THE SIGNIFICANCE OF SUUWASSEA EMILIEAE (Dinosauria: Sauropoda) FOR FLAGELLICAUDATAN INTRARELATIONSHIPS AND EVOLUTION

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SYNOPSIS Suuwassea emilieae is a recently described dinosaur taxon discovered in the Upper Jurassic Morrison Formation of the western United States and the only non-diplodocid flagellicaudatan (Dinosauria: Sauropoda) known from North America. It retains sauropod symplesiomorphies that are unexpected in a Late Jurassic taxon and thus sheds light on the evolutionary origins of the Flagellicaudata. Despite being comparatively small, the holotype of Suuwassea demonstrates hallmarks of relatively advanced age. A phylogenetic analysis of 30 taxa and 331 characters retains Suuwassea in a trichotomy with the Diplodocidae (Apatosaurus + (Diplodocus + Barosaurus)) and the Dicraeosauridae (Dicraeosaurus + Amargasaurus). This lack of resolution is probably due to a combination of missing data, character conflict and poor incorporation of specimens referred to diplodocid taxa that differ from their holotype specimens and species holotypes. Middle Jurassic palaeobiogeographical reconstructions conflict with the hypothetical distribution of flagellicaudatans in the Middle and Late Jurassic based on their phylogeny, implying that physical barriers, such as epeiric seas, were not responsible for limiting their initial radiation. The postparietal foramen shared by Suuwassea, Dicraeosaurus, Tornieria and Amargasaurus may correlate to preferred existence in near-shore, terrestrial environments.

KEY WORDS Sauropoda, palaeobiogeography, phylogeny, vertebrate palaeontology, Saurischia

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INTRODUCTION

Although by no means required (Kearney & Clark 2003; Norell & Wheeler 2003; Wiens 2003; Wilkinson 2003), complete and abundant specimens (representing the fullest possible data sets) of any taxon are still ideal for establishing and testing morphology-based phylogenetic hypotheses. For a variety of reasons, many sauropod taxa remain known from incomplete and often unique skeletons. Few localities worldwide can conform to the ideal by producing abundant, intact individuals. For most of the time that sauropods have been studied, the Upper Jurassic Morrison Formation of the western United States has remained virtually unequalled in this respect and its sauropod fauna has thus been a keystone of sauropod research. The Morrison Formation has produced multiple, often spectacular specimens of Apatosaurus, Camarasaurus and Diplodocus, all of which have played critical roles in sauropod phylogenetic and palaeoecological
In 1999–2000, a joint team from the University of Pennsylvania and the Academy of Natural Sciences (ANS) recovered a new diplodocoid from the Upper Jurassic Morrison Formation of south-central Montana. ANS 21122, discovered by Dr William Donawick (University of Pennsylvania) and Will Tillett of Lovell, Wyoming, was named *Suuwassea emilieae* by Harris & Dodson (2004: see Fig. 1). ANS 21122 clearly represents a diplodocoid as it displays numerous synapomorphies of that clade. The preliminary phylogenetic analysis presented by Harris & Dodson (2004) recovered a trichotomous Flagellicaudata (the clade consisting of the most recent common ancestor of *Diplodocus* and *Dicraeosaurus* and all its descendants), consisting of *Suuwassea*, the Diplodocidae (*Apatosaurus* + (*Diplodocus* + *Barosaurus*)) and the Dicraeosauridae (*Dicraeosaurus* + *Amargasaurus*). *Suuwassea* is of particular interest because although it is a diplodocoid from the Morrison Formation of North America, it possesses a mosaic of plesiomorphic sauropodan features and character states otherwise diagnostic of either the Gondwanan Dicraeosauridae or Morrison diplodocids. Furthermore, *Suuwassea* is important because it originated from exposures in Montana, farther north than most other described Morrison sauropods. This may demonstrate a palaeobiogeographical division in Morrison sauropod palaeoecology. As a diplodocoid that retains plesiomorphies not seen in *Apatosaurus* and *Diplodocus* (cf. Harris & Dodson 2004), *Suuwassea* sheds light on the origin and evolution of the Flagellicaudata. It is necessary to place *Suuwassea* in a proper historical, chronological and palaeobiogeographical framework to fully understand its importance.

