THE AXIAL SKELETON OF THE DINOSAUR *SUUWASSEA EMILIEAE* (SAUROPODA: FLAGELLICAUDATA) FROM THE UPPER JURASSIC MORRISON FORMATION OF MONTANA, USA

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Abstract: Vertebrae of *Suuwassea* demonstrate an interesting combination of plesiomorphies and autapomorphies among known members of the Flagellicaudata. The cranial cervical vertebrae have proportions close to *Diplodocus* but resemble those of *Apatosaurus* except by having greatly reduced cranial and caudal spinozygapophyseal laminae. As a result, they have craniocaudally compressed, caudally positioned spinous processes excavated on all sides by fossae. The cranial thoracic vertebrae are again similarly proportioned as those of *Diplodocus* but are morphologically similar to those of *Apatosaurus*. The most distinguishing feature of *Suuwassea* caudal vertebrae are the short, amphiplatyan, distalmost 'whiplash' caudal vertebrae. These may be either a retention of or a reversal to the plesiomorphic sauropod condition because classic flagellicaudatan, biconvex distalmost caudals occur in the Middle Jurassic of England.

Key words: *Suuwassea*, sauropod, Diplodocoidea, Flagellicaudata, Late Jurassic, Morrison Formation, Montana.

Vᴇʀᴛᴇʙʀᴀʟ morphology is of primary importance in sauropod studies. For phylogenetic purposes, vertebrae have figured prominently in recent cladistic analyses, comprising just under or just over one-third of the total number of characters analysed by Upchurch (1998) and Wilson (2002), respectively. Perhaps more importantly, vertebrae form the core of many studies on sauropod functional morphology and their resultant palaeoecology (Martin 1987; Alexander 1989; Christian and Heinrich 1998; Martin *et al.* 1998; Stevens and Parrish 1999; Seymour and Lillywhite 2000). Flagellicaudatan sauropods, particularly taxa from the Upper Jurassic Morrison Formation of western North America, have been integral to those studies. This is undoubtedly because very complete, and often articulated, material exists for these taxa, but is also due to the fact that many flagellicaudatans demonstrate some peculiarities either rarely seen or unique within the Sauropoda (e.g. cervical costal processes shorter than their respective vertebral bodies and spinous processes bifid through the cranial cervicals).

Harris and Dodson (2004) briefly described the axial skeleton of the new flagellicaudatan sauropod *Suuwassea emilieae* from the Morrison Formation of Montana. Though not represented by a complete series, the preserved vertebrae of *Suuwassea* are distinct from contemporary flagellicaudatans and display a mosaic of features seen otherwise in either *Apatosaurus* or *Diplodocus* as well as some autapomorphic structures.

MATERIAL AND METHODS

Terminology. Terminology used herein follows Harris (2004) because it emphasizes homology between anatomical structures, widely accepted as the basis for modern phylogenetic practice, with the following addendum. A useful and elucidatory descriptive nomenclatural system for the numerous pneumatic openings into each vertebra and their respective bounding laminae was created by Britt (1993) and Wilson (1999) based on older, non-standardized terminology (e.g. 'centrodiapophyseal lamina', utilizing 'centrum' and 'parapophysis', terms that have been abandoned in favour of 'corpus vertebra [body]' and 'eminentia costolateralis', respectively). Avian vertebrae have been substantially modified from their archosaurian ancestors and lack most of the structures of sauropods, so these terms only rarely apply to them. Nevertheless, some homologies exist: for example, the avian crista transverso-obliqua, though less complex, shares an identical course and endpoints with the caudal

spinozygapophyseal ('spinopostzygapophyseal') lamina of Wilson (1999). In addition, many of the terms created by Wilson (1999) utilize the roots 'anterior' and 'posterior' (e.g. 'posterior centrodiapophyseal lamina'), terms that are, for logical reasons, abandoned in favour of 'cranial' and 'caudal'. Constructing literal modifications of Britt's and Wilson's terms to conform to Baumel *et al.* (1993) produces awkward, cacophonous terms (e.g. 'lamina corporo-processus transversus' for 'centrodiapophyseal lamina'). Thus, the terms introduced by Britt and Wilson are retained here, unchanged, though modified such that 'anterior' and 'posterior' and the prefixes 'pre' and 'post' have been replaced with 'cranial' and 'caudal', and 'centro-' has been replaced with 'corporo-'. Also, for the sake of topographic and terminological consistency, 'caudal spinozygapophyseal lamina' is retained over crista transverso-obliqua. The avian 'lateral lamina' is surrendered for 'corporozygapophyseal lamina' because it is easy to confuse 'lateral lamina' as a noun with the same terms as an adjectival descriptor of any of the numerous laminae on the lateral surfaces of sauropod vertebrae. Similarly, the avian 'pneumatic foramen' requires elaboration for the more complex sauropod vertebra. Sauropod vertebrae often exhibit fossae around the foramina (frequently a single fossa contains multiple foramina) on the vertebral body; these are therefore 'corporal pneumatic fossae' ('pleurocoelous fossae') with attendant directional adjectival modifiers. Other fossae on the vertebral arches that are almost certainly pneumatic in origin are named following Wilson (1999) and Britt (1993), again with applicable modifications. See Text-figures 1–2 for labelled illustrations of terminology used herein.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; ANS, Academy of Natural Sciences, Philadelphia, USA; BYU, Brigham Young University, Provo, USA; CM, Carnegie Museum of Natural History, Pittsburgh, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; ML, Museu da Lourinhã, Portugal; MNB, Museum für Naturkunde der Humbolt-Universität zu Berlin, Institut für Paläontologie, Berlin, Germany; NHM, The Natural History Museum, London, UK; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, USA; NMST, National Science Museum of Tokyo, Japan; OU, Oxford University Museum of Natural History, Oxford, UK; TM, Tate Museum, Casper, USA; USNM, US National Museum, Smithsonian Institution, Washington, DC, USA; UW, University of Wyoming, Laramie, USA; YPM, Yale Peabody Museum, New Haven, USA.

Anatomical abbreviations. cam, camera; cap, capitulum; cdbzl, caudal intrazygapophyseal lamina; cdcdl, caudal corporodiapophyseal lamina; cdcpl, caudal corporoparapophyseal lamina; cdczl, caudal corporozygapophyseal lamina; cdelf, caudal elastic ligament fossa; cdidf, caudal infradiapophyseal fossa; cdizf, caudal infrazygapophyseal fossa; cdizl, caudal infrazygapophyseal lamina; cdszl, caudal spinozygapophyseal lamina; cdz, caudal zygapophysis; cdzdl, caudal zygadiapophyseal lamina; cem, costolateral eminence; cpr, costal process; crbzl, cranial intrazygapophyseal lamina; crcdl, cranial corporodiapophyseal lamina; crcpl, cranial corporoparapophyseal lamina; crczl, cranial corporozygapophyseal lamina; crelf, cranial elastic ligament fossa; cridf, cranial infradiapophyseal fossa; crizf, cranial infrazygapophyseal fossa; crizl, cranial infrazygapophyseal lamina; crpzl, cranial parazygapophyseal lamina; crszl, cranial spinozygapophyseal lamina; crz, cranial zygapophysis; crzdl, cranial zygadiapophyseal lamina; cta, costotransverse ansa; cti, capitulotubercular incisure; cvr, cervical rib; den, dens process; dt, dorsal torus; elf, elastic ligament fossa; fv, fovea; hpr, hemispinous process; idf, infradiapophyseal fossa; inc, intercentrum; ipf, infraparapophyseal fossa; iss, intraspinous sulcus; kn, knob; lcpf, lateral corporal pneumatic fossa; nep, neurapophysis; psf, paraspinous fossa; pdl, paradiapophyseal lamina; posf, postspinous fossa; posl, postspinous lamina; prsf, prespinous fossa; prsl, prespinous lamina; pzf, parazygapophyseal fossa; sdl, spinodiapophyseal lamina; sp, spinous process; tpr, transverse process; tub, tuberculum; vccr, ventral corporal crest; vcpf, ventral corporal pneumatic fossa; vf, vertebral foramen; vlpr, ventrolateral process.

SYSTEMATIC PALAEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878
DIPLODOCOIDEA Marsh, 1884 (Upchurch, 1995)
FLAGELLICAUDATA Harris and Dodson, 2004

SUUWASSEA Harris and Dodson, 2004

*Type species.* *Suuwassea emilieae* Harris and Dodson, 2004

Suuwassea emilieae Harris and Dodson, 2004
Text-figures 3–18

Holotype. ANS 21122, a disarticulated but associated partial skeleton including premaxilla, fragment of maxilla, squamosal, quadrate, complete braincase, first–seventh cervical vertebrae and other fragments, three cranial thoracic vertebrae and several

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TEXT-FIG. 1. Nomenclature for vertebral laminae and fossae used in this paper. A, cervical, B, cranial thoracic and C, caudal thoracic vertebrae of *Apatosaurus louisae* (from Gilmore 1936) in cranial (left), left lateral (middle) and caudal (right) views. Terminology applicable across taxa and throughout axial column. Anatomical structure names follow Britt (1993) and Wilson (1999), with emended nomenclatural terminology following Clark (1993) and Harris (2004).
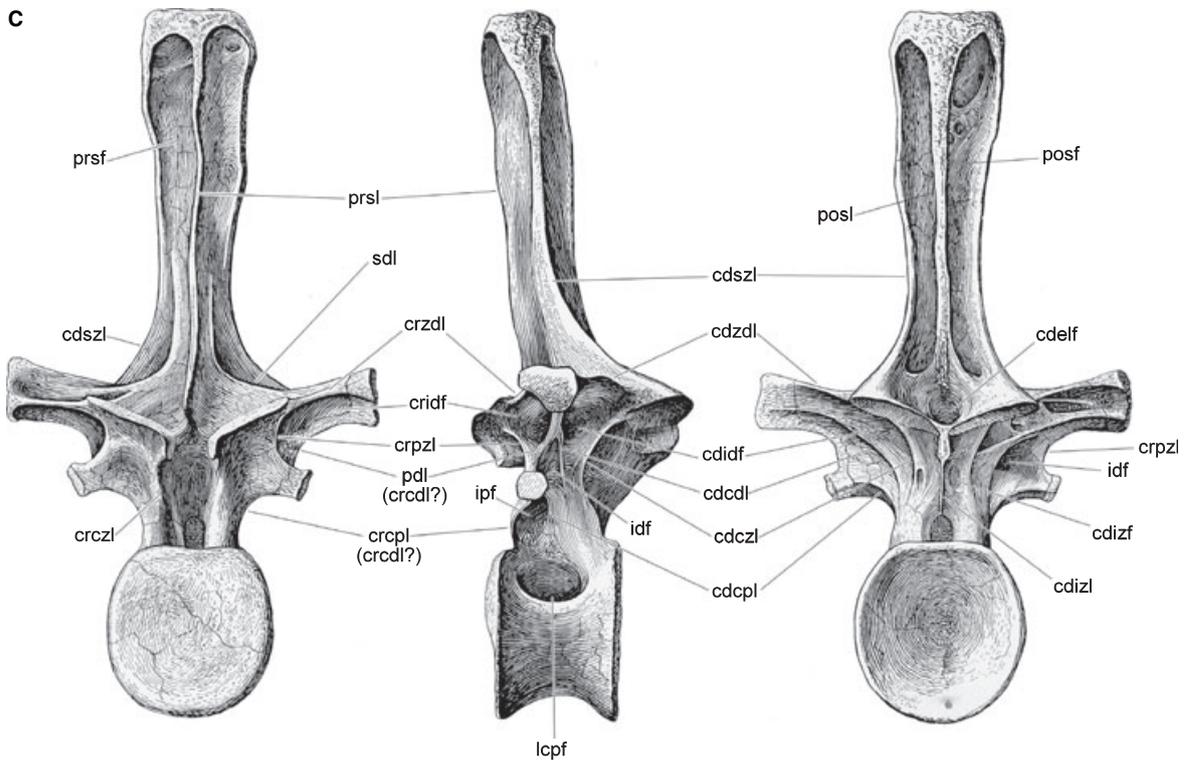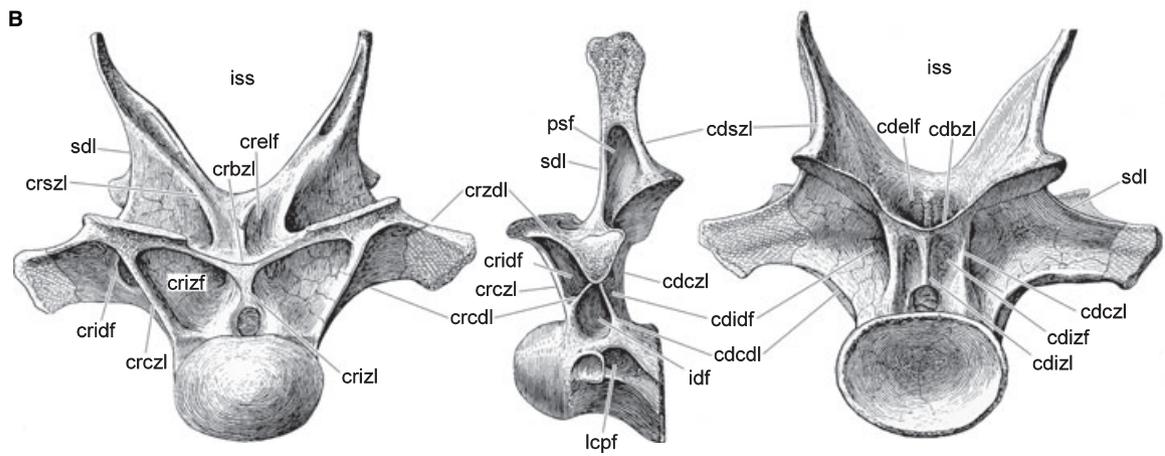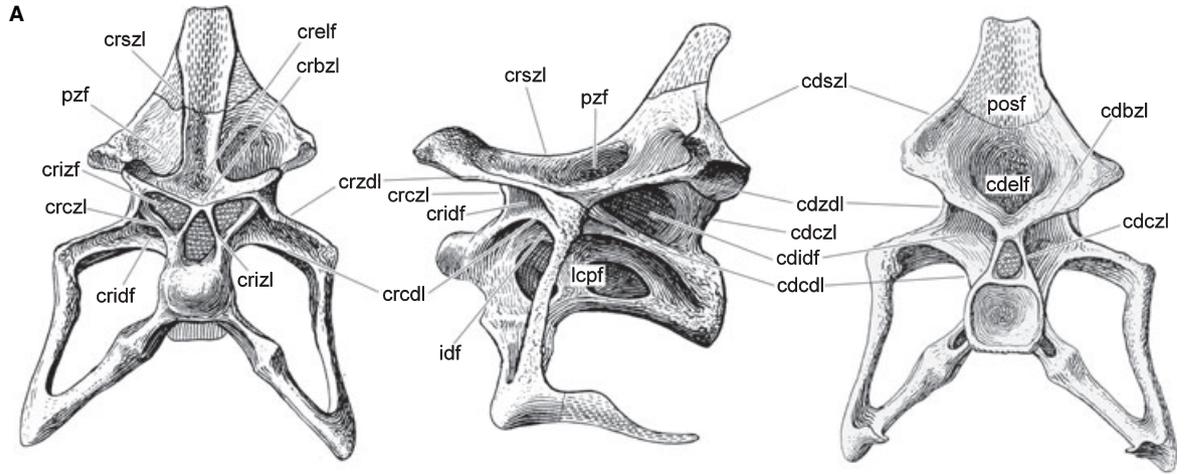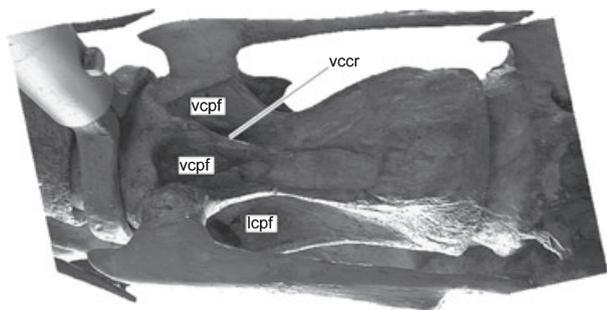
TEXT-FIG. 2. Additional nomenclature for cervical vertebrae based on *Dicraeosaurus* in ventral view.

ribs, numerous proximal-, mid- and distal caudal vertebral bodies, scapula, coracoid, humerus, partial tibia, fibula, calcaneum, several metatarsals, and two phalanges.

Type locality. Southern Carbon County, Montana, USA. 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.

Horizon. Lower Morrison Formation, Late Kimmeridgian–Tithonian.

Referred specimens. None.

Description

Except where specifically provided below, all vertebral measurements are provided in Table 1.

Cervical vertebrae and ribs
For the purposes of the following discussion, the neck is divided as follows (based on *Diplodocus*): cranial cervicals, 1–5, mid-cervicals, 6–10; caudal cervicals, 11–15. Preserved cervical vertebrae were found in line with each other, though not articulated (see 'Taphonomy', below).

Atlas (first cervical). The atlas of ANS 21122 (Text-fig. 3A–D) preserves an intact body (intercentrum) fused with incomplete neurapophyses (the traditional term is retained here over the avian 'atlantal arch' because, in most sauropods, the two elements never join dorsally to form the contiguous structure seen in birds). Sutures remain clearly visible between the body and neurapophyses. As preserved, the entire atlas is 92·6 mm tall dorsoventrally, although its missing zygapophyseal alae may have increased the height.

The atlantal body is dorsally concave in cranial profile and measures 56·3 mm across its widest dimension, the facets for the neurapophyses. The condyloid fossa embays the cranial face; in lateral view, the cranioventral portion projects further cranially and ventrally than any other portion of the body. Along the ventral (longest) margin, the element measures 33·8 mm cranio-

caudally. The caudal face is, in contrast, orientated in a vertical plane but slopes craniodorsally where it abuts the ventral surface of the dens of the axis. Two small, trapezoidal processes project caudally and ventrolaterally from the caudal face. The caudal articular surface of the atlantal body continues smoothly onto the caudal surfaces of these processes but terminates distally where the processes hook slightly caudodorsally. These processes have been interpreted as articular facets for a single-headed cervical rib (Hatcher 1901; Gilmore 1936), but in ANS 21122, these processes extend neither further ventrally nor laterally than the face of the axis ventral to the dens. Though diagenetic distortion of the atlas prevents proper articulation of the two vertebrae, it is clear that the articular surfaces on the ventrolateral processes of the atlas would articulate with (or come close to contacting) indistinct facets on the cranial sides of the axial costolateral eminences. This precludes the existence of a monocapitate, caudally projecting cervical rib articulating with the caudal surface such as the one reconstructed in *Apatosaurus louisae* by Gilmore (1936, fig. 6).

The left neurapophysis is more complete than the right. In comparison with the more tightly fused right side, the left has pivoted from its natural position, swinging the caudal end further laterally than it should be. The suture between its proximal end and the atlantal body is steeply inclined ventrolaterally. Distal to the articulation, the neurapophysis is waisted. Distal to the constriction, the base of the zygapophyseal ala flares into a flattened, obliquely orientated process. Both the dorsomedial and the caudal portions of the process are broken on the left side; the right neurapophysis preserves a portion of its dorsomedial edge, demonstrating the lack of dorsal fusion between the two neurapophyses. The zygapophyseal ala probably extended caudally, and curved ventrally, approximately 28 mm further to articulate with the cranial zygapophysis of the axis.

Axis (second cervical). The axial body (Text-fig. 4A–F) is opisthocoelous. The cranially rounded dens is trapezoidal in dorsal view, widening caudally. Its dorsal surface is flat but the remainder is ovoid and thickens in all caudal directions. As seen in cranial view, the dens is part of a larger atlantal pleurocentral assembly that is fused to the cranial surface of the axis but for which sutures are clearly visible ventrally and laterally. The base of the assembly is roughly rectangular in cranial view, but its ventral margin is irregular. Ventral to the assembly, a low, rounded keel occupies the midline of the cranial face, disappearing caudally between the costolateral eminences. On either side of the cranial face of the ventral swelling are poorly demarcated facets that articulate with the caudoventral processes of the atlas.

The axis is excavated on both sides by deep lateral corporal pneumatic fossae that are separated from each other by a thin, sagittal lamina. On both sides, the internal fossa progresses further cranially than its external outline to invade the space medial to the costolateral eminence and into the base of the pleurocentral complex. On the left side, this space is divided into two foramina: a small, ventral opening that leads ventromedially, and the larger, cranial opening. On the right side, no such pronounced division exists but the pneumatic fossa as a whole is very weakly divided into cranial and caudal portions by a modest swelling on the ventral margin. Cranial to this swelling, the fossa deepens both ventrally and cranially. On the left side, the

TABLE 1. Cervical (CV), thoracic (T) and caudal (CD) vertebral measurements of *Suuwassea emilieae* (in mm or degrees).

