



## ***The Late Triassic sauropod track record comes into focus: Old legacies and new paradigms***

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## THE LATE TRIASSIC SAUROPOD TRACK RECORD COMES INTO FOCUS: OLD LEGACIES AND NEW PARADIGMS

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**Abstract.**—Vertebrate tracks assigned to the ichnogenera *Tetrasauropus* and *Pseudotetrasauropus* (cf. *Otozoum*) have traditionally been attributed to robust and gracile prosauropods, respectively. Based on track morphology, we propose that the former ichnogenus (*Tetrasauropus*), as represented in the uppermost Triassic (Norian-Rhaetian) of western North America, and other regions, can be attributed to the Sauropoda. The suggestion that sauropod tracks exist in the Upper Triassic is no longer at variance with the body fossil record, as it was until recently. Previous failure to attribute *Tetrasauropus* to the Sauropoda provides a good example of the reluctance of ichnologists to make interpretations that do not concur with the skeletal record. While such caution is advisable in the still-specialized and immature science of vertebrate ichnology, it may also lead us to misinterpret important, even abundant, ichnological evidence that is easily accessible. Hindsight has revealed many other instances of the predictive potential of ichnology, and the reluctance of mainstream paleontology to accept predictions that have not been absolutely confirmed by osteological evidence.

Parallel evolutionary trends towards larger size in theropod tracks (e.g., *Grallator*), prosauropod tracks (*Pseudotetrasauropus* and *Otozoum*) and presumed sauropod tracks (*Tetrasauropus* and *Brontopodus*, or *Brontopodus*-like ichnotaxa) suggest that the interpretations proposed here are the most parsimonious and internally consistent. They indicate a convergent unfolding of evolution among all saurischian clades during the Late Triassic into the Jurassic.

### INTRODUCTION

It has long been known that the tracks of dinosaurs and other vertebrates may occur in strata that lack body fossils. In fact, skeletal remains of a particular trackmaker, known only from some corresponding ichnospecies (or higher ichnotaxon) designation, may be completely unknown in the body fossil record. This has been referred to as the "Cinderella syndrome" (Lockley, 1998). Similarly, because tracks are often abundant, particular types may occur in strata that predate the earliest skeletal remains that have been reliably attributed to corresponding skeletal forms.

This seems to have happened in the case of various sauropodomorph track types from South Africa and North America, and we reinterpret a number of tracks assigned to "prosauropod ichnotaxa" as sauropodan. Our conclusions are based on a number of lines of evidence, including the discovery of body fossils of true sauropods in the Triassic (Buffetaut et al., 2000). However, equally important from the ichnological perspective is that, despite a significant literature that assumes a prosauropod affinity for the tracks, based on age and size, the track types in question (ichnogenus *Tetrasauropus sensu lato*) show morphological features of true sauropod tracks. Therefore, they cannot be considered prosauropodan (or "pre-sauropodan") without taking the unwarranted step of proposing a hypothetical sauropod-like, non-sauropodan trackmaker that coexisted with the earliest true sauropods. It is true that large prosauropods like *Riojasaurus* may have been the trackmakers, but this assumption simply postulates more sauropod-like (large) and less sauropod-like (small) forms (VanHeerden, 1997), still leaving open the question of whether there is also a record of true sauropod tracks at this time.

Other lines of evidence that support the interpretation of at least the North American *Tetrasauropus* trackmakers as sauropods is their small size, in comparison to post-Triassic sauropod tracks, and their co-occurrence with other small saurischians (theropods and true prosauropods). However, all three saurischian

groups show consistent and convergent trends in increasing maximum size during the latest Triassic and earliest Jurassic.

The implications of these conclusions are twofold. First, in a strictly paleontological sense, we learn an object lesson about our reluctance to accept track evidence, no matter how abundant or compelling, unless it is backed up by the corresponding skeletal evidence of matching trackmakers, in strata of the same or similar age (Lockley, 1998, 1999a). Indeed, we may now conclude that the track evidence of Late Triassic sauropods has been staring us in the face for some time, and that despite mentioning or hinting at the possibility of such interpretations (Ellenberger, 1972; Conrad et al., 1987), the main reason for our reluctance to advance such conclusions has been the lack of corresponding skeletal remains.

Second, in a more general sense we must recognize that such instances of "reinterpretation" point to various inherent biases in science. Mainstream paleontology generally regards the hard "material" evidence of skeletal remains as reliable and views "soft," ichnological evidence as ambiguous and unreliable, despite repeated examples of track discoveries (e.g., *Chirotherium*) that are retrospectively acknowledged as prophetic and highly significant. Further examples are given in the discussion below. For these reasons we tend to approach the objects of our study with excessive skepticism. Although the inherent nature of track evidence requires a certain caution, too often such restraints create self-fulfilling prophecies and we fail to appreciate fully what the track evidence has to offer. This paper aims to rectify one such oversight.

### HISTORY OF RESEARCH

Although the possibility of Upper Triassic sauropods had been speculated upon, based on cladistic extrapolations (e.g., Wilson and Sereno, 1998; Upchurch, 1993), it has not been proven with actual fossils until comparatively recently (Buffetaut et al., 2000). The existence of Upper Triassic prosauropods, and their tracks,

however, has been known for some time. Even the famous *Chirotherium* ichnites, discovered in Europe during the 1820s and 1830s, were interpreted as prosauropodan (by Baron von Nopsca) despite being incompatible morphologically and, as we now know, too old: i.e., Early to Middle Triassic in age (see Lockley and Meyer, 2000 for recent summary). This interpretation left us with the legacy of perceiving a relationship between prosauropods and chirothere tracks (Olsen and Galton, 1984; Conrad et al., 1987; VanHeerden, 1997). Such perceptions are understandable given that various chirothere and chirothere-like tracks are found throughout the Triassic, and overlap the time range of well-known Late Triassic prosauropods such as *Plateosaurus*.

The first serious study of Upper Triassic track successions in which abundant sauropodomorph tracks occur was conducted by Ellenberger (1972, 1974) in southern Africa. Due to the remote location of most of his sites, the publication of his main work (in French), in an obscure monograph series, and the unproven assumption that his description of these ichnofaunas was "oversplit" (Olsen and Galton, 1984), many of his conclusions have been ignored or not taken as seriously as they deserve (Lockley and Meyer, 2000). Subsequent work, particularly in North America (Lockley and Hunt, 1995; Lockley et al., 2000), but also in Europe (Lockley et al., 1996; Lockley and Meyer, 2000), confirms the validity of much of Ellenberger's work. More important than the possibility of different interpretations is the need to take the actual track evidence seriously and study it as objectively as possible. This is what we have attempted to do in the sections that follow.

