

ONE

Overview of Sauropod Phylogeny and Evolution

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SAUROPOD STUDIES FROM OWEN TO THE PRESENT

This year marks the one hundred sixty-fourth anniversary of Richard Owen's (1841) description of the first sauropod—*Cetiosaurus*, the “whale lizard”—on the basis of vertebrae and limb elements from localities across England. Although these remains “had been examined by Cuvier and pronounced to be cetaceous” (Buckland 1841:96), Owen (1841:458–459) demonstrated the saurian affinities of *Cetiosaurus* on the basis of several features, including the absence of epiphyses (growth plates) on caudal vertebrae (fig. 1.1). He differentiated *Cetiosaurus* from other extinct saurians on the basis of its large size and characteristics of its vertebrae (see Upchurch and Martin 2003:215). Owen (1841:462) concluded his initial description with this assessment: “The vertebræ, as well as the bones of the extremities, prove its marine habits . . . the surpassing bulk and strength of the *Cetiosaurus* were probably assigned to it with carnivorous habits, that it might keep in check the Crocodilians and Plesiosaurs.” He regarded *Cetiosaurus* as a crocodilian by the “form of the

long bones” and “the toes being terminated by strong claws” (Owen 1842:102), but this assessment was based on limited anatomical evidence (Owen 1875:27). Key data emerged with the discovery of abundant *Cetiosaurus* bones in Oxfordshire by John Phillips. Thomas Huxley examined this “splendid series of remains” before the publication of Phillips' (1871) monograph and was the first to place *Cetiosaurus* within Dinosauria (Iguanodontidae [Huxley, 1869:35]). Phillips (1871) interpreted *Cetiosaurus* as a plant-eating dinosaur and hypothesized that its limb bones were “suited for walking.” He could not rule out the possibility that it was amphibious, however, concluding that it was a “marsh-loving or riverside animal.” Owen (1875:27) later acquiesced, referring *Cetiosaurus* to the Dinosauria because of its four sacral vertebrae. He admitted that it may have had some terrestrial capabilities but concluded that *Cetiosaurus* was an estuarine or marine animal based on its “organ of swimming,” the tail (Owen 1875:41).

These early interpretations, based on somewhat limited samples, were followed by the discovery of abundant sauropod skeletons in western North America and eastern Africa during



FIGURE 1.1. Sagittally sectioned posterior caudal vertebra of *Cetiosaurus oxoniensis* (OUM-J13697) with label in Owen's hand. This sectioned vertebra was used to demonstrate the lack of epiphyses at either end of the caudal centrum. Scale equals 5 cm.

the late nineteenth and early twentieth centuries. O. C. Marsh and E. D. Cope described numerous new and well represented sauropod genera from the Morrison Formation of the western United States, including the first complete sauropod skull (*Diplodocus* [Marsh 1884]), reconstructions of the skeletons of *Brontosaurus* by Marsh (1883; fig. 1.2) and *Camarasaurus* by Cope (Osborn and Mook, 1921:pl. 82; fig. 1.2), and the first mount of a complete sauropod skeleton (*Diplodocus* [Anonymous 1905]). These discoveries provided the first examples of ontogenetic variation and phylogenetic diversity in sauropods. Later, German expeditions to East Africa (present-day Tanzania) produced sauropod material rivaling that from North America. Janensch and others led field crews at Tendaguru, where they collected more than 235,000 kg of fossils (Maier 2003:105) that represented many new genera described over the course of 50 years (e.g., Janensch, 1914, 1929a, 1935–36, 1950, 1961). The abundance and diversity of sauropod remains unearthed in North America and Africa not only answered many of the queries posed by early sauropod researchers (e.g., dinosaurian affinities and terrestrial habits of sauropods) but also posed new ones. One of the major controversies that

extended across the Atlantic surrounded the posture of sauropods. American scientists favored an upright, columnar posture, whereas their German colleagues deemed a lacertilian pose more appropriate (Holland 1910; Desmond 1975). A second question, less controversial but farther-reaching, emerged from the study of these two large collections of sauropod material—How should sauropod diversity be classified?

TRADITIONAL CLASSIFICATION

When Marsh (1878) coined the suborder Sauropoda, it included only a single family, Atlantosauridae. Several of the features Marsh (1878:412) listed in that initial diagnosis of Sauropoda are now well-corroborated synapomorphies for the group or for more exclusive sauropod subgroups that were not identified at the time of Marsh's writing. Marsh invented new families to accommodate the increasing sauropod diversity revealed by new discoveries worldwide (e.g., Atlantosauridae, Morosauridae, Diplodocidae, Pleurocoelidae, Titanosauridae). The formal familial diagnoses for these groups (Marsh 1884, 1895) also recognized features currently considered synapomorphies for sauropod subclades. These diagnoses, however, did not resolve how these groups were interrelated; Marsh's ranked classifications did not function as hypotheses of evolutionary descent.

On the basis of his burgeoning Tendaguru collection, Janensch (1929a) produced a very different classification of Sauropoda that employed higher level groupings. He recognized two principal sauropod subgroups, one with broad, laterally facing nares and spatulate tooth crowns and the other with elevated, dorsally facing nares and narrow tooth crowns. Janensch named these two families Bothrosauropodidae and Homalosauropodidae, and recognized three and four subfamilies within each, respectively. Huene (1956) followed this dichotomous scheme, raising Janensch's subfamilies to familial rank and Janensch's families to "family-group" rank. In contrast to that of Marsh, Janensch's classification could be interpreted as an evolutionary

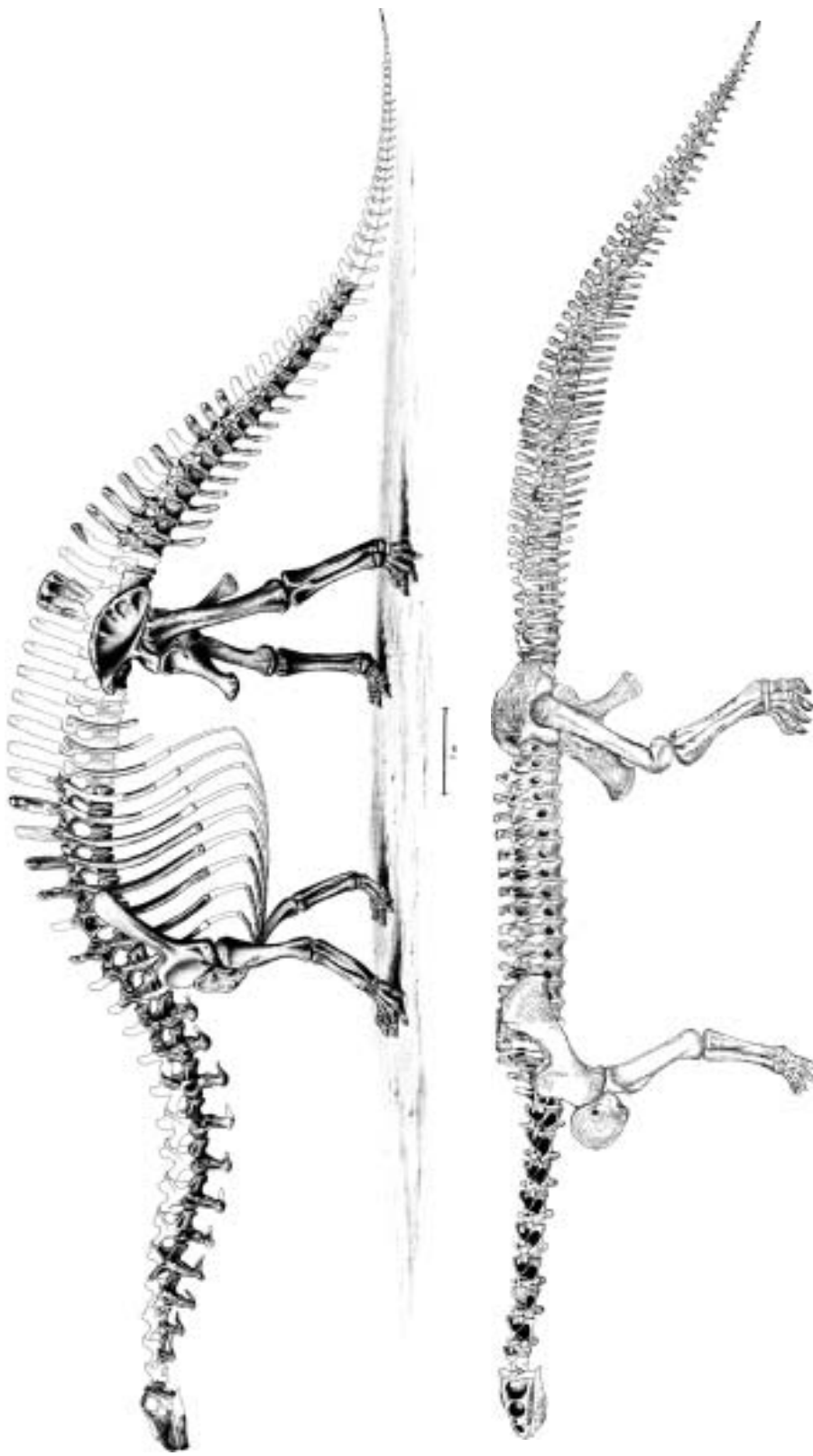


FIGURE 1.2. First reconstruction of sauropod dinosaurs. Top: "*Brontosaurus*" (= *Apatosaurus*) *excelsus* from Marsh (1883). From a lithograph later published in Ostrom and McIntosh (1966). Bottom: *Camarasaurus supremus*, as drawn by Ryder in 1877 under the direction of Cope. Later published in Osborn and Mook (1921:pl. 82).

hypothesis that involved divergence between two lineages differing in tooth morphology.

A dichotomous scheme for higher-level classification of sauropods based on tooth form and narial position became widely accepted, despite nomenclatural differences (Brachiosauridae versus Titanosauridae [Romer 1956, 1966]; Camarasauridae versus Atlantosauridae [Steel 1970]). Other traditional classifications of sauropods, however, follow Marsh in recognizing taxa of equivalent rank (usually families) with no higher-level hierarchical information (e.g., McIntosh 1990). Bonaparte (1986a) also utilized serially ranked families, but he regarded Late Jurassic and younger sauropod families (“Neosauropoda”) as advanced relative to older forms (“Eosauropoda”).

Numerical methods for assessing phylogenetic relationships in sauropod dinosaurs were first introduced by Gauthier (1986) in his analysis of saurischian dinosaurs. His character choice reflected those cited by previous authors (e.g., Romer 1956; Steel 1970) and his topology consequently conformed to the traditional dichotomy. Since then, more than a dozen cladistic analyses focusing on Sauropoda or its subgroups have appeared (Russell and Zheng 1993; Calvo and Salgado 1995; Upchurch 1995, 1998; Salgado et al. 1997; Wilson and Sereno 1998; Sanz et al. 1999; Curry 2001; Curry Rogers and Forster, 2001; Wilson 2002; Calvo and González Riga 2003; González Riga 2003; Upchurch et al. 2004). Together these analyses have scored 1,964 characters in 229 sauropod taxa, resulting in a variety of phylogenetic hypotheses that are discussed briefly below.

CLADISTIC HYPOTHESES

The main topological disagreement among early cladistic analyses of Sauropoda centered on the relationships of broad- and narrow-crowned sauropods. Upchurch (1995) presented the first large-scale cladistic analysis of sauropods, in which he proposed a slightly modified version of the traditional dichotomy that resolved broad tooth crowns as a primitive feature and narrow tooth crowns as a uniquely

derived feature characterizing *Diplodocus*-like taxa (i.e., Diplodocoidea) and titanosaurs. Salgado et al. (1997) were the first to depart from this traditional dichotomy by providing character evidence linking narrow-crowned titanosaurs to the broad-crowned *Brachiosaurus*, rather than to the other narrow-crowned group (Diplodocoidea). This result was corroborated by Wilson and Sereno (1998). In a subsequent analysis, Upchurch (1998) produced a topology that agreed in many ways with those of Salgado et al. (1997) and Wilson and Sereno (1998) but also explored the relationships of genera not treated by either. These three analyses agree on several topological points, including the separation of early-appearing genera (e.g., *Vulcanodon*, *Shunosaurus*, *Barapasaurus*, *Omeisaurus*) from a derived clade called Neosauropoda (Bonaparte 1986a), the identification of the two constituent neosauropod lineages Diplodocoidea (e.g., *Apatosaurus*) and Macronaria (e.g., *Camarasaurus*), and the positioning of the titanosaur lineage within Macronaria (fig. 1.3).

Despite points of agreement, other topological differences persist. The most significant of these centers on the phylogenetic affinities of two groups of Asian sauropods: the Chinese “euhelopodids” (*Shunosaurus*, *Omeisaurus*, *Mamenchisaurus*, *Euhelopus*) and the Mongolian nemegtosaurids (*Nemegtosaurus*, *Quaesitosaurus*). Upchurch (1995) proposed “Euhelopodidae” as a clade that evolved while China was geographically isolated from Europe from Middle Jurassic until Early Cretaceous times (Russell 1993; Z. Luo 1999; Barrett et al. 2002; Upchurch et al. 2002; Zhou et al. 2003). It evolved independently of its sister-taxon Neosauropoda but was eventually replaced by it during the Cretaceous (Upchurch 1995, 1998). In contrast, Wilson and Sereno (1998) suggested that Chinese sauropods are paraphyletic, with *Omeisaurus* occupying the sister-taxon to Neosauropoda (as in Upchurch 1995, 1998), but *Shunosaurus* positioned basally and *Euhelopus* positioned apically. This result was corroborated by Wilson (2002), whose analysis

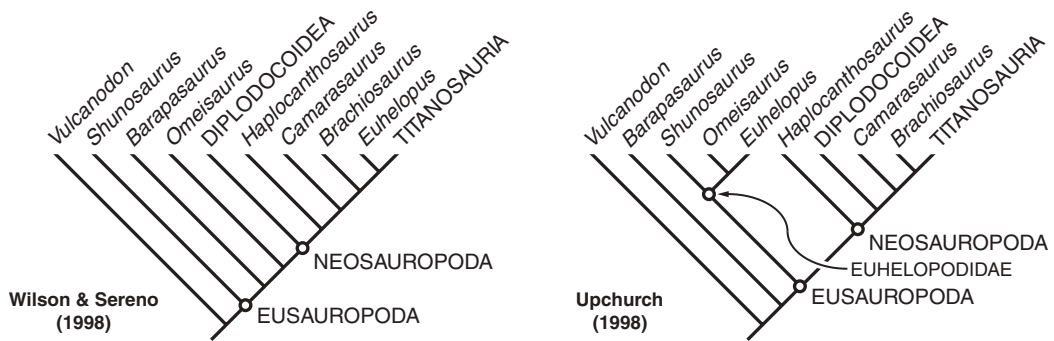


FIGURE 1.3. Hypotheses of the relationships of sauropod dinosaurs based on (left) Wilson and Sereno (1998) and (right) Upchurch (1998).

resolved some of Upchurch's (1998) "euhelopodid" characters as supporting the monophyly of *Omeisaurus* and *Mamenchisaurus* (Omeisauridae). A Templeton test (e.g., Larson 1994) showed that "euhelopodid" paraphyly could not be statistically rejected by the matrix of Upchurch (1998), but the "euhelopodid" monophyly could be rejected by the matrix of Wilson (2002). Thus far, no other analysis has specifically investigated the relationships of these Chinese sauropods, but Upchurch's most recent analysis supported paraphyly of some "euhelopodid" genera (see Upchurch et al. 2004; Barrett and Upchurch, chapter 4).

A second area of disagreement involves the relationships of the isolated skulls of the sauropods *Nemegtosaurus* and *Quaesitosaurus* from the Late Cretaceous of Mongolia. These slender-crowned taxa were originally described as *Dicraeosaurus*-like (Nowinski 1971), a designation consistent with the presumed diplodocid affinities of the Late Jurassic Chinese *Mamenchisaurus* (McIntosh 1990), as well as the conventional division of sauropods into narrow-crowned and broad-crowned groups. More recently, cladistic analyses have produced new hypotheses of relationships for *Nemegtosaurus* and *Quaesitosaurus*, including the monophyletic sister-taxon of diplodocoids (Yu 1993; Upchurch 1998, 1999; Upchurch et al. 2002), basal members of a clade including diplodocoids and titanosaurs (Upchurch 1995), and, most recently, titanosaurs (Salgado et al. 1997; Curry

Rogers and Forster 2001; Wilson 2002, 2005a). Although the weight of the evidence is in favor of titanosaur affinities for *Nemegtosaurus* and *Quaesitosaurus*, convergences with diplodocoids are noteworthy (Upchurch 1999; Curry Rogers and Forster 2001; see below).

