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MEMOIR 5

Early Evolution and Higher-level Phylogeny of Sauropod Dinosaurs

Jeffrey A. Wilson and Paul C. Sereno

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Cover Illustration: Skeletal silhouette of *Camarasaurus.*

Society of Vertebrate Paleontology

Memoir 5

EARLY EVOLUTION AND HIGHER-LEVEL PHYLOGENY OF SAUROPOD DINOSAURS

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EARLY EVOLUTION AND HIGHER-LEVEL PHYLOGENY
OF SAUROPOD DINOSAURS

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ABSTRACT—Although sauropods played a major role in terrestrial ecosystems during much of the Mesozoic Era, little effort has been directed toward diagnosing Sauropoda and establishing higher-level interrelationships among sauropods. As a consequence, the origin and evolution of major skeletal adaptations in sauropods has remained largely speculative.

The cladistic analysis presented here focuses on higher-level relationships among sauropods. Based on 109 characters (32 cranial, 24 axial, 53 appendicular) for 10 sauropod taxa, the most parsimonious arrangement places four genera (*Vulcanodon, Shunosaurus, Barapasaurus,* and *Omeisaurus*) as a sequence of sister-taxa to a group of advanced sauropods, defined here as Neosauropoda. Neosauropoda, in turn, is composed of the sister-clades Diplodocoidea and Macronaria; the latter is a new taxon that includes *Haplocanthosaurus, Camarasaurus,* and Titanosauriformes. Titanosauriformes includes Brachiosauridae and Somphospondyli, a new taxon uniting *Euhelopus* and Titanosauria. Among macronarians, the position of *Haplocanthosaurus* is the least stable as a result of the absence of cranial remains.

The basic structure of the phylogeny is resilient to various tests and establishes the evolutionary sequence of many functionally significant sauropod adaptations, such as the digitigrade posture of the manus in neosauropods. Other characteristic sauropod adaptations, such as narrow tooth crowns, increases in length and number of cervical vertebrae, and bifid neural spines, are shown to have evolved more than once. As these results underscore, the higher-level phylogeny of sauropods must be based on a broad sampling of character data.

The fossil record of sauropods, although relatively limited during the early phase of the radiation (Late Triassic through Early Jurassic), nonetheless indicates that all major clades were established prior to the Late Jurassic, when substantial faunal interchange among major continental regions was still possible. The functional, temporal, and biogeographic implications of the higher-level phylogeny of sauropods are explored.

RESUMEN—Los saurópodos habrían sido un componente importante de las comunidades terrestes durante gran parte del Mesosoico; se ha dirigido poco esfuerzo al estudio de la diagnosis de Sauropoda o a establecer las relaciones entre los distintos subgrupos. Por esto, el origen y la evolución de sus adaptaciones esqueletales han sido especulativos.

El análisis cladístico aquí presentado enfoca en las relaciones de alto-nivel de los saurópodos, sobre la base de 109 caracteres (32 cráneanos, 24 axiales y 53 apendiculares) de diéz grupos terminales. Se establece a los cuatro generos (*Vulcanodon, Shunosaurus, Barapasaurus* y *Omeisaurus*) como una sucesión de grupos-hermanos a un grupo de saurópodos avanzados, aquí definido como Neosauropoda. Neosauropoda es compuesto por los clados-hermanos Diplodocoidea y Macronaria; el último es un nuevo grupo que incluye *Haplocanthosaurus, Camarasaurus* y Titanosauriformes. Titanosauriformes incluye Brachiosauridae y Somphospondyli, un nuevo grupo unificando *Euhelopus* y Titanosauria. La ausencia de restos cráneanos hace menos segura la posición de *Haplocanthosaurus* entre macronarios.

La estructura de la filogenía es confirmada por varios análisis, y pone de manifesto la evolución de adaptaciones importantes, como por ejemplo la mano digitigrada en los neosauropodos. Otras adaptaciones tradicionalemente mencionadas—tales como las coronas angostas, aumentos del largo y numero de vértebras cervicales y las espinas neurales dobles en los vértebras presacras—fueron adquiridas mas de una vez. Esto subraya la importancia de una prueba con amplio muestreo de caracteres para análisis filogenéticos de saurópodos.

El registro fósil de los saurópodos, aunque relativamente limitado en los primeros tiempos de su radiación (Triásico tardío hasta Jurásico medio), indica que todos los clados mayores habrían estado establecidos antes del Jurásico tardío, cuando aún era posible el intercambio faunistico entre las mayores regiones continentales. Las implicaciones funcionales, temporales y biogeográficos de la filogenía de alto-nivel de los saurópodos son analizadas.

INTRODUCTION

In 1841 Richard Owen described the scattered remains of the first sauropod known to science as *Cetiosaurus,* or "whale lizard." Since that time, abundant sauropod remains have been discovered on every continent except Antarctica. Sauropods constitute a major proportion of the large herbivores in most continental faunas of Jurassic and Cretaceous age. Despite their rich and long fossil record, higher-level relationships among sauropods have received little attention.

We provide a phylogenetic framework for more focused work within Sauropoda by analyzing a broad range of character data across the most completely known taxa. First, we summarize historical and more recent efforts to resolve natural (monophyletic) groups among sauropods. Second, we define and diagnose the sauropod taxa that we have selected for analysis. Third, we

define and diagnose the ingroups supported by this phylogenetic analysis. Finally, we assess the reliability of these phylogenetic results and their evolutionary implications.

HISTORICAL BACKGROUND

Traditional Classification

Traditional (pre-cladistic) classifications divided sauropods into families and subfamilies (Fig. 1). When Marsh (1878) coined the suborder Sauropoda, it included only one family (Atlantosauridae) and was based principally on skeletal material of *Camarasaurus* (=*Morosaurus*; Riggs, 1901; Mook, 1914). Later Marsh (1882) erected a new family for *Camarasaurus* (Morosauridae), leaving other sauropods in Atlantosauridae (principally the diplodocids *Apatosaurus* and *Diplodocus*; Fig. 1A). Although Marsh's (1882) familial diagnoses differed only in an

A

Atlantosauridae
Morosauridae

B

Atlantosauridae
Diplodocidae
Pleurocoelidae
Morosauridae
Titanosauridae

C

Cetiosauridae
Morosauridae
Dicraeosauridae
Diplodocidae
Apatosauridae
Titanosauridae

D

Bothrosauropodidae
  Cetiosaurinae
  Brachiosaurinae
  Camarasaurinae
Homalosauropodidae
  Dicraeosaurinae
  Diplodocinae
  Apatosaurinae
  Titanosaurinae

E

Bothrosauropodidae
  Cetiosauridae
  Astrodontidae
  Brachiosauridae
  Camarasauridae
Homalosauropodidae
  Dicraeosauridae
  Diplodocidae
  Apatosauridae
  Titanosauridae

F

Brachiosauridae
  Cetiosaurinae
  Euhelopodinae
  Brachiosaurinae
  Camarasaurinae
Titanosauridae
  Dicraeosaurinae
  Diplodocinae
  Apatosaurinae
  Titanosaurinae

G

Vulcanodontidae
Cetiosauridae
Brachiosauridae
Camarasauridae
Diplodocidae
Dicraeosauridae
Titanosauridae

H

Vulcanodontidae
Cetiosauridae
  Cetiosaurinae
  Shunosaurinae
Brachiosauridae
Camarasauridae
  Camarasaurinae
  Opisthocoelicaudiinae
Diplodocidae
  Diplodocinae
  Dicraeosaurinae
  Mamenchisaurinae
Titanosauridae

FIGURE 1. Traditional higher-level classifications of Sauropoda. **A**, Marsh (1882); **B**, Marsh (1895); **C**, Huene (1927); **D**, Janensch (1929a); **E**, Huene (1956); **F**, Romer (1956); **G**, Bonaparte (1986a); **H**, McIntosh (1990a).

erroneous observation regarding the ischium, he had earlier noted major differences in vertebral structure between these two groups (Marsh, 1881).

Later, Marsh (1895, 1898) created new families (Diplodocidae, Pleurocoelidae, Titanosauridae) for *Diplodocus, Pleurocoelus,* and poorly known genera from southern continents (*Argyrosaurus, Titanosaurus*), respectively (Fig. 1B). Marsh's expanded familial classification recognized several significant features, such as the elevated position of the external nares in *Diplodocus* and the biconvex form of the first caudal centrum in *Titanosaurus.* Other features were noted and listed as better material began to accumulate (e.g., Huene, 1927; Fig. 1C). As was common in all pre-cladistic classifications, however, familial and subfamilial diagnoses functioned more as taxonomic keys than as lists of shared derived characters.

A scheme for sauropod classification recognizing two principal subgroups, one with broad nares and spatulate crowns and the other with elevated nares and narrow crowns, can be traced back to Janensch (1929a; Fig. 1D). Janensch recognized two families, Bothrosauropodidae and Homalosauropodidae, with three and four subfamilies, respectively. Huene (1956; Fig. 1E) followed this dichotomous scheme, raising the subfamilies to familial rank and the families to "family group" rank. Although the "family group" names Bothrosauropodidae and Homalosauropodidae were never adopted, a dichotomous scheme for higher-level classification of sauropods based on crown form and narial position became widely accepted (Brachiosauridae versus Titanosauridae, Romer, 1956, 1966, 1968; Camarasauridae versus Atlantosauridae, Steel, 1970; Fig. 1F).

Assessments of the higher-level relationships among sauropods were also influenced by the mistaken association between a skull of *Camarasaurus* and a skeleton of *Apatosaurus* (McIntosh and Berman, 1975). Until recently, these divergent forms were often included within the same subgroup. *Apatosaurus,*

for example, was referred to Camarasauridae rather than Diplodocidae by Lapparent and Lavocat (1955).

In summary, traditional classifications of sauropods most commonly contain a list of taxa of identical rank (usually at the family level), reflecting the absence of higher-level hierarchical information. Although some recent studies follow this format (Bonaparte, 1986a; McIntosh, 1990a, b; Fig. 1G, H), we focus attention below on analyses and character data that attempt to discriminate hierarchical relationships among the best known genera and distinctive subgroups.

Recent Studies

Recent discussions and analyses of sauropod phylogeny are briefly reviewed below in chronological order.

Gauthier (1986)—In the appendix of a paper on saurischian monophyly and theropod phylogeny, Gauthier (1986:45) listed synapomorphies for Sauropoda and several of its subgroups. He regarded *Vulcanodon* and *Barapasaurus* as the most primitive sauropods, and, following a traditional dichotomy, divided other sauropods into "camarasaurs" and "titanosaurs." Without any particular justification, he restricted Sauropoda to include only "camarasaurs" and "titanosaurs" and accorded *Euhelopus* special status as the possible sister-taxon to "titanosaurs."

Gauthier listed 27 synapomorphies uniting *Vulcanodon, Barapasaurus,* and other sauropods. Several of these (e.g., "spatulate teeth") are not preserved in *Vulcanodon* or *Barapasaurus* but are present in several other sauropods. Several other characters appear to be correlates of large body size (e.g., "texture of articular surfaces of long bones indicates retention of thick pads of cartilage" or "tibia to femur ratio less than 0.63") or are features that are not shared by all sauropods (e.g., "tibia compressed side to side," "enlarged descending flange on posterior face of distal end of tibia," and "metatarsals subequal in length"). Under the heading Ingroup Relationships, we describe several of the remaining synapomorphies on Gauthier's list and many others that characterize Sauropoda.

Gauthier (1986:45) listed synapomorphies to unite all sauropods other than *Vulcanodon* and *Barapasaurus,* many of which were listed previously by Steel (1970:59–60). Many of these synapomorphies, however, no longer characterize all remaining sauropods, given recent discovery of basal forms such as *Shunosaurus* and *Omeisaurus* (Zhang et al., 1984; Zhang, 1988; He et al., 1984, 1988). Furthermore, several of these synapomorphies were only vaguely defined, such as "massive proximal caudals" or "tibia with narrow descending flange." Several others involve complex descriptions composed of several discrete characters, such as "manus elephantine, only digit one retains the ancestral phalangeal formula and a large, clawlike ungual, with the others being reduced to single phalanges supporting hooflike unguals" or "relatively broad sacrum with enlarged sacral transverse processes that are level with top of deeply arched ilium." Under the heading Ingroup Relationships, we describe several of the remaining synapomorphies, such as retraction of the external nares.

The synapomorphies listed to support the "camarasaur" subgroup are based largely on *Camarasaurus* and *Brachiosaurus,* whereas those of the "titanosaur" subgroup rely on *Diplodocus* and *Apatosaurus* (Gauthier, 1986:45; Steel, 1970:63, 73). Several of the synapomorphies used by Gauthier to unite "camarasaurs" actually characterize a larger subset of sauropods that includes titanosaurs (sensu stricto). A "snout that is strongly demarcated" and ischial blades that are "horizontally disposed" characterize *Haplocanthosaurus, Euhelopus, Camarasaurus, Brachiosaurus,* and titanosaurs. Most of Gauthier's "titanosaur" synapomorphies, on the other hand, have a more restricted distribution. Features such as "external nares are confluent on midline and situated high on skull" and "pencil-like
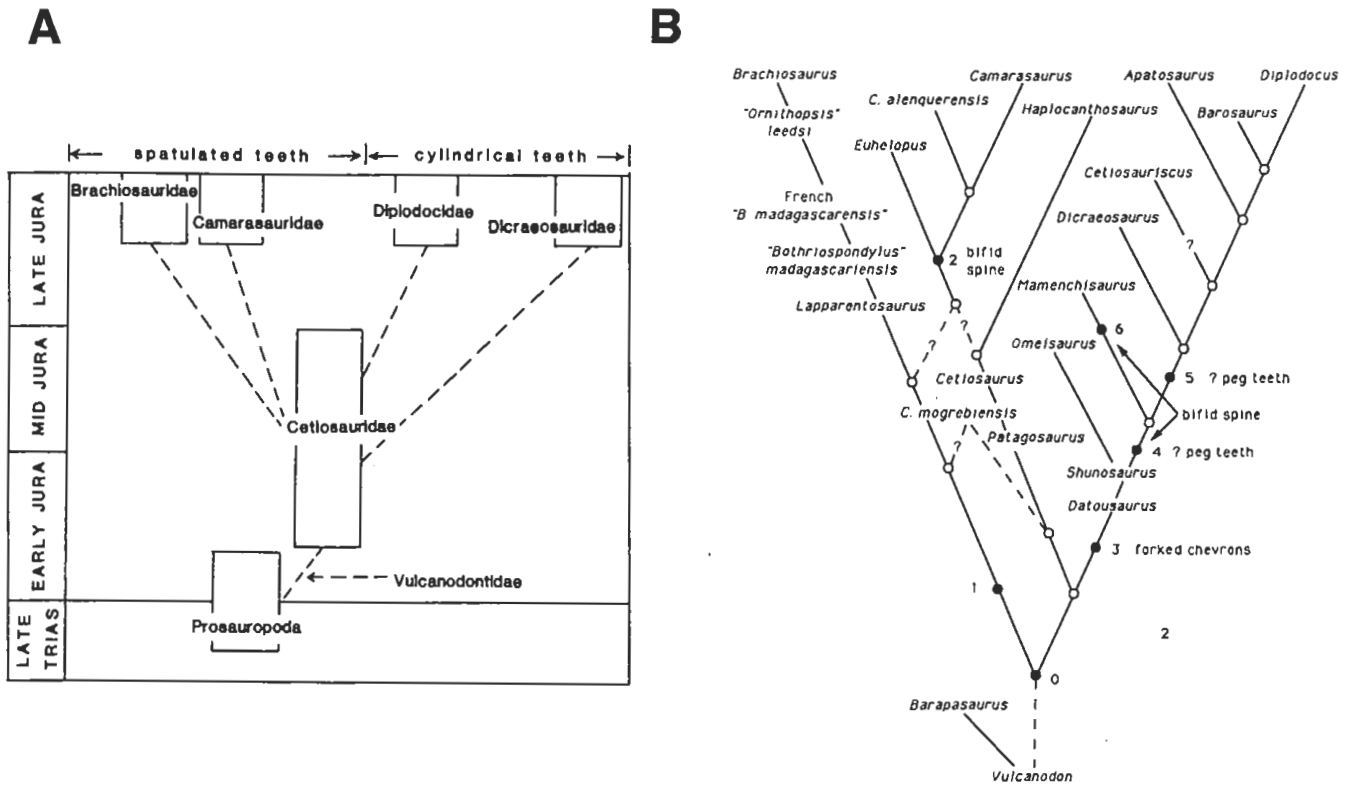
A

B

FIGURE 2. Recent phylogenetic hypotheses for Jurassic sauropods. **A**, Bonaparte (1986a:fig. 19.13); **B**, McIntosh (1990a:fig. 16.20). Numbers in **B** were used to label particular clades ("2" was accidentally displaced to the right).

teeth confined to the anteriormost part of jaws" actually characterize diplodocids rather than titanosaurs (sensu stricto). Gauthier's "titanosaurs" included "antarctosaurs" (i.e., titanosaurs sensu stricto) and diplodocids, which he assumed were similar, cranially and postcranially. There is now considerable evidence that this is not the case (Gimenez, 1992; Powell, 1992; Jacobs et al., 1993; Salgado and Coria, 1993; Wilson and Sereno, 1994; Wilson, unpubl. data).

In summary, the synapomorphies listed by Gauthier (1986) constitute a useful starting point toward establishment of a cladistic diagnosis for Sauropoda but do not resolve the higher-level relationships among sauropods.

Bonaparte (1986a)—In a comparative study of presacral vertebrae in sauropods, Bonaparte drew attention to advanced features present in most sauropods but absent in the basal forms *Vulcanodon, Barapasaurus,* and several "cetiosaurids." These features, notably the presence of invaginated pleurocoels and marked opisthocoely in presacral vertebrae, are regarded in the present analysis as synapomorphies that appeared early in sauropod phylogeny.

These characteristics formed the basis for his evolutionary diagram (Fig. 2A), which distinguished a grade of "eosauropods" (pre-Late Jurassic sauropods; Bonaparte, 1986b:40) as ancestral to a more advanced group he termed "neosauropods" (Late Jurassic sauropods; Bonaparte, 1986b:45). Curiously, Bonaparte did not include titanosaurs within his definition of neosauropods. Nonetheless, his recognition of a group of advanced sauropods distinguished from a group of early, basal sauropods on the basis of vertebral characteristics anticipates the cladistic definition of Neosauropoda presented by Upchurch (1995) and in this analysis.

McIntosh (1989, 1990a, b)—McIntosh has provided the most detailed review of sauropod genera and families. His clas-

sification, based on careful consideration of 17 variable regions in the skeleton (McIntosh, 1990b:54), recognized six families, which were listed serially (Vulcanodontidae, Cetiosauridae, Diplodocidae, Camarasauridae, Brachiosauridae, Titanosauridae; Fig. 1H). The lack of hierarchical structure among his sauropod families was purposeful, because McIntosh maintained that the traditional dichotomous classification of Sauropoda is naïve. He argued that titanosaurs have little in common with diplodocids, and have been grouped together largely on the basis of incorrect association and misidentification. McIntosh (1990a:375, 401) suggested that *Nemegtosaurus* and *Quaesitosaurus,* for example, may well represent titanosaurs that have been misidentified as diplodocids, whereas *Antarctosaurus* may represent a diplodocid misidentified as a titanosaur. He maintained that sorting out proper associations and identifications is necessary before one can obtain meaningful phylogenetic results.

Although few higher-level relationships are specified in his classification, McIntosh (1989:fig. 1; 1990a:fig. 16.20; Fig. 2B) presented phylogenetic trees that include additional phylogenetic structure. *Vulcanodon,* the earliest known sauropod, is positioned at the base of the tree as the ancestor to subsequent sauropods. Five important characters that vary among sauropods are plotted on the tree, but most branch points are not supported by character data.

Russell and Zheng (1994)—This brief analysis is the first numerical cladistic treatment of sauropod phylogeny. Russell and Zheng scored 21 characters in eight sauropod genera, using *Plateosaurus* as an outgroup. Titanosaurs were not included. They reported three minimum-length trees of 41 steps with a consistency index of 0.59 (Russell and Zheng, 1994:2094). Their results, however, were presented as a fully-resolved cladogram (Fig. 3A), which represents only one of the minimum-length trees.
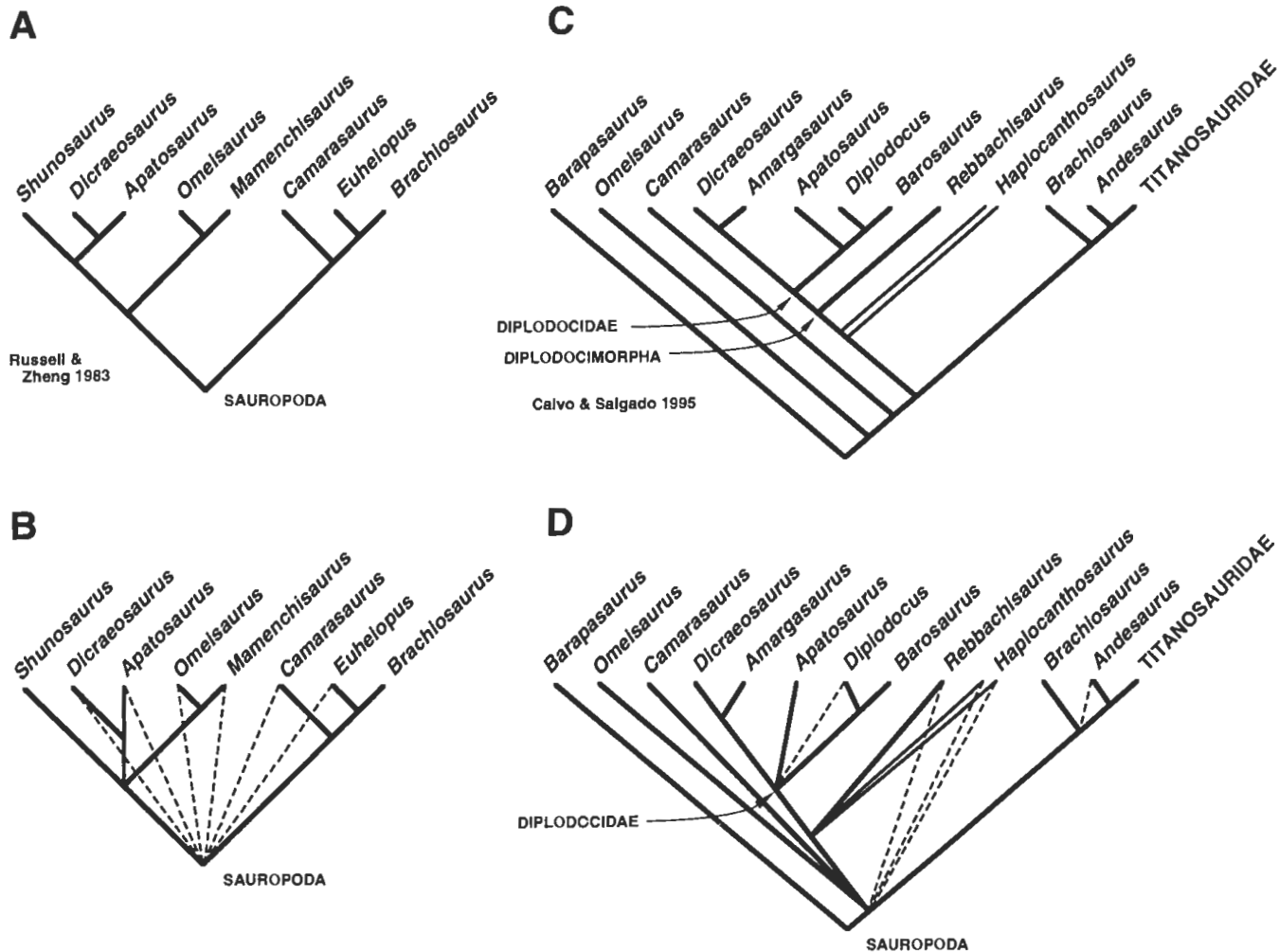
FIGURE 3. Recent cladistic hypotheses for sauropod phylogeny. **A**, fully resolved tree presented by Russell and Zheng (1994); **B**, strict consensus of 3 minimum-length trees based on the data matrix in Russell and Zheng (1994), with dashed lines showing loss of resolution for trees two steps longer than the minimum; **C**, fully resolved tree presented by Calvo and Salgado (1995); **D**, strict consensus of 5 minimum-length trees based on the data matrix in Calvo and Salgado (1995), with dashed lines showing loss of resolution for trees two steps longer than the minimum.

Reexamination of their data, however, revealed little hierarchical structure, and thus we have little reason to trust their preferred tree. Two of the characters (1, 7) are autapomorphies for *Apatosaurus* and, therefore, are uninformative with regard to ingroup relationships. There are 19 informative characters in eight taxa that yield three minimum-length trees (39 steps) with a consistency index of 0.56. When allowing just one additional step (40 steps), there are 29 trees that yield a strict-consensus tree that retains only one node in their preferred tree—*Dicraeosaurus* plus *Apatosaurus* (Fig. 3B). No phylogenetic structure remains when trees two steps longer than the minimum (41 steps) are considered. A more concerted search and analysis of character data is necessary to resolve higher-level relationships within Sauropoda.

Upchurch (1995)—Upchurch has presented the most detailed consideration of sauropod interrelationships to date, based on cladistic analysis of 174 characters in 27 sauropodomorph taxa (6 prosauropods, 21 sauropods; Fig. 4a). Unfortunately, his evaluation of previous hypotheses of sauropod interrelationships is marred by misrepresentation and over-interpretation. He represented Gauthier's (1986) phylogenetic comments and McIntosh's (1989, 1990a) trees as fully-resolved cladograms when such specificity is not apparent in the original

text or figures. Gauthier (1986:45), for example, did not mention synapomorphies that resolved the positions of *Vulcanodon* and *Barapasaurus* as shown by Upchurch (1995:fig. 2). Similarly, McIntosh's trees show several sauropods as ancestors with others connected by dashed or multiple (alternative) branches, yet these relationships were shown as fully resolved (Upchurch, 1995:figs. 3, 4) rather than as polytomies on a cladogram. Finally, although Upchurch (1995:fig. 7) presented a cladogram that is consistent with the phylogenetic hypothesis of Wilson and Sereno (1994), he ignored fundamental differences in phylogenetic arrangement, stating (Upchurch, 1995:368): "On reviewing all of these cladograms and phylogenies, it is possible to pick out certain points in common. Most of the recent work has concluded that *Barapasaurus* and *Vulcanodon* are successively more distant outgroups to the rest of Sauropoda; brachiosaurids and camarasaurids are sister groups; titanosaurids and diplodocids are sister groups; and the Cetiosauridae represents a primitive sauropod stock that gave rise to most of the Upper Jurassic and Cretaceous forms." Nevertheless, Wilson and Sereno (1994) and other authors (e.g., Salgado, 1993) have proposed an alternative arrangement for the major clades of sauropods as discussed in more detail below.

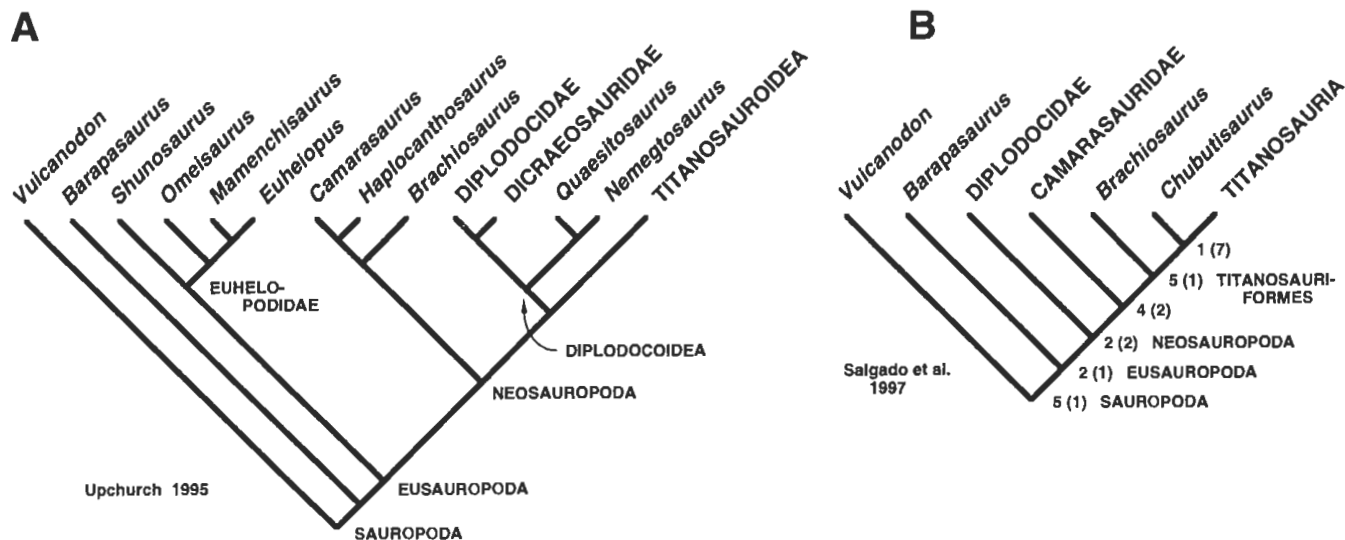Evaluation of Upchurch's phylogeny is important because it

FIGURE 4. Additional cladistic hypotheses for sauropod phylogeny. **A**, fully resolved tree given by Upchurch (1995) with some genera in the original cladogram subsumed into appropriate suprageneric taxa; **B**, strict consensus tree given by Salgado, Coria, and Calvo (1997) with titanosaurian genera subsumed within Titanosauria. In **B**, the number of unambiguous synapomorphies supporting each node is indicated (with the number of ambiguous synapomorphies shown in parentheses).

constitutes the most substantial cladistic work to date on sauropod phylogeny and because it apparently corroborates several aspects of traditional dichotomous classifications (Fig. 1D–F). Upchurch, however, did not provide the minimal information necessary for such an evaluation. Although based on a quantitative analysis of character data, his published study does not include a data matrix or any other information about the data (e.g., consistency indices, weighting schemes, number of multistate characters) or about the resulting trees (e.g., treelengths, number of trees obtained, topological differences). Nor was there any quantitative assessment of phylogenetic robustness (e.g., nodes retained in slightly longer trees) or comparison of results under competing topologies. Based on available information, it is impossible to evaluate rigorously Upchurch's (1995:fig. 8) nearly fully-resolved cladogram, which was based on an "unequally weighted heuristic analysis."

Nonetheless, several observations cast serious doubt on the quality of the character data and reliability of the results. Upchurch stated that his analysis was based on 174 characters in 27 sauropodomorphs yet listed only 118 characters in the text at nodes on the cladogram (Upchurch, 1995:368–369, fig. 8). Therefore, one-third of the data is not included in the text, and one must presume that these characters either reside at nodes within Prosauropoda, characterize terminal taxa, or simply were not reported. Of the 118 characters listed in the text at particular nodes, 52 diagnose well-established families or superfamilies and are not involved in determining higher-level relationships (Brachiosauridae, 7; Camarasauridae, 3; Diplodocidae, 14; Dicraeosauridae, 5; Titanosauridae, 7; Nemegtosauridae, 3; Diplodocidae plus Dicraeosauridae, 13). Thus only 66 (38%) of the 174 characters reportedly involved in this analysis appear at higher-level nodes on the cladogram.

Upchurch's cladogram exhibits only one polytomy—a trichotomy at the base of Neosauropoda—despite the inclusion of 21 sauropod genera as terminal taxa, many of which are based on very incomplete material (Fig. 4). To obtain such a result, one must presume an extraordinarily high consistency for the data, although no comment was made to this effect. Two conditions must hold to obtain such a fully-resolved result: (1) data are available to resolve all relationships, and (2) competing,

equally parsimonious topologies do not exist. Upchurch's preferred cladogram is unusually, indeed unreasonably, well-resolved given the amount of missing data and homoplasy that obtain in any realistic large-scale analysis of sauropod relationships.

Upchurch based character polarity on two outgroups, Theropoda and Ornithischia. Character polarity established by real outgroups rarely yields an ancestral condition that is uniformly plesiomorphic because of missing data, character transformation, and homoplasy among the outgroups. According to Upchurch (1995:fig. 8), however, these two outgroups yielded the plesiomorphic condition for all 174 characters in the analysis. If this were the case, two conditions must hold for all 174 characters: (1) at least one of the outgroups (Theropoda or Ornithischia) must be available for scoring (i.e., preserve a recognizable character-state), and (2) neither outgroup can be scored as apomorphic. If either condition is not met, the outgroup condition is ambiguous.

The outgroup condition, following this reasoning, cannot be plesiomorphic for several of Upchurch's synapomorphies. The outgroup condition for the synapomorphy "[n]umber of coossified sacral vertebrae increases from four to five" (Upchurch, 1995:375), for example, must be ambiguous because basal ornithischians have at least five sacral vertebrae. Likewise, the outgroup condition for the synapomorphy "[e]ach infraprezygapophyseal lamina, on the middle and posterior cervicals, bifurcates toward its dorsal end" (Upchurch, 1995:381) must also be ambiguous, because ornithischians do not possess an infraprezygapophyseal lamina.

Many synapomorphies listed by Upchurch are dimensional comparisons, such as "[s]hortened skull roof" (Upchurch, 1995:372). This kind of synapomorphy is difficult to evaluate when expressed without a comparative metric and in the absence of a list of characters and character states. The primitive condition, number of states, and scored condition for particular ingroups were not reported.

In the absence of a data matrix, we focus further comment on six synapomorphies listed by Upchurch (1995:378) to support a diplodocoid-titanosaur clade (Fig. 4)—a traditional grouping that our analysis specifically does not support.

(1) "Lingual surfaces of tooth crowns are convex mesiodistally." Known diplodocids have cylindrical crowns that exhibit the derived condition. Of the titanosaurs in Upchurch's analysis, in contrast, only *Malawisaurus* has associated teeth and can be scored. The lingual surface of its tooth crowns are nearly flat, rather than convex, and the cross-section at mid-crown level is D-shaped (Jacobs, Winkler, Downs, and Gomani, 1993:figs. 1D, 2A; pers. obs.). Although some titanosaurs have cylindrical crowns, other titanosaurs resemble *Malawisaurus* (e.g., *Ampelosaurus*; Le Loeuff, 1995:fig. 2).

(2) "Teeth relatively long and slender." This synapomorphy is difficult to evaluate without a more precise relative measure. We assume that Upchurch is referring to subcylindrical crowns that characterize diplodocoids and a subgroup of titanosaurs. Basal titanosaurs, however, have broader, weakly spatulate tooth crowns with proportions similar to those in brachiosaurids. Slender crown proportions will not support a diplodocoid-titanosaur clade without significant homoplasy.

(3) "Teeth taper at midlength or near to the crown tip." As defined by Upchurch, this condition is present in a much broader suite of sauropods including *Omeisaurus* (He, Li, and Cai, 1988:fig. 16a–f), *Brachiosaurus* (Janensch, 1935–1936:pl. 11, figs. 1, 4, 8, 9), and *Mamenchisaurus* (Russell and Zheng, 1994: pl. 2) and appears to characterize all sauropods more advanced than *Shunosaurus*.

(4) "Dorsal neural spines have a postspinal lamina." This feature is more broadly distributed than suggested by Upchurch. A postspinal lamina is present in most neosauropods including *Haplocanthosaurus* (Hatcher, 1903:pl. 1, fig. 3) and *Brachiosaurus* (Janensch, 1950:figs. 61, 64, 66).

(5) "Anterior caudal centra are at least mildly procoelous." This feature is difficult to defend as a diplodocoid-titanosaur synapomorphy, because of variation within each subgroup. *Opisthocoelicaudia*, for example, has opisthocoelous, rather than procoelous, anterior caudal vertebrae, as its name suggests. Because Upchurch positioned this genus as the sister-group to other titanosaurs, procoelous anterior caudal vertebrae should have an ambiguous distribution on his cladogram. If delayed character-state optimization was implemented as claimed (Upchurch, 1995:369), this feature should not have been listed as evidence supporting a diplodocoid-titanosaur clade. Other coding problems are manifest. When considering vertebral form, for example, care must be taken when coding is based on descriptive terms such as "amphicoelous" and "procoelous." Several sauropods have amphicoelous anterior caudal vertebrae with concave anterior and posterior central articular surfaces (e.g., *Brachiosaurus*, Riggs, 1904; *Haplocanthosaurus*, Hatcher, 1903). The derived "procoelous" condition, in which the anterior face is concave and the posterior face convex, must be scored specifically on the convexity of the posterior centrum face and not solely on the concavity of the anterior face.

(6) "Loss of calcaneum." Although ossified calcanea have not been reported in diplodocoids, the condition in titanosaurs remains uncertain. Among titanosaurs, only *Opisthocoelicaudia* has well-preserved hindlimbs and apparently lacks ossified calcanea. Huene (1929:pl. 17, fig. 2), however, described an ossified calcaneum in the South American titanosaur *Neuquensaurus* ("*Titanosaurus*") *australis*.

In summary, although Upchurch pointed out several synapomorphies of basal sauropod clades, his cladistic support for the traditional association of diplodocoids and titanosaurs is weak and based mainly on ambiguous dental characters and poorly substantiated postcranial features.

Calvo and Salgado (1995)—Calvo and Salgado presented a phylogenetic analysis of major sauropod genera and subgroups based on 49 characters in 12 taxa (Calvo and Salgado, 1995: fig. 18; Fig. 3C). Using *Omeisaurus, Barapasaurus,* and Prosauropoda as outgroups, they presented their results as a single, fully-resolved, minimum-length tree of 85 steps, with a consistency index of 0.655 (Calvo and Salgado, 1995:29). To obtain a single tree with the distribution of synapomorphies shown by Calvo and Salgado, it is necessary to order character 32, which describes the shape of the transverse processes of the anterior caudal vertebrae. These processes are "wing-shaped" in other diplodocoids but are developed as two struts in *Rayososaurus* (=*Rebbachisaurus*) *tessonei* (see comments on Diplodocoidea in the Ingroup Taxa section for discussion of *Rayososaurus*). Calvo and Salgado argued that the condition in *Rayososaurus* was derived from an antecedent wing-shaped condition because they assert that wing-shaped processes are present in the closely related African form *Rebbachisaurus garasbae* (Calvo and Salgado, 1995:22). Although Lavocat (1954) commented on the structure of the anterior caudal vertebrae in his description of the holotypic material of *Rebbachisaurus garasbae,* "[t]he first caudals, recognizable with large, aliform expansions of the apopophyseal laminae, have not been able to be removed from their plaster jackets" (Lavocat, 1954:68; translated from the original French text), these vertebrae can no longer be located to confirm this assessment. Regardless of the condition in *Rebbachisaurus,* however, there no basis to assume the condition in *Rayososaurus* is a modification of the "wing-shaped" condition present in diplodocoids.

Leaving this character unordered, their matrix yields five minimum-length trees (85 steps), one of which corresponds to their preferred tree. Strict or semistrict consensus of these minimum-length trees collapses 5 of 11 ingroup nodes on their preferred tree, including the node "Diplodocimorpha" (Fig. 3D). In two of the five minimum-length trees, ingroup taxa form a monophyletic clade with outgroups as shown by Calvo and Salgado (1995:fig. 18). A strict or semistrict consensus tree for these two minimum-length trees still results in collapse of two nodes among ingroup taxa.

Resolution decreases with only modest increase in treelength. When considering trees just one step longer (86 steps), there are 26 trees that yield a strict or semistrict-consensus tree with only four ingroup nodes. When accepting treelengths up to two steps longer than the minimum, there are 125 trees with only three ingroup nodes in common (Fig. 3D).

The two most stable nodes in their analysis identify higher-level groups that overlap with our results. The first involves Diplodocimorpha, a clade uniting dicraeosaurids, diplodocids, and close relatives. We use the available name Diplodocoidea for this clade (Upchurch, 1995), which has been used elsewhere in this manner (Wilson and Smith, 1996), and which includes two subgroups normally accorded familial rank (Dicraeosauridae and Diplodocidae; both were placed as subfamilies within Diplodocidae by Calvo and Salgado [1995]). Calvo and Salgado (1995) described 11 supporting "diplodociform" synapomorphies, five of which correspond with features listed below in our diagnosis of Diplodocoidea (2, pencil-shaped teeth; 24, posterior dorsal vertebrae with tall neural aches; 33, anterior caudal vertebrae with tall neural aches; 36, whiplash tail; 48, humerus less than 70 percent femoral length). We regard their characters 24 and 33 as a single feature (heightened neural arches in middorsal to mid-caudal vertebrae) and note that they have mislabeled (reversed) the character states for character 48.

The remaining six diplodocoid (i.e., "diplodocimorph") synapomorphies are present in dicraeosaurids and diplodocids but are problematic in *Rayososaurus*. Two appear to be artifacts of postmortem dorsoventral crushing of the holotypic skull of *Rayososaurus tessonei* (MUCPv-205; see Terminal Taxa for choice of generic and specific designation). The slit-shaped laterotemporal fenestra and anterior extension of the quadratojugal (characters 9, 11) appear to have been created or enhanced in this manner. The marked anterior orientation of the basipterygoid processes and strong anteroventral angle of the quadrate shaft

(characters 5, 6) are poorly substantiated; the former appears to be an artifact of the orientation of the braincase (with the supraoccipital wedge held vertically rather than sloping posteroventrally; Calvo and Salgado, 1995:figs. 3, 4), and the latter is speculative because the bone was not found in articulation and does not closely resemble the diplodocoid condition. A retracted position for the external nares above the orbits (character 7) is likewise poorly substantiated; the left nasal bone, which was reported to preserve a portion of the narial margin, does not meet its opposite in the midline as in *Diplodocus* and must be incomplete if properly identified as the nasal. The location of the external nares cannot be reliably determined. Finally, the transverse processes of the anteriormost caudals are not "wing-shaped" (character 32) as in diplodocoids (McIntosh, 1990a: fig. 16.7), nor is there justification to presume that they passed through a "wing-shaped" stage. If the redundant character 33 is deleted and the six problematic characters mentioned above are rescored as unknown in *Rayososaurus*, *Rayososaurus* groups with one or both species of *Haplocanthosaurus*. Thus support for diplodocoid monophyly (*Rayososaurus* plus other diplodocoids) is poorly established by the character evidence provided by Calvo and Salgado (1995).

The second clade that also appears in our analysis unites brachiosaurids (or *Brachiosaurus*) and titanosaurs (or "Titanosauridae"). Calvo and Salgado (1995:fig. 18) listed six synapomorphies uniting titanosaurids and *Brachiosaurus* (14, ascending maxillary process posterior to center; 35, neural arch anteriorly displaced on mid to posterior caudal vertebrae; 40, iliac preacetabular process expanded dorsally; 47, femoral shaft bulge; 49, metacarpus more than 45 percent radial length), omitting two others that also appear under delayed character-state optimization of their data (2, "cone and pencil chisel-like" crowns; 26, mid-prespinal lamina present on dorsal portion of spine). Two of these also appear as synapomorphies in our analysis (characters 40, 47).

In our opinion, the other titanosauriform synapomorphies are problematic. Brachiosaurids and titanosaurs do not share a common derived crown shape (character 2); the former characterized by moderately broad, spatulate crowns and the latter varying between somewhat narrower, spatulate crowns and subcylindrical crowns. In titanosaurs, the position of the ascending process of the maxilla relative to the remainder of the bone (character 14) is poorly known and difficult to evaluate; in diplodocids such as *Diplodocus,* the ascending ramus is centrally situated and cannot reasonably be scored as anteriorly displaced (Calvo and Salgado, 1995). The mid-prespinal lamina (character 26) is more variable than suggested. Although brachiosaurids and titanosaurs share a deep puboischial contact (character 41) and high metacarpal/radial length ratio (45% or more; character 49), both features are also present in *Camarasaurus,* and these synapomorphies support a more inclusive node. For example, the metacarpal/radius ratio for *Camarasaurus* (44–47%; Gilmore, 1925; McIntosh, Miller, Stadtman, and Gillette, 1996) is as high as in the titanosaur *Opisthocoelicaudia* (46%; Borsuk-Bialynicka, 1977) and significantly higher than in other sauropods, which average approximately 30%. With characters 2, 14, and 26 deleted, the union between brachiosaurids and titanosaurs remains stable in all trees, including those two steps longer than the minimum. Relationships outside this clade, however, are very poorly resolved.

In summary, the cladistic analysis of Calvo and Salgado (1995) supports the uncontroversial union of dicraeosaurids and diplodocids (Diplodocoidea) and provides the first cladistic evidence supporting a clade uniting brachiosaurids and titanosaurs. The association of other genera with diplodocoids (e.g., *Haplocanthosaurus* and *Rayososaurus*), the general relationships among neosauropods, and the position of *Omeisaurus* outside Neosauropoda are not resolved decisively. The monophyly

of titanosaurs and brachiosaurids, in contrast, is robust even with deletion of problematic characters 2, 14, and 26, as discussed above.

Salgado, Coria, and Calvo, 1997—In a phylogenetic study of titanosaurid relationships, Salgado, Coria, and Calvo (1997) analyzed 35 postcranial characters in 10 titanosaurids, six basal sauropod taxa (*Vulcanodon, Barapasaurus,* Diplodocidae, Camarasauridae, *Brachiosaurus, Chubutisaurus*), and two outgroups (Prosauropoda and Theropoda). Two most parsimonious trees (length: 54 steps, C.I.: 0.815) were generated (Fig. 4b).

Only 14 unambiguous synapomorphies support the arrangement of the eight nodes within Titanosauria, and many of the clades are supported only by a single character. A strict consensus of 33 trees generated allowing one extra step (54 steps) yields a polytomy involving all titanosaurian taxa.

The topological arrangement of the basalmost six nodes (i.e., those which are more inclusive than Titanosauria) is supported by nearly twice as much character evidence (19 synapomorphies for six nodes) than are the nodes within Titanosauria. The integrity of these basal nodes, however, was not evaluated, nor was there discussion of alternative hypotheses. Moreover, the resultant hierarchy is essentially identical to that of Wilson and Sereno (1994), and is similar to the basal arrangement presented by Upchurch (1995), although there is no discussion of these or other preceding studies (e.g., Gauthier, 1986; Bonaparte, 1986a; McIntosh, 1990a).

The monophyly of Sauropoda is supported by five unambiguous synapomorphies, three of which are included in our own diagnosis of Sauropoda (2, four or more sacral vertebrae; 3, ilium with pubic peduncle much longer than ischial articulation; 4, femur straight in lateral view). Upchurch (1995) also listed characters 2 and 4 in his diagnosis of Sauropoda. Character 1 (opisthocoelous cervical and anterior dorsal centra) cannot be substantiated in the most primitive sauropod, *Vulcanodon,* and is here regarded as an ambiguous synapomorphy of *Shunosaurus* and all more derived sauropods. Upchurch (1995) placed this synapomorphy at the same level of inclusiveness, characterizing *Barapasaurus, Shunosaurus,* and all more derived sauropods. Character 5 (metatarsals shorter than metacarpals) cannot be scored as derived in *Vulcanodon,* which has metapodials of roughly equal length (Raath, 1972:tabs. 6,7).

Salgado, Coria, and Calvo (1997) defined the clade that includes *Barapasaurus* and Neosauropoda as "Eusauropoda" and regarded it as a new taxon. Eusauropoda, however, was first coined by Upchurch (1995) for a slightly more exclusive group that included *Shunosaurus* (and other "euhelopodids") plus Neosauropoda (*Shunosaurus* was not scored in the analysis of Salgado et al. [1997]). Neither Upchurch's original definition of Eusauropoda nor the character evidence presented by him to defend its monophyly were discussed by Salgado, Coria, and Calvo (1997). Furthermore, the phylogenetic definition of Eusauropoda by Salgado, Coria, and Calvo (1997) differs from the original one by Upchurch (1995). Salgado, Coria, and Calvo (1997:7) defined Eusauropoda as a node-based taxon, "the clade including the most recent common ancestor of *Barapasaurus tagorei* and Neosauropoda and of its descendants," whereas Upchurch's (1995:372) original definition was a stem-based, "all sauropods, except for vulcanodontids, formed a monophyletic assemblage . . . 'Eusauropoda.'" In this analysis, we follow the original stem-based definition of Eusauropoda presented by Upchurch (see further discussion under Ingroup Relationships).

The character evidence presented by Salgado, Coria, and Calvo (1997) in defense of eusauropod monophyly is sparse. Eusauropoda is not preserved in a strict consensus of the 250 trees that are two steps longer than the most parsimonious tree. Only two characters (6, anterior trochanter of femur absent; 7, anteroposterior diameter of distal tibia subequal/greater than width)

are listed in the diagnosis of Eusauropoda. Character 7 is problematic because the primitive condition (distal tibia more expanded transversely than anteroposteriorly) is present in all sauropods except some titanosaurs. As Salgado, Coria, and Calvo (1997) noted, the transversely expanded distal portion of the tibia is related to the shape of the astragalus. As in basal saurischians, the astragalus of all sauropods except some titanosaurs is more broadly expanded transversely than anteroposteriorly.

The two neosauropod synapomorphies presented by Salgado, Coria, and Calvo (2:2, five or more sacral vertebrae; 8, pleurocoels on presacral vertebrae) were included among the 14 characters listed by Upchurch (1995) in his diagnosis of the same clade. We regard character 2 as a neosauropod synapomorphy, but scoring of a broader sample of basal sauropod taxa suggests that character 8 is present in a slightly more inclusive group (*Omeisaurus* + Neosauropoda).

Three of the four synapomorphies listed by Salgado, Coria, and Calvo (1997) as uniting *Camarasaurus, Brachiosaurus,* and titanosaurs (9, opisthocoelous trunk and sacral centra; 12, relatively long metacarpals; 13, dorsoventrally expanded pubic articulation of ischium) have been included in our diagnosis of the group. Upchurch (1995) listed character 12 as a synapomorphy of camarasaurids and brachiosaurids (to the exclusion of titanosaurs). Character 11 (open haemal canal on anterior caudal vertebrae) also characterizes *Haplocanthosaurus,* which was not included as a terminal taxon in the analysis of Salgado, Coria, and Calvo (1997).

Salgado, Coria, and Calvo (1997) provided strong support for the monophyly of Titanosauriformes, the newly proposed clade that unites *Brachiosaurus* and Titanosauria. Titanosauriform synapomorphies include several characters also used in this analysis (16, claw on manual digit I reduced or absent; 17, broadly expanded and upwardly directed preacetabular lobe of ilium; 19, presence of lateral bulge below greater trochanter). Character 15 (caudal neural arches shifted anteriorly) appears to be enhanced by presence of a prominent posterior convexity on anterior and middle caudal vertebrae. We regard character 18 (pubic peduncle perpendicular to sacral axis) as a correlate of character 17.

The major contribution of Salgado, Coria, and Calvo (1997) is the proposal of and support for Titanosauriformes, a new clade that includes *Brachiosaurus* and Titanosauria. This novel arrangement implies polyphyly of forms with narrow tooth crowns, although it was not evaluated in light of traditional broad-vs.-narrow-crowned arrangement. Titanosauriform synapomorphies and others are discussed in the section Ingroup Relationships. In contrast, the scheme of titanosaur interrelationships proposed by Salgado, Coria, and Calvo (1997) is not strongly supported by the evidence presented. Their hierarchy of basal sauropod genera, though not defended by substantial character evidence, is nevertheless stable, and is in general agreement with the analysis by Wilson and Sereno (1994), aspects of the analysis by Upchurch (1995), and the analysis presented here.

OUTGROUP RELATIONSHIPS

We assume an arrangement at the base of Dinosauria in which Ornithischia and Saurischia are monophyletic (Gauthier, 1986), Saurischia is composed of Theropoda and Sauropodomorpha, and Sauropodomorpha is composed of Sauropoda and Prosauropoda (Gauthier, 1986; Sereno, Forster, Rogers, and Monetta, 1993; Sereno, unpubl. data). Saurischian synapomorphies include, among others, a subnarial foramen between the premaxilla and maxilla, hyposphene-hypantrum articulations between dorsal vertebrae, and broad, mutual overlap of the proximal shafts of metatarsals II–IV (Gauthier, 1986; Sereno, Forster, Rogers, and Monetta, 1993). Sauropodomorph syna-

pomorphies include enlarged external nares, a paddle-shaped metatarsal V, and an enlarged ungual on pedal digit I (Sereno, unpubl.).

Prosauropods have been viewed as a paraphyletic assemblage in which some genera more closely related to sauropods than others (Colbert, 1964; Charig et al., 1965; Gauthier, 1986; Romer, 1956; Bonaparte, 1986a, b; McIntosh, 1990a, b; Benton, 1990). A suite of synapomorphies, however, has been identified that supports prosauropod monophyly, such as an unusual carpal-metacarpal articulation that involves inset of the base of metacarpal I into the carpus, and marked torsion in the shaft of the first phalanx of manual digit I (rotating the ungual medially) (Sereno, 1989, unpubl. data; Galton, 1990; Gauffre, 1995).

The traditional paraphyletic arrangement of prosauropods as a sequence of sister-taxa to Sauropoda ensures that the condition in prosauropods, which is remarkably uniform, is plesiomorphic in an analysis of sauropod interrelationships. But if Prosauropoda constitutes a monophyletic sister-taxon to Sauropoda, as assumed in this analysis, then character polarity must also be assessed in Theropoda, the second outgroup to Sauropoda.

TERMINAL TAXA

Ten sauropod taxa were selected for analysis on the basis of completeness and as a representative sample of sauropod morphology. Silhouette reconstructions of several of these genera are presented in Foldout 1 at the end of this paper. Establishing the relationships among these taxa will provide a phylogenetic framework for subsequent studies within more speciose subgroups, such as Diplodocoidea and Titanosauria. Below, we define each terminal taxon, give its presumed stratigraphic age or temporal range, and list supporting autapomorphies. The description of autapomorphies (and of synapomorphies in the section Ingroup Relationships) is accompanied by a set of anatomically arranged illustrations (Figs. 5–43) chosen as representative of the sauropod skeleton. Foldout 2 at the end of this paper provides a key to the anatomical and institutional abbreviations used here. Node- and stem-based phylogenetic definitions (de Quieroz and Gauthier, 1990, 1992) are employed to enhance taxonomic stability (see Taxonomic Definitions).

Vulcanodon karibaensis Raath, 1972

Hypodigm—Based on a partial postcranial skeleton consisting of a partial cervical, two sacral, and 12 caudal vertebrae, portions of both forelimbs lacking the carpus and manus, and a nearly complete pelvis and left hindlimb (NMZ QG 24). Referred material includes a right scapula (NMZ QG 152; Cooper, 1984:fig. 3).

Recorded Temporal Range—Early Jurassic (?Hettangian) (Raath, 1972).

Autapomorphies—Marked dorsoventral flattening of the unguals of pedal digits II and III, which have proximal dimensions that are significantly broader than deep.

