complete histological studies place these data into phylogenetic and ontogenetic contexts.

INTRODUCTION

Dinosaurs vary tremendously in adult body size. Even if birds, which range down to a few grams for some hummingbird weights (McGowan, 1994), are excluded from consideration, small Mesozoic non-avian dinosaurs such as *Compsognathus*, *Microraptor*, and *Caudipteryx* could scarcely have weighed more than a few kilograms. On the other end of the scale, sauropod giants such as various brachiosaurids and *Supersaurus* may have exceeded 30–40 metric tons (90 by some estimates; Alexander, 1997), producing a range amounting to five orders of magnitude (seven if birds are included) and approaching the range in mammals from the tiniest shrew to the blue whale (Eisenberg, 1984).

To reach large sizes, extant mammals grow more quickly than typical reptiles that reach large size, even the rapidly growing Nile and Komodo monitors (Buffrénil and Castanet, 2000; Auffenberg, 1981). Furthermore, within a given group, large taxa generally grow to adult size at more rapid rates than smaller taxa do (Case, 1978). Erickson and Brochu (1999) showed that the giant Cretaceous crocodile *Deinosuchus* reached its great size by continuing a somewhat higher pace of growth until the age of 50 years or more; but it still grew along more or less typical crocodylian growth curves (Fig. 1), and so fulfilled the “good reptile” model of physiology (e.g., Spotila, 1980; Paladino and Spotila, 1994). Most dinosaurs, however, do not fulfill that model of growth, as far as available evidence indicates (contra Seebacher 2003). Contrary to Spotila’s (1980) reasonable predictions, large dinosaurs grew to great size relatively quickly, as Dunham et al. (1989) inferred. Estimates from several lines of evidence indicate that hadrosaurs such as *Maiasaura* and *Hypacrosaurus* reached an adult size of about seven meters in approximately seven years

(Horner et al., 1999, 2000), and large sauropods such as *Apatosaurus* may have reached sub-adult size in ten to twelve years (Rimbot-Baly et al., 1995; Curry, 1999; Sander, 2000).

Evidence for this rapid growth comes largely from patterns of bone histology (Fig. 2), which show quantum differences in inferred growth rates between pseudosuchians (crocodiles and their archosaurian relatives) and ornithosuchians (dinosaurs, pterosaurs, and their relatives) (Padian et al., 2001; Ricqlès et al., 2003a). The actualistic inference, documented by empirical studies (e.g., Castanet et al., 1996, 2000), is that the general type of bone tissue primarily reflects its rate of growth (Amprino, 1947). Recently, Margerie et al. (2002) have demonstrated that within the fibro-lamellar complex of tissues that are typical to most dinosaur and pterosaur bones, the proportion of primary osteons is correlated with growth rate, but the orientation of the osteons is not (contra their earlier work: Castanet et al., 1996; see also Padian et al., 2001). Nevertheless, tissues in the fibro-lamellar context grow much more quickly than lamellar-zonal bone does. Hence, tissue types in living and extinct animals may be compared to approximate the amount of time that it took to lay down a given thickness of bone in an animal in which this can no longer be measured directly.

A second line of evidence comes from lines of arrested growth (LAGs), which are found in the bones of many basal birds as well as those of nearly all non-avian dinosaurs and pterosaurs at some stage of growth (Chinsamy et al., 1995, 1998; Reid, 1996, 1997; Ricqlès, 1980, 2000; Ricqlès et al., 2000). These LAGs may be annually deposited, as growth lines in many living ectotherms (and some endotherms) are, and so can be counted to assess age (Castanet et al., 1993; Klevezal, 1996). However, this hypothesis had not been tested by independent lines of evidence in fossil

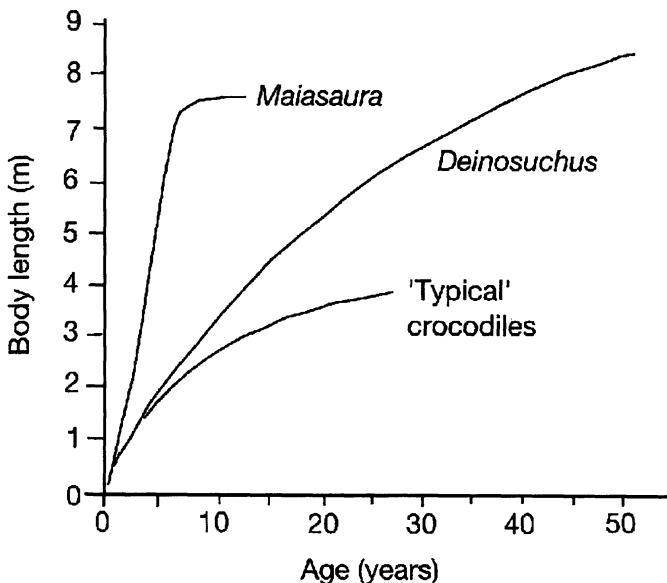


FIGURE 1. Comparative growth histories of the hadrosaurian dinosaur *Maiasaura* and the giant Cretaceous crocodile *Deinosuchus*, with "typical" crocodiles for comparison (crocodile data from Erickson and Brochu, 1999). *Deinosuchus* grows slightly more rapidly and extends its active growth curve more than typical crocodiles, but the curve for *Maiasaura*, a typical large dinosaur with respect to its growth profile, is qualitatively different, reaching approximately the same adult size in about seven years, rather than forty years or more (Horner et al., 1999). Although data on partial growth series have been collected for some dinosaurs, none but *Maiasaura* (Horner et al., 1999) and *Orodromeus* (Ricqlès, Horner, and Padian, unpubl. data) are currently represented from embryo to adult.

taxa until our work on *Maiasaura* (Horner et al., 2000) sustained it. Even so, in some extinct forms the presence and spacing of LAGs is so irregular as to cast doubt on the hypothesis (Horner et al., 1999), so it must be carefully assessed and not assumed. Furthermore, different bones of the same skeleton can have different numbers of LAGs (Horner et al., 1999).

If dinosaurs and pterosaurs could grow so rapidly, does it follow that they always did? The long bone cortex in large dinosaurs and pterosaurs is almost always composed primarily of well-vascularized fibro-lamellar bone, which reflects rapid growth rates (Ricqlès, 1980; Ricqlès et al., 1991; Castanet et al., 1993; Reid, 1996, 1997). Similar tissues are seen in living cows, horses, elk, and other large mammals, as well as among large birds. But as we will show, this pattern is not always true for small avian and non-avian dinosaurs and pterosaurs. The question we ask in this paper is why not: why do the tissues vary among dinosaur and pterosaur bones? To investigate it, we place known dinosaurian and pterosaurian osteohistological data in phylogenetic and ontogenetic contexts.

MATERIALS AND METHODS

Transverse and longitudinal thin-sections of cortical bone were taken from the specimens described below in the collec-

tions of the University of California Museum of Paleontology (UCMP), the Museum of the Rockies (MOR), and the National Geological Museum of China (NGMC). These were supplemented by specimens from the Yale Peabody Museum (YPM), the Carnegie Museum of Natural History, Pittsburgh (CM), the Ray Alf Museum, Claremont, CA (RAM), the Geologisk Museum, University of Copenhagen (MGUH), and the Virginia Museum of Natural History (VMNH). The thin-sections were processed according to standard techniques of preparing fossil bone tissues (e.g., Wilson, 1994). The specimens of *Scutellosaurus*, described by Rosenbaum and Padian (2000), were collected by James M. Clark during a UCMP field expedition to the Kayenta Formation of northern Arizona in 1983 (locality data on file at UCMP).

Sections were taken from the mid-shaft regions of the long bones specified in the text and figure captions. Although there can be substantial variations in tissue growth and expressions of histological features such as growth lines, endosteal bone, and secondary (Haversian) osteons among bones of a single skeleton (e.g., Horner et al., 1999), in each case we have tried to select well-preserved elements that are representative of the tissues reflected by the growth dynamics of the skeleton.

RESULTS

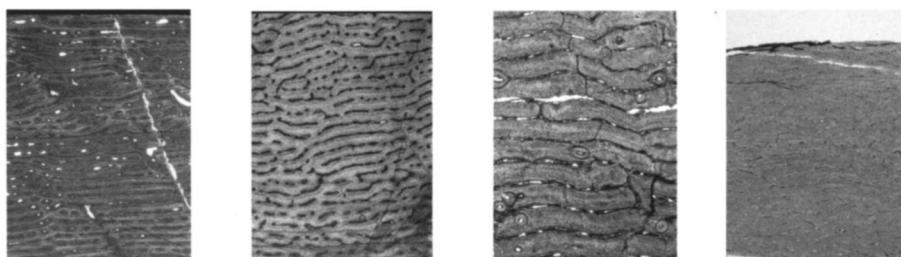
Histology of Small Dinosaur Bones

By "small dinosaurs" we mean those with total adult lengths of 1.5 meters or less. Although the ontogenetic stage of a given fossil vertebrate is not always obvious, there are several ways to assess adult size in fossil reptiles, using both gross anatomical (Bennett, 1993), and histological (e.g., Castanet et al., 1993; Padian et al., 1995; Horner et al., 2000) criteria. The embryonic bone tissues of dinosaurs and other reptiles have been described for comparative purposes (Horner et al., 2001), and do not require further discussion here.

Scutellosaurus—*Scutellosaurus* is the most basal thyreophoran ornithischian dinosaur (Colbert, 1981; Sereno, 1986). Like fabrosaurids, which are regarded as the most basal clade or paraclide of the Ornithischia (Peng, 1997), *Scutellosaurus* is small (femoral length about 5 cm) and ostensibly bipedal, judging from its forelimb-hindlimb disparity. The thin-sections of radius, femur, and tibia were taken from two specimens, one about 20% larger than the other (Rosenbaum and Padian, 2000).

The mean diameter of the bone wall of the femur (UCMP 170829, Fig. 2) is about 1.25 mm. The inner cortex is fairly well vascularized, but less than in most ornithosuchians (e.g., Cretaceous pterodactyloid pterosaurs [Ricqlès et al., 2000], theropods [Chinsamy, 1990; Varricchio, 1993 and see below], sauropodomorphs [Chinsamy, 1993; Rimblot-Baly et al., 1995; Curry, 1999; Sander, 2000], and derived ornithopods [Chinsamy, 1995; Horner et al., 1999, 2000]). Woven bone tissue of periosteal origin surrounds the numerous primary osteons, most of which are parallel and oriented longitudinally. A few secondary osteons are scattered in the deep cortex; there is a thin layer of first-generation secondary osteons on the sides of the bone where cortical drift takes place, and also an accumulation of endosteal lamellated bone. Vascular canals are mostly longitudinal, but occasionally there are some mostly oblique or circular

FIGURE 2. Histological patterns in dinosaurs and other archosaurs. Large dinosaurs (first row) show the "typical" fibro-lamellar pattern of large birds and mammals described by Ricqlès (1980), Reid (1996, 1997), and others. However, small dinosaurs and pterosaurs (second and third rows) have bone tissues that suggest slower growth. Crocodylians (fourth row), like other pseudosuchians, generally grow even more slowly than the small ornithosuchians, but some, such as captive-bred alligators and the small, gracile Triassic form *Terrestrisuchus*, show evidence of more rapid growth in their greater vascularization and occasional deposition of fibro-lamellar bone. Other dinosaurs (bottom row) are illustrated for comparative purposes (see text). Scale bar is 444 μm for *Eudimorphodon*, 4 mm for *Herrerasaurus* and *Troodon*, and 1 mm for all others. Femur of *Psittacosaurus* courtesy of G. R. Erickson. Other specimens from MOR and UCMP histological collections.

