

Paleontology series

Assessing dinosaur growth patterns: a microscopic revolution

Gregory M. Erickson

Department of Biological Science, Florida State University, Tallahassee, FL 32306-1100, USA

Some of the longest standing questions in dinosaur paleontology pertain to their development. Did dinosaurs grow at slow rates similar to extant reptiles or rapidly similar to living birds and mammals? How did some forms attain gigantic proportions? Conversely, how did birds (avian dinosaurs) become miniaturized? New data on dinosaur longevity garnered from bone microstructure (i.e. osteohistology) are making it possible to assess basic life-history parameters of the dinosaurs such as growth rates and timing of developmental events. Analyses of these data in an evolutionary context are enabling the identification of developmental patterns that lead to size changes within the Dinosauria. Furthermore, this rich new database is providing inroads for studying individual and population biology. All in all, paleohistological research is proving to be the most promising avenue towards gaining a comprehensive understanding of dinosaur biology.

Introduction

Dinosaurs have fascinated scientists and laypersons alike for nearly 200 years [1]. The largest animals to ever walk the Earth, dinosaurs share a unique blend of reptilian and mammal-like anatomical attributes that, together with their kinship with birds (avian dinosaurs), has evoked substantial scientific investigation [1]. Considerable insight into the diversity [1], anatomy [1], biogeography [2,3] and phylogenetic relationships of dinosaurs has been gained [1,4]. Nevertheless, some of the longstanding questions in vertebrate paleontology pertain to dinosaur development where little headway has been made. Namely, it is not known how dinosaurs attained giant size, how birds became miniaturized, or the means by which birds acquired their unprecedented rapid growth rates. Answers to these questions, derived from assumptions about dinosaur growth based on analogies drawn with living animals, have been disparate, speculative and controversial [5–8]. Recently however, paleontologists have found means to assess dinosaur life-history parameters such as growth rates and longevity through osteohistology (the study of bone microstructure [9]). Using these data, developmental patterns can now be compared in an evolutionary context and models about dinosaur development scrutinized empirically [10–13]. Surprisingly, the findings suggest

that dinosaur growth, including that in the earliest birds, was unique and not precisely the same as that in living reptiles, birds or mammals [10,14]. Hence, re-evaluation of theories about dinosaur and avian evolutionary biology is underway. Besides addressing major evolutionary questions, researchers are now using the same life-history data to explore other aspects of dinosaur biology such as sexual dimorphism and dwarfism [15,16], as well as aspects of population demographics [12].

Here I review the methodological advances in osteohistology that precipitated the major evolutionary findings and present exciting new avenues of research using life-history data. Finally, I explore future directions for this paleontological sub-discipline from which an unprecedented, comprehensive empirical understanding of the biology and evolution of these enigmatic animals stands to be gained.

Assessing growth patterns

The key to understanding evolutionary changes in dinosaur development is the ability to reconstruct growth curves. These age-versus-size (i.e. length or body mass) plots provide a basic, quantified depiction of post-hatching growth from which the timing of developmental events (e.g. onset of maturity) and growth rates can be garnered and used in interspecific comparisons [5,17,18].

The primary requisite for making growth curves is information on longevity. This was first provided for dinosaurs in the 1980s when researchers such as Reid as well as de Ricqlès began making total growth-line counts in bones from individual dinosaurs [8,19,20]. In the early 1990s, Chinsamy estimated the age of specimens spanning various developmental stages. By coupling these data with measures of size, she produced the first fully quantified age-versus-size growth curves for dinosaurs [21].

Recently, a second aging method using a principle called ‘Amprino’s rule’ (*sensu* [11]), where bone tissue formation rates are used to predict the length of development, was introduced [22]. The strength of this method lies in its being broadly applicable to all dinosaurs, including those that do not show growth lines. However, unlike growth-line aging, which has gained broad scale acceptance in vertebrate paleontology because of its proven efficacy in previous studies on living animals, the accuracy of aging determined via Amprino’s rule is still being tested (see below).

Corresponding author: Erickson, G.M. (gerickson@bio.fsu.edu).

Available online 8 September 2005

Box 1. Assessing dinosaur longevity from growth-line counts

Making growth curves for dinosaurs requires estimations of longevity for various individuals throughout development. To do this, osteohistologists sample bones from specimens spanning juvenile through adult developmental stages. The bones that are utilized show minimal remodeling (i.e. replacement or loss of the original bone during life because of metabolic, reproductive, biomechanical, or skeletal repair considerations [9]) and therefore provide a nearly complete record of development. Traditionally, dinosaur researchers have used the femur, but other bones have been shown to be equally or more efficacious in some taxa.

For example, multi-element sampling in tyrannosaurs has shown (Figure 1a) that the bones shown in blue [pubis, fibula, ribs, gastralia (i.e. belly ribs) and some post-orbital skull bones] work better than the femur in these animals [12,24]. The bones are sectioned transversely at mid-shaft using a slow-speed saw fitted with a diamond-tipped blade (Figure 1b). The sections (Figure 1c) are then affixed to glass petrographic slides and sanded/polished for viewing with polarized and/or reflected microscopy. On very large specimens for which making entire cross-sectional slides is difficult, researchers polish the cut faces of the bones to reveal 'polished lines' that reflect hardness differences between individual growth lines [20,23,31].

