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Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour

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A preliminary study of the Humaca dinosaur tracksite, in the Departamiento Chuquisaca (Bolivia), has revealed 11 parallel trackways of subadult sauropods travelling to the WNW as a group. The nearby Cal Orcko site preserves more variable trackway orientations produced by larger individuals. The Humaca trackways are interpreted as evidence of social behaviour among small titanosaurids. Together with the Toro Toro site it represents one of the few Late Cretaceous examples of evidence of sauropod herding. All three Bolivian sites provide useful evidence on the morphology of the titanosaurid manus and pes, and on trackway gauge. When considered in conjunction with trackway data from another Maastrichtian titanosaur tracksite, near Fumanya (Spain), it appears that titanosaurids were slightly to moderately wide-gauged as adults, with a large manus (manus-pes ratio, or heteropody about 1:2). Small individuals (sub-adults) may have been narrow-gauge in some cases, becoming wider-gauged as adults. The newly described Humaca and Cal Orcko sites also reveal an abundance of theropod tracks of various sizes, suggesting a theropod-sauropod, or 'saurischian' dominated assemblage as also recorded at Toro Toro. The detailed context and preservation of the sauropod and theropod tracks at all three sites are different and require further study, but at the Cal Orcko site indicate a well-developed perennial lake basin with a rich aquatic fauna. Other tracksites are known in the region, which has rich ichnological potential.

KEY WORDS: Dinosauria; Sauropoda; Titanosauridae; tracks; Upper Cretaceous; Bolivia.

1. Introduction

Until recently, the ichnological potential of Bolivia remained largely unexplored, though four dinosaur tracksites were reported by Leonardi (1994) from Toro Toro, Paratani, Arampampa and Camargo (Figure 1). Of these, the Toro Toro site was the most famous, largest and best documented (Leonardi, 1984, 1994), until the Cal Orko site, near Sucre, was discovered, in the 1980s, subsequently becoming a popular tourist destination. Such sites demonstrate the rich ichnological potential of the track-bearing El Molino Formation (Upper Puca Supergroup) and related deposits (Figure 2). Tracks from both the Toro Toro and Cal Orcko sites have been attributed to sauropods, theropods and ankylosaurs (Leonardi, 1994; Meyer *et al.*, 2001).

In July and August of 1998 an international expedition to the Sucre area (Departamiento de Chuquisaca), was launched with the primary purpose of studying a huge track site at the Cal Orcko limestone quarry. Initial results of this study have been published recently, but deal specifically with ankylosaur tracks (McCrea *et al.*, 2001) and other general aspects of the context of track-bearing beds (Meyer *et al.*, 2001). During the course of this investigation, however, some of the expedition members visited another, much more remote tracksite at Humaca and obtained preliminary documentation of the locality.

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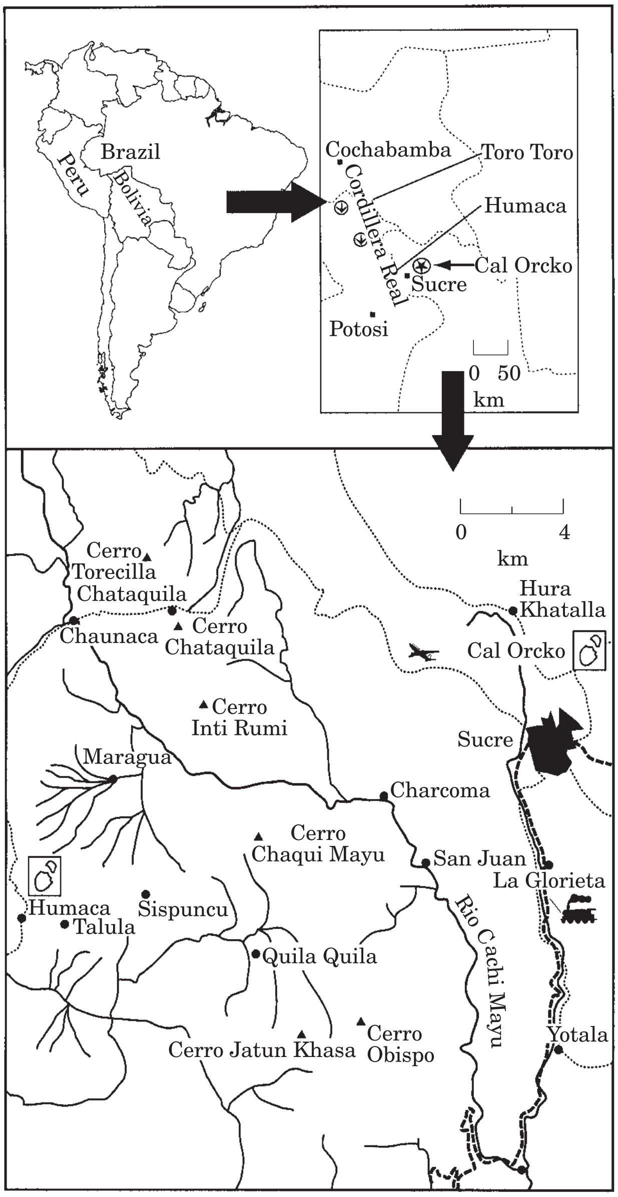

Figure 1. Top, location of dinosaur tracksites in Bolivia (modified after Leonardi, 1994) with, below, detail of location of Cal Orcko and Humaca sites near Sucre.

The purpose of this paper therefore is to describe the Humaca site, at which sauropod (presumably titanosaurid) tracks predominate, and compare these trackways with those reported from Cal Orcko and Toro Toro, and the only other known Maastrichtian sauropod tracksite at Fumanya in Spain. The Toro Toro site was not visted during this expedition, but was previously studied in detail by one of us (Leonardi, 1984, 1994).

All three Bolivian sites are reported as being in the Upper Cretaceous, Upper Puca Supergroup, which includes the El Molino Formation of probable Maastrichtian age (Sempere *et al.*, 1997). The Toro Toro site and the Humaca site are associated with sandstone track-bearing units in the Toro Toro and Chaunaca formations respectively, whereas the Cal Orcko site represents predominantly limestone substrates of the Molino Formation (Figure 2). In all areas there is evidence of multiple track-bearing surfaces and levels, as shown by detailed stratigraphic studies of the Cal Orcko site (Hippler, 2000; Meyer *et al.*, 2001; see section 6 below).

2. Localities

2.1. *Humaca*

The Humaca site is situated about 25 km WSW of Sucre (Figure 1) and is only accessible on foot after a 80 km (three hour) drive on unpaved roads which are of very poor quality for the last 15 km approaching the pueblo of Humaca. Access to the site is not advised without official authorization and a guide.

The site was discovered by one of us (DKM) in 1995 and visited by the remaining four authors on two separate occasions in 1998. Owing to the logistic difficulties of gaining access to the site it was only possible to conduct a preliminary study. This involved mapping the site with a traditional compass and tape-measure grid system. We also obtained tracings and photographs of the best preserved and most representative tracks using acetate film, and collected standard measurements of the sauropod tracks (Table 1). Tracings (T 650 and 674) are on file at the University of Colorado at Denver.

The site consists of a large sandstone dip slope (about 100 × 20 m), dipping NE at about 20° and best viewed from high ground to the north (Figures 3, 4). The up dip and down dip portions of this surface contain no immediately recognizable vertebrate ichnites. The central portion, however, reveals eleven parallel sauropod trackways that are deep and easily recognizable from a distance. This central area, measuring about 20 × 60 m was mapped (Figure 4). On close inspection there are many smaller theropod tracks preserved as brown ‘stains’, without relief, among the sauropod trackways. This mode of preservation requires further study, but the brown colouration of tracks within a greyish matrix suggests that the clear outline of these theropod tracks is caused by iron oxide.

