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Adaptive radiation in sauropod dinosaurs: bone histology indicates rapid evolution of giant body size through acceleration

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Abstract

The well-preserved histology of the geologically oldest sauropod dinosaur from the Late Triassic allows new insights into the timing and mechanism of the evolution of the gigantic body size of the sauropod dinosaurs. The oldest sauropods were already very large and show the same long-bone histology, laminar fibro-lamellar bone lacking growth marks, as the well-known Jurassic sauropods. This bone histology is unequivocal evidence for very fast growth. Our histologic study of growth series of the Norian *Plateosaurus* indicates that the sauropod sistergroup, the Late Triassic and early Jurassic Prosauropoda, reached a much more modest body size in a not much shorter ontogeny. Increase in growth rate compared to the ancestor (acceleration) is thus the underlying process in the phylogenetic size increase of sauropods. Compared to all other dinosaur lineages, sauropods were not only much larger but evolved very large body size much faster. The prerequisite for this increase in growth rate must have been a considerable increase in metabolic rate, and we speculate that a bird-like lung was important in this regard.

Keywords: Dinosauria; Sauropoda; Prosauropoda; Acceleration; Gigantism; Respiration

Introduction

The famed American paleontologist and zoologist E.D. Cope observed that large body size in vertebrate animals is generally attained by a gradual size increase within an evolutionary lineage that began with a small ancestral form. This evolutionary pattern is known as "Cope's rule".

Sauropods were a highly successful group of dinosaurs which was widespread in the Jurassic and Cretaceous. Sauropods were the largest animals ever to inhabit the land, culminating in truly gigantic forms in at least three lineages (Upchurch 1998; Wilson 2002). These giants are unique in exceeding the body mass of any other large terrestrial tetrapods (i.e. large mammals and other dinosaurs) by an order of magnitude (Burness

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et al. 2001), which raises the question whether Cope's rule applies to them as well. Recent finds (Buffetaut et al. 2000, 2002) indicate that the group arose already in the Late Triassic, but they also document the very rapid evolution (within a few million years after their origin) of very large body size in sauropods (Buffetaut et al. 2002). Sauropods therefore did not follow Cope's rule and are apparently unique among dinosaurs in this respect, because all major dinosaur lineages show a gradual size increase over tens of millions of years, lacking large representatives before the Middle or Late Jurassic, with the possible exception of the Theropoda (Thulborn 2003).

The discrepancy in body size between other dinosaurs and sauropods has recently been highlighted by the availability of more accurate mass estimates calculated from volume estimates based on photogrammetric measurements of actual skeletons (Gunga et al. 1999) or on scientific reconstructions (Seebacher 2001). These estimates place common sauropods consistently in the 15–50 t category (e.g. *Diplodocus* 10–20 t, *Apatosaurus* 20–35 t, *Brachiosaurus* 30–50 t; Seebacher 2001). In addition, there are a number of very large sauropods, e.g. the diplodocid *Seismosaurus*, the brachiosaurid *Sauroposeidon* (see Wedel et al. 2000), and the titanosaur *Argentinosaurus*, that are estimated to have attained a body mass of 80–100 t, whereas sauropod species with an adult body mass below 4–5 t are virtually unknown (Seebacher 2001). The largest representatives of other dinosaur lineages, despite generally being perceived as very big, rarely exceeded the 10 t threshold and thus actually are in the size range of very large terrestrial mammals such as extant and fossil elephants and the fossil indricotheres. Among animals only whales grow to a larger body mass, but a direct comparison between these two groups is difficult because of the vastly different constraints of the aquatic versus the terrestrial environment.

What made the gigantism of sauropods possible? This question obviously must center on a closer examination of sauropod evolutionary origins. The earliest currently known sauropod material is from the Late Triassic of Thailand (Buffetaut et al. 2000, 2002), from the Nam Phong Formation which is late Norian to Rhaetian in age (Racey et al. 1996). The material consists of the remains of two individuals. The first was relatively small (total length about 6.5 m) and possibly juvenile (although histologic samples were not available to confirm this), but the femur and other bones offered sufficient morphological characters for description as a separate genus and species, *Isanosaurus attavipachi* Buffetaut et al. (2000). The second individual (Buffetaut et al. 2002) is represented by various bones (primarily a right and an incomplete left humerus) which clearly pertain to a larger animal (Fig. 1). Because of the size difference and insufficient overlap in skeletal elements, it is uncertain if the second individual also belongs to *I. attavipachi* or represents a different sauropod taxon.

Based on the humerus length of 105 cm, the large individual is in the size range of the well-known large sauropods from the Late Jurassic (e.g. a medium-sized *Apatosaurus* has a humerus about 1 m long). The entire animal was at least 12–15 m long but, based on its bone histology, was not fully grown yet (see below). This documents the evolution of very large body size in sauropods already by the late Norian or Rhaetian (Buffetaut et al. 2002), at most 15 million years after the appearance of the closest relatives of the sauropods, the Prosauropoda, in the early Norian.

