

Paleoecology and Systematics of the Diplodocoid Sauropods

by

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To Wendy, mo mhíle stór

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ABSTRACT

Diplodocoid sauropods were among the most successful and largest herbivores of the Mesozoic. Here, the systematics and paleoecology of these animals are examined in five parts: a reassessment of the relationships of *Australodocus bohetii*, a phylogenetic analysis of the clade Diplodocoidea, an investigation of feeding behavior in diplodocoid sauropods, an examination of ontogenetic variation in the skull of *Diplodocus*, and a study of the evolution of tooth shape and replacement rate in Sauropodomorpha.

The sauropod *Australodocus* was originally described as a diplodocid (one of three clades of diplodocoid), the second such animal from the Late Jurassic of Tanzania. Comparative study suggests instead that *Australodocus* is a member of the distantly related Titanosauriformes, similar in many regards to *Brachiosaurus brancai*.

A phylogenetic analysis confirms the assessment from the previous chapter, and also identifies several key relationships for the understanding of diplodocoid evolution. The first of these is the resolution of the plesiomorphic taxon *Suuwassea* as a basal dicraeosaurid (the sister clade to Diplodocidae). Also presented is a fully-resolved Rebbachisauridae, with two sub-clades recovered (Limysaurinae, Nigersaurinae).

Using this hypothesis of relatedness as a backbone, the evolution of feeding strategies in the clade was examined. Hypotheses of various browsing behaviors (selective and nonselective browsing at ground-height, mid-height, or in the upper canopy) were examined using snout shape (square vs. round) and dental microwear. The square snouts, large proportion of pits, and fine subparallel scratches in *Apatosaurus*, *Diplodocus*, *Nigersaurus*, and *Rebbachisaurus* suggest ground-height nonselective browsing; the narrow snouts of *Dicraeosaurus*, *Suuwassea*, and *Tornieria* and the coarse scratches and gouges on the teeth of *Dicraeosaurus* suggest mid-height selective browsing in those taxa. This distribution does not match the recovered phylogeny (*Tornieria* is nested in a clade of ground-height browsers), although it did correspond perfectly with reconstructions of regional ecology, such that ground-height nonselective browsers lived in savanna-type environments, and mid-height selective browsers lived in forested environments.

Ontogenetic shape variation in at least one of the ground-height nonselective browsers (*Diplodocus*) suggests the possibility of ontogenetic variation in feeding strategy as well, where subadults may have fed selectively.

Although Diplodocoidea is diagnosed in part by narrow-crowned teeth, the inference of at least two distinct feeding strategies for this clade suggests that it is unlikely that the development of narrow crowns in this clade was an adaptation

for a particular feeding mode. Histological and proportional data suggest instead that the development of narrow crowns in this clade (and elsewhere) was an adaptation that enabled more rapid tooth replacement and may not have been tied directly to any particular feeding strategy or strategies.

CHAPTER 1

INTRODUCTION

The long-necked, shovel-nosed dinosaurs belonging to the Superfamily Diplodocoidea were some of the largest animals ever to walk the earth. Their immense size was achieved despite a head that in some cases was less than 0.4% of the total body volume (Gunga et al., 1999), severely limiting the total amount of forage that could be ingested with each bite. Even more remarkable are the rates at which these animals grew, perhaps as high as 5,500 kg/year, roughly equivalent to growth rates seen in grey whales today (Curry, 1999). Given the immense amount of forage these animals ingested daily using their comparably small skulls and jaws, understanding how and what these animals ate is an important step in reconstructing their impact on terrestrial ecosystems of the past.

Hypotheses of feeding behavior in diplodocoids are strongly influenced by their unusual skulls, which feature elongate, square snouts formed by forward expansion of the tooth-bearing facial bones, the premaxilla and maxilla. The face itself is rotated ventrally relative to the occiput, such that it faces the ground to a greater or lesser degree. This elongation and rotation of the face are accompanied by the restriction of teeth to the very front of the broad, flat muzzle. The teeth themselves are also unusual, with wear patterns that are unlike those

expected from a normal bite stroke (Barrett and Upchurch, 1994; Calvo, 1994); in fact, the pencil-like teeth appear to not contact each other at all. This combination of characteristics—an antorbitally elongate skull with a broad, variably rectangular muzzle, filled only at its distal extreme with long, narrow-crowned teeth and deflected ventrally relative to the braincase and neck—has come to diagnose the clade, although ontogenetic (Chapter 6) and ecological (Chapter 5) variation in shape will be demonstrated later. Although sauropods are notable early in their evolutionary history for their lack of cranial adaptations, such as the beaks, cheeks, and other adaptations seen in Ornithischian dinosaurs (Chure et al., 2010), the development of this ‘diplodocoid morphology’ represents a drastic departure from the anatomy of both basal and contemporaneous sauropods (Sereno et al., 2007).

Hypotheses of feeding in these taxa have typically focused on a unique feeding strategy, such as branch stripping (Dodson, 1990; Barrett and Upchurch, 1994) or predation on bivalves (Sternfeld in Holland, 1924). Other hypotheses of diplodocoid feeding behavior include aquatic plant grazing (Hatcher, 1901), and low-height, non-selective browsing (similar to grazing behavior in mammals; Sereno et al., 2007; Whitlock, 2007; 2009). However, there has not yet been a comprehensive and quantitative examination of feeding behavior in the group.

Here, I examine the ecology and evolution of diplodocoid sauropods in eight parts. Chapter 2 introduces the general taxonomy of the group and is intended as a reference for relevant anatomy, clade names, and relationships. Chapter 3 deals with the relationships of the putative diplodocoid *Australodocus*

bohetii from the Late Jurassic of Tanzania, removing it from Diplodocoidea and placing it with the titanosauriform sauropods. This chapter also discusses the impact of this reassignment on the content of Late Jurassic sauropod faunas, and attempts to explain the pattern of faunal diversity as a consequence of local ecology. Chapter 4 presents a taxonomically inclusive, well-resolved phylogeny of Diplodocoidea, which is used to interpret the results of Chapter 5, which uses dental wear, snout shape, and paleoecology to examine feeding behavior in each lineage. Chapter 6 examines ontogenetic variation in morphology and feeding behavior in *Diplodocus*. Chapter 7 presents preliminary results of tooth replacement rate in sauropods, including data from *Diplodocus* and the contemporaneous *Camarasaurus*. Chapter 8 presents a summary of the results and their interpretation.

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CHAPTER 2
INTRODUCTION TO DIPLODOCOID SAUROPODS: TAXONOMY,
DISTRIBUTION, AND BASIC ANATOMY

Sauropod dinosaurs, such as *Apatosaurus* (Fig. 2.1), are easily recognizable among dinosaurs by their iconic bauplan: long necks balanced by long tails, on either end of a barrel-chested torso supported by four columnar limbs. Although the strict adherence to this body type has led to the perception that sauropod anatomy is “monolithic” (sensu Wilson, 2005) and largely invariant, even among dinosaur workers, close examination reveals a tremendous amount of informative variation (Wilson, 2005:p. 2). In this chapter, a brief overview of diplodocoid taxonomy is followed by an examination of the anatomical variation that defines Diplodocoidea and its clades. The chapter concludes with an overview of diplodocoid distribution, in both geographic and temporal contexts.

DIPLODOCOID TAXONOMY

Diplodocoidea is one of two clades (alongside Macronaria) within the larger clade Neosauropoda. Taylor and Naish (2005) reviewed the taxonomy of Diplodocoidea in detail; here, discussion of taxonomy will be limited to defining the major clades, beginning with the most inclusive clade, Diplodocoidea. Although there has been some debate over the use of the stem-based

Diplodocoidea and the node-based Diplodocimorpha, Diplodocoidea is used here, due to the uncertain relationships and concomitant impacts on taxonomy of basal neosauropods such as *Haplocanthosaurus*. Diplodocoidea includes all sauropods more closely related to *Diplodocus* than *Saltasaurus* (Wilson and Sereno, 1998; Fig. 2.2).

Diplodocoidea itself is subdivided into three clades: Dicraeosauridae, Diplodocidae, and Rebbachisauridae. Dicraeosauridae and Diplodocidae are stem-based clades (specified by *Dicraeosaurus* and *Diplodocus*, respectively), completing a node-stem triplet (Sereno, 1999b) with Flagellicaudata, their containing clade (Fig. 2.2). Rebbachisauridae is also a stem-based clade, defined as everything more closely related to *Rebbachisaurus* than *Diplodocus*.

SAUROPOD ANATOMY

Although most of the morphology that characterizes basal sauropods is in the appendicular skeleton (a result of a shift from bipedality to obligate quadrupedality early in their evolutionary history), derived sauropod groups are most readily distinguishable by cranial and axial characters (Sereno, 1999a; Wilson, 2002; Chapter 4). Although some appendicular characters will be discussed later in this work, here the discussion is limited to the cranial and axial regions. Anatomical terminology here and in later chapters is of “Romerian” type (e.g. trunk vertebrae are “dorsal” rather than “thoracic” or “lumbar”, “anterior” is preferred over “rostral”), following Wilson (2006).

CRANIAL SKELETON

Sauropod skulls are, surprisingly, both small for their body size and simple in design, lacking the obvious hallmarks of herbivory (e.g., beaks, cheeks, and crushing dentition) seen in other dinosaurian herbivores (Chure et al., 2010). What variation does occur in sauropod crania is largely related to antorbital elongation of the facial skeleton, as exemplified by the diplodocoids (Fig. 2.3).

VERTEBRAL LAMINAE

The vertebral centra, arches, and spines of derived sauropods (some eusauropods and all neosauropods) were invaded by pneumatic diverticula, which excavated fossae in the external surface of the vertebrae. Because the vertebrae must still retain structural integrity, even heavily pneumatized vertebrae retain thin struts, or laminae, of bone. The distribution, orientation, and development of these laminae are diagnostic for clades at multiple scales of measurement (Upchurch, 1995, 1998; Wilson and Sereno, 1998; Wilson, 1999, 2002).

Wilson (1999) codified a nomenclatural system for these laminae, based upon identification of two landmarks connected by them. These laminae are identified by a four-letter acronym (e.g., cprl) abbreviating a name constructed from the two landmarks (e.g., centroprezygapophyseal lamina). This system has the advantage of identifying homologous structures across a wide range of sauropod dinosaurs, enabling comparisons between them. A full discussion of the system is more completely presented by Wilson (1999), but a brief overview

of laminae is presented in Table 2.1 and illustrated in Figure 2.4. This nomenclature will be referred to throughout this work, although the relevant names will be repeated in a list of abbreviations at the beginning of each chapter.

DIPLODOCROID-SPECIFIC ANATOMY

Diplodocoid sauropods are generally distinguishable from other sauropods by a combination of easily recognizable derived character states in the cranial and axial skeletons. The following is not intended to be a comprehensive list of synapomorphies (see Appendix 4.4 for a more complete listing than is presented here), but is instead intended to be a broad overview of the salient anatomy as an introduction to the study of diplodocoid sauropods.

Cranial skeleton

In diplodocoids, two major modifications to the cranial elements occurred, although the order in which they evolved is uncertain. The first major alteration is the extreme antorbital elongation of the face, caused not by elongation of the nasal bones, as in many mammals with elongate faces (Gilbert, 1980), but by elongation of the premaxilla and maxilla; this distinction is likely the result of the narial retraction that characterizes all neosauropods, which would have precluded the elongation of the nasals. The second modification is a ventral rotation of the face relative to the occiput, such that the snout was held in a downward-facing position when the head and neck were in a neutral posture (Sereno et al., 2007). For further discussion of the impact of these modifications

on behavior and ecology, see Chapters 5 and 6.

Additional characteristics of note are the development of a “chin” on the dentary (Fig. 2.3B) and narrow-crowned teeth. Typical sauropod teeth are large, broad-bladed elements with a D-shaped cross-section at mid-height; the teeth of diplodocoids are narrow and sub-cylindrical in cross-section (Wilson and Sereno, 1998). In the “mid-“ to Late Cretaceous, as diplodocoid diversity waned, titanosauriform sauropods diversified and developed narrow-crowned teeth (Chure et al., 2010). This was once believed to have united diplodocoids with derived titanosaurs (McIntosh, 1990; Upchurch 1995; 1998; Upchurch et al., 2004) but is now believed to be a convergent acquisition (Salgado and Calvo, 1992; Calvo and Salgado, 1995; Wilson, 2002; Wilson and Upchurch, 2009). As a result, the presence of narrow-crowned teeth is no longer considered diagnostic at coarser taxonomic scales.

Axial skeleton

Several features of the axial skeleton are now recognized as uniting diplodocoids to the exclusion of all other sauropods: short cervical ribs, patterns of lamination in dorsal and caudal vertebrae, and a string of elongate posterior-most caudal vertebrae known as a “whiplash” (Wilson, 2002; Upchurch et al., 2004; Figs. 2.4, 2.5).

In most sauropods, ribs on the cervical vertebrae were oriented roughly anteroposteriorly and overlap at least one vertebra posterior to the centrum that bears the rib. The cervical ribs of basal sauropods, such as *Shunosaurus*, only overlapped one vertebra posterior; in more derived neosauropods, the cervical

ribs became increasingly elongate, eventually overlapping three or four vertebrae posterior (Wilson, 2002). Diplodocoids were the exception to this trend, as their cervical vertebrae bore ribs that did not overlap any vertebrae posterior, and terminated posteriorly at or anterior to the posterior margin of the centrum (Fig. 2.4B).

As noted above, the pattern of lamination caused by invasion of pneumatic diverticula is commonly used to distinguish between sauropod clades. Diplodocoids are generally distinguished from other sauropods by the presence of a composite prespinal lamina in dorsal vertebrae, formed by the paired spinoprezygapophyseal laminae (Fig. 2.4F), and the presence of pre- and postzygodiapophyseal, anterior centrodiapophyseal, and posterior centrodiapophyseal laminae on anterior caudal vertebrae (Fig. 2.4A). Flagellicaudatans are further distinguished by bifurcation of the centropostzygapophyseal laminae in dorsal vertebrae (Fig. 2.4D). Diplodocoids are diagnosed by bifurcation of the centroprezygapophyseal laminae in cervical vertebrae (Fig. 2.4C).

The distal-most caudal vertebrae in diplodocoids had elongate centra (length:posterior height greater than 4) with biconvex articular surfaces (Fig. 2.5). Some workers have hypothesized that the tails were used as a “whiplash” for display or defense (e.g., Bakker, 1994), most recent work suggests that this was unlikely (Christiansen, 1996); the term “whiplash” remains in common use for this type of distal tail section. Although other sauropods have been discovered with biconvex caudals (Charig, 1980; Wilson et al., 1999), they are all proportionally

shorter than those of diplodocoids.

Diplodocoids were once thought to have been united by the presence of bifurcate cervical and anterior dorsal neural spines. Although this remains true for the sub-clade Flagellicaudata, containing Diplodocidae and Dicraeosauridae (Fig 2.5), rebbachisaurids and basal diplodocoids had single, undivided neural spines throughout the axial column.

TEMPORAL AND GEOGRAPHIC DISTRIBUTION

Prior to the inclusion of the Cretaceous *Rebbachisaurus* in the clade by McIntosh (1990), diplodocoids were thought to have been restricted to the Late Jurassic of North America and East Africa. As South America, North Africa, and Europe become more heavily sampled, however, our picture of their distribution has grown more complete (Figs. 2.6–2.8).

DICRAEOSAURIDAE

Dicraeosaurids are first known from the Late Jurassic (Kimmeridgian, 155 Ma; Fig. 2.6). Two genera (*Brachyrachelopan* and *Dicraeosaurus*) occur at this time in southern South America and southern Africa at nearly equivalent paleolatitudes (Fig. 2.6). These genera are typically resolved as sister taxa in recent phylogenetic analyses (Rauhut et al., 2005; Sereno et al., 2007). A land connection between Africa and South America persisted well into the Cretaceous, until at least 120 Ma (Krause et al., 2006) and perhaps as late as 100 Ma (Sereno, et al., 1999; 2004; Sereno and Brusatte, 2008). A third Late

Jurassic taxon, *Suuwassea* from North America, is potentially also a dicraeosaurid, the first lineage known outside Gondwana (Fig. 2.6; see Chapter 4).

Amargasaurus is the latest occurring genus, not appearing in the fossil record until the Early Cretaceous (Barremian-Aptian; 130-112 Ma) of South America (Salgado and Bonaparte, 1991; Fig. 2.7).

DIPLODOCIDAE

Diplodocidae, despite having more species assigned to it (13) than any other diplodocoid family, has the shortest chronologic record and is known only from the Kimmeridgian and Tithonian (155-145 Ma; Upchurch et al., 2004; Fig. 2.6). Representatives of Diplodocidae are known from both Laurasia and Gondwana, occurring in both the Morrison Formation of the western United States and the Tendaguru formation of Tanzania, and are a rare component of the fauna of the Camadas de Alcobaça Formation in Portugal.

REBBACHISAURIDAE

The rebbachisaurids are the most temporally widespread clade within Diplodocoidea, persisting from the Barremian (ca. 130 Ma) into the Santonian (83 Ma; Figs. 2.7, 2.8). *Histriasaurus* appears in the Early Cretaceous of Europe, possibly as early as the Late Hauterivian and contemporaneous with the earliest age estimate of *Zapalasaurus* in South America (Dalla Vecchia, 1998; Salgado et al., 2006). The rebbachisaurid from Burgos, Spain may have appeared as early

as the Late Barremian also. *Amazonsaurus* and *Limaysaurus* in South America and *Nigersaurus* in North Africa all occur in rocks datable only to the Aptian-Albian (Calvo and Salgado, 1995; Sereno et al., 1999; Carvalho et al., 2003). *Rayososaurus* is known from the Aptian of South America (Bonaparte, 1997). *Rebbachisaurus* and *Cathartesaura* occur in the Late Cretaceous of North Africa and South America, respectively (Lavocat, 1954; Gallina and Apesteguía, 2005).

SUMMARY

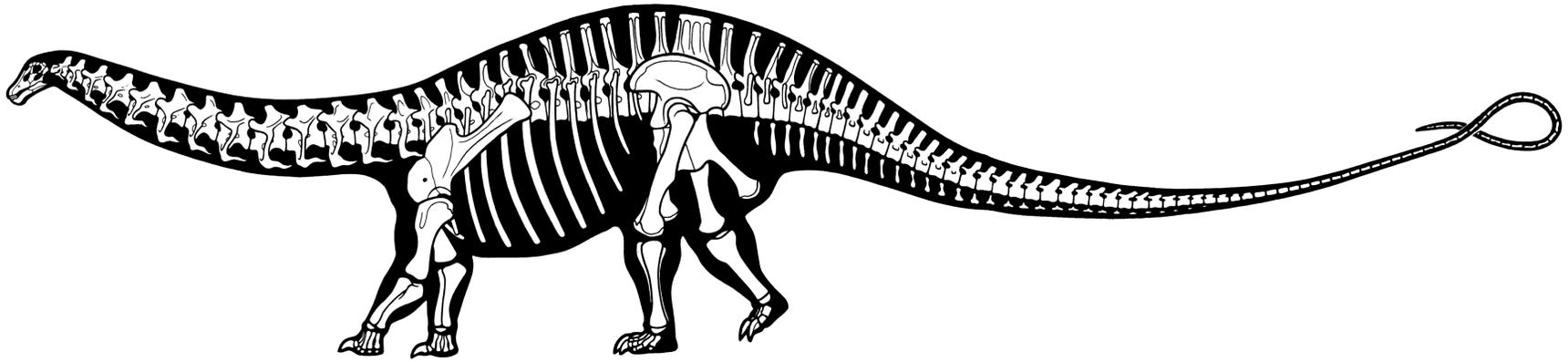
The diplodocoid sauropods were a taxonomically diverse dinosaur clade, with a geographically and temporally expansive range. This preceding review of anatomy, taxonomy, and distribution is intended as a primer and basic anatomical reference for the following chapters, starting with Chapter 3, a re-evaluation of a recently named taxon assigned to Diplodocidae.

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Fig. 2.1. Silhouette reconstruction of *Apatosaurus*, illustrating basic sauropod bauplan. From Wilson and Sereno (1998).

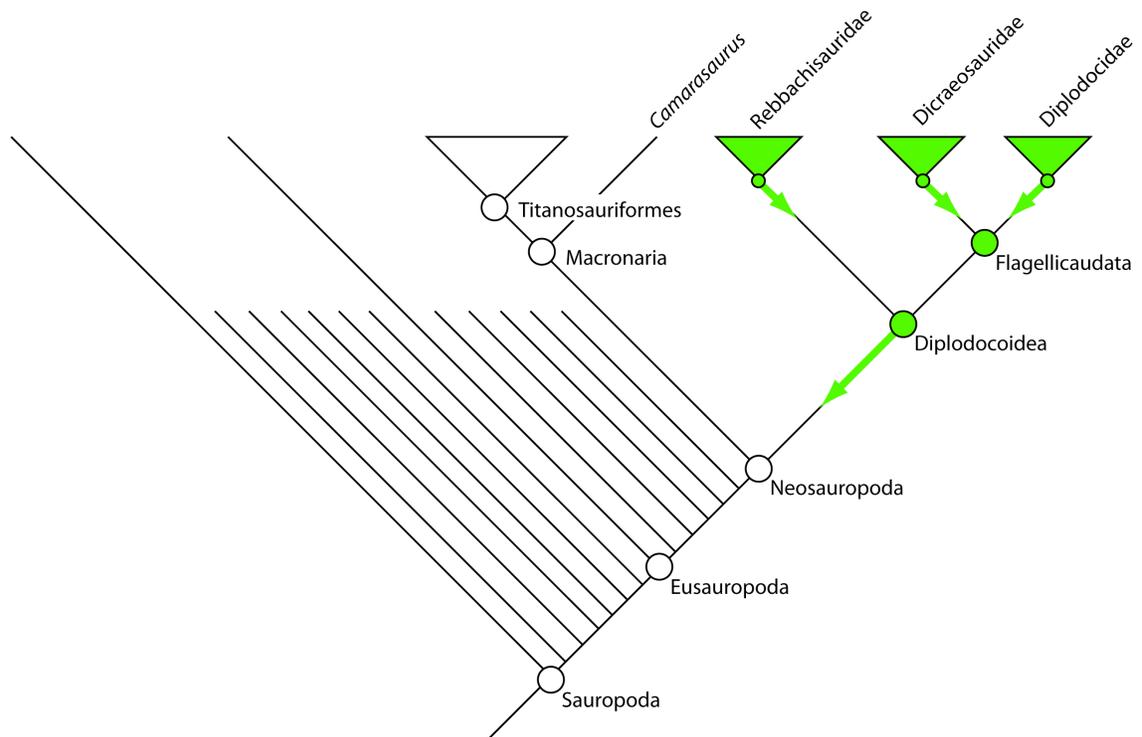


Figure 2.2. Simplified phylogeny of Sauropoda, illustrating relationships of relevant clades. Clades highlighted in green include diplodocoid sauropods. Arrows beneath nodes indicate that clade definition is stem based. Cladogram based on Wilson (2002).

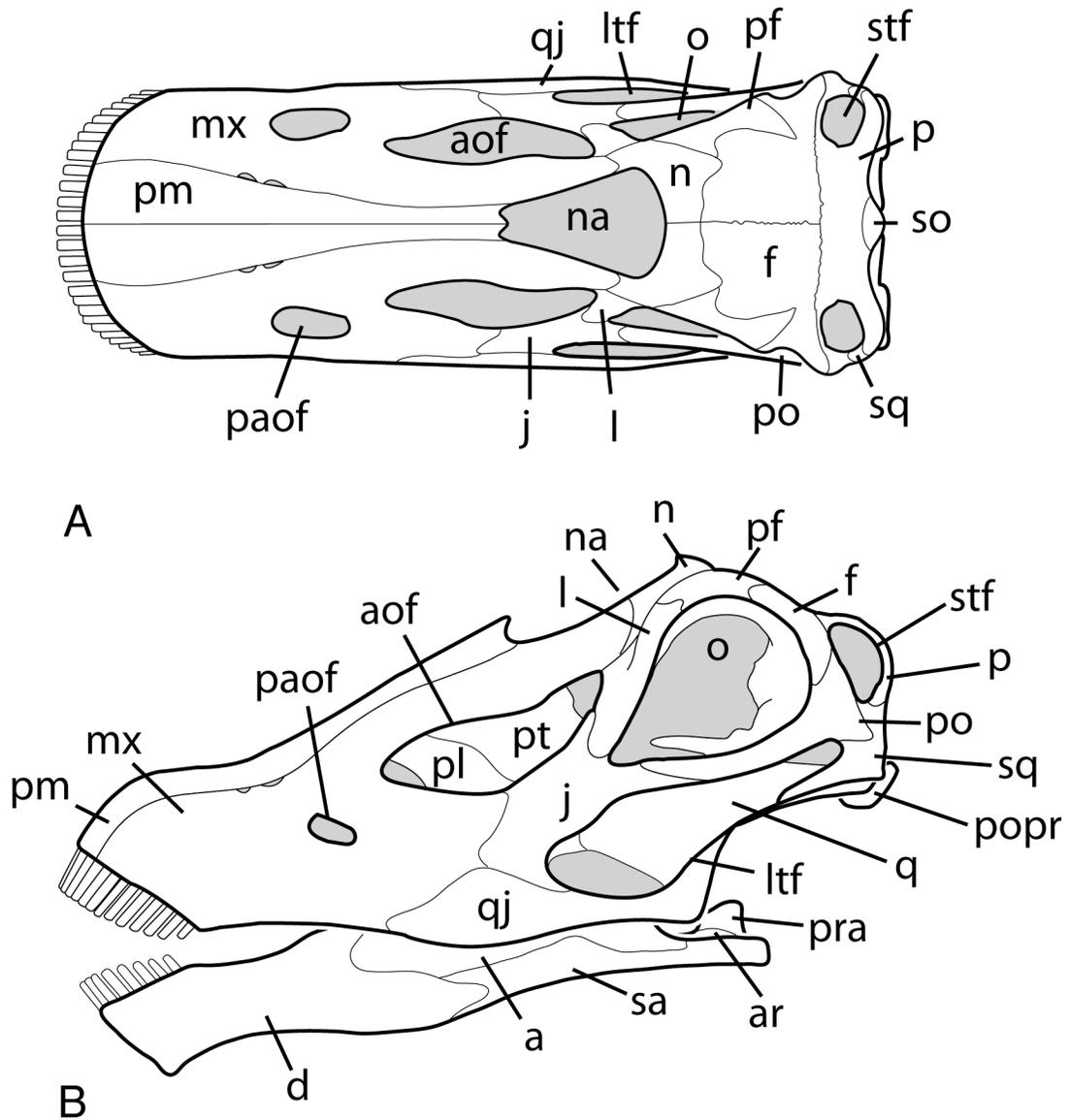


Figure 2.3. Cranial anatomy of the diplodocoid sauropod *Diplodocus* in dorsal (A) and left lateral (B) views. Abbreviations: a, angular; aof, antorbital fenestra; ar, articular; d, dentary; f, frontal; j, jugal; l, lacrimal; ltf, lateral temporal fenestra; mx, maxilla; n, nasal; na, narial opening; o, orbit; p, parietal; paof, preantorbital fenestra; pl, palatine; pm, premaxilla; po, postorbital; popr, paroccipital process; pra, prearticular; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; stf, supratemporal fenestra. Modified from Wilson and Sereno (1998).

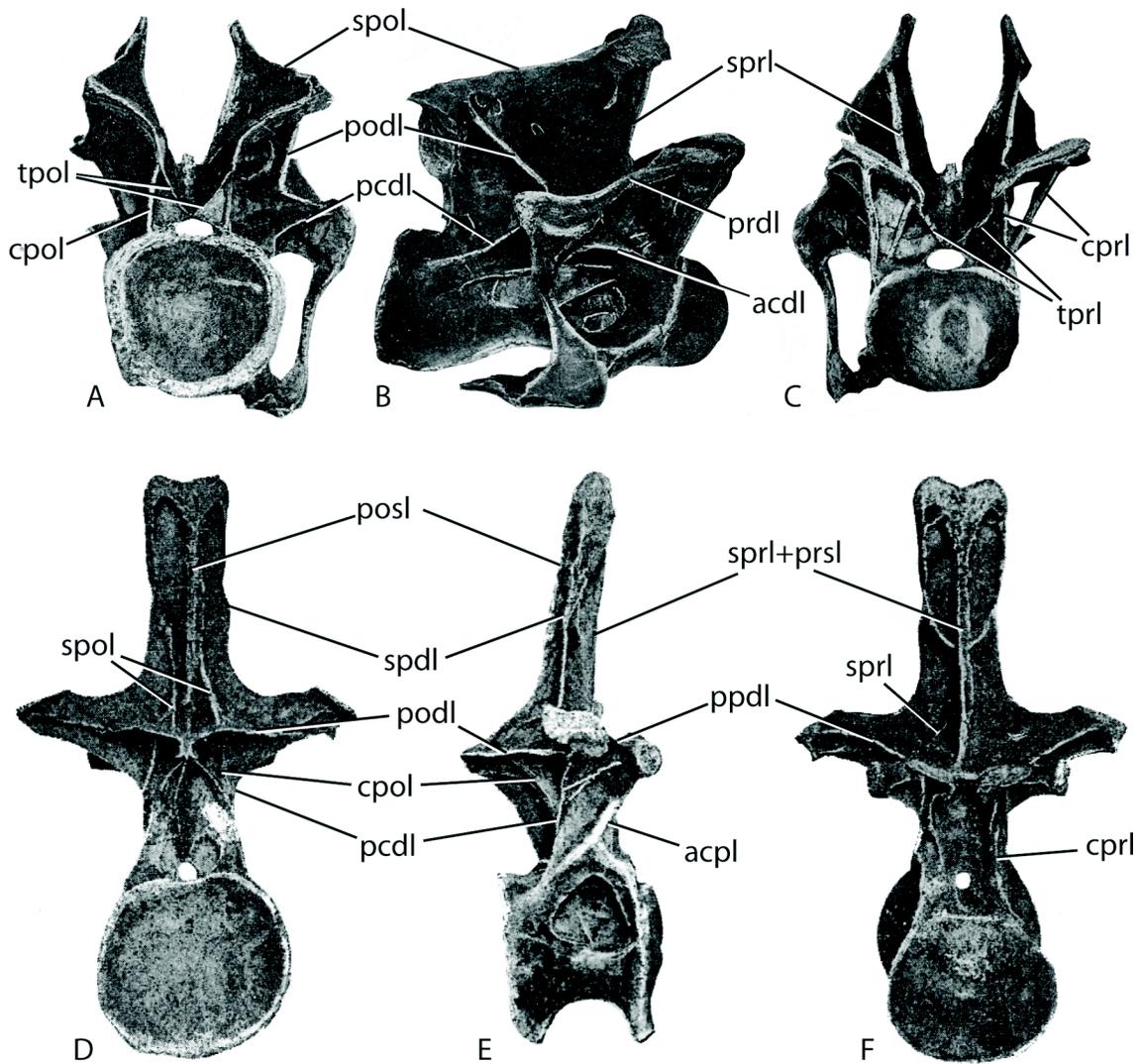


Figure 2.4. Cervical (A, B, C) and dorsal (D, E, F) vertebrae of *Diplodocus* illustrating locations of vertebral laminae. A, D: posterior view; B, E: right lateral view; C, F: anterior view. Abbreviations: acdl, anterior centrodiaepophyseal lamina; acpl, anterior centroparapophyseal lamina; cprl, centroprezygapophyseal lamina(e); cpol, centropostzygapophyseal lamina; pcdl, posterior centrodiaepophyseal lamina; podl, postzygodiaepophyseal lamina; posl, postspinal lamina; ppdl, parapophyseal-diaepophyseal lamina; prdl, prezygodiaepophyseal lamina; prsl, prespinal lamina; spdl, spinodiaepophyseal lamina; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tpol, intrapostzygapophyseal lamina; tprl, intraprezygapophyseal lamina. Nomenclature based on Wilson (1999). Figure modified from Hatcher (1901). Vertebrae not to scale.

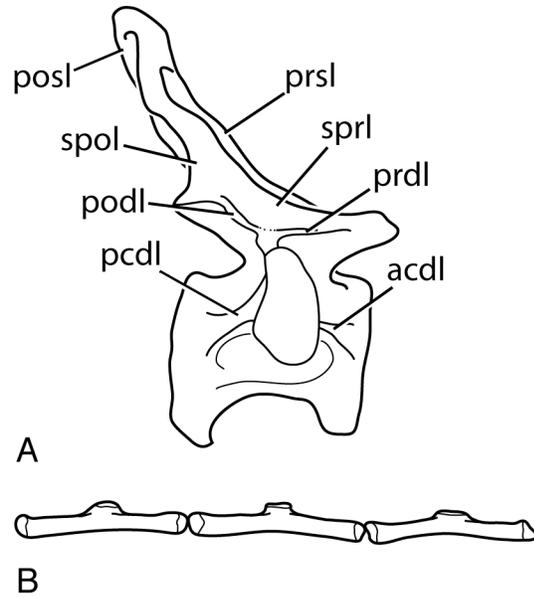


Figure 2.5. Caudal vertebrae of *Diplodocus*, illustrating diagnostic features of Diplodocoidea. A: anterior caudal vertebra in right lateral view. B: distalmost caudal vertebrae, showing elongate, biconvex structure. Redrawn from Hatcher (1901). Vertebrae not to scale. Abbreviations as in Fig. 2.4.

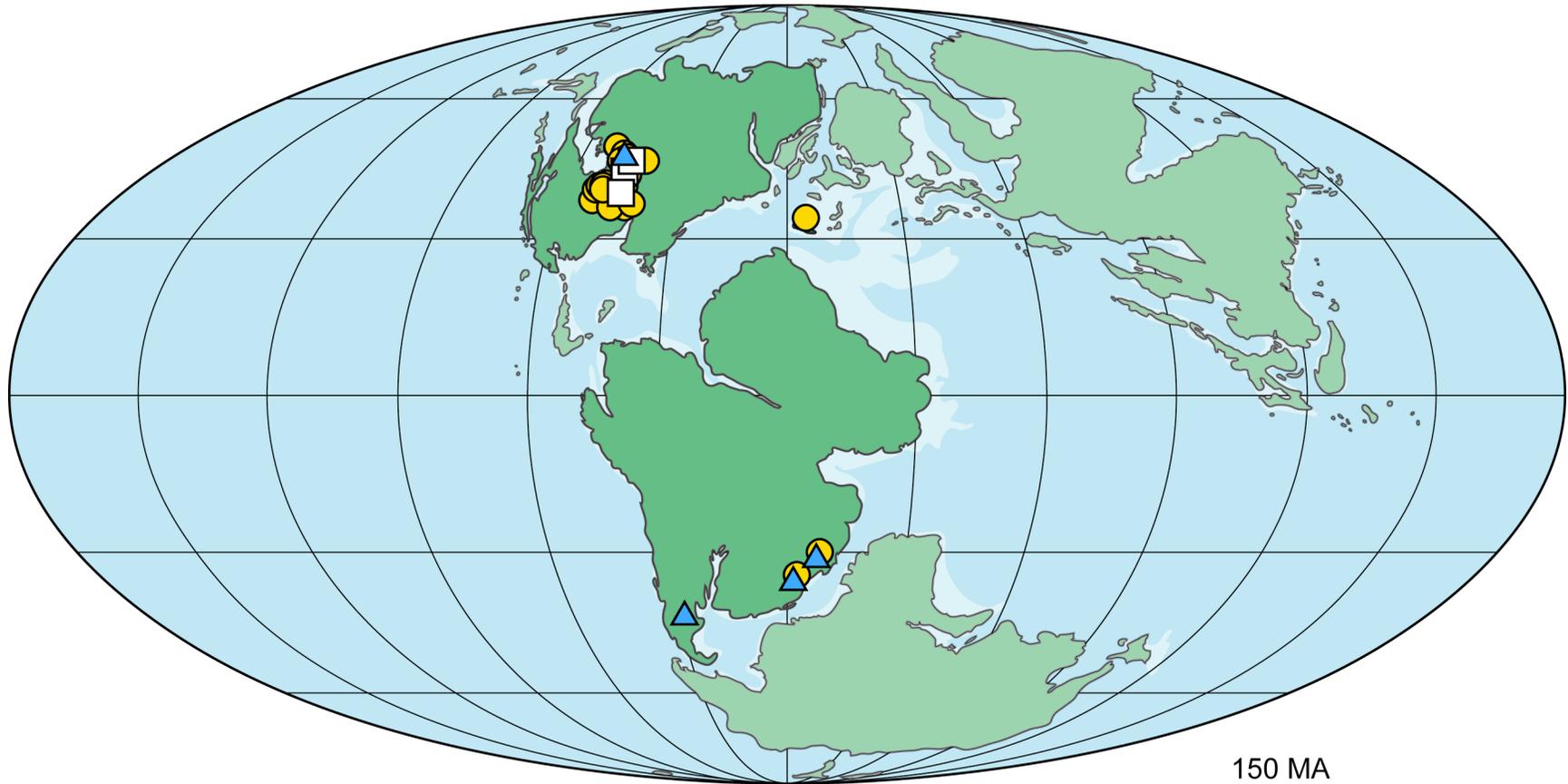


Figure 2.6. Paleogeographic reconstruction of the Late Jurassic (Kimmeridgian-Tithonian), showing distribution of diplodocoid sauropods. Fossils present on landmasses represented in solid green. Localities indicated by symbols. Key to symbols: gold circles, Diplodocidae; blue triangles, Dicraeosauridae; white squares, Diplodocoidea indet. Note presence of all clades except Rebbachisauridae. Locality data from the Paleobiology Database (paleodb.org), recovered 2/10/2010. Figure modified from Blakey (2006).

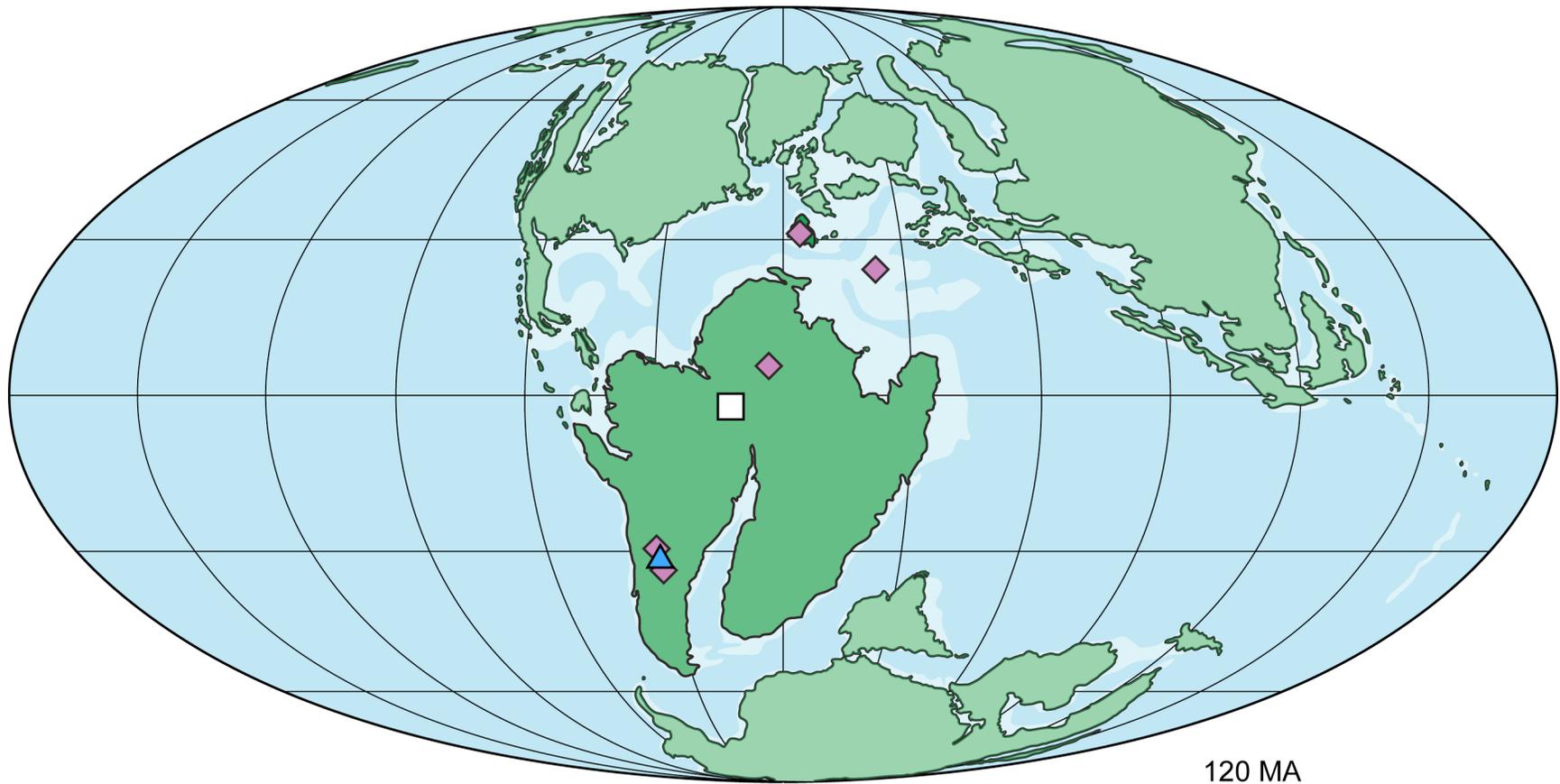


Figure 2.7. Paleogeographic reconstruction of the Early Cretaceous (Aptian), showing distribution of diplodocoid sauropods. Fossils present on landmasses represented in solid green. Localities indicated by symbols. Key to symbols: blue triangles, Dicraosauridae; violet diamonds, Rebbachisauridae; white squares, Diplodocoidea indet. Note reduced geographic distribution and first appearance of rebbachisaurids. Locality data from the Paleobiology Database (paleodb.org), recovered 2/10/2010. Figure modified from Blakey (2006).

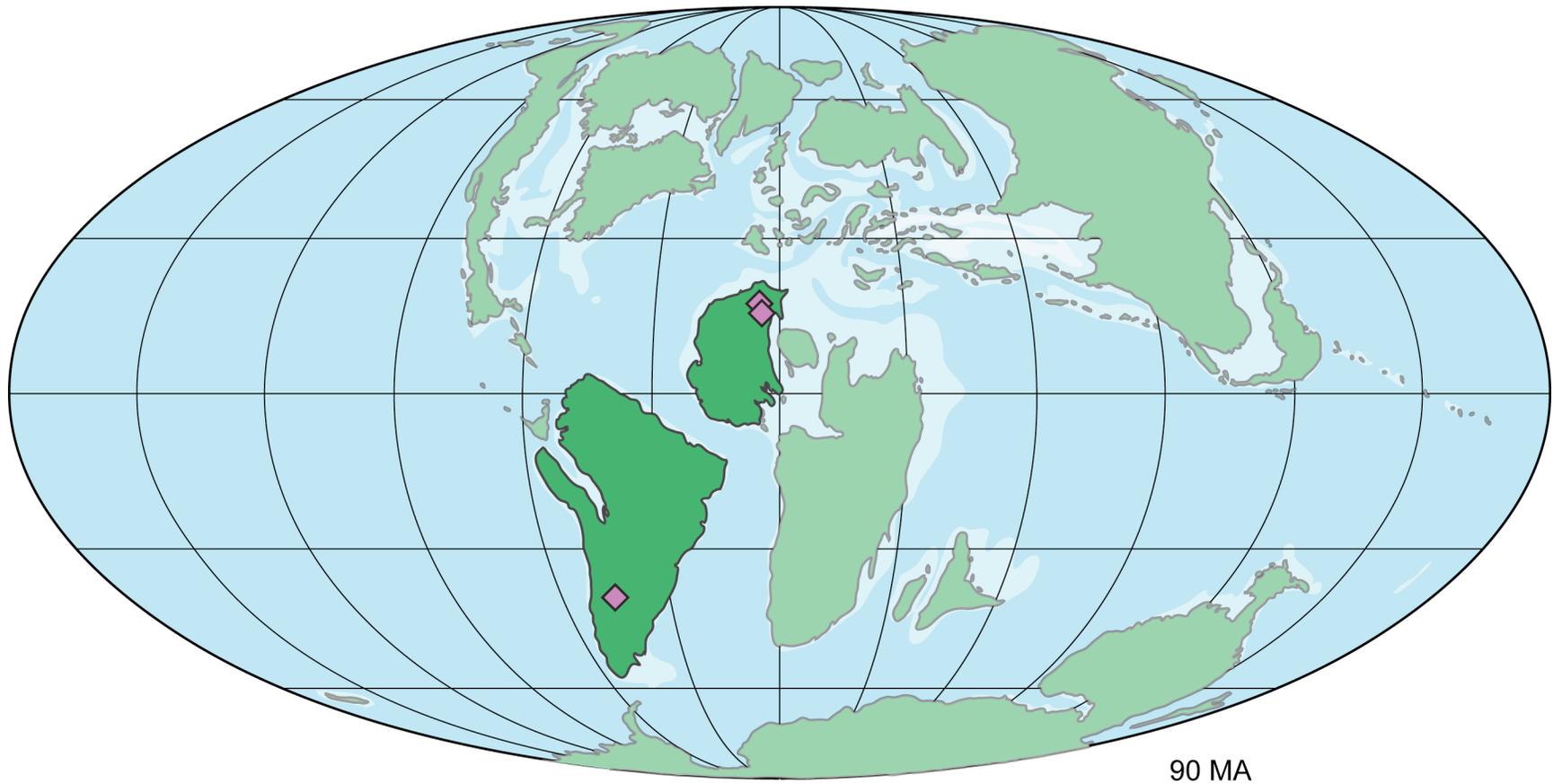


Figure 2.8. Paleogeographic reconstruction of the Late Cretaceous (Turonian), showing distribution of diplodocoid sauropods. Fossils present on landmasses represented in solid green. Localities indicated by symbols. Key to symbols: violet diamonds, Rebbachisauridae. Note reduced geographic distribution and first appearance of rebbachisaurids. Locality data from the Paleobiology Database (paleodb.org), recovered 2/10/2010. Figure modified from Blakey (2006).

Table 2.1. Abbreviations and landmarks for vertebral laminae. Adapted from Wilson (1999).

Lamina	Abb.	Landmark 1	Landmark 2
anterior centrodiapophyseal lamina	acd1	diapophysis	anterior margin of neurocentral junction (lateral aspect)
anterior centroparapophyseal lamina	acpl	parapophysis	anterior margin of neurocentral junction (lateral aspect)
centropostzygapophyseal lamina	cpol	postzygapophysis	posterior margin of neurocentral junction (lateral aspect)
centroprezygapophyseal lamina	cprl	prezygapophysis	anterior margin of neurocentral junction (lateral aspect)
posterior centrodiapophyseal lamina	pcdl	diapophysis	posterior margin of neurocentral junction (lateral aspect)
posterior centroparapophyseal lamina	pcpl	parapophysis	posterior margin of neurocentral junction (lateral aspect)
postzygodiapophyseal lamina	podl	postzygapophysis	diapophysis
postspinal lamina	posl	neural spine base (posterior aspect)	neural spine summit (posterior aspect)
parapophyseal-diapophyseal lamina	ppdl	parapophysis	diapophysis
prezygodiapophyseal lamina	prdl	prezygapophysis	diapophysis
prezygoparapophyseal lamina	prpl	prezygapophysis	parapophysis
prespinal lamina	prsl	neural spine base (anterior aspect)	neural spine summit (anterior aspect)
spinodiapophyseal lamina	spdl	neural spine (lateral aspect)	diapophysis
spinopostzygapophyseal lamina	spol	neural spine (posterior aspect)	postzygapophysis
spinoprezygapophyseal lamina	sprl	neural spine (anterior aspect)	prezygapophysis
intrapostzygapophyseal lamina	tpol	postzygapophysis	dorsal median margin of neural canal (posterior)
intraprezygapophyseal lamina	tprl	prezygapophysis	dorsal median margin of neural canal (anterior)

CHAPTER 3

A RE-EVALUATION OF *AUSTRALODOCUS BOHETII*, A PUTATIVE DIPLODOCOID SAUROPOD FROM THE LATE JURASSIC OF TANZANIA

The 1909–1913 German Tendaguru Expedition collected over 22,000 kg of fossil material from the Upper Jurassic (Tithonian) Tendaguru Formation of Tanzania (Maier, 2003). Most famous among these fossils were the remains of sauropods, both immense (*Brachiosaurus brancai*) and diminutive (*Dicraeosaurus hansemanni* and *D. sattleri*). With brachiosaurids, dicraeosaurids, and diplodocids (*Tornieria*) all present, the outcrops at Tendaguru provided a chance to examine a sauropod community nearly on par with that of the contemporaneous Morrison Formation of the western United States, the only other fauna to preserve multiple diplodocoid taxa living together (Dodson et al., 1980; Russell et al., 1980). In 2007, the Tendaguru Formation became only the second formation known with multiple diplodocids following the description of *Australodocus*, erected from materials previously assigned to *Tornieria africana* (formerly *Barosaurus africanus*; Remes, 2007). The assignment of *Australodocus* to Diplodocidae (and Diplodocoidea) is challenged, and evidence presented to suggest that *Australodocus* is instead the second *Brachiosaurus*-like Titanosauriform from Tendaguru.

HISTORY OF THE TENDAGURU '*BAROSAURUS*' MATERIAL

Adding to the diversity exemplified by the towering *Brachiosaurus brancai* and the tall-spined *Dicraeosaurus*, bones belonging to multiple individuals were referred to the then-exclusively North American diplodocid genus *Barosaurus* as *B. africanus* (Janensch, 1922). Later, McIntosh (1990) referred to this taxon as ?*Barosaurus*, and the material went without formal assignment for some time.

Upchurch et al. (2004) re-established the taxon under the generic name *Tornieria*, originally used by Sternfeld (1911) for the material, changing the specific epithet from *africanus* to *africana* to match the new gender of the genus. Remes (2006) provided the first modern review of the material assigned to *T. africana*, covering the 194 remaining specimens referred by Janensch to '*Barosaurus*' *africanus*. Despite to the fragmentary nature of the holotype specimen, this material has historically been assigned to *Tornieria* sp., on the assumption that no other diplodocid genera existed alongside *Tornieria* at Tendaguru (Remes, 2006).

Remes (2007) erected a new genus, *Australodocus*, based on a pair of isolated, articulated cervical vertebrae previously referred to "*Barosaurus*" (= *Tornieria*) in the collections of the Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany (MB). Using four diagnostic characters (see below), Remes (2007) assigned this new genus to Diplodocidae; if this assignation is correct, almost all of the referred material of *Tornieria* sp. should now be referred to Diplodocidae indet. instead (Remes, 2007), greatly reducing the anatomical completeness of *Tornieria*. The validity of *Australodocus* as a

diplodocoid taxon therefore has several major impacts: first, it introduces a new (and anatomically restricted, being based solely on two vertebrae) taxon for inclusion; second, it dramatically reduces the anatomical completeness of *Tornieria*, restricting it to a braincase, a single cervical vertebra, several caudal vertebrae, and fore- and hind-limb elements (Remes, 2006); third, the addition of a new taxon (regardless of its final referral) has an impact on our understanding of sauropod diversity, not only in Tendaguru, but also throughout the Late Jurassic world.

NOTE ON TAXONOMY

It has been suggested recently that the Tendaguru *Brachiosaurus* (*B. brancai*) and the North American *Brachiosaurus* (*B. altithorax*) belong to separate genera, and that *B. brancai* should instead be referred to as *Giraffatitan brancai* (Taylor, 2009). Although there are recognizable differences between the taxa, it has yet to be demonstrated that these represent generic-level differences and not simply differences between species of the same genera. Phylogenetic analyses demonstrate that the taxa form a monophyletic clade to the apparent exclusion of all other taxa (Taylor, 2009), and in the absence of evidence to the contrary, *Brachiosaurus* will be retained here for both taxa for simplicity's sake.

ABBREVIATIONS

Institutions. AMNH, American Museum of Natural History, New York City, U.S.A.; CM, Carnegie Museum of Natural History, Pittsburgh, U.S.A.; MB, Museum für

Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; USNM, United States National Museum of Natural History, Washington D.C., U.S.A.

SYSTEMATIC PALEONTOLOGY

Saurischia Seeley, 1887

Sauropodomorpha Huene, 1932

Sauropoda Marsh, 1878

Titanosauriformes Salgado, Coria, and Calvo., 1997

Genus *Australodocus* Remes, 2007

Diagnosis—As for type and only known species.

Australodocus bohetii Remes, 2007

Revised diagnosis. Titanosauriform sauropod characterized by bifurcate cervical neural spines, a robust accessory anterior process of the prezygapophysis, and an anteroventral expansion of the prezygapophyseal-diapophyseal lamina (podl) in mid-cervical vertebrae, enclosing the lateral margin of an anteriorly-facing, triangular cavity beneath the prezygapophysis.

Association of the elements. As noted by Remes (2007), the locality from which the *Australodocus* holotypic materials were collected has not been formally reviewed in the literature. It is known, however, that materials from both *Brachiosaurus* (a caudal vertebra) and a small diplodocoid (?*Barosaurus*; two small humeri) were found at the site (Remes, 2007).

COMPARATIVE ANATOMY

Below, the evidence for placing *Australodocus* with either Titanosauriformes or Diplodocoidea is discussed. Evidence is cited from internal and external pneumaticity, elongation of the centrum, form of the neural spine, and lamination of the centrum, neural arch, and spine.

Internal Pneumatic Texture

Centrum. Titanosauriforms can be easily distinguished from other neosauropods by the presence of a particular internal texture in the presacral vertebrae (Wilson, 2002). These sauropods had a somphospondylous or camellate internal bone texture, characterized by tiny internal cavities (2–20 mm) with angular walls and an irregular branching pattern (Wedel et al., 2000). Outside titanosauriforms, only the basal eusauropod *Mamenchisaurus* has a similar internal structure (Young and Zhao, 1972; Russell and Zheng, 1993).

Diplodocoids and other neosauropods, in contrast, had larger internal cavities (5–150 mm) with rounded walls and a regular, bifurcating branching pattern—a texture termed polycamerate (Wedel et al., 2000). Remes (2007) did not discuss the internal bone texture in *Australodocus*. Most of the exposed broken surfaces of the type vertebrae of *Australodocus* are either heavily eroded or covered by hard matrix, although in certain places the internal structure of the centra can be observed.

One such location, on the ventrolateral surface of the paratypic centrum (MB.R. 2454) just anterior to the parapophysis, appears to show evidence for

multiple millimeter-scale, angular cavities invading the internal portions of the element (Fig. 3.1A, B). Similarly located but morphologically distinct, centimeter-scale features are visible on the eroded surface of some *Barosaurus* vertebrae (CM 11984; Fig. 3.1 C). If the condition seen in *Australodocus* does represent somphospondylous internal bone texture, then it would be clear evidence for a titanosauriform relationship for that taxon. The absence of such a texture, however, does not indicate diplodocoid affinities, because this is the primitive condition for sauropods. Internal imaging techniques, such as CT scanning, are necessary to fully resolve this question.

Neural arch. In some basal titanosauriforms, such as *Brachiosaurus*, the internal pneumatic texture of the centrum also invades the neural arch, most commonly in the pre- and postzygapophyses (Wedel et al., 2000). In some instances, these camellae may open directly to the outside as a small pneumatic coel just posterior to the articular surface of the prezygapophysis (MB.R. 2180.24–28, MB.R.2181.42–44, MB.R.2181.47; Fig. 3.2). No similar structure has been noted outside Titanosauriformes.

Similar pneumatic features can be seen on both the prezygapophyses and postzygapophyses of *Australodocus* (Figs. 3.2, 3.3; Remes, 2007:text-fig. 5a). The holotype also has a sharp-bordered, ovate coel opening to an internal pneumatic chamber on both right and left sides, just anterior to the postzygapophysis (Fig. 3.3); a similar coel is present only on the left side in the paratype (Remes, 2007:text-fig. 2B).

External Pneumaticity

Centrum. External pneumatic features are reduced in titanosauriforms, such as *Brachiosaurus brancai*. In those taxa, the posterior one-third of the centrum is not pneumatized (Fig. 3.2A); a single *B. brancai* vertebra has a shallow fossa on one side (MB.R. 2180.25). Diplodocid vertebrae, in contrast, have extensive external pneumatization of the centrum, with a sharp-bordered coel continuing into the posterior one-third of the centrum and, in some taxa, nearly to the posterior margin of the centrum (e.g., *Apatosaurus*; Gilmore, 1936; Fig. 3.2C, D, E).

Pneumatization of the centrum is somewhat limited in *Australodocus*, and the pleurocoels do not extend into the posterior third of the centrum. The extreme posterior extension of the coel on the right lateral surface of the paratype centrum as illustrated by Remes (2007:text-fig.2C), appears to be slightly exaggerated. The centrum posterior to the coel does bear a shallow fossa that appears to correspond to the size and location of the posterior margin of the coel, but it is not continuous with the coel and does not represent the posterior bound of it.

Diplodocids are further distinguished by an elongate, shallow fossa that develops beneath the pleurocoel along the posteroventral margin of the centrum, visible in lateral view (Fig. 3.2C, D, E). This is irregularly developed in *Diplodocus*, but is a consistent feature of the mid-cervical vertebrae in *Barosaurus* (AMNH 6341, CM 11984) and *Tornieria* (Janensch, 1929). No similar fossa is developed in either *Brachiosaurus brancai* or *Australodocus*.

Ventral fossae. *Brachiosaurus* cervical centra commonly have a longitudinal concavity or fossa on their ventral surfaces (MB.R. 2180.24–28, MB.R.2181.42–44, MB.R.2181.47). Some diplodocoids, such as *Diplodocus* (CM 84) and *Barosaurus* (AMNH 6341), also have a strong ventral concavity.

Remes (2007) listed a concave ventral surface of the centrum as a synapomorphy uniting *Australodocus* with Flagellicaudata. This concavity is poorly developed in *Australodocus*, unlike the deeply excavated concavity seen in *Diplodocus* or *Barosaurus*. Furthermore, because a concave ventral surface also occurs in *Brachiosaurus*, this character is not useful in distinguishing between these taxa.

“Triangular Pneumatic Cavity”. Remes (2007:656) listed a “triangular pneumatic cavity” lateral to the neural canal and visible in anterior view as an autapomorphy of *Australodocus*. This structure does appear to be somewhat unique in its appearance, although the system of laminae and the presence of a pneumatic cavity in that location are also present in other sauropods. This cavity is bordered medially by the centroprezygapophyseal lamina (cprl), laterally by the prdl, and dorsally by the prezygapophysis. The extreme anterior expansion of the prdl present in *Australodocus* results in a more distinct cavity, although a similar cavity is present in *Brachiosaurus brancai* (MB.R. 2180.24–28, 2181.42–44, 2181.47). The prdl does not extend as far anteriorly in *Brachiosaurus*, however, and as a consequence the cavity faces anterolaterally and is not entirely visible in anterior view. These laminae do not appear to bound a similarly oriented cavity

in *Apatosaurus* (AMNH 550, Gilmore, 1936), *Barosaurus* (AMNH 3461; CM 19984), or *Diplodocus* (USNM 4712; CM 84; Hatcher, 1906). Thus, the condition in *Australodocus* is more similar to that of *Brachiosaurus* than it is to that of any diplodocid.

Elongation Index

Although highly homoplastic at broader taxonomic scales, the elongation index (centrum length divided by either posterior centrum width or posterior centrum height, depending on author) has commonly been used to compare sauropod neck vertebrae (e.g., Upchurch, 1998; Wilson and Sereno, 1998; Wedel, 2000; Rose, 2007). Both basal titanosauriform and diplodocoid sauropods display some degree of elongation, and their ranges overlap (Tables 3.1, 3.2).

Remes reported an elongation index (EI) of <4.1 for *Australodocus*, using the metric of Upchurch (1998; centrum length divided by posterior centrum width). When measured using a different EI ratio (centrum length divided by posterior centrum height), following Wilson and Sereno (1998), Wedel (2000), and Rose (2007), the paratype of *Australodocus* has an EI of 4.00. The cotyle of the holotype vertebrae is too damaged to make an accurate measurement, and so no EI is reported. Using the aEI (centrum length divided by the average of posterior centrum height and width; Chure et al., 2010), a method designed to account for changes in cross-sectional shape as well as deformation, returns a slightly lower score still (3.80; Tables 3.1, 3.2).

The EI and aEI of *Australodocus* is much lower than that of mid-cervical vertebrae of *Barosaurus* (5.37, 5.04) and *Diplodocus* (4.95, 4.74), and much higher than that of *Apatosaurus* (3.24, 2.79), but very close to that of *Brachiosaurus brancai* (3.92, 3.7) (Tables 3.1, 3.2). It should be noted, however, that the scores of both *B. brancai* and *Australodocus* are substantially lower than the EI and aEI scores of other brachiosaurids, such as *Paluxysaurus* and *Sauroposeidon*, and that both *Australodocus* and *Brachiosaurus* are within the range exhibited within Diplodocidae.

Bifurcation of the Neural Spine

Sauropod cervical neural spines are typically undivided, rising as a single unit above the neural canal. Diplodocid and dicraeosaurid sauropods are diagnosed, in part, by the presence of a two-part, or bifurcate neural spine. Bifurcate neural spines do occur outside that clade, however, and macronarian sauropods with bifid spines are becoming increasingly common finds. Bifid-spined macronarian taxa include *Camarasaurus* (Osborn and Mook, 1921), *Dongyangosaurus* (Lü et al., 2008), *Euhelopus* (Wiman, 1929), *Erketu* (Ksepka and Norell, 2006), *Huabeisaurus* (Pang and Cheng, 2000), *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977), *Phuwiangosaurus* (Martin et al., 1999), *Qiaowanlong* (You and Li, 2009), and *Tangvayosaurus* (Allain et al., 1999). Bifid neural spines are also present in the probable titanosauriforms *Mongolosaurus* (Gilmore, 1933) and an unnamed taxon from Inner Mongolia (M. D'Emic, pers. comm).

Remes (2007) listed bifid neural spines in *Australodocus* as a synapomorphy linking that taxon with diplodocids. The bifid neural spine in *Australodocus* differs in form from those seen in diplodocids, however. In *Australodocus*, the metapophyses are connected medially by a horizontally oriented, dorsoventrally compressed “shelf.” In the mid-cervical vertebrae of *Apatosaurus* and *Diplodocus*, which are more deeply bifid than those of *Australodocus*, there is no lamina connecting the two metapophyses. *Barosaurus*, which in one specimen (CM 11984) probably preserves cervical vertebrae 6 and 7, has only shallowly bifid anterior and mid-cervical neural spines, similar in some regard to those of *Australodocus*. These spines lack the horizontal “shelf” seen in *Australodocus*, however. More posterior vertebrae (AMNH 3461, CM 11984) are increasingly bifid, and also lack the horizontal shelf.

Pre-Epipophysis on Prezygapophyses

The prezygapophyses in some sauropod cervical vertebrae carry an accessory process that extends anterior to the margin of the prezygapophysis. This structure has been variously termed the “pre-epipophysis” (Wilson and Upchurch, 2009) and the “accessory anterior process” (Serenó et al., 1999). This process is common in titanosauriforms, appearing in at least *Brachiosaurus* (MB.R. 2180.25; SII; Janensch, 1950:fig. 37), *Erketu* (cervical vertebrae 4 and 5, IGM 100/1803; Ksepka and Norell, 2006), *Euhelopus* (Wilson and Upchurch, 2009), *Malawisaurus* (anterior- and mid-cervical vertebrae, Mal-278-2, Mal-278-3, Mal-

280-2; Gomani, 2005), *Phuwiangosaurus* (mid-cervical vertebra, P.W.1-2; Martin et al., 1999), and *Sauroposeidon* (cervical vertebrae 8, OMNH 53062; Wedel et al., 2000). This process also rarely occurs in diplodocids as a narrow lateral shelf along the prezygapophysis, but only rarely does it form a process, as seen in *Apatosaurus* (CM 3018; Gilmore, 1936) and (in one vertebra) in *Diplodocus* (CM 84; Holland, 1906). A process appears with slightly more regularity in the diplodocid *Barosaurus* (CM 11984). In *Barosaurus*, the pre-epipophysis is a dorsoventrally tall, laterally compressed sheet unlike the dorsoventrally compressed, laterally prominent pre-epipophysis seen in the titanosauriforms above. A pre-epipophysis also appears in the non-neosauropods *Jobaria* (Serenio et al., 1999), *Mamenchisaurus* (cervical vertebrae 15 and 16, ZDM0083; Ouyang and Ye, 2002) and *Shunosaurus* (Dong et al., 1983).

