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# The appendicular skeleton of *Suuwassea emilieae* (Sauropoda: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana (USA)

## Le squelette appendiculaire de *Suuwassea emilieae* (Sauropoda : Flagellicaudata) de la formation de Morrison, Jurassique supérieur aux Montana (États-Unis)

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#### Abstract

Appendicular elements of the sauropod dinosaur *Suuwassea emilieae*, from the Upper Jurassic Morrison Formation of Montana, USA, display a peculiar mix of autapomorphic and plesiomorphic features. While more similar in overall morphology to *Apatosaurus* than other flagellicaudatans, the coracoid of *Suuwassea* lacks the quadrangular shape of *Apatosaurus*. The humerus of *Suuwassea* bears a pronounced proximal tuberculum, a feature seen elsewhere only in saltasaurine titanosaurian sauropods. The rectangular proximal articular surface of the tibia is proportioned neither like *Diplodocus* nor *Apatosaurus* type specimens, although this region may be intraspecifically variable. The pes of *Suuwassea* possesses plesiomorphically elongate phalanges and a small, uncompressed ungual, unlike other flagellicaudatans except *Dyslocosaurus*. The localization of tooth marks on the pedal elements suggests that sauropod feet may have been singled out by scavengers, as has been noted for elephants. © 2007 Elsevier Masson SAS. All rights reserved.

#### Résumé

Les os appendiculaires du dinosaure sauropode *Suuwassea emilieae*, de la Formation de Morrison du Montana, États-Unis, montrent un mélange particulier de traits autapomorphes et plésiomorphes. Bien qu'il soit plus proche morphologiquement d'*Apatosaurus* que les autres Flagellicaudata, le coracoid de *Suuwassea* ne présente pas la forme quadrangulaire d'*Apatosaurus*. L'humérus de *Suuwassea* possède un tuberculum proximale prononcé, un caractère présent seulement dans les sauropodes titanosauriens saltasaurinés. La surface articulaire proximale du tibia est rectangulaire et ses proportions diffèrent des spécimens-type de *Diplodocus* et d'*Apatosaurus*, bien que cette région puisse présenter une variabilité intraspécifique. Le pied de *Suuwassea* a les phalanges allongées plesiomorphiquement et un petit unguéal qui n'est pas comprimé, à l'inverse des autres Flagellicaudata excepté *Dyslocosaurus*. La localisation des marques de dent sur les os du pied suggère que des pieds de sauropodes aient pu être choisis par des nécrophages, comme cela a été noté pour ceux des éléphants.

Keywords: Suuwassea; Flagellicaudata; Diplodocoidea; Sauropod; Morrison Formation; Late Jurassic

Mots clés : Suuwassea ; Flagellicaudata ; Diplodocoidea ; Sauropode ; Formation Morrison ; Jurassique supérieur

#### 1. Introduction

As with their vertebrae (Harris, 2006a), characters associated with limb bones have been major components of

both sauropod phylogenetic (Upchurch, 1998; Wilson, 2002) and biomechanical (Alexander, 1998; Christian et al., 1999; Gunga et al., 1999; Bonnan, 2003) research. In particular, studies of sauropod limbs have been used, either alone or coupled with ichnological research, to clarify functional, paleoecologic, paleobiogeographic, and biostratigraphic issues

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(Bird, 1944; Lockley et al., 1986, 1994; Christiansen, 1997; Wilson and Carrano, 1999). Owing to their large size and generally solid construction, limbs are also some of the most frequently preserved sauropod fossils. Despite the fact that some sauropod taxa have been based solely on isolated limbs (e.g. *Argyrosaurus* (Lydekker, 1893), *Dyslocosaurus* (McIntosh et al., 1992)), variation in limb element characters remains understudied at present. They have proven more useful in diagnosing higher clades (Upchurch, 1998; Wilson, 2002).

Harris and Dodson (2004) described the new flagellicaudatan sauropod *Suuwassea emilieae* from the Upper Jurassic Morrison Formation of Montana, USA. The holotype specimen, Academy of Natural Sciences (ANS) 21122 does not retain complete limbs but includes numerous, well-preserved limb elements. These include an unfused scapula and coracoid, fragments of sternal plates, a possible clavicle fragment, a complete humerus, a proximal tibia, a complete fibula, a calcaneum, several metatarsals, and some pedal phalanges. With the exception of one ungual, all elements are well preserved, including articular surfaces and muscle scars. Terminology used herein follows Harris (2004).

Institutional abbreviations: ACM: Amherst College, Amherst; ANS: Academy of Natural Sciences, Philadelphia; BYU: Brigham Young University, Provo; CM: Carnegie Museum of Natural History, Pittsburgh; HMNH: Houston Museum of Natural History, Houston; MACN: Museo Argentino de Ciencias Naturales, Buenos Aires; MNB: Museum für Naturkunde der Humbolt-Universität zu Berlin, Institut für Paläontologie, Berlin; NMMNH: New Mexico Museum of Natural History, Albuquerque; NSMT-PV: National Science Museum of Tokyo, Vertebrate Paleontology Collections, Tokyo; TM: Tate Museum, Casper; USNM: U.S. National Museum, Smithsonian Institution, Washington, DC; UW: University of Wyoming, Laramie; YPM: Yale Peabody Museum, New Haven.

#### 2. Pectoral girdle and limb

#### 2.1. Scapula

Only the right scapula (Fig. 1(1, 4)) is well preserved and nearly complete in ANS 21122. This robust element exhibits gentle but pronounced lateral convexity. The rugose coracoid articular surface is tear-drop-shaped, tapering dorsally. Its dorsal two-thirds is concave. It lies more or less perpendicular to both the medial and lateral faces of the element. The medial surface of the entire scapula is smooth, flat, and featureless except for a low, rough eminence near the dorsal margin at the base of the body, immediately caudal to the acromion (Fig. 1(4, inset)).



Fig. 1. Right scapula and coracoid of ANS 21122. Scapula in 1, lateral; and 4, medial views; inset of 4 shows close-up of elevated rugosity. Coracoid in 2, cranial (lateral); and 3, caudal (medial) views. Abbreviations: acpr = acromion process; cfo = coracoid foramen; dcr = deltoid crest; em = eminence; glfo = glenoid fossa. Scale bar 10 cm.

The scapula attains its maximum height (510 mm) across the acromion process. In lateral view, the dorsalmost point of the process lies closer to the level of the glenoid than to the midpoint of the scapular body. The cranial and caudal margins of the process, as well as its dorsoventral bisector, are roughly perpendicular to the long axis of the scapular body. A low but pronounced, flat-topped deltoid crest (crista deltoideus, term nov.; = deltoid ridge per Filla and Redman (1994)) divides the acromion approximately three-fourths the distance along its craniocaudal width. The crest angles only slightly caudally from the perpendicular to the long axis of the scapular blade. Ventrally, the crest expands craniocaudally and branches into two parts: a long ridge that curves suddenly caudally to parallel the long axis of the scapular body, and a shorter branch that angles cranioventrally and blends into the caudoventral margin of the glenoid. Thus, the thin (11.4 mm minimum), cranial three-fourths of the acromion process consists of a broad. shallow fossa. It is unclear what muscles originated in this fossa in vivo: Borsuk-Bialynicka (1977) reconstructed there the Mm. scapulohumeralis cranialis and supracoracoideus, whereas Filla and Redman (1994), more in line with modern avians, placed the Mm. supracoracoideus and deltoideus in that space. In crocodylians, the M. coracobrachialis has part of its origin in this region as well (Meers, 2003).

The scapular body is 1072 mm long. The scapular portion of the glenoid fossa is angled slightly medially and thus more visible in medial than in lateral view. The caudal branch of the deltoid crest occupies the ventral half of the lateral surface of the body and persists for most of its length, giving most of the body a laterally convex, 'D'-shaped cross sectional morphology, with the lateral convexity offset slightly ventrally. Both dorsal and ventral to the ridge, the body thins toward the margins. In lateral view, the dorsal margin of the blade is gently concave dorsally; the ventral margin is gently sinuous. The narrowest dorsoventral dimension of the scapular body (164.2 mm) occurs slightly caudal to the halfway point through its length. The body caudal to this point becomes increasingly expanded dorsoventrally due to a gradual upward migration of the dorsal margin. The caudodorsal portion of the blade is missing, so the degree of maximum expansion cannot be assessed, but it almost certainly was not as tall as the acromion process. The broadest preserved portion (located proximal to the distal end) measures 244.7 mm. The distal end of the blade thickens and presents a rugose surface caudally for the insertion of suprascapular cartilage.

## 2.2. Coracoid

The right coracoid preserved in ANS 21122 (Fig. 1(2, 3)) is separate from the scapula. Corresponding to its scapular counterpart, the scapular articular surface is tear-drop-shaped, expanding ventrally. It measures 317.7 mm long, slightly less than the mediolateral dimension of the element. Although the entire surface is rugose, much of its surface is angled such that, when articulated with the scapula, the coracoid angles toward the midline of the animal, causing the primary surface of the element to face cranially (probably cranioventrally). When articulated with the scapula, there is only a modest ventral indentation of the dorsal margin between the acromion process and the coracoid.

At its widest (from the scapular articular surface toward the sagittal plane of the animal) the bone measures 337.6 mm; in dorsoventral height (from the cranialmost edge of the glenoid facet dorsally, paralleling the scapular articular margin), it measures 388.1 mm. In profile, the scapular articular and glenoid surfaces sit at an obtuse angle to each other, while the dorsal and medial margins form a continuous and relatively regular curve. The rugose bone at the dorsal margin is thin (11 mm) but the coracoid steadily thickens ventrally to 25 mm. The ventral edge is short (61.1 mm) and again thin; it is gently concave ventrally, forming a shallow notch between the glenoid and a more ventrally protruding, broad and flattipped ventromedial process. The glenoid facet is roughly triangular, tapering craniomedially and measuring 141.7 mm long and 114.2 mm at its widest, where it is expanded beyond the plane of the remaining cranial surface of the element. Its articular surface is somewhat visible in lateral view, and a small portion of it actually wraps onto the lateral surface.

The coracoid is slightly convex cranially, with the apex of the convexity forming a broad, low ridge that persists dorsomedially from the medial margin of the coracoid foramen. The latter is a roughly circular opening  $(36.6 \times 31.1 \text{ mm})$ whose center sits 74.7 mm medial to the scapular articular surface, just under one-fourth the distance to the medial margin. The foramen opens caudolaterally, toward the scapular articular surface. A weak ridge divides the dorsal portion of the cranial face into vague medial and lateral fossae.

#### 2.3. Sternum

Two bone fragments represent the remains of one or more sternal plates (Fig. 2). The larger and more recognizable of the two, a thin, flat, parabolic piece (Fig. 2(1, 3)), is too sharply angled to be a portion of the missing left coracoid and is too thin to pertain to any portion of the right or left scapula. All preserved, unbroken edges are rugose and verrucate, and both dorsal and ventral surfaces are planar. The terminal, unbroken end of the fragment is thickened beyond the rest of the plate and bears an elongate, flat, rugose coracoid articular face set at an angle to both the dorsal and ventral surfaces.

