

Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach

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Abstract.—Fossil vertebrate distributions are typically based on body fossils, which are often poorly sampled at the margins of their true temporal and spatial ranges. Because vertebrate ichnofossils can be preserved in great abundance and in different environments than vertebrate body fossils, inclusion of ichnofossil data may improve sampled ranges. However, if ichnofossils are to serve as an independent source of distributional data, then their attribution to a body fossil group (i.e., trackmaker identification) cannot rely on temporal and spatial coincidence. Ichnofossils identified by synapomorphies can act as an independent source of distributional data that can modify spatial, temporal, and character distributions, which in turn may influence hypotheses of locomotor evolution.

In this paper I evaluate the spatial, temporal, and character distributions of early sauropod dinosaurs by using a combined ichnofossil and body fossil data set. Sauropod ichnofossils supplement the spatiotemporal distributions of early sauropods and provide important information on early sauropod foot posture that is rarely preserved or can only be inferred from body fossils. The presence of derived features in early-appearing ichnofossils challenges previous hypotheses of character transformation, implying either parallelism, reversal, or ghost lineages.

Stratocladistics can be used to resolve conflicting character and temporal distributions from body fossils and ichnofossils. Stratocladistic analysis of a combined ichnofossil and body fossil data set suggests a richer, more widely distributed diversity of early sauropods than currently recognized in body fossils and suggests that several locomotor characters originated much earlier than implied by body fossils.

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Introduction

Sauropod dinosaurs are the largest animals known to have walked on land. Their terrestrial capabilities are evident from the morphology of sauropod limb and axial bones (Mantell 1850; Phillips 1871; Hatcher 1901, 1902; Riggs 1904; Bakker 1971; Coombs 1975), but most strikingly in the sauropod footprint record (Bird 1944; Farlow 1992; Lockley et al. 1994). In addition to providing evidence of the terrestrial capabilities of sauropods, footprints provide temporal, spatial, and character data that can inform hypotheses of sauropod locomotor evolution.

Spatiotemporal distributions based on sauropod ichnofossils and body fossils overlap, but some strata and areas are recorded by only one of these sources. This partial disjunction between ichnofossil and body fossil data sets indicates that no one source provides the best hypothesis of sauropod distributions. The im-

port of ichnofossils on sauropod distributions is especially relevant early in sauropod history, when body fossils are rare and fragmentary (Lockley et al. 1994). In addition to spatiotemporal information, early sauropod ichnofossils provide information about locomotor posture that often cannot be discerned from the earliest body fossils, which rarely preserve manual and pedal remains. For example, the Middle Jurassic *Shunosaurus* (Zhang 1988) is the earliest appearing sauropod that preserves complete manual and pedal remains. Because sauropods had already evolved a fairly stereotyped manus and pes by the Middle Jurassic, the timing and nature of the transformation leading to this basic sauropod foot plan cannot yet be inferred from body fossils. However, recently described Late Triassic and Early Jurassic sauropod ichnofossils may provide insight into early sauropod locomotor evolution, suggesting a Triassic origin for certain features that do not appear in

the body fossil record until the Middle Jurassic.

The spatiotemporal distribution and locomotor posture of early sauropods are discussed below. First, I discuss the definition, ancestry, and content of Sauropoda. Second, I evaluate sauropod spatiotemporal distributions by using a combined ichnofossil and body fossil data set. Third, I compare the temporal distribution of locomotor characters preserved in early sauropod ichnofossils with the appearance of those same characters as implied by recent phylogenetic analyses of body fossils. Fourth, I use stratocladistic analysis to reconcile conflicting body fossil and ichnofossil distributions. And last, I propose a revised chronology for early postural changes within Sauropoda.

Sauropoda: Definition, Ancestry, and Content

The concept of “sauropod” has remained relatively unchanged since the taxon was introduced by Marsh in 1878. This may be due, in part, to the morphological gap separating sauropods from other sauropodomorphs. That is, perception of a sauropod “body plan” relies on the absence of intermediate forms that possess some, but not all, sauropod features. There were no “near-sauropod” sauropodomorphs hypothesized to bridge this morphological gap until the recent discovery and reinterpretation of several Late Triassic forms. To provide a nomenclatural context for the discussion that follows, the phylogenetic definition, hypothesized ancestry, and implied content of Sauropoda are briefly discussed below.

Definition.—Although the earliest cladistic analyses of Sauropoda did not specify a phylogenetic definition for the group (Russell and Zheng 1993; Calvo and Salgado 1995; Upchurch 1995, 1998), more recent analyses have adopted a definition of Sauropoda as a stem-based group that includes all sauropodomorphs more closely related to *Saltasaurus* than to *Plateosaurus* (Sereno 1998; Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004). This definition is mirrored by a stem-based definition for Prosauropoda that uses the same reference taxa: all sauropodomorphs

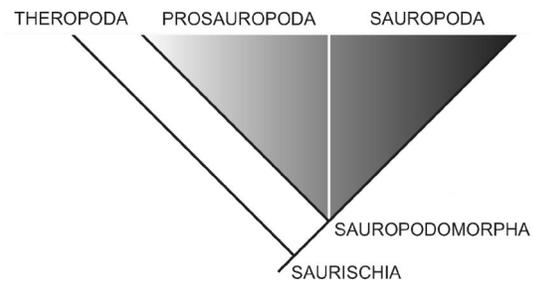


FIGURE 1. Simplified cladogram indicating the phylogenetic relationships amongst saurischians as well as phylogenetic taxonomy within Sauropodomorpha (based on Gauthier 1986; Sereno 1998, 1999; Wilson and Sereno 1998). Sauropodomorpha and its two constituent subgroups are arranged into a “node-stem triplet” (Sereno 1998) that nests the stem-based groups Sauropoda and Prosauropoda within the node-based group Sauropodomorpha. As shown by the gray tone, the stem-based groups (Prosauropoda or Sauropoda) include all sauropodomorphs more closely related to the reference taxon within the clade (*Plateosaurus* or *Saltasaurus*) than to the reference taxon within the opposing clade (*Saltasaurus* or *Plateosaurus*). By this definition, all sauropodomorphs are either sauropods (represented by tones more dark than light), prosauropods (represented by tones more light than dark), or their common ancestor (represented by white line).

more closely related to *Plateosaurus* than to *Saltasaurus* (Sereno 1998). These two stem-based clades comprise the node-based Sauropodomorpha, which includes *Plateosaurus*, *Saltasaurus*, and all descendants of their most recent common ancestor (Sereno 1998). This node-stem triplet configuration of phylogenetic definitions (Fig. 1) implies that (1) any sauropodomorph must be either a sauropod, a prosauropod, or their common ancestor; (2) any taxon more closely related to one reference form than the other must be a sauropodomorph; and (3) any taxon with equal affinity to these two reference forms is either their ancestor or not a sauropodomorph.

Ancestry.—The closest relatives to sauropods have been sought amongst small- to medium-sized sauropodomorphs common in Upper Triassic and Lower Jurassic horizons. Their stratigraphic distribution in rocks predating the then-known sauropods led Huene (1920) to coin the taxon “Prosauropoda” for these “before sauropods.” As stratigraphically older sauropods and younger prosauropods were discovered, however, temporal overlap precluded placement of prosauropods *en toto* as the direct ancestors of Sauropoda

(Charig et al. 1965). Since then, both traditional (Galton 1990) and cladistic (Sereno 1999; Benton et al. 2000; Galton and Upchurch 2000, 2004) analyses of sauropodomorph relationships have suggested that prosauropods form a monophyletic group. Although the strength of these claims varies between analyses, numerous synapomorphies of Prosauropoda have been proposed. Among these are several discrete characters that include a premaxillary beak, a highly modified first manual digit, and an hourglass-shaped proximal metatarsal II (Sereno 1999). Prosauropod monophyly was contested by Yates (2001, 2003), who disbanded prosauropods into a paraphyletic array of sequential outgroups to Sauropoda. More recently, Yates has proposed a more moderate hypothesis that recognizes a monophyletic core of prosauropods (including *Plateosaurus*) flanked basally by primitive forms and apically by sauropod-like forms (Yates and Kitching 2003; Yates 2004). Applying the phylogenetic definitions of Sereno (1998) to this topology, the monophyletic core that includes *Plateosaurus* should be called Prosauropoda, the derived sauropod-like forms should be included in Sauropoda, and taxa resolved as outgroups to those clades should be excluded from Sauropodomorpha. For the purposes of this analysis, I will assume a monophyletic Prosauropoda that includes genera accepted as such by all recent cladistic analyses (Sereno 1999; Yates and Kitching 2003; Yates 2004; Galton and Upchurch 2004). Theropoda and Ornithischia will be considered sequential outgroups to Sauropodomorpha (Fig. 1). *Thecodontosaurus* (Yates 2003) and *Saturnalia* (Langer et al. 1999), whose phylogenetic affinities remain controversial, were not included in this analysis. The focus group for this analysis, then, will include sauropods and near-sauropod sauropodomorphs identified by Yates (Yates 2003, 2004; Yates and Kitching 2003).

Content.—The sauropod “body plan” comprises numerous osteological characters that support the monophyly of Sauropoda and its subgroup Eusauropoda (Upchurch 1995, 1998; Wilson and Sereno 1998; Wilson 2002). Owing to its morphological distinctiveness, the taxonomic content of Sauropoda is uncontroversial for all Jurassic and Cretaceous sau-

ropodomorphs (although lower-level affinities are controversial for some). However, the affinities of five Upper Triassic–Lower Jurassic sauropodomorphs (*Blikanasaurus*, *Anchisaurus*, *Antenonitrus*, *Melanorosaurus*, *Lessemsaurus*) have received attention because they are hypothesized to possess some, but not all, sauropod body plan characters (Bonaparte 1999; Yates 2003, 2004; Yates and Kitching 2003).

Galton and van Heerden (1985, 1998) described the partial hindlimb of the Upper Triassic (Carnian–Norian) sauropodomorph *Blikanasaurus cromptoni*, which they considered “an early experiment in the direction of heavily-built quadrupedal saurischians, but. . . not on the evolutionary line that gave rise to the Sauropoda” (1985: p. 511). Some recent cladistic analyses, however, have resolved *Blikanasaurus* as more closely related to sauropods than to prosauropods (Upchurch et al. 2002, 2004; Yates 2003, 2004), but this hypothesis is not yet strongly supported. Yates and Kitching (2003: p. 1757) excluded *Blikanasaurus* from their analysis because of its topological instability, and *Blikanasaurus* possesses at least one hypothesized synapomorphy of prosauropods (hourglass-shaped proximal metatarsal II [Sereno 1999]). Although there are features that seem to support sauropod affinities for *Blikanasaurus*, many of these are proportional measures that could be related to body size (e.g., relative length of metatarsus, breadth of metatarsals I and V). Although I will provisionally treat *Blikanasaurus* as a basal sauropod in the discussion below, further inquiry into its phylogenetic position is required.

The small, facultatively bipedal *Anchisaurus* is usually considered part of a monophyletic Prosauropoda (Sereno 1999; Galton and Upchurch in press), but a recent review of the holotypic and referred remains has suggested sauropod affinities (Yates 2004). In the latter context, the small body size of *Anchisaurus* was interpreted as a reversal in the overall trend toward large body size in Sauropodomorpha (Yates 2004: Fig. 14). Although Yates (2004) reported a relatively high decay index (5) for the node positioning *Anchisaurus* at the base of Sauropoda, its Early Jurassic (Pliensbachian–Toarcian) age implies a 20-million-year ghost lineage preceding its appearance in

the fossil record. Implied stratigraphic debt and character evidence supporting its prosauropod affinities (Sereno 1999; Galton and Upchurch 2004) cast doubt on the hypothesis that *Anchisaurus* is a sauropod.

Yates and Kitching (2003: p. 1753) recently described the new genus *Antenonitrus* on the basis of a partial postcranial skeleton from the Upper Triassic (Norian) of South Africa that they suggest represents the “earliest known sauropod.” If the holotype constitutes a single individual, then the limb proportions suggest a quadrupedal pose for *Antenonitrus*. In fact, most of the features linking *Antenonitrus* to sauropods are proportional features; few discrete characters support this relationship. I will provisionally treat *Antenonitrus* as a potential sauropod, but the association among the holotypic remains and characters evidencing this affinity require further evaluation.

The Upper Triassic *Melanorosaurus* (Houghton 1924) from South Africa is an enigmatic sauropodomorph that is traditionally placed, along with the South American genus *Riojasaurus*, in Melanorosauridae (Galton 1985), widely regarded as a sauropod-like family of prosauropods (Galton 1990; Bonaparte and Pumares 1995; van Heerden and Galton 1997). However, Yates (2003) and Yates and Kitching (2003) have recently suggested that *Melanorosaurus* is a true sauropod. This assessment is based in part on the shape of the femoral shaft, which lacks the mediolateral sigmoid curvature typical of saurischians. However, the constituency of the holotype remains controversial (Houghton 1924; van Heerden 1979), and referral of better-preserved remains to the genus (van Heerden and Galton 1997; Welman 1999) must await restudy of the holotype.