Remes (2007) listed a pre-epipophysis as an autapomorphy of *Australodocus*. This process is most strongly developed on the right prezygapophysis of the holotypic vertebrae, as a large, laterally keeled process, beginning just anterior to the prezygapophyseal pneumatic cavity dorsally and extending well beyond the lateral anteroventral corner of the prezygapophysis. The robust nature of this process is most similar to that seen in titanosauriforms and unlike the weakly developed pre-epipophysis seen occasionally in diplodocids.

Prezygapophyseal facet shape in cervical vertebrae

The diplodocid sauropods *Barosaurus* and *Diplodocus* have transversely convex

articular facets on the prezygapophyses. Remes (2007) identified these facets as being present in *Australodocus* also, uniting that taxon with Diplodocidae. This character is also present in examined specimens of *Brachiosaurus brancai* (MB.R. 2180.24–28, MB.R.2181.42–44, MB.R.2181.47), however, and may be more widely distributed than previously thought.

Vertebral Laminae

Accessory laminae. In some specimens of *Brachiosaurus brancai* (MB.R. 2180.22), an accessory lamina occurs slightly ventral and parallel to the posterior centrodiapophyseal lamina (pcdl). This lamina is wholly distinct from the dorsal margin of the lateral pleurocoel. No such lamina is present in *Apatosaurus*, *Barosaurus*, or *Diplodocus*, and it is probably absent in *Tornieria*, although the only well-preserved cervical vertebra has since been lost (Remes, 2006) and the condition cannot be determined with certainty from the published photograph (Janensch, 1929:pl. VIII).

An identical lamina occurs on the left side of the centrum in the holotype vertebra of *Australodocus*, and on the right side of the centrum in the paratype. These laminae bound a teardrop-shaped cavity with its deepest concavity just posteroventral to the diapophysis, as in *Brachiosaurus*.

Prespinal laminae. A prespinal lamina (prsl) is occasionally noted in cervical vertebrae of sauropod taxa with single neural spines, but never in the cervical spines of taxa with bifid neural spines (Wilson, 1999). A prsl is reported by

Remes (2007:text-fig. 3) in the holotype vertebra, although it is absent in the paratype. It appears roughly confluent with the “median tubercle” at its dorsal terminus in *Australodocus*, and is in an equivalent position to an elongate tubercle seen in multiple specimens of *B. brancai* (i.e. MB.R.2180.24, MB.R.2180.25, MB.R.2180.27).

Bifurcate centroprezygapophyseal laminae. A bifurcate centroprezygapophyseal lamina (cprl) is characteristic of diplodocid sauropods. In those taxa, the two branches of the cprl originate along the same plane along the anteroposterior axis, and both connect the centrum with the prezygapophyses (see Chapter 2:Fig. 2.3C). A superficially similar condition exists in some other taxa, including *Brachiosaurus brancai*, although the cprl is not truly bifurcate. In those taxa, the dorsal margin of the neural canal often appears in the form of a thin ridge, due to the presence of pneumatic cavities dorsolateral to the neural canal. This thin ridge is commonly mistaken for a medial branch of the cprl (Chapter 4), although the left and right halves of this ridge meet at the midline and do not go to the prezygapophyses.

Although a bifurcate cprl was reported by Remes (2007) as being present in *Australodocus*, it could not be verified in either the holotype or paratype. The condition in *Australodocus* appears to be nearly identical to that of *B. brancai*, with a single lamina connecting the centrum and prezygapophysis, and a narrow, ridge-like neural canal dorsal margin (Fig. 3.3).

Taxonomic Affinities of Australodocus

Australodocus was originally referred to Diplodocidae on the basis of four characters that Remes (2007:662) claimed were unambiguous: bifurcate neural spines with median tubercle, concave ventral surface of centra, bifurcated cprl, and transversely convex prezygapophyseal articular facets. Although *Australodocus* does have apparently bifid neural spines, such structures are regularly observed within Macronaria (e.g., *Camarasaurus*, *Erketu*, *Opisthocoelicaudia*, *Phuwiangosaurus*). Several taxa share ventrally concave centra, including both diplodocids and *Brachiosaurus*. The ‘bifurcated’ cprl is similar in form to the unbifurcated cprl of *Brachiosaurus*, consisting of a robust cprl and a thin lamina overarching the neural canal and meeting the tpri as a rectilinear mass. Finally, transversely convex prezygapophyseal articular facets, although known in diplodocids, are also present in *B. brancai*.

Remes (2007) listed five additional character states that, in combination, were posited to be unique to *Australodocus* within Diplodocidae: 1) mid-cervical vertebrae moderately elongate ($EI > 4.0$); 2) broad, shelf-like pleurocentral lamina; 3) broad, robust parapophyses; 4) neural arch deep relative to centrum; and 5) lateral ramus of cprl “pillar-like.” In this study, *Australodocus* was found to have an EI significantly smaller than that of *Diplodocus* and *Barosaurus*, but quite similar to that of *Brachiosaurus brancai*. The remaining four characters are all expressed in *B. brancai*, with one caveat—the cprl is not truly divided (sensu Wilson, 2002) in either *Brachiosaurus* or *Australodocus*. *Australodocus* also lacks

the accessory pneumatic fossa on the lateral centrum, a feature present in all diplodocids.

In addition, *Australodocus* shares five putative synapomorphies with *B. brancai*: 1) somphospondylous internal bone texture in presacral centra, 2) internal pneumatization of neural arch, including pre- and postzygapophyses, 3) posterior one-third of centrum without pneumatic camerae, 4) accessory lamina ventral and roughly parallel to pcdl enclosing teardrop-shaped coel, and 5) presence of prsl in mid-cervical vertebrae. Therefore, it is suggested that *Australodocus* be considered a titanosauriform similar to *Brachiosaurus brancai* and not a diplodocid as previously suggested (Remes, 2007). The strong pre-epipophysis and the anteriorly expanded prdl in *Australodocus* distinguish it from *Brachiosaurus brancai*. Whether these differences are sufficient to differentiate them at the generic level is uncertain. In a purely utilitarian sense, the argument is unnecessary—the names as known serve to distinguish between the taxa, regardless of the signifier used—and so *Australodocus* is retained here.

Following the reassessment of this taxon, only a single diplodocid (*Tornieria*) is known from Tendaguru, and tentative referral of all diplodocid materials to that genus is recommended pending further revision of the genus. If there was indeed only a single diplodocid taxon—and only two diplodocoids total—in Tanzania during the Late Jurassic, this suggests that although diplodocids were widely distributed in the Late Jurassic, they were only taxonomically diverse in North America.

LATE JURASSIC SAUROPOD FAUNAS: A COMPARISON

Mateus (2006) briefly reviewed the similarities between Late Jurassic faunas in Portugal, the United States, and Tanzania, and found significant taxonomic overlap, particularly in Theropoda, but also in two genera of sauropods: *Apatosaurus*, found in the United States and Portugal, and *Brachiosaurus*, known from the United States and Tanzania. *Brachiosaurus* is indeed known from distinct species on both continents (but see Taylor, 2009); no specimen of *Apatosaurus*, however, is currently recognized from Europe. The only published record of *Apatosaurus* outside the United States, *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957), has since been revised and *A. alenquerensis* is now a junior synonym of *Lourinhasaurus alenquerensis* (Dantas et al., 1998). Although both *Apatosaurus* and *Lourinhasaurus* appear in Mateus' (2006) faunal list, no reference was listed for the *Apatosaurus* material. *Lourinhasaurus* is generally considered a macronarian similar to *Camarasaurus* (McIntosh, 1990; Wilson and Sereno, 1998; Mateus, 2006), and is not a member of the diplodocoid lineage. There is no known generic overlap between the Late Jurassic sauropod fauna of Patagonia and other Late Jurassic faunas, although an unnamed, fragmentary sauropod from Chubut (Argentina) was indistinguishable from *Brachiosaurus* in a phylogenetic analysis (Rauhut, 2006). Below and in Table 3.3, I review the distribution of macronarian and diplodocoid genera in the Late Jurassic.

Macronaria

Macronarians appear in Late Jurassic faunas in all four regions: the United States, Portugal, Tanzania, and Patagonian Argentina. Basal macronarians (*Camarasaurus*, *Lourinhasaurus*) are definitively known only from Portugal and the United States. Although some materials from the Kadzi Formation of Zimbabwe (equivalent to Tendaguru in Tanzania) have been tentatively referred to *Camarasaurus* (Raath and McIntosh, 1987), they are notably incomplete. *Camarasaurus* is quite common throughout the Morrison formation, however (Dodson et al., 1980).

Titanosauriforms also appear in all four faunas, being notably more generically diverse in Gondwana than in Laurasia. *Lusotitan* in Portugal and *Brachiosaurus altithorax* in the United States are the only Laurasian representatives, while Tanzania has three (*Australodocus*, *Brachiosaurus brancai*, and *Janenschia*) and Argentina two (*Tehuelchesaurus* and the unnamed Chubut brachiosaur). *Tehuelchesaurus* has been suggested to be a basal macronarian, however, more closely allied with *Camarasaurus* (Salgado and Bonaparte, 2007). *Brachiosaurus* is by far the most common sauropod in Tendaguru (Russell et al., 1980), although it is rare in Morrison deposits and restricted to the Brushy Basin (Wyoming, USA; Dodson et al., 1980).

Although the United States has at least twice the generic sauropod diversity of the other three faunas individually, it has a proportionally small number of macronarian genera (25%). Elsewhere, macronarians make up 60-66% of sauropod faunas. Absolute generic diversity is relatively consistent among

faunas, however, with each fauna having either two or three macronarians present. Basal forms are definitively present only in Laurasia, although an argument could be made that *Tehuelchesaurus* and the referred Kadzi *Camarasaurus* materials indicate the coexistence of basal macronarians and titanosauriforms worldwide.

Diplodocoidea

Representatives of Diplodocoidea are known from all four faunas. Diplodocids are known only from the United States, Portugal, and Tanzania. Dicraeosaurids are definitively known only from Gondwana, although the Morrison sauropod *Suuwassea* has been suggested to be a dicraeosaurid (Salgado et al., 2006; Whitlock and Harris, in press; Chapter 4), and certainly displays a number of characteristics of that group (Harris, 2006; Whitlock and Harris, in press; Chapter 4).

Diplodocids are by far most commonly found in the Morrison Formation of the United States, with at least five valid genera known (excluding *Suuwassea*), more than any other sauropod group, diplodocoid or otherwise, from a single formation in the Late Jurassic. *Dinheirosaurus* in Portugal and *Tornieria* are the remaining representatives of the group. Although it has been suggested (Remes, 2006; 2009) that there may be another diplodocid from Tanzania, distinct from *Tornieria*, this has not yet been demonstrated. Dicraeosauridae is represented by at least two genera, *Dicraeosaurus* in Tanzania and *Brachytrachelopan* in Argentina; as mentioned previously, *Suuwassea* may also be a member of this

group.

Aside from the Morrison Formation, diplodocoids make up a proportionally small percentage of most faunas. In those faunas, absolute generic diversity is relatively constant, with only one or two genera known from each formation.

PALEOENVIRONMENTAL RECONSTRUCTIONS

One potential explanation for the taxonomic richness of diplodocids in North America (and the lack thereof elsewhere) is the comparatively unusual ecology of much of the Morrison Formation, particularly with regard to floral assemblages. Although there has not yet been an examination of the flora of the Cañadón Cálcareo Formation (Argentina), comment is possible on the Late Jurassic formations of Portugal, Tanzania, and the United States.

Alcobaça and Lourinhã Formations (Portugal)

Myers (2006) reconstructed the paleoclimate of this region using paleosol data. The recovered data suggest that Late Jurassic Portugal was arid to semi-arid with seasonal variation, similar to the Morrison Formation. Plant fossils also show a great deal of overlap between Portugal and North America, with conifers, cheirolepidiaceans, bennettitales, and true ferns all represented in both regions (Mateus, 2006). Both the Alcobaça and Lourinhã formations have some marine component to them, consistent with near-shore environments (Mateus, 2006).

Morrison Formation (United States)

Plant fossils representing a wide diversity of conifers, ginkophytes, podocarpaceans, ferns, cheirolepidiaceans, and horsetails are known from multiple localities in the Morrison (Tidwell, 1990; Ash and Tidwell, 1998; Parrish et al., 2004). Based on these floras and the inferred requirements of herbivorous dinosaurs, the Morrison Formation was originally interpreted as lush and wet (Tidwell, 1990). However, recent work indicates that the Morrison was largely an arid to semi-arid environment, with a flora dominated by herbaceous (non-woody) plants and low- to mid-height woody shrubs, such as those in the family Podocarpaceae (Parrish et al., 2004). Tall trees and other upper canopy browse were restricted to riparian environments, except in a few localities, such as those of the Salt Wash member (Parrish et al., 2004). The revised view of the Morrison Formation is of an environment roughly equivalent to modern tropical savanna grasslands, with low-growing herbaceous flora such as ferns occupying the vegetation layer dominated by grasses in modern ecosystems (Parrish et al., 2004; Turner and Peterson et al., 2004).

Tendaguru (Tanzania)

The rocks of the Tendaguru formation were deposited in both uplands and tidal flats/coastal regions, although the near-shore environments appear to have been poorly vegetated (Aberhan et al., 2002). The uplands, on the other hand, were highly vegetated, dominated by conifers (including the very tall araucarians; Jarzen, 1981) that would have provided a food source for high-browsing

sauropods. Evergreen shrubs and smaller trees in the family Podocarpaceae are also quite common. Other macroflora include cycads and ginkophyte trees; only two varieties of ferns, either *Dicroidium* or *Pachypteris*-type, have been reported from Tendaguru (Aberhan et al., 2002). Tendaguru, therefore, was dominated by tall, conifer forests (Cheirolepidiaceae and Araucariaceae) and mid-height browse (Podocarpaceae, cycads), with comparatively little ground-level bulk forage (ferns).

SUMMARY

Sufficient data exist to compare both flora and fauna in the Late Jurassic paleoenvironments of two countries: Tanzania and the United States. Paleofloral data for Late Jurassic Portugal and Argentina are too incomplete to make a useful comparison. The Morrison was dominated by low browse and diplodocoid sauropods, whereas Tendaguru was dominated by high browse and macronarian sauropods. If diplodocoids were low-browsers, as has been suggested (Serenon et al., 2007), this may explain their diversification where low-browse dominated.

CONCLUSIONS

Based upon the morphological evidence presented here, *Australodocus* is more likely to have been a titanosauriform sauropod than a diplodocoid. As a consequence, the relative diversity of macronarian and diplodocoid sauropods in the Tendaguru is more like that of other Late Jurassic sauropod faunas, which are dominated by macronarians. Although most faunas are macronarian-rich,

generic diversity is similar between macronarian and diplodocoid sauropods in the Late Jurassic. This pattern may be related to paleoecology: the lone diplodocoid-dominated paleoecosystem (the Morrison Formation) is also the only one dominated by low browse, and the diversity of diplodocoids in the Morrison exceeds that of any individual macronarian fauna. The other well-known paleoecosystem, Tendaguru, was dominated by high browse and macronarian sauropods. This relationship will be explored in more depth in Chapter 5, in a discussion of feeding ecology of diplodocoid sauropods.

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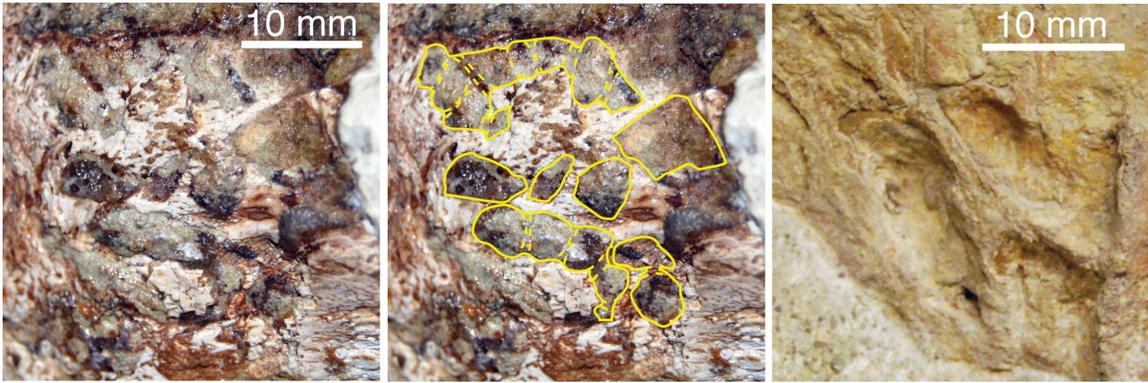


Figure 3.1. Internal bone texture. A, B: Paratypic vertebra (MB.R. 2454) of *Australodocus*, displaying multiple small (millimeter-scale) pneumatic cavities, or camellae. A, unaltered photo; B, photo from A with sediment-filled cavities highlighted. C: Seventh (?) cervical vertebra of *Barosaurus* (CM 11984), illustrating size and shape difference between internal pneumatic structures associated with diplodocids and those of *Australodocus*.

Figure 3.2 (Facing page). Representative mid-cervical vertebrae in right lateral view, scaled to centrum length. A: *Australodocus bohetii* holotype vertebra (MB.R. 2455). B: *Brachiosaurus brancai* (MB.R. 2160.25). C: *Barosaurus lentus* (CM 11984). D: *Diplodocus carnegii* (CM 84, redrawn from Holland, 1906). E: *Tornieria africana* (specimen lost, redrawn from Janensch, 1929). Abbreviations: na pnc, neural arch pleurocoel; poz, postzygapophysis; prep, pre-epipophysis; prz pnc, prezygapophyseal pleurocoel; vlpf, ventrolateral pneumatic fossa. Note the presence of na pnc and prz pnc on *Australodocus* and *Brachiosaurus* only, and the restriction of the vlpf to diplodocids *Barosaurus*, *Diplodocus*, and *Tornieria*.

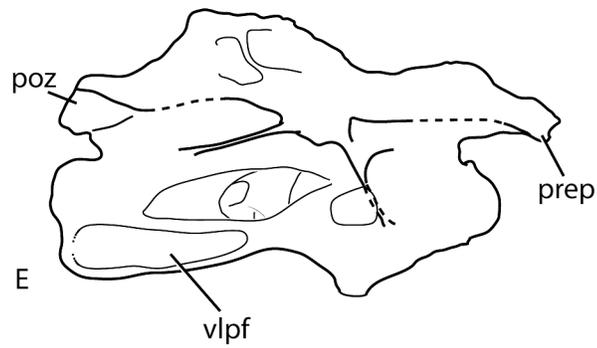
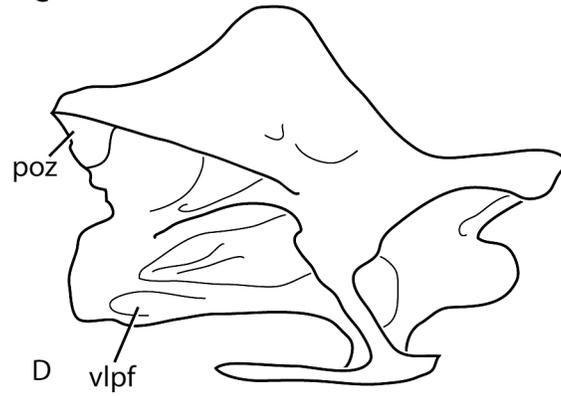
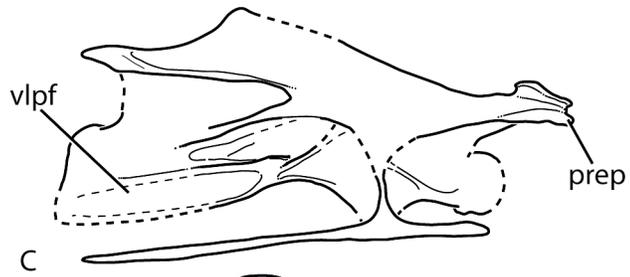
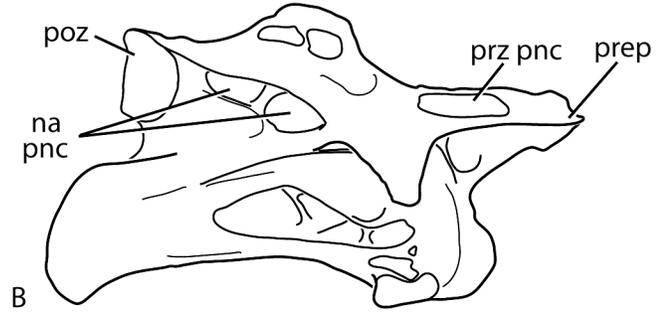
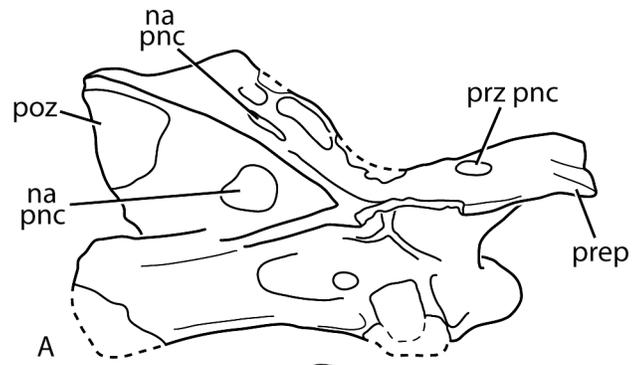


Figure 3.3 (Facing page). Holotype vertebra of *Australodocus bohetii* (MB.R. 2455) in right lateral (A), anterior (B), and left lateral (C) views. Note presence of prespinal lamina (prsl) and undivided centroprezygapophyseal laminae (cpri). Grey areas represent plaster reconstruction; hatching indicates broken bone. Abbreviations: acdl, anterior centrodiaepophyseal lamina; apcdl, accessory posterior centrodiaepophyseal lamina; cpol, centropostzygapophyseal lamina; cpri, centroprezygapophyseal lamina; nc, neural canal; pcdl, posterior centrodiaepophyseal lamina; podl, postzygodiaepophyseal lamina; poz, postzygapophysis; prdl, prezygodiaepophyseal lamina; prsl, prespinal lamina; sprl, spinoprezygapophyseal lamina. Scalebar = 5 cm.

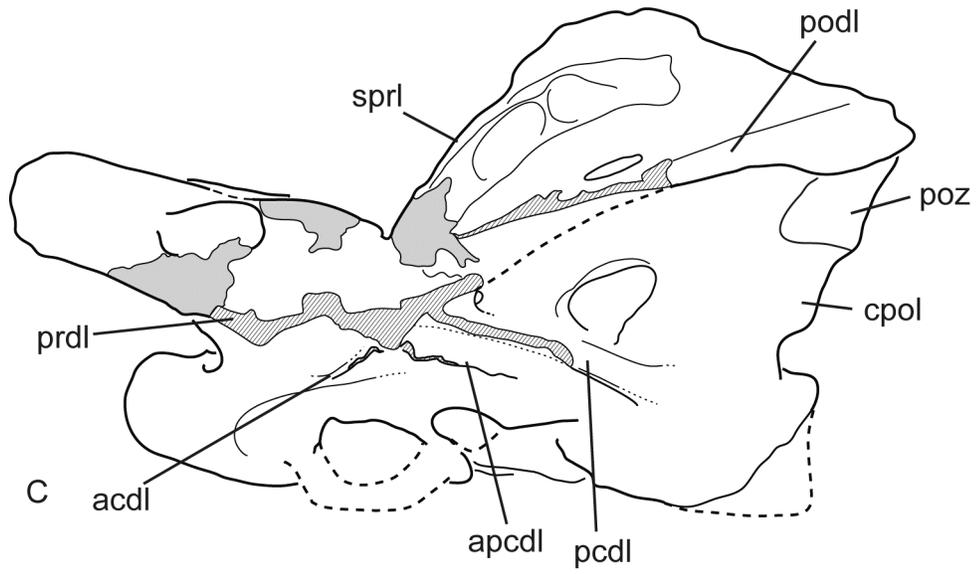
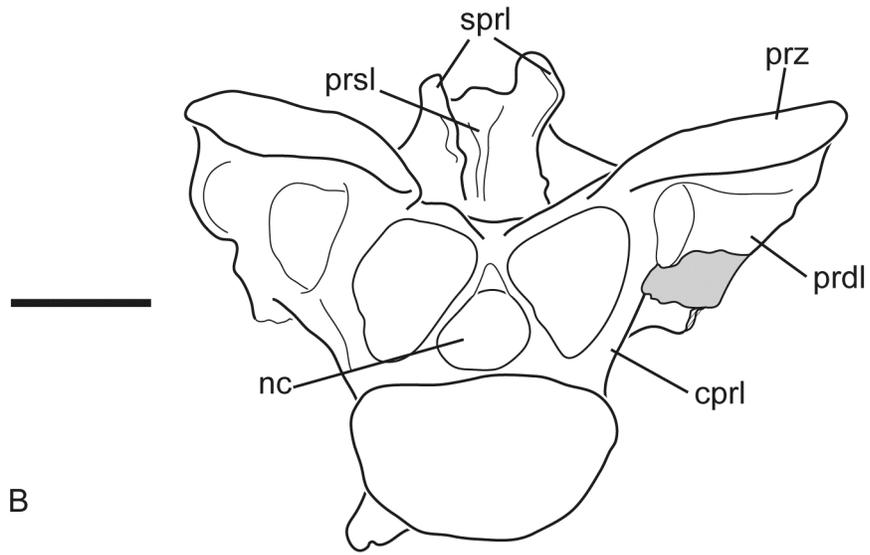
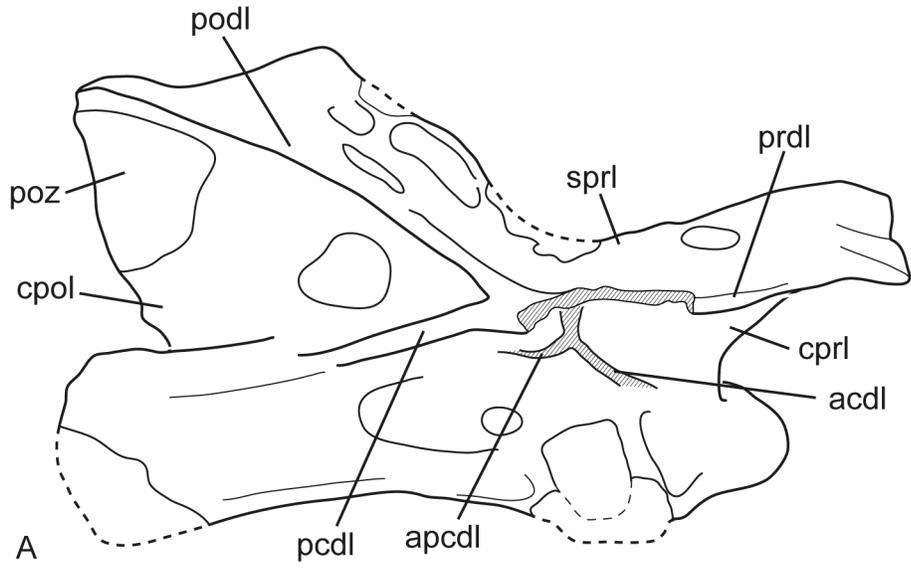


Table 3.1. Elongation index (EI) for *Australodocus* and six relevant sauropod taxa, reported for cervical vertebrae 6-8. No aEI is reported for *Sauroposeidon*; posterior centrum widths are unavailable for that taxon.

Taxon	Specimen	#	EI	aEI	Reference
<i>Australodocus bohetii</i>	MB. R. 2454	7?	4.00	3.80	Remes, 2007
<i>Barosaurus lentus</i>	AMNH 6341	8	5.37	5.04	McIntosh, 2005
<i>Diplodocus carnegii</i>	CM 84	6	5.26	4.91	Hatcher, 1906
<i>Diplodocus carnegii</i>	CM 84	7	5.05	4.69	Hatcher, 1906
<i>Diplodocus carnegii</i>	CM 84	8	4.53	4.63	Hatcher, 1906
<i>Apatosaurus lousiae</i>	CM3018	6	3.27	3.09	Gilmore, 1936
<i>Apatosaurus lousiae</i>	CM3018	7	3.14	2.72	Gilmore, 1936
<i>Apatosaurus lousiae</i>	CM3018	8	3.30	2.56	Gilmore, 1936
<i>Brachiosaurus brancai</i>	SI (?)	6	4.61	3.73	Janensch, 1950
<i>Brachiosaurus brancai</i>	be	6	4.07	3.75	Janensch, 1950
<i>Brachiosaurus brancai</i>	SI (?)	7	3.13	3.33	Janensch, 1950
<i>Brachiosaurus brancai</i>	SII	8	4.02	3.99	Janensch, 1950
<i>Sauroposeidon proteles</i>	OMNH 53062	6	6.10	n/a	Wedel et al., 2000
<i>Sauroposeidon proteles</i>	OMNH 53062	7	5.59	n/a	Wedel et al., 2000
<i>Sauroposeidon proteles</i>	OMNH 53062	8	4.63	n/a	Wedel et al., 2000
<i>Paluxysaurus jonesi</i>	FWMSH 93B-10-28	6	4.82	5.48	Rose, 2007

Table 3.2. Average elongation index (EI) and average elongation index (aEI) for *Australodocus* and six relevant sauropods, based on Table 3.1. No aEI is reported for *Sauroposeidon*; posterior centrum widths are unavailable for that taxon.

Taxon	EI	aEI
<i>Australodocus bohetii</i>	4.00	3.80
<i>Barosaurus lentus</i>	5.37	5.04
<i>Diplodocus carnegii</i>	4.95	4.74
<i>Apatosaurus lousiae</i>	3.24	2.79
<i>Brachiosaurus brancai</i>	3.92	3.68
<i>Sauroposeidon proteles</i>	5.44	n/a
<i>Paluxysaurus jonesi</i>	4.82	5.48

Table 3.3. Distribution of taxa in each of four Late Jurassic terrestrial faunas. Note high diplodocid diversity in the Morrison, combined with relative paucity of Macronarian taxa. Data from Harris and Dodson (2004), Rauhut (2006), Rauhut et al. (2005), Remes (2007), and Upchurch et al. (2004). Asterisks denote tentative assignment to that clade.

	Formation			
	Lourinhã	Morrison	Tendaguru	Cañadon Cálcareo
Diplodocidae	<i>Dinheirosaurus</i>	<i>Amphicoelias*</i> <i>Apatosaurus</i> <i>Barosaurus</i> <i>Diplodocus</i> <i>Supersaurus</i>	<i>Tornieria</i>	
Dicraeosauridae		<i>Suuwassea*</i>	<i>Dicraeosaurus</i>	<i>Brachyrachelopan</i>
Macronaria	<i>Lusotitan</i> <i>Lourinhasaurus</i>	<i>Brachiosaurus</i> <i>Camarasaurus</i>	<i>Australodocus</i> <i>Brachiosaurus</i> <i>Janenschia*</i>	Chubut TSF <i>Tehuelchesaurus</i>

CHAPTER 4

PHYLOGENETIC ANALYSIS OF DIPLODOCOIDEA

Diplodocoid sauropods, such as *Diplodocus* and *Apatosaurus*, with their long necks and tails and immense size, are among the most iconic and easily-recognized dinosaurs, with a rich palaeontological history dating back into the late 19th century. In particular, diplodocoids have been identified by their unique cranial anatomy: an antorbitally elongate skull with a broad, variably-rectangular muzzle, filled only at its distal extreme with long, narrow-crowned teeth. This morphology varies both taxonomically and ontogenetically; the narrowest snouts are known from juveniles (Whitlock, Wilson & Lamanna, 2010), although intraspecific adult variation also occurs, from the round-snouted *Dicraeosaurus* to the extremely square snout of *Nigersaurus*, with its nearly linear, orthogonally oriented tooth row (Sereno et al., 1999). This variation in shape has been suggested to correspond with specialized feeding behavior (Calvo, 1994), including low-browsing (Barrett & Upchurch, 1994; 2005; Christiansen, 2000; Upchurch & Barrett, 2000; Sereno et al., 2007; Whitlock et al., 2010). This hypothesis is supported by work demonstrating a semi-horizontal neck posture in the clade, in contrast to the more vertical neck posture of other sauropods (Stevens & Parrish, 1999). In addition, diplodocoids are easily recognized by a

series of elongate, biconvex caudal vertebrae, forming a ‘whiplash’ at the posterior extreme of the tail (Wilson, 2005a).

Diplodocoids also display an impressive range of adult body sizes, from the immense, ≥ 30 m long *Supersaurus* (Lovelace et al., 2008) to the diminutive *Brachytrachelopan*, which is no greater than 10 m in length (Rauhut et al., 2005). Similar size variation is also found within a single subgroup, Rebbachisauridae: *Rebbachisaurus* is represented by a very large dorsal vertebra and scapula that imply an animal roughly equivalent in size to *Apatosaurus*, whereas *Nigersaurus* was probably no more than 9 m in total length (Serenó et al., 2007).

Although diplodocoids were once known almost exclusively from the Late Jurassic Morrison and Tendaguru formations, recent discoveries in South America and northern Africa have resulted in the addition of 13 new diplodocoid genera since 1991, increasing the known diversity by nearly 150%. The greatest surge in known diversity has occurred post-2002, representing almost one-third of the total known generic diversity (Fig. 4.1). A basic phylogenetic arrangement of these sauropods into three groups—Dicraeosauridae, Diplodocidae and Rebbachisauridae—has emerged as a result of these new discoveries (Fig. 4.2). The rebbachisaurid sauropods in particular represent an important temporal range extension from the Late Jurassic into the Late Cretaceous (Calvo and Salgado, 1995). Unfortunately, much remains uncertain about the intergeneric relationships of many taxa, including both long-known but fragmentary genera

like *Haplocanthosaurus* and newly-discovered genera like *Suuwassea* and the rebbachisaurids.

Because these relationships remain uncertain, the morphological, geographic and temporal diversity of the group cannot be fully understood in an evolutionary context. Many prior analyses have had varying degrees of success in answering these questions, but to date no analysis has satisfactorily presented a well-resolved hypothesis of descent from which to begin. This study begins by reviewing recent analyses and explaining why so much uncertainty remains in diplodocoid phylogeny. In the second section, a new phylogeny, inclusive of all diplodocoid taxa, is presented and the results compared with prior analyses. The final section examines the paleobiogeographic relationships of the group in light of this new phylogeny.

ABBREVIATIONS

Institutions. AMNH, American Museum of Natural History, New York; ANS, Academy of Natural Sciences, Philadelphia; BYU, Brigham Young University, Vertebrate Paleontology Collection, Provo; CCC, Casa de Cultura do Município de Coroaá, Coroaá; CM, Carnegie Museum of Natural History, Pittsburgh; CMC, Cincinnati Museum Center, Cincinnati; CMNH, Cleveland Museum of Natural History, Cleveland; MACN, Museo Argentino de Ciencias Naturales “B. Rivadavia,” Buenos Aires; MB, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin; MIWG, Dinosaur Isle Visitor Centre, Sandown; MNHN, Muséum National d’Histoire Naturelle, Paris; MNN, Musée National du Niger, Niamey;

MOR, Museum of the Rockies, Bozeman; MOZ, Museo “Prof. Dr. Juan Olsacher,” Zapala; MPCA, Museo Provincial Carlos Ameghino, Cipolletti; MPEF, Museo Paleontológico Egidio Feruglio; MUCPv, Museo de Geología y Paleontología, Neuquén; PMU, Palaeontological Museum, University of Uppsala, Uppsala; USNM, United States National Museum, Washington D.C.

PRIOR CLADISTIC ANALYSES

Since 1995, there have been 11 numerical phylogenetic analyses dealing specifically with diplodocoid interrelationships, and several other, larger analyses that also included a large number of diplodocoids (Table 4.1). The results of these analyses are largely consistent with each other, not only in the relationships of the taxa that are fully resolved, but also in the taxa whose relationships remain uncertain; in particular, the relationships of *Amazonsaurus*, *Suuwassea*, *Haplocanthosaurus* and all interrelationships within Rebbachisauridae are ambiguous. The relationships that are most consistent (e.g., *Apatosaurus* as sister taxon to a clade containing *Barosaurus* and *Diplodocus*; Rebbachisauridae as sister clade to the clade containing Diplodocidae and Dicraeosauridae) are the oldest hypothesized relationships, many of which pre-date the use of numerical phylogenetic analyses. Despite nearly 15 years of continuous effort on the part of multiple workers to resolve additional relationships, little traction has been gained on that front. It would be hard to argue that the relationships examined here are not highly complex and difficult to resolve, but with so many workers remaining largely unsuccessful, there may be more to the problem than internal complexity.

One such potential stumbling block is the incompleteness of materials. Many of the earliest described taxa, such as *Diplodocus* and *Apatosaurus*, are known from relatively complete skeletons, including skulls. Those taxa, along with other mostly complete taxa of a more recent coinage, such as *Amargasaurus*, are commonly recovered in well-resolved relationships. Poorly-known taxa, such as *Rayososaurus*, are universally unresolved when included in phylogenetic analyses. However, some taxa (e.g., *Limaysaurus*, *Nigersaurus*, *Suuwassea*) preserve many elements from multiple body regions but are still unresolved phylogenetically. This ambiguity demonstrates that the effects of fragmentary or otherwise incomplete taxa are more dependent on the characters and other taxa included in the matrix than pure incompleteness (Kearney, 2002; Kearney and Clark, 2003).

More probably, then, the ambiguity is a result of the data included in each analysis. Taxonomic scope varies greatly among analyses (Table 4.2), although it is always narrower than the recognized diversity of diplodocoids (Fig. 4.3). Novel character data are typically a low proportion of the total, and of those there are few generic-level synapomorphies (Table 4.1). This influx of new character data are typically swamped by the influx of additional taxa (Table 4.2), diluting the pool of potential synapomorphies and reducing the power of the matrix to resolve relationships. Therefore, in order to examine the causes behind the observed pattern—old relationships consistently recovered, old uncertainties maintained and new taxa recovered in uncertain positions—a comparison of the underlying data and not simply the topologies resulting from them must be

undertaken. A subset of the comparative cladistic methods proposed by Sereno (2009) can be used to directly compare the data behind the four most complete analyses (Rauhut et al., 2005; Salgado et al., 2006; Harris, 2006c; Sereno et al., 2007) with each other and with (Wilson, 2002), the analysis explicitly used as a starting point for these and other recent diplodocoid-centric phylogenetic analyses (e.g., Lovelace et al., 2008). Of the 234 characters used in the matrix assembled by Wilson (2002), 64% were re-sampled from prior sources, primarily Wilson and Sereno (1998) but also others (e.g., Salgado and Bonaparte, 1991; Calvo and Salgado, 1995; Upchurch, 1995; 1998; Sereno et al., 1999). The overall proportion of resampled character data is lower (46%) if we also consider the autapomorphies listed in appendices, but the issue is not the quantity of resampling but the degree to which those data make up the basis for subsequent analyses focused on questions at different taxonomic scales. Comparisons to the analysis of Wilson (2002), therefore, are both consistent with the data attribution given by the relevant authors and a convenient way to examine the effects of a re-used dataset originally compiled for a different scale of analysis. Each of the four analyses is introduced below, followed by further comparative analysis.

Rauhut et al. (2005)

The analysis of Rauhut et al. (2005) was, prior to this analysis, the most taxonomically inclusive, with 15 diplodocoids (Table 4.2). Twelve additional outgroup taxa were also included, and all 27 taxa were scored for 154 characters.

The recovered topology is primarily interesting here for its resolution of *Suuwassea* as a basal diplodocid. The relationships of the rebbachisaurids and the diplodocids *Barosaurus*, *Dinheirosaurus*, *Diplodocus* and *Tornieria* are unresolved. *Amazonsaurus* was recovered as a titanosauriform, and *Haplocanthosaurus* was recovered outside Neosauropoda.

Salgado et al. (2006)

Salgado et al. (2006) included 12 diplodocoid taxa scored for 37 characters (Table 4.2). This analysis recovered *Amazonsaurus* in a polytomy with the rebbachisaurid taxa *Limaysaurus*, *Nigersaurus*, and *Rebbachisaurus*, linked by the presence of petal-shaped neural spines in either the posterior dorsal, sacral, or anterior caudal vertebrae, a reformulation of the Wilson (2002) character which concerned the dorsal vertebrae only. This result is in conflict with the recovered topology of Rauhut et al. (2005), although the analysis of Salgado et al. (2006) did not include any titanosauriform taxa and therefore could not have arrived at the same conclusion, regardless of the final position of *Amazonsaurus* in their cladogram. *Suuwassea* was resolved by Salgado et al. (2006) as a basal dicraeosaurid. *Zapalasaurus* and *Haplocanthosaurus* were recovered as basal diplodocids.

Harris (2006c)

Harris (2006c) included 10 diplodocoids in a sample of 30 sauropods scored for 331 total characters (Table 4.2). No resolution regarding the internal

relationships of Rebbachisauridae or the phylogenetic placement of *Suuwassea* within Flagellicaudata was recovered. *Haplocanthosaurus* was recovered as a non-neosauropod.

Sereno et al. (2007)

The analysis of Sereno et al. (2007) included a large number of rebbachisaurids but comparably few other diplodocoids (Table 4.2). Those taxa and three outgroups (*Jobaria*, *Macronaria* and *Omeisaurus*) were scored for 102 characters.

Sereno et al. (2007) were unable to resolve the position of *Suuwassea* relative to Dicraeosauridae and Diplodocidae. The analysis did recover a fully resolved Rebbachisauridae, however, inclusive of *Zapalasaurus*.

Comparative Cladistics

As noted by Sereno (2009) and Sereno and Brusatte (2009), topological comparisons are incapable of assessing the fundamental similarities and differences in data, specifically those that resulted in the differences in topologies previously discussed. Neither are they capable of fully exploring areas where data coverage (and thereby phylogenetic resolution and accuracy) might be improved. As noted above, the data behind each analysis must be compared to that of other analyses in order to establish areas of data deficiency and conflict. The comparative method used here, following Sereno (2009), involves two steps:

(1) establishing shared taxonomic scope, and (2) isolating and characterizing relevant data.

Shared taxonomic scope. The shared taxonomic scope (those taxa common to multiple analyses) is a way of visually representing the degree to which these analyses address the same problems (Sereno, 2009). In this case, the problem involves the interrelationships of diplodocoids. Although each of the recent analyses includes a different taxonomic sample, using the method outlined by Sereno (2009), each of the four analyses being compared can be reduced to a shared taxon set, and a consensus cladogram generated (Fig. 4.4). For two cladograms (Salgado et al., 2006; Sereno et al., 2007), the outgroup taxon (Camarasauromorpha and Macronaria, respectively) was represented by an exemplar taxon (*Camarasaurus*) to match the remaining analyses.

The shared taxonomic scope illustrates that some phylogenetic hypotheses were investigated by each analysis (i.e., the interrelationships of some rebbachisaurids, the position of *Suuwassea*), but others—the relationships of *Amazonsaurus*, *Haplocanthosaurus* and many putative rebbachisaurids such as *Zapalasaurus*—were outside their comparative scope.

Data characterization. There are 96 unique, informative characters among the reduced analyses as described above. Of these, 63 (66%) first appeared in the matrix of Wilson (2002), and a further 13 (14%) were taken from the matrix of

Upchurch et al. (2004; Fig. 4.5). The vast majority (80%) of the pooled character data, then, was taken from analyses that did not, and in some cases (i.e., *Suuwassea*) could not, resolve the outstanding phylogenetic questions common to all more recent analyses: the phylogenetic placement of *Suuwassea* and the interrelationships of rebbachisaurids. No analysis included more than 77 informative characters (80% of the total; Sereno et al., 2007). Harris (2006c; 65) and Rauhut et al. (2005; 48) included fewer informative characters. The analysis of Salgado et al. (2006) included only 24 informative characters after pruning.

If the analyses of Wilson (2002) and Upchurch et al. (2004) are taken as the starting points for subsequent analyses, only two of the four analyses add relevant characters: Rauhut et al. (2005) and Sereno et al. (2007; Fig. 4.5). The analysis of Sereno et al. (2007) is the only one to add characters that are informative regarding rebbachisaurid interrelationships; it is not surprising, then, that it is the only analysis—including those not directly compared here—to resolve relationships within the group. The second question, the affinities of *Suuwassea*, requires more investigation.

Two analyses, Harris (2006c) and Sereno et al. (2007), were unable to resolve the position of *Suuwassea* relative to Diplodocidae and Dicraeosauridae. Although the analysis of Rauhut et al. (2005) resolved the position of *Suuwassea* as a basal diplodocid, it did not add any character data supporting that conclusion, which was supported only by a combination of characters used in previous analyses (decay index = 1). However, one character added in that

analysis, narrowly diverging posterior cervical and anterior dorsal neural spines, supports the alternative placement of *Suuwassea* as a basal dicraeosaurid. Similarly, the analysis of Salgado et al. (2006) did not add any relevant character data to resolve the position of *Suuwassea*, although that taxon was resolved as a basal dicraeosaurid. Despite sharing nearly all of the pertinent character data regarding the relationship of *Suuwassea*, the analyses of Rauhut et al. (2005) and Salgado et al. (2006) recover different results. The character state similarity index, or CSSI (Sereno, 2009), may help explain this result. The CSSI measures the discrepancy in scorings for shared characters in two analyses, and is obtained using the following formula (from Sereno, 2009):

$$\text{CSSI} = (\text{tcs} - (\text{csc} + 0.5(\text{csd}))) / \text{tcs}$$

where tcs = total number of character states, csc = character state conflicts (e.g., 0 vs. 1), and csd = character state discrepancies (e.g., ? vs 1).

The analyses of Rauhut et al. (2005) and Salgado et al. (2006) share 200 total character states (eight taxa scored for 25 characters). Within those 200, there are 14 character state conflicts and 17 character state discrepancies, for a CSSI of 0.89 (Table 4.3). One character, (Rauhut et al., 2005 character 75; Salgado et al., 2006 character 11) has an apparent scoring conflict, but this is instead the result of the reformulation of a multi-state character into a binary character by Salgado et al. (2006); the states 1 and 3 are equivalent for this analysis and so are not considered in conflict. Other instances where this occurs (e.g., characters 8 and 31 in Salgado et al., 2006) do in fact represent distinct

states and are considered scoring conflicts. None of the character state conflicts involved the scorings of *Suuwassea*.

The CSSI indicates that 11% of the scorings in the two analyses differ; this is a surprisingly high amount of disparity. However, reversing the scorings for Salgado et al. (2006) does not result in reversing the placement of *Suuwassea*. Character state conflict does not appear to be the root cause of the ambiguous position of *Suuwassea*. In light of the fact that the original sources for much of the character data (Wilson, 2002; Upchurch et al., 2004) could not score *Suuwassea* and that only a single relevant character has been added that impacts its relationships, it appears that character data have had little impact on the placement of *Suuwassea* in any way. Instead, *Suuwassea* appears to be difficult to place because of a lack of relevant character data.

Comparative cladistics summary

The uncertainty surrounding some relationships, particularly rebbachisaurids, can be explained by a combination of poor taxonomic sampling and the addition of few, or more commonly, no characters that act as lower-level synapomorphies. The vast majority of data in each analysis are recycled from analyses (Wilson, 2002; Upchurch et al., 2004) that were themselves unable to resolve the phylogenetic relationships of some groups (i.e., Rebbachisauridae), either because they pre-date the description of those taxa (e.g., *Suuwassea*) or because no characters were included in the matrices (but see Wilson, 2002;

appendix 4) that could serve as lower-level synapomorphies in their respective matrices.

When new character and taxon data are incorporated, such as in the analysis of Sereno et al. (2007) regarding rebbachisaurid relationships, phylogenetic resolution appears to follow.

In other cases, such as with *Suuwassea*, appropriate character data have yet to be added, and its ambiguous placement is the result of a lack of new character data that tie it to a particular clade.

GENERIC-LEVEL RELATIONSHIPS OF DIPLODOCROID SAUROPODS

ANALYSIS

Twenty-six operational taxonomic units (OTUs) were scored for 189 morphological character statements (169 parsimony-informative). These included three outgroup taxa and 23 ingroup taxa, which included 20 diplodocoids. The character-taxon matrix was created using Mesquite (Maddison and Maddison, 2009). Interrelationships were resolved by parsimony analysis (PAUP* 4.0b10; Swofford, 2002). Due to the high number of OTUs, branch and bound search methods were used in lieu of an exhaustive search. Nine characters are multi-state. Outgroup choice and strategies for scoring character states are discussed below.

Outgroup choice and relationships

The eusauropod outgroups assumed in this study are based on the pattern of lower-level relationships presented by Wilson (2002). The non-neosauropod *Omeisaurus* and the probable non-neosauropod *Jobaria* were chosen as outgroups because a) they are relatively complete and b) they are relatively untransformed, minimizing the number of inapplicable characters and c) they provide the most proximal estimate of character polarity. Two additional non-diplodocoid OTUs, *Brachiosaurus* and *Camarasaurus*, although not explicitly included as outgroup taxa, were chosen to represent basal members of the clades Macronaria and Titanosauriformes. Using two OTUs instead of a single composite Macronaria allows these taxa to link to taxa outside of Diplodocoidea, thus providing a test of membership within that group (see Wilkinson et al., 1998)

Terminal taxa

All valid putative diplodocoid genera (sensu Upchurch et al., 2004) were included in the initial matrix, including *Losillasaurus* and *Australodocus*. The relative paucity of species-level autapomorphies necessitated consolidation of more speciose genera (i.e., *Apatosaurus* and *Diplodocus*) into single generic OTUs. The age, occurrence and original reference for each are summarized in Table 4.4.

Scoring was based on personal observation for *Amargasaurus*, *Amphicoelias*, *Apatosaurus*, *Australodocus*, *Barosaurus*, *Brachiosaurus*, *Brachytrachelopan*, *Camarasaurus*, *Cathartesaura*, *Dicraeosaurus*, *Diplodocus*,

Haplocanthosaurus, *Jobaria*, *Limaysaurus*, *Nigersaurus*, *Rayososaurus*, *Rebbachisaurus*, *Suuwassea*, *Tornieria* and *Zapalasaurus*. *Amazonsaurus*, *Dinheirosaurus*, *Histriasaurus*, *Losillasaurus*, *Nopcsaspondylus*, *Omeisaurus*, *Supersaurus* and the Spanish rebbachisaurid were based on published illustrations, photographs and descriptions. References and specimens used for scoring are listed in Appendix 4.1.

Certain taxa merit further comment to clarify what material was used for scoring. *Amphicoelias* was scored based on the holotype materials (AMNH 5764), exclusive of the tooth crown which was not mentioned in the initial description (Cope, 1877b) and may not belong to the genus (Osborn and Mook, 1921). The additional material provisionally referred to the genus (MOR 592; Wilson and Smith, 1996) was not scored, as the referral is tentative (Wilson JA, pers. comm.). *Barosaurus* was scored entirely on postcranial elements, not including the juvenile anterior cervical vertebrae and partial skull (AMNH 6530 and 7535), because these have not yet been convincingly referred to the genus. *Tornieria* was scored based on the materials assigned to the genus by Remes (2006) as well as on three premaxillae (MB.R. 2343, 2344, 2346), a maxilla (MB.R. 2345), a partial dentary (MB.R. 2348) and a mid-cervical vertebrae figured by Janensch (1929b; pl. 9, fig. 2) that has been subsequently been destroyed (Remes, 2007). *Brachiosaurus* was based entirely on *Brachiosaurus brancai*, the African species; no material from the North American *B. altithorax* was included. *Haplocanthosaurus* was scored from the holotype (*H. priscus*, CM 572), a referred partial skeleton (*H. priscus*, CM 879), the holotype of *H. delfsi*

(CMNH 10380) and two referred hindlimbs, CM 2043 (McIntosh, 1981) and USNM 4275 (McIntosh and Williams, 1988). Following Wilson and Sereno (1998), *Limaysaurus* was considered distinct from both *Rebbachisaurus* and *Rayososaurus*, and the taxa are scored separately. An isolated tooth crown of the appropriate size and type (MNHN MRS 1524a), from the Kem Kem Formation and likely to belong to *Rebbachisaurus garasbae* was included in the scored materials (see 'Rebbachisauridae', below). *Suuwassea* was scored for the holotype materials, as well as a dentary assigned to the holotype later (Whitlock and Harris, in press).

Nemegtosaurus and *Quaesitosaurus*, considered diplodocoids by McIntosh (1990), Upchurch (1995; 1998) and Upchurch et al. (2004), have since been convincingly placed within Titanosauria (Curry Rogers and Forster, 2001; Wilson, 2002; 2005b; Curry Rogers, 2005). They were not been included here.

Additional taxa of note: Three additional specimens, all putative rebbachisaurids, have been recently described but are not yet assigned to a genus. These specimens, a dorsal neural spine (CCC 017; Castro et al. 2007), a dorsal neural arch (MACN PVN35; Apesteguía, 2007) and a partial scapula (MIWG 6544; Mannion, 2008), were scored but not included in the final analysis (see 'Taxon removal', below).

Characters

A total of 189 characters was coded from all regions of the skeleton. Character scoring is summarized in the character-taxon matrix in Appendix 4.2, and character statements are listed in Appendix 4.3. These statements are composed of 75 (40%) cranial, 80 (42%) axial and 34 (18%) appendicular characters. Character data presented result from collections research or are taken from prior analyses, primarily Wilson (2002), Upchurch et al. (2004), Rauhut et al. (2005) and Sereno et al. (2007).

Most character statements are binary, although eight (characters 32, 35, 55, 61, 65, 67, 118, 157) code for two derived states. Two of these characters (35, 65) code for positional changes and are fully ordered. A third (32) codes for a variation in shape that can be reasonably interpreted as directly transformational—the reduction in size of the articular surface of the quadrate from quadrangular to triangular and eventually curvilinear—and is also considered fully ordered. Four (55, 61, 67, 157) that code for variation in shape cannot realistically be interpreted as transformational and are left unordered. For example, the shape of the palatobasal contact has three states: pterygoid with a small facet, a dorsomedially oriented hook, or a rocker-like surface. Unlike the previous example with its successive reduction in size and polygonal complexity, there is no rationale for ordering these states linearly. The final multi-state character (118) codes for variation in size of the neural spine. Wilson (2002) argued that similar characters should be coded as ‘easy loss’ characters. The mechanism by which spine length varies between generations and thus

eventually lineages is uncertain, however, and here coding is based solely on a posteriori examination of character scoring distribution. Those taxa scored a '2' are consistently nested within a grouping of taxa scored '1,' and although there is a single reversal from '1' (*Jobaria* + more derived taxa [MDT]) to '0' (Macronaria) there are no reversals from '2' to '1' or from '2' to '0'. This suggests that this character represents a linear transformation, and is coded as fully ordered.

Several character states listed by Wilson (2002:appendix 4) as autapomorphies were included in the analysis; more inclusive taxon sampling revealed their distribution to be wider than previously hypothesized. The inclusion of autapomorphies in an analysis of this type can also be useful in distinguishing otherwise morphologically similar taxa.

Missing information

Despite representing rather different issues, it is commonly suggested that authors score characters whose states are inapplicable to a taxon (or taxa) as missing, so-called 'reductive coding' (Strong and Lipscomb, 1997). However, the reductive approach inappropriately homologizes the two different conditions; therefore, following Wilson (2002), this analysis uses 'absence coding'—scoring taxa for which a character is inapplicable as '9'.

Taxon removal

After scoring, it was discovered that four OTUs were indistinguishable from other, more complete OTUs: MACN PVN35, MIWG 6544, *Nopcsaspondylus* and

Rayososaurus. MACN PVN35 is represented only by a partial dorsal neural arch, MIWG 6544 by a partial scapula and *Rayososaurus* by two partial scapulae and a partial femur. *Nopcsaspondylus* is now known only from photographs of a single vertebra (Nopcsa, 1902); the original specimen has subsequently been lost. All four OTUs were pruned using the safe taxonomic reduction criteria of Wilkinson and Benton (1995) prior to the final analysis. An assessment of their probable phylogenetic position within Diplodocoidea is discussed below (see 'Relationships of fragmentary taxa', below).

TOPOLOGY

Three equally parsimonious trees (273 steps) were recovered (Fig. 4.6). Clade names discussed in this section are shown on Figure 4.2 and defined in Table 4.5. Both the consistency index (0.740) and the retention index (0.844) are high, indicating a good fit between the morphologic data and the recovered topology. The distribution of synapomorphies was optimized using delayed transformation (DELTRAN) and is reported in Appendix 4.4; autapomorphies are listed in Appendix 4.5. Optimization using accelerated transformation (ACCTRAN) indicates several ambiguous synapomorphies due to missing data at the root of the clade in question; those characters and their optimization under DELTRAN and ACCTRAN are listed in Table 4.6. Below, the content and support for each clade are discussed and compared to previous topologies. Following Wilson (2002), Upchurch, Barrett & Galton (2007) and others, appropriate alternative

hypotheses are tested using Templeton tests; see Larson (1994) for discussion of methodology.

Diplodocoidea

Diplodocoidea, as recovered here, includes Rebbachisauridae, Dicraeosauridae and Diplodocidae, *Haplocanthosaurus*, *Amazonsaurus* and *Amphicoelias* (decay index = 2). As many as 31 additional characters may unite the group but cannot be scored for basal taxa (Table 4.6). As in all previous analyses, Dicraeosauridae and Diplodocidae are united to the exclusion of all other diplodocoids in the clade Flagellicaudata, and Rebbachisauridae is the sister clade to that group. No taxa are recovered on the stem of Flagellicaudata. *Amazonsaurus*, *Amphicoelias* and *Haplocanthosaurus* are recovered on the stem of Diplodocoidea, outside of the clade Rebbachisauridae + Flagellicaudata. These three taxa are commonly recovered within Diplodocoidea, but, with the exception of *Haplocanthosaurus*, are typically placed with more derived taxa.

Haplocanthosaurus

Haplocanthosaurus is recovered here as the basal-most diplodocoid, a placement supported by three synapomorphies: dorsal neural spines with prespinal lamina formed by conjoined spinoprezygapophyseal laminae (character 107); cervical ribs shorter than centrum (152); posterolaterally facing fibular facet of the astragalus (186). This is congruent with the findings of Calvo and Salgado (1995; n.b. *Haplocanthosaurus* was polyphyletic in their analysis), Wilson (2002),

Salgado et al. (2004), Remes (2006), Salgado et al. (2006) and Lovelace et al. (2008). In contrast, Upchurch (1998), Rauhut et al. (2005) and Harris (2006) recovered *Haplocanthosaurus* outside Neosauropoda. A re-analysis of Upchurch (1998) by Upchurch & Martin (2002) was unable to resolve a single position for *Haplocanthosaurus* relative to Neosauropoda, recovering it outside the Neosauropoda, outside Macronaria and outside Titanosauriformes. Re-scoring the matrix of Rauhut et al. (2005) for *Amazonsaurus* (see '*Amazonsaurus*,' below) reduces much of Eusauropoda to a polytomy, including *Haplocanthosaurus*, Rebbachisauridae and Flagellicaudata. In the analysis of Harris (2006), *Haplocanthosaurus* is excluded from Neosauropoda on the basis of one character, morphology of the lateral pneumatic cavity in cervical vertebrae; all other synapomorphies of Neosauropoda in that analysis were unscorable in *Haplocanthosaurus*. This character, with three derived states, has a low CI (0.30) and the most number of steps (10) found in that author's analysis, and *Haplocanthosaurus* itself is scored as having multiple states (0/1), including the state that appears to be primitive for Neosauropoda (1).

Upchurch (1995), Wilson & Sereno (1998), Casanovas et al. (2001) and Gallina & Apesteguía (2005) recovered *Haplocanthosaurus* as a macronarian. Both Upchurch (1995) and Wilson & Sereno (1998) were superseded by more recent analyses (Upchurch, 1998; Upchurch et al., 2004; Wilson, 2002) that are discussed elsewhere in this section. Neither Upchurch (1995) nor Wilson & Sereno (1998) were able to reject the alternative hypothesis that *Haplocanthosaurus* was a basal diplodocoid ($P > 0.10$). In the analysis of

Casanovas et al. (2001), the macronarian position of *Haplocanthosaurus* was supported by two synapomorphies: pleurocoels in dorsal vertebrae deep; and pleurocoels present in sacral vertebrae. Both derived states are also present in *Diplodocus*, however. The small sample of diplodocids included in that analysis—only *Barosaurus*, *Dicraeosaurus* and *Diplodocus*—may have contributed to that result. Adding *Apatosaurus* to their matrix produces two equally parsimonious trees. Strict, semi-strict and 50% consensus trees reduce Neosauropoda to a polytomy between Flagellicaudata, *Brachiosaurus*, *Camarasaurus*, *Haplocanthosaurus* and *Losillasaurus*; *Apatosaurus* is recovered in a polytomy with *Dicraeosaurus* and the clade *Barosaurus* + *Diplodocus*.

Gallina and Apesteguía (2005) recovered a polyphyletic *Haplocanthosaurus*, with *H. priscus* and *H. delfsi* members of distinct lineages, as in the analysis of Calvo and Salgado (1995). Unlike the results of Calvo and Salgado (1995), however, *Haplocanthosaurus* was recovered within Macronaria. *H. delfsi* was recovered as the more derived of the two, with *H. priscus* basal to the clade *H. delfsi* + *Camarasaurus*. The placement of both *Haplocanthosaurus* species in Macronaria is supported by two synapomorphies in the Gallina and Apesteguía (2005) analysis: posteriorly curved anterior caudal neural spines; and anterodorsally oriented prezygapophyses in mid-caudal vertebrae. Constraining both *Haplocanthosaurus* species to a position equivalent with this analysis requires five additional steps, suggesting that within that analysis, its position is robust; a topology with *Haplocanthosaurus* as a diplodocoid is rejected by a Templeton test ($P < 0.01$) for the Gallina & Apesteguía (2005) dataset.

Wilson (2002) and Upchurch et al. (2004), the two most recent comprehensive studies of sauropod relationships, disagree on the position of *Haplocanthosaurus*. Wilson (2002) recovered *Haplocanthosaurus* as a basal diplodocoid, a position supported only by the presence of short cervical ribs. Character support for this node in Wilson's analysis is also low (decay index = 1). Conversely, Upchurch et al. (2004) recovered *Haplocanthosaurus* as a macronarian, sister taxon to the clade *Brachiosaurus* + MDT. Constraining *Haplocanthosaurus* to be a member of Diplodocoidea in that analysis requires five additional steps, although a Templeton test reveals that the data cannot reject this alternative hypothesis ($P > 0.10$). The analyses of Wilson (2002) and Upchurch et al. (2004) also disagree in other content of Diplodocoidea. Upchurch et al. (2004) recovered *Nemegtosaurus* and *Quaesitosaurus* as basal diplodocoids; these taxa are considered titanosaurs by Wilson (2002; 2005b) and other authors (Curry Rogers and Forster, 2001; Apesteguía, 2004; Curry Rogers, 2005). *Haplocanthosaurus* is securely nested in Macronaria within Upchurch et al.'s (2004) analysis, but given the large topological differences between that tree and almost all others, there must remain some uncertainty in the position of *Haplocanthosaurus*, not only in Upchurch et al.'s (2004) analysis, but also in that of Wilson (2002).