**A history of Morrison Formation sauropods**

Sauropods were initially discovered in Middle and Upper Jurassic and Lower Cretaceous sediments of Europe and the Upper Cretaceous of India (*Titanosaurus* indicus; see review in Upchurch et al. 2004). However, even after over 150 years of collecting, all European and Cretaceous Indian sauropods remain described from only fragmentary skeletons or single elements and were enmeshed in something of a taxonomic morass until largely cleared by Upchurch & Martin (2002, 2003) and Wilson & Upchurch (2003). The first sauropod specimens recovered from the Morrison Formation (Table 1) also follow this pattern: many holotypes consist of fragmentary skeletons or single bones. Many of the holotypes were established in the famous ‘Bone Wars’ competition of the 19th century between Othniel C. Marsh and Edward D. Cope without the benefit of modern taphonomic understanding, so they often consist of elements from multiple taxa. Reconciling the consequent, convoluted specimen assignments has proven a difficult task (e.g. McIntosh & Carpenter 1998) and many taxa were not described more extensively until later in the early 20th century (Table 1). To this day, however, some Morrison discoveries from this era cannot be referred to existing genera, although they have not yet received restudy in a modern context (*Morosaurus* agilis (Marsh 1889; Gilmore 1907) and ‘*Apatosaurus* minimus’ (Mook 1917)).

A long hiatus followed, during which no new sauropod taxa were established from the Morrison Formation, although several significant advances were made, such as the recognition and description of the skull of *Apatosaurus* (Berman & McIntosh 1978). It was not until the description of specimens from the Dry Mesa Quarry in western Colorado...
Table 1  Chronological timeline of Morrison Formation sauropod discoveries and the status of each taxon.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Author and Year of Description</th>
<th>Status</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphicoelias</td>
<td>Cope 1877c, 1878</td>
<td>Uncertain</td>
<td>Often considered nomen dubium or synonymous with either Diplodocus or Supersaurus (McIntosh 1997b; Foster 2001); see also Osborn &amp; Mook (1921)</td>
</tr>
<tr>
<td>Apatosaurus</td>
<td>Marsh 1877, 1879a, b</td>
<td>Valid</td>
<td>Additional specimens described by Riggs (1903b); Gilmore (1936); see also Berman &amp; McIntosh (1978)</td>
</tr>
<tr>
<td>Camarasaurus</td>
<td>Cope 1877b</td>
<td>Valid</td>
<td>Additional specimens described by Osborn &amp; Mook (1921); Gilmore (1925)</td>
</tr>
<tr>
<td>Dystrophaeus</td>
<td>Cope 1877a</td>
<td>Nomen dubium</td>
<td>From the Tidwell Member of the Summerville Formation, not the Morrison Formation (Anderson &amp; Lucas 1992; Lucas &amp; Anderson 1997); see also Gillette (1996a, b) and McIntosh (1997a)</td>
</tr>
<tr>
<td>Diplodocus</td>
<td>Marsh 1878</td>
<td>Valid</td>
<td>Additional specimens described by Hatcher (1901); Holland (1906, 1924)</td>
</tr>
<tr>
<td>‘Morosaurus’ agilis</td>
<td>Marsh 1889</td>
<td>Uncertain</td>
<td>See also Gilmore (1907)</td>
</tr>
<tr>
<td>Barosaurus</td>
<td>Marsh 1890</td>
<td>Valid</td>
<td>See also Lul (1919)</td>
</tr>
<tr>
<td>Brachiosaurus</td>
<td>Riggs 1903a</td>
<td>Valid</td>
<td>See also Carpenter &amp; Tidwell (1998)</td>
</tr>
<tr>
<td>Haplocanthosaurus</td>
<td>Hatcher 1903a, b, 1906</td>
<td>Valid</td>
<td>Additional species named by McIntosh &amp; Williams (1988); see also Bilbey et al. (2000)</td>
</tr>
<tr>
<td>‘Apatosaurus’ minimus</td>
<td>Mook 1917</td>
<td>Uncertain</td>
<td>Type scapulocoracoid ref. to Brachiosaurus; type thoracic vertebra ref. to Supersaurus (Curtice et al. 1996; Curtice &amp; Wilhite 1996)</td>
</tr>
<tr>
<td>Ultrasaurus</td>
<td>Jensen 1985 emend. Olshesvky 1991</td>
<td>Nomen dubium</td>
<td>Type caudal vertebra ref. to Supersaurus (Curtice &amp; Stadtman 2001)</td>
</tr>
<tr>
<td>Dystylosaurus</td>
<td>Jensen 1985</td>
<td>Nomen dubium</td>
<td>Type caudal vertebra ref. to Supersaurus (Curtice &amp; Stadtman 2001)</td>
</tr>
<tr>
<td>Supersaurus</td>
<td>Jensen 1985</td>
<td>Provisionally valid</td>
<td>See also Curtice (1995) and Curtice &amp; Stadtman (2001)</td>
</tr>
<tr>
<td>Cathetosaurus</td>
<td>Jensen 1988</td>
<td>Nomen dubium</td>
<td>Synonymised with Camarasaurus but retained as C. lewisi McIntosh et al. 1996b)</td>
</tr>
<tr>
<td>Dyslocosaurus</td>
<td>McIntosh et al. 1992</td>
<td>Valid</td>
<td>Possibly from the Lance Formation (Upper Cretaceous), not Morrison Formation</td>
</tr>
<tr>
<td>Suuwassea</td>
<td>Harris &amp; Dodson 2004</td>
<td>Valid</td>
<td></td>
</tr>
</tbody>
</table>