## 2.4. Clavicle?

A peculiar fragment (Fig. 3) is possibly a partial clavicle. It superficially resembles the distal end of a dorsal rib but displays a peculiar series of knobs, ridges, and grooves. The shaft proximal to the ornamented region is smooth and rapidly decreases in circumference (Fig. 3(1, 3)). The rugose end is expanded both cranially and caudally on its lateral surface, swollen sagittally slightly on the ?lateral surface, and much more greatly on the ?medial surface. The ?medial surface is dominated by a flattopped swelling (Fig. 3(2, inset)) that is separated from the ?lateral surface by shallow fossae. Numerous parallel striae scar the ?medial swelling. The shaft is more sharply curved than



Fig. 2. Sternal fragments of ANS 21122. Large fragment in 1, ventral; and 3, dorsal views. Views uncertain for small fragment (2 and 4). Abbreviations: caf = coracoid articular facet. Scale bar 10 cm.

expected for a dorsal rib (Fig. 3(1, 3)). No fracture line or offset, implying healing of an infected break, can be discerned, and the symmetry of the specimen argues against a pathologic interpretation. The distinctive curvature renders it unlike the flat sternal ribs and gastralia of Apatosaurus excelsus (Marsh, 1896: Fig. 12-15) or Eobrontosaurus (Filla and Redman, 1994: Fig. 11). It also lacks the marginal rugosities of the latter, so the element appears not to be gastral in origin. The curvature and rapid tapering of the element recall the purported clavicles (interpreted as os penii by Nopsca (1905)) of Diplodocus carnegii (Hatcher, 1901) except that it bears unusual rugosities instead of the flat, smooth articular surface of the latter. This could conceivably be an ontogenetic feature as well. The striae on the elevated platform on the distal end of the fragment imply an overlapping articulation with another element. If the element is gastral, this could be interpreted either as the articular site for another gastral element; if perceived as a clavicle, either its counterpart or the coracoid. The preserved coracoid lacks a matching surface, however, and is much thinner on its dorsal end than the ?clavicle fragment implies.

## 2.5. Humerus

The 752 mm long right humerus is well preserved and complete (Fig. 4). The entirety of the element is craniocaudally compressed. The body is gently twisted such that, in distal view, the deltopectoral crest directly overhangs the midline of the

distal end. Its rugose, convex proximal end is expanded mediolaterally (379 mm) beyond all points distal. The head is not distinctly set off from the remainder of the proximal surface, but it forms the thickest craniocaudally (131.8 mm) proximal apex of the element. It is most visible as a distinct, hemiovoid, caudally tilted swelling on the caudal surface. The rugose proximal surface forms a distinct lip craniomedially that overhangs the shallow tricipital fossa; it also slopes toward the distal end both medially and laterally. Proximal to the deltopectoral crest, there is a modest, hemispherical proximal tuberculum (= proximal process of Upchurch (1998); Fig. 4(1, 2, 4)) that caps a pronounced, triangular, laterally projecting proximolateral process. This process has its origin approximately halfway down the humeral body and contributes to the lateral concavity of the element in cranial view. Both the lateral and medial margins of the main humeral body meet the sloping proximal end at rounded, approximately  $90^{\circ}$  angles.

The deltopectoral crest is a low, thick, and craniolaterally convex process spanning about one-third the humeral length distal to its origin under the proximal tuberculum – although the crest does not attain the same level proximally as the proximalmost point of the humerus, the distance from the proximalmost point to the distal end of the crest is roughly 48% the length of the entire element. The medial surface of the crest bears a pronounced convexity that invades the craniolateral corner of the tricipital fossa. At its tallest point, the crest flares into a low, rectangular protuberance that marks the insertion of the supracoracoideus muscles by homology with crocodylians (Meers, 2003) and/or the Mm. deltoideus major and pectoralis by homology with birds (Baumel and Witmer, 1993). Distal to the crest, the humeral body is 'D'-shaped in cross-section, with the flat surface facing cranially. Here it attains its narrowest width (142.8 mm) and smallest circumference (402 mm) before expanding rapidly toward the distal articular surface. No intercondylar incisure indents the distal articular surface but rough condyles can be delineated on the cranial surface by a pair of closely appressed, short, rugose, triangular eminences (Fig. 4(2, 3)). Of the two eminences, the smaller, medial one lies approximately on the midline of the long axis of the humerus, while the larger, lateral one is offset laterally. On the caudal surface, the distal condyles are separated by an elongate, shallow brachial fossa that is centered on the midline of the element and is bounded laterally by low, rounded ridges that do not extend very far proximal to the distal end. The lateral condyle projects farther caudally and is wider than its medial counterpart. A low, ovoid, rugose lateral epicondyle on the caudolateral margin is visible just proximal to the distal end. The distal articular surface measures 295.2 mm mediolaterally (about 78% the width of the proximal end) and a maximum of 163 mm craniocaudally. The planar but rugose distal articular surface is angled neither laterally nor medially with respect to the long axis of the humerus.

#### 3. Pelvic girdle and limb

Measurements of long bones from the hind limb are provided in Table 1; pedal ungual measurements are provided in Table 2.



Fig. 3. Fragment of possible clavicle of ANS 21122 in 1, ?caudal; 2, ?medial; and 3, ?lateral views. Inset on 2 shows close-up of probable articular surface. 4, oblique angle view of ?distal end showing knobby rugosities. Scale bar 10 cm.

#### 3.1. Femur

A large, wedge-shaped piece of bone dominated by a convex articular surface is the only femoral fragment preserved in ANS 21122. The bulbousness of the articular surface makes it unlikely to pertain to an ulna or radius. A small, rounded bulge on one side slopes obtusely toward the broken end. This does not project far enough to make the fragment represent the caput; coupled with the size and projected angle of continuation of the articular surface, this morphology indicates that the fragment belongs to the medial condyle. The preserved portion of the caudal intercondylar (flexor) sulcus indents just under one-half the craniocaudal dimension of the distal end. In contrast, the distal intercondylar sulcus is shallow.

#### 3.2. Tibia

Using the length of the intact fibula (see Table 1) as a guide, the preserved portion of the right tibia (Fig. 5) is the proximalmost two-thirds. The proximal articular face is markedly rectangular, though rounded on its craniomedial corner. The face is wider than long, and the longest axis parallels the direction in which the cnemial crest points. Ignoring its marked rugosity, it is virtually perpendicular to the long axis of the tibial body and planar save for a shallow depression craniolateral to center that tapers toward the cnemial crest. The low, straight cnemial crest has a low, hyperbolic cranial profile. The crest is thinnest proximally; distally, its internal face bears a thick, low, rugose, proximodistally elongate, caudally-facing fibular tuberculum (tuberculum fibularis, term nov.) that separates the narrow, concave fibular incisure and a shallower, narrower sulcus that lines the external edge of the cnemial crest. A second proximodistal ridge, shorter and less pronounced than the former, is roughly centered on the fibular articular facet.

The remainder of the preserved tibial shaft is unremarkable. The lateral and medial sides of the shaft taper gradually toward the distal end and grade imperceptibly into a parallel-sided, craniocaudally flattened shaft. Where broken, the acoelous shaft has a lightly reniform cross-section, shallowly convex cranially.

#### 3.3. Fibula

The right fibula is complete (Fig. 6). Its proximal articular face is subrectangular, flattened mediolaterally and tapering somewhat cranially. The slightly concave tibial articular face on the medial side is not topographically demarcated, but is discernable as a texturally rough, trapezoidal area that is proximodistally deepest along the cranial edge. The craniodistally tapering



Fig. 4. Right humerus of ANS 21122 in 1, proximal; 2, cranial; 3, distal; 4, lateral; 5, caudal; and 6, medial views. Abbreviations: bfo = brachial fossa; cap = caput of humerus; dpc = deltopectoral crest; dtb = proximal tuberculum; em = eminence; plpr = proximolateral process; trfo = tricipital fossa. Scale bar 10 cm.

portion of this trapezoid rises into a low, rounded tibial tuberculum (tuberculum tibialis, term nov.) that fits neatly into the incisure between the fibular tuberculum and secondary ridge on the tibia (see above). A second low, rugose ridge lies on the proximocaudal end of the trapezoid. The tibial articular face spans roughly the proximal one-fourth of the shaft. The face grades gradually into smoother bone distally and caudally. The tibial tuberculum continues as a decreasingly-pronounced ridge along the caudomedial margin of the shaft, but just over halfway along the length of the fibula, the ridge curves medially, dividing the medial side of the element into craniomedially-facing proximal and caudomedially-facing distal portions.

The lateral side of the fibular shaft is interrupted only by a proximodistally rhomboidal fossa roughly halfway along its length; it is demarcated both cranially and caudally by low, rounded ridges. The caudal ridge is less pronounced than the cranial. Both ridges converge and grade gently into the body of the shaft both proximally and distally, but only the caudal ridge, like the fossa itself, is rugose, marking the insertion of the M. iliofibularis (Borsuk-Bialynicka, 1977; Wilson and Sereno,

1998). This ridge was termed the 'lateral trochanter' by Wilson and Sereno (1998), but is more precisely described as the tuberculum M. iliofibularis (term nov.), following Baumel and Witmer (1993). The fossa is then the sulcus M. iliofibularis (term nov.).

The distal end of the fibula expands in all directions but most prominently craniomedially. The distal articular face is ovoid, longest mediolaterally.

#### 3.4. Calcaneum

Although no astragalus is preserved in ANS 21122, a small, rugose nubbin of bone (Fig. 7(1–3)) probably represents a calcaneum based on comparisons with the similarly shaped element ascribed to *Diplodocus* by Bonnan (2000; Fig. 7(4, 5)). The element is largely spherical, though in ?proximal and ?distal views, it takes the shape of an elliptical (non-Euclidean) triangle. It measures  $50.7 \times 44.3 \times 43.4$  mm. The knob is rugose over its entire surface, though especially so on the two aforementioned faces.

	Max prox-dist	Min prox-dist	Min shaft cran-caud	Min shaft med-lat	Min shaft circumf	Max PAF cran-caud	Min PAF cran-caud	Max PAF med-lat	Min PAF med-lat	Max DAF cran-caud	Min PAF cran-caud	Max DAF med-lat	Min DAF med-lat
Right Tibia	535 <sup>b</sup>	n/a	88.0 <sup>b</sup>	141.0 <sup>b</sup>	371 <sup>a</sup>	218	n/a	260	n/a	ż	i	i	ć
Right Fibula	839	n/a	78.9	45.6	240	175	n/a	95.0	83.7	141.4	n/a	116.7	n/a
Right metatarsal I	130.7	96.8	60.6	77.9	248	110.4	n/a	90.6	83.9	67.0	60.5	112.9	102.5
Right metatarsal II	154.3	133.4	57.4	56.5	200	110.9	88.8	83.2	62.6	72.3	67.1	89.2	85.0
Right metatarsal IV	172.8	167.3	45.0	38.7	150	100.4	n/a	64.2	50.2	62.1	53.9	74.6	71.3
Large Phalanx (Right I-1)	74.0	67.0	48.8	61.9	200	66.7	n/a	76.6	n/a	60.9	49.8	74.8	72.2
Small Phalanx	60.9	61.3	36.4	49.4	160	49.8	n/a	65.9	n/a	44.2	36.8	62.3	n/a

Table

? = measurement unavailable; Max = maximum; Min = minimum; Prox-dist = proximodistal measurement; cran-caud = craniocaudal measurement; dors-vent = dorsoventral measurement; PAF = proximal articular

for preserved portion, real value larger.

<sup>a</sup> measurement on broken element;

measurement

р

face; DAF = distal articular face.