Alternatively, Sanders has developed a method whereby a diamond-tipped drill coring-bit is used to extract a cylinder of bone from which polished-line preparations or petrographic slides can be made [23]. Aging is conducted by making total growth line counts within elements [28]. Here (Figure 1c), a thin-sectioned, dorsal rib from *Tyrannosaurus rex* (Field Museum of Natural History, Chicago, FMNH PR 2081) shows growth lines (arrows) that were counted to age this specimen. Each line represents a period of slowed and/or potential stoppage in tissue deposition [9]. The highly vascularized regions between the rings are known as zones and represent periods of active growth [8,9]. The inset box denotes a region late in development composed of tightly stacked growth rings known as an external

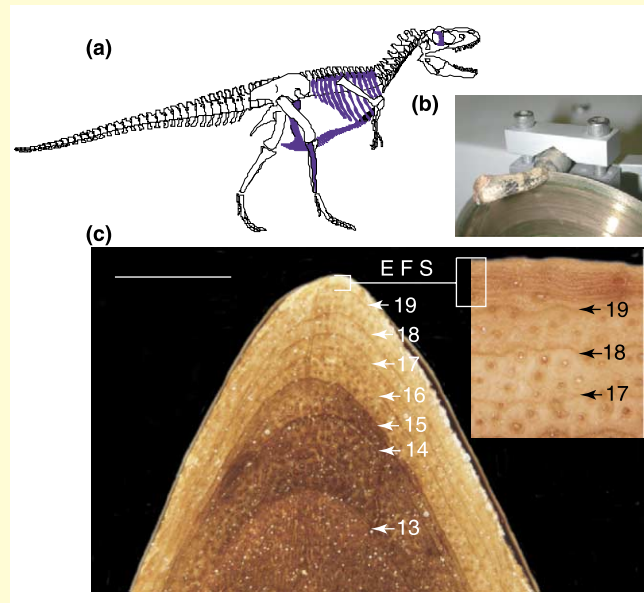


Figure 1.

fundamental system that indicates when growth slowed precipitously [22,27]. At this point in development, somatic maturity and full-adult size was reached. (Figure 1 redrawn and reproduced with permission from [12]. Scale bar = 10 mm.)

Determining longevity using growth-line counts

Total counts of growth lines is the most common method by which paleohistologists age dinosaurs (Box 1). The tree-ring-like growth lines (of which there are several variants [8,9,17,20,23–25]) appear as thin, circumferentially oriented, avascular regions in thin-sectioned bones. For a time, it was believed that dinosaurs by and large lacked growth lines in their skeletons (as is the case in most birds and living mammals [9,26]). However, Reid argued that dinosaurs without growth lines throughout their skeleton are the exception rather than the rule [19]. The burgeoning histological database has since supported his contention [27]. Hence, it is clear that most dinosaurs showed disrupted growth patterns characterized by periods of rapid growth followed periodically by temporary slow-downs or cessations of growth [19].

The accuracy of aging dinosaurs using growth lines hinges on the premise that these structures are formed annually. A substantial body of evidence supports this contention. By and large, the lines are structurally comparable to those found in outgroup clades to the Dinosauria – Actinopterygia (ray-finned fish), Amphibia (amphibians), Lepidosauria (tuatara and squamates) and Crocodylia (crocodilians) – where numerous studies have confirmed their annual genesis [12,28–30]. Thus, a comparable formative rhythm is predicted in dinosaurs as a result of the shared common ancestry. Moreover, recent studies have shown that the amount of bone tissue deposited between the dinosaur growth lines is consistent

with an annual genesis [11,22,31]. Spacing of the lines is also in conformity with an annual genesis, with widths becoming progressively smaller as development progresses [21,22]. (Random widths would be anticipated had they formed under non-cyclical influences.) Additionally, a recent, novel study on sauropods using oxygen isotopes by Tütken and colleagues showed patterns consistent with this hypothesis [32]. Finally, I am unaware of any studies that definitively link growth lines to non-annual environmental perturbations.

Determining longevity using Amprino's rule

The aging of dinosaurs using the principle of Amprino's rule (which honors the 1940s work by the pioneering histologist who argued that a correlation between bone tissue patterns and depositional rates exists [33]) is a less commonly used means to assess longevity. However, it is the only method currently available (although isotopic studies show promise [32]) for a minority of dinosaurs (some theropods, hypsilophodontids, iguanodontids and sauropods [19,21,27,34,35]) where the bones apparently lack growth lines or are produced only late in development. These animals appear to have maintained a level of year-round tissue formation (as occurs in the majority of bones from living mammals and modern birds) such that growth lines did not form [9,19,21]. It is not known why this occurred, but it might reflect selection for the more rapid attainment of adult size or for the capacity to exploit

environments with adverse climatic conditions (e.g. polar regions [35]).

Using the technique based on Amprino's rule, the predominant bone type in a dinosaur bone is determined and the total amount of this tissue that was deposited during the animal's life determined [11,22,31,36] (Box 2). The rate of formation of this bone type is deduced from living vertebrates and divided into the total to reveal the age of the dinosaur. Rigorous testing of the principle has only recently begun by periodically administering chemical bone markers to living birds where growth was monitored simultaneously [31,37–40] and by surveying tissue growth rates from the literature [29]. The findings have been frustrating insofar as aging dinosaurs is concerned. Tissue formation rates for specific bone types, particularly moderate to highly vascularized types such as those of dinosaurs, vary by as much as tenfold or more, and rates for different bone types show considerable overlap [31,37–40]. Furthermore, correlations between formation rate and both bone size and function have been revealed [37–39]. The influences of size and function on formation rates are problematic in that the bones of most dinosaurs were considerably larger than those of the birds used to model the principle and birds are a poor analogy for non-avian dinosaur locomotion [41]. Stark and Chinsamy [37] have surmised that aging and tissue-formation characterizations using Amprino's rule have been 'premature and inaccurate' and some of the original proponents have expressed similar reservations [42,43]. Given these problems, further understanding of the relationships between bone histology, scaling, biomechanics, phylogeny and growth rates in living animals is needed if this principle is to be implemented for dinosaurs. In the meantime, this rule (perhaps referred to more aptly as a hypothesis or, at most, a principle) is probably best

utilized as a means to roughly bound the potential ranges of tissue growth rates and longevity.

