Unique bone histology in partial large bone shafts from Upper Triassic of Aust Cliff, England: An early independent experiment in gigantism

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Two giant partial bone shafts, possible femora, from the Rhaetian Bone Bed (Upper Triassic) of Aust Cliff in SW England continue to conceal their origin. The most striking characteristic of these bones is their size, showing that dinosaur-like gigantism had already evolved by the Late Triassic. Based on their characteristic, columnar shaft morphology, it was previously suggested they came from a prosauropod or stegosaur. The bone histology of both specimens is very similar: the cortex is always rather thin, not exceeding 10 mm, and is of fibrolamellar type with longitudinal primary osteons. The primary osteons show a rather unusual feature, the development of a secondary osteon inside the primary one. The bone surface in both specimens shows open vascular canals, suggesting that the animals were still growing at the time of death, but an external fundamental system (EFS) is visible in the outermost cortex of specimen BRSMG Cb3870. The external cortex shows dense growth marks, but their annual nature is difficult to ascertain. The bones are probably dinosaurian, as indicated by the fibrolamellar bone, and possibly belong to an unknown basal sauropodomorph lineage. Alternatively, some very large pseudosuchians may have evolved fibrolamellar bone independently as an adaptation for reaching giant size.

Key words: Reptilia, Dinosauria, bone histology, fibrolamellar bone, primary osteon, secondary osteon, Triassic, England.

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Introduction

Identification of fossils can be challenging, especially if only isolated bones or, even worse, incomplete isolated bone fragments are preserved. Such fragments can be significant if they are of an unusual size and/or shape. In total, five partial shafts of large long bones have been found in the historically important Rhaetic Bone Bed near the base of the Westbury Formation (Upper Triassic) at Aust Cliff near Bristol, SW England (Storrs 1994; Galton 2005). The Westbury Formation was deposited in a shallow marine sedimentary environment during a transgressive period of the Westbury Sea, as indicated by finds of a rich fish fauna mainly represented by teeth (summarised by Storrs 1994). Rhaetian fissure fills and cave deposits are also known from SW England, indicating nearby landmasses that were inhabited by large terrestrial animals (e.g., Galton 1998, 2007; Whiteside and Marshall 2008). This is indicated by the find of the basal sauropodomorph *Camelotia borealis* represented by a partial skeleton (femur length of 1008 mm) discovered near the base of Westbury Formation of nearby Wedmore, Somerset (Galton 1998). This skeleton was identified as a basal sauropodomorph (melanorosaurid prosauropod), but is now regarded as a basal sauropod (Yates 2007, 2010).

Two of the long bone shafts were destroyed in November, 1940 but, based on the original unillustrated descriptions (Stutchbury 1850; Sanders 1876; Reynolds 1946), they were tentatively assigned by Galton (2005) to Dinosauria incertae sedis and *Camelotia borealis*. Because of the large size and

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columnar form of the bone shafts, Galton (2005) considered only dinosaurian bones in his comparison. Of the surviving elements, Galton (2005) assigned one to Dinosauria incertae sedis and the other two tentatively to Stegosauria, because of their distinctive columnar shape with an oval cross-section, the width being greater transversely than anteroposteriorly. If this is correct, these specimens would push the fossil record of stegosaurs back into the Late Triassic.

Currently, the earliest evidence for stegosaurs are the footprints and trackways of *Deltapodus brodricki* from the Middle Jurassic (Aalenian) of Yorkshire, NE England (Whyte and Romano 2001; Whyte et al. 2007). The earliest skeletal evidence consists of isolated bones from the Lower and Middle Bathonian of Oxfordshire and Gloucestershire, England (Galton and Powell 1983) and associated bones from the Bathonian of western Siberia (Averianov and Krasnolutskii 2009). Articulated skeletons are known of *Huayangosaurus taibaii* from the Bathonian–Callovian of China (Zhou 1984; Sereno and Dong 1992; Maidment et al. 2006) and of "*Lexovisaurus durobrivensis*" from the early–middle Callovian near, Peterborough, England (Galton 1985; now *Loricatosaurus priscus*, Maidment et al. 2008).

Butler et al. (2006) noted that the Aust Cliff bones lack any stegosaurian synapomorphies, a result of their being weathered fragments, as well as the absence of Early Jurassic stegosaurs, and the small size of all known Triassic ornithischians. They concluded that, although the bones "probably represent fragmentary femora of large dinosaurs (possibly sauropods)", they cannot be identified "with confidence beyond Reptilia indet." (Butler et al. 2006: 627). Irmis et al. (2007: 15) argued that extensive cancellous bone or trabeculae do not provide a phylogenetic signal because it can relate to biomechanics and life history, and they identified the bones as indeterminate Tetrapoda. Maidment et al. (2008: 385), who regarded them as indeterminate reptiles, also noted the presence of other large reptiles, such as thecodontians, in the Late Triassic. As regards the absence of Early Jurassic Stegosauria, the group would have been present at least in the Toarcian as indicated by the earliest occurrence of its sister group, the Ankylosauria (Thompson et al. 2012), the first record of which is a nodosaurid represented by a collection of 30 associated plates of four types from the upper unit of the Kota Formation of the Pranhita-Godavari Valley, India (Nath et al. 2002; for stratigraphy see Bandyopadhyay and Sengupta 2006; Bandyopadhyay et al. 2010; P. Yadagiri, personal communication 2001; S. Bandyopadhyay, personal communication 2012).

