

## Mammal Track Assemblages from the Early Tertiary of China, Peru, Europe and North America

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*Recent discovery of small, tridactyl vertebrate tracks in a remote region of northwestern China has expanded the data set for the interpretation of similar trackways elsewhere in the world. Previously, similar tracks reported found in Peru from the Formation des Couches Rouges, were attributed to ornithopod dinosaurs, and then used to reinterpret the age of the section as Late Cretaceous. Similarly, the Chinese trackways were, prior to this study, assigned to the very broad chronological interval Cretaceous through Oligocene.*

*Comparison with the similar ichnofaunas in North America and Europe where the age of the tracks is well constrained to Paleogene, and where the tracks are attributed to odd-toed ungulates (perissodactyls), necessitates careful analysis of the affinity and age of the Chinese and Peruvian trackways. In all regions the track assemblages are mammalian (i.e., of ungulate affinity). The Northern hemisphere tracks may be attributed to perissodactyls, but the South American tracks probably represent native ungulate groups such as the Notungulata and Litopterna, that show convergent foot morphology. Even at the high taxonomic level of odd toed ungulate such broad biostratigraphic (palichnostratigraphic) correlations are useful in providing insights into the geologic and tectonic history of terrestrial successions, where the age and faunas are poorly known.*

### INTRODUCTION

Despite the recent renewed interest in vertebrate tracks (Leonardi, 1987, 1994; Gillette and Lockley, 1989; Thulborn, 1990; Lockley, 1991; Lockley and Hunt, 1995; Treise and Sarjeant, 1997), there is still much to learn about the global spatial and temporal distribution of ichnofaunas. For example, while some Late Cretaceous ichnofaunas are reasonably well known (Lockley and Hunt, 1995) and contain tracks of large dinosaurs such as ceratopsians, hadrosaurs, and tyrannosaurs, few small vertebrate tracks, other than bird footprints, are known from this epoch. Thus reports of small vertebrate tracks of purported Late Cretaceous age (Noblet et al., 1995) pose problems of interpretation, owing to the lack of comparative material. This problem is compounded by the paucity of reliable information on early Tertiary (Paleocene—Eocene) tracks.

In this paper we compare a purported Late Cretaceous

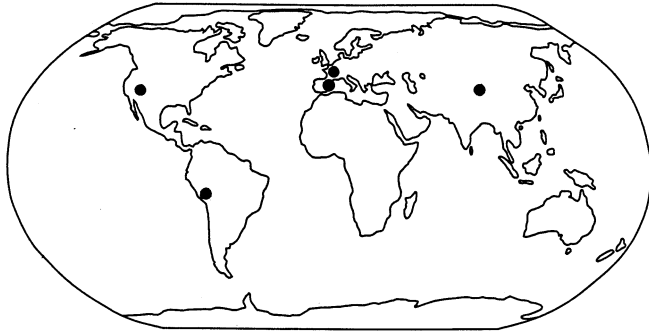
ichnofauna from southern Peru (Noblet et al., 1995) with a similar newly-discovered ichnofauna from Xinjiang Province, China (Fig. 1). Examination of both ichnofaunas suggests that the tracks are similar to Early Tertiary mammal tracks from North America. Owing to convergence, it is possible to confuse the tracks of different mammal groups either with the tracks of other more or less closely related forms, or even with those of small dinosaurs and certain ground-dwelling birds. Such potential confusion is largely avoided by analyzing individual footprints in the context of trackways, track assemblages, and the stratigraphic-paleobiogeographical context in which they occur. However, as discussed in the case of ungulates, this is not always easy. Tracks can nevertheless be useful in dating terrestrial sedimentary successions, making regional and global correlations (palichnostratigraphy), and reconstructing vertebrate paleocommunities. For the first time we bring together a number of obscure Paleogene track reports that previously have not been cross referenced, and suggest their potential to assist with geological interpretation.

### TRACKS FROM CHINA

The impetus for this study was the discovery by the second author of small tridactyl tracks from the extreme northwestern Qaidam Basin in Xinjiang Province, NW China (Figs. 2,3). The tracks were recovered from a sequence of nonmarine strata consisting of fluvial and shallow lacustrine facies mapped as the Cretaceous Quyangou Formation (XBGMR, 1993) in Qiemu County, south of Tura at N 37° 34' 56.9" E 86° 55' 01.2'.

