

PRELIMINARY OBSERVATIONS ON THE BONE HISTOLOGY OF THE MIDDLE TRIASSIC PSEUDOSUCHIAN ARCHOSAUR *Batrachotomus kupferzellensis* REVEAL FAST GROWTH WITH LAMINAR FIBROLAMELLAR BONE TISSUE

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ABSTRACT—The bone tissue of femur, rib, and gastralia from three different individuals of the Middle Triassic pseudosuchian *Batrachotomus kupferzellensis* from southern Germany is studied. The femoral bone tissue comprises laminar fibrolamellar bone tissue throughout and is stratified by three annual growth cycles, indicating that the individual died early in its fourth year of life, at which time it had reached 87% of maximum known femur length. Thus, compared with most other Pseudosuchia (e.g., phytosaurs, aetosaurs, and most crocodylomorphs, including marine taxa), *Batrachotomus* achieved its large body size in a very short time by fast, although interrupted, growth and not by protracted longevity. Such fast growth as well as the organization of the tissue is similar to the condition observed in ornithodirans. The pseudosuchians *Effigia* and *Postosuchus* also show fibrolamellar tissue, but vascular density is lower when compared with *Batrachotomus* and dominated by a longitudinal organization of primary osteons. The rib and gastralia of *Batrachotomus* both show an inner spongy organization surrounded by a ring of compact, avascular, highly organized parallel-fibered and/or lamellar bone largely covered by short fibers. Maximal growth cycle count in the proximal rib sample suggests an age of at least 11 years for this individual with a reduction of growth rate after the sixth cycle.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Understanding aspects of growth provides crucial data for the reconstruction of life history strategies in long-extinct clades, because the pattern of growth is impacted by ontogenetic development, metabolism, and external environmental factors (Karkach, 2006). Two divergent tissue types are found in extant tetrapods, reflecting two main growth patterns: lamellar-zonal bone (LZB) and fibrolamellar bone tissue type (FLB). According to Francillon-Vieillot and colleagues (1990:204), LZB is dominated by a bone tissue matrix of parallel-fibered or lamellar bone, extensively stratified by cyclical growth marks. Vascular density is low or tissue may be even avascular. FLB consists largely of woven and centripetally deposited lamellar bone (primary osteons), and the matrix shows a high vascular density (Francillon-Vieillot et al., 1990; Cubo et al., 2005; Legendre et al., 2016). Like LZB, FLB can be stratified by growth marks, as was described for some dinosaurs (Horner et al., 2000; Horner and Padian, 2004; Klein and Sander, 2007) and mammals (e.g., Sander and Andrassy, 2006; Köhler et al., 2012). Amprino (1947) recognized that there is a connection between bone tissue and growth rate (the slower the deposition rate, the more regular is the orientation of the collagen fibers), although this has been difficult to quantify (Castanet et al., 2000; de Margerie et al., 2002; Montes et al., 2007).

Recent lissamphibians and non-avian reptiles typically form LZB (Castanet et al., 1993). By contrast, most living birds and mammals deposit FLB (Chinsamy and Elzanowski, 2001; Köhler et al., 2012). There is consensus that bone tissue type (reflecting growth rates) and metabolism are related (e.g., Legendre et al., 2013), but growth rates of endothermic and ectothermic extant taxa can overlap.

In Mesozoic diapsids, the variety of combinations among bone tissues and vascular systems (e.g., Ricqlès et al., 2003, 2008; Chinsamy-Turan, 2005; Botha-Brink and Smith, 2011; Sander et al., 2011; Houssaye, 2013; Erickson, 2014; Houssaye et al., 2014; Klein et al., 2015a, 2015b) documents a much higher histological diversity that correlates with various growth patterns and life history strategies, as well as an implied broader metabolic range/diversity than observed in modern tetrapods (e.g., Castanet et al., 1993; Köhler et al., 2012). Ichthyosaurs (Buffrénil and Mazin, 1992; Houssaye et al., 2014) and some Sauropterygia (Buffrénil and Mazin, 1990; Wiffen et al., 1995; Klein et al., 2015a) are so far the only known non-archosaur diapsids that formed FLB throughout most of their ontogeny, which might be related—at least in Triassic forms—to a constant warm environment.

Archosauria is divided into two major clades: the Pseudosuchia, which includes modern crocodilians and all archosaurs more closely related to crocodilians than to birds, and the Avemetatarsalia or Ornithodira, which contains pterosaurs, silesaurids, and dinosaurs, including birds (Nesbitt, 2011). The

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Pseudosuchia were most successful and diverse (both ecologically and morphologically) during the Late Triassic (Brusatte et al., 2008; Foth et al., 2016), including quadrupedal and (facultative) bipedal forms, terrestrial and semiaquatic life styles, as well as piscivorous, carnivorous, or omnivorous diet preferences (e.g., Desojo and Vizcaíno, 2009; Gauthier et al., 2011; Nesbitt et al., 2013). According to Nesbitt (2011), Pseudosuchia contain Ornithosuchidae, Aetosauria, Poposauroidea, Rauisuchidae, and Crocodylomorpha, but probably also the long-snouted Phytosaurs (see Brusatte et al., 2010; Ezcurra, 2016). Except for Crocodylomorpha, the group went extinct at the end of the Triassic (Nesbitt, 2011; Toljagic and Butler, 2013).

Within Pseudosuchia, *Batrachotomus kupferzellensis* was a large (~6 m body length), common apex predator in the Middle Triassic Lower Keuper deposits of southern Germany (Kupferzell and Vellberg, Baden-Württemberg) (Gower, 1999; Gower and Schoch, 2009; Schoch and Seegis, 2016). It was quadrupedal, and its postcranial morphology suggests an erect posture (see Benton, 1984). *Batrachotomus* was formerly thought to be a member of Prestosuchidae (Gower, 2002; Brusatte et al., 2010), but other phylogenetic analyses found it more closely related to Crocodylomorpha and Rauisuchidae (Nesbitt, 2011; Li et al., 2012; Sues and Schoch, 2013).

Previous Works on Basal Archosaur Bone Histology

Ricqlès and colleagues (2003, 2008) were among the first who studied bone tissue of several pseudosuchian and basal archosauriforms. Since then, more studies on archosauromorphs, archosauriforms, and pseudosuchian archosaurs have been conducted. Most studied taxa comprise a mixture of bone tissues that usually early in ontogeny form FLB to later switch to LZB (e.g., Ricqlès et al., 2003, 2008; Botha-Brink and Smith, 2011; Werning and Nesbitt, 2016). Their tissue is interrupted by a high number of cyclical growth marks with broad zones alternating with broad annuli capped by a line of arrested growth (LAG; e.g., Ricqlès et al., 2003, 2008; Botha-Brink and Smith, 2011; Werning and Nesbitt, 2016). Osteoderm histology of phytosaurs and aetosaurs (Scheyer et al., 2014) as well as that of several ‘rauisuchians,’ including *Batrachotomus* (Scheyer and Desojo, 2011; Cerdá et al., 2013), documents a similar diverse distribution of bone tissues in these taxa, as is seen in their long bones.