2.2. *Cal Orcko*

The Cal Orcko site is in the outskirts of Sucre, in a large limestone quarry operated by the FANCESA cement company. According to Suárez Riglos (1995),

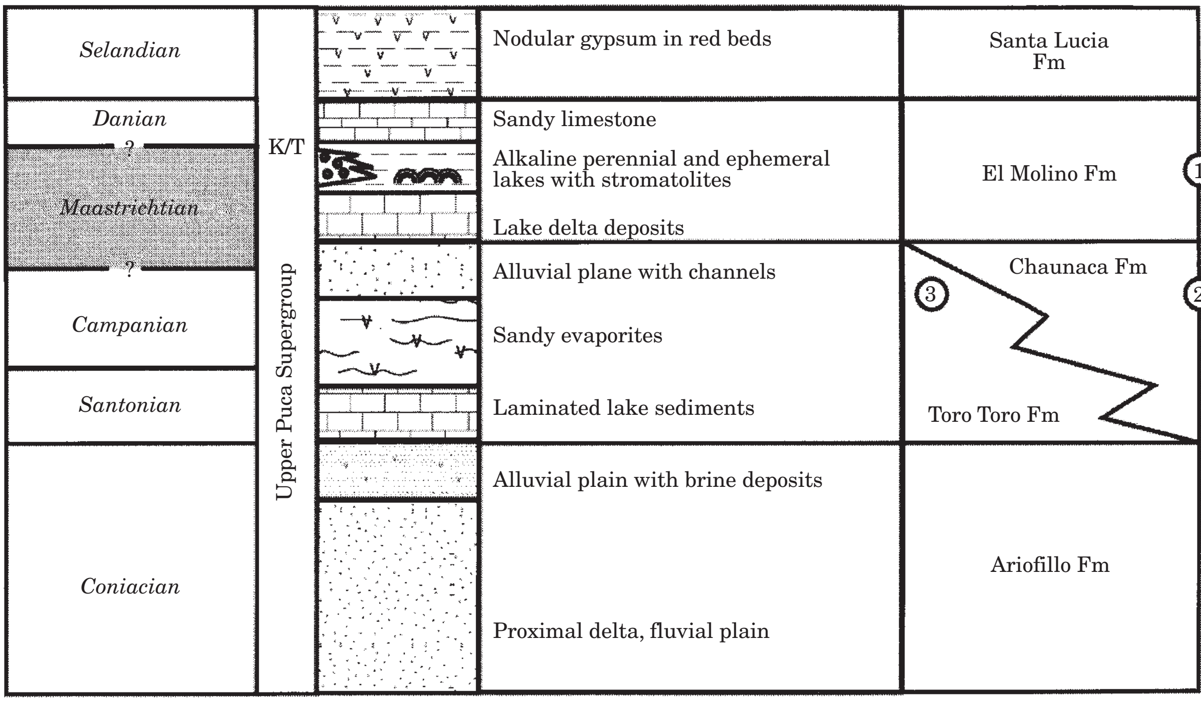

Figure 2. Stratigraphy of the Upper Cretaceous, Sucre region, Bolivia, showing inferred stratigraphic location of Cal Orcko (1), Humaca (2) and Toro Toro (3) sites; after Sempere *et al.* (1997) and Meyer *et al.* (2001).

Table 1. Measurements for Humaca sauropod tracks.

Trackway number	Pes track length	Pes track width	Manus length	Manus width	Stride in cmsT	Trackway width:out	Trackway width:in
1	43	37	22	18	138		0
2	45	34	16	27	148	78	0
3	50	33	–	–	142	72	15
4	42	28	19	29	130–140	65	0–5
5	(55)	40	–	–	185	–	–
6	40	26	–	–	142	–	–
7	43	36	35	27	160–180	–	10
8	45	33	–	–	180	–	–
9	(43)	35	–	–	200	–	–
10	40	28	–	–	192–206	–	–
11	–	(35)	–	–	185	–	–
Mean	44.6	33.2	23	25.3	165.8	(71.7)	(5.5)

the site was first noted or 'discovered' by the geologist José H. Heymann in the 1980s, and contains evidence of a pair of visually spectacular titanosaurid trackways heading from east to west (Figure 5). It is outside the scope of this paper to discuss the Cal Orcko site in detail, though the ankylosaurian tracks have recently been described (McCrea *et al.*, 2001). However, we note the presence of a few other sauropod trackways that are less well preserved than the spectacular pair illustrated in Figure 4. We consider it important to compare these trackways with those known from Toro Toro and Humaca in order to obtain a complete picture of the Upper Cretaceous sauropod trackway record known at present from Bolivia. We also note the presence of various theropod tracks at the Cal Orcko Site (Figure 6). Tracings (T 646–649, 651–659, 670–672 and 674–677) are on file at the University of Colorado at Denver. Representative silicon rubber molds are housed at the Natural History Museum in Basel, Switzerland.

Figure 3. Photograph, looking south, of the Humaca dinosaur tracksite, Chuquisaca, Bolivia. Compare with Figure 4.

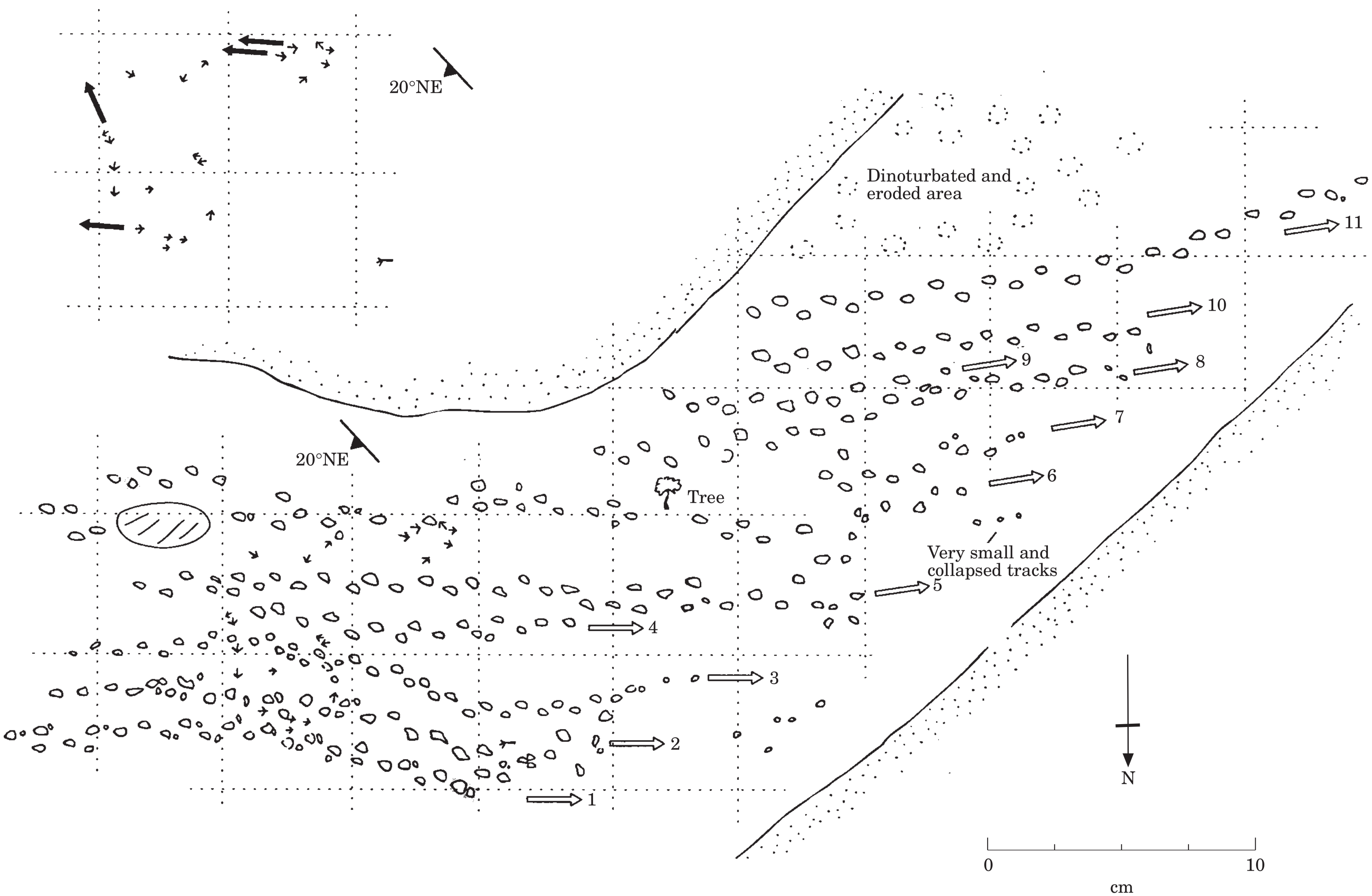

Figure 4. Map of the Humaca dinosaur tracksite, Chuquisaca, Bolivia. Note that the theropod tracks are shown both in their actual map location, and again on a separate grid (top left) so that trackway segments (black arrows) can be recognized. Because the site can only be viewed effectively from the north (looking south) as shown in Figure 3, the north arrow is shown to the bottom of the page.