The track-bearing slab (Figs. 4, 5), which was photographed in the field prior to transportation to the University of California Museum of Paleontology collections, reveals at least five tracks (A-E), all with approximately the same orientation. Two of the tracks (A+B) are overprinted. The tracks are all tridactyl and quite small (about 6 cm in length, 8 cm in width) with three equidimensional, elongately-oval to "fusiform" or cigar-shaped digit impressions that lack digital pad impressions. This configuration suggests a well-padded foot. The toe impressions are subparallel to slightly divergent in most cases, although some reveal somewhat larger digit divarication angles. The track is mesaxonic, with the central digit protruding anteriorly more than the lateral digits, but only by a relatively small amount in comparison with tridactyl dinosaurs or birds. The heel appears broad and bilobed in most cases, but is typically not as deeply impressed as the toes. The texture on some tracks is reminiscent of skin impressions of the type seen on the padded feet of modern mammals, such as dogs and cats.

The trackways were recovered from rocks mapped as Upper Jurassic through Paleogene (XBGMR, 1993), with the slab coming from the interval mapped as Cretaceous. The basis for this age assignment is tenuous. An Upper Jurassic age for the base of the section is inferred because Lower-Middle Jurassic coals and associated plant fossils are not found at the base of the section. Undocumented reports of the ostracods *Cyprinotus* sp., *Eucypris* sp., and *Cypris* sp. from elsewhere in the section are thought to represent an Oligocene age (XBGMR, 1993). However, the section lacks any radiometric, magnetostratigraphic, or



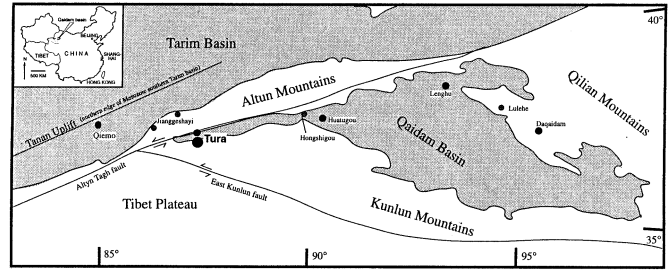
**FIGURE 1**—General Locality map for early Tertiary ungulate track sites mentioned in this paper, from China, Peru, France, Spain and North America. Localities are marked by black circles.

documented paleontologic age constraints. Hence, the age of the strata from which the sample was recovered is essentially unconstrained within the late Mesozoic—Paleogene time interval. Our correlation, herein, of the discovered tracks to similar trackways in well-dated North American and European sequences (Lockley and Hunt, 1995; Lockley and Meyer, 1999) is the most robust biostratigraphic data available from the Tura section.

**TRACKS FROM PERU**

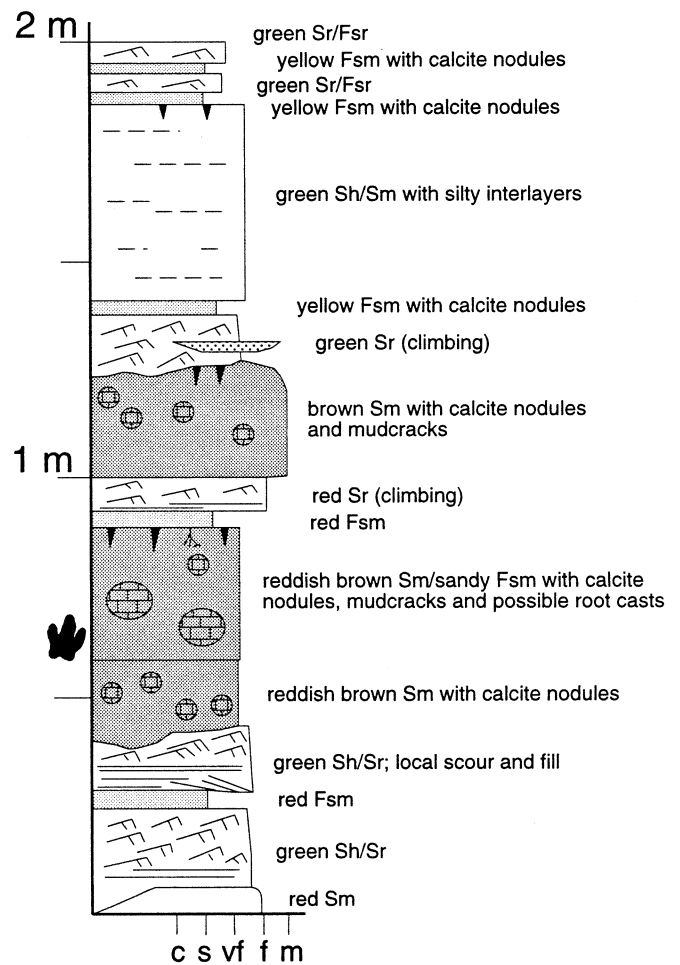
Tracks were first described from the Formation des Couches Rouges by Gregory (1916). The trackmaker was purported to be “a small animal of the dinosaur type” (Gregory, 1916). Noblet et al. (1995) also documented small tracks from the Formation des Couches Rouges at a higher stratigraphic level than those described by Gregory (1916). The tracks described by Noblet et al. (1995) are 6–8 cm wide and up to 10 cm in length (Fig. 6), although some of the tracks in the assemblage appear to be as small as 3 cm by 4 cm based on the illustrations published by Leonardi (1994). Noblet et al. (1995) interpreted the sample and, thus, a large part of the formation as Cretaceous in age. This interpretation was possibly influenced by the interpretation of Gregory (1916) that the trackmakers were dinosaurs and, therefore, Mesozoic in age. No other information was given by Gregory to support the suggestion that these tracks are dinosaurian. It should be noted, however, that this report did not deal with the same tracks discussed by Noblet et al. (1995) and those herein.