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#### 3.5. Metatarsal I

Right metatarsal I (Fig. 8, left column) is a short, broad, compact element. Its proximal end is broadest craniocaudally; both the cranial and caudal ends overhang the remainder of the element. When the body of the element is held vertically, the proximal surface slopes sharply distomedially at a 74° angle to the long axis of the body. The lateral margin of the proximal articular face is gently concave; the medial margin is more conspicuously convex medially, rendering the facet roughly 'D'-shaped with the cranio- and caudolateral corners flaring the furthest cranio- and caudolaterally, respectively. The facet is rugose only along its lateral and caudolateral margins.

The distolateral (= caudolateral) condyle of the metatarsal projects farthest distally, contributing to the sharp proximomedial slope of the distal articular face, which forms an angle of  $75^{\circ}$  to the body and converges on the proximal facet. Five tiny, probably nutrient, foramina are arranged irregularly approximately midway along the cranial face of the body. The dorsal and lateral surfaces of the element grade into one another distally, unobstructed by a ridge, but proximally the boundary between them is indicated by the buttress supporting the craniolateral process of the proximal articular surface. The proximal end of the lateral side is deeply concave. A triangular depression is bounded cranially and caudally by low ridges that connect the distolateral process to both the proximocaudal and proximocranial corners of the proximal articular surface. The deepest portion of this fossa is pitted and rugose where the interosseous ligament inserted. A shallower fossa adorns the distal end of the lateral surface, caudodistal to the distolateralproximocranial ridge. The caudal and medial faces of the shaft are featureless except for rugosities along the proximal margin and several nutrient foramina on both surfaces.

The distal end of the metatarsal is sinusoidal in cranial view and cartouche-shaped (rectangular with rounded corners) in distal view, with the long axis oriented mediolaterally. Its articular facet is divided into weak medial and lateral condyles by a depression that is deepest caudally. The lateral condyle is the more pronounced of the two. Its surface is mostly smooth. The distal articular surface wraps onto the caudal face of the shaft, particularly on the distomedial corner.

## 3.6. Metatarsal II

Right metatarsal II (Fig. 8, middle column) is longer than metatarsal I but similarly stocky. Unlike metatarsal I, the proximal articular surface is hourglass-shaped in proximal view, with the long axis oriented roughly craniocaudally. Both its lateral and medial margins are concave, rendering the facet narrowest across its midpoint. The entirety of the surface is relatively rugose but particularly so on the cranial and caudomedial margins.

Both the proximal and distal articular surfaces angle medially toward one another in cranial view, though not as strongly as on metatarsal I. The cranial surface is smooth and featureless except for a low, rugose eminence on its distolateral corner and two nutrient foramina roughly centered on the face.

Table	2					
Pedal	ungual	measurements	of	Suuwassea	emilieae	(in mm)

	Max prox-dist	Max ext tub-tip	Max dors-vent	Max prox dors-vent	Max med-lat	PAF max dors-vent	PAF max med-lat
Ungual, Right I-2	157.4 <sup>a</sup>	159.8 <sup>a</sup>	79 <sup>a</sup>	77.8	48.3	73.7	52.6
Ungual, Left II-3	165.0	188.7	118.0	102.0	53.7	95.8	49.1
Ungual, Left IV-?3	75.0	80.3	36.9	36.9	28.1	40.4	24.6

Maximum proximodistal length measured in lateral view as horizontal line through axis of articular end from intersections with vertical lines tangential to articular and distal ends, respectively. Straight-line measurement from proximalmost point on extensor tubercle to distal ungual tip provided separately. Maximum dorsoventral height measured in lateral view as vertical line (parallel to articular face) from intersections with horizontal lines tangential to dorsalmost and ventralmost (tip) points on ungual body, respectively. Maximum proximal dorsoventral measurement incorporates flexor tubercle, whereas maximum dorsoventral measurement of proximal articular face does not.

<sup>a</sup> measurement for preserved portion, real value greater; Max = maximum; prox-dist = proximodistal measurement; dors-vent = dorsoventral measurement; ext tub = extensor tubercle; PAF = proximal articular face

The lateral surface of the shaft is divided into two shallow fossae like those on metatarsal I, though they are much shallower, lack marked rugosities, and are perforated by two nutrient foramina. The caudal face is pierced by a single, large nutrient foramen. The dominant feature on the smooth medial face is a second low, rugose eminence located at the proximocaudal corner.

The rugose distal articular face is again cartouche-shaped, longest mediolaterally. The surface is divided only cranially by a shallow depression. The caudolateral corner protrudes from the shaft caudolaterally, tapering into a short, blunt process. The articular surface wraps onto the cranial face of the metatarsal.

#### 3.7. Metatarsal IV

The remaining metatarsal (Fig. 8, right column) is longer and more slender than the previous elements. The rugose proximal articular surface is craniocaudally elongate; it is essentially reniform but bears a blunt, off-center point caudomedially. The cranial surface of the element is smooth and featureless. A shallow, rugose fossa indents the proximal end of the medial surface; the fossa is bounded proximocaudally by a pronounced ridge that supports the jutting caudomedial end of the proximal articular surface. The caudal and lateral surfaces of the shaft blend together into a single caudolaterally-facing surface that bears the only visible nutrient foramen on the bone.

Even though it lacks the caudomedial corner, the distal articular surface is only slightly wider mediolaterally than craniocaudally. It is rugose and has rounded edges; the caudal margin is concave. The surface is barely divided into medial and lateral halves by a shallow fossa that tapers and shallows cranially. In distal view, the lateral condyle is more compressed mediolaterally than its medial counterpart. With the missing corner restored the caudomedial condyle projects farther caudally than its lateral counterpart. As before, the articular surface wraps onto the cranial surface of the shaft.

#### 3.8. Non-terminal phalanges

Two phalanges are preserved with ANS 21122 (Fig. 9). Both are longer than wide at their narrowest (at mid-length); the lengths, however, are subequal to the greatest widths of their

proximal and distal ends. The robust elements have well formed, cotylar proximal and trochlear distal articular surfaces. Since only early, basal eusauropods retain robust phalanges with typical phalangeal morphology in the manus (e.g. Shunosaurus (Zhang, 1988; Wilson, 2002)), the well-formed elements in ANS 21122 most likely make them pedal elements. The two phalanges do not articulate with each other, but the larger (Fig. 9, left column) articulates moderately well with both metatarsal I and the largest preserved ungual (see below). However, in morphology, the larger resembles phalanx II-1 and the smaller III-1 of the pes of Apatosaurus louisae (Gilmore, 1936: Fig. 28 D-II and D-III). This comparison holds for the smaller phalanx (Fig. 9, right column) with USNM 4287 (referred by Marsh (1896: Pl. 28, Fig. 2) to Diplodocus longus but noted as attributable to Apatosaurus instead by McIntosh and Carpenter (1998)), which is also longer than wide, but in the latter specimen, phalanx I-1 compares better with the larger preserved in ANS 21122. A phalanx mounted as IV-1 with CM 94 is virtually identical to the small phalanx of ANS 21122. Nevertheless, the identification of the phalanges as II-1 and III-1 is held here; if correct, then their subequal dimensions are a surprising, autapomorphic reversal to (or plesiomorphic retention of) a pre-neosauropod state (Upchurch, 1998; Wilson, 2002).

Both phalanges are craniocaudally compressed and lack collateral ligament fossae. The proximal articular surfaces of both are ovoid, tapering gently to one side (probably lateral, per Upchurch (1998)). The proximal articular surfaces of both are divided into two extremely shallow but roughly equal fossae by barely discernible, dorsoplantarly oriented ridges. The larger phalanx is trapezoidal in cranial view, with the distomedial end projecting furthest distally.

#### 3.9. Unguals

Three unguals are preserved. The two larger (Fig. 10, left and middle columns) are typically sauropodan, robust, mediolaterally compressed, blunt claws with only modest curvature. The higher but shorter claw tapers nearly to a point. In both, when the articular face is held vertically, the distal ends extend much further ventrally than the ventralmost portion of the face. In these aspects, the larger two differ from the manual ungual of *Apatosaurus louisae* (Gilmore, 1936: Fig. 18) that



Fig. 5. Right tibia of ANS 21122 in 1, proximal; 2, caudal; 3, lateral; and 4, cranial views. Abbreviations: cncr = cnemial crest; fbtr = fibular trochanter. Scale bar 10 cm.

tapers to a tall, squared-off point that ends only slightly farther ventrally than the proximal articular face. The proximal articular faces are oblique to the sagittal plane of each element, a feature not noted in manual claws. In USNM 4287, a pes of *Apatosaurus*, ungual I is longer but lower than that of ungual II and possesses an extensor tubercle. However, a manual ungual of an indeterminate Morrison Formation sauropod (USNM 337921) is extremely similar to the incomplete, longer, large ungual of ANS 21122. In general, all preserved unguals of ANS 21122 compare more favorably with the pedal unguals of *Apatosaurus*, *Camarasaurus* (McIntosh et al., 1996) and *Dyslocosaurus* (McIntosh et al., 1992), and are thus attributed here to the pedes of *Suuwassea*, but it remains conceivable that one of the two larger unguals actually belongs on the manus.

The two larger claws are asymmetrical in that the narrowest ventral edge lies parasagittally; the remainder of the rugose ventral surface angles dorsally. In articulation, the lateral side of the ungual tilts to face more plantarly, while the medial side faces dorsally. This creates the aforementioned asymmetry and an offset, proximodistally flat ventral surface that contacted the substrate. As is typical for derived sauropod claws, the proximal articular face of each occupies only the proximoventral portion of the element. Based on comparison with USNM 4287 and the direction of angulation of the proximal articular surfaces, the longer but proximally lower ungual of ANS 21122 (Fig. 10, left column) belongs to digit I of the left foot and the shorter but proximally taller (Fig. 10, middle column) to digit II of the right foot (the articular surface of the smallest ungual is not offset, rendering determination of its right/left position equivocal). This is the opposite assignment given by Harris and Dodson (2004) (but see above and Table 3). This also accords roughly with the condition in A. ajax (NSMT-PV 20375) where the ungual of the second pedal digit is the more equidimensional (Upchurch et al., 2004a), though smaller overall. However, it contrasts with the usual sauropod condition in which the ungual of digit I is the longest, so whether or not this assignment is accurate remains to be seen.

Ungual I lacks a topographic extensor tubercle, having instead a markedly rugose, but otherwise planar, surface in the same position. The remaining two unguals possess small extensor tubercula. Extremely shallow grooves, probably neurovascular sulci, ornament the lateral surface of the largest and the more ventral surface of the larger left ungual. The sulci probably extended to the distal ends, but this is difficult to demonstrate because each surface is marred by pathologies (see below). The ungual of digit II is more heavily weathered than the right and lacks its distal end.

The smallest ungual (Fig. 10, right column) is much smaller and less laterally compressed than known sauropod manual unguals. It is also less recurved and less laterally compressed. Its proximal articular face is more centered dorsoventrally than on its larger counterparts. A short, shallow sulcus on the distal one-third of one lateral surface terminates in a tiny but deep nutrient foramen; the other surface lacks a neurovascular sulcus but has a similar foramen.

