Jesper Milàn, Per Christiansen & Octávio Mateus

A three-dimensionally preserved sauropod manus impression from the Upper Jurassic of Portugal: Implications for sauropod manus shape and locomotor mechanics

Author's address: Jesper Milàn, Geological Institute, University of Copenhagen, Øster Voldgade 10, DK. 1350 Copenhagen, Denmark, milan@geol.ku.dk; **Per Christiansen**, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK. 2100 Copenhagen, Denmark, p2christiansen@zmuc.ku.dk; **Octávio Mateus**, Universidade Nova de Lisboa, Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia UNL, 2825 Monte de Caparica, Portugal; Museu da Lourinhã, Rua João Luis de Moura, 2530-157 Lourinhã, Portugal, omateus@dinocasts.com

Abstract

Sauropods were the largest animals ever to walk the earth, and evolved several specializations in their limbs in order to support their body mass. Their legs became columnar and their manual digits became reduced and encapsulated in tissue to form a single weight-bearing unit in the derived sauropods. A new three-dimensionally preserved cast of a sauropod manus, found in the Upper Jurassic Lourinhã Formation, Portugal, demonstrates not only the shape, but also the actual movements of the sauropod manus during the stride. The manus cast is 32 cm deep, and show the manus to be hoof-shaped and lacking any impressions of individual digits, except for digit I, the pollex. Well preserved striations from skin on the sides of the cast show that the manus was covered in rough, tubercular skin. The width of the manus cast is consistent from top to bottom, demonstrating that the manus was brought down and lifted vertically before any parasaggital movement of the upper limb took place.

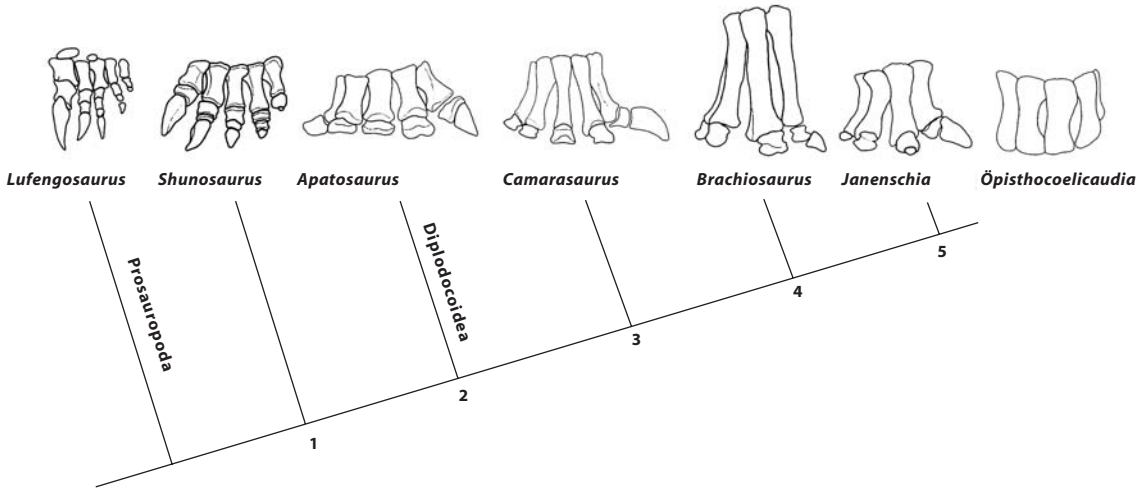


Fig. 1: Diagram showing sauropod relationships and manual morphology. 1, Eusauropoda; 2, Neosauropoda; 3, Macronaria; 4, Titanosauriformes; 5, Titanosauria. Figures not drawn to same scale.

Introduction

Incorporating both ichnological and osteological data is important when reconstructing extinct animals and formulating and testing hypotheses of locomotory behavior and evolution. The discovery of well preserved fully articulated and conjugated sauropod manus specimens (Gilmore 1925, 1936), studies of osteology and functional morphology, and of numerous tracks and trackways (Lockley et al., 1994 and references therein) have demonstrated that at least neosauropod dinosaurs had a highly unusual manual structure (Fig.1). This comprises erectly positioned metacarpals, that were tightly interlocked proximally and formed a semicircle, as well as abbreviated phalanges that usually did not leave individual traces in even well preserved tracks. This has implications for sauropod locomotor evolution and functional morphology. In this paper we present new evidence for the shape and function of the sauropod manus, based on a three-dimensionally preserved cast of a sauropod manus from the Late Jurassic of Portugal.