While these views may be correct from the point of view of a synapomorphy-based identification, certain taxa such as dicynodonts can be excluded from consideration because they do not have a straight shaft in any long bone. Also the marine reptiles of the Latest Triassic (ichthyosaurs and plesiosaurs) can be excluded from consideration because they do not reach anywhere near the size of the Aust Cliff bone shafts, do not have long straight shafts in their long bones, and differ completely in their histology.

Institutional abbreviations.—BRSMG, Bristol City Museum and Art Gallery, Bristol, UK.

Other abbreviations.—EFS, external fundamental system; LAG, line of arrested growth.

Material and methods

The two large partial bones (BRSMG Cb3869 and BRSMG Cb3870) sampled by us were collected from the Rhaetic Bone Bed of the Westbury Formation at Aust Cliff, SW England. Judging from their straight, columnar shape and large size (Table 1), the specimens most likely represent midshafts of femora (Galton 2005). Measurements are given in Table 1. *Camelotia borealis* was not accessible for histological sampling because it is known only from the holotype femur.

We sampled both bone shafts using the core drilling method described in Sander (2000) and Stein and Sander (2009). The sampling location in BRSMG Cb3870 and Cb3869 was determined by the area of the shaft showing the seemingly best preserved bone surface (Fig. 1A, B, respectively). To obtain the thickest cortex possible, i.e., the optimal growth record, from a core sample, long bones need to be sampled exactly at midshaft (Sander 2000), but this could not be controlled sufficiently in the two Aust Cliff specimens. The drill cores were processed into thin sections and studied with a Leica DMLP microscope at University of Bonn and a Nikon Eclipse E200 Microscope at University of Cape Town.

Table 1. Preserved lengths and circumferences measured and total lengths estimated for BRSMG Cb3869 and Cb3870. Note disagreement with growth mark counts.

Collection number	Preserved length	Circumference	Estimated length	Growth marks
BCM Cb3869	380 mm	430 mm	1100 mm	13-14 annuli
BCM Cb3870	380 mm	373 mm	1000 mm	30-31 LAGs

Results

Notably, both samples show a very similar but rather unusual bone histology (Fig. 2A, B), suggesting that they pertain to the same taxon. The cortex is thin in BRSMG Cb3870, not exceeding 10 mm, and surrounds a large medullary area filled with an extensive web of trabeculae (Fig. 2A), while in BRSMG Cb3869, the cortex is about three times thicker (Fig. 2B). The primary bone is fibrolamellar, consisting of primary osteons in a matrix of woven-fibred bone. Primary osteons are oriented exclusively longitudinally. They are relatively immature in that the vascular canal remains large, and there are only a few lamellae of centripetally deposited bone. Both samples show one striking feature, however, that only becomes apparent upon close inspection, which is that, towards the deeper cortex, many of the primary osteons harbour a secondary osteon (Fig. 3A_1, A_2, B_1, B_2). These second-

