CRANIAL OSTEOLOGY OF *SUUWASSEA EMILIEAE* (SAUROPODA: DIPLODOCOIDEA: FLAGELLICAUDATA) FROM THE UPPER JURASSIC MORRISON FORMATION OF MONTANA, USA

JERALD D. HARRIS

Science Department, Dixie State College, 225 South 700 East, St. George, Utah 84770, U.S.A., jharris@dixie.edu

ABSTRACT—Cranial elements of *Suuwassea emilieae* (Sauropoda: Diplodocoidea) from the Upper Jurassic Morrison Formation of Montana, U.S.A., represent one of only a few flagellicaudatan skulls known. Preserved elements include a left premaxilla, a fragment of right maxilla, a right squamosal, a right quadrate, a basicranium and skull roof lacking only the rostral end of the frontals, basipterygoid processes, and parasphenoid rostrum. Autapomorphic features of the skull include: premaxillary teeth projecting parallel to long axis of premaxilla; single optic nerve foramen; postparietal foramen present and larger than parietal foramen; supraoccipital with elongate ventral process contributing little to dorsal margin of foramen magnum; basioccipital not contributing to floor of median condylar incisure; and antotic processes with no dorsal contact with frontals. The basicranium more closely resembles that of *Apatosaurus* rather than *Diplodocus* and is also unlike the skull of *Dicraeosaurus*, despite its possession of a similar postparietal foramen, a feature unique among Morrison Formation sauropods. Pending reanalysis of *Tornieria africana*, which also possesses it, the postparietal foramen must be viewed as a symplesiomorphic retention in the Dicraeosauridae, with its loss a synapomorphy of the Diplodocidae, or at least of the North American members of the latter clade.

INTRODUCTION

The Morrison Formation has been one of the premier sources of sauropod fossils for over a century. Spectacular quarries on (Colorado, New Mexico, Utah) and immediately adjacent to (Wyoming) the Colorado Plateau have produced numerous partial and complete skeletons of some of the most famous and well-studied sauropods. In particular, the diplodocids *Apatosaurus* and *Diplodocus* have been studied not only for their phylogenetic information (Upchurch, 1998; Wilson, 2002) but also as models for understanding sauropod functional morphology (Alexander, 1989; Myhrvold and Currie, 1997; Stevens and Parrish, 1999) and paleoecology (Upchurch, 1994; Fiorillo, 1998; Upchurch and Barrett, 2000).

Traditionally, the Morrison Formation of Montana has been largely ignored in paleontological studies dealing with the formation as a whole. Indeed, though he knew the Morrison was exposed in southern Montana, Marsh (1896:175) lamented that it was barren of fossils. Vertebrate fossils in particular remained rare after that; only in the latest 19th and early 20th centuries was a single specimen recovered, consisting of a fore- and hind limb referred to *Diplodocus* by Mook (1917). The somewhat better-known and more-fossiliferous Morrison outcrops in the Black Hills of Wyoming and South Dakota (Marsh, 1896; Foster, 1996, 2003) and the southern end of the Bighorn Basin in Wyoming (Siber, 1997; Ayers, 2000; Wilborn, 2002) were generally considered the northernmost extent of Morrison faunal provenance. However, an abundance of new research has demonstrated that, at least in south-central and central Montana (the northern end of the Bighorn Basin and farther north), Morrison deposits are indeed fossiliferous (Curry, 1994; Wilson and Smith, 1996; Storrs and Garcia, 2001; Myers, 2003, 2004). Interestingly, the majority of reported specimens from Montana thus far consist entirely of 'small' diplodocoid sauropods, although camarasaurids, allosauroid theropods, stegosaurs, non-dinosaurian reptiles, and fishes have been noted in faunal lists (e.g., Turner and Peterson, 1999; Foster, 2003) but not yet described.

In 1999–2000, a joint team from the University of Pennsylvania and the Academy of Natural Sciences (ANS) recovered a new sauropod taxon from the Upper Jurassic Morrison Formation of south-central Montana (Fig. 1). The specimen, ANS 21122, was discovered by Dr. William Donawick (University of Pennsylvania) and Will Tillett of Lovell, Wyoming. It was named *Suuwassea emilieae* by Harris and Dodson (2004), described briefly, and subjected to a preliminary phylogenetic analysis that recovered a trichotomy consisting of *Suuwassea* and the two components of the clade Flagellicaudata, the Diplodocidae (*Apatosaurus* + (*Diplodocus* + *Barosaurus*)) and Dicraeosauridae (*Dicraeosaurus* + *Amargasaurus*). To elucidate the position of *Suuwassea* within the Flagellicaudata and flagellicaudatan intrarelationships in general, a more detailed description and phylogenetic analysis is necessary. The cranial anatomy of *Suuwassea* is described in detail herein; the postcranial anatomy will be presented elsewhere, as will an expanded phylogenetic analysis.

Despite the relative increase in sauropod discoveries over the last few years, sauropod cranial materials remain more rare than postcrania, though they are perhaps better represented in diplodocoids than in other sauropod clades. The handful of *Diplodocus* skulls (including the partial skull of 'D.' *hayi* Holland, 1924) represent the most complete information on the cranial anatomy of the clade. Elsewhere in the Morrison Formation, only two skulls, one fragmentary and one largely complete, have been reported for *Apatosaurus* (Berman and McIntosh, 1978). Additional information comes from cranial material of the dicraeosaurid *Dicraeosaurus* and the probable diplodocine *Tornieria* (sensu Upchurch et al., 2004) from Tanzania (Janensch, 1935–1936). More recent discoveries include the caudal ends of the skulls of the rebbachisaurid *Limaysaurus* (sensu Salgado et al., 2004; = '*Rebbachisaurus*' *tessonei* per Calvo and Salgado, 1995), still largely undescribed material of the probable rebbachisaurid *Nigersaurus* (Sereno et al., 1999), and the dicraeosaurid *Amargasaurus* (Salgado and Calvo, 1992). More information doubtlessly resides in an as-yet undescribed, complete skull (TM 001) possibly referable to *Apatosaurus* (Bakker, 1998). The perception of cranial evolution within the Diplodocoidea, particularly the Flagellicaudata, thus suffers large gaps. The partial skull of *Suuwassea*, including a virtually complete braincase and skull roof, therefore deserves detailed description.

Cranial elements of *Suuwassea* were found separated both from each other and from the cervical vertebral series. Dissoci-

FIGURE 1. Locality information for Rattlesnake Ridge locality in Carbon County, Montana, source for ANS 21122. More specific locality information not provided to protect site from fossil poaching; specific information on file at the Academy of Natural Sciences, Philadelphia, and available to qualified workers.

ated cranial elements preserved in ANS 21122 include a nearly complete left premaxilla and fragment of the right maxilla (both dentigerous), a partial right quadrate, a right squamosal, and a virtually complete basicranium that also includes the caudal skull roof and occipital elements. The fragmentary rostral elements cannot be precisely oriented with respect to the basicranium, but their similarities to those of known diplodocoid skulls suggest comparable relative positions, which are assumed here.

Terminology used here follows Harris (2004), with the following addendum. Because the neutral position of the sauropod neck is a subject of some debate (Stevens and Parrish, 1999, 2000; Upchurch, 2000), it is unclear how the skull was normally held with respect to horizontal. Some authors (e.g., Holland, 1906; Nowinski, 1971; McIntosh and Berman, 1975; Bakker, 1986; Salgado and Calvo, 1997; Wilson and Sereno, 1998) have reconstructed diplodocoid (and diplodocoid-like titanosaurian) skulls with a 'domed' skull roof, with the nasal-frontal suture at the dome apex. In the lateral view of this configuration, the ventral margins of the maxillae and premaxillae are roughly horizontal, the frontals and parietals slope caudoventrally (thus facing caudodorsally), and the supraoccipital and exoccipital-opisthotic complex tilt rostroventrally (thus facing caudoventrally). This renders the axis of the occipital condyle and its neck roughly vertical. While this is not necessarily incorrect, an alternative is to place the skull roof in a horizontal plane, facing dorsally, rendering the supraoccipital and exoccipital-opisthotic complex more or less vertical and resulting in a caudoventral orientation for the occipital condyle. Further variation exists within the Flagellicaudata (see Comparisons, below) that affects the coding of some characters that depend on external criteria for orientation. For terminological convenience, the skull of ANS 21122 is described here using the latter method. De Beer (1947) discussed the possibility that the 'normal' head position may be determined by discerning the plane of the lateral semicircular canal, but the canals and their angular relationships to the remainder of the skull have been studied in only a few dinosaurs, none of them diplodocoids (e.g., *Brachiosaurus* [Janensch, 1935–1936] and *Plateosaurus* [Galton, 1985]).

Institutional Abbreviations—ANS, Academy of Natural Sciences, Philadelphia; **CM**, Carnegie Museum of Natural History, Pittsburgh; **HMNH**, Houston Museum of Natural History, Houston; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MNB**, Museum für Naturkunde der Humbolt-Universität zu Berlin, Institut für Paläontologie, Berlin, Germany; **TM**, Tate Museum, Casper; **USNM**, U.S. National Museum, Smithsonian Institution, Washington, DC; **YPM**, Yale Peabody Museum, New Haven.

DESCRIPTION

Premaxilla

The partial left premaxilla (Figs. 2A–D) consists of the rostral end of the bone, including the dentigerous end and a short portion of the nasal process. The preserved portion measures 72.1 mm rostrocaudally, 33.8 mm mediolaterally, and 15.2 mm dorsoventrally on its medial side (it thins laterally to 11.9 mm thick at the lateral margin). The dentigerous portion is more or less rectangular in rostrodorsal view and tapers gently toward the process. The ventral surface is flat, but the dorsal surface is gently convex and possesses several small, irregularly placed foramina. Four alveoli are present at the rostral end of the bone, the third of which retains a portion of a small, slightly compressed, cylindrical tooth. The thin bone forming the lateral plate of the dorsal margin has been broken away, exposing the alveolus in longitudinal section. The lateral margin of the bone bears a small, rostrocaudally elongate fossa approximately even with the alveolar margin; this fossa is hidden in dorsal view by a thin, laterally projecting bony shelf.

Caudally, the bone narrows mediolaterally and thickens dorsoventrally at the base of the nasal process. Thus, while the medial margin of the element remains straight, the lateral margin is sigmoid where the bone narrows suddenly, marking the rostral end of the narial fossa. A modest, dorsally projecting ridge of bone flares abruptly from the flat, dorsal surface and is associated only with the narial fossa. A small, ovoid foramen occurs on the lateral side of the ramus dorsal to the ridge. The medial margin of the process bears a shallow, longitudinal groove.

Maxilla

The preserved portion of the right maxilla (Fig. 2E–H), from the rostral end of the bone, was recovered as float. The fragment, which measures 72.8 mm rostrocaudally and 50.3 mm mediolaterally, is too deep to represent a portion of the dentary. The fragment possesses 7 alveoli, two of which retain tooth roots. In cross section, the bone is slightly concave medially and is 18.1 mm thick at its maximum (the bone thins slightly dorsally and caudally). As with the premaxilla, the lateral surface of the bone is riddled with numerous tiny foramina, most of which open rostroventrally. The foramina near the dentigerous margin of the bone open into shallow grooves; the more dorsal foramina open more laterally and lack these grooves.

The ventral perimeter of the bone is dominated by a shallow fossa that makes the margin ventrally concave. The fossa shallows and disappears near the preserved caudodorsal portion of the fragment. The medial surface of the bone is flat and smooth except for a row of circular, rostroventrally open foramina, each of which is located just above its corresponding alveolus. The more caudoventral foramina are broken open to expose the interior chambers of the alveoli and, in one, the root of a tooth.