There are three tracksite locality numbers (111, 112 and 113 of Leonardi, 1994) known from the top of the Formation des Couches Rouges. The first (111), which is named K'ayra, has yielded a single track about 14 cm long (Fig. 4) that was attributed to a dinosaur by Leonardi (1994). The second locality (112), named Paruro, reveals a 25 cm<sup>2</sup> surface on which pairs of overlapping tridactyl tracks, on the order of 5 cm long, are arranged in clear trackways; these were described by Leonardi (1994, p. 83) as “mammaloid . . . the size of a cat or little dog.” Other small 4-cm-long, tridactyl, vertebrate tracks with elongate subparallel digit traces bear some relationship to purported condylarth tracks from the Paleocene Paskapoo Formation of Alberta (Russell, 1930). The third locality (113), named Langui (Sicuan), reveals a slab of 2 m<sup>2</sup> with tridactyl tracks 10–18 cm long as illustrated herein (Fig. 4). The stratigraphic po-

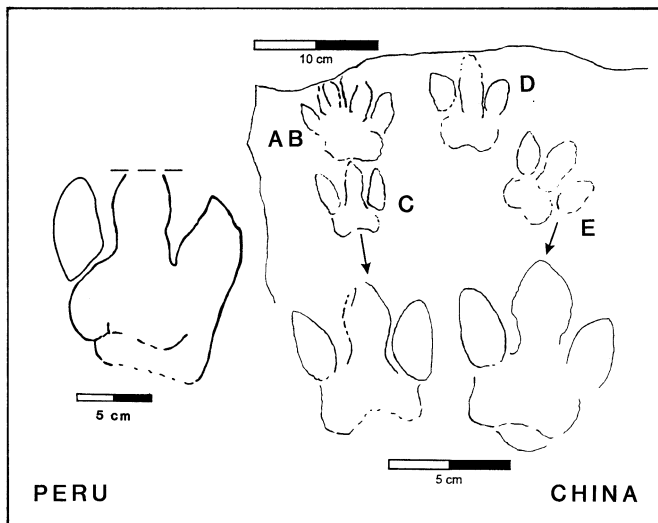


**FIGURE 2**—Location of Qaidam tracksite in Xinjiang province, south of the town of Tura (sample site marked by large black circle). Towns are marked by small black circles. Type sections for Cretaceous (Hongshigou, Jianggeshayi) through Tertiary (Lulehe) strata are marked by small gray circles.

sition of all three localities is given as the top of the Formation des Couches Rouges. All tracks remain *in situ*, and are on steeply inclined bedding surfaces. We have not visited these sites, but good photographic documentation, provided by Christophe Noblet, was published in detail by



**FIGURE 3**—Stratigraphic section of track-bearing beds, Qaidam Basin, showing typical marginal lacustrine facies. Grain size scale is: c, clay; s, silt; vf, very fine sand; f, fine sand; m, medium sand. Lithofacies codes are: Fsm, massive mudstone; Fsr, rippled siltstone; Sm, massive sandstone; Sr, rippled sandstone; Sh, planar laminated sandstone (after Miall, 1978; Ritts, 1995).



**FIGURE 4**—Chinese track assemblage (right) drawn from photo, with edge of block shown. Note that tracks from China (A-E) all have the same orientation, and that A and B are an overprinted set. Enlargements of C and E are shown for comparison with the Peruvian track (left).

one of us (Leonardi, 1994, Pl XXXIV, figs 1–4 and Pl. XXXV, figs 1–6).