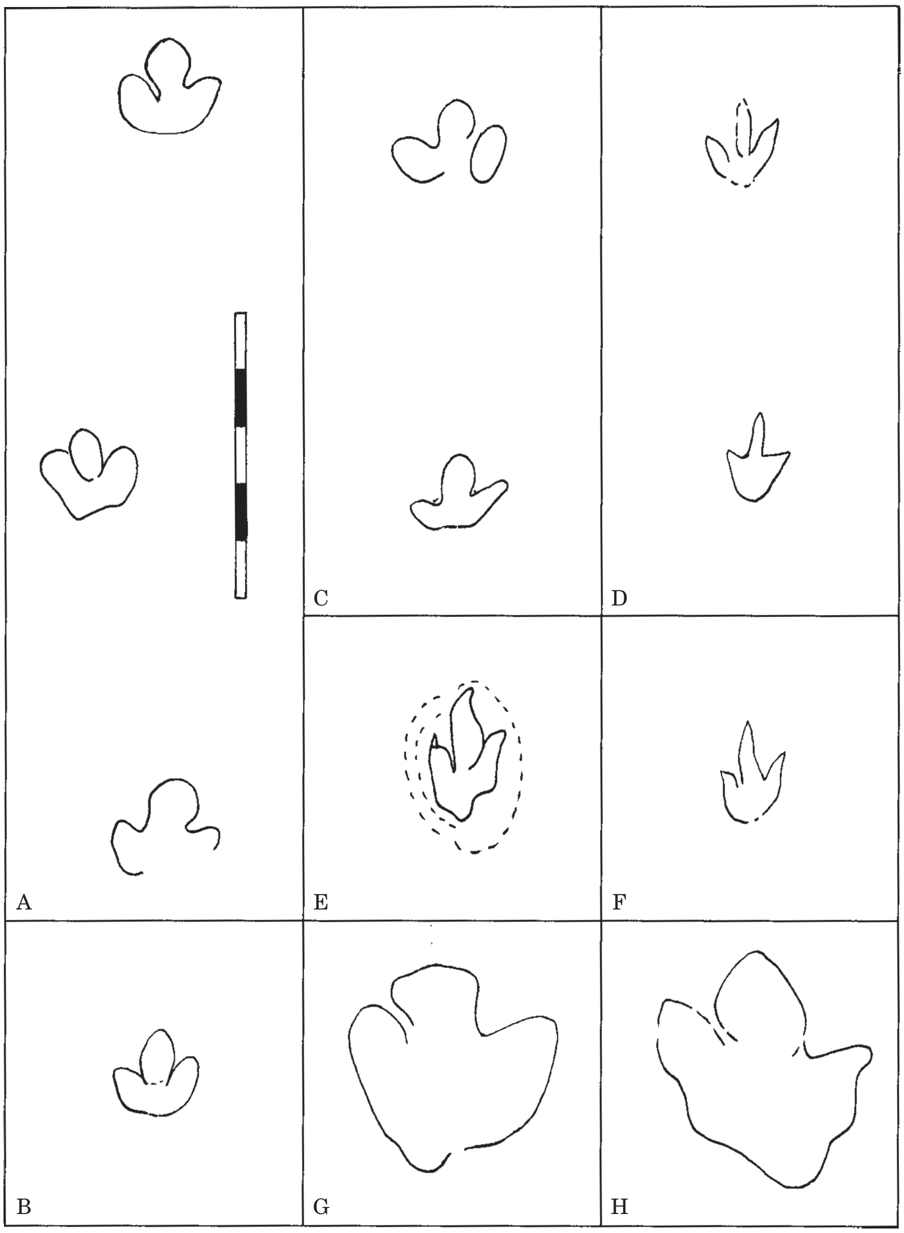

Figure 6. Representative tridactyl trackways and tracks from the Cal Orcko site, drawn to same scale (bar represents 50 cm). A–C, G, wide, blunt-toed forms of possible ornithopod affinity. D–F, H, elongate, theropod tracks. E shows mud rim. F from trackway of running individual with stride of 1.55 m. Compare with Figures 10 and 11.

2.3. Toro Toro

The Toro Toro site was the first in Bolivia from which sauropod tracks were reported (Leonardi 1984, 1994). He recorded them as being in the Toro Toro Formation (Figure 2). Although the site has not been described in great detail, a map has been published which reveals part of an exposure in which there are eight sauropod trackways heading in the same direction (Leonardi 1984). These are associated with dozens of parallel trackways of theropods. Six of the

Figure 5. Two spectacular parallel titanosaurid trackways at the Cal Orcko site, Sucre, Bolivia. Direction of progression is down dip, towards bottom of picture. Scale of photo is about 25 m from top to base of exposure. Note the theropod trackway orientated from right to left in middle of photograph. Compare with Figure 12.

Figure 7. Photographs of representative sauropod manus–pes track sets from the Humaca site. Left, trackway 1; right, trackway 4. Compare with Table 1 and Figure 9. Scales represent 1 m.

sauropod trackways are described as those of adults and two represent juveniles. In contrast to the Humaca trackways, which are spread out on a front of less than 20 m, perhaps implying that they all passed at about the same time, or at least without following in line, the Toro Toro sauropod trackways are spread out on a front of 200 m. The Toro Toro tracks are also described as having ''fore footprints'' that are ''extremely large in relation to the habitual pattern of sauropods'' (Leonardi, 1994, p. 40). The significance of this observation and its bearing on the interpretation of sauropod trackmakers is discussed below.

3. Preservation of the Humaca sauropod tracks

In comparison with the Toro Toro and Cal Orcko sites, the Humaca tracks are distinctive. First, at Humaca there are no prominent sediment rims or bulges around the tracks as there are at both the other two sites. This appears to be related in some way to greater track depth. All of the Humaca sauropod tracks are deep, of the order of 15–20 cm in depth in many cases (Figures 7, 8), whereas at Toro Toro, and at Cal Orcko in particular, the tracks are relatively shallow, indicating that the substrate was firm only a few centimetres below the surface. Another consistent feature of the preservation at the Humaca site is that the track margins are vertical to overhanging (Figure 8). In some cases the tracks have collapsed inwards to such an extent that footprints that originally measured 30–40 cm in diameter have been reduced to small holes only 5–10 cm in diameter. In some trackways one can follow a sequence of footprints from completely uncollapsed to collapsed examples (Figure 4). This suggests that the consistency of the sediment varied within short distances across the site. In some

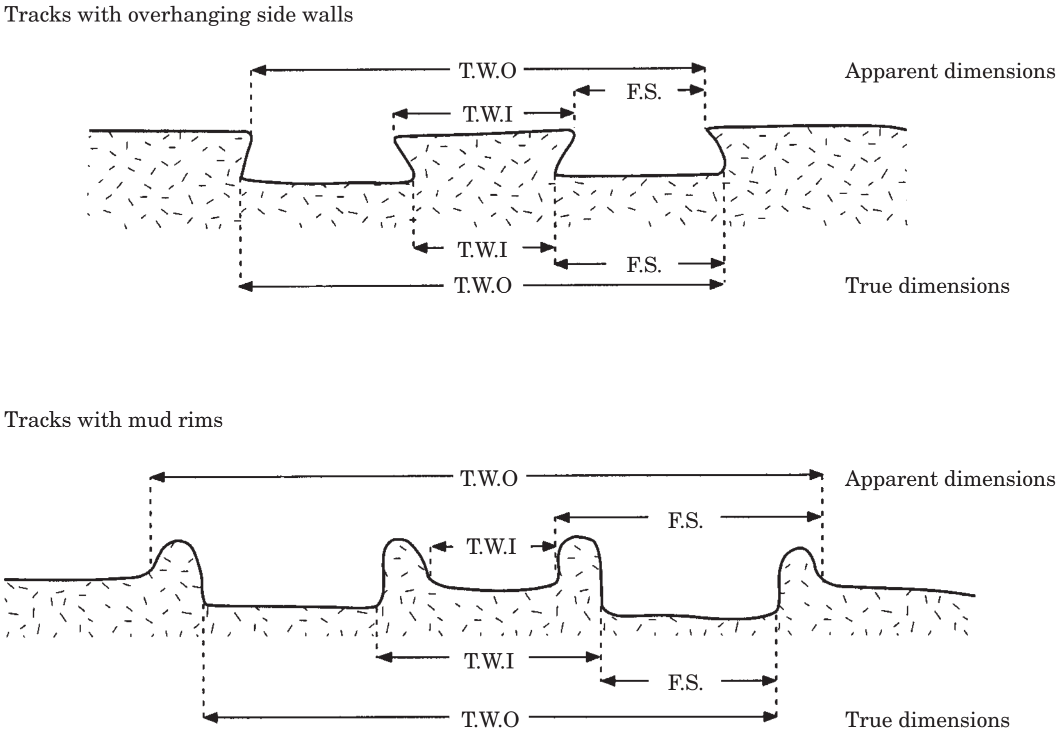

Figure 8. Preservational influences that affect the determination of the exact margin of tracks can also affect the estimation of trackway gauge parameters if true and apparent dimensions are not clearly distinguished. Above, the case of tracks with overhanging side walls. Below, the case of tracks with mud rims. T.W.I, inner trackway width, and T.W.O, outer trackway width is correctly indicated below, but overestimated above. F.S., footprint size, measured as length or width, may also be measured correctly (below) or incorrectly (above) depending on where one infers the periphery of the imprint.

tracks where the side walls are partly overhanging, the floor of the footprints is quite well preserved, showing in some cases impressions of morphological details of the foot such as toe impressions, as described below. Such observations suggest that the sediment was coherent enough, in some areas, to preserve useful information on sauropod foot morphology, whereas in other areas the sediment lacked coherence, presumably owing to high water content.