Frontal

Only the caudal 41.4 mm of the frontals (Figs. 3A–D, 4A–D) are preserved, so their precise morphology cannot be determined. The dorsal, median suture between the bones has been diagenetically offset dextrolaterally. A small (10.9 × 11.7 mm) opening, bisected by the line of contact, is situated 11.8 mm rostral to the parietal suture. This is a result of the incomplete fusion of the frontals and does not represent a natural opening.
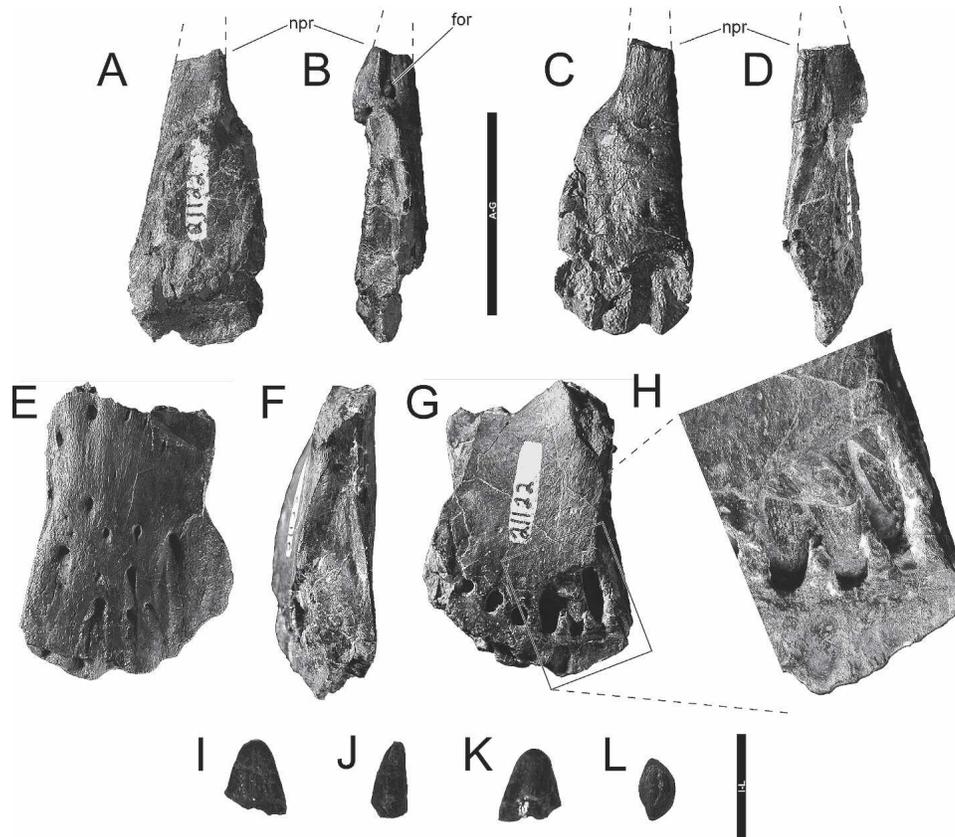
FIGURE 2.   Left premaxilla of ANS 21122 in **A**, dorsal; **B**, lateral; **C**, ventral; and **D**, medial views. Fragment of right maxilla of ANS 21122 in **E**, lateral; **F**, caudal; and **G**, medial views. Scale bar 5 cm. **H**, close-up of the caudal-most alveolus showing replacement teeth. Premaxillary tooth tip in **I**, labial; **J**, mesial; **K**, lingual; and **L**, apical views. **Abbreviations**: **for**, foramen; **npr**, nasal process. Scale bar equals 1 cm.

Laterally, each frontal curves ventrally into a rostrocaudally flattened and rostrally hooked postorbital process that bounds the caudodorsal margin of the orbit. It is across these processes that the frontals attain their maximum width (189 mm). The caudal margin of this process is flat and relatively smooth where it had been overlapped by the postorbital. The lateral margins of these processes have a rugose texture. There is no supratemporal fossa surrounding the supratemporal fenestra.

The frontal-parietal suture is predominantly straight and transverse, but the line curves slightly caudally at its lateral ends. The frontals measure 108.5 mm from the dorsal-most points of the supratemporal fenestrae and along the frontal-parietal suture. Within the supratemporal fenestra, the frontal-parietal contact produces a short ridge contiguous with the antotic process. Rostroventrally, the frontals form the dorsal and lateral margins of the olfactory canal; they are bolstered on either side of the canal by broad pedestals of the orbitosphenoids. The olfactory foramen itself is only slightly tilted rostrodorsally; it lies in virtually the same plane as the optic foramen. This markedly contrasts with the condition in other flagellicaudatans (e.g., *Apatosaurus*, *Dicraeosaurus*, and *Diplodocus*) and perhaps indicates that the external nares were not as caudally retracted as in more derived forms. A small region of contact exists between the frontals and laterosphenoids on the braincase; laterally, they do not contact the antotic processes (see below).

Parietal

In dorsal view (Figs. 3D, 4D), the parietals are rostrocaudally narrow (26.6 mm wide at their narrowest point, rostral to the postparietal foramen). Their rostral margin, in contact with the frontals, is interrupted only by a small midline opening that leads directly into the braincase. Topographically, this coincides with a parietal foramen (the correct term for the structure often called the pineal foramen or parapineal foramen [Jarvik, 1980] because the parietal organ, not the pineal, is generally the photoreceptive body [Edinger, 1955; Northcutt, 1979] as in many lepidosaurs [Edinger, 1955; Northcutt, 1979; Quay, 1979]). However, this opening is accepted to be lost in all archosaurs save a few basal forms (Quay, 1979; Roth and Roth, 1980). The periodic occurrence of this structure in some sauropod specimens has been a cause of controversy (McIntosh, 1990:356); the reason for this apparent reversal from the ancestral condition in these specimens remains unknown.

The caudal margin of the parietal is convolute in dorsal view as a result of two caudodorsal indentations (the nuchal fossae) on either side of the low but prominent sagittal nuchal crest of the supraoccipital. In caudal view, the parietals are not exposed medially, but their exoccipital processes arch ventrolaterally, creating rostrocaudally compressed, hooked processes that form the caudodorsal margins of the supratemporal fenestrae and the dorsal margins of the posttemporal fenestrae. As with the postorbital processes of the frontals, these processes taper distally, initially bend caudally, then begin to curve rostrally prior to their termination. The bone on the caudal surface of these processes is striated and rough as a result of muscle insertion (probably the M. complexus, based on comparisons with birds [Vanden Berge and Zweers, 1993], but possibly also involving the M. splenius, M. depressor mandibulae, and/or Mm. rectus and spinalis capitis based on comparisons with crocodylians [Cong, 1998]). The
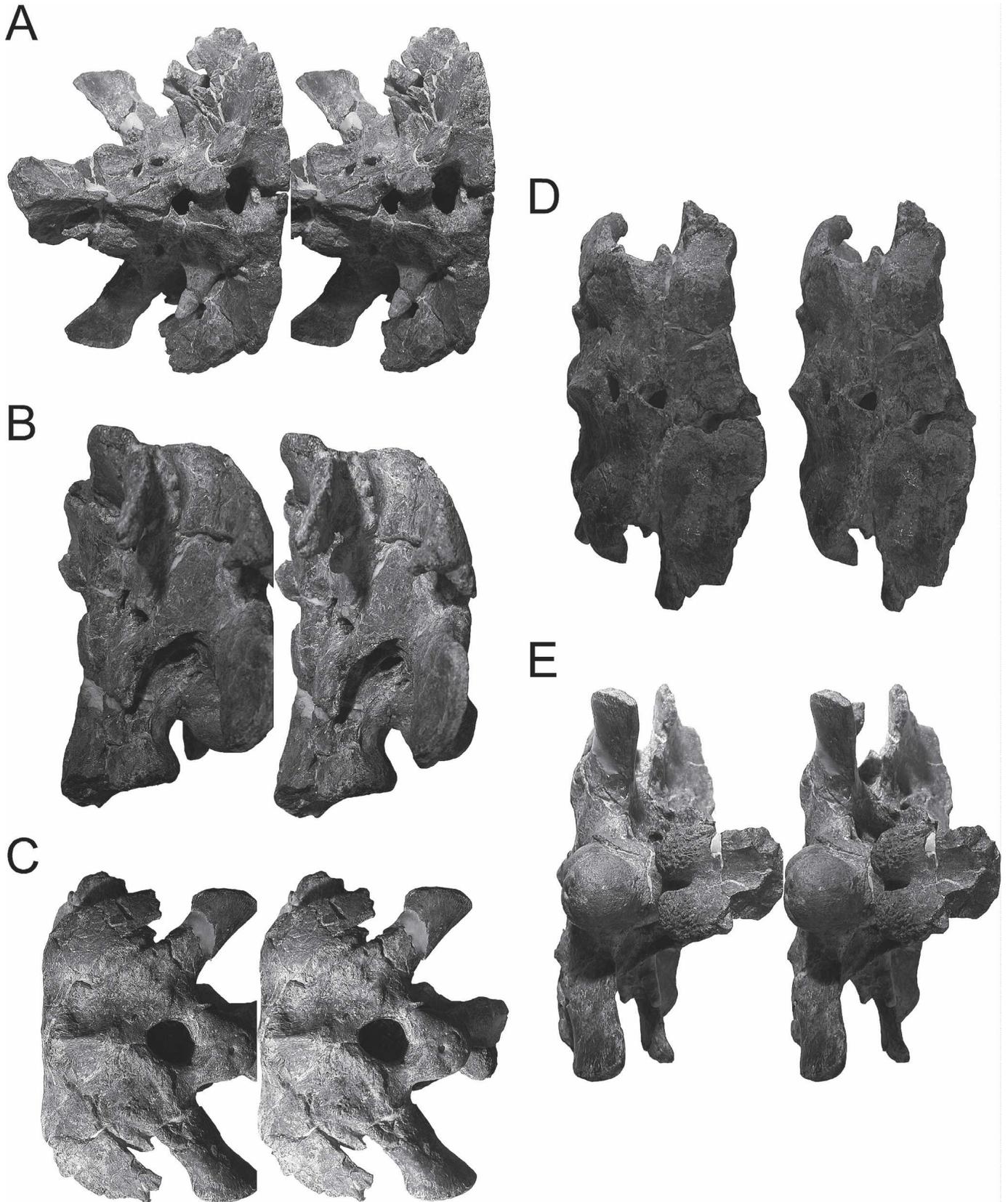
FIGURE 3.   Stereo photos of skull roof and basicranium of ANS 21122 in **A**, rostral; **B**, left lateral; **C**, caudal; **D**, dorsal; and **E**, ventral views. For features and scale, see Figure 4.
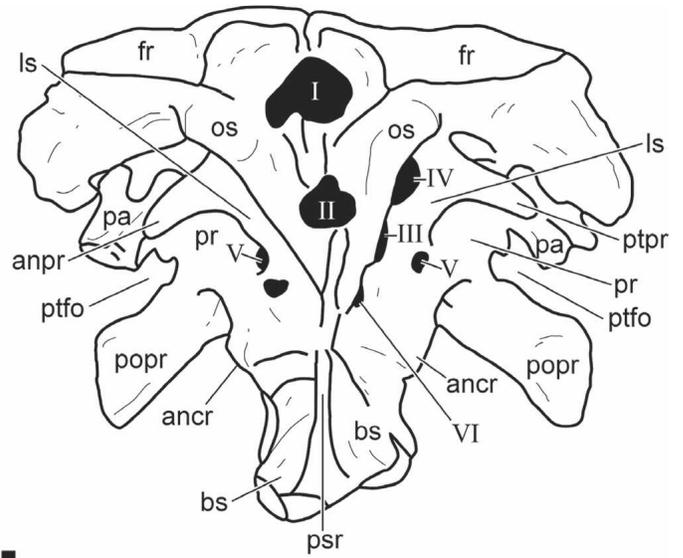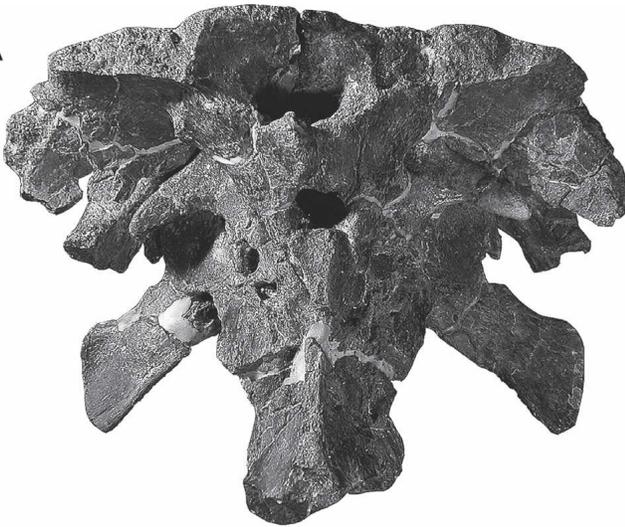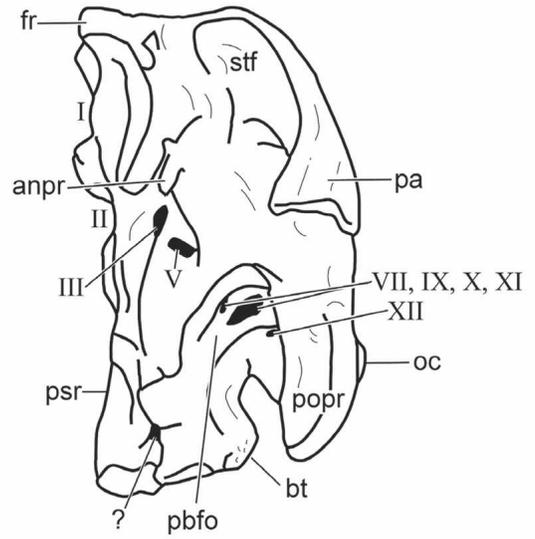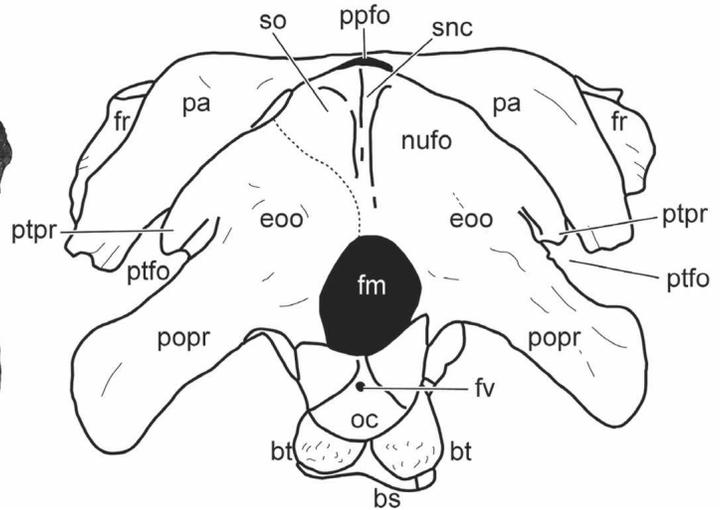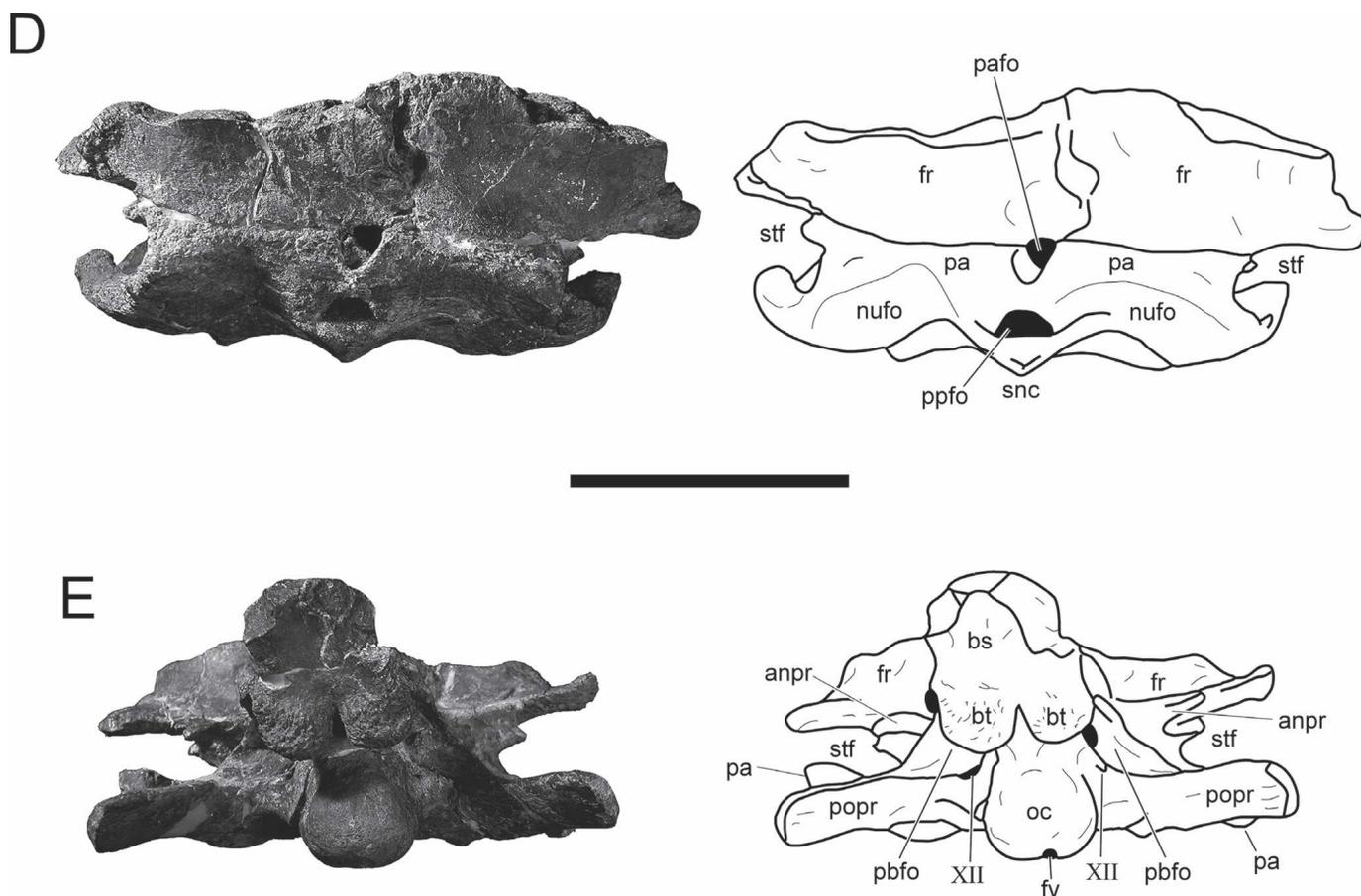
FIGURE 4. Skull roof and basicranium of ANS 21122 in **A**, rostral; **B**, left lateral; **C**, caudal; **D**, dorsal; and **E**, ventral views. **Abbreviations**: **ancr**, antotic crest; **anpr**, antotic process; **bs**, basisphenoid; **bt**, basal tuberculum; **eoo**, exoccipital-opisthotic complex; **fm**, foramen magnum; **fr**, frontal; **fv**, fovea; **ls**, laterosphenoid; **nufo**, nuchal fossa; **oc**, occipital condyle; **os**, orbitosphenoid; **pa**, parietal; **pbfo**, parabasal fossa; **popr**, paroccipital process; **pr**, prootic; **psr**, parasphenoid rostrum; **ptfo**, posttemporal fenestra; **ptpr**, posttemporal process; **snc**, sagittal nuchal crest; **so**, supraoccipital; **stf**, supratemporal fenestra; **I–XII**, cranial nerve foramina; **?**, opening of unknown function. Scale bars equal 10 cm.