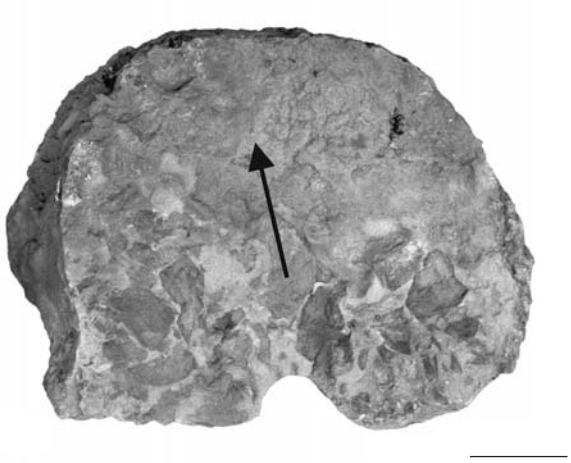
Sauropod manual morphology and evolution

Sauropod dinosaurs were the largest terrestrial vertebrates in evolutionary history and thus faced severe problems with support of mass. The limb bones were sturdy and limb postures columnar, with inferred locomotory capabilities similar to elephants. The hind feet in all known taxa appear to have had a digitigrade posture with a posterior heel pad, as in elephants (Christiansen 1997). Forefoot postures and presumable functional morphology did, however, change markedly throughout evolution (Fig. 1).

The most primitive sauropod known with a complete manus is *Shunosaurus* (Zhang 1988). *Shunosaurus* has 3 carpals, decreasing in size mediolaterally, and the medial carpal is flattened, although not block-like, having distinct articulating facets for the medial and lateral carpals (Zhang 1988, Christiansen 1997). The abbreviated phalanges (digital formula 2-2-2-2-1) probably did not have much mobility, but carpal structure indicates more suppleness than in later forms (Christiansen 1997). Manual posture appears to have been semidigitigrade (Christiansen 1997, Wilson & Sereno 1998), and gently posteriorly concave. *Omeisaurus* also has 3 carpals (He et al., 1988, Christiansen 1997), and these were more block-like, showing greater size heterogeneity, the medial one being the largest. Lavocat (1955) reported on 3 carpals in a »*Bothriospondylus*« from Madagascar, but this find has yet to be studied in detail. All later sauropods, Neosauropoda, (Wilson & Sereno 1998) had but two, distinctly block-like carpals and highly abbreviated digits, albeit with a prominent ungual on digit I. Their metacarpals were maintained in an erect posture, tightly bound together proximally and formed a wide, U-shaped semicircle, as indicated by long, intermetacarpal articulating facets (Christiansen 1997, Wilson & Sereno 1998), fully articulated specimens (Gilmore 1925, 1936), and numerous trackway finds. Some genera, such as *Janenschia*, *Brachiosaurus* (Janensch 1922, 1961) and *Apatosaurus* (Gilmore 1936) appear to have had only one ossified carpal.

Titanosauriformes (Wilson & Sereno 1998) supposedly had a reduced ungual on digit I (Salgado et al., 1997) but this character is ambiguous as its most basal member, *Brachiosaurus*, did indeed have a small ungual (Fig. 1, see also Upchurch 1994), but the basal titanosaurian *Janenschia* did not (Fig. 1, see also Janensch 1922, 1961). Supposedly Titanosauridae lacked not only a digit I ungual, but ossified manual phalanges altogether (Salgado et al., 1997), as evidenced by the absence of digits recovered with even well preserved specimens, such as *Opisthocoelicaudia* (Borsuk-Bialynicka 1977) and *Epachthosaurus* (Salgado et al., 1997). This graphically illustrates that the neosauropod manus was adapted for columnar support of mass, having little mobility and a limited contribution to forward propulsion relative to the hind limb (Christiansen 1997). The studies of osteology predict that sauropods initially retained some manual flexibility and that sauropod evolution favoured support of mass over flexibility. The manual morphology of neosauropods must have severely restricted mobility, and the manus appears to have been largely inflexible. The forelimb was essentially columnar during support of mass (Bonnan 2003),