The groups ancestral to the Sauropoda are the prosauropod dinosaurs. Although it has long been recognized that there is a close relationship between these small (<100 kg) to large (3 t; Seebacher 2001) animals and the sauropods, the exact nature of this relationship has not yet been resolved. Prosauropods may be monophyletic and in their entirety form the sistergroup of sauropods. Alternatively, it could be that only certain prosauropods, namely the melanorosaurids, are the sistergroup of sauropods, the other prosauropod taxa such as plateosaurids being successively more distantly related to the Sauropoda (Benton et al. 2000). Sauropod monophyly, however, is unanimously accepted, as is the monophyly of Sauropoda plus all prosauropods, which are united in the taxon Sauropodomorpha (Upchurch 1998; Wilson 2002).

The evolution of gigantism in sauropod dinosaurs from prosauropods, and of the body plan changes linked to this, are an obvious case of a pattern of heterochrony termed peramorphosis (Long and McNamara 1997) in which the descendant has a larger body size than the ancestor, and the juvenile descendant resembles the adult ancestor whereas the adult descendant is more 'developed'. However, which process of heterochrony produced the gigantic body size of sauropod dinosaurs had not been understood until recently. Because a number of recent studies (Rimblot-Baly et al. 1995; Curry 1999; Erickson et al. 2001; Sander 2000) detected very fast growth in several taxa of Middle and Late Jurassic sauropods based on examinations of their bone histology, it was suggested that an increase in growth rate (acceleration) compared to primitive dinosaurs was responsible (McNamara 1997). At the time, however, the very large Late Triassic sauropod was not known yet, and a model of prolonged acceleration from the Late Triassic to the Late Jurassic, i.e. a gradual phyletic size increase, seemed tenable to account for sauropod gigantism.

Heterochrony describes the evolutionary effects of changes in rate or timing of ontogenetic processes of a descendant compared to the ancestor, affecting its shape

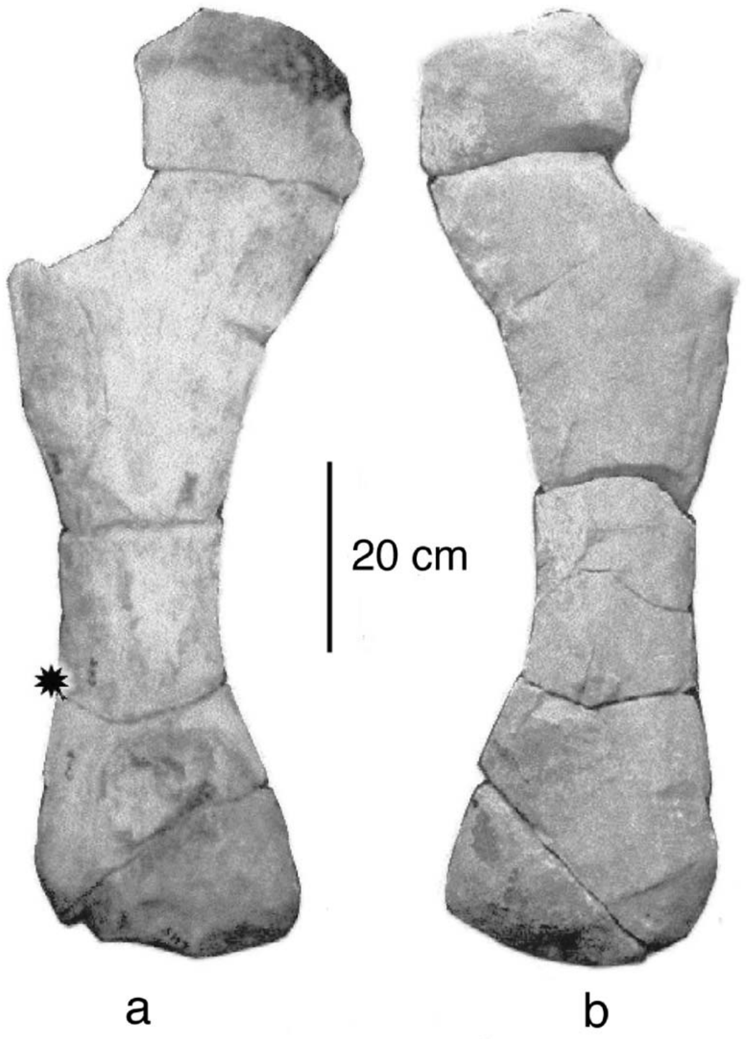


Fig. 1. Sampling location for the large sauropod from the late Norian to Rhaetian Nam Phong Formation at Khok Hin Poeng (Chaiyaphum Province, Thailand). The sample was taken from the fragmentary left humerus (Paleontological Collection, Department of Mineral Resources, Thailand CH 5). The sampling location (∗) is marked here on an image of the right humerus. (a) Cranial view and (b) Caudal view of the right humerus.

and size (Gould 1977; Alberch et al. 1979; McNamara 1997). As we concentrate here on the change of size, not so much on change of shape, we follow the more general terminology of McNamara (1997) and Long and McNamara (1997). "Acceleration" thus also refers to an increase in the rate of overall body growth and not only to an increase in the rate of shape change of a particular structure, the latter being the original definition of Alberch et al. (1979).