broadest transverse span of the parietals, the distal-most preserved ends of these processes, is 170.3 mm, while at its narrowest, between the supratemporal fenestrae, the span is only 107.8 mm.

The supratemporal fenestrae have a subrectangular morphology, with the longest axis oriented dorsoventrally. They are fully visible in lateral view but retain slight dorsal exposure (Figs. 3B,D, 4B,D). The preserved dorsal margin is subrectangular, parallels the plane of the skull roof, and lies perpendicular to both the rostral and caudal margins. The longest rostrocaudal axis of the fenestra is 32.3 mm; the ventral margin is not preserved, so a precise dorsoventral measure cannot be determined, but the preserved portion is 56.2 mm. It would be slightly, but not substantially, longer than this because the preserved ventrolateral ends of the frontals and parietals are unbroken, marking the points of contact with the squamosal and postorbital, which form the lower border of the fenestra. As a result, *Suuwassea* technically fails to meet the neosauropod apomorphy in which the intraparietal distance is twice the maximum length of the fenestra, but only by a few millimeters. Where the fronto-parietal suture contacts the dorsomedial margin of the supratemporal fenestrae, the parietals emit dorsoventrally long but mediolaterally low processes; the postorbital abutted the rostrolateral face of this process, blocking the frontal from contributing to the fenestra.

Situated at and centered on the parietal-supraoccipital contact is a small (15.4 × 6.3 mm), trapezoidal foramen (with the longest margin of the trapezoid at the caudal margin). This corresponds in position with the postparietal foramen of Janensch (1935–1936:figs. 72–3, 97) and Salgado and Calvo (1992:fig. 1A). The rim of the foramen is slightly elevated above the surrounding skull roof and sits on the dorsalmost portion of the low, tetrahedral eminence formed by the union of the transverse and sagittal nuchal crests (see below). The foramen opens dorsally and slightly caudally. Its purpose is unclear, but the fact that it enters the brain cavity close to the egress of the canal from the parietal foramen suggests that it may have been for photoreception. As proposed by Janensch (1935–1936:figs 128, 134), it may have enhanced the nominal function of the parietal organ (or other portion of the larger pineal-parietal complex) that is normally exposed only via the parietal foramen. In 'lower' tetrapods, the parietal organ is photoreceptive and has effect on thermoregulation, gonad and pigment development, and maintenance of circadian rhythms (Roth and Roth, 1980; Kardong, 1995). The parietal organ is wholly glandular, a part of the endocrine system in birds (Kardong, 1995); its exposure via the parietal (and possibly postparietal) foramen in *Suuwassea* and other sauropods indicates that similar transformation had not occurred in more basal saurischians. Hopson (1979) concluded that the space into which the parietal and postparietal foramina open, which he

termed the 'fontanelle,' either was cartilage-filled or housed a dorsal venous sinus; both would obstruct photoreception by a parietal organ through either opening.

Supraoccipital

The supraoccipital (Figs. 3C–D, 4C–D) is 48.9 mm tall dorsoventrally and 56.6 mm in its widest mediolateral dimension. Most of its rhomboidal body is centrally located on the occipital surface of the skull and composed of broad wings that are dorsolaterally convex in caudal view. The lateral alae taper laterally to low, blunt, ventrally projecting processes. A low but prominent, 36.6 mm long sagittal nuchal crest extends from a point 15.7 mm dorsal to the foramen magnum to the caudal margin of the postparietal foramen, where it expands laterally into a low, caudally projecting, triangular eminence that forms a transverse nuchal crest. The ventral end of the sagittal nuchal crest also flares slightly laterally on either side. This is the only portion of the element visible in dorsal view. On either side of the nuchal crest, the bone slopes rostrolaterally, forming the lateral borders of the nuchal fossae that continue onto the parietals (see above). Ventral to the lower extent of the nuchal crest, the supraoccipital thins to a mediolaterally narrow, ventrally projecting pillar that forms a small portion (approximately one-seventh) of the dorsal margin of the foramen magnum. Its suture with the exoccipital-opisthotic complex is visible on the left side. Within the foramen magnum, the suture indicates that the bone again flares laterally but is entirely overlapped by the exoccipital-opisthotic complex.

Exoccipital-Opisthotic

The exoccipitals and opisthotics (Figs. 3C–D, 4C–D) are fused and form the majority of the margin of the dorsoventrally ovoid (30.3 × 22.7 mm) foramen magnum. The exoccipital-opisthotic complexes also form the dorsolateral portions of the caudoventrally projecting occipital condyle. Pronounced, thickened condylar processes project from the ventrolateral margins of the foramen magnum and converge toward the distal end of the occipital condyle; at their distal ends, these processes flare and meet at the midline, excluding the basioccipital from the floor of the median condylar incisure. The planes of the nuchal surface of the skull and the foramen magnum are virtually the same.

Each complex tapers toward the ventral process of the supraoccipital. Dorsolateral to the foramen magnum, the bones widen dorsoventrally into broad quadrangular plates; from these, two processes project laterally. The small, dorsal posttemporal processes (processus posttemporalis, term. nov.) project laterally and curve ventrally, tapering to blunt points. They measure 9.6 mm mediolaterally and 7.7 mm dorsoventrally at their bases and project into the posttemporal fenestra (see Holland, 1906) between the parietals dorsally and the paroccipital processes ventrally, creating the bifid medial morphology of the posttemporal fenestra (Figs. 3C, 4C). Both the dorsal and ventral margins of each posttemporal process are thus free of contact with surrounding elements.