Instead, ornithodirans such as dinosaurs (e.g., Ricqlès, 1968; Horner et al., 2000; Chinsamy-Turan, 2005; Erickson, 2005, 2014; Sander et al., 2011) and pterosaurs (e.g., summarized in Steel, 2008) formed FLB through most of their ontogeny, indicating sustained high growth rates. Their tissue is interrupted by a relatively lower number of broad zones alternating with thin annuli or LAGs (Ricqlès et al., 2003). In addition, the vascular system differs between ornithodirans and pseudosuchians: dinosaurs usually show a laminar or plexiform and pterosaurs a reticular organization, whereas in pseudosuchians vascularization is dominated by longitudinal canals (Ricqlès et al., 2003). Despite the presence of FLB in the inner cortex, the tissue type of pseudosuchians is usually categorized as LZB due to the dominance of parallel-fibered and lamellar bone throughout the cortex (Ricqlès et al., 2003, 2008). However, some exceptions occur, such as the large archosauriformes *Erythrosuchus* and crocodylomorph *Terrestrisuchus*, which largely grew with FLB (Ricqlès et al., 2003; Botha-Brink and Smith, 2011).

In summary, most pseudosuchians had high growth rates only early in development, and large adult sizes were reached through protracted cyclical growth, resulting in high numbers of growth marks (Ricqlès et al., 2003, 2008). Contrary to this is the potential of ornithodirans to reach large body sizes quickly, resulting in a lower number of growth marks until attaining maximum size (Ricqlès et al., 2008; see also Sander et al., 2004, for accelerated growth in Sauropoda). However, due to limited sampling, the

evolution of growth patterns in basal archosauromorphs, including pseudosuchians, is still poorly understood.

In the current study, we analyze bone histology and microanatomy of a femur, a rib, and parts of gastral ribs of three different individuals of the large-bodied pseudosuchian *Batrachotomus kupferzellensis* and compare bone tissue and growth pattern with those of other basal archosauromorphs, on a morphological and a phylogenetic level.

Institutional Abbreviation—SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

MATERIALS AND METHODS

The midshaft of an almost complete but dorsoventrally heavily crushed left femur of *Batrachotomus kupferzellensis* (SMNS 90509; Gower and Schoch, 2009) from the locality of Kupferzell was sampled (Fig. 1A). The crushed condition of the femur is most likely the result of the compaction of argillites and marls between diagenetic cemented dolomite banks, characterizing the rocks of the locality (Schoch and Seegis, in press). Here, another midshaft break of a non-compacted femur (SMNS 52970) helps to confirm that the medullary cavity in SMNS 90509 is actually small and not secondarily compacted (Fig. 1D). The sampled femur measures approximately 42 cm, which is 87.9% of the thus far longest known femur (SMNS 52970) of *Batrachotomus*, which measures 47.8 cm (Gower and Schoch, 2009). In addition, three thin sections along the midshaft region of a dorsal rib (SMNS 92130) and of a gastral rib (SMNS 92131) were sampled, respectively (Fig. 1B, C). The samples all originate from the same locality and horizon but belonged to different individuals.

The thin sections were produced following standard petrographic methods (Klein and Sander, 2007) and had a thickness of between 55 and 72 μm . Thin sections were studied and photographed with a Leica DM 750P compound polarizing microscope equipped with a digital Leica ICC50HD camera. Cross-sections were scanned with an Epson V740 PRO high-resolution scanner (Fig. 2). The bone histological terminology follows Francillon-Vieillot et al. (1990).

Due to compression of the cross-section, the overall femoral growth rate was calculated by measuring the cortical thickness of all four bone sides and dividing the resulting average value by four. This value was then divided by the number of years counted from the sample, using a year of 380 days (see Botha-Brink and Smith, 2011).

To trace evolutionary patterns of growth in basal archosauromorphs from the Permian and Triassic periods, we mapped the occurrence of different types of bone tissue onto a phylogenetic hypothesis for basal archosauromorphs, using the ‘trace history’ function in the program Mesquite 3.2 (Maddison and Maddison, 2017). Three different growth pattern states were defined: formation of LZB through whole ontogeny (0), formation of FLB only during early ontogenetic stages with subsequent formation of LZB for remaining life time (1), and intense formation of FLB over longer ontogenetic period (2). The histological data were taken from the literature (see Supplementary Data, Table S1). For the phylogeny of archosauromorphs, an informal supertree was created. The relationships of stem archosaurs follows Ezcurra (2016), whereas the topology of crown archosaurs is based on Nesbitt (2011). Because of conflicting results, we considered two different phylogenetic positions for phytosaurs: as a sister group to Archosauria (Nesbitt, 2011) and as the most basal member of Pseudosuchia (Brusatte et al., 2010; Ezcurra, 2016). To test the strength of the phylogenetic signal for the growth patterns in archosauromorphs, we reshuffled the character states 10,000 times across the tree while the topology was held constant. Afterwards, we compared the number of steps with the original character mapping. If the original number of steps was smaller than in 95% of the randomized character states, growth

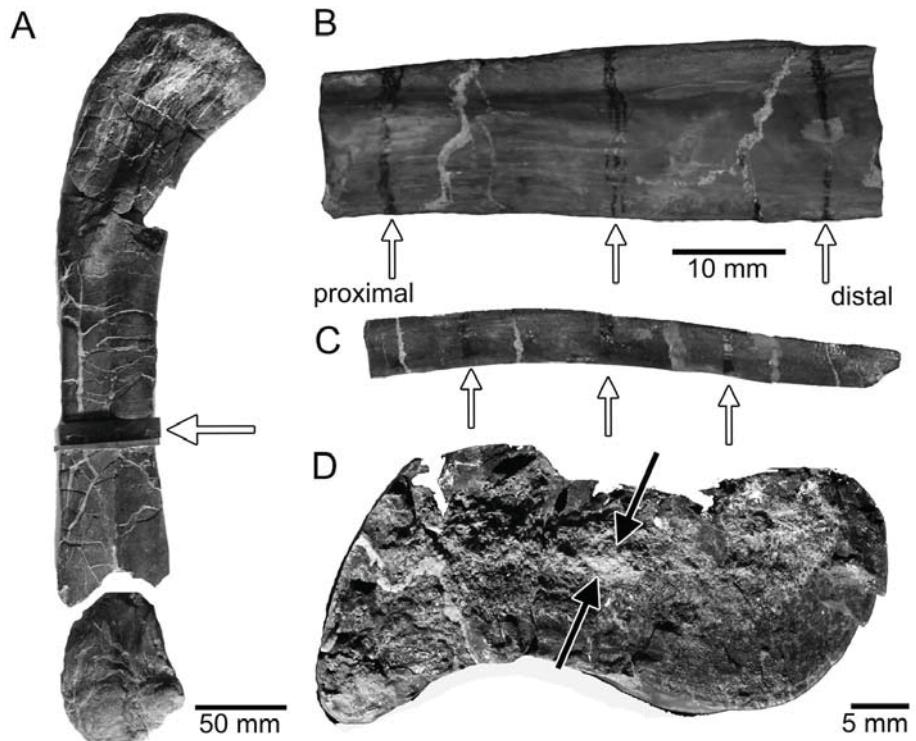


FIGURE 1. Sampled bones of *Batrachotomus kupferzellensis* from the late Ladinian (Middle Triassic) of southern Germany with the respective sampling locations marked by white arrows. **A**, left femur (SMNS 90509) in ventral view; **B**, fragment of *Batrachotomus kupferzellensis* dorsal rib (SMNS 92130); **C**, fragment of gastralia (SMNS 92131); **D**, midshaft cross-section (natural break) of largest known femur (SMNS 52970) of *Batrachotomus kupferzellensis* exhibiting a central free medullary cavity now filled with dolomitic marlstone (black arrows).

patterns in archosauromorphs are considered to be phylogenetically constrained.