Pedal unguals I–III of *Apatosaurus louisae* scale gradually and sequentially from larger to smaller (Gilmore, 1936: Fig. 30; Table 3). If this pattern holds for *Suuwassea*, the great size disparity between the smallest ungual and the others suggests that it cannot belong to digit III and that *Suuwassea* therefore has four pedal unguals. In fact, the small ungual bears some

![](_page_9_Figure_2.jpeg)

Fig. 6. Right fibula of ANS 21122 in 1, proximal; 2, lateral; 3, cranial; 4, medial; 5, caudal; and 6, distal views. Abbreviations: silf = M. iliofibularis sulcus; tarf = tibial articular facet; tilf = M. iliofibularis trochanter; ttb = tibial tuberculum. Scale bar 10 cm.

resemblance to the ungual assigned to digit IV of the enigmatic diplodocoid *Dyslocosaurus* (McIntosh et al., 1992: Fig. 3K, 4J). However, the pedal unguals of USNM 4287, USNM 11656 (cf. *Diplodocus*), and the holotype of *Janenschia robusta* (Fraas, 1908: Pl. 7) decrease much more rapidly, and their third pedal unguals more closely resemble those of *Suuwassea*, although in USNM 11656, the small third ungual is still quite compressed mediolaterally. The precise number of pedal unguals in *Suuwassea* is assumed to be three, but this awaits confirmation by further discoveries.

#### 4. Comparisons with other flagellicaudatans

Given the flagellicaudatan relationships of *Suuwassea* (Harris and Dodson, 2004; Harris, 2006b), comparisons are restricted here to other members (and purported members) of

that clade, including Amargasaurus cazaui (MACN-N 15), Apatosaurus spp., Barosaurus lentus, Dicraeosaurus spp., Diplodocus spp., Dyslocosaurus polyonychius (ACM 663), Eobrontosaurus yahnahpin (TM 001), Supersaurus vivianae, and Tornieria ('Barosaurus') africana. Little can be said about the appendicular skeleton of sole known specimen of Amargasaurus because its description is only preliminary, and it lacks pedes. For Apatosaurus, as in Harris (2006a, 2006c), A. ajax, A. louisae, A. excelsus, and A. sp. are considered together unless otherwise noted (discussion here of A. excelsus is based on UW 15556, which was placed in A. parvus by Upchurch et al. (2004a)). The holotype of B. lentus, YPM 429, does not preserve any appreciable appendicular elements that overlap with ANS 21122, obviating direct comparison of the two taxa. However, additional specimens that do possess limb bones have been referred to this taxon and

![](_page_10_Figure_1.jpeg)

Fig. 7. Calcaneum of ANS 21122 in 1, ?proximal; 2, ?distal; and 3, ?lateral views. Outline schematics of calcaneum attributed to *Diplodocus* by Bonnan (2000) in 4, ?proximal; and 5, lateral views. Scale bar 5 cm.

are used here. As revised by McIntosh and Carpenter (1998), no appendicular material is present in the genoholotype of *Diplodocus*, *D. longus*, YPM 1920. However, several other specimens have been referred to this genus, including the articulated material of the cotypes of *D. carnegii* (CM 84 and 94). '*Diplodocus*' hayi, based on a partial skeleton including the caudal end of the cranium (Holland, 1906, 1924), may belong to one of the two other species, but demonstrates some cranial and postcranial peculiarities (McIntosh, 1990b). For the purposes of this comparison, all three species are considered together except where specifically noted. For graphic comparisons, see Fig. 11.

## 4.1. Scapula

Scapulae are well known in Apatosaurus, Diplodocus, Eobrontosaurus, and both the holotype (BYU 9025; specimen numbering per Curtice and Stadtman (2001)) and referred material (BYU 12962) of Supersaurus. The scapula of Dicraeosaurus is poorly known: only two, partial specimens, both referred to D. sattleri, have been illustrated: MNB 2721 (O8) (Janensch, 1961: Pl. 15, Fig. 6) and MNB 2723 (E19) (Janensch, 1961: Pl. 15, Fig. 5). The latter more closely resembles other, more complete scapulae referred to Tornieria africana (see below), so it remains possible that at least some scapulae attributed to Tornieria actually belong to Dicraeosaurus (in which case the comparisons below under that genus apply here). The scapula of *T. africana* figured by Fraas (1908: Pl. 9, Fig. 3) resembles an ischium and does not match other specimens referred to the same taxon, such as MNB 2729 (A4) and 2730 (K34), that are used in the following comparisons.

The cranial end of the scapula of *Eobrontosaurus*, including its acromion process, is indistinguishable from that of *Suuwassea*. For *Amargasaurus*, Salgado and Bonaparte (1991) describe the acromion process as 'modest', which differs from the robust process in *Suuwassea*. The acromion of A. louisae is markedly different from that of Suuwassea because its deltoid crest lies directly on the caudal margin of the process, obviating a caudal fossa (Gilmore, 1936: Fig. 9A). The caudal margin of the process also possesses a short, blunt, caudally-projecting process that is absent in other flagellicaudatans. The acromion process of A. ajax reportedly also lacks a caudal fossa, although its deltoid crest lies cranial to the caudal margin of the acromion process (Upchurch et al., 2004a), and A. excelsus possesses a caudal fossa that is much smaller than that of Suuwassea (Gilmore, 1936: Fig. 10, 32). Although Janensch (1961) seems to have thought the acromion of Dicraeosaurus scapula MNB 2721 (O8) complete (because he did not dash in his estimate of a missing margin as he did for the distal end and for other figured Tendaguru scapulae), the entire margin of the bone from the dorsal surface of the preserved portion of the acromion to the glenoid fossa is heavily abraded and more likely indicates that the bulk of the process was destroyed. Certainly the more cranial fossa is absent; whether or not the preserved portion represents part of the deltoid crest or the caudal fossa is unclear. What is preserved of the acromion process, and indeed the entire lateral surface of the bone, is smooth, unladen by any pronounced ridges or crests, such as those seen in Suuwassea and other sauropods. On MNB dd3038 (mounted with specimen m and referred to D. hansmanni by Janensch (1961)), the deltoid crest angles toward the caudal margin of the acromion, as in Tornieria (see below) but dissimilar to Suuwassea. Also, the deltoid crest on dd3038 is much lower and less sharply distinguished from the surrounding fossae than in Suuwassea and other North American flagellicaudatans. The preserved lateral surfaces of both the acromion process and the scapular body, however, are both convex dorsoventrally, and the long axes of the convexities may be homologous with the more pronounced ridges in other sauropods. The convexity of the scapular body is broader dorsoventrally and lies much more dorsally on MNB 2721 (O8) than it is in Suuwassea and diplodocids.

![](_page_11_Figure_2.jpeg)

Fig. 8. Right metatarsals I (left column), II (middle column), and IV (right column) of ANS 21122 in row 1, proximal; row 2, cranial; row 3, lateral; row 4, caudal; row 5, medial; and row 6, distal views. Abbreviation: dlpr = distolateral process. Scale bar 10 cm.

![](_page_12_Figure_2.jpeg)

Fig. 9. Large (left column) and small (right column) preserved pedal phalanges of ANS 21122 in row 1, dorsal; row 2, lateral; row 3, plantar; and row 4, distal views. See text for discussion of placement on foot. Scale bar 10 cm.

Scapulae of Diplodocus and Supersaurus can be immediately distinguished from Suuwassea by the distinctive caudal angulation and placement of their acromion processes, in which the dorsalmost point lies much closer to the midpoint of the scapular body than in the Montana taxon (Hatcher, 1901: Fig. 14; Mook, 1917; McIntosh, 1990a). However, at least one scapula, that of a small juvenile currently referred to Diplodocus (USNM 337842), does not display this feature, so the development of this angulation may be ontogenetic. Contra Janensch (1961: 182), the caudal margin of the acromion of the ostensibly diplodocine Tornieria, as in Suuwassea, lies at a much more obtuse angle to the dorsal margin of the scapular body than in North American diplodocines. As a result, the dorsalmost point of the acromion of Tornieria retains the plesiomorphic proximity to the level of the glenoid than to the midpoint of the scapular body, unlike Diplodocus. However, both the deltoid crest and the acromial dorsoventral bisector angle much more caudally in Tornieria than in ANS 21122, approaching the condition in *Diplodocus*. As a result, the deltoid crest of the former lies much closer to the caudal margin of the acromion, rendering the caudal acromial fossa comparatively small and less pronounced.

The distal ends of scapulae vary widely in morphology among flagellicaudatans. The distal scapular bodies of Eobrontosaurus (TM 001, Filla and Redman, 1994) and A. louisae progressively expands in dorsoventral depth almost immediately caudal to the acromion (Gilmore, 1936; pers. obs.), but other specimens referred to Apatosaurus are more similar to Suuwassea in lacking this progressive expansion (McIntosh, 1995). In A. ajax, the caudal branch from the deltoid crest persists and is pronounced all the way to the distal end of the body, but there is reportedly no distal expansion (Upchurch et al., 2004a). The scapular bodies of Diplodocus and Supersaurus differ from that of Suuwassea by being shorter (because of the displacement of their acromion processes). Along with Tornieria (MNB 2730 (K34)), they also differ by possessing ventrally deflected ventral margins of their distal ends, effectively creating a ventral expansion of the distal end.

An elevated, rugose ridge or eminence situated immediately caudal to the acromion and close to the dorsal margin of the medial scapular surface like that of *Suuwassea* also occurs in at least some *Apatosaurus* (e.g. USNM 4268) and *Tornieria* (MNB 2729 (A4), 2723 (E19)) scapulae, plus a morphologically similar but unnumbered specimen in the MNB Tendaguru collection. A scapula of *Brachiosaurus* (MNB 2727 (Y10)) also displays this, although other scapulae of that taxon do not. The feature is expressed sporadically and probably has more to do with individual variation than phylogeny.

#### 4.2. Coracoid

The autapomorphic, quadrilateral coracoid of *Apatosaurus* (e.g. Marsh, 1896: Pl. 19, no. 1; McIntosh, 1995; Upchurch et al., 2004a) is immediately distinguishable from the (presumably plesiomorphic) morphology of *Suuwassea*, and all other flagellicaudatans, in which the dorsal and medial margins are rounded and form a continuous, uninterrupted arc. The coracoids of *Apatosaurus*, *Dicraeosaurus*, and *Diplodocus* also lacks the distinct ridge from the coracoid foramen to the dorsal margin, although they are similarly 'flexed' and convex in that area. The coracoid of *Eobrontosaurus* is rounded, as in *Suuwassea*, but appears to be shallower craniocaudally than in the latter (Filla and Redman, 1994; Bakker, 1998).

The coracoid of *Dicraeosaurus* (based on MNB 2718 and 2719, both from the dd quarry) is a much thicker and more robust bone than in *Suuwassea*. The various low ridges and shallow fossae discernible on the cranial surface of the *Suuwassea* coracoid are absent in *Dicraeosaurus*, which presents instead a simple, smooth, convex surface. In the more complete MNB 2179, the dorsomedial margin of the otherwise arcuate bone is autapomorphically interrupted by a fairly deep, abrupt, and parabolic notch (Janensch, 1961: Fig. 2).

In some specimens of *Diplodocus* (e.g. USNM 4268, CM 94), the coracoid foramen on the cranial surface is located much closer to the scapular articular surface than in the Montana

![](_page_13_Figure_2.jpeg)

Fig. 10. Pedal unguals I (left column), II (middle column) and ?III (right column) of ANS 21122 in row 1, proximal; row 2, lateral; row 3, medial; row 4, dorsal; and row 5, plantar views. Scale bar 10 cm.

taxon. The coracoid foramen in *Dicraeosaurus* sits directly against the scapular articular surface and tunnels at a straight, rather than oblique, angle so there is no offset between the openings on the cranial and caudal surfaces.