In addition to areas of disagreement, there are unresolved areas resulting from lack of information. Two such areas involve the origin of sauropods and the diversification of their latest surviving lineage, Titanosauria. Sauropods have long been absent from Triassic rocks, but their two saurischian sister-taxa (Prosauropoda, Theropoda) are found in lowermost Upper Triassic horizons. Recent discoveries of Triassic sauropod body fossils and ichnofossils (see below) have provided the first opportunity to resolve sauropod origins, but additional field and museum research is needed. Renewed interest in titanosaurs, whose interrelationships remain resolved, have been fueled by descriptions of many new discoveries in the field (Curry Rogers, chapter 2). These include the first titanosaur with associated cranial and cranial remains (*Rapetosaurus* Curry Rogers and Forster 2001, 2004), the first embryonic titanosaur remains (Chiappe et al. 1998, 2001; Salgado et al. 2005), and nearly complete associated or articulated postcranial skeletons from South America (*Mendozasaurus* González Riga 2003; *Epachthosaurus* Martínez et al. 2004; *Gondwanatitan* Kellner and Azevedo 1999), Asia (*Phuwiangosaurus* Martin et al. 1994;

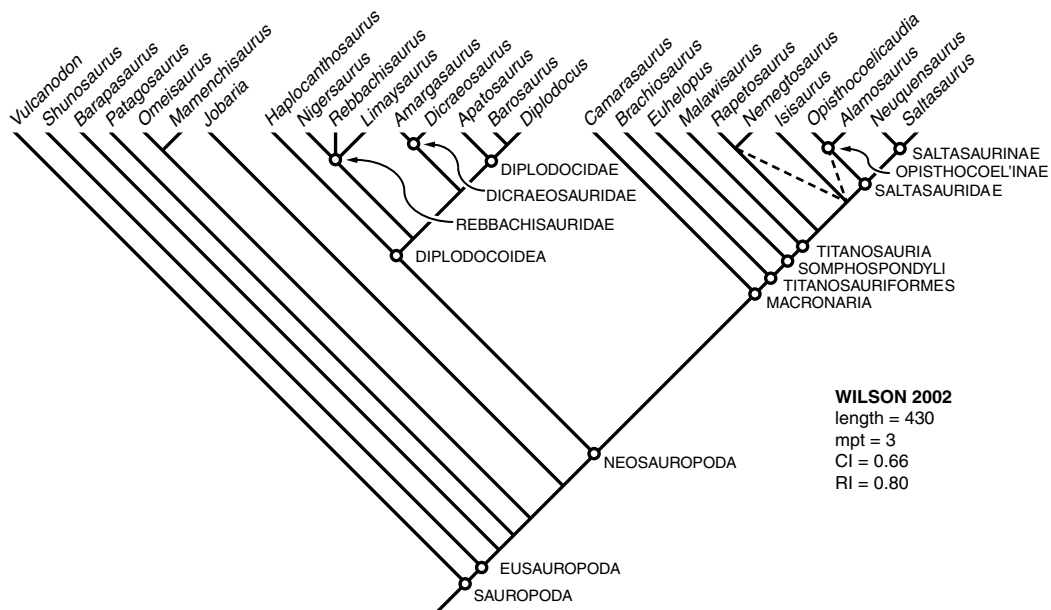


FIGURE 1.4. Phylogenetic relationships of sauropod genera based on Wilson (2002). Dashed lines indicate nodes that are lost in trees two steps longer than the most parsimonious tree. Taxonomy has been updated for *Rayosaurus* (= *Limaysaurus* [Salgado 2004]) and “*Titanosaurus*” *colberti* (= *Isisaurus* [Wilson and Upchurch 2003]).

Tangvayosaurus Allain et al. 1999), India (*Isisaurus* Jain and Bandyopadhyay 1997), Europe (*Lirainosaurus* Sanz et al. 1999; *Ampelosaurus* Le Loeuff 1995, 2003), and Africa (*Malawisaurus* Jacobs et al. 1993; *Paralattitan* Smith et al. 2001). Several analyses have investigated titanosaur phylogeny (most notably Curry [2001] and Curry Rogers and Forster [2001]), and there are several points of agreement among them (Wilson and Upchurch 2003). These preliminary analyses are the first step toward establishing a framework for titanosaur evolutionary history, but at least a dozen valid titanosaur genera have yet to be accommodated by a phylogenetic analysis, in addition to the many undescribed specimens uncovered in recent years.

The topology of Wilson’s (2002) analysis of Sauropoda, based on 27 taxa scored for 234 characters, is assumed in this paper (fig. 1.4). Outgroup choice, character descriptions, character coding assumptions, character–taxon matrix, and tree statistics are given by Wilson (2002). Below, the evolutionary events diagnosing several major sauropod clades are discussed. For each event, a set of synapomorphies

is presented that has been identified in various analyses (table 1.1). Appendix 1.1 lists each character and its states.

MAJOR EVOLUTIONARY EVENTS IN SAUROPODA AND ITS SUBGROUPS

Sauropoda is a monophyletic group whose body plan (fig. 1.2) is supported by more than 40 synapomorphies, many of which were not lost within the 150 million-year history of the group (McIntosh 1990; Upchurch 1995, 1998; Wilson and Sereno 1998). Modification of this basic architecture, as it pertains to the evolution of herbivory, neck elongation, and locomotion within five clades (Sauropoda, Eusauropoda, Neosauropoda, Diplodocoidea, Macronaria) is explored here. Important to this discussion is the presumed ancestry of Sauropoda, which is not yet agreed on. Whereas most researchers favor a monophyletic Prosauropoda (Sereno 1989; Galton 1990; Wilson and Sereno 1998; Galton and Upchurch 2000, 2004; Benton et al. 2000), recent analyses of sauropodomorph relationships (Yates 2001, 2003, 2004; Yates and Kitching

TABLE 1.1.
Synapomorphies for the Five Sauropod Clades Discussed

	CHARACTER NUMBER, BY CLADISTIC ANALYSIS			
	SALGADO ET AL. (1997)	UPCHURCH (1998)	WILSON & SERENO (1998)	WILSON (2002)
Columnar, quadrupedal posture (Sauropoda)				
elongate forelimbs	—	158	1	172
elongate metatarsal V	—	—	15	225
straight limb elements	4	186	1	149
reduction of olecranon	—	161	4	167
femur with eccentric cross-section	—	191	10	198
unossified limb articular surfaces	—	—	—	—
unossified distal carpals	—	164	—	173
unossified distal tarsals (3 & 4)	—	197	13	216
Herbivorous specializations (Eusauropoda)				
tooth rows shortened	—	73	67	66
precise occlusion	—	—	35	67
tooth rows arched	—	59	31	65
teeth overlap	—	—	34	69
enamel wrinkling	—	—	33	71
broad crowns	—	71	32	70
dentary deepens anteriorly	—	57	30	55
Neck elongation (Eusauropoda)				
number of neck vertebrae	5	76	37	80
number of dorsal vertebrae	—	95	70	91
Hindfoot posture (Eusauropoda)				
pes shortened relative to tibia	—	—	50	223
spreading metatarsus	—	—	52	217
metatarsal I broader than II–V	—	—	51	221
pedal phalangeal count reduced	—	200	57	233
metatarsal II broader than III–IV*	—	—	73	224
pedal unguals directed laterally*	—	—	64	228
Reduced ossification of wrist & ankle (Neosauropoda)				
reduction to two carpals	—	163	79	173
astragalus reduced	—	195	85	210
Forefoot posture (<i>Jobaria</i> + Neosauropoda)				
bound metacarpus	—	169	80	175
tightly arched metacarpus	—	169	81	176
Herbivorous specializations (Diplodocoidea)				
tooth row restricted anteriorly	—	74	—	66
mandible squared in dorsal view	—	59	—	65
jaw articulation shifted forward	—	?27	—	46, 53
pterygoid flange and adductor fossa shifted forward	—	—	—	37
loss of crown overlap	—	—	—	69
cylindrical tooth crowns	—	70	—	70
enhanced tooth replacement rate	—	—	—	74

TABLE 1.1. (continued)

	CHARACTER NUMBER, BY CLADISTIC ANALYSIS			
	SALGADO ET AL. (1997)	UPCHURCH (1998)	WILSON & SERENO (1998)	WILSON (2002)
Presacral specializations (Flagellicaudata)				
forked neural spines	—	92	106	85, 89
elongate neural spines*	—	—	—	93
number of cervical vertebrae*	—	77	37	80
number of dorsal vertebrae*	—	95	70	91
Tail specializations (Diplodocoidea)				
elongate caudal centra	—	134	—	137
biconvex caudal centra	—	134	—	136
30 or more archless caudal centra*	—	128	—	138
Wide-gauge limb posture (Saltasauridae)				
femur distal condyles beveled	—	—	—	201
eccentric femoral midshaft	—	—	—	198
coracoid quadrangular†	29	153	—	156
scapular blade deflected dorsally†	—	—	—	151
crescentic sternal plates†	26	154	—	158
humeral distal condyles exposed anteriorly	—	—	—	163
humeral distal condyles divided	—	—	—	164
humeral deltopectoral crest expanded	—	—	3	161
prominent olecranon†	—	161	4	167
distal radius expanded transversely†	—	—	—	170
distal tibia expanded transversely†	7	—	—	205
iliac blade directed laterally†	28	172	—	187
femur deflected medially†	19	187	100	199
carpus unossified*	—	165	79	173
manual phalanges absent*	27	—	43	181

NOTE: Character numbers are those employed in four major cladistic analyses of sauropod relationships. Asterisks (*) denote synapomorphies that apply at slightly *less* inclusive nodes; daggers (†) denote synapomorphies that apply at slightly *more* inclusive nodes (see text for details).

2003) resolve taxa considered “prosauropods” to be paraphyletic. Although the earliest of these analyses supports a fully pectinate arrangement of “prosauropods” (Yates 2001, 2003:fig. 22), the most recent analyses resolve a monophyletic core of prosauropods flanked basally by primitive forms and apically by sauropod-like forms (Yates and Kitching 2003:fig. 4; Yates 2004:fig. 13). Sereno (1998) specified phylogenetic definitions that designate Prosauropoda and Sauropoda reflexive stem-based clades that comprise the node-based Sauropodomorpha. Applying this phylogenetic definition to the Yates and Kitching (2003:fig. 13) topology, the monophyletic core

should be called Prosauropoda, the derived sauropod-like forms should be included in Sauropoda, and taxa resolved as outgroups to those clades are non-sauropodomorph saurischians. The phylogenetic definitions for this node–stem triplet are as follows (Sereno 1998:table 4) (boldface type indicates node-based definitions; regular type indicates stem-based definitions):

Sauropodomorpha Huene 1932—

Plateosaurus engelhardti, *Saltasaurus lorica-*
tus, their most recent common ancestor
and all descendants.

Prosauropoda Huene 1920—All sauropodomorphs closer to *Plateosaurus engelhardti* than to *Saltasaurus loricatus*.

Sauropoda Marsh 1878—All sauropodomorphs closer to *Saltasaurus loricatus* than to *Plateosaurus engelhardti*.

Below, I summarize the major specializations relating to herbivory, neck elongation, and locomotion for each of five major sauropod clades. The synapomorphies discussed are listed in table 1.1, alongside their usage in various cladistic analyses of sauropod relationships. Appendix 1.1 gives a full character list with primitive and derived states.

SAUROPODA

Probable sauropod body fossils and ichnofossils are present in Upper Triassic (Carnian) sediments, but their referrals require confirmation (summarized in Wilson 2005b). The partial hindlimb of *Blikanasaurus* is proportioned similarly to those of later sauropods (Yates 2003, 2004; Yates and Kitching 2003; Upchurch et al. 2004), but correlation with body size cannot yet be ruled out. Likewise, trackways from the Upper Triassic (Carnian) Portezuelo Formation of West-Central Argentina resemble those of later sauropods, but their identification remains tentative (Marsicano and Barredo 2004). The oldest definitive sauropod fossils are the *Tetrasauropus* trackways preserved in the Chinle Group of western North America, which are Norian-Rhaetian in age (ca. 210 mya [Lockley et al. 2001; see Wright, chapter 9]). Slightly younger or coeval ?Rhaetian strata in Thailand preserve the fragmentary remains of *Isanosaurus* (Buffetaut et al. 2000). *Isanosaurus* may be more derived than the slightly younger *Vulcanodon* (Raath 1972), which is generally considered the most primitive sauropod (Wilson 2002: fig.13, table 13). Because the basalmost sauropods *Vulcanodon*, *Isanosaurus*, and *Gongxianosaurus* (fig. 1.5) lack complete cranial remains and much of the vertebral column, the majority of the features diagnosing Sauropoda are appendicular synapomorphies. Of these, many are related to the adoption of a

columnar, graviportal posture, which involved independent changes in limb proportions, posture, and ossification.

COLUMNAR, QUADRUPEDAL POSTURE

Outgroups to Sauropoda are primitively bipedal and characterized by relatively short forelimbs that generally represent less than half the length of the hindlimb. In these forms, the proximal hindlimb is shorter than the distal hindlimb, nearly half of whose length is provided by the metatarsus. Sauropoda is characterized by modifications of proportions both within and between the fore- and the hindlimbs, a modification related to quadrupedalism. Sauropods have elongate forelimbs that are at least 70% of the hindlimb length, nearly twice that of their outgroups (table 1.2, fig. 1.5). This change was accommodated by an overall lengthening of the forelimb, especially the distal elements (fig. 1.6), and an overall shortening of distal hindlimb elements relative to the proximal element (fig. 1.7). Reduction of the distal hindlimb did not include metatarsal V, which attains at least 70% of the length of metatarsal IV in all sauropods, effecting a more symmetrical pes with five weight-bearing digits. Although lengthening of the forelimb and relative shortening of the distal hindlimb characterize all sauropods, future discoveries may suggest that these features are not correlated. Both early sauropod body fossils and ichnofossils suggest that quadrupedalism evolved in sauropods sometime prior to the Late Triassic (Wilson 2005b). Adoption of a quadrupedal pose within Sauropoda represents one of four such acquisitions within Dinosauria, each of which is associated with body size increase (Carrano 2000, 2005; see Carrano, chapter 8).

Associated with the proportional changes that facilitate a quadrupedal pose are specializations that allow a columnar, rather than flexed, limb posture. In basal dinosaurs, the disposition of limb articular surfaces and shaft curvature suggest a slightly flexed resting pose for the hip, knee, shoulder, and elbow joints. In sauropod outgroups, for example, the anteroposterior curvature of the femur offsets proximal and distal

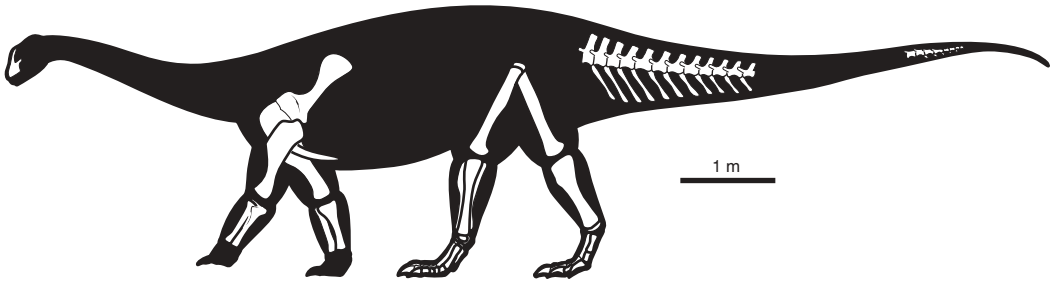


FIGURE 1.5. Silhouette skeletal reconstruction of *Gongxianosaurus shibeiensis* in left lateral view. Reconstruction based on unnumbered specimens pertaining to three individuals described by He et al. (1998). The majority of the skeleton pertains to a possibly subadult individual represented by an articulated pectoral girdle and forelimb and an articulated hindlimb that were discovered in association (He et al. 1998:1). The two series of articulated caudal vertebrae likely pertain to a distinct, adult individual, as does the premaxilla. Both the caudal series and the premaxilla have been scaled to the size of the appendicular elements. The relative size of missing elements (i.e., skull, neck, trunk, manus) was based on the basal sauropods *Vulcanodon* and *Shunosaurus*. Additional elements attributed to *Gongxianosaurus* (Luo and Wang 2000) are not included in this reconstruction because they have not yet been figured or described in detail.

condyles of the femur approximately 20° from horizontal (fig. 1.8A, B). Likewise, bony extensor processes on the ulna (olecranon) and tibia (cnemial crest) are prominent in immediate sauropod outgroups but do not project above the

dorsal surface of the ulna and tibia, respectively, in *Vulcanodon*, *Gongxianosaurus* (fig. 1.5), and most other sauropods (fig. 1.7). Reduction of these processes suggests a more columnar alignment of the elbow and knee joints. In addi-

TABLE 1.2
Limb Proportions in Selected Saurischian Genera

	FORE:HIND	MT III:TIBIA	REFERENCE(S)
Theropoda			
<i>Eoraptor</i>	0.43	0.43	Sereno (pers. comm.)
<i>Herrerasaurus</i>	0.47	0.52	Sereno (1993), Novas (1993)
Prosauropoda			
<i>Jingshanosaurus</i>	0.42	0.57	Zhang & Yang (1994)
<i>Lufengosaurus</i>	0.50	0.57	Young (1941)
<i>Plateosaurus</i>	0.52	0.48	Huene (1926)
?Sauropoda			
<i>Blikanasaurus</i>	—	0.36	Galton & van Heerden (1985)
<i>Antenonitrus</i>	0.81	0.38	Yates & Kitching (2003)
Sauropoda			
<i>Vulcanodon</i>	0.78	0.37, 0.32	Raath (1972), Cooper (1984)
<i>Gongxianosaurus</i>	0.62	0.38	He et al. (1988)
<i>Shunosaurus</i>	0.67	0.27	Zhang (1988)
<i>Omeisaurus</i>	0.90	0.28	He et al. (1988)
<i>Jobaria</i>	0.88	0.28	Sereno et al. (1999)
<i>Apatosaurus</i>	0.72	0.21	Gilmore (1936)
<i>Camarasaurus</i> *	0.83	0.24	Gilmore (1925)
<i>Camarasaurus</i>	(0.85)	0.24	McIntosh & al. (1996)
<i>Opisthocoelicaudia</i>	0.79	0.25	Borsuk-Bialynicka (1977)

NOTE: Forelimb length equals the sum of the lengths of the humerus, radius, and longest metacarpal; hindlimb length equals the sum of the lengths of the femur, tibia, and longest metatarsal. Asterisk(*) indicates measurement of a juvenile individual; parentheses indicate an estimated value. Abbreviation: mt, metatarsal.

