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Jeffrey A. Wilson; Matthew T. Carrano

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Titanosaurs and the origin of “wide-gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion

Jeffrey A. Wilson and Matthew T. Carrano

Abstract.—Two major ichnotypes of sauropod trackways have been described: “narrow-gauge,” in which both manus and pes prints approach or intersect the trackway midline, and “wide-gauge,” in which these prints are well apart from the midline. This gauge disparity could be the result of differences in behavior, body size, or morphology between the respective trackmakers. However, the biomechanics of locomotion in large terrestrial vertebrates suggest that sauropods were probably restricted in locomotor behavior, and the lack of systematic size differences between footprint gauges argues against body-size-related influences. We argue that skeletal morphology is responsible for gauge differences and integrate data from locomotor biomechanics and systematics with the track record to predict the hindlimb morphology of wide-gauge trackmakers. Broader foot stances in large, graviportal animals entail predictable mechanical consequences and hindlimb modifications. These could include outwardly angled femora, offset knee condyles, and a more eccentric femoral midshaft cross-section. A survey of sauropod hindlimb morphology reveals that these features are synapomorphies of titanosaurs, suggesting that they were the makers of wide-gauge trackways. The temporal and geographic distribution of titanosaurs is consistent with this hypothesis because wide-gauge trackways predominate during the Cretaceous and are found worldwide. Additional appendicular synapomorphies of titanosaurs are interpreted in light of identifying these animals as wide-gauge trackmakers. We suggest that titanosaurs may have used a bipedal stance more frequently than did other sauropods. These correlations between ichnology, biomechanics, and systematics imply that titanosaurs were unique among sauropods in having a more varied repertoire of locomotor habits.

Jeffrey A. Wilson and Matthew T. Carrano. *Department of Organismal Biology and Anatomy, University of Chicago, 1027 East Fifty-seventh Street, Chicago, Illinois 60637.*
E-mail: jawilson@midway.uchicago.edu and mcarrano@midway.uchicago.edu

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Introduction

Footprints and trackways were among the first dinosaur remains to receive scientific attention (e.g., Hitchcock 1836) and have seen a renaissance of study in recent decades as an increasing number and diversity have been discovered (see Lockley 1986; Thulborn and Wade 1989). Trackways are particularly promising records of dinosaur locomotion because they represent the trace of an act—a moment in time—and therefore can provide information that is usually unavailable from skeletal morphology alone (Alexander 1976; Thulborn 1982, 1989; Gatesy and Middleton 1996). Despite these potential benefits, however, footprints have been of limited use because of difficulties in identifying the trackmakers. This problem is underscored in depositional settings where footprints are preserved better than body fossils, and estimates of taxonomic

diversity must depend solely on these tracks. This problem is partially mitigated by a system of ichnotaxonomy that categorizes tracks on the basis of general trackmaker types (e.g., ceratopsian, sauropod, hadrosaur), but this system precludes examining footprint data at any lower taxonomic levels. As a result, analyses that attempt to integrate skeletal and ichnological data (Farlow 1992; Lockley, Farlow, and Meyer 1994) must focus on these broad taxonomic categories and generally cannot examine within-group patterns of locomotor diversity.

Significant ichnological evidence of within-group locomotor diversity has come to light recently. Several authors (Farlow et al. 1989; Farlow 1992; Lockley, Farlow, and Meyer 1994; Moratalla et al. 1994) have noted that sauropod trackways fall into two general categories, “wide-gauge” and “narrow-gauge,” referring to the relative distance of the prints from the

trackway midline. These trackways are typified by *Brontopodus* (Farlow et al. 1989) and *Parabrontopodus* (Lockley, Farlow, and Meyer 1994). Although it is reasonable to infer locomotor variation between wide- and narrow-gauge trackmakers given other differences between these trackway types (e.g., temporal distribution, additional ichnomorphological features), it is not clear if the locomotor variation results from contrasting behavior, morphology, body size, or some combination of these factors (Farlow 1992). Although brachiosaurids (including the genus *Pleurocoelus*) have been forwarded as candidate wide-gauge trackmakers (Farlow 1992; McIntosh in Lockley and Hunt 1995a; Salgado and Calvo 1997), this suggestion has not been corroborated by morphological features that identify an osteological basis for gauge width. Moreover, no consideration has been given to the sequential appearance of such features in sauropod history. The implications of trackway gauges for sauropod locomotor evolution are difficult to evaluate without specific trackmaker identifications, recognition of the morphological features underlying gauge width, and the historical context of these features.

Sauropod trackways are notable in that they document distinct gauges. Variation in track and trackway morphology of other dinosaur clades appears to be circumstantial rather than systematic, serving to differentiate speeds, sizes, or individual ichnotaxa. For example, although hadrosaur trackways may preserve either bipedal or quadrupedal locomotor habit, all hadrosaur taxa are thought to have been capable of engaging in either form of locomotion; other widespread differences between groups of hadrosaur tracks are not apparent. The same is true for identifiable tracks of other ornithopods, theropods, ceratopsians, and prosauropods—none of these groups show systematic within-group clustering of trackway variation.

In this paper, we integrate data from locomotor biomechanics, skeletal morphology, and systematics with the ichnological record in an attempt to identify the makers of wide-gauge sauropod trackways. Furthermore, we propose a biomechanical framework for sauropod locomotion that predicts that the

makers of wide-gauge trackways would have differed in several aspects of hindlimb morphology from the makers of narrow-gauge trackways. Guided by these morphological predictions, we then survey sauropod hindlimb morphology within a systematic framework in order to identify which sauropods are most likely to have made wide-gauge trackways.

Sauropod Trackways: Gauge Width in Time and Space

The temporal distribution of sauropod trackways generally parallels the record of sauropod body fossils. The oldest sauropod trackways are found in Lower Jurassic deposits of Africa, North America, and Asia; trackways are abundant throughout the rest of the Jurassic and Lower Cretaceous, but fewer are recorded in Upper Cretaceous rocks (Lockley, Meyer, Hunt, and Lucas 1994 and references therein). Sauropod footprints have an easily recognizable, conservative morphology. Manus impressions are generally U-shaped, subtending an arc of approximately 270 degrees. The median axis of the print (passing through digit III) is oriented anterolaterally relative to the line of travel, and a trace of the large pollex claw is occasionally preserved. Pes impressions are always larger in area than those of the manus, and the manus-to-pes ratio (referred to as heteropody) ranges from 1:2 to 1:5 in sauropods (Lockley, Farlow, and Meyer 1994). Additionally, pes prints are characteristically subcircular in outline, with a well-developed heel print and impressions of three or four laterally directed claws. The pes impression can partially or totally obscure that of the manus in sauropod trackways, as the pes was apparently often placed in the same location following removal of the manus from the substrate. This overlap is common in "short-coupled" forms (Leonardi 1987).

