A PRELIMINARY NOTE ON THE FIRST TETRAPOD TRACKWAYS FROM THE LITHOGRAPHIC LIMESTONES OF LAS HOYAS (LOWER CRETACEOUS, CUENCA, SPAIN)

JOSÉ J. MORATALLA, MARTIN G. LOCKLEY, ANGELA D. BUSCALIONI, MARIA A. FREGENAL-MARTINEZ, NIEVES MELÉNDEZ, FRANCISCO ORTEGA, BERNARDINO P. PÉREZ-MORENO, ESTHER PÉREZ-ASENSIO, JOSÉ L. SANZ & REBECCA J. SCHULTZ

MORATALLA J.J., LOCKLEY M.G., BUSCALIONI A.D., FREGENAL-MARTINEZ M.A., MELÉNDEZ N., ORTEGA F., PÉREZ-MORENO B.P., PÉREZ-ASENSIO E., SANZ J.L. & SCHULTZ R.J 1995. A preliminary note on the first tetrapod trackways from the lithographic limestones of Las Hoyas (Lower Cretaceous, Cuenca, Spain). [Note préliminaire sur les premières traces de tétrapodes observées dans les calcaires lithographiques de Las Hoyas (Crétacé inférieur, Cuenca, Espagne]. GEOBIOS, **28, 6** : 777-782. Villeurbanne le 29.12.1995.

Manuscrit déposé le 21.04.1994 ; accepté définitivement le 28.09.1994.

ABSTRACT

Although famous as a fossil lagerstätte that has produced numerous well-preserved vertebrates, recent discoveries indicate that the lithographic limestones of Las Hoyas (Calizas de la Huérguina Formation) also contain vertebrate trackways. We herein report on at least two distinctive tetrapod track types tentatively assigned to crocodilians and to turtles. Turtle tracks are isolated while the crocodile ones are forming a trackway showing an animal walking with a very regular step and stride length on an emergent surface. It is interesting to note the similarity between the inferred turtle tracks from Las Hoyas and those from the Late Jurassic lithographic limestones of Cerin, France. The occurrence of tracks in both environments suggests that the ichnofaunas are similar.

KEY-WORDS : PALEOICHNOLOGY, CROCODILES, TURTLES, LOWER CRETACEOUS, SPAIN.

RÉSUMÉ

Le gisement de Las Hoyas a délivré de nombreux vertébrés avec un bon état de préservation. Plus récemment on a découvert dans les calcaires lithographiques de Las Hoyas (Formation "Calizas de la Huérguina") des empreintes de pas de vertébrés. On a trouvé deux types d'empreintes de tétrapodes identifiés comme appartenant vraisemblablement à des crocodiles et des tortues. Tandis que les empreintes de tortues sont isolées, celles de crocodiles sont disposées selon une piste indiquant un animal qui marche avec un pas et une enjambée réguliers. La piste crocodilienne indique un animal qui marche sur une surface émergée. Il est intéressant de remarquer la similitude des empreintes de tortues de Las Hoyas avec celles des calcaires lithographiques de Cerin, France (Jurassique supérieur). En conséquence, on peut supposer une étroite similarité entre les ichnofaunes respectives.

MOTS-CLÉS : PALÉOICHNOLOGIE, CROCODILES, TORTUES, CRÉTACÉ INFÉRIEUR, ESPAGNE.

INTRODUCTION

The lithographic limestones of Las Hoyas form part of the Calizas de la Huérguina Formation, that outcrop in the Province of Cuenca, east central Spain (Fig. 1). These limestones have been considered as Hauterivian to Early Barremian in age (Sanz *et al.* 1988a, 1988b ; Sanz & Bonaparte 1992).

The limestones of Las Hoyas are famous as a fossil lagerstätte, and have, to date, produced a number of very important fossils including *Iberomesornis* and *Concornis*, which are two of the most important avian fossils currently known (Sanz *et al.* 1988a, 1988b ; Sanz & Buscalioni 1992). Other important and equally well preserved specimens include articulated remains of crocodilians and small dinosaurs (Sanz & Buscalioni 1992).

