

Constraints on the Lamina Density of Laminar Bone Architecture of Large-Bodied Dinosaurs and Mammals

Authors: Hofmann, Rebecca, Stein, Koen, and Sander, P. Martin

Source: Acta Palaeontologica Polonica, 59(2) : 287-294

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2012.0149>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Constraints on the lamina density of laminar bone architecture of large-bodied dinosaurs and mammals

REBECCA HOFMANN, KOEN STEIN, and P. MARTIN SANDER



Hofmann, R., Stein, K., and Sander, P.M. 2014. Constraints on the lamina density of laminar bone architecture of large-bodied dinosaurs and mammals. *Acta Palaeontologica Polonica* 59 (2): 287–294.

Laminar bone tissue is commonly found in Dinosauria (including birds) and Mammalia. The tissue emerged convergently several times, and its frequent occurrence among amniotes has stimulated researchers to study some of its geometric features. One such feature is lamina thickness or lamina density (LD, expressed as number of laminae per mm). We measured LD in a sample of sauropodomorph dinosaur taxa (basal sauropodomorphs, basal sauropods and Neosauropoda) and compared it with LD of a selection of mammals. LD is relatively constrained within the groups; nonetheless mean sauropodomorph LD differs significantly from mean mammal LD. However, increasing sample size with other dinosaur groups and more perissodactyls and artiodactyls may alter this result. Among sauropods, LD does not change drastically with increasing femur length although a slight tendency to decrease may be perceived. We conclude that the laminar vascular architecture is most likely determined by a combination of structural and functional as well as vascular supply and physiological causes.

Key words: Dinosauria, Mammalia, bone histology, laminar bone, lamina thickness, lamina density.

Rebecca Hofmann [rebecca_hofmann@gmail.com] and P. Martin Sander [martin.sander@uni-bonn.de], Division of Paleontology, Steinmann Institute, University of Bonn, Nussallee 8, 53115 Bonn, Germany;
Koen Stein [koen_stein@yahoo.co.uk], Division of Paleontology, Steinmann Institute, University of Bonn, Nussallee 8, 53115 Bonn, Germany; current adress: Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany (corresponding author).

Received 21 December 2012, accepted 16 October 2013, available online 18 October 2013.

Copyright © 2014 R. Hofmann et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Highly vascularized bone tissues (HVBT) occur in long bones of several extinct and extant vertebrate groups. These include therapsids (Ray et al. 2004, 2009), large pterosaurs, some basal archosaurs and some derived Crurotarsi (Ricqlès et al. 2003, 2008; Padian et al. 2004; Cubo et al. 2012), but HVBT are most widespread in mammals and dinosaurs. Today only extant endotherms with high growth rates produce HVBT (Amprino 1947), and thus following Case (1978) and Brown (2004), high resting metabolic rates can be inferred for extinct taxa with HVBT.

A very common type of highly vascularized bony tissue is laminar bone (laminar or plexiform bone sensu Ricqlès 1968). In laminar bone, the vascular canals of the bony tissues are mainly oriented circumferentially, i.e., parallel with the periosteal surface. Laminar bone is a composite tissue built up by two different matrix types (Stein and Prondvai 2012, 2014). The first matrix type secreted by stationary osteoblasts (Ferretti et al. 2002; Marotti 2010) forms a vas-

cular framework of woven bone (not fibrous bone; see Stein and Prondvai 2014). This woven bone framework provides a rapid volumetric size increase of the bone but the woven bone trabeculae are very thin, isotropic and structurally not very stable (Stein and Prondvai 2014). This is why dynamic osteoblasts compact the tissue with a different and anisotropic bone matrix type soon after ossification of the woven bone (Ferretti et al. 2002). The anisotropic highly organized primary bone tissue (HOPB; sensu Stein and Prondvai 2014) gradually compacts the vascular spaces. Combined, these two matrix types give the tissue all the positive aspects of both matrices. A schematic overview of laminar bone formation is provided in Fig. 1.

Laminar bone architecture evolved convergently at least twice, namely in the ancestors of dinosaurs and those of mammals. Within dinosaurs, laminar bone is well documented from the long bones of enormous sauropods like *Brachiosaurus*, *Barosaurus*, and *Dicraeosaurus* (Sander 2000), in theropods such as *Coeolophysis*, *Allosaurus* (Padian et al. 2004; Bybee et al. 2006) and *Tyrannosaurus rex* (Horner and Padian 2004), and hadrosaurs, e.g., *Maiasau-*