We examined the bone histology of the oldest sauropod dinosaur and, by comparing it histologically to numerous Late Jurassic sauropods and the ancestral prosauropods, are now able to paint a detailed picture of the evolution of the very large body size of sauropod dinosaurs. The results may have a bearing on what made the unique gigantism of sauropods possible.

Methods and material

The record of growth provided by bone histology

Fossil bone is generally characterized by good to excellent preservation of its histology, which allows comparisons with fossils of different geological ages and with recent vertebrates. Bone histology records the growth of the individual and thus provides information about the growth strategies and life-history parameters of species and higher taxa, making it uniquely suited to detect heterochronic processes in evolution by comparing life-history parameters in phylogenetic lineages. This has been pointed out some time ago by Ricqlès (1980), and applied to archosaurs by Erickson and Brochu (1999), Padian et al. (2001), and Ricqlès and Buffrénil (2001).

Bone may show growth marks, most commonly lines of arrested growth (LAGs), which record cessation of bone apposition, albeit for an unknown duration. Other types of growth marks are modulations (Rimblot-Baly et al. 1995) and polish lines (Sander 2000). Making the well-founded assumption of annual growth cyclicity (Castanet et al. 1993; Chinsamy 1993), the growth mark record can be quantified (this technique, called skeletochronology, is regularly used in the study of recent vertebrates), and estimates of growth and important life-history parameters become possible (Ricqlès 1980; Castanet et al. 1993; Castanet 1994).

A more general record of growth is contained in the type of bone laid down; because a specific bone type is linked to a particular rate of bone apposition, a relationship known as "Amprino's rule" (Ricqlès et al. 1991; Castanet et al. 2000; Sander 2000; Padian et al. 2001; Margerie et al. 2002). This relationship is difficult to quantify because of the limited number of tissue types which are deposited within wide (but non-overlapping) rate brackets. The fastest-growing bone is fibro-lamellar bone without LAGs (found today in large mammals), intermediate rates are indicated by fibro-lamellar bone with LAGs, and low rates are indicated by lamellar-zonal bone (found today in most reptiles) (Ricqlès et al. 1991; Castanet et al. 2000; Margerie et al. 2002).

Sampling

Bone histology was studied in thin sections, polished sections, and high-resolution digital photographs of fracture surfaces. The fracture surfaces were located around mid-shaft of the bones to capture a cross section of the neutral growth region of the shaft. This contains the longest record of an individual's growth. The thin sections and polished sections can be ground either from samples cut off a fracture surface or from a core sample. We obtained core samples by drilling with a diamond drill bit at a standardized sampling location, also at mid-shaft (for details see Sander 2000). After embedding in polyester resin, the sample was cut perpendicular to the long axis of the bone, revealing a segment of the cross section of the shaft. One half of the sample was ground into the thin section, the other half into the polished section.

The oldest sauropod from the Late Triassic

The sample was taken from the fragmentary left humerus of the large individual from the Nam Phong Formation of Thailand (Buffetaut et al. 2002). The sampling location is in the lateral side of the mid-shaft, somewhat distal to the neutral region (Fig. 1). Sampling would ideally have taken place 8 cm farther proximally but was constrained by natural breaks in the specimen. The medullary region is small and filled with cancellous bone. The sections show conspicuous diagenetic alteration in some regions, but this is not widespread enough to preclude histological evaluation.

Late Triassic prosauropod bones

We sampled numerous prosauropod post-cranial bones, concentrating on limb and girdle bones of *Plateosaurus* from the German locality of Trossingen and the Swiss locality of Frick (Sander 1992), but also from the basal prosauropod *Thecodontosaurus* from the Late Triassic of England (Benton et al. 2000). Techniques employed for sampling the prosauropod bones were mainly coring and high-resolution digital photography of fracture surfaces (not possible with the Frick material because of a mineral cover on the fracture surfaces).

Late Jurassic sauropod bones

The bone histology of later sauropods was studied by us in extensive growth series of long bones of several Late Jurassic taxa (*Barosaurus*, *Brachiosaurus*, *Dicraeosaurus*, *Janenschia*) from the Tendaguru beds of Tanzania (Sander 1999, 2000), and from the Morrison Formation of the western United States (*Apatosaurus*, *Camarasaurus*, *Diplodocus*; work in progress by the first author), using the core sampling technique. Sauropod limb bones such as the humerus and femur are ideal for studying growth because they have a thick cortex that is little affected by remodeling (Rimblot-Baly et al. 1995; Sander 2000).

