*Paleobiology,* 26(3), 2000, pp. 466–488

# Longbone histology of the Tendaguru sauropods: implications for growth and biology

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*Abstract.*—A new sampling technique for fossil bone (coring with a 5/8'' bit) was used to sample longbones of all four sauropod genera from the Upper Jurassic Tendaguru beds of Tanzania for paleohistological study. *Brachiosaurus* and *Barosaurus* are represented by growth series of humeri and femora, while *Dicraeosaurus* could be sampled in fewer specimens and only one bone of *Janenschia* was available. Although all samples are dominated by fibrolamellar bone tissue, taxa can be distinguished by the degree and nature of bone remodeling and the presence and spacing of a peculiar kind of growth line (here termed ''polish lines''). In addition, *Barosaurus* bone revealed two types of histology, tentatively interpreted as sexual morphs. The Tendaguru sauropods show a common growth pattern in which growth is determinate but sexual maturity is achieved well before maximum size is reached. For *Brachiosaurus* and *Barosaurus,* size at sexual maturity can be estimated and was reached at about 40% and 70% maximum size, respectively. Quantification of growth is possible in *Janenschia* using polish lines: the specimen studied reached sexual maturity at ≥11 years, attained maximum size at ≥26 years, and died at ≥38 years.

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Accepted: 21 December 1999

## Introduction

Sauropod dinosaurs are among the biologically most interesting vertebrates because they were typically one magnitude larger than any other terrestrial animal, living or extinct. This sheer size leads to scale effects in their biology and physiology that are only inadequately understood with the application of modern analogues.

Modern analytical techniques offer a way out of this dilemma, providing direct evidence for certain biological or physical aspects. One such technique is paleohistology, the study of fossilized bone in thin-section. At the histological level, bone is remarkably little altered during fossilization, and direct inferences about its mode of deposition can be drawn from comparison with recent animals (Ricqlès 1976, 1980; Ricqlès et al. 1991; Francillon-Vieillot et al. 1990). Growth patterns in turn are controlled by various biological parameters in the living animal.

Paleohistological studies of sauropod bone can thus potentially address questions about life history (such as age at sexual maturity and longevity) as well as about the nature of the metabolism of these gigantic herbivores. Following the pioneering work of Ricqlès, a substantial body of literature on dinosaur bone histology has accumulated, some of which specifically pertains to sauropods. Ricqlès (1968) noted that sauropods (in this case the early sauropod *Lapparentosaurus,* assigned to *Bothriospondylus* at the time) were characterized by abundant fibrolamellar bone which is the exception in reptiles but the rule in large mammals and birds and indicative of sustained fast growth. As in large mammals, Haversian bone is also commonly present in sauropods. In his early work, Ricqlès viewed this as suggestive of a metabolic rate elevated above that of typical reptiles and possibly indicating a homeothermic metabolism for these animals. Later studies of sauropod bones (Ricqlès 1983) and Reid (1981, 1990), however, noted the presence of bone-growth cycles and even of lines of arrested growth (LAGs). Such structures form in living animals as the result of cyclical growth and are particularly common in ectotherms. This and other paleohistological lines of evidence as well as theoretical predictions form the basis for the current belief that sauropods (and most other dinosaurs) had some intermediate type of metabolism, neither typically reptilian nor typically mammalian (for reviews see Ricqlès 1980;

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Reid 1990, 1997a; Chinsamy 1994; Chinsamy and Dodson 1995; Rimblot-Baly et al. 1995; Farlow et al. 1995; Farlow and Brett-Surman 1997; Padian 1997).

One problem with paleohistological work is its destructive nature. Samples must be broken off or cut out of the bones to be studied, which understandably leads to reluctance on the part of curators and collection managers to allow sampling of complete and accordingly well-identified bones. Because of poor sampling, therefore, paleohistological work has remained anecdotal, with an often patchy coverage of the taxa in question, sauropod dinosaurs being no exception.

In this paper, I present the first results of extensive paleohistological work on the famed Tendaguru sauropod fauna from the Upper Jurassic of Africa. Much of the material is housed at the Naturkundemuseum of the Humboldt-Universität Berlin (NHUB), including fairly good growth series of limb bones (Janensch 1961) of the two more common taxa, *Brachiosaurus brancai* and *Barosaurus africanus.* The two other genera, *Dicraeosaurus* with *D. hansemanni* and *D. sattleri,* and *Janenschia robusta* (formerly *Tornieria robusta* [see Wild 1991]) were studied as well. It should be noted that the four sauropods differ significantly in size and body shape (for a review and comparative reconstructions of all taxa except *Janenschia,* see McIntosh et al. 1997), with *Brachiosaurus* having been an order of magnitude heavier than *Dicraeosaurus. Barosaurus* and *Janenschia* were intermediate in size but also differ greatly in bauplan. *Barosaurus* was a gracile, very long necked form while the poorly known *Janenschia* is characterized by extremely stout and massive bones (Janensch 1961).

## Methods and Materials

### Sample Selection

The taxonomy and bone identification of the sauropod longbones from the Tendaguru beds follow Janensch (1961), who figured several and listed most of the specimens sampled. Because the collection was initially curated by Janensch, the information on the specimen labels is also based on his taxonomic assignments. Later scientific visitors to the Berlin collections sometimes expressed doubts in notes left with the specimens about the identifications of Janensch, but a taxonomic revision of the material is beyond the scope of this paper. Furthermore, the paleohistological results are compatible with Janensch's identifications.

This study focused on longbones, primarily the humerus and femur, of the Tendaguru sauropods for two reasons. First, these elements are by far the most abundant in the collections, representing the largest number of individuals and encompassing a great size range (Table 1). Second, sauropod longbones have an exceedingly simple morphology that is largely the product of appositional growth. In other words, there are no distinctive bends in the shaft, no crests, and no trochanters that would be correlated with extensive remodeling of the bone during growth simply to maintain the shape of the bone. Sauropod longbone internal histologic structure thus closely approximates the general mode of longbone growth in which two terminal epiphysial cones of endochondral bone are surrounded by a mantle of periosteal bone that is thickest at or near the middle of the diaphysis (Francillon-Vieillot et al. 1990). Observation of cortical thickness in cross-fractures of sauropod longbones in the NHUB collections indeed reveals that the cortex is thickest at the narrowest part of the diaphysis, which is usually in the middle of the bone or slightly distal to it. The narrowest part of the diaphysis thus provides the ideal sample location because a core drilled there will encounter the thickest, as well as the oldest, compact bone.

This was the rationale for choosing the sample location in the Tendaguru longbones. To further minimize any effect of shape changes of the bone resulting from growth, all humeri were cored in the middle of the convex side of the diaphysis which correlates with the posterior side of the bone. Because the relationships are reversed in the femora, they were sampled on the convex anterior side of the bone. Exceptions were only made if superficial damage was encountered, because the last stage of growth of the animal, as recorded in the outermost cortex, is of particular importance in assessing its ontogenetic stage.

TABLE 1. Sauropod longbones sampled for this study. All specimens are from the Tendaguru beds (Upper Jurassic, Tanzania) and are housed in the NHUB collections. ID for hist. = sample number for histological study, MSM = Middle Saurian Marls, USM = Upper Saurian Marls. It must be noted that the stratigraphic provenance of some of the specimens is not beyond doubt as there are discrepancies in the stratigraphic position of certain localities between Janensch 1914b and Janensch 1961 as well as within this last paper.

| Genus | Specimen no. | ID for hist. | Bone | Side | Length (in cm) | Bed | Remarks |
|---|---|---|---|---|---|---|---|
| *Brachiosaurus* | XX 19 | Br1 | humerus | l | 69 | MSM | |
| *Brachiosaurus* | cc 2 | Br2 | humerus | r | 108 | USM | |
| *Brachiosaurus* | T 8 | Br3 | humerus | l | 128 | USM | |
| *Brachiosaurus* | t 7 | Br4 | humerus | r | 153 | MSM | |
| *Brachiosaurus* | J 12 | Br5 | humerus | r | 170 | USM | |
| *Brachiosaurus* | II 28e | Br6 | humerus | l | 176 | USM | |
| *Brachiosaurus* | MB.R.1990.1 | Br7 | ulna | l | 90 | ? | |
| *Brachiosaurus* | g 1 | Br8 | femur | r | 69 | ? | |
| *Brachiosaurus* | St 134 | Br9 | femur | r | 74 | MSM | |
| *Brachiosaurus* | IX 1 | Br10 | femur | l | 88 | USM | |
| *Brachiosaurus* | dd 452 | Br11 | femur | l | 135 | MSM | |
| *Brachiosaurus* | Nr. 305 | Br12 | femur | r | 156 | ? | |
| *Brachiosaurus* | St 291 | Br13 | femur | r | 183 | MSM | |
| *Brachiosaurus* | XV | Br14 | femur | l | 219 | USM | |
| *Brachiosaurus* | No 85 | Br15 | tibia | ? | 85 | USM | |
| *Barosaurus* | G 91 | Ba1 | humerus | r | 43.5 | USM | type A |
| *Barosaurus* | MB.R.2625 | Ba2 | humerus | l | 61 | ? | type B |
| *Barosaurus* | IX 94 | Ba3 | humerus | l | 64 | USM | type A |
| *Barosaurus* | XVI 641 | Ba4 | humerus | l | 73 | USM | type A |
| *Barosaurus* | XI a7 | Ba5 | humerus | l | 80.5 | USM | type A |
| *Barosaurus* | A1 | Ba6 | humerus | r | 99 | USM | type A |
| *Barosaurus* | XVI 5 | Ba7 | femur | l | 79 | USM | type B |
| *Barosaurus* | Ki 71a | Ba8 | femur | 1 | 102 | MSM | type A |
| *Barosaurus* | k 10 | Ba9 | femur | r | 110 | ? | type A |
| *Barosaurus* | Ki 2 | Ba10 | femur | r | 119 | MSM | type B |
| *Barosaurus* | Ki 4 | Ba11 | femur | l | 120 | MSM | type B |
| *Barosaurus* | NW 4 | Ba12 | femur | l | 135 | ? | type A |
| *Barosaurus* | Nr. 76 | Ba13 | femur | l | 135 | ? | type A |
| *Barosaurus* | Ki 5 | Ba14 | tibia | r | 84 | MSM | type B |
| *Barosaurus* | H 5 | Ba15 | fibula | ? | 96 | USM | type A |
| *Dicraeosaurus* | ab 10 | Di1 | humerus | l | 58 | USM | *D. sattleri* |
| *Dicraeosaurus* | O 3 | Di2 | humerus | r | 61 | USM | *D. sattleri* |
| *Dicraeosaurus* | ab 2 | Di3 | humerus | r | 62 | USM | *D. sattleri* |
| *Dicraeosaurus* | O 2 | Di4 | femur | r | 98 | USM | *D. sattleri* |
| *Dicraeosaurus* | M 1 | Di5 | femur | r | 112 | USM | *D. sattleri* |
| *Dicraeosaurus* | dd 3032 | Di6 | femur | r | 114 | MSM | *D. hansemanni* |
| *Janenschia* | P 8 | Ja1 | humerus | l | 89 | USM | |
| *Janenschia* | Nr. 22 | Ja2 | femur | l | 127 | ? | |

In total, 38 cores were drilled, 15 of which pertain to *Brachiosaurus,* 15 to *Barosaurus,* six to *Dicraeosaurus,* and two to *Janenschia* (Table 1). In general, mostly humeri and femora were sampled, between one-third and one-half of all the specimens per element in the collections, with some lower limb bones included for comparison. For both *Brachiosaurus* and *Barosaurus,* the smallest and the largest humeri and femora in the NHUB collection, and between four and five consecutively larger bones in between, were chosen for sampling (Table 1). In *Brachiosaurus,* however, the two largest humeri (210 and 213 cm long) could not be sampled because they are on exhibit and make up part of the famous mounted skeleton at the NHUB. In addition, some of the smallest specimens listed by Janensch (1961) could not be found in the collections, presumably having been destroyed during World War II. The largest size range, representing a more than threefold size increase, could be sampled in *Brachiosaurus* femora (Br8: 69 cm, Br14: 219 cm, my measurements). *Dicraeosaurus,* on the other hand, shows little size variation (Table 1), but some associated material could be sampled, e.g., the right humerus, Di2, and the right femur, Di4, both pertaining to individual ''O'' (see also Janensch 1914a,b, 1961).

