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NEW ICHNOLOGICAL RECORD FROM THE LATE CAMPANIAN TORO TORO FORMATION AT TORO TORO, POTOSÍ (BOLIVIA): FIRST PROBABLE DROMAEOSAURID TRACKS FROM SOUTH AMERICA

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Palabras clave. Huellas. Terópodo. Dromeosauridae. Unenlagiinae. Cretácico. Bolivia. Gondwana.

Dromaeosaurids have a characteristic pes with a larger central third digit, a slightly smaller fourth one, and a second one represented by a ball-shaped pad that supported a retracted, deeply curved claw that did not come into contact with the ground (Ostrom, 1969). The group had hitherto been reported only from Late Jurassic to Cretaceous deposits in northern continents. However a substantial change in the perception of their paleobiogeographic history arose when several South American and Malagasy maniraptorans were discovered (Novas and Puerta, 1997; Forster *et al.*, 1998; Calvo *et al.*, 2004; Makovicky *et al.*, 2005; Novas and Pol, 2005; Novas *et al.*, 2008).

The record of vertebrate tracks in Bolivia is one of the most important and diverse of the world (Branisa, 1968; Bonaparte *at el.*, 1984; Leonardi, 1994; Meyer *et al.*, 2001; Lockley *et al.*, 2002). The aim of this paper is to describe and analyze ichnotaxonomically some tracks with peculiar features that suggest probable dromaeosaurid affinities. These tracks were found in the Toro Toro Formation (Upper Cretaceous) at Toro Toro, Potosí Department, Bolivia. Aspects of the paleobiology of the putative trackmakers are also discussed.

The specimens examined –briefly mentioned by Apesteguía *et al.* (2007)– are tracks preserved as natural molds. The original material is still *in situ*, but two plaster replicas of one of the footprints were made. One of these is housed in the collection of the Félix de Azara Foundation, Buenos Aires, Argentina (CFA-PA-852), while the other is in the Toro Toro National Park headquarters, Bolivia, with no collection number.

LOCALITY AND GEOLOGICAL SETTING

Toro Toro is a small town located in northern Potosí Department in Bolivia (Fig. 1). The area contains a large vertebrate tracksite, spreading across 10 km, from Huayra Khasa Hill to the Huayllas Hill, and with additional outcrops closer to the Umajalanta Caves. The tracksite comprises several layers in the upper part of the Toro Toro Formation (Campanian), a local equivalent to the more widespread Chaunaca Formation (Kennan and Pindell, 2000), that is overlain by the Maastrichtian El Molino Formation (Lohmann and Branisa, 1962; Camoin *et al.*, 1997; Sempere *et al.*, 1997) (Fig. 1). This stratigraphic unit represents part of the postrift stage (Mertmann and Fiedler, 1997) in an alluvial to deltaic environment within the Potosí Basin.

The sediments are mainly reddish mudstones and sandstones with a few gypsum intercalations (Sempere *et al.*, 1988), and are also exposed in the Otavi and Sarcarca areas (Mertmann and Fiedler, 1997; Hippler *et al.*, 1999).

The main track-bearing level of the Toro Toro tracksite is a non-continuous bedding surface that crops out along the banks of the Toro Toro River before it flows in to the Condor Mayu River. The footprints here described were found in a creek parallel to the eastern bank of the Toro Toro River, immediately after the first natural stone bridge, before the junction of this river and the Mayu Mayu River (Fig. 1).

The Toro Toro Formation also outcrops at other secondary localities that yielded an abundant and diverse ichnological record that remains still unpublished. However, as intermediate zones are not exposed, these hills and creeks render uncertain their correspondence to the same level (see details in Fig. 1).

SYSTEMATIC PALEONTOLOGY

Ichnofamily Dromaeopodidae Li *et al.*, 2008

Ichnogenus ***Dromaeopodus***? Li *et al.*, 2006

Type ichnospecies. *Dromaeopodus shandongensis* Li *et al.*, 2008.

***Dromaeopodus*? isp.**

Figure 2

Referred material. Ten *in situ* tracks from the Toro Toro tracksite (18°07′S–65°45′W), at Toro Toro, Potosí Department, Bolivia; CFA-PA-852 and one unnumbered specimen, were preserved as plaster replicas of one of those footprints (Fig. 2; Tab. 1).

