The Evolution of Sauropod Locomotion

MORPHOLOGICAL DIVERSITY OF A SECONDARILY QUADRUPEDAL RADIATION

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SAUROPOD DINOSAUR LOCOMOTION, like that of many extinct groups, has historically been interpreted in light of potential modern analogues. As these analogies—along with our understanding of them—have shifted, perspectives on sauropod locomotion have followed. Thus early paleontologists focused on the "whalelike" aspects of these presumably aquatic taxa (e.g., Osborn 1898), reluctantly relinquishing such ideas as further discoveries began to characterize sauropod anatomy as more terrestrial. Although this debate continued for over a century, the essentially terrestrial nature of sauropod limb design was recognized by the early 1900s (Hatcher 1903; Riggs 1903). Aside from a few poorly received attempts (e.g., Hay 1908; Tornier 1909), comparisons have usually been made between sauropods and terrestrial mammals, rather than reptiles. Particular similarities were often noted between the limbs of sauropods and those of elephants and rhinos (Holland 1910; Bakker 1971).

With respect to sauropod locomotion, these comparisons with proboscideans have been

fruitful but also have tended to become canalized. In this regard, the words of paleontologist W. C. Coombs (1975:23) remain particularly apt, as much for their still-relevant summary of the status quo in sauropod locomotor research as for their warning to future workers:

> It is a subtle trap, the ease with which an entire reptilian suborder can have its habits and habitat preferences deduced by comparison not with all proboscideans, not with the family Elephantidae, not with a particular genus or even a single species, but by comparison with certain populations of a single subspecies.
>
> Deciding that a particular modern animal is most like sauropods is no guarantee of solving the problem of sauropod behavior.

Similarly, modern analogues play a limited role in illuminating the evolution of sauropod locomotion. What information may be gleaned from terrestrial mammals and applied to sauropods is more likely to inform aspects of general limb design, for the simple reason that such information is likely to be rather general in scope. For example, it has been suggested

that sauropods employed a limited locomotor repertoire relative to other, smaller dinosaurs in order to maintain limb safety factors (e.g., Wilson and Carrano 1999). This was based on structural limits and behavior changes that had been observed between large- and small-bodied extant mammals (Biewener 1990).

For finer-scale patterns of locomotor evolution to be understood, data on locomotor morphology must first be brought into a phylogenetic context. Fortunately, several recent cladistic studies have greatly clarified systematic relationships within Sauropoda (e.g., Upchurch 1995, 1998; Salgado et al. 1997; Wilson and Sereno 1998; Curry Rogers and Forster 2001; Wilson 2002), although greater resolution is still needed, and many taxa have yet to be studied in detail. Furthermore, the changes apparent within sauropod evolution will almost certainly be subtler than those between sauropods and other dinosaurs. Therefore interpretations cannot rely solely on general analogies with extant taxa, but must also address the specific differences perceived between different taxa. In this regard, not all aspects of sauropod locomotor morphology may be interpretable, or even explicable, although their presence may still be noteworthy.

In this chapter, I use a phylogenetic framework to analyze sauropod locomotor evolution. This aspect of sauropod biology is approached quantitatively with measurements taken directly from specimens and is integrated with qualitative morphological observations. I interpret the resultant patterns in light of the evolution of body size and quadrupedalism, and note several sauropod locomotor specializations. Finally, three large ingroups (diplodocoids, basal macronarians, and titanosaurians) are described in greater detail, to illustrate a portion of the smaller-scale diversity evident in sauropod locomotor morphology.

BODY SIZE AND BODY-SIZE EVOLUTION

Body size likely played a central role in sauropod evolution. As Dodson (1990:407) noted, "Large size with all its biological implications was intrinsic to sauropod biology and was established at the outset of sauropod history." Even the most primitive known sauropods were large relative to other dinosaurs, usually reaching at least 5 metric tons; this is often close to the largest size attained by most other dinosaur clades (e.g., Anderson et al. 1985; Peczkis 1994). Ultimately, some sauropods achieved maximum body sizes exceeding 40 metric tons, with some estimates suggesting even higher masses (e.g., Colbert 1962).

Not surprisingly, several morphological features associated with early sauropod evolution appear to be size-related. This implies that the morphological hallmarks of the earliest sauropods (and, by extension, the diagnosis of Sauropoda itself) cannot be entirely separated from the acquisition of large body size.

These features include (1) a columnar, graviportal limb posture, (2) increased limb bone robusticity, (3) shortened distal limb segments (Carrano 2001), and (4) increased femoral midshaft eccentricity (Wilson and Carrano 1999; Carrano 2001). In other groups of terrestrial amniotes, these features are correlated with increased body size (e.g., Alexander et al. 1979; Scott 1985; Carrano 1998, 1999, 2001). Most are similarly correlated within other dinosaur clades and across Dinosauria as a whole (Carrano 2001). Additionally, the acquisition of a graviportal limb posture may be tied to reduction of lower-limb flexion and extension, implying a functional correlation with reduction in the lower-limb extensor attachments sites such as the olecranon and cnemial crest (see "Sauropod Locomotor Specializations," below).

The simultaneous appearance of these characters at the base of Sauropoda (Upchurch 1995, 1998; Wilson and Sereno 1998; Wilson 2002) is probably an artifact of an insufficiently resolved and recorded early sauropod history. Nonetheless, their close ties to large size in other vertebrate groups suggest that they may be genuinely intercorrelated. In other words, the appearance of more than one of these characters within a single clade or large-bodied taxa may be predictable.

Limb scaling relationships in dinosaurs were examined by Carrano (2001), although sauropods were not highlighted in that study. The results of that analysis demonstrated that dinosaur hindlimb bones scale strongly linearly regardless of posture, with the only evident differences being attributed to changes in body size. Specifically, although hindlimb elements of quadrupedal dinosaurs often appear to be more robust than those of bipedal forms, they are similarly robust at any given body size (fig. 8.1). Indeed, quadrupedalism is associated with an increase in body size over the primitive condition in all dinosaur clades in which it evolves. Dinosaur forelimb elements showed a trend opposite to that expected, becoming relatively longer and less robust in quadrupeds. This shift in scaling was interpreted as a response to the need for a longer forelimb to accompany the hindlimb in generating stride length.

Among thyreophorans and ceratopsians, scaling trends are consistent with this overall pattern, indicating that hindlimb bones did not undergo significant proportional changes during the transition to quadrupedalism apart from those associated with size increases. Forelimb changes are similar to those seen in quadrupeds generally (fig. 8.2). "Semibipedal" dinosaurs, such as prosauropods and derived ornithopods, tend to scale intermediately between bipeds and quadrupeds in both fore- and hindlimb elements (fig. 8.1). They do not show significant differences from either but, instead, overlap the two postures in forelimb scaling. The general picture available from these analyses is one of remarkable uniformity among all dinosaurs regardless of posture, and of the overwhelming influence of body size (versus posture) on limb bone dimensions. These patterns are apparent whether comparisons are made using anteroposterior, mediolateral, or circumferential femoral dimensions (Carrano 2001).

Other features of sauropod limbs are also best viewed as responses to increased body size. Femoral midshaft eccentricity increases in all

dinosaurs with increasing body size (Carrano 2001). The apparent disparity between sauropod femora and those of other dinosaurs is an artifact of the size discrepancy between them; extraordinarily large ornithopod and thyreophoran femora show eccentricities comparable to those of sauropods. Similarly, the proportionally short distal limb segments of sauropods are also mirrored among large thyreophorans, ceratopsians, and ornithopods, as well as large terrestrial mammals. Furthermore, the length of the distal limb decreases with increasing body mass in dinosaurs and terrestrial mammals generally (Carrano 1999, 2001). Thus, sauropod limb scaling properties are again entirely consistent with size-related trends.

Beyond this, body-size evolution has not received specific attention in sauropods, except in the larger context of body-size evolution in dinosaurs (Carrano 2005). Here I used squared-change parsimony to reconstruct ancestral body size values using terminal taxon body sizes and a composite phylogeny (fig. 8.3). Femoral length and midshaft diameters were used as proxies for body size because they scale strongly linearly with it (see appendix 8.1). Once ancestral values are reconstructed, ancestor–descendant comparisons can be made throughout Sauropoda. Specifically, I analyzed evolutionary patterns by comparing each ancestor to its descendants (including all internal nodes), as well as by comparing the reconstructed ancestral value for Sauropoda with each terminal taxon (table 8.1). In addition, I used Spearman rank correlation to investigate correlations with patristic distance from the base of the phylogeny, testing whether more derived taxa tend to be larger than more primitive forms (table 8.2).

