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
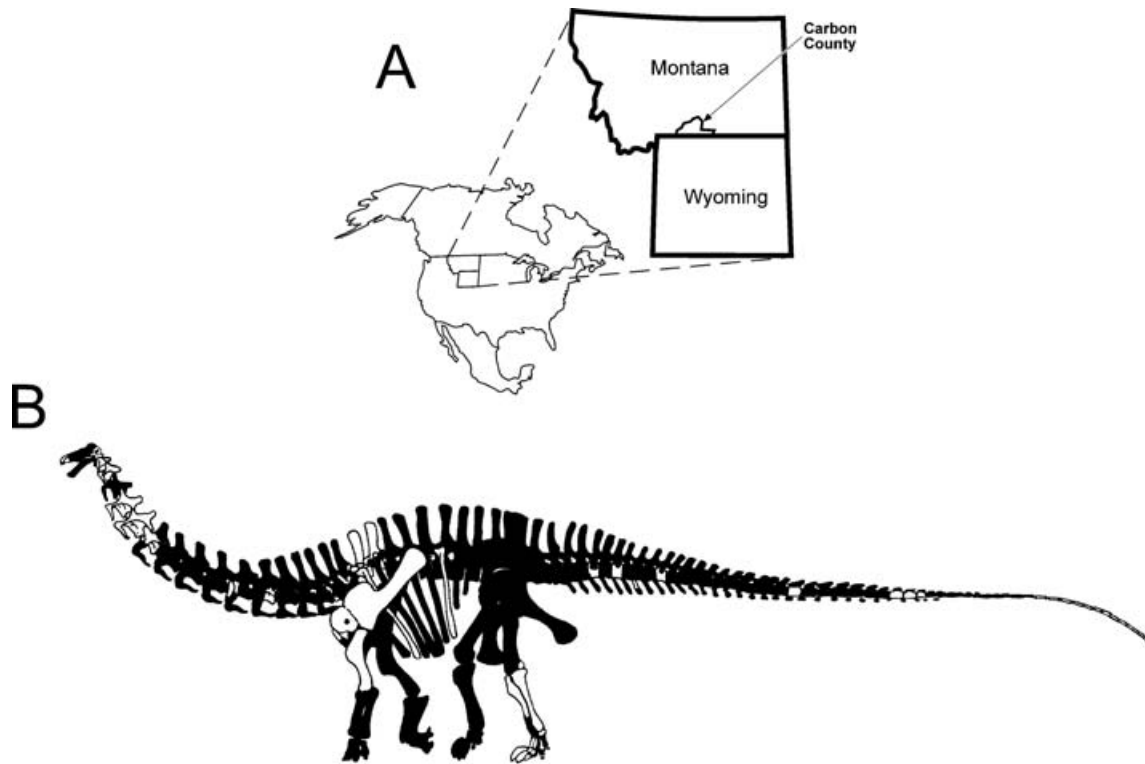
Figure 1 **A**, Locality information for ANS 21122. More specific information has not been provided to prevent unlawful exploitation of site. **B**, Reconstruction of *Suuwassea emilieae* Harris & Dodson, 2004, with preserved elements indicated in white (drawing by Jason Poole).

research. The highly distinctive and derived morphologies of *Apatosaurus* and *Diplodocus* in particular stand out among sauropods and their origins have remained unclear.

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.