Description. The specimens are represented by eight isolated tracks (Figs. 2.3 –7), and two probably associated imprints in a partial trackway (Figs. 2.1 –2).

The specimens, produced by a large-sized bipedal trackmaker, show poor to moderate preservation, some of them probably being undertracks. The footprints are didactyl, asymmetric with respect to the central axis of the digit III

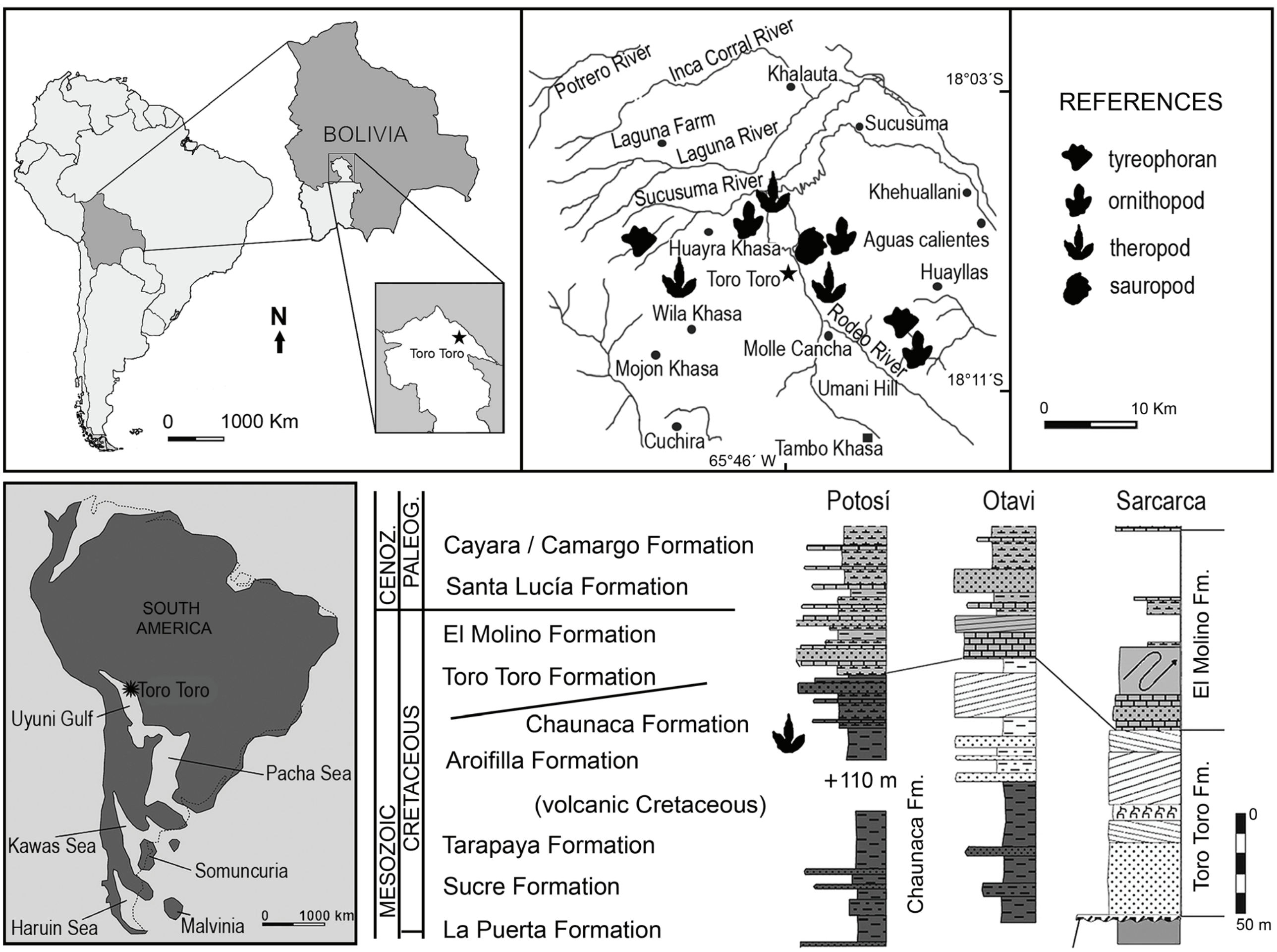

Figure 1. Top, left: location map of Toro Toro, Potosí Department, Bolivia, South America; right: detailed map with the main ichnological sites. Bottom: paleogeographical reconstruction of South America during the Late Campanian (modified from Pascual *et al*., 1996) and the lithostratigraphic framework of three trace-fossil bearing sections (modified from Hippler *et al*., 1999)/ *Arriba, izquierda: mapa de localización de Toro Toro, departamento de Potosí, Bolivia, América del Sur; derecha: mapa detallado con los principales sitios icnofosilíferos. Abajo, reconstrucción paleogeográfica de América del Sur durante el Maastrichtiano (modificado de Pascual* et al.*, 1996) y la litoestratigrafía de tres secciones portadoras de icnofósiles (modificado de Hippler* et al.*, 1999).*

impression, with no hallux imprint preserved (Fig. 2). The tracks may display complete digit III and IV impressions, with the digit II imprint incomplete or even missing (Figs. 2.3 –4,7), or may have the impressions of digits III and IV joined into a single mark with no evidence at all of digit II (Fig. 2.1 –2). The tridactyl condition of the foot is evident in some specimens, but it appears functionally didactyl.

The average length: width ratio is 1.4 (average length 22 cm, average width 15.9 cm). The impression of digit III is the longest, usually with a large claw mark, while digit IV –in some cases curved inwards– is shorter and with a smaller claw mark. When present, digit II impression is represented only by the first digital pad and no claw mark. Average lengths of the digit impressions are: II: 3 cm, IV: 10.1 cm, and III: 13.8 cm. The average angle between the impressions of digits II –III is 16°, while between digits III –IV it is 17.8°, and the total divarication is 32.2°. Metatarsal pads are wide when compared with typical tridactyl tracks.