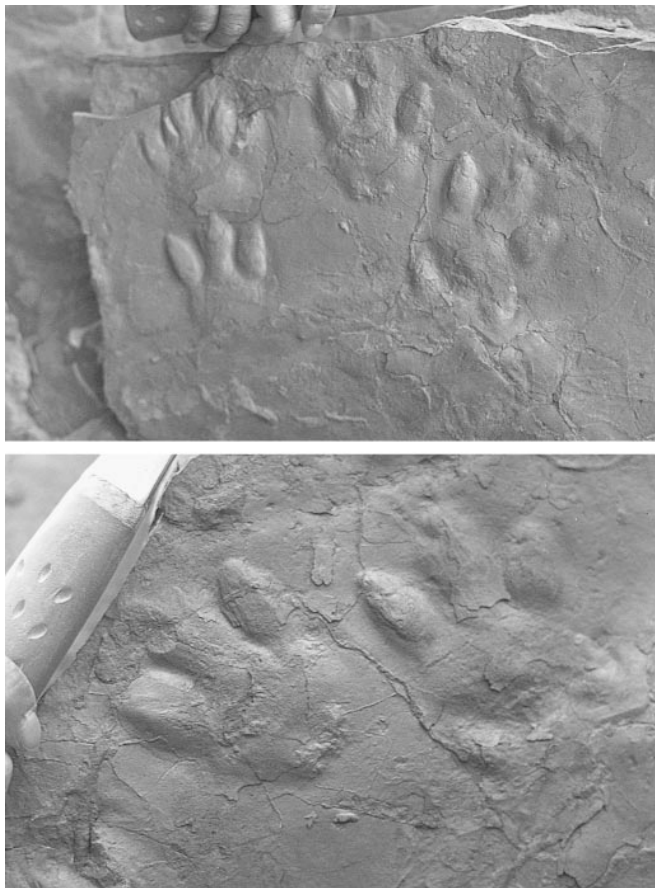
The Peruvian tracks appear similar to those from the Xinjiang sample in both size and morphology, although as discussed below, the trackmakers were probably different. Both have low digit divarication angles and a broad, bilobed heel (Figs. 4, 6), though some of the Peru tracks have a wider digit divarication angle and a more rounded heel. Other tracks from the sample show overprinting of manus and pes (Leonardi, 1994, Pl. XXXIV, fig. 2).

#### TRACKS FROM NORTH AMERICA

Tracks similar to those found in Peru and China have been reported in chronostratigraphically well-constrained Tertiary strata of western North America. Examples have been documented in the Eocene Green River Formation (Anonymous, 1960 a, b), the Eocene Debeque Formation of western Colorado, and certain Tertiary formations of Utah (Lockley and Hunt, 1995). In addition, tracks attributed to perissodactyls have been reported from the late Eocene of Texas (Sarjeant and Langston, 1994). These latter tracks have been named *Apoxypus*, as have tridactyl, perissodactyl tracks from other regions such as Europe (discussed below).

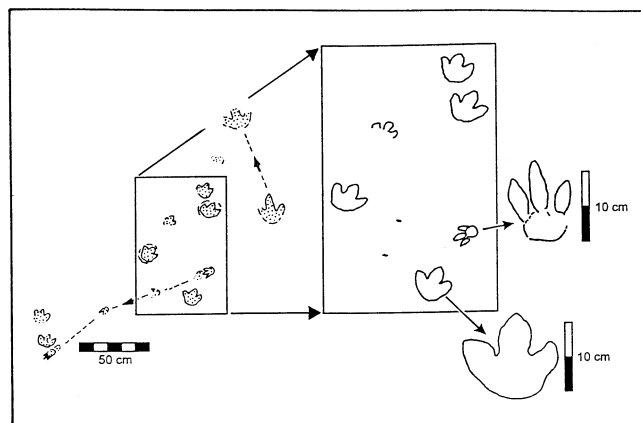
Two of the Colorado tracks (Fig. 7) are similar to the majority of tracks from the Peruvian sample, having wide digit divarication angles and a rounded heel. However, other specimens have less divergent toes and demonstrate overprinting of manus and pes as do the remaining Peruvian tracks and the tracks from China. Thus, the Peruvian tracks appear to cover much the same range of morphological variation as seen in the small Chinese and Colorado samples.