Not surprisingly, early sauropod evolution is characterized by a steady increase in body size from the condition seen in *Vulcanodon* and larger prosauropods to that in basal neosauropods, representing at least a doubling in size over some 40 million years (Fig. 8.4). This pattern predominates throughout basal sauropods and into Neosauropoda, but the pattern within Neosauropoda is more complex.
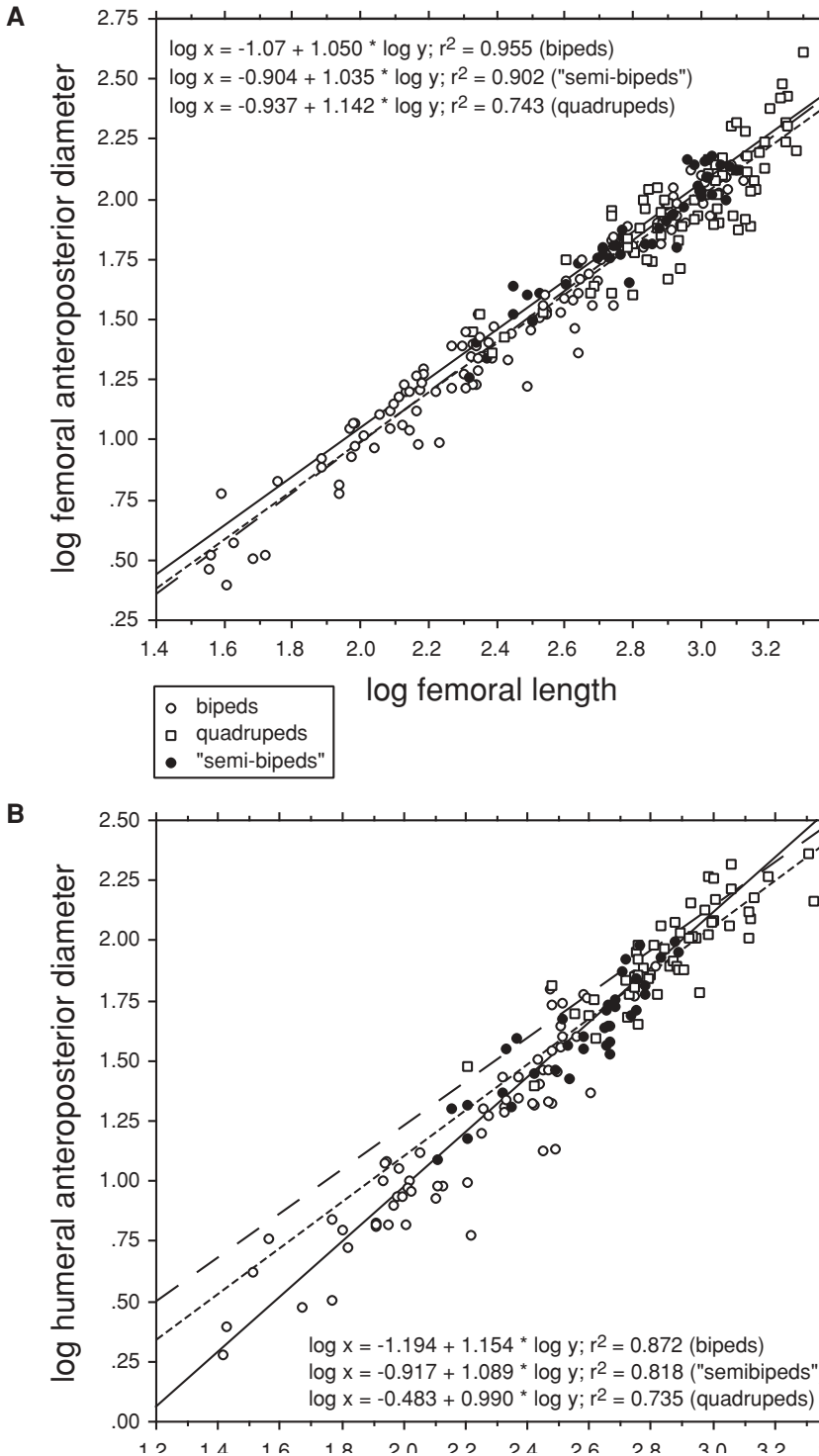
A

log x = -1.07 + 1.050 * log y; r^2 = 0.955 (bipeds)
log x = -0.904 + 1.035 * log y; r^2 = 0.902 ("semi-bipeds")
log x = -0.937 + 1.142 * log y; r^2 = 0.743 (quadrupeds)

log femoral anteroposterior diameter

log femoral length

○ bipeds
□ quadrupeds
● "semi-bipeds"

B

log humeral anteroposterior diameter

log x = -1.194 + 1.154 * log y; r^2 = 0.872 (bipeds)
log x = -0.917 + 1.089 * log y; r^2 = 0.818 ("semibipeds")
log x = -0.483 + 0.990 * log y; r^2 = 0.735 (quadrupeds)

FIGURE 8.1. Limb bone scaling associated with limb posture in dinosaurs. Reduced major axis regressions showing bipeds (open circles, solid lines), "semi-bipeds" (filled circles, dotted lines), and quadrupeds (open squares, dashed lines) from all dinosaur clades. (A) Femoral anteroposterior diameter versus length; (B) humeral anteroposterior diameter versus length. There are few scaling differences among the femora of different groups, but increasingly negative scaling of the humerus accompanies quadrupedalism.
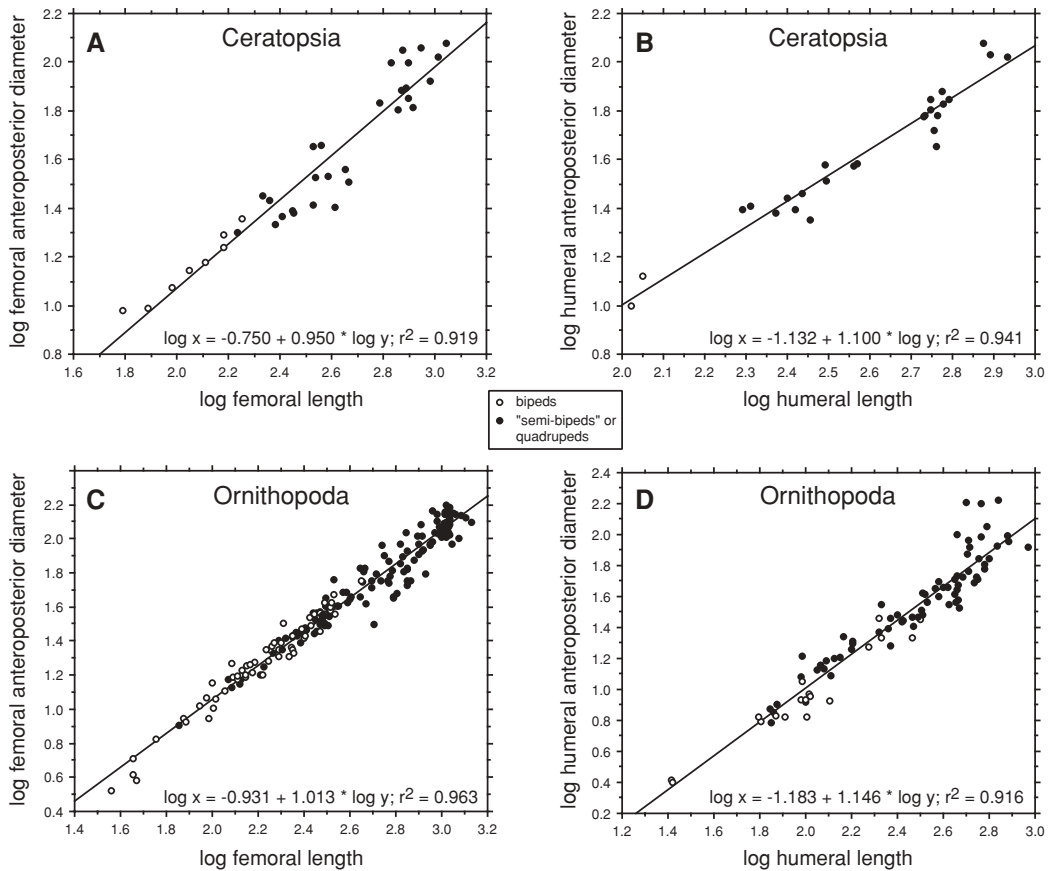
FIGURE 8.2. Limb bone scaling associated with changes in limb posture in nonsauropod dinosaurs. Reduced major axis regressions showing bipeds (open circles) and either "semibipeds" or quadrupeds (filled circles) in two clades for which the transition to quadrupedalism is represented. (A) Femoral diameter versus length in Ceratopsia; (B) humeral diameter versus length in Ceratopsia; (C) femoral diameter versus length in Ornithopoda; (D) humeral diameter versus length in Ornithopoda. Different postural types scale very similarly within each group.

Diplodocoids and macronarians both show divergences in body-size evolution, with members of each group having increased and decreased in size from the primitive condition. The largest members of both clades (*Apatosaurus* among diplodocoids, *Brachiosaurus, Argyrosaurus,* and *Argentinosaurus* among macronarians) are similar in size, but macronarians reach substantially smaller adult body sizes (*Saltasaurus, Neuquensaurus, Magyarosaurus;* ~1.5–3 metric tons) than the smallest diplodocoids (*Dicraeosaurus, Amargasaurus;* ~5–10 tons). More notable is the steady, consistent decrease in body size among derived macronarians, from some of the largest (e.g., *Argentinosaurus;* ~50 tons) to some of the smallest (e.g., *Saltasaurus;* ~3 tons) sauropod

body sizes over about 30 million years. This trend includes titanosaurians and reaches its nadir among saltasaurines.