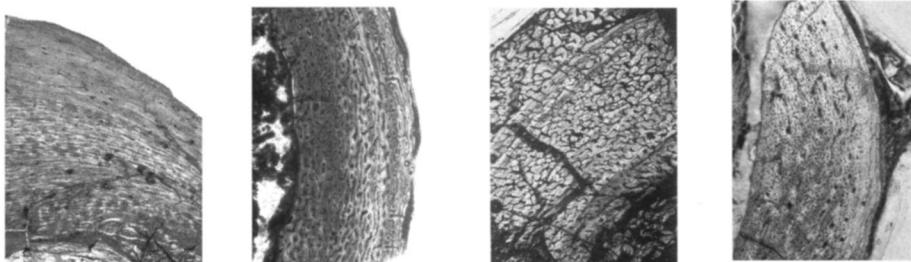
**Large Dinosaurs
and Pterosaurs**

Maiasaura

Allosaurus

Apatosaurus

Pteranodon

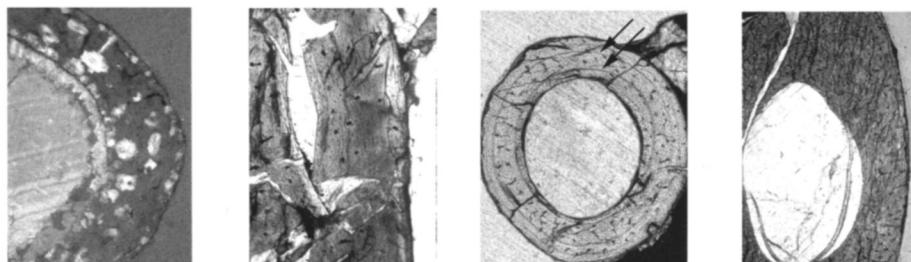
Small Dinosaurs

Scutellosaurus

Orodromeus

Psittacosaurus

Confuciusornis

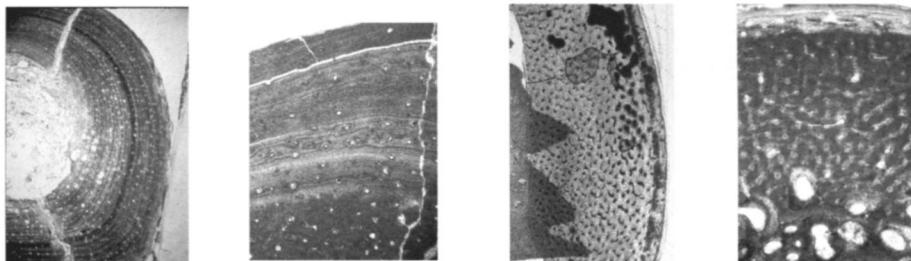
Small Pterosaurs

Eudimorphodon

Dimorphodon

Rhamphorhynchus

Pterodactylus

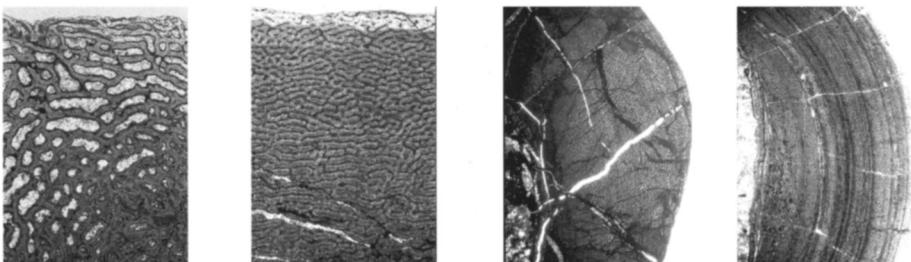
Crocodylians

Wild Alligator

?Leidyosuchus

Terrestrisuchus

Lab Alligator

Other Dinosaurs

Young Lambeosaurus

Coelophysis

Herrerasaurus

Troodon

anastomoses, especially in the middle of the cortex. There is less vascularization toward the most external cortex, where the vascular canals are smaller, but there is no sub-periosteal avascular bone tissue. The bone wall thickness is relatively high for a dinosaur—nearly 30% of the diameter—and the vascularization in the inner cortex is not substantially higher than in the outer cortex, suggesting that a roughly constant growth rate was maintained for most of the animal's life. No LAGs are observed. In sum, the growth profile suggested by this femur is very much like that of the captive, optimally raised alligator described below.

A radius sectioned close to the midshaft (UCMP 130580, Fig. 3A) has a few vascular canals close to the endosteal surface, but hardly any canals through the rest of the cortex, and those are tiny. Osteocyte lacunae are uncommon and scattered. There are some recognizable fibers in the bone, but the bone is best characterized as lamellar-zonal. There is a perimedullary layer of endosteal bone. In these respects this bone strongly resembles the bones of lizards (Buffrénil and Castanet, 2000), and suggests very slow growth at this stage, especially near the periosteal edge where the bone is almost acellular. At least seven LAGs are visible in the outer half of the cortex alone. A number of structures superficially resemble Sharpey's fibers.

A radius from another specimen (UCMP 170829, Fig. 3B) was sectioned through the metaphysis. The periosteal bone has no endosteal lining because the endosteal edge of the cortex is endochondral bone. The outer cortex is parallel-fibered, with a few

scattered longitudinal vascular canals (some regions have more, some have none). The osteocyte lacunae are flattened and organized into more or less circumferential layers. Again, there is no evidence of fibro-lamellar tissue. Some Sharpey's fibers appear in the external cortex. There is no evidence of secondary (Haversian) tissue, but the periosteal surface is rough and suggests that some of the most external tissue may be missing. In longitudinal section (Fig. 3C), the same radius shows well-ossified bone right up to the surface. There is a very slight thickness of calcified cartilage at the "epiphyseal" surface; some small islands of calcified cartilage persist deep in the metaphysis. (The term "epiphyseal" is used advisedly because the actual cartilage plate is not preserved; only the underlying calcified cartilage remains.) These features suggest that this animal is not a juvenile (Horner et al., 2000).

In the tibia, the vascular canals are nearly all longitudinal, small in diameter, and commoner in the mid-cortex than in the outer cortex, which is nearly avascular (UCMP 130580, Fig. 3D). At least three LAGs are present. One is in the deep cortex, and another is in the upper third, delineated by a layer of primary osteons. Above this point vascular canals are very rare. A third LAG appears in the outer cortex at the base of a lamellar, nearly avascular layer in which osteocytes are still common. Through the rest of the cortex, osteocytes are organized as in parallel-fibered bone; that is, they are flattened and in more or less circumferential layers. There is no evidence of fibro-lamellar

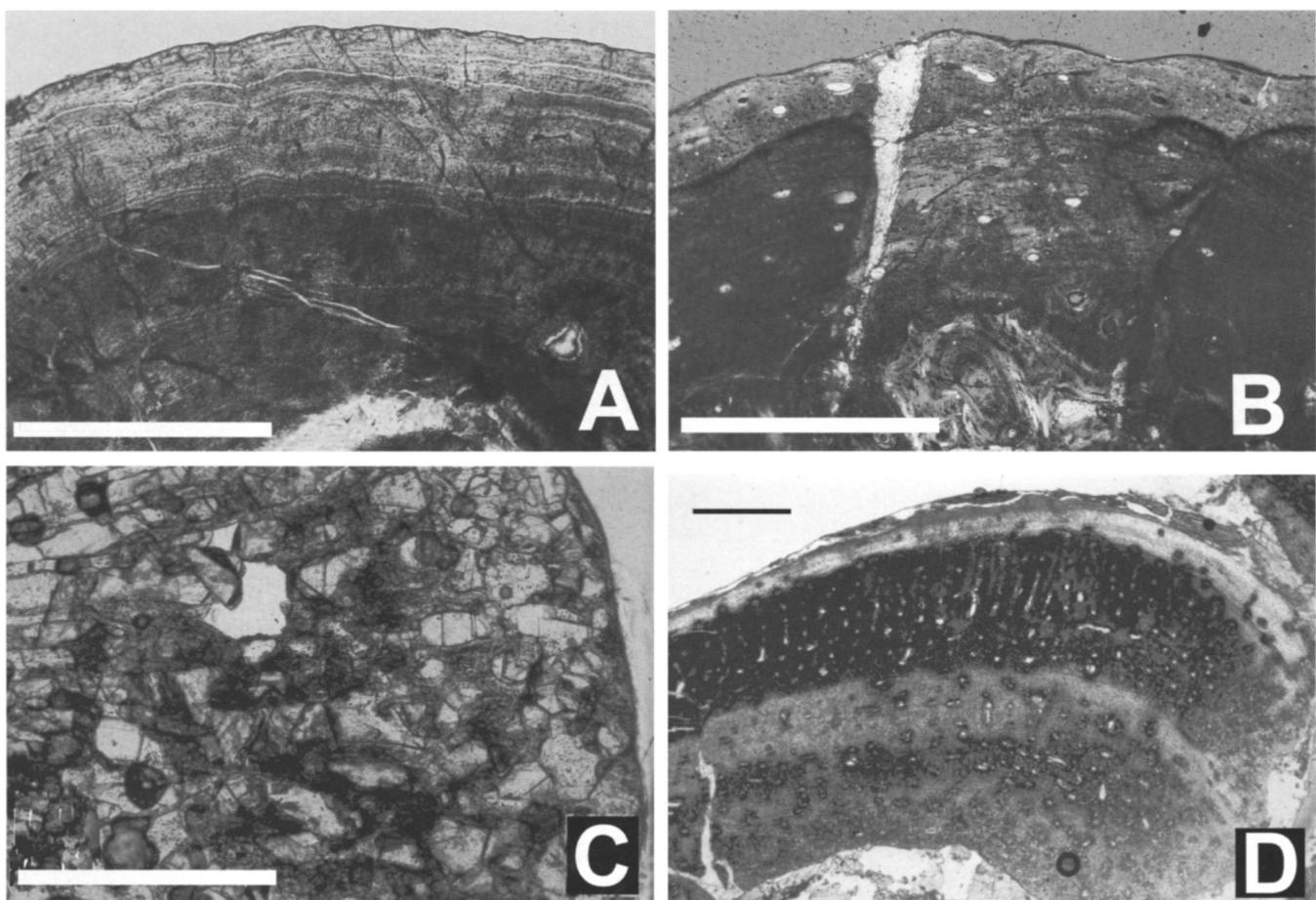


FIGURE 3. The early Jurassic basal thyreophoran *Scutellosaurus* (Colbert, 1981; Rosenbaum and Padian, 2000). **A**, general view of the cortex of a radius (UCMP 130580), with few, small vascular canals and uncommon scattered osteocytes. This is a "lamellar-zonal" pattern. **B**, transverse section, detail of the external cortex through the metaphysis of another radius (UCMP 170829), showing parallel-fibered matrix with few vascular canals. **C**, longitudinal section through the same specimen, depicting well ossified bone right to the "epiphyseal" surface, formed by a thin coat of calcified cartilage cells. **D**, tibia of UCMP 130580, showing externally decreasing abundance of narrow, longitudinal vascular canals. The deep cortex does not suggest high growth rates earlier in ontogeny. Femur illustrated in Figure 2. Scale bars are 1 mm.

organization except perhaps deep in the cortex, associated with some primary osteons. There is no evidence of endosteal bone.