Comments—*Vulcanodon,* the oldest known sauropod, was originally interpreted as a prosauropod by Raath (1972). Cruickshank (1975) first identified *Vulcanodon* as a sauropod on the basis of the length of metatarsal V, which approaches the length of the other metatarsals. Other sauropod features were noted by Cooper (1984) in his detailed redescription of the holotypic skeleton.

Raath (1972:4) provided the only diagnosis for the genus and species, which consists in large part of resemblances to prosauropods (symplesiomorphies) and sauropods (sauropod synapomorphies). He mentioned, however, the unusual "nail-like" unguals on pedal digits II and III, which indeed appear to be diagnostic. Although not found in articulation, the relative size and symmetry of these unguals support their assignment to pedal digits II and III. Proximally, the maximum width of each
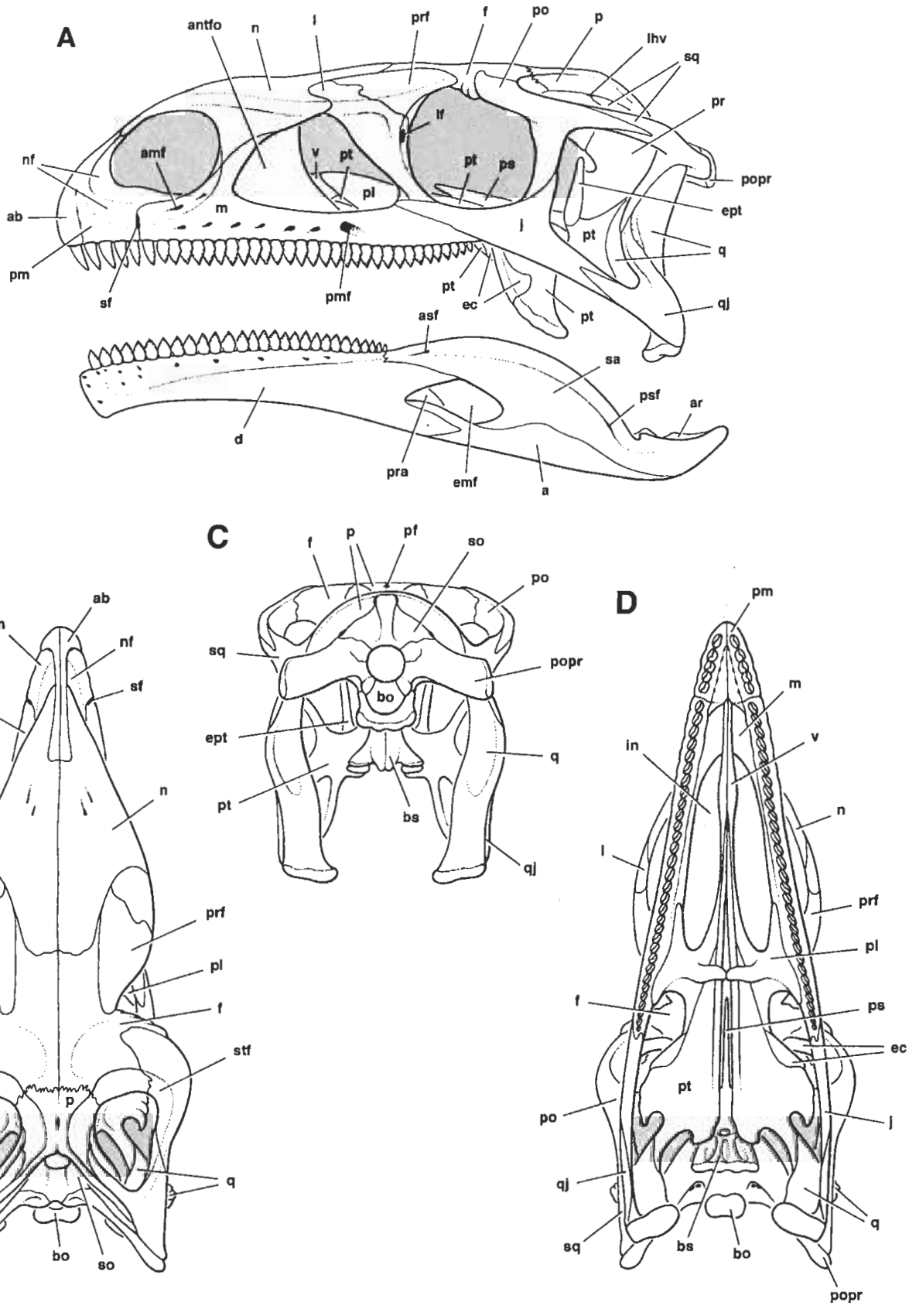
FIGURE 5. Skull reconstruction of the prosauropod *Plateosaurus engelhardti* in lateral (**A**), dorsal (**B**), posterior (**C**), and ventral (**D**) views. For key to anatomical abbreviations refer to foldout.
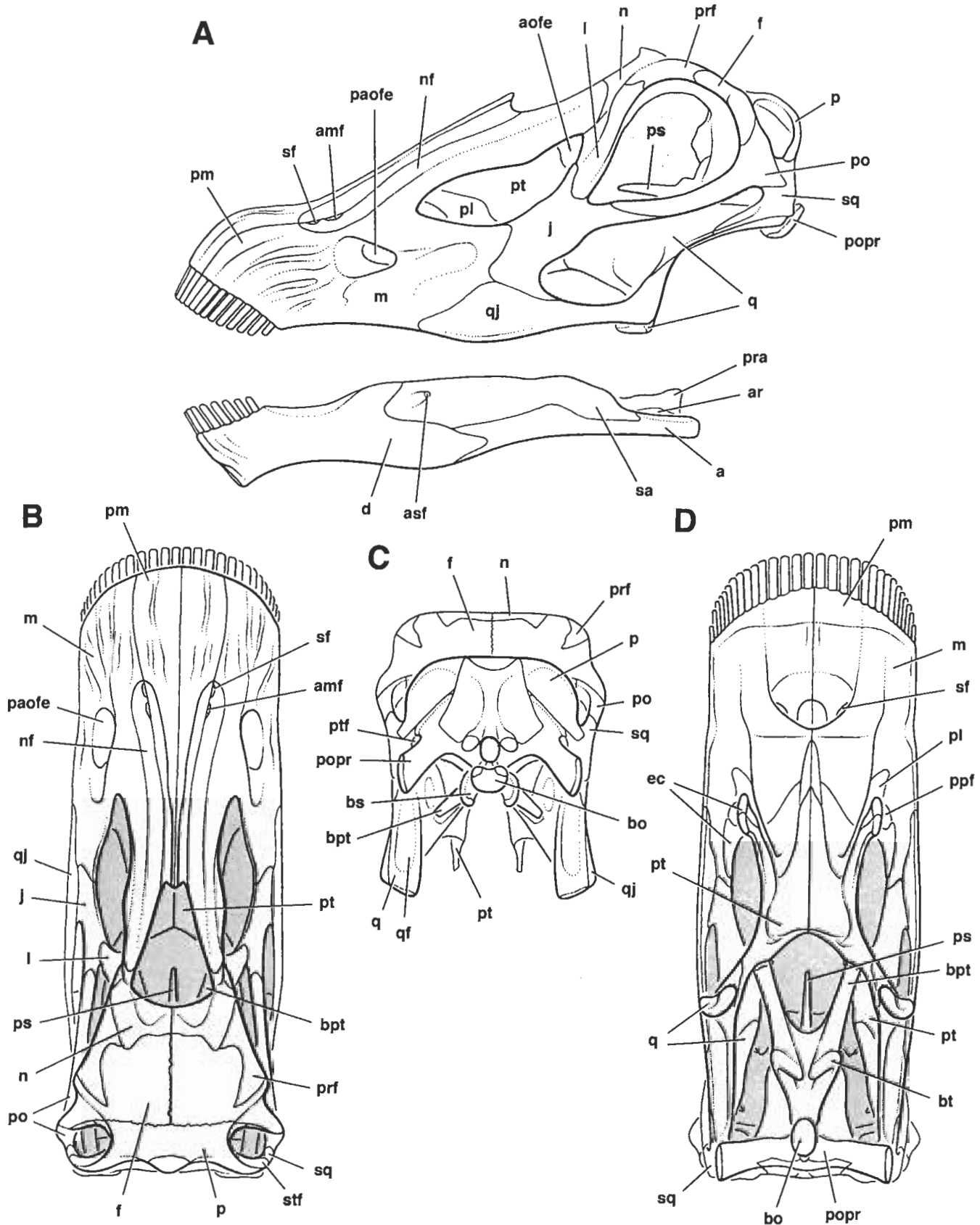
FIGURE 6.   Skull reconstruction of the diplodocoid *Diplodocus* in lateral (**A**), dorsal (**B**), posterior (**C**), and ventral (**D**) views.
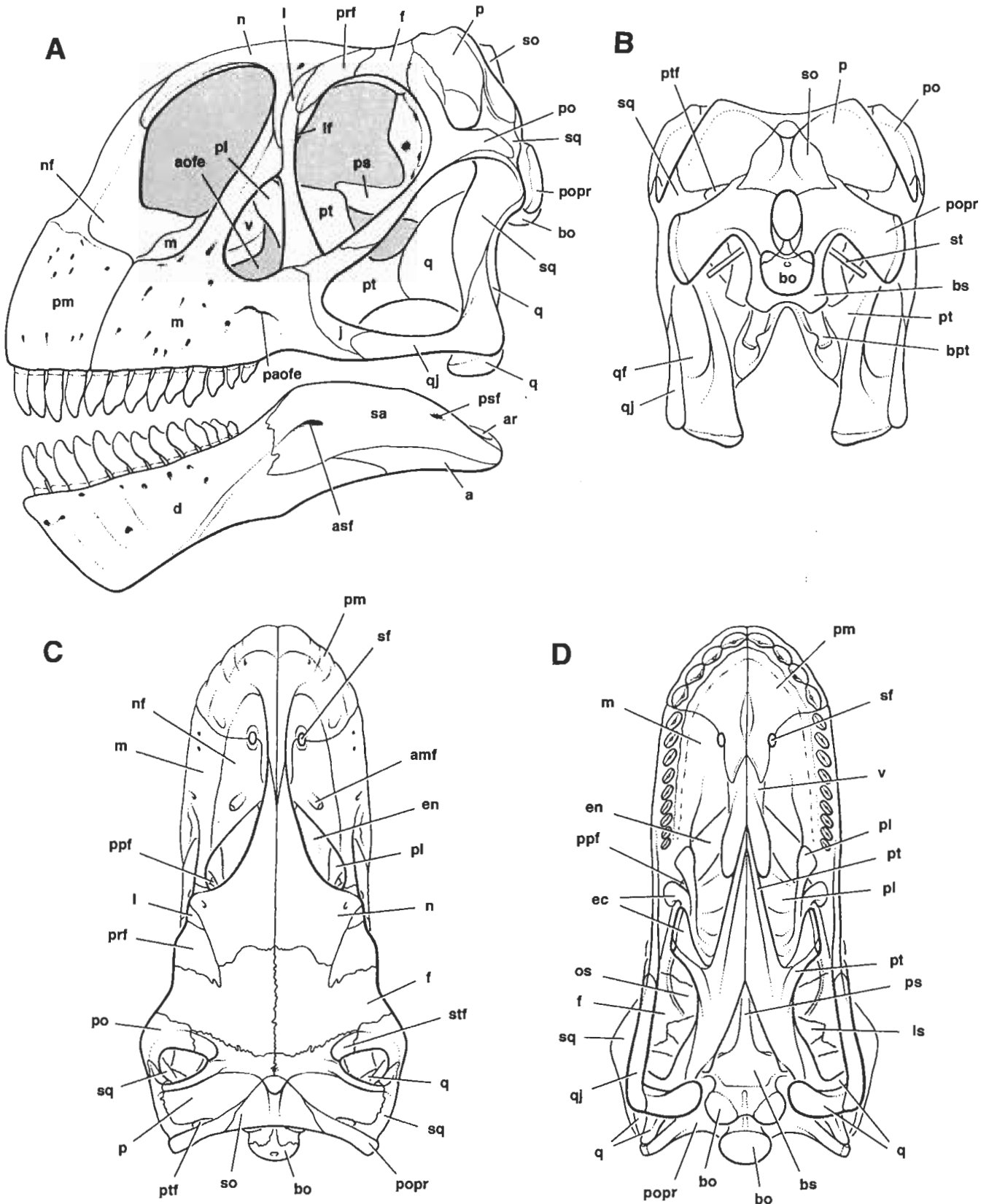
FIGURE 7. Skull reconstruction of a subadult individual of the basal macronarian *Camarasaurus lentus* (based on CM 11338) in lateral (**A**), posterior (**B**), dorsal (**C**), and ventral (**D**) views.
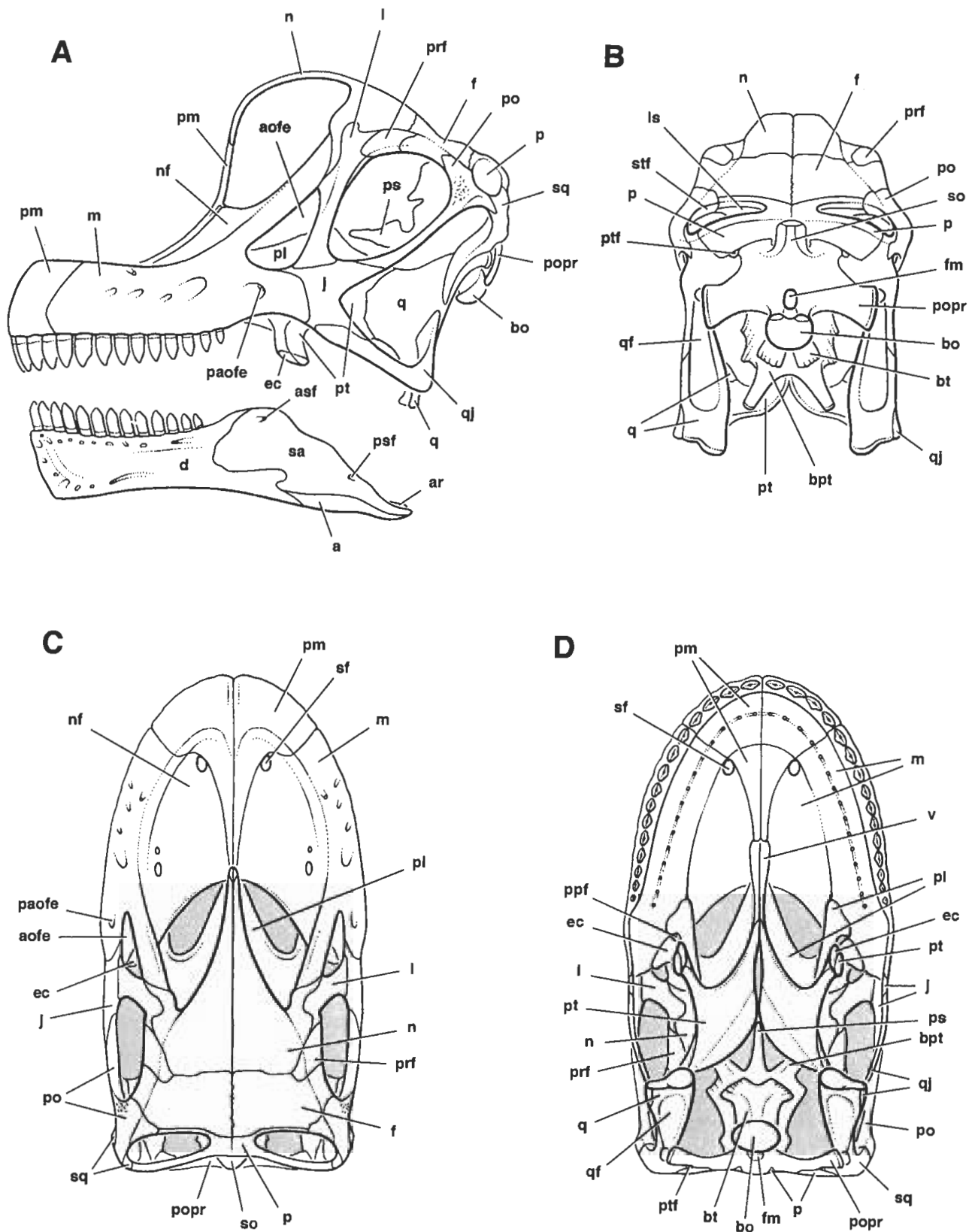
FIGURE 8. Skull reconstruction of the brachiosaurid *Brachiosaurus brancai* (based on HMN t1, S66, and S116) in lateral (**A**), posterior (**B**), dorsal (**C**), and ventral (**D**) views.
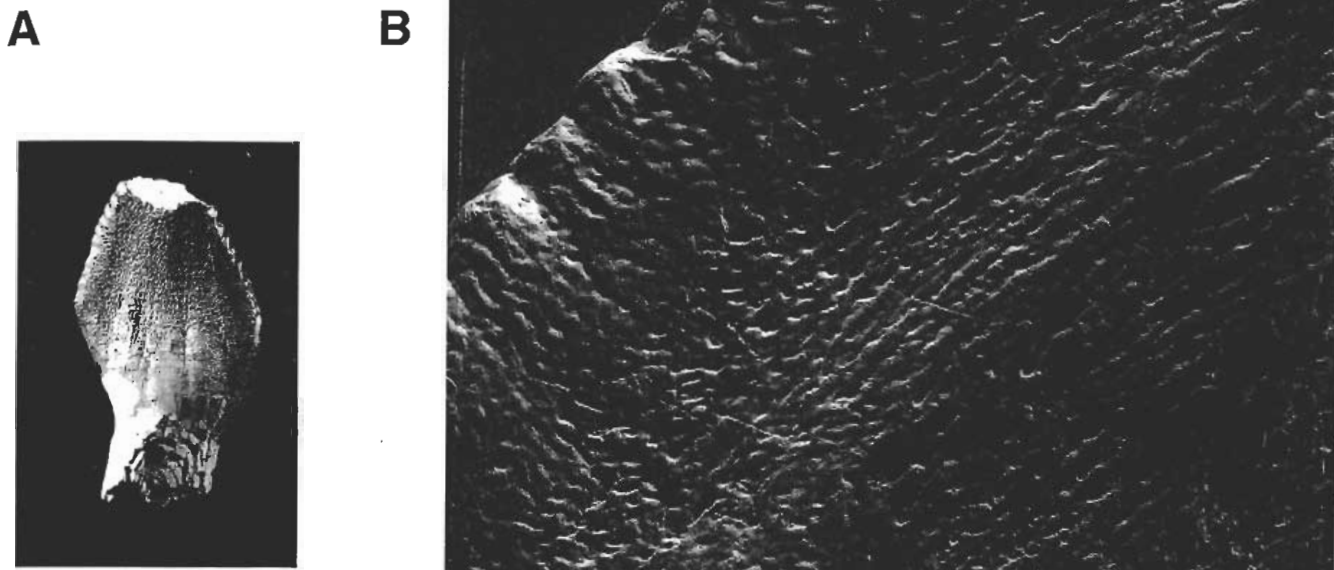
FIGURE 9. Enamel texture in sauropods as preserved on the crown from an unnamed neosauropod from the Lower Cretaceous of Niger (Sereno et al., 1994). **A**, lingual view; **B**, SEM photograph of the same showing the enamel texture and marginal denticles. Scale bars equal 1 cm in **A** and 1 mm in **B**.

ungual exceeds its height, especially the smaller third ungual, which is twice as wide as deep (Raath, 1972:pl. 7; Cooper, 1984:figs. 35I–L, 36). In prosauropods, the unguals of pedal digits II–IV are moderately flattened with subequal height and depth proximally (Cooper, 1981:fig. 79, 80). In other sauropods, in contrast, these unguals more closely resemble that of pedal digit I and are always claw-shaped, with depth significantly greater than width throughout their length (e.g., McIntosh et al., 1992:figs. 3, 4). The unusually broad proportions of the unguals in pedal digits II and II appear to be unique to *Vulcanodon* among sauropodomorphs.

Shunosaurus lii Dong, Zhou, and Zhang, 1983

Hypodigm—Based on an articulated skeleton lacking the distal bones of the forelimbs and hindlimbs (ZDM T5401; Zhang, 1988:fig. 1). Numerous referred specimens include nearly complete skeletons (ZDM 5402, 5404; Zhang, 1988:figs. 2, 58), nearly complete skulls (ZDM T5403; Zhang, 1988:fig. 12,13; IVPP V7261), and a tail club (ZDM 5006; Dong, Peng, and Huang, 1989).

**Recorded Temporal Range**—Middle Jurassic (Bathonian-Callovian) (Dong, Zhou, and Zhang, 1983).
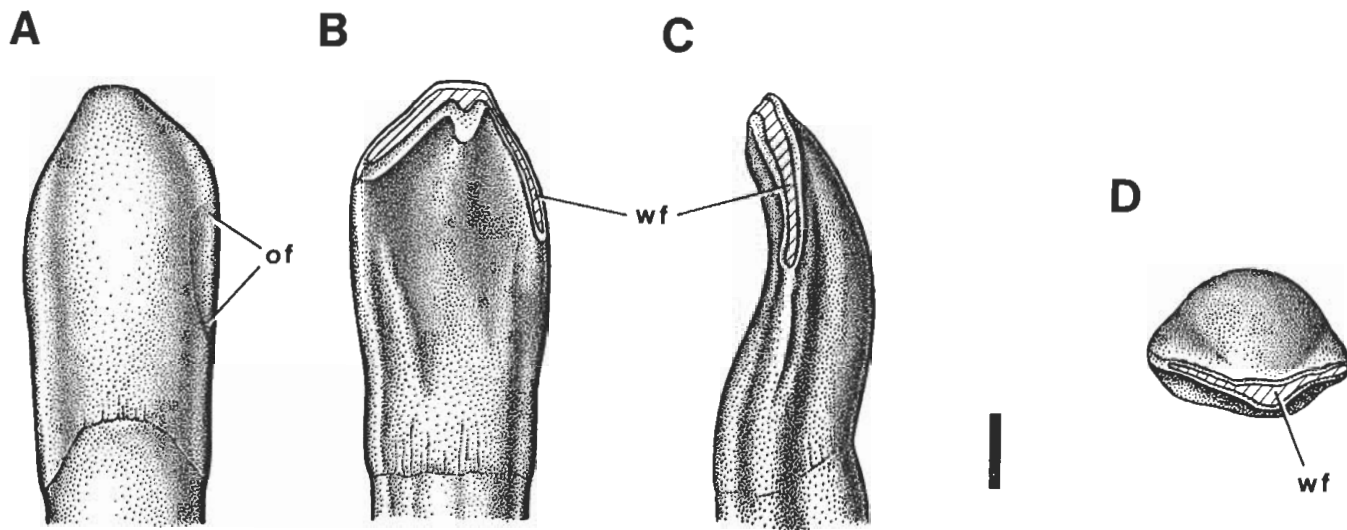
FIGURE 10. Worn crown of *Camarasaurus grandis* (YPM 1905) in labial (**A**), lingual (**B**), anterior (**C**), and apical (**D**) views (from Ostrom and McIntosh, 1966:pl. 7). V-shaped wear facet indicated by cross-hatching. Scale bar equals 1 cm.
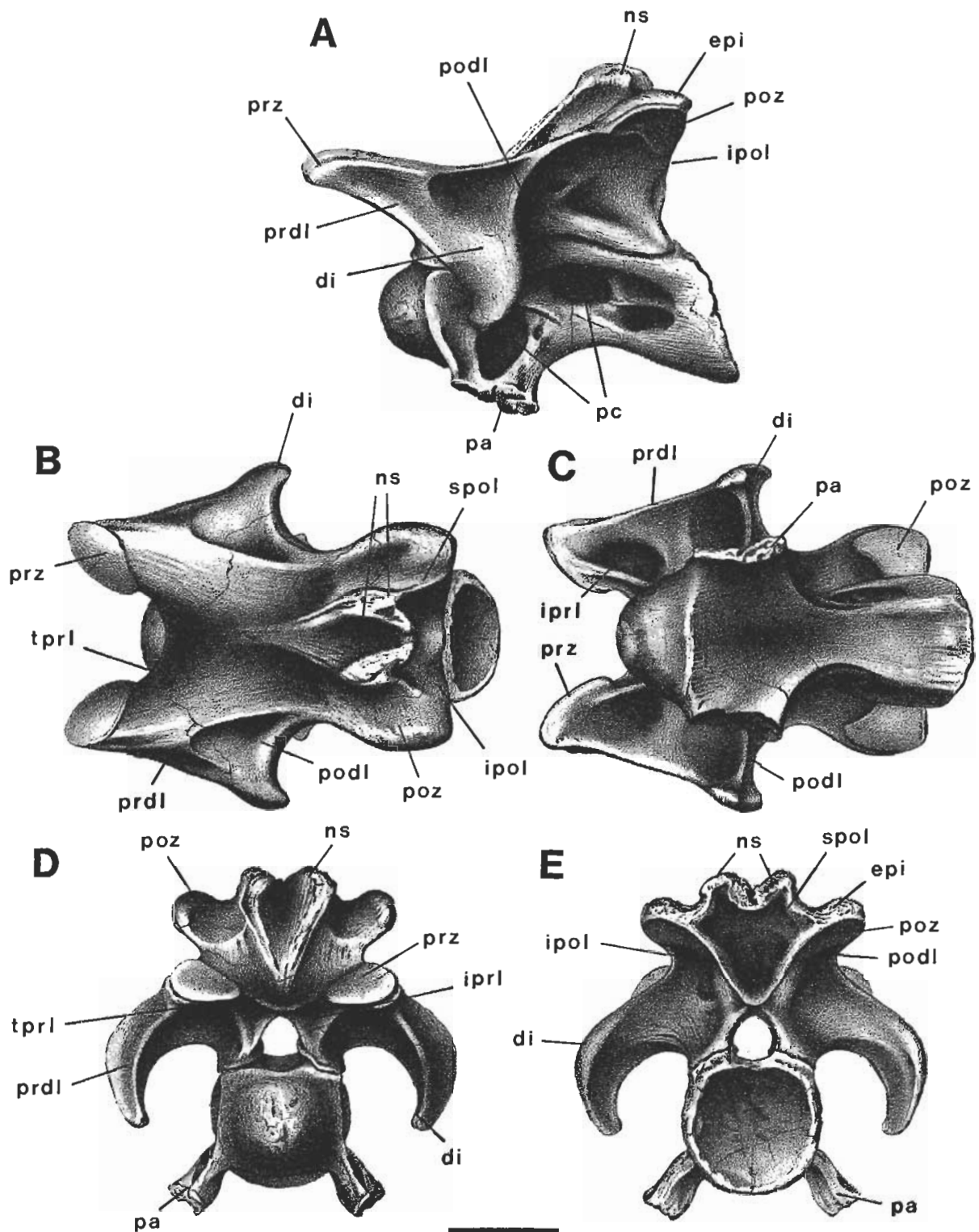
FIGURE 11.   Fifth cervical vertebra of *Camarasaurus grandis* (YPM 1905) in lateral (**A**), dorsal (**B**), ventral (**C**), anterior (**D**), and posterior (**E**) views (from Ostrom and McIntosh, 1966:pl. 11). Scale bar equals 10 cm.

Autapomorphies—Anterior portion of axial neural spine prominent; "postparapophyses" on posterior dorsal vertebrae; terminal tail club composed of at least three enlarged, coossified caudal vertebrae with two dermal spines.

Comments—Zhang's (1988:78–79) diagnosis listed numerous features, only a few of which appear to be autapomorphies of *Shunosaurus lii*. One of the more striking autapomorphies is an unusual articulation between the ribs and the posterior dorsal vertebrae. The parapophyseal articulation is split between adjacent vertebrae, with a portion of the articulation in its usual
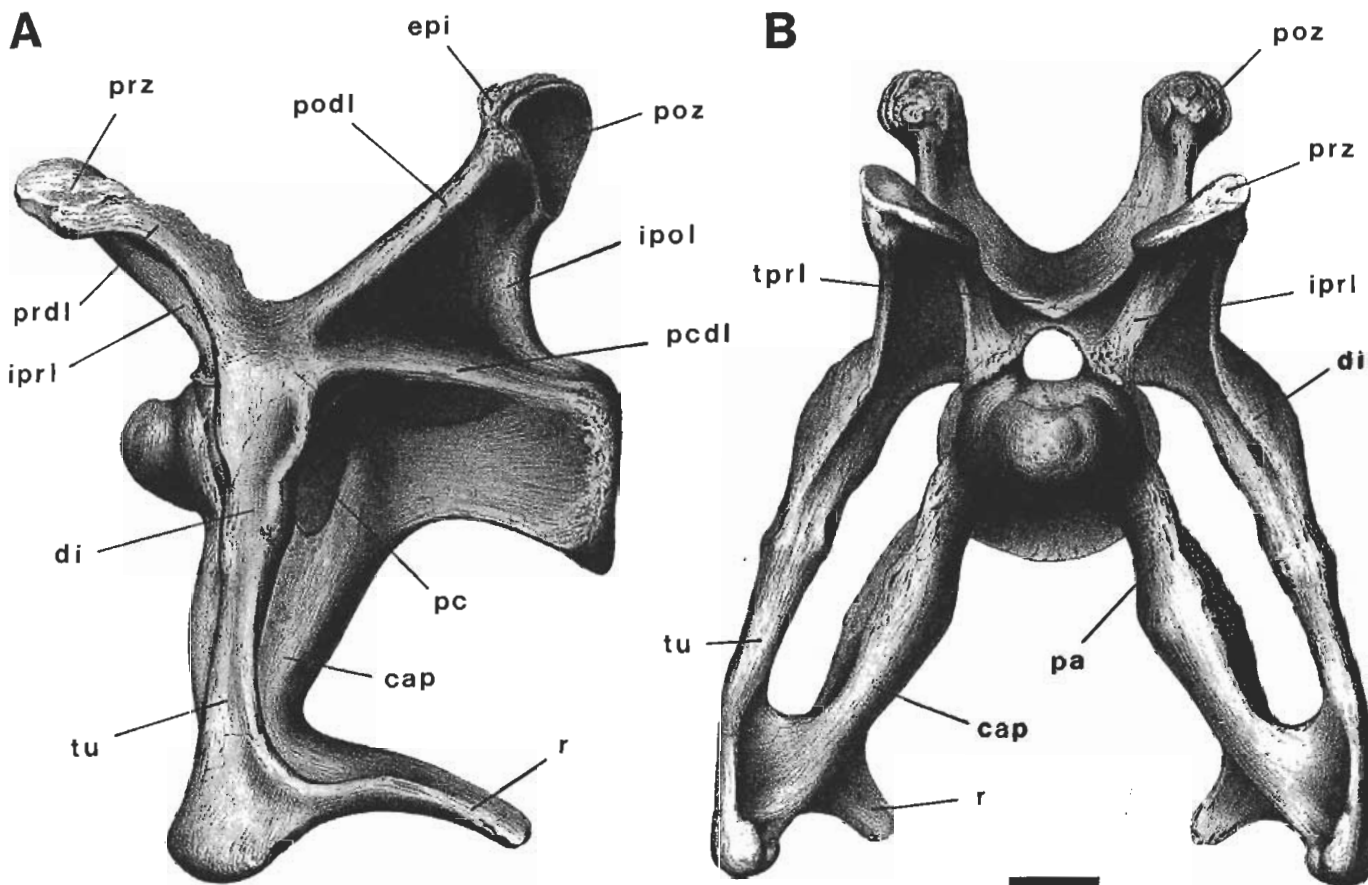
FIGURE 12. Eighth cervical vertebra and coossified rib of *Apatosaurus excelsus* (YPM 1980) in lateral (**A**) and anterior (**B**) views (from Ostrom and McIntosh, 1966:pl. 12). Scale bar equals 10 cm.

position by the prezygapophyses and an anterior extension located near the postzygapophysis on the preceding vertebra (Zhang, 1988:figs. 31, 32; "postparapophysis"). The tail club, which appears to fuse late in growth, is surmounted by at least two spine-shaped ossifications (Zhang, 1988:fig. 39; Dong et al., 1989).

Barapasaurus tagorei Jain, Kutty, and Roy-Chowdhury, 1975

Hypodigm—Based on a sacrum (ISI R50; Jain, Kutty, and Roy-Chowdhury, 1975:fig. 2), with referred material consisting of isolated teeth and many disarticulated postcranial bones.

Recorded Temporal Range—Early Jurassic (Jain, Robinson, and Roy-Chowdhury, 1962).

Autapomorphies—Posterior dorsal vertebrae with slit-shaped neural canal, the margins of which are deeply inset both fore and aft, and an infradiapophyseal fossa opening into the neural canal (Jain et al., 1979:pl. 100, 101).

Comments—The diagnosis for *Barapasaurus tagorei* provided by Jain, Kutty, and Roy-Chowdhury (1975:223, 226) listed general descriptive features and highlighted the specializations of the dorsal vertebrae, which are the most distinctive part of the postcranial skeleton. Scoring of *Barapasaurus* was based on published ·illustrations as well as observations made on the material housed in the collections of the Indian Statistical Institute (Wilson, unpubl. data).

Omeisaurus Young, 1939

Definition—*O. jungsiensis, O. tianfuensis,* their ancestor, and all its descendants.

Recorded Temporal Range—Late Jurassic (Weishampel, 1990; Dong, 1995).

Autapomorphies—Ascending ramus of maxilla with dorsoventrally expanded distal end; increase in number of cervical vertebrae (probably three added for a total of 16 cervical vertebrae); increase in cervical length (mid-cervical centra nearly five times longer than deep) with reduction in height of cervical neural spines.

Comments—Although five species of the genus *Omeisaurus* have been named, three (*O. changshouensis, O. fuxiensis,* and *O. luoquanensis*) are based on fragmentary material that is difficult to compare to the type species (*O. jungsiensis*) and are probably invalid. He, Li, Cai, and Gao (1984) and He, Li, and Cai (1988:figs. 1, 2) described several well preserved skeletons of *O. tianfuensis* (ZDM T5701–T5705), from which we have derived our character data.

Dong, Peng, and Huang (1989:figs. 1, 2) described sauropod tail clubs from the Dashanpu quarry near Zigong (Sichuan), attributing some to *Shunosaurus* and others to *Omeisaurus*. A tail club is clearly present in *Shunosaurus,* as preserved in associated skeletons (ZDM T5401; Zhang, 1988). The basis for referral of several of the tail clubs to *Omeisaurus,* on the other hand, has not been demonstrated. No tail clubs were associated with the skeletons that form the basis for the description of *Omeisaurus* (He, Li, and Cai, 1988), although the distalmost caudal vertebrae were not preserved. Until the presence of a terminal tail club is properly documented in *Omeisaurus,* we believe it is premature to use this feature to link this genus with *Shunosaurus* (e.g., Upchurch, 1995:373–374).
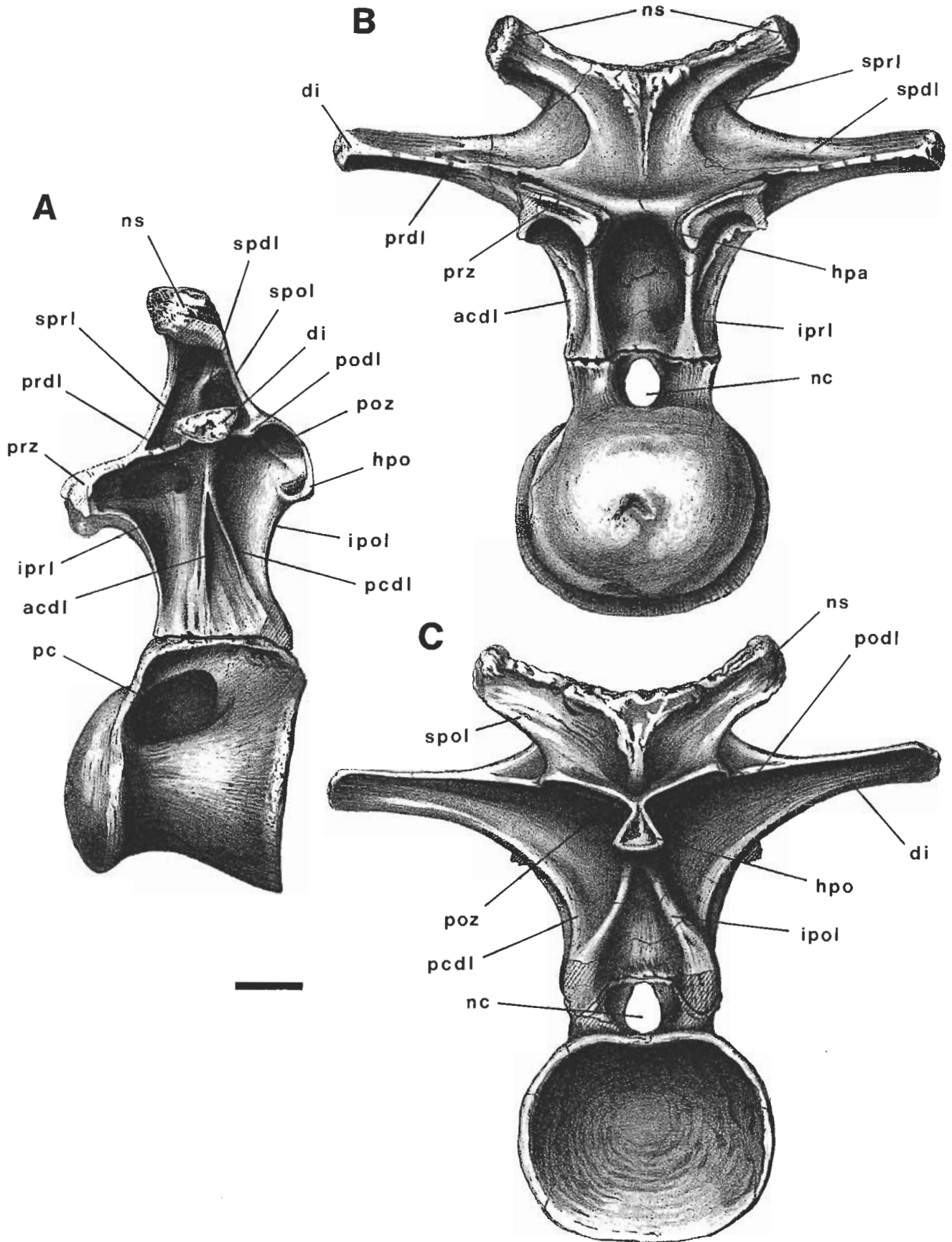
FIGURE 13. Mid-dorsal vertebra of *Camarasaurus grandis* (YPM 1901 or 1902) in lateral (**A**), anterior (**B**), and posterior (**C**) views (from Ostrom and McIntosh, 1966:pl. 24). Scale bar equals 10 cm.
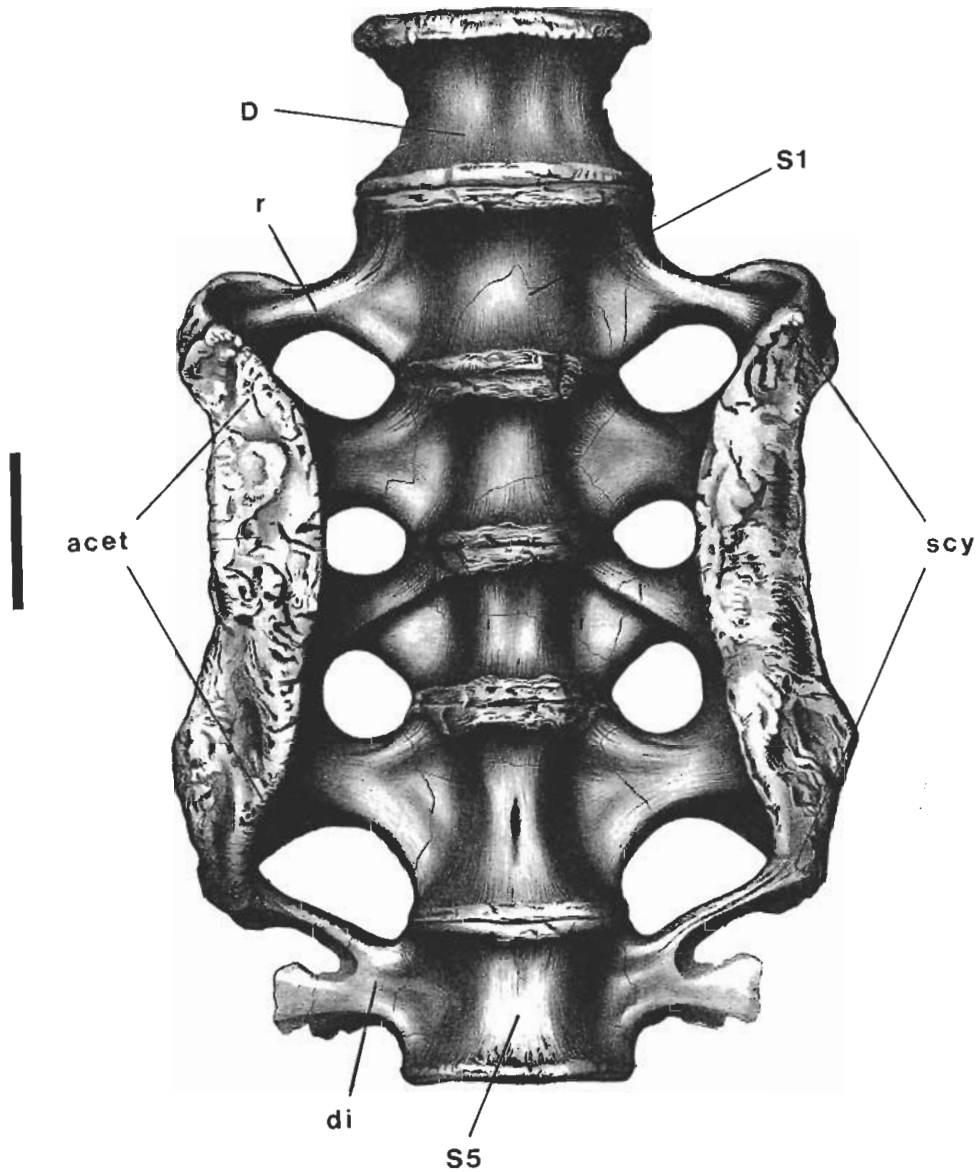
FIGURE 14. Posteriormost dorsal and sacral vertebrae 1–5 of *Apatosaurus excelsus* (YPM 1980) in ventral view (from Ostrom and McIntosh, 1966:pl. 27). Scale bar equals 30 cm.

Diplodocoidea Marsh, 1884
(=Diplodocimorpha Calvo and Salgado, 1995)

Definition—Neosauropods more closely related to *Diplodocus* than to *Saltasaurus*, including *Rayososaurus, Amphicoelias,* dicraeosaurids, and diplodocids.

Recorded Temporal Range—Late Jurassic (Kimmeridgian) to Early Cretaceous (Hauterivian) (McIntosh, 1990a; Salgado and Bonaparte, 1991), and possibly surviving into the Late Cretaceous (Campanian-Maastrichtian) (Huene, 1929:pl. 29).

Synapomorphies—Dentary with ventrally projecting "chin" and transversely narrow symphysis; subcylindrical tooth crowns; narrow subcylindrical basipterygoid processes (length at least four times basal diameter) that project anteroventrally or anteriorly (Fig. 6); atlantal intercentrum with anteroventrally expanded occipital fossa; cervical ribs shorter than their respective centra (Fig. 12); dorsal and anterior caudal vertebrae with tall neural arches (more than two and one-half times dor-

soventral centrum height); whiplash tail (30 or more elongate, biconvex posterior caudal vertebrae).

Comments—The monophyly of the best known diplodocoids—dicraeosaurids (*Amargasaurus, Dicraeosaurus*) and diplodocids (*Apatosaurus, Barosaurus, Diplodocus*)—is well established (Berman and McIntosh, 1978; Yu, 1993; Calvo and Salgado, 1995; Wilson and Smith, 1996). The most basal diplodocoids, however, lie outside these subgroups and include *Rayososaurus tessonei* (="*Rebbachisaurus*" *tessonei,* Calvo and Salgado, 1995) and *Amphicoelias altus* (Osborn and Mook, 1921; Wilson and Smith, 1996). Based largely on single partial skeletons, their anatomy is not fully known. Most of the synapomorphies listed in the above diagnosis are preserved in one or the other of these basal genera. Those that are present in other diplodocoids but cannot be scored may eventually be shown to characterize these basal genera and include the extreme elevation of the external nares above
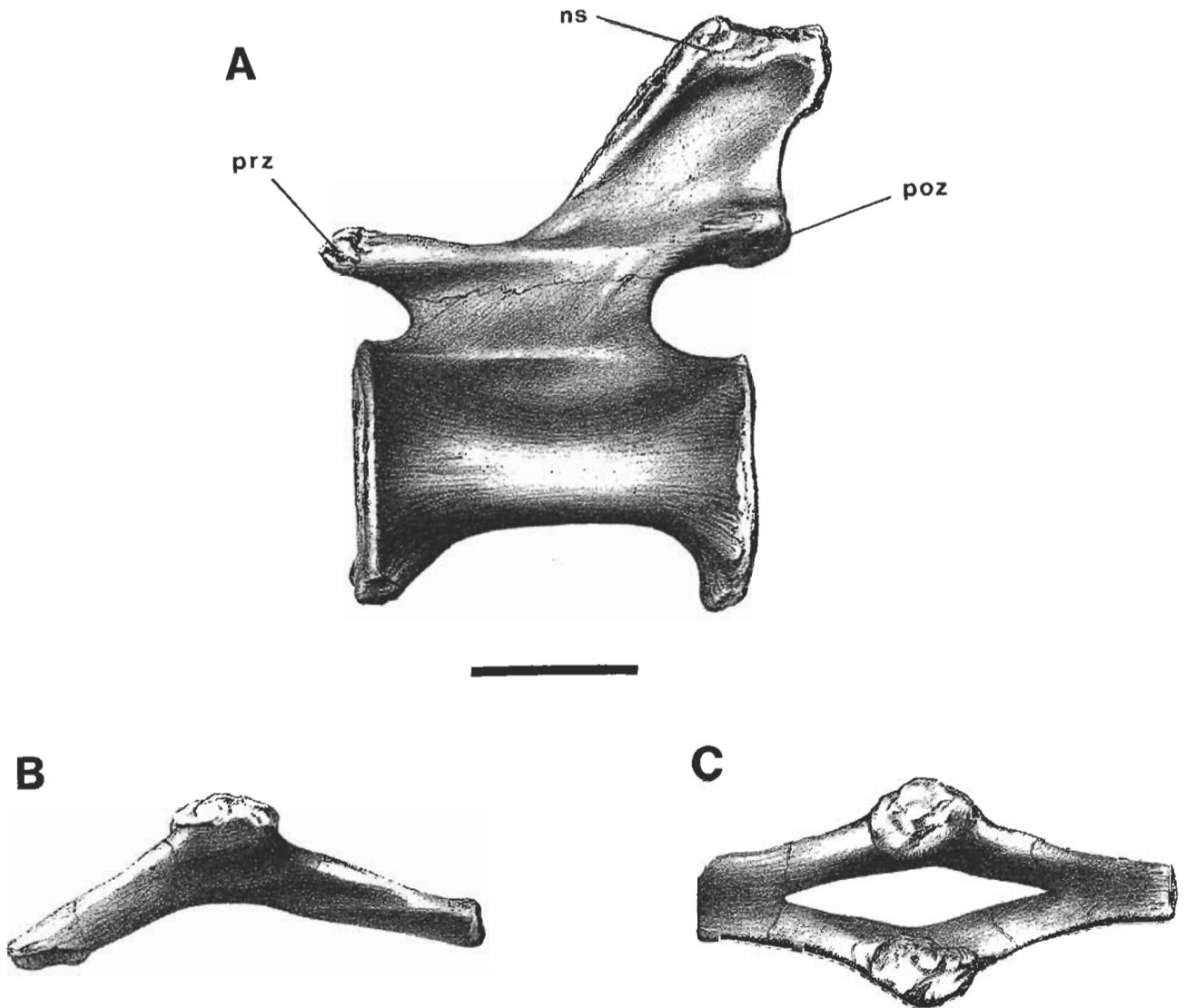
FIGURE 15.   Distal caudal vertebra (YPM 1878) and distal chevron (YPM 4675) of *Diplodocus longus* in lateral (**A**, **B**) and dorsal (**C**) views (from Ostrom and McIntosh, 1966:pl. 36). Scale bar equals 10 cm.

the orbits, the lack of an ossified calcaneum, and the laterally flaring lateral distal condyle on metatarsal I.

The sauropod remains from Neuquén, Argentina, referred to *Rebbachisaurus* by Calvo and Salgado (1995) show several similarities to the type species, *R. garasbae,* including a broadly expanded scapular blade and broad dorsal neural spines composed of four prominent, perpendicularly oriented laminae. These features appear to be synapomorphic at some level, but enough differences exist between the two taxa to suggest that they may in fact represent two separate genera. For example, the neural arches of *R. garasbae* exhibit a complex lamination pattern ventral to the diapophyses and zygapophyses (Wilson, pers. obs.). These accessory "infradiapophyseal" and "infrazygapophyseal" laminae are not present in the Neuquén specimen. Moreover, the shape of the dorsal neural spines differs in the two taxa. In *R. garasbae,* the dorsal neural spines broaden to nearly twice their minimum width through the proximal twothirds of their height, and then taper sharply towards their summit. In contrast, the dorsal neural spines of the Neuquén specimen they broaden gently towards their distal end. More fragmentary remains of a second sauropod from coeval beds in

Neuquén Province were described by Bonaparte (1996) as a new taxon, *Rayososaurus agrioensis.* The type scapula of this form very closely resembles that of the type of "*Rebbachisaurus*" *tessonei,* sharing with it the narrow acromion process, which forms a U-shaped with the long axis of the scapula. Given the differences apparent in the dorsal vertebrae alone of *Rebbachisaurus garasbae* and "*Rebbachisaurus*" *tessonei* (not to mention those that may exist in the cranial or appendicular skeleton, complete remains of which are unknown in the former) and the close resemblances between the latter and *Rayososaurus agrioensis,* we suggest that the both Neuquén species be referred *Rayososaurus.* The aforementioned similarities between *Rebbachisaurus* and *Rayososaurus,* as well as those mentioned in Calvo and Salgado (1995:15) and Bonaparte (1996: 109), represent shared derived characters supporting their close phylogenetic relationship.

Charig (1980) referred *Cetiosauriscus stewarti* to Diplodocidae on the basis of its forked caudal chevrons and biconvex distal caudal vertebrae. The phylogenetic affinities of *Cetiosauriscus* are important in view of its Middle Jurassic (Callovian) age. If properly referred, it would constitute the earliest
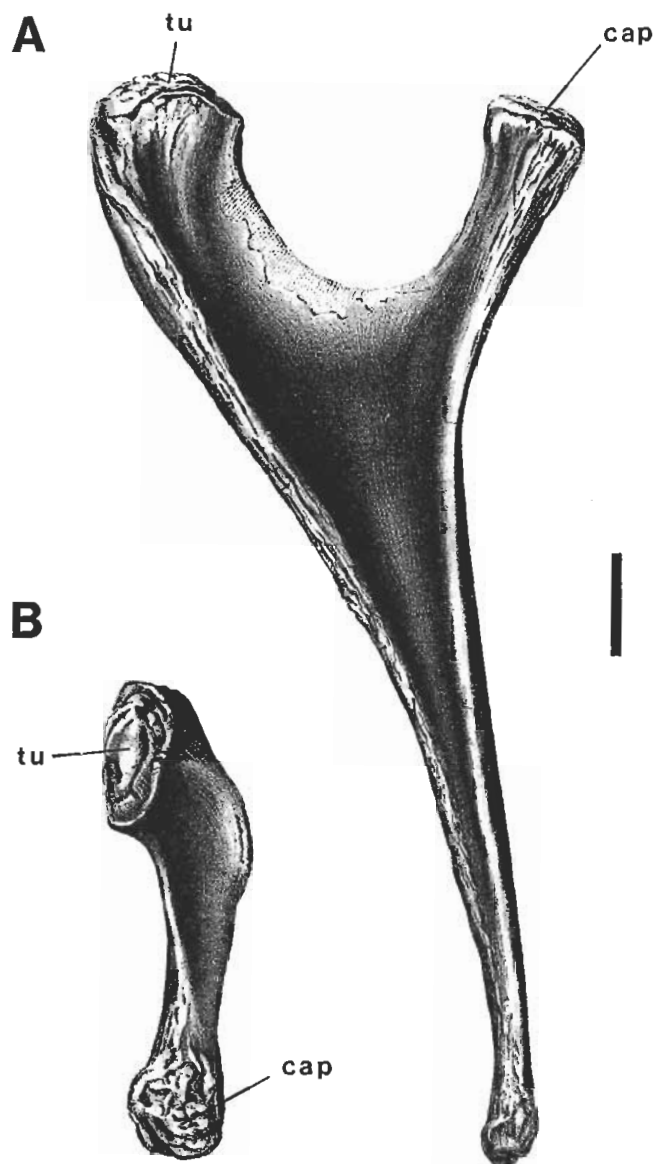
FIGURE 16. Left anterior dorsal rib of *Apatosaurus excelsus* (YPM 1980) in posterior (**A**) and proximal (**B**) views (from Ostrom and McIntosh, 1966:pl. 39). Scale bar equals 10 cm.

FIGURE 17. Left scapula (**A**) and right coracoid (reversed) (**B**) of *Camarasaurus grandis* (YPM 1901) in lateral view (from Ostrom and McIntosh, 1966:pls. 43, 46). Scale bar equals 30 cm.

known record of a diplodocoid. As discussed below, however, forked chevrons and elongate biconvex distal caudal vertebrae are present in other sauropod subgroups, and so we regard the referral of *Cetiosauriscus stewarti* to Diplodocoidea as requiring further justification.

Haplocanthosaurus Hatcher, 1903

Definition—*H. priscus, H. delfsi,* their ancestor, and all its descendants.

Recorded Temporal Range—Late Jurassic (Kimmeridgian-Tithonian) (Hatcher, 1903; McIntosh and Williams, 1988).

Autapomorphies—Dorsal vertebrae with neural arches lacking anterior central diapophyseal lamina and with elongate infrapostzygapophyseal laminae; dorsal diapophyses projecting dorsolaterally at 45° and approaching the height of neural spines; scapular blade with dorsally and ventrally expanded distal end.

