Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

Dromaeosaurid tracks from the Upper Cretaceous Candeleros Formation of northwestern Patagonia provide additional data on the palaeobiology and palaeoecology of 'raptor' dinosaurs

ARTURO M. HEREDIA, FEDERICO A. GIANECHINI, FLAVIO BELLARDINI, IGNACIO J. MANIEL, ALBERTO C. GARRIDO, GUILLERMO J. WINDHOLZ, MATTIA A. BAIANO, ALESSIO CIAFFI AND IGNACIO DÍAZ-MARTÍNEZ

LETHAIA

This contribution documents several strongly asymmetrical and functionally didactyl tracks from the Cenomanian Candeleros Formation of northwestern Patagonia, Argentina. This new record includes at least six tracks preserved as concave epireliefs in medium-grained sandstone from alluvial plain deposits. Each track is approximately 10 cm long, showing impressions of digits III and IV, and a proximal impression of digit II with a separated and well-developed claw trace. This type of footprint is commonly referred to dromaeosaurid dinosaurs; however, the sickle claw impression is barely known in the track record. These tracks suggest that the trackmaker had a well-developed ungual phalanx on digit II and could rest on the substrate, possibly while was stationary. The Cretaceous dromaeosaurid record in Argentina is limited to the Neuquén Basin and includes unenlagiine dromaeosaurids. Thus, it is likely that the tracks were made by a small member of this clade, such as *Buitreraptor gonzalezorum*. As they are the first dromaeosaurid tracks from the Candeleros Formation, and from Patagonia, these finds enhance track diversity and provide a more comprehensive correlation between ichnological and osteological evidence from this unit. This discovery contributes to our understanding of the limited dromaeosaurid track record in Gondwana and the Cenomanian age globally. □ *Functionally didactyl footprints, dromaeosaurids, Unenlagiinae, palaeobiology, Late Cretaceous, Patagonia.*

Arturo M. Heredia ✉ [heredia.arturomiguel@gmail.com], Flavio Bellardini [fbellardini@unrn.edu.ar] and Guillermo J. Windholz [gwindholz@unrn.edu.ar], Instituto de Investigación en Paleobiología y Geología (IIPG), CONICET-Universidad Nacional de Río Negro, Av. General Julio Argentino Roca 1242, R8332 General Roca, Río Negro, Argentina; Federico A. Gianechini [fgianechini@email.unsl.edu.ar], Instituto Multidisciplinario de Investigaciones Biológicas de San Luis (IMIBIO-SL), CONICET-Universidad Nacional de San Luis, Av. Ejército de los Andes 950, D5700 San Luis, Argentina; Ignacio J. Maniel [imaniel@mendoza-conicet.gob.ar], Instituto de Evolución, Ecología Histórica y Ambiente (IDEVEA), CONICET-Universidad Tecnológica Nacional, Av. J.J. Urquiza 314, M5600 San Rafael, Mendoza, Argentina; Alberto C. Garrido [albertocarlosgarrido@gmail.com], Museo Provincial de Ciencias Naturales 'Prof. Dr. Juan A. Olsacher', Dirección Provincial de Minería, Ejército Argentino y Etcheluz, Q8340AUB Zapala, Neuquén, Argentina; Centro de Investigación en Geociencias de la Patagonia (CIGPat), Departamento de Geología y Petróleo. Facultad de Ingeniería. Universidad Nacional del Comahue. Buenos Aires 1.400, Q8300IBX Neuquén, Argentina; Mattia A. Baiano [mbaiano@unrn.edu.ar], Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina; Universidad Nacional de Río Negro, General Roca, Argentina; Museo Paleontológico 'Ernesto Bachmann', Dr. Natali S/N, Q8311 Villa El Chocón, Argentina; Alessio Ciaffi [al.ciaffi@gmail.com], Universita La Sapienza di Roma, Piazzale Aldo Moro 5, 00185 Roma, Italy; Ignacio Díaz-Martínez [ignacio.diaz@unican.es], Departamento de Ciencias de la Tierra y Física de la Materia Condensada, Facultad de Ciencias, Universidad de Cantabria, Avda. de los Castros 48, 39005 Santander, Cantabria, Spain; *manuscript received on 20/11/2024; manuscript accepted on 11/04/2025; manuscript published on 12/08/2025 in Lethaia 58*(3).

The Dromaeosauridae is a family of theropod dinosaurs that are informally referred to as 'raptors' and have long attracted popular and scientific attention due to their distinctive body plan (Ostrom 1990; Norell & Makovicky 2004), their close phylogenetic relationship to birds (Turner *et al*. 2007, 2012), and their probable gregarious behaviour (Ostrom 1990, but see also Roach & Brinkman 2007 for an alternative opinion).

One of the most distinctive anatomical features of these deinonychosaurian theropods is the

https://doi.org/10.18261/let.58.3.4

morphology of the foot, which is characterized by a digit II with the capacity of hyperextension and with a hypertrophied sickle-shaped claw. Among deinonychosaurians, the dromaeosaurid fossil record is diversified and widespread, with finds from North America, Europe, Africa, Asia and South America (Ostrom 1990; Norell & Makovicky 2004; Turner *et al*. 2012). The earliest confirmed dromaeosaurid fossil record comes from the Early Cretaceous (*Utahraptor ostrommaysi* Kirkland *et al*., 1993 and other records from the Yellow Cat Member of the Cedar Mountain Formation, Berriasian–Valanginian, Joeckel *et al*. 2023) and they survived until the end of the Cretaceous (Maastrichtian), although in South America, dromaeosaurids are restricted to the Late Cretaceous (Norell & Makovicky 2004; Makovicky *et al*. 2005; Turner *et al*. 2012; Gianechini *et al*. 2024).

Historically, most research on dromaeosaurids has focused on skeletal material; however, recent ichnological evidence has significantly improved our knowledge of this clade (Lockley *et al*. 2016a; Kim *et al*. 2018; Qin & Xing 2021; Enriquez *et al*. 2021). For instance, the documentation of trackways with functionally didactyl footprints suggests that the sickle claw of digit II was usually held retracted during locomotion (e.g. Kim *et al*. 2008, 2012, 2018; Lockley *et al*. 2016a, 2016b; Qin & Xing 2021). Additionally, some authors suggest that the presence of multiple parallel and closely spaced trackways with the same orientation, track morphology and size, on the same tracking surface, represents evidence of gregarious behaviour for dromaeosaurids (Li *et al*. 2008; Xing *et al*. 2018). The functionally didactyl tracks assigned to dromaeosaurids are well known in China, South Korea, North America, and Europe, from the earliest Early Cretaceous (Berriasian) to the end of the Late Cretaceous (Maastrichtian) (Lockley *et al*. 2016a; Enriquez *et al*. 2021). Thus, the oldest dromaeosaurid ichnological record is similar in age to the oldest osteological record. However, this record is poorly known in South America, with evidence referred to as *Dromaeopodus*? isp. from the Toro Toro Formation (Campanian) and undetermined tracks from the El Molino Formation (Maastrichtian), both of Bolivia (Apesteguía *et al*. 2011; Meyer *et al*. 2021).

In this contribution, several strongly asymmetrical and functionally didactyl tracks documented in a new tracksite at El Sauce locality from the Cenomanian Candeleros Formation of northern Patagonia, Argentina, are analysed. This record consists of at least six tracks preserved as concave epireliefs in medium-grained sandstone from alluvial plain deposits. The aim of this study is fourfold: 1) to describe in detail the track morphology and preservation; 2) to provide an ichnotaxonomical analysis; 3) to identify the possible trackmakers; and 4) to discuss their palaeobiological and palaeoecological implications.

Geological setting

The Neuquén Basin is in the west-central region of Argentina, extending from 32° to 40° S latitude along the Andean foothills (Fig. 1A). Spanning approximately 120,000 km², the basin preserves a continuous Late Triassic to Palaeogene stratigraphical succession, with more than 7000 m of sedimentary deposits that reflect both marine and continental environments (Howell *et al*. 2005). During the Late Cretaceous–Palaeogene interval, the basin was part of a foreland basin system, predominantly composed of continental deposits, with subordinate marine intervals (Howell *et al*. 2005). South of the Huincul High, in the Picún Leufú depocenter, the strata between the Mendoza and Neuquén groups are assigned to the Bajada del Agrio Group, which is composed of a set of continental sediments known as the La Amarga and Lohan Cura formations (Leanza & Hugo 2011). The Cenomanian–Campanian Neuquén Group rests unconformably on the Bajada del Agrio Group, forming an angular unconformity that marks the transition to the foreland basin phase. The Neuquén Group is characterized by more than 1200 m of continental deposits, accumulated during a period of complete palaeogeographical disconnection of the basin with the Pacific Ocean (Howell *et al*. 2005; Garrido 2010).