The only measurable trackway parameter is the pace length of the partial trackway, which is about 1.6 m.

Remarks and comparisons. The morphology of the tracks studied herein allows including them in the ichnofamily Dromaeopodidae Li *et al.*, 2008. It was originally proposed to include the ichnotaxa *Dromaeopodus shandongensis* Li *et al.*, 2008, as the type ichnogenus, and *Velociraptorichnus sichuanensis* Zhen *et al.*, 1994. Later, *Dromaeosauripus hamanensis* Kim *et al.*, 2008, and *Menglogipus sinensis* Xing *et al.*, 2009 were also included. The ichnofamily was based on the particular morphology of the tracks, not on producer identity or biology, as required by the ICZN (2000).

Dromaeopodus Li *et al.*, 2008 (type ichnospecies: *Dromaeopodus shandongensis* Li *et al.*, 2008), from the Early Cretaceous of Shandong Province (China), includes several large didactyl footprints, with imprints of digits III and IV subparallel, subequal in length, displaying a laterally convex curvature, a suboval heel pad mark, and a hemispherical depression representing the proximal portion of digit II. The Bolivian tracks are provisionally assigned to this ichnogenus based on overall morphology. Although some differences exist, more and better preserved specimens are necessary to confirm an ichnotaxonomic separation.

Dromaeosauripus hamanensis Kim *et al.*, 2008, established to distinguish didactyl tracks from the Early Cretaceous of Korea, displays a similar morphology to the tracks included in *Dromaeopodus*, being almost half the size. Both ichnotaxa seem to be similar kind of tracks, but the Korean tracks lack a pad trace for digit II, perhaps because of different preservational conditions. However, more details are necessary for a confident ichnotaxonomic assignment.

Menglogipus sinensis Xing *et al.*, 2009, includes didactyl footprints from the Late Jurassic –Early Cretaceous of Hebei Province (China), and differs from the Bolivian specimens by displaying a longer digit III imprint respect to IV, and a wider angle between these digit impressions.