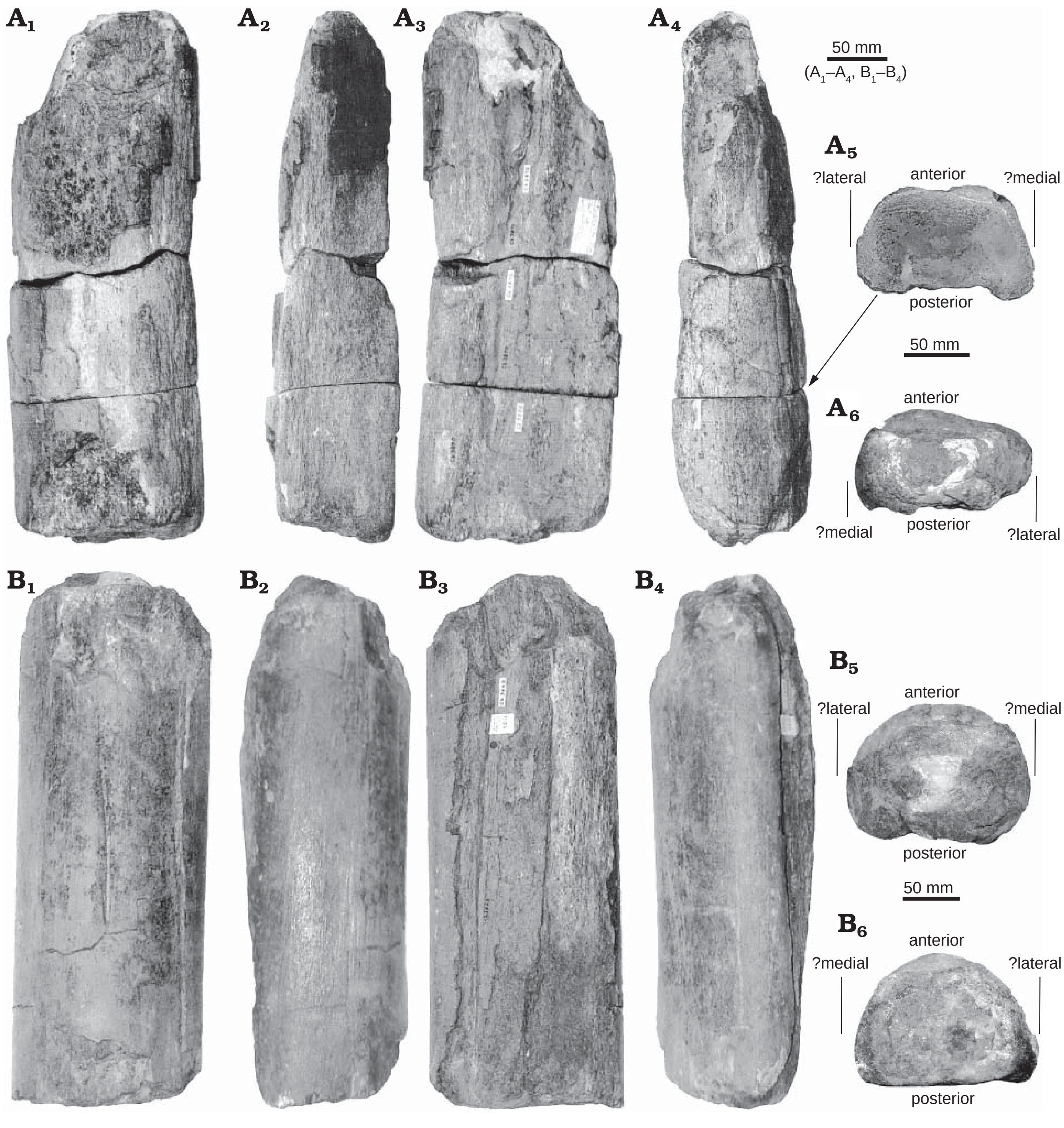
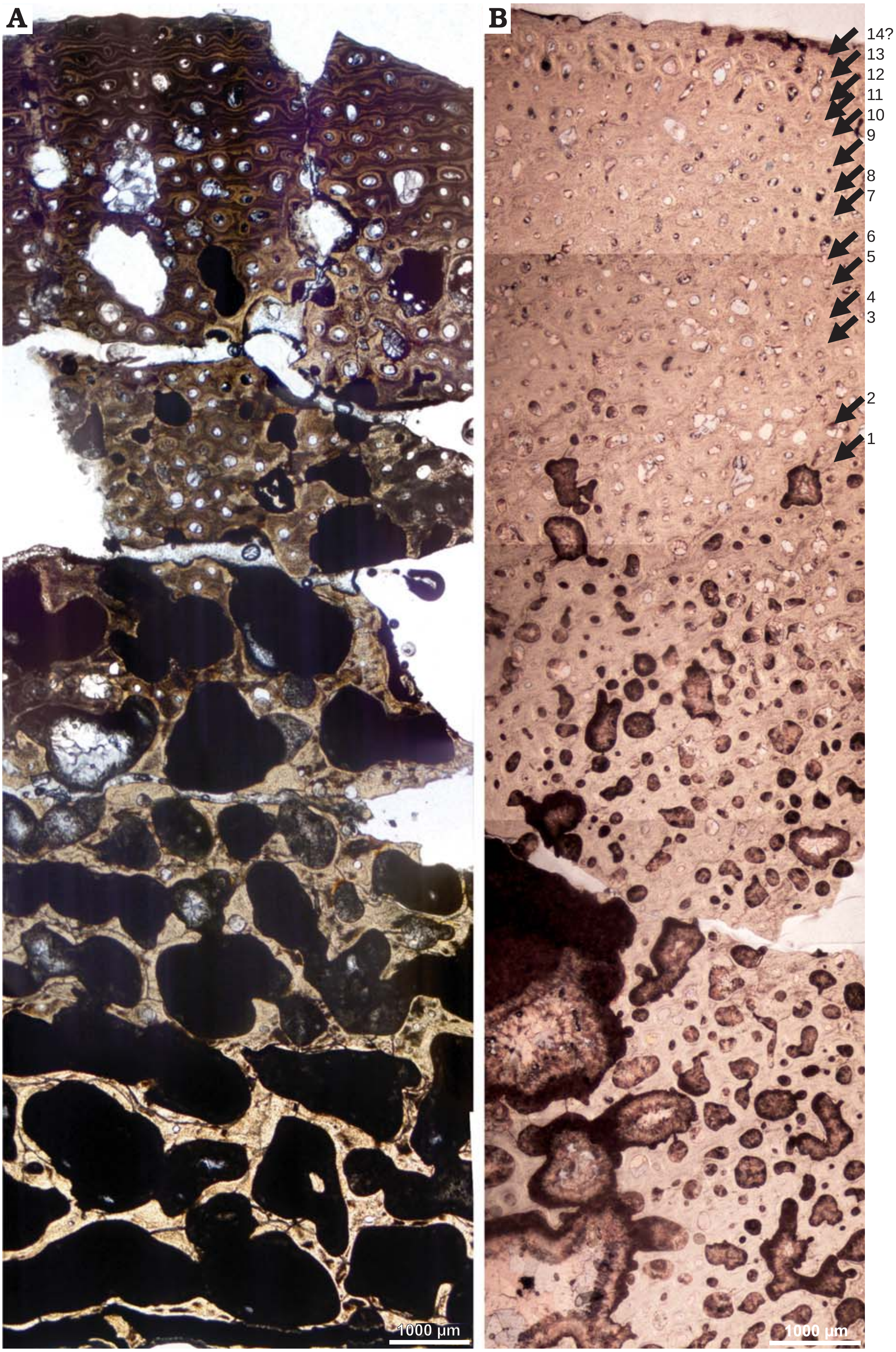


