

Dinosaurian growth rates and bird origins

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Dinosaurs, like other tetrapods, grew more quickly just after hatching than later in life. However, they did not grow like most other non-avian reptiles, which grow slowly and gradually through life. Rather, microscopic analyses of the long-bone tissues show that dinosaurs grew to their adult size relatively quickly, much as large birds and mammals do today. The first birds reduced their adult body size by shortening the phase of rapid growth common to their larger theropod dinosaur relatives. These changes in timing were primarily related not to physiological differences but to differences in growth strategy.

For most of the 160 years since dinosaurs were named, they have been considered typical, if overgrown, reptiles, and it was assumed that they grew at rates broadly similar to those of extant reptiles¹. Indeed, there was no particular reason to think otherwise, even though their upright stance and parasagittal gait led Richard Owen, in naming them, to put them in a completely new group of Reptilia. However, in the 1970s interest in the question of dinosaur metabolism renewed ideas about their growth strategies and rates^{2–5}. Some physiological models concluded that dinosaurs could have been perfectly ‘good reptiles’⁶ whose large size gave them the metabolic benefits of inertial homoiothermy without truly departing from an ectothermic strategy⁷. However, a growing body of literature on bone growth rates suggests that, whereas dinosaurs may not have grown at rates exactly like those of extant birds and mammals, they seem generally to have been more like them than like other extant reptiles.

Evidence for this shift in perspective comes largely from bone histology, the microstructural characteristics of bone that reflect ontogenetic, environmental, mechanical and phylogenetic factors⁸. Recently renewed efforts have begun to use these routinely sampled bone tissues to calculate growth rates^{9–20}.

Timing the growth of extinct animals

To time the growth of extinct animals, two lines of evidence are generally used, and both depend on homologous features in extant vertebrates and on simple actualistic reasoning (using the features of extant organisms to interpret the fossil record). First, the type of primary (appositional) bone tissue indicates the overall range of growth rate. A given type of primary bone tissue grows at the same range of rates in any taxon²¹; hence, it is presumed that a certain kind of tissue deposited in an extinct animal would have grown at the approximate rates that it does in animals today. Second, bone growth is often punctuated by the deposition of various rings, lines or annular structures that may reflect cyclical annual growth, seasonal stress or other endogenous rhythms^{2,4,22,23}, so they may be skeletochronological indicators. However, consideration of extant vertebrates demonstrates that the biological meaning of these indicators must be assessed on a case-by-case basis. Some growth rings are of relatively avascular bone that interrupts vascular tissues, representing a real change in the type of deposition^{2,4}; others merely comprise lines of temporary cessation of growth and even slight erosion of the bone surface^{2,11,24}; and some simply represent indefinite pauses with no erosion^{9,16,24}. Generally, ectothermic animals extensively produce rest lines that are annual or seasonal, but endothermic animals can also do so, even when temperature and food supply are maintained through the year^{23,25}. Moreover, different bones in the same skeleton can have sharply differing numbers of growth lines^{11,24}; the distance between successive growth lines does not always decrease regularly in some taxa¹²; and some taxa

closely related to those with copious growth lines may show none at all²⁶. Obviously the whole issue of bone ‘growth lines’ is linked more to organ-specific developmental dynamics, species-specific life-history strategies, and population-level interactions with their environments, than to overall patterns of thermometabolic Gestalt¹¹.

Dinosaurian versus reptilian growth rates

Comparing these two histological lines of evidence, our own investigations of extant and extinct archosaurs (including birds), as well as a survey of the published literature on bone histology, reveal a dichotomy between those archosaurs related to crocodiles and those related to birds and dinosaurs (Fig. 1). This distinction can be traced back to the division of the two lineages at least by the Middle Triassic, over 230 million years ago. In the hadrosaur *Maiasaura*, for example, the kinds of tissue typically deposited throughout the cortex of the long bones imply growth rates which suggest that maturity was reached at about seven years old and seven metres long¹¹. This estimate is consistent with counts of growth lines in the largest long bones, and the amount of tissue deposited between successive lines is commensurate with expected annual growth at rates reflected by the given bone tissues¹¹. (However, like extant mammals and birds, and other extinct dinosaurs, *Maiasaura* appears to have been growing too rapidly to lay down a growth line in its first year.) Similar growth rates are now estimated even for large sauropod dinosaurs^{9,13,14} and large pterosaurs²⁷. Such rates are in sharp contrast to those assessed for crocodiles, even gigantic ones like the Cretaceous *Deinosuchus*, which could exceed eight metres in length but took 50 years to do so¹⁵ (Fig. 2).