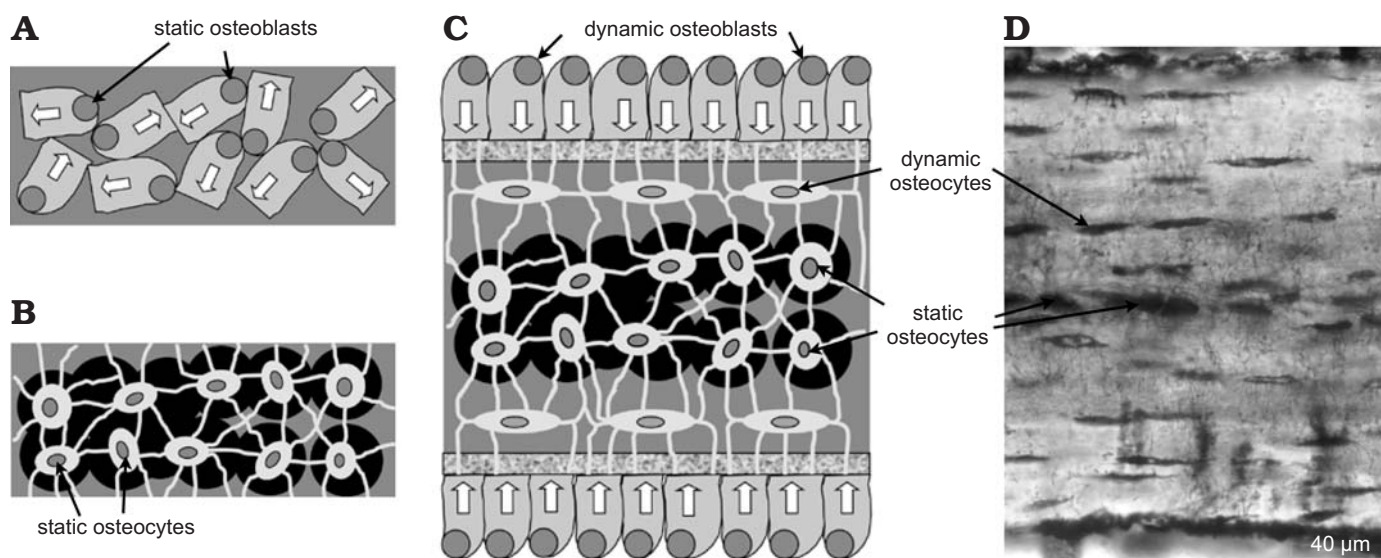


Fig. 1. Static and dynamic osteogenesis. **A.** Static osteogenesis by static osteoblasts proliferating in situ from mesenchymal tissue. The random orientation of the osteoblasts creates a random local fibre orientation of the produced matrix. **B.** Static osteoblasts turn into static osteocytes as they become entrapped in the mineralizing woven bone matrix. **C.** Dynamic osteoblasts arrange themselves on the woven bone and start producing highly organized primary bone, occasionally trapping a dynamic osteoblast, which will then become a dynamic osteocyte. **D.** Static and dynamic osteocyte lacunae in a longitudinal section of a humerus of the titanosaur *Alamosaurus*. A–C modified from Marotti (2010), D modified from Stein and Prondvai (2014).

ra and *Hypacrosaurus* (Horner et al. 1999; Cooper et al. 2008). The Recent ostrich and emu, living relatives of dinosaurs (Castanet et al. 2000), and several extinct birds e.g., *Hesperornis* (Starck and Chinsamy 2002) also have bones with laminar tissues. In the mammalian line, laminar bone appears in medium to large sized extinct and extant mammals (Enlow and Brown 1958) like artiodactyls such as *Sus scrofa*, *Bos primigenius* (Currey 1962), *Bison priscus*, *Cervus elaphus*, *Megaloceros giganteus* (Sander and Andr  ssy 2006); perissodactyls (e.g., *Equus* and *Coelodonta*; Sander and Andr  ssy 2006), and elephantids like *Loxodonta africana*, *Elephas maximus*, and *Mammuthus columbi*, but also the dwarfed *Mammuthus exilis* (Curtin et al. 2012). The high growth rate of long bones with laminar bone enables animals to grow large in a relatively short time, the circular organization of the vascular canals and bony laminae providing optimal support for high strain and stress under torsional loads (Margerie et al. 2004, 2005). Some studies suggest that the high values of apposition rate this tissue can reach vary between 20 and 110 $\mu\text{m}/\text{day}$ depending on the taxon (Castanet et al. 2000; Margerie et al. 2002; Sander and T  ckmantel 2003).

Starck and Chinsamy (2002) observed that the vascular spaces are much larger than the blood vessels contained within them. We believe that the maximal size of the cells that need to pass through the blood vessels not only determines minimal blood vessel diameter, but also, perhaps indirectly, influences the minimal width of the vascular spaces. Vascular spaces are compacted through ontogeny, narrowing the space for soft tissues contained within them. Concurrently, maximal width of the vascular spaces as well as the thickness of the laminae is probably limited by the interplay between biomechanical and nutritional require-

ments. If the vascular canals are too wide, and the bony constituents are too thin, the bone tissue will be brittle. On the other hand, when bone laminae become too thick, the tissue will be less porous, and blood flow limited. If these hypotheses are correct, it means there are functional and biological constraints acting on the architectural dimensions of laminar bone.

In this paper, we aim to test if laminar bone histomorphometry is altogether constrained. To do this, we focussed on a particular feature of laminar bone: the lamina thickness and corresponding lamina density (LD, number of laminae per mm). The definition of one lamina follows Sander and T  ckmantel (2003) and Francillion-Vieillot (1990). This means the thickness of one lamina is defined from the centre of one vascular canal to the center of the following vascular canal as illustrated in Fig. 2. Despite the promising preliminary results of Sander and T  ckmantel (2003) on sauropod laminar bone, and the results of Curtin et al. (2012) on elephantid laminar bone, lamina density has been largely neglected in other histological investigations. Curtin et al. (2012) clearly distinguished pre- and postnatally deposited laminar bone tissues, and furthermore observed much stronger variation in the dwarfed mammoths compared to the non-dwarfed Columbian mammoth. Sander and T  ckmantel (2003) studied the lamina density and the bone apposition rate in humeri and femora of five sauropod taxa (*Apatosaurus*, *Barosaurus*, an indetermined gracile diplodocid, *Brachiosaurus*, and *Janenschia*). With regard to some variation, Sander and T  ckmantel (2003) found that lamina density is quite constant at 4–6 laminae per mm independent of taxon, bone, and ontogenetic age. This led to the assumption that the low variation of lamina density and thickness is a result of underlying structural formation