In summary, there is very little if any typical fibro-lamellar bone in most of these elements; instead, the bone is parallel-fibered and not highly vascularized compared to the bones of most dinosaurs (e.g., Reid, 1996). Its “lamellar-zonal” structure is similar to that of crocodylians. The vascular canals are almost entirely longitudinally oriented and tend to be more sparsely distributed toward the outer cortex. The thickness of the bone wall suggests that this relatively poorly vascularized bone tissue was not a recent change from the more highly vascularized bone laid down earlier in life, but was fairly typical of the animal’s overall growth (Fig. 3D). The general histological features of the bones of the larger specimen of *Scutellosaurus* suggest that growth was slowing, and was probably near completion.

Orodromeus—This is a genus of hypsilophodontid dinosaur known from the Late Cretaceous Two Medicine Formation of Montana (Horner and Weishampel, 1988; Scheetz, 1998), about 1.5 meters in adult length. Scheetz (1998) provides a complete description of the osteology, and Ricqlès, Horner, and Padian (in press) summarize the histology; here, we describe for comparison only the adult femur.

The diameter of the femur (Fig. 2) is approximately 15 mm and the length 17 cm long (approximately three times the length of the femur in *Scutellosaurus*); the bone wall thickness is 2–3 mm. A thin endosteal layer of lamellated bone is present; there are at least three LAGs, which have not been observed in some other hypsilophodontid specimens (Chinsamy, 1995; Chinsamy et al., 1998). The vascular canals are mostly longitudinally oriented; the bone is more vascularized than in crocodylians and *Scutellosaurus*, but not as much as in hadrosaurs such as *Maiasaura* at this general size (Horner et al., 2000). As expected, there is higher vascularization in the deep cortex, decreasing toward the periosteum. The cortex is formed of fibro-lamellar and parallel-fibered bone, the latter especially toward the outer edge. Some secondary osteons occur very deep in the cortex. The tissue organization of this bone is intermediate in many respects between crocodiles and *Scutellosaurus* on the one hand and *Maiasaura* on the other.

Psittacosaurus—The bone histology of this basal ceratopsian (Fig. 2), known from the late Early Cretaceous of China and the early Late Cretaceous of Mongolia, was recently described by Erickson and Tumanova (2000). Femur length of the available specimens of *P. mongoliensis* ranged up to 21 cm, reflecting the typical adult size of the species, about 2 m in total length. Although Erickson and Tumanova lacked the early stages of growth, they identified seven further stages distinguished by femoral length and numbers of LAGs, which they took to be annual.

Psittacosaurus shows a pattern reported for the first time among dinosaurs, large and small, in that some of its bones seem to have experienced a growth spurt as it reached adult size. The bone matrix was woven-fibered throughout, already suggesting higher growth rates than in typical reptiles of today, such as crocodiles and lizards. But Erickson and Tumanova found that the orientation of the vascular canals in the femur and tibia progressed from predominantly reticular to radial, and vascularization appears to increase, reflecting rapid circumferential growth (Erickson and Tumanova, 2000:figs. 1C, 2C).

Avascular and poorly vascularized layers of parallel-fibered bone occasionally and irregularly interrupt the cortical matrix, as do typical LAGs. These structures could be taken for annual respires in active growth and deposition of bone. However, the tissue matrix between some of the more broadly separated annuli is highly vascularized. Extensively anastomosing canals radiate in all directions and frequently traverse the annuli of parallel-fibered bone, suggesting a higher rate of growth than the 6–7 μm per day that would characterize a yearly cycle (Amprino,

1947; Castanet et al., 1996, 2000; Margerie et al., 2002). Indeed, some intervals between annuli are an order of magnitude thinner than this, yet are composed of the same kind of well vascularized tissue, which would seem to question the inference that the annuli are truly annual.

Erickson and Tumanova estimated nine years to reach 2-meter adult size, though they lacked the early stages of ontogeny (younger than their “3-year-old” stage). Their growth curve of extrapolated mass for *Psittacosaurus* was sigmoidal, despite no evidence of slowing to the maximal size and an absence of early ontogenetic stages. The sigmoidal curve assumes very little growth until the “3-year-old” stage, based on their Developmental Mass Extrapolation. No external fundamental system (Cormack, 1987) or other indicator of termination of growth was reported, though some intracortical osteoclastic resorption cavities without lamellar infilling were found. Nevertheless, the known maximal size of 2 m seems to be well established for the genus (Sereno, 1997), so these specimens are ostensibly adults. Furthermore, although the growth curve for long bone lengths (as opposed to body mass) of *Maiasaura* is hemiparabolic, reflecting tapering rates with age, and that of *Psittacosaurus* is sigmoid, according to Erickson and Tumanova (2000), both dinosaurs show linear curves (Fig. 4) in the percentage of adult growth reached per year, suggesting a steadier overall growth.

As we explain below, however (see Discussion: alternative hypotheses), the specific kinds of fibro-lamellar tissue patterns may have more overlap in their depositional rates than previously supposed; if so, this will affect reconstructions of patterns of growth trajectories.

Maiasaura—This hadrosaur is quite a large dinosaur, reaching its seven meters of adult length in about seven years (Horner et al., 2000). We include it here to contrast its histology with those of smaller forms, using a very young ontogenetic stage (only a few months old). The diameter of the nestling femur (MOR GS400 F-4; Fig. 2, bottom row), approximately 5 cm long, is approximately 15 mm, but the marrow cavity is larger and so the bone wall is thinner than in *Scutellosaurus*. The cortex comprises mostly densely vascularized fibro-lamellar tissue of the laminar or plexiform types, depending on the region of the bone. The canals are mostly circularly and longitudinally oriented, with some radial and oblique canals. There is no discrete endosteal or periosteal layer at all and the bone matrix is homogeneous in texture. Osteonal development has begun with abundant osteocytes oriented around the vascular spaces. This is typically fast-growing tissue from an individual that would be characterized as a nestling (Horner and Makela, 1979; Horner and Weishampel, 1988; Horner et al., 2000). Obviously this animal was growing far more rapidly than *Scutellosaurus* was at the same size.

Coelophysis—This femur is from a nearly adult specimen (UCMP 129618) that may have reached nearly 1.7 meters in length (Padian, 1986). The femur (Fig. 2) is nearly 25 cm long, its mean diameter is 22 mm, and its mean cortical thickness is 5 mm. Therefore it is considerably larger than the *Scutellosaurus* specimen, but still small for a typical Mesozoic dinosaur. The cortex of this highly vascularized bone, previously figured by Colbert (1995), is dominated by well-organized fibro-lamellar bone in which most vascular canals are circumferential and longitudinal, anastomosing radially. There is an endosteal layer of lamellar bone around the medullary cavity, but no LAGs. This cortical tissue is typical of the cortical matrix of some large living birds, such as the rhea or turkey vulture, and is comparably well vascularized. Similar tissue was figured by Chinsamy (1993) for the closely related *Syntarsus*, in which LAGs were identified. The sub-periosteal bone in the present specimen is characterized locally by a thin, less vascularized layer in which longitudinal canals are scattered, suggesting the onset of cessation of growth and perhaps the initiation of the EFS (Ricqlès et al., 2001). Even though this may be a nearly adult individual, the tissues through-

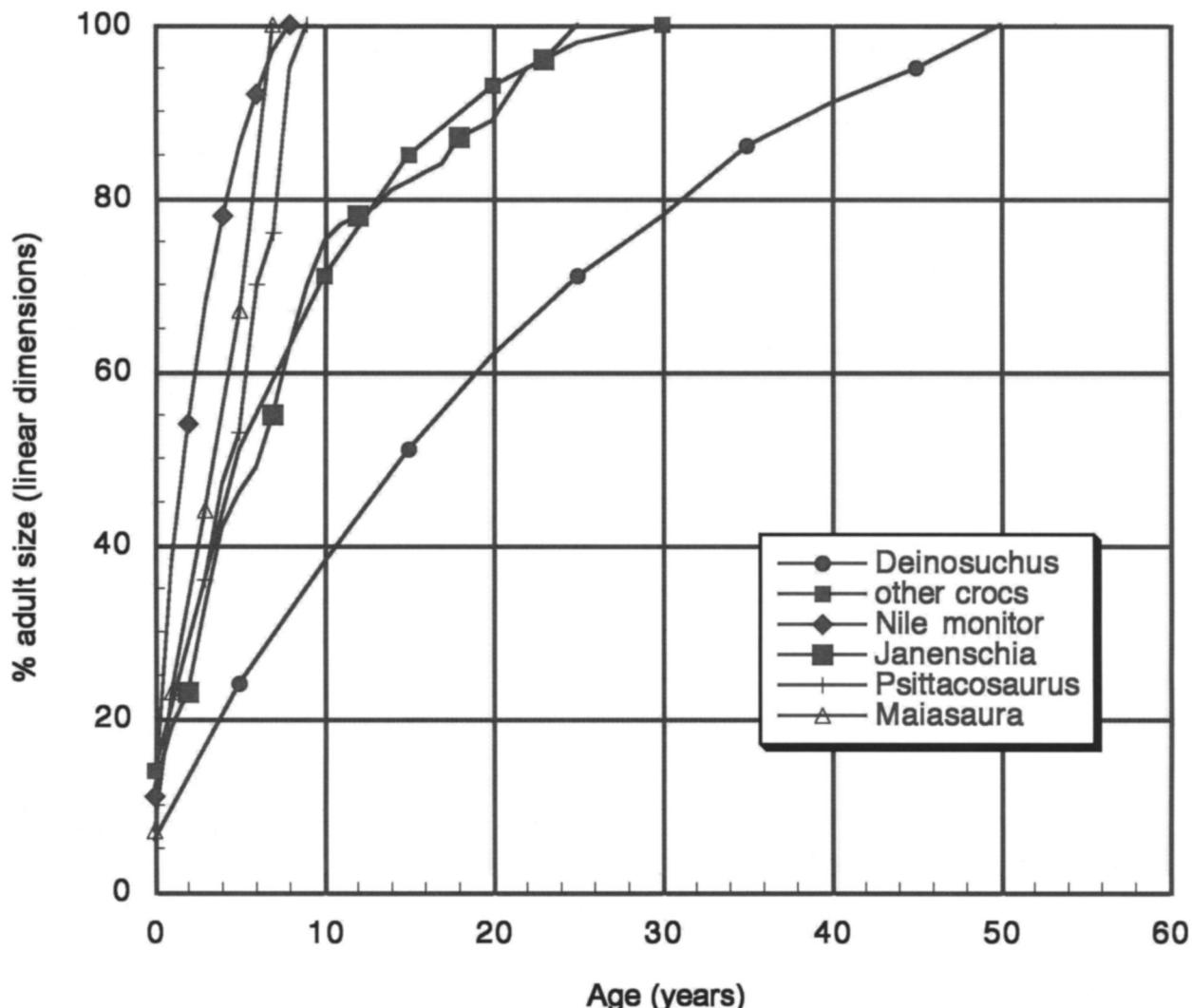


FIGURE 4. Small animals tend to reach adult size faster than large related animals do; but even so, some kinds of animals grow much more rapidly than others (see Figure 1). This graph plots the pace at which adult size is reached. The Nile monitor (de Buffrénil and Castanet, 2000) reaches its adult size at a pace comparable to dinosaurs such as *Maiasaura* (Horner et al., 2000) and *Psittacosaurus* (Erickson and Tumanova, 2000), and mid-sized crocodiles (Erickson and Brochu, 1999) have a pace relatively similar to the sauropod *Janenschia* (Sander, 2000). However, the Nile monitor has a snout-vent length of a meter or less, whereas this length is nearly five meters in *Maiasaura*; *Janenschia*'s mass was nearly 200 times that of an average crocodile. *Deinosuchus*, as the curves in Erickson and Brochu (1999) show, largely extends the trajectory of typical crocodiles. Hence in this figure it appears to reach its gigantic adult size at a slower rate than in smaller crocodiles, but this merely reflects its larger adult size.

out the cortex suggest much higher growth rates than in the smaller, nearly contemporaneous *Scutellosaurus*.

