SAUROPOD TRACKS AND TRACKMAKERS: INTEGRATING THE ICHNOLOGICAL AND SKELETAL RECORDS*

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RESUMEN

 Los primeros huesos y pistas de saurópodos o de parientes cercanos se encuentran en el principio del Jurásico. Los saurópodos fueron miembros importantes de la fauna de dinosaurios durante el Jurásico Medio y continuaron destacando en la mayor parte del mundo, durante el resto de la era mesozoica. Resulta difícil identificar los autores de las huellas saurópodas debido a que la estructura de la mano y pie de muchos de ellos es similar y también porque las trazas fósiles no suelen conservarse bien. Hay rastrilladas de saurópodos anchas y estrechas, pero no se sabe si esta diferencia del rastro es el reflejo de la diferencia en la estructura del animal. No se puede determinar si los saurópodos preferían hábitat o latitud concretos si se considera la distribución geográfica o paleoambiental de sus huellas. Si se combina el registro icnológico y el de huesos fósiles, se obtienen algunas conclusiones. Los saurópodos del Cretácico Superior (titanosáuridos) son probablemente miembros más prominentes de la fauna de dinosaurios del Hemisferio Sur que los ornitópodos, mientras que ocurre lo contrario en Asiamérica. Tanto el registro óseo como el icnológico, indican que muchas especies de saurópodos se encuentran con más facilidad en hábitats que al menos tienen una estación seca. Algunos otros, sin embargo, vivieron en regiones de clima indiscutiblemente húmedo.

 Palabras clave: Saurópodos, Titanosaurios, Cretácico Superior, Pisadas, Distribución paleogeográfica, Paleoecología.

 Skeletal remains of sauropods, as well as trackways made by sauropods or their near relatives, first occur in the Early Jurassic. By the Middle Jurassic sauropods were important members of dinosaur faunas, and they continued to be prominent in dino-

saur faunas from most of the world for the remainder of the Mesozoic Era. Identifying the makers of sauropod footprints is made difficult by the rather uniform construction of the hand and foot in most sauropods, and by the often poor preservation of sauropod trace fossils. Some sauropod trackways are wide-gauge, and others are narrower, but whether this difference in trackway pattern reflects structural differences between different sauropod trackmakers is unknown. The geographic and paleoenvironmental occurrences of sauropod tracksites are presently inadequate for determining latitudinal and habitat preferences of sauropods. Combined with the skeletal record, however, the ichnological record of sauropods does permit some conclusions. Late Cretaceous sauropods (titanosaurids) were probably more prominent members of dinosaur faunas in the Southern Hemisphere than were ornithopods, and ornithopods were more important than sauropods in Asiamerica. Both the skeletal and ichnological records suggest that many sauropod species were most common in at least seasonally dry habitats. However, some sauropods lived in regions that had fairly wet climates.

Key words: Sauropodae, Titanosauridae, Upper Cretaceous, Footprints, Paleogeographical distribution, Paleoecology.

0. INTRODUCTION

Sauropod dinosaurs were the largest land-living animals in the history of the earth. They were in addition among the most successful groups of dinosaurs, occurring from early in the Jurassic Period until the end of the Cretaceous Period, with numerous genera known from every continent except Antarctica (McIntosh, 1990a; Dodson, 1990b). Their immense size has made sauropods irresistibly intriguing subjects for speculation about the morphological, physiological, and ecological correlates of gigantism (Dodson, 1990b; Spotila, 1991; Daniels and Pratt, 1992).

Although most of our understanding of sauropod biology and evolution has come from study of the skeletal remains of these reptiles, sauropod trace fossils provide a significant, complementary source of information about the locomotion, behavior, habitats, and stratigraphic and geographic occurrences of these dinosaurs (Valenzuela et al., 1988; Lockley et al., 1989; Lockley, 1991; Thulborn, 1990). In the present paper I briefly review the record of sauropod body and trace fossils, and describe the morphological features of better-preserved sauropod tracks. I then discuss the implications of the occurrences of sauropod ichnofossils and skeletal remains for interpretations of the paleolatitudinal zonation and habitat preferences of these dinosaurs.

1. EARLY JURASSIC SAUROPODS AND POSSIBLE SAUROPOD TRACKS

Although there is universal agreement that sauropods and prosauropods together comprise a monophyletic group, the Sauropodomorpha, within the Saurischia,

the question of whether sauropods are derived from prosauropods, or instead share a common ancestor with a cladistically monophyletic (holophyletic) Prosauropoda, remains unresolved (Bonaparte, 1986; Benton, 1990; Dodson, 1990a; Galton, 1990; McIntosh, 1990a). All presently known prosauropods are too specialized to be sauropod ancestors. Of particular interest for the study of footprints, presently known prosauropods show much more size reduction of the outer digit of the foot than do sauropods.

Early Jurassic sauropods were placed by McIntosh (1990a, b) within the family Vulcanodontidae. These dinosaurs retain many prosauropod skeletal features, and lack synapomorphies of sauropods in a stricter sense, and so some workers (e.g. Benton, 1990) regard them as prosauropod outgroups to the Sauropoda proper.

Raath (1972) described an incomplete left pes of *Vulcanodon karibaensis* from the? Hettangian of Zimbabwe, Africa. Metatarsals I-III were preserved in articulation, and metatarsals IV and V were found nearby. "The hallux was articulated, as was the first phalanx of the second toe. The remaining phalanges have been allocated on the basis of comparative sizes and configurations of articular surfaces" (Raath, 1972:20). Unfortunately, the two outer digits were not preserved. As reconstructed by Raath (Fig. 1), the foot is like that of later sauropods in having a well-developed claw on digit I. Metatarsal I is a stout bone, but is not as massive in comparison with the other metatarsals as in later sauropods. The phalanges of digits II and III are considerably longer in comparison with their respective metatarsals in *Vulcanodon* than in later sauropods, and the unguals of these digits are shorter in comparison with more proximal phalanges in *Vulcanodon* than in more derived sauropods. Digit III is relatively much longer in *Vulcanodon* than in later sauropods.

The foot skeleton is unknown in other vulcanodontids, which are known from Early Jurassic rocks of Germany, India, and China. McIntosh (1990b) speculated that these early sauropods originated from prosauropod (melanorosaurid?-McIntosh, 1990a) ancestors in the latest Triassic or earliest Jurassic, perhaps in Gondwanaland.

Large footprints (pes track lengths of 50-100 cm) attributed to sauropods are known from the Pliensbachian of Morocco (Jenny and Jossen, 1982; Ishigaki, 1986, 1988). As figured by Ishigaki, these tracks seem to fall into two morphological groups (Fig. 2A-D; Ishigaki himself, however, did not consider these discrete groups). The first group (Fig. 2C, D) has pes tracks with four large digit impressions, a suggestion of an outward bulge in the outer wall of the track possibly corresponding to a very reduced fifth digit, and a very long heel mark; manus prints show no digit impressions. The second morphological group (Fig. 2A, B) has manus prints somewhat like those of the first, but pes tracks with very short, clawless digital impressions. Left and right manus and pes tracks of the first morphological group are some distance away from the trackway midline ("wide-gauge", to use a railroad analogy), and the pace angulations of manus and pes footprints are about the same. Left and right pes tracks of the second morphological group are much closer to the trackway midline ("narrow-gauge"). Pes tracks in this latter
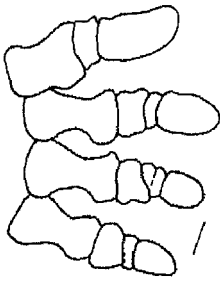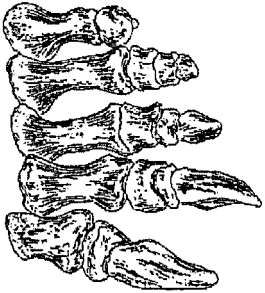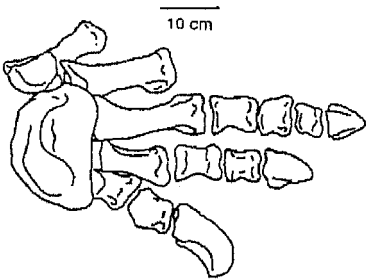
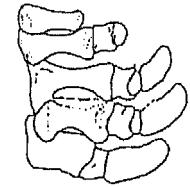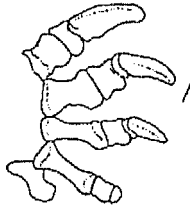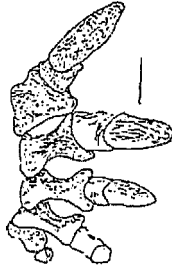Fig. 1: Hindfoot skeletons of sauropod dinosaurs. Scale bars = 10 cm. Vulcanodontidae: Vulcanodon, incomplete left pes; redrawn from Raath (1972). Cetiosauridae: Shunosaurus, left pes; redrawn from Zhang (1988). Rhoetosaurus, right pes; redrawn from a figure provided by the Queensland Museum. Brachiosauridae: Pleurocoelus, left pes; redrawn from Gallup (1989). Camarasauridae: Camarasaurus, left pes; redrawn from Farlow (1987). Diplodocidae: Apatosaurus, right pes; redrawn from Hatcher (1901). Diplodocus, right pes; redrawn from Farlow (1987). Barosaurus, left pes; redrawn from Janensch (1961); the pes may have had three unguals, rather than the two shown here (Farlow et al., 1989). Titanosauridae: Janenschia (formerly Tornieria-Wild, 1991), right pes; redrawn from Janensch (1961).
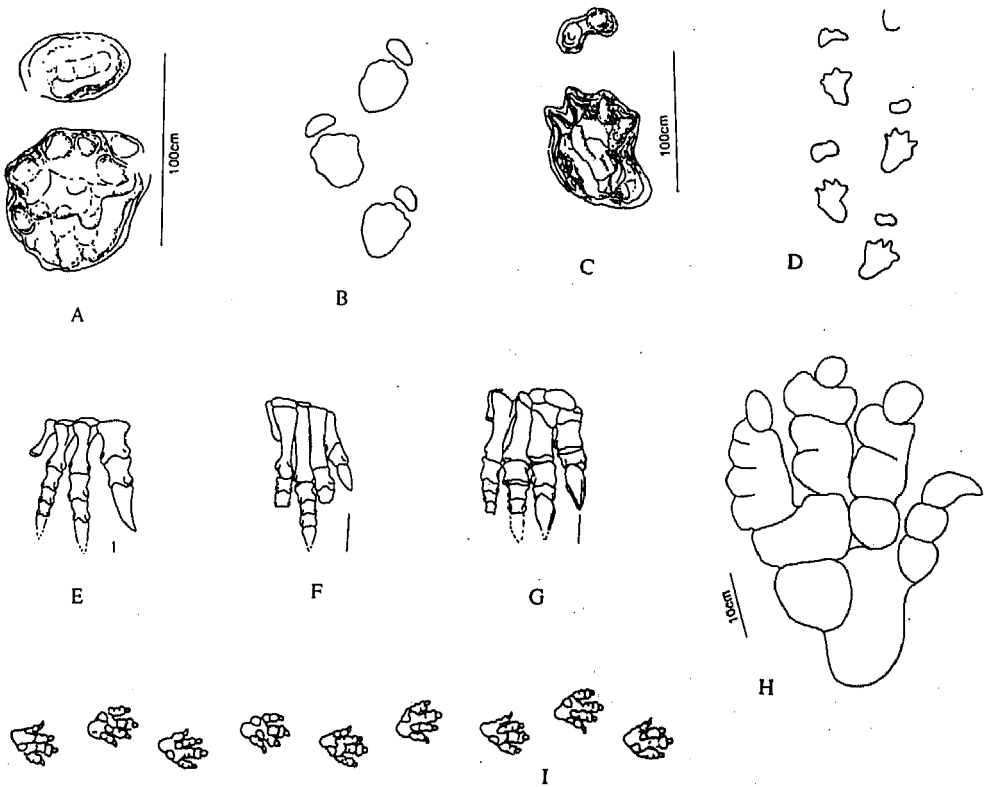
Fig. 2: Early Mesozoic sauropodomorphs and sauropodomorph footprints.
A, B: *Manus-pes set and trackway pattern from the Pliensbachian of Morocco, here called "morphological group 2". Redrawn from Ishigaki (1988). C, D: Manus-pes set and trackway pattern from the Pliensbachian of Morocco, here called "morphological group 1". Redrawn from Ishigaki (1988). E: Right manus of the melanorosaurid prosauropod* Riojasaurus. *Scale bar = 1 cm. Redrawn from Galton (1990).*
F: *Incomplete right pes of* Riojasaurus. *Scale bar = 5 cm. Redrawn from Galton (1990). G: Incomplete right pes of blikanasaurid prosauropod* Blikanasaurus. *Scale bar = 10 cm. Redrawn from Galton (1990). H, I: Left pes track and trackway pattern of prosauropod trace fossil,* Otozoum, *from the Early Jurassic of the Connecticut Valley, U.S.A. Redrawn from Hitchcock (1858: plates XXII, XXXIII).*

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group have a higher pace angulation than do manus tracks; the centers of manus prints are farther away from the trackway midline than are the centers of pes tracks. Traces of the tail occur in neither of the two groups of putative sauropod prints.

The second Moroccan ichnomorphological group has features similar to those of typical narrow-gauge sauropod ichnites (e.g. *Breviparopus*-see below), but there are no suggestions of the large claw marks that one would expect to see on the pes, particularly on digit I, although this might be due to the generally poor preservation of these footprints. The shape of pes tracks of the first Moroccan ichnomorphological group is rather different from that usually seen in well-preserved sauropod hindfoot tracks, in which claw marks are laterally directed, and digit I usually leaves the largest, most clearly visible impression. On the basis of the morphology of the pes of *Vulcanodon*, I would expect digit I to leave the stoutest, although not necessarily the longest, digital impression in hindfoot tracks of even the earliest sauropods. Ishigaki's drawing of the Moroccan tracks does depict the inner digit mark as being stouter than the others, but not by much.

The footprints of the first Moroccan ichnological group may well have been made by sauropods, but given their somewhat unusual morphology and their Early Jurassic age another possibility is worth considering. Basal sauropodomorphs (prosauropods and the ancestors of sauropods, if these were not themselves prosauropods) included one or more lineages of herbivorous dinosaurs that were evolving toward gigantic size. Melanorosaurid prosauropods include forms that attained lengths of as much as 10 meters (Galton, 1990). *Blikanasaurus* is the only presently-known member of the Blikanasauridae; although more modest in size (length perhaps 5 meters) than the larger melanorosaurids, *Blikanasaurus* nonetheless was "an early experiment in the direction of heavily-built quadrupedal saurischians" (Galton and van Heerden, 1985:511).

The hindfeet of melanorosaurids, and even more the hindfeet of *Blikanasaurus*, have four stout digits, like the pes tracks of the first Moroccan ichnomorphological group (Fig. 2F, G). The manus of *Blikanasaurus* is unknown, but the manus of the melanorosaurid *Riojasaurus* has three well-developed digits (Fig. 2E), and so is a poor match for the forefoot tracks of the first Moroccan ichnomorphological group.

Blikanasaurus comes from the late Carnian or early Norian of Lesotho, and well-known melanorosaurids are likewise Late Triassic in age (although this group possibly occurs as late as the Pliensbachian-Galton, 1990). There may therefore be a time gap between these prosauropods and the Pliensbachian footprints from Morocco.

Given the differences in hindfoot track shape between known sauropod trace fossils and the first Moroccan ichnomorphological group, it is tempting to speculate that the latter tracks were made not by true sauropods, but rather by specialized descendants of melanorosaurids or blikanasaurids that had independently achieved gigantic size. Such hypothetical "parasauropods" would have to have reduced the construction of the manus from the condition seen in *Riojasaurus* to the more elliptical shape seen in the Moroccan forefoot tracks, in a manner analogous to the

way that true sauropods developed their own compactly constructed manus. However, McIntosh's (1990a, b) suggestion that the ancestors of sauropods were presently unknown melanorosaurids in which reduction of metatarsal V had not proceeded to the point seen in known members of this family would, if true, mean that my hypothetical "parasauropods" were near cousins of the true sauropods, and not a completely independent lineage of huge sauropodomorphs.

Before leaving this speculative line of thought, it is intriguing to note that the hindfoot tracks of the first Moroccan ichnomorphological group are at least superficially similar to those of the Early Jurassic Connecticut Valley ichnogenus *Otozoum* (an observation independently made by M.G. Lockley). *Otozoum*, like the Moroccan pes tracks, has four stout digits on the hindfoot track (Fig. 2H). Unlike the Moroccan trace fossils, *Otozoum* trackways are rather narrow (Fig. 2I), with a high pace angulation (cf. Lockley, 1990), but this may be the consequence of a bipedal rather than quadrupedal style of locomotion of the *Otozoum*-maker (cf. Thulborn, 1990:284). The alleged *Otozoum* manus (Hitchcock, 1858; Lull, 1953) is quite different from what one would expect in any known sauropodomorph. However, manus impressions are associated with pes tracks in only one specimen, Amherst College 5/14, and the case for putting these prints into the same trackway does not seem very strong to me (a conclusion independently reached by M.G. Lockley); in fact, Lull (1953:191) concluded that "the two manus prints were apparently not made by the animal that made the pes prints at that time, but subsequently".

Otozoum occurs in the Portland Formation of the Newark Supergroup of the Hartford Basin, and so is roughly Hettangian-Pliensbachian in age (Haubold, 1986; Olsen et al., 1989). Consequently it is not inconceivable that the *Otozoum*-maker was a relative of the maker of the first Moroccan ichnomorphological group. Like (Lull 1953) and (Lockley 1990, 1991), I would argue that the *Otozoum*-maker may have been a prosauropod, although this interpretation is not without problems (Baird, 1980); other candidates include "crocodylomorphs" (Baird, 1980; Olsen and Padian, 1986 "crurotarsians" in the usage of Sereno, 1991) and ornithopods (Thulborn, 1990).