The South American Upper Triassic (upper Norian) genus *Lessemsaurus* (Bonaparte 1999) was named on the basis of several presacral and sacral neural arches and associated presacral centra from the Los Colorados Formation of La Rioja, Argentina. Although Bonaparte (1999: p. 133) referred *Lessemsaurus* to the prosauropod family Melanorosauridae, he grouped it with the sauropods *Lapparentosaurus* and *Volkheimeria* as having vertebrae of the “saurópodo primitivo” type. He based this on

the height of the dorsal neural spines, presence of an infrapostzygapophyseal fossa on dorsal neural arches, and the presence of a “supraneural” constriction below the postzygapophyses (Bonaparte 1999: p. 134). Although no presacral features diagnose Sauropoda, three were resolved as synapomorphies of Eusauropoda by Wilson (2002: Appendix 3): opisthocoelous cervical centra, mid-cervical neural arches taller than height of posterior centrum face, and dorsal neural spines broader transversely than anteroposteriorly. Unfortunately, none of these features can be adequately scored in *Lessemsaurus*. Cervical centra are part of the holotype of *Lessemsaurus*, but Bonaparte (1999) did not comment on the morphology of their articular faces. The cervical neural spines do not appear elongate relative to the presumed height of the centra, which were associated but not articulated (Bonaparte 1999: Fig. 13B). Bonaparte mentions that the dorsal neural spines are transversely thick, but did not provide measurements or figures that allow comparison of neural spine dimensions. Thus, despite superficial similarities, as yet there is no strong evidence that *Lessemsaurus* is a sauropod. It will be regarded here as an indeterminate sauropodomorph pending discovery of more complete skeletal remains.

Spatiotemporal Distribution of Early Sauropods

Until recently, sauropod body fossils and ichnofossils were known only from Jurassic and Cretaceous sediments. This distribution was inconsistent with the Late Triassic first appearances of the sauropod sister lineages Prosauropoda and Theropoda (Figs. 1, 2) (Gauthier 1986). The 15–20-Myr missing interval preceding the first appearance of sauropods in the fossil record was recently reduced by the discovery of Late Triassic sauropod body fossil taxa, including *Isanosaurus* and a second, unnamed form (Buffetaut et al. 2000, 2002), *Antenonitrus* (Yates and Kitching 2003), and *Blikanasaurus* (Upchurch et al. 2002, 2004; Yates 2003).

Well before the discovery of these body fossils, however, trackways from the Upper Triassic of North America were described and at-

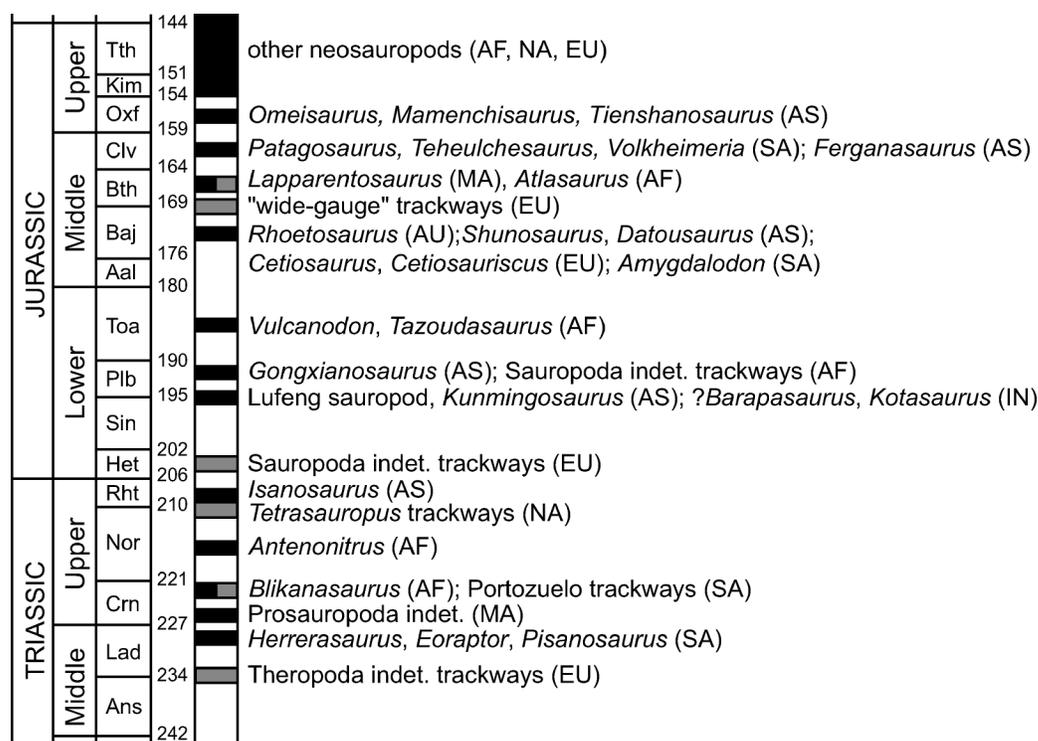


FIGURE 2. Temporal and spatial distributions of early sauropods and related theropod (*Herrerasaurus*, *Eoraptor*), prosauropod, and ornithischian (*Pisanosaurus*) dinosaurs. Tracks and trackways are represented by gray bars; body fossils are represented by black bars. The age of the Kota Formation is not resolved beyond Early Jurassic; the Kota sauropods *Barapasaurus* and *Kotasaurus* have been placed in the middle of that range. Abbreviations: AF, Africa; AS, Asia; AU, Australia; EU, Europe; IN, India; MA, Madagascar; NA, North America; SA, South America. Abbreviations for geological stages are from Benton 1993, and timescale is based on Gradstein et al. 1999.

tributed to the ichnotaxon *Tetrasauropus* (Lockley 1986; Conrad et al. 1987). Despite their similarity to Jurassic and Cretaceous sauropod trackways, *Tetrasauropus* was not identified as such by traditional methods of trackmaker identification, which rely on phenetic similarity and coincident spatial and temporal distributions of body fossils and ichnofossils. It was not until after the discovery of *Isanosaurus* body fossils that *Tetrasauropus* trackways were attributed to a sauropod trackmaker, which "reflects the convention of using osteological evidence as the ultimate arbiter [sic] in deciding at least the temporal, if not the spatial, range of major vertebrate groups" (Lockley et al. 2001: p. 189). (As Lockley et al. [2001: p. 185] noted, the North American *Tetrasauropus* trackways differ from the holotypic *Tetrasauropus* trackway from South Africa, which Rainforth [2003: p. 829]) considers "incompatible with dinosaurian pedal struc-

ture." Here and elsewhere, "*Tetrasauropus*" refers to the North American trackways described by Lockley et al. [2001], which may be referred to a different ichnogenus.)

Ichnofossils are an important source of spatiotemporal information for tetrapods because of their abundance (one trackmaker can make many tracks) and their preservation in environments distinct from those preserving body fossils (Lockley 1991; Lucas 2003). Although Mesozoic mammals remain notable exceptions, perhaps because of their small body size and relatively indistinct manual and pedal skeleton, ichnofossils enhance distributional data (Lockley and Foster 2003). Ichnofossils, however, can extend distributions based on body fossils only when trackmaker identification is spatially and temporally independent. In contrast to traditional methods that rely on phenetic similarity and temporal and spatial coincidence, synapomorphy-based

trackmaker identification (Olsen 1995; Carrano and Wilson 2001) relies on the recognition of osteological synapomorphies from trackway evidence. Synapomorphy-based trackmaker identification frees tracks from preconceived distributions based on body fossils, a distinction especially relevant to early sauropod distributions because (1) a lengthy missing interval precedes the first appearance of body fossils, and (2) the sauropod manus and pes are characterized by numerous synapomorphies that facilitate their identification from trackways. Below, I discuss the spatial and temporal distributions of early sauropods, based on combined body fossil and ichnofossil data.

Temporal Distribution.—The earliest known dinosaur skeletal remains are preserved in Middle to Late Triassic sediments of the Ischigualasto Formation of northwestern Argentina, which have been radiometrically dated at 228 Myr B.P. (Rogers et al. 1993) (Fig. 2). Represented in the Ischigualasto fauna are the basal ornithischian *Pisanosaurus* (Casamiquela 1967) and the saurischian theropods *Herrerasaurus* (Reig 1963) and *Eoraptor* (Serenó et al. 1993). Sauropodomorpha first appears approximately 5 Myr later in the Carnian of Madagascar (Flynn et al. 1999), Africa (Dutuit 1972), South America (Langer et al. 1999), and North America (Chatterjee 1984; Sereno 1991). Theropod trackways of Anisian–?Ladinian age (ca. 238 Ma; Demathieu 1990) suggest an even earlier divergence for Theropoda and Sauropodomorpha (Carrano and Wilson 2001).

An Upper Triassic (Carnian) first appearance for Sauropoda is suggested by both body fossil and ichnofossil remains, but both require confirmation. As mentioned above, the partial hindlimb of the Upper Triassic (Carnian) *Blikanasaurus* preserves several features of Sauropoda (Yates 2003, 2004; Yates and Kitching 2003; Upchurch et al. 2004), some of which may be body size-related. Likewise, tracks from the lower Upper Triassic (Carnian) Portozuelo Formation of west-central Argentina may possess sauropod synapomorphies (see below), but their identification remains tentative (Marsicano and Barredo 2004).

The oldest definitive sauropod fossils are the *Tetrasauropus* trackways preserved in the Chinle Group of western North America, which are Norian–Rhaetian in age (ca. 210 Ma; Lockley et al. 2001). Other Upper Triassic trackways from South Africa (*Pentasauropus*, *Sauropodopus*, *Tetrasauropus* [Ellenberger 1972]) and eastern North America (*Agrestipus* [Weems 1987]) do not appear to preserve diagnostic sauropod features and cannot yet be referred to that group. Slightly younger ?Rhaetian strata in Thailand preserve the fragmentary remains of *Isanosaurus* (Buffetaut et al. 2000) (Fig. 2). *Isanosaurus* may be more derived than the Toarcian *Tazoudasaurus* (Alain et al. 2004) and the probably Toarcian *Vulcanodon* (Raath 1972; Yates et al. 2004), which is generally considered the most primitive sauropod (Wilson 2002: Fig. 13, Table 13).

Sauropod ichnofossils are preserved in Lower Jurassic sediments in Italy (Dalla Vecchia 1994), Poland (Gierlinski 1997), and Morocco (Ishigaki 1988). The two European trackways are preserved in slightly older (Hettangian, ca. 206–202 Ma) horizons than are the Moroccan trackways (Pliensbachian, ca. 195–190 Ma). Still younger sauropod body fossils are known from Lower Jurassic horizons of India (*Barapasaurus* [Jain et al. 1975]; *Kotasaurus* [Yadagiri 2001]) and China (*Kunmingosaurus* [Zhao in Dong 1992]; *Gongxianosaurus* [He et al. 1998]; “Lufeng sauropod” [Barrett 1999]). Of these early sauropod body fossils, only *Gongxianosaurus* preserves complete pedal remains. The first complete sauropod skeleton is *Shunosaurus*, from Middle Jurassic sediments of China (Zhang 1988), which also preserve other sauropods (e.g., *Datousaurus*). Ichnofossils from the Middle Jurassic (Bathonian) of Europe (Santos et al. 1994; Day et al. 2002) provide the first record of the derived sauropod subgroup Neosauropoda. These wide-gauge trackways have been attributed to titanosaur trackmakers (Wilson and Carrano 1999). Neosauropod body fossils first appear in the Callovian of Kirghizia (*Ferganasaurus* [Alifanov and Averianov 2003]) and persist throughout the remainder of the Jurassic and Cretaceous.

Figure 2 identifies several intervals during which no definitive sauropods have been re-

corded, including the Aalenian, Sinemurian, and intervals preceding the Carnian. Until recently, a lengthy missing interval (about 20 Myr) spanned the Carnian, Norian, and Rhaetian ages, between the first appearance of prosauropods and the appearance of the first sauropods. However, the recent discoveries of *Isanosaurus*, *Antenonitrus*, and *Tetrasauropus*, as well as the reinterpretation of *Blikanasaurus* have begun to bridge this temporal gap. Likewise, a Toarcian gap was filled recently by the discovery of *Tazoudasaurus* (Allain et al. 2004) and the revised Toarcian age for the *Vulcanodon* beds (Yates et al. 2004), which were previously considered to be ?Hettangian (e.g., McIntosh 1990; Wilson and Sereno 1998).

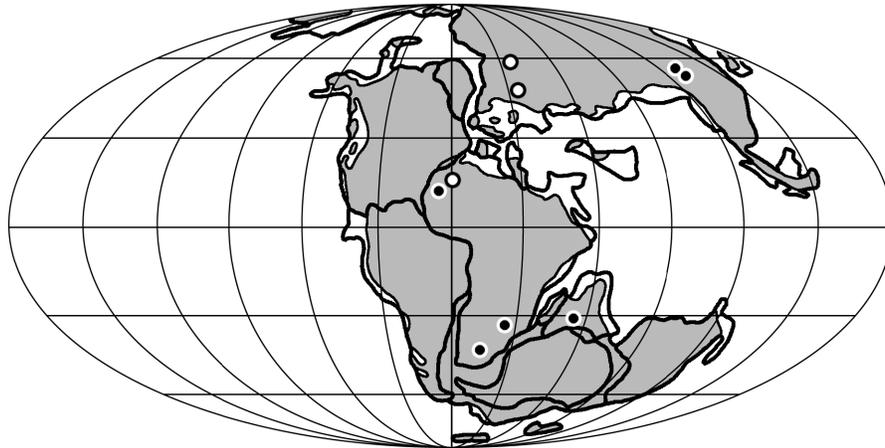
Spatial Distribution.—The spatial distribution of early sauropod body fossils is restricted to fairly small areas in southern, central, and eastern Pangea (Fig. 3, black-filled circles). Sauropod body fossils from uppermost Triassic sediments of Thailand (*Isanosaurus* and an unnamed form) and Lower Jurassic sediments of China (*Gongxianosaurus*, “Lufeng sauropod”) delimit a northeastern area, body fossils from the Upper Triassic and Lower Jurassic of southern Africa (*Antenonitrus*, *Blikanasaurus*, *Vulcanodon*) and the Lower Jurassic of India (*Barapasaurus*, *Kotasaurus*) delimit a southern area, and a single body fossil from the Lower Jurassic of Morocco (*Tazoudasaurus*) forms a central area. If we accept that Sauropoda is a monophyletic group that includes these body fossils, and that sauropods could not cross the Tethys Sea, then this distribution suggests that sauropods previously inhabited the intervening land area. Thus, body fossils suggest that early sauropods may have been present in Madagascar, central Africa, eastern North America, western Europe, and the Middle East. These data, however, do not imply that early sauropods were present in Australia, Antarctica, South America, or western North America. Recently, Gillette (2003: p. 687) interpreted the distribution of sauropod body fossils as suggesting an “initial geographic distribution limited to southeastern Asia” followed by an Early Jurassic “[e]xpansion of distribution. . . through southern Laurasia and eastern Gondwana” and later “geographic expansion in the Middle Jurassic to include Aus-

tralia and South America, but not North America” until the Late Jurassic. Although this interpretation appears consistent with body fossil data, incorporation of ichnofossil data yields a different pattern of early sauropod distributions.