Confuciusornis—Chiappe et al. (1999) summarized the osteology of this Early Cretaceous genus from the Liaoning province of China, perhaps the most basal known bird after *Archaeopteryx*. Our histological study (Ricqlès et al., 2003b) was based on a full analysis of the long bones of a single, ostensibly adult specimen (MOR 1063 for the histological thin-sections; NGMC 98-8-2 for the skeleton). Here we briefly discuss the femur (Fig. 2), which is 5.6 cm long in an animal approximately the size of a small crow. The most external part of the cortex of the femur is formed by mostly nonvascular, parallel-fibered tissue, and the bulk of the cortex comprises the typical fibrolamellar tissue where the vascular canals are primarily longitudinal and circular, forming primary osteons. Some faintly circular organization of the woven matrix can be observed. Numerous secondary osteons appear in the deep periosteal cortex, sometimes overlapping an earlier generation; some of these have been eroded and resorbed

during the centripetal deposition of endosteal bone around the marrow cavity. The secondary osteons appear relatively uniformly around the circumference of the inner cortex of the femur, which is not always the case in other bones.

A dinosaur with a relatively short growth period (perhaps as short as 8–13 weeks; Ricqlès et al., 2003b), *Confuciusornis* flew and had feathers, so was ostensibly endothermic. Yet it seems not to have grown as quickly as living birds of similar size do; and some enantiornithines (another basal group of Mesozoic birds) apparently grew even more slowly (Chinsamy et al., 1995; Ricqlès et al., 2001, 2003b; Padian et al., 2001). However, evidence for an early phase of rapid post-hatching growth may have been completely eroded away by the marrow, and hence not recorded in the adult skeleton (Ricqlès, 2000; also possible for pterosaurs; see below and Ricqlès et al., 2001). The fibrolamellar tissue typical of its cortex is of a type commonly laid down by birds at 6–8 μm or more per day, based on rates derived from the mallard (Castanet et al., 1996). At such rates, *Confuciusornis* may have

reached adult size in as little as half a year (Ricqlès et al., 2003b); but Margerie et al. (2002) have significantly revised upward the rates for avian tissues first based on the mallard alone. These tissue patterns suggest growth rates that may have been comparable to or perhaps slightly lower than in the larger immediate relatives of *Confuciusornis*, the coelurosaurian dinosaurs, as well as in large extant birds, which reach their large adult size relatively quickly (Padian et al., 2001).

Histology of Small Pterosaur Bones

In a previous study of the bone histology of pterosaurs, Ricqlès et al. (2000) described and discussed tissues from nine taxa of pterosaurs. Two of these (*Dimorphodon* and *Dorygnathus*) are basal pterosaurs from the Early Jurassic, and the rest are pterodactyloids from the Late Cretaceous (Aptian-Albian through Maastrichtian). All but *Dimorphodon* displayed highly vascularized fibro-lamellar cortical tissues that are extremely similar to those of birds such as the duck, the hawk, and the guinea fowl (Enlow and Brown, 1957) and to those of large dinosaurs (Reid, 1996; Horner et al., 1999, 2000). And, like birds, pterosaurs resorbed all but a thin shell of the outer cortex, making it difficult to reconstruct the ontogenetic history of bone tissue deposition without a full series of specimens. Ricqlès et al. (2000) noted that the cortical tissues of *Dimorphodon*, sampled from three specimens that appeared to be full grown to nearly so, seemed to reflect relatively thicker bone walls and slower growth than in other pterosaurs. It was not possible to determine why: the ontogenetic slowing of growth with age, a primitive condition for the group, or a reflection of overall low growth rates commensurate with relatively small size were all possibilities that could not be eliminated. It now appears that the tissues in question—fibro-lamellar bone formed of longitudinally oriented primary osteons embedded in a woven periosteal matrix—may grow at rates that overlap those of other tissue patterns (reticular, laminar, plexiform; see *Discussion*). The specimen of *Dorygnathus* described by Gross (1934) had more typical fibro-lamellar cortical tissues, but again, ontogenetic status could not be ascertained. These taxa were relatively smaller than other pterosaurs studied by Ricqlès et al. (2000): *Dimorphodon* had a total length of about 120 cm and a wingspan of about 1.7 m, whereas *Dorygnathus* was about 100 cm long with a wingspan of about 1.2 m.

Eudimorphodon—Jenkins et al. (2001) described a new species of the Late Triassic basal pterosaur *Eudimorphodon* as *E. cromptonellus*, based on a single specimen (MGUH VP 3393) from the Fleming Fjord Formation of Greenland. This specimen bears characters that make it perhaps the oldest, and certainly the smallest known pterosaur. To try to determine the ontogenetic status of the animal, we thin-sectioned a fragment from the mid-shaft of the femur (Fig. 2; Ricqlès et al., 2000).

Although the shafts of the long bones are generally not crushed, the osteocytes appear flattened. Much of the original tissue structure is obscure under the microscope (Figs. 2, 5A). The primary osteons are relatively numerous for the thickness of the cortex; they are longitudinally oriented and numerous around three-quarters of the cortical circumference. They are nearly always secondarily filled by mineral crystals, which obscure their structure so that it cannot be determined whether grossly woven periosteal tissues surrounded the osteons, which appears unlikely. Mineral crystals likewise cling to much of the inner cortical wall that surrounds the medullary cavity, which is also filled by crystals; so it is not possible to tell whether there was an endosteal lining of bone. A longitudinal view of the end of the bone (Fig. 5B) shows remnants of a chondral plate and subjacent trabecular bone struts that surround extensive metaphyseal spaces in large adult pterosaurs (Ricqlès et al., 2000). At the “epiphyseal” surface, islands of hypertrophied calcified cartilage may be suggested by tiny clear crystals that appear to

replace them in places in the “epiphysis.” “Ghosts” of calcified cartilage even appear to form part of the bony struts in the epiphyseal region. The large amount of cortical space that the minerals now occupy in the cortex suggests high vascularization and fairly rapid growth commensurate with the early stages of growth (Horner et al., 2001). However, given the condition of the specimen, all that can really be said is that there is no sign either of mature bone or of very fast-growing tissues of a small juvenile. The nearly equal lengths of the major long bones are typical of young pterosaurs (Bennett, 1995).

Dimorphodon—Ricqlès et al. (2000) briefly described some bone tissues from this Early Jurassic pterosaur, but at the time the somewhat anomalous tissue structures were difficult to interpret in broader context (see above). With the consideration of further material, along with that of *Rhamphorhynchus* and *Pterodactylus* (see below), a different pattern emerges that suggests limited if not slow growth in these genera of small pterosaurs. Here we consider two specimens, YPM 350 (the larger) and YPM 9182, each represented by a second wing-phalanx and a tibia-fibula (see Padian, 1983 for osteological descriptions).

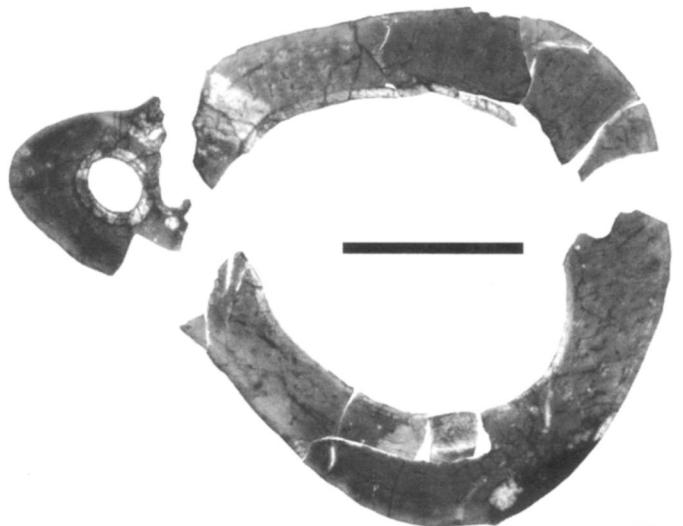
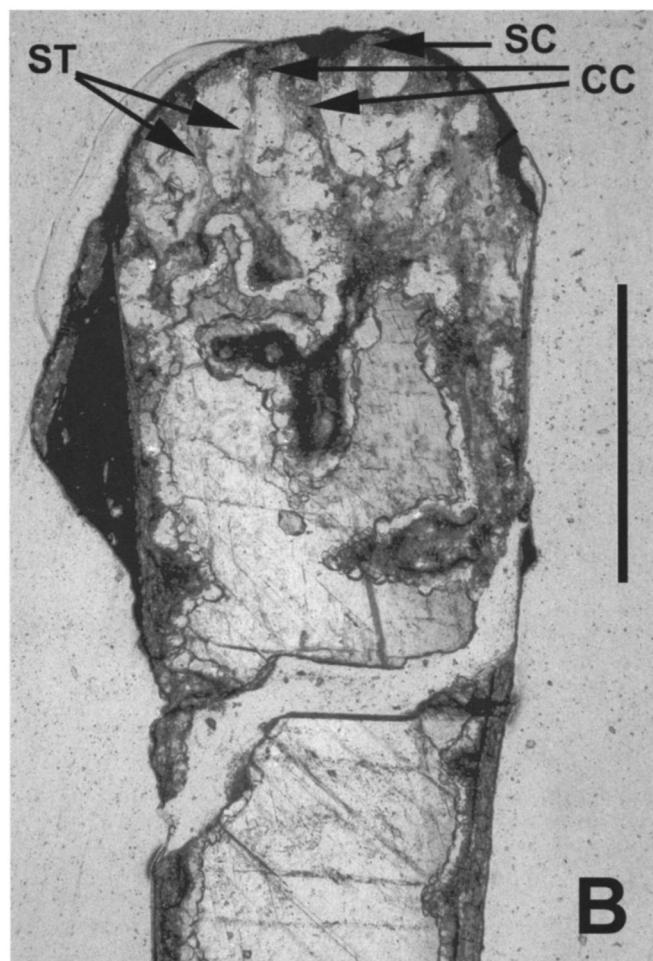
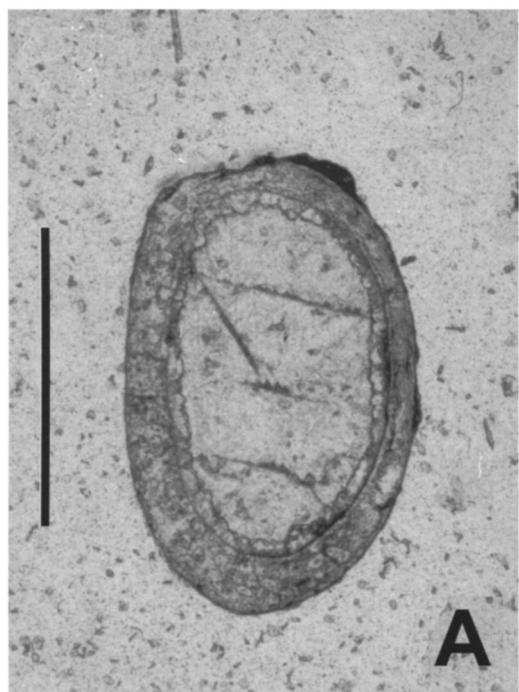
The smaller wing-phalanx (74 mm long) has a cortex with numerous, relatively large (for the cortical diameter, which is thin as in all pterosaurs) secondary osteon-like structures that are oriented longitudinally. This compacted coarse cancellous tissue has well-organized circumferential osteocytes that are tightly packed, and is completed by endosteal trabeculae. A few circumferential, radial, and oblique vascular anastomoses can be observed between the large osteons. One reversal line is present in the outer cortex, lining the tissue of periosteal origin in which the vascular pattern abruptly changes to small and sparser longitudinally oriented vascular canals in a poorly organized matrix; the outermost cortex appears nearly avascular. As in all these bones, a substantial layer of endosteal bone surrounds the medullary cavity. Some areas of the deep cortex suggest formation by endosteal compaction of an earlier spongiosa through processes of metaphyseal relocation. Because this section is submetaphyseal, not diaphyseal, it provides little information about radial growth dynamics.