2. TYPICAL SAUROPOD FOOTPRINTS AND THEIR MAKERS

During the remainder of the Jurassic Period the Sauropoda split into five groups (Figs. 3-6) recognized as families by McIntosh (1990a, b): Cetiosauridae, Brachiosauridae, Camarasauridae, Diplodocidae (Salgado and Bonaparte, 1991; remove dicraeosaurines from the diplodocids as a family of their own, the Dicraeosauridae), and Titanosauridae; the last of these families became more prominent during the Cretaceous Period. The criteria by which these groups are diagnosed include features of the skull, teeth, vertebral column, tail, ribs, pelvic girdle, and limbs, but not —apart from the slim and elongate metacarpals of the brachiosaurids— the manus and pes.
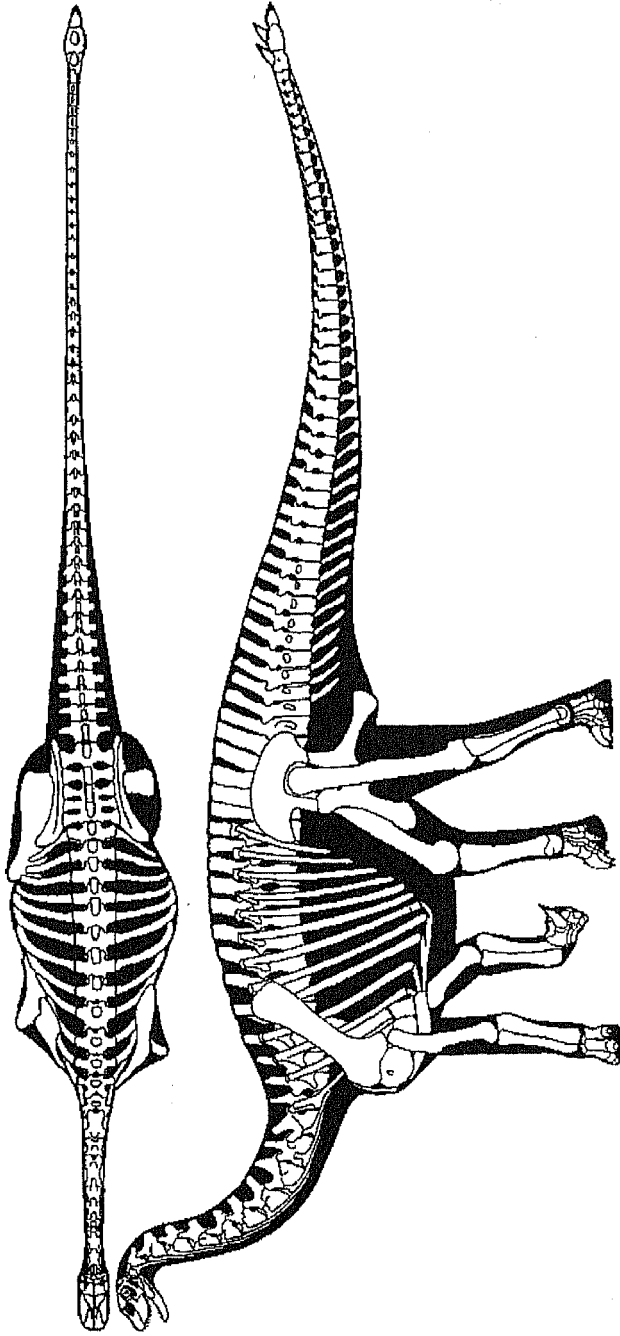
Fig. 3: Skeletal reconstruction of Shunosaurus (Cetiosauridae). Total length from nose to tailtip about 9 meters. Drawing by Gregory S. Paul.
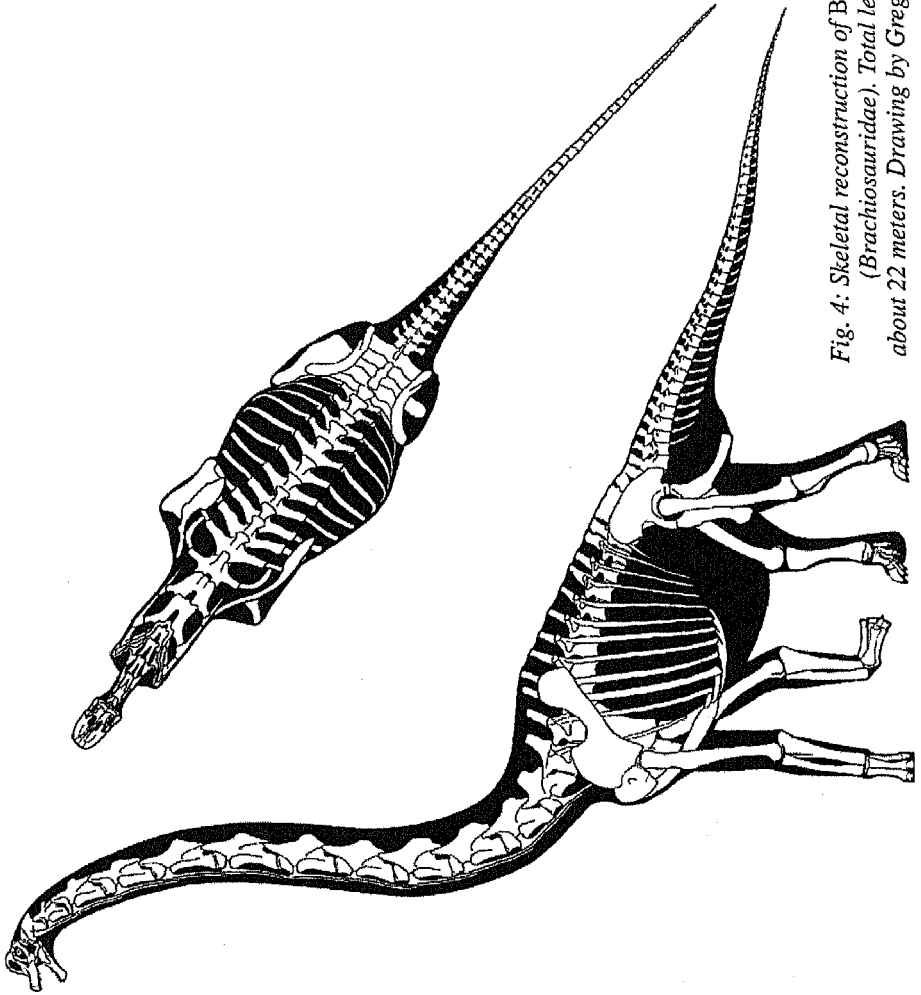
Fig. 4: Skeletal reconstruction of Brachiosaurus (Brachiosauridae). Total length about 22 meters. Drawing by Gregory S. Paul.
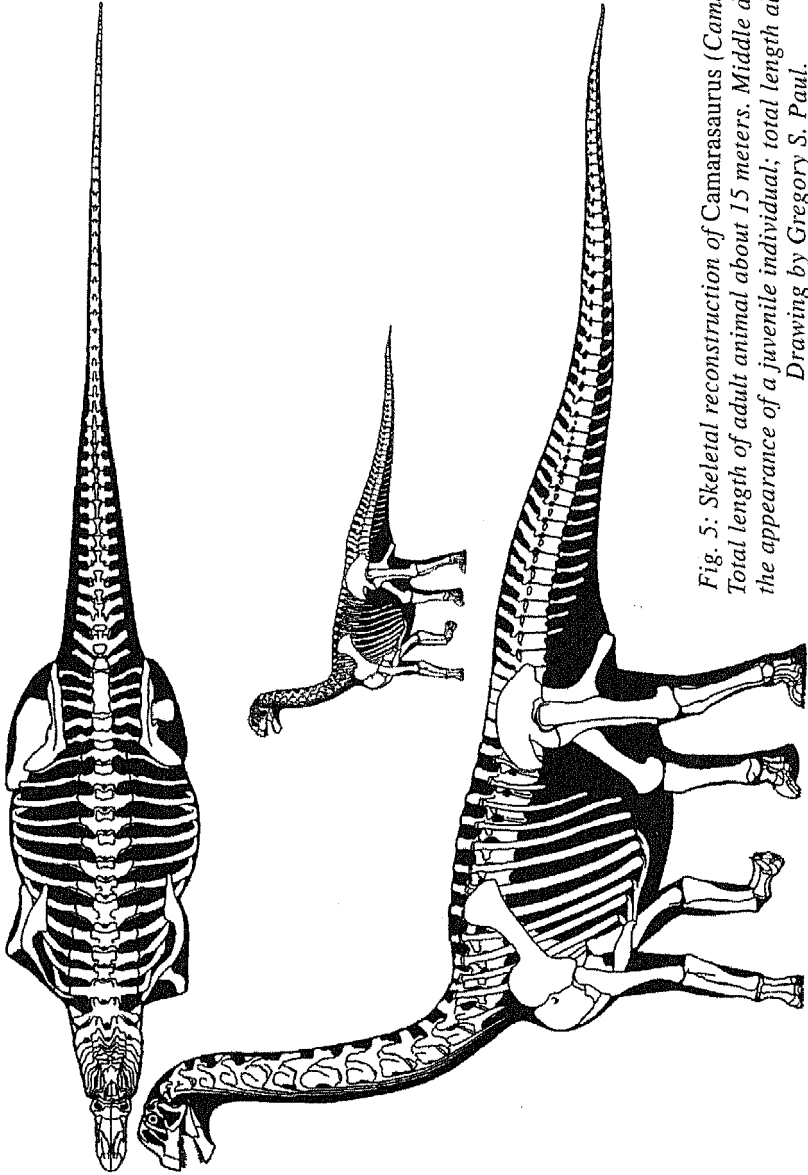
Fig. 5: Skeletal reconstruction of Camarasaurus (Camarasauridae). Total length of adult animal about 15 meters. Middle drawing shows the appearance of a juvenile individual; total length about 5 meters. Drawing by Gregory S. Paul.
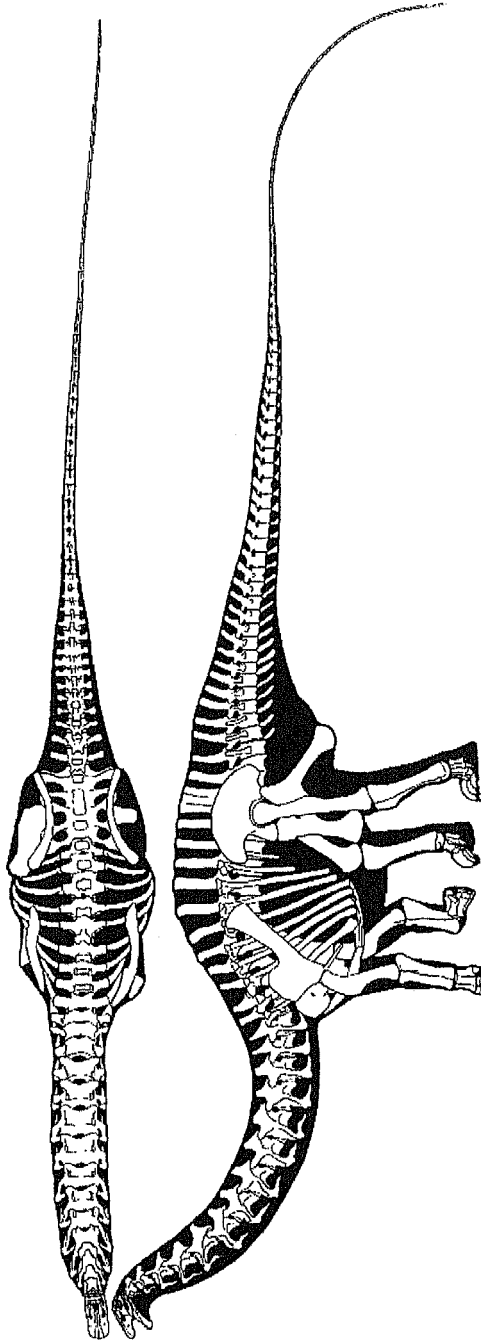
Fig. 6: Skeletal reconstruction of Apatosaurus (Diplodocidae). Total length about 23 meters. A median row of conical spines may have run along the top of the backbone (Czerkas, 1992). Drawing by Gregory S. Paul.

The pes skeletons of most sauropods (Fig. 1) are fairly uniform in their construction (Farlow et al., 1989), with the first metatarsal being the most massive, and more lateral metatarsals becoming more slender. There are stout unguals on at least the three inner digits, that of digit I being the largest. The phalanges of digits IV and V are mere nubs of bone except in the cetiosaurid *Rhoetosaurus*, the brachiosaurid *Pleurocoelus*, and the diplodocid *Dyslocosaurus*, in which digit IV bears a small ungual (Gallup, 1989; McIntosh et al., 1992); *Dyslocosaurus* may also bear an ungual on digit V. The manus of *Brachiosaurus* differs from that in other sauropods (Fig. 7) in having, in addition to long, slim, stilt-like metacarpals, a relatively much smaller claw on digit I.

These observations do not permit much confidence about the possibility of identifying the makers of most sauropod trace fossils even to the family level, with the possible exception of brachiosaurids. The manus and the pes of most sauropods were fairly compact structures, with very short toes whose relative lengths will probably seldom, if ever, be discernible in footprints. Correlating sauropod tracks with skeletal taxa will probably remain a matter of assessing the likelihood that a given skeletal taxon in a particular stratigraphic unit might have made footprints found in the same or a correlative unit.

This problem is compounded by the poor quality of preservation of most sauropod tracks, which are frequently little more than round or elliptical depressions identifiable as sauropod tracks only on the basis of their size and arrangement in trackways. Unfortunately, some such nondescript sauropod trace fossils have received formal names (e.g. *Neosauropus* [which is probably not even sauropod; Santos et al., in press], *Elephantopoides, Sauropodichnus*), a procedure that I cannot endorse (Lockley et al., 1986; Farlow et al., 1989).

Probably the best-preserved sauropod tracks in the world are those from the Early Cretaceous (Comanchean; late Aptian-early Albian) Glen Rose Formation of Texas, U.S.A. (Figs. 8-12), particularly those exposed in the limestone bed of the Paluxy River at Dinosaur Valley State Park, near Glen Rose (Somervell County). These tracks were first seen by local residents in 1934, and came to the attention of Roland T. Bird, a fossil collector for the American Museum of Natural History (New York), in 1938 (Bird, 1985). In 1940 Bird collected portions of a beautifully preserved Paluxy River sauropod trackway for the American Museum and the Texas Memorial Museum (Austin). This trackway was made the type specimen of *Brontopodus birdi*, an ichnotaxon named in Bird's honor by Farlow et al. (1989). Additional information about these sauropod tracks and their occurrence was presented by Langston (1974), Farlow (1987), Farlow and Hawthorne (1989), Gallup (1989), Pittman (1984, 1989, 1990), Pittman and Gillette (1989), and Hawthorne (1990).

Well-preserved manus tracks (length and width about 40-50 cm) in the type specimen of *Brontopodus* are somewhat horseshoe-shaped, being most deeply impressed along the anterior and the inner and outer edges of the footprint, and shallowest in the central and rear portion of the track. Slight indentations in the medial and lateral sides of manus tracks suggest that digits I and V of the forefoot

Brachiosaurus brancai

Janenschia robusta

Shunosaurus lii

Apatosaurus excelsus
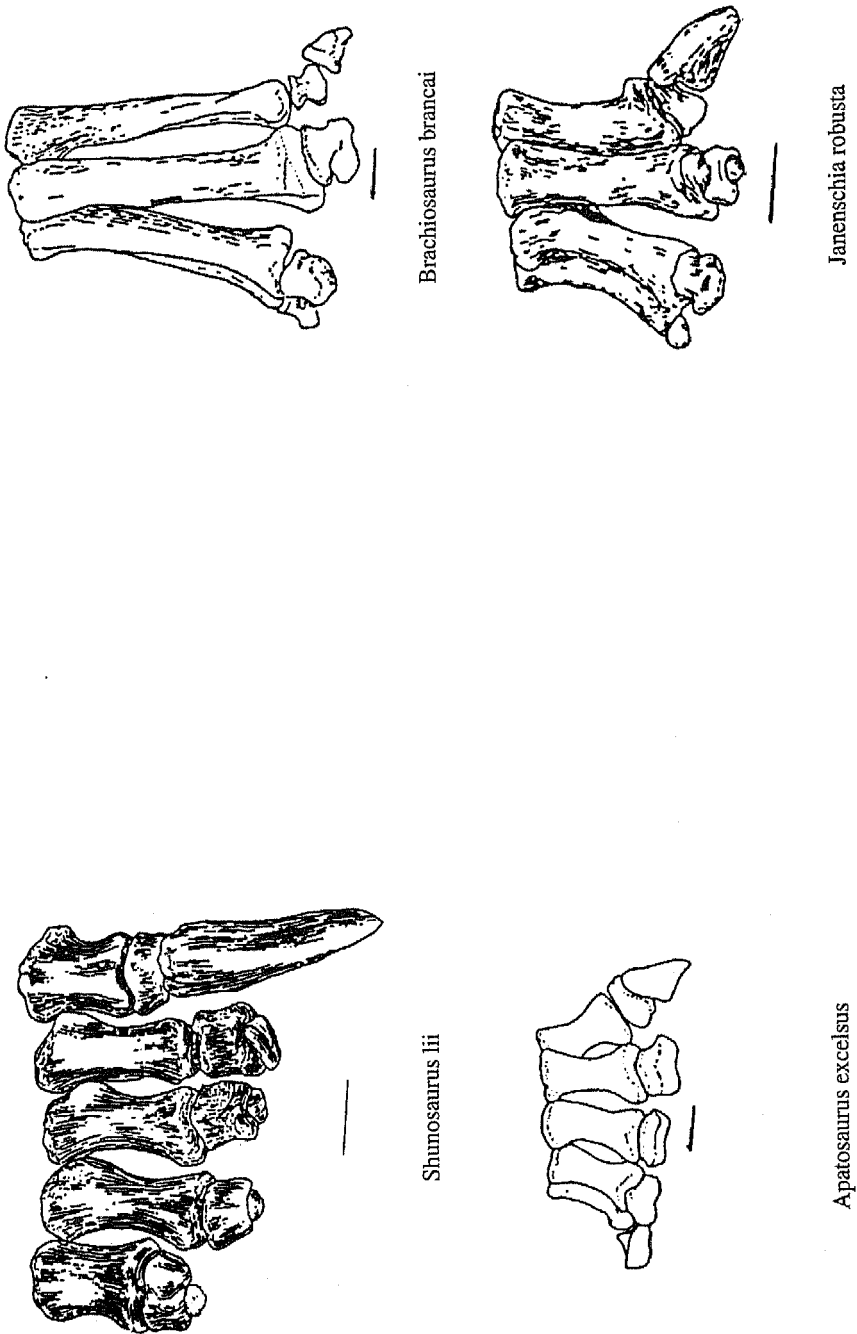
Fig. 7: Forefoot skeletons of sauropods. Scale bars = 10 cm. Illustrations redrawn from sources cited in caption to Fig. 1.