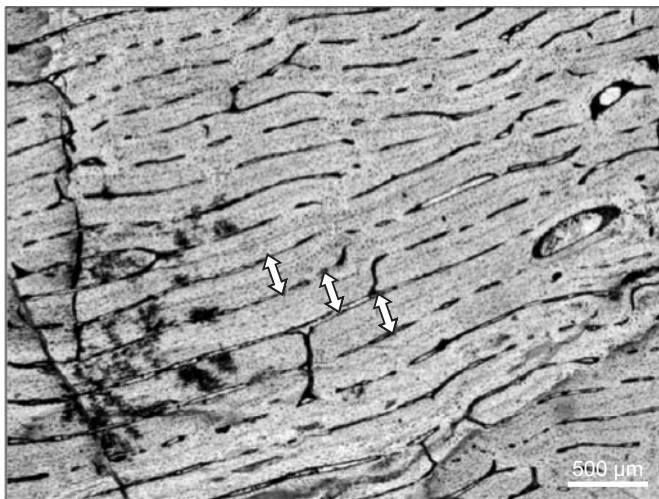


Fig. 2. Laminar bone tissue in a *Brachiosaurus* humerus (MFN t7). One lamina is defined as the distance from the center of a vascular canal to the center of the following vascular canal, as indicated by the arrows (cf. Sander and Tückmantel 2003).

principles of laminar bone. Further testing of this hypothesis and measuring lamina thickness may thus provide better insight into the formation of the tissue itself (e.g., Curtin et al. 2012). Histomorphometric features corresponding to functional and structural requirements should have similar shape and size. We therefore expect mammal and dinosaur laminar bone to have similar lamina thicknesses and densities. A comparison of laminar bone histomorphometry in mammal and dinosaur long bones is important because of the convergent nature of laminar bone in these groups.

Institutional abbreviations.—BYU, Museum of Earth Sciences, Brigham Young University, Provo, USA; CM, Carnegie Museum of Natural History, Pittsburgh, USA; DFMH/FV, Dinosaurier-Freilichtmuseum Münchshagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Münchshagen, Germany; FGGUB, Facultatea de Geologie și Geofizică, Universitatea București, Bucharest, Romania; IPB, Steinmann Institute, University of Bonn, Bonn, Germany; MDE, Musée des Dinosauriens, Esperaza, France; MSF, Municipal Sauriermuseum Frick, Frick, Cantone of Aargau, Switzerland; MQB, Museum für Ur- und Ortsgeschichte Quadrat, Bottrop, Germany; MFN, Museum für Naturkunde, Berlin, Germany; OMNH, Oklahoma Museum of Natural History, Norman, USA; PC.DMR, Palaeontological collection, Department of Mineral Resources, Khon Kaen, Kalasin, Thailand; SGP, Sino-German Project, University of Tübingen, Germany; SMA, Sauriermuseum Aathal, Aathal, Canton Zürich, Switzerland; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TMM, Texas Memorial Museum, Austin, USA.

Other abbreviations.—LD, lamina density; HOPB, highly organized primary bone tissue; HVBT, highly vascularized bone tissue.

Material and methods

For this study, we used long bones (humeri, femora, ulnae, and tibiae, but also metatarsals and one metacarpal) of dinosaurs and mammals for histological analysis of lamina density. Most of these materials have been described previously (e.g., Sander 2000; Klein and Sander 2008) and are kept in the thin section collection of the IPB. However, some new thin sections were made from a number of mammal long bones. Samples for these thin sections were obtained either by histological coring (Stein and Sander 2009) or by complete cross sectioning of the long bone midshaft. Of all 134 samples (listed in tables S1 and S2 in Supplementary Online Material available at http://app.pan.pl/SOM/app59-Hofmann_et_al_SOM.pdf), 95 belong to dinosaurs and include bones from 12 neosauropods, two basal sauropods, and one basal sauropodomorph. The remaining 39 samples come from 17 mammal taxa, some Recent, but most Pleistocene. The low numbers of mammal samples reflect difficulties in making consistent measurements (see following paragraph), and in finding a variety of histologically well-preserved specimens, especially among the Pleistocene mammals.

Thin sections were examined under a Leica DM LP 2500 polarization microscope. To provide a proper measurement of lamina density, an area of laminar bone without any anastomoses or extensive remodelling is required, with laminae parallel to each other and without extensive perturbations by features such as Sharpey's fibres or other connective fibres (Suzuki et al. 2003; Petermann and Sander 2013). We measured lamina density from actual specimens, but also from published histological images.

LD was quantified by counting the number of laminae per mm by superimposing an stage micrometer onto the sample. A whole number of lamina was counted (usually four to five) and their total thickness measured. This number was then standardized to laminae/mm. Following Sander and Tückmantel (2003), LD was measured in the innermost, outermost, and central parts of the cortex. In fully cross-sectioned specimens, measurements were made where possible, permitting preservation and limited remodelling. Sander and Tückmantel (2003) already found insignificant differences between different locations within one sample. Lamina density did not vary much between these zones, maximally by 3 laminae/mm, but often less. For this reason, LD for each specimen was averaged to provide a representative value. Whenever insufficient suitable locations could be identified, e.g., in some of the *Plateosaurus* samples, only one measurement was noted.

All measurements are in SOM: table S1. Tests for normality and statistical validation of comparisons were performed with Statistics Open For All (SOFA, version 1.3, <http://www.sofastatistics.com>). Reported statistics (mean, SD, etc.) were calculated from the original data, but in some cases, we also reported on statistical bins of the histograms.

