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TRACKWAY EVIDENCE FOR A HERD OF JUVENILE SAUROPODS FROM THE LATE JURASSIC OF PORTUGAL[1]

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ABSTRACT: **Studies of fossil footprints in Upper Jurassic carbonates at Lagosteiros Bay - Cabo Espichel, Sesimbra Region, Portugal, reveal the presence of multiple track-bearing levels with abundant trackways of sauropods. One level reveals good evidence for a herd of at least seven small sauropods that moved towards the southeast. All had similar foot sizes and wide-gauge trackways indicative of an age group of a single species. They were evidently accompanied by at least three larger individuals, also with wide-gauge trackways, that were also moving in approximately the same direction. This is the first convincing example of sauropod herd behavior reported from a European tracksite. It also provides the best known example of herding amongst juvenile sauropods. The Cabo Espichel trackway evidence for herding is compared with other tracksite evidence for brontosaur gregarious behavior and the implications for social behavior are considered.**

RESUMO: **Os estudos sobre pegadas de dinossáurios realizados no Jurássico superior da Baía dos Lagosteiros - Cabo Espichel (Sesimbra, Portugal), permitiram localizar várias camadas com abundantes pistas de saurópodes. Um dos níveis icnológicos possui um bom testemunho de uma manada de, pelo menos, sete saurópodes de pequenas dimensões que se moviam para sudeste. Todos os animais deixaram pegadas com dimensões idênticas e pistas largas ("wide-gauge"), o que indica um grupo etário de uma única espécie. Este grupo estava acompanhado por três indivíduos de grandes dimensões, que também deixaram pistas largas e se deslocavam aproximadamente na mesma direcção. Este é o primeiro exemplo convincente de comportamento gregário nos saurópodes, reconhecido numa jazida icnológica europeia, bem como o melhor testemunho conhecido de tal comportamento entre saurópodes juvenis. A jazida da Baía dos Lagosteiros, com o conjunto de pistas que evidenciam comportamento gregário, é comparável a outras jazidas e fornece importante informação com implicações no conhecimento do comportamento social dos dinossáurios.**

INTRODUCTION AND PREVIOUS WORK

The present study is part of a cooperative study of dinosaur tracksites in Portugal aimed at revealing new insights into the paleobiology of Late Mesozoic dinosaurs. As previous work has shown, evidence of dinosaurs is quite common in Portugal (see GOMES, 1915-1916; ANTUNES, 1976, 1989 and SANTOS, 1990,

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for preliminary reports on tracksites and DANTAS, 1990, for review of skeletal evidence). Prior to the 1990's there had been no systematic attempt to study dinosaur tracksites in Portugal. However, in the wake of the so called "Dinosaur Footprint Renaissance" (LOCKLEY & GILLETTE, 1987; LOCKLEY, 1991a), there has been growing interest in dinosaur ichnology around the world, and a corresponding increase in publications in this field (LOCKLEY, 1991b; THULBORN, 1990). For example the authors are currently engaged in a systematic survey of dinosaur tracksites in Portugal (SANTOS, 1990), and have now published preliminary reports and new interpretations on a number of sites (see SANTOS *et al.*, 1992; LOCKLEY *et al.*, 1992b; LOCKLEY & SANTOS, 1993; DANTAS *et al.*, 1994; MEYER *et al.*, 1994; LOCKLEY *et al.*, 1994a, b and this paper). Taken together, this new spate of publications on Portuguese dinosaur ichnology indicates that the late Mesozoic, in particular the Late Jurassic carbonates of the Sesimbra region, are a particularly fruitful area for research. To date we have reported on the first good examples of Late Jurassic brontosaur tracks with well-preserved manus and pes digit impressions, what is probably the smallest sauropod trackway in Europe (smallest individual sauropod trackmaker), evidence of a limping sauropod and the first european examples of manus dominated sauropod trackways (see references cited above). The purpose of this paper is therefore to report on another new tracksite that provides compelling evidence for a herd of juvenile brontosaurs.

GEOLOGY AND STUDY METHODS

Between the autumn of 1992 and the summer of 1993 we conducted field work in the Sesimbra region to determine the extent of dinosaur track-bearing horizons in the Late Jurassic carbonates of this region. Maps and preliminary results from the Avelino tracksite (LOCKLEY & SANTOS, 1993) and the Zambujal quarry site (LOCKLEY *et al.*, 1992b) have already been published, indicating a rich pre-Portlandian (Kimmeridgian) track record in this area. The focus of this study however, is the Portlandian track-bearing deposits that crop out on the south side of Lagosteiros Bay below the monastery at Cabo Espichel.