The 58.5 mm long paroccipital processes (Figs. 3B–C, 4B–C,E) project ventrolaterally farther from the midline (160.4 mm) than any preserved portion of the skull; modest caudal inclination is also present. In caudal view, the ventral margin of each process is linear but the dorsal margin is concave dorsally. The distal ends are expanded dorsoventrally and are mildly convex laterally. The rostral side of the distal end of each process is concave, producing a crescentic cross-sectional shape. The medial half of each dorsal margin of the paroccipital process bears a shallow sulcus. The sulcus is bounded caudally by a low ridge, visible in caudal view, that parallels the posttemporal process. Rostrally, the sulcus is bounded by a lower crest that continues dorsomedially close to the ventral margin of the posttemporal process.

The ventral margin of each paroccipital process continues as a low, rostroventrally oriented ridge that persists rostroventrally to form the caudolateral margins of the basal tubercles. At their ventral ends, the crests curve caudally to bound shallow, dorsoventrally elongate fossae immediately dorsal to the basal tubercula. These ridges form the caudoventral margins of the parabasal fossae, which are dorsoventrally elongate depressions that curve caudally and laterally at their dorsal ends onto the roots of the paroccipital processes. This fossa probably housed the stapes as it coursed toward the oval foramen as in modern birds (Baumel and Witmer, 1993). The fossae are widest at their dorsal ends and gradually narrow ventrally. The fossa on each side contains two large foramina that open ventrolaterally, though postmortem breakage has removed part of the bar that separates the foramina on the right side. Cranial nerves VII, IX, and X, and possibly XI, plus the internal carotid arteries and jugular veins, exited between the dual openings on each side.

Basioccipital and Basisphenoid

The basioccipital (Figs. 3C,E, 4C,E) forms most of the caudoventrally projecting occipital condyle. The condyle is roughly spherical, measuring 31.2 mm mediolaterally and 26.8 mm dorsoventrally, and its dorsal margin is indented by the median condylar incisure. A tiny, caudally oriented fovea on the caudodorsal part of the condyle marks the insertion point for a capitular ligament. Rostral and slightly lateral to the neck of the occipital condyle on either side, beneath the thick dorsolateral ridges, are small hypoglossal (cranial nerve XII) foramina that open laterally. Ventral to the occipital condyle, the basioccipital and basisphenoid conjoin in a rostrocaudally thick, columnar, medial process that bears the basal tubercles on the caudal surface. This columnar process measures 39.9 mm rostrocaudally from the point just ventral to the occipital condyle to the base of the parasphenoid rostrum, and 48.0 mm including the basal tubercles. The basal tubercles are not distinct processes but exist primarily as paired, 23.1 mm-long, rugose knobs that jut caudoventrally and slightly laterally from the main basioccipital pillar. The tubercles conjoin rostrally such that, in caudal view, the remainder of the pillar-like process is visible between them. A narrow channel that connects a small, ovoid, caudally open basioccipital foramen to a ventrally open sulcus separates the tubercles medially. The caudolateral surfaces of the tubercles are embayed by dorsoventrally elongate fossae.

The notch separating the basal tubercles opens ventrally into a broad, shallow, rostrocaudally oriented sulcus on the ventral surface of the basioccipital that flares abruptly mediolaterally onto the basisphenoid. The broken bases of the basipterygoid processes indicate that their diameters were narrow; the angle between them (as seen in rostral view) appears to be 65°, but this is likely an artifact of the differing manners in which each process is broken. The apparent angle between the preserved base of the right process and the skull roof is roughly 45°. In rostral view, a broken surface along the midline of the skull, measuring 51.4 mm dorsoventrally, marks the base of the parasphenoid rostrum. The only intact portion of the rostrum is a low ridge that extends from the ventral margin of the optic foramen towards the broken surface; overall, the rostrum was 78.4 mm long dorsoventrally at its base. If the dorsal margin of the parasphenoid rostrum bore a groove, it did not persist onto the basisphenoid because it is not indicated by the broken base.

Small (4.5 mm diameter) foramina are nested within shallow, triangular fossae on the ventrolateral surfaces of the pillar, just dorsal to the ventral margin of the basisphenoid. Their function is unknown.

Orbitosphenoid

The orbitosphenoids (Figs. 3A–B, 4A–B) are completely fused medially. Their medial margin forms a continuous and, in lateral view, straight line with the broken base of the parasphenoid

rostrum. In rostral view, they are broadly Y-shaped (apex pointed ventrally). At their dorsal contact with the frontals, paired pedestals flare dorsolaterally and overlap the ventral surface of the frontals with a dorsolateral-ventromedially oblique suture. These form the ventrolateral edges of the large (24.7 × 16 mm), sagittal, transversely oval olfactory nerve (cranial nerve I) foramen. This opening faces mostly rostrally but is also tilted to possess a slight dorsal component as well. Roughly 15 mm ventral to this opening, also along the sagittal line, occurs the smaller (14 × 9.6 mm), more subcircular, unpaired optic nerve (cranial nerve II) foramen. A short, midline process invades this opening on its dorsal margin, but both the end of this process and the ventral margin of the opening consist of finished bone, indicating that a dividing bar was absent. Lateral to the olfactory foramen, where the orbitosphenoid pillars brace the frontals, two tiny foramina pierce the bone; similar openings were interpreted by Holland (1924) as transmitting veins in '*Diplodocus*' *hayi*. Caudal and lateral to these openings, each element angles caudally toward their contact with the laterosphenoids, with which they are completely fused. The laterosphenoid suture is, however, indicated by the presence of the oculomotor (cranial nerve III) and trochlear (cranial nerve IV) foramina (Berman and McIntosh, 1978; Salgado and Calvo, 1992). The trochlear foramen measures 6.2 × 4.2 mm and opens rostrolaterally just ventral to the dorsolateral contact with the frontals. The oculomotor (III) foramen is situated 14.3 mm ventral and slightly rostral to the trochlear foramen, just caudolateral to the optic foramen; it is 11.8 × 3.9 mm long dorsoventrally and also opens rostrolaterally. Farther ventromedial to the oculomotor foramina, just lateral to the dorsalmost point where the parasphenoid rostrum would have attached, are two tiny foramina, probably for transmission of the abducens (cranial nerve VI) nerves.

Laterosphenoid

The laterosphenoids (Figs. 3A–B, 4A–B) are fused to all the surrounding bones, so their morphology cannot be precisely discerned. The most prominent feature of each is a 30.8 mm long, laterally projecting antotic process (processus antotica, term nov.) that curves slightly ventrally toward its distal end. The ventral margin of the process continues ventrally as a low, thin crest that terminates at the dorsal edge of the roughly triangular trigeminal (cranial nerve V) foramen. The latter opening is located just caudolateral to the oculomotor foramen. Dorsomedial to the antotic process is a pronounced and sharply bounded fossa. The caudodorsal end of this elongate, 19 mm-long fossa deepens and may form a tiny slit, but this region is obscured by matrix. The fossa empties laterally into the notch that separates the antotic process from the orbital process of the frontal.

Prootic

As with the laterosphenoids, fusion of the prootics (Figs. 3A–B, 4A–B) to other braincase elements is complete, and thus their precise morphologies cannot be discerned except by a crack on the left side and a corresponding, roughened linear feature on the right that represent sutures. Both lines continue caudodorsally, then arc laterally to connect with the ventral margin of the supratemporal processes of the parietals. A long, thin prootic crest extends rostroventrally from the rostromedial surface of the paroccipital process, forming the rostral boundary of the parabasal fossa and the rostral margin of the basal tubercles. The trigeminal foramen is considered to lie on the contact of the laterosphenoid and prootic in *Diplodocus* (Berman and McIntosh, 1978), *Amargasaurus* (Salgado and Calvo, 1992), and *Shunosaurus* (Chatterjee and Zheng, 2002) and presumably does so in *Suuwassea*. The remainder of the prootic, ventral and lateral to the antotic processes and caudodorsal to the trigeminal foramina, consists of flat, rostrolaterally facing, roughly pentagonal plates of bone that lie rostromedial and dorsal to the bases of the paroccipital processes.

Squamosal

The right squamosal (Fig. 5A–D) was recovered disarticulated from the remainder of the skull. It is an elongate, arcuate bone with its quadratojugal process tapering rostroventrally. At its dorsal end, it bears a deep, rectangular fossa that received a process from the postorbital. Dorsal to the fossa is a rectangular plateau of bone, the dorsal side of which drops off sharply onto the lateral surface of the parietal process. Thus, the distal end of the parietal abuts the caudodorsal surface of the rectangular plateau. The medial surface of the squamosal is deeply embayed by a smooth-surfaced fossa that shallows and ultimately disappears at the base of the quadratojugal process. However, the medial surface of the latter also houses a deep fossa, separated from the former by a sharp crest of bone. This fossa apparently formed a scarf joint with the quadratojugal, which it overlapped laterally.

Quadrate

The preserved portion of the right quadrate (Fig. 5E–I) includes all of the main shaft but lacks all but the base of the thin, plate-like pterygoid process. In lateral view (Fig. 5H), the element is concave caudally. The shaft is 154.9 mm long dorsoventrally. The mediolaterally compressed squamosal end is 24.5 mm rostrocaudally and lies at an acute angle to the long axis of the mandibular end. Its head is formed by a modest swelling at its dorsal end. Ventral to the head, a shallow furrow dominates the caudal surface of the shaft, disappearing just dorsal to the mandibular condyles. The lateral margin of the sulcus is formed by a thin, caudolaterally projecting ridge of bone. Distally, the ridge splits into two divergent crests that bound a shallow, triangular fossa on the caudolateral surface. The caudal crest spans the caudolateral margin of the bone and forms a small, rugose eminence before terminating proximal to the medial mandibular condyle. The more rostral crest continues rostrolaterally as a low, thin crest on the base of the pterygoid process. The space bounded by the two crests is narrow proximally but widens distally into a shallow, triangular fossa that does not extend onto the medial mandibular condyle.

The lateral margin of the caudal sulcus grades into a much thicker, medially projecting ridge that forms the entirety of the medial margin. This ridge broadens ventrally, extending onto the base of the pterygoid process. It does not extend onto the lateral condyle.

The rostromedial surface of the quadrate is lightly concave. A low, short, laterally projecting ridge ventrolateral to the squamosal head bounds and narrows the concavity at its proximal end. The base of the pterygoid process, which projects rostromedially from the shaft, thins toward the mandibular head; its base is located 27.0 mm dorsal to the lateral condyle and is the thickest portion of the process. The rostral face of the distal articular condyles is flat except for a swelling above the lateral side. A shallow, triangular fossa on the ventral surface of the pterygoid process roofs the space rostral to the condyles. The notch described by the rostral margin of the condyle and the ventral edge of the pterygoid process is hyperbolic in lateral view.

The mandibular articular head measures 31.6 mm mediolaterally and 18.8 mm in its greatest rostrocaudal dimension. Separate medial and lateral condyles are not evident; in fact, the distal end is unfinished and even concave instead of forming true, convex condyles; whether this is due to breakage, ontogeny, or another factor is unclear. In articular view (Fig. 5I), the articular surface is roughly D-shaped, bulging caudally and lightly indented rostrally.
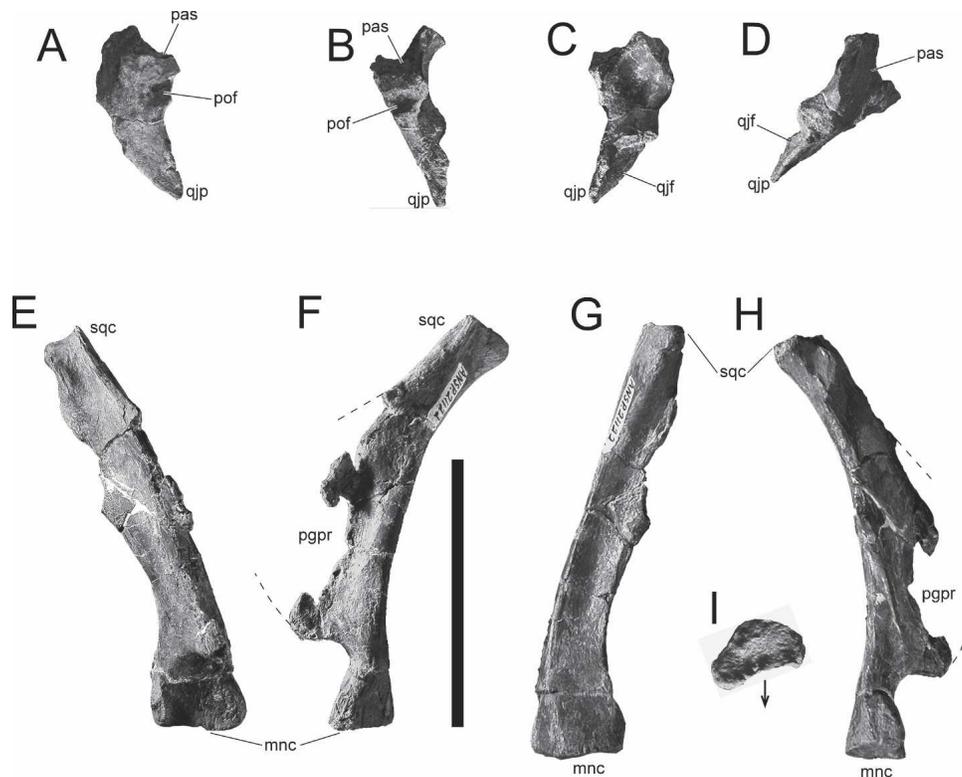
FIGURE 5.   Right squamosal of ANS 21122 in **A**, caudolateral; **B**, rostrolateral; **C**, rostrolateral; and **D**, ventromedial views. Right quadrate of ANS 21122 in **E**, rostral; **F**, medial; **G**, caudal; **H**, lateral; and **I**, distal (articular) views. Arrow in **I** points rostrally. **Abbreviations**: **mnc**, mandibular capitulum; **pas**, articular surface for squamosal process of parietal; **pof**, fossa for squamosal process of postorbital; **pgpr**, pterygoid process; **qjf**, fossa for squamosal process of quadratojugal; **qjp**, quadratojugal process; **sqc**, squamosal capitulum. Scale bar equals 10 cm.