Comments—*Haplocanthosaurus priscus,* one of the rarest

sauropods in the Morrison Formation of the western United States, was described on the basis of two partial skeletons found in proximity to one another (CM 572, 879; Hatcher, 1903:figs. 1, 2). These two skeletons were originally regarded as separate species (*H. priscus* and *H. utterbacki*; Hatcher, 1903), but were later synonymized by McIntosh and Williams (1988). A third partial skeleton, discovered a few kilometers from the type lo-

FIGURE 18. Left scapulocoracoid of *Euhelopus zdanskyi* (**A**) and *Opisthocoelicaudia skarzynskii* (**B**) in medial view (modified from Young [1935] and Borsuk-Bialynicka [1977], respectively). Scale bar equals 30 cm.
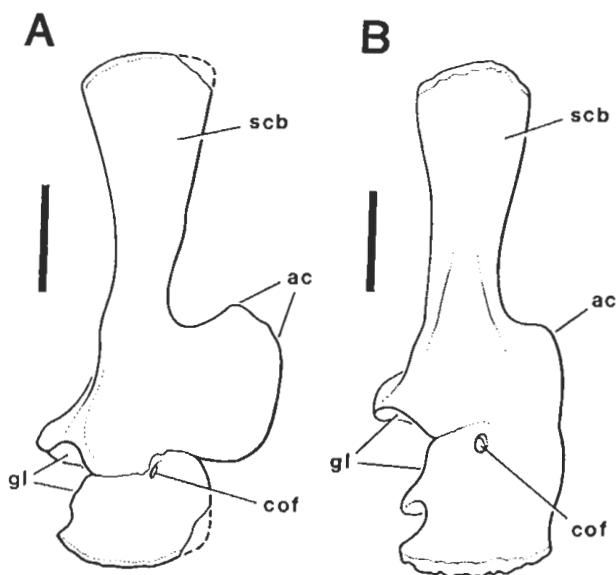

FIGURE 19. Left humerus of *Camarasaurus grandis* (YPM 1901) in posterior (**A**) and lateral (**B**) views (from Ostrom and McIntosh, 1966: pl. 49). Scale bar equals 30 cm.

cality, has been described recently as a second species, *Haplocanthosaurus delfsi* (McIntosh and Williams, 1988). We base our character data for the genus on these specimens, which lack any part of the skull and many bones of the fore- and hindlimbs. A partial braincase and the first three cervical vertebrae (USNM 5384) and a paired ischia and a complete hindlimb (USNM 4275) have been referred to *Haplocanthosaurus* (Gilmore, 1907; McIntosh and Williams, 1988), but we regard this assignment as tentative because of the lack of sufficient overlapping elements.

Based only on the relative width of the scapular blade, Calvo and Salgado (1995:fig. 18) suggested that the genus *Haplocanthosaurus* is paraphyletic, with one species (*H. priscus*) more closely related to diplodocoids than the other (*H. delfsi*). They scored scapular blade proportions as a ratio between the minimum width at the neck of the scapula and its maximum width at the end of the blade. *H. priscus* and *Rayososaurus tessonei* are scored as having a distal scapular blade width three times or more its proximal width. In *H. priscus*, however, this proportion is clearly less than three (Hatcher, 1903:fig. 18); in *Rayososaurus tessonei*, the ratio is even lower, just exceeding two (Calvo and Salgado, 1995:fig. 12A). Furthermore, the proximal portion of the scapular blade in *H. delfsi* has been restored (McIntosh and Williams, 1988:16); therefore, the ratio in this specimen is unknown, although the preserved portion of the distal blade resembles that in *H. priscus*. Given these inconsistencies and the aforementioned autapomorphies, there is no basis for claiming that *Haplocanthosaurus* is paraphyletic.

Camarasaurus Cope, 1877

Definition—*C. grandis, C. lentus, C. lewisi, C. supremus,* their ancestor, and all its descendants.

Recorded Temporal Range—Late Jurassic (Kimmeridgian-Tithonian) (McIntosh, 1990a).

Autapomorphies—Lacrimal with long axis directed anterodorsally; quadratojugal with short anterior ramus that does not extend anterior to laterotemporal fenestra; quadratojugal-squamosal contact; conspicuous groove passing anteroventrally
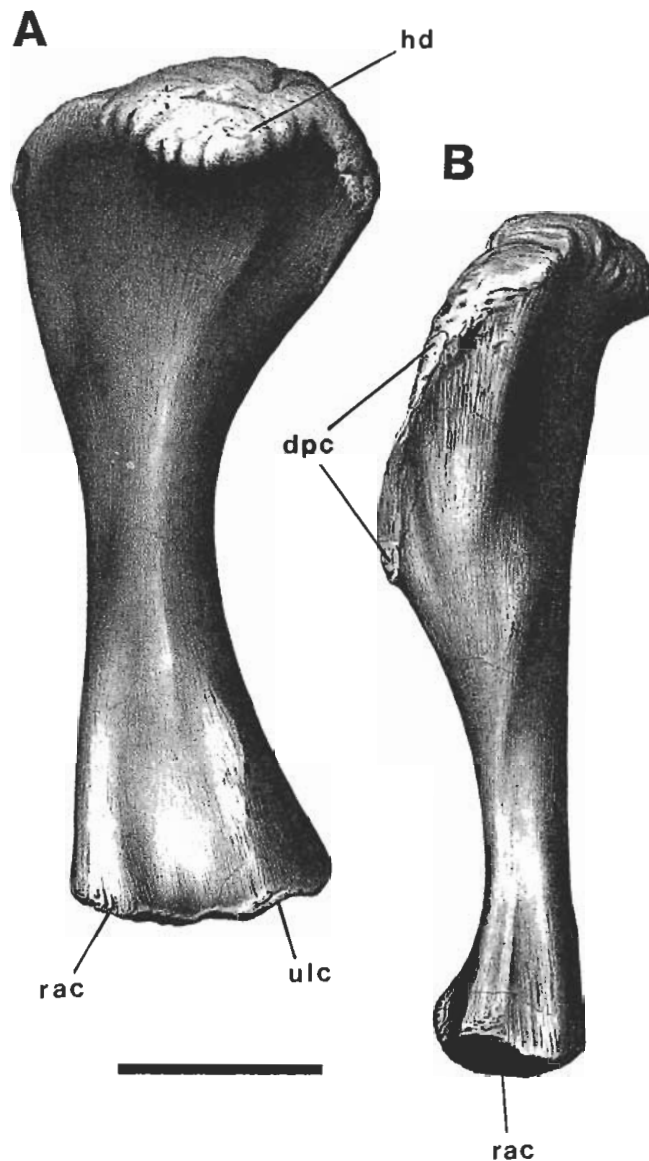
from surangular foramen to ventral margin of dentary (Fig. 7A); ischial blade directed posteriorly so that long axis of its shaft passes though pubic peduncle (Fig. 29); fibula with dorsoventrally deep tibial scar (Fig. 32G).

Comments—The four species within the genus *Camarasaurus* are in need of revision. McIntosh (1990a) referred a fifth species to *Camarasaurus*, one that was originally referred to *Apatosaurus* (as *A. alenquerensis*; Lapparent and Zbyszewski, 1957). Based on material from the Upper Jurassic of Portugal, *A. alenquerensis* has an ischium with a slender shaft that closely resembles that of *Camarasaurus* (Lapparent and Zbyszewski, 1957:pl. 19, figs. 51, 52) and is probably correctly referred to this genus. Additional features distinguishing the Portuguese specimen from other species of *Camarasaurus*, however, are not apparent from the preserved material.

Brachiosauridae Riggs, 1904

Definition—Titanosauriforms more closely related to *Brachiosaurus* than to *Saltasaurus*, including, by this definition, the
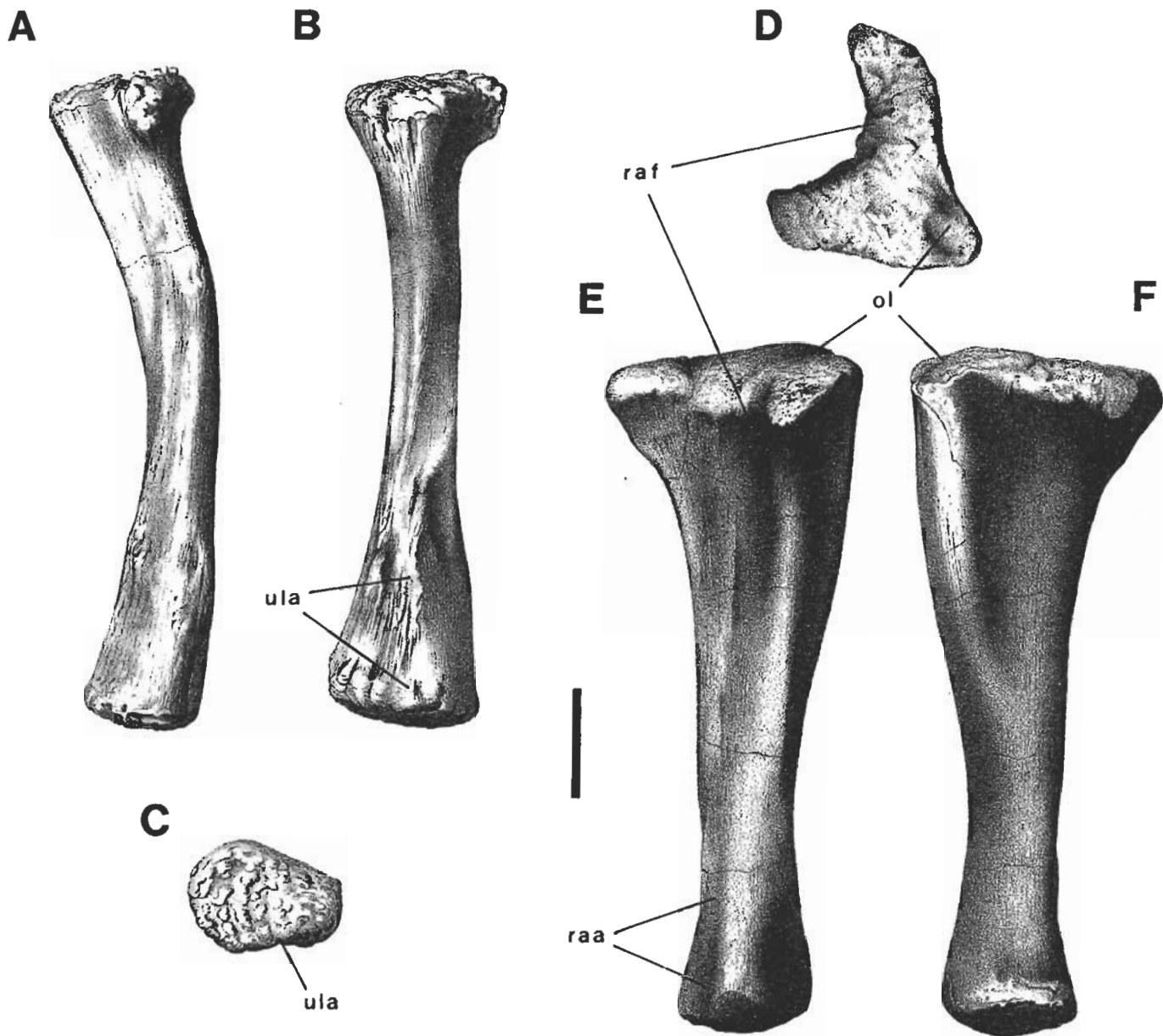
FIGURE 20. Left radius and ulna of *Camarasaurus grandis* (YPM 1901), with the radius in medial (**A**), posterior (**B**), and distal (**C**) views and the ulna in proximal (**D**), lateral (**E**), and posterior (**F**) views. **A–C** are from a previously unpublished lithograph completed under the direction of O. C. Marsh (another lithograph of the same bone, proximodistally inverted, was published by Ostrom and McIntosh [1966:pl. 51]). **D–F** are from Ostrom and McIntosh (1966:pl. 53). Scale bar equals 10 cm.

French "*Bothriospondylus*" *madagascarensis* (i.e., not the material from Madagascar), *Brachiosaurus*, *Eucamerotus*, and *Pleurocoelus*.

Recorded Temporal Range—Late Jurassic (Kimmeridgian) to Early Cretaceous (?Albian) (Riggs, 1904; McIntosh, 1990a; Bonaparte and Coria, 1993).

Synapomorphies—Subrectangular muzzle (twice as long as deep; Fig. 8A); elongate cervical centra (reaching a maximum of seven times as long as deep); centra with deep accessory depressions; elongate humerus (subequal to the femur in length); humerus with prominent deltopectoral crest.

Comments—Our observations on *Brachiosaurus* are based on the well-preserved material from Tendaguru (Janensch, 1922, 1935–1936, 1950) and western North America (Riggs, 1904). We regard as dubious the assignment of additional spe-

cies to *Brachiosaurus* based on fragmentary material from Portugal (*B. atalaiensis*, Lapparent and Zbyszewski, 1957) and Algeria (*B. nougaredi*, Lapparent, 1960).

Whether there should be subgeneric, rather than specific, distinction between the African *Brachiosaurus brancai* and the western North American *B. altithorax* (Paul, 1988) amounts to an arbitrary taxonomic distinction. Paul (1988) based his preference for subgenera on erroneous comparisons, basing his distinction—the lack of "withers" (tall anterior dorsal neural spines) in *B. altithorax*—on an isolated (?middle) dorsal vertebra previously assigned to "*Ultrasauros*" *macintoshi* and quite possibly pertaining to a diplodocid (Curtice and Curtice, 1996). New articulated material is needed to increase current knowledge of the skeletal structure of *Brachiosaurus altithorax* from western North America.

A

B
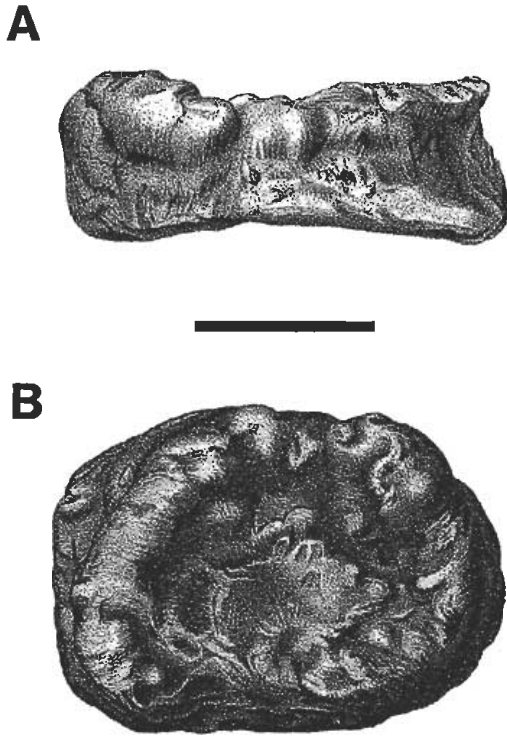
FIGURE 21. Left distal carpal of *Camarasaurus* sp. (YPM 4633) in lateral (**A**) and proximal (**B**) views (from Ostrom and McIntosh, 1966: pl. 54). Scale bar equals 5 cm.

Euhelopus zdanskyi Wiman, 1929

Hypodigm—Based on two skeletons (PMU 233, 234) including a partial skull with lower jaw, presacral and sacral vertebrae, pectoral and pelvic girdles, humerus, and hindlimb (Wiman, 1929; Mateer and McIntosh, 1985).

Recorded Temporal Range—Early Cretaceous (?Neocomian) (Wu, Brinkman, and Lü, 1994; Dong, 1995).

Autapomorphies—Procumbent teeth with asymmetrical enamel (i.e., anterior crown-root margin is closer to apex of crown) and well-developed crown buttresses on lingual crown surface; anteroventral margin of naris acute; presacral neural spines with divided coel above prezygapophyseal-postzygapophyseal lamina; increase in number of cervical vertebrae (three or four added for a total of 16 or 17 cervical vertebrae).

Comments—The *Brachiosaurus*-like limb proportions (humerus:femur = 0.99) mentioned by Mateer and McIntosh (1985) and more tentatively suggested by McIntosh (1990a) may be an artifact of the incompleteness of the proximal portion of the femur. *Euhelopus* was discovered in the Mengyin Formation of eastern China (Shandong) in beds regarded as Early Cretaceous in age (Wiman, 1929). Subsequently, a Late Jurassic age has been proposed on the basis of the dinosaurian fauna (Young, 1958; Dong, 1992) and conchostrachans (Chen, 1982). Wu, Brinkman, and Lü (1994:227) correlated the Mengyin Formation with Early Cretaceous deposits in the Ordos Basin of Inner Mongolia. Most recently, Dong (1995:94) referred the Mengyin Group to the Early Cretaceous *Psittacosaurus* Complex.

Titanosauria Bonaparte and Coria, 1993

Definition—Titanosauriforms more closely related to *Saltasaurus* than to either *Brachiosaurus* or *Euhelopus*. Currently included by this definition are *Aeolosaurus, Alamosaurus, Am-*

pelosaurus, Andesaurus, Argentinosaurus, Epachthosaurus, Magyarosaurus, Malawisaurus, Nemegtosaurus, Neuquensaurus, Opisthocoelicaudia, and *Saltasaurus.*

Recorded Temporal Range—Late Jurassic (Kimmeridgian) to Late Cretaceous (Maastrichtian).

Synapomorphies—Anterior caudal centra with prominently convex (hemispherical) posterior face; anterior and middle caudal vertebrae with prespinal and postspinal laminae; sternal plates large with strongly concave lateral margins; ulna with prominent olecranon process; carpals unossified or absent; ischium longer than pubis.

Comments—Until recently, titanosaurs have been known from skull fragments, partial skeletons, and disarticulated material of relatively derived taxa. This situation has begun to change with the discovery of more completely preserved material (*Saltasaurus,* Powell, 1992), basal taxa (e.g., *Andesaurus,* Calvo and Bonaparte, 1991; *Malawisaurus,* Jacobs, Winkler, Downs, and Gomani, 1993), and the realization that the Mongolian sauropod *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977) is actually a titanosaur (Gimenez, 1992; Salgado and Coria, 1993; Upchurch, 1995; Salgado et al., 1997).

Basal titanosaurs such as *Andesaurus* and *Malawisaurus* demonstrate that several features formerly used to characterize the group actually apply only to more derived members. These features include subcylindrical tooth crowns, middle and posterior caudal centra with cone-shaped posterior centrum faces, strong proximal and distal expansion of the humerus, transverse expansion of the distal ends of the radius and tibia, and metacarpals I and II subequal in length (Powell, 1986, 1992; Salgado, 1993; Salgado et al., 1997; Wilson, unpubl. data).

The presence of plesiomorphic features in the basal titanosaurs *Andesaurus, Epachthosaurus,* and *Argentinosaurus* (e.g., hyposphene-hypantrum articulations in dorsal vertebrae, amphiplatyan middle and posterior caudal vertebrae) formed the basis for the family Andesauridae (Bonaparte and Coria, 1993). Together, Andesauridae and Titanosauridae (all other titanosaurs) form Titanosauria, which was diagnosed by (1) the presence of small pleurocoels located in the anterior portion of an elongate, ovoid depression, and (2) the presence of two or more deep, well-defined, sharp-cornered depressions on the lateral face of the inferior half of dorsal neural arches (Bonaparte and Coria, 1993:272). Although Andesauridae is now regarded as a paraphyletic assemblage because *Epachthosaurus* is more closely related to other titanosaurs than is *Andesaurus* (Salgado and Martinez, 1993; Salgado, Coria, and Calvo, 1997), and the features used to unite "andesaurids" with titanosaurids are not present in the majority of the latter, the monophyly of Titanosauria is well supported as defined here and by Salgado, Coria, and Calvo (1997).

The oldest record of titanosaurs comes from the Upper Jurassic Tendaguru beds of Tanzania, as pointed out by McIntosh (1990a) and others. Several bones now referred to *Janenschia* ("*Tornieria*" *robusta*; Janensch, 1961; Wild, 1992) exhibit titanosaurian synapomorphies such as the prominent olecranon process on the ulna. Whether these bones pertain to a single taxon is not yet clear.

The Mongolian sauropods *Nemegtosaurus* and *Quaesitosaurus* have remained phylogenetic enigmata, in part because they are based on isolated skulls without clear association with any postcranial elements. In addition, postmortem distortion of these skulls (flattening of the posterior vault and rotation of the quadrate) has strongly influenced their initial interpretation. Since their original descriptions by Nowinski (1971) and Kurzanov and Bannikov (1983), *Nemegtosaurus* and *Quaesitosaurus* have been regarded as dicraeosaurids, based in large part on the preserved orientation of the quadrate and the relatively narrow proportions of the crowns (McIntosh, 1990a; Yu, 1993; Upchurch, 1995).
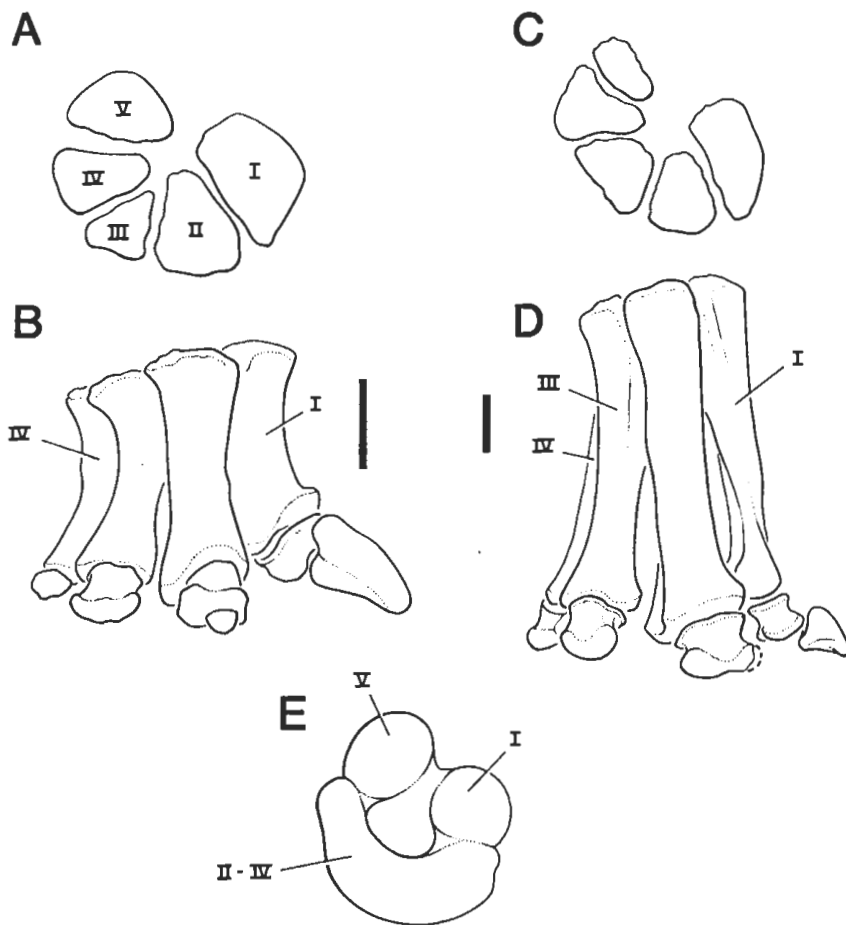
FIGURE 22. Right manus of cf. *Janenschia robusta* (**A, B**) and *Brachiosaurus brancai* (**C, D**) in proximal (**A, C**) and anterior (**B, D**) views (modified from Janensch, 1922). **E**, right manus print of *?Brontopodus* (modified from Thulborn, 1990:fig. 16.6b). Print is oriented relative to the trackway midline; anterior toward bottom of figure. Scale bars for **A–D** equal 10 cm.

Realization that these Mongolian sauropods may not be properly placed within Diplodocoidea first came with the description of the dicraeosaurid *Amargasaurus* (Salgado and Calvo, 1992). These authors restricted Dicraeosauridae to *Amargasaurus* and *Dicraeosaurus,* recognizing several synapomorphies that were not present in *Nemegtosaurus* and *Quaesitosaurus*. Later, Calvo (1994) suggested that the Mongolian skulls were titanosaurs, basing his reidentification on the similarity in crown shape between *Nemegtosaurus* and the North American titanosaur *Alamosaurus,* and on the low-angle wear facets that were present on some tooth crowns in *Nemegtosaurus*. Some of the crowns in *Nemegtosaurus,* however, bear V-shaped wear facets (Nowinski, 1971:pl. 13, fig. 3a), a primitive feature that occurs in nearly all sauropods except diplodocoids and titanosaurs.

Salgado and Calvo (1997) presented additional evidence for the interpretation of *Nemegtosaurus* and *Quaesitosaurus* as sauropods that are probably related to titanosaurs. They suggested that "the primitive architecture of the skull (occipital condyle and paroccipital processes posteroventrally oriented, basipterygoid processes ventrally directed and 'camarasauroid' conformation, and disposition of nares in the skull), coupled with the presence of certain derived characters (charaters [sic] a–d), indicate that *Nemegtosaurus* and *Quaesitosaurus* are not diplodocids but they are closely related to Titanosauridae" (Salgado and Calvo, 1997:42). Characters a–d refer to (a) the presence of "cylindrical, peg-like dentition confined to the extremity of the snout"; (b) the presence of "sharply inclined wear facets";

(c) "the mandibular symphysis is parallel to the long axis of the lower jaw"; and (d) "the supratemporal fenestra is very narrow." Neither the primitive skull architecture nor the putative titanosaurian synapomorphies, however, provide unambiguous evidence for a close phylogenetic relationship between the Mongolian taxa and titanosaurs. Characters (a) and (d) are also present in diplodocids and dicraeosaurids, respectively, (b) is primitive for eusauropods, and (d) has only been confirmed in *Antarctosaurus,* the assignment of which to Titanosauridae is at least controversial (McIntosh, 1990a; Jacobs, Winkler, Downs, and Gomani, 1993).

Several synapomorphies support the allocation of *Nemegtosaurus* and *Quaesitosaurus* to Macronaria rather than Diplodocoidea, such as the exclusion of the jugal from the orbital margin, a broad quadrate fossa, and presence of a prominent coronoid process (Wilson, 1997). In the following analysis, we have not included *Nemegtosaurus* or *Quaesitosaurus* as terminal taxa, as additional features support their inclusion within the terminal taxon Titanosauria, as first suggested by Calvo (1994). These features include the presence of thin, sheet-like basal tubera and of paroccipital processes with slender, ventrally directed non-articular processes. On the basis of several shared features (e.g., exclusion of squamosal from the margin of the supratemporal fenestra) and the absence of significant differences between the two specimens, Wilson (1997) suggested that *Nemegtosaurus* and *Quaesitosaurus* may, in fact, represent the same taxon.
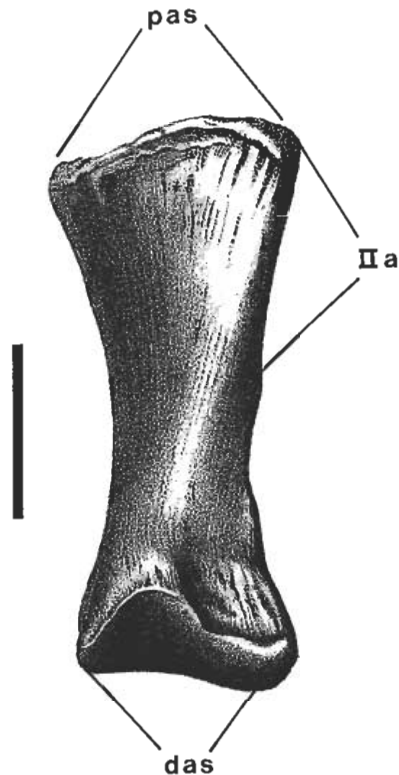
FIGURE 23.   Left metacarpal I of *Camarasaurus lentus* (YPM 1910) in anterior view (from Ostrom and McIntosh, 1966:pl. 60). Scale bar equals 5 cm.

INGROUP RELATIONSHIPS

Ingroup taxa derived from the phylogenetic analysis are described below. Phylogenetic definitions and diagnoses are given for each taxon. Phylogenetic definitions are designed for taxonomic stability (see Taxonomic Definitions), and phylogenetic diagnoses are based on supporting synapomorphies, which are described in detail for each ingroup. Synapomorphies are listed by their corresponding character number (followed by a colon and state number for multistate characters) under delayed-transformation optimization (Swofford, 1993). Character codings and character-state distributions are listed in Table 2 and in the Appendix.

Sauropoda Marsh, 1878

Definition—Sauropodomorphs more closely related to *Saltasaurus* than to *Plateosaurus*.

Recorded Temporal Range—Earliest Jurassic (Hettangian) to latest Cretaceous (Maastrichtian).

Diagnosis—Characterized by an obligatory quadrupedal posture with columnar orientation of the principal limb-bones (humerus, radius-ulna, femur, tibia-fibula); four or more sacral vertebrae (one caudosacral added); deltopectoral crest of humerus low; olecranon absent; ulna with triradiate proximal end; distal end of radius subrectangular and with flattened posterior margin for ulna; ilium with low ischial peduncle; ischial blade equal to or longer than pubic blade; ischial shafts with dorsoventrally flattened distal ends; femoral cross-section elliptical (with transverse long axis); fourth trochanter of femur reduced to low crest or ridge; astragalus lacking anterior fossa and foramina at base of ascending process; distal tarsals 3 and 4 absent (no ossified distal tarsals); metatarsals I and V with proximal ends subequal

in area to that of metatarsals II and IV; metatarsal V 70 percent or more of the length of metatarsal IV; pedal digit I ungual enlarged, deep and narrow (sickle-shaped).

(1) *Obligatory quadrupedal posture with columnar limbs and short metapodials*. Nearly all prosauropods and theropods are small to medium-sized dinosaurs that exhibit features associated with an habitual bipedal stance, the ancestral dinosaurian posture. The resting posture, for example, includes some flexure at the hip, knee, shoulder, and elbow joints, and the long axes of the femur and metatarsals show at least subtle curvature. Limb proportions include a forelimb that is substantially shorter than the hindlimb and metapodials that are 40% to 50% the length of respective epipodials.

In contrast, all sauropods including *Vulcanodon* increased body mass, with femoral length always exceeding one meter (Table 3) and with limb orientations and proportions suitable to accommodate extreme loading. The first and second segments of the forelimbs and hindlimbs assume a columnar orientation with no curvature in the femoral shaft and with reduction of the ulnar olecranon and tibial cnemial processes (Figs. 19, 20, 30–32). The forelimb is lengthened relative to the hindlimb (to at least 65% of the hindlimb), and the metapodials are reduced relative to the epipodials (nearly always less than 40% of that of the radius and tibia, respectively, except in some advanced sauropods that increase metacarpal length). These features are regarded here as correlates of large body size and an obligatory quadrupedal posture, because similar patterns are present in large graviportal mammals such as extant proboscideans.

(2:1) *Sacral vertebrae four or more in number (one caudosacral vertebra added)*. Prosauropods (e.g., *Massospondylus, Plateosaurus*; Cooper, 1981; Galton, 1990) and basal theropods (*Eoraptor, Herrerasaurus*; Sereno and Novas, 1992; Sereno, Forster, Rogers, and Monetta, 1993) have three sacral vertebrae with ribs that attach to the ilium. Although in all ornithischians and most theropods, there are five or more sacral vertebrae, three sacral vertebrae is the ancestral condition for Sauropodomorpha. The acquisition of a fourth sacral vertebra in *Melanorosaurus readi* (Van Heerden and Galton, 1997) and possibly *Massospondylus* (Cooper, 1981) is interpreted as an independent acquisition of a fourth sacral vertebra, not necessarily reflecting the origin of additional sacral vertebrae in basal sauropods. Based on the condition in these two outgroups, we suggest that the primitive sauropodomorph sacrum consisted of three vertebrae, and basal sauropods increased the number of sacral vertebrae by one, whereas *Omeisaurus* and neosauropods increased the number of sacral vertebrae by two (Fig. 14).

Fusion of sacral vertebrae in sauropod genera varies with the age of the individual (Hatcher, 1903; Riggs, 1904; Mook, 1917; Osborn and Mook, 1921; Gilmore, 1925; McIntosh et al., 1996). Riggs (1904) compared the timing of ossification of individual vertebrae in known sauropod sacra. He noticed that of the five vertebrae typically present in sauropod sacra (at that time only neosauropods were known), the median three elements fuse earliest in development, whereas the posterior dorsal or "dorsosacral" vertebra and the anterior caudal or "caudosacral" vertebra are incorporated into the sacrum later in development. Riggs suggested that the median three were the "true" sacral vertebrae present in early sauropods, while the others were incorporated more recently in sauropod evolution. Although early fusion of the median three sacral vertebrae appears to be the general case in most neosauropods, the first three sacral vertebrae are fused in *Haplocanthosaurus* (Hatcher, 1903) and *Brachiosaurus* (Janensch, 1950) .

The timing and extent of ossification of the dorsosacral and caudosacral vertebrae may indicate which of these was acquired first in the early evolution of sauropods. Sacra consisting of only four vertebrae have been reported for *Diplodocus* (Osborn, 1899; Hatcher, 1901), *Apatosaurus* (Riggs, 1904; Gilmore,

A

B   C   D
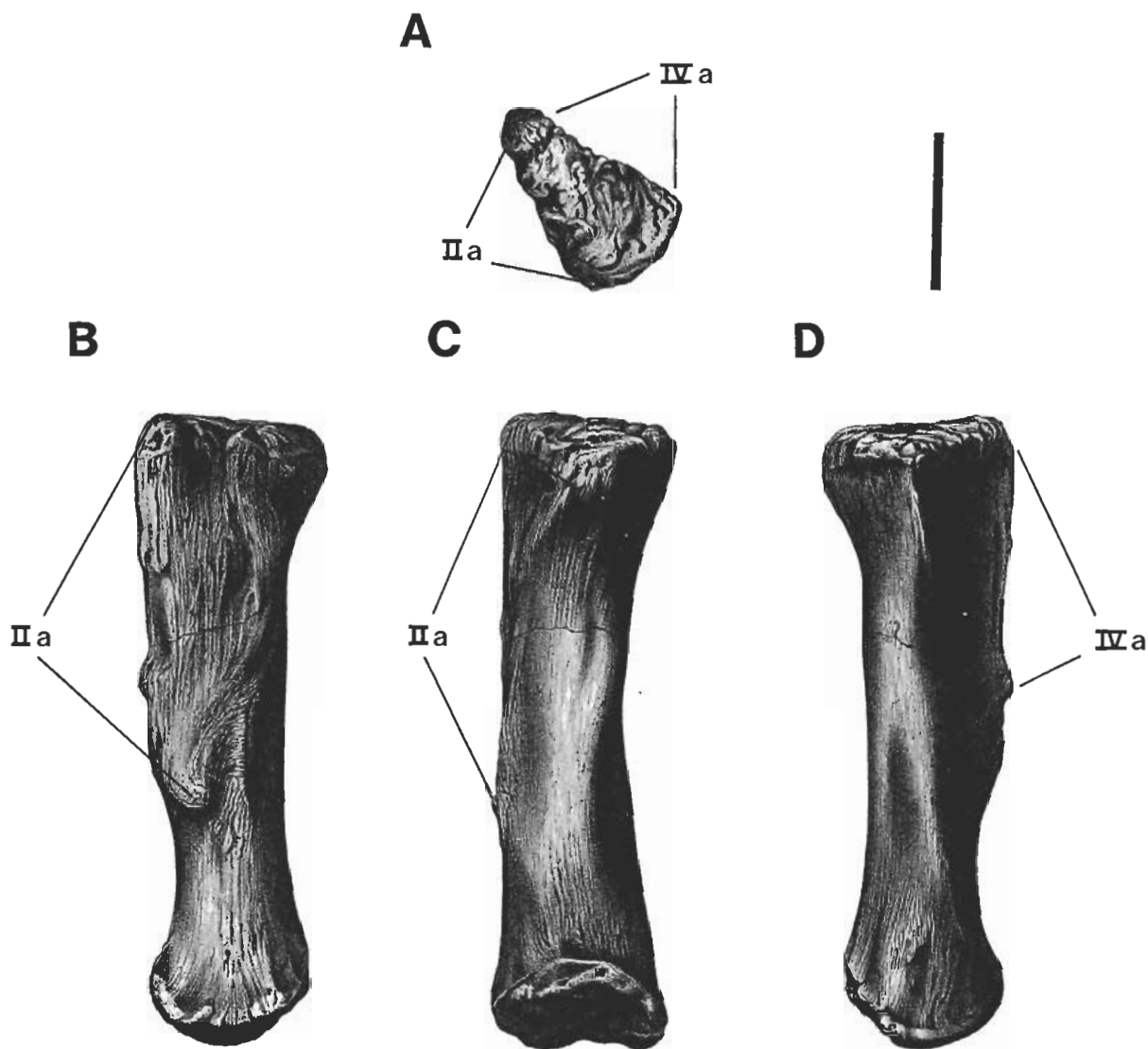
FIGURE 24. Left metacarpal III of *Camarasaurus* sp. (YPM 4633) in proximal (**A**), medial (**B**), anterior (**C**), and lateral (**D**) views (from Ostrom and McIntosh, 1966:pl. 57). Scale bar equals 10 cm.

1936), and *Camarasaurus* (Osborn and Mook, 1921; Fig. 27). In each case, the three fused "true" sacral vertebrae are followed by an incorporated caudosacral vertebra. This suggests that of the two recent incorporations into the sacrum, the caudosacral vertebra tends to fuse to the other sacrals before the dorsosacral vertebra, and may have been acquired earlier in evolution. Thus the inclusion of a fourth vertebra into the sacrum of sauropods may represent an incorporated anterior caudal vertebra.

In this character and later discussions of sacral number, we define a sacral vertebra by its attachment to the pelvic girdle, not by its fusion to other sacral vertebrae (although the two usually coincide in mature individuals).

(3) *Deltopectoral crest of humerus low.* Prosauropods and most theropods have prominent, hatchet-shaped deltopectoral crests that project anterolaterally from the shaft of the humerus. In prosauropods, for example, the crest extends as a robust, curved flange along the proximal half of the humerus. In contrast, the deltopectoral crest in *Vulcanodon* (Raath, 1972:fig. 4) and nearly all other sauropods is developed only as a low rugose ridge (Fig. 19). Brachiosaurids constitute a notable excep-

tion. The deltopectoral crest is developed as a significant flange that arches anterolaterally away from the shaft of the humerus (Janensch, 1961:pl. 16, fig. 1).

(4) *Olecranon reduced or absent.* In prosauropods and basal theropods, a rounded olecranon projects proximally from the humeral articular surface of the ulna (e.g., *Lufengosaurus,* Young, 1947; *Massospondylus,* Cooper, 1981). In contrast, in *Vulcanodon* (Cooper, 1984:fig. 7) and most sauropods, the proximal end of the ulna is nearly flat (e.g., *Camarasaurus*; Fig. 20E, F). Some sauropods, such as *Apatosaurus* (Gilmore, 1936:fig. 13) and *Barosaurus* (Janensch, 1961:pl. 17, fig. 2a, b), show an intermediate condition in which there is a distinct rounded olecranon. But the olecranon is well developed in sauropods only among titanosaurs (*Janenschia, Opisthocoelicaudia, Saltasaurus*; Janensch, 1961:pl. 17, fig. 7a; Borsuk-Bialynicka, 1977:fig. 8; Powell, 1992:fig. 32). The condition in titanosaurs is considered a reversal in light of all of the character evidence.

(5) *Proximal end of ulna triradiate, with deep radial fossa.* In prosauropods and theropods, the proximal articular end of the ulna is subtriangular with at best a shallow concavity along

A   **B**   **A**
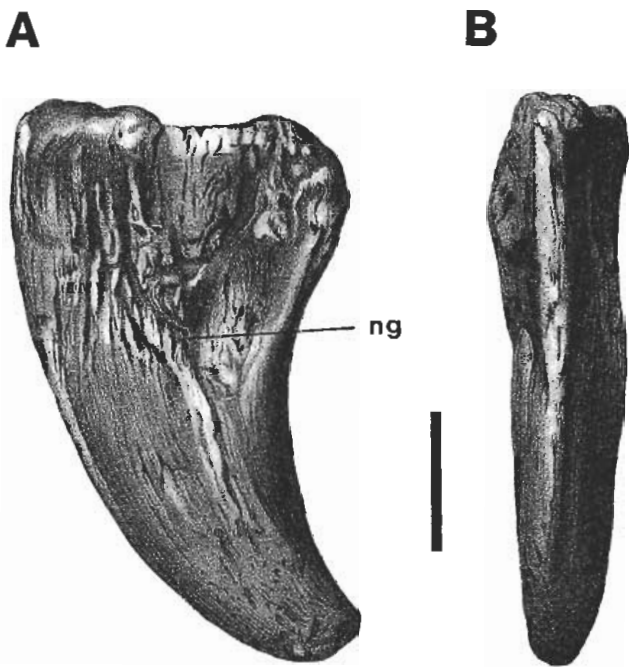

FIGURE 25.   Ungual of digit I of right manus of *Camarasaurus* sp. (YPM 4633) in medial (**A**) and dorsal (**B**) views (from Ostrom and McIntosh, 1966:pl. 63). Scale bar equals 5 cm.

FIGURE 26.   Right ilium (reversed) of *Camarasaurus grandis* (YPM 1901) in lateral (**A**) and ventral (**B**) views (from Ostrom and McIntosh, 1966:pl. 65). Scale bar equals 30 cm.

its lateral margin to accommodate the head of the radius (e.g., *Massospondylus, Herrerasaurus*; Cooper, 1981:fig. 30; Sereno, 1993:fig. 8).

In sauropods, in contrast, the ulna is triradiate in proximal view, with a broad trough facing anterolaterally for the head of the radius (McIntosh, 1990a:367; Fig. 20D). The trough is bounded by anterior and lateral projections; the former is the longer of the two. These features are well developed in *Vulcanodon,* in which the anterior process is particularly long (Cooper, 1984:fig. 8; note that Cooper [1984:fig. 9B] has mislabeled an anterior view of the radius and ulna as "posterior," and a lateral view as "medial"), in other basal sauropods such as *Omeisaurus* (He, Li, and Cai, 1988:fig. 46B), and in other sauropods including titanosaurs (Powell, 1992:fig. 32).

(6) *Distal condyle of radius subrectangular, with flat posterior margin for ulna.* In prosauropods and theropods, the radius has a straight shaft and a subcircular or oval distal end that abuts the distal end of the ulna along a small portion of its margin. This condition is present in all prosauropods (e.g., *Massospondylus,* Cooper, 1981:figs. 29, 30; *Lufengosaurus,* Young, 1947:fig. 4.4; *Plateosaurus,* Huene, 1926:pl. 3, fig. 10) and basal theropods (e.g., *Herrerasaurus,* Sereno, 1993:fig. 8).

In sauropods, in contrast, the shaft of the radius usually follows a gentle sigmoidal curve, and the distal end is flattened anteroposteriorly. In *Vulcanodon,* the radial shaft is curved, and, despite some erosion of the distal end of the radius, the distal shaft is clearly flattened anteroposteriorly (Cooper, 1984:fig. 9). The condition in *Shunosaurus* is more difficult to evaluate from available figures, but the distal end appears to be relatively broad (Zhang, 1988:fig. 47). In *Omeisaurus,* the radial shaft is gently curved and the distal end flattened (He, Li, and Cai, 1988:fig. 45). Other sauropods show the advanced condition, varying most in the degree to which the shaft is curved, from weakly (e.g., *Apatosaurus*; Gilmore, 1936) to strongly curved (e.g., *Camarasaurus,* Fig. 20A–C; *Saltasaurus,* Powell, 1992:fig. 33).

All known sauropods appear to have been obligatory quadrupeds with columnar limbs. Given those postural constraints,
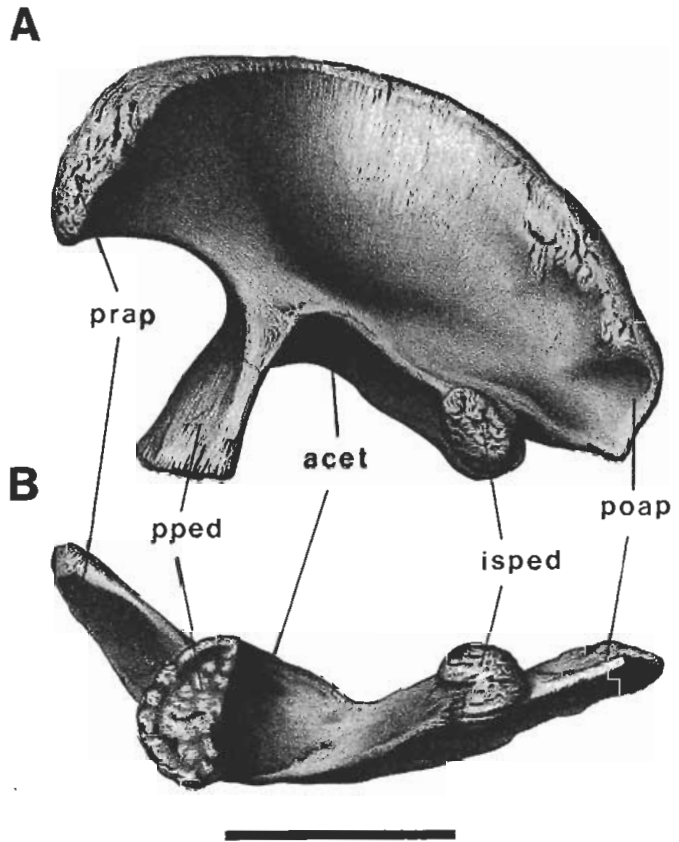
some degree of rotation in the forearm is required if the manus is to be directed laterally, or especially, anteriorly. In the largest quadrupedal mammals, the proximal end of the radius has shifted from a lateral to an anterior position relative to the ulna, and the shaft of the radius crosses that of the ulna so that the distal end is located on the medial side of the ulna. In this way, the manus points almost directly anteriorly.

In sauropods, the bones of the forelimb and the manus prints in trackways suggest that pronation of the manus in sauropods is well developed but less pronounced than in the largest mammalian quadrupeds. In sauropods, the proximal end of the radius is lodged within a deep radial fossa on the anterolateral side of the ulna. The curvature in the radial shaft accommodates its partial crossover of the ulnar shaft, and the flattened distal end of the radius articulates against the flat anterior margin of the ulna. The resultant median axis of the manus is directed mostly anteriorly and laterally as shown by many trackways (Fig. 22E). Although varying by as much as 30°, the median axis of the manus in natural articulation appears to be directed somewhat more anteriorly than laterally.

(7) *Ilium with low ischial peduncle.* In prosauropods and most theropods, the ischial peduncle is developed as a distinct ventral projection that separates the ramus of the postacetabular process of the ilium from the ischium by a substantial distance. The ischial peduncle is typically subtriangular in lateral view.

In sauropods, in contrast, the ischial peduncle is low and sometimes broader than deep, as in *Vulcanodon* (Cooper, 1984: fig. 16). In most sauropods, it has a low, subrectangular or trapezoidal shape in lateral view (e.g., *Apatosaurus, Barapasaurus*; Gilmore, 1936:fig. 19; Jain, Kutty, Roy-Chowdhury, and Chat-
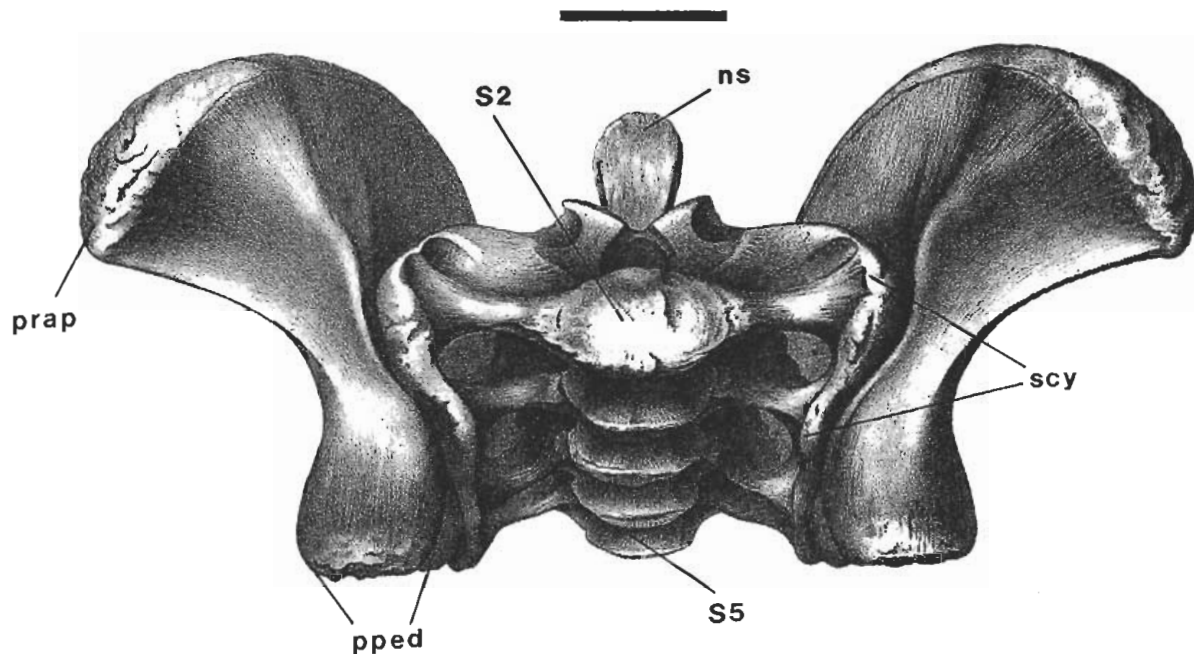
FIGURE 27. Ilia (YPM 1901 or 1905) and sacrum (YPM 1900) of *Camarasaurus grandis* in anterior view (from Ostrom and McIntosh, 1966: pl. 89). Scale bar equals 30 cm.
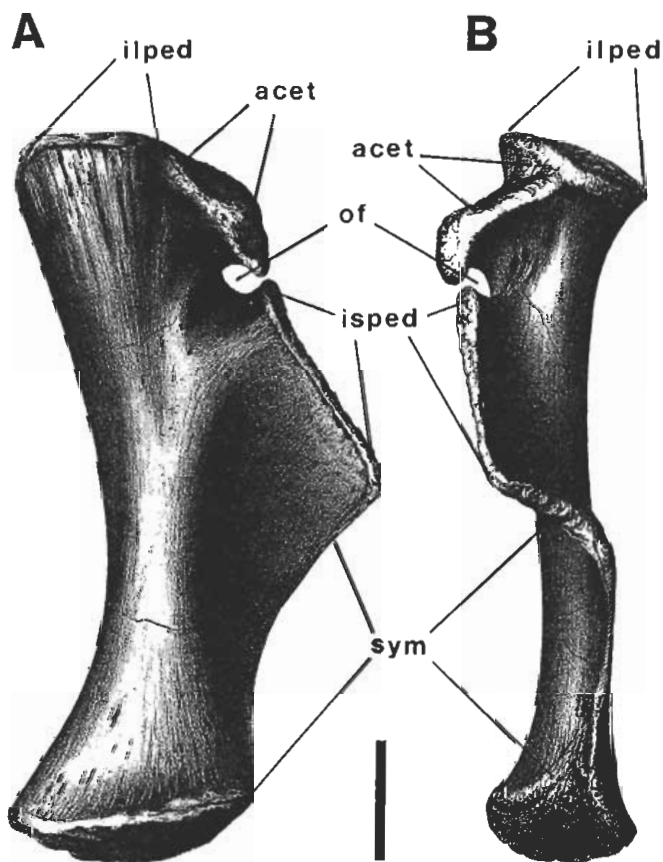
FIGURE 28. Right pubis (reversed) of *Camarasaurus lentus* (YPM 1910) in anterolateral (**A**) and posteromedial (**B**) views (from Ostrom and McIntosh, 1966:pl. 70). Scale bar equals 10 cm.

terjee, 1979:pl. 93B). In some individuals, the posterior margin of the peduncle is poorly defined, whereas, in others, there is a distinct notch between the ischial peduncle and the postacetabular process (e.g., *Apatosaurus, Camarasaurus*; Fig. 26). In all sauropods, however, the peduncle is low with only a short distance between the ventral margin of the postacetabular process and the ischium. The shortening of the ischial peduncle of the ilium is at least partially compensated for by an increase in the height of the iliac peduncle of the ischium. As a result, the long axis of the iliac blade, as seen in lateral view in natural articulation, is only tipped moderately anterodorsally, and the pubic peduncle extends ventral to the ischial peduncle (*Diplodocus, Apatosaurus, Opisthocoelicaudia, Shunosaurus*; Osborn, 1899: fig. 7; Gilmore, 1936:fig. 19; Borsuk-Bialynicka, 1977:fig. 12; Zhang, 1988:fig. 51).

(8) *Ischial shaft equal to, or longer than, pubic shaft.* In prosauropods and theropods, the shaft of the pubis is moderately to markedly longer than the shaft of the ischium. In prosauropods, the pubic blade is approximately 15% longer than the shaft of the ischium, with the latter measured from the base of the obturator expansion. A similar proportion is found in allosauroid theropods, although the differential in length is often considerably greater in other theropods.

In sauropods, the shaft of the ischium is as long as or longer than the shaft of the pubis. These altered proportions are largely the result of shortening of the length of the pubic shaft relative to the base of the pubis, because the overall length of the pubis is usually equal to, or greater than, that of the ischium (e.g., *Shunosaurus*; Zhang, 1988:fig. 51). The derived length of the ischial shaft is present in the basal titanosauriform *Euhelopus* (Wiman, 1929:pl. 4), but the shaft is shorter than the pubic shaft in all titanosaurs, which have markedly reduced the overall size of the ischium (e.g., *Opisthocoelicaudia*; Borsuk-Bialynicka, 1977:fig. 12).

(9) *Ischial shaft with dorsoventrally flattened distal end.* In prosauropods and theropods, the ischial shafts usually become rod-shaped toward their distal ends. In prosauropods, the distal portion of the ischial shaft is distinctly triangular, and the cross-
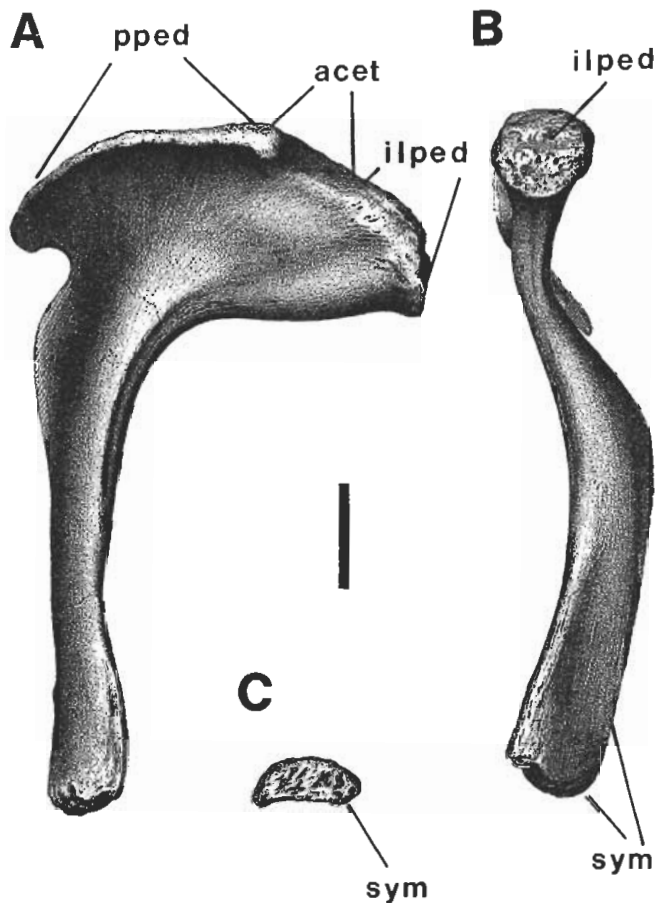
FIGURE 29. Right ischium (reversed) of *Camarasaurus grandis* (YPM 1905) in ventrolateral (**A**), oblique (posterodorsal and somewhat lateral) (**B**), and distal (**C**) views (from Ostrom and McIntosh, 1966:pl. 68). Scale bar equals 10 cm.

