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A reappraisal of the Middle Triassic chirotheriid *Chirotherium ibericus* Navás, 1906 (Iberian Range NE Spain), with comments on the Triassic tetrapod track biochronology of the Iberian Peninsula

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Triassic vertebrate tracks are known from the beginning of the 19th century and have a worldwide distribution. Several Triassic track ichnoassemblages and ichnotaxa have a restricted stratigraphic range and are useful in biochronology and biostratigraphy. The record of Triassic tracks in the Iberian Peninsula has gone almost unnoticed although more than 25 localities have been described since 1897. In one of these localities, the naturalist Longinos Navás described the ichnotaxon *Chirotherium ibericus* in 1906. The vertebrate tracks are in two sandy slabs from the Anisian (Middle Triassic) of the Moncayo massif (Zaragoza, Spain). In a recent revision, new, previously undescribed vertebrate tracks have been identified. The tracks considered to be *C. ibericus* as well as other tracks with the same morphology from both slabs have been classified as *Chirotherium barthii*. The rest of the tracks have been assigned to Chirotheriidae indet., *Rhynchosauroides* isp. and undetermined material. This new identification of *C. barthii* at the Navás site adds new data to the Iberian record of this ichnotaxon, which is characterized by the small size of the tracks when compared with the main occurrences of this ichnotaxon elsewhere. As at the Navás tracksite, the Anisian *C. barthii*-*Rhynchosauroides* ichnoassemblage has been found in other coeval localities in Iberia and worldwide. This ichnoassemblage belongs to the upper Olenekian-lower Anisian interval according to previous biochronological proposals. Analysis of the Triassic Iberian record of tetrapod tracks is uneven in terms of abundance over time. From the earliest Triassic to the latest Lower Triassic the record is very scarce, with *Rhynchosauroides* being the only known ichnotaxon. *Rhynchosauroides* covers a wide temporal range and gives poor information for biochronology. The record from the uppermost Lower Triassic to the Middle Triassic is abundant. The highest ichnodiversity has been reported for the Anisian with an assemblage composed of *Dicynodontipus*, *Procolophonichnium*, *Rhynchosauroides*, *Rotodactylus*, *Chirotherium*, *Isochirotherium*, *Coelurosauroichnus* and *Paratrisauropus*. The Iberian track record from the Anisian is coherent with the global biochronology proposed for Triassic tetrapod tracks. Nevertheless, the scarcity of track occurrences during the late Olenekian and Ladinian

prevents analysis of the corresponding biochrons. Finally, although the Iberian record for the Upper Triassic is not abundant, the presence of *Eubrontes*, *Anchisauripus* and probably *Brachychirotherium* is coherent with the global track biochronology as well. Thus, the Triassic track record in the Iberian Peninsula matches the expected record for this age on the basis of a global biochronological approach, supporting the idea that vertebrate Triassic tracks are a useful tool in biochronology.

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INTRODUCTION

Triassic tetrapod tracks have a Pangea-wide distribution (see Lucas, 2007; Klein & Lucas, 2010a; and references herein). The Triassic track record is archosaur, lepidosauromorph/archosauromorph-(*Rhynchosauroides*) and synapsid-dominated (Haubold, 1971, 1984; Klein & Haubold, 2007), and includes the oldest known dinosaur tracks (Klein & Lucas, 2010a). Several recent papers have asserted the usefulness of Triassic ichnotaxa for establishing correlations between different stratigraphic units on a global scale, with emphasis on the German and North American records (Lucas, 2007; Klein & Haubold, 2007; Klein & Lucas, 2010a). Nevertheless, Klein & Lucas (2010a) have suggested that the “single largest problem with Triassic footprint biostratigraphy and biochronology is the nonuniform ichnotaxonomy and evaluation of footprints that show extreme variation in shape due to extramorphological (substrate-related) phenomena”. For instance, the ichnogenus *Chirotherium* Kaup, 1935a, is one of the described ichnotaxa with most ichnospecies, but in several recent papers some of the ichnospecies described have been considered to be extramorphological variations or synonyms of well-established taxa (Klein & Haubold, 2007; Klein & Lucas, 2010a; Xing et al., 2013).

In the Iberian Peninsula the Triassic track record has gone almost unnoticed because of its scarcity and the fact that many of the tracks were described more than a century ago (e.g. Calderon, 1897; Navás, 1904, 1906; Gómez de Llarena, 1917). In the last few years new discoveries and reviews of previous material have notably increased what is known of the Iberian Triassic tetrapod track record (Gand et al., 2010; Díaz-Martínez & Pérez-García, 2011, 2012; Fortuny et al., 2011). The latter authors made an exhaustive review of the Triassic bone and track record in the Iberian Peninsula, putting special emphasis on the paleobiogeography. Taking into account these recent papers, 26 localities with Triassic vertebrate tracks have been described since 1897 in the Iberian Peninsula (see Díaz-Martínez & Pérez-García, 2011; Díaz-Martínez & Pérez-García, 2012; Fortuny et al., 2012; Meléndez & Moratalla, 2014). Most of the studies predate the 1990s, and almost all the Iberian tracks have been studied just once and only taking into account their ichnotaxonomical affinities. There are some examples where the material has been reassessed, such as *Chirotherium catalaunicum* Casanovas Cladellas, Santafé Llopis & Gómez Alba, 1979 (Fortuny et al., 2011), the *Chirotherium* tracks from

64 Mallorca (Calafat et al., 1986-1987; Gand et al., 2010), *Chirotherium barthii* Kaup, 1935b from
65 Catalonia (Calzada, 1987; Valdiserri, Fortuny & Galobart 2009), and the “Rillo de Gallo footprint” in
66 Guadalajara (Calderón, 1897; Díaz-Martínez & Pérez-García, 2012). These reassessments have
67 changed the initial identifications, and the age of the track-bearing layers has been taken into
68 consideration. A number of researchers (Gand et al., 2010; Fortuny et al., 2011; Díaz-Martínez &
69 Pérez-García, 2012) have emphasized the need to reappraise the Iberian Triassic vertebrate record in
70 order to compare it with that from other coeval basins.

71 In the present work, we reassess the two slabs from the Moncayo massif (NE Spain) where
72 *Chirotherium ibericus* (Navás, 1906) was defined (Navás, 1904, 1906). Since its definition, no one has
73 yet reanalyzed this material first hand, although it has been addressed in some ichnotaxonomic
74 discussions (Leonardi, 1959; Kuhn, 1963; Haubold, 1971). During visits to the Natural Science
75 Museum of the University of Zaragoza (Zaragoza, Spain), we have identified in the slabs new
76 vertebrate tracks and anatomical details undescribed by Navás (1904, 1906) and Leonardi (1959).
77 Moreover, on the basis of recent geological studies (e.g. Díez et al., 2007; Bourquin et al., 2007, 2011),
78 we are able to refine the geological location of these slabs (Navás site from here). The main aim of this
79 paper is to discuss the ichnotaxonomy of all the vertebrate tracks found in the two slabs (those
80 classified as *Chirotherium ibericus* and the other new material associated with them). Furthermore, we
81 review the main tetrapod track assemblages of the Iberian Triassic (only including those localities that
82 are well dated) in order to compare them with the biochrons based on tetrapod footprints (e.g. Klein &
83 Haubold, 2007; Klein & Lucas, 2010a) proposed for the Triassic.

86 HISTORY OF *CHIROTHERIUM IBERICUS*

88 Longinos Navás (1858-1938) was a Spanish Jesuit naturalist and a prominent entomologist in
89 his time (Bastero Monserrat, 1989). He also made notable contributions to vertebrate paleontology with
90 the recognition of several new species of tetrapods from the Miocene *Lagerstätte* of Libros in Teruel
91 province (Navás, 1922) as well as the erection of the Triassic ichnospecies *Chirotherium ibericus*
92 (Navás, 1906). His publications on Triassic tracks (Navás, 1904, 1906) reported the first occurrence of
93 vertebrate tracks in Spain following the finding of a chirotheriid footprint in the Triassic of Molina de
94 Aragón, Guadalajara province (Calderón, 1897; Díaz-Martínez & Pérez García, 2012). The tracks were

found in the summer of 1895. Longinos Navás was on a fieldtrip in the Moncayo area when a summer visitor (Mr. Ignacio de Inza) showed him the place where “two dog-like traces” were imprinted cloven on the rock. Navás (1904, 1906) went on to identify six fossil tracks in this outcrop. The first report of the discovery was in 1904, when Navás (1904) cited the presence of *Cheirotherium* in the Moncayo massif, including a first drawing of the slab bearing six ichnites made in the field by himself (Fig. 1). Subsequently, Navás (1906) assigned the tracks to a new ichnotaxon, *Chirosaurus ibericus*, but without a distinctive diagnosis. Nevertheless, it cannot be considered a *nomen nudum* because he provided a detailed description and compared it with other ichnotaxa (see art. 10.1 ICZN). At the end of Navás’s (1906) paper, he proposed the possibility of using the name *Chirotherium ibericum* instead of *Chirosaurus ibericus*. In this case, *Chirosaurus ibericus* has priority over *Chirotherium ibericum*, which is a junior synonym, since the former was used before the latter. On the other hand, the ichnogenus *Chirotherium* has priority with respect to *Chirosaurus* (see Sarjeant, 1990) so the correct way to name the ichnotaxon proposed by Navás is *Chirotherium ibericus*.