The Neuquén Group is subdivided into three primary subgroups: Río Limay, Río Neuquén, and Río Colorado (Fig. 1B). The lower subgroup, the Río Limay Subgroup (Cenomanian–Turonian), is represented by the Candeleros Formation at its base (Fig. 1B). Known for its characteristic purple to red continental deposits, the Candeleros Formation is overlain by the Huincul Formation, which is easily distinguished by its yellow to white sandstone beds (Garrido 2010).

The Candeleros Formation consists of massive coarse- to medium-grained sandstones and conglomerates, with interbedded thin claystone and siltstone layers, reaching a thickness of approximately 200–300 m. This unit preserves different continental palaeoenvironments, including alluvial, fluvial, and aeolian settings related to arid to semiarid conditions during its deposition, with a temperate climate characterized by alternating dry and wet periods (Garrido 2010; Calvo & Rivera 2018; Krapovickas *et al*. 2018; Heredia *et al*. 2020; Apesteguía *et al*. 2023).

The study site is located in the southern part of the Neuquén Basin, where the Candeleros Formation

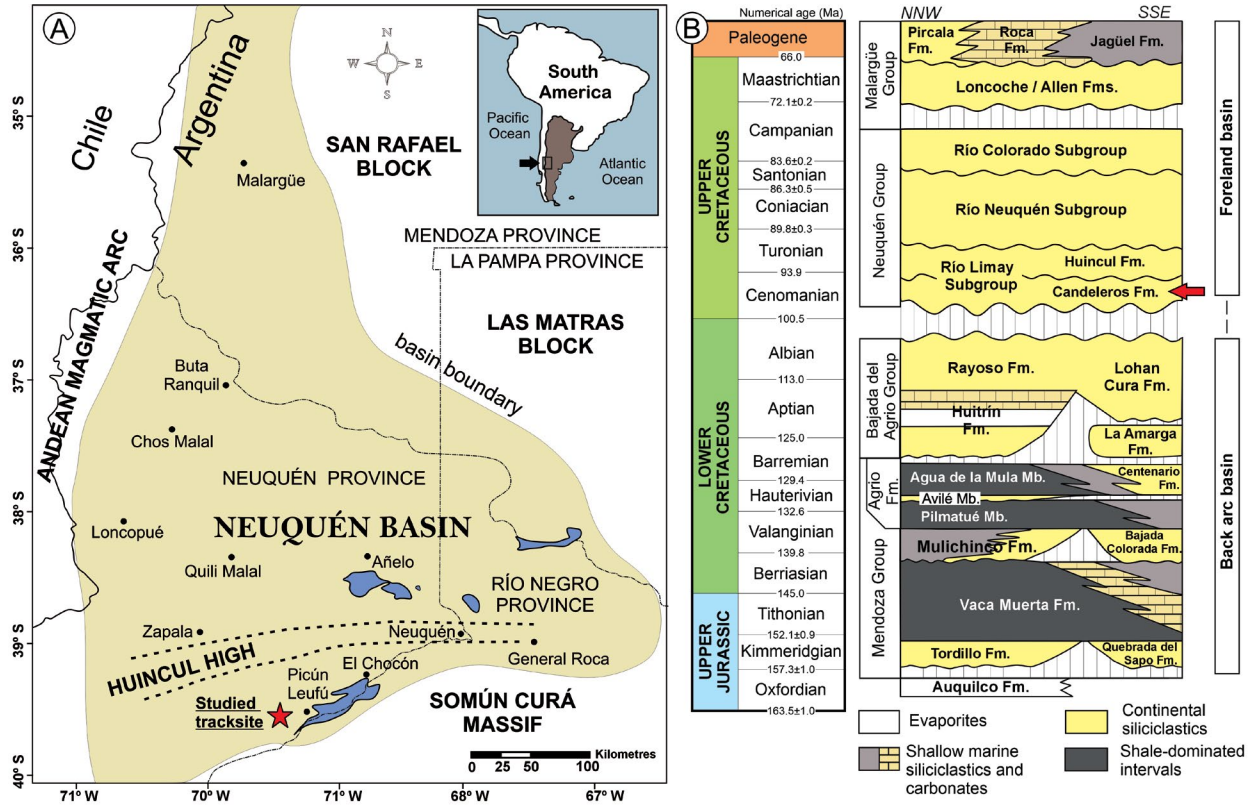

Fig. 1. A, the Neuquén Basin (north-western Patagonia, Argentina) showing the studied site (El Sauce) by a red star. B, stratigraphical chart of the Upper Jurassic–Palaeogene interval of the Neuquén Basin (modified from Howell *et al.* 2005). The Candeleros Formation, the lower unit of the Neuquén Group, is highlighted by a red arrow.

(Cenomanian) is exposed extensively (Fig. 1A). At this site, the lower section of the Candeleros Formation is dominated by playa lake and ephemeral fluvial deposits, likely developed within a distal alluvial fan zone. Playa lakes are represented by interbedded massive to laminated fine-grained sandstones, mudstones and claystones. Ephemeral fluvial channels are characterized by fining-upward deposits, beginning with massive sandstones and transitioning upward into horizontally laminated and ripple cross-laminated sandstones. Toward the upper section of this unit, sandy braided fluvial system deposits become predominant. The tracks are found within levels of the lower section, generally associated with sheetflood deposits formed in depressed areas and associated with the playa lake facies.

Material and methods

The new material consists of at least six tracks preserved in a single block that was collected in proximity of El Sauce locality (GPS point for reference: 39° 30’ 19” S, 69° 24’ 19” W) to the west of the Picún Leufú city, in the Neuquén Province, northern Patagonia, Argentina. This material (collection number 58-MES-IC-09) was deposited in the Museo ‘Carlos Hermosilla’ of El Sauce (Fig. 1A). The logged section in the study site includes about 32 m in thickness of sandstones interbedded with claystones, mudstones and limestones, with thin tuff layers occasionally preserved (Fig. 2). The new track-bearing level is found in medium-grained sandstones with horizontal stratification in the upper part of the logged section (Fig. 2).

Track measurements have been carried out following the works of Thulborn (1990), Heredia *et al.* (2021) and Lallensack (2025). The tracks have been studied through field descriptions and photogrammetric models obtained using Agisoft Metashape 1.5.0 Professional Edition (Educational License, www.agisoft.com) following the procedures indicated by Mallison & Wings (2014), Falkingham *et al.* (2018), and Lallensack (2025). The false depth colour images of the tracks have been produced with the free software Paraview (www.paraview.org).