Wide-gauge trackways have been defined as those in which manus and pes impressions are "well away from the trackway midline," whereas those of narrow-gauge tracks "are close [to] or even intersect the trackway midline" (Farlow 1992: pp. 108, 109) (Fig. 1). Farlow (1992) has identified several additional ichnomorphological correlates of narrow- and

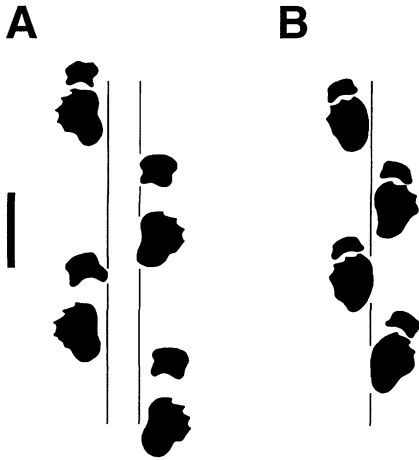


FIGURE 1. Diagram of sauropod trackway types. A, Wide-gauge trackways from the Cretaceous of Texas, and B, Narrow-gauge trackways from the Upper Jurassic of Portugal. Note the greater distance separating prints in wide-gauge tracks (indicated by vertical lines), as compared with narrow-gauge tracks (single vertical line). Modified from Lockley, Farlow, and Meyer (1994). Scale bar, 1m.

wide-gauge trackways. For example, whereas claw impressions are occasionally preserved in narrow-gauge manus prints, they are not typically associated with wide-gauge trackways. Additionally, manus prints are positioned closer to the midline than are pes prints in wide-gauge trackways, whereas the opposite is true of narrow-gauge trackways. Farlow (1992) also described indentations in the manus prints of *Brontopodus* (wide-gauge) that indicate a separation of digits II–IV from the marginal digits. This morphology is not known to occur in narrow-gauge tracks.

Patterns in the temporal distribution of narrow- and wide-gauge trackways have been identified by Lockley, Farlow, and Meyer (1994) and Lockley, Meyer, Hunt, and Lucas (1994). The latter authors state, "Narrow-gauge sauropod trackways (cf. *Parabrontopodus*) dominate the Jurassic track record (especially prior to the Tithonian) and wide-gauge trackways (cf. *Brontopodus*) dominate the Cretaceous track record" (1994: p. 245). Such a clear-cut distribution is not well supported by their data, however, as narrow-gauge trackways account for only 56% of total Jurassic sauropod trackways and 58% of total Jurassic tracksites (ichnocoenoses or aggregations of

trackways) (Lockley, Meyer, Hunt, and Lucas 1994: Table 1). Although narrow-gauge tracks do form the majority of Jurassic sauropod ichnocoenoses, wide-gauge tracks are well represented, particularly in the Late Jurassic. Their data do, however, support predominance of wide-gauge tracks in the Cretaceous, as such tracks constitute at least 96% of total trackways and 97% of total tracksites. Rather than a clear temporal segregation of track types in the Jurassic and Cretaceous, then, the data of Lockley, Meyer, Hunt, and Lucas (1994) suggest a more complex pattern: a mixed distribution of Jurassic track types followed by increasing rarity of narrow-gauge tracks through the Late Jurassic and Early Cretaceous, culminating in the complete absence of narrow-gauge trackways by the Late Cretaceous.

Despite the commonness of Cretaceous wide-gauge tracks, however, only the genus *Pleurocoelus* (or another, as yet unknown, brachiosaurid) has been identified as a potential wide-gauge trackmaker. Describing wide-gauge trackways from Glen Rose, Texas, Langston (1974) proposed that *Pleurocoelus*, a brachiosaurid found in adjacent deposits, might be the trackmaker. More recently, several authors have supported Langston's hypothesis of a brachiosaurid or *Pleurocoelus*-like trackmaker, noting that the lack of pollex impressions in wide-gauge trackways is consistent with brachiosaurid manual morphology (Farlow 1992; Lockley, Farlow, and Meyer 1994; Lockley and Hunt 1995a). Salgado and Calvo reiterated claims of *Pleurocoelus* as the *Brontopodus* trackmaker, and stated that the absence of unguals in the preserved manus print "supports the inclusion of *Pleurocoelus* sp. within the Titanosauria" (1997: p. 45). However, both brachiosaurids and titanosaurs are equally plausible as the *Brontopodus* trackmaker because both possess reduced manual unguals (Salgado et al. 1997). For the same reason, therefore, the absence of ungual impressions in supposed *Pleurocoelus* tracks cannot be used to support its inclusion within Titanosauria. A more rigorous correlation between skeletal and trackway morphology must be developed before we can attempt to identify the makers of sauropod (or other dinosaur) trackways

and interpret patterns in their distribution and abundance.

Tracks and Trackmakers

Paleoichnologists have faced the problem of associating tracks and trackmakers since the earliest discoveries of dinosaur tracks (Hitchcock 1836). In subsequent decades, a diverse ichnotaxonomy flourished alongside a comparatively poor understanding of trackmaker identity (e.g., Lull 1915). In recent years, however, a renaissance in dinosaur ichnology has led to the application of theoretical biomechanics (Alexander 1976), the mechanics of trackmaking in extant vertebrates (Padian and Olsen 1989), and the effects of different substrates (Farlow 1989) for discriminating and interpreting dinosaur tracks.

Farlow (1997, 1998, personal communication) asked whether dinosaur tracks could be expected to distinguish their respective trackmakers, given the assumption that such tracks preserved the original morphology with perfect fidelity. His data from birds (extant dinosaurs) show that even under idealized conditions of preservation, the tracks of certain major taxonomic groups (i.e., most ground-dwelling birds) can be difficult to distinguish from one another. This conclusion is corroborated by data from non-avian dinosaur pedal skeletons (Farlow 1998). By implication, the morphology preserved in footprints alone may not be sufficient to distinguish between lower-level non-avian dinosaur taxa.

It is not surprising, therefore, that the majority of trackmaker identifications are based largely on coincidental evidence such as temporal and spatial proximity. For example, Lockley and Hunt (1995b) stated that the print of a large theropod from the Laramie Formation "could be the track of *Tyrannosaurus*" (1995b: p. 605). They also identified the probable *Ceratopsipes* trackmaker as *Triceratops* on the basis of abundant remains of the latter in nearby, contemporaneous strata. Although *Triceratops* is the most common Maastrichtian ceratopsian in the Western Interior, the possibility that the tracks were made by *Torosaurus*, a chasmosaurine ceratopsid of similar size and distribution, cannot be ruled out. Moreover, general conclusions about ceratopsian

locomotion are unlikely to rest on such generic-level identifications. Although it is tempting to designate specific dinosaur genera as the makers of specific tracks, coarser taxonomic designations would better reflect the limitations of information from trackways.

Temporal and spatial coincidence can be used to draw more general and reasonable conclusions about potential dinosaur trackmakers. For example, Schulp and Brokx (in press) described a wide-gauge sauropod trackway from the Maastrichtian of Fumanya, Spain. The authors noted that titanosaurs were the only sauropods known from the Maastrichtian of Europe and cited this as evidence that titanosaurs were the makers of wide-gauge trackways. This is consistent with the currently known geographic and temporal distribution of titanosaur body fossils, although this association remains coincidental.

Trackmaker identity will probably never be confirmed without the fortuitous discovery of a titanosaur skeleton fossilized at the end of a wide-gauge trackway. Although direct trackmaker-trackway associations are known in the fossil record, they are exceedingly rare. In this instance we feel that additional evidence from systematics and biomechanics can be brought to light to provide a stronger basis for claims of titanosaurs as wide-gauge trackmakers.

