

A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA

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Harris, J.D. and Dodson, P. 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. *Acta Palaeontologica Polonica* 49 (2): 197–210.

A partial skeleton of a new sauropod dinosaur from the Upper Jurassic Morrison Formation (?Tithonian) of Montana is described. *Suuwassea emilieae* gen. et sp. nov. is diagnosed by numerous cranial, axial, and appendicular autapomorphies. The holotype consists of a premaxilla, partial maxilla, quadrate, braincase with partial skull roof, several partial and complete cranial and middle cervical, cranial dorsal, and caudal vertebrae, ribs, complete scapulocoracoid, humerus, partial tibia, complete fibula, calcaneus, and partial pes. It displays numerous synapomorphies of the Diplodocoidea, including characters of both the Diplodocidae (*Apatosaurus* + (*Diplodocus* + *Barosaurus*)) and Dicraeosauridae (*Dicraeosaurus* + *Amargasaurus*). Preliminary phylogenetic analysis indicates that *Suuwassea* is a diplodocoid more derived than rebbachisaurids but in a trichotomy with both the Diplodocidae and Dicraeosauridae. *Suuwassea* represents the first well-supported, North American, non-diplodocid representative of the Diplodocoidea and provides new insight into the origins of both the Diplodocidae and Dicraeosauridae.

Key words: Dinosauria, Diplodocoidea, Diplodocidae, Dicraeosauridae, paleobiogeography, phylogeny, Morrison Formation, Jurassic.

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Introduction

The Morrison Formation of the western United States is arguably one of the most expansive and productive Mesozoic terrestrial units anywhere in the world, producing ichnites, plants, invertebrates, and, most spectacularly, vertebrates, especially dinosaurs (see papers in Carpenter et al. 1998). However, in contrast to numerous quarries in Colorado, New Mexico, Oklahoma, Utah, and Wyoming, vertebrate fossils from Morrison Formation outcrops in Montana have historically been somewhat rarer than their southern counterparts. The only Montana vertebrate fossils from the Morrison Formation formally attributed to specific genera are a set of fore- and hind limb elements ascribed to *Diplodocus* by Mook (1917) and a partial skeleton tentatively placed in the poorly-understood genus *Amphicoelias* by Wilson and Smith (1996) based the cross-sectional morphology of the femur as well as general dissimilarity to well-known, typical Morrison Formation diplodocids (J. Wilson, personal communication 2002). The northern extent of the well-known Morrison Formation fauna occurs otherwise in the southern Bighorn Basin, Wyoming (e.g., the Howe Quarry—see Breithaupt 1996; Ayers 2000).

Recent reports and investigations (Horner 1989; Curry 1994; Turner and Peterson 1999; Storrs and Garcia 2001), however, have produced a substantial number of vertebrate fossils from the Morrison Formation in Montana. Interestingly, these reports are dominated by small sauropod individu-

als. In contrast, specimens from more southern outcrops tend to be larger individuals, and juveniles are uncommon (Weishampel and Horner 1994, but see Carpenter and McIntosh 1994, and Curry 1999 for exceptions). None of these Montana specimens has yet been formally described, so it is not yet known whether they pertain to juveniles of either known or new sauropod taxa that would have attained larger sizes as adults, or to new taxa that remain comparatively small as adults. If the former, they are important because despite a comparative wealth of specimens, ontogenetic change is poorly understood for Morrison Formation sauropods, and accumulations of juveniles may have important paleoecological and behavioral implications thus far hypothesized only using footprint data (e.g., Lockley et al. 1994). If the latter, then the northern end of the Morrison Formation depositional basin may contain a unique fauna from a heretofore unrecognized paleoecosystem that contrasts with the general portrait of the formation's fauna based on material from outcrops south of the Bighorn Basin. The sauropod described in this preliminary report pertains to a new diplodocoid (Table 1), *Suuwassea emilieae* gen. et sp. nov., that appears to fit into this "small sauropod" pattern, measuring an estimated 14–15 m long, approximately two-thirds the size of the holotypes of *Diplodocus carnegii* and *Apatosaurus louisae*.

Institutional abbreviation.—ANS, Academy of Natural Sciences, Philadelphia.

Table 1. Synapomorphies of the Diplodocoidea and inclusive clades per Upchurch (1998), Wilson and Sereno (1998), and Wilson (2002). Only those states that could be diagnosed in *Suuwassea* are listed.

Upchurch 1998	Wilson and Sereno 1998	Wilson 2002
<p>Diplodocoidea</p> <ul style="list-style-type: none"> + premaxilla narrow at rostral end and elongate rostrocaudally + ratio of rostrocaudal width of supratemporal fenestra: mediolateral width of occiput ≤ 0.10 + long axis of quadrate oriented caudodorsal-rostroventral + loss of lingual concavity on worn tooth crowns + ratio of tooth crown height: mesiodistal width ≥ 5.0 + worn tooth crowns with subparallel mesial and distal margins <p>Diplodocidae</p> <ul style="list-style-type: none"> + rounded distal ends of paroccipital processes + laterally compressed parasphenoid rostrum lacking dorsal sulcus + grooves on labial surfaces of tooth crowns absent + pedal phalanx II-2 craniocaudally compressed <p>Dicraeosauridae</p> <ul style="list-style-type: none"> – frontals coalesced + supratemporal fenestra face laterally + postparietal foramen present – leaf-shaped processes projecting dorsolaterally from crista prootica – angle between basiptyergoid processes $\sim 20^\circ$ – deep pit between basiptyergoid processes – pleurocoels on cervical vertebrae absent ~ fossae on dorsal surfaces of costal eminences absent – ratio of height of cervical vertebra: length of centrum ≥ 1.5 	<p>Diplodocoidea</p> <ul style="list-style-type: none"> + subcylindrical tooth crowns + atlantal intercentrum with cranioventrally expanded occipital fossa + cervical ribs shorter than their respective centra – dorsal and proximal caudal vertebrae with neural arches $\geq 2.5x$ height of centrum + whiplash tail present 	<p>Diplodocoidea</p> <ul style="list-style-type: none"> + cervical ribs shorter than respective vertebra bodies <p>Rebbachisauridae + (Diplodocidae + Dicraeosauridae)</p> <ul style="list-style-type: none"> + rostralmost margin of premaxilla not stepped – parietal excluded from margin of posttemporal fenestra + tooth crowns do not overlap + neural spines not triangular – biconvex distalmost caudal centra + distal caudal centra elongate (“whiplash” tail present) <p>Diplodocidae + Dicraeosauridae</p> <ul style="list-style-type: none"> + atlantal intercentrum with cranioventrally expanded occipital fossa – cranial cervical neural spines bifid + caudal cervical and cranial dorsal spinous processes bifid – medial tubercle between bifid neural spines + metatarsal I with caudolateral projection on distal condyle <p>Diplodocidae</p> <ul style="list-style-type: none"> + quadrate fossa shallow + proximal caudal vertebrae procoelous – ≥ 30 biconvex caudal vertebrae <p>Dicraeosauridae</p> <ul style="list-style-type: none"> – frontals fused in adults + postparietal foramen present – supratemporal fenestra smaller than foramen magnum – crista prootica with enlarged, “leaf”-like processes – low angle between basiptyergoid processes + basal tubera narrower than occipital condyle – ratio of dorsal neural spine length: vertebral body length ~ 4.0

+ state listed is present in *Suuwassea*; – state listed is absent in *Suuwassea*; ~ state listed is variable in *Suuwassea*.

Systematic paleontology

Saurischia Seeley, 1887

Sauropoda Marsh, 1878

Diplodocoidea Marsh, 1884 (Upchurch 1995)

Flagellicaudata clade nov.

Definition: A node-based taxon consisting of the most recent common ancestor of *Dicraeosaurus* and *Diplodocus* and all of its descendants (the clade “Dicraeosauridae + Diplodocidae” of numerous authors).

Etymology: Latin *flagellum*, meaning whip, and Latin *cauda*, meaning tail. In reference to the “whip tail” of most included taxa, consisting of a long chain of elongate, minimally arcuate or anarcuate (lacking arches) centra at the distal end of the tail.

Genus *Suuwassea* nov.