We measured the stratigraphic section in this area, and determined that there were at least eight track-bearing levels in this sequence (Fig. 1). The succession consists of shallow water carbonates assigned to the Upper Portlandian or Portlandian B (RAMALHO, 1971, 1988). ANTUNES (1976) published a photograph of sauropod tracks that are easily visible just above the high tide line on what we now refer to as level 5 (see MEYER *et al.*, 1994: fig. 2). These are the tracks that have been referred to as "Pegadas de Mula" (ANTUNES, 1976; SANTOS, 1990; SANTOS *et al.*, 1992; LOCKLEY *et al.*, 1994a). However, prior to this study, no other tracks had been documented at any other levels.

We herein report on our preliminary efforts to map and document trackways at level number three (Fig. 1-3). Due to the very extensive, uncovered or "clean" and steeply-dipping bedding planes, the cliffs at Cabo Espichel present an excellent opportunity to see well-exposed trackways. In our preliminary reconaissance we scanned the cliffs with binoculars then photographed the outcrops to obtain enlarged photographs. This revealed an abundance of trackways, but it was not possible to identify the trackway types, their orientations or detailed trackway parameters from such long-distance surveys. Thus we had to climb the cliffs to map and measure the trackways on the outcrop.

The inclination of the cliffs at 40° or more is such that they are difficult to ascend safely. An experienced mountaineer could probably climb them without ropes, but this is not recommended. In order to work safely, and for prolonged periods of time, we ascended the cliffs with ropes and secured climbing bolts every 25 m. In this position we were secure, though not protected from the danger of falling rocks dislodged by wind, seagulls, curious spectators and tourists looking down from above. We used a tape measure, laid out directly up and down dip, as a base line or transect and mapped in at least six consecutive steps in the area where each trackway crossed the transect line. We also obtained measurements of footprint size, step and stride length and trackway width, for all trackways except number 1, which was difficult to access safely. Subsequently with enlarged photographs we were able to fill in the remaining sequence of steps in each trackway and complete an accurate scale map (Fig. 2). The two large sauropod trackways and the theropod trackway exposed on the same surface at the bottom of the cliff were also mapped, but without the need for safety ropes.

RESULTS

We recorded details of the carbonate lithology and fossil content at all levels in the section, including track-level three. These details will be published elsewhere, and are summarized only briefly herein. The track bed is rich in the remains of invertebrates including foraminifera, bivalves and gastropods. We also recovered isolated turtle bones attributable to the Plesiochelydae. The surface and upper part of the track bed also exhibits extensive invertebrate bioturbation (cf. *Thalassinoides*).

The results of our mapping indicate that at least twelve trackways are preserved on the surface of track bed three (Fig. 2-3). Of these eleven are those of sauropods and one is attributed to a tridactyl biped, probably a theropod. We numbered the trackways from the top of the exposure (the south) down the