Among the most significant of Ellenberger's conclusions were those that pointed to the widespread distribution of sauropodomorph trackmakers in the Late Triassic and Early Jurassic. He described *Sauropodopus* (Ellenberger, 1972, p. 73), which, as the name implies, is a relatively large track (pes length 26 cm) of possible sauropodan affinity, though this was questioned by Olsen and Galton (1984) and Lockley and Meyer (2000, p. 87-89). Ellenberger (1972, p. 88-91) also described *Deuterosauropodopus*, a larger trackmaker (pes length 40 cm) that he considered better adapted to quadrupedal progression than *Sauropodopus*. Thulborn (1990) included *Deuterosauropodopus* (but not *Sauropodopus*) in his catalog of miscellaneous tracks attributed to sauropods.

Of much greater interest are the two related ichnogenera, *Tetrasauropus* and *Pseudotetrasauropus* (Ellenberger, 1972), both of which have been widely accepted as probable examples of prosauropod/sauropodomorph tracks and recognized in both North America and Europe (Thulborn, 1990; Lockley and Hunt, 1995; Lockley et al., 1996, 2000; Hunt et al., 2000; Gand et al., 2000; Lockley and Meyer, 2000). In general, *Tetrasauropus* was made by a quadrupedal animal with large fleshy feet (pes length 44 cm), in which only the distal ends of the digits (claws) are separate from the plantar surface of the foot. In contrast, *Pseudotetrasauropus* represents a predominantly bipedal animal that had all pes digits widely separated and characterized by distinctive digital pads (Fig. 1). Ellenberger (1972, p. 59) noted that *Pseudotetrasauropus* is very similar to the probable prosauropod ichnogenus *Otozoum* from the Lower Jurassic (see Olsen and Galton, 1980; Thulborn, 1990; and Lockley and Meyer, 2000 for further

re-evaluation of this material). A smaller track of this same general type was assigned by Ellenberger (1972) to the ichnogenus *Kalosauropus* (Lockley and Meyer, 2000, p. 91-93).

Although the ichnological community has limited access to the original South African specimens, some replicas are available in the University of Montpellier collections, and it is now clear that *Pseudotetrasauropus* (which is similar to *Otozoum*) is a good match for the prosauropod foot. Digit I in this ichnogenus is shorter, and usually much less deeply-impressed than digits II-IV. In contrast, in *Tetrasauropus* digits I, II and III are almost equally large and pronounced, as is typically seen in the tracks of later (Jurassic and Cretaceous) sauropods. In an attempt at standardization, the two ichnogenera *Tetrasauropus* and *Pseudotetrasauropus* have been applied to purported sauropodomorph tracks from North America and Europe (Lockley and Hunt, 1995; Lockley et al., 1996, 2000). However, due to the lack of skeletal evidence, it was assumed that they represent robust and gracile prosauropods, respectively. As indicated below, further examination of the abundant material now available suggest that the robust, fleshy forms are better assigned to true sauropods.

Baird (1980) described the trackway of a small quadruped from the Navajo Sandstone (Lower Jurassic) of Arizona as an example of a prosauropod trackway and named it *Navahopus*. He made much of the purported impression of a large pollex claw characteristic of prosauropods. Some authors (e.g., Olsen and Galton, 1984; Thulborn, 1990) have accepted the purported pollex claw impression as evidence of prosauropod affinity. Others, however, including ourselves, have not. The claw impression is by no means clearly a morphological feature, and as pointed out by Lockley and Hunt (1995), the trackway is typical of mammal-like reptiles, whose footprints are the dominant type in the Navajo dune facies. As noted below, the introduction of this name, and its subsequent use by Olsen and Galton (1984), has led to various ichnotaxonomic complications.

Prior to our present claim that Upper Triassic *Tetrasauropus* tracks from western North America are sauropodan in origin, the oldest tracks attributed to sauropods from North America were those reported by Foster et al. (2000) from a poorly-dated (?late Middle or ?early Late Jurassic) part of the Entrada Formation, near Escalante, Utah. Elsewhere in the world the oldest tracks attributed to sauropods include examples from the Lower Jurassic of Morocco (Jenny and Josen, 1982; Ishigaki, 1988) and from the Lower Jurassic of Italy (Lanzinger and Leonardi, 1991; Leonardi and Avanzini, 1994).

## ICHNOTAXONOMIC USAGE

When first studied in North America, the tracks (up to about 30 cm long) that we now assign to *Tetrasauropus* and which "at first sight...resemble those of small sauropods." (Fig. 2; Conrad et al., 1987, p. 132) were tentatively assigned to the ichnogenus *Chirotherium*. This error was based more on interpretation of the manus than on pes morphology. As pointed out by H. Haubold (personal communication, 1997), *Chirotherium* pes digits are straight and not curved outward as in *Tetrasauropus*. Conrad et al. (1987) also suggested that the tracks might have been made

