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Orientation and Characteristics of Theropod Trackways from the Las Losas Palaeoichnological Site (La Rioja, Spain)

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The Las Losas site (approximately 500 m^2) was cleared in July 1998 and revealed 375 theropod dinosaur footprints. Statistical surveys of their biomorphical and morphometrical data are congruent with a continuous morphological transition among the theropod footprints—a transition which does not allow us to differentiate ichnogroups.

Certain footprints show a longitudinal groove in their toes. The foot movement of their trackmakers can be inferred from these grooves. There are also, in this outcrop, i) trackways whose ichnites are either regular or anomalous according to the position of crossing, ii) semiplantigrade trackways with digitigrade sections and iii) trackways that cross the footprint site without variation in their footprints. These facts allow us to infer that: i) the substrate hardness was different in different zones at particular moments, and ii) the variation in the regularity and shape of the footprints depended upon the mud conditions at the moment they were made. Three preferential directions of march are shown by the trackways, suggesting different phases of activity.

Keywords Dinosaur, footprints, semiplantigrade, shape variations, mud conditions, Lower Cretaceous, Spain

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INTRODUCTION

La Rioja, Spain, is an area rich in dinosaur footprints, and more than 60 scientific papers and more than 10 popular accounts have been published. During summer fieldwork in 1998, a new site—Las Losas in Enciso (La Rioja)—was cleared (Fig. 1), and 375 theropod footprints of different kinds were recorded on a surface of 500 m^2. The footprint bed extends down slope, and laterally, to other sites exposing the same bed where further ichnites are to be found, even more than 100 m away. The tracks were carefully described by Blanco et al. (2000). The 375 footprints are grouped into (a) 59 trackways, comprising 303 footprints; (b) 36 other footprints, grouped as 18 pairs; and (c) 36 prints which apparently do not have any relationship to the others. All are attributable to the theropod ichnogroup (large and small teropods); there are no ornithopod trackways. The shape and distribution of the footprints and trackways have been studied using both biomorphological and biometrical methods of classification and analysis. The names Theropod, large and small theropod, are used in this paper to distinguish kinds of ichnites and not to identify particular dinosaurs, thus having the same meaning as in the classification of Casanovas et al. (1989).

The site can be located on the 1:50.000 scale National Topographic Map sheet number 280 (ENCISO), its UTM coordinates being 30TWM596671. The geological stratum where the footprints occur is included in the C_{113}^{4c} Unit, according to

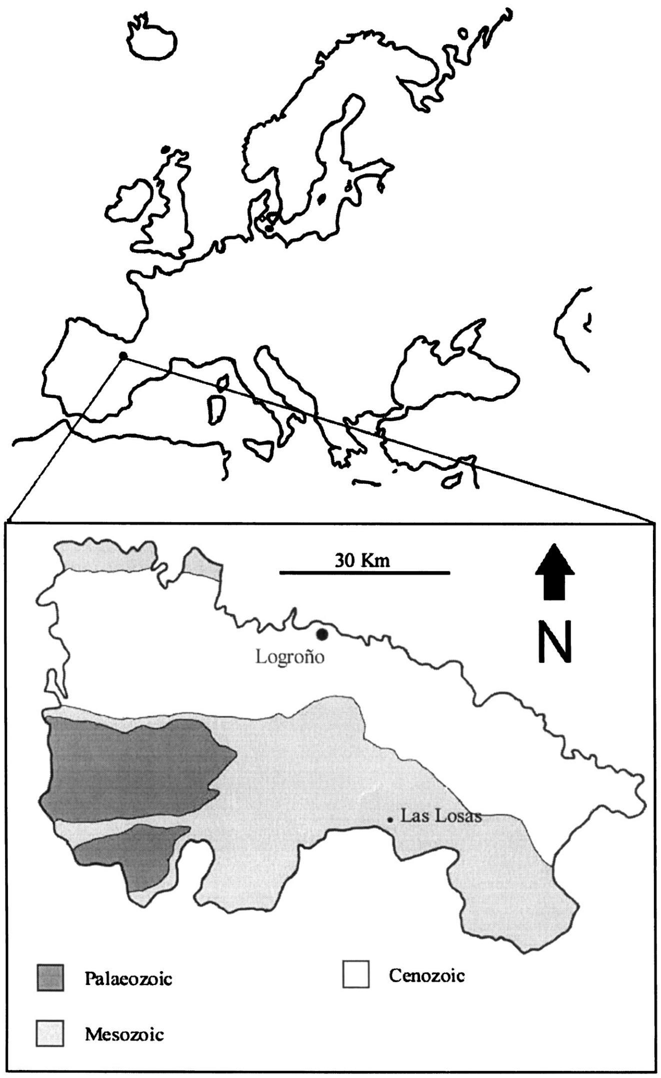

FIG. 1. Location map of the Las Losas site.

Camara and Durantez (1981). This unit is composed of "lime-marl sediments with included sandstone levels." The latest dating indicates that this unit belongs to the Enciso Group (Tischer, 1966) of the Aptian, late Early Cretaceous (Mas and Alonso, 1991; Alonso and Mas, 1993).

According to Blanco et al. (2000), "The footprints are in the surface of a sandstone bed whose direction and dip are N164E, 26E. In addition to the footprints there are many irregularities in the form of small holes, probably due to bioturbation. The present composition of the rock is probably quite different from the original, because of two generalized processes affecting this area, which is close to the highest temperature of the Alpine metamorphism: recrystallization and decalcification. The original composition of this rock would have been a calcareous mud with an unknown quantity of detrital elements of sand and particles of finer size" (translated from Spanish).

FOOTPRINTS AND TRACKWAYS NUMERICAL ANALYSIS

Here the mean values of the different variables (Fig. 2) and ratios obtained for each trackway are analyzed to find out what type of dinosaur footprints are present, the possible differences among them (small and large), and the gaits of their trackmarks.

At this site, the theropod ichnological characteristics are very evident. All are tridactyl or tetradactyl foot marks (when the hallux is printed). The toes are relatively long and well separated. They have an acuminate tip, which indicates that their makers had sharp claws. The α (angle II–III) digital angle is smaller than the β (angle III–IV) one. In some prints there are digital pad-marks.

1. By graphically comparing the footprint length (**L**) and width (**W**) variables, we tried to see whether these dinosaurs had a pes that was longer than wide, as many authors claim. When the straight line **W** = **L** has been drawn, we see (Fig. 3) that most values fall below it, so the proposition is true in this case. If this figure is compared with a similar one (Pérez-Lorente, 1996: Fig. 3) made from a larger population (208 trackways), more values fall above the straight line. In the Las Losas site there are deformed (irregular) footprints and footprints with the interdigital angle value above 60°, so their **II** and **IV** digital tips are widely separate. The soft mud, into which the foot was emplaced, may have been the principal agent determining the great width of the footprints. This fact might explain the values above the straight line.
2. The (**L–W**)/**W** ratios (variation of the foot length in relationship with its width) show that, among 77 trackways and sets studied, there are 51 in which the prints are longer than wide, while just 9 where the reverse is true; in the remaining 7 this ratio cannot be calculated.
3. If the scattering plot (Fig. 4), obtained by comparing the **III** digit length (**LIII**) and pes length (**L**) variables, is compared with the similar one obtained by Pérez-Lorente (1996) from a larger number of cases, we can see that:
   a. All of the cases are also below the **LIII** = **L** straight line and above the **LIII** = 0.5 **L** straight line; in other words, all values, except for two, are higher than 0.5, so they are theropod ichnites.
   b. The Fig. 4 field is correlated with the central zone of Fig. 8 in the above-mentioned paper.