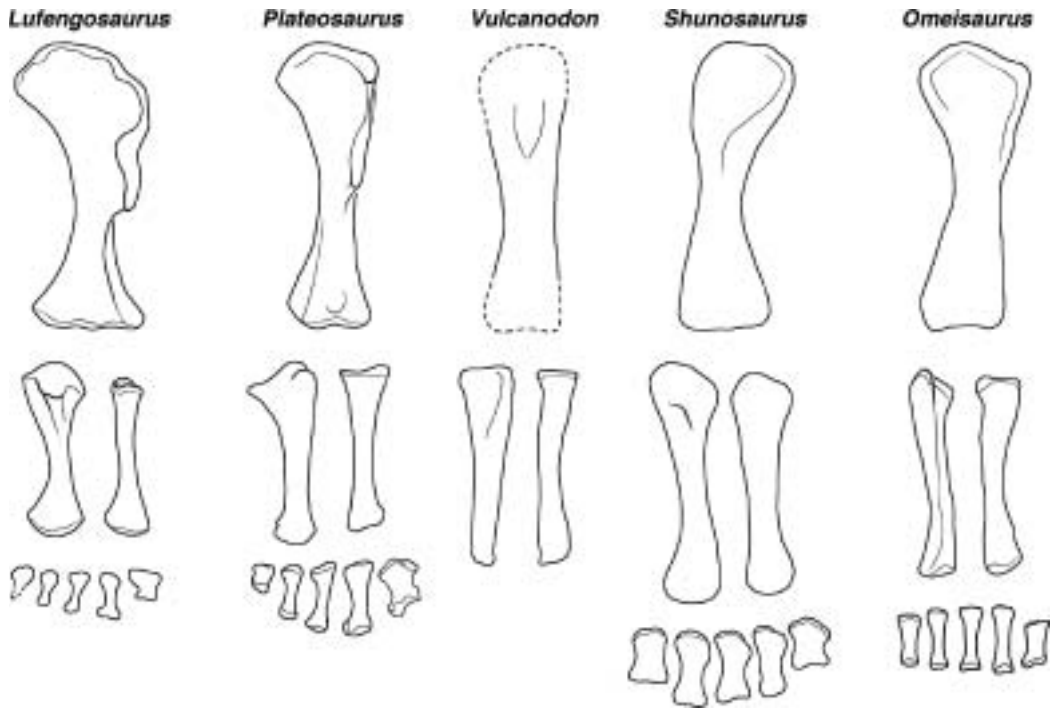


FIGURE 1.6. Forelimb proportions in the prosauropods *Lufengosaurus* and *Plateosaurus* and the basal sauropods *Vulcanodon*, *Shunosaurus*, and *Omeisaurus*. Forelimbs have been scaled to the same humeral length. Based on Young (1947), Huene (1926), Raath (1972), Zhang (1988), and He et al. (1998), respectively.

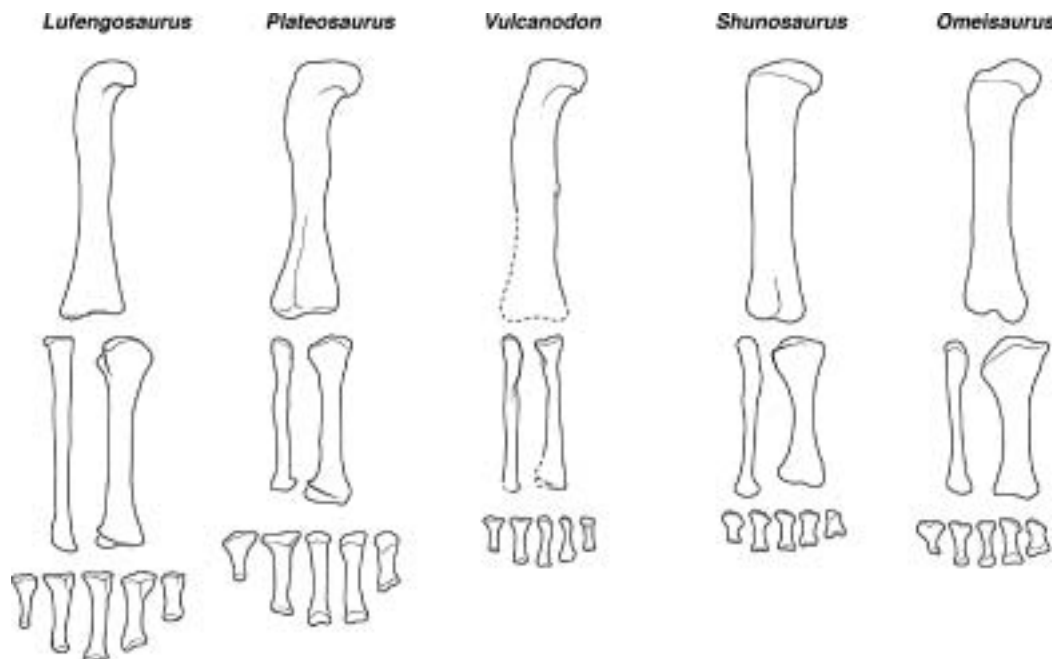


FIGURE 1.7. Hindlimb proportions in the prosauropods *Lufengosaurus* and *Plateosaurus* and the basal sauropods *Vulcanodon*, *Shunosaurus*, and *Omeisaurus*. Hindlimbs have been scaled to the same femoral length. Based on Young (1947), Huene (1926), Raath (1972), Zhang (1988), and He et al. (1998), respectively.

FIGURE 1.8. Femoral curvature in the saurischian dinosaurs *Herrerasaurus* (A), *Massospondylus* (B), *Vulcanodon* (C), and *Isanosaurus* (D). Femora are figured in right medial view and have been scaled to the same length to facilitate comparison. The left femur of *Isanosaurus* has been reversed. Based on Novas (1993), Cooper (1981), Cooper (1984), and Buffetaut et al. (2000), respectively.

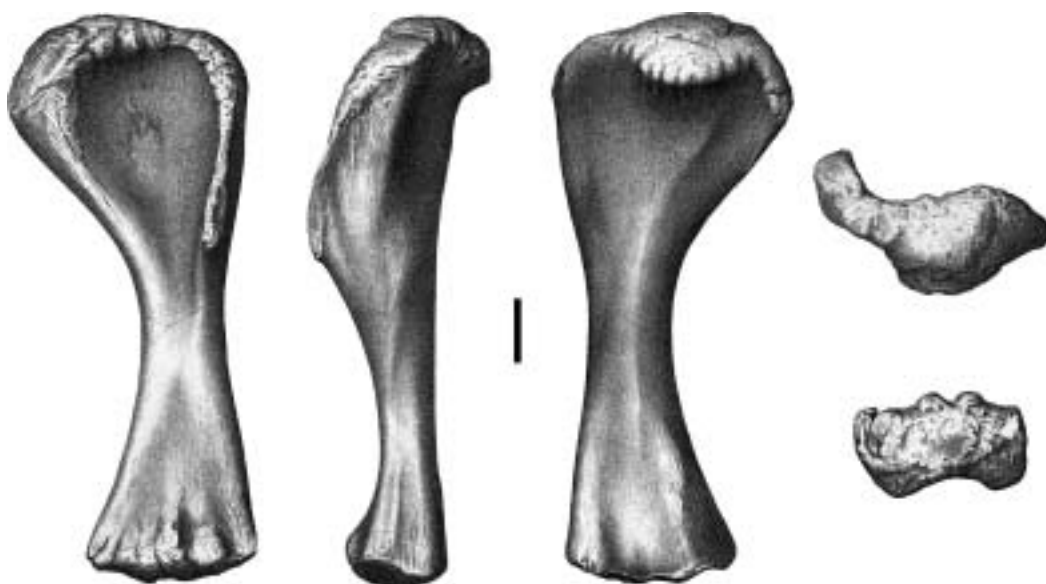
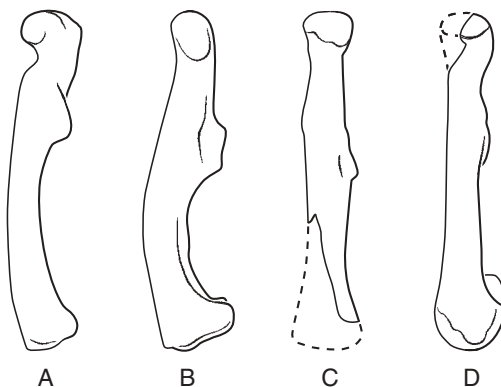


FIGURE 1.9. Left humerus of *Camarasaurus grandis* (YPM 1901) in anterior (left), lateral (middle), posterior (right), proximal (top), and distal (bottom) views (from Ostrom and McIntosh 1966:pl. 49). Scale bar equals 30 cm.

tion, the longest weight-bearing elements in the skeleton (humerus, femur) have eccentric mid-shaft cross sections that are broader mediolaterally than anteroposteriorly. Distal limb elements (radius/ulna, tibia/fibula) do not share this cross-sectional geometry, but they bear weight in tandem and are together broader mediolaterally than anteroposteriorly.

Reduced ossification of limb elements represents the third major appendicular specialization characterizing Sauropoda. A conspicuous feature of sauropod limb elements is that their artic-

ular ends have a rugose, irregular surface, whereas their shafts are smooth. Owen (1841:461) recognized this feature in *Cetiosaurus*, noting that “the articular surfaces which are preserved are covered with large tubercles for the attachment of thick cartilage.” Similarly, Marsh (1878:413) described the humerus of *Camarasaurus* as “rough, and well covered with cartilage” (fig. 1.9). The thickness of this cartilage cap has not yet been estimated but is implied in articulated skeletons by the difference in volumes of the acetabulum and femoral head. The

proximal carpal and tarsal elements have few to no nonarticular surfaces and are completely made up of rough, rugose bone. Consequently, the configuration of sauropod wrist and ankle elements relative to adjacent elements is difficult to determine because little of the articular surfaces remains. Distal carpals have not been identified in any sauropod skeleton, and distal tarsals have only been recovered for *Gongxianosaurus*, in which discoidal ossifications are preserved atop metatarsal III and between metatarsal IV and metatarsal V (He et al. 1998:fig. 4C; fig. 1.5). Retention of ossified distal tarsals may suggest that *Gongxianosaurus* is the most primitive sauropod, but their absence in other basal sauropods (e.g., *Vulcanodon*) has not yet been confirmed by articulated material.

EUSAUROPODA

Eusauropoda is the node-based group including *Shunosaurus lii*, *Saltasaurus loricatus*, their most recent common ancestor, and all descendants (fig. 1.4). This definition specifies all named sauropods except *Vulcanodon*, *Gongxianosaurus*, and *Rhoetosaurus*, as well as the possible early sauropods *Blikanasaurus* and *Antenonitrus*. The oldest well-preserved eusauropod is the Middle Jurassic *Shunosaurus*, which is known from several complete skeletons (Zhang 1988). Consequently, many of the synapomorphies diagnosing Eusauropoda are ambiguous and may obtain a broader distribution once basal forms are known more completely. Eusauropod synapomorphies greatly outnumber those of any other node within Sauropoda—Wilson (2002) reported 53, fewer than half of which could be scored in more basal taxa. Thus, the ambiguous (i.e., cranial and axial) synapomorphies may have evolved as early as the divergence of Sauropoda from Prosauropoda in earliest Late Triassic (Carnian, 220 mya [Flynn et al. 1999]). The unambiguous (i.e., hindlimb) synapomorphies, on the other hand, signal more recent modifications since the divergence of Eusauropoda from Sauropoda in the Late Triassic (Rhaetian, 210 mya [Buffetaut et al. 2000]).

HERBIVOROUS SPECIALIZATIONS

The Middle Jurassic *Shunosaurus* is the earliest-appearing sauropod known from well-preserved cranial remains. All cranial synapomorphies of Eusauropoda are ambiguous and may later be shown to characterize more inclusive groups. *Shunosaurus* possessed a sophisticated dental apparatus that is highly modified relative to that of prosauropods, indicating that eusauropods modified the shape of the crowns as well as their arrangement along the tooth row. Principal among these changes is the acquisition of precisely occluding dentition, a feature that is unknown elsewhere in Saurischia.

Prosauropods and theropods primitively have lower tooth rows that extend the length of the dentary but upper tooth rows that extend farther posteriorly to midorbit. With different lengths and numbers of teeth, upper and lower teeth have mismatched occlusion that generates no regular wear pattern. Additionally, prosauropods and theropods have tooth rows that are relatively straight in dorsal or ventral view. Right and left sides meet at an acute angle, and none of the teeth are oriented transversely (fig. 1.10A, B). Sauropods differ in all of these respects. Nearly all sauropods known by cranial remains have tooth rows that are of even length and contain similar numbers of teeth. The upper tooth row terminates at or in front of the antorbital fenestra, and the dentary always has an edentulous region posterior to the last tooth. In dorsal view, the tooth rows are curved rather than straight, and at least two teeth are oriented transversely (fig. 1.10C, D). Together, these changes signal precise occlusion in sauropods, as evidenced by crown wear facets generated by tooth-to-tooth wear (Calvo 1994). In dorsal view, the tooth rows are outwardly arched rather than straight, and at least two teeth are oriented transversely (fig. 1.10C, D). The entire tooth row is transversely oriented in some sauropods (see “Diplodocoidea,” below). Most sauropods develop an imbricate arrangement of teeth in which the mesial edge of each tooth is overlapped by the distal edge of the preceding tooth.

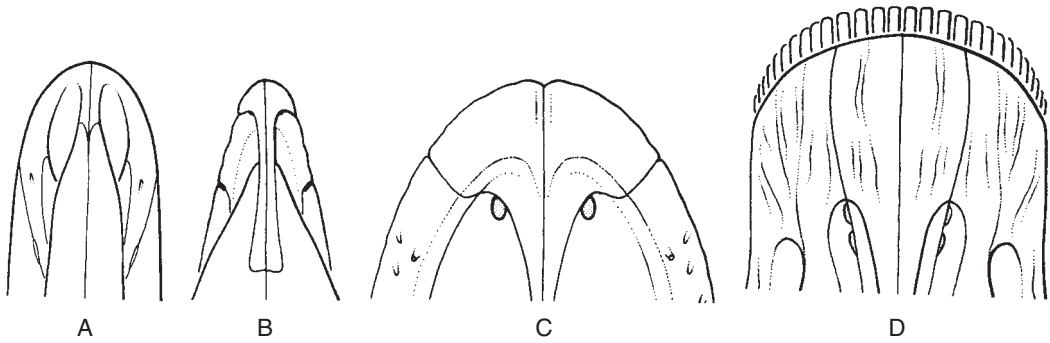


FIGURE 1.10. Snouts of the theropod *Herrerasaurus* (A), the prosauropod *Plateosaurus* (B), and the sauropods *Brachiosaurus* (C) and *Diplodocus* (D) in dorsal view. Based on reconstructions from Sereno (1993) and Wilson and Sereno (1998)

Eusauropod tooth crowns also have distinctive shape and texture. All teeth have a characteristically wrinkled enamel texture whose function is unknown. Coarseness of enamel wrinkling varies to some extent within sauropods, with narrow-crowned teeth usually exhibiting much finer wrinkling than broad tooth crowns. Sauropod tooth crowns are primitively spatulate, with a D-shaped cross section.