	Max Body Ln	Min Body Ln	Costolat Emin Wd	Trans Proc Wd	Max Vert Ht	Pleur Foss Ln	Cran Artic Surf Ht	Cran Artic Surf Wd	Caud Artic Surf Ht	Caud Artic Surf Wd	Cran Zyg Wd	Caud Zyg Wd	Vert Arch Ht[2]	Spin Proc Ht[3]	Spin Proc Ht[4]	Spin Proc Max Med-Lat Wd	Spin Proc Max Cran-Caud Wd[5]	Spin Proc Ang (°)[6,7]
CV2	133·2	109·6	58·4	62·4+	186·3	64·6	45·5	58·4	42·2	45·1	70·4	82·6[e]	135·6	25·7	105·0	61·0	19·4	−37
CV3	156·2	136·1	69	84·0+*	181+	99·2	36·5	43·0	45·0	56·2	64·6	80·6+	124·9+	25+	97·2+	30·2+	68+	−33
CV5	215·4	185·8	68·9	94·1+*	231	133·5	40·2	48·2	61·8	59·5	60·5*	91·5*	177·3	65·5*	144·6	73·9	4·7	−32/ −12*
CV6	257·0	228·8	60·6[e]*	122+*	268·0	166·5	52·0	54·6	74·6	72·6	119·3	130·1	192·5	69·5	161	76·9	31·1/ 16·5[8]	10
CV7	280·8*	251*	160[e]*	144·1+*	113+	196·3*	42·9*	60·4*	59·4*	91·2*	139·3*	146·9*	?	?	?	?	?	?
Cran end frag	?	?	208[e]*	?	147+	?	80·7*	102·4*	?	?	194·3*	?	?	?	?	?	?	?
Caud end frag	?	?	?	?	160+*	?	?	?	137*	173·6[e]*	?	?	?	?	?	?	?	?
T2	307·-*	268·-*	?	?	351+*	181·2*	183·5*	92*	?	198·2*	?	?	180·3+*	?	?	?	?	?
T3	259·-*	179·-*	?	?	455*	72	166·1*	?	191·1*	135·7*	?	?	320*	99*	282*	18·4[L]	74·8[L]	+20*
T4	253·3*	168·9-*	75+*	391	549·-*	43·2*	178·-*	92+*	176·7	1164+*	227·4*	117·6*	361*	133*	310*	63·3[B]/ 20·3[L]	54·8[R]/ 65·8[L]	−16*
Prox CD A	101·6	60·4	n/a	?	189+	n/a	171·4	220·5	156·0	181·4	?	?	?	?	?	?	?	?
Prox CD B	124·8	81·0	n/a	?	163+	n/a	146·9	164·2	c. 125	144·9	?	?	?	?	?	?	?	?
Prox CD C	120·6	89·8-	n/a	?	184+	n/a	173·3*	159·0*	152·1*	145·7*	?	?	?	?	?	?	?	?
Mid CD	164	139·3	n/a	?	120+	n/a	112·0	115·8	106·1	115·6	?	?	?	?	?	?	?	?
Dist CD	123·3	114·8	n/a	?	53·9+	n/a	47·8	49·4	47·0	46·8	n/a	n/a	?	n/a	n/a	n/a	n/a	n/a
Dist CD	114·6	103·6	n/a	?	51·8+	n/a	41·4	40·3	37·6	37·1	n/a	n/a	?	n/a	n/a	n/a	n/a	n/a
Dist CD	103·6	97·1	n/a	?	43+	n/a	34·5	38·8	32·5	32·9	?	?	?	?	?	?	?	?
Dist (wl) CD	58·1	57·4	n/a	n/a	17·6	n/a	17·6	13·0	16·4	14·0	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Dist (wl) CD	53·4*	53·2*	n/a	n/a	11·8*	n/a	15·1*	11·2*	16·9*	9·9*	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

wl, whiplash; n/a, not applicable; [1]measured on the ventral surface; [2]measured from the ventral margin of the vertebral canal; [3]measured from cranialmost point on caudal spinozygapophyseal lamina; [4]measured from dorsal margin of vertebral foramen on the caudal end; [5]measured perpendicular to vertebral body (positive value, cranial tilt, negative angle, caudal tilt); [6]measured on sagittal plane; does not incorporate laterally flared edges; [7]if two values given, first, angle of main shaft of spine, second, angle of distal end of spine; [8]first value measured at lateral margin, second sagittally; [e]distance represents measurement from sagittal plane to one side doubled; +, measured distance on broken or distorted element; real value larger; −, measured distance on broken or distorted element; real value lower; *measured distance based on diagenetically distorted element; [L]left half of bifurcate spinous process; [R]right half of bifurcate spinous process; [B]measurement incorporates both halves of bifurcate spinous processes.
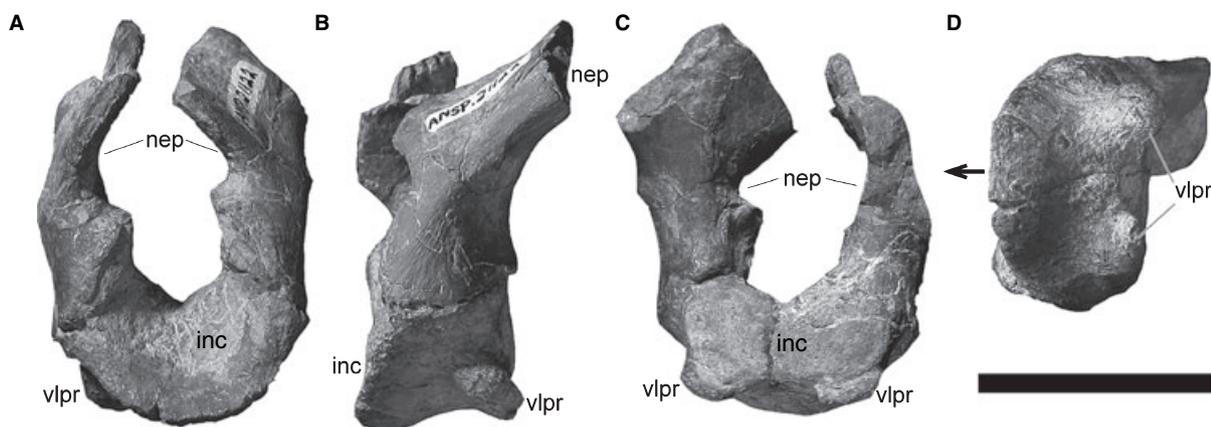
TEXT-FIG. 3. Atlas of ANS 21122. A, cranial, B, left lateral, C, caudal, and D, ventral views. Arrow in D points cranially. Scale bar represents 10 cm.

caudal termination of the fossa corresponds to the external margin of the fossa, but on the right side the fossa again continues into a pocket beyond its respective external margin. The fossa on the right side progresses further dorsally than on the left.

The costolateral eminences are ovoid bulges at the cranioventral margins of the vertebral body. They project markedly laterally and ventrally beyond any other portion of the body. Their articular fossae are fairly shallow.

In ventral view, the axial body is spool-shaped. The cranial expansion is occupied by the costolateral eminences and caudal end by the caudal articular facet. Between the costolateral eminences and the midway point along the length of the body, an extremely weak median keel can be discerned. A wide, weakly developed median sulcus embays the caudal half of the body, bounded by two equally weak ridges. The groove and its bounding ridges originate caudal to the costolateral eminences and become more pronounced caudally. The axial body lateral to this median trough and ventral to the lateral corporal pneumatic fossae is again shallowly grooved. This ventrolaterally open groove is bounded dorsally by a low, weakly developed ridge that originates on the caudal margin of the costolateral eminence; it too is more pronounced at its caudal end. The caudal articular facet of the body is roughly circular but flattened at its dorsal margin.

The vertebral foramina are dorsoventrally ovoid at both ends. The articular surfaces of the cranial zygapophyses are small, axially elongate ovals that face dorsolaterally and are only slightly elevated above the remainder of the surrounding vertebral arch. Immediately caudoventral to the zygapophyses on both sides are broken surfaces at the bases of the transverse processes that overhang moderately deep, craniomedially orientated, infradiapophyseal fossae just dorsal to the lateral corporal pneumatic fossae. The base of the transverse process on each side emits a short caudal corporodiapophyseal lamina that bounds the infradiapophyseal fossa caudodorsally and forms the cranioventral margin of a caudally open caudal infradiapophyseal fossa.

The craniodorsal margin of the vertebral arch consists of two flat, craniolaterally facing, cranial spinozygapophyseal laminae whose union forms a sagittal, alaminar, prespinous ridge. This ridge decreases in height but increases in width as it progresses from a point just dorsal to the vertebral foramen to the distal end of the spinous process. The spinous process is thus V-shaped in cross-section and sits entirely over the caudal half of the vertebral body. The spine gradually widens mediolaterally toward the distal end, which is rendered heart-shaped by a 12-mm-deep, sagittal, parabolic notch. The caudal surface of the spinous process is markedly concave, overhanging a deep postspinous fossa that penetrates as far cranially as the cranial base of the spinous process. The fossa tapers in mediolateral width between the caudal zygapophyses.

Only the right caudal zygapophysis is preserved. It is suspended by a narrow, caudal spinozygapophyseal lamina that projects caudolaterally from the margin of the spinous process. Its articular facet is a craniocaudally elongate oval that likewise faces caudolaterally. It projects further both caudally and laterally than both the spinous process and the vertebral body and sits higher dorsally than the cranial zygapophyses. Caudodorsal to the facet, a short dorsal torus is present.

Identification of the remaining cervical vertebrae is problematic because the cervical column is disarticulated and incomplete. The vertebra identified here as the third cervical is only slightly larger than the axis but articulates with it only moderately well, probably the result of differences in distortion plus the absence of one caudal zygapophysis on the axis. Subsequent cervical position assignments are based both on general morphological and size trends and on comparison of percentage differences in vertebral body craniocaudal dimensions with other diplodocoids (Table 2).

Third cervical. The strongly opisthocoelous vertebral body is generally similar to that of the axis (Text-fig. 5A–F). The cranial articular condyle occupies approximately the dorsal three-quarters of the cranial face; the remainder of the face is a broad, flat, crescentic, dorsally concave surface that extends laterally onto the cranial surfaces of the costolateral eminences. The cranial articular condyle is slightly wider than tall. The caudal articular cotyle is circular.

As on the axis, the lateral corporal pneumatic fossae of both sides deeply excavate the lateral surfaces, are separated by only a thin, sagittal sheet of afenestrate bone, and occupy virtually the entirety of the lateral surfaces of the vertebral body. The right fossa is weakly divided by a low, oblique ridge into a cranial portion that covers about one-quarter of the body and a complementary caudal portion; no such ridge is present on the left
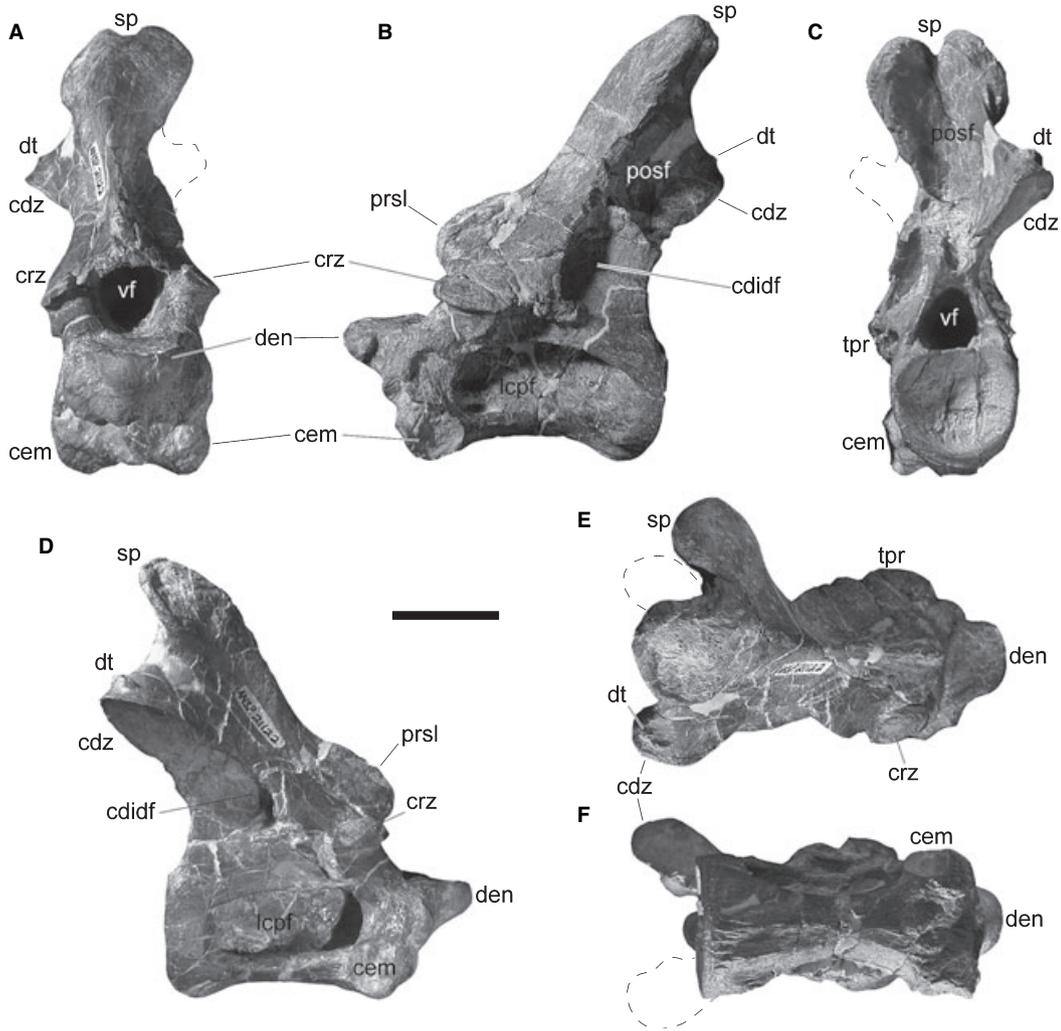
TEXT-FIG. 4. Axis of ANS 21122. A, cranial, B, left lateral, C, caudal, D, right lateral, E, dorsal, and F, ventral views. Scale bar represents 10 cm.

side. The left fossa contains smaller dorsal and larger ventral foramina craniodorsal to the costolateral eminence. These open craniomedially into the flat area ventral to the cranial articular condyle. On the right side, the fossa instead extends cranially, medially, and ventrally into a deep pocket. The lateral corporal pneumatic fossa invades the body more deeply both caudodorsally and caudoventrally on the right side than on the left.

Though still constricted at mid length, the vertebral body is less hourglass-shaped than in the axis in ventral view. The ventral surface is, instead, transversely concave on the cranial half, between the costolateral eminences, but flat and rectangular caudal to that. The lateral margins of the ventral surface form low, ventrolaterally flaring ridges at the caudal end. A low, rugose median crest is discernible at the caudal end. Cranially, the body expands laterally into the costolateral eminences. A pronounced sagittal bulge positioned at the cranioventral edge of the body interrupts the ventral surface between the costolateral eminences. This swelling probably housed a portion of the pneumatic invasion from the right lateral corporal pneumatic fossa. It rapidly tapers caudally and disappears before the midpoint.

The costal foveae face cranially, ventrally and laterally. The right side bears 70·7 mm of the proximal end of a cervical rib (where unfused to the vertebral bodies, this term is retained in favour of the avian 'costal process'). The bicapitate rib has a short capitulum separated from the remainder of the rib by a short neck. The diagenetically diminished angle between the capitulum and tuberculum, as seen in cranial view, is 55 degrees. The dorsal surface of the capitulum is not invaded by the lateral corporal pneumatic fossa. A mediolaterally flattened process is all that is preserved of the tuberculum. There is no cranial process, but the craniolateral surface is rugose where the Mm. intertransversarii and/or lateral flexor colli inserted (Wedel and Sanders 2002). The shaft of the rib is flattened dorsomedially but otherwise roughly circular in cross-section.

The cranial zygapophyses, unlike those on the axis, are borne on long and distinct cranial spinozygapophyseal laminae that curve craniodorsally, forming distinctly concave caudodorsal margins in lateral view. The zygapophyses project about as far cranially as the articular condyle of the body. The roughly circular articular surfaces face dorsomedially. The cranial spino-

TABLE 2. Craniocaudal lengths (in mm) of flagellicaudatan cervical vertebral (CV) bodies. For *Apatosaurus excelsus* (*A. parvus sensu* Upchurch *et al.* 2004*a*) (row 1) and *A. louisae* (row 2; from Gilmore 1936), *Dicraeosaurus hansemanni* (row 3; from Janensch 1929*a*), and *Diplodocus carnegii* (row 4; from Hatcher 1901), the numbers in parentheses indicate the per cent change in length of each vertebral body from its sequential precedent; for CV5, per cent differences from both CV4 (first number) and CV3 (second number) are given. For *Suuwassea emilieae*, the measurement of CV2 (including dens) is real; all subsequent numbers in row 5 represent the predicted craniocaudal length based on the per cent differences calculated for *Diplodocus*. Row 6 presents actual measurements and per cent craniocaudal vertebral body lengths for preserved *Suuwassea* cervicals. For the fifth cervical, per cent differences are given from both the third and the fourth cervical. Note the similarities in per cent differences between the actual values for CV 5–7 of *Suuwassea* and *Diplodocus*.

	CV2	CV3	CV4	CV5	CV6	CV7	CV8	CV9	CV10	CV11	CV12	CV13	CV14
Apatosaurus excelsus UW 15556	n/a	250	300(20%)	342(14%/36·8%)	n/a	415(n/a)	415(0%)	445(7·2%)	475(6·7%)	n/a	n/a	n/a	n/a
Apatosaurus louisae CM 3018	190	280(47·4%)	370(32·1%)	n/a	440(n/a)	450(2·3%)	485(7·8%)	510(5·2%)	530(3·9%)	550(3·8%)	490(−10·9%)	480(−2·0%)	n/a
Dicraeosaurus hansemanni MHN m	160	185(15·6%)	275(48·6%)	225 (−18·2%/21·6%)	230(2·2%)	230(0%)	235(2·2%)	220(−6·4%)	210(−4·5%)	155(−26·2%)	140(−9·7%)	130(−7·1%)	140(7·7%)
Diplodocus carnegii CM 84	165	243(47·3%)	289(18·9%)	372(28·7%/53·1%)	442(18·8%)	485(9·7%)	512(5·6%)	525(2·5%)	595(13·3%)	605(1·7%)	627(3·6%)	638(1·8%)	642(0·6%)
Suuwassea emilieae ANS 21122 predicted	133·2	196·2	233·3	300·2/300·4	356·6	391·2	413·1	423·4	479·7	487·8	505·4	514·5	517·6
Suuwassea emilieae ANS 21122 actual	133·2	141·1(5·9%)	n/a	217·4(54·1% [CV3])	258·4(18·9%)	284·3*(10·0%)	n/a	n/a	n/a	n/a	n/a	n/a	n/a

*Measured distance based on diagenetically distorted element.

zygapophyseal laminae are supported ventrally by moderately thick cranial corporozygapophyseal laminae and caudolaterally by cranial zygadiapophyseal laminae. Although the cranial zygapophyses conjoin ventromedially via the cranial intrazygapophyseal lamina, the thick cranial spinozygapophyseal laminae are separated dorsally by a deep, craniodorsally facing, dorsoventrally ovoid elastic ligament (= intrazygapophyseal) fossa at the base of the spinous process. Cranial infrazygapophyseal fossae (term nov., = peduncular fossae *sensu* Britt 1993) are represented only by shallow indentations dorsolateral to the vertebral foramen. The cranial spinozygapophyseal, together with both cranial and caudal zygadiapophyseal laminae, surround pronounced, triangular cranial parazygapophyseal fossa (fossa parazygapophysealis cranialis, term nov.) on the lateral sides of the bases of the cranial spinozygapophyseal laminae; the fossa on the left is further subdivided into two by a low ridge that parallels the cranial spinozygapophyseal lamina.