This analysis supports previous assertions of body-size increase in sauropods, emphasizing its persistence throughout much of the clade. However, it also highlights an unappreciated complexity to this pattern, demonstrating that most body-size increases occur early in sauropod evolution and were largely complete by the Upper Jurassic neosauropod radiation. Subsequent decreases are also evident, particularly among macronarians. These may be a response to having reached an upper bound on body size or represent size-based diversification in later sauropod lineages. In this study,
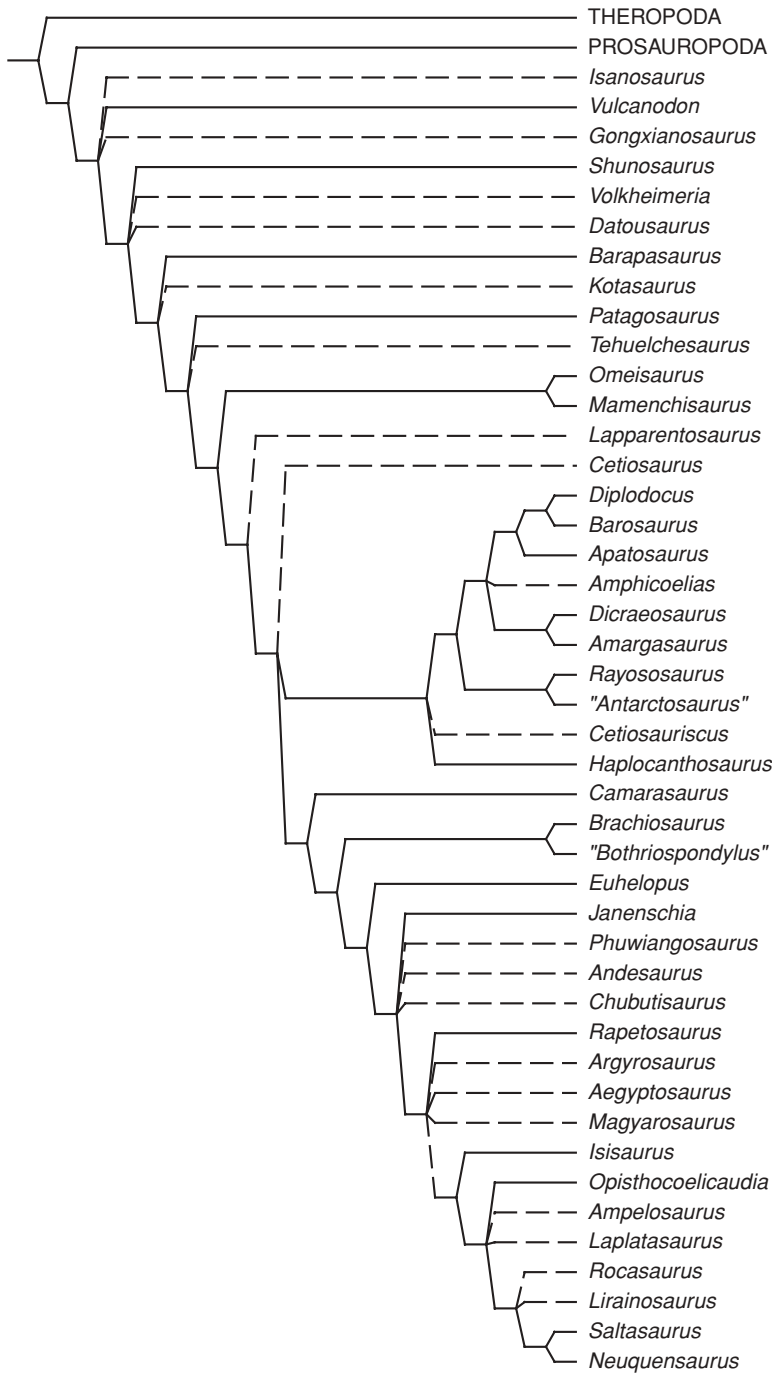
FIGURE 8.3. Sauropod phylogeny used for this chapter. Based primarily on Wilson (2002), but also Salgado et al. (1997), Wilson and Sereno (1998), Upchurch (1998), and Curry Rogers (pers. comm.). Taxa with dashed lines were not analyzed cladistically but are placed according to their presumed position in table 13 of Wilson (2002).

TABLE 8.1

TABLE 8.1
Results of Body-Size Analyses for Sauropoda

	MEAN	SUM	SKEW	MEDIAN	N	+	−
A. All ancestor–descendant comparisons							
FL	0.014	1.203	0.771	0.006	89	47	42
FAP	0.009	0.641	0.331	0.011	70	38	32
FML	0.013	0.911	0.239	0.008	70	41	29
B. Basal node–terminal taxon comparisons							
FL	0.209	10.879	−0.588	0.239	52	46	8

NOTE: Results using squared-change parsimony reconstructions based on measurements of femoral length. In A, comparisons are between each reconstructed ancestral node and each descendant taxon; in B, they are between the basal reconstructed ancestral node for each clade and all its descendant terminal taxa. These results are drawn from a larger study (Carrano 2005), in which all available dinosaur taxa were included. Abbreviations: skew, skewness; +, number of positive ancestor–descendant changes; −, number of negative ancestor–descendant changes; FAP, femoral anteroposterior diameter; FL, femoral length; FML, femoral mediolateral diameter.

TABLE 8.2
Spearman Rank Correlations of Body Size and Patristic Distance for Sauropoda

	ρ	z	P	$\rho^{\dagger}$	$z^{\dagger}$	$P^{\dagger}$
All Sauropoda						
FL	−0.104	−0.973	0.331	−0.106	−0.998	0.318
FAP	−0.201	−1.671	0.095*	−0.204	−1.697	0.090*
FML	−0.219	−1.833	0.067*	−0.223	−1.863	0.063*
Diplodocoidea						
FL	0.526	2.409	0.016*	0.519	2.377	0.018*
FAP	0.456	1.766	0.078*	0.449	1.738	0.082*
FML	0.705	2.639	0.008*	0.700	2.618	0.009*
All non-macronarian Sauropoda						
FL	0.663	4.499	<0.001*	0.662	4.491	<0.001*
FAP	0.415	2.490	0.013*	0.413	2.478	0.013*
FML	0.379	2.208	0.027*	0.376	2.193	0.028*
Macronaria						
FL	−0.718	−3.515	<0.001*	−0.727	−3.526	<0.001*
FAP	−0.205	−0.869	0.385	−0.211	−0.894	0.371
FML	−0.552	−2.467	0.014*	−0.563	−2.519	0.012*

NOTE: Abbreviations as in Table 8.1, Note. Daggers (†) indicate values corrected for ties; asterisks (*) indicate significant *p* values.

Magyarosaurus—which has been described as a "dwarf" sauropod (Jianu and Weishampel 1999)—is not a unique taxon but instead represents the size endpoint for an entire clade of relatively small taxa. Because smaller sauropods tend to be the end products of their respective lineages (and therefore have relatively high patristic distance values), there is a weak negative size correlation within Sauropoda. However, when macronarians are analyzed separately, they show a significant size decrease, while other sauropod groups (diplodocids and all nonmacronarians) exhibit significant size increases (table 8.2).

Trend analyses (McShea 1994; Alroy 2000a, 2000b; Carrano 2005) suggest that sauropod
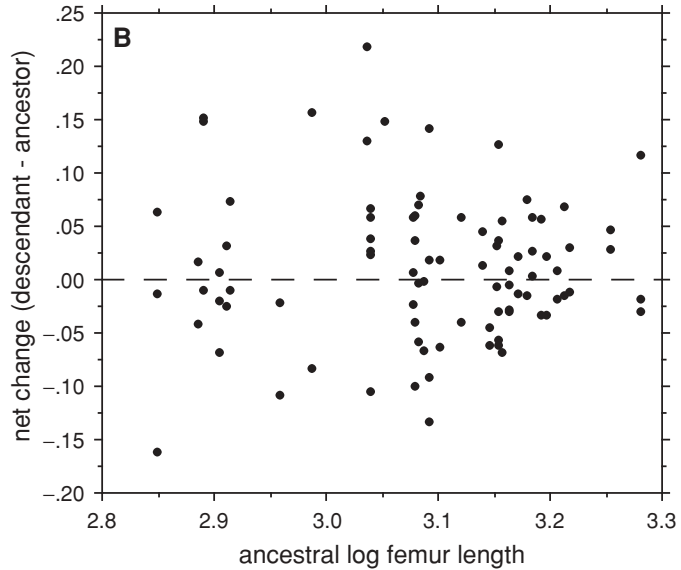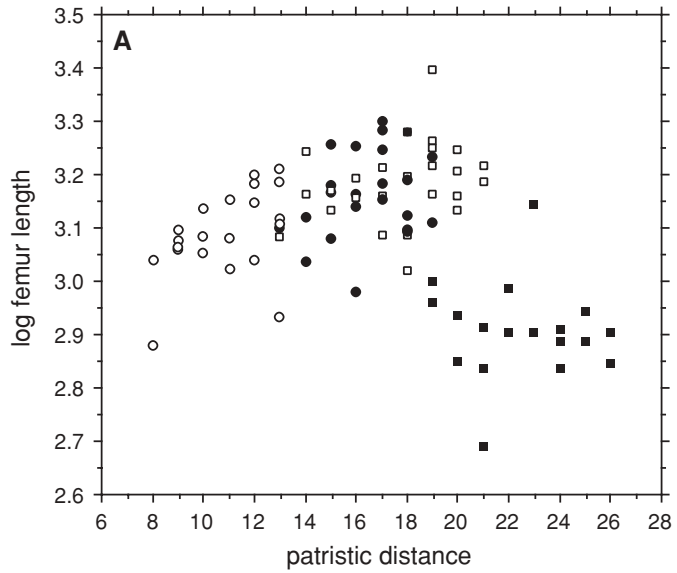
FIGURE 8.4. Body-size evolution in Sauropoda, based on measurements of femur length. (A) Body size versus patristic distance, showing increases throughout most of sauropod evolution, particularly from basal sauropods (open circles) to diplodocoids (open squares) and basal macronarians (filled circles). Note the steady size decrease in derived macronarians (filled squares). (B) Net change (descendant size minus ancestral size) versus ancestral body size, showing that changes during sauropod evolution are nearly random (i.e., no correlation).

body-size evolution is largely characterized by "active" macroevolutionary processes. Two details of this pattern support such an interpretation: (1) the range of sauropod body sizes expands through time (and through the phylogeny), with concomitant loss of smaller taxa as larger taxa appear; and (2) there is a weak positive correlation between ancestor–descendant changes and ancestral sizes. The apparent upper size bound for sauropods (which may well be altered by subsequent discoveries) is minimally about 50 metric tons, substantially greater than those for other dinosaur groups (which tend to be between 5 and 10 tons). Their apparent lower size bound, approximately 1–3 metric tons, is also considerably larger than that for other dinosaurs (usually between 0.05 and 0.5 tons) (Carrano 2005).