RESULTS

Histological Description

Femur—Due to compaction of the femur (SMNS 90509), the entire cross-section is traversed by cracks and fissures (Fig. 2A, B). The outer bone surface is in many places incomplete or crushed. The medial and lateral bone sides are best preserved, whereas the dorsal and ventral sides experienced most damage, indicating dorsoventrally directed pressure. Ventrolaterally, a funnel-shaped, sediment-filled crack reaches deep into the cortex (Fig. 2A, B).

In the lateromedial direction, an elongated crack runs through the center of the cross-section, most likely tracing and expanding the free, but small medullary cavity (Fig. 2A, B). The free cavity was surrounded by secondary trabeculae comprising erosion cavities, which are now largely collapsed and compressed due to damage/compaction during fossilization (Fig. 3A). Thicker fragments of lamellar (endosteal) bone aligned parallel to the dorsoventral bone surfaces indicate partial lining of the cavity margin by endosteal bone (Fig. 3A). Large erosion cavities occur scattered up into the middle cortex (Figs. 2, 3A). True Haversian bone is not deposited, but some of the smaller round erosion cavities lined by lamellar (endosteal) bone can be interpreted as young (immature) secondary osteons (Currey, 2002; Fig. 3A).

The vascular system is dominated by a laminar organization but can become locally (sub-)plexiform (Figs. 2–4). The shape of the vascular canals is circumferential, longitudinal, and reticular. Vascular density is higher on the lateral side of the bone (Fig. 2). Vascular canals are surrounded by primary osteons (Fig. 4).

The primary bone tissue consists of woven-fibered bone with numerous round osteocyte lacunae and primary osteons, resulting in fibrolamellar bone tissue (Figs. 2, 4A, B). Locally, the

woven-fibered bone component is intermixed with parallel-fibered bone (Fig. 4C, D).

The cortex is stratified by annual growth cycles consisting of broad zones, forming most of the cortex, and narrow/thin annuli (Figs. 2, 3B–D). The zones start with numerous and large primary osteons in the inner, but their number gradually decreases towards the outer zone. Zones are made of woven-fibered and low-organized parallel-fibered bone. Annuli are avascular and narrow/thin, consisting of highly organized parallel-fibered bone tissue. Three distinct annuli can be counted, of which one forms the outer cortex (Fig. 3B–D).

Except for the lateral bone side (Fig. 3D), vascular density decreases somewhat and tissue organization increases towards the outer cortex, but a change to an external fundamental system (*sensu* Horner et al., 2000) is not observed (Fig. 3B, C). The cortex of the dorsal and ventral bone sides is generally more organized and contains locally thin layers of avascular parallel-fibered bone that, however, cannot be followed throughout the entire cross-section and are thus interpreted as non-annual cycles (subcycles; see Klein et al., 2015b). Growth rate had decreased in the outer cortex of the ventral and dorsal bone sides due to higher organization of bone tissue and decreased vascular density (Fig. 3C), but vascular density is still high medially and laterally (Figs. 2, 3B, D), indicating that the individual was not fully grown. During the recorded growth period, this individual grew on average (see Materials and Methods) at a daily rate of ca. 16.0 $\mu\text{m}/\text{day}$ (assuming 3 years of fast growth).

Dorsal Rib—The shape of the cross-sections taken from the dorsal rib (SMNS 92130) changes from the proximal to the distal part from roundish-triangular to elliptical (Fig. 5A–B). Over all, the area accommodating the prominent ventral ridge is concave, whereas the other margins are convex or straight. The rib samples all share a spongy inner structure (Fig. 5A–B, F–G). The spongiosa consists internally of large central erosion cavities connected by secondary trabeculae forming a medullary region. The medullary region grades into a remodeling zone that is