Navás (1906) proposed these tracks as a new ichnotaxon mainly on the basis of their age, size and shape. He suggested a Silurian age for the tracks but all the other known *Chirotherium* tracks were Triassic. In addition, he compared the size of these tracks with the tracks from Molina de Aragon (Guadalajara, Spain) and those from the “British Museum of London” (today the Natural History Museum of London), concluding that the latter were much bigger. He also suggested that the digit impressions of *C. ibericus* were more slender than the other tracks with which he compared them.

The slab was excised and new tracks appeared inside that were only cited but not described by Navás (1906). Finally, Navás (1906) proposed an amphibian as the trackmaker.

Subsequently, Leonardi (1959) re-studied the material of Navás (1906) on the basis of the previous publications and assigned the tracks from one slab to *Chirotherium ibericus* and the tracks from the other slab to *Chirotherium coltoni* (= *Isochirotherium coltoni*) Peabody (1957). Leonardi (1959) proposed that the presence of *Chirotherium* indicated a Triassic age.

Finally, Kuhn (1963) and Haubold (1971) analyzed the entire bibliography on pre-Cenozoic amphibian and reptile tracks and considered the tracks of the Navás site to be *Chirotherium ibericum* and *Chirotheriidae* indet. respectively.

GEOLOGICAL SETTING

126

127 The tracks studied here are located in two excised slabs of fine-grained, bluish gray sandstones.
128 According to the known data (Navás, 1906; Leonardi, 1959; Bastero Monserrat, 1989), the Navás site
129 was located in a block of rock within Holocene deposits from the Moncayo massif, in the western part
130 of Zaragoza province, NE Spain. The exact location is beside the road to the Moncayo Sanctuary, 700
131 meters before the sanctuary (Fig. 2). The Navás site is located in the Aragonese Branch of the Iberian
132 Range (Fig. 2). The Triassic of this region is composed of typical Germanic facies: detritic
133 Buntsandstein, dolomitic Muschelkalk and lutitic-evaporitic Keuper (Arribas, 1985). The Moncayo
134 massif is a structural relief that stands out from the surrounding topography and has a great richness of
135 glacial and periglacial landforms (e.g. Pellicer & Echeverría, 2004). These Holocene deposits (e.g.
136 block slopes) are formed from reworked material from the outcropping Buntsandstein facies of the
137 Moncayo anticline (Fig. 2, Ramírez del Pozo, 1980).

138 The local series in the Moncayo outcrops is formed from Permo-Triassic detritic deposits lying
139 unconformably on a Variscan basement (Arribas, 1985; Díez et al., 2007). This detritic series,
140 lithologically composed of conglomerates, sandstones and lutites, is divided into four units: the
141 Araviana, Tierga, Calcena and Trasobares units, in ascending stratigraphic order (Arribas, 1985). The
142 basal conglomerates and lutites of the Araviana unit are attributed to the Permian, whereas above them
143 a noticeable hiatus has been recognized for the Lower Triassic (Díez et al., 2007). The Buntsandstein
144 facies *sensu stricto* is represented by the Tierga, Calcena and Trasobares units, which are Anisian
145 (Middle Triassic) in age (Díez et al., 2007; Bourquin et al., 2007, 2011).

146 The studied track-bearing slabs were recovered within Holocene deposits from the NE slope of
147 the Moncayo peak (Fig. 2); their exact stratigraphic origin cannot be specified with certainty. However,
148 the lithological features and the nearest outcrops allow us to assign these slabs to Anisian
149 Buntsandstein s. s. deposits, it being impossible to pinpoint their provenance specifically to one of the
150 three local units. These deposits constitute a major cycle that can be divided into two minor cycles
151 (Díez et al., 2007). The sandy nature of the slabs suggests that they probably belong to the Tierga-
152 Calcena cycle in its retrogradational phase (mainly the Tierga unit), which is attributed to the lower
153 Anisian (Díez et al., 2007). The Tierga unit – about 250 meters thick and mainly composed of fine to
154 medium-grained sandstones, with interbedded silty claystones – shows an evolution from a braided
155 river to a fluvio-lacustrine environment, whereas the overlying Calcena unit – far less thick and rich in
156 lutite – represents heterolithic coastal plain deposits (Díez et al., 2007).

Buntsandstein facies in the Iberian Range have traditionally been considered to be fluvial in origin (e.g. Arche & López-Gómez, 2006). Nonetheless, it should be noted that recently the red Buntsandstein sandstones of the south-eastern Aragonian Branch of the Iberian Chain have been reported as an evolving erg system (Soria et al., 2011), in accordance with the highly arid conditions predicted by paleoclimatic models for Western Europe during the Early Triassic (Péron et al., 2005).

MATERIAL AND METHODS

The analysed materials are two slabs, CS.DA.38 and CS.DA.39, which are housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain. The slabs have been deposited in the current institution since the late 20th century and were previously part of the collection of the Jesuit school of Zaragoza (Colegio El Salvador) at which Longinos Navás was teaching. The tracks were drawn using a large sheet of plastic. All the tracks were photographed individually, were measured (Fig. 3) and were labeled with the acronyms CS.DA.38.X or CS.DA.39.X (Figs. 4-6), depending on the slab and the position within the slab. CS.DA is the official label assigned by the Jesuit school and later maintained in the Natural Science Museum of the University of Zaragoza. In addition, m/p refers to manus and pes tracks respectively.

The slabs have dimensions of 1.3 m length by 0.88 m width and 0.14 m thickness. The tracks which Navás sketched and identified as a single trackway in the papers of 1904 and 1906 in slab CS.DA.39 (Navás, 1904) are in fact part of two incomplete trackways (CS.DA.39.1.1p, CS.DA.39.1.1m, CS.DA.39.1.2p, CS.DA.39.1.2m and CS.DA.39.2.1m and one isolated track CS.DA.39.9) (Fig. 1, 4-6). The tracks in slab CS.DA.39 are at the bottom and are stratigraphically beneath slab CS.DA.38. The natural casts of CS.DA.38 are located on the top of CS.DA.39.

Within slab CS.DA.38 (Figs. 4, 6) we have identified three partial trackways (CS.DA.38.1-CS.DA.38.2 and CS.DA.38.4), a manus-pes track set (CS.DA.38.3) and three isolated tracks (CS.DA.38.5-CS.DA.38.7). In slab CS.DA.39 (Figs. 5-6), three partial trackways (CS.DA.39.1-CS.DA.39.3), five tracks (CS.DA.39.4-CS.DA.39.8) that could represent a trackway, and two isolated tracks (CS.DA.39.9-CS.DA.39.10) have been studied. In total, 28 vertebrate tracks have been studied (12 in CS.DA.38 and 18 in CS.DA.39).

Measurements were taken mainly according to Demathieu & Wright (1988) and Clark, Aspen & Corrance (2002) (see Fig. 3). Ichnotaxonomic discussions are mainly based on Avanzini & Renesto (2002), Demathieu & Demathieu (2004), Fichter & Kunz (2004), King et al. (2005) and Valdiserri & Avanzini (2007). In analyzing and describing the skin marks we follow Avanzini (2000) and Kim et al. (2010).

The measurements taken were (Fig. 3; Table 1-3): L, track length; l, track width; M, length set of I-IV; m, width set I-IV; I, length digit I; II, length digit II; III, length digit III; IV, length digit IV; V, length digit V; t, divarication II-IV; t', divarication I-IV; f, divarication I-V; PL, pace length; Apm, angle between pes and manus; and Dpm, distance between pes and manus. All parameters are given and compared in cm, except t, t', f, and Apm, which are given in degrees.

Further, the entire bibliography relating to the record of Iberian Triassic tracks is revised in order to allow comparison with the global tetrapod track biochronology proposed by Klein & Haubold (2007) and Klein & Lucas (2010a). The information that we use is presented in simplified form in Table 4 and in the Supplementary Data.

SYSTEMATIC ICHNOLOGY

Ichnofamily Chirotheriidae Abel, 1935

Ichnogenus *Chirotherium* Kaup 1835a

Chirotherium barthii Kaup 1835b

(Figs. 4-8)

1904 *Cheirotherium* Navás, p. 149.

1906 *Chirosaurus ibericus* Navás, p. 208, fig. 2-3.

1906 *Chirotherium ibericum* Navás, p. 213, fig. 2-3.

1959 *Chirotherium ibericus* Leonardi, p. 243, photograph 3.

1959 *Chirotherium coltoni* Leonardi, p. 243.

1963 *Chirotherium ibericum* Kuhn, p. 71.