Etymology: From the Crow (Native American) “suuwassa”. Intended pronunciation: “SOO-oo-WAH-see-uh”. In combination, “suuwassa” means “the first thunder heard in Spring”, but use of the root words, “suu”, meaning “thunder”, and “wassa”, meaning “ancient”, are an homage to

the traditional appellation “thunder lizard” often applied to sauropods (following *Brontosaurus* Marsh, 1879). The use of a Crow term further reflects the position of the type locality in ancestral Crow territory as well as its proximity to the present Crow Reservation. The spelling of the name follows the best current orthography for the Crow language, which does not use Latin characters; the pronunciation is approximate and simplified.

Diagnosis.—Supraoccipital with ventral end drawn out into narrow, elongate process that contributes very little to dorsal margin of foramen magnum; basioccipital does not contribute to dorsal side of occipital condylar neck; antotic processes of laterosphenoid separated from frontals by deep notches; cranial cervical neural spines restricted to caudal halves of their respective centra, craniocaudally compressed, expanded distally, concave on all sides, and not bifurcate; distal caudal (“whiplash”) centra amphiplatyan; dorsal tuberculum of humerus well developed; proximal articular surface of tibia wider mediolaterally than long craniocaudally; calcaneus spheroidal; pedal phalanges longer proximodistally than wide mediolaterally.

Suuwassea emiliae sp. nov.

Figs. 1–3, Tables 2, 3.

Holotype and only known specimen: ANS 21122, disarticulated but associated partial skeleton including dentigerous, partial left premaxilla; dentigerous fragment of maxilla; quadrate; complete braincase; atlas, axis, and four cranial-middle cervical vertebrae and other fragments; three cranial dorsal vertebrae and several ribs; numerous proximal-, mid- and distal caudal centra; right scapula, coracoid, and humerus; partial right tibia; complete right fibula; calcaneus; several metatarsals and pedal phalanges.

Type locality: Southern Carbon County, Montana, U.S.A. Because the locality lies on land accessible to the public and managed by the Bureau of Land Management (BLM) and thus has the potential for illegal exploitation by non-scientific interests, more specific locality information is not provided here, but is on file at the ANS and available to qualified individuals.

Type horizon: Morrison Formation (?Brushy Basin Member equivalent), ?Tithonian.

Etymology: In honor of the late Emilie deHellebranth, paleontology advocate who generously funded the expeditions in 1999–2000 that recovered the specimen.

Diagnosis.—Same as for genus.

Description and comparison.—The diplodocoid affinities of *Suuwassea emiliae* are clear based on the possession of multiple synapomorphies identified by Upchurch (1998), Wilson and Sereno (1998), and Wilson (2002) (Table 1). Cranial elements preserved in ANS 21122 include fragmentary dentigerous elements and a largely complete braincase. The distinction between the body of the premaxilla and the nasal process is minimal (Fig. 1A), as in all diplodocoids (Upchurch 1998, 1999). Of its four alveoli, one retains a portion of a small, unworn tooth with a cylindrical root and tapering crown. The medial margin of the element remains straight but the lateral edge is sinuous, marking the rostral end of the nasal fossa. A small, ovoid foramen occurs on the lateral side of the nasal process.

The preserved portion of the right maxilla has seven alveoli. Numerous small foramina perforate the lateral surface; some open into shallow grooves. The medial surface of the bone is flat and smooth except for a row of foramina, one above each alveolus. The caudalmost foramen is broken open, exposing portions of at least two, possibly three, unerupted tooth crowns above a third situated in the alveolar opening; room is available for a fourth and possibly fifth tooth as well, as might be expected in a diplodocoid (Wilson 2002).

In lateral view, the right quadrate (Fig. 1B) is markedly curved (caudally concave), as in all known diplodocoids (Calvo and Salgado 1995; Upchurch 1998). In caudal view, the element is similarly curved so that the distal articular condyles sit lateral to the squamosal articular end. Ventral to the squamosal end, a shallow furrow incises the caudal surface of the shaft as in *Apatosaurus* and *Diplodocus*, rather than the deep fossa of other sauropods. The condition is unknown in dicraeosaurids, but the lack of the fossa is possibly synapomorphic for the Flagellicaudata (Upchurch 1998, 1999). The mandibular articular surface of the quadrate is flat and tilts ventromedially, as in *Apatosaurus* (Berman and Mc-

Intosh 1978). The articular surface is roughly D-shaped, bulging caudomedially and lightly indented rostrally.

The braincase, including partial skull roof bones (Fig. 1C), is nearly complete. Only the caudal ends of the frontals are preserved; laterally, each curves ventrally into a curved postorbital process that forms the caudodorsal margin of the orbit and the rostradorsal margin of the supratemporal fenestra. The frontals are unfused, unlike the condition in dicraeosaurids (Salgado and Calvo 1992). The frontal-parietal suture is interrupted by a small, midline, parietal foramen. In dorsal view, the parietals are very short rostrocaudally. A small, trapezoidal postparietal foramen (Fig. 1C₁), known elsewhere only in dicraeosaurids and *Tornieria* (“*Barosaurus*”) *africanus* (Janensch 1935–1936), sits centered on the parietal-supraoccipital contact. *Suuwassea* differs from both *Dicraeosaurus* and *Tornieria* (“*Barosaurus*”) *africanus* in that its postparietal foramen is larger than the parietal opening. In caudal view, the parietals are exposed only laterally as squamosal processes that form the caudodorsal margins of the supratemporal fenestrae. The dorsoventrally oblong supratemporal fenestrae are exposed in dorsal view but have much greater exposure laterally (Fig. 1C₂). However, they are longer dorsoventrally than either rostrocaudally or mediolaterally, and situated caudal, not ventral, to the orbit, more similar to both *Diplodocus* and *Apatosaurus* (Berman and McIntosh 1978) than to dicraeosaurids (Janensch 1935–1936; Salgado and Calvo 1992).

The supraoccipital bears a low but sharp sagittal nuchal crest (Fig. 1C₃) that increases in prominence from a point just dorsal to the foramen magnum to the caudal margin of the postparietal foramen, where it merges with very short transverse nuchal crests to form a low, tetrahedral eminence similar to, but smaller than, that of dicraeosaurids (Salgado 1999). Ventral to the sagittal crest, the supraoccipital thins to a narrow, sagittal pillar that forms only the dorsalmost margin of the foramen magnum. In *Apatosaurus* and *Diplodocus* (Berman and McIntosh 1978), the ventral portion of the supraoccipital is not distinctly set off from the remainder of the element and contributes broadly to the dorsal margin of the foramen magnum. The exoccipital-opisthotic complex forms the remainder of the margin of the foramen magnum and the entirety of the dorsolateral portions of the roughly spherical occipital condyle so that the basioccipital is not exposed on the dorsal surface of the condylar neck. Dorsal to the paroccipital processes, small, ventrally hooked processes project laterally into the posttemporal fossa, giving it a bifurcate medial margin. The distal ends of the paroccipital processes are expanded slightly dorsoventrally and convex laterally.

The basioccipital forms most of the occipital condyle. Ventral to the condyle, the fused basioccipital-basisphenoid descends as a thick, columnar, median process. Paired, closely appressed, hemiovoid, verrucate basal tubera (Fig. 1C₂, C₃) jut from the caudoventral margin of this process and are conjoined rostrally such that, in caudal view, the remainder of the columnar process is visible between them, similar to *Dicraeo-*