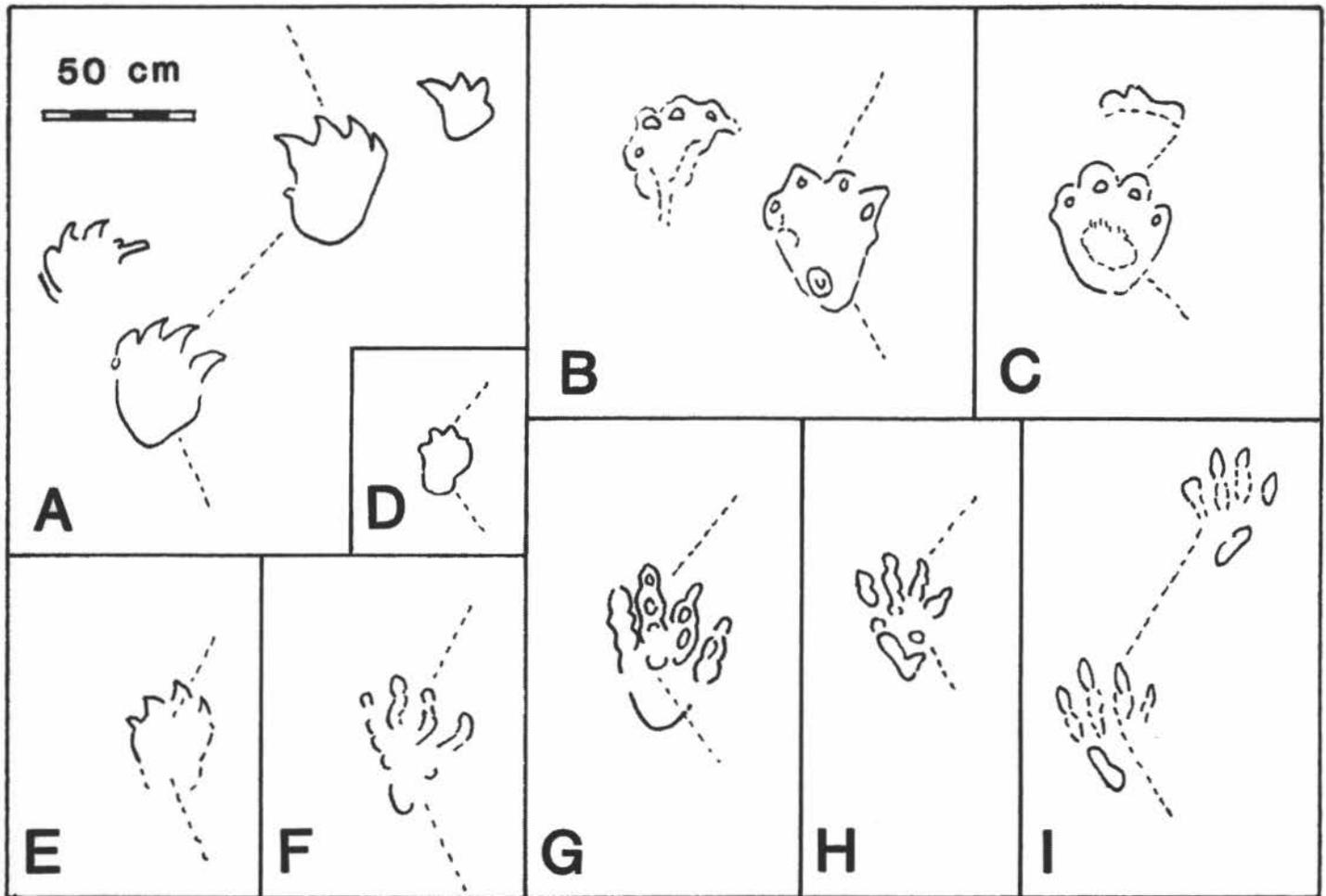


FIGURE 1. *Tetrasauropus* and *Pseudotetrasauropus* tracks, based on type specimens from southern Africa after Ellenberger (1972). Note that the latter ichnogenus resembles *Otozoum* (redrawn after Lockley and Meyer, 2000). A. *Tetrasauropus unguiferous*, B. *Pseudotetrasauropus jaquesi*, C. *P. elegans*, D. *P. dulcis*, E. *P. acutungis*, F. *P. angustus*, G. *P. mekalingensis*, H. *P. bidedoidea*, I. *Otozoum*.

by phytosaurs, because they were abundant on an exposure of exhumed fluvial channel deposits.

As more of these tracks came to light, and their similarity to *Tetrasauropus* became apparent, Lockley and Hunt (1995, p. 91) explicitly asked "What do prosauropod tracks look like?" and concluded that the label *Chirotherium* was questionable and best replaced by *Tetrasauropus* – implying sauropodomorph rather than phytosaur affinity. At the same time it became clear that the ichnogenus *Pseudotetrasauropus* was also common in North America and that it too was of probable prosauropod affinity, and similar to younger (Early Jurassic) *Otozoum*. One of the most significant differences between the South African and North American assemblages, besides the greater ichnotaxonomic diversity generated by Ellenberger's liberal naming procedures, is that both *Tetrasauropus* and *Pseudotetrasauropus* are generally represented by smaller forms in North America.

A further level of complexity was added to the prosauropod tracks debate when Baird (1980) described *Navahopus* as a prosauropod track. This caused Olsen and Galton (1984) to consider "*Tetrasauropus* a synonym of *Navahopus* and although the former has historical priority (they) erected the ichnofamily Navahopidae

to accommodate both ichnogenera" (Lockley et al., 1996, p. 36). We consider this conclusion untenable because *Navahopus* is evidently the track of a mammal-like reptile similar to *Brasilichnium* (Lockley and Hunt, 1995). It is not morphologically similar to *Tetrasauropus*, nor does it originate from deposits of the same age.

One of the most significant implications of regarding *Tetrasauropus* as a probable sauropod track is that we are encouraged to compare it with well-known sauropod tracks such as *Brontopodus* (Fig. 3; Farlow et al., 1989). This raises the possibility that *Brontopodus* could be a junior synonym of *Tetrasauropus* (Ellenberger, 1972). However, as discussed below, although the similarities are marked, especially in pes morphology, there are noteworthy differences in the shape of the manus and the overall trackway configuration.

It is worth noting that the type specimen of *Tetrasauropus* (Fig. 2) from South Africa shows claws that turn inward, not outward, as in most North American examples. This may indicate some subtle, or perhaps quite significant, differences in the morphology of the trackmakers, as discussed below, but may simply represent variable substrate conditions. Variation in the angle of claw impressions is found among Jurassic and Cretaceous sauro-

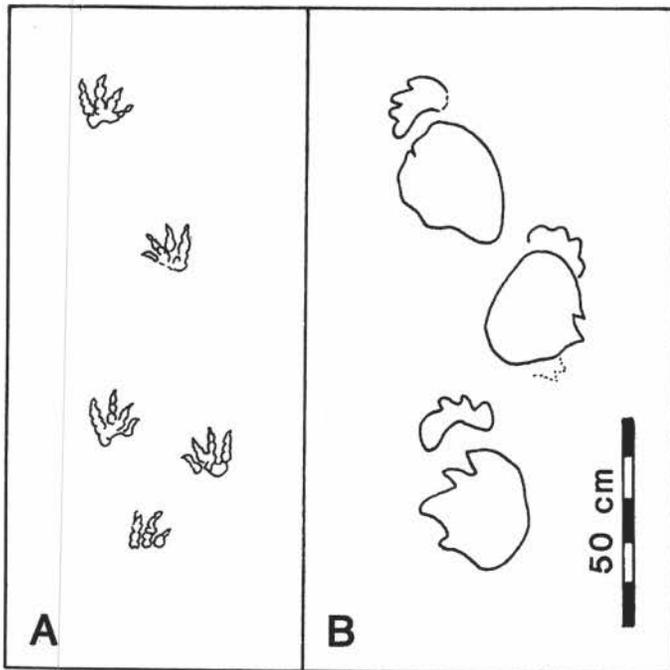


FIGURE 2. *Pseudotetrasauropus* (A) and *Tetrasauropus* (B) tracks based on North American sample (modified after Lockley and Hunt, 1995)

pod tracks, though most point outward or forward, not medially.

