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SHORT COMMUNICATION

THE DENTARY OF *SUUWASSEA EMILIEAE* (SAUROPODA: DIPLODOCOIDEA)

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Sauropod cranial elements, despite their rarity, contain a significant proportion of the known phylogenetically important character data (see Wilson, 2002; Upchurch et al., 2004). In particular, cranial characters are important in distinguishing between the two main neosauropod lineages, Diplodocoidea and Macronaria, as well as between the various lineages of diplodocoid sauropods. One recently described diplodocoid, *Suuwassea emilieae*, has proven difficult to place phylogenetically despite a relative wealth of cranial data (Harris, 2006a). As a putatively basal member of the Late Jurassic radiation of diplodocoids, *Suuwassea* is an important taxon for the understanding of diplodocoid sauropod evolution. Although it has been variously recovered as a member of either the primarily Laurasian diplodocids or the Gondwanan dicraeosaurids, the precise relationship between those lineages and *Suuwassea* has remained uncertain.

Here we describe a recently discovered dentary assignable to the holotypic specimen of *Suuwassea emilieae* (Academy of Natural Sciences 21122). This dentary possesses important character data that suggest dicraeosaurid affinities for *Suuwassea*; as a consequence, *Suuwassea* is potentially the only recognized Laurasian member of Dicraeosauridae. The description of this dentary also adds to our scarce knowledge of sauropod dentaries.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York City, U.S.A.; **ANS**, Academy of Natural Sciences, Philadelphia, U.S.A.; **CM**, Carnegie Museum of Natural History, Pittsburgh, U.S.A.; **CMC**, Cincinnati Museum Center, Cincinnati, U.S.A.; **MB**, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; **MNN**, Musée National du Niger, Niamey, Niger; **MOR**, Museum of the Rockies, Bozeman, U.S.A.; **USNM**, United States National Museum, Washington, D.C., U.S.A.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878
DIPLODOCOIDEA Marsh, 1884
FLAGELLICAUDATA Harris and Dodson, 2004
SUUWASSEA EMILIEAE Harris and Dodson, 2004

Association of the Material

The two fragments comprising the dentary were recovered from the main *Suuwassea* locality (Rattlesnake Ridge Quarry No. 1), disassociated from each other (Fig. 1): the dentigerous portion was recovered near cervical vertebra 5, whereas the edentulous posterior section was surface collected near cervical 3. This material was originally collected with the rest of ANS 21122 but only recently prepared and identified. ANS 21122 was the only individual recovered from this quarry; given the close association with the rest of the skeleton and the similarity in size between the dentary and the recovered premaxilla and maxilla, we assign this element to ANS 21122 with confidence. No additional mandibular elements (e.g., the splenial) were recovered.

Description

Dentary—The left dentary is nearly complete, lacking only the surangular process, the dorsal margin posterior to the dentigerous portion, and part of the ventromedial 'chin.' The dentary contacted its counterpart anteriorly at the symphysis, and would have contacted the splenial and coronoid medially, and the surangular and angular posterolaterally. The anterior one-third is dentigerous. The dentary itself is small, only 177 mm in length and a maximum of 40 mm tall, making it proportionally similar in size to the preserved elements of the upper jaw (Harris, 2006b). Based on proportions displayed by other diplodocoids, the dentary probably comprised approximately one-half of the total mandibular length. The element, as preserved, is slender, similar to those of *Apatosaurus* (CMC VP 7180), *Diplodocus* (AMNH 969; CM 3452, 11161, 11255; USNM 2672, 2673), and *Nigersaurus* (MNN GAD512), but unlike the robust dentary of *Dicraeosaurus* (MB R.2372).

In external and internal views, the posterior two-thirds of the ventral margin of the dentary is nearly linear; this changes only anteriorly, where the element deepens significantly to form the ventrally projecting 'chin' characteristic of diplodocoid sauropods (Wilson, 2002). The ventral margin of this 'chin' is broken, but enough remains to be confident of the presence of a significant expansion in this region. The Meckelian canal, visible on the internal surface of the dentary (Fig. 2A), is very tall posteriorly, reaching the ventral margin and surpassing the dorsal margin of the angular process. The canal narrows sharply and arches dorsally near mid-length of the dentary before descending ventrally on the anterior half of the element. The narrowing of the canal coincides with the posterior portion of the tooth row: as the teeth become sequentially larger anteriorly, the canal narrows to allow room for the alveoli. This canal does not continue onto the ventral surface of the dentary, as occurs in *Nigersaurus* (MNN GAD512). The ventral margin of the canal is eroded anterior to a large break (Fig. 2A), artificially inflating the apparent exposure of the canal in internal view. Nine replacement foramina lie near the preserved dorsal margin of the dentary, beneath the alveolar margin.