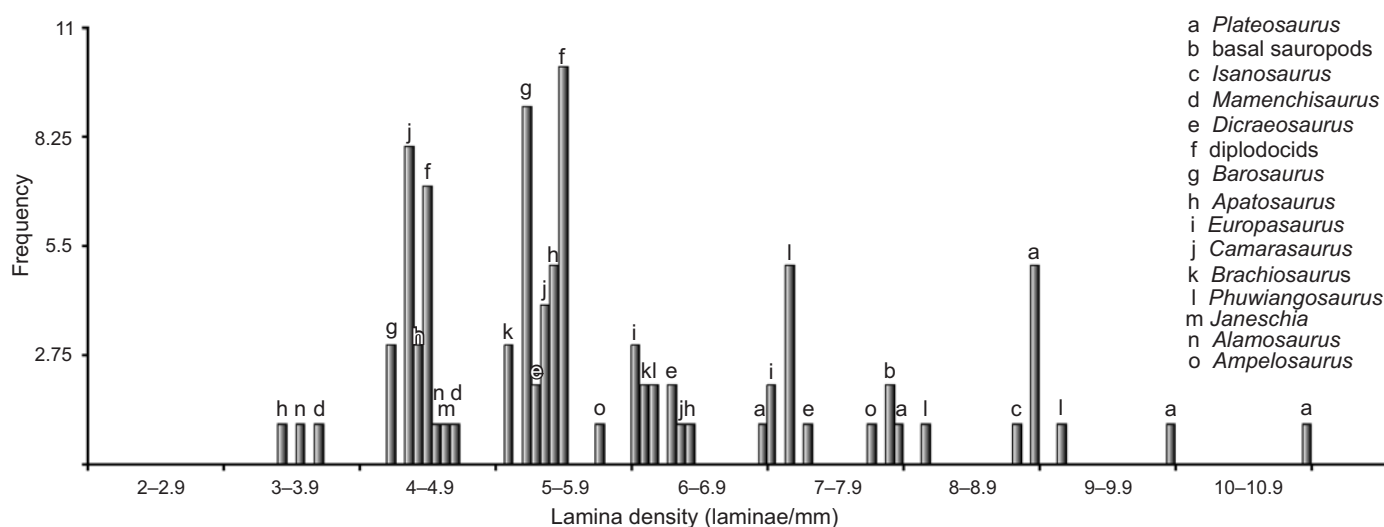


Fig. 3. Comparison of the frequency distributions of lamina density of sauropodomorph dinosaur taxa. The distribution follows a normal distribution. Descriptive statistics for sauropod lamina density: mean = 5.76 laminae/mm; SD = 1.386 laminae/mm; skew = 0.842; kurtosis = 0.021. For further discussion please refer to the main text.

Data obtained from literature

Some additional measurements of lamina density were taken from published micrographs (SOM: table S2). Strong differences in LD were observed in some of these published specimens. An example is *Herrerasaurus* sp. with 17 laminae/mm (Ricqlès et al. 2003) and *Herrerasaurus ischigualastensis* with 11.2 laminae/mm (Starck and Chinsamy 2002). It is difficult to say whether or not these variations reflect individual differences, especially without full control over sample location, and sometimes lacking further information on the specimen. Therefore these theropods were excluded from the analysis, but will be accounted for in the discussion. Measurements of elephantid LD in Curtin et al. (2012), with control over element, element length and sample location were used in our analysis.

Results

Variation within specimens and specimen average LD.—

As mentioned in the Material and methods section, variation within specimens was low, and lamina density values were averaged for each specimen.

Comparison of LD between taxa

Variation among dinosaurs.—The frequency distribution of LD of dinosaurs (Fig. 3) follows a more or less normal distribution (mean = 5.76 laminae/mm; SD = 1.386 laminae/mm; skew = 0.842; kurtosis = 0.021). A test for normality, based on D'Agostino and Pearson's (1973) test that combines skew and kurtosis to produce an omnibus test of normality, confirms this ($p < 0.05$). Most common LD are in the range of 4–7 laminae/mm. The more derived dinosaur taxa like

Europasaurus, *Brachiosaurus*, *Barosaurus*, *Dicraeosaurus*, *Camarasaurus*, *Apatosaurus*, *Alamosaurus*, *Mamenchisaurus*, and the indeterminate Diplodocidae show a LD within this range. The derived sauropod *Phuwiangosaurus*, with LD ranging 6–9 laminae/mm, can be considered a moderate outlier from this distribution. *Plateosaurus* and *Isanosaurus* and two indeterminate basal sauropods (cf. *Isanosaurus*) are the strongest outliers, with noticeably thinner laminae and a LD between 6 and 10 laminae/mm.

Variation among mammals.—Initial inspection of the distribution of mammal LD (Fig. 4) does not show a definite normal distribution as for the dinosaurs. However, the distribution passed the test for normality ($p < 0.05$; mean = 4.154 laminae/mm; SD = 1.517 laminae/mm; skew = 0.964 and kurtosis = 0.289). Some of the larger mammal

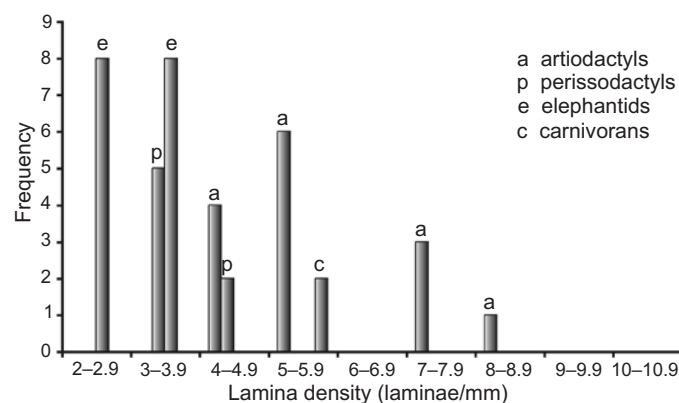


Fig. 4. Comparison of the frequency distributions of lamina density of the different mammal groups. These data represent 24 of our own samples complemented with 15 elephantid samples from Curtin et al. (2012). Mammal lamina density follows a normal distribution. Descriptive statistics of mammal lamina density: mean = 4.154 laminae/mm; SD = 1.517 laminae/mm; skew = 0.964 and kurtosis = 0.289. For further discussion please refer to the main text.

taxa (e.g., *Equus* and *Mammuthus*) have a very low LD in a range of 2–4.3 laminae/mm. Only the domestic and the feral *Sus scrofa* form outliers, with very high LD of 7–8.5 laminae/mm.