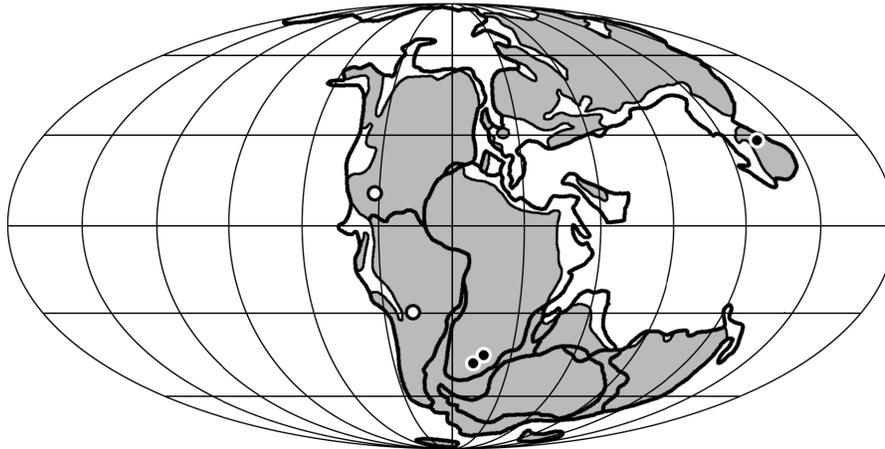
Sauropod footprints confirm the prediction that sauropods inhabited land areas within the area enclosed by sauropod body fossils, and they extend the geographical range of early sauropods to western North America and possibly South America (Fig. 3, white-filled circles). Combined ichnofossil and body fossil data indicate that sauropods achieved a broad east-west distribution (western North America to eastern Asia) by the Late Triassic and extended their range to Africa, Europe, India, and southern South America by the Early Jurassic. Later body fossils indicate that sauropods attained their broadest geographic distribution by the Middle Jurassic, when they also occupied both Madagascar (*Lapparentosaurus* [=“*Bothriospondylus*”] [Ogier 1975; see also Buffetaut 2003]) and Australia (*Rhoetosaurus* [Longman 1926]) (Fig. 2). The only major continental landmass that has not yet produced sauropod fossils is Antarctica. However, because sauropods have been recovered from each of the landmasses adjoining Antarctica during the Middle Jurassic (India, Australia, southern Africa, southern South America, Madagascar), it is likely that sauropods were present on Antarctica by that time.

Distribution of Morphological Features

The quadrupedal posture and distinctive manus and pes skeletons of sauropods have facilitated identification of their footprints in the fossil record since Bird’s (1941) discovery of sauropod trackways in the Early Cretaceous of Texas, which were later named *Brontopodus birdi* in his honor (Farlow et al. 1989). The sauropod manus and pes skeleton and their corresponding impressions in sauropod ichnotaxa such as *Brontopodus* share numerous similarities (Fig. 4), including several synapomorphies of Sauropoda and its subgroups (Table 1). The ability to observe these synapomorphies varies with preservation of the trackway. Whereas several features can be observed in coarsely preserved footprints (e.g.,



Early Jurassic (Sinemurian, 200 mya)



Late Triassic (Rhaetian-Norian-Carnian, 220 mya)

FIGURE 3. Geographic distribution of early sauropod fossils mapped onto paleogeographic reconstructions of the Earth during the Late Triassic (Rhaetian–Norian–Carnian, 220 Ma) and Early Jurassic (Sinemurian, 200 Ma). Black-filled circles represent body fossils; white-filled circles represent ichnofossils. Late Triassic body fossils include *Blikanasaurus* (South Africa; Galton and van Heerden 1985), *Antenonitrus* (South Africa; Yates and Kitching 2003), and *Isanosaurus* (Thailand; Buffetaut et al. 2000); Late Triassic ichnofossils include *Tetrasauropus* (U.S.A.; Lockley et al. 2001) and an unnamed form from the Portozuelo Formation (Argentina; Marsicano and Barredo 2004). Early Jurassic body fossils include *Vulcanodon* (Zimbabwe; Raath 1972; South Africa; Yates et al. 2004), *Tazoudasaurus* (Morocco; Allain et al. 2004), *Barapasaurus* (India; Jain et al. 1975), the “Lufeng sauropod” (China; Barrett 1999), and *Gongxianosaurus* (China; He et al. 1998), and Early Jurassic ichnofossils include unnamed forms from Holy Cross Mountains (Poland; Gierlinski 1997), Lavini di Marco (Italy; Dalla Vecchia 1994), and Atlas Mountains (Morocco; Ishigaki 1988). Paleogeographic reconstructions are based on Smith et al. 1994.

large body size, digitigrade manus, spreading pes), some features can be identified only in trackways (e.g., quadrupedal stance, wide-gauge posture) or finely preserved tracks (e.g., shaft width of metatarsal I > metatarsals II–IV). One of the more conspicuous features associated with sauropod trackways is the heel

impression, which may be regarded as a “reciprocal illuminant”—a soft tissue feature preserved in trackways that have been attributed to a certain trackmaker by other means (Carrano and Wilson 2001: p. 571). The presence of a well-marked heel trace in all sauropod trackways thus far identified indicates

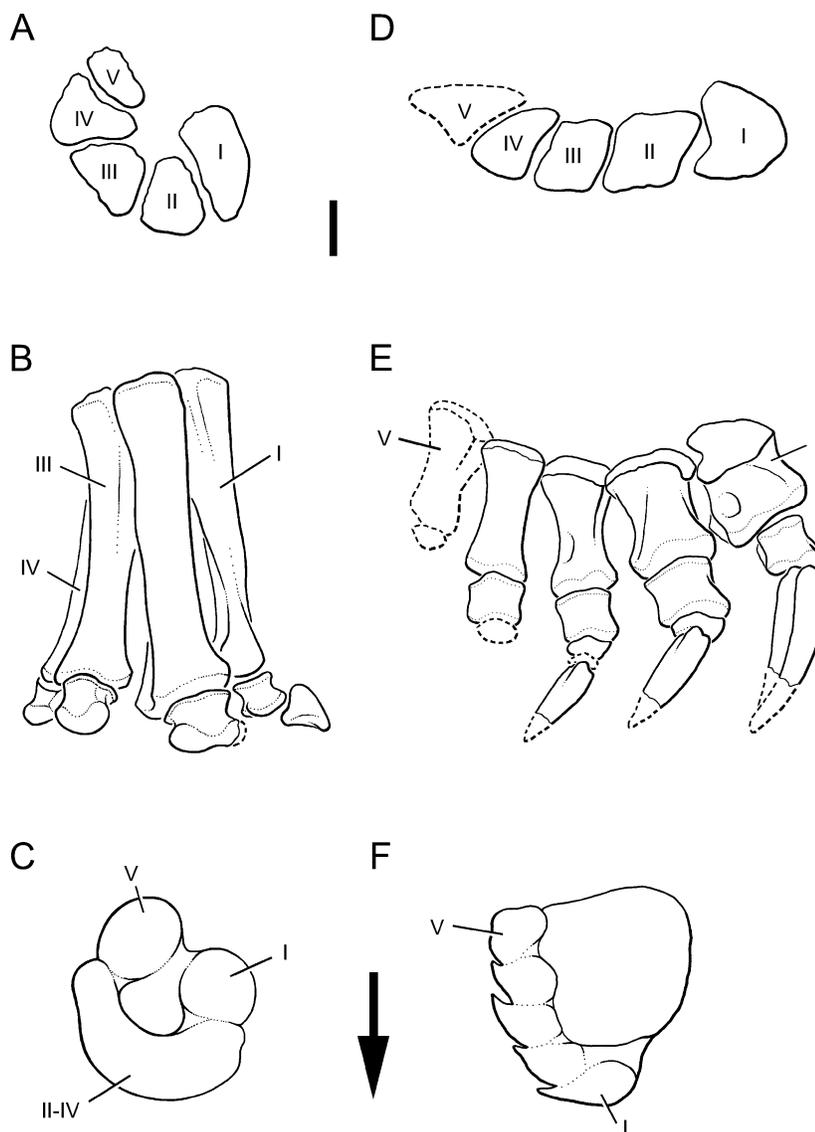


FIGURE 4. Sauropod manus, pes, and footprints. A, B, *Brachiosaurus*. Right manus in proximal (A) and anterior (B) views. C, F, *?Brontopodus*. Right manus print (C) and right pes print (F), oriented relative to the trackway midline (arrow). Modified from Thulborn 1990: Fig. 6.16f. D, E, *Apatosaurus*. Right pes in proximal (D) and dorsal (E) views. Modified from Gilmore 1936: Figs. 25, 27, 28. A–C from Wilson and Sereno 1998: Fig. 22. Roman numerals indicate digit numbers. Scale bar, 10 cm for A, B, D, and E; C and F not to scale.

that a fleshy pad supported the pes, a feature that may be related to the acquisition of a spreading metatarsus and semi-digitigrade pedal posture (Wilson and Sereno 1998). As such, presence of a heel impression can be used as a synapomorphy that identifies a eu-sauropod trackmaker.

Trackway features suggest that *Brontopodus* trackways were made by a titanosauriform sauropod, perhaps a saltosaurid (sensu Wil-

son 2002; Wilson and Upchurch 2003). Because these Early Cretaceous trackways do not predate the estimated origin of Titanosauriformes (Late Jurassic) or Saltosauridae (Early Cretaceous), *Brontopodus* does not modify the hypothesized temporal distributions of titanosauriforms, saltosaurids, or their defining synapomorphies (Table 1). However, Middle Jurassic trackways preserving saltosaurid features (Santos et al. 1994; Day et al. 2002) alter

TABLE 1. Synapomorphies of Sauropoda and its subgroups that can be identified in the trackways of *Brontopodus birdi* (Fig. 4C,F). The asterisk indicates a “reciprocal illuminant”—a soft tissue feature associated with trackways securely identified by osteological synapomorphies. Synapomorphies are based on Wilson 2002 and references therein; trackway features are modified from Carrano and Wilson 2001. Osteological features for Neosauropoda have been resolved as eusauropod synapomorphies by Upchurch (1998).

Clade	Osteological character	Trackway feature
Sauropoda	Columnar, obligately quadrupedal posture	Quadrupedal tracks
Eusauropoda	Large body size	Large track size
	Manual phalangeal count reduced	Short digit impressions
	Minimum shaft width of metatarsal I exceeds those of metatarsals II–IV	Digit I more deeply impressed than others
	Semi-digitigrade pes	Metatarsals spreading in pes print
	Pedal ungual IV reduced/absent	No pedal ungual IV print
<i>Barapasaurus</i> + more derived taxa	Sickle-shaped pedal unguals II, III	Pedal ungual II, III impressions deep, sickle-shaped
	*Pes supported by heel pad	Heel trace
	Laterally directed pedal unguals	Pedal ungual prints offset laterally
Neosauropoda	Metacarpus bound	Anteroposteriorly narrow manus print that lacks digit divergence
Titanosauriformes Saltasauridae	Metacarpus forming 270° arc	Tightly arched manus print
	Femoral shaft deflected medially	Wide-gauge tracks
	Femoral distal condyles offset 10° relative to shaft	Wide-gauge tracks
	Femoral midshaft, transverse diameter at least 185% anteroposterior diameter	Wide-gauge tracks

existing distributions because they predate the hypothesized origin of both Titanosauriformes and Saltasauridae. Either these lineages appeared earlier than the body fossil record shows, or their defining characters appeared homoplastically in earlier sauropods. Thus, if trackways are attributed to body fossil clades through the use of synapomorphies, then any diagnostic trackway that extends the temporal distribution of a body fossil clade alters the distributions of characters, taxa, or both.

Late Triassic (Fig. 5) and Early Jurassic (Fig. 6) trackways outside the spatiotemporal range delimited by body fossils can be referred to Sauropoda on the basis of osteological synapomorphies. Because few appendicular synapomorphies of or within Sauropoda are estimated (on the basis of body fossils) to have evolved before the Early Jurassic, these early appearing trackways have the potential to modify either character distributions or temporal distributions. There are three resolutions to distributional conflicts implied by ichnotaxa bearing characters that appear outside the tem-

poral range of body fossil clades they diagnose (Fig. 7) (Carrano and Wilson 2001):

1. *parallelism*—the ichnotaxon is not a member of the body fossil clade, but represents an as-yet-undiscovered body fossil that evolved the character independently;
2. *reversal*—the ichnotaxon is more primitive than both the body fossil clade diagnosed by the feature and its body fossil outgroups (which lack the feature), and the character diagnoses the clade including all four but was lost in the body fossil outgroups;
3. *synapomorphy*—the ichnotaxon is a member of the body fossil clade, extending the temporal range of the body fossil clade, all later-appearing body fossil outgroups, and the character.

