

Bone microstructure and relative age of the holotype specimen of the diplodocoid sauropod dinosaur *Suuwassea emilieae*

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We present the first study of bone microstructure in *Suuwassea emilieae*, a diplodocoid sauropod from the Morrison Formation. Although the holotype of *Suuwassea* was recently identified as a subadult, bone histology demonstrates that this individual had reached sexual maturity at approximately 75–80% of maximum adult size. The smaller size of the holotype of *Suuwassea* relative to contemporary sauropods is due to ontogeny rather than a true reflection of adult size. A fully adult individual would have likely been similar in size to a fully adult specimen of *Apatosaurus*. *Suuwassea* has a number of plesiomorphic characters that might have been explained by its supposed early ontogenetic status, and would then have called the validity of the taxon into question. However, our demonstration that it was an adult confirms that these features represent retention of plesiomorphic character states or evolutionary reversals in a derived animal. Additionally, the specimen shows extensive cortical drift and secondary osteon formation related to skeletal loading, which is often obscured by complete remodeling of Haversian systems in sauropod taxa. There are substantial differences in the microstructure across the bone, which could make histologic samples not based upon complete cross sections problematic. *Suuwassea* is one of four currently recognized dicraeosaurid taxa, and this study contributes potential taxonomic characters in sauropod bone microstructure.

Key words: Dinosauria, Sauropoda, *Suuwassea*, histology, Jurassic, Morrison Formation, Montana, USA.

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Introduction

Suuwassea emilieae Harris and Dodson, 2004 is a diplodocoid sauropod from the Upper Jurassic Morrison Formation of Montana. The holotype (ANS 21122), a partial skeleton that includes numerous cranial, axial, and appendicular elements, is currently the only known specimen (Harris and Dodson 2004). In phylogenetic analyses, *Suuwassea* originally created a trichotomous clade Flagellicaudata, as the sister taxon to diplodocids and dicraeosaurids (Harris and Dodson 2004). However, a newly described dentary added three dicraeosaurid characters to *Suuwassea*, so strengthening its placement as a basal dicraeosaurid (Salgado et al. 2006; Whitlock and Harris 2010; Whitlock 2011). This made *Suuwassea* the first dicraeosaurid found on the Laurasian

continent, extending the geographic range for dicraeosaurids substantially (Whitlock and Harris 2010). Even though there is only one specimen, *Suuwassea* has been extensively studied (Harris and Dodson 2004; Harris 2006a–c, 2007; Whitlock and Harris 2010).

The holotype specimen of *Suuwassea* was originally characterized by its small size and was estimated to be approximately two-thirds the size of the fully adult contemporary Morrison sauropods, *Apatosaurus* and *Diplodocus* (Harris 2006b, c). The complete humerus of *Suuwassea* (ANS 21122) measures 752 mm in length and the complete tibia (based on the fibula) is 839 mm. *Apatosaurus* (CMNH 3018) has a humerus measuring 1150 mm and a tibia of 1115 mm (Gilmore 1936). *Diplodocus* (CMNH 94) has a tibia 1006 mm long (Hatcher 1901). Therefore, based on the tibia, ANS 21122

is actually 83% the size of *Diplodocus* and 75% the size of *Apatosaurus* rather than a mere 66%. However, it should be noted that differing allometry of the tibia between these taxa could cause discrepancies in determining absolute size using simple ratios. Further, *Suuwassea* retains a number of plesiomorphic characters (amphiplatyan distal caudals, post-parietal foramen, elongate pedal phalanges with a small, un-compressed ungual). These and other characters distinguish it from contemporary sauropod taxa (Harris 2006a–c; 2007). Plesiomorphies are often found in juvenile specimens, which make it advisable to name new taxa based only on adult individuals (Rozhdestvensky 1965; Gould 1966; Sereno 2010).

Woodruff and Fowler (2012) suggested that *Suuwassea* was a subadult specimen of another Morrison sauropod because its phylogenetic position was difficult to discern owing to plesiomorphic characters and that it appeared to be small in body size. The subadult status of ANS 21122 was inferred on the basis of neurocentral fusion and some fusion in the skull and braincase (Harris 2006c). All of the cervical neural arches are fused with the synostoses completely obliterated, the dorsal neural arches are fused with the synostoses visible, and the caudal neural arches are unfused (Harris 2006b).