A

B

Fig. 8: Sauropod footprints from the Early Cretaceous Glen Rose Formation, Paluxy River, Dinosaur Valley State Park, Somervell County, Texas, U.S.A. A-D: Footprints from the type trackway of Brontopodus birdi (Farlow et al., 1989). A, B: Well-preserved right manus track, print S2M in the American Museum portion of the type specimen, AMNH 3065. A is a view from directly overhead, and B is a posterolateral oblique view. Track length and width about 50 cm. C: Well-preserved right pes track S2M from AMNH 3065, part of a manus-pes set with the manus track shown in A and B. Length 87 cm.

C

D
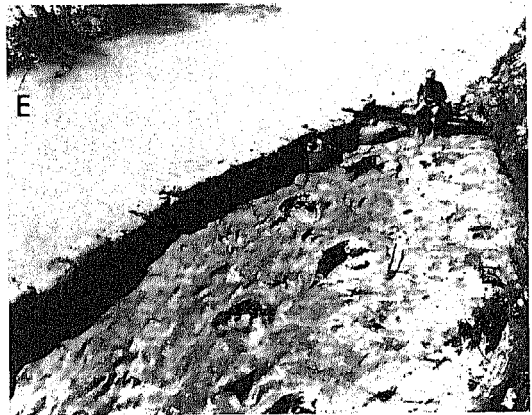
D: Footprints of the type trackway in situ. *Large black arrow, positioned near the trackway midline, shows direction of travel. Note the wide separation of left from right footprints, making this a "wide-gauge" sauropod trackway. The trackway segments collected for the American Museum and the Texas Memorial Museum are immediately to the left of the trench cut into the river bedrock, near the top of the photograph. Photograph by R.T. Bird. E: Trackway of a very large sauropod (S5, the "Giant") near the south end of R.T. Bird's Paluxy River footprint quarry (Farlow, 1987: Fig. 28). Only pes tracks are preserved; track lengths about 110 cm. Black arrow near the trackway midline shows the dinosaur's approximate direction of travel. Photograph by R.T. Bird.*

OZARK SAUROPOD TRAILS

Dinosaur Valley State Park
Paluxy Riverbed, Glen Rose, Texas

© 1982-1992. Glen J. Kuban

Based on photographs, measurements,
and sketches by Glen Kuban 1980-1988.
1988 measurements assisted by Nora Lan.
Positions and shapes of tracks A1 through A3
are tentative and based on W. Fields (1978)

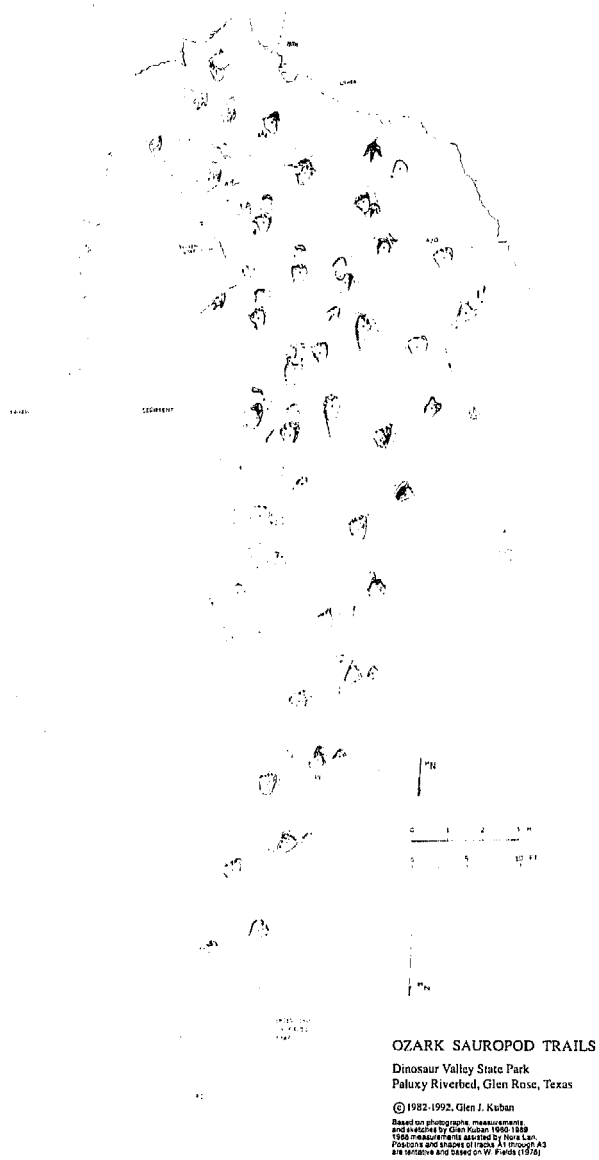*Fig. 9: Four sauropod trackways and associated theropod footprints along the east bank of the Paluxy River, Dinosaur Valley State Park, Texas. The four trackmakers were all traveling in a southerly direction (toward the top of the page);*
^{M}N = *magnetic North. The two middle trails intersect near the spot where they are first seen. Note the wide gauge of these trackways. Map drawn by Glen Kuban.*
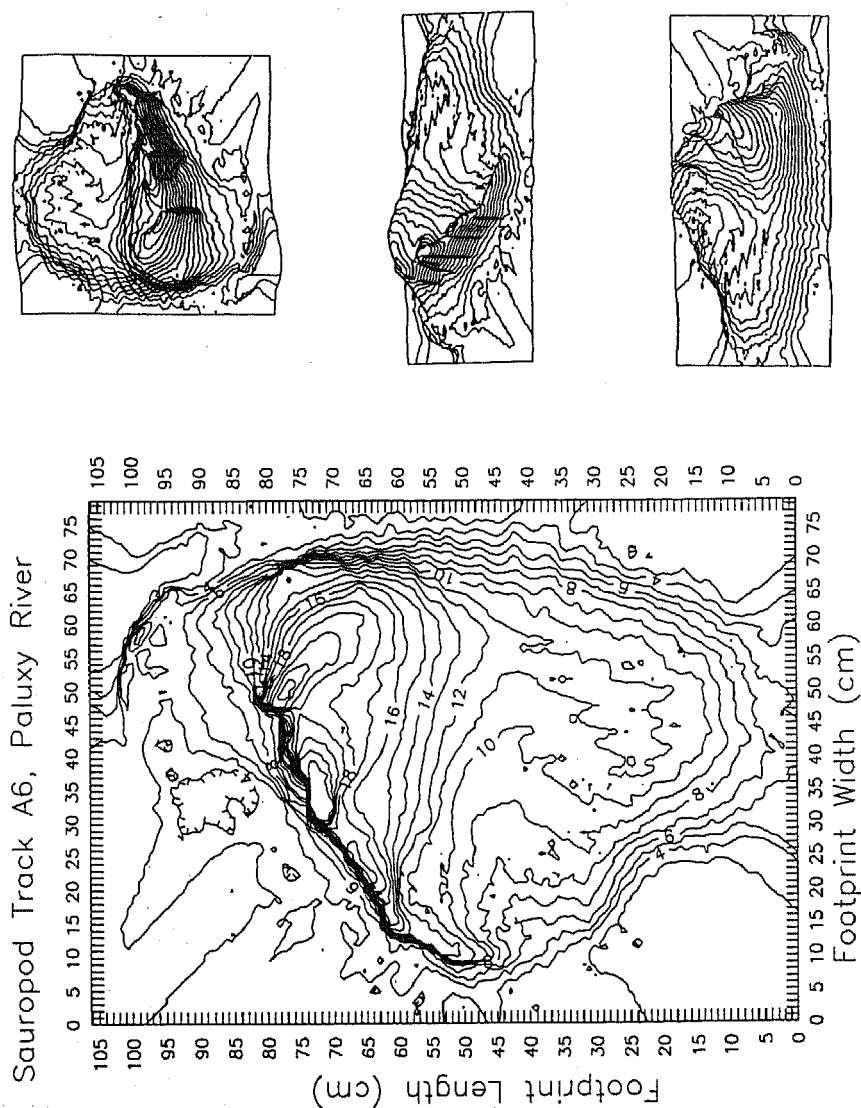
Fig. 10: Contour map and perspective views of sauropod right manus-pes set A6 from the Main Tracksite, Dinosaur Valley State Park (Farlow, 1987). The contour map was made from a cast of the original footprint, and so left-right symmetry and topography are reversed from the original footprint. The manus print is shallow and poorly preserved, but the pes track of this set is superb. Contours indicate depths of different regions of the pes track; contour interval = 1 cm. Note the shallowness of the lateral portion of the track, and the great depth of the footprint's medial edge.

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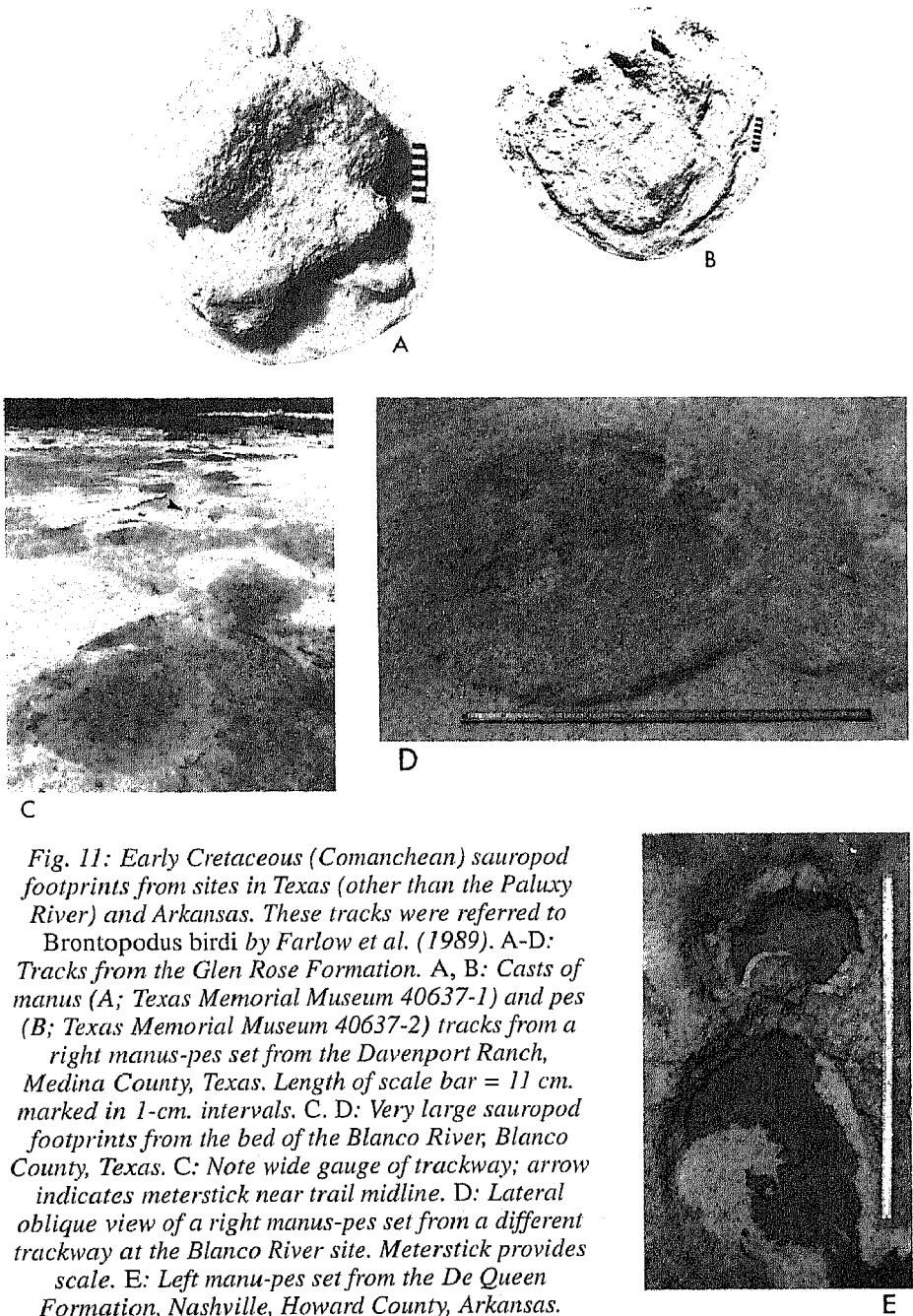
Fig. 11: Early Cretaceous (Comanchean) sauropod footprints from sites in Texas (other than the Paluxy River) and Arkansas. These tracks were referred to Brontopodus birdi by Farlow et al. (1989). A-D: Tracks from the Glen Rose Formation. A, B: Casts of manus (A; Texas Memorial Museum 40637-1) and pes (B; Texas Memorial Museum 40637-2) tracks from a right manus-pes set from the Davenport Ranch, Medina County, Texas. Length of scale bar = 11 cm. marked in 1-cm. intervals. C. D: Very large sauropod footprints from the bed of the Blanco River, Blanco County, Texas. C: Note wide gauge of trackway; arrow indicates meterstick near trail midline. D: Lateral oblique view of a right manus-pes set from a different trackway at the Blanco River site. Meterstick provides scale. E: Left manu-pes set from the De Queen Formation, Nashville, Howard County, Arkansas.

Fig. 12: "Wide-gauge" sauropod trackways. Scale bars = 1 meter, except where otherwise indicated. Use of ichnotaxon names does not necessarily mean that I regard those names as valid. A-D: Brontopodus birdi. A, B: Trackways from 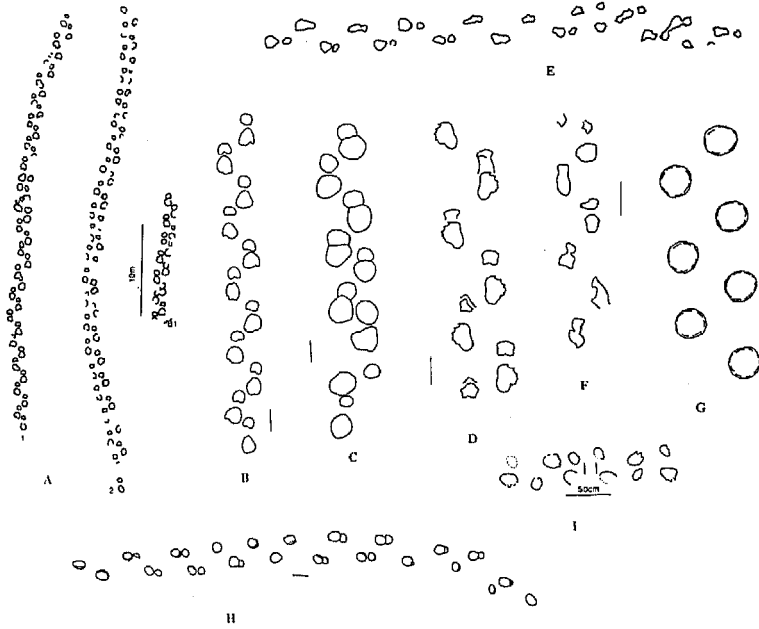the Early Cretaceous De Queen Formation, Howard County, Arkansas. Redrawn from Pittman and Gillette (1989). A: Trackways, 1, 2, and B1. B: Detail of the first several footprints of Trackway 1. C: Sauropod trackway from the Glen Rose Formation, Miller Creek, Blanco County, Texas. Redrawn from Pittman (1990). D: R.T. Bird's drawing of the American Museum portion of the type specimen of Brontopodus birdi (AMNH 3065), drawn to eliminate distortions of the shape of some tracks caused by superposed carnosaur footprints (cf. Farlow, 1987: Fig. 31). E, F: Sauropod trails "Grupo H" (E) and "Grupo I" (F), Enciso Group (Early Cretaceous), Valdecevillo, Spain. Redrawn from Casanovas Cladellas et al. (1989: Figs. 8, 9). G: Sauropodichnus giganteus, Río Limay Formation (middle Cretaceous), Neuquén Province, Argentina. Redrawn from Calvo (1991). H: Rotundichnus munchehagensis, Bückeberg Formation (Early Cretaceous), Rehburg, Germany. Redrawn from Hendricks (1981). Additional sauropod trackways from this site were described by Fischer et al. (1988). I: Trackway of a very small sauropod, Jindong Formation (Early Cretaceous), South Korea. Redrawn from Lim et al. (1989).

were separated by soft tissues from digits II-IV, which were themselves bound together by soft tissues to form a crescent-shaped anterior portion of the foot. There are no indications of either a large digit I (thumb) claw or a cushioning pad of connective tissue behind the bones of the manus.

Well-preserved pes tracks (length about 87 cm; width about 60-65 cm) in the type specimen are strongly assymetrical, with large, laterally directed claw marks on digits I through III, and smaller ungual or callosity marks in the positions of digits IV and V. Pes tracks are deepest along their inner margins, indicating that the trackmaker carried the bulk of its weight on the inner side of its hindfoot, a conclusion consistent with the stout construction of the inner metatarsals of the sauropod pes. There is a deep "heel" mark at the rear of the footprint, indicating the presence of a substantial, elephant-like (Sikes, 1971:32), shock-absorbing pad of connective tissue behind and beneath the bones of the foot.

The trackway is wide-gauge, with manus and especially pes tracks well away from the trackway midline; the centers of pes tracks are farther away from the midline than are the centers of manus prints. Both manus and pes tracks angle outward with respect to the dinosaur's direction of travel. The pace and stride are about the same for manus and pes tracks; the stride is about 3 1/2 times the length of pes prints. The pace angulation ranges from 100°-120° for both manus and pes tracks.

Other sauropod trackways at the Paluxy River site, and at other sites in Texas and Arkansas, are fairly similar in morphology to those of the type trackway. There is, however, a considerable size range of sauropod tracks from Texas. Some sauropod trails from the Davenport Ranch site (Medina County) have tracks that are considerably smaller (pes track lengths of 40-50 cm) than those of the type trackway, and were probably made by juveniles (Bird, 1985; Farlow et al., 1989; Lockley, 1991). Other trackways have pes tracks with lengths in excess of a meter.