The larger wing-phalanx (97 mm long), in contrast, is primary in structure with numerous longitudinal primary osteons that are surrounded by some woven tissue. The matrix shows little organization. Nearly all the osteons are longitudinal, with some radial anastomoses. It thus resembles the outer cortex of the smaller specimen.

The tissue patterns in the tibia-fibula are much like those of the wing-phalanx. The smaller specimen (85 mm long) has a thin cortex with fewer osteons than in the wing-phalanx; these sometimes anastomose radially (Fig. 5C). The fibula is completely fused at this midshaft level, as it is to the proximal end (Padian, 1983). It has three central cavities lined with endosteal bone that represent the medullary cavity. The larger tibia-fibula (104 mm long; Fig. 5D) illustrates coossified elements, with tissues similar to those of the previous specimen; the fibula has only a single central cavity. The canaliculi of the osteocytes are very well developed, which is typical of pterosaurs. The cortex is well vascularized; the longitudinal osteons are not large and show little woven tissue surrounding them.

In summary, most of the cortex is formed by a fibro-lamellar bone tissue with longitudinally oriented osteons, regardless of the bone element. The tissue structures suggest a period of rapid growth to at least the size represented by the smaller specimen, then a gentle slowing of growth that seems to be suggested at the end of bone deposition in the larger specimen. The cortex, then, shows typically “dinosaurian” rates, likely succeeded by lower rates more characteristic of a later phase of ontogeny.

Rhamphorhynchus—Cortical bone tissues from this Late Jurassic genus are described here for the first time (Figs. 2, 6). Two specimens were available to us: the smaller specimen (CM



11433) has a second wing-phalanx approaching 35 mm in length, and so fits Bennett's (1995) first size-class; in the larger specimen, from the Ray Alf Museum (V97017/258), the same bone is 90 mm long, and so approximates Bennett's (1995) second size-class. Apart from some notable features, the long bones are quite similar in most histological respects, but also quite unlike those of larger pterosaurs (Ricqlès et al., 2000). Typical of pterosaurs and some other clades (Rensberger et al., 2000), the radiating elongate and branching patterns of the osteocytic canaliculi are visible at high magnifications.

The radius (Fig. 6A) is between one-half and two-thirds the diameter of the ulna, and this is also true for the bone wall thickness. Despite its minuscule thickness, the smaller radius is well vascularized by minute primary osteons. The larger radius also has many vascular canals; most are longitudinal with some oblique radial anastomoses. There is no sign of an external fundamental system. The radius of the larger specimen has three lines of arrested growth, and the ulna has two, but part of the inner cortex of the ulna has been removed by cortical drift. There is no sign of a change in tissue type deposited on either side of any growth line, except a loss of vascular canals external to the mid-cortical LAG. The lines lack any kind of scalloped surface that would suggest the erosion of pre-existing tissue. The cortex of the smaller ulna is well vascularized throughout; in the larger specimen, the inner cortex resembles the smaller specimen in being nearly plexiform in vascular construction, and it has many more canals than its outer cortex or than the cortex of the radius, suggesting slower growth for the radius. The outer cortex of the larger ulna changes from mostly longitudinal canals of small diameter with radial and sometimes circumferential anastomoses, to less vascularized tissue with longitudinal canals, finally becoming avascular near the surface. Unlike the typical long bones of larger pterosaurs, this bone lacks a fibrolamellar matrix with the typical “bright lines” described by Currey (1984); instead, it is made of a finely parallel-fibered tissue of periosteal origin. A very thin coating of endosteal bone circles the marrow cavity in the larger specimen.

The second wing-phalanx of the larger specimen (Fig. 6B) is both well preserved and unusual in construction. A thin ring of endosteal bone lines the medullary cavity. Overall, the cortex has few vascular canals; most are in the inner cortex, which forms an “island” of fibro-lamellar bone tissue inside an essentially lamellar outer cortex. In this “island,” vascular canals are irregularly oriented and small in diameter. (In the corresponding bone of the smaller specimen, this same region forms most of the cortex and some of these canals open to the bone’s surface, suggesting that growth was quite active and not complete.) The outermost cortex, except near the leading edge of the bone, has no canals at all and is formed of parallel-fibered tissue. However, there is no sign of an EFS signaling curtailment of growth, as seen in other pterosaurs, especially large ones (Ricqlès et al., 2000). Two LAGs can be observed: one is between the inner fibro-lamellar cortex and the more external cortex, and has been partially destroyed by expansion of the medullary cavity; a second more external one loops around the circumference of the bone. Behind the medullary cavity, which has received a significant complement of endosteal bone, and below the trailing edge of the bone, the cortex becomes lamellar, but unfortunately the ventral edge of the bone has been lost.

The second wing phalanx of the smaller specimen is as just described, with a tiny fibro-lamellar cortex and a thin preserved layer of endosteal bone that surrounds the medullary cavity. There are few vascular canals, and they are all longitudinally oriented and small in diameter.

The femur and tibia of the larger specimen have a thin layer of endosteal bone that surrounds the medullary cavity. The bulk of the periosteal bone of the cortex is parallel-fibered. The canals of the moderately vascularized cortex are mostly longitudinal, and become slightly radial along half the circumference; in the tibia there are very few of them, all longitudinal. There are one to three LAGs in the femur (Fig. 2); the innermost LAG is resorbed by cortical drift along much of the circumference. Up to four LAGs can be seen in the tibia (Fig. 6C), which is nearly avascular with few osteocytes; its outermost cortex may show the onset of the EFS.

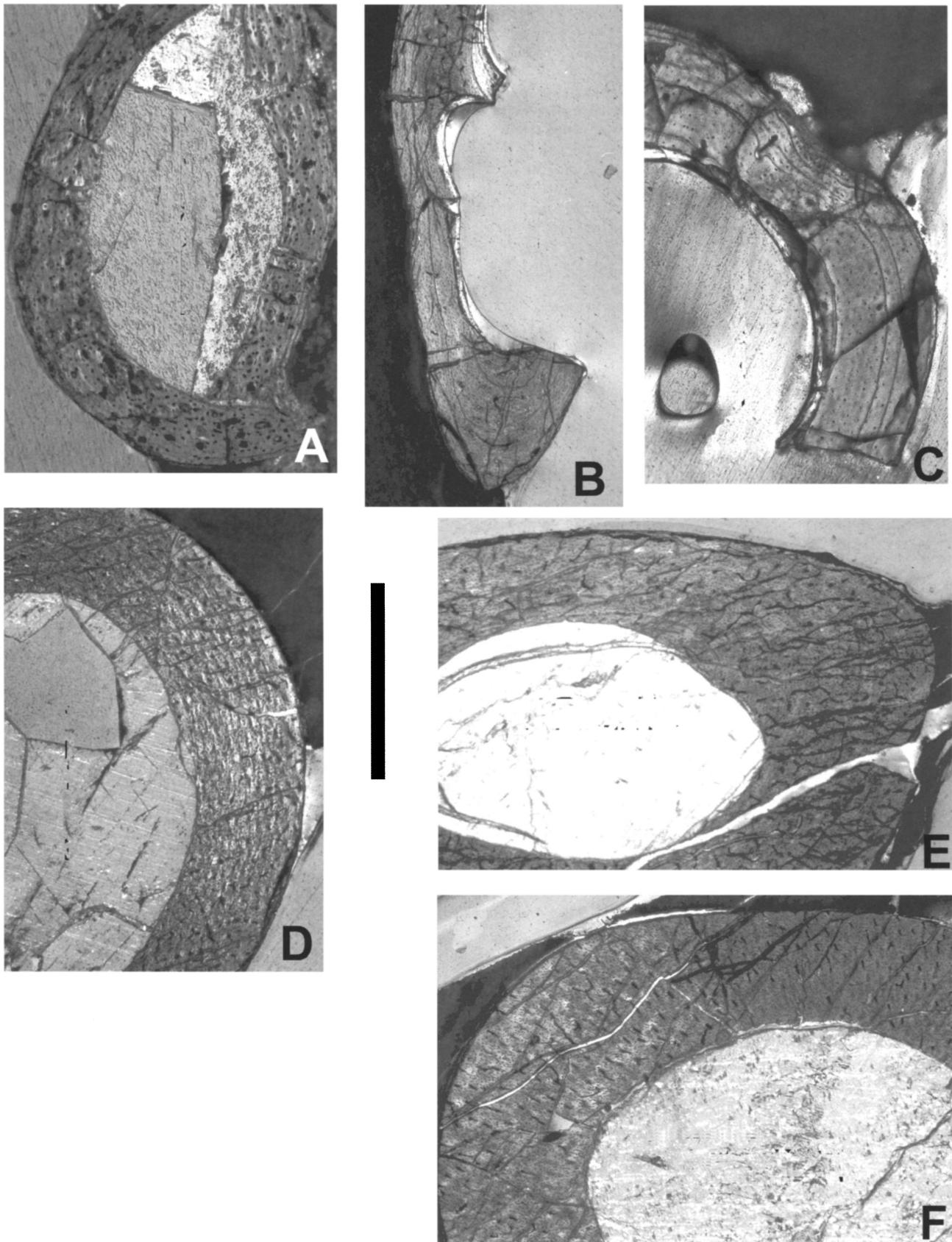
Like other bones, the coracoid of the smaller specimen has numerous but narrow vascular canals. The alternation of color patterning along one side suggests a “plywood” construction described for the pectoral girdle in large pterodactyloids by Ricqlès et al. (2000). There is a visible endosteal lining inside the thin periosteal bone wall, with remnants of what appear to be internal struts, as seen in other pterosaurs and birds, here made partly of typical endosteal tissue.