The dentary symphysis is nearly complete, missing only the ventral-most portion. The preserved portion is subtriangular, with a significantly broader dorsal portion and a narrower ventral tail that extends down to and beyond the broken margin of the bone (Fig. 2A). The long axis of the symphysis is inclined anterodorsally approximately 40° from perpendicular to the long axis of the dentary.

Several large, irregularly placed foramina adorn the external surface of the dentary below the tooth row (Fig. 2B). Similar vascular foramina are also present on the premaxilla and maxilla (Harris, 2006b), and on the dentaries of *Dicraeosaurus* (MB R.2372) and *Tornieria* (MB R.2347, R.2348; but see Remes, 2006, 2009). A 'lateral plate' (sensu Upchurch, 1995), which borders the labial surfaces of the teeth in eusauropods, is not preserved,

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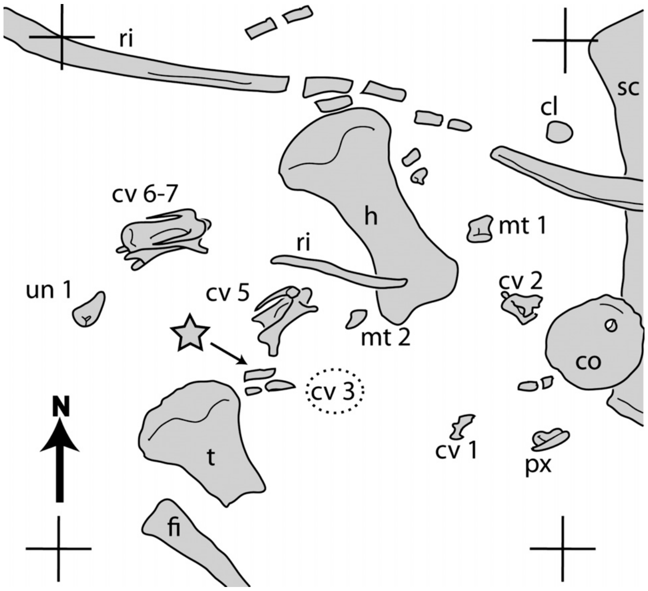

FIGURE 1. Detail of quarry map showing location of dentary (starred) relative to the rest of ANS 21122. Grid marks 1 m square. Modified from Harris (2006c). **Abbreviations**: **cl**, calcaneum; **co**, coracoid; **cv**, cervical vertebrae; **fi**, fibula; **h**, humerus; **mt**, metatarsals; **px**, premaxilla; **ri**, ribs; **sc**, scapula; **t**, tibia; **un**, unguals.

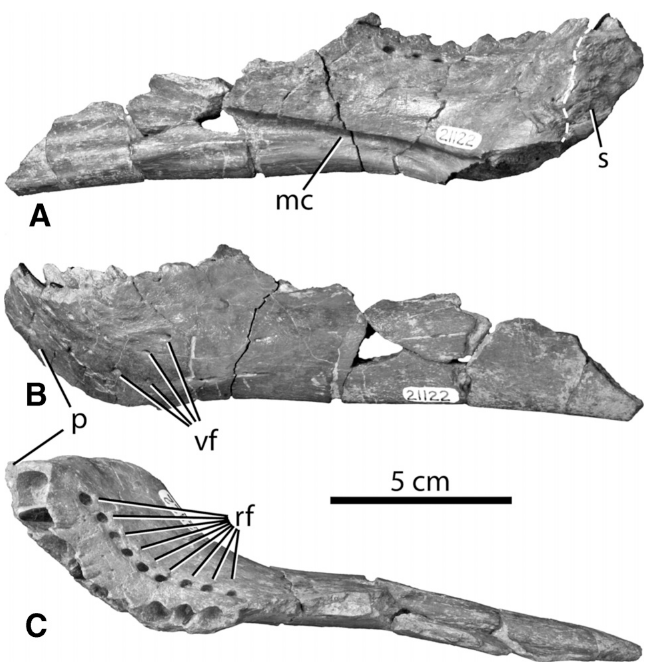

FIGURE 2. Dentary of *Suuwassea emilieae* (ANS 21122). **A**, medial view. **B**, lateral view. **C**, dorsal view. **Abbreviations**: **mc**, Meckelian canal; **p**, anterior prominence; **rf**, replacement foramina; **s**, symphysis; **vf**, vascular foramina. Scale bar equals 5 cm.

although a broken edge indicates its probable position. Posterior to the tooth row, the dorsal margin becomes mediolaterally compressed above a longitudinally directed, mid-height bulge on the external surface. As a result, the dentary has a D-shaped cross-section in this region.