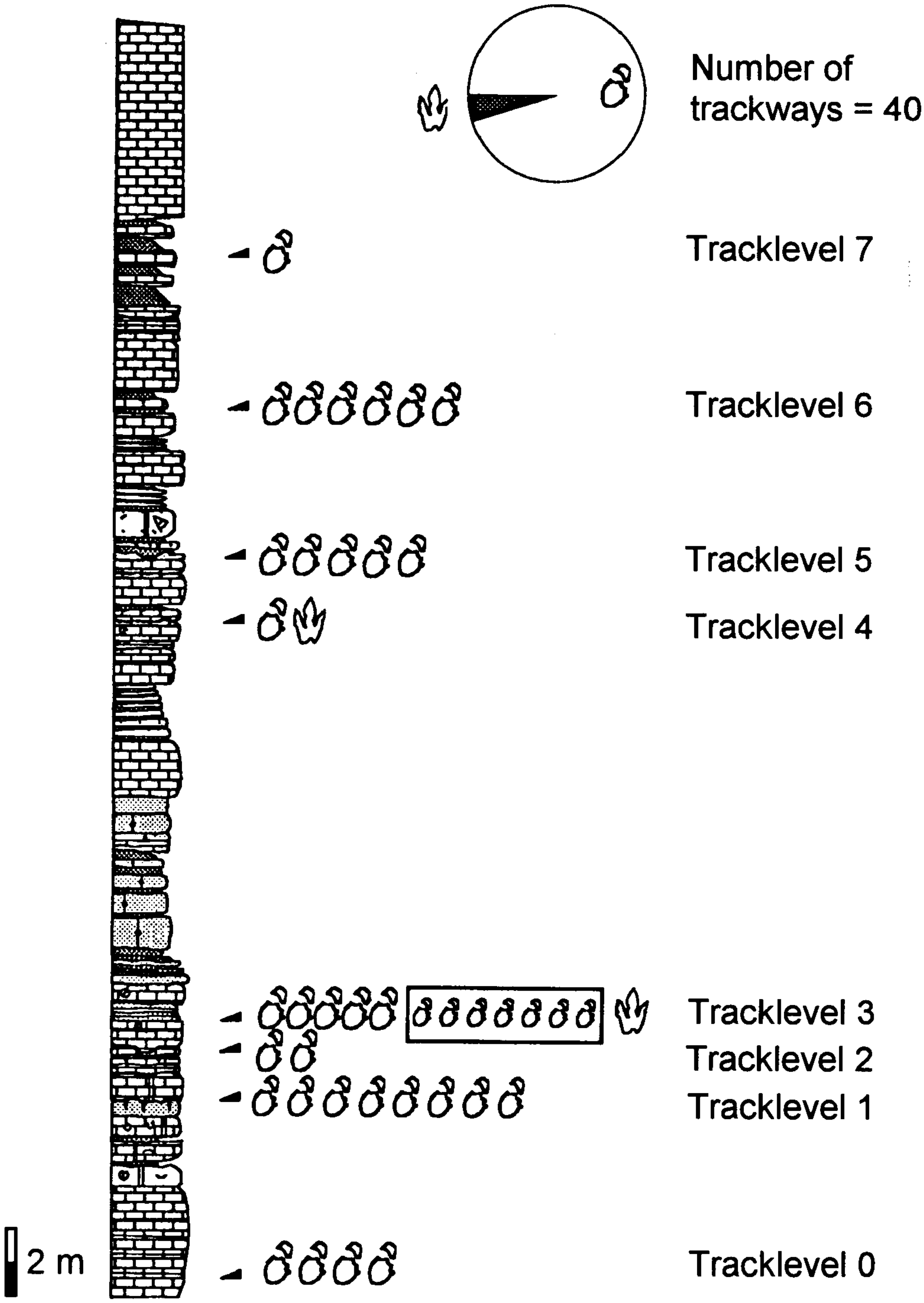

Fig. 1 - Stratigraphic section of Portlandian rocks on the south side of Lagosteiros Bay, showing track-bearing levels discussed in text.

cliff (to the north). Trackways 1-7 represent small individuals with pes lengths between 38 cm and 46 cm, and trackways 8, 10 and 11 represent larger individuals with pes lengths between 70 cm and 73 cm (TABLE I). Trackway 9 represents a manus-only trackway of a large sauropod in which only the right manus is well preserved (shown in black in Fig. 2). Trackway 12 represents a theropod dinosaur with a footprint length of 42 cm and width of 35 cm.

To determine the sauropod trackway gauge, we measured the distance between the inside margins of the pes tracks on all trackways except numbers 1 and 9. Our results clearly show that all the sauropod trackways on this surface have relatively wide-gauge