### Sampling Technique

Traditionally, bone thin-sections are cut from samples of bone that are removed from the skeletal element in question by breaking or cutting off the bone with preparation tools or a rock saw. Alternatively, material that is already fragmentary is used. In addition to damaging the bone specimens, this method has the disadvantage that the sample site on the skeletal element can rarely be chosen freely but must follow preexisting fractures or damaged areas. This makes interspecific and intraspecific comparisons of bones difficult because most features of histology are influenced, if not determined, by the position of the sample in the bones (Francillon-Vieillot et al. 1990; Reid 1997b). In addition, whole and well-identified bones are rarely available for sectioning.

The technique used in this study largely avoids the problems of destruction and imprecise sample location by using a coring device for sampling. The setup is rather simple, consisting of a normal electric power drill mounted in a small-workshop drill press. The small coring bit (diamond studded, 1.5 cm in diameter, 5 cm long, as supplied by The Company, Lakewood, Colorado) can then be used to drill a core of bone at a precisely determined location on the longbones. This allows precise sampling of equivalent locations in different bones of a growth series or in the same bones of different species and thus ensures the comparability of the samples. Because of the limited damage, complete and well-identified specimens can be sampled, including figured specimens, as was the case in this study.

The bone was placed under the drill press, moved to the desired position, and stabilized with wet sand or cushioning material. The core was then carefully drilled to the desired depth using water as a lubricant and coolant. A normal lab spray bottle proved sufficient for the task of supplying the water, although the spent water had to be mopped up periodically. If the drill had penetrated somewhat less than halfway through the bone, it had reached well into the cancellous bone or medullary cavity at the center of the element. The core was broken loose with a slender steel blade and could then be ground into one or several thin-sections and polished sections. If the cortex was thicker than 40 mm, the core barrel was too short, and the core had to be drilled in two sections, which were later glued together. For the thick cortex of the large *Brachiosaurus* and *Janenschia* bones, a custom-made extension of the coring bit was necessary to drill through the entire cortex.

It is important to record the orientation of the core with respect to the element's long axis to facilitate controlled sectioning. The resulting hole in the bone compromises the morphology and stability of the specimen very little and provides a permanent and unobtrusive record of the sample site.

For sectioning, the core was embedded in polyester resin and cut in half with a rocksaw using a 0.5-mm-thin blade to minimize loss of material. One half of the core was ground and polished to a high gloss while the other was used for thin-sectioning. The thin-sections were ground to a thickness of 30 μm to 60 μm, depending on bone preservation. Although 30-μm sections are almost too thin for paleohistologic study, some bones have such heavy diagenetic growth of dark ore minerals emanating from the osteocyte lacunae that very thin-sections were necessary to render the tissue translucent.

The thin-sections and polished sections were then examined using standard techniques including transmitted normal- and polarized-light microscopy as well as incident-light microscopy. Incident-light microscopy was primarily used for the study of the polished sections. At low magnifications, the polished sections were viewed with a Wild stereomicroscope using two different illumination techniques: standard oblique lighting, which gives the normal color image of the section, and vertical lighting with the source placed very close to the optical axis of the microscope. This creates a reflection on the surface of the polished section, the resulting image providing information about surface reflectivity only. At high magnifications, a Zeiss Axioplan incident-light compound microscope with dark-field and bright-field illumination was used. In the compound microscope, the dark-field image provides the color information and the bright-field image the reflectivity information.

### Terminology

The terminology of bone histology used here is largely that reviewed by Francillon-Vieillot et al. (1990). However, two aspects of terminology need special mention. First, in this study two types of growth lines are recognized: lines of arrested growth (LAGs) (Castanet 1974; Francillon-Vieillot et al. 1990; Castanet et al. 1993) and a peculiar type of growth mark for which I use the informal term ''polish lines'' after the process that makes them visible. Second, the large sample base including growth series allowed the observation of size- and presumably age-related variation in cortical bone, which was described using an ontogenetic terminology. After careful description and definition, I chose to use simple terms like ''juvenile'' bone instead of the technically correct but cumbersome ''laminar fibrolamellar bone with wide lumina.'' In addition, as I argue below, the biological implications of this terminology are justified.

## Results

### Polish Lines

Before discussing the histology of the individual taxa, the peculiar kind of growth mark common to all Tendaguru sauropods needs to be described, the polish line. A polish line is defined as a growth line in fibrolamellar bone that is visible in polished section but not in thin-section. Polish lines are readily observed with the naked eye or a stereomicroscope by tilting the polished surface to create a reflection (Fig. 1). Under an incident-light compound microscope, polish lines are only visible in bright-field illumination (Fig. 2). Their mode of study is thus similar to that of coal petrographic samples and polished ore samples. In bright-field illumination, it can be seen that polish lines mark an abrupt outward decrease of reflectivity that is caused by an abrupt softening of the fossil bone tissue. Pos-

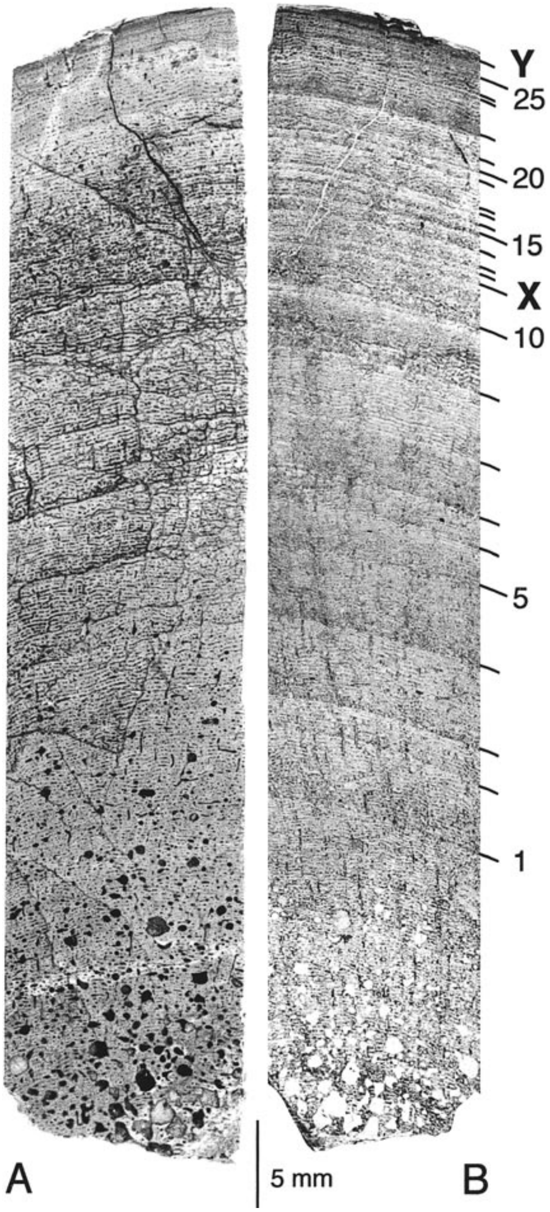

FIGURE 1. Photograph of polished section of *Janenschia* core femur Ja2. The bone surface is at the top. For ease of comparison, left image is reversed. A, Normal illumination. The laminar organization of the bone tissue is clearly visible. The erosional cavities in the inner cortex (bottom) are filled with clear calcite and appear dark. B, Reflection on the polished surface. Numerous polish lines (tick marks) are visible. The erosional cavities in the inner cortex (bottom) appear light because they create a large, even reflection. The count of the polish lines is based on examination of the core under a compound microscope using bright-field illumination. Note the wide spacing of the first 11 lines. X = presumable onset of sexual maturity as indicated by sudden decrease in polish line spacing. Y = change from fibrolamellar bone to lamellar-zonal bone, recording the near cessation of growth.

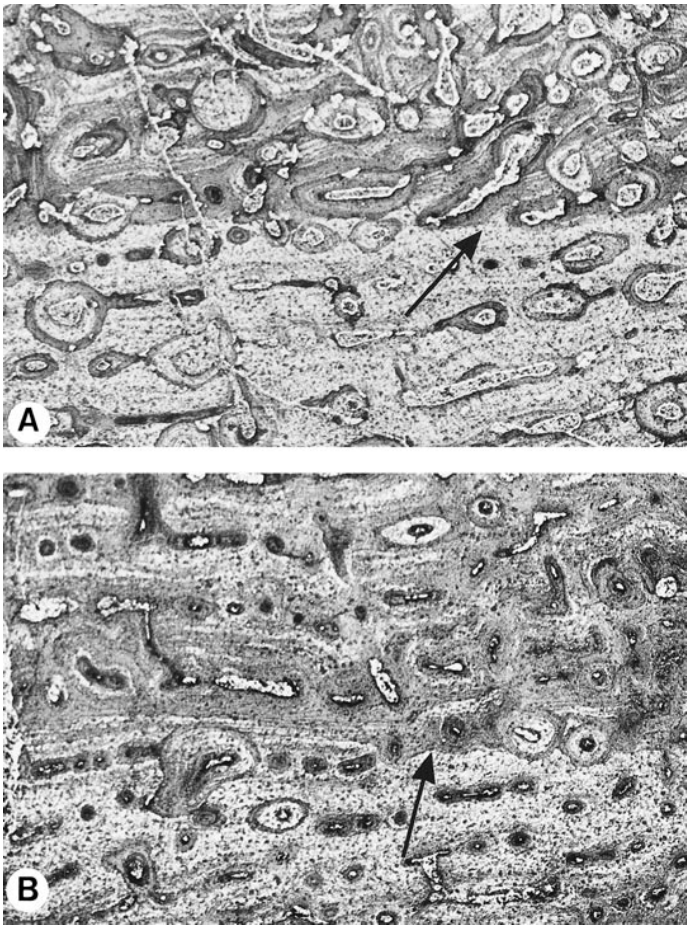

FIGURE 2. Reflected-light micrograph (bright-field illumination) of polish lines in *Janenschia* femur Ja2. The top of the frames is toward the bone surface. The width of the frames is 2.7 mm. A, Line No. 4 (arrow). The polish line is marked by a sharp decrease in bone reflectivity. B, Line No. 22 (arrow). Note secondary osteons cutting polish line in the right half of the frame.

sibly this softening is due to a decrease in mineralization or a change in crystallite size of the bone apatite. Interestingly, the softening does not seem to be correlated with the type of arrangement of the bone fibers (i.e., woven vs. lamellar) as polish lines do not show up in polarized light in thin-section, even if those are rather thick (>60 μm).