QUADRUPEDALISM

Quadrupedalism represents a second fundamental, dominant characteristic of all sauropods,

having been achieved in the earliest known forms and retained in all known descendants. Much of the appendicular skeleton shows adaptations for quadrupedal posture, particularly in the manus and forelimb (McIntosh 1990; Upchurch 1995, 1998; Wilson and Sereno 1998). These changes include lengthening of the forelimb elements relative to those of the hindlimb, as well as morphological modifications of the distal forelimb elements associated with locomotion and weight bearing (see below).

Based on such criteria, the primitive sauropod *Vulcanodon* appears to have been fully quadrupedal (Cooper 1984). Its more primitive relatives *Blikanasaurus* and *Isanosaurus* entirely lack forelimb materials, so their postural status cannot be assessed. The recently described basal sauropod *Antetonitrus* (Yates and Kitching 2003) has a relatively long forelimb but retains prosauropod-like manual elements, suggesting that quadrupedalism may have been facultative in this taxon. More complete forelimb materials are needed to better elucidate its postural and locomotor capabilities.

Other outgroup sauropodomorph taxa (prosauropods and stem-sauropodomorphs) all appear to have retained at least facultative bipedalism (e.g., Galton 1990). Thus the transition to quadrupedalism in sauropods is only hinted at by the known fossil record. Nonetheless, it can be examined indirectly through comparison with other dinosaur groups in which the transition is recorded (Ceratopsia, Thyreophora), along with "semibipedal" taxa such as prosauropods and derived ornithopods.

Among thyreophorans and ceratopsians, the shift to quadrupedalism is also accompanied by marked changes in forelimb morphology. Not surprisingly, hindlimb morphology is usually little altered, instead retaining many of the locomotor features already present in the bipedal members of each clade. Most differences in the hindlimb can be attributed to those associated with concomitant body size increases (Carrano 2001; see also "Body Size and Body-Size Evolution," above). In the forelimb, however, the manus is modified to become weight-bearing through consolidation of the carpus (via fusion and/or loss) and reduction in its mobility, incorporation of the metacarpals into a bound unit, and transformation of the unguals into blunt, hooflike structures. Aside from relative lengthening of the forelimb, these are the primary features used to infer quadrupedalism in dinosaur taxa.

Most of these changes are already present in basal sauropods (e.g., *Shunosaurus, Barapasaurus*), indicating that these animals were already fully (and probably obligatorily) quadrupedal. The manus of *Vulcanodon* is incomplete, but the long humerus and forearm suggest that this taxon was also probably fully quadrupedal (Raath 1972; Cooper 1984). Nevertheless, the transition to permanent quadrupedalism likely involved a series of morphological changes that occurred across a range of facultatively quadrupedal taxa. *Antetonitrus* may represent one such intermediate, combining a relatively long forelimb with a primitive manus (Yates and Kitching 2003).

More derived basal sauropods record the completion of this evolutionary process (fig. 8.5). Despite our fragmentary understanding of its early stages, relics of the transition to quadrupedalism remain in basal sauropods such as *Shunosaurus, Barapasaurus, Omeisaurus, Mamenchisaurus*, and "cetiosaurs" (e.g., *Lapparentosaurus, Patagosaurus, Cetiosaurus*). Although these forms were fully quadrupedal, they document the continued acquisition of additional characters related to this posture. Their phylogenetic positions help to clarify the original sequence of character acquisition in earlier forms by "removing" later-appearing features from the early stages of the evolution of sauropod quadrupedalism.

The primitive saurischian manus was probably digitigrade, as suggested by the posture of manus prints of otherwise bipedal dinosaurs (e.g., Lull 1953; Baird 1980). Additionally, other dinosaur clades that underwent a transformation to quadrupedalism also appear to have passed through (and sometimes remained at) a phase involving a digitigrade manus. The major
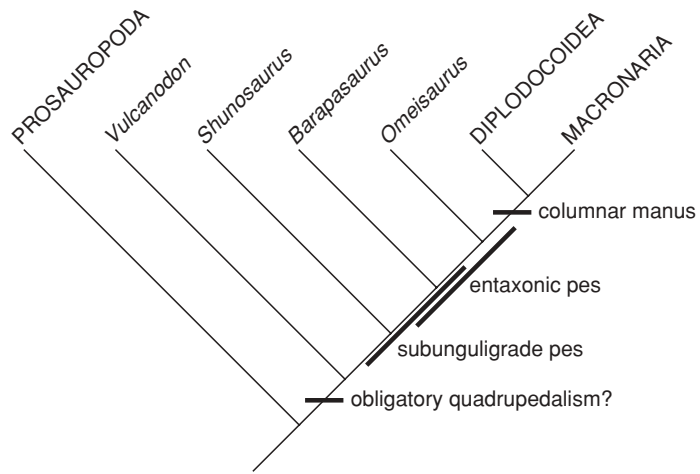
FIGURE 8.5. The transition to quadrupedalism in Sauropoda. Although basal sauropods were likely obligate quadrupeds, numerous additional modifications for this posture were developed in basal taxa. Phylogeny from Wilson and Sereno (1998).
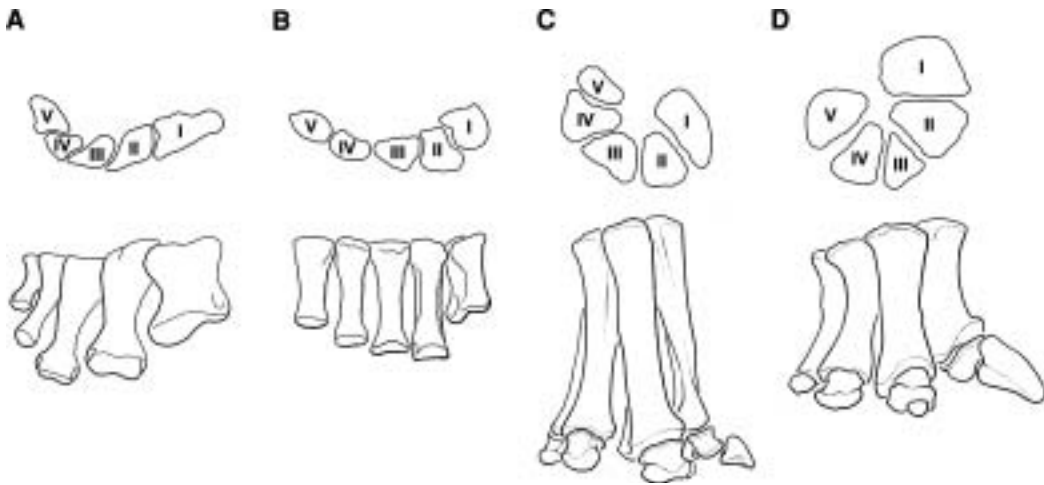

FIGURE 8.6. Changes in the metacarpus in Sauropoda. The metacarpals acquire a semicircular, columnar arrangement within sauropods, with a reduction in length disparities between elements. Proximal (top row) and dorsal (bottom row) views of the articulated right metacarpus; proximal views are shown with the palm toward the top of the page. (A) *Massospondylus carinatus* (modified from Cooper 1981). (B) *Shunosaurus lii* (modified from Zhang 1988). (C) *Brachiosaurus brancai* (modified from Janensch 1922; Wilson and Sereno 1998). (D) *Janenschia robusta* (modified from Janensch 1922; Wilson and Sereno 1998). Numbers refer to metacarpals I through V. Not to scale.

changes in manus morphology, therefore, began from a primitively digitigrade structure in which the individual metacarpals are most firmly interconnected proximally, arranged in a dorsoventral arch, and held at an oblique angle to the substrate (fig. 8.6). This morphology would have served to resist long-axis bending during flexion and extension at the carpus by allowing the metacarpals to act together in distributing and deflecting these loads. In the most primitive sauropods for which complete manus remains are known (e.g., *Shunosaurus*,

Omeisaurus), the intermetacarpal facets are already somewhat elongated distally, indicating that the bones were arranged into a tight, amphiaxonic arch while being held nearly vertically relative to the substrate (Osborn 1904; Gilmore 1946; Christiansen 1997). Coombs (1975) described this arrangement as mimicking columns beneath a supported floor (i.e., the carpus), an analogy that is probably mechanically appropriate. Compressional loading was likely increased relative to bending in such a structure.
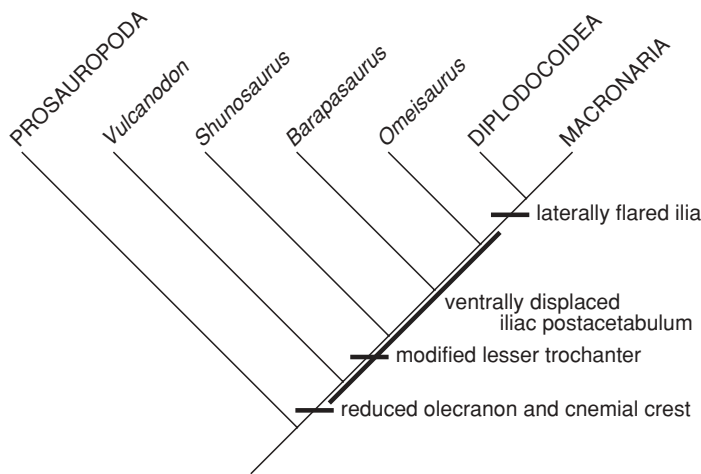
FIGURE 8.7. Sauropod locomotor specializations. The acquisition of unique morphological features within sauropods occurred throughout basal taxa, prior to the divergence of diplodocoids and macronarians. Phylogeny from Wilson and Sereno (1998).