Only the bases of the transverse processes are preserved on both sides, more so on the left. The processes overhang tetrahedral infradiapophyseal and cranial infradiapophyseal fossae that are separated by short, thick, cranioventrally orientated cranial corporodiapophyseal laminae. In addition to the cranial zygadiapophyseal lamina, the transverse processes are supported by two structures. One, the low, thick, caudal corporodiapophyseal laminae, merges with the caudodorsal margin of the lateral corporal pneumatic fossae cranial to the caudal end of the vertebral body. The second set, the longer and thinner caudal zygadiapophyseal laminae, originate on the dorsal surfaces of the transverse processes and curve caudodorsally to form the ventrolateral margins of the caudal zygapophyses. The caudal zygadiapophyseal laminae overhang axially elongate but mediolaterally narrow caudal infrazygadiapophyseal fossae. These fossae deepen cranially and invade the region dorsomedial to the transverse processes.

As on the axis, the caudodorsally orientated spinous process is located entirely over the caudal half of the body. Its craniodorsal surface, unlike that of the axis, is flat and narrow (15·9 mm) mediolaterally, bearing a short (31·8 mm), low ridge just dorsal to the elastic ligament fossa. Distally, the flat surface grades into a shallow, craniodorsally open concavity that is bounded laterally by the cranial spinozygapophyseal laminae. The distal end of the spine is missing.

Also as on the axis, a postspinous fossa dominates the caudal portion of the vertebral arch. Unlike the axis, however, the fossa widens between the zygapophyseal alae, narrowing only at its ventralmost end, dorsal to the vertebral foramen. The fossa is thus deep and dorsoventrally ovoid. Only the right caudal zygapophysis is intact: its face is gently sinuous (slightly convex cranially and slightly concave caudally), ovoid, and faces ventrolaterally. A pronounced and rugose dorsal torus projects caudodorsally well beyond the articular facet.

Fifth cervical. This vertebra (Text-fig. 6A–F) is substantially larger than the third cervical, indicating that the fourth cervical was not preserved. This element is somewhat crushed mediolaterally and the spinous process was twisted dextrally by diagenetic pressures. In most respects, the fifth cervical is similar to the third, including the caudally concave cranial spinozygapophyseal
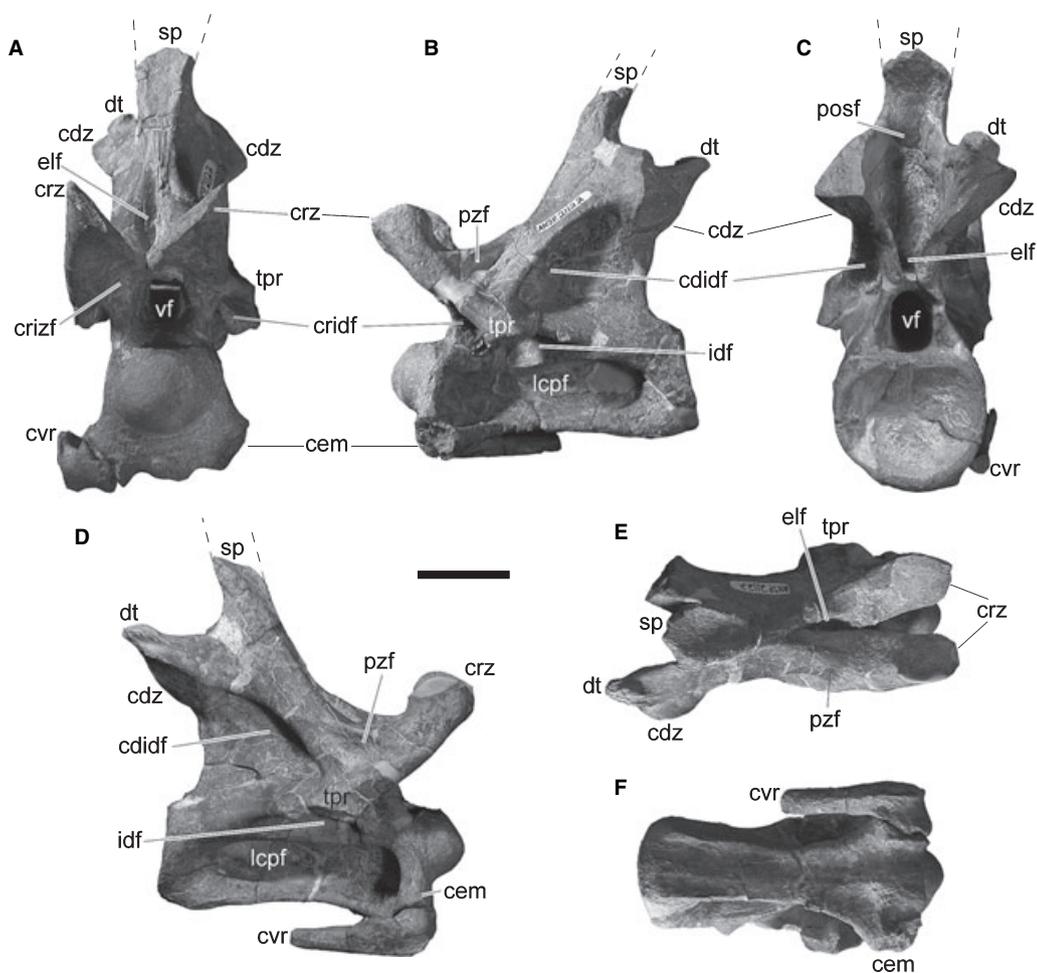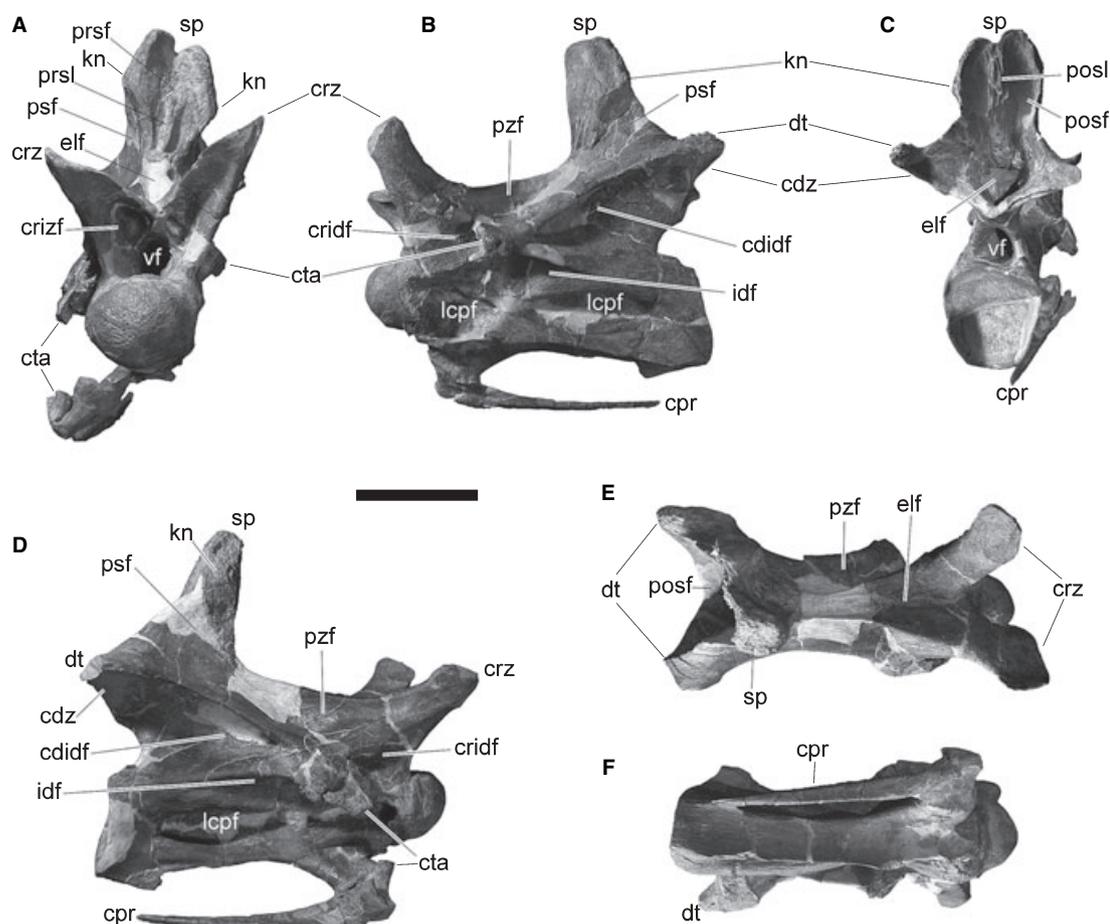
TEXT-FIG. 5. Third cervical of ANS 21122. A, cranial, B, left lateral, C, caudal, D, right lateral, E, dorsal, and F, ventral views. Scale bar represents 10 cm.

laminae and caudally inclined spinous process. However it displays several distinguishing features. The cranial articular condyle is somewhat compressed dorsoventrally and occupies the entire cranial end of the vertebral body; it is not bounded ventrally by a cranially flat face as on the third cervical. The lateral corporal pneumatic fossae are dorsoventrally constricted where low, thick ridges feebly divide the fossae into cranial and caudal portions as in its predecessor (i.e. the ridges do not attain the same topographic level as the margins of the fossae). Unlike on the third cervical, the lateral corporal pneumatic fossae extend onto the dorsal surfaces of the costolateral eminences. Also unlike the third cervical, the cranial portion of the ventral surface is deeply concave and bears no median swelling. The caudal end, however, bears an diminutive sagittal bulge. The costolateral eminences project more ventrally than laterally, but the angle between the rib capitulum and tuberculum is acute as a result of crushing. Cervical rib capitula are articulated with, but not fused to, the costolateral eminences; in lateral view, the capitula and ribs were located entirely ventral to the vertebral body. The rib tubercula are fused to the transverse processes, forming long, slender, columnar costotransverse ansae.

The cranial zygapophyses project slightly further cranially than the vertebral body and have somewhat oblong, dorsomedially facing articular surfaces. They are undercut ventromedially by two cranial infrazygapophyseal fossae, each smaller than the vertebral canal. Tetrahedral cranial parazygapophyseal fossae remain but are less pronounced and open more caudally. The sinuous caudal zygapophyseal articular surfaces face somewhat more ventrally, though this again may be the result of crushing. They are capped by elongate, rugose, caudodorsally projecting dorsal tori.

The spinous process is indented by pre-, para- and postspinous fossae. A rugose ridge at the cranioventral end of the cranial elastic ligament fossa may be considered a prespinous lamina. The spinous process expands mediolaterally toward its apex, attaining maximal width just proximal to its terminus. A long, narrow crack at the distal end gives the appearance of bifurcation, but the collinear dorsal margin indicates that no true split was present. The caudoventral side of the spinous process roofs a deep postspinous fossa, as on previous cervicals. The expanded distal portion is rimmed by low, thick cranial and thinner caudal ridges that form the boundaries of the elongate fossae; these fos-
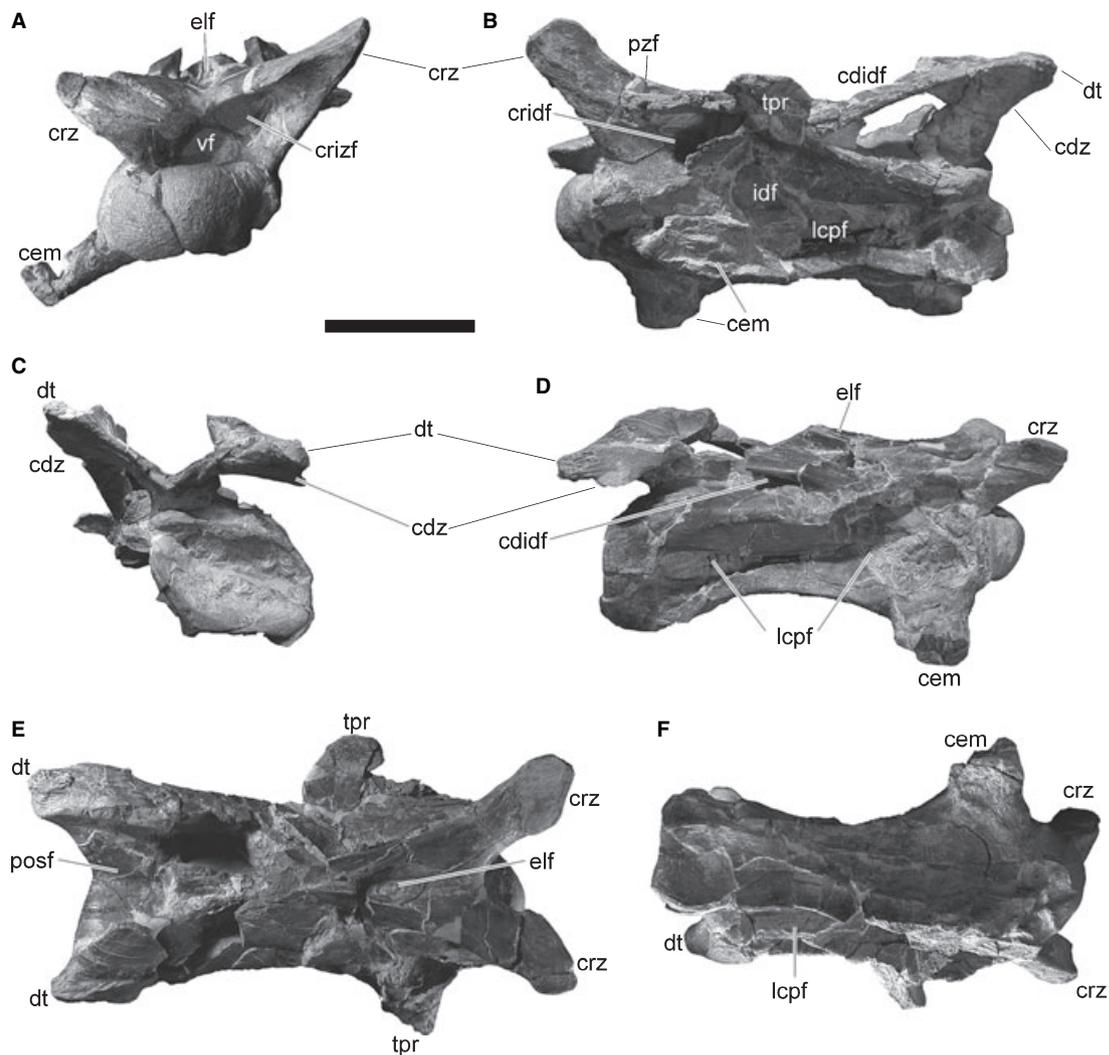
TEXT-FIG. 6. Fifth cervical of ANS 21122. A, cranial, B, left lateral, C, caudal, D, right lateral, E, dorsal, and F, ventral views. Scale bar represents 10 cm.

sae parallel the long axis of the spine to the point of maximum lateral expansion. These paraspinous fossae (fossae paraspinosus, term nov.) are interrupted near the distal end by small, low, rugose, laterally protruding knobs. The fossae extend ventrally nearly to the base of the spine and are more or less contiguous with the parazygapophyseal fossae. Both fossae sets are deeper and more pronounced on the left than the right side, endorsing a pneumatic interpretation.

Sixth cervical. Beginning with the sixth, the cervical vertebral bodies become increasingly elongate craniocaudally (Text-fig. 7A–F). Preserved cervicals also become increasingly distorted. The cranial articular condyle is more hemispherical than on previous cervicals. The lateral corporal pneumatic fossa is shorter dorsoventrally than on the preceding vertebrae. The oblique ridge that divides the fossa into unequal cranial and caudal parts is more topographically pronounced, almost level with the external surface of the vertebra dorsal to the fossa. The ventral surface of the vertebral body is transversely concave and only slightly constricted at mid length. The ventral lip of the caudal

articular face protrudes further caudally than its dorsal counterpart, thus appearing in lateral view as at an angle to the long axis of the vertebral body, unlike previous cervicals. The caudal articular cotyle, however, remains facing caudally, rather than caudodorsally.

The dorsal surface of the costolateral eminence bears a triangular fossa that is separated from the cranial end of the lateral corporal pneumatic fossa by a thick, pronounced ridge. The cervical rib capitulum is fused with the eminence, producing a true costal process that is widest mediolaterally and concave dorsally. Crushing has again reduced the natural angle between the rib articular processes to 43 degrees. The costal process is shorter than the vertebral body but remains wholly ventral to it.

The dorsal margins of the cranial spinozygapophyseal laminae are less concave than on the preceding vertebrae; the zygapophyses themselves project substantially further cranially than the vertebral body. The cranial zygadiapophyseal laminae form decreasingly pronounced, laterally projecting ridges that terminate ventral to the articular faces. They contribute less to the support of the zygapophyses than on preceding cervicals. The

TEXT-FIG. 7. Sixth cervical of ANS 21122. A, cranial, B, left lateral, C, caudal, D, right lateral, E, dorsal, and F, ventral views. Scale bar represents 10 cm.

articular facets are mediolaterally oblong instead of more equidimensional, as on the previous vertebra, and are again lightly sinuous (concave laterally and convex medially). The deep, tetrahedral cranial infrazygapophyseal fossae are subequal in size to the vertebral foramen; the left fossa is further divided by a thin, oblique lamina. As on the fifth cervical, the caudal zygapophyses face more ventrally than laterally and are capped by long, robust dorsal tori. The parazygapophyseal fossae merge with the shallow paraspinous fossae caudally.

The slight cranial inclination of the spinous process appears to be genuine, but some effect of diagenetic distortion cannot be ruled out completely. It is similar to its predecessor in possessing a prespinous fossa interrupted at its base by a sagittal prespinous lamina that divides the larger concavity into two dorsoventrally oblong, parasagittal fossae. The low prespinous lamina fades roughly half-way towards the distal end of the spine. As with the previous vertebra, the spinous process expands laterally towards the distal end. Similarly, its paraspinous fossae are interrupted by low, rugose, lateral knobs, but they are much larger on this vertebra. The distal end of the spine is cleft by a parabolic, 11·8-mm-deep intraspinous sulcus, marking the initial stage of bifurcation. The caudal surface of the spine also bears two dorsoventrally oblong, postspinous fossae divided by a rugose, postspinous lam-

ina that becomes increasingly pronounced ventrally as it curves into the deep, elastic, ligament-bearing region of the fossa.

Seventh cervical. This is the caudalmost somewhat complete cervical vertebra; it lacks its spinous process and is more severely distorted by dorsoventral crushing than its predecessors (Text-fig. 8A–F). It does not articulate well with the sixth cervical due to this distortion. In most respects, it is similar to the sixth cervical but is longer craniocaudally. Crushing is probably responsible for the cranial articular condyle being wider than tall. The caudal articular face retains the apparent slope in lateral view seen in the previous vertebra. The lateral corporal pneumatic fossa of the left side lacks the prominent, oblique dividing lamina visible on the right and on preceding cervicals, but has several smaller internal laminae instead. Costolateral eminences project ventrolaterally well below the level of the vertebral body. Cranial parazygapophyseal fossae remain present. The base of the missing spinous process indicates that it continued the trend of restriction to the caudal half of the element. The caudal zygapophyses retain long, robust dorsal tori. A low rugose ridge floors the cranial elastic ligament fossa; its caudal counterpart ramifies cranially to the base of the spinous process.

TEXT-FIG. 8. Seventh cervical of ANS 21122. A, cranial, B, left lateral, C, caudal, D, right lateral, E, dorsal, and F, ventral views. Scale bar represents 10 cm.

Other cervicals. Two other, heavily crushed fragments, much larger than the seventh cervical, represent caudal cervicals. One fragment preserves the cranial end of a vertebra (Text-fig. 9A–C), including the cranial articular condyle, cranial zygapophyses and costal processes. On this element, the cranial articular condyle is wider mediolaterally than tall dorsoventrally; it was not greatly affected by diagenetic deformation. It is overlain by a vertebral foramen subequal in size to the paired cranial infrazygapophyseal foramina. The cranial zygapophyseal alae are straight, project craniodorsally, and maintain the articular facet morphology of the sixth and seventh cervicals. The small distance by which they protrude further cranially than the vertebral body may be due to distortion. The cranial ends of the lateral corporal pneumatic fossae deeply invade the cranial articular condyle and contain several accessory laminae and foramina. The dorsolateral surface of the costolateral eminence remains concave and separated from the lateral corporal pneumatic fossa by a low ridge.