FIGURE 30. Left femur of *Camarasaurus grandis* (YPM 1901) in anterior (**A**) and medial (**B**) views (from Ostrom and McIntosh, 1966: pls. 72, 73). Scale bar equals 30 cm.

section of the conjoined shafts forms an inverted triangle (Cooper, 1981:fig. 55). In basal theropods, the ischial shafts tend to be more rod-shaped, as in *Coelophysis* (Padian, 1986:fig. 5.3). In *Herrerasaurus,* the narrow distal shafts of the ischia have an inverted triangular cross-section, as in prosauropods (Novas, 1993:fig. 5C). In more derived theropods, the distal ischial shaft is transversely compressed as it approaches the distal foot (e.g., *Allosaurus,* Madsen, 1976).

In sauropods, in contrast, the ischial shaft is flattened into a blade distally, as in many ornithischians. In *Vulcanodon,* the blade is somewhat transitional between that typical of prosauropods and sauropods. Its distal half, however, is flattened into a blade with a maximum width (measured from ischial symphysis to lateral margin of blade) approximately three times its minimal thickness (measured perpendicular to maximum width; see Cooper, 1984:fig. 19). Most sauropods have flattened the distal shaft to a greater degree, so that its maximum width is more than three times its minimum thickness (e.g., *Apatosaurus*; Ostrom and McIntosh, 1966:pl. 67). Even in *Camarasaurus,* which has an unusually narrow distal ischial blade, its width approaches three times its thickness (Fig. 29).

(10) *Femoral shaft with elliptical cross-section, long axis oriented mediolaterally.* In theropods and prosauropods, the femoral midshaft is suboval in cross-section. In the prosauropods *Lufengosaurus* and *Massospondylus,* the anteroposterior diameter is slightly greater than the transverse diameter in midshaft cross-sections (Young, 1947:fig. 6.1; Cooper, 1981:fig. 60E).

Herrerasaurus exhibits a nearly subcircular midshaft cross-section.

Nearly all sauropods, in contrast, show marked anteroposterior compression of the femoral shaft, as seen in *Vulcanodon* (Raath, 1972:31; Cooper, 1984:fig. 22). The long axis of the cross-section is always oriented transversely (McIntosh, 1990a; Fig. 30). The only exception is the diplodocoid *Amphicoelias,* in which the femoral shaft has a circular cross-section (Osborn and Mook, 1921:fig. 125; Wilson and Smith, 1996). The anteroposteriorly compressed form of the femoral shaft in sauropods may be associated with large body size, but similar modification of the shaft does not occur in large terrestrial mammals such as proboscideans.

(11) *Fourth trochanter of femur developed as a low crest.* The fourth trochanter in prosauropods and theropods projects from the shaft as a distinct flange with a characteristic subrectangular profile among prosauropods (e.g., *Massospondylus*; Cooper, 1981:fig. 60) and crescentic profile among theropods (e.g., *Allosaurus*; Madsen, 1976:pl. 50). In sauropods, the fourth trochanter is reduced to a low crest, as noticed by Riggs (1904) and others (Raath, 1972; Gauthier, 1986; McIntosh, 1990a; Fig.

FIGURE 31.   Left tibia, fibula, and astragalus of *Apatosaurus excelsus* (YPM 1980) in anterior view (from Ostrom and McIntosh, 1966:pl. 74). Scale bar equals 30 cm.

30B). The fourth trochanter is also reduced in all large quadrupedal ornithischians (ankylosaurs, stegosaurs, ceratopsids) and in the largest theropods (tyrannosaurs), and thus its reduction in sauropods may be related to their obligatory quadrupedal posture and large body size.

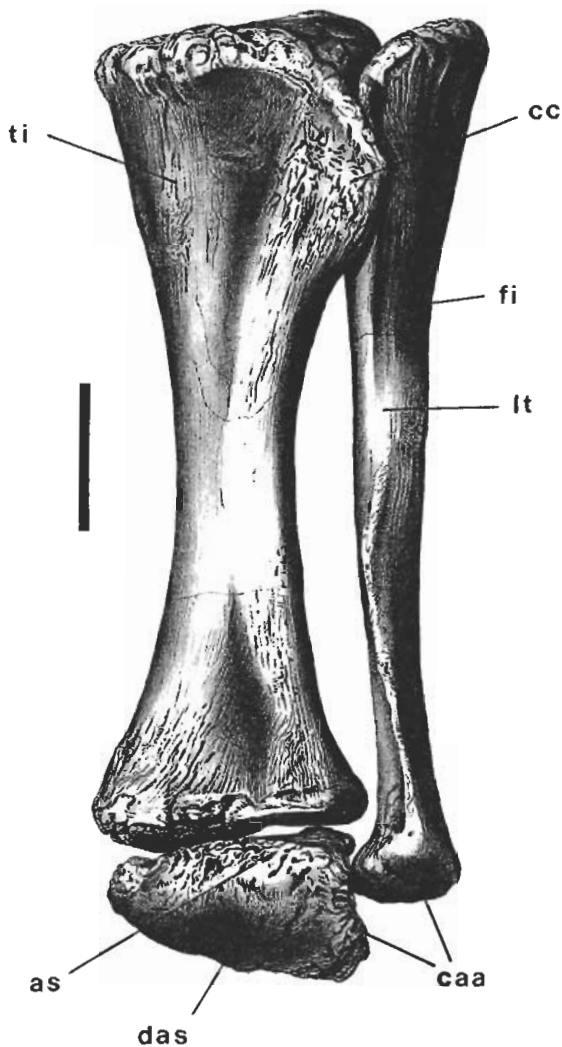(12) *Astragalar fossa and foramina at base of ascending process absent.* In prosauropods and theropods, conspicuous neurovascular foramina are located in an oval depression of variable size at the base of the ascending process, and are broadly exposed in anterior view of the astragalus. Accessory foramina are also present in a nonarticular hollow on the posterior aspect of the ascending process.

In sauropods, only the posterior foramina are present and are often enlarged. The fossa and foramina at the base on the anterior aspect of the ascending process are absent (Fig. 33). The articular surface of the ascending process and that of the distal roller meet along the anterior margin of the astragalus. These features are present in *Vulcanodon* (Cooper, 1984:fig. 25) and all other sauropods in which the astragalus is preserved (e.g., *Apatosaurus*; Fig. 31).

(13) *Distal tarsals 3 and 4 absent or unossified.* In prosauropods, theropods, and more distant outgroups, a pair of discshaped distal tarsals are present proximal to, and closely artic-

ulating with, metatarsals II–IV. These are identified as distal tarsals 3 and 4, the latter usually the thicker of the two with a posterior articular facet for metatarsal V (*Plateosaurus, Massospondylus*; Huene, 1926:pl. 6; Cooper, 1981:fig. 70). The condition in the basal theropods *Eoraptor* and *Herrerasaurus* is virtually identical. The only notable exception is found in the prosauropod *Blikanasaurus,* in which the pair of distal tarsals is located more medially over metatarsals I–III (Galton and Van Heerden, 1985), a configuration that seems unlikely to represent their natural articulation.

No ossified distal tarsals have ever been reported in sauropods. Either these bones were eliminated altogether or never ossified in sauropods.

(14) *Metatarsals I and V with proximal ends subequal in area to that of metatarsals II and IV.* In prosauropods and theropods, the proximal ends of the outer metatarsals (I, V) are smaller than the adjacent metatarsals (II, IV). As all currently known theropods have already begun to reduce pedal digit I, including *Eoraptor* (Sereno, Forster, Rogers, and Monetta, 1993) and *Herrerasaurus* (Novas, 1993), the condition in prosauropods is more relevant for outgroup comparisons. The ends of metatarsals I and V are smaller than adjacent metatarsals, but only by a small margin (e.g., *Lufengosaurus, Massospondylus*; Young, 1947:fig. 7; Cooper, 1981:fig. 72j).

In sauropods, the proximal ends of the external metatarsals (I, V) have an area as large as, or larger than, any of the internal metatarsals (II–IV), as seen in *Vulcanodon* (Cooper, 1984:fig. 27) or *Apatosaurus* (Gilmore, 1936:fig. 15). The increase in the proximal area of metatarsal I is dramatic, often exceeding that of metatarsal II and reflecting the full participation of pedal digit I in bearing the weight of the hindlimb in sauropods.

(15) *Length of metatarsal V 70 percent or more that of metatarsal IV.* In prosauropods and theropods, the length of metatarsal V is approximately half that of metatarsal IV (*Massospondylus,* Cooper, 1981; *Eoraptor,* Sereno, Martinez, and Alcober, in prep.). In sauropods, in contrast, the length of metatarsal V is 75% that of metatarsal IV in *Vulcanodon* and 85% in other sauropods (e.g., *Apatosaurus*; Gilmore, 1936:fig. 16). As with digit I, digit V in sauropods assumed an active role in bearing the weight of the hindlimb (Raath, 1972; Cruickshank, 1975; Van Heerden, 1978; Gauthier, 1986).

(16) *Ungual of pedal digit I enlarged.* The pedal unguals in sauropodomorphs are unusual in that the ungual on the first digit is always slightly longer than those on more lateral digits. In prosauropods such as *Lufengosaurus* and *Massospondylus,* this difference is subtle; the ungual of digit I is only about 10% longer than the ungual of digit II (Young, 1947:fig. 7; Cooper, 1981:figs. 78–80). The length of the first ungual can also be compared to the proximal phalanx of digit I, which is subequal in length.

In sauropods, in contrast, the ungual of pedal digit 1 is approximately 25% longer than the ungual of the second digit, as seen in the articulated pedes of *Apatosaurus* and *Dyslocosaurus* (Gilmore, 1936; McIntosh, Coombs, and Russell, 1992). Although the unguals of digits II and III in *Vulcanodon* are not preserved, the large first ungual can be compared to the ungual of digit IV, which is approximately half as long (Cooper, 1984: fig. 35). The marked size difference between these unguals in *Vulcanodon* indicates that sauropods exhibit a strong decreasing gradient in ungual size from digit I to digit IV.

(17) *Ungual of pedal digit I deep and narrow.* In prosauropods and theropods, the ventral surface each pedal ungual is flat, so that a cross-section of the ungual at midlength is subtriangular. In lateral view, the pedal unguals in these outgroups are gently recurved and taper uniformly toward their apices.

In sauropods, in contrast, the pedal unguals are transversely compressed, and most lack a distinct, flattened ventral surface. The first ungual in *Vulcanodon,* for example, is platelike in
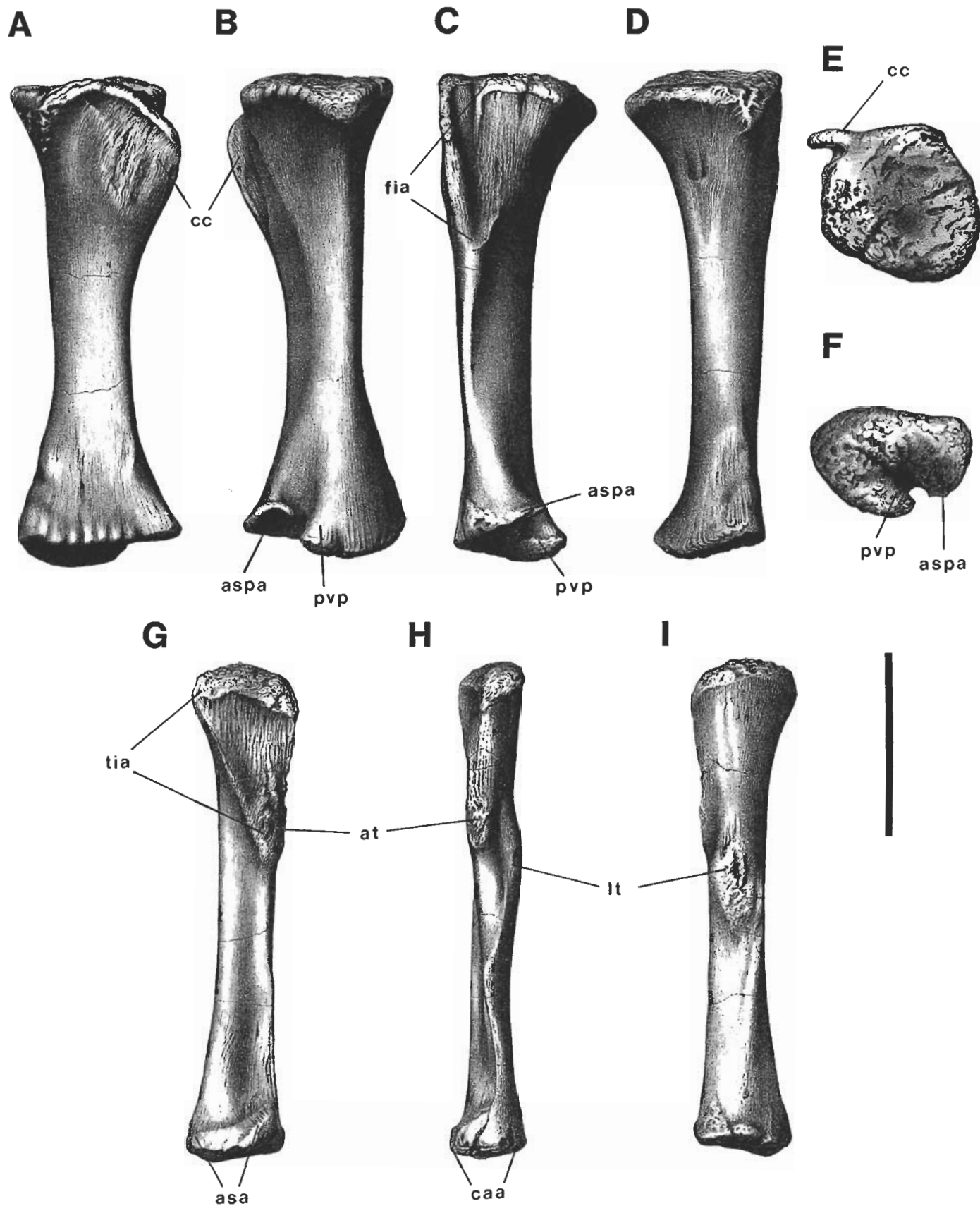
FIGURE 32.   Left tibia and fibula of *Camarasaurus grandis* (YPM 1905) with the tibia in anterior (**A**), posterior (**B**), lateral (**C**), medial (**D**), proximal (**E**), and distal (**F**) views and the fibula in medial (**G**), anterior (**H**), and lateral (**I**) views (from Ostrom and McIntosh, 1966:pls. 75–77). Scale bar equals 30 cm.
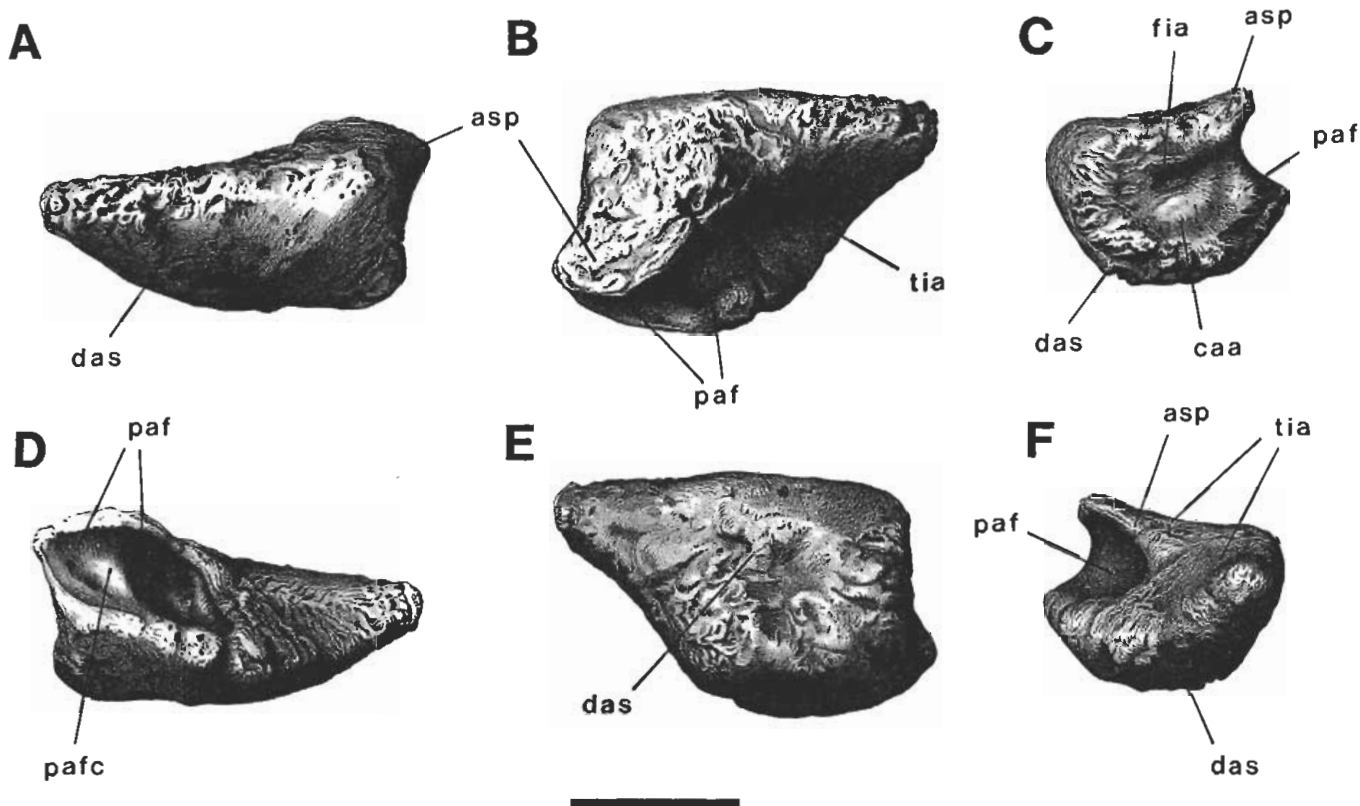
FIGURE 33. Left astragalus of *Camarasaurus grandis* (YPM 1901 or 1905) in anterior (**A**), proximal (**B**), lateral (**C**), posterior (**D**), distal (**E**), and medial (**F**) views (from Ostrom and McIntosh, 1966:pl. 78). Scale bar equals 10 cm.

dorsal view (Cooper, 1984:fig. 33C). In other sauropods, a narrow ventral surface is present but is often offset to one side of the ungual (e.g., *Camarasaurus*; Fig. 35). In lateral view, the pedal unguals in sauropods are proportionately deep and maintain depth throughout much of their length. As a result, the pedal unguals of sauropods are sickle-shaped (*Vulcanodon,* Cooper, 1984:fig. 33A, B; *Apatosaurus*; Gilmore, 1936:fig. 30). In *Vulcanodon,* at least the first ungual is sickle-shaped; the fourth ungual is flattened dorsoventrally, an unusual shape that may be peculiar to *Vulcanodon.*

Eusauropoda Upchurch, 1995

Definition—Sauropods more closely related to *Saltasaurus* than to *Vulcanodon.*

Recorded Temporal Range—Early Jurassic (Pliensbachian) to latest Cretaceous (Maastrichtian).

Diagnosis—External nares retracted posterodorsally; snout with stepped subnarial margin; antorbital fossa absent; maxillary border of external naris long; anterior process of prefrontal absent; squamosal-quadratojugal contact absent; anterior ramus of quadratojugal elongate and distally expanded; infraorbital region of cranium shortened anteroposteriorly; supratemporal region of cranium shortened anteroposteriorly; supratemporal fossa broadly exposed laterally; quadrate shaft with elongate posterior fossa; lateral ramus of palatine narrow; maximum depth of anterior end of dentary ramus approximately 150 percent minimum depth of ramus; tooth rows broadly arched anteriorly; spatulate tooth crowns; enamel with wrinkled texture; crown overlap; precise crown-to-crown occlusion; V-shaped wear facets (interdigitating occlusion); 13 or more cervical vertebrae; cervical centra opisthocoelous; mid-cervical neural arches tall (height greater than posterior face of centrum); dorsal neural

spines broader transversely than anteroposteriorly; distal chevrons with anterior and posterior processes; block-shaped carpals; phalanges on manual digits II and III reduced (II-ungual, III-3 and ungual absent; manual phalangeal formula 2-2-2-2-2 or lower); manual phalanges (other than unguals) broader than long; iliac blade with semicircular dorsal margin and expanded preacetabular process; pubic apron canted posteromedially; cnemial crest of tibia projecting laterally; posteroventral process of tibia reduced; fibula with lateral trochanter; metatarsal III length 25 percent or less that of tibia; metatarsal I with minimum shaft width greater than that of metatarsals II–IV; metatarsals with spreading configuration; nonterminal phalanges of pedal digits short; ungual of pedal digit I longer than metatarsal I; penultimate phalanges of pedal digits II–IV rudimentary or absent; pedal digits II–III with sickle-shaped unguals; ungual of pedal digit IV rudimentary or absent.

Comments—As noted above, we follow Upchurch's (1995) original stem-based definition of Eusauropoda, rather than the node-based definition by Salgado, Coria, and Calvo (1997). It appears, however, that Upchurch did not follow his own definition of Eusauropoda as "all sauropods, except for vulcanodontids" (1995:372). The problem arises from the use of Vulcanodontidae, a group that is paraphyletic by Upchurch's own definition, as the reference taxon to the stem-based definition. Because *Barapasaurus* is included within Vulcanodontidae (although linked with other sauropods by six synapomorphies), Eusauropoda is placed at the next most exclusive node, which, in Upchurch's arrangement, includes *Shunosaurus* (and other "euhelopodids") and neosauropods. As applied here, a stem-based definition restricts Eusauropoda to those sauropods more closely related to *Saltasaurus* than to *Vulcanodon.*

(18:1) *External nares retracted posterodorsally.* In prosau-

FIGURE 34.   Left proximal pedal phalanx of *Camarasaurus grandis* (YPM 1901 or 1905) in dorsal (**A**), proximal (**B**), and distal (**C**) views (from Ostrom and McIntosh, 1966:pl. 86). Scale bar equals 10 cm.
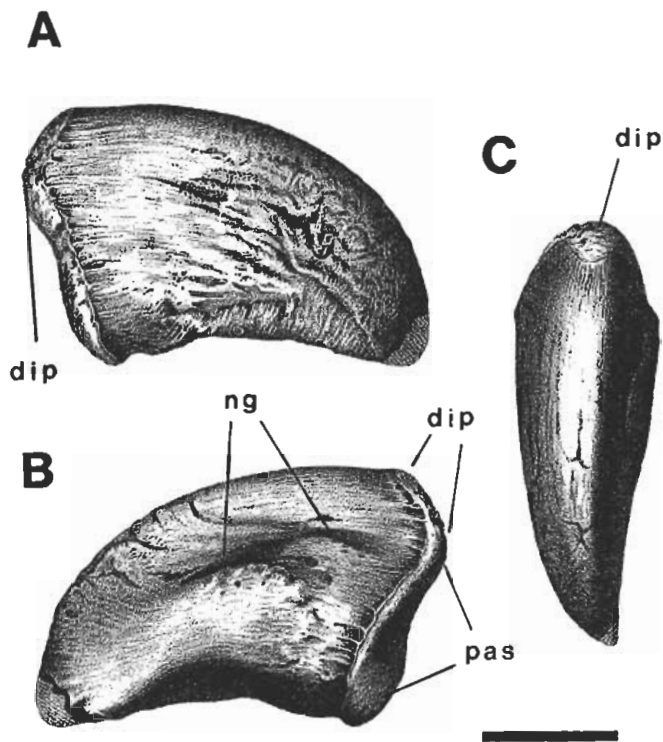
FIGURE 35.   Left ungual of pedal digit I of *Camarasaurus grandis* (YPM 1901 or 1905) in medial (**A**), lateral (**B**), and dorsal (**C**) views (from Ostrom and McIntosh, 1966:pl. 88). Scale bar equals 5 cm.
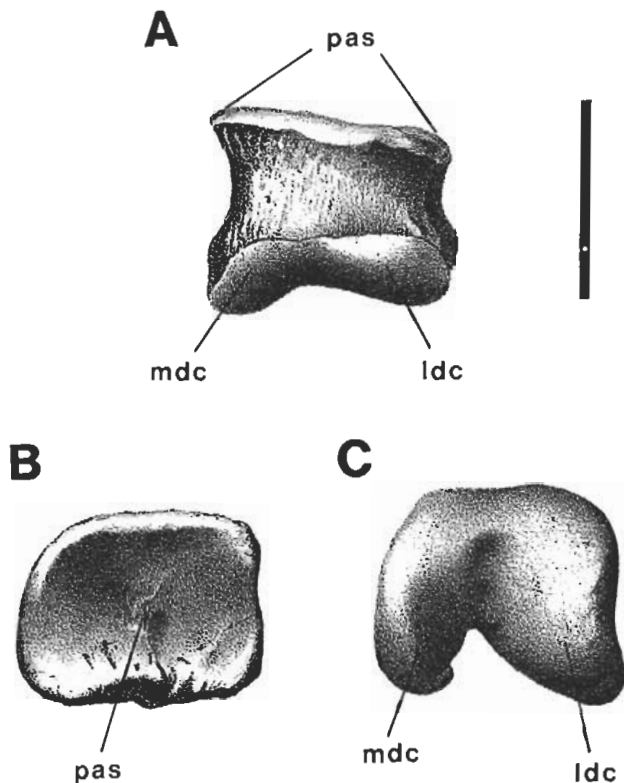
ropods and nonavian theropods, the external nares are located near the anterior end of the snout (Fig. 5). As cranial material is not available for *Vulcanodon,* the retracted position of the external nares and other eusauropod cranial synapomorphies listed below are ambiguous, and may eventually be shown to characterize all sauropods.

The external nares in *Shunosaurus* and all other eusauropods are retracted so that the dorsal margin of the narial opening is level with, or dorsal to, the dorsal margin of the orbit (Steel, 1970; Gauthier, 1986; McIntosh, 1990a; Upchurch, 1995; Fig. 37). The margin below the nares is deeper than that below any other cranial opening. In diplodocoids, the external nares are retracted farther posteriorly, so that their posterior margin is positioned dorsal to the orbit (Fig. 6). As in hadrosaurs that are characterized by marked narial retraction, the anterior and posterior position of the premaxilla and nasal, respectively, relative to the external naris in sauropods is maintained despite the posterior migration of the narial openings (Figs. 6–8).

Characters regarded by us as correlated with narial retraction include the deep body of the premaxilla, proximity of the external naris and orbit, proximity of the maxilla and prefrontal, and absence of an anterior ramus on the lacrimal. We regard the shorter proportions of the postnarial portion of the skull roof ("shortened skull roof"; Upchurch, 1995:372) as an additional correlate of narial retraction.

(19) *Snout with stepped anterior margin.* In prosauropods and theropods, the profile of the snout follows a smooth curve from the internarial bar to the alveolar margin (Fig. 5). The alveolar and subnarial regions (muzzle) do not protrude in advance of the external nares.

In eusauropods, on the other hand, the subnarial portion of the snout protrudes anteriorly and laterally beyond the external

nares. In lateral view, the anterior margin of the snout of *Shunosaurus* has a distinct step, with the subnarial portion of the premaxilla projecting slightly anterior to the internarial bar (Zhang, 1988:figs. 3, 12). The rounded rim of this subnarial projection, which is marked by low rugosities in *Shunosaurus* and *Camarasaurus,* continues posteriorly on the maxilla. Specimens of both of these genera, furthermore, show that the stepped margin of the snout becomes more distinct with maturity (Zhang, 1988; Madsen et al., 1995). The snout is sharply demarcated in *Omeisaurus* (He, Li, and Cai, 1988:figs. 12, 14), and in *Camarasaurus* and *Brachiosaurus* (Figs. 7, 8), where the anterior projection of the snout is maximally developed. In *Shunosaurus, Euhelopus* (Mateer and McIntosh, 1985:fig. 5), and the titanosaur *Malawisaurus* (Jacobs, Winkler, Downs, and Gomani, 1993:fig. 1A), the step in the snout margin remains more moderate.

(20) *Antorbital fossa absent.* In prosauropods and theropods, the smooth inset surface of the antorbital fossa is present along most of the border of the external antorbital fenestra. In prosauropods, this margin is broadest on the maxilla, as in *Plateosaurus* (Fig. 5). In most theropods, the smooth medial wall of the fossa is well developed (Witmer, 1997). Eusauropods, in contrast, lack any development of an inset margin around the antorbital fenestra (Figs. 6–8). Persistence of the antorbital fenestra in sauropods, however, supports the continued presence of an antorbital sinus, which may be associated with a depression on the medial side of the maxilla along the border of the fenestra (Madsen et al., 1995:fig. 10B; Witmer, 1997:27). Nevertheless, as seen in lateral view of the eusauropod skull, there is no development of a smooth supporting flange for the antorbital sinus, a unique condition among dinosaurs.

(21) *Maxillary border of external naris long.* In prosauropods, there is a short maxillary border on the external nares (e.g., *Plateosaurus;* Fig. 5). In basal theropods, such as *Eorap-*
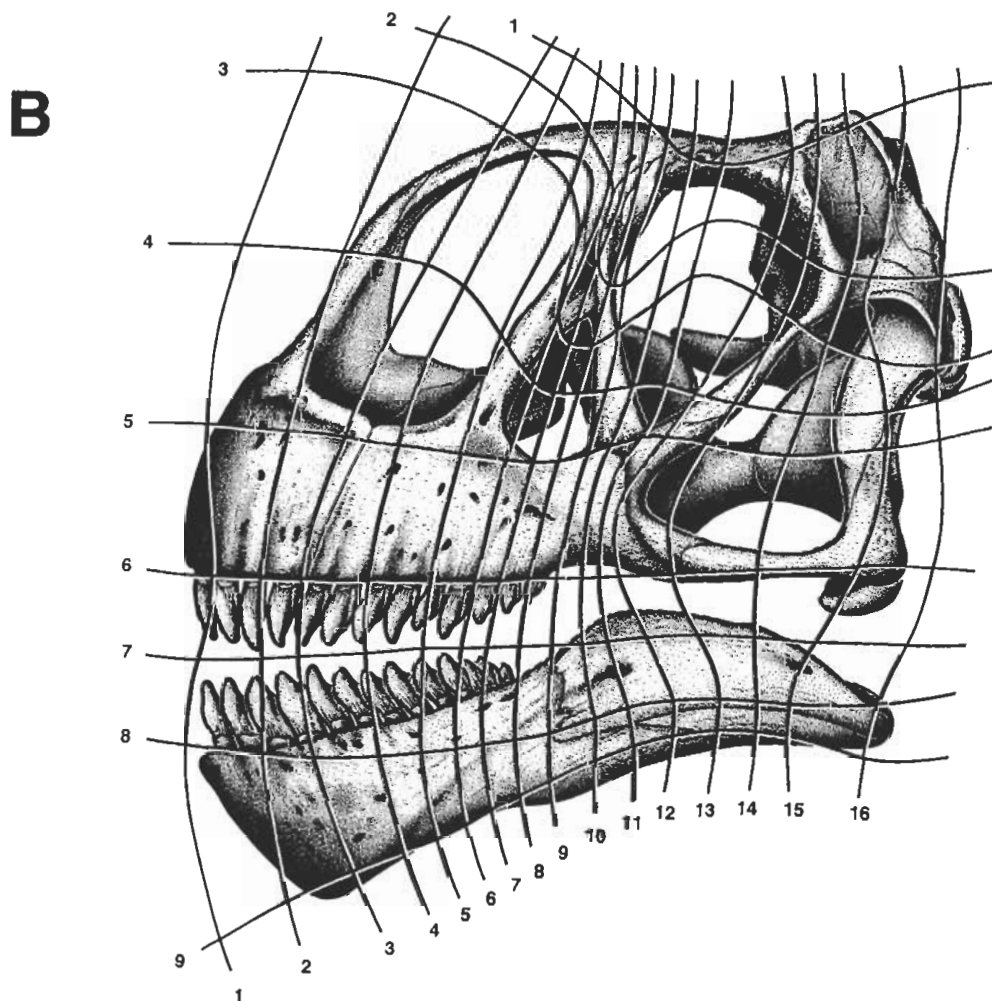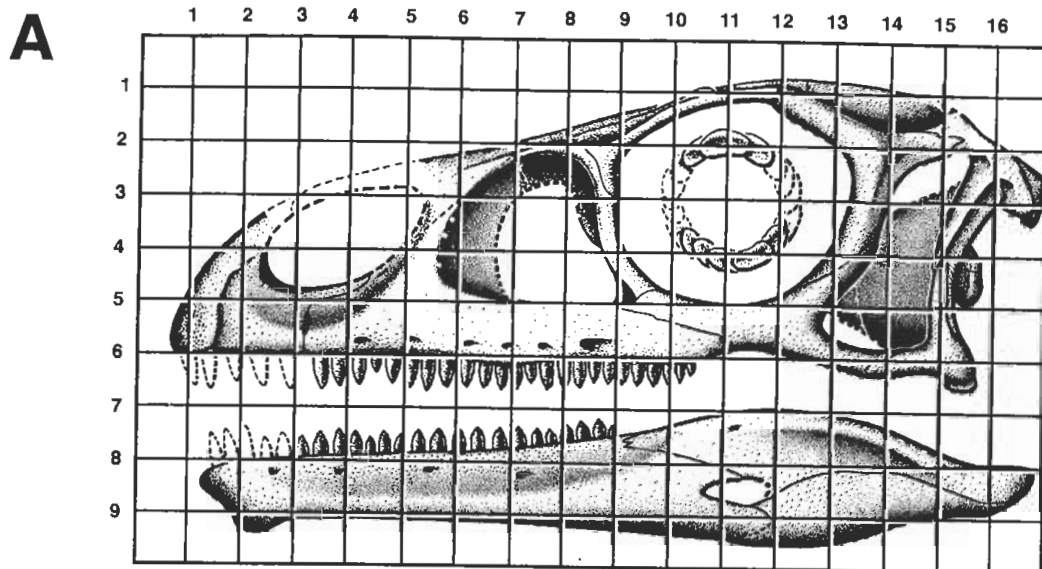
FIGURE 36. Transformation grid based on sutures and other landmarks showing the regions of the sauropod skull that have undergone the greatest shape change. **A**, reconstruction of the skull of the prosauropod *Riojasaurus incertus* (based on ULR 56) in lateral view; **B**, reconstruction of the skull of a subadult individual of *Camarasaurus lentus* (based on CM 11338).
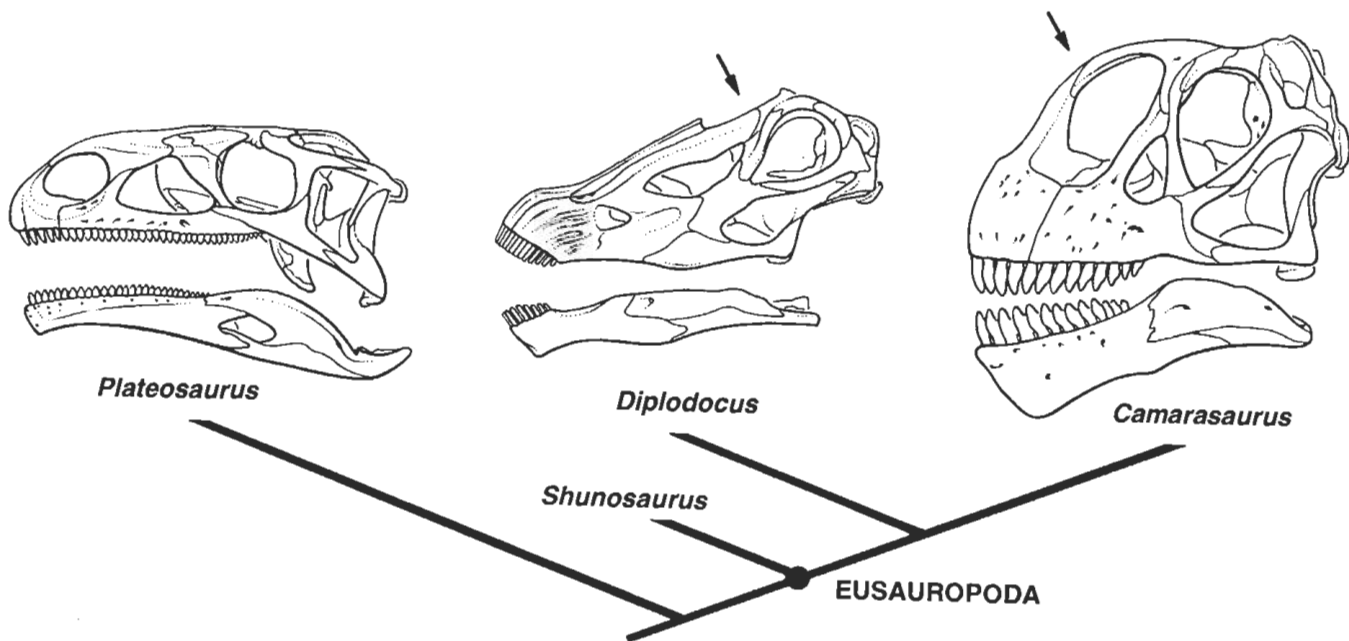
FIGURE 37.   Phylogenetic diagram comparing the skulls (in lateral view) of *Plateosaurus engelhardti, Diplodocus,* and a subadult individual of *Camarasaurus lentus.* Retraction of the external nares (arrows; character 18:1) is a synapomorphy for Eusauropoda.
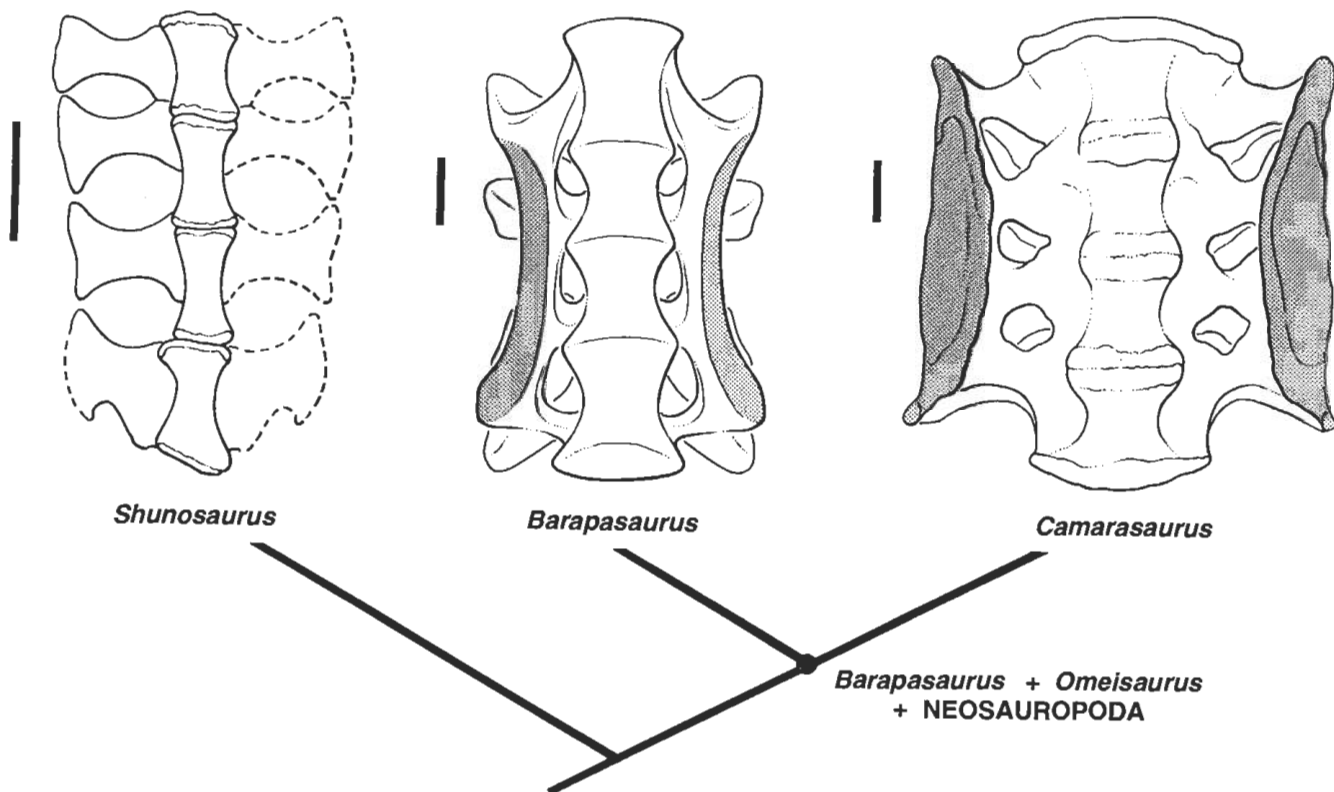
FIGURE 38.   Phylogenetic diagram comparing the sacra (in ventral view) of *Shunosaurus lii* (after Zhang, 1988), *Barapasaurus tagorei* (after Jain, Kutty, and Roy-Chowdhury, 1975), and *Camarasaurus supremus* (after Osborn and Mook, 1921). Anterior is toward the top of the page. Fusion of the distal ends of the sacral ribs forms a sacricostal yoke (stippled) in the adult (character 61), which is a synapomorphy for the subgroup of sauropods including *Barapasaurus, Omeisaurus,* and Neosauropoda. Scale bars equal 10 cm.

FIGURE 39. Phylogenetic diagram comparing the posterior cervical vertebrae (in lateral view) of *Shunosaurus lii* (after Zhang, 1988; note that the view is slightly dorsal), *Omeisaurus tianfuensis* (after He, Li, and Cai, 1988), and *Diplodocus carnegii* (after Hatcher, 1901). Deeply invaginated cervical pleurocoels (stippled) that are subdivided by at least one major septum (characters 68, 69) are synapomorphies for *Omeisaurus* plus Neosauropoda.
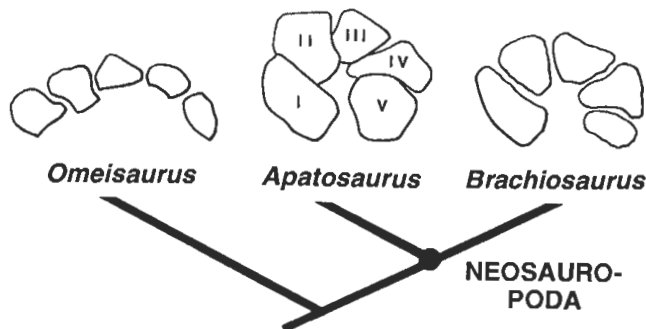
FIGURE 40. Phylogenetic diagram comparing the shape and articular configuration of the left metacarpals (in proximal view) of *Omeisaurus tianfuensis* (after He, Li, and Cai, 1988), *Apatosaurus excelsus* (after Gilmore, 1936), and *Brachiosaurus brancai* (after Janensch, 1961). The wedge-shaped proximal ends of the metacarpals together form an arc of approximately 270° in proximal view (character 81), a synapomorphy for Neosauropoda.

tor (Sereno, Forster, Rogers, and Monetta, 1993:fig. 1b) and *Herrerasaurus* (Sereno and Novas, 1993:fig. 12A), and in ornithischians, the maxilla is excluded from the narial margin by the posterolateral process of the premaxilla.

In eusauropods, on the other hand, the maxilla forms a long section of the posteroventral margin of the external naris (Gauthier, 1986), broadly separating the posterolateral process of the premaxilla and anteroventral process of the nasal (Figs. 7, 8). This condition is maintained in diplodocoids despite the extreme posterodorsal location of the external nares (Fig. 6).

(22) *Anterior process of prefrontal absent.* In prosauropods and theropods, the prefrontal has a short process that extends anteriorly between the lacrimal and nasal, as best seen in dorsal view of the skull (Fig. 5). In eusauropods, there is no development of this process and no separation of lacrimal and nasal by the prefrontal (Figs. 6–8).

(23) *Squamosal-quadratojugal contact absent.* In prosauropods and basal theropods, the squamosal and quadratojugal usually join at their tips, excluding the quadrate from the posterior margin of the laterotemporal fenestra (Fig. 5). These relations are preserved in many prosauropods, *Eoraptor* (Sereno, Forster, Rogers, and Monetta, 1993:1b), *Herrerasaurus* (Sereno and Novas, 1993:fig. 8A), and in the basal ornithischian *Lesothosaurus* (Sereno, 1991:fig. 12A).

In eusauropods, the squamosal fails to contact the quadratojugal, and the quadrate forms a short portion of the posterior border of the laterotemporal fossa (Gauthier, 1986). *Camarasaurus* is an exception, which we regard as a reversal (Fig. 7). Upchurch (1995) listed the absence of squamosal-quadratojugal contact as a synapomorphy of "euhelopodids" and diplodocids, but the condition is much more widespread within Sauropoda, characterizing *Shunosaurus* (Zhang, 1988:figs. 3, 12), diplodocoids (Fig. 6), *Brachiosaurus* (Fig. 8), and *Euhelopus* (Mateer and McIntosh, 1985:fig. 6).

(24) *Anterior ramus of quadratojugal elongate, distally expanded.* In prosauropods, theropods, and basal ornithischians, the dorsal ramus of the quadratojugal is slightly longer than the anterior ramus, as measured from the corner of the laterotemporal fenestra (Fig. 5). This condition is well-developed in several prosauropods, *Eoraptor* (Sereno, Forster, Rogers, and Monetta, 1993:fig. 1b), *Herrerasaurus* (Sereno and Novas, 1993: fig. 8A), and *Lesothosaurus* (Sereno, 1991:fig. 12A). Furthermore, in all of these taxa, the anterior ramus tapers distally.

In eusauropods, the opposite conditions are uniformly present. The anterior ramus of the quadratojugal is approximately twice as long as the dorsal ramus and expands toward its anterior end. This derived form of the quadratojugal is present in *Shunosaurus* (Zhang, 1988:figs. 3, 12), diplodocoids (Fig. 6), *Camarasaurus* (Fig. 7), *Brachiosaurus* (Fig. 8), and titanosaurs (*Nemegtosaurus*; Nowinski, 1971:fig. 1; *Quaesitosaurus*; Kurzanov and Bannikov, 1983:fig. 1).

(25) *Infraorbital region of cranium shortened anteroposteriorly.* In prosauropods and theropods, the jugal separates the antorbital and laterotemporal openings by a significant distance on either side of the orbit (Fig. 5). In eusauropods, in contrast, the infraorbital region of the cranium is very short anteroposteriorly, and the antorbital and laterotemporal openings approach one another (Gauthier, 1986; Upchurch, 1995). As described by McIntosh (1990a:354), the sauropod cranium appears as if it were "squeezed," the orbit being forced upward as the antorbital and lateral temporal fenestrae have come together (Figs. 6–8). The laterotemporal fenestra, in particular, extends anteriorly ventral to at least the posterior half of the orbit. Although there is modest expression of this anterior extension of the laterotemporal fenestra in some prosauropods (e.g., *Lufengosaurus*; Young, 1941:figs. 3, 4) and *Herrerasaurus* (Sereno and Novas, 1993:fig. 8A), the condition in sauropods is more extreme.

Other characters that we regard as correlated with infraorbital shortening include the subtriangular orbit with sharply notched ventral margin, absence of a posteriorly tapering lacrimal pro-
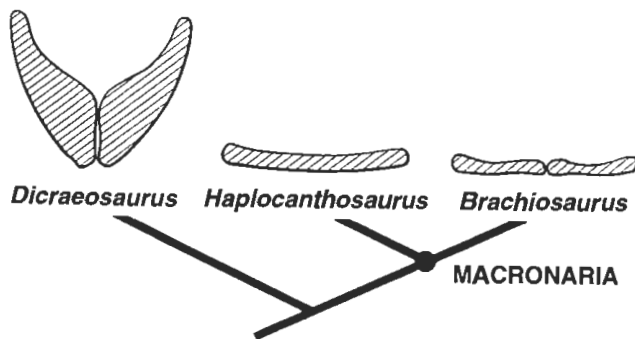
FIGURE 41. Phylogenetic diagram comparing a cross-section near the distal ends of the ischial shafts of *Dicraeosaurus hansemanni* (after Janensch, 1961), *Haplocanthosaurus priscus* (after Hatcher, 1903), and *Brachiosaurus brancai* (after Janensch, 1961). Coplanar distal ischial shafts (character 88) is a synapomorphy for Macronaria.
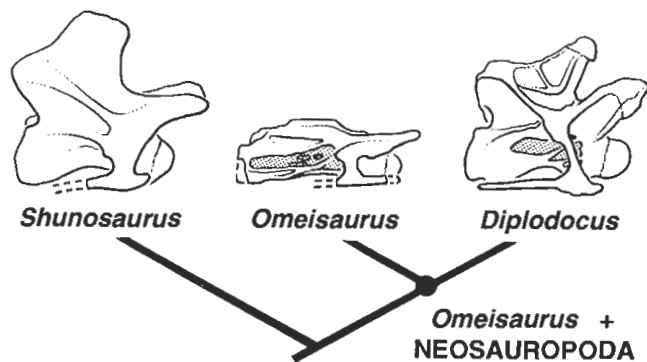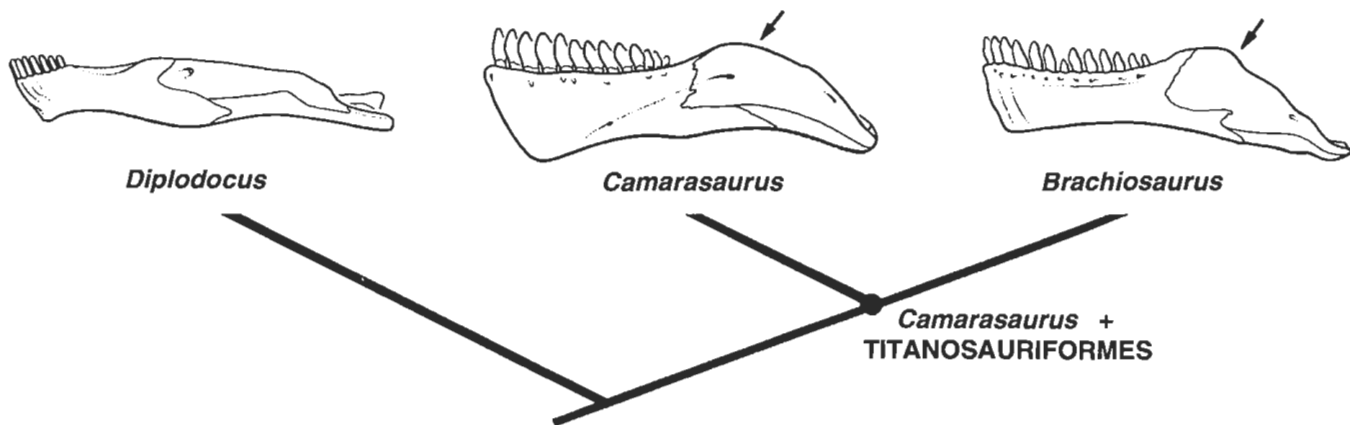
FIGURE 42.   Phylogenetic diagram comparing the lower jaws (in lateral view) of *Diplodocus* (based on CM 11131), *Camarasaurus lentus* (based on CM 11338), and *Brachiosaurus brancai* (after Janensch, 1935–1936). A pronounced coronoid process on the surangular (arrows; character 91) is a synapomorphy for *Camarasaurus* plus Titanosauriformes.

cess along the anteroventral border of the orbit, shortening or elimination of the contribution of the jugal to the ventral margin of the cranium, and the proximity of the maxilla and quadratojugal.

(26) *Supratemporal region of cranium shortened anteroposteriorly.* In prosauropods and theropods, the temporal bar is longer anteroposteriorly than deep transversely (Fig. 5). In eusauropods, in contrast, the temporal bar is very short, and, as a result, the upper portion of the laterotemporal fenestra is narrow (Figs. 6–8). In general, the supratemporal region appears to be compressed anteroposteriorly in sauropods.

(27) *Supratemporal fossa broadly exposed laterally.* In prosauropods and theropods, the supratemporal fossa faces dorsally and is largely obscured in lateral view by the postorbital-squamosal temporal bar (Fig. 5). In eusauropods, in contrast, the

FIGURE 43.   Phylogenetic diagram comparing the right femora (in anterior view) of *Camarasaurus supremus* (after Osborn and Mook, 1921), *Brachiosaurus brancai* (after Janensch, 1961), and the titanosaur *Saltasaurus loricatus* (after Powell, 1992). Medial deflection of the proximal end of the femur (arrows; character 100) is a synapomorphy for Titanosauriformes.

supratemporal fossa is broadly exposed in lateral view, which appears to be largely the result of a ventral shift in the position of the temporal bar (Figs. 6–8). The quadrate head is also fairly low in position (at mid-orbit level) in sauropods, but a similarly low position for the quadrate head in some prosauropods does not result in lateral exposure of the supratemporal fossa. The lateral exposure of the supratemporal fossa is clearly present in the basal sauropod *Shunosaurus* (Zhang, 1988:fig. 3).

(28) *Quadrate shaft with elongate posterior fossa.* In prosauropods and theropods, the dorsal two-thirds of the quadrate shaft is transversely narrow, and the quadrate foramen is located approximately at mid-height along the shaft adjacent to the suture with the quadratojugal (e.g., *Plateosaurus*; Fig. 5C).

In eusauropods, in contrast, the dorsal two-thirds of the quadrate shaft is occupied by a vertically elongate fossa, as is best exposed in posterior view of the skull. In this view, the fossa is bounded by the principal strut of the quadrate shaft medially, and the quadratojugal and squamosal laterally. In basal eusauropods such as *Shunosaurus* (Zhang, 1988:fig. 5), *Omeisaurus* (He, Li, and Cai, 1988:fig. 10) and diplodocoids (Hatcher, 1903: fig. 1; Fig. 6C), the fossa is modestly developed. In more advanced eusauropods, such as *Camarasaurus* (Fig. 7B), the fossa is deep and sharply defined.