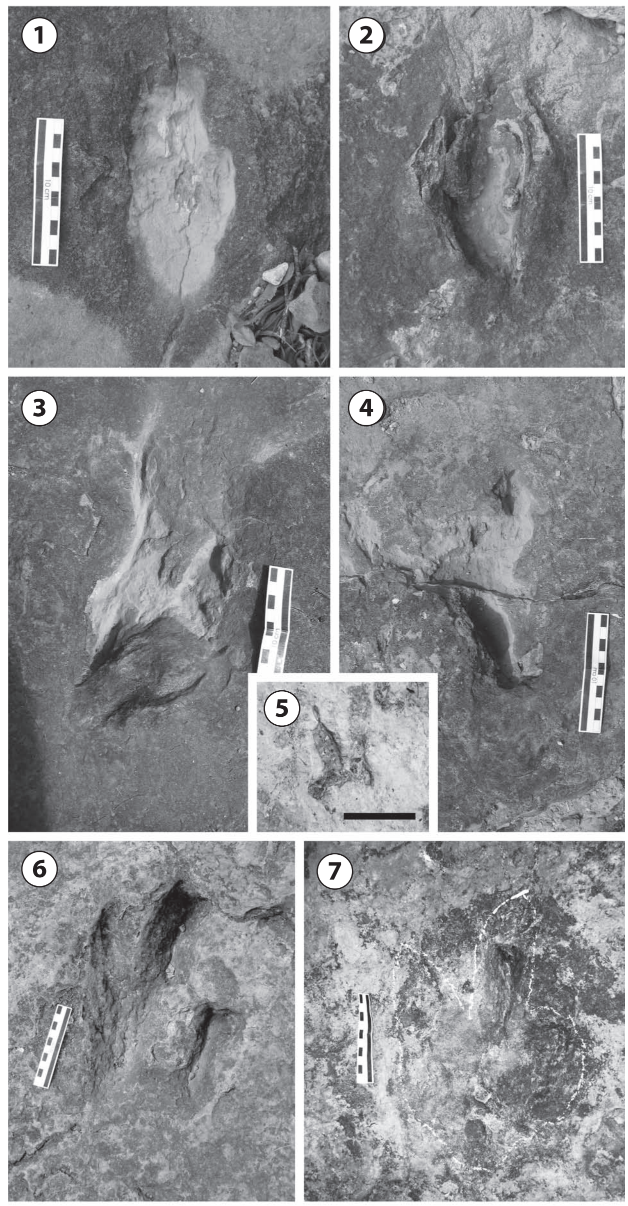

Figure 2.1–7, Tracks assignated to Dromaeosauridae from Toro Toro; **1 –2**, probably associated footprints; **3 –7,** isolated footprints. Scale bars: 10 cm. Abbreviations: II: digit II imprint; III: digit III imprint; IV: digit IV imprint/ *Huellas de Toro Toro asignadas a Dromaeosauridae.* ***1 –2,*** *huellas probablemente asociadas;* ***3 –7,*** *huellas aisladas. Escalas: 10 cm. Abreviaturas:* ***II****: impresión del dígito II;* ***III****: impresión del dígito III;* ***IV****: impresión del dígito IV.*

Velociraptorichnus sichuanensis Zhen *et al.*, 1995, from the Early Cretaceous of Sichuan and Shandong provinces (China) (Zhen *et al.*, 1995; Li *et al.*, 2008) is represented by small tracks with small digit II impressions. It differs from the Bolivian footprints by having straight digit impressions.

Two isolated medium-sized didactyl footprints from the Lower Cretaceous of Utah, were suggested to match with the foot of *Utahraptor* (Lockley and Peterson, 2002; White and Lockley, 2002; Lockley *et al.*, 2004). Furthermore, Gierliński (2007, 2008) reported two didactyl tracks in a partial trackway from Mount Mlynarka, Poland, as *Velociraptorichnus* isp. Subsequently, Gierliński (2009) claimed that they were more similar to *Dromaeopodus*. All the non-Chinese tracks are poorly preserved and the morphological details available are insufficient to confidently confirm similarity with the Bolivian specimens.

Earlier rocks from the Chinle Group (Late Triassic) from western Colorado yielded three didactyl tracks (Gaston *et al.*, 2003). They display curved impressions of digits III and IV and an enlarged digital pad at the base of digit II. They are both temporally and anatomically incongruent with a deinonychosaurian origin (Li *et al.*, 2008), according to current chronological knowledge of the group.