Taxon	Author and Year of Description	Status	Notes
Amphicoelias	Cope 1877*c*, 1878	Uncertain	Often considered *nomen dubium* or synonymous with either *Diplodocus* or *Supersaurus* (McIntosh 1997*b*; Foster 2001); see also Osborn & Mook (1921)
Apatosaurus	Marsh 1877, 1879*a, b*	Valid	Additional specimens described by Riggs (1903*b*); Gilmore (1936); see also Berman & McIntosh (1978)
Camarasaurus	Cope 1877*b*	Valid	Additional specimens described by Osborn & Mook (1921); Gilmore (1925)
Dystrophaeus	Cope 1877*a*	*Nomen dubium*	From the Tidwell Member of the Summerville Formation, not the Morrison Formation (Anderson & Lucas 1992; Lucas & Anderson 1997); see also Gillette (1996*a, b*) and McIntosh (1997*a*)
Diplodocus	Marsh 1878	Valid	Additional specimens described by Hatcher (1901); Holland (1906, 1924)
'*Morosaurus*' *agilis*	Marsh 1889	Uncertain	See also Gilmore (1907)
Barosaurus	Marsh 1890	Valid	See also Lull (1919)
Brachiosaurus	Riggs 1903*a*	Valid	See also Carpenter & Tidwell (1998)
Haplocanthosaurus	Hatcher 1903*a, b*, 1906	Valid	Additional species named by McIntosh & Williams (1988); see also Bilbey *et al.* (2000)
'*Apatosaurus*' *minimus*	Mook 1917	Uncertain	
Ultrasauros	Jensen 1985 emend. Olshevsky 1991	*Nomen dubium*	Type scapulocoracoid ref. to *Brachiosaurus*; type thoracic vertebra ref. to *Supersaurus* (Curtice *et al.* 1996; Curtice & Wilhite 1996)
Dystylosaurus	Jensen 1985	*Nomen dubium*	Type caudal vertebra ref. to *Supersaurus* (Curtice & Stadtman 2001)
Supersaurus	Jensen 1985	Provisionally valid	See also Curtice (1995) and Curtice & Stadtman (2001)
Cathetosaurus	Jensen 1988	*Nomen dubium*	Synonymised with *Camarasaurus* but retained as *C. lewisi* McIntosh *et al.* 1996*b*)
Seismosaurus	Gillette 1991	*Nomen dubium*	Synonymised with *Diplodocus*; possibly distinct species (Lucas 2000; Lucas *et al.* 2004)
Dyslocosaurus	McIntosh *et al.* 1992	Valid	Possibly from the Lance Formation (Upper Cretaceous), not Morrison Formation
Eobrontosaurus	Filla & Redman 1994, Bakker 1998	*Nomen dubium*	Synonymised with *Camarasaurus* (Upchurch *et al.* 2004)
Suuwassea	Harris & Dodson 2004	Valid	

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. Kirby 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
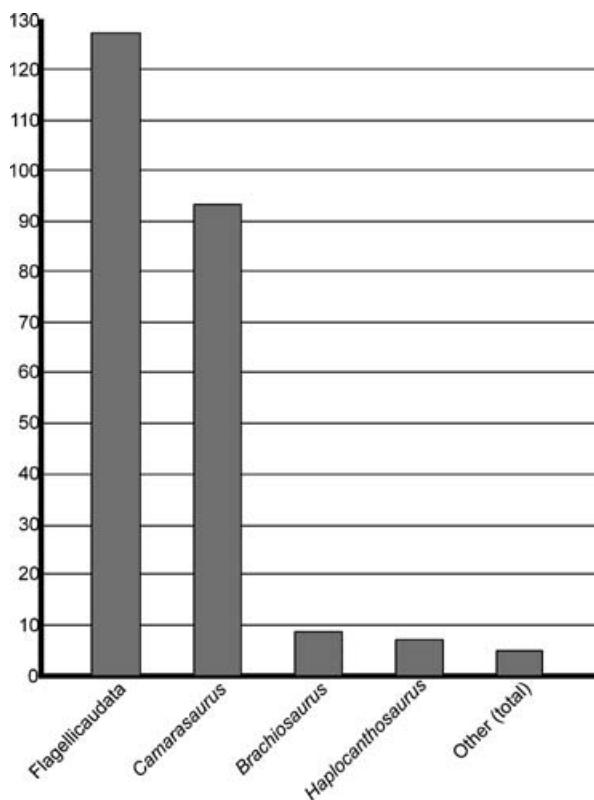
Figure 2 Abundances of sauropod taxa in the Morrison Formation based on number of sites producing material identifiable to genus (modified and simplified from Foster 2003). The Flagellicaudata consists of *Apatosaurus*, *Barosaurus*, *Diplodocus*, *Supersaurus* and *Suuwassea*, and is largest because it contains multiple taxa; individually, each taxon is less common. *Camarasaurus* is the single most common sauropod genus. The category 'Other' sums occurrences of very rare or unique sauropod specimens (*Amphicoelias*, '*Apatosaurus*' *minimus*, *Dyslocosaurus* and '*Morosaurus*' *agilis*.)