The second fragment represents the caudal end of a vertebra (Text-fig. 9D–E). The retention of a pendant caudal zygadiapophyseal lamina long enough to overlap the vertebral body indicates that it is a caudal cervical. The caudal articular face retains the angled profile of the sixth and seventh cervicals. The ventral surface of the vertebral body is mediolaterally broad and transversely concave. The caudal end of the lateral corporal pneumatic fossa sits much further cranially with respect to the caudal margin of the body than on any other preserved cervical. Two shallow caudal infrazygapophyseal fossae are visible dorsolateral to the vertebral foramen. The caudal zygapophysis faces mostly ventrally and is capped by a short dorsal torus that does not surpass the articular face in length.

Thoracic vertebrae and ribs
Two partial and one complete, heavily (mostly mediolaterally) distorted thoracic vertebrae are preserved. They can be identified as cranial thoracics because their short costolateral eminences
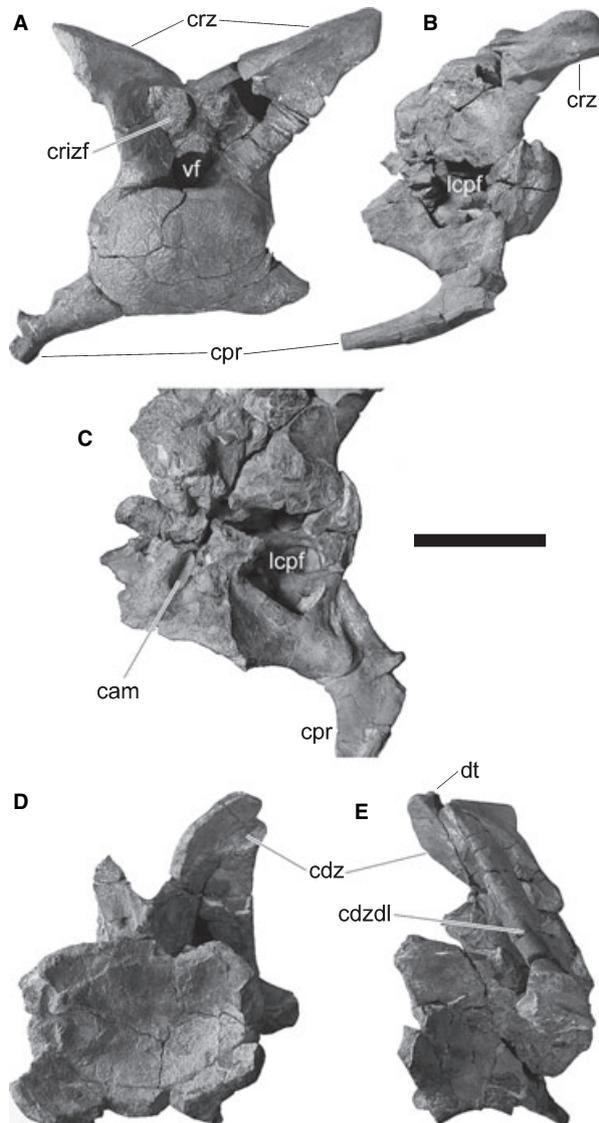
TEXT-FIG. 9. Middle or caudal cervical vertebral fragments preserved with ANS 21122. Cranial end fragment. A, cranial, B, right lateral, and C, oblique right caudolateral views. Caudal end fragment. D, caudal, and E, right lateral views. Scale bar represents 10 cm.

remain largely on the vertebral body or very near the arch-body junction, but do not project ventrally beyond their respective bodies. More specific placement in the column is problematic, however: the preserved bodies display relative proportions more similar to *Diplodocus* than to *Apatosaurus* cranial thoracics (Table 3), but are morphologically more like the latter. Harris and Dodson (2004) reported the vertebrae of ANS 21122 as the second–fourth thoracics, which also matches the pattern of gradual costolateral eminence dorsal migration reported for *Diplodocus* by Hatcher (1901) but contrasts with the abrupt condition in *Apatosaurus louisae*, in which the eminence is situated high on the vertebral arch by the third thoracic (Gilmore 1936, pl. 25; McIntosh 1995). However, the pattern in *A. excelsus* matches

both those of *Diplodocus* and ANS 21122 (Gilmore 1936, pl. 32). Certainly, none of the elements in ANS 21122 can be the caudal-most cervical vertebra because in other flagellicaudatans, costo-transverse ansae are retained throughout the mid- and caudal cervical series. Given the similarities between *Apatosaurus* and *Suuwassea*, the assignments of Harris and Dodson (2004) are revised here to the first–third thoracics, though the caveat that they are indeed the second–fourth (or some combination from the cranial thoracic region) remains.

First thoracic vertebra. The cranialmost thoracic (Text-fig. 10A–C), with the most ventrally placed, costolateral eminence, is better preserved on the left side. The vertebral body is shorter but taller than any preserved cervical. The lateral corporal pneumatic fossa tapers caudally but deepens to invade the articular condyle cranially. The costolateral eminence is located at the cranioventral edge of the fossa but it projects laterally and does not extend past the ventral margin of the vertebral body.

The vertebral arch, measured as the distance from the dorsal margin of the vertebral body to the base of the caudal zygapophyses, is relatively low. The cranial and caudal corporodiapophyseal laminae converge dorsal to the costolateral eminence, forming the roof of a tetrahedral infradiapophyseal fossa that opens laterally. The caudal corporodiapophyseal lamina bifurcates toward its cranial end into dorsal and ventral ridges that bound between them a shallow sulcus. The transverse process is missing. The caudal corporo- and zygadiapophyseal laminae form the cranial and dorsal margins of the caudal infradiapophyseal fossa. The caudal zygapophyseal articular face is a large, dorsoventrally elongate oval. Only the base of the spinous process is preserved dorsal to the caudal zygapophysis, but the spine must have been deeply bifid because the entire medial surface of the zygapophyseal ala consists of smooth, unbroken bone. On the most craniolateral preserved portion of the spine, a short, thin, lamina divides a small, ovoid fossa dorsal to the apex of the infradiapophyseal fossa. The intraspinous sulcus (sulcus intraspinosus, term nov., the space between halves of a bifid spinous process) persists ventrally to the roof of the vertebral canal. No median pseudospinous tuberculum (tuberculum pseudospinosus, term nov., = median spine *sensu* Hatcher 1901 and Gilmore 1936; wirklicher Neuralstachel *sensu* Wiman 1929; Ansatzknopf *sensu* Janensch 1929a; median tubercle *sensu* Wilson 2002) is preserved. The shape and orientation of the hemispinous processes (processus hemispinosus, term nov., one half of a bifurcate spinous process; = metapophysis *sensu* Borsuk-Bialynicka 1977) cannot be assessed.

Second thoracic vertebra. The second thoracic vertebra (Text-fig. 10D–F) is similarly opisthocoelous but has a much taller vertebral arch. Its costolateral eminences have been obscured by distortion and breakage, but are located near the body-arch junction, at least on the right side. Both sides of the vertebral body are intact but as before, only the left half of the arch is intact. The lateral corporal pneumatic fossae of both sides are reduced compared with preceding vertebrae in both length and height. As before, they taper and shallow caudally but contain additional lamina and foramina cranially.

TABLE 3. Craniocaudal lengths (in mm) of flagellicaudatan cranial thoracic (T) vertebral bodies. For *Apatosaurus excelsus* (*A. parvus sensu* Upchurch *et al.* 2004*a*) (row 1) and *A. louisae* (row 2; from Gilmore 1936), *Dicraeosaurus hansemanni* (row 3; from Janensch 1929*a*) and *Diplodocus carnegii* (row 4; from Hatcher 1901), the numbers in parentheses indicate the per cent change in length of each vertebral body from its sequential precedent; for each vertebra after T1, per cent differences from each subsequent vertebra are given in reverse order. For *Suuwassea emilieae*, the measurement of the cranialmost preserved thoracic vertebra is real; its position as T1 and T2 are considered in rows 5 and 6, respectively. All subsequent numbers in rows 5 and 6 represent the predicted craniocaudal length based on the per cent differences calculated for *Diplodocus*. Row 7 presents actual measurements and per cent craniocaudal vertebral body lengths for preserved *Suuwassea* thoracics. Note the closer similarities in per cent differences between the actual values for *Suuwassea* and *Diplodocus* than other flagellicaudatans.

	T1	T2	T3	T4
Apatosaurus excelsus UW 15556	345	285 (−17·4%)	280 (−1·8%/−18·8%)	213 (− 23·9%/−25·3%/−38·3%)
Apatosaurus louisae CM 3018	310	315 (1·6%)	310 (−1·6%/0%)	260 (−16·1%/−17·5%/−16·1%)
Dicraeosaurus hansemanni MHN m	125	130 (4·0%)	129 (−0·8%/3·2%)	133 (3·1%/2·3%/6·4%)
Diplodocus carnegii CM 84	510	416 (−18·4%)	326 (−21·6%/−36·1%)	318 (−2·4%/−23·6%/−37·6%)
Suuwassea emilieae ANS 21122 predicted (as T1–3)	307	250·5	196·4	n/a
Suuwassea emilieae ANS 21122 predicted (as T2–4)	n/a	307	240·7	234·9
Suuwassea emilieae ANS 21122 actual	n/a	307	259* (−15·6%)	253·3* (−2·2%/−17·5%)

*Measured distance based on diagenetically distorted element.

The elongate vertebral arch has a conspicuous craniodorsal angulation, though how much of this is the result of crushing and distortion is difficult to assess. The arch appears to house paired caudal infrazygapophyseal foramina dorsal to the vertebral foramen. No paraspinous fossa is present. The intraspinous sulcus persists ventrally only to a point level with the midpoint of the caudal zygapophyses. As before, no pseudospinous tuberculum is present. The caudal zygapophyses are preserved close to the midline, again possibly an artefact of distortion, and have greatly enlarged, ovoid articular faces. The hemispinous process dorsal to the zygapophysis is short and distally rounded. It is moderately convex both laterally and, especially, medially. The distal margin thickens to form a rugose rim. The spine curves slightly medially toward its distal end.

Third thoracic vertebra. The remaining thoracic vertebra (Text-fig. 11A–D) is relatively complete. Its costolateral eminences are located just dorsal to the body-arch junction. Its body is shorter craniocaudally than the previous two, but it remains opisthocoelous. The vertebral body has, as on previous thoracic vertebrae, been compressed mediolaterally but also demonstrates some dorsoventral displacement. The lateral corporal pneumatic fossae are reduced to small, roughly circular openings centrally located dorsal to the craniocaudal midline of the vertebral body. The fossa on the right contains no visible foramina; the left fossa may possess a foramen leading cranially into the body, but this area has been crushed virtually shut. The same crushing gives the ventral margin of the body the appearance of being keeled, but it was almost certainly flat or convex. The costolateral eminences are only slightly elevated above the lateral surfaces of the vertebral body.

The dorsoventrally elongate vertebral arch is fused to the vertebral body, but a vague line of suture can be discerned for most of its basal circumference. The lateral surfaces of the arch are occupied entirely by the still tetrahedral infradiapophyseal and cranial infradiapophyseal fossae, separated by a thin, cranioventral–caudodorsally orientated cranial infradiapophyseal lamina. The cranial infradiapophyseal fossa on the right side deeply invades the arch, although the medialmost surface is broken. The cranial corporozygapophyseal laminae are robust, dorsolaterally projecting pillars of bone that spawn craniomedially orientated cranial infrazygapophyseal laminae. Presumably these met at the midline, but this region is broken. Shallow fossae adorn the cranial surfaces of these sheets just ventral to the cranial zygapophyses; these may represent rudimentary infrazygapophyseal fossae. Visible in the interior of the vertebral arch dorsal to the vertebral canal, exposed by breakage of the lamina, are several small, irregularly spaced, probably pneumatic camerae.

The cranial zygapophyses consist of planar, mediolaterally ovoid articular facets that are barely elevated above, and project only slightly craniolaterally from, the surrounding bone. The facets are coplanar with the dorsal surfaces of the cranial zygadiapophyseal laminae, but are set off from them by a barely discernible rim. A thick and rugose prespinous lamina rises abruptly from the cranial interzygapophyseal lamina. At its proximal end, the prespinous lamina consists of a series of short vertical ridges and fossae, but more dorsally they merge to form a single, pronounced sheet. At its distal end, its left surface houses a small pneumatic fossa.

The transverse processes are essentially horizontal sheets, braced ventrally by the conjoined cranial and caudal corporodiapophyseal laminae. Their distal ends expand to form rugose, triangular, laterally facing, costal articular surfaces. The right transverse process is orientated caudolaterally; the left has a strong dorsal angulation as well. Plastic deformation has clearly had an influence, and the true amount of dorsal angulation, if any, cannot be assessed; if they follow the pattern of *Apatosaurus*, then the horizontal right process is closer to the correct orientation. The caudal surface of each transverse process is deeply concave, housing a mediolaterally elongate, tetrahedral caudal
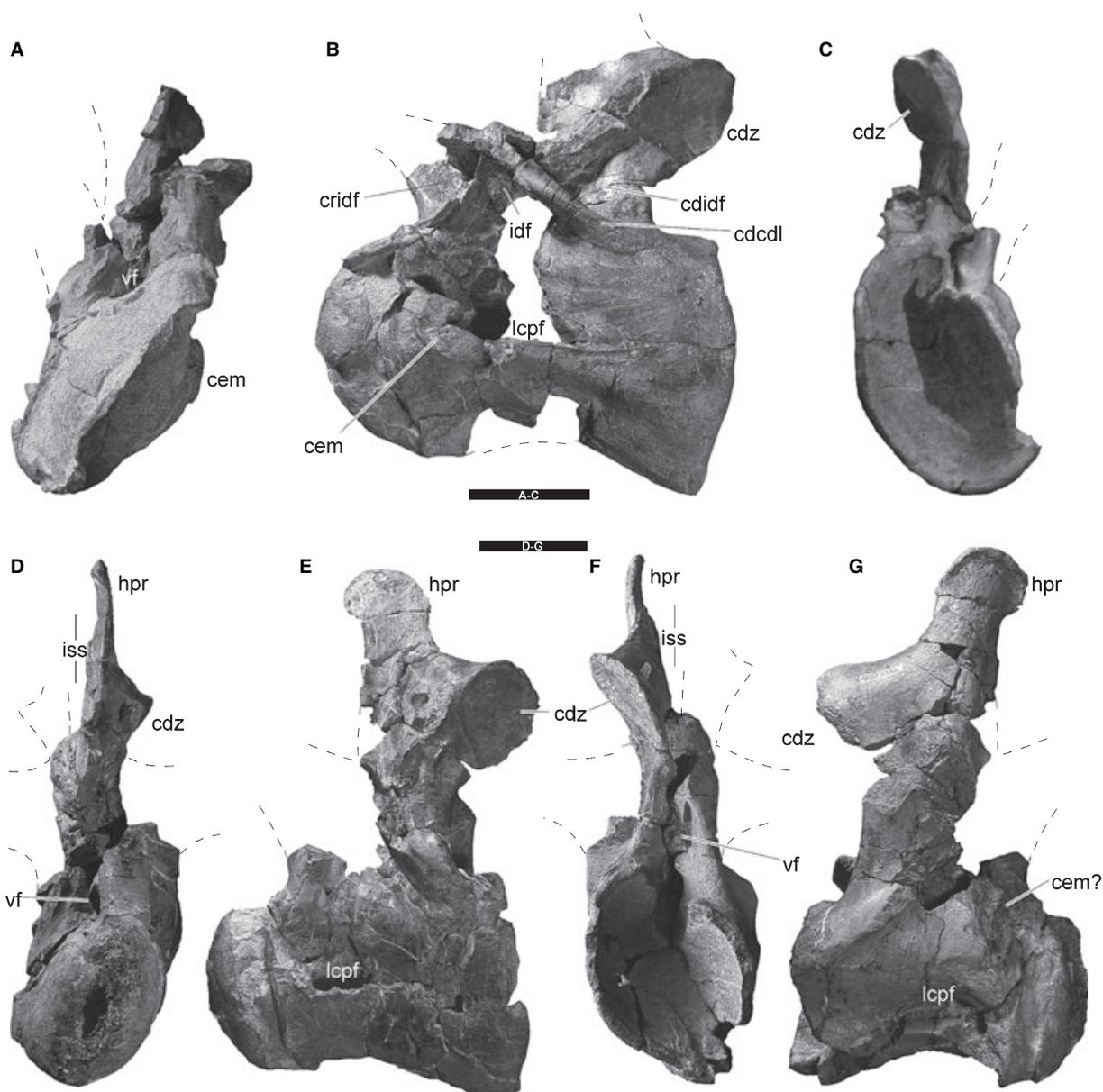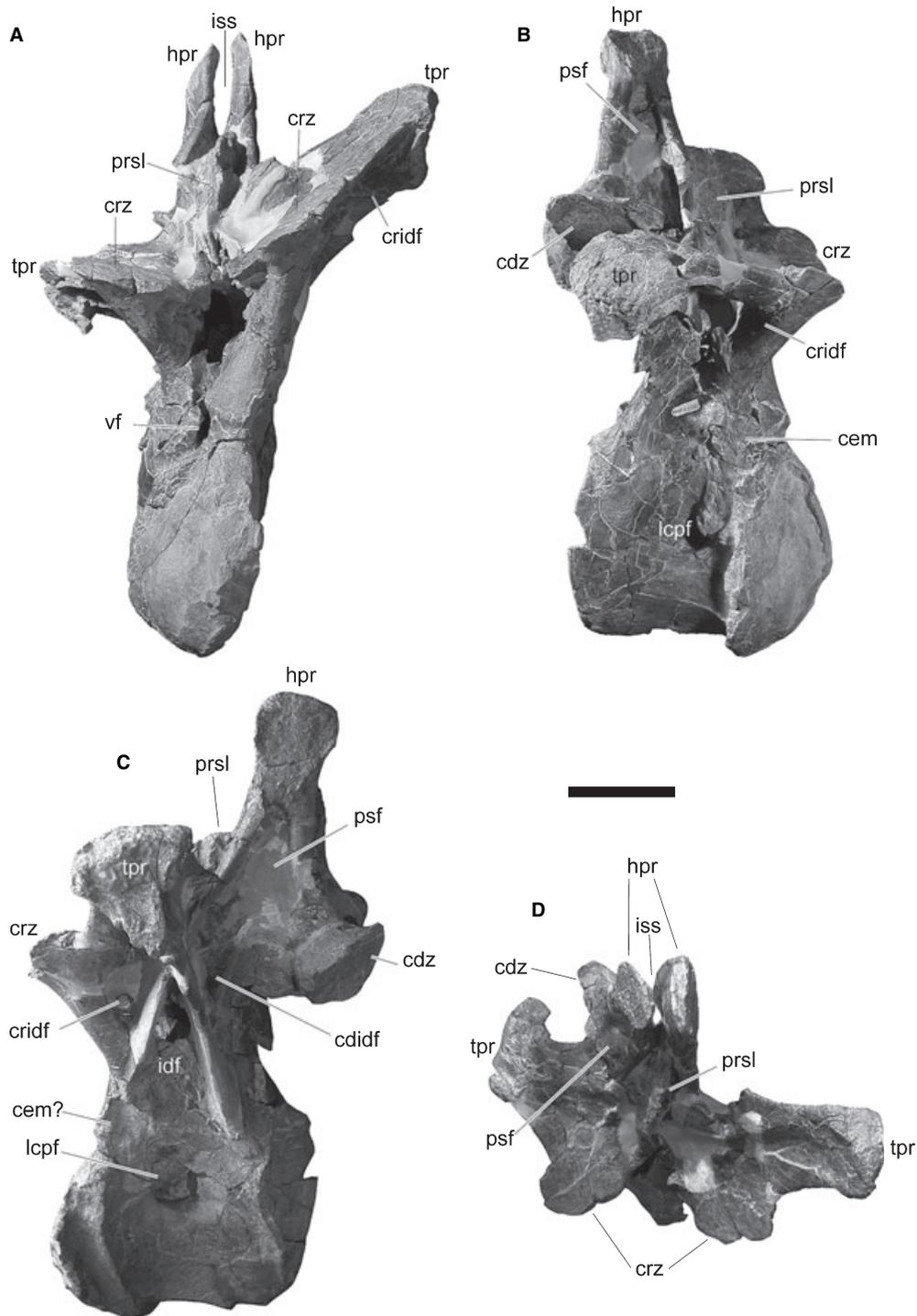
TEXT-FIG. 10. First thoracic vertebra of ANS 21122. A, cranial, B, left lateral, and C, caudal views. Second thoracic vertebra of ANS 21122. D, cranial, E, left lateral, F, caudal, and G, right lateral views. Scale bars represent 10 cm.

infradiapophyseal fossa that is bounded ventrolaterally by the caudal corporodiapophyseal lamina, ventromedially by the caudal corporozygapophyseal lamina, and dorsally by the roughly horizontal caudal zygadiapophyseal lamina. The caudal zygapophyses jut caudally, each supported by its own corporozygapophyseal and spinozygapophyseal lamina. There is no sign of either an infrazygapophyseal lamina or of hypantral articular facets. The zygapophyseal articular facets are mediolaterally elongate, oval facets that face ventrolaterally (again augmented by crushing).