Middle–Upper Jurassic deposits in Niger yielded five trackways –totaling 120 didactyl tracks lacking heel pad imprints– assigned to dromaeosaurids (Mudroch *et al.*, 2009). However, these authors did not provide a detailed description or pictures; thus it is not possible to discuss the taxonomic assignation of these tracks.

A trackway from the Late Cretaceous from northeastern México was mentioned as belonging to dromaeosaurids (Meyer *et al.*, 2008), but there is not enough information about these tracks to confirm their taxonomic placement.

DISCUSSION

The Dromaeosauridae (Matthew and Brown, 1922) were defined as all deinonychosaurs closer to *Velociraptor* than to *Troodon* (Sereno, 1998). The revised phylogeny by Makovicky *et al.* (2005) unites *Buitreraptor*, *Unenlagia*, and *Rahonavis* within a Gondwanan lineage of Dromaeosauridae, the Unenlagiinae (Bonaparte, 1999). This clade includes large forms, such as the large *Austroraptor* from the uppermost Cretaceous of Argentina (Novas *et al.*, 2008), that shares derived traits with *Buitreraptor* and other still unnamed forms (Calvo *et al.*, 2004).

Although more and better preserved specimens are necessary to confirm this taxonomic placement, the morphology of the Toro Toro footprints prompts relating them to

Table 1 - Summary of measured track. Linear measurements in centimeters and angles in degrees / *Resumen de los parámetros medidos de huellas. Mediciones lineales en centímetros y ángulos en grados.*

Specimens	L	W	II	III	IV	II-III	III-IV	II-IV
Isolated tracks								
Track 1	*28.8 inc*	*19.9*	*9.2*	*17.8*	*15.3*	*10*	*11*	*18*
Track 2	*19.4*	--	--	--	--	--	--	--
Track 3	*27.4*	--	--	*14.6*	--	--	--	--
Track 4	*19.4 inc*	*10.8*	*1*	*10.5*	*7.6 inc*	*13*	*14*	*22*
Track 5	*22*	*16.5*	*1.5*	*12.3*	*4.7*	*20*	*30*	*48*
Track 6	*26.8*	*20*	*2.1*	*15.8*	*10.4*	*16*	*16*	*36*
Track 7	--	*22.4*	--	*17.5*	--	*17*	--	--
Track 8	*25 inc*	*19.4*	*1.4*	*17.8*	*10.1*	*20*	*18*	*37*
Trackway? ~~2~~ (partial)								
Track 1	*16.4*	*7.5*	--	*6.2*	--	--	--	--
Track 2	*20*	*10.5*	--	*11.4*	--	--	--	--
Mean	*22*	*15.9*	*3.0*	*13.8*	*10.1*	*16*	*18*	*32*

Abbreviations: **L**, *track length*; **W**, *track width*; **II**, *length of digit II*; **III**, *length of digit III*; **IV**, *length of digit IV*; **II-III**, *divarication angle between digits II and III*; **III-IV**, *divarication angle between digits III and IV*; **II-IV**, *divarication angle between digits II and IV* / Abreviaturas: **L**, largo de la huella; **W**, ancho de la huella; **I**, largo del dígito I; **II**, largo del dígito II; **III**, largo del dígito III; **IV**, largo del dígito IV; **II-III**, ángulo formado por los ejes de los dígitos II y III; **III-IV**, ángulo formado por los ejes de los dígitos III y IV; **II-IV**, ángulo formado por los ejes de los dígitos II y IV.

the dromaeosaurids. If this were confirmed, they represent the first tracks referable to South American dromaeosaurids, also known as unenlagines, and the second record of these tracks for Gondwana, after the Nigerian tracks (Murdoch *et al.*, 2009).