emendations of vertebral laminae from Harris (2006*b*) Some basicranial sutures are obliterated by fusion, but others are visible; some elements (e.g. the supraoccipital) demonstrate both conditions on opposite sides (Harris 2005). The dens is fused to the axis, although the suture line is visible (Harris 2006*b*). All cervical vertebral arches are seamlessly coalesced with their respective bodies. In crocodylians, both of these features indicate a high maturity index (Brochu 1996). In contrast, the cervical vertebral arches are completely separate from their respective bodies in a juvenile specimen referred to *Apatosaurus* (Carnegie Museum 555/556) despite the fact that these elements are roughly the same size as in ANS 21122. In *Suuwassea*, arches of the preserved thoracics are fused, although suture lines remain discernible. Those of the proximal and middle caudal vertebrae were unfused (Harris 2006*b*: fig. 13A), but they were apparently fused on the more distal caudals (Harris 2006*b*: figs 13E–I). This contrasts with the caudal-to-cranial pattern of fusion during ontogeny seen in crocodylians (Brochu 1996), so it is possible that the crocodylian model does not apply to sauropods. Overall, however, the vertebral features imply that ANS 21122 was by no means a juvenile animal, despite its comparatively small size, but nor was it fully grown.

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 vertebrae (Harris & Dodson 2004, Harris 2006*a*, *b*) that, as muscle and tendon 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 PALAEOBIOGEOGRAPHY