Note: The 80-year hiatus between the discoveries of the valid taxa Haplocanthosaurus and Supersaurus as well as the predominant tendency of taxa named from 1985 onward to be later synonymised with previously named taxa.

(Miller et al. 1991) that new taxa were named (Table 1). Most recently, however, Suuwassea has been joined by several, as yet undescribed, specimens, particularly those from the northern reaches of the Morrison Formation depositional basin, which demonstrate some peculiarities when compared to well-known Morrison genera and may ultimately prove to represent additional, distinctive taxa (Wilson & Smith 1996; Erickson & Hanks 2001; H.-J. Kiry Siber, pers. comm. 2003; N. Murphy, pers. comm. 2003).

In point of fact, most of the recently-proposed Morrison sauropod genera have been met with a great deal of skepticism and their fate has generally been synonymy (Table 1). Therefore, proposition of a new Morrison Formation sauropod genus such as Suuwassea requires substantial support. Many of the distinguishing characteristics of Suuwassea are subtle, but certainly no more – and often much less – so than those that are universally accepted as separating Diplodocus and Barosaurus. The possibility that differences are ontogenetic is discussed below.

The current, genus-level, sauropod inventory of the Upper Jurassic Morrison Formation consists of Apatosaurus, Barosaurus, Brachiosaurus, Camarasaurus, Diplodocus, Haplocanthosaurus and Suuwassea. Supersaurus is less well-known but is provisionally valid (Curtice 1995; Curtice & Stadtman 2001) pending a full reanalysis. At a higher taxonomic level, the Morrison Formation sauropod fauna is dominated (in terms of number of individuals) by the basal macronarian (cf. Wilson 2002) Camarasaurus, but flagellicaudatan diplodocoids (Apatosaurus, Barosaurus, Diplodocus, Supersaurus, Suuwassea) are the most diverse (Foster 2003; Fig. 2). Brachiosaurus and Haplocanthosaurus remain comparatively rare and are restricted to the lower half of the formation (Carpenter 1998, Turner & Peterson 1999).

**Flagellicaudatan ontogeny**

Whether the unusual features exhibited by Suuwassea are the result of ontogenetic, rather than phylogenetic, differences (Brochu 1996) must be considered. Aside from the fact that it was not a hatchling or very young juvenile, the age of ANS 21122 at the time of death is equivocal. The anatomical terminology used herein follows Harris (2004) with...
The ends of preserved limb bones are well-formed. The deltoid ridge on the scapular acromion process is pronounced, which may be an adult feature in sauropods (Bonaparte 1986), although the scapula and coracoid are unfused. Conceivably, calcanei ossify with age in diplodocoids; if so, then ANS 21122 represents a fairly old individual because that element is large and robust (Harris & Dodson 2004; Harris 2005).