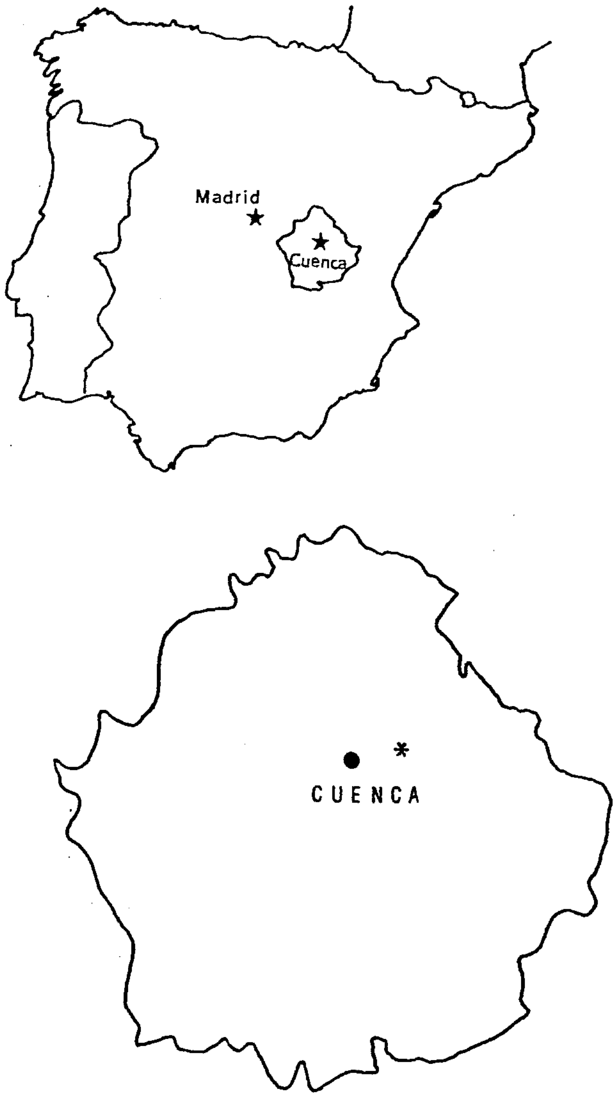

Figure 1 - Map showing the location of Las Hoyas outcrop (asterisk) in the province of Cuenca (Spain). *Situation du gisement de Las Hoyas dans la province de Cuenca (Espagne).*