Constraining the position of *Haplocanthosaurus* outside Neosauropoda, to a node either above or below *Jobaria*, in the present analysis requires only a single additional step; all other relationships outside Neosauropoda require two

or more additional steps. Placing *Haplocanthosaurus* at the base of Macronaria also requires only a single additional step, although moving it to a position more derived than *Camarasaurus* requires at least seven additional steps. This low resistance to re-arrangements may be the result of critical anatomical data that are absent in *Haplocanthosaurus*, such as cranial characters. Neosauropoda is supported by five synapomorphies, only a single one of which can be identified in *Haplocanthosaurus*: anterior chevrons without 'crus' (character 155). Further confounding the issue with that character is the reversal of that state within Flagellicaudata and the absence of information regarding its state in *Amphicoelias* and basal rebbachisaurids. The elements from which *Haplocanthosaurus* is known are also quite plesiomorphic, making it difficult to assign to a particular group because it necessarily shares so few synapomorphies with any other clade. It is likely that the description of more complete *Haplocanthosaurus* remains (Bilbey, Hall and Hall, 2000) could result in that taxon moving to any number of positions around the base of Neosauropoda.

Removing *Haplocanthosaurus* from this analysis results in three equally parsimonious trees of length 264. The topology is unaltered from that recovered from the unpruned matrix.

Excluding the referred hindlimb elements (CM 2043 and USNM 4275) from the scored material does not change the topology or the number of recovered trees, but it does negatively impact the robustness of the node Diplodocoidea. One of the three recovered synapomorphies of the group, posterolaterally facing tibial articular facet of the astragalus (186), is recovered

instead as a synapomorphy of the more restrictive group Flagellicaudata + Rebbachisauridae when this material is excluded.

Amazonsaurus

The recovery of *Amazonsaurus* as a basal diplodocoid contrasts with the position of that genus in previous analyses as basal to Flagellicaudata (Salgado et al., 2004), in a four-way polytomy with rebbachisaurids (Salgado et al., 2006) or within Macronaria (Rauhut et al., 2005). In this analysis, *Amazonsaurus* shares three unambiguous synapomorphies with the clade *Amphicoelias* + more derived diplodocoids (MDD): petal shaped anterior caudal neural spines (character 127; reversed in Diplodocidae); anterior neural spines broader than anteroposteriorly long (character 128); and spinoprezygapophyseal laminae (spr1) present on anterior caudal neural spines (character 138). It cannot be scored for any of the synapomorphies reported here for the clades Rebbachisauridae, *Rebbachisaurus* + MDD, or Limaysaurinae + Nigersaurinae. *Amazonsaurus* is excluded from the clade *Amphicoelias* + MDD by its proportionally short dorsal neural spines (character 118). It is excluded from the clade Rebbachisauridae + Flagellicaudata by its proportionally short mid-caudal vertebrae (character 145); it is unscorable for all other synapomorphies uniting that clade. The proportional height of the neural spine is estimated from the neural spine MN 4558-V and the dorsal centrum MN 4558-V. Although the two were not recovered in association, the height of the neural spine and the length of the centrum are nearly equal. It is

highly unlikely then that either derived state (neural spine either twice or four times the centrum length) is present.

Amazonsaurus was united with Flagellicaudata in the analysis of Salgado et al. (2004), based on two characters: a divided centropostzygapophyseal lamina in posterior dorsal vertebrae and the presence of diapophyseal laminae on anterior caudal vertebrae. Neither character could be confirmed here, as very little of the neural arch below the diapophyses is preserved in the holotype specimen, and both are scored as ‘?’.

Salgado et al. (2006) recovered *Amazonsaurus* as a rebbachisaurid, but few synapomorphies listed for the group could be scored. Of four rebbachisaurid synapomorphies—lack of hyposphene-hypantrum in dorsal vertebrae, dorsal neural spines four times taller than centrum, dorsal and anterior caudal neural spines ‘petal’-shaped and distally expanded scapula—only petal-shaped anterior caudal neural spines can be scored for *Amazonsaurus*. This analysis recovers this feature as a synapomorphy of a larger group, rather than Rebbachisauridae. Constraining *Amazonsaurus* to a position at the base of Rebbachisauridae incurs an additional parsimony debt of two steps.

Rauhut et al. (2005) recovered *Amazonsaurus* within Macronaria based on two characters: opisthocoelous posterior dorsal centra and forked chevrons restricted to the distal tail. The preserved dorsal centrum is slightly opisthocoelous and is presumably a mid- to posterior dorsal, although the cotyle is damaged. However, there are only eight preserved chevrons for *Amazonsaurus*, apparently consecutive, and based upon their size it is

reasonable to assume they are anterior or anterior mid-caudal chevrons. The state of mid- and distal chevrons therefore cannot be determined. Re-running the analysis with only that single cell rescored as '?' returns 855 equally parsimonious trees (Table 4.7). A strict consensus of those trees results in a polytomy between the clades Flagellicaudata, Rebbachisauridae, *Euhelopus* + MDT, *Omeisaurus* + *Cetiosauriscus* and all other taxa excluding *Shunosaurus*. The placement of *Amazonsaurus* as a macronarian in the analysis of Rauhut et al (2005) is poorly supported, and its placement there cannot be distinguished from a placement basal to any of the above clades within Eusauropoda. *Amazonsaurus* is well-supported as a basal diplodocoid in the current analysis, but the fragmentary nature of this taxon and the taxa immediately below and above it in the tree necessitate caution in any interpretation that relies on *Amazonsaurus* occupying this position. Templeton tests are unable to reject any of the previously published hypotheses of relationship based on the current dataset ($P > 0.10$).

Amphicoelias

In addition to the unambiguous synapomorphy listed above (height of mid-dorsal neural spines twice centrum length), *Amphicoelias* shares an additional ambiguous synapomorphy with more derived diplodocoids: the greatest anteroposterior thickness of the femoral shaft is much greater than 50% of the anteroposterior depth of the distal articular condyles (character 179). The recovery of *Amphicoelias* as a basal diplodocoid agrees with the findings of

Rauhut et al. (2005), although the latter result may hinge on one or two key scorings. As mentioned above, re-scoring *Amazonsaurus* in the Rauhut et al. (2005) matrix results in the placement of *Amphicoelias* in a large polytomy with essentially all other eusauropods. Removing *Amazonsaurus* entirely from the analysis of Rauhut et al. (2005) returns fewer trees (324) and greater resolution in a strict consensus—the clades Macronaria and Rebbachisauridae + Flagellicaudata are both resolved—although there is still a large polytomy at the node above *Shunosaurus* that includes *Amphicoelias*. No other analysis has examined *Amphicoelias* using modern computational methods (Table 4.2).

Diplodocidae

Diplodocidae is a well-supported node (decay index = 7, 20 synapomorphies) inclusive of six taxa: *Apatosaurus*, *Barosaurus*, *Dinheirosaurus*, *Diplodocus*, *Supersaurus* and *Tornieria*. *Apatosaurus* is recovered as the basal-most member of the clade. *Supersaurus* is recovered one node higher. *Dinheirosaurus* and *Tornieria* are recovered in a polytomy with the clade (*Barosaurus*, *Diplodocus*) in both strict and 50% majority-rule consensus trees. Similarly, Rauhut et al. (2005) recovered *Barosaurus*, *Dinheirosaurus*, *Diplodocus* and *Tornieria* in a four-way polytomy; a 50% majority-rule tree obtained using a rescored matrix (see ‘*Amazonsaurus*’ and ‘*Amphicoelias*’, below) recovers a fully resolved Diplodocidae, with *Apatosaurus* basal to all other diplodocids and *Tornieria* basal to the clade (*Dinheirosaurus* (*Barosaurus*, *Diplodocus*)). *Dinheirosaurus* and *Tornieria* are difficult to confidently differentiate, as no elements overlap between

them: *Dinheirosaurus* is known primarily from two posterior cervical vertebrae and a series of articulated dorsal vertebrae (Bonaparte and Mateus, 1999) whereas *Tornieria* is known primarily from cranial, caudal and appendicular elements (Remes, 2006). Any hypothesis of their relative relationships is therefore predicated entirely on synapomorphies and symplesiomorphies with the surrounding members of Diplodocidae and not with each other, and must be treated with caution.

The arrangement of the three best-known taxa in both trees—(*Apatosaurus* (*Barosaurus*, *Diplodocus*))—is consistent with the relationships recovered by traditional (non-computational) studies and all previous cladistic analyses (Calvo and Salgado 1995; Casanovas et al., 2001; Wilson, 2002; Harris and Dodson, 2004; Upchurch et al., 2004; Gallina and Apesteguía, 2005; Harris, 2006; Remes, 2006; Salgado et al., 2006; Lovelace et al., 2008). The relationship (*Apatosaurus* (*Tornieria* (*Barosaurus*, *Diplodocus*))) is also consistent with Remes (2006). As in all previous analyses, *Barosaurus* and *Diplodocus* are well-supported sister taxa. They share seven synapomorphies (Appendix 4), three of which are ambiguous and may characterize a group inclusive of *Dinheirosaurus*, *Tornieria*, or both (Table 4.6).

The recovery of *Supersaurus* as a basal diplodocine in this analysis is at odds with the result of Lovelace et al. (2008), which recovered *Supersaurus* as the sister taxon to *Apatosaurus*. Examination of their matrix reveals that the *Apatosaurus* + *Supersaurus* sister relationship in their analysis is supported by a single synapomorphy: scapular glenoid strongly bevelled medially. The two taxa

also share four plesiomorphic characters: anterior caudal centra not doubling in length over the first 20 vertebrae; cylindrical anterior caudal centra; ulnar proximal condylar processes subequal; short neural spines on first caudal (reversal); and short posterior dorsal neural arches. Three of these characters (anterior caudal centra not doubling in length over the first 20 vertebrae, cylindrical anterior caudal centra and short posterior dorsal neural arches) are ambiguously resolved, and do not differentiate the preferred tree of Lovelace et al. (2008) from this analysis. *Supersaurus* and the diplodocines, however, share two derived states in their analysis: mid-cervical centra with an elongation index (EI; centrum length:posterior centrum height; Upchurch, 1998) greater than or equal to 4.0; and anterior caudal centra with pneumatopores.

Supersaurus cannot be scored for character 166 in Lovelace et al. (2008), ulnar proximal condylar processes subequal, as the referred ulna (BYU 13744) was removed from the taxon by those authors earlier in the same paper. After rescored that single cell, a PAUP* search returns twice as many equally parsimonious trees (48). A strict consensus of those trees drops *Apatosaurus*, *Suuwassea* and *Supersaurus* into a polytomy at the base of Flagellicaudata with Dicraeosauridae and what remains of Diplodocidae. The 50% majority-rule tree agrees with the conventional topology, with *Apatosaurus* and *Supersaurus* in a polytomy at the base of Diplodocidae and *Suuwassea* in a polytomy with Dicraeosauridae and Diplodocidae. In the current analysis, the clade *Supersaurus* + MDD is supported by three unambiguous synapomorphies

(Appendix 4), suggesting that this clade is more probably correct than a sister relationship between *Apatosaurus* and *Supersaurus*.

Dicraeosauridae

Dicraeosauridae is well supported (decay index = 11; 13 unambiguous synapomorphies) and contains *Amargasaurus*, *Brachyrachelopan*, *Dicraeosaurus* and *Suuwassea*. The recovered relationship (*Amargasaurus* (*Brachyrachelopan*, *Dicraeosaurus*)) is consistent with the two prior hypotheses of their relationships (Rauhut et al., 2005; Sereno et al., 2007) and is well supported (decay index = 7; 8 unambiguous synapomorphies).

Salgado et al.'s (2006) analysis is the only other to recover *Suuwassea* as a basal dicraeosaurid. Harris and Dodson (2004), Harris (2006) and Sereno et al. (2007) all recovered *Suuwassea* in a polytomy with Dicraeosauridae and Diplodocidae. Harris (2006), after pruning *Alamosaurus*, *Euhelopus*, *Haplocanthosaurus*, *Losillasaurus*, *Jobaria*, *Malawisaurus*, *Nigersaurus* and *Rebbachisaurus* from the matrix, recovered *Suuwassea* as a basal dicraeosaurid supported by three synapomorphies: subtriangular lateral temporal fenestra; tall cervical neural spines; and elongate distalmost caudal vertebrae.

Gallina and Apesteguía (2005), Rauhut et al. (2005), Remes (2006) and Lovelace et al. (2008) recovered *Suuwassea* as a basal diplodocid. This result was supported in the analysis of Rauhut et al (2005) by only a single derived character, presence of a divided centroprezygapophyseal lamina (cp1) in middle and posterior cervical vertebrae. *Suuwassea*'s position in the analyses of Gallina

and Apesteguía (2005), Remes (2006) and Lovelace et al. (2008) was based on that same synapomorphy and one sympleisomorphy, either presence of dorsal pleurocoels (Gallina and Apesteguía, 2005) or lack of a basisphenoid/basipterygoid recess (Remes, 2006; Lovelace et al., 2008). In the present analysis, the cprl of *Suuwassea* is not considered to be divided, although there is a superficially similar morphology present. In many sauropods, the roof of the neural canal forms an anteriorly projecting 'lip' that grades gently on its lateral margins into the cprl; in some taxa (i.e., *Suuwassea*) the lateral narrowness of the pedicel and the robustness of this neural canal lip can create the appearance of a divided cprl. A true divided cprl can be distinguished by the lack of an anteroposterior 'offset' between the anterior margin of the cprl and its medial branch. In *Suuwassea* and similar taxa, the lip of the neural canal is set back from the cprl and the two are easily distinguished. Rescoring this character from '1' to '0' in all three analyses (Table 4.7) results in equally parsimonious topologies with *Suuwassea* as either a basal dicraeosaurid or a basal diplodocid. The position of *Suuwassea* in the present analysis is supported by a Templeton test, which rejects the placement of *Suuwassea* either as a basal diplodocid ($P < 0.01$) or as a basal diplodocine ($P < 0.01$).

Suuwassea represents the only recorded instance of a Laurasian member of Dicraeosauridae, and the second recorded instance of sympatric dicraeosaurids and diplodocids (*Tornieria* and *Dicraeosaurus* occur in the same layers in Tendaguru). *Suuwassea* lacks a number of unambiguous synapomorphies with *Amargasaurus* and more derived dicraeosaurids—fused

frontals (character 19), decreased pneumaticity in vertebrae (characters 81, 111), bifid anterior cervical vertebrae (character 85) and tall neural spines (characters 87, 93, 118)—suggesting that it is a basal dicraeosaurid. Harris (2006a; 2006b; 2006c; 2007) and Lovelace et al. (2008) have noted the coarse similarities between *Suuwassea* and *Apatosaurus*, although as both are basal members of their respective clades, they may be expected to retain many plesiomorphic characters. The presence of basal members of both clades in North America may indicate a Laurasian origin for Flagellicaudata (see ‘Paleobiogeographic Implications’, below).

Rebbachisauridae

Rebbachisauridae is recovered as a monophyletic group containing *Histriasaurus*, *Rebbachisaurus*, *Cathartesaura*, *Limaysaurus*, *Zapalasauros*, *Nigersaurus* and the unnamed Spanish rebbachisaurid. Other sauropods that are included in this group are *Nopcsaspondylus*, *Rayososaurus* and three unnamed elements, CCC 017, MACN PVN35 and MIWG 6544 (Table 4.8). *Histriasaurus* is recovered as the basal-most member of the group, just outside the clade *Rebbachisaurus* + MDD, primarily due to the retention of the hyposphene-hypantrum articulation. As in the analysis of Sereno et al. (2007), the remaining taxa are divided into two distinct lineages, here named Limaysaurinae and Nigersaurinae (Table 4.5; see ‘Nomenclature’, below). *Cathartesaura* and *Limaysaurus* are recovered as sister taxa, as are *Nigersaurus* and the Spanish rebbachisaurid, similar to Sereno et al. (2007). Here, however, *Zapalasauros* is

recovered as the basal-most member of Nigersaurinae, unlike the position at the base of Limaysaurinae recovered by Sereno et al. (2007). This change in position is due to a combination of updated character scorings based on first-hand observations (Table 4.9) and the addition of novel characters not present in the analysis of Sereno et al. (2007). The phylogenetic position of *Zapalsaurus* is supported here by two unambiguous synapomorphies: presence of an epipophyseal-prezygapophyseal lamina (eprl) on cervical vertebrae (character 78); and caudal neural spines with triangular lateral processes derived from the lateral lamina (123). The recovery of *Zapalsaurus* at the base of Nigersaurinae breaks up the geographic (South America (Europe, Africa)) distribution of derived rebbachisaurids recovered by Sereno et al. (2007) and requires a more complicated explanation (see 'Paleobiogeographic Implications', below). Limaysaurinae is supported by two unambiguous synapomorphies: accessory lateral lamina connecting postzygodiapophyseal lamina (podl) and the sprl on posterior cervical vertebrae (character 96); and sprl-spinopostzygapophyseal lamina (spol) contact on anterior caudal vertebrae (137).

Zapalsaurus was recovered outside the clade Rebbachisauridae + Flagellicaudata by Salgado et al. (2006), on the basis of anterior caudal neural spines without spinoprezygapophyseal laminae present and extending onto the lateral surface of the neural spine. Here, *Zapalsaurus* is scored '?' for this character (138); spinoprezygapophyseal laminae are definitely present on the anterior-most preserved caudal vertebrae, although they do not appear to extend onto the lateral surfaces. The preservation of the anterior-most caudal is

somewhat ambiguous. It is possible that in more anterior caudal vertebrae, these laminae would take on the form seen in other diplodocoids. For this reason, it was scored here as '?'. Constraining *Zapalasauros* (as presently scored) outside the clade Rebbachisauridae + Flagellicaudata requires an additional step (274 total). Rescoring *Zapalasauros* as primitive for this state (0), without changing its position in the topology, adds an additional step to the tree (274); constraining the rescored *Zapalasauros* outside the clade Rebbachisauridae + Flagellicaudata in this rescored analysis requires still one more step (275), making the placement of *Zapalasauros* within Rebbachisauridae a more parsimonious hypothesis than alternative positions. Differences between these topologies are too small to calculate meaningful test statistics for comparison, such as with a Templeton test.

The clade Rebbachisauridae is not as strongly supported as either Diplodocidae or Dicraeosauridae (decay indices = 2, 7, 11, respectively), largely as a consequence of fragmentary taxa at the base of the clade. There are, however, three non-homoplastic synapomorphies uniting Rebbachisauridae (Appendix 4.4). The clade Limaysaurinae + Nigersaurinae is supported by 22 synapomorphies, but all of these are ambiguous due to missing data. Some, all or none may in fact be recovered as synapomorphies of Rebbachisauridae once scorings for basal forms are known (Table 6). Support for internal nodes is less robust, and the fragmentary nature of all but *Limaysaurus* and *Nigersaurus* pushes a number of potential synapomorphies of more inclusive groups farther up the tree.

Removing the isolated crown MNHN MRS 1524a from the scoring of *Rebbachisaurus* does not affect the results of the analysis. The presence of a second, lingual planar wear facet (character 67) is suggested by this crown, but cannot be definitively identified and so was scored as unknown here. This character is potentially a synapomorphy of a larger group than was recovered here (Limaysaurinae + Nigersaurinae; Appendix 4.4).

Relationships of Fragmentary Taxa

Four taxa referred to Diplodocoidea (MACN PV N35, MIWG 6544, *Nopcsaspondylus* and *Rayososaurus*) were too fragmentary to be distinguishable from other taxa, but preserve enough phylogenetic information to formulate a tentative hypothesis of their membership in Rebbachisauridae (Table 4.8). MACN PV N35 is indistinguishable in this analysis from *Histriasaurus* and shares all three synapomorphies of Rebbachisauridae recovered here (Appendix 4.4). The Isle of Wight taxon (MIWG 6544) and *Rayososaurus* are assignable to Rebbachisauridae based on the presence of a U-shaped concavity on the dorsal margin of the scapular acromion process and a racquet-shaped distal scapular blade, although the absence of a known scapula of *Histriasaurus* prevents further diagnosis. *Nopcsaspondylus* shares the three synapomorphies of Rebbachisauridae and can be further resolved as belonging to the clade *Rebbachisaurus* + MDD due to the lack of a hyosphene. Apesteguía (2006) assigned MACN PV N35 to *Nopcsaspondylus*, which is contradicted by the presence of a hyosphene in MACN PV N35 and its absence in

Nopcsaspondylus (Nopcsa, 1902). For this reason, MACN PV N35 cannot be assigned to *Nopcsaspondylus*.

Three isolated vertebral elements (CCC 017, CCC 030 and CCC 060) from the Albian of Brazil have been referred to Rebbachisauridae (Castro et al., 2007). CCC 017, a posterior dorsal/anterior caudal neural arch, shares a ventrally bifurcate spot with Rebbachisauridae. CCC 017 may also have a hyposphene, suggesting that it belongs to a basal part of the lineage (Table 4.8). The remaining materials, a fragmentary neural arch (CCC 030) and neural spine (CCC 060), cannot be confidently assigned to any clade at this time.

A partial braincase, skull roof and dentary (MOR 592), previously referred to the basal diplodocoid *Amphicoelias* (Wilson and Smith, 1996), appear to belong instead to a dicraeosaurid. A sharp crest on the supraoccipital (character 45) and the presence of a tuberosity near the dentary symphysis (character 61) both suggest dicraeosaurid affinities, although the dentary symphysis is intermediate between the subtriangular dicraeosaurid and the ovate diplodocid conditions. This and other minor differences between these elements and *Suuwassea emilieae* (Harris, 2006a) preclude referral of MOR 592 to that taxon, but it is probable that the two are closely related.

Rejected Putative Diplodocoids

Two taxa, *Australodocus* (Remes, 2007) and *Losillasaurus* (Casanovas et al., 2001), have previously been suggested to be members of Diplodocoidea. The results of this study suggest that these two taxa do not belong to this group.

Three other taxa, too fragmentary to include in this study, are also provisionally excluded from Diplodocoidea: BMNH R1967, a string of distal caudal vertebrae; ‘*Cetiosaurus glymptonensis*,’ a series of mid-caudal vertebrae; and PMU R263, an anterior caudal vertebra.

Australodocus: *Australodocus bohetii* is recovered within Macronaria, as a sister taxon to *Brachiosaurus brancai*. Remes (2007) suggested that *Australodocus* was a diplodocid closely related to *Diplodocus*, *Barosaurus* and *Tornieria* on the basis of four characters: bifurcate neural spines with median tubercle, concave ventral surface of centra, bifurcated crpl and transversely convex prezygapophyseal articular facets. Subsequent re-examination suggests that the crpl is not bifurcate. Of the remaining characters, only bifurcate neural spines differentiate *Australodocus* from *B. brancai*, and bifid neural spines are known from multiple macronarian taxa (e.g., *Camarasaurus*, *Erketu*, *Opisthocoelicaudia*, *Phuwiangosaurus* and *Qiaowanlong*). *Australodocus* and *Brachiosaurus* are united by three synapomorphies: camellate internal bone structure in presacral vertebrae (character 76); pleurocoel reduced, restricted to area above parapophysis (81); and elongation index of mid-cervical vertebrae 4.0 or greater (90; independent derivation in Diplodocidae).

Losillasaurus: *Losillasaurus* is recovered in a polytomy with *Omeisaurus* at the base of the tree, outside the clade *Jobaria* + Neosauropoda. Although initially recovered as a basal diplodocoid (Casanovas et al., 2001), all subsequent

analyses including *Losillasaurus* (Harris and Dodson, 2004; Gallina and Apesteguía, 2005; Rauhut et al., 2005; Harris, 2006; Royo-Torres, Cobos and Alcalá, 2006; Lovelace et al., 2008) have recovered it outside that clade. Of those analyses, only Gallina and Apesteguía (2005) recovered it as a neosauropod; all others recovered it in a position outside the clade *Jobaria* + Neosauropoda, as in this analysis. Here, *Losillasaurus* is excluded from more derived sauropods by the lack of pre- and post-spinal laminae on anterior caudal neural spines (characters 129, 130).

BMNH R.1967. Referred to *Cetiosauriscus leedsi* (but see Harris, 2006), BMNH R.1967 is a string of 10 elongate, biconvex distal caudal vertebrae. All known diplodocoid distal caudal vertebrae have EI scores above 5.0; the vertebrae of BMNH R.1967 are “less elongated” (EI = 3.2; Woodward, 1905: 239). It is possible that basal diplodocoids may have had lower distal caudal EI scores—no distal caudals are known for *Haplocanthosaurus*, *Amphicoelias*, or *Amazonsaurus*—but because moderately elongate (EI < 4.0), biconvex distal caudal vertebrae are also known in titanosaurs (Wilson, Martinez, & Alcober, 1999), their presence in BMNH R.1967 is not sufficient to assign this specimen to Diplodocoidea.

‘*Cetiosaurus glymptonensis*.’ Upchurch & Martin (2003) suggested that these caudal vertebrae could belong to a basal diplodocoid, based on the relative elongation of the centra. The maximum EI reported for ‘*C. glymptonensis*’ by

those authors is 2.17, which is below that reported for mid-distal caudal vertebrae of diplodocids such as *Diplodocus* (EI = 2.28) and *Apatosaurus* (EI = 3.44), but greater than that of macronarians such as *Camarasaurus* (EI = 1.66). The EI of '*C. glymptonensis*' is also similar to that reported by those authors for caudal vertebra 35 in the incertae sedis taxon *Cetiosauriscus stewarti* (EI = 2.00) and the basal eusauropod *Mamenchisaurus* (EI = 2.09), however. Mid-caudal centrum elongation varies greatly across taxa (Upchurch and Martin, 2003: table 1), and may not ultimately be as useful as distal caudal elongation in distinguishing between clades. In the absence of any shared synapomorphies with Diplodocoidea, the referral of '*C. glymptonensis*' to that clade can neither be supported nor refuted here.

PMU R263. As noted above, an anterior caudal vertebra from Shandong, China (PMU R263) was recently described as belonging to a diplodocid (Upchurch & Mannion, 2009). If true, this specimen would represent a temporal and geographic range extension for the diplodocids, and would also be the first non-titanosauriform from the Cretaceous of Asia. However, it has also been suggested that this caudal vertebra belongs instead to a titanosaur (Whitlock et al., in press). In particular, the presence of somphospondylous or camellate internal bone texture in PMU R263 indicates titanosauriform affinities. The matrix presented in this study cannot resolve PMU R263 with regard to a position within Neosauropoda, except to exclude it from the clade *Amazonsaurus* + MDD; this is likely a result of the high degree of convergence and overall morphological

similarity present in basal neosauropods such as *Haplocanthosaurus* and *Camarasaurus*. An analysis encompassing a wider diversity of titanosauriform taxa may be able to more confidently resolve the position of PMU R263 within Neosauropoda. It is highly probable that this taxon does not represent a diplodocoid, and therefore does not impact palaeobiogeographic hypotheses concerning the group.

DATA ANALYSIS

Character data in a phylogenetic analysis are often seen as being trapped in a 'black box', hidden from outside observers (Rieppel and Kearney, 2007). In addition to the obvious difficulties this poses for independent assessment of the results of an analysis, important patterns within the data may go unnoticed without further examination. Below, the character data presented in this analysis are summarized in two contexts: regional character inclusion and missing data.

Regional character inclusion

The importance of individual anatomical regions for character data is highly dependent on the taxa in question. The distribution of that character data can potentially serve as a shorthand way of examining which anatomical regions have undergone the most modification in a group. Understanding the regional specificity of those specializations may also serve as a way to identify broad patterns between clades, such as between various herbivore groups. Figure 4.7

presents one method for visually comparing regional importance of character data in phylogenetic analyses at various scales and between various clades.

In this analysis, cranial (40%) and axial (42%) characters make up the majority of character data (Fig. 4.7A). In contrast, the analysis of Wilson (2002), encompassing all of Sauropoda, has regional character distributions more evenly distributed between the cranial (33%), axial (31%) and appendicular/dermal regions (36%; Fig. 4.7B). The analysis of Upchurch et al. (2004), which also examined relationships across Sauropoda, had similar character distributions (31%, 34%, and 35%, respectively). The importance of the appendicular skeleton in these analyses is likely related to their broader taxonomic scope, which includes two important locomotor transitions: the acquisition of quadrupedalism in sauropods and the acquisition of wide-gauge limb posture in titanosaurs. Wilson (2002:appendix 3) listed 21 synapomorphies for Sauropoda and 53 for Eusauropoda; of these 74 synapomorphies, 38 (14% of total included characters) are appendicular (19 in each clade). If that 14% is excluded from the total, cranial (38%) and axial (36%) characters make up a proportion of the matrix in Wilson (2002) that is more similar to that seen in this analysis, although the importance of particular subregions (e.g., dermal skull) differs.

In the current analysis, characters from the dermal skull (20%), caudal vertebrae (16%) and cervical vertebrae (13%) make up the largest proportion of character data of the individual sub-regions. In the analysis of Wilson (2002), dermal skull (11%) and caudal vertebrae (11%) characters were again the most important, but cervical vertebrae were less important (5%) than the braincase

(10%) and the pes (10%). Dermal skull characters make up a larger proportion of both the total data and the regional data in the current analysis, indicating the relative importance of those characters for distinguishing diplodocoids, both from other sauropod groups and between smaller groups within the clade. This is potentially related to specializations in herbivory seen in this group, such as the development of a broad, square snout and a dental battery (Sereno et al., 2007).

Cranial characters, particularly relating to the dermal skull, also make up a significant proportion of the character data in a recent phylogenetic analysis of Ornithischia (Butler et al., 2008; Fig. 4.7C). Dental characters also make up a significant proportion of skull characters in both analyses (15% in this analysis; 17% in Butler et al. 2008). The evolution of special cranial adaptations for herbivory, such as a square jaw and the development of a dental battery, occurred in both groups (Weishampel, 2004; Sereno and Wilson, 2005), although the variation in ornithischian cranial morphology dwarfs that in seen Diplodocoidea (e.g., beaks, cheeks and neomorphic midline jawbones). Nonetheless, this illustrates the relative importance of herbivorous specializations in Diplodocoidea, even in comparison to other neosauropods. A recent large-scale analysis of Titanosauria (Curry Rogers, 2005; Fig. 4.7D) included a similar but slightly lower proportion of total characters as cranial data (30%) than Wilson (2002), although the proportion of cranial characters regarding dermal skull elements is similar to that seen in this analysis (51%). This may reflect the importance of snout shape for derived titanosaurs, based upon the apparent

convergence on the diplodocoid condition seen in some taxa (e.g. *Rapetosaurus*; Curry Rogers and Forster, 2004).

Missing data

Missing data, expressed as the percent of cells unscorable in each morphological region, are listed for each taxon (Table 4.10); higher percentages indicate more unscored matrix cells. Fifteen taxa had at least 50% missing data, and ten had more than 75%. Of these latter ten, most are rebbachisaurids; the Spanish rebbachisaurid, *Cathartesaura*, *Histriasaurus*, *Rebbachisaurus* and *Zapalasaurus* had more than 79% missing data. Relatively complete taxa, with less than 25% missing data, are present in each major radiation of ingroup taxa (e.g., Rebbachisauridae) as well as in all outgroups.

Twelve taxa could not be scored for any cranial characters; a thirteenth, *Rebbachisaurus*, was scored only for a single cranial character, based on a referred tooth crown (MNHN MRS 1524a). All but nine taxa (*Apatosaurus*, *Brachiosaurus*, *Camarasaurus*, *Dicraeosaurus*, *Diplodocus*, *Jobaria*, *Limaysaurus*, *Nigersaurus* and *Omeisaurus*) had more than 50% of cranial data missing. The most complete region is the axial region, with a majority of taxa missing less than 50% of character data, and all but four missing less than 75%. The majority of taxa were missing less than 50% of the appendicular character data, and all but eight were missing less than 75%.

As a consequence of the relative completeness of this region across taxa, axial characters make up the largest proportion of support for Diplodocoidea as

well as for each of its sub-groups (Table 4.11). With the exception of Dicraeosauridae, the cranial region is again the most incompletely scored, although in each clade it provides the second-most amount of support; in Rebbachisauridae, cranial characters provide equivalent levels of support to the axial region.

There are very few appendicular synapomorphies recognized in this analysis. Although Rebbachisauridae receives nearly 20% of its total support from this region, the other two major clades have little support from the appendicular region, and in fact only two appendicular characters unite Diplodocoidea. The proportion of support for Diplodocoidea from the cranial and appendicular regions (88%) is similar to that reported by Wilson (2002; 85%). The relative importance of cranial characters over appendicular characters, despite typically higher percentages of missing data in the former, has been suggested to be a function of innovations focused on the cranial region over the limbs and girdles (Wilson, 2002), and indeed, such specializations as the ventral rotation of the dermal skull relative to the braincase and the anterior displacement of the jaw joint to a point beneath the orbit are unknown elsewhere in Sauropoda (Wilson, 2005a). Furthermore, the greatest degree of sauropod cranial specialization is seen in the more recently surviving diplodocoids, such as *Nigersaurus* (Sereno and Wilson, 2005; Sereno et al., 2007).

PALEOBIOGEOGRAPHIC IMPLICATIONS

The first definitive diplodocoid remains appear in the Kimmeridgian, representing the first of two diplodocoid radiations and marked by the appearance of seven genera (*Amphicoelias*, *Apatosaurus*, *Barosaurus*, *Dicraeosaurus*, *Dinheirosaurus*, *Diplodocus* and *Haplocanthosaurus*) on three continents (North America, Europe, Africa; Fig. 4.8), followed by the appearance of *Brachytrachelopan* and *Suuwassea* in the Tithonian of South and North America, respectively. This initial radiation is of interest to paleobiogeographers primarily because it provides information about the area of origin for Diplodocoidea. This radiation also overlaps with the initial breakup of Gondwana, and preserves a vicariant signal related to that breakup.

The second radiation of diplodocoids occurred in the mid-Early Cretaceous with the first appearance of Rebbachisauridae. Contemporaneously, the southern Atlantic Ocean was widening and South America and Africa began to break apart, beginning at the southern end of the burgeoning continental divide (Fig. 4.8). The exact timing of this series of events is debated, and several models of breakup have been proposed (Upchurch, 2008). Krause et al. (2006) argued for complete breakup of South America and Africa by 100 Ma (the Africa-first model); Sereno, Wilson and Conrad (2004) suggested that contact between the continents was at least intermittent up to at least 100 Ma (the Pan-Gondwana model). More recently, Upchurch (2008) proposed an Early Cretaceous (140–120 Ma) breakup of Gondwana into 'Samafrica' (South America and Africa) and East Gondwana, a model that is distinct from, but potentially congruent with, the

Africa-first model. Because the geographic and temporal distribution of Rebbachisauridae overlaps the time periods and continents in question, the pattern of descent in Rebbachisauridae is of potential paleobiogeographic interest.

Area of origin

Determining the area of origin for a clade is necessarily a dispersalist procedure, inasmuch as it implies that the original lineage dispersed to other regions prior to cladogenesis and/or vicariance. Under these conditions, use of computational methods such as are typically employed (i.e. COMPONENT; Page, 1993) may not be the best approach. Instead, we may consider a modification of a cladistic approach first proposed by Bremer (1992). In this approach, the paleobiogeographic condition may be understood as a character with multiple transformation states, with each state represented by a landmass or other discrete location. In other words, instead of a transformation between alternate morphological conditions, the transformation might be dispersal from North America to South America. Additionally, because we generally understand the connectivity of continents during the Middle to early Late Jurassic (Fig. 4.8), it is possible to create a character model that addresses the patterns of connectivity between them (Table 4.12). In this case, direct connectivity can be assumed between some landmasses (North America with Europe and South America, Africa with Europe and South America) but not others (North America and Africa, Europe and South America). It is then a simple matter to map this character onto

a tree or trees in a program such as Mesquite (Maddison and Maddison, 2009) and calculate an ancestral condition, equivalent in this case to an ancestral landmass, for each node.

Reconstructing the ancestral state in Mesquite using a parsimony criterion unambiguously recovers an ancestral origin in North America for those clades with representatives in the Late Jurassic (Dicraeosauridae, Diplodocoidea and Diplodocidae; Fig. 4.8). This is in contrast to the hypothesis of Remes (2006; 664), which postulated a Gondwanan origin for Diplodocoidea on the basis that “most Gondwanan diplodocoids are less derived.” Reconstructing the ancestral state using the topology presented by Remes (2006) returns the same unambiguous North American origin, however. Most of the plesiomorphic diplodocoid taxa (e.g., *Haplocanthosaurus* and *Amphicoelias*), as well as the most plesiomorphic members of Diplodocidae (*Apatosaurus*) and Dicraeosauridae (*Suuwassea*) are North American. North America is also the only continent for which basal diplodocoids, diplodocids and dicraeosaurids are known, which also suggests a North American origin.

Paleobiogeographic patterns

The influence of vicariance on intergeneric relationships can be examined using computational biogeographic software, in this case COMPONENT 2.0 (Page, 1993). The significant time gap (ca. 22 million years) between the first definitive appearance of a flagellicaudatan (Kimmeridgian) and the first rebbachisaurid (Late Hauterivian) provides a convenient breaking point to separate the two

clades and consider the paleobiogeographic patterns of each individually. Additionally, because the critical interval (Late Jurassic–Late Cretaceous) encompasses nearly the entirety of the breakup of Pangaea, connectivity varies greatly between stages. Following other studies of paleobiogeography that encompass long time durations (e.g., Upchurch, Hunn and Norman, 2002; Butler et al., 2006), paleobiogeographic patterns were examined in two stages: Late Jurassic and Cretaceous. Randomization tests were conducted in TREEMAP 2.0β (Charleston & Page, 2002) for each recovered area cladogram (10,000 replicates of the taxon cladogram).

Late Jurassic. A pruned cladogram containing only taxa present in the Late Jurassic was input into COMPONENT 2.0, and one most-parsimonious area cladogram—(Europe (North America (South America, Africa)))—was recovered (Fig. 4.8). Including the Cretaceous taxa *Amazonsaurus* and *Amargasaurus* in the input cladogram results in the same area cladogram. This is congruent with many paleogeographic reconstructions (e.g., Smith, Smith and Funnell, 1994; Blakey, 2006), which suggest at least intermittent discontinuity of Europe from Africa, North America and South America by the Middle Jurassic, and the Callovian separation of North America from Gondwana (Sereno, 1997; 1999; Fig. 4.8). Although this area cladogram does fail a randomization test ($P > 0.46$), such failure does not indicate the lack of signal, only the absence of evidence for a repeated signal (Upchurch et al., 2002), and is probably influenced in large part by the small sample size ($n = 11$).

From North America, diplodocids dispersed into Africa (*Tornieria*) and Europe (*Dinheirosaurus*); the relationship between *Tornieria*, *Dinheirosaurus* and more derived diplodocids is uncertain, however, and little else can be said about their particular relationship. Dicraeosaurids dispersed into South America (*Brachytrachelopan*) and Africa (*Dicraeosaurus*). Including the Cretaceous-age *Amargasaurus* in the analysis suggests a dispersal of dicraeosaurids into Africa via South America, and this seems a likely route, particularly given the predominantly Gondwanan relationships of many Late Jurassic African taxa (Mateus, 2006). The fragmentary *Amazonsaurus*, from the Cretaceous of South America, may represent an additional incursion into that continent from North America.

Cretaceous. A single area cladogram with the form (South America (Africa, Europe)) was derived from a pruned input cladogram containing only rebbachisaurids (Fig. 4.8). The same area cladogram is recovered if *Amazonsaurus* is placed as the basal-most rebbachisaurid, at an additional parsimony cost of 2 steps. As before, this area cladogram fails a randomization test ($P > 0.99$).

If correct, this arrangement suggests that Europe and Africa remained in contact after the breakup of South America from the rest of Gondwana, as has been suggested previously (Upchurch et al., 2002). The timing of these splits (ca. Hauterivian–Valanginian, based upon the *Zapalasaurus–Nigersaurus*/Spanish rebbachisaurid relationship) is much earlier than the purported 100 Ma date for

the final separation of South America from Africa in both the Africa-first and Pan-Gondwana models. This signal may be the result of an Early Cretaceous opening of the South Atlantic acting as a barrier to these taxa, but not to others (e.g., abelisaurid theropods; Sereno et al., 2004). It may also be a function of missing data, although this may be a less likely hypothesis, as rebbachisaurids are known from appropriate time periods on both continents (*Limaysaurus*, *Nigersaurus*).

CONCLUSIONS

The three main lineages of diplodocoid sauropods (Dicraeosauridae, Diplodocidae and Rebbachisauridae) are recovered by phylogenetic analysis in their traditional relationship: Dicraeosauridae and Diplodocidae as sister clades, with Rebbachisauridae basal to both. Although many taxa at the base of both Rebbachisauridae and Diplodocoidea are fragmentary, a phylogenetic signal can be detected and the relationships of those taxa can be resolved. *Haplocanthosaurus*, *Amazonsaurus* and *Amphicoelias* are recovered as sequentially more derived taxa at the base of Diplodocoidea. *Suuwassea* is well-supported as a basal dicraeosaurid. Two main lineages of derived rebbachisaurids are identified, the South American Limaysaurinae and the more cosmopolitan Nigersaurinae.

Diplodocoidea appears to have experienced two main diversifications. The first, likely occurring in the mid-Jurassic of North America, gave rise to Diplodocidae and Dicraeosauridae. Diplodocidae dispersed into at least western

Europe and east Africa and potentially South America. Dicraeosauridae dispersed into, and was most taxonomically diverse in, Gondwana, with known representatives in South America and eastern Africa. The dicraeosaurid *Amargasaurus* is the only known Cretaceous survivor of either lineage.

The second radiation occurred prior to the Early Cretaceous and involved the diversification of rebbachisaurids. The long ghost lineage at the base of Rebbachisauridae prohibits well-informed speculation on the geographic origins of the group. At some point prior to about 135 Ma, the group entered South America, where the greatest generic diversity is found. Members of the nigersaurine lineage also dispersed into north Africa and western Europe no later than 130 Ma; the two continents must have been in at least intermittent contact up until that point.

This phylogenetic hypothesis serves as a starting point for examining the development of herbivorous adaptation—particularly the development of the rebbachisaurid tooth battery—and patterns of body size and shape evolution, from the gigantic, long-necked diplodocids to the diminutive, short-necked dicraeosaurids and derived rebbachisaurids.

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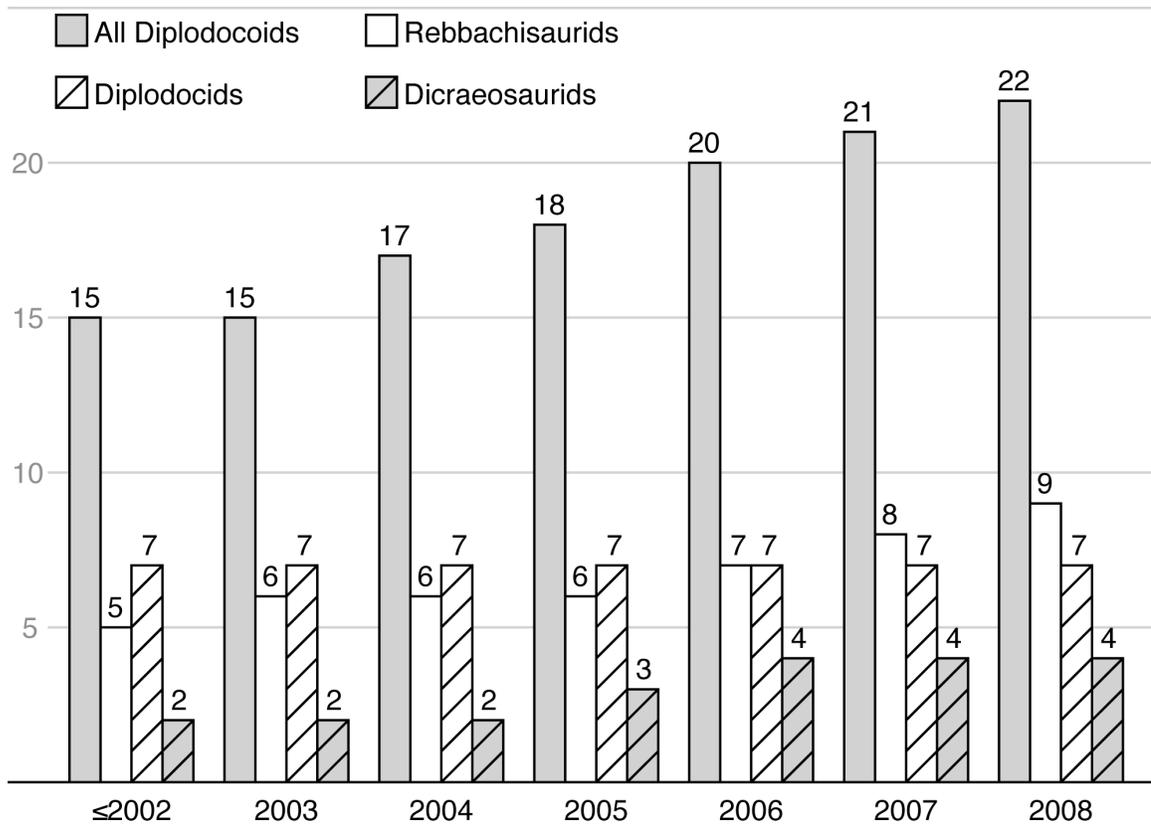


Figure 4.1. Diplodocoid genera known to science at the beginning of each calendar year. Diplodocid diversity has remained stable, but Dicraeosauridae and Rebbachisauridae have experienced large diversity gains, as have taxa at the base of Diplodocoidea. Classification following the results of this study.

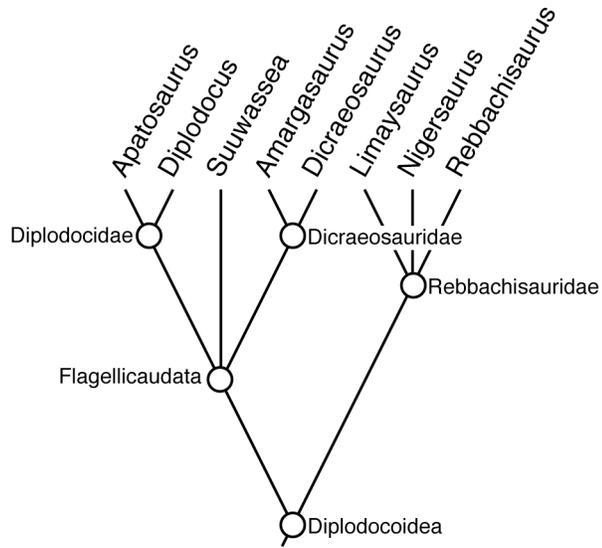


Figure 4.2. Strict consensus cladogram of Diplodocoidea, summarizing the results of all previous analyses including *Suwassea* and at least three rebbachisaurids.

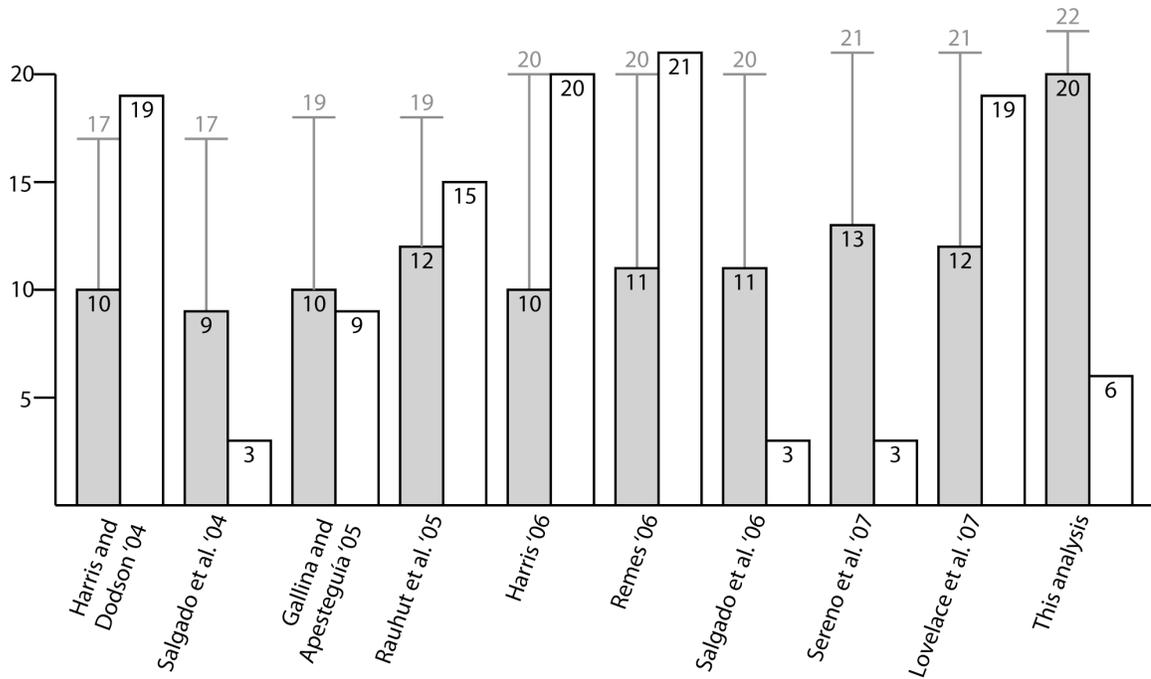


Figure 4.3. Taxa included in all analyses post-dating 2004, following the recognition of 75% of all currently recognized diplodocoid genera. Grey bars indicate diplodocoid taxa (following the results of this analysis); white bars indicate non-diplodocoids. 50% grey lines and numbers above grey bars indicate the total number of then-recognized diplodocoid taxa.

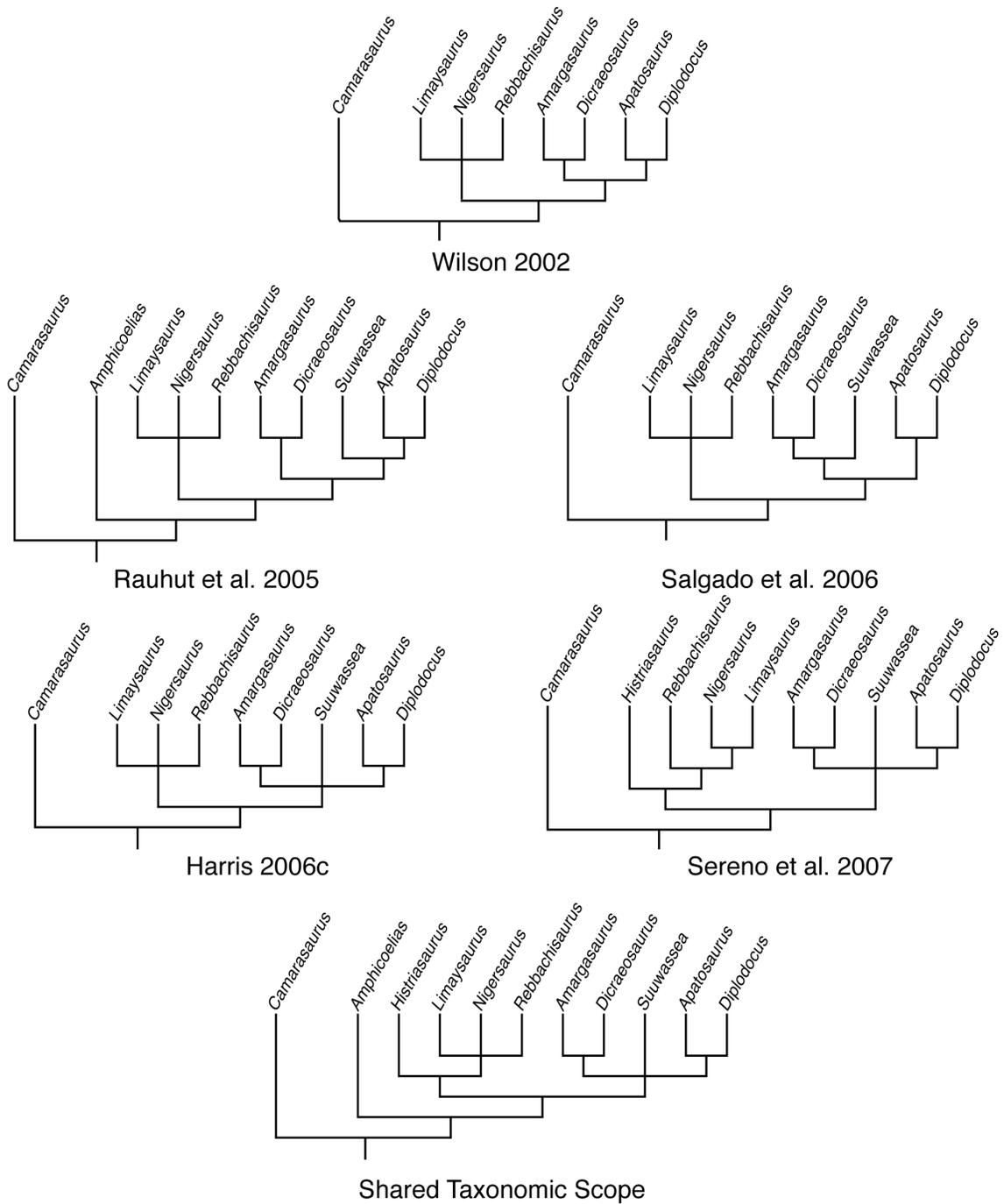


Figure 4.4. Shared taxonomic scope and pruned topologies from Wilson (2002) and four recent analyses: Rauhut et al. (2005), Salgado et al., (2006), Harris (2006), and Sereno et al. (2007).

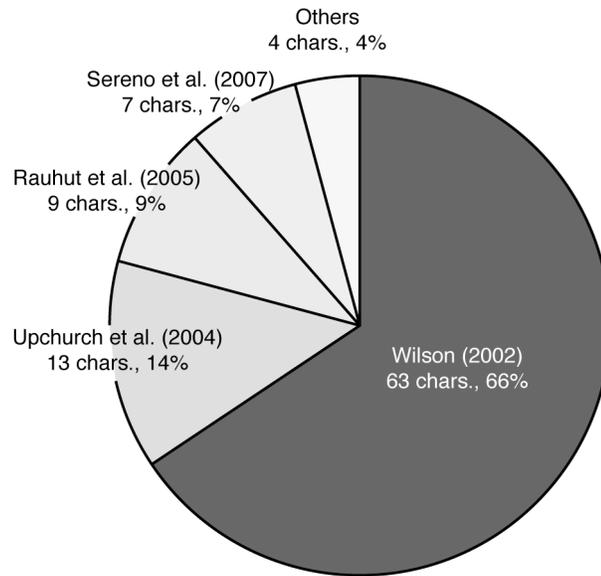


Figure 4.5. Character authorship for the 96 pooled relevant characters. Notice the predominance of two analyses (Wilson, 2002; Upchurch et al., 2004), both of which predate the description of many problematic taxa, and neither of which presents data that resolve the interrelationships of Rebbachisauridae.

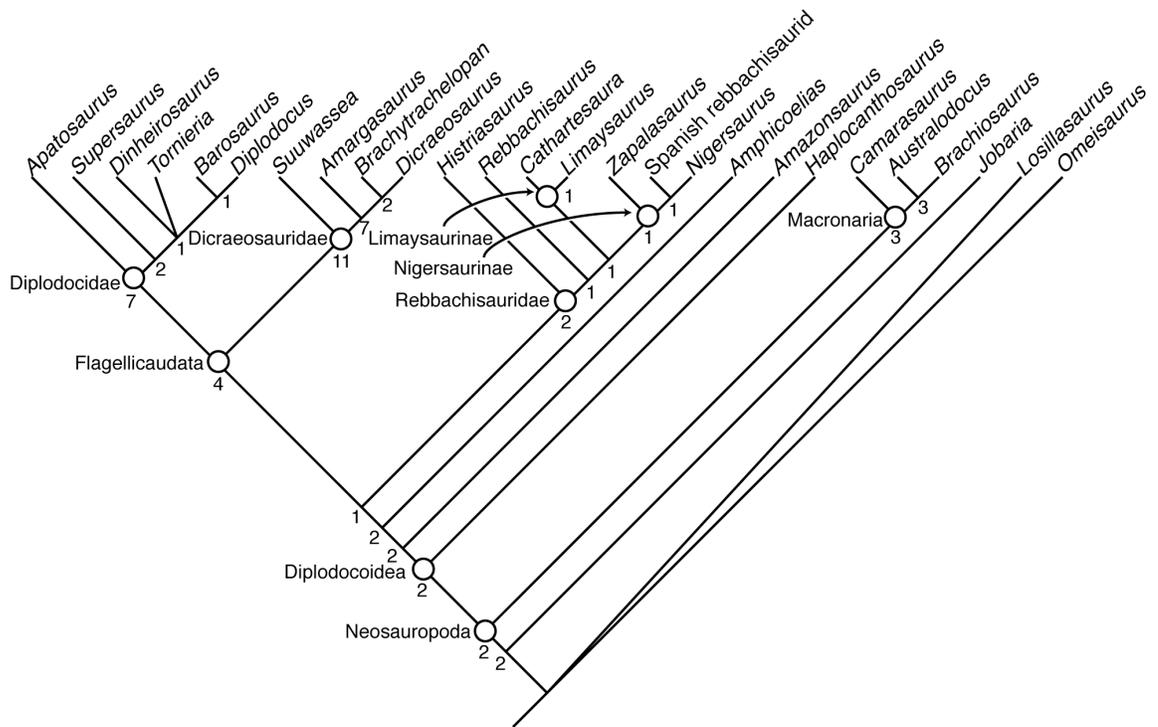


Figure 4.6. Phylogenetic hypothesis presented in this analysis. Cladogram represents a strict consensus of three equally parsimonious trees (273 steps), labelled with relevant clade names. Decay indices reported below each node.

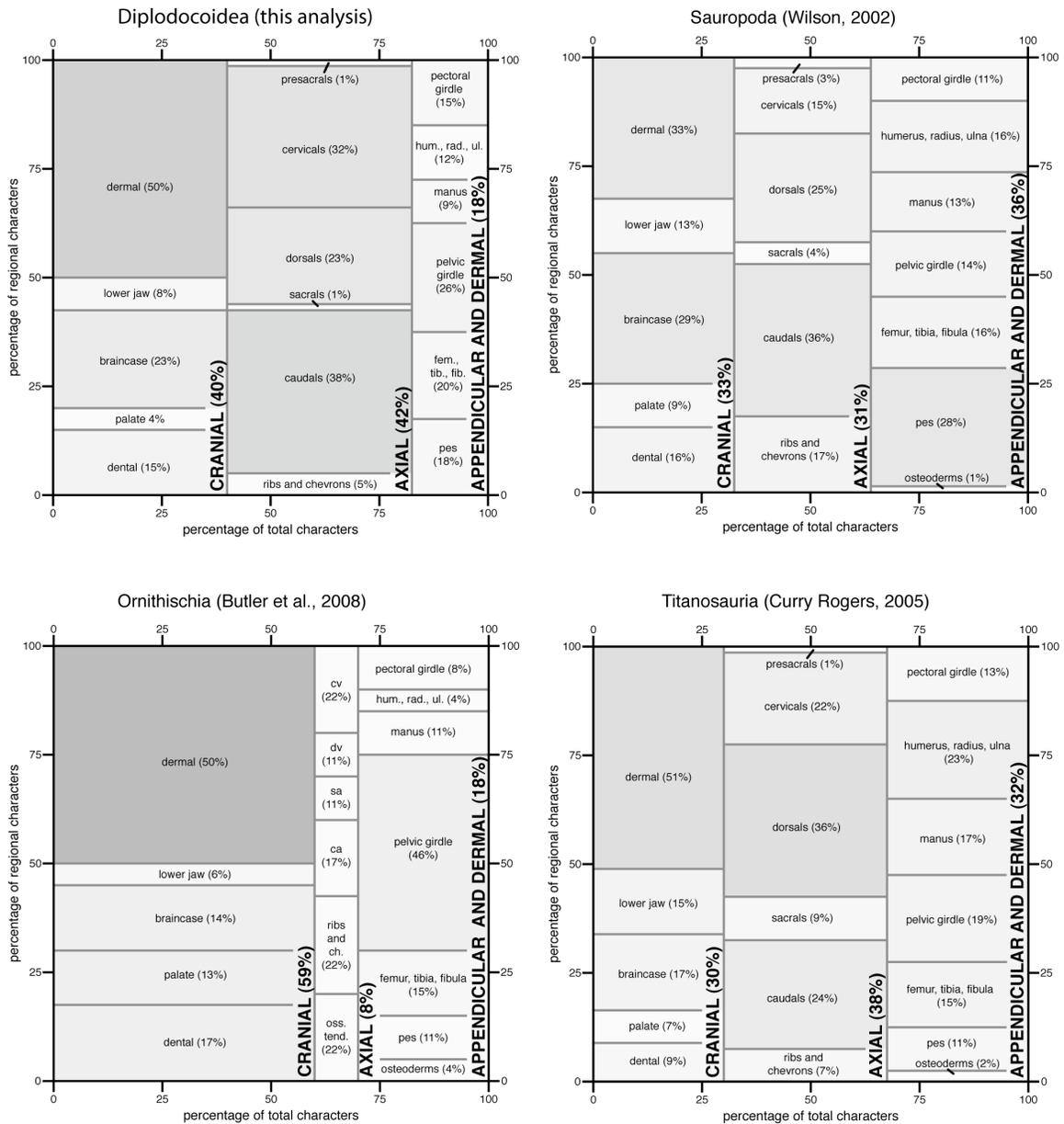
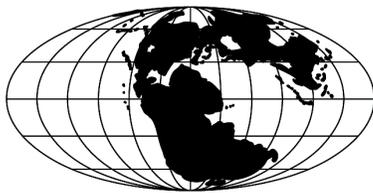
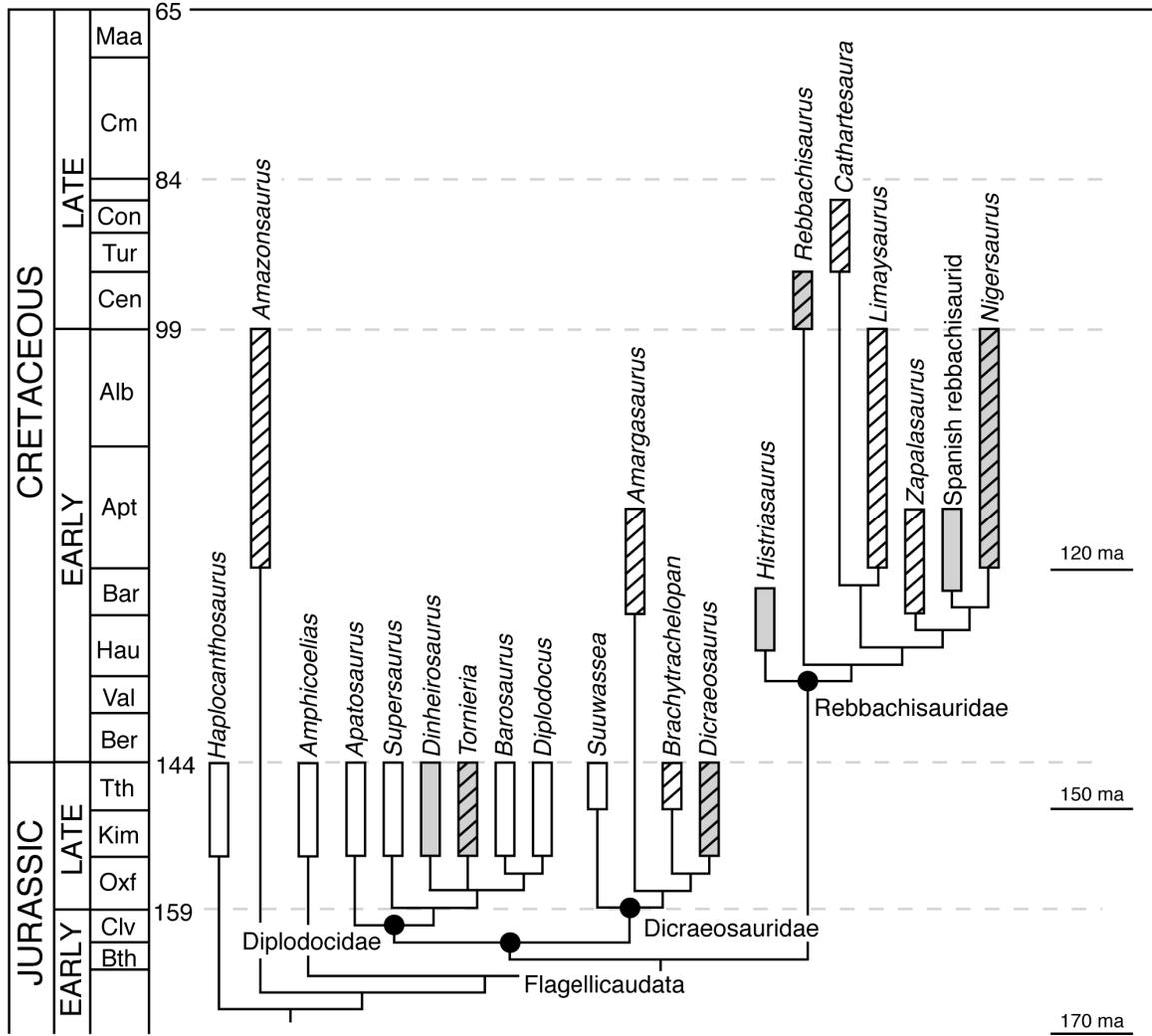


Figure 4.7. Character maps illustrating the relative importance of character data by region to various analyses. Broader analyses of dinosaur interrelationships, such as the Wilson (2002) analysis of sauropoda, incorporate data from all three body regions fairly equally. Analyses of specialized herbivore groups, such as Diplodocoidea (this analysis) or Ornithischia (Butler et al., 2008) must take into account the special importance of cranial anatomy for those taxa.