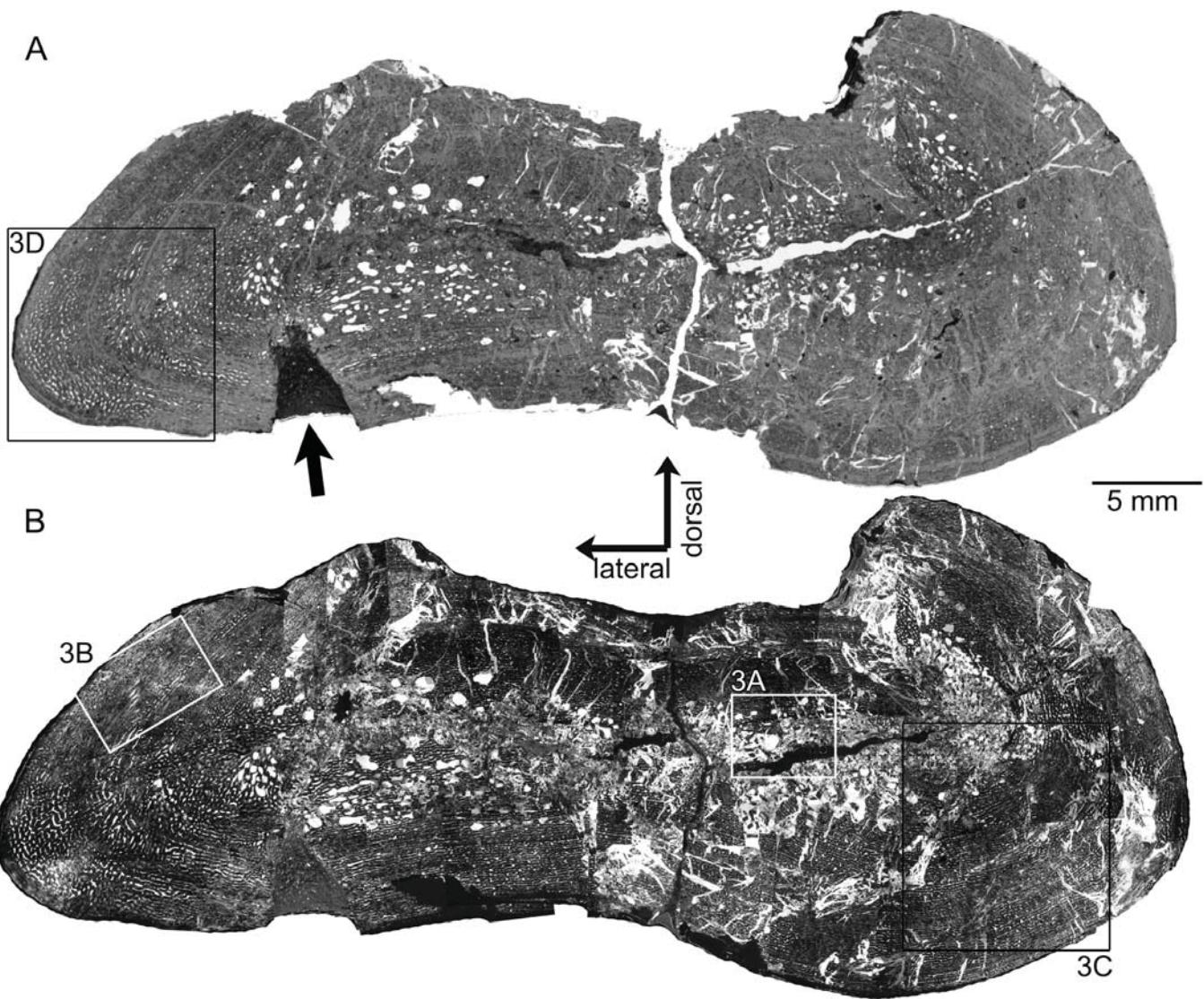


FIGURE 2. Cross-sections of the femur of *Batrachotomus kupferzellensis* (SMNS 90509). **A**, midshaft cross-section in plane polarized light. Ventrolaterally, a funnel-shaped crack reaches deep into the cortex (black arrow); **B**, composite photograph of midshaft cross-section under crossed nicols depicting the mainly laminar vascular organization. The rectangles correspond to the microphotographs depicted in Figure 3.

characterized by smaller erosion cavities transforming locally into secondary osteons. Scattered erosional cavities reach far into the outer cortex, mainly in a lateromedial direction (Fig. 5A–B). Vascularization is low and consists of small, simple vascular canals and few primary osteons all arranged longitudinally (Fig. 5F). The inner cortex, if visible between the erosional cavities, consists of parallel-fibered bone tissue. In the outer cortex, higher-organized parallel-fibered bone tissue grades into lamellar bone, which is stratified by numerous rest lines. Additionally, the primary bone tissue in the outer cortex is dominated by long Sharpey's fibers and shorter fibers (Fig. 5G–H). Osteocyte lacunae are numerous but remain small. The middle to outer rib cortex is stratified by LAGs. At least 11 LAGs are counted in the proximal section, which reveals according to Waskow and Sander (2014) the most complete growth record in the rib. The last five LAGs deposited in the outer cortex are more closely spaced than the LAGs in the middle cortex (Fig. 5A), indicating a reduction in growth rate.

Gastralium—A part of a gastralium was thin-sectioned three times along its shaft. The cross-sections are all elliptical (Fig. 5C–D). All three samples show large de-central medullary regions that contain large erosion cavities connected by secondary trabeculae. Mainly towards the mediolateral side, smaller erosion cavities are scattered in the cortex. The bone tissue of the gastralium is avascular and consists of highly organized parallel-fibered bone interspersed with short fibers (Fig. 5I). Osteocyte lacunae are very small but numerous. The cortex is stratified by numerous rest lines.

DISCUSSION

The three elements of *Batrachotomus* clearly demonstrate interelemental histovariability. The femur indicates fast growth by the presence of fibrolamellar bone tissue in a laminar to (sub-)plexiform organization, whereas rib and gastralium show low-vascularized to nearly avascular lamellar-zonal bone tissue