Until the discovery of basal taxa (the rebbachisaurids *Rebbachisaurus garasbae*, *Limaysaurus* [?=*Rebbachisaurus*] *tessonei* 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 diplodocoids. The data matrix (see Supplementary Data available on Cambridge Journals Online on: http://www.journals.cup.org/abstract_S14772019 06001805) 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
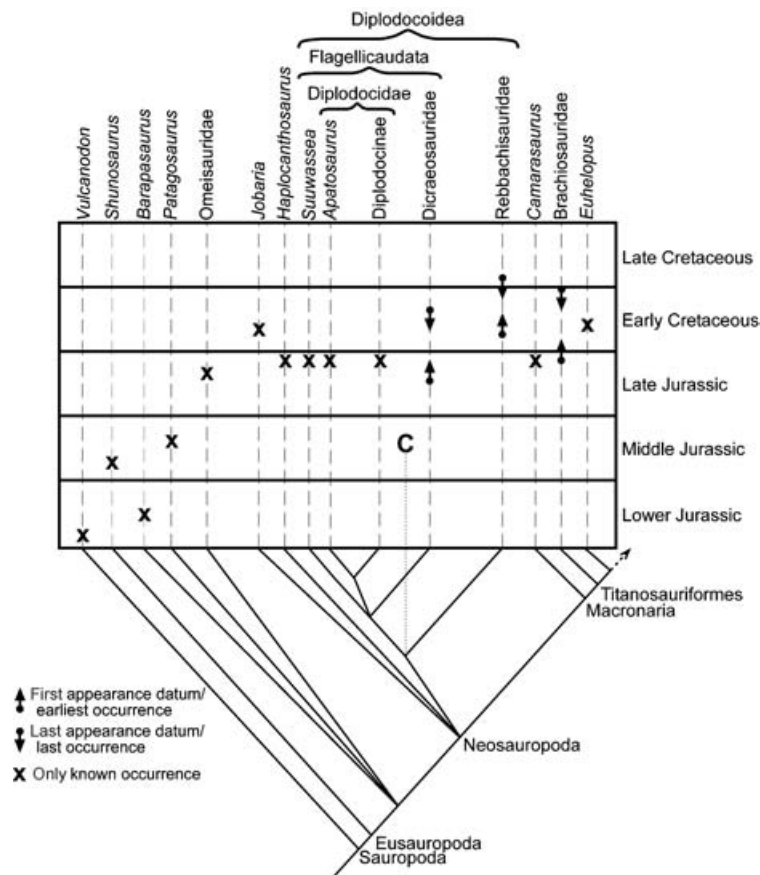
Figure 3   Sauropod phylogeny (simplified from Harris & Dodson 2004) showing occurrences and ranges of non-titanosaurian taxa, emphasising diplodocoids. The 'C' indicates occurrence of British Museum (Natural History) specimen (BMNH) R.1967, a string of articulated, biconvex distal caudal vertebrae incorrectly 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 = 500 000. 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
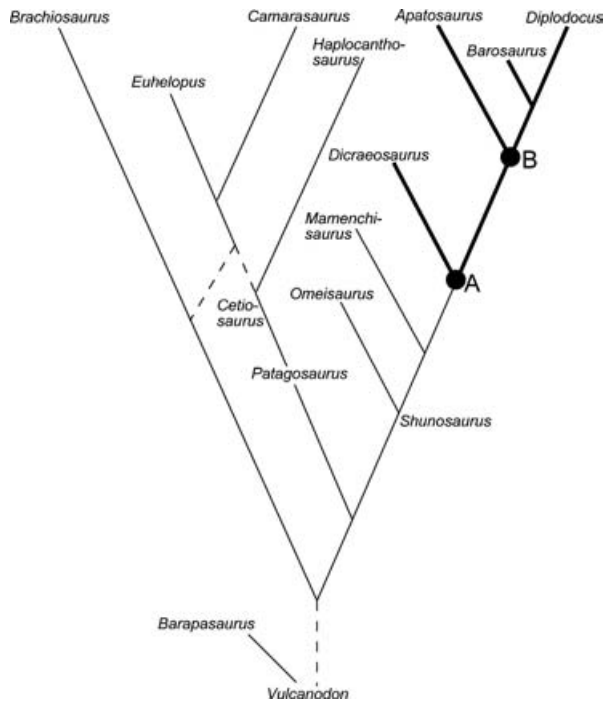
Figure 4 The 'traditional' phylogeny of the Sauropoda (modified and simplified from McIntosh 1990). Everything within node A represents what is currently understood as the Diplodocoidea; node B represents the Diplodocidae. In this phylogeny, the position occupied by *Dicraeosaurus* can represent the Dicraeosauridae.