Tracks from a second North American site from the Green River Formation of northeastern Utah occur on the Strawberry Slab (Anonymous, 1960a, b). This remarkable



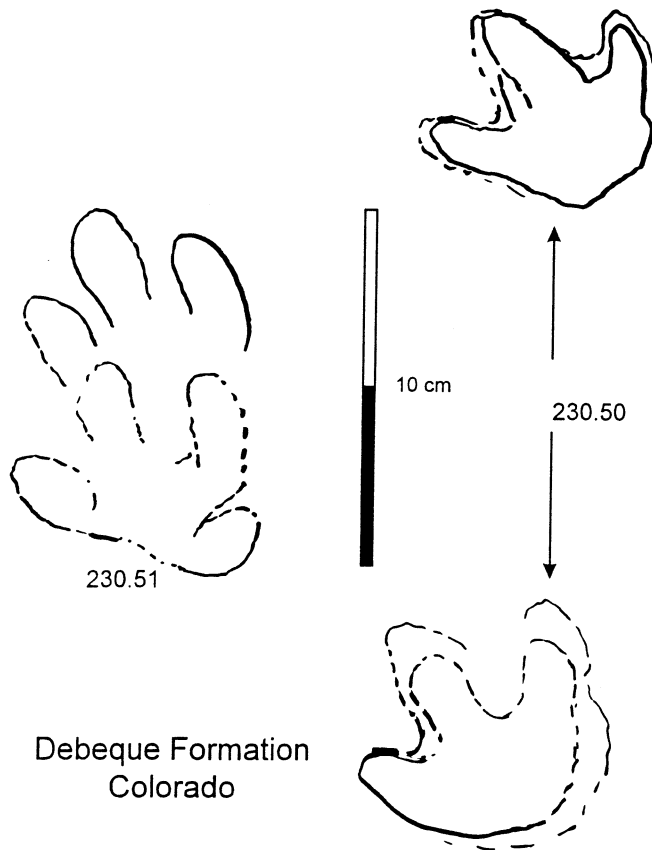
**FIGURE 5**—Photo of Chinese track-bearing slab, now in the University of California at Berkeley Museum of Paleontology collections.

specimen, found in Strawberry Canyon in Northeast Utah, has never been studied seriously, even though it was on display at the National Museum (Smithsonian Institution) for many years. An accurate scale drawing was made, by the senior author, of the Strawberry slab tracing all tracks and other obvious features such as mud cracks (Fig. 8). The slab displays more than 130 footprints, all of



**FIGURE 6**—Peruvian track assemblage (left) redrawn from Leonardi (1994) and Noblet et al. (1995) with box area enlarged to show individual track morphologies.

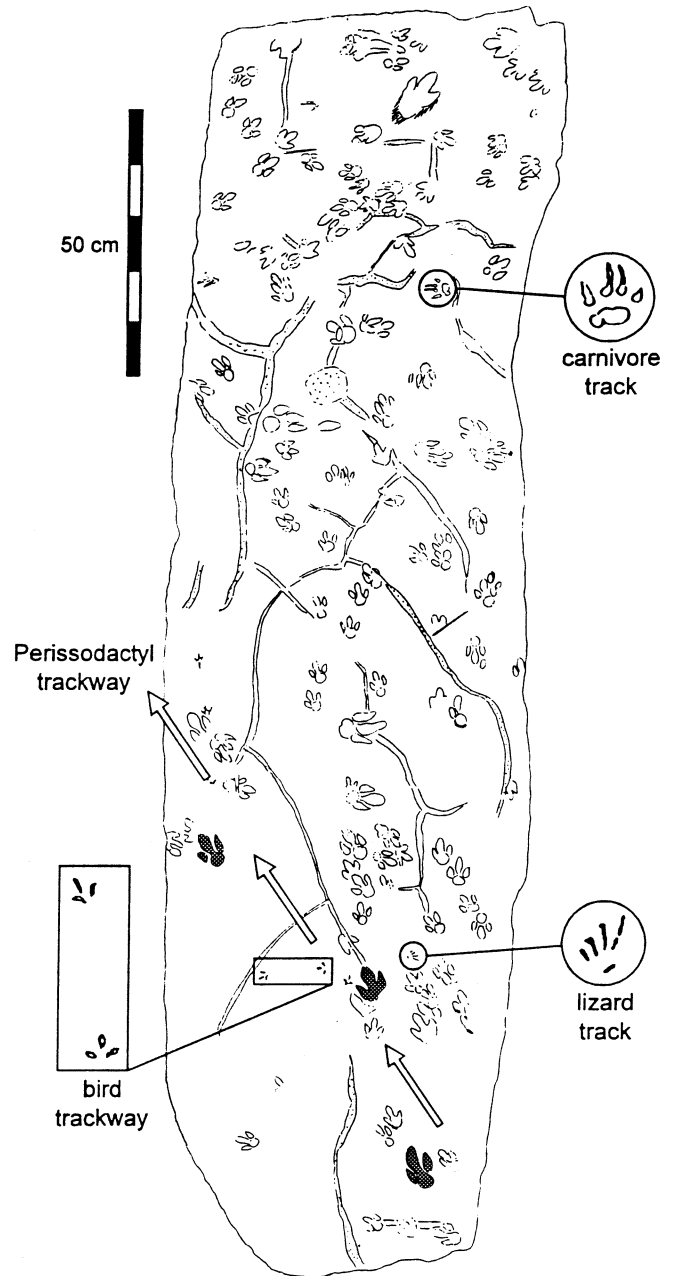




**FIGURE 7**—CU-MWC track specimens 230.50–51 from the Debeque Formation (Eocene) of Colorado (from Lockley and Hunt, 1995, fig. 6.12).