   The ratio **LIII/L** x 100 frequency histogram (Fig. 5) shows most of the values to be above 50, which means these values are adjusted to the posted theropod ichnite limits.
4. If the slenderness (**Sl/L**, Fig. 6) of the hind limb is estimated, we obtain the maximum value of this ratio; this is 10 in large theropod prints (**L** > 25 cm) and 13 in small

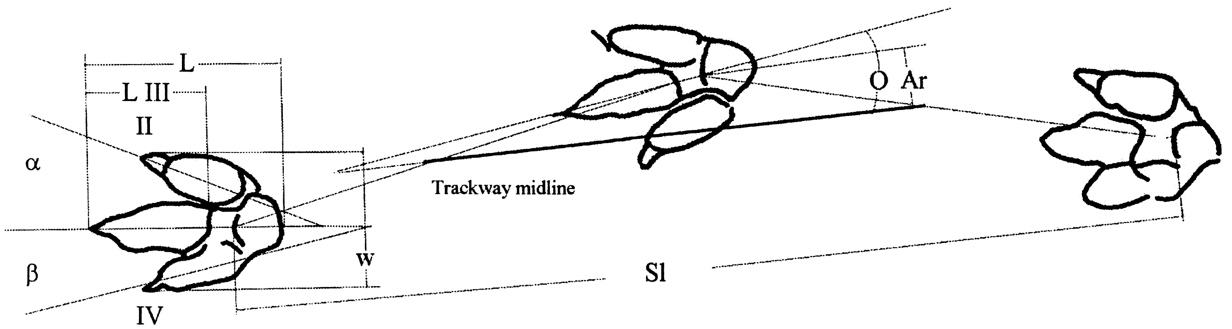

FIG. 2. Trackway and footprint parameters. **L**: footprint length, **W**: footprint width, **LIII**: digit III length, **α**: II-III interdigital angle, **β**: III–IV interdigital angle, **O**: footprint orientation, **Ar**: tackway amplitude, **Sl**: Stride length.

theropod ones (**L** < 25 cm). The maximum modal number of cases is between the values of 6 and 7, which indicates that their makers had relatively slender limbs (Casanovas et al., 1995b).

The 375 footprints are theropods and, according to the division proposed by Thulborn (1990, pp. 145–166), these would include 50 carnosaur (large theropod) and 9 coelurosaur (small theropod) trackways. However, we question that allocation, since there is a continuous size intergradation (see below).

If histograms of the footprint length values are drawn, the columns obtained from the two footprint types (large and small theropod) are complementary, with no abrupt change or variation in modal values. These values do not allow discrimination between the two size-based footprint types. We must therefore utilize other criteria.

The height at the hip (**h**) has been estimated using the Thulborn formula (1990, p. 254). The mode is between 130 and 140 cm, utilizing 12 cases. There is no discontinuity between small dinosaur prints, with lengths less than 25 cm, and larger ones with lengths greater than 25 cm (Fig. 7); consequently we consider the distinction between large and small footprints in Thulborn's scheme (>25 or <25 cm) to be artificial.

Finally, the gait of the tackmakers, their speed and the way in which they put their foot in relationship with the trackway midline are analysed as follow:

- The ratio **Sl/h** (relative stride length) (Fig. 8) has a maximum mode value of between 1.2 and 1.4, so that most of the dinosaurs from this site walked at a moderate speed (Thulborn, 1990, pp. 157–158).
- In Pérez-Lorente's study (1996), the pedal length correlated closely with the stride. This correlation is also observed in the trackways discussed herein (Fig. 9). A lineal regression analysis has been made using the minimal square method (Cao Abad et al. 2001, pp. 84–100) and the following results have been obtained.

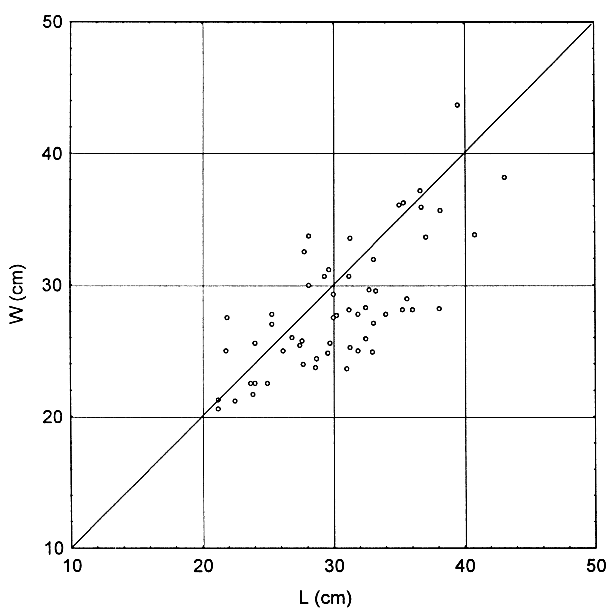

FIG. 3. Footprint length (**L**) and width (**W**) relationship. Arithmetic mean values for footprints in each trackway.

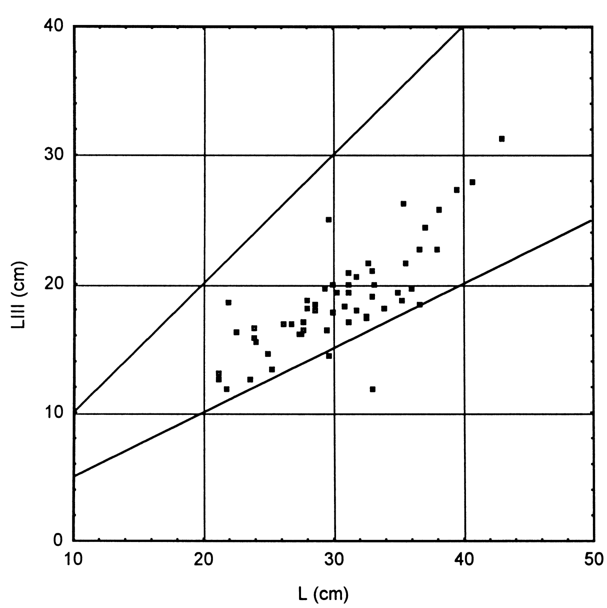

FIG. 4. Footprint length (**L**) and digit III length (**LIII**) relationship. Arithmetic mean values for footprints in each trackway.