#### 4.3. Clavicle

The only other flagellicaudatan for which possible clavicles have been described is *Diplodocus*. Both CM 84 and 662 ('*D*.' *hayi*, HMNH 175) include peculiar bones that have generally been considered clavicles (Holland, 1906: Figs. 29, 30). These bones share with the possible clavicle of *Suuwassea* a sharp bend that separates a smaller, narrow region (that, in CM 662, terminates in a bifurcation) from a broader, flatter region. If the element in ANS 21122 is correctly identified, it is unclear to which end of CM 662 it correlates: certainly, it lacks the bifurcation of the former, but the broad terminus of the bone in CM 662 is farther from the sharp bend than if that were the proper homology in ANS 21122.

## 4.4. Humerus

Among flagellicaudatans, the humerus of *Suuwassea* is most similar to that of *Apatosaurus* (particularly *A. louisae*): both

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and, Ior digits	III and 1V, ungual two	digits previous (three	TOT Dyslocosaurus)						
	Suuwassea emilieae (ANS 21122)	Suuwassea emilieae (ANS 21122) <sup>a</sup>	Apatosaurus louisae (CM 3018)	cf. Apatosaurus (USNM 4287)	Diplodocus carnegi (CM 94)	Diplodocus longus (CM 30767)	Diplodocus sp. (USNM 11656)	Tornieria africana (MNB 2370 (28))	Dyslocosaurus polyonychyius (ACM 663)
Ln ext tub-tip, digit	159.8°	188.7	270.2 <sup>b</sup>	229.0	235.5	220.4	177.1	192.8°	195.0°
I unguar Ln ext tub-tip, digit II unanal	188.7(18.1%°)	159.8°(-15.3% <sup>d</sup> )	245.1 <sup>b</sup> (-9.3%)	$154.8^{c,e}(-32.4\%-)$	175.5(-25.5%)	$171.0^{\rm b}(-22.4\%)$	134.8(-23.9%)	$120.1^{\rm c}(-37.7\%)$	138.5°(-29%)
Ln ext tub-tip, digit	$80.3^{\rm f}(-57.4\%/-49.7\%^{\circ})$	$80.3^{\rm f}(-49.7\%^{\rm d}/-57.4\%)$	$170.4^{\rm b}(-30.5\%/36.9\%)$	$96.0^{c.g}(-38.0\%/-58.1\%)$	n/a	$153.9^{\rm b,d}(-10.0\%^{\rm c}/-30.2\%)$	$86.5^{\circ}(-35.8\%^{\rm d}/-51.2\%^{\rm d})$	n/a	n/a
III ungual Ln ext tub-tip, digit	ţ	ſ	n⁄a	n/a	n/a	n/a	n/a	n/a	65.6(-52.6%/-66.4%)
PAF max dors-vent	73.7	95.8	136.5	24)	109.8	122.6	101.3	110.3	66.5
PAF max dors-vent	95.8(30.0%)	73.7(-23.1%)	116.1(-14.9%)	24)	88.1(-19.8%)	$96.0^{ m b}(-21.7\%)$	76.5(-24.5%)	94.1(-14.7%)	52.5(-21.1%)
PAF max dors-vent	$40.4^{\rm f}(-57.8\%/-45.2\%)^{\rm f}$	$40.4^{\rm f}(-45.2\%/-57.8\%)^{\rm f}$	$79.9(-31.2\%h^{\rm l}-41.5\%)$	50	n/a	73.0(-24.0%/-40.5%)	41.0(-46.4%/-59.5%)	n/a	45.5(-13.3%/-31.6%)
digit III ungual PAF max dors-vent digit IV ungual	ſ	J	n⁄a	n/a	n/a	n/a	n/a	n/a	32.5(-28.6%/-38.1%/-51.19
<sup>a</sup> same as columr <sup>b</sup> estimate based o	1 one but with assignments of on partly reconstructed elemen	unguals I and II reversed (see nts.	e text for details).						

shement embedded in mount, so full value unable to be measured; In = length; max = maximum; dors-vent = dorsoventral measurement; ext tub = extensor tubercle; PAF = proximal articular face; n/a = not applicable. text for details). ungual placement on this digit questionable (see

measurement for reconstructed element, real value probably lower.

element diagenetically distorted.

measurement for preserved portion, real value greater.

have widely expanded proximal and distal ends compared to the proximodistally short, mediolaterally narrow diameter at midbody, though the humerus of Montana taxon is even more waisted than in Apatosaurus. Both taxa, as well as specimens of Tornieria, in which its development varies between specimens, also share a medial bulge of the deltopectoral crest. However, a partial juvenile humerus of Apatosaurus sp. (USNM 337827) and humeri of Dicraeosaurus lack this swelling, so it may be an ontogenetic or size-related feature. The humeri of A. louisae (CM 3018), Barosaurus (CM 21719; McIntosh, 1981), Diplodocus, and some specimens of Tornieria bear a second eminence, centered at the proximal end of the tricipital fossa, that is absent in Suuwassea. Like most muscle scars, this may be a size-related feature. The deltopectoral crest of A. ajax spans a comparatively smaller percentage of the overall humeral length than in Suuwassea or other species of Apatosaurus (Upchurch et al., 2004a). The lateral margin of

ANS 21122. On *Dicraeosaurus* humerus MNB 2631 (ab1), the apex of the proximal end is similarly situated near the sagittal axis of the bone as in *Suuwassea*, but on 2655 (ab2), it is displaced more medially, as in *Tornieria africana*. Similarly, the caudally less-pronounced caput of *Diplodocus* is, in cranial view, generally offset medially from the midline of the element more than in *Suuwassea* or *Apatosaurus*, where it appears more centered.

the bone in *A. ajax* is straighter than in *Suuwassea*, lacking a pronounced proximolateral process and flaring of the distolateral corner (Upchurch et al., 2004a: Fig. 5A, D). Humeri of other flagellicaudatans, including *Amargasaurus* (Salgado and Bonaparte, 1991), *Dicraeosaurus* (MNB 2631 (ab1) and 2655 (ab2); Janensch, 1961: Tab. 5), *Diplodocus*, and several elements from various stages of growth assigned to *Tornieria* (Janensch, 1961: Tab. 4), are less constricted at midshaft than in

*Suuwassea* remains the only flagellicaudatan to possess a pronounced proximal tuberculum. In *Diplodocus*, the combination of the aforementioned offset of the caput and absence of a proximal tuberculum forces the dorsal end of the deltopectoral crest to have a more ventral position compared to the dorsalmost point on the humerus than in *Suuwassea*, where the proximal tuberculum is only slightly lower than the top of the element. An exception to this is CM 21721, which is referred to *Diplodocus* but is much more similar to *Suuwassea* and *Apatosaurus*.

All flagellicaudatan humeri exhibit the small, closely appressed, cranial processes at the distal end seen in *Suuwassea*, though in *Dicraeosaurus* (MNB 2655 (ab2)) they are proportionately larger compared to the distal end overall and more centered on the shaft. Where visible in *Tornieria* (e.g. MNB 2656 (g81), 2639 (Ki68a) and 2673 (k37)), they are generally less pronounced and separated by a shallower sulcus than in *Suuwassea*.

## 4.5. Tibia

Variation in proximal tibial morphology has been undocumented among flagellicaudatans. Certainly, in *Apatosaurus* and *Tornieria*, the morphology is quite variable as demonstrated by

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![](_page_15_Figure_2.jpeg)

Fig. 11. Comparisons of flagellicaudatan appendicular elements (labeled by column): row 1, scapula and coracoid in lateral view; row 2, humerus in cranial view; row 3, right tibia in proximal view (with cnemial crests oriented in the same direction); and row 4, pedal unguals in side view. Drawings for *Apatosaurus* from Gilmore (1936), for *Diplodocus* humerus from Osborn and Granger (1901) and tibia from Hatcher (1901). Not to scale.

numerous referred specimens; whether these differences are intra- or interspecific remains to be seen. The shape in A. louisae (CM 3018) contrasts sharply with that of ANS 21122 by having opposite long and short axes (Gilmore, 1936: Fig. 23C). However, a second tibia referred to A. louisae (CM 33964) and that of A. ajax (NSMT-PV 20375) more closely approaches the equidimensionality of Suuwassea, though the caudal face of CM 33964 may be crushed, and that of A. ajax is only about 5% wider than long (Upchurch et al., 2004a), meeting the criterion of Wilson and Sereno (1998) for "subcircularity". Still other tibiae referred to Apatosaurus (e.g. CM 21729) are intermediate in morphology between ANS 21122 and CM 3018; CM 85 and 21729 even exceed the ratio seen in Suuwassea. Tibiae assigned to Dicraeosaurus, except for that recovered with MNB m (D. hansemanni), are either incomplete or damaged (Janensch, 1961: Fig. L1–5). (Based on its proximal proportions, MNB 2578 (H2) may also pertain to this taxon but is labeled as belonging to Tornieria). In MNB 2591 (Q12), the proximal articular surface is wider than long (at least 75%) parallel to the cnemial crest, more so than Suuwassea, even though part of the surface proximal to the cnemial crest is missing. Specimen MNB 2583 (O4) (Janensch, 1961: Fig. L4), a severely abraded specimen attributed to D. sattleri, is also wider than long but much less so than MNB 2591 (Q12). These both contrast with the tibia of MNB m that, though having its longest proximal axis across the cnemial crest, is somewhat more congruent in dimensions. Even so, it is still 28% wider than long. In Diplodocus carnegii, the proximal articular surface of the tibia, as seen in proximal view, is triangular (Hatcher, 1901: Fig. 18; pers. obs.), not quadrangular as in Suuwassea. This is also true of the proximal tibia of Dyslocosaurus (McIntosh et al., 1992). However, in a small tibia referred to Diplodocus, CM 33953, the mediolateral axis exceeds the craniocaudal by more than 50%, though this specimen has suffered a degree of crushing. All proximal tibial articular surfaces in *Tornieria* are wider mediolaterally than long craniocaudally, but the ratios vary such that the differences are as little as 10% or as great as 21%. If assignments of referred specimens are correct (and crushing accounted for), the variation greatly weakens the utility of the proximal articular surface dimensions as a phylogenetically useful character, at least for flagellicaudatans.

The cnemial crest of the tibia of *Apatosaurus ajax* (NSMT-PV 20375) does not project beyond the remainder of the tibial body in proximal view (Upchurch et al., 2004a: Fig. 12D), unlike *Suuwassea*. The cnemial crests of *Apatosaurus* and *Diplodocus* (CM 94) both bear fibular tubercula; a barely pronounced eminence may be discerned on *Dicraeosaurus* MNB 2591 (Q12) and in several specimens referred to *Tornieria*, but the feature is completely absent in *Dicraeosaurus* specimen MNB m, although the cnemial crest in this specimen swells distally. In *Apatosaurus*, though, the tuberculum is situated at the end of the cnemial crest.

## 4.6. Fibula

The gracile fibula of *Diplodocus* is virtually identical to that of Suuwassea. Apatosaurus fibulae are much more massive, stocky, and less waisted than the gracile element in Suuwassea, even specimens approximately the same size (e.g. CM 555/ 556). The fibula in Apatosaurus is less waisted at midlength but is otherwise similar in morphology. The M. iliofibularis tuberculum in CM 3018 is less well-defined and not delineated by pronounced ridges; on CM 22952, it is much more proximally placed than in ANS 21122. The fibula of Dicraeosaurus sattleri figured by Janensch (1961: Fig. L5), MNB 2628 (O5), is fairly heavily reconstructed in plaster, but its morphology compares favorably with MNB 2618 (Sa28), also referred to this species. As in Apatosaurus, both are shorter, somewhat stockier elements than the fibula of Suuwassea. Both retain a rough, triangular tibial articular surface but neither possesses a distinct tibial tuberculum. However, unlike Suuwassea, the caudal margin of the tibial articular surface is demarcated by a ridge where it abruptly transitions to smooth bone. Tornieria tibiae also lack a distinct tibial tuberculum.