1971 Chirotheriidae indet. Haubold, p. 58.

218 **Referred specimens:** CS.DA.38.1.1p, CS.DA.38.1.1m, CS.DA.38.1.2p, CS.DA.38.2.1p,
219 CS.DA.38.2.1m, CS.DA.38.2.2p, CS.DA.38.2.2m, CS.DA.38.3.1p, CS.DA.38.3.1m, CS.DA.39.1.1p,
220 CS.DA.39.1.1m, CS.DA.39.1.2p, CS.DA.39.1.2m, CS.DA.39.2.1p, CS.DA.39.2.1m and
221 CS.DA.39.2.2p.

222 **Material:** 16 tracks (four partial trackways and one pes/manus set) in the two slabs (nine in CS.DA.38
223 and seven in CS.DA.39); some of them show skin and phalangeal pad impressions (Figs. 4-8; Table 1).
224 .

225 **Horizon and locality:** Buntsandstein facies, Anisian (Middle Triassic); Navás site (Moncayo massif,
226 Zaragoza, Spain).

227 **Description:**

228 Manus: There are seven manus tracks but only one is complete, CS.DA.39.1.2m. It is
229 pentadactyl, mesaxonic, asymmetric and digitigrade (Fig. 7). The length of the manus tracks varies
230 from 4.7 cm to 6.1 cm, and the width of the only complete track is 6.1 cm. Four digit impressions (I–
231 IV) are directed forward, and one, the digit V impression, is directed laterally. Digit I is often poorly
232 preserved or absent. There is little difference in the length of digits III and IV, which are longer than
233 digits I (the smallest) and II. Digit V is situated proximally below digit IV. It is divergent (from the
234 long axis through digit III) and separated from the other digits. Digits I, II, III and IV fuse at their
235 proximal ends but do not present clear metacarpal pads. At least four of the digits (I–IV) have an
236 acuminate end, although these are not as prominent as those on the pes. The divarication angle II–IV is
237 from 30° to 48°. The angulation between digits I–IV and I–V is 65° and 145° respectively in
238 CS.DA.39.1.2m (see Table 1).

239 The manus tracks are more poorly-preserved than the pes tracks. The manus is relatively small
240 compared to the pes, with the manus-pes length ratio ranging from 0.4 to 0.46.

241 Pes: These are pentadactyl, mesaxonic, asymmetric and semiplantigrade tracks (see Fig. 7).
242 Four digit impressions (I–IV) are directed forward, and one, the digit V impression, is directed
243 laterally. They are longer than wide. The length of the pes print varies from 11.2 cm to 14.5 cm, and
244 the width ranges from 7.5 cm to 8.9 cm. The length to width ratio varies from 1.5 to 1.65. Digits I–IV
245 form an isolated group that is longer (from 8 to 8.9 cm) than wide (from 5.6 to 7.9 cm). The digits are
246 longer than wide and have an acuminate end. Digit III is slightly longer than digit IV and digit II. Digit
247 I is the smallest (III > IV > II > I); it is located posteriorly and is usually the worst preserved. The
248 divarication angle II–IV varies from 18° to 29° and I–IV from 28° to 45°. Digits I–IV show clear

impressions of digital pads, but not metatarsal pads. Digit V is rotated outwards with respect to digit IV. It shows a subovoid impression of the metatarsal pad. The angulation between digit I–V varies from 78° to 86°. In the pes track CS.DA.38.1.2p skin impressions are recognizable. They are very small in size, about 1 mm on the digit V surface (Fig. 8). Their shape is predominantly subrounded and does not show a distinct ornamentation. Impressions are separated by a thin and non-imbricated depression. Another part of the slab with skin-like marks has been found, but there are not any tracks associated with it.

Trackway: There are four partial trackways and one manus-pes set (see Figs. 4-7). The manus is rotated outward 14°-30° with respect to the pes. The manus/pes distances range from 11.3 cm to 16.4 cm. The manus is placed in front of, and to the inside of, the pes (usually with the outer edge of the manus in line with the outer edge of the pes). The pace length between pes tracks is from 33.8 cm to 42 cm, and between manus tracks from 36 cm to 38.5 cm.

Remarks:

The tracks in both slabs have the same general shape. Although there is slight variability among them, we consider that this variability is a consequence of preservational factors. The main difference between the tracks is the size. The tracks in CS.DA.38 are slightly smaller than the CS.DA.39 tracks (see Table 1). Nevertheless, we consider that size is not a valid ichnotaxobase (see Bertling et al., 2006), and therefore we have classified all of them in the same way.

Since the pes tracks are semiplantigrade and pentadactyl with a compact anterior digit I–IV group and a posterolaterally positioned digit V, and the manus tracks are smaller than the pes tracks, pentadactyl, mesaxonic, asymmetric and digitigrade, they can be attributed to the ichnofamily Chirotheriidae (cf. Demathieu & Demathieu, 2004; King et al., 2005). Demathieu & Demathieu (2004) and King et al. (2005) proposed the proportions of digits I–IV as the most important feature for distinguishing chirotheriid ichnogenera, whereas the length, shape and position of digit V are variable (Klein and Haubold, 2003).

The ichnofamily Chirotheriidae is composed of nine ichnogenera: *Brachychirotherium* Beurlen, 1950; *Chirotherium*; *Isochirotherium* Haubold, 1971; *Paleochirotherium* Fichter & Kunz, 2011; *Parachirotherium* Kuhn, 1958; *Protochirotherium* Fichter & Kunz, 2004; *Parasynaptichnium* Mietto, 1987; *Sphingopus* Demathieu, 1966; and *Synaptichnium* Nopcsa, 1923. Five of these, *Brachychirotherium*, *Chirotherium*, *Isochirotherium*, *Parachirotherium* and *Sphingopus*, are

mesaxonic, and only in three of these, *Brachychirotherium*, *Chirotherium* and *Isochirotherium* do the digit I-IV impressions form an isolated group. The tracks from the Navás site belong to *Chirotherium* because the digit IV impression is normally longer than II and the digit II-IV impressions are similar in thickness. In *Isochirotherium* and *Brachychirotherium* (*sensu* Haubold, 1971; King et al., 2005) digit II is always longer than digit IV, and in the latter digits II and III are thicker than digits I, IV and V.

The studied material, classified as *C. ibericus* by Navás (1906), and other material of the same shape, presents the digit III impression slightly longer than digits II and IV. This character differentiates it from *C. vorbachii* Kirchner, 1927 (Fig. 8A), which is much more mesaxonic. Furthermore, it is characterized by a digit IV impression that is slightly longer and often thinner than digit II. It differs from *C. sickleri* Kaup, 1835c, *C. lulli* Bock, 1952, and *C. eyermani* Baird, 1957, which present digit IV clearly longer than digit II (Figs. 8B-D), and from *C. storetonense* Morton, 1863, which has digit II thinner than digit IV (Fig. 8E). Additionally, the digit I impression is smaller and thinner than the digit II-IV impressions, and located forwardly and slightly independently with respect to digits II-IV. These characters differentiate it from *C. rex* Peabody, 1948, *C. wondrai* Heller, 1952, and *C. coureli* Demathieu, 1970, which have a more robust digit I impression positioned at the same proximal position as the other digits and forming a more compact group I-IV (Fig. 8F-H). The only ichnotaxon that shares all the above-described characters with the studied material is *C. barthii* (Fig. 8I). Only the size differentiates them from one another. The Navás site tracks (Fig. 8J-L) are smaller than the holotype of *C. barthii*. Nevertheless, we consider that size is not a valid ichnotaxobase because it can represent a merely ontogenetic variation. Accordingly, we regard the two types of track as the same. *C. barthii* was defined in 1835 by Kaup on the basis of Middle Triassic tracks from Germany. Therefore, *C. barthii* has temporal priority with respect to the ichnotaxon *C. ibericus*, and the latter is a junior synonym of *C. barthii*.

Ichnofamily Chirotheriidae Abel, 1935

Chirotheriidae indet.

(Figs. 4-6, 9)

Referred specimens: CS.DA.39.3.1 and CS.DA.39.3.2

Material: A possible partial trackway of pes tracks in slab CS.DA.39 (Figs. 4-6, 9D; Table 2).

Horizon and locality: Buntsandstein facies, Anisian (Middle Triassic); Navás site (Moncayo massif, Zaragoza, Spain).

Description:

The tracks are poorly-preserved and could be two consecutive pes tracks. The first track is pentadactyl, mesaxonic, asymmetric and semiplantigrade (Fig. 8D). Four digit impressions (I–IV) are directed forward, and one, the digit V impression, is directed laterally. It is longer than wide. The second track preserves the digit V impression, which is also directed laterally, and some impressions directed forwards, which could belong to any of the digit I–IV impressions. The pace length is 72 cm.

Remarks:

As pointed out in the previous section, pes tracks that are semiplantigrade and pentadactyl with a compact anterior digit I–IV group are related with the ichnofamily Chirotheriidae (cf. Demathieu & Demathieu, 2004; King et al., 2005). Nevertheless, we are not assigning these tracks to a concrete chirotheriid ichnogenus because the proportions of digits I–IV are the most important feature for classification (Demathieu & Demathieu, 2004; King et al., 2005) and this information cannot be extracted from the tracks due to their state of preservation.

Ichnofamily Rhynchosauroidea Haubold, 1966

Ichnogenus *Rhynchosauroides* Maidwell, 1911

Rhynchosauroides isp.