Dentition

Aside from a lone, compressed cylindrical fragment of a tooth shaft, the only teeth preserved in ANS 21122 are those in the premaxilla and fragment of the maxilla. These teeth are barely erupted and provide limited information regarding important dental characters such as length, width, and wear patterns. The crown morphology described herein is based on the apical end of a single crown removed from the premaxilla so that both labial and lingual sides could be examined (Fig. 2I–L).

The crown tapers to a blunt, parabolic tip. Both lingual and labial surfaces are convex, the lingual more so. There are neither denticles nor grooves on either surface, but enamel on both is convolute (i.e., wrinkled). The enamel is subequal in thickness on the labial and lingual sides. The crown is not separated from the root by a constriction. This morphology is almost identical to that of unworn crowns of *Diplodocus* (Marsh, 1896:pl. 26, figs. 1–2) and *Apatosaurus* (pers. obs.).

COMPARISONS WITH OTHER FLAGELLICAUDATANS

In addition to highlighting the distinctive characters of *Suuwassea*, detailing specific differences between the crania of *Suuwassea* and other sauropods illuminates characters that may be phylogenetically useful but have not yet been included in a formal analysis and characters that may have too much intraspecific variation to be phylogenetically useful. Given the flagellicaudatan affinities of *Suuwassea* (Harris and Dodson, 2004), comparisons herein will be limited to other members (and purported members) of that clade (see Figure 6 for graphic comparisons). These taxa include: *Amargasaurus cazaui* (MACN-N 15); the most complete described skull of *Apatosaurus* (CM 11162),

which almost certainly pertains to *A. louisae* (Berman and McIntosh, 1978; McIntosh, 1981), with notes from a partial braincase (YPM 1860) that probably pertains to *A. ajax* (Berman and McIntosh, 1978:figs. 11A–D); *Dicraeosaurus* (Janensch, 1935–1936); *Diplodocus* (several specimens), including both *Diplodocus* spp. and those attributed to *D.* cf. *longus* (Marsh, 1884; Holland, 1924; McIntosh and Carpenter, 1998); and *Tornieria* (Janensch, 1935–1936). No skulls are currently known for *Barosaurus*. Though noting that its numerous cranial differences from skulls of other *Diplodocus* species probably warranted genus-level separation, Holland (1924) granted only species-level distinction for *Diplodocus hayi* (CM 662, now at the HMNH but unnumbered). The holotype of the latter taxon includes an intact braincase and caudal skull roof that was described in detail by Holland (1906). Doubt has been cast on the referral of this specimen to *Diplodocus*; it is referred to herein as '*Diplodocus*' *hayi* following Foster (2001, 2003), pending restudy. Some misgivings have been voiced (Hay, 1908) about the positions of sutures figured by Holland (1906); therefore, only gross morphological comparisons will be made here. Other Morrison Formation sauropod cranial materials for which no taxonomic assignment has yet been made are discussed below, following the comparisons of individual elements.

The premaxillae of *Apatosaurus*, *Dicraeosaurus*, and *Diplodocus* cf. *longus* (USNM 2673 and CM 3452) are much larger and more massive elements than the small, thin bone of *Suuwassea*. However, a premaxilla assigned to *Diplodocus* (CM 11255) and the premaxillae of *Tornieria africana* are of similar size and slenderness. The dorsal and ventral surfaces of the premaxilla of *Suuwassea* are parallel; this feature is also seen in a premaxilla referred to *Tornieria* (MNB 2343 [Ki125]). However, the premaxillae of *Apatosaurus*, *Dicraeosaurus*, *Diplodocus*, and other
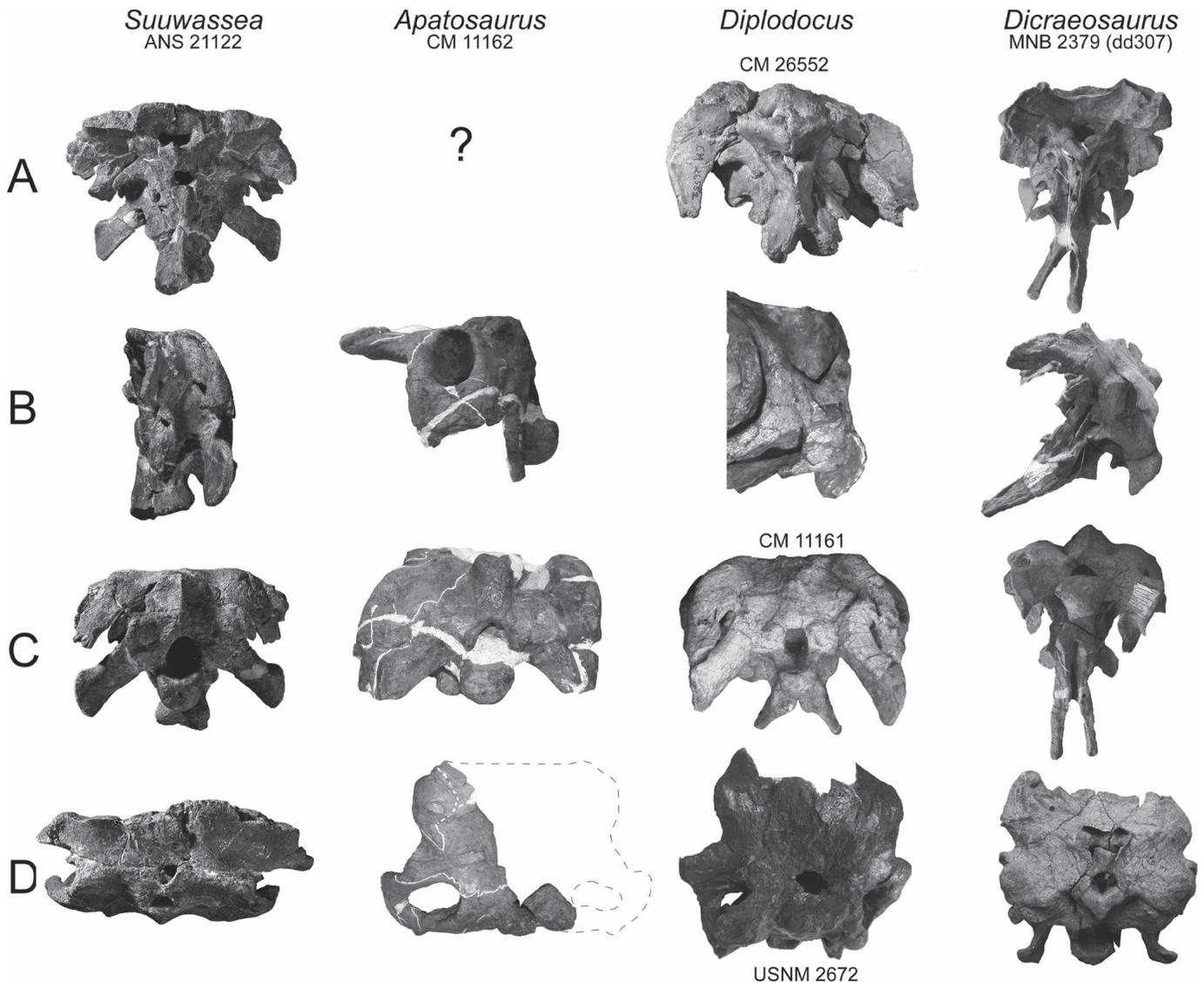
FIGURE 6. Comparisons of basicrania of flagellicaudatan sauropods (by column) in **A**, rostral; **B**, left lateral; **C**, caudal; and **D**, dorsal views. Not to scale.

premaxillae referred to *Tornieria* (MNB 2344 [dd416], 2346 [Ki126]) possess rostrodorsally convex dorsal and ventral surfaces, rendering the bone ventrally hooked in lateral view. The premaxillae of *Apatosaurus* and *Tornieria* have much longer bodies rostral to the narial process than *Suuwassea*. The premaxillae in *Apatosaurus* and *Diplodocus* lack the abrupt ridge at the base of the narial process, adjacent to the narial fossa, possessed by *Suuwassea*. The offset between the main corpus and the nasal process is less pronounced in *Dicraeosaurus* than in *Suuwassea*. The degree of offset between the nasal process and main premaxillary body varies in *Tornieria*; only in one specimen (MNB 2344 [dd416]) is it similar to that of *Suuwassea*. The bases of the nasal processes of two premaxillae of *Tornieria* (MNB 2344 [dd416] and 2346 [Ki126]), but not a third (MNB 2243 [Ki125]), are perforated not only by a deep foramen on their lateral surfaces, like the one in *Suuwassea*, but also by a second, shallower excavation rostral to the first (Janensch, 1935–1936:figs. 81–84).

Though only slightly larger in absolute terms than that preserved with ANS 21122, the braincases of *Dicraeosaurus* (MNB 2738 [dd307] and 2739 [dd495], both assigned to *D. hansemanni*),

and one specimen of *Diplodocus* (USNM 2673) are much more massive overall; other braincases of *Diplodocus* (CM 3452, 11844, 26552, and, especially, 11161) are, however, of similar size and proportions. Two braincases (with associated skull roofs) ascribed to *Tornieria* (MNB 2387 [dd316] and 2388 [dd130]) are of similar gracile proportions to *Suuwassea*, but both differ in significant ways from the holotype braincase (MNB 2386 [K1]) which is much larger and more massive than either of the former or that of *Suuwassea*.

Characteristic for dicraeosaurids, the frontals of *Amargasaurus* (Salgado and Calvo, 1992) and *Dicraeosaurus* (Janensch, 1935–1936) are seamlessly fused, unlike those of *Suuwassea*. Interfrontal sutures cannot be discerned in any specimen referred to *Tornieria*, which in this respect is more similar to dicraeosaurids than to *Suuwassea*. In general, the frontals of *Apatosaurus* and *Diplodocus* are similar to those of *Suuwassea* though the midline region of the frontals in CM 11162 is missing, so that the status of interfrontal fusion cannot be assessed.

The fronto-parietal sutures of *Apatosaurus* (Berman and McIntosh, 1978:fig. 3D) and *Diplodocus* (except USNM 2673,

where it cannot be discerned) are less linear than those of *Suuwassea*. Specifically, as their sutures course laterally from the midline, they veer rostrally at the supratemporal foramen before resuming a lateral track—thus, their lateral ends lie entirely rostral to the supratemporal fenestra. The fronto-parietal suture in *Dicraeosaurus* is similarly nonlinear, but it sweeps caudally before entering the supratemporal fenestrae. Parietal exposure on the dorsal surface of the skull is much more substantial in *Dicraeosaurus* and *Tornieria* than in *Suuwassea*, and where they meet, the parietals of *Dicraeosaurus* rise to form a distinct, sagittal ridge between the parietal and postparietal foramina. The skull roof of '*D.*' *hayi* is dominated by large, paired frontals that confine dorsal exposure of the parietals to a narrow band at the caudal end of the skull, as in *Suuwassea*. Fronto-parietal sutures can be discerned in *Tornieria* (MNB 2386 [K1] and 2388 [dd130]) in approximately the same position as in ANS 21122. The postorbital process of the frontal in the remaining known *Tornieria* braincase (MNB 2387 [dd316]) sweeps caudally to such an extent that all but its hooked distal end are virtually horizontal, unlike the more vertical process in *Suuwassea*.