Resolution of conflicting ichnological and body fossil distributions as either parallelism or reversal results in modification of previous character distributions, whereas resolution of this conflict as synapomorphy results in modified temporal distribution of taxa. The distribution of several locomotor characters among

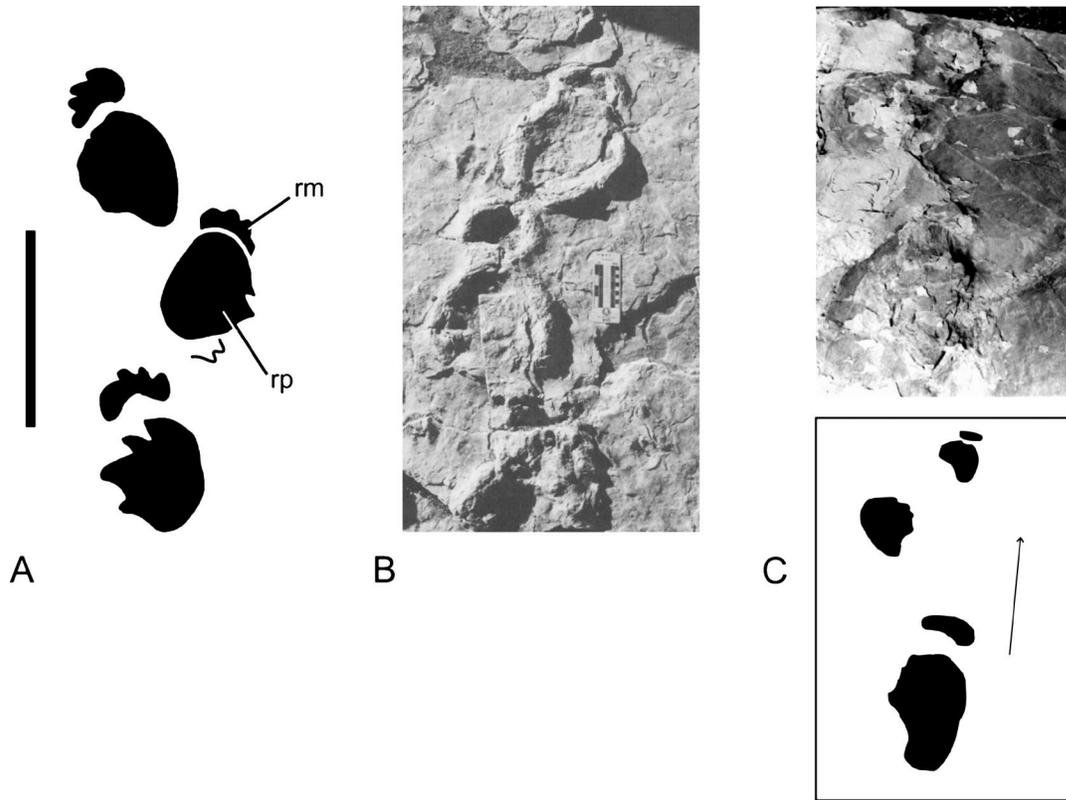


FIGURE 5. Late Triassic sauropod footprints. A, B, *Tetrasauropus* trackways from the Upper Triassic (Chinle Group) of Cub Creek (A) and Peacock Canyon (B), Colorado (from Lockley et al. 2001). C, Possible sauropod trackways from the Portozuelo Formation (Carnian) of Argentina (modified from Marsicano and Barredo 2004). This photograph was not taken from directly above tracks; relative sizes are distorted (upper tracks appear smaller than lower ones). Abbreviations: rm, right manus print; rp, right pes print. Scale bar, 50 cm for A, 10 cm for B.

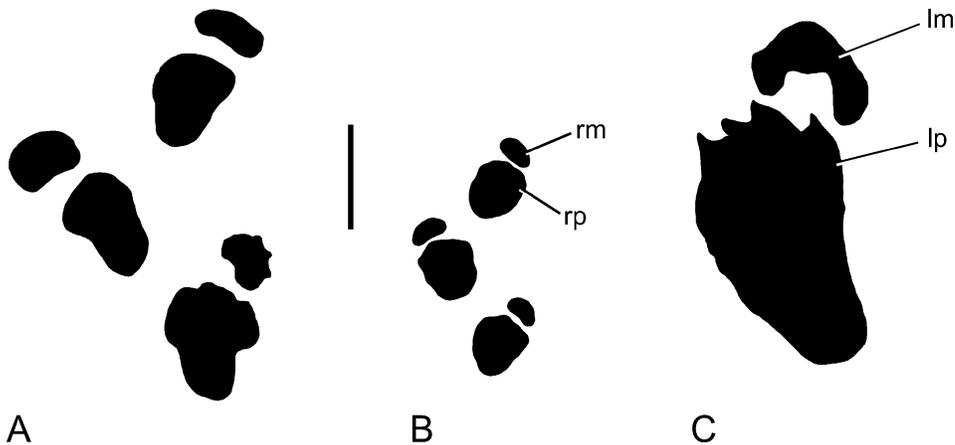
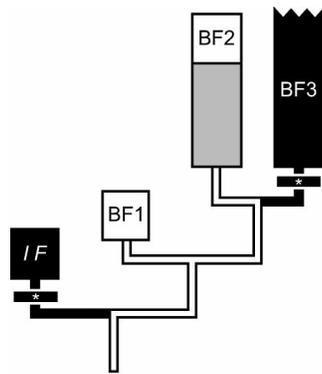
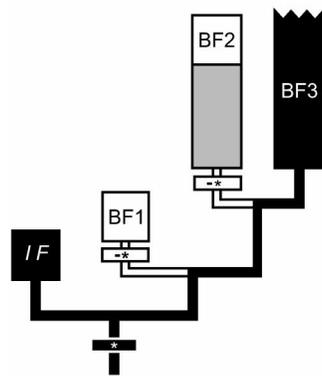


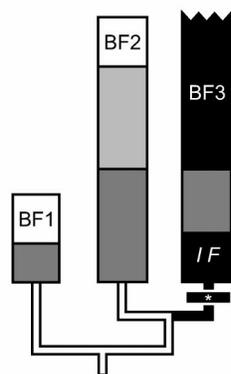
FIGURE 6. Early Jurassic sauropod footprints. A, Trackway from the Pliensbachian of the Atlas Mountains, Morocco (based on Farlow 1992: Fig. 2a–b). B, Trackway ROLM 28 from the Hettangian of Lavini di Marco, Italy (based on Dalla Vecchia 1994: Fig. 2); C, Manus-pes pair of *?Parabrontopodus* from the Hettangian of the Holy Cross Mountains, Poland (based on Gierlinski 1997: Fig. 1b). The trackways from Morocco (A) and Italy (B) are oriented relative to the trackway midline, which could not be determined for the Polish specimen (C). Abbreviations: lm, left manus print; lp, left pes print; rm, right manus print; rp, right pes print. Scale bar, 10 cm.



(1) parallelism



(2) reversal



(3) synapomorphy

FIGURE 7. Three resolutions to the conflict in character and taxon distributions from body fossil and ichnofossil data. In this example, the early appearance in an ich-

nofossil (IF) of a derived morphological feature (*) known to be absent in the later-appearing body fossils (BF1 and BF2) but present in a derived body fossil (BF3) can be resolved three ways. Parallelism (1) interprets the ichnofossil as basal to the body fossils and resolves the feature as evolving in parallel in the ichnofossil and body fossil 3. Reversal (2) also interprets the ichnofossil as basal to the body fossils, but instead resolves the feature as a synapomorphy of all four taxa that was reversed in two of the body fossils. Synapomorphy (3) interprets the ichnofossil as an early appearing member of the BF3 lineage, which implies three ghost lineages. Resolutions (1) and (2) imply homoplasy but no additional ghost lineages; resolution (3) implies additional ghost lineages (dark gray bars) but no homoplasy. Vertical distances reflect hypothetical age differences. Pale gray bars indicate ghost lineages implied by body fossils; dark gray bars indicate ghost lineages implied by ichnofossils. Black indicates the derived condition; white indicates the primitive condition.

Quadrupedal Posture.—Determination of locomotor posture in extinct tetrapods typically relies on indirect evidence derived from skeletal remains. Primary among these are intermembral indices, but relative trunk length and qualitative assessments of the robustness of forelimb elements are also used. Trackway data, in contrast, offer direct evidence of locomotor posture, but generalizations based on them are not without ambiguity. In order for them to be useful indicators of locomotor behavior, trackways should be interpreted in the context of behavioral variation (is the trackway representative of “typical” trackmaker behavior?), taphonomic variation (is trackway morphology altered by preservation?), and taxonomic variation (is the trackmaker “typical” of the larger taxon it represents?).

In some cases, osteological and trackway data offer an unambiguous determination of locomotor posture. Theropods are considered obligate bipeds because their forelimbs are no more than 40–50% of hindlimb length, their slender manus bears narrow, sickle-shaped unguals, and only bipedal trackways have

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nofossil (IF) of a derived morphological feature (*) known to be absent in the later-appearing body fossils (BF1 and BF2) but present in a derived body fossil (BF3) can be resolved three ways. Parallelism (1) interprets the ichnofossil as basal to the body fossils and resolves the feature as evolving in parallel in the ichnofossil and body fossil 3. Reversal (2) also interprets the ichnofossil as basal to the body fossils, but instead resolves the feature as a synapomorphy of all four taxa that was reversed in two of the body fossils. Synapomorphy (3) interprets the ichnofossil as an early appearing member of the BF3 lineage, which implies three ghost lineages. Resolutions (1) and (2) imply homoplasy but no additional ghost lineages; resolution (3) implies additional ghost lineages (dark gray bars) but no homoplasy. Vertical distances reflect hypothetical age differences. Pale gray bars indicate ghost lineages implied by body fossils; dark gray bars indicate ghost lineages implied by ichnofossils. Black indicates the derived condition; white indicates the primitive condition.

been attributed to the group. Osteological and ichnological data are similarly compelling for the locomotor posture of most sauropods, which have relatively elongate forelimbs (at least 70% hindlimb length) and only quadrupedal trackways attributed to them.

In contrast, these data are ambiguous for the locomotory posture of prosauropods, whose phylogenetic affinities affect the polarity of basal sauropod characters (see "Ancestry" above). Many prosauropods have hindlimb and trunk proportions intermediate between those of theropods (bipeds) and sauropods (quadrupeds), which may suggest an intermediate locomotory posture (Huene 1926; Galton 1976, 1990, 2000; Cooper 1981; van Heerden 1997). Trackways attributed to prosauropods exhibit both bipedal (e.g., *Pseudotetrasauropus* [Ellenberger 1972], *Otozoum* [Rainforth 2003]) and quadrupedal locomotion (e.g., *Navahopus* [Baird 1980]; cf. *Otozoum* [Lockley and Hunt 1995: Figs. 4.17–4.19; Lockley and Meyer 2000: Fig. 4.3]). It is not yet clear whether these tracktypes represent one or more prosauropod trackmakers, each capable of two locomotor modes (i.e., a facultative biped), or two prosauropod trackmakers, each capable of a single locomotor mode (i.e., a biped and a quadruped).

The nearest outgroups to Dinosauria, *Lagerpeton* and *Marasuchus*, are regarded as bipedal (Sereni and Arcucci 1993, 1994), as are the ropods. The sauropodomorphs *Saturnalia* and *Thecodontosaurus*, which have been regarded as either basal prosauropods or outgroups to Sauropodomorpha, are likewise considered to be bipedal (Langer et al. 1999; Yates 2001). Thus, Dinosauria and Saurischia are primitively bipedal (Carrano 2000). Sauropodomorpha was probably primitively bipedal, but the ancestral state is contingent on relationships within Prosauropoda and the locomotor posture assigned to basal prosauropods.

Sometime after their hypothesized divergence from Theropoda and Prosauropoda 238–228 Myr ago (see above "Spatial Distribution"), sauropods acquired an obligate quadrupedal stance. If the Upper Triassic *Antenonitrus* is shown to be a sauropod and an associated individual, then its relatively robust, elongate forelimb suggests that it is the earliest

quadrupedal sauropod body fossil. The Lower Jurassic *Barapasaurus*, *Gongxianosaurus*, and *Vulcanodon* are the first definitive sauropod body fossils for which a quadrupedal pose can be inferred. The earlier appearing, Upper Triassic *Isanosaurus* is too fragmentary to determine its locomotor posture.

North American *Tetrasauropus* trackways (Figs. 2, 5A,B), which are coeval with the body fossil *Antenonitrus*, suggest that sauropod quadrupeds evolved before the Upper Triassic (Norian). Even older trackways from the Portozuelo Formation of Argentina (Figs. 2, 5C) record a quadruped in the Carnian (ca. 225 Ma), 5–10 Myr before the appearance of *Antenonitrus* and approximately 25 Myr before the appearance of a definitive quadrupedal body in the Lower Jurassic. However, as Marsicano and Barredo (2004) noted, the presence of manus prints in these trackways is irregular and the trackmaker may have been a facultative, rather than an obligate, quadruped.