Polish lines follow the fabric of the primary bone, commonly in the middle of a lamina of fibrolamellar bone. They represent former bone surfaces and are thus growth markers and not diagenetic artifacts. Outwards from a polish line, reflectivity often gradually increases again to initial values, only to drop sharply at the next polish line. This pattern is akin to many kinds of cyclical growth, including some seen in bone (Castanet et al. 1993). However, polish lines should not be confused with the modulations described by Ricqles (1983) and the cyclic deposition of periosteal bone described by Curry (1998), both of which are apparent in the relative vascularization of the bone. In fact, polish lines may be the intermediate stage between modulations and lines of arrested growth, resulting from a slow-down in growth more pronounced than that producing a modulation but not pronounced enough to arrest growth completely. The idea of a spectrum of growth marks was already discussed in some detail by Ricqlès (1983). As to the question why polish lines have not been observed in fossil bone before, a likely explanation is that bone histology is rarely studied in polished sections (e.g., this method is not mentioned in the comprehensive review by Castanet et al. [1993]).

*Barosaurus africanus.*—The sample of six humeri, seven femora, one tibia, and one fibula (Table 1) is very remarkable in that two distinctive histologic patterns are encountered: one, termed type A (Fig. 3), in five humeri, four femora, and a fibula, and the other, termed type B (Fig. 3), in one humerus, three femora, and a tibia. The types are linked neither to stratigraphic origin nor to ontogenetic stage (Table 1).

The smallest bone of type A, humerus Ba1 (43 cm) clearly is a juvenile, as evidenced by its size and bone structure. The innermost part of the section preserves primary bone with irregularly oriented, wide lumina. This tissue is best described as plexiform to reticulate fibrolamellar bone, although the bone is mainly fibrous with only thin regions of lamellar bone in the primary osteons. The wide lumina, the irregular arrangement of the vascular canals, and the predominance of woven-fibered bone suggest a rather early ontogenetic origin for this tissue, either embryonic or early posthatching. This bone type will be termed ''hatchling'' bone hereafter (see also Fig. 5A).

The outer cortex of Ba1 is made up of primary bone of the laminar fibrolamellar type. It is not known if Ba1 possessed an inner region of cancellous bone because the core does not show any. However, some remodeling of the center of the bone is evident by the sparse secondary osteons in the ''hatchling'' bone.

The tissue in the outer cortex of Ba1 differs from that of adult *Barosaurus* in its much wider lumina, i.e., in a higher ratio of vascular space to bone tissue. Other differences can be observed as well: there are more radial vascular canals than in adults, the osteocyte lacunae in this tissue have a rounded, ''plump'' appearance as opposed to the flattened osteocytes of adults, the bright line in the middle of the lamina is lacking or only poorly developed, and sometimes the middle of the lamina is marked by densely spaced osteocytes. Bone with at least some of these characteristics is regularly encountered in the Tendaguru sauropods and will be termed ''juvenile bone'' (see also Figs. 4C, 5B) because it is the bone type seen in small individuals.

Humeri from 64 cm (Ba3) to 99 cm (Ba6, the largest) in length show a thick cortex of primary bone with increasingly common although generally sparse secondary osteons. The cortex of humerus Ba3 consists entirely of laminar fibrolamellar bone with wide lumina (''juvenile'' bone). Humeri Ba5 (88 cm) and Ba6 show a cortex consisting entirely of laminar fibrolamellar bone with narrow lumina. In addition to the narrow lumina, this bone type differs from'' juvenile'' bone in its fewer radial vascular canals, the flattening of the osteocyte lacunae, presence of a bright line in the middle of the laminae, the presence of numerous incremental lines in the primary osteons, and the predominantly lamellar arrangement of the bone fibers. Bone with at least some of these characteristics is regularly encountered in medium-sized to large individuals of the Tendaguru sauropods and will be termed ''adult'' bone (see also Figs. 4C, 5B).

It should be noted that lumen width alone is an insufficient criterion for distinguishing ''juvenile'' from ''adult'' bone because immature ''adult'' bone may have rather wide lumina as well. This is because laminar fibrolamellar bone grows centripetally, gradually narrowing the vascular canals as the tissue matures. This explains the observation that in some cases an *increase* of lumen width can be

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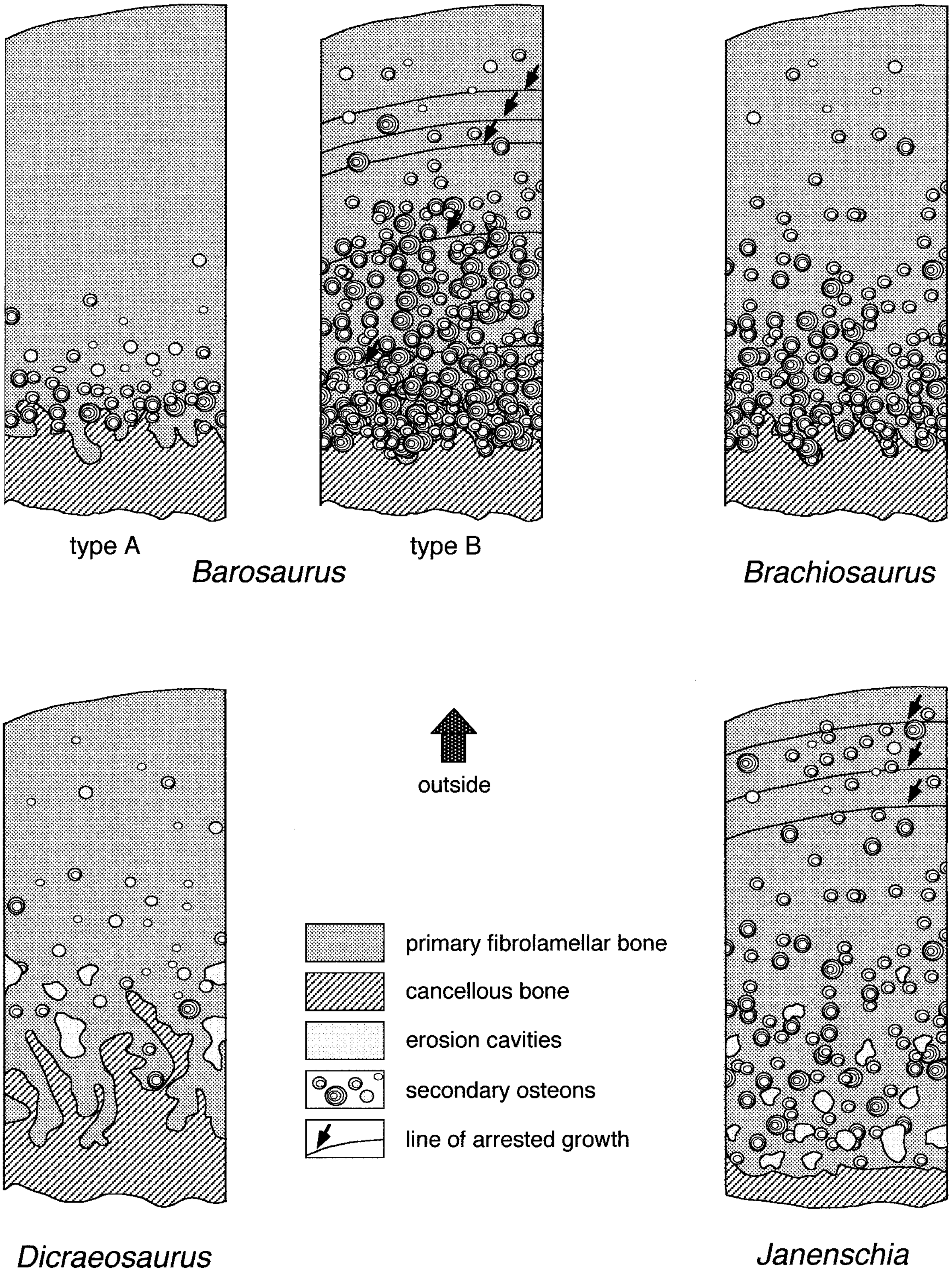
FIGURE 3. Schematic comparison of bone histology of all four Tendaguru sauropod genera. *Barosaurus* shows two different histologic types: type A is characterized by continuous deposition of fibrolamellar bone and only few secondary osteons, whereas in type B numerous LAGs are found throughout the cortex, and many secondary osteons are present as well. *Barosaurus* in general is characterized by an abrupt transition from cancellous bone to compact bone. In comparison, that of *Brachiosaurus* is more gradual. This genus also differs from *Barosaurus* type A and *Dicraosaurus* in the considerable number of secondary osteons, especially in large individuals. *Dicraeosaurus* is characterized by erosion cavities throughout the cortex and a very gradual transition between cancellous bone and compact bone. *Janenschia* shows many erosion spaces in the inner cortex, secondary osteons throughout the cortex, and LAGs in the outer cortex.


type A
type B
Barosaurus
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outside
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cancellous bone
erosion cavities
secondary osteons
line of arrested growth
Dicraeosaurus
Janenschia