In caudal view, the suture between the parietals and exoccipital-opisthotic complex in both *Apatosaurus* and *Diplodocus* (CM 11161, 11844, and 26522) is interrupted by two pronounced but short, broad, triangular processes of the parietal that invade the complex (Berman and McIntosh, 1978:fig. 3B, E), rendering the contact sinuous, unlike the linear suture in *Suuwassea*. Although the sutures cannot be discerned in one *Tornieria* braincase (MNB 2387 [dd316]), the missing parietal in MNB 2388 (dd130) indicates that *Tornieria* too has a sinuous, nonlinear suture and had similar processes of the parietal (Janensch, 1935–1936:figs. 72, 77). The condition in *Amargasaurus* and *Dicraeosaurus* is uncertain because of fusion.

The caudal surface of the braincase meets the skull roof at an abrupt angle in one braincase of *Dicraeosaurus* (MNB 2379 [dd307]), but in another (MNB 2378 [dd495]), the transition is much smoother and more rounded. The entire caudal surface of the skull dorsal to the foramen magnum angles abruptly rostrodorsally in all skulls of *Diplodocus* and in the holotype specimen of *Tornieria* (MNB 2386 [K1]). Thus, when held with its sagittal nuchal crest in a vertical plane, the occipital condyles in these specimens project almost entirely ventrally. In *Apatosaurus*, *Dicraeosaurus* (MNB 2379 [dd307]), *Suuwassea*, and other skulls referred to *Tornieria*, the foramen magnum and the sagittal nuchal crest lie in parallel (and nearly identical) planes, such that their occipital condyles project caudoventrally (in *Tornieria*, orientation is more ventral in MNB 2388 [dd130] than in MNB 2387 [dd316]). Salgado and Calvo (1992) reported a ventral angulation for the occipital condyle in *Amargasaurus*.

Only the left supratemporal fenestra is intact in *Apatosaurus* (CM 11162); like *Suuwassea*, it faces more laterally than dorsally. The rostrocaudally narrow, dorsoventrally elongate supratemporal fenestrae of *Dicraeosaurus* have migrated even farther ventrolaterally and are barely visible in dorsal view; they open entirely laterally. Most remarkably, the supratemporal fenestrae of *Amargasaurus* have either shrunk compared to overall skull size and migrated ventrally to occupy the caudoventral corner of the orbit (Salgado and Calvo, 1992) or been entirely lost (Wilson, 2002). The supratemporal fenestrae in *Diplodocus* specimens exhibit a variety of states: in most, they are visible dorsally but face more laterally (especially in CM 11844), as in *Suuwassea*. It is unclear how much of this is due to crushing in USNM 2673. In USNM 2672, the left fenestra faces almost entirely dorsally, but on the right (the more distorted side), it faces almost entirely laterally. In CM 26522, the fenestrae are similarly situated to ANS 21122 but face slightly more dorsally. The orientation of the supratemporal fenestrae in '*D.*' *hayi* has a much smaller lateral component than in *Suuwassea*. The supratemporal fenestrae of *Tornieria* (MNB 2387 [dd316]) are similar in morphology

to those of *Suuwassea* in all respects, though slightly narrower rostrocaudally.

The presence or absence of a parietal foramen cannot be assessed in *Amargasaurus* or *Apatosaurus*; some braincases of *Diplodocus* (e.g., USNM 2672) lack this opening (Berman and McIntosh, 1978), but in others, the skull roof is embayed in this area, sloping inward medially. In two *Diplodocus* specimens (CM 11161 and USNM 2673), these fossae house large parietal foramina. Breakage and crushing of both of these specimens (Holland, 1906; Pompeckj, 1920) may be partly responsible for the size of the foramina. In *Dicraeosaurus*, the enormous parietal opening is elevated above the surrounding skull roof in MNB 2379 (dd307), but less so in 2378 (dd495). The only braincase of *Tornieria* with an intact skull roof (MNB 2387 [dd316]) bears a large, circular parietal foramen that floors a shallow, rostrocaudally asymmetrical fossa centered on the parietals (possibly including part of the frontals). Pompeckj (1920) suggested that the openings in the Tendaguru sauropods were either unnatural or unnaturally enlarged by breakage and or preparation, but their rims are formed of unbroken bone.

In *Amargasaurus*, *Dicraeosaurus*, and *Tornieria*, the parietal foramen is larger than the postparietal foramen, the reverse of the condition in *Suuwassea*. Postparietal foramina are absent in all known specimens of *Apatosaurus* and *Diplodocus*, including '*D.*' *hayi*. An additional *Diplodocus* skull (CM 11161) has a small, triangular opening in the same position as the postparietal foramen in *Suuwassea*, but this is simply a broken surface that does not open into a channel and is, therefore, not a homologous structure. Even though the skull roof is broken in this area in *Apatosaurus* (CM 11162), the rostral surface of the supraoccipital is not embayed by a vertical sulcus that would lead to an opening on the missing surface; thus, the absence appears to be genuine. Like the parietal foramen, the postparietal foramen in *Dicraeosaurus*, a large opening that ranges from subcircular (MNB 2379 [dd307]) to trapezoidal (MNB 2378 [dd495]) in shape, is elevated above the skull roof, but it opens caudodorsally instead of dorsally as it does in *Suuwassea*. In *Tornieria* (MNB 2388 [dd130]), the foramen is roughly trapezoidal, but with its long axis on the opposite side from that of *Suuwassea*. The opening also does not sit on a raised platform constructed by the nuchal crests, but instead sits in its own depression below a thin, caudally projecting shelf of the parietals. This shelf sits more dorsal even than the dorsal-most extent of the supraoccipital. The rostrodorsal margin of the supraoccipitals in the two referred braincases (MNB 2387 [dd316] and 2388 [dd130]) are concave in dorsal view, indented by the channel into which the postparietal foramen opens. The holotype (MNB 2386 [K1]), however, lacks this notch and may not have possessed a postparietal foramen.

The supraoccipitals of *Amargasaurus* and *Dicraeosaurus* (MNB 2379 [dd307]) each form a large tetrahedral eminence created by the conjunction of sagittal and transverse nuchal crests, similar to, but much larger than, those of *Suuwassea*. Possibly the result of minor abrasion, the eminence is less pronounced in a second *Dicraeosaurus* braincase (MNB 2378 [dd495]). Eminences are also present in *Apatosaurus* and *Diplodocus*, but they are more rectangular than tetrahedral and much less pronounced than in *Suuwassea* because the sagittal and transverse nuchal crests are lower, broader, and less sharp (crushing has artificially enhanced the eminence in *Diplodocus* specimen USNM 2673). In *Tornieria*, the sagittal nuchal crest of MNB 2387 (dd316) is low and broad as in ANS 21122 and similarly joins with short, transverse nuchal crests to form a low, tetrahedral eminence. In the other braincase referred to this taxon (MNB 2388 [dd130]), however, the same eminence has much more emphasis because the sagittal crest is thinner and protrudes farther caudally and the transverse crests are pronounced ridges.

In *Amargasaurus* and *Apatosaurus*, nuchal fossae deeply invade the skull roof in dorsal view. The situation in *Diplodocus* is equivocal: the fossae deeply invade the dorsal surface of the skull in some specimens (CM 3452 and 11844) but in others (CM 11161 and 26522), they are shallow as in ANS 21122. Similarly, in one specimen of *Dicraeosaurus* (MNB 2378 [dd495]), the nuchal fossae are shallow, but in another (MNB 2379 [dd307]), they are relatively deep and are invaded laterally by dorsoventrally elongate pits that are absent in *Suuwassea* and MNB 2378 (dd495). The rostral invasion reaches an extreme in *Tornieria* (MNB 2387 [dd316]), where they extend as far rostrally as the parietal foramen. In both MNB 2387 (dd316) and 2388 (dd130), the nuchal fossae also continue ventrolaterally onto the bases of the paroccipital processes, creating a raised rim along the dorsolateral margin of the foramen magnum.

The supraoccipitals in *Amargasaurus* and *Dicraeosaurus* are fused seamlessly with their respective exoccipital-opisthotic complexes, disguising their true morphologies. The supraoccipital of *Apatosaurus* (CM 11162) does not narrow sharply into an elongate ventral process as in *Suuwassea*; thus, the element makes a relatively large contribution to the dorsal margin of the foramen magnum (Berman and McIntosh, 1978). The transverse nuchal crests are expressed as two knobs at the lateral ends of this process rather than as distinct ridges, again in contrast to the condition in *Suuwassea*. In *Diplodocus*, sutures are apparent only in CM 26522 (Berman and McIntosh, 1978:fig. 3B) where they demonstrate that, like *Apatosaurus*, the bone has broad exposure on the dorsal margin of the foramen magnum, with sutures trending laterally from that contact.

As with the supraoccipital, the precise morphology of the exoccipital-opisthotic complex has been obfuscated by fusion in most flagellicaudatans, except on the neck of the occipital condyle. *Amargasaurus* lacks posttemporal processes, and its paroccipital processes are far more robust than in *Suuwassea*, greatly reducing the posttemporal fenestrae. Posttemporal processes are present in *Apatosaurus*, but they abut the exoccipital processes of the parietal along their entire length, endowing the small posttemporal fenestra with a rounded, rather than forked, medial margin, unlike the condition in *Suuwassea*. The paroccipital processes of *Apatosaurus* are similar to those of *Suuwassea*; they angle somewhat caudally in CM 11162, but this may be a diagenetic artifact. Sutures on the occipital condylar neck are not discernible in CM 11162, but in YPM 1860 (Berman and McIntosh, 1978:figs. 11A, C), there appears to be a thin, median exposure of the basioccipital; this is also true in *Dicraeosaurus* and *Diplodocus*. *Dicraeosaurus* completely lacks posttemporal processes; its paroccipital processes sweep sharply caudally in both specimens, but they are intact only in MNB 2379 (dd307). Diagenetic distortion has affected the morphology of the latter, but the caudal surfaces of the paroccipital processes appear concave caudally, in contrast to *Suuwassea*, though the resultant fossae are not contiguous with the nuchal fossae as they are in *Tornieria*. The paroccipital processes themselves are much shorter mediolaterally and taller dorsoventrally in *Dicraeosaurus* than in *Suuwassea*. The distal ends of the processes in the former are greatly elongate, forming pendant, pointed ventral processes and shorter, more rounded dorsal ones.

As in *Suuwassea*, the medial ends of the rostral faces of the paroccipital processes contact the antotic crests, but rather than forming the site of its origin, the crest continues uninterrupted as the lateral margins of thin laminae that ascend to contact the parietal. Diagenetic distortion has pressed together the squamosal processes of the parietal and the paroccipital processes of *Diplodocus* skulls USNM 2672 and 2673 and angled them caudolaterally, obliterating the posttemporal fenestra. In CM 3452 and 26522, the processes are in similar positions, and of similar morphology, to those of *Suuwassea*; those of CM 11161 and 11844 twist so that the caudal-most surfaces face caudomedially.

A small posttemporal process bifurcates the medial margin of the posttemporal fenestra of *Diplodocus* (Berman and McIntosh, 1978), though it is shorter mediolaterally and taller dorsoventrally than in ANS 21122. The paroccipital processes in '*Diplodocus*' *hayi* are deeply invaded by fossae lateral to the occipital condyle, unlike the condition in *Suuwassea* or any other flagellicaudatan. The posttemporal processes in '*D.*' *hayi* and *Tornieria* (MNB 2388 [dd130]) also bifurcate the posttemporal fenestra. This may also be true for the holotype of *Tornieria* (MNB 2386 [K1]), but if so, the posttemporal processes are shorter and much more massive. The paroccipital processes, intact only in MNB 2388 (dd130), are similar to those of ANS 21122 except for their involvement in the nuchal fossae and their lack of rostral concavity. The distinctive crest that connects the ventral margin of the processes to the basal tubercles in *Suuwassea* is absent in *Tornieria*. The dorsal expansion at the distal end is more pointed and abrupt in *Tornieria* than in *Suuwassea*.