Reconstructing growth curves

Once the ages of specimens from a developmental series of the same species have been established, measures of size are needed to enable growth-curve reconstruction [17] (Box 3). Most studies have used element length and, in a few cases, the total length of the dinosaur as a measure of size [21,23,24] (Box 3). Such linear measures are useful for studying size increases within a species, but have less utility for making interspecific growth comparisons where shape differences come into play. (An extreme illustration of the problem would be concluding that a 5000-kg elephant and 100-kg boa had the same growth rates because both reached similar adult lengths in 20 years. Obviously, total mitotic activity and cell growth in the elephant greatly outpaced those in the snake during this time span.) To account for interspecific differences in size and shape, comparative physiologists have adopted standardization to body mass [5,17]. Body mass can be estimated in dinosaurs by several means [44]. A common practice in dinosaur paleontology is to utilize circumference measures of weight-bearing long bones such as the femur and humerus [17,44]. Recently, mass estimates have been coupled with longevity data to provide the first age-mass growth curves for dinosaurs [10,12,17] (Box 3). From this, useful mass standardized growth-rate comparisons have been made not only between dinosaurs, but also with members of living clades [10] (Box 4).

Data from body mass and a few linear growth curves have been incorporated into phylogenetic character analyses to provide quantified perspectives on how heterochronic changes (i.e. evolutionary changes in

Box 2. Assessing dinosaur longevity using the principle of Amprino's rule

A less commonly utilized aging technique for dinosaurs and basal birds uses a principle called 'Amprino's rule' (*sensu* [11,22]). The formative rate of tissue types from living animals is used to estimate lengths of time for bone development and thus determine longevity. This aging technique is the only tested means to age animals in cases where growth lines were not deposited throughout life. The method has seen limited application in assessing dinosaur [11,22,31] and basal bird [11,36]

longevity. In Figure 1a, the bones of an ostrich (*Struthio camelus*) were labeled by periodically administering fluorochromic chemical labels to establish the formative rate of the bone tissue (marked yellow and red; photo courtesy of Kristina Curry Rogers). Note that the values shown here are hypothetical and intended only to illustrate the methodology. The formation rate is divided into the amount of bone that formed during development (measured radially; Figure 1b) to reveal longevity.

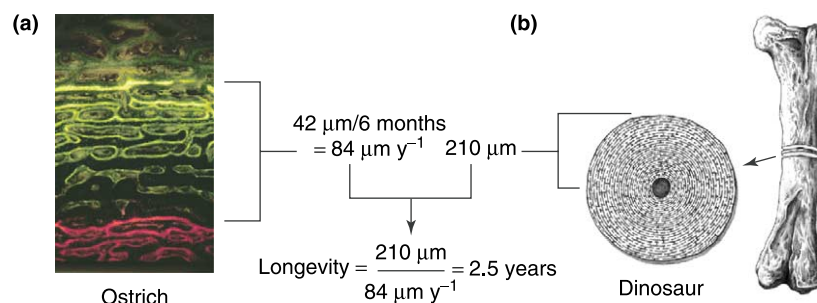


Figure 1.

Box 3. Making dinosaur growth curves

Longevity estimates are coupled with size data (from direct measures of length or mass estimates from bone circumferences) for dinosaurs to make age-versus-size growth curves. In Figure 1a, femur length was used for the sauropod *Janeschia* to produce a simple growth curve. This plot was used for determining the age of sexual maturity (hypothesized as occurring when the growth rates initially slowed) and somatic maturity (full adult size as indicated by the asymptote [23]). The curve can also be used to assess linear growth rates at various points in development. (Redrawn and reproduced with permission from [23].)

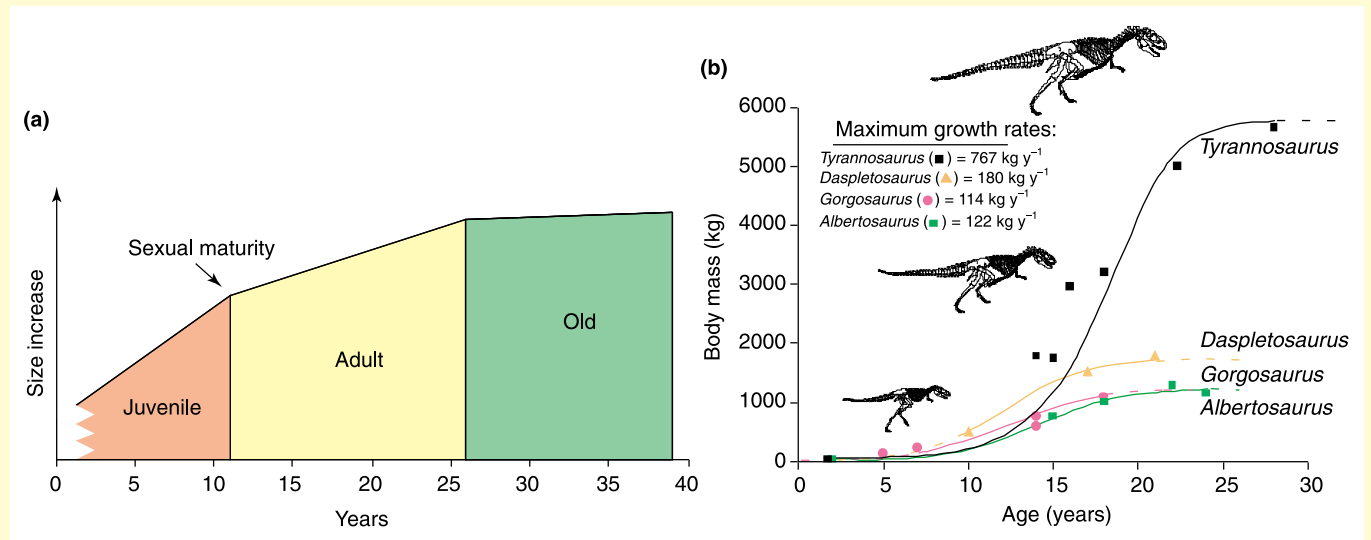


Figure 1.

developmental rates or timing) occurred in dinosaurs [10,12,13] (Box 3).