A Model for Correlating Trackways and Locomotor Habit

The systematic distinction between sauropod trackway gauges probably reflects some locomotor difference, but this difference could result from several factors. Animals of similar general body form may exhibit variations in limb, joint, and girdle morphology. Additionally, individual animals may also vary locomotion because of growth, behavior, or substrate type and consistency.

Locomotor variation in extant animals illustrates several generalizations that seem to apply across most terrestrial vertebrate taxa. For example, although mammals shift gaits and crocodilians can alter limb posture, the options for such modifications become more restricted as body size increases (Biewener 1989, 1990a,b). Once terrestrial vertebrates reach megaherbivore size—such as modern probos-

cideans and hippos—locomotor variation decreases markedly. Specifically, these animals are constrained to an essentially columnar, parasagittal limb posture. This posture aligns the limb more closely with the ground reaction force and increases the mechanical advantage of the muscles acting at the limb joints. Megaherbivores are also constrained to lower levels of maneuverability and acceleration because of the risk of bone fracture (Biewener 1989, 1990a,b). Additionally, larger animals tend to use fewer gaits and gait changes than smaller animals. It is reasonable to infer that sauropods, the only dinosaurs that were consistently larger than the largest mammals by a full order of magnitude, were at least as restricted as large modern mammals in these locomotor features. In view of these structural and behavioral limitations, it is unlikely that any single sauropod was capable of producing both wide- and narrow-gauge trackways.

Although trackway width is greater in wide-gauge trackways, the individual prints making up such trackways are, on average, of a size comparable to those making up narrow-gauge trackways (J. Farlow personal communication 1998). Similarly, both types of prints are found in a variety of substrate types, ranging from fine-grained fluvial mud (Meyer et al. 1994) to nearshore pond and marsh deposits (Meyer and Pittman 1994) to marginal marine carbonates (Lockley, Meyer, and Santos 1994; Moratalla et al. 1994). Substrate variations do not correspond with gauge width and therefore cannot be invoked to explain gauge differences.

Differences in trackway width imply specific differences in limb bone posture and orientation. The biomechanical consequences of such differences should be reflected as differences in hindlimb morphology. A simple model relating hindlimb posture to the forces imposed by support and locomotion can be formulated from biomechanical principles. This model can then be used to make predictions about hindlimb morphology, thereby constraining the potential identities of wide-gauge trackmakers.

The similar sizes of individual wide- and narrow-gauge trackway prints suggest that the trackmakers were on average similar in

body size. This is not a surprising conclusion because foot size does not appear to change substantially relative to body mass throughout neosauropod evolution (Wilson and Sereno 1998). One implication of this is that because wide-gauge trackmakers were not simply larger animals, they would have had to employ a wider foot stance in order to generate these tracks (Farlow 1992; Moratalla et al. 1994). An increase in width of foot stance could be accomplished by increasing the overall width of the body carriage (pectoral and pelvic girdles), by angling the limbs outward from the body, or by combining the two. These possibilities suggest morphological expectations for wide-gauge trackmakers: (1) wider sacra or (2) limb morphologies suggesting an angled posture (angled femoral axis, offset knee and/or ankle articulations). Both of these correlates will involve a third expectation in any erect-limbed vertebrate: any postural change resulting in a wider foot stance would also increase the eccentricity of the femoral midshaft—that is, wide-gauge femora should be proportionally wider mediolaterally relative to their anteroposterior width than narrow-gauge femora.

The limbs of terrestrial vertebrates are designed to resist the forces imposed on them by locomotion and trunk support, and body weight is the primary factor in determining the magnitudes of these forces. In addition to compressive forces (due to columnar support) and anteroposterior bending forces (due to swinging the limbs forward and back during locomotion), limb bones are also subjected to mediolateral bending. Because the limbs are parasagittal and not directly underneath the body, the center of mass causes rotation of the proximal limbs toward the midline (Fig. 2). This mediolateral bending is increased by any factor that furthers the distance between the limb and the center of mass. Thus, several factors can increase mediolateral bending, including greater body mass, more widely separated hip joints, and a wider foot stance.

This does not necessarily mean that mediolateral forces are those most important to limb morphology, or that such forces predominate during either locomotion or trunk support. Although anteroposterior forces are likely to

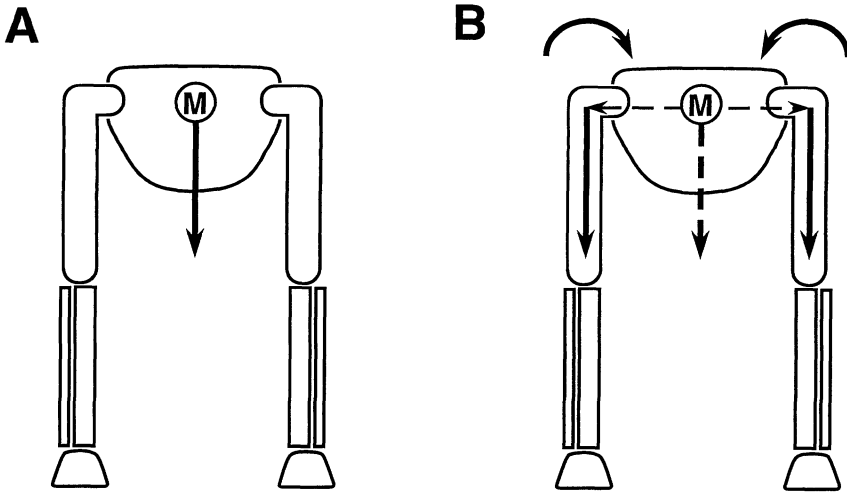


FIGURE 2. Effects of limb position on center of mass. A, Any animal with paired limbs will suspend its center of mass (M) between the two limbs and girdles because each limb is lateral to, not directly beneath, this center of mass. B, As a result, although the limbs are subjected to a compressive force (straight arrows) by their support of the mass of the animal, they cannot act as strict columns. To determine the force acting on the limbs, the compressive force of the center of mass must be shifted over the limbs, resulting in the addition of a mediolateral couple, or bending moment (curved arrows). Thus the limbs are subjected to both mediolateral bending and compression.

be high during locomotion, unlike mediolateral forces, they can be balanced by forces generated by the substantial anterior and posterior limb muscles. By contrast, few limb muscles have a predominately mediolateral orientation, resulting in little muscular ability to counter these forces. We suggest that, given no changes in stance or posture that might affect longitudinal forces, an increase in mediolateral force is likely to cause an alteration in limb morphology—specifically, a femoral cross-section that is elongate mediolaterally—simply by changing the overall pattern of forc-

es on the limb. Thus, larger or wider animals (i.e., animals that have relatively increased mediolateral bending on their limbs) would be expected to show more eccentric femoral cross-sections.