In dorsal view, the dentary arches gently toward the symphysis, although the tooth row bows outward near the anterolateral corner of the dentary and does not follow the ventral margin of the element (Figs. 2C, 3B). In comparison, the dentaries of adult *Diplodocus* (AMNH 969; CM 11161; USNM 2672, 2673), *Apatosaurus* (CMC VP 7180), and *Nigersaurus* (MNN GAD512) are more typically square. The dentary of *Dicraeosaurus* (MB R.2372) is also superficially more square than *Suuwassea*, but this is largely a result of a similar outward bowing of the tooth row at the anterolateral corner (Fig. 3C). The shape of the dentary of *Suuwassea* is somewhat similar to that of juvenile *Diplodocus* (CM 11255; Whitlock et al., 2010) as well as similarly sized dentaries from *Tornieria* (MB R.2347) and two indeterminate diplodocoids (MOR 592; USNM 5473), although in each of those specimens the tooth row closely matches the curvature of the dentary.

The dentary bears nine alveoli. The last alveolus occurs at a position just over one-third of the total dentary length from the symphysis (Fig. 2C). The posterior margin of the last preserved alveolus is much thicker than any of the septae separating the preceding alveoli, indicating that there were no subsequent alveoli. Posterior to this point, the preserved, edentulous dorsal margin of the dentary constricts severely to form a thin lamina. This lamina continues the medial curvature of the posterior tooth row until it reaches the internal margin of the dentary, at which point it smoothly curves back laterally to follow the lateral ramus of the element. This curvature gives the dorsal margin a gentle, sigmoid appearance in dorsal view, similar to that seen in *Dicraeosaurus* (MB R.2372), *Diplodocus carnegii* (CM 11161), and, superficially, *Nigersaurus* (MNN GAD512), but not in other diplodocoid taxa.

A conspicuous, dorsoventrally oriented prominence protrudes anteriorly from the external surface of the dentary, coincident with the first alveolus (Fig. 3A). The medial margin of this prominence contributes to the symphyseal articular surface. A similar prominence, accompanied by a labial displacement of the first alveolus, is seen in *Dicraeosaurus* (MB R.2372), but not in *Diplodocus* (AMNH 969; CM 3452, 11161, 11255; USNM 2672, 2673), *Apatosaurus* (CMC VP 7180), or *Nigersaurus* (MNN GAD512). When in articulation with the opposing dentary, this prominence would have formed half of a large midline process. The function of this process is uncertain, and there are no similar prominences on the preserved premaxillae of either *Suuwassea* or *Dicraeosaurus*.

Dentition—No functional teeth are preserved, but replacement teeth are visible in the second, fourth, sixth, and eighth alveoli, as well as in cross-section through a break just posterior to the last alveolus. As discussed above, there were nine teeth in each dentary, four fewer than are seen in *Dicraeosaurus* and five fewer than in some adult *Diplodocus* individuals (Holland, 1924), but similar to the count seen in juvenile *Diplodocus* (Whitlock et al., 2010). Upper (5.0–5.5 mm) and lower (4.4–4.8 mm) crowns were similar in size, based on comparison with teeth exposed in the maxilla and premaxilla. Crowns are elliptical in cross-section, with low, blunt carinae developed on the mesial and distal margins.

The replacement tooth visible in cross-section indicates that replacement teeth formed very deep in the bone—in this case, almost on top of the margin of the Meckelian canal—and in *Suuwassea*, as in other small or young sauropods (Whitlock et al., 2010), replacement teeth in posterior alveoli were often strongly anteriorly inclined. The ‘every other alveolus’ pattern of visible replacement teeth suggests that replacement occurred in waves, or zahnreihen, as in crocodylians (Edmund, 1962).