These results support the hypothesis that large dinosaurs grew more like large extant birds and mammals than like extant reptiles, even large ones^{2,4,11,18}. And, if growth rates provide any indication of underlying basal metabolic rates, they suggest that these dinosaurs were not like typical ectotherms^{2,3,6,10,11}. Finally, although most extant birds reach maturity too rapidly to lay down growth lines^{28,29}, some extinct birds, such as the two-metre-tall Eocene neognath *Diatryma* and the three-metre-tall moa, *Dinornis*, produced growth lines in their long bones (Fig. 3), suggesting not that they were ectothermic, but that the production of these lines was merely a function of endogenous rhythms^{17,24,30}.

In contrast to large dinosaurs and pterosaurs, small ones apparently grew more slowly. Their long bone cortices were less well vascularized, the vessels were primarily longitudinal, and the bones may show more closely spaced growth lines. These data would seem to fit a model describing dinosaurs as essentially reptilian, perhaps with somewhat higher basal metabolic rates, and large dinosaurs would grow quickly merely by virtue of inertial homoiothermy. Against this quite reasonable model, however, small mammals and birds also deposit bone of relatively low vascularity, with predominantly longitudinal vessels and lines of arrested growth (LAGs)^{28,29},

but are clearly endothermic^{2,3}. Moreover, the cortical bone of small dinosaurs and pterosaurs is primarily fibro-lamellar (not lamellar-zonal as in crocodiles and other ectotherms), reflecting more rapid growth, and the tissues are typically far better vascularized than in typical reptiles. These differences in patterns seem to begin before hatching¹⁰. Furthermore, extant taxa of large adult size typically grow at rates absolutely higher than related smaller taxa, regardless of their physiologies¹, so this pattern would be expected in dinosaurs. Even the most basal dinosaurs, such as the 2.5-metre-long *Herrerasaurus* and the 1.5-metre-long *Coelophysis*, grew at high rates, suggesting that smaller dinosaurs (for example, *Scutellosaurus* and *Orodromeus*) grew at secondarily slow rates (Fig. 1).

How ancient birds grew

These generalizations relating bone-tissue type and growth rates, when seen in phylogenetic perspective, can provide insight into how ancient birds grew and how their small size evolved. Compared with nearly all of their immediate relatives among the theropod dinosaurs, the dromaeosaurs and troodontids, the first birds were small³¹ (Fig. 4). Close bird relatives generally ranged from 1.1 to 3.0 metres in body length, with femur lengths of 14 to 30 centimetres. An exception is the recently discovered *Microraptor*³², which—if truly adult—is small enough (femur length 5.3 centimetres) to demonstrate that non-avian maniraptorans of suitable size for avian ancestry indeed existed. By comparison, *Archaeopteryx*, the most basal bird, reached a body length of approximately 50–60 centimetres

(femur length about 3.2–7.0 centimetres), smaller than its feathered non-avian dinosaur relatives³³.

Previous analyses³⁴ of the bone tissue histology of two types of basal Mesozoic birds reported generally low vascularization and even a nearly avascular cortex in two enantiornithine femora, with several LAGs (Fig. 3). The lack of vascular canals and the persistence of LAGs are features commonly found in ectothermic extant reptiles and amphibians^{22,30}. Such features prompted the inference³⁴ that these basal birds had not fully attained avian physiological levels and may even have been intermediate between ‘typical’ reptilian metabolism and endothermy. Analyses of *Hesperornis* and *Ichthyornis*, two Cretaceous birds closer to extant forms, showed higher vascularity and an absence of LAGs, suggesting gradual attainment of the fully endothermic metabolism of extant birds³⁵. Other workers³⁶ suggested from similar histological studies that the basal bird *Confuciusornis* was endothermic, but that its endothermy had evolved independently of neornithine (extant) birds.