2a 10 cm



2b 10 cm

Fig. 2: The new three-dimensionally preserved cast of a sauropod manus track. A: frontal view of the cast. B: horizontal section through the cast, notice the prominent semilunate shape without any indications of free digits, except from the cast of the pollex impression which is present as a triangular protrusion in the lower left corner of the picture, indicated by a P. The position of the pollex claw identifies the cast as a impression of a right manus. Arrow indicates direction of progression.

and the main propulsive force came from the hind limbs, unlike any extant quadrupedal animals, and probably early sauropods as well (Christiansen 1997). Neosauropods thus evolved not only a manual morphology that was different from more primitive forms, but also changed their locomotor mechanics. Thus, neosauropods could have touched the ground and subsequently lifted their forefeet in a near vertical manner, with the main flexion mobility being in the elbow, very different from extant animals, even elephants (Gambaryan 1974, Christiansen 1997).

The new three-dimensionally preserved manus cast

New evidence for the shape and function of the sauropod manus comes from a deep, three-dimensionally preserved, natural cast of a sauropod manus found in the Upper Jurassic (Tithonian-Kimmeridgian) Lourinhã Formation, central west Portugal, during field work the summer 2003. The Lourinhã Formation is part of the Lusitanian Basin and consists of approximately 140 m of terrestrial sediments, deposited during the initial rifting of the Atlantic in the Kimmeridgian and Tithonian. The sediments consist mainly of thick red and green clay layers, interbedded with massive fluvial sandstone lenses and heterolithic horizons. The sandstone lenses appear as horizontally extensive, lenticular beds; some are traceable for several kilometres along the sections exposed along the coast. The sandstone lenses have been interpreted as distal alluvial fan facies originating from periods of extensive faulting (Hill 1989).

The Late Jurassic sediments of Portugal have yielded a rich dinosaurian fauna, including numerous sauropod remains as well as extensive finds of tracks and trackways. The first dinosaur fossils were collected in 1863 in Porto das Barcas, near Lourinhã. Since then, at least five sauropod forms have been recognized in Portugal: *Lusotitan atalaiensis*, *Camarasaurus* sp., *Apatosaurus* sp., *Lourinhasaurus alenquerensis* and *Dinheirosaurus lourinhanensis* (Antunes & Mateus 2003).

The new track was found in-situ in the coastal cliffs west of Lourinhã and is preserved as a fine-grained sandstone cast in a layer of silt and clay. The cliff section at the site is vertical due to continuous coastal erosion. Additional tracks from the trackway are still buried in the cliff section and are inaccessible on account of approximately 20 metres of overburden. Several less well-preserved casts of tracks have been found under similar circumstances in the coastal cliffs in the Lourinhã area.

The cast was collected and is stored at Museu da Lourinhã (ML 965). The depth of the cast is 32 cm, measured from the original tracking surface, and it is 45 cm wide. A horizontal fracture approximately in the middle of the cast caused it to split during excavation. When viewed in horizontal section, as allowed by the crack, the cast revealed a distinct semi-lunate shape where the whole front of the manus is smooth and semi-circular, lacking any indication of free digits, except from the posteriomedially orientated pollex claw, which is present as a narrow triangular protrusion along the side of the cast (Fig. 2). The sides and front of the manus cast are covered with prominent, vertical, 2–10 mm wide striations flanked by 1–2 mm deep furrows, originating from the movement of a rough and tubercular skin through the sediment (Fig. 3).

Discussion

Evidence from well preserved Middle Jurassic sauropod tracks and trackways (Santos et al., 1994) show the shape of the sauropod manus to be semilunate and lacking impressions of free digits except for digit I. Trackways from the Upper Cretaceous of Bolivia, purported to be titanosaurid, display evidence of separate, albeit very abbreviated manual digits (Lockley et al., 2002). These, however, appear more like depressions in the bottom of the tracks and do not seem to affect the outline shape of the manus imprint. Additionally, the impressions of digit I in these tracks indicate a very short pollex claw.

In the cast described in this study, the impression of the pollex claw is proportionally smaller relative to manus size than in similar sauropod tracks from the Middle Jurassic of Portugal (Santos et al., 1994). This shows that the trackmaker possesed a relatively small pollex claw, consistent with the brachiosaurid manual morphology (Fig. 1, see also Upchurch 1994).