Although synostosis (fusion) is often used to infer ontogenetic status (Brochu 1996), the most precise method for determining relative age is bone histology. Recent years have seen an explosion of studies of bone histology in Sauropodomorpha (see SOM: table S1, Supplementary Online Material at http://app.pan.pl/SOM/app59-Hedrick_etal_SOM.pdf; Chinsamy 1995; Curry 1999; Sander 1999, 2000; Sander and Tückmantel 2003; Klein and Sander 2008; Woodward and Lehman 2009; Stein et al. 2010; Sander et al. 2011). Not only does this large body of work reinforce the validity of characters distinguishing histologic ontogenetic stages (Klein and Sander 2008) in sauropods, but it also provides a basis for meaningful comparisons among the bone microstructures of groups within Sauropodomorpha. To better understand the ontogenetic stage and phylogenetic position of *Suuwassea*, we sectioned the tibia to examine the internal microstructure of the bone.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; ANS, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA; BYU, Brigham Young University, Provo, Utah, USA; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; DMNH, Denver Museum of Natural History, Denver, Colorado, USA; GCP, Grupo Cultural Paleontológico de Elche, Elche, Spain; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; ISIR, Palaeontological Collection, Geology Museum, Indian Statistical Institute, Calcutta, India; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN,N, Argentine Museum of Natural Sciences “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP, Museo de la Plata, La Plata, Argentina; MNN, Musée National du Niger, Niamey, Republic of Niger; MUCPv, Geology and Paleontology Museum of

the National University of Comahue, Neuquén, Argentina; NMNH, National Museum of Natural History, Washington, DC, USA; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; T, Chongqing Natural History Museum, Chongqing, China; UNPSJB,PV, Universidad Nacional de la Patagonia “San Juan Bosco”, Paleovertebrados, Comodoro Rivadavia, Argentina; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; ZDM, Zigong Dinosaur Museum, Zigong, China; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—BOS, biological ontogenetic stage; HOS, histologic ontogenetic stages; LAG, line of arrested growth.

Material and methods

We took our histologic section from the mid-diaphysis of the right tibia. As there is presently only one specimen of *Suuwassea*, destructive sampling had to be kept to a minimum. The tibia was chosen because the bone was originally broken at midshaft, allowing for minimal destruction and information loss. It is 535 mm in preserved length and the section was taken 30 mm from the distal preserved end (Fig. 1). ANS 21122 also preserves a complete fibula and humerus, but the data from the tibia were sufficient to make sectioning these bones unnecessary. In other studies of Sauropodomorpha (Sander 2000; Klein and Sander 2008; Sander et al. 2011), humeri and femora are preferentially used over tibiae. However, other authors argue that the tibia is the ideal bone to section (Horner and Padian 2004).

The terminology for ontogenetic stages (juvenile, subadult, adult) has not been standardized. Often sexual maturity is used as the transition between subadult and adult. This is often defined in fossil taxa by the inflection point in a taxon growth curve (Erickson et al. 2001; Erickson 2005). However, Lee and Werning (2008) suggest that the inflection point may not demonstrate the onset on sexual maturity in dinosaurs based on data from extant animals. Other authors define adulthood by the attainment of maximum body size (Scannella and Horner 2010). The distinction between juveniles and subadults is even less clear. As ANS 21122 is a single specimen and its ontogenetic stage cannot be related to a growth curve, we use the biologic ontogenetic stage correlated with its HOS as defined by Klein and Sander (2008), which defines growth stage via the supposed inflection point along a growth curve. This technique was developed in order to determine the biologic ontogenetic stage of a sauropod based on bone histology. The term senescent adult is used here for animals that had reached maximum body size.

The large size of the cross section (total circumference, 370 mm) meant the entire bone could not fit on a single thin section slide. The transverse cut section was subdivided into five portions, which were mounted on five 50 mm x 75 mm glass slides. Overall data loss during histologic preparation



Fig. 1. The right tibia of the holotype (ANS 21122) of the diplodocoid sauropod *Sunwassea emilieae* Harris and Dodson, 2004, Morrison Formation, Late Jurassic. For ease of sectioning, the tibia was dismantled at a natural break and then sectioned 3 cm from the preserved distal end (red line) to ensure a complete cross section. The proximal end of the distal segment was then re-attached to the proximal segment.

was minimal. There was some loss of trabecular bone from the center of the cross-section following uneven grinding of one of the slides during preparation. However, the trabecular bone does not preserve ontogenetically diagnostic features (Francillon-Vieillot et al. 1990), so this data loss is negligible. Methods for thin sectioning follow Chinsamy and Raath (1992), and the terminology follows Francillon-Vieillot et al. (1990).

Results

The bone microstructure is very well preserved and clearly shows histologic patterns and structures (Fig. 2A). The hollow cavities (trabecular bone and interior of osteons) are filled with calcite. The bone material itself is preserved as fluorapatite. There is cortical drift leading to a disproportionate amount of compact bone on the caudolateral side where the thickness is 1.5–2 times greater than on the medial, cranial, or caudal sides (30–40 mm on the lateral side compared with 15–20 mm on the other aspects of the bone). The compacta are thinnest caudally.

The bone is fibrolamellar with a high density of well-developed primary osteons throughout the entire compact bone wall, indicating a high degree of vascularization (Fig. 3A). The primary osteons have a parallel arrangement throughout the cavity. This arrangement is evident even in the inner cortex where the primary osteons are partially overprinted by secondary osteons. There are five total growth cycles pre-

served with alternating highly vascularized zones and poorly vascularized annuli (Fig. 2B). The cycles are most completely visible in the caudolateral region of the bone (Fig. 3A). Other regions only preserve three clear cycles of alternating vascularization. Fibrolamellar and lamellar zonal bone are gradational and are not dichotomous (Francillon-Vieillot et al. 1990), so these cycles indicate differences in growth rate.