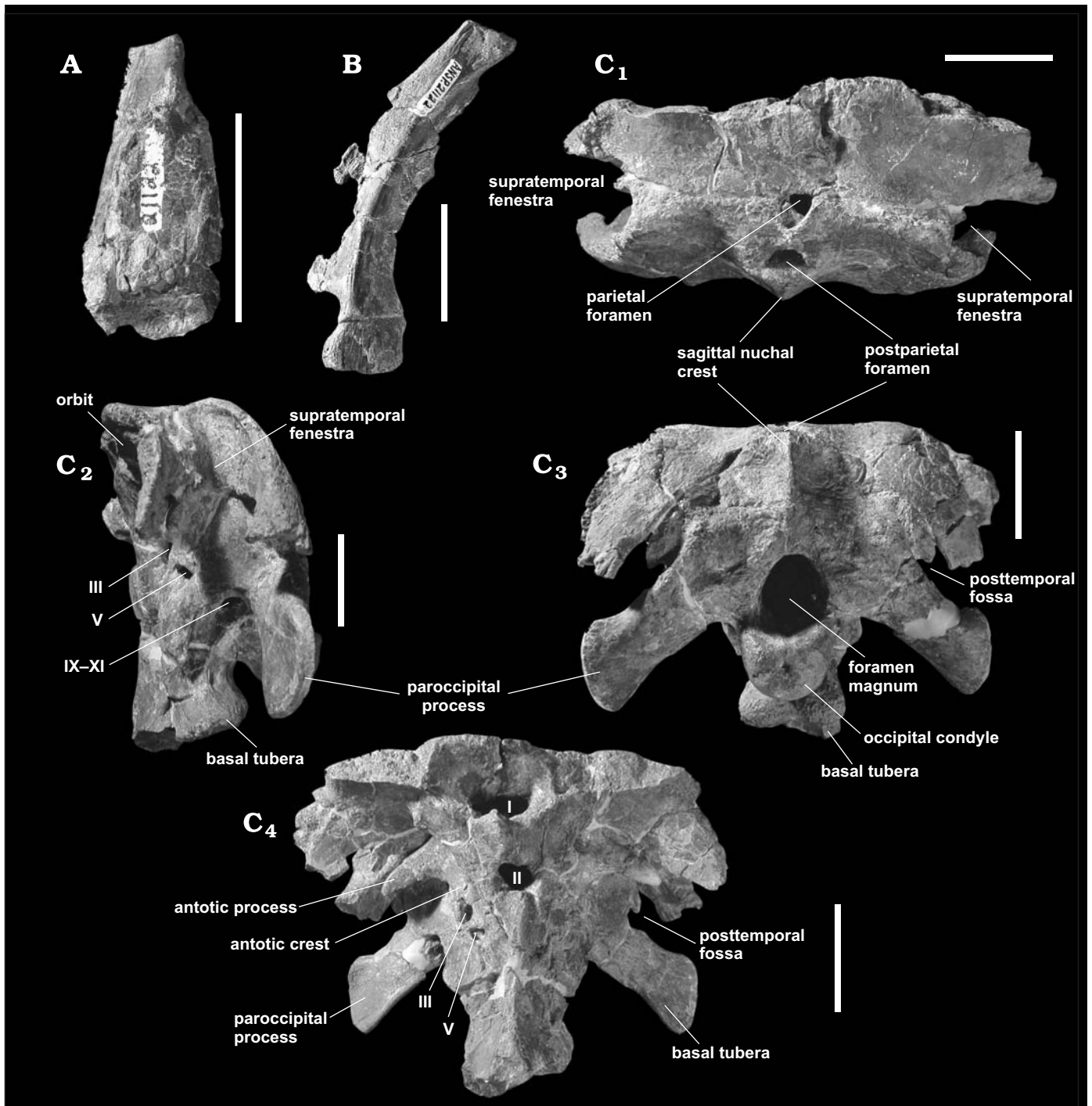


Fig. 1. Cranial elements of *Suuwassea emilieae* ANS 21122. **A.** Left premaxilla in rostradorsal view. **B.** Right quadrate in medial view. **C.** Basicranium in dorsal (C_1 , rostral toward top), left lateral (C_2 , dorsal toward top), caudal (C_3), and rostral (C_4) views. Scale bars 5 cm.

saurus (Janensch 1935–1936) and *Amargasaurus* (Salgado and Calvo 1992). The tubera do not project laterally as in *Diplodocus*. The basal tubera are separated medially by a narrow sulcus that runs ventrally from a small, median subcondylar foramen, located dorsal to the tubera, to a ventrally open sulcus running sagittally along the ventral surface of the columnar process. The latter continues as a shallow, rostrocaudally-oriented sulcus that separates the basiptyergoid pro-

cesses, unlike the deep pits of dicraeosaurids (Upchurch 1998). Too much of the bases of the processes are broken to allow for an estimate of their angle of divarication.

Ventral to the olfactory foramen, the orbitosphenoids form the dorsolateral margins of an unpaired optic (II) foramen (Fig. 1C₄); incompletely divided optic foramina are also known in some specimens of *Diplodocus* (Osborn 1912; Berman and McIntosh 1978). The most prominent feature of

each laterosphenoid is a long, laterally projecting, ventrally curved antotic process that is separated from the frontals dorsally by a deep notch (Fig. 1C₄), unique within the Diplodocoidea. The bulk of each prootic is a flat, roughly pentagonal plate of bone that lies rostromedial to the bases of the paroccipital processes. The prootic crest lacks the peculiar “leaf”-like processes of dicraeosaurids (Salgado and Calvo 1992; Upchurch 1998). A second low crest caudally bounds a fossa at the contact with the exoccipital-opisthotic complex; the fossa contains two foramina: a large ventral opening for the exits of cranial nerves IX–XI plus the perilymphatic duct, and a smaller, more dorsal one for cranial nerve VII, as in *Apatosaurus* (Berman and McIntosh 1978: fig. 6). Tiny foramina for cranial nerve XII pierce the base of the occipital condylar neck.

Vertebral measurements are provided in Table 2. The body of the atlas (Fig. 2A) is trapezoidal in lateral view, widest along the ventral margin, identical to the apomorphic condition of diplodocids (Wilson and Sereno 1998). Two small, trapezoidal processes project caudoventrally from the caudoventral end to abut indistinct facets on the cranial sides of the axial parapophyses, precluding the articulation of a caudally-projecting cervical rib like the one hypothesized in *Apatosaurus louisae* by Gilmore (1936: fig. 6). Distal to their articulations with the body, the neurapophyses are waisted; the zygapophyses are missing.

The body of the axis is opisthocelous and slightly wider mediolaterally than tall dorsoventrally. Ventral to the fused pleurocentral assembly, a low keel occupies the midline cranial to the parapophyses. Both sides of the centrum contain pleurocoelous fossae, but only on the right side is the fossa very weakly divided into cranial and caudal portions by a modest swelling on the ventral margin. The parapophyses project markedly laterally and ventrally beyond any other portion of the body. The laminar lateral surfaces of the neural arch cover infraprediapophyseal and infradiapophyseal fossae. Two flat, craniolaterally-facing plates separated by a sagittal, non-laminar prespinal ridge, create a neural spine that is V-shaped in cross section and that angles caudo-dorsally approximately 60° from the horizontal to sit entirely over the caudal half of the centrum. The distal end of the spine is laterally expanded and rendered heart-shaped by a sagittal notch. The caudal surface overhangs a deep postspinal fossa that lacks the postspinal lamina seen in *Dicraeosaurus* (Janensch 1929). A short epiphysis protrudes caudodorsal to the postzygapophyseal facet.

The positions of remaining cervical vertebrae were determined using relative sizes and goodness of articulation with each other. They thus appear to consist of virtually complete cervicals 3, 5, and 6; cervical 7 has been diagenetically distorted and lacks most of the neural arch. All are strongly opisthocelous and generally similar to the axis (Fig. 2B, C). The centrum of cervical 3 is, like the axis, wider mediolaterally than tall dorsoventrally, but those of cervicals 5 and 6 are the opposite. On the more cranial vertebrae, the pleurocoelous fossae are either undivided or only weakly divided

Table 2. Measurements of vertebrae of ANS 21122, holotype of *Suuwassea emilieae*. All measurements in mm.