Dinosaurs show a general pattern of femoral morphology that is consistent with this prediction: mediolateral diameter becomes greater than anteroposterior diameter as body size increases, and sauropods show the most marked femoral eccentricity (in a sense, cross-sections of their femora resemble I-beams designed to resist mediolateral forces) (Carrano 1998). Any dinosaur groups that exhibit increases in other factors, such as sacral breadth and gauge width, should also show increases in femoral eccentricity. Specifically, the authors of wide-gauge trackways are expected to show increased femoral eccentricity as well as the aforementioned hindlimb features.

Sauropod Systematic Morphology

Sauropoda is a monophyletic group of saurischian dinosaurs (Fig. 3) whose earliest representatives are found in Lower Jurassic sediments and whose latest survivors are present in uppermost Cretaceous beds. Sauropoda and its successive sister taxa Prosauropoda

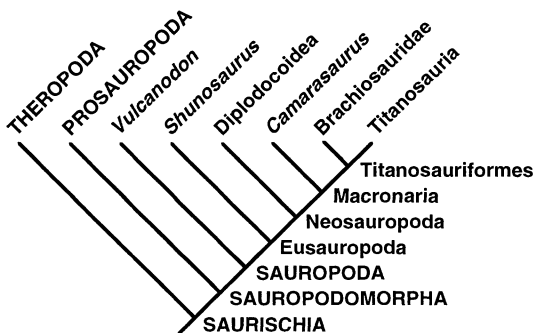


FIGURE 3. Cladogram showing basic phylogenetic relationships of the sauropods and sauropod subgroups discussed in the text. Based on Wilson and Sereno (1998).

and Theropoda constitute the clade Saurischia, which is the sister-clade to all other dinosaurs (Gauthier 1986; Galton 1990; Sereno et al. 1993). All known sauropods are large-bodied (estimated body masses usually in the tens of tons [Peckzis 1994]) and habitually quadrupedal. Quadrupedalism in sauropods, whose ancestors were small-to-medium sized bipedal dinosaurs, was acquired secondarily. Early sauropod evolution is distinguished by the acquisition of a columnar, graviportal limb posture. (Many of the characters mentioned below are listed in McIntosh 1990, Upchurch 1995, and Salgado et al. 1997; all are described in detail in Wilson and Sereno 1998.)

The fragmentary skeleton of *Vulcanodon*, the earliest and most primitive sauropod known, already displays a suite of sauropod synapomorphies related to the acquisition of quadrupedal progression at large body size; many of these features are also reflected in sauropod trackways. The forelimb is longer relative to the hindlimb than it is in other saurischians, with proportions similar to those of most mammalian quadrupeds. Unlike the condition in many mammals, however, the flat articular surfaces of the distal humerus and proximal radius and ulna of sauropods would not have allowed full pronation of the manus. Instead, it appears that the radius was positioned lateral to the ulna at the elbow and anterior to the ulna at the wrist. This resulted in a manus that was (permanently) laterally rotated (supinated) relative to the direction of travel (Wilson and Sereno 1998). Sauropod limb elements lack the sigmoid curvature present in those of prosauropods and theropods, suggesting reduced bending moments in weight-bearing bones. Several changes in the pes reflect full participation of digits I and V as weight-bearing elements. *Vulcanodon* and all other sauropods are characterized by a pentadactyl pes in which the well-developed metatarsal V is at least 70% of the length of metatarsal IV. In sauropod outgroups the fifth metatarsal is small or rudimentary and does not function as a weight-bearing element. Similarly, the proximal surfaces of metatarsals I and V are subequal in area to that of the central metatarsals in all sauropods, supporting

the inference that these outer digits participated as weight-bearing elements.

In the Middle Jurassic, sauropods still constituted a relatively small component of sampled dinosaur diversity, with approximately ten genera known worldwide (Hunt et al. 1994). A number of specializations in these eusauropods (= sauropods more derived than *Vulcanodon* [Upchurch 1995]) suggest that they had already acquired a characteristically graviportal manus and pes. Although three-clawed mani are primitive for prosauropods and theropods, eusauropods lose the unguals on digits II and III, retaining only a single, large ungual on the pollex. The nonterminal manual phalanges are broader than long and reduced in number: the manual phalangeal formula for eusauropods is 2-2-2-2 (or fewer).

The eusauropod pes is characterized by a major postural change. Prosauropods and theropods have elongate metatarsals that are closely appressed proximally and assume an elevated, digitigrade orientation. In eusauropods, however, metatarsal III is reduced to 25% of tibial length and the metatarsals attain a spreading, plantigrade position and articulate on the anterior surface of the astragalus. The presence of a heel impression in all sauropod footprints suggests that the metatarsus was supported by a fleshy pad. The ungual phalanx on pedal digit I is enlarged (longer than metatarsal I) and that of digit IV is rudimentary or absent. Similarly, the minimum shaft diameters of the metatarsals are unequal, with that of metatarsal I always greater than those of metatarsals II-IV. This suggests the inner metatarsals were increasingly important in weight-bearing relative to the outer ones. Farlow (1992) has noted that well-preserved trackways confirm this hypothesis, with the pedal digit I impression substantially deeper than those of II-V (e.g., *Brontopodus*). Additionally, eusauropod pedal unguals are asymmetrical and their articular surfaces are beveled anterolaterally. This indicates that the claws were deflected laterally relative to the digit III axis, as confirmed in pes prints (Farlow et al. 1989: Fig. 42.5; Pittman 1989: Fig. 15.12).

A second major postural change character-

izes neosauropod dinosaurs, the clade uniting diplodocoids, camarasaurids, brachiosaurs, and titanosaurs (Upchurch 1995; Wilson and Sereno 1998). In contrast to the pes, the neosauropod manus obtains a more vertically oriented, digitigrade posture in which the individual metacarpals serve as columnar, supportive elements. The five metacarpals are elongate (at least 1/3 of radius length) and articulate proximally in a tight arc. Distally, the metacarpals and phalanges are arranged in a slightly broader arc, resulting in the U-shaped manus print characteristic of sauropod trackways.

Titanosaurs represent the most diverse neosauropod clade, comprising at least 25 genera with a worldwide distribution (Hunt et al. 1994). Despite their diversity, titanosaurs remain the most phylogenetically enigmatic sauropod subgroup; their origins and interrelationships have remained obscure and controversial for over a century. Although recent work has begun to cast light on these problems (Calvo and Salgado 1995; Salgado et al. 1997; Salgado and Calvo 1997; Wilson and Sereno 1998), analyses of titanosaur morphology and biogeography are in their infancy. Titanosauria consists of a series of basal taxa based on fragmentary material that serve as successive outgroups to the well-diagnosed clade Saltasauridae, which includes *Saltasaurus* (Powell 1992), *Opisthocoelicaudia* (Borsuk-Bialynicka 1977), *Alamosaurus* (Gilmore 1946), and *Neuquensaurus* (Huene 1932), among others (Powell 1992). Although the neck and skull are undescribed in titanosaurs, the limb skeleton is well documented and furnishes many of the diagnostic features of the clade and its inclusive subclades. Moreover, several of these appendicular synapomorphies suggest a departure from the basal sauropod locomotor style, one that may be discernible in trackway morphology.