Figure 4.8 (Facing page). Calibrated phylogeny of diplodocoid sauropods. Cross-hatched bars indicate Gondwanan affinities, hollow bars indicate Laurasian. Grey bars indicate 'old world' (Europe/Africa), white bars indicate 'new world' (North/South America). Temporal boundaries based on Gradstein, Ogg and Smith (2004). Paleogeographic reconstructions below phylogeny illustrate continental connectivity at three key time intervals: the Middle Jurassic (170 ma), likely time of origin for Diplodocoidea; the Late Jurassic (150 ma), interval of greatest diversity within Flagellicaudata; and Early Cretaceous (120 ma), interval of greatest rebbachisaurid diversity. Paleogeographic reconstructions based on Blakey (2006).



Middle Jurassic
170 ma



Late Jurassic
150 ma



Early Cretaceous
120 ma

Table 4.1. Comparisons of the 11 phylogenetic analyses of diplodocoid relationships. Abbreviations: GSA = generic-level synapomorphies added; MPT = number of most-parsimonious trees; NC = novel characters; NG = new genera. *Two additional synapomorphies separating Diplodocidae from *Suuwassea* are also added.

Analysis	Taxa	Characters	MPT	NG	NC	GSA
Calvo and Salgado (1995)	15	49	1	1	—	—
Casanovas, Santafé and Sanz (2001)	10	48	1	1	0 (0%)	0
Harris and Dodson (2004)	29	124	24	1	0 (0%)	0
Salgado et al. (2004)	12	52	3	1	0 (0%)	0
Gallina and Apesteguía (2005)	19	77	5	2	22 (28.6%)	3*
Rauhut et al. (2005)	27	154	88	4	13 (8.4%)	2
Harris (2006c)	30	331	72	0	0 (0%)	0
Remes (2006)	32	234	9	0	0 (0%)	0
Salgado et al. (2006)	14	37	1	1	4 (10.8%)	0
Sereno et al. (2007)	16	102	5	2	12 (11.8%)	9
Lovelace et al. (2008)	31	238	3	1	4 (1.7%)	3

Table 4.2. Comparison of taxonomic inclusion by taxa for nine recent analyses. Analyses which have been clearly superceded by subsequent work by the primary author (e.g. Salgado et al., 2004) have not been included. Abbreviations: CS95, Calvo and Salgado (1995); C&01, Casanovas et al. (2001); GA05, Gallina and Apesteguía (2005); R&05, Rauhut et al. (2005); H06, Harris (2006c); R06, Remes (2006); S&06, Salgado et al. (2006); S&07, Sereno et al. (2007); L&08, Lovelace et al. (2008).

Taxon	CS95	C&01	GA05	R&05	H06	R06	S&06	S&07	L&08
<i>Amargasaurus</i>	X		X	X	X	X	X	X	X
<i>Amazonsaurus</i>							X		
<i>Amphicoelias</i>				X					
<i>Apatosaurus</i>	X		X	X	X	X	X	X	X
<i>Australodocus</i>									
<i>Barosaurus</i>	X	X	X	X	X	X	X		X
<i>Brachytrachelopan</i>				X				X	
<i>Cathartesaura</i>			X					X	
<i>Dicraeosaurus</i>	X	X	X	X	X	X	X	X	X
<i>Dinheirosaurus</i>				X					
<i>Diplodocus</i>	X	X	X	X	X	X	X	X	X
<i>Haplocanthosaurus</i>	X	X	X	X	X	X	X		X
<i>Histriasaurus</i>								X	
<i>Limaysaurus</i>	X		X	X	X	X*	X	X	X*
<i>Losillasaurus</i>		X	X	X	X	X			X
<i>Nigersaurus</i>			X	X	X	X	X	X	X
<i>Nopcsaspondylus</i>									
<i>Rayososaurus</i>			X						
<i>Rebbachisaurus</i>			X	X	X	X	X	X	X
Spanish Taxon								X	
<i>Supersaurus</i>									X
<i>Suuwassea</i>			X	X	X	X	X	X	X
<i>Tornieria</i>				X		X			
<i>Zapalasaurus</i>							X		

Table 4.3. Character state variation in 16 characters shared between the conflicting analyses of Rauhut et al. (2005) and Salgado et al. (2006). Character S30/R114 (asterisk) has the same scoring in both, but the character coding is reversed in Salgado et al. (2006). Abbreviations: S, Salgado et al. (2006); R, Rauhut et al. (2005); *Am*, *Amargasaurus*; *Ap*, *Apatosaurus*; *Ca*, *Camarasaurus*; *Dc*, *Dicraeosaurus*; *Dp*, *Diplodocus*; *Li*, *Limaysaurus*; *Ni*, *Nigersaurus*; *Re*, *Rebbachisaurus*; *Su*, *Suuwassea*.

Char. #	Taxa (character state score)								
	<i>Am</i>	<i>Ap</i>	<i>Ca</i>	<i>Dc</i>	<i>Dp</i>	<i>Li</i>	<i>Ni</i>	<i>Re</i>	<i>Su</i>
S3									?
R33									0
S12								0	0
R76								?	?
S8		1			1				
R57		2			2				
S9	0		0	0			?		?
R62	1		1	1			0		0
S7			0						
R72			1						
S16						1			
R78						?			
S13	0					1			1
R88	?					?			?
S17									0
S89									?
S21	1								1
R92	0								?
S24	1					1			

Taxa (character state score)

Char. #	<i>Am</i>	<i>Ap</i>	<i>Ca</i>	<i>Dc</i>	<i>Dp</i>	<i>Li</i>	<i>Ni</i>	<i>Re</i>	<i>Su</i>
R96	?					0			
S27						?			
R97						0			
S25	1			1				1	
R101	?			0				?	
S29						?			
R103						0			
S30			0*						
R114			0						
S31			0			1	1	1	
R119			1			2	2	2	
S34								?	
R143								1	

Table 4.4. Age, provenance, and original reference for 26 included taxa. Age abbreviations: EK = Early Cretaceous; LJ = Late Jurassic; LK = Late Cretaceous. Area abbreviations: AF = Africa; AS = Asia; EU = Europe; NA = North America; SA = South America.

Taxon	Age	Area	Reference
<i>Amargasaurus cazau</i>	EK	SA	Salgado and Bonaparte (1991)
<i>Amazonsaurus maranhensis</i>	LK	SA	Carvalho et al. (2003)
<i>Amphicoelias</i>	LJ	NA	Cope (1877b)
<i>Apatosaurus</i>	LJ	NA	Marsh (1877)
<i>Australodocus bohetii</i>	LJ	AF	Remes (2007)
<i>Barosaurus</i>	LJ	NA	Marsh (1890)
<i>Brachiosaurus brancai</i>	LJ	AF	Janensch (1914)
<i>Brachytrachelopan mesai</i>	LJ	SA	Rauhut et al. (2005)
Spanish Taxon	EK	EU	Pereda Suberbiola et al. (2003)
<i>Camarasaurus</i>	LJ	NA	Cope (1877a)
<i>Cathartesaura anaerobica</i>	LK	SA	Gallina and Apesteguía (2005)
<i>Dicraeosaurus</i>	LJ	AF	Janensch (1914)
<i>Dinheirosaurus lourinhanensis</i>	LJ	EU	Bonaparte and Mateus (1999)
<i>Diplodocus</i>	LJ	NA	Marsh (1878)
<i>Haplocanthosaurus</i>	LJ	NA	Hatcher (1903)
<i>Histriasaurus boscarolli</i>	EK	EU	Dalla Vecchia (1998)
<i>Jobaria tiguidensis</i>	EK	AF	Sereno et al. (1999)
<i>Limaysaurus tessonei</i>	EK	SA	Calvo and Salgado (1995)
<i>Losillasaurus giganteus</i>	LJ-EK	EU	Casnovas et al. (2001)
<i>Nigersaurus taqueti</i>	EK	AF	Sereno et al. (1999)
<i>Omeisaurus</i>	LJ	AS	Young (1939)
<i>Rebbachisaurus garasbae</i>	LK	AF	Lavocat (1954)
<i>Supersaurus vivianae</i>	LJ	NA	Jensen (1985)
<i>Suuwassea emilieae</i>	LJ	NA	Harris and Dodson (2004)
<i>Tornieria africana</i>	LJ	AF	Sternfeld (1911)

Taxon	Age	Area	Reference
<i>Zapalasauros bonapartei</i>	EK	SA	Salgado et al. (2006)

Table 4.5. Recommended phylogenetic definitions for clades discussed in this analysis. Clades are listed in decreasing order of inclusiveness within lineages. MRCA = most recent common ancestor and all descendants.

Clade	Definition	Author of Definition
Neosauropoda	MRCA (<i>Diplodocus</i> + <i>Saltasaurus</i>)	Wilson and Sereno (1998)
Diplodocoidea	<i>Diplodocus</i> not <i>Saltasaurus</i>	Wilson and Sereno (1998)
Rebbachisauridae	<i>Rebbachisaurus</i> not <i>Diplodocus</i>	Wilson, in Salgado et al. (2004)
Limaysaurinae	<i>Limaysaurus</i> not <i>Nigersaurus</i>	New
Nigersaurinae	<i>Nigersaurus</i> not <i>Limaysaurus</i>	New
Flagellicaudata	MRCA (<i>Dicraeosaurus</i> + <i>Diplodocus</i>)	Harris and Dodson (2004)
Dicraeosauridae	<i>Dicraeosaurus</i> not <i>Diplodocus</i>	Sereno (1998)
Diplodocidae	<i>Diplodocus</i> not <i>Dicraeosaurus</i>	Sereno (1998)

Table 4.6. Ambiguous character optimizations attributable to missing data, based on two optimization strategies: accelerated transformations (ACCTRAN) and delayed transformations (DELTRAN). ACCTRAN favors reversals over parallelism, whereas DELTRAN favors parallelism over reversals. Characters are listed in their approximate order of appearance in the cladogram. MDD = more derived diplodocoids.

Character number	DELTRAN	ACCTRAN
1, 3, 4, 5, 6, 8, 9, 13, 15, 28, 30, 31, 34, 35, 49, 50, 56, 64, 65, 70, 71, 149, 152, 163	Rebbachisauridae + Flagellicaudata	Diplodocoidea
141	Rebbachisauridae + Flagellicaudata	<i>Amazonsaurus</i> + MDD
126, 145	Rebbachisauridae + Flagellicaudata	<i>Amphicoelias</i> + MDD
69	<i>Amphicoelias</i> + MDD	Diplodocoidea
39	Flagellicaudata	Neosauropoda
32, 67, 84	Flagellicaudata	Diplodocoidea
86	Diplodocidae, Dicraeosauridae	Flagellicaudata
187	Diplodocidae	Flagellicaudata
102, 136	<i>Barosaurus</i> + <i>Diplodocus</i>	(<i>Dinheirosaurus</i> , <i>Tornieria</i> (<i>Barosaurus</i> + <i>Diplodocus</i>))
52, 80, 162	Dicraeosauridae, <i>Nigersaurinae</i> + <i>Limaysaurinae</i>	Diplodocoidea
105	<i>Amargasaurus</i> + MDD, Rebbachisauridae	Diplodocoidea
48, 86, 108, 115, 125	<i>Amargasaurus</i> + MDD	Dicraeosauridae
156, 157, 158, 161	<i>Rebbachisaurus</i> + MDD	Rebbachisauridae
20, 21, 22, 24, 26, 27, 32, 33, 35, 39, 43, 44, 46, 51, 53, 67, 73, 74, 87, 88, 95, 125	<i>Nigersaurinae</i> + <i>Limaysaurinae</i>	Rebbachisauridae
90, 94, 122, 173, 181	<i>Nigersaurus</i> + Burgos	<i>Nigersaurinae</i>

Table 4.7. Suggested rescorings for the matrix of Rauhut et al. (2005).

Taxon	Character	Original	Rescored
<i>Amazonsaurus</i>	113	1	?
<i>Suuwassea</i>	66	1	0

Table 4.8. Age, provenance, and probable attribution of fragmentary taxa not included in the final analysis. Age abbreviations: EK = Early Cretaceous; LK = Late Cretaceous. Area abbreviations: EU = Europe, SA = South America. Clade abbreviation: MDT = more derived taxa.

Taxon	Age	Area	Clade	Characters
CCC 017	EK	SA	Rebbachisauridae	116
MACN PV N35	EK	SA	Rebbachisauridae	104, 105, 116
MIWG 6544	EK	EU	Rebbachisauridae	156, 157
MOR 592	LJ	NA	Dicraeosauridae	45, 61
<i>Nopcsaspondylus</i>	LK	SA	<i>Rebbachisaurus</i> + MDT	104, 105, 109, 116, 120
<i>Rayososaurus</i>	EK	SA	Rebbachisauridae	156, 157, 158

Table 4.9. Rescored cells from the Sereno et al. (2007) matrix. Character state abbreviations: '0' = primitive; '1' = derived; '?' = unknown.

Taxon	Character	Original	Rescored
<i>Cathartesaura</i>	80	0	1
<i>Dicraeosaurus</i>	81	1	0
<i>Histriasaurus</i>	71	?	0
<i>Limaysaurus</i>	18, 75, 80, 94	0	1
<i>Limaysaurus</i>	12	1	?
<i>Limaysaurus</i>	78	?	1
<i>Nigersaurus</i>	55, 69	?	1
<i>Nigersaurus</i>	78	?	0
<i>Suuwassea</i>	49	1	0
<i>Zapalasaurus</i>	51	?	1

Table 4.10. Percent missing data in terminal taxa, broken down by region.

Taxon	Cranial (74)	Axial (79)	Appendicular (34)	Total
<i>Amargasaurus cazau</i>	63%	16%	50%	41%
<i>Amazonsaurus maranhensis</i>	100%	64%	94%	84%
<i>Amphicoelias altus</i>	100%	77%	77%	86%
<i>Apatosaurus</i>	4%	0%	0%	2%
<i>Australodocus bohetii</i>	100%	82%	100%	93%
<i>Barosaurus</i>	100%	6%	26%	47%
<i>Brachiosaurus brancai</i>	3%	4%	0%	3%
<i>Brachytrachelopan mesai</i>	100%	54%	97%	80%
Spanish Taxon	100%	69%	80%	83%
<i>Camarasaurus</i>	0%	1%	0%	1%
<i>Cathartesaura anaerobica</i>	100%	57%	80%	78%
<i>Dicraeosaurus</i>	30%	1%	15%	15%
<i>Dinheirosaurus lourinhanensis</i>	100%	71%	100%	88%
<i>Diplodocus</i>	0%	0%	3%	1%
<i>Haplocanthosaurus</i>	100%	6%	44%	50%
<i>Histriasaurus boscarolli</i>	100%	86%	100%	94%
<i>Jobaria tiguidensis</i>	11%	13%	15%	12%
<i>Limaysaurus tessonei</i>	43%	9%	15%	23%
<i>Losillasaurus giganteus</i>	96%	48%	80%	73%
<i>Nigersaurus taqueti</i>	8%	18%	21%	14%
<i>Omeisaurus</i>	11%	13%	6%	11%
<i>Rebbachisaurus garasbae</i>	97%	77%	85%	87%
<i>Supersaurus vivianae</i>	100%	43%	77%	72%
<i>Suuwassea emilieae</i>	53%	50%	77%	56%
<i>Tornieria africana</i>	64%	63%	26%	57%
<i>Zapalasaurus bonapartei</i>	100%	63%	71%	79%

Table 4.11. Data support for each major clade of ingroup taxa. Percent missing data (cells) and relative percent of character support (characters) for each region are reported. Percent missing data was based on Table 10. Percent support was calculated by summing the characters supporting each node within each lineage (Appendix 3). *Although not included in this study, at least two taxa (*Nopcsaspondylus* and *Rayososaurus*) should be considered rebbachisaurids, and therefore also diplodocoids. †The percent support in this group totals only 99% as a result of rounding; cranial and axial characters provide nearly 40.5% support each.

	Diplodocoidea	Dicraeosauridae	Diplodocidae	Rebbachisauridae
# Taxa	20 (+2)*	4	6	7 (+2)*
Cranial				
% missing	73%	55%	61%	78%
% support	41%	31%	30%	40%
Axial				
% missing	42%	49%	31%	55%
% support	47%	66%	63%	40%
Appendicular				
% missing	57%	60%	38%	64%
% support	12%	3%	7%	19% [†]

Table 4.12. Step-matrix coding for the paleobiogeographic character used to determine area of origin.

From/To	North America	Europe	Africa	South America
North America	0	1	2	1
Europe	1	0	1	2
Africa	2	1	0	1
South America	1	2	1	0

APPENDIX 4.1 — MATERIAL EXAMINED

Taxon	Basis for scoring
<i>Amargasaurus cazau</i>	MACN-N 15 (holotype)
<i>Amazonsaurus maranhensis</i>	Carvalho et al. (2003)
<i>Amphicoelias</i>	AMNH 5764 (holotype), 5765
<i>Apatosaurus</i>	AMNH 339, 460, 550, 675, 696, 969, 4676, 7533, 30016; CM 85, 87, 89, 555, 556, 566, 577, 3018, 3378, 3390, 3391, 11253, 11162, 21708, 21748, 21752, 21785, 33996, 36687; CMC VP7800; USNM 4287, 4712
<i>Australodocus bohetii</i>	MB.R. 2455 (holotype), 2454 (paratype)
<i>Barosaurus</i>	AMNH 6341; CM 11984, 21744; Lull (1919)
<i>Brachiosaurus brancai</i>	MB.R. 2180, 2181, 2390
<i>Brachytrachelopan mesai</i>	MPEF-PV 1716 (holotype)
Spanish Taxon	Pereda Suberbiola et al. (2003)
<i>Camarasaurus</i>	AMNH 461; CM 8942, 11069, 11338, 11393, 12020, 21712, 21730, 21733, 21781, 33925, 33929, 36663; UMMP 16995; USNM 13786; McIntosh et al. (1996)
<i>Cathartesaura anaerobica</i>	MPCA-232 (holotype)
<i>Dicraeosaurus</i>	MB.R. 2195–2197, 2204, 2336–2340, 2371, 2373, 2377– 2380, 2550, 2551, 2569, 2628, 2631, 2634, 2655, 2695, 2696, 2711, 2717–2719, 2737, 3719–3732, 3772–3783, 3785, mounted skeleton (holotype)
<i>Dinheirosaurus lourinhanensis</i>	Bonaparte and Mateus (1999)
<i>Diplodocus</i>	AMNH 223, 380, 401, 594, 614, 694, 5855; CM 84, 94, 307, 2098, 2099, 3492, 11161, 11255, 21749, 21763, 21738, 26552, 30767; USNM 2672, 2673, 4713, 4713, 4728, 5368, 10865
<i>Haplocanthosaurus</i>	CM 572 (holotype), 879, 20443; CMNH 10380; USNM 4275
<i>Histriasaurus boscarolli</i>	Dalla Vecchia (1998)
<i>Jobaria tiguidensis</i>	MNN TIG 3 (holotype), 4–12
<i>Limaysaurus tessonei</i>	MUCPv-205 (holotype), 153, 206, 272, 273; Pv-6722-MOZ, 6729, 6733, 6734, 6738, 6741, 6745, 6747, 6751, 6753, 6756, 6759, 6760, 6766, 6767
<i>Losillasaurus giganteus</i>	Casanovas et al. (2001)
<i>Nigersaurus taqueti</i>	MNHN 75, 1966; MNN GAD-512 (holotype), 15–18

Taxon	Basis for scoring
<i>Nopcsaspondylus</i>	Nopcsa (1902)
<i>Omeisaurus</i>	He, Li and Cai (1988); Tang et al. (2001)
<i>Rayososaurus agrioensis</i>	MACN-N 41 (holotype)
<i>Rebbachisaurus garasbae</i>	MNHN 1957 (holotype)
<i>Supersaurus vivianae</i>	Jensen (1985); Lovelace et al. (2008)
<i>Suuwassea emilieae</i>	ANS 21122 (holotype)
<i>Tornieria africana</i>	MB.R. 2343, 2345, 2346, 2348, 2386, 2387, 2572, 2586, 2669, 2672, 2713, 2726, 2728, 2730, 2733, 2956–2960, 2913; Janensch (1929b); Remes (2006)
<i>Zapalasaurs bonapartei</i>	Pv-6127-MOZ (holotype)

APPENDIX 4.2—CHARACTER-TAXON MATRIX

		0	0	0	0	0	0
		1	2	3	4	5	6
		0	0	0	0	0	0
<i>Omeisaurus</i>	1000000000	0900000001	0010010000	0000000000	000000??00	?????00000	
<i>Jobaria</i>	1000000000	0900010001	??110100?0	0000000000	0000000?00	00?0?0?000	
<i>Camarasaurus</i>	1010000000	1000010001	0001110010	0010000010	0000000000	0000100100	
<i>Brachiosaurus</i>	1010000000	1000010001	000?110010	00100?0000	0000000000	0001000000	
<i>Australodocus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Haplocanthosaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Amphicoelias</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Losillasaurus</i>	??????????	??????????	??????????	??????????	??????????0	?00???????	
<i>Dinheirosaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Amazonsaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Apatosaurus</i>	0021111111	1011101101	00011101?1	1101110110	0100000011	000001?100	
<i>Barosaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Diplodocus</i>	0021111111	1111101101	0001110111	1101110110	0100000011	0001011100	
<i>Supersaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Tornieria</i>	002111?1??	??????????	00????????	????????11?	?100000?1?	??01??????	
<i>Amargasaurus</i>	??????????	?????1?0011	0000?00???	???????1111	1001101111	0100??????	
<i>Brachytrachelopan</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Dicraeosaurus</i>	01211111??	10??1?0011	0000??0???	???????1111	0001101111	01001??101	
<i>Suuwassea</i>	?12111????	?????1?????	00?0??????	?101?01111	0000101???	0100???	
<i>Histriasaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Rebbachisaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Limaysaurus</i>	??????????	?????1?0000	1119101??1	?211200090	0019010011	1110?1????	
<i>Cathartesaura</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Zapalasaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Nigersaurus</i>	002111011?	1010100000	11191011?1	121120009?	0119010011	1110?1?012	
<i>Spanish Rebbach.</i>	??????????	??????????	??????????	??????????	??????????	??????????	

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0	0	0	1	1	1
7	8	9	0	1	2
0	0	0	0	0	0

<i>Omeisaurus</i>	00?0000001	?000001000	000??001?1	0000000009	9?00000000	1?00000000
<i>Jobaria</i>	00?0000000	0000001010	0100?001?0	0000000109	900000?001	001?0??100
<i>Camarasaurus</i>	0010000001	0000101001	0100000100	0000001000	0000000?01	1000000010
<i>Brachiosaurus</i>	0010000101	0000111001	1100000101	0000000009	9000001001	1010000010
<i>Australodocus</i>	??????????	?????11001	110?????01	?0000?????	??????????	??????????
<i>Haplocanthosaurus</i>	??????????	?????01000	010??00110	0000000019	9000101011	1000000000
<i>Amphicoelias</i>	?????????1?	??????????	??????????	??????????	??00001?00	1010000100
<i>Losillasaurus</i>	??????????	?????01000	00???0????	??????????	??0010?001	10?0?0?00?
<i>Dinheirosaurus</i>	??????????	??????1001	010???????	??????101?	??000??100	1111??0100
<i>Amazonsaurus</i>	??????????	?????0????	??????????	??????????	??00??0?0?	1????0?01?
<i>Apatosaurus</i>	01?1111111	1000101001	0101110110	0001001001	0000001000	1111000100
<i>Barosaurus</i>	??????????	?????01001	011??101?1	0001001111	0100001100	1111000?00
<i>Diplodocus</i>	0101111111	1100101001	0101010101	0001001111	0100001100	1111000100
<i>Supersaurus</i>	??????????	?????01001	010?????11	??1?01???	?00000?000	?1?1?0???
<i>Tornieria</i>	???1??111	?1??101001	011?????1	000???????	??????????	??????????
<i>Amargasaurus</i>	??????????	?????01010	1101011110	1110001000	1010101100	0?1110120?
<i>Brachytrachelopan</i>	??????????	?????01010	1?0??11??0	111??01?11	10101?1110	01111?020?
<i>Dicraeosaurus</i>	1??1101111	1??0101010	1101011110	1110001011	1010101110	0111100200
<i>Suuwassea</i>	1??????11?	??001?1010	0101000010	0100001??0	1?10?0???	1?0????1??
<i>Histriasaurus</i>	??????????	?????0????	??????????	??????????	??0110???	10???1???
<i>Rebbachisaurus</i>	?????????1?	??0?0?0???	??????????	??????????9	9?011?1?1?	101101?201
<i>Limaysaurus</i>	?????02?1?	??11101010	010??00000	0000110009	900110?010	100101?101
<i>Cathartesaura</i>	??????????	?????01010	010???????	??00110019	9?????????	??????????
<i>Zapalasaurus</i>	??????????	?????01110	01??00???	??????????	??????????	??????????
<i>Nigersaurus</i>	00?1202110	1011101110	010??00001	0001100009	900111101?	101?010101
Spanish Rebbach.	??????????	??????1110	?????00??1	??1???0??	??0???????	1???????

	1	1	1	1	1	1	1
	3	4	5	6	7	8	
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<i>Omeisaurus</i>	000000000	00?000000	000?0000??	?000000?00	1000000000	0000000100	
<i>Jobaria</i>	0000??0011	00?0000000	0000000?00	9000000?00	1011000000	0100000?10	
<i>Camarasaurus</i>	0000000011	0000000000	0000000100	9000101000	1001111001	0100000000	
<i>Brachiosaurus</i>	0000000011	0000000000	00000000??	?000101000	1001111101	0100000000	
<i>Australodocus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Haplocanthosaurus</i>	0000000011	0000000000	00000001??	?10010000?	????????000	010?000100	
<i>Amphicoelias</i>	??????????	??????????	??????????	????????00?	??????????	????????1110	
<i>Losillasaurus</i>	?00?000000	01?0?0000?	000????0??	??????????	??0????00?	010??0????	
<i>Dinheirosaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Amazonsaurus</i>	?00?0?1111	0?????0100	??000000??	????1?????	????????10?	??????????	
<i>Apatosaurus</i>	1001010111	0000001101	1100100011	1111000010	1010001010	1000100110	
<i>Barosaurus</i>	1001010111	0101111111	1111101011	?1??000000	101?00?01?	10001001??	
<i>Diplodocus</i>	1001010111	0101111111	1111101011	1100000000	101100?010	1000100111	
<i>Supersaurus</i>	?00?0001??	01?100?101	11?0??????	?100?00?0?	?????????1?	??001?????	
<i>Tornieria</i>	?00?010111	0101?11101	?1011000??	?????0000?	?011????0??	10001?0111	
<i>Amargasaurus</i>	100?1?11??	00100001?0	10?011????	?10000000?	1110????0??	???????0110	
<i>Brachytrachelopan</i>	1?????????	??????????	??????????	?10???????	????????0??	??????????	
<i>Dicraeosaurus</i>	1001111111	1010000100	1000110011	?10000000?	1111???010	1000110110	
<i>Suuwassea</i>	??????????	?110?0????	???011??00	?10?000?0?	111???????	??????????	
<i>Histriasaurus</i>	??????????	??????????	??????????	??????????	??????????	??????????	
<i>Rebbachisaurus</i>	??????????	??????????	??????????	?????1210?	0?????????	??????????	
<i>Limaysaurus</i>	0000111111	0000001100	1000100011	?1??112101	011100??00	0110000110	
<i>Cathartesaura</i>	?00?11????	??00??1100	1000?00???	?????12???	??????????	???????0110	
<i>Zapalasaurus</i>	??1?1?11??	0000000?00	10?01000??	??????????	?????????00	0100000??0	
<i>Nigersaurus</i>	?11??111??	0000??0100	??00100011	?100?1210?	0111????000	0111000110	
Spanish Rebbach.	?11??1?1??	00?0????100	?00???????	??????????	??????????	01110?????	

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Omeisaurus ?00000100
Jobaria ?0?11100?
Camarasaurus 000110000
Brachiosaurus 000110000
Australodocus ?????????
Haplocanthosaurus 00???1???
Amphicoelias 00???????
Losillasaurus ?????????
Dinheirosaurus ?????????
Amazonsaurus ?????????
Apatosaurus 001111101
Barosaurus 001???1?1
Diplodocus 001111101
Supersaurus ??1??????
Tornieria 001111?0?
Amargasaurus ??0111???
Brachytrachelopan ??????????
Dicraeosaurus 01011110?
Suuwassea ??0???1??
Histriasaurus ?????????
Rebbachisaurus ?????????
Limaysaurus 00?1?101?
Cathartesaura ?0????????
Zapalasaurus ?????????
Nigersaurus 101111???
Spanish Rebbach. 10????????

APPENDIX 4.3—CHARACTER LIST

Character codings used in this analysis are listed below in anatomical order.

1. Premaxillary anterior margin, shape: without step (0); with marked step, anterior portion of skull sharply demarcated (1).
2. Premaxilla, external surface: without anteroventrally orientated vascular grooves originating from an opening in the maxillary contact (0); vascular grooves present (1).
3. Ascending process of the premaxilla, shape in lateral view: convex (0); concave, with a large dorsal projection (0); sub-rectilinear and directed posterodorsally (1).
4. Premaxilla, angle between lateral and medial margins of premaxilla as seen in dorsal view: greater than 20° (0); less than or equal to 20° (1).
5. Premaxilla, shape in dorsal view: main body is massive, with proportionally short ascending process distinct (0); single elongate unit, distinction between body and process absent (1).
6. Posterolateral process of the premaxilla and the lateral process of the maxillary, shape: with midline contact forming a marked narial depression, subnarial foramen not visible laterally (0); without midline contact (1).
7. Subnarial foramen and anterior maxillary foramen, position: well distanced from one another (0); separated by narrow bony isthmus (1).
8. Subnarial foramen: not visible laterally (0); visible in lateral view (1).

9. Dorsal process of maxilla, posterior extent: anterior to or even with posterior process (0); extending posterior to posterior process (1).
10. Maxilla-quadratojugal contact: absent or small (0); broad (1).
11. Preantorbital fenestra: absent (0); present (1).
12. Preantorbital fenestra: without sharply defined fossa (0); with (1).
13. Antorbital fenestra, maximum diameter: much shorter than orbital maximum diameter, less than 85% of orbit (0); subequal to orbital maximum diameter, greater than 85% orbit (1).
14. Antorbital fenestra, shape of dorsal margin: straight or convex (0); concave (1).
15. External nares, position: retracted to level of orbit, facing laterally (0); retracted to position between orbits, facing dorsally or dorsolaterally (1).
16. External nares, maximum diameter: shorter than orbital maximum diameter (0); longer than orbital maximum diameter (1).
17. Prefrontal, posterior process size: small, not projecting far posterior of frontal-nasal suture (0); elongate, approaching parietal (1).
18. Prefrontal, posterior process shape: flat (0); hooked (1).
19. Frontals, midline contact (symphysis): patent suture (0); fused in adult individuals (1).
20. Frontal, anteroposterior length: approximately twice transverse breadth (0); less than transverse breadth (1).

21. Frontal-Nasal suture, shape: flat or slightly bowed anteriorly (0); v-shaped, pointing posteriorly (1).
22. Frontals, dorsal surface: without paired grooves facing anterodorsally (0); grooves present, extend on to nasal (1).
23. Frontal, contribution to dorsal margin of orbit: roughly equal or less than contribution of prefrontal (0); approximately twice contribution of prefrontal (1).
24. Frontal, contribution to margin of supratemporal fenestra/fossa: present (0); absent, frontal excluded from anterior margin of fenestra/fossa (1).
25. Orbit, anterior-most point: anterior to the anterior extremity of lateral temporal fenestra (0); roughly even with or posterior to anterior extent of lateral temporal fenestra
26. Orbital ventral margin, anteroposterior length: broad, with subcircular orbital margin (0); reduced, with acute orbital margin (1).
27. Postorbital, posterior process: present (0); absent (1).
28. Jugal, contribution to antorbital fenestra: very reduced or absent (0); large, bordering approximately one-third its perimeter (1).
29. Jugal, contact with ectopterygoid: present (0), absent (1).
30. Quadratojugal, position of anterior terminus: posterior to middle of orbit (0), anterior margin of orbit or beyond (1).
31. Quadratojugal, angle between anterior and dorsal processes: less than or equal to 90° (0); greater than 90°, approaching 130° (1).

32. Quadrate, articular surface shape: quadrangular in ventral view, oriented transversely (0); roughly triangular in shape (1); thin, crescent-shaped surface with anteriorly directed medial process (2).
33. Quadrate fossa, depth: shallow (0); deeply invaginated (1).
34. Quadrate, orientation: subvertical (0); strongly inclined posterodorsally (1).
35. Squamosal, anterior extent: restricted to postorbital region (0); extends well past posterior margin of orbit (1); extends beyond anterior margin of orbit (2).
36. Squamosal-quadratojugal contact: present (0); absent (1).
37. Squamosal, posteroventral margin: smooth (0); with prominent, ventrally directed 'prong' (1).
38. Parietal, contribution to post-temporal fenestra: present (0); absent (1).
39. Parietal, distance separating supratemporal fenestrae: less than the width of the long axis of the supratemporal fenestra (0); twice the length of the long axis of the supratemporal fenestra (1).
40. Postparietal foramen: absent (0); present (1).
41. Paroccipital processes, shape: ventral margin flat (0); ventral margin with marked excavation (1).
42. Paroccipital process distal terminus: straight, slightly expanded surface (0); rounded, tonguelike process (1).
43. Supratemporal fenestra: present (0); absent (1).

44. Supratemporal fenestra, maximum diameter: much longer than that of foramen magnum (0); subequal to greatest length of foramen magnum (1).
45. Supraoccipital: sagittal nuchal crest: broad, weakly developed (0); narrow, sharp and distinct (1).
46. Supraoccipital, height: twice height of foramen magnum (0); subequal to or less than height of foramen magnum (1).
47. Crista prootica, size: rudimentary (0); expanded laterally into dorsolateral process (1).
48. Basipterygoid processes, shape: thin, widely diverging (0); massive, narrowly diverging (1).
49. Basipterygoid processes, orientation: perpendicular to (0) or angled approximately 45° to (1) skull roof.
50. Basipterygoid processes, length: short, approximately twice basal diameter (0); elongate, at least four times basal diameter (1).
51. Basal tubera, anteroposterior depth: approximately half dorsoventral height (0); sheet-like, 20% dorsoventral height (1).
52. Basal tubera, breadth: much broader than occipital condyle (0); narrower than occipital condyle (1).
53. Basal tubera: distinct from basipterygoid (0); reduced to slight swelling on ventral surface of basipterygoid (1).
54. Basal tubera, shape of posterior face: convex (0); slightly concave (1).

55. Palatobasal contact, shape: pterygoid with small facet (0); dorsomedially orientated hook (1); rocker-like surface (2).
56. Pterygoid, transverse flange (i.e. ectopterygoid process) position: between orbit and antorbital fenestra (0); anterior to antorbital fenestra (1).
57. Pterygoid position relative to ectopterygoid on transverse palatal hook: lateral (0); medial (1).
58. Dentary, anteroventral margin shape: gently rounded (0); sharply projecting triangular process or 'chin' (1).
59. Dentary, anterolateral corner: not expanded laterally beyond mandibular ramus (0); expanded beyond lateral mandibular ramus (1).
60. Dentary, cross-sectional shape of symphysis: oblong or rectangular (0); subtriangular, tapering sharply towards ventral extreme (1); subcircular (2).
61. Dentary, tuberosity on labial surface near symphysis: absent (0); present (1).
62. Mandible, coronoid eminence: strongly expressed, clearly rising above plane of dentigerous portion (0); absent (1).
63. Splenial posterior process, position: overlapping angular (0); separating anterior portions of prearticular and angular (1).
64. Snout shape in dorsal view: rounded/pointed, PMI below 70% (0); square/blunt, PMI above 75% (1).

65. Tooth rows, length: extending to nearly to or past antorbital fenestra (0); restricted to the jaw anterior of the antorbital fenestra (1); restricted anterior to subnarial foramen (2).
66. Crown-to-crown occlusion: present (0); absent (1).
67. Occlusal pattern: v-shaped, paired wear facets (0); single planar facet (1); paired planar facets (2)
68. Tooth crowns, orientation: aligned slightly anterolingually, tooth crowns overlap (0); tooth crowns, orientation: aligned along jaw axis, crowns do not overlap (1)
69. Tooth crowns, cross-sectional shape at midcrown: D-shaped (0); cylindrical (1).
70. Dentary teeth, number: greater than 20 (0); 17 or fewer (1).
71. Replacement teeth per alveolus, number: two or fewer (0); three or more (1).
72. Teeth, orientation relative to long axis of jaw: perpendicular (0); inclined anteriorly (1).
73. Teeth, longitudinal grooves on lingual aspect: absent (0); present (1).
74. Thickness of enamel asymmetric labiolingually: absent (0); present (1).
75. Teeth, marginal denticles: present (0); absent (1).
76. Presacral bone texture: solid (0); spongy, with large internal cells (camellate) (1).
77. Cervical pneumatopores (pleurocoels): absent (0); present (1).

78. Cervical vertebrae, epipophyseal-prezygapophyseal lamina (eprl): absent (0); present (1).
79. Cervical vertebrae, longitudinal ridge on ventral surface: absent (0); present (1).
80. Cervical vertebrae, longitudinal sulcus present on ventral surface: absent (0); present (1).
81. Cervical vertebrae, pneumatization of lateral surface of centra: large, divided pleurocoel over approximately 1/2 of centrum (0); reduced, large fossa but sharp-bordered coel, if present, restricted to area above parapophysis (1).
82. Cervical vertebrae, pleurocoel: undivided (0); with lamina dividing pleurocoel (1).
83. Cervical vertebrae, second lateral pneumatic fossa: absent (0); shallow, anteroposteriorly elongate fossa present, posteroventral to pleurocoel (1).
84. Atlantal intercentrum, occipital facet shape: rectangular in lateral view, length of dorsal aspect subequal to that of ventral aspect (0); expanded anteroventrally in lateral view, anteroposterior length of dorsal aspect shorter than that of ventral aspect (1).
85. Atlantal neural arch: without foramen (0); with foramen (1).
86. Anterior cervical neural spines, shape: single (0) bifid (1).
87. Anterior cervical vertebrae, height:length ratio: height less than or roughly equal to length of centrum (0); height 1.5 times length of centrum (1).

88. Anterior cervical vertebrae, pleurocoel extending onto dorsal surface of parapophysis: absent (0); present (1).
89. Anterior cervicals, paired pneumatic fossae on ventral surface: absent (0); present (1).
90. Mid-cervical centra, anteroposterior length/height of posterior face: 2.5-3 (0); 4+ (1).
91. Mid-cervical vertebrae, angle between postzygodiapophyseal and spinopostzygapophyseal laminae: acute (0); right angle (1).
92. Mid-cervical neural spines, orientation: vertical (0) anteriorly inclined (1).
93. Mid-cervical neural spines: less than or approximately equal in height to neural arch (distance centrum-postzygapophysis) (0); considerably higher than neural arch (1).
94. Mid- and posterior cervical neural arches, centroprezygapophyseal lamina (cp1), shape: single (0); divided (1).
95. Mid- and posterior cervical vertebrae, pleurocoel extending onto dorsal surface of parapophysis: present (0); absent (1).
96. Posterior cervical vertebrae, accessory lateral lamina connecting postzygodiapophyseal and spinoprezygapophyseal laminae in posterior cervical vertebrae: absent (0) present (1).
97. Posterior cervical neural spines, shape: single (0); bifid (1).

98. Posterior cervical neural arches, accessory spinal lamina: absent (0); present, running vertically just posterior to spinoprezygapophyseal lamina (1).
99. Posterior cervical neural and/or anteriormost dorsal neural spines, orientation: vertical (0); inclined anteriorly (1).
100. Posterior cervical and anterior dorsal bifid neural spines, median tubercle: absent (0); present (1).
101. Posterior cervical and anterior dorsal bifid neural spines: widely diverging (0) narrow, parallel to converging (1).
102. Posterior cervical and anterior dorsal vertebrate, roughened lateral aspect of prezygodiapophyseal lamina: absent (0); present (1).
103. Dorsal pneumatopores (pleurocoels): present (0); absent (1).
104. Dorsal vertebrae, spinodiapophyseal webbing: laminae follow curvature of neural spine and diapophysis in anterior view (0); laminae "festooned" from spine, dorsal margin does not closely follow shape of neural spine and diapophysis (1).
105. Dorsal transverse processes, orientation: horizontal or only slightly inclined dorsally (0); more than 30° inclined dorsally from the horizontal (1).
106. Dorsal neural arches, paired, subdivided pneumatic chambers dorsolateral to neural canal: absent (0), present (1).

107. Single (not bifid) dorsal neural spines, spinprezygapophyseal laminae: separate along entire length (0); joined distally, forming single prespinal lamina (1).
108. Mid-dorsal neural spines, form: single, bifid form (if present) does not extend past the second or third dorsal (0); bifid, inclusive of at least the fifth dorsal vertebrae (1).
109. Mid- and posterior dorsal vertebrae, height of neural arch below the postzygapophyses (pedicel): less than height of centrum (0); subequal to or greater than height of centrum (1).
110. Mid- and posterior dorsal neural spines: without laterally flared, triangular lateral processes (0); with laterally flared, distal triangular processes (1).
111. Mid- and posterior dorsal vertebrae, lateral pleurocoels present in centra: absent (0); present (1).
112. Mid- and posterior dorsal neural arches, centropostzygapophyseal lamina (cpol), shape: single (0); divided, left and right medial cpols uniting beneath hyposphene (1).
113. Mid- and posterior dorsal neural arches, posterior centroparapophyseal lamina (pcpl): absent (0); present (1).
114. Mid- and Posterior dorsal neural arches: height above postzygapophyses (neural spine) equal to height below (pedicel) (0); neural spine much taller than pedicel (1).

115. Mid- and posterior dorsal neural arches, prezygoparapophyseal lamina (prpl): present (0); absent (1).
116. Posterior dorsal neural arches: spinopostzygapophyseal lamina single (0); spol divided near postzygapophyses (1).
117. Posterior dorsal neural arches: parapophysis subequal in height or below height of diapophysis (0); parapophysis well above height of diapophysis (1).
118. Dorsal neural spine (not including arch), height: less than 2x centrum length (0); 2x centrum length (1); 4x centrum length (2).
119. Posterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1).
120. Posterior dorsal neural arches, hyposphene-hypantrum articulations: present (0); absent (1).
121. Sacral neural spines, height: twice centrum length (0); nearly four times centrum length (1).
122. Caudal neural spines, elliptical depression between spinodiapophyseal lamina and postspinal lamina on lateral neural spine: absent (0); present (1).
123. Caudal neural spines with triangular lateral processes: absent (0); present (1)
124. First caudal centrum, articular face shape: flat (0); procoelous (1); opisthocoelous (2); biconvex (3).

125. Anterior caudal vertebrae, transverse processes: ventral surface directed laterally or slightly ventrally (0); directed dorsally (1).
126. Anterior caudal neural spine (not including arch), height: less than 1.5 times centrum height (0); 1.5 times centrum height or more (1).
127. Anterior caudal neural spines, shape in anterior/posterior view: rectangular through most of length (0); 'petal' shaped expanding transversely through 75% of its length and then tapering (1).
128. Anterior caudal neural spines, transverse breadth: approximately 50% of anteroposterior length (0); greater than anteroposterior length (1).
129. Anterior caudal neural arches, prespinal lamina: absent (0); present (1).
130. Anterior caudal neural arches, postspinal lamina: absent (0); present (1).
131. Anterior caudal neural spines, prespinal and postspinal laminae: terminate at or beneath dorsal margin of neural spine (0); project dorsally above neural spine (1).
132. Anterior caudal centra (excluding the first), articular face shape: amphiplatyan (0); procoelous(1).
133. Anterior caudal centra, ventral surface: without irregularly placed foramina (0); irregular foramina present on some anterior caudals (1).
134. Anterior caudal centra, pneumatopores (pleurocoels): absent (0); present (1).
135. Anterior caudal centra, length: subequal among first 20 (0); doubling over first 20 (1).

136. Anterior caudal vertebrae, anterior face shape: cylindrical (0); quadrangular (1).
137. Anterior caudal neural spines, sprl-spol contact: absent (0) present (1).
138. Anterior caudal neural spines, sprl: absent (0); present, extending onto lateral aspect of neural spine (1).
139. Anterior caudal neural spines, shape: single (0); slightly bifurcate anteriorly (1).
140. Anterior caudal neural spines, lateral expansion at distal extremity: absent (0); present, distolateral margins flared slightly over last 1/3 without tapering. (1).
141. Anterior caudal transverse processes, shape: triangular, tapering distally (0); winglike (1).
142. Anterior caudal transverse processes, diapophyseal laminae (acdl, pc dl, prdl, podl): absent (0); all present, well defined (1).
143. Anterior caudal vertebrae, concavo-convex zygapophyseal articulation: absent (0); present (1).
144. Anterior and mid-caudal centra, ventral longitudinal hollow: absent (0); present (1).
145. Mid-caudal vertebrae, ratio of centrum length to height: less than 2:1 (0); greater than or equal to 2:1 (1).

146. Mid-caudal vertebrae, lateral surface of centra: without longitudinal ridge at mid-height (0); longitudinal ridge present, centra hexagonal in anterior/posterior view (1).
147. Mid-caudal neural spines, orientation: posterodorsally inclined (0); vertical (1).
148. Anterior and mid-caudal neural spines, shape: rectangular in anterior/posterior view (0); with distinct distal swelling in anterior/posterior view (1).
149. Distalmost caudal centra, articular face shape: platycoelous (0); biconvex (1).
150. Distalmost caudal centra, length-to-height ratio: less than 4 (0); greater than 5 (1).
151. Distalmost biconvex caudal centra, number: 10 or fewer (0); more than 30 (1).
152. Cervical ribs, length: overlapping several centra posterior (0); shorter than or roughly equivalent to centrum length (1).
153. Cervical ribs, position relative to centrum: not projecting far beneath centrum (0); projecting well beneath centrum, such that height of vertebra exceeds length (1).
154. Cervical ribs, length of posterior process: greater than length of fused diapophysis/tuberculum (0); subequal in length to fused diapophysis/tuberculum

155. Chevrons, "crus" bridging haemal canal: present (0); absent on most (1).
156. Scapular acromion process dorsal margin: convex or straight (0), u-shaped concavity (1).
157. Scapular blade, shape: acromial edge straight, without rounded expansion (0); rounded expansion on acromial side (1); racquet-shaped (2).
158. Scapula: without semi-ovate, flat muscle scar just distal to glenoid on scapular shaft (0); scar present (1).
159. Scapular glenoid, orientation: relatively flat or laterally facing (0); strongly bevelled medially (1).
160. Sternal plates, shape: ovate (0); crescentic (1)
161. Humerus, midshaft cross-section, shape: circular, major and minor axes subequal (0); elliptical, major axis twice width of minor axis (1).
162. Humerus, pronounced proximolateral corner: (0) absent; (1) present
163. Humerus, proximal end expanded laterally in anterior/proximal view: not expanded (0); expanded, lateral margin concave in anterior/posterior view (1)
164. Ulna, proximal condylar processes: subequal in length (0); anterior arm longer (1).
165. Metacarpus, ratio of longest metacarpal to radius: close to 0.3 (0); greater than 0.45 (1).
166. Metacarpal I, length: shorter than IV (0); longer than IV (1).
167. Carpus, number of carpal bones: more than 2 (0); two or fewer (1).

168. Iliac preacetabular process, shape: sharply pointed (0); blunt to semi-circular anterior margin (1).
169. Pubis, ambiens process development: small, confluent with anterior margin of pubis (0); prominent, projecting anteriorly(1).
170. Pubis, length of puboischial contact: one third total length of pubis (0); one-half total length of pubis (1).
171. Ischial distal shaft, shape: bladeliike, medial and lateral depths subequal (0); triangular, depth of ischial shaft increases medially (1).
172. Ischial distal shafts, cross-sectional shape: V- shaped, forming an angle of nearly 50° with each other (0); flat, nearly coplanar (1).
173. Ischium, iliac peduncle: iliac peduncle straight or widening in smooth curve distally (0); narrow, with distinct "neck" (1).
174. Ischium, elongate muscle scar on proximal end: absent (0); present (1).
175. Ischial shaft, transverse distal expansion: absent (0); present (1).
176. Ischium, lateral fossa at base of shaft: absent (0); present (1).
177. Femur, cross-sectional shape: transversely broad (0); subcircular (1).
178. Femur, fourth trochanter: prominent, visible in anterior view (0); not visible in anterior view (1).
179. Femur, greatest anteroposterior thickness of shaft: less than or approximately equal to 1/2 the anteroposterior depth of the distal articular condyles (0); much greater than 1/2 the anteroposterior depth of the distal articular condyles (1).

180. Femur, shape of distal condyles: articular surface restricted to distal portion of femur (0); expanded onto anterior portion of femoral shaft (1).
181. Femur, pronounced ridge on posterior surface between greater trochanter and head: absent (0); present (1).
182. Femur, large nutrient foramen opening midshaft anteriorly on femur: absent (0), present (1).
183. Fibula, insertion of the m. iliofibularis: located approximately at mid-shaft (0); proximal, located, above midshaft (1).
184. Astragalus, shape: rectangular (0); wedge-shaped, with reduced anteromedial corner (1).
185. Astragalus, ascending process length: limited to anterior two-thirds of astragalus (0); extending to posterior margin of astragalus (1).
186. Astragalus, fibular facet: faces laterally (0); faces posterolaterally, anterior margin visible in posterior view (1).
187. Metatarsal I distal condyle, posterolateral projection: absent (0); present (1).
188. Metatarsal I, transverse axis of proximal and distal condyles: at an angle to the axis of the shaft (0); perpendicular to the axis of the shaft (1).
189. Pes, phalanx I-1: proximal and ventral surfaces meet at approximately 90° (0); proximoventral corner drawn out into thin plate underlying metatarsal I (1).

APPENDIX 4.4—SYNAPOMORPHIES

Shared, derived characters supporting relevant subgroups are listed below, from most to least inclusive. Characters listed here were optimized using delayed transformation (DELTRAN). Synapomorphies with ambiguous optimization are listed in Table X. MDT = more derived taxa. Numbers in square brackets refer to character number in Appendix 2.

Neosauropoda + *Jobaria*

1. Divided pleurocoel in cervical vertebrae (Upchurch, 1995). [82]
2. Prespinal lamina present on anterior caudal neural spines (Wilson, 2002).
[129]
3. Postspinal lamina present on anterior caudal neural spines (Wilson, 2002).
[130]

Neosauropoda (Bonaparte, 1986)

1. Preantorbital fenestra present (Berman and McIntosh, 1978). [11]
2. Anterior terminus of the lateral temporal fenestra is anterior to the anterior margin of the orbit (Upchurch, 1995). [25]
3. Marginal denticles absent on teeth (McIntosh, 1990). [75]
4. ‘Crus’ bridging haemal canal usually absent on anterior chevrons (Upchurch, 1995). [155]
5. Two or fewer carpal elements (Wilson and Sereno, 1998). [167]

Diplodocoidea (Marsh, 1884; Upchurch, 1995)

1. Spinoprezygapophyseal laminae in dorsal vertebrae fuse to form single prespinal lamina. [107]
2. Cervical ribs short, not overlapping posterior centra (Wilson, 2002). [152]
3. Fibular facet of astragalus faces posterolaterally. [186]

***Amazonsaurus* + more derived diplodocoids**

1. Anterior caudal neural spines petal-shaped. [127]
2. Anterior neural spines broader than anteroposteriorly long (Wilson, 2002). [128]
3. Spinoprezygapophyseal lamina on anterior caudal neural spines extends onto the lateral aspect of the neural spine (Wilson, 2002). [138]

***Amphicoelias* + more derived diplodocoids**

1. Mid-dorsal neural spine height at least twice centrum length (Upchurch et al., 2004). [118]
2. Greatest anteroposterior thickness of femur over 50% maximum anteroposterior depth at distal condyle. [179]

Rebbachisauridae + Flagellicaudata

1. Premaxilla anterior margin without step (reversal; Wilson, 2002). [1]

2. Ascending process of the premaxilla subrectilinear in lateral view, directed posteriorly (Upchurch, 1995). [3]
3. Angle between lateral and medial margins of premaxilla in dorsal view less than or equal to 20° (Harris, 2006c). [4]
4. Premaxilla without sharp distinction between main body and ascending process (Upchurch, 1998). [5]
5. Posterolateral process of the premaxilla and lateral process of the maxilla without midline contact (Wilson, 2002). [6]
6. Subnarial foramen not visible in lateral view (Wilson, 2002). [8]
7. Dorsal process of maxilla extending posterior to posterior process (Wilson, 2002). [9]
8. Antorbital fenestra subequal in length to maximum orbital diameter (Wilson, 2002; Harris, 2006c). [13]
9. External nares retracted to between orbits, facing dorsally (Wilson, 2002). [15]
10. Jugal large, contributing to approximately one-third of the total antorbital fenestra perimeter (Wilson, 2002). [28]
11. Quadratojugal extends anteriorly to at least the anterior margin of orbit (Rauhut et al., 2005). [30]
12. Angle between anterior and dorsal processes of quadratojugal greater than 90° (Upchurch, 1998). [31]
13. Quadrate strongly inclined posterodorsally. [34]

14. Squamosal extends anteriorly past posterior margin of orbit. [35]
15. Basipterygoid processes angled approximately 45° to skull roof (Wilson, 2002). [49]
16. Basipterygoid processes elongate, at least four times basal diameter (Wilson, 2002). [50]
17. Transverse flange of pterygoid located anterior to antorbital fenestra (Wilson, 2002). [56]
18. Snout shape square or blunted (Wilson, 2002). [64]
19. Tooth rows restricted to the jaw anterior to the antorbital fenestra (Wilson, 2002). [65]
20. Tooth crowns aligned along jaw axis, not overlapping (Wilson, 2002). [68]
21. Three or more replacement teeth per alveolus (Wilson, 2002). [71]
22. Neural spine much taller than pedicel in mid- and posterior dorsal vertebrae. [114]
23. Anterior caudal neural spine height at least 150% of centrum height (Calvo and Salgado, 1995). [126]
24. Winglike anterior caudal transverse processes (Wilson, 2002). [141]
25. Mid-caudal vertebral centra length at least twice height (Upchurch et al., 2004). [145]
26. Biconvex distalmost caudal centra (Wilson, 2002). [149]
27. Distalmost caudal centra at least five times longer than tall (Wilson, 2002). [150]

28. Proximal margin of humerus expanded, lateral margin concave in anterior/posterior view (Janensch, 1961). [163]

Flagellicaudata (Harris and Dodson, 2004)

1. Subnarial foramen separated from anterior maxillary foramen by narrow bony isthmus (Wilson, 2002). [7]
2. Quadrate articular surface roughly triangular in shape. [32]
3. Parietal without contribution to the post-temporal fenestra (Wilson, 2002). [38]
4. Distance between supratemporal fenestrae twice the length of the longest axis of the supratemporal fenestrae (Wilson, 2002). [39]
5. Dentary with sharply projecting ventral “chin” (Wilson, 2002). [58]
6. Single planar occlusal facet on teeth (Wilson, 2002). [67]
7. Anteriorly expanded ventral margin of atlantal intercentrum (Wilson, 2002). [84]
8. Bifid posterior cervical neural spines (Wilson, 2002). [97]
9. Divided centropostzygapophyseal laminae (Wilson, 2002). [112]
10. Height of sacral neural spines nearly four times length (Wilson, 2002). [121]
11. Procoelous first caudal centrum (Wilson, 2002). [124]
12. Anterior chevrons with ‘crus’ bridging haemal canal (reversal; Wilson, 2002). [155]
13. Pubis with prominent ambiens process (Wilson, 2002). [169]
14. Ischial distal shaft triangular, depth increasing medially (Wilson, 2002). [171]

15. Ischial distal shafts with V-shaped cross-section, forming approximately a 50° angle with each other (reversal; Wilson, 2002). [172]
16. Ischial shaft with transverse distal expansion (Riggs, 1903). [175]
17. Metatarsal I distal condyle with posterolateral projection (Wilson, 2002). [187]

Diplodocidae (Marsh, 1884)

1. Maxilla-quadratojugal contact broad (Rauhut et al., 2005). [10]
2. Antorbital fenestra with concave dorsal margin (Wilson, 2002). [14]
3. Prefrontal posterior process elongate (Wilson, 2002). [17]
4. Prefrontal posterior process with “hooked” shape (Wilson, 2002). [18]
5. Frontal contribution to dorsal margin of orbit roughly equal to contribution of prefrontal (reversal). [23]
6. Squamosal-quadratojugal contact absent (Wilson, 2002). [36]
7. Paroccipital process distal terminus rounded and tongue-like (Upchurch et al., 2004). [42]
8. Mandible without strong coronoid eminence. [62]
9. Direct crown-to-crown occlusion absent (Wilson, 2002). [66]
10. Cervical vertebrae with longitudinal sulcus on ventral surface (Upchurch, 1998). [80]
11. Anterior cervical neural spines bifid (Wilson, 2002). [86]

12. Mid- and posterior cervical neural arches with divided centroprezygapophyseal laminae (Serenio et al., 2007). [94]
13. Posterior cervical and anterior dorsal bifid neural spines with median tubercle. [100]
14. Anterior caudal neural spines rectangular in anterior/posterior view (reversal). [127]
15. Spinoprezygapophyseal and spinopostzygapophyseal laminae contact each other on anterior caudal neural spines (Wilson, 2002). [137]
16. Anterior caudal neural spines distally-flattened and laterally expanded. [140]
17. Diapophyseal laminae present on anterior caudal transverse processes (Wilson, 2002). [142]
18. More than 30 distal biconvex caudal vertebrae (Wilson, 2002). [151]
19. Insertion of the M. iliofibularis on the fibula located above midshaft. (Wilson and Sereno, 1998). [183]
20. Proximoventral corner of phalanx I-1 drawn out into thin plate underlying metatarsal I (Upchurch et al., 2004). [189]

***Supersaurus* + more derived diplodocids**

1. Mid-cervical centra at least four times longer than tall (Wilson, 2002). [90]
2. Anterior caudal centra (excluding the first) procoelous (Wilson, 2002). [132]
3. Anterior caudal vertebrae with pleurocoels (Wilson, 2002). [134]

Diplodocus + Barosaurus

1. Posterior cervical neural arches with accessory spinal laminae just posterior to spinoprezygapophyseal laminae (Wilson, 2002). [98]
2. Prezygapophyseal lamina on posterior cervical and anterior dorsal vertebrae with roughened lateral aspect (Wilson, 2002). [102]
3. Length of anterior caudal centra doubling over first 20 (Wilson, 2002). [135]
4. Anterior caudal neural spines slightly bifurcate distally. [139]
5. Anterior caudal vertebrae with concavo-convex zygapophyseal articulation (Wilson, 2002). [143]
6. Mid-caudal neural spines vertically oriented (Wilson, 2002). [147]

Dicraeosauridae (Huene, 1927)

1. Premaxilla with anteroventrally oriented vascular grooves originating from an opening in the maxillary contact (Wilson, 2002). [2]
2. Frontal contributes to margin of supratemporal fenestra (reversal; Wilson, 2002). [24]
3. Ventrally directed prong on squamosal. [37]
4. Postparietal foramen absent (Wilson, 2002). [41]
5. Supraoccipital with sharp-edged nuchal crest (Salgado, 1999). [46]
6. Crista prootica expanded laterally into dorsolateral process (Wilson, 2002). [47]
7. Basal tubera narrower than occipital condyle (Wilson, 2002). [52]

8. Dentary symphysis subtriangular in shape. [60]
9. Dentary with tuberosity on labial surface near symphysis. [61]
10. Cervical vertebrae with longitudinal ridge on ventral surface (Sereno et al., 2007). [79]
11. Mid-cervical neural spines anteriorly inclined (Rauhut et al., 2005). [92]
12. Posterior cervical and anterior dorsal bifid neural spines narrow and parallel to converging in anterior/posterior view (Rauhut et al., 2005). [101]
13. Dorsal vertebrae without pleurocoels (Wilson, 2002). [103]
14. Anterior caudal centra with irregularly placed foramina on ventral surface (Harris, 2007). [133]
15. Mid-caudal vertebral centra with mid-height longitudinal ridge on lateral surface, centra hexagonal in anterior/posterior view. [146]
16. Humerus with pronounced proximolateral corner (Wilson, 2002). [162]

***Amargasaurus* + more derived dicraeosaurids**

1. Frontals completely fused (Wilson, 2002). [19]
2. Greatest dimension of supratemporal fenestra subequal to that of foramen magnum (Wilson, 2002). [44]
3. Basipterygoid processes massive, narrowly diverging (Wilson, 2002). [48]
4. Cervical vertebrae with reduced pneumatization, coel (if present) restricted to area above parapophysis. [81]
5. Bifid anterior cervical neural spines (Wilson, 2002). [86]

6. Anterior cervical vertebrae height at least 150% of length (Casanovas et al., 2001). [87]
7. Angle between postzygodiapophyseal and spinopostzygapophyseal laminae roughly 90° (Rauhut et al., 2005). [91]
8. Mid-cervical neural spines considerably taller than pedicel (Rauhut et al., 2005). [93]
9. Dorsal transverse processes inclined dorsally at least 30° from the horizontal (Rauhut et al., 2005). [105]
10. Bifid dorsal neural spines extend to at least fifth dorsal. [108]
11. Mid- and posterior dorsal vertebrae without pleurocoels (reversal; Rauhut et al., 2005) [111]
12. Prezygoparapophyseal laminae present in mid- and posterior dorsal neural arches (Wilson, 2002). [115]
13. Dorsal neural spine height 400% centrum length (Wilson, 2002). [118]
14. Anterior caudal transverse processes directed dorsally. [125]

Dicraeosaurus + Brachytrachelopan

1. Mid-cervical neural spines inclined anteriorly (Rauhut et al., 2005). [92]
2. Posterior cervical and anterior dorsal neural spines inclined anteriorly (Rauhut et al., 2005). [99]

Rebbachisauridae (Bonaparte, 1997)

1. Spinodiapophyseal webbing “festooned” from spine (Sereno et al., 2007). [104]
2. Dorsal transverse processes inclined dorsally more than 30° from the horizontal (Rauhut et al., 2005). [105]
3. Spinopostzygapophyseal lamina divided near the postzygapophyses in posterior dorsal vertebrae. [116]

***Rebbachisaurus* + more derived rebbachisaurids**

1. Mid- and posterior dorsal pedicel height subequal to or greater than centrum height (Sereno et al., 2007). [109]
2. Posterior dorsal neural arches without hyposphene-hypantrum articulation (Wilson, 2002). [120]
3. Scapular acromion process with u-shaped dorsal margin (Sereno et al., 1999). [156]
4. Scapular blade racquet-shaped (Wilson, 2002). [157]
5. Ovate, flat muscle scar distal to glenoid on posteroventral scapular blade. [158]
6. Humerus with circular mid-shaft cross-section (reversal; Wilson, 2002). [161]

Limysaurinae* + *Nigersaurinae

1. Anteroposterior length of frontal less than breadth (reversal; Wilson, 2002). [20]
2. Frontal-nasal suture v-shaped, pointing posteriorly. [21]

3. Paired, anterodorsally facing grooves on frontal. [22]
4. Frontal excluded from anterior margin of supratemporal fenestra (Wilson, 2002). [24]
5. Orbital ventral margin subcircular (reversal; Wilson, 2002) [26]
6. Postorbital posterior process absent (Wilson, 2002). [27]
7. Quadrate articular surface thin and crescent-shaped in ventral view. [32]
8. Quadrate fossa deep (Wilson, 2002). [33]
9. Squamosal extends anteriorly beyond anterior margin of orbit. [35]
10. Supratemporal fenestra absent (Wilson, 2002). [39, 43, 44]
11. Height of supraoccipital subequal to or less than height of foramen magnum (Wilson, 2002). [46]
12. Basal tubera sheet-like, 50% dorsoventral height (Wilson, 2002). [51]
13. Basal tubera narrower than occipital condyle (Wilson, 2002). [52]
14. Basal tubera reduced to a slight swelling on the ventral surface of the basipterygoid. [53]
15. Worn crowns with paired labial and lingual planar facets (Wilson, 2002). [67]
16. Longitudinal grooves on lingual aspect of teeth (Wilson, 2002). [73]
17. Asymmetric labiolingual enamel thickness (Wilson, 2002). [74]
18. Cervical vertebrae with longitudinal ridge on ventral surface (Sereno et al., 2007). [79]
19. Anterior cervical vertebrae without external pneumatization on the dorsal surface of the parapophysis (reversal; Upchurch, 1998) [88]

20. Anterior cervicals without paired pneumatic fossae on ventral surface (reversal) [89]
21. Mid- and posterior cervical vertebrae without external pneumatization on the dorsal surface of the parapophysis (Sereno et al., 2007). [95]
22. Anterior caudal vertebrae with dorsally directed transverse processes. [125]
23. Humerus with pronounced proximolateral corner (Wilson, 2002). [162]

***Nigersaurinae* (new taxon)**

1. Epipophyseal-prezygapophyseal lamina present on cervical vertebrae (Sereno et al., 2007). [78]
2. Caudal neural spines with triangular lateral processes (Sereno et al., 2007). [123]

***Nigersaurus* + Burgos taxon**

1. Mid-cervical central, anteroposterior length 400% height of posterior face (Wilson, 2002). [90]
2. Mid- and posterior cervical neural arches with divided centroprezygapophyseal laminae (Sereno et al., 2007). [94]
3. Caudal neural spines with elliptical depression between spinodiapophyseal lamina and postspinal lamina on lateral surface of neural spine (Sereno et al., 2007). [122]
4. Iliac peduncle of ischium with constriction or “neck” (Sereno et al., 2007). [173]

5. Ischium with elongate muscle scar on proximal end (Sereno et al., 2007). [174]
6. Femur with pronounced ridge on posterior surface between greater trochanter and femoral head (Sereno et al., 2007). [181]

Limaysaurinae (new taxon)

1. Posterior cervical vertebrae with accessory lateral lamina connecting postzygodiapophyseal and spinoprezygapophyseal laminae (Calvo and Salgado, 1995). [96]
2. Anterior caudal neural spines with sprl-spol contact (Wilson, 2002). [137]

APPENDIX 4.5—AUTAPOMORPHIES

Amargasaurus

1. Paroccipital processes with marked ventral excavation (Wilson, 2002). [41]
2. Parapophysis dorsal to diapophysis in posterior dorsal vertebrae. [117]
3. Ulna, proximal condylar processes subequal in length (reversal; Wilson, 2002). [164]

Amazonsaurus

1. Posterior dorsal centra opisthocoelous (Wilson, 2002). [119]
2. Iliac acetabular process sharply pointed (reversal; Salgado et al., 1997). [168]

Apatosaurus

1. Mid-cervical vertebrae anteroposterior length:height of posterior face ratio 2.5-3 (reversal; Wilson, 2002). [90]
2. Cervical ribs projecting well beneath centrum (Wilson, 2002). [153]
3. Cervical ribs with posterior process equal in length to fused diapophysis/tuberculum (Wilson, 2002). [154]
4. Scapular glenoid bevelled medially (Wilson, 2002). [159]
5. Ulna, proximal condylar processes subequal in length (reversal; Wilson, 2002). [164].