	Centrum Length	Max Vert Height	Cran Artic Surf Height	Cran Artic Surf Width	Caud Artic Surf Height	Caud Artic Surf Width
CV2	133.2	186.3	45.5	58.4	42.2	45.1
CV3	156.2	181+	36.5	43.0	45.0	56.2
CV5	215.4	231	40.2	48.2	61.8	59.5
CV6	257.0	268.0	52.0	54.6	74.6	72.6
CV7	280.8*	113+	42.9*	60.4*	59.4*	91.2*
D2	307-*	351+*	183.5*	92*	?	198.2*
D3	259*	455*	166.1*	?	191.1*	135.7*
D4	253.3*	549-*	178-*	92+*	176.7	116.4+*
Prox CD A	101.6	189+	171.4	220.5	156.0	181.4
Prox CD B	124.8	163+	146.9	164.2	~125	144.9
Prox CD C	120.6	184+	173.3*	159.0*	152.1*	145.7*
Mid CD	164	120+	112.0	115.8	106.1	115.6
Dist CD	123.3	53.9+	47.8	49.4	47.0	46.8
Dist CD	114.6	51.8+	41.4	40.3	37.6	37.1
Dist CD	103.6	43+	34.5	38.8	32.5	32.9
Dist (wl) CD	58.1	17.6	17.6	13.0	16.4	14.0
Dist (wl) CD	53.4*	11.8*	15.1*	11.2*	16.9*	9.9*

+ measured distance on broken or distorted element; real value larger;
 – measured distance on broken or distorted element; real value smaller;
 * measured distance based on diagenetically distorted element; ? measurement not possible. CV = cervical, D = dorsal, CD = caudal, wl = whiplash.

by low, oblique ridges. More caudally, these dividing ridges become more pronounced; the 7th has multiple laminae. Most fossae contain asymmetrical internal foramina that deeply invade the cranio- and caudodorsal portions of the body and basal neural arches. Centra become markedly more elongate with the sixth cervical. The ventral surfaces lack the unusual combination of fossae and keels seen in *Dicraeosaurus*. Caudally in the sequence, the ventral surfaces become increasingly concave transversely. The parapophyses protrude ventrolaterally beyond their respective centra. Those on cervical 3 bear no dorsal fossae, similar to *Dicraeosaurus*. However, such fossae are present on cervicals 5–7, but only on 6 and 7 are the fossae separated from the pleurocoelous fossae by ridges. The differences among these cervicals represent a mosaic of states displayed by primitive sauropods and derived diplodocids (see Upchurch 1998).

The prezygapophyses are borne on long, distinct arms that curve craniodorsally, as in both *Apatosaurus* (Gilmore 1936) and *Dicraeosaurus* (Janensch 1929). Their cranial extent equals (cervicals 3 and 5) or exceeds (6 and 7) that of the articular condyle of the centrum. The prezygapophyses conjoin ventromedially via the cranial intrazygapophyseal lamina, while thick spinoprezygapophyseal laminae are separated at the base of the neural spine by a deep, probably elastic ligament fossa. Cranial infrazygapophyseal fossae split the centroprezygapophyseal laminae dorsally; the fossae are

only shallow indentations on cervical 3 but become deep pits on 5–7. The spinoprezygapophyseal, pre-, and postzygadiapophyseal laminae surround distinct, triangular fossae on the lateral sides of the bases of the spinoprezygapophyseal laminae. The prezygadiapophyseal lamina on cervicals 3 and 5 retain the sheet-like morphology of the axis and form the entirety of the zygapophyseal processes, but from cervical 6 on, the lamina becomes a laterally-projecting ridge that only trails onto the lateral side of the zygapophysis.

From cervical 5 caudally, transverse processes and parapophyses are fused with their ribs. The transverse processes overhang tetrahedral infradiapophyseal and infraprediapophyseal fossae that are separated by short, thick cranial centrodiapophyseal laminae that stem from the caudodorsal margins of the pleurocoelous fossae. Longer, thinner postzygadiapophyseal laminae originate on the dorsal surfaces of the transverse processes and curve caudodorsally to form the ventrolateral margins of the postzygapophyseal alae. On cervicals 3 and 5, the postzygadiapophyseal laminae are less shelf-like than in other diplodocoids and instead form laterally-facing sheets. These sheets overhang craniocaudally elongate but mediolaterally narrow caudal infrapostdiapophyseal fossae that open only ventrally.

The neural spines of all preserved cervicals are located entirely over the caudal half of their respective centra, as in *Apatosaurus excelsus* (Gilmore 1936), cervical 4 of *A. louisae* (Gilmore 1936), and cervicals 2–3 of *Dicraeosaurus* (Janensch 1929). They are caudodorsally inclined on cervicals 3 and 5 but slightly craniodorsally inclined on cervical 6, a pattern identical to *Apatosaurus louisae* (Gilmore 1936) and similar to those of *A. excelsus* (Gilmore 1936) and *Dicraeosaurus* (Janensch 1929). The craniodorsal surface of each spine is occupied by a shallow fossa bounded laterally by the spinoprezygapophyseal laminae. The fossae on cervicals 5 and 6 are further subdivided by low prespinal laminae at their proximal ends (Fig. 2C); a similar postspinal lamina is also present on cervical 6. The spines of cervicals 5 and 6 (that of 3 is broken) progressively widen distally, forming craniocaudally compressed spines very unlike those of *Apatosaurus louisae*, *Dicraeosaurus*, or *Diplodocus*, but vaguely similar to *Apatosaurus excelsus* (Gilmore 1936). The craniocaudally narrow lateral surfaces of the spines are also indented by elongate fossae that terminate at the spine's widest point against rugose, laterally-projecting knobs (Fig. 2B, C). The spine of cervical 5 shows no sign of bifurcation, but the distal end of the 6th bears a shallow, parabolic notch, presumably representing the initiation of bifurcation. Thus, bifurcation only occurs caudal to cervical 5 in *Suuwassea*, compared to commencement at cervical 5 in *Apatosaurus louisae* and cervical 6 in *A. excelsus* (Gilmore 1936), cervical 2 in *Dicraeosaurus* (Janensch 1929), and cervical 3 in *Diplodocus* (Hatcher 1904). All spines overhang deep postspinal fossae. Pronounced and rugose epipophyses project caudodorsally well beyond the postzygapophyseal articular facets (Fig. 2B); epipophyses are known elsewhere in the Diplodocoidea, but do not project as far in any other taxon.

Each cervical rib has a short articular processes that is separated from the remainder of the rib by a very short neck. The shafts are flattened dorsomedially but otherwise roughly circular in cross section. The only complete rib, on cervical 6, is only slightly shorter than the centrum to which it is articulated, as in all diplodocoids. The ribs lack cranial processes, as in *Apatosaurus louisae*, although this probably is not a useful phylogenetic character (Wedel and Sanders 2002).

Three heavily (mostly mediolaterally) distorted dorsal vertebrae are preserved; they are probably the 2nd–4th based on the positions of their parapophyses. Dorsal 4 (Fig. 2D) is the most complete. The opisthocoelous centra are craniocaudally shorter but dorsoventrally taller than the preserved cervical centra. The pleurocoelous fossae taper caudally on 2–3, but on 4, they are smaller, rounder, and both restricted to and centered on the dorsal half of the centrum. The neural arches increase in height through the sequence; the complete arches on dorsals 3 and 4 measure less than twice the height of the centrum, but this may be the result of distortion. The transverse processes, preserved only on dorsal 4, are topped by expansive, flat prezygadiapophyseal laminae and are invaginated caudally by deep sulci. The prezygapophyseal facets are not elevated above the level of this lamina. Hyposphene/hypantrum articulations are absent. Neural spines are preserved only on 3 and 4; both are modestly bifid and lack median tubercles. Spinodiapophyseal and spinopostzygapophyseal laminae merge to form mediolaterally flattened spine halves that have craniocaudally expanded distal ends as in *Dicraeosaurus*, *Diplodocus*, and *Apatosaurus* (Hatcher 1904; Janensch 1929; Gilmore 1936). The lateral surface of the spine on dorsal 4 houses a moderate fossa, also as in *Apatosaurus* (Gilmore 1936). Dorsal 4 also possesses a pronounced prespinal lamina ventral to the intraspinal sulcus. The spine of dorsal 3 angles slightly cranially, but that of dorsal 4 angles caudally; how much of either is the result of crushing and distortion is difficult to assess.

Two fairly complete dorsal ribs and several fragments all lack pneumatic foramina and are not hollow. In the most complete rib, the shaft cross-section is triradiate proximally but becomes chevron-shaped distally. The distal end is flattened mediolaterally and both expanded and rectangular.