#### DATABASE

Upper Triassic track evidence from the western United States, compiled by the present authors and their colleagues, provides a coherent body of data which makes it possible to base ichnological conclusions, censuses and interpretations on a large data set and a significant body of literature. Almost all of the track-sites are found in the upper part of the Chinle Group (Rock Point sequence and Apachean land-vertebrate faunachron, *sensu* Lucas 1991, 1993, 1998). In recent years, several additional track-sites have been reported in the Rock Point sequence, including the important Furnish Canyon site described below.

Upper Triassic rock successions in the western United States that are replete with diverse vertebrate track assemblages have been recorded in three large regions within the Chinle Group outcrop belt (i.e., the southern Colorado Plateau region, the northern Colorado Plateau region, and the eastern region, *sensu* Lockley and Hunt, 1995). *Tetrasauropus* and *Pseudotetrasauropus* tracks occur in both the northern and eastern regions, notably around Dinosaur National Monument (Lockley et al., 1992) and Gateway, Colorado. In eastern New Mexico, track-bearing outcrops have been reported from east of Folsom, New Mexico, downstream in the Dry Cimarron Valley to the vicinity of Kenton, Oklahoma, as well as in southeastern Colorado (Conrad et al., 1987; Lockley and Hunt, 1993, 2000). For example, a hitherto undescribed site in Furnish Canyon, Colorado northeast of Kenton, is characterized by large bedding plane exposures imprinted with long, sub-parallel trackways attributed to the ichnogenus *Tetrasauropus* (Fig. 4). Late Triassic track assemblages similar to

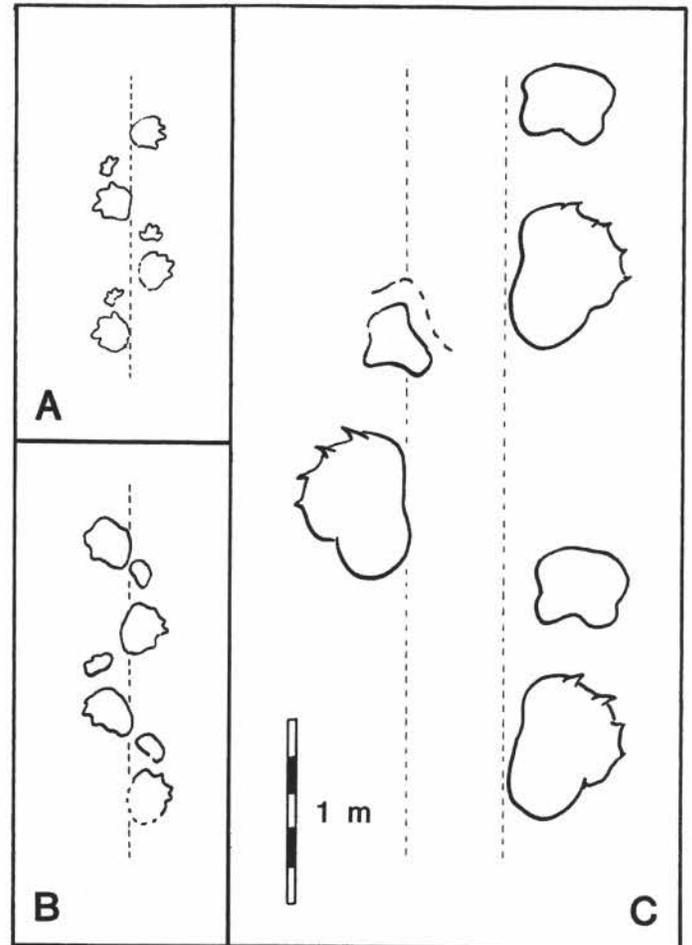


FIGURE 3. Comparison between North American *Tetrasauropus* (A and B from Cub Creek and Peacock Canyon, respectively) and *Brontopodus birdi* (C) from the Cretaceous of Texas (modified after Lockley and Hunt, 1995, and Farlow et al., 1989).

those found in the Dry Cimarron Valley also occur elsewhere in east-central New Mexico, notably at Redonda Mesa and Apache Canyon (Hunt et al., 2000; Lockley et al., 2000).

#### TETRASAUROPLUS MORPHOLOGY

*Tetrasauropus unguiferous*, the type ichnospecies of the ichnogenus *Tetrasauropus*, has a large pes (44 cm long) with a smaller manus situated antero-lateral to the pes. The digits on both the manus and the pes appear to curve inward toward the trackway midline. The step is short (79–83 cm); i.e., less than twice foot length. Pace angulation is about 100–110° (Ellenberger, 1972, fig. 36; Lockley and Meyer, 2000, fig. 4.7). It is not possible to determine if the trackway is narrow- or wide-gauge. However, if the partial type trackway, shown in Figure 1A, were extrapolated, using the pace distances and angulation angles indicated by Ellenberger's diagram, the trackway would appear to be narrow-gauge or very slightly wide-gauge (i.e., with little or no space between the inner margins of the pes prints). The space between the manus prints, however, is quite considerable. A second ichnospecies (*T. gigas*) originally assigned to ichnogenus *Tetrasauropus*

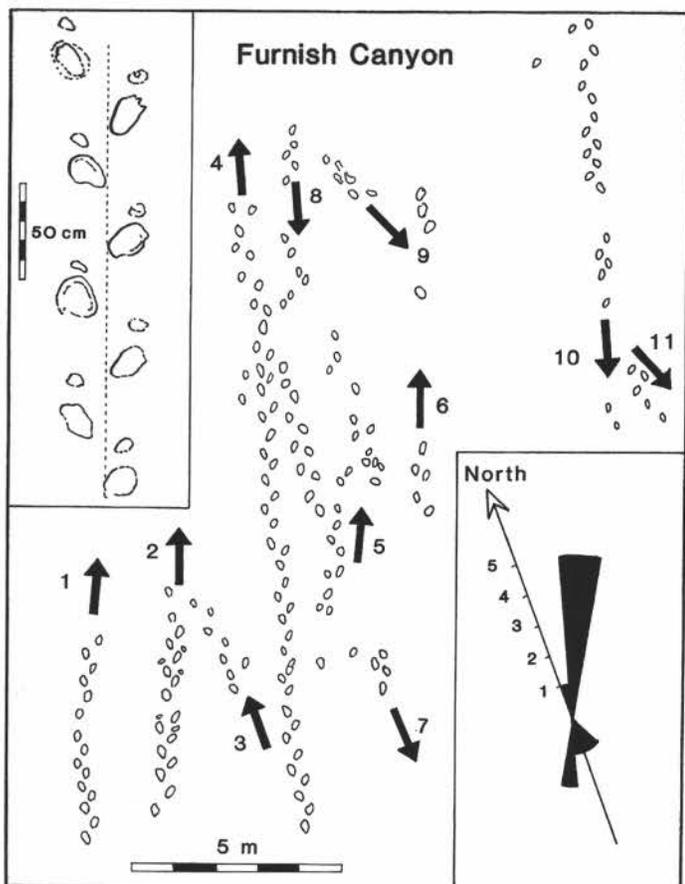


FIGURE 4. Map of Furnish Canyon *Tetrasauropus* tracksite, southeastern Colorado. Note preferred NNE and SSW trackway trends. Inset show details of trackway 2 (based on CU Denver tracing number 508).