(29) *Lateral ramus of palatine narrow.* In prosauropods, theropods, and ornithischians, the lateral portion of the palatine is plate-shaped with a long contact laterally with the maxilla (Fig. 5). In eusauropods, the palatine is reduced to a relatively narrow process that projects anterolaterally toward its contact with the maxilla on the ventral surface of the palatal shelf. The palatine is well-preserved in *Diplodocus, Camarasaurus,* and *Brachiosaurus* (Figs. 6–8), and also has the derived form and orientation in *Shunosaurus* (Zhang, 1988:fig. 11).

(30) *Dentary ramus, maximum depth of anterior end approximately 150 percent minimum depth of ramus.* In prosauropods and theropods, the depth of the anterior end of the dentary ramus is not markedly different from its depth midway along the ramus. In some prosauropods, the anterior end of the dentary has a modest ventral expansion (e.g., *Riojasaurus*). The depth of the anterior end of the dentary, however, is almost always slightly less than the depth of the ramus at midlength (Fig. 5). The condition in *Vulcanodon* unknown.

Shunosaurus and more advanced sauropods have increased the depth of the anterior ramus to approximately 150% of the minimum depth of the ramus. In scoring this character, it is important to consider carefully the completeness of the anterior
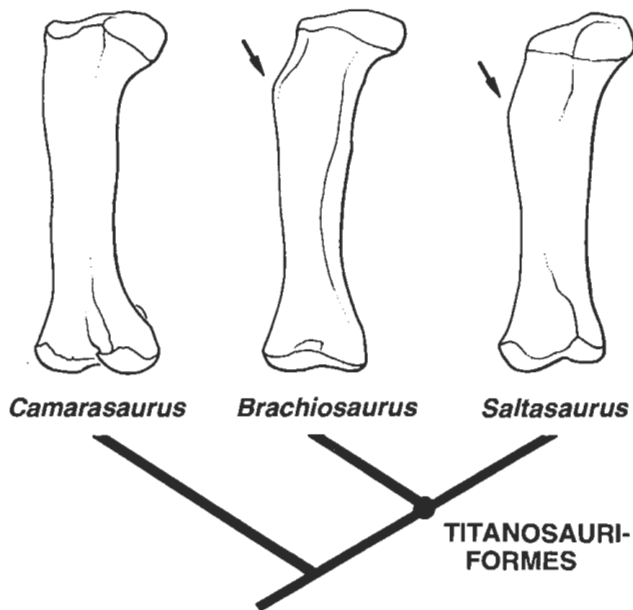
TABLE 1. Completeness of cranial, vertebral, and appendicular remains of sauropod terminal taxa used in this analysis. Abbreviations: +, represented; ?, not represented; P, partially represented.

Taxon	Skull	Teeth	Cerv.	Dorsal	Sacral	Caudal	Fore	Hind
Vulcanodon	?	?	?	P	P	P	P	P
Shunosaurus	+	+	+	+	+	+	+	+
Barapasaurus	?	P	P	+	+	+	P	P
Omeisaurus	+	+	+	+	+	+	+	+
Diplodocoidea	+	+	+	+	+	+	+	+
Haplocanthosaurus	?	?	+	+	+	P	?	P
Camarasaurus	+	+	+	+	+	+	+	+
Brachiosauridae	+	+	+	+	+	+	+	+
Euhelopus	P	+	+	+	+	?	P	P
Titanosauria	P	P	+	+	+	+	+	+

end of the ramus. In many specimens, either the anteroventral corner or portions of the alveolar margins are broken away. In *Shunosaurus,* the anterior end of the dentary is not expanded as preserved in one skull (Zhang, 1988:fig. 16). In another sketch of the same skull, the anterior end of the dentary is shown as expanded (Zhang, 1988:fig. 18), although a photograph demonstrates that the first drawing accurately shows the portions that are preserved (Zhang, 1988:pl. 1). A third skull (ZG65430; Zheng, 1996:fig. 15) demonstrates the derived condition, with an anterior dentary expanded to 147% the minimum depth of the ramus. In *Omeisaurus,* well preserved dentaries show that the anterior end expands to a width of approximately 170% of the minimum width of the ramus (He, Li, and Cai, 1988: fig. 17. The anterior end of the dentary is expanded to approximately 150% of the minimum depth of the ramus in the diplodocoids *Dicraeosaurus* (Janensch, 1950: fig. 111) and *Diplodocus* (Fig. 6A) and in *Camarasaurus* (Fig. 7A). In the titanosaur *Nemegtosaurus* (Nowinski, 1971: pl. 14, fig. 1d), the anterior end of the dentary is expanded (to approximately 145%), as is also true of the much more slender dentary of the titanosaur *Malawisaurus* (to approximately 150%; Jacobs, Winkler, Downs, and Gomani, 1993:fig. 1B, C).

(31) *Tooth rows broadly arched anteriorly (U-shaped).* In prosauropods and basal theropods, the tooth rows join anteriorly at a relatively sharp angle, and the premaxillary palate is narrow and deep (Fig. 5). Among prosauropods, *Massospondylus* (Attridge et al., 1985; Gow et al., 1990) and *Lufengosaurus* (Young, 1941) have the broadest skull proportions, but even in these prosauropods, the snout and anterior arch of the tooth rows remain relatively narrow and V-shaped as compared to the

condition in sauropods. The tooth rows in *Shunosaurus* (Zhang, 1988:figs. 11, 13) and all subsequent sauropods (Figs. 6–8) are broadly arched (U-shaped) anteriorly.

(32:1) *Spatulate tooth crowns.* In prosauropods and most theropods, cross-sections of upper or lower tooth crowns (perpendicular to the long axis of the crown) are nearly always elliptical, because the lateral and medial surfaces of the crowns are convex anteroposteriorly and flat or convex dorsoventrally. In many prosauropods, the crowns of the premaxillary teeth show a gentle posteromedial curvature, such that the medial crown surface is gently concave dorsoventrally (e.g., *Plateosaurus,* Galton, 1984:pl. 1, fig. 9; *Yunnanosaurus,* Young, 1951:fig. 14). Gentle inward curvature of the premaxillary crowns also characterizes the anterior premaxillary crowns in many ornithischians. As in prosauropods, however, this curvature is weak or absent in more posterior crowns in the upper tooth row.

The tooth crowns of most eusauropods, in contrast, have a characteristic spatulate form because the lingual surface of the crown is anteroposteriorly and dorsoventrally concave, particularly in the distal half of the crown. The crown, therefore, has a cup-shaped appearance, with a crescentic, or at least a D-shaped, cross-section in its distal half. This derived crown shape is present in *Shunosaurus* (Zhang, 1988:fig. 20), *Omeisaurus* (He, Li, and Cai, 1988:fig. 16), *Camarasaurus* (Fig. 10), *Brachiosaurus* (Janensch, 1935–1936:pl. 11), *Pleurocoelus* (Lull, 1911:figs. 7, 8), *Euhelopus* (Wiman, 1929:pl. 2), and basal titanosaurs (*Malawisaurus,* Jacobs, Winkler, Downs, and Gomani, 1993:fig. 2A). Diplodocoids and advanced titanosaurs have evolved subcylindrical crowns. Even in these species, however, the distal end of an unworn crown is usually gently spatulate

TABLE 2. Tabulation of ambiguity in the optimization of character states under delayed-transformation (DELTRAN) and accelerated-transformation (ACCTRAN) algorithms of PAUP (Swofford, 1993). Nodes are numbered as follows: 1—Sauropoda; 2—Eusauropoda; 3—*Barapasaurus* + *Omeisaurus* + Neosauropoda; 4—*Omeisaurus* + Neosauropoda; 5—Neosauropoda; 6—Macronaria; 7—*Camarasaurus* + Titanosauriformes; 8—Titanosauriformes; 9—Somphospondyli. Listed terminal taxa indicate autapomorphies, a negative sign indicates character-state reversal. Numbers in parentheses indicate transformations of multi-state characters.

Character	DELTRAN	ACCTRAN
4, 44	−Titanosauria	−Node 8
18–33, 35–36, 38–40, 42–45, 48	Node 2	Node 1
34	*Shunosaurus, Omeisaurus*	Node 2, −Node 5
37	Prosauropoda (0–>1), Node (0–>3)	Theropoda (0<–>1), Node 1 (1–>3)
41	Node 2, −Titanosauria	Node 1, −Node 8
62–63	Node 3	Node 2
65–67, 71–73	Node 4	Node 3
70	Prosauropoda (0–>1), *Shunosaurus* (0–>2), Node 4 (0–>3)	Theropoda (0–>1), Node 1 (1–>2), Node 3 (2–>3)
75–76	Node 5	Node 3
89–91, 95–95	Node 7	Node 6
106	*Camarasaurus,* Brachiosauridae	Node 6, −Node 9
109	Diplodocoidea, Titanosauria	Node 5, −*Camarasaurus*

TABLE 3. Femoral length (mm) in representative sauropodomorphs based on individuals recognized as adult. () = estimated.

Prosauropoda		
Massospondylus	330	Cooper, 1981
Lufengosaurus	740	Young, 1947
Riojasaurus	600	Bonaparte, 1969
Plateosaurus	900	Huene, 1926
Sauropoda		
Vulcanodon	(1,100)	Raath, 1972
Shunosaurus	1,200	Zhang, 1988
Barapasaurus	1,365	Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1977
Omeisaurus	1,310	He, Li, and Cai, 1988
Diplodocoidea		
Amargasaurus	1,050	Salgado and Bonaparte, 1991
Amphicoelias	1,770	Osborn and Mook, 1921
Apatosaurus	1,830	Gilmore, 1936
Dicraeosaurus	1,220	Janensch, 1950
Diplodocus	1,542	Hatcher, 1901
Haplocanthosaurus	1,745	Hatcher, 1903
Camarasaurus	1,800	Osborn and Mook, 1921
Brachiosaurus	2,140	Janensch, 1961
Titanosauria		
Opisthocoelicaudia	1,395	Borsuk-Bialynicka, 1977
T. araukanicus	1,050	Huene, 1932

or D-shaped (e.g., *Dicraeosaurus*, Janensch 1935–1936:pl. 12; *Nemegtosaurus*, Nowinski, 1971:pl. 8; "*Laplatasaurus*," Powell, 1979:fig. 2; *Malawisaurus*, Jacobs, Winkler, Downs, and Gomani, 1993).

Galton (1985:figs. 6A–O, 7G–O, 1990:fig. 15.4F–G) described several isolated teeth from the Lower Lufeng Formation in China, accepting Simmon's (1965) referral of these specimens to the prosauropod *Yunnanosaurus.* These tooth crowns, however, are not correctly referred to *Yunnanosaurus,* because the crowns in that genus are not as strongly medially curved and the roots are not as robust (Young, 1951:fig. 14). Furthermore, wear facets are not present in the any of the crowns in *Yunnanosaurus,* whereas the isolated crowns described by Galton have well developed V-shaped facets similar to those observed in many eusauropods. These isolated teeth from the Early Jurassic of China may belong to an as yet unknown eusauropod, although, unlike known eusauropods, the enamel lacks the characteristic wrinkled texture described below.

(33) *Enamel with wrinkled texture.* In prosauropods, theropods, and ornithischians, the enamel covering on the crowns of the teeth has a smooth external surface. Although often ornamented with ridges, the enamel surface itself is smooth. Eusauropods, in contrast, have a unique surface texture characterized by an irregular pattern of rugosities and vertical striae (Fig. 9). Owen (1840–1845:291, pl. 75) recognized this unusual feature more than a century ago, describing "wavy longitudinal ridges with widish intervals where it was sculptured with minute rugae." All sauropod teeth, regardless of shape, are characterized by this surface texture, the function of which remains unknown.

(34) *Crown overlap.* In prosauropods and theropods, the crowns of adjacent teeth do not overlap or contact each other. In eusauropods, in contrast, the crowns are designed for an overlapping arrangement, as preserved in situ in *Shunosaurus* (Zhang, 1988:figs. 2, 21), *Omeisaurus* (He, Li, and Cai, 1988: fig. 17), *Camarasaurus* (Fig. 7A, D), and in many other eusauropods. Although the distribution of this character in the taxa included this analysis does not affect the topology, the presence of overlapping crowns in probably several basal taxa not included in this analysis (e.g., *Mamenchisaurus,* Russell and Zheng, 1994:pl. 2; *Patagosaurus,* Bonaparte, 1986b:fig. 34), suggests this feature is a eusauropod synapomorphy.

The tooth crowns have an imbricate arrangement, in which the leading edge of each crown is overlapped labially by the next most anterior crown. A gentle depression, or overlap facet, is present along the posterior margin of each crown on the labial side of the crown. This facet accommodates the lingual aspect of the posterior margin of the next most anterior crown. Crown overlap appears to have been lost independently within Diplodocoidea and Titanosauria, subgroups that evolved narrow subcylindrical crowns incapable of significant overlap. In addition, the crowns do not contact one another in *Brachiosaurus,* despite the moderately broad tooth crowns in this genus (Janensch, 1935–1936:pls. 11, 12; Fig. 8A, D).

(35) *Precise crown-to-crown occlusion.* In prosauropods and theropods, the crowns of the upper and lower teeth generally do not contact each other when the jaws close, and regular wear facets are not developed. As a consequence, it is not necessary that the tooth rows be equal in length, and the upper row almost always extends farther posteriorly than the lower (Fig. 5A).

In eusauropods, in contrast, upper and lower tooth crowns occlude precisely, resulting in a regular pattern of wear facets as described below. Precise occlusion appears to occur even in narrow-crowned sauropods, such as diplodocids and titanosaurs, because wear facets in these subgroups have a uniform appearance, namely a single plane of truncation from the stroke of a single opposing crown. Furthermore, in all eusauropods, the tooth rows are equal in length, so that crown-to-crown contact involved the entire upper and lower tooth rows (Figs. 6–8).

(36:1) *V-shaped wear facets (interdigitating occlusion).* Regular wear facets are not present in prosauropods and theropods, and as a result, they cannot provide outgroup information regarding particular patterns of crown wear or occlusion in sauropods. Among basal ornithischians such as *Lesothosaurus,* wear facets are not as uniform as in sauropods, and no regular pattern is apparent (Sereno, 1991).

In eusauropods, a common pattern of wear results in a V-shaped facet developed along the mesial and distal margins of each crown (except in some of the smallest crowns at the posterior end of the tooth rows; Fig. 10). This characteristic wear pattern is present in the basal eusauropods *Shunosaurus* (Zhang, 1988:fig. 20) and *Omeisaurus,* and in many other eusauropods including *Brachiosaurus* (Janensch, 1935–1936), *Euhelopus* (Wiman, 1929), and the titanosaur *Nemegtosaurus* (Nowinski, 1971). In light of the present analysis, V-shaped wear facets were lost twice in favor of elliptical wear facets in diplodocoids and narrow-crowned titanosaurs.

(37:3) *Cervical vertebrae 13 or more in number.* Prosauropods and basal theropods have 10 cervical vertebrae. The distinction between cervical and dorsal vertebrae is based on rib form, the first dorsal rib being much more robust than the last cervical rib. Presumably this would be the first rib to contact the sternum, and therefore the first dorsal rib. In prosauropods, the cervical-dorsal transition is best preserved in *Plateosaurus* (SMNS 58958), which preserves the last cervical rib and the longer and much more robust first dorsal rib on presacral vertebrae 10 and 11, respectively. A cervical count of 10 is also consistent with the condition in the basal theropod *Eoraptor* (Sereno, Martinez, and Alcober, in prep.). The neck is not preserved in the basal sauropod *Vulcanodon.*

In all eusauropods, at least two vertebrae have been added to the cervical series for a minimum count of 12 (Upchurch, 1995). Somewhat surprisingly, the two sauropods with only 12 cervical vertebrae (*Dicraeosaurus* and *Camarasaurus*) are not the most basal sauropods when considering all of the evidence. Likewise, the two terminal taxa in the analysis that have more than 15 cervical vertebrae (*Omeisaurus* and *Euhelopus*) are not closely related. Thus, it seems probable that as many as 13 cervical vertebrae were present in sauropods ancestrally, and

that the number of cervical vertebrae increased on several occasions independently. We consider the problem of neck elongation in sauropods in more detail below in the section on Neck Elongation.

(38) *Cervical centra opisthocoelous.* In prosauropods and in the basal theropods *Herrerasaurus* and *Eoraptor,* the cervical vertebrae are gently amphicoelous (Sereno and Novas, 1993; Sereno, Martinez, and Alcober, in prep.). Among theropods, well-developed opisthocoely (i.e., centra with a distinctly convex anterior face and concave posterior face) occurs first among large ceratosaurs (e.g., *Dilophosaurus, Ceratosaurus*) and tetanurans (allosauroids) but is not present in smaller coelophysoid ceratosaurs (e.g., *Coelophysis*) and is not primitive for Theropoda or Neotheropoda (Ceratosauria + Tetanurae). No cervical vertebrae are preserved in *Vulcanodon,* and so the basal condition in Sauropoda remains unknown.

In eusauropods, the cervical vertebrae are strongly opisthocoelous in *Shunosaurus* (Zhang, 1988:figs. 24–28), *Barapasaurus* (Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1979:fig. 98A), *Omeisaurus* (He, Li, and Cai, 1988:figs. 19–23), and more advanced sauropods (Figs. 11, 12).

(39) *Mid-cervical neural arches deep (greater than centrum diameter).* The mid-cervical neural arches in prosauropods and basal theropods are proportionately low. Most prosauropods, such as *Plateosaurus,* have elongate mid-cervical vertebrae (C3–C6) with very low neural arches and broad, low neural spines (Huene, 1926). *Riojasaurus* has the most robust cervical vertebrae and deepest neural arches, which are approximately as deep as the vertical diameter of the posterior face of the centrum (Bonaparte and Pumares, 1995). Basal theropods differ in the proportions of the neural arches. Those with relatively slender necks, such as *Eoraptor* (Sereno, Martinez, and Alcober, in prep.) or coelophysoid ceratosaurs (Colbert, 1989), have very low cervical neural arches and spines. *Herrerasaurus* has a proportionately shorter neck with mid-cervical neural arches that are approximately as deep as the posterior face of the centrum (Sereno and Novas, 1993:fig. 12). Other theropods with proportionately larger skulls and shorter necks, such as *Allosaurus* (Madsen, 1976), have deeper mid-cervical neural arches and spines. There are no complete cervical vertebrae known for *Vulcanodon.*

In eusauropods, mid-cervical neural arches and spines are well developed, so that the vertical height of the neural arch is greater than the vertical diameter of the centrum. The increased height of the mid-cervical neural arches in eusauropods was noted by Bonaparte (1986a). In *Shunosaurus* both the neural arch and spine are relatively deep (Zhang, 1988:figs. 24, 25). In *Camarasaurus,* the spine is reduced (probably as a result of its bifid form), but the neural arch remains deep (Fig. 11). In diplodocoids (*Apatosaurus*; Fig. 12), *Brachiosaurus* (Janensch, 1950:figs. 34, 37), and *Euhelopus* (Wiman, 1929:pl. 1), the neural arches of the mid-cervical vertebrae remain deeper than the centrum face despite the extreme length of the vertebrae. *Omeisaurus* is an exception, with very low mid-cervical neural arches on very elongate centra (He, Li, and Cai, 1988:fig. 19).

(40) *Dorsal neural spines broader transversely than anteroposteriorly.* In prosauropods and theropods, the dorsal neural spines are plate-shaped with broad lateral surfaces and relatively narrow anterior and posterior edges (e.g., *Plateosaurus,* Huene, 1926:pl. 2, fig. 1; *Massospondylus,* Cooper, 1981: figs. 5, 9; *Herrerasaurus,* Sereno and Novas, 1993:fig. 12). In *Vulcanodon,* no dorsal vertebrae are preserved.

In eusauropods, in contrast, the dorsal neural spines are broader transversely than anteroposteriorly, as noted by Bonaparte (1986a). This feature is clearly present in the basal eusauropods *Shunosaurus* (Zhang, 1988:pl. 3), *Barapasaurus* (Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1979), and *Omeisaurus* (He, Li, and Cai, 1988:fig. 26B) as well as in more

derived genera. In *Shunosaurus,* anteroposterior compression of the neural spine is expressed first in the last two cervical vertebrae (C12, C13; Zhang, 1988:fig. 28). In *Omeisaurus,* the last cervical (C17) has a low subquadrate spine, and anteroposterior compression of the neural spine is apparent in the first dorsal (He, Li, and Cai, 1988:fig. 24). In taxa with bifid neural spines, we have measured the transverse width of the base of the spine and regard these taxa as having transversely broadened proportions.

Among theropods, similar broadening of the neural spines of the posterior cervical and anterior dorsal vertebrae occurs in large-skulled tetanuran theropods such as *Allosaurus* (Madsen, 1976:pls. 14–16). The greater transverse width of the neural spines increases the area of attachment for interspinous ligaments.

(41) *Distal chevrons with anterior and posterior projections.* In prosauropods and basal theropods, all chevrons are simple strut-shaped bones in lateral view. Distal chevrons are not known in *Vulcanodon.* In most eusauropods, the distal chevrons have distinct anterior and posterior prongs which extend away from the base of the chevron (Fig. 15B, C). These distal chevrons, often described as "boat-shaped" or "forked," have a wider distribution among sauropods than previously recognized. Upchurch (1995) regarded their occurrence in diplodocoids and "euhelopodids," and independent acquisitions. Their presence in *Barapasaurus* (Wilson, pers. obs.) and *Camarasaurus* (Gilmore, 1925:374), as well as in *Shunosaurus* (Zhang, 1988:fig. 41), *Omeisaurus* (He, Li, and Cai, 1988:fig. 40), and diplodocoids suggests that forked distal chevrons are a eusauropod synapomorphy. Titanosaurs lack such chevron processes, which is regarded as a reversal in the present analysis. The condition in *Haplocanthosaurus, Brachiosaurus,* and *Euhelopus* is unknown.

(42) *Block-shaped carpals.* In prosauropods and most theropods, the distal carpals are the largest carpal elements. In prosauropods, a large distal carpal is situated over metacarpals I and II, with a rounded proximal articular surface and a tightly articulating distal articular surface for the metacarpals. Distal carpals 2 and 3 are always present in prosauropods, but the proximal carpals are very reduced if present at all (Young, 1947; Cooper, 1981). In basal theropods such as *Eoraptor* and *Herrerasaurus,* the proximal carpals (radiale and ulnare) are large and well-ossified and the distal carpals are generally smaller (Sereno, 1993). In tetanuran theropods, however, a large distal carpal is situated over metacarpals I and II and appears to have evolved independently from that in prosauropods.

It is unknown whether sauropod carpals correspond to proximal ossifications, distal ossifications, or both. Because of their well-developed metacarpal facets as well as their overall similarity to the relative size and position of the three principal carpals in prosauropods, the three carpals present in the most primitive sauropods probably represent distal carpals 1–3. No carpals are known for *Vulcanodon,* but three are present in *Shunosaurus* (Zhang, 1988:pl. 14) and *Omeisaurus* (He, Li, and Cai, 1988:pl. 14, fig. 6). In *Shunosaurus,* the carpals, particularly the medial pair, are block-shaped and with distinct, flattened proximal and distal articular surfaces. Block-shaped carpals are also known in *Camarasaurus* (Osborn and Granger, 1901; Osborn, 1904; Fig. 21), and *Bothriospondylus madagascariensis* (Lavocat, 1955:1796). The block-like or discoid shape of these carpals is apparent when they are well preserved. No carpals are known in titanosaurs, and it is possible that they were not ossified (Borsuk-Bialynicka, 1977).

(43) *Manual phalanges on digits II and III reduced (II-ungual, III-3 and ungual absent; digital formula 2-2-2-2-2).* In prosauropods and basal theropods, the manual digits functioned in grasping and other manipulative capacities and were not specialized for weight support. Thus unguals are present on digits

II and III, which are successively longer than digit I. Digits IV and V retain at least a pair of vestigial phalanges in prosauropods (e.g., *Lufengosaurus,* Young, 1947) and usually fewer in basal theropods (*Eoraptor,* Sereno, Martinez, and Alcober, in prep.; *Herrerasaurus,* Sereno, 1993). The manual phalangeal formula regarded by us as primitive at the outgroup node is 2-3-4-2-2, with unguals on digits I, II, and III. No manual phalanges were recovered with the known skeletal material of *Vulcanodon.* The modifications noted here in the manus of all eusauropods, therefore, may eventually be shown to characterize *Vulcanodon,* which clearly was also an obligatory quadruped.

In eusauropods, manual digits II and III are shortened so that all but the first (with its enlarged ungual) are subequal in length. Eusauropods, thus, are characterized by loss of unguals in digits II and III and loss, in addition, of at least one nonterminal phalanx in digit III, which yields a manual phalangeal formula of 2-2-2-2-2, as preserved in *Shunosaurus* (Zhang, 1988:fig. 49). The shortening of the middle digits (II and III) of the manus and loss of their respective unguals reduces the disparity in the length of digits II–V and appears to be an adaptation for weight support.

We code this phalangeal reduction as a single character, representing one of two major changes of the phalangeal formula within sauropods. The other major change involves the loss of all manual phalanges within Titanosauria. Loss of the second vestigial phalanx in manual digits II–V has been recorded in *Camarasaurus* and *Brachiosaurus,* but we regard this alleged reduction with some suspicion as these small wedge-shaped phalanges are easily lost or overlooked. The proximal phalanges in these sauropods have divided distal condyles as in those genera that preserve the second vestigial phalanx, suggesting that terminal vestigial elements may have been present.

(44) *Manual phalanges (other than unguals) broader than long.* In prosauropods and theropods, all of the nonterminal phalanges are longer than broad. No manual phalanges are known in *Vulcanodon.* In all eusauropods, all of the phalanges except the ungual of digit I are broader than long and lack well-formed collateral ligament pits. Although clearly an adaptation for weight support in an elephantine manus, we score this condition separately from other correlates of large body size, because it is clear that similar changes in the pes in eusauropods are not present in *Vulcanodon.*

(45) *Iliac blade with semicircular dorsal margin and expanded preacetabular process.* In prosauropods and the basal theropods *Eoraptor* and *Herrerasaurus,* the small preacetabular process of the ilium is either subtriangular or subquadrate and does not extend beyond the pubic peduncle. Although the preacetabular portion of the iliac blade is not preserved in *Vulcanodon,* the form of the remainder of the ilium is remarkably like that in other sauropods, and this feature may eventually be shown to characterize *Vulcanodon* as well.

Nevertheless, the iliac blade in eusauropods has a semicircular dorsal margin, and the preacetabular process is expanded anteriorly (Fig. 26). Usually the preacetabular blade has a half-crescent shape and extends anterior to the pubic peduncle when the long axis of the blade is oriented along the horizontal.

(46) *Pubic apron canted posteromedially.* In *Vulcanodon,* prosauropods, and theropods, the pubic apron is developed as a plate-shaped sheet of bone that extends transversely to meet its opposite along the midline. The apron, thus, has a transverse orientation. The pubic apron in *Vulcanodon,* in particular, is very similar to that in prosauropods and forms a single planar sheet composed of both right and left pubes (Raath, 1972:fig. 4). There is a sharp bend between the pubic apron and the portion of the pubis leading to the ischial peduncle.

In eusauropods, in contrast, the surface of the blade curves more gradually away from the transverse orientation of the pubic foot and toward the posteriorly directed ischial peduncle

(Fig. 28). As a result, most of the apron is canted posteromedially and has a V-shaped cross-section at midlength.

(47) *Cnemial crest of tibia projecting laterally.* The cnemial crest is oriented anteriorly in *Vulcanodon* (Cooper, 1984:fig. 24), prosauropods (*Massospondylus,* Cooper, 1981:fig 66; *Plateosaurus,* Galton, 1990:fig. 15.7), and basal theropods. In eusauropods, on the other hand, the cnemial crest is directed laterally as a thin plate-shaped flange, partially obscuring the proximal end of the fibula in anterior view (e.g., *Shunosaurus,* Zhang, 1988:fig. 54; *Apatosaurus,* Fig. 31; *Camarasaurus,* Fig. 32). The functional significance of this reorientation is not clear. A medially directed cnemial process occurs in some cursors (e.g., *Mononykus*) and within birds, but no other dinosaurs have reoriented the cnemial process in this manner.

(48) *Posteroventral process of tibia reduced.* In prosauropods and theropods, the posteroventral process of the tibia extends laterally toward the calcaneum, completely obscuring the posterior fossa of the astragalus in posterior view. In the prosauropod *Massospondylus* and the theropod *Herrerasaurus,* for example, the flange extends just lateral to the remainder of the distal end of the tibia (Cooper, 1981:fig. 66; Novas, 1993:fig. 8). In *Vulcanodon,* the distal end of the tibia is incomplete and the shape of the posteroventral process is unknown (Raath, 1972:fig. 8; Cooper, 1984:fig. 24).

In eusauropods, in contrast, the posteroventral process does not extend laterally to approach the calcaneum. As a result, the posterior fossa of the astragalus is exposed in posterior view. This condition is present uniformly among eusauropods, as seen in *Shunosaurus* (Zhang, 1988:fig. 54) and *Camarasaurus* (Fig. 32B).

(49) *Fibular lateral trochanter.* In *Vulcanodon,* prosauropods, and theropods, an anterior trochanter is present along the anterolateral margin of the shaft of the fibula, located approximately one-third of the distance from the proximal end of the bone. There are no other marked trochanters or rugosities on the external surface of the fibular shaft in these taxa.

In eusauropods, in contrast, an additional elliptical rugosity is present on the lateral side of the shaft of the fibula, located just proximal to midshaft. This raised rugosity, visible as a swelling on the shaft in anterior or posterior view of the fibula, is clearly present in *Shunosaurus* (Zhang, 1988:fig. 54), *Barapasaurus* (Wilson, pers. obs.), and more advanced sauropods (*Apatosaurus,* Gilmore, 1936:fig. 24A; *Camarasaurus,* Fig. 32H, I; *Opisthocoelicaudia,* Borsuk-Bialynicka, 1977:fig. 16A2). The shape of the rugosity is variable. In most eusauropods, the rugosity is oval with long axis oriented proximo-distally (e.g., *Camarasaurus,* Fig. 32H, I). In the stocky, short-limbed titanosaurs, such as *Opisthocoelicaudia,* the trochanter is elliptical with a transverse long axis (Borsuk-Bialynicka, 1977:fig. 16A2). In all of these eusauropods, a low crest descends from the posterior margin of the rugosity down the posterior margin of the shaft.

The lateral trochanter has been interpreted in two ways in the descriptive literature on sauropods. Huene (1929) and Powell (1992) suggested that this trochanter marks the insertion of either the peroneus longus or iliofibularis muscles, respectively—muscles that have been regarded as the best candidates for insertion on the anterior trochanter in other dinosaurs. Borsuk-Bialynicka (1977), on the other hand, regarded the rugosity as a novel structure marking the origin of the flexor digitorum longus muscle. We support the latter interpretation specifically because most sauropods clearly maintain a distinct anterior trochanter, which is located as in sauropod outgroups on the anterior margin of the fibula just proximal to the lateral trochanter (Fig. 32G–I). The suggested function of the muscle(s) that originate on the lateral trochanter, flexion of the pes (Borsuk-Bialynicka, 1977:17A), may be related to the shift in eusauropods from a digitigrade to a more plantigrade posture for the pes.

(50) *Metatarsal III length 25 percent or less that of tibia.* The length of metatarsal III is approximately 40 to 50% that of the tibia in eusauropod outgroups, including *Vulcanodon* (37% using the measurements provided by Raath [1972]; Cooper [1981] listed 32%), *Lufengosaurus* (52%; Young, 1947), *Plateosaurus* (40–56%; Cooper, 1981:tab. 6), and *Herrerasaurus* (52%).

The metatarsals in eusauropods are considerably shorter relative to the tibia. The length of metatarsal III is 25% or less that of the tibia in *Apatosaurus* (21%; Gilmore, 1936), *Camarasaurus*, 22–25%) and other eusauropods. Thus, in relation to the tibia, the eusauropod metatarsus is shortened to less than 60% of its relative length in *Vulcanodon*. Marked shortening of the metatarsus relative to the tibia in eusauropods may reflect the adoption of a semi-digitigrade pedal posture, as discussed below.

(51) *Metatarsal I minimum shaft width greater than that of metatarsals II–IV.* In *Vulcanodon* and prosauropods, the shaft diameter for metatarsals I–IV is remarkably uniform. Minimum transverse shaft width differs by less than 10% across metatarsals I–IV in prosauropods (e.g., *Lufengosaurus,* Huene, 1947: fig. 7) and across metatarsals I–V in *Vulcanodon* (Cooper, 1984: fig. 27B). In *Vulcanodon,* metatarsal I has a shaft diameter comparable to that of the other metatarsals, but the diameter is somewhat dependent on the orientation of the metatarsal. All theropods have a functionally tridactyl pes. As a result, even the basal theropod *Herrerasaurus* shows reduction in the length and diameter of the external metatarsals I and V, which were not involved in weight support.

In eusauropods, in contrast, metatarsal I is the most robust, with a minimum transverse shaft width that always exceeds that of any other metatarsal. This strength of metatarsal I cannot be directly related to the large size of the first ungual, because *Vulcanodon* has the enlarged ungual but retains a slender metatarsal I. Rather, the asymmetrical robustness of pedal digits must be related to the unequal weight distribution across the plantigrade pes in eusauropods. As seen in sauropod trackways and as is also true for the manus, the pes is directed laterally relative to the axis of the trackway (Pittman and Gillette, 1989: fig. 34.17). Despite its shorter overall length as compared to digits II and III, digit I is the leading digit of the pes. Furthermore, the leading margin of the pes print (the medial side of the pes) is consistently deeper than the trailing margin, or lateral side of the pes (Pittman and Gillette, 1989:322). At least during walking, therefore, a greater load is carried by the inner digits of the pes in eusauropods.

(52) *Metatarsals with spreading configuration.* In *Vulcanodon*, prosauropods, and theropods, the metatarsals are bound together by ligaments with the proximal portions of the metatarsal shafts overlapping broadly and closely appressed. This "bound" metatarsus helped support the habitually digitigrade posture of the pes, which is shown by prosauropod and theropod footprints (Thulborn, 1990). The tight arrangement of metatarsals is present in *Vulcanodon,* in which the proximal ends of the metatarsals are flattened and broadly overlapping. In addition, the shape of the metatarsals in proximal view (Cooper, 1984:fig. 27) is extremely similar to that in prosauropods (e.g., *Massospondylus,* Cooper, 1981:fig. 72j).

Eusauropods, in contrast, have a spreading configuration of the metatarsals and, at best, a semi-digitigrade pedal posture. In *Shunosaurus,* the proximal ends of the metatarsals do not contact each other as broadly as in *Vulcanodon,* and the proximal portions of the metatarsal shafts do not appear to be in mutual contact (Zhang, 1988:fig. 55). In other eusauropods, the metatarsal shafts are clearly separated by intervening spaces (e.g., *Apatosaurus,* Gilmore, 1936:fig. 25; *Opisthocoelicaudia,* Borsuk-Bialynicka, 1977:pl. 14, fig. 2b). Eusauropods probably had a fleshy pad that elevated the heel and, in this way, sup-

ported a sloping orientation for the metatarsals and a semi-digitigrade pedal posture (Janensch, 1922; Lapparent and Lavocat, 1955; Cooper, 1984; Gauthier, 1986; McIntosh, 1990a; Thulborn, 1990).

(53) *Pedal phalanges (other than unguals) broader than long.* In prosauropods and theropods, the phalanges of the pes other than unguals all have greater maximum lengths than widths. This is also true for all of the nonungual phalanges in the pes in *Vulcanodon,* with the exception of the second phalanx of digit III, which has subequal dimensions (Raath, 1972: fig. 9f; Cooper, 1984:figs. 34, 35). Several of the phalanges in *Vulcanodon,* furthermore, have well-formed collateral ligament pits, suggesting the retention of considerable digital flexibility in the pes.

In eusauropods, nonungual pedal phalanges are proportionately very short. Maximum transverse width always exceeds maximum length, with rare exceptions in which the proportions are subequal (Fig. 34). The short proportions of the nonungual phalanges of the pes and the lack of well formed collateral ligament pits suggest that the pedal digits of eusauropods were proportionately shorter and capable of less flexion or extension than in *Vulcanodon.*

An apparent exception to these short phalangeal proportions occurs in the diplodocid *Dyslocosaurus,* which was shown with a proximal phalanx in digit IV that is longer than broad (McIntosh, Coombs, and Russell, 1992:fig. 3G). The same phalanx in *Apatosaurus,* however, is broader than long (Gilmore, 1936: fig. 28D). The pedal phalanges in *Apatosaurus,* moreover, have robust shafts and deep distal condyles in lateral view. In two of the phalanges attributed to *Dyslocosaurus,* the shafts taper in depth toward small distal condyles with well-formed collateral ligament pits (McIntosh, Coombs, and Russell, 1992:fig. 4E, H). Only *Vulcanodon* among sauropods has nonterminal phalanges that bear any similarity to these. A small dorsoventrally flattened ungual, tentatively attributed to the fifth digit, is also unlike the unguals preserved in any other sauropod (McIntosh, Coombs, and Russell, 1992:fig. 3L). We suggest here that the two nonterminal phalanges discussed above and the small dorsoventrally flattened ungual do not pertain to a sauropod and should not be associated with the other skeletal elements that comprise the only known specimen of the diplodocid *Dyslocosaurus.*

(54) *Pedal digit I ungual as long as, or longer than, metatarsal I.* In *Vulcanodon* the length of the ungual of digit I (142 mm) is less that that of metatarsal I (159 mm), or approximately 89% the length of the metatarsal (Raath, 1972). The same is true in prosauropods (e.g., *Lufengosaurus;* 84% metatarsal I length) and in basal theropods that maintain a complete metatarsal I, such as *Eoraptor* and *Herrerasaurus* (30% metatarsal I length). In the first pedal digit, plesiomorphically, metatarsal I always exceeds the length of the ungual.

In eusauropods, the reverse relation holds; the first ungual nearly always exceeds the length of metatarsal I. In *Shunosaurus* (Zhang, 1988), the ungual is particularly long (length 173% that of metatarsal I). In *Omeisaurus* (He, Li, and Cai, 1988), on the other hand, the first ungual is only moderately longer (103%), and it is as long as metatarsal I in the short pes of the titanosaur *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977). Most eusauropods fall somewhere in between, such as *Apatosaurus* (Gilmore, 1936) and *Dyslocosaurus* (McIntosh, Coombs, and Russell, 1992) with a first pedal ungual that is 127% and 141% of the length of metatarsal I, respectively.

The increased relative length of the first ungual to metatarsal I and other pedal phalanges may be a consequence of the significant reduction in length of the metatarsus and phalanges other than unguals in eusauropods that we describe above. Eventually it may be shown that the first pedal ungual maintains

its size in the face of a general reduction in length of other pedal elements in eusauropods.

(55) *Penultimate phalanges of pedal digits II–IV rudimentary or absent.* Prosauropods and basal theropods retain a full complement of pedal phalanges in digits I–IV that invariably number 2-3-4-5, respectively, each bearing an ungual phalanx. Although the pedal phalangeal formula and number of unguals are not certain in the basal sauropod *Vulcanodon,* the penultimate phalanges resemble those in prosauropods and are not drastically shortened (Cooper, 1984:figs. 34E–H, 35A–D).

In eusauropods, reduction in the pedal phalangeal formula occurs in the phalanges immediately preceding the ungual. The penultimate phalanx in pedal digits II–IV is reduced to a disc or lost in *Shunosaurus* (Zhang, 1988:fig. 55), *Omeisaurus* (He, Li, and Cai, 1988:pl. 17, fig. 6), diplodocoids (*Apatosaurus, Diplodocus,* Hatcher, 1901:figs. 21, 22), *Camarasaurus* (Ostrom and McIntosh, 1966:pl. 87, figs. 7–12), *Pleurocoelus* (Gallup, 1989:fig. 1), *Euhelopus* (Wiman, 1929:pl. 4, fig. 12), and titanosaurs (*Opisthocoelicaudia,* Borsuk-Bialynicka, 1977).

Although all of the nonterminal pedal phalanges are proportionately short in eusauropods (character 53), the penultimate phalanges are extremely reduced and are easily lost during excavation or mistaken as sesamoids. The well-preserved pes of the diplodocid *Apatosaurus,* for example, has a full complement of phalanges on the inner digits I–III, numbering 2-3-4, respectively (CM 89; Hatcher, 1901:fig. 22). A second individual is missing the diminutive penultimate phalanx in pedal digit III (CM 3018; Gilmore, 1936:fig. 25). The missing disc-shaped phalanx either failed to ossify or was lost during burial or excavation. We regard as a similar case the reported count of three phalanges in pedal digit III in *Shunosaurus* and *Omeisaurus;* a very reduced penultimate phalanx may have been present or may have failed to ossify.

The greatest number of phalanges recorded among sauropods in pedal digit IV is three (*Shunosaurus,* Zhang, 1988; *Omeisaurus,* He, Li, and Cai, 1988; *Camarasaurus,* Jensen, 1988)—down two from the outgroup condition of five phalanges. In these sauropods, the terminal phalanx of pedal digit IV is an ungual, indicating that two intervening (nonterminal) phalanges were lost.

Therefore, eusauropods clearly exhibit nonterminal phalangeal reduction in the pes; this pattern is unknown elsewhere among dinosaurs in either the manus or pes. This pattern of reduction maintains the size and functional integrity of the unguals despite considerable digital shortening. A similar change occurred in the evolution of mammalian manual and pedal phalanges.

(56) *Pedal digits II–III with sickle-shaped unguals.* In *Vulcanodon,* prosauropods, and basal theropods, the pedal unguals of digits II–III have a distinctly flattened plantar surface. In *Vulcanodon,* only the unguals of pedal digits II and III (or IV) are known, and these are particularly dorsoventrally flattened. In prosauropods (e.g., *Massospondylus;* Cooper, 1981:fig. 79) and basal theropods (*Herrerasaurus;* Novas, 1993:fig. 9), the pedal unguals of digits II-IV always have a flattened plantar surface, which distinguishes them from the manual unguals. Furthermore, in lateral view (e.g., *Massospondylus;* Cooper, 1981:fig. 80), these unguals taper gradually toward their distal ends.

In eusauropods, in contrast, the pedal unguals on digits II and III resemble the sickle-shaped ungual of pedal digit I. These unguals are transversely narrow with rounded, frequently asymmetric, ventral margins. In lateral view, they are dorsoventrally deep, and often round abruptly distally. Although always considerably smaller than the first pedal ungual, these unguals have the same sickle-shaped form, as is well seen in *Shunosaurus* (Zhang, 1988:pl. 15), *Omeisaurus* (He, Li, and Cai, 1988:fig. 57), *Apatosaurus* (Gilmore, 1936), *Dyslocosaurus* (McIntosh,

Coombs, and Russell, 1992:figs. 1, 3, 4), *Camarasaurus* (Ostrom and McIntosh, 1966:pl. 88) and *Pleurocoelus* (Gallup, 1989). When present, the ungual of pedal digit IV varies in form from sickle-shaped (*Pleurocoelus,* Gallup, 1989: fig. 1; *Camarasaurus,* Jensen, 1988:fig. 7C) to hoof-shaped (*Shunosaurus,* Zhang, 1988:fig. 55; *Omeisaurus,* He, Li, and Cai, 1988:pl. 17, fig. 6).

(57) *Pedal digit IV ungual rudimentary or absent.* In prosauropods and basal theropods, the ungual of pedal digit IV is only slightly shorter than that of pedal digits II and III. In *Vulcanodon,* the ungual of pedal digit IV has similar proportions (if correctly identified; Cooper, 1984).

In eusauropods, in contrast, the ungual of pedal digit IV is rudimentary or absent (e.g., *Shunosaurus;* Zhang, 1988:fig. 55). The largest of these unguals occur in *Pleurocoelus* (Gallup, 1989) and *Dyslocosaurus* (McIntosh, Coombs, and Russell, 1992), both of which require further documentation. In the former, the disposition of the original elements has yet to be described, and in the latter, non-sauropod bones were also incorporated into the pes, raising some doubt regarding the association of the ungual (see character 53). In other eusauropods that retain this element, the ungual on pedal digit IV is very reduced in size (e.g., *Camarasaurus;* Jensen, 1988:fig. 7C). The absence of a substantial ungual on pedal digit IV agrees with the observed record of sauropod pedal prints (Farlow et al., 1989).

Barapasaurus + Omeisaurus + Neosauropoda

Recorded Temporal Range—Early Jurassic (Pliensbachian) to latest Cretaceous (Maastrichtian).

Diagnosis—Posterior cervical and anterior dorsal neural arches with interprezygapophyseal laminae; opisthocoelous anterior dorsal centra; middle and posterior neural arches with composite lateral laminae (spinodiapophyseal plus supraprezygapophyseal); sacricostal yoke; fibula with triangular articular scar for tibia; astragalar posterior fossa divided by crest; asymmetrical pedal unguals.

(58) *Posterior cervical and anterior dorsal neural arches with interprezygapophyseal lamina.* In *Shunosaurus* (Zhang, 1988:fig. 30), prosauropods, and theropods, a simple notch separates the prezygapophyses, as seen in anterior view. The condition in *Vulcanodon* remains unknown.

The prezygapophyses in other sauropods are joined on the midline at the dorsal margin of the neural canal by a bony lamina here termed the interprezygapophyseal lamina. This web of bone is present in the anterior dorsal vertebrae of *Barapasaurus* (Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1979:pl. 101a), *Omeisaurus* (He, Li, and Cai, 1988:fig. 28) and other sauropods (e.g., *Apatosaurus,* Fig. 12B; *Camarasaurus,* Fig. 13B; *Saltasaurus,* Powell, 1992, fig. 10). The interprezygapophyseal lamina is usually separated from the infraprezygapophyseal lamina, which joins the prezygapophysis and the centrum, by a well-developed circular fossa. The interprezygapophyseal lamina is not present in the middle and posterior dorsal neural arches, in which the wedge-and-notch hyposphene-hypantrum articulation stiffens intervertebral connections (Fig. 13A).

(59) *Anterior dorsal centra opisthocoelous.* In prosauropods and basal theropods, the centra of the presacral vertebrae are gently amphicoelous (*Plateosaurus,* Huene, 1926:pl. 2, fig. 2; *Herrerasaurus,* Novas, 1993:fig. 1). Most large tetanuran theropods, such as *Allosaurus* (Madsen, 1976), have opisthocoelous cervical and anterior dorsal centra, but this condition is not primitive for Theropoda or Saurischia. The condition is unknown in the basal sauropod *Vulcanodon.* In *Shunosaurus,* the last cervical and first dorsal centra are weakly opisthocoelous, while the succeeding dorsal centra are gently amphicoelous.

In *Barapasaurus, Omeisaurus,* and other sauropods, opisthocoelous centra characterize more of the dorsal column. In *Om-*

eisaurus, for example, the anteriormost dorsal centra are strongly opisthocoelous, with this condition gradually diminishing by the seventh dorsal vertebra (He, Li, and Cai, 1988:figs. 26–30). Dorsal opisthocoely is taken to its extreme in *Camarasaurus* (Mook, 1914:fig. 1; McIntosh, Miller, Stadtman, and Gillette, 1996; Fig. 13), *Brachiosaurus* (Janensch, 1950), and titanosaurs, such as *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977), in which the entire dorsal series is strongly opisthocoelous.

(60) *Middle and posterior dorsal neural arches with composite lateral lamina (spinodiapophyseal plus supraprezygapophyseal).* In many dinosaurs, bony laminae connect the various processes of the neural arch and also span the neural arch and centrum. In prosauropods (e.g., *Plateosaurus,* Huene, 1926: pl. 2, fig. 2) and theropods (e.g., *Herrerasaurus,* Novas, 1993: fig. 1A), four laminae extend from the distal end of the transverse process. These four diapophyseal laminae are regarded here as primitive for saurischians. Each of these laminae is named according to the vertebral structures joined by it: prezygapophyseal-diapophyseal lamina (prdl), postzygapophyseal-diapophyseal lamina (podl), anterior centrodiapophyseal lamina (acdl), and posterior centrodiapophyseal lamina (pcdl) (Wilson, in preparation; Figs. 11–13). The condition in *Vulcanodon* remains unknown as no dorsal vertebrae have been preserved. In *Shunosaurus,* a rudimentary lateral lamina is present in the posterior dorsal neural arches but is not developed as in the sauropods described below (Zhang, 1988:figs. 30–32).

Barapasaurus and all more advanced sauropods are characterized by a fifth diapophyseal lamina, the spinodiapophyseal lamina (spdl). This lamina extends from the dorsal surface of the transverse process to the lateral surface of the neural spine (e.g., *Barapasaurus,* Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1979:pl. 101; *Camarasaurus,* Fig. 13). An anterior branch of a lamina that is common among saurischians, the suprapostzygapophyseal lamina (spol), often joins the spinodiapophyseal lamina to form a composite lateral lamina.

In *Omeisaurus,* the spinodiapophyseal lamina is present in nearly all of the dorsal vertebrae (He, Li, and Cai, 1988:figs. 28, 29). In *Apatosaurus,* this lamina is present in all dorsal vertebrae more posterior than the fifth (Gilmore, 1936:pl. 25). In *Haplocanthosaurus* (Hatcher, 1903:pl. 2) and *Brachiosaurus* (Janensch, 1950:fig. 62), it is present in dorsal vertebrae more posterior than the ninth and 10th or 11th, respectively. It is also present in the basal titanosaurs *Andesaurus* (Calvo and Bonaparte, 1991:fig. 3), *Malawisaurus* (Jacobs, Winkler, and Gomani, 1996:fig. 5D), and *Saltasaurus* (Powell, 1992:figs. 14, 15).

(61) *Sacricostal yoke.* In prosauropods and theropods, the expanded ends of the ribs of adjacent sacral vertebrae rarely establish significant contact with each other but rather attach independently to the iliac blade (e.g., *Massospondylus,* Cooper, 1981:fig. 12; *Plateosaurus,* Huene, 1926:pl. 2, fig. 3). The sacral ribs, in addition, do not participate in the articular surface of the acetabulum. This appears to be the case in the one figured specimen of *Shunosaurus* (Zhang, 1988:fig. 34; Fig. 38). The distal ends of the sacral ribs remain separate, and the middle pair attach close to the rim of the acetabulum but do not participate in the articular surface. The absence of a sacricostal yoke in *Shunosaurus,* however, should be treated with caution as the figured individual (ZDM T5401) is immature and it is clear that fusion of the ribs to each other occurred late in development in *Camarasaurus* (CM 11,338). In *Vulcanodon,* the poorly preserved sacral ribs do not provide solid evidence for distal fusion and the formation of a sacricostal yoke (Cooper, 1984:fig. 12).

In all eusauropods more advanced than *Shunosaurus,* the ends of the sacral ribs coossify, enclosing oval intervertebral fenestrae (Fig. 38). The distal ends of the middle sacral ribs form the medial edge of the acetabulum (Fig. 14). The coossified distal ends of the sacral ribs are referred to as the "sac-

ricostal yoke," which fuses to the pelvic girdle very late in development and, as a result, is often preserved as a separate coossified series of sacral vertebrae and ribs. The intervertebral fenestrae are large in *Omeisaurus* (He, Li, Cai, 1988:fig. 32) and smaller in the titanosaurs *Saltasaurus* (Powell, 1992:fig. 17) and *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977).

(62) *Fibula with broad triangular scar for tibia.* In prosauropods and basal theropods, the articular surface for the tibia on the proximal end of the fibula is usually limited to a poorly defined flattened area marked by striae (*Massospondylus,* Cooper, 1981:fig. 69A). In basal theropods, one or two low ridges may be present on the articular surface near the proximal end of the fibula (e.g., *Herrerasaurus,* Novas, 1993:fig. 8F). In *Vulcanodon,* the articular surface for the tibia appears to be rather small; a gap separates all but the dorsal margins of these bones in natural articulation (Cooper, 1984:fig. 24). Cooper (1984: 218) remarked, however, that there is a "large, distinctly striated, subtrigonal area" that contacts the tibia. Thereferore, the derived condition described may be present in *Vulcanodon.* Likewise, the condition in *Shunosaurus* remains uncertain because the medial aspect of the fibula has not been figured (Zhang, 1988).

In other eusauropods, the articular surface for the tibia is developed as a well defined, rugose, triangular area that occupies the full width of the fibula near its proximal articular end and deepens proximodistally toward its ventral terminus in the anterior trochanter. This distinctive attachment scar is present in *Barapasaurus* (Wilson, pers. obs.), *Omeisaurus* (He, Li, and Cai, 1988:fig. 53C), *Camarasaurus* (Fig. 32G), and titanosaurs, including *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977:fig. 16A) and *Argentinosaurus* (Bonaparte and Coria, 1991:fig. 8; note that this figure of a right fibula has been misidentified as a right tibia). The scar is present in a fibula of *Brachiosaurus* (HMN St 149; Wilson, pers. obs.), although it is not illustrated by Janensch (1961:pl. 218:fig. 2C).

(63) *Astragalar posterior fossa divided by crest.* In prosauropods and basal theropods, the posterior fossa of the astragalus is shaped as a single depression with several small vascular foramina (e.g., *Massospondylus,* Cooper, 1981:fig. 71h; *Herrerasaurus,* Novas, 1989:fig. 2.6). The posteroventral process of the tibia partially overlaps the medial portion of the fossa, as appears to be the case in *Vulcanodon* (Raath, 1972:pl. 6).

In *Barapasaurus, Omeisaurus,* and neosauropods, the posterior fossa is divided unequally by a rounded crest that descends ventromedially from the ascending process, as best seen in posterior view of the astragalus. The medial portion of the fossa is broader than the lateral, much of which is covered by the posteroventral process of the tibia. Both depressions are pierced by large foramina, which provide the principal vascular supply to the astragalus (given the absence in sauropods of an anterior depression with associated foramina). The divided posterior fossa is exposed in *Omeisaurus* (He, Li, and Cai, 1988: fig. 54A), *Mamenchisaurus* (Young and Zhao, 1972:fig. 11.1), diplodocoids (*Diplodocus,* Hatcher, 1901:fig. 20; *Apatosaurus,* Gilmore, 1936:fig. 26C), *Camarasaurus* (Fig. 33D), *Brachiosaurus* (Janensch, 1961:pl. 22, fig. 2a), and titanosaurs (*Opisthocoelicaudia,* Borsuk-Bialynicka, 1977:pl. 14, fig. 8). The condition in *Shunosaurus* is not clear from available figures, and the condition in *Euhelopus* cannot be determined because the posterior fossa of the only available astragalus (in the holotype) is obscured by matrix.

(64) *Pedal unguals asymmetrical (canted ventrolaterally in articulation).* In prosauropods and theropods, the pedal unguals are more or less symmetrical about a vertical plane. In lateral or medial views, little if any of the proximal articular surface or flattened plantar aspect of the ungual is exposed (Cooper, 1981:fig. 80). In *Vulcanodon,* the ungual of the first digit is slightly asymmetrical, so that more of the proximal articular

surface and plantar surface is visible in medial view (Cooper, 1984:fig. 33A, B). The other pedal unguals are flattened dorsoventrally and are not readily comparable.