None of the preserved proximal or middle caudal vertebrae are complete: all lack neural arches and associated processes. Although they are wider mediolaterally than long proximodistally, the most proximal preserved caudals are not similar to the heavily craniocaudally compressed first three to four centra of *Diplodocus* (Hatcher 1904). They are, however, weakly procoelous. It is thus unclear whether or not they represent the proximalmost caudals, rendering *Suuwassea* more similar to *Dicraeosaurus* (Janensch 1929), or somewhat more distal caudals (in the vicinity of the tenth), as in *Apatosaurus* (Gilmore 1936) and *Diplodocus* (Hatcher 1904). The centra are roughly pentagonal in transverse cross section, tapering ventrally to relatively narrow, flat-bottomed ridges. All lack pleurocoelous fossae. Broken surfaces ventrolateral to the base of the neural

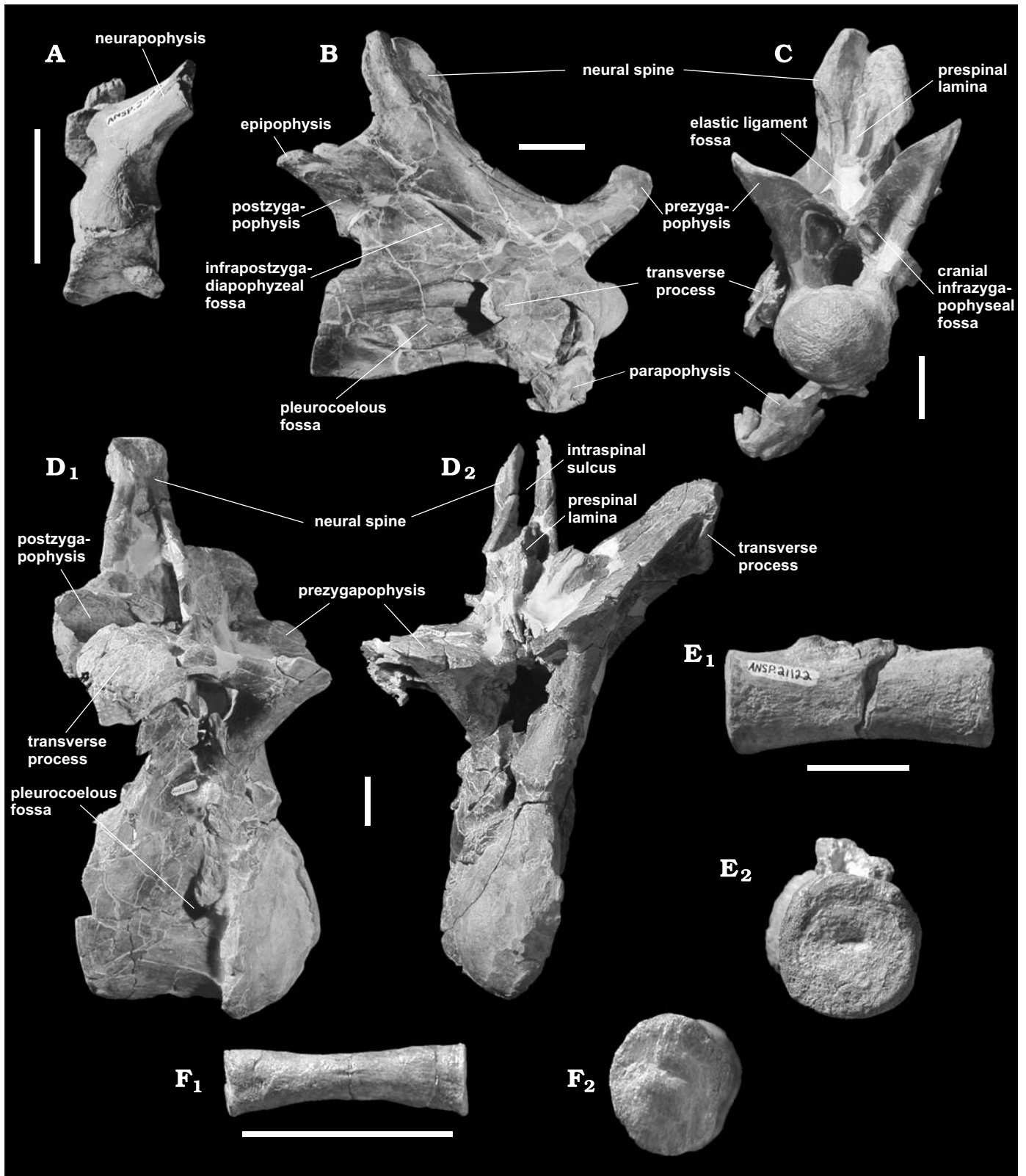


Fig. 2. Axial elements of *Suuwassia emilieae* ANS 21122. **A.** Atlas in left lateral view. **B.** Fifth cervical vertebra in right lateral view. **C.** Sixth cervical vertebra in cranial view. **D.** ?Fourth dorsal vertebra in right lateral (**D₁**) and cranial (**D₂**) views. **E.** Distal caudal vertebra in lateral (**E₁**) and end (**E₂**) views. **F.** “Whiplash” caudal vertebra in lateral (**F₁**) and end (**F₂**) views. Scale bars 5 cm; scales do not apply to close-ups **E₂** and **F₂**.

arches indicate that the transverse processes extended onto their respective centra. Chevron articular facets are indis-

tinct. Each articular face of the proximal centra is subequal in mediolateral and dorsoventral dimensions; both of these

dimensions are greater than the proximodistal lengths of the centra.

Four elongate, slightly waisted, spool-shaped, middle to distal caudals (Fig. 2E) are amphicoelous and have roughly circular proximal and distal articular faces. The largest (middle-most) preserves a pronounced longitudinal ridge ventral to the attachment site of the neural arch. Its ventral surface is only modestly concave ventrally in lateral view and lacks the sulcus seen in comparable vertebrae of *Diplodocus*, *Seismosaurus*, and at least some specimens of *Barosaurus* (Lull 1919; Gillette 1991; Upchurch 1998). The smaller, more distal three are much more cylindrical. Tiny foveae, sometimes bounded ventrally by low, convex eminences, adorn each face of each. The articular surfaces of two extreme distal, “whiplash” caudals (Fig. 2F) similarly bear tiny foveae bounded both dorsally and ventrally by convex eminences as on the previous vertebrae, but these eminences do not dominate the entire, otherwise amphiplatyan face and are barely visible laterally. *Suuwassea* is, in this respect, markedly different from *Apatosaurus* (Gilmore 1936) and more similar to *Diplodocus* (Holland 1906), though the “whiplash” caudals of that genus appear still more biconvex than in *Suuwassea*.

Appendicular element measurements are provided in Table 3. The dorsalmost point on the acromion process of the scapula (Fig. 3A) lies closer to the level of the glenoid than to the midpoint of the scapular blade, similar to *Apatosaurus* (Gilmore 1936) and *Eobrontosaurus* (Filla and Redman 1994) but opposite the condition of *Diplodocus* (Hatcher 1904) and *Supersaurus* (Jensen 1985). A low deltoid crest angles slightly caudally from the vertical and divides the acromion approximately three-fourths the distance along its craniocaudal width. The distoventral branch of the deltoid crest occupies the ventral half of the blade and persists for most of its length, making the blade laterally convex. The caudodorsal portion of the blade is missing, so the degree of maximum expansion cannot be assessed, but it appears minimal. The glenoid facet angles slightly medially and is thus somewhat more visible in medial than in lateral view, reflecting the plesiomorphic sauropod condition (Wilson and Sereno 1998). The medial surface of the scapula bears a low, rugose eminence near the dorsal margin, just caudal to the acromion process.

The right coracoid (Fig. 3B) is slightly wider craniocaudally than dorsoventrally. In profile, the dorsal and medial margins form a continuous and relatively regular curve, similar to that of *Diplodocus* (Hatcher 1904) but unlike the subrectangular element of *Apatosaurus* (Gilmore 1936; Filla and Redman 1994). The flat glenoid facet faces only slightly laterally. It is roughly triangular and expanded beyond the plane of the remaining cranial surface of the element. The coracoid foramen on the lateral surface is well inset from the scapular articular margin.

The dorsally convex proximal end of the craniocaudally compressed right humerus (Fig. 3C) is mediolaterally wider than any other portion of the element. The head forms a distinct swelling on the caudal surface. Proximal to the delto-

Table 3. Measurements of appendicular elements of ANS 21122, holotype of *Suuwassea emilieae*. All measurements in mm.