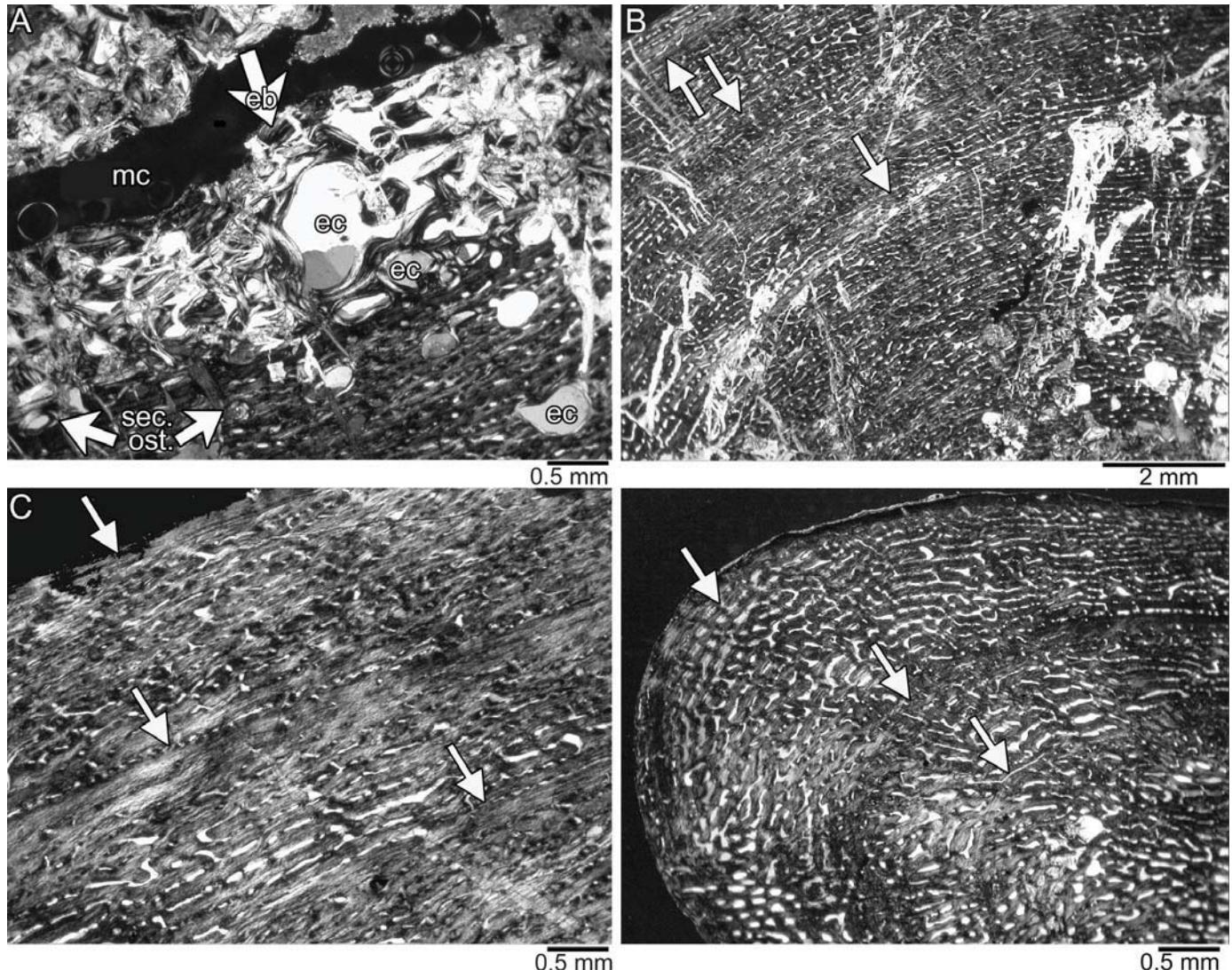


FIGURE 3. Details of medulla and annual growth cycles consisting of broad zones and narrow/thin annuli in femur (SMNS 90509) of *Batrachotomus kupferzellensis*. **A**, area of medulla with scattered erosion cavities reaching into the primary cortex at its margin under crossed nicols. The medullary cavity is partially lined by a layer of endosteal bone; **B**, growth marks in the medial half under crossed nicols; **C**, growth cycles in the dorsal half under crossed nicols; **D**, growth cycles in the lateral half in plane polarized light. **Abbreviations:** eb, endosteal bone; ec, erosion cavities; mc, medullary cavity.

type and the presence of fibers all over the primary cortex. Sauropodomorph dinosaurs such as *Plateosaurus* and *Camarasaurus* also show fibrolamellar bone tissue in their long bones and zonal primary bone dominated by fibers in their ribs (N.K., pers. observ., 2007; Waskow and Sander, 2014). Differences in the annual growth mark count (three growth marks in the femur vs. 11 growth marks in the rib) are related to the fact that different individuals were sampled representing different ontogenetic stages with different individual ages. Based on the femur histology, our study documents that *Batrachotomus* had the ability to grow very fast and reached its large body size within a few years and not by protracted longevity as do most pseudosuchians (including extant crocodylians).

Bone histological data of dinosaurs and pterosaurs are numerous, and all support the general statement of Ricqlès et al. (2003) that ornithodirans formed FLB throughout most of their ontogeny, indicating sustained high growth rates. Fast growth rates in ornithodirans throughout most of ontogeny were also supported by Cubo et al. (2012). Data on archosauromorphs,

archosauriforms, and pseudosuchian archosaurs, however, are still rare (and less well understood) but so far show a variety of bone tissues and vascular systems, resulting in a mixture of bone tissue patterns (Botha-Brink and Smith, 2011). The primary bone tissue type of non-ornithodiran archosauromorphs can be characterized (with a few exceptions, see below) as lamellar-zonal bone tissue type/LZB (Ricqlès et al., 2003, 2008; Botha-Brink and Smith, 2011; Werning and Irmis, 2011; Ezcurra et al., 2014; Mukherjee, 2015; Veiga et al., 2015; Werning and Nesbitt, 2016). Differences with modern reptiles that also grow with LZB are mainly related to vascularity (density and organization) and a higher organization of tissue.

The character mapping (Fig. 6), however, indicates that the last common ancestor of Archosauromorpha already possessed the ability to form FLB in ontogeny (see also Ricqlès et al., 2003, 2008; Botha-Brink and Smith, 2011; Legendre et al., 2013), with three independent secondary losses (characterized by the formation of LZB only) in stem archosaurs (i.e., *Tritylodon*, *Stenaulorhynchus*, and *Vancleavea*) and one or two times in the