Results

Histology of the oldest sauropod

The primary bone of the cortex of the large sauropod humerus from the Late Triassic of Thailand consists entirely of laminar fibro-lamellar bone tissue (Fig. 2). Growth marks are not very well developed, as there are neither LAGs nor polish lines but only modulations. The modulations are more closely spaced in the outer cortex than in the inner cortex. The inner cortex shows resorption cavities and incipient secondary osteons but no secondary bone. The medullary cavity is small and completely filled with cancellous bone.

This histology of the humerus is unequivocal evidence of very rapid and uninterrupted growth at rates comparable to those of modern large terrestrial mammals such as large ungulates and elephants (Curry 1999; Sander 1999, 2000). However, due to the lack of sufficiently developed growth marks, the life history of the individual cannot be quantified. It is also important to note that the histology of the large Thai humerus conforms in all aspects to that seen in later sauropod long bones and differs clearly from that of prosauropod long bones. This provides independent histologic confirmation of the assignment of the material to the Sauropoda which was based on morphology alone.

Bone histology also indicates that the individual was not fully grown yet. Firstly, it lacks closely spaced LAGs in the outermost cortex. The presence of this feature in large individuals of the Late Jurassic sauropods indicates the near termination of growth (Curry 1999; Sander 1999, 2000). In addition, the lack of Haversian remodeling in the cortex of the large Thai humerus argues against an advanced ontogenetic stage, because Haversian remodeling is seen to occur only in fully grown individuals of Late Jurassic sauropods (Curry 1999; Sander 1999, 2000).

Prosauropod histology

Plateosaurus limb bones (humerus, femur, tibia, fibula) exhibit a different histology (Fig. 2). There is a large medullary cavity bordered by a thin inner zone of remodeled cortex. The remainder of the cortex consists of primary bone of the laminar fibro-lamellar type containing regularly spaced LAGs. *Plateosaurus* girdle bones (scapula, pubis) also show LAGs, but the latter are more distinctive and set in fibro-lamellar bone with longitudinal vascular canals. These differences in the primary bone of long and girdle bones are due to the lower bone apposition rates in the latter. In the girdle bones, there is no medullary cavity but a limited internal region of secondary cancellous bone. The growth mark record is therefore longer and more distinctive in the girdle bones than in the long bones. *Thecodontosaurus* limb bone histology is essentially the same as that of *Plateosaurus*, but the sample size is insufficient for quantitative estimates.

Individuals of *Plateosaurus* with a femur length between 56 and 89 cm (the longest known femora are nearly 1 m long) display between 5 and 15 cycles in their cortex, usually between 6 and 13. This is a minimum count, because several cycles were destroyed by expansion of the medullary cavity of the long bones and by the formation of secondary cancellous bone in the girdle bones. An abrupt decrease in LAG spacing in the middle to outer cortex of some specimens (Fig. 2) indicates a decrease in growth rate fairly late in observed ontogeny.

The abundance of fibro-lamellar bone in combination with regularly spaced LAGs in *Plateosaurus* and *Thecodontosaurus* indicates that growth was cyclical but rapid, at least until sexual maturity was reached. Afterwards, growth rate decreased but still was substantial and elevated above typical reptilian rates. Eventually, growth plateaued as indicated by a thin layer of poorly vascularized lamellar-zonal bone with very closely spaced LAGs in the outermost cortex of some individuals.