Semi-Digitigrade Pes.—Acquisition of a spreading pes with metatarsals oriented nearly horizontally is a synapomorphy for Eusauropoda (Upchurch 1995), a clade that includes all sauropods but the basalmost forms *Vulcanodon*, *Tazoudasaurus*, *Gongxianosaurus*, *Antenonitrus*, and *Blikanasaurus*. Wilson and Sereni (1998: p. 41) hypothesized that the morphology of the eusauropod tarsus and pes suggested a "semi-digitigrade" foot posture, in which the relatively short metatarsals (~1/4 tibia length) were oriented nearly horizontally and supported by a fleshy heel pad (Fig. 4D–F). Non-eusauropods such as *Vulcanodon* and *Gongxianosaurus*, in contrast, have a relatively elongate metatarsus (>1/3 tibial length) that resembles those of prosauropods and theropods.

In the absence of qualifying terms, "semi-digitigrady" does not have explicit meaning in existing classifications of tetrapod locomotor posture. Specifically, "digitigrady" refers to a range of postures intermediate between the extremes of "plantigrady," in which the metatarsals and phalanges are oriented horizontally and contact the substrate, and "unguligrady," in which the metatarsals are oriented nearly vertically and only the distal-most phalanges contact the substrate (Carra-

no 1997: p. 78). By this definition, the sauropod pes is digitigrade but closer to the plantigrade extreme than the unguligrade extreme. Somewhat confusingly, the specialized foot posture of hippopotamids, rhinocerotids, and proboscideans, in which a fleshy pad supports the pes, has been termed “sub-unguligrade” because the penultimate and ungual phalanges contact the substrate (Carrano 1997: Fig. 1B, Appendix 1). Although the hypothesized sauropod hind foot posture is in some ways similar to “sub-unguligrady” (viz. the fleshy heel pad), the metatarsus is not held vertically as in sub-ungulates, nor are the non-ungual phalanges hypothesized to be held off the substrate. For the purposes of this discussion, the term “semi-digitigrady” will be applied to the foot posture hypothesized for Eusauropoda.

Body fossils provide unambiguous support for the hypothesis that a semi-digitigrade pes originated in Eusauropoda, which first appears in the Lower Jurassic, and was absent in eusauropod outgroups, which first appear in the Upper Triassic. Although the earliest eusauropod is Sinemurian–Pliensbachian in age (*Kunmingosaurus*), a semi-digitigrade pes is first documented in the Middle Jurassic (Bajocian) *Shunosaurus*. These hypothesized temporal and character distributions are challenged by semi-digitigrade pes impressions present in Upper Triassic *Tetrasauropus* trackways (Fig. 5A,B) and Lower Jurassic sauropod trackways (Fig. 6). Additionally, Upper Triassic trackways from the Portozuelo Formation (Fig. 5C) seem to indicate an even earlier origin for semi-digitigrade pedal posture, although the unguals appear to be directed medially rather than laterally (see “Laterally Directed Pedal Unguals” below). Conflicting ichnological and osteological estimates for the first appearance of semi-digitigrady in sauropods can be reconciled in one of three ways (Fig. 7). Semi-digitigrady either (1) evolved in parallel in Eusauropoda and in Upper Triassic and Lower Jurassic trackmakers, (2) diagnoses all sauropods but was reversed in *Vulcanodon* and *Gongxianosaurus*, or (3) implies that Upper Triassic and Lower Jurassic trackmakers are eusauropods. Resolutions (1) and (2) accept the stratigraphic data at face value and inter-

pret the trackmakers as the basalmost sauropods, outgroups to *Vulcanodon* and Eusauropoda. As such, these two resolutions represent equally parsimonious solutions to an ambiguous character distribution: resolution (1) delays transformations, and a semi-digitigrade pes is assumed to have been acquired in parallel in the trackmakers and Eusauropoda, whereas resolution (2) accelerates transformations, and a semi-digitigrade pes is assumed to evolve at the base of the clade and later reverse in non-eusauropod body fossils such as *Vulcanodon*. Alternatively, resolution (2) could imply that the hind foot posture of non-eusauropod body fossils has not been interpreted correctly, and that the feature diagnoses Sauropoda and has not reversed. A recent study of skeletal remains referred to *Plateosaurus* has inferred a less digitigrade posture than traditionally posited for prosauropods (Sullivan et al. 2003), which may imply that some prosauropods had a more sauropod-like pedal posture. This preliminary result underscores the need for additional investigation into osteological correlates of foot posture. Resolution (3) accepts the character data at face value, interpreting the Upper Triassic and Lower Jurassic trackmakers as eusauropods. In this scenario, the early appearance of the ichnofossils suggests a Late Triassic origin for Eusauropoda and a 50-Myr missing lineage prior to the Bajocian appearance of *Shunosaurus*, the earliest eusauropod with a demonstrably semi-digitigrade pes.

Reduction of Manual Phalanges.—Prosauropods retain the primitive manual phalangeal count of 2*-3*-4*-3-2, in which the first three digits bear unguals (noted by asterisks). Theropods, too, retain the primitive phalangeal complement on the first three digits but apomorphically reduce the outer two digits for a 2*-3*-4*-0-0 count (Serenio and Novas 1992). All eusauropods, in contrast, are characterized by a shortened manus in which each digit bears two or fewer phalanges, and only the pollex bears an ungual (Wilson and Serenio 1998; Fig. 4B). The second ungual attributed to the manus of *Ferganasaurus*, which is now lost, has been interpreted as a misassociation (Alifanov and Averianov 2003: p. 364). Reduction of manual phalanges, however, remains an

ambiguous synapomorphy of Eusauropoda, because their outgroups do not preserve complete manual remains (e.g., *Vulcanodon*, *Gongxianosaurus*). Although osteological evidence for reduction of manual phalanges does not appear until the Middle Jurassic (*Shunosaurus*), it likely evolved much earlier, as suggested by older, but more derived eusauropods such as *Barapasaurus* (Lower Jurassic), which does not preserve a complete manus.

Manual phalangeal reduction can be identified in well-preserved trackways, such as that of the Cretaceous ichnogenus *Brontopodus* (Fig. 4C). The manus print is complete, but there is no indication of individual digits or unguals. However, the degree of reduction cannot be ascertained in even exceptionally well preserved sauropod forefoot impressions, because they do not preserve phalangeal impressions. This may in itself indicate the extreme phalangeal reduction in eusauropods. Lower Jurassic trackways suggest that early sauropods possessed a reduced set of manual phalanges similar to those of Middle Jurassic eusauropods. Manual impressions preserve neither evidence of free digits nor ungual impressions (Fig. 6). The three small convexities on the outer margin of one manual print (Fig. 6A), do not appear in others and may be preservational defects. Upper Triassic *Tetrasauropus* trackways, in contrast, appear to be more primitive in this character than both *Shunosaurus* and the Lower Jurassic trackmakers. The presence of free digits is indicated by the consistent appearance of extensions from the central, fleshy portion of the manus (Fig. 5A). However, the number of phalanges retained cannot be determined. The absence of similar extensions in other North American *Tetrasauropus* trackways (Fig. 5B) suggests either a difference in preservation or the presence of a second, more derived sauropod present in the Upper Triassic. Likewise, the Upper Triassic Portozuelo trackways do not preserve evidence of manual digits and resemble those of Lower Jurassic trackways.

Trackway evidence suggests that manual phalangeal reduction began prior to the Lower Jurassic, perhaps even the Upper Triassic.

Laterally Directed Pedal Unguals.—*Barapasaurus* and more derived sauropods evolved ped-

al unguals that are deflected laterally relative to the long axis of each digit and of the foot itself. This conspicuous feature derives from changes in the shape of the articular facet of the ungual, as well as asymmetry of the blade of the ungual (Wilson and Sereno 1998). This feature can be detected in partial pedes and even in isolated unguals. The presence of laterally directed pedal unguals is an unambiguous synapomorphy because the basal sauropods *Vulcanodon*, *Tazoudasaurus*, *Gongxianosaurus*, and *Shunosaurus*—each of which preserve pedal unguals—appear to retain the primitive condition (but further documentation of this condition is required [Wilson and Sereno 1998: p. 44]). The presence of this feature can be easily determined in well-preserved trackways (Fig. 4F) but may be more difficult to detect as preservation quality declines. Upper Triassic *Tetrasauropus* trackways (Fig. 5A,B) clearly preserve impressions of pedal unguals deflected laterally relative to the axis of the pes. Likewise, Lower Jurassic footprints from Poland preserve ungual impressions that are only slightly laterally directed from the axis of the pes, but their orientation relative to the direction of travel cannot be determined (Fig. 6C). Lower Jurassic trackways from Morocco and Italy do not bear ungual traces and cannot be scored for this feature (Fig. 6A,B). The Upper Triassic Portozuelo trackways (Fig. 5C), in contrast, preserve ungual impressions that are oriented medial to the axis of the pes and line of travel.

The early appearance of laterally directed pedal unguals in Upper Triassic *Tetrasauropus* trackways predates the first osteological evidence of this feature in the Lower Jurassic *Barapasaurus*. This conflict can be resolved as either (1) parallelism, (2) reversal, or (3) synapomorphy. Each of these resolutions requires ad hoc hypotheses of either homoplasy or ghost lineages. Parallelism implies that *Tetrasauropus* evolved laterally directed pedal unguals independent of the clade uniting *Barapasaurus* and other sauropods. Reversal implies that laterally directed pedal unguals diagnoses the clade including *Tetrasauropus* and more derived sauropods, but was reversed in intervening basal sauropods. Synapomorphy resolves *Tetrasauropus* as a member of the clade

uniting *Barapasaurus* and more derived sauropods and implies ghost lineages for several taxa.

Digitigrade Manus.—In sauropods with a digitigrade manus, the metacarpus is arranged vertically, and the five metacarpals are subequal in length and tightly appressed proximally (Fig. 4B). The manus contacts the substrate at the metacarpal-phalangeal joint and creates an abbreviated forefoot print (Fig. 4C). Some sauropods are also characterized by wedge-shaped proximal metacarpal heads that articulate in a tight arc of approximately 270° (Fig. 4A), a tubular arrangement of the metacarpus that results in a tightly arched forefoot print (Fig. 4C). Upchurch (1998) considered these two features (digitigrade manus, tubular metacarpus) to be correlated and diagnostic of all sauropods preserved with manual remains (i.e., Eusauropoda). More recently, Bonnan (2003: pp. 599, 610–611) further suggested that a digitigrade, tubular metacarpus is phylogenetically linked to the acquisition of a quadrupedal posture, and that these three correlated features will be shown to characterize all sauropods once manual remains are known for basal forms. In contrast, Wilson and Sereno (1998) and Wilson (2002) regarded the digitigrade manus and tubular metacarpus as independent features that are present in neosauropods but absent in more basal forms such as *Shunosaurus* (Zhang 1988: Fig. 49, Pl. 14) and *Omeisaurus* (He et al. 1988: Figs. 47–48; Pl. 14, Figs. 4–6), whose metacarpals appear to have poorly defined intermetacarpal articular surfaces that were only slightly arched (~90°) in articulation.

Upper Triassic *Tetrasauropus* trackways from North America (Fig. 5) and Lower Jurassic trackways from Italy, Poland, and Morocco (Fig. 6) document sauropod trackmakers with a digitigrade manus, identified by an antero-posteriorly narrow manus print that lacks digit divergence (Table 1). However, unlike more derived sauropods (Fig. 4C), the manus prints appear to be only slightly arched. Although more and better-preserved trackways are required to confirm this, the presence of one feature (digitigrade manus) and the absence of the other (tightly arched metacarpus) in these trackways suggests they are independent

(Wilson and Sereno 1998; Wilson 2002). Although quadrupedal posture and digitigrade manus are present in these early trackways, this does not provide evidence that these characters are correlated. If we accept the character scoring of Wilson and Sereno (1998), in which *Shunosaurus* and *Omeisaurus* are regarded as primitive (i.e., manus not digitigrade), then the early appearance of a digitigrade forefoot posture in *Tetrasauropus* and Lower Jurassic trackways can be interpreted as either (1) parallelism, (2) the early appearance of digitigrade foot posture in non-neosauropods with subsequent reversals, or (3) the early appearance of Neosauropoda. Parallelism implies two independent origins of the digitigrade manus posture, whereas reversal implies that intervening taxa have reverted to a primitive forefoot posture. Synapomorphy resolves *Tetrasauropus* and Lower Jurassic trackmakers as neosauropods and implies several ghost lineages. However, if we accept the Upchurch (1998) and Bonnan (2003) interpretations of *Shunosaurus* and *Omeisaurus* as having the derived, digitigrade forefoot posture, then trackway evidence suggests that digitigrade forefoot posture evolved in the Triassic and characterized all sauropods more derived than *Tetrasauropus*. These early sauropods, however, had not yet evolved the tightly arched arrangement of metacarpals diagnostic of neosauropods.

Using Stratocladistics to Resolve Conflicting Distributions

In the preceding section, I attempted to reconstruct individual character transformations by using data from both ichnofossils and body fossils. In each case, ichnofossil and body fossil character and temporal distributions were nonoverlapping, so hypotheses of character transformation required ad hoc hypotheses of character change (homoplasy) or of stratigraphic intervals in which taxa were not sampled (ghost lineages). The optimal character transformation minimizes both of these. I have suggested that for a given topology, only three alternate hypotheses of character transformation exist for conflicting ichnological and body fossil data—parallelism, reversal, and synapomorphy (Fig. 7). The

number of ad hoc hypotheses implied by each of the three possible transformations can be determined, and the transformation implying the fewest ad hoc claims can be chosen for a single character and a given topology. However, when several characters are considered simultaneously, such as the locomotor characters discussed here, minimizing ad hoc hypotheses amongst multiple character transformations quickly becomes intractable. Moreover, these additional character data and temporal data should be allowed to influence the cladistic topology itself, and a general method is required. Stratocladistics is the only method of phylogenetic inference that explicitly selects the tree or trees that minimize both character debt and stratigraphic debt (Fisher 1992, 1994; Fisher et al. 2002).