Brachytrachelopan

1. Accessory articulation between dorsal vertebrae, distinct from hyosphene-hypantrum.

Cathartesaura

1. Posterior cervical neural spines inclined anteriorly (Rauhut et al., 2005). [99]

Dicraeosaurus

1. Median tubercle present in posterior cervical and anterior dorsal vertebrae (Wilson, 2002). [100]
2. Pedicel in mid- and posterior dorsal vertebrae greater than height of centrum (Sereno et al., 2007). [109]
3. Mid- and posterior dorsal neural arches with pcpl (Wilson, 2002). [113]
4. Anterior caudal neural arches with posl. [130]
5. Ischium with lateral fossa present at base of shaft (Wilson, 2002). [176]
6. Femur with large nutrient foramen opening anteriorly at mid-shaft (Wilson, 2002). [182]

Diplodocus

1. Preantorbital fenestra with well-defined fossa (Wilson, 2002). [12]

2. Pterygoid medial to ectopterygoid on transverse palatal hook (Wilson, 2002). [57]
3. Teeth inclined anteriorly relative to axis of jaw (Wilson, 2002). [72]

Haplocanthosaurus

1. Pedicel in mid- and posterior dorsal vertebrae greater than height of centrum (Sereno et al., 2007). [109]
2. Anterior and mid-caudal neural spines with distinct distolateral expansion. [148]

Limaysaurus

1. Mid- and posterior dorsal neural arches with pcpl (Wilson, 2002). [113]
2. Sternal plates crescentic (Wilson, 2002). [160]
3. Ischium with distal constriction on iliac peduncle (Sereno et al., 2007). [173]
4. Metatarsal I with transverse axes of proximal and distal condyles perpendicular to shaft (Wilson, 2002). [188]

Nigersaurus

1. Paroccipital process terminates distally in a rounded, tongue-like process (Upchurch et al., 2004). [42]

2. Anterolateral corner of dentary expanded laterally beyond lateral mandibular ramus (Wilson, 2002). [59]
3. Dentary symphysis subcircular (Wilson, 2002). [60]
4. Tooth rows restricted anterior to subnarial foramen (Wilson, 2002). [65]
5. Dorsal neural arches with paired, subdivided pneumatic chambers dorsolateral to neural canal (Serenio et al., 1999). [106]
6. Insertion of m. iliofibularis located above midshaft on fibula (Wilson, 2002). [183]

Rebbachisaurus

1. Dorsal neural spine height 400% centrum length (Wilson, 2002). [118]

Supersaurus

1. Anterior caudal neural spine height less than 150% centrum height (reversal; Calvo and Salgado, 1995). [126]

Suuwassea

1. Anterior cervical parapophyses not pneumatic on dorsal margin (reversal). [88]
2. Anterior caudal centra procoelous (Wilson, 2002). [132]
3. Distalmost caudal centra articular face shape platycoelous (reversal; Wilson, 2002) [149]

4. Distalmost caudal centra length-to-height ratio less than 4 (reversal; Wilson, 2002). [150]

Tornieria

1. Anterior and mid-caudal vertebrae without ventral longitudinal hollow (reversal; Wilson, 2002). [144]

CHAPTER 5

INFERENCES OF DIPLODOCOID FEEDING BEHAVIOR FROM SNOUT SHAPE AND MICROWEAR ANALYSES

Herbivory evolved multiple times within Archosauria, the group uniting crocodiles and birds and containing a variety of fossil forms such as dinosaurs, aetosaurs, phytosaurs, rauisuchians, and pterosaurs. Among living archosaurs, however, herbivory is restricted to birds and potentially turtles (e.g., Zardoya and Meyer, 1998; Kumazawa and Nishida, 1999), which are highly derived (e.g., secondary loss of teeth) and provide a poor analog for the vast majority of extinct, herbivorous archosaurs. Without a direct behavioral analog, progress in understanding the behavior of herbivorous archosaurs has not reached the level of sophistication seen in studies of extinct mammals, whose craniodental anatomy is readily interpreted using modern analogues and dental wear features. As a result, studies of Mesozoic ecology are often hampered by an incomplete understanding of herbivore behavior—an aspect that carries great weight due to the relative abundance of herbivores in any ecosystem. As a major link between primary productivity and secondary and tertiary consumers, they represent the base of the animal food pyramid and therefore influence the flow of energy through an ecosystem.

Of particular importance to the understanding of Mesozoic ecology are sauropod dinosaurs, which were the dominant megaherbivores during most of

the Jurassic and Cretaceous, a span of approximately 135 million years. Sauropods were typically quite large, with the largest reaching over 30 m in total body length (Lovelace et al., 2007). Although estimates of metabolic rates and food requirements vary (Weaver, 1983; Curry, 1999; Lehman and Woodward, 2008), it is clear that these organisms required a large amount of browse daily. There is also evidence of herding behavior (Lockley, 1991), increasing the local impact of sauropods on a community—higher population density results in greater stress on plant communities as more animals utilize the available (and limited) resources. Disregarding all other impacts, these animals must have had major effects on communities in terms of bulk mass consumed daily.

Although sauropods lack the obvious adaptations for herbivory (e.g., beaks and cheeks) present in the other major clade of herbivorous dinosaurs, Ornithischia (Chure et al., 2010), ongoing work suggests that sauropods were equally specialized for the task. Tooth replacement rate in sauropods, examined through histological study of thin-sectioned teeth, reveals that sauropod dinosaurs had the fastest known tooth replacement rates among vertebrates—some sauropods replaced their teeth every 30 days (Sereno et al., 2007). Even the slowest replacing teeth in neosauropods (~62 days; see chapter 7) were replaced at a rate similar to the fastest replacing non-sauropod herbivores (Erickson, 1996). Given the remarkable degree of wear seen on shed teeth—perhaps 25–40% crown height lost, based on estimated *Nigersaurus* crown heights from Sereno and Wilson (2005)—the implication is that sauropod teeth experienced extreme wear throughout their short life span. As the plant materials

a sauropod would have encountered are not particularly abrasive in comparison to modern floras (Chure et al., 2010), it is likely that a combination of feeding behavior and sheer volume of plant material ingested is responsible for high wear. Debate continues, however, on how and what sauropods, particularly diplodocoid sauropods, were eating. In this chapter, I examine the diet and behavior of diplodocid sauropods, using data from analyses of snout shape and dental wear (both micro- and macrowear features).

DIPLODOCOID DIETS: PREVIOUS STUDIES

Within Sauropoda, no group has received as much attention with regard to diet as Diplodocoidea (Osborn, 1899; Hatcher, 1901; Holland, 1906, 1924; Hay, 1908; Tornier, 1911; Coombs, 1975; Bakker, 1986; Dodson, 1990; Fiorillo, 1991, 1995, 1998; Barrett and Upchurch, 1994, 2005; Calvo, 1994; Stevens and Parrish, 1999, 2005; Christiansen, 2000; Upchurch and Barrett, 2000; Barrett and Willis, 2001; Sereno et al., 2007; Whitlock et al., 2010). This is due in large part to their unusual skulls, which feature elongate, horse-like faces ending in a squared-off snout and a comparably short arcade of tiny, narrow-crowned teeth (see Chapter 2). Because this morphology has typically been regarded as poorly suited for biting or slicing through vegetation, many other hypotheses of feeding behavior have been put forth, including eating plants from riverbeds (Hatcher, 1901), scraping algae from rocks (Holland, 1906), stripping leaves from branches by using the teeth as a sort of 'comb' or 'rake' (Coombs, 1975; Bakker, 1986; Barrett and Upchurch, 1994), and at least partial reliance on carnivory, either on

bivalves (Sternfeld in Holland, 1924) or fish (Tornier, 1911). Other workers have suggested that diplodocoid sauropods fed in a manner similar to modern large-bodied herbivores: ground-level browsing (Barrett and Upchurch, 1994; Stevens and Parrish, 1999, 2005; Upchurch and Barrett, 2000; Barrett and Willis, 2001; Sereno et al., 2007). This latter hypothesis has the benefit of being directly observable in modern animals and thus requires the invoking of no novel behaviors. Testing this hypothesis is consequently more straightforward, and can be accomplished using methods proven to be effective in studies of both mammals and dinosaurs.

RECONSTRUCTING DIETS

The reconstruction of diet in fossil taxa has a long methodological history, dating back to the 19th century (e.g., Osborn, 1899). Two morphological features in particular, snout shape and tooth wear, have been proven to be informative in mammals. Here, I discuss methods historically used to examine those features, and their relevance to the reconstruction of diets in diplodocoid sauropods.

Snout shape

The shape of the premaxilla, constituting the entirety of the anterior-most extremity of the skull, or 'snout', in most mammals, has long been suggested to be related to dietary preference or selectivity in herbivorous mammals (Boué, 1970; Bell, 1971; Owen-Smith, 1982; Bunnell and Gillingham, 1985). Boué (1970) provided the first quantitative measurement of snout shape in ungulates,

the Arcade Index (AI). The AI measured the shape of the incisive arcade in the dentary in ruminants and was calculated by dividing the breadth of the arcade by its anteroposterior depth. An AI of over 1.0 (a square jaw) was found to be associated with grazers, whereas scores below 1.0 (pointed jaws) were found most commonly in browsers, although this measurement is primarily a measure of breadth and does not fully capture snout shape .

Janis and Erhardt (1988) found that although both palatal breadth and muzzle breadth scale with body size, palatal breadth was more strongly correlated with dietary selectivity (e.g., grazing vs. browsing behavior) in ungulates. The narrowest muzzle breadths occurred in animals browsing in upper story vegetation (Janis and Erhardt, 1988). Gordon and Illius (1988) expanded on these observations, noting that incisor arcade structure is also correlated with selectivity, such that broader arcades are maladaptive for selective browsing behavior, as this morphology is more likely to result in the unintentional ingestion of unpalatable, undigestible, or dangerous woody parts of browse plants (e.g., thorns). Narrow arcades, conversely, are maladaptive for grazing (a non-selective feeding behavior) because the small breadth of the arcade results in reduced intake efficiency when consuming sward-like growth forms such as grasses. Gordon and Illius (1988) also noted that grazers, in addition to having broader snouts, also have sublinear arcades with a more transversely oriented anterior tooth row. So-called 'intermediate' feeders, which may utilize both selective and non-selective behaviors, have snout shapes more similar to those of browsers than grazers. Gordon and Illius (1988) concluded

that snout shapes have evolved to maximize food intake within a particular nutritional quality constraint. There also appears to be a size component to behavioral and morphological differentiation: larger animals were found to be less selective than smaller taxa, although at body sizes below about 100 kg, morphological differentiation between snouts seems to be minor (Gordon and Illius, 1988).

Solounias et al. (1988) and Solounias and Moelleken (1993) demonstrated that a similar relationship between snout shape and diet was also present in extinct ungulates. These two studies used a method originally proposed by Walker (1984) for use in hominids. Snout shape was quantified along a profile defined using the midline and the intersection of the snout with a line drawn at 26° from the midline, originating at the anterior-most point of the premaxillary symphysis. These profiles were then digitized and analyzed using spline-fit functions. Upon examining both reconstructed fossil premaxillae and those of extant ruminants, Solounias et al. (1988) and Solounias and Moelleken (1993) found that snout shape correlates well with selectivity in extant species. Solounias et al. (1988) also confirmed their inferences from snout shape using dental microwear data (see below).

Dompierre and Churcher (1996) modified the method used in Walker (1984), Solounias et al. (1988), and Solounias and Moelleken (1993) for their study of diet in extinct camelids. The original method, which relied on the curvature of snout profiles, necessitated scaling each profile to an equivalent size; the Premaxillary Shape Index (PSI) of Dompierre and Churcher (1996) used

area ratios and so removed the size component. The PSI was calculated using a similar approach to the Walker (1984) method, utilizing a line drawn at 26° from the midline. The intercepts of this line with the premaxillary profile form two vertices of a right triangle, with the chord between them forming the hypotenuse; the third vertex is located anterolateral to the margin of the snout. The PSI itself is the ratio of the area of the premaxilla within the triangle to the total area of the triangle, expressed as a percentage ($0 \leq \text{PSI} \leq 100$); higher scores indicate squarer snouts. PSI scores were found to correlate with diet in extant herbivores, such that the highest PSI scores were present in grazers and lower scores were present in selective browsers (Dompierre and Churcher, 1996). Dompierre and Churcher (1996) concluded that PSI scores are potentially indicative of diet in extinct animals as well .

The relationship between snout shape and dietary habit has also been demonstrated outside of ungulate mammals. Carrano et al. (1999) examined the relationship between a suite of morphological characters (including muzzle breadth) and dietary preference in hadrosaur dinosaurs. The two subclades within Hadrosauridae, Lambeosaurinae and Hadrosaurinae, were found to be differentiated by relative muzzle breadth and limb proportions, similar to the pattern seen in ungulates. Carrano et al. (1999) used this to infer an open-habitat, non-selective feeding behavior for the broad-snouted hadrosaurines and a closed-habitat, selective-feeding behavior for the narrow-snouted lambeosaurines. One hadrosaurine, *Prosaurolophus*, has a relative muzzle breadth within the range seen in the selectively browsing lambeosaurines

(Carrano et al., 1999); this may suggest that there is not a perfect correlation between phylogeny and behavior. Carrano et al. (1999) also examined the impact of missing data on their results and found that artificially degraded datasets returned similar results and significance to the original dataset, suggesting that missing data did not greatly impact their conclusions.

Significance for reconstructing sauropod diets. Although sauropods were typically much larger than both large ungulates and large hadrosaurs, absolute skull size does not differ greatly between the two dinosaurian clades. Volume estimates in sauropods range from ca. 0.05 m³ in *Dicraeosaurus* (Gunga et al., 1999) to 0.2 m³ in *Brachiosaurus* (Gunga et al., 2008), compared to ca. 0.3 m³ in the hadrosaur *Edmontosaurus* (Bates et al., 2009). As a result, muzzle breadths are roughly constrained within a similar morphospace (although some sauropod taxa greatly exceed the range of breadths seen in hadrosaurs, e.g., *Nigersaurus*; Sereno et al., 1999). Sauropod snouts also display a range of variation in shape, from narrow-snouted taxa like *Camarasaurus* to broader snouted taxa like *Diplodocus*, that is reminiscent of the pattern observed in modern ungulates (Fig. 5.1). It is reasonable to hypothesize that the snout morphologies noted in sauropods would have impacted selectivity and intake rate in much the same way that they do in extant ungulates, although in the absence of direct behavioral observations, additional evidence may need to be presented. One source of such evidence is dental wear.

Dental microwear

Dental microwear is the study of damage done to teeth by contact with other surfaces, in particular the interactions between a tooth and food, grit, and opposing teeth. Studies of microwear typically include the quantification of features falling into one of the following three categories (Fig. 5.2A, B, C):

scratches: features that are at least 4x longer than wide

pits: deep, subcircular features

gouges: oblate features with irregular margins; intermediate
between scratches and pits

Such features preserve information about the last few meals an organism ate, and are one of the few direct lines of evidence we have for interpreting the diets of extinct organisms, particularly when those organisms have no extant descendants for comparison. Although caution must be used when interpreting diets of extinct organisms, broad dietary categories are often assignable. By providing direct evidence of what organisms were eating, microwear features can also indicate overlap in resource exploitation and behavior.

Previous work. The majority of microwear studies to date involve the reconstruction of diets in extinct and extant mammals (Puech et al., 1986; Solounias et al., 1988; Anyonge, 1996; Solounias and Semprebon, 2002; Merceron et al., 2005; Nelson et al., 2005; Merceron et al., 2007; Townsend and Croft, 2008), based primarily on wear features recovered from molars and premolars. Increasingly, however, studies focusing on the dental microwear of

non-mammalian organisms have begun to appear, including cynodonts (Goswami et al., 2005), dinosaurs (Fiorillo, 1991, 1998; Upchurch and Barrett, 2000; Goswami et al., 2005; Sereno et al., 2007; Williams et al., 2009; Garcia and Cerda, 2010), and fish (Purnell et al., 2006; Purnell et al., 2007). Of these, only the analyses of microwear in stickleback fish (Purnell et al., 2006; Purnell et al., 2007) were able to control diet experimentally; the rest relied upon comparisons with studies of mammalian microwear.

This reliance is a potential concern, due to broad differences in shape and function between the majority of teeth in question and the molariform teeth examined in the mammalian studies. Molars are used for oral processing of food in mammals, using a combination of puncturing, slicing, and crushing to break down foodstuffs. Non-mammalian animals typically have no oral processing, and use their teeth solely for food-acquisition behaviors involving puncturing or slicing. Incisiform teeth, therefore, may prove a more useful analogue to archosaur teeth than molariform teeth.

The majority of incisor microwear studies have been done on primates, although isolated studies of non-primate incisor microwear exist (Young and Marty, 1986; Young et al., 1990; Domning and Beatty, 2007). There is evidence for a correlation between incisor wear and diet in primates (Ungar, 1990, 1994; Ungar and Spencer, 1999) although some (Kelley, 1990) suggest that incisor microwear is useful only for determining finer-scale dietary preference, once a broader category (e.g., frugivory) has been determined by other means.

Although the degree to which the manual manipulation of foodstuff by

primates alters the character of wear is uncertain, some behaviors, such as leaf stripping, are strong candidates to broadly correspond with potential food acquisition behaviors in other organisms. Importantly, leaf stripping is known to leave characteristic microwear patterns on incisors in *Gorilla* (Ryan, 1981). Additionally, there is evidence that browse height also impacts incisor microwear in predictable ways, with larger features appearing on the teeth of upper canopy feeders than on those of ground-level feeders, the result of a lower concentration of grit relative to phytoliths in food obtained at those greater heights (Walker, 1976; Ungar, 1994, 1998).

Significance for reconstructing sauropod diets. As noted above, several studies have discussed microwear features in sauropod dinosaurs, most commonly in diplodocoid sauropods (Fiorillo, 1991, 1998; Upchurch and Barrett, 2000; Sereno et al., 2007). Although the features recovered from diplodocoid teeth (*Diplodocus* in Fiorillo, 1991, 1998; Upchurch and Barrett, 2000; *Nigersaurus* in Sereno et al., 2007) are typically the same, primarily fine scratches, the interpretation of the behavior that caused these features differs, from high browsing (e.g., feeding on upper canopy vegetation; Fiorillo 1991, 1998) to branch stripping (Upchurch and Barrett, 2000) to ground-level browsing (Sereno et al., 2007). The confusion over the functional significance of these wear features is likely exacerbated by two factors: first, sauropod microwear has previously been examined in the absence of other data, unlike what has been done for modern and extinct mammals; and second, only a very narrow sample of sauropod diversity has been sampled, and

so there has been little relevant comparative data.

Although the relationship between incisor microwear and diet is uncertain, inferences can still be drawn about the character of foodstuffs ingested. In particular, feature size and texture are expected to correspond with browse height and certain intrinsic plant properties, such as woody vs. herbaceous stems.

Dental macrowear

The accumulation of wear, over time, often results in larger wear features (called facets) visible to the naked eye (Fig. 5.2D). These wear facets are direct evidence of jaw motion, because their orientation, size, and position on the tooth are directly linked to the motion of the jaw relative to the surface causing wear, be it food, the opposing dentition, or a substrate. When the upper dentition overlaps the lower, as in most animals, an orthal bite is expected to produce facets on the lingual surfaces of the upper dentition, and the labial surfaces of the lower teeth.

Interpreting the functional cause of wear facets is often quite difficult, even in organisms that are well-known. Although the ornithischian dinosaur *Psittacosaurus* has been described from hundreds of individuals since the 1920s, only recently have the wear facets on their cheek teeth, which imply a more mobile jaw than is reasonable given the akinetic skulls of psittacosaurus, been understood as part of a complex bite with multiple jaw motions (Sereno et al., 2010).

Significance for reconstructing sauropod diets. In most sauropods for which macrowear is known, facets form either as V-shaped wear patches on the apical, mesial, and distal portions of the occlusal surface (as in the macronarian *Camarasaurus*) or as single planar wear facets, typically on the lingual apical surface in upper dentitions and on the labial apical surface in lower dentitions (as in the titanosauriform *Nemegtosaurus*; Nowinski, 1971; Wilson and Sereno, 1998). In diplodocid and rebbachisaurid sauropods, however, wear facets commonly form on the labial surface of the upper dentition, sometimes accompanied by lingual facets (as in *Nigersaurus*). Until recently, similar facets were not known in titanosaurs, the other narrow-crowned sauropod clade, although several recently described teeth from the Allen Formation of Argentina have multiple wear facets, including facets on both the labial and lingual surfaces (García and Cerda, 2010). Labial facets on the upper dentition have commonly been cited as evidence for branch-stripping behavior (e.g., Upchurch and Barrett, 2000), caused by the friction of a branch or stem being passed over the surface of the tooth. These labial facets have also been cited as evidence for a non-orthal bite (Dodson, 1990; Calvo, 1994; Barrett and Upchurch, 1994). Under this interpretation, propalinal motion of the lower jaw, in which the lower dentition overlaps the upper during the bite stroke, is required to form the upper facets.

Therefore, if the low-browsing hypotheses of feeding in square-snouted sauropods are supported by microwear data, the unusual wear facets on the labial surfaces of the upper dentition need to be explained. García and Cerda

(2010) proposed that labial wear facets on the upper dentition are a function of the lingual-labial trajectory of a replacing tooth, such that a replacing tooth in the upper dentition is effectively lingual to its opposite(s) in the dentary through the early portion of its functional life, although this is difficult to demonstrate in the absence of an exceptionally preserved fossil and seems unlikely given the rapid turnover in narrow-crowned teeth (see Chapter 7). Modern mammals are typically a poor analogue also, as modern ruminants typically lack the upper incisors and the effect of the transverse power stroke on incisor wear in other grazers (e.g. *Equus*) is uncertain. Some older domesticated horses do show development of a labial wear facet on the incisors, however (Roberts, 1905:fig. 77).

To develop a testable hypothesis for diplodocoid feeding behavior, evidence from snout shape, microwear, and macrowear will be compared, not just with data from modern herbivores, but also with each other. In this way, an approximation of the “total evidence” approach will be brought to bear on this question.

ABBREVIATIONS

Institutions: AMNH, American Museum of Natural History, New York City; ANS, Academy of Natural Sciences, Philadelphia; CM, Carnegie Museum of Natural History, Pittsburgh; CMC, Cincinnati Museum Center, Cincinnati; CMN, Canadian Museum of Nature, Ottawa; MB.R., Humboldt Museum für Naturkunde, Berlin; MNN, Musée National du Niger, Niamey; MOR, Museum of the Rockies,

Bozeman; ROM, Royal Ontario Museum, Toronto; USNM, United States National Museum, Washington D.C.; YPM, Yale Peabody Museum, New Haven.

MATERIALS AND METHODS

Morphological data, in this case snout shape and microwear features, can be used to distinguish between several combinations of browse height (ground-height, mid-height, and upper canopy) and browse strategy (selective and nonselective) in diplodocoid sauropods. Here, ground-level feeding is defined as feeding on vegetation within 1 m of ground height, mid-height feeding is defined as feeding between ground height and 10 m, and upper canopy feeding is feeding at all heights above 10 m. Ten meters is chosen as the upper limit for mid-height browsing based on estimated maximum head height of diplodocoids in quadrupedal stance, using combined neck and forelimb height (Barrett and Upchurch, 2000; table 4.2) The following is also summarized in Table 5.1.

Evidence for browse height

Browse height will be examined primarily through the examination of dental microwear features. The primary influence of browse height on microwear is through the creation of pits as a consequence of ingested grit. Grit, exogenous mineral particles, are suspended and transported in the air through aeolian processes and through the actions of animals (e.g. walking). These particles then fall out of suspension and are then deposited on the ground or on plants. A proportionally larger amount of grit is deposited on plant surfaces at lower

heights than those that greater heights (Mainland, 2003; Sanson et al., 2007). Taxa that browse at lower heights therefore typically ingest more extraneous grit, and their teeth may have a higher proportion of pits in their microwear features, as is seen in ground-height browsing ungulates (DeMiguel et al., 2008). Ground-height browsing sauropods will therefore be expected to have the highest proportion of pits in their microwear features, followed by mid-height and upper canopy browsers.

The incisors of ground-height feeding primates also display a slightly different character than those of taxa browsing at greater heights. Ungar (1992, 1994, 1996) showed that, as a function of the ratio of soil particles to opal phytoliths, mean scratch breadth is lower in taxa browsing at or near ground height. Because the teeth of sauropod dinosaurs are functionally analogous to the incisors of mammalian herbivores, it is expected that the scratch breadth in ground-height browsing sauropods will also be smaller than in those that browse at different heights.

Evidence for browsing strategy

Browsing strategy (selective vs. nonselective) will be examined using both microwear and snout shape indices. Snout shapes in selective browsers are predicted to be narrower than those of nonselective browsers, as in herbivorous mammals. Two microwear features can indicate browse type: scratch orientation consistency and feature size. Consistency of scratch orientation has been related to food texture, such that softer (eg., herbaceous) foods result in more

unimodally distributed scratch orientations, whereas low consistency of orientation is related to eating harder or more brittle foods (Grine, 1986; Van Valkenburgh et al., 1990). Harder or more brittle foods are likely to have included brittle stems, indicating woody browse that is selectively browsed upon. Larger features also indicate selective browsing, either as a result of woody stems (coarse scratches) or large particles such as seeds (gouges).

SNOUT SHAPE

Six genera of diplodocoid sauropod dinosaur (*Apatosaurus*, *Dicraeosaurus*, *Diplodocus*, *Nigersaurus*, *Suuwassea* and *Tornieria*) preserve enough of the dermal skull to reconstruct the snout shape. The skulls of these six genera were reconstructed in dorsal view based on examination of the original materials (Appendix 5.1). These reconstructions are prone to some error, and the amount of material available necessarily influences their accuracy; *Diplodocus*, for example, is known from multiple articulated skulls, whereas *Dicraeosaurus* is known only from disarticulated braincases and fragmentary dermal elements. Nonetheless, these were produced with as much rigor as possible and are consistent with each other, and so should vary in ways consistent with their variation in life.

These reconstructions (Fig. 5.3) were then measured using two squareness indices: the upper arcade index (uAI) and the premaxillary-maxillary index (PMI). A third method, measuring the divergence angle of the premaxillae, was utilized after some complications arose with the PMI due to the laterally expanded snout

observed in *Nigersaurus*. These indices were then compared among taxa, first to test the null hypothesis that there is no difference in snout squareness among diplodocoids, and second to test the hypothesis that any variation in snout shape is correlated with phylogeny, not diet. Student's t-tests were performed to determine statistical significance between groups. The non-diplodocoid neosauropods *Brachiosaurus* and *Camarasaurus* were also examined, as taxa widely recognized as selective browsers and as outgroups to the diplodocoids.

uAI. The uAI is a modification of the AI introduced by Boué (1970). Although the original metric measured the ratio of the lower dental arcade, the uAI utilizes the upper jaw instead, because upper jaws are more commonly preserved in diplodocoid dinosaurs. In order to retain 1.0 as the dividing score between square and round jaws, the uAI measures only the right or left half of the snout (Fig. 5.4), although Boué's metric included both right and left jaws in its width measurement. In both metrics, the measured variable is the width of the dental arcade (in the uAI, the half-width) divided by the depth..

PMI. The PMI is also a modification of an older metric; in this case it is a modification of the premaxillary shape index (PSI; Dompierre and Churcher, 1996). Because the sauropod snout includes both the premaxilla and the maxilla, the PSI is only slightly modified as the premaxillary-maxillary index (PMI). This index is otherwise calculated in much the same way as the PSI (Fig. 5.4). First, a line is drawn perpendicular to the long axis of the skull and tangent to the

anterior-most point on the skull. A second line is drawn parallel to the midline tangent to the broadest point of the snout. A third line is then drawn at 26° from the long axis of the skull connecting the first two lines, forming a right triangle; 26° is used to be consistent both with the PSI and with work predating the PSI. The area of the skull within that triangle is calculated and compared to the area of the triangle as a whole to compute the PMI. In cases where the snout narrows behind its broadest part (e.g., *Nigersaurus*, certain hadrosaurs), the shape posterior to the broadest point is disregarded, and the snout is considered to have continued in a straight line to the point of intersection with the hypotenuse. Although this may inflate the PMI score slightly, it more accurately reflects the shape of the snout.

Premaxilla Divergence Angle. Due to the often fragmentary or deformed nature of fossil material, the prior two metrics rely on reconstructions of skulls. Although every effort was made to accurately reconstruct morphology, this has resulted in a small sample size. One method to measure squareness directly from fossil material (reducing potential error inherent in reconstruction) and increase sample size involves comparing the angles of divergence on the anterior margin of the premaxilla (PMDA). This is measured here by orienting the specimen in strict dorsal or ventral view and measuring the angle formed between the anterolateral and anteromedial corners and a line drawn perpendicular to symphysis (Fig. 5.4).

MICROWEAR ANALYSIS

Thirty-eight teeth belonging to seven genera were examined for microwear features (Appendix 5.2). Damaged or heavily weathered teeth were deemed unsuitable and not examined, following Teaford (1988). The suitable teeth were molded using a high-resolution polyvinylsiloxane dental molding material (Coltene Whaledent President microSystem 6012). Casts were made in water-clear epoxy and examined at 70x using transmitted light microscopy, following the methods of Solounias and Semprebon (2002). Images were taken using a Spot CCD camera (Spot Insight 11.2 Color Mosaic, Diagnostic Instruments) at the highest resolution available (36 bits/pixel, 300 dpi), mounted on a Nikon SMZ 1500 microscope. Image analysis was performed in Microware 4.02 (Ungar, 2002). Where possible, wear was examined from multiple sites on the same tooth and averaged. Features measured were scratch number, scratch orientation, pit density, and pit size. Patterns of microwear were examined against patterns characteristic of feeding behavior in modern mammals (see below).

Although sauropod remains are abundant globally, skulls are a rare component of sauropod fossil assemblages (Whitlock et al., 2010: table 1). Even Diplodocoidea, the clade most completely represented by cranial material, contains only six genera with dermal tooth-bearing elements associated with them (see above). Isolated, shed teeth are common finds, but are not identifiable to a useful degree, and can only be assigned to large clades (e.g., Diplodocoidea). In some instances, particularly involving Morrison Formation

sauropods, isolated dentigerous elements are also not identifiable to the genus level, due to the paucity of non-basicranial autapomorphies in the clade. Even among those teeth that are both worn and assignable to a particular taxon, preserved wear features are rare. Despite an effort to comprehensively sample as much of the available data as possible, only nine teeth were suitable.

MACROWEAR ANALYSIS

Preliminary results from an ongoing experiment designed to reproduce wear facets in sauropod dinosaurs were obtained, using a purpose-built 'macrowear machine,' designed to simulate an orthal bite stroke (Fig. 5.5). This machine consists of two plexiglas 'jaws,' one fixed to a table and representing the immobile upper jaw. The second jaw is attached to an oscillating motor, such that the jaw swings back and forth simulating the movement of the lower jaw. The oscillating motor was affixed to a micromanipulator, enabling fine control over the relative position of the jaws when in occlusion. The dentition was represented by epoxy casts of four teeth (upper and lower), representing the premaxillary dentition and the teeth opposing it in the dentary. The upper dentition was created using casts of the dentition of YPM 4677, a premaxilla of *Diplodocus*. The lower dentition was constructed using casts of the upper teeth, which were surface scanned using a NextEngine desktop 3D scanner. These scans were used to create a 3D wireframe model of the teeth, which mirrored (to correct for left-right asymmetry in the teeth), scaled, and rapid prototyped. The rapid prototypes were then assembled in a block of four, molded, and cast in the same

epoxy. The relative position of the upper and lower dentitions, tooth spacing, tooth size, and the orientation of the teeth (e.g., degree of procumbency) were based on examination of intact dentitions and skulls of *Diplodocus* (CM 11161; USNM 2673, 2674; AMNH 969).

These dentitions were then placed in opposition in the macrowear machine, with a specially constructed sandpaper vegetation model in between them. This model was created using 100 grit sandpaper, folded over and cut along the folded margin to create multiple ribbon-shaped 'leaves' that were free to move independently of each other. The sandpaper was suspended using monofilament and weighted using clay, to simulate initial resistance and subsequent release of plant material as the stem or leaf is sheared during the bite stroke. Results were checked every three hours, and the experiment was discontinued when labial facets began to appear.

RESULTS

SNOUT SHAPE

Results of the snout shape analyses (uAI, PMI, PMDA) are summarized in Tables 5.2 and 5.3.

uAI

Four taxa (*Apatosaurus*, *Dicraeosaurus*, *Diplodocus*, and *Nigersaurus*) preserve enough of the maxilla that the position of the last tooth in the tooth row can be determined, the uAI calculated. This metric could not be determined for *Suuwassea* and *Tornieria*; the only known maxillae of those taxa are distally

incomplete and the position of the posteriormost tooth cannot be accurately determined. *Nigersaurus* had the highest uAI score (4.0), followed by *Apatosaurus* (1.5) and *Diplodocus* (1.2). *Dicraeosaurus* has the lowest uAI score (0.6). The non-diplodocoid sauropods *Brachiosaurus* and *Camarasaurus* have uAI scores similar to those of *Dicraeosaurus* (0.6 and 0.4, respectively).

PMI

As above, *Nigersaurus* had the highest PMI value (95%). *Apatosaurus* (84%) and *Diplodocus* (84%) had the next highest PMI, followed by *Dicraeosaurus* (74%) and *Suuwassea* (74%). *Tornieria* (71%) had the lowest PMI score of the ingroup taxa. Diplodocoids had higher PMI scores than all outgroup taxa (*Brachiosaurus* = 68%; *Camarasaurus* = 63%).

The PMI scores for *Apatosaurus*, *Nigersaurus*, and *Diplodocus* group significantly (based on a two-tailed unpaired t-test; $p = 0.02$) to the exclusion of *Dicraeosaurus*, *Suuwassea*, and *Tornieria*, but low sample size limits the degrees of freedom and the power of discrimination is low. The ingroup (Diplodocoidea) and outgroup (*Brachiosaurus* and *Camarasaurus*) conditions cannot be statistically separated ($p = 0.1$), although when considered apart from the other diplodocoids *Apatosaurus*, *Nigersaurus*, and *Diplodocus* are distinct from the macronarians ($p = 0.02$).

Premaxillary Divergence Angle

The initial sample included 16 premaxillae. Of those 16, 12 were deemed

complete enough for measurement (Table 5.3). In the incomplete premaxillae, the thin 'lateral plate' (Upchurch and Barrett, 2000:88) that extends ventrally from the labial margin of the premaxilla and forms the ventral-most portion of the element was missing or heavily damaged, preventing accurate assessment of the PMDA from those elements.

The diplodocoids again segregated into two groups, with *Dicraeosaurus* (24°), *Suuwassea* (25°), and *Tornieria* (25°) having high divergence angles compared to *Apatosaurus* (6°), *Diplodocus* (7°), and *Nigersaurus* (4°). Although sample sizes are low, a two-tailed unpaired t-test suggests that the two groups are statistically significant ($p < 0.0001$). *Nigersaurus* is again the squarest; *Suuwassea* and *Tornieria* are the roundest. The difference between *Nigersaurus* and *Apatosaurus* is less marked (2°) than with previous metrics.

The PMDA of *Brachiosaurus* (35°, 30°; average = 33°) and *Camarasaurus* (27°, 45.4°, 46.5°; average = 40°) are higher than for any diplodocoid. The variation observed in *Camarasaurus* is potentially the result of ontogeny; the element that provided the 27° PMDA measurement (UUVP 3999) is much larger and presumably came from an adult, whereas CM 11338 is a subadult individual. A two-tailed, unpaired t-test indicates that the values found for the macronarians are not statistically different ($p = 0.07$) from those observed in the round-snouted diplodocoids (*Dicraeosaurus*, *Suuwassea*, and *Tornieria*).

MICROWEAR

Although 39 teeth were examined for microwear features, only nine (23%) were

found to have features consistent with a record of diet. Of these, only seven teeth belonging to three taxa (*Dicraeosaurus*, *Diplodocus*, and *Nigersaurus*) appeared to preserve an accurate sample of wear. The others preserved no wear features, primarily as a result of post-mortem damage. The teeth of *Apatosaurus* and *Rebbachisaurus* are described below and compared qualitatively, but not quantitatively. Figure 5.6 illustrates representative wear features for these five taxa. Full results are presented in Table 5.4.

Apatosaurus

The probable *Apatosaurus* skull CMC VP 7180 contains multiple teeth in-situ, although the majority of these teeth were broken apically. Wear features were recovered from one tooth, the first tooth in the left dentary. Although this tooth was heavily abraded post-mortem, as indicated by a “sugary” texture, 109 small ($410.41 \mu\text{m}^2$) features can be seen dotting the surface of the dentin. The shape of these features was generally subcircular (long axis:short axis ratio = 1.27:1), indicating that the majority of these features are pits and not gouges. No scratches are recorded in the dentin, and no features were recovered from the enamel of any tooth.

Dicraeosaurus

Two teeth (MB.R. 2204 and 2197), tentatively assigned to *D. hansemanni*, preserve some microwear features. Features are recovered from both dentine and enamel surfaces.

MB.R. 2204. A total of 588 features was recorded on the dentine surface of the labial wear facet. Of these, the majority (359) were large pits and gouges (average area = 438.07 μm^2 , average circumference = 41.07 μm). These features were consistently oblong rather than subcircular (long axis:short axis ratio = 1.64:1), indicating the dominance of gouges over pits. In addition, 229 scratches were recorded, with an average length of 72.03 μm and an average breadth of 4.89 μm . Scratches are generally without a preferred orientation, and cross-scratches are common.

The labial enamel margin of the wear facet preserved 227 features. Of these, the majority (227) were large pits (average area = 523.82 μm^2 , average circumference = 43.75 μm) with an oblate shape (long:short axial ratio = 1.75:1). One hundred seventy-six scratches were also recovered, with an average length of 64.41 μm and an average breadth of 6.47 μm . As in the dentine, scratches lack a single preferred orientation and cross-scratches are common.

MB.R. 2197. Although this tooth does not preserve a large amount of microwear, some features are present on the labial enamel edge. Here, two exceptionally large (85,670.85 μm^2) gouges are preserved. No scratches or smaller pits were observed, and it is probable (although not certain) that these are not the result of tooth-food or tooth-tooth contact.

Diplodocus

Three teeth from two specimens (CM 11161 and USNM 2673) preserve microwear features on the enamel.

CM 11161. Microwear features were recovered from small areas of the labial enamel margin of the facet on the second right premaxillary tooth and the first left premaxillary tooth. Identification of features was hampered here and on other diplodocid specimens by the application of a preservative lacquer, likely around the turn of the century. Attempts to remove this lacquer were generally unsuccessful.

Ninety-six features—45 scratches and 51 pits—were recovered. Average scratch length is 91.96 μm , with an average breadth of 4.04 μm . Pits are subcircular (ratio of axes = 1.35:1) and small (average area = 127.13 μm^2 , average circumference = 20.2 μm). Scratches are generally subparallel, although cross-scratching does rarely occur, and oriented roughly along the apicobasal axis. Scratches extend over the edge of the facet and onto the lingual surface of the tooth for a short distance.

USNM 2673. Seven loose teeth are associated with the *Diplodocus longus* skull USNM 2673. None of these teeth have wear facets, and based on the size and position of one tooth, some of them may have been replacement teeth. One tooth, however, an incomplete crown recovered separately from the other six loose teeth, does preserve what appear to be wear features on the presumed

labial surface distant from the apex. Based on size comparisons with the intact teeth of USNM 2673, this crown appears to be an upper tooth.

The 52 wear features (37 scratches, 15 pits) recovered from this surface differ from those seen on the labial facet in CM 11161 in both size and character. Scratches are substantially longer (309.69 μm) and broader (5.68 μm) than those from the facet margin. They are generally sub-parallel with rare-cross scratching, but the orientation is nearly perpendicular to the long axis of the tooth, with only a slight apicobasal component. Pits are also larger than those observed on the facet (average area = 1,466.33 μm^2 , average circumference = 69.17 μm), although they are proportionally identical to those from CM 11161 (ratio of axes = 1.32:1). Because these features do not come from either a facet or from the apical surface of the crown, they cannot be confirmed as the result of a bite stroke.

Nigersaurus

Wear features were recovered from two crowns in the G2 and G100 assemblages.

G2. Wear features (138 scratches, 276 pits) were observed on the labial enamel margin of the labial facet on the G2 crown. As in *Diplodocus*, scratches are elongate (89.69 μm) and narrow (average breadth = 3.53 μm). Scratch orientation is generally apicobasal, without cross-scratching. Pits are small (average area = 21.95 μm^2 , average circumference = 26.8 μm). Pit proportions

(1.48:1) are more oblate than those of *Diplodocus* and *Apatosaurus*, but substantially rounder than those observed in the enamel of *Dicraeosaurus*.

G100. No wear features were recovered from the facet of this crown, perhaps as a result of post-mortem wear. Features were observed on the lingual surface of the enamel basal to the actively worn surface. Of the 39 features observed, the majority (30) were scratches. All features were generally larger than those observed on the facet of G2. Scratch length (180.34 μm) and breadth (5.03 μm) are greater than those from G2. Similar to the wear recovered from USNM 2673, scratch orientation is more mesiodistal than apicobasal, although there is still a minor apicobasal component. Cross scratching occurs but is rare. Pit size (average area = 1,154.58 μm^2 , average circumference = 70.2 μm) and shape (ratio of axes = 2.28:1) were also substantially larger. Because these features are located away from surfaces of active wear, it is likely that they were caused by some contact outside of the bite stroke.

Rebbachisaurus. A single loose tooth of rebbachisaurid type (MNHN 1512a; see Chapter 4 for full referral) is referable to *Rebbachisaurus*. Wear features (eight scratches, 12 pits) were recovered from the enamel near the smaller facet (presumably the labial surface). Scratches were very long (218.05 μm) and narrow (4.51 μm). Cross scratching did occur, although scratches appear to be predominantly mesiodistally oriented. Pits were quite large (average area =

1,016.22 μm^2 , average circumference = 69.17 μm) but generally subcircular (ratio of axes = 1.2:1).

MACROWEAR

The development of wear features is discussed below in three stages. Observations were discontinued after the onset of distinct labial facets on the upper dentition on at least one crown. Experiments were reproduced three times with identical results. Interpretations are based on a model of *Diplodocus*; wear facet development on divergent dentitions (such as that of *Nigersaurus*) is likely to have been similar, but may have differed slightly.

Stage 1

Wear on the upper dentition began with the development of a small, apicobasally elongate facet on the lingual surface of the tooth. A similar facet developed on the labial surface of the lower teeth.

Stage 2

Increasing tooth usage results in the enlargement of the facets on both upper and lower teeth. Upper teeth, but not the lower, begin to develop an apical facet. The continued wear on the lingual surface in combination with wear on the apical surface results in a subhorizontal apical margin.

Stage 3

As apical wear increases and tooth height diminishes, the lingual curvature of the tooth brings the labial face of the upper teeth into contact with the foodstuff. As a result, the apical facet begins to expand basally onto this labial side, until it is clearly visible on the labial surface of the tooth. The lower dentition does not develop a similar facet, and wear continues on these teeth only as an enlargement of the original labial facet.

DISCUSSION

SNOUT SHAPE

The six ingroup taxa examined can be broadly divided into two categories: square and round. Square-snouted diplodocoids include the diplodocids *Apatosaurus* and *Diplodocus* and the rebbachisaurid *Nigersaurus*. Round-snouted diplodocoids include the dicraeosaurids *Dicraeosaurus* and *Suuwassea*, and the diplodocid *Tornieria*. Round-snouted diplodocoids are generally squarer than outgroup taxa such as *Brachiosaurus* and *Camarasaurus*, however.

This pattern of snout shapes is reminiscent of the pattern seen in modern ungulates. In light of that comparison, the broad-snoutedness seen in *Apatosaurus*, *Diplodocus*, and *Nigersaurus* is interpreted as an adaptation to ground-level, non-selective browsing in at least some diplodocoid sauropods. The narrower, rounded snouts of *Dicraeosaurus*, *Suuwassea*, and *Tornieria* are

interpreted as evidence for greater subsistence on mid-height, selective browse, although the intermediacy of these shapes between the squarest diplodocoids and the roundest outgroups may indicate at least partial reliance on non-selective browsing in these taxa.

The snout shapes of macronarian sauropods like *Brachiosaurus* and *Camarasaurus* are consistently rounder than those of diplodocoid sauropods, although not significantly so ($p > 0.05$). If this difference is reflective of a difference in feeding behavior, it may well be due to the difference in browse height. *Brachiosaurus* and *Camarasaurus* were both probably mid- to upper-canopy browsers, based on studies of neck posture (Stevens and Parrish 1999, 2005; Christian and Dzemski, 2007; Christian, in press) and limb proportions (Wilson and Sereno, 1998). Diplodocids and dicraeosaurids, however, were likely browsing near or at ground level (Stevens and Parrish, 1999, 2005). Differences in available vegetation at such lower heights (herbaceous plants at low heights, woody browse at mid- and upper heights), potentially resulting in the occasional non-selective exploitation of browse, may have influenced the relative breadth of the snout in *Dicraeosaurus*, *Suuwassea*, and *Tornieria*. Alternatively, there may be a phylogenetic component to the difference in snout shapes between selectively browsing diplodocoids and macronarians—if broad snouts are pleisomorphic for Diplodocoidea, there may be some constraint on the degree of roundness attained.

Comparisons with hadrosaurids

As discussed previously (see *Reconstructing Diets*, above), Carrano et al. (1999) noted a general dichotomy of form between hadrosaurine and lambeosaurine hadrosaurs—hadrosaurines had broad snouts, lambeosaurines had narrow snouts—and related this difference to a division in dietary habit, such that the hadrosaurines (H) were non-selective browsers and the lambeosaurines (L) were selective browsers. As large bodied dinosaurian herbivores, hadrosaurids are a potentially useful comparison for sauropods, particularly with regard to snout shape. PMI scores were determined for *Anatotitan copei* (H; Chapman and Brett-Surman, 1990:fig. 12.1), *Edmontosaurus regalis* (H; Chapman and Brett-Surman, 1990:fig. 12.1), *Maiasaura peeblesorum* (H; Horner, 1983:fig. 1), *Prosaurolophus maximus* (H; Brown, 1916:fig. 3), *Saurolophus osborni* (H; Brown, 1912:fig. 2), *Corythosaurus casuarius* (L; CMN 34825), *Hypacrosaurus altispinus* (L; ROM 702), *Lambeosaurus sp.* (L; ROM 758) and *Velafrons coahuilensis* (L; Gates et al., 2007:fig. 3). Because the premaxillae are edentulous in hadrosaurs, the uAI could not be calculated. The PMDA could not be calculated due to the difference in form between hadrosaurids and sauropods. The margin of the snout in hadrosaurids is formed entirely by the premaxilla, which continues posterior to the snout itself, and thus the metric does not accurately model the shape of the anterior margin of the snout in these taxa.

Broad-snouted diplodocids group within the range of PMI scores seen in hadrosaurines; in both clades, scores cluster around 80–85% (Fig. 5.8; only

those taxa examined by Carrano et al. [1999] are plotted). The exceedingly square snout of *Nigersaurus* (95%) is nearly matched by that of *Anatotitan* (93%). Lambeosaurines, particularly *Hypacrosaurus* (76%) and *Lambeosaurus* (74%), typically have rounder snouts than hadrosaurines, although there is some overlap (e.g., *Corythosaurus*, 80%). There is also overlap in the range of scores between the upper end of the round-snouted diplodocoid range (*Dicraeosaurus*, 74%) and lower end of the lambeosaurines range (*Lambeosaurus*, 74%), although the PMI of *Tornieria* (71%) is lower than any hadrosaurid examined. The lambeosaurine *Velafrons*, which was not included in the dataset of Carrano et al. (1999) and was not plotted in Figure 5.8, has a PMI score (85%) more similar to those of square-snouted diplodocids and hadrosaurines, which suggests the potential for non-selective browsing in Lambeosaurinae.

The overall similarity between snout shape in putatively nonselective and selective browsers in both diplodocoids and hadrosaurids suggests that a) PMI is a valid measure of an ecomorphological variable and b) hypotheses of non-selective and selective browsing based on snout shape in diplodocoid sauropods are well-founded. The similarity in snout shape between the two dinosaur groups may also indicate the presence of direct resource competition between them.

MICROWEAR

Although the relationship between wear on molar and incisiform teeth is uncertain, the pattern of variation in wear features between round-snouted (*Dicraeosaurus*) and square-snouted (*Apatosaurus*, *Diplodocus*, *Nigersaurus*)

diplodocoids is quite similar to that expressed in molariform teeth of mammals. *Dicraeosaurus* featured larger, coarser features in general, with less orientational consistency than in the square-snouted taxa. These features can be tentatively interpreted as evidence for variation in both browse height and type (e.g., woody vs. herbaceous, selective vs. non-selective).

Browse height

Dicraeosaurus, *Diplodocus*, and *Nigersaurus* all had a large proportion of pits in their microwear features. *Nigersaurus* had the highest proportion of pits to scratches (2:1), followed by *Diplodocus* (1.1:1); *Dicraeosaurus* had the lowest ratio (0.8:1). Furthermore, the ratio of pits to scratches in *Diplodocus* may be artificially low; only 96 total features were recovered from two teeth (compared to 414 in *Nigersaurus* and 403 in *Dicraeosaurus*). The proportion of those features varies between teeth, such that the first left premaxillary tooth has a pit:scratch ratio of 0.7:1, while the second right premaxillary tooth has a ratio of 1.4:1. Regardless, it is clear that *Nigersaurus* has a higher proportion of pits to scratches than *Dicraeosaurus*, which suggests that *Nigersaurus* ate at a lower browse height. The same is potentially true for *Diplodocus*, which, even allowing for the potentially misleading results from the left premaxillary tooth, had a higher density of pits than *Dicraeosaurus*.

Browse type

Square-snouted diplodocoids *Diplodocus* and *Nigersaurus* are characterized by

an abundance of fine (breadth $\leq 5 \mu\text{m}$), subparallel scratches; round-snouted *Dicraeosaurus* is dominated by coarse (breadth $>6 \mu\text{m}$) scratches, including a large proportion of cross-scratches. The greater orientational consistency in *Diplodocus* and *Nigersaurus* suggests that these animals were biting through softer stems, consistent with a hypothesis of browsing on herbaceous plants, such as low-growing ferns. Conversely, the low consistency of scratches in *Dicraeosaurus* is indicative of harder, more brittle foods, possibly including the shearing of woody stems. The significantly coarser scratches and larger pits/gouges observed in *Dicraeosaurus* also suggest a diet including coarser plants and a large proportion of larger particles than those ingested by *Diplodocus* and *Nigersaurus*, and probably *Apatosaurus* and *Rebbachisaurus* as well. The larger particles in question may have been hard objects such as seeds; an abundance of such high-quality foodstuffs in the diet indicates selective browsing behavior (Chin and Kirkland, 1998).

In addition to their significantly larger size, the pits recovered from *Dicraeosaurus* are notably more oblate and gouge-like than the subcircular features recovered from the other taxa. Although the meaning of this shape difference is uncertain, it may be related to physical differences in the particles causing the wear, or to the orientation of the force compressing the particle into the tooth (e.g., meeting the enamel edge obliquely vs. orthogonally). In either case, the shape difference suggests some significant difference in diet or behavior between *Dicraeosaurus* and the square-snouted diplodocoids.

Comparison with previous results

Diplodocus. Fiorillo (1991, 1998), Calvo (1994), and Upchurch and Barrett (2000) previously examined wear features on the teeth of *Diplodocus*. All studies agree on the dominance of fine, subparallel scratches oriented generally along the labiolingual axis. Neither Fiorillo (1991, 1998) nor Calvo (1994) recovered pits, although Upchurch and Barrett (2000:106) did recover some “pit like areas,” but these were considered larger than normally produced by grit or phytoliths. These features appear to have been recovered from the dentine of a heavily worn tooth, however (Upchurch and Barrett:fig. 4.5), where larger features may be expected. The lack of pits led Fiorillo (1991, 1998) and Calvo (1994) to suggest an upper-canopy browsing behavior for *Diplodocus*, which is counter to much of the evidence for ground-level browsing presented in subsequently (e.g. Stevens and Parrish, 1999, 2005; Upchurch and Barrett, 2000; Sereno et al., 2007; this study). High browsing was also inferred as a possible feeding mechanism for *Diplodocus* by Upchurch and Barrett (2000), based on macrowear features.

The absence of pits in previous studies is somewhat perplexing, given their relative abundance in all teeth examined in this study. The difference may be a result of methodology, given the reliance of previous studies on SEM images (at extremely high magnification) as opposed to the use of low-magnification microscopy here. It may also be the result of sample size, as all studies include relatively few teeth per taxon compared to studies of mammals. The ubiquity of pits in all teeth examined here, their similarity in form among broad-snouted taxa,

and their difference in form in the round-snouted *Dicraeosaurus*, however, all reinforce the validity of the interpretation presented here.

Nigersaurus. Sereno et al. (2007) examined microwear features on the teeth of *Nigersaurus*. The results of that study are essentially identical to those presented here, although this study identified a significantly larger number of small pits. Both Sereno et al. (2007) and this work infer a diet based on ground-level browsing of herbaceous plant materials based on the consistent labiolingual orientation of fine scratches on the labial surface of the enamel and a high pit/scratch ratio.

Leaf stripping behavior?

Ryan (1981) suggested that some features of incisor microwear in *Gorilla*, *Pan*, and *Papio* were indicative of leaf-stripping behavior: polished surfaces and a preponderance of subparallel, fine scratches on the apical surface of the incisors. However, the proportion of features (scratches and pits) in the microwear assemblages reported here for sauropods differ from wear produced by leaf-stripping. In all but one sample (left premaxillary tooth 1 of *Diplodocus*) from the occlusal surface of sauropod teeth, pits outnumber scratches significantly, whereas scratches substantially outnumber pits in each of the samples reported by Ryan (1981). This latter result was suggested to have been a consequence of repeated drawing of plant materials over the enamel surface. In leaf stripping behavior, grit causes striations rather than compressional features (i.e., pits) as

seen in wear caused by a bite. Because of the high proportion of pits in the sauropod microwear sampled, leaf stripping behavior is considered to be less plausible than ground-level browsing behavior, although it is noted that leaf stripping and ground-level browsing do leave superficially similar traces on incisiform teeth.

Non-facet microwear features

Features recorded from the non-occlusal surfaces of presumptive ground-level browsing taxa such as *Diplodocus* and *Nigersaurus* differ from the features recorded from facets in both taxa. Specifically, larger features are recovered, and those features (particularly scratches) are in a different orientation relative to the tooth, nearly orthogonal to the long axis of the tooth rather than subparallel to it. Because these features are located a substantial distance from the occlusal surface, it is highly unlikely that they represent wear formed during the bite stroke. The implication, therefore, is that the wear was caused by nearby vegetation, which in turn suggests a dense (perhaps sward-like) growth form for the food resource in question. The orientation of the wear at nearly 90° to the occlusal features may have been the result of vegetation scraping against the labial margin of the upper dentition as the head and neck are moved laterally to obtain the next bite; this would fit with the interpretation of some authors (Stevens and Parrish, 1999; 2005) of the long neck as a means to increase the feeding envelope without moving the body. Such features were not recorded from the selectively browsing *Dicraeosaurus*.

FEEDING SUMMARY

Snout shape and microwear indices suggest the presence of both a ground-level, nonselective browsing behavior and a mid-height, selective browsing behavior in diplodocoid sauropods. Here, feeding behavior is examined in relation to body size, phylogeny, and paleoecology, to determine the influence of each on behavior in diplodocoid sauropods.

Body size and feeding behavior

Among flagellicaudatans, selectively browsing taxa had smaller skulls, and were smaller overall, than non-selective browsers (Janensch, 1929, 1935–36; Wilson and Sereno, 1998; Harris and Dodson, 2004; Remes, 2006). The rebbachisaurid *Nigersaurus*, however, was the most specialized non-selective browser sampled and was of approximately similar size to *Dicraeosaurus* and *Tornieria*. Although this rules out the hypothesis that feeding behavior was entirely size-dependent, it does not necessarily mean that there is no relationship between size and behavior. It is possible that above 10–12 meters in body length, selective browsing behavior became untenable as a feeding mode (although this restriction does not appear to upper-canopy feeders like *Brachiosaurus* and *Camarasaurus*); non-selective browsing behavior was clearly effective even at small (by sauropod standards) body sizes. Other dinosaurs hypothesized to have been ground- and mid-height selective browsers, such as ceratopsians (Dodson et al., 2004; Sereno et al. 2010), heterodontosaurs (Norman and Weishampel,

1991), lambeosaurines (Carrano et al., 1999), and stegosaurs (Weishampel, 1984) also tended to be small in comparison to sauropods, and even the largest rarely exceeded 12 m in body length (You and Dodson, 2004; Dodson et al., 2004; Norman et al., 2004; Horner et al., 2004; Galton and Upchurch, 2004). It is possible that above this size, handling and forage time for selective browsing exceeded some metabolic threshold when an animal is limited to lower-canopy browse. Competition in the understory may also have played a role; macronarian sauropods successfully grew large while selectively browsing in the upper canopy, but they also had exclusive dominion over those heights as no other clade of dinosaurian herbivore was able to access those resources (Fastovsky and Smith, 2004).

Phylogenetic signal

Within individual diplodocoid clades, feeding behavior was reasonably consistent, although snout shape can be determined for only one rebbachisaurid (*Nigersaurus*; Fig. 5.9A). However, the diplodocid *Tornieria* has microwear features and a snout shape most similar to those of the dicraeosaurids *Dicraeosaurus* and *Suuwassea*. Because *Tornieria* is a relatively derived diplodocid (see Chapter 4), it appears that the feeding behavior inferred for this taxon is an independent derivation within this lineage, rather than a retained plesiomorphic behavior. This in turn suggests that the behavior was not strictly governed by inheritance, and that some plasticity was possible.

The ancestral condition for snout shape in diplodocoids is difficult to

determine. Although both diplodocids and rebbachisaurids appear to have square snouts, there is not overwhelming evidence to suggest that this is the original condition for the group as a whole. The ancestral state in Flagellicaudata is equivocal: basal diplodocids have square snouts and basal dicraeosaurids have round snouts. Furthermore, the only rebbachisaurid for which snout shape can be determined (*Nigersaurus*), is a highly derived taxon that likely does not represent the basal condition for the group. Juvenile *Diplodocus* have narrow snouts (Chapter 6; Whitlock et al., 2010), which may suggest that the square-snouted condition seen in adults is derived from an ancestral round-snoutedness. Outgroup taxa (e.g., macronarians, basal eusauropods) are unequivocally round-snouted, but where, when, and how many times the transition to square-snoutedness occurred in diplodocoidea cannot be said with certainty. If square-snoutedness is taken as the ancestral diplodocoid condition, one origination (at the base of Diplodocoidea) and two reversals (one at the base of Dicraeosauridae, once in *Tornieria*) are required (three evolutionary steps). If round-snoutedness is basal for sauropods, then at least two originations (once at the base of Diplodocidae and once somewhere within Rebbachisauridae) and one reversal (*Tornieria*) are required (three steps) are required.

Environmental signal

Similar morphological plasticity in other dinosaurian groups (e.g., hadrosaurids) has typically been interpreted in relation to behavior, although often behavior and morphological divergence are correlated with phylogeny (Carrano et al., 1999),

and it can be difficult to tease apart the influences of phylogeny and behavior on morphology. However, as noted above, phylogeny is not a perfect explanation for the diversity of snout shapes seen in diplodocoids. It is likely, then, that this morphological variability was driven in larger part by the browse flora available to these animals.