Secondary osteons have varying degrees of density and distribution in different regions of the bone (Fig. 2B). The medial, caudolateral, and cranial regions have the highest density of secondary osteons, whereas other regions have sparse secondary osteons confined to the deeper cortex close to the trabecular bone. The lowest density is in the caudal region where secondary osteons do not extend more than 1.5 mm from the edge of the trabecular bone. The medial region has the highest density of secondary osteons, which extend 10 mm from the edge of the trabecular bone. This region also has overprinting of the first generation of secondary osteons by a second generation (Fig. 3B). Additionally, there are clusters of multiple generations of secondary osteons in the outer cortex surrounded by primary osteons (Fig. 3C).

A single line of arrested growth (LAG) is preserved at the outer edge of the fourth annulus along the entire circumference of the bone, although it is discontinuous in some areas (Figs. 2B, 3D). It is most evident on the medial and lateral sides. The cortical drift is also evident by the position of this LAG approximately 1.5 mm from the periosteal surface of the bone on all sides except for the caudolateral side where it is 4.5 mm from the surface (Fig. 2B). Additionally, the lateral

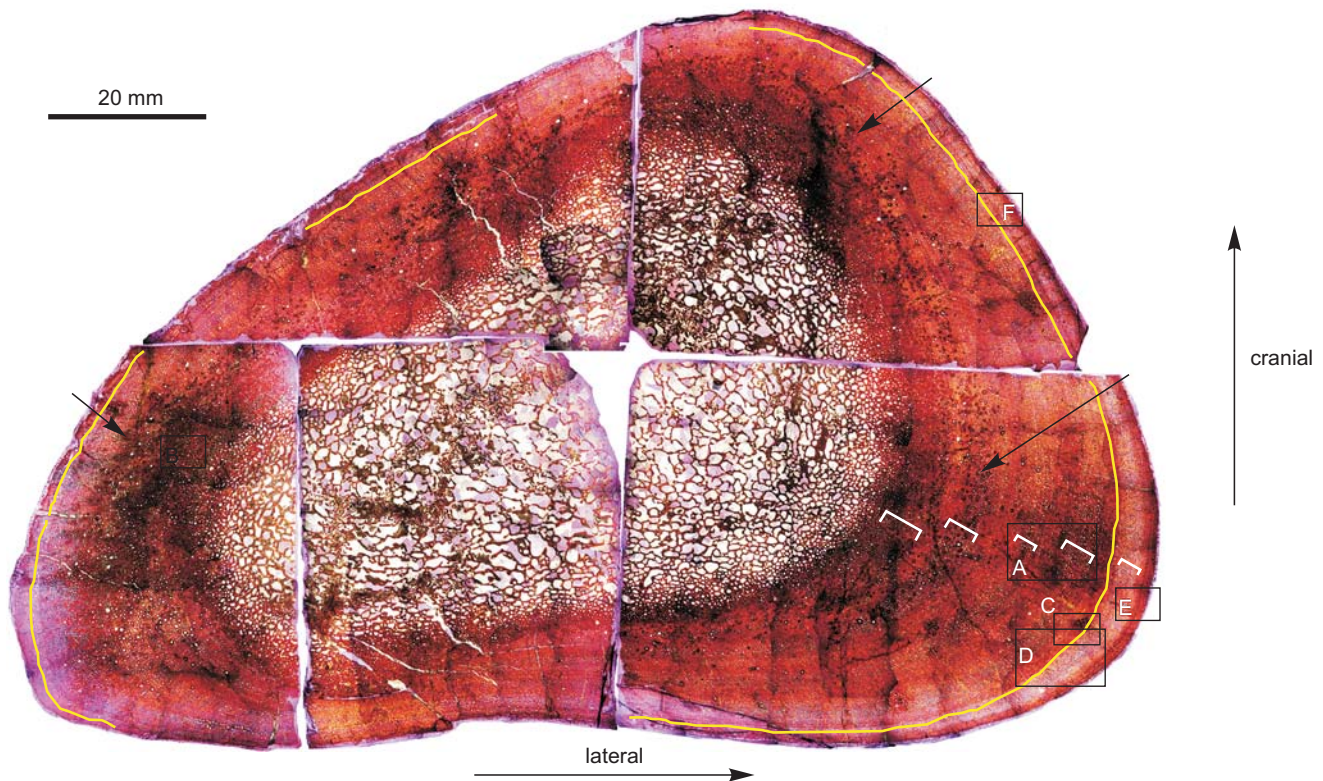


Fig. 2. The right tibia of the holotype (ANS 21122) of the diplodocoid sauropod *Suuwassea emilieae* Harris and Dodson, 2004, Morrison Formation, Late Jurassic. The full cross section under cross-polarized light. Cortical drift and changes in compact bone thickness in different sections of the bone is evident. Arrows indicate areas with the highest densities of secondary osteons. The yellow line demonstrates locations where the LAG (line of arrested growth) following the fourth annulus can be traced along the circumference of the bone. White brackets show the five highly vascularized zones in the lateral region of the bone. Between the brackets are poorly vascularized annuli. The lettered boxes correspond to the locations of the images in Fig. 3.