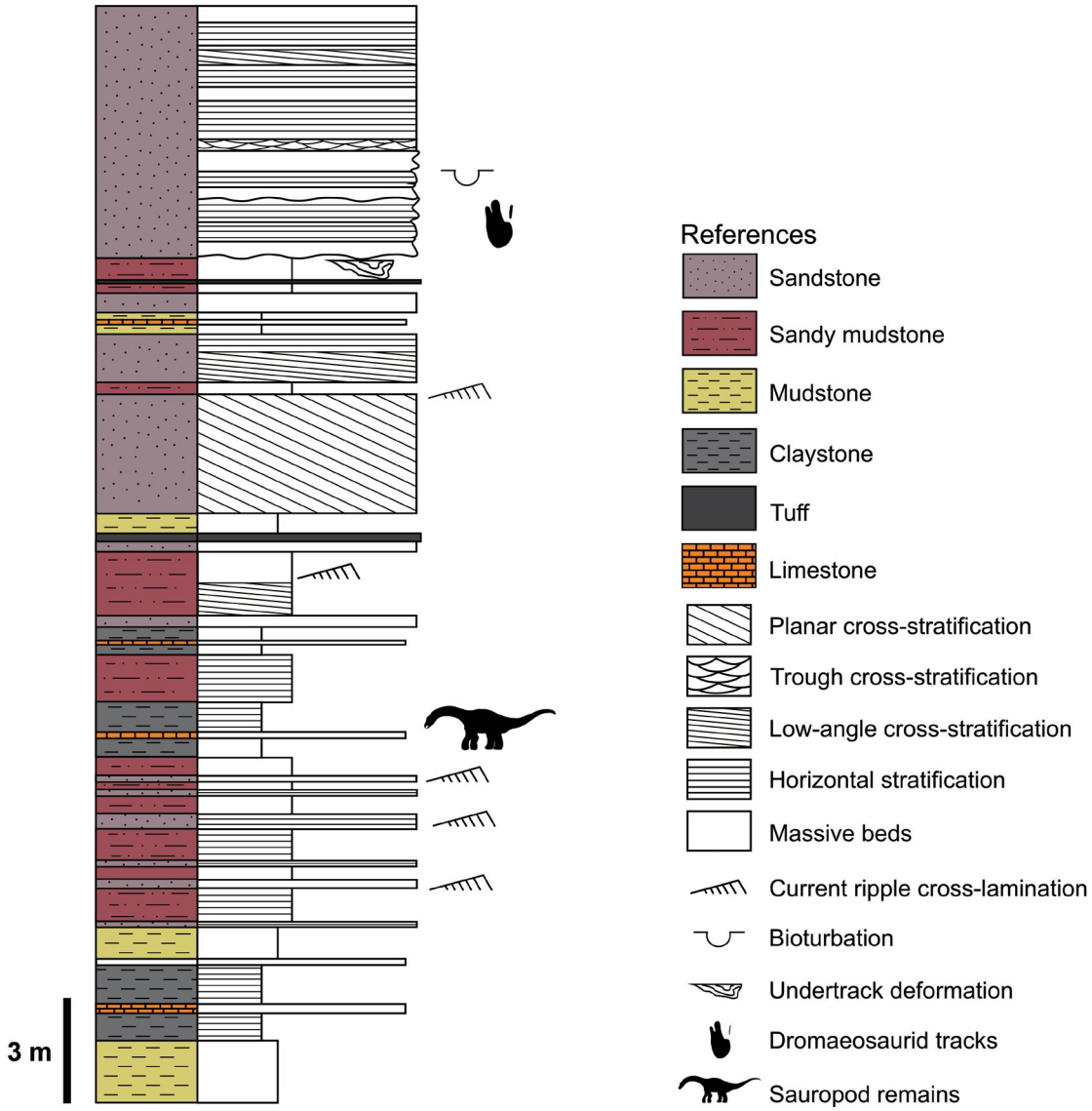

Fig. 2. Stratigraphical section of the Candeleros Formation at El Sauce locality with the position of the studied dromaeosaurid tracks. The top of the profile represents the actual erosion surface. The sauropod remains have been documented by Bellardini *et al.* (2023).

The terminology proposed for vertebrate tracks by Lallensack (2025) and Lallensack *et al.* (2025) was used in this work. Although the term 'didactyl track' for tracks that imprint only two digits (digits III and IV) without any impression of digit II (e.g. see Fig. 5B–C, I) is widely used in the literature, this descriptive term has also been used for tracks that fully imprint digits III and IV but only a very proximal part of digit II (e.g. see Fig. 5A, D–H). In the present work the term 'functionally didactyl tracks' will be used to refer both to the cases mentioned above and to the tracks studied here, in which the claw impression of digit II is preserved, whether the impression of such digit is complete or not.

Considering that the hypex is not very well-preserved in most tracks, to have a better comparison between the digits within and between each track, the length of digit impression was measured following Moratalla *et al.* (1988) as the distance between the 'heel' and the tip of each digit impression.

Results

Description of the tracks

The studied tracks consist of at least six impressions preserved as concave epireliefs in a medium-grained

sandstone (Figs 3, 4). No clear trackway has been recognized, although one couple or pair of tracks (left track 1 with right track 6) could belong to a trackway with a pace length of about 24 cm. Five tracks have a similar orientation (tracks 1–2, 4–6), and only one is oriented in the opposite direction (track 3). The tracks lack delicate

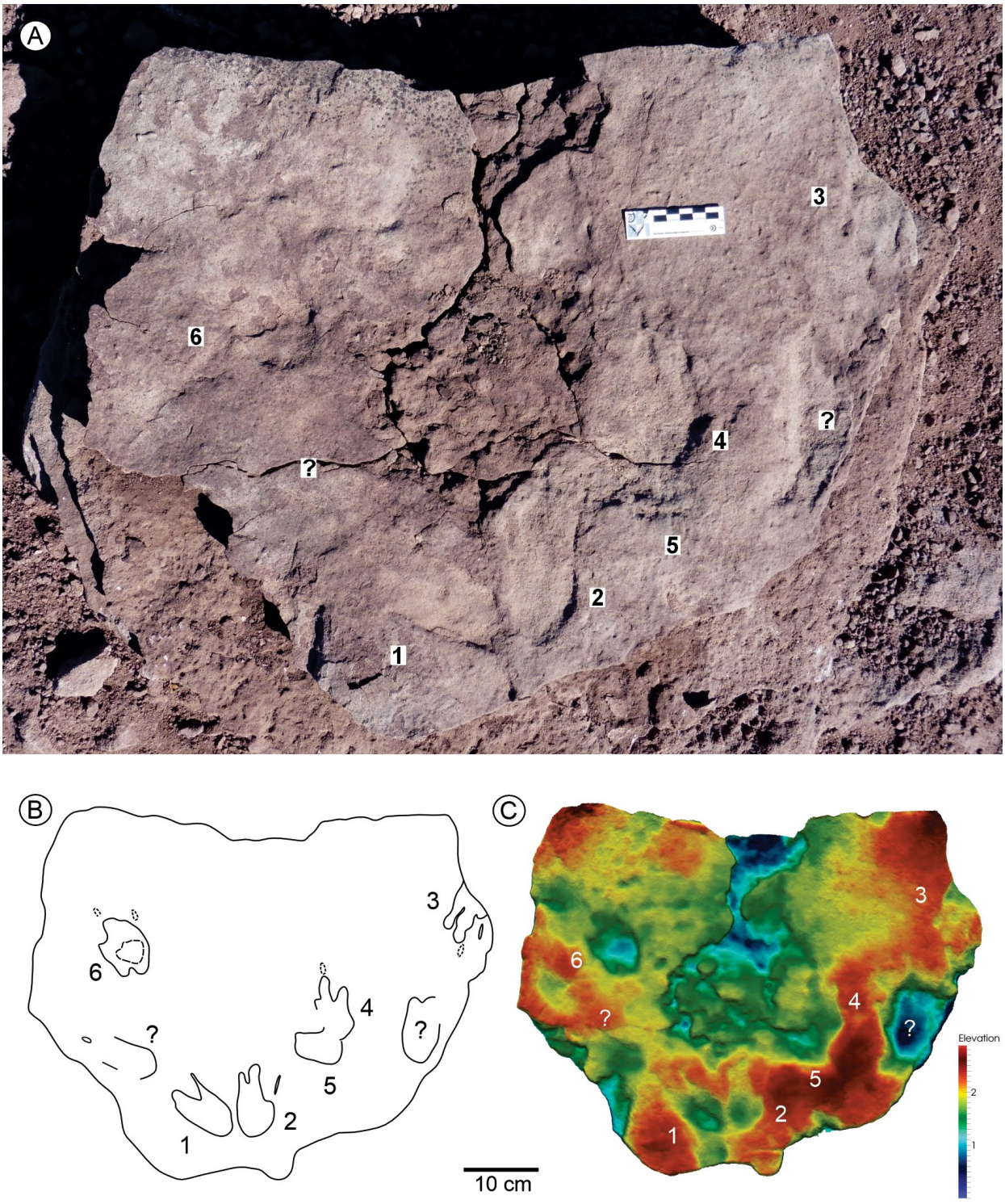

Fig. 3. A, dromaeosaurid tracks documented in the El Sauce locality. B, interpretative scheme of the tracks. C, false-colour depth image of the tracks.