Meanwhile, the sauropod pes also underwent significant changes in morphology and posture. Primitively, the saurischian (and dinosaurian) pes was a digitigrade structure with four primary weight-bearing digits, an arrangement retained by prosauropods, primitive theropods (*Herrerasaurus, Eoraptor*), and basal ornithischians (*Pisanosaurus, Lesothosaurus*). Basal sauropods enlarged digit V into an additional support element (Raath 1972; Cruickshank 1975), representing a reversal to a more primitive archosaurian condition. These same taxa also show a shift in metatarsal orientation from relatively upright (subvertical) to more horizontal. Sauropod footprints show evidence that these low-angled metatarsals were supported by a fleshy pad (Coombs 1975; Gallup 1989), analogous to those of modern proboscideans and rhinocerotids, indicating that the sauropod pes was subunguligrade rather than strictly digitigrade.

SAUROPOD LOCOMOTOR SPECIALIZATIONS

Other changes documented in basal sauropod evolution do not appear to be related to either quadrupedalism or large body size but, instead, represent unique components of the sauropod locomotor apparatus. Like the changes discussed previously, these modifications occurred early in sauropod evolution and were essentially in place by the appearance of Neosauropoda (fig. 8.7).

All sauropods show evidence of reduction in the lower-limb muscle attachments. This occurs in both the fore- and the hindlimbs, where the insertion areas for these muscles are reduced relative to the condition in other saurischians (and other dinosaurs). In the forelimb, the ulnar olecranon process is reduced to a flat, rugose surface in primitive sauropods; this condition is reversed only in titanosaurians (Christiansen 1997; Wilson and Sereno 1998). This process represents the insertion of musculi (mm.) triceps, which are the major forearm extensors (e.g., Christiansen 1997). The hindlimb shows reduction of the cnemial crest on the tibia, representing the insertion for the knee extensors (mm. iliotibiales, musculus [m.] ambiens, and mm. femorotibiales). These changes suggest a shift in basal sauropods away from significant use of the lower limb during locomotion and toward relying primarily on protraction and retraction at the hip and shoulder to generate stride length.

As in other quadrupedal dinosaurs, both the manus and the pes of sauropods show phalangeal reduction (Osborn 1904; Coombs 1975; Upchurch 1995, 1998; Wilson and Sereno 1998). Usually reduction occurs primarily in length, with individual phalanges becoming

TABLE 8.3
Loss of Manual Phalanges in Sauropoda

	SPECIMEN	PRESERVED	RECONSTRUCTED
Theropoda			2-3-4-2*-0
Prosauropoda			2-3-4-3*-2*
Shunosaurus lii	ZDM T5402	2-2-2*-2*-2*	2-2-2*-2*-2*
Omeisaurus tianfuensis	ZDM T	2-2-?-?-1	2-2-2-2-2*
Jobaria tiguidensis	MNN TIG3	2-2-2-2-2	2-2-2-2-2
Apatosaurus louisae	CM 3018	2-2*-1-1-1	2-2*-1-1-1
Apatosaurus excelsus	CM 563	2-1-1-1-1	2-2*-1-1-1
Camarasaurus sp.	FMNH 25120	2-1-1-1-1	2-2*-1-1-1
Camarasaurus sp.	AMNH 823	2-1-1-1-1	2-2*-1-1-1
Camarasaurus grandis	GMNH-VP 101	2-1-1-1-1	2-2*-1-1-1
Brachiosaurus brancai	HMN S II	2-1-1-1-1	2-2*-1-1-1
Janenschia robusta	HMN Nr. 5	2-2*-1-1-1	2-2*-1-1-1
Opisthocoelicaudia skarzynskii	ZPal MgD-I/48	0-0-0-1*-0	0-0-0-1*-0
Alamosaurus sanjuanensis	USNM 15660	0-0-0-0-0	0-0-0-0-0

NOTE: Formulas list numbers of phalanges in order from digit I through digit V. Asterisks (*) indicate vestigial phalanges; question marks (?) indicate questionable numbers.

compact and often disclike. However, sauropods continue this trend to its extreme, eliminating many of the manual and pedal phalanges altogether. In the manus particularly, this reduction is carried to the point that all the unguals, and nearly all the phalanges, are eventually lost (Osborn 1904, 1906; Gilmore 1946; Wilson and Sereno 1998; table 8.3). Phalanges typically serve as points of flexion and extension for the manus, and their loss indicates the loss of these functions within this portion of the limb. This represents the end point of the transformation from a propulsive, digitigrade manus to one that was almost entirely dedicated to columnar support.

Tracking this set of changes is problematic, however, because phalanges are often lost prior to discovery of the specimen. This is particularly true of vestigial, nubbinlike phalanges such as those in the manus of *Shunosaurus* (Zhang 1988). Conservatively, manual phalangeal reduction appears to occur primarily at two points in sauropod evolution. First, most of the phalanges on digits II–V were lost in Neosauropoda, and then the remainder were lost in derived titanosaurs. However, some evidence suggests that this pattern is more complex. For example, *Apatosaurus louisae* (CM 3018) retains two phalanges on digit II (Gilmore 1936). Many other neosauropods (perhaps most nontitanosaurs) retain a distal articular facet on II-1 that implies the presence of an additional phalanx, albeit a small one. The vestigial IV-1 in *Opisthocoelicaudia* (Borsuk-Bialynicka 1977) might also be a genuine relic. Thus, additional stages of reduction may have existed between Neosauropoda and titanosaurs (table 8.3).

In addition, the primitive dinosaurian pes is a mesaxonic structure, with the weight-bearing axis passing down the central digit (III) (fig. 8.8). This condition, in which the central metatarsals are the longest and most robust, is evident in prosauropods and in basal sauropods (*Vulcanodon*). However, it is altered in more derived sauropods (e.g., *Shunosaurus, Omeisaurus*) such that the medial metatarsals are larger than the central elements. In particular, metatarsal I becomes the most robust, and the weight-bearing axis shifts to a more medial, entaxonic position (Coombs 1975). This type of pedal structure is highly unusual among tetrapods, being evident elsewhere among
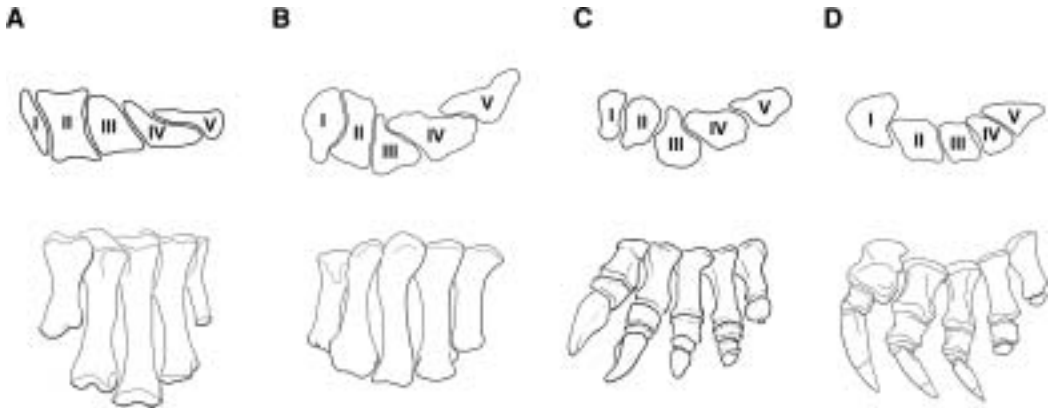
FIGURE 8.8. Changes in the metatarsus in Sauropoda. The metatarsals change from mesaxonic to entaxonic, as the medial digits become relatively larger. Proximal (top row) and dorsal (bottom row) views of the articulated left metatarsus; the proximal views are shown plantar-upward. (A) *Massospondylus carinatus* (modified from Cooper 1981) . (B) *Vulcanodon karibaensis* (modified from Cooper 1984). (C) *Shunosaurus lii* (modified from Zhang 1988; Wilson and Sereno 1998). (D) *Apatosaurus louisae* (modified from Gilmore 1936). Numbers refer to metatarsals I through V. Not to scale.
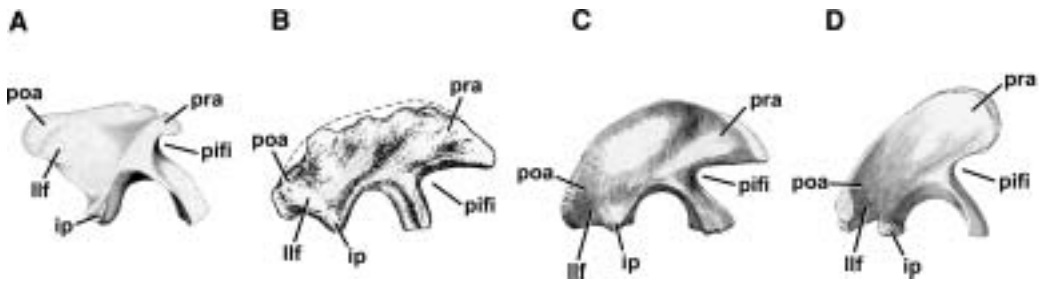

FIGURE 8.9. Changes in the ilium in Sauropoda. The ilium is expanded anteroposteriorly, and the postacetabulum is depressed ventrally to the level of the ischial peduncle. Right pelves are shown in lateral view. (A) *Massospondylus carinatus* (modified from Cooper 1981). (B) *Shunosaurus lii* (modified from Zhang 1988). (C) *Dicraeosaurus hansemanni* (modified from Janensch 1961). (D) *Brachiosaurus brancai* (modified from Janensch 1961). Abbreviations: ip, ischial peduncle; llf, origination area for lower limb flexors; pifi, space anterior to ilium for passage of m. puboischiofemoralis internus 2; poa, postacetabulum; pra, preacetabulum. Not to scale.

megatheriid xenarthrans. This shift may have accompanied a more general change from narrow-bodied, predominantly bipedal taxa in which the limbs were positioned well under the body to wider-bodied quadrupedal taxa in which the limbs were more laterally positioned. In such wider-bodied taxa, the weight-bearing axis would pass through the medial portion of the pes instead of the central portion, as reflected in the modified proportions of metatarsals I and II.