The *Brontopodus*-maker is usually interpreted as the brachiosaurid *Pleurocoelus* (Langston, 1974; Farlow, 1987; Farlow et al., 1989; Gallup, 1989; Pittman, 1989), based on the inferred absence or very small size of the digit I ungual of the manus of the trackmaker (a presumed brachiosaurid feature), and the fact that skeletal remains of this dinosaur are known from the Glen Rose Formation. The nomenclature of the genus *Pleurocoelus* is very untidy (Ostrom, 1970; Langston, 1974; Lucas and Hunt, 1989; McIntosh, 1990). McIntosh (1990:348) referred skeletal material from Texas to *P. nanus*, a species based on bones from the Arundel Formation of Maryland (U.S.A.), even though the Arundel specimens are older (Hauterivian-Barremian) and smaller than specimens from Texas (Langston, 1974; Weishampel, 1990); however, larger specimens of *Pleurocoelus (P. altus)* do occur in the Arundel. A relatively large specimen identified as *Pleurocoelus* is also known from the Cedar Mountain Formation (Aptian-Albian) of Utah (DeCourten, 1991), and a large *Pleurocoelus* may occur in the Cloverly Formation (Aptian-Albian) of Montana (Weishampel, 1991). If the Texas skeletal remains do represent *P. nanus*, and if the Texas trackmaker was this taxon, then *P. nanus* was not a small form, as suggested by McIntosh on the basis of the (juvenile?) skeletal material from Mary-

land, but rather a species that attained a body size comparable to that of *Apatosaurus*, or even larger.

McIntosh et al. (1992) noted that the *Brontopodus*-maker might not have been a brachiosaurid, but rather a presently unknown diplodocid which, like *Dyslocosaurus*, bore unguals on digits IV and V of the pes. The cautionary remark is well taken, but had the *Brontopodus*-maker been a diplodocid I would have expected to see a pollex claw mark on manus tracks. However, the manus of *Dyslocosaurus* is unknown, and sauropod manus prints seldom show claw marks, and so I cannot exclude the possibility that the *Brontopodus*-maker was a diplodocid, although I consider it unlikely.

Sauropod ichnites similar in trackway pattern to *Brontopodus* are known from the Bückeberg Formation (Berriasian) of northwestern Germany (Fig. 12H), and have been given the name *Rotundichnus münchehagensis* (Hendricks, 1981; Fischer et al., 1988). Like *Brontopodus*, *Rotundichnus* is a wide-gauge sauropod trackway. Both manus and pes tracks are deeper at their anterior than their posterior ends. Pes tracks are deeper, with a steeper edge, on their inner than on their outer sides ("Die Trittsiegel sind entweder schüsselformig eingeprägt oder sie besitzen eine gerade Sohlfläche, die vorne und/oder innen die maximale Eindrucktiefe aufweist und nach hinten flach ausläuft"; Hendricks, 1981:20). *Rotundichnus* is so similar in its observable features to *Brontopodus* that Farlow et al. (1989) considered designating the Paluxy River sauropod tracks a species of *Rotundichnus*, but decided against this because the German tracks are not well enough preserved to reflect morphological features of the feet that made them.

Other wide-gauge sauropod trackways are known from sites in Spain, Switzerland, Argentina, and Korea (Fig. 12) (Meyer, 1990; Casanovas et al., in press). Few of these ichnites have been described in detail, and those that have been described show little interpretable footprint morphology.

In contrast to wide-gauge sauropod trails are trackways from numerous sites in which pes (and sometimes manus) tracks are close to or even intersect the trackway midline (Fig. 13). One such trail, made by a huge sauropod from the Late Jurassic or Early Cretaceous of Morocco (Fig. 13I, J), has been named *Breviparopus taghbaloutensis* (Dutuit and Ouazzou, 1980; Ishigaki, 1989). The trackmaker was comparable in size to the largest Early Cretaceous sauropod trackmakers in Texas. Outline drawings of the footprints published by Dutuit and Ouazzou (1980) differ somewhat from drawings published by Ishigaki (1989), and published photographs suggest that the individual footprints were not well preserved. Consequently a detailed comparison of morphological features between the tracks of *Breviparopus* and *Brontopodus* is not possible. In some *Breviparopus* pes tracks claw marks appear to be directed outward, as in *Brontopodus*, but in other pes prints from the same trackway the claw marks seem to point anteriorly. Manus prints of *Breviparopus* lack the indentations in the lateral and medial walls seen in well-preserved *Brontopodus* manus tracks, but this might be due to poor preservation of the Moroccan footprints (Farlow et al., 1989).
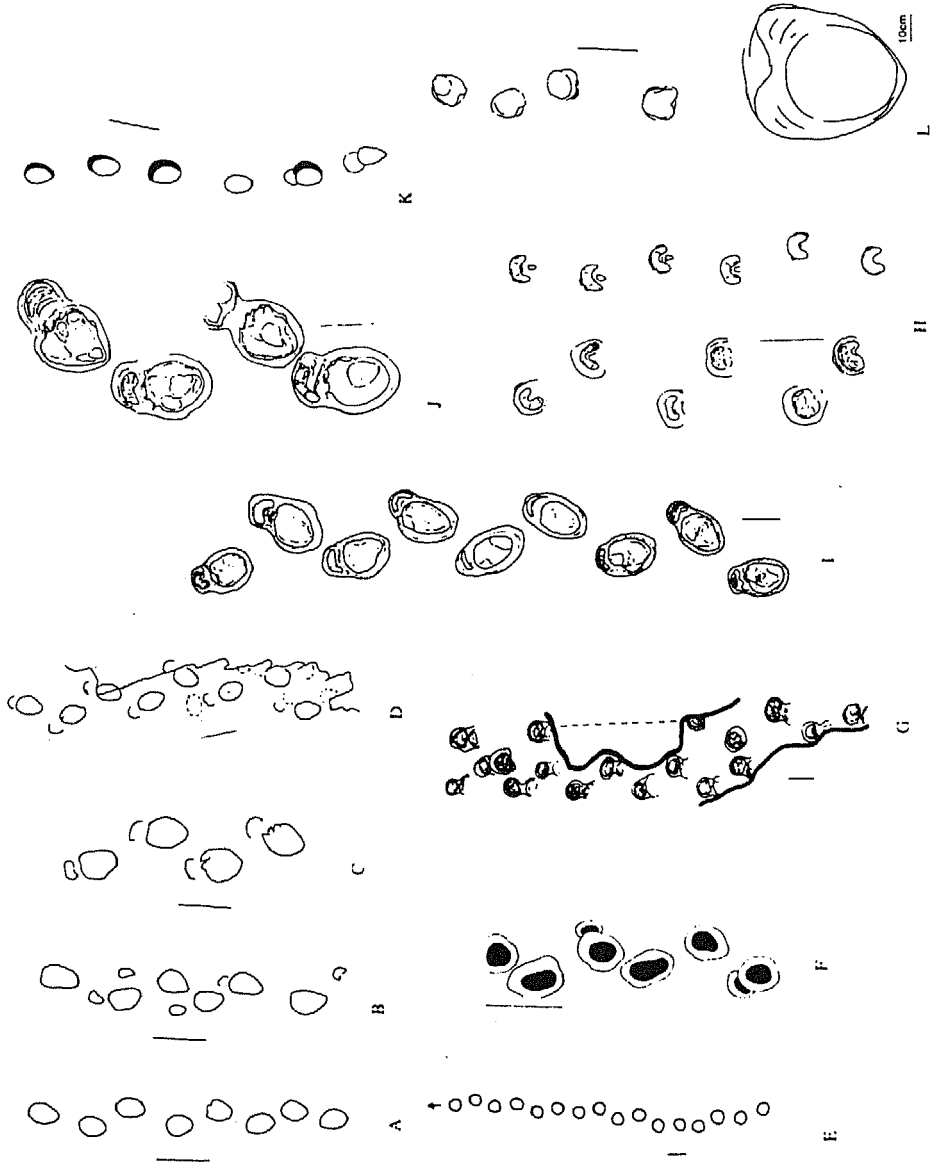
The trackway pattern of *Breviparopus* is quite different from that usually seen in *Brontopodus*. In addition to being narrow-gauge, the *Breviparopus* trail has manus prints that are farther away from the trackway midline than are the centers of pes tracks, in contrast to sauropod trails from the Early Cretaceous of Texas.

Differences in trackway gauge between *Brontopodus* and other wide-gauge sauropod trails on the one hand, and *Breviparopus* and other narrow-gauge trackways on the other, conceivably reflect differences in the skeletal structure of the trackmakers, with the former group having been wider-bodied animals than the latter group. Inspection of the dorsal views of skeletal reconstructions of sauropods in Figures 3-6, for example, suggests the possibility that some sauropod taxa may have differed from others in the ratio of width across the girdles to glenoacetabular length. However, an alternative explanation for differences in trackway gauge is also possible (Fig. 14). The makers of wide-gauge sauropod trackways may have walked with their legs directly beneath their shoulder and hip joints, while the makers of narrow-gauge trails may have angled their legs (particularly their hind-legs) inward a bit from their limb girdles. Proboscideans walk in this fashion,

Fig. 13: "Narrow-gauge" sauropod (real and alleged) trackways. Scale bars = 1 meter, except where otherwise indicated. Use of ichnotaxon names does not necessarily mean that I regard those names as valid. A-D: Trackways from the Morrison Formation (Late Jurassic), Colorado. Redrawn from Lockley et al. (1986). A: Sauropod trackway, near Fort Collins. B, C: Trackways 31 and 34, respectively, Purgatoire River. D: Trackway near State Bridge. E: Neosauropus lagosteirensis, Early Cretaceous, Lagosteiros, Portugal. Redrawn from Telles Antunes (1976). These are probably not sauropod footprints (Santos et al., in press), although they were originally described as such. F: Elephantopoides barkhausensis, Late Jurassic, Barkhausen, Germany. Redrawn from Friese and Klassen (1979). G-J: Middle Jurassic trackways from the central High Atlas Mountains, Morocco. G: Trackways A (left) and B (right). Redrawn from Ishigaki (1989). H: Trackways C (left) and D (right). Redrawn from Ishigaki (1989). Trackways A-D were interpreted by Ishigaki (1989) as having been made by swimming or half-floating dinosaurs, a conclusion questioned by Lockley and Rice (1990). I, J: Trackway pattern (I) and more detailed drawing of some of the tracks (J) of Breviparopus taghbaloutensis. Redrawn from Ishigaki (1989) and Ishigaki (personal communication). K, L: Early Cretaceous sauropod trackways from the Babouri-Figuil Basin, Cameroon. Redrawn from Dejax et al. (1989). The authors did not attribute these footprints to sauropods (but thought that sauropod tracks were questionably present at some of their sites). I show these as possible sauropod trackways because of their similarity to other narrow-gauge trackways attributed (rightly or wrongly) to sauropods. Ishigaki (1988) illustrated somewhat similar trackways from the Pliensbachian of Morocco, but like Dejax et al. (1988) considered them to have been made by bipedal dinosaurs. K: Trackway Group D. L: Trackway Group C1-C4; entire trackway (above) and individual footprint (below).
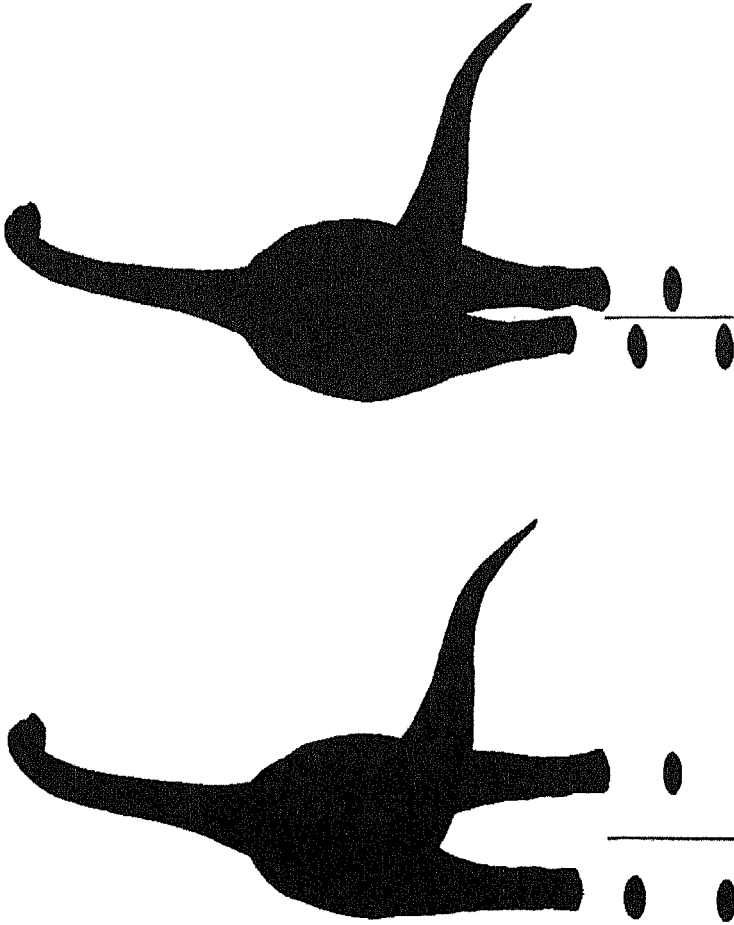
Fig. 14: Possible effect of sauropod body carriage on trackway gauge. Two sauropods of the same body width are walking away from the viewer. The sauropod on the left holds its limbs directly beneath its girdles, while the legs of the sauropod on the right angle inward in an elephant-like fashion. Line segments and dots diagrammatically illustrate trackway midlines and footprints, respectively. The sauropod on the left makes a wide-gauge trackway, and the sauropod on the right makes a narrow-gauge trackway.

making very narrow trackways (Muybridge, 1957:plate 111; Sikes, 1971:fig. 8; Leakey, 1987:467).

Whether differences in trackway pattern correlate with taxonomic differences between trackmakers thus remains uncertain. Comparison of Figures 12 and 13 suggests that the difference between narrow-gauge and wide-gauge trails is more a matter of degree than of kind. Sauropods may have created different trackway patterns when walking across substrates of different consistency, or when walking at different speeds. If so, differences in trackway pattern will have rather little systematic value.

3. PALEOGEOGRAPHIC AND PALEOECOLOGICAL OCCURRENCE OF SAUROPOD TRACE AND BODY FOSSILS

Lockley (1991:123-124) argued that "from their first appearance in Early Jurassic North Africa right through to Cretaceous times, brontosaur tracksites are associated with limy substrates in tropical and subtropical latitudes. In contrast, the ornithopod-dominated Cretaceous assemblages are mainly associated with middle to high latitudes, in some cases even as far north as the Arctic circle". This intriguing hypothesis prompted me to examine the paleogeographic occurrence of sauropod fossils more generally, to see if any correlations between the occurrence of sauropods and paleogeographic or paleoclimatological features could be detected.

3.1. Mesozoic geography and climates

The break-up of Pangaea had barely begun in the Early Jurassic, and so the existence of this gigantic landmass had a profound impact on the world's climates. The shape of Pangaea was such that large land masses occurred on either side of the low-latitude Tethyan seaway (Scotese, 1991; Scotese and Golonka, 1992). This resulted in a double monsoonal air circulation, with southeastern Asia and northern Gondwana experiencing significant rainfall during their respective summers (Parrish et al., 1982; Hallam, 1985; Dubiel et al., 1991). Monsoonal conditions probably disrupted the flow of equatorial easterly winds, with the result that much of tropical Pangaea had dry climates. Moister conditions prevailed in coastal areas of high-latitude portions of Pangaea.

Climatic conditions in the interiors of the Asian and Gondwanan portions of Pangaea are controversial. Mathematical models suggest that high-latitude interior regions should have experienced freezing winter temperatures (Crowley and North, 1991). This conclusion contradicts floral and faunal evidence of warm temperatures at high latitudes (Hallam, 1985; Vakhrameev, 1991). Warmer winter temperatures can be achieved by invoking CO_2-generated greenhouse conditions in the mathematical models, but this exacerbates already high summertime temperatures in the interior of Pangaea (Crowley and North, 1991). This problem of reconciling retrodictions of severe high-latitude winter temperatures in continental interiors, based

on numerical models, with paleontological evidence of milder conditions, is a recurring theme in the interpretation of Mesozoic climates (Barron, 1989; Sloan and Barron, 1990; Crowley and North, 1991; Horrell, 1991). Whatever the annual temperature range, interior regions of Pangaea may have been very dry (Parrish et al., 1982), particularly if greenhouse warming did prevail during the Early Jurassic (Crowley and North, 1991).

Apart from modest growth in the nascent Atlantic Ocean, the configuration of continental blocks and deep ocean basins in the Middle and Late Jurassic (Figs. 15, 16) remained much the way it had been earlier in the period (Scotese, 1991). Monsoonal conditions still existed in southeastern Asia and Gondwana, but equatorial Pangaea may have been less arid than before (Parrish et al., 1982; Moore et al., 1992). Conditions had become drier in Europe and south-central Asia, however (Hallam, 1984, 1985; Vakhrameev, 1991), and interior regions of Pangaea remained arid (Parrish et al., 1982; Moore et al., 1992). A sophisticated general circulation model of the Late Jurassic atmosphere (Moore et al., 1992) suggests that greenhouse conditions were still necessary to account for the occurrence of presumed warm-temperature organisms at high latitudes (Hallam, 1985), but wintertime temperatures in high-latitude interior regions remained cold in this model.

The break-up of Pangaea proceeded apace during the early and middle portions of the Cretaceous Period (Scotese, 1991; Scotese and Golonka, 1992), with enlargement of the Atlantic and Tethys (Fig. 17). Temperatures were warm over most of the planet (Hallam, 1984, 1985), except perhaps during the winter in the interiors of high-latitude continents, and there was probably still a significant greenhouse effect caused by high levels of CO_2 in the atmosphere (Barron, 1989; Crowley and North, 1991; Berner, 1992).

The atmospheric circulation had become more latitudinally zonal, due to the diminished influence of monsoons in a world of smaller continental masses (Parrish et al., 1982). Climates were more humid in Europe and the Mideast than they had been in the Late Jurassic, and the geographic extent of arid regions would continue to shrink over the remainder of the Cretaceous (Hallam, 1984, 1985). Forests occurred at middle and high latitudes of North America, Eurasia, and Gondwana (Ziegler et al., 1987).