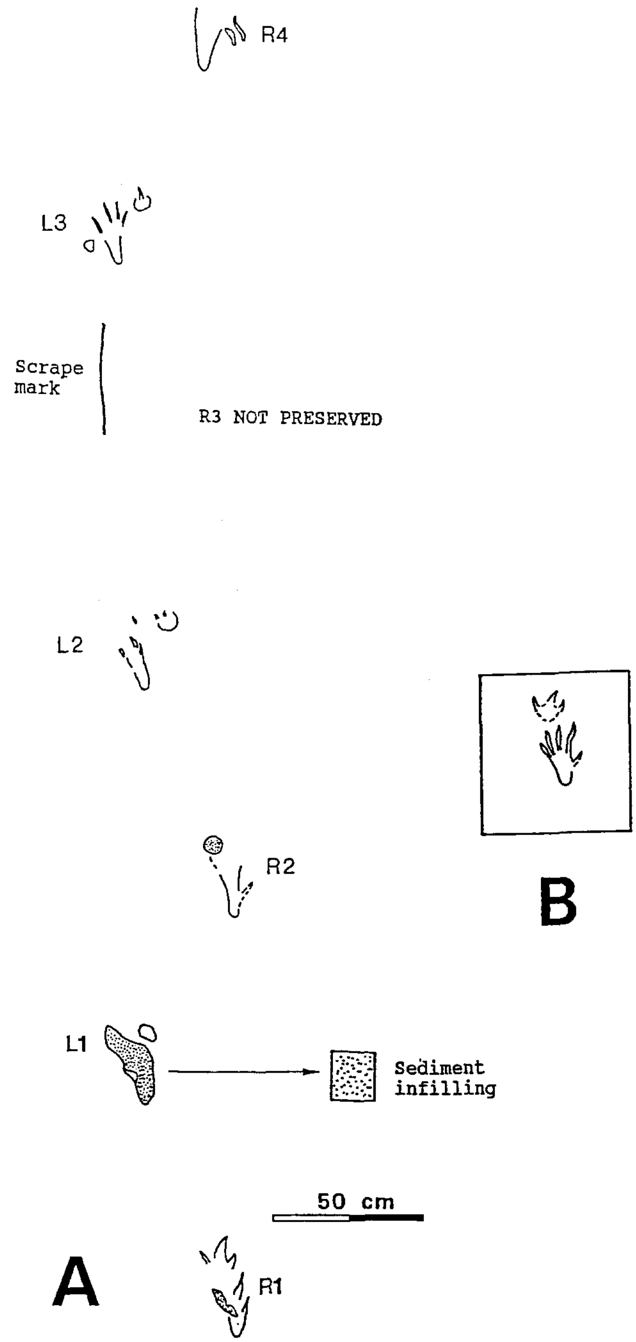

Figure 2 - **A**, ? crocodile trackway (LH-6501) at Las Hoyas outcrop. **B**, morphology of the tracks inferred by the overlay method of Baird (1952). ***A***, *piste de crocodile ? (LH-6501) dans le gisement de Las Hoyas.* ***B***, *morphologie des empreintes obtenue par la méthode de superposition de Baird (1952).*

DESCRIPTION OF TRACKS

? CROCODILIAN TRACKWAY

To date we have only discovered one complete trackway (Fig. 2) that we assign to a ? crocodilian trackmaker. The trackway consists of six poorly-preserved sets of manus and pes tracks numbered R1, L1, R2, L2, --, L3, R4 (tracks assigned to R3 in the sequence are missing due to a fracture in the bedding plane). The tracks are all very shallow, presumably indicating that the original substrate was quite firm, relative to the weight of the trackmaker.

Despite the poor preservation, the trackway pattern is clear, and it is possible to demonstrate quite clearly that the animal was walking with a very regular step and stride length (Table 1). The size of individual footprints is not easy to mea-

	(R1-R2)	(L1-L2)	(L2-L3)		Average
λ	132	131	132		131.6
	(R1-L1)	(L1-R2)	(R2-L2)	(L3-R4)	
P	80	70	80	70	73.3
	(R1-L1-R2)				
γ	130°				130°
	(R1-L1-R2)	(L1-R2-L2)			
TW	33	32			32.5

Table 1 - Trackway measurements of LH-6501. λ, stride length ; P, pace length ; γ, pace angle ; TW, trackway width ; R, footprint belonging to the right side ; L, the sale for the left side (see also Fig. 1). Measurements in cms. *Mesures de la piste LH-6501. λ, longueur de l'enjambée ; P, longueur du pas ; γ, angle du pas ; TW, largeur de la piste ; R, empreinte de pas du côté droit ; L, la même pour le côté gauche (voir aussi Fig. 2). Mesures en cm.*

sure precisely, but the combination of a relatively clear pes heel impression, and faint digit impressions in at least some of the tracks, suggests an animal with a pes length of about 20 cm and width of about 14 cm. We used the overlay method of Baird (1952) to make a composite manus-pes set outline (Fig. 2B). The shape of the manus impressions are harder to determine, but, based on a composite of faint outlines traced from the map, appears to have been about 10 cm in length and width.