Skeletal information shows that dromaeosaurids bear a retractable sickle-shaped claw on their second toe, which is held off the ground. Available reconstructions show the sickle-claw in a very high position (see Fig. 3.1). On the basis of preserved morphology, the deep imprint of the first proximal part of digit II in some of the Toro Toro tracks suggests that the foot either stepped into soft mud or else that the second digit was held much lower and closer to the ground than expected (Fig. 3.2). Supporting the latter assumption we note that some of the tracks are not too deep and that digit I is not impressed in any of them. Comparison with the skeletal evidence provided by the sickle-clawed unenlagine *Neuquenraptor argentinus* (Novas and Pol, 2005; Fig. 3.3) shows no evident differences, except that the latter has a longer first phalanx. The pes of *Deynonychus antirrhopus* was reconstructed by Ostrom (1969) in an intermediate posture between the two possible configurations (Fig. 3.4).

It is interesting to remark that the size of the Toro Toro tracks matches that of those large representatives of the deynonychosaurian clade (*e.g.*, *Austroraptor*) existing in South America at that time. For this reason –and although during the Late Campanian North American faunas entered South America increasing the taxonomical diversity of southern theropods– the studied tracks are likely referable to southern dromaeosaurids. While large dromaeosaurids also existed in North America (*e.g.*, *Utahraptor*), this occurred during the Early Cretaceous, whereas the larger known unenlagines are late Campanian.

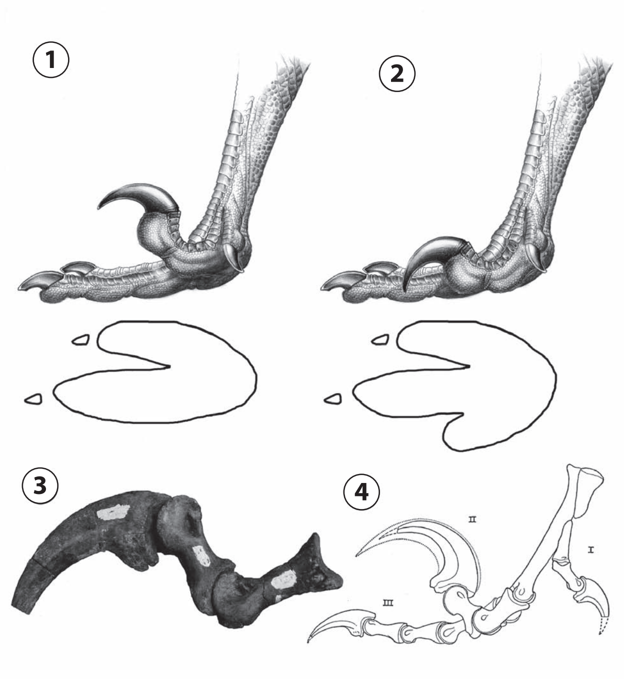

Figure 3. 1, Reconstruction of pes and track of a dromaeosaurid showing a low position for the raptorial sickle-claw; **2,** reconstruction of pes and track of a dromaeosaurid as previously proposed with the sickle-claw and corresponding phalanges holding it far from the ground; **3,** sickle-claw in the unenlagine ***Neuquenraptor argentinus*** (Novas and Pol, 2005); **4**, pes and sickle-claw in the dromaeosaurid ***Deynonychus antirrhopus*** by Ostrom (1969) showing a posture intermediate between two proposals. Not to scale/ ***1,*** *reconstrucción de pata y huella de dromeosáurido mostrando una posición baja de la garra falciforme raptorial;* ***2,*** *reconstrucción de pata y huella de dromeosáurido como fue propuesto anteriormente, con la garra falciforme raptorial y las falanges correspondientes elevadas distantes del suelo;* ***3,*** *garra falciforme en el unenlagino* **Neuquenraptor argentinus** *(Novas and Pol, 2005);* ***4****, pata y garra falciforme en el dromeosáurido* **Deynonychus antirrhopus** *según Ostrom (1969) con una postura intermedia entre las dos propuestas. No a escala.*

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REFERENCES

Apesteguía, S., de Valais, S., Meyer, C.A., Ríos Cordero, G. and Medina, O. 2007. Reduced inner toe theropod trackways from El Molino Formation (Maastrichthian) at Toro Toro (Bolivia). *5ra Reunión Argentina de Icnología y 3era Reunión de Icnología del Mercosur* (Ushuaia), *Abstracts*, p. 47.