(Figs. 4–6, 9)

Referred specimens: CS.DA.39.4, CS.DA.39.5, CS.DA.39.6, CS.DA.39.7, CS.DA.39.8 and CS.DA.39.9.

Material: Part of a possible trackway (CS.DA.39.4, CS.DA.39.5, CS.DA.39.6, CS.DA.39.7 and CS.DA.39.8) and an isolated track (CS.DA.39.9) in slab CS.DA.39 (Figs. 4–6, 9A–C; Table 2).

Horizon and locality: Buntsandstein facies, Anisian (Middle Triassic); Navás site (Moncayo massif, Zaragoza, Spain).

Description:

Manus: the best-preserved manus track, CS.DA.39.4 (Fig. 9B), is pentadactyl, ectaxonic, very asymmetric and plantigrade. Four digit impressions (I–IV) are directed forward, and one, the digit V impression, is directed more laterally. The length of the track is 3.7 cm and the width 2.4 cm (length / width ratio 1.54). The digits are longer than wide and rotated medially. Digit IV is the longest. Digit IV>III>II>I>V. The divarication angle II–IV is 10°, I–IV is 50° and I–V is 78°. The digit impressions

show clear impressions of claw marks. The palm impression is well-marked and bilobed. Similar to this track is CS.DA.39.9 4 (Fig. 9A), but one of the digit impressions (probably the digit IV impression) is not preserved.

Pes: track CS.DA.39.5 4 (Fig. 9C) is tetradactyl, very asymmetric and digitigrade. The four digit impressions (I–IV) are longer than wide, directed forward and rotated medially. It is not possible to measure the length or width of the track due to its state of preservation. Digit IV is the longest. Digit IV>III>II>I>V. The divarication angle II–IV is 15° and I–IV is 30°. The digit impressions do not show clear impressions of claw marks.

Tracks CS.DA.39.6, CS.DA.39.7 and CS.DA.39.8 are tridactyl and didactyl. The shape and size of the preserved digit impressions are similar to those of tracks CS.DA.39.4 and CS.DA.39.5, and they are located close to them.

Remarks:

There is clear variability among all the tracks. Some of them, CS.DA.39.4–CS.DA.39.8, could be part of the same trackway given their shape, size and location. Therefore, this variability is probably a consequence of the state of preservation and not because they are different morphotypes. The best-preserved tracks present the following main features: four digit impressions (I–IV) directed forward; digits longer than wide and rotated medially; and digits increasing in length from I to IV. In addition, in CS.DA.39.4 and CS.DA.39.10 (manus tracks) there is a digit V impression, which is shorter than the others and is turned outwards. These characters are typical of the ichnogenus *Rhynchosauroides* (Melchor & de Valais, 2006; Avanzini, Piñuela & García-Ramos, 2010). However, more than 20 ichnospecies of *Rhynchosauroides* have been defined (see Haubold, 1971), and the validity of some of them has not been discussed. As we have suggested above, moreover, the shape of the tracks studied here is variable, and they are not well enough preserved for a confident determination of the ichnospecies. Accordingly, we have decided to be cautious in assigning these tracks to *Rhynchosauroides* isp.

Undetermined material

Unnamed Morphotype

(Figs. 4–6, 9)

Referred specimens: CS.DA.38.4, CS.DA.38.5, CS.DA.38.6, CS.DA.38.7 and CS.DA.39.10.

Material: six footprints in the two slabs (five in CS.DA.38 and one in CS.DA.39); two of them are a pair 4 (Figs. 4-6, 9E; Table 3).

Horizon and locality: Buntsandstein facies, Anisian (Middle Triassic); Navás site (Moncayo massif, Zaragoza, Spain).

Description:

These are tridactyl, mesaxononic, symmetric and digitigrade tracks. The length is from 2 cm to 2.4 cm, and the width from 1.6 cm to 2.8 cm. The three digit impressions are directed forward. There is little difference in the length of the digits, the central one being the longest. The divergence between the lateral digits is variable. The tracks of the pair CS.DA.38 (Figs. 4-6, 9E) present a greater divarication angle than the other tracks. The digit impressions of these tracks are the thinnest as well. At least three tracks (CS.DA.38.4.1, CS.DA.38.4.2 and CS.DA.38.5) have an acuminate end.

The pace length in the pair CS.DA.38.4 is 37 cm.

Remarks:

Although some tracks are thinner than others, all the tracks present the same features. Tridactyl, mesaxononic and digitigrade tracks could be associated with non-avian or avian theropod tracks (cf. Thulborn, 1990; de Valais & Melchor, 2008). However, non-avian theropod tracks are generally asymmetric, and there are no avian remains in the Anisian. The tracks are very shallow and are not well-preserved. It is possible that these tracks are formed from the preserved parts of other kinds of track. Because of the poor state of preservation of the specimens, any attribution would be tentative.

DISCUSSION

The Navás site tracks and the Triassic Iberian record

After a reassessment of the Navás site, *Chirotherium barthii*, Chirotheriidae indet., *Rhynchosauroides* isp., and an unnamed morphotype have been identified. As at the Navás site, chirotheriid tracks are well-represented in other Iberian localities. This kind of tracks is the most abundant compared to other ichnogroups. According to the revision of Díaz-Martínez & Pérez-García (2011) and the most recent articles (Díaz-Martínez & Pérez-García, 2012; Fortuny et al., 2012;

Meléndez & Moratalla, 2014; this work) on 63 classified remains in 26 publications, 26 correspond to chirotheriid tracks. These tracks have been attributed to *Brachychirotherium* (2), *Chirotherium* (13), *Isochirotherium* (3), *Synaptichnium* (5) and indeterminate chirotheriids (3). The re-evaluation of the type material of *C. ibericus* has demonstrated that it is a junior synonym of *C. barthii*. This latter ichnospecies has also been found at other Iberian localities such as Corral d'en Parera (Calzada, 1987) and in the Eslida Formation (Gand et al., 2010), both Anisian in age. Gand et al. (2010) suggested that the presence of *C. barthii* is "rather uncommon in Spain". What is remarkable is the small size of the Iberian tracks assigned to *C. barthii* (Figs, 7A-D), since in the emended description of the diagnosis of this ichnospecies provided by King et al. (2005), the authors proposed that *C. barthii* has a pes length of about 19–22 cm. In the case of the Iberian tracks, the tracks from the Navás site have a pes length of between 11–14 cm, while the tracks described by Gand et al. (2010) are even smaller (pes length 8.4 cm). Calzada (1987) did not measure the total length of the tracks but the length of digit III (9.5– 9.6 cm) according to the scale of the track pictures also seems small in size. Small-sized *C. barthii* tracks have also been described in the Middle Triassic of the United States (Klein & Lucas, 2010b; Lovelace & Lovelace, 2012), Morocco (Tourani et al., 2010; Klein et al., 2011), and China (Xing et al. 2013), and possibly also Switzerland (Cavin et al., 2013). The small size of the Iberian tracks assigned to *C. barthii* would fit better with the pes length of *C. sickleri*. In fact, King et al. (2005) proposed that "there is a strong possibility that *C. sickleri* may represent the tracks of a juvenile reptile, whose adult tracks might be attributed to *C. barthii* or *C. storetonense* Morton, 1863". Klein & Haubold (2003) also showed the similarities between the two ichnotaxa with a landmark analysis and suggested that "one could suspect a juvenile *C. barthii*". The authors pointed out that some features of *C. sickleri*, such as the manus print morphology and the trackway pattern, were not included in the analysis, which was mainly done with the pes morphology. The Navás site, as well as the recent publications of small-sized *C. barthii* tracks, thus adds valuable data to this debate, and an exhaustive comparison of the two ichnotaxa is needed in order to discern whether *C. sickleri* is an ontogenetic variation of *C. barthii* or in fact a different ichnospecies.

The *C. barthii* pes track CS.DA.38.1.2p has preserved skin traces (Fig. 4) that are not noted in previous reports on the material. Other skin traces were found in the same slab (Fig. 9F), but they are not related with any visible track. The skin impressions were only created because the integument registered on a receptive substrate (Gatesy, 2001; Pérez-Lorente, 2001), and the motion of the skin relative to the sediment during separation strongly influences the morphology of the skin impression

(Gatesy, 2001; Avanzini, Piñuela & García-Ramos, 2011). In this case, the ornamentation reveals scales that are sub-rounded to polygonal in shape, and it is present in digit V. These scale marks are similar to other chirotheriid skin impressions studied by Avanzini (2000), suggesting that these kinds of scales are similar to those of birds and extant Archosauria.