The trackway also reveals at least two examples of very narrow, elongate "scrape marks" that appear to have been made by individual toes during locomotion. The first is about 30 cm long and is situated posterior to pes track L3, and was evidently made by the animal as it moved its pes (or manus) forward prior to placing it on the substrate. The second example of such traces consists of a pair of subparallel traces situated laterally and exterior to the anterior part of pes track R4, and presumably made by the manus immediately before it was placed on the substrate. Such traces are very similar to those made by modern and ancient crocodiles walking on soft substrates (Padian & Olsen 1984). The preservation of such fine traces suggest that the trackway is a true trackway, not an undertrackway, and that its poor, or faint preservation is due to the firmness of the substrate, not subsequent taphonomic deterioration of the substrate.

We conclude that the trackmaker was a crocodilian on the basis of footprint morphology and trackway configuration. Our interpretations are supported by the following similarities noted between the Las Hoyas trackway and those of modern crocodilians : 1) pes tracks larger than manus tracks, 2) pes tracks longer than wide, 3) pes tracks pentadactyl with impression of digit V much shorter than other digit impressions, 4) trackway moderately wide with low pace angulation values (130° in the Las Hoyas trackway, about 120° for the Jurassic trackmaker cited by Padian and Olsen), and 5) the presence of very narrow, elongate, curved scrape marks caused by the toes touching the substrate between consecutive footfalls.

RECONSTRUCTION OF THE TRACKMAKER

Clearly the Las Hoyas trackmaker was quite a large animal, especially in relation to the diminutive (dwarf) crocodile skeletons currently known from the same deposits. For example, the atoposaurid illustrated by Buscalioni (1992, Fig. 21) is only about 25 cm long with a pes length of only 2 cm and a glenoacetabular distance of about 6 cm. A new specimen (Neosuchia indet.) is also quite small (foot length about 4 cm, glenoacetabular dimension 12 cm and overall length about 50 cm). Based on the trackway, we estimate a glenoacetabular dimension of about 80 cm (see Fig. 2), which would scale up to an animal that probably reached as much as 3 meters in length.

? TURTLE TRACKS

The Las Hoyas lithographic limestones have also produced two isolated tridactyl footprints of large size that, to date, have not been found as part of recognizable trackways. These tracks (Fig. 3b) are reminiscent of turtle tracks found in the Upper Jurassic lithographic limestones of Cerin (Fig. 3a). These tracks were initially interpreted as the tracks of hopping dinosaurs, and named *Saltosauropus* (Bernier *et al.* 1984), but later reinterpreted, correctly in our opinion, as the tracks of large turtles (Thulborn 1989).