The inferences drawn from these histological observations are reasonable if one considers the distributions of such features only in extant vertebrates (ectothermic reptiles versus endothermic mammals and birds). However, the same evidence in a phylogenetic and ontogenetic context, including extinct forms (Fig. 4), suggests a different picture for basal birds^{5,17} (Fig. 3). Like all other theropod outgroups of birds studied, ranging from troodontids and tyrannosaurs out to allosaurs, coelophysids and even herrerasaurs, the small theropods from which birds evolved had well vascularized bone tissues¹⁶ (K.P. *et al.* unpublished observations). The long bones of the hindlimbs in particular consist almost entirely of tissues displaying a fibro-lamellar pattern⁴. This pattern, which also predominates in large extant birds and mammals, typically grows continuously at rates of 10–60 micrometres per day, much faster than the tissues of ‘typical’ extant reptiles^{8,22,37}. LAGs are observed throughout the cortices of the long bones of most non-avian theropods and other dinosaurs, but they are also known in the long bones of mammals and some extant birds, especially in the outermost cortex where growth slows^{28,29}. Thus, in these taxa they may represent little more than evidence of environmentally mediated endogenous patterns of cyclical growth with no general physiological implications²⁴. Slow-growing bone does not necessarily imply low metabolic rates, as can be seen from humans, whose bones grow much more slowly than those of most mammals, but who are obviously endothermic.

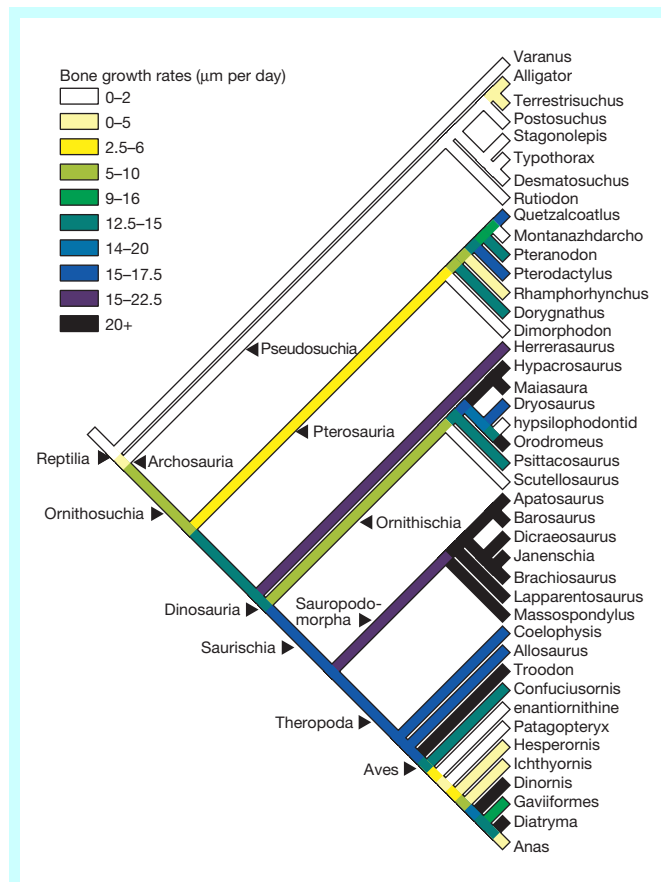


Figure 1 Cladogram of archosaurian taxa, after various sources, with subadult long-bone growth rates. Rates are estimates based on histological structure, vascularity, and vascular patterns of cortical tissues of subadult femora and tibiae, compared to the same types of tissues of known growth rate in the mallard, ostrich and emu^{19,37}. 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.