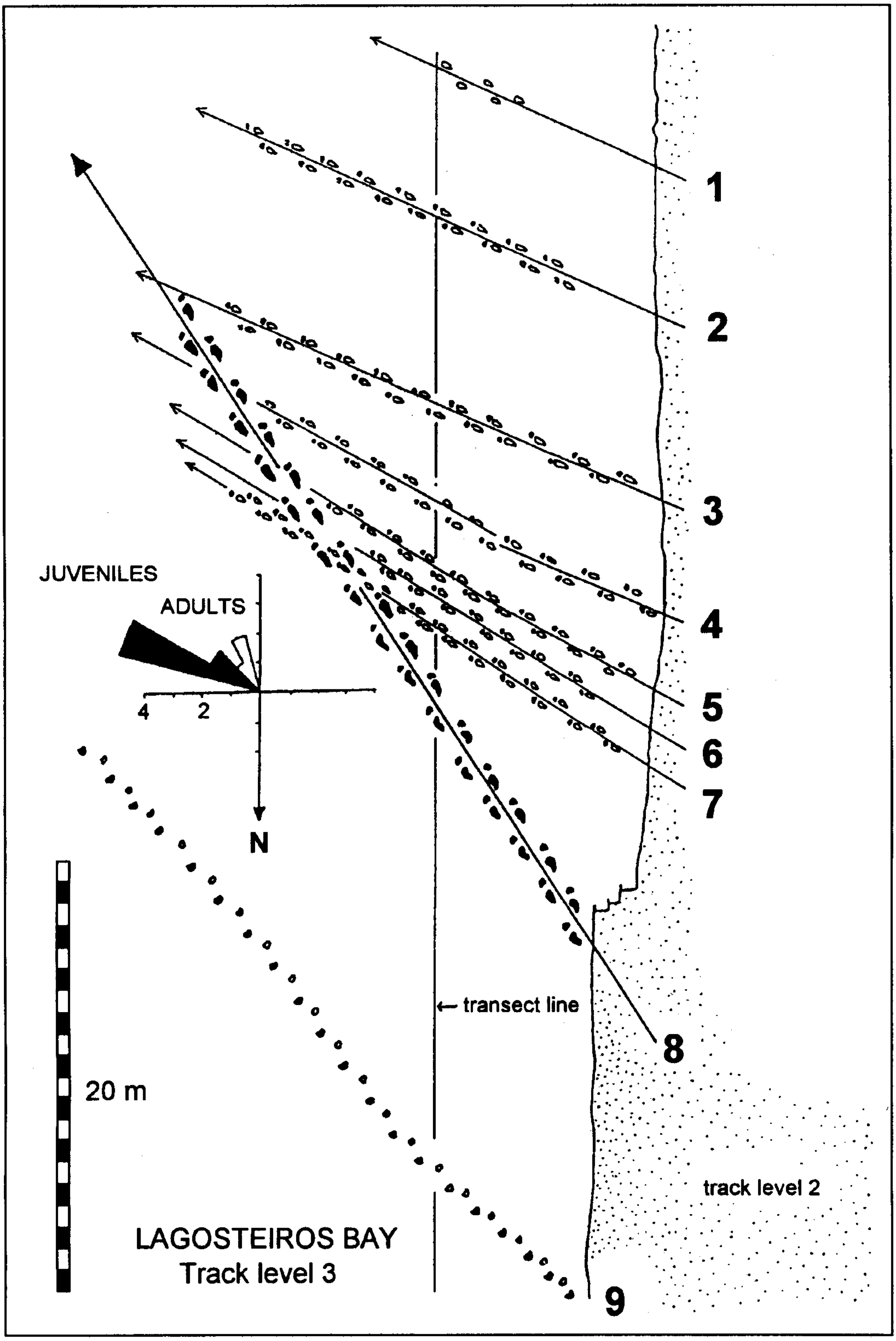

Fig. 2 - Map of track-bearing bedding plane number 3 exposed on upper part of cliff, south side of Lagosteiros Bay. Trackways of small brontosaurs numbered 1-7; trackways of large brontosaurs numbered 8-11 (see Fig. 3 for Nº 10 and 11). Trackway Nº 9 is dominated by right manus tracks.

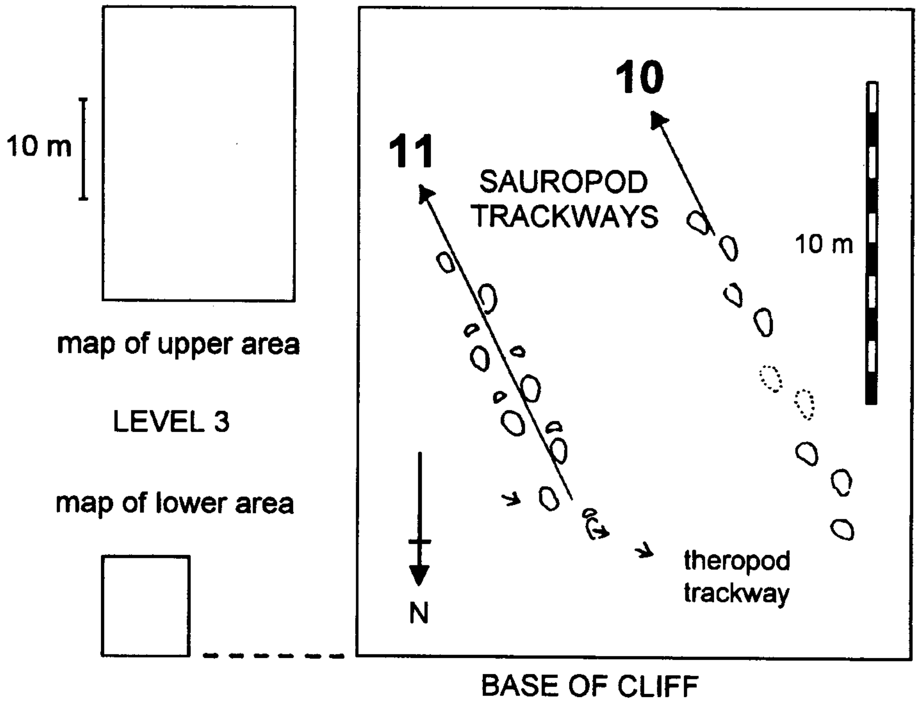

Fig. 3 - Map of track-bearing bedding plane Nº 3 exposed on lower part of cliff, south side of Lagosteiros Bay. Note orientation of sauropod trackways in relation to those recorded on map of upper area (Fig. 2). Both mapped areas presented with the same orientation.

TABLE I
Trackway measurements for track bed 3, Lagosteiros Bay (Upper Jurassic).