Methods.—No computer program is yet available that evaluates character data and stratigraphic data together. Stratocladistic analysis usually employs two programs, a parsimony algorithm that finds the shortest tree or trees given a character-taxon matrix (e.g., PAUP* [Swofford 2001]) and a program that tracks changes in a multistate, polymorphic character (e.g., MacClade 4.0 [Maddison and Maddison 2000]). Protocol for stratocladistic analysis has been presented elsewhere (Fisher 1992; Polly 1997; Fox et al. 1999; Bloch et al. 2001; Bodenbender and Fisher 2001) and will only be summarized here. The first stage of stratocladistic analysis proceeds as does standard cladistic analysis. That is, operational taxonomic units are scored for characters and this information is coded into a character-taxon matrix. A parsimony algorithm such as PAUP* obtains the shortest tree or trees that explain this character information. The second stage of stratocladistic analysis begins with the cladistically shortest tree (or trees), which MacClade converts to a phylogenetic tree by the addition of a stratigraphic character (typically the last character in the matrix) not included in the cladistic analysis. The length of the phylogenetic tree identical to the cladistic topology is the “stratigraphically augmented treelength,” which is the starting point from which shorter trees are sought using the “make ancestor” tool in MacClade. Because stratocladistics compares trees with zero-

length branches (i.e., ancestors), it is important to include autapomorphies in the character-taxon matrix. The shortest phylogenetic tree isomorphic with the shortest cladistic tree can be shortened further by evaluating alternate topologies, either by manual branch swapping or the “Search Above” tool in MacClade, or by searching in PAUP* for all trees below the “debt ceiling” implied by the stratigraphically augmented treelength.

Stratocladistic analysis of early sauropod and sauropod-like taxa evaluated 172 morphological characters and a single stratigraphic character in three ichnofossils and 12 body fossils (see Appendix online at <http://dx.doi.org/10.1666/03047.S1>). Terminal taxa included all relevant Upper Triassic and Lower Jurassic sauropods, as well as three of the ichnofossils discussed above (the Portozuelo form [Argentina], *Tetrasauropus* [U.S.A.], the Lavini di Marco form [Italy]; Figs. 5, 6). Many of the terminal taxa have been included in previous analyses (e.g., Upchurch 1995, 1998; Wilson and Sereno 1998; Wilson 2002), but *Gongxianosaurus*, *Isanosaurus*, *Tazoudasaurus*, and the ichnofossils have not. Morphological characters included only those characters resolved as synapomorphies or autapomorphies at nodes basal to Neosauropoda, as well as uniquely derived autapomorphies (Wilson 2002: Appendices 2–4). I have emended scorings to accommodate recently described materials of *Omeisaurus* (Tang et al. 2001), *Mamenchisaurus* (Ouyang and Ye 2002), and *Barapasaurus* (Bandyopadhyay et al. 2003). The stratigraphic character scores the presence of a terminal taxon in any of the 14 Triassic and Jurassic stratigraphic stages from the Anisian to the Oxfordian. Because no sauropods in this analysis are preserved in two stages (Ladinian, Aalenian), these states were not coded and did not contribute to total debt. The remaining 12 stratigraphic stages were coded as character states 0–9 and A or B. The ampersand symbol (&) denotes polymorphism, in which a taxon occupied multiple stratigraphic levels; the forward slash (/) indicates uncertainty, in which a taxon occupies one of several possible stratigraphic levels (Maddison and Maddison 2000). Character polarity was

determined by successive outgroups to Sauropoda (Prosauropoda, Theropoda).

Results.—Cladistic analysis of the 12 body fossil ingroup taxa produced a single tree (Fig. 8A). The Upper Triassic and Lower Jurassic forms *Blikanasaurus* and *Antenonitrus* were resolved as the basalmost sauropods, but this analysis does not test the possibility that they are prosauropods, which remains an open question (see above, "Content"). Rather, this analysis assumes they are sauropods and examines their affinities within the group. *Gongxianosaurus*, *Isanosaurus*, *Tazoudasaurus*, and *Vulcanodon* were resolved as sequential outgroups to Eusauropoda. The basal portion of the topology was the most poorly supported (decay indices = 1), but the derived, eusauropod portion of this topology is better supported. Addition of three ichnofossils to this ingroup resulted in two equally parsimonious trees, a strict consensus of which preserves the relationships of eusauropod outgroups but provides no resolution within Eusauropoda (Fig. 8B). The Portozuolo and *Tetrasauropus* ichnotaxa were resolved as proximate outgroups to Eusauropoda, and the Lavini di Marco ichnotaxon was in an unresolved position within Eusauropoda. An Adams consensus tree offers more resolution, retaining a single polytomy at the base of Eusauropoda between *Shunosaurus*, the Lavini di Marco ichnotaxon, and a clade of more derived eusauropods (Fig. 8C).

The Adams consensus tree (Fig. 8C) was used as the best cladistic tree in the stratocladistic analysis, with the Lavini di Marco trackmaker positioned as the most primitive eusauropod. Addition of the stratigraphic character resulted in a phylogenetic tree 36 steps longer than the cladistic topology. An isomorphic phylogenetic tree two steps shorter could be created by making Prosauropoda and *Barapasaurus* ancestors, and a tree 14 steps shorter was discovered by three rearrangements of terminal taxa: (1) the Portozuolo and *Tetrasauropus* trackmakers were placed basal to *Isanosaurus*, (2) *Gongxianosaurus* was made more derived than *Isanosaurus*, and (3) the Lavini di Marco trackmaker was made more primitive than *Tazoudasaurus*. Thus, the optimal stratocladistic solution is 16 steps shorter

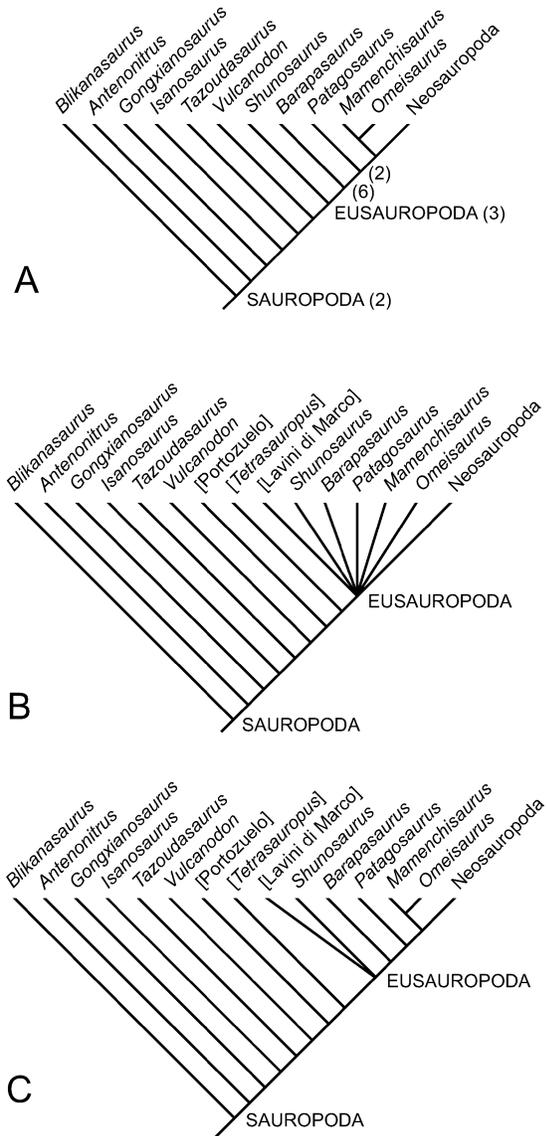


FIGURE 8. Cladistic results. A, Single most parsimonious tree produced in analysis of body fossil taxa only. Treelength equals 214 steps, Consistency Index, excluding uninformative characters = 0.81, Retention Index = 0.86; numbers in parentheses at nodes indicate decay indices greater than 1. B, Strict consensus of two trees produced in an analysis of body fossils and ichnofossils (square brackets). Several basal taxa can be resolved from Eusauropoda, whose interrelationships are uncertain. Treelength equals 218 steps, Consistency Index, excluding uninformative characters = 0.80, Retention Index = 0.86. C, Adams consensus of two most parsimonious trees in B.

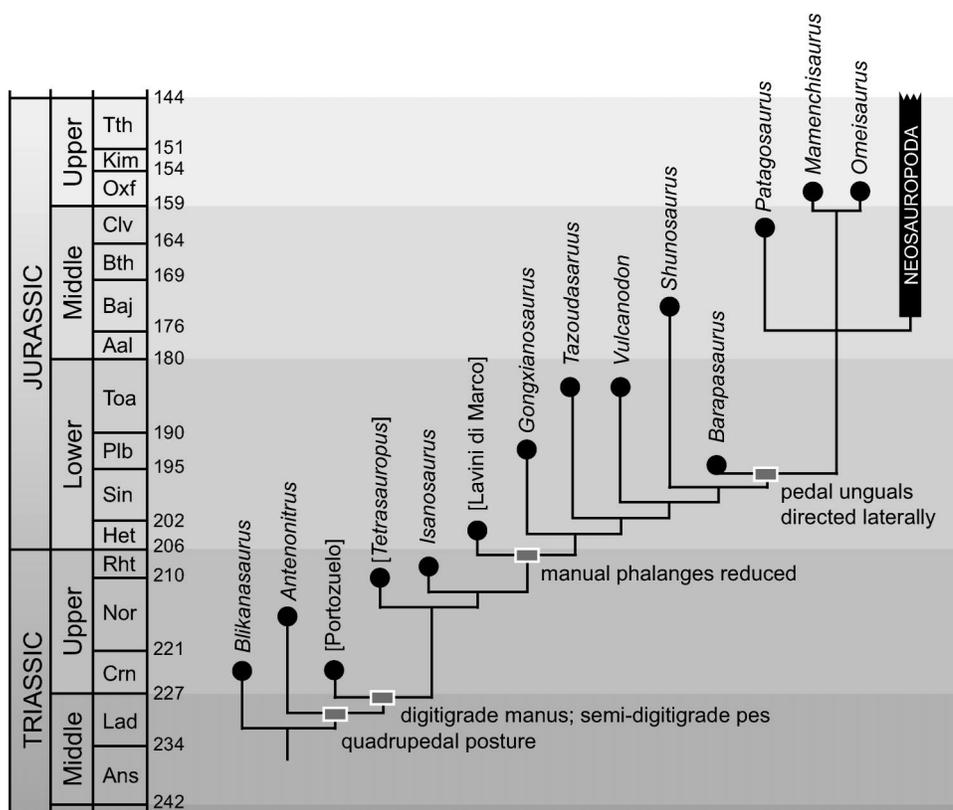


FIGURE 9. Stratocladistic results for basal sauropod body fossils and ichnofossils (square brackets) with hypothesized optimizations for locomotor characters discussed in text. This phylogenetic hypothesis implies two homoplastic characters. Semi-digitigrade pedal posture was lost in *Vulcanodon*, and laterally directed pedal claws evolved in parallel in *Tetrasauropus* and *Barapasaurus* plus more derived sauropods. Abbreviations for geological stages are from Benton 1993; timescale is based on Gradstein et al. 1999.

than the phylogenetic tree implied by the cladistic topology. Two equally parsimonious stratocladistic trees differ in the position of *Patagosaurus* relative to *Omeisaurus*, *Mamenchisaurus*, and Neosauropoda; Theropoda, the Portozuelo trackway, *Gongxianosaurus*, and *Isanosaurus* can be made ancestors without augmenting treelength. By using the "Character Trace" function in MacClade, transformations for each of the locomotory synapomorphies discussed above could be examined. The phylogenetic tree presented in Figure 9 shows the optimization of the locomotory synapomorphies discussed above, each of which is implied to originate earlier than in the cladistic result (Table 2).

Early Sauropod Foot Posture

Tetrasauropus and other early trackways not only record the presence of sauropod track-

makers in time and space, but they also record the presence of character states and have the potential to revise the hypothesized timing of their appearance in the fossil record. Morphological features in early sauropod ichnofossils suggest the early acquisition of several synapomorphies whose osteological distributions are restricted to body fossil subgroups that appeared later in time (Table 2, Fig. 9).

The Upper Triassic (Carnian) Portozuelo Formation trackways from Argentina record a sauropod-like trackmaker with a quadrupedal posture, digitigrade manus, and semi-digitigrade pes much earlier than these features appear in body fossils. If the Portozuelo trackmaker is a sauropod, as these features suggest, it implies that many hallmark sauropod locomotor features appeared at the beginning of the Upper Triassic. The early appearance of

TABLE 2. Estimated temporal origin for several sauropod synapomorphies based on body fossils and ichnofossils. Differences between these estimates are tallied at right; in all cases the origin based on ichnology precedes that based on osteology. The two entries for the “digitigrade manus” character reflect alternate interpretations of *Shunosaurus* and *Omeisaurus*. Upchurch (1998) scored them as derived and resolved digitigrady as a synapomorphy of Eusauropoda; Wilson and Sereno (1998) scored them as derived and resolved digitigrady as a synapomorphy of Neosauropoda. Because the age of *Barapasaurus* is not agreed upon, a range of ages was used. Stage name abbreviations are as in Figure 2 (based on Benton 1993); timescale based on Gradstein et al. 1999. Abbreviation: Myr, million years.