Saltasaurids are the only dinosaur group with unossified manual phalanges (as with other such characters, caution must be taken to distinguish "absent" from "not preserved"). Free phalanges have not been found associated with manual elements in any titanosaur and are not present among the articulated manual elements of *Alamosaurus* and *Opistho-*

coelicaudia (Gilmore 1946; Borsuk-Bialynicka 1977). Furthermore, the metacarpals have reduced phalangeal articular surfaces that are not exposed on their anterior aspect (Salgado et al. 1997). The distributions of these features are not known within basal titanosaurs and therefore are ambiguous saltosaurid synapomorphies. The apparent absence of manual phalanges (and thus the pollex claw) in saltosaurids is consistent with the absence of a pollex claw impression in wide-gauge trackways, though it does not preclude the possibilities that the trackmaker (1) engaged in a behavior in which the thumb claw was habitually retracted (Thulborn 1989; Upchurch 1994), or (2) had a significantly reduced (rather than absent) thumb claw, as in brachiosaurs.

Sauropod femora are primitively straight shafted and the femoral distal condyles are oriented such that the mediolateral axis of their articular surfaces is orthogonal to the long axis of the bone (mean: $92 \pm 4^\circ$). In other words, an axis drawn across their articular surfaces mediolaterally will intersect the long axis of the shaft at approximately 90° . Thus the tibial articular surface is oriented horizontally when the femur is held vertically (Fig. 4A). Two morphological features, one characterizing titanosaurs and brachiosaurs (= Titanosauriformes) and the other synapomorphic for titanosaurs, however, suggest a unique hindlimb posture for titanosaurs. Titanosauriform femora bear a characteristic bulge on the lateral portion of the proximal one-third of the shaft; in anterior view the proximal portion appears to be deflected medially (Fig. 4B) (McIntosh 1990; Salgado et al. 1997; Wilson and Sereno 1998). Whereas in *Brachiosaurus* the distal condyles remain perpendicular to the long axis of the femur, in titanosaurs the condylar surfaces are angled dorsomedially relative to the long axis of the femur (Fig. 4C). As a result, the distal femoral condyles in titanosaurs (e.g., *Opisthocoelicaudia*, *Saltasaurus*, and *Neuquensaurus*) appear to be "beveled," requiring an outwardly angled femur (i.e., leveling the distal condyles) to create a horizontal articular surface with the vertically oriented tibia. The mediolateral condylar axis forms an acute angle with the long

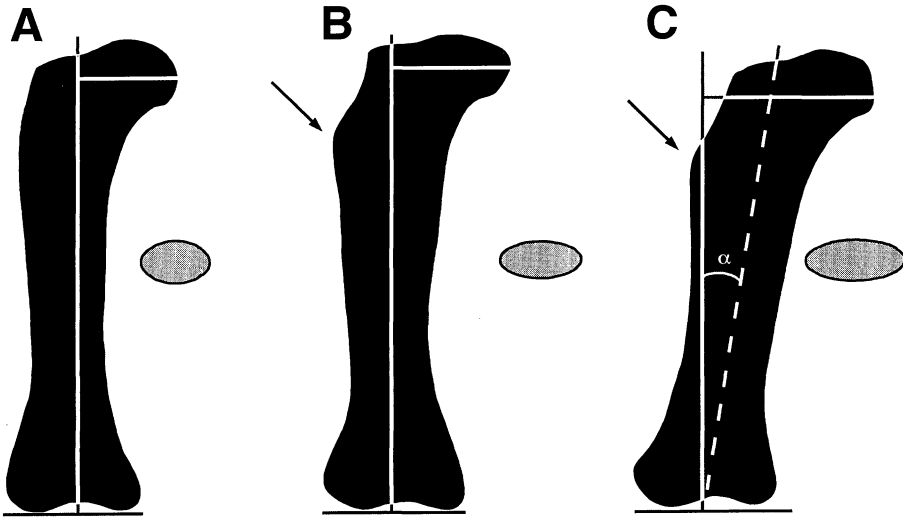


FIGURE 4. Trends in femoral morphology within Sauropoda. Right femora in anterior view of *Diplodocus* (A), *Brachiosaurus* (B), and *Saltasaurus* (C). Ellipses at right of each femur are reconstructed midshaft cross-sections. Solid lines centered at base of femora mark the vertical and horizontal; solid line at proximal end of femur represents the horizontal distance between the femoral head (hip) and the center of distal condyles (knee). Dashed line in C passes through the long axis of the femur. Primitively, sauropod femora show some eccentricity between the mediolateral and anteroposterior femoral diameters, but are only slightly elliptical (*Diplodocus*). The femur of *Brachiosaurus* has a more eccentric profile, and titanosaurs (such as *Saltasaurus*) have the most elliptical sauropod femora. The femoral shafts of *Brachiosaurus* and *Saltasaurus* display a prominent lateral bulge on the lateral surface (indicated by arrow), whereas other sauropods have straight-shafted femora (*Diplodocus*). More primitive sauropods also have a nearly perpendicular relationship between the long axis of the femur and the mediolateral axis of the distal femoral condyles, while this angle (indicated by α) is acute in titanosaurs. See text for statistical analyses. Modified from Hatcher (1901: Pl. 11), Janensch (1961: Fig. 208), and Powell (1992: Fig. 37). Femora are normalized to the same length for comparison.

axis (mean: $85 \pm 5^\circ$), suggesting that the femora of these sauropods were angled laterally outward from the acetabulum. This difference is significant in both unpaired, two-group *t*-tests and Mann-Whitney *U*-tests (Table 1). Complete femora are not preserved in basal titanosaurs (e.g., *Andesaurus*, *Malawisaurus*), so this is an ambiguous saltosaurid synapomorphy.

Sauropods are also characterized by a marked eccentricity between the anteroposterior and mediolateral femoral midshaft di-

ameters, so that the femur is elliptical in cross-section with the longer axis oriented mediolaterally. Only *Amphicoelias* appears to lack this morphology, which has been noted as an autapomorphy of this genus (Osborn and Mook 1921; Wilson and Smith 1996). This eccentricity is widely present in other dinosaur taxa, notably stegosaurs, ankylosaurs, some ceratopsians, and very large hadrosaurs (Carrano 1998), but is most marked in sauropods (and synapomorphic for this group within Saurischia) (Wilson and Sereno 1998). A Mod-

TABLE 1. Results of unpaired, two-group *t*-tests and Mann-Whitney *U*-tests comparing morphological features in titanosaurs and other sauropods. Femoral axis angle was measured between the mediolateral femoral condyle axis and long axis of femur; the tangent was taken in order to normalize the distribution of angle measurements (angle minus 60° was used because angles were clustered around 90°); femoral eccentricity was calculated as mediolateral diameter divided by anteroposterior diameter. $\bar{x}(T)$ = mean value for titanosaurs; $\bar{x}(S)$ = mean value for other sauropods; $n(T)$ = number of titanosaurs sampled; $n(S)$ = number of other sauropods sampled.

Variables	$\bar{x}(T)$	$\bar{x}(S)$	$n(T)$	$n(S)$	<i>t</i>	<i>p</i>	<i>Z</i>	<i>p</i>
Femoral axis angle	85.00	91.59	14	29	4.233	0.001	3.719	0.002
Tangent of (angle - 60°)	0.47	0.62	14	29	4.038	0.002	3.719	0.002
Femoral eccentricity	1.85	1.50	21	34	2.675	0.001	2.599	0.009

TABLE 2. A, Model II log-log regressions of mediolateral diameter versus anteroposterior diameter for titanosaur and non-titanosaur sauropod femora. B, *t*-test and Mann-Whitney *U*-test on residuals from regressions. Abbreviations as in Table 1. Data from Carrano (1998) and Wilson (unpublished data).