The southern portion of the site appears to be more deeply affected by modern erosion than the northern part, and may originally have been an area where the details of track morphology were less well preserved, possibly owing to trampling (i.e., dinoturbation). The striking contrast between the deep sauropod tracks and the complete lack of relief on the coloured theropod tracks suggests potential for a rewarding sedimentological study to determine whether preservational differences arose from differences in the timing of track-making activity. In this regard it should be noted that at the Cal Orcko and Toro Toro sites the theropod tracks are generally preserved in the same way as the sauropod tracks; i.e., as impressions with similar depths and mud displacement rims developed to various degrees in proportion to track size and local substrate variability.

4. Ichnology

4.1. Sauropod tracks

The most striking feature of the site is the set of 11 parallel sauropod trackways numbered 1–11 from north to south (Figures 3, 4). Several lines of evidence suggest that the trackmakers were part of a herd passing through the area. First, there is a regular trackway orientation with all trackways trending in almost exactly the same direction between west and WSW (240–270°). Second, the well-preserved tracks in each trackway are all similar in size (Table 1) with pes length varying from about 40–50 cm. Pes width (26–40 cm) is probably the most reliable measurement as the margin of the heel is not always clear, thus creating variable length measurements. Third, there is a fairly regular inter-trackway spacing of about 1.5–2.0 m. Fourth, some of the trackways, notably

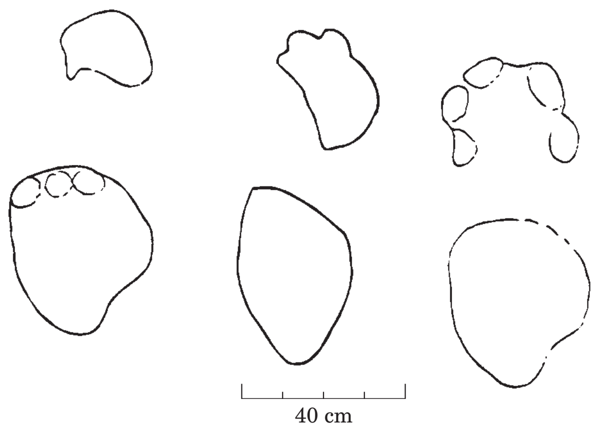

Figure 9. Line drawings of representative sauropod tracks from the Humaca site. Manus-pes sets on left and centre correspond to left and right in Figure 7, and come from trackways 1 and 4 respectively. Manus-pes set on right is a composite based on manus from trackway 7 (note five digit impressions) and pes from trackway 1, which matches trackway 7 for size.

trackways 1–3, show similar parallel patterns of curvature. For example, these three trackways veer slightly to the right, and then back to the left as if the animals were making slight changes in direction at the same time (cf. Lockley 1999, fig. 5.5).

Pes tracks are subtriangular in outline, sometimes revealing the presence of three blunt, equidimensional claw impressions representing digits I, II, and III, with I being located in the most anterior position (Figures 7, 9). This morphology is generally similar to that recorded for Maastrichtian titanosaurid tracks from the Fumanya site in northern Spain (Schulp and Brokx, 1999), and from the two other Bolivian titanosaurid tracksites at Toro Toro and Cal Orcko.

Manus tracks are semicircular with the long axis (length) rotated somewhat outwards relative to the trackway midline. Some show impressions of up to five rounded callosities or blunt claw impressions (Figures 7, 9).

There appears to be some variation in the relative size of manus tracks in relation to pes tracks. In the case of relatively small tracks this is probably attributable, in part, to slight or incipient collapse. With the pes track being registered after the manus there is a high possibility of distortion of the manus track, if not complete obliteration by overlap. We infer, especially in the sedimentological circumstances just described, that relatively large manus prints (Figures 7–9) are the most representative, in part for reasons discussed further below. Given the evidence for a herd, presumably of monospecific composition, it seems unlikely that there would be pronounced morphological variation among individuals already known to be approximately the same size.

The most reliable measurements were generally obtained for the better-preserved trackways in the northern sector of the site (e.g., trackways 1–7). There does, however, appear to be a fairly clear pattern of increasing stride lengths from north to south (Table 1). There is no obvious indication that stride length is related to size. However, it does appear that with increasing stride length to the north there is a corresponding decrease in the frequency of discernible manus tracks. This appears to be the predictable result of overstepping that can arise as step and stride length increases. It is tempting to speculate that to the south, where substrate conditions were softer, the animals instinctively adjusted their locomotion to place their hind feet in their front footprints, perhaps, in the process, speeding up a little so as to negotiate a potential quagmire more rapidly, and attain firmer footing beyond what was clearly an area of soft substrate. This speculative hypothesis could be tested by further detailed study of the site.

We also attempted to measure trackway width (internal and external) on the better-preserved trails. It appears that in general the trackways are quite narrow gauge, that is, there is little or no space between the inner margin of pes tracks and the trackway midline. In some cases a slight space is observed. It also appears that these internal trackway-width measurements are variable and depend to some degree on the curvature of the trackway. The significance of such measurements is discussed further below.

4.2. *Theropod tracks*

As indicated above, theropod tracks at the Humaca site are preserved as colour stains rather than in relief. Despite this, the outlines of various tracks are very clear and we present representative examples taken from acetate tracings (Figures 10, 11). In a few cases it is possible to discern sequential steps, but such measurements were not systematically collected. The apparent concentration of tracks towards the north is in part a reflection of the fact that the relatively smooth surface of the track-bearing layer is less damaged by erosion in this region. There is at least one probable example of a theropod track that is preserved as a relatively deep impression with a metatarsal impression. Most tracks are small to medium-sized, though we do not claim that the size range (foot length 12–30 cm) recorded in this preliminary study represents the entire size spectrum.

Theropod tracks from the Humaca site can be compared with those found at the Cal Orko site