In other respects, the fibulae of both *Apatosaurus* and *Diplodocus* are similar to that of *Suuwassea*. The muscle scar at midshaft in *Dicraeosaurus* MNB 2618 (Sa28) bears parallel ridges bounding its M. iliofibularis sulcus, somewhat similar to *Suuwassea*, but the sulcus is shallower. MNB 2628 (O5) differs in that the entire area is elevated above the surrounding bone; it bears neither distinct trochanters nor sulci, although the surface is somewhat abraded. This insertion site is situated somewhat more proximal on 2628 (O5) than on 2618 (Sa28). M. iliofibularis sulci on *Tornieria* fibulae MNB 2612 (H3) and 2626 (K1) each bear a longitudinal crest that bisects the fossa, unlike *Suuwassea*, but other fibulae assigned to the genus lack this feature, so it may either be ontogenetically or intraspecifically variable.

#### 4.7. Calcaneum

Bonnan (2000) demonstrated that a calcaneum is present in at least in one specimen of *Diplodocus* (CM 30767). One may also be preserved in *Apatosaurus* specimen CM 30766. This small element shares with its counterparts in *Suuwassea* and *Diplodocus* a non-Euclidean triangular morphology, but unlike *Suuwassea*, it is flattened proximodistally, and thus almost identical to the element in *Diplodocus* (CM 30767). CM 30766 also preserves a tibia and astragalus, so this isolated element could be supported as a tarsal element, but an ulna and manus have also been referred to it (McIntosh, 1981), so it remains possible that the bone is a carpal. A calcaneum in the MNB collections labeled 'Sauropoda gen. et sp. indet.' is virtually identical to a larger one assigned to *Brachiosaurus* and probably does not pertain to *Dicraeosaurus* or *Tornieria*.

#### 4.8. Metatarsal I

The morphology of metatarsal I appears to be conserved across most flagellicaudatan taxa, and so most differ from Suuwassea only in relatively minor details. Apatosaurus, as exemplified by USNM 4287 and NSMT-PV 20375, has a more rectangular proximal articular surface (McIntosh and Carpenter, 1998: Fig. 5E; Upchurch et al., 2004b: Fig. 13A), lacking the rounded, medial protrusion and cranio- and caudolateral processes seen in Suuwassea. The proximal articular surface in Diplodocus is similarly rectangular. The same elements in Apatosaurus specimens CM 89 and 3018, however, are more 'D'-shaped, as in the Montana taxon; CM 3018 is much more sharply indented on the lateral margin than in Suuwassea. MNB 2272 (O15), a metatarsal I referred to Dicraeosaurus sattleri, though abraded on many surfaces, agrees with metatarsal I of Suuwassea in all respects, including being riddled with nutrient foramina. Metatarsal I of Dyslocosaurus is typically diplodocoid and even 'D'-shaped in proximal view, as in Suuwassea. USNM 11656 (Diplodocus sp.) possesses a more pronounced notch on the medial surface between the cranial and caudal ends of the distal articular surface that is lacking in ANS 21122.

Exceptions to this overall similarity include MNB 2397 (dd113), referred to Dicraeosaurus hansemanni. Its proximal articular surface slopes sharply medially, but the distal articular surface is almost perpendicular to the long axis of the bone. Its proximal articular surface is rhomboidal and not indented laterally. A marked fossa at the distal end of the cranial face separates and defines medial and lateral distal condyles, unlike Suuwassea. Similarly, a sharp, oblique ridge, absent in ANS 21122, defines the proximocaudal extent of the distal articular surface. The large fossae on the lateral surface of metatarsal I in Suuwassea are completely absent in MNB 2397 (d113). The condition in a metatarsal I referred to Tornieria, MNB 2730 (28), resembles that of the aforementioned D. hansemanni element in that its the proximal articular surface, in cranial view, appears roughly horizontal while the distal surface slopes dorsomedially, whereas in caudal view, the proximal articular surface slopes sharply medially while the distal surface is horizontal. This specimen also possesses a distinctive protuberance on the lateral surface just distal to the proximal articular surface (Janensch, 1961: Fig. P1a) that is absent in *Suuwassea*. This specimen contrasts with others of more typical flagellicaudatan morphology referred to *Tornieria* (e.g. MNB 2284 (IXt4), 2286 (XVI28), and 2400 (XVI21)). The proximal articular surface of metatarsal I in the African taxon does not protrude as far medially as in *Suuwassea*, and is thus less 'D'-shaped and more trapezoidal.

Despite general morphological similarity, metatarsal I of *Suuwassea* is more slender than those of many other flagellicaudatans, having a smaller "stoutness" ratio (0.69, as defined by Upchurch et al., 2004a: 84–85) than *Apatosaurus ajax* (0.84), *A. louisae* (0.85), 0.82 in *Diplodocus*, and 0.85 in *Barosaurus* (Upchurch et al., 2004a). It is closer to the ratio of 0.70 for *Dyslocosaurus* (McIntosh et al., 1992).

#### 4.9. Metatarsal II

Apatosaurus exhibits some variability in the morphology of metatarsal II: the proximal articular surface of USNM 4287 has a more triangular, craniocaudally broader proximal articular surface than does ANS 21122; those of CM 89 and 3018 again more closely match Suuwassea but bear marked pits at their craniolateral corners. USNM 4287 also has a more pronounced eminence at the distolateral corner of the cranial surface. In NSMT-PV 20375, the surface is largely rectangular with a rounded caudolateral corner (Upchurch et al., 2004a: Fig. 13A), very unlike Suuwassea. The rhomboidal proximal ends of metatarsal II in Dicraeosaurus specimens MNB 2270 (dd113) and MNB 2395 (St593) are longer craniocaudally than wide and not embayed as in Suuwassea because the fossae on the medial and lateral surfaces of the bone do not extend far enough proximally to affect the shape of the proximal articular surface. Like Suuwassea, a rugose knob at the distolateral corner interrupts the otherwise smooth cranial face of MNB 2395 (St593). The distal articular surface of metatarsal II in Dicraeosaurus is more rectangular than in Suuwassea and its condyles are not separated at its caudal end by a notch. In contrast, the distal articular surface in Diplodocus (USNM 11656) is more hourglass-shaped than in Suuwassea. The Montana taxon lacks the pronounced, ridge-like muscle insertion on the distolateral surface of metatarsal II seen in Dyslocosaurus. As with its metatarsal I, the proximal and distal articular surfaces of metatarsal II of Tornieria do not angle toward each other like they do in ANS 21122, but the bone is otherwise similar. Where there is a rugosity on the distolateral corner of the cranial surface on metatarsal II of Suuwassea, Tornieria possess a marked knob of rugose bone.

#### 4.10. Metatarsal IV

Metatarsal IV of *Apatosaurus*, based on USNM 4287 and CM 89, is very similar to that of *Suuwassea* in all-visible respects; that on CM 3018 is pathologic and does not lend itself to comparison. In *A. ajax* (NSMT-PV 20375), the proximal articular surface is much more ovoid than in *Suuwassea* – it actually more closely matches the morphology of the proximal

articular surface of metatarsal II of the latter (Upchurch et al., 2004a: Fig. 13A). The element in Diplodocus (USNM 10865 and 11656) is very similar to that of Suuwassea, lacking only the waisting seen in the proximal articular surface of the Montana taxon. Metatarsal IV of Dicraeosaurus, as exemplified by MNB 2273 (bb7), differs from its counterpart in ANS 21122 in having a mediolaterally compressed, tear-drop-shaped proximal articular surface whose caudal process projects caudally rather than caudomedially and is thus not visible in cranial view. Its distal articular surface is roughly circular, again in contrast to Suuwassea. In morphology, metatarsal IV of Tornieria is similar in morphology to its complement in Suuwassea, but roughly equal in length to its own metatarsal II, unlike the Morrison taxon. The element identified as metatarsal IV in ANS 21122 also resembles metatarsal III of Tornieria. which is longer than metatarsal II. The distal articular surface of metatarsal III in the Tanzanian sauropod is much more square than the element in Suuwassea. Metatarsal IV of Tornieria more closely matches that of Suuwassea in that the long axis of its proximal articular surface is closer to perpendicular to that of the distal end, a feature not present in its metatarsal III.

#### 4.11. Non-ungual phalanges

As discussed above (under 'Non-terminal phalanges'), the smaller phalanx of ANS 21122 is virtually identical to that of III-1 of Apatosaurus specimen USNM 4287. However, the larger phalanx has the opposite length:width proportions of phalanx II-1 in the same specimen. Phalanx I-1 in USNM 4287 is embedded in plaster in articulation with its metatarsal and ungual and thus not fully visible, but it is much wider proximally, and shorter both at midlength and distally than it is long, only somewhat similar to the larger phalanx in ANS 21122. Phalanges II-1 and III-1 on the type specimen of A. louisae (CM 3018) and all preserved phalanges in the pes of A. ajax (NSMT-PV 20375) are much shorter proximodistally than those of Suuwassea but are otherwise of similar morphology except that the distal articular surface in phalanx I-1 in A. *louisae* is much more mediolaterally compressed and there is a shallow, possibly collateral ligament, fossa on the medial surface of II-1. Phalanx II-1 of CM 89 is similarly broader than long, but III-1 on this specimen displays the opposite condition, as does its IV-1, both of which are similar to the phalanges in ANS 21122. Pedal phalanges I-1 of all Diplodocus specimens are both short, almost shapeless elements, but phalanges II-1, III-1, and IV-1 have more typical phalangeal morphology. In USNM 11656 and CM 30767, all of the latter are wider mediolaterally than they are long, unlike those of Suuwassea, but are otherwise similar. However, in CM 94, phalanges III-1 and IV-1 are longer than wide; in gross morphology, both (but particularly IV-1) are much more similar to the small than to the large phalanx recovered for ANS 21122, and is conceivable that the phalanx ascribed here to III-1 of Suuwassea actually belongs to IV-1. More distal phalanges are short, disc-like elements in Diplodocus that have no comparable elements preserved in ANS 21122. The large phalanx of ANS 21122 is similar in morphology to MNB 2730 (28), a phalanx II-1 of *Tornieria* (Janensch, 1961: Fig. Q–A II1a) but is much longer and less asymmetrical at its distal end. The smaller phalanx is vaguely similar to III–1 of the latter specimen, but again longer. Neither preserved phalanx of ANS 21122 is similar to MBR 2300 (68); (Janensch, 1961: Fig. Q A I1 and B I1, a proximodistally compressed, almost amorphous phalanx I–1 also assigned to *Tornieria*.

Pedal phalanges have not been identified for *Dicraeosaurus*. Some pedal phalanges attributed to *Dyslocosaurus* may not pertain to that taxon (Wilson and Sereno, 1998); those pictured by McIntosh et al. (1992) are dissimilar to those preserved in ANS 21122.