The basal tubercula of *Amargasaurus* are separated from the occipital condyle by a narrow, acute notch. The distances between the occipital condyle and the basal tubercula in *Diplodocus* and *Tornieria* are much greater than in *Suuwassea*, and their angles more obtuse. The occipital condyles in both specimens of *Dicraeosaurus* possess capitular foveae, and the subcondylar space between the condyle and basal tubercles is comparatively wider than in *Suuwassea*. In *Tornieria*, two parasagittal foveae are present in MNB 2386 (K1) but none are present on the two referred braincases.

The basal tubercula of *Amargasaurus* resemble those of *Suuwassea* by being low, rugose, and closely appressed, but they are not separated by a narrow groove, and the basisphenoid depression dorsal to the tubercula is much larger than in *Suuwassea* (Salgado and Calvo, 1992). Characteristic for dicraeosaurids but absent in *Suuwassea*, a deep sulcus on the ventral surface of the basisphenoid connects to a deep pit between the basipterygoid processes in both *Amargasaurus* and *Dicraeosaurus*. The entire basisphenoid pillar assembly in *Dicraeosaurus* is much more elongate and sweeps more rostrally than that of *Suuwassea*. The large, globular basal tubercula of *Apatosaurus* are widely separated and lack the small dorsal fossa seen in *Suuwassea*. However, the ventral surface of the basisphenoid rostral to the tubercula is only shallowly concave, as in *Suuwassea*. The tubercles of *Dicraeosaurus* are similar to those of *Suuwassea* for the same reasons as in *Amargasaurus*. In one *Dicraeosaurus* specimen (MNB 2379 [dd307]), the tubercles are, as in *Suuwassea*, separated by a notch, but unlike the latter, the notch continues uninterrupted as a sulcus to the pit between the basipterygoid processes. In another specimen (MNB 2378 [dd495]), there is a fovea between the dorsal margins of the tubercles, but ventral to that, the tubercles are connected by a short but thick lamina of bone. Ventrally, they are again separated and morphologically similar to 2379 (dd307). The basal tubercula in *Diplodocus* skulls (except CM 3452) are, as in *Suuwassea*, closely appressed, but differ by being rostrocaudally flattened and projecting ventrally, rather than caudoventrally. CM 3452 contrasts with other skulls of *Diplodocus* because its basal tubercula are widely separated mediolaterally, and separated caudally only by a barely discernible fossa. In other specimens, the tubercula are separated caudally by a shallow, parabolic notch (a deep fovea in USNM 2673). The caudal surfaces of the basal tubercula also bear pronounced fossae, as in *Suuwassea*. Ventrally, the basisphenoid of *Diplodocus* becomes so concave that it cannot be seen caudally, even through the notch between the basal tubercula, in contrast with the more pillar-like configuration in *Suuwassea*. The markedly pendant tubercula of '*D.*' *hayi* are not divided caudally as they are in *Suuwassea*. '*Diplodocus*' *hayi* bears a small foramen between the basipterygoid processes. In none of the three specimens referred to *Tornieria* are the tubercles separated caudodorsally by a vertical sulcus; in contrast, they are connected by a

transverse crest of bone. The tubercles themselves are cranio-caudally flat rather than rugose, hemispheroidal knobs as in ANS 21122. Ventrally, the tubercles in MNB 2387 (dd316) and 2388 (dd130) are separated by a deep, narrow, pit-like fossa, and they project directly from the bases of the basipterygoid processes—in other words, there is no space between them in lateral view, a *Dicraeosaurus*-like character. MNB 2386 (K1) differs in that its basal tubercles are virtually nonexistent and there is a much larger, pit-like fossa separating them from the roots of the basipterygoid processes. Though they are about the same size, the basisphenoid pillars of MNB 2387 (dd316) and MNB 2388 (dd130) are shorter dorsoventrally than in ANS 21122.

Amargasaurus possesses a very short and ventrally displaced parasphenoid rostrum compared to that of *Suuwassea.* The parasphenoid rostrum in *Dicraeosaurus* is similarly dorsoventrally short. In some braincases of *Diplodocus* (CM 11161 and 26522), *Dicraeosaurus* (MNB 2379 [dd307]), and *Tornieria* (MNB 2388 [dd130]), the dorsal end of the base of the parasphenoid rostrum is marked by a small but fairly deep fossa immediately ventral to the optic foramina. This fossa is absent in *Suuwassea*. Presuming the broken surface on the midline of the braincase of ANS 21122 to be an indication of the depth of the parasphenoid rostrum, it was substantially taller than the 'spike'-like process in *Diplodocus*.

Amargasaurus, *Dicraeosaurus*, and '*Diplodocus*' *hayi* retain separate, paired optic foramina. In these taxa, *Diplodocus* (USNM 2672 and 2673), and *Tornieria* (except MNB 2386 [K1]), the olfactory foramen is canted rostrodorsally to face the overlying frontals; in *Dicraeosaurus* (MNB 2379 [dd307]), the angle is almost 90° to the plane of the optic foramina, indicating extreme caudal retraction of the bony nares. This is in stark contrast to *Suuwassea*, in which the olfactory foramen lies virtually in the same plane as the optic foramina—comparatively, its nares appear to have been far less retracted (Fig. 7). The pattern of the remaining cranial nerve openings in *Dicraeosaurus* (as exemplified by MNB 2379 [dd307]) is identical to that of *Suuwassea*, though the trigeminal foramen is separated from the oculomotor foramen by thin, topographically high crest, unlike *Suuwassea*. The other cranial nerve openings are similar across the remaining flagellicaudatan taxa.

Breakage in ANS 21122 occurs proximal to the position of the diagnostic 'leaf'-like processes on the antotic crest of dicraeosaurids, but because the antotic crest in *Suuwassea* greatly decreases in prominence rostral to the basal tubercles, it may be predicted that such 'leaf'-like processes were absent. Distinct, separate antotic processes are lacking in *Amargasaurus*, but it does possess the peculiar, flat extensions of the antotic crest. *Dicraeosaurus* possesses distinct antotic processes, but instead of the rostrocaudally flattened, laterally projecting structures in *Suuwassea*, they are mediolaterally flattened, rounded protrusions that either directly abut the postorbital process of the frontal (as on the right side of MNB 2379 [dd307]) or are separated from it only by a narrow gap (as on the left side). Antotic processes are present in *Diplodocus*, but they contact the frontals along their entire dorsal margins, separated only by a narrow, non-perforating sulcus. The antotic crests in *Diplodocus* (CM 26522) flare laterally into short, rostrocaudally flat processes, much smaller than the 'leaf'-like processes of *Dicraeosaurus* but larger than the virtually absent processes in *Suuwassea*. The crests in CM 11161 also lack such distinctive processes, but the crests themselves are more laterally extensive than in other specimens. '*D.*' *hayi* also lacks distinct antotic processes but has large, flat lateral extensions from the antotic crest ventral to the trigeminal foramina (Holland, 1906:fig. 8, labeled as part of the alisphenoid) that are similar in morphology to the 'leaf'-like processes of dicraeosaurids. *Tornieria* (MNB 2387 [dd130] and MNB 2387 [dd316], but not MNB 2386 [K1]) also possesses small, rostrocaudally flattened, laterally rounded projections from the antotic crest (figured but not highlighted by Janensch, 1935–1936:figs.
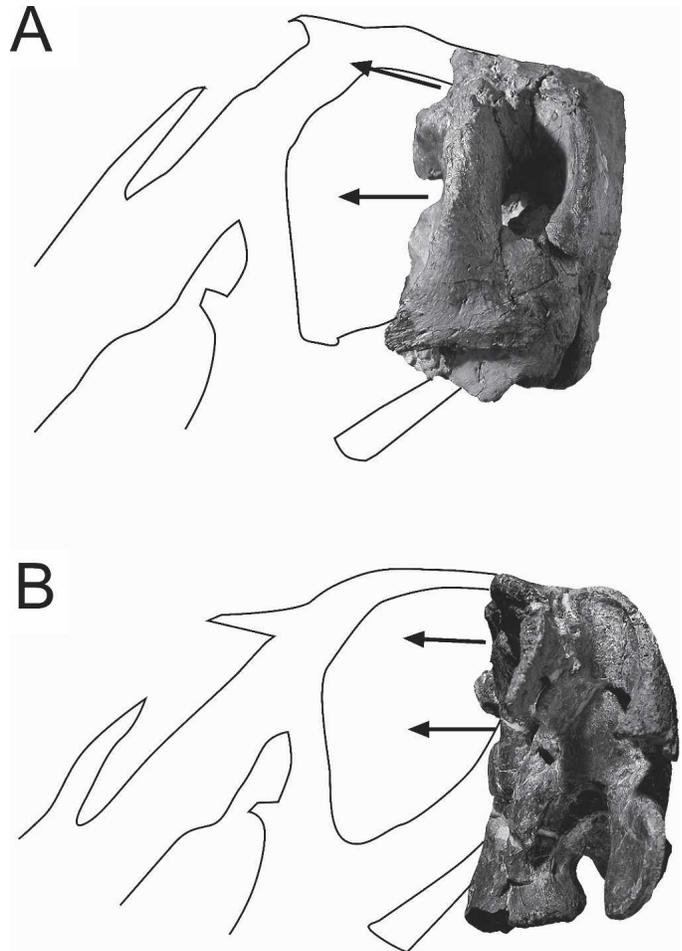
FIGURE 7. Left lateral views and reconstructions of the skulls of **A**, *Diplodocus* (CM 26522); and **B**, *Suuwassea* showing relative orientations of olfactory and optic nerve foramina (arrows). Note the roughly parallel orientation in *Suuwassea* indicates a lesser degree of narial retraction than in *Diplodocus*.

70–72). MNB 2388 (dd130) possesses antotic processes ventral to the laterosphenoid-frontal contact, though they are shorter and more blunt than in *Suuwassea*.

The squamosals of *Amargasaurus* (Salgado and Calvo, 1992:figs. 1B and 3) and *Dicraeosaurus* (Janensch, 1935–1936:figs. 103–104) are much broader, more plate-like bones than those of *Suuwassea*; the quadratojugal process of the squamosal of *Amargasaurus* extends much further rostrally than in the Montana sauropod. The squamosal of *Apatosaurus* appears very similar to that of *Suuwassea*, but much of it is hidden by the postorbital and paroccipital processes. The caudodorsal end of the squamosal in *Diplodocus* (e.g., CM 11844) is virtually identical to that of ANS 21122, but its quadratojugal process is more elongate, forming a long, slender process that overlaps much of the quadratojugal. Janensch (1935–1936:figs. 79–80) illustrated a bone he considered a left prefrontal of *Tornieria*, but this is almost certainly a left squamosal. It differs from that of *Suuwassea* in that the fossa on the medial side of its parietal process is more abbreviated, failing to extend rostroventrally onto the quadratojugal process. It is more elongate than that of *Suuwassea*, but not nearly as much as that of *Diplodocus*. At the rostroventral end of the fossa, the element in *Tornieria* emits a short, hooked accessory process rostrally where no such process exists in *Suuwassea*. The fossa on the quadratojugal process for

the quadratojugal sits more ventrally than it does in the Montana taxon, such that it is invisible in rostromedial view.

The slender quadrate of *Diplodocus* is virtually identical to that of *Suuwassea* except in CM 11161, where the medial portion of the mandibular head is more convex. The quadrate of *Apatosaurus* (Berman and McIntosh, 1978:fig. 10) is identical to that of *Suuwassea* in all respects.

Among other Morrison Formation sauropod skulls, an isolated braincase (USNM 5384) was assigned to '*Morosaurus*' *agilis* by Marsh (1889) and later referred to *Haplocanthosaurus* by Gilmore (1907). Numerous features distinguish this specimen from *Suuwassea*, including: frontoparietal suture not linear (parietals with short rostral processes at skull midline); postparietal foramen absent; and posttemporal fenestra small and not medially bifid. The supraoccipital is broader than in *Suuwassea*. Gilmore (1907) reported that the paroccipital processes in USNM 5384 angle caudally, but this may be the result of distortion. The skull shares at least one feature with *Suuwassea*, however: the lack of exposure of the basioccipital on the dorsal side of the occipital condyle.