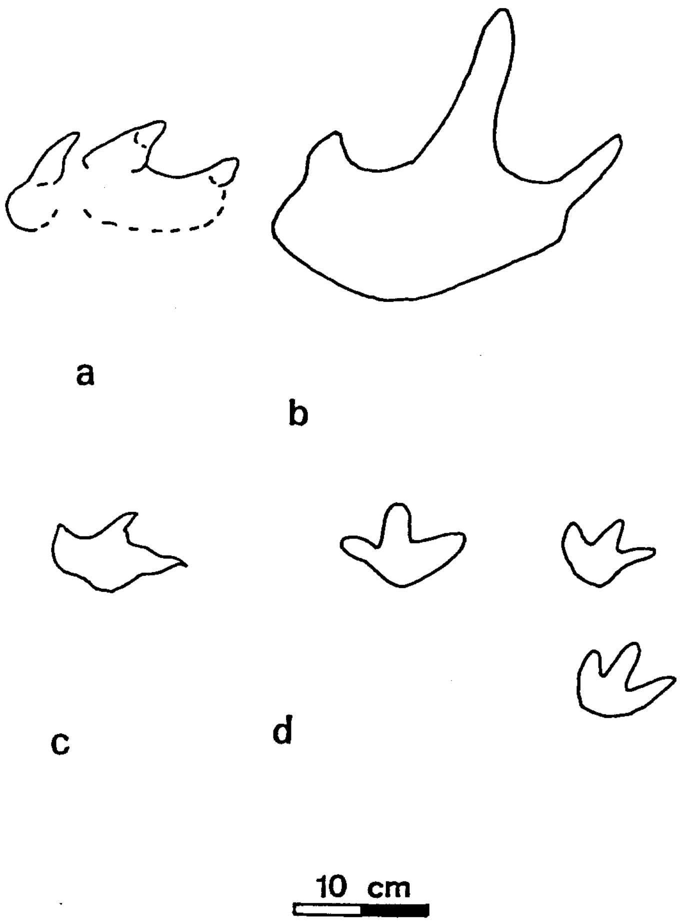

Figure 3 - Several examples of tracks attributed to turtles in the fossil record. **a, *Saltosauropus*** of the Upper Jurassic of Cerin (France) ; **b**, track (LH-6500) of the Las Hoyas site (Cuenca province, Spain) ; **c**, track from the Santa Cruz de Yanguas site, Lower Cretaceous (Soria province, Spain) ; **d**, several tracks of the Los Cayos A site, Lower Cretaceous, (Cornago township, La Rioja province, Spain). *Quelques exemples d'empreintes de pas attribuées à des tortues dans le registre fossile.* ***a, Saltosauropus,*** *du Jurassique supérieur de Cerin (France) ;* ***b,*** *empreinte (LH-6500) de Las Hoyas (province de Cuenca, Espagne) ;* ***c,*** *empreinte de Santa Cruz de Yanguas, Crétacé inférieur (province de Soria, Espagne) ;* ***d,*** *quelques empreintes de Los Cayos A, Crétacé inférieur (commune de Cornago, province de La Rioja, Espagne).*

It is outside the scope or this paper to present a detailed description of these tracks, but a few observations are pertinent. Existing ichnotaxonomy and interpretation of purported turtle tracks is both confused and controversial, and therefore in need of review and revision (Lockley *et al.* in prep.). This revision is being aided by a significant number of discoveries of new turtle trackways (Moratalla 1993) (Figs. 3c,d). For the purposes of this paper therefore we need only briefly review the history of work in this field in order to understand this latest discovery in its proper context.

Walther (1904) reported trackways, which he named *Ichnium megapodium*, from the lithographic limestones of Solnhofen. These were later renamed *Emydichnium* by Nopsca (1923) and attributed to swimming turtles (see also Lessertisseur 1955, fig. 58f). Seilacher (1963) later attributed these traces to roll marks produced by ammonites (cf. Viohl 1983, fig. 8 for a photograph of a different specimen showing such markings). Although there is doubt about the origin of many purported vertebrate traces in the Solnhofen limestone, the possibility of turtle tracks cannot be ruled out.

In 1982 vertebrate trackways were reported from the Upper Jurassic lithographic limestones of Cerin, France (Bernier *et al.* 1982, 1984). The trackway of a large turtle was described and named *Chelonichnium cerinense* by Demathieu & Gaillard (*in* Bernier *et al.* 1982), and attributed to a walking animal. Demathieu & Gaillard (*in* Bernier *et al.* 1982) used the name *Chelonichnium*, originally coined to denote a Lower Triassic trace from the Buntsandstein (Schimper 1850), despite the fact that it has been declared a *nomen dubium* by many authors (Abel 1935 ; Haubold 1971). They indicated that they based their choice on the antiquity of the name, and that they were aware of the name (*Emydichnium*) and interpretation proposed by Nopsca (1923), but that they did not like it because it indicated the wrong type of turtle, not to mention the doubt cast on the interpretation by Seilacher (1963).