In sum, the bone tissues of these specimens suggest animals that may have grown in their earlier stages much as rapidly growing juvenile dinosaurs do (Horner et al., 2000), and in their later stages, about as slowly as (or more slowly than) *Scutellosaurus* (see below). The size ranges of the two available specimens approximately correspond to each of Bennett's (1995) two year-classes. The tissues of the larger specimen suggest growth rates on the order of 2.5–5 µm per day, if based on the mallard (Castanet et al., 1996), from which one might extrapolate a diametral growth of roughly 2 to 4 mm per year. The actual diametral growth in the wing-phalanges is 3 mm, and this would appear to be commensurate with the difference between Bennett's (1995) size classes. These wing bones are not round, however, but much like a posteriorly tapered wing in cross-section; the actual diametral expansion is closer to 0.20 mm (Fig. 6B), which would take only 40–80 days to grow at observed rates. These same tissues may have grown at faster rates than those observed in the mallard, as Margerie et al. (2002) have shown (see also Starck and Chinsamy, 2002). Clearly, more analysis of these complex bones is needed.

Pterodactylus—Cortical bone tissues from this Late Jurassic genus, the most basal pterodactyloid, are also described here for the first time, based on CM 11430. It is identified in the CM catalogue as a *Rhamphorhynchus*, but its long wing metacarpal indicates otherwise. Although the skull is missing, the specimen is in the size range of the larger pterodactylids (e.g., *Pt. longicollum* but smaller and with different proportions than *Gallo-dactylus*: Wellnhofer, 1978). The bone tissues of this specimen are remarkably homogeneous both within and among elements. In general, its histological profile is not similar to that of *Rhamphorhynchus*, just described, although this specimen is close in size to the larger *Rhamphorhynchus* specimen described above. By size alone it would be expected to be at the sub-adult or nearly adult stage; however, this interpretation is not clearly supported by the bone histology.

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FIGURE 5. Histology of early basal pterosaurs. **A–B**, *Eudimorphodon cromptonellus*; **C**, *Dimorphodon macronyx*. **A**, cross-section of the femoral shaft of *E. cromptonellus* (Jenkins et al., 2001). A detail of this section is shown in Figure 2. Mineral crystals have invaded and obscured details of the large primary osteons of the cortex, as well as its internal border. **B**, Longitudinal view of the end of the femur, showing chondral plate (sc) and subjacent trabecular struts (st), both of which contain islands of hypertrophied calcified cartilage (cc). **C**, cross-section of tibia-fibula of *D. macronyx* (YPM 9182H) at midshaft, showing generally slow-growing tissue with fewer osteons. **D**, cross-section of tibia-fibula of *D. macronyx* (YPM 350) at midshaft. Note complete fusion of fibula to tibia in both specimens. The wing-phalanx of YPM 9182 is illustrated in Figure 2. Scale bars are 1 mm.



The cortex of the ulna has a fibrous matrix with some evidence of “bright lines” (Ricqlès et al., 2000) and well developed lamellae of the primary osteons (Fig. 6D). The osteocytes are regularly distributed and more numerous than in the *Rhamphorhynchus* specimen just described. The vascular canals form an extremely dense network; they are mostly longitudinal, with some circular and radial anastomoses. A thin layer of endosteal bone surrounds most of the medullary cavity.

In the first wing phalanx, the vascular canals of the primary osteons are at least as numerous as in the ulna. These are also mostly longitudinal with some radial or irregular anastomoses that are extensive in places. Endosteal layering of the medullary cavity is extensive, and part of the deep cortex is formed by a crescent of compacted coarse cancellous tissue. This region has in turn been eroded internally and overlaid by the thickest part of the endosteal complement. The second wing phalanx (Fig. 6E) is generally similar to the first, but has more irregular vascular anastomoses; the third has a slightly more extensive endosteal layer. Both the second and third phalanges lack the region of secondary reworking in the deep cortex.

The femur and tibia are much like the wing phalanges histologically. They are extensively vascularized and show the typically extensive canalicular development of osteocytes in pterosaur bones. The wing phalanx (Fig. 2) has a crescentic region of secondary compacted coarse cancellous tissue along one internal edge, and endosteal bone covers only this part internally. The tibia (Fig. 6F) also lacks secondary osteons, and has mostly radial and longitudinal primary osteons that form a fibro-lamellar bone tissue with the periosteal matrix. A very thin layer of endosteal bone with few osteocytes surrounds the medullary cavity. Again, much of the earlier ontogenetic history of the bone is resorbed but the tissue patterns that remain suggest high growth rates at earlier stages.

Histology of Small and Large Crocodile Bones

For the purpose of comparison, we briefly describe the cortical tissues of a few members of the Crocodylia (Fig. 2): first, the Late Cretaceous–Early Tertiary crocodile *Leidyosuchus*; second, the small, gracile crocodylomorph *Terrestrisuchus*, from the Late Triassic or Early Jurassic (Crush, 1984); and third, a three-year-old laboratory-reared *Alligator mississippiensis*. Because these crocodiles are rather different from each other and accordingly show somewhat different growth patterns, they are useful in discussing growth rates of large and small dinosaurs and pterosaurs.

Leidyosuchus—The femur of *Leidyosuchus* (MOR 266) is composed of poorly vascularized lamellar-zonal tissue with longitudinal canals. Most canals are restricted to the deeper regions of the bone; large sections of the older bone have little or no vascularization. There are at least eight LAGs. This specimen is quite typical of the Crocodylomorpha in its bone histology, which has been detailed extensively by Enlow and Brown (1957), Buffrénil (1980), Hutton (1986), and Hua and Buffrénil (1996), and does not require description here. As Ricqlès et al. (2003a) showed, this pattern is also typical of pseudosuchians in general. An exception is the next form to be considered.

Terrestrisuchus—The humerus (VMNH 2274, Fig. 2; see also Ricqlès et al., 2003a) has a thick, homogeneous cortex that is well vascularized by narrow longitudinal canals with some radial

anastomoses locally. This pattern even becomes reticular in some regions, as in the mallard (Castanet et al., 1996). The fibers of the cortex show little spatial organization, and it is isotropic under polarized light. Some of the interstitial matrix is parallel-fibered. Many fibers are organized circularly toward the outer cortex, where one or two LAGs appear. The osteons that surround the vascular canals are small but well defined. Osteocytes are few but relatively large, and have many (mostly peripherally) radiating canaliculi. The organization of the cortical bone tissue exemplifies a simple form of the fibro-lamellar complex, in which the vascular channels are longitudinally arranged. Growth appears to slow only in the outermost quarter of the cortex. A thin coating of finely lamellar endosteal bone surrounds the marrow cavity.

The histological features suggest a growth regime that, based on Castanet et al. (1996; but see *Discussion*) is mostly continuous and relatively rapid for pseudosuchians, perhaps on the order of 7–10 µm per day or more. Growth appears to become more cyclical later in life, but was apparently not finished. The pre-adult stage of the specimen is also suggested by the absence of secondary osteons in the deep cortex often observed in larger pseudosuchians (Ricqlès et al., 2003a). This inference has now been strengthened by the suggestion that *Terrestrisuchus* is a juvenile form of *Saltoposuchus* (Allen, 2003).

Captive-bred *Alligator mississippiensis*—The growth of this specimen (MOR 95-9 F2-2) was artificially accelerated by keeping it at a constant temperature of 27°C, living in a fish hatchery with constantly available high-protein food supply. The specimen hatched at a length of approximately 30 cm, and was sacrificed at three years of age, when its length was approximately 150 cm. (Normal rates of growth in wild alligators initially approximate 30 cm per year or more, though this slows with age. Hatchlings of the Nile crocodile raised on a crocodile farm in Zimbabwe, kept at a constant temperature of 37°C and fed a diet of crocodile meat, grow a meter a year, twice their mean growth in the wild [Padian, unpub. data]). Despite its age, this specimen deposited no LAGs, unlike individuals in the wild (Buffrénil, 1980). Hence its rate of growth is known to be unusually high for an alligator.

The femoral cortex (Fig. 2), relative to the medullary cavity, is substantially thicker than in dinosaurs, and much thicker than in pterosaurs. The bone matrix is mostly parallel-fibered, with extensive osteonal development. Most vascular canals are longitudinally oriented. There is no endosteal layer surrounding the perimedullary cavity; some endosteal bone appears as reworked trabeculae in the cavity. Secondary osteons appear in the deep cortex. The periosteal tissue is variably vascularized: along part of the circumference there are few or no circular canals, whereas in other parts the canals are more numerous, round to flattened, and sometimes even anastomosing as in the deeper cortex. A LAG may be forming at the periosteal surface, but because it has not yet divided into zones, this tissue cannot be called lamellar-zonal. It is very similar in most respects to the *Scutellosaurus* tibia, and so it could be suggested that *Scutellosaurus* was growing like a young alligator with artificially accelerated growth rates, at least twice that of extant wild alligators (Buffrénil, 1980).

Reid (1996, 1997) has figured the bone tissues of a wild-caught alligator that show anomalous patterns from those of typical

FIGURE 6. Histology of Late Jurassic pterosaurs. **A–C**, *Rhamphorhynchus*, **D–F**, *Pterodactylus*. **A**, cross-section of radius of *Rhamphorhynchus* (CM 11443), showing woven-fibered matrix with tiny longitudinal vascular canals. **B**, cross-section of second wing-phalanx of RAM V97017/258, showing gradation from vascularized internal cortex (top) to nearly avascular external cortex. **C**, cross-section of tibia of CM 11443, showing nearly avascular cortex with few osteocytes. The femur of the same specimen is pictured in Figure 2. **D**, cross-section of ulna of *Pterodactylus* (CM 11400), showing fibrous matrix with longitudinal canals that may anastomose radially. **E**, cross-section of second wing-phalanx. **F**, cross-section of tibia. The femur of the same specimen is pictured in Figure 2. Scale bars is 1 mm.

crocodylians and pseudosuchians (Ricqlès et al., 2003a), reflecting high growth rates at a post-nestling stage that would be unusual. However, examinations of other crocodiles shown here (see also Buffrénil, 1980), plus a variety of pseudosuchian relatives (Ricqlès et al., 2003a), clearly indicate a common phylogenetic pattern and invite further examination of Reid's specimen.

DISCUSSION

"Typically Dinosaurian" Growth

The long bone histology of most dinosaurs studied to date is characterized by well-vascularized fibro-lamellar bone in which most vascular canals are circumferential and longitudinal, with oblique and radial anastomoses (Padian et al., 2001; note discussion of *Coelophysis*, above). During ontogeny, a perimedullary layer of endosteal bone may form, and secondary (Haversian) osteons may invade the cortex, generally beginning in the deep cortex and spreading centrifugally through life. These patterns vary from bone to bone and from region to region within a bone, and depend largely on body size, bone size, ontogenetic stage, and functional-mechanical factors (Horner et al., 1999, 2000). Lines of arrested growth (LAGs), without the distinct avascular annulus seen in most basal tetrapods, may begin to appear in the skeletons of what can be termed "late juveniles" and "subadults" (Horner et al., 2000), but their onset may be delayed or they may be completely absent.