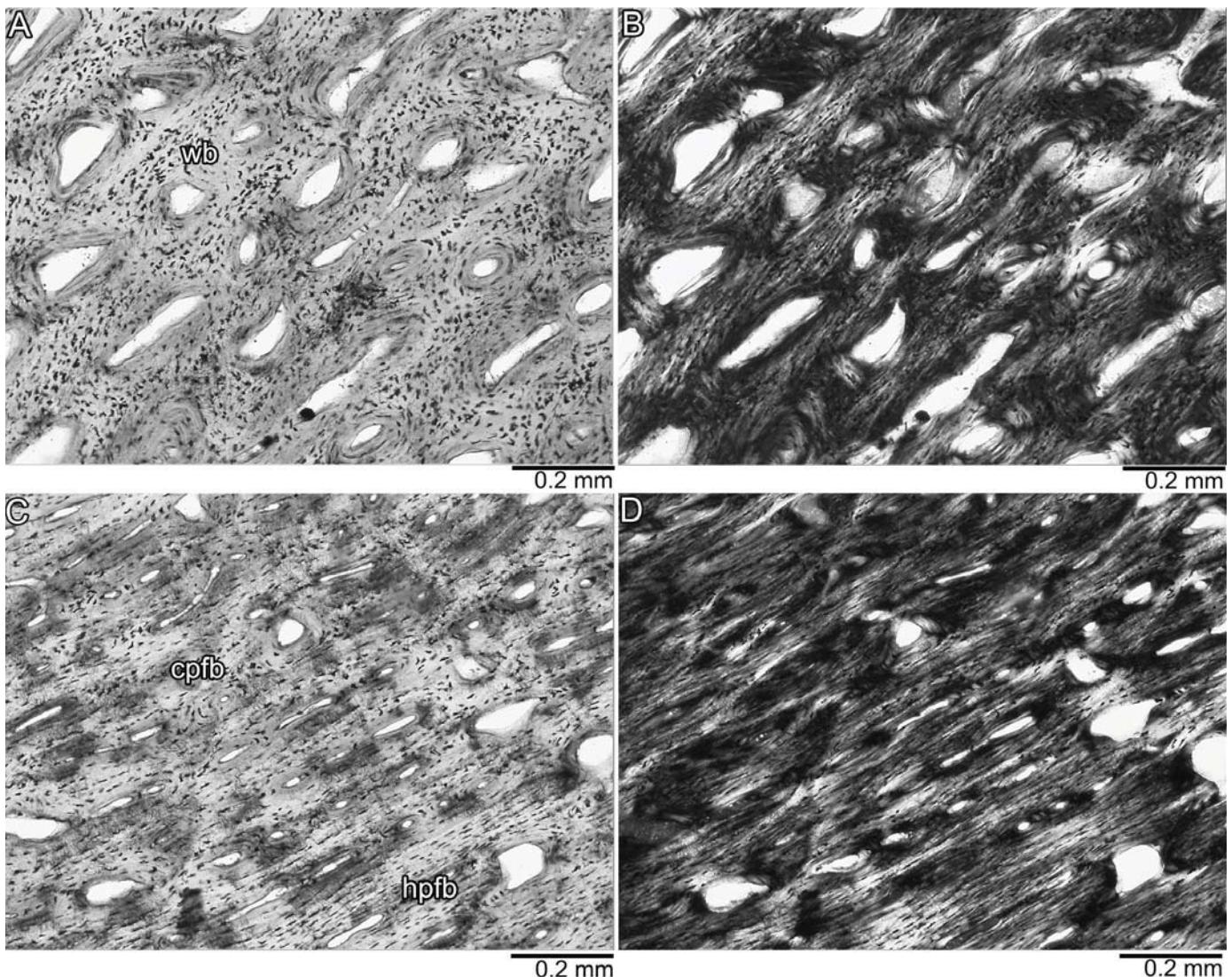
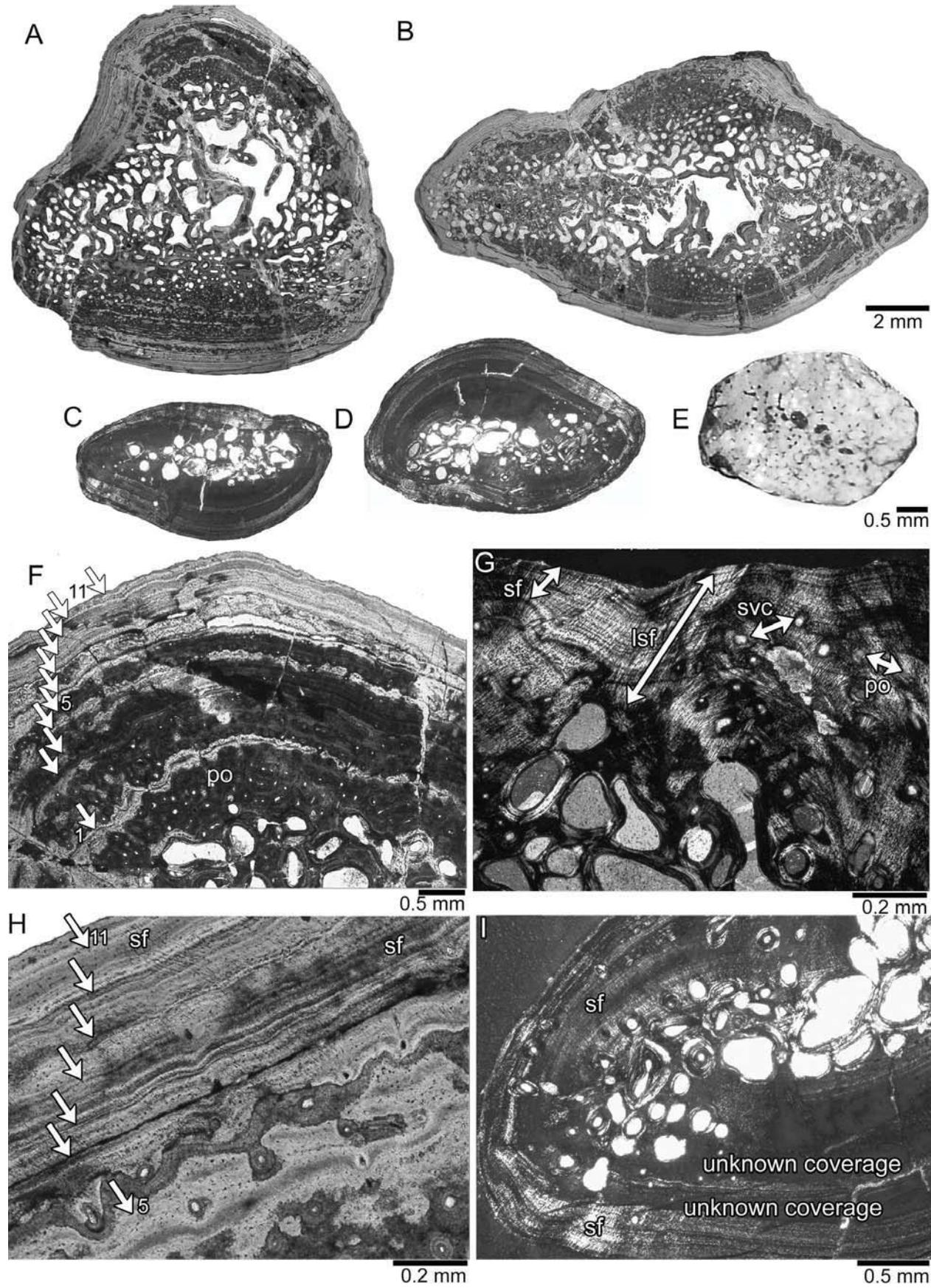


FIGURE 4. Details of primary bone tissue of femur (SMNS 90509) of *Batrachotomus kupferzellensis*. **A, B**, primary bone tissue of the inner cortex consisting of woven-fibered bone and primary osteons in plane polarized light (**A**) and under crossed nicols (**B**). Note the numerous round osteocyte lacunae accumulated in the woven-fibered bone. **C, D**, primary bone tissue of the middle cortex consisting of coarse parallel-fibered bone and higher-organized parallel-fibered bone in plane polarized light (**C**) and under crossed nicols (**D**). **Abbreviations:** **cpfb**, coarse parallel-fibered bone; **hpfb**, higher-organized parallel-fibered bone; **wb**, woven bone.

crown group (i.e., Crocodylomorpha). Here, the presence of FLB in *Terrestrisuchus* indicates a more complex history (see below). For the clade including Erythrosuchidae and Archosauria, the character evolution is ambiguous: if the last common ancestor formed FLB only in early ontogeny (as presumed for the last common ancestor of Archosauromorpha), the ability to grow FLB for a longer period of time (indicating a prolonged fast growth) evolved six times independently in Erythrosuchidae, *Chanaresuchus* (Proterochampsia), Ornithodira, *Effigia* (Poposauridae), basal Loricata (i.e., *Batrachotomus* and *Postosuchus*), and *Terrestrisuchus* (Crocodylomorpha). In contrast, if the last common ancestor of Erythrosuchidae and Archosauria already formed FLB for a longer period of time, this ability was secondarily reduced to early ontogeny four times: in *Euparkeria* (Euparkeriidae), *Rutiodon* (Phytosaurs), Aetosauria, and *Luperosuchus* (basal Loricata). Permuting the character states across the tree shows that the original distribution of growth patterns (defined by bone tissue structure) is

more parsimonious (10 steps for both topologies) than in 95% of all randomized data set (Fig. 6). In consequence, the bone tissue structure shows a clear phylogenetic signal.