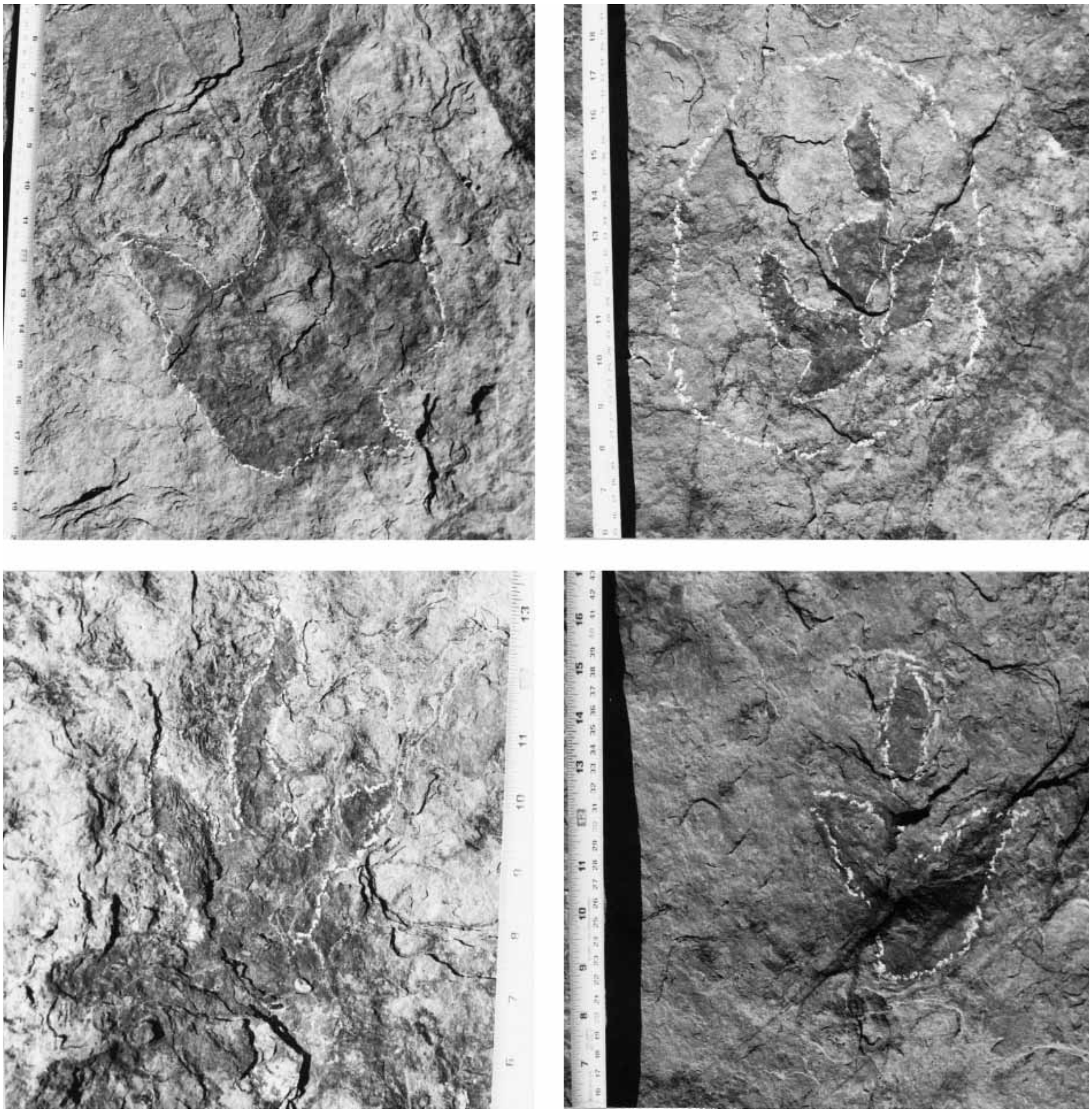

Figure 10. Photographs of representative theropod tracks from the Humaca site. Compare with Figure 11.

(Figure 6), which include a number of much larger examples, up to 40 cm or more in length. Although little can be inferred from these differences without further detailed study, we can at least report that the Cal Orcko tracks occur in extensive trackway sequences, including one that is 350 m in length and hence the longest dinosaur trackway on record (Meyer *et al.*, 2001). It is also evident that many of the Cal Orcko theropod tracks are rather short, i.e., length /width ratio is 1.0 or less, which is unusual for theropods. Some of these may be attributed to non-theopodan bipeds such as ornithopods, but like ankylosaurs, and ornithischians in general, skeletal records of ornithopods are rare in South America.

5. Sauropod track morphology and its implications

5.1. Sauropod heteropody

Leonardi (1994, p. 40, pl. 8, fig. 1a) was the first to make an explicit statement about the morphology of Upper Cretaceous sauropod tracks when he noted that tracks at the Toro Toro site had “fore

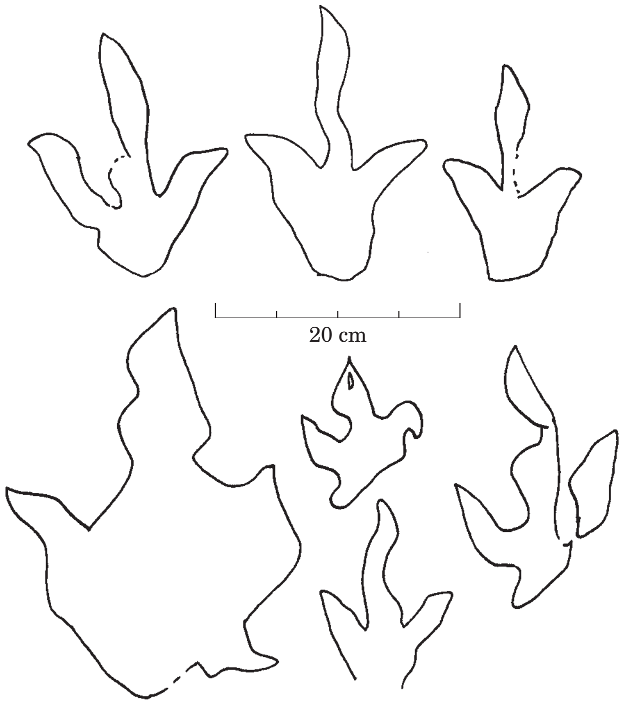

Figure 11. Line drawings of representative theropod tracks from the Humaca site. Compare with Figures 6 and 10.

footprints" that are "extremely large in relation to the habitual pattern of sauropods." Thus the manus:pes ratio indicates a low degree of heteropody. We are now in a position to compare the morphology of manus pes sets from four sites (Figures 7, 9, 12) and see these in the context of trackway morphology (i.e., trackway gauge).

Beginning with pes track morphology, the Humaca footprints seem to confirm observations made at Fumanya and Toro Toro that the titanosaurid pes has at least three discernible claw impressions. These are relatively short and equidimensional, though the inner claw (digit I) protrudes more anteriorly than the others as appears to be common for all sauropods.

The Humaca manus prints are particularly interesting because they show the presence of up to five blunt digit impressions. Manus tracks from the Toro Toro site appear to be characterized by three sharper, centrally located manus claw traces (Figure 12). Before concluding that the difference in sharpness between these and the traces from the Humaca site, might represent true differences in track morphology, we should remember that at both sites there are

Figure 12. Comparison of titanosaurid track and trackway morphologies from Toro Toro, Cal Orcko, Humaca and Fumanya. Dotted lines indicate mud rims. Solid lines indicate inner trackway width for trackways from Cal Orcko and Toro Toro.

significant, and different preservational factors to consider.

When considered together the relative size (surface area) of manus and pes tracks, or heteropody, is important in differentiating different sauropod track types, and may ultimately be important in deciding formal ichnotaxonomic labels (Lockley *et al.*, 1994a, in press). Collectively the Bolivian and Spanish titanosaur trackway sample provides us with sufficient information to estimate, with some confidence, the ratio of manus:pes area in titanosaurid footprints.

To date sauropod trackways with manus:pes ratios ranging from between 1:2 and 1:5 have been identified (Lockley *et al.*, 1994a; Santos *et al.*, 1994). Using this scheme, the manus:pes ratio of the Toro Toro trackway (Leonardi, 1994, pl. 7, fig. 1a) approaches 1:1, and the tracks from the Cal Orcko site reveal a ratio of 1:2. Those from the Humaca site (trackway 7) reveal a ratio of between 1:2 and 1:3, and those from Fumanya (Schulp and Brokx, 1999) a ratio of about 1:1. These results generally confirm the observations that the manus is relatively large Leonardi (1994). We consider the relatively small manus from trackways 1 and 4 at the Humaca site (Figure 9) to be anomalous and an artifact of preservation. The manus in trackway 7 is relatively large by comparison (Figure 9). It is possible that there is a variation in the heteropody ratio during ontogeny. In this regard some Humaca manus tracks are smaller in relation to the pes than those from other sites. Such ontogenetic variation may also be a factor in trackway gauge as discussed below.

5.2. Sauropod trackway gauge

Recent advances in our knowledge of the morphology and spatio-temporal distribution of sauropod track types (Lockley *et al.*, 1994b, 2001 and references therein) suggest that it is important to understand titanosaurid track morphology from the perspective of trackway width (gauge) as well as relative manus–pes size (heteropody) and claw impression morphology. For example, it has recently been proposed that titanosaurids can be considered, collectively with brachiosaurids, as a group whose skeletal morphology indicates a wide gauge posture and gait (Farlow, 1992; Lockley *et al.*, 1994b; Wilson and Carrano, 1999). The trackway data now available allows us to begin to test this gauge hypothesis and provide additional data on heteropody and actual footprint morphology.

Observations of trackway width from the Toro Toro, Cal Orcko and Fumanya sites suggest that titanosaurids were wide-gauged. The first explicit observations of purported titanosaurid tracks (Schulp and Brokx, 1999), based on observations of trackways from Fumanya in Spain, suggest that as much as one full pes width separated the inner margins of pes tracks (inner or interior trackway width: Table 1; Figure 12). Drawings published by Leonardi (1994) for the Toro Toro site suggest a similar separation (Figure 12). At the Cal Orcko site where two moderately well-preserved trackways have been documented, approximately 25 cm separates the inner margin of pes tracks in trackways where pes width is about 50 cm. At Humaca we were not able to measure internal trackway width in all trackways. In those where it was possible to obtain measurements we recorded inner trackway widths between zero and 15 cm. Bearing in mind that these were small trackmakers (average pes track width about 30 cm) the larger measurement is approximately half pes width. It is also important to note that various degrees of inward collapse or contraction of tracks in soft sediment (Figure 8) will affect inner and outer trackway width measurements. In such cases it is important to try and differentiate between the margin of the footprint at its point of maximum penetration of the substrate and the margin at the top of the ‘side wall’ (Figure 8). In this regard ichnologists must always be careful to measure the margin of the sediment rim.