Bonaparte, J.F. 1999. Tetrapod faunas from South America and India: A palaeobiogeographic interpretation. *Proceedings of the Indian National Science Academy* 65: 427 –437.

Bonaparte, J.F., Colbert, E.H., Currie, Ph., de Ricqles, A., Kielan-Jaworowska, Z., Leonardi, G., Morello, N. and Taquet, P. 1984. *Sulle orme dei dinosauri*. Erizzo Editrice, Venice, 337 p.

Branisa, L. 1968. Hallazgo del amonite *Neolobites* en la Caliza Miraflores y de huellas de dinosaurios en la Formación El Molino y su significado para la determinación de la edad del "Grupo Puca". *Boletín del Instituto Boliviano del Petróleo* 8: 16 –29.

Calvo, J.O., Porfiri, J.D. and Kellner, A.W. 2004. On a new maniraptoran dinosaur (Theropoda) from the Upper Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional Rio de Janeiro* 62: 549 –566.

Camoin, G., Casanova, J., Rouchy, J-M., Blan-Valleron, M-M. and Deconinck, J-F. 1997. Environmental controls on perennial and ephemeral carbonate lakes: the central palaeo-Andean Basin of Bolivia during Late Cretaceous to early Tertiary times. *Sedimentary Geology* 113: 1 –26.

Forster, C.A., Sampson, S.D., Chiappe, L.M. and Krause, D. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279: 1915 –1919.

Gaston, R., Lockley, M.G., Lucas, S.G. and Hunt, A.P. 2003. *Grallator*-dominated fossil footprint assemblages and associated enigmatic footprints from the Chinle Group (Upper Triassic), Gateway Area, Colorado. *Ichnos* 10: 153 –163.

Gierliński, G.D. 2007. New dinosaur tracks in the Triassic, Jurassic and Cretaceous of Poland. *4as Jornadas Internacionales sobre Paleontología de Dinosaurios y su entorno* (Burgos), *Resúmenes*, p. 13 –15.

Gierliński, G.D. 2008. Late Cretaceous dinosaur tracks from the Roztocze Hills of Poland. *2nd International Congress on Ichnology* (Warsaw), *Abstracts*, p. 44.

Gierliński, G.D. 2009. A preliminary report on new dinosaur tracks in the Triassic, Jurassic and Cretaceous of Poland. *4as Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno* (Burgos), *Resúmenes*, p. 75 –90.

Hippler, D., Bucher, S., Meyer, Chr.-A. and Fügenschuh, B. 1999. Preliminary results on the sedimentology of the Late Cretaceous El Molino Formation (Sucre, Bolivia). *7th Swiss Sedimentologists Meeting* (Fribourg), *Abstracts*, p. 22.

ICZN (International Commission for Zoological Nomenclature). 2000. *International Code of Zoological Nomenclature, adopted by the International Union of Biological Sciences , 4th edition*. International Trust for Zoological Nomenclature, London, 232 p.

Kennan, L. and Pindell, J. 2000. *Exploration Framework Atlas Series: Volume 3, The Central Andes*. Tectonic Analysis Ltd., Duncton (West Sussex), 65 p.

Kim, J.Y., Kim, K.S., Lockley, M.G., Yang, S.Y., Seo, S.J., Choi, H.I. and Lim, J.D. 2008. New didactyl dinosaur footprints (*Dromaeosauripus hamanensis* ichnogen. et ichnosp. nov.) from the Early Cretaceous Haman Formation, south coast of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 262: 72 –78.

Leonardi, G. 1994. *Annotated Atlas of South American Tetrapod footprints (Devonian to Holocene)*. Serviço Geológico de Brasil, Brasilia, 248 p.

Li, R., Lockley, M.G., Makovicky, P.J., Matsukawa, M., Norell, M.A., Harris, J.D. and Liu, M. 2008. Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China. *Naturwissenschaften* 95: 185 –191.

Li, D., Azuma, Y., Fujita, M., Lee, Y-N. and Arakawa, Y. 2006. A preliminary report on two new vertebrate tracks sites including dinosaurs from the Early Cretaceous Hekou Group, Gansu province, China. *Journal of the Paleontological Society of Korea* 22: 29 –49.