Fig. 1. Photographs in different views of long bone shafts of BRSMG Cb3870 (**A**) and Cb3869 (**B**) from the Westbury Formation of Aust Cliff near Bristol, UK; in anterior (A_1, B_1), ?lateral (A_2, B_2), posterior (A_3, B_3), ?medial (A_4, B_4), proximal (B_5) and distal (A_6, B_6) views; cut and ground surface in distal view (A_5). The specimens represent notably straight shafts of large long bones, presumably femora. Core sample location indicated by the black circle. Note that in BRSMG Cb3870 only a small area of outer bone surface is preserved, constraining the sample location. Modified from Galton (2005).

ary osteons may also be termed immature in that only a few lamellae are present (arrows in Fig. 3A_1, A_2, B_1, B_2). The secondary osteon is clearly separated from the primary osteon surrounding it by a resorption line, which appears slightly undulating and, unlike a LAG (line of arrested growth), cuts into structures of the previously deposited tissue of the primary osteon (Fig. 3A_1, A_2, B_1, B_2). Erosion cavities decrease in size towards the bone surface (white arrow in Fig. 3B_5) and, in most cases, show an at least partial thin lining of lamellar bone (black arrow in Fig. 3B_5).

In BRSMG Cb3870, an almost avascular outermost cortex is visible (Figs. 2A, 3B_3), which still retains a few vascu-


A
B
14?
13
12
11
10
9
8
7
6
5
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3
2
1
1000 µm
1000 µm

lar canals opening to the surface. Just below the bone surface, the specimen shows 10 or 11 distinctive and closely spaced growth marks that form a characteristic convoluted pattern because of their incorporation of the superficial blood vessels during growth (Fig. 3B$_4$). These LAGs may represent a rather thick external fundamental system (EFS; Fig. 3B$_4$), but this is difficult to determine because of the thinness of the cortex. Alternatively, they may represent slow growth in a zonal pattern. There are 30 or 31 LAGs in total (Fig. 3B$_3$), including the 10 or 11 below the bone surface (Fig. 3B$_4$), but the annual nature of these LAGs is difficult to evaluate because of their close spacing.

BRSMG Cb3869 represents a younger individual. The drill bit did not penetrate the entire cortex, the recovered thickness being about 10 mm. However, the inner to mid cortex appears cancellous due to numerous erosion cavities (Fig. 2B), suggesting that it was not much thicker. Erosion cavities are scarce and unfilled in the outer cortex (arrows in Fig. 3A$_3$) and more frequent in the inner cortex. Here, the cavities are either filled by a thin line of lamellar bone or remain unfilled. The secondary osteons inside the primary osteons are filled with lamellar bone only up to half of their diameter (Fig. 3A$_3$), giving them the characteristic immature appearance as noted above. The outermost cortex is less vascularised with simple longitudinal vascular canals, some of which are open to the bone surface, suggesting that the animal was still growing slowly at the time of death. There appears to be an annulus in the outermost cortex, which is quite broad and has a stripey appearance, similar to an accumulation of growth marks, and may thus be interpreted as an EFS (Fig. 3A$_3$). Growth marks are much less distinctive in BRSMG Cb3869 than in BRSMG Cb3870. Up to possibly 13 or 14 annuli (arrows in Fig. 2B) occur in the mid to outer cortex of this sample (number 14 may be an EFS).