This tissue pattern obtains through most of life, but a different pattern of faster-growing tissue generally prevails in early ontogeny (Horner et al., 2001), and another pattern prevails late in life as growth slows and eventually nearly ceases. These late ontogenetic tissues are generally far less well vascularized, and a longitudinal orientation of the canals tends to predominate. An external fundamental system (EFS) of nearly avascular, lamellar periosteal tissue, often separated from the cortex by a LAG, and often containing a variable number of growth-related inflection lines within it, finishes the growth of the bone in many specimens. Because most Mesozoic dinosaurs were large and grew in this fashion, we term this general pattern of histological ontogenesis and maturation "typically dinosaurian." Many or most of its features are shared by typical large extant birds and mammals (see also Klevezal, 1996).

Although growth stages are known for very few taxa that have been examined so far, these patterns seem to be shared by most (especially large) dinosaurs and pterosaurs. As the data presented above indicate, however, *Scutellosaurus* and some other small dinosaurs and perhaps small pterosaurs do not appear to follow the "typically dinosaurian" pattern. Even in the deep cortex they do not reveal an early history of rapidly growing, well-vascularized fibro-lamellar bone typical of larger dinosaurs. If such a pattern was present at earlier stages it has been eroded, but (e.g., in *Scutellosaurus*) the thickness of the preserved cortex suggests that the stage of rapid growth seen in the embryos and perinates of extant amniotes and extinct dinosaurs (Horner et al., 2001) did not persist into later stages.

Two further factors need to be considered in analyzing growth of these bones and in comparing them to those of other animals. First, the speed of bone deposition is reflected largely by the process of deposition of the bone matrix (e.g., Castanet et al., 1996). One depositional process, which forms the so-called "lamellar-zonal" patterns of relatively slow growth, is simply accretional: lamellar bone matrix forms by periosteal deposition, although this may involve fairly dense vascularity at the osteogenic surface. The other process, which forms the so-called "fibrolamellar" patterns associated with rapid growth, is biphasic: the woven or "fibrous" bone matrix first formed by the periosteum creates open clefts full of unmineralized connective tissues that are later filled in by the "lamellar" component of primary os-

teons. This woven scaffolding can form at much higher rates than the incremental process of lamellar-zonal bone. For this reason, the "pseudosuchian" (primarily lamellar-zonal) and "ornithosuchian" (primarily fibro-lamellar) patterns of bone tissues within archosaurs have a relatively sharp evolutionary divergence reflected in their growth rates (Padian et al., 2001). The second factor to be considered is that the growth rates of the various tissue types within the fibro-lamellar pattern itself can overlap extensively; growth rates may not be correlated principally with the orientation of vascular canals but rather with the degree of vascularization (Margerie et al., 2002; see below).

Growth Rates and Strategies

Our artificially accelerated specimen of *Alligator*, as noted, grew nearly twice as fast as typical young (up to 3 years) crocodylians do. It shares some similarities, such as a preponderance of longitudinally oriented vascular canals and not much evidence of fibro-lamellar bone, with *Scutellosaurus*. There is no independent evidence for the age of the *Scutellosaurus* specimens, but the avascular periosteal layers in UCMP 130580 suggest that this specimen was at least nearly full grown. Up to this point, however, its tissues suggest that it had been growing much like those of the "accelerated" alligator.

Retrocalculating an average growth rate of 40 cm in length per year, *Scutellosaurus* could have reached adult length (about a meter) in two to three years from a reconstructed hatchling length of 10 cm, and this correlates with the number of LAGs found in the tibia of UCMP 130580. Assuming that the diameter of the femur at hatching was 2 mm, it could have grown at the average diametral rate of 3.5 mm per year (given a daily radial growth rate of 2.5–5 μm per day) to reach its eventual diameter in UCMP 170829 of 12.5 mm in three years. This diametral growth rate is 70% of the 5-mm average yearly rate seen in growing bones of *Maiasaura* (Horner et al., 2000) and is commensurate with rates initially observed in the mallard (Castanet et al., 1996).

In comparison, *Orodromeus* at this size is more highly vascularized than *Scutellosaurus* and the accelerated alligator, but not as much so as *Maiasaura*. *Confuciusornis*, in contrast, may have grown fairly rapidly in early stages of growth, but slowed in later ontogeny so that it shows the typical features of age seen in other dinosaurs. This slowing is clearly a departure from the pattern of more rapid growth in typical theropods, including larger living birds (such as the turkey vulture: Enlow and Brown, 1957, 1958; Ricqlès et al., 2000) and many extinct non-avian forms (e.g., *Troodon*, *Coelophysis*; Fig. 2), which show less slowing of growth in the external cortex (Ricqlès et al., 2001; Padian et al., 2001).

The differences in tissue patterns and, by implication, growth rates observed in these dinosaurs and the crocodile suggest different life-history strategies of growth. Small basal dinosaurs, with some exceptions, appear to have grown more slowly and steadily than typical dinosaurs, although generally faster than typical crocodiles and other reptiles do. The "typical dinosaurs" studied so far, such as *Maiasaura*, *Hypacrosaurus*, *Allosaurus*, and various sauropods (Fig. 2), are mostly of large size, so their growth strategy appears to have been to reach this large size as rapidly as possible, perhaps to avoid predation. However, even relatively basal saurischians, including the sauropodomorphs *Euskelosaurus* (Ricqlès, 1968) and *Massospondylus* (Chinsamy, 1990) and the theropod *Coelophysis*, as well as the basal dinosaur (or close relative) *Herrerasaurus* (Padian et al., 2001) appear to have grown more rapidly than *Scutellosaurus* and *Orodromeus*, and this is also true to a lesser extent for the small derived theropod *Troodon* (Varricchio, 1993) (Fig. 2).

A parallel situation can be seen in pterosaurs (Fig. 2): large Cretaceous pterodactyloids (wingspan 3–11 m) such as *Montanazhdarcho*, *Pteranodon*, *Quetzalcoatlus*, and related forms show

“typical dinosaurian” and even typical large birdlike bone growth (Padian et al., 1995; Ricqlès et al., 2000). However, as seen here, some smaller, basal pterosaurs of the Jurassic and Late Triassic (wingspan up to 1.5 m), especially *Rhamphorhynchus*, appear to have growth patterns more similar to those of smaller birds. More specifically, *Dimorphodon* and especially *Pterodactylus* share particular kinds of fibro-lamellar tissues with birds of similar size; this suggests elevated growth rates (Ricqlès et al., 2000; Padian et al., 2001). It is not clear whether the simpler tissue patterns observed in *Dimorphodon* could match the growth rates suggested by the more densely vascularized patterns of *Pterodactylus* (Margerie et al., 2002). There is no evidence of the slowing or cessation of growth in the external cortex of the *Pterodactylus* bones that we studied.

The extensive size range observed in the two specimens of *Rhamphorhynchus* is of interest to the question of pterosaur growth rates and possible “year-classes” represented in the Solnhofen Limestone (Bennett, 1995). The bone tissues of the smaller individual that we studied strongly suggest high growth rates, but almost no traces of this early stage of rapid growth are preserved in the larger specimen, except in the second wing phalanx. In the larger specimen, the more “mature,” slowly growing parallel-fibered bone suggests an adult condition and an age of perhaps three to four years. In summary, this situation again parallels that observed in small birds, whose adult skeletons provide little or no information about their very high growth rates early in ontogeny (Ricqlès et al., 2001, 2003b; Castanet, 2001).

The Evolution of Growth Rates in Dinosaurs and Pterosaurs: a Hypothesis

Fig. 7 shows a phylogeny of archosaurs, based on standard phylogenetic analyses (Sumida and Brochu, 2000), using the taxa discussed herein and in Padian et al. (2001). When features of bone histology are superimposed on this phylogeny, a general trend emerges but convergences and reversals of growth strategies are also apparent. Unfortunately, we do not have evidence for many crucial basal taxa, within and outside Dinosauria, such as basal ornithopods and dinosauromorphs such as *Lagosuchus* and *Lagerpeton*.

The relatively slow growth rates observed in crocodiles, and the well-known slow growth in other living reptiles (compared to extant endotherms of similar size), indicate that this slow growth pattern may have been primitive for amniotes, and possibly for archosaurs. Histological samples taken from the bones of basal pseudosuchian relatives of crocodiles, such as phytosaurs and aetosaurs in the UCMP collections, substantiates this inference of polarity among archosaurs (Padian et al., 2001; Ricqlès et al., 2003a). Relatively more rapid, but still not “typically dinosaurian” rates of growth are implied for basal ornithischians such as *Scutellosaurus* and *Orodromeus*. Rapid “typically dinosaurian” growth rates appear to have evolved independently at least in large pterodactyloid pterosaurs, large derived ornithopods, and saurischians. These rates are so far unstudied in larger thyreophorans, pachycephalosaurs, and ceratopsids.

The patterns of “typically dinosaurian” growth rates in ornithodirans are correlated to some extent with size, at least in the animals sampled so far. These patterns are in accordance with observations of growth rates in extant vertebrates: taxa of larger adult size generally grow at higher rates than taxa of smaller adult size (Case, 1978), although they usually do not reach their adult size sooner. However, the instantaneous growth rate in small taxa can temporarily equal or exceed that of large taxa (J. Castanet, pers. comm.). And, as the extensive studies of Klevezal (1996) show, there are substantial similarities between the bone growth patterns of some small mammals and those of small pterosaurs and basal birds such as *Confuciusornis*. However, we must stress that the relationship of body size to bone tissue pat-

terns is indirect at best, because it is entirely mediated by growth rates. (Small and large animals can grow at high or low rates, depending on the taxon.) In this case we are using actualistic indicators of growth rates in given tissues to characterize fossil bone (see Enlow and Brown, 1958, and a summary of later work in Ricqlès, 1976).

It is not known at what size the transitions to “typically dinosaurian” tissue patterns (and associated growth rates) have taken place, if the hypothesis is correct. However, based on our analysis they appear to fall between the adult sizes of *Scutellosaurus* and *Orodromeus* (up to 1.2 m) on one hand and *Coelophysis* (1.5 m and larger) on the other. Among pterosaurs, even small taxa with wingspans not greater than 1.7 meters or so appear to have evolved high growth rates, at least during early life.

The comparatively slow-growing tissues and persistence of LAGs seen in some limited available specimens of some basal Mesozoic birds (e.g., enantiornithines and to a lesser extent *Patagopteryx*) have suggested to some workers that these birds had not yet reached avian levels of endothermy and metabolism (Chinsamy et al., 1995, 1998). This is one possibility if physiology is inferred directly from a limited sample of bone tissue, which is often inevitable in extinct taxa. However, in phylogenetic context it would have to be inferred that these taxa are secondarily slow-growing (either in those individuals or in the lineages they represent). Thus, they would reflect a change in growth strategy that seems to return in some respects to the pattern of slow-growing basal dinosaurs discussed here (Ricqlès et al., 2001; Padian et al., 2001).

Alternate Hypotheses to Explain Tissue Patterns

We have couched our explanation of different tissue patterns in terms of growth rates reflected in living bone tissues, following “Amprino’s Rule.” Here we discuss two possible modifications of our overall theory (there may well be other possibilities). The first comes from phylogeny, and the second from new experimental results on growth rates.