Herbivory imposes two major constraints on behavior: foraging time and digestive time (Searle and Shipley, 2008). Digestive time is a function of the length of the digestive tract and may be loosely interpreted from body size, although soft tissue structures (e.g., the rumen), which are not typically preserved in the fossil record, can substantially impact retention time (Hummel et al., 2008). Foraging time, however, can be inferred from skeletal evidence based on models of intake rate. Intake rate has a major influence on feeding behavior in modern herbivores (Stephens and Krebs, 1986); which is to say that an organism will attempt to maximize intake rate in a given environment. Broad- or square-snouts have been demonstrated to maximize intake rate in non-selectively browsing mammals (Gordon and Illius, 1988); a broad snout in selective herbivores decreases intake rate by increasing handling time and minimizing bite mass cropped (Myers and Bazely, 1992).

Variation in forage quality may also have had some influence on behavior. Two hypotheses in particular, the forage abundance hypothesis (FAH) of MacArthur and Pianka (1966) and the selective quality hypothesis (SQH) of Jarman and Sinclair (1979), might be useful in explaining a relationship between ecology and behavior in these sauropods. The FAH suggests that when

resources are perceived to be abundant, animals may choose to be more selective; grazing behavior increases when resource levels are low. In this hypothesis, forage abundance is the controlling factor. SQH, conversely, predicts that herbivores are actually less selective when high quality resources are plentiful and homogeneously distributed. Under SQH, food quality is the key variable. If the regional ecology can be reconstructed for sauropods, support for one or both of these hypotheses in the feeding behavior may be found.

Although the ecological conditions of Niger during the Aptian-Albian are largely unknown (particularly with regard to flora), the paleoecology of the Late Jurassic Morrison and Tendaguru formations, where the remaining five taxa have been found, is better understood.

Morrison Formation. The Morrison Formation of North America is dominated by diplodocoid sauropods, in particular the square-snouted diplodocids. Diplodocids (primarily *Apatosaurus* and *Diplodocus*) are both the most common sauropod fossils found in these beds and the most widespread, occurring in more localities than any other clade (Foster, 2003; n.b., the macronarian *Camarasaurus* is the most numerous single genus of dinosaur). Only a single round-snouted diplodocoid taxon (*Suuwassea*) is known from the Morrison Formation.

As discussed earlier (see Chapter 3), plant fossils from the Morrison include a wide diversity of conifers, ginkophytes, podocarpaceans, ferns, cheirolepidiaceans, and horsetails (Tidwell, 1990; Ash and Tidwell, 1998; Parrish et al., 2004). Most recent work suggests that much of the Morrison Formation

was an arid to semi-arid savanna-like environment, dominated by ground-height herbaceous browse (e.g., ferns, bryophytes) and low- to mid-height woody shrubs (Parrish et al., 2004; Turner and Peterson, 2004). Taller browse (primarily conifers; e.g., *Pagiophyllum*, *Podozamites*) was restricted to areas near watercourses and isolated pockets, such as that preserved by the Salt Wash member (Ash and Tidwell, 1998; Parrish et al., 2004; Turner and Peterson, 2004). It is in these isolated pockets that high-browsing sauropods like *Brachiosaurus altithorax* are found (Turner and Peterson, 2004).

Low browse in the southern Morrison, particularly the ferns and small trees, appears to have been highly nutritious and digestible, on par with extant browse (Hummel et al., 2008). The abundance of high quality, broadly distributed low browse and the appearance of multiple lineages of non-selectively browsing sauropods fit well with the predictions of the SQH, and suggest a relationship between ecology and behavior in the southern Morrison Formation.

The northern end of the Morrison Formation (e.g., Montana) has been recognized for its unusual sauropod fauna, composed of smaller adults and more juveniles than is typical of more southern localities (Weishampel and Horner, 1994; Harris and Dodson, 2004). Additionally, dicraeosaurids such as *Suuwassea* and MOR 592 are known exclusively from Montana (Harris and Dodson, 2004; Whitlock and Harris, in press). Paleoenvironmental reconstructions of the northern Morrison Formation are also quite different from those of the southern localities. This region was likely to have been a wetter environment than the southern Morrison Formation (Parrish et al., 2004).

Morrison Formation sediments found near central Montana are believed to have been deposited in mires, coal swamps and/or peat bogs, and associated riparian environments (Parrish et al., 2004). Forested habitats have previously been thought to lead to a greater reliance on selective browsing in other dinosaurs (Carrano et al., 1999) and in modern mammals (Janis and Erhardt, 1988; Searle and Shipley, 2008). It is probable that the restriction of round-snouted, selectively browsing dicraeosaurids to this type of environment in the Morrison Formation indicates a similar constraint on sauropod dinosaurs. The less homogenous environments of the northern Morrison may likely have resulted in patches of highly nutritious vegetation, such as *Equisetum* and the conifer *Araucaria* (Hummel et al., 2008); the increase in selectivity when high-quality resources are restricted matches the predictions of SQH. The relatively high concentration of juvenile diplodocoids in the northern Morrison Formation, with their narrow snouts (Chapter 6; Whitlock et al., 2010), is also consistent with this interpretation.

Tendaguru Formation. The sauropod fauna of Tendaguru is made up exclusively of round-snouted taxa, including *Brachiosaurus*, *Dicraeosaurus*, and *Tornieria*. The African *Brachiosaurus* taxon is a much more important component of the fauna compared to its American relative, particularly in the Middle Saurian Beds where it is the most common sauropod found (Russell et al., 1980). The most common fossil sauropod in the Upper Tendaguru is the diplodocid *Tornieria*, which is rare in the Middle Saurian Beds but common elsewhere (Russell et al.,

1980). *Dicraeosaurus* is a minor component of all dinosaur-bearing layers (Russell et al., 1980).

The sediments preserved in the Tendaguru Formation encompassed both strictly terrestrial uplands and tidal flats/coastal regions, but the latter appear to have been poorly vegetated (Aberhan et al., 2002). In contrast, the uplands seem to have been heavily vegetated by conifer forests (including the very tall araucarians; Jarzen, 1981) that would have provided a food source for high-browsing sauropods. Also present were evergreen shrubs and small (<25 m) trees in the family Podocarpaceae. Minority components of the flora included cycads and ginkophyte trees. Ferns were exceptionally rare, and only two varieties, either *Dicroidium* or *Pachypteris*-type, have been reported from Tendaguru (Aberhan et al., 2002). The uplands of Tendaguru, therefore, were a heterogenous mix of upper-canopy browse dominated by conifers (Cheirolepidiaceae and Araucariaceae) and mid-height woody browse (Podocarpaceae, cycads); comparatively little low-height bulk forage (ferns) would have been found.

No ground-height, non-selectively browsing sauropod dinosaurs have been recovered from Tendaguru. The sauropods that have been found there are exclusively mid-height (*Dicraeosaurus*, *Tornieria*) or upper canopy (*Brachiosaurus*) feeders, which corresponds well with the recovered vegetation, which is dominated by woody browse. Although cycads and podocarpaceans evergreens would have been abundant mid-height browse, they are substantially less nutritious than the ferns, horsetails, and other low browse plants common to

the southern Morrison Formation (Hummel et al., 2008). Here, where high-quality food resources are limited, SQH predicts an increase in selectivity. The lack of evidence for large bodied, non-selective browsers in Tendaguru fits well with this prediction.

Summary. Forested habitats that are linked with riparian environments are also associated with round-snouted sauropods in both the Morrison (*Brachiosaurus altithorax*, *Camarasaurus*, *Suuwassea*) and Tendaguru (*Brachiosaurus brancai*, *Dicraeosaurus*, *Tornieria*) Formations. Square-snouted sauropods (*Apatosaurus*, *Diplodocus*) are found in the open, savanna-like environment proposed for the southern Morrison Formation, although the round-snouted *Camarasaurus* is also found in these beds. Evidence suggests that the riparian environments cutting through the savanna-type environments of the Morrison had substantial tree coverage (Turner and Peterson, 2004), which could explain the presence of *Camarasaurus* in those regions. The selective quality hypothesis of Jarman and Sinclair (1979) predicts non-selective browsing when high-quality resources are abundant and broadly distributed and selective browsing when high-quality resources are restricted; both predictions match the inferences of diplodocoid feeding strategy and floral ecology made for the Morrison and Tendaguru Formations. The general robustness of the relationship between diplodocoid anatomy and paleoecology suggests that square-snoutedness is linked with ground-height, non-selective browsing, and round-snoutedness is associated with mid- to upper-canopy selective browsing (Fig. 5.9).

MACROWEAR

Experimental results from the macrowear machine indicate that an orthal bite stroke, when used to crop vegetation at low heights, will produce labial wear facets on the upper dentition. Food items are pushed up against the upper dentition by the lower during the closing of the jaw. On an unworn crown, this results in the development of a lingual facet on the upper dentition occurs and an apicobasally elongate, labially positioned facet on the lower. As wear increases, an apical facet on the upper dentition occurs as an apical expansion of the lingual facet. Continued apical wear, in combination with the lingual curvature of the apex of the crown, results in the development of a labial wear facet on the upper crowns (Fig. 5.10). This facet occurs well before the crown is eroded to the point observed in fossil crowns. The apex of the crown on the upper dentition is nearly horizontal as a result of continued wear on both lingual and labial margins. The labial facet has similar mesiodistal and apicobasal dimensions whereas the lingual facet is distinctly apicobasally elongate. These results are similar to the labial and lingual facets seen on the tooth crowns of *Nigersaurus* (Sereno and Wilson, 2005; Sereno et al., 2007).

These results may also explain the facets in *Nigersaurus*. In *Nigersaurus*, the lingual facet has a smooth margin, indicative of tooth-tooth contact, whereas the labial facet has a 'dished' or 'scooped' appearance, indicative of tooth-food contact (Sereno et al., 2007). Although the labial facet in the experimental teeth is caused entirely by passage of foodstuffs over the apex of the crown, the

lingual facet was caused by the actions of the lower dentition (although production of the facet is directly caused by passage of the sandpaper). In an actual bite, the foodstuff would be sheared by the passage of the crown apices, and would likely not have been trapped between the labial surface of the lower dentition and the lingual surface of the upper dentition as it was in the experiment. Thus, the teeth would pass each other on those margins free of foodstuffs, forming a tooth-tooth facet on the upper dentition. A tooth-food facet would still form on the lower dentition, as that facet is also formed in part by contact with the food item. The dominance of the labial facet over the lingual facet with increasing wear time may explain the absence of a lingual facet in diplodocids; the teeth of diplodocids were replaced less often than those of *Nigersaurus* (D'Emic et al., 2009; Chapter 8), which may have provided time for the labial facet to overprint the lingual facet in those taxa.

Although the labial facets could also have been formed by branch-stripping activities as has been suggested (Upchurch and Barrett, 2000), these results indicate that such behavior is not required to form these facets, and in fact the results of this experiment closely match observed wear patterns in the ground-level browser *Nigersaurus*. Further study, with more sophisticated tooth models (e.g., two-part casts, materials with more appropriate hardness values) and more accurate food analogs, is required to fully test this interpretation, however.

CONCLUSIONS

Hypotheses of feeding behaviors typical of modern mammalian herbivores (e.g.,

non-selective and selective browsing) are supported for diplodocoid sauropods using evidence from snout shape and dental microwear. Snout shapes in diplodocoids include both rounded and square snouts, similar to those seen in hadrosaurid dinosaurs. Square snouts have been correlated with non-selective feeding behavior in modern and extinct mammals and in hadrosaurine dinosaurs, whereas round snouts correlate with selective browsing behaviors in those taxa. Dental microwear features indicative of ground-height browsing on herbaceous plants correspond with square snouts in diplodocoid sauropods; microwear features suggestive of mid-height browsing on brittle, potentially woody plants correspond with round snouts.

There is potential correspondence between body size and feeding behavior in diplodocoids: above 12–15 m body length, diplodocoids are exclusively non-selective, ground-height browsers; small diplodocoids include both selective and non-selective browsers, however. There is not a strong phylogenetic signal to morphology and behavior, although most diplodocids (except *Tornieria*) and rebbachisaurids were ground-height browsers, whereas dicraeosaurids (and *Tornieria*) were mid- to high-browsers. Feeding behavior corresponds well to environmental associations, such that closed environments dominated by upper-canopy browse lacked the ground-height, nonselective browsers that dominated open environments.

Experimental results indicate that the characteristic high-angled wear facets seen on the labial surfaces of upper teeth in diplodocids and rebbachisaurids can occur during ground-height browsing, and do not require alternative explanations (e.g., branch stripping).

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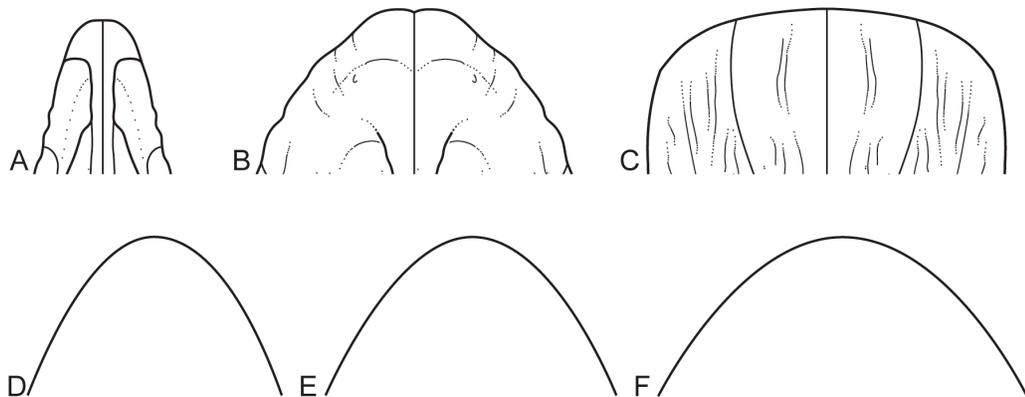


Figure 5.1. Snout shapes of sauropodomorph dinosaurs compared to similar shapes seen in ungulate mammals. Above: *Plateosaurus*, *Camarasaurus*, and *Diplodocus* snouts. Below: Outlines of snouts from a browser, an intermediate feeder, and a grazer. Sauropod snouts modified from Wilson (2005); mammal snout outlines modified from Gordon and Illius (1988).

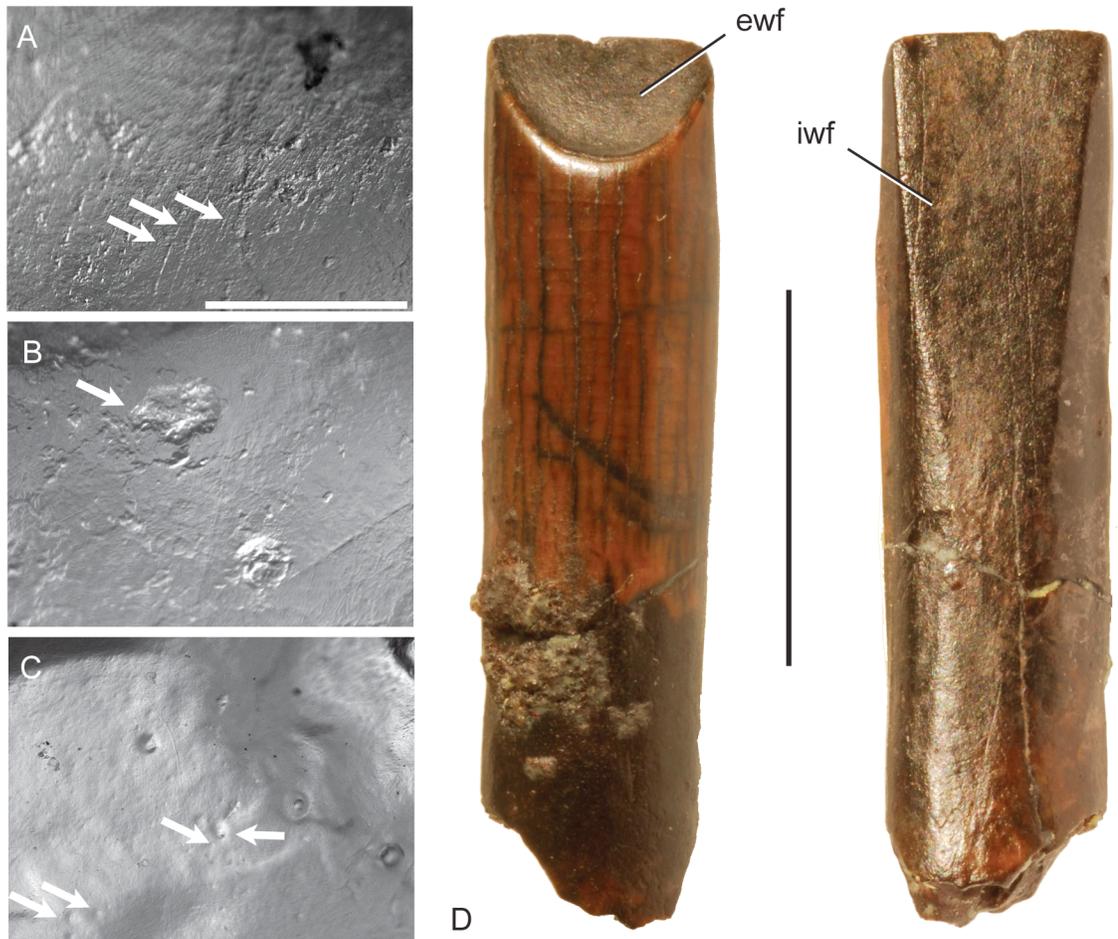


Figure 5.2. Examples of microwear features (exemplars indicated by arrows). A: Scratches, features at least 4x longer than wide. B: Gouges, large features with irregular margins. C: Pits, subcircular features, typically small. D: A tooth of *Nigersaurus*, illustrating the paired wear facets, labial (ewf) and lingual (lwf), seen on rebbachisaurid teeth. The labial facet is seen in most diplodocoid dentitions. Scale in A, B, C = 0.5 mm. Scale in D = 1 cm. D is modified from Sereno et al. (2007).

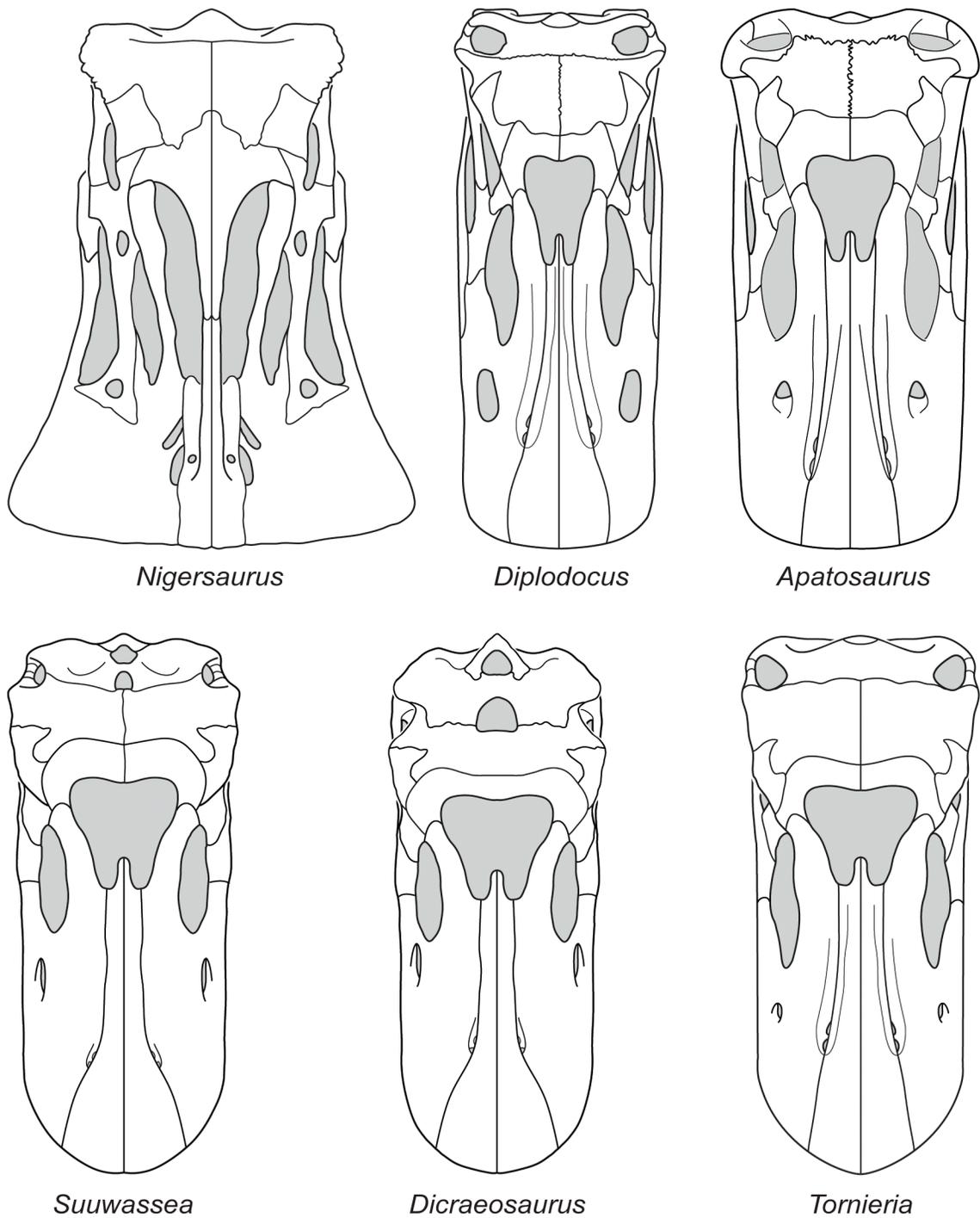


Figure 5.3. Reconstructions of diplodocoid skulls used in this analysis. Reconstructions of *Nigersaurus* and *Diplodocus* modified from Sereno et al. (2007) and Wilson and Sereno (1998), respectively. All other reconstructions based on material listed in Appendix 5.1. Skulls scaled to equivalent anteroposterior lengths.

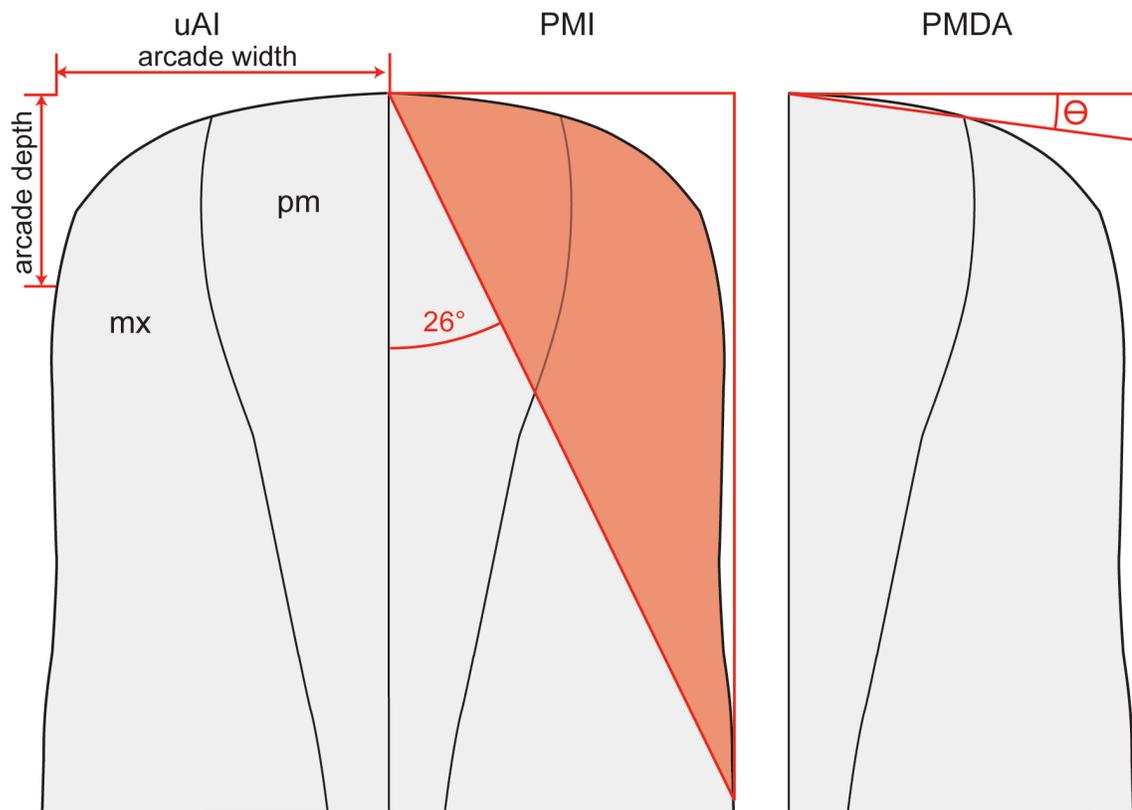


Figure 5.4. Metrics used to determine snout shape in this study. Snout depicted based on *Diplodocus* in Figure 5.3, anterior towards top of page.

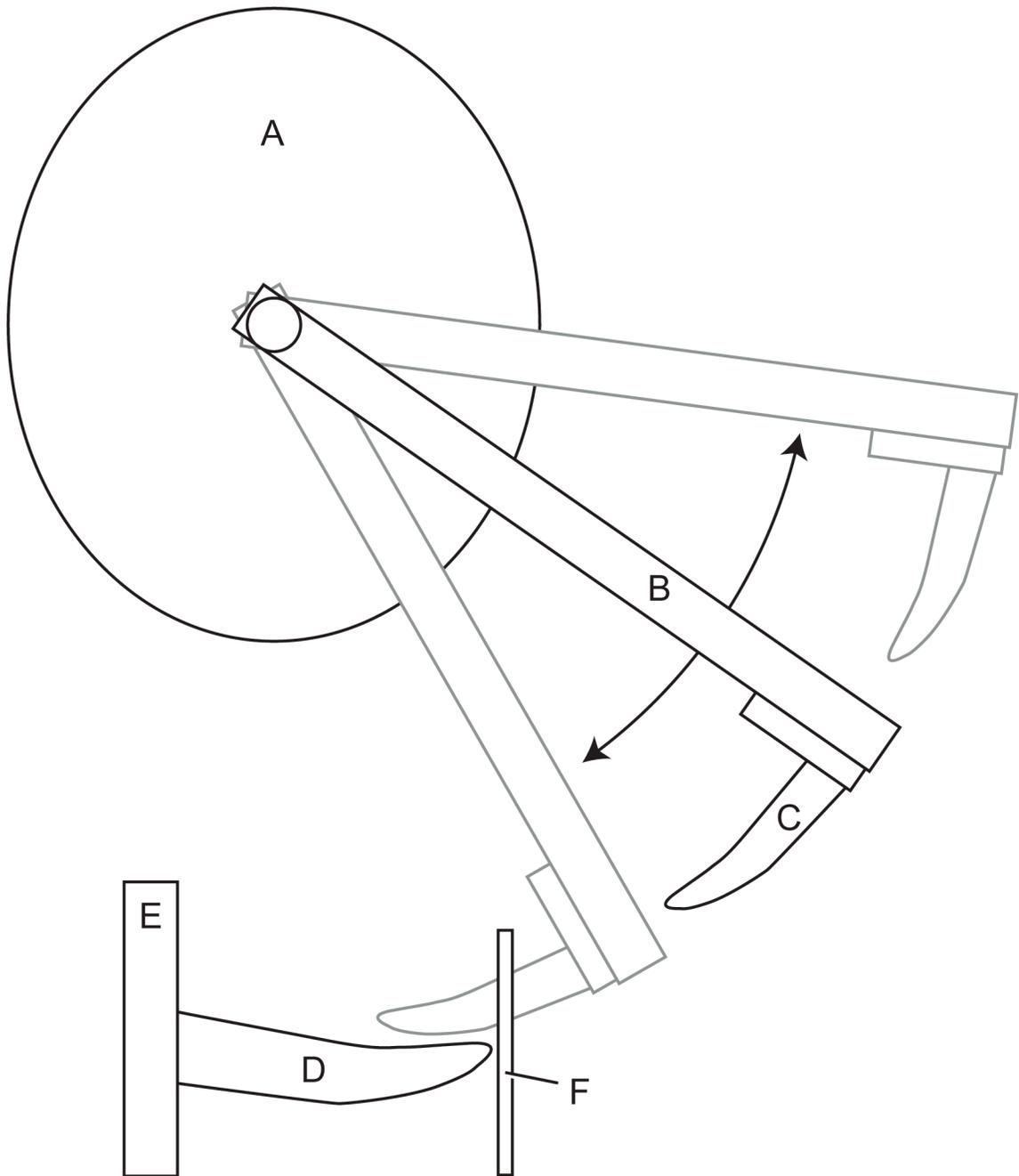


Figure 5.5. Schematic illustration of the ‘macrowear machine’ in lateral view. The machine consists of an oscillating motor (A), which moves a plexiglas sheet representing the lower jaw (B) and bearing epoxy casts of the lower dentition (C) in a representation of an orthal bite. The lower jaw occludes with epoxy casts of the upper dentition (D), fixed to a plexiglas plate (E). Sandpaper is introduced between the teeth (F) to simulate foodstuffs.

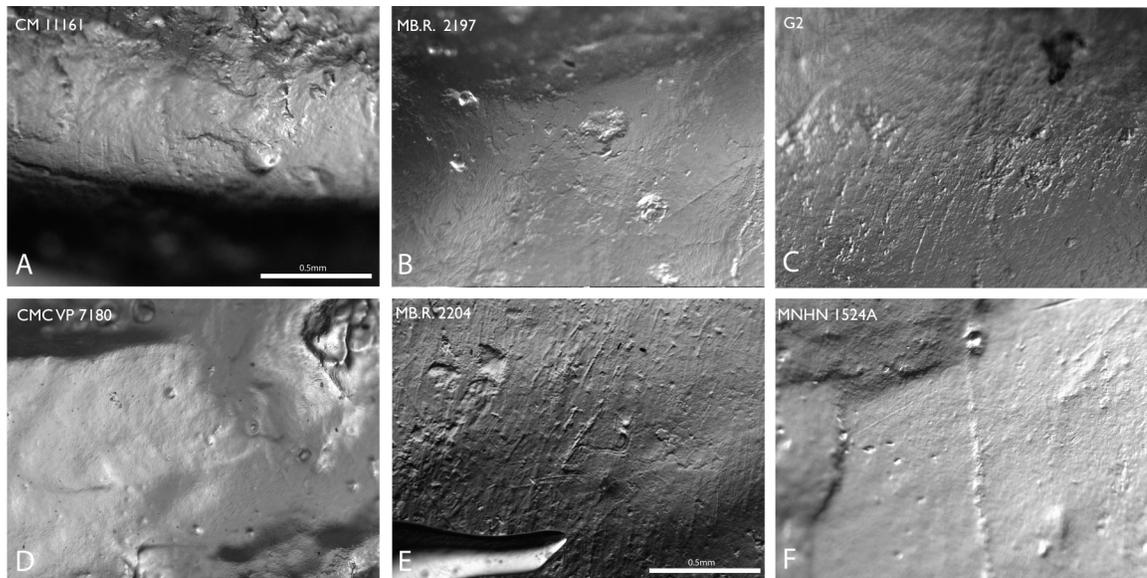


Figure 5.6. Microwear features recovered from sauropod dinosaurs. A, *Diplodocus*. B, E, *Dicraeosaurus*. C, *Nigersaurus*. D, *Apatosaurus*. F. c.f. *Rebbachisaurus*. A, C, D, F dominated by small pits and fine scratches, interpreted as indications of ground-height, non-selective browsing; B, E dominated by large gouges and coarse scratches, interpreted as indications of mid-height, selective browsing.

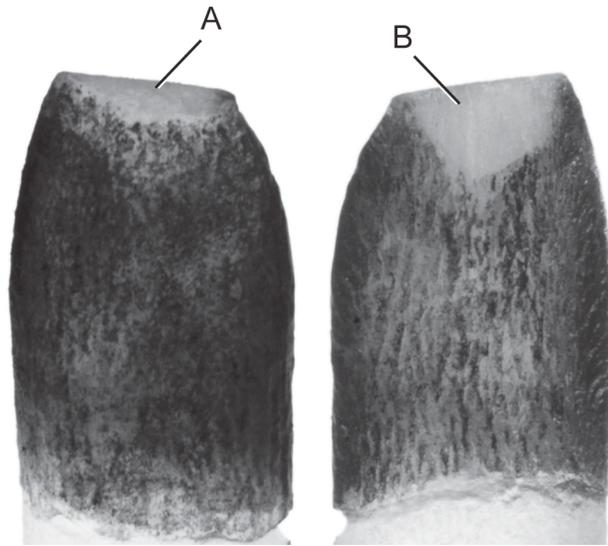


Figure 5.7. Labial (A) and lingual (B) facets formed on an upper tooth using the 'macrowear machine.'

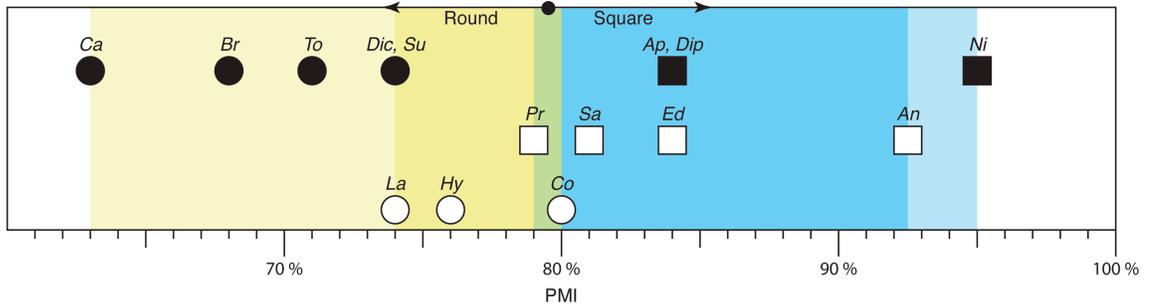


Figure 5.8. Plot of PMI scores for hadrosaurid (open symbols) and sauropod (closed symbols) dinosaurs. The vertical axis separates taxa into sauropods (top), hadrosaurines (middle) and lambeosaurines (bottom). Squares represent taxa considered to have been non-selective browsers, circles represent taxa considered to have been selective browsers. Blue tones indicate the range of square snouts and yellow tones indicate the range of round snouts; green tone indicates overlap. Overlap in snout shape occurs between behavioral guilds in hadrosaurs, but not in sauropods, although sample size is limited for sauropods. Sauropod snout shapes are also more diverse than snout shapes in hadrosaurids. Inferences of hadrosaur diet based on Carrano et al. (1999). Abbreviations: An, *Anatotitan*; Ap, *Apatosaurus*; Br, *Brachiosaurus*; Ca, *Camarasaurus*; Co, *Corythosaurus*; Dic, *Dicraeosaurus*; Dip, *Diplodocus*; Ed, *Edmontosaurus*; Hy, *Hypacrosaurus*; La, *Lambeosaurus*; Ni, *Nigersaurus*; Pr, *Prosauroplophus*; Sa, *Sauroplophus*; Su, *Suuwassea*; To, *Tornieria*.

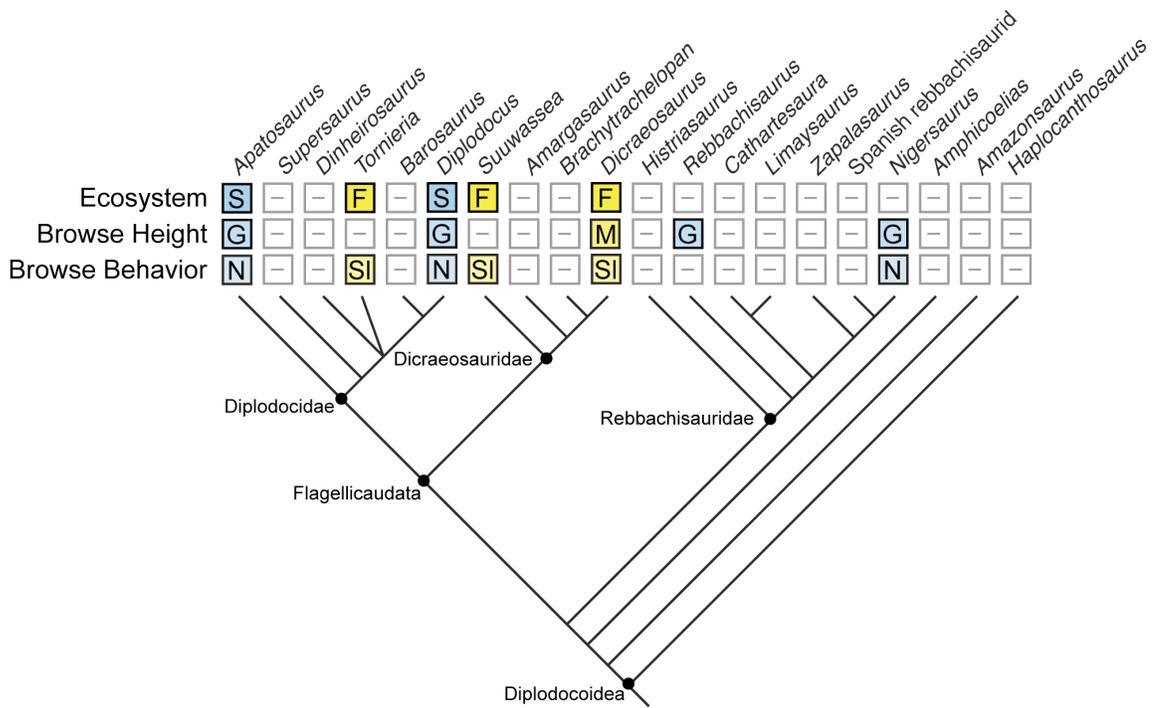


Figure 5.9. Phylogeny of diplodocoid sauroptiles (modified from Chapter 4), with ecosystem, inferred browse height, and inferred browse behavior plotted above terminals. Data suggest that ground-height, non-selective browsing evolved in open, savanna-like environments, whereas selective, mid-height browsing was most common in diplodocoids living in closed environments dominated by mid- and upper-canopy browse. Blue tones indicate data suggestive of ground-height, non-selective browsing; yellow tones indicate data suggestive of mid-height, selective browsing. Inferences for which insufficient data exists are represented in 50% grey tones. Abbreviations: S, savanna type ecosystem; F, forested ecosystem; G, ground-height browser; M, mid-height browser; N, nonselective browser; SI, selective browser.

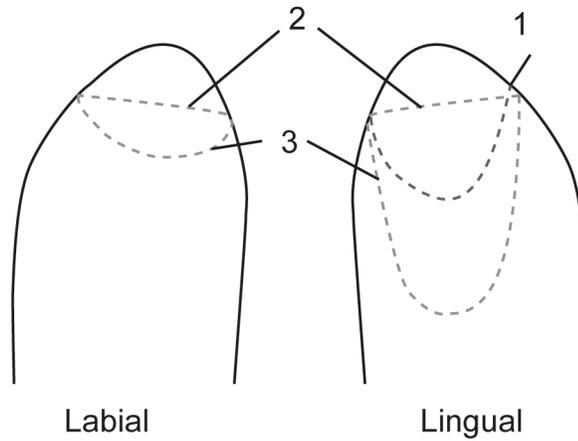


Figure 5.10. Development of wear facets on an upper tooth of *Diplodocus*. Initial wear develops as a planar, low-angled wear facet on the lingual surface, caused by passage of the lower teeth past the apices of the upper dentition (1). Apical wear develops next (2), caused by contact between the upper dentition and the stem of the food item. Apical wear, in conjunction with continued wear on the lingual surface, results in a flat apical margin; imperfect occlusion between upper and lower teeth results in the sub-perpendicular orientation of this apical margin. The final stage of wear occurs when apical wear progresses far enough to encroach on the labial margin of the lingually-curving crown (3).

Table 5.1. Feeding strategies and the predicted snout shape and microwear features associated with each.

Feeding strategy	Snout Shape	Microwear features
Browsing: Ground-height	Square	high proportion of pits relative to other features, fine scratches
Browsing: Mid-height	N/A	fewer pits relative to other features
Browsing: Upper canopy	N/A	few pits
Browsing: Non-selective	Square	cross-scratches, large features (i.e. coarse scratches, gouges)
Browsing: Selective	Round	subparallel scratches, fine features (i.e. fine scratches, no pits)

Table 5.2. Snout shape scores by taxon

	uAI	PMI	PMDA
<i>Apatosaurus</i>	1.5	84%	6.3°
<i>Dicraeosaurus</i>	0.6	74%	24.4°
<i>Diplodocus</i>	1.2	84%	7.4°
<i>Nigersaurus</i>	4.0	95%	3.5°
<i>Suuwassea</i>	—	74%	25°
<i>Tornieria</i>	—	71%	25.4°
<i>Brachiosaurus</i>	0.6	68%	33°
<i>Camarasaurus</i>	0.4	63%	40°

Table 5.3. PMDA scores by element.

Containing clade	Family	Genus	Species	Specimen #	PMDA	Position	
Diplodocoidea	Diplodocidae	<i>Diplodocus</i>	<i>longus</i>	AMNH 969	4.5	L	
					7	R	
				USNM 2673	9.8	L	
			<i>carnegii</i>	CMNH 11161	8.3	L	
		<i>Apatosaurus</i>	<i>sp.</i>	CMNH 11162	12.4	L	
					4	R	
			<i>sp.</i>	CMC VP 7800	3	L	
					5.8	R	
			<i>Tornieria</i>	<i>africana</i>	MB.R.2346	25.4	L
		Dicraeosauridae	<i>Suuwassea</i>	<i>emilieae</i>	ANS 21122	25	L
			<i>Dicraeosaurus</i>	<i>sp.</i>	MB.R.2339	24.4	L
Rebbachisauridae	<i>Nigersaurus</i>	<i>taqueti</i>	MNN GAD-512	3.5	L		
	Macronaria	<i>Brachiosaurus</i>	<i>brancai</i>		34.5	L	
				30.2	R		
<i>Camarasaurus</i>		<i>lentus</i>	CM 11338	45.4	R		
				46.5	L		
	<i>sp.</i>	UUVP 3999	27	R			

Table 5.4. Microwear features recovered from teeth. Teeth marked with an asterisk (*) indicate features recovered from areas outside the facet.

<i>Apatosaurus</i>			
	CMC VP 7180		
Pit Length	12.89 μm		
Pit Breadth	10.14 μm		
Pit Number	109		
L:B Ratio	1.27		
Average Area	410.41 μm^2		
Circumference	46.43 μm		
Scratch Length	n/a		
Scratch Breadth	n/a		
Orientation	n/a		
Consistency	n/a		
Scratch Number	n/a		
<i>Dicraeosaurus</i>			
	MB.R.2204 Dentine 1	MB.R.2204 Dentine 2	MB.R.2204 Enamel
Pit Length	13.44 μm	18.10 μm	17.11 μm
Pit Breadth	8.58 μm	10.57 μm	9.75 μm
Pit Number	177	182	227
L:B Ratio	1.57	1.71	1.75
Average Area	362.09 μm^2	600.74 μm^2	523.82 μm^2
Circumference	35.42 μm	46.56 μm	43.75 μm
Scratch Length	75.86 μm	69.36 μm	64.41 μm
Scratch Breadth	4.21 μm	5.36 μm	6.47 μm
Orientation	54.97	35.55	20.76
Consistency			
Scratch Number	94	135	176
<i>Diplodocus</i>			
	CM 11161 LP1	CM 11161 RP2	USNM 2673*
Pit Length	8.84 μm	6.72 μm	24.80 μm
Pit Breadth	6.90 μm	4.87 μm	18.83 μm
Pit Number	14	37	15
L:B Ratio	1.28	1.38	1.32
Average Area	191.53 μm^2	102.76 μm^2	1466.33 μm^2
Circumference	24.90 μm	18.43 μm	69.17 μm
Scratch Length	123.72 μm	68.79 μm	309.69 μm
Scratch Breadth	3.47 μm	4.46 μm	5.68 μm
Orientation			
Consistency	68.67	128.06	167.73
Scratch Number	19	26	37

<i>Nigersaurus</i>		
	G2	G100*
Pit Length	10.00 μm	28.93 μm
Pit Breadth	6.75 μm	12.71 μm
Pit Number	276	9
L:B Ratio	1.48	2.28
Average Area	211.95 μm^2	1154.58 μm^2
Circumference	26.80 μm	70.19 μm
Scratch Length	889.69 μm	180.34 μm
Scratch Breadth	3.53 μm	5.03 μm
Orientation		
Consistency	61.83	1.93
Scratch Number	138	30
<i>Rebbachisaurus</i>		
	MNHN 1512a	
Pit Length	19.71 μm	
Pit Breadth	16.42 μm	
Pit Number	14	
L:B Ratio	1.20	
Average Area	1016.22 μm^2	
Circumference	69.17 μm	
Scratch Length	218.05 μm	
Scratch Breadth	4.51 μm	
Orientation		
Consistency	32.57	
Scratch Number	8	

APPENDIX 5.1—MATERIAL EXAMINED FOR CRANIAL RECONSTRUCTIONS

Taxon	Material Examined
<i>Apatosaurus</i>	CM 11162, CMC VP7180
<i>Dicraeosaurus</i>	MB.R. 2336, MB.R. 2337, MB.R. 2338, MB.R. 2339, MB.R. 2340, MB.R. 2372, MB.R. 2378, MB.R. 2379
<i>Diplodocus</i>	AMNH 969, CM 11161, USNM 2672, USNM 2673
<i>Nigersaurus</i>	MNN GAD 512
<i>Suuwassea</i>	ANS 2112
<i>Tornieria</i>	MB.R. 2343, MB.R. 2346, MB.R. 2348, MB.R. 2374, MB.R. 2387, MB.R. 2388

APPENDIX 5.2—TEETH EXAMINED FOR MICROWEAR FEATURES

Taxon	Material Examined
<i>Apatosaurus</i>	CMC VP 7180: right maxillary tooth 4, right dentary tooth 2
<i>Dicraeosaurus</i>	MB.R.2195:one tooth; MB.R.2197:one tooth; MB.R.2204:one tooth
<i>Diplodocus</i>	CM 11161: left premaxillary teeth 1–4, left maxillary teeth 1, 4, right premaxillary teeth 2, 3, right maxillary tooth 1; USNM 2672: left dentary tooth 1, left maxillary teeth 5, 6, right premaxillary tooth 2, right maxillary teeth 2, 5–7; USNM 2673: six loose teeth
<i>Limaysaurus</i>	MUCPv-205: two teeth
<i>Nigersaurus</i>	MNN GAD 512: G2: one tooth; G89: three teeth; G110: three teeth
<i>Rebbachisaurus</i>	MNHN 1524a: one tooth
<i>Suuwassea</i>	ANS 2112: one tooth
<i>Tornieria</i>	MB.R.2193: right maxillary teeth 1, 2

CHAPTER 6

ONTOGENETIC VARIATION IN THE SKULL OF *DIPLODOCUS*

The skull of *Diplodocus* was first described by Marsh in 1884, and several additional, nearly complete skulls have been discovered and described since, making diplodocid cranial elements some of the best-known among Sauropoda (Marsh, 1884; Hatcher, 1901; Holland, 1906, 1924; Gilmore, 1932; Janensch, 1935-36; Haas, 1963; McIntosh and Berman, 1975; Berman and McIntosh, 1978, Connely, 1997). Since its discovery, the skull of *Diplodocus* has played a prominent role in distinguishing diplodocids from other sauropods. Cranial characters represent four of the seven features Marsh (1884) used in his initial diagnosis of the Family Diplodocidae, a trend that continues to this day. Wilson (2002) listed ten cranial characters as synapomorphies of Diplodocoidea (sauropods more closely related to *Diplodocus* than to *Saltasaurus*), as well as seven cranial synapomorphies for the subgroup Diplodocidae (sauropods more closely related to *Diplodocus* than to *Dicraeosaurus*) and six for Dicraeosauridae (sauropods more closely related to *Dicraeosaurus* than *Diplodocus*). Cranial characters made up 39.5% of the support for the node Diplodocoidea, nearly 10% more than for Macronaria (Wilson, 2002:table 14). Likewise, cranial specializations contributed much of the character support for Diplodocoidea and Diplodocidae in the analysis of Upchurch et al. (2004). Even at lower taxonomic

levels, cranial characters are important qualifiers. Wilson (2002:appendix 4) lists 25 cranial characters as autapomorphies for the six included diplodocoid genera for which cranial material is preserved and that were included in his analysis. Both their unusual shape and their relative abundance—40% of diplodocoid genera are represented by some cranial material, compared to less than 33% of macronarians (Table 1)—have contributed to what has become an iconic impression of the diplodocoid skull.

The diplodocoid skull is typically described as elongate antorbitally, with the nares retracted to a position dorsomedial to the orbits and the jaws transversely expanded anteriorly, terminating in a blunt, square snout containing narrow-crowned teeth. The shape of the *Diplodocus* skull has been regarded as poorly suited to chewing or biting through stems (e.g., Hay, 1908; Holland, 1924), and, as a consequence, great interest has been taken in the potential uses of the skull for gathering food in other ways (Osborn, 1899; Hatcher, 1901; Holland, 1906, 1924; Hay, 1908; Tornier, 1911; Coombs, 1975; Bakker, 1986; Dodson, 1990; Fiorillo, 1991, 1995, 1998; Barrett and Upchurch, 1994; Calvo, 1994; Stevens and Parrish, 1999, 2005; Christiansen, 2000; Upchurch and Barrett, 2000). The unique skull shape of *Diplodocus* has led researchers to propose equally unique modes of feeding, including uprooting aquatic succulents (Hatcher, 1901), scraping algae from rocks (Holland, 1906), branch stripping (Coombs, 1975; Bakker, 1986; Barrett and Upchurch, 1994), and prehension of fish (Tornier, 1911) or bivalves (Sternfeld in Holland, 1924), as well as a feeding strategy employed by modern megaherbivores: low height cropping (Barrett and

Upchurch, 1994; Upchurch and Barrett, 2000; Barrett and Willis, 2001; Stevens and Parrish, 1999; Sereno et al., 2007). Regardless of their specific functional interpretation, all studies agree that the feeding ecology of *Diplodocus* was clearly distinct from those employed by contemporaneous macronarian sauropods such as *Camarasaurus* and *Brachiosaurus*.

Here, I describe a juvenile skull attributable to *Diplodocus* that provides new insights into the life history and paleoecology of this giant herbivore. The reconstructed shape of the facial skeleton, particularly the anterior, tooth-bearing region, is transversely narrow and rounded anteriorly, in contrast to the square, blunt shape characteristic of adult diplodocids. This disparity in shapes between age classes implies a pattern of ontogenetic remodelling of the facial skeleton. This pattern is interpreted as an indication of resource partitioning between rapidly growing juveniles and adults, which were primarily invested in maintaining body existing body mass, and then compared and contrasted with the known record of cranial ontogeny in other dinosaurs.

DISCOVERY OF THE JUVENILE *DIPLODOCUS* SKULL

Several expeditions led by Earl Douglass in the early 20th century to the Carnegie Quarry in what is now Dinosaur National Monument yielded some of the most spectacular sauropod discoveries in North America, including several complete or nearly complete skulls (McIntosh, 1981). Most famous of these is probably the complete and largely undistorted adult *Diplodocus* skull (Carnegie Museum [CM] 11161) collected by Douglass in 1912. Three years later, a large sub-adult skull

of this genus (CM 3452) was the first—and, to date, only described—diplodocid skull found articulated with postcranial elements. Following these successes, a third, much smaller *Diplodocus* skull was collected by Douglass and his team in 1921, near the discovery site of CM 11161 (Fig. 1; McIntosh, 1981). This skull was mentioned and figured by Holland (1924:pl. 43), but until now has never been fully described.

ABBREVIATIONS

Institutions. AMNH, American Museum of Natural History, New York, 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, Germany; SMM, Science Museum of Minnesota, St. Paul, U.S.A.; USNM, United States National Museum, Washington D.C., U.S.A.; YPM, Yale Peabody Museum, New Haven, U.S.A. Z. PAL, Polish Academy of Science, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887

SAUROPODOMORPHA Huene, 1932

SAUROPODA Marsh, 1878

DIPLODOCOIDEA Marsh, 1884

FLAGELLICAUDATA Harris and Dodson, 2004

DIPLODOCIDAE Marsh, 1884

DIPLODOCUS Marsh, 1878

(Figs. 2–5)

CM 11255 is a diplodocid sauropod, sharing the following synapomorphies with other representatives of this clade: elongate prefrontal with a posterior projection approaching the parietal; squamosal-quadratojugal contact absent; paroccipital process with rounded, tongue-like ventrolateral end; shallow quadrate fossa. CM 11255 displays a single autapomorphy of *Diplodocus*: sharply defined fossa surrounding preantorbital fenestra. CM 11255 is distinguishable from *Apatosaurus* by the following features: presence of a long quadratojugal process of the squamosal that nearly contacts the quadratojugal; basiptyergoid recess present; basiptyergoid process without marked anteroventral flaring; closely appressed, sheet-like basal tubera with posteriorly facing concavity; paroccipital processes strongly ventrally oriented. CM 11255 cannot be compared to the

other Morrison Formation diplodocids, *Barosaurus* and *Supersaurus*, due to their lack of recognized cranial material. CM 11255 is distinguishable from the East African diplodocid *Tornieria* by the presence of a basipterygoid recess and the comparatively larger contribution of the prefrontal to the margin of the orbit. It can also be tentatively distinguished by the location of the frontal-parietal suture, which is located near the anterior margin of the supratemporal fenestra in *Diplodocus* and probably CM 11255, but located more posteriorly in *Tornieria*. Lastly, CM 11255 is distinguishable from the indeterminate flagellicaudatan *Suuwassea* in the following characters: anteroposteriorly compressed basal tubera; basisphenoid concave ventrally, not visible in posterior view; basal tubera widely separated from occipital condyle, spike-like, dorsoventrally narrow parasphenoid rostrum.

Few characters have been shown to consistently distinguish the skulls of different diplodocid taxa, particularly *Apatosaurus* and *Diplodocus* (Berman and McIntosh, 1978). In the only description of a mostly complete skull referable to *Apatosaurus* (CM 11162), Berman and McIntosh (1978) noted several cranial distinctions between that genus and *Diplodocus*, although these are primarily proportional in nature. Due to the early ontogenetic stage of CM 11255, proportional characters are potentially unreliable. Nevertheless, the anteroventral flaring of the basipterygoid processes noted by those authors for *Apatosaurus* (CM 11162) is not present in CM 11255 or in any other specimen of *Diplodocus*, regardless of ontogenetic stage; the remainder of the characters listed by

Berman and McIntosh (1978) cannot be evaluated on CM 11255 due to incomplete preservation.

Wilson (2002) distinguished between *Apatosaurus* and *Diplodocus* on the basis of the basipterygoid recess, which is absent in the former but present in the latter. The presence of a sharply defined fossa surrounding the preantorbital fenestra is listed as an autapomorphy of *Diplodocus* by Wilson (2002); this fossa is present in CM 11255, but cannot be adequately evaluated in CM 11162; as such, its state is here considered unknown in *Apatosaurus*. The basal tubera, which are globose and laterally expanded in *Apatosaurus* (CM 11162, YPM 1860), are pendant and more anteroposteriorly compressed in CM 11255 and in other specimens of *Diplodocus* (CM 11161, CM 3452, USNM 2672).

Although there are no cranial remains known for two other Morrison diplodocids (*Supersaurus*, *Barosaurus*), the identification of two novel probable *Diplodocus* autapomorphies and the ease with which CM 11255 is distinguished from *Apatosaurus*, *Suuwassea*, and *Tornieria* support the current assignment of this specimen to *Diplodocus*. CM 11255 is not here assigned to a species within *Diplodocus*: no cranial characters yet known serve to differentiate between the various species of the genus, which currently remain distinguishable solely by postcranial features. As such, the lack of associated postcranial material for CM 11255 currently prevents a specific diagnosis.

DESCRIPTION

ONTOGENETIC STAGE

The early ontogenetic stage assigned to CM 11255 is based on the small size of the specimen and on the presence of a visible suture between the left and right parietal bones. The skull measures 29.2 cm from its anterior-most point to the posterior margin of the occipital condyle, which is approximately 58% the length of the adult *Diplodocus* CM 11161 and approximately 66% the length of the large sub-adult CM 3452. CM 11255 is therefore the ontogenetically youngest *Diplodocus* skull ever fully described.

PRESERVATION

CM 11255 was recovered in isolation, with no associated postcrania or elements belonging to other individuals (Fig. 1). It was recovered from, and to some extent is still obscured by, a poorly-sorted sandstone matrix. The skull is crushed laterally, such that its left and right halves are disarticulated along the midline sutures, continuing posteriorly through the unfused parietals. Parts of the maxillae and premaxillae have been damaged or destroyed, although the tooth row is well represented in these regions by in-situ replacement teeth, preserved when sediment filled in around the highly resistant teeth after the thin bone surrounding them had been eroded away. This type of preservation is not uncommon (e.g., CM 21718 [McIntosh, 1981; pers. observ.], YPM 1922), although it is not typically found in direct association with other skull elements. The skull roof and occiput are represented primarily by elements from the right

side, although median elements (supraoccipital, occipital condyle, basioccipital) are largely complete. The dermal skull roof (nasal, prefrontal, frontal, and parietal) is rotated away from the midline of the facial skeleton by approximately 7.5°.

The left and right elements of the lower jaw are disarticulated, and the left mandible is displaced slightly medially and posterodorsally. As seen in ventral view, the curvature of the jaws is similar in both elements. The lower jaw of the well-preserved skull of *Nemegtosaurus* (Z. PAL MgD-I/9) has a similar translation of one mandible relative to the other (Wilson, 2005). No deformation of the tooth-bearing elements was noted in that specimen, although the left and right mandibles were translated relative to each other; this suggests that the curvature seen in the preserved mandibular elements of CM 11255 is likely natural and undistorted.

DERMAL ROOF COMPLEX

Premaxilla

The premaxillae are elongate tooth bearing elements that contact each other medially and the maxillae laterally, terminating posteriorly at the external naris. Due to the lateral crushing, the anterior portion of the skull is deformed along the median suture between the premaxillae, creating an unusually steep angle between these bones and exaggerating their visibility in lateral view.

Four tooth positions are preserved in the right premaxilla and are presumed present in the left (Fig. 2). The anterior margins of the premaxillae are

represented only by narrow, medial portions of the left and right premaxillae. Harris (2006) regarded the premaxillae of CM 11255 as similar in proportion and size to those of *Suuwassea*; however, the premaxillae in the present specimen appear to expand laterally without the distinct 'step' of *Suuwassea*, in which the transversely wide anterior portion is clearly demarcated by sharp lateral curvature in dorsal and ventral view. The narial fossae are not distinctly preserved.

The posterior extremes of the premaxillae are partially complete, preserving a portion of the anterior margin of the narial opening. There is no evidence for an elongate internarial bar, such as has been observed in some adult (USNM 2673) and sub-adult (CM 3452) *Diplodocus* skulls.

Maxilla

The maxillae are thin, sheet-like bones that are divided by the antorbital fenestra into an ascending process and a posteriorly-directed process that contacts the jugal and quadratojugal (Fig. 2). As in adult *Diplodocus*, the preserved portion of the maxilla-jugal suture is coarsely sinuous in lateral view. The ascending process remains in contact with the premaxilla until they both reach the external naris. Posteriorly, the ascending process contacts the nasal and the lacrimal.

Similar to adult *Diplodocus* (AMNH 696, CM 11161, CM 3452, USNM 2672) and other diplodocoids (*Dicraeosaurus*, MB.R. 2336; *Apatosaurus* CM 11162, CMC VP 7180), the external surfaces of the maxillae in this region are ornamented by several shallow, elongate depressions, roughly corresponding to

the positions and orientations of tooth families within the bone. The lateral plate of the maxilla is partially preserved posteriorly. The poor anterior preservation contributes to the convex shape of the ventral margin as preserved.

Immediately posterior to the preserved dentigerous margin of the maxilla is a large, distinct fossa that dorsally overlaps the three posterior-most replacement teeth. The fossa is pierced posteriorly by a large, subcircular preantorbital fenestra. The sharp outline of the fossa is best preserved on the left side (Fig. 2D). In other *Diplodocus* skulls (CM 11161, CM 3452, USNM 2672), the subnarial foramen and anterior maxillary foramen reside in a shallow groove situated slightly anterodorsal to the preantorbital fossa, along the contact with the premaxilla; neither these foramina nor the groove are distinctly preserved in CM 11255.

Nasal

The nasal is a roughly quadrangular element with anteriorly projecting rami that form the right and left posterolateral margins of the naris. The preserved portions of these rami contact the lacrimal and maxilla anteriorly; the main body of the nasal contacts the prefrontal laterally and would have contacted the frontal posteriorly, forming the anterior-most medial element of the braincase. The main body of the nasal rises dorsally above the orbit, elevating the posterior margin of the naris, as seen in some other individuals of *Diplodocus* (AMNH 696, CM 11161, CM 3452, USNM 2672; Figs. 2B, 3D). A small (~1 cm long) piece of the anterior ramus is preserved on the left side (Figs. 2D, 3C, 4C). This process

forms the posterolateral margin of the naris. It is probable that the orientation of the rami and the main body of the nasal obscured the naris in lateral view and that the naris pointed strictly anterodorsally in life.

Jugal

The jugal is a V-shaped element that connects the maxilla and quadratojugal with the lacrimal and postorbital. Its contact with the maxilla is a broadly sinuous suture, whereas its contacts with the remaining three elements are more linear (Fig. 2C, D). A dorsally-directed process along the lacrimal/jugal contact, as illustrated by Wilson and Sereno (1998:fig. 6) in their reconstruction of *Diplodocus*, appears to be at least incipiently present, although less substantial in this specimen. Medially, the jugal has a small contact with the palate via a lateral process of the pterygoid.

As in adult *Diplodocus*, the jugal is broad, flat, and excluded from the ventral margin of the skull. It forms parts of the margins of three skull openings: the orbit, the antorbital fenestra, and the lateral temporal fenestra.

Lacrimal

The lacrimal is a bar-shaped element, oriented approximately dorsoventrally. It contacts the jugal ventrally, the nasal and prefrontal dorsally, and the maxilla along the dorsal portion of its anterior margin. The suture with the jugal is nearly linear, with a reduced version of the “stepped” contact in some adult skulls (CM 11161; Fig. 2). Ventral to its anterior contact with the maxilla, the lacrimal forms

an anteroposteriorly elongate portion of the margin of the antorbital fenestra; the cross-sectional shape becomes more mediolaterally elongate dorsal to this fenestra. There, a strong ridge on the lateral surface of the lacrimal extends dorsally to join the laterally expanded prefrontal and form the anterior portion of the dorsal orbital margin.

The long axis of the lacrimal in CM 11255 is much more vertically oriented than is typical of more ontogenetically mature skulls, suggesting that the infraorbital and antorbital regions experienced a greater degree of anteroposterior and anteroventral lengthening during growth than did neighboring regions. A consequence of the orientation of the lacrimal is that the tear-drop shape typical of eusauropod orbits is not as strongly expressed; although there is still an anteroventral 'corner' on the orbit, the shape is generally subcircular.

Prefrontal

The prefrontal meets and slightly overlaps the lacrimal at a scarf joint. Along with the frontal, which it contacts posteriorly, the prefrontal forms most of the dorsal margin of the orbit. In lateral view, the prefrontal is anteroposteriorly broad, with only a gentle ventral concavity. In dorsal view, it is arcuate and contacts the frontal and nasal along a concave medial margin. This concavity lends the posterior half of the prefrontal a 'hooked' shape, which has been recognized as a diplodocid feature (Berman and McIntosh, 1978; Wilson, 2002). The prefrontal forms much of the lateral margin of the skull roof in dorsal view.