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 Dicraeosauridae (*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 flagellicaudatan). In some trees, *Losillasaurus* continued to pair with *Mamenchisaurus* (or as sister to an (*Omeisaurus* + *Mamenchisaurus*) 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*, *Nigersaurus*, *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-diplodocoid 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 *Mamenchisaurus*. *Haplocanthosaurus* occurs as a non-diplodocoid, 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.
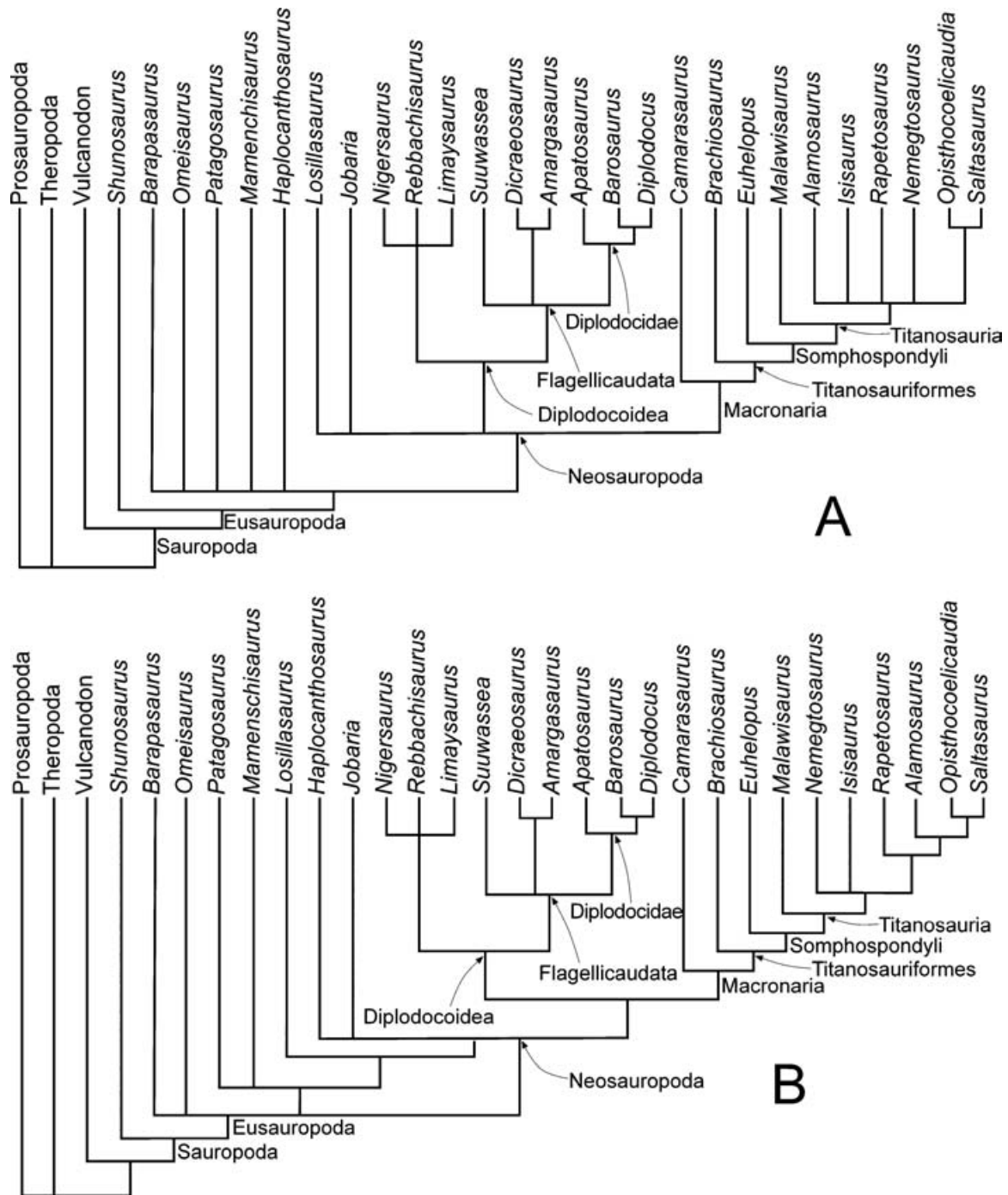