Some features present in ANS 21122 that could be perceived as ontogenetic variants are absent in other flagellicaudatans, regardless of size. These features include such structures as the dorsal tuberculum on the humerus and the enormous, elongate dorsal tori on the cranial cervical vertebral arches of the preserved thoracics (Harris & Dodson 2004, Harris 2006a, b) that, as muscle insertion points, are in an advanced state of development. These imply advanced age (Brochu 1996), again despite the small size of the specimen compared to other flagellicaudatans, particularly other Morrison Formation taxa, and the fact that significantly larger specimens of those taxa either lack these same features or have much less developed versions. Therefore, these characters in *Suuwassea* are more likely to be of genuine phylogenetic value than attributable to issues of maturity.

**DIPLODOCOID PALEOBIOGEOGRAPHY**

Until the discovery of basal taxa (the rebbachisaurids *Rebbachisaurus garasbae*, *Limaysaurus* [? = *Rebbachisaurus*] tessaoni and, possibly, *Losillasaurus*), members of the Diplodocoidea were perceived as phylogenetically split into two fundamental radiations: the Dicraeosauridae and the Diplodocidae (Figs 3 & 4). Even in the most comprehensive recent analyses that incorporate them, the Rebbachisauridae invariably fall out as the sister taxon to a flagellicaudatan (Diplodocidae + Dicraeosauridae) dichotomy. The Dicraeosauridae is limited to Africa and South America, but the diplodocid identity of *Tornieria africana* (K. Remes, pers. comm. 2003) demonstrates that members of the more diverse Diplodocidae were more widespread. Why dicraeosaurids apparently never moved into Laurasia while diplodocids did has not been examined (but see below).

**PHYLOGENETIC ANALYSIS**

**Methods and materials**

The analysis performed by Harris & Dodson (2004) recovered a position for *Suuwassea* in a trichotomy with the previously recognised clade Diplodocidae + Dicraeosauridae (i.e. the Flagellicaudata). To see if more recent sauropod phylogenetic analyses could resolve this trichotomy, a second cladistic analysis of apomorphic character distributions was performed to elucidate the most parsimonious placement of *Suuwassea* with respect to other sauropods, particularly diplodocids. The data matrix (see Supplementary Data available on Cambridge Journals Online on: http://www.journals.cup.org/abstract_S1477201906001805) combines the matrices and character lists (which can be thought of as incipient or tacit matrices) of Calvo & Salgado (1995), Salgado (1999), Wilson (2002), and Upchurch et al. (2004), which receive as prefixes for each character in...
Figure 3  Sauropod phylogeny (simplified from Harris & Dodson 2004) showing occurrences and ranges of non-titanosaurian taxa, emphasising diplodocoids. The ‘C’ indicates occurrence of British Museum (Natural History) specimen (BMNH) R.1967, a string of articulated, biconvex distal caudal vertebrae incorrectly referred to *Cetiosauriscus stewarti* (Heathcote 2003), possibly marking the earliest known occurrence of the Diplodocoidea.

this matrix C, S, W and U, respectively (see Supplementary Data: Appendices 1 and 2). Updates for some taxa outlined in Harris & Dodson (2004) were also included. Where possible, duplicate characters were joined into a single character; in some instances, when two characters were similar but not identical, one character was preferentially selected, generally where one state was much more clearly defined than the other. Some characters had to be revised entirely; details are provided in Supplementary Data: Appendix 2. The resultant matrix had 331 characters, six of which were ordered: characters 14, 89, 93 and 284 were ordered following Wilson (2002), while characters 6 and 324 were also ordered because they were combined from two sequential (i.e. tacitly ordered) sets of characters by Upchurch et al. (2004; see Supplementary Data: Appendix 2). The matrix was otherwise similar to that used by Harris & Dodson (2004), utilising the taxon set of Wilson (2002), adding only *Suuwassea* and *Losillasaurus*. As in Wilson (2002) and Upchurch et al. (2004), character polarity was assessed using the Theropoda and Prosauropoda as outgroups. *Losillasaurus*, originally recovered as a basal diplodocoid (Casanovas et al. 2001), was retained to see if the new, enlarged matrix used would also clarify its relationships. *Tornieria africana* was specifically left out of the analysis pending restudy (K. Remes, pers. comm. 2003), although if much of the material attributed to this taxon genuinely pertains to a single species, it is more complete than many other taxa that have been included in previous sauropod phylogenetic analyses. The titanosaurian *Neuquensaurus* was also omitted owing to the incomplete state of its description at the time of the analysis. The final matrix therefore included 30 operational taxonomic units (OTUs). Including, and in addition to, the character state revisions of *Mamenchisaurus* and *Omeisaurus* utilised by Harris & Dodson (2004), several other sources of information (see Supplementary Data: Appendix 1) provided additional data on character states for included taxa. *Suuwassea* was coded for 118 out of the 331 characters (roughly 36%).