region of the bone also preserves two closely spaced LAGs in the outermost cortex (Fig. 3E). These are not traceable along the entire margin of the bone. The fact that the cortex is significantly thicker with a higher density of primary osteons in the lateral region suggests faster bone appositional rates specific to this region. The LAGs in the outermost cortex indicate growth cessation in this region. These closely spaced LAGs should not, however, be considered an external fundamental system, because primary osteons are seen in the outermost cortex in all other regions of the bone, indicating the individual was still growing rapidly at the time of its death (Fig. 3F).

In order to make meaningful comparisons between *Suuwassea* and other sauropods, it is first necessary to understand the relative size of ANS 21122 in comparison with other sauropods. As only one specimen of *Suuwassea* is known, it is not possible to estimate adult weight and construct a growth curve as has been done in other studies using techniques such as developmental mass extrapolation (Erickson and Tumanova 2000; Erickson et al. 2001; Lehman and Woodward 2008). However, it is possible to make length estimates of unknown limb elements (radius, ulna, femur) from known elements (humerus, tibia) to compare ANS 21122 to similarly sized individuals (SOM: table S2). ANS 21122 has a humerus length, L_H , of 752 mm and a tibia length, L_T , of 839 mm (based on the fibula). Regression over a dataset of

16 sauropods with known humerus and radius lengths, L_R , produces the equation:

$$L_R = 52.320 + 0.603 (L_H) \quad (1)$$

with an R^2 value of 0.936 suggesting an excellent correlation between humerus and radius length (Fig. 4A). Similar equations can be found for the ulna, L_U , ($n = 15$; $R^2 = 0.938$) using the humerus (Fig. 4B), and for the femur, L_F , ($n = 18$; $R^2 = 0.939$) using the tibia (Fig. 4C).

$$L_U = 30.271 + 0.634 (L_H) \quad (2)$$

$$L_T = 87.215 + 0.553 (L_F) \quad (3)$$

These equations allow estimation of missing elements in ANS 21122 (radius = 505 mm, ulna = 507 mm, femur = 1359 mm), and comparison with similarly sized sauropod elements of different taxa that have been examined histologically.

Discussion

Many different methods have been proposed for approximating individual age in fossil taxa. Often this determination is based on the number of growth lines present and a retrocalculated number of resorbed juvenile growth rings based on