Variation between dinosaurs and mammals.—The combined distribution of mammal and dinosaur lamina density (Fig. 5) failed the ideal normality test. However, most real-world data sets with as many results (134) would fail for even slight differences from the perfect normal curve. Skew is 0.449 and kurtosis is -0.107, probably an appropriate sign to assume normality. An O'Brien's (1978) test for homogeneity suggests mammal and dinosaur LD distributions have equal variances ($p > 0.5$), allowing comparison of the distributions with conventional methods. Comparison of means of dinosaur and mammal LD shows a statistically significant difference when assuming normality (independent t-test, $t = 5.928$; $p < 0.001$). Assuming non-normal distributions, a non-parametric alternative suggests an equally significant difference between the medians (Mann-Whitney U statistic = 752.0; Two-tailed p value < 0.001).

LD as a function of femur length

Scaling and ontogenetic effects may interfere with LD comparison, so it is necessary to test for correlation with body size. We used femur length as a proxy for body size (Anderson et al. 1985; Seebacher 2001). For a sensible comparison, only those taxa were included for which a minimum of four known femur lengths were available. This excluded all the mammals, and reduced the sample to one basal sauropodomorph and four neosauropod dinosaurs: *Plateosaurus*, *Barosaurus*, *Camarasaurus*, *Apatosaurus*, and the diplodocids. In Fig. 6, LD of these five taxa is plotted against the respective individual femur lengths. Among the neosauropods, LD remains almost constant, with little variation between 4 to 6.5 laminae/mm with increasing femur length. Nonetheless, a tendency of decreasing LD with increasing femur length may be present (Slope = -0.001; Intercept = 5.61; Pearson's R statistic = -0.372, two-tailed $p = 0.052$). The LD of the basal sauropodomorph *Plateosaurus* is striking, showing very strong variation. A first impression may be the strong decrease of LD with increasing femur length, but with only four data points, a regression analysis would be meaningless, and a clear trend cannot be predicted.

Discussion

Dinosaur lamina density.—Sauropodomorph LD follows a normal distribution, with the most frequent LD between 4–6 laminae/mm, independent of sampled taxon or element. This supports the hypothesis of Sander and Tückmantel (2003) that structural constraints shape laminar bone in sauropods. However, *Plateosaurus* (a basal sauropodomorph), *Isanosaurus*,

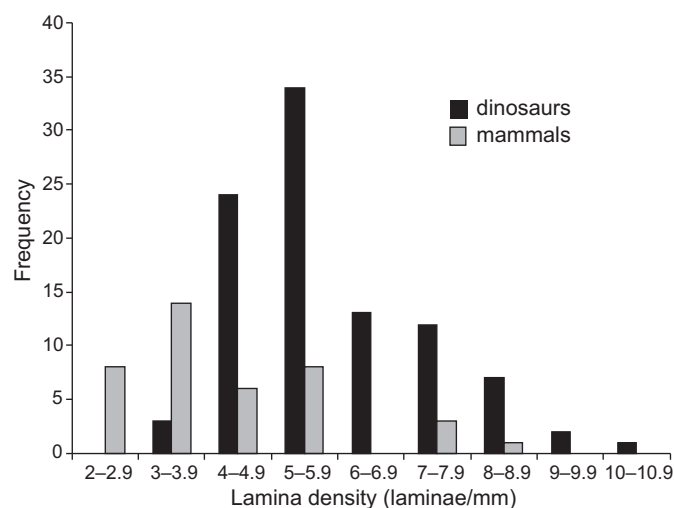


Fig. 5. Comparison of dinosaur and mammal lamina density. A test for normality of the combined distributions failed (which is common for large datasets), but descriptive statistics suggest the dataset may still be normal (skew [lopsidedness] = 0.449; kurtosis [peakedness or flatness] = -0.107). Mean mammal lamina density differs significantly from mean dinosaur lamina density (independent t-test, $t = 5.928$; $p < 0.001$). A non-parametric alternative suggests an equally significant difference between the medians (Mann-Whitney U statistic = 752.0; two-tailed p value < 0.001). For discussion of these results, please refer to the main text.

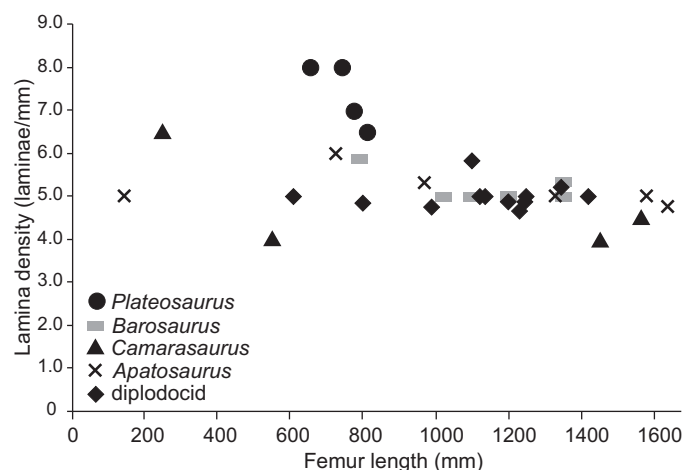


Fig. 6. Lamina density vs. femur length of sauropodomorph dinosaur taxa (*Plateosaurus* and neosauropods). Among the neosauropods, lamina density does not correlate with femur length, although a slight decrease may take place with increasing femur length (Slope = -0.001; Intercept = 5.61; Pearson's R = -0.372, two-tailed $p = 0.052$). High variability of lamina density in *Plateosaurus* may be related to its developmental plasticity (cf. Sander and Klein 2005).

and two other indeterminate basal sauropods are strong outliers. *Isanosaurus* (Buffetaut et al. 2000) and the indeterminate basal sauropods were all found in terrestrial sediments of the Upper Triassic to Lower Jurassic Nam Pong Formation of Thailand. The affinity of the basal sauropods is still uncertain, and they may or may not be related to *Isanosaurus*. Either way, their high LD values (6 to 10 laminae/mm) indicates that the basal sauropod(omorph)s in general have more, but thinner laminae than the more derived sauropods.