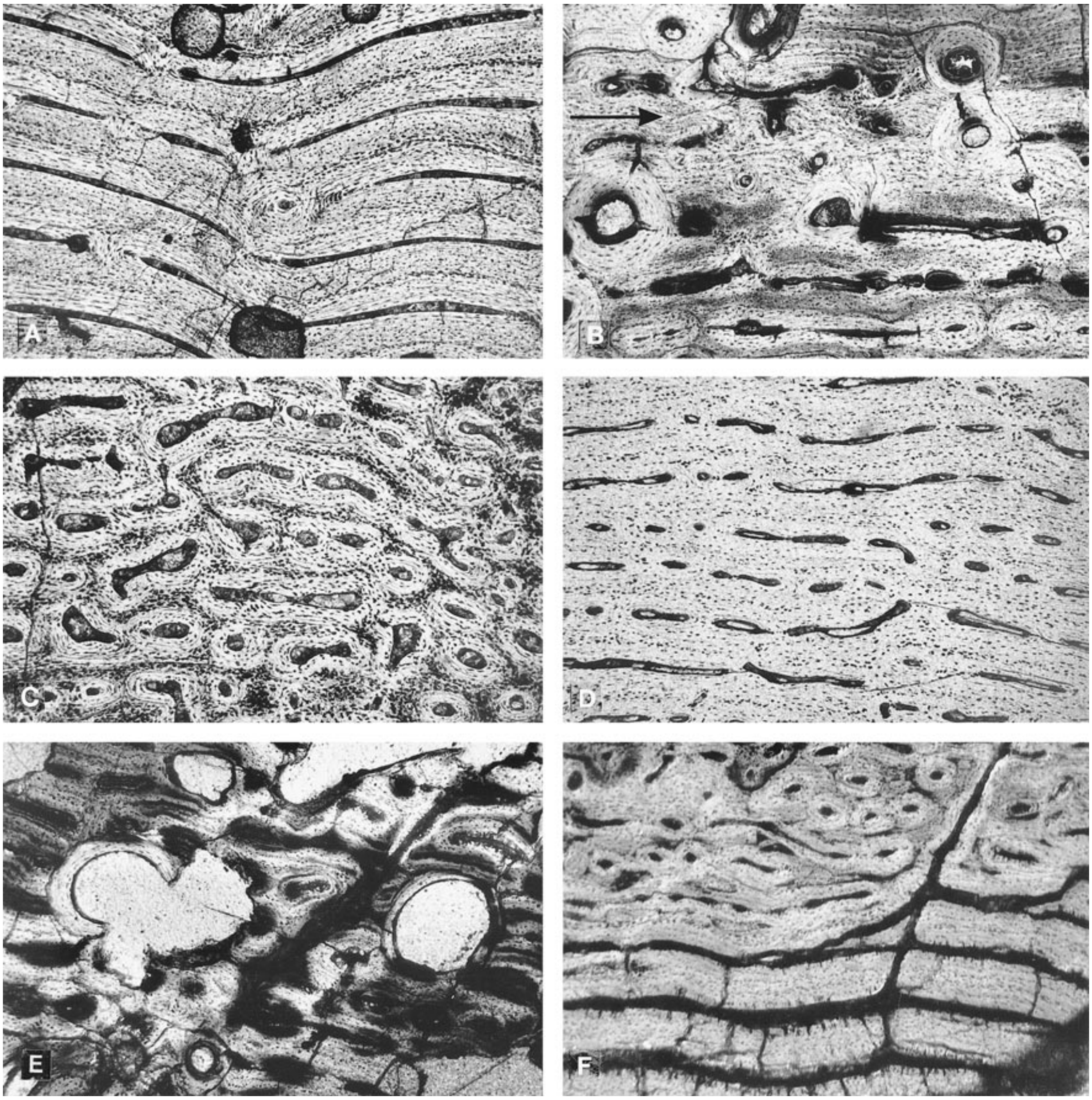

FIGURE 4. Differences in bone histology among the four sauropod dinosaur genera from the Tendaguru beds (Upper Jurassic, Tanzania). The photomicrographs show the histology of various longbones at the middle of the diaphysis. The top of the frame is toward the bone surface. The width of all frames is 1.9 mm. A, *Barosaurus* humerus Ba4, type A, laminar fibrolamellar bone with narrow lumina of the outer cortex. B, *Barosaurus* femur Ba10, type B, laminar fibrolamellar bone with narrow lumina of the outer cortex with some secondary osteons and a line of arrested growth (arrows). C, *Brachiosaurus* humerus Br1, fibrolamellar bone with wide lumina of the middle cortex. D, *Brachiosaurus* humerus Br4, laminar fibrolamellar bone with narrow lumina of the outer cortex. E, *Dicraeosaurus* femur Di4, midcortex. Note the large cavities eroded into the fibrolamellar bone. They have only an incomplete lining of secondary bone. F, *Dicraeosaurus* femur Di4, fibrolamellar bone of the outer cortex with regions of differing vascular canal architecture.

observed in the outermost cortex of medium-sized to large individuals, owing to incomplete osteogenesis of the ''adult'' bone at the time of death. The transition from ''juvenile'' to ''adult'' bone, on the other hand, is marked by an outward *decrease* of lumen width (Fig. 6).

The medium-sized humerus Ba4 (73 cm) records the outward transition from laminar fibrolamellar bone with wide lumina (''juvenile'' bone) to laminar fibrolamellar bone with narrow lumina (''adult'' bone) in its outer cortex (Figs. 4A, 6A). However, even the largest

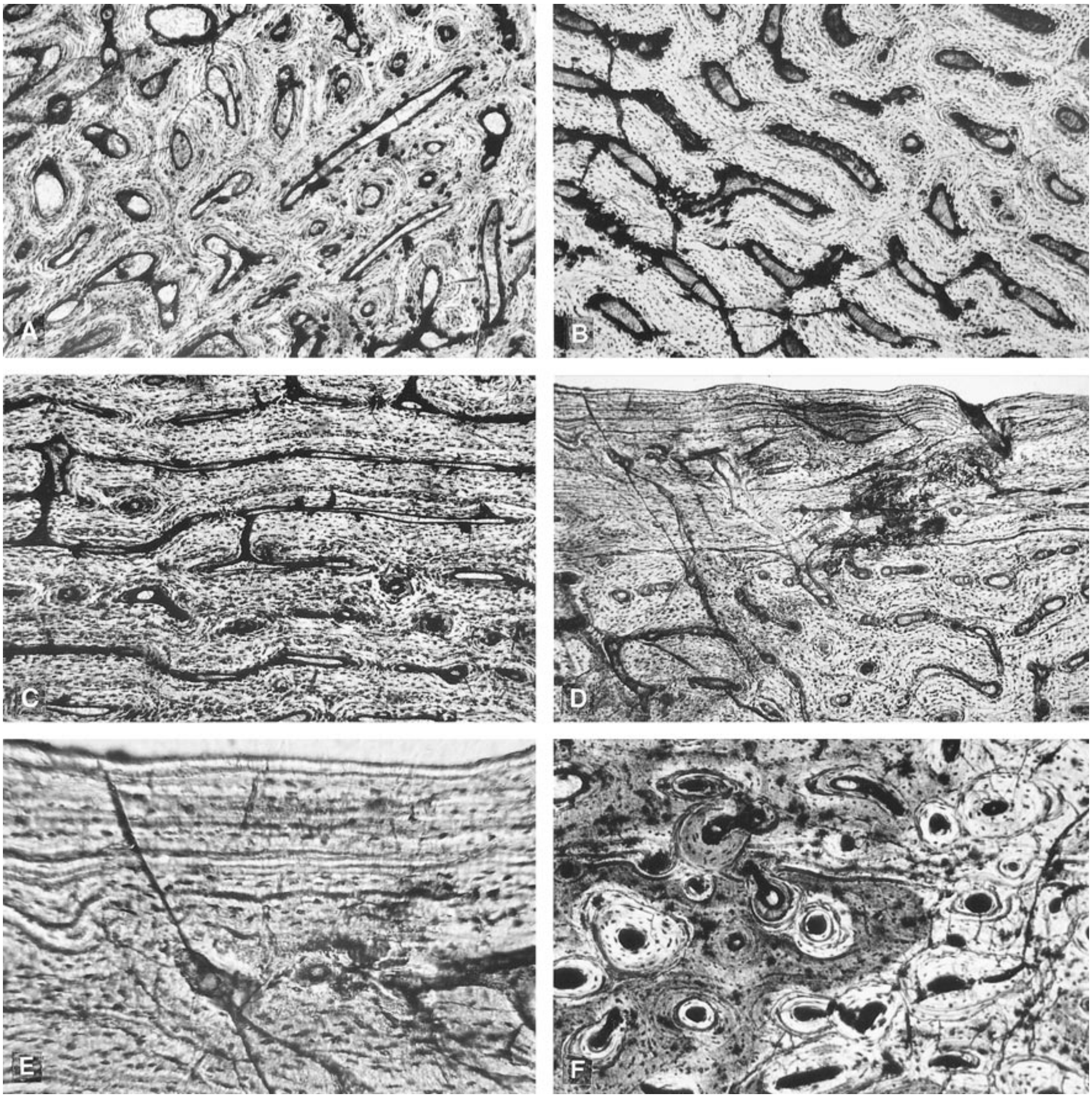

FIGURE 5. The four types of primary bone observed in the sauropod dinosaurs from the Tendaguru beds (Upper Jurassic, Tanzania). Vascularization pattern and lines of arrested growth (LAGs) indicate ontogenetic age of fibrolamellar bone. The top of the frame is toward or at the bone surface. A, ''Hatchling'' bone in the innermost cortex of *Barosaurus* femur Ba12. ''Hatchling'' bone is characterized by an irregular arrangement of large vascular canals. B, ''Juvenile'' bone in the inner cortex of *Barosaurus* femur Ba12. ''Juvenile'' bone shows a more laminar arrangement of the vascular canals but still very large lumina. C, ''Adult'' bone in the middle and outer cortex of *Barosaurus* femur Ba12. The vascular system is well organized in a circumferential pattern and the lumina are small. D, *Dicraeosaurus* femur Di6, ''adult'' fibrolamellar bone of the outer cortex followed by the thin layer of lamellar-zonal bone of the outermost cortex with closely spaced LAGs. The bone surface is visible at the top. E, *Dicraeosaurus* femur Di6, close-up of the lamellar-zonal bone with LAGs. F, *Barosaurus* humerus Ba2 with LAG in the middle cortex. Also note the secondary osteons, one of which cuts through the LAG. The width of frames A–D is 1.9 mm, that of E is 0.6 mm, and that of F is 1.15 mm.

bone (Ba6) preserves islands of ''juvenile'' bone in the spongiosa because spongiosa formation proceeds directly into primary bone without an intermediate stage of secondary osteons.