*pus*, is here considered a synonym of *Pentasauropus*, a suggestion endorsed by Ellenberger (Lockley and Meyer, 2000, p. 88).

Tracks now assigned to *Tetrasauropus* (Fig. 5) from North America were first illustrated by Lockley (1986, pl. 1, fig. 16) and Conrad et al. (1987, figs. 4-5), and assigned tentatively to the ichnotaxon *Chirotherium* sp. In an attempt to relate abundant North American ichnofaunas to comparable material described from other regions, many additional ichnites were subsequently illustrated (cf. Lockley and Hunt, 1995, fig 3.13 and Lockley et al., 2000, fig 4) and assigned to the ichnogenus *Tetrasauropus*. We note, however, that the North American ichnites have pes digit impressions that consistently curve outwards. Whether the North American ichnites really belong in this ichnogenus (*Tetrasauropus*) depends on the degree to which the material is considered similar to material from southern Africa. As pointed out by Lockley and Meyer (2000), no one is really familiar with large samples of material from both regions. It is nonetheless our opinion that the North American material is not attributable to *Chirotherium*, and that its similarity to South African *Tetrasauropus* is noteworthy.

In the North American sample assigned to *Tetrasauropus*, the size of the tracks ranges from about 20–30 cm (pes length) with quite a large differential between the size of the manus (small) and the pes (large). Pes pace angulation varies (120–140°) as does

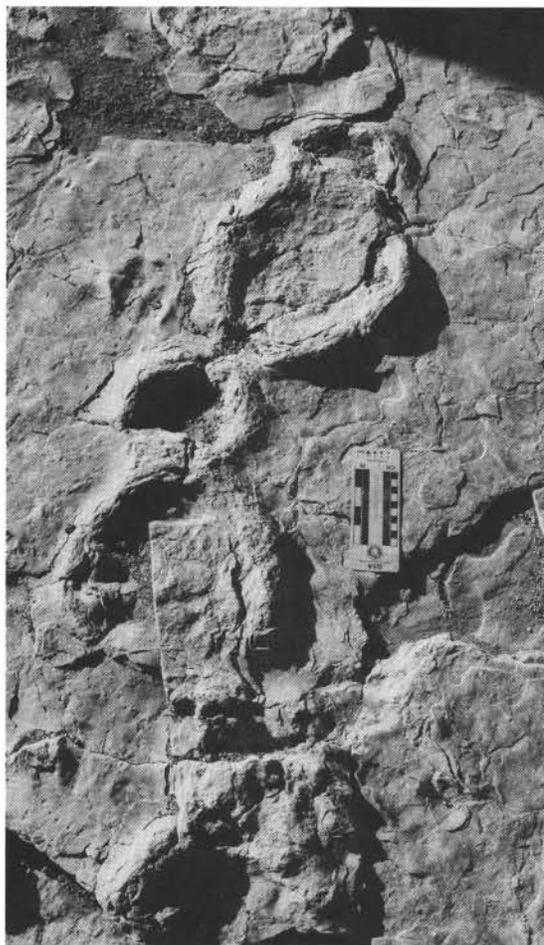


FIGURE 5. Photograph of *Tetrasauropus* trackway from Peacock Canyon. Compare with Lockley (1986, pl. 1, top left).

manus pace angulation (90–140°). It is also noticeable that the long axis of the pes is rotated outwards much more than in the type trackway from southern Africa (compare Fig. 1A with 2B and 3A,B). The North American trackways are also consistently narrow-gauge. Differences between North American and South African *Tetrasauropus*, especially in size, digit curvature directions and, to a lesser extent, probable pes axis alignment and trackway gauge, may argue for placing the North American ichnites in a different ichnotaxon, at least at the ichnospecies, if not at the ichnogenus level. However, in the interests of caution, no formal ichnotaxonomic revision is attempted here.

In contrast to *Tetrasauropus*, *Pseudotetrasauropus* almost invariably appears to have been made by a bipedal trackmaker (Ellenberger, 1972; Lockley and Hunt, 1995; Lockley and Meyer, 2000), causing Olsen and Galton (1984) to suggest, erroneously in our opinion, that the tracks were made by bipedal chirotheres of the ichnogenus *Brachychirotherium* (VanHeerden, 1997, p. 253). The *Tetrasauropus* pes track is morphologically very similar to later sauropod tracks such as *Brontopodus* and related forms. However, the manus is different in that the individual digits, though relatively blunt, are more clearly defined. Viewed from the morphodynamic perspective proposed by Lockley (1999a,b), there is a coherent relationship between saurischian feet and

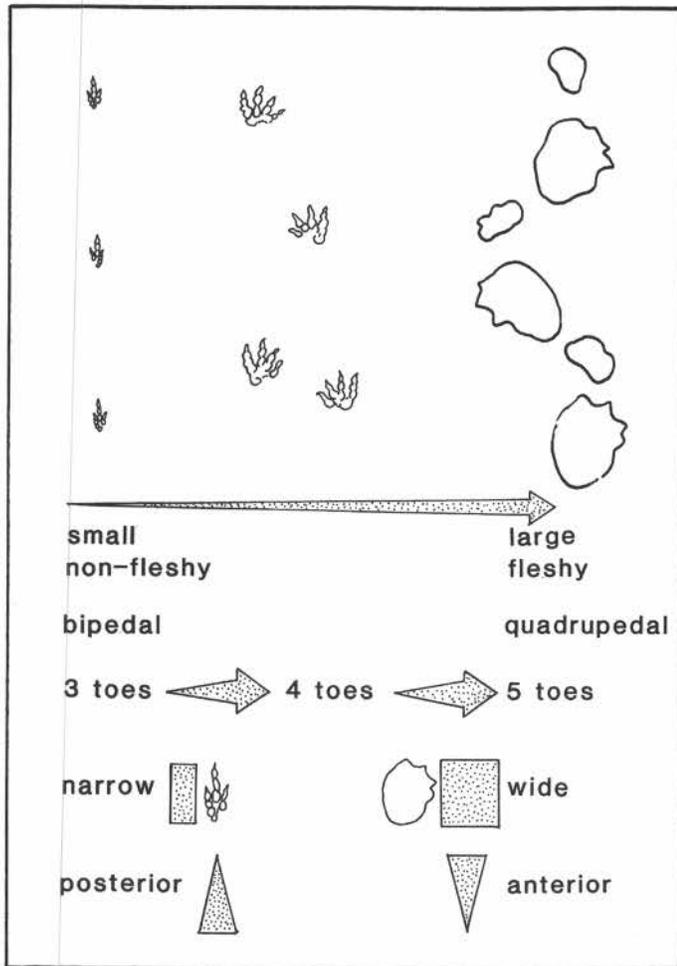


FIGURE 6. Morphodynamic relationships among saurischian (theropod, prosauropod and sauropod) tracks based on Triassic ichnofaunas of western North America. Note increase in size, fleshiness, number of digits, and trend from bipedal narrow trackways (posterior emphasis) to wide quadrupedal configuration (anterior emphasis).