Despite overall greater humidity than in the Late Jurassic, dry environments were still present (Ziegler et al., 1987). A greater annual latitudinal fluctuation of the Intertropical Convergence Zone than in the modern world may have prevented the existence of equatorial forests, resulting instead in savanna-like vegetations at low latitudes. Desert conditions may have prevailed in the central portion of a continental block composed of Africa and South America, along a belt extending from China to the vicinity of the Caspian Sea, and in portions of eastern Africa, India, and southern North America (Ziegler et al., 1987).

The various features of the early to middle Cretaceous atmospheric and oceanic circulations were related, either directly or indirectly, to plate tectonic phenomena. Dispersion of the continental fragments of Pangaea created an equatorial seaway that stretched across the entire planet, and increased vulcanism, expressed in rapid

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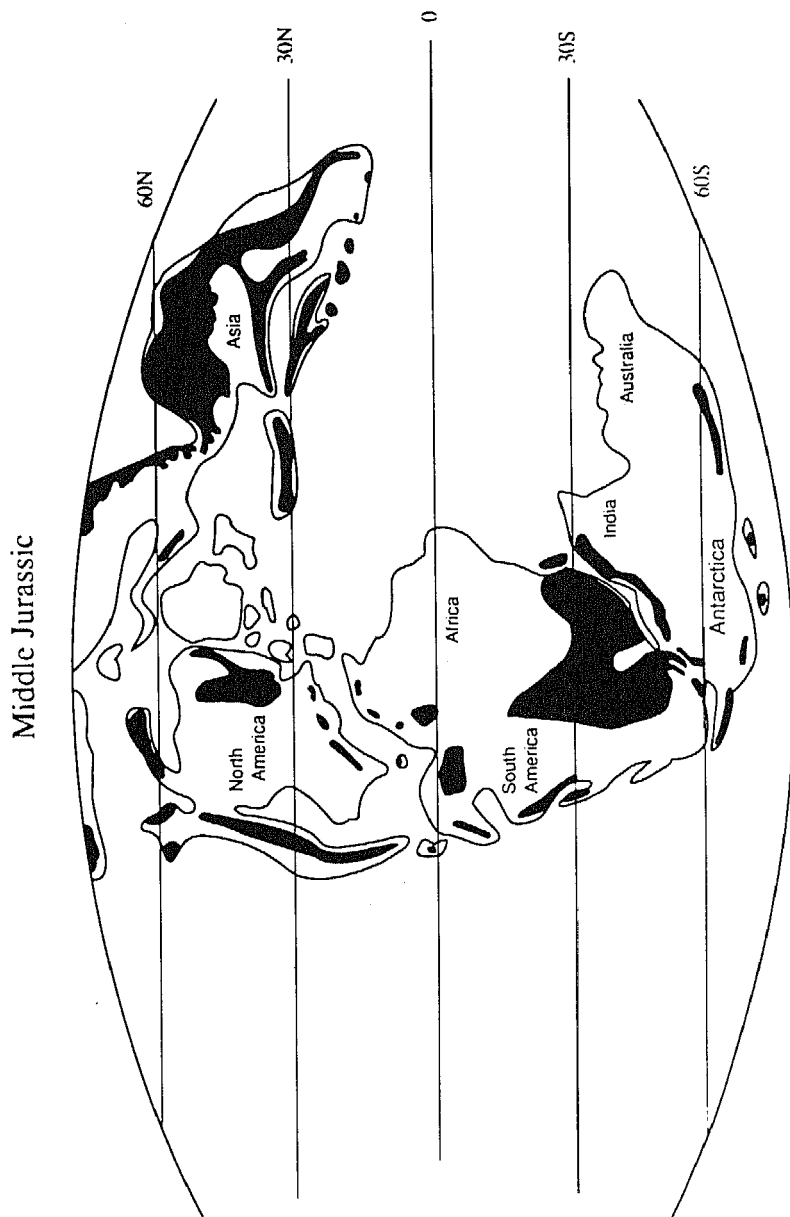
Fig. 15: Reconstruction of the Middle Jurassic (Callovian) continents. White = lowlands, black = mountainous regions. Redrawn from Scotese and Golonka (1992).

Late Jurassic
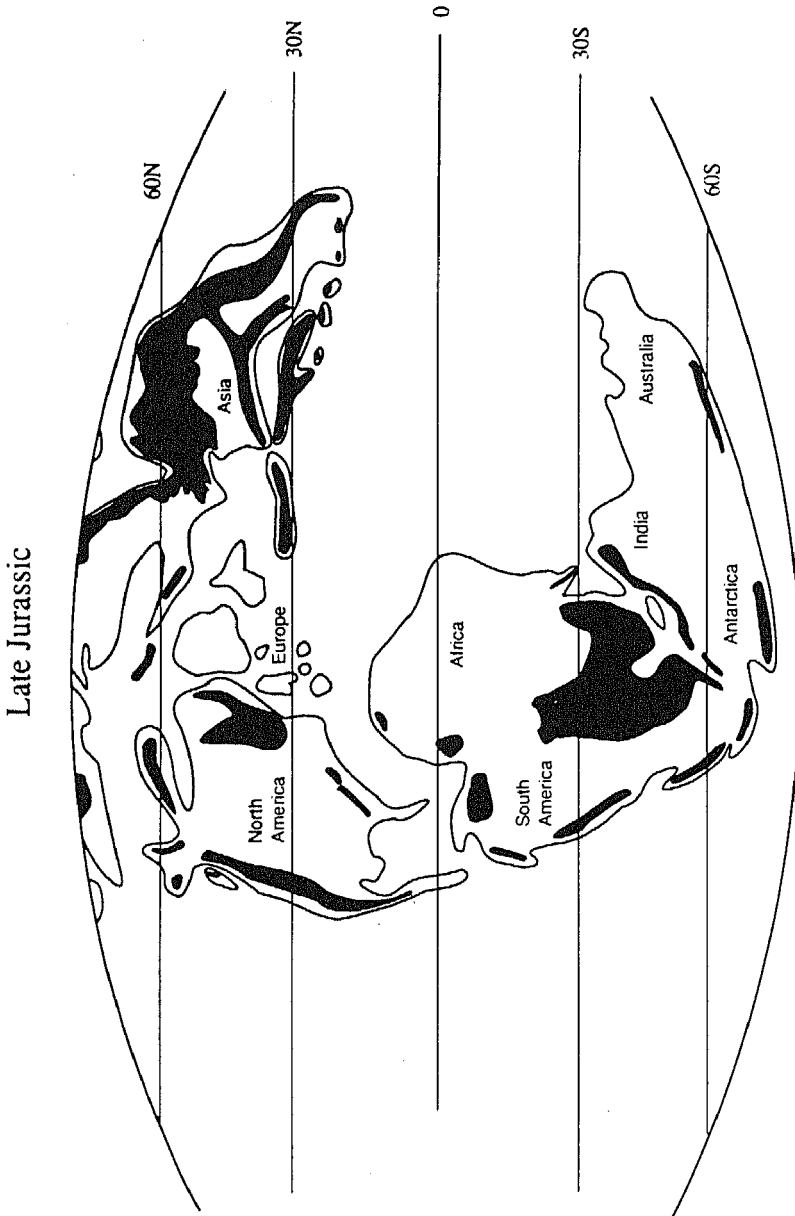

Fig. 16: Reconstruction of the Late Jurassic (Kimmeridgian) continents. Color shadings as in Fig. 11. Redrawn from Scotese and Golonka (1992).
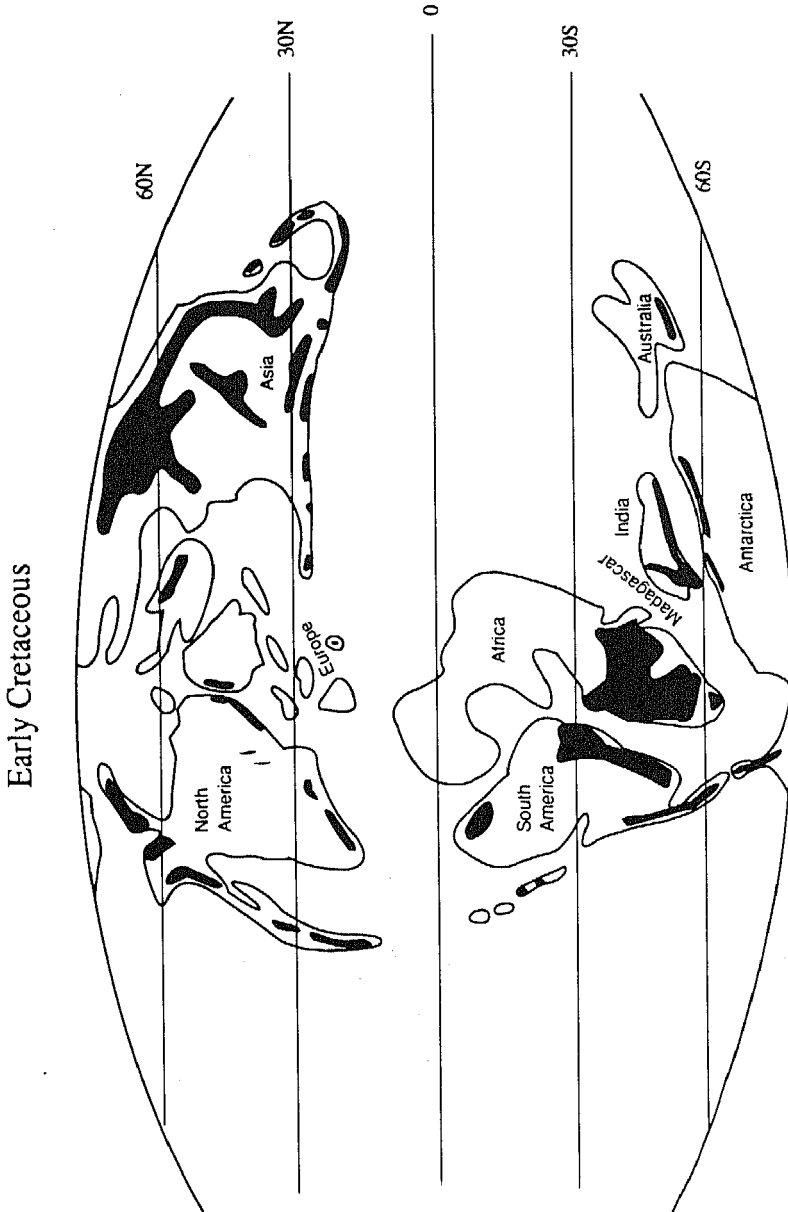
Early Cretaceous

Fig. 17: Reconstruction of the Early Cretaceous (Aptian) continents. Color shadings as in Fig. 11. Redrawn from Scotese and Golonka (1992).

rates of sea-floor spreading and the formation of huge oceanic plateaus, resulted in eustatic sea level rise and high atmospheric CO_2 levels (Hallam, 1984, 1985; Barron, 1989; Crowley and North, 1991; Winterer, 1991).

Global temperatures probably declined after the middle Cretaceous, but the Late Cretaceous earth remained warmer than the modern world (Crowley and North, 1991; Horrell, 1991; Vakhrameev, 1991). The relative positions of the continents were starting to approximate their present-day configuration (Fig. 18) (Scotese, 1991; Scotese and Golonka, 1992), and the global atmospheric circulation showed features reminiscent of the modern circulation (Horrell, 1991; Patzkowsky et al., 1991).

Terrestrial plant biomes roughly comparable to those of the modern world, zoned according to latitude in a fashion broadly reminiscent of the vegetation zones of the Early Cretaceous (Ziegler et al., 1987), existed in the Maastrichtian (Horrell, 1991). Tropical ever-wet forests were present along the equator, but how widely this biome occurred is unclear (Horrell, 1991; Patzkowsky et al., 1991). Seasonally wet vegetations were widely distributed in the tropics (Horrell, 1991). Wet warm-temperate biomes occurred in both northern and southern hemispheres, and cool temperate vegetations in both polar regions (Horrell, 1991). Arid regions had become restricted in geographic extent (Hallam, 1984, 1985); the largest remaining expanse of desert was in central Asia (Horrell, 1991; Patzkowsky et al., 1991).

3.2. Geographic distribution of sauropod fossil sites

I now consider the paleogeographic occurrence of sauropod body and trace fossils. By examing the geographic distribution of skeletal and footprint sites simultaneously, it may be possible to eliminate taphonomic or other artifacts that might bias the body fossil or ichnological records by themselves. Any biogeographic signal that can be detected in both kinds of sauropod fossil record is probably more reliable than one seen only in footprint or bone sites. My analysis is done for the Early, Middle, and Late Jurassic, and also the Early and Late Cretaceous. I recognize that these stratigraphic intervals were of unequal duration, but the uncertain age of many terrestrial vertebrate assemblages makes any temporal breakdown of sites other than the one employed here problematic. I followed Weishampel (1990) in assigning sites to the five stratigraphic subdivisions used here. Paleogeographic locations of sites were estimated from maps published by Scotese and Golonka (1992). Geographic data on dinosaur body and trace fossil sites are taken from Weishampel (1990), with additional site information from Hendricks (1981), Fischer et al. (1988), Moratalla et al. (1988), Casanovas Cladellas et al. (1989), Dejax et al. (1989), DeCourten (1990), Calvo (1991), and Salgado and Bonaparte (1991).

3.2.1. Early Jurassic (Hettangian-Toarcian)

Vulcanodontid sauropods are known from Zimbabwe, Germany, India, and China, and brachiosaurids from China; additional indeterminate sauropod material
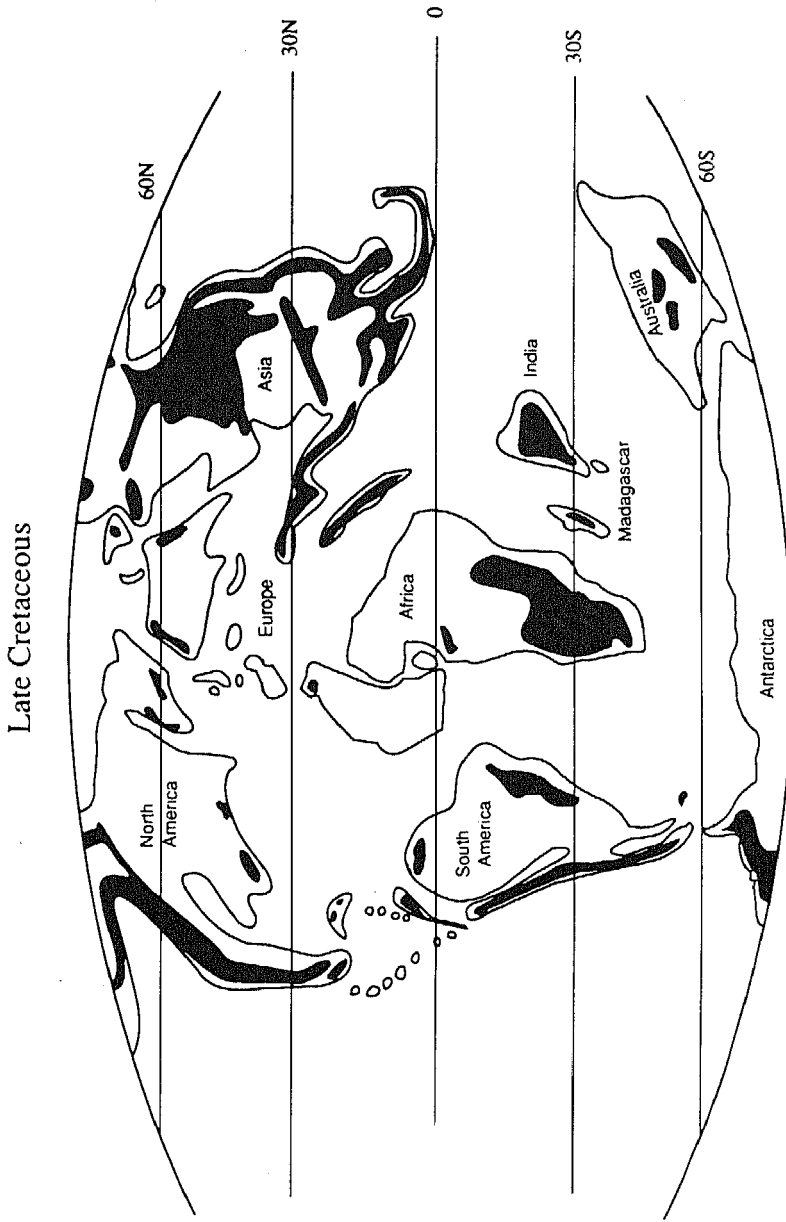
Fig. 18: Reconstruction of the Late Cretaceous (Maastrichian) continents. Color shadings as in Fig. 11. Redrawn from Scotese and Golonka (1992).

has been found in Morocco. Possible sauropod tracksites occur in Morocco (see section 1) and Afghanistan. The Afghan, German, and Moroccan sites were located near the edge of Tethys, but not in regions that received monsoonal rains; these were probably areas that had low rainfall (Parrish et al., 1982; Hallam, 1985). The Zimbabwean site was also in a dry region, and one that may as well have experienced extreme temperatures over the annual cycle (Crowley and North, 1991). The Chinese and Indian sites were in portions of Pangaea that Parrish et al. (1982) infer to have had low rainfall, but that Hallam (1985) thought were seasonally wet. All of these Early Jurassic sauropod sites seem to have been in areas that were at least seasonally dry, but that is not very surprising, given the likely occurrence of dry conditions over much of Pangaea.

3.2.2. Middle Jurassic (Aalenian-Callovian)

Middle Jurassic sauropod (mainly cetiosaurid) sites are much more numerous than those of the Early Jurassic. There is, however, a significant geographic bias in the data; most Middle Jurassic sites are in western Europe, at sites close to 30° North paleolatitude (Fig. 15). Because of this bias, it is inappropriate to look for patterns in the geographic distribution of sauropod sites by themselves; this distribution might merely reflect artifacts in the occurrence of dinosaur bone and footprint sites more generally. A more useful approach is to examine the distribution of sauropod bone and footprint sites in comparison with sites at which bones and tracks of non-sauropod dinosaurs occur, and with the geographic distribution of all sites containing dinosaur skeletal and footprint fossils. This allows us to filter out any artifacts in the paleogeographic record of sauropod fossils of the kind just mentioned. If the distribution of sauropod sites shows any marked differences from the distribution of sites containing fossils of other kinds of dinosaurs, this might indicate the existence of real differences in the paleogeographic occurrences of sauropods that could have biological significance.