A. Regressions statistics							
Group	y-intercept	Slope	<i>p</i>	<i>r</i> ²	<i>n</i>		
Titanosaurs	0.792 ± 0.247	0.904 ± 0.121	0.001	0.661	21		
Other sauropods	0.355 ± 0.262	1.152 ± 0.125	0.001	0.620	34		
All sauropods	0.606 ± 0.193	1.048 ± 0.093	0.001	0.583	55		

B. Residual statistics								
	$\bar{x}(T)$	$\bar{x}(S)$	<i>n</i> (T)	<i>n</i> (S)	<i>t</i>	<i>p</i>	<i>Z</i>	<i>p</i>
Residuals	0.052	-0.032	21	34	2.654	0.010	-2.668	0.008

el II regression (Table 2) of these two femoral diameters in sauropods produces a slope of 0.793; in other words, the rate of increase for anteroposterior diameter is only 79% of that for mediolateral diameter. Regression statistics indicate a high significance for this equation, although the data show a high variance about the slope ($r^2 = 0.583$; $p < 0.001$; $n = 55$).

Titanosauria, however, is characterized by an even more marked disparity between these two femoral diameters. Model II regression (Table 2) shows that titanosaur femora are systematically more eccentric than those of other sauropods: the y-intercepts of these two regressions are significantly different (other sauropods: 0.355 ± 0.262 ; titanosaurs: 0.792 ± 0.247), indicating an overall increase in femoral eccentricity in titanosaurs. The slopes of these two regressions are also different (other sauropods: 1.152; titanosaurs: 0.904), demonstrating that the femora of other sauropods show a greater increase in eccentricity as size increases. Although titanosaur femoral eccentricity shows lower allometry than that of other sauropods, titanosaur femora are more eccentric in absolute dimensions (as indicated by the y-intercepts), such that they remain more eccentric at all sizes regardless of these slope differences. Mean values for femoral eccentricity (= anteroposterior diameter divided by mediolateral diameter) are significantly larger in titanosaurs when compared with values for other sauropods with *t*-tests and *U*-tests (Table 1). Mean residual values of the two

groups about the regression are also significantly different, with titanosaurs tending to fall above the regression line (i.e., have more eccentric femora than predicted) and other sauropods tending to fall below (Table 2). It is interesting to note that the most eccentric femora among non-titanosaur sauropods belong to *Euhelopus* and *Brachiosaurus*, which are considered to be successive sister-taxa to Titanosauria (Wilson and Sereno 1998). The presence of these locomotor adaptations in saltasaurids suggests that they are wide-gauge trackmakers. The angled femoral axis and beveled knee joint of titanosaurs require a broader foot stance than those of narrow-gauge sauropods (Fig. 5).

Trackway evidence indicates that wide-gauge locomotor adaptations evolved prior to the Late Jurassic, before the predominance of wide-gauge tracks in the Cretaceous (Fig. 6). However, the first appearance of wide-gauge tracks in the geologic record predates the first appearance of titanosaur body fossils by approximately ten million years. This suggests that the titanosaur lineage may extend back to the Middle Jurassic. Confirmation awaits further additions to the skeletal record of these wide-gauge trackmakers.

Implications for Titanosaur Biology

This analysis suggests substantial locomotor variation within Sauropoda. Currently, this is the only evidence for such large-scale variation within a major dinosaur clade, al-

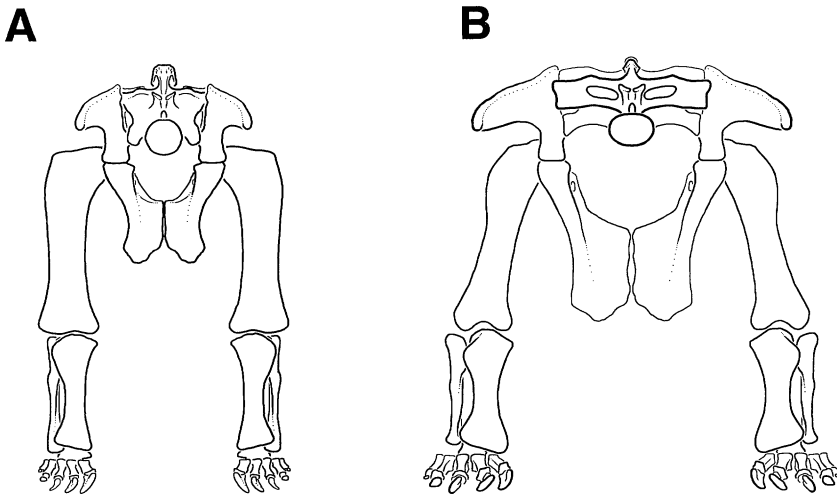


FIGURE 5. Reconstructed pelvic girdles and hindlimbs of *Camarasaurus* (A) and the titanosaur *Opisthocoelicaudia* (B) in anterior view, at the level of the first sacral vertebra. Note that when the distal femoral condyles are articulated in a horizontal plane with the proximal tibia, the proximal femur of *Opisthocoelicaudia* is angled medially from the knee joint, whereas that of *Camarasaurus* is nearly vertical. As a result, the titanosaur hindlimb is reconstructed as having been canted outwardly at its distal end, resulting in a wide-gauge stance. These reconstructions represent standing animals, in which the limb stance is typically wider than during locomotion. The *Camarasaurus* reconstruction is based on measurements and figures from McIntosh, Miles, Cloward, and Parker (1996: Tables I, K, L, Fig. 79) and illustrations in Osborn and Mook (1921: Figs. 45, 109, 111). The *Opisthocoelicaudia* reconstruction is based on Borsuk-Bialynicka (1977: Fig. 11, 12, Pls. 13, 14); the ilia have been reconstructed on the basis of *Titanosaurus colberti* (Jain and Bandyopadhyay 1997: Fig. 23). Both figures are normalized to the same height for comparison.

though systematic comparisons of this kind have not yet been applied to other groups. More interesting, however, are the implications for dinosaur locomotion in general and for titanosaur locomotion in particular.

Unlike modern terrestrial mammals, the majority of which are small in body mass (<10 kg), dinosaurs apparently had quite a large modal size (>100 kg [Peczki 1994]). Very few modern terrestrial mammals attain body sizes within the range of large dinosaurs (e.g., hadrosaurs, theropods, ceratopsians), and none reach the sizes attained by sauropods. Large terrestrial mammals—proboscideans, rhinos, and hippos—tend to display a reduced repertoire of locomotor behaviors, in terms of both speed and gait; elephants, in particular, are notable as the only terrestrial mammals incapable of running (i.e., they lack a suspension phase during locomotion at any speed [Hildebrand 1985; Biewener 1989, 1990a,b]). In this light, the distinction between locomotor styles in sauropods becomes more significant, as it implies the possibility for locomotor variation at body sizes an order of

magnitude above those seen in terrestrial mammals today.