We arrive at the preliminary conclusion that while moderately large titanosaurid tracks from Toro Toro, Fumanya and Cal Orcko are moderately wide gauge, smaller tracks from Humaca are sometimes narrow gauge or tending only very slightly towards the wide-gauge condition. This is probably in part a function of ontogeny. For example, if a trackway in which the pes track width is 50 cm shows an inner trackway width of 25 cms, as at Cal Orcko, then the ratio is the same as for a smaller track (30 cm width) with an inner trackway width of 15 cm. If however other tracks in the sample of smaller individuals consistently show a narrow gauge condition, then the possibility of ontogeny from narrow to wide gauge must be considered, at least in some individuals. Further study is required to determine whether such differences are a function of size, substrate conditions, inherent variability in titanosaurid locomotor repertoires, or a combination of these factors.

Recently it has been suggested that there were systematic morphodynamic trends in dinosaur evolution that resulted in the progressive anteriorization of overall morphology in all clades with a corresponding widening of the body and trackways (Lockley, 1999, 2001; Lockley *et al.*, 2001, in press). The sauropodomorphs provide a particularly good example. Prosauropods had a strong posterior emphasis, being facultative bipeds with relatively short necks, long tails and small mani. The more primitive sauropods such as the Diplodocidea (*sensu* Wilson and Carrano, 1999) also had long tails, small heads, and relatively small front limbs and mani. By contrast the most derived sauropods, the brachiosaurids and titanosaurs, generally had the longest necks, largest heads, and longest front limbs and the shortest tails. It is, therefore, not surprising that the front feet were relatively large producing the largest manus pes ratios.

5.3. Sauropod social behaviour

Trackway evidence for social behavior among sauropods has so far been reported mainly from Upper Jurassic and Lower Cretaceous sites, though a possible Upper Triassic site is also known (Lockley *et al.*, 2001). The best Upper Jurassic examples are those from the Purgatoire site of Colorado (Lockley *et al.*, 1986; Lockley 1991, 1995) and from Cabo Espichel in Portugal (Lockley *et al.*, 1994c). In both cases the majority of parallel trackways represent small individuals with a pes size comparable to the group recorded from Humaca.

Parallel trackways from two Lower Cretaceous sites in the Glen Rose Formation of Texas indicate the passage of a herd of 12 large individuals and 23 individuals of variable size from the famous Paluxy and Davenport Ranch sites respectively (Bird, 1939, 1941, 1944, 1954, 1985). These four sites along with sites such as the Upper Jurassic Hidden Canyon locality in Utah, where three parallel trackways are recorded (Barnes and Lockley, 1994), give the impression that gregarious behavior among sauropods was relatively common.

Recent studies of dinosaur tracksites in China (Lockley *et al.*, in press) reveal at least two Cretaceous sites with parallel sauropod trackways. The older is a Lower Cretaceous (Barremian–Aptian) site near Otog Qi in Inner Mongolia, with four parallel trackways. The younger is an Upper Cretaceous (Turonian–Coniacian) site near Chuxiong in Yunnan Province (Chen and Hunag, 1993; Lockley *et al.*, in press) which reveals ten trackways of which five have parallel orientations.

Eight parallel trackways recorded by Leonardi from the Toro Toro site represented the first documentation of probable social behaviour among Late Cretaceous sauropods (presumably titanosaurids) in South America. At this site the predominantly adult sauropods were widely spread out over 200 m (average spacing about 25 m) suggesting a low density, or widely dispersed group. A preliminary map of the site was published by Leonardi (1984).

By contrast, trackway evidence from the Humaca site allows us to infer that a group of at least 11 sub-adult titanosaurids moved WSW as a social group. They appear to have been travelling close together, as the total spacing perpendicular to the direction of travel is only 20 m (average spacing about 2 m). No trackways were recorded with other orientations. Such evidence might lead to the conjecture that trackway spacing is less (greater density) among small individuals than among adults, as might be predicted from a simple consideration of the minimum space necessary for the passage of small rather than large individuals. Certainly several of the aforementioned sites (Purgatoire, Cabo Espichel, Davenport Ranch, Inner Mongolia and Yunnan Province) reveal relatively close spacing or tight packing in groups composed of, or dominated by, sub-adults. This suggestion needs to be tested by quantitative analysis of trackway spacing in relation to footprint size in all available samples.

The Humaca site adds to available information on the subject of Late Cretaceous sauropod herding behaviour by suggesting that titanosaurids travelled in groups as sub-adults, as well as adults, and that such groups may have maintained a high density. At the Cal Orcko site two larger animals left parallel trackways (Figure 5), though at this site all other trackways appear to represent the activity of individuals moving in different directions, often at different times (different stratigraphic levels). Tracks from the Fumanya site indicate about 30 individuals in one area, presumably at about the same time (Schulp and Brokx, 1999; Lockley and Meyer, 2000). Although the trackway orientations are quite variable a few adjacent trackways are parallel, suggesting social behaviour.

Thus, leaving aside the early Late Cretaceous (Turonian–Coniacian) site in Yunnan Province, two of the other four known Late Cretaceous (Maastrichtian) sites strongly suggest social behavior among titanosaurids while the two remaining sites also hint at this possibility. Such evidence is consistent with evidence that sauropods exhibited social behavior throughout most, if not all of their history (see Coria, 1994 for Middle Jurassic evidence based on skeletal remains, and citations above for Upper Jurassic and Lower Cretaceous trackway evidence). There is no reason to infer that Late Cretaceous titanosaurids were an exception to this rule or that they lost their social inclinations at the end of the Mesozoic.

6. Palaeoecological observations

6.1. Cal Orcko palaeoecology and palaeoenvironment

The Cal Orcko stratigraphy has been studied in detail (Hippler, 2000), and a preliminary summary can be given here to place the track beds in palaeoenvironmental and palaeoecological context (Meyer *et al.*, 2001). As indicated in Figure 13, the section at Cal Orcko Quarry consists of at least 125 m of limestone, sandy oolitic limestone and clay assigned to the El Molino Formation, which overlies the more sandstone-rich Chaunaca Formation (Sempere *et al.*, 1997). Much of the El Molino Formation is fossiliferous, containing the remains of algae, snails, bivalves, ostracods, fish, turtles and crocodiles as well as coprolites, invertebrate traces and footprints. Tracks have been recorded at a minimum of seven stratigraphic levels (Figure 13).

According to Meyer *et al.* (2001) these facies represent a mosaic of lacustrine and marginal lacustrine facies. Sandstones represent the influence of fluvial and deltaic sedimentation encroaching on a perennial lake basin, whereas the fossiliferous limestones and claystones represent a well-established lake system that supported abundant life (Figure 14). The presence of carbonate units and many track-bearing layers indicates that the lake basin was shallow, with high productivity and significant evaporation, leading to fluctuating (lowering) of lake levels that probably encouraged track-making activity over wide expanses of the lake basin during dry spells.

The track assemblage represents something of an ichnological bonanza. More than 300 trackways were recorded on a single outcrop representing a sandy limestone bedding plane that extends as a vertical wall for more than 1.2 km along strike, with an average height of about 80 m (total area = 96,000 m^2). This represents a sample of lake shoreline of about 1/10 km^2. Approximately 90.5% of the sample is made up of sauropod and theropod tracks (about 34.5 and 46 % respectively; Meyer *et al.*, 2001), with small theropods and various ornithischians (notably ankylosaurs) making up the remaining 9.5%. Given that the ornithischian affinity of many three toed tracks is uncertain the fauna could fairly be characterized as saurischian (i.e., theropod-sauropod) dominated.