Precise tooth-to-tooth occlusion is not lost within Sauropoda, but many of the other herbivorous innovations are modified in later lineages, principally Diplodocoidea (see Sereno and Wilson, chapter 5). Because all known sauropod skulls share these features, their sequence of acquisition is not yet known.

NECK ELONGATION

The primitive saurischian precaudal vertebral count is 27, although the relative number of cervical, dorsal, and sacral vertebrae vary in Theropoda (9-15-3, respectively) and Prosauropoda (10-14-3). Vertebral counts are not known for non-eusauropods, but *Vulcanodon* has a sacrum with four coossified vertebrae (Raath 1972). The fourth sacral vertebra in sauropods is a caudosacral, based on osteological and developmental evidence (Wilson and Sereno 1998). The eusauropod *Shunosaurus* (13-13-4) is the basalmost sauropod genus for which the vertebral count is known. Compared to outgroups, eusauropods are characterized by two neck elongation events: (1) incorporation of one dorsal vertebra into the cervical series and (2) duplication of two cervical

vertebrae to achieve the primitive eusauropod precaudal count of 13-13-4.

Later, *Patagosaurus*, *Omeisaurus*, and more derived sauropods acquire a fifth sacral without changing the precaudal count (13-12-5), which most likely represents the incorporation of a dorsal vertebra into the sacrum (rather than the addition of a cervical and loss of a dorsal). Nearly all of the dozen subsequent neck-lengthening events characterize individual neosauropod genera and are not synapomorphies of larger clades. The exception is Diplodocidae (15-10-5), which incorporated two dorsal vertebrae into the cervical series. Thus, there is no progressive increase in neck length within Sauropoda; rather, individual genera were specialized for their neck length. All three means of neck lengthening (incorporation, duplication, elongation) were employed within Sauropoda.

HINDFOOT POSTURE

Theropods and prosauropods are interpreted as having a digitigrade pes, a posture in which the heel and proximal metatarsals were held off the ground, and the distal metatarsals and phalanges contacted the substrate (Carrano 1997). Eusauropods are characterized by several changes that together result in a unique hind-foot posture that is easily recognized in footprints (fig. 1.11). These include the independent modification of the length, arrangement, and robustness of the metatarsus, as well as the reduction in the number and size of the pedal phalanges.

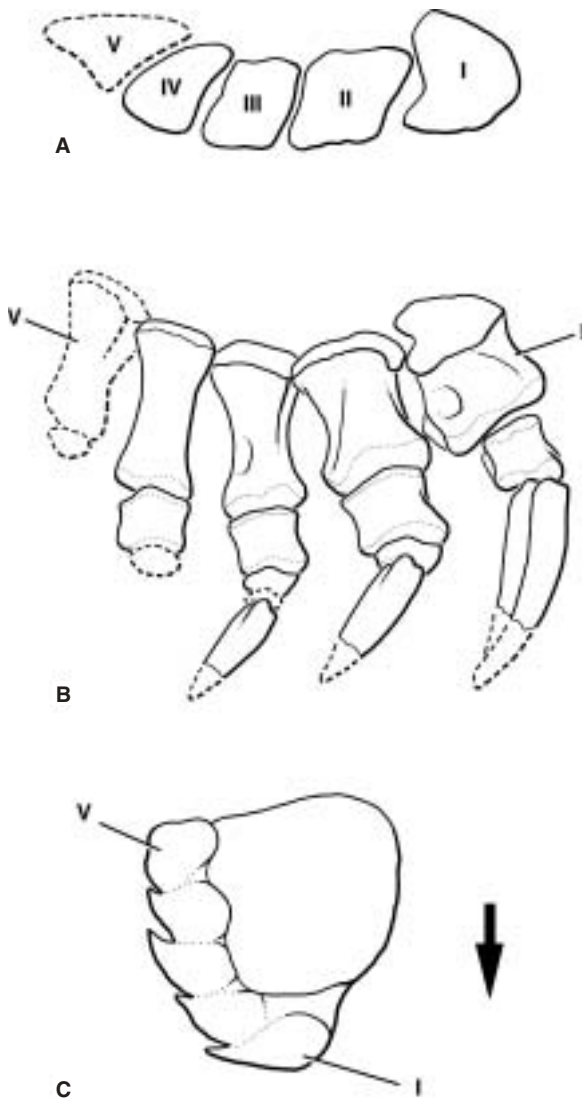


FIGURE 1.11. Right pes of *Apatosaurus* in proximal (A) and dorsal (B) views; C, right pes print of *?Brontopodus* oriented relative to the trackway midline (arrow). *Apatosaurus* modified from Gilmore (1936:figs. 25, 27, 28); *?Brontopodus* modified from Thulborn (1990:fig. 6.16f). Abbreviations: I-V, digits I-V.

Sauropod outgroups have long distal hindlimbs, in which the metatarsus accounts for 40% to 50 of the tibial length (table 1.2). In contrast, the eusauropod metatarsus is markedly abbreviated and comprises less than 25% of the tibial length. The proportions of the basal sauropods *Vulcanodon* and *Gongxianosaurus*, as well as those of *Blikanasaurus* and *Antenonitrus*, are intermediate between sauropod outgroups and eusauropods such as *Shunosaurus* (figs. 1.5, 1.7, table 1.2). In addition to these proportional changes, the eusauropod metatarsus attains a spreading configuration in which the proximal

ends are not in mutual contact, as they are in sauropod outgroups. In dorsal view, for example, the metatarsal shafts are separated by intervening spaces (fig. 1.11B). These changes effect a more spreading hindfoot posture in which the metatarsus was held in a subhorizontal, rather than subvertical, orientation. Wilson and Sereno (1998:41) recognized this as a “semi-digitigrade” foot posture. Carrano (1997:fig. 1B) termed the inferred foot posture in sauropods “subunguligrade,” referring to the specialized foot posture of hippopotamids, rhinocerotids, and proboscideans, in which the metatarsus is held

vertically, a fleshy pad supports the foot, and the penultimate and ungual phalanges contact the substrate. Although the hypothesized sauropod hindfoot posture is similar to “sub-unguligrady” (viz. the fleshy heel pad), the metatarsus is thought to have been held in a nearly horizontal rather than a vertical orientation, and the nonungual phalanges are hypothesized to have contacted the substrate. The term *semi-digitigrady* is used here to refer to the foot posture hypothesized for Eusauropoda.

Although the earliest sauropods are interpreted as having a digitigrade posture, there are no footprints attributed to sauropods that indicate such a foot posture. Rather, the earliest sauropod trackways bear elongate pes prints that indicate a semidigitigrade hindfoot posture (e.g., Portezuelo trackways [Marsicano and Barredo 2003], *Tetrasauropus* [Lockley et al. 2001]). This 22 million- to 44 million-year discrepancy between the first appearance of semi-digitigrade pedal posture in the body fossil and that in the ichnofossil records may indicate early appearance of eusauropods, homoplasy, or that hindfoot posture has been erroneously interpreted in early sauropods. Based on a stratocladistic analysis of ichnological and body fossil data, Wilson (2005b) suggested that semi-digitigrady evolved in the Late Triassic and was either reversed or misinterpreted in the early sauropods *Vulcanodon* and *Gongxianosaurus*. A preliminary study of skeletal remains referred to *Plateosaurus* has inferred a less digitigrade posture than traditionally posited for prosauropods (Sullivan et al. 2003), which underscores difficulties in determining locomotor posture from osteology.

In addition to revising the temporal origin of semi-digitigrade hindfoot posture in early sauropods, ichnofossils indicate that the subhorizontal foot was supported by a fleshy heel (fig. 1.11C).

Eusauropods are also characterized by a departure from the within-pes proportions that characterize other saurischians. Body weight in theropods and prosauropods is accommodated by three and four pedal digits, respectively. In these taxa, shaft breadth varies little across the

metatarsus (table 1.2), implying that body weight was borne subequally by its constituent elements. The eusauropod pes, in contrast, displays marked asymmetry of metatarsal shaft diameters in which metatarsal I is broader than all others. The disparity among metatarsals II–V becomes more pronounced in more derived sauropods. *Omeisaurus*, *Mamenchisaurus*, and Neosauropoda are diagnosed by a metatarsus in which the minimum shaft diameters decrease laterally such that the diameters of metatarsals III and IV are 50% to 60% that of metatarsal II (table 1.3). Hatcher (1901:51) noted this pattern and suggested that “the weight of the body was borne by the inner side of the foot.” This feature is manifest in well-preserved sauropod footprints, in which the inner margin is more deeply impressed than the outer margin (e.g., Pittman and Gillette 1989:322).

The acquisition of a semidigitigrade hindfoot posture is accompanied by reduction of the phalangeal portion of the pes. Prosauropods and basal theropods retain a full complement of pedal phalanges on digits I–IV that invariably number 2-3-4-5, each digit bearing an ungual phalanx (table 1.4). The possible basal sauropod *Blikanasaurus* retains the same count. Although the pedal phalangeal formula is not known in *Vulcanodon*, its penultimate phalanges resemble those of prosauropods and are not drastically shortened (Cooper 1984:figs. 34, 35). The articulated hindfoot of *Gongxianosaurus* confirms that basal sauropods maintained a high number of phalanges (2-3-4-5), which themselves were longer than broad (fig. 1.5). The pes of eusauropods is reduced in both the number and the size of phalangeal elements. The penultimate phalanx in digits II–IV is reduced to a plate-shaped disc or lost in *Shunosaurus*, *Omeisaurus*, and various neosauropods. The greatest number of phalanges retained in eusauropod digit IV is three (e.g., *Shunosaurus*, *Omeisaurus*, *Camarasaurus*), two fewer than the outgroup condition of five. Despite the loss of two phalanges, an ungual is maintained on digit IV. Eusauropods clearly demonstrate non-terminal phalangeal reduction, which maintains the size and functionality of the unguals amid substantial

TABLE 1.3
Pedal Proportions in Select Saurischian Genera

	MT I:II:III:IV	MT V:IV
	(MINIMUM BREADTH)	(LENGTH)
Theropoda		
<i>Eoraptor</i>	—	0.56
<i>Herrerasaurus</i>	0.60:0.90:0.95:1	0.59
Prosauropoda		
<i>Jingshanosaurus</i>	1.0:1.0:1.0:1.0	0.55
<i>Lufengosaurus</i>	0.84:0.84:0.84:1	0.56
<i>Plateosaurus</i>	1.0:1.0:1.0:1.0	0.61
?Sauropoda		
<i>Blikanasaurus</i>	1:1:0.89:0.65	0.53
<i>Antenonitrus</i>	0.62:0.86:1?	—
Sauropoda		
<i>Gongxianosaurus</i>	—	0.64
<i>Vulcanodon</i>	0.73:0.64:0.82:1	0.75
<i>Shunosaurus</i>	1:0.92:0.85:0.85	0.70
<i>Omeisaurus</i>	1:0.87:0.56:0.62	0.90
<i>Apatosaurus</i>	1:0.75:0.50:0.55	—
<i>Camarasaurus</i> *	—	0.75
<i>Camarasaurus</i>	1:0.69:0.44:0.50	0.81
<i>Opisthocoelicaudia</i>	1:0.78:0.67:0.44	0.78
" <i>Barosaurus</i> "	1:0.68:0.41:0.36	0.95

NOTE: References as in Table 1.2; "*Barosaurus*" data from Janensch (1961). Asterisk (*) indicates measurement of a juvenile individual.

digital shortening. Non-terminal phalangeal reduction may have also produced a mammal-like phalangeal count in cynodont-grade synapsids (Hopson 1995).

Further modification of the pedal configuration described above diagnoses sauropods more derived than *Shunosaurus*. In *Barapasaurus*, *Omeisaurus*, and all neosauropods, the four pedal unguals are directed laterally with respect to the digit axis. This reorientation of the pedal unguals is accomplished by a beveled proximal articular surface and twisting of the axis of the ungual. Wilson and Sereno (1998) scored the basal sauropods *Vulcanodon* and *Shunosaurus* with the primitive condition (i.e., anteriorly directed unguals), and the primitive condition appears to characterize *Blikanasaurus*, *Antenonitrus*, and *Gongxianosaurus*. Although laterally directed pedal unguals first appear in the body fossil

record in the Lower Jurassic *Barapasaurus*, they appear 13 million to 35 million years earlier in the ichnofossil record. Upper Triassic *Tetrasauropus* trackways (fig. 1.11) clearly preserve impressions of unguals deflected laterally relative to the axis of the pes (Lockley et al. 2001), indicating that this feature evolved earlier than implied by body fossils alone (Wilson 2005b).

NEOSAUROPODA

Neosauropoda is the node-based group including *Diplodocus longus*, *Saltasaurus loricatus*, and all descendants of their most recent common ancestor (Wilson and Sereno 1998; fig. 1.4). Within this node-based group, the two reflexive stem-groups (*Diplodocoidea*, *Macronaria*) form a stable node–stem triplet (boldface type indicates node-based definitions; regular type indicates stem-based definitions).

TABLE 1.4
Manual and Pedal Phalangeal Counts in Select Saurischian Genera

	MANUS	PES
Theropoda		
<i>Eoraptor</i>	2*-3*-4*-1-0	2*-3*-4*-5*-1
<i>Herrerasaurus</i>	2*-3*-4*-1-0	2*-3*-4*-?-1
Prosauropoda		
<i>Jingshanosaurus</i>	2*-3*-4*-3*-1	2*-3*-4*-5*-1
<i>Lufengosaurus</i>	2*-3*-4*-3-1	2*-3*-4*-5*-1
<i>Plateosaurus</i>	2*-3*-4*-3-2	2*-3*-4*-5*-2
?Sauropoda		
<i>Blikanasaurus</i>	—	2*-3*-4*-?5*-?
<i>Antenonitrus</i>	—	—
Sauropoda		
<i>Vulcanodon</i>	—	—
<i>Gongxianosaurus</i>	—	2*-3*-4*-5*-?
<i>Shunosaurus</i>	2*-2-2-2-2	2*-3*-3*-3*-2
<i>Omeisaurus</i>	2*-2-?-?-1	2*-3*-3*-3*-2
<i>Diplodocus</i>	—	2*-3*-3?-2-0
<i>Camarasaurus</i>	2*-1-1-1-1	2*-3*-4*-2*-?
<i>Brachiosaurus</i>	2*-1-1-1-1	—
<i>Opisthocoelicaudia</i>	0-0-0-0-0	2*-2*-2*-1?-?

NOTE: Asterisk (*) indicates a clawed digit. References as in Table 1.2; *Diplodocus* data from Hatcher (1901).

Neosauropoda Bonaparte 1986b—

Diplodocus longus, *Saltasaurus loricatus*, their most recent common ancestor, and all descendants.

Diplodocoidea Upchurch 1995—All

neosauropods more closely related to *Diplodocus longus* than to *Saltasaurus loricatus*.

Macronaria Wilson and Sereno 1998—All

neosauropods more closely related to *Saltasaurus loricatus* than to *Diplodocus longus*.

Bonaparte (1986b:369) originally referred to neosauropods as the “end-Jurassic” sauropods—members of Dicraosauridae, Diplodocidae, Camarasauridae, and Brachiosauridae. Although no definitive skeletal remains referable to this group have been recorded prior to the “end Jurassic,” the phylogenetic definition of Neosauropoda is not temporally bounded.

Cretaceous neosauropods include rebbachisaurid diplodocoids and Titanosauria (left out of Bonaparte’s definition), and the near-simultaneous appearance of the principal neosauropod lineages in the Late Jurassic implies that one or more of them were present in the Middle Jurassic. Neosauropoda accommodates the majority of sauropod genera and encompasses most of its morphological diversity.

The recently described *Jobaria* has been resolved as the outgroup of Neosauropoda (Sereno et al. 1999; Wilson 2002; fig. 1.4) on the basis of a number of advanced features they share. *Jobaria* has been alternatively resolved within Neosauropoda as a basal macronarian (Upchurch et al. 2004), but the evidence supporting this hypothesis is presently outweighed by the retention of several primitive characters. The relevant synapomorphies of *Jobaria* + Neosauropoda is discussed alongside those distinguishing Neosauropoda. *Jobaria* and

Neosauropoda can be distinguished by a novel forefoot posture in which the manus is arranged into a tight semicircle and held vertically. Neosauropoda, in turn, is distinguished by marked reduction in the number and ossification of carpal and tarsal elements.