Femoral histology of *Batrachotomus* differs from pseudosuchians such as aetosaurs, phytosaurs (when considered as pseudosuchians), and many crocodylomorphs (including marine forms from the Jurassic; see Hua and Buffrénil, 1996) by the general presence of laminar to (sub-)plexiform FLB, resulting in a fast, but periodically interrupted growth rate in the recorded time. *Batrachotomus* reached 87% of its maximum known size (corresponding to ~5.6 m body length) within 3 years, which is contrary to, for example, phytosaurs and aetosaurs that take well over 10 years to attain their maximum size (Ricqlès et al., 2003). *Batrachotomus* shares with other pseudosuchians, such as the poposaurid *Effigia* (Nesbitt, 2006), the rauisuchid *Postosuchus*, and the crocodylomorph *Terrestrisuchus* (Ricqlès et al., 2003), a prolonged deposition of FLB (beyond the first one or two inner growth cycles) and therefore an increased



growth rate. The latter still differ by their vascular system, which shows a mainly longitudinal orientation of vascular canals, whereas that of *Batrachotomus* is dominated by a laminar to (sub-)plexiform organization. *Postosuchus* and *Effigia* further form secondary osteons and have an EFS deposited in their outer cortex (Ricqlès et al., 2003; Nesbitt, 2006), indicating that ontogenetically older individuals were sampled. The lack of an EFS as well as of secondary osteons in the *Batrachotomus* femur could be related to the relatively young age of the individual sampled. Further, *Postosuchus* has a much higher preserved number of growth cycles (20 in the humerus; Ricqlès et al., 2003), when compared with *Batrachotomus*, whereas in *Effigia* the number of annual growth cycles is similar (around six growth cycles in the femur according to Nesbitt, 2006). By contrast, the sample of *Terrestrisuchus* clearly originated from a young individual, as is indicated by the low number of growth marks (two LAGs) and by the lack of any remodeling and an EFS (Ricqlès et al., 2003), similar to the femur sample of *Batrachotomus*. The calculation of the daily growth rate revealed 14.52 $\mu\text{m}/\text{day}$ for *Postosuchus* (Legendre et al., 2013), 11.3 $\mu\text{m}/\text{day}$ for *Proterosuchus* (Botha-Brink and Smith, 2011), 7–10 $\mu\text{m}/\text{day}$ for *Terrestrisuchus* (Padian et al., 2004), and around 16.0 $\mu\text{m}/\text{day}$ in *Batrachotomus*. The high growth rate documented in the femur of *Batrachotomus* might be related to its young age, whereas one has to consider that growth rate decreases with further age (see Erickson, 2005). *Batrachotomus* is so far unique from the others, because it is the only member of Pseudosuchia growing with laminar to (sub-)plexiform FLB until over two-thirds of maximum body/femoral length is reached.

A bone tissue structure with broad growth zones and narrow annuli as well as fast growth in early ontogeny is more typical for ornithodirans. Likewise, Ornithodira typically grew with FLB, in which the growth rates of non-avian dinosaurs range from 3 to 24 $\mu\text{m}/\text{day}$ (Sander and Tückmantel, 2003), with 10.5 $\mu\text{m}/\text{day}$ in the sauropod *Apatosaurus* (Curry, 1999) and 7.6 $\mu\text{m}/\text{day}$ in the prosauropod *Plateosaurus engelhardti* (this study; femur 1 of Klein and Sander, 2007). However, these growth rates overlap with those found for some pseudosuchians (independent of whether they grew with FLB or LZB, see above), indicating that growth rates (in contrast to the bone tissue structure itself) may not be a good proxy for phylogenetic or physiological analyses.

However, the comparison of growth rates of extinct vertebrates remains difficult for many reasons, including methodical problems with the calculation itself. Further problems are related, for example, to an unclear number of annual growth cycles due to loss of inner cycles or how the annual growth marks are counted, that is, whether all annual growth cycles are considered (average growth rate) or only those of juvenile growth or those during fast growth periods, respectively. Further methodological problems concern differences in cortex thickness around the cross-section due to natural shape and postburial compaction or to the number of days per year that are considered for the period of active growth. A second problem concerns the wide range of growth rates of a tissue type resulting in an overlap of growth rates of different tissues (Starck and Chinsamy, 2002; Montes et al., 2010), and finally, the problem due to “substantial variation [...] among different elements of a single individual and within a single bone type” (Botha-Brink and Smith,

2011:1250; see also Woodward et al., 2014). Such distinct variations are also supported by the differences in histology between the femur and the rib and gastralia of *Batrachotomus*.

Based on the current data situation, however, *Batrachotomus* and some other pseudosuchians represent an exception from the observation made by Montes et al. (2010) and Cubo et al. (2012), who found a successive decrease in bone growth rates from the last common ancestor of Pseudosuchia to extant crocodiles. However, the common high growth rates and the possibility to grow with FLB in early archosauromorphs and pseudosuchians support the hypothesis of Ricqlès et al. (2003, 2008) who stated that “reaching and maintaining very high growth rates through ontogeny could have been a basal characteristic of archosauriforms.” The reason why some pseudosuchians grow faster than others, however, remains unclear. Possible triggers for fast growth in *Batrachotomus* might be in response to environmental parameters (Botha-Brink and Smith, 2011; Botha-Brink et al., 2016), respiration and metabolic rates (Cubo et al., 2012; Seymour et al., 2004), large body size (Padian and Horner, 2004), a possible earlier onset of sexual maturity (Karkach, 2006), or an erect stance combined with an active predatory life style (Benton, 1984; Seymour et al., 2004). For instance, in an unstable environment, fast growth and earlier maturity may have been favorable (Botha-Brink et al., 2016), which is in agreement with the supposed habitat of *Batrachotomus*. In the Kupferzell locality, fluctuating growth marks in the temnospondyl *Gerrothorax pulcherrimus* have been interpreted as evidence for unstable environmental parameters (Witzmann et al., 2012) so that the fast growth rates present in *Batrachotomus* may have been an advantage to an apex predator niche in the ecosystem (Botha-Brink et al., 2016). Thus, besides phylogenetic constraints, the bone tissue of *Batrachotomus* probably includes an adaptational signal, as was suggested several times before (Ricqlès et al., 2003, 2008; Botha-Brink and Smith, 2011; Veiga et al., 2015).

The rib and gastralia of *Batrachotomus* both follow the lamellar-zonal pattern and do not show FLB. However, in both elements, the tissue consists largely of short fibers. The inner cortex of the dorsal rib samples is built of low-vascularized parallel-fibered tissue interrupted by widely spaced LAGs. The outer cortex consists of avascular tissue containing several closely spaced LAGs. The proximal rib sample reveals a reduction in growth rate, indicated by a closer spacing of LAGs after LAG 6. The comparison of the rib of *Batrachotomus* with several modern taxa (lepidosaurs, archosaurs, and mammals) supports the results of Canoville et al. (2016) that rib microstructure is largely related to body size (and to a lesser amount to life style), because *Batrachotomus* shares with most larger taxa the presence of a spongiosa surrounded by a ring of compact cortex (Canoville et al., 2016).