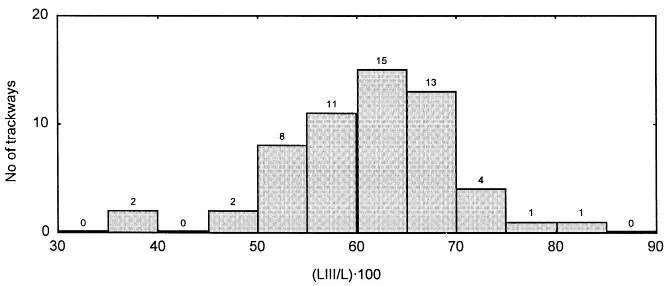

FIG. 5. **LIII/L** x 100 ratio histogram (digit III length/footprint length). Arithmetic mean values for footprints in each trackway.

— Correlation coefficient r = 0.97
— Determination coefficient $R^2 = 0.94$
— Regression coefficient m = +0.2037

This direct relationship (Fig. 9) shows that the theropods, which have longer pedes, also have longer strides. This does not mean, that, with longer pedes, the speed is greater. The speed depends on the stride and also on the height at the hips (see the ratio **Sl/h**, the relative stride length that define three dinosaur gaits: walk, trot and run; Thulborn, 1990).

• The frequency histogram of the footprint orientation (**O**, Fig. 10), or footprint rotation, in sexagesimal degrees, is presented taking in terms of the average footprint orientation value for each trackway. In most trackways the angle between the footprint axis and the midline is 0 to –5 degrees (*sensu* Leonardi, 1987); 65.4% of the trackways have negative or 0° orientation and 34.6% have positive orientation. This proportion is not clearly evident in Fig. 10, since the 0° orientation values are included in the (0,5) intervals. Even so, we can see that most of the trackways indicate a *varus* gait; that is, a gait in which the feet deviate from the direct line-an inward rotated gait. (This is the mechanism by which a bipedal animal, with the body in a horizontal position walks. It puts the centre of gravity over its foot, on the same vertical line, without any appreciable swinging of the body, even at slow speed; the swinging would be very much heigher if the animal had a *valgus* gait or outward rotation—Pérez-Lorente, 2001, p. 196).

• Next we examined whether the larger footprints have negative rotation and the smallest ones positive; or, as Pérez-Lorente (1996) stated, whether the largest theopods have a more *varus* gait than the smallest. The ratio between **L** and **O** (see Fig. 11) shows the following tendencies:

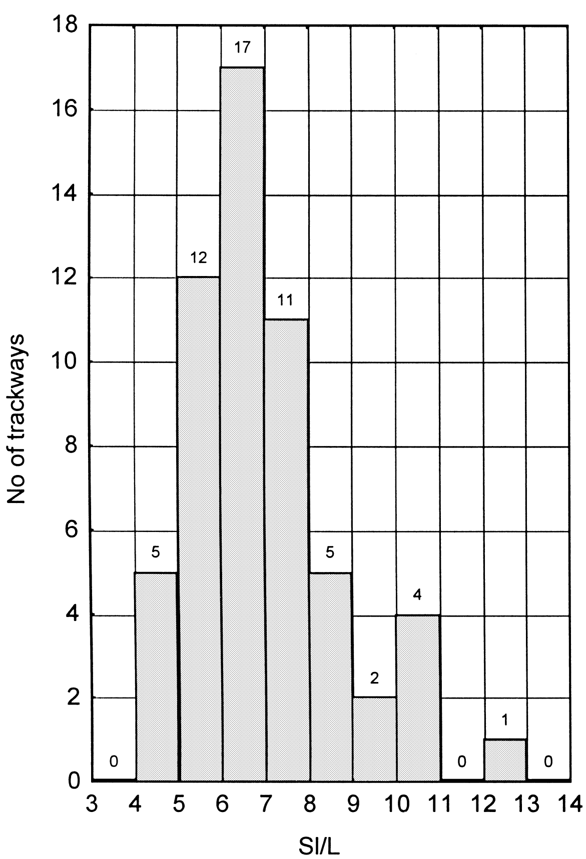

FIG. 6. Histogram of **Sl/L** values (stride length/pes length, or slenderness). Arithmetic mean values for each trackway.

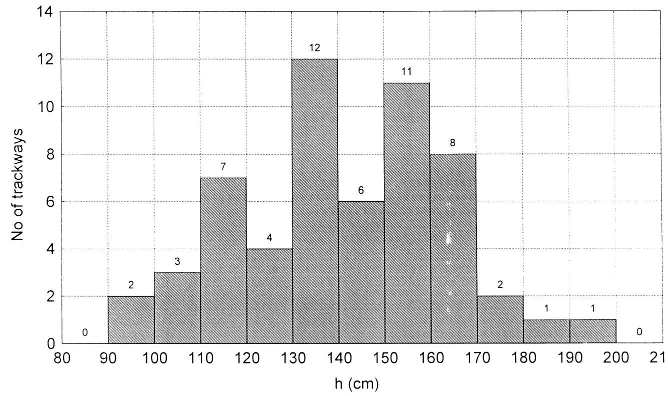

FIG. 7. Histogram of acetabulum height (**h**). Arithmetic mean values for each trackway.

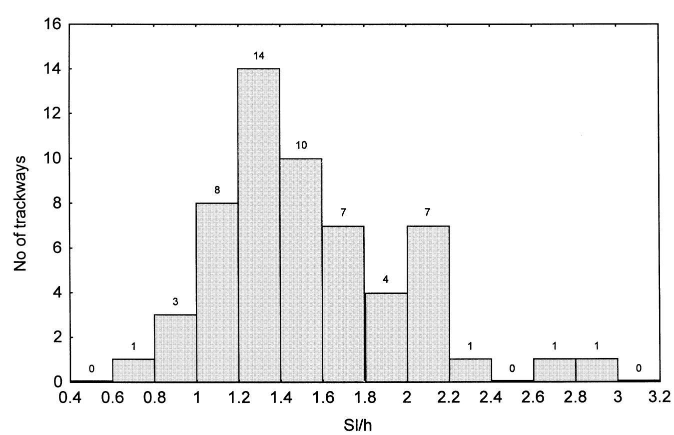

FIG. 8. Histogram of relative stride length (**Sl/h**). Arithmetic mean values for each trackway.

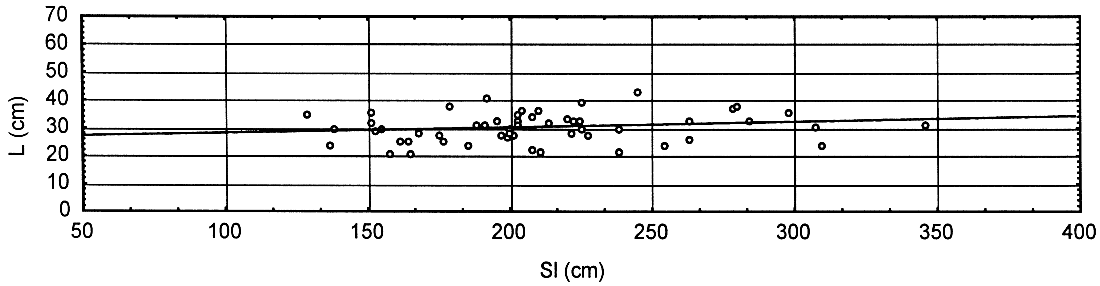

FIG. 9. Stride length (**Sl**) and pes length (**L**) relationship. Arithmetic mean values for each trackway.