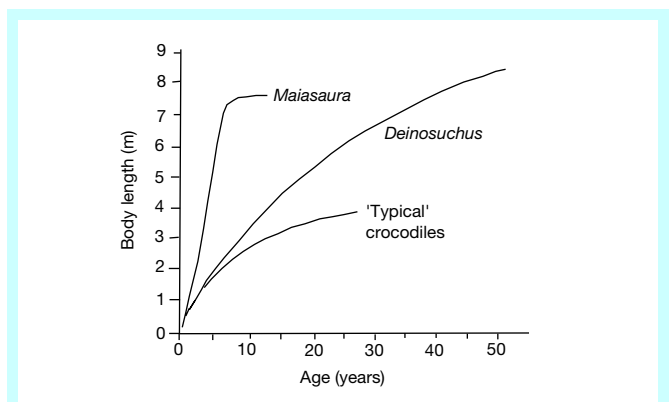


Figure 2 Comparative growth histories of the hadrosaurian dinosaur *Maiasaura*¹¹ and the giant Cretaceous crocodile *Deinosuchus*, with ‘typical’ crocodiles for comparison¹⁵. *Deinosuchus* grows slightly more rapidly and extends its active growth curve more than typical crocodiles, but the curve for *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 40 years or more. Although data on partial growth series have been collected for some dinosaurs^{9,10,12–14,16,18,20}, none but *Maiasaura* is currently represented from embryo to adult.

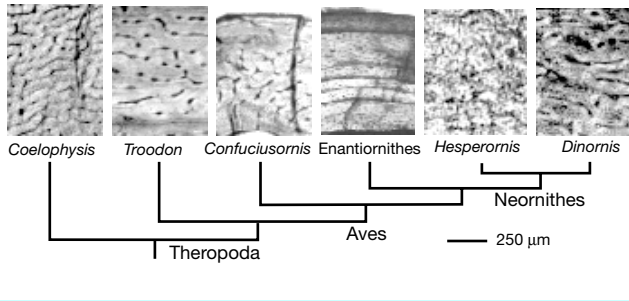


Figure 3 Transverse mid-shaft thin-sections of cortical bone of representative theropod taxa, showing the evolution of tissue from basal theropods to crown-group birds. The anomalous slow growth patterns in enantiornithines and in the external cortex of *Confuciusornis* are reflected by the nearly avascular, non-fibrolamellar tissue. (Enantiornithes from ref. 34; *Hesperornis* from ref. 35.)

If avian precursors had well vascularized, fast-growing bone, how can the relatively avascular, slow-growing patterns seen in some basal birds be explained? One possibility is that the limited tissue samples of enantiornithines may simply represent old individuals, in which growth has nearly ceased. Birds, like other theropods, have a thin cortex in which 75 per cent or more of earlier deposited tissue is resorbed, leaving no record in adults of presumably faster-growing juvenile tissues^{16,17}.

How birds got small

We propose an alternative hypothesis that takes into account both ontogeny and phylogeny. Preliminary histological observations of the basal bird *Confuciusornis*³⁶ (Fig. 3) do not suggest overall low growth rates, and a thorough study of this bird confirms active growth during a large part of its ontogeny at least (K.P. *et al.* unpublished observations). Conversely, bone tissue patterns indicate

that some basal birds, such as some enantiornithines and perhaps *Patagopteryx*, grew more slowly than extant birds of similar size^{34,35}. Thus they reached a much smaller adult size than other theropods, but they still took longer to grow to this smaller size than do extant birds. Their bone cortices suggest that they could have accomplished this by shortening the early rapid-growth phase and extending the more adult-like, slower-growth phase seen in some enantiornithine bones^{5,17,34}.