Of special interest in large longbones of *Barosaurus* and the other Tendaguru sauropods is the outermost cortex, which commonly consists of a very thin layer of lamellar-zonal bone with closely spaced LAGs. Humerus Ba6,

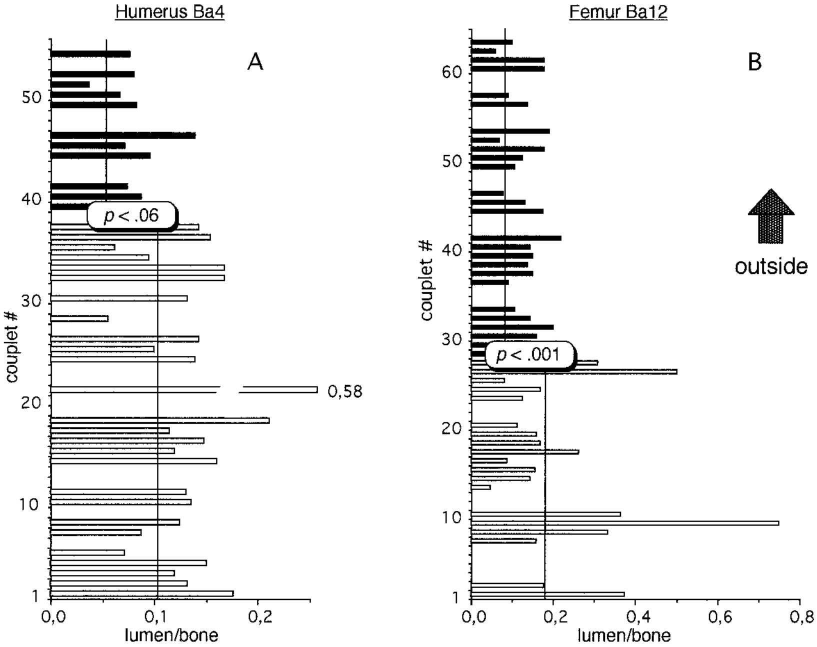

FIGURE 6. Quantification of transition from ''juvenile'' to ''adult'' bone in *Barosaurus* humerus Ba4 and femur Ba12. Relative amount of vascular space is expressed as width of vascular space (lumen) divided by width of the lamina directly external to it (x-axis). ''Couplet'' refers to a lumen and the lamina directly external to it. The outward change of relative amount of vascular space is charted couplet-by-couplet across the transition (y-axis). White indicates ''juvenile'' bone, black indicates ''adult'' bone. The vertical lines connected by the probability value are the means for the ''juvenile'' and ''adult'' bone, respectively. The *p*-value indicates the probability, as computed by *t*-test, that the relative amount of vascular space is different in the two bone types. A, Humerus Ba4; the entire cortex was measured. The significance is not very high but this is likely due to the low number of couplets of ''adult'' bone that are preserved in this section. B, Femur Ba12; the ''hatchling'' bone and most of the outer cortex was not included in the analysis of this bone. The significance is very high, statistically supporting the observation of a rapid transition from ''juvenile'' to ''adult'' bone.

however, lacks these closely spaced LAGs in the outermost cortex. On the other hand, as the surface of this bone is very poorly preserved, closely spaced LAGs may have been present but lost to weathering.

The two largest femora of type A (Ba12, 135 cm; Ba13, 135 cm) differ in this respect because they do have a very thin outermost layer of lamellar-zonal bone with closely spaced LAGs. The femora essentially show the same histology as the humeri, with no free medullary cavity, a thick cortex of primary bone, and few secondary osteons. Specimen Ba12 (Figs. 5A–C, 8) is especially informative because, owing to the low degree of remodeling, it preserves the entire ontogeny of the animal, from reticulate fibrolamellar bone (''hatchling'' bone) to the very thin layer of lamellar-zonal bone with LAGs in the outermost cortex. Femora of type A differ from humeri of this type, however, in the occurrence of polish lines. Four are seen in Ba8 and about 11 are seen in Ba12.

Type B histology is shown by five bones (Ba2, Ba7, Ba10, Ba11, Ba14). It is characterized by an inner cortex with heavy remodeling with dense Haversian bone, by isolated secondary osteons in the outer cortex, commonly occurring all the way to the outer surface of the bone (Fig. 4B), and by several irregularly spaced LAGs throughout the cortex (Fig. 4B). In addition, the primary bone in all type B specimens except Ba7 has more longitudinal canals and fewer circular canals than in type A. The lumina are narrow, and there are even more incremental lines in the primary osteons than in the ''adult'' bone of type A. One humerus, a rather small one (Ba2, 61 cm), exhibits a type B histology (Fig. 5F). It has a central spongiosa instead of a medullary cavity. Among the femora, the smallest (Ba7, 79 cm) is also of type B. The heavy remodeling

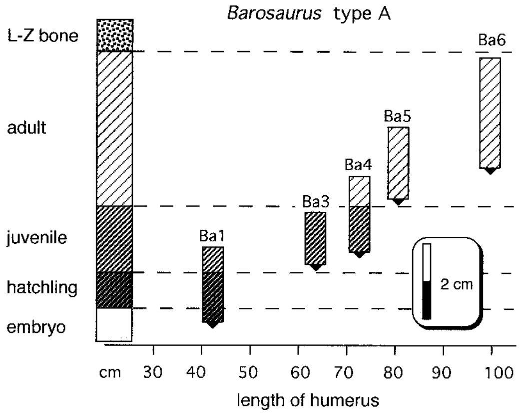

FIGURE 7. Bone type correlated with bone size in a growth series of *Barosaurus* (type A) humeri. This growth series serves to establish the size at which the transition from ''hatchling'' to ''juvenile'' bone deposition occurred as well as that from ''juvenile'' to ''adult'' bone deposition, thereby establishing size at sexual maturity. Embryonic bone could not be distinguished from'' hatchling'' bone in this study. However, the thickness of the cortex in humerus Ba1 suggests that the inner cortex of this bone was already laid down in the embryo. ''L-Z bone'' in this and the following figures is the thin layer of lamellar-zonal bone with closely spaced LAGs resulting from greatly decreased growth rates. The scale indicates cortex thickness in the respective samples.

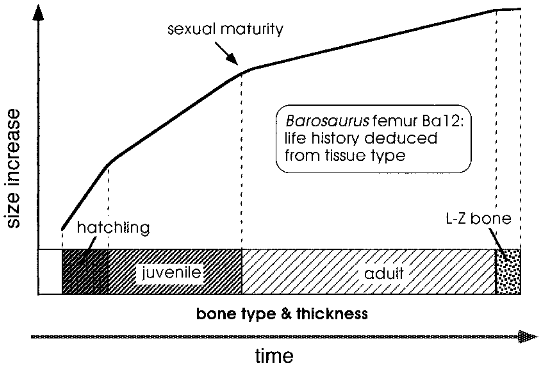

FIGURE 8. Change of bone type during ontogeny in a single *Barosaurus* (type A) femur, specimen Ba12. This bone is exceptional in that nearly the entire life history of the individual is recorded in a single location of the cortex. The changes in tissue type record the stepwise decrease in growth rate. The second decrease is best interpreted as the onset of sexual maturity. Size increase can only be plotted qualitatively because the exact relationship between cortex thickness at any one time and bone size is unknown.

of the inner cortex of this small bone is particularly striking. On the other hand, it shows the least development of isolated secondary osteons and LAGs among all type B bones. The two other type B femora are rather large (Ba10, 119 cm; Ba11, 120 cm).

The two types in *Barosaurus* longbone histology (Fig. 3) thus record rather different growth strategies. Type A grew rapidly and continuously, and remodeling was very limited. In contrast, the growth that produced type B was slower and interrupted, at least partially cyclical, and accompanied by much remodeling—the most extensive seen in any Tendaguru sauropod.

*Brachiosaurus brancai.*—Six humeri, seven femora, one ulna, and one tibia of *Brachiosaurus brancai* were sampled (Table 1). All bones show a rather uniform histologic pattern (Fig. 3), with variation being introduced mainly by differences in individual age. Humerus histology will be discussed first, starting with the smallest individual to trace the ontogenetic changes in bone histology.

The smallest humerus, Br1, with a length of 69 cm, has a cortex of primary bone of the laminar fibrolamellar type with wide lumina (''juvenile'' bone) (Fig. 4C), similar to that seen in the smaller *Barosaurus* humeri. However, in the ''juvenile'' bone of *Brachiosaurus*, the middle of the laminae is particularly well marked by densely spaced osteocytes. In humerus Br1, the transition from the spongiosa to the cortex is gradual, and there are only a few secondary osteons in the inner cortex but none in the outer. In the polished section, three polish lines can be discerned.

The next largest individual (Br2, 108 cm) does not preserve any ''juvenile'' bone. The primary cortex of Br2 consists of fibrolamellar bone with narrow lumina instead (''adult'' bone). As in *Barosaurus,* in *Brachiosaurus* this bone type is characterized by a distinctive flattening of the osteocyte lacunae, more incremental lines in the primary osteons, and the largely lamellar arrangement of the bone fibers. Humeri Br3 (128 cm) and Br4 (153 cm) (Fig. 4D) have histologies very similar to that of Br2 except for their greater cortical thicknesses. As in the juvenile, the transition between the spongiosa and cortex is rather gradual. Secondary osteons are scattered throughout the inner cortex, decreasing in abundance outwards and lacking entirely in the outer cortex.

The two largest *Brachiosaurus* humeri sampled (Br5, 170 cm; Br6, 176 cm) differ from the previous ones mainly in the increasing proportions of secondary bone in their cortex. Humerus Br5 has a distinctive inner region of Haversian bone in the inner cortex that is turned into spongiosa by remodeling. There is no primary bone left in this region. Humerus Br6 shows even more extensive Haversian replacement with isolated secondary osteons occurring throughout the outer cortex. The specimen shows no outer thin layer of closely spaced LAGs. Br5 differs from the other adult specimens in the development of several LAGs that were seen in a fracture across the bone as well as in the thin-sections.

Although femur histology is generally similar to that of the humerus, there are some differences. Most notable are the generally thinner cortex in the midsized specimens Br11 and Br12 and the almost universal visibility of irregularly spaced polish lines in the four largest femora. As in the humerus, the secondary osteons spread outward with increasing bone size, but only in the largest specimen (Br14, 219 cm) is an amalgamation of the secondary osteons to Haversian bone found, although it does not affect the entire cortex.

The cortices of the smallest (Br8) and second smallest (Br9) femora consist entirely of ''juvenile'' bone of the kind seen in the small humerus Br1. In accordance with this is the unfinished outer surface of the bones with the vascular system frequently opening up to the periosteum. The second smallest femur (Br9) with a length of 74 cm is larger than the smallest humerus (Br1) and derives from a significantly larger individual than Br1 because in *Brachiosaurus,* as opposed to the other sauropods, the humerus is longer than the femur. Another juvenile feature of Br9 appears to be the lack of polish lines, also seen in Br8 (69 cm) and Br10 (88 cm). A thin outer layer of densely spaced LAGs set in lamellar-zonal bone was observed only in the second largest specimen (Br13, 183 cm), but not in the largest (Br14, 219 cm).

Ulna and tibia, each sampled only once (Br7 and Br15), seem to offer no radical departure from the histology observed in the larger humeri and femora. Both bones lack polish lines. However, both are characterized by much Haversian bone in the inner cortex.

*Dicraeosaurus spp.*—As opposed to the other Tendaguru sauropod genera, *Dicraeosaurus* is represented by two species in the fauna (Janensch 1914a, 1961): *D. hansemanni* from the Middle Saurian Marls (*mittlere Sauriermergel*) and *D. sattleri* from the Upper Intercalated Beds (*obere Zwischenschichten*) and the Upper Saurian Marls (*obere Sauriermergel*) (see Table 1). As *Dicraeosaurus* is much less common than the two previous taxa, only three humeri and three femora were sampled. Two of these, humerus Di2 and femur Di4 (Fig. 4E,F), belong to a single individual, specimen ''O,'' of *D. sattleri.* Both bones indeed show the same history of growth.