The intraspinous sulcus is not as deep as in the previous vertebra. Both hemispinous processes angle slightly caudally from the vertical and are closely appressed; the predeformational mor-

phology of the intraspinous sulcus is unclear. The ventralmost point of the sulcus lacks a pseudospinous tuberculum and lies dorsal to the caudal zygapophyses, well above the roof of the vertebral canal, indicating that bifurcation was dying out and did not persist much further caudally in the series. As on the previous thoracic vertebra, each hemispinous process is mediolaterally compressed, but unlike its predecessors, its base is invaded by a dorsoventrally elongate paraspinous fossa that is bounded by stout ridges formed by the spinodiapophyseal and caudal spinozygapophyseal laminae. Each fossa tapers distally; the left fossa is shallow but the cranioventral corner of the right appears to have deeply invaded the vertebral arch craniomedially and itself contains a series of short, accessory laminae. The cra-

TEXT-FIG. 11. Third thoracic vertebra of ANS 21122. A, cranial, B, right lateral, C, left lateral, and D, dorsal views. Scale bar represents 10 cm.

nial margins of the hemispinous processes are formed not by cranial spinozygapophyseal laminae but by spinodiapophyseal laminae that twist abruptly from lying in a transverse to a parasagittal plane just dorsal to the base of each hemispine. The caudal margins of the hemispinous processes consist entirely of caudal spinozygapophyseal laminae. The deep postspinous fossa bifurcates distally along with the spine, but neither branch persists to the distal end of its spine. The portions of the hemispinous process medial surfaces not indented by these fossae are roughly planar, but thicken proximal to the distal ends into low, axial ridges. The bone texture, both distal and immediately proximal to these ridges, is rough. The distal ends of both hemispin-

ous processes expand slightly craniocaudally and angle slightly medially, thus presenting rugose surfaces dorsolaterally. These surfaces are not rimmed as on the previous vertebra.

Ribs. Two thoracic ribs are fairly complete; several other fragments are also present. None possesses pneumatic foramina, nor are any hollow. One (Text-fig. 12), from the middle of the series, measures 1·4 m along its inside curvature. This rib has an elongate and dorsally directed tuberculum but a short capitulum

TEXT-FIG. 12. Middle thoracic rib of ANS 21122. Proximal end. A, caudal, and B, cranial views. Distal end. C, medial, and D, lateral views. Scale bar represents 10 cm.

(Text-fig. 12A–B). The two processes diverge at an acute angle from the costal body and are conjoined through the capitulotubercular incisure by a thin lamina. In cross-section, the shaft below the proximal end is triradiate, indented on its cranial and caudal surfaces by broad grooves. The groove on the cranial surface gradually diminishes distally, becoming non-existent halfway down the body. The caudal groove persists almost to the distal end of the rib, rendering the cross-sectional morphology of the distal shaft chevron-shaped. The distal end (Text-fig. 12B–C) is flattened mediolaterally and both expanded and squared off by a rugose distal surface. The second rib, probably positioned further caudally in the series, is more strongly recurved. Its tuberculum, capitulum and extreme distal ends are missing, but the body follows the pattern of the preceding rib.

Caudal vertebrae

Of all the caudal vertebrae preserved in ANS 21122, only the distal, 'whiplash' caudals are complete. All the remaining vertebrae consist only of vertebral bodies that lack all phylogenetically informative portions of their respective arches. On the proximal and middle caudals, this absence is due to lack of fusion as evidenced by the deeply fluted articular surfaces for the arches on the bodies. In contrast, the arches on the most distal vertebrae that retain them are seamlessly fused, but everything dorsal to the bases of the corporozygapophyseal laminae are broken.

Proximal caudals. Of the preserved caudal vertebrae, none appears to be from the most proximal portion of the tail (i.e. first through fourth caudals); in *Diplodocus*, the vertebral bodies of the proximalmost caudals are extraordinarily compressed proximodistally and the bases of the aliform transverse processes extend far down the lateral sides of their respective bodies. Instead, the three bodies of proximal caudals of ANS 21122 (labelled A, B and C here for convenience of reference) are more similar to those of the fifth–tenth caudals of *Diplodocus* (Hatcher 1901; Gilmore 1936). However, the proximalmost caudal vertebrae of *Apatosaurus* and *Dicraeosaurus* (of which only the first two are weakly procoelous) lack the extreme compression of *Diplodocus* and are instead much more like those of *Suuwassea* in proportion. It is thus possible that the degree of compression seen in diplodocines is autapomorphic. All three preserved *Suuwassea* proximal caudals (Text-fig. 13) are longer along their dorsal than ventral margins. These elements are procoelous/distoplatyan (*sensu* Tidwell *et al.* 2001). Possibly the vertebrae were more procoelous than they appear: the distal articular surfaces and the thin, outermost margins of the proximal articular cotyles have been abraded. The latter artefact enhances the pentagonal morphology of the bodies: each lateral side is divided into two unequal, distinct faces. The more dorsal faces are shorter dorsoventrally, face dorsolaterally, and bear the abraded bases of the vertebral arches. The larger, more ventral portions face ventrolaterally and are perforated by several large and irregularly distributed nutrient foramina. Lateral corporal pneumatic fossae are absent. The ventral margin of each body is so narrow that it effectively creates a transversely broad 'keel' (Text-fig. 13C, I) The ventral surface is flat to slightly transversely convex on vertebrae A and C but slightly concave on B. Distinct articular facets for haemal arches cannot be discerned.
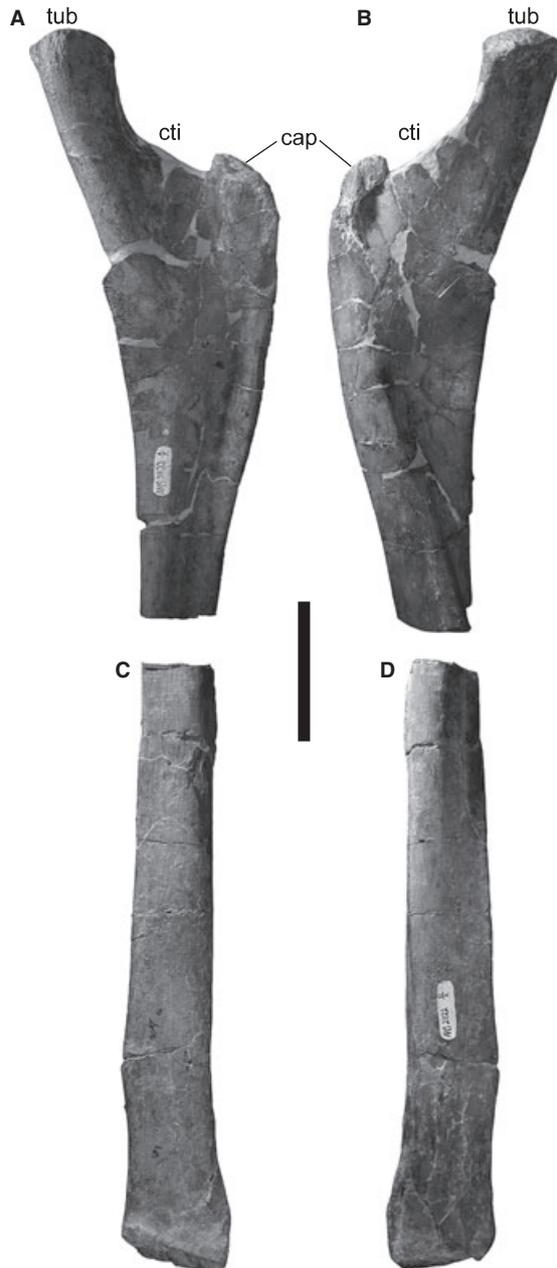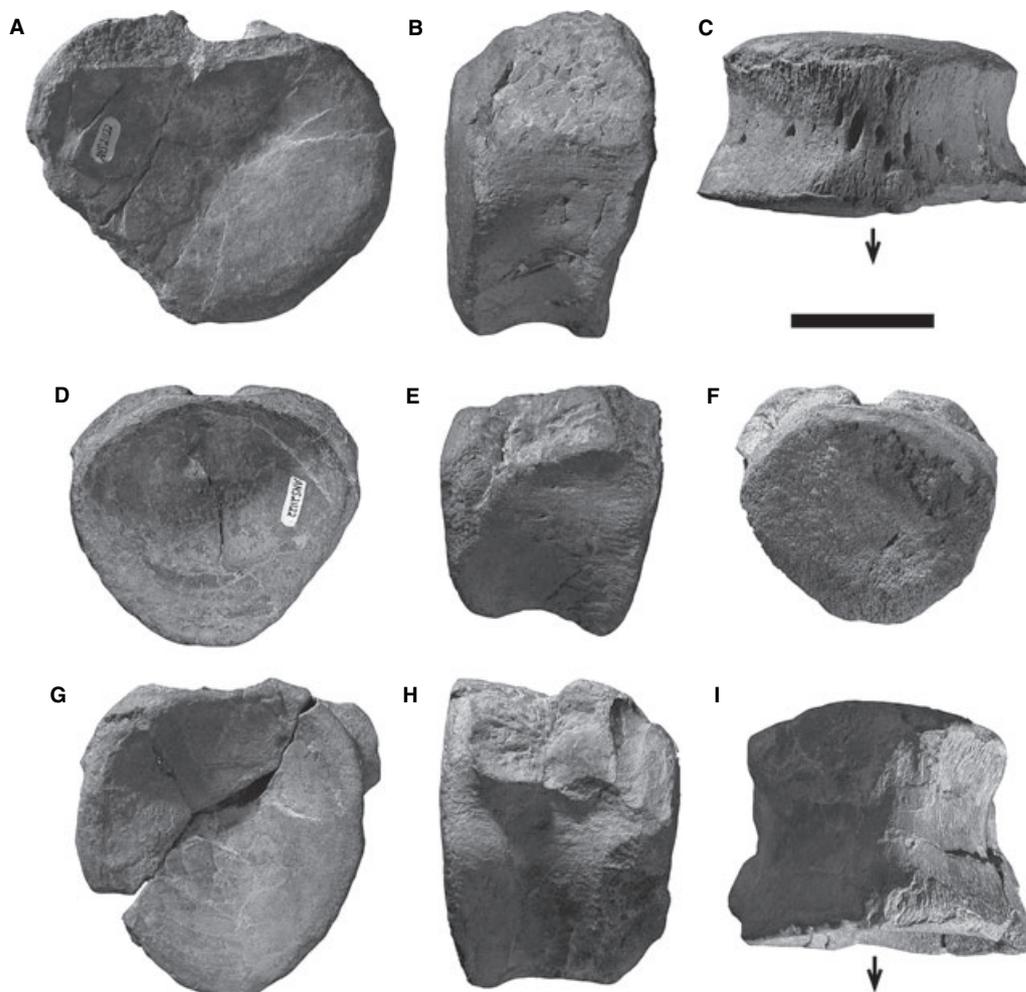
TEXT-FIG. 13. Proximal caudal vertebrae of ANS 21122. Proximalmost preserved caudal (A). A, proximal, B, right lateral, and C, ventral views. Caudal B. D, proximal, E, left lateral, and F, distal views. Caudal C. G, proximal, H, left lateral, and I, ventral views. Arrows in C and I point cranially. Scale bar represents 10 cm.

Middle caudals. An elongate, waisted, spool-shaped middle caudal (Text-fig. 14A–D) is amphicoelous and has roughly circular proximal and distal articular faces. The preserved base of the vertebral arch is located closer to one end (presumably the proximal) of the body than the other. The concavity of the caudal articular face is offset dorsally. As on more proximal caudals, the lateral surfaces consist largely of two parts. The ventral, laterally facing, planar surface takes up the majority of the lateral side. It is separated by a low, rounded, linear ridge from shorter, proximodistally elongate, slightly concave surfaces that border the vertebral canal. The ventral surface of the vertebra is mostly flat, but becomes lightly transversely concave at the proximal and distal ends, between the articular eminences for the haemal arches.

Three similar, though smaller and more elongate, amphiplatyan distal caudals (Text-fig. 14E–L), and fragments of several others, have subcircular to subrectangular articular faces, but unlike their predecessor, most bear tiny, deep, collateral ligament foveae on the centre of each articular face. On most, such foveae are bounded by low, convex, transverse eminences. The lateral ridge of the larger middle caudal vertebra is absent on these smaller elements, so their spool-shaped bodies have more circular cross-sections.

Distal caudals. Two complete and 11 end fragments representing between six and 11 other, extreme distal, 'whiplash' caudals are preserved. Their amphiplatyan bodies entirely lack vertebral arches as well as the median waisting of the middle caudal and more proximal caudal vertebrae (Text-fig. 15). Both articular faces bear tiny foveae bounded both dorsally and ventrally by convex eminences. Only a single fragment, by far the smallest preserved (8.8×10.1 mm in maximum diameters) appears to be convex, but it is unclear whether or not this fragment is truly a distal caudal or the distal end of a process from some other element (or taxon).

Haemal arches. Only a single fragment of a haemal arch (chevron) was recovered (Text-fig. 14M). It represents the dorsal end of an arch that probably originated in the proximal portion of the tail. This placement is based on size and on the unproven
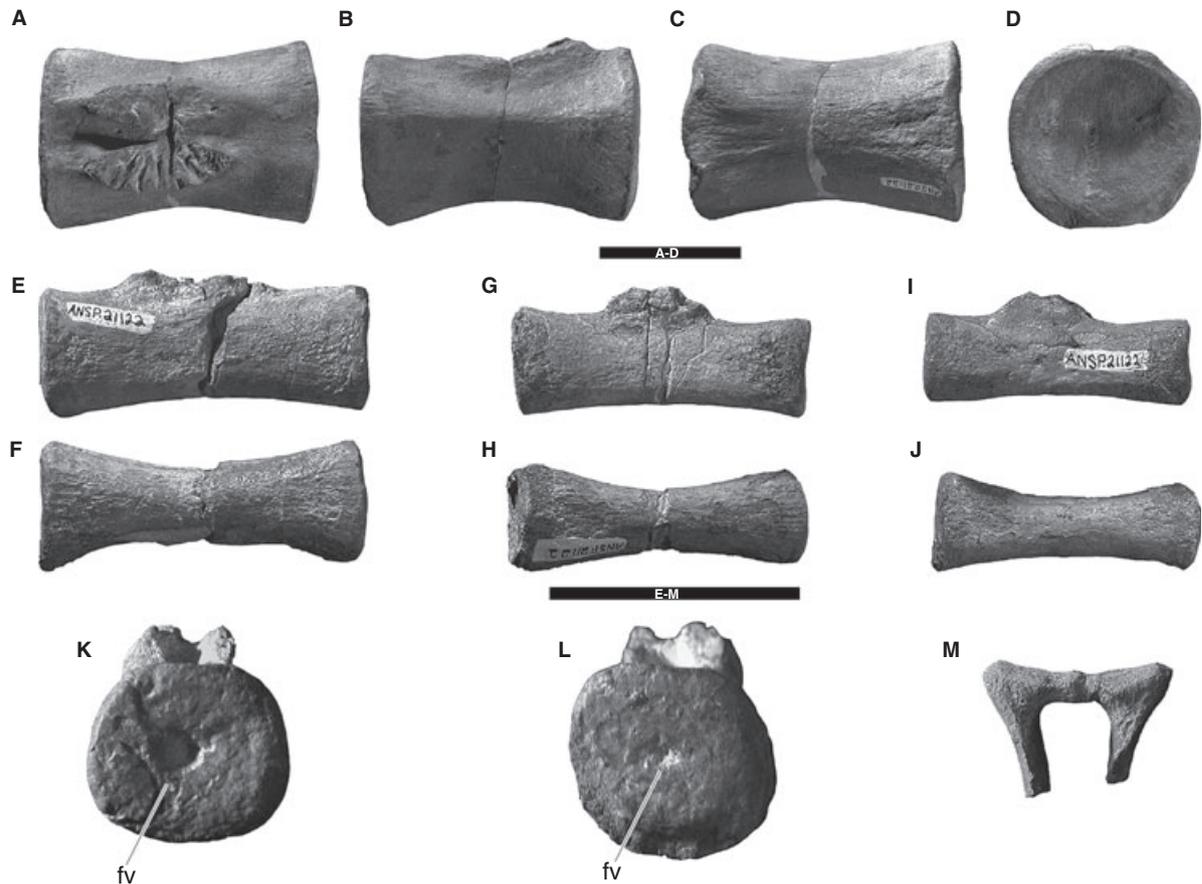
TEXT-FIG. 14. Middle and distal caudal vertebrae of ANS 21122. Middle caudal vertebral body. A, dorsal, B, right lateral, C, ventral, and D, proximal views. More distal caudals. E, G, I, left lateral, and F, H, J, ventral views. K, proximal, and L, distal views of vertebra shown in I–J. M, proximal haemal arch fragment. Scale bars represents 10 cm for A–D, 5 cm for E–M.

assumption that *Suuwassea*, like other flagellicaudatans, possessed bifurcate, 'skid'-like arches on the distal portion of the tail. Other than the fact that it is not open dorsally, the fragment is unremarkable.

Axial pneumaticity
The cranial cervicals are so deeply invaded by fossae that little internal space remains available to house camellae, so presumably these vertebrae qualify as camerate. Breakage in the seventh cervical and the caudal cervical fragments demonstrate that the base of the vertebral arch is largely solid, though near the dorsal surface the cranial-end fragment displays a few small, ovoid spaces lined with smooth bone (Text-fig. 9C). In both fragments, the interiors of the sagittal septa between the lateral corporal pneumatic fossae can be seen. In the cranial-end fragment, a small, craniocaudally ovoid fossa sits on the dorsal surface; how (or whether) it connected to the lateral corporal pneumatic fossa is unclear. A similar fossa floors the bone (Text-fig. 9C). It is separated by a very thin lamina from a second, narrower fossa that appears to invade the lamina that connects the costolateral eminence to the vertebral body. The pattern of breakage around these spaces suggests that these were not open externally. These fossae appear to qualify as camerae

because the overall surrounding bone is thick and much more solid. The vertebrae thus qualify as polycamerate (*sensu* Wedel *et al.* 2000).

COMPARISONS WITH OTHER FLAGELLICAUDATANS

Given the flagellicaudatan nature of *Suuwassea* outlined by Harris and Dodson (2004), comparisons will be limited here to other members (and putative members) of that clade. Graphic comparison of flagellicaudatan cervical vertebrae is presented in Text-figure 16, cranial thoracic vertebrae in Text-figure 17 and distal ('whip') caudal vertebrae in Text-figure 18. Particular attention and detail is focused on comparative patterns and distributions of laminae and fossae because they have been specified in the past as taxonomically diagnostic features in some sauropods, such as *Amazonsaurus* (de Souza Carvalho *et al.* 2003) and have proven important in specimen-level and interspecific phylogenies (e.g. Upchurch *et al.* 2004a).

A

B

C

fv
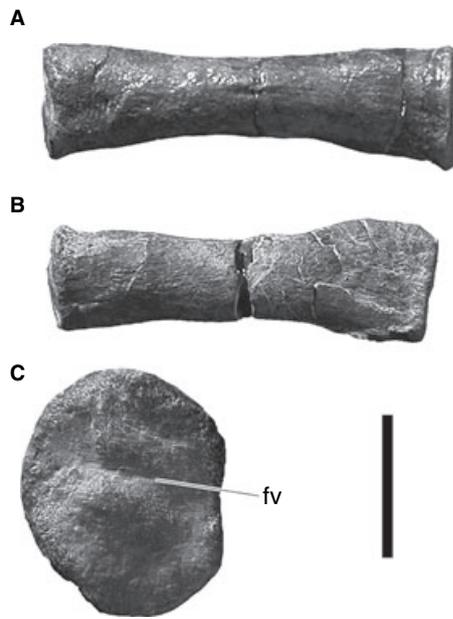
TEXT-FIG. 15. Distal 'whiplash' caudals of ANS 21122. A–B, lateral, and C, end views. Scale bar represents 2 cm for A–B, 1 cm for C.