Six tracks belonging to *Rhynchosauroides*, including pes and manus tracks, were found at the Navás site. *Rhynchosauroides* is the best-known ichnogenus in the Triassic record of Iberia. It has been found at 13 localities in the provinces of Barcelona, Cantabria, Castellón, Guadalajara, Teruel and Zaragoza (Demathieu & Saiz de Omeñaca, 1976, 1977; Demathieu, Ramos & Sopeña; Demathieu & Saiz de Omeñaca, 1979; Calzada, 1987; Demathieu & Saiz de Omeñaca, 1990; Ezquerro et al., 1995; Valdiserri, Fortuny & Galobart, 2009; Gand et al., 2010; this work). Four *Rhynchosauroides* ichnospecies have been described in the Iberian Peninsula: *Rhynchosauroides santanderensis* Demathieu & Saiz de Omeñaca, 1976; *Rhynchosauroides virgiliae* Demathieu, Ramos & Sopeña, 1978; *Rhynchosauroides extraneus* Demathieu & Saiz de Omeñaca, 1979; and *Rhynchosauroides simulans* Demathieu & Saiz de Omeñaca, 1979. The temporal record of this ichnotaxon is predominantly Anisian, as exemplified by the Navás site, although it has also been described in the Permian (Valentini, Conti & Mariotti, 2007) and even in the Late Jurassic (Avanzini, Piñuela & García-Ramos, 2010).

Finally, undetermined material has also been found at the Navás site. These tracks are tridactyl and mesaxonitic, but they are probably the preserved part of other tracks. In the Iberian record other Triassic tracks with problematic affinities have been cited (see Supplementary information Table S1). The tracks classified as type 3 and type 4 of Demathieu & Saiz de Omeñaca (1976, 1977) are similar to those from the Navás site. In the former case, the shape of the tracks suggests that they are part of *Rhynchosauroides* tracks. It is therefore possible that the Navás tracks might be as well.

The Navás tracksite presents the *Chirotherium barthii*-*Rhynchosauroides* ichnoassemblage. This ichnoassemblage is common in other Middle Triassic localities in Iberia (Calzada, 1987; Gand et al., 2010), as well as in other ichnoassemblages with greater ichnodiversity described in the Middle Triassic of Europe (e.g. France, Gand, Demathieu & Montenat, 2007; Italy, Avanzini Bernardi, Nicosia, 2011; Poland, Niedzwiedzki et al., 2007), North Africa (e.g.: Morocco, Tourani et al., 2010; Klein et al., 2011) and North America (e.g. Hunt et al., 1993; Heckert, Lucas & Hunt, 2005). Analysis of the ichnoassemblage from the Navás site within the context of the global tetrapod track biochronology of the Triassic shows it to belong to biochron II (*sensu* Klein & Haubold, 2007) or the

466 *Chirotherium barthii* biochron (*sensu* Klein & Lucas, 2010a). Both biochrons are defined for the upper
467 Olenekian-lower Anisian age, which is coherent with the age of the Navás site, which is here
468 considered Anisian.

469

470 **The Triassic record of vertebrate tracks in the Iberian Peninsula and the tetrapod-track-based** 471 **biochrons**

472

473 Several characteristic track assemblages and ichnotaxa have a restricted stratigraphic range and
474 can therefore be repeatedly observed in the global record in distinct time intervals (Klein & Lucas,
475 2010a). Several authors (e.g. Haubold, 1969; Demathieu & Haubold, 1974; Olsen, 1980; Lockley &
476 Hunt, 1995; Hunt & Lucas, 2007; Lucas, 2007; Klein & Haubold, 2007; Klein & Lucas, 2010a; and
477 references therein) have proposed the possibility of a tetrapod ichnostratigraphy of Triassic sequences.
478 Nevertheless, vertebrate track biochronology faces three main problems that result in it being not as
479 refined as tetrapod body fossils can be: the ichnotaxonomy, the evolutionary turnover rates and facies
480 restrictions (Lucas, 2007). The last two biases are conditioned by the habitat and rate of evolution that
481 is proper to each animal group (see discussion in Lucas, 2007). Thus the main problem with Triassic
482 footprint biostratigraphy and biochronology is the nonuniform ichnotaxonomy and the evaluation of
483 footprints that show extreme variation in shape due to extramorphological (substrate-related)
484 phenomena (Klein & Lucas, 2010a). For instance, 75 chirotherian ichnospecies have been described
485 from Triassic deposits in Europe, North America, South America, northern and southern Africa, and
486 China (Klein & Haubold, 2007; Klein & Lucas, 2010a), but most of them may be synonyms and/or
487 extramorphological variations of perhaps 35 valid ichnotaxa (Xing et al., 2013).

488 Since 1897, when the first work on Triassic vertebrate tracks from the Iberian Peninsula was
489 published, 25 scientific works on the topic have been published (see Díaz-Martínez & Pérez-García,
490 2011; Díaz-Martínez & Pérez-García, 2012; Fortuny et al., 2012; and Meléndez & Moratalla, 2014)
491 (Supp. Table 1). Vertebrate tracks have been reported from 26 sites, and six new ichnotaxa have been
492 defined: *Chirotherium ibericus*, *R. santanderensis*, *R. virgiliae*, *Chirotherium catalaunicum*, *R.*
493 *extraneus* and *R. simulans*. More than half of the papers on Triassic tracks were published before the
494 1990s, and almost none of the Iberian tracks have been re-studied. In all the papers that reassess
495 previously studied tracks, the initial ichnotaxonomic identifications and the age of the track-bearing
496 layers were subsequently modified (e. g. Leonardi, 1959; Gand et al., 2010; Fortuny et al., 2011; Díaz-

Martínez & Pérez-García, 2012; this work). In addition to the nonuniform ichnotaxonomy, the Iberian record presents another problem when it comes to comparisons with the biostratigraphy and biochronology proposed for the Triassic tracks. This is the temporal geological context of the ichnological localities. In some papers the age of the tracksite is well defined in terms of chronostratigraphic ages such as Anisian, Ladinian or Rhaetian (e.g. Pascual-Arribas & Latorre-Macarrón, 2000; Gand et al., 2010; Fortuny et al., 2011). In other papers, however, authors have located the tracks within the classic Germanic facies (Buntsandstein, Muschelkalk and Keuper) (see Díaz-Martínez & Pérez-García, 2011; Supplementary information Table S1), which are not considered time intervals, as the development of the different rift systems in central and western Europe was not coeval, causing diachronous facies changes (López-Gómez, Arché & Pérez-López, 2002; and references therein). In this context, we have only compared the Iberian record that is located in a concrete chronostratigraphic age (Table 4; Fig. 10) with the tetrapod track biochronology of the Triassic proposed by Klein & Haubold (2007) and Klein & Lucas (2010a).

Lowest Triassic-upper Lower Triassic

Klein & Lucas (2010a) define the “dicynodont-tracks” biochron for the latest Changhsingian-Induan stratigraphic interval, during which earliest Triassic dicynodont tracks are characteristic. The authors suggest that this biochron is so far restricted to Gondwana.

For the late Induan-late Olenekian stratigraphic interval, Klein & Haubold (2007) propose biochron I, and Klein & Lucas (2010a) the *Protochirotherium* biochron. The typical ichnological assemblage of these biochrons is based on the ichnotaxa *Protochirotherium* (*Synaptichnium*), *Rhynchosauroides* and *Procolophonichnium* Nopcsa, 1923 (Klein & Lucas, 2010a).

In the Iberian Peninsula the only record of Triassic tracks for this interval is composed solely of *Rhynchosauroides* tracks considered to be Olenekian-Anisian in age (Gand et al., 2010). This is the oldest Triassic track record in the Iberian Peninsula. The ichnotaxon *Rhynchosauroides* has a broad temporal distribution. Klein & Lucas (2010a) represented it throughout the Triassic, and Avanzini, Piñuela & García-Ramos (2010) even identified *Rhynchosauroides* tracks in the Upper Jurassic of Asturias (Spain). The appearance of this ichnotaxon in Iberia is thus coherent with the global distribution proposed by Klein & Lucas (2010a). Nevertheless, the record is very scarce and does not

give concrete data on the biochron, which could be within the Olenekian-Anisian time range given the dominance of *Rhynchosauroides* in some footprint assemblages (Fig. 10).

Uppermost Lower Triassic-Middle Triassic

For this interval Klein & Haubold (2007) proposed three biochrons, and Klein & Lucas (2010a) two. For the late Olenekian-early Anisian, biochron II (Klein & Haubold, 2007) and the *Chirotherium barthii* biochron (Klein & Lucas, 2010a) were defined. The typical assemblage for this temporal interval is composed of *C. barthii*, *C. sickleri*, *Isochirotherium*, *Synaptichnium* (“*Brachychirotherium*”), *Rotodactylus* Peabody, 1948, *Rhynchosauroides*, *Procolophonichnium*, dicynodont tracks and *Capitosauroides* Haubold, 1970 (Klein & Lucas, 2010a).

Klein & Haubold (2007) proposed biochron III for the late Anisian-early Ladinian interval and biochron IV for the late Ladinian. Biochron III is composed of the ichnotaxa *Sphingopus*, *Atreipus* Olsen & Baird, 1986, *Grallator* Hitchcock, 1858, *Rotodactylus*, *Isochirotherium* and *Synaptichnium* (“*Brachychirotherium*”). Typical of biochron IV are *Parachirotherium*, *Atreipus*, *Grallator*, and *Synaptichnium* (“*Brachychirotherium*”). For almost the same temporal range as biochrons III and IV, Klein & Lucas (2010a) defined the *Atreipus-Grallator* biochron in the late Anisian-lowermost Carnian. The typical assemblage of this biochron comprises *Atreipus*, *Grallator* (“*Coelurosaurichnus*”), *Synaptichnium* (“*Brachychirotherium*”), *Isochirotherium*, *Sphingopus*, *Parachirotherium*, *Rhynchosauroides* and *Procolophonichnium*.