All of the *Dicraeosaurus* bones were from subadult to adult animals as suggested by their large size (Table 1). No differences in bone histology were observed between the two species of *Dicraeosaurus.* However, both species differ in bone histology from all other Tendaguru sauropods (Fig. 3). Histological differences are especially useful in conjunction with size because, for example, any *Barosaurus* humerus small enough to be confused with *Dicraeosaurus* would show signs of immaturity (wide lumina in the inner region of fibrolamellar bone).

The cortex of *Dicraeosaurus* consists of primary fibrolamellar bone (Figs. 3, 4E,F), which is generally similar to the laminar fibrolamellar bone with narrow lumina (''adult'' bone) of large *Barosaurus* type A. However, there are several differences in addition to the size correlation that serve to distinguish it from both *Barosaurus* and *Brachiosaurus.* In most but not all specimens there is a peculiar regionalization in vascular canal architecture in the fibrolamellar bone of *Dicraeosaurus.* Regions of laminar fibrolamellar bone with circular vascular canals (as seen in the primary bone of *Brachiosaurus* and *Barosaurus*) alternate with regions of fibrolamellar bone dominated by longitudinal to plexiform vascular canals (Fig. 4F). Depending on cortex thickness, several alternating regions can be observed. Humerus Di2 and femur Di4 of specimen ''O'' show the same sequence of regions, suggesting that some life-history signal is preserved in this regionalization.

In the fibrolamellar bone of *Dicraeosaurus*, the osteocyte lacunae are evenly scattered throughout the thickness of a lamina but have the same flattened shape as in ''adult'' bone of *Barosaurus.* There are fewer incremental lines in the primary osteons than in *Barosaurus* and *Brachiosaurus* but this feature is combined with a predominantly lamellar arrangement of the bone fibers in the primary osteons.

A very characteristic feature of *Dicraeosaurus* longbones is that the spongiosa arises directly from erosion of primary bone, which reaches deeply into the cortex (Fig. 3). Large erosion cavities can be found in the inner and middle cortex, occasionally also in the outer cortex. These erosion cavities show only a thin lining of secondary bone and sometimes none at all (Fig. 4E). Secondary osteons are very widely scattered (Fig. 3). The development of a medullary cavity within the spongiosa is variable; e.g., the femur Di4 has one whereas the humerus Di2 seems to lack it. The two largest bones in the sample, the femur Di5 (*D. sattleri*) and the femur Di6 (*D. hansemanni*), have densely spaced LAGs set in a thin layer of lamellar-zonal bone in the outermost cortex (Fig. 5D,E). Polish lines are irregularly spaced and variable in number. Femur Di4 has four lines, while femur Di6 has at least five.

*Janenschia robusta.*—*Janenschia,* being the rarest and most unusual sauropod of the Tendaguru fauna, was sampled only from two specimens, the humerus Ja1 and the femur Ja2 (Figs. 1, 3). The bone microstructure of Ja1 was strongly affected by diagenesis (the most extreme case encountered in the Tendaguru material). What little could be observed essentially corroborates the observations made in Ja2. This femur (127 cm long), on the other hand, proved most interesting. The specimen had macroscopically shown clear indication of numerous ''growth lines'' in a fracture across the diaphysis.

The cortex is very thick (over 6 cm at the core location; Fig. 1), in keeping with the general robustness of *Janenschia* bones. The degree of vascularization of the primary fibrolamellar bone of the cortex decreases toward the outside. However, the distinction between laminar fibrolamellar bone with wide lumina (''juvenile'' bone) and laminar fibrolamellar bone with narrow lumina (''adult'' bone) of *Janenschia* is not as clear-cut as in the other taxa investigated, and the transition between the tissue types is more gradual. Only the outer 1.5 cm of the cortex consists clearly of ''adult'' bone. This part is also characterized by the occurrence of LAGs in the fibrolamellar bone (Figs. 1, 3). The last phase of bone growth consists of a narrow layer (about 2 mm thick) of lamellar-zonal bone with numerous, closely spaced LAGs.

Remodeling rate is moderate in *Janenschia.* The transition between spongiosa and cortex is fairly abrupt, with remodeling affecting only the inner one-fourth of the cortex. There is no region of dense Haversian bone, only outwardly decreasing amounts of vascular canals expanded by erosion and of secondary osteons situated in laminar fibrolamellar bone (Fig. 3). Very isolated secondary osteons extend nearly to the outermost region of fibrolamellar bone.

Polish lines and their spacing in *Janenschia* are rather remarkable because they are much more numerous and more regularly spaced than in the other taxa, suggesting that they record regular time increments (Fig. 1). The *Janenschia* sample also suggests that polish lines are not fundamentally different from LAGs. They may simply represent a less-pronounced drop in growth rate because a few of the outer polish lines are also expressed as LAGs in thin-section.

The first polish line is found about 1 cm into the cortex (Fig. 1). It is followed by another ten lines that are spaced between 1. 5 mm and 4 mm apart. Farther outwards, another 15 polish lines can be counted with line spacing decreasing abruptly to between 0. 25 mm and 2 mm (Fig. 1). The record of cyclical growth is continued by LAGs in the thin outer layer of lamellar-zonal tissue. A precise count of these LAGs is difficult, but there are at least six and at most 12 of them.

## Comparison of Histology

A notable and rather surprising result of this study is that all four Tendaguru sauropod genera clearly show distinctive histologic patterns in their longbone diaphysis (Fig. 3), which are indicative of differences in growth strategy and possibly life history. However, they have a number of histologic features in common, notably the dominance of primary fibrolamellar bone in the cortex and the generally low degree of remodeling of the cortex by bone erosion and redeposition (Fig. 3). Also in common are polish lines, the peculiar kind of growth mark in the primary fibrolamellar bone that can only be seen in reflected light on polished sections.

Another important feature shared by all four Tendaguru sauropods, with the exception of *Barosaurus* type B, is the great scarcity or absence of LAGs and modulations in the fibrolamellar part of the cortex. Such LAGs and modulations (Ricqlès 1983) have been observed repeatedly in many dinosaurs (review by Reid 1990) and early birds (Chinsamy et al. 1995) as well as occasionally in large mammals (Klevezal 1996; A. de Ricqlès personal communication 1997). Their absence in the longbones of the Tendaguru sauropods may be linked to the fact that only the largest and therefore fastest growing bones were sampled, i.e., the longbones. Smaller bones in other parts of the skeleton may have well preserved LAGs or modulations because of the much lower rate of bone deposition in small bones. The same is seen in the mammalian skeleton (Klevezal 1996). In addition, as noted above, the polish lines may represent the histological markers equivalent to LAGs and modulations if only very subtle slow-downs in growth occurred.

## Qualitative Aspects of Life History

### Methods

Cortical growth in the longbones of sauropod dinosaurs records life-history traits in a qualitative and sometimes quantitative fashion. First, I will focus on the qualitative aspects of bone histology in *Barosaurus*, *Brachiosaurus*, and *Dicraeosaurus*. (Qualitative aspects of growth in *Janenschia* will be discussed in conjunction with the quantitative discussion because *Janenschia* was studied in only one bone.) Important to both the qualitative and quantitative aspects of bone growth is ''Amprino's rule'' (Amprino 1947), which states that bone of the same tissue type is deposited with the same relative and presumably absolute speed. Amprino's rule has recently been tested by measuring bone deposition rates in a variety of extant taxa and has generally been found to be valid (Ricqlès et al. 1991; Castanet et al. 1996), although these authors take a cautious stance, noting that the database is still rather limited.

Three types of fibrolamellar bone tissue were observed in the juvenile and adult sauropod longbones sampled for this study. They differ in the arrangement and diameter of the vascular canals as well as in a number of other criteria and were termed ''hatchling,'' ''juvenile,'' and ''adult'' bone for descriptive purposes (Fig. 5A–C). The justification for this suggestive ontogenetic terminology will become fully apparent in the discussion of the individual taxa. To review the salient features of these bone types, ''hatchling'' bone is characterized by large, irregularly shaped vascular canal spaces (lumina) that are arranged in a reticular or plexiform pattern (Fig. 5A). ''Juvenile'' bone, on the other hand, still retains the large lumina but now they are elongate and arranged parallel to the bone surface in a laminar pattern (Fig. 5B). ''Adult'' bone also displays the laminar pattern, but the lumina are distinctly smaller (Figs. 5C, 6). Immature ''adult'' bone also may have rather wide lumina but can be distinguished from ''juvenile'' bone by having both fewer radial vascular canals and a bright line in the middle of the lamina.

Because lumen size, shape, and arrangement reflect the vascular system in the living bone, the transition from ''hatchling'' via ''juvenile'' to ''adult'' bone documents the stepwise decreasing volume and increasing organization of the vascular system during ontogeny. It also records a decrease in growth rate, more precisely the rate of bone deposition, as indicated by the decrease in vascularization and the increase in spatial organization of the vascular system. At the subvascular level, this same decrease in growth rate is also documented by the increase of lamellar bone and the decrease of woven-fibered bone (Francillon-Vieillotet al. 1990, Ricqlès et al. 1991), the increase in number and prominence of incremental lines in the primary osteons, and the increased flattening of the osteocyte lacunae (Francillon-Vieillot et al. 1990).

Applying ''Amprino's rule'' to the Tendaguru sauropod longbones, the type and relative thickness of any of these three bone types in the cortex in correlation with the size of the bone can be used to reconstruct life history because each bone type is characterized by a specific growth rate.

Yet another tissue type is of importance in this respect, however—the thin layer of lamellar-zonal bone with LAGs, seen in the outermost cortex of some of the bones studied (Fig. 5D,E). It records a dramatic decrease in growth rate by a magnitude or more, amounting to a near-complete cessation of growth in bone circumference, although limited growth in length still may have been possible (Rimblot-Baly et al. 1995). The common presence of the thin layer of lamellar-zonal bone with LAGs indicates that growth in the Tendaguru sauropods was essentially determinate. The lack of the thin layer in some large bones cannot be taken as evidence against determinate growth. It is more likely that growth terminated at somewhat variable body size in these species than that some individuals of the same species exhibited a determinate growth pattern while others did not. Although great care was taken to avoid weathered bone surfaces as sample sites, one cannot entirely exclude the possibility that in some large bones the lack of the thin outer layer of lamellar-zonal bone is due to post-mortem effects such as weathering.

The sequence of three distinctive types of fibrolamellar bone followed by lamellar-zonal bone suggests that the growth curve derived from the outward changes in cortical bone tissue will be characterized by three consecutive decreases in growth rate, the last of which is most dramatic. This sequence can be observed in a growth series of bones or, ideally, in the cortex of a single, large bone. Growth rate apparently did not decrease gradually, because the bone types are distinct and the transitions between them are rather abrupt (Fig. 6).