	Prox-dist Length	Min Shaft Circumference	Prox Artic Face Cran-caud	Prox Artic Face Med-lat	Dist Artic Face Cran-caud	Dist Artic Face Med-lat
Right humerus	752	402	131.8	379	163	295.2
Right tibia	535+	371*	249.1	218	?	?
Right fibula	839	240	175	95.0	141.4	116.7
Right MtI	130.7	248	110.4	90.6	67.0	112.9
Right MtII	154.3	200	110.9	83.2	72.3	89.2
Right MtIV	172.8	150	100.4	64.2	62.1	74.6
Large phalanx	74.0	200	66.7	76.6	60.9	74.8
Small phalanx	66.9	160	49.8	65.9	44.2	62.3

+ measured distance on broken or distorted element; real value larger; * measured distance based on broken element; ? measurement not possible.

pectoral crest is a modest, hemispherical supracoracoideus process (per Upchurch 1998) (Fig. 3C₁), purportedly a synapomorphy of the clade *Opisthocoelicaudia* + *Saltasaurus* (Upchurch 1998). The proximomedial corner forms an angle of approximately 90° but is not squared off, sitting instead on a triangular proximolateral process, as in all non-titanosauriform sauropods (Wilson 2002). Ventral to the low deltopectoral crest, the humeral body is D-shaped in cross section. There is no intercondylar incisure on the distal articular surface but the articular condyles are demarcated on the caudal surface by a shallow olecranon fossa. The reniform distal surface is flat, acondylar, and much wider mediolaterally than craniocaudally, as in all non-titanosaurians (Wilson 2002). The ratio of humeral length to minimum circumference much more closely matches that of *Apatosaurus* than *Diplodocus* (per McIntosh 1990).

The largely planar proximal articular face of the right tibia (Fig. 3D) is markedly rectangular though rounded on its craniomedial corner. It is markedly different from the more triangular proximal tibial faces of *Diplodocus* (Hatcher 1901: fig. 18) and *Dyslocosaurus* (McIntosh et al. 1992: fig. 2D); that of *Apatosaurus* is also rectangular but has its major axis in the opposite direction (Gilmore 1936: fig. 23). The face is roughly 19% greater mediolaterally than craniocaudally. This contrasts with the primitive (largely pre-sauropodan) state in which the proximal end is expanded craniocaudally, but also technically fails the definition of “subcircular” set by Wilson and Sereno (1998: 48) of 15% for the derived condition. The short, straight cnemial crest appears to point laterally and bears a thick, longitudinally elongate lateral process on its internal face. The remainder of

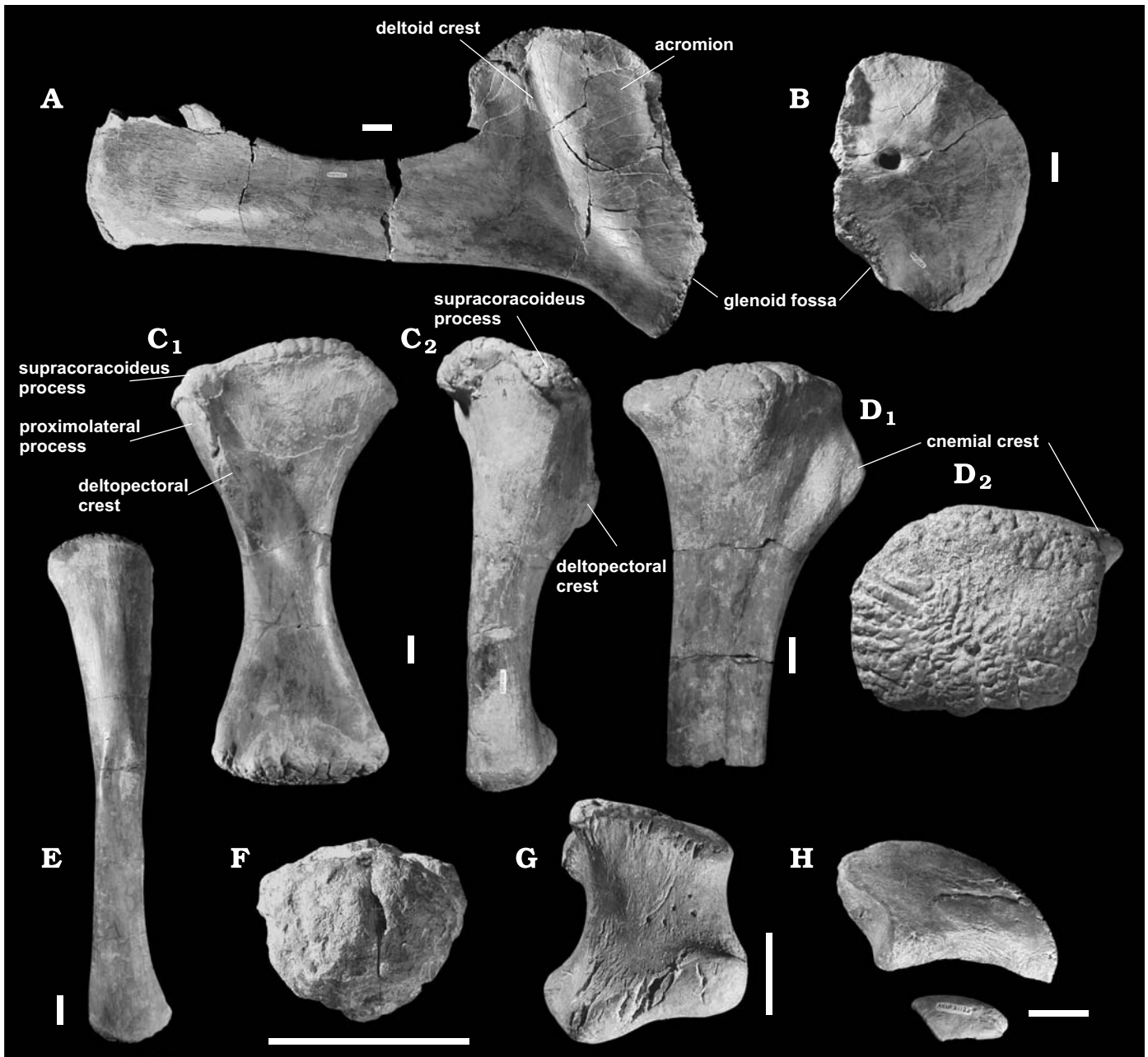


Fig. 3. Appendicular elements of *Suuwassea emilieae* ANS 21122. **A.** Right scapula in lateral view. **B.** Right coracoid in craniolateral view. **C.** Right humerus in cranial (C₁) and lateral (C₂) views. **D.** Right tibia in caudal (D₁) and proximal (D₂) views. **E.** Right fibula in lateral view. **F.** Calcaneus in ?proximal view. **G.** Right metatarsal I in cranial view. **H.** Pedal unguals I (top) and ?III in lateral view. Scale bars 5 cm; scale bars do not apply to close-up D₂.

the preserved, craniocaudally compressed tibial shaft is unremarkable; the distal end was not recovered.

The proximal articular surface of the complete right fibula (Fig. 3E) is subrectangular, flattened mediolaterally and tapers somewhat cranially. A rough, trapezoidal area on the proximomedial surface marks the articulation with the tibia and spans roughly the proximal one-fourth of the shaft. The lateral side of the fibular shaft bears a proximodistally rhomboidal muscle insertion scar roughly halfway along its length. The distal articular face is ovoid, longest craniocaudally, but is shorter than the proximal end.

A small, globular, rugose bone probably represents a calcaneus (Fig. 3F) based on comparisons with the similarly shaped element described for *Diplodocus* by Bonnan (2000). It shares with *Diplodocus* (Bonnan 2000: figs. 3E, 3H) a subtriangular morphology on what are probably the proximal and distal articular surfaces. Unlike that ascribed to *Diplodocus*, however, the element in *Suuwassea* is largely spherical rather than flattened dorsoventrally (Bonnan 2000: fig. 3F).