REDUCED OSSIFICATION OF CARPALS AND TARSALS

The evolutionary history of sauropod dinosaurs documents reduced ossification of carpal and tarsal elements. This tendency may be related to the reduced ossification that characterizes all sauropod weight-bearing elements (fig. 1.9; see Sauropoda, above). In the carpus of *Herrerasaurus* (Sereno 1993:fig. 15) and *Eoraptor* (P. Sereno, pers. comm.), a large radiale, ulnare, and series of four distal carpals are present. In prosauropods, the proximal carpals are very reduced or absent (unossified), but the medial three distal carpals (dc 1–3) are present and articulate with the proximal ends of metacarpals I–III, respectively (e.g., *Massospondylus* [Cooper 1981:figs. 35, 36], *Lufengosaurus*, [Young 1941:fig.15]). The earliest sauropod for which a carpus is known preserves only three block-shaped carpals that decrease in size laterally, based on their presumed position (*Shunosaurus* [Zhang 1988:figs. 2, 48]). Because they were found closely associated with metacarpals I–III, rather than with the radius and ulna, Wilson and Sereno (1998:47) regarded them as distal carpals. Other nonneosauroopods show a similar pattern: *Omeisaurus* has three carpals of decreasing size (He et al. 1988), as does *Jobaria* (Sereno et al. 1999). In *Jobaria*, one surface of the largest carpal has two triangular facets that match the proximal surfaces of metacarpals I and II, suggesting that it is a distal carpal; the other surface bears no discernible articular surface. Thus prosauropods and basal sauropods retain only three ossified distal carpals and lack ossified proximal carpals. Neosauropods further reduce the number of ossified carpals to two or fewer. In *Camarasaurus*, two block-shaped carpals are present and fitted to the metacarpals. As Osborn (1904:182) noted, the fitted articulation between the carpals and the

metacarpals suggests that the primary axis of the wrist joint was positioned more proximally, between these carpals and the bones of the forearm. Other neosauroopods have a single carpal element positioned above metacarpals II and III (e.g., *Apatosaurus* [Hatcher 1902; Gilmore 1936]). One individual of *Apatosaurus*, however, preserves a carpal element hypothesized to articulate with metacarpals IV and V (Filla and Redman 1994). As discussed later, some sauropods lack ossified carpus altogether (see “Macronaria” below).

In prosauropods and basal theropods, the body of the astragalus (i.e., the portion below the ascending process) is trapezoidal. In the prosauropod *Massospondylus* and the basal theropod *Herrerasaurus*, the proximodistal and anteroposterior depth of the medial side of the astragalus equals or exceeds that of the lateral side (Cooper 1981:fig. 71f; Novas 1989:figs. 2.5–10). The basal sauropod *Shunosaurus* appears to retain the primitive condition, based on the only available view (anterior) of the astragalus (Zhang 1988:fig. 54). In contrast, the astragalus in *Jobaria* and Neosauropoda appears wedge-shaped in both proximal and anterior views. In *Jobaria*, for example, the proximodistal and anteroposterior depth of the astragalus diminishes markedly toward its medial side. In addition, in proximal and distal views, the primitive posteromedial corner of the astragalus is absent, and the astragalus has a subtriangular, rather than subrectangular, shape.

FOREFOOT POSTURE

Prosauropods and basal ornithischians retain the primitive dinosaur condition in which the proximal ends of the metacarpals are not closely appressed and are only slightly arched in articulation. The metacarpals are subrectangular in proximal view, and their intermetacarpal articular surfaces do not extend down the shaft. For example, the articulated manus of *Massospondylus* is cupped approximately 90° between metacarpal I and metacarpal V, and most of this arch occurs in metacarpals I and III, whose lateral articular surfaces form an acute angle with the anterior surface (Cooper 1981:fig. 37). A similar condition is present in basal ornithischians (e.g.,

Lesothosaurus [Sereno 1991]). The condition in theropods, however, differs from that of prosauropods and basal ornithischians. Although the manus is bound proximally in theropods, the metacarpus retains the same 90° proximal curvature present in prosauropods and ornithischians (*Herrerasaurus* [Sereno 1993, fig. 15], *Deinonychus*, [Ostrom 1969:fig.62]). The configuration and pose of the metacarpus of basal sauropods such as *Shunosaurus* and *Omeisaurus* are not agreed on. Whereas Wilson and Sereno (1998) suggested that their forefoot posture resembles that of prosauropods and basal ornithischians, in which the manus is spreading and only slightly arched ventrally, both Upchurch (1998) and Bonnan (2003) interpreted them as having the derived, digitigrade forefoot posture that characterizes *Jobaria* and neosauropods.

The metacarpus of *Jobaria* and neosauropods is arranged into a tightly bound, digitigrade structure that is hypothesized to have contacted the substrate at the metacarpal-phalangeal joints. The metacarpals arranged into a vertical cylinder in which all are subequal in length and have well-developed intermetacarpal articular surfaces that extend distally to midshaft (e.g., *Camarasaurus* [Ostrom and McIntosh 1966:figs. 55–59]). Proximally, the metacarpal heads are wedge-shaped and articulate in a tight arc of approximately 270°. This tubular arrangement of the metacarpals is due to their medial and lateral articular surfaces meeting the external (anterior) aspect of the metacarpal at an acute angle. A tightly curled, digitigrade manus, defined by these osteological features, is present without exception in Neosauropoda.

Although cladistic studies have regarded digitigrade forefoot posture as diagnostic of Eusauropoda (Upchurch 1998), Neosauropoda (Upchurch 1995; Wilson and Sereno 1998), or *Jobaria* + Neosauropoda (Wilson 2002), ichnofossils suggest a much earlier origin. Upper Triassic trackways from North America (Lockley et al. 2001) and South America (Marsicano and Barredo 2004), as well as Lower Jurassic trackways from Italy (Dalla Vecchia 1994), Poland (Gierlinski 1997), and Morocco (Ishigaki 1988),

document sauropod trackmakers with a digitigrade manus (fig. 1.12). These trackways record the appearance of a digitigrade forefoot posture 22 million to 44 million years earlier than predicted by Upchurch (1998) and 57 million years earlier than predicted by Wilson and Sereno (57 my). This discrepancy can be interpreted as the early appearance of Neosauropoda or the early appearance of digitigrade foot posture in non-neosauropods. Assessment of forefoot posture in non-neosauropods was based solely on the published illustrations of the only basal taxa preserving manual remains, *Shunosaurus* (Zhang 1988:fig. 49, pl. 14) and *Omeisaurus* (He et al. 1988:figs. 47, 48; pl. 14, figs. 4–6). On the basis of these illustrations, Wilson and Sereno (1998:48) argued that *Shunosaurus* and *Omeisaurus* lacked a digitigrade forefoot posture because their metacarpals have poorly defined intermetacarpal articular surfaces. Other dinosaurs with a vertically oriented, digitigrade foot posture have metapodials that are tightly appressed (bound) proximally and have well-marked intermetapodial facets that extend down their shafts (e.g., *Herrerasaurus* pes, *Iguanodon* manus). Additionally, the metacarpals of *Shunosaurus* and *Omeisaurus* are subrectangular proximally, implying that they were only slightly arched proximally (~90°) in articulation, unlike *Jobaria* and neosauropods (Wilson and Sereno 1998:fig. 40). Upchurch (1998:68), however, argued that despite these considerations, *Shunosaurus* and *Omeisaurus* had forefeet that were both digitigrade and U-shaped proximally, features he regarded as a single character (table 1.1). Trackways from Italy, Poland, and Morocco preserve a digitigrade manus that is not tightly arched (fig. 1.12), suggesting that the bound metatarsus and its tightly arched configuration are independent characters. The trackways further suggest that the bound metacarpus was acquired earlier in sauropod history than was the tubular metacarpus.

DIPLODOCOIDEA

One of two reflexive neosauropod stem-groups, Diplodocoidea includes all neosauropods more

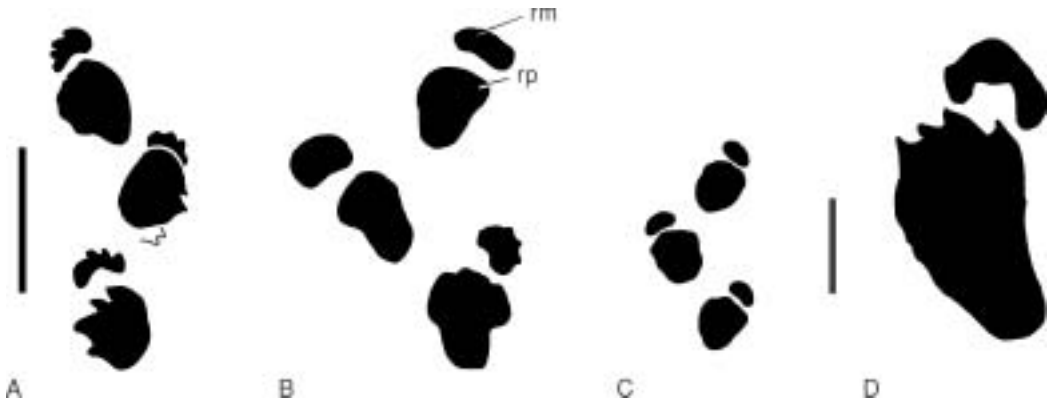


FIGURE 1.12. Early sauropod footprints. (A), *Tetrasauropus* trackway from the Upper Triassic (Chinle Group) of Cub Creek (based on Lockley et al. (2001); (B), trackway from the Lower Jurassic (Pliensbachian) of the Atlas Mountains, Morocco (based on Farlow 1992:fig. 2a, b); (C), trackway (ROLM 28) from the Lower Jurassic (Hettangian–Pliensbachian) of Lavini di Marco, Italy (based on Dalla Vecchia 1994:fig. 2); (D) manus–pes pair of *?Parabrontopodopus*, from the Hettangian of the Holy Cross Mountains, Poland (based on Gierlinski 1997:fig. 1b). (A–C) are oriented relative to trackway midline; trackway midline cannot be determined for (D). Scale equals 50 cm for (A), 10 cm for (B–D).

closely related to *Diplodocus longus* than to *Saltasaurus loricatus* (Wilson and Sereno 1998). By this definition, Diplodocoidea unites *Haplocanthosaurus*, Rebbachisauridae, Dicraeosauridae, and Diplodocidae. The position of *Haplocanthosaurus* as the basalmost diplodocoid is weakly supported and awaits further confirmation by additional material. Apart from the position of *Haplocanthosaurus*, the relationships within and between diplodocoid families are stable. The three families have stem-based definitions specifying all taxa more closely related to their namesake genus than to either of the other two namesake genera. Sereno (1998) formally defined Dicraeosauridae and Diplodocidae; Rebbachisauridae is phylogenetically defined for the first time here. A revised phylogenetic nomenclature for Diplodocoidea and its subgroups is proposed below (boldface type indicates node-based definitions; regular type indicates stem-based definitions):

Diplodocoidea Upchurch 1995—All neosauropods more closely related to *Diplodocus longus* than to *Saltasaurus loricatus*.

Rebbachisauridae Bonaparte 1997—All diplodocoids more closely related to *Rebbachisaurus garasbae* than to *Diplodocus longus*.

Flagellicaudata Harris and Dodson 2004—*Diplodocus longus*, *Dicraeosaurus hansemanni*, their most recent common ancestor, and all descendants.

Dicraeosauridae Janensch 1929b—All diplodocoids more closely related to *Dicraeosaurus hansemanni* than to *Diplodocus longus*.

Diplodocidae Marsh 1884—All diplodocoids more closely related to *Diplodocus longus* than to *Dicraeosaurus hansemanni*.

This arrangement of taxon names affords a node–stem triplet within Diplodocoidea that unites two well known stem-based groups (Diplodocidae, Dicraeosauridae) whose sister-taxon relationship has been long recognized.

Like all neosauropod lineages, earliest diplodocoids are found in Upper Jurassic rocks. Diplodocidae is currently restricted to the Late Jurassic of North America (*Diplodocus*, *Apatosaurus*, *Barosaurus*, *Seismosaurus*) and Africa (“*Barosaurus*” *africanus*). Dicraeosauridae is also known from the Late Jurassic of Africa (*Dicraeosaurus*) but survives into the Early Cretaceous of South America (*Amargasaurus*). Rebbachisauridae is the latest surviving diplodocoid clade and is restricted to the Cretaceous of Africa (*Nigersaurus*, *Rebbachisaurus*),

TABLE 1.5
Data Support in the Two Neosauropod Lineages Macronaria and Diplodocoidea

	MACRONARIA	DIPLODOCOIDEA
number of taxa	11	9
cranial		
% missing data	58	55
% character support	30	39.5
axial		
% missing data	35	33
% character support	37	45.5
appendicular		
% missing data	41	55
% character support	33	15

NOTE: The relative proportions of cranial, axial, and appendicular characters supporting the interrelationships of these clades are compared below. Missing data scores were based on Wilson (2002:table 8). Total percentage missing data was higher in Diplodocoidea (48%) than Macronaria (44%).

South America (*Limaysaurus*), and Europe (*Histriasaurus*, *Salas rebbachisaurid*).

The features supporting the relationships within Diplodocoidea and differentiating its composite genera are supported by a predominance of cranial and axial synapomorphies (table 1.5). These include a major transformation in skull shape and a highly modified vertebral column, discussed below.

HERBIVOROUS SPECIALIZATIONS

As discussed above, the basic sauropod skull plan is quite distinct from those of basal saurischians (see “Eusauropoda” below). The set of features comprising this plan evolved sometime prior to the first appearance of Eusauropoda (Middle Jurassic) and, with few exceptions, was retained until their last appearance (latest Cretaceous). The diplodocoid skull is perhaps the most unique among Sauropoda, and may be thought of as the result of exaggeration of several eusauropod features combined with novelties that evolved stepwise within Diplodocoidea.

The broadening of the snout and shortening of the tooth row that characterizes Eusauropoda is exaggerated in diplodocoids, which evolved upper and lower tooth rows that are restricted

anterior to the antorbital fenestra and arranged in jaws that are rectangular in dorsal view (fig. 1.10). In dicraeosaurids and diplodocoids, most teeth are positioned on the transverse portion of the jaw ramus. Rebbachisaurids further this trend by restricting all teeth to the transverse portion of the jaw, which extends lateral to the ramus (see Sereno and Wilson, chapter 5). Transversely oriented tooth rows are unknown elsewhere in Dinosauria.

Other modifications of the diplodocoid skull are novelties that have no precedent in sauropod evolution. One set of such features that characterizes Diplodocoidea is the reorientation of the braincase and part of the palate relative to the dermal skull. In sauropod outgroups and in most sauropods, the jaw articulation lies at the posterior extreme of the skull, behind the orbit. Likewise, the basiptyergoid processes are short and point ventrally, and the adductor fossa is positioned on the posterior half of the lower jaw, just below the orbit. The diplodocoid skull differs in each of these respects, due to a reorientation of the dermal skull relative to the braincase. In diplodocoids the quadrate is oriented anteriorly such that the jaw joint is positioned below the orbit in lateral view. The pterygoid and

its connection to the braincase via the basiptyergoid processes are shifted forward. These two changes effectively shorten the lower jaw and shift anteriorly the adductor fossa. Although they diagnose the same node, these features are not considered to be correlated. Some but not all of these changes are manifest in other taxa, such as pachycephalosaurs, which have anteriorly oriented basiptyergoid processes with otherwise typical quadrate articulation and lower jaw length. This change in the shape of the diplodocoid skull effects an inclined line of action for the principal jaw closing musculature, which may have resulted in more fore-aft motion than present in other sauropods (Upchurch and Barrett 2000).

One aspect of diplodocoid skulls represents a reversal from the basic eusauropod condition. Relative to their outgroups, eusauropods have broad crowns that overlap one another along the tooth row. Diplodocoids, in contrast, reduce crown size and lose the crown overlap diagnostic of Eusauropoda. These features are correlated, because crown overlap requires some expansion of the crown relative to the root. Reduction of crown size may also be correlated with the relative shortening of the tooth row, if tooth number remains constant. A significant consequence of crown reduction is that additional replacement teeth can pack the jaw ramus. Up to five replacement teeth fill a given position in *Diplodocus* (Holland 1924:fig. 3), whereas up to seven are present in *Nigersaurus* (Sereno et al. 1999:fig. 2D). This specialization may allow enhanced tooth replacement rates (see Sereno and Wilson, chapter 5).

PRESACRAL SPECIALIZATIONS

Neural spines vary in length, shape, and orientation throughout Dinosauria, but only within sauropods are they completely divided. Forked neural spines appear several times in Sauropoda, usually as an autapomorphies for genera (e.g., *Camarasaurus*, *Euhelopus*, *Opisthocoelicaudia*). Flagellicaudata (Diplodocidae + Dicraeosauridae) is the only suprageneric group characterized by forked neural spines. These usually extend from

the anterior cervical neural spines to those of the mid-dorsal region, but they may extend to the anterior caudal neural spines in some taxa (e.g., *Diplodocus*). The forked neural spines are longest in *Amargasaurus* and *Dicraeosaurus*, in which they are more than four times the centrum height, and shortest in *Apatosaurus*, in which they are shorter than the centrum height. A median tubercle may occasionally be present between the two rami of the neural spines of the pectoral region, but this feature is not present in all diplodocoids. Forked neural spines may have been a specialization that allowed passage of elastic ligaments (Janensch 1929b; Alexander 1985), such as the ligamentum nuchae and ligamentum elasticum interspinale (Tsuihiji 2004). The presence of forked neural spines and implied ligaments in some taxa but not in others remains unexplained.