The next question to ask is which events in the life history of the animal can the three transitions between the four tissue types and the attendant drops in growth rate be correlated with? The first transition must have happened during preadult ontogeny, simply because of the small absolute size of the bones in which it occurs. Probably it is correlated with an event such as leaving the nest or termination of parental care. The interpretation of the second transition, occurring at roughly between 40% and 80% maximum size (depending on taxon, see below) is crucial for the reconstruction of life history. Conceivably, it could represent an event during juvenile ontogeny, but it is unclear what this event could be because juveniles normally show a uniformly high or only gradually decreasing growth rate. More likely, the second transition represents sexual maturity. A growth pattern with sexual maturity attained at well below maximum size is normal in living reptiles and is also comparable with that observed in the largest terrestrial mammal, the African elephant, which shows considerable adult growth in males (Jarman 1983).

If the second transition does not represent sexual maturity, it would have had to occur at the third transition, close to maximum size, suggesting a determinate growth pattern not observed in living reptiles. Viewing the second transition as an expression of sexual maturation is thus the most parsimonious interpretation, providing justification for the terminology of ''hatchling,'' ''juvenile,'' and ''adult'' fibrolamellar bone.

## Qualitative Life-History Assessments

*Barosaurus Type A.*—The best information on qualitative aspects of life history is provided by *Barosaurus*, particularly humeri of type A (Fig. 7). The smallest humerus (Ba1, 43 cm long) records the transition from ''hatchling'' bone to ''juvenile'' bone about two-thirds through the cortex, suggesting that humeri of hatchlings would have been less than about 35 cm long. It should be noted that this and the following values of bone length derived from histological observations of the mid-diaphysial cortex are only approximate because cortical thickness is only loosely correlated with bone length (probably less a result of intrinsic

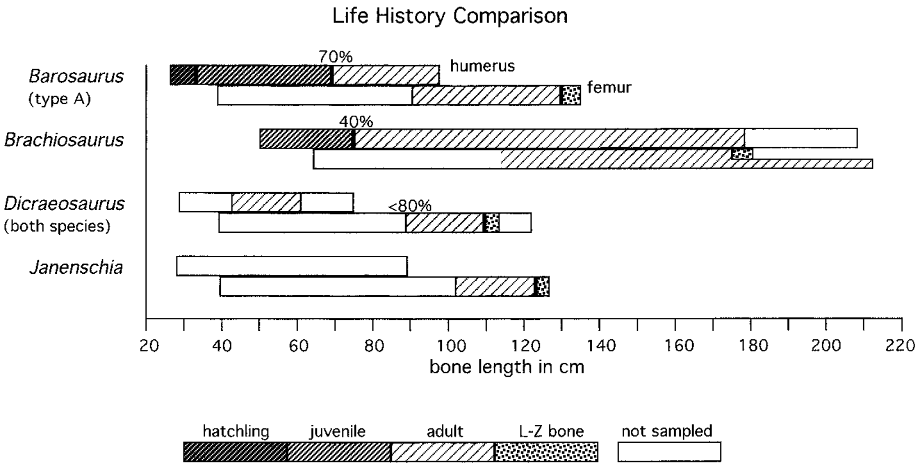

FIGURE 9. Comparison of life history of all four Tendaguru sauropod genera based on tissue type. The bar graphs for each genus are based on all available specimens. The percentage value is that of size at sexual maturity relative to maximum size. Intraspecific variation in life history can be observed in *Brachiosaurus.* Note that *Barosaurus* and *Brachiosaurus* reach sexual maturity at nearly the same size although maximum size differs greatly.

variation in cortex thickness than of variation introduced by imprecise sample location).

A humerus of 73 cm length (Ba4) records the transition from ''juvenile'' to ''adult'' bone in its outer cortex (Fig. 6), while the cortex of an 80.5-cm humerus (Ba5) consists entirely of ''adult'' bone. Assuming again that this transition occurred at sexual maturity, humeri longer than about 70 cm would belong to adult animals (Fig. 7). Growth continued at a high rate considerably into adulthood, as evidenced by the largest *Barosaurus* humerus from Tendaguru (Ba6, 99 cm). Its cortex consists entirely of ''adult'' bone, and there is no outer layer of lamellar-zonal bone with LAGs. As noted above, however, this layer may have been lost to weathering. At any rate, sexual maturity in *Barosaurus* occurred at no more than 70% maximum size.

Independent confirmation of these life-history traits for type A of *Barosaurus* is provided by one of the two largest femora (Ba12, 135 cm; Fig. 8), the innermost cortex of which consists of ''hatchling'' bone while the outermost cortex preserves a thin layer of lamellar-zonal bone with one or two LAGs (Figs. 5A–C, 8). This specimen also documents the transition from ''juvenile'' to ''adult'' bone well, and the decrease of relative lumen space can be quantified (Fig. 6B).

*Barosaurus Type B.*—Growth of type B of *Barosaurus* can be documented in much less detail because of the smaller sample size. humerus Ba2 (61 cm) and Femur Ba7 (79 cm) seem to derive from an adult individual because there is much ''adult'' bone in their outer cortex (Fig. 5F). Any remaining ''juvenile'' bone in the inner cortex has been obliterated by Haversian remodeling. Femora Ba10 (119 cm) and Ba11 (120 cm) are clearly derived from much larger animals than are humerus Ba2 and femur Ba7; nonetheless, they, too, show only ''adult'' bone (Fig. 4B) but no outer layer of the lamellar-zonal tissue. The scanty data suggest that *Barosaurus* type B reached sexual maturity at a considerably smaller size than type A but that it also grew very much after sexual maturity and that maximum size was not much smaller.

*Brachiosaurus.*—Although the data for *Brachiosaurus* are less conclusive than for *Barosaurus* type A, *Brachiosaurus* seems to have achieved sexual maturity at a smaller relative size than *Barosaurus* (Fig. 9). humerus Br1, at a length of 69 cm clearly a juvenile, has a cortex consisting entirely of ''juvenile'' bone (Fig. 4C). Femur Br10 (88 cm), on the other hand, preserved no obvious ''juvenile'' bone. As the humerus is longer than the femur in *Brachiosaurus* (hu/fe ratio = 1. 08), the individual from which Br10 is derived was somewhat larger than the bearer of Br1. A rough estimate of humerus length at sexual maturity is thus about 85 cm (Fig. 9). This is in accordance with humerus Br2 (108 m) that preserves no ''juvenile'' bone in its inner cortex.

Growth was determinate but maximum size was apparently variable, with femur Br13 (183 cm) largely having stopped growing (as evidenced by the thin lamellar-zonal bone with LAGs in the outermost cortex) while the largest known *Brachiosaurus* femur (Br14, 219 cm) belonged to an individual that was still growing. The largest humerus sampled (Br6, 176 cm) also was still growing. This is not surprising because it is much smaller than the largest specimen known (213 cm, NHUB S II). It should be noted that Gross (1934) already observed lamellar-zonal bone with LAGs in the outermost cortex of a *Brachiosaurus* bone from the Tendaguru beds and correctly concluded it to indicate a determinate growth pattern.

Remarkably, *Brachiosaurus* and *Barosaurus* thus seem to have reached sexual maturity at about the same humerus size, but *Brachiosaurus* continued to grow much longer. Its size at sexual maturity apparently was only about 40% of maximum size as opposed to 70% in *Barosaurus* (Fig. 9)

*Dicraeosaurus.—Dicraeosaurus* shows little size variation in the Tendaguru sample, and only adult bones seem to be represented. This is suggested by bone histology as well. The three humeri drilled were 58–62 cm long, somewhat smaller than known maximum length (74 cm, NHUB Q 11), and all preserve ''adult'' bone only. The same is true for the three femora, the smallest of which (Di4, 98 cm; Fig. 4E,F)) belongs to the same individual as humerus Di2 (61 cm). The larger femora (Di4, 112 cm; Di6, 114 cm) already show closely spaced LAGs in their outermost cortex, suggesting that the animals had largely stopped growing (Fig. 5D,E). As these femora are close to maximum size (122 cm in the femur of skeleton ''m,'' the skeleton mounted at the NHUB), the presence of closely spaced LAGs in their outermost cortex is not surprising.

Sexual maturity in *Dicraeosaurus* was thus reached at a femur length significantly less than 98 cm, equivalent to less than 80% maximum size (Fig. 9). As in *Brachiosaurus,* maximum size apparently shows some variability.

### Quantitative Aspects of Life History

Although there are other ways emerging to quantitatively estimate life-history parameters from bone histology (e.g., bone deposition rates [Curry 1998]), in this study only growth lines were used. Growth lines are the standard source of data for histologic aging of modern tetrapods (Castanet and Smirina 1990; Castanet et al. 1993; Klevezal 1996) and have successfully been used for this purpose in fossils (Sander 1990). As noted in the descriptions of the individual taxa, two types can be observed in the Tendaguru sauropod longbones: lines of arrested growth (Fig. 5D–F) and polish lines (Figs. 1, 2).

LAGs are commonly encountered in the outermost cortex of large longbones where they are closely spaced and set in lamellar-zonal bone. Assuming annual deposition, they record the number of years the animal lived after rapid growth ceased. Thus the number varies from one in the largest *Barosaurus* femur (Ba12) to 12 in the *Janenschia* femur (Ja2), with *Brachiosaurus* and *Dicraeosaurus* specimens showing intermediate numbers (Fig. 5D,E).

LAGs also occur rarely and are irregularly spaced in the ''adult'' fibrolamellar bone of some Tendaguru sauropods such as *Barosaurus* type A, *Brachiosaurus,* and *Janenschia.* Most prominently, of course, they are developed in the fibrolamellar bone of *Barosaurus* type B (Figs. 3, 5F). In this, however, they allow age estimates only for the humerus Ba2, which preserves about seven. Because of extensive cortical remodeling, this represents a minimum number, thus putting the minimum age of the animal at eight years. The large femur Ba10 preserves LAGs only in the outer region of fibrolamellar bone. They are more closely and irregularly spaced than in humerus Ba2, suggesting a slower growth rate than in the humerus.

Polish lines are potentially more informative, especially in *Janenschia.* Their spacing in femur Ja2 suggests that they were developed annually and record life history in a quantitative manner (Figs. 1, 10). The first 11 widely spaced polish lines thus would represent the

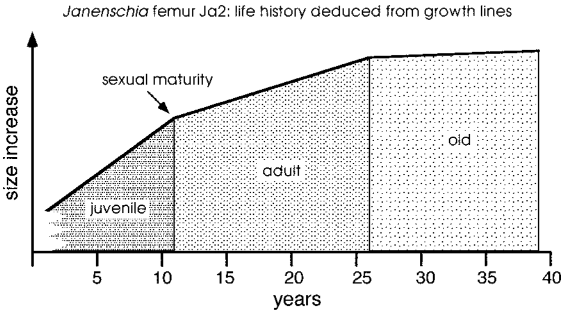

FIGURE 10. Quantitative estimate of life history of *Janenschia* (femur Ja2) based on growth lines. Growth lines are either polish lines in the fibrolamellar part of the cortex or LAGs in the thin outer layer of lamellar-zonal bone.

years of juvenile growth, sexual maturity taking at least 11 years to achieve. This represents a minimum number because one or two innermost lines may have been destroyed by remodeling.