tracks attributed to theropods, prosauropods and sauropods, as follows. They widen from three to four to five functional toes and become progressively wider and more fleshy, as the animals in question attain progressively larger maximum sizes. The fleshiness is also added progressively from the posterior as the morphological center of gravity of the whole animal moves forward. This anteriorization trend—also observed in other dinosaurian clades—is also very evident in the shift from obligatory bipedal to facultative biped to obligatory quadruped, and is accompanied by a general increase in overall body size, a lengthening of limbs and, perhaps counter-intuitively, a corresponding shortening of the step. This can be seen by arranging typical Late Triassic theropod, prosauropod and sauropod tracks (*Grallator*, *Pseudotetrasauropus* and *Tetrasauropus*, respectively) along this morphodynamic gradient (Fig. 6).

Most notable among these trends is the shift to quadrupedal locomotion in *Tetrasauropus*. Again, using the morphodynamic perspective, the earliest quadrupeds in many archosaurian and dinosaurian clades appear to have belonged to the small manus

type (cf. Peabody, 1948; Lockley, 1999a). For example, there is a clear pattern of increasing manus size among sauropods during the Jurassic and Cretaceous, with the former small manus varieties being attributed to “primitive” diplodocids, which generally had narrow gauge trackways, and the latter, large manus varieties being attributed to “derived” brachiosaurids/titanosaurids, which generally had wider gauge trackways (Wilson and Carrano, 1999). North American *Tetrasauropus* ichnites fit this predictable pattern. They are smaller than most post-Triassic sauropod tracks, have a narrow-gauge trackway (primitive condition), and the manus is small and incompletely enclosed in a fleshy pad in comparison with later sauropods (also a primitive condition). The femoral morphology of the Triassic sauropod *Isanosaurus* (Buffetaut et al., 2001) suggests a diplodocid-like configuration of the distal condyles in which the femora are angled slightly inward towards the trackway midline, thus retaining the narrow gait (and gauge) characteristic of the primitive condition in saurischians.

It is also noteworthy that many *Tetrasauropus* trackways show partial or complete pes overlap of the manus. This, in addition to the strong outward rotation of the hind feet, is very characteristic of sauropod trackways. However, as noted above, overlap configurations, variabilities and other trackway parameters in *T. unguiferous*—the type *Tetrasauropus* trackway—are not known with certainty.

#### PALEOECOLOGICAL CENSUS

As noted above, tracks are abundant at many Chinle Group sites, and data are relatively easy to collect quickly. Even though there is doubt about the affinity of trackmakers, distinctive track types can be recorded and assigned to ichnotaxonomic categories. We also advocate the making of site maps so that other researchers can assess the significance of the track data. This has been done at many sites. For example, the map of the Cub Creek site near Dinosaur National Monument (Lockley and Hunt, 1995, fig 3.23) shows the distribution of 35 trackways attributed to dinosaurs (*Grallator* and *Pseudotetrasauropus*) and other archosaurs (*Brachychirotherium*). Two of the 22 known sites in this area reveal the presence of *Tetrasauropus*, and a census based on 111 trackways from all tracksites in the region reveals a total of 16 trackways of this type (see Lockley and Hunt, 1995, fig 3.24). We suggest one revision to the conclusions presented by Lockley et al. (1992a, Fig. 5) in which three trackways, from site 91-6, are attributed to phytosaurs (Fig. 7; Conrad et al., 1987). These trackways are probably best assigned to *Tetrasauropus*. Here, the relationship between trackways with manus-pes separation (1 and 2) and overlap (3) is clearly seen as a function of stride length.

In the region of Gateway, Colorado, similar trackways have been reported, both in the upper part of the Chinle Group (Rock Point sequence) and in the basal Wingate, which, based on the presence of *Brachychirotherium*, are also Late Triassic in age, as is the basal Glen Canyon Group (or Navajo-Nugget sequence) at Dinosaur National Monument (Lockley et al., 1992a). Many of these trackways are deep, and details of foot morphology are poorly preserved. Thus, few have been described in detail. Nevertheless, at least one visually distinctive trackway has been illus-

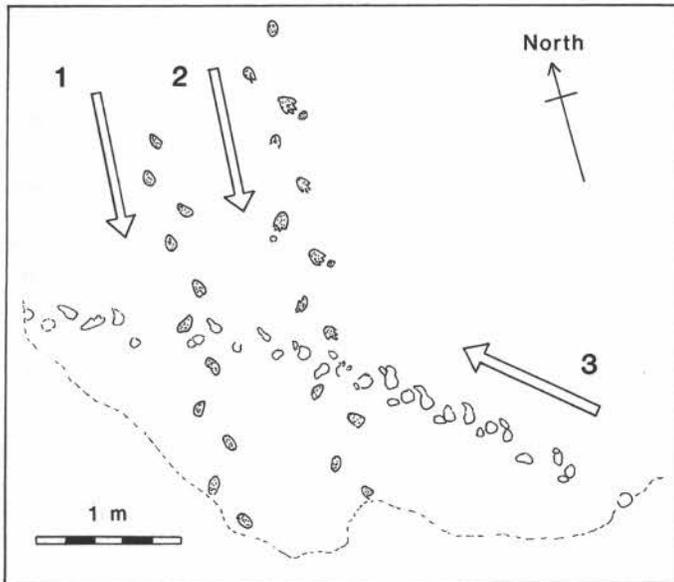


FIGURE 7. Dinosaur National Monument site 91-6 shows three trackways that we assign to the ichnogenus *Tetrasauropus* (after Lockley et al., 1992). Note the two parallel trackways (1 and 2), which are shallow, show a long step, and have no pes on manus overlap, and the third (3), which is deep, and shows a short step with partial pes on manus overlap.

trated (Lockley and Hunt, 1995, fig 4.4). Although some of these trackways appear to have been made by bipeds, there are many sites, including Dinosaur National Monument sites (Cub Creek and 91-6), Peacock Canyon, New Mexico and Furnish Canyon, Colorado where it is easy to distinguish both manus and pes tracks (Figs. 2-7). Thus, it appears that the *Tetrasauropus* morphology is relatively common in the Late Triassic. This conclusion is supported by an examination of sites in northeastern New Mexico and southeastern Colorado.