**Results**

Analyses were performed in PAUP* 4b10 (Swofford 2002). The large number of taxa used precluded an exhaustive search, so following the guidelines used by Wilson (2002), an initial heuristic analysis was performed using random stepwise addition (with 50 replicates) with Maximum trees = 500000. This analysis produced 72 equally most parsimonious trees (MPTs) with length = 783, consistency index (CI) = 0.526 and retention index (RI) = 0.687. Among these, *Suuwassea* occurs in only one of two positions. In half the trees (36), *Suuwassea* falls as the sister taxon to the
Diplodocidae (Apatosaurus + (Diplodocus + Barosaurus)), united by the following synapomorphies (see Supplementary Data: Appendix 2 for character definitions): 50(1), 65(1), 168(1), 314(1) and 319(1). In the remaining 36 MPTs, Suuwassea occurs as the sister taxon to the Diplodocidae (Dicraeosaurus + Amargasaurus), united by synapomorphies 28(0), 33(1), 118(1)* and 194(1), where an asterisk (*) denotes a character for which states on the stem below the branch are equivocal. These results reduce by half the number of possible positions recovered by Harris & Dodson (2004) in which Suuwassea also occurred as either the sister taxon to Apatosaurus within the Diplodocidae or as the sister taxon to the Flagellicaudata (in this latter case, Suuwassea is not, by definition (Harris & Dodson, 2004), a flagellicauditan). In some trees, Losillasaurus continued to pair with Manchchisaurus (or as sister to an (Omeisaurus + Manchchisaurus) clade), but in others, it branched one step further up the tree than the Chinese taxon, often as a sister taxon to Patagosaurus with Barapasaurus out one further step.

Consensus trees were computed as follows: both strict and semistrict consensus trees are identical (Fig. 5A) and, predictably, recovered Suuwassea in a trichotomy with the Diplodocidae and Dicraeosauridae, the identical position recovered in the less expansive analysis of Harris & Dodson (2004). Losillasaurus remained a non-neosauropod. An Adams consensus (Fig. 5B) also recovered the flagellicaudatan trichotomy. This tree differs from the former largely in its fragmentation of the polytomies among the non-neosauropodan eusauropods and within the Titanosauria. Losillasaurus retained its prior non-neosauropodan position.

Despite the lack of demonstrable correlation between the information obtained concerning the phylogenetic affinities of a taxon and its degree of completeness in a given data matrix ( Kearney & Clark 2003; Wiens 2003; see below), an heuristic analysis that excludes the more poorly known (represented by a high percentage of missing data), non-flagellicaudatan taxa from the matrix (Haplocanthosaurus, Euhelopus, Jobaria, Malawisaurus, Nigerlisaurus, Rebbachisaurus, Alamosaurus, Losillasaurus) produced only two trees, with somewhat better statistics (length = 679, CI = 0.602, RI = 0.709). Interestingly, in both trees, Suuwassea remained within the Flagellicaudata but as the sister taxon to the Dicraeosauridae, united by synapomorphies 33(1), 104(0)*, 118(1)* and 194(1). When Haplocanthosaurus and Malawisaurus (a presumed basal neosauropod and basal titanosaurian, respectively) were reintroduced, this number increased to four trees (length = 710, CI = 0.577, RI = 0.700), three of which retained a Suuwassea + Dicraeosauridae clade (united by synapomorphies 28(0), 33(1), 104(0)*, 118(1)* and 194(1)) and one of which found a Suuwassea + Diplodocidae clade (united by synapomorphies 50(1), 101(1), 168(1), 314(1) and 319(1)). Strict, semistrict and Adams consensus trees of this analysis recovered, as before, a flagellicaudatan trichotomy, but a 50% majority-rule consensus retained the Suuwassea + Dicraeosauridae grouping.