which are preserved as natural casts. Although most of the footprints are tridactyl and attributable to perissodactyls, there are a few tracks attributable to birds, one attributable to a tetradactyl tetrapod (possibly a carnivore/creodont), and one attributable to a lizard. Many of the perissodactyl tracks belong in trackway segments, although it is not possible to assign all tracks to trackways with certainty. However, it is possible to measure a step and stride of 37 cm and 70 cm, respectively, for one of the larger trackways (Fig. 8).

The Strawberry slab tracks range in length from approximately 5 cm to 9 cm, and are similar in size to those from China and Peru. The observation that the footprints are “almost perfectly preserved” (Anonymous 1960a,b) is confirmed by the observation that some tracks appear to show skin impressions. The texture of these skin impressions is similar to that seen on the paws of a modern dog. In other words the skin texture is very fine and granular, something like fine sand paper. Such an observation would seem to provide morphological evidence to rule out dinosaurian (hadrosaurian) trackmakers, which had an integument displaying a much coarser polygonal pattern (Currie et al., 1990). Although such verification is not necessary to establish that the Utah trackmakers were not dinosaurs, owing to a confirmed Eocene age, it is useful in helping establish the similarity of the Utah tracks with those from China and Peru. Some of the tracks from China appear to show the same fine skin texture seen in tracks



**FIGURE 8**—Scale drawing of the Eocene Strawberry Slab from North-eastern Utah (National Museum Specimen, no number). Reversed to appear as impressions not casts. Details of non-perissodactyl tracks also shown.

from the Strawberry Slab. We cannot demonstrate that the Peruvian tracks are characterized by similar skin texture; this may be due to sub-optimal preservation or lack of search for such subtle features. There is, however, no evidence of dinosaurian (hadrosaurian) skin morphology in the Peruvian sample.

**TRACKS FROM EUROPE**

Ellenberger (1980) described wide, 10.5-cm-long tridactyl, perissodactyl tracks from the upper Eocene of Gar-

rigues-Ste-Eulaine, Province of Gard, Southern France, and named them *Paleotheripus*. This ichnogenus name suggests that the trackmaker was *Paleotherium*—a member of the paleothere clade described by Kurten (1971, p. 70) as “a side branch of horse-like animals” that did not reach the New World. Ellenberger also named *Lophiopus*, a more elongate tridactyl perrisodactyl track from the same locality, implying that the trackmaker was *Lophiodon* or a lophiodontid—a group of semi tapirs (Kurten (1971).

Santamaria et al. (1989) reported an Oligocene mammal tracksite from the vicinity of Agramunt in the Leida region of Spain. Although younger than the French material, they described the new ichnogenus *Plagiolophustipus* which implies the presence of the genus *Plagiolophus*, which belongs to the paleothere clade. Both the Spanish and French studies are notable for explicitly stating that the makers of the tracks were ancestral horses and tapirids.

Even if European trackmakers were not conspecific or congeneric with their counterparts in North America or Asia, it appears that they were related at higher taxonomic levels (i.e. families, superfamilies etc.). Moreover assumptions or inferences about the affinity of trackmakers should neither precede or preclude careful description of track assemblages in their geological context.

#### AFFINITY OF THE TRACKMAKERS

It is clear that early Tertiary mammal tracks are widely distributed but have not been studied in great detail. Nevertheless, Eocene tridactyl tracks from both France and Texas, and Oligocene tracks from Spain, have been assigned ichnogenus names. In addition we can infer, with reasonable certainty, that the tracks from all other northern hemisphere localities are those of perissodactyls. Tracks from Peru, however, though made by ungulates with three functional toes, were probably not perissodactyls. The skeletal record of early Tertiary South American ungulates indicates that the dominant groups were the native “Notungulata and Litoperna, both of which were present in the oldest South American fossil beds of late Paleocene age” (Romer, 1996, p. 255). A more comprehensive treatment of the South American mammal fauna is provided by Simpson (1980).