Figure 5 Strict and semistrict (identical: **A**) and Adams (**B**) consensus trees of phylogenetic analysis of relationships of *Suuwassea emilieae* using the data matrix presented in the Supplementary Data. Note that, in both consensus trees, the Flagellicaudata consists of a trichotomy containing *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.
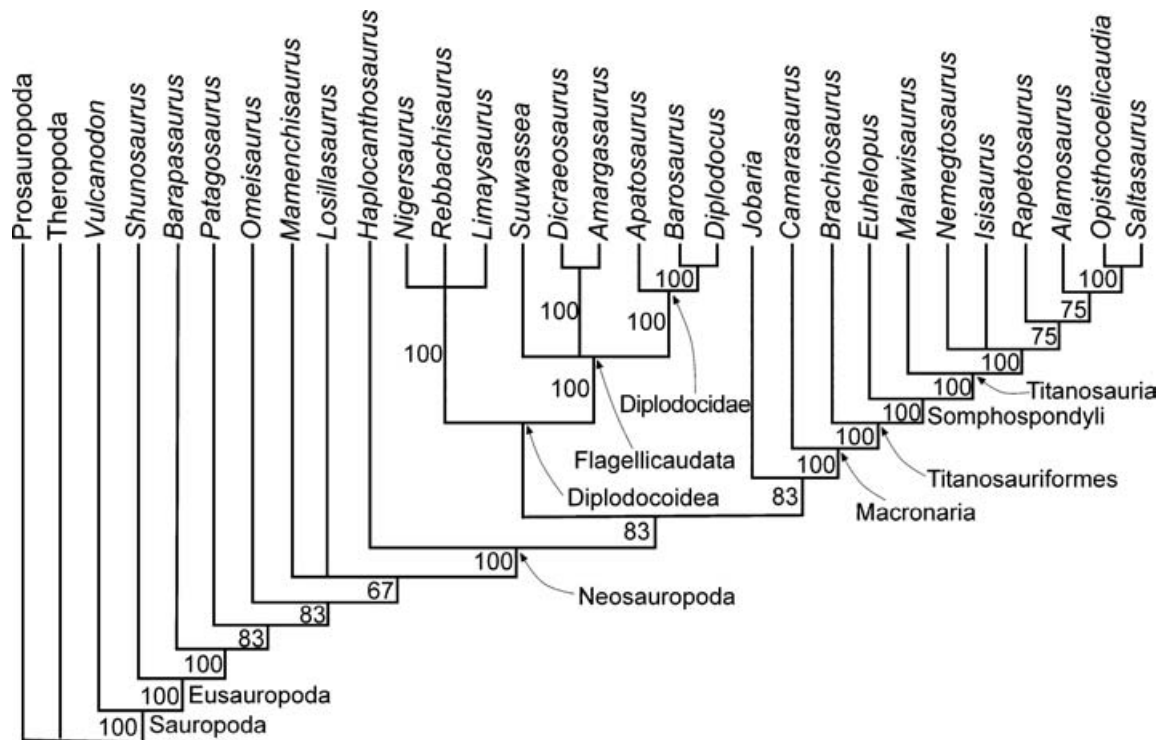
Figure 6 Phylogenetic analysis of relationships of *Suuwassea emilieae* produced by 50% majority rule analysis of the data matrix presented in the Supplementary Data. Note that the Flagellicaudata consists of a trichotomy containing *Suuwassea*, the Diplodocidae (*Apatosaurus* + (*Diplodocus* + *Barosaurus*)) 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