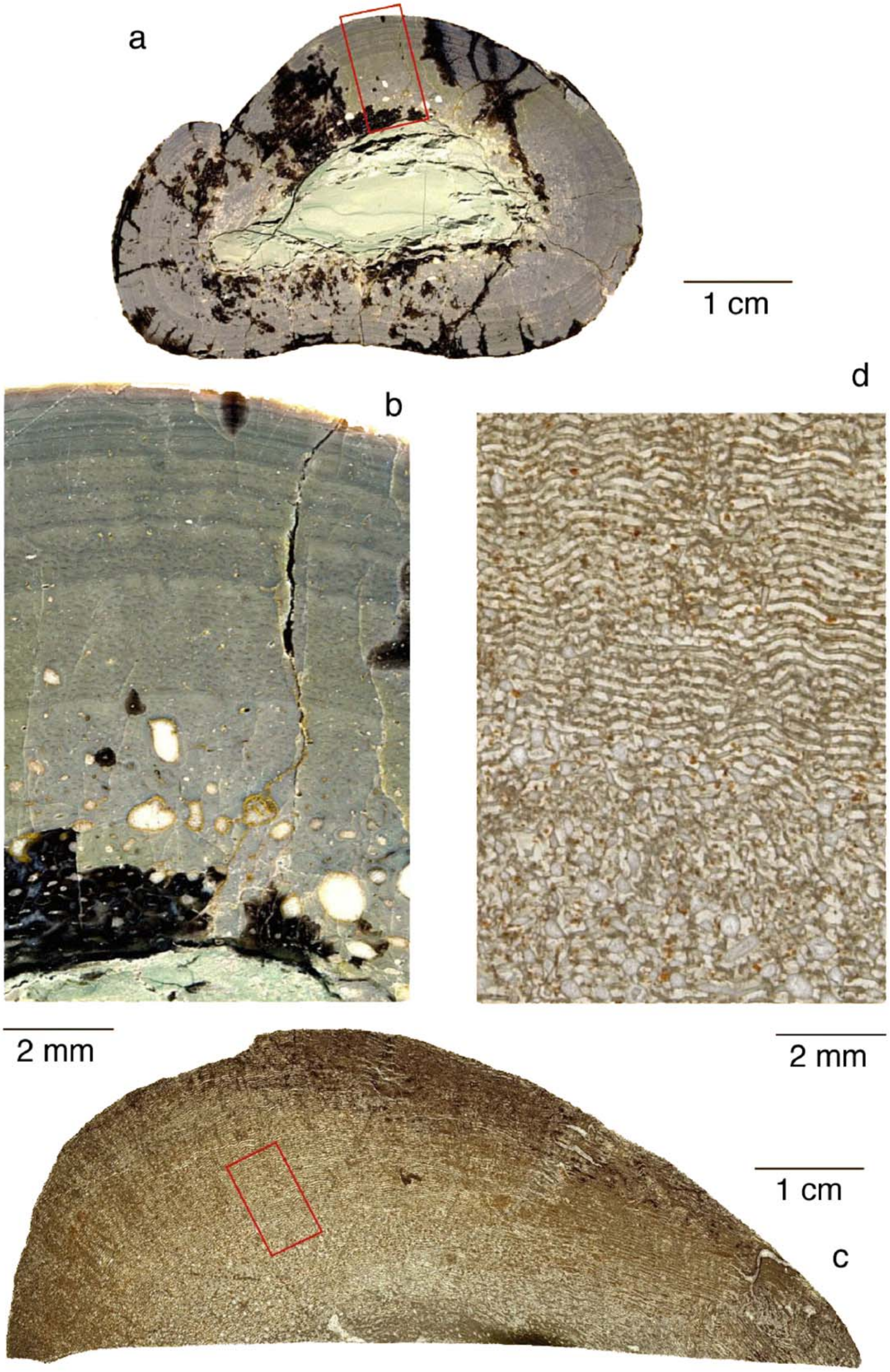
Brief published descriptions of limb bone histology are also available for the prosauropods *Massospondylus* (Chinsamy 1993) and *Euskelosaurus* (Ricqlès 1968). The quantitative data obtained for *Massospondylus* are consistent with those for *Plateosaurus* (see also Seitz 1907; Gross 1934). However, the largest individuals of *Massospondylus* do not show any indication of a growth plateau. This was interpreted as evidence for an indeterminate growth strategy in this taxon (Chinsamy 1993) but could also be due to a taphonomic bias against very large individuals of this species. *Euskelosaurus* is of particular interest because it belongs to the Melanorosauridae, generally considered to be the prosauropod group most closely related to the sauropods. It, too, shows the combination of fibro-lamellar bone and LAGs (and also dense Haversian bone), but precise counts were not given (Ricqlès 1968).

Histology of the Late Jurassic sauropods

As in the oldest sauropods, the primary bone of the long-bone cortex of later sauropods consists entirely of laminar fibro-lamellar tissue. Commonly, the primary bone lacks growth marks entirely. If present, most are weakly expressed (as modulations; Ricqlès 1983) and polish lines (Sander 1999, 2000), and irregularly spaced LAGs are very rare.

As in the prosauropods and in modern reptiles, but unlike in most large mammals, sauropod dinosaurs apparently reached sexual maturity well before maximum size. An abrupt decrease in vascularization and an increase in tissue organization in the fibro-lamellar bone of the middle to outer cortex document a sudden slowdown in growth best explained by the onset of sexual maturity (Ricqlès et al. 1991). Sauropods reached a distinctive growth plateau which is indicated by a thin layer of lamellar-zonal bone with closely spaced growth marks in the outermost cortex of large individuals (Curry 1999; Sander 2000).

Because of the poor expression or complete lack of growth marks in their fibro-lamellar bone, quantitative estimates of sauropod life-history parameters are the exception. *Janenschia* from Tendaguru (Sander 2000) and *Apatosaurus* from the Morrison Formation (Curry 1999) reached sexual maturity at >11 and >10 years, respectively. One large individual of *Janenschia* stopped growing at >26 years and died at >38 years (Sander 2000). A large individual of *Apatosaurus* (femur length 164 cm) was estimated to be 33 years old and still growing (Sander and Tückmantel 2003). An age estimate of only 15 years for another large *Apatosaurus*


a
1 cm
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2 mm
2 mm
1 cm
c

(Erickson et al. 2001) appears too low in comparison with these estimates. Longevity data are not yet available for any other sauropods.