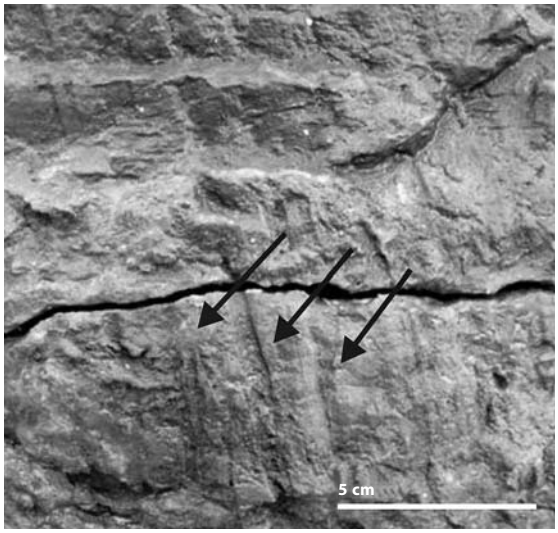


Fig. 3: Close up showing the rough striations from the rough tuberculate skin (arrows) covering the front of the manus.

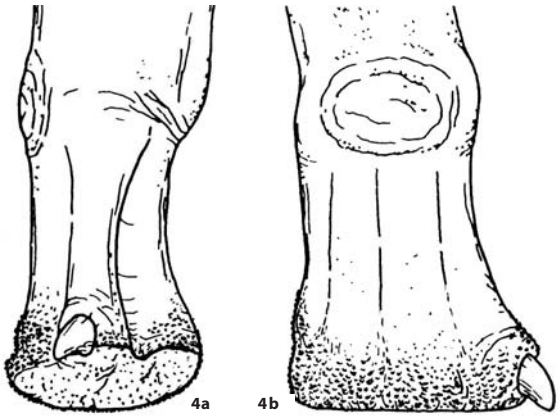


Fig. 4: Reconstruction of a brachiosaurid manus based on the new track evidence presented. A: rear view. B: frontal view. Notice the lack of free digits, except the pollex claw. The front and sides of the manus are covered with rough tubercular skin. Figure modified from PAUL (1987).

The abundance of brachiosaurid material found in the area (Antunes & Mateus 2003) together with the manus shape, suggests a brachiosaurid origin of the track. Because the cast was found as a single find, and the circumstances prohibited excavation of further tracks from the trackway, it is not possible to refer the track to a wide, intermidate or narrow-gauge trackway.

Sauropod tracks usually fall into one of two categories: either a »narrow-gauge« type in which the respective tracks from the left and right sides intersect the midline of the trackway, or a »wide-gauge« type, where the imprints lie further away from the midline (Farlow 1992). The wide-gauge trackways first occur in the Middle Jurassic Galinha tracksite in Portugal (Santos et al., 1994) and the Middle Jurassic Ardley Quarry in England (Day et al., 2002, 2004) and become dominant up through the Cretaceous (Wilson & Carrano 1999). The temporal distribution and analyses of anatomy (Wilson & Carrano 1999) support a titanosaurian origin for the wide-gauge trackways. Based on evidence from the Galinha and Ardley Quarry tracksites, Day et al. (2004) suggests four different morphologies of sauropod trackways: (1) narrow-gauge trackways showing a well-developed pollex claw impression, supposed to be of non-titanosauriform origin; (2) intermediate-gauge trackways with either well-developed or reduced pollex claw impression, formed by brachiosaurs or the most basal titanosaurs; (3) wide-gauge trackways characterized by reduced pollex claw impression and formed by basal titanosaurs like *Janenschia* and (4) wide-gauge trackways showing no indication of manual digits, formed by advanced titanosaurs.

The shape and dimensions of the herein described cast of a manus track is constant from top to bottom, demonstrating the absence of a horizontal component in the lifting of the manus. Even the width of the pollex claw impression is constant from top to bottom of the cast, showing that the manus was brought down vertically, maintained vertical in the weight-supporting phase and subsequently lifted clear of the sediment before any parasaggital movements of the forelimb occurred.