6.2. Bolivian vertebrate ichnofaunas

It is outside the scope of this study to discuss the palaeoecology of all possible titanosaurid tracksites in detail; however, it is worth noting that all three Bolivian tracksites are associated with low-latitude palaeoenvironments, which appear to have been the preferred habitat of sauropods (Lockley *et al.*, 1994b). The Toro Toro site, which was the first to be reported, can be described as a theropod-sauropod (i.e., saurischian) track assemblage with two additional trackways attributed to ankylosaurs, associated with a siliciclastic track-bearing layer. In this regard it is quite similar to the Humaca tracksite where we also find sauropod and theropod (saurischian) tracks associated with a sandy substrate. By contrast the Cal Orcko track beds are predominantly calcareous. However, they also reveal a theropod-dominated track assemblage with sauropods, ankylosaurs and possible ornithopods. In this regard it is interesting to note that well-documented remains of ornithischian dinosaurs (especially anklosaurs) are scare in the Cretaceous of South America. Thus the occurrence of ankylosaur tracks (Leonardi, 1994; McCrea *et al.*, 2001) is particularly significant.

Lockley *et al.* (1994b) suggested that sauropod tracks are usually found in association with carbonate substrates, as at Cal Orcko (Figures 13 and 14), and this is the case in as many as 90% of tracksites worldwide, most of which fall in tropical and subtropical latitudes, i.e., within 30° of the equator. At present, however, the local stratigraphic sections at Humaca and Toro Toro have not been described in sufficient detail to determine the frequency and degree of intergrading of carbonate and siliciclastic units. Clearly, however, there are strong similarities between the track assemblages at the three Bolivian sites, which reflects their close geographic and stratigraphic proximity. More significantly perhaps, the ichnofaunas strongly support the data on dinosaur distributions in South America, which show that almost all recorded localities are heavily dominated by saurischians, i.e., theropods and sauropods (Weishampel *et al.*, 1991).

7. Conclusions

Prior to the late 1990s the only convincing examples of multiple Upper Cretaceous sauropod trackways were those provided by Leonardi (1984, 1994) from Toro Toro, Bolivia, and an obscure report by Chen & Huang (1993) from Yunnan Province, southern China. To this meagre record we can now add the Fumanya site in Spain (Schulp & Brokx, 1999), the Cal Orcko site in Bolivia (Suárez-Riglos, 1995 and this paper), the Humaca site reported by Meyer *et al.* (2001) and herein, and the updated description of the Yunnan site (Lockley *et al.* in press). Together these sites give us a much better idea of the morphology of Late Cretaceous sauropod tracks, and in particular shed light on the tracks of latest Cretaceous titanosaurs from South America and the palaeoenvironmental settings in which they were active.

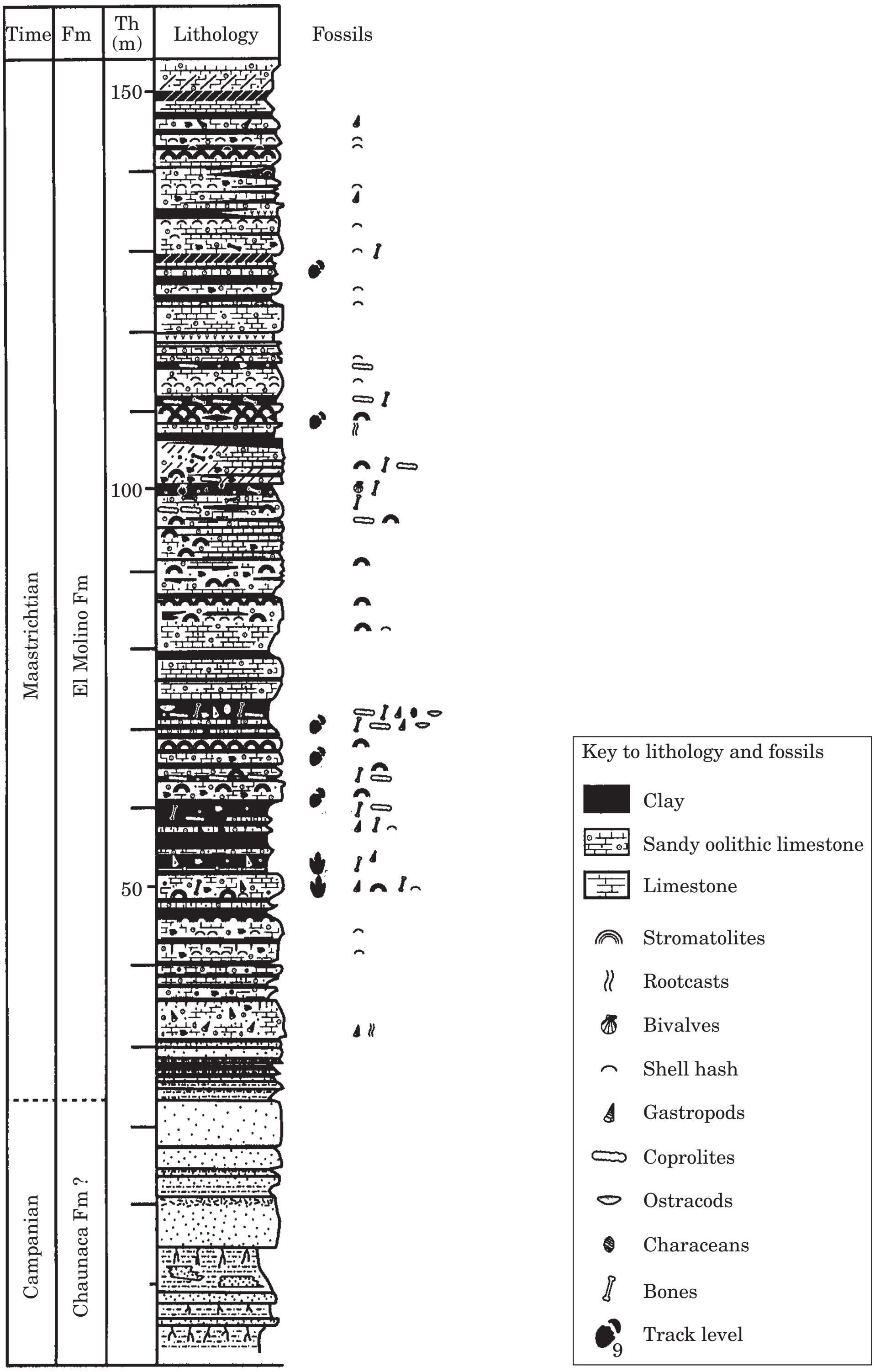

Figure 13. Stratigraphic section of the El Molino Formation at Cal Orcko Quarry, Sucre Bolivia (modified after Meyer *et al.*, 2001).

The assumption that these animals were all titanosaurids cannot be proven unequivocally. However, the abundance of this group in the latest Cretaceous and the lack of evidence for other sauropods strongly favours a titanosaurid origin. We can, therefore, draw the following four conclusions:

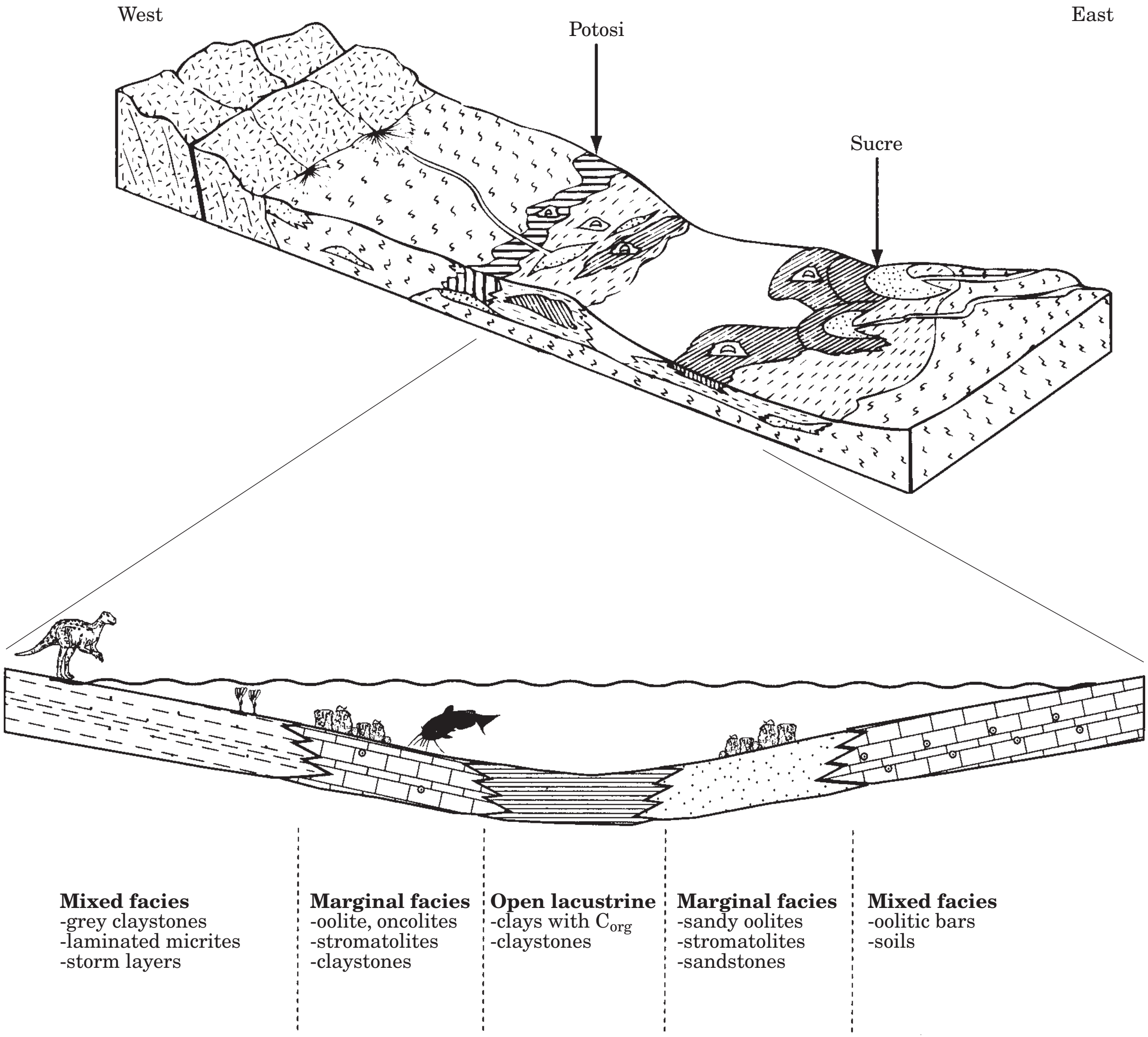

Figure 14. Schematic reconstruction of generalized facies relationships in the El Molino Formation and contiguous Upper Cretaceous facies of the Cal Orcko region, Sucre, Bolivia. Compiled from various sources including Sempere *et al.* (1997) and Hippler (2000).

(1) All sites evidently support the conclusion that adult titanosaurs had a large manus relative to the size of the pes (average ratio of about 1:2). Titanosaurids also appear to have had hind feet with relatively short unguals or blunt callosities and fore feet with blunt digit traces (unguals or callosities).

(2) All sites support the conclusion that titanosaurids produced wide-gauge trackways, at least when adult. The typical gauge of juveniles is not clearly established, but appears to have ranged from narrow gauge to moderately wide gauge (i.e., inner trackway width from 0 to half pes width).

(3) The Humaca site, the Toro Toro and the Cal Orcko sites reveal 11, 8 and 2 parallel trackways respectively, and so suggest that titanosaurids sometimes travelled in social groups. Trackways at the Fumanya (Spain) site are also abundant and so suggest a congregation of many individuals in the same area, and occasional passage of several individuals in the same direction.

(4) Titanosaurid tracks are typically associated with theropod footprints in what we may call 'saurischian dominated' ichnofaunas, in which evidence of ornithischian dinosaurs (e.g., ankylosaurs and ornithopods) is scare or lacking.

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References

Barnes, F. A. & Lockley, M. G. 1994. Trackway evidence for social sauropods from the Morrison Formation, eastern Utah (USA). *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 37–42.

Bird, R. T. 1939. Thunder in his footsteps. *Natural History* **43**, 254–261.

Bird, R. T. 1941. A dinosaur walks into the museum. *Natural History* **47**, 74–81.

Bird, R. T. 1944. Did *Brontosaurus* ever walk on land? *Natural History* **53**, 61–67.

Bird, R. T. 1954. We captured a live brontosaur. *National Geographic Magazine* **105**, 707–722.

Bird, R. T. 1985. *Bones for Barnum Brown. Adventures of a dinosaur hunter*, 225 pp. (Texas Christian University Press, Forth Worth, Texas).

Chen, S. & Huang, X. 1993. Preliminary study of dinosaur tracks in Changling, Chuxiong Prefecture. *Journal of Yunnan Geology* **12** (3), 266–276.

Coria, R. A. 1994. On a monospecific assemblage of sauropod dinosaurs from Patagonia: implications for gregarious behavior. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 209–213.

Farlow, J. O. 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. *Zubia* **10**, 89–138.

Hippler, D. 2000. *Geology and sedimentology of the Cal Orcko Syncline* (*Sucre, Chuquisaca*). Unpublished Masters thesis, University of Basel, 121 pp.

Leonardi, G. 1984. Le impromte fossili di dinosauri. In *Sulle orme dei dinosauri* (eds Bonaparte, J. F., Colbert, E. H., Currie, P. J., de Ricqles, A., Kielan-Jaworowska, Z., Leonardi, G., Morello, N. & Taquet, P.), pp. 165–186 (Errizo Editrice, Venice).

Leonardi, G. 1994. *Annotated atlas of South America tetrapod footprints (Devonian to Holocene)*, 248 pp., 35 pls (Companhia de Pesquisa de Recursos Minerais, o Servico Geologico do Brasil, Brasilia).

Lockley, M. G. 1991. *Tracking dinosaurs: a new look at an ancient world*, 238 pp. (Cambridge University Press, Cambridge).

Lockley, M. G. 1995. Track records. *Natural History* **104**, 46–51.

Lockley, M. G. 1999. *The eternal trail: a tracker looks at evolution.* 334 pp. (Perseus Books, Reading, MA).

Lockley, M. G. 2001. Trackways–dinosaur locomotion. In *Paleobiology: a synthesis* (eds Briggs, D. E. G. & Crowther, P.), pp. 412–416 (Blackwell, Oxford.

Lockley, M. G. & Meyer, C. A. 2000. *Dinosaur tracks and other fossil footprints of Europe*, 323 pp. (Columbia University Press, New York).

Lockley, M. G., Farlow, J. O. & Meyer, C. A. 1994a. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia: Revista de Geocíencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 135–146.

Lockley, M. G., Houck, K. & Prince, N. K. 1986. North America's largest dinosaur tracksite: implications for Morrison Formation paleoecology. *Geological Society of America, Bulletin* **97**, 1163–1176.

Lockley, M. G., Meyer, C. A., Hunt, A. P. & Lucas, S. G. 1994b. The distribution of sauropod tracks and trackmakers. *Gaia: Revista de Geocíencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 233–248.

Lockley, M. G., Meyer, C. A. & Santos, V. F. 1994c. Trackway evidence for a herd of juvenile sauropods from the Late Jurassic of Portugal. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 27–36.

Lockley, M. G., Wright, J. L., Lucas, S. G. & Hunt, A. P. 2001. The late Triassic sauropod track record comes into focus. Old legacies and new paradigms. *New Mexico Geological Society, Guidebook, 52nd Field Conference*, pp. 181– 190.

Lockley, M. G., Wright, J. L., White, D., Matsukawa, M., Li, J., Feng, L. & Li, H. 2002. The first sauropod trackways from China. *Cretaceous Research* **23**, 363–381.

McCrea, R., Lockley, M. G. & Meyer, C. A. 2001. Global distribution of purported ankylosaur track occurrences. In *The armored dinosaurs* (ed. Carpenter, K.), pp. 413–454 (Indiana University Press, Bloomington).

Meyer, C. A. Hippler, D. & Lockley, M. G. 2001. The Late Cretaceous vertebrate ichnofacies of Bolivia – facts and implications. In *VII International Symposium on Mesozoic Terrestrial Ecosystems. Associación Paleontológica Argentina, Publicatión Especial* 7, 133–138.

Santos, V. F., Lockley, M. G., Meyer, C. A., Carvalho, J., Galopim de Carvalho, A. M. & Moratalla, J. J. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* (Lisbon) **10**, 5–14.

Schulp, A. S. & Brokx, W. A. 1999. Maastrichtian sauropod footprints from the Fumanya Site, Berguedà, Spain. *Ichnos* **6**, 239–250.

Sempere, T., Butler, R. F., Richards, D. R., Sharp, W. & Swisher, C. C. III. 1997. Stratigraphy and chronology of Upper Cretaceous–lower Paleogene strata in Bolivia and northwest Argentina. *Geological Society of America, Bulletin* **109**, 709–727.

Suárez Riglos, M. 1995. Huellas de dinosaurios en Sucre. *Association Sucrenes de Ecologia Anuario* **95**, 44–48.

Weishampel, D., Dodson, P. & Osmolska, P. 1991. *The Dinosauria*, 733 pp. (University of California Press, Berkeley).

Wilson, J. A. & Carrano, M. T. 1999. Titanosaurs and the origin of wide gauge trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* **25**, 252–267.