In a recent review of dinosaur tracksites in New Mexico (Lockley et al., 2000, Table 1), we reported on the number of trackways attributed to dinosaurs in the following four categories: *Grallator* and cf. *Grallator*, *Pseudotetrasauropus* and *Tetrasauropus*, attributed respectively to small and medium-sized theropods and gracile and robust prosauropods. We present here a revised version of this tabulation (Table 1) to include the data from five sites: Redonda Mesa (RM), Apache Canyon (AC), Peacock Canyon (PC), Sloan Canyon (SC) and Furnish Canyon (FC). We revisited the Peacock Canyon site, where some of the best *Tetrasauropus*

tracks occur, and also identified at least two good examples of *Pseudotetrasauropus*. Other changes to the table were made based on re-examination of available data.

From the tabulated data, it is easy to determine that *Tetrasauropus* trackways are quite common, and that they are among the dominant elements at both the Peacock Canyon and Furnish Canyon sites, though non-dinosaurian trackmakers such as *Rhynchosauroides* (a lacertilian) are common at the former site. A total of 53 *Tetrasauropus* trackways have been recorded to date. When combined with at least 16 from the Dinosaur National Monument area and at least five from Gateway, Colorado, we estimate a sample in excess of 70 trackways. In all areas where *Tetrasauropus* tracks occur they are associated with abundant *Grallator* tracks and several *Pseudotetrasauropus* trackways. Thus we infer that the *Grallator-Pseudotetrasauropus-Tetrasauropus* ichnological assemblage is a widespread and significant indicator of the archosaurian/dinosaurian ichnofauna of the entire region in which upper Chinle Group (Rock Point sequence) strata crop out.

If we rank the four track types listed in Table 1 by relative abundance, we find that the sample (N= 90) is dominated by *Tetrasauropus* (59%), with theropod tracks (two ichnospecies of *Grallator sensu lato*) comprising 29% and *Pseudotetrasauropus* comprising 12%. To this census for northeastern New Mexico and Furnish Canyon, Colorado, we should add at least 20 trackways known from the Sheep Pen Sandstone of the tristate area, near Kenton, Oklahoma (Conrad et al., 1987; Lockley and Hunt, 1995; Lockley et al., 2000). This increases the census to 110 trackways, of which about 47% are *Tetrasauropus*, 43% theropod and 10% attributed to prosauropods (i.e., *Pseudotetrasauropus*). This census is probably a better reflection of the high proportion of *Grallator* tracks found at most Late Triassic sites, and, moreover, once presumed non-dinosaurian ichnotaxa are removed, the census size and percentages are very similar to estimates reported from the Dinosaur National Monument area (Fig. 8).

Our reinterpretation of *Tetrasauropus* as a probable sauropod track remains consistent with inferences made by Lockley et al (2000, p. 12), who stated that "small dinosaurian trackmakers were more widely distributed geographically than large trackmakers." By this we mean to stress that small animals are more common than large ones (Bonner, 1988). This is still essentially true because small *Grallator* and *Pseudotetrasauropus* tracks occur at four of the five sites tabulated above, whereas *Tetrasauropus* occurs at only three. This difference is even greater in the case of the data cited for the Dinosaur National Monument area, where *Tetrasauropus* occurs at only 2 of 22 sites. Because sauropod tracks are statistically most abundant at low latitude sites (Lockley et al., 1994), it may be worth plotting the paleogeographic distribution (and abundance) of *Tetrasauropus* tracksites as more data become available. Present evidence suggest that *Tetrasauropus* tracks are somewhat larger and more abundant in the Dry Cimarron Valley than in the Gateway and Dinosaur National Monument areas.

In addition to the South African sites, we know of at least four other regions where dinosaur tracks of the *Tetrasauropus* type have been reported. In South Wales (Lockley et al., 1996) a census based on 88 trackways of presumed dinosaurian origin

Table 1. Distribution of four purported dinosaur track types from five sites in northeastern New Mexico and southeastern Colorado. (Updated after Lockley et al., 2000, table 1). RM= Redonda Mesa; AC = Apache Canyon; PC = Peacock Canyon; SC = Sloan Canyon; FC = Furnish Canyon.

Ichnotaxon and inferred trackmaker	Number of trackways reported from:					
	RM	AC	PC	SC	FC	TOTAL
<i>Grallator</i> small theropod	(1)	1	2	1	-	15
<i>Grallator</i> larger theropod	-	-	-	11	-	11
<i>Pseudotetrasauropus</i> prosauropod	1	7	2	1	-	11
<i>Tetrasauropus</i> sauropod	-	-	40	1	12	53
Subtotals	2	8	44	24	12	90

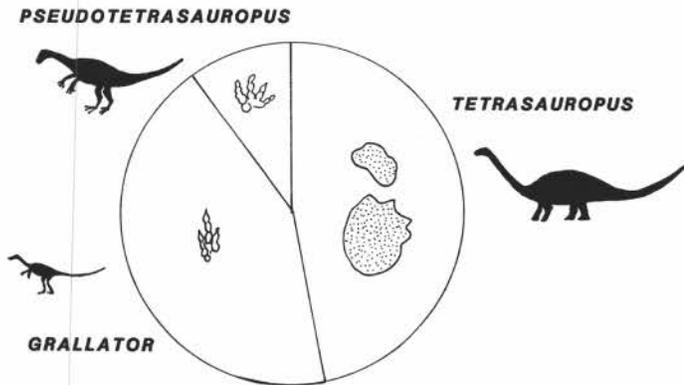


FIGURE 8. Proportions of inferred dinosaurian ichnotaxa ( $n=110$ ) from northeastern New Mexico and southeastern Colorado. The data compare favorably with similar census data from strata of the same age from the Dinosaur National Monument area. See text for details.

reveals 66 theropod trackways (75%), 18 attributed to *Pseudotetrasauropus* and *Otozoum* (i.e., prosauropods) and 4 attributed to *Tetrasauropus*. Furrer (1984, 1993) reported a large *Tetrasauropus*-like trackway in the Upper Triassic of the Swiss Alps, Jenkins et al. (1994) reported a similar trackway from the Upper Triassic of Greenland (also illustrated by Lockley and Meyer, 1995, fig. 4.14), and trackways that are remarkably similar to both *Tetrasauropus* and *Pseudotetrasauropus* have been reported from the Italian Alps (Mietto, 1991; Lockley and Meyer, 2000). Some of the rounded tracks, which resemble their North American counterparts (cf. *Tetrasauropus*), have been attributed to sauropodomorphs (prosauropods).