The depth and shape of the present cast yields evidence about the locomotor mechanics of the particular sauropod that made the track. When tracks are emplaced in deep substrates, any horizontal component of the foot movements during the stride will result in an elongate morphology of the tracks, as demonstrated by Upper Triassic theropod tracks from East Greenland (Gatesy et al., 1999). In two of the Middle Jurassic sauropod trackways described from the Ardley Quarry, England, the manus impressions occurred as elongated disturbed structures indicating the manus was dragged through the mud during the stride (Day et al., 2004). On the contrary, deep well preserved, Upper Cretaceous, sauropod tracks from Humaca, Bolivia are 15-20 cm deep, and the manus tracks appears as steep-walled cavities with no sign of deformation from horizontal movements (Lockley et al., 2002). Upper Jurassic tracks from track level 5 (Lockley et al., 1994, Meyer et al., 1994), Cabo Espichel, Portugal, have sauropod manus tracks in excess of 20 cm depth, again appearing as steep-walled cavities with no indication of a horizontal component in the stride (J.M. pers. obs.). These examples from tracks reflects an evolution in sauropod locomotor mechanics from the Middle Jurassic tracks from the Arden Quarry (Day et al., 2004), where the manus is dragged forward, to the Upper Jurassic (Lockley et al., 1994, Meyer et al., 1994) examples, the Upper Cretaceous examples (Lockley et al., 2002), and the herein described cast, where the manus is emplaced and lifted vertically clear off the ground.

Eusauropods, like *Shunusaurus* from the Middle Jurassic had a semi-digitigrade manus stance (Christiansen 1997, Wilson & Sereno 1998) and are likely trackmakers to the manus tracks who show a forward drag of the foot, while the Neosauropods, which appear from the Upper Jurassic and onward, has the more erect and reduced manus, likely to have made the tracks where the manus is lifted vertically clear off the ground.

The striations from the skin tubercles preserved on the sides of the cast of the manus track are similar to, although larger than, striations known from theropod and ornithopod tracks (Gatesy 2001, Currie et al., 2003) and from tracks of the extant emu (Milàn in press). This demonstrates uniformity in the pedal skin texture between a variety of non-avian and avian dinosaurs.
Based on the evidence herein presented, the brachiosaurid manus should be reconstructed with digits II to V encapsulated by tissue to form a semilunate unit, with only a short digit I, the pollex, free and the skin texture roughly tubercular (Fig. 4).

Conclusion

A newly found three-dimensionally preserved cast of a manus track, probably from a brachiosaurid, demonstrates that the manual digits of advanced sauropod dinosaurs were encapsulated in tissue to form a hoof-like unit. Only digit I, the pollex, was separated and had a short triangular claw. The cast shows that the manus was brought down and lifted vertically without any parasaggital components of movements before it was lifted well clear of the ground, and thus the entire forelimb retained its columnar form during the weight supporting phase, as predicted from anatomy, and here confirmed by a well preserved ichnofossil.

Acknowledgments

JM is financed by the University of Copenhagen, Faculty of Natural Science. The research by OM was partly financed by fellowship Praxis XXI BD|21616|99 of the Portuguese Fundação para a Ciência e Tecnologia. Richard G. Bromley, Geological Institute, University of Copenhagen kindly read and commented on the manuscript. And finally a big thanks to the geology students Geological Institute, University of Copenhagen who helped excavate and carry the specimen up from the beach.

References

Antunes, M. T. & Mateus, O. (2003): Dinosaurs of Portugal. - Comptes Rendus Palevol, **2**: 77–95; Paris.

Bonnan, M. F. (2003): The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. - Journal of Vertebrate Palaeontology, **23**: 595–613; Lawrence|Kansas.

Borsuk-Bialynicka, M. (1977): A new camarasaurid *Opisthocoelicaudia skarzynskii* gen. n., n. sp. from the Upper Cretaceous of Mongolia. - Palaeontologica Polonica, **37**: 5–64; Warszawa.

Christiansen, P. (1997): Locomotion in sauropod dinosaurs. - Gaia, **14**: 45–75; Athens.

Currie, P. J., Badamgarav, D. & Koppelhus, E. B. (2003): The First Late Cretaceous Footprints from the Nemegt Locality in the Gobi of Mongolia. - Ichnos, **10**: 1–13; Philadelphia.

Day, J. J., Upchurch, P., Norman, D., Gale, A. S. & Powell, H. P. (2002): Sauropod trackways, evolution, and behaviour. - Science, **296**: 1659; Washington.

Day, J. J., Norman, D. B., Gale, A. S., Upchurch, P. & Powell, H. P. (2004): A Middle Jurassic dinosaur Trackway site from Oxfordshire, U.K. - Palaeontology, 47: 319–348; Oxford.

Farlow, J. O. (1992): Sauropod tracks and trackmakers: Integrating the ichnological and skeletal records. - Zubia, **10**: 89–138; Logroño.