Amargasaurus cazaui. The most obvious difference in cervical and thoracic vertebral morphology between *Amargasaurus* (MACN-N 15) and *Suuwassea* is that the former autapomorphically possess hyperelongate spinous (on the axis) and hemispinous (on all postaxial cervicals) processes (Salgado and Bonaparte 1991). As with *Dicraeosaurus* (see below), the intraspinous sulcus of *Amargasaurus* appears on the third cervical where it cleaves down to a point just dorsal to the vertebral canal. Spinous bifurcation persists through the seventh (*sensu* Salgado and Bonaparte 1991) thoracic (21st presacral) vertebra, a much more extensive span than is apparent for *Suuwassea*. The shallow lateral corporal pneumatic fossa morphology in *Amargasaurus* cervicals much more closely resembles that of *Dicraeosaurus* than *Suuwassea*. Small dorsal tori appear to be present on at least some cervicals (Salgado and Bonaparte 1991, fig. 5) of *Amargasaurus*. The caudal vertebrae of the Argentine taxon have only been briefly described and not figured (Salgado and Bonaparte 1991), so no meaningful comparison can be made.

Amphicoelias altus. Because no elements in their respective holotypes overlap, *Suuwassea* cannot be compared to *Amphicoelias* (the type specimen of which, AMNH 5764, consists of a caudal thoracic vertebra and a femur). New material from Montana reported to pertain to *Amphicoelias* by Wilson and Smith (1996) has not been fully described and comes from a locality different from that of the genoholotype, and thus cannot belong to the same individual. The referral of that material to the genus was

based on a combination of femoral proportions and the more general lack of similarity to other known Morrison diplodocoids, and it may be referable to either *Suuwassea* or yet another new Morrison taxon. If *Amphicoelias* is as similar to *Diplodocus* and *Barosaurus* as is typically presumed, then it is unlikely that it is congeneric with *Suuwassea*, but until referrals are secured and material described, it remains possible.

Apatosaurus spp. All three widely accepted species of *Apatosaurus* (*A. ajax*, *A. excelsus* and *A. louisae*), as well as some specimens referred to these species or simply as *A.* sp., are considered together below, except where noted. The only axial elements shared between the holotype of *A. ajax* (YPM 1840) and YPM 1860 are cranial thoracic vertebrae. A new specimen of *A. ajax*, NSMT-PV 20375, includes many other shared elements. Features supposedly separating *A. ajax* from *A. excelsus* have been questioned (Riggs 1903; McIntosh 1995; Wedel and Sanders 2002; Upchurch *et al.* 2004a), and these two species may not be distinct. Specimen CM 563, now UW 15556, was described as *A. excelsus* by Gilmore (1936) but was referred to the new taxon *A. parvus* by Upchurch *et al.* (2004a); most of the following references to *A. excelsus* refer to this specimen; at any rate, none of the diagnostic characters of *A. parvus* can be assessed on *Suuwassea* with presently known material.

The atlas of *Apatosaurus louisae*, CM 3018, is fused to its axis. This may be an ontogenetic feature and although it differs in this respect from *Suuwassea*, the element does not greatly differ morphologically from that of ANS 21122. However, a proportionately enormous atlas associated with CM 555/556, a small juvenile referred to *A. excelsus* (McIntosh 1981), is more elongate than those of either CM 3018 or ANS 21122, despite the fact that its associated axial body is smaller and shorter than both. The atlas of CM 555/556 is convex caudally (apparently owing to fusion with the dens, which is absent from the axis), bears a ventral keel, and has ventral processes that protrude laterally beyond any other portion of the atlantal body, all unlike ANS 21122. The neurapophysis of *Suuwassea* lacks the foramen present in *A. louisae* (Gilmore 1936, fig. 5; Wilson 2002).

Preserved postatlantal cervical vertebrae of *Suuwassea* more closely resemble those of *Apatosaurus*, especially *A. excelsus* (UW 15556) than any other flagellicaudatan. *Suuwassea* differs most notably from CM 3018 (*A. louisae*) and NSMT-PV 20375 (*A. ajax*) in its extreme craniocaudal compression of the spinous processes (Gilmore 1936, pl. 24; Upchurch *et al.* 2004a, pl. 1). The spines of *A. louisae*, from the sixth cervical onward, and all spines in *A. ajax*, are craniocaudally broader than in *Suuwassea*. Those of NMST-PV 20375, beyond the third cervical, are also lower and more *Diplodocus*-like. A condition similar
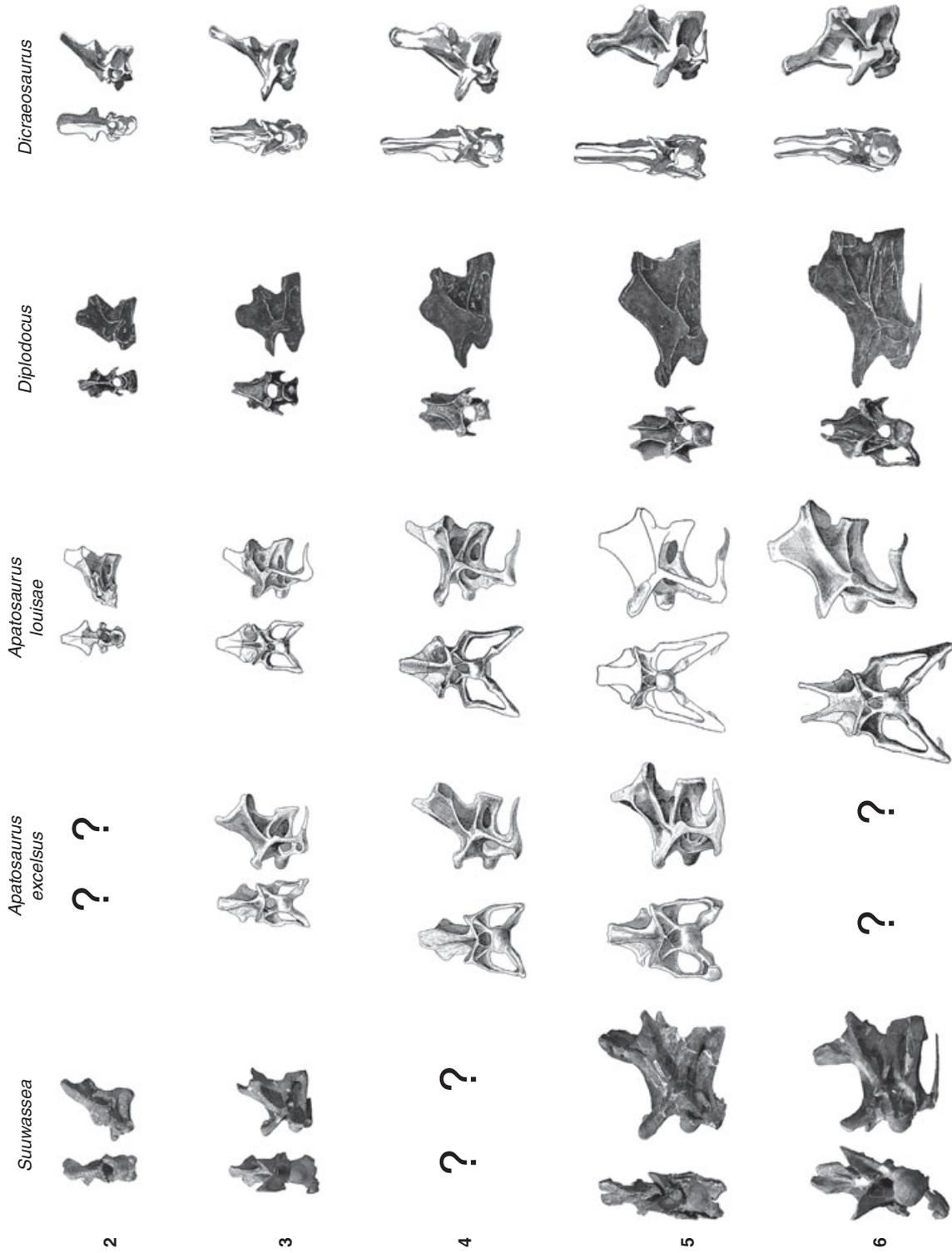
TEXT-FIG. 16. Comparisons of cranial–mid cervical vertebrae of flagellicaudatans in cranial (left) and left lateral (right) views. Row numbers represent vertebral number. Illustrations for *Apatosaurus excelsus* (*A. parvus sensu* Upchurch *et al.* 2004*a*) and *A. louisae* from Gilmore (1936), for *Diplodocus* from Hatcher (1901) (lateral views reversed), and *Dicraeosaurus* from Janensch (1929*a*) (lateral views reversed).
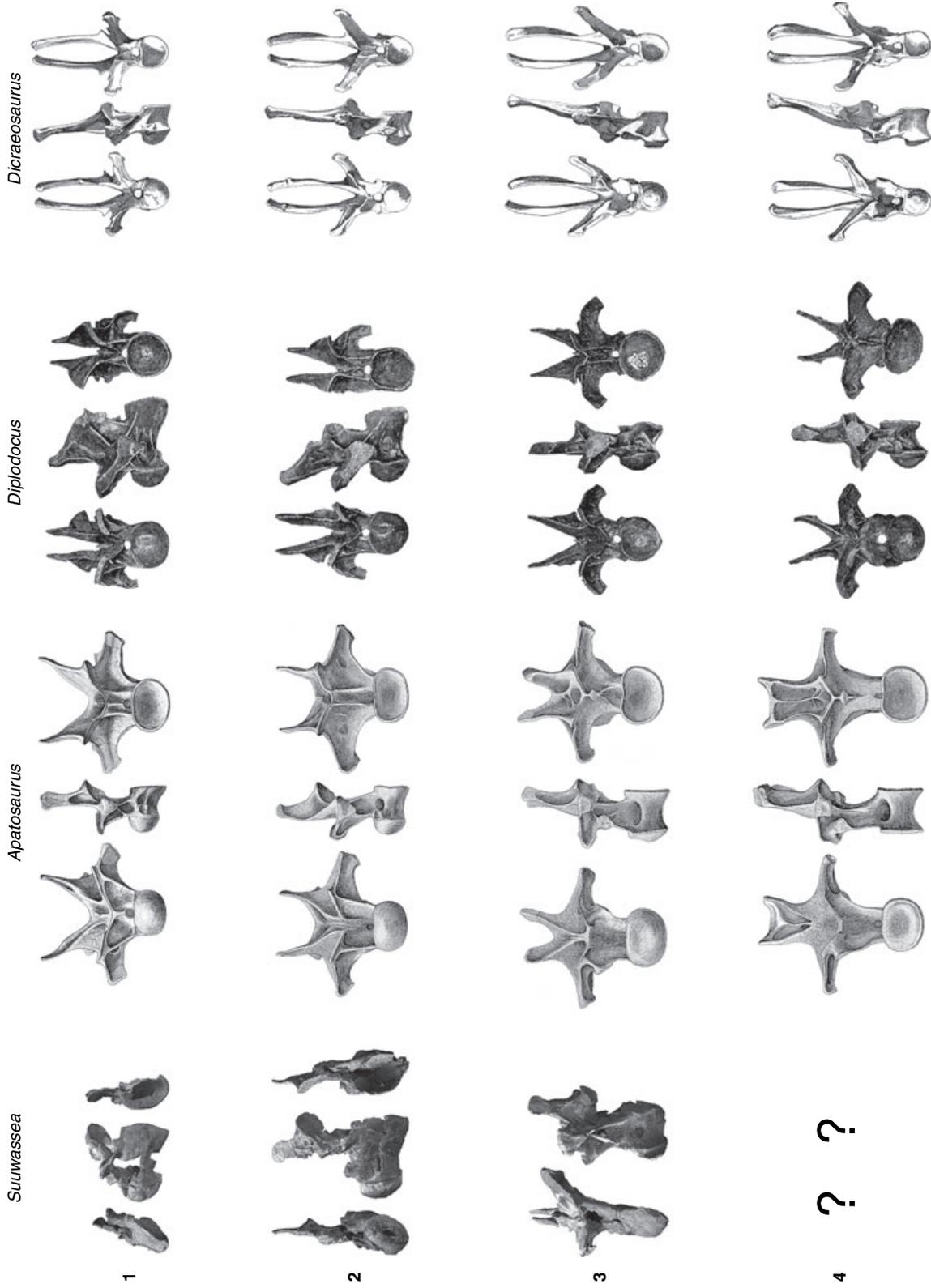
TEXT-FIG. 17. Comparisons of cranial thoracic vertebrae of flagellicaudatans in cranial (left), left lateral (middle) and caudal (right) views. Row numbers represent vertebral number. Illustrations for *Apatosaurus* from Gilmore (1936), for *Diplodocus* from Hatcher (1901) (lateral views reversed), and *Dicraeosaurus* from Janensch (1929a) (lateral views reversed).
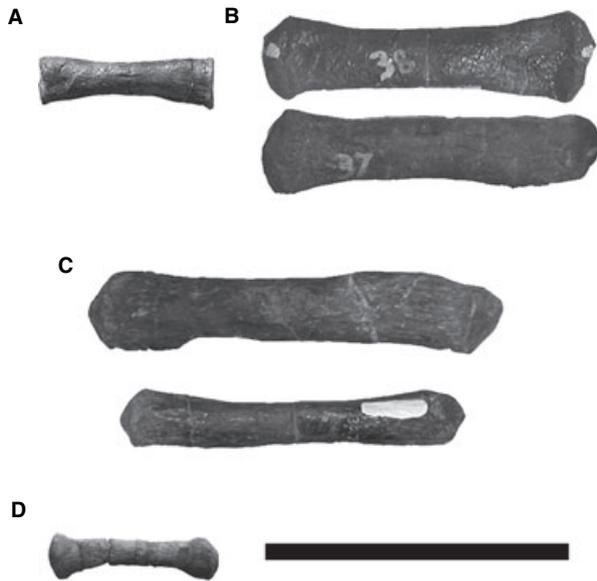
TEXT-FIG. 18. Comparison of distal 'whiplash' caudal vertebrae. A, *Suuwassea* ANS 21122. B, *Apatosaurus* CM 3378. C, *Diplodocus* CM 307. D, *Dicraeosaurus* MNB dd. All illustrations to scale. Scale bar represents 10 cm.

to *Suuwassea* is observed in CM 555/556, which is only slightly smaller than ANS 21122 but in which all cervical vertebral arches are unfused to their respective centra.

None of the preserved spines in *A. louisae* or *A. ajax* (NSMT-PV 20375) bears either pre- or postspinous laminae, but have cranial elastic ligament and deep, postspinous fossae as well as paraspinous fossae. Some prebifurcation and foremost bifurcate spines of CM 555/556, however, have long, sagittal, pre- and postspinous laminae. Whether the pattern and distribution of the various laminae and fossa among these specimens is due to taxonomic or individual variation remains to be explored. Differences between *A. excelsus* (UW 15556) and ANS 21122 are less pronounced. The spines of the preserved cervicals are similar to those of *Suuwassea* in positions over their respective vertebral bodies, apparent pattern of bifurcation (also in *A. ajax*, NSMT-PV-20375), and in angulation, but their caudal spinozygapophyseal laminae protrude further laterally than in ANS 21122. The spines of the Montana sauropod also seem to be proportionately longer than in UW 15556. No spine in UW 15556 possesses pre- or postspinous laminae as on the sixth cervical of *Suuwassea*.

Lateral corporal pneumatic fossae on the cranial cervicals of *A. excelsus* (UW 15556), *A. ajax* (NSMT-PV 20375) and *A. louisae* are divided into marked cranial and caudal portions by a pronounced ridge, in *A. louisae* as far cranially as the axis (Gilmore 1936, pl. 24; pers. obs.) and in *A. ajax* as far as the third cervical, unlike the less derived condition in ANS 21122. The cranialmost vertebral bodies of juvenile CM 555/556, however, display

undivided fossae, so again differences may reflect ontogeny in *Apatosaurus*. The dorsal surfaces of the dorsoventrally compressed costolateral eminences in *A. louisae* only bear fossae on the third and fourth cervicals, where they are best described as rudimentary. In CM 555/556, the lateral corporal pneumatic fossae extend a short distance onto the eminences, terminating against low ridges. The eminences of *A. ajax* (NSMT-PV 20375) are reportedly fossate from the sixth cervical onward, and fossae are separate from the lateral corporal pneumatic fossae, similar to *Suuwassea*.

None of the cranial cervicals of *A. louisae* possesses well-defined parazygapophyseal fossae like *Suuwassea*, but they are present in UW 15556, where they connect directly to paraspinous fossae in all preserved cervicals, unlike *Suuwassea*. The prezygapophyseal alae of *A. ajax* (NSMT-PV 20375) lack the upturned, facet-bearing distal ends seen in *A. louisae* and *Suuwassea* (Upchurch *et al.* 2004*a*, pl. 1) and are instead more similar to the straight processes seen in *Diplodocus*. The wider vertebral arches of *A. ajax* bear caudal infrazygapophyseal fossae on the sixth cervical, unlike *Suuwassea*. Dorsal tori are present on most *Apatosaurus* cervicals but are never as long or rugose as in *Suuwassea*. Cervical rib tubercula, and their fused ansa counterparts, are shorter in *Suuwassea* than in *Apatosaurus*; in this respect, the Montana taxon bears greater resemblance to *Diplodocus*.

Although they are fragmentary and crushed in ANS 21122, the cranial thoracic vertebrae of *Apatosaurus* and *Suuwassea* are somewhat similar. If the vertebra referred here to the third thoracic (see above) of *Suuwassea* is actually the fourth, as its proportions compared with *Diplodocus* indicate (Table 3), then its opisthocoely distinguishes it from the same element in *A. louisae* (Gilmore 1936, pl. 25) and more closely resembles the condition in *A. ajax* (Upchurch *et al.* 2004*a*, pl. 3) and *Diplodocus* (Hatcher 1901). The lateral corporal pneumatic fossae appear to be smaller in *Suuwassea* than *Apatosaurus*, possibly a size-related feature. The vertebral arches and hemispines of both *Suuwassea* and *A. louisae* angle craniodorsally in the first two thoracic vertebrae and switch to caudal angulation by the third (Gilmore 1936); those of *A. excelsus* are missing in the first two, but the hemispines are vertical in the third and angle caudodorsally in the fourth. In *A. ajax*, the hemispines are caudally inclined on the second through fourth thoracic vertebrae (Upchurch *et al.* 2004*a*). *Suuwassea* and *Apatosaurus* both display prespinous laminae in some cranial thoracics, but *Suuwassea* lacks both the paired cranial spinozygapophyseal laminae and the postspinous laminae that occur in *Apatosaurus*. Similarly, both thoracics in ANS 21122 that preserve vertebral arches lack the marked spinodiapophyseal laminae seen in cranial and caudal views of the second to fourth thoracics of

Apatosaurus louisae (Gilmore 1936, pl. 25) and *A. ajax* (Upchurch *et al.* 2004*a*, pl. 3) and are thus, in this respect, somewhat more similar to *A. excelsus* (*A. parvus sensu* Upchurch *et al.* 2004*a*). In *Suuwassea*, *A. louisae* and *A. excelsus*, bifurcate spinous processes are deep in the first and second thoracic vertebrae, shallower on the third, and almost extinct by the fourth vertebra (Gilmore 1936); the intraspinous sulcus in *A. ajax* remains fairly deep and wide on the third and fourth thoracics (Ostrom and McIntosh 1966, pl. 16; Upchurch *et al.* 2004*a*, pl. 3). Both taxa lack pseudospinous tubercula but possess paraspinous fossae caudal to the second thoracic (Gilmore 1936). However, some specimens of *Apatosaurus* (e.g. USNM 4713, NSMT-PV 20375) display a paraspinous fossa on more cranial thoracics, rendering this character variable. In *A. louisae*, the fossae invade the arch more deeply than in ANS 21122. *Suuwassea* lacks the numerous accessory foramina seen in the infrazygapophyseal, cranial and caudal infradiapophyseal fossae, and on the dorsal surface of the transverse processes illustrated by Gilmore (1936, pl. 32) in the cranial thoracics of *A. excelsus* (*A. parvus sensu* Upchurch *et al.* 2004*a*), but again, pneumatic invasions are not necessarily symmetrical or uniform between individuals, or even within an individual, let alone taxa.