Soon after a large number of additional trackways were found at seven different stratigraphic levels in the same deposits (Bernier *et al.* 1984). These additional trackways were attributed to hopping dinosaurs and named *Saltosauropus latus* by Demathieu & Gaillard (*in* Bernier *et al.* 1984). Illustrations and further discussion of these trackways have been repeated, with the same interpretation, in many articles (cf. Barale *et al.* 1985). Thulborn (1989) challenged the interpretation of the hopping dinosaurs and proposed instead that the tracks were made by a swimming turtle. We agree with this interpretation (cf. Lockley 1991). Further publication by Bernier and his colleagues (1993) repeat their original interpretations, and do not discuss the alternative interpretation of Thulborn (1989).

New discoveries of trackways similar to *Saltosauropus* in shape, but of smaller size, from the Jurassic and Cretaceous of North America and Spain (Schultz *et al.* 1994 ; Moratalla 1993 respectively) (Figs. 3c,d) have been attributed to turtles and, at least in a general sense, support the conclusions of Thulborn (1989).

Las Hoyas material is very scarce, only two isolated tracks without trackway. This fact makes very difficult the comparison with *Saltosauropus* or other related tracks and also to make inferences on locomotion, trackway pattern or simply to know if the tracks are caused by the hand or pes. However, based on the size and shape of the tracks from Las Hoyas (Fig. 3b) we conclude that they could be included within the variability of *Saltosauropus* from Cerin, and hence could be tentatively attributed to large turtles, that were presumably swimming. The depth of the tracks, relative to the inferred light weight of a turtle when buoyed up by water, would suggest a very soft substrate at the time the tracks were made, and provides a striking contrast with the shallow crocodile trackway.

DISCUSSION

The presence of trackways of large animals in the lithographic limestones adds considerably to our knowledge of the vertebrate fauna. The presence of large crocodiles, up to 3 meters in length, indicates the presence of species the size of *Goniopholis* from the Wealden of Belgium and Galve (Teruel province, Spain) (Buscalioni & Sanz 1987), in addition to the dwarf species already known (Sanz *et al.* 1988b).

The presence of tracks relatively similar to *Saltosauropus* would indicate large turtles with a body width of at least a meter if not more. The tridactyl condition of the Las Hoyas turtle tracks (see Fig. 3b) is relatively similar to that of the other Spanish outcrops : Los Cayos A (La Rioja province) (Fig. 3d) and Santa Cruz de Yanguas (Soria province) (Moratalla 1993 ; Lockley *et al.* in press) (Fig. 3c). This morphology seems to be the common pattern of that tracks, despite the pentadactyl condition of the turtle autopodia. So, the turtles that made such tracks should have autopodia with three digits more developed than the other two, probably with longer ungual phalanges. These characters are present, for instance, in Trionychoidea, that is, the soft carapace turtles. In the Chelonioidea members (marine turtles) the limbs have become highly modified as paddles that propel the body through the water (Carrol 1988 ; p. 213). Therefore, it is difficult to reconcile the tracks with the foot skeleton unless we propose that the tracks are caused by a particular pattern of locomotion. The large size of the tracks also suggests a very big animal, perhaps a member of the Testudinoidea group, first known as snapping turtles from the Paleocene. We propose that the Las Hoyas turtle tracks could have been made by a member of the Trionychoidea or at least a Trionychoidea-like turtle. However, the skeletal record of turtles from Las Hoyas currently consists of two small turtle specimens identified as Toxochelyidae indet (Sanz *et al.* 1988b). Whatever interpretation is put on these tracks, they clearly represent vertebrates that were previously unknown in the Las Hoyas fossil record.

Finally we note that the presence of turtle tracks in lithographic limestones in France (Cerin), Spain (Las Hoyas) and possibly in Germany (Solnhofen) appears to be more than mere coincidence. From an ichnological viewpoint, repeat assemblages (ichnocoenoses) in the same sedimentary facies, as for example at Cerin, imply a distinct ichnofacies (Lockley *et al.* in press). Thus it could be proposed that the Las Hoyas ichnofacies, and perhaps the Solnhofen ichnofacies, are similar to the Cerin ichnofacies, at least in a general sense. Further ichnological work is necessary to test this hypothesis.