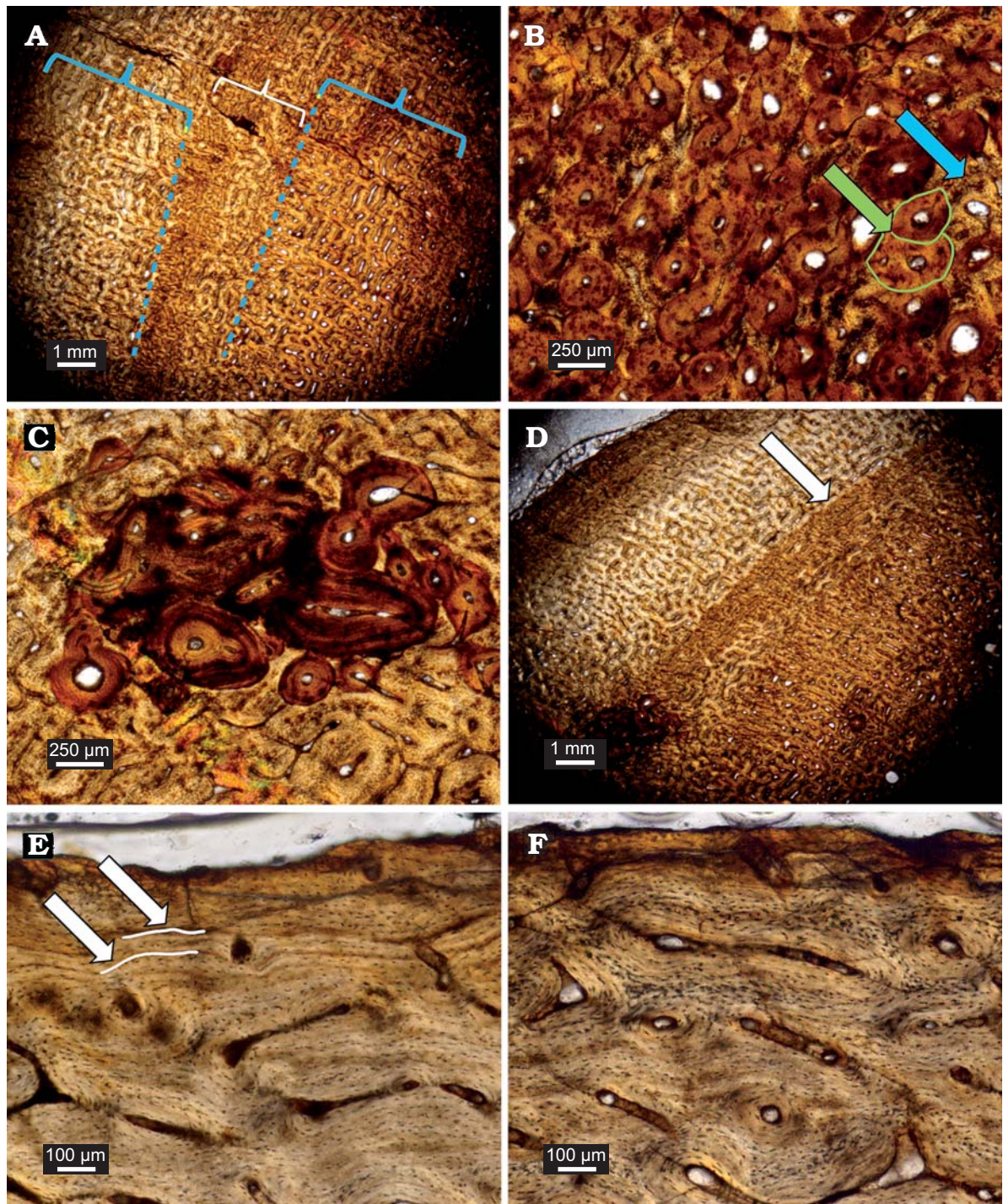


Fig. 3. Histologic structures visible in the tibia of the holotype (ANS 21122) of the diplodocoid sauropod *Suuwassea emilieae* Harris and Dodson, 2004, Morrison Formation, Late Jurassic, photographed under plane-polarized light. **A.** Successive growth cycles in the caudolateral region of the bone. Brackets indicate successive highly and poorly vascularized zones. Highly vascularized zone with dense primary osteons (right), followed by a poorly vascularized annulus (middle). The leftmost region shows the subsequent zone characterized by higher vascularization (outermost cortex to left). **B.** The high density of secondary osteons (outlined in green) in the medial inner cortex, showing overprinting by a second generation (green arrow). Additionally, primary osteons are visible between secondary osteons showing that the bone is not completely remodeled (blue arrow). **C.** A cluster of secondary osteons in the outer cortex of the craniomedial region. This cluster is surrounded by primary osteons. **D.** Outer cortex of the caudolateral region, showing the LAG (line of arrested growth) (arrow) associated with the fourth annulus. **E.** Two LAGs in the outermost cortex of the lateral region. **F.** Primary osteons in the outermost cortex of the craniolateral region leading up to the periosteal surface of the bone.

width between successive annuli (Amprino 1947; Sander and Tückmantel 2003). However, sauropods pose the problem of

both fast growth with few growth stops before adulthood, and extensive secondary remodeling throughout the cor-