—The average orientation value in these trackways is mostly negative.

— If a distinction is made between large and small theropod prints, we can see that there are more positive orientations in small theropod prints and more negative orientations in large theropod prints.

Taking into account the latter tendency (including both types of theropod pints), we can infer that the increase in the pes length is proportional to the increase in the negative orientation. This trend was also found by Casanovas et al. (1995a) in ornithopod footprints; they suggested that it might have anatomical causes.

- The trackways are mostly narrow (Casanovas et al., 1995b). There are 34 trackways with the ratio **Ar/W** below 0.5 (which sugessts that their makers trod the midline). **Ar** is the distance between pes midpoint and the trackway midline. Another 7 trackways whose value is 0.5 (showing they were lightly touching or setting their feet tangentially to the midline), with 9 that trod outside it (Table 1 and Fig. 12). As the **Ar/W** values indicate, the trackways are very narrow, so that most feet trod the midline.

- It is postulated that, when the speed increases, the trackway width must be smaller. The ratio between $\mathbf{v_2}$ (Demathieu, 1986 speed formula) and **Ar** (trackway width) is shown in Fig. 13. When the speed is higher the trackway is narrower, whereas when the trackway width is greater, the speed is slower. The Demathieu speed formula is used here because its values are less variable than those calculated using the Alexander (1976) speed formula.

IRREGULAR FOOTPRINT DISTRIBUTION

Normal footprints and *irregular footprints* have been distinguished from this site. Normal footprints are characterized by three separate and acuminate toes; they were imprinted without any slippage of the foot on the ground or any slumping of the mud into the print. In contrast, the outline shapes of the irregular footprints are due to slippage of the foot on the ground during the W phase (Weight-bearing phase: the foot sinks into the substrate), its movement during the K phase (Kick-off: the foot take off from the substrate) (Thulborn and Wade, 1989), and/or later mud slumping into the prints. The semiplantigrade footprints are placed in the irregular category.

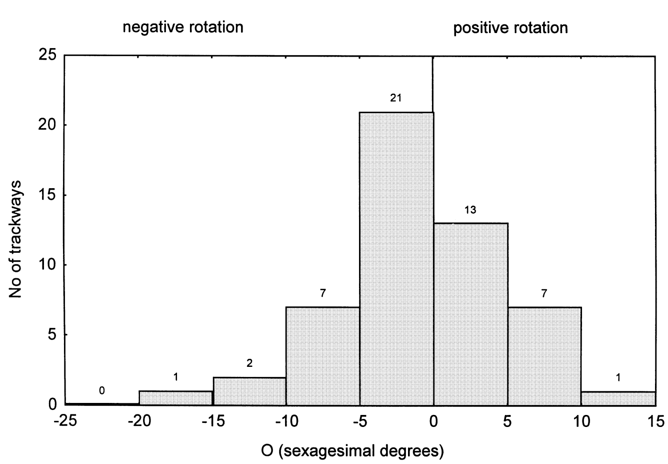

FIG. 10. Histogram of footprint orientation (**O**). Arithmetic mean values for each trackway.

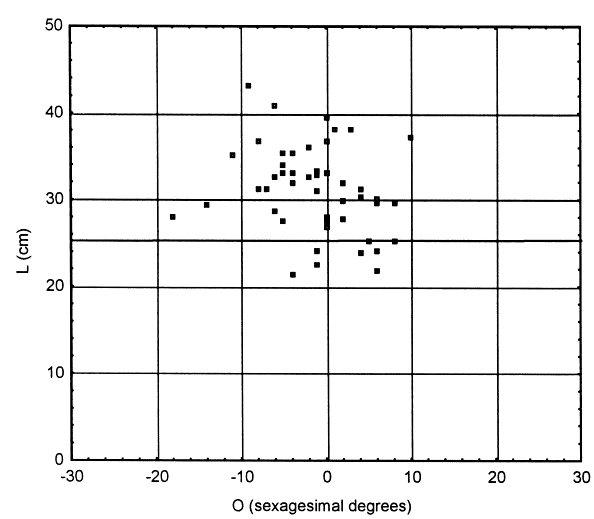

FIG. 11. Footprint orientation (**O**) and length (**L**) relationship. The horizontal line is Thulborn's cut-off between "carnosaurs" (large teropods) and "coelurosaurs" (small teropods). Arithmetic mean values for each trackway.

TABLE 1
Wide trackways.

Trackway	Ar/W	Justification
LL3	0.7	Trackway with not many footprints (3); only one value of **Ar**
LL5	0.9	Trackway with footprints, many strained by the soft mud
LL11	0.7	Trackway with not many footprints (3); only one value of **Ar**
LL12	0.6	Trackway with footprints, many strained by the soft mud
LL13	0.7	
LL40	0.7	**Ar** height in LL40.4 and LL40.5 tracks; the trackway goes out from a flooded zone
LL41	0.6	At the end of the trackway, the midline turns
LL44	0.9	Turning trackway
LL46	0.6	Plantigrade trackway where the trackmaker decreased its speed

If the irregular print areas are mapped, seven sectors (A to G) are recognized, separated by regular print zones. Sector D has been divided into two parts (upper and lower), in relation to the topography of the site (Fig. 20). The criterion used to delineate these zones is that there are many deformed footprints inside, but not outside them. This does not mean that all the footprints in the zones are irregular, since some clearly are not (e.g., LL29, LL32, trackways). In Table 2, we show the trackway distribution in relation to the zones in which they occur. This illustrates how the deformed footprints change into normal ones when they leave one of these soft zones and progress onto a firmer surface. Consequently, it is evident that there were soft mud zones (zones A, B, C, D, E, F, G) between firmer surfaces. When the dinosaur crossed these zones, its footprints might be normal or irregular, according to exactly where it trod (Table 3).

However, some dinosaurs crossed all zones without showing any deformation of the footprints. So there was a period, we do not know whether before or after the implanting of the other footprints, when the whole site area had the same (firmer) mud consistency.

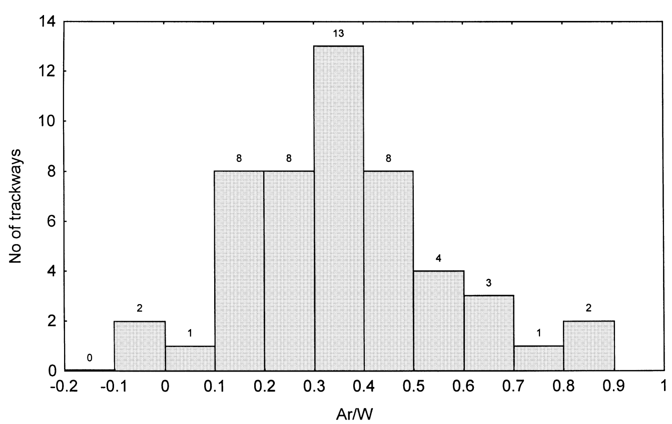

FIG. 12. Histogram of **Ar/W** ratio values (trackway narrowness). **Ar**: distance between pes mid point and the trackway midline; **W**: footprint width. Arithmetic mean values for each trackway.