two possible positions, as sister taxon to either of the terminal clades (the Diplodocidae and Dicraeosauridae). The resultant consensus trees collapsed the Flagellicaudata into a (probably 'soft') polytomy with those two terminal clades. While the influence of missing data has not been assessed with respect to this lack of resolution, some of it is certainly due to character conflict, particularly with characters indicating diplodocid affinities (50(1), 65(1), 101(1), 168(1), 314(1) and 319(1)) versus those supporting dicraeosaurid affinities (28(0), 33(1), 104(0)*, 118(1)* and 194(1)). Conflicting characters may either be perceived as variable within a single taxon (in this case, assuming ANS 21122 were perceived as a specimen of another taxon, such as *Apatosaurus*) or as genuine autapomorphies diagnostic at a lower taxonomic level (a 'genus' or species). Possession of novel characters that have physiological ramifications (such as the postparietal foramen), render less likely intraspecific variation as a valid explanation (i.e. it is unlikely that some individuals of a species have the structure and others lack it). Thus, in addition to its autapomorphies, the conflicting characters most parsimoniously support interpretation of *Suuwassea* as a valid taxon.

For the purpose of facilitating future field identification of a Morrison Formation sauropod specimen as *Suuwassea* (as opposed to as *Apatosaurus*, *Barosaurus*, or *Diplodocus*), and since many of its autapomorphies (Harris & Dodson 2004) are somewhat subtle, it is useful to list traits that, although not autapomorphic for *Suuwassea*, allow a specimen to be distinguished from other currently-known diplodocoids in the Morrison Formation. These include (based on personal observation as well as references listed in Table 1): overall size smaller than *Apatosaurus* or *Diplodocus*, despite relatively advanced age (see 'Flagellicaudatan ontogeny,' above); postparietal foramen present (absent in *Apatosaurus* and *Diplodocus*), small trapezoidal, not recessed below level of skull roof; occipital surface of skull and foramen magnum lie in roughly the same plane (noticeably angled in *Diplodocus*); sagittal nuchal crest sharp (low, rounded and broad in *Apatosaurus* and *Diplodocus*); post-temporal processes lacking dorsal contact with squamosal processes of parietals (contact present in *Apatosaurus*); basal tubercula project caudoventrally (ventrally in *Apatosaurus* and *Diplodocus*); basisphenoid visible between basal tubercula in caudal view (absent in *Apatosaurus* and *Diplodocus*); cranial spinozygapophyseal laminae in cranial cervicals reduced or non-existent (prominent in *Apatosaurus louisae* and *Diplodocus*, reduced in *A. excelsus*); cranial cervical spinous processes situated entirely over caudal margin of vertebral bodies (seen elsewhere only in *Apatosaurus excelsus*); bifurcation of cervical spinous processes begins at cervical 6 (cervical 2 in *Dicraeosaurus*, 3 in *Diplodocus*, 5 in *Apatosaurus louisae*, 5 or possibly 6 in *A. excelsus*); cranial-mid cervical spinous processes broader mediolaterally than craniocaudally with distal lateral expansions (absent in *Diplodocus* and *A. louisae*); spinous processes of cervicals 2–5 with pronounced caudal inclination, reverts to cranial inclination at cervical 6 (no angulation in *Diplodocus*, reversion by cervical 5 in *A. excelsus*); cranial zygapophyseal alae of cervicals 2–5 with caudodorsally concave margins in lateral view (seen elsewhere only in *Apatosaurus louisae* and *Dicraeosaurus*); cervicals 2–6 (at least) with distinct, elongate dorsal tori; dorsalmost point on acromion closer to glenoid fossa than to midpoint of scapular body (opposite condition in *Diplodocus*

and *Barosaurus*); coracoid with rounded craniomedial margin (square in *Apatosaurus*); humerus robust, with proximal and distal ends greatly expanded with respect to mid-body (humerus comparatively slender, with less expanded ends, in *Diplodocus*); one of the first two pedal unguals longer but lower than the other (not present in *Apatosaurus* or *Diplodocus*).

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 flagellicaudatans 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 Kirgyzstan (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 one or more of the following: (1) flagellicaudatans did not evolve until the Bathonian (and the European discoveries are close to being true first appearance data); (2) other physical and/or palaeoecological barriers prevented spread into Asia; (3) taphonomic biases in Asia have precluded the discovery of flagellicaudatans there; or (4) the palaeogeographical understanding of Europe and Asia during this time is incomplete.

Flagellicaudatans have not yet been recognised in the Middle Jurassic of Argentina (Casamiquela 1963; Bonaparte 1986; Rich *et al*. 1999; Weishampel *et al*. 2004), implying either a true absence, taphonomic bias, or the presence of other physical and/or ecological barriers that restricted the earliest flagellicaudatans geographically. However, epicontinental seaways similar to that between Europe and Asia in the Bathonian 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 flagellicaudatans 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 landmasses 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 flagellicaudatans or non-flagellicaudatan 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, flagellicaudatan-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 flagellicaudatan, 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 palaeoecological 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 (Malumián *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 flagellicaudatans and dicraeosaurids in the Morrison Formation would be in the northern part of the depositional basin, closer to the sea.

Acknowledgements

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