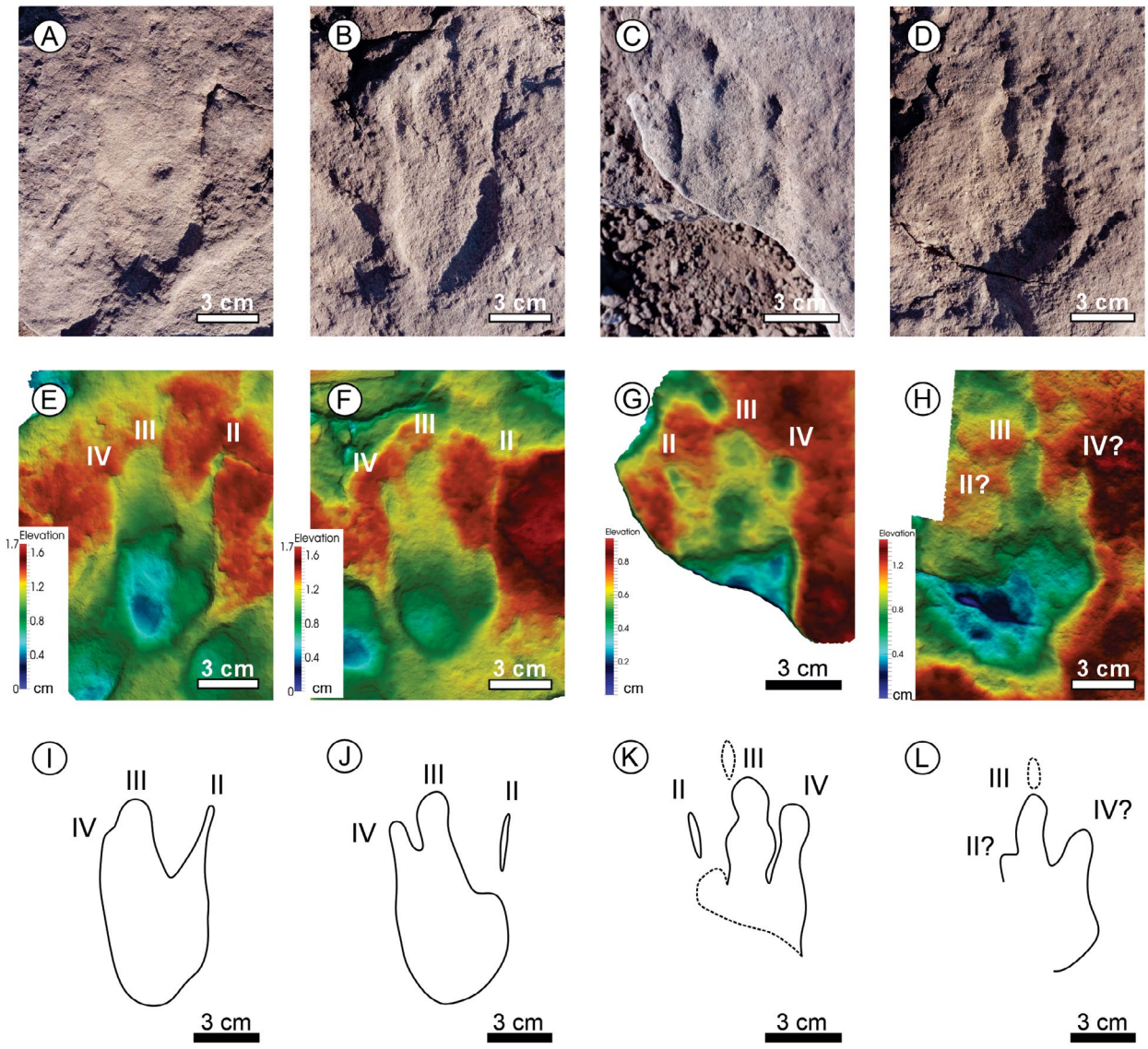

Fig. 4. Detail of the best preserved dromaeosaurid tracks documented in the El Sauce locality. A–D, photographs of tracks 1, 2, 3 and 4, respectively. E–H, false-colour depth image of tracks 1, 2, 3 and 4, respectively. I–L, interpretative scheme of the tracks 1, 2, 3 and 4, respectively.

impressions, such as pad (except for digits III and IV of track 3) and skin impressions, but they are sufficiently well-preserved to clearly identify their outline (grade 1 *sensu* Marchetti *et al*. 2019). Considering the preservation and outlines of the tracks and the claw impression of digit II, they could be poorly preserved true tracks or shallow undertracks. The tracks are strongly asymmetric, preserving always the impression of digits III and IV and sometimes a complete impression of digit II (e.g. track 1) or a partial digit II associated with a well-developed claw impression separated from the distal part of digit II (e.g. tracks 2, 3). Measurements of the tracks are presented in Table 1. The tracks are longer than they are wide, 8.3–10.0 cm long (average 9.2 cm) and 4.8–6.0 cm wide (average 5.1 cm), and the length/width ratio ranges between 1.48–2.08 (average 1.80). In all the tracks, the impression of digit III is longer than digit IV, with digit III ranging 8.8–10.1 cm in length (average 9.6 cm) and digit IV ranging 7.6–9.0 cm in length (average 8.4 cm). The length of the impression of digit II, without taking into account the impression of the claw (6.0–6.3 cm long and 6.2 cm in average), is shorter than the impression of the other two digits. Nevertheless, considering the impression of this claw trace the impression of digit II is 9.4–9.8 cm long, which in some cases is shorter than that of digit

Table 1. Measurement of the studied tracks (58-MES-IC-09)

Track	Length	Width	L/W	LII	LIII	LIV	II–III	III–IV	II–IV
1 (left)	9.8	4.9	2.00	6.2 (9.8)	9.8	8.5	17	6	22
2 (left)	10.0	4.8	2.08	6.0 (9.4)	10.1	9.0	10	7	17
3 (right)	–	–	–	–	–	–	9	4	6
4 (right?)	8.8	5.1	1.73	6.3	8.8	7.6	11	7	18
5	8.3	4.8	1.73	–	–	–	–	–	–
6	8.9	6.0	1.48	–	–	–	–	–	–
Average	**9.2**	**5.1**	**1,80**	**6.2 (9.6)**	**9.6**	**8.4**	**12**	**6**	**1**6

Length of track in cm; width of track in cm; L/W length/width ratio without units; LI, LII and LIII length of digit impressions I, II and III, respectively, in cm (for LII the value in parentheses includes the claw impression); II–III, III–IV and I–IV, divarication angle of the digit impressions I, III and IV, respectively, in degrees (°).

III (e.g. in tracks 2, 3) and in others it is longer (e.g. tracks 1). There are several recognizable claw impressions, some of them corresponding to digit II (tracks 1, 2 and 3) and other to digit III (tracks 3, 4). The claw impressions of digit II are longer and narrower than those of digit III. For example, the claw impression of digit II in track 2 is long and narrow, about 2.7 cm long and 0.3 cm wide, but unlike the tack 1 there is a gap of about 1.1 cm between this claw impression and the rest of the same digit impression (Fig. 5B, G, L). The angle of divarication between the impression of digit II and digit III is greater than the angle between the impressions of digits III and IV (average 12° and 6°, respectively).

Ichnotaxonomy

Several functionally didactyl ichnotaxa have been documented mainly in the Early Cretaceous of Asia and North America: *Velociraptorichnus sichuanensis* Zhen *et al*., 1994 from the Jiaguan Formation of China (Fig. 5A), *Dromaeosauripus hamanensis* Kim *et al*., 2008 from the Haman Formation of South Korea (Fig. 5B), *Dromaeosauripus yongjingensis* Xing *et al*., 2013 from the Yanguoxia Formation of China (Fig. 5C), *Dromaeosauripus* isp. from the South Platte Formation (Dakota Group) of USA (Lockley *et al*. 2016b) (Fig. 5D), *Velociraptorichnus zhangi* Xing *et al*., 2015 from the Xiaoba Formation of China (Fig. 5E, F), *Dromaeopodus shandongensis* Li *et al*., 2008 from the Tianjialou Formation of China (Fig. 5G) *Menglongipus sinensis* Xing *et al*., 2009 from the Tuchengzi Formation of China (Fig. 5H), *Dromaeosauripus jinjuensis* Kim *et al*., 2012 from the Jinju Formation of South Korea (Fig. 5I), and *Dromaeosauriformipes rarus* Kim *et al*., 2018 from the Jinju Formation of South Korea. On the other hand, the record of functionally didactyl tracks is poorly known in the southern hemisphere and is restricted to the lattermost Cretaceous of South America. It includes didactyl tracks recorded in Bolivia from the Campanian Toro Toro Formation referred to as *Dromaeopodus*? isp. (Apesteguía *et al*. 2011) and undetermined tracks from the Maastrichtian El Molino Formation (Meyer *et al*. 2021; Fig. 5J).