	TRACKWAY Nº	PES LENGTH	PES WIDTH	STRIDE	GAUGE*	SPEED $m.s^{-1}$
Small Brontosaurs (1-7)	1	-	-	-	wide	-
	2	46	30	210	42	1.32
	3	38	25	190	45	1.39
	4	40	28	182	54	1.21
	5	42	25	200	28	1.35
	6	45	30	175	42	1.00
	7	40	30	170	35	0.95
Large Brontosaurs (8-11)	8	70	55	230	(45)	0.93
	9	-	-	200	-	-
	10	70	45	260	-	1.15
	11	73	44	265	50	1.45
Theropod		42	35			

All measurements in cm. Speed (v) calculated using: $v = 0.25g^{0.5}.\lambda^{1.67}.h^{-1.17}$; where g - gravitational acceleration, λ - stride length and h - hip height (estimated as 4 x footprint length). (*) Distance between inside margin of hind footprints, measured perpendicular to the trackway axis, see text for details.

trackways (*sensu* FARLOW, 1992; MEYER *et al.*, 1994: fig. 4). In addition we measured trackway orientations and found that the small trackmakers (1-7) were heading towards the east south east (ESE) and the larger ones, 8, 10 and 11 were progressing towards the southeast (SE) (Fig. 2-3). The manus dominated trackway indicates an animal moving in the opposite direction towards the northwest (NW). We also calculated the speed of the sauropods using the formula of ALEXANDER (1976), see TABLE I. The results show that the small brontosaurs were travelling at between 0.95 and 1.39 $m.s^{-1}$ ($=3.4$-5.0 $km.h^{-1}$) and the large ones at 0.93-1.45 $m.s^{-1}$ ($=3.3$-5.2 $km.h^{-1}$). These are typical walking speeds for sauropods (LOCKLEY, 1987; THULBORN, 1990), and suggest no significant difference in velocities of the small and large individuals.

INTERPRETATION OF TRACKWAYS

It is clear from the trackway maps (Fig. 2-3) that there is a strong preferred orientation for the small trackmakers (between 114 and 122°) and for the large trackmakers (between 145 and 155° for numbers 8, 10 and 11). This suggests a small herd or group of subadult or juvenile individuals moving purposefully together in the same direction (Fig. 4), and a smaller number of larger (adult) individuals moving in the same general direction, but with their own distinct orientation that was slightly oblique (about 30°) to the direction of travel of the smaller group. It seems highly unlikely that the seven small trackways heading ESE, or the three large trackways heading SE, bear no relationship to one another. On the contrary, evidence from other tracksites suggests that sauropods and other dinosaurs sometimes travelled in distinctive size groups, each with distinctive preferred directions. Such evidence argues against the trackways representing isolated individuals that passed by at different times. The NW orientation (towards 320°) of the manus dominated trackway, and the obviously different mode of preservation, can be used to suggest that the trackmaker passed by at a different time from all the other sauropods, when substrate conditions were different.

DISCUSSION

Large samples of sauropod trackways are now known from several sites around the world including Texas (BIRD, 1944), Colorado (LOCKLEY, HOUCK & PRINCE, 1986; LOCKLEY & RICE, 1990), South Korea (LIM, YANG & LOCKLEY, 1989; LIM *et al.*, 1994), Morocco (ISHIGAKI, 1989), Portugal (LOCKLEY & SANTOS, 1993) and Switzerland (MEYER, 1990, 1993). In the former two examples, Texas and Colorado, parallel trackways provide compelling evidence for gregarious behavior among the trackmakers. The Texas examples, from the Paluxy River and Davenport Ranch sites respectively, were the first reported trackway evidence for herds of at least 12 and 23 sauropods (BIRD, 1941, 1944). These reports have become classic examples of trackway evidence for social behavior that have been cited on many occasions (OSTROM, 1972; LOCKLEY, 1987, 1989, 1991b; THULBORN, 1990). The Colorado site, known as the Purgatoire Valley dinosaur tracksite, has revealed evidence of at least twelve parallel trackways including five very well-preserved examples made by subadult sauropods that were very similar in size. The Korean sites have yielded a large sample that includes many of the smallest known sauropod trackways, but no good evidence of herding.

Comparisons of the size of the Texas and Colorado trackmakers with those from Portugal reveal the following. Trackways from Davenport Ranch, Texas, average 53 cm long (range 35-78 cm) with no obvious clustering of larger and smaller animals. Tracks from the Purgatoire Valley site, Colorado, are also variable in size, but include one obvious grouping of 5 parallel trackways with an average foot length of 57 cm (range 52-60 cm). By contrast the six measured, small sauropod trackways from Lagosteiros Bay, Portugal, show an average length of 42 cm (range 38-46 cm; TABLE I). Thus the Portuguese tracks are only 79 and 74% respectively of the size of the tracks from Texas and Colorado, and are thus the best evidence available for small brontosaurs travelling in groups.