The Iberian record in the uppermost Lower Triassic-Middle Triassic time interval is abundant. As suggested above, the oldest remains are Olenekian-Anisian in age and are composed only of *Rhynchosauroides* tracks (Gand et al., 2010). Calzada (1987) proposed a late Olenekian or early Anisian age for the tracks that he studied in the Buntsandstein of Catalonia, whereas Valdiserri, Fortuny & Galobart (2009) and Fortuny et al. (2012) suggested an Anisian age for these tracks. In the Anisian, the Iberian assemblage consists of *Dicynodontipus* Lilienstern, 1944, *Procolophonichnium*, *Rhynchosauroides*, *Rotodactylus*, *Brachychirotherium*, *Chirotherium barthii*, *Isochirotherium*, *Synaptichnium*, *Coelurosaurichnus* Huene, 1941, and *Paratrisauropus* Ellenberger, 1972 (Calzada, 1987; Valdiserri, Fortuny & Galobart., 2009; Gand et al., 2010; Fortuny et al., 2012; this work). In the Ladinian only three localities with vertebrate tracks have been described to date (Demathieu, Pérez-López & Pérez-Lorente, 1999; Fortuny et al., 2012; Meléndez & Moratalla, 2014). Demathieu,

558 Pérez-López & Pérez-Lorente (1999) described tridactyl tracks and referred them to a
559 crurotarsal/dinosauroid trackmaker. Fortuny et al. (2012) studied some vertebrate ichnites that were
560 recovered from the Middle Muschelkalk (Ladinian-early Carnian) and classified them as belonging to
561 the *Chirotheriidae* ichnofamily. Finally, Meléndez & Moratalla (2014) cited the presence of tracks with
562 the general footprint morphology of the “group” formed by the *Chirotherium*-*Isochirotherium*-
563 *Brachychirotherium* ichnogenera.

564 When the Iberian record for this temporal interval is compared with the tetrapod-track-based
565 biochrons, it can be seen that several characteristic Triassic track assemblages and ichnotaxa with a
566 restricted stratigraphic range are present. For instance, the ichnotaxon *Chirotherium barthii* has been
567 found in four localities of an Anisian age (Table 4). The presence of this ichnotaxon is typical of
568 biochron II of Klein & Haubold (2007) and the *Chirotherium barthii* biochron of Klein & Lucas
569 (2010a), both from the late Olenekian-early Anisian interval. The latter authors suggest that
570 *Chirotherium barthii* disappears during the Anisian. The ichnotaxa *Isochirotherium* and *Rotodactylus*
571 have been found in the Anisian of the Iberian Peninsula as well. Both ichnotaxa have a broader
572 distribution (late Olenekian-early Ladinian) than *C. barthii*, forming part of biochrons II and III of
573 Klein & Haubold (2007) and the *C. barthii* and *Atreipus-Grallator* biochrons of Klein & Lucas
574 (2010a). These ichnotaxa disappear before the end of the Ladinian (Klein & Lucas, 2007). Also present
575 in the Anisian of the Iberian Peninsula are the ichnotaxa *Coelurosaurichnus* and *Paratrisauropus*.
576 *Coelurosaurichnus* is present in biochron III (late Anisian-early Ladinian) of Klein & Haubold (2007)
577 and in the *Atreipus-Grallator* biochron (late Anisian-lowermost Carnian) of Klein & Lucas (2010). The
578 ichnotaxon *Synaptichnium*, present in the Anisian of Iberia, is typical of biochrons II, III and IV of
579 Klein & Haubold (2007) and the *C. barthii* and *Atreipus-Grallator* biochrons of Klein & Lucas (2010a)
580 for the late Olenekian-Ladinian time range. The ichnotaxon *Brachychirotherium* was cited in the
581 Anisian of the Iberian Peninsula by Gand et al. (2010). Nevertheless, Klein & Haubold (2007) and
582 Klein & Lucas (2010a) placed this ichnotaxon in biochrons V and VI, and in the *Brachychirotherium*
583 biochron of the lowermost Carnian to Rhaetian respectively. After analyzing the tracks classified as
584 *Brachychirotherium* by Gand et al. (2010), we conclude that they present a *Chirotherium* affinity (the
585 digit IV impression is longer than II, and the digit II-IV impressions are similar in thickness). In this
586 case, the age of these tracks matches with the distribution of *Chirotherium* in the biochronological
587 approaches. Other ichnotaxa with a broad temporal distribution (see Klein & Lucas, 2010a), such as

588 *Dicynodontipus*, *Procolophonichnium* and *Rhynchosauroides*, have also been found in the Anisian of
589 the Iberian Peninsula.

590 For the Ladinian, chirotheriid tracks and tracks referred to a crurotarsal/ dinosauroid trackmaker
591 have been found in Iberia. However, these tracks are not useful in biostratigraphic and
592 biochronological studies.

593 In sum, the Iberian record from the Anisian is coherent with the global biochronology of
594 Triassic tetrapod tracks, but in the late Olenekian and the Ladinian the record is very scarce (Fig. 10).

595 596 **Upper Triassic**

598 For the Carnian to Rhaetian, Klein & Haubold (2007) propose two biochrons. Biochron V has a
599 temporal range from lower Carnian to lower Norian and is composed of the ichnotaxa *Atreipus*,
600 *Grallator* and *Brachychirotherium* (Klein & Haubold, 2007); biochron VI, ranging from the middle
601 Norian to Rhaetian, consists of *Grallator*, *Eubrontes* Hitchcock, 1845 and *Brachychirotherium* (Klein
602 & Haubold, 2007). By contrast, Klein & Lucas (2010a) propose the *Brachychirotherium* biochron for
603 almost all the Late Triassic (from lowermost Carnian to Rhaetian). This biochron is composed of the
604 assemblage comprising *Brachychirotherium*, *Atreipus*, *Grallator*, *Eubrontes*, *Apatopus*,
605 *Rhynchosauroides* and dicynodont tracks (Klein & Lucas, 2010a).

606 In the Iberian Peninsula there are only two localities in the Upper Triassic. Pérez-López (1993)
607 classified a trackway found in the Keuper facies as *Brachychirotherium* cf. *gallicum*. In Europe this
608 facies spans from the late Middle Triassic (Ladinian) through the entire Late Triassic (Carnian to
609 Rhaetian) (Sues & Fraser, 2010). The presence of *Brachychirotherium* is typical of the lowermost
610 Carnian-Rhaetian, and this could be the age of these Spanish tracks. The other tracksite from the Upper
611 Triassic presents *Eubrontes* and *Anchisauripus* and is dated as Rhaetian in age (Pascual-Arribas &
612 Latorre-Macarrón, 2000). The ichnotaxon *Eubrontes* is typical of biochron VI (early Norian-Rhaetian)
613 of Klein & Haubold (2007) and the *Brachychirotherium* biochron (lowermost Carnian-Rhaetian) of
614 Klein & Lucas (2010a). Although the Iberian record for the Upper Triassic is not abundant, the data on
615 these tracks are coherent with the global biochronology of Triassic tetrapod tracks (Fig. 10).

616 A noteworthy point that emerges from the previous review is the high ichnodiversity during the
617 Anisian when compared with the other ages in the Iberian Peninsula. This high ichnodiversity can be
618 explained in at least three ways (see Díaz-Martínez, García-Ortiz, Pérez-Lorente, 2015). The first

619 explanation would be that this is a consequence of a greater diversity of trackmakers in the Anisian
620 than in other ages, this diversity being reflected in the track record. It is also possible that in the
621 Anisian there were more suitable facies for preserving the tracks, so although the diversity might in
622 fact be similar in all the ages, in the Anisian it seems highest; there would thus be a preservational bias
623 against the other ages. Finally, the high ichnodiversity could also be explained by weathering and
624 erosion processes that affect the Anisian rock outcrops less than the facies of other ages. Unfortunately,
625 we have no data to support any of these hypotheses. In order to have a more complete vision of the
626 Triassic track record in the Iberian Peninsula, it is therefore important to reassess the rest of the
627 Triassic Iberian ichnological localities not included here because these do not yet have a concrete
628 temporal geological context.