Among these ichnospecies, only *D. hamanensis*, *D. jinjuensis* and *D. rarus* preserve two digits (digits III and IV) without any impression of digit II, whereas other ichnospecies fully imprint digits III and IV only imprint a very proximal part of digit II (e.g. *V. sichuanensis*, *D. yongiingensis*, *D. shandongensis*, *M. sinensis*). Only *V. zhangi* has digits II, III and IV fully impressed. Nevertheless, the study tracks show a smaller divarication angle between the digits III and IV than those of these ichnotaxa, excluding *D. shangdongensis,* which displays similar values. Nevertheless, unlike the last ichnospecies, the tracks studied here do not preserve the impression of the phalangeal pads, except for the impression of digits III and IV of track 3, and they preserve a complete impression of digit II. Although *V. zhangi* preserves a complete digit II impression, the studied tracks from El Sauce show a higher length/width ratio range (1.8 vs. 1.1), a smaller divarication angle between digits II and IV (16° vs 52°) and a narrower impression of digit II, compared with digits III and IV, of *V. zhangi*. As a result, the El Sauce tracks are different from the rest of the functionally didactyl known ichnotaxa, representing a potential new form. However, following Marchetti *et al*. (2019), we consider the new tracks as undetermined tracks due to the poor preservation conditions, pending better-preserved finds to justify the erection of a new ichnotaxon.

Discussion

Trackmaker

The tracks from El Sauce exhibit a strongly asymmetrical morphology with a partial or complete impression of digit II, which has led to their interpretation as

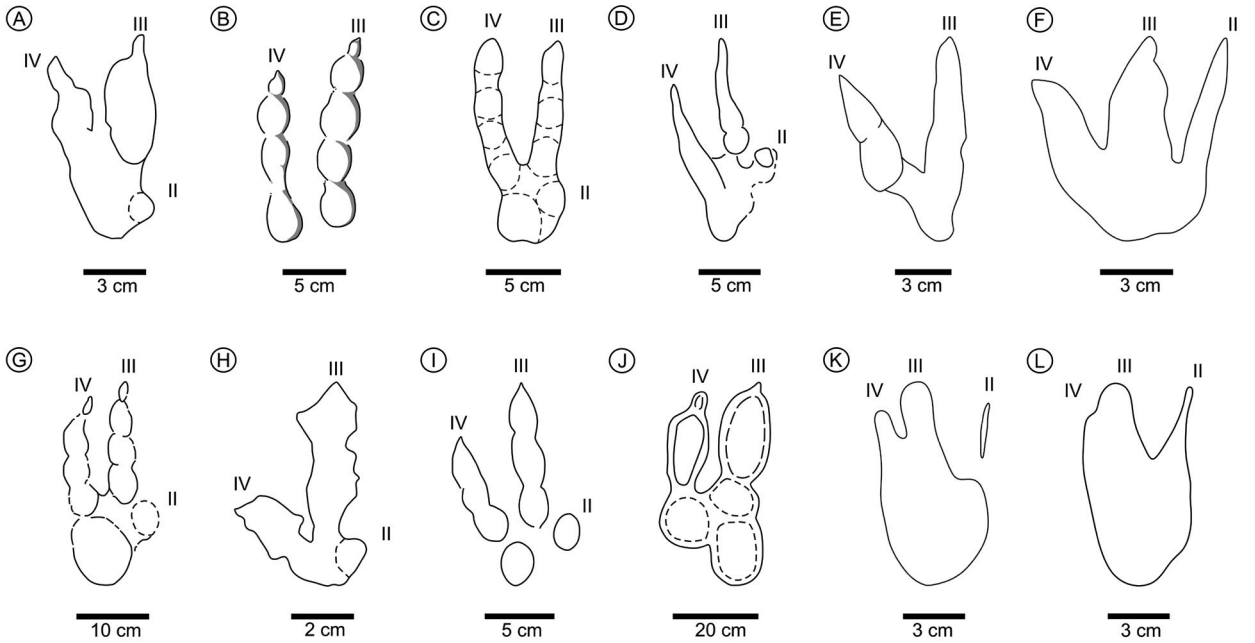

Fig. 5. Interpretative schematic drawings of dromaeosaurid ichnotaxa. A, *Velociraptorichnus sichuanensis* from the Lower Cretaceous Jiaguan Formation, China, redrawn from Zhen *et al.* (1994). B, *Dromaeosauripus hamanensis* from the Lower Cretaceous Haman Formation, South Korea, redrawn from Kim et al. (2008). C, *Dromaeosauripus yongjingensis* from the Lower Cretaceous Yanguoxia Formation, China, redrawn from Xing et al. (2013); D) *Dromaeosauripus* isp. from the Albian South Platte Formation (Dakota Group), USA, redrawn from Lockley et al. (2016a). E, F, *Velociraptorichnus zhangi* from the Lower Cretaceous Xiaoba Formation, China, redrawn from Xing et al. (2015), without impression of digit II and with complete impression of digit II, respectively. G, *Dromaeopodus shandongensis* from the Barremian–Aptian Tianjialou Formation, China, redrawn from Li *et al.* (2008). H, *Menglongipus sinensis* from the Jurassic–Cretaceous transition Tuchengzi Formation, China, redrawn from Xing et al. (2009). I, *Dromaeosauripus jinjuensis* from the Aptian Jinju Formation, South Korea, redrawn from Kim *et al.* (2018). J, undetermined didactyl tracks from the Maastrichtian El Molino Formation, Bolivia, redrawn from Meyer *et al.* (2021). K, L, El Sauce tracks from the Cenomanian Candeleros Formation, Argentina (this study), with the partial impression of digit II and the full impression of digit II, respectively.

functionally didactyl tracks. There are cases of tracks that appear to be functionally didactyl due to preservation issues, but are actually functionally tridactyl (see Lockley *et al.* 2016a). Nevertheless, the recurrent pattern in the morphology of the studied tracks reflects with some confidence the functionally didactyl morphology of the producer, in particular, due to the long and narrow claw trace only present in digit II (e.g. tracks 1, 2, and 3).

The only group of Cretaceous bipedal dinosaurs capable of making this type of tracks are the deinonychosaurian theropods, which are characterized by a hyperextensible digit II with a hypertrophied sickle-shaped claw and a functionally didactyl track. Deinonychosauria includes two families: Dromaeosauridae and Troodontidae; however, only dromaeosaurids have been documented in Gondwana, and among dromaeosaurids, only the unenlagiine are known in South America (Gianechini & Apesteguía 2011; Turner *et al.* 2012; Gianechini *et al.* 2024). The unenlagiine fossil record of Argentina is restricted to the Upper Cretaceous of the Neuquén Basin and includes: *Buitreraptor gonzalezorum* Makovicky *et al.*, 2005 from the Cenomanian Candeleros Formation; *Unenlagia comahuensis* Novas & Puerta, 1997; *Unenlagia paynemili* Calvo *et al.*, 2004; *Neuquenraptor argentinus* Novas & Pol, 2005 and *Pamparaptor micros* Porfiri *et al.*, 2011 from the late Turonian–early Coniacian Portezuelo Formation; *Diuqin lechiguanae* Porfiri *et al.*, 2024 from the Santonian Bajo de la Carpa Formation; and *Austroraptor cabazai* Novas *et al.*, 2009 from the Campanian–Maastrichtian Allen Formation.

The only dromaeosaurid known from the Cenomanian Candeleros Formation is the small-sized unenlagiine *B. gonzalezorum*, from La Buitrera locality, a fossiliferous site located less than 100 km away from El Sauce. The size range (foot length) of most known deinonychosaurian trackmakers *sensu* Lockley *et al.* (2016a) is between ~10 and 28 cm, except for the diminutive didactyl tracks (~1.0 cm long) of *D. rarus* (Kim *et al.* 2016). Accordingly, the study tracks 8.3–10.1 cm long (average 9.4 cm) would be among the smallest documented for this group. The track length

of the foot of a bipedal dinosaur comprises the total sum of lengths of phalanges in digit III (ΣP) together with the claw sheath, joint capsules, base of the metatarsus, and possibly a fleshy heel (Thulborn & Wade 1984). ΣP of a specimen of *B. gonzalezorum* was measured from fig. 6 of Gianechini *et al.* (2024), resulting in about 8 cm in length. Considering the measurement of ΣP for *B. gonzalezorum* and that this represents about 80% of the total length of the theropod foot (Thulborn & Wade 1984, fig. 18), it is possible to estimate a footprint size of about 10 cm long.

Taking into account the temporal and geographical correlation of the studied tracks and fossil record from the Candeleros Formation, together with the anatomical features and the size of the functional didactyl tracks, we suggest a small-sized unenlagiine dromaeosaurid, such as *B. gonzalezorum* as a producer of the new tracks from El Sauce (Fig. 6).