Based on their bone histology, the two partial femoral shafts are likely from the same species, one being somatically mature and the other younger.

Discussion

Life history variation.—Based on shaft circumference, the histologically younger BRSMG Cb3869 is slightly larger than histologically older BRSMG Cb3870 (Table 1). However, circumference measurements may be in error in the latter because extensive pre-burial erosion and/or weathering resulted in partial loss of the cortex. The differences between the two specimens may, however, also be a result of different growth histories. BRSMG Cb3869 formed annuli instead of LAGs, i.e., growth was slowed down periodically but not arrested at any time as far as the record shows in the unremodelled primary bone. Continuous, although not even, growth may impact on the specimen's terminal size, e.g., periodically arrested growth results in smaller body size than periodically slowed down growth. This is supported by the distinctly thicker cortex in the younger, annuli-forming specimen BRSMG Cb3869. The presence of LAGs in the one and of annuli in the other specimen may be (i) an ecological signal, (ii) sexual dimorphism, or (iii) intraspecific variation.

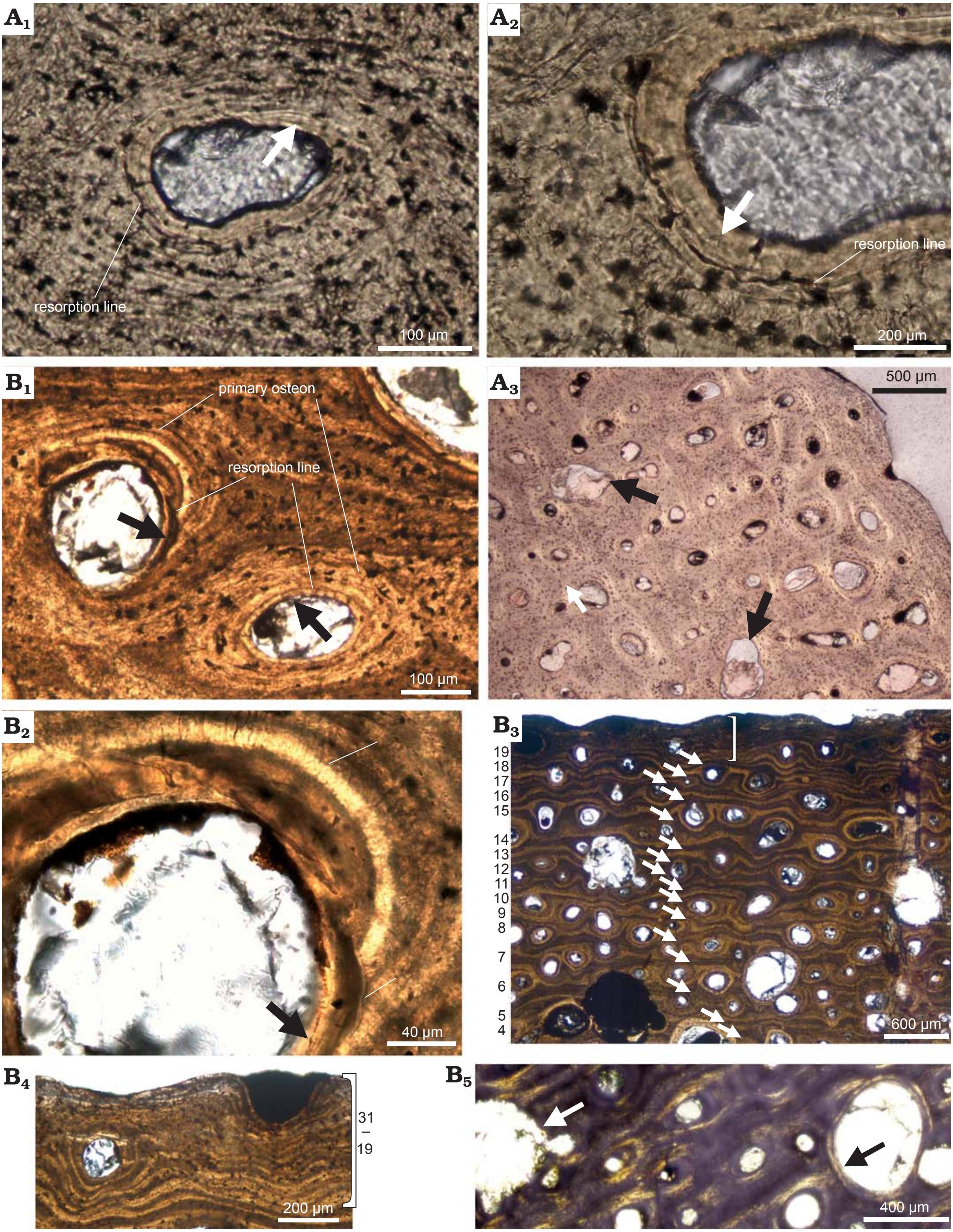
← Fig. 2. Bone histology of long bone shafts from the Upper Triassic near Bristol, UK. **A**. BRSMG Cb3870, a thin cortex, consisting of fibrolamellar bone with longitudinal vascular architecture. The deeper part of the cortex shows abundant erosion cavities and secondary osteons, grading into cancellous bone. **B**. BRSMG Cb3869, the cortex is thicker and has less distinctive growth marks but shows the same histology as BRSMG Cb3870. Up to 13 or 14 annuli (arrows) occur in the middle and outer cortex of the primary compact bone. The deep cortex becomes increasingly cancellous as a result of abundant large erosion cavities.