In all eusauropods except *Shunosaurus,* in contrast, the unguals are asymmetric. The proximal articular surface is beveled anteriorly toward its lateral margin, and the narrow plantar surface is beveled dorsolaterally (e.g., *Camarasaurus*; Fig. 35). The beveled proximal end deflects the ungual laterally, and the beveled plantar surface faces ventrally when the ungual is inclined ventrolaterally. In natural articulation, the unguals appear to have been deflected lateral to the midline axis of the pes and canted so that the sagittal plane of the ungual is inclined ventrolaterally (*Pleurocoelus,* Gallup, 1989:figs. 1, 4; *Dyslocosaurus,* McIntosh, Coombs, and Russell, 1992:fig. 1A). Pedal prints confirm the lateral deflection and ventrolateral inclination of the pedal unguals (Thulborn, 1990:fig. 6.16f; Pittman and Gillette, 1989:fig. 34.16).

These asymmetries can be verified in disarticulated unguals by comparing medial and lateral views, with the ungual held so that its sagittal plane is vertical. In lateral view, the proximal articular end and the narrow plantar surface are exposed, whereas, in medial view, neither of these surfaces can be seen (e.g., *Omeisaurus,* He, Li, and Cai, 1988:fig. 57). The condition in *Shunosaurus* is nevertheless uncertain because the unguals have only been figured in dorsal view (Zhang, 1988:fig. 55). Although they do not appear to be deflected laterally or canted ventrolaterally, the condition of the unguals in this genus (as well as that in digit I in *Vulcanodon*) requires further documentation.

Omeisaurus + Neosauropoda

Recorded Temporal Range—Late Jurassic (Oxfordian) to latest Cretaceous (Maastrichtian).

Diagnosis—Frontal excluded from the supratemporal fossa; supratemporal fenestra oriented transversely; 17 or fewer dentary teeth; presacral pleurocoels deep and invaginated; cervical pleurocoels divided; 12 or fewer dorsal vertebrae; 5 or more sacral vertebrae (at least one dorsosacral vertebrae added); cervical rib shafts positioned below centra; acromion more than 150% of minimum width of the scapular blade; metatarsals III and IV with minimum transverse shaft diameters 65% or less than that of metatarsals I and II.

(65) *Frontal excluded from supratemporal fossa.* In prosauropods and basal theropods, the frontal contributes to the anterior margin of the supratemporal fossa (Fig. 5). This is also true in the basal ornithischian *Lesothosaurus* (Sereno, 1991:figs. 11, 12) and clearly constitutes the primitive condition for Sauropoda. The condition is not known in *Vulcanodon,* but the frontal participates in the anterior wall of the fossa in *Shunosaurus* (Zhang, 1988:fig. 8; Zheng, 1996:fig. 8A).

In *Omeisaurus* (He, Li, and Cai, 1988:figs. 8, 9) and more advanced sauropods, the frontal is excluded from the supratemporal fossa, the anterior margin of which is formed entirely by the postorbital and parietal (Figs. 6–8).

(66) *Supratemporal fenestra, long axis oriented transversely.* In prosauropods (Fig. 5) and basal theropods (e.g., *Herrerasaurus,* Sereno and Novas, 1993:figs. 7, 8), the long axis of the supratemporal fossa is oriented anteroposteriorly. In other words, the fossa is longer anteroposteriorly than broad transversely. Although the condition is unknown in *Vulcanodon,* these proportions are present in *Shunosaurus* (Zheng, 1996:fig. 8A).

In *Omeisaurus* (He, Li, and Cai, 1988:fig. 8) and more advanced sauropods, the long axis of the supratemporal fossa is oriented transversely rather than anteroposteriorly (Figs. 6–8). This modification of the shape of the fossa may be correlated with the absence of frontal participation in the fossa. We have

scored these independently because such is not the case in other dinosaurs (e.g., *Allosaurus*; Madsen, 1976:pl. 2A).

(67) *Dentary tooth count 17 or fewer.* In prosauropods and basal theropods, the number of dentary teeth varies between 15 and 30. The number of teeth increases during growth and is somewhat positively correlated with body size and negatively correlated with relative tooth size. *Plateosaurus* has between 25 and 30 dentary teeth (Fig. 5), *Massospondylus* varies between 20 and 26 (Attridge et al., 1985; Gow et al., 1990), and basal theropods such as *Eoraptor* and *Herrerasaurus* average between 15 and 20 (Sereno and Novas, 1993). Thus, plesiomorphically, mature prosauropods probably had between 20 to 25 dentary teeth, and mature basal theropods probably averaged somewhat less, between 15 and 20 dentary teeth. The number of dentary teeth is unknown in *Vulcanodon.* In *Shunosaurus,* several adult skulls have more than 25 dentary teeth (Zheng, 1996:38). The dentary tooth count usually reported for *Shunosaurus* (18–21 teeth; Zhang, 1988; McIntosh, 1990a) appears to be based on a subadult specimen (Zhang, 1988). Thus the ancestral eusauropod probably had between 20 and 30 dentary teeth as an adult.

In *Omeisaurus* and more advanced sauropods, there are always fewer than 20 dentary teeth and, with one exception, fewer than 17. *Omeisaurus* averages between 14 and 17 dentary teeth in mature individuals (Dong et al., 1983; He et al., 1988: fig. 17). Tooth counts in diplodocoids vary between 9–11 (*Diplodocus*; Holland, 1924) and 16 (*Dicraeosaurus*; Janensch, 1935–1936), and, in *Camarasaurus, Brachiosaurus,* and the titanosaur *Nemegtosaurus* (Nowinski, 1971), range from 12 to 15 dentary teeth (Figs. 6–8).

(68) *Presacral pleurocoels deep and invaginated.* In prosauropods and basal theropods, pleurocoels are absent. In *Herrerasaurus,* a very shallow depression is present on the side of the anterior cervical centra above the parapophysis. No wellformed pleurocoels, however, are present in basal theropods, and the appearance of presacral pleurocoels among neotheropods represents an independent acquisition. The condition in *Vulcanodon* remains unknown. In *Shunosaurus,* a noticeable depression is present on the sides of the cervical centra, and surely represents a rudimentary pleurocoel (Zhang, 1988:fig. 27). Thus pneumatization of the vertebral column was already in place among basal eusauropods but had yet to invade the centra of the presacral vertebrae significantly.

In *Omeisaurus* and all more advanced sauropods, pleurocoels are developed as sizable invaginations of the presacral centra (Fig. 39). The invaginations excavate most of the body of the centrum, often leaving only a bony septum in the midline. Although varying in their expression along the presacral series, most of these advanced sauropods have well marked pleurocoels along the entire series (Figs. 11–13). Dicraeosaurids and *Euhelopus* constitute partial exceptions. In the former, discrete presacral pleurocoels are present, but the depression is not as deep and the ventral rim is poorly developed (e.g., *Amargasaurus*; Salgado and Bonaparte, 1991). In *Euhelopus,* well-formed pleurocoels are present in the dorsal vertebrae but are reduced in size in the cervical vertebrae (Wiman, 1929:pl. 3; Wilson, pers. obs.).

(69) *Cervical pleurocoels divided.* We regard the outgroup condition for this character as too transformed to score, because the pleurocoels are either absent or rudimentary. In *Omeisaurus* and more advanced sauropods, the pleurocoels are subdivided by a bony septum that extends posteroventrally (He, Li, and Cai, 1988:fig. 21C). Sometimes this septum is absent in the smaller pleurocoels of the anteriormost cervical vertebrae (e.g., *Omeisaurus*; He, Li, and Cai, 1988:fig. 19). In *Camarasaurus* and the diplodocids *Diplodocus* and *Apatosaurus,* the septum is either vertical or posteroventrally inclined (Figs. 11, 12). In *Diplodocus, Omeisaurus,* and *Brachiosaurus,* the septum is

joined by various thinner secondary septa. In *Euhelopus,* even the smallest of the reduced cervical pleurocoels retains a septum (Wilson, pers. obs.).

(70:3) *Dorsal vertebral number 12 or fewer.* Prosauropods (Galton, 1990) and the basal theropods *Eoraptor* and *Herrerasaurus* (Novas, 1993; Sereno, Martinez, and Alcober, in prep.) have 15 dorsal vertebrae, and this probably constitutes the ancestral condition for sauropods. The number of dorsal vertebrae is not known in the basal sauropods *Vulcanodon* or *Barapasaurus. Shunosaurus* has 13 dorsal vertebrae (Zhang, 1988). As no other sauropod has been shown to have more than 13 dorsal vertebrae, a loss of two dorsal vertebrae may constitute a synapomorphy for Eusauropoda. Reconstructing the numbers of vertebrae in different sections of the column, however, is complicated by the fact that dorsal vertebrae may have been transferred into the neck or incorporated into the sacrum. An increase in sacral number, therefore, may result in a decrease in dorsal number and should not be scored in duplicate. In addition, identifying a given vertebra as a dorsal rather than a posterior cervical is fraught with uncertainty. A fuller discussion of vertebral counts is presented in the section on Neck Elongation.

With two exceptions, *Omeisaurus* and all more advanced sauropods have 12 or fewer dorsal vertebrae. *Euhelopus* has 13 dorsal vertebrae, while *Haplocanthosaurus* appears to have at least 13 dorsal vertebrae, although the unusual number reported is 14 (McIntosh and Williams, 1988:11, 12). The number of dorsal vertebrae in this case is based on two skeletons with overlapping portions of the presacral column. We have chosen the more conservative number, given that no other eusauropod is known to have as many as 14 dorsal vertebrae. Dorsal number varies from 12 to as few as 10 in remaining sauropods. There are 12 dorsal vertebrae in *Camarasaurus* (Gilmore, 1925) and the diplodocoid *Dicraeosaurus* (Janensch, 1929a), probably 11 or 12 in the titanosaur *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977) and *Brachiosaurus* (Janensch, 1950), and 10 in the diplodocids *Apatosaurus* (Gilmore, 1936) and *Diplodocus* (Hatcher, 1901). The diplodocoids *Barosaurus* (Lull, 1919) and *Amargasaurus* (Salgado and Bonaparte, 1991) have been reported to have only 9 dorsal vertebrae.

(2:2). *Sacral vertebral number five or more (at least one dorsosacral vertebra added).* As discussed above, it is clear from the form of the neural arches in the sacral vertebrae of prosauropods and basal theropods that a posterior dorsal vertebra was incorporated into the sacrum as the first of three sacral vertebrae present in the ancestral dinosaur. Prosauropods and the basal theropods *Eoraptor* and *Herrerasaurus* (Sereno, Martinez, and Alcober, in prep.) all have three sacral vertebrae (contra Novas, 1993), the posterior two of which have broad ribs and constitute the primordial pair. Thus three sacral vertebrae that contact the pelvic girdle constitutes the ancestral condition for Sauropoda rather than two (contra Hatcher, 1901: 32; McIntosh, Miller, Stadtman, and Gillette, 1996:81).

The basal sauropods *Vulcanodon, Shunosaurus,* and *Barapasaurus* have added a caudal vertebra to the posterior end of the sacrum, judging from the form of the fourth sacral vertebra. The initial dinosaurian sacral vertebrae (now comprising the first three of four sacral vertebrae) form the majority of the acetabular articular surface on the sacricostal yoke and are the first to coossify (Ostrom and McIntosh, 1966:pl. 29; McIntosh, Miller, Stadtman, and Gillette, 1996). In *Barapasaurus,* all four sacral vertebrae contribute to the acetabulum articular surface (Fig. 38).

In *Omeisaurus* (He, Li, and Cai, 1988:fig. 32) and all other sauropods, a fifth sacral vertebra has been added to the anterior end of the sacrum (McIntosh, 1990a; Upchurch, 1995; Fig. 14). With maturity, this dorsosacral vertebra contacts the pelvic girdle and fuses to the centrum of the succeeding sacral vertebra

and to the sacricostal yoke. This dorsosacral vertebra rarely contributes significantly to the articular surface of the acetabulum and is the last sacral to fuse, often resulting in sacra with only four coossified vertebrae in immature individuals.

Euhelopus (Wiman, 1929) and titanosaurs (*Opisthocoelicaudia,* Borsuk-Bialynicka, 1977:fig. 11; *Saltasaurus,* Powell, 1986:pl. 31) are characterized by the incorporation of a third dorsal vertebra into the sacrum. This dorsosacral vertebra fuses to the anteriormost sacral vertebra and has a weak contact with the ilium. Complete coossification of this sixth sacral vertebra is a derived condition shared by *Euhelopus* and titanosaurs (see character 2:3).

(71) *Cervical rib shafts positioned below centra.* In prosauropods and basal theropods, the slender shafts of the cervical ribs usually overlap one another to form a composite shaft of bone alongside the cervical centra (e.g., *Plateosaurus,* Huene, 1926:pl. 2, fig. 1). In lateral view, the cervical rib shafts are positioned a little below the parapophyseal articulation and level with the ventral margin of the cervical centra. The transverse processes project ventrolaterally, and the short parapophyses are situated on the lateral side of the centrum near its ventral margin. Nothing is known about the condition of the cervical vertebrae and associated ribs in *Vulcanodon.* In *Shunosaurus,* these features are present (Zhang, 1988:figs. 23–28), although few of the ribs are preserved in articulation due to the immaturity of the specimen. The parapophyses are positioned on the sides of the cervical centra, and the transverse processes extend ventrally only to midheight on the centra (note that the apparent ventral position of the cervical rib shaft of *Shunosaurus* in Fig. 39 is the result of the partial lateral rotation of the vertebra).

In contrast, in *Omeisaurus* and more advanced sauropods, the cervical rib shafts are always positioned ventrolateral to the cervical column, as is preserved in articulation in the eusauropod *Euhelopus* (Wiman, 1929:pl. 1). The more ventral position of the rib shafts is the result of several modifications. First, the cervical transverse processes project more strongly ventrally so that the articular end for the tuberculum of the rib is already near the ventral margin of the centrum (e.g., *Saltasaurus*; Powell, 1992:fig. 6). Second, the parapophyses are located on the ventrolateral, rather than lateral, side of the centrum. This is the case in all presacral centra and is evident in ventral view (e.g., *Omeisaurus*; He, Li, and Cai, 1988:fig. 21A). Third, the processes of the cervical vertebrae (transverse processes, parapophyses) and cervical ribs (capitulum, tuberculum) are lengthened. In some genera, the parapophyses project away from the centra as columnar processes (e.g., *Camarasaurus,* Fig. 11). In others, the lengthening of all of these processes places the rib shafts far below the centra (e.g., *Apatosaurus*; Fig. 12).

(72) *Acromion more than 150 percent of the minimum width of the blade.* In prosauropods, the anteroposterior length of the acromion ranges from 100% to 150% of the minimum width of the scapular blade (*Plateosaurus,* Huene, 1926:pl. 5, fig. 9; *Lufengosaurus,* Young, 1947:fig. 3). Much of the apparent variation in size is related to the difficulty in accurately measuring the length of the acromion. In prosauropods, the acromion curves gradually away from the blade, its margin never achieving a full 90° angle to the anterior margin of the blade. Nevertheless, its anteroposterior length is clearly less than that in most eusauropods. We have scored the condition in theropods as too transformed for comparison because of the reduction in width of the blade of the scapula that occurs in basal theropods (i.e., *Eoraptor, Herrerasaurus*).

Shunosaurus has an acromial region that appears intermediate in form between that in prosauropods and that typical of most eusauropods. As in prosauropods, the acromial region expands gradually away from the shaft, its posterior margin never achieving a 90° angle to the axis of the shaft (Zhang, 1988:fig.

42). In general, however, the acromion appears expanded relative to that in prosauropods. Its overall dimensions, for example, are similar to that of the coracoid, whereas the acromion is always relatively smaller in prosauropods. In most sauropods, nevertheless, the acromion is even more expanded. More information is needed for *Shunosaurus,* as the acromial end of the scapula differs in available figures (Zhang, 1988:figs. 42, 43).

In *Omeisaurus,* the acromion curves away from the blade at an angle of 90° (He, Li, and Cai, 1988:fig. 41). Its anteroposterior length is twice that of the neck of the blade and greater than the anteroposterior length of the coracoid. Except for most titanosaurs, these expanded dimensions of the acromion are typical of that in more advanced sauropods (McIntosh, 1990a:fig. 16.8; Fig. 17). In *Euhelopus,* for example, the acromion curves at an angle greater than 90° to the scapular margin, achieving a length approximately 270% of the width of the neck of the scapula (Young, 1935:fig. 2). Among titanosaurs, *Alamosaurus* has the broadest acromion (Gilmore, 1946:fig. 6), with an anteroposterior width approximately 150% that of the neck of the blade. Other titanosaurs have reduced the length and relative size of the acromion (*Opisthocoelicaudia,* Borsuk-Bialynicka, 1977; *Saltasaurus,* Powell, 1986:pl. 3, 37; 1992:fig. 28). This reduction is accentuated by the overall expansion of the size of the coracoid in all known titanosaurs.

(73) *Metatarsals III and IV with minimum transverse shaft diameters 65 percent or less those of metatarsals I or II.* In prosauropods and basal theropods, the minimum transverse diameters of the shafts of metatarsals II and IV are slightly greater than those of metatarsals I and II. The length and transverse diameter of the shaft of metatarsal V is significantly less than in metatarsals I–IV in prosauropods and theropods, but this inequality is not found in basal sauropods. In *Vulcanodon* and *Shunosaurus,* the transverse shaft diameters of the metatarsals are remarkably uniform. In *Shunosaurus,* the diameter of metatarsal I is slightly greater, and metatarsal V slightly less, than the others. Leaving aside metatarsal V (which, as a non-weight-bearing element, is small or reduced in the outgroups for sauropods), it is clear that the outer metatarsals (III and IV) have shaft diameters comparable to those of the inner metacarpals (I and II) in outgroups for sauropods and basal sauropods. The condition in *Barapasaurus* remains unknown.

In *Omeisaurus* and more advanced sauropods, the minimum transverse shaft diameters of metatarsals III and IV are 60% or less than those of metatarsals I and II. Given that an increase in the shaft diameter of metatarsal I is a synapomorphy for Eusauropoda, comparison to metatarsal II is perhaps the most appropriate. In *Omeisaurus,* the minimum shaft diameters of metatarsals III and IV are 50% to 60% that of metatarsal II (He, Li, and Cai, 1988:fig. 55). The same difference in shaft diameter is present in *Camarasaurus* (Jensen, 1988:fig. 7C), *Apatosaurus* (Gilmore, 1936:fig. 27C), *Pleurocoelus* (Gallup, 1989: fig. 1), and titanosaurs (*Opisthocoelicaudia,* Borsuk-Bialynicka, 1977:pl. 14, fig. 2b).

Neosauropoda Bonaparte, 1986b

Definition—*Diplodocus, Saltasaurus,* their common ancestor, and all its descendants, including by this definition Diplodocoidea and Macronaria.
Recorded Temporal Range—Late Jurassic (Oxfordian) to latest Cretaceous (Maastrichtian).
Diagnosis—Preantorbital fenestra developed; ventral process of postorbital broader transversely than anteroposteriorly; lack of a jugal-ectopterygoid contact; external mandibular fenestra closed; tooth crowns lacking denticles; two or fewer carpal elements; metacarpals bound and with long intermetacarpal articular surfaces; metacarpus with U-shaped proximal articular sur-

face (270° arc); iliac preacetabular processes laterally divergent; proximal end of tibia subcircular; astragalar ascending process extending to posterior margin of astragalus; astragalus wedge-shaped in anterior view.

(74) *Preantorbital fenestra.* In most dinosaurs, a row of large neurovascular foramina open on the lateral surface of the maxilla above the alveolar margin. In prosauropods, the posteriormost foramen (Fig. 5A; posterior maxillary foramen) is slightly larger than the others and opens posteroventrally rather than anteroventrally. These foramina lead to a canal within the maxilla that opens on the floor of the antorbital fossa. In *Plateosaurus* (AMNH 6810), the posterior opening of the canal is located in a groove on the floor of the antorbital fossa, medial and slightly anterior to the posterior maxillary foramen (Fig. 5A). In basal eusauropods, the largest neurovascular foramina on the lateral surface of the maxilla are also positioned near the alveolar margin, and as in prosauropods and theropods, none is unusually large (e.g., *Omeisaurus;* He, Li, and Cai, 1988:fig. 9).

In neosauropods, in contrast, a large opening is located ventral, or anteroventral, to the antorbital fenestra. Originally identified in diplodocids (Fig. 6A), this opening is connected directly to the antorbital space by a short posteromedial canal that opens medially above the narrow palatal shelf of the maxilla (e.g., *Brachiosaurus,* Janensch, 1935–1936:figs. 41, 42; Ostrom and McIntosh, 1966:pl. 5). The opening is large enough and the canal short enough that the bones of the palate are visible through the preantorbital fenestra in *Diplodocus* (Fig. 6) and *Brachiosaurus* (Fig. 8). In these taxa, the canal may house a pneumatic extension of the antorbital sinus. This is suggested, in particular, in diplodocids, in which a well-marked depression is present along the anterior and ventral margins of the fenestra (Fig. 6; USNM 11255; Witmer, 1997:fig. 17A, B). In *Dicraeosaurus* (Janensch, 1935–1936:fig. 108), *Camarasaurus* (Fig. 7A), and the titanosaur *Nemegtosaurus* (Nowinski, 1971:pl. 9, fig. 1), the preantorbital fenestra is more slit-shaped. In a well-preserved subadult skull of *Camarasaurus,* the opening is very narrow and subdivided (Fig. 7A; CM 11338). In adult *Camarasaurus,* the preantorbital opening may be reduced considerably in size or absent altogether (Madsen, McIntosh, and Berman, 1995:figs. 9A, 10A, 11A). Likewise, *Euhelopus* shows no development of the preantorbital fenestra in the available adult skull (Mateer and McIntosh, 1985:fig. 5A, D).

As discussed above (character 20), we regard the preantorbital fenestra and fossa as novel features rather than as a subdivision of the antorbital fenestra and fossa (contra Witmer, 1997:27). Basal eusauropods show no development of a preantorbital opening and, as is true of all sauropods, no development of an antorbital fossa on the maxilla.

(75) *Ventral process of postorbital broader transversely than anteroposteriorly.* In prosauropods, basal theropods, and nearly all ornithischians, the ventral process of the postorbital is broader anteroposteriorly than transversely. This relation holds in the basal eusauropod *Shunosaurus,* in which the anteroposterior width at midlength along the process is slightly greater than the transverse width (ZDM 65430).

In neosauropods, the opposite proportions are present. The width of the gently concave orbital surface, best seen in anterior view (Madsen et al., 1995:fig. 18B), always exceeds that of the same process in lateral view. The broadened orbital surface and reduced anteroposterior width also characterizes diplodocoids (Fig. 6A), *Camarasaurus* (Fig. 7A; Madsen, McIntosh, and Berman, 1995:fig. 18), *Brachiosaurus* (Fig. 8A; Janensch, 1935–1936:fig. 13). It also appears to be the case in *Euhelopus* (Wiman, 1929:pl. 1, fig. 9) and the titanosaur *Nemegtosaurus* (Nowinski, 1971:fig. 1), both of which have ventral processes that are very narrow in lateral view.

(76) *Jugal-ectopterygoid contact absent.* In prosauropods and

theropods, the lateral process of the ectopterygoid arches toward the lateral margin of the skull roof, butting against the jugal (Fig. 5D; *Herrerasaurus*, Sereno and Novas, 1993:figs. 7D, 8D). The lateral contact of the ectopterygoid is close to the posterior end of the maxilla in prosauropods and the basal ornithischian *Lesothosaurus* (Sereno, 1991), and, in other ornithischians, the contact often involves both the jugal and maxilla. In the basal eusauropod *Shunosaurus*, the ectopterygoid articulates laterally with the jugal (Zhang, 1988:fig. 3; Zheng, 1996). In *Omeisaurus*, the condition remains uncertain.

In neosauropods, on the other hand, the lateral process of the ectopterygoid projects anterolaterally, abutting against the maxilla anterior to the jugal. This anterior shift in the lateral contact of the ectopterygoid is present in *Diplodocus* (Fig. 6D), *Camarasaurus* (Fig. 7D; Madsen, McIntosh, and Berman, 1995: fig. 10B), and *Brachiosaurus* (Fig. 8D). Among titanosaurs, the palate is most completely known in *Nemegtosaurus*, but the ectopterygoid is not preserved (Nowiński, 1971).

(77) *External mandibular fenestra closed.* The external mandibular fenestra is bordered by the dentary, surangular, and angular in prosauropods and in basal theropods and ornithischians. *Plateosaurus*, for example, maintains the primitive condition, with the dentary, surangular, and angular forming the anterior, dorsal, and ventral margins of the fenestra, respectively (Fig. 5A). It is now clear that several basal sauropods maintain at least a small external mandibular fenestra, including *Shunosaurus* (Zhang, 1988:figs. 3, 16; Zheng, 1996), *Omeisaurus* (He, Li, and Cai, 1988:figs. 13, 15), and *Mamenchisaurus* (Russell and Zheng, 1994:pl. 2, fig. 2). In these genera, the border of the fenestra is formed by three bones as described above (the angular is shown as excluded from the border in one specimen of *Omeisaurus* but clearly participates in the ventral margin in another; He, Li, and Cai, 1988:fig. 15). Previous remarks that only *Shunosaurus* among sauropods retains a mandibular fenestra are overstated (McIntosh, 1990a:358). Upchurch (1995: 372) recognized the presence of a fenestra in these basal eusauropods but also tried to distinguish between the size of the fenestra, linking "euhelopodids" (*Shunosaurus, Omeisaurus,* and *Mamenchisaurus*) and neosauropods on the basis of a "greatly reduced" opening. No distinguishing proportion was given, however, and a tangible difference between adult *Shunosaurus* (Zhang, 1988:fig. 12) and other basal eusauropods and prosauropods (e.g., *Riojasaurus*; Fig. 36A; *Jingshanosaurus,* Zhang and Yang, 1994:fig. 10) does not appear to exist.

The external mandibular fenestra is closed in neosauropods. In *Diplodocus* (USNM 11161; McIntosh and Berman, 1975:fig. 5), a shallow depression is developed at the juncture of the dentary, surangular, and angular, but there is no actual fenestra. The subadult skull of *Camarasaurus* (Fig. 7A) also shows that the external mandibular fenestra became closed before adult size was reached.

(78) *Tooth crown denticles absent.* In prosauropods, subconical denticles are present on the margins of the premaxillary and maxillary crowns as an adaptation to an exclusively herbivorous diet. Independently evolved in ornithischians, the denticles are approximately 5 to 10 times the size of the marginal serrations that characterize most theropods and the majority of basal archosaurs. The long axis of each denticle is angled toward the apex of the crown, rather than oriented perpendicular to the crown margin as is usually the case with serrations. As discussed above (character 32), there exist no solid grounds for the referral of certain isolated subconical tooth crowns with V-shaped wear facets to *Yunnanosaurus* (contra Galton, 1985). Furthermore, Galton (1985:117) remarked that these crowns resembled sauropods by the absence of denticles. It is now clear, however, that basal sauropods such as *Shunosaurus* (Zhang, 1988:fig. 19E), *Barapasaurus* (Jain, Kutty, and Roy-Chowdhury, 1975), *Omeisaurus* (He, Li, and Cai, 1988:16), and *Mamen-*

chisaurus (Russell and Zheng, 1994) have denticulate crown margins. In *Omeisaurus* and *Mamenchisaurus,* for example, the denticles are best developed on the convex anterior crown margin and are often few in number or absent on the concave posterior margin. Denticles also appear to be better developed on smaller, posterior crowns than on larger, anterior ones.

Among neosauropods, denticles are restricted to the posteriormost tooth crowns, for example in *Camarasaurus* (CM 11,338) and *Brachiosaurus* (Janensch, 1935–1936:pl. 12, figs. 2, 3). In *Shunosaurus*, marginal denticles were reduced to a similar extent independently, as they are present only on the posteriormost crowns (ZDM 65430). In most neosauropods, such as diplodocoids (*Diplodocus,* Holland, 1924:figs. 2, 3), *Euhelopus* (Wiman, 1929:pl. 2, figs. 12–23), and titanosaurs (*Malawisaurus,* Jacobs, Winkler, Downs, and Gomani, 1993:fig. 2A), even posterior tooth crowns lack denticles. Although denticles have been reported as present (McIntosh, 1990a; Russell and Zheng, 1994) in the crowns of the possible titanosaur from Mongolia, *Mongolosaurus* (Gilmore, 1933:fig. 4), this rudimentary ridge-like ornamentation is common among titanosaurs (e.g., *Nemegtosaurus,* Nowiński, 1971:pl. 13, fig. 3a) and does not extend from the crown margin as distinct subconical projections, as is the case with the denticles in basal sauropods. One neosauropod with well-developed marginal denticles comes from the Lower Cretaceous of Niger (Fig. 9). Smaller posterior crowns have many denticles; large anterior crowns, nevertheless, have only a few rudimentary denticles near the tip of the crown.

(79) *Carpal number two or fewer.* In basal theropods and basal ornithischians, both proximal and distal carpals are present and usually well ossified. In *Eoraptor* (Sereno, Martinez, and Alcober, in prep.) and *Herrerasaurus* (Sereno, 1993:fig. 15), for example, a large radiale and ulnare and a series of four distal carpals are present. In prosauropods, the proximal carpals are very reduced or absent, but the medial three distal carpals (1–3) are always present and articulate, respectively, with the proximal ends of metacarpals I–III (e.g., *Massospondylus,* Cooper, 1981:figs. 35, 36; *Lufengosaurus,* Young, 1941:fig. 15). In *Shunosaurus* (Zhang, 1988:figs. 2, 48), the basalmost sauropod for which the carpus is known, three block-shaped carpals of decreasing size are present and were found closely associated with metacarpals I–III, rather than with the radius and ulna (as might be expected if they represented proximal carpals). In *Omeisaurus,* a similar configuration of three carpals is preserved in one individual (He, Li, and Cai, 1988:pl. 14, fig. 6) but may not have been found in articulation (He, Li, and Cai, 1988:fig. 2). We regard these as distal carpals 1–3 and this configuration as primitive within Sauropoda.

In neosauropods, the number of carpals is reduced to two or less. In *Camarasaurus,* two block-shaped carpals are present and fitted to the metacarpals. As Osborn (1904:182) noted, the fitted articulation between the carpals and metacarpals not only suggests that they are properly identified as distal carpals but also that the primary axis of the wrist joint was positioned more proximally, between these carpals and the bones of the forearm. Furthermore, Osborn identified the large medial carpal as fused distal carpals 1–3 and the lateral element as fused distal carpals 4 and 5, based on the articular relations with the metacarpals (Osborn, 1904:fig. 1). This particular assessment of homology, although plausible, remains only one of several possibilities, because of the lack of intervening fusion lines, the potentially centered position of the single disc-shaped carpal found in other neosauropods (e.g., cf. *Janenschia,* Janensch, 1922:469–470; *Apatosaurus,* Gilmore, 1936:fig. 14; *Diplodocus,* Hatcher, 1902: fig. 10), and the absence of lateral distal carpals (4 and 5) in basal sauropods and prosauropods. Finally, titanosaurs appear to have eliminated any ossification of the carpus, as evidenced by the lack of carpals in specimens that preserve all of the other

bones of the forelimb (*Opisthocoelicaudia,* Borsuk-Bialynicka, 1977; *Alamosaurus,* Gilmore, 1946).

(80) *Metacarpals bound (long intermetacarpal articulations).* In prosauropods, contact between the bases of the metacarpals is limited. In proximal view, the bases of the metacarpal are in contact (e.g., *Massospondylus;* Cooper, 1981:fig. 37), but this intermetacarpal articulation does not extend down the metacarpal shafts, as seen in dorsal view (e.g., *Massospondylus,* Cooper, 1981:fig. 35; *Lufengosaurus,* Young, 1941:fig. 15). A similar condition is present in basal ornithischians (e.g., *Lesothosaurus;* Sereno, 1991:fig. 8B). In theropods, however, intermetacarpal contact is more extensive. Opposing flattened surfaces are present on the bases of the inner three metacarpals (e.g., *Herrerasaurus;* Sereno, 1993:fig. 14). Basal sauropods more closely resemble the pattern in prosauropods than in theropods. In *Shunosaurus* and *Omeisaurus,* the metacarpal bases are in mutual contact, but there are no intermetacarpal articular surfaces extending down their shafts (Zhang, 1988:fig. 49; He, Li, and Cai, 1988:fig. 41B). When the metacarpals are brought into articulation, significant space remains between the proximal halves of the metacarpals; this space cannot be eliminated by simply moving the metacarpals closer to one another (Zhang, 1988:pl. 14, fig. 1; He, Li, and Cai, 1988:pl. 14, fig. 6). Although theropods had evolved a ligament-bound metacarpus that was enhanced in some theropod subgroups, this condition does not appear to be primitive for Saurischia, Sauropoda, or Eusauropoda.

In neosauropods, all five metacarpals are characterized by long intermetacarpal articular surfaces that abut one another in the articulated metacarpus (Figs. 22, 24). Thus the metacarpals were united by ligaments into a rigid column, and the manus in neosauropods assumed a digitigrade posture. This condition is present in diplodocoids (Hatcher, 1902; Gilmore, 1936), *Camarasaurus* (Fig. 24; Osborn, 1904; McIntosh, Miller, Stadtman, and Gillette, 1996:pl. 19B, C), brachiosaurids (Fig. 22B; Ogier, 1975), and titanosaurs (*Alamosaurus,* Gilmore, 1946; *Opisthocoelicaudia,* Borsuk-Bialynicka, 1977; *Laplatasaurus,* Huene, 1929). The condition appears to be primitive in *Vulcanodon* (Raath, 1972:fig. 12) and remains unknown in *Haplocanthosaurus* and *Euhelopus.*

(81) *Metacarpal proximal ends subtriangular, composite proximal articular surface U-shaped.* In prosauropods and basal theropods, the proximal articular surfaces of the metacarpals form a composite arc of approximately 90° (*Massospondylus,* Cooper, 1981:fig. 36; *Lufengosaurus,* Young, 1941:fig. 15.1a; *Herrerasaurus,* Sereno, 1993:fig. 15). There is, in other words, an approximately 90° rotation between the dorsal surface of metacarpal I and that of metacarpal V. In the basal eusauropods *Shunosaurus* and *Omeisaurus,* the metacarpals are shown in articulation with very little arc in proximal view (Zhang, 1988: fig. 49; He, Li, and Cai, 1988:pl. 14, fig. 6), but these restorations are surely incorrect. The shapes of the proximal articular ends in these two genera, nonetheless, are not transversely compressed and do not have triangular proximal articular surfaces with angular apices. Rather, they have a subquadrate or rounded triangular shape, which probably formed a composite arc of approximately 90° in natural articulation (Fig. 40).

In neosauropods, in contrast, the proximal ends of the metacarpals are transversely compressed and form a composite arc of approximately 270° (Figs. 21, 23, 40). Thus the articular arc is tighter than a U-shape, which would place metacarpals I and V in opposition, facing medially and laterally, respectively. These metacarpals actually face slightly posteriorly when the midline of the metacarpal arc is directed anteriorly (Fig. 22). The tightly arched configuration of the proximal articular surface is a reflection of the transversely compressed, wedge-shaped form of the proximal shafts of the metacarpals. The central metacarpals (II–IV) are often deeper than broad (Figs.

22, 24). The tightly arched form of the proximal articular end of the metacarpus is maintained to a large extent distally, with the digitigrade manus composed principally of an arched metacarpal "colonnade" (Gauthier, 1986). This derived configuration of the metacarpus is confirmed by available manual prints of sauropods (Fig. 22E).

We regard the ligament-bound structure of the neosauropod metacarpus and its tightly arched form as independent characters, because the former has evolved in other dinosaurian subgroups (e.g., theropods, advanced iguanodontian ornithischians) but the latter is unique to neosauropods.

(82) *Iliac preacetabular blade laterally divergent (width across ilia greater than iliac length).* In prosauropods, theropods, and ornithschians, the width across the iliac preacetabular processes is equal to, or less than, the maximum length of the ilium. The greatest width relative to the length of the ilium occurs in prosauropods and basal theropods, because in these forms the preacetabular process is short (and thus iliac length is relatively shorter). In prosauropods, the width across the preacetabular processes is approximately 70 to 80% of the length of the ilium (e.g., *Plateosaurus,* Huene, 1926:pl. 2, fig. 3). In *Herrerasaurus,* these dimensions are subequal (Novas, 1993:fig. 3). In *Eoraptor* and other theropods, the width of the pelvic girdle across the ilia is similar to that in prosauropods or proportionately narrower. In *Shunosaurus,* the preacetabular processes do not project strongly laterally (Zhang, 1988:fig. 51). In *Barapasaurus* (Wilson, pers. obs.) and *Omeisaurus* (He, Li, and Cai, 1988:fig. 32), the width across the preacetabular processes is approximately 80% of the length of the ilium.

In neosauropods, the width of the pelvic girdle across the preacetabular processes is always greater than the length of the ilia, which is largely the result of the strong lateral flare of the preacetabular processes (Fig. 27). In some neosauropods, the tip of the preacetabular process projects almost directly laterally (e.g., *Saltasaurus*). The maximum width across the ilia compared to the maximum length of the ilium is approximately 140% in *Haplocanthosaurus* (Hatcher, 1903:pl. 5, fig. 1) and *Camarasaurus* (Osborn and Mook, 1921:fig. 49), 150% in *Apatosaurus* (Mook, 1917:fig. 1) and *Diplodocus* (Hatcher, 1901: fig. 9), and 200% in *Euhelopus* (Wiman, 1929:pl. 1, fig. 3) and *Saltasaurus* (Powell, 1992:fig. 17).

(83) *Tibia with subcircular proximal end.* In prosauropods and theropods, the transverse dimension of the proximal end of the tibia is always less than its anteroposterior dimension, the former measuring approximately 55% to 75% of the latter (e.g., *Lufengosaurus,* Young, 1941:pl. 5, fig. 1a; *Herrerasaurus,* Novas, 1993:fig. 8C). Among basal sauropods, this primitive proportion is present in *Vulcanodon* (Cooper, 1984:fig. 23B) and *Barapasaurus* (Wilson, pers. obs.). The proportions of the proximal end of the tibia are not available in *Shunosaurus.* In *Omeisaurus,* a figured tibia appears to have been severely anteroposteriorly crushed, because its proximal end is more than twice as wide as anteroposteriorly deep (He, Li, and Cai, 1988:fig. 53B).

In neosauropods, the proximal end of the tibia is subcircular with subequal anteroposterior and transverse dimensions. The transverse width of the proximal end is within 15% of its anteroposterior dimension in diplodocoids (*Diplodocus,* Hatcher, 1901:fig. 18; *Apatosaurus,* Gilmore, 1936:fig. 23; *Dyslocosaurus,* McIntosh et al., 1992:fig. 2D), *Camarasaurus* (Fig. 32E), *Brachiosaurus* (Janensch, 1961:fig. 210), *Euhelopus* (Wiman, 1929:pl. 1, fig. 9), and titanosaurs (*Opisthocoelicaudia,* Borsuk-Bialynicka, 1977:pl. 14, fig. 2a, b; cf. "*Titanosaurus,*" Huene, 1929:pl. 19, fig. 4c). The condition in *Haplocanthosaurus* is available in a specimen that may be correctly referred to the genus (USNM 4275; McIntosh and Williams, 1988), but the relative dimensions of the proximal end have not been reported. It is possible that the subcircular shape of the proximal end of

tibia will also characterize *Omeisaurus* as well as *Mamenchisaurus* (Young, 1954:fig. 4) when additional information is available.

(84) *Astragalar ascending process extends to the posterior margin of astragalus.* In prosauropods and theropods, the ascending process is limited to the anterior two-thirds of the astragalus in proximal view. The posterior third is occupied by a posterior fossa that, at least in part, accommodates the posteroventral flange of the tibia. The wedge-shaped form of the ascending process and its location on the anterior two-thirds of the astragalus are remarkably similar in prosauropods (e.g., *Massospondylus,* Cooper, 1981:fig. 71f) and basal theropods (*Eoraptor,* Sereno, Martinez, and Alcober, in prep.; *Herrerasaurus,* Novas, 1989:fig. 2.6). The ascending process also forms about two-thirds or less of the medial side of the astragalus in the basal sauropods *Vulcanodon* (Raath, 1972:fig. 9a), *Omeisaurus* (He, Li, and Cai, 1988:fig. 54, pl. 17, fig. 3a), and *Mamenchisaurus* (Young and Zhao, 1972:fig. 11.1). In *Shunosaurus,* proximal or medial views of the astragalus are not available, and so the relative size and position of the ascending process are uncertain. The opposing strongly beveled articular surface on the tibia, however, suggests that the articular surface of the ascending process sloped to a significant degree (Zhang, 1988:fig. 54).

In neosauropods, in contrast, the ascending process extends to the posterior end of the astragalus in proximal view, as preserved in diplodocoids (*Diplodocus,* Hatcher, 1901:fig. 20; *Apatosaurus,* Gilmore, 1936:fig. 26A), *Camarasaurus* (Fig. 33B, C), *Brachiosaurus* (Janensch, 1961:pl. 22, figs. 1, 2a), *Euhelopus* (Wilson, pers. obs.), and titanosaurs (*Opisthocoelicaudia,* Borsuk-Bialynicka, 1977:pl. 14, fig. 8). This may represent a reorientation of the astragalus as much as an actual posterior extension of the ascending process. The astragalus in neosauropods appears as if it were rotated posterodorsally, so that the sloping articular surface of the ascending process is oriented at a much shallower angle (approximately 10 to 15° from the horizontal) than in prosauropods or basal sauropods (25 to 40°). The shallow angle of the ascending process in neosauropods clearly represents its natural orientation (Fig. 31). The orientation of a neosauropod astragalus in isolation, however, is less obvious, and some have been tipped anteriorly so that, in proximal view, the ascending process stops short of the posterior margin and its articular surface assumes a sharper angle to the horizontal (e.g., *Dicraeosaurus;* Janensch, 1961:pl. 22, fig. 4b). Likewise, the astragalus in *Vulcanodon,* which has a more primitive form, has been tipped posteriorly so that in proximal view the ascending process appears to extend to the posterior margin of the astragalus (Cooper, 1984:fig. 25D). We regard the apparent rotation of the astragalus, the posterior extension of the ascending process, and the near horizontal orientation of the articular surface of the ascending process as correlates of a single neosauropod synapomorphy.

(85) *Astragalus wedge-shaped in anterior view.* In prosauropods and basal theropods, the body of the astragalus (i.e., without the ascending process) appears subrectangular in anterior view (e.g., *Massospondylus,* Cooper, 1981:fig. 71g; *Eoraptor,* Sereno, Martinez, and Alcober, in prep.; *Herrerasaurus,* Novas, 1989:fig. 2.5). The medial side of the astragalus has approximately the same proximodistal depth as the lateral side. Likewise, in proximal view, the medial side of the astragalus is subrectangular, with rounded anteromedial and posteromedial corners.

In neosauropods, in contrast, the medial side of the astragalus is reduced. In anterior and posterior views, the astragalus appears wedge-shaped, with the proximodistal depth of the astragalus decreasing markedly toward its medial side (Figs. 31, 33A, D). In addition, in proximal and distal views, the primitive posteromedial corner of the astragalus is absent, and the as-

tragalus has a subtriangular, rather than subrectangular, shape (Fig. 33B, E). The posterior margin passes from the posterior fossa, laterally, to the anteromedial corner, medially, without any development of a posteromedial corner. The reduction of the medial end of the astragalus—i.e., the reduction in thickness and loss of the posteromedial corner—can be observed in diplodocoids (*Diplodocus,* Hatcher, 1901:fig. 20; *Apatosaurus,* Gilmore, 1936:fig. 26A; *Dyslocosaurus,* McIntosh, Russell and Coombs, 1992:fig. 2F, H), *Camarasaurus* (Fig. 33B, C), *Brachiosaurus* (Janensch, 1961:pl. 22, fig. 1), *Euhelopus* (Wiman, 1929:pl. 4, fig. 10), and titanosaurs (*Opisthocoelicaudia;* Borsuk-Bialynicka, 1977:pl. 14, fig. 8).

Macronaria, new taxon

Definition—Neosauropods more closely related to *Saltasaurus* than to *Diplodocus.*

Etymology—*Macros,* (Greek), long and *naris* (Latin), nostril, in reference to the diameter of the external naris, which exceeds that of the orbit.

Recorded Temporal Range—Late Jurassic (Kimmeridgian) to latest Cretaceous (Maastrichtian).

Diagnosis—Middle and posterior dorsal neural spines with transversely flared distal ends; chevrons with open proximal articulations; coplanar distal ischial shafts.

(86) *Middle and posterior dorsal neural spines with transversely flared distal ends.* In the basal sauropods *Barapasaurus* and *Omeisaurus,* the lateral margins of the posterior dorsal neural spines are nearly parallel (Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1979:pl. 101a, c; He, Li, and Cai, 1988:fig. 30). In anterior view, these posterior dorsal neural spines appear as vertically oriented rectangles. In diplodocoids, in which the anterior and middle dorsal neural spines are bifid, the succeeding single neural spines of the posterior dorsal vertebrae are also parallel-sided in anterior view (*Apatosaurus,* Gilmore, 1936:pl. 25, figs. 7–9). Thus, although eusauropods are characterized by transversely expanded dorsal neural spines (character 40), the extent of this broadening in basal forms is roughly equal throughout the height of the neural spine.

In macronarians, posterior dorsal neural spines flare sharply near their apices to form distinct triangular lateral processes. In the single-spined forms *Haplocanthosaurus* and *Brachiosaurus,* these flared neural spines follow relatively parallel-sided anterior and mid-dorsal neural spines (Hatcher, 1903:pl. 1, figs. 8–10; Janensch, 1961:figs. 57, 61, 66). As in diplodocoids, the anterior and middle dorsal neural spines in *Camarasaurus* (Osborn and Mook, 1921:pl. 71, figs. 8–10) and *Euhelopus* (Wiman, 1929:pl. 3, figs. 3, 4) are cleft, whereas those of the posteriormost dorsal vertebrae are single. In contrast to diplodocoids, however, the lateral margins of these posterior dorsal vertebrae are concave. Upchurch (1995:376) listed distally flared posterior dorsal neural spines as a synapomorphy uniting camarasaurids (including *Haplocanthosaurus*) and brachiosaurids, but did not comment on its distribution within titanosaurs. Distally flared posterior dorsal neural spines are also present in titanosaurs, though they are not as strongly developed as in *Brachiosaurus* and *Camarasaurus.* In *Ampelosaurus* (Le Loeuff, 1995:fig. 4) and *Saltasaurus* (PVL 4017-135), for example, expansion of the distal neural spines resembles that in *Haplocanthosaurus.* The shape of the posterior dorsal neural spines is not known in the basal titanosaurs *Malawisaurus, Epachthosaurus,* and *Andesaurus.* The derived condition is also present in an isolated dorsal neural spine from the Upper Cretaceous of India (Huene and Matley, 1933:fig. 21).

(87) *Anterior caudal chevrons with open proximal articulation.* The anterior caudal chevrons of most saurischians form the bony enclosure of the haemal canal. In *Eoraptor* and *Massospondylus,* the dorsal margin of the haemal canal is concave

in anterior view, while in lateral view the anterior and posterior margins of the proximal articular surface are beveled for contact with the preceding and succeeding caudal vertebrae, respectively. This condition is present in the basal sauropods *Vulcanodon, Barapasaurus,* and *Omeisaurus,* in which the anterior and middle caudal chevrons are bridged proximally (Raath, 1972: fig. 7; He, Li, and Cai, 1988:fig. 39). Whereas in *Barapasaurus* even the posteriormost, "forked" chevrons are bridged proximally, they are open proximally in *Omeisaurus* (He, Li, and Cai, 1988:fig. 40). In the diplodocoids *Diplodocus* and *Dicraeosaurus,* the forked chevrons appear near the thirteenth to seventeenth caudal vertebrae and are open proximally. The anterior chevrons preceding these have completely enclosed haemal canals (Osborn, 1899:fig. 12; Janensch, 1929b:fig. 53).

In macronarians, the dorsal margin of the haemal canal is formed by ventral surfaces of adjacent caudal centra. The chevrons are Y-shaped in anterior view, with free arms forming the ventral and lateral margins of the haemal canal. All known anterior caudal chevrons of *Haplocanthosaurus* and *Brachiosaurus* have open proximal articulations (Hatcher, 1903:figs. 7–10; McIntosh and Williams, 1988:15; Janensch, 1950:figs. 123–136). In titanosaurs, the proximal articular surface of caudal chevrons is not bridged by bone, and the haemal canal is particularly deep, especially in the middle caudal chevrons (*Andesaurus,* Calvo and Bonaparte, 1991:fig. 4F; *Saltasaurus,* Powell, 1991:figs. 26, 27; *Alamosaurus,* Gilmore, 1946:fig. 4). There is, however, some variation in chevron structure among species of *Camarasaurus.* Chevrons of *C. supremus* and *C. grandis* are open proximally (Osborn and Mook, 1921:figs. 62–64; McIntosh, Miller, Stadtman, and Gillette, 1996:88), whereas chevrons 2–5, 13, and 16 are bridged proximally in *C. lewisi* (McIntosh, Miller, Stadtman, and Gillette, 1996:pl. 17). Anterior caudal chevrons are not known for the juvenile specimen of *C. lentus.* We consider the condition in *C. lewisi* aberrant in this regard, with the derived macronarian condition being more general for the genus. Open anterior caudal chevrons are also in *Shunosaurus,* which is here interpreted as independent event (Zhang, 1988:fig. 40).

(88) *Ischial distal shafts nearly coplanar.* The ischia of basal sauropods and diplodocoids meet on an angle, forming a triangle in distal view (*Apatosaurus,* Gilmore, 1936:fig. 20A; *Dicraeosaurus,* Janensch, 1961:fig. 12). In these taxa, the ischial shafts are somewhat twisted, so that the long axes of their distal extremes are oriented 30° to 35° from vertical.

In macronarians, the dorsoventral depth of the medial and lateral extremes of the distal portions of the ischia are subequal, and the distal ischia twist nearly 90° from vertical to form a broad, nearly horizontal plate at their distal extremes (Fig. 29, 41). Upchurch (1995:377) considered ischial shafts "strongly twisted relative to the plane of the proximal plate" a camarasaurid synapomorphy, uniting *Camarasaurus* and *Haplocanthosaurus,* without comment on the distribution of this feature within brachiosaurids or titanosaurs. In *Brachiosaurus* and the basal titanosaur *Malawisaurus,* the ischial shafts are platelike and twist distally to form a nearly horizontal surface (Janensch, 1961:fig. 10; Jacobs, Winkler, Downs, and Gomani, 1993:fig. 1G). This condition is present in *Andesaurus* and *Aeolosaurus,* though the ischia are not as platelike (Calvo and Bonaparte, 1991:fig. 5A; Salgado and Coria, 1993:fig. 9). In more derived titanosaurs, the ischial shafts are much shorter than the pubic shafts, and although they are flattened, the ischial shafts do not twist quite as much distally.

Camarasaurus + Titanosauriformes

Recorded Temporal Range—Late Jurassic (Kimmeridgian) to latest Cretaceous (Maastrichtian).

Diagnosis—Maximum diameter of naris greater than orbital maximum diameter; quadrate fossa deep; surangular depth more than twice the depth of angular; opisthocoelous posterior dorsal centra; length of longest metacarpal 45% of more that of radius; metacarpal I longer than metacarpal IV; puboischial contact deep dorsoventrally.

(89) *External naris, maximum diameter greater than orbital maximum diameter.* Enlarged external nares characterize sauropodomorph dinosaurs (Sereno, unpubl. data). Whereas in the basal theropods *Eoraptor* and *Herrerasaurus* the maximum diameter of the external naris is less than half that of the orbit (41–42%, Sereno, Forster, Rogers, and Monetta, 1993:fig. 1; Sereno and Novas, 1993:fig. 8A), prosauropods and basal sauropods are characterized by nares nearly twice that size (81% in *Plateosaurus* [Fig. 5A, B]; 75% in *Shunosaurus,* Zhang, 1988:fig. 3; 80% in *Diplodocus* [Fig. 6A, B]).

The size of the external nares relative to that of the other skull openings is further increased in *Camarasaurus,* brachiosaurids, and titanosaurs. In these taxa, the external nares are the largest skull openings; the ratio of the long axis of the naris to that of the orbit is 50% larger than in prosauropods and basal sauropods. In *Camarasaurus,* the long axis of the naris is 110–130% that of the orbit (DNM 28, DNM 975, Madsen et al., 1995), whereas it is 121% the length of the long axis of the orbit in *Brachiosaurus* (Fig. 8A). The size of the naris relative to other skull openings varies with maturity in *Camarasaurus,* as the orbit and naris are subequal in size in juvenile specimens (Fig. 7A). The relative sizes of the naris and orbit are unknown in *Haplocanthosaurus, Euhelopus,* and titanosaurs.

(90) *Quadrate fossa deep.* Eusauropods are characterized by the presence of an elongate fossa on the posterior aspect of the quadrate (character 28). In *Shunosaurus* and *Omeisaurus,* this fossa is well-marked, but shallow. In *Diplodocus* and *Apatosaurus,* the quadrate fossa forms a transversely narrow, gentle depression, which covers approximately two-thirds of the quadrate. In all of these taxa, the quadrate fossa is completely formed by the quadrate.

The quadrate fossa of *Camarasaurus* and titanosauriforms is broad, deep, and extends dorsally to the lateral aspect of the quadrate head (Madsen et al., 1995:fig. 20; *Brachiosaurus,* Janensch, 1935–36:fig. 26; *Nemegtosaurus,* Nowinski, 1971:pl. 12, fig. 2). The fossa is deeply incised on the medial portion of the quadrate and becomes more shallow laterally (*Camarasaurus,* Madsen et al., 1996:fig. 20). This shallow lateral margin of the quadrate abruptly meets the quadratojugal and squamosal, which form the lateral margin of the quadrate fossa. In *Camarasaurus* and *Brachiosaurus,* the quadrate fossa faces posteriorly, whereas it appears to be slightly posterolaterally oriented in *Nemegtosaurus* and *Quaesitosaurus* (Figs. 7D, 8D; Nowinski, 1971:pl. 12, fig. 2; Kurzanov and Bannikov, 1983: fig. 1). The laterally facing quadrate fossa and "resonator depression" reconstructed by Kurzanov and Bannikov (1983:92) for *Quaesitosaurus,* however, appear to be exaggerated, as this orientation causes the pterygoid process of the quadrate to contact the basal tubera (Kurzanov and Bannikov, 1983:fig. 2). No cranial remains are known for *Haplocanthosaurus,* so this feature may be found to characterize all macronarians. A broad quadrate fossa is also present in the diplodocoid *Rayososaurus tessonei,* although the weight of other characters in this analysis suggests that it represents an independent acquisition (Calvo and Salgado, 1995:fig. 6A).