The proximal caudal vertebra of *A. ajax* (NSMT-PV 20375) resemble those of *Suuwassea* in being procoelous/distoplatyan (Upchurch *et al.* 2004*a*), unlike the more traditional procoely, with convex distal articular facets, of other *Apatosaurus* species. Some specimens referred to *Apatosaurus* (e.g. CM 3018, 30766, NMST-PV 20375, USNM 337919) have proximal caudal vertebral bodies that resemble those of *Suuwassea* by lacking the extreme proximodistal compression seen in *Diplodocus*. However, other specimens (e.g. CM 21740) possess more flattened proximal caudals. Regardless of their sequential position, uncompressed *Apatosaurus* proximal caudals taper ventrally into thick, longitudinal ridges (McIntosh 1995), but they lack the numerous, irregular foramina of *Suuwassea*. The second–third and fifth–sixth caudals of *A. louisae* bear small, moderately deep fossae approximately where lateral corporal pneumatic fossae are expected (Gilmore 1936, pl. 26); these fossae are much too small and restricted to be considered lateral corporal pneumatic fossae, but are much larger than typical for nutrient foramina, and may indicate incipient pneumatization. *A. ajax* proximal caudals are non-fossate (Upchurch *et al.* 2004*a*). With the present understanding of ANS 21122, the proximal caudal vertebral bodies cannot be reliably used to distinguish *Suuwassea* from *Apatosaurus*.

Similarly, mid-caudal vertebral bodies in *A. louisae* are virtually identical to those of *Suuwassea*, including possessing lateral, longitudinal ridges. However, some mid-caudals referred to *Apatosaurus* (e.g. CM 3378) are markedly polygonal, rather than smoothly rounded, and even possess shallow, longitudinal, superficially pneumatic fossae-like depressions near the body-arch junction. Some distal caudals exhibit small foveae on their articular surfaces in USNM 337924 (referred to *Apatosaurus* sp.); most of those of CM 3018, however, do not. *Apatosaurus* 'whiplash' caudals are much longer than those of *Suuwassea*. In CM 3018 and CM 3378, most are biconvex (McIntosh 1995), though a few vertebrae bear one relatively flat face (but never both); a few individual vertebrae near the extreme distal end tend toward amphiplatyan (Holland 1915, pl. 59), but not in sequence. It requires a peculiar happenstance to restrict the preserved 'whiplash' caudals and caudal fragments (8–13 in total) in ANS 21122 to such oddities. Thus, the most parsimonious explanation is that *Suuwassea* differs from *Apatosaurus* in possessing, as the norm, short, amphiplatyan 'whiplash' caudals that are dissimilar to those of *Apatosaurus*.

Barosaurus lentus. The holotype of *B. lentus*, YPM 429, includes a string of vertebrae from the mid-cervical to the mid-caudal region (Lull 1919). The only axial elements overlapping with ANS 21122, however, are the cranial thoracic and proximal and mid-caudal vertebrae. Given the overarching similarity of *Barosaurus* to *Diplodocus*, it is unlikely that *Barosaurus* and *Suuwassea* cervicals were very similar.

The first thoracic vertebra of *Barosaurus* appears to possess a more complex set of laminae than does the same element in *Suuwassea*, including a 'horizontal lamina' dorsally bounding the lateral corporal pneumatic fossa (Lull 1919) that is not pronounced in ANS 21122. The bone in *Barosaurus* also possesses large caudal infrazygapophyseal fossae that are not evident in either of the most cranial thoracics of *Suuwassea*. However, the first thoracic of *Barosaurus* bears a craniodorsally directed spinous process, similar to *Suuwassea*. The bases of its hemispinous processes appear to be much wider than in *Suuwassea* and they bound a much deeper intraspinous sulcus.

Proximal caudal vertebrae of YPM 429 differ significantly from those of ANS 21122 by possessing deep lateral corporal pneumatic fossae and ventral sulci that are entirely absent in the Montana taxon. Ventral sulci persist into the mid-caudals of *Barosaurus*, further distinguishing this taxon from *Suuwassea*.

Cetiosauriscus stewarti. Heathcote (2003) noted that a string of articulated, biconvex, 'whiplash' caudal vertebrae (NHM R. 1967) attributed to *C. stewarti* cannot be shown to belong to that taxon. The holotype of *C. stewarti* is that of a primitive eusauropod; the biconvex string of 'whiplash' caudals, however, may pertain to a diplodo-

coid. Their biconvexity clearly differentiates them from the amphiplatyan elements in *Suuwassea*, but their much older age may indicate that the condition in *Suuwassea* is secondarily derived rather than a retained plesiomorphy.

'Cetiosaurus' glymptonensis. Originally described by Phillips (1871), Upchurch and Martin (2003) considered that the British middle–distal caudal vertebrae that comprise the holotype (OU J13750–13758) may pertain to a genuine Middle Jurassic (Bathonian) diplodocoid. They are diagnosed by the possession of two parallel, longitudinal ridges on the lateral surfaces, giving each an octagonal cross-sectional morphology, unlike *Suuwassea*. At least one middle caudal assigned to *Dicraeosaurus* (MNB dd173) is also octagonal in cross-section (pers. obs.).

Dicraeosaurus spp. Both species of *Dicraeosaurus*, *D. hansemanni* and *D. sattleri*, are considered together here except where otherwise noted. An atlantal body assigned to *D. hansemanni*, MNB 2380 (dd511), possesses the prominent cranioventral extension of the cranial articular surface diagnostic of diplodocoids, but unlike *Suuwassea*, its caudal face is divided into two shallow, semicircular fossae by a sagittal ridge. The ventrolateral corners of the face project slightly ventrolaterally, but there are no distinct, trapezoidal processes such as those seen in *Suuwassea*. Vague facets dorsal to these corners may be articular surfaces for an atlantal rib. A right neurapophysis [MNB 2381 (dd512)] resembles that of *Suuwassea* but is somewhat stockier. The axis of *Dicraeosaurus* is similar to that of *Suuwassea* but its spinous process lacks the distal notch, and it has a pronounced postspinous lamina.

The highly distinctive postaxial cervical vertebrae of *Dicraeosaurus*, as exhibited by the articulated specimen MNB m, differ substantially from those of *Suuwassea*. Most obviously, the elongate spinous processes of *Dicraeosaurus* cervicals are deeply bifid by the third vertebra (Janensch 1929*a*). The spines are thus formed by two laterally compressed, hemispinous processes rather than the craniocaudally compressed, single spines seen in ANS 21122. The third cervical of *Dicraeosaurus* lacks the expansive, flat area ventral to the cranial articular condyle visible in *Suuwassea*. From the third cervical, *Dicraeosaurus* displays cranial infrazygapophyseal fossae like those in *Suuwassea* (although they are not figured by Janensch 1929*a*) but, interestingly, from the fifth it also possesses caudal ones (pers. obs.) that are absent in the Montana sauropod. The lateral corporal pneumatic fossae of *Dicraeosaurus* form only shallow fossae on the lateral surfaces of the vertebral bodies, not invading the bone deeply enough to be separated only by a thin median septum as in *Suuwassea* and most other diplodocoids. However, the cranial ends of the fossae in many *Dicraeosaurus* cervicals

give way to deep foramina that invade the cranial articular condyle, as in *Suuwassea*. Lateral corporal pneumatic fossae in *Dicraeosaurus* are never subdivided by internal ridges, but the ventral surfaces (most emphasized at the cranial ends) of most cervicals are excavated by fairly deep, parasagittal ventral corporal pneumatic fossae separated by a distinct keel (Text-fig. 2). The parasagittal fossae are themselves sometimes further subdivided by thin laminae. In lateral view, cranial cervicals in *Dicraeosaurus* have strongly but asymmetrically arched ventral margins (Janensch 1929*a*, pl. 1, figs 3*a*, 4*a*) that give the impression that the cranial articular surface of the vertebral body projects further ventrally than the remainder of the body; *Suuwassea* lacks this morphology. Dorsal tori are present in *Dicraeosaurus* but as a consequence of spinous bifurcation, are mediolaterally flattened, in contrast to those in ANS 21122.

Despite these differences, the cervicals of *Dicraeosaurus* bear some similarities to *Suuwassea*. The cranial zygapophyseal alae are directed craniodorsally and have primarily concave-up dorsal margins. Cranial parazygapophyseal fossae are present on all postaxial *Dicraeosaurus* cervicals, but they all extend onto the proximolateral surfaces of their respective hemispinous processes, a feature seen only on the fifth and sixth cervicals of *Suuwassea*. Spinous process orientation shifts from caudodorsal to craniodorsal at around the fourth cervical, more similar to *Suuwassea* than other diplodocoids. The caudal cervicals and cranial thoracics of *Dicraeosaurus* bear rugose pseudospinous tubercula, unlike *Suuwassea*.

Only the first few thoracic vertebrae of *Dicraeosaurus* (*Dicraeosaurus* has 11, not 12, cervicals; pers. obs., contra McIntosh 1990) possess lateral corporal pneumatic fossae, and those are shallow and lack internal foramina, differing from those of *Suuwassea*. Deep spinous process bifurcation persists until the 17th presacral (sixth thoracic) vertebra and is gone entirely by the 19th (eighth thoracic) in the Tanzanian taxon, much further caudal than is apparent for *Suuwassea*.

Dicraeosaurus lacks the heavily compressed proximal caudals of American diplodocids, so vertebrae with uncompressed bodies similar to those preserved in ANS 21122 begin immediately caudal to the sacrum. Some proximal caudal vertebrae of *Dicraeosaurus hansemanni* (e.g. MNB m caudal 4 and up, dd 475, dd 78) possess shallow, longitudinal sulci on their ventral surfaces, in contrast to the planar surface in *Suuwassea*; the sulci, however, are so shallow on others as to render the ventral surfaces virtually flat (e.g. MNB m caudals 1–2 and dd unnumbered). The bodies of the first–sixteenth caudals (especially the third–sixth) of *D. hansemanni* (MNB m) are perforated by irregularly placed foramina, as in proximal caudal A of ANS 21122. The condition in the first three caudals of *D. sattleri* cannot be assessed, but by the

fourth, the ventral surface becomes planar except at the distal end. MNB dd 475 displays the roughly pentagonal corporal cross-sectional morphology of *Suuwassea* proximal caudals, but others in this portion of the column have smoother, more planar lateral surfaces. The initial appearance of a lateral ridge in MNB m does not occur until the ninth caudal.

Middle caudal vertebrae of *Dicraeosaurus* possess a lateral ridge as in *Suuwassea* but they are more pronounced, more ventrally located and less crescentic. Some *Dicraeosaurus* middle caudals possess an additional ridge at the body-arch junction (probably a remnant of the transverse process), and others a modest ridge at the junction between the ventrolateral and lateral surfaces. The ventral surface of *Dicraeosaurus* middle caudals is more strongly concave transversely than in ANS 21122 (Janensch 1929*a*, figs 74b–77b; pers. obs.).

Pre-'whip' distal caudal bodies are similar to (though larger than) those of *Suuwassea* but display variable articular surface morphology. Only one of the anarcuate, 'whip' caudal vertebrae of *Dicraeosaurus* (specimens apparently from the dd quarry mounted with specimen m) is biconvex, but not nearly as much as in *Diplodocus* or *Apatosaurus*. The rest are better defined as either proximoplatyan or distoplatyan (*sensu* Tidwell *et al.* 2001), and a few elements as amphiplatyan (Janensch 1929a, figs 17–20; pers. obs.). Where flat, the articular faces of *Dicraeosaurus* 'whip' caudals are irregular, but they do not bear any marks as distinctive or regular as the foveae and associated tumescences visible in ANS 21122. It is unclear whether the distal caudals from the dd quarry utilized in the mount of skeleton m were found in sequence, but it is almost certain that these vertebrae pertain to *Dicraeosaurus*, as it was the most common (but not the only) taxon in the dd quarry (Janensch 1929*b*; Maier 2003).

Dinheirosaurus lourinhanensis. Comparison with *Dinheirosaurus* (ML 414) is hampered because the holotype has not been fully prepared or described at present (Bonaparte and Mateus 1999). Only limited comparison of cranial thoracic vertebrae is possible. In most respects they are similar to the mostly complete fourth thoracic of *Suuwassea*, and share cranially displaced, lateral corporal pneumatic fossae. However, *Suuwassea* lacks the diagnostic caudal corporoparapophyseal lamina on the fourth thoracic of the Portuguese sauropod. The spinous processes on the cranial thoracic vertebrae of *Dinheirosaurus* do not possess the deep fossae or craniocaudally expanded distal ends of *Suuwassea*.

Diplodocus spp. The genoholotype of *Diplodocus longus*, YPM 1920, consists only of two middle caudal vertebrae and a haemal arch (McIntosh and Carpenter 1998), but several other specimens have been referred to this species.

Better associated postcranial material comprises the cotypes of *D. carnegii* (CM 84 and 94). Whether or not the disparities in proportion, details of vertebral arch lamination, and spinous process angulation between *D. longus* and *D. carnegii* are best perceived as species-level differences (McIntosh and Carpenter 1998) or as simple intraspecific variation (Gilmore 1932), awaits a thorough reanalysis of all *Diplodocus* specimens. For the purposes of this comparison, both species plus '*D.*' *hayi* and '*Seismosaurus*' (NMMNH 3690, *sensu* Lucas *et al.* 2004) are considered together except where specifically noted.

An atlas (USNM 2672) attributed to *D. longus* (McIntosh and Carpenter 1998) is generally similar to that of *Suuwassea* but has a much more pronounced cranioventral process and much less pronounced caudoventral processes. It is also mediolaterally broader and craniocaudally narrower than that of ANS 21122. *Diplodocus* appears to lack an atlantal rib, as does *Suuwassea*.

Cranial cervical vertebrae of *Diplodocus* are readily distinguished from those of *Suuwassea* by their much lower spinous processes that bifurcate more cranial in the series, longer vertebral bodies, and their straight cranial zygapophyseal alae. *Diplodocus* cervicals also lack parazygapophyseal fossae and have more complex lateral corporal pneumatic fossae than *Suuwassea*. The third and fourth cervical vertebrae of CM 84 possess shallow fossae on the dorsal surfaces of their costolateral eminences that are separated from their respective corporal fossae by low ridges. Dorsal tori are mostly absent in *Diplodocus*; where present, they are short and rounded protuberances, unlike the long, rugose processes in *Suuwassea*.

The bodies of the first through fourth thoracic vertebrae of *Diplodocus*, though longer than in *Suuwassea*, retain pronounced opisthocoely (Hatcher 1901, pl. 8), possibly similar to the apparent pattern in *Suuwassea* (see above). Lateral corporal pneumatic fossae in *Diplodocus* thoracics retain the complex series of laminae and foramina of the cervical series, unlike ANS 21122. The transverse processes in *Diplodocus* thoracic vertebrae curve ventrally toward their distal ends, unlike the more linear morphology in the Montana taxon. Deeply ventrally sagging caudal intrazygapophyseal laminae seen in the caudal cervicals and first two thoracics of *Diplodocus* (Hatcher 1901, pl. 8) are not evident in *Suuwassea*. Thoracic vertebrae in *Diplodocus* retain deeply cleft spinous processes into the middle thoracic region; the intraspinous sulcus in the cranial thoracics invades further ventrally than in *Suuwassea* (Hatcher 1901, pl. 8). Some cranial thoracics of CM 84 retain pseudospinous tubercula (Hatcher 1901, pl. 8). Paraspinous fossae in the latter, present on all cranial thoracic vertebrae, are deeper, more complex and more foraminate than in *Suuwassea*.

Proximal caudal vertebral bodies of *Diplodocus* are noted for their remarkable proximodistal compaction (Osborn

1899; Hatcher 1901). As above, none of the preserved *Suuwassea* caudals matches this morphology, but they are more similar in proportions to those of CM 84 immediately distal to the highly compressed, proximalmost ones. However, *Suuwassea* proximal caudals are starkly different because they lack the lateral corporal pneumaticity, ventral sulci and ventral proximodistal concavity (in lateral view) of *Diplodocus* (Hatcher 1901, pl. 9).

Suuwassea mid-caudal vertebral bodies also lack the distinctive ventral, sagittal sulcus and the pronounced ventral concavity (in lateral view) of the same elements in *Diplodocus* (Osborn 1899; Hatcher 1901; McIntosh and Carpenter 1998; Upchurch 1998; Wilson 2002). They are also shorter (McIntosh 1990) and less laterally compressed than those of *Diplodocus*, although the latter are somewhat crushed. Some vertebral bodies of NMMNH 3690 possess marked lateral fossae (Gillette 1991, fig. 7). Distal caudals of *Diplodocus* are similar to those of *Suuwassea* but proportionately longer. The 'whiplash' caudals, however, are substantially longer and almost exclusively strongly biconvex.

Eobrontosaurus yahnahpin. Bakker (1998) stated that *Eobrontosaurus* retains cervical ribs/costal processes that project beyond the limits of their associated vertebral bodies, which differentiates that taxon from *Suuwassea*. Although cranial thoracic vertebrae form part of the holotype of *Eobrontosaurus* (TM 001), they have only been briefly described and not figured (Filla and Redman 1994). Upchurch *et al.* (2004b) considered *Eobrontosaurus* to be congeneric with the non-diplodocoid sauropod *Camarasaurus*.

Supersaurus vivianae. Axial elements referred to *Supersaurus* that have counterparts present in ANS 21122 consist of a mid-cervical vertebra (BYU 9024), thoracic vertebrae (BYU 4053, 9044 and 12814), and several proximal and middle caudal vertebrae (BYU 4839, 9045, 9077, 9084, 12639, 12819 and 12843). The purported fourth thoracic vertebrae of *Supersaurus* (BYU 4053), the former holotype of *Dystylosaurus edwini*, lacks a bifid spinous process and lateral spinous fossae, possesses hypantral facets and has a much more elevated parapophysis than the possible fourth thoracic of *Suuwassea*. Like the Montana taxon, however, *Supersaurus* may possess a smaller number of bifurcate cervical and thoracic spinous processes than in other flagellicaudatans (Curtice and Stadtman 2001). BYU 4503 also possesses a deep fossa that completely divides the cranial infrazygapophyseal lamina that is absent in ANS 21122, although Curtice and Stadtman (2001) noted that this feature is likely to be ontogenetic and occurs only in the oldest diplodocid individuals.

*Tornieria ('Barosaurus') africana.* Presacral vertebrae of *Tornieria*, especially previously unpublished cervical vertebrae, are currently being restudied (K. Remes, pers. comm. 2002), so no details are presented here that would render moot that analysis. Proximal caudal vertebrae figured by Fraas (1908, pl. 8, fig. 3) more closely resemble *Diplodocus* than *Suuwassea* in being deeply and complexly pneumatic and in possessing a deep ventral sulcus. Deep lateral corporal pneumatic fossae persist well distal in the caudal sequence; they eventually shallow but persist to the middle portion of the tail, unlike *Suuwassea*. The proximal and distal articular faces of middle and more distal caudals of *Tornieria* project much further ventrally than the remainder of their respective vertebral bodies (Fraas 1908, pl. 8, fig. 8; Janensch 1929b, figs 19, 21). The ventral surfaces are mediolaterally concave as well, and thus they differ significantly from those of *Suuwassea*.

Other sauropods. Although it has been considered either more primitive (McIntosh 1990) or more derived (Upchurch *et al.* 2004b) than Morrison diplodocoids, it remains possible that the hexavertebral sacrum AMNH 675 that forms part of the holotype of '*Apatosaurus*' *minimus* (Mook 1917) may pertain to *Suuwassea*. Because ANS 21122 does not preserve sacral elements, the two cannot be directly compared, but the distinctly non-diplodocoid features noted in the former by Upchurch *et al.* (2004a, b) make synonymy unlikely. The addition of a sixth sacral vertebra in AMNH 675, plus its laterally deflected cranial iliac processes, implies that this specimen pertains to a titanosauriform, or at least a somphospondylian.

The first three cervical vertebrae associated with the braincase USNM 5384 assigned to '*Morosaurus*' *agilis* by Marsh (1889), and considered referable to *Haplocanthosaurus* by Gilmore (1907), are significantly different than comparable elements in ANS 21122. In particular, the simple, laterally compressed and cranially tilted spinous process on the third cervical (possibly the result of crushing, however) and more complex lateral corporal pneumatic fossae on the preserved cervical vertebrae indicate that USNM 5384 is not congeneric with *Suuwassea*. It shares with the Montana sauropod the rostrodorsally curved cranial zygapophyses and the presence of parazygapophyseal fossae.