Regarding hypothesis (i), BRSMG Cb3869 may have experienced more agreeable, consistent weather conditions than BRSMG Cb3870. Wikelski and Thom (2000) described changes in the growth history of an individual of the marine iguana *Amblyrhynchus christatus* from Galapagos, the original body length of which decreased about 20% in only two years as a result of low availability of food during "El Nino" events and resumed growing after environmental conditions normalised.

Regarding hypothesis (ii), female reproduction requires a vast amount of energy and, thus, growth may be arrested during reproduction periods. Egg-shelling requires additional calcium, which in crocodilians is resorbed from the bones (e.g., Wink and Elsey 1986; Wink et al. 1987; Schweitzer et al. 2007), hence the resorption (erosion) cavities. The latter are indeed extensive in the LAG-forming specimen BRSMG Cb3870, implying a possible female sex. Linking LAGs with reproduction would imply annual reproduction cycles, which does occur in wild crocodiles but their reproduction frequency is usually rather variable from annually to every 2–5 years (Joanen and McNease 1971; Lance 1989; Kofron 1990).

Uniqueness of the bone tissue of the Aust Cliff specimens.—The cortical bone histology of the long bone shafts from Aust Cliff is unlike any described in the literature so far. Since the histology of both bones is the same, showing the same peculiarities, they very likely pertain to the same taxon. While the cortex of both bones is rather thin in the sections, this represents only a minimum thickness because of the poorly controlled sampling location. However, Galton (2005) pointed out the rather thin cortex of the Aust Cliff shafts apparent in the terminal fracture surfaces. Only serial sectioning or μCT imaging would resolve the true cortex thickness of these bones.

The uniqueness of the histology lies in the development of the primary and secondary osteons, with the latter developed within the former (Fig. 3A$_1$, A$_2$, B$_1$, B$_2$). Normal secondary osteons, while commonly following preexisting primary vascularity, cut across existing primary osteon boundaries and other existing structures. This is because the cutting cone of normal secondary osteons is roughly the size of primary osteons and thus obliterates the primary osteon. Cutting across primary osteons is only rarely the case in the Aust Cliff bones where the cementing line of the secondary


A1
resorption line
100 µm
A2
resorption line
200 µm
B1
primary osteon
resorption line
100 µm
A3
500 µm
B2
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B3
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
600 µm
B4
31
–
19
200 µm
B5
400 µm

osteon is within the lamellae of the primary osteon. In fact, the cementing line only becomes apparent at close inspection with the compound microcope, using higher magnifications, a nearly closed diaphragm, and a condensor. The cutting cone of the secondary osteons must have been distinctly smaller than usual, and osteoclast activity was influenced by the preexisting lamellae of the primary osteon. In fact, we are unsure whether to call these structures proper secondary osteons or, more descriptively, primary osteons with a two-phase centripetal deposition.

A clue to understanding this remodelling pattern may be the numerous resorption cavities deeper in the cortex, which show a similar thin lining of lamellar bone as the secondary osteons (Fig. 3B$_5$). The secondary osteons inside the primary ones may be part of the same remodelling process acting in the inner cortex, except that it was less extensive in the outer cortex, resulting in only a little resorption before redeposition commenced again (Fig. 4). During a later resorption phase, the unfilled resorption cavities were possibly formed. For the lack of modern examples of the peculiar tissue of the Aust Cliff bone shafts, its exact mode of formation remains difficult to understand.