The ilium is substantially modified in sauropods (fig. 8.9). Primitively (in prosauropods and basal theropods), this bone is dorsoventrally narrow and relatively short anteroposteriorly (Carrano 2000). In all known sauropods, both the preacetabular and the postacetabular processes are expanded anteroposteriorly and dorsoventrally. The preacetabulum is large and lobate (Raath 1972; Wilson and Sereno 1998), arching above a large space anteroventral to the ilium through which m. puboischiofemoralis internus 2 likely passed (Romer 1923; Carrano and Hutchinson 2002). This space is larger than that seen in neotheropods, implying that m. puboischofemoralis internus 2 did not undergo the alterations in size or position seen in that group (Carrano and Hutchinson 2002).

The preacetabular ilium is also flared laterally in most neosauropods, with the blade curving outward from a point just dorsal to the pubic peduncle. This is carried to an extreme in titanosaurians (Powell 1986, 1990, 2003; Wilson
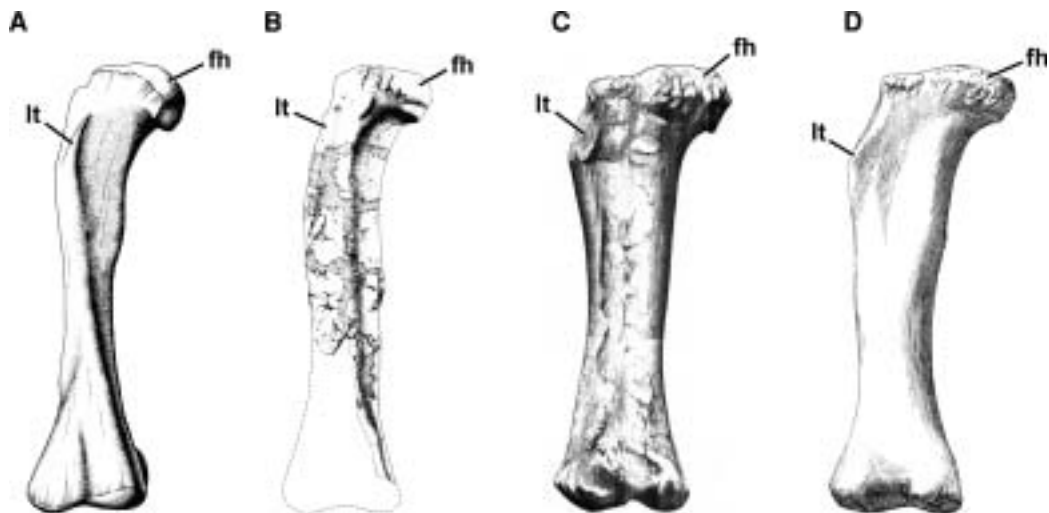
FIGURE 8.10. Changes in the femoral lesser trochanter within Sauropoda. The lesser trochanter is reduced from a distinct process to a rugose bump and shifts in position from anterolateral to lateral. Right femora are shown in anterior view. (A) *Massospondylus carinatus* (modified from Cooper 1981). (B) *Vulcanodon karibaensis* (modified from Cooper 1984). (C) *Apatosaurus excelsus* (modified from Riggs 1903). (D) *Brachiosaurus brancai* (modified from Janensch 1961). Abbreviations: fh, femoral head; lt, lesser trochanter. Not to scale.

and Sereno 1998), in which the preacetabular ilium reaches laterally nearly as far as the greater trochanter of the femur. A similar condition is seen in ankylosaurs, and in both groups the effect would have been to shift the origins of m. iliotibialis 1 and m. iliofemoralis externus laterally. As a result, these muscles would have had reduced mediolateral actions relative to their anteroposterior and/or dorsoventral ones.

The iliac postacetabulum is also large but extends much farther ventrally than the preacetabulum. In *Vulcanodon* (Raath 1972; Cooper 1984) and *Shunosaurus* (Zhang 1988), the postacetabulum is depressed close to the level of the ischial peduncle, much more so than the condition in prosauropods and theropods. It reaches the level of the ischial peduncle in many diplodocoids, and actually exceeds it in many titanosaurians. Several lower-limb flexors originated on the iliac postacetabulum, including mm. flexores tibiales internii, m. flexor tibialis externus, and m. iliofibularis (Cooper 1984), although the exact placement and bounds of these muscles are not clear (Carrano and Hutchinson 2000). In most neosauropods, this portion of the ilium often bears complex fossae

and rugosities that mark the origins of several of these muscles. Therefore, depression of the postacetabulum would have brought the lower-limb flexor origins farther ventrally, reducing their dorsoventral components relative to their anteroposterior actions.

On the femur, the lesser trochanter was primitively part of the dinosauriform trochanteric shelf, a ridge running around the anterolateral corner of the proximal femur that served as the insertion for m. iliofemoralis externus (Hutchinson 2001). In most dinosaurs, this shelf is differentiated into a distinct process (the lesser trochanter, for portions of mm. iliotrochanterici) as well as a rugose mound (for m. iliofemoralis externus) (Hutchinson 2001; Carrano and Hutchinson 2002). This occurs independently in several dinosaur clades (Carrano 2000), but sauropods are a persistent exception to this trend (fig. 8.10). Instead, although the trochanteric shelf is modified in sauropods, the lesser trochanter is reduced to a rounded anterolateral ridge in *Vulcanodon* (Cooper 1984) and a rugose lateral bump in other sauropods. The m. iliofemoralis insertion was not drawn proximally as in other

dinosaurs (Carrano 2000), instead remaining well below the femoral head.

This transition would have accomplished two things. First, m. iliofemoralis externus would have been placed laterally, not anteriorly as in most dinosaurs (Carrano 2000). Thus this muscle would have retained a role in femoral abduction (and possibly rotation), rather than femoral protraction. Second, it remained relatively distal in position and was (apparently) never elaborated into separate muscles; no analogues to mm. iliotrochanterici of theropods and birds were present. Therefore sauropods likely relied on m. puboischiofemoralis internus for femoral protraction, as did most non-theropod dinosaurs.

LOWER-LEVEL PATTERNS IN SAUROPOD LOCOMOTOR EVOLUTION

Although acquired stepwise in basal sauropods, the morphological specializations discussed above characterize nearly all known sauropod taxa. Their appearances mark the emplacement of the sauropod locomotor apparatus, which remained fundamentally unaltered throughout subsequent neosauropod evolution for the next 100 million years. Yet on this functional and morphological foundation was built a diversity of sauropod locomotor habits that has gone mostly unappreciated. This is largely thanks to the perceived uniformity of the sauropod appendicular skeleton, which, while genuine at one scale (and in that sense remarkable), has also helped to obscure smaller-scale patterns in sauropod locomotor evolution (e.g., Hatcher 1903:55). Discovering and interpreting lower-level evolutionary patterns require an understanding of smaller-scale differences between sauropod groups.

Here I discuss the differences among three major sauropod groups—diplodocoids, basal macronarians, and titanosaurians. I do not seek to present a detailed study of these taxa; my goal is rather to demonstrate that existing information is sufficient to illustrate marked morphological (and, by inference,

functional) differences among these taxa. Future work in this area is likely to be quite fruitful.

DIPLODOCOIDEA

Diplodocoids are the sister-group to Macronaria within Neosauropoda (fig. 8.3). The group includes three major clades (Diplodocidae, Dicraeosauridae, and Rebbachisauridae) and over 25 taxa, of which at least 15 are well known. They are generally perceived as smaller and more slender than other sauropods, based largely on reconstructions of *Diplodocus, Amargasaurus,* and *Dicraeosaurus.* However, specimens of *Apatosaurus* (YPM 1860) and *Seismosaurus* (NMMNH P-3690; possibly synonymous with *Diplodocus* [Lucas and Heckert 2000]) rival the largest macronarians in overall size. (As noted earlier, this gigantism was achieved independently in these two clades.)

Diplodocoids have gracile limbs that are short relative to the trunk, making them somewhat low-slung animals (fig. 8.11A). Compared to basal macronarians, diplodocoids would have had shorter strides relative to their trunk length. A marked discrepancy between the fore- and the hindlimb lengths exaggerates the condition typically present in other quadrupedal dinosaurs. The manus remains relatively short, similar to that in more primitive sauropods. A few diplodocoids (*Diplodocus* and particularly *Amphicoelias*) are notable in having a reduced femoral midshaft eccentricity (Osborn and Mook 1921) compared to other, similar-sized sauropods.