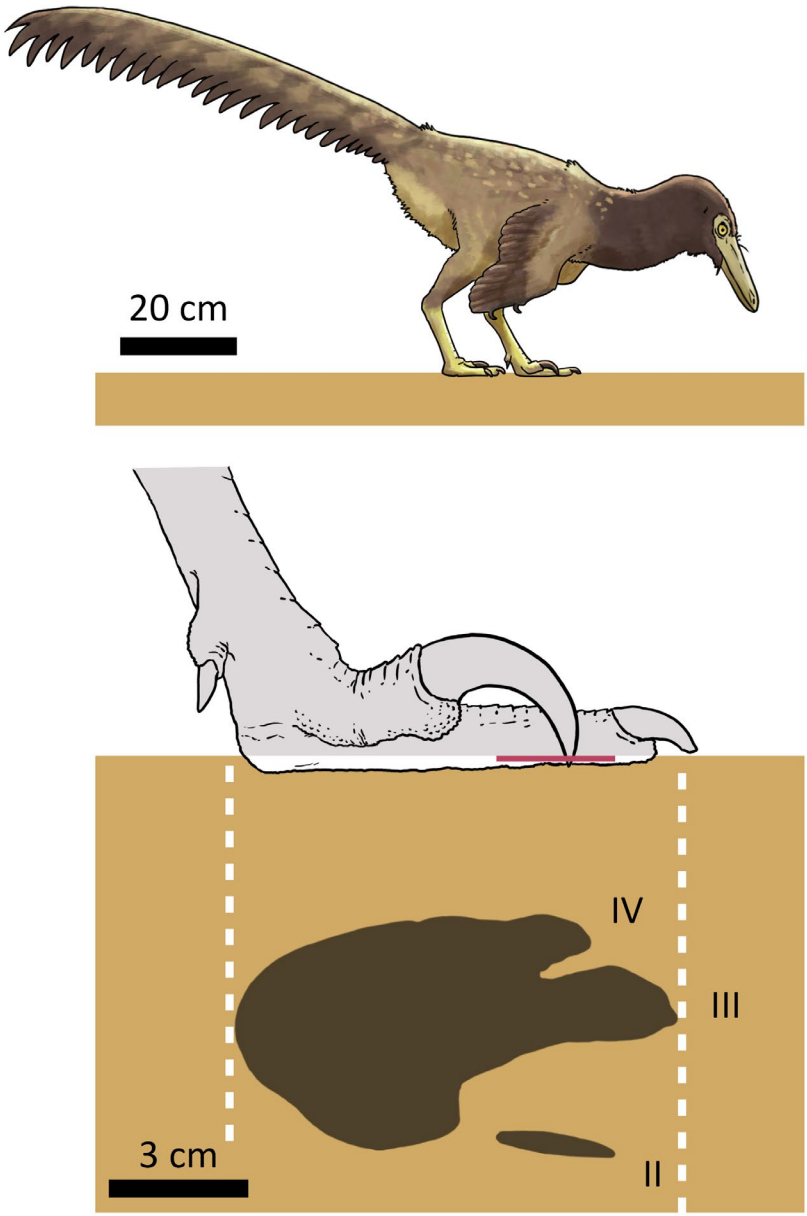

Fig. 6. Interpretative illustration of the possible dromaeosaurid trackmaker of El Sauce tracks: above, a small size unenlagiine in a slow walking posture, and below, detail of the unenlagiine producer imprinting their left foot on the substrate and producing a strongly symmetrical track with the sickle-shaped claw trace of digit II. Illustrator: Alessio Ciaffi.

Palaeoecological inferences

Dromaeosaurids were bipedal theropods with functionally didactyl tracks, which suggest that they usually kept the digit II off the ground in a hyperextended position, with only the third and fourth digits supporting the weight of the animal (Lockley *et al*. 2016a). Digit II had an unusually large and curved falciform (sickle-shaped) claw, held off the ground or retracted during the locomotion, which is thought to have been used for capturing prey (Bishop 2019).

All documented functionally didactyl trackways referred to dromaeosaurids typically maintain the same stride length and therefore a constant speed: e.g. trackway of *D. hamanensis* consisting of four tracks shows a stride range of 204–205 cm, mean 204 cm (Kim *et al*. 2008); trackway of *D. jinjuensis* consisting of 12 tracks shows a stride range of 71–105 cm, mean 80.4 cm (Kim *et al*. 2012); trackway of *D. rarus* consisting of 7 tracks shows a stride range of 8.41–13.1 cm, mean 10 cm (Kim *et al*. 2018); trackway HMT-T22 consisting of 18 tracks shows a stride range of 73.0–90 cm, mean 82.4 cm (Xing *et al*. 2018). Taking into account that no trackway has been documented in this study, as in the case of the tracks of *D. zhangi* which also shows the impression of digit II, it is most parsimonious to assume that a sickle-shaped claw impression of digit II would have been produced in a slow-moving stance or a non-moving posture. The tracks are very shallow for the digit II to have been imprinted in a retractable position. Furthermore, none of the El Sauce tracks are deep enough to have imprinted the digit I or metatarsal impressions (Gatesy *et al*. 1999; Heredia *et al*. 2021). Considering that the depth of the tracks is uniform, it is inferred that the impression of the claw of digit II is not due to a deep step of the producer but rather to the fact that this digit was not retracted (Fig. 6).

The early Late Cretaceous of northern Patagonia is characterized by a diversified tetrapod fauna, especially of dinosaurs and pterosaurs, evidenced by both osteological and ichnological records (Novas 2009; Calvo & Rivera 2018; Krapovickas *et al*. 2018; Apesteguía *et al*. 2023; Heredia *et al*. 2019, 2020, 2021, 2023, 2024a). In particular, the Cenomanian of the Candeleros Formation records a great diversity of theropod dinosaurs, including carcharodontosaurids, abelisaurids, basal coelurosaurs, alvarezsaurids, and dromaeosaurids (Heredia *et al*. 2020 and references therein). Among these theropods, both alvarezsaurids and unenlagiine dromaeosaurids include species with body-lengths ranging approximately between 0.5 m and 1.5 m, which are the smallest in body size (Makovicky *et al*. 2005; Makovicky *et al*. 2012). Despite their small size, unenlagiines such as *Buitreraptor* are considered primarily terrestrial predators (Gianechini *et al*. 2020). The Candeleros Formation also records a great diversity of theropod tracks, among which carcharodontosaurids, abelisaurids and basal coelurosaurs have been proposed as their trackmakers, except for dromaeosaurids and alvarezsaurids (Calvo & Rivera 2018; Krapovickas *et al*. 2018; Heredia *et al*. 2020, 2021, 2024b). Thus, the new tracks here described, not only improve the theropod track diversity of the Candeleros Formation, but also provide a new correlation between the ichnological and osteological evidence of theropod dinosaurs from this geological unit.

Conclusions

Several strongly asymmetrical and functionally didactyl tracks from the Cenomanian Candeleros Formation, El Sauce locality of northwestern Patagonia, Argentina, are documented. This record consists of at least six tracks preserved as concave epireliefs in medium-grained sandstone from alluvial plain deposits. This type of footprint is associated with dromaeosaurid dinosaurs; however, few sickle claw impressions have been recorded so far. These tracks indicate that the trackmaker had a developed ungual phalanx on digit II and could rest it on the substrate, possibly while was stationary. Considering that the osteological dromaeosaurid record from the Upper Cretaceous of Argentina only includes the unenlagiines, it is likely that the producer of the tracks presented here was a small-sized unenlagiine, such as *Buitreraptor gonzalezorum*. The new find improves the theropod track diversity of the Candeleros Formation and the Upper Cretaceous of the Neuquén Basin. Moreover, the new find from El Sauce improve not only our knowledge on the dromaeosaurids of northwestern Patagonia, but also increase the scarce dromaeosaurid track record of South America and particularly of the Cenomanian worldwide.

Acknowledgements.– We thank the reviewers Nathan Enriquez (University of New England, Australia) and James Farlow (Purdue University Fort Wayne, USA) and the Associate Editor Gabriela Mángano (University of Saskatchewan, Canada) for their constructive comments and suggestions that improved the manuscript. We also thank the International Ichnological Association Travel Grants for their support to Arturo M. Heredia to present the advances of this research at the 5th International Congress on Ichnology (ICHNIA), held in Florianopolis, Brazil, in April 2024. Moreover, we would like to thank the Comisión de Fomento de El Sauce and El Sauce 'Carlos Hermosilla' Museum of the Neuquén Province, and Javier E. Guevara and Mattia Y. Messina for their help in the fieldwork. This research was financially supported by the Paleontological Society Arthur James Boucot Research Grant 2022 to Arturo M. Heredia, Agencia Nacional de Promoción

Científica y Tecnológica (ANPCyT) -Proyectos de Investigación Científica y Tecnológica (PICT) 2019-00994 to Ignacio J. Maniel, the Ramón y Cajal fellowship (RYC-2022) and the Ministry of Science and Innovation of Spain to Ignacio Díaz-Martínez.