#### 4.12. Unguals

An ungual referred to the pes of Apatosaurus (USNM 5383) is long and low in lateral aspect, much more similar to the ungual assigned here to digit I than II of ANS 21122 but is broader mediolaterally and does not taper toward its distal end. Instead, it is squared off, more like the pollex claw of CM 3018 (Gilmore, 1936: Fig. 18), but the element is longer than the latter. The claw also lacks a distinctive extensor tubercle as in ungual I of ANS 21122. USNM 5383 may pertain to Camarasaurus (M. Bonnan, note with specimen, 1999). However, it is also similar to ungual I of Apatosaurus pes USNM 4287. The ungual of pedal digit I of A. ajax (NSMT-PV 20375) is long, low, and terminated in a bluntly rounded tip, but possesses an extensor tubercle. In CM 89, ungual II is essentially a smaller version of ungual I, and neither closely resembles the elongate ungual of ANS 21122. Unguals III of USNM 4287 and CM 89 are unlike the small ungual of ANS 21122 because they are laterally compressed. Digits IV and V of Apatosaurus lack onychiform terminal unguals, having rounded nubbins of bone instead.

The only ungual phalanx ascribed to Dicraeosaurus, MNB 2333 (dd113), is somewhat similar to the largest of Suuwassea except its ventral distoplantar margin is not as concave in lateral view. The neurovascular sulcus on one of its sides turns sharply and extends all the way to the distal end of the element (Janensch, 1961: Fig. R 5a; pers. obs.), unlike either of the large unguals preserved in ANS 21122. The pedal phalangeal formula of Diplodocus may allow some variation (McIntosh, 1990a) and the unguals of CM 94 and USNM 11656 differ significantly. Most prominently, CM 94 lacks an onychiform ungual on digit III, whereas one is present in USNM 11656. Whether the absence in CM 94 is real (McIntosh, 1981) or taphonomic (Hatcher, 1901) is unknown. Unguals I of USNM 11656 and CM 94 and 30767 are similar to the larger, complete ungual of Suuwassea, including possessing a pit rather than an extensor tubercle. In USNM 11656, however, the claw tapers to a more round and blunt point distally. Ungual II in all three specimens, however, is more like a smaller version of ungual I than is the longer, lower claw in ANS 21122. Ungual III, present only in USNM 11656 and CM 30767, is unlike the small ungual in ANS 21122 by being laterally compressed and generally onychiform. Digits IV and V lack unguals in Diplodocus. The largest ungual of Tornieria, MNB 273 (28) (Janensch, 1961: Fig. Q–A I2a), is intermediate in length and morphology between the two largest unguals preserved in ANS 21122. Its proximal articular surface is much more planar than in *Suuwassea*, and its neurovascular sulci are largely invisible. None of the several small unguals in the MNB collections labeled only as 'Sauropoda gen. et sp. indet.' that could pertain to either *Dicraeosaurus* or *Tornieria* resemble the small ungual of *Suuwassea* because they are all laterally compressed.

Dyslocosaurus (ACM 663) deserves especial scrutiny because of its peculiar possession of four onychiform pedal unguals. If, as discussed above, ANS 21122 also possesses four onychiform pedal unguals, it raises the possibility that the two taxa are congeneric, with Dyslocosaurus the senior synonym. However, as above, the tibiae and second metatarsals of the two taxa differ. The ungual ascribed to pedal digit IV of Dyslocosaurus is similar to the small ungual of Suuwassea by being less laterally compressed and less recurved than the larger unguals. There are proportional differences, however (Table 3). Concern voiced over the inclusion of some elements of the holotype of this genus (Wilson and Sereno, 1998: 41) indicates that it is possible that the ungual assigned to that digit does not properly belong there. Given what differences exist, coupled with the problems of whether or not ACM 663 represents (a) a Morrison Formation sauropod, and (b) a single individual (McIntosh et al., 1992; Wilson and Sereno, 1998), it is most prudent to maintain Suuwassea and Dyslocosaurus as separate taxa until further material of the latter is identified.

#### 4.13. Other sauropods

As noted by Harris (2006a), some workers have proposed that *Seismosaurus* may be synonymous with *Diplodocus*. The lone distinguishing (autapomorphic) feature (per Upchurch et al., 2004b) of NMMNH 3690, the type specimen of *S. hallorum*, is its caudally-hooked distal ischia. Ischia are not preserved in ANS 21122, obviating direct comparison, but overall similarity of *Seismosaurus* to *Diplodocus* suggests that it cannot be conspecific with *Suuwassea*.

Wilson and Sereno (1998) note that both possession of an onychiform ungual on pedal digit II and great reduction or absence of the ungual on digit IV are eusauropod apomorphies, present in all adequately described sauropods except Vulcanodon (Gongxianosaurus was not included in their analysis). More than three is therefore a secondary reversal. Wilson and Sereno (1998) questioned the validity of claims of supratrinary polyonychy in a specimen referred to the poorly understood Lower Cretaceous sauropod *Pleurocoelus* by Gallup (1989) citing, in part, ichnological evidence that sauropod pedes possess large unguals only on digits I-III (Farlow et al., 1989). However, some sauropod hind footprints, including some from the ?Upper Jurassic or Lower Cretaceous of Morocco (Ishigaki, 1988, 1989; Farlow, 1992) and Lower Cretaceous of Texas (Farlow, 1987; Farlow et al., 1989) reportedly show impressions from four pedal unguals (but see Meyer and Monbaron (2002) concerning the Moroccan prints). The impression of the ungual on digit IV is indeed small in these tracks, but is similar to those of digits I-III in morphology (laterally compressed) and orientation. Although not adequately described, Gallup (1989) briefly discussed the taphonomy of the cf. *Pleurocoelus* foot: it was found upright in originally thixotropic sediments, implying the animal to which it belonged was trapped and originally preserved at least partially upright, similar to articulated, vertically-oriented manus specimens from Tendaguru referred to *Brachiosaurus* and *Janenschia* (Aberhan et al., 2002). If this interpretation is correct, the cf. *Pleurocoelus* foot was most likely articulated, making Gallup's description of four pedal unguals accurate. Together, the osteological and ichnological records indicate that tetronychy may be more common than previously thought in post-Early Jurassic sauropods.

### 5. Taphonomy

The biostratinomic taphonomy of ANS 21122 was reviewed by Harris (2006a). Evidence for scavenging is preserved on the pedal elements. All three preserved metatarsals and the largest phalanx display tooth marks (scores), particularly at the margins of their proximal articular surfaces (Figs. 8(2, 4) and 9(1)). The bulk of these marks scar the distal ends of the bones, but metatarsals I and II bear a few proximally and metatarsal II has two on the shaft. Most of the marks are deep, mostly parallel grooves on the boundaries between the shaft and the proximal and distal articular faces. Most are oblique to the long axes of their respective elements. Similar patterns of tooth marks on the ends of sauropod limb elements have been previously noted (Hunt et al., 1994; McIntosh et al., 1996). The taxonomic affiliation of the carnivore(s) responsible for the marks is indeterminate. The spacing between many of the parallel grooves is small; if they were made simultaneously by single events, and thus reflect actual labiolingual distances between successive teeth, then the maker was a small animal, almost certainly too small to have been preying on the sauropod. Instead, it implies scavenging. Yet the depth of the grooves on the thick, solid bone implies an animal with strong jaw muscles, possibly crocodylomorphs (e.g. Hallopus) or juveniles of a large, robust theropod. A small, shed, allosauroid-style theropod tooth recovered in sediments immediately around the Suuwassea specimen supports the latter assessment.

The localization of the marks on the distal ends of the metapodials is intriguing. The tendency of mammalian carnivores (especially hyaenas) to gnaw the ends of limb bones is well-known (e.g. Miller, 1969; Haynes, 1980, 1983; Hill, 1980). Some Mesozoic carnivores clearly exhibited the same behavior, as evidenced by tooth marks (e.g. ANS 21122 and a Camarasaurus grandis femur (McIntosh et al., 1996)). Fiorillo (1991), however, discussed reasons why theropods probably gnawed bones less frequently than their mammalian counterparts. Hyaenas in particular try to crack the ends of metapodials to get to the marrow cavities inside, but except for tyrannosaurids (Farlow et al., 1991; Chin et al., 1998), theropods were not adept bone crackers. Instead, scavengers responsible for the marks on ANS 21122 may have been attempting to get at protein-rich synovial fluids, fatty synovial pads, and even articular and meniscus cartilages. Because sauropod appendages were compact and held vertically as a functional response to load bearing as in large modern mammals (e.g. proboscideans), it seems likely that the soft tissue surrounding the metapodials and within the joint capsules was more substantial than in most other taxa, although elephants lack substantial menisci (Forstenpointner et al., 2001). Thus, sauropod appendicular joints may have been singled out by scavengers able to tear off and remove digits from the proximity of the carcass.

#### 6. Discussion

As with the cranial and axial skeleton (Harris, 2006a, 2006c), the appendages of *Suuwassea* display an amalgamation of features seen in other flagellicaudatans. The scapula lacks the diagnostic caudal offset of the acromion and caudoventral expansion of diplodocines and the progressive expansion of the body seen in *Apatosaurus louisae*. Similarly, the coracoid retains the plesiomorphic arcuate margin, unlike the quadrilateral morphology of *Apatosaurus*. The humerus is peculiar by possessing a pronounced proximal tuberculum unlike any other sauropod except saltasaurine titanosaurians (Upchurch, 1998), though it is placed on a distinct, laterally-projecting proximolateral process that has a typical, non-titanosaurian morphology.

The rectangular proximal articular surface of the tibia contrasts with the triangular shape of Diplodocus, and has oppositely oriented long and short axes from A. louisae, but specimens referred to these and other flagellicaudatan taxa display a wide variety of proportions, rendering the utility of this character dubious. Metatarsal I bears the distinctive distolateral process of other flagellicaudatans, but the pedal phalanges have unusual proportions compared to its relatives. One claw preserved in ANS 21122 is low and long, unlike other known flagellicaudatan pedal unguals; whether this truly belongs on the foot remains to be seen. The unusually small, non-onychiform pedal ungual of Suuwassea, belonging either to pedal digit III or IV, is unlike those of either Apatosaurus or Diplodocus but bears some similarity to the enigmatic Dyslocosaurus, from which Suuwassea differs in tibial and second metatarsal morphology.

Again as with the skull and vertebrae, the limb elements of *Suuwassea* are closer to those of *Apatosaurus* in morphology than to other flagellicaudatans, but much of this similarity is to specimens referred to *Apatosaurus* spp., not to the holotypes of the three species. Further work is required to sort out intraspecific diversity and variation within *Apatosaurus* and other diplodocids before these characters can be incorporated into a formal phylogenetic analysis. In the interim, Harris (2006b) provides a phylogenetic analysis of *Suuwassea* using currently recognized characters.