(91) *Surangular depth more than twice depth of angular.* The dorsal margin of the posterior half of the lower jaw in basal sauropods is relatively flat, and the ratio of the depth of the surangular to that of the angular is low. In *Shunosaurus,* the depth of the surangular is 1.5 times that of the angular (Zhang, 1988:fig. 3), whereas, in *Omeisaurus,* this ratio is 1.7 (He, Li, and Cai, 1988:fig. 13B). The coronoid region is particularly low

in diplodocoids, in which the depth of the surangular is 1.4 times that of the angular in *Diplodocus* (Fig. 6A).

Camarasaurus and titanosauriforms are characterized by an enlarged coronoid process on the lower jaw (Fig. 42). The prominent, rounded bulge is formed by the dorsoventrally expanded surangular, which is more than twice the depth of the angular. In the relatively short-jawed *Camarasaurus,* the surangular is more than two and one-half times the height of the angular in lateral view, whereas it is more than three in *Brachiosaurus* (height measured perpendicular to tooth row; Figs. 7A, 8A). The surangular is nearly two and one-half times the depth of the angular in *Nemegtosaurus* and *Quaesitosaurus* (Nowinski, 1971:pl. 9, fig. 1B; Kurzanov and Bannikov, 1983: fig. 1). Neither the surangular nor the angular are completely preserved on the lower jaws of *Euhelopus,* but the distinct surangular prominence preserved just posterior to the dentary indicates that the derived condition is present (Wiman, 1929:pl. 1, figs. 2, 6).

(92) *Posterior dorsal centra opisthocoelous, convexity present on anterior face of centrum.* Whereas the cervical and anterior dorsal centra of most eusauropods are opisthocoelous (characters 38, 59), their posterior dorsal centra are generally amphicoelous to platycoelous, with flattened anterior faces and slightly concave posterior faces (*Barapasaurus,* Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1979:pls. 100, 101; *Omeisaurus,* He, Li, and Cai, 1988:fig. 30). The same condition holds for the diplodocoids *Apatosaurus* and *Dicraeosaurus* (Gilmore, 1936:pl. 32, figs. 5–9; Janensch, 1929b:pl. 1, figs. 19–23). *Haplocanthosaurus,* however, retains a low convexity on the dorsal half of the anterior face of the posterior dorsal centra, but this prominence is much more reduced than the anterior convexities present in the first five dorsal centra (Hatcher, 1903:pl. 2, figs. 7–14).

All presacral vertebrae of *Camarasaurus* and titanosauriforms are strongly opisthocoelous. As mentioned above, basal sauropods retain the posterior depression in the posterior dorsal centra, so opisthocoely must be defined on the presence of a well-marked, hemispherical convexity on the anterior face of the centrum. In *Camarasaurus* and *Brachiosaurus,* all presacral centra are strongly opisthocoelous, and the dorsal centra are arched ventrally, which accentuates the anterior convexity in lateral view (Osborn and Mook, 1921:pls. 70–74; Janensch, 1961:figs. 56–65). The posterior dorsal centra of *Euhelopus* and titanosaurs (e.g., *Argentinosaurus, Saltasaurus*), though not strongly arched ventrally, are nonetheless strongly opisthocoelous (Young, 1935:fig. 1; Bonaparte and Coria, 1993:fig. 5A, B; Powell, 1992:figs. 14, 15). Increased opisthocoely may have increased mobility of the posterior half of the trunk, although the presence of accessory hyposphene-hypantrum articulations in many of these taxa may have maintained some stiffness in the trunk. Hyposphene-hypantrum articulations between posterior dorsal vertebrae are lost in a subgroup of titanosaurs, potentially increasing trunk flexibility even more within this clade.

(93) *Length of longest metacarpal 45 percent or more that of radius.* Eusauropods primitively have a short metacarpus that is oriented at a relatively low angle to the substrate. In *Shunosaurus* and *Omeisaurus,* the longest metacarpal constitutes between 32% and 35% the length of the radius (Zhang, 1988: tabs. 9, 11; He, Li, and Cai, 1988:tabs. 14, 15). In diplodocoids, which have a more vertically oriented, digitigrade manus, the metacarpus is short relative to the radius (0.36–0.38 in *Apatosaurus*; Gilmore, 1936:219, 226).

In *Camarasaurus,* brachiosaurids, and titanosaurs, the metacarpus is lengthened relative to the radius. It is unknown whether this characterizes all macronarians, as *Haplocanthosaurus* lacks a forelimb. The metacarpus-to-radius ratio is high in *Brachiosaurus,* in which the elongate metacarpus comprises 51% the length of the radius (Janensch, 1961:tabs. 7, 8). This ratio

is 0.44 in an adult specimen of *Camarasaurus* (McIntosh, Miller, Stadtman, and Gillette, 1996:tabs. 11, 13), while it is 0.47 in a juvenile specimen (Gilmore, 1925:382). The metacarpus is also elongate in titanosaurs, including *Opisthocoelicaudia* (0.46; Borsuk-Bialynicka, 1977:tabs. 9, 10) and *Argyrosaurus* (0.59; Huene, 1929:77). The distal forelimb is unknown in *Euhelopus.* Upchurch (1995:376) listed "relatively long and slender" metacarpals as a synapomorphy uniting brachiosaurids and camarasaurids, although the metacarpus is equally elongate in titanosaurs. It is unclear whether Upchurch considered the elongate metacarpus of titanosaurs an independent acquisition, or simply scored it as plesiomorphic.

(94) *Metacarpal I subequal in length to metacarpal IV.* The outer metacarpals (i.e., I and V) of basal sauropods are the shortest metacarpal elements. In *Shunosaurus, Omeisaurus* and the diplodocids *Diplodocus* and *Barosaurus,* metacarpal I accounts for 75 to 90% the length of metacarpal IV (Zhang, 1988: tab. 11; He, Li, and Cai, 1988:tab. 15; Osborn and Granger, 1901:202, 205). Among non-macronarian sauropods, *Apatosaurus* represents the only exception, with metacarpal I being longer than metacarpal IV (Gilmore, 1936:226). Thus, primitively for sauropods, metacarpals II–IV are the longest elements, whereas metacarpals I and V are significantly shorter. In most of these taxa, the metacarpus is roughly symmetrical about the central element; metacarpal III is the longest element, metacarpals II and IV are the next longest elements, and metacarpals I and V are the shortest.

In *Camarasaurus, Brachiosaurus,* and titanosaurs, metacarpal I is elongated relative to other metacarpals. In *Camarasaurus* and *Brachiosaurus,* metacarpal I is as long as metacarpal IV (McIntosh, Miller, Stadtman, and Gillette, 1996:13; Janensch, 1961:tab. 8). Metacarpal I in the titanosaurs *Alamosaurus* and *Opisthocoelicaudia* is longer than metacarpal IV and represents the longest metacarpal (Gilmore, 1946:39; Borsuk-Bialynicka, 1977:tab. 10). Thus, in this clade, the medial three metacarpals (I–III) are the longest elements in the metacarpus.

(95) *Puboischial contact deep dorsoventrally.* In eusauropods, the ischium and pubis meet below the acetabulum along a dorsoventral contact, which represents approximately one-third of the total length of the pubis, as measured from the iliac peduncle to the pubic foot (*Shunosaurus,* Zhang, 1988:fig. 52B; *Omeisaurus,* He, Li, Cai, and Gao, 1988:fig. 50). The same condition obtains in *Apatosaurus* and *Haplocanthosaurus,* in which the puboischial contact is shallow relative to the pubic shaft (Gilmore, 1936:figs. 20, 36; Hatcher, 1903:pl. 5, fig. 2).

In *Camarasaurus* and titanosauriforms, the puboischial contact is relatively much deeper, constituting nearly half the total length of the pubis. For example, in *Camarasaurus* and *Andesaurus,* the length of the ischial peduncle of the pubis is 45% the total length of the pubis, whereas it makes up more than 50% of the total length of the pubis in *Brachiosaurus* (Fig. 28; Calvo and Bonaparte, 1991:fig. 6A; Janensch, 1961:fig. 200). The condition in *Euhelopus,* as in several titanosaurs, is unknown because the margins of the ischial process of the pubis are incomplete.

Titanosauriformes Salgado, Coria, and Calvo, 1997

Definition—*Brachiosaurus, Saltasaurus,* their common ancestor, and all of its descendants, including by this definition Brachiosauridae and Somphospondyli.

Recorded Temporal Range—Late Jurassic (Kimmeridgian) to latest Cretaceous (Maastrichtian).

Diagnosis—Pterygoid lacking dorsomedially oriented basipterygoid hook; dorsal ribs with pneumatic cavities; distal condyle of metacarpal I undivided and with reduced articular surface; iliac preacetabular process semicircular; femur with proximal one-third of shaft deflected medially.

(96) *Pterygoid lacks dorsomedially oriented basipterygoid hook.* In *Shunosaurus* and *Camarasaurus,* the palatobasal articulation involves a pronounced, dorsomedially oriented pterygoid hook, which wraps around the basipterygoid process (Zheng, 1996:fig. 11; Fig. 7B). The condition is ambiguous within diplodocoids, as this hook-like process is present on the isolated pterygoid of *Dicraeosaurus,* but there is no such hook involved in the palatobasal articulation of *Diplodocus.* Cranial remains are not definitely known for *Haplocanthosaurus.*

In titanosauriforms, the pterygoid lacks the basipterygoid hook, resulting in an open palatobasal articulation. In *Brachiosaurus,* the basipterygoid process rests in a very shallow depression in the ventromedial portion of the quadrate ramus of the pterygoid (Fig. 8B). Similarly, in the titanosaurs *Nemegtosaurus* and *Quaesitosaurus,* the articulation between the basipterygoid process and pterygoid is open medially. These taxa are characterized by a "rocker"-like palatobasal articulation, in which basipterygoid process rests in an anteroposteriorly concave facet in the pterygoid.

(97) *Dorsal ribs with pneumatic cavities.* The proximal portions of cervical ribs are occasionally pneumatized in *Omeisaurus* and neosauropods, as the anterior division of the pleurocoel may invade the capitulum of the rib. The dorsal ribs of *Omeisaurus,* diplodocoids, and *Camarasaurus,* in contrast, do not contain pneumatic openings, although their posterior surfaces often contain shallow fossae.

Titanosauriforms are characterized by pneumatic dorsal ribs. As noted by Riggs (1904:239, pl. 75, fig. 5) in *Brachiosaurus altithorax,* the anterior surfaces of the dorsal ribs are perforated by large foramina, which lead to a spongy internal cavity. In *B. brancai,* both the anterior and posterior surfaces are pierced by pneumatic openings (Janensch, 1950:figs. 107–108). Upchurch (1995:376) listed among his synapomorphies for Brachiosauridae that "thoracic ribs possess foramina that lead into internal cavities." Pneumatic ribs, however, characterize a larger group that includes *Euhelopus* and titanosaurs. Pneumatic openings are present between the posterior surface of the tuberculum and capitulum in the isolated dorsal ribs of *Euhelopus,* but the position of these ribs within the dorsal series is unknown (PMU R233E; Wilson, pers. obs.). Titanosaurs including *Magyarosaurus* and *Ampelosaurus* also have pneumatic ribs (BM R4891, MDE C391; Wilson, pers. obs.). The extent of pneumatization along the dorsal column is unknown, though it appears that pneumatization is more common in anterior dorsal ribs. An as yet undescribed titanosaur from Mendoza, Argentina, also possesses pneumatic ribs, and various exposed cross-sections indicate that the proximal one-third of most thoracic ribs are pneumatized and composed of large-celled, spongy bone (Wilson, in prep.).

(98) *Distal condyle of metacarpal I undivided, phalangeal articular surface reduced.* The distal condyles of metacarpal I of most saurischians are divided and asymmetrical. In *Herrerasaurus* and *Massospondylus,* for example, the lateral distal condyle of metacarpal I extends further distally than does the medial condyle, such that the distal condyles are canted 20° to 30° from a line orthogonal to the axis of the shaft (Sereno, 1993:fig. 9; Cooper, 1981:figs. 38, 39D, F). Likewise in sauropods, including *Apatosaurus* and *Camarasaurus,* the distal condyles are offset, but other asymmetries exist: the medial condyle is much broader anteroposteriorly and transversely in distal aspect, and its articular surface has more of an excursion anteriorly and posteriorly than does the medial condyle (Gilmore, 1936:fig. 16C; Fig. 23). The distal articular surfaces of the other metacarpals do not display this pronounced asymmetry.

In titanosauriforms, the distal end of metacarpal I is not divided into distinct condyles, and its distal surface is flat relative to the shaft axis. In *Brachiosaurus,* the distal condyle is level

and the articular surface has little exposure on the external (anterior) or internal (posterior) surfaces of the metacarpal (Janensch, 1961:pl. 18, figs. 1–3). Flat, undivided distal condyles are also present in *Pleurocoelus* and the titanosaurs *Opisthocoelicaudia* and *Alamosaurus* (Lull, 1911:pl. 17, fig. 1; Borsuk-Bialynicka, 1977:pl. 7, fig. 3; Gilmore, 1946:fig. 10B). The metacarpus is unknown in *Euhelopus.* The loss of distinct distal condyles (and thus their asymmetry) and the concomitant reduction of the distal articular surface may be related to diminution of ungual of digit I, which is small in *Brachiosaurus* and absent in titanosaurs (Salgado, Coria, and Calvo, 1997). Gimenez (1992:154) considered metacarpal I with a symmetrical distal end a titanosaur synapomorphy, whereas Salgado, Calvo, and Coria (1995) listed absence of phalangeal articular surfaces on the distal metacarpals as a synapomorphy supporting a sister-group relationship between *Pleurocoelus* and Titanosauria (though only metacarpal I is known for *Pleurocoelus*). Loss of distinct distal condyles and reduction of the distal articular surface are here considered correlated, and the distribution recognized here implies that this feature characterizes all titanosauriforms.

(99) *Iliac preacetabular process semicircular and with posteroventral excursion of its cartilage cap.* As discussed above, eusauropods are characterized by an iliac blade which has a semicircular dorsal margin (character 45). In most sauropods, the highest point of this arc is directly above the acetabulum, and the blade is roughly symmetrical about this point. Anteriorly, the preacetabular process tapers to an acute terminus, which is the anteriormost projection of the ilium (horizontal formed by a line between the ventralmost points of the pubic and ischial peduncles of the ilium). This acute tip also delimits the margin of the cartilage cap of the ilium (Fig. 26). The short, triangular preacetabular process is present in the basal sauropods *Barapasaurus* and *Omeisaurus* (Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1979:fig. 93B; He, Li, and Cai, 1988: fig. 49). The same condition is present in the ilia of neosauropods, despite the lateral divergence of their preacetabular processes (*Camarasaurus,* Fig. 26; *Diplodocus, Apatosaurus, Haplocanthosaurus,* Hatcher, 1903:pl. IV, figs. 1–3). The dorsal margin of the ilium is not preserved in *Vulcanodon* or indicated in available figures of *Shunosaurus* (Raath, 1972; Zhang, 1988).

In titanosauriforms, the preacetabular lobe of the ilium is semicircular in profile, and the rudimentary projection marking the posteriormost excursion of the iliac cartilage cap is positioned posterior to the anterior margin of the ilium. The lobe-shaped expansion of the preacetabular process of *Brachiosaurus* causes the ilium to appear asymmetrical, with its dorsal margin rising to its highest point anterior to the acetabulum (Janensch, 1961:fig. 198). The ventral prong marking the margin of the cartilage cap is positioned on the ventral surface of the preacetabular process, between the anterior margin of the ilium and the pubic peduncle. In *Euhelopus,* the more complete of the two ilia of "specimen b" exhibits the characteristic posteroventral excursion of the preacetabular cartilage cap (Wiman, 1929:pl. 4, fig. 1). Both the semicircular expansion of the preacetabular process and the more posterior excursion of its cartilage cap are readily observable in titanosaurs, including *Saltasaurus* and *Titanosaurus colberti* (Powell, 1991:fig. 18; Jain and Bandyopadhyay, 1997:fig. 23B).

(100) *Femur with proximal one-third of shaft deflected medially.* Sauropod femora lack the sigmoid curvature present plesiomorphically in saurischian dinosaurs (see character 1). Although the femoral head projects medially from the femoral shaft, the long axis of the femur is straight in anterior and lateral views, as demonstrated by *Camarasaurus* (Fig. 30A).

Titanosauriform femora bear a characteristic bulge on the lateral portion of the proximal one-third of the shaft (Fig. 43). Relative to its long axis, the proximal portion of the femur is

deflected medially in anterior view. This "sharp deflection of the proximal third of the lateral margin" of the femur was first noted by McIntosh (1990a:370) and later listed as a titanosauriform synapomorphy by Salgado (1993:268) and Salgado, Coria, and Calvo (1997:fig. 10). This lateral bulge on the lateral margin of the femur is distinct in *Brachiosaurus* and titanosaurs, such as *Saltasaurus* and *Opisthocoelicaudia* (Janensch, 1961:fig. 208; Powell, 1991:fig. 37; Borsuk-Bialynicka, 1977: fig. 15A, pl. 13, figs. 1–2). This feature has not been previously noted in *Euhelopus*, possibly because of the missing proximolateral portion of the femur of "specimen a" (Wiman, 1929:pl. 3, figs. 20–22). The femur of a second individual ("specimen b"), on the other hand, is well-preserved and exhibits the characteristic titanosauriform medial deflection of the proximal one-third of the femoral shaft (Wiman, 1929:pl. 4, figs. 4, 5). This titanosauriform synapomorphy is also present in the fragmentary skeletons of *Aegyptosaurus* (Stromer, 1932:pl. 1, fig. 7a), *Austrosaurus* (Coombs and Molnar, 1981:pl. 5, fig. B), and *Phuwiangosaurus* (Martin et al., 1994:fig. O). These genera are here considered Titanosauriformes incertae sedis.

Somphospondyli, new taxon

Definition—Titanosauriforms more closely related to *Saltasaurus* than to *Brachiosaurus*.

Recorded Temporal Range—Late Jurassic (Kimmeridgian) to latest Cretaceous (Maastrichtian).

Etymology—*somphos* (Greek), spongy or porous, in reference to the typical bone texture within the presacral column; *spondylos* (Greek), vertebra.

Diagnosis—Reduced lamination on cervical neural arches; presacral vertebrae composed of spongy bone; anterior and mid-dorsal neural spines posterodorsally inclined; six sacral vertebrae (one dorsosacral vertebra added); scapular glenoid deflected medially.

(101) *Cervical neural arch laminae rudimentary.* The various bony projections of sauropod neural arches are connected and supported by a complex framework of bony laminae. In the anterior cervical vertebra of *Camarasaurus*, for example, strut-like processes buttress the zygapophyses, diapophyses, parapophyses, and spine to each other and to the centrum (Fig. 11). At the junction of two or more of these vertebral laminae, deep, well defined fossae are formed.

In *Euhelopus* and titanosaurs, neural arch laminae of cervical vertebrae are rudimentary. In *Euhelopus* and *Malawisaurus*, only two laminae, the postzygapophyseal-diapophyseal lamina (pzdl) and the posterior centrodiapophyseal lamina (pcdl), are distinctly developed on the cervical neural arches, but even these are not as well-developed as those in *Camarasaurus* and other sauropods (Wiman, 1929:pl. 3, fig. 3; Jacobs, Winkler, and Gomani, 1996:fig. 5A). Moreover, the small fossa between these two laminae and posterior to the diapophysis is the only well-defined neural arch fossa present. This reduced neural arch lamination also characterizes the titanosaur from Peirópolis, Brazil (Powell, 1987:pl. 1, figs. 1–4). In all of these taxa, the extent of neural lamination increases towards the cervical-dorsal transition, so that the lamination in posterior cervical vertebrae is somewhat intermediate between that of the anterior cervical and the typically laminate dorsal vertebrae.

(102) *Presacral vertebrae composed of spongy bone.* Omeisaurus and neosauropods are characterized by the presence of pneumatic openings on the lateral portion of presacral centra (character 68). These pleurocoels are always divided by a bony strut in cervical centra. In a transverse section through the centrum, the paired pleurocoels excavate nearly all of the interior of the centrum except for a median vertical lamina (Ostrom and McIntosh, 1966:pl. 23, figs. 4, 5). Thus, within these sauropods,

relatively large pleurocentral openings lead into large, paired cavities.

In *Euhelopus* and titanosaurs, the presacral vertebrae are composed of spongy bone. In these forms, relatively small pleurocoels open internally into a series of interconnected bony cells. In transverse of longitudinal sections, the interior of the centrum is composed of a fine network of bony struts. In *Saltasaurus*, for example, the entire vertebra of is highly pneumatic, so that cross-sections through the centrum and bony processes of the neural arch reveal a spongy internal structure (Powell, 1992:fig. 16). This feature has been previously recognized as characterizing titanosaurs; as Powell (1986:238) noted, "The cervical, dorsal, sacral, and in some cases caudal vertebrae of the titanosaurids are not solid, but are internally composed of large cells in the vertebral centrum and other large structures, such as the neural spine, diapophysis, parapophysis, etc. . ." (translated from the original Spanish text). This highly spongy internal bone structure, however, also characterizes *Euhelopus*. As in many titanosaurs, the pleurocoels of cervical and dorsal vertebrae are small in *Euhelopus*, and open into a series of small cells (Wilson, pers. obs.).

(103) *Anterior and mid-dorsal neural spines posterodorsally inclined.* In the long-spined diplodocoid *Dicraeosaurus*, the dorsal neural spines are oriented perpendicular to the axis of the dorsal centra (Janensch, 1929b:pl. 1, figs. 12–23). Similarly, in *Camarasaurus*, the dorsal neural spines are oriented vertically, although in each of the four composite dorsal series figured by Osborn and Mook (1921:pls. 70–73), the neural spine of one vertebra (placed in the center of the series) is slightly deflected posteriorly. In *Haplocanthosaurus*, the anterior and posterior dorsal neural spines are vertically oriented, whereas the middle dorsal neural spines are tilted slightly posteriorly. The maximum posterior inclination of these middle dorsal neural spines is 20° from vertical (dorsal 7; Hatcher, 1903:pl. 2, fig. 1.8).

The anterior and middle dorsal neural spines of *Euhelopus* and titanosaurs are posterodorsally inclined, forming an angle of approximately 45° with the vertical. In the articulated vertebral column of *Euhelopus*, the neural spines of the fifth through the eighth dorsal vertebrae are inclined posteriorly (Wiman, 1929:pl. 3, figs. 1, 3, 4). Among titanosaurs, articulated dorsal series are only known for *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977:pl. 3, figs. 1–5, 7–9) and the titanosaur from Peirópolis, Brazil (Powell, 1987:pl. 2, figs. 2–5). In these forms, posteriorly deflected neural spines are present on the second or third through the ninth dorsal vertebrae. The neural spines of isolated posterior dorsal vertebrae of *Malawisaurus* and *Saltasaurus* are also posteriorly inclined, but the extent of this inclination throughout the dorsal series is unknown.

(2:3) *Sacral vertebral number six (one dorsosacral vertebra added).* Omeisaurus and neosauropods are characterized by a sacrum composed of five coossified vertebrae (character 2:2). Based on the structure and relative timing of fusion, these five sacral vertebrae are interpreted as representing the two primordial sacral vertebrae, two incorporated dorsosacral vertebrae, and an incorporated caudosacral vertebra (Fig. 47).

Euhelopus and titanosaurs are characterized by the presence of a sixth sacral vertebra, which has been incorporated from the dorsal series. The centrum and neural arch of this dorsosacral vertebra are completely coossified to those of the second sacral vertebra. In *Titanosaurus colberti* and *Euhelopus*, the slender rib of the dorsosacral vertebra contacts the ilium, though it does not contribute to the formation of the sacricostal yoke (Jain and Bandyopadhyay, 1997:fig. 10; Wiman, 1929:pl. 4, figs. 2, 3).

(104) *Scapular glenoid deflected medially.* In *Herrerasaurus* and *Massospondylus*, the surfaces of both the scapular and coracoid glenoid are flat, and oriented roughly perpendicular to the

plane of the base of the scapula and the coracoid (Sereno, 1993: fig. 1; Cooper, 1981:figs. 22, 23). In these taxa and in other basal saurischians, neither portion of the glenoid is well exposed medially or laterally. In *Shunosaurus*, the surface of the glenoid is relatively flat, whereas in *Barapasaurus* and *Omeisaurus*, both scapular and coracoid portions of the glenoid are slightly exposed medially (Zhang, 1988:fig. 43; Jain, Kutty, Roy-Chowdhury, and Chatterjee, 1979:fig. 93A; He, Li, Cai, and Gao, 1988:fig. 41). The glenoid cavity in *Camarasaurus* is similarly flat and slightly exposed in lateral view (Fig. 17). In *Brachiosaurus*, the scapular glenoid is clearly beveled laterally in anterior view (Janensch, 1961:pl. 15, fig. 3A). Thus, the glenoid is flat in most sauropods, and forms a surface which is roughly perpendicular to the base of the scapula and coracoid. In some forms, the glenoid is slightly visible laterally or medially. In all of these taxa, however, the scapular and coracoid portions of the glenoid are not offset with respect to each other.

In *Euhelopus* and titanosaurs (e.g., *Opisthocoelicaudia*), the scapular and coracoid glenoid are offset with respect to each other, so that the scapular glenoid faces medially whereas the coracoid glenoid faces laterally (Fig. 18). The scapular glenoid is deep mediolaterally and strongly beveled medially in *Euhelopus*, *Opisthocoelicaudia*, and *Saltasaurus* (Powell, 1991:fig. 28C). The scapular glenoid appears relatively narrow in *Titanosaurus colberti*, but is nonetheless beveled medially (Jain and Bandyopadhyay, 1997:fig. 18A).

PHYLOGENETIC RESULTS

One hundred and nine morphological characters were scored for outgroups and for 10 terminal taxa encompassing the majority of known sauropod diversity (see Appendix). Approximately one-half of the characters are introduced in this work are used in a novel manner. The remaining characters have been used by one or more previous authors, although most have been coded as cladistic characters and character states or recoded from previous cladistic analyses (Huene, 1929, 1932; Gilmore, 1936, 1946; Romer, 1956; Steel, 1970; Cruickshank, 1975; Berman and McIntosh, 1978; Cooper, 1984; Gauthier, 1986; Bonaparte, 1986a, b; McIntosh, 1990a, b; McIntosh and Williams, 1988; Salgado, 1993; Salgado, Coria, and Calvo, 1997; Upchurch, 1995). Character polarity was determined by outgroup comparison, and minimum-length trees were generated using the Branch-and-Bound algorithm in PAUP (Phylogenetic Analysis Using Parsimony; Swofford, 1993). Characters were optimized under delayed and accelerated transformation, and optimization ambiguity in the data set is tabulated in Table 2.

Robustness Tests

The data supports a single minimum-length tree of 153 steps, with relatively high consistency and retention indices (Figs. 44, 45; C.I.: 0.77; R.I.: 0.79). The overall robustness of this tree and of particular nodes in the tree were tested by accepting trees several steps longer than the minimum. Sets of trees of were generated by incrementally increasing the number of additional steps. A 50 percent majority-rule consensus tree was calculated for each set of trees. For trees up to two steps longer, there are no rearrangements of the single minimum-length tree. At three steps longer than the minimum, two trees are generated that differ in the position of *Haplocanthosaurus* and yield an unresolved trichotomy at the base of Neosauropoda in a consensus tree. At four steps longer than the minimum, 11 trees are generated by rearrangements of *Haplocanthosaurus* and *Barapasaurus*. At seven steps longer than the minimum, 64 trees are generated. These trees yield a strict consensus tree lacking any structure within Sauropoda save for the basal position of *Vulcanodon* (Eusauropoda). At 10 steps longer than the minimum,
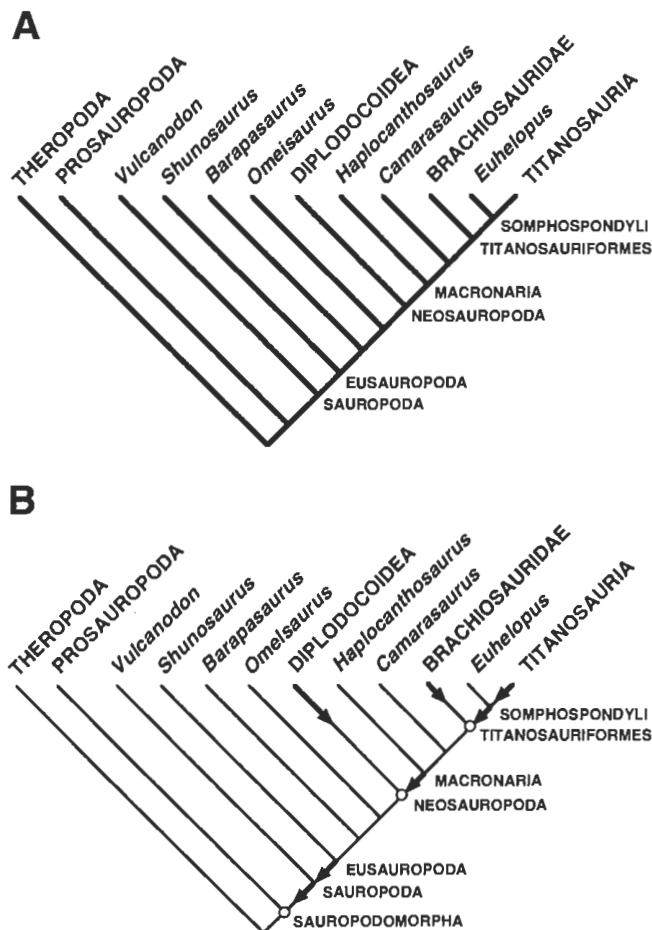
FIGURE 44. Cladistic arrangement and taxonomic definitions for 10 sauropod taxa based on an analysis of 109 characters, using Prosauropoda and Theropoda as successively more remote outgroups. **A**, single minimum-length tree (153 steps; CI, 0.81; RI, 0.86) was determined by maximum parsimony analysis; **B**, cladogram for Sauropodomorpha showing the locations of the stem-based (arrows) and node-based (open circles) taxonomic definitions used in this study.

that node disappears as well in a strict consensus of 238 possible trees.

The loss of resolution with increasing steps, however, is largely the result of missing data in two of the terminal taxa, *Barapasaurus* and *Haplocanthosaurus*, neither of which are represented by adequate cranial material. *Barapasaurus* and *Haplocanthosaurus* are scored as unknown for 53% and 65% of the 109 characters in the matrix, respectively. The only other ingroup taxon with a comparably high amount of missing data (*Vulcanodon*, 62%), maintains a more stable phylogenetic position because of 11 postcranial characters that are derived in all other sauropods and do not exhibit any homoplasy. The phylogenetic positions of *Barapasaurus* and especially *Haplocanthosaurus* are less secure, and the great amount of missing information for these taxa allows many equally parsimonious rearrangements with relatively few additional steps.

The basic structure of the minimum-length tree, nevertheless, appears to be robust. Even when accepting all trees 10 steps greater than the minimum-length tree (i.e., 163 steps), all nodes in the minimum length tree are present in more than 50% of the 238 possible trees. Clearly the collapse of structure with additional steps is the result of one or two weak nodes and a few taxa known only from partial skeletons.
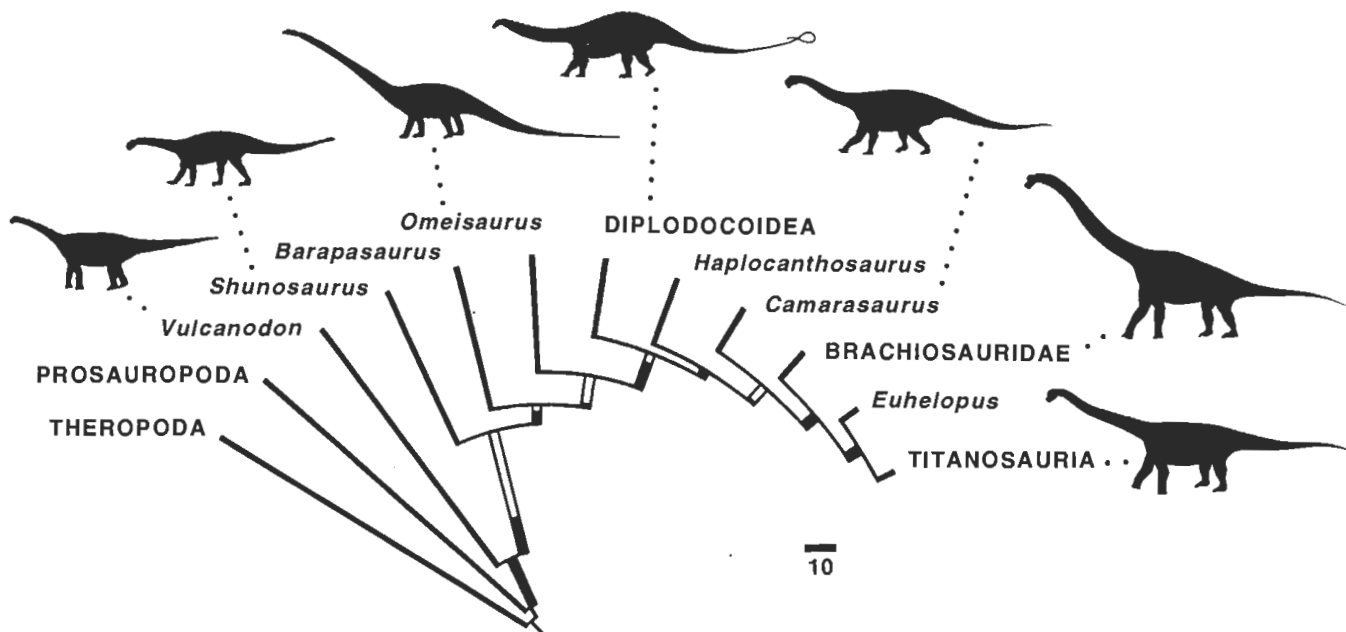
FIGURE 45. Circular cladogram with internal branches scaled according to the number of synapomorphies under delayed character-state optimization (unambiguous synapomorphies shown as black). Icons are not to scale. Scale bar shows 10 synapomorphies.

An Implausible Dichotomy

The data were fitted to the traditional two-family topology using MacClade (Maddison and Maddison, 1993). The traditional topology, based primarily on tooth structure, unites Diplodocoidea and Titanosauria in one clade and *Camarasaurus* and Brachiosauridae in another (Huene, 1932, 1956; Romer, 1956; Steel, 1970; Gauthier, 1986; Upchurch, 1995). Thirteen additional steps are necessary to accommodate this traditional topology, a substantial increase in length that casts serious doubt on the plausibility of the traditional hypothesis. The consistency index remains relatively high (C.I.: 0.73) due to the large number of higher-level synapomorphies present in both hypotheses (below Neosauropoda). The shift in the consistency index is far more dramatic (C.I.: 0.79 versus 0.60; R.I.: 0.82 versus 0.42) when restricting the ingroups to neosauropods and examining only the 35 synapomorphies that vary principally within Neosauropoda (i.e., characters 75–109). Furthermore, there are more than 800 equally parsimonious alternative trees of comparable length to that embodying the traditional dichotomy.

These results suggest that the morphological characters used to generate the shortest tree contain significant phylogenetic signal, and that the traditional dichotomous arrangement within Neosauropoda is untenable.

Taxonomic Definitions

The utility of taxon names based on phylogenetic definitions has been emphasized recently, and node-based or stem-based phylogenetic definitions have been applied methodically to differentiate crown groups (node-based) from more inclusive groups that incorporate the intervening extinct taxa (stem-based) (de Quieroz and Gauthier, 1990, 1992).

The use of various combinations of phylogenetic definitions, however, has not been explored within groups that are known only from either living or extinct taxa. In this study, we define several higher taxa as stable node-stem triplets (Sereno, in press). A node-stem triplet is an association of three higher

taxa, in which a node-based group is composed of two stem-based subgroups. Higher taxa defined as node-stem triplets remain stable in the face of new taxa or rearrangements within each subgroup. Thus, if Neosauropoda is defined as a node-based taxon composed of two stem-based taxa, Diplodocoidea and Macronaria, a triplet of phylogenetically defined higher taxa is formed and can be defined to enhance stability. To increase stability, the reference taxa selected on either side of a particular node in a phylogenetic definition are best chosen at some phylogenetic distance from the node. Thus, in the example above, we have based the definitions on the well-known genera *Diplodocus* and *Saltasaurus*:

Neosauropoda: *Diplodocus, Saltasaurus,* their common ancestor and all descendants.

Diplodocoidea: All neosauropods closer to *Diplodocus* than to *Saltasaurus.*

Macronaria: All neosauropods closer to than to *Saltasaurus Diplodocus.*

The hierarchical scheme presented below summarizes the phylogenetic definitions used in this study. Bold-face type indicates node-based taxa; regular type indicates stem-based taxa. Three nested node-stem triplets form the spine of the classification.

Sauropodomorpha
  Prosauropoda
  Sauropoda
    Neosauropoda
      Diplodocoidea
      Macronaria
        Titanosauriformes
          Brachiosauridae
          Somphospondyli
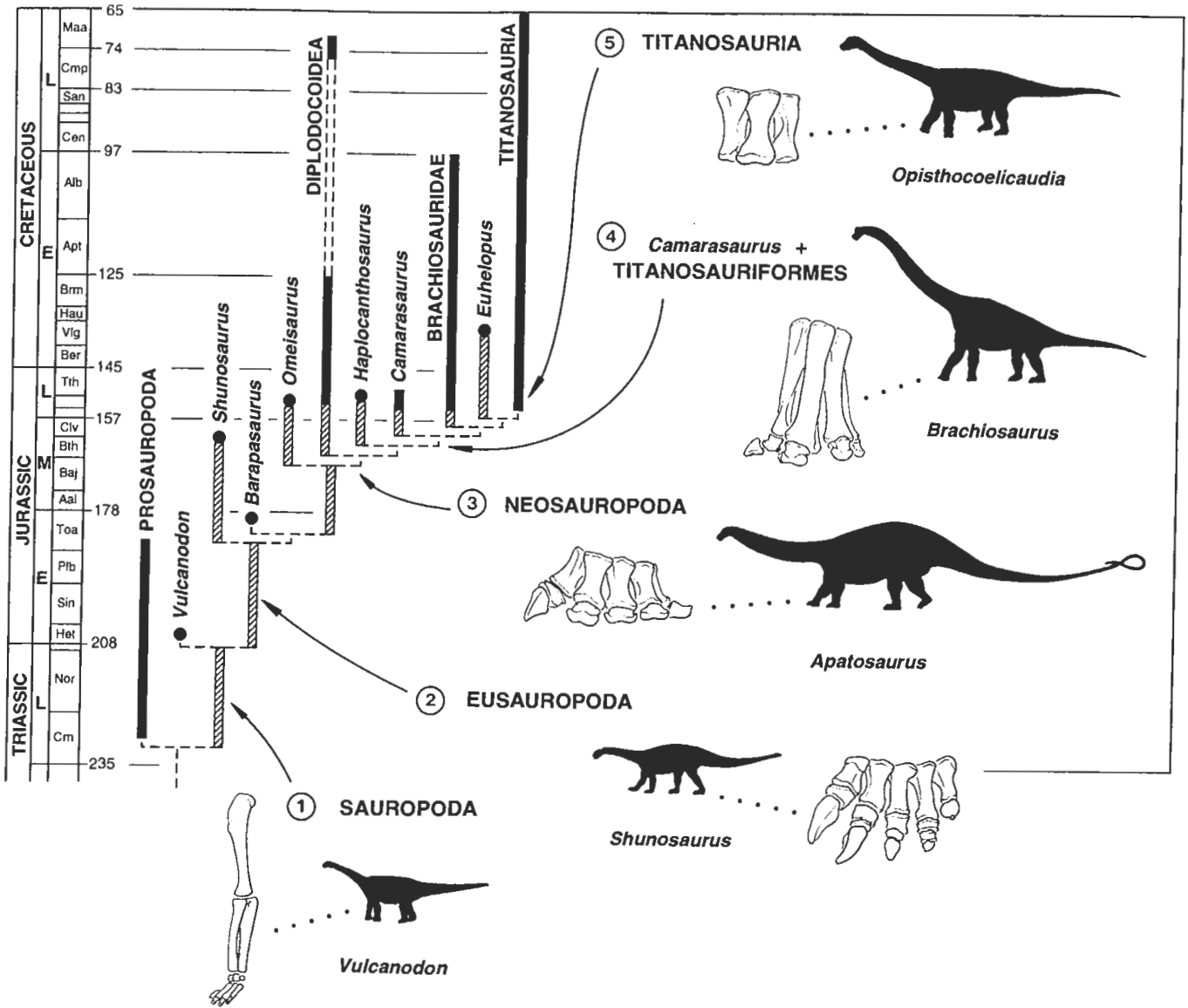   *Euhelopus*
          Titanosauria

FIGURE 46.   Evolution of principal postural changes in the fore and hindlimbs of Sauropoda. Node 1, evolution of columnar posture among obligatory quadrupeds of large body size; Node 2, collapse of the pes from a digitigrade to a sub-plantigrade or graviportal posture with a substantial heel pad; Node 3, elevation of the metacarpus from a plantigrade to a digitigrade posture with a rigid, ligament-bound metacarpus; Node 4, elongation of the metacarpus to equal 45 percent or more of the length of the radius; Node 5, lack of carpal ossification and loss of all manual phalanges. The calibrated phylogeny of sauropodomorphs is based on their cladistic relationships and recorded temporal ranges (black), with cross-hatched bars represent missing ranges and missing ancestral lineages and dashed bars indicating uncertainty in the identification of specimens of young age. Icons are to scale, line drawings are not. The time-scale is based on data in Harland et al. (1990).

DISCUSSION

Early Body Size and Posture

The ancestral body size and posture for Sauropoda can only be inferred from the outgroups Prosauropoda and Theropoda. Judging from the basal taxa in each of these successive outgroups, the ancestral sauropod had an overall length of 3–4 m or less, with at least a facultative bipedal posture. Sauropods, therefore, were secondarily obligate quadrupeds and doubled their body size early in their evolution (Table 3). With few exceptions (possibly dicraeosaurids and *Euhelopus*), sauropods maintained or increased in body size throughout their history. Many early sauropod modifications may reflect size-related constraints on skeletal structure (Fig. 46).

With increased body weight, the long bones of the limbs assumed a more vertical orientation. Limbs are effective in weight-bearing when loaded axially, transmitting forces along the long axis of limbs and limb elements to the ground. The shafts of the femur, humerus, and metatarsal IV lose the sigmoid curvature present in most saurischians and many ornithischians (character 1), allowing these elements to be loaded more in compression than in bending. The olecranon process on the ulna is very poorly developed (character 4), which facilitates a columnar rather than flexed forelimb stance. Titanosaurs, which secondarily developed a prominent olecranon process, have a fossa on posterior surface on the humerus that permitted full extension of the forelimb.

The articular ends of sauropod limb bones have a character-

istic rugose texture, with sculpted groves and pits. This texture, which is better developed in sauropods than in other dinosaurs, enhances the attachment of a thick cartilage cap. Carpal and tarsal elements are partially and sometimes completely enclosed in thick cartilage, and the calcaneum and carpal elements are unossified in several sauropods, presumably retained in cartilage (character 79). This kind of cartilage joint may be necessary at body weights in excess of 10 tons (i.e., twice that of an African elephant and presumably twice that calculated for *Tyrannosaurus*). The hydrostatic organization of cartilage allows it to absorb compressional forces and then recover quickly when the load is removed (Wainwright et al., 1976). Its ability to respond to repeated loading makes cartilage more effective than bone in absorbing shock and transmitting forces from the end of one bone to a surface involving several bones.

The cross-sectional shape of the femoral shaft in most sauropods is distinctly elliptical, with the long axis of the ellipse oriented transversely (character 10). This cross-sectional geometry and orientation increases the resistance of the shaft to mediolateral bending because more of the resistant material is located in the region experiencing high stress. Because the head of the femur projects dorsomedially into the acetabulum, body weight is loaded off-axis, medial to the long axis of the femur. The elliptical cross-section of the femoral shaft may be important in resisting this eccentric loading of the femoral shaft when body weight is borne by the hindlimb during locomotion.

Evolutionary Trends

Tooth Form—Differences in crown proportions (broad versus narrow) had been regarded as the signposts of two major clades of sauropods, the camarasaurid-brachiosaurid lineage and the diplodocid-titanosaur lineage (Huene, 1929, 1956; Romer, 1956; Steel, 1970; Gauthier, 1986; Upchurch, 1995). The phylogenetic results presented above challenge that hypothesis, as have other recent studies (Calvo, 1994; Jacobs et al., 1993; Salgado, 1993; Salgado et al., 1997; Wilson and Sereno, 1994). The narrow-versus-broad-crown dichotomy fails to characterize monophyletic groups and represents an oversimplification of crown form. Several tooth crown shapes and feeding styles are found among sauropods. Calvo (1994) identified four crown "types" and assigned titanosaurian and diplodocoid teeth to different "types" based on differences in the form of the crown and pattern of wear facets.

The phylogenetic results presented above suggest two general conclusions regarding the evolution of tooth crown form among sauropods. First, crown breadth relative to crown height in most sauropods is not distinct from that of prosauropods. Moderately broad crown proportions (basal-apical crown length relative to maximum anteroposterior crown width) appear to be primitive for sauropodomorphs and have become particularly broad as a specialization in some sauropods such as *Camarasaurus*.

Second, the narrow, subcylindrical crowns that characterize diplodocoids and some titanosaurs clearly arose independently, because basal titanosaurs have spatulate crowns. The basal titanosaurs *Malawisaurus* and *Ampelosaurus*, for example, have tongue-shaped, spatulate crowns that are D-shaped in cross-section at mid-crown level. In this regard, they resemble the crowns of *Omeisaurus*, *Camarasaurus*, and *Brachiosaurus* (character 32:1). Teeth with cylindrical cross-sections at mid-crown level (character 32:2) are restricted to most diplodocoids and a subgroup of titanosaurs. Narrow, subcylindrical crowns arose independently within these two groups (see above). Because titanosaurs were the dominant sauropod subgroup during the Late Cretaceous, nearly all teeth were narrow-crowned during the final episode of sauropod evolution.

Sauropod teeth are characterized by textured tooth enamel consisting of minute ridges and grooves (character 33), and this

texture is always maintained. Eusauropods evolved a sophisticated overlapping, interlocking dentition that produced characteristic V-shaped wear facets (characters 34–36). Overlapping crowns are asymmetrical: anteriorly, a thick lingual ridge buttresses the overlapping crown, and, posteriorly, a small facet on the labial side of the crown marks the overlap of the succeeding tooth. It now appears that this widespread pattern of interlocking crowns with V-shaped wear facets was lost independently in diplodocoids and a subgroup of titanosaurs. Both subgroups evolved a derived pattern of wear, suggesting different masticatory styles (Calvo, 1994). Titanosaurs have elliptical wear facets that cut across the crown at a low angle to the tooth axis (character 35:2), whereas, in diplodocids, the wear facets are subcircular and truncate the crowns at a high angle (character 35:1; Calvo, 1994). These dental specializations all appear to have been in place before the close of the Jurassic period, long before the rise of angiosperms in the mid-Cretaceous.

Narial Retraction—The external nares are at least partially retracted from the anterior end of the snout to a position level with, or above, the dorsal margin of the orbit (character 18:1). Although at least partially retracted, the external nares in most sauropods still face laterally. The external nares of *Camarasaurus* and *Brachiosaurus* are enlarged but are no further retracted relative to the orbit than in more primitive eusauropods (character 89). Diplodocoids, in contrast, evolved fully retracted, confluent nares that open above the orbits (character 18:2). The premaxilla of the basal titanosaur *Malawisaurus* preserves a large, laterally facing external naris similar to those of *Camarasaurus* and *Brachiosaurus* (Jacobs, Winkler, Downs, and Gomani, 1993). Basal titanosaurs, therefore, clearly do not have fully retracted external nares as had often been presumed.

Two isolated sauropod skulls from the Upper Cretaceous Nemegt Formation of Mongolia, *Nemegtosaurus* and *Quaesitosaurus*, have been interpreted as diplodocoids and reconstructed with fully retracted, dorsally facing external nares (Nowinski, 1971; Kurzanov and Bannikov, 1983; McIntosh, 1990a; Yu, 1993; Upchurch, 1995). Their diplodocoid status was based on general skull shape and similarities that, on reexamination, prove to be preservational artifacts (e.g., anteriorly displaced jaw articulation; Wilson, pers. obs.). Calvo (1994) suggested that these taxa were titanosaurs, basing this conclusion on the close resemblance of tooth shape and wear in *Alamosaurus* and *Nemegtosaurus*. Some of the teeth of *Nemegtosaurus*, however, have V-shaped wear facets unlike the planar wear facets in known titanosaurs (Nowinski, 1971:pl. 13, fig. 3a).

We agree that *Nemegtosaurus* and *Quaesitosaurus* are macronarians (characters 89–91, 97) and that their affinities lie with Titanosauria on the basis of thin, sheet-like basipterygoid processes and paroccipital processes with ventrally directed distal projections (Wilson, 1997). Although they are not completely preserved, it is unlikely that either *Nemegtosaurus* or *Quaesitosaurus* had retracted external nares as in diplodocoids (see discussion in Titanosauria).

Thus, although narial retraction appeared early in sauropod evolution and is advanced further in many forms, full retraction of the external nares above the orbits appears to have occurred only once among diplodocoids.

Neck Elongation—Although it is clear that some sauropods have elongated the cervical series, neck elongation has not been examined in phylogenetic perspective in the light of a cladogram. There has also not been a serious attempt to tease apart the three means by which the cervical series could become elongated: lengthening of cervical vertebrae, duplication of cervical vertebrae, or incorporation of dorsal vertebrae in the cervical series.

In our analysis of trends in this region of the vertebral column, vertebral number or length were treated as unordered characters. Transitions from one character state to any other require only one step. Loss (or gain) of three vertebrae, for example, entails
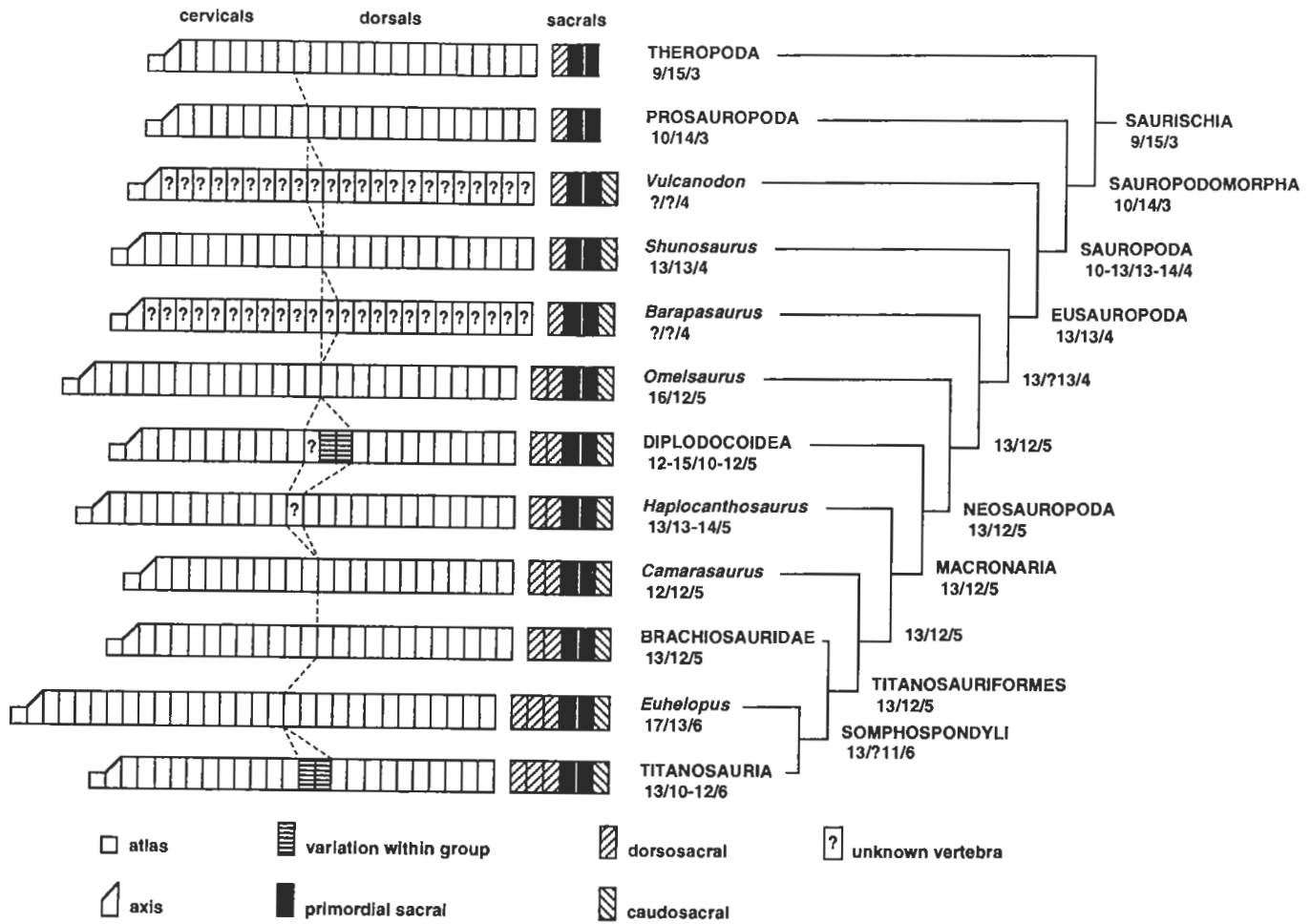
FIGURE 47. Phylogenetic diagram showing the evolution in the number of presacral and sacral vertebrae in sauropods and their immediate outgroups. Vertebral formulae (cervicals, dorsals, sacrals) are given for internal nodes and terminal taxa, based on delayed character-state optimization of characters 2, 37, and 70 and data from the literature. Diagrammatic presacral and sacral vertebrae (left) are aligned by the pair of primordial sacral vertebrae. Dashed line divides the presacral column into cervical and dorsal vertebrae.

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only a single step. Presacral counts were scored as follows. Among basal theropods, *Eoraptor* has 9 cervical and 15 dorsal vertebrae (Sereno, Martinez, and Alcober, in prep.). The cervical-dorsal region of the vertebral column is incompletely known in *Herrerasaurus,* and the number of presacral vertebrae is unknown (Sereno and Novas, 1993). *Plateosaurus* and most other prosauropods have 10 cervical and 15 dorsal vertebrae (Galton, 1990), and this is probably the primitive condition.