CONCLUSION

The skull of *Suuwassea* shares with *Apatosaurus* a short quadratojugal process of the squamosal, coplanar foramen magnum and nuchal surface of the skull, and virtually identical squamosal and quadrate, but it shares with *Diplodocus* a bifid medial margin of the posttemporal fenestra and exclusion of the basioccipital from the dorsal surface of the occipital condyle. *Apatosaurus* does not appear to possess a parietal foramen, though this feature has variable expression in the larger sample of skulls of *Diplodocus*. *Apatosaurus*, *Diplodocus*, and *Tornieria* (i.e., diplodocid) skulls share several features not seen in *Suuwassea*, including sinuous parietal-exoccipital sutures, ventrally projecting basal tubercula, and a rostrodorsally angled olfactory foramen. However, a cladistic analysis incorporating these features is premature until (a) the axial skeleton of *Tornieria* is better described, and (b) the intrarelationships of specimens referred to *Apatosaurus* and *Diplodocus* are established.

The premaxilla of *Suuwassea emilieae* is unique among the known Flagellicaudata in lacking any angulation between the axis of the nasal process and the direction of tooth eruption. The squamosal is virtually identical to that of *Apatosaurus*, and the quadrate is not distinct from that of other Morrison Formation flagellicaudatans. The most prominent, distinctive feature of the cranium is the postparietal foramen, unknown in any other Morrison Formation sauropod. In other respects, however, the skull demonstrates a mosaic of features. Possession of a postparietal foramen, the sharp, sagittal nuchal crest and prominent tetrahedral process of the supraoccipital, and the visibility of the basisphenoid between the basal tubercula are reminiscent of the Dicraeosauridae (and, except for the last, the diplodocine *Tornieria*), but in most other ways, the skull is much more similar to that of diplodocids. Given that Harris and Dodson (2004) recovered *Suuwassea* outside both the Diplodocidae and Dicraeosauridae but still within the Flagellicaudata, the most parsimonious interpretation is that possession of a postparietal foramen is plesiomorphic for the Flagellicaudata (and possibly the Diplodocoidea), and retained in dicraeosaurids but lost in diplodocids.

ACKNOWLEDGMENTS

LITERATURE CITED

Alexander, R. M 1989. Dynamics of Dinosaurs & Other Extinct Giants. Columbia Press, New York, 167 pp.

Ayers, J. 2000. The Howe Ranch Dinosaurs. Sauriermuseum Aathal im Zürcher Oberland, Aathal, 95 pp.

Bakker, R. T. 1986. The Dinosaur Heresies. William Morrow and Company, Inc., New York, 481 pp.

Bakker, R. T. 1998. Channeling the thunder in the thunder lizards: cranial/cervical adaptations for infra-sound control in apatosaurine dinosaurs. Journal of Vertebrate Paleontology 18(3, supplement):25A.

Baumel, J. J., and L. M. Witmer. 1993. Osteologia; pp. 45–132 in J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge (eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium, Second Edition. Publications of the Nuttall Ornithological Club 23. Nuttall Ornithological Club, Cambridge.

Berman, D. S, and J. S. McIntosh. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). Bulletin of the Carnegie Museum of Natural History 8:5–35.

Calvo, J. O., and L. Salgado. 1995. *Rebbachisaurus tessonei* sp. nov. A new Sauropoda from the Albian–Cenomanian of Argentina; new evidence of the origin of the Diplodocidae. Gaia 11:13–33.

Chatterjee, S., and Z. Zheng. 2002. Cranial anatomy of *Shunosaurus*, a basal sauropod dinosaur from the Middle Jurassic of China. Zoological Journal of the Linnean Society 136:145–169.

Cong, L. 1998. The Gross Anatomy of *Alligator sinensis* Fauvel. China Forestry Publishing House, Beijing, 388 pp. [Chinese 1–319; English 321–388]

Curry, K. A. 1994. Juvenile sauropods of the Morrison Formation of Montana. Journal of Vertebrate Paleontology 14(3, supplement): 22A.

de Beer, G. R. 1947. How animals hold their heads. Proceedings of the Linnean Society of London 159:125–139.

Edinger, T. 1955. The size of parietal foramen and organ in reptiles. A rectification. Bulletin of the Museum of Comparative Zoology 114: 3–34.

Fiorillo, A. R. 1998. Dental microwear patterns of the sauropod dinosaurs *Camarasaurus* and *Diplodocus*: evidence for resource partitioning in the Late Jurassic of North America. Historical Biology 13:1–16.

Foster, J. R. 1996. Fossil vertebrate localities in the Morrison Formation (Upper Jurassic) of western South Dakota; pp. 255–263 in M. Morales (ed.), The Continental Jurassic. Museum of Northern Arizona, Flagstaff. Museum of Northern Arizona Bulletin 60.

Foster, J. R. 2001. Relative abundances of the Sauropoda (Dinosauria,

Saurischia) of the Morrison Formation and implications for Late Jurassic paleoecology of North America; pp. 47–60 in R. D. McCord and D. Boaz (eds.), Western Association of Vertebrate Paleontologists and Southwest Paleontological Symposium—Proceedings 2001. Mesa Southwest Museum Bulletin 8.

Foster, J. R. 2003. Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain region, U.S.A. New Mexico Museum of Natural History and Science Bulletin 23:1–95.

Galton, P. M. 1985. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. II. All the cranial material and details of soft part anatomy. Geologica et Palaeontologica 19:119–159.

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.

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.

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

Hay, O. P. 1908. Dr. W. J. Holland on the skull of *Diplodocus*. Science, n.s. 28:517–519.

Holland, W. J. 1906. The osteology of *Diplodocus* Marsh, with special reference to the restoration of the skeleton of *Diplodocus carnegiei* Hatcher. Memoirs of the Carnegie Museum 2:225–264.

Holland, W. J. 1924. The skull of *Diplodocus*. Memoirs of the Carnegie Museum 9:379–403.

Hopson, J. A. 1979. Paleoneurology; pp. 39–146 in C. Gans (ed.), Biology of the Reptilia Volume 9: Neurology A. Academic Press, London.

Janensch, W. 1935–1936. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguru-schichten Deutsch-Ostafrikas. Palaeontographica 2:145–298.

Jarvik, E. 1980. Basic Structure and Evolution of Vertebrates, Volume 2. Academic Press, London, 337 pp.

Kardong, K. V. 1995. Vertebrates: Comparative Anatomy, Function, Evolution. Wm. C. Brown Publishers, Dubuque, Iowa, 777 pp.

Marsh, O. C. 1884. Principal characters of American Jurassic dinosaurs. Part VII. On the Diplodocidae, a new family of the Sauropoda. American Journal of Science (Third Series) 27:161–168.

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

Marsh, O. C. 1896. The dinosaurs of North America. Papers Accompanying the Annual Report of the U.S. Geological Survey 1895–1895: 135–244.

McIntosh, J. S. 1981. Annotated catalogue of the dinosaurs (Reptilia, Archosauria) in the collections of Carnegie Museum of Natural History. Bulletin of the Carnegie Museum of Natural History 18:1–67.

McIntosh, J. S. 1990. Sauropoda; pp. 345–401 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, First Edition. University of California Press, Berkeley, California.

McIntosh, J. S., and D. S Berman. 1975. Description of the palate and lower jaw of the sauropod dinosaur *Diplodocus* (Reptilia: Saurischia) with remarks on the nature of the skull of *Apatosaurus*. Journal of Paleontology 49:187–199.

McIntosh, J. S., and K. Carpenter. 1998. The holotype of *Diplodocus longus*, with comments on other specimens of the genus; pp. 85–110 in K. Carpenter, D. J. Chure, and J. I. Kirkland (eds.), The Upper Jurassic Morrison Formation: An Interdisciplinary Study. Modern Geology 23.

Mook, C. C. 1917. The fore and hind limbs of *Diplodocus*. Bulletin of the American Museum of Natural History 37:815–819.

Myers, T. 2003. Catastrophic mass mortality of a herd of young diplodocid sauropods from the Morrison Formation of Montana. Journal of Vertebrate Paleontology 23(3, supplement):81A.

Myers, T. M. 2004. Evidence for age segregation in a herd of diplodocid sauropods. Journal of Vertebrate Paleontology 24(3, supplement): 97A.

Myhrvold, N. P., and P. J. Currie. 1997. Supersonic sauropods? Tail dynamics in the diplodocids. Paleobiology 23:393–403.

Northcutt, R. G. 1979. The comparative anatomy of the nervous system and the sense organs; pp. 615–770 in M. H. Wake (ed.), Hyman's Comparative Vertebrate Anatomy, Third Edition. University of Chicago Press, Chicago, Illinois.

Nowinski, A. 1971. *Nemegtosaurus mongoliensis* n. gen., n. sp. (Sauropoda) from the uppermost Cretaceous of Mongolia. Palaeontologia Polonica 25:57–81.

Pompeckj, J. F. 1920. Das angebliche Vorkommen und Wandern des Parietalforamens bei Dinosauriern. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 3:109–129.

Quay, W. B. 1979. The parietal eye-pineal complex; pp. 245–406 in R. G. Northcutt and P. Ulsinki (eds.), Biology of the Reptilia Volume 9: Neurology A. Academic Press, London.

Roth, J. J., and E. C. Roth. 1980. The parietal-pineal complex among paleovertebrates: evidence for temperature regulation; pp. 189–231 in R. D. K. Thomas and E. C. Olson (eds.), A Cold-blooded Look at the Warm-blooded Dinosaurs. AAAM Selected Symposium. Westview Press, Boulder, Colorado.

Salgado, L., and J. O. Calvo. 1992. Cranial osteology of *Amargasaurus cazaui* Salgado & Bonaparte (Sauropoda, Dicraeosauridae) from the Neocomian of Patagonia. Ameghiniana 29:337–346.

Salgado, L., and J. O. Calvo. 1997. Evolution of titanosaurid sauropods. II: the cranial evidence. Ameghiniana 34:33–48.

Salgado, L., A. Garrido, S. E. Cocca, and J. R. Cocca. 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada del León (Lohan Cura Formation), Neuquén Province, northwestern Patagonia, Argentina. Journal of Vertebrate Paleontology 24:903–912.

Sereno, P. C., A. L. Beck, D. B. Dutheil, H. C. E. Larsson, G. H. Lyon, B. Moussa, R. W. Sadleir, C. A. Sidor, D. J. Varricchio, G. P. Wilson, and J. A. Wilson. 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. Science 286:1342–1347.

Siber, H. J. K. 1997. The Bighorn Mountain Dinosaur Project. Sauriermuseum Aathal Bulletin 9:1–28.

Stevens, K. A., and J. M. Parrish. 1999. Neck posture and feeding habits of two Jurassic sauropod dinosaurs. Science 284:798–800.

Stevens, K. A., and J. M. Parrish. 2000. Neck posture of sauropod dinosaurs. Science 287:547b–548b.

Storrs, G. W., and W. J. Garcia. 2001. Preliminary analysis of a monospecific sauropod locality from Carbon County, Montana. Journal of Vertebrate Paleontology 21(3, supplement):105A.

Turner, C. E., and F. Peterson. 1999. Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior, U.S.A.; pp. 77–114 in D. D. Gillette (ed.), Vertebrate Paleontology in Utah. Utah Geological Survey Miscellaneous Publication 99–1.

Upchurch, P. 1994. Sauropod phylogeny and palaeoecology; pp. 249–260 in M. G. Lockley, V. F. Dos Santos, C. A. Meyer, and A. Hunt (eds.), Aspects of Sauropod Paleobiology. Gaia 10.

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

Upchurch, P. 2000. Neck posture of sauropod dinosaurs. Science 287: 547b.

Upchurch, P., and P. M Barrett. 2000. The evolution of sauropod feeding mechanisms; pp. 79–122 in H.-D. Sues (ed.), Evolution of Herbivory in Terrestrial Vertebrates. Cambridge University Press, Cambridge.

Upchurch, P., P. M. Barrett, and P. Dodson. 2004. Sauropoda; pp. 259–322 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, Second Edition. University of California Press, Berkeley, California.

Vanden Berge, J. C., and G. A. Zweers. 1993. Myologia; pp. 189–250 in J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge (eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium, Second Edition. Publications of the Nuttall Ornithological Club 23. Nuttall Ornithological Club, Cambridge.

Wilborn, B. 2002. Vertebrate bonebeds from the Morrison Formation, Bighorn Basin, Wyoming: a revised stratigraphic analysis. Journal of Vertebrate Paleontology 22(3, supplement):119A.

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

Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memoir 5:1–68.

Wilson, J. A., and M. B. Smith. 1996. New remains of *Amphicoelias* Cope (Dinosauria: Sauropoda) from the Upper Jurassic of Montana and diplodocoid phylogeny. Journal of Vertebrate Paleontology 16(3, supplement):73A.