How did dinosaurs grow?

Some of the most fundamental questions about dinosaur development pertain to how their growth rates compare with those of living taxa and how modifications in such rates enabled some forms to be gigantic and others, including birds, to become miniaturized.

A recent integrative study set out to test the three competing hypotheses about dinosaur growth rates [10], namely that they grew at rates (i) comparable to reptiles [5], (ii) similar to those of birds and mammals [6], or (iii) somewhere in between [8]. The results showed that, with respect to body size, dinosaurs grew more rapidly than living reptiles (Box 4). However, rate increases with greater size were not similar to those predicted by any of these hypotheses. Insofar as physiology can be inferred from growth rates, dinosaurs appear to have been unique.

Padian, de Ricqlès and colleagues have been looking at bone tissue types in outgroup taxa to learn whether the growth pattern in dinosaurs is unique or reflects earlier ancestry [11,45–47]. Using Amprino's rule, their data suggest that the relatively rapid growth rates of dinosaurs stemmed from a common ancestor shared with pterosaurs.

One of the oldest questions in paleontology is how dinosaurs attained giant size. Increased phylogenetic resolution has enabled Carrano to conclude that dinosaurian lineages attained enormous proportions (3+ tons) on at least seven or eight occasions [48]. How did these

Age-versus-mass growth curves, such as the one shown in Figure 1b for North American tyrannosaurs [12], are generally sigmoidal in shape, except in cases where older adult animals are not represented and the asymptote is absent. Timing to somatic maturity, mass standardized maximal growth rates and other life-history parameters can be assessed and used in both interspecific comparative and evolutionary contexts from this type of curve. (Redrawn and reproduced with permission from [12].)

events occur? Evolutionary theory offers three possible solutions: (i) acceleration, whereby growth rates increased from those present in their ancestors; (ii) delay in the onset of maturity; or (iii) through a combination of both processes [49]. A growth-curve study published by my research group focused on the evolution of the enormous *Tyrannosaurus* within Tyrannosauria [12] and showed that acceleration in growth rates of fourfold or more was the key to the great stature of this taxon (Box 3). A subsequent study by Sander and colleagues looked at the same phenomenon within the Sauropodomorpha and interestingly revealed the same pattern [13].

These findings stand in contrast to three earlier osteohistological studies on gigantism in the dinosaurian outgroups Lepidosauria [30], Crocodyliformes [50] and Crocodylia [51], which all revealed retention of ancestral growth rates and delays in the onset of maturity. It will be interesting to see in the future if all cases of dinosaurian gigantism involved acceleration.

Of course, not all dinosaurs were large. By which heterochronic mechanism(s) did dinosaurs become smaller? There have been several explorations of this phenomenon using osteohistology. One of the most interesting relates to the idea that relatively small dinosaurs found in Eastern Europe (e.g. hadrosaurs and sauropods) are island dwarfs [52]. Sander and colleagues tested this hypothesis using diminutive sauropod specimens from Germany [15,16]. They believe that they have found evidence that individuals just 8–9 years of age show histological attributes (tightly packed growth lines called an external

Box 4. Comparison of maximal growth rates in dinosaurs to those in extant vertebrates

In Figure 1, Maximal growth rates for dinosaurs were deduced from age-mass growth curves for six dinosaurs represented by lettered boxes (from smallest to largest: *Shuvuuia* (Sh), *Psittacosaurus* (P), *Syntarsus* (Sy), *Massospondylus* (Ms), *Maiasaura* (Ma) and *Apatosaurus* (A); [10]). These data were then plotted with similar data for major living vertebrate clades [5]. A regression line was fitted to the dinosaur data spanning the bounds of known dinosaur size. The results show that whole-organism growth rates for dinosaurs were faster than those of living reptiles of equivalent size. This finding supports qualitative conclusions to the same effect based on tissue-level signal and the reasoning underlying Amprino's rule [11,26]. However the data do not conform to theories that dinosaurs grew in the same manner as living birds, mammals [6], or at rates between reptiles and birds and/or mammals [8]. Rather, dinosaur growth rates show a unique scaling trajectory. The regression [Maximal growth rate = $0.002215 (M_{adult})^{0.925}$, $R^2 = 0.961$] also reveals that small size in dinosaurs involved decreases in absolute growth rates [10].

One caveat of this being the first plot of its kind is that only a small sampling of species was available at the time. The addition of further data, particularly for large sauropods, where Sander [23] has found what appear to be considerably lower growth rates than those reported by Curry [25], might force reanalysis of the aforementioned trends. (Redrawn and reproduced with permission from [10].)

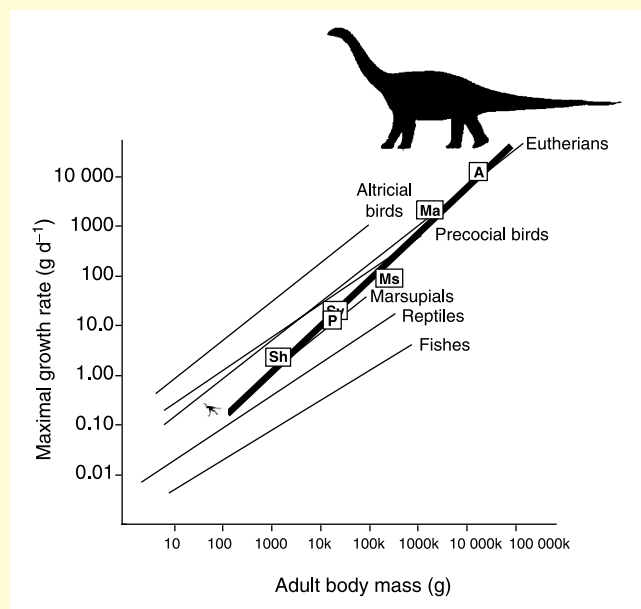


Figure 1.

fundamental system or EFS that suggest growth was plateauing) indicating full adult size. The same EFS structures occurred at ages of 15 years or later in their giant relatives [15]. As in cases of dwarfism in proboscidi-ans (elephants) on islands [53], it is believed that selection for smaller sizes enabled these animals to maintain viable population sizes with limited resources.