Despite the presence of laminar bone histology in some individuals, *Plateosaurus* had a lower growth rate than most sauropods (Klein and Sander 2007). Sander et al. (2004) suggested that a growth rate acceleration took place at the base of Sauropoda. This could imply that the thinner laminae of basal sauropodomorphs and basal sauropods are associated with a lower volumetric expansion rate of the laminae. Among derived sauropods, *Phuwiangosaurus* also has relatively high LD (7–9 laminae/mm). Klein et al. (2009) suggested that *Phuwiangosaurus* had a lower growth rate than other neosauropods of comparable size, which may support the hypothesis that lamina thickness is related to growth rate.

The dwarfed sauropod *Europasaurus* is considered a sister taxon of Brachiosauridae but more derived than *Camarasaurus*, and most likely adapted to the life on an island by decreasing its growth rate (Sander et al. 2006). Contrary to *Camarasaurus* with 4–6.5 laminae/mm and *Brachiosaurus* with 5–6.3 laminae/mm, *Europasaurus* has generally higher lamina density (6–7 laminae/mm), which might also be associated with a lower growth rate. However, if a strict linear correlation exists between bone growth rate and LD, a LD similar to that of *Plateosaurus* would be expected for *Europasaurus*. Lamina densities for these taxa overlap, but the LD of *Europasaurus* is on average still lower compared to the similar sized *Plateosaurus*. Possibly also a phylogenetic constraint limits the increase of LD in this dwarfed sauropod. A single sample, which was not included in the analysis, of the dwarfed ornithomimid *Telmatosaurus* (Tibia FGGUB R.7) has an average LD of 6.3 laminae/mm. This is similar to the LD in *Europasaurus*, but further measurements of large ornithomimids are needed to make any further inferences about the influence of the evolution of nanism.

Mammal lamina density.—The domestic and feral form of *Sus scrofa* can be considered outliers compared to the whole dataset. Their much higher LD (6.5 up to 8.5 laminae/mm) than other mammals remains unexplained. The wild boar has slightly higher LD than the domestic pig, perhaps an effect of domestication and higher growth rate. Nevertheless it is certainly of interest for future studies to explore whether other mammal groups generally have lower LD than artiodactyls.

Comparing LD of dinosaurs and mammals.—Mammal LD averages in the same bins (4–4.9 and 5–5.9 laminae/mm) as that of sauropods. A statistical comparison, however, shows that despite these similar values, the means are significantly different. The dinosaur sample was biased for sauropods, whereas the mammalian sample was taken from different mammal subclades, but had a comparatively low sample size. Ideally, more theropods and ornithischians of different body sizes would be included, as well as more artiodactyls and perissodactyls. Pending access to further specimens, this will be the subject of another paper. An alternative explanation for the observed differences may be convergence in the tissues of mammals and dinosaurs. The difference in the means of the two distributions is slightly more than one standard deviation. The convergently evolved laminar bone

tissues of dinosaurs and mammals thus have mean LD very close to each other, which suggests structural and biological limiting factors constrain the dimensions of the vascular spaces. The vascular spaces certainly have a lower size limit, in order to allow a supply of blood in the tissue. Sander and Tückmantel (2003) also suggested that only a specific range of thicknesses may provide mechanical stability in the tissues. If these variables were known, it would thus be possible to calculate a theoretical maximal LD (cf. Mishra and Knothe Tate, 2003). The reason for the low variation in LD may thus be found in the formation principles of laminar bone (Stein and Prondvai 2014). Here we predict that the low variation of LD applies to all laminar bone of large bodied sauropods. Unfortunately, our sample size is too small to predict if the same is applicable for specific mammal groups, and further testing is necessary.

Dependency of LD on femur length.—The slight decrease of LD with increasing femur length in sauropods may indicate a requirement for thicker laminae at larger body sizes. The strong variation in LD of the basal sauropodomorph *Plateosaurus* compared to the sauropods suggests that throughout sauropod ontogeny, high adult body weights mean that LD experiences stronger histomorphometrical constraints. The sudden drop in LD through the ontogeny of *Plateosaurus* may represent a threshold body size in this taxon where lamina thickness increase is required. *Plateosaurus* has been found to have strong developmental plasticity in adult body size compared to the more derived sauropods (Sander et al. 2004; Sander and Klein 2005), therefore a higher variation of LD in this taxon is not so surprising. Unfortunately, the preliminary data for *Plateosaurus* restrict us from making further claims. A topic for further study is whether other basal sauropodomorphs (e.g., *Massospondylus*) and any other dinosaurs also have such high LD. Interestingly, the LD data from published micrographs of *Allosaurus* are as high as those of *Plateosaurus*, and *Herrerasaurus* and *Coelophysis* even exceed the high LD of *Plateosaurus*. The overall smaller body sizes of these non-sauropod dinosaurs further suggests an adult body size-driven threshold for the low variation in the LD of sauropods in general. Curtin et al.'s (2012) observation that LD varies greatly in dwarfed mammoths compared to large-bodied taxa, furthermore suggests structural constraints operating on the formation of laminar tissues at large body size. An alternative explanation for the observed decrease in LD of sauropods may be an increase in growth rate up to the point of sexual maturity (cf. Lehman and Woodward 2008 and Klein and Sander 2008).