Frontal

In lateral view, the frontal is a narrow, arcuate element that contacts the prefrontal anteriorly and the postorbital laterally. In dorsal view, the frontals can be seen to contact the parietals posteriorly and the nasal anteriorly. The frontal-parietal suture is obscured and so cannot be compared to the relatively linear suture of *Suuwassea* or the sinuous sutures known in *Apatosaurus* (CM 11162) and *Diplodocus* (CM 11161) (Harris, 2006). The frontal forms much of the dorsal skull roof, and contacts the orbitosphenoid ventrally.

The lateral margin of the right frontal has been eroded away, exposing the trabecular internal structure of the bone, bordered by a thin veneer of cortical bone on the dorsal and ventral faces. In other specimens of *Diplodocus* (CM 11161, CM 3452, USNM 2672, USNM 2673), the lateral portion of the frontal that forms the orbital margin is greatly expanded laterally, creating a broad shelf dorsal to the orbit. A notch is commonly associated with the anterior margin of this expanded margin. In *Apatosaurus* (CM 11162), this expansion is well developed, and increases the width of the skull in this region well beyond the lateral extent of the parietals. Based on the mediolateral position of the posterior-most preserved portion of the postorbital, CM 11255 did not have such a prominent lateral expansion.

Postorbital

The postorbital is a triradiate element, with elongate processes contacting the frontal dorsally and the jugal anteriorly. The third process is comparatively short

and inserts into a groove in the squamosal. CM 11255 preserves the jugal process, which forms most of the ventral margin of the orbit. The contact with the jugal occurs along a shallowly-angled, planar suture. Although the postorbital and lacrimal are closely situated in adult specimens, this relationship in CM 11255 appears unusually close. There is a longitudinal ridge along the lateral surface of the jugal process, expanding the element into a flat shelf dorsally and rendering it triangular in cross-section. This creates a narrow fossa surrounding the lateral temporal fenestra.

Squamosal

The squamosal is an arcuate element when viewed laterally, contacting the parietal, postorbital, and quadrate, and forming a portion of the margin of both temporal fenestrae. The right side of CM 11255 preserves a small portion of the anteriorly-directed process that overlies the head of the quadrate in lateral view. In CM 11255, this process is partially obscured by matrix (Fig. 2A), but is revealed by computed tomography (CT) to extend anteriorly to nearly contact the posterodorsally-directed squamosal process of the quadratojugal, which contrasts with the widely-spaced position of these elements in adult *Diplodocus* (CM 11161). In posterior view, the preserved portion of the squamosal is almost entirely obscured by the paroccipital process, although a small portion of the lateral margin can be seen overlapping the quadrate (Fig. 3B, D).

Quadratojugal

The quadratojugal of CM 11255 is an anteroposteriorly elongate, dorsoventrally narrow element that contacts and laterally overlaps the quadrate; its elongate squamosal process extends 2.3 cm along the lateral margin of the quadrate toward the squamosal. This process tapers dorsally and terminates in a broken surface; it can be inferred to have extended to near the midpoint of the quadrate, within a centimeter of contact with the squamosal. The anteroventral corner of the lateral temporal fenestra is preserved on the left side only. Much of the anterior contact with the maxilla is not preserved.

The dorsal margin of the quadratojugal is broadly sinuous. It is dorsally convex anteriorly along the contacts with the maxilla and jugal, and it is concave posteriorly where it forms the anteroventral corner of the lateral temporal fenestra. In dorsal and ventral views, the quadratojugal bulges laterally as it overlaps the articular head of the quadrate (Fig. 4).

Parietal

The parietal of CM 11255 contacts the frontal anteriorly and delimits the dorsomedial margin of the supratemporal fenestra. The partially preserved median contact between the parietals is a highly interdigitated suture. In adult and large sub-adult *Diplodocus* (CM 11161, CM 3452, USNM 2672, USNM 2673), the parietals are fused. Coupled with the small size of the specimen, the presence of a patent interparietal suture in CM 11255 suggests that fusion of these elements only occurred as the animal approached maturity.

The lateral wing of the parietal arches strongly dorsolaterally, obscuring the supratemporal fenestra in posterior view—a condition described as characterizing *Diplodocus* by Berman and McIntosh (1978). The dorsolateral margin of the parietal in *Apatosaurus* is nearly linear, unlike the state preserved in CM 11255.

In dorsal view, a nuchal fossa can be seen between the lateral wing of the parietal and the parietal-supraoccipital suture. Although the depth of this fossa is somewhat exaggerated by an area of broken bone in the center of the concavity, the nuchal fossa appears to invade quite deeply, reaching nearly to the depth of the parietal-frontal suture, and is therefore more strongly concave than that seen in *Suuwassea* (Harris, 2006) and some specimens of *Diplodocus* (CM 11161). It is quite similar to the fossae in some other *Diplodocus* specimens, however, including other presumed sub-adult skulls (CM 3452), as well as in *Apatosaurus* (CM 11162).

The supratemporal region is narrow in dorsal view. The preserved mediolateral width of the right parietal at the greatest extent of the lateral wing is 4.1 cm, resulting in a minimum total transverse width estimate of 8.2 cm, roughly 24% of the total skull length (compared to ~29% in adult *Diplodocus* and ~46% in *Apatosaurus*). The proportional width of CM 11255 is more congruent with smaller *Diplodocus* skulls (SMM P84.15.3; Erickson and Hanks, 2001).

PALATAL COMPLEX

The palatal complex of CM 11255 is represented by the quadrates, pterygoids, ectopterygoids, palatines, and vomers (Fig. 5). The latter four structures are visible entirely or in large part only through CT scanning.

Quadrate

The quadrate connects the palate with the dermal skull roof through its insertion into a recess of the squamosal posterodorsally and with the facial skeleton by contact with the quadratojugal laterally. The quadrate also contacts the paroccipital process posteriorly (Fig. 3B, D). The wing-like pterygoid flange of the quadrate extends anteromedially, and is visible in lateral view through the lateral temporal fenestra. This flange is broad and flat, terminating in a broad, arcuate contact with pterygoid.

In lateral view, the quadrate is distinctly concave posteriorly, unlike the relatively straight or only slightly bent condition seen in adult exemplars of *Apatosaurus* (CM 11162), *Diplodocus* (CM 11161), and *Suuwassea* (Harris, 2006). This curvature is slightly exaggerated by breakage at mid-shaft, but even allowing for some distortion the quadrate was much more strongly curved than those of larger *Diplodocus* skulls. The quadrate fossa is shallow, as in other diplodocoids, and does not continue onto other elements laterally.

The articular surface of the quadrate condyle is visible in lateral view, with the medial aspect projecting well beyond the ventral margin of the quadratojugal.

The articular face is roughly triangular with a peak facing posteriorly. The surface is beveled such that it faces slightly ventrolaterally.

Pterygoid

The pterygoid forms much of the posterior portion of the palate, contacting the pterygoid wing of the quadrate posteriorly, the palatine and ectopterygoid laterally, and the vomer anteriorly. Anteriorly, the pterygoid bifurcates into anterodorsally and anteroventrally-directed processes. The anterodorsal process is broad and sheet-like and has a slightly concave, elongate dorsal margin that extends anteriorly to contact the palatine and the vomer (Fig. 5). Much of the ventral portion of this process is indistinguishable from matrix in the CT images, suggesting that portion of the element was quite thin. The pterygoid anteroventral process contacts the ectopterygoid to form the transverse pterygoid hook. In contrast to the autapomorphic condition described for adult *Diplodocus* by Wilson (2002), the pterygoid is situated posterolateral to the ectopterygoid when the two elements are articulated (Fig. 5).

Like the other dermal skull elements of the left side, the left pterygoid is displaced dorsally, posteriorly, and slightly medially. The pterygoids are vaulted inward at an angle of approximately 37.3° from vertical and arch dorsally as they approach their midline contact (Fig. 5C). The right pterygoid is more strongly inclined dorsomedially (35° from the vertical) than the left (2.3°). In adult *Diplodocus* (CM 11161), the pterygoids are inclined at approximately 30° from the vertical (McIntosh and Berman, 1975).

Palatine

The palatine is thin and arcuate in CM 11255, contacting the pterygoid posteriorly along a concave, anterodorsally inclined suture. The dorsal portion of the palatine and the contact with the vomer is not well preserved (see “Vomer”, below). The anteroventral portion of the palatine forms a dorsoventrally flattened process that contacts the maxilla along its lateral and anterior margins. The anterior-most portion of this process is overlapped by a posterior process of the maxilla that projects from the floor of the preantorbital fenestra. The ectopterygoid contacts the palatine along the palatine’s ventral margin, near the posterior margin of the maxillary contact.

Vomer

The vomer is trapezoidal in lateral view, contacting the maxilla anteriorly and the pterygoid posteriorly. It is overlapped to some degree along its posteroventral margin by the palatine, although that contact is poorly preserved. The vomers are strongly vaulted, although this is probably exaggerated by the minor lateral compression of the skull.

Ectopterygoid

The ectopterygoid is an arched, strap-like element that articulates laterally with the maxilla and posteromedially with the pterygoid in a ventrally-directed, anteroposteriorly elongate “hook” that extends to near the level of the ventral

margin of the maxilla. As discussed above, the articulation of the ectopterygoid with the pterygoid appears to position the former anteromedial to the latter, unlike the condition described for adult *Diplodocus* by Wilson (2002). In both cases, the articulation is primarily along the posterior margin of the ectopterygoid, and the ectopterygoid process of the pterygoid curves laterally to meet the ectopterygoid, so the variation seen here is perhaps not significant.

BRAINCASE

The braincase is largely missing, particularly those elements surrounding the foramen magnum. As with the circumorbital and skull roof elements, the right side preserves more of these bones than does the left. The braincase is oriented at the same slight angle to the facial skeleton as is the skull roof.

Basioccipital

The basioccipital makes up the main body of the occipital condyle, and in CM 11255 it is mostly complete. Little of the foramen magnum remains dorsal to it, including the portion of the margin that was presumably formed by this element. The condyle is D-shaped in occipital view, with a nearly flat posterodorsal margin. Including allowances for ventral rotation of the structure, the occipital condyle is oriented strongly ventrally. The suture between the basioccipital and the exoccipital-opisthotic that forms the dorsolateral “shoulder” of the condyle is plainly visible on both sides (Fig. 3B, D).

Supraoccipital

The supraoccipital is a midline element that contacts the parietals and the exoccipital-opisthotics. In CM 11255, the supraoccipital is represented primarily by a large, triangular eminence formed by the confluence of two crests: a transverse crest that extends laterally towards the nuchal fossa, the insertion of which is obscured by a broken surface; and a prominent, sagittal crest that extends down the midline of the element, flaring slightly at its dorsal terminus (Fig. 3B, D). In *Apatosaurus*, *Suuwassea*, and other crania of *Diplodocus*, a narrow isthmus of the supraoccipital extends ventrally to form a small portion of the dorsal margin of the foramen magnum, although this cannot be determined in CM 11255 due to a lack of preservation.

Exoccipital-Opisthotic

The exoccipital-opisthotic forms part of the posterior braincase, contacting the supraoccipital and basioccipital medially, the parietal dorsally, and the squamosal laterally. Together, the right and left exoccipital opisthotics form much of the lateral margin of the foramen magnum. In CM 11255, these elements are primarily represented by the left and right paroccipital processes. The blade-like paroccipital processes are strongly angled ventrally, as in other *Diplodocus* specimens (CM 11161, CM 3452). This is in contrast to the more laterally-directed processes seen in *Suuwassea* (Harris, 2006) and *Apatosaurus* (CM 11162). As in other diplodocid sauropods, the paroccipital process expands

ventrolaterally, predominantly on its dorsal margin. The exoccipital-opisthotic makes a small contribution to the 'shoulders' of the occipital condyle (Figs. 3, 4).

Basisphenoid

In diplodocoids, the basisphenoid serves as the only bony connection between the braincase and palate, contacting the pterygoids via elongate basipterygoid processes. Posteriorly, it meets the basioccipital at the base of the neck of the occipital condyle. Dorsally, the basisphenoid projects anteriorly as the parasphenoid rostrum, visible through the left orbit. This process is rod-like and elongate, reaching anteriorly to near the anterior margin of the orbit. It is generally similar in shape and proportion to its homologues in adult *Diplodocus*, and is unlike the much larger, dorsoventrally expanded parasphenoid rostrum of *Suuwassea* (Harris, 2006). A prominent ridge just dorsal to the parasphenoid rostrum is identified as the ventral extreme of the antotic crest.

Near its contact with the basioccipital, the basisphenoid is expanded into paired basal tubera that are separated from each other by a narrow sulcus. A narrow pit (the 'basipterygoid recess'; Wilson, 2002) is present just posterior to this sulcus, as in other specimens of *Diplodocus*. The basal tubera of CM 11255 are diagnostic for this genus in two ways. First, unlike the more massive, globose basal tubera seen in *Apatosaurus*, those of in CM 11255 are flat and semi-concave posteriorly, as in other *Diplodocus* skulls (CM 11161, CM 3452). Second, as in other specimens of *Diplodocus*, the basal tubera of CM 11255 are pendulous, primarily visible ventral to the occipital condyle in occipital view. In

Apatosaurus (CM 11162, CMC VP 7180, YPM 1860), the basal tubera do not descend as far ventrally and are more laterally oriented, such that they are primarily visible lateral to the condyle.

Anteroventral to the basal tubera, a deep concavity separates the paired basiptyergoid processes. In CM 11255, the basiptyergoid processes are thin and elongate, similar in shape to those of other *Diplodocus* crania. Anteroventrally, there is a condyle for articulation with the pterygoid. Unlike their counterparts in *Apatosaurus*, the basiptyergoid processes of CM 11255 do not flare anteroventrally. The angle between the basiptyergoid processes cannot be determined due to deformation of the left process and breakage of the right process.

Orbitosphenoid and Laterosphenoid

Posterodorsal to the parasphenoid, the right orbitosphenoid and laterosphenoid are visible in medial view (Fig. 2C, D). Much of the internal surface of the orbitosphenoid has been destroyed, including the foramina for cranial nerves I and IV, respectively. A small foramen for the passage of cranial nerve III is preserved near the ventral margin of the orbitosphenoid. An ovate, anteroposteriorly oriented foramen situated slightly posterodorsal to the foramen for cranial nerve III may have accommodated the endolymphatic sac. Ventrally, the orbitosphenoid meets the parietal in a sinuous, patent suture. Posteriorly, the orbitosphenoid abuts the supraoccipital in a straight, dorsoventrally oriented patent suture. The internal surface of the laterosphenoid is marked by a large,

approximately anteroposteriorly oriented tuberosity, the dorsal margin of which forms the ventral margin of the foramen for cranial nerve V. The anteroventral corner of this tuberosity, where the openings for cranial nerves IX–XI are expected, has been destroyed.

CRANIAL OPENINGS

Six cranial openings can be identified in CM 11255: the preantorbital fenestra, the antorbital fenestra, the orbit, the external naris, the supratemporal fenestra, and the lateral temporal fenestra. The subnarial foramen, anterior maxillary foramen, and posttemporal fenestra are not preserved.

Preantorbital Fenestra

The preantorbital fenestra is a small, elliptical opening that pierces the maxilla in the posterodorsal corner of a sharply defined fossa that extends anteriorly and ventrally. As in other neosauropods, the preantorbital fenestra is internally connected with the antorbital fenestra by a narrow bridge of bone composed of a posteromedial projection of the maxilla and an anterior projection of the palatine, inserting on the ventral margin of the preantorbital fenestra. The preantorbital fenestra may therefore represent a pneumatic continuation of the antorbital fenestra, similar to the invasions of the maxilla by the antorbital sinus in some theropods (Witmer, 1997).

Antorbital Fenestra

Located posterodorsal to the preantorbital fenestra, the antorbital fenestra opens laterally and is without a distinct fossa surrounding it. It is bound largely by processes of the maxilla; the ascending process surrounds the fenestra on its dorsal margin, and the posterior process contributes most of the anteroventral margin. The remainder of the antorbital fenestra is enclosed by the jugal and the lacrimal; the nasal is excluded from its margin.

As in adult *Diplodocus*, the outline of the antorbital fenestra of CM 11255 is roughly teardrop-shaped, with the acute posterodorsal corner formed by the confluence of the maxilla and lacrimal. The dorsal margin is not as concave as in adult *Diplodocus* (CM 11161, USNM 2672, USNM 2673), more closely resembling the condition seen in other sub-adult *Diplodocus* (CM 3452).

Orbit

Five bones bound the orbit: the lacrimal, prefrontal, frontal, postorbital, and jugal. It is a subcircular opening in CM 11255, with the sharply notched ventral margin typical of eusauropods weakly expressed (Wilson and Sereno, 1998). The primary cause of this shape disparity is the vertical orientation of the lacrimal, creating a wider angle between that element and the postorbital process of the jugal. The expansion of this angle gives the orbit its rounded appearance. The orbit is more strongly arched dorsally, where it is bounded by the prefrontal and frontal, than it is ventrally, where it is proscribed by the postorbital. The

anteroposterior length of the orbit is difficult to determine due to the loss of the frontal process of the postorbital.

External Naris

The external naris is bounded posteriorly and posterolaterally by the nasal, anterolaterally by the maxillae, and anteriorly by the premaxillae. From the position of preserved elements surrounding it, the naris faced entirely dorsally. The transverse breadth of the naris expands posteriorly, giving the opening a triangular shape in dorsal view. There is no evidence for a large internarial bar dividing the naris anteriorly, although such bars have been observed in other *Diplodocus* crania (CM 3452, USNM 2762).

Supratemporal Fenestra

In adult skulls of *Diplodocus*, the supratemporal fenestrae are bounded by the frontals and postorbitals anteriorly, the parietals posteriorly, and the squamosal ventrally. However, due to the incomplete preservation of these elements in CM 11255, little is known about the condition of the supratemporal fenestra in this specimen. It was likely a mediolaterally elongate, oval opening, largely obstructed in posterior view by the large lateral wing of the parietal. The partially preserved right supratemporal fenestra is fully visible in lateral view.

Lateral Temporal Fenestra

The lateral temporal fenestra is poorly preserved, although an estimate of its shape can be inferred from the bones forming its margin. As in other diplodocids, it is roughly divisible into two sections: a rounded, anterior portion and a dorsoventrally compressed, anteroposteriorly elongate posterior portion. In CM 11255, its anterior margin is approximately even with the anterior margin of the orbit in lateral view. This is unlike the condition in larger *Diplodocus* skulls (e.g. CM 11161), in which the lateral temporal fenestra extends well anterior to the orbit.

LOWER JAW

The lower jaw is similar to that described for larger specimens of *Diplodocus*, save only for its rounded anterior end, which distinguishes it from the iconic squared shape of adults.

Dentary

As in other *Diplodocus* (CM 11161, USNM 2672), the dentary of CM 11255 comprises approximately one-half the length of the mandible. The internal surfaces of both dentaries are preserved medially, and the ventral margin is visible in both elements as well. As a consequence of the lateral crushing of the skull, the dentaries are disarticulated from each other at the symphysis, and the left is displaced posteriorly, dorsally, and medially. In ventral view, the dentaries are similar, although the better-preserved right element is slightly more strongly

curved. The orientation of the symphysis suggests that the two dentaries would have met at a sharp angle, unlike the symphysis in adult *Diplodocus*, which was oriented essentially perpendicular to the anterior rami of the dentaries. The Meckelian groove is visible on the medial surface of the right dentary, arching dorsally to the broken edge of the bone.

Surangular

The surangular forms the dorsal portion of the posterior half of the mandible. In lateral view, it contacts the dentary anteroventrally and the angular ventrally. Medially, it contacts the dentary anteriorly and the splenial and prearticular ventrally. The surangular contacts the articular posteriorly in other exemplars of *Diplodocus*, but this cannot be confirmed in CM 11255. The surangular is broad and sheet-like, and there is no evidence for a well-developed coronoid eminence. There is also no evidence of the anterior surangular foramen that occurs in other *Diplodocus* (CM 11161, CM 3452).

The surangular and angular (along with the articular) form the retroarticular process, which protrudes farther posterior to the quadrate in CM 11255 than is seen in adult *Diplodocus*. In this way, it is more similar to the condition of the large sub-adult CM 3452. As in that specimen, however, the mandibular cotyle does not extend greatly posterior to the articular head of the quadrate, being instead quite rounded dorsally. This indicates that the lower jaw of CM 11255 was not capable of being significantly displaced anteriorly during the bite stroke, in contrast to what has been previously proposed for adult

Diplodocus (Barrett and Upchurch, 1994; Calvo, 1994; Upchurch and Barrett, 2000; Barrett and Upchurch, 2005).

Angular

The angular forms the ventral margin of the mandible and contributes to the unusually well developed retroarticular process. In lateral view, it contacts the surangular dorsally and the dentary anteriorly. Medially, it contacts the splenial anterodorsally and the prearticular dorsally.

Splenial

The splenial is a triradiate bone with two closely appressed anterior processes that contact the dentary and a posterior process that separates the prearticular from the angular. The anteroventral process is elongate and triangular in shape. The anterodorsal process is also triangular in shape, but much broader at the base and does not extend far anteriorly. Whether the anterodorsal process is further subdivided (as in CM 11161; McIntosh and Berman, 1975) cannot be determined.

Prearticular

The prearticular is a subquadrangular element that contacts the surangular dorsally and the angular and splenial ventrally. It arches slightly dorsally at mid-length, where it forms a portion of the ventral margin of the adductor fossa, and is

very similar to the prearticular described for the adult *Diplodocus* CM 11161 (McIntosh and Berman, 1975).

DENTITION

The teeth of CM 11255 are of the narrow-crowned type typical of diplodocoids (Calvo, 1994). As in other *Diplodocus*, they lack marginal denticles. Seven functional maxillary tooth positions are preserved on the right side, and 10–11 are estimated on the left. This is the standard *Diplodocus* condition (AMNH 696, CM 11161, CM 3452, USNM 2672). In the lower jaw, there are eight preserved functional teeth in the left dentary and six in the right. Based on other *Diplodocus* skulls, CM 11255 would have had between 10–11 dentary teeth total. The upper teeth are larger than their lower counterparts, and are generally in a better state of preservation. None show definite traces of wear.

Similar to adult teeth, those of CM 11255 are subcircular in cross-section near the apicobasal midpoint of the crown, and become labiolingually compressed more apically. The upper teeth are unusual for a diplodocoid, however, in having mesiodistal asymmetry. Unlike the teeth preserved in specimens of adult *Diplodocus* (AMNH 696, CM 11161, USNM 2672, USNM 2673), the apices of each tooth of CM 11255 are slightly distally inclined. The teeth are sharply pointed, a condition Holland (1924) considered unusual. However, *in situ* teeth in other *Diplodocus* skulls (CM 3452, USNM 2672, and USNM 2673) are also pointed, suggesting that this shape is in fact typical for unworn crowns. As in those skulls (but not CM 11161), the teeth of CM 11255

are also closely appressed, occasionally contacting their mesial and/or distal neighbors.

In adult diplodocoids, the dentition is restricted to the anterior extremity of the snout. Although much of the ventral margins of the maxillae of CM 11255 are missing, a large proportion of the dentition is represented by both functional (Fig. 2A, B) and replacement (Fig. 2C, D) teeth. The preservation of the replacement teeth allows the reconstruction of the position of the distal-most maxillary tooth, which is located farther posteriorly than is typical for adult *Diplodocus* (Fig. 2). That is, the tooth row in adults ends well anterior to the preantorbital fenestra, and often anterior to the subnarial foramen. Conversely, in CM 11255, the tooth row appears to end posterior to at least the subnarial foramen, and perhaps quite close to the anterior margin of the preantorbital fenestra.

The replacement teeth in each maxillary tooth family are first formed well within the bone, with the most distally located replacement tooth forming nearly within the preantorbital fossa (Fig. 2B, D). The most mesially-positioned upper teeth (i.e., those in the premaxilla and the mesial-most positions of the maxilla) appear to travel in an arcuate path through the jaw bones as a result of the 'stepped' shape of the snout visible in lateral view; more distal teeth seem to form in more linear families. The erupted teeth are oriented at a slight angle to the ventral margin of the jaw and tilted slightly mesially (Fig. 2A, C), as in other sub-adult *Diplodocus* (CM 3452). Visual estimates of the size and position of the replacement teeth of CM 11255 suggest that, even as juveniles, *Diplodocus* individuals carried in excess of four or five replacement teeth per alveolus in the

maxilla. In the dentary of CM 11255, replacement teeth are present within 7 mm of the preserved ventral margin of the jaw, possibly explaining the ventrally projecting 'chin' of diplodocids as a reservoir for replacement teeth (Wilson and Sereno, 1998). The presence of so many teeth in such a small jaw may be evidence of rapid replacement rates, such as that observed in the rebbachisaurid diplodocoid *Nigersaurus* (Sereno et al., 2007).

DISCUSSION

RECONSTRUCTING THE SNOUT

Adult individuals of *Diplodocus* and most other diplodocoids are well-known for having snouts that are broad and square in dorsoventral view, with anteriorly sequestered teeth. The youngest known juvenile *Diplodocus* (CM 11255), however, has a highly rounded snout and a tooth row that extends farther posteriorly than in adults (Figs. 6, 7). Although taphonomic processes have slightly distorted the snout, there are three main lines of evidence that suggest that I have correctly reconstructed its shape: the preserved position of the teeth, the orientation and size of the palatal elements, and the shape of the dentary.

Evidence from Teeth

In adult *Diplodocus*, the posterior-most tooth in the maxillary tooth row (tooth 10 or 11) is located very far anteriorly in the jaw, well anterior to the preantorbital fenestra. The lateral compression experienced by CM 11255 is unlikely to have

displaced its tooth row posteriorly; displacement of that type would result in visible damage or deformation to the pre-preantorbital region of the skull, which is not evident in the specimen. In contrast, the most likely consequence of lateral crushing is exaggeration of the length of the skull due to folding at the premaxillary symphysis, causing the anterior ends of the premaxillae to protrude farther anteriorly than they did in life. This can be refuted as a major impactor here due to the close association of the anterior end of the preserved upper tooth row with the anterior end of the right dentary.

Evidence from the Palate

The pterygoids are elements with multiple local angles when viewed in cross-section (Fig. 5C). In *Diplodocus* and *Apatosaurus*, the angle between the pterygoids at mid-height is approximately 60° (Berman and McIntosh, 1978). The right pterygoid of CM 11255—the better preserved of the two—has an angle with the vertical of 35°. If the right pterygoid is mirrored, the resultant median angle is 70°, greater than that seen in adult *Diplodocus*. This suggests that the right pterygoid is largely undistorted, and when mirrored provides a conservative estimate of palatal width. Using the right pterygoid to reconstruct the width of the palate indicates that the width to be added is only 11 mm, for a maximum skull width of 88 mm at the quadrates. If the entire right side of the skull, to the midline suggested by the right pterygoid, is mirrored, the maximum skull width is only 102 mm. Even using this higher estimate, the reconstructed snout is still quite round in comparison to adults (see Comparisons with Adult *Diplodocus*, below).

Evidence from the Dentary

As noted above, lateral crushing of the skull has displaced the left mandible, disarticulating it from the right at the dentary symphysis. This disarticulation and subsequent displacement appears to have been the main impact of compression on the mandibles because their longitudinal rami appear to be relatively straight and the anterior curvature of each dentary is similar (Fig. 4B, D). These elements are gently rounded in ventral view, not squared as seen in larger *Diplodocus* skulls.

Lateral crushing of this extent is not typically seen in larger *Diplodocus* skulls, although slight crushing is apparent in two other specimens, one adult (USNM 2672), and a larger sub-adult (CM 3452). In both of these latter specimens, the dentaries are symmetrical and appear to retain their original morphology (squared in USNM 2672, more gently rounded in CM 3452) and are, again, disarticulated along the symphysis, with one mandible displaced. Even in a clearly distorted skull (USNM 2673), the deformation occurs along the lateral ramus of the mandible, not at its anterolateral corner. The only observed case of deformation altering the anterior shape of the dentary is the dicraeosaurid diplodocoid *Dicraeosaurus* (MB.R. 2372), in which the squareness of the dentary is exaggerated, although the ventral margin is itself undeformed. It is unlikely, then, that taphonomic deformation has greatly altered the shape of the dentaries of CM 11255, and consequently these elements constitute a reasonable proxy for snout shape in this specimen.

COMPARISONS WITH ADULT *DIPLODOCUS*

Varricchio (1997) listed ten ways in which the crania of dinosaurs have been shown to vary ontogenetically, two of which (increase in tooth count, shortening and deepening of the skull) are potentially related to changes in feeding behavior. Others (relative decrease in size of the orbit, relative increase in antorbital length) are common in many amniote groups and are not directly related to feeding behavior.

As expected, the relative contributions of the orbit and braincase to overall skull size are dramatically larger in CM 11255 relative to large adult skulls (Fig. 7). Accordingly, there is a smaller contribution of the antorbital region to skull length in CM 11255, which has the effect of shortening the face. This shorter proportional length is accompanied by a snout that is narrower and rounder in dorsal view. The upper tooth row occupies a much larger proportion of the jaw margin and extends much farther posteriorly than in adults. This suggests a large-scale ontogenetic remodeling of the facial skeleton involving rearrangement of the food-gathering apparatus, which has not been previously reported for any sauropodomorph dinosaur.

Implications for Facial Remodeling in Diplodocus

In mammals, snout shape has been shown to serve as a proxy for feeding behavior (Boué, 1970; Solounias et al., 1988; Dompierre and Churcher, 1996). Broad, anteriorly flat snouts belong to mammals that crop low-lying grasses near the ground, and narrow, pointed snouts belong to mammals that selectively

browse for particular plants or plant parts. Using a modification of a metric used by Solounias et al. (1988), the snout shape of sauropods can be quantified. The premaxillary-maxillary index (PMI) is calculated by superimposing a triangle over a dorsal view of the snout with the hypotenuse drawn at 26°. The area of this triangle that is covered by snout is divided by the total area of the triangle to determine the PMI; higher numbers indicate squarer snouts. The most conservative reconstruction of CM 11255 has a PMI of 56%; this is well below that of adult *Diplodocus* (PMI=84%; Whitlock, 2007). This pointed snout is also seen in other juvenile specimens of *Diplodocus* (CMC VP 8300; Whitlock, 2006). The ontogenetic disparity in snout shapes in this genus may be evidence of resource partitioning between adults and juveniles that might have had vastly different energetic needs.

Fiorillo (1998) presented patterns of enamel microwear as evidence for resource partitioning between adults and juveniles of a different Morrison sauropod, *Camarasaurus*. Ongoing research has shown a difference in wear patterns between relatively round snouted (*Dicraeosaurus*) and relatively square snouted (*Apatosaurus*, adult *Diplodocus*) diplodocoids that is consistent with selective browsing vs. non-specific browsing similar to the 'grazing' behavior of ruminants (Whitlock, 2007). Unfortunately, microwear has not yet been recovered from a definitive juvenile *Diplodocus* tooth for comparison with adult patterns.

Curry (1999) and Lehman and Woodward (2008) presented sigmoidal growth curves for the diplodocid *Apatosaurus*. Assuming that these curves accurately represent the pattern of growth rates through diplodocid ontogeny,

juvenile *Diplodocus* in the exponential growth phase may have required more energy-rich foodstuffs than adults that had reached their growth plateau. Barrett (2000) suggested a similar scenario for basal sauropodomorphs involving opportunistic carnivory in juveniles. Jarman (1974) noted that small ungulates, which have comparably higher metabolic rates than large ungulates, have narrow snouts for selective browsing of plant parts with high digestibility and high caloric content. It is possible that a similar scenario could have occurred in an organism whose growth curve involves many orders of magnitude increase in mass. Earlier ontogenetic stages likely required easily digestible, high calorie foods to maintain a higher metabolism, and used a narrow, pointed snout to selectively obtain them. Once full size had been reached, energetic goals may have been attained by higher-volume, less nutritious, non-specific browsing by blunt-snouted adult *Diplodocus* individuals. Resource partitioning may also have occurred out of necessity, easing intraspecific competition between adults and their offspring, or, as noted by Jarman (1974), because a larger skull (such as that of adult *Diplodocus*) is less suited for selective herbivory.

COMPARISONS WITH OTHER DINOSAURS

Of the numerous dinosaurian taxa that have been examined for ontogenetic cranial variation, six are of particular interest. Three related taxa, the sauropodomorphs *Camarasaurus*, *Rapetosaurus*, and *Massospondylus*, are examined, as well as the theropods *Albertosaurus* and *Tyrannosaurus*. To

elucidate the condition in an ornithischian, the basal ceratopsian *Psittacosaurus* is also discussed.

Camarasaurus

Camarasaurus is known from multiple skulls, including a juvenile preserving most of the facial skeleton (CM 11338). Ikejiri (2004) and Ikejiri et al. (2005) suggested that there was little remodelling of the craniofacial skeleton throughout the ontogeny of this genus. McIntosh et al. (1996) posited that a reduction in alveolar count did occur with advancing ontogenetic stage, contrary to the typical dinosaurian condition (Varricchio, 1997; but see Carr, 1999). Fiorillo (1998) used enamel microwear patterns to suggest resource partitioning between adults and juveniles in browse height, but not necessarily browse type. For sauropods like *Camarasaurus*, whose relatively high forelimb-to-hindlimb and low neck-to-torso ratios suggest a higher browse height than is posited for diplodocoids, browse height was most likely a function of body size and therefore maturity. In other words, given their smaller size, younger individuals necessarily browsed at lower heights than older individuals. In contrast *Diplodocus* has been interpreted as a mid- to low-height feeder throughout its ontogeny (Barrett and Upchurch, 1994; Upchurch and Barrett, 2000; Stevens and Parrish, 1999, 2005). The variation in resource acquisition may have been as much a function of behavior as it is of physiology.

Rapetosaurus

The derived titanosaurian sauropod *Rapetosaurus* is known from cranial elements belonging to an adult and a juvenile, including facial bones from each (Curry Rogers and Forster, 2004). However, the reconstructed skull of this taxon is based almost entirely on the adult, as very little of the facial skeleton is preserved in the juvenile (Curry Rogers and Forster, 2004:fig. 1). Although the reconstructed snout is somewhat rounded in dorsal view, the preserved dentary (Curry Rogers and Forster, 2004:fig. 28) approaches a square shape, more so than in the juvenile *Diplodocus* but less than in adults. In the absence of more complete juvenile skulls, little can be said about the ontogenetic development of the blunt snout in *Rapetosaurus*.

Massospondylus

Sues et al. (2004) described four skulls attributable to *Massospondylus carinatus*, representing several stages of growth. *M. carinatus* appears to have added maxillary tooth positions with age, and there are more denticles per crown in juvenile specimens than in adults, but the general shape of the snout does not appear to have varied greatly (Sues et al., 2004). Gow (1990) noted a few ontogenetic changes in the braincase of *M. carinatus*, primarily the late ossification of a posterior extension of the laterosphenoid separating the vena cerebialis media and cranial nerve V, and increased muscle scarring on the supraoccipital. Reconstructions of three skulls of *M. carinatus* (Gow et al., 1990:fig. 7) suggest that the orbit became proportionally smaller and the

antorbital region proportionally longer with increasing size, as is typical of many other dinosaurian taxa (Varricchio, 1997).

Albertosaurus and *Tyrannosaurus*

The premaxillae and maxillae of *Albertosaurus* were subject to ontogenetic variation, particularly in the later sub-adult stages, when the snout broadened transversely (Carr, 1999). Additionally, the skull as a whole became more robust with age, a pattern also seen in *Tyrannosaurus*. Carr (1999) hypothesized that this variation may be the result of variation in foraging behaviors, such that older individuals were more capable of grasping and holding live prey or tearing apart large carrion; an alternate explanation proposed was that the increased robustness and broadness was a physiological response to increased skull size and bite force. Additionally, the teeth became more robust throughout ontogeny, with a corresponding reduction in the number of alveoli. The implication is that, as in *Diplodocus*, tyrannosaurid theropods were capable of variation in response to differing feeding behaviors or requirements at different ontogenetic stages.

Psittacosaurus

The basal ceratopsian *Psittacosaurus* is known from many individuals of varying sizes and stages of ontogeny. In *P. mongoliensis*, alveolar count more than doubles throughout ontogeny, eventually reaching 12 maxillary and dentary teeth from approximately five in the youngest individuals (Serenó, 1990). In *P. mongoliensis* and *P. xinjiangensis*, the large sagittal crest is not present in young

individuals and developed as the animal matured (Sereno and Chao, 1988). Additionally, Makovicky et al. (2006) demonstrated that the presence of a well-developed flange on the dentary is age-related, only appearing in older sub-adults. Those authors also found that overall skull shape, however, did not significantly vary with age. Unlike in *Diplodocus*, it appears that the ontogenetic variation in *Psittacosaurus* was not related to a substantial change in feeding behavior, but was instead a response to increased body size and muscle development with age.

CONCLUSION

CM 11255 is the smallest recognized skull of *Diplodocus*. It shares several synapomorphies with adult skulls, but the presence of unfused parietal bones and the small size of the specimen (60% of the anteroposterior length of the adult skull CM 11161) indicate that it pertains to a juvenile individual. Unique to this individual are the extreme posterior position of the distal-most tooth in the maxillary tooth row and the rounded dental arcade, in contrast to the squared snout and anteriorly sequestered tooth row in adults. The larger sub-adult *Diplodocus* CM 3452 strongly resembles CM 11255 in both conditions, and it is hypothesized that juvenile and sub-adult individuals of *Diplodocus* share a facial morphology that is distinct from that of adults, particularly with regard to the tooth bearing elements and the dental arcade. Similar morphologies (rounded vs. blunt snouts) have been shown to be related to food gathering in mammals. The

condition in *Diplodocus* indicates ontogenetic niche partitioning, as has been suggested for *Camarasaurus* and tyrannosaurid theropods. Juvenile and sub-adult *Diplodocus* appear to have been selective browsers, whereas square-snouted adults were likely low-height non-selective browsers, similar to what has been proposed for the diplodocoids *Brachytrachelopan* (Rauhut et al., 2005), *Dicraeosaurus* (Upchurch and Barrett, 2000; Barrett and Upchurch, 2005), and *Nigersaurus taqueti* (Sereno et al., 2007).

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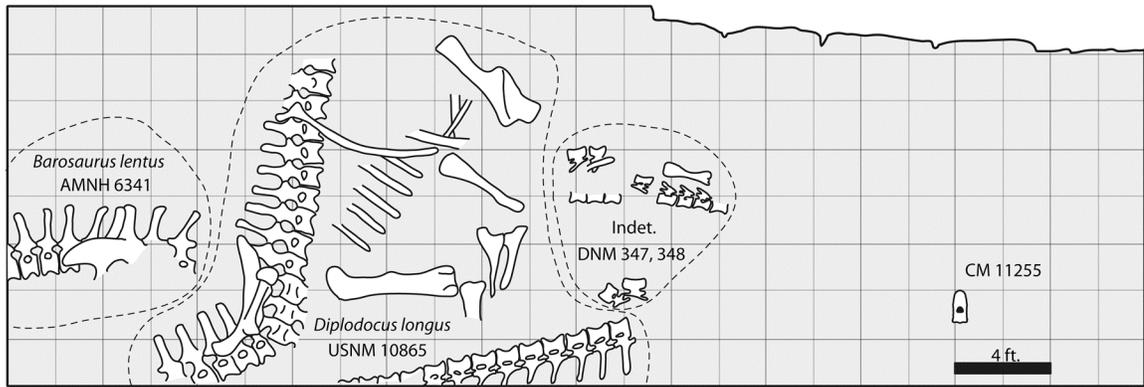
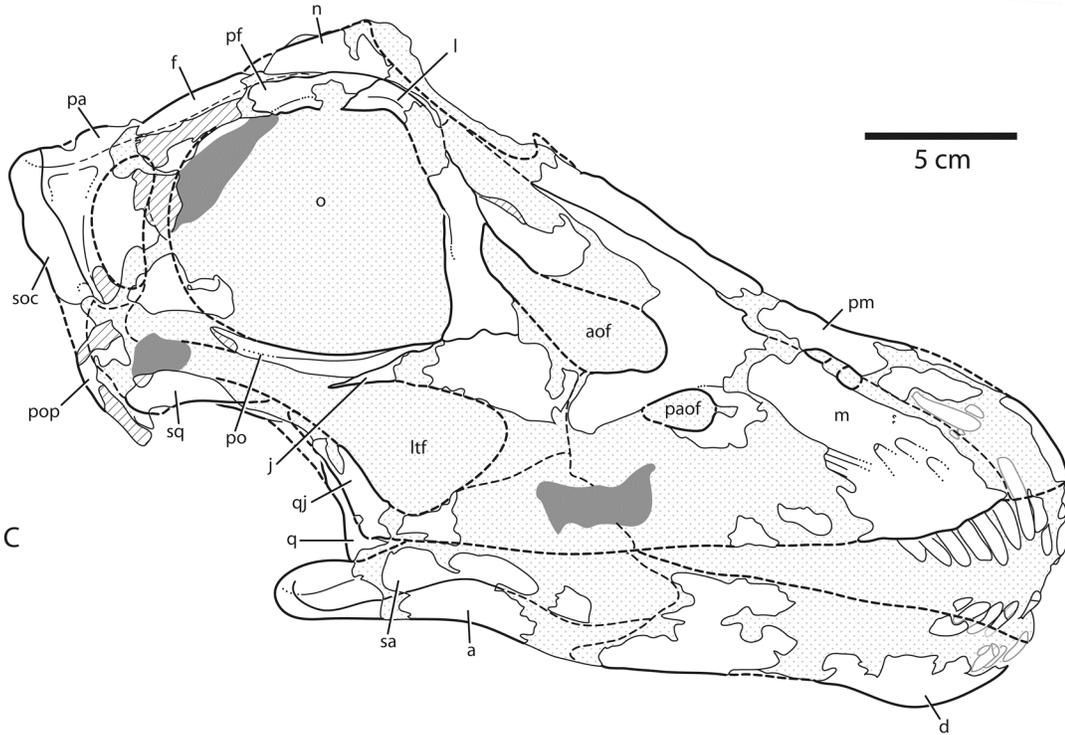


Figure 6.1. Quarry map showing the original location of the juvenile *Diplodocus* skull (CM 11255) relative to other dinosaurs excavated from Carnegie Quarry at Dinosaur National Monument. Redrawn from original quarry map at Carnegie Museum of Natural History. North at top of figure; grid lines are two feet (~0.61 m) apart.

Figure 6.2 (Next two pages). Photographs and interpretive line drawings of the juvenile skull of *Diplodocus* (CM 11255). A, B, right lateral view; C, D, left lateral view. Stippled areas indicate matrix; hatching indicates broken bone. Scale bar equals 5 cm. Abbreviations: a, angular; aof, antorbital fenestra; bo, basioccipital; d, dentary; eo, exoccipital-opisthotic; f, frontal; j, jugal; ltf, lateral temporal fenestra; l, lacrimal; m, maxilla; mc, Meckelian canal; n, nasal; o, orbit; os/l, orbitosphenoid/laterosphenoid; pa, parietal; paof, preantorbital fenestra; pf, prefrontal; pm, premaxilla; po, postorbital; pop, paroccipital process; ps, parasphenoid; psaf, posterior surangular foramen; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; soc, supraoccipital; spl, splenial; sq, squamosal.



A



C

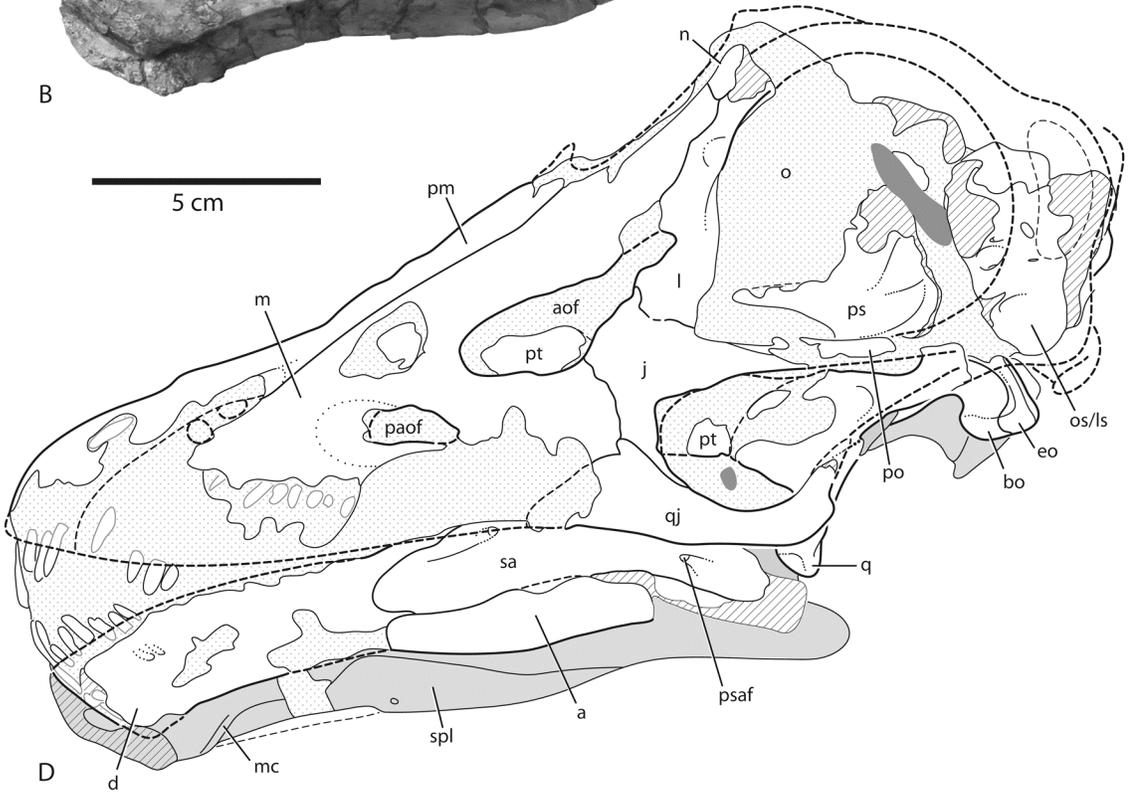


Figure 6.3 (Facing page). Photographs and interpretive line drawings of the skull of *Diplodocus* (CM 11255). A, C, anterior view; B, D, posterior view. Stippled areas indicate matrix, hatching indicates broken bone. Scale bar equals 5 cm. Abbreviations: a, angular; bo, basioccipital; bt, basal tubera; btp, basipterygoid processes; d, dentary; eo, exoccipital-opisthotic; f, frontal; l, lacrimal; m, maxilla; mc, Meckelian canal; n, nasal; os/l, orbitosphenoid/laterosphenoid; pa, parietal; pf, prefrontal; po, postorbital; popr, paroccipital process; pm, premaxilla; ps, parasphenoid; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; soc, supraoccipital.

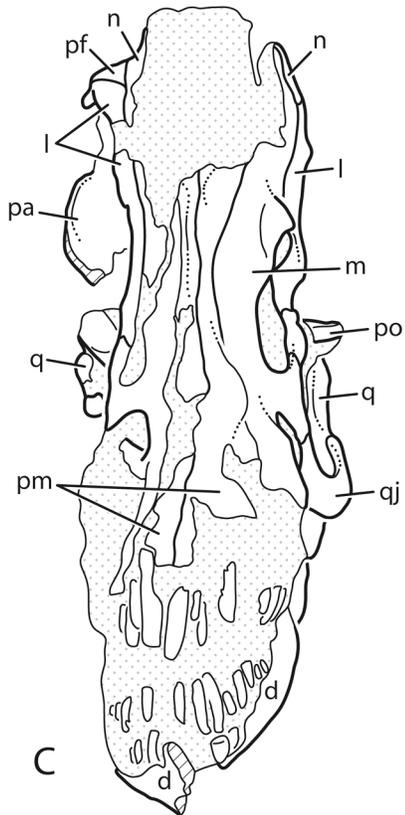


A

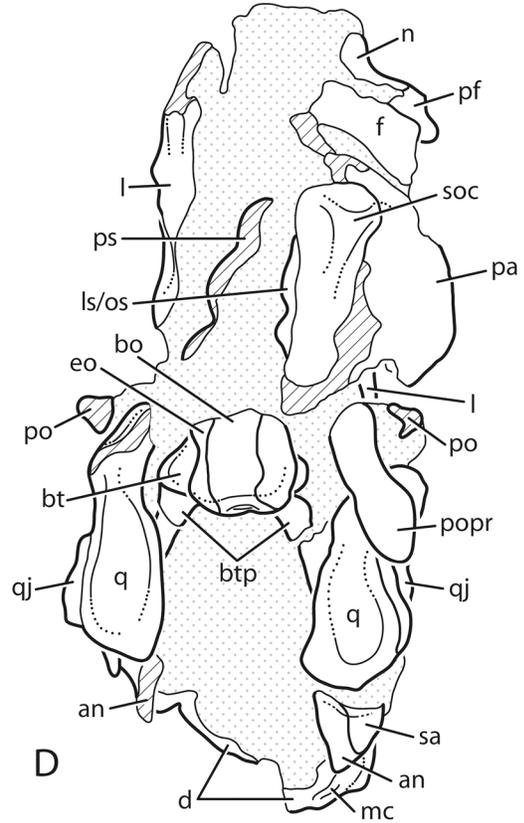


B

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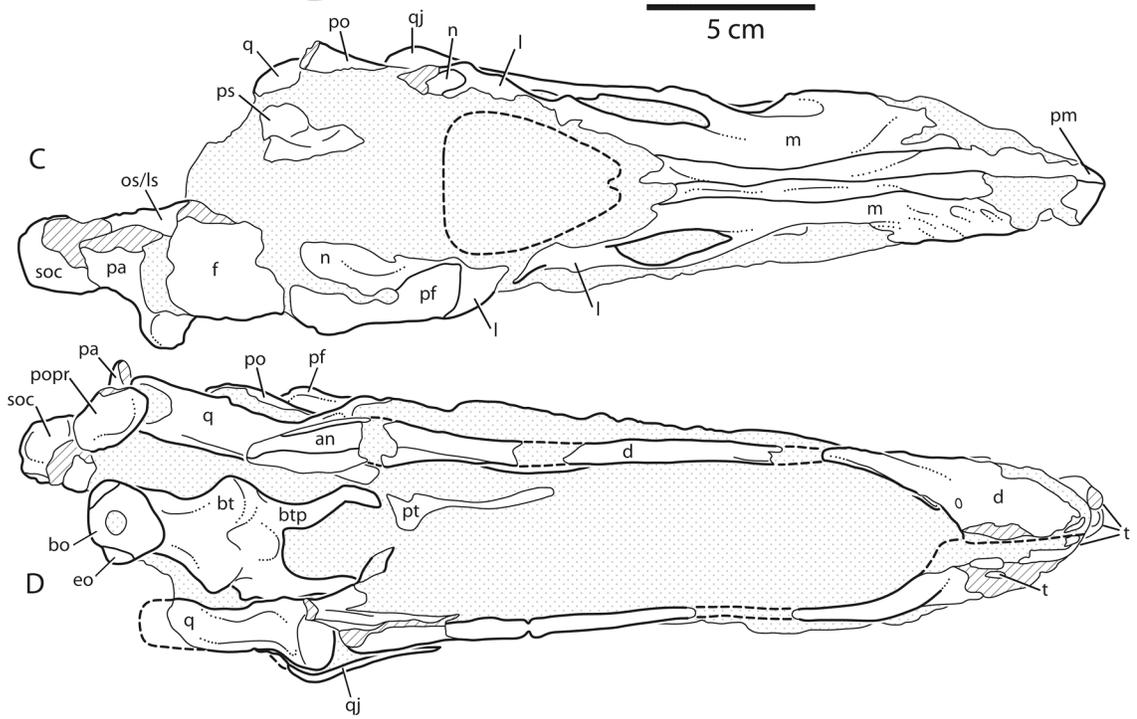


C



D

Figure 6.4 (Facing page). Photographs and interpretive line drawings of the juvenile skull of *Diplodocus* (CM 11255). A, C, dorsal view; B, D, ventral view. Stippled areas indicate matrix, hatching indicates broken bone. Scale bar equals 5 cm. Abbreviations: a, angular; bo, basioccipital; bs, basisphenoid; bt, basal tubera; btp, basipterygoid processes; d, dentary; eo, exoccipital-opisthotic; f, frontal; l, lacrimal; m, maxilla; n, nasal; nf, nuchal fossa; os/l, orbitosphenoid/laterosphenoid; pa, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; popr, paroccipital process; pt, pterygoid; q, quadrate; qj, quadratojugal; soc, supraoccipital; t, teeth.



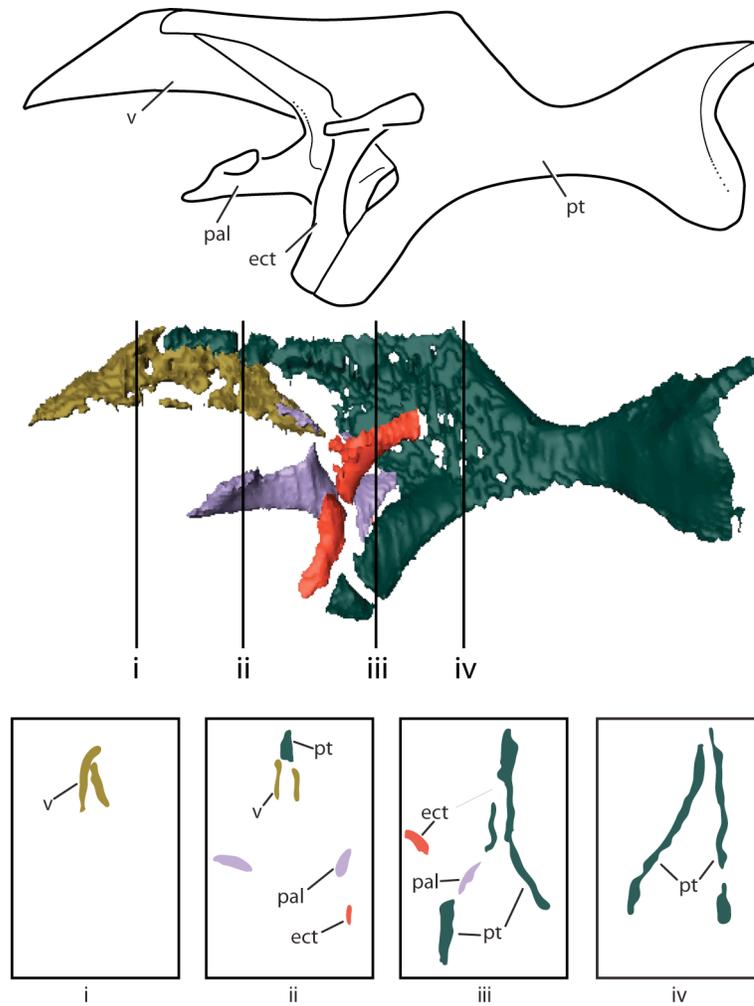


Figure 6.5. Palatal complex of juvenile *Diplodocus* (CM 11255), based on data obtained using computed tomography (CT) scanning. A, Reconstruction of the palate in left lateral view; B, palatal complex in lateral view; C, Cross sections taken through B at transects i–iv. Cross-sections in anterior view. Scale bar equals 5 cm. Abbreviations: ect, ectopterygoid; pal, palatine; pt, pterygoid; v, vomer.

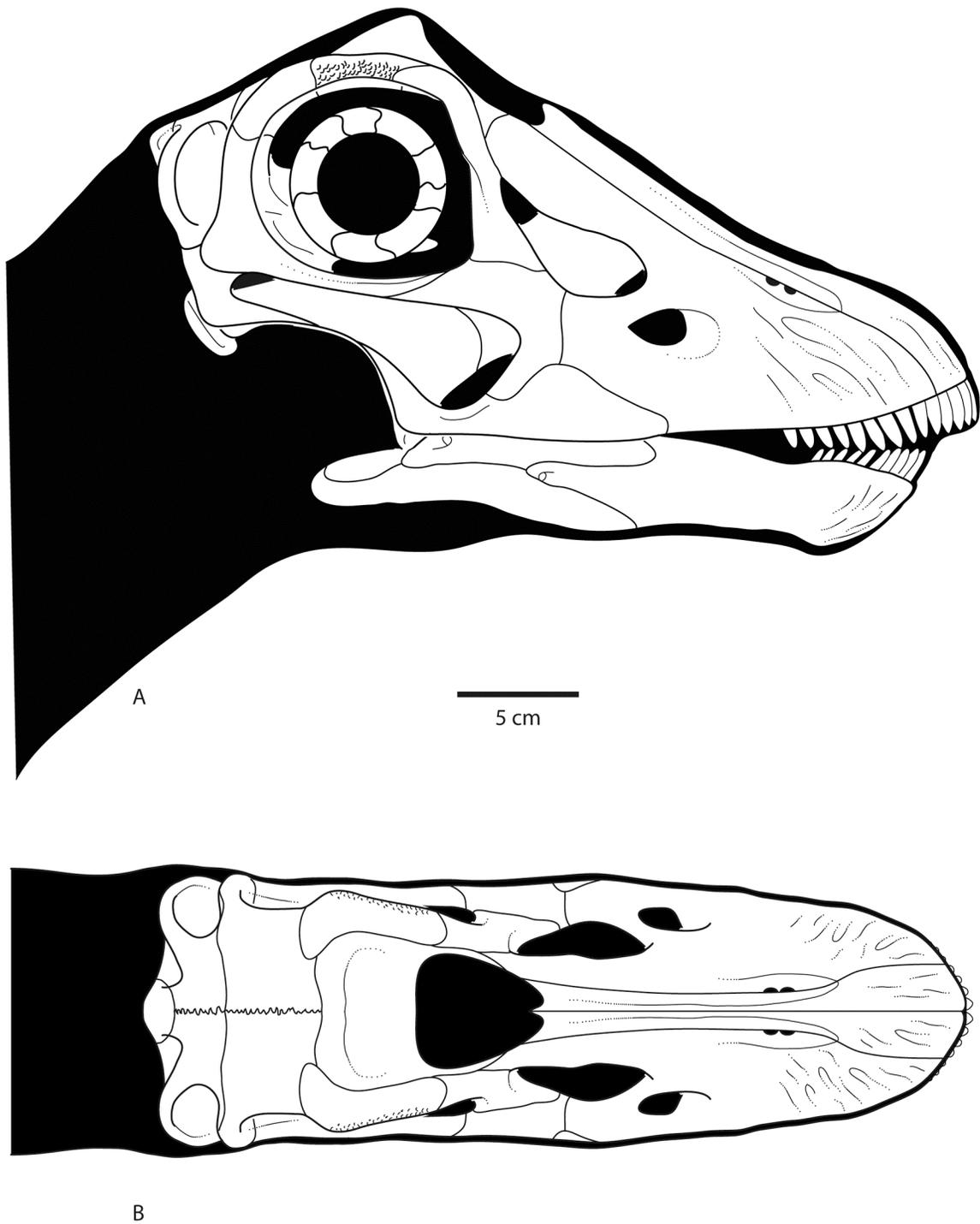
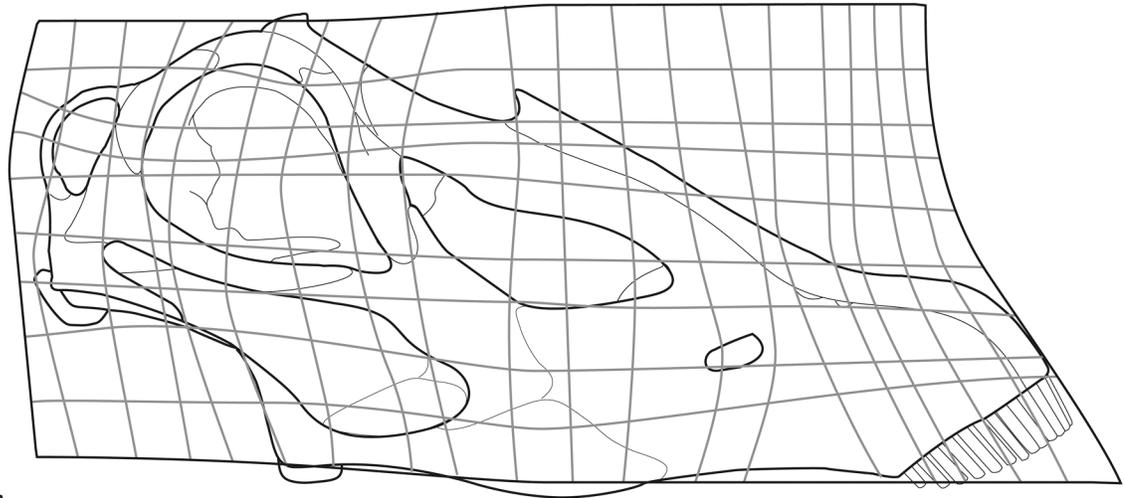
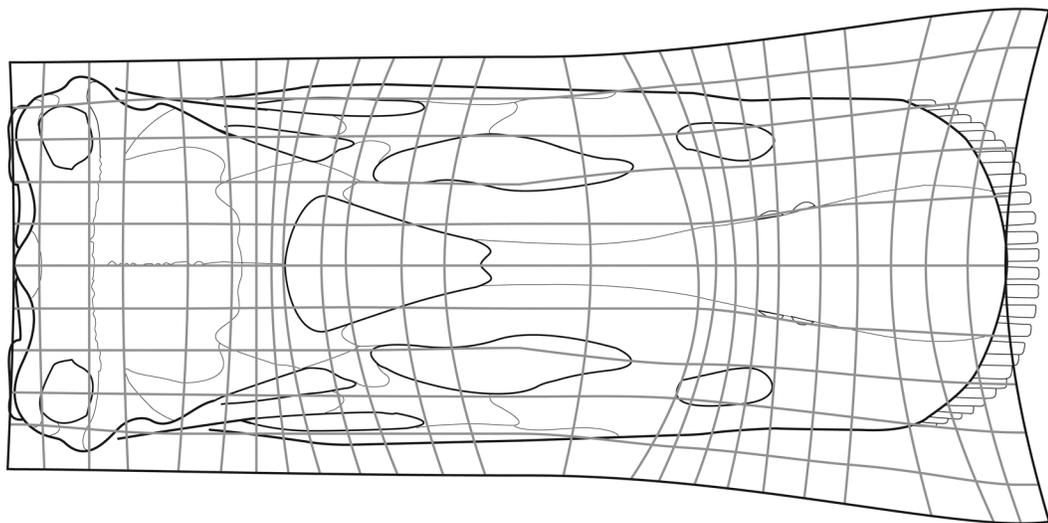


Figure 6.6. Reconstruction of CM 11255. A, lateral view; B, dorsal view. Scale bar equals 5 cm.



A



B

Figure 6.7 Transformation grids based on sutures and other landmarks showing the regions of the Diplodocus skull that underwent the greatest amount of shape change through ontogeny. Grids based on Fig. 6 and a reconstruction of the adult skull of Diplodocus (Wilson and Sereno, 1998:fig. 6). A, lateral view; B, dorsal view.

Table 6.1. Described sauropod taxa known from cranial elements, not including taxa known solely from teeth.