Lockley, M.G., Kim, J.Y., Kim, K. S., Kim, S.H., Mastukawa, M., Rihui, L., Jianjun, L., Yang, S-Y. 2008. *Minisauripus* the track of a diminutive dinosaur from the Cretaceous of China and South Korea: implications for stratigraphic correlation and theropod foot morphodynamics. *Cretaceous Research* 29: 115 –130.

Lockley, M.G. and Peterson, J. 2002. *A guide to fossil footprints of the world*. Lockley-Peterson Publications, St. George, Utah, 124 p.

Lockley, M.G., Lucas, S.G., Hunt, A.P. and Gaston, R. 2004. Ichnofaunas from the Triassic-Jurassic boundary sequences of the Gateway area, Western Colorado: implications for faunal composition and correlations with other areas. *Ichnos* 11: 89 –102.

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

Lohmann, H.H. and Branisa, L. 1962. Estratigrafía y paleontología del Grupo Puca en el sinclinal de Miraflores, Potosí. *Petróleo Boliviano* 4: 9 –16.

Makovicky, P.J., Apesteguía, S. and Agnolín, F.L. 2005. The earliest dromaeosaurid theropod from South America. *Nature* 437: 1007 –1011.

Matthew, W.D. and Brown, B. 1922. The family Deinodontidae, with notice of a new genus from Cretaceous of Alberta. *Bulletin of the American Museum of Natural History* 46: 367 –385.

Mertmann, D. and Fiedler, K. 1997. Sedimentary evolution of the Cretaceous to Palaeocene Potosí Basin (Eastern Cordillera, southern Bolivia). *1er Congreso Latinoamericano de Sedimentología, Sociedad Venezolana de Geología (*Margarita, Venezuela), *Resúmenes volumen 2*, p. 95 –101.

Meyer, C.A., Frey, E.D. and Thüring, B. 2008. The pitfalls of interpreting incomplete dinosaur trackways – an example of a dromaeosaurid trackway from the Late Cretaceous of the Sierra Madre Oriental (Cerro del Pueblo Formation, Late Campanian; Parras Basin, Coahuila, NE Mexico). *6th Meeting of the European Association of Vertebrate Palaeontologists* (Spišská Nová Ves), *Abstracts*, p. 69 –73.

Meyer, C.A., Hippler, D. and Lockley, M.G. 2001. The Late Cretaceous vertebrate ichnofacies of Bolivia - facts and implications. *7th International Symposium on Mesozoic Terrestrial Ecosystems. Asociación Paleontológica Argentina* 7: 133 –138.

Mudroch, A., Richter, U., Joger, U. and Kosma, R. 2009. Dinosaur tracks from the Tiouraren Formation near Azènak (Republic of Niger). *7th Annual Meeting European Association of Vertebrate Palaeontologists* (Berlin), *Abstracts*, p. 52.

Novas, F.E. and Pol, D. 2005. New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. *Nature* 3285: 858 –861.

Novas, F.E., Pol, D., Canale, J., Porfiri, J. and Calvo, J. 2008. A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. *Proceedings of the Royal Society B -Biological Scineces* 276: 1101 –1107.

Novas, F.E. and Puerta, P.F. 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* 387: 390 –392.

Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History* 30: 1 –165.

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

Sempere, T., Oller, J. and Barrios, L. 1988. Evolución tectosedimentaria de Bolivia durante el Cretácico. 5° *Congreso Geológico Chileno* (Santiago de Chile), *Resúmenes* 3: H37 –H65.

Sereno, P.C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 210: 41 –83.

White, D. and Lockley, M.G. 2002. Probable dromeosaur tracks and other dinosaur footprints from the Cedar Mountain Formation (Lower Cretaceous), Utah. *Journal of Vertebrate Paleontology* 22: 119A.

Xing, L.D., Harris, J.D., Sun, D-H. and Zhao, H-Q. 2009. The Earliest known deinonychosaur tracks from the Jurassic –Cretaceous boundary in Hebei province, China. *Acta Palaeontologica Sinica* 48: 662 –671.

Zhen, S., Li, J. and Zhang, B. 1995. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan, China. *Memoirs of the Beijing Natural History Museum* 54: 105 –120.

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