Conclusions

This study aimed to gain further insight into lamina thickness and lamina density in the convergently evolved laminar bone of dinosaurs and mammals. LD does not vary with taxon or element. Mean mammal and dinosaur lamina thickness

is significantly different, but biased (mostly sauropods in the dinosaur group) and limited sampling (mammal sample significantly smaller than dinosaurs) may have influenced this result. Further sampling of theropods and ornithischian dinosaurs as well as more perissodactyls and artiodactyls may significantly alter these results. Our results for the sauropod sample, however, support the hypothesis of Sander and Tückmantel (2003) that LD is underlined by structural constraints. High LD outliers like *Plateosaurus* may be correlated with a lower growth rate, or developmental plasticity. A lower growth rate may also be the cause of high LD of the titanosaur *Phuwiangosaurus* (cf. Klein et al. 2009). Among mammals, the suids (domestic pig and wild boar) form outliers as well. The LD in these artiodactyls is higher than in other mammals, but more specimens are needed to test whether this is a general feature of artiodactyls. Comparison of LD in dinosaurs and mammals shows low variation despite convergence of laminar tissues. We speculate that structural and biomechanical as well as vascular and nutritional demands limit the variation of LD (see also Mishra and Knothe Tate 2003; Margerie et al. 2005). LD does not change drastically with femur length, although there is a slight decreasing trend. As observed in *Plateosaurus* and other non-sauropod dinosaur samples, an adult body size-driven threshold may cause low variation in sauropod LD. Among sauropods, a barely significant decrease in LD through ontogeny may represent an increase in growth rate before reaching sexual maturity.

Acknowledgements

We thank Olaf Dülfer (University of Bonn, Germany) for technical assistance with making thin sections, Louise Roth (Duke University, Durham, USA) and Holly Woodward (Oklahoma State University, Tulsa, USA) for reviewing and significantly improving this manuscript, and Michael Benton for final editing. We also thank Holger Petermann (University of Bonn, Germany) for thin sectioning the wild boar sample on short notice. Our greatest gratitude goes to all the curators from the numerous institutions across the globe, who have allowed consumptive sampling of all the specimens in their care. Part of this research was performed by RH as part of her B.Sc. thesis at the University of Bonn. KS and PMS greatly acknowledge the DFG for funding. This is contribution 158 of the DFG Research Unit 533 “Biology of the Sauropod Dinosaurs: The Evolution of Gigantism”.

References

- Amprino, R. 1947. La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l'accroissement. *Archives de Biologie* 58: 315–330.
- Anderson, J.F., Hall-Martin, A., and Russell, D.A. 1985. Long bone circumference and weight in mammals, birds, and dinosaurs. *Journal of Zoology Series A* 207: 53–61.
- Brown, J.H. 2004. Towards a metabolic theory of ecology. *Ecology* 85: 1771–1789.
- Buffetaut, E., Suteethorn, V., Le Loeuff, J., Cuny, C., Tong, H., and Khan-subha, S. 2000. The first giant sauropod from the Late Triassic of Thailand. *Comptes rendus Palevol* 1: 103–109.
- Bybee, P.J., Lee, A.H., and Lamm, E.-T. 2006. Sizing the Jurassic theropod dinosaur *Allosaurus*: Assessing growth strategy and evolution of ontogenetic scaling of limbs. *Journal of Morphology* 267: 347–359.
- Case, T.J. 1978. On the evolution and adaptive significance of post-natal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* 53: 243–282.
- Castanet, J., Rogers, K.C., Cubo, J., and Boisard, J.-J. 2000. Periosteal bone growth rates in extant ratites (ostrich and emu). Implications for assessing growth in dinosaurs. *Comptes rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes* 323: 543–550.
- Cooper, L.N., Lee, A.H., Taper, M.L., and Horner, J.R. 2008. Relative growth rates of predator and prey dinosaurs reflect effect of predation. *Proceedings of the Royal Society B* 275: 2609–2615.
- Cubo, J., Le Roy, N., Martinez-Maza, C., and Montes, L. 2012. Paleohistological estimation of bone growth rate in extinct archosaurs. *Paleobiology* 38: 335–349.
- Currey, J.D. 1962. The histology of the bone of a prosauropod dinosaur. *Paleontology* 5: 238–246.
- Curtin, A., MacDowell, A., Schaible, E., and Roth, V.L. 2012. Non-invasive histological comparison of bone growth patterns among fossil and extant neonatal elephantids using synchrotron radiation X-ray microtomography. *Journal of Vertebrate Paleontology* 32: 939–955.
- D'Agostino, R.B. and Pearson, E.S. 1973. Testing for departures from normality. *Biometrika* 60: 613–622.
- Enlow, D.H. and Brown, S.O. 1958. A comparative histological study of fossil and recent bone tissues. Part III. *Texas Journal of Sciences* 10: 187–230.
- Ferretti, M., Palumbo, C., Contri, M., and Marotti, G. 2002. Static and dynamic osteogenesis: two different types of bone formation. *Anatomy and Embryology* 206: 21–29.
- Francillon-Vieillot, H., Buffrénil, V. de, Castanet, J., Géraudie, J., Meunier, F.J., Sire, J.Y., Zylberberg, L., and Ricqlès, A.J. de 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: J.G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Vol. 1*, 471–530. Van Nostrand Reinhold, New York.
- Horner, J.R. and Padian, K. 2004. Age and growth dynamics of *Tyrannosaurus rex*. *Proceedings of the Royal Society of London B* 271: 1875–1880.
- Horner, J.R., Ricqlès, A. de, and Padian, K. 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. *Paleobiology* 25 (4): 295–304.
- Klein, N. and Sander, P.M. 2007. Bone histology and growth of the prosauropod *Plateosaurus engelhardti* Meyer, 1837 from the Norian bonebeds of Trossingen (Germany) and Frick (Switzerland). *Special Papers in Paleontology* 77: 169–206.
- Klein, N. and Sander, P.M. 2008. Ontogenetic stages in the long bone histology of sauropod dinosaurs. *Paleobiology* 34: 247–263.
- Klein, N., Sander, P.M., and Suteethorn, V. 2009. Bone histology and its implications for the life history and growth of the Early Cretaceous titanosaur *Phuwiangosaurus sirindhornae*. *Geological Society, London, Special Publications* 315: 217–228.
- Lehman, T. and Woodward, H. 2008. Modeling growth rates for sauropod dinosaurs. *Paleobiology* 34: 264–281.
- Margerie, E. de, Cubo, J., and Castanet, J. 2002. Bone typology and growth rate: testing and quantifying “Amprino's rule” in the mallard (*Anas platyrhynchos*). *Comptes Rendus Biologies* 325: 221–230.
- Margerie, E. de, Robin, J.-P., Verrier, D., Cubo, J., Groscolas, R., and Castanet, J. 2004. Assessing a relationship between bone microstructure and growth rate: a fluorescent labelling study in the king penguin chick (*Aptenodytes patagonicus*). *Journal of Experimental Biology* 207: 869–879.
- Margerie, E. de, Sanchez, S., Cubo, J., and Castanet, J. 2005. Torsional resistance as a principal component of the structural design of long bones: comparative multivariate evidence in birds. *Anatomical Record* 282: 49–66.