The D-shaped proximal articular face of the compact right metatarsal I (Fig. 3G) is broadest craniocaudally and concave laterally. In cranial view, the element is trapezoidal,

longest along its lateral margin and with the proximal and distal surfaces sloping medially, all features of advanced eusauropods (Wilson 2002). Its lateral condyle sends a pronounced process distolaterally, as in all flagellicaudatans (Upchurch 1998; Wilson 2002). A fossa on the lateral side of the metapodial is divided by low, oblique ridge similar to that seen in *Apatosaurus louisae* (Gilmore 1936) and *Tornieria* (“*Barosaurus*”) *africanus* (Janensch 1961). The distal articular surface of the metatarsal is rectangular with rounded corners (cartouche-shaped) and its long axis is oriented medio-laterally. Its articular facet is divided into weak medial and lateral condyles.

Right metatarsal II is longer than metatarsal I but similarly stocky. Unlike metatarsal I, the proximal articular surface is spool-shaped in proximal view, with the long axis oriented craniocaudally. Both the proximal and distal articular surfaces angle medially towards one another in cranial view, though not as strongly as on metatarsal I. The lateral surface bears two fossae similar to those on metatarsal I, but it lacks the pronounced crest of the same element in *Dyslocosaurus* (McIntosh et al. 1992: fig. 4F). The rugose distal articular face is again cartouche-shaped, longest mediolaterally. The caudolateral corner protrudes markedly from the shaft, tapering into a short, blunt process.

The remaining metapodial is longer and more slender than the previous metapodials and appears to be a right metatarsal IV based on comparison with those of *Apatosaurus* (Gilmore 1936), *Tornieria* (“*Barosaurus*”) *africanus*, and *Dicraeosaurus* (Janensch 1961). The caudal and lateral surfaces of the shaft blend together into a single caudolaterally-facing surface. The distal articular surface is only slightly wider mediolaterally than craniocaudally and only weakly separated into asymmetrical medial and lateral condyles.

Two probable proximal pedal phalanges are longer than wide at their narrowest (mid-body), proportions unseen in any other eusauropod. Morphologically, the larger resembles II-1 and the smaller III-1 of *Apatosaurus louisae* (Gilmore 1936: figs. 28 D-II and D-III), though the larger articulates moderately well with both metatarsal I and the largest preserved ungual. Both phalanges are dorsoplantarly compressed and lack collateral ligament fossae, as in all eusauropods (Upchurch 1998). The ovoid proximal articular surfaces taper to one side (probably lateral, per Upchurch 1998). The larger phalanx is trapezoidal in dorsal view with the distomedial end projecting farthest distally.

Three unguals taper to blunt points that extend further ventrally than the ventralmost portion of their proximal articular surfaces; these features identify them as pedal rather than manual. The two larger claws are asymmetrical: their proximal articular faces occupy only the proximoventral portions of the elements and each angles distolaterally. The largest (Fig. 3H, top) appears to belong to right digit I; the large left ungual is longer but lower than the previous and is provisionally assigned to digit II. Ungual I lacks an extensor tubercle. The smallest ungual (Fig. 3H, bottom) is far smaller,

less laterally compressed, less recurved than the others, and resembles ungual IV of *Dyslocosaurus* (McIntosh et al. 1992: figs. 3K and 4J) more than ungual III of *Apatosaurus louisae* (Gilmore 1936: fig. 30, no. III), but its position on the foot of *Suuwassea* is unclear.

Discussion

A preliminary phylogenetic analysis was performed by adding *Suuwassea* to the data matrix of Wilson (2002) that was specifically designed to test sauropod phylogeny at the genus level (Fig. 4A). The Spanish sauropod *Losillasaurus giganteus* was also added to the matrix because Casanovas et al. (2001) recovered it as a basal diplodocoid (although it should be noted that no rebbachisaurids were included in the analysis presented along with the description of the taxon). The matrix thus had 31 operational taxonomic units scored for 234 characters. Further modifications to the matrix of Wilson (2002) were made by emending or updating character state entries for *Omeisaurus* based on Tang et al. (2001), and *Mamenchisaurus* based on Ouyang and Ye (2002). Emended codings are provided in the Appendix. A NEXUS file of the whole matrix is available upon request from the senior author.

Cladistic analyses were performed using PAUP* 4b10 (Swofford 2002). An heuristic search (maxtrees = 1000) using the same settings specified by Wilson (2002: 238) produced 24 equally parsimonious trees with length = 427, CI = 0.611, and RI = 0.776. In the resultant trees, *Losillasaurus* is not supported as a basal diplodocoid, and falls out surprisingly instead as a sister taxon to the more primitive Chinese sauropod *Mamenchisaurus*. This is almost certainly the result of lack of data coded for the Spanish taxon, as noted by Wilson (2002), and requires further testing when more data are available on the latter. *Suuwassea* occurs in one of four places: as the sister taxon to all other flagellicaudatans (Diplodocidae + Dicraeosauridae), as the sister taxon to an *Apatosaurus* + Diplodocinae clade, as the sister taxon to *Apatosaurus* within the Diplodocidae, or as the sister taxon to the Dicraeosauridae. A strict consensus of these 24 trees produced a single, fairly uninformative tree characterized by a four-way flagellicaudatan polytomy comprising *Suuwassea*, *Apatosaurus*, the Diplodocinae (*Diplodocus* + *Barosaurus*), and the Dicraeosauridae (*Dicraeosaurus* + *Amargasaurus*), as well as a rebbachisaurid trichotomy. An heuristic search with the same parameters as above but having removed *Losillasaurus* still produced 24 equally parsimonious trees but with length = 418, CI = 0.624, and RI = 0.784. *Suuwassea* still fluctuates between the same four positions as in the analysis that included *Losillasaurus*, and the consensus tree produced the same polytomy of the Flagellicaudata.

Subsequently, a 50% majority rule bootstrap analysis of the full matrix (i.e., including *Losillasaurus*) using a full heuristic search with 1000 replicates produced a single tree