Unfortunately, no such differences are seen in the Middle Jurassic record (Fig. 19). Sauropod body fossils are most common at sites where the remains of other kinds of dinosaurs also occur. There is no suggestion of any latitudinal separation between ornithopod and sauropod sites.

The only potential sauropod tracksite occurs at very high latitude in the Southern Hemisphere, but the putative sauropod track from this locality does not look very sauropod-like (Molnar [1991: fig. 37E]), and I suspect that it was made by some other kind of quadrupedal dinosaur. Therefore the high-latitude sauropod footprint occurrence shown in Fig. 19 is very questionable.

3.2.3. Late Jurassic (Oxfordian-Tithonian)

Late Jurassic sauropod sites are abundant and widespread, occurring in North America, Europe, China, southeast Asia, South America, India, and Africa. The
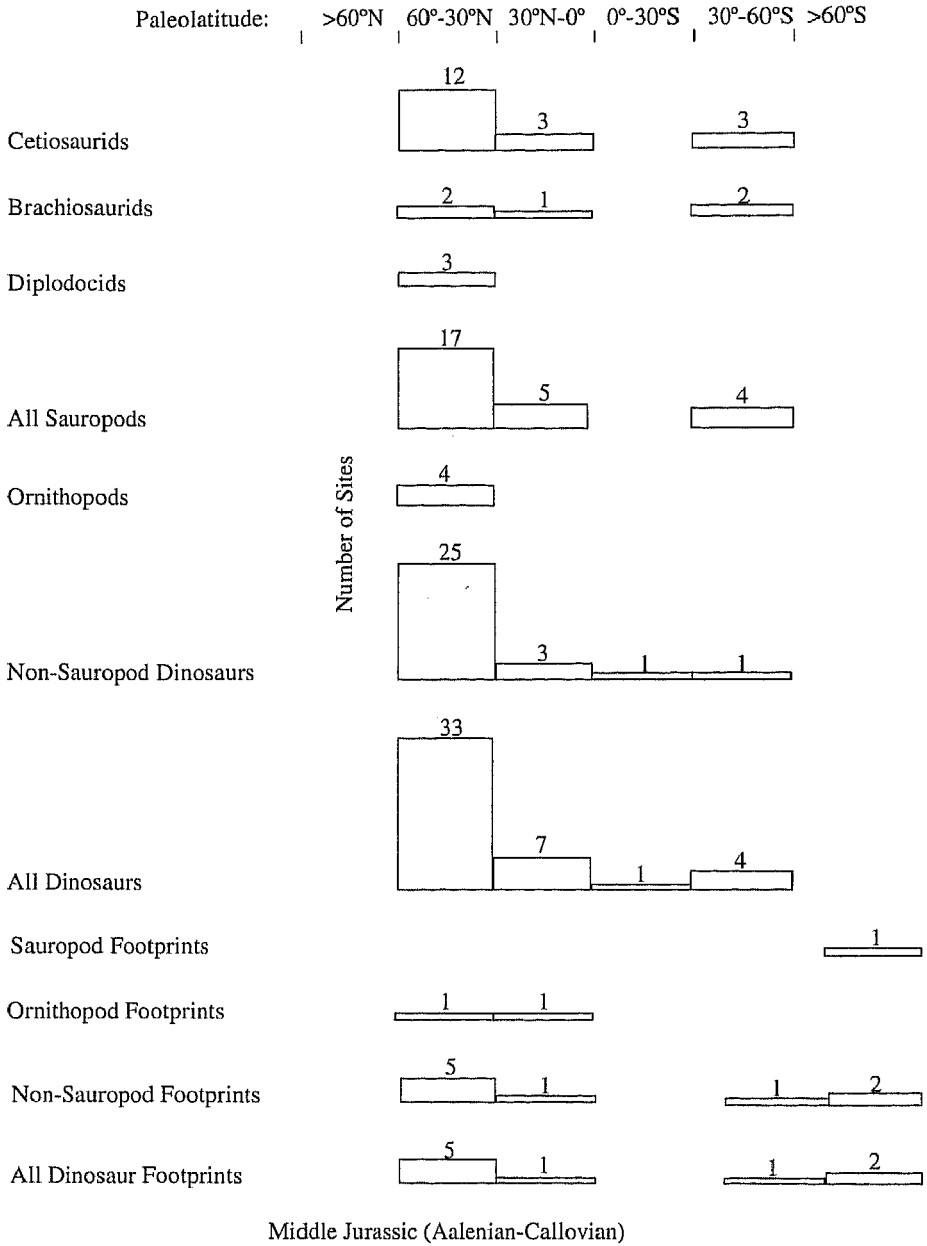
Fig. 19: Counts of the number of Middle Jurassic skeletal and footprint sites in which sauropods and other dinosaur groups occur, as a function of paleolatitude.

classic Morrison Formation localities in western North America occur in a region (Fig. 16) that was probably at least seasonally dry, and the same may have been true of some of the Chinese sites (Bilbey et al., 1974; Dodson et al., 1980; Parrish et al., 1982; Hallam, 1984, 1985; Dodson, 1990; Turner and Fishman, 1991; Bilbey, 1992; Moore et al., 1992). European and Indian sites may have been wetter, and the Tendaguru dinosaur beds in eastern Africa may have accumulated under conditions in which water was abundant at least on a seasonal basis (Parrish et al., 1982; Moore et al., 1992; cf. Russell et al., 1980). Sauropod sites in Thailand probably experienced monsoonal conditions (Parrish et al., 1982; Moore et al., 1992).

As with the Middle Jurassic, there is no obvious difference between the latitudinal distribution of sauropod and other dinosaur bone and footprint sites (Fig. 20), although it is probably significant from a biogeographic standpoint that the only titanosaurid localities are in the Southern Hemisphere (see below). Sauropods and ornithopods frequently occur at the same localities. The greatest diversity of sauropods (in terms of number of presently recognized taxa) occurs in the Morrison Formation (between 0° and 30° North paleolatitude), the Shangshaximiao Formation of China (between 30° and 60° North paleolatitude-although I am less confident about my paleolatitude determinations for Mongolian and Chinese than most other sites), and the Tendaguru Beds of Tanzania (close to 30° South paleolatitude). There is thus no clear latitudinal pattern in the peak diversity of sauropods, and the diversity of other dinosaur groups shows no obvious latitudinal difference from that of sauropods.

I can recognize no paleoclimatic or other factor that restricted the geographic distribution of sauropods as a group, whatever the factors that might have influenced the occurrence of individual species.

3.2.4. Early Cretaceous (Berriasian-Albian)

Sauropod bone and footprint localities are known from North America, Europe, Mongolia, China, Korea, South America, Africa, and Australia. Representatives of all five non-vulcanodontid sauropod families recognized by McIntosh (1990) occur in the Wealden and equivalent faunas of western Europe, found in sediments that accumulated in rather humid environments (Hallam, 1984, 1985; Ziegler et al., 1987). In contrast, some of the Chinese, African, and South American sauropods may have lived in seasonally dry, savanna-like situations, or even desert environments (Ziegler et al., 1987; Leonardi, 1989). Most presently-known sauropod tracksites occur at low paleolatitudes, between 30° North and South, while ornithopod tracksites are prevalent at higher latitudes in the Northern Hemisphere (Fig. 21), in accord with Lockley's hypothesis. However, sauropod skeletal sites, even though they peak at 0°-30° North, show little latitudinal difference from ornithopod or "all-dinosaur" skeletal sites. The greatest diversity of sauropods occurs at sites from the Wealden of England (30°-60° North paleolatitude), and also at sites close to the paleoequator in Africa. The Wealden sites also have many ornithopod taxa. There
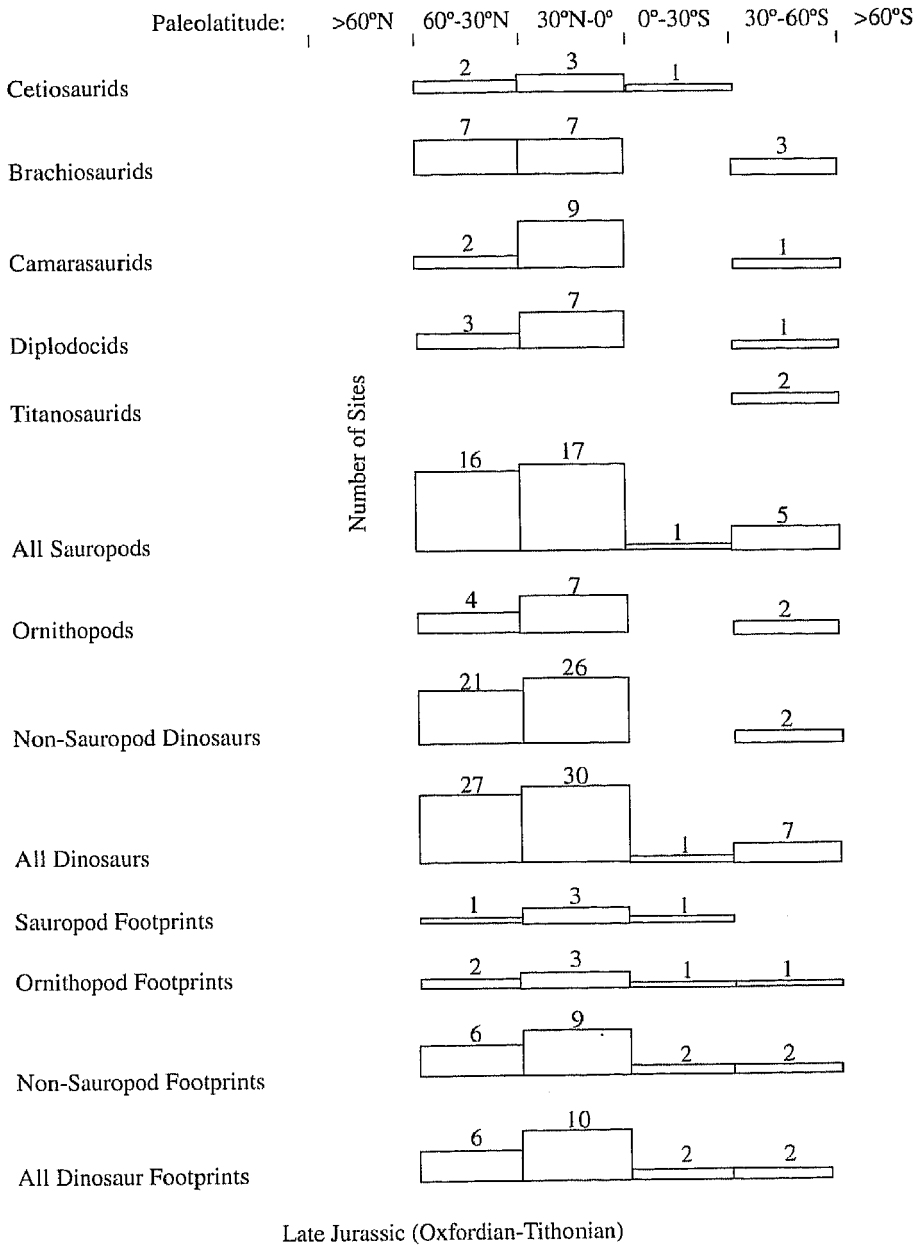
Fig. 20: Counts of the number of Late Jurassic skeletal and footprint sites in which sauropods and other dinosaur groups occur, as a function of paleolatitude.
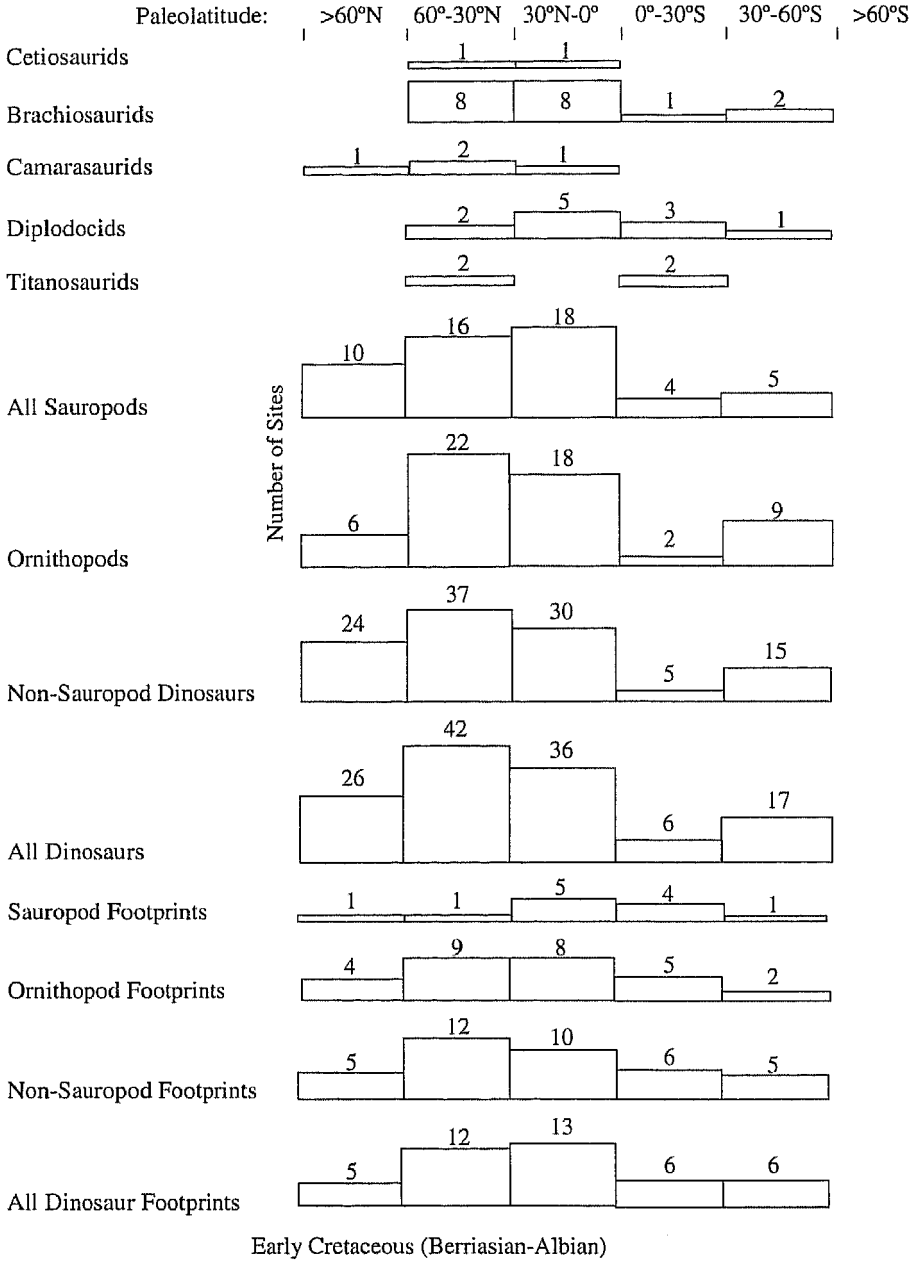
Fig. 21: Counts of the number of Early Cretaceous skeletal and footprint sites in which sauropods and other dinosaur groups occur, as a function of paleolatitude.

is therefore no obvious difference in the latitudinal occurrences of peak diversity between sauropods and other dinosaur groups.

3.2.5. Late Cretaceous (Cenomanian-Maastrichtian)

The Late Cretaceous skeletal record of sauropods is dominated by titanosaurids, which are known from sites in North America, Europe, central Asia, southeast Asia, Africa, Madagascar, India, and South America. As for the Early Cretaceous, Late Cretaceous sauropod localities occur both in what were relatively wet and what were fairly dry regions (Horrell, 1991; Patzkowsky et al., 1991). Most presently-known dinosaur skeletal and footprint sites are in the Northern Hemisphere, a pattern also shown by ornithopod skeletal and footprint sites alone (Fig. 22). Sauropod bone sites are also most common in the Northern Hemisphere, but show a second peak at middle latitudes of the Southern Hemisphere; for titanosaurids alone, there are slightly more Southern than Northern Hemisphere sites. Given that this second, southern peak does not occur so strongly in the ornithopod or "all-dinosaur" distributions, it is probably a real biogeographic signal that indicates the relatively greater importance of sauropods, and titanosaurids in particular, in Late Cretaceous dinosaur faunas of the Southern than of the Northern Hemisphere. This conclusion is bolstered by diversity patterns; ornithopods (particularly hadrosaurids) are extraordinarily diverse in the Late Cretaceous of Asiamerica, where sauropods are usually absent or uncommon (cf. Lucas and Hunt, 1989; Holtz 1992; the Nemegt Formation of Mongolia is a notable exception to this generalization-Osmólska, 1980), and titanosaurids are very diverse in faunas from India, South America, and even eastern Europe (although the great diversity of titanosaurids may in part be the artifact of an over-split taxonomy; McIntosh, 1990).