Given that much of the material from Peru, China, and North America is being illustrated, herein, for the first time, and that none of it has been assigned ichnotaxonomic labels, it would be premature to attempt detailed comparisons with the named ichnotaxa from Europe. However, it is worth illustrating the range of size (foot length from about 5–18 cm) and shape (digit divarication and heel morphology) among the various tridactyl tracks currently known from early Tertiary sites (Figure 9). Such variation in size and shape suggests a potential to differentiate morphotypes in cases where the quality of track preservation is suitable. Indeed, it is only careful documentation of track morphologies from various localities that will help determine their utility in establishing trackmaker affinity, and the significance of biogeographic and biostratigraphic track distributions in space and time. Ultimately, full documentation of diverse ichnofaunas from such sites may be more useful in establishing the age of ichnofaunas,

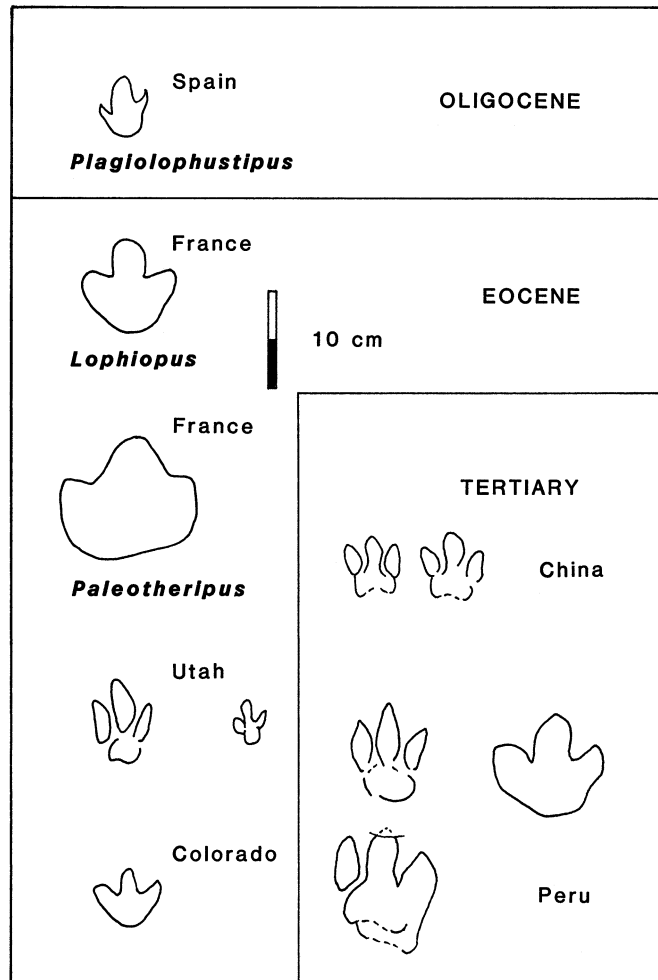


FIGURE 9—Line drawings of tridactyl Paleogene ungulate tracks from Asia, Europe, North America, and South America, show a range of sizes and shapes. All drawn to the same scale.

using simple assemblage zone principles. In this regard, the aforementioned assemblages from Texas, Utah, France, and Spain all contain a variety of tracks in addition to those of perissodactyls.

#### IMPLICATIONS OF TRACKS FOR STRATIGRAPHY AND BASIN ANALYSIS

It is often difficult to reliably constrain chronostratigraphy in nonmarine basins, particularly for non-volcanic, arid-climate, unfossiliferous sequences. In such settings, reliable age constraints are rare. Hence, identification of a new age indicator has the potential to shift the age assignment of large sections of strata. These drastic shifts in age assignment may have dramatic impact on the way that the stratigraphy and tectonic history of basins are reconstructed.

In both the China and Peru examples cited in this paper, the trackways were recovered from thick, nonmarine deposits that were considered to be Cretaceous through Tertiary in age, but had no reliable age constraints within the section. In both cases the trackways described in this paper are the most reliable age constraints on that part of

the section. Furthermore, in both cases, this has led to a reassignment of strata from Cretaceous to early Tertiary. It is important to note the result of revised age determinations for these tracks. In the case of the Peruvian trackways, the earlier, erroneous assignment of the tracks to a dinosaurian fauna near the top of the red beds, thought to be "Santonian to Upper Eocene" in age (Leonardi, 1994; Noblet et al., 1995), initially led to an incorrect reassignment of much of the Formation des Couches Rouges to Mesozoic, and a subsequent misinterpretation of sedimentation and tectonics in the Cuzco-Sicuani basin (Noblet et al., 1995).