In addition, diplodocoids have a modified metatarsus in which metatarsals III and IV are "twinned" in morphology. This contrasts (albeit subtly) with the condition in other sauropods, where these two bones are similar in length but distinct from one another in shape. The functional implications of such a pedal structure are unclear; it may belie some minor locomotor specialization or simply be a product of increased limb bone slenderness. In other respects, however, the diplodocoid appendicular skeleton is relatively conservative, retaining
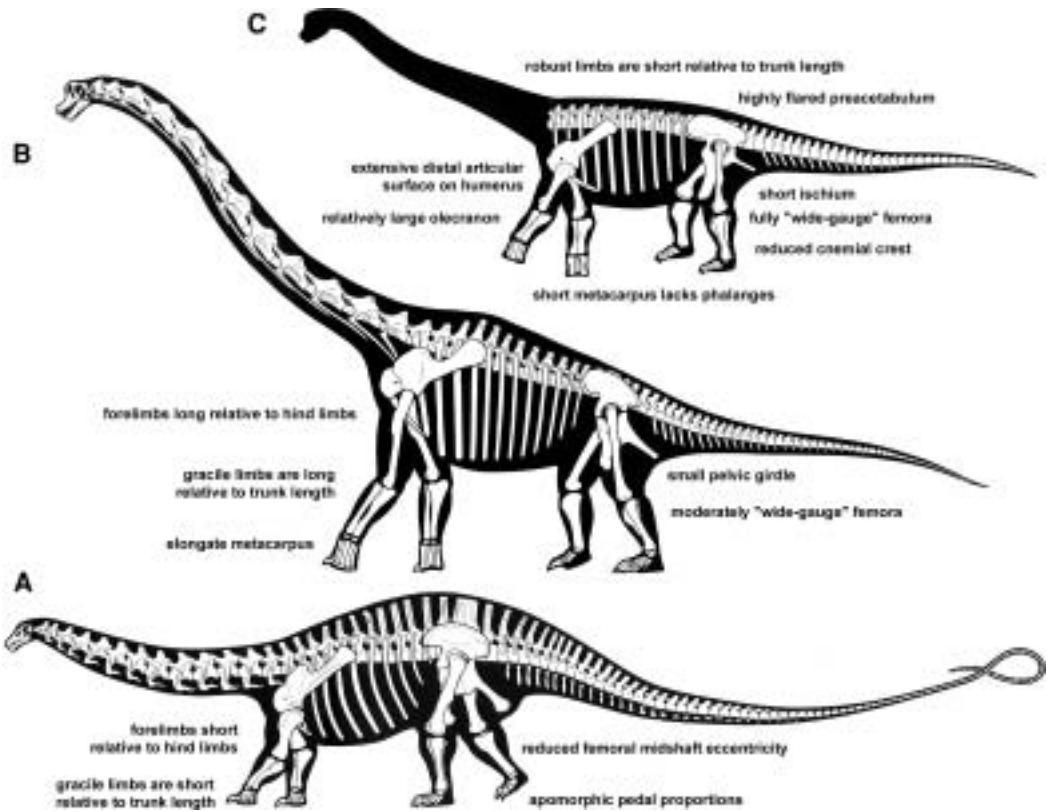
FIGURE 8.11. Comparative morphology of three sauropod groups. (A) Diplodocoidea (*Apatosaurus louisae*); (B) basal Macronaria (*Brachiosaurus brancai*); (C) Titanosauria (*Opisthocoelicaudia skarzynskii*). Skeletal reconstructions modified from Wilson and Sereno (1998). Approximately to scale.

many sauropod and neosauropod symplesiomorphies.

BASAL MACRONARIA

"Basal macronarians" are a paraphyletic assemblage of more than 20 species of taxa including the Brachiosauridae, *Camarasaurus*, *Euhelopus*, *Janenschia*, and the most basal titanosaurians (e.g., *Aeolosaurus*, *Pleurocoelus*) (Wilson and Sereno 1998; Wilson 2002). Many of these forms are large even among sauropods, with taxa such as *Brachiosaurus*, *Sauroposeidon*, and *Argentinosaurus* representing some of the largest known terrestrial vertebrates.

Basal macronarians are characterized by relatively gracile limbs that are long relative to the trunk (fig. 8.11B). As a result, these taxa would have had longer stride lengths compared to diplodocoids. The forelimbs are long relative to

the hindlimbs (again, opposite to the diplodocoid condition), a tendency most evident in *Brachiosaurus* (FMNH P25107, HMN D) but also seen in other taxa ("*Bothriospondylus madagascariensis*," MNHN specimen [Lapparent 1943]; *Euhelopus*, PMU R234 [Wiman 1929]; *Lusotitan atalaiensis*, MIGM holotype [Lapparent and Zbyszewski 1957]). In addition, the metacarpus is elongate relative to that of diplodocids and primitive sauropods, allowing it to contribute increasingly to stride length. Overall, most of these changes would have allowed the forelimb to approach or exceed the hindlimb in its ability to contribute to forward progression. This represents a reversal of the typical (and primitive) dinosaurian condition.

Many of these forms also show a reduction in the size of the pelvic girdle relative to the pectoral girdle. This would have reduced the origination

areas for most of the proximal hindlimb musculature, again suggesting a shift in locomotor dominance toward the forelimb. Some of the "wide-gauge" features that exemplify titanosaurians (see below) are present in these taxa, but to a much lesser degree. For example, brachiosaurids show a medial offset of the femoral head, moderate flaring of the preacetabular ilium, and reduction of the pollex ungula—all changes eventually carried further by titanosaurians (Wilson and Carrano 1999).

Recently, Stevens and Parrish (1999) suggested that sauropods generally did not raise the neck above the level of the shoulder. The resulting clade of long-necked but low-browsing animals stands in marked contrast to conventional reconstructions of sauropods with giraffe-like neck postures (e.g., Paul 1988). I do not attempt to evaluate this hypothesis here, but it is worth noting that an additional effect of forelimb lengthening in basal macronarians would be to raise the height of the shoulder, thereby elevating the maximum potential height of the neck in animals otherwise constrained to low browsing. Thus basal macronarians may have been relatively high-browsing sauropods thanks to their forelimb adaptations.

TITANOSAURIA

Titanosaurian sauropods comprise approximately 50 taxa of derived macronarians (Wilson and Sereno 1998; Curry Rogers and Forster 2001; Wilson 2002) such as *Rapetosaurus, Ampelosaurus*, and the Saltasaurinae. Of these, approximately 35 are known from diagnostic materials, and many fewer from relatively complete specimens. As noted above, titanosaurians are unusual in being markedly smaller than most other sauropods, but in addition, they display a suite of features that readily distinguish them from other neosauropods (fig. 8.11C). These include an outward-canted femur with a correspondingly angled distal articular surface, a widened sacrum, and a significantly more elliptical femoral midshaft relative to body size (Wilson and Sereno 1998; Wilson and Carrano 1999). Such features are consistent with an

interpretation of titanosaurians as the authors of "wide-gauge" sauropod trackways (Wilson and Carrano 1999).

Titanosaurians are also characterized by highly flared iliac preacetabular processes (Powell 1986, 1990, 2003; Christiansen 1997), somewhat analogous to the condition seen in ankylosaurs. This flaring would have displaced the origins of m. iliofemoralis and m. iliotibialis 1 more laterally, as noted above (Carrano 2000). The pelvic elements are relatively small, as in basal macronarians. In addition, the ischium is very short relative to the pubis (Wilson and Sereno 1998), and the anterior caudals have ball-in-socket articulations, perhaps associated with an increased predominance of bipedal rearing in these taxa (Borsuk-Bialynicka 1977; Wilson and Carrano 1999).

Reversing the primitive condition for sauropods, titanosaurian humeri have anteroposteriorly long distal articular surfaces (Wilson and Sereno, 1998; table 8.4), indicating a wider range of flexion–extension at the elbow than in other sauropods (Osborn 1900). Although the limb joint surfaces are not well modeled and are now missing what were probably substantial cartilage caps (Hatcher 1901; Coombs 1975), it is reasonable to assume that the true articular cartilage would have been at least as anteroposteriorly extensive as the bony attachment surface. I measured the linear height of the articular surface on the anterior face of the distal humerus and compared it among sauropod groups relative to total humerus length. These differences are significant when compared using both the unpaired, two-group t-test ($t = -5.346$, df = 16; $p < 0.001$) and the Mann–Whitney U-test ($U = 2.000$, $Z = -3.184$; $p = 0.015$).

Both fore- and hindlimbs are short relative to the trunk. The particularly short titanosaurian forefoot is the most derived among sauropods in having entirely lost the carpus and phalanges (including the manual ungual) or having both reduced to cartilage (Gilmore 1946; Salgado et al. 1997; Wilson and Sereno 1998). Whatever function the enlarged pollex had originally evolved

TABLE 8.4
Humeral Articulation Angles in Sauropods

	SPECIMEN	HL	AHD	%
Shunosaurus lii	T5401	648	37	5.7
Omeisaurus tianfuensis	T5701	790	27	3.4
Mamenchisaurus constructus	IVPP V.947	1,080	52	4.8
"Cetiosaurus" mogrebiensis	Tamguert n'Tarit	1,370	42	3.1
Barosaurus africanus	HMN k 37	970	16	1.6
Dicraeosaurus hansemanni	HMN Q 11	740	24	3.2
Camarasaurus grandis	YPM 1901	1,288	90	7.0
Brachiosaurus altithorax	FMNH P25107	2,040	105	5.1
Brachiosaurus brancai	HMN S II	2,130	104	4.9
Euhelopus zdanskyi	GSC specimen	1,090	40	3.7
Tehuelchesaurus benitezii	MPEF-PV 1125	1,140	41	3.6
Janenschia robusta	HMN P 8	890	40	4.5
Gondwanatitan faustoi	MN 4111-V	729	71	9.7
Aegyptosaurus baharijensis	BSP 1912 VIII 61	1,000	83	8.3
Alamosaurus sanjuanensis	USNM 15560	1,360	90	6.6
Opisthocoelicaudia skarzynskii	ZPAL MgD-I/48	1,000	58	5.8
Saltasaurus loricatus	PVL 4017-67	611	66	10.8
Isisaurus colberti	ISIR 335/59	1,480	148	10.0

NOTE: Measurements are in millimeters. Abbreviations: AHD, anterior height of distal articulation; HL, humeral length.
% = (AHD/HL) × 100.

for in ancestral bipedal saurischians, its conversion into an entirely locomotor structure was complete in titanosaurians. These barrel-chested taxa also exhibit a modified shoulder joint (Powell 1986, 2003; Wilson and Sereno 1998) that, in conjunction with changes at the elbow, suggests increased forelimb mobility and flexibility compared to other sauropods.