Presacral counts for the basal sauropods *Vulcanodon* and *Barapasaurus* are unknown. *Shunosaurus* preserves 13 cervical and 13 dorsal vertebrae (Zhang, 1988). He, Li, and Cai (1988) described *Omeisaurus* with 17 cervical and 11 dorsal vertebrae. McIntosh (1990a:330), however, suggested that the position of the cervical-dorsal transition was incorrect, and that there were actually 16 cervical and 12 dorsal vertebrae.

Among diplodocoids, the diplodocids *Diplodocus* and *Apatosaurus* are known to have 15 cervical and 10 dorsal vertebrae. The dicraeosaurid *Dicraeosaurus* was reported as having 12 cervical and 12 dorsal vertebrae (Janensch, 1929a), but the cervical-dorsal transition may have been one vertebra further anterior (McIntosh, 1990a:392). *Amargasaurus* was reported as having 13 cervical and 9 dorsal vertebrae (Salgado and Bonaparte, 1991), but the parapophysis of the ninth dorsal vertebra is still relatively low on the neural arch, suggesting that it is

not the posteriormost dorsal. Given the variation in presacral counts and the lack of articulated vertebral columns for basal forms, the ancestral diplodocoid condition is difficult to determine. The ancestral dicraeosaurid would have had 12 or 13 cervical vertebrae and 9 to 12 dorsal vertebrae. The ancestral vertebral number in diplodocoids was estimated to have been 12, 13, or 15 cervical and 10 or 12 dorsal vertebrae.

Among macronarians, *Camarasaurus* had 12 cervical and 12 dorsal vertebrae. The number of cervical vertebrae in *Haplocanthosaurus* is unknown, but it had at least 13 cervical and probably 13 dorsal vertebrae. The pectoral region of *Brachiosaurus* is incompletely known, and the counts for cervical vertebrae are uncertain (McIntosh, 1990a:381). The presacral count for *Brachiosaurus* is estimated to be 13 cervical and 11 or 12 dorsal vertebrae. Among titanosaurs, articulated presacral vertebrae are only known for *Opisthocoelicaudia,* which had 10 or 11 dorsal vertebrae (Borsuk-Bialynicka, 1977), and an unnamed titanosaur from Brazil, which had 13 cervical and 12 dorsal vertebrae (Powell, 1987). The presacral count for titanosaurs was estimated to be 13 cervical and 10 to 12 dorsal vertebrae.

Presacral counts (characters 37, 70) and a cervical length metric (108) were mapped on to the minimum-length tree to show the distribution of states, and then these characters were traced using MacClade (Maddison and Maddison, 1993) to de-
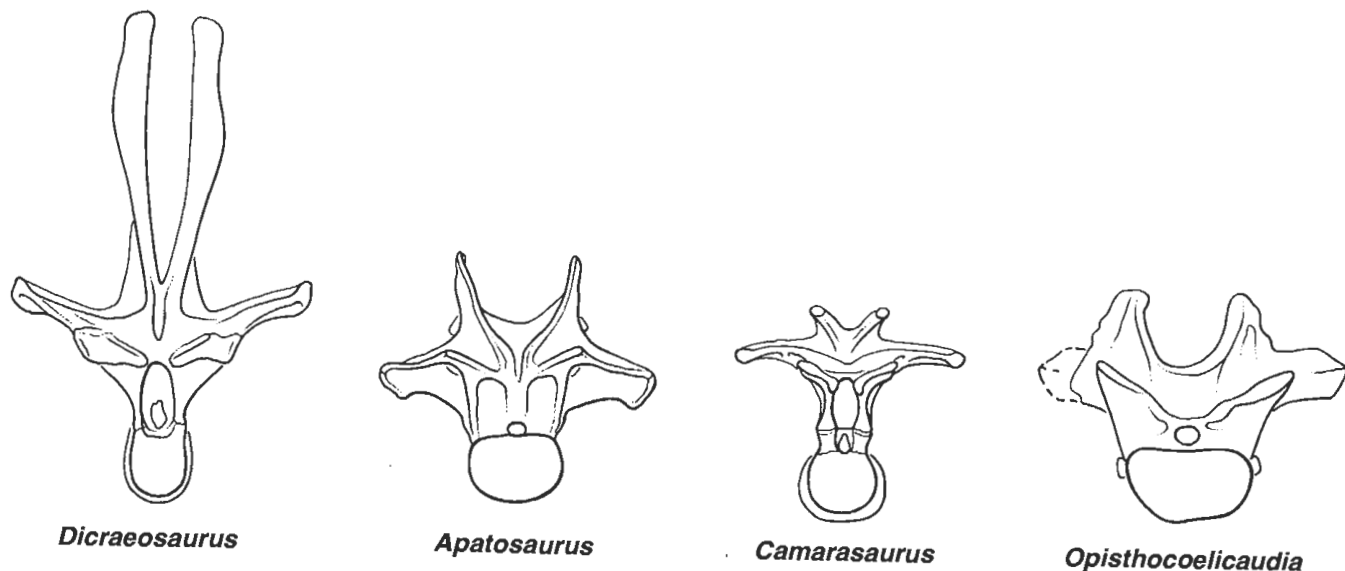
FIGURE 48. Anterior dorsal vertebrae (anterior view) showing the bifid form of the neural spines (character 106) in the diplodocoids *Dicraeosaurus hansemanni* (after Janensch, 1929b) and *Apatosaurus excelsus* (after Gilmore, 1936), *Camarasaurus supremus* (after Osborn and Mook, 1921), and the titanosaur *Opisthocoelicaudia skarzynskii* (after Borsuk-Bialynicka, 1977).

termine the ancestral state at ingroup nodes (Fig. 47). Because PAUP does not accept a range of values for terminal taxa for which vertebral counts are not known with certainty, the data were either entered as "?" or scored with the most plausible state. Determination of the ancestral state at ingroup nodes was based on character tracing with MacClade.

Assuming unordered characters, the results of character tracing indicate that there was an increase in cervical number at the level of Eusauropoda (character 37:3, 13 or more cervical vertebrae), but that this result is ambiguous since the presacral count is unknown in *Vulcanodon*. A decrease in the number of dorsal vertebrae (12 or 13 dorsal vertebrae) characterizes *Omeisaurus* and neosauropods, but this feature is also equivocal because the number cervicals and dorsals is unknown in *Barapasaurus* and *Vulcanodon*.

Assuming ordered transformations, the presacral count of *Shunosaurus* becomes the ancestral count for eusauropods, and the dorsal count of *Omeisaurus* becomes the primitive count for *Omeisaurus* plus Neosauropoda. This would suggest that the ancestral presacral count for all neosauropod lineages was 13 cervical and 12 dorsal vertebrae. This tentative result suggests independent modification of presacral number in three lineages. *Camarasaurus* and *Haplocanthosaurus* are interpreted as having lost one cervical vertebra and gained one dorsal vertebra, respectively. And within Diplodocoidea, diplodocids are interpreted as having incorporated two dorsal vertebrae into the cervical column.

The addition of three cervical vertebrae at Eusauropoda and the possible loss of three dorsal vertebrae at *Omeisaurus* plus Neosauropoda may also indicate that trunk vertebrae were incorporated into the neck. Because of ambiguities at the nodes ancestral to these clades, however, the ancestral condition at the intervening nodes cannot be reconstructed. It is not known at what hierarchical level(s) these changes took place.

The number of sacral vertebrae (character 2), however, may add some information that could constrain the ancestral vertebral number at intervening nodes. As noted earlier (see *Omeisaurus* + Neosauropoda), morphological evidence suggests that the fifth sacral vertebra was probably incorporated from the dorsal column (Hatcher, 1903). If this is correct, the ancestral dorsal count for the clade including *Barapasaurus* and all more

derived sauropods can be tentatively placed at 13. As *Barapasaurus* is known to have 4 sacral vertebrae and its phylogenetic position suggests it had 13 cervicals, for the loss of one dorsal vertebrae (i.e., becoming incorporated into the sacrum) to result in 12 dorsals in the clade *Omeisaurus* plus Neosauropoda, the number of dorsal vertebrae in *Barapasaurus* should be 13. Similarly, the ancestral eusauropod would have had 13 cervical and 13 dorsal vertebrae, which agrees with the known vertebral count for *Shunosaurus*. At one or both of the intervening branches between Sauropodomorpha and Eusauropoda, three cervical vertebrae were then added and two dorsal vertebrae were lost. The most parsimonious explanation of this pattern involves two events, namely (1) the incorporation of two trunk vertebrae into the neck and (2) the duplication of one cervical vertebra. These two events may have occurred simultaneously at either the level of Sauropoda or Eusauropoda, or they may have occurred independently at each of the nodes.

Increase in cervical length (character 108) also constitutes a repeated trend within sauropods, occurring at least three times (*Omeisaurus*, *Brachiosaurus*, and a subgroup of diplodocoids).

At least 7 neck-lengthening events occurred in sauropod evolution. All three mechanisms appear to have been involved: 3 vertebral lengthenings, 2 incorporations, and 2 duplications.

Neural Spine Form—Our analysis supports the independent derivation of bifid neural spines in the posterior cervical and anterior dorsal vertebrae (character 107) at least three times in sauropod evolution. Forked neural spines are present in *Camarasaurus*, *Euhelopus*, diplodocoids, and at least one titanosaur (*Opisthocoelicaudia*) (Fig. 48). Janensch (1929b) and later Alexander (1985) suggested that a large median nuchal ligament occupied the space between bifid neural spines, between and anterior dorsal vertebrae and the occiput. This structure would support the skull and neck, as it does in several extant ungulates. Dimery, Alexander, and Deyst (1985) examined the role of nuchal ligaments in supporting the head of sheep, deer, and camels. They found that attachment of the nuchal ligaments to the cervical vertebrae differs in these animals. Anchored at the base of the neck, nuchal ligaments of deer and sheep attach distally at one point on the anterior cervicals and terminate on the occiput, whereas those of camels have branches attaching
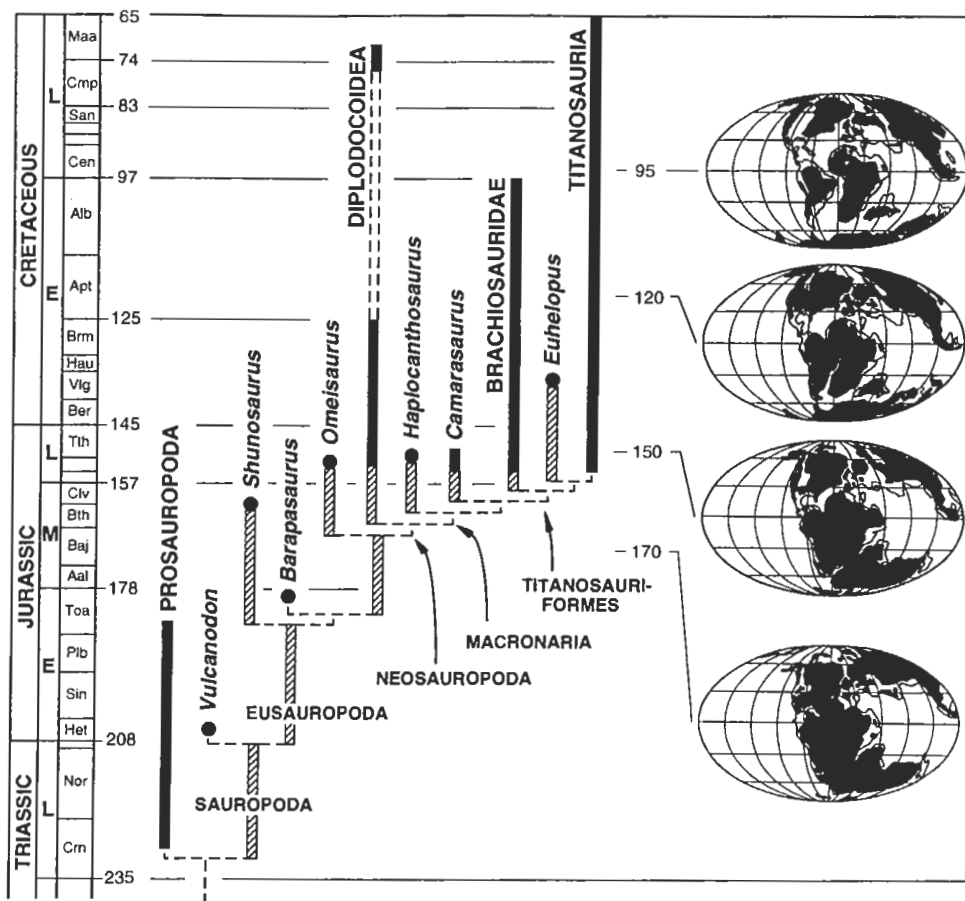
FIGURE 49. A calibrated phylogeny of sauropodomorphs compared with the geographic distribution of land areas during the Jurassic and Cretaceous. The calibrated phylogeny is based on their cladistic relationships, as established in this study, and their recorded temporal ranges (black). Cross-hatched bars represent missing ranges and missing ancestral lineages; dashed bars indicate uncertainty in the identification of specimens of young age. The time-scale is based on Harland et al. (1990) and the paleogeographic reconstructions are based on Smith et al. (1994), with land areas shown as black and epeiric seas shown as white areas inside the continental margins.

to each cervical vertebrae. The camel-type nuchal ligament resists the downward buckling of intervertebral joints because each is supported by a branch of the nuchal ligament (Dimery et al., 1985). More importantly, these nuchal attachments to the cervical vertebrae allow tensile forces in the ligament to decrease from thorax to occiput. In this manner, a long neck is feasible without excessively long neural spines (Dimery et al., 1985), and perhaps this was also the case in sauropods (as has been reconstructed by Janensch [1929b:pl. 4] for *Dicraeosaurus*). In any case, the repeated occurrence of split neural spines among sauropods indicates that a strong nuchal ligament was present.

Biogeography

A central question in historical biogeography is the influence of continental fragmentation on the evolution of terrestrial vertebrate faunas (Duellman, 1990; Buffetaut and Rage, 1993). Sauropod dinosaurs are a useful model because they achieved a nearly Pangaean distribution by the Middle Jurassic and persisted until the peak of continental isolation at the end of the Cretaceous (McIntosh, 1990a; Smith et al., 1994).

Although sauropods are first recorded from the Early Jurassic, their sister-taxon, Prosauropoda, is already present in the Late Triassic (late Carnian; Fig. 49). This places a "minimum origin" for Sauropoda in the Late Triassic. The 15–20 million year gap between the first prosauropod and first sauropod represents the time period during which the diagnostic features of sauropods arose.

Upchurch (1995) argued for a geographically isolated East Asian "euhelopodid" fauna (including *Shunosaurus, Omeisaurus,* and other Chinese sauropods) from the Middle Jurassic to the Early Cretaceous. Although geological evidence for possible geographic isolating mechanisms is presented, support for the evolutionary isolation (i.e., monophyly) of "Euhelopodidae" is weak. Of the five characters diagnosing Euhelopodidae, three have a more general distribution, characterizing eusauropods (loss of squamosal-quadratojugal contact [Upchurch's character 22], forked caudal chevrons [31], increase from 12 to 13 cervical vertebrae [28]), one occurs in other sauropods (fan-shaped first caudal rib), and the fifth has only been reliably reported in one of the four taxa (bony tail club). The present analysis presents strong evidence in favor of a paraphyletic Euhelopodidae, with 17 characters uniting *Omeisaurus* more closely with Neosauropoda than *Shunosaurus,* and 34 characters supporting a closer relationship between *Euhelopus* and Titanosauria than to *Omeisaurus.* The phylogenetic affinities of several other Chinese forms (e.g., *Bellusaurus, Datousaurus, Mamenchisaurus*) are unresolved at present.

Because the oldest known neosauropod material dates from the Late Jurassic, it is clear that the neosauropod radiation took place prior to this time. The apparent restricted distribution of

certain neosauropod lineages on southern continents has been interpreted as a Gondwanan signal in sauropod evolution (Bonaparte and Kielan-Jaworowska, 1987). Upchurch (1995) also suggested that, during the Late Jurassic, camarasaurids and diplodocids were restricted to Laurasia, while dicraeosaurids and titanosaurids were restricted to Gondwana. Occurrences of these sauropod taxa outside their presumed area of endemism (e.g., *Brachiosaurus* and *Barosaurus* in Africa and titanosaurs in Europe) were interpreted as the result of dispersal events. Because neosauropod origins predate the breakup of Pangaea, it seems more likely that these "aberrant" taxa are relics of a primitive, widespread neosauropod fauna that survived differentially on isolated continental landmasses.

Titanosaurs were the dominant large herbivores in South America throughout the Cretaceous, and are represented in fewer numbers in North America, Europe, Asia, and Africa. Titanosaur-like sauropods were present in the Early Cretaceous of North America (Ostrom, 1970; Langston, 1974), and are represented in the Late Cretaceous of New Mexico and Utah by *Alamosaurus* (Gilmore, 1922, 1946). The implied mid-Cretaceous (Cenomanian-Campanian) sauropod hiatus in North America has been regarded as an extinction event attributed to various factors, including falling sea levels (Kues et al., 1980; Lucas and Hunt, 1989) and replacement by ornithischian dinosaurs (Buffetaut, 1989). The occurrence of *Alamosaurus* in the Maastrichtian of North America has been explained as the result of an austral immigration (Sloan, 1970; Bonaparte, 1984; Lucas and Hunt, 1989).

Is the mid-Cretaceous sauropod hiatus in North America related to an extinction event followed by an austral immigration, or had titanosaurs a more global distribution during the Cretaceous, and is the gap in the sauropod record the result of poor sampling? Evaluation of the austral immigrant hypothesis depends on the lower-level relationships of *Alamosaurus,* the geographic distribution of closely related genera, and the divergence time of these taxa relative to the loss of connections between North America and other continental landmasses. If *Alamosaurus* is an austral immigrant, one would minimally expect its first two sister-taxa to (1) be from a southern continent and (2) have their first occurrence in the fossil record postdating the loss of connections between the southern continents and North America. No synapomorphies, however, have been mentioned to link *Alamosaurus* to specific Late Cretaceous titanosaurs from a southern continent. Shared derived characters in the pectoral girdle, forelimb, and pelvic girdle indicate that *Alamosaurus* may belong to a clade of Late Cretaceous titanosaurs including *Opisthocoelicaudia* (Asia) and *Saltasaurus* (South America) (Wilson, unpubl. data). If true, a northern dispersal event from Asia is an equally plausible scenario. A third possibility is that this titanosaur lineage had a deeper history than indicated by the current fossil record, originating before continental connections were severed and attaining a wide geographic distribution.

In his review of the European titanosaurian record, Le Loeuff (1993:112) proposed a sauropod extinction event coeval with the sauropod hiatus in North America. Furthermore, Le Loeuff suggested that the occurrence of titanosaurs in the late Campanian of Europe was the result of immigration from Africa. The lack of titanosaurs during this period, however, may be due to the generally poor vertebrate record in Europe during the 10-million-year gap between the late Cenomanian and late Campanian. Claims of extinction or dispersal are impossible to evaluate in the absence of strong evidence for a genuine hiatus in the sauropod record and a cladogram for the taxa that inhabit the areas of interest. As for the South American immigrant hypothesis, the appearance of titanosaurs in the late Campanian of Europe as an immigration event from Africa has not yet been supported by phylogenetic data. The European forms should

have African sister-taxa with origins postdating the appearance of boundaries separating Africa and Europe.

CONCLUSIONS

Phylogenetic results from a numerical cladistic analysis of 109 characters in 10 ingroup taxa support a monophyletic Sauropoda consisting of several basal lineages which diverged early (Early–Middle Jurassic) from an advanced neosauropod group. Within Neosauropoda, Macronaria and Diplodocoidea are sister-taxa, the latter consisting of *Haplocanthosaurus, Camarasaurus,* and Titanosauriformes. The phylogenetic positions of the poorly known genera *Barapasaurus* and *Haplocanthosaurus* within basal eusauropods and macronarians, respectively, remains uncertain.

The topology was shown to be robust to the addition of extra evolutionary steps, and the minimum-length tree is substantially shorter than that suggested by the traditional dichotomy between the brachiosaur-camarasaur and diplodocid-titanosaur lineages. Traditional characters supporting a diplodocoid-titanosaur sister-group relationship are shown to be homoplastic with respect to a broad survey of sauropod morphology. Shared similarities between these two taxa, including cylindrical tooth crowns, procoelous anterior caudal centra, and unossified calcanea were shown to appear independently within both diplodocoids and titanosaurs, as well as in other sauropod lineages.

The early evolution of sauropod dinosaurs was characterized by appendicular adaptations facilitating columnar support of body weight. Specialized dentitions—interlocking and overlapping tooth crowns, V-shaped wear facets—are present in basal sauropods and further modified within some subgroups. These modifications, which include loss of overlapping tooth crowns, narrow crown proportions, and decreases in the number of teeth, occurred before the Late Jurassic and well before the diversification of angiosperms in the Cretaceous. Early in their evolution, sauropods increased the number of cervicals by three by incorporating two trunk vertebrae into the neck (effectively moving the shoulder girdle posteriorly), and adding one cervical vertebra. Several subsequent events of neck lengthening characterize specific sauropod subgroups.

The distribution of several classic sauropod features was shown to be homoplastic. Narrow crown proportions, bifid neural spines, elongate cervical centra, and increased length and numbers of cervical vertebrae appear independently in many sauropod subgroups.

Biochronological data indicate that neosauropods originated in the Middle Jurassic and diversified by the Late Jurassic. There is no evidence of a tectonic signal in higher-level sauropod phylogeny. Instead, it seems that an initially global distribution of neosauropods in the Late Jurassic persisted into the Cretaceous, with neosauropod lineages flourishing and diversifying in some areas and decreasing in diversity or becoming extinct in others.

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APPENDIX

The distribution and coding of 109 characters is shown below for the two outgroups (Theropoda, Prosauropoda) and 10 sauropod taxa considered in the analysis. Synapomorphies are listed for each ingroup as optimized under delayed character-state transformation (see Table 2 for optimization ambiguity). For multi-state characters (2, 18, 32, 36, 37, 70), character-states are listed parenthetically after the character number. Homoplastic characters with complex distributions (105–109) are listed with other characters.

SYNAPOMORPHIES

Sauropoda

1. Obligatory quadrupedal posture with columnar limbs and short metapodials.
2(1). Sacral vertebral number four or more (one caudosacral vertebra added) (Jain, Kutty, and Roy-Chowdhury, 1975; Upchurch, 1995).
3. Humeral deltopectoral crest low.
4. Olecranon reduced or absent (Raath, 1972; McIntosh, 1990a).
5. Ulna proximal end triradiate, with deep radial fossa.
6. Radial distal condyle subrectangular with flat posterior margin for ulna.
7. Ilium with low ischial peduncle (Jain, Kutty, and Roy-Chowdhury, 1975; McIntosh, 1990a).
8. Ischial shaft equal to, or longer than, pubic shaft.
9. Ischial shaft with dorsoventrally flattened distal end.
10. Femoral shaft with elliptical cross-section, long axis of ellipse oriented mediolaterally (Raath, 1972; Gauthier, 1986; McIntosh, 1990a).
11. Femoral fourth trochanter developed as a low crest (Riggs, 1904; Raath, 1972; Gauthier, 1986; McIntosh, 1990a).
12. Astragalar fossa and foramina at base of ascending process absent.
13. Distal tarsals 3 and 4 absent or unossified (Raath, 1972; Gauthier, 1986).
14. Metatarsals I and V with proximal end subequal in area to that of metatarsals II and IV.
15. Metatarsal V length at least 70 percent that of metatarsal IV (Cruickshank, 1975; Van Heerden, 1978; Gauthier, 1986).
16. Pedal digit I ungual enlarged.
17. Pedal digit I ungual deep and narrow (sickle-shaped).

Eusauropoda

18(1). External nares retracted posterodorsally (Steel, 1970; Gauthier, 1986; McIntosh, 1990a; Upchurch, 1995).
19. Snout with stepped anterior margin.
20. Antorbital fossa absent.
21. Maxillary border of external naris long.

22. Anterior process of prefrontal absent.
23. Squamosal-quadratojugal contact absent (Gauthier, 1986).
24. Anterior ramus of quadratojugal elongate, distally expanded.
25. Infraorbital region of skull shortened anteroposteriorly (Gauthier, 1986; McIntosh, 1990a; Upchurch, 1995).
26. Supratemporal region of cranium shortened anteroposteriorly.
27. Supratemporal fossa broadly exposed laterally.
28. Quadrate shaft with elongate posterior fossa.
29. Palatine lateral ramus narrow.
30. Dentary ramus, maximum depth of anterior end approximately 150 percent minimum depth of ramus.
31. Tooth rows broadly arched anteriorly (U-shaped).
32(1). Spatulate crowns.
33. Tooth enamel with wrinkled texture.
34. Tooth crown overlap.
35. Precise crown-to-crown occlusion.
36(1). V-shaped wear facets (interdigitating occlusion).
37(3). Cervical vertebrae 13 or more in number (Upchurch, 1995).
38. Cervical centra opisthocoelous.
39. Mid-cervical neural arches deep, greater than centrum diameter (Bonaparte, 1986a).
40. Dorsal neural spines broader transversely than anteroposteriorly (Bonaparte, 1986a).
41. Distal chevrons with anterior and posterior projections.
42. Block-shaped carpals.
43. Manual phalanges on digits II and III reduced (II-ungual, III-3 and ungual absent; digital formula 2-2-2-2-2 or lower).
44. Manual phalanges (other than unguals) broader than long.
45. Iliac blade with semicircular dorsal margin and expanded preacetabular process (McIntosh, 1990a).
46. Pubic apron canted posteromedially.
47. Tibial cnemial crest projecting laterally.
48. Tibial posteroventral process reduced.
49. Fibular lateral trochanter.
50. Metatarsal III length 25 percent or less that of tibia.
51. Metatarsal I minimum shaft width greater than that of metatarsals II–IV.
52. Metatarsals with spreading configuration (Janensch, 1922; Lapparent and Lavocat, 1955; Cooper, 1984; McIntosh, 1990a).
53. Pedal phalanges (other than unguals) short.
54. Pedal digit I ungual equal to or longer than metatarsal I.
55. Pedal digits II–IV, penultimate phalanges rudimentary or absent.
56. Pedal digits II–III with sickle-shaped unguals.
57. Pedal digit IV ungual rudimentary or absent.

Barapasaurus + Omeisaurus + Neosauropoda

58. Posterior cervical and anterior dorsal neural arches with interprezygapophyseal lamina.
59. Anterior dorsal centra opisthocoelous.
60. Middle and posterior dorsal neural arches with composite lateral lamina (spinodiapophyseal plus supraprezygapophyseal).
61. Sacricostal yoke.
62. Fibula with broad triangular articular scar for tibia.
63. Astragalar posterior fossa divided by crest.
64. Pedal unguals asymmetrical (canted ventrolaterally in articulation).

Omeisaurus + Neosauropoda

65. Frontal excluded from supratemporal fossa.
66. Supratemporal fenestra, long axis oriented transversely.
67. Dentary tooth count 17 or fewer, teeth restricted anterior of the antorbital fenestra.
68. Presacral pleurocoels deep, invaginated (Calvo and Salgado, 1995).
69. Cervical pleurocoels divided.
70(3). Dorsal vertebral number 12 or fewer.
2(2). Sacral vertebral number five or greater (at least one dorsosacral added) (McIntosh, 1990a; Upchurch, 1995).

71. Cervical rib shafts positioned below centra.
72. Acromion more than 150 percent of the minimum width of scapular blade.
73. Metatarsals III and IV with minimum transverse shaft diameters 65 percent or less than that of metatarsals I or II.

Neosauropoda

74. Preantorbital fenestra.
75. Ventral process of postorbital broader transversely than anteroposteriorly.
76. Jugal-ectopterygoid contact absent.
77. External mandibular fenestra closed (McIntosh, 1990a; Upchurch, 1995).
78. Crown denticles absent (McIntosh, 1990a; Calvo and Salgado, 1995).
79. Carpal number two or fewer.
80. Metacarpals bound (long intermetacarpal articular surfaces).
81. Metacarpals, proximal end subtriangular, composite proximal articular surface U-shaped (McIntosh, 1990a; Upchurch, 1995).
82. Iliac preacetabular blade laterally divergent (width across ilia greater than iliac length).
83. Tibia with subcircular proximal end.
84. Astragalar ascending process extends to posterior margin of the astragalus.
85. Astragalus wedge-shaped in anterior view.

Macronaria

86. Middle and posterior dorsal neural spines with transversely flared distal ends (Upchurch, 1995).
87. Anterior caudal chevrons with open proximal articulation (Upchurch, 1995).
88. Ischial distal shafts platelike and nearly coplanar.

Camarasaurus + Titanosauriformes

89. External naris, maximum diameter greater than orbital maximum diameter (McIntosh, 1990a; Upchurch, 1995).
90. Quadrate fossa deep.
91. Surangular depth more than twice depth of the angular.
92. Posterior dorsal centra opisthocoelous, convexity present on anterior face of centrum (Salgado, Coria, and Calvo, 1997).
93. Length of longest metacarpal 45 percent or more that of the radius (Salgado, Coria, and Calvo, 1997).
94. Metacarpal I subequal in length to metacarpal IV.
95. Puboischial contact deep dorsoventrally (Salgado, Coria, and Calvo, 1997).

Titanosauriformes

96. Pterygoid lacking dorsomedially oriented basipterygoid hook.
97. Dorsal ribs with pneumatic cavities.
98. Metacarpal I distal condyle undivided, phalangeal articular surface reduced.
99. Iliac preacetabular process semicircular, with posteroventral excursion of its cartilage cap (Salgado, Coria, and Calvo, 1997).
100. Femur with proximal one-third of shaft deflected medially (McIntosh, 1990a; Salgado, 1993; Calvo and Salgado, 1995; Salgado, Coria, and Calvo, 1997).

Somphospondyli

101. Cervical laminae rudimentary.
102. Presacral vertebrae composed of spongy bone.
103. Anterior to mid-dorsal neural spines posterodorsally inclined.
2(3). Sacral vertebral number six (one dorsosacral added).
104. Scapular glenoid deflected medially.

CHARACTER–TAXON MATRIX

Taxon	10	20	30	40	50	60	70	80	90	100	109
Theropoda	00000 00000	00000 00000	00000 00000	00000 50000	00000 00000	00000 00000	00000 00050	05000 00500	00000 00005	00010 00000	10000 0000
Prosauropoda	00000 00000	00000 00000	00000 00000	00000 51000	00000 00000	00000 00000	00000 00051	00000 00000	00000 00005	00000 00000	10000 0000
Vulcanodon	11111 11111	11111 11???	????? ?????	????? ?????	????? 00?00	00000 00???	0000? ?????	??0?? ?????	??000 ?00??	??0?0 ????0	????? ???0
Shunosaurus	11111 111?1	11111 11111	11111 11111	11111 13111	11111 11111	11111 11000	0??00 00052	000?0 00100	00?00 01000	00000 00000	10000 0000
Barapasaurus	11111 11111	111?? ?1???	????? ?????	?1??? ??111	1???1 1111?	????? ??111	1111? ??05?	????? ??0??	?00?? 000??	?0?70 ????00	0000? 0000
Omeisaurus	12111 111?1	11111 11111	11111 111?1	11111 14101	11111 111?1	11111 11111	11111 11113	111?? ?0000	00000 00000	00000 ?0000	00000 0100
Diplodocoidea	12111 11111	11111 11201	11111 11111	12101 22111	11111 11111	11111 11111	11111 11113	11111 11111	11111 00000	00000 ?0000	00000 1010
Haplocanthosaurus	12??? ?1111	1???? ?????	????? ?????	????? ?3111	????1 1????	????? ??111	1???? ??112	10??? ?????	?1??? 111??	?0?70 ?0?00	0000? 00?0
Camarasaurus	12111 11111	11111 11111	11011 11111	11111 12111	11111 11111	11111 11111	11111 11113	11111 11111	11111 11111	11111 00000	00001 1001
Brachiosauridae	12011 11111	11111 11111	11111 11110	11101 13111	?1111 11111	11111 11111	11113 11111	11111 11111	11111 11111	11111 11111	00001 01?1
Euhelopus	131?? ?1111	111?? 11111	1?11? ??111	11111 14111	????1 11111	1111? 1?111	???1? ?1112	11101 ?11??	?11?1 1?1?0	11??? ?1?11	11110 10?0
Titanosauria	13101 11011	11111 11111	?1111 11111	11101 33111	0?151 11111	11111 11111	11111 11113	10111 ?1111	11111 111?1	11111 11111	11110 0010

Character-state abbreviations: "0" = primitive state; "1"–"4" = derived states; "?" = missing information; "5" = not applicable; underlining indicates variation within the terminal taxon.

CHARACTERS ORDERED BY ANATOMICAL REGION

Skull

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). (105)

Premaxilla, anterior margin, shape: without step (0); with marked step, anterior portion of skull sharply demarcated (1). (19)

Maxillary border of external naris, length: short (0); long (1). (21)

Preantorbital fenestra: absent (0); present (1). (74)

Antorbital fossa: present (0); absent (1). (20)

Jugal-ectopterygoid contact: present (0); absent (1). (76)

External nares, position: terminal (0); retracted to a level with orbit (1); retracted above orbit (2). (18)

External naris, maximum diameter: shorter (0), or longer (1) than orbital maximum diameter. (89)

Orbit, ventral margin, anteroposterior width: broad, subcircular orbital margin, laterotemporal fenestra posterior to orbit (0); reduced, acute orbital margin, laterotemporal fenestra extends under orbit (1). (25)

Frontal contribution to supratemporal fossa: present (0); absent (1). (65)

Prefrontal, anterior process: present (0); absent (1). (22)

Supratemporal fenestra, long axis orientation: anteroposterior (0); transverse (1). (66)

Supratemporal region, anteroposterior width: temporal bar longer anteroposteriorly than transversely (0); temporal bar shorter anteroposteriorly than transversely (1). (26)

Supratemporal fossa, lateral exposure: not visible laterally, obscured by temporal bar (0); visible laterally, temporal bar shifted ventrally (1). (27)

Postorbital, ventral process, shape: transversely narrow (0); broader transversely than anteroposteriorly (1). (75)

Squamosal-quadratojugal contact: present (0); absent (1). (23)

Quadratojugal, anterior process, length: short, anterior process shorter than dorsal process (0); long, anterior process approximately twice as long as the dorsal process (1). (24)

Quadrate, posterior fossa: absent (0); present (1). (28)

Quadrate, posterior fossa, depth: shallow (0); deep (1). (90)

Pterygoid, dorsomedially oriented basipterygoid hook: present (0); absent (1). (96)

Palatine, lateral ramus, shape: plate-shaped (long maxillary contact) (0); rod-shaped (narrow maxillary contact) (1). (29)

Dentary, anterior end of ramus, depth: slightly less than that of dentary at midlength (0); 150 percent minimum depth (1). (30)

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). (31)

External mandibular fenestra: present (0); absent (1). (77)

Surangular, depth: less than twice (0); or more than two and one-half times (1) maximum depth of the angular. (91)

Dentary teeth, number: greater than 20 (0); 17 or fewer (1). (67)

Crown-to-crown occlusion: absent (0); present (1). (35)

Occlusal pattern: V-shaped facets (interlocking) (0); high-angled planar facets (1); low-angled planar facets (2). (36)

Tooth crowns, orientation: aligned along jaw axis, crowns do not overlap (0); aligned slightly anterolingually, tooth crowns overlapping (1). (34)

Enamel surface texture: smooth (0); wrinkled (1). (33)

Marginal tooth denticles: present (0); absent (1). (78)

Tooth crowns, cross-sectional shape at mid-crown: elliptical (0); D-shaped (1); cylindrical (2). (32)

Postcranial Axial Skeleton

Presacral vertebrae, bone texture: solid (0); spongy, with internal cells (1). (102)

Presacral pleurocoels, shape: shallow lateral depressions (0); deep lateral excavations bordered by a sharp lip (1). (68)

Cervical vertebrae, number: 9 or fewer (0); 10 (1); 12 (2); 13 (3); 15 or greater (4). (37)

Cervical vertebrae, neural arch lamination: well-developed, with well-defined laminae and coels (0); rudimentary; diapophyseal laminae only feebly developed if present (1). (101)

Cervical centra, articular face shape: amphicoelous (0); opisthocoelous (1). (38)

Cervical centra, anteroposterior length/height of posterior face: 2.5–3.0 (0); >4 (1). (107)

Cervical pleurocoels, shape: simple, undivided (0); complex, divided by bony septa (1). (69)

Cervical rib, tuberculum-capitulum angle: greater than 90° (0); less than 90°, rib ventrolateral to centrum (1). (71)

Anterior and mid-cervical neural spines, orientation: nearly vertical with respect to the vertebral axis (0); posterodorsally inclined, approximately 45° from vertical in lateral view (1). (103)

Mid-cervical neural spines, height: less than that of posterior centrum face (0); greater than height of posterior centrum face (1). (39)

Posterior cervical and anterior dorsal neural arches, intraprezygapophyseal lamina: absent (0), present (1). (58)

Posterior cervical and anterior dorsal neural spines, shape: single (0); bifid (1). (106)

Dorsal vertebrae, number: 15 (0); 14 (1); 13 (2); 12 or fewer (3). (70)

Dorsal neural spines, breadth: narrower transversely than anteroposteriorly (0); much broader transversely than anteroposteriorly (1). (40)

Anterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1). (59)

Middle and posterior dorsal neural spines, shape: tapering or not flaring distally (0); flared distally, with triangular lateral processes (1). (86)

Middle and posterior dorsal neural spines, spinodiapophyseal and suprapostzygapophyseal laminae: separate (0); joined in composite lateral lamina (1). (60)

Posterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1). (92)

Sacral vertebrae, number: 3 or fewer (0); 4 (1); 5 (2); 6 (3). (2)

Sacrum, sacricostal yoke: absent (0); present (1). (61)

Distalmost caudal centra, articular face shape: platycoelous (0); biconvex (1). (108)

Dorsal ribs, proximal pneumatocoels: absent (0); present (1). (97)

Chevrons, shape: Y-shaped (0); "forked" with anterior and posterior projections (1). (41)

Chevrons, proximal "crus" bridging superior margin of haemal canal: present (0); absent (1). (87)

Appendicular Skeleton

Posture: bipedal (0); columnar, obligately quadrupedal posture (1). (1)

Scapula, acromion process, size: narrow (0); width more than 150 percent minimum width of blade. (72)

Scapula, distal blade, shape: acromial edge not expanded (0); with rounded expansion on acromial side (1). (109)

Scapular glenoid, orientation: relatively flat (0); strongly beveled medially (1). (104)

Humerus, deltopectoral attachment, development: prominent (0); reduced to a low crest or ridge (1). (3)

Ulna, proximal condyle, shape: subtriangular (0); triradiate, with deep radial fossa (1). (5)

Ulna, olecranon process: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1). (4)

Radius, distal condyle, shape: round (0); subrectangular, flattened posteriorly and articulating in front of ulna (1). (6)

Carpal bones, shape: round (0); block-shaped, with flattened proximal and distal surfaces (1). (42)

Carpal bones, number: 3 or more (0); 2 or fewer (1). (79)

Metacarpus, shape: spreading (0); bound, with subparallel shafts, and articular surfaces extending half their length (1). (80)

Metacarpals, shape of proximal surface: gently curving, forming a 90° arc (0); U-shaped, subtending a 270° arc (1). (81)

Highest metacarpal-to-radius ratio: close to 0.3 (0); 0.45 or more (1). (93)

Metacarpal I, length: shorter than metacarpal IV (0); longer than metacarpal IV (1). (94)

Metacarpal I, distal condyle shape: divided and asymmetrical (0); undivided and flat with respect to axis of shaft (1). (98)

Manual digits II and III, phalangeal number: 2-3-4-3-2 or more (0); reduced, 2-2-2-2-2 or fewer (1). (43)

Manual phalanges (other than unguals), shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1). (44)

Pelvis, anterior width: narrow, ilia longer anteroposteriorly than distance between preacetabular processes (0); broad, distance between preacetabular processes exceeds anteroposterior length of ilia (1). (82)

Ilium, ischial peduncle, size: large, prominent (0); low, rounded (1). (7)

Iliac blade, dorsal margin, shape: flat (0); semicircular (1). (45)

Ilium, preacetabular process, shape: pointed, arching ventrally; semicircular, oriented anterodorsally (1). (99)

Pubic apron, orientation: transverse (0); canted posteromedially (1). (46)

Puboischial contact, length: approximately one-third (0) or one-half (1) total length of pubis. (95)

Ischial blade, length: much shorter than (0), or equal to or longer than pubic blade (1). (8)

Ischial distal shaft, shape: triangular, depth of ischial shaft increases medially (0); bladelike, medial and lateral depths subequal (1). (9)

Ischial distal shafts, cross-sectional shape: V-shaped, forming an angle of nearly 50° with each other (0); flat, nearly coplanar (1). (88)

Femur, cross-sectional shape: round (0); elliptical, with long axis oriented mediolaterally (1). (10)

Femur, fourth trochanter, development: prominent (0); reduced to crest or ridge (1). (11)

Femoral shaft, lateral margin: straight (0); proximal one-third deflected medially (1). (100)

Tibia, proximal condyle, shape: narrow, long axis anteroposterior (0); expanded transversely, condyle subcircular (1). (83)

Tibia, cnemial crest, orientation: projecting anteriorly (0); laterally (1). (47)

Tibia, distal posteroventral process, size: broad transversely, covering posterior fossa of astragalus (0); reduced, posterior fossa of astragalus visible posteriorly (1). (48)

Fibula, proximal tibial scar, shape: not well-marked (0); well-marked and deepening anteriorly (1). (62)

Fibula, lateral trochanter: absent (0); present (1). (49)

Astragalus, shape: rectangular (0); anteromedial corner truncated (1). (85)

Astragalus, foramina at base of ascending process: present (0); absent (1). (12)

Astragalus, ascending process, length: limited to anterior two-thirds of astragalus (0); extending to posterior margin of astragalus (1). (84)

Astragalus, posterior fossa, shape: undivided (0); divided by vertical crest (1). (63)

Distal tarsals 3 and 4: present (0); absent (1). (13)

Metatarsus, configuration: bound (0); spreading (1). (52)

Metatarsal I, minimum shaft width: less than (0) or greater than (1) that of metatarsals II–IV. (51)

Metatarsal I and V proximal condyle, size: smaller than (0), or subequal to metatarsal II and IV (1). (14)

Metatarsal III length: 30 percent or more (0), or 25 percent or less (1), that of tibia. (50)

Metatarsals III and IV, minimum transverse shaft diameters: subequal to (0) or less than 65 percent (1) that of metatarsals I or II. (73)

Metatarsal V, length: shorter than (0), or at least 70 percent length of metatarsal IV (1). (15)

Pedal phalanges (other than unguals), shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1). (53)

Pedal digits II–IV, penultimate phalanges, development: subequal in size to more proximal phalanges (0); rudimentary or absent (1). (55)

Pedal unguals, orientation: aligned with (0), or deflected lateral to (1), digit axis. (64)

Pedal digit I ungual, length: subequal to (0), or 25 percent larger than ungual of digit II (1). (16)

Pedal digit I ungual, length: shorter than metatarsal I (0); longer than metatarsal I (1). (54)

Pedal ungual I, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1). (17)

Pedal unguals II–III, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1). (56)

Pedal digit IV ungual, size: subequal in size to unguals of pedal digits II and III (0); rudimentary or absent (1). (57)

→

FOLDOUT 1.   Skeletal silhouettes of *Shunosaurus, Apatosaurus, Camarasaurus, Brachiosaurus,* and *Opisthocoelicaudia.* Silhouettes are drawn to scale.
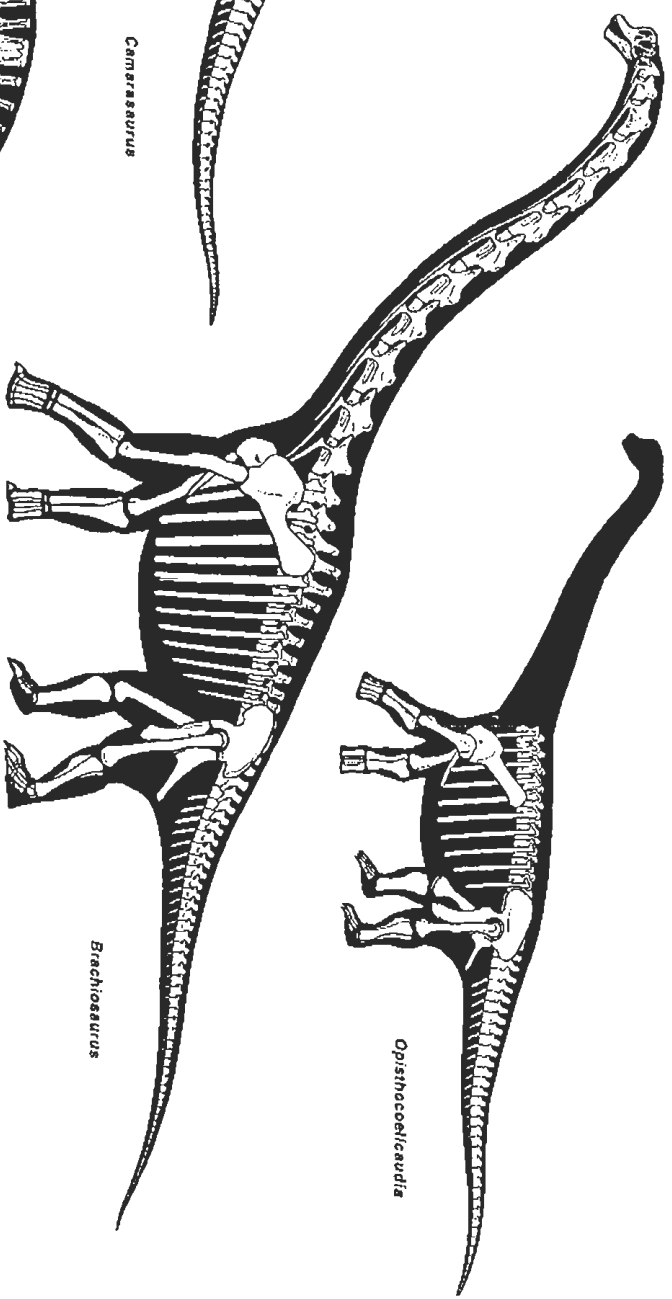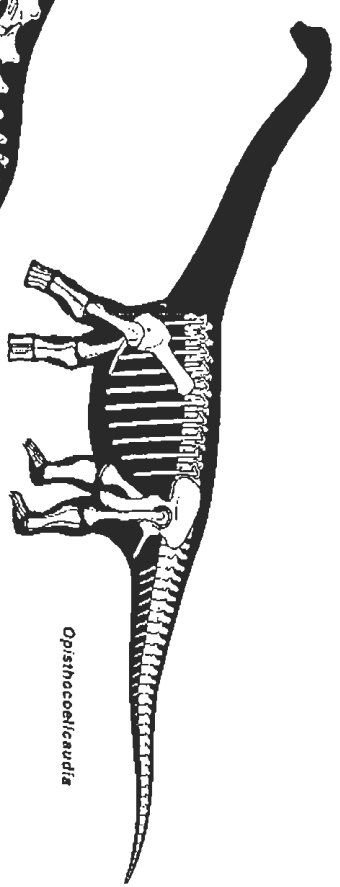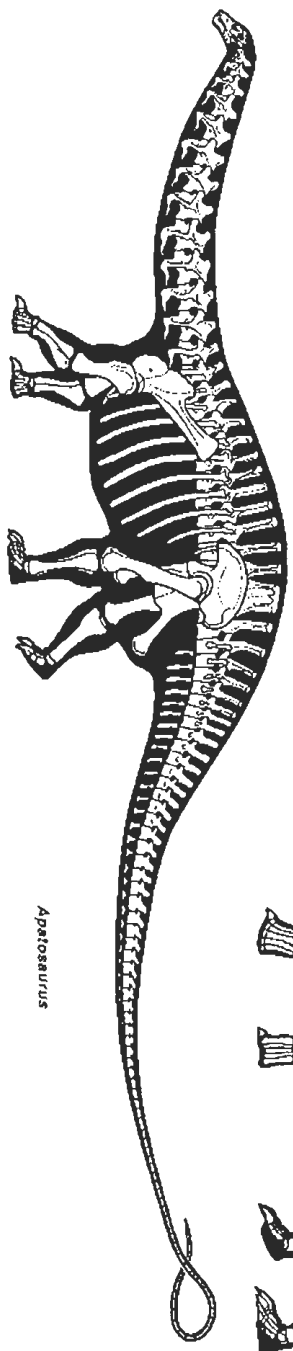
FOLDOUT 2.   Abbreviations used in text.
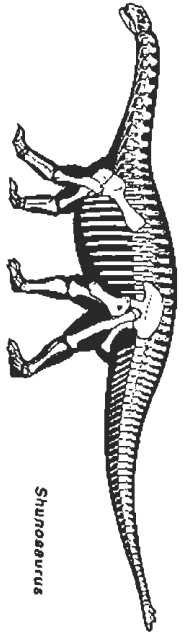
Shunosaurus
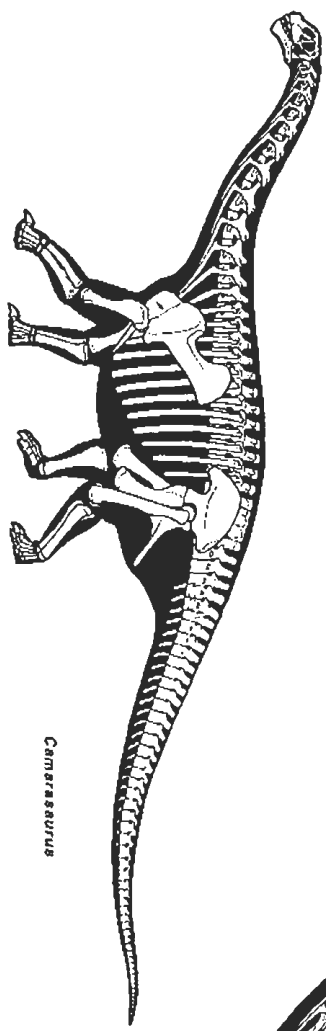
Camarasaurus

Apatosaurus

Brachiosaurus

Opisthocoelicaudia

Institutional Abbreviations

AMNH	American Museum of Natural History, New York
BM	Natural History Museum (formerly British Museum [Natural History]), London
BYUVP	Brigham Young University, Provo
CM	Carnegie Museum of Natural History, Pittsburgh
HMN	Museum für Naturkunde der Humboldt-Universität, Berlin
ISI	Indian Statistical Institute, Calcutta
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires
MDE	Musée des Dinosaures, Espéraza
MPCA	Museo Provincial "Carlos Ameghino," Plaza Huincul
MUCP	Museo de la Universidad Nacional del Comahue, Neuquén
NMZ	National Museum of Zimbabwe, Bulawayo
PMU	Palaeontological Museum, Uppsala
PVL	Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán
SMU	Southern Methodist University, Shuler Museum, Dallas
ULR	Universidad de La Rioja, La Rioja
USNM	National Museum of Natural History (formerly United States National Museum), Washington, DC
UUVP	University of Utah, Salt Lake City
ZDM	Zigong Dinosaur Museum, Zigong

Anatomical Abbreviations

a	angular
ab	attachment surface for horny bill
ac	acromion
acet	acetabulum
acdl	anterior centrodiapophyseal lamina
adf	anterior dentary foramen
af	adductor fossa
amf	anterior maxillary foramen
aofe	antorbital fenestra
aofo	antorbital fossa
apmf	anterior premaxillary foramen
ar	articular
as	astragalus
asa	astragalar articular surface
asf	anterior surangular foramen
asp	ascending process
aspa	articular surface for the ascending process
at	anterior trochanter
bo	basioccipital
bpt	basipterygoid process
bs	basisphenoid
caa	calcaneal articular surface
cap	capitulum
cc	cnemial crest
cof	coracoid foramen
d	dentary
das	distal articular surface
di	diapophysis
dip	dorsal intercondylar process
dpc	deltopectoral crest
ec	ectopterygoid
emf	external mandibular fenestra

en	external naris
eo	exoccipital
epi	epipophysis
ept	epipterygoid
f	frontal
fi	fibula
fia	fibular articular surface
fic	fibular condyle
ft	fourth trochanter
gl	glenoid
hd	head
hpa	hypantrum
hpo	hyposphene
ilped	iliac peduncle
imf	internal mandibular foramen
in	internal nares
ipol	infrapostzygapophyseal lamina
iprl	infraprezygapophyseal lamina
isped	ischial peduncle
j	jugal
l	lacrimal
ldc	lateral distal condyle
lf	lacrimal foramen
lhv	foramen for the lateral head vein
ls	laterosphenoid
lt	lateral trochanter
m	maxilla
mdc	medial distal condyle
n	nasal
nc	neural canal
nf	narial fossa
ng	nail groove
ns	neural spine
o	overlap facet
oc	occipital condyle
of	obturator foramen
ol	olecranon
op	opisthotic
p	parietal
pa	parapophysis
paf	posterior astragalar fossa
pafc	crest in posterior astragalar fossa
paofe	preantorbital fenestra
pas	proximal articular surface
pc	pleurocoel
pcdl	posterior centrodiapophyseal lamina
pf	parietal foramen
pl	palatine
pm	premaxilla
pmf	posterior maxillary foramen
po	postorbital
poap	postacetabular process
podl	postzygapophyseal-diapophyseal lamina
popr	paroccipital process
poz	postzygapophysis
pped	pubic peduncle
ppf	postpalatine fenestra
pr	prootic
pra	prearticular
prap	preacetabular process
prdl	prezygapophyseal-diapophyseal lamina
prf	prefrontal
prz	prezygapophysis
ps	parasphenoid
psf	posterior surangular foramen

pt	pterygoid	sq	squamosal
ptf	posttemporal foramen	st	stapes
pvp	posteroventral process	stf	supratemporal fossa
q	quadrate	sym	symphysial surface
qf	quadrate fossa	ti	tibia
qj	quadratojugal	tia	tibial articular surface
r	rib	tic	tibial condyle
raa	radial articular surface	tprl	interprezygapophyseal lamina
rac	radial condyle	tu	tuberculum
raf	radial fossa	ula	ulnar articular surface
sa	surangular	ulc	ulnar condyle
scb	scapular blade	v	vomer
scf	supracoracoideus fossa	wf	wear facet
scy	sacricostal yoke		
sf	subnarial foramen	I–V	metapodials or digits I–V
so	supraoccipital	IIa, IVa	metacarpal II, IV articular surface
sp	spine		
spdl	supradiapophyseal lamina	C	cervical
spol	suprapostzygapophyseal lamina	CA	caudal
sprl	supraprezygapophyseal lamina	D	dorsal
		S	sacral

MEMOIRS OF THE SOCIETY OF VERTEBRATE PALEONTOLOGY

EDITORIAL POLICY AND PROCEDURES FOR MEMOIR SERIES

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