SEMIPLANTIGRADE ICHNITES

Among the above footprints designated as irregular, some stand out in having a front part with all three main toes (**II**, **III**, **IV**) impressed and an elongated and narrower posterior part. The posterior area may be as long as the front part and may have the hallux impressed (Fig. 14).

The shape of these footmarks might be due to the movement of the foot during the step in a really soft mud (the mud being displaced from where the toe sinks until its withdrawal), or to gravitational collapse of the footprint mud wall toward the inside of the impression. Certain arguments refuting the latter interpretation were set forth by Kuban (1989) and these might apply to this outcrop.

- There are hallux marks whose shape does not indicate foot displacement but the opposite: the foot is supported by the toes and the metatarsus, while the rear of the foot does not trail along the ground. Pes and metatarsus axes are both horizontal during the rest.

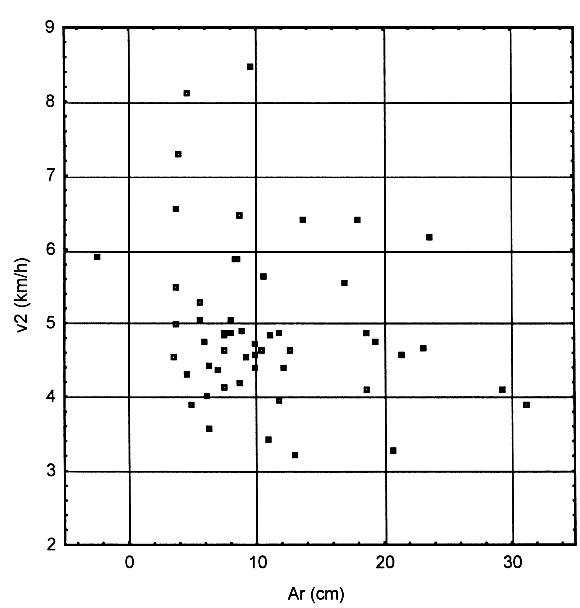

FIG. 13. **Ar** (Trackway amplitude) and $\mathbf{v_2}$ (Demathieu speed formula) relationship. Arithmetic mean values for each trackway.

TABLE 2
Morphological variation of the footprints.

Trackways with deformed footprints in soft mud areas but undeformed in hard areas															
Nº Trackway	A	hard	B	hard	C soft	hard	D upper	hard	D lower	hard	E	Hard	F	hard	G
1	------														
2	----														
4	----														
5			---=												
7		-	---												
8		-	---												
9			-	--											
10			--	-											
12			------												
13				--	==										
14				--	--										
15					--	-									
16					==-=										
17						--	-								
19						---									
20						-	--								
21						--	-	--	-						
22							-	--	-						
24							--	--	-						
25							----	-		----					
27										-----	=				
28										-	====				
30											-----				
31													==--=		
34									---	-	----	--			
36											---	--			
37									---	-	=--	--			
38												--	=--		
40											---	---	-		
41													===--		
42													--		
43													--=--		
44													====		
45													-------	-	
46													====		
47													=---		
51													-	---	
52													----	---	
53													-------	-	
54														---	=-
55														---	--
58														---	--

(continued on next page)

TABLE 2
Morphological variation of the footprints *(continued).*

Trackways with NOT deformed footprints in any area															
3	---														
6			---												
11	---														
18						---									
23							----	---	-						
26										---					
29											----				
32												-	----		
33											-	--			
35												---			
39													--		
Nº Trackway	A	hard	B	hard	C soft	hard	D upper	hard	D lower	hard	E	hard	F	hard	G

(-) footprint
(=) semiplantigrade footprint

- Toe marks survive in the anterior part of the trace, which indicate that although there was a mud collapse, the ichnite shape is not due to distortion of the footprint. We can distinguish the front part (with toe impressions) from the hind part (without toe impressions).
- Except in LL44.2, there are no grooves that indicate movement of the toe to disturb the footprint morphology.
- The footmarks are always wider where the toes are impressed rather than at the metatarsal.

We conclude that the unusual features of the footprints studied are due to the impression of both the toes and the metatarsus (Kuban, 1989), so they are semiplantigrade ichnites. This term is utilized in accordance with Leonardi et al. (1987, pp. 48–49) since the phalanges and metapodium are impressed, but not the basipodium. (The term "plantigrade" has been applied to such footprints by Thulborn (1990, p. 79), Kuban (1989, p. 69), and Lockley (1991, p. 182) but this is incorrect since, as Leonardi et al. (1987) pointed out, that word should be used only when the basipodium is also impressed, which is not the case in these footprints).

The semiplantigrade ichnites occur in two configurations:

1. Traces of the metapodium are as large as those of the acropodium and usually are rounded posteriorly.
2. Marks of the metapodium are smaller than those of the acropodium, with a rounded or angular posterior.

In the first case, the dinosaur probably placed the whole metatarsus on the ground, while in the second scenario, the posterior trace could be due to sinking of the foot, which caused the only most distal part of the metatarsus to be impressed (Aguirrezabala and Viera, 1980).

The metapodium impression axis is at an angle with the digitigrade foot impression axis in footprints LL16.5; LL28.2,.3,.4; LL46.1,.2; LL54.2. This divergence from the normal situation

TABLE 3
Trackway properties.

Crossing a soft mud zone		Crossing a soft and a hard zone		Crossing more than two zones	
Deformed	**Not deformed**	**Deformed in the soft zone**	**Not deformed**	**Deformed in the soft zones**	**Not deformed**
LL1, LL2, LL5, LL12, LL16, LL30, LL31, LL41, LL42, LL43, LL44, LL46, LL47	LL29, LL39	LL4, LL7, LL8, LL10, LL13, LL14, LL15, LL17 LL19, LL27, LL28, LL36, LL38, LL45, LL51, LL52, LL53, LL54, LL55, LL58	LL18, LL32, LL33, LL49	LL9, LL20, LL21, LL22, LL24, LL25, LL34, LL37, LL40	LL23

FIG. 14. LL28 and LL44 trackways.

was explained by Pérez-Lorente (1993); it is related to the non-parasagital anatomical disposition of the digital region respect to the metatarsus. This divergence may be the reason for the arched feature cited by Kuban (1990), although that author related it to the supposed elevation of the metatarsus (as if it were a plantar arch).

The only trackways consisting wholly of semiplantigrade footprints are: LL16, LL28, LL44 and LL46. In most of the trackways, deformed ichnites alternate with normal ones (Table 4). Some trackways show very deep footmarks (e.g. LL44), whereas others are shallow. In LL44 there is a footprint (LL44.2) that has grooves behind it, parallel to the metatarsal axis. The grooves end where the metapodium sinks, so the marks were made by the metapodium when it scraped the ground before sinking.