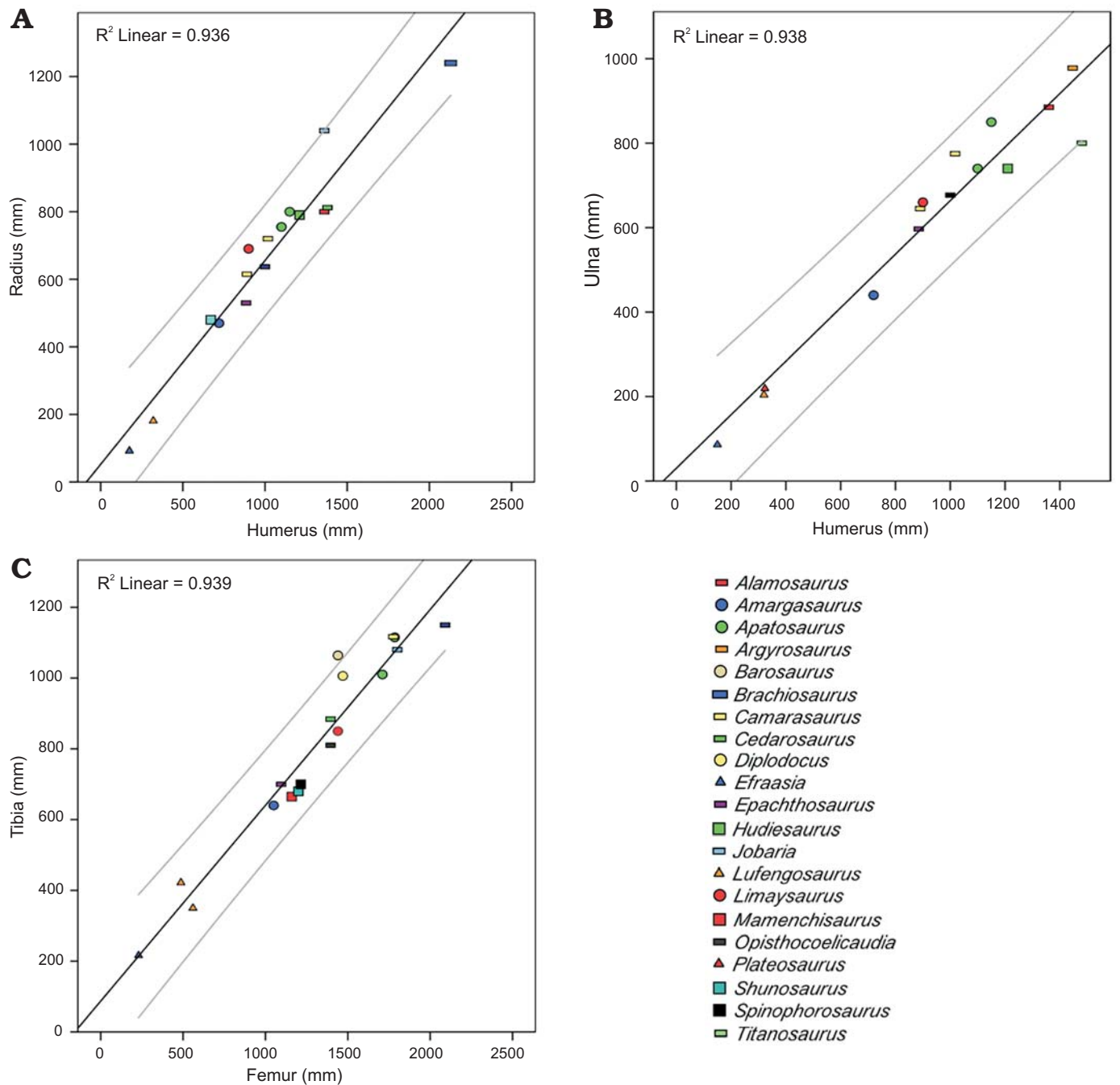


Fig. 4. Allometric graphs of sauropodomorph appendicular elements. Gray lines delineate 95% confidence interval. A. Plot of sauropod humerus length versus radius length. $R^2 = 0.936$. B. Plot of sauropod humerus length versus ulna length. $R^2 = 0.938$. C. Plot of sauropod femur length versus tibia length. $R^2 = 0.939$.

text obscuring potential growth lines after adulthood (Stein et al. 2010). Because of these complications, growth lines were not found in sauropods until 1981 (Reid 1981; Ricqlès 1981). Therefore, sauropods require careful consideration to interpret specimen age, as even presumably old individuals often do not preserve growth lines (Ricqlès 1980). Klein and Sander (2008) proposed such a system, which served to standardize the determination of relative age in sauropods based on the ontogenetic succession of tissue types as revealed by bone histology.

The HOS technique includes 13 separate stages, later expanded to 14 stages to accommodate *Magyarosaurus* (Stein et al. 2010), which document the transition from embryo to senescent adult (Klein and Sander 2008). These stages assess age based upon a combination of histologic structures: development of primary osteons, development and degree of vascularity, relative amount of different types of fibrolamellar bone, development and density of secondary osteons, and occurrence of LAGs (Klein et al. 2009). It is crucial to assess ontogenetic stage based upon all of these factors rather than a subset of

them, as each structure can show some individual variation. Sander et al. (2011) outline the characters distinguishing each HOS and the biological ontogenetic stage (BOS) correlated with the HOS. BOS is a hypothetical relative age correlate to different histologic structures whereby sexual maturity is recognized by a decrease in growth rate on a growth curve rather than attainment of full adult size (Klein and Sander 2008).

ANS 21122 is transitional between type D and type E bone (as defined by Klein and Sander 2008) with well-formed primary osteons, high vascularization, and somewhat dense secondary osteons in certain areas of the bone, as well as the presence of LAGs. These structures give ANS 21122 a HOS of 8–9, which are correlated to a BOS ranging from sexually mature to Adult stage I (of three possible adult stages). The LAGs suggest an older HOS (9–10), but the lack of secondary osteons in many parts of the bone and the high vascularity suggest a somewhat younger animal. Therefore, although ANS 21122 is not a senescent adult, it is certainly older than subadult and has reached sexual maturity.

Recently, Woodruff and Fowler (2012) suggested that *Suuwassea* was an immature version of a different Morrison sauropod taxon based on its modest amount of neural spine bifurcation, which they interpreted as an ontogenetically variable character. However, on the basis of the present analysis, ANS 21122 is a young adult (based on HOS). After sexual maturity, characters are not simply early ontogenetic stages of characters seen in senescent adults of other taxa, but are taxonomically viable (Gould 1966). This implies that the modest neural spine bifurcation in ANS 21122 at a relatively late ontogenetic stage is a taxonomic character separating it from other diplodocoids (Harris 2006b), but a detailed analysis comparing the HOS of diplodocoids with degree of neural spine bifurcation has yet to be performed.