References

Apesteguía, S., de Valais, S., Cordero, G.R. & Ramírez, O.M. 2011. New ichnological record from the late Campanian Toro Toro Formation at Toro Toro, Potosí (Bolivia): first probable dromaeosaurid tracks from South America. *Ameghiniana 48*, 662–667.

Apesteguía, S., Díaz-Martínez, I., Mayoral, J.P., Riguetti, F., Veiga, G.D., de Valais, S. & Dumont, L.F. 2023. Dinosaur tracks with skin impressions in the La Buitrera Paleontological Area (Candeleros Formation, Cenomanian), Río Negro Province, Argentina. *Cretaceous Research*, 105584. https://doi.org/10.1016/j.cretres.2023.105584

Bellardini, F., Windholz, G.J., Baiano, M.A., Garrido, C.A., Maniel, I, Heredia, A.M., Ciaffi, A., Guevara Lucero, J.E. & Messina, M.Y. 2023. How diversified was the sauropod fauna at the base of the Neuquén Group? new evidence from Candeleros Formation (Cenomanian) of southern Neuquén Basin (Patagonia, Argentina). *IV Jornadas de Paleontología de la Cuenca Neuquina, Libro de Resúmenes*. Malargüe, Mendoza, 7–8.

Bishop, P.J. 2019. Testing the function of dromaeosaurid (Dinosauria, Theropoda) 'sickle claws' through musculoskeletal modelling and optimization. *PeerJ 7*, e7577. https://doi.org/10.7717/peerj.7577

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

Calvo, J.O. & Rivera, C. 2018. Huellas de dinosaurios en la costa oeste del embalse Ezequiel Ramos Mexía y alrededores (Cretácico Superior, Provincia de Neuquén, República Argentina). *Boletín de la Sociedad Geológica Mexicana 70*, 449–497. https://doi.org/10.18268/bsgm2018v70n2a11

Enriquez, N.J., Campione, N.E., Sullivan, C., Vavrek, M., Sissons, R.L., White, M.A. & Bell, P.R. 2021. Probable deinonychosaur tracks from the Upper Cretaceous Wapiti Formation (upper Campanian) of Alberta, Canada. *Geological Magazine 158*, 1115–1128. https://doi.org/10.1017/S0016756820001247

Falkingham, P.L., Bates, K.T., Avanzini, M., Bennett, M., Bordy, E.M., Breithaupt, B.H., Castanera, D., Citton, P., Díaz-Martínez, I., Farlow, J.O., Fiorillo, A.R., Gatesy, S.M., Getty, P., Hatala, K.G., Hornung, J.J., Hyatt, J.A., Klein, H., Lallensack, J.N., Martin, A.J., Marty, D., Matthews, N.A., Meyer, C.A., Milàn, J., Minter, N.J., Razzolini, N.L., Romilio, A., Salisbury, S.W., Sciscio, L., Tanaka, I., Wiseman, A.L.A., Xing, L.D. & Belvedere, M. 2018. A standard protocol for documenting modern and fossil ichnological data. *Palaeontology 61*, 469–480. https://doi.org/10.1111/pala.12373.

Garrido, A.C. 2010. Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (Argentina): nueva propuesta de ordenamiento litoestratigráfico. *Revista del Museo Argentino de Ciencias Naturales 12*, 121–177.

Gatesy, S.M., Middleton, K.M., Jenkins F.A. Jr & Shubin, N.H. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature 399*, 141–144. https://doi.org/10.1038/20167

Gianechini, F.A. & Apesteguia, S. 2011. Unenlagiinae revisited: dromaeosaurid theropods from South America. *Anais da Academia Brasileira de Ciências 83*, 163–195.

Gianechini, F.A., Ercoli, M.D. & Díaz-Martínez, I. 2020. Differential locomotor and predatory strategies of Gondwanan and derived Laurasian dromaeosaurids (Dinosauria, Theropoda, Paraves): inferences from morphometric and comparative anatomical studies. *Journal of Anatomy 236*, 772–797. https://doi.org/10.1111/joa.13153

Gianechini, F.A., Colli, L. & Makovicky, P.J. 2024. Pelvic and hindlimb muscular reconstruction of the paravian theropod *Buitreraptor gonzalezorum* and its palaeobiological implications. *Historical Biology*, 1–27. https://doi.org/10.1080/08912963.2023.2301674

Heredia, A.M., Díaz-Martínez, I., Pazos, P.J., Comerio, M. & Fernández, D.E. 2020. Gregarious behaviour among non-avian theropods inferred from trackways: a case study from the Cretaceous (Cenomanian) Candeleros Formation of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology 538*, 109480. https://doi.org/10.1016/j.palaeo.2019.109480

Heredia, A.M., Pazos, P.J. & Díaz-Martínez, I. 2021. Morphological variations in dinosaur tridactyl tracks from the Candeleros Formation (Upper Cretaceous) of northwestern Patagonia, Argentina. *Journal of South American Earth Sciences 108*, 103212. https://doi.org/10.1016/j.jsames.2021.103212

Heredia, A.M., Bellardini, F., Garrido, A., Maniel, I.J., Windholz, G.J., Guevara Lucero, J.E. Messina, M.Y., Ciaffi, A. & Baiano, M.A. 2023. A preliminary report on a new dinosaur trackssite from the Candeleros Formation (Cenomanian, Upper Cretaceous) of southern Neuquén Basin, Patagonia, Argentina. *IV Jornadas de Paleontología de la Cuenca Neuquina, Libro de Resúmenes*. Malargüe, Mendoza, 13–14.

Heredia, A.M., Díaz-Martínez, I., Pazos, P.J. & de Valais, S. 2024a. Pterosaur tracks from the Upper Cretaceous (Cenomanian) Candeleros Formation of northwestern Patagonia, Argentina: ichnotaxonomic and paleoecological perspectives from Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology 650*, 112338. https://doi.org/10.1016/j.palaeo.2024.112338

Heredia, A.M., Bellardini, F., Baiano, M.A, Maniel, I.J., Garrido, A.C., Windholz, G.J., Guevara, J.E., Ciaffi, A., Messina, M.Y. & Díaz-Martínez, I. 2024b. First report of deinonychosaurian tracks from the Upper Cretaceous Candeleros Formation of northwestern Patagonia, Argentina. *Abstracts, 5th International Congress on Ichnology (ICHNIA)*, Florianopolis, Brazil, 138–139.

Howell, J.A., Schwarz, E., Spalletti, L.A. & Veiga, G.D. 2005. The Neuquén basin: an overview. *Geological Society, London, Special Publications 252*, 1–14. https://doi.org/10.1144/GSL.SP.2005.252.01.01

Joeckel, R.M., Suarez, C.A., McLean, N.M., Möller, A., Ludvigson, G.A., Suarez, M.B., Kirkland, J.I., Andrew, J., Kiessling, S. & Hatzell, G.A. 2023. Berriasian–Valanginian geochronology and carbon-isotope stratigraphy of the Yellow Cat member, Cedar Mountain Formation, eastern Utah, USA. *Geosciences 13*, 32. https://doi.org/10.3390/geosciences13020032

Kim, J.Y., Kim, K.S., Lockley, M.G., Yang, S.Y., Seo, S.J., Choi, H.I. & 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. https://doi.org/10.1016/j.palaeo.2008.02.003

Kim, J.Y., Lockley, M.G., Woo, J.O. & Kim, S.H. 2012. Unusual didactyl traces from the Jinju Formation (Early Cretaceous, South Korea) indicate a new ichnospecies of *Dromaeosauripus*. *Ichnos 19*, 75–83. https://doi.org/10.1080/10420940.2012.664054

Kim, K.S., Lim, J.D., Lockley, M.G., Xing, L., Kim, D.H., Piñuela, L., Romilio, A., Yoo, J.S., Kim, J.H. & Ahn, J. 2018. Smallest known raptor tracks suggest microraptorine activity in lakeshore setting. *Scientific Reports 8*, 16908. https://doi.org/10.1038/s41598-018-35289-4

Kirkland, J.I., Burge, D. & Gaston, R. 1993. A large dromaeosaur (Theropoda) from the Lower Cretaceous of eastern Utah. *Hunteria 2*, 1–16.

Krapovickas, V., Garrido, A.C. & Canale, J.I. 2020. Dinosaur tracks at Cañadón de las Campanas and Villa El Chocón area (Late Cretaceous, Candeleros Formation), Patagonia, Argentina. *Revista De La Asociación Geológica Argentina 77*, 447–462.