Acknowledgments - This paper has been supported by the DGICYT (project number PB-88/0174). We wish to thank also to "Junta de Comunidades de Castilla-La Mancha" for financial support of the excavation and to Jesús Madero, director of the "Museo de la Diputación de Cuenca", for helping with the fieldwork. We thank also to G.R. Demathieu and C. Gaillard for critically reading the manuscript and make valuable suggestions.

REFERENCES

ABEL O. 1935 - Vorzeitliche Lebensspuren XV. Gustav Fischer Verlag, Jena : 644 p.

BAIRD D. 1952 - Revision of the Pennsylvanian and Permian footprints *Limnopus, Allopus and Baropus. Journal of Paleontology,* **26**, 5 : 832-840.

BARALE G., BERNIER P., BOURSEAU J.P., BUFFETAUT E., GAILLARD C., GALL J.C. & WENZ S. 1985 (coord. Bernier P.) - Cerin : une lagune tropicale au temps des dinosaures. *Centre National de la Recherche Scientifique, Museum d'Histoire naturelle de Lyon* : 136 p.

BERNIER P., BARALE G., BOURSEAU J.P., BUFFETAUT E., DEMATHIEU G.R., GAILLARD C. & GALL J.C. 1982 - Trace nouvelle de locomotion de chélonien et figures d'émersion associées dans les calcaires lithographiques de Cerin (Kimméridgien supérieur, Ain, France). *Geobios,* **15,** 4 : 447-467.

BERNIER P., BARALE G., BOURSEAU J.P., BUFFETAUT E., DEMATHIEU G.R., GAILLARD C., GALL J.C. & WENZ S. 1984 - Découverte de pistes de dinosaures sauteurs dans les calcaires lithographiques de Cerin (Kimméridgien supérieur, Ain, France) : implications paléoécologiques. *In* DAVID L. & GALL J.C. (eds) : Paléoécologie. *Geobios*, **M.S. 8** : 177-185.

BERNIER P., BARALE G., BOURSEAU J.P., BUFFETAUT E., GAILLARD C., GALL J.C. & WENZ S. 1993 - The paleontological excavation at Cerin, Southern French Jura Mountains. *First European Paleontological Congress* : 18 p.

BUSCALIONI A.D. 1992 - Historia evolutiva de los Crocodylomorpha. Actas del II Curso de Paleontología en Cuenca. Instituto "Juan de Valdés". Excmo. Ayuntamiento de Cuenca : 307-344.

BUSCALIONI A.D. & SANZ J.L. 1987 - Cocodrilos del Cretácico inferior de Galve (Teruel, España). *Estudios geológicos*, vol. extr. Galve-Tremp : 23-43.

CARROLL R.L. 1988 - *Vertebrate Paleontology and Evolution*. W.H. Freeman and Company, New York : 698 p.

GALL J.C. 1989 - Die Grabungsstelle der oberjurassischen Plattenkalke von Cerin (Sudjura, Frankreich). *Archaeopteryx*, **7** : 11 p.

HAUBOLD H. 1971 - *Handbuch der Paläeoherpetologie : Ichnia Amphibiorum et Reptiliorum fossilium*. Gustav Fischer Verlag : 124 p.

LESSERTISSEUR J. 1955 - Traces fossiles d'activité animale et leur signification paléobiologique. *Mémoires de la Société géologique de France*, **74** : 150 p.

LOCKLEY M.G. 1991 - *Tracking Dinosaurs : a new look at an ancient world*. Cambridge University Press : 238 p.

LOCKLEY M.G. & HUNT A.P. (in press) - Dinosaur Tracks and other fossil footprints of the Western United States.

MELÉNDEZ N., MELÉNDEZ A. & GÓMEZ-FERNÁNDEZ J.C. 1989 - Los sistemas lacustres del Cretácico inferior de la Serranía de Cuenca (Cordillera Ibérica). Guía de Campo, IV Reunión del Grupo Español de Trabajo : 70 p.