Lastly, both exhaustive and heuristic analyses pruning all taxa except Suuwassea, the outgroups (Prosauropoda and Theropoda), diplodocids (Apatosaurus, Barosaurus, Diplodocus), dicraeosaurids (Amargasaurus, Dicraeosaurus) and the best known rebbachisaurid (Limaysaurus) produced a single tree (length = 323, CI = 0.904, RI = 0.884) in which Suuwassea was recovered as the sister taxon to the Diplodocidae. These abbreviated analyses demonstrate that some character states convergently evolved by many non-diplodocid and non-diplodocid taxa have powerful effects on resolution within the Diplodocoidea. This encourages both better descriptions of poorly known taxa as well as the search for more characters that may reduce these effects and clarify resolution within this clade.

A 50% majority bootstrap analysis was also performed on the full matrix (again with Maximum trees = 500 000 and 50 replicates) using the heuristic setting and random stepwise addition (following Wilson 2002). This recovered a single tree (Fig. 6) in which, as in the heuristic consensus trees, Suuwassea, the Diplodocidae and the Dicraeosauridae form three trichotomous branches of the Flagellicauda, a clade that has excellent support, higher than that recovered by Harris & Dodson (2004). Losillasaurus is retained as a non-neosauropod, close to Manchchisaurus. Haplocanthosaurus occurs as a non-diplodocid, basal neosauropod, contrasting with the position recovered in the non-pruned analysis of Wilson (2002). More exact (i.e. less plastic) positions of Haplocanthosaurus, Jobaria and Losillasaurus across trees may follow more complete descriptions of the latter two taxa and new specimens of Haplocanthosaurus (Bilbey et al. 2000; Southwell et al. 2003). The low tree statistics in the full analyses are probably due in large part to the inclusion of wildcard taxa that are either poorly described (e.g. Losillasaurus), poorly known (e.g. Vulcanodon, Nemegtosaurus), or poorly resolved (either non-neosauropodan eusauropod or titanosaurian). Again, redescriptions using new material of these taxa might increase confidence and resolution in the trees.
**Figure 5** Strict and semistrict (identical: A) and Adams (B) consensus trees of phylogenetic analysis of relationships of *Suuwassea emilieae* using the data matrix presented in the Supplementary Data. Note that, in both consensus trees, the Flagellicaudata consists of a trichotomy containing *Suuwassea*, the Diplodocidae (*Apatosaurus* + (*Diplodocus* + *Barosaurus*)) and the Dicraeosauridae (*Dicraeosaurus* + *Amargasaurus*). Node (arrows) and stem clade names from Wilson (2002) and Harris & Dodson (2004).

**DISCUSSION AND CONCLUSIONS**

**The flagellicaudatan trichotomy**

Despite an expanded data matrix, including a 41% increase in the number of characters over the analysis of Harris & Dodson (2004), the phylogeny of the Flagellicaudata was not clarified and the trichotomy remains. In part, this is probably due to the presence of equivocal states on the stems below the Flagellicaudata for characters 104(1) and 118(1) that otherwise support dicraeosaurid affinities. If these characters are later shown to be present in more primitive taxa, it would diminish support for a *Suuwassea* + Dicraeosauridae clade while strengthening support for a *Suuwassea* + Diplodocidae clade.
Figure 6  Phylogenetic analysis of relationships of *Suuwassea emilieae* produced by 50% majority rule analysis of the data matrix presented in the Supplementary Data. Note that the Flagellicaudata consists of a trichotomy containing *Suuwassea*, the Diplodocidae (*Apatosaurus* + (*Diplodocus* + *Barosaurus*)) and the Dicraeosauridae (*Dicraeosaurus* + *Amargasaurus*). Node (arrows) and stem clade names from Wilson (2002) and Harris & Dodson (2004). Numbers are bootstrap values (percentages) for each stem.