631 CONCLUSIONS

633 The ichnotaxonomy of historic vertebrate tracks found in two sandy slabs from the Anisian
634 (Middle Triassic) of the Moncayo massif (Iberian Range, NE Spain) has been re-studied. The tracks
635 previously considered *Chirotherium ibericus* by Navás, and other tracks of the same shape found in the
636 two slabs, have been reassessed and have been classified as *Chirotherium barthii*. *Chirotherium*
637 *ibericus* has been deemed to be a junior synonym of *Chirotherium barthii*. The rest of the studied
638 tracks have been assigned to *Chirotheriidae* indet., *Rhynchosauroides* isp. and undetermined material.
639 All the tracks classified as *Chirotherium barthii* in the Iberian Peninsula are characterized by their
640 small size. This point and other reports of small-sized *C. barthii* in other localities around the world
641 shed new light on the differentiation between small-sized *C. barthii* and *C. sickleri*. The *C. barthii*-
642 *Rhynchosauroides* ichnoassemblage present in the Navás tracksite (Anisian in age) is typical of
643 biochron II or the *Chirotherium barthii* biochron, of an Olenekian-lower Anisian age. This
644 ichnoassemblage has also been found in other coeval Iberian localities. Although the Iberian record of
645 Triassic tracks is not continuous and in some ages is more abundant than others, in general it is
646 coherent with the global biochronology of Triassic tetrapod tracks. This further corroborates the
647 usefulness of vertebrate Triassic tracks in biochronology. In the Lowest Triassic-upper Lower Triassic
648 interval, the record is very scarce and only the ichnotaxon *Rhynchosauroides* is cited. The record for
649 the uppermost Lower Triassic-Middle Triassic is abundant. The most complete record is the

ichnoassemblage from the Anisian, which is composed of *Dicynodontipus*, *Procolophonichnium*, *Rhynchosauroides*, *Rotodactylus*, *Chirotherium*, *Isochirotherium*, *Coelurosaurichnus*, and *Paratrisauropus*. The late Olenekian and Ladinian record is not well represented. Finally, *Eubrontes*, *Anchisauripus* and probably *Brachychirotherium* have been identified although the Iberian record for the Upper Triassic is not abundant. The analysis could be more complete if the whole of the Iberian record were analyzed. With this paper, therefore, we emphasize the need to reassess the Triassic vertebrate track record of the Iberian Peninsula and specify the age of the localities, in order to have a complete image of this record and compare it with the tetrapod-track-based biochronology and biostratigraphy.

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- FIGURE CAPTIONS:
- Figure 1. Reproduction of the original drawing of slab CS.DA.39 bearing Triassic ichnites from the Moncayo massif, made by Longinos Navás in 1895 in the field and reported by Navás (1904, p. 149).
- Figure 2. Geological setting of the Navás tracksite. Map redrawn from MAGNA (Ramirez del Pozo, 1980). General map of the Triassic outcrops and pictures from the Navás site.
- Figure 3. Scheme used for the measurements of the tracks and trackways after Demathieu & Wright (1988) and Clark Aspen & Corrance (2002) for: a) chirotheriid tracks, b) *Rhynchosauroides* tracks, c) tridactyl tracks, d) trackways. Abbreviations in Material and Methods.
- Figure 4. Picture and sketch map of slab CS.DA.38
- Figure 5. Picture and sketch map of slab CS.DA.39
- Figure 6. Sketch map of slabs CS.DA.38 and CS.DA.39 with the acronyms of each track
- Figure 7. Pictures of the studied tracks assigned to *Chirotherium* *barthii*. A: CS.DA.38.1.1p and CS.DA.38.1.1m. B: CS.DA.38.1.2p. C: CS.DA.39.1.1p. D: CS.DA.39.1.2m (see location in Fig.6).
- Figure 8. Main *Chirotherium* ichnospecies compared with the Navás site tracks. A: *C. vorbachi* (redrawn from King et al., 2005). B: *C. sickleri* (redrawn from Haubold, 1971). C: *C. lulli* (redrawn from Baird, 1954). D: *C. lomasi* (redrawn from Baird, 1957). E: *C. storetonense* (redrawn from King et al., 2005). F: *C. rex* (redrawn from Peabody, 1957). G: *C. wondrai* (redrawn from Haubold, 1971). H:

1010 *C. coureli* (redrawn from Demathieu, 1970). I: *C. barthii* (redrawn from Haubold, 1971). J:
1011 CS.DA.38.1.1p. K: CS.DA.38.1.2p. and L: CS.DA.39.1.1p.

1012

1013 Figure 9 Photographs of the new identified material assigned to *Rhynchosauroides*. A: CS.DA.39 .9. B:
1014 CS.DA.39 .4. C: CS.DA.39.5. D: Chirotheriidae indet. (CS.DA.39.3.2p). E: Undetermined material
1015 (Unnamed Morphotype, CS.DA.38.4.1). F: Isolated set of skin impressions from the slab CS.DA.38
1016 (see location in Fig.6).

1017

1018 Figure 10. Stratigraphic distribution of tetrapod track ichnotaxa and form groups in the Triassic with
1019 the global biochrons recognized by Klein & Haubold (2007) and Klein & Lucas (2010a). The red lines
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1021 *Coelurosau.*, *Coelurosaurichnus*; *Dicy.*, *Dicynodont* tracks; *Prot.*, *Protochirotherium*.

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1024 TABLE CAPTIONS:

1025

1026 Table 1. Measurements (in cm and degrees) of the *Chirotherium barthii* tracks from the Navás site.
1027 Abbreviations in Material and Methods.

1028

1029 Table 2. Measurements (in cm and degrees) of the *Rhynchosauroides* tracks from the Navás site.
1030 Abbreviations in Material and Methods.

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1032 Table 3. Measurements (in cm and degrees) of the undetermined tracks from the Navás site.
1033 Abbreviations in Material and Methods.

1034

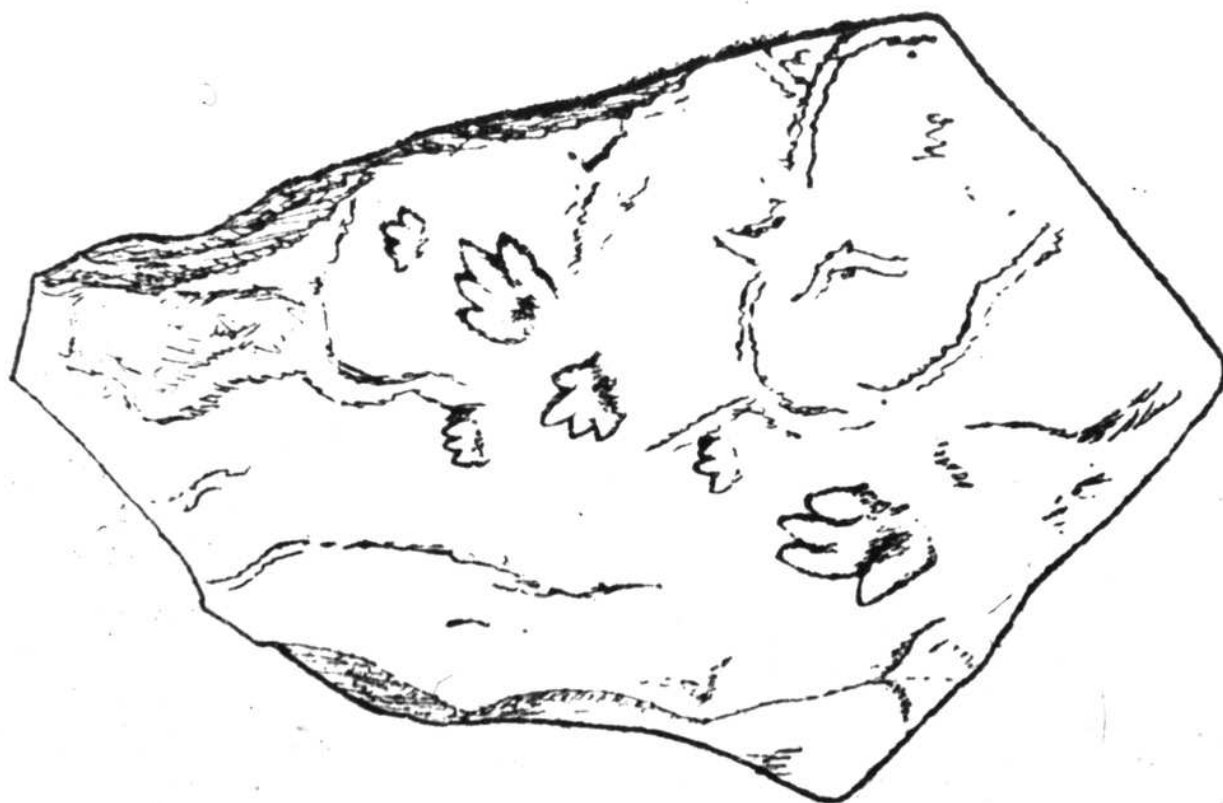
1035 Table 4. Summary of the published Triassic tracks from the Iberian Peninsula that are located in a
1036 concrete chronostratigraphic age. Only the most recent ichnotaxonomic determination is considered.

1037

1038 Supplementary information Table S1: Summary of all the Iberian Triassic tracks published in the
1039 Iberian Peninsula.

Reproduction of the original drawing of Triassic ichnites f made by Longinos Navás in 1895 in the field and reported by Navás (1904).