So far, only gastralia of aquatic vertebrates have been histologically studied (summarized in Klein and Scheyer, 2017), all of which are more osteosclerotic when compared with that of *Batrachotomus*. For comparison, we examined the midshaft break of a gastralia of the terrestrial prosauropod dinosaur *Plateosaurus* (Fig. 5E). The microstructure is also much more

← FIGURE 5. Histology and microanatomy of rib and gastralia of *Batrachotomus kupferzellensis*. **A**, composite of proximal cross-section of dorsal rib (SMNS 92130) in plane polarized light; **B**, composite of distal cross-section of dorsal rib (SMNS 92130) in plane polarized light; **C**, cross-section of proximal gastralia (SMNS 92131) under crossed nicols; **D**, cross-section of distal gastralia (SMNS 92131) under crossed nicols; **E**, cross-section (natural break) of a gastralia of *Plateosaurus* (SMNS F5). **F–H**, histological details of dorsal rib samples (SMNS 92130). Note the spongyous inner structure and the large amount of fibers in the primary bone tissue; **F**, single-headed arrows mark LAGs in the proximal rib sample in plane polarized light; **G**, transitional area between medullary region and primary tissue largely made of fibers under crossed nicols; **H**, transition between inner and outer cortex where LAGs become more closely spaced in plane polarized light; **I**, histological details of the gastralia (SMNS 92131) depicting the spongyous inner and primary tissue made of short fibers under crossed nicols. **Abbreviations:** **ISf**, long Sharpey's fibers; **po**, primary osteons; **ssf**, short fibers; **svc**, simple vascular canal.

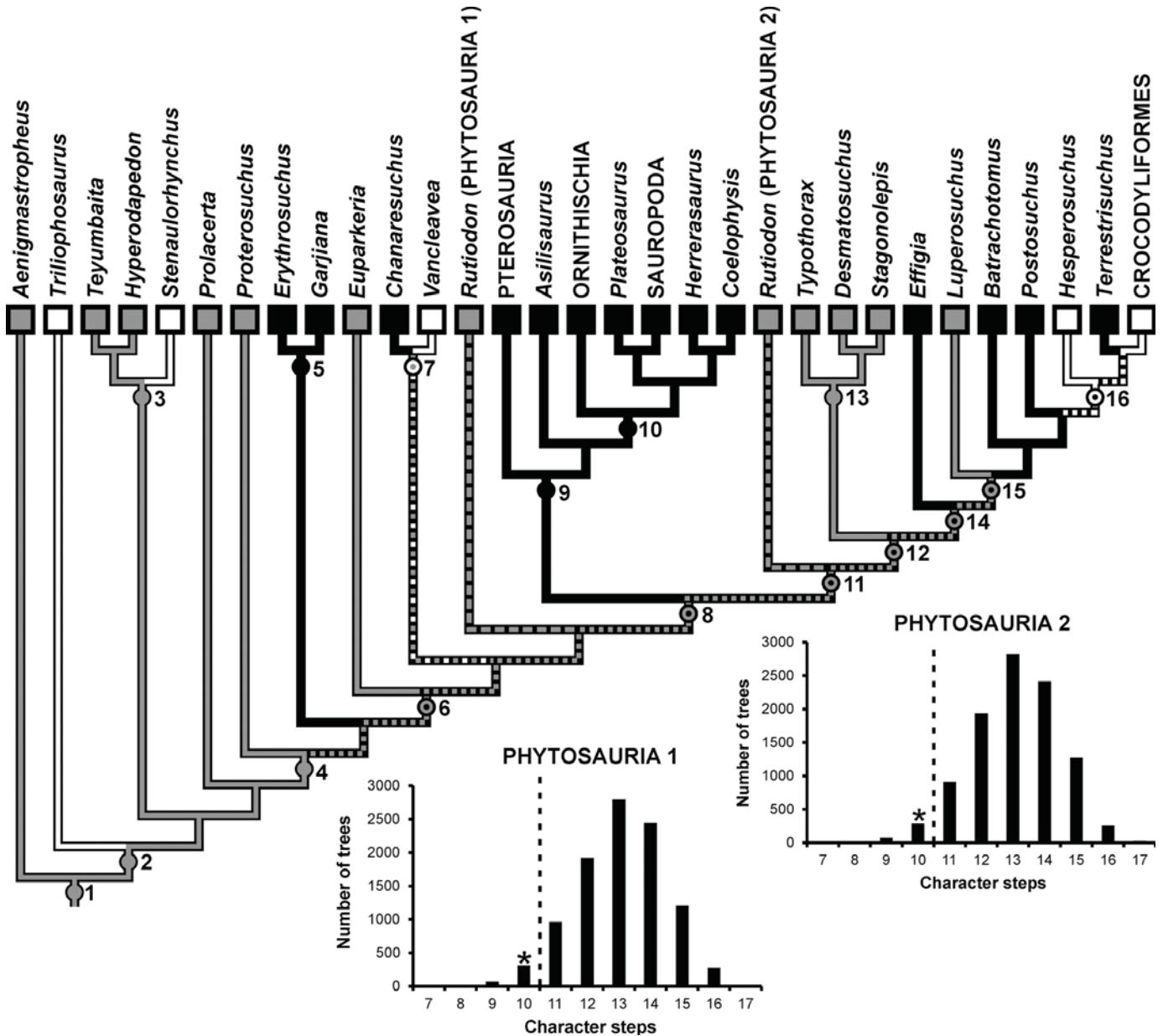


FIGURE 6. Evolution of growth patterns (defined by bone tissue structure) in basal archosauromorphs (with two alternative positions for phytosaurs, gray dashed lines) for which histological data are available. 1, Archosauromorphia; 2, Crocodaformes; 3, Rhynchosauria; 4, Archosauriformes; 5, Erythrosuchidae; 6, Eucrocopoda; 7, Proterochampsia; 8, Archosauria; 9, Ornithodira; 10, Dinosauria; 11, Pseudosuchia; 12, Suchia; 13, Aetosauria; 14, Paracrocodylomorpha; 15, Loricata; 16, Crocodylomorpha. White boxes indicate growth with only LZB, gray boxes indicate growth with FLB early in ontogeny, which then switches to LZB, and black boxes indicate fast growth with FLB over a longer period. Bar charts below phylogeny show the result of the character permutation across the tree for two alternative positions of phytosaurs. Asterisks mark the number of character steps of the original analysis; dashed lines mark the 95% threshold for the phylogenetic signal.

compact and lacks a comparable cancellous inner structure to that of *Batrachotomus*.

The large amount of fibers in the rib and gastralia of *Batrachotomus* is striking. The long fibers in the rib samples run through different growth layers (Fig. 5G) and most likely are Sharpey's fibers, which represent muscle and tendon attachments of gross morphology. The short fibers that are visible in the rib samples (Fig. 5A–D) and all over the cortex of the gastralia samples may point to an embedding of these elements in the periost (Witzmann, 2009; Konietzko-Meier and Klein, 2013). The high amount of fibers indicate a strong association with thorax musculature, which may have played

a crucial role in costal and gastral breathing (Carrier and Farmer, 2000; Perry and Sander, 2004). In contrast, cervical ribs of sauropod dinosaurs that show a similar presence of short fibers in their cortex are interpreted as ossified tendons (Cerda, 2009; Klein et al., 2012a).

Finally, histological differences between the femur, gastralia, and rib of *Batrachotomus* are remarkable and clearly show that elements to be compared need to be carefully chosen (see Woodward et al., 2014). The understanding of the presence of the high amount of fibers in the rib and gastralia of *Batrachotomus* as well as their spongy inner organization prompts further study and comparison.

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