Histological comparison with other Late Triassic large tetrapods.—Based on morphology and microanatomy, i.e., the large size and the straight shaft of the partial femora and their thin cortex, Galton (2005) suggested affinity of the giant Aust Cliff bones with two types of dinosaurs, namely prosauropods or stegosaurs. A similarly straight shaft is also found in Sauropoda, which had been excluded by Galton (2005) based on their thicker cortex, and in large pseudosuchian archosaurs (Niedźwiedzki et al. 2012). As noted above, the apparent thinness of the cortex may be an artefact of the location of sampling sites and fracture planes. Thus, we will enter into a closer comparison of the histology of the Aust Cliff specimens with these four taxa, namely Pseudosuchia, basal Sauropodomorpha, Sauropoda, and Stegosauria.

← Fig. 3. Detailed bone histology of the femoral shafts from the Upper Triassic near Bristol, UK. **A**. BRSMG Cb3869, primary osteon modified by a secondary osteon that developed inside the primary one; A$_2$, close-up of A$_1$, a secondary osteon within a primary osteon clearly shows a resorption line (white arrows indicate lamellae deposited in the secondary osteon); A$_3$, the outermost cortex poorly vascularized and containing unfilled erosion cavities (black arrows). **B**. BRSMG Cb3870, resorption cutting through the lamellae of the primary osteon (discordant) or following them (concordant); B$_2$, close-up of B$_1$, the resorption line of the secondary osteon clearly cuts through the tissue of the primary osteon (black arrows indicate lamellae deposited in the secondary osteon); B$_3$, up to 19 LAGs (white arrows) occuring in the primary cortex, complemented by 11 or 12 in the external fundamental system (B$_4$); B$_5$, erosion cavities showing a thin lining of lamellar bone (black arrow) or none at all (white arrow). Image in polarised light.

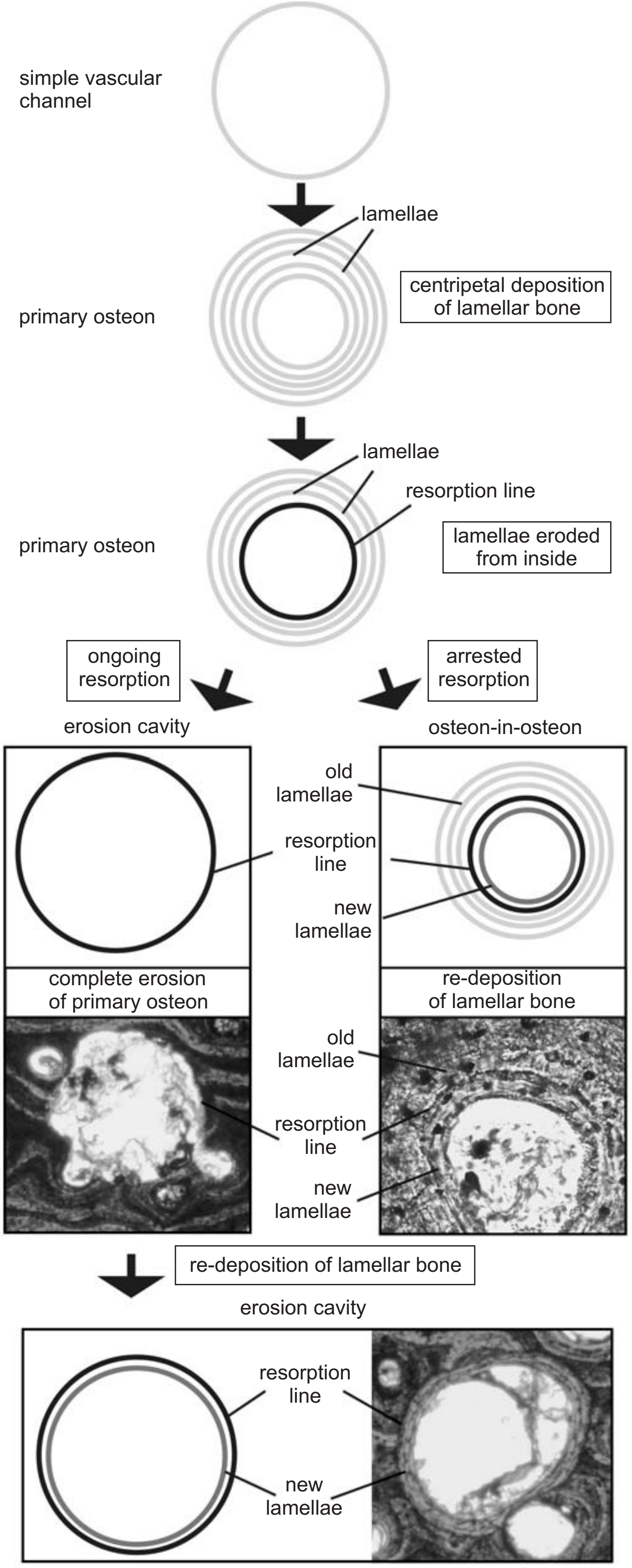

Fig. 4. Flow diagram explaining the peculiar patterns of remodelling seen in the Aust Cliff bones BRSMG Cb3869 and Cb3870. In a simple vascular canal, lamellar bone is deposited centripetally forming a primary osteon. In the Aust Cliff shafts, the inner lamellae of this primary osteon are later resorbed from the inside. When erosion stops before the entire primary osteon is resorbed, leaving a resorption line within the primary osteon, new lamellae can be deposited and a secondary osteon forms within the primary one. With ongoing resorption, an erosion cavity forms, the size of which exceeds the one of the former primary osteon. When resorption stops, deposition of lamellar bone can resume.