The semiplantigrade ichnites were probably formed due to one or more of the following reasons (Aguirrezabala and Viera, 1980; Kuban, 1989; Thulborn, 1990):

- This was the resting posture of the dinosaur, where the dinosaur supported its weight on the metatarsus. Some resting traces appear with the impression of the breastbone and ischial callosity as well as the footprints; examples are: *Sauropus barrattii* Lull 1953, *Moyenisauropus natator* Ellenberger 1974 (Thulborn, 1990: pp. 90–91) and *Anomoepus major* Hitchcock 1858 (Gierlinski, 1997).
- The mud was so wet that the animal left the metatarsal print due to two different processes:
  - — The impression was made because the toes sank very deep and because the metatarsus was inclined; it was not perpendicular to the ground (Gatesy et al.,1999).
  - — The impression was made because the dinosaur deliberately leaned on the metatarsus so as not to sink too much. Kuban (1989) inferred that in this scenario the steps should be shorter but this does not happen in many semiplantigrade trackways.
- The prints were made by an animal which progressed in jumps, so the impulse and the cushioning are made principally with the metatarsal segment, which would lean on the ground.
- The impressions are left by a dinosaur with its body near to the ground. The dinosaur might adopt such a posture while eating something from shallow waters.
- The animal walked stooped because it wished to be hidden from its potential prey.

In the Las Losas outcrop, there are ichnites in which all or part of the metatarsus is impressed. One can observe that the semiplantigrade and deformed footprints are grouped in areas where the mud was probably softer. In many trackways the deformed footprints and the semiplantigrade footmarks are intermingled suggesting that they are mainly controlled by the ground conditions.

With regard to Kuban's (1989) claim: ". . . one might expect such prints to show relatively short paces, reflecting more cautious steps. In contrast, many elongate tracks in Glen Rose have moderate to long paces. . . ." In this outcrop, the estimated speed in trackways with semiplantigrade footprints fluctuates between 3 and 11 km/h, quite distinct values although not unusual. This may be because, when walking through the soft ground, the stride changes since the dinosaur was afraid of sinking or slipping, or because the animal wanted to depart quickly. In LL44.2 there are some grooves behind the heel, across the bottom, which indicate the slipping of the toe leaning on the mud. In this case, the pace (155 cm) is much longer than in the rest of the trackway (70 cm approximately), which implies that the dinosaur emphasized the distance between the feet on the ground, probably for one of the reasons suggested above.

Footprints LL46.5 (Fig. 15) and LL46.6 have the metatarsal mark higher than the bottom of the toes, possibly due to the jumping gait mentioned earlier. What is certain is that the pressure made by the digits of the pes was greater than the pressure made by the metatarsal part. Another interpretation is that the dinosaur first set down its foot in the plantigrade position and afterwards raised the metatarsus (Fig. 15). At that moment, the

TABLE 4
Characteristics of the trackways with semiplantigrade prints.

Trackway	Direction	**l** (cm)	$\mathbf{v_2}$ (km/h)	$\mathbf{v_1}$ (km/h)	Semiplantigrade ichnites	Observations
LL4	N195E	37	4	5	LL4.5	
LL5	N295E	61	4	4	LL5.4	
LL13	N286E	40	6	8	LL13.3,.4	
LL16	N200E	39	4	4’5	LL16.1,.2,.3,.5	LL16.2,.4 with metapodium
LL22	N270E	33	4	4’5	LL22.5	
LL25	165E	35	4	5	LL25.7,.9	
LL27	N270E	30	4	5	LL27.4	
LL28	N275E	53	4’5	5’5	LL28.2,.3,.4,.5,.6	LL28.2,.3,.4 with metapodium; LL28.3,.4 hallux mark
LL31	N320E	51	8	11	LL31.1,.2,.5	LL31.1,.2 with metapodium
LL37	N145E	41	6	8	LL37.6	
LL38	N235E		4’5	5’5	LL38.3	Hallux mark
LL41	N85E	40	5	6	LL41.1,.2	
LL43	N165E	40	7	10	LL43.3	
LL44	Variable	67	3	3	LL44.1,.2,.3,.4,.5,.6	All with metapodium; the last four with hallux mark
LL46	N255E	54	4’5	5’5	LL46.1,.2,.3,.4,.5,.6,.7	All with metapodium; the first two with hallux mark
LL47	N225E	39	6	10	LL47.1	
LL54	N185E		6	7	LL54.2	With metapodium
Sets					LL61.2	
					LL70.2	
					LL71.1	
Isolate					LL88	
Footprints					LL98	

$\mathbf{v_1}$ speed calculated using Alexander (1979) formula.
$\mathbf{v_2}$ speed calculated using Demathieu (1986) formula.

TABLE 5
Orientation and characteristics of the trackways.

Direction of trackway	**Trackways**	**Semiplantigrade trackways**	**Not deformed**	**With longitudinal grooves**
WNW	LL1, LL5, LL6,LL9, LL13, LL17, LL22, LL27, LL28, LL29, LL30, LL31, LL38, LL39, LL42, LL43, LL46, LL47, LL48, LL50, LL55, LL57	LL5, LL13, LL27, LL28, LL31, LL38, LL43, LL46, LL47	LL29, LL50	LL13, LL30, LL48, LL55, LL57
E-ESE	LL3, LL11, LL12, LL14, LL18, LL20, LL21, LL23, LL24, LL26, LL36, LL41, LL49	LL41	LL3, LL11, LL18, LL23, LL26, LL36, LL49	LL18, LL36, LL49
Variable	LL4, LL7, LL8, LL10, LL15, LL16, LL19, LL25, LL33, LL34, LL35, LL37, LL40, LL43, LL44, LL45, LL51, LL52, LL53, LL54, LL58, LL59	LL4, LL16, LL25, LL37, LL44, LL54	LL34, LL35	LL51, LL52, LL53, LL58

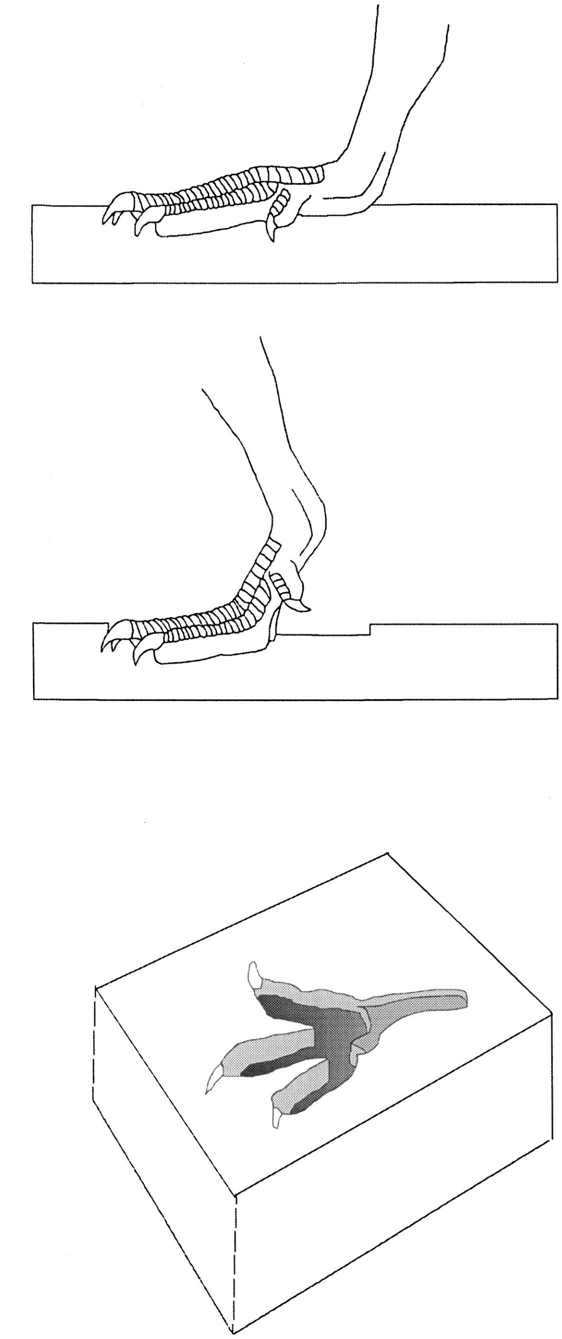

FIG.15. LL46.5 footprint and supposed dinosaur foot movements.