Further evidence for differences in growth curves between basal and neornithine birds comes from estimates of growth rates in the long bones of *Confuciusornis*^{17,31} (K.P. *et al.* unpublished observations). If the tibia is accorded a relatively slow growth rate of 4–6 micrometres per day, as its moderately vascularized cortex and mostly longitudinally oriented vascular canals indicate by comparison with the growth curves of extant birds³⁷, it would have reached adult size in just over half a year. This estimate is commensurate with those for the humerus (26 weeks), radius (21–31 weeks), and femur (35–48 weeks), if allowances are made for the range of growth curves³⁷ reflected in their respective tissues¹⁷. In contrast, most extant birds of the size of *Confuciusornis* reach adult size in four to eight weeks³⁸, but the larger theropod dinosaurs must have taken much longer, even at higher growth rates.

This hypothesis presumes that cortical bone tissue types that grow at specific rates in extant animals grew at similar rates in extinct forms. If these basal birds grew at such moderate overall rates (comprising a short phase of rapid growth and a protracted later phase of slower growth), it would explain why the known specimens of *Archaeopteryx* have a twofold size range, yet fit a single allometric growth trajectory³⁹.

A strict test for heterochrony⁴⁰, often invoked in connection with the origin of birds^{5,17}, requires complete comparative ontogenies of all forms under study, which is not possible in extinct tetrapods. However, the distribution of primitive and derived features in a phylogenetic series of related taxa provides a secondary test that reflects the direction of evolutionary changes and allows inferences about specific developmental mechanisms.