The long-bone histology of Late Jurassic sauropods is in agreement with that of the Middle Jurassic *Lapparentosaurus* from Madagascar (Rimblot-Baly et al. 1995). Detailed histologic data are not yet available for Cretaceous sauropods, but there is no reason to believe that their histology differed from that of the earlier forms.

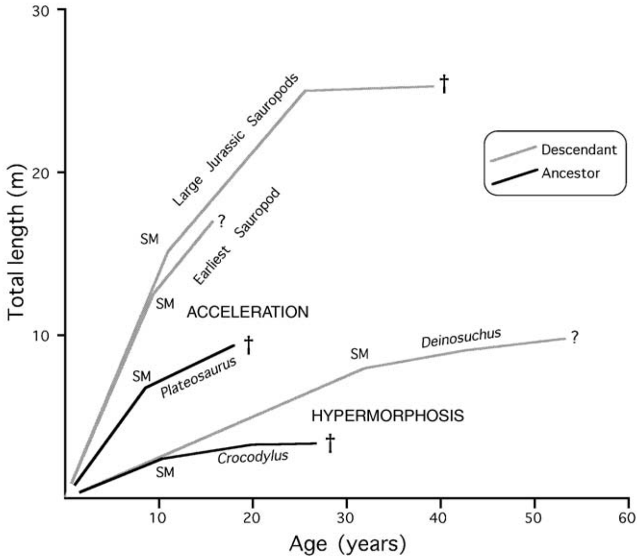

Fig. 3. Heterochronic processes in the evolution of gigantism. Large size in the Late Cretaceous crocodilian *Deinosuchus* was achieved by hypermorphosis (prolonged phase of growth at juvenile rate), whereas large size in the Triassic and later sauropods was primarily achieved by acceleration (increase in growth rate). The growth curve for the large Jurassic sauropods summarizes observations for several taxa (Rimblot-Baly et al. 1995; Curry 1999; Sander 1999, 2000). The duration of the juvenile growth phase in the large Triassic sauropod is an estimate. Age data for *Plateosaurus* were obtained during this study, those for crocodiles are from Erickson and Brochu (1999). SM = sexual maturity.

Discussion

The qualitative comparison of the bone histology of the large humerus from the Late Triassic of Thailand with that of prosauropods provides unequivocal evidence that the oldest sauropods grew considerably faster than the much smaller prosauropods and at the same rate as in the Late Jurassic sauropods. The quantitative figures for age at sexual maturity and life span for the Late Jurassic sauropods are roughly comparable to those for prosauropods, also indicating that sauropods grew considerably faster than the much smaller prosauropods because they reached a much larger body size in a not much longer life span (Fig. 3).

The occurrence of a typical sauropod bone histology in the oldest known sauropod clearly indicates that the evolutionary process of acceleration (increase in growth rate; McNamara 1997) produced the large body size of sauropods (Fig. 3), and that acceleration was very strong. An alternative scenario, which would call first for phylogenetic size increase by hypermorphosis (prolonged growth at the rate of the ancestor), followed later by an increase in growth rate resulting in a shortened ontogeny, apparently did not take place. This suggests that the key innovation that enabled sauropods to reach gigantic size was present from the beginning of the lineage. The early evolution of very large body size apparently allowed sauropods to be the dominant terrestrial herbivores for at least the entire Jurassic, and thus may well have been the key to the evolutionary success of the Sauropoda.

Acceleration in growth rate was also at work in other dinosaur lineages (Erickson et al. 2001; Padian et al. 2001) and by itself cannot explain the unique body size of sauropods. Gradual phylogenetic size increase produced by acceleration is probably also seen in other endothermic amniote lineages such as proboscidean mammals. The difference between sauropod dinosaurs and all other terrestrial tetrapod lineages leading to very large representatives is the initial massive increase in growth rate in sauropods, resulting in ‘instantaneously’ very large animals. The increase in growth rate must have required an equally dramatic increase in metabolic rate.