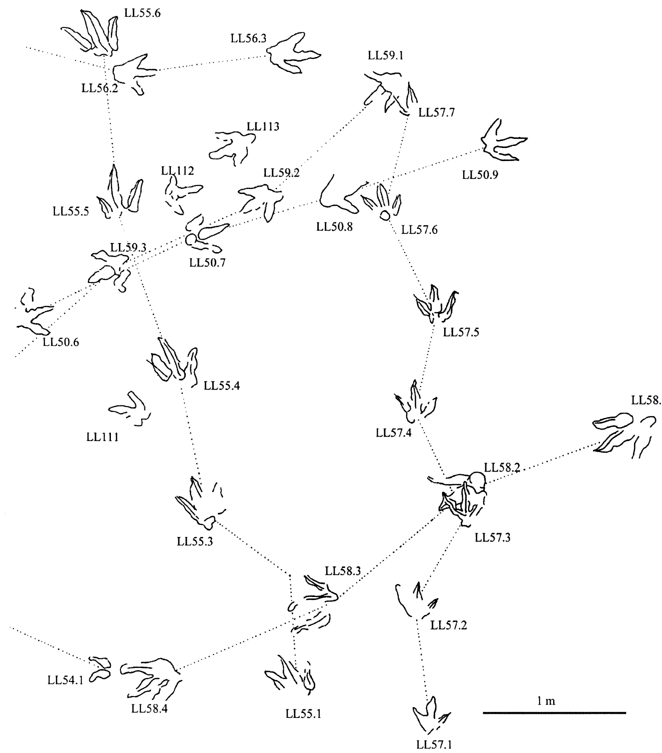

FIG. 16. Footprints with longitudinal toe grooves.

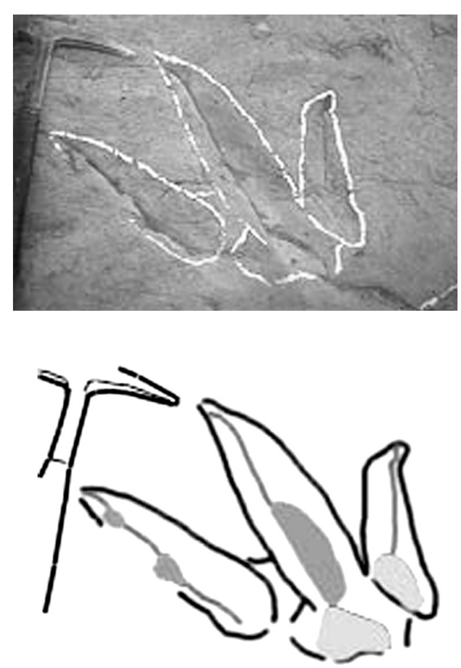

FIG. 17. LL55.6 footprint. The lines in the toes axes are the longitudinal grooves, the dark grey areas are the mud gravitational collapse areas and the clear grey areas are mud mound at the posterior ends of the grooves.

whole weight would be on the toes, in such a way that they sank much deeper.

To sum up, the ichnites of the Los Losas outcrop were made due to a variable gait, from digitigrade to semiplantigrade, when the dinosaurs crossed areas with softer mud.

FOOTPRINTS WITH LONGITUDINAL TOE GROOVES

Some trackways (Table 5) and isolated ichnites have a long, narrow, and shallow longitudinal groove in their toes (Fig. 16). This groove starts at the distal end of the digital impression, or a bit further forward, and it ends in a variable position but in general inside the footprint, near the proximal part of the impression of the toes.

Depending on the ichnite examined, one, two, or three grooves can be observed. The course of the grooves may be straight, curved, or with a sigmoid shape, but always converges on the back part of the footprint. Sometimes there is a little mud mound at the posterior ends of these grooves. In other cases, the grooves are interrupted by mud lumps that were caused by the mud falling after the claws passed (Fig. 17). These traces were caused by the claws on the ground during the B and K phases (Thulborn and Wade, 1989).

Some footprints are deformed by the mud collapse after the K phase. Some longitudinal grooves are irregular due to lateral mud collapse. The accumulated mud at the end of the grooves may fall into the groove, covering a portion of it.

An important feature is the convergence of the three grooves on the proximal part of the print (Figs. 17, 18), which indicates that the toes were closing during the backward movement of the pes, as was the joint angle between the zeugopodium and metapodium. These movements aided the flexion of the toes.

TRACKWAY ORIENTATIONS AND DIRECTIONS

The trackways directions or movement have been measured to determine the trackway arrangements (Fig. 19). Four maxima, E-ESE, S, SW, and WNW, are observable in these graphic measures. By using the above maxima, the trackways with the same direction were grouped on the site map (Fig. 20). When this trackway direction map is examined, the E-ESE and WNW direction tracks are especially noteworthy (Figs. 21, 22).

The remaining tracks, most of whose directions are S, SW and even SE, indicate a rotational movement of the trackmakers, as can be seen in Fig. 23. By examining the site in this way, the initial chaos disappears and all the trackways, except four, are grouped by common directions (groups: E-ESE: Fig. 21, WNW: Fig. 22 and S-SW-SE: Fig. 23).

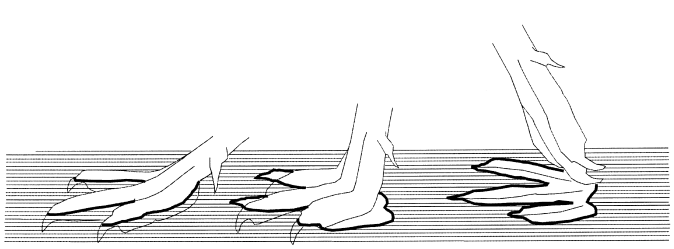

FIG. 18. Supposed dinosaur foot movement.

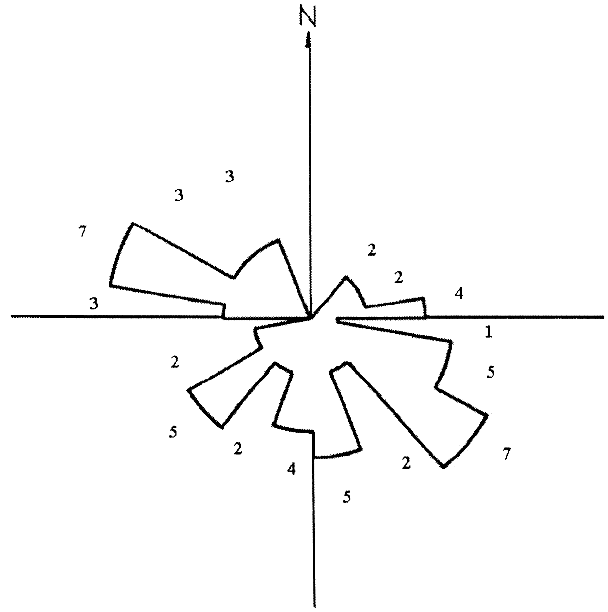

FIG. 19. Trackway orientations. The numbers indicate the number of trackways in each lobe.