3.2.6. Paleogeographic occurrence of sauropod sites: conclusions

Whatever the features that limited the geographic distributions of individual sauropod species, sauropods as a group were too diverse to permit simple characterization of their occurrences in terms of paleogeography or paleoclimatic regimes. Sauropods occurred in both wet and dry regions, at low, middle, and even high paleolatitudes. Lockley's (1991) hypothesis of a latitudinal separation of sauropods and ornithopods is unsupported for Jurassic footprint and bone sites, weakly supported for Early Cretaceous sites, and strongly supported by the Late Cretaceous separation of titanosaurid and ornithopod sites. However, the Late Cretaceous pattern is not so much one of high-latitude ornithopods and low-latitude sauropods, but rather of Asiamerican ornithopod-dominated faunas and Southern Hemisphere faunas in which titanosaurids were prevalent. Holtz (1992) takes this even further, suggesting that Late Cretaceous dinosaur faunas of Asiamerica were atypical, reflecting the development of this landmass as an island continent isolated from the
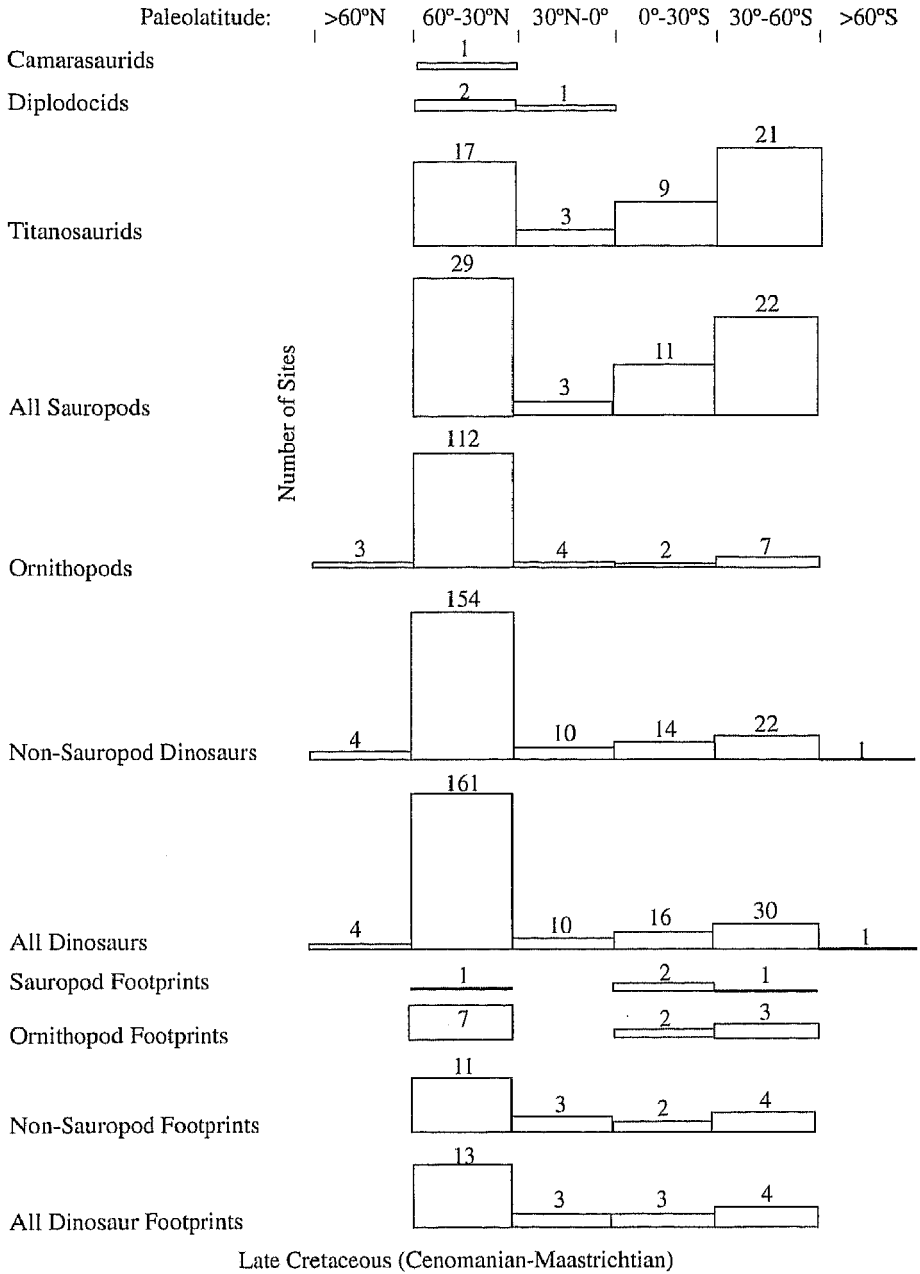
Fig. 22: Counts of the number of Late Cretaceous skeletal and footprint sites in which sauropods and other dinosaur groups occur, as a function of paleolatitude.

rest of the world. The results of my analysis are consistent with Holtz' interpretation.

3.3. Paleoenvironmental distribution of sauropod fossil sites

In addition to proposing a latitudinal separation of ornithopod-dominated assemblages and those in which sauropods were common, Lockley (1991:112) suggested that "Cretaceous ornithopod-dominated communities evolved an ecological preference for well-vegetated, humid, coastal plain environments. By contrast the sauropoddominated track assemblages are usually characterized by a high proportion of theropod tracks but a distinct lack of ornithopod tracks. Moreover, they usually occur in environments that represent limy and salty lakes and coastal lagoons". This conclusion was based on work summarized in Leonardi (1989) and Lockley and Conrad (1989). Lockley (1991) contrasted tracksites from the Wealden of England, the Enciso Group of Spain, and the Gething Group and the Dakota, Mesaverde, and Laramie beds of North America, where ornithopod tracks are common and sauropod prints rare or absent, with tracksites from the Glen Rose Formation of Texas and the Toro-Toro beds of Bolivia, where sauropod prints are common and ornithopod tracks rare. In other ichnofaunas, like those of the Sousa beds of Brazil and the Jindong beds of Korea, sauropod and ornithopod tracks occur at the same sites, but usually not in the same track layers.

Interpretation of the habitat preferences of sauropods on the basis of the occurrence of bone or footprint sites is complicated by geographic considerations of the kind already discussed. For example, the absence of sauropods in many coastal plain faunas from pre-Maastrichtian Late Cretaceous units of western North America may be due to sauropod extinction in this region after the Albian, rather than the lack of favored sauropod habitats (Lucas and Hunt, 1989; McIntosh et al., 1992). We must compare paleoenvironmental situations in which sauropods are common or uncommon for regions and times when sauropods are known to have been present.

Leonardi (1989) summarized the paleoenvironmental occurrences of South American dinosaur trackways; I re-tabulated his data for the Early and Late Cretaceous, the geologic intervals with the largest samples of dinosaur trackways (Table 1). However, I changed the interpretation of the kinds of trackmakers represented and the paleoenvironment of one site (Baños del Flaco) from those given by Leonardi to the interpretations of M.G. Lockley (written communication; see also Santos et al., in press).

Leonardi concluded that sauropods were most common in fluvial, lacustrine, and marginal marine situations. It must be noted, however, that dinosaur tracksites formed in these environments are more common than those from other situations, and that these are among the environments in which footprints are most likely to be preserved. Consequently there may be a significant preservational artifact in Leonardi's data.

There may be an artifact due to sauropod behavior as well. Many authors have concluded that some sauropod species were gregarious on the basis of footprint

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Table 1: Counts of the number of dinosaur trackways from sites representing various paleoenvironments from the Cretaceous of South America. Identification of paleoenvironments follows those of the author. Data from Leonardi (1989)

	Arid	"Semi-Arid Continental"	Semi-Arid Fluvial	Semi-Arid Lacustrine	Marine Platform
Early Cretaceous:					
Theropods	3		62	228	4
Sauropods			13	9	3
Ornithopods			13	21	
Unidentified Dinosaurs			12+	1	
Total Number of Trackways	3		100+	259	7+
Number of Tracksites	2		·7	11	1
Late Cretaceous:					
Theropods	1	2			101+
Sauropods					8
Ornithopods		1			c. 4
Unidentified Dinosaurs					2
Total Number of Trackways	1	3			c. 115
Number of Tracksites	1	1			3

Assignment of sites to paleoenvironments: **Arid**: Cianorte, Indianópolis, Plottier. **"Semi-Arid Continental"**: El Chocón. **Semi-Arid Fluvial**: São Domingos, Antenor Navarro Formation, Piranhas Formation, São Romão, Cabeça de Negro. **Semi-Arid Lacustrine**: Sousa Formation. **Marine Platform**: Baños del Flaco, Quebrada de la Escalera, Toro-Toro, Parotani.

evidence (Kaever and Lapparent, 1974; Bird, 1985; Lockley et al., 1986; Farlow, 1987; Fischer et al., 1988; Lockley, 1991), a conclusion consistent with the taphonomy of sauropod skeletal assemblages (Dodson et al., 1980; Dodson, 1990). Leonardi (1989) likewise inferred that sauropods were herding animals on the basis of his tracksites. It is therefore possible that the dispersion of sauropods in Mesozoic ecosystems was rather clumped, due to the gregarious behavior of these dinosaurs. The absence of sauropod footprints at any particular site may frequently have been a function of chance-the fact that a sauropod herd did not happen to be in the vicinity when a bedding surface was collecting tracks-rather than due to the absence of sauropods from that environment. Consequently a tabulation of the environmental breakdown of the number *of sites* at which sauropod footprints (and skeletal remains?) occur, rather than a breakdown of the number of sauropod *trackways* in different palæoenvironments, might provide the most informative basis for speculation about sauropod habitat preferences.

The total number of Cretaceous sites in Leonardi's sample is small, and the number of sites at which sauropod trackways occur is even smaller. Sauropod tracks

occur at 2 of the 7 sites that Leonardi identified as occurring in semi-arid fluvial environments, and at 2 of the 4 of the marine platform sites. Leonardi did not report the breakdown of trackways by individual site for his semiarid lacustrine, Sousa Formation localities. Given the possible artifacts already described, Leonardi's data-even consituting as large a sample of trackways as they do-may not be adequate for identifying sauropod habitat preferences.

Even so, comparison of the footprint and skeletal records of sauropods permits tentative conclusions about the habitat preferences of at least some sauropod species. Sauropod remains are common over a wide geographic extent in the Morrison Formation of western North America. Sauropod bones (many found in partially articulated skeletons) are common in all lithofacies (Dodson et al., 1980), and sauropods are among the most abundant dinosaurs in the Morrison fauna, although this might in part reflect a sizerelated taphonomic bias in favor of these immense reptiles (Dodson et al., 1980; Coe et al., 1987). Sauropod trackways are also abundant at some sites (Lockley et al., 1986; Prince and Lockley, 1989). In contrast, ornithopod skeletons and trackways are less common in the Morrison Formation (Dodson et al., 1980; Coe et al., 1987; Prince and Lockley, 1989 [contra Lockley et al., 1986]).

The most important herbivores in the Early Cretaceous Cloverly Formation of the western United States were the ankylosaur Sauropelta and the ornithopod Tenontosaurus (Dodson et al., 1980). However, these dinosaurs tend not to occur together; Tenontosaurus occurs in "plant-rich sediments of swampy aspect" (Dodson et al., 1980:92), while Sauropelta is found in sediments that accumulated under drier conditions. The rare occurrences of Cloverly sauropods are in found in association with Sauropelta (Dodson et al., 1980); both Ostrom (1970) and Langston (1974) felt that sauropods were much less important members of the Cloverly fauna than were ornithopods and ankylosaurs.

Although sauropod skeletal remains occur in the Early Cretaceous Wealden beds of England, they often consist of isolated elements, perhaps suggesting that they were transported into the Wealden's wet, coastal, depositional environments (Coombs, 1975). However, the scarcity of articulated sauropod material in the Wealden could instead be due to a smaller number of bone-rich dinosaur quarries in the Wealden beds than in the Morrison Formation (J. McIntosh, pers. com.). On the other hand, Ostrom (1970) reported his "qualitative" impression that ornithopods were about five times as abundant in the Wealden skeletal fauna as sauropods. Sauropod footprints are uncommon in Wealden or Wealden-equivalent rocks of western Europe, while footprints attributed to ornithopods are abundant (Lockley, 1991). Taken together, the skeletal and the footprint records of the Wealden are consistent with the interpretation that sauropods were less important in this humid coastal environment (see section 3.2.4) than were other kinds of dinosaurs, particularly ornithopods.

Sauropod footprints of the Glen Rose Formation of Texas occur in coastal carbonate sediments that accumulated in tidal flat and salt marsh-environments (Pittman, 1989, 1990; Bergan, 1990; Hawthorne, 1990)- Although Langston (1974) suggested that the probable trackmaker, Pleurocoelus, preferred these littoral habi-

tats, it is hard to believe that animals as big as sauropods were restricted to such situations. It seems more likely that the Glen Rose sauropod tracks were made by dinosaurs passing through shoreline environments that either were not their normal habitats (Farlow, 1987; Pittman, 1990), or were only a small portion of the habitat spectrum that they frequented.

This conclusion is supported by the occurrence of Comanchean sauropod skeletal material (including teeth) in clastic sedimentary rocks that accumulated farther away from the shoreline than did the carbonate rocks of the Glen Rose Formation (Langston, 1974; Gallup, 1989; Winkler et al., 1990), and by the occurrence of *Pleurocoelus* in other Early Cretaceous faunas (Ostrom, 1970; DeCourten, 1990). In fact, *Pleurocoelus* is the most abundant dinosaur in the Early Cretaceous Arundel Formation of Maryland (Lull, 1911; Ostrom, 1970), a unit that accumulated in a paludal setting reminiscent of the Wealden environment (Langston, 1974). However, Hatcher (1903:13) noted that "No two bones or fragments of all that material collected in the Potomac beds in Maryland were found in such relation to one another as to demonstrate that they belonged to the same individual"-a taphonomic circumstance reminiscent of the occurrence of skeletal remains of sauropods in the Wealden fauna. As with the Wealden fauna, one can therefore question whether the Arundel sauropod remains represent dinosaurs that lived in the depositional environments where their bones were preserved. Consequently the habitat preferences of *Pleurocoelus*-assuming that this dinosaur did prefer certain environments over others-are hard to identify.

Lehman (1987) recognized three major sedimentary depositional provinces in the Late Maastrichtian of western North America, each with its own characteristic dinosaur fauna. The *Leptoceratops* fauna occurred in relatively cool piedmont situations, and the *Triceratops* fauna occupied lowland coastal swamps and floodplains. The *Alamosaurus* fauna occurred in southerly, "markedly seasonal, semi-arid environments of the intermontane basins" (Lehman, 1987:189)-a situation rather like that inferred for the Morrison paleoenvironment. The titanosaurid *Alamosaurus* is a major constituent of this fauna.

The camarasaurid *Opisthocoelicaudia* and the diplococid *Nemegtosaurus* of the slightly older Nemegt Formation of Mongolia lived under climatic conditions that were "warm, subhumid and seasonal, with dry and rainy periods alternating" (Osmólska, 1980:147). Like the *Alamosaurus* fauna, the Nemegt fauna occurred in a region subject to at least seasonally dry conditions (cf. Horrell, 1991; Patzkowsky, 1991), but Osmólska's description makes the Nemegt environment sound somewhat more mesic-which may account for the abundant occurrence of hadrosaurs as well as sauropods in this unit.

In conclusion, trackway data alone do not at present provide conclusive evidence about the habitats in which sauropods were most common, given taphonomic artifacts that may be inherent in the footprint record. Combined with the skeletal record, however, the ichnological record is very informative. It is certainly intriguing

that in units which have both abundant skeletal and footprint samples, like the Morrison Formation and the Wealden beds, the two fossil records are consistent (cf. Lockley, 1991:85) in their picture of the importance of sauropods as opposed to ornithopods in the living fauna.

Although Dodson (1990:403) interpreted the fossil record of sauropods to suggest that these dinosaurs "prospered under humid conditions", with "the adaptation of Morrison sauropods to seasonally dry environments...an extreme rather than a typical situation for sauropods", my review of the skeletal and ichnological records suggests that Morrison sauropods may indeed be representative of the habitat preferences of many sauropod species. However, this does not mean that all sauropods were most abundant in seasonally dry situations; as previously noted, sauropods occur in fossil faunas that accumulated in regions that probably had wet climates, as well as places that were fairly dry. The great diversity of these dinosaurs may itself reflect the success of sauropods in adapting to a wide range of terrestrial environments.

4. ACKNOWLDEGEMENTS

5. BIBLIOGRAPHY

Baird, D., 1980. A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. In *Aspects of vertebrate history: essays in honor of Edwin Harris Colbert*. Ed. Jacobs, Museum of Northern Arizona Press, 219-230.

Barron, E.J., 1989. Studies of Cretaceous climate. In *Understanding climate change*. Ed. Berger, Dickinson, and Kidson, American Geophysical Union 52/International Union of Geodesy and Geophysics 7, 149-157.

Benton, M.J., 1990. Origin and interrelationships of dinosaurs. In *The Dinosauria*. Ed. Weishampel, Dodson, and Osmolska, Cambridge Univ. Press, 11-30.

Bergan, G.R., 1990. Nearshore clastic-carbonate facies in the Glen Rose Formation (Lower Cretaceous) in North-Central Texas. In *Nearshore clastic-carbonate fa-*

cies and dinosaur trackways in the Glen Rose Formation (Lower Cretaceous) of central Texas. Ed. Bergan and Pittman. Field Trip Guidebook 8, Geological Society of America, 1-45.

Berner, R.A., 1992. Palaeo-CO_2 and climate. *Nature*, (358), 114.

Bilbey, S.A., 1992. *Stratigraphy and sedimentary petrology of the Upper Jurassic-Lower Cretaceous rocks of the Cleveland-Lloyd Dinosaur Quarry, with a comparison to the Dinosaur National Monument Quarry,* Utah. PhD Thesis, University of Utah, 1-295.

Bilbey, S.A., Kerns, R.L., Jr., Bowman, J.T., 1974. Petrology of the Morrison Formation, Dinosaur Quarry Quadrangle, Utah. *Utah Geology Mineral Survey Special Studies 48.*

Bird, R.T., 1985. *Bones for Barnum Brown: adventures of a dinosaur hunter,* Texas Christian University Press, 1-225.

Bonaparte, J.F., 1986. The early radiation and phylogenetic relationships of the Jurassic sauropod dinosaurs, based on vertebral anatomy. In *The beginning of the age of dinosaurs. Faunal change across the Triassic-Jurassic boundary.* Ed. Padian, Cambridge Univ. Press, 247-258.

Calvo, J., 1991. Huellas de dinosaurios en la Formacion Río Limay (Albiano-Cenomaniano?), Picun Leufu, Provincia de Neuquen, República Argentina. (Ornithischia-Saurischia: Sauropoda-Theropoda). *Ameghiniana*, (28), 241-258.

Casanovas, M.L., Ezquerra, R., Fernández, A., Pérez-Lorente, F., Santafé, J.V., Torcida, F., in press. "Un grupo de sauropodos en el yacimiento Soto 2", La Rioja (España). *Zubía.* (In litt.).