What evolutionary innovations could have allowed this massive increase in metabolic rates? We speculate that a major adaptation was a bird-like lung, although the performance of other organs and organ systems such as the heart and circulatory systems also would have had to increase greatly. The lungs of living birds, with their unidirectional flow, are twice as efficient as mammalian

Fig. 2. Comparison of the bone histology of the prosauropod *Plateosaurus* from the Triassic of Frick (Switzerland) and the large sauropod from the Triassic of Thailand. (a) Cross section of a *Plateosaurus* humerus at mid-shaft, showing a large medullary cavity and clear growth cycles which are more closely spaced with increasing age of the individual; rectangle marks location of sample in (b). (b) Detail of cortical bone; the cortex consists of laminar fibro-lamellar bone with regularly spaced LAGs. (c) Cortex of the large sauropod humerus, note the lack of obvious growth marks; rectangle marks location of sample in (d). (d) Detail; the cortical bone is of the laminar fibro-lamellar type seen in later sauropods.

lungs, greatly decreasing the energetic cost of breathing (Perry and Reuter 1999). While nothing is known about the lungs of prosauropods, there is considerable osteological evidence for bird-like lungs in sauropods, e.g. the highly pneumatized vertebrae of derived sauropods, pointing to the presence of an extensive air sac system (Wedel et al. 2000; Wedel 2003). In addition, features of the axial skeleton of the trunk region suggest that the sauropod lung was attached dorsally (Perry and Reuter 1999).

Even more evidence, osteological (pneumatization of the skeleton) as well as phylogenetic (birds as the descendants of maniraptoran theropods), is strongly suggestive of derived theropod dinosaurs possessing a bird-like lung (Perry 2001). Possibly, a bird-like lung thus arose much earlier than in derived theropods and is a synapomorphy of Saurischia in general. The ability of predators such as *Tyrannosaurus rex* to grow to giant size may have created the evolutionary pressure on size increase in the sauropodomorph lineages. Of course, this pressure must have been met with the ability of the prey to ‘outgrow’ the predator, resulting in giant size of the prey. The adaptive radiation of saurischian dinosaurs may thus be seen as the arms race between giant carnivores and giant herbivores, the unique gigantism of which (Burness et al. 2001) was facilitated by a super-efficient lung, among other improvements to the organ systems. This would not only answer the question what made gigantism in sauropods possible, but also which selection pressure actually pushed up body size in sauropods as well as theropods.

The hypothesis of super-efficient lungs in saurischian dinosaurs can be tested in at least two ways: (1) by further study of skeletal correlates of lung anatomy, especially in prosauropods; and (2) by modeling saurischian respiratory physiology. Respiratory physiology is well studied in extant vertebrates, and insights from it could be combined with the baseline data for growth rates in saurischians obtained from this and other studies to see if lung efficiency would make a difference.

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References

Alberch, P., Gould, S.J., Oster, G.F., Wake, D.B., 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5, 296–317.

Benton, M.J., Juul, L., Storrs, G.W., Galton, P.M., 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of Southwest England. J. Vertebr. Paleontol. 20, 77–108.

Buffetaut, E., Suteethorn, V., Cuny, C., Tong, H., Le Loeuff, J., Khansubha, S., Jongautchariyakul, S., 2000. The earliest known sauropod dinosaur. Nature 407, 72–74.

Buffetaut, E., Suteethorn, V., Le Loeuff, J., Cuny, C., Tong, H., Khansubha, S., 2002. The first giant dinosaurs: a large sauropod from the Late Triassic of Thailand. C. R. Palevol. 1, 103–109.

Burness, G.P., Diamond, J., Flannery, T., 2001. Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. Proc. Natl Acad. Sci. USA 98, 14518–14523.

Castanet, J., 1994. Age estimation and longevity in reptiles. Gerontology 40, 174–192.

Castanet, J., Francillon-Vieillot, H., Meunier, F.J., Ricqlès, A. de, 1993. Bone and individual aging. In: Hall, B.K. (Ed.), Bone. Volume 7: Bone Growth — B. CRC Press, Boca Raton, FL, pp. 245–283.

Castanet, J., Rogers, K.C., Cubo, J., Boisard, J.-J., 2000. Periosteal bone growth rates in extant ratites (ostrich and emu). Implications for assessing growth in dinosaurs. C. R. Acad. Sci. Paris Sci. Terre 323, 543–550.

Chinsamy, A., 1993. Bone histology and growth trajectory of the prosauropod dinosaur *Massospondylus carinatus* (Owen). Mod. Geol. 18, 319–329.

Curry, K.A., 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. J. Vertebr. Paleontol. 19, 654–665.

Erickson, G.M., Brochu, C.A., 1999. How the “terror crocodile” grew so big. Nature 398, 205–206.

Erickson, G.M., Rogers, K.C., Yerby, S.A., 2001. Dinosaurian growth patterns and rapid avian growth rates. Nature 412, 429–433.

Gould, S.J., 1977. Ontogeny and Phylogeny. Harvard University Press, Cambridge, MA.

Gross, W., 1934. Die Typen des mikroskopischen Knochenbaues bei fossilen Stegocephalen und Reptilien. Z. Anat. Entwicklungsgesch. 203, 731–764.

Gunga, H.-C., Kirsch, K., Rittweger, J., Röcker, L., Clarke, A., Albertz, J., Wiedemann, A., Mokry, S., Suthau, T., Wehr, A., Heinrich, W.-D., Schultze, H.-P., 1999. Body size and body volume distribution in two sauropods from the Upper Jurassic of Tendaguru (Tanzania). Mitt. Mus. Natk. Humboldt-Univ. Berlin Geowiss. Reihe 2, 91–102.