A full review of dinosaur tracksites that reveal evidence of gregarious behavior is outside the scope of this paper, so we have mainly confined ourselves to a discussion of sauropod tracksites. However it is worth mentioning that a number of Cretaceous ornithopod tracksites have been described where there is evidence of gregarious behavior. At the Mosquero Creek site in New Mexico for example trackways indicate that small ornithopods were travelling in one direction, and large ones in the opposite direction (LOCKLEY *et al.*, 1992a; LOCKLEY, MATSUKAWA & HUNT, 1993). This strongly suggest that trackways allow ichnologists to identify various size or age groups, particularly in the large trackway samples that are attributable to gregarious dinosaur species (LOCKLEY, 1994). Based on tentative age estimates recently proposed by LOCKLEY (1994) the Portuguese sauropod trackmakers would probably have been no more than one to two years old.

We note that the dinosaur track assemblages (ichnocoenoses) in the Upper Jurassic carbonates of the Sesimbra region are heavily dominated by the trackways of sauropods. This means that they can be assigned to the *Brontopodus* ichnofacies (*sensu* LOCKLEY, HUNT & MEYER, 1994; LOCKLEY & HUNT, *in press*). This ichnofacies is particularly well represented in the Upper Jurassic of Portugal, the Upper Jurassic of Switzerland (MEYER, 1993) and the Lower Cretaceous of Texas.

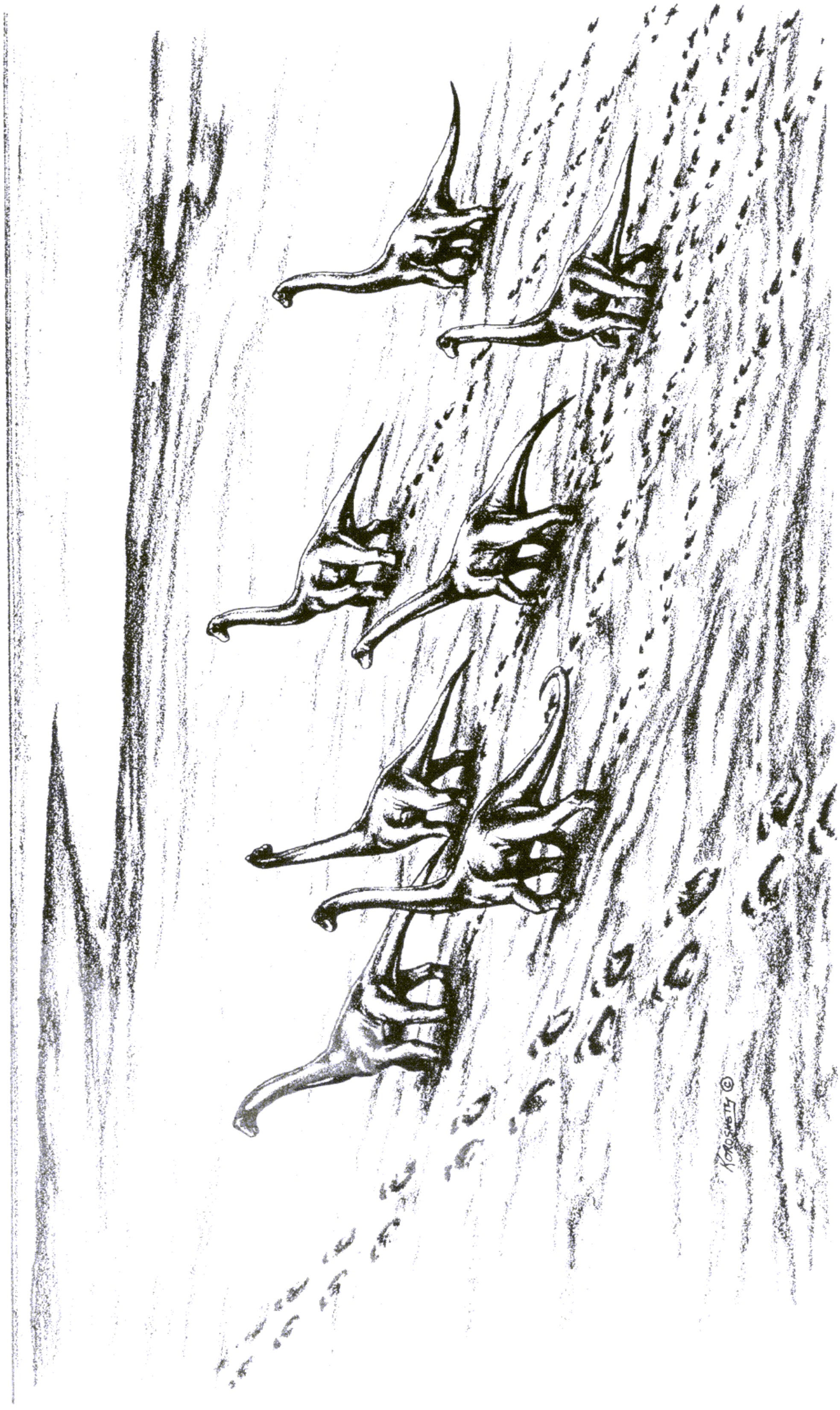

Fig. 4 - Reconstruction of a herd of seven juvenile sauropods travelling east-south-east. Based on trackway configurations shown in Figure 2. Artwork by Paul Koroshetz.