Along the same lines, a heated debate surrounds whether *Nanotyrannus*, a purported dwarf species of tyrannosaur, is in fact just a juvenile of *Tyrannosaurus* [54,55]. Anatomical studies have revealed juvenile attributes in support of the latter hypothesis [55,56]. However, if the dwarfing event simply involved early sexual maturation, immature features might still be expected. I recently aged one of these specimens (Burpee

Museum of Natural History, Rockford, BMR P2002.4.1) to see if it has adult histological features or falls outside the confidence interval for *Tyrannosaurus* development [12]. The 11-year-old specimen plots on the growth curve. This lends support to it being a juvenile of the larger taxon (unless of course maturity occurred somewhat later in development) and suggests there was only one large carnivorous taxon in the Latest Maastrichtian of North America.

The rediscovery that birds are theropod dinosaurs [57,58] has led to interest in how early birds, such as *Archaeopteryx*, attained small size [10,11,43]. A survey of dinosaurian and avian osteohistological types and formative rates using Amprino's rule led to the conclusion that the diminutive size of the first birds was brought about by a decrease in the length development compared with that of their dinosaurian ancestors [11]. It was posited that selection favored reduced body size because it enabled decreases in wing loading and improved power-to-weight ratios. However, the latest discoveries of *Archaeopteryx*-sized theropods, such as *Microraptor* and *Sinosauropteryx* have led by Xu, Hwang and colleagues to conclude that this miniaturization event actually occurred before the cladogenesis of birds and was not driven by selection related to flight [59–61]. How then did these dinosaurs become small? The aforementioned dinosaur growth-rate regression (Box 4) and associated theropod growth curves suggest that absolute decreases in growth rates and truncated development facilitated dwarfing [10].

Late developmental patterns

In addition to revealing aspects of evolutionary changes in growth rates, osteohistology has utility for analyzing late developmental patterns in dinosaurs. Some of the first dinosaur growth studies reported the absence of EFS structuring that would indicate the specimens were full adult size [21,26,62]. It was theorized that these dinosaurs had an indeterminate growth strategy [19,21,26,62] (i.e. the capacity to grow appreciably throughout life; this is not to be confused with the more common use of this term in ecology, where it refers to sexual maturation before the attainment of maximal body size [63,64]). Subsequent osteohistological analyses have since revealed that EFS structuring is in fact commonplace and it appears that all dinosaurs had determinant growth strategies [10,12,19,21,22,24,31,65]. Growth curves graphically reveal these size plateaus and show that some species of sauropods and tyrannosaurs spent as much as 30% of their total lifespan as full-grown adults [10,12,23]. These growth curve studies also point to an interesting taphonomic conclusion: most specimens in museums are not full-sized adults. Perhaps this is to be expected given that for every specimen that reached late adulthood, many younger individuals perished and are more likely to be represented in the fossil record.

When did the dinosaurs reach somatic maturity (i.e. adult body size)? Growth curves derived from various laboratories reveal that this occurred at an age of 2.5–3.0 years in tiny theropods such as *Shuvuuia* [10], at ~4–12 years in small- to moderate-sized dinosaurs such

as *Syntarsus* and *Massospondylus* [21], at ~16.0–18.5 years in large dinosaurs such as *Albertosaurus* and *Tyrannosaurus* [12,24], and at ~20–26 years in giant sauropods, such as *Lapparentosaurus* [62] and *Janeschia* [23].

It has been speculated that precipitous rate changes in growth curves [23] (Box 3) or EFS bone structuring [19,26,63] (Box 1) could reflect the onset of sexual maturity, whereby energy allocation shifted from growth to reproduction. However, pending evidence for definitive correlations with sexual reproduction, this deduction is tenuous. Sexual maturity in most animals, including living reptiles, occurs well before full adult size is reached [66]. In birds (which are avian dinosaurs), however, it occurs once growth has come nearly to a standstill [67]. Furthermore, in most vertebrates, there are multiple pulses in growth rates [18]. Discerning which pulse, if any, reflects the onset of sexual maturity remains unclear.

How long did dinosaurs live?

Estimates of dinosaur longevity have been highly variable, and similar to the aforementioned growth-rate estimates, depend on the extant model adopted. An extreme example includes contentions that large sauropods lived hundreds of years based on rates in living reptiles [5]. The picture emerging from the current research is revealing how longevity relates to body mass. Tiny theropods, such as *Shuvuuia*, lived to ~3–4 years [10], small- to moderate-sized dinosaurs, such as *Syntarsus* and *Massospondylus*, to ~7–15 years [21], and large dinosaurs, such as *Albertosaurus* and *Tyrannosaurus*, to ~24–30 years [12,24]. The giant sauropods, such as *Brachiosaurus* and *Bothriospondylus* lived upwards of 50 years [20,31]. In no case has credible evidence suggested that any dinosaur topped a century in age.

Intraspecific studies

Besides helping to provide evolutionary insight to major developmental questions about dinosaurs, a few researchers have recently shown that growth-curve data can be used to better understand species biology. Several anatomical studies have suggested that the presence of purported robust and gracile post-cranial elements from the same species indicates that these animals showed whole-body sexual size dimorphism [63,68,69]. Testing of such hypotheses has been difficult because the field lacks a proven means to assess gender from the skeletons of any dinosaur. Given this, alternative explanations such as age differences or individual variation are tenable.