Long, J.A., McNamara, K.J., 1997. Heterochrony. In: Currie, P.J., Padian, K. (Eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 311–317.

Margerie, E. de, Cubo, J., Castanet, J., 2002. Bone typology and growth rate: testing and quantifying ''Amprino's rule'' in the mallard (*Anas platyrhynchos*). C. R. Acad. Sci. Paris Biol. 325, 221–230.

McNamara, K., 1997. Shapes of Time. The Evolution of Growth and Development. Johns Hopkins University Press, Baltimore.

Padian, K., Ricqles, A. de, Horner, J.R., 2001. Dinosaurian growth rates and bird origins. Nature 412, 405–408.

Perry, F.S., Reuter, C., 1999. Hypothetical lung structure of *Brachiosaurus* (Dinosauria: Sauropoda) based on functional constraints. Mitt. Mus. Natk. Humboldt-Univ. Berlin Geowiss. Reihe 2, 75–79.

Perry, S.F., 2001. Functional morphology of the reptilian and avian respiratory system and its implications for theropod dinosaurs. In: Gauthier, J., Gall, L.F. (Eds.), New Perspectives on the Origin and Early Evolution of Birds. Peabody Museum of Natural History. Yale University, New Haven, pp. 429–441.

Racey, A., Love, M.A., Canham, A.C., Goodall, J.G.S., Polochan, S., Jones, P.D., 1996. Stratigraphy and reservoir potential of the Mesozoic Khorat Group, NE Thailand. J. Petrol. Geol. 19, 5–40.

Ricqlès, A. de, 1968. Recherches paléohistologiques sur les os longs des Tétrapodes I—origine du tissu osseux plexiforme des Dinosauriens Sauropodes. Ann. Paléontol. 54, 133–145.

Ricqlès, A. de, 1980. Croissance périodique, ontogenèse, phylogenèse et stratégies démographiques: le cas des reptiles captorhinomorphes. Bull. Soc. Zool. Fr. 105, 363–369.

Ricqlès, A. de, 1983. Cyclical growth in the long limb bones of a sauropod dinosaur. Acta Palaeontol. Pol. 28, 225–232.

Ricqlès, A. de, Buffrénil, V. de, 2001. Bone histology, heterochronies and the return of tetrapods to life in water: where are we? In: Mazin, J.-M., Buffrénil, V. de. (Eds.), Secondary Adaptation of Tetrapods to Life in Water. Dr. Friedrich Pfeil, Munich, pp. 289–310.

Ricqlès, A. de, Meunier, F.J., Castanet, J., Francillon-Vieillot, H., 1991. Comparative microstructure of bone. In: Hall, B.K. (Ed.), Bone. Volume 3: Bone Matrix and Bone Specific Products. CRC Press, Boca Raton, FL, pp. 1–78.

Rimblot-Baly, F., Ricqlès, A. de, Zylberberg, L., 1995. Analyse paléohistologique d'une série de croissance partielle chez *Lapparentosaurus madagascariensis* (Jurassique moyen): Essai sur la dynamique de croissance d'un dinosaure sauropode. Ann. Paléontol. (Invertebr.–Vertebr.) 81, 49–86.

Sander, P.M., 1992. The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. Palaeogeogr. Palaeoclim. Palaeoecol. 93, 255–299.

Sander, P.M., 1999. Life history of the Tendaguru sauropods as inferred from long bone histology. Mitt. Mus. Natk. Humboldt-Univ. Berlin Geowiss. Reihe 2, 103–112.

Sander, P.M., 2000. Long bone histology of the Tendaguru sauropods: implications for growth and biology. Paleobiology 26, 466–488.

Sander, P.M., Tückmantel, C., 2003. Bone lamina thickness, bone apposition rates, and age estimates in sauropod humeri and femora. Paläontol. Z. 76, 161–172.

Seebacher, F., 2001. A new method to calculate allometric length–mass relationships of dinosaurs. J. Vertebr. Paleontol. 21, 51–60.

Seitz, A.L., 1907. Vergleichende Studien über den mikroskopischen Knochenbau fossiler und rezenter Reptilien. Nova Acta Leopold. 87, 230–370.

Thulborn, T., 2003. Comment on ''Ascent of dinosaurs linked to an iridium anomaly at the Triassic–Jurassic boundary''. Science 301, 169b.

Upchurch, P., 1998. The phylogenetic relationships of sauropod dinosaurs. Zool. J. Linn. Soc. Lond. 124, 43–16103.

Wedel, M.J., 2003. Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. Paleobiology 29, 243–255.

Wedel, M.J., Cifelli, R.L., Sanders, R.K., 2000. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. Acta Palaeontol. Pol. 45, 343–388.

Wilson, J.A., 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zool. J. Linn. Soc. 136, 217–276.