MORATALLA J.J. 1993 - Restos indirectos de dinosaurios del registro español : Paleoicnología de la Cuenca de Cameros (Jurásico superior-Cretácico inferior) y Paleoología del Cretácico superior. Vol. I y II. Universidad Autónoma de Madrid. Facultad Ciencias, Departamento de Biología : 729 p. (unpublished Ph. D. Thesis).

NOPSCA F.V. 1923 - Die fossilen Reptilien. *Fortschr. Geol. Pal.*, **2**, 6 : 210 p.

PADIAN K. & OLSEN P.E. 1984 - The fossil trackway *Pteraichnus* : not pterosaurian but crocodilian. *Journal of Paleontology,* **58** : 178-184.

SANZ J.L. & BONAPARTE J.F. 1992 - A new order of birds (Class Aves) from the Early Cretaceous of Spain : 39-49. *In* CAMPBELL K.E. (ed.) : Papers in Avian Paleontology. Honoring Pierce Brodkorb. Science Series n° 36. *Natural History Museum of Los Angeles County* : 491 p.

SANZ J.L., BONAPARTE J.F. & LACASA A. 1988a - Unusual Early Cretaceous birds from Spain. *Nature*, **331** : 433-435.

SANZ J.L. & BUSCALIONI A.D. 1992 - A new bird from the Early Cretaceous of Las Hoyas, Spain, and the early radiation of birds. *Palaeontology*, **35,** 4 : 829-845.

SANZ J.L., WENZ S., YÉBENES A., ESTES R., MARTÍNEZ-DELCLOS X., JIMÉNEZ-FUENTES E., DIÉGUEZ C., BUSCALIONI A.D., BARBADILLO L.J. & VIA L. 1988b - An Early Cretaceous faunal and floral continental assemblage : Las Hoyas fossil site (Cuenca, Spain). *Geobios*, **21**, 5 : 611-635.

SCHIMPER W.P. 1850 - Palaeontologia Alsatica ou fragments paléontologiques en Alsace. *Mémoire de la Société d'Histoire naturelle de Strasbourg*, **4.**

SCHULTZ R.J., LOCKLEY M.G. & ROBINSON J. 1994 - Subaqueous turtle tracks from the Middle Jurassic Summerville Formation of eastern Utah.

SEILACHER A. 1963 - Umlagerung und Rootransport von Cephalopoden-Gehausen. *Neues Jahrbuch für Geologie und Paläontologie*, Monatshefte : 593-615.

THULBORN R.A. 1989 - The Gaits of Dinosaurs. *In* GILLETTE D.D. & LOCKLEY M.G. (eds) : *Dinosaur Tracks and Traces*. Cambridge University Press : 39-50.

VIOHL G. 1983 - Forschungsprojekt "Solnholfener Plattenkalke". *Archaeopteryx*, **1** : 3-23.

WALTHER J. 1904 - Die Fauna der Solnhofener Plattenkalke bionomisch betrachtet. *Festschrift der Medizinisch naturwissenschafftlichen Gesellschaft zu Jena*, **11** : 135-214.

MORATALLA J., BUSCALIONI A.D.,ORTEGA F., PÉREZ-MORENO B.P., PÉREZ-ASENSIO E. & SANZ J.
Unidad de Paleontología
Departamento de Biología
Facultad de Ciencias, Universidad Autónoma
Cantoblanco
28049 Madrid, Spain

LOCKLEY M.G. & SCHULTZ R.J.
Geology Department
University of Colorado at Denver
Box 172
1200 Larimer Street
Denver, Colorado 80204, USA

FREGENAL-MARTINEZ M.A. & MELÉNDEZ N.
Departamento de Estratigrafía
Facultad de Ciencias Geológicas
Universidad Complutense
28040 Madrid, Spain