In addition, three other factors probably contribute to this lack of resolution:

1. **Specimen incompleteness.** Although the data matrix was expanded, the only additional element recognised and described for *Suuwassea* after Harris & Dodson (2004) was a squamosal (Harris, 2005). No new specimens have been recognised that could replace missing with actual data, so expanding the data matrix did not add many additional diagnosable character states. In short, *Suuwassea* retained virtually as much missing data as it had previously: it was codable for 34% of the characters in Harris & Dodson (2004) versus 36% here. Along with character conflict, this is probably the factor contributing most to the lack of resolution and the resultant ‘soft’ polytomy (sensu Maddison 1989).

2. **Character set incompleteness.** Compounding the incompleteness of the specimen, the characters added to the matrix are not applicable to ANS 21122. This does not mean that these characters were poor or should not have been added; only that further characters whose states may be determined in ANS 21122 have not yet been identified (Wiens 2003). Many characters that might clarify flagellicaudatan intrarelationships await fuller description of *Tornieria africana* and analysis of specimens referred to *Apatosaurus*, *Diplodocus* and *Barosaurus*. This could result in the removal of some characters that have variable expression within an OTU, or it could identify previously unrecognised taxa that can be coded separately, thus allowing finer resolution.

3. **Common ancestor fecundity.** Parsimony-based cladistic analyses preferentially seek out evolutionary events that produce dichotomous results (i.e. only two branches at any node). It remains possible, however, that any ancestral (meta)taxon may give rise to multiple descendant taxa (multiple speciation, which produces a ‘hard’ polytomy, sensu Maddison (1989)), even with the fullest possible data set, this is represented by a trichotomy (or polytomy for particularly fruitful ancestral (meta) taxa). Hypothetically, *Suuwassea* and other flagellicaudatans truly share a common ancestor that is not more closely related to either *Suuwassea*, the Diplodocidae, or the Dicraeosauridae than any other. The Flagellicaudata would be an ambitaxon *sensu* Archibald (1994). With presently available data, this hypothesis is essentially untestable as far as *Suuwassea* and the Flagellicaudata are concerned, but it must be considered as a possible, albeit remote, contributing factor.

*Suuwassea* as a distinct taxon

The 36% of character states coded for *Suuwassea* in this analysis is greater than or equal to some other included taxa (e.g. *Barosaurus* with 117/331 = 35%, *Vulcanodon* with 99/331 = 29%, *Nemegtosaurus* with 91/331 = 27%) that are unquestionably valid. Nevertheless, there is no currently accepted threshold of missing data (as a percentile) at which taxa should be pruned from an analysis to ‘enhance’ resolution (Kearney & Clark 2003). The models explored by Wiens (2003) indicate that the lack of identified characters, not the lack of character state data for a given taxon in a matrix, is a bigger factor.

Furthermore, while *Suuwassea* behaved as a wildcard taxon in the heuristic analyses, it alternated between only
Significance of *Suuwassea emilieae* for Flagellicaudatans

Flagellicaudatan Palaeobiogeography

The oldest flagellicaudatan remains are from the Middle Jurassic (see above), at which time Pangaea was still in the early stages of fragmentation (e.g. Smith et al. 1994). The proximity of most continental land masses at this time may have enabled the earliest flagellicaudatan and their immediate ancestors to disseminate widely during the Middle Jurassic. Their apparent absence in Asia, as reflected by the prolific Middle Jurassic Dashanpu and Late Jurassic Shaximiao and related sauropod localities in China (He et al. 1988; Zhang 1988; Ouyang 1989; Dong 1990, 1997; Zhao 1993; Zhang et al. 1998; Maisch et al. 2001, 2003) and Kirgystan (Alifanov & Averianov 2003), may also date to this period, since Asia was separated from Europe (and all other continents) by an epeiric sea (Russell 1993; Upchurch 1995; Upchurch et al. 2002). This marine barrier was not in place in the Bajocian (Smith et al. 1994), implying either a true absence, taphonomic bias, or the presence of other physical and/or ecological barriers that restricted the earliest flagellicaudatan geographically. However, epicontinental seaways similar to that between Europe and Asia in the Bajocian are reconstructed as separating Europe from North America and Gondwana since the Early Triassic (Smith et al. 1994). It is then possible that the earliest flagellicaudatan were truly restricted to Europe. If they were more widespread in the Middle Jurassic, then the seaway separating Europe and Asia at the same time should not have proven an impassable physical barrier to flagellicaudatan dispersal.