Woodruff and Fowler (2012) base their assessment of *Suuwassea* on a sample set of 18 sauropod individuals, with only four preserving a relatively complete vertebral series. Neural spine bifurcation varies through the vertebral column inter- and intraspecifically, which may account for some of the variation interpreted by Woodruff and Fowler (2012) as ontogenetic (Wedel and Taylor 2013). This would only be evident from a larger sample set of complete individuals. Additionally, other characters in *Suuwassea*, such as the postparietal foramen (Harris 2006a) are not seen in juvenile specimens of other Morrison taxa (Whitlock et al. 2010) and must be accounted for in order to justify synonymization. The postparietal foramen is seen in large, presumably adult individuals of dicraeosaurid taxa such as *Dicraeosaurus* and *Amargasaurus* (Salgado and Calvo 1992), but not in any other known Morrison sauropod taxa. Though a potentially intriguing idea (Woodruff and Fowler 2012), degree of neural spine bifurcation cannot be used as a reliable method for inferring ontogeny until a complementary histologic analysis is performed confirming ontogenetic stages in examined specimens using a larger sample set of individuals with complete vertebral columns.

Some sauropodomorphs exhibit developmental plasticity such that body size and animal age are poorly correlated.

This is especially apparent in the basal sauropodomorph *Plateosaurus* (Sander and Klein 2005; Klein and Sander 2007). Some derived taxa such as the macronarian *Camarasaurus* and titanosaur *Phuwiangosaurus* also exhibit a modest amount of developmental plasticity, though much less than *Plateosaurus* (Klein and Sander 2008). This could also be the case in the basal sauropod *Shunosaurus*, which does not have any secondary osteons even at a large size (Ye et al. 2007). Non-avian theropods and birds also commonly show variable degrees of developmental plasticity (Starck and Chinsamy 2002). Therefore, it could be that *Suuwassea* was also developmentally plastic. However, other flagellicaudatans (*Apatosaurus*, *Diplodocus*, *Barosaurus*, *Dicraeosaurus*) and *Brachiosaurus* show strong correlation between histologic stage and body size (Klein and Sander 2008), as do other basal sauropodomorphs such as *Massospondylus* (Chinsamy 1995). There is variation in the sizes of different species of *Apatosaurus* (Upchurch et al. 2004), but this is likely interspecific variation rather than developmental plasticity. Since related taxa are generally not developmentally plastic, it is reasonable to assume *Suuwassea* also was not.

The ontogenetic status of the holotype of *Suuwassea* compares well with similarly sized diplodocoid individuals that had not reached senescence at their time of death. *Apatosaurus* specimens (CMNH 21715, BYU 681-11940, BYU 6812-4749) with femur lengths of 1218 mm (estimated), 1330 mm, and 1354 mm (estimated) respectively are HOS 8–10 (Klein and Sander 2008). Similarly sized *Diplodocus* specimens are also within this HOS range (Klein and Sander 2008). *Phuwiangosaurus* has much older histologic patterns for smaller individuals (~1000 mm femur = HOS 12) and likely had a maximum body size smaller than these diplodocoids (Klein et al. 2009). In contrast, *Alamosaurus* has young histologic patterns in large individuals suggesting much larger size than *Suuwassea* and other diplodocoids (Woodward and Lehman 2009). This is supported by findings of Fowler and Sullivan (2011) who describe a gigantic specimen of *Alamosaurus* based on a partial femur and two vertebrae. A histologic study of *Apatosaurus* by Curry (1999) suggested that specimens of equivalent size to *Suuwassea* were late juveniles rather than subadults or adults. However, in that study, sexual maturity was inferred at the onset of full body size rather than at a slowing of growth rate (Curry 1999). The presence in the *Apatosaurus* samples of secondary osteons and remodeling make them minimally HOS 7. Given the larger number of sampled sauropods (including more specimens of *Apatosaurus*) and amount of work done to determine sauropod BOS since Curry's (1999) pioneering study, it is likely these animals were older than originally recognized (implying somewhat slower growth rates than originally inferred).

Considering the close similarity in HOS between ANS 21122 and similarly sized *Apatosaurus* and *Diplodocus* specimens, we inferred that a fully adult *Suuwassea* would likely be approximately the size of a fully adult *Apatosaurus* or *Diplodocus*. Though *Suuwassea* was originally considered a small Morrison sauropod when compared to the largest

contemporary Morrison sauropod taxa (Harris and Dodson 2004), the smaller size of the holotype is ontogenetic and does not indicate senescent adult size.

Recent phylogenetic studies have clarified the dicraeosaurid affinities of *Suuwassea* (Whitlock 2011). *Dicraeosaurus* was the only dicraeosaurid prior to this study to be sectioned histologically, based on a sample of six specimens (three femora and three humeri; Sander 2000). In that study, femur length (or equivalent femur length based on humerus length) was fairly small, ranging from 865 mm to 1140 mm. All of these animals were considered subadult to early adult based on histology (Sander 2000). *Dicraeosaurus* has a pattern in orientation of vascularity alternating between radial canals and longitudinal canals in the outermost cortex as well as large erosional cavities towards the inner cortex. These characters are not observed in ANS 21122, so are probably not dicraeosaurid apomorphies. However, sectioning the two other known dicraeosaurids, *Brachytrachelopan* and *Amargasaurus* would be the only method of confirming this, assuming the dicraeosaurid affinities of *Suuwassea*.