The histological diversity of Triassic crurotarsan archosaurs has been described comprehensively by de Ricqlès et al. (2003, 2008), including large-bodied forms such as phytosaurs and rauisuchians. Longitudinal vascular canals, primary and secondary osteons as well as numerous growth marks are shared with the Aust Cliff bones. A modification of the fibro-lamellar bone complex, which is characterised by not highly developed woven bone, occurs in the deep cortex, i.e., during early development, of some archosaurs (de Ricqlès et al. 2003, 2008). Among basal sauropodomorphs, the histology of Plateosauridae such as *Plateosaurus* (Klein and Sander 2007) and *Massospondylus* (Chinsamy 1993) is well known and differs from that of the Aust Cliff specimens in having laminar fibrolamellar bone and few secondary osteons. The histology of other basal sauropodomorphs is similar to that of Plateosauridae (e.g., de Ricqlès 1968; Chinsamy 1993; Klein and Sander 2007). The Aust Cliff bones are also unlike Sauropoda, which uniformly have laminar fibrolamellar bone usually lacking growth marks (Sander 2000; Klein and Sander 2008; Sander et al. 2011). This histology is even seen in the earliest sauropods such as the large cf. *Isanosaurus* from the Late Triassic of Thailand (Buffetaut et al. 2000, 2002; Sander et al. 2004). Finally, stegosaur bone histology resembles that of the Aust Cliff bones in having fibrolamellar bone with predominantly longitudinal primary osteons (Redelstorff and Sander 2009; Hayashi et al. 2009), but stegosaurs lack the peculiar secondary osteons inside the primary osteons and show normal secondary osteons instead.

The Aust Cliff bones simply do not offer a good match with any previously described histologies. The presence of fibrolamellar bone would suggest dinosaurian affinity, possibly with an unknown lineage of sauropodomorphs. Alternatively, very large pseudosuchian archosaurs may have had a bone histology different from that described for other non-dinosaurian archosaurs, particularly the smaller rauisuchians, by de Ricqlès et al. (2003, 2008). Pseudosuchian affinities of the Aust Cliff bones have gained in credibility because a very large one (femur length ca. 700 mm) has recently been described from Poland, *Smok wawelski* (Niedźwiedzki et al. 2012), that occurs in sediments only slightly older than the Westbury Formation. Previously, Late Triassic non-dinosaurian archosaurs of such large size (up to 6–7 m), with pillar-like hind limbs, had been known only from Argentina (Bonaparte 1981). Very large size in such non-dinosaurian archosaurs could have evolved by an increase in growth rate, resulting in the fibrolamellar bone seen in the Aust Cliff specimens. Testing this hypothesis would require histological sampling of this material. To narrow down the affinities of the large Aust Cliff bones, we furthermore hope that the *Camelotia* material can be histologically sampled in the future.

Conclusions

The unique bone histology of the two sampled partial femoral shafts from the Rhaetian Westbury Formation at Aust Cliff, England, encompasses fibrolamellar bone with longitudinal primary osteons, most of which are modified by secondary remodelling. Growth marks are common as either LAGs or annuli, indicating cyclical growth. In the older specimen, BRSMG CB3870, LAGs become gradually more narrow-spaced towards the bone surface, where they form an EFS. The bone tissue of the younger but slightly larger specimen, BRSMG Cb3869, contains annuli rather than LAGs. This variation in type of growth marks in combination with body size may indicate stronger and weaker interruptions of growth as a response to ecological variation or sexual dimorphism.

Based on the geological age, the bone size and the straight shaft, the affinity of the Aust Cliff bones can only be sought among certain dinosaurs (basal sauropodomorphs, Sauropoda and Stegosauria) or large pseudosuchian archosaurs. However, all sauropodomorphs have a laminar vascular architecture, pseudosuchians lack fibrolamellar bone, and stegosaurs, while having longitudinal primary osteons, lack the secondary modification seen in the Aust Cliff bones. In addition, the fossil record of the latter only begins in the Middle Jurassic, at least 25 Ma years later than the age of the Westbury Formation. While it is clear that the Aust Cliff femora represent an early experiment in a graviportal stance and gigantism, it is unclear at present in which (presumably archosaurian) lineage this experiment took place.

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