The paucity of Middle Jurassic vertebrate fossils globally makes it impossible to assess any of these options: such faunas are well represented only in Patagonia, China, western Europe (Heathcote 2003; Upchurch & Martin 2003) and Morocco (Monbaron 1983; Monbaron et al. 1999). Despite the recent recognition of probable ichnological differences between wide-gauge, ‘titanosauriform’ and narrow-gauge, non-‘titanosauriform’ taxa (Wilson & Carrano 1999), which broadens the dataset with which to perform such a test, even the trackway record of Middle Jurassic sauropods is sparse, with specimens stemming largely from the same land-masses as the body fossil record, i.e. Europe (Santos et al. 1994; Whyte & Romano 1994; Avanzini 1997; Day et al. 2002, 2004) and northwestern Africa (Ishigaki 1988, 1989;
Meyer & Monbaron 2002). Narrow-gauge (*Parabrontopodus* sensu Lockley et al. (1994)) trackways dominate in the Jurassic (Wilson & Carrano 1999) and, although these trackways include ichnotaxa that possess neosauropodan morphology, it is presently impossible to specify whether their makers were flagelllicaudatans or non-flagelllicaudatan neosauropods.

By the Callovian, North America was physically separated from Gondwana and Europe was isolated by epeiric seas (Smith et al. 1994). The presence of diplodocines in the Late Jurassic of both Laurasia (Morrison Formation, Portugal, Germany) and Gondwana (Tendaguru, presuming *Tornieria* to be diplodocine) thus implies that the Diplodocidae must have been present on both land masses prior to this time. Since the Dicraeosauridae is the sister taxon to the Diplodocidae, the first dicraeosaurids must also predate this split. This means that there is no *a priori* reason to presume that dicraeosaurids did not exist in Laurasia and that the lack of any definitive dicraeosaurid fossils in any of the Late Jurassic, flagelllicaudatan-producing, Laurasian formations reflects either a pseudo-absence or a regional extinction *sensu* Upchurch et al. (2002). Vicariance, therefore, cannot explain the observed restriction of dicraeosaurids to Gondwana. The presence of *Suuwassea*, a non-diplodocid, non-dicraeosaurid flagelllicaudatan, in the Morrison Formation alongside true diplodocids supports the hypothesis that dicraeosaurids could also have inhabited North America. Similarly, the lack of diplodocid fossils in Gondwana after the Late Jurassic also reflects either a pseudo-absence or a regional extinction. Both hypotheses remain based on negative evidence.

One feature of *Suuwassea* is particularly interesting in a palaeobiogeographical and palaeocological light: the postparietal foramen. *Suuwassea* has been hypothesised as belonging to a somewhat different Morrison Formation fauna (or faunal province) than the ‘typical’ fauna known from more southern parts of the depositional basin (Harris & Dodson 2004), perhaps reflecting a palaeoenvironmental preference, possibly for a palaeoecosystem closer to the sea. Of the three other taxa that possess a postparietal foramen, two – *Dicraeosaurus* and *Tornieria*, both from Tendaguru – are also found in near-shore terrestrial deposits. The palaeoenvironment of the La Amarga Formation in which the remaining taxon, *Amargasaurus*, was preserved, has been interpreted as wholly terrestrial (Leanza & Hugo 2001), although others have interpreted its setting also as being in close proximity the sea (Malumian et al. 1983; Montanelli 1987; Andreis 2001; but see discussion in Prámparo & Volkheimer 2002). Even though its function remains unknown, the concurrence of a postparietal foramen in sauropods in near-shore palaeoenvironments is unexpected and may be correlative. If true, the best place to seek other basal flagelllicaudatans and dicraeosaurids in the Morrison Formation would be in the northern part of the depositional basin, closer to the sea.

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**References**


Supplementary data is available on Cambridge Journals Online on: http://www.journals.cambridge.org/abstract_S1477201906001805.