TAPHONOMY

In situ, ANS 21122 displays only a very approximate pattern of articulation (Text-fig. 19). The most evident pattern is retained in the ordering of the cranial cervical vertebrae and basicranium, although the scapula, coracoid and humerus remain in close association, as do the tibia and fibula. Scavenging may have been responsible for some of the existing disarticulation because evidence of scavengers is present (see below). The basicranium and
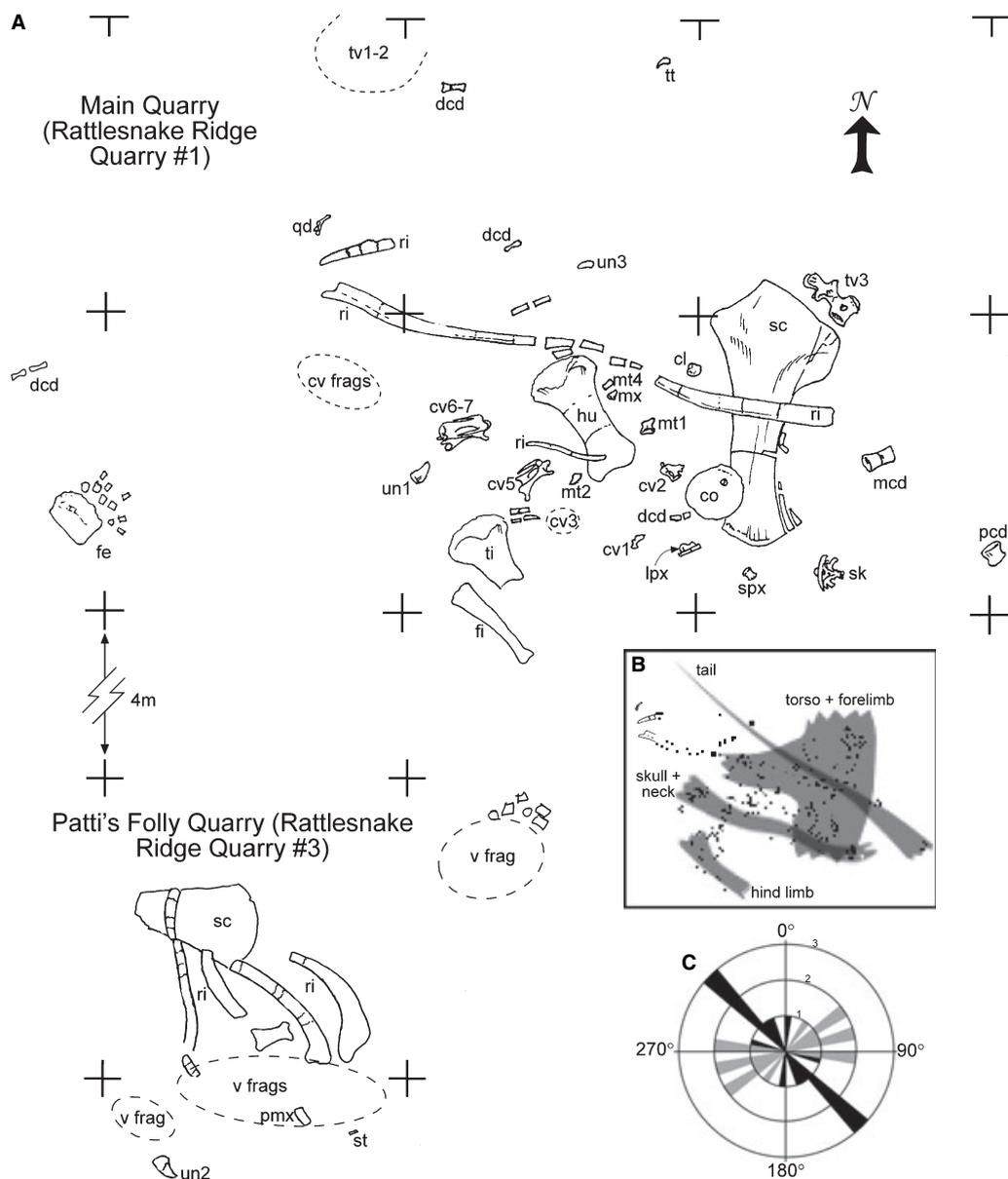
TEXT-FIG. 19. A, quarry map of ANS 21122 *in situ*. Grid marks 1-m squares. B, schematic drawing showing remnants of articulation in cranio-cervical, thoracic-pectoral, caudal, and hind limb elements superimposed on map of Quarry 1. C, rose diagram showing alignments of long axes of selected elements from quarry 1. Black denotes heavy elements (third thoracic vertebrae, thoracic rib, scapula, humerus, tibia and fibula); grey denotes smaller, lighter elements (quadrate, cervical vertebrae, caudal vertebral bodies, thoracic rib fragments). Note the almost perpendicular orientations of the two groups. Abbreviations: cl, calcaneum, co, coracoid; cv, cervical vertebra; dcd, distal caudal vertebra; fe, femur; fi, fibula; frag, fragment; hu, humerus; lpx, large phalanx; mcd, mid caudal vertebra; mt, metatarsal; mx, maxilla fragment; pcd, proximal caudal vertebra; pmx, premaxilla; qd, quadrate; ri, rib; sc, scapula; sk, skull (basicranium); spx, small phalanx; st, isolated sauropod tooth; tt, theropod tooth; tv, thoracic vertebra; un, ungual; v, vertebra (position undetermined).

cervical vertebrae are largely distributed in sequence along a single line (Text-fig. 19B), indicating that they remained articulated for some time, probably even after detaching from the remainder of the body. Caudal vertebrae are widely dispersed but show a decrease in size, indicating that the tail was sharply arched; the majority of the tail

lay parallel to the neck though pointing in the opposite direction.

A rose diagram (Text-fig. 19C) demonstrates a bimodal distribution for the long axes of elongate elements. Interestingly, the large, heavier elements (third thoracic vertebra, thoracic rib, scapula, humerus, tibia, fibula) have

orientations almost perpendicular to those of elongate, small, light elements (quadrate, cervical vertebrae, caudal vertebral bodies, thoracic rib fragments). Because the number of elements involved in creating the rose diagram was small (six large, eight small), this bimodality may be a random effect, but if water was responsible for most or all of the deposition of the specimen, it may have been the result of the differential effect of current velocity. In this scenario, the heavier elements may have had one end (the heavier end) anchored while the rest of the bone aligned parallel to current direction, whereas smaller, lighter elements rolled along with their long axes perpendicular to the current direction (Voorhies 1969). However, given that many of the 'light' elements retained fragile laminae and processes (e.g. the costal processes on the cervical vertebrae), extended periods of rolling after soft tissue degradation seem unlikely.

The preservation in ANS 21122 of many small, light elements (portions of the skull, distal caudals, calcaneum) that are often lost in other sauropod specimens, contrasts with the absence of many of the large, robust elements (sacrum, pubes, ischia, femora, ulnae, thoracic vertebrae) frequently present in sauropod specimens. The degree of bone weathering (e.g. caudal cervicals, femur) increases toward a cliff face just north of the quarry; this, coupled with the recovery of sizable but unidentifiable, weathered fragments of bone on the slopes below the quarry, indicates that more of the individual was originally present post-interment but has since been lost to erosion: in short, this discrepancy is artefactual. Some elements were undoubtedly removed by scavengers (see below), but it also conceivable that the preserved, sedimentologically lighter elements were separated from the heavier ones by water transport. As above, two features of ANS 21122 support the contention that such transport was non-violent: the retained anatomical sequence (though not articulation) of some elements (neck, tibia and fibula) and the presence in many elements (braincase, cervical vertebrae) of intact, extremely thin bony laminae, that would probably have been destroyed in a high-energy event.

Proximal caudal vertebra A bears a single prominent, deep, oblique groove across its proximal articular face. This is probably a post-mortem, sedimentological tool mark, though it could also be a tooth mark, although why surrounding teeth of a scavenger did not leave parallel grooves is uncertain. However, evidence of scavenging is present on several podial elements.

CONCLUSIONS

Among well-known flagellicaudatans, vertebrae of *Suuwassea* are readily distinguished from those of *Barosaurus*, *Diplodocus* and *Tornieria* by possessing tall, craniocaudally compressed spinous processes on the cranial–mid-cervical vertebrae that do not bifurcate until the sixth cervical and persist only into the cranial thoracic vertebrae, simple lateral corporal pneumatic fossae through at least the sixth cervical, the lack of elongate mid- and distal caudals, and the presence of amphiplatyan 'whip' caudal vertebral bodies.

Suuwassea is radically different from *Dicraeosaurus* and *Amargasaurus* by lacking both highly elongate cervical spinous processes that bifurcate at the third cervical and ventral corporal pneumatic fossae, and by possessing more complex and invasive lateral corporal pneumatic fossae through at least the cranial thoracics. Cranial thoracics in *Dicraeosaurus* lack the deep lateral corporal pneumatic fossae of *Suuwassea*, and deep bifurcation in the spinous processes of *Dicraeosaurus* persist further caudally than in *Suuwassea*. Proximal caudal vertebral bodies of *Suuwassea* and *Dicraeosaurus* are very similar, but the mid- and distal (including the 'whip') caudals are different, being more elongate and gracile in the Montana taxon.

In morphology, the axial skeleton of *Suuwassea* most closely resembles that of *Apatosaurus*, to the point at which isolated cranial thoracic and proximal–distal (non-'whip') caudal vertebrae cannot be reliably distinguished between the two taxa. Among presently known axial skeleton elements, only the cranial cervicals and amphiplatyan 'whip' distal caudals readily distinguish the two. In the cranial–mid-cervicals, the craniocaudally compressed and mediolaterally expanded spinous processes with pronounced fossae and, occasionally, laminae are slightly more similar to *A. excelsus* (*A. parvus sensu* Upchurch *et al.* 2004a) than *A. louisae* and *A. ajax*. *Apatosaurus* cranial cervicals bear more complex lateral corporal pneumatic fossae and lack the massive dorsal tori of *Suuwassea*, though both of these features may vary between individuals and may not be ideal separators. *Suuwassea* cervical ribs and costal processes lack the cranial processes of *A. excelsus* (*A. parvus sensu* Upchurch *et al.* 2004a). Specimens currently referred to *Apatosaurus* exhibit either a marked range of individual variation or there are more species present than currently recognized (see Upchurch *et al.* 2004a for some discussion). Despite the axial similarities, *Suuwassea* also possesses numerous cranial and appendicular features that distinguish it from *Apatosaurus* (Harris 2006a and in prep.), but the similarities, though not strictly apomorphic, strongly suggest a closer relationship between the two taxa than either possesses to other flagellicaudatans, despite the results of two phylogenetic analyses (Harris and Dodson 2004; Harris 2006b). More material of *Suuwassea* and a thorough re-analysis of specimens referred to *Apatosaurus*, as well as possible ontogenetic changes in the latter, may shed light on this issue.

REFERENCES

ALEXANDER, R. M. 1989. *Dynamics of dinosaurs and other extinct giants*. Columbia Press, New York, 167 pp.

BAKKER, R. T. 1998. Dinosaur mid-life crisis: the Jurassic-Cretaceous transition in Wyoming and Colorado. 67–77. *In* LUCAS, S. G., KIRKLAND, J. I. and ESTEP, J. W. (eds). *Lower and middle Cretaceous terrestrial ecosystems*. New Mexico Museum of Natural History and Science, Bulletin, **14**, 330 pp.

BAUMEL, J. J., KING, A. S., BREAZILE, J. E., EVANS, H. E. and VANDEN BERGE, J. C. (eds). 1993. *Handbook of avian anatomy: Nomina Anatomica Avium*. Nuttall Ornithological Club, Cambridge, 779 pp.

BONAPARTE, J. F. and MATEUS, O. 1999. A new diplodocid, *Dinheirosaurus lourinhanensis* gen. et sp. nov., from the Late Jurassic beds of Portugal. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*, **5**, 13–29.

BORSUK-BIALYNICKA, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologica Polonica*, **37**, 5–63.

BRITT, B. B. 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. Unpublished PhD dissertation, University of Calgary, 383 pp.

CHRISTIAN, A. and HEINRICH, W.-D. 1998. The neck posture of *Brachiosaurus brancai*. *Mitteilungen aus dem Museum für Naturkunde in Berlin: Geowissenschaftliche Reihe*, **1**, 73–80.

CLARK, G. A. Jr 1993. Termini situm at directionem partium corporis indicantes. 1–6. *In* BAUMEL, J. J., KING, A. S., BREAZILE, J. E., EVANS, H. E. and VANDEN BERGE, J. C. (eds). *Handbook of avian anatomy*: Nomina anatomica avium. Nuttall Ornithological Club, Cambridge, 779 pp.

CURTICE, B. and STADTMAN, K. 2001. The demise of *Dystylosaurus edwini* and a revision of *Supersaurus vivianae*. 33–40. *In* McCORD, R. D. and BOAZ, D. (eds). *Western Association of Vertebrate Paleontologists and Southwest Paleontological Symposium – Proceedings 2001*. Mesa Southwest Museum, Bulletin, **8**, 143 pp.

DE SOUZA CARVALHO, I., DOS SANTOS AVILLA, L. and SALGADO, L. 2003. *Amazonsaurus maranhensis* gen. et sp. nov. (Sauropoda, Diplodocoidea) from the Lower Cretaceous (Aptian–Albian) of Brazil. *Cretaceous Research*, **24**, 697–713.

FILLA, J. and 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.' 159–178. *In* NELSON, G. E. (ed.). *The dinosaurs of Wyoming*. Wyoming Geological Association, 44th Annual Field Conference Guidebook, 187 pp.

FRAAS, E. 1908. Ostafrikanische Dinosaurier. *Palaeontographica*, **55**, 105–144.

GILLETTE, D. D. 1991. *Seismosaurus halli* gen. et sp. nov., a new sauropod dinosaur from the Morrison Formation (Upper Jurassic/Lower Cretaceous) of New Mexico, USA. *Journal of Vertebrate Paleontology*, **11**, 417–433.

GILMORE, C. W. 1907. The type of the Jurassic reptile *Morosaurus agilis* redescribed, with a note on *Camptosaurus*. *Proceedings of the United States National Museum*, **32**, 151–165.

—— 1932. On a newly mounted skeleton of *Diplodocus* in the United States National Museum. *Proceedings of the United States National Museum*, **81**, 1–21.

—— 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum*, **11**, 175–271.

HARRIS, J. D. 2004. Confusing dinosaurs with mammals: tetrapod phylogenetics and anatomical terminology in the world of homology. *Anatomical Record Part A*, **281**, 1240–1246.

—— 2006a. Cranial osteology of *Suuwassea emilieae* (Sauropoda: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana, U.S.A. *Journal of Vertebrate Paleontology*, **26**, 88–102.

—— 2006b. The significance of *Suuwassea emilieae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. *Journal of Systematic Paleontology*, **4**, 185–198.

—— and 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.

HEATHCOTE, J. 2003. The relationships of *Cetiosauriscus stewarti* (Dinosauria: Sauropoda): implications for sauropod phylogeny. *Journal of Vertebrate Paleontology*, **23** (Supplement to No. 3), 60A.

HOLLAND, W. J. 1915. Heads and tails, a few notes relating to the structure of the sauropod dinosaurs. *Annals of the Carnegie Museum*, **9**, 273–278.

JANENSCH, W. 1929*a*. Die Wirbelsäule der Gattung *Dicraeosaurus*. *Palaeontographica*, **2**, 35–133.

—— 1929*b*. Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru-Expedition. *Palaeontographica*, **2**, 1–34.

LUCAS, S. G., HERNE, M. C., HECKERT, A. B., HUNT, A. G. and SULLIVAN, R. M. 2004. Reappraisal of *Seismosaurus*, a Late Jurassic sauropod dinosaur from New Mexico. *Geological Society of America, Abstracts with Programs*, **36**, 422.

LULL, R. S. 1919. The sauropod dinosaur *Barosaurus* Marsh. *Memoirs of the Connecticut Academy of Arts and Sciences*, **6**, 1–42.

MAIER, G. 2003. *African dinosaurs unearthed: the Tendaguru expeditions*. Indiana University Press, Bloomington, 380 pp.

MARSH, O. C. 1889. Notice of new American Dinosauria. *American Journal of Science (Third Series)*, **37**, 331–336.

MARTIN, J. 1987. Mobility and feeding of *Cetiosaurus* (Saurischia, Sauropoda) – why the long neck? 154–159. *In* CURRIE, P. J. and KOSLER, E. H. (eds). *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Occasional Papers of the Tyrrell Museum of Palaeontology, **3**, 239 pp.

—— MARTIN-ROLLAND, V. and FREY, E. 1998. Not cranes or masts, but beams: the biomechanics of sauropod necks. *Oryctos*, **1**, 113–120.

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.

—— 1990. Sauropoda. 345–401. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 733 pp.

—— 1995. Remarks on the North American sauropod *Apatosaurus* Marsh. 119–123. *In* SUN, A. and WANG, Y. (eds). *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press, Beijing, 250 pp.

—— and CARPENTER, K. 1998. The holotype of *Diplodocus longus*, with comments on other specimens of the genus. 85–110. *In* CARPENTER, K., CHURE, D. J. and KIRKLAND, J. I. (eds). *The Upper Jurassic Morrison Formation: an interdisciplinary study*. Modern Geology, **23**, 537 pp.

MOOK, C. C. 1917. Criteria for the determination of species in the Sauropoda, with description of a new species of *Apatosaurus*. *Bulletin of the American Museum of Natural History*, **37**, 355–360.

OSBORN, H. F. 1899. A skeleton of *Diplodocus*. *Memoirs of the American Museum of Natural History*, **1**, 191–214.

OSTROM, J. H. and McINTOSH, J. S. 1966. *Marsh's dinosaurs: the collections from Como Bluff*. Yale University Press, New Haven, 388 pp.

PHILLIPS, J. 1871. *Geology of Oxford and the valley of the Thames*. Clarendon Press, Oxford, 529 pp.

RIGGS, E. S. 1903. Structure and relationships of opisthocoelian dinosaurs. Part I. *Apatosaurus* Marsh. *Field Columbian Museum Publication*, **82**, Geological Series, **2**, 165–196.

SALGADO, L. and BONAPARTE, J. F. 1991. Un nuevo sauropod Dicraeosauridae, *Amargasaurus cazaui* gen. et sp. nov., de la Formacion La Amarga, Neocomiano de la Provincia del Neuquen, Argentina. *Ameghiniana*, **28**, 333–346.

SEYMOUR, R. S. and LILLYWHITE, H. B. 2000. Hearts, neck posture and metabolic intensity of sauropod dinosaurs. *Proceedings of the Royal Society of London, B*, **267**, 1883–1887.

STEVENS, K. A. and PARRISH, J. M. 1999. Neck posture and feeding habits of two Jurassic sauropod dinosaurs. *Science*, **284**, 798–800.

TIDWELL, V., CARPENTER, K. and MEYER, S. 2001. New titanosauriform (Sauropoda) from the Poison Strip Member of the Cedar Mountain Formation (Lower Cretaceous), Utah. 139–165. *In* TANKE, D. H. and CARPENTER, K. (eds). *Mesozoic vertebrate life*. Indiana University Press, Bloomington, 577 pp.

UPCHURCH, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society*, **124**, 43–103.

—— and MARTIN, J. 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. *Journal of Vertebrate Paleontology*, **23**, 208–231.

—— TOMIDA, Y. and BARRETT, P. M. 2004*a*. A new specimen of *Apatosaurus ajax* (Sauropoda: Diplodocidae) from the Morrison Formation (Upper Jurassic) of Wyoming, USA. *National Science Museum Monographs*, **26**, 1–108.

—— BARRETT, P. M. and DODSON, P. 2004*b*. Sauropoda. 259–322. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. Second edition. University of California Press, Berkeley, 733 pp.

VOORHIES, M. R. 1969. Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska. *University of Wyoming, Contributions to Geology, Special Paper*, **1**, 1–69.

WEDEL, M. J. and SANDERS, R. K. 2002. Osteological correlates of cervical musculature in Aves and Sauropoda (Dinosauria: Saurischia), with comments on the cervical ribs of *Apatosaurus*. *Paleobios*, **22**, 1–6.

—— CIFELLI, R. L. and SANDERS, R. K. 2000. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Palaeontologica Polonica*, **45**, 343–388.

WILSON, J. A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology*, **19**, 639–653.

—— 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society*, **136**, 217–276.

—— and SMITH, M. B. 1996. New remains of *Amphicoelias* Cope (Dinosauria: Sauropoda) from the Upper Jurassic of Montana and diplodocoid phylogeny. *Journal of Vertebrate Paleontology*, **16** (Supplement to No. 3), 73A.

WIMAN, C. 1929. Die Kriede-dinosaurier aus Shantung. *Palaeontologia Sinica, Series C*, **6**, 1–67.