Gambaryan, P. P. (1974): How mammals run. - 367 pp.; New York (John Wiley & Sons).

Gatesy, S. M., Middleton, M. K., Jenkins Jr, F. A. & Shubin, N. H. (1999): Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. - Nature, **399**: 141–144; London.

Gatesy, S. M. (2001): Skin impressions of Triassic theropods as records of foot movement. - Bulletin of the Museum of Comparative Zoology, **156**: 137–149; Cambridge|Massachusetts.

Gilmore, C. W. (1925): A nearly complete, articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument, Utah. - Memoirs of the Carnegie Museum, **10**: 347–384; Pittsburgh.

Gilmore, C. W. (1936): Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. - Memoirs of the Carnegie Museum, **11**: 175–300; Pittsburgh.

Hill, G. (1989): Distal alluvial fan sediments from the Upper Jurassic of Portugal: Controls on their cyclicity and channel formation. - Journal of the Geological Society London, **146**: 539–555; London.

He, X., Li, K., Cai, K. & Gao, Y. (1988): The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan, IV. - 143 pp.; Peking (Chengdu Science and Technology Publishing House).

Janensch, W. (1922): Das Handskelett von *Gigantosaurus* und *Brachiosaurus* aus der Tendaguru-Schichten Deutsch-Ostafrikas. - Zentralblatt für Mineralogie, Geologie und Paläontologie, **1922**: 464–480; Stuttgart.

Janensch, W. (1961): Die Gliedmassen und Gliedmassengürtel der Sauropoden der Tendaguru-Schichten. - Palaeontographica (suppl. 7), **3**: 177–235; Stuttgart.

Lavocat, R. (1955): Sur un member antérieur du dinosaurien sauropode *Bothriospondylus recueilli* à Madagascar. - Comptes Rendus de l'Academie des Sciences, Paris, **240**: 1795–1796; Paris.

Lockley, M. G., Meyer, C. A. & Santos, V. F. (1994): Trackway evidence for a herd of juvenile sauropods from the Late Jurassic of Portugal. - Gaia, **10**:27–35; Athens.

Lockley, M. G., Santos, V. F., Meyer, C. A. & Hunt, A. P. (eds.) (1994): Aspects of sauropod paleobiology. - Gaia, **10**: 1–279; Athens.

Lockley, M. G., Schulp, A. S., Meyer, C. A., Leonardi, G. & Mamani, D. K. (2002): Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. - Cretaceous Research, **23**: 383–400; London.

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, **10**: 57–64; Athens.

Milàn, J. (in press). Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks, due to differences in walking pattern and substrate consistency: ichnotaxonomical implications. - Palaeontology; Oxford.

Paul, G. S. (1987): The science and art of restoring the life appearance of dinosaurs and their relatives. - In: Czerkas, S. J. & Olson, E. C. (eds.): Dinosaurs Past and Present II. Natural History Museum Los Angeles County: pp 5–39; Los Angeles (University of Washington Press).

Salgado, L., Coria, R. A. & Calvo, J. O. (1997): Evolution of titanosaurid sauropods. I: Phylogenetic analyses based on the postcranial evidence. - Ameghiniana, **34**: 3–32; Buenos Aires.

Santos, V. F., Lockley, M. G., Meyer, C. A., Carvalho, J. Carvalho, A. M. G. D. & Moratalla, J. J. (1994): A new sauropod tracksite from the Middle Jurassic of Portugal. - Gaia, **10**: 5–13; Athens.

Upchurch, P. (1994): Manus claw function in sauropod dinosaurs. - Gaia, **10**: 161–171; Athens.

Wilson, J. A. & Sereno, P. C. (1998): Early evolution and higher-level phylogeny of sauropod dinosaurs. - Society of Vertebrate Palaeontology, Memoir, **5**: 1–68; Chicago (supplement to Journal of Vertebrate Palaeontology 18).

Wilson, J. A. & Carrano, M. T. (1999): Titanosaurs and the origin of »wide-gauge« trackways: a biomechanical and systematic perspective on sauropod locomotion. - Palaeobiology, **25**: 252–267; Lawrence|Kansas.

Zhang, Y. (1988): The Middle Jurassic dinosaur fauna from dashanpu, Zigong, Sichuan. - Journal of the Chengdu College of Geology, **3**: 1–87; Chengdu.