Titanosaur Locomotion: Adaptations for Mobility.—Saltosaurids (and perhaps other titanosaurs) share additional synapomorphies that, although not directly involved in creating a particular trackway morphology, nonetheless become explicable in the light of our conclusions. Saltosaurids, particularly *Neuquensaurus* and *Saltasaurus*, are characterized by an elongate, nearly transversely oriented preacetabular process of the ilium (Fig. 5B). This would, among other effects, move the origination sites of femoral protractor muscles laterally and more closely align the lines of action of these muscles with the anteroposterior direction of travel. These flared ilia also increase the distance of the insertion points of abdominal oblique muscles from the midline, suggesting a broad abdominal cavity. Reconstructions of saltosaurid pelvises (e.g., of *Opisthocoelicaudia* and *Saltasaurus*) suggest that the acetabulum in these taxa faced ventrolaterally, in contrast to the laterally facing acetabula of other sauropods. Additionally, the pubis is

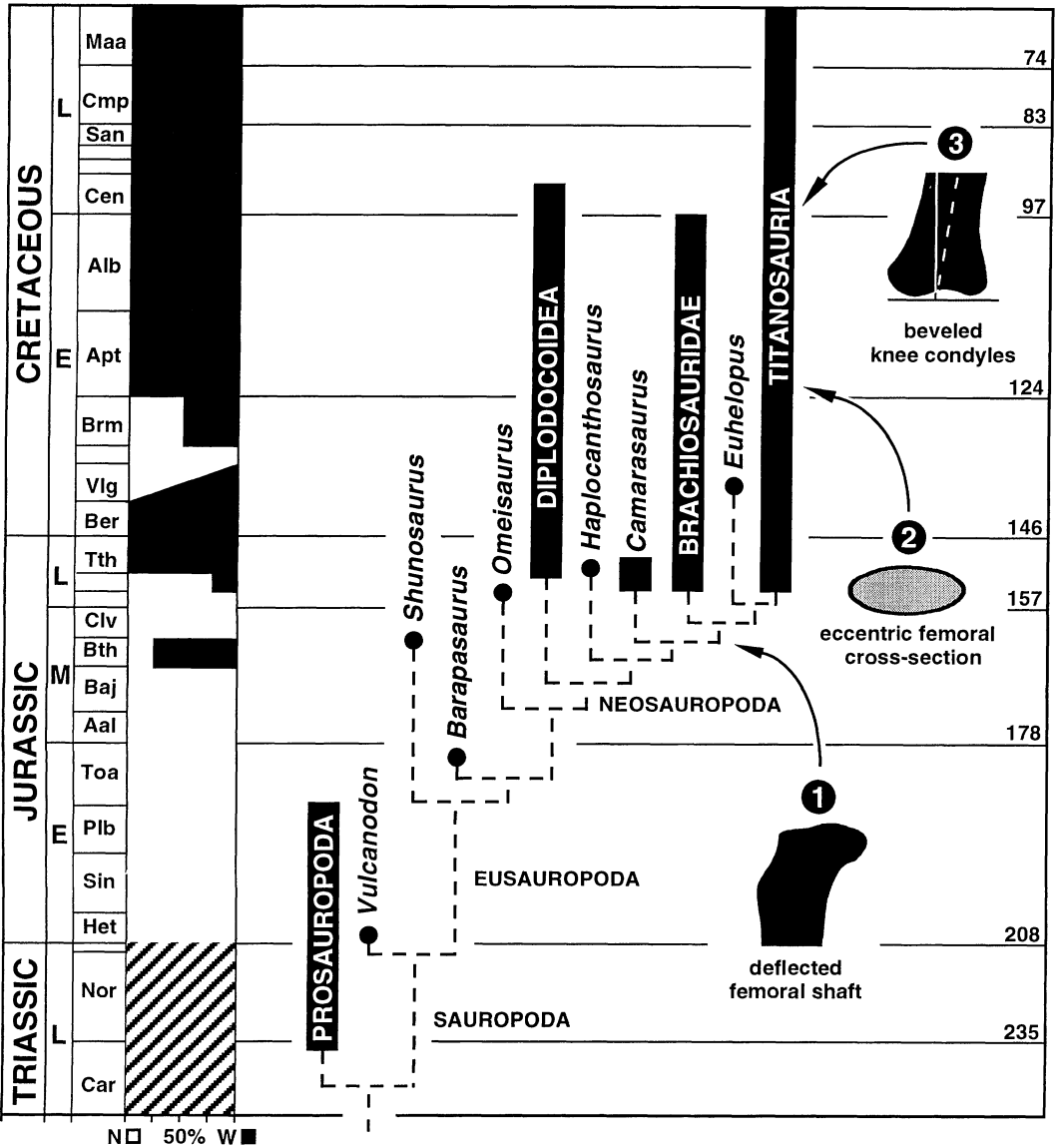


FIGURE 6. Abundance of wide- and narrow-gauge sauropod trackways through time. Using data reported in Lockley, Meyer, Hunt, and Lucas (1994), we have plotted abundance of each trackway type as a percentage of all known sauropod trackways. The Triassic is marked with hatching because no definitive sauropod trackways are known from this time period. Note that narrow-gauge tracks (white area of graph on left) predominate during the Early and Middle Jurassic, whereas wide-gauge trackways (black area of graph) predominate during the Cretaceous. These data are synchronized with the temporal appearance of different sauropod clades and their respective locomotor synapomorphies. Synapomorphies discussed in the text appear by the beginning of the Late Jurassic (1 = medial deflection of proximal femur [Titanosauriformes]; 2 = increased femoral midshaft eccentricity [Titanosauria]; 3 = beveled distal femoral condyles [Saltasauridae]).

substantially longer than the ischium, a reversal of the primitive sauropod condition (Wilson and Sereno 1998). In many titanosaurs, the convex articular surfaces of the distal femoral condyles are enlarged to the extent of being exposed on the anterior surface. Correspond-

ingly, the anteroposterior dimension of the femoral articular surface of the tibia is expanded, forming a laterally compressed ellipse in proximal view. Both of these features seem to indicate an increased anteroposterior excursion of the tibia at the knee joint.

Saurischian dinosaurs are characterized by accessory intervertebral (i.e., hyposphene-hypantrum) articulations below the prezygapophyses and postzygapophyses of dorsal vertebrae (Gauthier 1986; Sereno et al. 1993). These interlocking wedge-and-notch articulations likely added rigidity to the trunk by constraining rotational, mediolateral, and dorsoventral motion between dorsal vertebrae. Saltasaurids are the only saurischians to reverse this feature (Salgado et al. 1997). Moreover, the posterior dorsal vertebrae of saltasaurids (as well as *Camarasaurus* and brachiosaurids) are strongly opisthoceolous, exhibiting a strongly convex anterior centrum surface and a concave posterior centrum surface. Combined, loss of hyposphene-hypantrum articulations and pronounced opisthoceoly suggest an increased range of trunk motion in saltasaurids. This flexibility was apparently extended into the short tail (approximately 35 vertebrae), where the first caudal centrum is biconvex, the majority of caudal vertebrae are procoelous, and the distalmost vertebrae are biconvex (Wilson et al. in press).