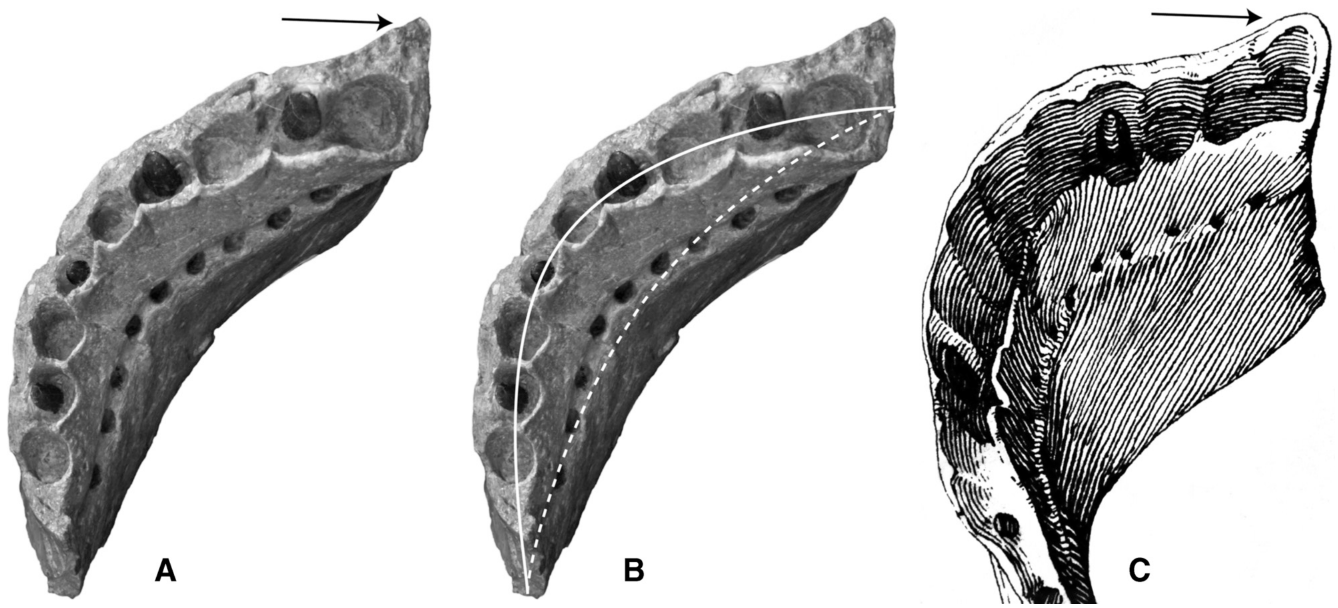

FIGURE 3. Anterior prominence at the dentary symphysis (arrow), shown in dorsal view. **A**, dentary of *Suuwassea* ANS 21122. **B**, dentary of *Suuwassea,* showing bowed-out curvature of tooth row (solid line) compared to curvature of dentary (dashed line). **C**, dentary of *Dicraeosaurus* MB R.2372. Modified from Janensch (1935–36:fig. 113). Figures not to scale.

DISCUSSION

The phylogenetic position of *Suuwassea* is ambiguous. Although consistently recovered as a member of Flagellicaudata (the clade containing the most recent common ancestor of *Diplodocus* and *Dicraeosaurus* and all of its descendants), the position of *Suuwassea* within that clade is less well resolved. Of the eight phylogenetic analyses that have included *Suuwassea* to date, three recover it in a polytomy with Dicraeosauridae and Diplodocidae (Harris and Dodson, 2004; Harris, 2006a; Sereno et al., 2007), three as a basal diplodocid (Gallina and Apesteguía, 2005; Rauhut et al., 2005; Remes, 2006), one in a diplodocid subclade along with *Apatosaurus* and *Supersaurus* (Lovelace et al., 2008), and one as a basal dicraeosaurid (Salgado et al., 2006). Of the five analyses fully resolving the position of *Suuwassea*, none recovered *Suuwassea* at a node with a decay index exceeding ‘1’.

The lack of a consensus placement may be the result of the plesiomorphic nature of *Suuwassea* (Harris, 2006a), as well as the restrictions of the matrices that have been used to examine it. *Suuwassea* appears to lack a number of the synapomorphies that have been used to identify derived members of Dicraeosauridae and Diplodocidae. Furthermore, because the matrices that have been used make primary use of character data that pre-date the discovery of *Suuwassea* (e.g., the matrix of Wilson, 2002), there is little new character data that might pull *Suuwassea* toward one branch or the other. In other words, if *Suuwassea* is to be resolved with regard to other flagellicaudatans, new character data must be added to the known set. Given the weak character support for hypotheses of both diplodocid and dicraeosaurid affinities, the identification of even a few additional synapomorphies with either group would do much to resolve the position of *Suuwassea*.