Character	Body fossil	Ichnofossil	Tally
Quadrupedal posture	<i>Antenonitrus</i> Late Triassic (Nor)	Portozuelo trackway Late Triassic (Crn)	9 Myr
Semi-digitigrade pes	<i>Barapasaurus</i> Early Jurassic (Sin-Toa)	Portozuelo trackway Late Triassic (Crn)	22–44 Myr
Reduction of manual phalanges	<i>Barapasaurus</i> Early Jurassic (Sin-Toa)	Lavini di Marco trackway Early Jurassic (Het)	2–24 Myr
Laterally directed pedal unguals	<i>Barapasaurus</i> Early Jurassic (Sin-Toa)	<i>Tetrasauropus</i> trackway Late Triassic (Nor)	13–35 Myr
Digitigrade manus (Upchurch 1998)	<i>Barapasaurus</i> Early Jurassic (Sin-Toa)	Portozuelo trackway Late Triassic (Crn)	22–44 Myr
Digitigrade manus (Wilson and Sereno 1998)	<i>Atlasaurus</i> Middle Jurassic (Bth)	Portozuelo trackway Late Triassic (Crn)	57 Myr

quadrupedal posture in the Portozuelo trackways slightly predates their appearance in the body fossil *Antenonitrus* (Table 2) but does not imply homoplasy. The early evolution of a digitigrade manus in the Portozuelo and *Tetrasauropus* trackmakers and the absence of sauropod trackways indicating a more horizontal forefoot posture is consistent with the hypothesis that *Shunosaurus* and *Omeisaurus* possessed a digitigrade manus (Upchurch 1998; Bonnan 2003). If correct, then a 22–44-Myr difference between the appearance of the feature in ichnofossils and body fossils is implied (Table 2). Likewise, the presence of a semi-digitigrade pes in the Portozuelo and *Tetrasauropus* trackmakers implies this feature evolved nearly 22–44 Myr earlier than recognized in body fossils and was reversed or misinterpreted in *Vulcanodon*. Neither the Portozuelo nor the *Tetrasauropus* trackmakers appear to have possessed reduced manual phalanges, which are interpreted to have evolved later in time, with the appearance of the Lavini di Marco trackmaker in the Hettangian. *Tetrasauropus* preserves laterally directed pedal unguals, but the absence of this feature in later-appearing but more derived forms such as *Tazoudasaurus*, *Vulcanodon*, and *Gongxianosaurus* implies that this feature was acquired in parallel with the clade including *Barapasaurus* and more derived sauropods.

Thus, by the early Late Triassic sauropods had relatively small forefeet that were held in a nearly vertical, digitigrade posture in which the five weight-bearing digits were arranged in a gentle arch. Distinctive projections from the forefoot print indicate an initial stage of phalangeal reduction in which vestigial digits are retained. In contrast, the relatively large pes was held in a nearly horizontal, semi-digitigrade pose that was supported by a large, fleshy heel. The pes retained four relatively large pedal unguals that were oriented along the digital axis. This basic eusauropod limb posture was modified in later sauropod subgroups, which developed a U-shaped manus, reduced the number of manual phalanges, and evolved laterally directed pedal unguals.

Conclusions

The deep history, broad distribution, and morphological sophistication of Late Triassic and Early Jurassic trackways suggests a richer diversity of early sauropods than currently appreciated. Whereas phylogenetic appraisals of sauropod descent recognize relatively few cladogenic events prior to the origin of Neosauropoda in the Late Jurassic, preservation of sauropod trackways and body fossils across a widespread area implies a diverse early sauropod fauna thus far absent from the body fossil record. The advanced locomotor anatomo-

my of these early sauropod trackmakers indicates that several signature locomotor features likely evolved during the 10–15-Myr interval preceding the appearance of *Tetrasauropus* and *Isanosaurus* in the fossil record. These results underscore the importance of ichnofossils to understanding vertebrate distribution and locomotor evolution.

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Appendix

Character-taxon matrix. The following are scorings for 173 characters in 15 terminal taxa and two outgroups. Square brackets surrounding terminal taxa indicate they are ichnofossils. Characters 1–172 are morphological characters scored with state 0 (primitive), states 1–4 (derived), ? (missing information), and 9 (inapplicable). All morphological characters are binary except four (characters 40, 44, 53, 63), which are unordered. (Please note that several characters have multiple states in the analysis of Wilson [2002], but only two of those states are present in the taxa analyzed here. The full list of states is given in the “Character List” below.) Character 173 is the stratigraphic character (within parentheses), with ordered states 0–9 and A–B. Taxa that traverse stratigraphic boundaries are polymorphic (&); those whose age is not well established are uncertain (/).

	10	20	30	40	50	60	70	80	90	100
<i>Theropoda</i>	000000000	000000000	900000000	000000000	0000109000	0000000009	0000900000	0000900010	1009000000	0000000000
<i>Prosauropoda</i>	000000000	000000000	900000000	000000000	0001109000	0010000009	0000900000	0000900000	0009000000	0000000000
[<i>Portozuelo</i>]	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	0?????????
<i>Blikanasaurus</i>	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Antenonitrus</i>	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
[<i>Tetrasauropus</i>]	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Isanosaurus</i>	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Tazoudasaurus</i>	?????????	?????????	9?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Vulcanodon</i>	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
[<i>Lavini di Marco</i>]	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Barapasaurus</i>	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Gongxianosaurus</i>	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Shunosaurus</i>	011011100	01?001111	0101100110	11?1111112	0003119101	002100?009	0010910000	1?01111101	011?111010	0110101111
<i>Neosauropoda</i>	111111111	111111111	111111111	11111?112	1013011001	0031111111	1024110011	1041?11111	0111111111	1011111111
<i>Patagosaurus</i>	1?1011????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Omeisaurus</i>	1110111??	11?1111111	11?1111110	1?21111111	1014011110	0031111111	0024110000	1?11100111	0110111010	00111?1111
<i>Mamenchisaurus</i>	111?11110?	?11011111	11?1111110	1111111111	0114010110	1131111101	002?211100	?11110?111	0111111?11	11????1111

	110	120	130	140	150	160	170
<i>Theropoda</i>	000000000	000000000	900000000	000000000	0010000900	0000000000	0000000001
<i>Prosauropoda</i>	000000000	000000000	900000000	000000000	0000000900	0000000000	0000000001
[<i>Portozuelo</i>]	?????????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Blikanasaurus</i>	?????????	?????????	010000000	000?0?0?0?	?????????	?????????	?????????
<i>Antenonitrus</i>	?0010??10	0??2??001	010000?01	?00?0?0?0?	????00900	0??2??0?0?	1?00001110
[<i>Tetrasauropus</i>]	????0????	?????????	?????????	?????????	?????????	?????????	????010?0?
<i>Isanosaurus</i>	?1010????	?????????	?????????	?????????	?????????	?????????	?01?000?0?
<i>Tazoudasaurus</i>	?????????	????0101???	?????????	100?1?0?0?	0??2??000?	????0001??	?????????
<i>Vulcanodon</i>	10101?00?0	00010010?1	0010010000	11001?2???	?00?0?0?0?	?????????	100000?0?
[<i>Lavini di Marco</i>]	????0????	?????????	?????????	?????????	?????????	?????????	?????????
<i>Barapasaurus</i>	1011110111	11?1?1?01	0??2??0?0?	?11?0?0?0?	0000?0000	0??2??000?0	000000???
<i>Gongxianosaurus</i>	?1110??1?	?0??0?000?	01?0000001	00000??0??	?????0?900	0??2??0?0?	010000???
<i>Shunosaurus</i>	?0111?11?	10010?111	0111011?1	111101110	0000000000	0000001000	00(8)
<i>Neosauropoda</i>	111111111	101111111	011111111	1111000000	0000000000	0111111100	0000000000
<i>Patagosaurus</i>	101111001?	?????????	011?0?0?0?	?????????	?????????	11110?0900	0000000?0
<i>Omeisaurus</i>	101?10111	?00101111	111111111	1111000000	0000110000	0000000000	0000000000
<i>Mamenchisaurus</i>	101111111?	11011111?1	01?1?11?1?	?1?000000	0000?01111	1000000?00	0000000000

Character List

The following list of characters is derived from numerous sources. Characters 1–158 are from Wilson 2002 and references therein; character 159 is from Galton and van Heerden 1998; characters 160–161 are from Yates and Kitching 2003; character 162 is from He et al. 1998; character 163 is from Buffetaut et al. 2000; characters 167–172 are from Sereno 1999; the stratigraphic character (173) is new to this analysis.

1. Posterolateral processes of premaxilla and lateral processes of maxilla, shape: without midline contact (0); with midline contact forming marked narial depression, subnarial foramen not visible laterally (1).
2. Premaxillary anterior margin, shape: without step (0); with marked step, anterior portion of skull sharply demarcated (1).
3. Maxillary border of external naris, length: short, making up much less than one-fourth narial perimeter (0); long, making up more than one-third narial perimeter (1).
4. Preantorbital fenestra: absent (0); present (1).
5. Antorbital fossa: present (0); absent (1).
6. External nares, position: terminal (0); retracted to level of orbit (1); retracted to a position between orbits (2).
7. Orbital ventral margin, anteroposterior width: broad, with subcircular orbital margin (0); reduced, with acute orbital margin (1).
8. Lacrimal, anterior process: present (0); absent (1).
9. Jugal-ectopterygoid contact: present (0); absent (1).
10. Postorbital, ventral process shape: transversely narrow (0); broader transversely than anteroposteriorly (1).
11. Frontal contribution to supratemporal fossa: present (0); absent (1).
12. Frontal, anteroposterior length: approximately twice (0) or less than (1) minimum transverse breadth.
13. Parietal occipital process, dorsoventral height: short, less than the diameter of the foramen magnum (0); deep, nearly twice the diameter of the foramen magnum (1).
14. Parietal, distance separating supratemporal fenestrae: less than (0) or twice (1) the long axis of supratemporal fenestra.
15. Supratemporal fenestra, long axis orientation: anteroposterior (0); transverse (1).
16. Supratemporal region, anteroposterior width: temporal bar longer (0) or shorter (1) anteroposteriorly than transversely.
17. Supratemporal fossa, lateral exposure: not visible laterally, obscured by temporal bar (0); visible laterally, temporal bar shifted ventrally (1).
18. Laterotemporal fenestra, anterior extension: posterior to orbit (0); ventral to orbit (1).
19. Quadratojugal, anterior process length: short, anterior process shorter than dorsal process (0); long, anterior process more than twice as long as dorsal process (1).
20. Quadrate fossa: absent (0); present (1).
21. Quadrate fossa, depth: shallow (0); deeply invaginated (1).
22. Pterygoid, transverse flange (i.e., ectopterygoid process) position: posterior of orbit (0); between orbit and antorbital fenestra (1); anterior to antorbital fenestra (2).
23. Pterygoid, palatine ramus shape: straight, at level of dorsal margin of quadrate ramus (0); stepped, raised above level of quadrate ramus (1).
24. Palatine, lateral ramus shape: plate-shaped (long maxillary contact) (0); rod-shaped (narrow maxillary contact) (1).
25. Epiterygoid: present (0); absent (1).
26. Vomer, anterior articulation: maxilla (0); premaxilla (1).
27. Basisphenoid/basipterygoid recess: present (0); absent (1).
28. Occipital region of skull, shape: anteroposteriorly deep, paroccipital processes oriented posterolaterally (0); flat, paroccipital processes oriented transversely (1).
29. Dentary, depth of anterior end of ramus: slightly less than that of dentary at midlength (0); 150% minimum depth (1).
30. External mandibular fenestra: present (0); absent (1).
31. Adductor fossa, medial wall depth: shallow (0); deep, prearticular expanded dorsoventrally (1).
32. Splenial posterodorsal process: present, approaching margin of adductor chamber (0); absent (1).
33. Coronoid, size: extending to dorsal margin of jaw (0); reduced, not extending dorsal to splenial (1); absent (2).
34. Tooth rows, shape of anterior portions: narrowly arched, anterior portion of tooth rows V-shaped (0); broadly arched, anterior portion of tooth rows U-shaped (1); rectangular, tooth-bearing portion of jaw perpendicular to jaw rami (2).
35. Tooth rows, length: extending to orbit (0); restricted anterior to orbit (1); restricted anterior to subnarial foramen (2).