In ontogenetically older sauropods, secondary reconstruction affects the entire bone, obscuring primary histologic structures (Stein et al. 2010). ANS 21122 was still relatively early in its adult development so it provides information on the way in which Haversian systems invade the outer cortex of the bone. It is not only ontogenetic changes that cause secondary osteon formation and overprinting by successive generations, but also skeletal loading (Klein and Sander 2007). Differential loading can also cause cortical bone drift (Ricqlès et al. 2003), evident in ANS 21122. Horner and Padian (2004) suggest the tibia is the ideal bone to section owing to its large size and rapid growth, which delay secondary osteon overprinting. The full cross section in ANS 21122 contains large regions of non-remodeled tissue supporting this assertion. However, cortical drift was extensive and caused a higher degree of secondary remodeling in many areas, obscuring regions of the inner cortex.

ANS 21122 shows overprinting of secondary osteons by a second generation in the innermost cortex (Fig. 3B). This extent of secondary remodeling has previously only been reported in the oldest sauropod individuals (Stein et al. 2010). It is possible this secondary reconstruction is related to a late ontogenetic stage, but in the absence of other factors indicating a higher HOS, it is most parsimonious to consider the reconstruction to be related to skeletal loading in ANS 21122. Overprinting of secondary osteons is still poorly understood and the implications behind their overprinting needs to be further examined.

It is evident that different regions of the tibia had different growth rates. The lateral and medial regions had higher cortical thicknesses than the caudal or cranial regions, indicating relatively more deposition and a faster bone apposition rate medially and laterally. These areas also had a larger number and higher density of secondary osteons than other regions. Further, the lateral region had an additional two LAGs (Fig. 3E), which were not present elsewhere in the bone and reflect

different growth rates in the different regions. It is possible that the lateral region, which preserves a larger number of annuli and a high number and density of primary osteons, originally grew faster than other regions of the bone, as suggested by the larger cortical thickness, but then stopped growing earlier than the other regions as indicated by the two outermost LAGs.

This study highlights issues with the coring technique, in which only a cylinder of bone is extracted from the cortex, rather than the entire cortex being sectioned (Sander 1999, 2000; Stein and Sander 2009). The degree of remodeling and vascularization can be very different depending on the section that is cored, as made clear by ANS 21122. Such differences are only visible in complete cross sections (Chinsamy-Turan 2005). The coring technique has been applied widely to humeri and femora to preserve specimen integrity (Klein and Sander 2008). In these bones, differences in regions of the cross section are not as pronounced as in the tibia of ANS 21122. This could be related to the presence of the fibula, which might offset skeletal loading in the tibia, causing variability across the cross section. However, currently there is too small a sample set of sauropod tibia cross sections to confidently make this assertion.

Tornieria was inferred to have had a sexually dimorphic bone microstructure: type A with little secondary osteon remodeling and type B with dense secondary osteon overprinting and LAGs (Sander 2000). In Sander (2000), this material was referred to *Barosaurus* and was subsequently assigned to *Tornieria* (Remes 2006). The cranio-lateral region of ANS 21122 has little remodeling as in *Tornieria* type A, whereas the caudolateral region has extensive secondary osteon remodeling similar to *Tornieria* type B. Based on results from this study, it is possible that the bone types merely reflect variation in remodeling across a cross section. In order to verify the validity of the sexual dimorphism hypothesis (Sander 2000), full cross sections of several individuals would be necessary to determine if the degree of remodeling is uniform. Despite the value of limiting the amount of destructive sampling, the coring technique is problematic when comparing bones unless the core is taken in the exact same location on the bone. Therefore, when applying this technique, close adherence to the instructions in Stein and Sander (2009) is paramount. Future studies should focus on understanding how sauropod bones other than the humerus and femur remodel in different regions of a single cross section through ontogeny in order to evaluate the potential limitations of this technique and to better understand sauropod histologic patterns as they relate to ontogeny, phylogeny, and skeletal loading.

Conclusions

A fully-grown adult *Suuwassea* was larger than previously suggested and was likely similar in size to *Apatosaurus* and *Diplodocus*, but did not reach sizes achieved by the largest

Morrison sauropods such as *Supersaurus*. The only known specimen of *Suuwassea* had reached sexual maturity (HOS 8–9) by the time of death and was likely 75–80% of its full adult size. This study provides the first histologic analysis of *Suuwassea* and confirms its validity as a separate Morrison taxon, as its plesiomorphic characters are not related to immaturity of the specimen. We also present allometric equations for determining the length of missing elements in sauropod bones based upon a dataset of 15–18 genera. Such equations will allow future histologic comparisons between similarly sized taxa in order to determine relative age and size of sauropod genera in specimens that do not have the same elements preserved. This study adds a new genus to the ever-growing number of sauropod dinosaurs that have been studied histologically and adds the second dicraeosaurid, further expanding the sauropod histologic database.

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