As mentioned earlier, more than a dozen neck lengthening events appear within Neosauropoda, whose basic complement of cervical, dorsal, and sacral vertebrae is 13-12-5. All are autapomorphies for genera, except for one event that characterizes Diplodocidae. The diplodocids *Apatosaurus* and *Diplodocus* incorporated two dorsal vertebrae into the neck to obtain the precaudal count of 15-10-5. Although precaudal counts are not known for other diplodocids, dicraeosaurids and rebbachisaurids do not appear to share this feature.

TAIL SPECIALIZATIONS

The number of caudal vertebrae comprising the tail is fairly similar in outgroups to Sauropoda. Caudal counts are known for the prosauropods *Jingshanosaurus* (44), *Lufengosaurus* (43), and *Plateosaurus* (41), as well as the basal theropods *Eoraptor* (45; Sereno, pers. comm.) and *Herrerasaurus* (43-45). This number is retained in the basal sauropod *Shunosaurus* (43) and slightly increased in more derived sauropods such as *Omeisaurus* (50-55) and *Camarasaurus* (53). A marked increase in the number of caudal vertebrae characterizes Diplodocidae, which nearly doubles the primitive count (*Diplodocus*, 80 + ; *Apatosaurus*, 82). Tail elongation in diplodocids is the result of supernumerary distal caudal verte-

brae, of which there are more than 30. These archless distal caudal centra are not only numerous, but also distinctly biconvex and elongate. Although biconvex distal caudal centra are known in other neosauropods, none are as elongate or numerous as in diplodocids (Wilson et al. 1999). Together, this series of 30 or more elongate, biconvex centra constitute a “whiplash” tail, which has been interpreted as a defensive (e.g., Holland 1915) or noisemaking (Myhrvold and Currie 1997) specialization. Although their caudal counts are unknown, the presence of elongate, biconvex caudal centra in the rebbachisaurids *Limaysaurus* (Calvo and Salgado 1995; Salgado 2004) and *Nigersaurus* (personal observation), as well as the dicraeosaurid *Dicraeosaurus* (Janensch 1929b), suggests that the whiplash tail may have been a general diplodocoid feature. However, this can only be confirmed by future discoveries of articulated remains.

MACRONARIA

The second of the two reflexive neosauropod stem-groups, Macronaria includes all neosauropods more closely related to *Saltasaurus loricatus* than to *Diplodocus longus* (Wilson and Sereno 1998). By this definition, Macronaria unites *Camarasaurus*, *Brachiosaurus*, *Euhelopus*, and Titanosauria (fig. 1.4). Two node–stem triplets are recognized within Macronaria, one for Titanosauriformes (Wilson and Sereno 1998) and the other for Saltosauridae Sereno (1998), a titanosaur subgroup. Phylogenetic definitions within Macronaria are as follows (boldface type indicates node-based definitions; regular type indicates stem-based definitions):

Macronaria Wilson and Sereno 1998—All neosauropods more closely related to *Saltasaurus loricatus* than to *Diplodocus longus*.

Titanosauriformes Salgado et al. 1997—*Brachiosaurus brancai*, *Saltasaurus loricatus*, their most recent common ancestor, and all descendants.

Brachiosauridae Riggs 1904—All titanosauriforms more closely related to

Brachiosaurus brancai than to *Saltasaurus loricatus*.

Somphospondyli Wilson and Sereno 1998—All titanosauriforms more closely related to *Saltasaurus loricatus* than to *Brachiosaurus brancai*.

Titanosauria Bonaparte and Coria 1993—*Andesaurus delgadoi*, *Saltasaurus loricatus*, their most recent common ancestor, and all descendants.

Saltosauridae Powell 1992—*Opisthocoelicaudia skarzynskii*, *Saltasaurus loricatus*, their most recent common ancestor, and all descendants.

Opisthocoelicaudiinae McIntosh 1990—All saltosaurids more closely related to *Opisthocoelicaudia skarzynskii* than to *Saltasaurus loricatus*.

Saltosaurinae Powell 1992—All saltosaurids more closely related to *Saltasaurus loricatus* than to *Opisthocoelicaudia skarzynskii*.

Macronaria is more taxonomically diverse and widespread than its neosauropod counterpart Diplodocoidea. Like other neosauropod lineages, macronarians first appear in the Late Jurassic. However, the simultaneous appearance of *Camarasaurus*, *Brachiosaurus*, and the possible titanosaur *Janenschia* suggests an earlier origin for the group. Furthermore, trackway evidence may suggest a Middle Jurassic origin for titanosaurs (Wilson and Carrano 1999; Day et al. 2002, 2004; see below) and thus all neosauropod lineages. Macronarians are the only sauropod subgroup to persist until the end of the Cretaceous, represented as titanosaurs in the Maastrichtian in North America (*Alamosaurus* [Gilmore 1946]), India (*Isisaurus* [Jain and Bandyopadhyay 1997]), Europe (*Magyarosaurus* [Huene 1932], *Ampelosaurus* [LeLoeuff 1995]), Asia (*Nemegtosaurus* [Nowinski 1971], *Opisthocoelicaudia* [Borsuk-Bialynicka 1977]), Madagascar (*Rapetosaurus* [Curry Rogers and Forster 2001]), Africa (cf. Titanosauria [Rauhut and Werner 1999]), and South America (*Gondwanatitan* [Kellner and Azevedo

1999)). Titanosauria includes several extremely large forms (e.g., *Antarctosaurus giganteus*, *Argyrosaurus*, *Argentinosaurus*; fig. 1.13, left), but also genera diminutive by sauropod standards (e.g., *Saltasaurus*, *Neuquensaurus*; fig. 1.13, right). The body size range in Titanosauria exceeds that in other sauropod subgroups and provides an opportunity to evaluate temporal and morphological patterns of body size change within the group, once a genus-level phylogeny is established.

Appendicular synapomorphies comprise a substantial proportion of character support within Macronaria, particularly within its latest-surviving clade, Titanosauria (table 1.5). Although several appendicular synapomorphies apply at basal macronarian nodes, perhaps the most striking changes occur within Titanosauria and are related to the acquisition of a wide-gauge limb posture.

WIDE-GAUGE LIMB POSTURE

Animals with parasagittal limb stance walk or run on land with their limbs held close to the body midline. In these forms, the supporting elements swing anteroposteriorly and contact the substrate near the body midline. As the animal reaches higher speeds, these contacts approach and sometimes touch or cross the midline. A parasagittal limb stance can be observed directly in living therian mammals and in birds (e.g., Muybridge 1957). Squamates and crocodylians, in contrast, have a sprawling gait in which the proximal limb elements are oriented close to the horizontal plane and the limbs contact the substrate at some distance from the body midline (e.g., Blob 2001). Fossilized trackways provide indirect evidence for parasagittal locomotion in extinct dinosaurs (e.g., Thulborn 1982). As observed in living therians and birds, theropod and ornithopod fore- and hindfoot impressions are quite close to or overlap the trackway midline. Likewise, sauropod trackways evidence a parasagittal limb stance, although the placement of the fore- and hindfeet relative to the midline varies within the clade. “Narrow-gauge” sauropod tracks are

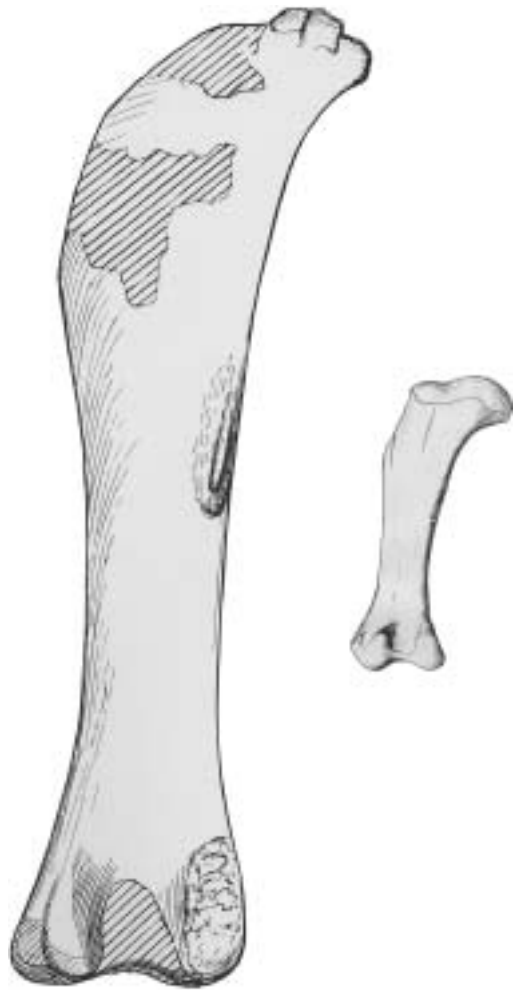


FIGURE 1.13. Left femora (posterior view) of the titanosaurs *Antarctosaurus giganteus* (length, 231 cm) and *Neuquensaurus australis* (length, 70 cm). To scale (from Huene 1929:pl. 20, 36). Both femora correspond to adult individuals.

defined as those in which manus and pes impressions are “close [to] or even intersect the trackway midline,” whereas “wide-gauge” trackways are “well away from the trackway midline” (Farlow 1992:108, 109). Variation in gauge width has been inferred to be taxonomic, with narrow-gauge stance presumed to be primitive and wide-gauge stance derived (Wilson and Carrano 1999). Further, the presence of certain morphological characteristics of saltasaurid titanosaurs has suggested that they are the wide-gauge trackmakers. Wilson and Carrano (1999) recognized three hindlimb features that support

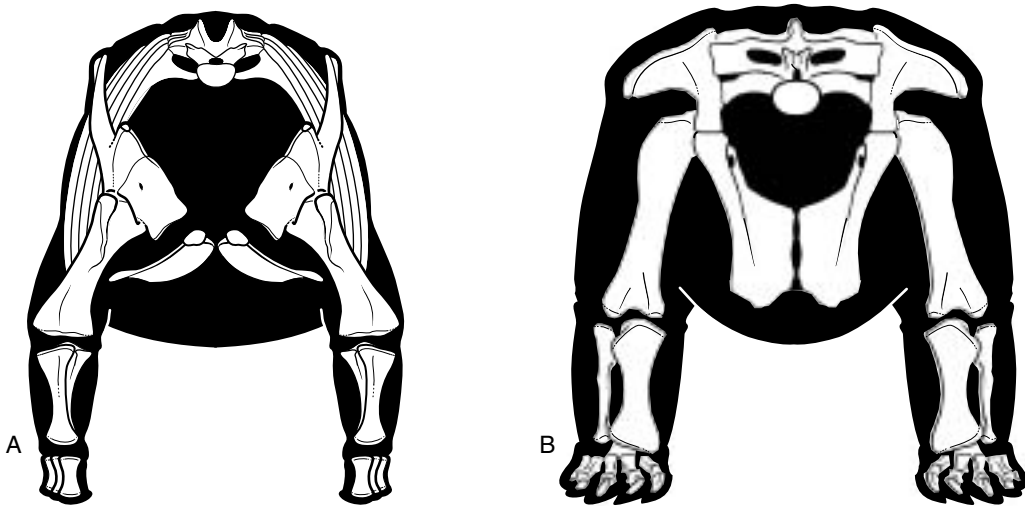


FIGURE 1.14. Limb skeleton of the wide-gauge saltasaurid *Opisthocoelicaudia*. Pectoral girdle and forelimb (A) and pelvic girdle and hindlimb (B) in anterior view. Forelimb reconstruction based on illustrations and photographs in Borsuk-Bialynicka (1977:fig. 9B, pl. 7–9, 11); hindlimb reconstruction modified from Wilson and Carrano (1999).

the hypothesis that saltasaurids were wide-gauge trackmakers. In addition, they recognized forelimb features that are related to wide-gauge locomotion. Still other features are merely associated with wide-gauge limb posture but are not required by it. These are discussed below.

Acquisition of wide-gauge limb posture requires the manus and pes to contact the ground at some distance from the midline. This was achieved in saltasaurids by two modifications that allowed the femur to angle outward from the body wall. First, the proximal third of the femur is canted inward relative to the rest of the shaft (fig. 1.14B). A similar characteristic is present in forest bovids that walk with their femora more abducted than do their closest relatives (Kappelman 1988). Second, the distal condyles are not aligned orthogonal to the long axis of the femur, as in other sauropods. Instead, the distal femoral condyles of saltasaurids are beveled 10° dorsomedially. As shown in figure 1.14, this conformation orients the axis of the knee parallel to the ground and perpendicular to the ground reaction force when the limb is angled away from the body. So far, this feature is restricted to saltasaurids. A third feature that may facilitate a wide-gauge limb posture in saltasaurids is the highly eccentric femoral midshaft cross section. It has already

been mentioned that all sauropod femora (except some diplodocines) are broader mediolaterally than anteroposteriorly. This shape provides greater resistance to mediolateral bending. Saltasaurids, however, exaggerate this feature well beyond that of typical sauropods. This increased femoral eccentricity may have offered greater resistance to the increased bending moment imposed by a wide-gauge limb posture. The distal tibia, whose distal end is diagnostically broader in titanosaurs than in other sauropods, may also be specialized to counter mediolateral bending.

A series of pectoral girdle and forelimb features is related to the acquisition of wide-gauge limb posture in saltasaurids. The anterior thorax and the shoulder girdle are broader in saltasaurids than in other sauropods, owing to the combined effects of the elongate coracoids and the enlarged, crescentic sternal plates (fig. 1.14A). However, because the pectoral girdle has no bony connection to the vertebral column, the absolute distance between the glenoid and the midline cannot be determined. The forelimb is characterized by several reversals of early sauropod synapomorphies associated with the evolution of a columnar, graviportal posture. The humerus in saltasaurids is unique in that it bears a prominent deltopectoral crest,

and its distal condyles are both divided and exposed anteriorly. These features are not present in other sauropods. Likewise, the ulna is characterized by a prominent olecranon process that projects above the articular surface of the ulna, as it does in sauropod outgroups but not in other sauropods. These reversals—particularly extension of the ulnar articular surface onto the anterior surface of the humerus and the prominent olecranon process—suggest a more habitually flexed forelimb posture in saltasaurids. Other features are consistent with this interpretation, including the increased transverse diameter of the distal radius, which is a shape that better resists mediolateral bending moments.

A third set of features is novelties of wide-gauge limb trackmakers that do not signal a modified limb posture but they may offer insight into the function of this novel locomotory specialization. Saltasaurids are characterized by a short tail that consists of approximately 35 stout caudals, many fewer than in sauropods primitively and less than half the number in diplodocids. The articular surfaces of all titanosaur caudal centra are concavo-convex; in all but *Opisthocoelicaudia* the anterior face of the centrum is concave (procoelous). Borsuk-Bialynicka (1977) and Wilson and Carrano (1999) suggested that this shortened tail may have functioned as a third support when saltasaurids reared during feeding or mating. A second saltasaurid synapomorphy may also be related to occasional bipedal stance or tripod rearing. The preacetabular processes or saltasaurid ilia are flared laterally such that they are oriented nearly perpendicular to the body axis. Wilson and Carrano (1999) suggested that, among other effects, flared ilia move the origination site of the femoral protractor muscles laterally, bringing them into anteroposterior alignment with the direction of travel. Finally, one feature peculiar to saltasaurids and their subgroups is a pronounced reduction in the ossification of the carpus, manus, and tarsus. Carpal elements have not been found associated with manual elements in any titanosaur and are not present

among the articulated forelimb elements of *Alamosaurus* and *Opisthocoelicaudia* (Gilmore 1946:pl. 4; Borsuk-Bialynicka 1977:29). In both cases, radius, ulna, and metacarpals were all preserved in articulation, but no intervening carpal elements were found. Manual phalanges have been reported only rarely in association with titanosaur skeletons, and never has an ungual been reported. The manual phalanges that have been reported are extremely reduced (e.g., Borsuk-Bialynicka 1977), and it is likely that the manus had no fleshy digits. Like the carpus and manus, the ankle is extremely reduced in the saltasaurids. The saltasaurid astragalus is distinct among dinosaurs in the extreme reduction of its mediolateral diameter, which is subequal to the anteroposterior and proximodistal diameters. In articulation, the pyramidal astragalus of the saltasaurid *Opisthocoelicaudia* contacts the fibula and the lateral aspect of the tibia but does not reach the medial extreme of the distal tibia (fig. 1.14B).

CONCLUSIONS

Sauropods were “successful” dinosaurs by virtue of their geographic distribution, temporal survivorship, biomass, generic diversity, higher-level diversity, and morphological complexity. Although historically studies of sauropod systematics have lagged behind those of other dinosaur subgroups, a burst of analyses in the last decade has begun to elucidate the evolutionary history of the group.