Few growth studies have sampled enough large adult individuals from which to statistically test these possibilities. Nonetheless, an exceptionally thorough aging study by Klein (N. Klein, PhD dissertation, Universität Bonn, 2004) on the prosauropod *Plateosaurus* might be amenable to this. The growth curves based on 27 specimens showed a single homogeneous cluster among adults of similar age and provide at least first-round evidence that sexual dimorphism was unlikely in this taxon. This contradicts an earlier Principle Components Analysis on *Plateosaurus* femora [69] that seemed to show two morphotypes and suggests instead that age differences can account for this variance. Biologically, this result

points to *Plateosaurus* utilizing other means for sexual recognition such as regionalized anatomical differences (e.g. thumb-claw differences) and/or other cues such as color differences, pheromones or dermal excrescences, among others, that were less likely to be preserved.

Several longevity and growth-curve studies have been made using specimens from dinosaur bone beds (mass aggregations of dinosaur remains), where temporary or permanent social groups met their demise in some cases [21–23]. A few researchers have recently embarked on investigations using such information to reveal dinosaur population demographics. One preliminary study [12] on a pack of the tyrannosaur *Albertosaurus* [70] showed individuals ranging from ~2 to 21 years of age and representatives from most developmental stages. Using a growth curve for the taxon (Box 3), it was possible to conclude that ~10% of the animals were adolescents, 10% were juveniles, 40% were actively growing sub-adults, 10% were young adults and 30% were older full-sized adults. This finding provides evidence that members of this taxon assimilated into such aggregations at very young ages and, assuming that these were not ephemeral gatherings, were members of packs throughout life.

Future directions

Growth-pattern reconstruction through osteohistology has become an important and exciting avenue for understanding the biology and evolution of dinosaurs. Insight into major, longstanding questions about dinosaur development has been gained and many positive directions for future research have been identified. Given that the field is in its infancy, there is a proximate need to broaden the database both intra- and interspecifically (several groups such as thyreophorans, for example, are unstudied) to help make taxonomic characterizations, reveal evolutionary patterns and provide for meaningful, statistically backed conclusions.

There also is a pressing need to better understand how skeletal microanatomy relates to growth. Particular emphasis needs to be paid to how and why growth lines do or do not form, and to developing more accurate means to age dinosaurs when growth lines are not present. Furthermore, a better understanding about the length of time over which growth lines form is needed because this will affect annual growth interpretations. Meeting such needs will require more experimentation on living animals, where it will be imperative to adopt standards whereby only statistically backed methods are accepted. Additionally, I encourage all researchers to garner experience working with known-age animals and to thoroughly study the techniques used in the herpetological literature before working on fossils. This will help alleviate uncertainties about how to age animals. It will also help to ensure the uniformity of methods between laboratories. There is also a need to test the means by which dinosaur sizes are estimated. Again more experimentation and validation of methodologies is required.

If these considerations are heeded, I believe that the emergent field of osteohistology will develop into a respected sub-discipline with a sound foundation from

which to gain the long-sought comprehensive understanding of dinosaur evolutionary paleobiology.

Acknowledgements

I thank the many people who have provided those of us in this line of research with access to specimens. A special thanks is owed to Armand de Ricqlès and John Horner for recognizing the scientific potential of osteohistology and for introducing many of us to the field. I personally want to thank Martin Sander for providing input on the latest work of his laboratory, Kristi Curry Rogers for access to her research photos, and the National Science Foundation for their continued support.