## DISCUSSION

While there is always doubt about the affinity of tracks, the progress made in vertebrate ichnology in recent years has allowed for the definition of distinctive track assemblages in well-defined stratigraphic intervals. The Upper Triassic of the western United States, in particular the Rock Point sequence of the Chinle Group (equivalent to the Apachean faunachron), is one such interval. There seems little doubt that abundant small *Grallator* tracks (many in the range of 6-10 cm foot length) represent the early radiation of small theropods, and the presence of a few larger tracks of this type in the latest Triassic indicates a phylogenetic size increase in a few groups. Similarly, it is now well established that tracks that are morphologically similar to *Pseudotetrasauropus* (Ellenberger, 1972) or *Otozoum* (Hitchcock, 1858) are highly reminiscent of prosauropod foot morphology. Again, these tracks are mostly small in Upper Triassic sequences and become progressively larger as one traces them into the Lower Jurassic. Similarly, the rounded (oval) fleshy foot tracks assigned to the ichnogenus *Tetrasauropus*, although large in the South African and Swiss samples (foot length up to 40-50 cm), are generally much smaller in the North American, Welsh, Greenland and Italian samples (15-30 cm). Given that post-Early Jurassic sauropod tracks reach much larger maximum sizes (80-100 cm), we again find evidence of a systematic size increase, which follows the

trends observed for theropod and prosauropod tracks. Given that we know of no published objections to the interpretation of such *Tetrasauropus*-like track morphologies as sauropodan, when found in post-Triassic deposits, it is most parsimonious to assume that those found in the Late Triassic belong to sauropodan clades, as now supported by body fossil evidence. The previously-mentioned alternative interpretation—that they represent a hitherto-unknown robust prosauropod with fleshy feet—is not supported by much evidence of true prosauropods with sauropod-like feet. Nonetheless, we cannot entirely rule out the possibility of candidates such as *Riojasaurus* and *Blikanasaurus* in the group that Van Heerden (1997, p. 259) calls “heavy-bodied prosauropods.”

It is not unusual to find that large ichnofaunas provide new evidence of the spatial and temporal distribution of important vertebrate groups that extends the knowledge derived from the skeletal record. Such data should be welcomed by paleontologists of an osteological bent. Too often such evidence is seen as contradictory to the skeletal record, when in fact it merely supplements it and extends temporal and spatial range boundaries, *without* seriously invalidating the general ranges established using body fossils. Nevertheless, when ichnological data extend the range of important groups closer to their origins, i.e., before the earliest known skeletal occurrence, such data usually prove controversial.

For example, abundant ichnological data now exist to indicate that tracks of shorebirds exist from the earliest Cretaceous (Berriasian) onwards, becoming very abundant, especially in Asia, by the late Neocomian (Lockley et al., 1992b; Lockley and Rainforth, in press). Skeletal evidence for these shorebird, or shorebird-like forms is not available, or at best very scarce and ambiguous, even though there is a steady increase in the discovery of other bird types proving high avian diversity early in the Cretaceous. Many other examples could be cited, including trackway evidence, which is the oldest evidence of Devonian tetrapods, and australopithecine tracks that, at the time of discovery, were older than known skeletal remains (Lockley, 1999a).

The interpretation of *Tetrasauropus* as a sauropodan track has several significant implications. First, as noted, *Tetrasauropus* can now be regarded as the oldest sauropod track type reported from North America. In fact, assuming an age of about 210 ma, these tracks are about 50 million years older than the unnamed sauropod trackway reported from the late Middle to early Late Jurassic (165-160 Ma) of Utah (Foster et al., 2000). Of equal significance is the implication that this interval defines a North American sauropod hiatus (*sensu* Lucas and Hunt, 1989). The original concept of a sauropod hiatus was applied to the chronostratigraphic interval between the late Albian and the Campanian-Maastrichtian boundary, an interval of about 25 million years (100-75 Ma). It now appears that this could be considered the “second sauropod hiatus,” the “first sauropod hiatus” being the longer interval between the late Norian-Rhaetian and the Callovian-Oxfordian occurrences.

Given that on a global scale sauropods were an extant group from the latest Triassic to the latest Cretaceous, these hiatuses evidently result from sauropod facies preferences and other large scale paleobiogeographical and geological influences on sauropod distribution. It is already known that sauropods preferred low lati-

tude habitats, where carbonate precipitation prevailed in "semi-arid" climatic regimes as evaporation often exceeded precipitation (Lockley et al., 1994). Retallack (1997, p 355) has confirmed that "sauropod soils" (indicating the substrates preferred by prosauropods as well as sauropods) are typically "red, weakly clayey and strongly calcareous paleosols (aridisols, calcic alfisols)." In many details upper Chinle Group sedimentary facies are similar to those of the Upper Jurassic Morrison Formation, which represents a typical sauropod habitat. Calcareous paleosols are present, and there is evidence of periodic aridity. Indeed, the uppermost Chinle Group facies underlie the massive Glen Canyon Group sequence, which represents sand-dominated deserts. Thus, it appears that after appearing in relatively large numbers, in late Chinle (Apachean) time, sauropods then disappeared from North America as excessively arid conditions developed. As part of any future study of the facies preferences of sauropods in North America, it may be fruitful to consider the relationship of stratal assemblages to paleolatitude (cf. Anderson and Lucas, 1996, fig. 3).

The possibility of the discovery of Upper Triassic brontosaurus footprints is perhaps not surprising, given that we now know of coeval skeletal remains. From the viewpoint of the formulation of new scientific paradigms, however, it is significant that ichnological evidence, which suggests the existence of more than 70 early sauropod trackways, found in Upper Triassic strata of three states (New Mexico, Utah and Colorado), has until now failed to generate the most parsimonious morphological interpretation, i.e., that they are most probably sauropodan in origin. Failure to consider seriously this possibility and present it, as done here, reflects several influences on how we do science. First, it reflects a lack of experience and boldness on the part of ichnologists, ourselves included, in presenting interpretations that previously would have appeared controversial. Second, it reflects the need for the acquisition of a large database before the "big picture" emerges. And third, as noted previously, it reflects the convention of using osteological evidence as the ultimate arbiter in deciding at least the temporal, if not the spatial, range of major vertebrate groups in the fossil record.

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