Lallensack, J.N. 2025. Methods and terminology in vertebrate track ichnology. In: Lucas, S.G., Hunt, A.P. & Klein, H. (Eds) *Vertebrate Ichnology: Tetrapod Tracks and Trackways*, 3-28, Elsevier, Amsterdam. https://doi.org/10.1016/B978-0-443-13837-9.00009-3

Lallensack, J.N., Leonardi, G. & Falkingham, P.L. 2025. Glossary of fossil tetrapod tracks. *Palaeontologica Electronica 27*, 1–105. https://doi.org/10.26879/1389

Leanza, H.A., & Hugo, C.A. 2024. Las formaciones La Amarga y Lohan Cura (Cretácico Temprano) en el depocentro de Picun Leufú. In: Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C. & Vallés, J.M. (Eds) *Geología y Recursos Naturales de la Provincia del Neuquén*. Relatorio del XVIII Congreso Geológico Argentino, 223–230.

Li, R., Lockley, M.G., Makovicky, P.J., Matsukawa, M., Norell, M.A., Harris, J.D. & Liu, M. 2008. Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China. *Naturwissenschaften 95*, 185–191. https://doi.org/10.1007/s00114-007-0310-7

Lockley, M.G., Harris, J.D., Li, R., Xing, L. & van der Lubbe, T. 2016a. Two-toed tracks through time: on the trail of 'raptors' and their allies. In: Falkingham, P., Marty, D. & Richter, A. (Eds) *Dinosaur Tracks: Next Steps*, 182–200. Indiana University Press, Bloomington.

Lockley, M.G., Xing, L., Matthews, N.A. & Breithaupt, B.H. 2016b. Didactyl raptor tracks from the Cretaceous, Plainview Sandstone at Dinosaur Ridge. *Cretaceous Research 61*, 161–168. https://doi.org/10.1016/j.cretres.2016.01.007

Makovicky, P.J., Apesteguía, S. & Agnolín, F.L. 2005. The earliest dromaeosaurid theropod from South America. *Nature 437*, 1007–1011. https://doi.org/10.1038/nature03996

Makovicky, P.J., Apesteguía, S. & Gianechini, F.A. 2012. A new coelurosaurian theropod from the La Buitrera fossil locality of Río Negro, Argentina. *Fieldiana Life and Earth Sciences 5,* 90–98. https://doi.org/10.3158/2158-5520-5.1.90

Mallison, H. & Wings, O. 2014. Photogrammetry in paleontology—a practical guide. *Journal of Paleontological Techniques 12*, 1–31.

Manning, P.L., Margetts, L., Johnson, M.R., Withers, P.J., Sellers, W.I., Falkingham, P.L., Mummery, P.M., Barrett, P.M. & Raymont, D.R. 2009. Biomechanics of dromaeosaurid dinosaur claws: application of X-ray microtomography, nanoindentation, and finite element analysis. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology 292*, 1397–1405. https://doi.org/10.1002/ar.20986

Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, S., Melchor, R.N. & Farlow, J.O. 2019. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. *Earth-Science Reviews 193*, 109–145. https://doi.org/10.1016/j.earscirev.2019.04.008

Meyer, C.A., Marty, D., Thüring, B., Thüring, S. & Belvedere, M. 2021. The Late Cretaceous dinosaur track record of Bolivia–Review and perspective. *Journal of South American Earth Sciences 106*, 102992. https://doi.org/10.1016/j.jsames.2020.102992

Moratalla, J.J., Sanz, J.L. & Jimenez, S. 1988. Multivariate analysis on Lower Cretaceous dinosaur footprints: discrimination between ornithopods and theropods. *Geobios 21*, 395–408. https://doi.org/10.1016/S0016-6995(88)80042-1

Motta, M.J., Agnolín, F.L., Brissón Egli, F. & Novas, F.E. 2020. New theropod dinosaur from the Upper Cretaceous of Patagonia sheds light on the paravian radiation in Gondwana. *The Science of Nature 107*, 1–8. https://doi.org/10.1007/s00114-020-01682-1

Mudroch, A., Richter, U., Joger, U., Kosma, R., Idé, O. & Maga, A. 2011. Didactyl tracks of paravian theropods (Maniraptora) from the ?Middle Jurassic of Africa. *PLoS One 6*, e14642. https://doi.org/10.1371/journal.pone.0014642

Norell, M.A. & Makovicky, P.J. 2004. Dromaeosauridae. In: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds). *The Dinosauria: Second Edition*. University of California Press, Berkeley, 196–209.

Novas, F.E. 2009 *The Age of Dinosaurs in South America*. Indiana University Press, Bloomington.

Novas, F.E. & Pol, D. 2005. New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. *Nature 433*, 858–861. https://doi.org/10.1038/nature03285

Novas, F.E., Pol, D., Canale, J.I., Porfiri, J.D. & Calvo, J.O. 2009. A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. *Proceedings of the Royal Society B: Biological Sciences 276*, 1101–1107. https://doi.org/10.1098/rspb.2008.1554

Novas, F. & Puerta, P. 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature 387*, 390–392. https://doi.org/10.1038/387390a0

Ostrom, J. H. 1990. Dromaeosauridae. In: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds) *The Dinosauria*. University of California Press, Berkeley, 269–279.

Porfiri, J.D., Calvo, J.O. & Santos, D.D. 2011. A new small deinonychosaur (Dinosauria: Theropoda) from the Late Cretaceous of Patagonia, Argentina. *Anais da Academia Brasileira de Ciências 83*, 109–116.

Porfiri, J. D., Baiano, M.A., Dos Santos, D.D., Gianechini, F.A., Pittman, M. & Lamanna, M.C. 2024. *Diuqin lechiguanae* gen. et sp. nov., a new unenlagiine (Theropoda: Paraves) from the Bajo de la Carpa Formation (Neuquén Group, Upper Cretaceous) of Neuquén Province, Patagonia, Argentina. *BMC Ecology and Evolution 24*, 77. https://doi.org/10.1186/s12862-024-02247-w

Qin, Y. & Xing, L. 2021. First report of deinonychosaurian trackway from the Cretaceous of Guizhou, China. *Biosis: Biological Systems 2*, 238–241. https://doi.org/10.37819/biosis.002.02.0099

Roach, B.T. & Brinkman, D.L. 2007. A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. *Bulletin of the Peabody Museum of Natural History 48*, 103–138. https://doi.org/10.3374/0079-032X(2007)48[103:AROCPH]2.0.CO;2

Thulborn, R.A. 1990. *Dinosaur Tracks*. Chapman and Hall, London.

Thulborn, R.A. & Wade, M. 1984. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum 21*, 413–517.

Turner, A.H., Pol., D., Clarke, J.A., Erickson, G.M. & Norell, M.A. 2007. A basal dromaeosaurid and size evolution preceding avian flight. *Science 317*, 1378–1381. https://doi.org/10.1126/science.1144066

Turner, A.H., Makovicky, P.J. & Norell, M.A. 2012. A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History 371*, 1–206. https://doi.org/10.1206/748.1

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

Xing, L.D., Lockley, M.G., Yang, G., Xu, X., Cao, J., Klein, H., Persons Iv, W.S., Shen, H.J. & Zheng, X.M. 2015. Unusual deinonychosaurian track morphology (*Velociraptorichnus zhangi* n. ichnosp.) from the Lower Cretaceous Xiaoba Formation, Sichuan Province, China. *Palaeoworld 24*, 283–292. https://doi.org/10.1016/j.palwor.2015.04.004

Xing, L., Lockley, M.G., Guo, Y., Klein, H., Zhang, J., Zhang, L., Person IV, W.S., Romilio, A., Tang, Y. & Wang, X. 2018. Multiple parallel deinonychosaurian trackways from a diverse dinosaur track assemblage of the Lower Cretaceous Dasheng Group of Shandong Province, China. *Cretaceous Research 90*, 40–55. https://doi.org/10.1016/j.cretres.2018.04.005

Xing, L., Lockley, M.G., Klein, H., Peng, G., Ye, Y., Jiang, S., Zhang, J., Persons IV, W.S. and Xu, T. 2016. A theropod track assemblage including large deinonychosaur tracks from the Lower Cretaceous of Asia. *Cretaceous Research 65*, 213–222. https://doi.org/10.1016/j.cretres.2016.05.003

Zhen, S.N., Li, J.J., Chen, W. & Zhu, S. 1994. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan. *Memoirs of the Beijing Natural History 54*, 105–120.