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#### References

- Aberhan, M., Bussert, R., Heinrich, W.-D., Schrank, E., Schultka, S., Sames, B., Kriwet, J., Kapilima, S., 2002. Palaeoecology and depositional environments of the Tendaguru beds (Late Jurassic to Early Cretaceous Tanzania). Mitteilungen aus dem Museum f
  ür Naturkunde in Berlin: Geowissenschaftliche Reihe 5, 19–44.
- Alexander, R.M., 1998. All-time giants: the largest animals and their problems. Palaeontology 41, 1231–1245.
- Bakker, R.T., 1998. Dinosaur mid-life crisis: the Jurassic-Cretaceous transition in Wyoming and Colorado. In: Lucas, S.G., Kirkland, J.I., Estep, J.W. (Eds.), Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science, Albuquerque, pp. 67–77.
- Baumel, J.J., Witmer, L.M., 1993. Osteologia. In: Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vanden Berge, J.C. (Eds.), Handbook of avian anatomy: Nomina anatomica avium, second edition. Nuttall Ornithological Club, Cambridge, pp. 45–132.
- Bird, R.T., 1944. Did *Brontosaurus* ever walk on land? Natural History 53, 60– 69.
- Bonnan, M.F., 2000. The presence of a calcaneum in a diplodocoid sauropod. Journal of Vertebrate Paleontology 20, 317–323.
- Bonnan, M.F., 2003. The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. Journal of Vertebrate Paleontology 23, 595–613.
- Borsuk-Bialynicka, M., 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. Palaeontologia Polonica 37, 5–63.
- Chin, K., Tokaryk, T.T., Erickson, G.M., Calk, L.C., 1998. A king-sized coprolite. Nature 393, 680–682.
- Christian, A., Heinrich, W.-D., Golder, W., 1999. Posture and mechanics of the forelimbs of *Brachiosaurus brancai* (Dinosauria: Sauropoda). Mitteilungen aus dem Museum f
  ür Naturkunde in Berlin: Geowissenschaftliche Reihe 2, 63–73.
- Christiansen, P., 1997. Locomotion in sauropod dinosaurs. Gaia 14, 45-75.
- Curtice, B., Stadtman, K., 2001. The demise of *Dystylosaurus edwini* and a revision of *Supersaurus vivianae*. In: McCord, R.D., Boaz, D. (Eds.), Western association of vertebrate paleontologists and southwest paleontological symposium - proceedings 2001. Mesa Southwest Museum, Mesa, pp. 33–40.

- Farlow, J.O., 1987. Lower Cretaceous dinosaur tracks, Paluxy River valley, Texas. Baylor University, Wacos, Texas.
- Farlow, J.O., 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. Zubía 10, 89–138.
- Farlow, J.O., Brinkman, D.L., Abler, W.L., Currie, P.J., 1991. Size, shape, and serration density of theropod dinosaur lateral teeth. Modern Geology 16, 161–198.
- Farlow, J.O., Pittman, J.G., Hawthorne, J.M., 1989. Brontopodus birdi, Lower Cretaceous sauropod footprints from the U. S. Gulf Coastal Plain. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 371–394.
- Filla, J., Redman, P.D., 1994. Apatosaurus yahnahpin a preliminary description of a new species of diplodocid dinosaur from the Late Jurassic Morrison Formation of southern Wyoming the first sauropod dinosaur found with a complete set of 'belly ribs'. In: Nelson, G.E. (Ed.), The dinosaurs of Wyoming. Wyoming Geological Association, Casper, pp. 159–178.
- Fiorillo, A.R., 1991. Prey bone utilization by predatory dinosaurs. Palaeogeography, Palaeoclimatology, Palaeoecology 88, 157–166.
- Forstenpointner, G., Weissengruber, G., Kübber-Heiss, A., Hittmair, K., Konar, M., 2001. Morphological features of the stifle joint of the African elephant (*Loxodonta africana* Blumenbach, 1797). Journal of Morphology 248, 230.
- Fraas, E., 1908. Ostafrikanische Dinosaurier. Palaeontographica 55, 105-144.
- Gallup, M.R., 1989. Functional morphology of the hindfoot of the Texas sauropod *Pleurocoelus* sp. indet. In: Farlow, J.O. (Ed.), Paleobiology of the dinosaurs. Geological Society of America Special Paper 238, pp. 71–74.
- Gilmore, C.W., 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. Memoirs of the Carnegie Museum 11, 175–271.
- Gunga, H.-C., Kirsch, K., Rittweger, J., Röcker, L., Clarke, A., Albertz, J., Wiedemann, A., Mokry, S., Suthau, T., Wehr, A., Heinrich, W.-D., Schultze, H.-P., 1999. Body size and body volume distribution in two sauropods from the Upper Jurassic of Tendaguru (Tanzania). Mitteilungen aus dem Museum für Naturkunde in Berlin: Geowissenschaftliche Reihe 2, 91–102.
- Harris, J.D., 2004. Confusing dinosaurs with mammals: tetrapod phylogenetics and anatomical terminology in the world of homology. Anatomical Record 281A, 1240–1246.
- Harris, J.D., 2006a. The axial skeleton of *Suuwassea emilieae* (Sauropoda: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana, USA. Palaeontology 49, 1091–1121.
- Harris, J.D., 2006b. The significance of *Suuwassea emilieae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. Journal of Systematic Palaeontology 4, 185–198.
- Harris, J.D., 2006c. Cranial osteology of *Suuwassea emilieae* (Sauropoda: Diplodocoidea: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana, USA. Journal of Vertebrate Paleontology 26, 88–102.
- Harris, J.D., Dodson, P., 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. Acta Palaeontologica Polonica 49, 197–210.
- Hatcher, J.B., 1901. *Diplodocus* (Marsh): its osteology, taxonomy, and probable habits, with a restoration of the skeleton. Memoirs of the Carnegie Museum 1, 1–63.
- Haynes, G., 1980. Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones. Paleobiology 6, 341–351.
- Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology 9, 164–172.
- Hill, A.P., 1980. Early postmortem damage to the remains of some contemporary East African mammals. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), Fossils in the making: vertebrate taphonomy and paleoecology. University of Chicago Press, Chicago, pp. 131–152.
- Holland, W.J., 1906. The osteology of *Diplodocus* Marsh, with special reference to the restoration of the skeleton of *Diplodocus carnegiei* Hatcher. Memoirs of the Carnegie Museum 2, 225–264.
- Holland, W.J., 1924. The skull of *Diplodocus*. Memoirs of the Carnegie Museum 9, 379–403.
- Hunt, A.P., Meyer, C.A., Lockley, M.G., Lucas, S.G., 1994. Archaeology, toothmarks and sauropod dinosaur taphonomy. In: Lockley, M.G., Dos

Santos, V.F., Meyer, C.A., Hunt, A. (Eds.), Aspects of sauropod paleobiology. Gaia 15, pp. 225–231.

- Ishigaki, S., 1988. Les empreintes de Dinosaures du Jurassique inférieur du Haut Atlas central Marocain. Notes et Mémoires du Service Géologique du Maroc 44, 79–86.
- Ishigaki, S., 1989. Footprints of swimming sauropods from Morocco. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur tracks and traces. Cambridge University Press, Cambridge, pp. 83–86.
- Janensch, W., 1961. Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. Palaeontographica supplement 7, 3, 177–235.
- Lockley, M.G., Houck, K.J., Prince, N.K., 1986. North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. Geological Society of America Bulletin 97, 1163–1176.
- Lockley, M.G., Meyer, C.A., Hunt, A.P., Lucas, S.G., 1994. The distribution of sauropod tracks and trackmakers. In: Lockley, M.G., Dos Santos, V.F., Meyer, C.A., Hunt, A. (Eds.), Aspects of sauropod paleobiology. Gaia 15, pp. 223–248.
- Lydekker, R., 1893. The dinosaurs of Patagonia. Anales del Museo de La Plata 2, 1–14.
- Marsh, O.C., 1896. The dinosaurs of North America. The Annual Report of the U. S. Geological Survey 1895–1895, 135–244.
- McIntosh, J.S., 1981. Annotated catalogue of the dinosaurs (Reptilia Archosauria) in the collections of Carnegie Museum of Natural History. Bulletin of the Carnegie Museum of Natural History 18, 1–67.
- McIntosh, J.S., 1990a. Sauropoda. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. University of California Press, Berkeley, pp. 345–401.
- McIntosh, J.S., 1990b. Species determination in sauropod dinosaurs with tentative suggestions for their classifications. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur systematics: perspectives and approaches. Cambridge University Press, Cambridge, pp. 53–69.
- McIntosh, J.S., 1995. Remarks on the North American sauropod Apatosaurus Marsh. In: Sun, A., Wang, Y. (Eds.), Sixth symposium on Mesozoic terrestrial ecosystems and biota, short papers. China Ocean Press, Beijing, pp. 119–123.
- McIntosh, J.S., Carpenter, K., 1998. The holotype of *Diplodocus longus*, with comments on other specimens of the genus. In: Carpenter, K., Chure, D.J., Kirkland, J.I. (Eds.), The Upper Jurassic Morrison Formation: an interdisciplinary study. Modern Geology, 23, pp. 85–110.
- McIntosh, J.S., Coombs Jr., W.P., Russell, D.A., 1992. A new diplodocid sauropod (Dinosauria) from Wyoming, USA. Journal of Vertebrate Paleontology 12, 158–167.

- McIntosh, J.S., Miles, C.A., Cloward, K.C., Parker, J.R., 1996. A new nearly complete skeleton of *Camarasaurus*. Bulletin of the Gunma Museum of Natural History 1, 1–87.
- Meers, M.B., 2003. Crocodylian forelimb musculature and its relevance to Archosauria. The Anatomical Record 274A, 891–916.
- Meyer, C.A., Monbaron, M., 2002. Middle Jurassic dinosaur tracks from Morocco - facts and fiction. In: The 7th European workshop of vertebrate paleontology. EWVP, Sibiu, p. 27.
- Miller, G.J., 1969. A study of cuts, grooves, and other marks on Recent and fossil bone I Animal tooth marks. Tebiwa 12, 20–26.
- Mook, C.C., 1917. The fore and hind limbs of *Diplodocus*. Bulletin of the American Museum of Natural History 37, 815–819.
- Nopsca, F., 1905. Remarks on the supposed clavicle of the sauropodous dinosaur *Diplodocus*. Proceedings of the Zoological Society of London 289–294.
- Osborn, H.F., Granger, W., 1901. Fore and hind limbs of Sauropoda from the Bone Cabin Quarry. Bulletin of the American Museum of Natural History 14, 199–208.
- Salgado, L., Bonaparte, J.F., 1991. In: Un nuevo sauropod Dicraeosauridae, *Amargasaurus cazaui* gen. et sp. nov., de la Formación La Amarga, Neocomiano de la Provincia del Neuquen, Argentina. Ameghiniana 28. 333–346.
- Upchurch, P., 1998. The phylogenetic relationships of sauropod dinosaurs. Zoological Journal of the Linnean Society 124, 43–103.
- Upchurch, P., Barrett, P.M., McIntosh, J.S., Dodson, P., 2004a. Sauropoda. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. second edition. University of California Press, Berkeley, pp. 259–322.
- Upchurch, P., Tomida, Y., Barrett, P.M., 2004b. A new specimen of *Apatosaurus ajax* (Sauropoda: Diplodocidae) from the Morrison Formation (Upper Jurassic) of Wyoming, USA. National Science Museum of Tokyo Monographs 26, 1–108.
- Wilson, J.A., 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society 136, 217–276.
- Wilson, J.A., Carrano, M.T., 1999. Titanosaurs and the origin of 'wide-gauge' trackways: a biomechanical and systematic perspective on sauropod locomotion. Paleobiology 25, 252–267.
- Wilson, J.A., Sereno, P.C., 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memoir 5, 1–68.
- Zhang, Y., 1988. In: The Middle Jurassic Dinosaur Fauna from Dashanpu, Zigong, Sichuan Vol. III. Sauropod dinosaur (I). *Shunosaurus*. Sichuan Publishing House of Science and Technology, Chengdu China. (in Chinese).