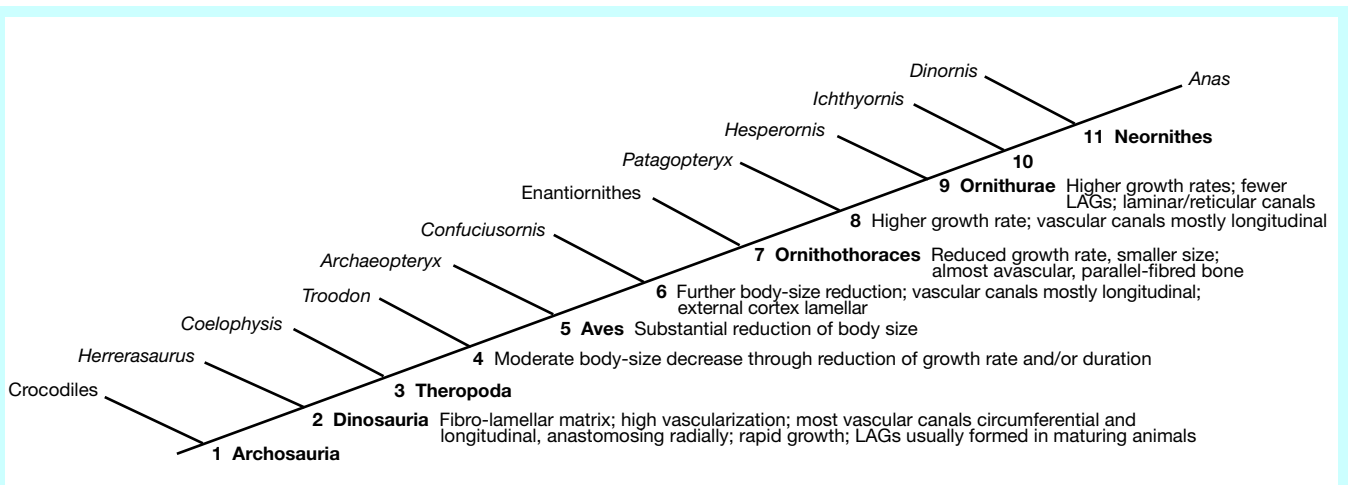


Figure 4 Cladogram of representative birds and other theropod dinosaurs, using crocodiles as an outgroup, to show the evolution of the growth strategies suggested by histological patterns, sampled in all taxa here except *Archaeopteryx*. These characters are treated as synapomorphies at the following nodes. **Node 1** (crocodiles): primarily parallel-fibred matrix; extensive LAGs; moderate vascularization; most vascular canals longitudinal; moderately slow growth. These features are common to Pseudosuchia basally but are not assumed here to be plesiomorphic for Archosauria. **Node 2** (Dinosauria): fibro-lamellar matrix extensively developed; dense vascularization with circular, longitudinal and radial canals; LAGs usually formed in maturing animals; rapid growth. **Nodes 4 and 5** (comprising the origin of birds and flight): as for Dinosauria; lamellar external cortex; reduction of body size through slowing of growth rate and/or shorter ontogeny, as reflected in bone tissues. **Node 6** (some features presumably apply to *Archaeopteryx*): longitudinal canals predominate with few anastomoses; body size reduced from theropod condition; lamellar external cortex and mostly longitudinal vascular canals in adults. **Node 7** (toward more advanced fliers): further reduction of vascularization; parallel-fibred or lamellar, almost non-vascular bone in adults; basally, further reduction of body size through further truncation of the early phase of fast growth. **Node 8**: fibro-lamellar cortex with longitudinal canals and few anastomoses; external cortex lamellar; fewer LAGs (?); higher growth rate reflected by faster-growing bone during a larger percentage of ontogeny. **Nodes 9–11** (toward the 'modern' condition): fibro-lamellar cortex with laminar or reticular vascularization in large birds; high to very high growth rates; fast-growing bone almost entirely resorbed in adults of small size; few or no LAGs.

If birds had simply reduced adult size by becoming paedomorphic (*sensu ref. 40*), they would have retained a juvenile shape at this reduced adult size (as, for example, if humans were to slow development so as to achieve adulthood and sexual maturity at a shape and size now characteristic of five-year-olds). Evidence for this pattern includes the persistence of features associated with juveniles of related taxa, and sometimes in the delay in, or absence of, fusion of skeletal elements commonly fused in the adults of outgroup taxa. However, in adult basal birds the forms and proportions of juvenile ancestors do not reappear. Rather, they show a derived development of proportional trends such as the further elongation of lower limbs, arms and hands, the beginnings of fusion of some skeletal elements (carpometacarpus, tibiotarsus, tarsometatarsus and pygostyle), and the further development of feathers^{5,17,31}. These patterns instead suggest a combination of overall dwarfing of adult size, accompanied by a form of peramorphosis of many skeletal forms and proportions. In other words, mosaic developmental changes carried some features of shape to more derived states even as body size was reduced⁴⁰. These changes are distinct from strict proportional dwarfism, because some shape parameters (such as the elongated arms and feathers) experienced positive allometry even as size decreased (acceleration *sensu ref. 40*). Reduction in body size was almost certainly associated with a reduction of the time needed to reach adult size. The relative elongation of forelimbs and feathers, coincident with a phyletic reduction in adult size, would have been advantageous to the inception of flight by decreasing wing loading and improving the power-to-weight ratio.

A boost in growth rates for later birds

Birds more closely related to extant groups (Neornithes, Fig. 4) gradually acquired the histological features of typical extant bird bone³⁵. Vascularity increased and LAGs were generally reduced or lost, although they persist at least in the outer cortex of some extant and fossil crown-group birds^{28,29}. The return to predominantly fast-growing bone tissue in more derived small birds (Neornithes and their relatives) suggests a trend to reach adult size quickly, within a shorter maturation time than in basal birds and non-avian theropods. (This pattern can be seen only in analysis of the 90 per cent of the growth trajectory comprising rapidly growing bone that is resorbed throughout ontogeny.) The acceleration of growth rates signalled further changes in life-history strategy that may have facilitated the rapid growth of some taxa to fledging size³⁸. Large ground birds such as ratites have converged in body size and bone histology with many Mesozoic non-avian theropods (Fig. 3). This seems to have resulted in large part from a secondary extension of the rapid-growth phase of their developmental trajectory that allows them to attain a large size quickly¹⁹.

Note added in proof: We are delighted that the independent results of Erickson *et al.*⁴¹ (this issue) so closely reflect and complement our own. Note that our measurements are linear, whereas theirs are extrapolated mass estimates, which accounts for many differences in the curves. Though more work is needed, we conclude that our independent studies generally characterize dinosaur growth strategies with substantial accuracy. □

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