36. Crown-to-crown occlusion: absent (0); present (1).
37. Tooth crowns, orientation: aligned along jaw axis, crowns do not overlap (0); aligned slightly anterolaterally, tooth crowns overlap (1).
38. Tooth crowns, cross-sectional shape at mid-crown: elliptical (0); D-shaped (1); cylindrical (2).
39. Enamel surface texture: smooth (0); wrinkled (1).
40. Marginal tooth denticles: present (0); absent on both anterior and posterior edges (2).
41. Dentary teeth, number: more than 20 (0); 17 or fewer (1).
42. Presacral bone texture: solid (0); spongy, with large, open internal cells, "camellate" (1).
43. Presacral centra, pneumatopores (pleurocoels): absent (0); present (1).
44. Cervical vertebrae, number: 9 or fewer (0); 10 (1); 12 (2); 13 (3); 15 or greater (4).
45. Cervical neural arch lamination: well developed, with well-defined laminae and coels (0); rudimentary; diapophyseal laminae only feebly developed if present (1).
46. Cervical centra, articular face morphology: amphicoelous (0); opisthocoelous (1).
47. Cervical pneumatopores (pleurocoels), shape: simple, undivided (0); complex, divided by bony septa (1).
48. Anterior cervical centra, height/width: less than 1 (0); approximately 1.25 (1).
49. Mid-cervical centra, anteroposterior length/height of posterior face: 2.5–3.0 (0); >4 (1).
50. Mid-cervical neural arches, height: less than that of posterior centrum face (0); greater than that of posterior centrum face (1).
51. Middle and posterior cervical neural arches, centroprezygapophyseal lamina (cppl), shape: single (0); bifid (1).
52. Posterior cervical and anterior dorsal neural spines, shape: single (0); bifid (1).
53. Dorsal vertebrae, number: 15 (0); 14 (1); 13 (2); 12 (3); 11 (4); 10 or fewer (5).
54. Dorsal neural spines, breadth: narrower (0) or much broader (1) transversely than anteroposteriorly.
55. Anterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1).
56. Middle and posterior dorsal neural arches, anterior centroparapophyseal lamina (acpl): absent (0); present (1).
57. Middle and posterior dorsal neural arches, prezygaparapophyseal lamina (prpl): absent (0); present (1).
58. Middle and posterior dorsal neural arches, spinodiapophyseal lamina (spdl): absent (0); present (1).
59. Middle and posterior dorsal neural arches spinopostzygapophyseal lamina (spol) shape: single (0); divided (1).
60. Middle and posterior dorsal neural arches, spinodiapophyseal lamina (spdl) and spinopostzygapophyseal lamina (spol) contact: absent (0); present (1).
61. Middle and posterior dorsal neural spines, shape: tapering or not flaring distally (0); flared distally, with pendant, triangular lateral processes (1).
62. Middle and posterior dorsal neural arches, "infradiapophyseal" pneumatopore between acdl and pcld: absent (0); present (1).
63. Sacral vertebrae, number: three or fewer (0); four (1); five (2); six (3).
64. Sacrum, sacrocostal yoke: absent (0); present (1).
65. Sacral vertebrae contributing to acetabulum: numbers 1–3 (0); numbers 2–4 (1).
66. Caudal transverse processes: persist through caudal 20 or more posteriorly (0); disappear by caudal 15 (1); disappear by caudal 10 (2).
67. First caudal centrum, articular face shape: flat (0); procoelous (1); opisthocoelous (2); biconvex (3).
68. Anterior caudal centra (excluding the first), articular face shape: amphiplatyan or platycoelous (0); procoelous (1); opisthocoelous (2).
69. Anterior caudal neural arches, prespinal lamina (prsl): absent (0); present (1).
70. Anterior caudal neural arches, postspinal lamina (posl): absent (0); present (1).
71. Anterior caudal transverse processes, proximal depth: shallow, on centrum only (0); deep, extending from centrum to neural arch (1).
72. Anterior and middle caudal centra, ventral longitudinal hollow: absent (0); present (1).
73. Cervical rib, tuberculum-capitulum angle: greater than 90° (0); less than 90°, rib ventrolateral to centrum (1).
74. "Forked" chevrons with anterior and posterior projections: absent (0); present (1).
75. "Forked" chevrons, "crus" bridging dorsal margin of haemal canal: present (0); absent (1).
76. Chevrons: persisting throughout at least 80% of tail (0); disappearing by caudal 30 (1).
77. Posture: bipedal (0); columnar, obligately quadrupedal posture (1).
78. Scapular acromion process, size: narrow (0); broad, width more than 150% minimum width of blade (1).
80. Humeral deltopectoral attachment, development: prominent (0); reduced to a low crest or ridge (1).
81. Humeral distal condyles, articular surface shape: restricted to distal portion of humerus (0); exposed on anterior portion of humeral shaft (1).

82. Humeral distal condyle, shape: divided (0); flat (1).
83. Ulnar proximal condyle, shape: subtriangular (0); triradiate, with deep radial fossa (1).
84. Ulnar proximal condylar processes, relative lengths: subequal (0); unequal, anterior arm longer (1).
85. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1).
86. Radial distal condyle, shape: round (0); subrectangular, flattened posteriorly and articulating in front of ulna (1).
87. Humerus-to-femur ratio: less than 0.60 (0); 0.60 or more (1).
88. Carpal bones, number: three or more (0); two or fewer (1).
89. Carpal bones, shape: round (0); block-shaped, with flattened proximal and distal surfaces (1).
90. Metacarpus, shape: spreading (0); bound, with subparallel shafts and articular surfaces that extend half their length (1).
91. Metacarpals, shape of proximal surface in articulation: gently curving, forming a 90° arc (0); U-shaped, subtending a 270° arc (1).
92. Metacarpal I distal condyle, transverse axis orientation: beveled approximately 20° proximodistally (0) or perpendicular (1) with respect to axis of shaft.
93. Manual digits II and III, phalangeal number: 2-3-4-3-2 or more (0); reduced, 2-2-2-2-2 or less (1); absent or unossified (2).
94. Manual phalanx I.1, shape: rectangular (0); wedge-shaped (1).
95. Manual nonungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1).
96. Pelvis, anterior breadth: narrow, ilia longer anteroposteriorly than distance separating preacetabular processes (0); broad, distance between preacetabular processes exceeds anteroposterior length of ilia (1).
97. Ilium, ischial peduncle size: large, prominent (0); low, rounded (1).
98. Iliac blade dorsal margin, shape: flat (0); semicircular (1).
99. Pubic apron, shape: flat (straight symphyysis) (0); canted anteromedially (gentle S-shaped symphyysis) (1).
100. Ischial blade, length: much shorter than (0) or equal to or longer than (1) pubic blade.
101. Ischial distal shaft, shape: triangular, depth of ischial shaft increases medially (0); blade-like, medial and lateral depths subequal (1).
102. Ischial distal shafts, cross-sectional shape: V-shaped, forming an angle of nearly 50° with each other (0); flat, nearly coplanar (1).
103. Femoral fourth trochanter, development: prominent (0); reduced to crest or ridge (1).
104. Femoral lesser trochanter: present (0); absent (1).
105. Femoral midshaft, transverse diameter: subequal to (0), 125–150%, or (1) at least 185% (2) anteroposterior diameter.
106. Femoral distal condyles, relative transverse breadth: subequal (0); tibial much broader than fibular (1).
107. Tibial proximal condyle, shape: narrow, long axis anteroposterior (0); expanded transversely, condyle subcircular (1).
108. Tibial cnemial crest, orientation: projecting anteriorly (0) or laterally (1).
109. Tibial distal posteroventral process, size: broad transversely, covering posterior fossa of astragalus (0); shortened transversely, posterior fossa of astragalus visible posteriorly (1).
110. Fibula, proximal tibial scar, development: not well marked (0); well marked and deepening anteriorly (1).
111. Fibula, lateral trochanter: absent (0); present (1).
112. Fibular distal condyle, size: subequal to shaft (0); expanded transversely, more than twice midshaft breadth (1).
113. Astragalus, shape: rectangular (0); wedge-shaped, with reduced anteromedial corner (1).
114. Astragalus, foramina at base of ascending process: present (0); absent (1).
115. Astragalus, ascending process length: limited to anterior two-thirds of astragalus (0); extending to posterior margin of astragalus (1).
116. Astragalus, posterior fossa shape: undivided (0); divided by vertical crest (1).
117. Distal tarsals 3 and 4: present (0); absent or unossified (1).
118. Metatarsus, posture: bound (0); spreading (1).
119. Metatarsal I proximal condyle, transverse axis orientation: perpendicular to (0) or angled ventromedially approximately 15° to (1) axis of shaft.
120. Metatarsal I distal condyle, transverse axis orientation: perpendicular to (0) or angled dorsomedially to (1) axis of shaft.
121. Metatarsal I distal condyle, posterolateral projection: absent (0); present (1).
122. Metatarsal I, minimum shaft width: less than (0) or greater than (1) that of metatarsals II–IV.
123. Metatarsal I and V proximal condyle, size: smaller than (0) or subequal to (1) those of metatarsals II and IV.
124. Metatarsal III length: more than 30% (0) or less than 25% (1) that of tibia.
125. Metatarsals III and IV, minimum transverse shaft diameters: subequal to (0) or less than 65% (1) that of metatarsals I or II (1).
126. Metatarsal V, length: shorter than (0) or at least 70% (1) length of metatarsal IV.

127. Pedal nonungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1).
128. Pedal digits II–IV, penultimate phalanges, development: subequal in size to more proximal phalanges (0); rudimentary or absent (1).
129. Pedal unguals, orientation: aligned with (0) or deflected lateral to (1) digit axis.
130. Pedal digit I ungual, length relative to pedal digit II ungual: subequal (0); 25% larger than that of digit II (1).
131. Pedal digit I ungual, length: shorter (0) or longer (1) than metatarsal I.
132. Pedal ungual I, shape: broader transversely than dorsoventrally (0); sickle shaped, much deeper dorsoventrally than broad transversely (1).
133. Pedal ungual II–III, shape: broader transversely than dorsoventrally (0); sickle shaped, much deeper dorsoventrally than broad transversely (1).
134. Pedal digit IV ungual, development: subequal in size to unguals of pedal digits II and III (0); rudimentary or absent (1).
135. [*Vulcanodon* autapomorphy: marked dorsoventral flattening of the unguals of pedal digits II and III.]
136. [*Shunosaurus* autapomorphy: strap-shaped pterygoid.]
137. [*Shunosaurus* autapomorphy: anterior portion of the axial neural spine prominent.]
138. [*Shunosaurus* autapomorphy: “postparapophyses” on posterior dorsal vertebrae.]
139. [*Shunosaurus* autapomorphy: terminal tail club composed of at least three enlarged, co-ossified caudal vertebrae with two dermal spines.]
140. [*Barapasaurus* autapomorphy: posterior dorsal vertebrae with slit-shaped neural canal.]
141. [*Patagosaurus* autapomorphy: cervical vertebrae with elongate centroprezygapophyseal laminae and “hooded” infra-prezygapophyseal coels.]
142. [*Patagosaurus* autapomorphy: anterior dorsal vertebrae with elongate centropostzygapophyseal and postzygodiapophyseal laminae.]
143. [*Patagosaurus* autapomorphy: transversely narrow third sacral vertebra.]
144. [*Patagosaurus* autapomorphy: proximal humerus with median ridge on posterior aspect.]
145. [*Omeisaurus* autapomorphy: maxillary ascending ramus with dorsoventrally expanded distal end.]
146. [*Omeisaurus* autapomorphy: distalmost caudal chevrons fused to anteriormost portion of ventral centrum.]
147. [*Mamenchisaurus* autapomorphy: accessory prezygodiapophyseal lamina in anterior dorsal vertebrae.]
148. [*Mamenchisaurus* autapomorphy: “forked” chevrons in mid-caudal region with anterior and posterior projections oriented less than 45° to each other.]
149. [*Mamenchisaurus* autapomorphy: ulna with anterior arm of proximal condyle nearly one-half the length of shaft.]
150. [*Mamenchisaurus* autapomorphy: femur with medially expanded tibial condyle.]
151. [*Mamenchisaurus* autapomorphy: proximal half of femoral shaft broader than distal half.]
152. [*Neosauropoda* autapomorphy: supratemporal fenestrae separated by twice longest diameter of one supratemporal fenestra.]
153. [*Neosauropoda* autapomorphy: pterygoid palatine ramus with stepped dorsal margin.]
154. [*Neosauropoda* autapomorphy: basiphenooid/basipterygoid recess.]
155. [*Neosauropoda* autapomorphy: external mandibular fenestra closed.]
156. [*Neosauropoda* autapomorphy: marginal tooth denticles absent on both anterior and posterior margins of crown.]
157. [*Neosauropoda* autapomorphy: chevrons lack “crus” bridging dorsal margin of haemal canal.]
158. [*Neosauropoda* autapomorphy: carpal bones number two or fewer.]
159. [*Blikanasaurus* autapomorphy: fibula with enlarged, ovoid, ventromedially oriented distal articular surface.]
160. [*Antenonitrus* autapomorphy: ventral ridge on hyposphenes of dorsal vertebrae.]
161. [*Antenonitrus* autapomorphy: humerus deep sulcus adjacent the laterodistal margin of the laterodistal margin of the deltopectoral crest.]
162. [*Gongxianosaurus* autapomorphy: coracoid foramen absent.]
163. [*Isanosaurus* autapomorphy: femur with sigmoid fourth trochanter.]
164. [*Lavini di Marco* autapomorphy.]
165. [*Tetrasauropus* autapomorphy.]
166. [*Portozuelo* autapomorphy.]
167. [*Prosauropoda* autapomorphy: dentary tooth 1 inset.]
168. [*Prosauropoda* autapomorphy: manual digit I-phalanx 1, axis through distal condyles rotated 60° ventrolaterally.]
169. [*Prosauropoda* autapomorphy: metatarsal II proximal articular surface hourglass-shaped.]
170. [*Theropoda* autapomorphy: intramandibular joint present.]
171. [*Theropoda* autapomorphy: cervical epiphyses prong-shaped.]
172. [*Theropoda* autapomorphy: internal cavitation of centra and long bones well developed.]
173. Stratigraphic character: Anisian (0); Carnian (1); Norian (2); Rhaetian (3); Hettangian (4); Sinemurian (5); Pliensbachian (6); Toarcian (7); Bajocian (8); Bathonian (9); Callovian (A); Oxfordian (B).