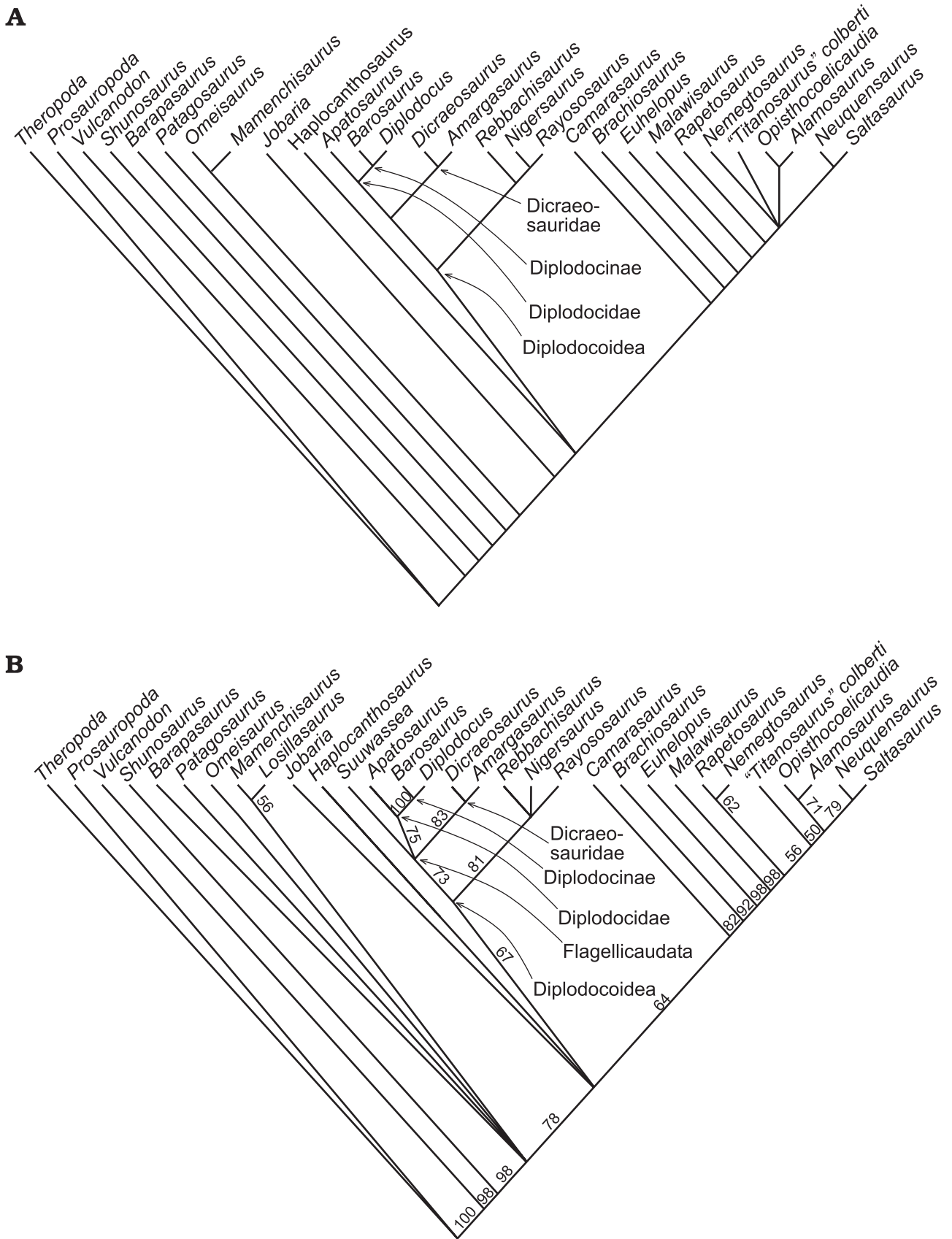


Fig. 4. **A.** Phylogenetic relationship of the Sauropoda as proposed by Wilson (2002). **B.** 50% majority heuristic bootstrap phylogeny using the updated matrix of Wilson (2002) and with *Suuwassea emilieae* and *Losillasaurus giganteus* added. Note the resultant trichotomic nature of the Flagellicaudata. Bootstrap values (percentages) indicated along each stem.

(Fig. 4B) with length = 441, CI = 0.592, and RI = 0.757. The topology of the tree is somewhat similar to that obtained by Wilson (2002; Fig. 4A) with the following changes. Some sorting has occurred within the Titanosauria. *Losillasaurus* continued to fall, albeit with weak support, as the sister taxon to *Mamenchisaurus*. *Barapasaurus* and *Patagosaurus* have been subsumed into a polytomy with the latter and *Omeisaurus*. *Jobaria* has been subsumed into a trichotomy with *Haplocanthosaurus* and the Diplodocoidea. Of most immediate interest is that the traditional flagellicaudatan dichotomy between the Diplodocidae and the Dicraeosauridae has been expanded into a trichotomy between those two terminal clades and *Suuwassea* (Fig. 4B), though this grouping has only moderate support. A more detailed and robust description, and an expanded phylogenetic analysis, are currently in preparation and aim to clarify the position of *Suuwassea* with respect to other members of the Flagellicaudata.

Conclusions

The mosaic of diplodocid and dicraeosaurid character states displayed by *Suuwassea emilieae* gen. et sp. nov. indicates that many of the character states presently thought autapomorphic of either the Diplodocidae or Dicraeosauridae may in fact be plesiomorphies either lost or retained in each terminal clade. The presence of a diplodocoid with what are currently perceived as dicraeosaurid features on a Laurasian landmass likewise raises questions about whether the ancestral flagellicaudatan enjoyed a Laurasian or Gondwanan distribution or both (Bonaparte 1986; Salgado and Bonaparte 1991; Upchurch et al. 2002). Currently, dicraeosaurid occurrences are restricted to Gondwanan continents, but diplodocids occur in Laurasia as well as alongside dicraeosaurids in Gondwana. If the primitive nature of *Suuwassea* indicates that the Flagellicaudata originated in Laurasia and migrated later into Gondwana (as might be indicated by the Middle Jurassic *Cetiosauriscus stewarti* in England), then it is conceivable that dicraeosaurids may also have been present there at one time before migrating (and becoming restricted) to Gondwana (creating in Laurasia a “pseudo-absence” per Upchurch et al. 2002). Alternatively, basal flagellicaudatans enjoyed a more global distribution but only after the breakup of Pangaea did a Gondwanan population give rise to dicraeosaurids. Given the occurrence of the apparent diplodocid *Tornieria* (“*Barosaurus*”) *africanus* in the Upper Jurassic of a Gondwanan land mass, it appears more likely that post-Pangaeian vicariance alone cannot explain the dicraeosaurid restriction to Gondwana. In either case, why dicraeosaurids were unable to obtain the pandemism enjoyed by their diplodocid cousins remains an unanswered question.

Furthermore, the discovery of *Suuwassea* is in line with the recent trend of “small” sauropod discoveries in the northern reaches of the Morrison Formation depositional basin (see above). Since the Morrison Formation can be re-

garded as time-transgressive, following the northward retreat of the Middle Jurassic Sundance Sea, it is possible that the environs closest to the regressing shoreline were home to a somewhat different fauna than is currently known from deposits in the more expansive southern portion of the basin. This hypothesis requires further testing with future discoveries.

Acknowledgements

We are grateful to Will Tillett of Lovell, WY, and Dr. William Donawick (University of Pennsylvania) for their role in the discovery ANS 21122, and for their invaluable logistic support in the field. Will and Melissa Tillett provided remarkable hospitality during the excavation. The authors emphasize that much of the research conducted on ANS 21122 was completed by Dr. William Donawick, Barbara Grandstaff, Matthew Lamanna, Doreena Patrick, Karen Poole, Dr. Allison Tumarkin-Deratzian (all University of Pennsylvania), Jason Poole, Patricia Kane-Vanni, Lisa Sachs, Sherry Michael Weller (all Academy of Natural Sciences), William E. Gottobrio (Bryn Mawr College), Paul Penkalski (Geology Museum, University of Wisconsin-Madison), and Dr. Hailu You (Chinese Academy of Geological Sciences), but nomenclatural etiquette prevented us from including them as authors on the paper. Recovery and preparation of the specimen was accomplished by many of the former and ANS volunteers Jenn Anne, Kahalia Boozer, Jean Caton, John Newman, Ken Newman, Tracey O’Kelly, and by Jesse and Lloyd Tillett. Rev. Randy Graczyk provided critical information regarding the Crow language, and Ben Creisler advised on its subsequent Latinization. The specimen was collected under BLM permit M 89354 administered by the Billings, MT, BLM office, and our sincerest thanks to Gary P. Smith for his support in expediting the permit. Funding for the excavation was graciously provided by the late Emilie deHellebranth, for whom the specimen is named, the University of Pennsylvania Research Foundation, the University of Pennsylvania Paleobiology Fund, the School of Veterinary Medicine (Alan M. Kelly, dean), and the Department of Animal Biology (Narayan Avadhani, chair). Thoughtful review comments made by Drs. Paul Upchurch (University of Cambridge) and Jeffrey A. Wilson (University of Michigan) greatly improved the manuscript.

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Appendix

Updated codings to Wilson (2002) used in the analyses performed to determine the phylogenetic relationships of *Suuwassea emilieae*.

<i>Omeisaurus</i>	1110001101 10000?0101 1000010111 ?11?0?1??1 1100?0?0?0 ?00110000? 1???111011 111?000104 0111010?0- 3101?11011 1000000211 01?0100100 0000001000 0?000???10 0?11000011 000?000001 0101101010 0101000000 1110110001 0101011100 0?01011??0 1010011111 1111111111 1110
<i>Mamenchisaurus</i>	1110-01110 10000?0?01 0000010?11 01110?10?1 11?00????0 ?0?1100001 1011111011 1100001104 0101010110 3101011011 101000021? 0??0110100 0000001000 0?000???10 001100?011 0???00?001 0101111010 011101?000 1???11000? ?101011101 001101?110 1110?11?10 1?1?1111?? 1??0
<i>Losillasaurus</i>	?????????? ???? ?????? ???? ?????? ???? ?????? ???? ?00?? ???? ?????? ?????????? ???? ????1?? 01000??10- ?0?? ?1?110 111?001?? ???? ?1?10? 0000?01100 ?0???????? ???? ?0???? ???? ??????001 0101????01 ?????????? ??????000? ?????????? ??????????? ??????????? ??????????? ???? ?
<i>Suuwassea</i>	?0???????1 ?????????0? ?111010?1? ??100????? ????0?0??1 0??1?????? ?????2???0? 12?0?0011? 011000?110 ??01?????? ??????????? ????0???0? ?????????? ????000--?1 0???????11 000100???1 0100?????? ??????????? ?????????? ???? ?????? ??11??11?? ????0?1111 10?1?1?101 1???