CONCLUSIONS

1 - Portlandian dinosaur trackways from the trackbed designated as number 3 at Lagosteiros Bay provide the first compelling evidence of gregarious sauropods so far reported from Europe.

2 - These gregarious sauropods were evidently travelling in two sub groups consisting of small animals (foot length 38-46 cm) and larger animals (foot length 70-73 cm). But all were travelling towards the southeast. No other trackway evidence for a gregarious group of brontosaurs is currently known in which the individuals consistently have such small foot sizes.

3 - The abundance of sauropod tracks in shallow water to marginal marine carbonates is typical of the *Brontopodus* ichnofacies (*sensu* LOCKLEY, HUNT & MEYER, 1994).

4 - Trackbed 3 also provides further evidence that manus only sauropod trackways are common in carbonate deposits.

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REFERENCES

ALEXANDER, R.M. (1976) - Estimates of speeds of dinosaurs. *Nature*, **261**: 129-130.

ANTUNES, M.T. (1976) - Dinossáurios Eocretácicos de Lagosteiros. *Ciências da Terra*, **1**, 35 pp.

ANTUNES, M.T. (1989) - Dinossáurios em Sesimbra e Zambujal - episódios de há cerca de 140 milhões de anos. *Sesimbra Cultural*, **0**: 12-14.

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**(2): 60-67.

DANTAS, P. (1990) - Dinossáurios de Portugal. *Gaia*, **2**: 17-26.

DANTAS, P.; SANTOS, V.F.; LOCKLEY, M.G. & MEYER, C.A. (1994) - Footprint evidence for limping dinosaurs from the Upper Jurassic of Portugal. *Gaia* (*this volume*).

FARLOW, J.O. (1992) - Sauropod Tracks and trackmakers: integrating the ichnological and skeletal records. *Zubia*, **10**: 89-138.

GOMES, J.P. (1915-1916) - Descoberta de rastos de sáurios gigantescos no Jurássico do Cabo Mondego. *Comun. Com. Serv. Geol. Portugal*, **11**: 132-134 (*in* "Manuscritos de Jacinto Pedro Gomes"). Publicação póstuma.

ISHIGAKI, S. (1989) - Footprints of swimming sauropods from Morocco *in* GILLETTE, D.D. & LOCKLEY, M.G. (Eds), *Dinosaur Tracks and Traces*, Cambridge Univ. Press, Cambridge, pp. 83-86.

LIM, S.-K.; YANG, S.-Y. & LOCKLEY, M.G. (1989) - Large Dinosaur Footprint assemblages from the Cretaceous Jindong Formation of Southern Korea *in* GILLETTE, D.D. & LOCKLEY, M.G. (Eds), *Dinosaur Tracks and Traces*, Cambridge University Press, Cambridge, pp. 333-336.

LIM, S.-K.; LOCKLEY, M.G.; YANG, S.-Y.; FLEMING, R.F. & HOUCK, K. (1994) - A preliminary report on sauropod tracksites from the Cretaceous of Korea. *Gaia* (*this volume*).

LOCKLEY, M. G. (1987) - Dinosaur Trackways *in* CZERKAS, S.J. & OLSEN, E.C. (Eds), *Dinosaur Past and Present*, Los Angeles County Nat. Hist. Mus. Symp., Los Angeles, pp. 80-95.

LOCKLEY, M.G. (1989) - Tracks and Traces: New Perspectives on Dinosaurian Behavior, Ecology and Biogeography *in* PADIAN, K. & CHURE, D.J. (Eds), *The Age of Dinosaurs, Short courses in Paleontology*, **2**, Paleontol. Soc., Knoxville, Tenn., pp. 134-145.

LOCKLEY, M.G. (1991a) - The Dinosaur Footprint Renaissance. *Modern Geol.*, **16**: 139-160.

LOCKLEY, M.G. (1991b) - *Tracking Dinosaurs: a new look at an ancient world.* Cambridge Univ. Press, Cambridge, 238 pp.

LOCKLEY, M.G. (1994) - Dinosaur ontogeny and population structure: interpretations and speculations based on footprints *in* CARPENTER, K.; HIRSCH, K. & HORNER, J. (Eds), *Dinosaur Eggs and Babies*, Cambridge Univ. Press, Cambridge, pp. 347-365.

LOCKLEY, M.G.; FLEMING, R.F.; YANG, S.-Y. & LIM, S.-K. (1991) - The distribution of dinosaur and bird tracks in the Jindong Formation of South Korea: implications for paleoecology *in Intern. Symp. on Origin, Sedimentation and Tectonics of Late Mesozoic to Early Cenozoic sedimentary basins at the eastern Margin of the Asian Continent*, Kyushu University, Fukuoka, Japan, Aug. 25-30, p. 61.