The addition of a dentary to the known material of *Suuwassea* adds a significant amount of phylogenetic information, because the bone can be directly compared to material from representatives of all three lineages of diplodocoid sauropods: Dicraeosauridae (*Dicraeosaurus*), Diplodocidae (*Apatosaurus*, *Diplodocus*, *Tornieria*), and Rebbachisauridae (*Nigersaurus*). The addition of this single element to the holotype of *Suuwassea* enables the scoring of six additional characters in the matrix of Harris (2006a; Table 1). Unfortunately, these characters do not differentiate members of Dicraeosauridae and Diplodocidae. Three new, potentially phylogenetically informative characters, described below, can be recognized in the dentary of *Suuwassea*, however. Although a full phylogenetic analysis is outside the scope of a short communication, recommended scorings for these characters are summarized in Table 2. Adding these characters to the matrix of Harris (2006a) recovers *Suuwassea* as a basal dicraeosaurid in the most parsimonious trees, two steps shorter than the shortest trees resolving *Suuwassea* as a basal diplodocid. A new phylogenetic analysis of Diplodocoidea, incorporating these characters and others, has been submitted for review elsewhere (Whitlock, in press).

(1) Dentary symphysis, shape in medial view: subovate (0); subtriangular (1). The transverse dentary rami of diplodocids such as *Apatosaurus* (CMC VP 7180), *Diplodocus* (CM 3452, 11161, 11255; USNM 2672), and *Tornieria* (MB R.2347, R.2348) are typically labiolingually thin and roughly of equivalent thickness along their margins. As a result, the symphyses of these taxa are roughly ovoid in shape. The highly derived rebbachisaurid *Nigersaurus* (MNN GAD512) has a subcircular symphysis. *Dicraeosaurus* (MB R.2372) in contrast, has a subtriangular symphysis with a labiolingually expanded dorsal portion and a tapering ventral portion. Although the symphysis in *Suuwassea* is incomplete ventrally

TABLE 1. Recommended additional scorings for *Suuwassea emilieae* for the matrix of Harris (2006a), based on the material described here.

	79	80	81	86	90	91	92
Suuwassea	1	1	0	0	1	1	1

Numbers reflect original numbering of characters from Harris (2006a).

TABLE 2. Recommended scorings for the three novel characters presented in this article.

	1	2	3
Apatosaurus	0	0	0
Dicraeosaurus	1	1	1
Diplodocus	0	0	0
Nigersaurus	0	0	1
Suuwassea	1	1	1
Tornieria	0	0	0

Character numbers correspond to numbers designated in the text.

as a result of the damaged 'chin,' the dorsal portion is clearly expanded both on the internal and external margins. Ventrally, those margins taper, narrowing the symphysis.

(2) External surface of dentary at symphysis: smooth, without anteriorly directed prominence (0); with large prominence on midline (1). The external margins of the dentaries of *Apatosaurus*, *Diplodocus*, *Nigersaurus*, and *Tornieria*, when viewed in occlusal orientation, are roughly curvilinear. In *Suuwassea* and *Dicraeosaurus*, a dorsoventrally oriented prominence appears on the external surface of the dentary at the symphysis. In *Dicraeosaurus*, this prominence is additionally accompanied by a slight anterior displacement of the first alveolus; *Suuwassea* does not share this condition. This prominence contributes to the derived state in character 1, and the two states overlap in distribution. It is possible to distinguish them, however: the dorsal expansion of the symphysis is not exclusively on the external margin, and the narrowed ventral tail extends beyond the ventral limits of the anterior prominence.

(3) Shape of tooth row in occlusal view: follows curvature of dentary (0); anterolateral corner of tooth row displaced labially (1). In *Apatosaurus, Diplodocus*, and *Tornieria* (MB R.2347), the tooth row closely matches the curvature of the dentary. In *Suuwassea* and *Dicraeosaurus*, the tooth row does not strictly follow the curvature of the ventral margin of the dentary, but instead bows outward toward the lateral margin. *Nigersaurus* also shares the derived state because its tooth row does not follow the curvature of the dentary, but in this taxon, the tooth row is instead sublinear, extending laterally well beyond the anterolateral corner (MNN GAD512; Sereno et al., 1999).

Each of these three characters appears to unite *Suuwassea* with *Dicraeosaurus* to the exclusion of other diplodocoids. When taken together with previously recognized potential synapomorphies uniting *Suuwassea* with Dicraeosauridae—frontal-parietal suture located between supratemporal fenestrae, presence of a post-parietal foramen, tall cervical neural spines, etc. (Harris, 2006a)—the placement of *Suuwassea* as a basal dicraeosaurid, first recovered by Salgado et al. (2006), seems to be the better-supported hypothesis. If true, *Suuwassea* would be the first dicraeosaurid recognized from Laurasia. This re-organization may have drastic implications for the inferred paleobiogeographic distributions of sauropod dinosaurs in the Late Jurassic, potentially favoring a Laurasian origin of the group over the Gondwanan origin proposed previously (Remes, 2006).

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