Casanovas, M.L., Fernández, A., Pérez-Lorente, F., Santafé, J.V., 1989. *Huellas de dinosaurio de La Rioja. Yacimientos de Valdecevillo, La Senoba y La Virgen del Campo.* I.E.R., *Cienc. Tierra,* 1-190.

Coe, M.J., Dilcher, D.L., Farlow, J.O., Jarzen, D.M., Russell, D.A., 1987. Dinosaurs and land plants. In *The origins of angiosperms and their biological consequences.* Eds. Friis, Chaloner, and Crane, Cambridge Univ. Press, 225-258.

Coombs, W.P., Jr., 1975. Sauropod habits and habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology,* (17), 1-33.

Crowley, T.J., North, G.R., 1991. *Paleoclimatology,* Oxford Univ. Press, 1-339.

Czerkas, S.A., 1992. The new look of sauropods. *Journal of Vertebrate Paleontology* (12 supplement 3), 26A.

Daniels, C.B., Pratt, J., 1992. Breathing in long necked dinosaurs, did the sauropods have bird lungs? *Comparative Biochemistry Physiology,* (101A), 43-46.

DeCourten, F.L., 1991. The Long Walk Quarry and Tracksite: unveiling the mysterious Early Cretaceous of the Dinosaur Triangle Region. In *Guidebook for dinosaur quarries and tracksites tour, western Colorado and eastern Utah.* Ed. Averett, Grand Junction (Colorado, U.S.A., Geological Society, 19-25.

Dejax, J., Michard, J.-G., Brunet, M., Hell, J., 1989. Empreintes de pas de dinosauriens datée du Crétacé inférieur dans la Bassin Babouri-Figuil (Fossé de la Bénoué, Cameroun). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, (178), 85-108.

Dodson, P., 1990a. Sauropodomorpha. In *The Dinosauria*. Eds. Weishampel, Dodson, and Osmólska, Univ. California Press, 318-319.

Dodson, P., 1990b. Sauropod paleoecology. In *The Dinosauria*. Eds. Weishampel, Dodson, and Osmólska, Univ. California Press, 402-407.

Dodson, P., Behrensmeyer, A.K., Bakker, R.T., McIntosh, J.S., 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology*, (6), 208-232.

Dodson, P., Behrensmeyer, A.K., Bakker, R.T., 1980. Taphonomy of the Morrison Formation (Kimmeridgian-Portlandian) and Cloverly Formation (Aptian-Albian) of the western United States. *Mémoires Societe géologique de France N.S.*, (139), 87-93.

Dubiel, R.F., Parrish, J.T., Parrish, J.M., Good, S.C., 1991. The Pangaean megamonsoon-evidence from the Upper Triassic Chinle Formation, Colorado Plateau. *Palaios* (6), 347-370.

Dutuit, J.-M., Ouazzou, A., 1980. Découverte d'une piste de dinosaure sauropode sur le site d'empreintes de Demnat (HautAtlas marocain). *Mémoires Societe géologique de France N.S.*, (139), 95-102.

Farlow, J.O., 1987. *Lower Cretaceous dinosaur tracks, Paluxy River Valley*, Texas. South Central Section, Geological Society of America, Baylor University, 1-50.

Farlow, J.O., Hawthorne, J.M., 1989. Comanchean dinosaur. footprints. In *Field guide to the vertebrate paleontology of the Trinity group, Lower Cretaceous of central Texas*. Eds. Winkler, Murry, and Jacobs, Southern Methodist University, 23-30.

Farlow, J.O., Pittman, J.G., Hawthorne, J.M., 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the U.S. Gulf Coastal Plain. In *Dinosaur tracks and traces*. Eds. grillette and *Lockley*, Cambridge Univ. Press, 371-394.

Fischer, R., Kulle-Battermann, S., Töneböhn, R., 1988. Das "Naturdenkmal Saurierfährten Münchehagen". *Natur und Museum*, (118), 385-392.

Friese, H., Klassen, H., 1979. *Die Dinosaurierfährten von Barkhausen im Wiehengebirge. Veröffentlichungen des Landkreises Osnabrück*, Heft 1, 1-36.

Gallup, M.R., 1989. Functional morphology of the hindfoot of the Texas sauropod *Pleurocoelus* sp. indet. In *Paleobiology of the dinosaurs*. Ed. Farlow, Geological Society of America Special. Paper 238, 71-74.

Galton, P.M., 1990. Basal Sauropodomorpha-Prosauropoda. In *The Dinosauria*. Eds. Weishampel, Dodson, and Osmólska, University of California Press, 320-344.

Galton, P.M., van Heerden, J., 1985. Partial hindlimb of *Blikanasaurus cromptoni*, n. gen. and n. sp., representing a new family of prosauropod dinosaurs from the Upper Triassic of South Africa. *Geobios*, (18), 509-516.

Hallam, A., 1984. Continental humid and arid zones during the Jurassic and Cretaceous. *Palaeogeography, Palaeoclimatology, Palaeoecology*, (47), 195-223.

Hallam, A., 1985. A review of Mesozoic climates. *Journal of the Geological Society of London*, (142), 433-445.

Hatcher, J.B., 1901. *Diplodocus* (Marsh): its osteology, taxonomy, and probable habits, with a restoration of the skeleton. *Memoirs Carnegie Museum*, (1), 1-64.

Hatcher, J.B., 1903. Discovery of remains of Astrodon *(Pleurocoelus)* in the *Atlantosaurus* beds of Wyoming. *Annals Carnegie Museum*, (2), 9-14.

Haubold, H., 1986. Archosaur footprints at the terrestrial Triassic-Jurassic transition. In *The beginning of the age of dinosaurs. Faunal change across the Triassic-Jurassic boundary*. Eds. Padian, Cambridge Univ. Press, 189-201.

Hawthorne, J.M., 1990. *Dinosaur track-bearing strata of the Lampasas Cut Plain and Edwards Plateau*, Texas. Baylor Geological Studies Bull. 49, 1-47.

Hendricks, A., 1981. Die Saurierfährte von Munchehagen bei Rehburg-Loccum (NW-Deutschland). *Münster Landesmuseum Naturkunde*, Abhandlungen, (43), 3-22.

Hitchcock, E.D., 1858. *Ichnology of New England. A report on the sandstone of the Connecticut Valley, especially its fossil footmarks*. William White, 1-199.

Holtz, T.R., Jr., 1992. Endemicity analysis of global Cretaceous dinosaurian faunas. *Fifth North American Paleontological Convention*, Abstracts and Program, Chicago, 132.

Horrell, M.A., 1991. Phytogeography and paleoclimatic interpretation of the Maestrichtian. *Palaeogeography, Palaeoclimatology, Palaeoecology*, (86), 87-138.

Ishigaki, S., 1986. *Morocco no kyoryu*. Tsukiji Publ., 1-261.

Ishigaki, S., 1988. Les empreintes de dinosaures du Jurasique inférieur du Haut Atlas central marocain. *Notes du Service géologique du Maroc* (44), 79-86.

Ishiqaki, S., 1989. Footprints of swimming sauropods from Morocco. In *Dinosaur tracks and traces*. Eds. Gillette and Lockley, Cambridge Univ. Press, 83-86.

Janensch, W., 1961. Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica* Suppl., (7), 177-235.

Jenny, J., Jossen, J.-A., 1982. Découverte d'empreintes de pas de dinosauriens dans le Jurassique inférieur (Pliensbachian) du Haut-Atlas central (Maroc). *Comptes Rendus Acad. de Sciences Paris*, (294), 223-226.

Kaever, M., de Lapparent, A.F., 1974. Les traces de pas de dinosaures du Jurasique de Barkhausen (Basse Saxe, Allemagne). *Societe Géologique de France, Bulletin* (16), 516-525.

Langston, W., Jr. 1974. Nonmammalian Comanchean tetrapods. *Geoscience and Man*, (8), 77-102.

Leakey, M.D., 1987. Animal prints and trails. In *Laetoli, a Pliocene site in northern Tanzania*. Eds. Leakey and Harris, Oxford Univ. Press, 451-489.

Lehman, T.M., 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western Interior of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, (60), 189-217.

Leonardi, G., 1989. Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation. In *Dinosaur tracks and traces*. Eds. Gillette and Lockley, Cambridge Univ. Press, 165-178.

Lim, S.-K., Yang, S.-Y., Lockley, M.G., 1989. Large dinosaur footprint assemblages from the Cretaceous Jindong Formation of southern Korea. In *Dinosaur tracks and traces*. Eds. Gillette and Lockley, Cambridge Univ. Press, 333-336.

Lockley, M.G., 1990. Tracking the rise of dinosaurs in eastern Utah. *Canyon Legacy, Dan O'Laurie Museum, Moab, Utah*, (2), 2-8.

Lockley, M.G., 1991. *Tracking dinosaurs. A new look at an ancient world*. Cambridge University Press, 1-238.

Lockley, M.G., Conrad, K., 1989. The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the western USA. In *Dinosaur tracks and traces*. Eds. Gillette and Lockley, Cambridge Univ. Press, 121-134.

Lockley, M.G., Houck, K.J., Prince, N.K., 1986. North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. *Geological Society of America Bulletin*, (97), 1163-1176.

Lockley, M.G., Rice, A., 1990. Did *"Brontosaurus"* ever swim out to sea?: evidence from brontosaur and other dinosaur footprints. *Ichnos*, (1), 81-90.

Lucas, S.G., Hunt, A.P., 1989. *Alamosaurus* and the sauropod hiatus in the Cretaceous of the North American Western Interior. In *Paleobiology of the dinosaurs*. Ed. Farlow, Special Paper 238, Geological Society of America, 75-85.

Lull, R.S., 1911. The Reptilia of the Arundel Formation. *Maryland Geological Survey Report, Lower Cretaceous Volume*, 174-178, 183-211.

Lull, R.S., 1953. *Triassic life of the Connecticut Valley*. State of Connecticut Geological and Natural History Survey, 1-331.

McIntosh, J.S., 1990a. Sauropoda. In *The Dinosauria*. Eds. Weishampel, Dodson, and Osmólska, Univ. California Press, 345-401.

McIntosh, J.S., 1990b. *Species determination in sauropod dinosaurs with tentative suggestions for their classification*. In *Dinosaur systematics, approaches and perspectives*. Eds. Carpenter and Currie, Cambridge Univ. Press, 53-69.

Meyer, C.A., 1990. Sauropod tracks from the Upper Jurassic Reuchenette Formation (Kimmeridgian; Lommiswil, Kt. Solothurn) of northern Switzerland. *Eclogae Geologicae Helvetiae*, (83), 389-397.

McIntosh, J.S., Coombs, W.P., Jr., Russell, D.A., 1992. A new diplodocid sauropod (Dinosauria) from Wyoming, U.S.A. *Journal of Vertebrate Paleontology*, (12), 158-167.

Molnar, R.E., 1991. Fossil reptiles in Australia. In *Vertebrate palaeontology of Australasia*. Eds. Vickers-Rich, Monaghan, Baird, and Rich, Pioneer Design Studio, 605-702.

135

Moore, G.T., Hayashida, D.N., Ross, C.A., Jacobson, S.R., 1992. Paleoclimate of the Kimmeridgian/Tithonian (Late Jurassic) world: I. Results using a general circulation model. *Palaeogeography, Palaeoclimatology, Palaeoecology*, (93), 113-150.

Moratalla, J., Sanz, J.L., Melero, I., Jiménez, S., 1988. *Yacimientos paleoicnológicos de La Rioja (huellas de dinosaurio)*. Gobierno de La Rioja e Iberduero, 1-95.

Muybridge, E., 1957. *Animals in motion*. Dover Publications, 1-74.

Olsen, P.E., Padian, K., 1986. Earliest records of *Batrachopus* from the southwestern United States, and a revision of some Early Mesozoic crocodylomorph ichnogenera. In *The beginning of the age of dinosaurs. Faunal change across the Triassic-Jurassic boundary*. Ed. Padian, Cambridge Univ. Press, 259-273.

Olsen, P.E., Schlische, R.W., Gore, P.J.W. (Eds.), 1989. *Tectonic, depositional, and paleoecological history of early Mesozoic rift basins, eastern North America*. Field Trip Guidebook T351, American Geophysical Union, Washington, D.C., 1-174.

Osmólska, H., 1980. The Late Cretaceous vertebrate assemblages of the Gobi Desert, Mongolia. *Mémoires Societe géologique de France*, N.S., (139), 145-150.

Ostrom, J.H., 1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. *Peabody Museum of Natural History, Yale University, Bulletin* 35, 1-234.

Parrish, J.T., Ziegler, A.M., Scotese, C.R., 1982. Rainfall patterns and the distribution of coals and evaporites in the Mesozoic and Cenozoic. *Palaeogeoqraphy, Palaeoclimatology, Palaeoecology*, (40), 67-101.

Patzkowsky, M.E., Smith, L.H., Markwick, P.J., Engberts, C.J., Gyllenhaal, E.D., 1991. Application of the Fujita-Ziegler paleoclimate model: Early Permian and Late Cretaceous examples. *Palaeogeography, Palaeoclimatology, Palaeoecology* (86), 67-85.

Pittman, J.G., 1984. Geology of the De Queen Formation of Arkansas. *Transactions-Gulf Coast Association of Geological Societies*, (34), 201-209.

Pittman, J.G., 1989. Stratigraphy, lithology, depositional environment, and track type of dinosaur track-bearing beds of the Gulf Coastal Plain. In *Dinosaur tracks and traces*. Eds. Gillette and Lockley, Cambridge Univ. Press, 135-153.

Pittman, J.G., 1990. Dinosaur tracks and trackbeds in the middle part of the Glen Rose Formation, western Gulf Basin, USA. In *Nearshore clastic-carbonate facies and dinosaur trackways in the Glen Rose Formation (Lower Cretaceous) of Central Texas*. Eds. Bergman and Pittman, Field Trip 8 Guidebook, Geological Society of America, 1990 Annual Meeting, 47-83.

Pittman, J.G., Gillette, D.D., 1989. The Briar Site: a new sauropod dinosaur tracksite in Lower Cretaceous beds of Arkansas, USA. In *Dinosaur tracks and traces*. Eds. Gillette and Lockley, Cambridge Univ. Press, 313-332.

Prince, N.K., Lockley, M.G., 1989. The sedimentology of the Purgatoire tracksite region, Morrison Formation of southeastern Colorado. In *Dinosaur tracks and traces*. Eds. Gillette and Lockley, Cambridge Univ. Press, 155-163.

Raath, M.A., 1972. Fossil vertebrate studies in Rhodesia: a new dinosaur (Reptilia: Saurischia) from near the Trias-Jurassic boundary. *Arnoldia* (National Museums of Rhodesia) (30[5]), 1-37.

Russell, D.A., Béland, P., McIntosh, J.S., 1980. Paleoecology of the dinosaurs of Tendaguru (Tanzania). *Mémoires Societe Géologique de France*, N.S. (139), 169-175.

Salgado, L., Bonaparte, J., 1991. Un nuevo sauropodo Dicraeosauridae, *Amargasaurus cazaui* gen. et sp. nov., de la Formacion la Amarga, Neocomiano de la Provincia del Neuquen, Argentina. *Ameghiniana*, (34), 333-346.

Santos, V.S., Lockley, M.G., Moratalla, J., Galopim, A.M., in press. Europe's longest dinosaur trackway? Interpretations of Cretaceous footprints from Carenque, near Lisboa, Portugal. *Gaia. Revista de Geociencias*, Museum Nacional de Historia Natural, Portugal.

Scotese, C.R., 1991. Jurassic and Cretaceous plate tectonic reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, (87), 493-501.

Scotese, C.R., Golonka, J., 1992. *Paleogeographic atlas. PALEOMAP Progress Report 20*, University of Texas at Arlington, 1-37.

Sereno, P.C., 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology*, (11[supplement 4]), 1-53.

Sikes, S.K., 1971. *The natural history of the African elephant*. Weidenfeld and Nicolson, 1-397.

Sloan, L.C., Barron, E.J., 1990. "Equable" climates during Earth history? *Geology*, (18), 489-492.

Spotila, J.R., O'Connor, M.P., Dodson, P., Paladino, F., 1991. Hot and cold running dinosaurs: body size, metabolism and migration. *Modern Geology*, (16), 203-227.

Telles Antunes, M., 1976. *Dinossáurios Eocretácicos de Lagosteiros*. Universidad Nova de Lisboa, Ciencias de Terra, 1-33.

Thulborn, R.A., 1990. *Dinosaur tracks*. Chapman and Hall, 1-410.

Turner, C.E., Fishman, N.S., 1991. Jurassic Lake T'oo'dichi': a large alkaline, saline lake, Morrison Formation, eastern Colorado Plateau. *Geological Society of America Bulletin*, (103), 538-558.

Vakhrameev, V.A., 1991. *Jurassic and Cretaceous floras and climates of the Earth*. Cambridge Univ. Press, 1-318.

Valenzuela, M., García-Ramos, J.C., De Centi, C.S., 1988. Las *Huellas de Dinosaurios del Entorno de Ribadesella*. Central Lechera Asturiana, 1-35.

Weishampel, D.B., 1990. Dinosaurian distribution. In *The Dinosauria*. Eds. Weishampel, Dodson, y Osmólska, Univ. California Press, 63-139.

Wild, R., 1991. *Janenschia* n. g. *robusta* (E. Fraas 1908) pro *Tornieria robusta* (E. Fraas 1908) (Reptilia, Saurischia, Sauropodomorpha). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 173, 1-4.

Winkler, D.A., Murry, P.A., Jacobs, L.L., 1990. Early Cretaceous (Comanchean) vertebrates of central Texas. *Journal or vertebrate Paleontology*, (10), 95-116.

Winterer, E.L., 1991. The Tethyan Pacific during Late Jurassic and Cretaceous times. *Palaeogeography, Palaeoclimatology, Palaeoecology*, (87), 253-265.

Zhang Y. 1988. *The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan. Vol. 3. Sauropod dinosaurs (I). Shunosaurus.* Sichuan Publishing House of Science and Technology, Chengdu, China, 1-90.

Ziegler, A.M., Raymond, A.L., Gierlowski, T.C., Horrell, M.A., Rowley, D.B., Lottes, A.L., 1987. *Coal, climate and terrestrial productivity: the present and early Cretaceous compared. In Coal and coal-bearing strata: recent advances.* Ed. Scott., Geological Society Special Publication, 25-49.