- Marotti, G. 2010. Static and dynamic osteogenesis. *Italian Journal of Anatomy and Embryology* 115: 123–126.
- Mishra, S. and Knothe Tate, M.L. 2003. Effect of lacunocanalicular architecture on hydraulic conductance in bone tissue: Implications for bone health and evolution. *Anatomical Record Part A* 273A: 752–762.
- O'Brien, R.G. 1978. Robust techniques for testing heterogeneity of variance effects in factorial designs. *Psychometrika* 43: 327–342.
- Padian, K., Horner, J.R., and Ricqlès, A.J. de 2004. Growth in small dinosaurs and pterosaurs: The evolution of archosaurian growth strategies. *Journal of Vertebrate Paleontology* 24: 555–571.
- Petermann, H. and Sander, P.M. 2013. Histological evidence for muscle insertion in extant amniote femora: implications for muscle reconstruction in fossils. *Journal of Anatomy* 222 (4): 419–436.
- Ray, S., Bandyopadhyay, S., and Bhawal, D. 2009. Growth patterns as deduced from bone microstructure of some selected neotherapsids with special emphasis on dicynodonts: Phylogenetic implications. *Palaeoworld* 18: 53–66.
- Ray, S., Botha, J., and Chinsamy, A. 2004. Bone histology and growth patterns of some non-mammalian therapsids. *Journal of Vertebrate Paleontology* 24: 634–648.
- Ricqlès, A.J. de 1968. Recherches paléohistologiques sur les os longs des tétrapodes I. – Origine du tissu osseux plexiforme des dinosauriens sauropodes. *Annales de Paléontologie* 54: 133–145.
- Ricqlès, A.J. de, Padian, K., and Horner, J.R. 2003. On the bone histology of some Triassic pseudosuchian archosaurs and related taxa. *Annales de Paléontologie* 89: 67–101.
- Ricqlès, A.J. de, Padian, K., Knoll, F., and Horner, J.R. 2008. On the origin of high growth rates in archosaurs and their ancient relatives: Complementary histological studies on Triassic archosauriforms and the problem of a “phylogenetic signal” in bone histology. *Annales de Paléontologie* 94: 57–76.
- Sander, P.M. 2000. Long bone histology of the Tendaguru sauropods: Implications for growth and biology. *Paleobiology* 26: 466–488.
- Sander, P.M. and Andrassy, P. 2006. Lines of arrested growth and long bone histology in Pleistocene large mammals from Germany: What do they tell us about dinosaur physiology? *Palaeontographica A* 277: 143–159.
- Sander, P.M. and Klein, N. 2005. Developmental plasticity in the life history of a prosauropod dinosaur. *Science* 310: 1800–1802.
- Sander, P.M. and Tückmantel, C. 2003. Bone lamina thickness, bone apposition rates, and age estimates in sauropod humeri and femora. *Paläontologische Zeitschrift* 76: 161–172.
- Sander, P.M., Klein, N., Buffetaut, E., Cuny, G., Suteethorn, V., and Le Loeuff, J. 2004. Adaptive radiation in sauropod dinosaurs: bone histology indicates rapid evolution of giant body size through acceleration. *Organisms, Diversity and Evolution* 4: 165–173.
- Sander, P.M., Klein, N., Stein, K., and Wings, O. 2011. Sauropod bone histology and implications for sauropod biology. In: N. Klein, K. Remes, C.T. Gee, and P.M. Sander (eds.), *Understanding the Life of Giants: Biology of the Sauropod Dinosaurs*, 276–302. Indiana University Press, Bloomington.
- Sander, P.M., Mateus, O., Laven, T., and Knötschke, N. 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature* 441: 739–741.
- Seebacher, F. 2001. A new method to calculate allometric length-mass relationships of dinosaurs. *Journal of Vertebrate Paleontology* 21: 51–60.
- Starck, J.M. and Chinsamy, A. 2002. Microstructure and developmental plasticity in birds and other dinosaurs. *Journal of Morphology* 254: 232–246.
- Stein, K. and Sander, P.M. 2009. Histological core drilling: A less destructive method for studying bone histology. In: M.A. Brown, J.F. Kane, and W.G. Parker (eds.), *Methods in Fossil Preparation: Proceedings of the First Annual Fossil Preparation and Collections Symposium*, 69–80. Petrified Forest National Park, Holbrook (<http://preparation.paleo.amnh.org/assets/FPCSvolume-Final.pdf>).
- Stein, K. and Prondvai, E. 2012. No fibrous (woven) bone in sauropod “fibrolamellar” bone? *Journal of Vertebrate Paleontology* 32: 178A.
- Stein, K. and Prondvai, E. 2014. Rethinking the nature of fibrolamellar bone: An integrative biological revision of sauropod plexiform bone formation. *Biological Reviews of the Cambridge Philosophical Society* 89: 24–47.