Most of the undeformed tracks in the soft mud zones are in the group of trackways with E-ESE directions. Most of the semiplantigrade tracks are in the other two groups. Footprints with longitudinal grooves are present in all three groups.

The first conclusion is that the trackmakers whose direction is E-ESE trod on this site when the mud conditions were uniform all over the area. The second is that these were dinosaurs going in the same direction. This can be explained either by gregarious behavior or by environmental conditions or natural barriers that caused their makers to go in these directions. The tracks indicating changing direction suggest a group of dinosaurs that did not walk so closely together.

CONCLUSIONS

First, the statistical survey of measurement data is concordant with other surveys suggesting that: a) Different types of theropod dinosaurs are not inferred as makers of the large (more than 25 cm) and (less than 25 cm) theropod footprints. b) Theropod dinosaurs had "varus" gait (inward rotation of their foots) and the largest theropods had more "varus" gait than the smaller ones. c) Theropod dinosaurs left narrow trackways and narrower when they increased their speeds.

Second, the longitudinal toe groove marks are proof of the backward retraction movement of the trackmaker's toes during the K phase.

Finally, careful study of the orientation and the different modes of deformation (depth, semiplantigrade or no semi-

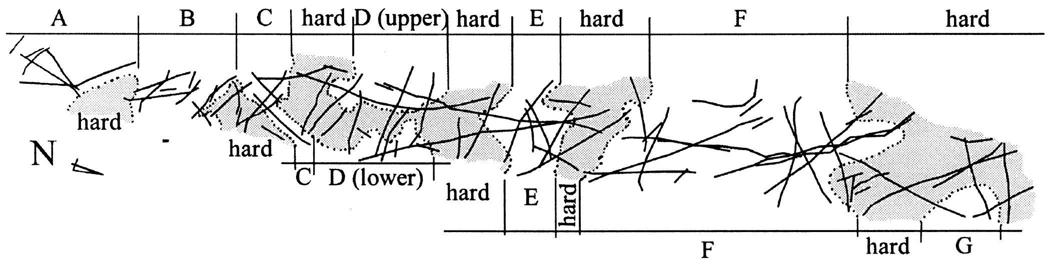

FIG. 20. Map of the Las Losas site. The lines are midline trackways, the shadow areas are the hard mud areas and the black areas (A, B, C, D upper, D lower, E, F and G) are the soft mud areas.

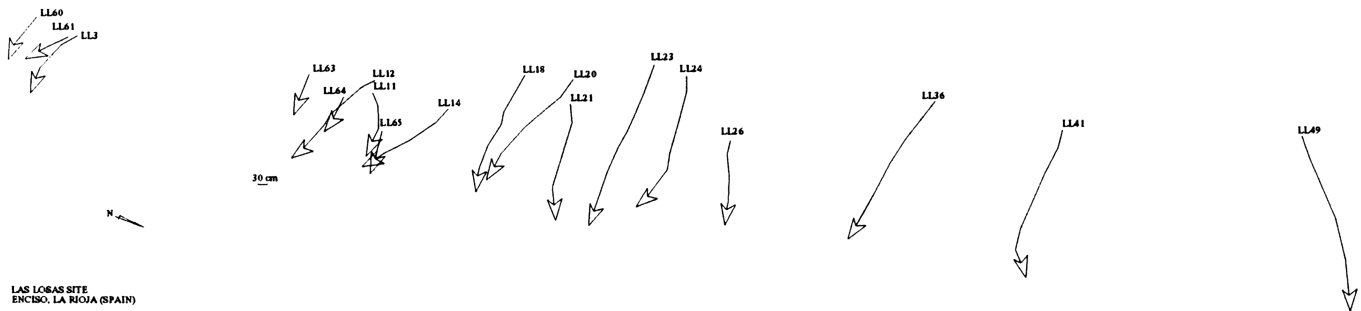

FIG. 21. Trackway midlines whose directions are E-ESE.

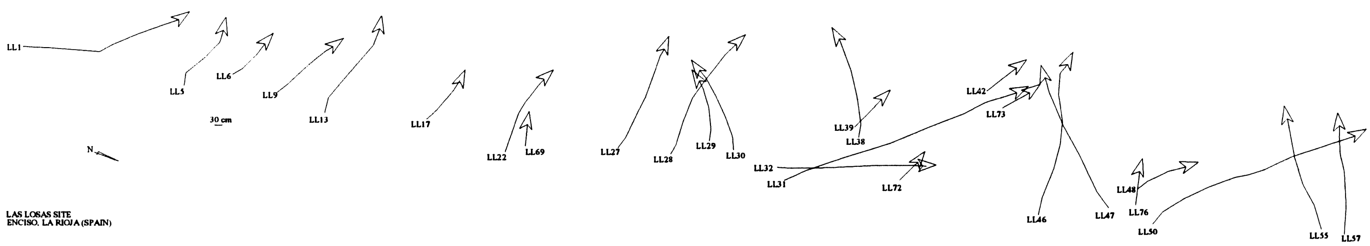

FIG. 22. Trackway midlines whose directions are W-WNW.

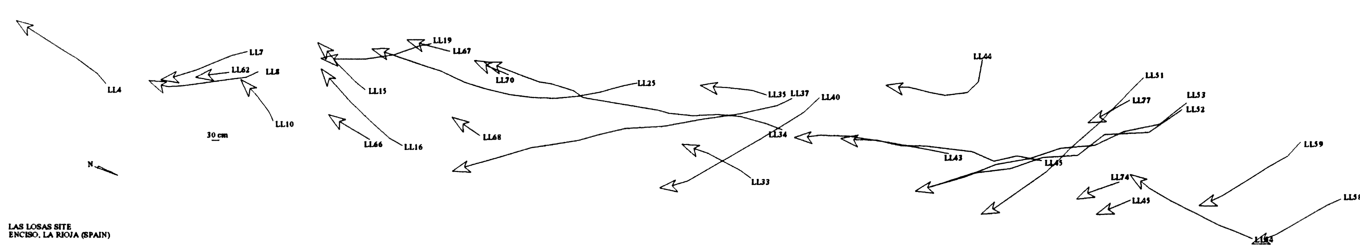

FIG. 23. Variable direction trackways.

plantigrade, mud collapse features, etc.) across a large site, with many trackways, show considerable variation within a small area. This allows us to identify soft and firm areas of substrate and to suppose different phases of activity, as suggested by track orientations. They show the potential of tracks for giving insight into the complex local substrate conditions that exist at tracksites, and how these relate to the spatial and temporal history of trackmaking activity.

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