CONCLUSIONS

The basic sauropod appendicular morphology, including its functional relationships to locomotion, is fundamentally tied to the constraints imposed by large size on a vertebrate in a terrestrial environment. Many sauropod appendicular synapomorphies are also found in other large dinosaurs and in large terrestrial mammals, and their appearance is likely size related. Body size within sauropods increases steadily throughout the clade, with subsequent size decreases in both diplodocoids (dicraeosaurids) and macronarians (saltasaurines). Trend analyses suggest that this

conforms to a "passive" rather than an "active" trend (*sensu* McShea 1994).

Features associated with the acquisition of obligate quadrupedalism—including a relatively long forelimb and supportive manus—are already present in the primitive sauropod *Vulcanodon*, but the transition is completed in successively more derived basal sauropods. Few scaling changes are inferred to have accompanied this postural shift aside from lengthening of the forelimb.

Other aspects of sauropod limb morphology are unique to the clade, including the development of a columnar, tightly arched manus with a reduced phalangeal count. The subunguligrade pes is entaxonic, indicating a shift in primary weight support toward the medial aspect of the pes. The femoral lesser trochanter is fully lateral and reduced to a rugose bump, representing the least elaborate such structure within Dinosauria. The iliac preacetabulum (and associated muscle origins) are flared laterally, whereas the postacetabulum (and associated muscle origins) are depressed ventrally.

These basic aspects of sauropod appendicular design are never radically altered, but sauropod locomotor evolution nevertheless includes an unappreciated morphological diversity. Diplodocoids, basal macronarians, and titanosaurians each show locomotor specializations that distinguish them from one another. Although many of these differences are subtle relative to those that distinguish sauropods from other dinosaurs, they nonetheless suggest that all sauropods did not employ identical locomotor styles or habits. Future studies should focus on these smaller-scale morphological differences to fully interpret and appreciate the true locomotor diversity within Sauropoda.

ACKNOWLEDGMENTS

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APPENDIX 8.1. TAXA AND MEASUREMENTS USED IN THIS CHAPTER

Taxa are listed in a general phylogenetic hierarchy, but see figure. 8.3 for details of their hypothesized interrelationships. All measurements are in millimeters and were log-transformed prior to analysis. Abbreviations as in table 8.1. Institutional abbreviations: AMNH, American Museum of Natural History, New York, New York; BMNH, The Natural History Museum, London, UK; BSP, Bayerische Staatssammlung für Paläontologie, München, Germany; CH/P.W., Department of Mineral Resources, Bangkok, Thailand; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; DINO, DINOLab, Fruita, Colorado; FMNH, Field Museum of Natural History, Chicago, Illinois; GMNH, Gunma Museum of Natural History, Gunma, Japan; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; ISI, Indian Statistical Institute, Kolkata, India; IVPP, Institute of Palaeoanthropology and Palaeontology, Beijing, China; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MCNA, Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz, Spain; MDE, Musée des Dinosaures, Esperaza, France; MIGM, Museu Geológico do Instituto Geológico e Mineiro, Lisboa, Portugal; MLP, Museo de La Plata, La Plata; Argentina; MN, Museu Nacional, Rio de Janeiro, Brazil; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MPCA, Museo Provincial "Carlos Ameghino," Cipoletti, Argentina; MPEF, Museo Paleontólogico "Egidio Feruglio," Trelew, Argentina; MUCP, Museo de Ciencias Naturales de la Universidad Nacional del Comahue, Neuquén, Argentina; OUM, Oxford University Museum, Oxford, UK; PMU, Palaeontological Museum, University of Uppsala, Uppsala, Sweden; PVL, Instituto Miguel Lillo, Tucumán, Argentina; QG, Queen Victoria Museum, Harare, Zimbabwe; State University of New York (SUNY), Stony Brook, New York; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut; ZDM, Zigong Dinosaur Museum, Zigong, China; ZPAL, Muzeum Ziemi Polska Akademia Nauk, Warsaw, poland.

	SPECIMEN	FL	FAP	FML
Sauropoda				
Gongxianosaurus shibeiensis	Holotype	1,164.0		270.0
Isanosaurus attavipachi	CH4-1	760.0	71.5	121.6
Vulcanodon karibaensis	QG 24	1,100.0	140.0	174.0
Eusauropoda				
Barapasaurus tagorei	Holotype	1,365.0	131.0	187.0
Cetiosaurus oxoniensis	OUM	1,626.0		305.0
Datousaurus bashanensis	IVPP V.7262	1,057.0	147.0	
Kotasaurus yamanpalliensis	111/S1Y/76	1,130.0	80.0	160.0
Lapparentosaurus madagascariensis	"Individu taille max"	1,590.0	240.0	
Mamenchisaurus constructus	IVPP V.948	1,280.0	207.0	
Mamenchisaurus hochuanensis	IVPP holotype	860.0		
Omeisaurus junghsiensis	IVPP holotype		103.0	
Omeisaurus tianfuensis	ZDM T5701	1,310.0		206.0
Patagosaurus fariasi	PVL 4076	1,542.0	135.5	
	PVL 4170			255.0
Shunosaurus lii	IVPP V.9065	1,250.0		188.0
Tehuelchesaurus benitezii	MPEF-PV 1125	1,530.0		243.0
Volkheimeria chubutensis	PVL 4077	1,156.0	148.0	75.1
Neosauropoda				
Diplodocoidea				
Amargasaurus cazaui	MACN-N 15	1,050.0	128.8	180.0
Amphicoelias altus	AMNH 5764	1,770.0	210.0	216.0
Apatosaurus ajax	YPM 1860	2,500.0		
Apatosaurus excelsus	FMNH 7163	1,830.0	310.0	310.0
Apatosaurus louisae	CM 3018	1,785.0	174.0	332.3
Barosaurus africanus	HMN NW 4	1,361.0	150.6	204.2

	SPECIMEN	FL	FAP	FML
Barosaurus lentus	AMNH 6341	1,440.0	120.2	204.3
Cetiosauriscus stewarti	BMNH R.3078	1,360.0	190.0	195.0
Dicraeosaurus hansemanni	HMN m	1,220.0	142.5	
	HMN dd 3032			192.3
Diplodocus carnegii	CM 84	1,542.0	174.0	
	CM 94			186.0
Diplodocus longus	YPM 1920	1,645.0		
	AMNH 223		143.0	
Haplocanthosaurus priscus	CMNH 10380	1,745.0		
	CM 572		207.0	
Rayososaurus tessonei	MUCPv-205	1,440.0		220.0
Macronaria				
"Bothriospondylus madagascariensis"	MNHN uncat.	1,460.0	110.0	
Brachiosaurus altithorax	FMNH P25107	2,000.0		365.0
Brachiosaurus brancai	HMN St	1,913.0	151.7	299.0
Camarasaurus lentus	DINO 4514	1,470.0		252.0
	CM 11338		86.5	
Camarasaurus supremus	AMNH 5761a	1,800.0	255.0	
	GMNH-PV 101			228.0
Euhelopus zdanskyii	PMU R234	955.0	100.0	142.0
Titanosauriformes				
Aegyptosaurus baharijensis	BSP 1912 VIII 61	1,290.0	75.0	223.0
Ampelosaurus atacis	MDE uncat. 1	802.0		157.5
	MDE uncat. 2		66.0	
Andesaurus delgadoi	MUCPv-132	1,550.0		226.0
"Antarctosaurus wichmannianus"	FMNH 3019	1,770.0		
	MACN 6904		77.5	217.0
Argyrosaurus superbus	PVL 4628	1,910.0	160.0	300.0
Chubutisaurus insignis	MACN 18222	1,715.0	265.0	
Janenschia robusta	HMN IX	1,330.0		
	HMN P		131.5	188.8
Laplatasaurus araukanicus	MLP-Av 1047/1128	1,000.0		
Lirainosaurus astibiae	MCNA 7468	686.0		97.0
Magyarosaurus dacus	BMNH R.3856	488.0	43.7	66.8
Neuquensaurus australis	MLP CS 1121/1103	700.0	110.0	
Neuquensaurus robustus	MLP CS 1094	799.0		134.5
	MLP CS 1480		120.0	
Opisthocoelicaudia skarzynskii	ZPAL MgD-I/48	1,395.0	108.0	280.0
Phuwiangosaurus sirindhornae	CH/P.W. 1-1/1-21	1,250.0	85.0	215.0
Rapetosaurus krausei	SUNY uncat.	687.0	91.2	63.1
Rocasaurus muniozi	MPCA-Pv 56	768.0		117.0
Saltasaurus loricatus	PVL 4017-80	875.0		164.6
	PVL 4017-79		90.0	
Titanosaurus indicus	BMNH R.5934	865.0	67.3	80.9