First, our phylogeny suggests that higher growth rates are basal to ornithodirans, and that lower rates were plesiomorphic to Archosauria and its immediate outgroups, as for Amniota in general (Ricqlès et al., 2003a). This would be falsified if the tissue patterns seen in these basal groups, notably Archosauriformes, reflected higher rates of growth. In this context we note the anomalously high (for non-ornithodirans) growth rates that can be inferred from the tissues of the Early Triassic archosauriform *Erythrosuchus* (Gross, 1934). *Erythrosuchus* is also unusual in showing suggestion of pneumatization of some bones, although the critical evidence of communication via foramina with an internal chamber is not yet established for this taxon (Gower, 2000). It remains to be seen whether these patterns of histology and pneumatization are generally correlated. It will be equally important to know more about the histological patterns of other basal ornithodirans, such as *Lagosuchus*, in order to test hypotheses of character polarity.

Second, there is progress in the calibration of growth rates based on actualistic comparisons to living taxa. Based on Amprino’s Rule, differences in growth rates observed or inferred for various tissues of the fibro-lamellar complex have been thought to be linked to the density and orientation of the vascular canals (Ricqlès, 1976–77), although considerable overlap has been acknowledged (Castanet et al., 1996). Current experimental studies designed to quantify such rates more precisely are now emphasizing this overlap in depositional rates among the various fibro-lamellar tissue types (Margerie et al., 2002; Starck and Chinsamy, 2002), although it is still unknown whether the overlap persists amid the highest rates of deposition. Accordingly, it cannot be securely concluded at present that *within the fibro-lamellar complex* a given tissue type indicates a significantly higher growth

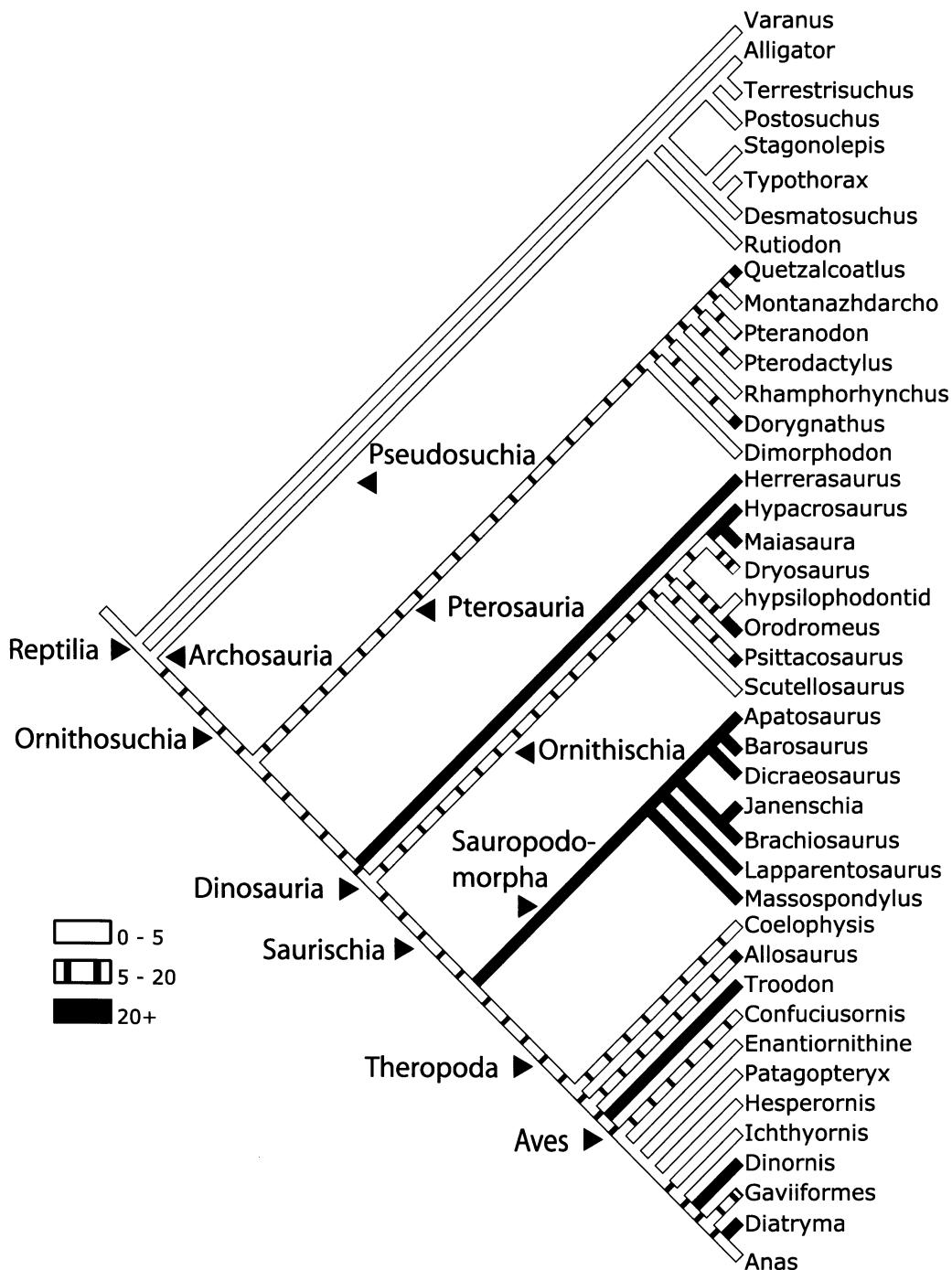


FIGURE 7. Cladogram of archosaurian taxa, after various sources, with estimated subadult long bone growth rates (in μm per day) superimposed. (Note that these are conservative values, and that there may be more overlap among rates for fibro-lamellar tissues than the key suggests; for explanation see text.) Rates were based on observations of cortical tissues of subadult femora and tibiae, compared to the same types of tissues of known growth rate in the mallard, ostrich, and emu (Castanet et al., 1996, 2000). Growth rate was optimized as a continuous-state character (with values adjusted from the key) on a standard phylogeny of archosaurs using squared-change parsimony in MacClade Version 3.08. Based on Padian et al. (2001), modified with new information on avian tissue growth rates provided by J. Castanet (pers. comm.).

rate than another. Hence the calibration of histological growth rates in our Fig. 7, based on rates for the mallard derived by Castanet et al. (1996), and modified following J. Castanet (pers. comm.), are conservative in their magnitude and may overlap more than indicated. However, all types of fibro-lamellar bone grow at demonstrably higher rates than do those of the lamellar-zonal type, which dominate the skeletons of most non-ornithodiran reptiles.

A question that proceeds from these new findings, then, is what factors besides growth rates might determine the depositional patterns of fibro-lamellar tissues? We have previously identified four major factors: phylogeny, ontogeny, mechanics, and environment (Ricqlès et al., 2000). If ontogenetic growth rates cannot entirely explain differential growth rates among fibro-lamellar tissue types, and if the animals are not physiologically different, we also cannot invoke phylogeny or environment,

because these organisms share common ancestors and they are found in the same faunas. The differences, then, especially between small and large taxa of the same clades, may relate to mechanical influences on growing tissues that modulate the types that are laid down (Margerie, 2002). In other words, the fibro-lamellar tissue types that we see in species of different sizes, and with different functions of their bones, may reflect mechanical stresses that are manifested differently in the expressions of bone tissues through ontogeny (e.g., Margerie, 2002). This productive area of research is outside our study presented here.

Erickson et al. (2001) quantified growth rates estimated from partial ontogenetic series of several dinosaurian groups, and concluded that growth in dinosaurs was sigmoidal, as it is in many extant vertebrate groups. We agree with them that dinosaurs and pterosaurs achieved their high growth rates probably in the Middle or early Late Triassic, certainly in the common ancestor of the two clades and perhaps as early as the divergence of these ornithosuchian groups from the pseudosuchians (Padian et al., 2001). Whereas the curves for these taxa may be sigmoidal, as they conclude, our findings suggest that a rapid phase of growth began earlier in ontogeny than the several years that they project. This difference would imply shorter times to maturity than Erickson et al. (2001) predict, but clearly more evidence from early post-eclosion stages are needed for nearly all dinosaurs, including the ones that they and we have studied.

In a related study, Chinsamy and Elzanowski (2001) inferred an early postnatal slowing of growth in two basal bird lineages from the Cretaceous. Our study of *Confuciusornis* (Ricqlès et al., 2003b) generally agrees with the idea that birds slowed the phase of growth that was rapid in their non-avian relatives, thus achieving small size (Padian et al., 2001; Ricqlès et al., 2001). However, none of these studies has been able to benefit from bone tissues of early post-eclosion stages, so it is difficult to substantiate patterns that are inferred to resemble those of precocial flying birds. We simply have insufficient evidence at present, though we agree that this idea is more plausible than the alternative that basal birds enjoyed long periods of altricial growth and intensive parental care.

CONCLUSIONS

The phylogenetic distribution of bone tissue patterns in archosaurs indicates that with few exceptions, pseudosuchians have maintained lower growth rates since their separation from ornithosuchians, at least by the mid-Triassic (Ricqlès et al., 2003a). Ornithosuchians, in contrast, are characterized by higher basal growth rates than those of crocodiles, but small taxa apparently grew at somewhat lower rates than larger taxa did. These high ("typically dinosaurian") rates seem to have evolved several times (at least in large pterodactyloids, large derived ornithopods, theropods, and sauropodomorphs). An alternative hypothesis is that moderately high to high growth rates are plesiomorphic for Archosauria, with secondary reversals to lower rates in some clades of small size as well as throughout Pseudosuchia (with few exceptions). These hypotheses require further testing of various ornithischian and dinosaurian outgroups among Ornithosuchia, especially basal fabrosaurs, heterodontosaurs, and other Dinosauriformes, as well as basal Archosauriformes and Archosauria (Ricqlès et al., 2003a). It may also eventuate that the differences among tissues within the fibro-lamellar complex reflect mechanical influences on the tissues that are related to body size or particular functions of the skeleton. We stress that single sections of isolated bones, without attention to skeletal variation and without ontogenetic control, are not likely to yield meaningful results (Horner et al., 1999, 2000; Erickson and Tumanova, 2000). Our sample is not ideal either phylogenetically or ontogenetically, though there is some control of both factors (Padian et al., 2001). An assessment of variation within skeletons

is not presented here for the sake of brevity, but is immaterial to the patterns that we discuss (Horner et al., 1999).

Our hypotheses could be falsified on at least two grounds. First, ontogenies of individual taxa, as more are elucidated, could show no patterns of histological change during the maturation of bone tissues. We think that this is unlikely, based on the range of living and extant taxa sampled so far, but we are prepared to accept anomalies into our generalization as part of the expected variation of nature. Second, as more ontogenetic patterns of archosaurian taxa are placed in phylogenetic context, it could turn out that the trends we see bear no correlation to size, even in phylogenetic context, and (or) that the patterns change so often in clades as to weaken statistically the evolutionary signal that we infer is present, based on evidence to date. Finally, improved calibration of depositional rates of tissues of living forms may force adjustments of the quantitative measures that we use here (Margerie, 2001; Margerie et al., 2002; see Fig. 7). However, unless these patterns turn out to be completely random, which studies do not suggest, it would not affect our overall conclusion that particular tissues reflect growth rates (following Amprino's Rule), and that these may change predictably as body size evolves in a clade. We further predict that the distinction between the growth rates of Pseudosuchia and Ornithosuchia, as reflected in their bone tissues, will remain clear.

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