References

- Weishampel, D.B. *et al.*, eds (2004) *The Dinosauria*, University of California Press
- Sereno, P. (1999) Dinosaurian biogeography: vicariance dispersal, and regional extinction. In *Proceedings of the Second Gondwana Dinosaur Symposium* (Tomida, Y. *et al.*, eds), pp. 249–257, National Science Museum, Tokyo Monogr. #15
- Weishampel, D.B. *et al.* (2004) Dinosaur distribution. In *The Dinosauria* (2nd edn) (Weishampel, D.B. *et al.*, eds), pp. 517–606, University of California Press
- Sereno, P. (1999) The evolution of dinosaurs. *Science* 284, 2137–2147
- Case, T.J. (1987) Speculations on the growth rate and reproduction of some dinosaurs. *Paleobiol.* 3, 320–328
- Bakker, R.T. (1986) *The Dinosaur Heresies*, William Morrow
- Thomas, R.D.K. and Olson, E.C., eds (1980) *A Cold Look at Warm-Blooded Dinosaurs*, Westview
- Reid, R.E.H. (1997) Dinosauria physiology: the case for “intermediate” dinosaurs. In *The Complete Dinosaur* (Farlow, J.O. and Brett-Surman, M.K., eds), pp. 449–473, Indiana University Press
- Francillon-Vieillot, H. *et al.* (1990) Microstructure and mineralization of vertebrate skeletal tissues. In *Biom mineralization: Patterns and Evolutionary Trends* (Carter, J.G., ed.), pp. 471–530, Van Nostrand Reinhold
- Erickson, G.M. *et al.* (2001) Dinosaur growth patterns and rapid avian growth rates. *Nature* 412, 429–433
- Padian, K. *et al.* (2001) Dinosaurian growth rates and bird origins. *Nature* 412, 405–412
- Erickson, G.M. *et al.* (2004) Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature* 430, 772–775
- Sander, P.M. *et al.* (2000) Adaptive radiation in sauropod dinosaurs: bone histology indicates rapid evolution of giant body size through acceleration. *Org. Div. Evol.* 206, 217–238
- Chinsamy, A. *et al.* (1994) Growth rings in Mesozoic birds. *Nature* 368, 196–197
- Sander, P.M. *et al.* (2004) Insular dwarfism in a brachiosaurid sauropod from the Upper Jurassic of Germany. *J. Vert. Paleontol.* 24, 108A
- Mateus, O. and Laven, T. (2004) A dwarf between giants? A new Late Jurassic sauropod from Germany. *J. Vert. Paleontol.* 24, 90A
- Erickson, G.M. and Tumanova, T.A. (2000) Growth curve and life history attributes of *Psittacosaurus mongoliensis* (Ceratopsia: Psittacosauridae) inferred from long bone histology. *Zool. J. Linn. Soc.* 130, 551–566
- Zullinger, E.M. *et al.* (1984) Fitting sigmoidal equations to mammalian growth curves. *J. Mammal.* 65, 607–636
- Reid, R.E.H. (1997) How dinosaurs grew. In *The Complete Dinosaur* (Farlow, J.O. and Brett-Surman, M.K., eds), pp. 403–413, Indiana University Press
- de Ricqlès, A. (1983) Cyclical growth in the long limb bones of a sauropod dinosaur. *Acta Palaeontol. Pol.* 28, 225–232
- Chinsamy, A. (1994) Dinosaur bone histology: implications and inferences. In *Dino Fest* (Rosenberg, G.D. and Wolberg, D.L., eds), pp. 213–227, Paleontological Society Publication #7
- Horner, J.R. *et al.* (2000) Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *J. Vert. Paleontol.* 20, 115–129
- Sander, P.M. (2000) Longbone histology of the Tendaguru sauropods: implications for growth and histology. *Paleobiol.* 26, 466–488
- Horner, J.R. and Padian, K. (2004) Age and growth dynamics of *Tyrannosaurus rex*. *Proc. R. Soc. London B Biol. Sci.* 271, 1875–1880
- Curry, K.A. (1999) Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. *J. Vert. Paleontol.* 19, 654–665
- de Ricqlès, A. (1980) Tissue structures of dinosaur bone: functional significance and possible relation to dinosaur physiology. In *A Cold Look at Warm-Blooded Dinosaurs* (Thomas, R.D.K. and Olson, E.C., eds), pp. 103–139, Westview
- Padian, K. and Horner, J.R. (2002) Typology versus transformation in the origin of birds. *Trends Ecol. Evol.* 17, 120–124
- Castanet, J. (1994) Age estimation and longevity in reptiles. *Gerontol.* 40, 174–192
- Castanet, J. *et al.* (1993) Bone and individual aging. In *Bone: Bone Growth* (Vol. 7) (Hall, B.K., ed.), pp. 245–283, CRC
- Erickson, G.M. *et al.* (2003) Vermiform bones and the evolution of gigantism in *Megalania* – how a reptilian fox became a lion. *J. Vert. Paleontol.* 23, 966–970
- Sander, P.M. and Tüchtmantel, C. (2003) Bone lamina thickness, bone apposition rates, and age estimates in sauropod humeri and femora. *Palaeontol. Z.* 77, 161–172
- Tütken, T. *et al.* (2004) Paleobiology and skeletochronology of Jurassic dinosaurs: implications from the histology and oxygen isotope compositions of bones. *Palaeogeog. Palaeoclimat. Palaeoecol.* 206, 217–238
- Amprino, R. (1947) La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l'accroissement. *Arch. Biol. (Liege)* 58, 315–330
- de Ricqlès, A. *et al.* (2001) The bone histology of basal birds in phylogenetic and ontogenetic perspectives. In *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom* (Gauthier, J. and Gall, L.F., eds), pp. 411–426, Special Publication Peabody Museum of Natural History
- Chinsamy, A. *et al.* (1998) Polar dinosaur bone histology. *J. Vert. Paleontol.* 18, 385–390
- de Ricqlès, A. *et al.* (2003) Osteohistology of *Confuciusornis sanctus* (Theropoda: Aves). *J. Vert. Paleontol.* 23, 373–386
- Starck, J.M. and Chinsamy, A. (2002) Bone microstructure and developmental plasticity in birds and other dinosaurs. *J. Morphol.* 254, 232–246
- Castanet, J. *et al.* (1996) Expression de la dynamique de croissance dans la structure de l'os périostique chez *Anas platyrhynchos*. *C. R. Acad. Sci.* 319, 301–308
- Castanet, J. *et al.* (2000) Periosteal bone growth rates in extant ratites (ostriche and emu). Implications for assessing growth in dinosaurs. *C. R. Acad. Sci.* 323, 543–550
- de Margerie, E. *et al.* (2002) Bone typology and growth rate: testing and quantifying “Amprino’s rule” in the mallard (*Anas platyrhynchos*). *C. R. Biol.* 325, 221–230
- Gatesy, S.M. and Dial, K.P. (1996) Locomotory modules and the evolution of avian flight. *Evolution* 50, 331–340
- Padian, K. and Horner, J.R. (2004) Dinosaur physiology. In *The Dinosauria* (2nd edn) (Weishampel, D.B. *et al.*, eds), pp. 660–671, University of California Press
- Padian, K. (2004) Basal Avialae. In *The Dinosauria* (2nd edn) (Weishampel, D.B. *et al.*, eds), pp. 210–231, University of California Press
- Seebacher, F.A. (2001) A new method to calculate allometric length-mass relationships of dinosaurs. *J. Vert. Paleontol.* 21, 51–60
- Padian, K. *et al.* (2004) Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies. *J. Vert. Paleontol.* 24, 555–571
- de Ricqlès, A. *et al.* (2000) Paleohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications. *Zool. J. Linn. Soc.* 129, 349–385
- de Ricqlès, A. *et al.* (2003) On the bone histology of some Triassic pseudosuchian archosaurs and related taxa. *Ann. Paléontol.* 89, 67–101
- Carrano, M.T. Body-size evolution in the Dinosauria. In *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles* (Carrano, M.T. *et al.*, eds), University of Chicago Press (in press)