The stratigraphic distribution of the first representatives of Sauropoda and of their sister-taxon Prosauropoda implies a 10 million- to 15-million year missing lineage during which the score of features diagnosing sauropods evolved. Synapomorphies related to precisely occlusion, neck elongation, and columnar posture evolved during the Late Triassic and Early Jurassic and characterize all sauropods. Although all main neosauropod lineages appear simultaneously around the globe in the Late Jurassic, it is probable that neosauropods were present in the Middle Jurassic and possible that they were

present in the Early Jurassic. Future sampling of these poorly sampled intervals will better illuminate early neosauropod evolution. The two principal neosauropod subgroups, Macro-*naria* and *Diplodocoidea*, are the predominant sauropods during the Late Jurassic and Cretaceous. The descent and diversification within these two groups were shaped by changes in different regions of the skeleton. *Diplodocoids* are characterized by cranial and axial synapomorphies that led to the evolution of a dental battery in *Rebbachisaurids* and a whiplash tail in *Flagellicaudatans*. In contrast, a series of appendicular changes led to the evolution of a wide-gauge limb posture in the *Macronarian* subgroup *Titanosauria*, which was the dominant sauropod lineage of the Cretaceous, represented on nearly all continental landmasses by more than 40 species.

Despite advances in understanding of the group, substantial gaps in our knowledge of sauropod history still exist. Like the animals themselves, our understanding of sauropod history is deepest in the middle but somewhat thinner on both ends. The sequence of changes leading to the sauropod body plan from the primitive saurischian condition is still poorly understood. For instance, it is not known whether herbivorous specializations preceded large body size and quadrupedality. New discoveries of basal sauropod taxa are needed to address this question. At the other end of sauropod history, phylogenetic understanding of the two latest-surviving sauropod groups, *Rebbachisauridae* and *Titanosauria*, are as yet unknown, but new discoveries have already begun to bring clarity to this problem. These two lineages are important biogeographically during the end of sauropod history and may signal an interesting survivorship pattern. Despite the fact that both broad- and narrow-crowned sauropod taxa were present on most continental landmasses, only narrow-crowned taxa survived into the Late Cretaceous each independent case (see Barrett and Upchurch, chapter 4). No broad-crowned sauropod teeth have been reported from Late Cretaceous sedi-

ments. Future discoveries and analyses are required to better understand the relationship, if any, between Late Cretaceous survivorship and narrow-crowned dentition.

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LITERATURE CITED

- Alexander, R. M. 1985. Mechanics of posture and gait of some large dinosaurs. *Zool. J. Linn. Soc.* 83:1–25.
- Allain, R., Taquet, P., Battail, B., Dejax, J., Richir, P., V éran, M., Limon-Duparcmeur, F., Vacant, R., Mateus, O., Sayarath, P., Khenthavong, B., and Phouyavong, S. 1999. Un nouveau genre de dinosaure sauropode de la formation des Grés supérieurs (Aptien-Albien) du Laos. *C.R. Acad. Sci. Paris Sci. Terre Planètes* 329: 609–616.
- Anonymous. 1905. The presentation of a reproduction of *Diplodocus carnegei* to the trustees of the

- British Museum. *Annals of the Carnegie Museum* 3: 443–452.
- Barrett, P.M., Hasegawa, Y., Manabe, M., Isaji, S., and Matsuoka, H. 2002. Sauropod dinosaurs from the Lower Cretaceous of eastern Asia: taxonomic and biogeographical implications. *Palaeontology* 45: 1197–1217.
- Benton, M.J., Juul, L., Storrs, G.W., and Galton, P.M. 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. *J. Vertebr. Paleontol.* 20: 77–108.
- Blob, R.W. 2001. Evolution of hindlimb posture in nonmammalian therapsids: biomechanical tests of paleontological hypotheses. *Paleobiology* 27: 14–38.
- Bonaparte, J.F. 1986a. The early radiation and phylogenetic relationships of sauropod dinosaurs, based on vertebral anatomy. In: Padian, K.(eds.). *The Beginning of the Age of Dinosaurs*. Cambridge University Press, Cambridge. pp. 247–258.
- . 1986b. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosaures) du Jurassique moyen de Cerro Cóndor (Chubut, Argentine). *Ann. Paléontol.* 72: 325–386.
- . 1997. *Rayososaurus agrioiensis* Bonaparte 1995. *Ameghiniana* 34: 116.
- Bonaparte, J.F., and Coria, R.A. 1993. Un nuevo y gigantesco sauropodo titanosaurio de la Formación Río Limay (Albiano-Cenomanio) de la Provincia del Neuquén, Argentina. *Ameghiniana* 30: 271–282.
- Bonnan, M.F. 2003. The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, limb orientation, and phylogeny. *J. Vertebr. Paleontol.* 23: 595–613.
- Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontol. Polonica* 37: 1–64.
- Buckland, W. 1841. *Geology and Minerology Considered with Reference to Natural Theology*, 2nd ed. Lea & Blanchard, Philadelphia. 468 pp.
- Buffetaut, E., Suteethorn, V., Cuny, G., Tong, H., Le Loeuff, J., Khansubha, S., and Jongautcharyakul., S. 2000. The earliest known sauropod dinosaur. *Nature* 407: 72–74.
- Calvo, J.O. 1994. Jaw mechanics in sauropod dinosaurs. *GAIA* 10: 183–193.
- Calvo, J.O. and González Riga, B.J. 2003. *Rinconsaurus caudamirus* gen. et sp. nov., a new titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia, Argentina. *Revista Geologica de Chile* 30: 333–353.
- Calvo, J.O., and Salgado, L. 1995. *Rebbachisaurus tessonei*, sp. nov. A new Sauropoda from the Albian-Cenomanian of Argentina; new evidence on the origin of Diplodocidae. *GAIA* 11: 13–33.
- Carrano, M.T. 1997. Morphological indicators of foot posture in mammals: a statistical and biomechanical analysis. *Zool. Linn. Soc.* 121: 77–104.
- . 2000. Homoplasy and the evolution of dinosaur locomotion. *Paleobiology* 26: 489–512.
- . 2005. Body-size evolution in the Dinosauria. In: Carrano, M.T., Gaudin, T.J., Blob, R.W., and Wible, J.R. (eds.). *Amniote Paleobiology: Phylogenetic and Functional Perspectives on the Evolution of Mammals, Birds and Reptiles*. Chicago: University of Chicago Press (in press).
- Chiappe, L.M., Coria, R.A., Dingus, L., Jackson, F., Chinsamy, A., and Fox, M. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature* 396: 258–261.
- Chiappe, L.M., Salgado, L., and Coria, R.A., 2001. Embryonic skulls of titanosaur sauropod dinosaurs. *Science* 293: 2444–2446.
- Cooper, M.R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occas. Papers Natl. Mus. Rhodesia B Nat. Sci.* 6: 689–840.
- . 1984. Reassessment of *Vulcanodon* and the origin of the Sauropoda. *Palaeontol. Africana* 25: 203–231.
- Curry, K.A. 2001. *The Evolutionary History of the Titanosauria*. Ph.D. thesis, State University of New York, Stony Brook.
- Curry Rogers, K.A., and Forster, C. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. *Nature* 412: 530–534.
- Curry Rogers, K.A., and Forster, C. 2004. The skull of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. *J. Verteb. Paleontol.* 24:121–144.
- Dalla Vecchia, F.M. 1994. Jurassic and Cretaceous sauropod evidence in the Mesozoic carbonate platforms of the southern Alps and Dinards. *GAIA* 10: 65–73.
- Day, J.J., Upchurch, P., Norman, D.B., Gale, A.S., and Powell, H.P. 2002. Sauropod trackways, evolution, and behavior. *Science* 296: 1659.
- Day, J.J., Norman, D.B., Gale, A.S., Upchurch, P., and Powell, H.P. 2004. A Middle Jurassic dinosaur trackway site from Oxfordshire, U. K. *Palaeontology* 47: 319–348.
- Desmond, A.J. 1975. *The Hot-Blooded Dinosaurs*. Blond and Briggs, London. 238 pp.
- Farlow, J.O. 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. *Zubía* 10: 89–138.

- Filla, B. J., and Redman, P. D. 1994. *Apatosaurus yahnapin*: a preliminary description of a new species of diplodocid dinosaur from the Late Jurassic Morrison Formation of southern Wyoming, the first sauropod found with a complete set of "belly ribs." Forty-fourth Annual Field Conference—1994 Wyoming Geological Association Guidebook 44: 159–178.
- Flynn, J. J., Parrish, J. M., Rakotosamimanana, B., Simpson, W. F., Whatley, R. L., and Wyss, A. R. 1999. A Triassic fauna from Madagascar, including early dinosaurs. *Science* 286: 763–765.
- Galton, P. M. 1990. Prosauropoda. In: Wieshampel, D. B., Dodson, P., and Osmólska, H. (eds.). *The Dinosauria*. University of California Press, Berkeley. Pp. 320–345.
- Galton, P. M. and Upchurch, P. 2000. Prosauropod dinosaurs: homeotic transformations ("frame shifts") with third sacral as a caudosacral or a dorsosacral. *J. Vertebr. Paleontol.* 20: 43A.
- . 2004. Prosauropoda. In: Weishampel, D. B., Dodson, P., and Osmólska, H. (eds.), *The Dinosauria*, 2nd ed. University of California Press, Berkeley. Pp. 232–258.
- Galton, P. M., and van Heerden, J. 1985. Partial hindlimb of *Blikanasaurus cromptoni* n. gen. and n. sp., representing a new family of prosauropod dinosaurs from the Upper Triassic of South Africa. *Géobios* 18: 509–516.
- Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. In: Padian K., ed. *The origin of birds and the evolution of flight*. *Memoirs of the California Academy of Sciences* 8: 1–55.
- Gierlinski, G. 1997. Sauropod tracks in the Early Jurassic of Poland. *Acta Palaeontol. Polonica* 42: 533–538.
- Gierlinski, G., Pienkowski, G., and Niedzwiedzki, G. 2004. Tetrapod track assemblage in the Hettangian of Soltyków, Poland, and its paleoenvironmental background. *Ichnos* 11: 195–213.
- Gilmore, C. W. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument, Utah. *Mem. Carnegie Mus.* 10: 347–384.
- Gilmore, C. W. 1936. Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. *Mem. Carnegie Mus.* 11: 175–300.
- . 1946. Reptilian fauna of the North Horn Formation of central Utah. *U. S. Geol. Surv. Prof. Paper* 210C: 1–52.
- González Riga, B. J. 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza Province, Argentina. *Ameghiniana* 40: 155–172.
- Harris, J. D., and Dodson, P. 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. *Acta Palaeontol. Polonica* 49: 197–210.
- Hatcher, J. B. 1901. *Diplodocus* (Marsh): its osteology, taxonomy, and probable habits, with a restoration of the skeleton. *Mem. Carnegie Mus.* 1: 1–63.
- . 1902. Structure of the forelimb and manus of *Brontosaurus*. *Ann. Carnegie Mus.* 1: 356–376.
- He, X.-L., Li, K., and Cai, K.-J. 1988. [The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan. Vol. IV. Sauropod Dinosaurs (2) *Omeisaurus tianfuensis*]. Sichuan Scientific and Technological Publishing House, Chengdu. 143 pp.
- He, X.-L., Wang, C., Liu, S., Zhou, F., Liu, T., Cai, K., and Dai., B. 1998. [A new sauropod dinosaur from the Early Jurassic in Gongxian County, South Sichuan]. *Acta Geol. Sichuan* 18: 1–6.
- Holland, W. J. 1910. A review of some recent criticisms of the restorations of sauropod dinosaurs existing in the museums of the United States, with special reference to that of *Diplodocus carnegiei* in the Carnegie Museum. *Am. Nat.* 44: 259–283.
- . 1915. Heads and tails: a few notes relating to the structure of the sauropod dinosaurs. *Annals of the Carnegie Museum* 9: 273–278.
- . 1924. The skull of *Diplodocus*. *Mem. Carnegie Mus.* 9: 379–403.
- Hopson, J. A. 1995. Patterns in evolution of the manus and pes of non-mammalian synapsids. *J. Vertebr. Paleontol.* 15: 615–639.
- Huene, F. V. 1920. Bemerkungen zur Systematik und Stammesgeschichte einiger Reptilien. *Z. Induktive Abstammungslehre Vererbungslehre* 22: 209–212.
- . 1926. Vollständige Osteologie eines Plateosauriden aus dem schwäbischen Keuper. *Geol. Palaeontol. Abhandlungen* 15: 129–179.
- . 1932. Die fossil Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monograph. Geol. Palaeontol.* 4: 1–361.
- . 1956. Paläontologie und Phylogenie der Niederen Tetrapoden. VEB Gustav Fischer Verlag, Jena. 716 pp.
- Huxley, T. H. 1869. On the classification of the Dinosauria, with observations on the Dinosauria of the Trias. *Q. Rev. Geol. Soc. London* 26: 32–51.
- Ishigaki, S. 1988. Les empreintes de dinosaures du Jurassique inférieur du Haut Atlas central marocain. *Notes Serv. Géol. Maroc* 44: 79–86.
- Jacobs, L. L., D. A., Winkler, Downs, W. R., and Gomani, E. M. 1993. New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. *Palaeontology* 36: 523–534.
- Jain, S. L., and Bandyopadhyay, S. 1997. New titanosaurid (Dinosauria: Sauropoda) from the

- Late Cretaceous of central India. *J. Vertebr. Paleontol.* 17: 114–136.
- Janensch, W. 1914. Übersicht über die Wirbeltierfauna der Tendaguru-Schichten, nebst einer kurzen Charakterisierung der neu aufgeführten Arten von Sauropoden. *Arch. Biontol.* 3: 81–110.
- . 1929a. Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru Expedition. *Palaeontographica (Suppl. 7)* 2: 1–34.
- . 1929b. Die Wirbelsäule der gattung *Dicraeosaurus*. *Palaeontographica (Suppl. 7)* 7: 39–133.
- . 1935–1936. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus*, und *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica (Suppl. 7)* 3: 147–298.
- . 1950. Die wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica (Suppl. 7)* 3: 27–93.
- . 1961. Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica (Suppl. 7)* 3: 177–235.
- Kappelman, J. 1988. Morphology and locomotor adaptations of the bovid femur in relation to habitat. *J. Morphol.* 198: 119–130.
- Kellner, A. W. A., and Azevedo, S. A. K. de 1999. A new sauropod dinosaur (Titanosauria) from the Late Cretaceous of Brazil. *Proc. Second Gondwanan Dinosaur Symp.* 15: 111–142.
- Larson, A. 1994. The comparison of morphological and molecular data in phylogenetic systematics. In: Schierwater, B. S. B., Wagner, G. P., and DeSalle, R. (eds.). *Molecular Biology and Evolution: Approaches and Applications*. Birkhauser Verlag, Basel. Pp. 371–390.
- Le Loeuff, J. 1995. *Ampelosaurus atacis* (nov. gen., nov. sp.), un nouveau Titanosauridae (Dinosauria, Sauropoda) du Crétacé supérieur de la Haute Vallée de l'Aude (France). *C. R. Acad. Sci. Paris (Ser. II)* 321: 693–699.
- Le Loeuff, J. 2003. The first articulated titanosaurid skeleton in Europe. In: Meyer, C. A. (ed.). *First European Association of Vertebrate Paleontologists Meeting*. Natural History Museum, Basel.
- Lockley, M. G., Wright, J. L., Hunt, A. G., and Lucas, S. G. 2001. The Late Triassic sauropod track record comes into focus: old legacies and new paradigms. *New Mexico Geological Society Guidebook, 52nd Field Conference, Geology of the Llano Estacado*. Pp. 181–190.
- Luo, Y., and Wang, C. 2000. A new sauropod, *Gongxianosaurus*, from the Lower Jurassic of Sichuan, China. *Acta Geol. Sinica* 74: 132–136.
- Luo, Z. 1999. A refugium for relicts. *Nature* 400: 23–25.
- Maier, G. 2003. *African Dinosaurs Unearthed*. Indiana University Press, Bloomington. 380 pp.
- Marsh, O. C. 1878. Principal characters of American Jurassic dinosaurs. Pt. I. *Am. J. of Sci. (Ser. 3)* 16: 411–416.
- . 1883. Principal characters of American Jurassic dinosaurs: Part VI. Restoration of *Brontosaurus*. *Am. J. Sci. (Ser. 3)* 26: 81–86.
- . 1884. Principal characters of American Jurassic dinosaurs. Part VII. On the Diplodocidae, a new family of the Sauropoda. *Am. J. Sci. (Ser. 3)* 27: 161–168.
- . 1895. On the affinities and classification of the dinosaurian reptiles. *Am. J. Sci. (Ser. 3)* 50: 413–423.
- Marsicano, C. A., and Barredo, S. P. 2004. A Triassic tetrapod footprint assemblage from southern South America: palaeobiogeographical and evolutionary implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 203: 313–335.
- Martin, V., Buffetaut, E., and Suteethorn, V. 1994. A new genus of sauropod dinosaur from the Sao Khua Formation (Late Jurassic or Early Cretaceous) of northeastern Thailand. *C. R. Acad. Sci. Paris (Ser. II)* 319: 1085–1092.
- Martínez, R., Giménez, O., Rodríguez, J., Luna, M., and Lamanna, M. C. 2004. An articulated specimen of the basal Titanosaurian (Dinosauria: Sauropoda) *Epachthosaurus sciuttoi* from the early Late Cretaceous Bajo Barreal Formation of Chubut Province, Argentina. *J. Vertebr. Paleontol.* 24: 107–120.
- McIntosh, J. S. 1990. Sauropoda. In: Weishampel, D. B., Dodson, P., and Osmólska, H. (eds.). *The Dinosauria*. University of California Press, Berkeley. Pp. 345–401.
- McIntosh, J. S., Miles, C. A., Cloward, K. C., and Parker, J. R. 1996. A new nearly complete skeleton of *Camarasaurus*. *Bull. Gunma Mus. Nat. Hist.* 1: 1–87.
- Myhrvold, N. P., and Currie, P. J. 1997. Supersonic sauropods? Tail dynamics in the diplodocids. *Paleobiology* 23: 393–409.
- Muybridge, E. 1957. *Animals in Motion*. Brown, L. S. (ed.). Dover, New York.
- Novas, F. E. 1989. The tibia and tarsus in Herrerasauridae (Dinosauria, incertae sedis) and the origin and evolution of the dinosaurian tarsus. *J. Paleontol.* 63: 677–690.
- . 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *J. Vertebr. Paleontol.* 13: 400–423.