Our treatment of titanosaur locomotion has largely overlooked the pectoral girdle and forelimb, principally because the positions of these elements relative to the trunk are not constrained by osteological connections. Controversy has surrounded attempts to reconstruct forelimb posture in other dinosaurs (Johnson and Ostrom 1995; Lockley and Hunt 1995b; Dodson and Farlow 1997), and in general the relationship between the pectoral girdle (and forelimb) and thorax can only be approximated. In this sense, the implications of the various shared derived features of the titanosaur forelimb and pectoral girdle are unclear. However, forelimb apomorphies appear to be consistent with the locomotor inferences based on hindlimb morphology, as both fore- and hindlimbs create prints that are well away from the midline in wide-gauge trackways. In the pectoral girdle, the large, crescentic sternal plates of saltasaurids suggest a broader shoulder carriage and an expanded attachment surface for the pectoral musculature. The presence of large sternal plates that articulate with the coracoids is consistent with a broad-chest-

ed animal whose scapular glenoid is well-distanced from the midline. As in the femur, the distal condyles of the humerus have a pronounced anterior exposure. The ulnar olecranon process is hypertrophied and the radial articular surface is shallow, suggesting that saltasaurids had a less columnar forelimb posture than other sauropods.

The collection of features described here begins to qualify the range of motion possible in the saltasaurid skeleton, thereby circumscribing the potential range of activities for these animals. Convex articular surfaces and fewer intervertebral articulations suggest that saltasaurid titanosaurs enjoyed increased mobility of the dorsal and caudal regions of the axial column. Expanded articular surfaces reveal greater flexibility and range of motion in the knee and elbow joints, while increased breadth of pectoral and pelvic regions are consistent with broader separation of the limbs during locomotion. Together, these features suggest that the locomotor repertoire of saltasaurids might have surpassed that of other sauropods.

Bipedal Posture in Titanosaurs.—Sauropod bipedalism was first proposed almost a century ago by Hatcher (1901), and since Bakker's (1971) reinterpretation of sauropods as fully terrestrial animals, several authors have envisioned these animals rearing into a bipedal or tripod stance for feeding, defense, copulation, and locomotion (Bakker 1978; Borsuk-Bialynicka 1977; Alexander 1985; Powell 1986; Jensen 1988). Although this assessment has not always been supported by specific osteological features (see Bakker 1971, 1978), some authors have pointed to a variety of characteristics that might have facilitated bipedalism in sauropods. Recent examinations of skeletal morphology in titanosaurs (Borsuk-Bialynicka 1977; Powell 1986) and camarasaurids (Jensen 1988), for example, have noted specific similarities to the morphology of (presumably) bipedal giant ground sloths.

Borsuk-Bialynicka listed three features of the skeleton of the saltasaurid *Opisthocoelicaudia* that implied "Megatherium-like habits" (1977: p. 51), or occasional bipedalism: a thickened acetabulum, opisthoceolous caudal vertebrae, and broadly flared ilia. In his treatise

on titanosaurs, Powell (1986) proposed occasional bipedalism in taxa such as *Saltasaurus* and *Neuquensaurus* based on a similar set of features. Jensen (1988) suggested that *Cathetosaurus lewisi* (= *Camarasaurus lewisi* [McIntosh, Miller, Stadtman, and Gillette 1996]) was also adapted for occasional bipedal progression. Jensen additionally cited the long series of bifid presacral neural spines, long caudal chevrons, and diagonal intervertebral bracings in support of this interpretation.

Jensen (1988) also noted several features that are present in large, occasionally bipedal mammals but are absent in sauropod dinosaurs. Sauropods lack osseous levers (bony protuberances) at the limb joints, retain "simple cartilaginous joints" rather than tightly fitting osseous joints, and lack "triad joints" (i.e., those incorporating sesamoids). However, dinosaur limb joints are notorious for being poorly ossified (Coombs 1975); it is not surprising that additional ossifications such as sesamoids are absent. As preserved, sauropod joint surfaces represent the contact surface between the articular joint cartilage and underlying bone; therefore it is impossible to determine whether sauropods had tightly fitting limb joints. Although most sauropods do lack osseous levers, titanosaurs retain an ulnar olecranon process that may have assisted in elevating the trunk, neck, and head. The antero-posterior expansion of the humeral condyles further suggests greater elbow flexion than in other sauropods.

Other saltasaurid features also suggest bipedalism. These include a more flexible back and a short, flexible tail, both of which would have been advantageous during a shift in posture. Sauropod ischia, primitively longer than the pubes, may have interfered with bipedal posture when tilting of the dorsal axis lowered the ischia toward the ground. Saltasaurid ischia are shorter than the pubes and might not have encountered this problem. Although many of the features described above are likely to have been beneficial to any sauropod standing bipedally, correlations have not been made between these features and the use of a bipedal stance in living animals.

These features are not proof of bipedalism in saltasaurids, and bipedalism is not required

to explain their presence. No single feature even implies this behavior. Taken as a whole, however, saltasaurid (and other titanosaur) postcranial morphology strongly suggests that these sauropods exhibited distinct locomotor specializations relative to other sauropod groups. Although bipedal posture was certainly possible in other sauropods (and probably necessary for reproduction), most of these taxa do not display specific adaptations for routine use of bipedalism. We suggest that the normal behavioral repertoire of saltasaurids may have included more frequent use of a bipedal posture than that of other sauropods.

Conclusions

The distinct morphologies of wide- and narrow-gauge sauropod trackways can be interpreted in the light of locomotor biomechanics, limb morphology, and sauropod systematics. This analysis suggests that wide-gauge trackways were the products of wide-gauge sauropods, rather than narrow-gauge sauropods of different sizes or engaged in different behaviors. Wider foot stances in large, graviportal animals such as sauropods would have had mechanical consequences resulting in modifications of the hindlimb skeleton. These modifications—an outwardly angled femoral posture and beveled knee condyles, along with a more asymmetrical femoral midshaft—are synapomorphies of titanosaurs, suggesting they are the wide-gauge trackmakers. The temporal distribution of wide-gauge trackways (present in the Jurassic, predominant in the Cretaceous) is consistent with current hypotheses concerning the origins of titanosaurs and their subsequent diversification.

Saltasaurids, the best-represented titanosaurs, show a suite of additional postcranial features unknown elsewhere in Sauropoda that suggest a derived locomotor repertoire that may have included bipedalism. These features include vertebral adaptations for increased trunk and tail mobility, changes in knee and elbow morphology resulting in greater flexibility, and wider foot stances for greater stability of the wider body carriage. More routine use of bipedal posture in saltasaurids is suggested by flared ilia for support of the viscera and by other features.

This represents the first instance among dinosaurs where trackways and trackmakers have been linked using more than coincident temporal and geographic evidence. Variation in trackways suggests that different locomotor styles and postures may have existed among sauropods. This type of variation in locomotor habit has not been observed in the fossil record of other major dinosaur clades. Sauropods may be unique in this regard, but additional work needs to be done before any further conclusions can be drawn. Clearly ichnological data have significant value in analyses of dinosaur locomotor evolution, especially when integrated with systematics and morphology.

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