- 49 McKinney, M.L. and McNamara, K.J. (1991) *Heterochrony: the Evolution of Ontogeny*, Plenum
- 50 Sereno, P.C. *et al.* (2001) The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science* 294, 1516–1519
- 51 Erickson, G.M. and Brochu, C.A. (1999) How the terror crocodile grew so big. *Nature* 398, 205–206
- 52 Grigorescu, D. (2003) Dinosaurs of Romania. *C. R. Palevol.* 2, 97–101
- 53 Lister, A. and Bahn, P. (1994) *Mammoths*, Macmillan
- 54 Holtz, T., Jr. (2001) The phylogeny and taxonomy of the Tyrannosauridae. In *Mesozoic Vertebrate Life* (Tanke, D.H. and Carpenter, K., eds), pp. 64–83, Indiana University Press
- 55 Carr, T.D. (1999) Craniofacial ontogeny in Tyrannosauridae. *J. Vert. Paleontol.* 19, 497–520
- 56 Brochu, C.A. (2002) Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high resolution computed tomographic analysis of the skull. *Mem. Soc. Vert. Paleontol.* 7, 1–38
- 57 Witmer, L.M. (2002) The debate on avian ancestry: phylogeny, function, and fossils. In *Mesozoic Birds: Above the Heads of Dinosaurs* (Chiappe, L.M. and Witmer, L.M., eds), pp. 3–30, University of California Press
- 58 Clark, J.M. *et al.* (2002) Cladistic approaches to the relationships of birds to other theropod dinosaurs. In *Mesozoic Birds: Above the Heads of Dinosaurs* (Chiappe, L.M. and Witmer, L.M., eds), pp. 31–61, University of California Press
- 59 Xu, X. *et al.* (2000) The smallest known non-avian theropod dinosaur. *Nature* 408, 705–708
- 60 Xu, X. *et al.* (2002) A basal troodontid from the Early Cretaceous of China. *Nature* 415, 780–784
- 61 Hwang, S.H. *et al.* (2002) New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from Northeastern China. *Am. Mus. Novit.* 3381, 1–44
- 62 Rimblot-Baly, F. *et al.* (1995) Analyse paléohistologique d'une série de croissance partielle chez *Lapparentosaurus madagascarensis* (Jurassique Moyen): essai sur la dynamique de croissance d'un dinosaure sauropode. *Ann. Paléontol. (Invert-Vert)* 81, 49–86
- 63 Carpenter, K. (1999) *Eggs, Nests, and Baby Dinosaurs*, Indiana University Press
- 64 Purves, W.K. *et al.* (1992) *Life: the Science of Biology*, Sinauer Associates
- 65 Horner, J.R. *et al.* (1999) Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. *Paleobiol.* 25, 295–304
- 66 Charnov, E.L. (1993) *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*, Oxford University Press
- 67 Ricklefs, R.E. (1968) Patterns of growth in birds. *Ibis* 110, 419–451
- 68 Larson, P. (2002) *Rex Appeal*, Invisible Cities
- 69 Weishampel, D.B. and Chapman, R.E. (1990) Morphometric study of *Plateosaurus* from Trossingen (Baden-Württemberg, Federal Republic of Germany). In *Dinosaur Systematics: Approaches and Perspectives* (Carpenter, K. and Currie, P.J., eds), pp. 43–51, Cambridge University Press
- 70 Currie, P.J. (1998) Possible evidence of gregarious behavior in tyrannosaurids. *GAIA* 15, 271–277

Articles of Interest in *Current Opinions and Trends* Journals

- James A. Fraser and Joseph Heitman (2005) Chromosomal sex-determining regions in animals, plants and fungi. *Current Opinion in Genetics & Development* doi:10.1016/j.gde.2005.09.002
- Duccio Medini, Claudio Donati, Hervé Tettelin, Vega Massignani and Rino Rappuoli (2005) The microbial pan-genome. *Current Opinion in Genetics & Development* doi:10.1016/j.gde.2005.09.006
- Filip Vandenbussche, Ronald Pierik, Frank F Millenaar, Laurentius A.C.J. Voesenek and Dominique Van Der Straeten (2005) Reaching out of the shade. *Current Opinion in Plant Biology* doi:10.1016/j.pbi.2005.07.007
- Anna Di Rienzo and Richard R. Hudson (2005) An evolutionary framework for common diseases: the ancestral-susceptibility model. *Trends in Genetics* doi:10.1016/j.tig.2005.08.007
- John M. Hancock (2005) Gene factories, microfunctionalization and the evolution of gene families. *Trends in Genetics* doi:10.1016/j.tig.2005.08.008
- Greg Gibson and Bruce Weir (2005) The quantitative genetics of transcription. *Trends in Genetics* doi:10.1016/j.tig.2005.08.010
- Sergey Sikora, Alex Strongin and Adam Godzik (2005) Convergent evolution as a mechanism for pathogenic adaptation. *Trends in Microbiology* doi:10.1016/j.tim.2005.08.010
- Scott J. Douglas, Ken Dawson-Scully and Marla B. Sokolowski (2005) The neurogenetics and evolution of food-related behaviour. *Trends in Neurosciences* doi:10.1016/j.tins.2005.09.006
- Katherine Denby and Chris Gehring (2005) Engineering drought and salinity tolerance in plants: lessons from genome-wide expression profiling in Arabidopsis. *Trends in Biotechnology* doi:10.1016/j.tibtech.2005.09.001
- Jens Nielsena and Stephen Oliver (2005) The next wave in metabolome analysis. *Trends in Biotechnology* doi:10.1016/j.tibtech.2005.08.005
- Xiang Lia and Ling Qin (2005) Metagenomics-based drug discovery and marine microbial diversity. *Trends in Biotechnology* doi:10.1016/j.tibtech.2005.08.006