LOCKLEY, M.G. & GILLETTE, D.D. (1987) - Dinosaur Tracks Symposium signals a renaissance in vertebrate ichnology. *Paleobiology*, **13**: 246-252.

LOCKLEY, M.G.; HOUCK, K.J. & PRINCE, N.K. (1986) - North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. *Bull. Geol. Soc. Am.*, **97**: 1163-1176.

LOCKLEY, M.G. & HUNT, A.P. (*in press*) - *Dinosaur Tracks and other fossil footprints from the western United States.* Columbia Univ. Press.

LOCKLEY, M.G.; HUNT, A.P.; HOLBROOCK, J.; MATSUKAWA, M. & MEYER, C.A. (1992a) - The dinosaur freeway: a preliminary report on the Cretaceous Megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains, Colorado Oklahoma and New Mexico *in* FLORES, R. (Ed.), *Mesozoic of the Western Interior*, SEPM Midyear Mtg. Fieldtrip Guidebook, pp. 39-54.

LOCKLEY, M.G.; HUNT, A.P. & MEYER, C.A. (1994) - Vertebrate tracks and the Ichnofacies Concept: implications for paleoecology and palichnostratigraphy *in* DONOVAN, S. (Ed.), *The Paleobiology of Trace Fossils*, Wiley & Sons, New York, pp. 241-268.

LOCKLEY, M.G.; MATSUKAWA, M. & HUNT, A. (1993) - *Tracking Dinosaurs: New interpretations based on footprints. An Exhibit Guidebook.* Univ. Colorado, Denver, 68 pp.

LOCKLEY, M.G.; NOVIKOV, V.; SANTOS, V.F.; NESSOV, L.A. & FORNEY, G, (1994a) - "Pegadas de Mula": an explanation for the occurrence of Mesozoic traces that resemble mule tracks. *Ichnos*, **3**: 125-133.

LOCKLEY, M.G.; PITTMAN, J.G.; MEYER, C.A. & SANTOS, V.F. (1994b) - On the common occurrence of manus-dominated sauropod trackways in Mesozoic carbonates. *Gaia* (*this volume*).

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

LOCKLEY, M.G. & SANTOS, V.F. (1993) - A preliminary report on sauropod trackways from the Avelino Site, Sesimbra Region, Upper Jurassic, Portugal. *Gaia*, **6**: 38-42.

LOCKLEY, M.G.; SANTOS, V.F.; RAMALHO, M.M. & GALOPIM DE CARVALHO, A.M. (1992b) - Novas jazidas de pegadas de dinosáurios no Jurássico superior de Sesimbra (Portugal). *Gaia*, **5**: 40-43.

MEYER, C.A. (1990) - Sauropod tracks from the Upper Jurassic Reuchenette Formation (Kimmeridgian: Lommiswil, Kt. Solothurn) of Northern Switzerland. *Eclogae Geol. Helv.*, **83**: 389-397.

MEYER, C.A. (1993) - A sauropod dinosaur megatracksite from the Late Jurassic of Northern Switzerland. *Ichnos*, **3**: 29-38.

MEYER, C.A.; LOCKLEY, M.G.; ROBINSON, J.W. & SANTOS, V.F. (1994) - A comparison of well-preserved sauropod tracks from the Late Jurassic of Portugal and the Western United States: evidence and implications. *Gaia* (*this volume*).

OSTROM, J.H. (1972) - Were some dinosaurs gregarious? *Palaeogeog., Palaeoclimatol., Palaeoecol.*, **11**: 287-301.

RAMALHO, M.M. (1971) - Contribution à l'étude micropaléontologique et stratigraphique du Jurassique supérieur et du Crétacé inférieur des environs de Lisbonne (Portugal). *Mem. Serv. Geol. Portugal*, **19**, 218 pp.

RAMALHO, M.M. (1988) - Microfaciès des couches à pistes de dinosaures au Portugal - considérations paléoécologiques. *Rev. Micropaleontol.*, **30**: 267-275.

SANTOS, V.F. (1990) - Icnofósseis de dinossáurios de Portugal. Alguns aspectos paleoecológicos. *Seminário Científico, Fac. Ciências, Univ. Lisboa*, 36 pp. (*unpublished*).

SANTOS, V.F.; LOCKLEY, M.G.; MORATALLA, J.J. & GALOPIM DE CARVALHO, A.M. (1992) - The longest dinosaur trackway in the world?: interpretations of Cretaceous footprints from Carenque, near Lisbon, Portugal. *Gaia*, **5**: 18-27.

THULBORN, R.A. (1990) - *Dinosaur Tracks*. Chapman Hall, London, 410 pp.