The age reassignment erroneously suggested a shortening of the duration of sedimentation in the basin (from 45 to 20 Ma), and a corresponding doubling of inferred sedimentation and subsidence rates. Such inferences, in turn, implied a more pronounced and rapid tectonism early in the history of Andean orogenesis and required postulating a previously unrecognized 20 Ma unconformity to explain the Oligocene age assigned to the overlying beds of the Puno Group (Noble et al., 1995). Our interpretation is far more parsimonious. It suggests that the top of the Red bed sequence is much younger (Tertiary, and probably Eocene), as originally asserted by Noblet et al. (1987), grading, without any evidence of a large unconformity, into the Oligocene Puno Group. Thus, we can return to the original interpretation of Noblet et al. (1987) that "sedimentation of the red beds . . . was achieved during an inactive tectonic period lasting 45 Ma, and occurring between two major short tectonic events . . . -the Peruvian phase about 85 Ma . . . (and) the Incaic phase about 40 Ma" (Noblet et al., 1995, p. 785-786). This case shows the importance of biostratigraphic control in the analysis of terrestrial sedimentary successions and, moreover, indicates that such control may be provided by vertebrate footprints.

## DISCUSSION

Based on the known affinity and age of tracks from Colorado, Utah, and Europe, we infer that the tracks from Peru and China are early Tertiary in age and of mammalian (ungulate) affinity. The basis for this conclusion is the morphological similarity between tracks from all four areas. All the northern hemisphere tracks have been attributed to perissodactyls, mainly of Eocene age. Even where age of the strata is not well-established, as is the case in China, a combination of typical mammalian track morphology and/or skin impressions with manus and pes overprinting patterns (Lockley and Hunt, 1995) rules out the possibility of dinosaur affinity for any of the samples discussed herein.

Leonardi (1994) and Noblet et al. (1995) argued that the Peruvian tracks were Cretaceous in age and produced by ornithomimid dinosaurs (iguanodontids or hadrosaurs). We recognize that some of the tracks with wider digit divarication angles look like miniature hadrosaur tracks, but all available evidence argues against this conclusion. First, and most important, the morphology of the tracks is typical of perissodactyl tracks found on three other continents. (Even though South American forms were not true perissodactyls, they were ungulates which were convergent in many aspects of gross morphology.) Second, almost all known hadrosaur tracks are much larger than any found

in the samples discussed herein. Purported juvenile hadrosaur tracks from the Late Cretaceous of Utah are of uncertain origin and should be interpreted with caution (Lockley and Hunt, 1995, p. 226, fig. 5.38). Third, typical ornithomimid trackways show regular spacing of steps with clear right and left tracks, and short intervals between footprints. Such trackway patterns are not observed in these samples. Fourth, all the tracks show low digit divarication angles and little anterior protrusion of the central digit (III) beyond the other two, which is not typical of hadrosaur track morphology. Hadrosaur tracks may have rounded or bilobed heels, but they are usually smaller, in proportion to the track width, than in the samples discussed herein. Fifth, as noted above, skin texture, in the known Eocene sample from Utah and possibly in the Chinese sample, is characteristically mammalian, and nothing in the Peruvian sample indicates an alternate, dinosaurian morphology.

The very fact that there is confusion regarding the identification of these trackmakers indicates that caution must be taken in attempting to establish their affinity. It is obviously helpful to have seen other similar tracks from stratigraphic units that reliably have been dated, before making correlations. However, the common lack of serious attention to vertebrate ichnology means that few vertebrate paleontologists have such experience. Hence, correlations are not often proposed or attempted. In this regard, we can understand, to some extent, the conclusions proposed by Leonardi (1994) and Noblet et al. (1995) that the Peruvian tracks are Cretaceous, because Tertiary mammal tracks were previously unknown in most of South America, and the possibility of mammaloid tracks in the Mesozoic can not be ruled out completely. However, none are known with the size and perissodactyl (or perissodactyl-like) characteristics described herein. For all the reasons given above, we argue that the Peruvian, and the newly discovered Chinese tracks, are Tertiary in age.

## CONCLUSIONS

(1) Small Tridactyl tracks of uncertain age from purported Cretaceous deposits in Peru and Cretaceous-Tertiary deposits in western China are inferred to be Paleogene in age based on correlations with similar tracks in North America and Europe.

(2) These Paleogene footprints are attributed to perissodactyls (early horses or tapiroids) in the Northern Hemisphere and to native ungulates (Nothungulata and/or Litoperna) in South America. They conceivably could be confused with the tracks of small dinosaurs or large ground-dwelling birds with well-padded feet. However, detailed study of track morphology, trackway patterns, skin impressions, and overprinting relationships, however, strongly argues in favor of a mammalian origin.

(3) Attribution of these tracks to Paleogene mammals is important in establishing the tectonic history of sedimentation sequences in Peru and China where other better age constraints are unavailable.

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