The polish lines indicate that the phase of rapid adult growth also seen in the other Tendaguru sauropods would have lasted from the twelfth to the twenty-sixth year of life of the *Janenschia* individual (Figs. 1, 10). After growth had largely ceased, 12 LAGs were laid down in the thin outer layer of lamellar-zonal bone, suggesting that the animal lived another 12 years, reaching an age of at least 38 years. The number of growth lines in *Janenschia* is in accord with observations of a fairly high number of LAGs in other sauropods (Reid 1981, 1990; Ricqlès 1983; Rimblot-Baly et al. 1995) but differs from the fairly low number of growth cycles observed for *Apatosaurus* by Curry (1998) and in the other Tendaguru sauropods.

This interpretation derived from the polish lines in *Janenschia* Ja2 is corroborated by tissue type. The first 11 polish lines are developed in ''juvenile'' bone, although this shows fairly narrow lumina. Polish lines No. 12 to No. 26 are developed in ''adult'' bone and, more significantly, some of them are also expressed as LAGs, including line No. 12. The decreased rate of bone growth after sexual maturity thus is documented not only by the lower degree of vascularization but also by interruptions of growth.

It is important to note that the growth line record in *Janenschia* suggests the same pattern of growth as derived from the succession of bone types in the other sauropods. In particular, the decrease in growth rate in mid-ontogeny (at 11 years in *Janenschia* and at the transition from ''juvenile'' to ''adult'' bone in *Barosaurus* and *Brachiosaurus*) is detected by both methods. Sexual maturity after 11 years seems more likely than after 26 years because it is in better agreement with the observations of Curry (1998) on *Apatosaurus* and with theoretical predictions about maximum age at sexual maturity by Dunham et al. (1989) for sauropod dinosaurs in general.

### Dimorphism of Bone Histology in *Barosaurus*

The dimorphism observed in the bone histology of *Barosaurus* longbones (Figs. 3, 4A,B) could be due to a number of causes, an obvious one being sexual dimorphism. Others are the presence of two taxa in the sample, climatic change over time, and an artifact of the sampling technique. This last hypothesis appears unlikely, as discussed in some detail in the next section. The hypothesis of climatic change over time can be discounted readily because both horizons sampled contained bones of both type A and type B (Table 1). Histological types are thus not linked to the gracile and robust variants described by Janensch (1961), the robust variant being found only in the Upper Saurian Marls.

Taxonomic difference as an explanation for the dimorphism cannot be ruled out, but there is no supporting evidence. Longbones of type A and type B show no morphological differences. There is also no suggestion of the presence of two taxa in the other *Barosaurus* material from Tendaguru (Janensch 1961).

Sexual dimorphism thus remains a distinct possibility and will be examined in more detail. The fast, continuous growth with little remodeling of type A contrasts strongly with the slower, discontinuous growth of type B (see Fig. 3). In addition, type B is characterized by extensive remodeling, the most extensive in any of the Tendaguru sauropods (Fig. 3). Type B could represent the female, with the extensive remodeling and possibly the interruptions in growth linked to reproduction.

The formation of eggshell and yolk would draw considerable amounts of calcium and phosphorus from the mother, and these two elements are primarily stored in the skeleton as bone apatite. Type A would then represent the male. Its fast and continuous growth would be compatible with selection pressure for large size early in ontogeny. This in turn might have been advantageous in competitions among the males for mates.

Such differences in growth patterns, with the males growing faster than the females, are not uncommon in living reptiles and are observed among others, in the American alligator (*Alligator mississippiensis*) (see graph in Varricchio 1997), as well as in box turtles (*Terrapene* spp.), agama lizards (*Agama* spp.), and copperhead snakes (*Agkistrodon contortrix*) (Bellairs 1970).

The proposal of sexual dimorphism in *Barosaurus* is clearly the most speculative of the interpretations derived here from bone histology, and better support by a larger size of the Tendaguru sample or independent confirmation in the North American *Barosaurus* is desirable.

## Discussion

An important premise in comparing bone histology and deriving growth patterns (including sexually dimorphic ones) in the Tendaguru sauropods just from samples from the middle of the humeral or femoral diaphysis is that these samples are representative of the growth strategy of the whole animal. How can we be sure that the sequence and relative thickness of tissues do not reflect local morphogenesis? What about allometric growth in the skeleton? As noted earlier, effects of local variations in osteogenesis due to morphogenesis are minimized by the choice of the sample site and by sampling exactly equivalent sites in the different bones.

A test of the premise is also provided by comparing different bones of the same individual. As noted earlier, both the right humerus and the right femur of *Dicraeosaurus* individual ''O'' were sampled and showed a remarkably similar growth record. In another instance, bone histology provides the only available evidence that certain bones belong to the same individual because of histologic similarity. Isolated sauropod longbones and bone accumulations are the rule in the Tendaguru beds, and associated or articulated material is the exception (Janensch 1914b; Heinrich 1999). Bones in bone accumulations usually cannot be assigned to specific individuals (Heinrich 1999). Such is the case with the specimens bearing the field number prefix ''Ki,'' indicating that they come from the Kindope locality (Janensch 1914b; Heinrich 1999). In the histologic sample of *Barosaurus* there are four bones bearing the ''Ki'' -prefix (Table 1): the right femur Ki 2, the left femur Ki 5, the right tibia Ki5, and the left femur Ki 71a. Initially, I had sampled only Ki 2, Ki 5, and Ki 71a, noticing that Ki 2 and Ki 5 show a type B histology. In the final sampling effort, I also sampled Ki 4 to broaden my database for *Barosaurus* femora. To my surprise, Ki 4 also showed type B histology. This might suggest that type B histologies are more common at Kindope than elsewhere. However, a closer look at the size and type of these type B bones suggests that they derive from the same type B individual because the femora are left and right bones and nearly of the same size (119 cm vs. 120 cm), and at 84 cm the tibia could well fit with a femur of that size. In addition, the growth records in the three samples are rather similar, with strong Haversian remodeling in the inner cortex and scattered secondary osteons and a few irregularly spaced LAGs in the outer cortex. The main difference between the femora on one hand and the tibia on the other is that the tibia has a relatively thicker region of Haversian bone. These observations suggest that the single cores taken from standardized locations in the diaphysis are indeed representative for the whole animal despite the influence of local osteogenesis on the histology of the samples.

Addressing the problem of the dimorphic bone histology in particular, an additional argument can be made against it being an artifact of local osteogenesis: In a bone cross-section, lateral change in tissue type in the cortex is not abrupt but gradual. This has also been shown to be the case in sauropod longbones (Ricqlès 1983; Rimblot-Baly et al. 1995). The two histologic types observed in *Barosaurus,* on the other hand, are rather distinct without intermediate histologies. If local tissue type variation were the cause for dimorphic bone histology, one would expect intermediate histologic types in the core samples.

Allometry is not likely to be a significant challenge to the premise because sauropod limb bones in general do not exhibit strong allometries (see also Ogier cited in Ricqlès 1983). Additional evidence that the samples are representative of the whole animal is that the same general growth pattern, sexual maturation well before termination of growth (see above), is documented by three different observations: tissue-type change in growth series of bones of *Barosaurus* and *Brachiosaurus,* tissue-type change in individual bones in *Barosaurus,* and number and spacing of growth lines in *Janenschia.* However, local morphogenesis as well as allometry probably would interfere with further quantification of the patterns observed.

Taxon recognition is also based on the premise that the histology of the core sample from the thinnest part of the longbone is not primarily controlled by local osteogenesis but is representative for the entire bone. A good test for the premise, of course, is provided by longbones in which the identification of Janensch (1961 and specimen labels) has been questioned by later workers. This occurs especially in bones of similar morphology and size, e.g., the humeri of small individuals of *Barosaurus* versus those of large individuals of *Dicraeosaurus.* As should have been apparent from the descriptions of the individual taxa, these can be readily identified by bone histology. Thus, although humerus Ba3 and Di3 are nearly of the same size (64 and 62 cm, respectively), their histologies are rather distinctive and corroborate the morphology-based assignment by Janensch. Another example involves the femur NHUB Nr. 76, which at 135 cm would be large for *Barosaurus* but smallish for *Brachiosaurus.* The bone was assigned to *Brachiosaurus* in a note left by a recent visitor to the collection. However, histology clearly shows it to pertain to *Barosaurus,* the original assignment by Janensch.

## Conclusions

The histology of the longbones, primarily humerus and femur, of the four Tendaguru sauropod genera is comparable in some respects but there are surprising differences in others (Fig. 3). These differences allow taxon recognition based on bone histology, especially if bones of the same size are compared. In addition, possible sexual morphs in one species, *Barosaurus africanus,* can be recognized. *Brachiosaurus brancai* shows a thick cortex of fibrolamellar bone that in older individuals is affected by considerable remodeling. *Barosaurus* ''males'' are similar to *Brachiosaurus* except that they show very little remodeling, resulting in the preservation of ''juvenile'' or even ''hatchling'' bone in the deep cortex. *Barosaurus* ''females,'' on the other hand, show strong remodeling of the fibrolamellar bone which also has LAGs. *Dicraeosaurus* spp. can be distinguished by the high degree of resorption activity in the cortex, resulting in a gradual transition from spongiosa to cortex, and commonly by a peculiar alternation of vascularization patterns in the fibrolamellar tissue. *Janenschia robusta* differs from the other taxa in its great cortical thickness and regularly spaced polish lines.

All taxa except the presumed female of *Barosaurus* exhibit continuous, fast growth with relatively little remodeling activity in the bone. In all taxa, remodeling increases with age, and growth appears to slow down dramatically in individuals approaching maximum size. Sexual maturity appears to have been attained at much less than maximum size (Fig. 9). This can be quantified for *Brachiosaurus* and *Barosaurus,* which reached sexual maturity at 40% and 70% maximum size, respectively. Only in *Janenschia* can a qualitative estimate of life history be made, based on growth lines, particularly polish lines. In the specimen studied, sexual maturity was reached at ≥11 years, growth essentially ceased at >26 years, and the animal died at ≥38 years (Fig. 10).

## Acknowledgments

This research would have not been possible without the open minds of W.-D. Heinrich und

H.-P. Schultze of the Naturkundemuseum der Humbolt-Universität zu Berlin, who gave me unprecedented opportunities to sample sauropod longbones for histologic work.

The paper benefited greatly from discussions with A. de Ricqlès (College de France) and K. Curry (State University of New York, Stony Brook) as well as members of the Tendaguru working group in Berlin. The thoughtful reviews of earlier versions of the manuscript by J. O. Farlow and especially J. Castanet also contributed a great deal to sorting out my sometimes tangled thoughts and messy use of terms. Help from G. Oleschinski and D. Kranz (Institut für Paläontologie, Universität Bonn) in preparing the photographic plates is greatly appreciated.

This research was funded by a grant from the Deutsche Forschungsgemeinschaft to the author.

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