Category	Genus	Material	Key Reference
Non-Neosauropods	<i>Archaeodontosaurus</i>	jaw fragment	Buffetaut, 2005
	<i>Chebsaurus</i>	skull fragments	Mahammed et al., 2005
	<i>Chinshakiangosaurus</i>	partial dentary	Upchurch et al., 2007
	<i>Datousaurus</i>	jaw fragments	Dong and Tang, 1984
	<i>Gongxianosaurus</i>	jaw fragment	He et al. 1998
	<i>Lamplughsauro</i>	partial skull	Kutty et al., 2007
	Lufeng taxon	partial maxilla	Barrett, 1999
	<i>Mamenchisaurus</i>	several partial skulls	Ouyang and Ye, 2002
	<i>Omeisaurus</i>	three partial skulls	He et al., 1988; Tang et al., 2001
	<i>Patagosaurus</i>	jaw fragments	Bonaparte, 1979; Rauhut, 2003
Diplodocoids	<i>Shunosaurus</i>	at least five partial skulls	Chatterjee and Zheng, 2002
	<i>Tazoudasaurus</i>	partial braincase, jaw fragments	Allain and Aquesbi, 2008
	<i>Amargasaurus</i>	braincase	Salgado and Bonaparte, 1991
	<i>Apatosaurus</i>	multiple braincases, nearly complete skull	Berman and McIntosh, 1978
	<i>Dicraeosaurus</i>	two braincases, jaw fragments	Janensch, 1935-36
	<i>Diplodocus</i>	multiple adult and sub-adult skulls	Holland, 1924
	<i>Limaysaurus</i>	braincase	Calvo and Salgado, 1995
	<i>Nigersaurus</i>	nearly complete skull	Sereno et al., 1999
	<i>Suuwassea</i>	braincase, jaw fragments	Harris, 2006
	<i>Tornieria</i>	braincase, possibly jaw fragments	Remes, 2006, 2009
Macronarians	<i>Abrosaurus</i>	skull	Ouyang, 1989
	<i>Ampelosaurus</i>	partial braincase	Le Loeuff, 1995
	<i>Antarctosaurus</i>	braincase, partial dentary	Huene, 1929
	<i>Atlasaurus</i>	braincase, jaw fragments	Monbaron et al., 1999
	Auca Mahuevo taxon	multiple embryonic skulls	Chiappe et al., 2001

Category	Genus	Material	Key Reference
Macronarians (cont.)	<i>Bonatitan</i>	braincase	Martinelli and Forasiepi, 2004
	<i>Bonitasaura</i>	partial skull	Apesteguía, 2004
	<i>Brachiosaurus</i>	at least three partial skulls	Janensch, 1935-36
	<i>Camarasaurus</i>	multiple adult and sub-adult skulls	Madsen et al., 1995
	<i>Euhelopus</i>	nearly complete skull	Wiman, 1929
	<i>Europasaurus</i>	at least 11 partial skulls	Sander et al., 2006
	Glen Rose taxon	partial braincase	Tidwell and Carpenter, 2003
	<i>Isisaurus</i>	partial braincase	Berman and Jain, 1982
	<i>Jainosaurus</i>	partial braincase	Huene and Matley, 1933
	<i>Jobaria</i>	partial adult skull and sub-adult braincase	Sereno et al., 1999
	<i>Lirainosaurus</i>	braincase fragment	Sanz et al., 1999
	? <i>Magyarosaurus</i>	braincase	Weishampel, 1991
	<i>Malawisaurus</i>	braincase, other dermal skull fragments	Gomani, 2005
	<i>Nemegtosaurus</i>	nearly complete skull	Nowinski, 1971; Wilson, 2005
	<i>Neuquensaurus</i>	skull fragments	Huene, 1929
	Neuquén taxon	partial braincase	Calvo and Kellner, 2006
	<i>Paluxysaurus</i>	skull fragments	Rose, 2007
	<i>Phuwiangosaurus</i>	jaw fragments	Martin et al., 1999
	<i>Qaesitosaurus</i>	partial skull	Kurzanov and Bannikov, 1983
	<i>Rapetosaurus</i>	partial adult and sub-adult skulls	Curry Rogers and Forster, 2004
Río Negro taxon	partial braincase	García et al., 2008	
<i>Saltasaurus</i>	partial braincase	Bonaparte and Powell, 1980	

CHAPTER 7

TOOTH REPLACEMENT PHENOMENA IN SAUROPOD DINOSAURS

Polyphyodonty, the condition of having continuous tooth replacement, has been recognized in most non-mammalian vertebrates for over 150 years (Owen, 1840-1845). One important expression of this phenomenon is in the dentition of herbivorous dinosaurs, where multiple age classes within a single tooth family (a functional tooth and all its replacement teeth) may sometimes be functional at the same time (Lambe, 1917; Edmund, 1960; Sereno and Wilson, 2005). In ornithischian dinosaurs, the transition to rapid replacement precedes the development of a tooth battery (a single functional dental unit composed of many smaller constituent teeth) independently in two lineages, and is well documented as part of an overall trend in cranial modification for herbivory, including the development of beaks and cheeks (Sereno, 1986).

Tooth replacement in sauropod dinosaurs is less well understood, however, which may be due in part to the popular conception that sauropod feeding behavior was “simple and stereotyped” (Barrett and Upchurch, 2005b: 126; n.b., those authors argue against that perception), which was in turn driven by the recognition of the typically spartan skull design in these animals (Chure et al.,

2010). However, long-term trends in tooth shape—the development of both increasingly broad and an increasingly narrow crowns by the Late Jurassic, both of which persist throughout the Early Cretaceous, followed by the extinction of broad crowns and the evolution of narrow crowns from broad-crowned ancestors—indicate that sauropod dentitions were variable and prone to selection by multiple forces (Fig. 7.1; Chure et al., 2010). One potential selective advantage for the development of broad, spatulate tooth crowns is an increase in oral processing efficiency (e.g., Barrett and Upchurch, 2005b: 141). However, sauropod-line sauropodomorphs lost a fleshy cheek, which enable animals to keep a food item near the chewing surface, early in their evolution (Upchurch et al., 2007), limiting the effectiveness of any oral processing that may have occurred in these organisms. The enlarged, spatulate teeth developed by basal eusauropods were subsequently lost in two clades of derived sauropods, where dentitions were reduced to a set of small, narrow-crowned teeth. This second trend has in turn been suggested to be related to trends in tooth replacement rate (Chure et al., 2010), inasmuch as tooth development time (and thus replacement rate) is limited by the rate of dentine apposition—smaller teeth can be grown faster, although this correlation has not yet been demonstrated for sauropods.

Both the initial increase in tooth size and the subsequent reduction in size seen in more derived taxa may be seen as different biological responses to the same stimulus: elevated rates of tooth wear. Erickson (1996b) recognized two potential biological responses to increased tooth wear: increased tooth longevity,

typically via increased tooth crown volume, or increased dentine formation rate (i.e., increased replacement rate). Sauropods may have responded in both ways at various points in their evolutionary history, and because longevity and replacement rate are inversely related it is likely that the two observed responses are also linked. In order to understand the evolution of sauropod dentitions, both trends must be quantified and examined in a phylogenetic context. Although tooth shape data have been compiled for nearly 100 sauropod taxa (Chure et al., 2010: electronic supplemental material [esm] 6), replacement rates have been estimated for only one taxon, the highly derived *Nigersaurus* (ca. 30 days; Sereno et al., 2007). Here, replacement rates are calculated for two neosauropod dinosaurs, the narrow-crowned *Diplodocus* and the broad-crowned *Camarasaurus*, and estimated for four additional sauropodomorph taxa (*Mamenchisaurus*, *Massospondylus*, *Shunosaurus*, and the Río Negro titanosaur). These data represent all major clades in Sauropodomorpha and will be combined with available tooth shape data to determine which, if any, of Erickson's (1996b) biological responses were potential influences on morphology throughout sauropodomorph evolution.

QUANTIFYING RATES OF REPLACEMENT

Studies of mammal (Schour and Steadman, 1935) and crocodile teeth (Erickson, 1996a) have revealed the existence of regular laminations in that have been shown to represent daily increments of growth via tetracycline labeling in extant

taxa (Erickson, 1996b; FitzGerald, 1998; Smith et al., 2006). This daily growth continues uninterrupted until the tooth is completely grown. The resultant lines, termed incremental lines of von Ebner, can be counted much like tree rings to determine tooth development time, and the difference in line counts between successive teeth within an alveolus represents tooth replacement rate (Fig. 7.2).

Incremental lines of von Ebner have been reported in multiple archosaur taxa, including representatives of Crocodylia (*Leidyosuchus*, *Alligator*), Saurischia (*Deinonychus*, *Troodon*, *Albertosaurus*, *Tyrannosaurus*), and Ornithischia (*Edmontonia*, *Triceratops*, *Prosaurolophus*, *Maiasaura*, *Edmontosaurus*) (Erickson 1996a,b; Straight et al., 2004), although only a single sauropodomorph (the derived neosauropod *Nigersaurus*) has been sampled (Sereno et al., 2007).

Erickson (1996b) published replacement rates for several dinosaurs using counts of incremental lines. In that study, replacement rate was found to be highly correlated with diet: carnivorous theropod dinosaurs had replacement rates on yearly time scales (290–777 days), herbivorous ornithischians had much more rapid replacement, on monthly time scales (50–83 days), even in cases where tooth formation time is equivalent (e.g., *Albertosaurus* and *Edmontosaurus*; Erickson, 1996b). Erickson (1996b) concluded that rapid replacement evolved in concert with the development of a tooth battery to combat heavy wear caused by a silica-rich plant diet.

More recently, the first rate for a sauropod dinosaur, *Nigersaurus*, was published (Sereno et al., 2007). This rate of replacement, approximately every 30

days, is the fastest rate yet reported—faster even than the fastest replacing ornithischians, which developed both fast replacement and a fully-formed tooth battery in response to tooth wear. *Nigersaurus* was relatively diminutive by sauropod standards and would have been similar in size to larger ornithischians, and had a tooth battery of its own (Sereno and Wilson, 2005; Sereno et al., 2007).

PATTERNS OF REPLACEMENT

In reptiles, it has long been noted that teeth typically replace in an alternating pattern, such that all odd-numbered teeth replace at approximately the same time, as do even-numbered teeth (Röse, 1893; Edmund, 1960; Stevens and Presch, 1979). However, subtle differences in the timing of those replacements between mesial and distal teeth suggested to Edmund (1960) that this pattern of replacement happens in ‘waves’ or ‘Zahnreihen’, such that tooth germination propagates from distal to mesial, or, rarely, from mesial to distal. In crocodyliforms, but apparently not other archosaurs, the consistency of Zahnreihen diminishes with age, and in some cases the directionality of the waves reverses (Edmund, 1960).

Tooth replacement phenomena have not been discussed for many sauropod dinosaurs, due in part to the rarity of skulls with intact dentitions. Janensch (1935-36), examining the degree of wear on intact dentitions of *Brachiosaurus brancai*, demonstrated what is most likely a back-to-front pattern

of alternate replacement in that taxon. White (1958) noted what he considered a front-to-back pattern in *Camarasaurus*, although Zheng (1996), in his re-examination of that material, found that *Camarasaurus* conformed to the standard back-to-front replacement pattern. Galton (1985) discussed replacement in the basal sauropodomorph *Plateosaurus*, noting the presence of one replacement tooth per alveolus and multiple Zahnreihen in each element (e.g., maxilla, dentary). Gow et al. (1990) briefly discussed replacement in *Massospondylus*, noting that it must have been rapid because of the lack of heavily worn teeth, but did not discuss the number of replacement teeth per alveolus. Chatterjee and Zheng (2002) found a back-to-front replacement pattern in the basal eusauropod *Shunosaurus*. Wilson (2005) and Whitlock and Harris (in press) demonstrated a pattern of alternate replacement in *Nemegtosaurus* and *Suuwassea*, respectively, but could not determine the directionality of Zahnreihen.

MECHANISMS OF REPLACEMENT

Derived sauropods developed a slightly modified version of the mechanism by which most archosaurs physically replaced their worn-out teeth. The ancestral condition, present in crocodyliforms, basal sauropodomorphs and theropods, is the development of replacement teeth in a resorption pit in the root of the functional tooth, on the lingual surface (Edmund, 1960). In crocodyliforms only, the replacing teeth physically intrude upon and enter the pulp cavity of the

functional tooth (Edmund, 1960). As replacing teeth grow, they eventually either resorb the entire root, leaving only the easily shed crown (crocodyliforms), or force the functional tooth up and out of the socket (theropods, prosauropods). Taxa where replacement teeth invade the pulp cavity of functional teeth typically have only a single replacement tooth per alveolus (Edmund, 1960), although in rare cases there may be two (e.g., *Allosaurus*; Edmund, 1960).

The condition in derived sauropods appears to be most similar to that of basal ornithischians (those without dental batteries), in which teeth move labially as they develop (Marsh, 1896; Holland, 1924; Edmund, 1960; Coria and Chiappe, 2001). As a tooth reaches the end of its functional life cycle, the next tooth pushes the worn-out tooth out of the alveolus and replaces it; as suggested by Coria and Chiappe (2001) this is likely a function of the growing replacement teeth pressing against the lingual wall of the functional tooth, the slightly conical shape of the tooth forcing the mature tooth anteriorly and out of the socket. Eusauropods have at least two (basal eusauropods; Ouyang and Ye, 1998) and commonly three or more replacing teeth per alveolus (neosauropods; Marsh, 1896; Coria and Chiappe, 2001)

ABBREVIATIONS

Institutions. IPB H, Goldfuß Museum of Palaeontology, University of Bonn, Bonn; MPCA, Museo Provincial Carlos Ameghino, Cipolletti; MPEF-PV, Museo Paleontológico Egidio Feruglio, Trelew; PVL, Colección de Paleontología de

Vertebrados de la Fundación Miguel Lillo, Tucumán; SAM-PK-K, Iziko South African Museum, Capetown; UMNH and UUVP, University of Utah Museum of Natural History, Salt Lake City; YPM, Yale Peabody Museum, New Haven.

MATERIALS AND METHODS

Replacement teeth from the premaxillae of two neosauropod dinosaurs, *Camarasaurus* (UUVP 3999) and *Diplodocus* (YPM 4677) were removed from each element. These teeth were then embedded in clear epoxy, and thin-sectioned along their long axis. Thin sections were examined at magnification and photographed using a Spot CCD camera (Spot Insight 11.2 Color Mosaic, Diagnostic Instruments) mounted on a Nikon SMZ 1500 microscope. Increment counts and thicknesses were calculated in ImageJ (Rasband, 1997–2009) using the IncMeas v1.11 plug-in (Rountrey, 2009). Replacement rates were calculated by subtracting the total number of incremental lines of von Ebner in a tooth from the number in the tooth preceding it (e.g., tooth A – tooth B = replacement rate), averaged over multiple sequential pairs.

The basal sauropodomorphs *Massospondylus* (maxilla, SAM-PK-K402; dentary, SAM-PK-K39) and *Plateosaurus* (dentary, IPB H 161) were μ CT scanned and the number and size of replacement teeth were quantified in each taxon, in order to estimate replacement rate (see below). Additional estimates of replacement rate were taken from published figures of a basal sauropod (*Shunosaurus*; Zheng, 1996), a basal eusauropod (*Mamenchisaurus*; Ouyang

and Ye, 2002), and a putative narrow-crowned titanosauriform (the Río Negro taxon; Coria and Chiappe, 2001). Although the identification of the Río Negro taxon as a titanosauriform (as opposed to a diplodocoid) is tentative, it is considered a titanosauriform here for two reasons: first, the Río Negro taxon has anteroventrally elongate (greater than 2:1 length:width ratio) replacement foramina on the ventral surface of the premaxilla, a character it shares with the titanosauriform *Nemegtosaurus* (Wilson, 2005) but not diplodocoids or basal macronarians, which have subcircular replacement foramina (pers. obs.); second, although Río Negro Province has provided many new neosauropod taxa (e.g., *Aeolosaurus*, *Antarctosaurus*, *Bonatitan*, *Bonitasaura*, “*Laplatasaurus*”), no non-titanosauriforms have been identified there (Salgado and Bonaparte, 2007). Replacement rates in these five taxa are estimated using a metric termed the height-corrected ratio (HCR). The HCR is calculated as:

$$\frac{\sum \left(\frac{H_1}{H_m}, \frac{H_2}{H_m} \dots \frac{H_x}{H_m} \right)}{H_m} \times \frac{1cm}{H_m}$$

where $H_1, H_2 \dots H_x$ are the heights of replacement teeth and H_m is the maximum height of a mature tooth (both in cm). The H_m term removes the influence of crown size: the time to finish building a 100 mm tooth that is 75% complete is not the same as that required of a 75% complete tooth that is 200 mm tall. When absolute height is corrected for, the closer in size successive teeth are, the smaller the gap in time between their initiations on the dental lamina and therefore the faster the replacement rate and the higher the HCR. This is a

qualitative measure only, and is probably not powerful enough to predict replacement rate in days.

Two elements, a dentary belonging to the basal eusauropod *Patagosaurus* (MPEV-PV 1670; Rauhut, 2003) and a premaxilla assigned to *Laplatasaurus* (PVL 3670-12; Powell, 1979), are discussed below but were not directly examined for replacement rate. Although replacement teeth are exposed in both elements, the teeth are either too damaged (PVL 3670-12) or incompletely exposed (MPEF-PV 1670), making a realistic estimate of the relative lengths impossible.

Premaxillary teeth were labeled using two positional descriptors: tooth family (e.g., the alveolus; Arabic numerals), ranging from 1 (the most mesial) to 4 (the most distal); and tooth position within the family (lower case Roman numerals), beginning with i (the first replacement tooth) and continuing to the youngest replacement tooth present (Fig 7.3). Thus, the third tooth in the second family would be tooth 2-iii.

RESULTS

Tooth replacement rate, formation time, number of replacement teeth per alveolus, and incremental line thicknesses are reported for *Diplodocus* and *Camarasaurus*. Qualitative estimates of tooth replacement rate are given for *Massospondylus*, *Shunosaurus*, *Mamenchisaurus*, *Nigersaurus* and the Río

Negro taxon. Estimates could not be obtained for *Plateosaurus*, due to the lack of visible replacement teeth in that specimen.

DIPLODOCUS

Average replacement time for the four pairs of consecutive teeth was 35 days, with a range of 32–38 days (Fig. 7.4). The HCR score for *Diplodocus* is 1.2 (Table 7.1). No results are reported from tooth family 2, because damage to the tip of tooth 2-ii made estimates excessively speculative. Formation times for the two largest teeth (presumed to be fully grown) were 187 and 183 days. A maximum of six replacement teeth are present in each alveolus. Average increment thickness is 16.14 μm , with a range of 13.73 μm in tooth 4-iii to 18.03 in tooth 4-i. Directionality of Zahnreihen is ambiguous, as different tooth positions (e.g. i, ii, iii) have different age relationships between mesial and distal teeth.

CAMARASAURUS

Average replacement time for the three pairs of replacement teeth is 62 days, with a range of 60–63 days (Figure 7.4). The HCR score (0.5) is lower than in *Diplodocus*, but greater than that of other spatulate crowned taxa like *Mamenchisaurus* (Table 7.1). Formation time for the largest tooth, which was moving into function position at the time of death and bears a small wear facet, was 315 days. As many as four replacement teeth may have been present; the imbrication of replacement teeth (see *Tooth packing*, below) within the jaw makes assigning teeth to a specific family difficult at small sizes. Average increment

thickness is 14.82 μm , with a range of 14.18 μm in tooth 4-iii to 15.76 in tooth 4-iv.

MASSOSPONDYLUS AND PLATEOSAURUS

Replacement teeth in both *Massospondylus* and *Plateosaurus* were rare, identifiable in only a single alveolus in the dentary of *Massospondylus* (SAM-PK-K39) and absent elsewhere. It is probable that the remaining replacement teeth were too small to be observable using μCT . The observed replacement tooth was much smaller than the functional tooth whose root it partially inhabits (38%). The small relative size of this replacement tooth, combined with the inferred smaller size of replacement teeth at earlier stages of development, suggests that a maximum of one replacement tooth was present per alveolus in both *Massospondylus* and *Plateosaurus*. The HCR score for *Massospondylus* is (22).

SHUNOSAURUS

Based on figures and measurements in Zheng (1996) and Chatterjee and Zheng (2002), replacement teeth in *Shunosaurus* are approximately 15% of functional teeth by length. HCR in *Shunosaurus* is approximately 0.2 (Table 7.1), indicating a slower replacement rate than is observed in *Camarasaurus*.

MAMENCHISAURUS

The replacing teeth figured by Ouyang and Ye (2002: fig. 12) in the premaxilla of *Mamenchisaurus* are approximately 31% of the preceding teeth by length. The HCR in this taxon is similar to that of *Camarasaurus* (0.4; Table 7.1), indicating that the rate of replacement was similar in both taxa, although slightly slower in *Mamenchisaurus*.

NIGERSAURUS

As reported by Sereno et al. (2007), *Nigersaurus* has the fastest known replacement rate of any dinosaur (ca. 30 days). Replacing teeth are similar in size to each other (89% by height), and the HCR is 1.9, the highest score for a sauropod, and the second highest for a sauropodomorph (Table 7.1).

RÍO NEGRO TAXON

Coria and Chiappe (2001) figured the premaxilla of an unnamed narrow-crowned titanosauriform from Río Negro Province, Argentina. Three replacing teeth were visible in CT images; based on the great similarity in heights (ca. 85% of the preceding tooth) between successive teeth and the size of the third replacement tooth, it is probable that at least one additional replacement tooth was present in life for a total of four (pers. obs.). HCR for the Río Negro taxon is 1.6, within the range of scores seen in diplodocoids (Table 7.1).

DISCUSSION

REPLACEMENT RATES

Rates of replacement in neosauropod dinosaurs appear to have been at least as fast as in other dinosaurian herbivores, and in narrow-crowned taxa such as *Diplodocus* and *Nigersaurus*, up to twice as fast. HCR scores also suggest faster replacement rates in narrow-crowned taxa relative to broad-crowned taxa. This trend towards faster replacement, coupled with trends in tooth size and shape, may illustrate a series of adaptations to herbivory, by increasing tooth longevity and increasing dentine formation rate.

Phylogenetic trends in replacement rates and tooth shape

Plotting tooth shape and replacement rate data on a simplified cladogram (Fig. 7.5) reveals a potential phylogenetic signal. The transition from taxa at the base of Sauropodomorpha, such as *Massospondylus* and *Plateosaurus*, to more derived taxa is marked by the development of spatulate tooth morphology. Such crowns have previously been recognized as a synapomorphy of Eusauropoda (Wilson, 2002), but new discoveries of basal sauropods as *Tazoudasaurus* (Allain and Aquesbi, 2008) and *Gongxianosaurus* (Luo and Wang, 2000) pull the development of that character down to at least the clade Sauropoda (Fig. 7.5). In the Middle Jurassic, some eusauropod taxa, such as cf. *Cetiosauriscus* (BMNH R3377; Barrett, 2006) and *Turiasaurus* (Royo-Torres et al., 2006), continued this trend by increasing crown breadth further (Fig. 7.1; Chure et al., 2010: esm 5, 6).

Within Neosauropoda, at least two secondary reductions in crown breadth occur: once in Diplodocoidea, and once within Titanosauriformes (Fig. 7.5).

The initial increase in tooth size that occurred at or around the node Sauropoda appears to have been accompanied by a reduction in replacement rate—the much smaller crowns of basal sauropodomorphs like *Massospondylus* grew (and thus were replaced) much faster than the larger crowns of taxa like *Shunosaurus*, as indicated by the HCI scores for those taxa. The rate implied by *Massospondylus*'s HCI is probably a reasonable estimate of rate for basal sauropodomorphs. Crown height in this specimen (66 mm) is lower than the largest observed crowns in *Massospondylus* and *Plateosaurus*, which are commonly in above 10 mm (e.g. Galton, 1985; Gow et al., 1990), but is substantially larger than the crowns of taxa such as *Pantyraco* (Yates, 2003) and *Saturnalia* (Langer et al., 1999).

The first increase in sauropod tooth replacement rate occurs somewhere within Eusauropoda, as inferred from an increase in the number of replacing teeth in an alveolus (Fig. 7.5). Basal sauropodomorphs, such as the 'prosauropods' *Plateosaurus* (IPB H 161) and *Massospondylus* (SAM-PK-K396, SAM-PK-K402), the sauropod *Tazoudasaurus* (Allain and Aquesbi, 2008), and the basal eusauropod *Shunosaurus* (Zheng, 1996; Chatterjee and Zheng, 2002) had only one replacement tooth per alveolus. More derived eusauropods such as *Mamenchisaurus* (Ouyang and Ye, 2002) and *Patagosaurus* (MPEF-PV 1670) had up to two replacement teeth per alveolus. A second increase in replacement

rate is observable in the Late Jurassic neosauropod radiation, as evidenced by the presence of at least three replacement teeth per alveolus (Fig. 7.5). *Camarasaurus*, despite having large, spatulate crowns, maintained as many as four replacement teeth per alveolus; it is likely that this represents the upper limit for replacement rate in broad-crowned sauropods. Additional increases in replacement rate may have occurred at least twice more, once within Diplodocoidea and probably again within Titanosauriformes. Diplodocoids had rapid tooth replacement (30–35 days), and given the similarity in HCR in narrow-crowned titanosauriforms (e.g., the Río Negro taxon, probably *Laplatasaurus*) to that in diplodocoids, it is likely that a high replacement rate was present in all narrow-crowned sauropods.

Why increase tooth size?

In sauropod dinosaurs, increased tooth volume is recognized by the presence of broad- or spatulate-crowned teeth. These crowns may be proportionally similar to or only slightly broader than the leaf-shaped teeth from which they evolved (Chure et al., 2010: Fig. 7.1), but their size in proportion to the skull is markedly increased (Upchurch and Barrett, 2000). The transition from leaf-shaped crowns to spatulate crowns in basal eusauropods appears to be roughly contemporaneous with (or lagging slightly) the transition from facultative herbivory in basal sauropodomorphs to obligate herbivory in sauropods (Barrett, 2000; Barrett and Upchurch, 2005b, Upchurch et al., 2007), suggesting that the

increase in tooth volume may be related to a change in feeding behavior, perhaps diet. A common biological response to increased reliance on herbivory (and thus wear rates) is to increase tooth volume, as seen in the hypsodont teeth of horses and other mammalian herbivores (e.g., Van Valen, 1960; Janis, 1988). It is probable that the evolution of spatulate tooth morphology in sauropods was a similar response to insufficient tooth longevity caused by wear.

Why decrease tooth size?

Narrow-crowned teeth evolved at least three times in derived sauropods: once in Diplodocoidea, once in the lineage leading to *Abydosaurus* (Chure et al., 2010), and a third time in the lineage (or lineages) leading to more derived Titanosauriformes (Fig. 7.5). Narrow crowns appear to have conferred an adaptive advantage over broad crowns late in the second half of sauropod evolution; during the Late Jurassic the sauropod trend of increasing tooth breadth reversed, and by the Late Cretaceous only narrow-crowned taxa remained (Chure et al., 2010; Fig. 7.1). Additionally, following the disappearance of diplodocoids from the record in the early Late Cretaceous, tooth crowns in titanosauriforms rapidly decreased in breadth, until they were similar in size to those of diplodocoids (Chure et al., 2010). Hadrosaur-level replacement rate (approximately bimonthly) was achieved by sauropods with broad-crowned teeth (e.g., *Camarasaurus*), which were also more resistant to wear than smaller teeth

by virtue of their larger volume. Why then, did both lineages of derived sauropods develop narrow-crowned teeth?

Erickson's (1996b) two biological responses to wear—increased tooth size and increased replacement rate—appear to be inversely related. Narrow crowns are more quickly replaced; dentine apposition rates across amniote taxa are relatively consistent (Erickson, 1996b), and so smaller crowns will form more rapidly than larger crowns. They will, however, wear out sooner than larger crowns. Tooth size and shape in sauropods, then, are the result of the interaction between these two competing responses—whichever is most biologically “important” at the time will hold the most influence.

A likely scenario is that those lineages that eventually developed narrow crowns were encountering even more abrasive browse than their broad-crowned relatives. If a large crown was unable to resist wear sufficiently, the crown would wear out before its time, and perhaps months would pass before it could be replaced. Replacing a tooth every month meant that an excessively worn crown would be ineffective for a much shorter length of time before being replaced.

For example, imagine a case of a diplodocoid (30 day rate) and a basal macronarian (60 day rate), for which wear rates exceed the functional life of a tooth for both taxa. The diplodocoid will produce 12 generations of teeth per year, compared to six for the macronarian. If the narrow-crowned tooth matches or exceeds just 51% of the functional life of a broad-crowned tooth (i.e., 29 functional days vs. 57 days) under similar wear conditions, the narrow-crowned

sauropod will have more functional days, per alveolus, than the broad crowned taxon. In this example, the diplodocoid would have 348 functional days per alveolus per year, compared to just 342 days per alveolus per year for the macronarian—a seemingly small difference that may nonetheless be significant for a multi-ton animal consuming large quantities of browse daily.

Increased wear rates may have been a result of a shift in diet. Some narrow-crowned taxa may have been low browsers (Chapter 5; Barrett and Upchurch, 2000; Sereno et al., 2007), a behavior that is related to increased ingestion of abrasive exogenous grit (e.g., Ungar, 1996). The sauropod most highly specialized for a low-browsing lifestyle, *Nigersaurus*, has the fastest known replacement rate of any dinosaur (Sereno et al. 2007). In contrast, sauropods with broader crowns, such as *Mamenchisaurus* and *Camarasaurus*, are thought to have been mid- to upper-canopy browsers, where exogenous grit is lower (Barrett and Upchurch, 2000; 2005). Some narrow-crowned sauropods, such as dicraeosaurids, were not low-browsers, however, and whether low-browsing or narrow crowns evolved first is uncertain (Chapter 5).

Because narrow crowns and low-height browsing appear at the same time in two different clades and never independently, it is possible that narrow crowns provide an adaptive advantage for that feeding habit. Because spatulate crowns were lost in low browsers, despite the increased grit intake due to their diet, it is also possible that larger crowns may actually have been maladaptive. If, as outlined above, wear rates in low-browsing taxa exceeded the replacement rate

of tooth crowns, narrow crowns may have been a biological response facilitating rapid replacement. A broader survey of wear patterns across Sauropoda and additional replacement rate data are necessary to fully test this hypothesis, however.

TOOTH PACKING AND REPLACEMENT PATTERNS

Similarly high numbers of replacement teeth in narrow-crowned and broad-crowned neosauropod dinosaurs necessitated some highly ordered packing to accommodate all of those teeth within the tooth-bearing elements. Because of the different relative sizes and shapes in each group, the packing was also different. Below, I discuss tooth packing in narrow- and broad-crowned sauropods, and the impact on replacement pattern in each.

Narrow-crowned sauropods. The tooth families in taxa with narrow-crowned teeth are organized in a regular fashion. As seen in the neosauropods *Diplodocus* (Holland, 1924; this study), *Nigersaurus* (Serenó et al., 2007), *Bonitasaura* (MPCA 300), *Laplatasaurus* (Powell, 1979), and the Río Negro taxon (MPCA-79), the teeth in each individual family line up in regular order, immediately lingual and slightly basal to the tooth that precedes it. Each successive tooth is significantly smaller than the tooth it will eventually replace. A lack of jaws with gaps in their dentition suggests the physical act of replacement happens rapidly; in crocodylian teeth, the replacement is essentially immediate (Edmund, 1962).

The relative size of equivalent teeth in adjacent tooth families suggest that replacement proceeds in waves, as suggested by Romer and Price (1940), White (1958), Edmund (1960, 1962) and Osborn (1973, 1974). In *Diplodocus*, this appears to occur in an even/odd pattern, such that tooth families 1 and 3 replace at approximately the same time, as do positions 2 and 4. Although this might serve to constrain tooth orientation in some dentitions (e.g., imbrication of functional teeth) , narrow-crowned teeth do not overlap, and in the majority of cases do not contact their mesial and distal neighbors when in functional position. Each replacing tooth is therefore free to develop in approximately the same orientation with regard to its mesial/distal axis that it will take when functional.

Broad-crowned sauropods. The replacing teeth of *Camarasaurus*, with their broad crowns, exceed the mesial and distal margins of the internal alveolus by the time they reach the “ready” position in the tooth family. This is caused in part by the diminution in alveolar diameter towards the body of tooth-bearing elements as well as a constriction of some of them (i.e., premaxilla, maxilla) proximally. As a result, the first replacing tooth of each family cannot be directly adjacent to its mesial and distal neighbors, as is the case in narrow-crowned sauropods. Instead, there is an every-other pattern, where adjacent teeth of the same cohort (i.e. the first replacement tooth in each family) are not adjacent in the alveoli, but are rather offset such that the teeth of families 1 and 3 are in-line

with each other, but the teeth in families 2 and 4 are either lingual or labial to their respective teeth in 1 and 3, depending on the position during the replacement cycle (Fig. 7.6). It is likely that the spaces between the largest replacing teeth are filled with the roots of functional teeth; the roots of the functional teeth ahead of the largest replacing teeth are most probably being pushed out by their replacements in a fashion similar to that proposed for narrow-crowned teeth. As in *Diplodocus*, the teeth of *Camarasaurus* (and potentially all other broad-crowned taxa) replace in an even/odd pattern, which is consistent with the packing pattern just described.

Unlike the condition in narrow-crowned sauropods, the teeth of broad-crowned taxa do overlap each other mesially and distally when in functional position. The teeth are imbricate, such that the distal edge of each tooth overlaps the mesial edge of the next tooth on the labial side. As suggested above, this would seem to restrict the orientation of replacing teeth, as a fresh tooth would be hedged in on two surfaces by teeth already in position. However, it appears that in at least the premaxilla of *Camarasaurus*, the teeth do not develop in their functional orientation as the teeth of *Diplodocus* do. The developing teeth are oriented such that their carinae are aligned tangential to the curvature of the jaw, and as such must rotate slightly clockwise (as seen in apical view) when dropping into functional position. The reason for this disparity in orientation is most probably due to a lack of internal alveolar space; by arranging the teeth in this manner, more teeth can fit in the same tightly constrained jawbone. Precisely

how this twisting occurred is unknown. One possible explanation may be that a combination of the curvature of the premaxilla, the orientation of the distal carina on the tooth mesial to the replacing tooth, and the curvature of the crown of the replacing tooth, which positions the mesial carina lingual to the distal carina of the mesial neighbor as the tooth drops into position, combine to facilitate the twisting of the tooth, which is otherwise held in place simply by soft tissue-cementum connections (White, 1958).

This forced twisting may account for what appears to be a fairly long duration of the replacement itself. Unlike narrow-crowned teeth, which do not appear to have wear on replacing teeth, a replacing tooth in tooth family 4 of *Camarasaurus* has a distinct wear facet on it, suggesting not only that the tooth became functional quite rapidly after passing the margin of the lateral plate, but also that it remained in that position long enough to form a distinct facet.

CONCLUSIONS

Derived sauropods like *Camarasaurus*, *Diplodocus*, and *Nigersaurus* replaced their teeth as fast as or faster than any other dinosaurian herbivore. Narrow-crowned taxa like *Diplodocus* and *Nigersaurus* were able to replace their teeth on approximately monthly timescales, approximately twice as fast as the most rapidly replacing spatulate-crowned sauropods; rapid replacement rates apparently evolved in diplodocoids prior to the development of a tooth battery in derived taxa such as *Nigersaurus*. Sauropod teeth display two adaptive trends for

dealing with an abrasive, plant-based diet. The first trend, from basal sauropodomorphs to sauropods, is an increase in tooth size, which acts to prolong the life of the tooth by increasing surface area at the expense of replacement rate. Sauropods also experimented with increased tooth breadth at this stage. Within Eusauropoda, some sauropods (e.g., *Patagosaurus*, *Mamenchisaurus*) developed slightly faster rates of replacement, as evidenced by increased numbers of replacement teeth, up to two per alveolus. Neosauropoda is marked by a second increase in replacement rate, demonstrated by the presence of three or more replacement teeth per alveolus. Narrow-crowned teeth, which were able to replace much more rapidly than the spatulate-crowned teeth of more basal sauropods, evolved at least three times within Neosauropoda: first in diplodocoids, followed later by at least two lineages within Titanosauriformes. It is apparent that replacement rate became a more important factor in dental evolution and may have been a driving force behind crown volume reduction in those taxa. This trend does not appear to be coupled with an increase in body size or a new chewing mechanic (e.g., more precise occlusion), but may be evidence of a dietary signal, as suggested by independent evidence for niche partitioning between broad- and narrow-crowned taxa.

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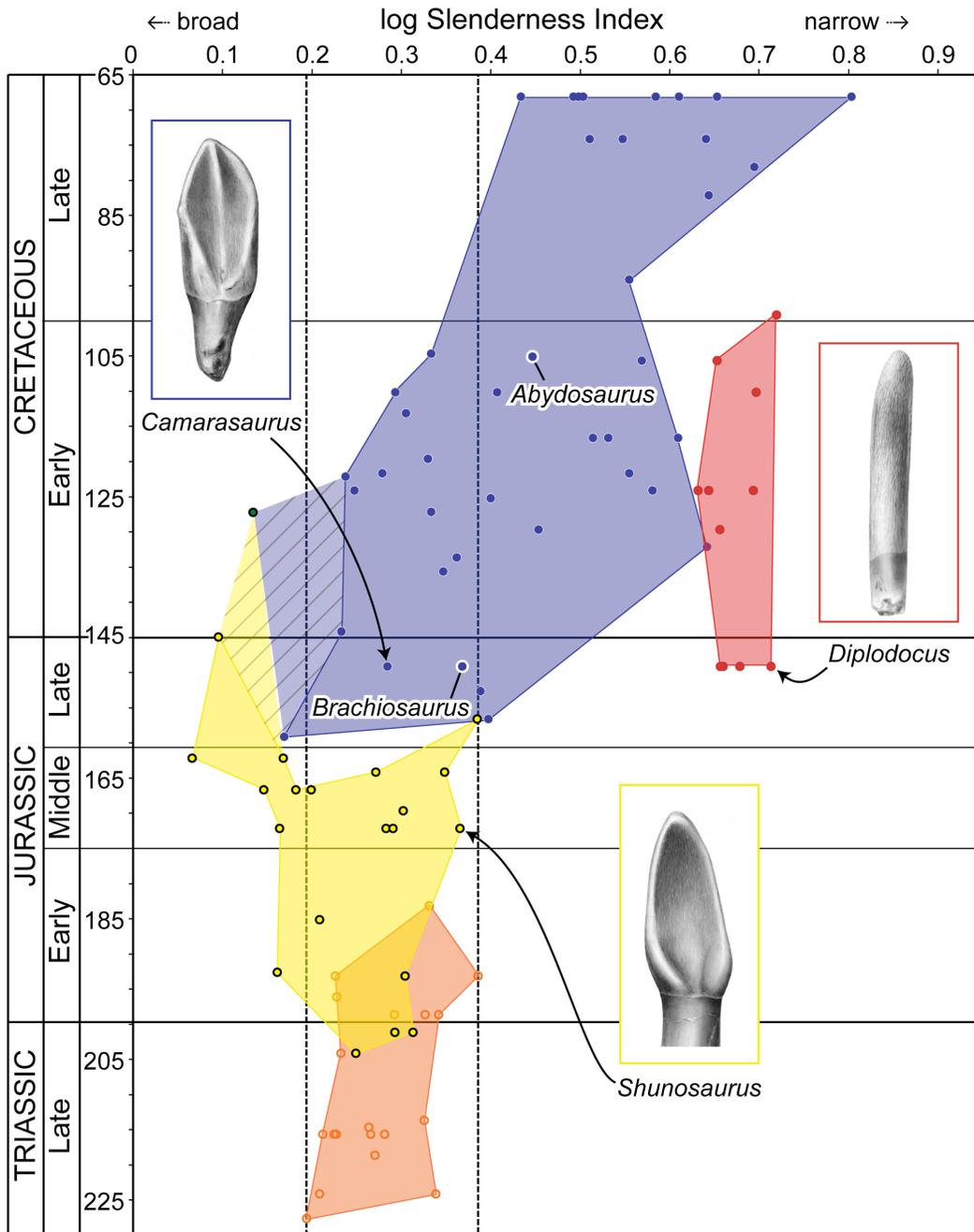
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Figure 7.1. (Facing page). Temporal trends in sauropod tooth morphology. Basal sauropods (yellow) developed broader crowns than their prosauropod ancestors (salmon). Two derived lineages of neosauropods, diplodocoids (red) and macronarians (purple) independently acquired extremely narrow crowns from ancestors with broad crowns. Reprinted from Chure et al., (2010). Image copyright Chure, Britt, Whitlock, and Wilson, 2010.



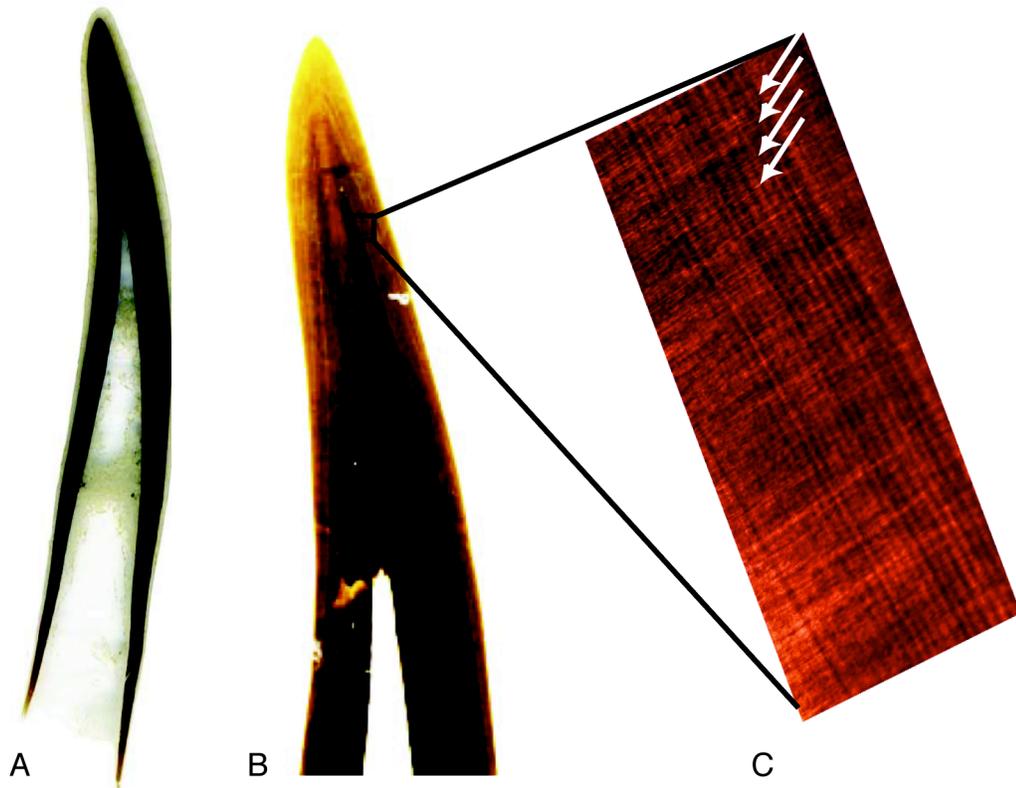


Figure 7.2. A thin-section of a *Diplodocus* tooth (YPM 4677), illustrating the whole tooth (A), detail of the apex (B), and a close up under low magnification (C; 20x) showing incremental lines of von Ebner, indicated by white arrows.

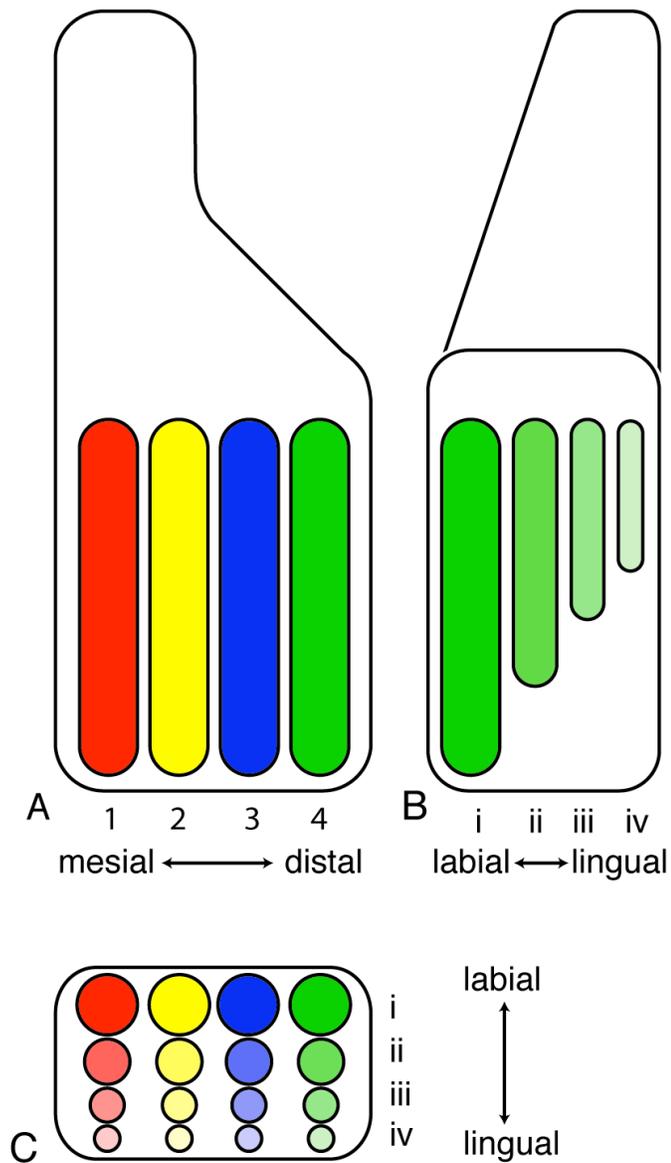


Figure 7.3. Diagrammatic representation of a left sauropod premaxilla in anterior (A), lateral/distal (B), and ventral (C) views, illustrating positional terminology. Arabic numerals represent position of the alveolus in the jaw; 1 being the tooth closest to the midline, with successively more distal positions receiving successively higher numbers (2, 3, 4...). Roman numerals represent position within the tooth family, with the most mature replacement tooth considered tooth i, and successively less mature teeth receiving successively higher numbers (ii, iii, iv...).

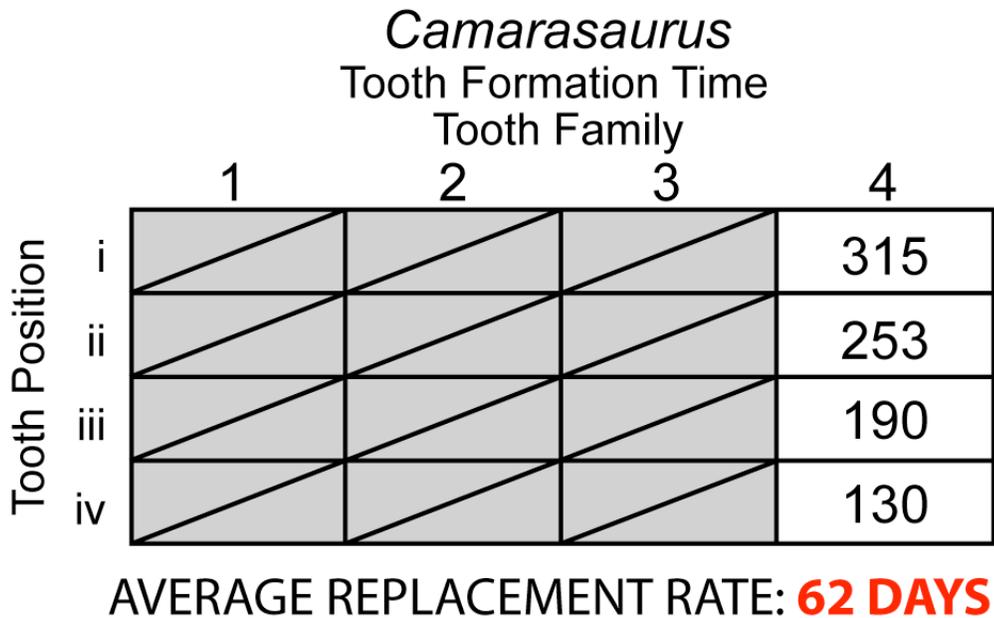
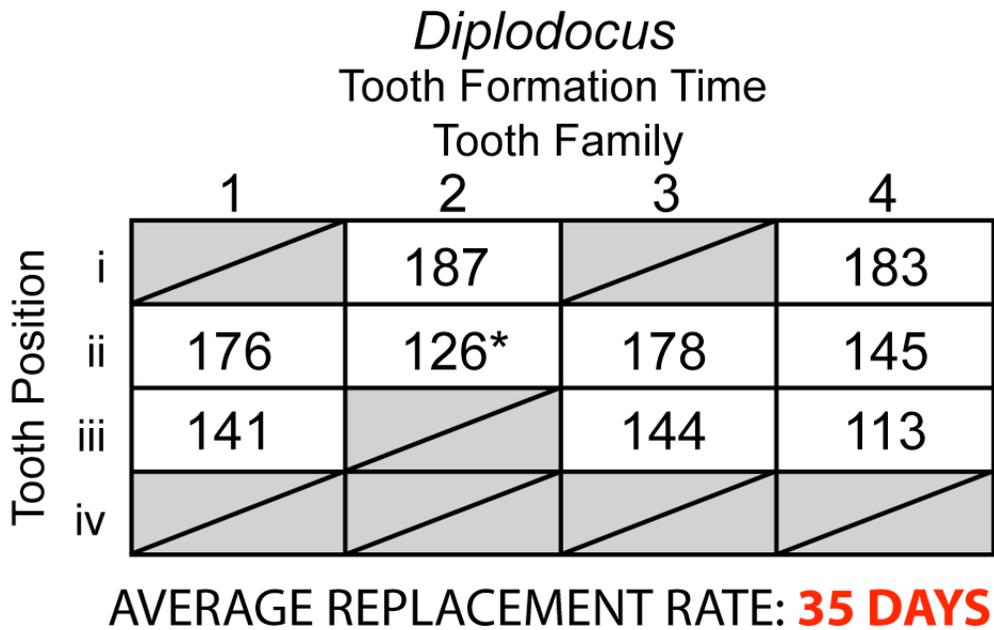


Figure 7.4. Tooth replacement rate and increment counts for the neosauropod dinosaurs *Diplodocus* and *Camarasaurus*. *Camarasaurus* teeth are larger and take longer to form than the teeth of *Diplodocus*, leading to the faster replacement rate (35 days vs. 65 days) seen in the narrow-crowned taxon.

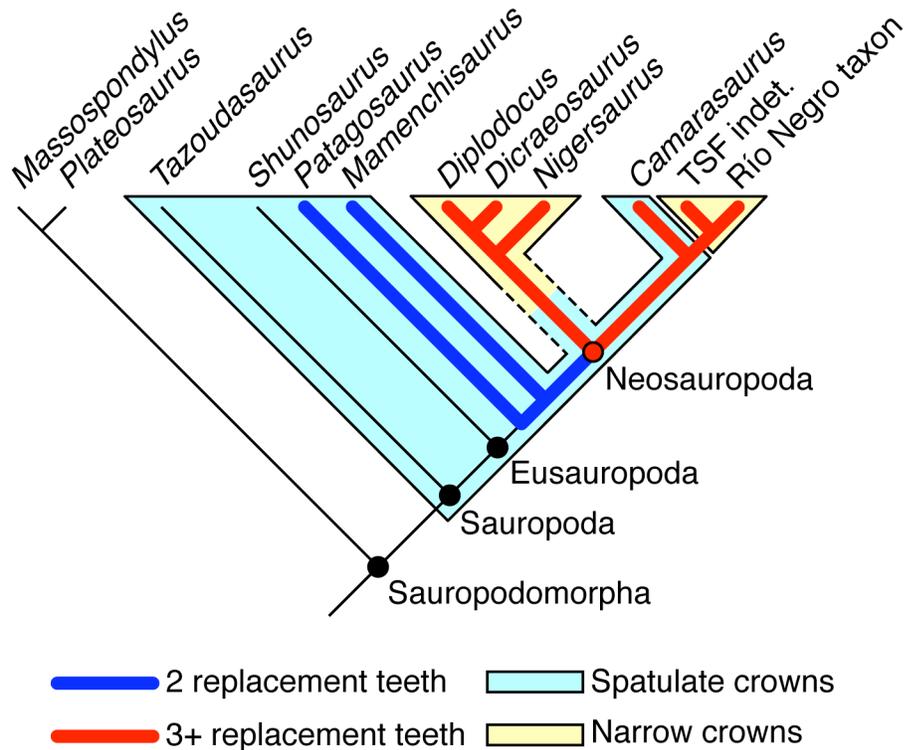


Figure 7.5. Simplified cladogram of Sauropodomorpha, illustrating the relationships of taxa for which replacement rate can be inferred. Large, spatulate tooth crowns evolved early in sauropod evolution, possibly as a response to increased tooth wear. This was followed by the first of two marked increases in replacement rate, within Eusauropoda, marked by an increase in the number of replacement teeth per alveolus (2). A second increase in replacement rate occurs at Neosauropoda, where at least three replacement teeth occur per alveolus. Within Neosauropoda, narrow crowns evolve twice, once somewhere on the diplodocoid lineage, and again within Titanosauriformes. Diplodocoid sauropods are known to have developed extremely fast replacement rates, on the order of 30-35 days; estimates for narrow-crowned titanosaurs (i.e., the Río Negro taxon) suggest similarly elevated replacement rates. Data for TSF indet. (UMNH-898) taken from Calvo (1994).



Figure 7.6. The premaxilla of *Camarasaurus* (UUVP 3999) in medial view, showing the relative positions of replacement teeth with respect to the labio-lingual axis. The external bone surface of the premaxilla and the teeth of the first tooth family have been prepared away, exposing the relative positions of equivalent teeth in tooth families 2 and 3, such that tooth 3II is located labial to tooth 2II. Replacement teeth of tooth families 1 and 3 are in the same plane, as are replacement teeth for families 2 and 4, although these two planes are not in sync. This may be a functional constraint due to the relative size of the teeth and the limited space within the jaw element. Scale bar represents 5 cm.

Table 7.1. Average height ratio and height-corrected ratio (HCR) for seven sauropodomorph dinosaurs, sorted by HCR. Height ratio is the proportion of the apicobasal length of a tooth to the tooth preceding it, expressed as a percentage. HCR is the height ratio, corrected for apicobasal length of a fully mature tooth. Tooth height is the apicobasal length of the largest tooth in the series, inclusive of both crown and root. Larger height ratio and HCR scores are related to faster tooth replacement rates.

Taxon	Height Ratio	Tooth Height	HCR
<i>Shunosaurus</i>	15%	7.5 cm	0.2
<i>Mamenchisaurus</i>	31%	7.7 cm	0.4
<i>Camarasaurus</i>	54%	11.8 cm	0.5
<i>Diplodocus</i>	73%	5.9 cm	1.2
Río Negro Taxon	85%	5.3 cm	1.6
<i>Nigersaurus</i>	89%	4.7 cm	1.9
<i>Massospondylus</i>	38%	1.7 cm	2.2

CHAPTER 8

CONCLUSION

This dissertation brought together techniques from multiple disciplines (comparative anatomy, phylogenetic systematics, biogeography, ecology and ecomorphology, and histology) to examine the evolution of diplodocoid sauropods and the feeding strategies they used while becoming dominant herbivores on a global scale. Here, I review the original research presented in the preceding pages and summarize the conclusions thereof.

Due in large part to their long history of study, the basic set of suprageneric diplodocoid interrelationships is well resolved, and the diagnostic features of most genera are well established. However, intergeneric relationships are less well resolved, particularly with regard to recently described taxa. Chapter 3 took an in-depth look at the relationships of one such taxon: *Australodocus*.

Australodocus was erected in 2007 as a new genus of diplodocoid sauropod, based on two cervical vertebrae from the collections of the Late Jurassic (Kimmeridgian-Tithonian) Tendaguru Formation (Tanzania). *Australodocus* was to be the second diplodocoid from Tendaguru, alongside *Tornieria*. All diplodocoid material from the region had previously been assigned to *Tornieria*, with the result that *Tornieria* was a reasonably well-known and phylogenetically informative taxon. If *Australodocus* was indeed a diplodocid, the affinities of much of the material assigned to *Tornieria* would need to be re-

evaluated, potentially resulting in two fragmentary taxa where once there was a single, relatively complete taxon.

Re-evaluating the holotypic and paratypic materials of *Australodocus* indicate that the four unambiguous synapomorphies listed by Remes (2007) as uniting *Australodocus* with Diplodocidae—bifurcate neural spines with median tubercle, concave ventral surface of cervical centra, bifurcated centroprezygapophyseal lamina (cp1), and transversely convex prezygapophyseal articular facets—are either incorrectly identified (bifurcate cp1) or ambiguous with regard to phylogenetic placement within Neosauropoda. Six characters suggest a relationship between *Australodocus* and the titanosauriform *Brachiosaurus brancai*, however: somphospondylous texture of presacral centra, pneumatization of the neural spine, posterior 1/3 of centrum without pneumatic cavities, accessory lamina connecting centroprezygapophyseal lamina and prezygodiapophyseal lamina anterior to the anterior centrodiapophyseal lamina, accessory lamina ventral and roughly parallel to the posterior centrodiapophyseal lamina enclosing teardrop-shaped coel, and presence of a prespinal lamina in mid-cervical vertebrae. Based on this evidence, *Australodocus* was removed from Diplodocoidea and was instead suggested to be a titanosauriform related to *Brachiosaurus*.

Questions of interrelationships also persist among taxa with more certain diplodocoid affinities, such as the putatively basal taxa *Amphicoelias* and *Haplocanthosaurus*, the flagellicaudatan *Suuwassea*, and the highly specialized rebbachisaurids. For the rebbachisaurids, this uncertainty is coupled with a

recent surge in discoveries of new taxa. Comparative cladistic methods demonstrate that character and taxon sampling need to be improved before greater phylogenetic resolution can be expected.

In Chapter 4, I presented a new phylogenetic analysis that resolves many of the outstanding questions regarding the relationships within Diplodocoidea and examines paleobiogeographic trends within the group. *Suuwassea* was recovered as a basal dicraeosaurid (the only Laurasian member of the group), and two distinct clades of rebbachisaurids were identified: a group closely allied with *Nigersaurus* and a clade associated with *Limaysaurus*. *Amphicoelias*, *Amazonsaurus* and *Haplocanthosaurus* were provisionally placed as successively less-derived taxa at the base of Diplodocoidea. A North American origin for Diplodocoidea and Flagellicaudata was hypothesized based on the geographic and temporal distribution of those taxa. Rebbachisaurid taxa demonstrate a South American/African vicariance pattern, but the timing of the event predates the proposed final rifting of those continents by ca. 40 million years; the meaning of this discrepancy is uncertain.

The unique skull shape of *Diplodocus* and other diplodocoids has led researchers to propose a wide range of feeding modes, including uprooting aquatic plants, scraping algae from rocks, branch stripping, as well as feeding strategies employed by modern megaherbivores such as low-level cropping. Despite over a century of discussion, however, no strongly-supported hypothesis has yet widespread acceptance.

In Chapter 5, the feeding behavior of these giant herbivores was

investigated using two techniques borrowed from studies of extinct and extant mammals: snout shape and dental microwear. Snout shape—the relative squareness or roundness of the arcade in dorsal/ventral view—has been shown to correlate with the time spent grazing (cropping of grasses at low vertical heights) or browsing (selective feeding on leaves or shoots at low, medium, or high heights). Dental microwear is the pattern of scratches, pits, and gouges that result from contact between teeth and foods. This pattern varies based on, among other qualities, coarseness of food, grit content, and the presence/absence of large seeds.

Snout shape analyses indicated the presence of two morphotypes within Diplodocoidea: a square morph and a round morph. Taxa with square snouts (*Apatosaurus*, *Diplodocus*, and *Nigersaurus*) also had microwear features indicative of low-height browsing on herbaceous vegetation: sub-parallel, fine scratches and an abundance of small, round pits. Of the three taxa with round snouts (*Dicraeosaurus*, *Suuwassea*, and *Tornieria*), only *Dicraeosaurus* could be examined for microwear features. The microwear features recovered from *Dicraeosaurus* indicate a very different diet from that of square snouted diplodocoids. Coarse scratches, large, oblong pits and gouges, and commonly occurring cross-scratches all indicate a diet of woody plants, browsed at a higher elevation than the plants browsed by square-snouted taxa.

When the morphological variables are mapped onto the phylogeny recovered in Chapter 4, it is apparent that shape and wear data correspond better with ecological signals than they do with phylogeny. The resolution of the

round-snouted *Tornieria* firmly within the otherwise square-snouted Diplodocidae is exemplary of this inference; also important is the resolution of *Suuwassea* as a dicraeosaurid. Square snouted taxa are apparently restricted to atypical environments dominated by low browse, although round-snouted taxa are common in all paleoenvironments. Dicraeosauridae is composed exclusively of round-snouted taxa (*Dicraeosaurus*, *Suuwassea*), but diplodocidae contains both square-snouted (*Apatosaurus*, *Diplodocus*) and round-snouted (*Tornieria*) members.

Although adult diplodocid sauropods were likely to have been low-height, nonselective browsers, the examination of a juvenile skull of *Diplodocus* suggests that may not have been true for sub-adults. Chapter six described that skull (Carnegie Museum 11255), noting the presence of typical juvenile characteristics (e.g., incomplete fusion of some dermal skull elements, relatively enlarged orbit, relatively short antorbital length) as well as some more atypical characteristics. In particular, this juvenile skull has an extraordinarily round snout and a posteriorly expanded dentition, in contrast to the square snout and anteriorly sequestered dentition of adults. Because the adult morphology is so intimately tied to interpretations of feeding behavior, it is inferred that this variation indicates ontogenetic variation in feeding behavior as well, such that juveniles may have been more selective browsers than adults. Morphologic variation of this type appears to be unique among sauropodomorphs, and potentially dinosaurs as a whole.

Finally, Chapter 7 examined the patterns of change in dental morphology

and replacement rate throughout sauropod evolution. Sauropods evolved from small, bipedal omnivores that over time became increasingly reliant on herbivory and achieved larger body sizes, eventually becoming obligate quadrupeds. With this increase in body size and dietary shift came an increase in tooth wear, which reduced dental effectiveness. Sauropods responded to increased tooth wear rates by increasing crown volume and/or increasing tooth replacement rate. Early in sauropod history, crown volumes were small, enabling rapid replacement. As the reliance on herbivory outstripped the ability of sauropodomorphs to replace their teeth, a rapid increase in crown size occurred, roughly coinciding with the base of the clade Sauropoda. This increase in crown volume resulted in decreased replacement rate; rates of dentine apposition are relatively constant across Amniota, so any increase in volume will result in an increase in tooth formation time. The primary solution to this issue is to increase the area of dentine apposition, which is typically expressed as an increase in the number of replacement teeth at one time within a single crypt. This first occurs within basal Eusauropods such as *Mamenchisaurus*, where the first evidence for multiple replacement teeth (2) is seen. A second increase in replacement rate (signalled by an increase in replacement teeth per crypt) occurs at Neosauropoda, in both broad-crowned (*Camarasaurus*) and narrow-crowned (*Diplodocus*) taxa. Here, histological study indicates extraordinarily rapid replacement rates of 62 days or less. The first of at least two significant reductions in crown volume (Diplodocoidea) appears at this node; this reduction appears to be related to an increase in replacement rate. Narrow crowned *Diplodocus* (35 days) and

Nigersaurus (30 days) have replacement rates approximately twice as fast as any other dinosaur yet examined. Reduction in crown volume is suggested to be an adaptation for increased replacement rate.

In summary, the relationships of diplodocoid sauropods are difficult but not impossible to reconstruct, and here a well-supported hypothesis of relationships based on data throughout the skeleton is presented. This hypothesis was used as a background on which to examine the evolution of various feeding strategies in the clade, which were recognized as ground-height nonselective browsing and mid-height selective browsing using snout shape (square vs. round) and dental microwear indices. The distribution of those feeding behaviors did not perfectly match the recovered phylogeny, although it did correspond perfectly with reconstructions of regional ecology, such that ground-height nonselective browsers lived in savanna-type environments, and mid-height selective browsers lived in forested environments. Ontogenetic shape variation in at least one of the ground-height nonselective browsers (*Diplodocus*) suggests the possibility of ontogenetic variation in feeding strategy as well, where subadults may have fed selectively. Although Diplodocoidea is diagnosed in part by narrow-crowned teeth, the inference of at least two distinct feeding strategies for this clade suggests that it is unlikely that the development of narrow crowns in this clade was an adaptation for a particular feeding mode. Histological and proportional data suggest instead that the development of narrow crowns in this clade (and elsewhere) was an adaptation that enabled more rapid tooth replacement and may not have been tied directly to any particular feeding strategy or strategies.