- Nowinski, A. 1971. *Nemegtosaurus mongoliensis* n. gen., n. sp., (Sauropoda) from the uppermost Cretaceous of Mongolia. *Palaeontol. Polonica* 25:57–81.
- Osborn, H. F. 1904. The manus, sacrum and forelimb of Sauropoda. *Bull. Am. Mus. Nat. Hist.* 20: 181–190.
- Osborn, H. F., and Mook, C. C. 1921. *Camarasaurus*, *Amphicoelias*, and other sauropods of Cope. *Mem. Am. Mus. Nat. Hist.* 3: 247–387.
- Ostrom, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Yale Peabody Mus. Nat. Hist.* 30: 1–165.
- Ostrom, J. H., and McIntosh, J. S. 1966. *Marsh's Dinosaurs, the Collections from Como Bluff*. Yale University Press, New Haven, CT, London. 388 pp.
- Owen, R. 1841. A description of a portion of the skeleton of *Cetiosaurus*, a gigantic extinct saurian occurring in the Oolitic Formation of different parts of England. *Proc. Geol. Soc. London* 3: 457–462.
- . 1842. Report on British fossil reptiles, Part II. Reptiles. *Rep. Br. Assoc. Adv. Sci.* 1841: 60–204.
- . 1875. *Monographs on the British fossil Reptilia of the Mesozoic formations. Part II. (Genera Bothriospondylus, Cetiosaurus, Omosaurus)*. *Palaeontol. Soc. Monogr.* 29: 15–93.
- Phillips, J. 1871. *Geology of Oxford and the Valley of the Thames*. Clarendon Press, Oxford. 529 pp.
- Pittman, J. G., and Gillette, D. D. 1989. The Briar Site: a new sauropod dinosaur tracksite in Lower Cretaceous beds of Arkansas. In: Gillette, D. D., and Lockley, M. G. (eds.). *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, New York. Pp. 313–332.
- Powell, J. E. 1992. Osteología de *Saltasaurus loricatus* (Sauropoda-Titanosauridae) del Cretácico Superior del Noroeste argentino. In Sanz, J. L. and Buscalioni, A. D., (eds.). *Los Dinosaurios y su Entorno Biotico*. Instituto “Juan de Valdes”, Cuenca. Pp. 165–230.
- Raath, M. 1972. Fossil vertebrate studies in Rhodesia: a new dinosaur (Reptilia, Saurischia) from the near the Trias-Jurassic boundary. *Arnoldia* 30: 1–37.
- Rauhut, O. W. M., and Werner, C. 1997. First record of a Maastrichtian sauropod dinosaur from Egypt. *Palaeontol. Africana* 34: 63–67.
- Riggs, E. S. 1904. Structure and relationships of opisthocoelian dinosaurs. Part II: The Brachiosauridae. *Field Columbian Museum Geological Series* 2: 229–248.
- Romer, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago, 772 pp.
- . 1966. *Vertebrate Paleontology*. University of Chicago Press, Chicago. 368 pp.
- Russell, D. A. 1993. The role of central Asia in dinosaurian biogeography. *Can. J. Earth Sci.* 30: 2002–2012.
- Russell, D. A., and Zheng, Z. 1993. A large mamenchisaurid from the Junggar Basin, Xinjiang, People's Republic of China. *Can. J. Earth Sci.* 30: 2082–2095.
- Salgado, L. 2004. Lower Cretaceous rebbachisaurid sauropods from the Cerro Aguada del León (Lohan Cura Formation), Neuquén Province, northwestern Patagonia, Argentina. *J. Vertebr. Paleontol.* 24: 903–912.
- Salgado, L., Coria, R. A., and Calvo, J. O. 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34: 3–32.
- Salgado, L., Coria, R. A., Chiappe, L. M. 2005. Osteology of the sauropod embryos from the Upper Cretaceous of Patagonia. *Acta Paleontol. Polonica* 50: 79–92.
- Sanz, J. L., Powell, J. E., Le Loeuff, J., Martínez, R., and Pereda-Suberbiola, X. 1999. Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain). Titanosaur phylogenetic relationships. *Estud. Mus. Ci. Nat. de Álava* 14: 235–255.
- Sereno, P. C. 1989. Prosauropod monophyly and basal sauropodomorph phylogeny. *J. Vertebr. Paleontol.* 9: 38A.
- . 1991. *Lesothosaurus*, “fabrosaurids,” and the early evolution of Ornithischia. *J. Vertebr. Paleontol.* 11: 168–197.
- . 1993. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *J. Vertebr. Paleontol.* 13: 425–450.
- . 1998. A rationale for phylogenetic definitions, with application to the higher-level phylogeny of Dinosauria. *Neues Jahrb. Geol. Paläontol. Abhandlungen* 210: 41–83.
- Sereno, P. C., and Novas, F. E. 1993. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *J. Vertebr. Paleontol.* 13: 451–476.
- Sereno, P. C., Beck, A. L., Duthiel, D. B., Larsson, H. C. E., Lyon, G. H., Moussa, B., Sadleir, R. W., Sidor, C. A., Varricchio, D. J., Wilson, G. P., and Wilson, J. A. 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. *Science* 286: 1342–1347.
- Smith, J. B., Lamanna, M. C., Lacovara, K. J., Dodson, P., Smith, J. R., Poole, J. C., Giengengack R., and Attia, Y. 2001. A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. *Science* 292: 1704–1706.
- Steel, R. 1970. Saurischia. *Handb. Paläoherpetol.* 13: 1–88.

- Sullivan, C., Jenkins, F.A., Gatesy, S.M., and Shubin, N.H. 2003. A functional assessment of hind foot posture in the prosauropod dinosaur *Plateosaurus*. *J. Vertebr. Paleontol.* 23: 102A.
- Thulborn, R.A. 1982. Speeds and gaits of dinosaurs. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 38: 227–256.
- . 1990. *Dinosaur Tracks*. Chapman and Hall, London. 410 pp.
- Tsuihiji, T. 2004. The ligament system in the neck of *Rhea Americana* and its implication for the bifurcated neural spines of sauropod dinosaurs. *J. Vertebr. Paleontol.* 24: 165–172.
- Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philos. Trans. Roy. Soc. London B* 349: 365–390.
- . 1998. The phylogenetic relationships of sauropod dinosaurs. *Zool. J. Linn. Soc.* 124: 43–103.
- . 1999. The phylogenetic relationships of the Nemegtosauridae (Saurischia, Sauropoda). *Journal of Vertebrate Paleontology* 19: 106–125.
- Upchurch, P., and Barrett, P.M. 2000. The evolution of sauropod feeding. In: Sues, H.-D. (ed.). *Evolution of Feeding in Terrestrial Vertebrates*. Cambridge University Press, Cambridge. pp.79–122.
- Upchurch, P., and Martin, J. 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. *J. Vertebr. Paleontol.* 23: 218–231.
- Upchurch, P., Hunn, C.A., and Norman, D.B. 2002. An analysis of dinosaurian biogeography: evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proc. Roy. Soc. London B* 269: 613–621.
- Upchurch, P., Barrett, P.M., and Dodson, P. 2004. Sauropoda. In: Weishampel, D.B., Dodson, P., and Osmólska, H. (eds.). *The Dinosauria*, 2nd ed. University of California Press, Berkeley. Pp. 259–322.
- Wilson, J.A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zool. J. Linn. Soc.* 136: 217–276.
- . 2005a. Redescription of the Mongolian sauropod *Nemegtosaurus mongoliensis* Nowinski (Dinosauria: Saurischia) and comments on Late Cretaceous sauropod diversity. *J. Syst. Palaeontol.* 3: 283–318.
- . 2005b. Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. *Paleobiology* 31: 400–423.
- Wilson, J.A., and Carrano, M.T. 1999. Titanosaurs and the origin of “wide-gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* 25: 252–267.
- Wilson, J.A., and Sereno, P.C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Soc. Vertebr. Paleontol. Mem.* 5: 1–68 (supplement to *J. Vertebr. Paleontol.* 18).
- Wilson, J.A., Martinez, R.A., and Alcobar, O.A. 1999. Distal tail of a titanosaurian sauropod from the Upper Cretaceous of Mendoza, Argentina. *Journal of Vertebrate Paleontology* 19: 592–595.
- Wilson, J.A., and Upchurch, P. 2003. A revision of *Titanosaurus* Lydekker (Dinosauria–Sauropoda), the first dinosaur genus with a ‘Gondwanan’ distribution. *Journal of Systematic Palaeontology* 1: 125–160.
- Yates, A.M. 2001. A new look at *Thecodontosaurus* and the origin of sauropod dinosaurs. *J. Vertebr. Paleontol.* 21: 116A.
- . 2003. A new species of the primitive dinosaur, *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *J. Syst. Palaeontol.* 1: 1–42.
- . 2004. *Anchisaurus polyzelus* Hitchcock: the smallest known sauropod dinosaur and the evolution of gigantism amongst sauropodomorph dinosaurs. *Postilla*. Pp 1–58.
- Yates, A.M., and Kitching, J.W. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod evolution. *Proc. Roy. Soc. London B* 270: 1753–1758.
- Young, C.C. 1941. A complete osteology of *Lufengosaurus huenei* Young (gen. et sp. nov.). *Palaeontol. Sinica (C)* 7: 1–53.
- . 1947. On *Lufengosaurus magnus* (sp. nov.) and additional finds of *Lufengosaurus huenei* Young. *Palaeontol. Sinica (C)* 12: 1–53.
- Yu, C. 1993. The skull of *Diplodocus* and the phylogeny of the Diplodocidae. PhD Thesis: University of Chicago.
- Zhang, Y. 1988. The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan. *J. Chengdu Coll. Geol.* 3: 1–87.
- Zhang, Y., and Yang, Z. 1994. [A New Complete Osteology of Prosauropoda in Lufeng Basin, Yunnan, China; *Jingshanosaurus*]. Yunnan Publishing House of Science and Technology, Kunming. 100 pp.
- Zhou, Z., Barrett, P.M., and Hilton, J. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421: 807–814.

APPENDIX 1.1. CHARACTER DESCRIPTIONS

Note: Complete character descriptions for synapomorphies discussed in text and listed in Table 1.1 (from Wilson 2002). Primitive state is indicated as 0; 1–5 represent derived states.

37. Pterygoid, transverse flange (i.e., ectopterygoid process) position: posterior of orbit (0); between orbit and antorbital fenestra (1); anterior to antorbital fenestra (2).
46. Basipterygoid processes, length: short, approximately twice (0); or elongate, at least four times (1) basal diameter.
53. Basipterygoid processes, orientation: perpendicular to (0) or angled approximately 45° to (1) skull roof.
55. Dentary, depth of anterior end of ramus: slightly less than that of dentary at midlength (0); 150% minimum depth (1).
65. Tooth rows, shape of anterior portions: narrowly arched, anterior portion of tooth rows V-shaped (0); broadly arched, anterior portion of tooth rows U-shaped (1); rectangular, tooth-bearing portion of jaw perpendicular to jaw rami (2).
66. Tooth rows, length: extending to orbit (0); restricted anterior to orbit (1); restricted anterior to subnarial foramen (2).
67. Crown-to-crown occlusion: absent (0); present (1).
69. Tooth crowns, orientation; aligned along jaw axis, crowns do not overlap (0); aligned slightly anterolingually, tooth crowns overlap (1).
70. Tooth crowns, cross-sectional shape at mid-crown: elliptical (0); D-shaped (1); cylindrical (2).
71. Enamel surface texture: smooth (0); wrinkled (1).
74. Replacement teeth per alveolus, number: two or fewer (0); more than four (1).
80. Cervical vertebrae, number: 9 or fewer (0); 10 (1); 12 (2); 13 (3); 15 or greater (4).
85. Anterior cervical neural spines, shape: single (0); bifid (1).
89. Posterior cervical and anterior dorsal neural spines, shape: single (0); bifid (1).
91. Dorsal vertebrae, number: 15 (0); 14 (1); 13 (2); 12 (3); 11 (4); 10 (5).
93. Dorsal neural spines, length: approximately twice (0) or approximately four times (1) centrum length.
136. Distalmost caudal centra, articular face shape: platycoelous (0); biconvex (1).
137. Distalmost biconvex caudal centra, length-to-height ratio: <4(0); >5(1).
138. Distalmost biconvex caudal centra, number: 10 or fewer (0); more than 30 (1).
149. Posture: bipedal (0); columnar, obligately quadrupedal posture (1).
151. Scapular blade, orientation: perpendicular to (0) or forming a 45° angle with (1) coracoid articulation.
156. Caracoid, anteroventral margin shape: rounded (0); rectangular (1).
158. Sternal plate, shape: oval (0); crescentic (1).
161. Humeral deltopectoral crest, shape: relatively narrow throughout length (0); markedly expanded distally (1).
163. Humeral distal condyles, articular surface shape: restricted to distal portion of humerus (0), exposed on anterior portion of humeral shaft (1).
164. Humeral distal condyle, shape: divided (0); flat (1).
167. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1).
170. Radius, distal breadth: slightly larger than (0) or approximately twice (1) midshaft breadth.
172. Humerus-to-femur ratio: <0.60 (0); ≥0.60 (1).
173. Carpal bones, number: three or more (0); two or fewer (1).
175. Metacarpus, shape: spreading (0); bound, with subparallel shafts and articular surfaces that extend half their length (1).
176. Metacarpals, shape of proximal surface in articulation: gently curving, forming a 90° arc (0); U-shaped, subtending a 270° arc (1).
181. Manual digits II and III, phalangeal number: 2-3-4-3-2 or more (0); reduced, 2-2-2-2-2 or less (1); absent or unossified (2).
187. Iliac preacetabular process, orientation: anterolateral to (0) or perpendicular to (1) body axis.

198. Femoral midshaft, transverse diameter: subequal to (o), 125%–150%, or (1) at least 185% (2) anteroposterior diameter.
199. Femoral shaft, lateral margin shape: straight (o); proximal one-third deflected medially (1).
201. Femoral distal condyles, orientation: perpendicular or slightly beveled dorsolaterally (o) or beveled dorsomedially approximately 10° (1) relative to femoral shaft.
205. Tibia, distal breadth: approximately 125% (o) or more than twice (1) midshaft breadth.
210. Astragalus, shape: rectangular (o); wedge-shaped, with reduced anteromedial corner (1).
216. Distal tarsals 3 and 4: present (o); absent or unossified (1).
217. Metatarsus, posture: bound (o); spreading (1).
221. Metatarsal I, minimum shaft width: less than (o) or greater than (1) that of metatarsals II–IV.
223. Metatarsal III length: more than 30% (o) or less than 25% (1) that of tibia.
224. Metatarsals III and IV, minimum transverse shaft diameters: subequal to (o) or less than 65% (1) that of metatarsals I or II (1).
225. Metatarsal V, length: shorter than (o) or at least 70% (1) length of metatarsal IV.
228. Pedal unguals, orientation: aligned with (o) or deflected lateral to (1) digit axis.
233. Pedal digit IV ungual, development: subequal in size to unguals of pedal digits II and III (o); rudimentary or absent (1).