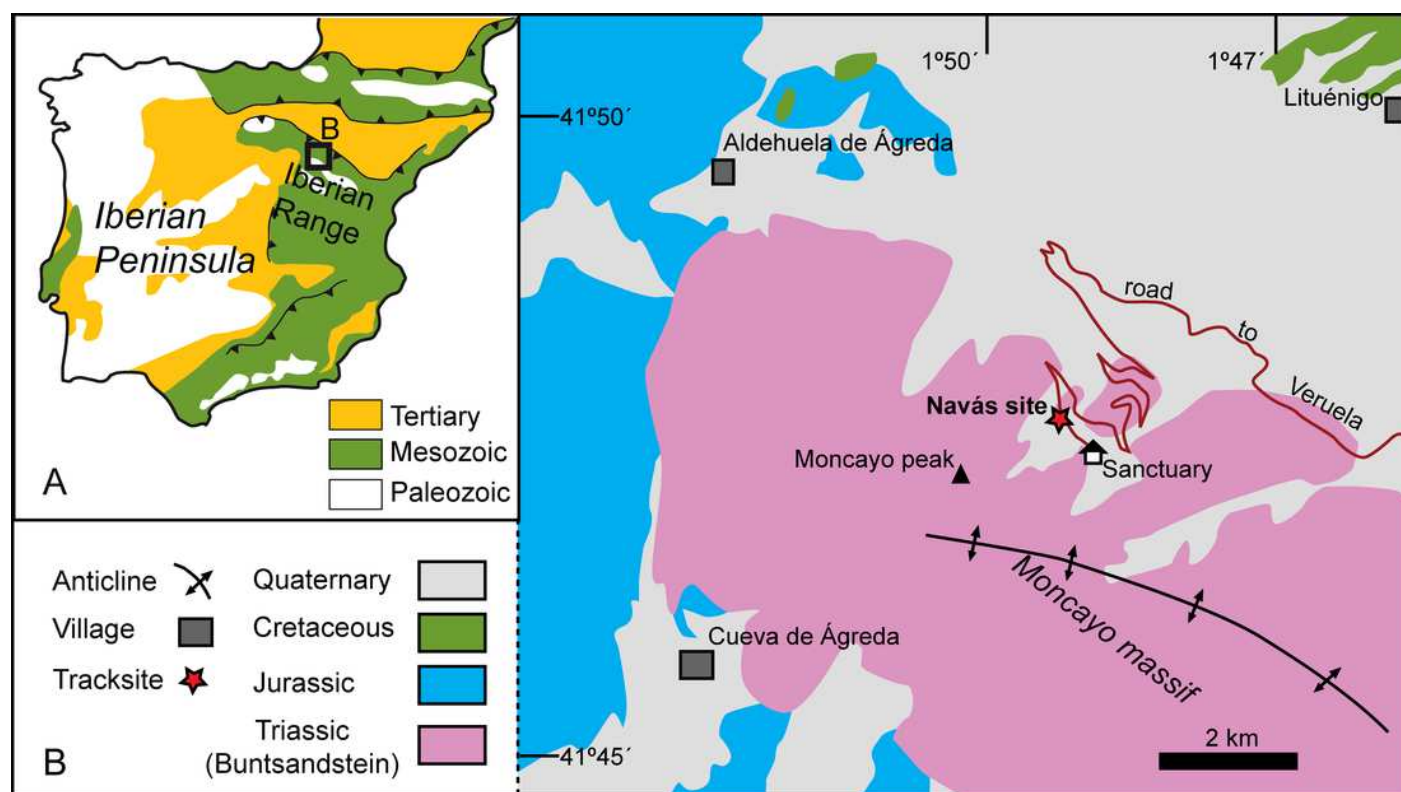
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HUELLAS DE CHEIROTHERIUM EN MONCAYO

Geological Setting of the Triassic outcrops in the Moncayo Massif.

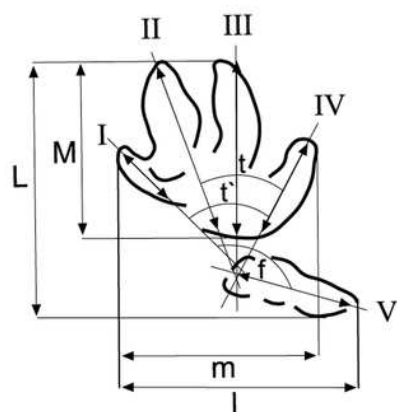
Figure 2. Geological setting of the Navás tracksite. Map redrawn from MAGNA (Ramirez del Pozo, 1980). General map of the Triassic outcrops and pictures from the Navás site.



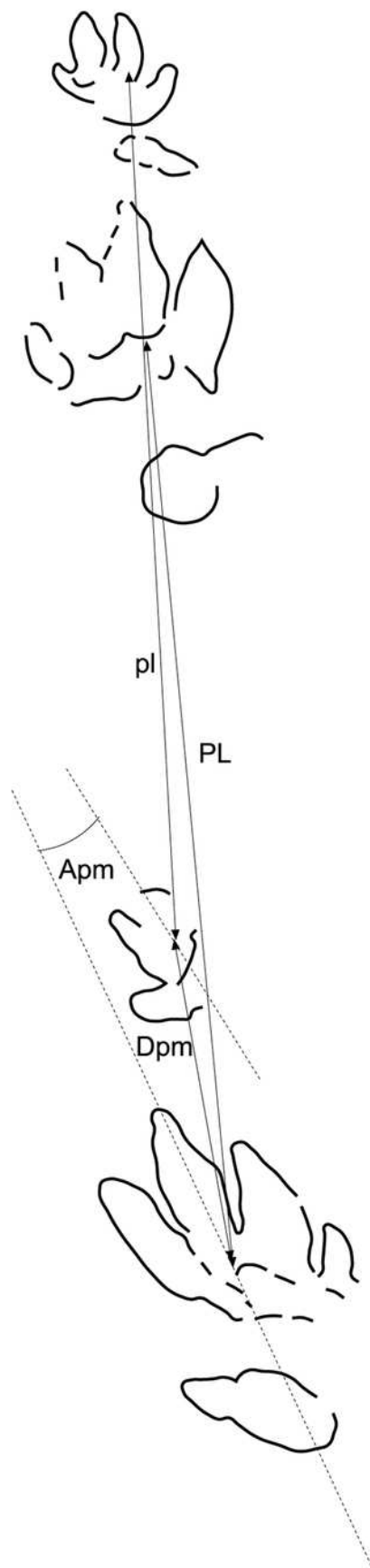
Scheme used for the measurements of the tracks and trackways

Figure 3. Scheme used for the measurements of the tracks and trackways after Demathieu & Wright (1988) and Clark Aspen & Corrance (2002) for: a) chirotheriid tracks, b) *Rhynchosauroides* tracks, c) tridactyl tracks, d) trackways. Abbreviations in Material and Methods.

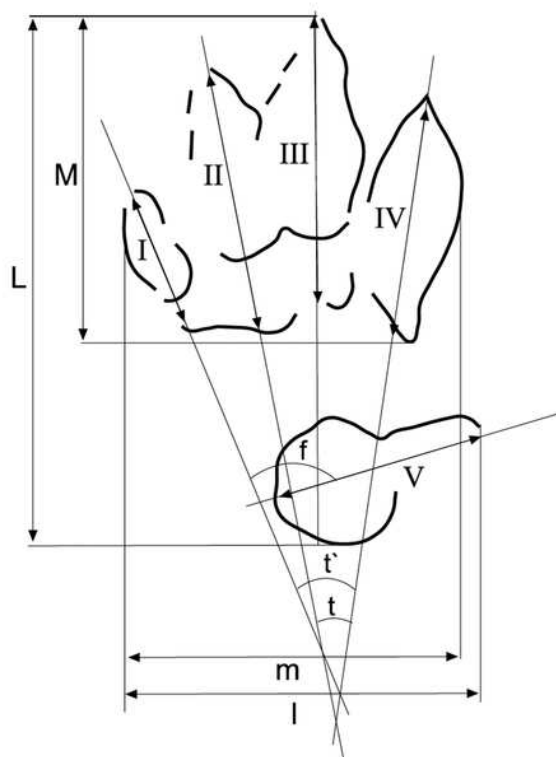
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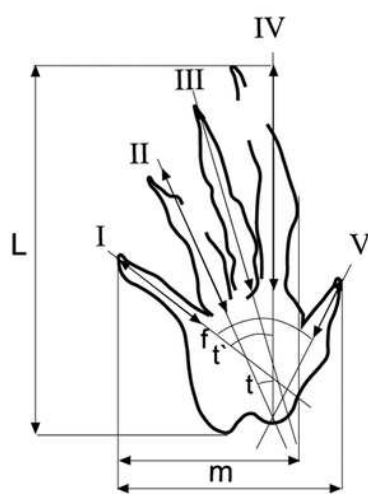
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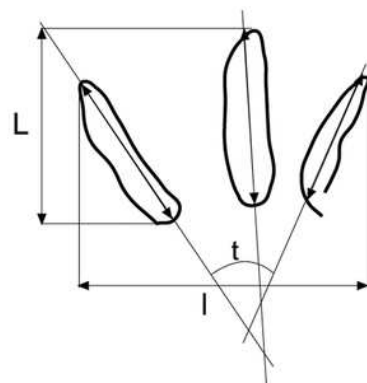
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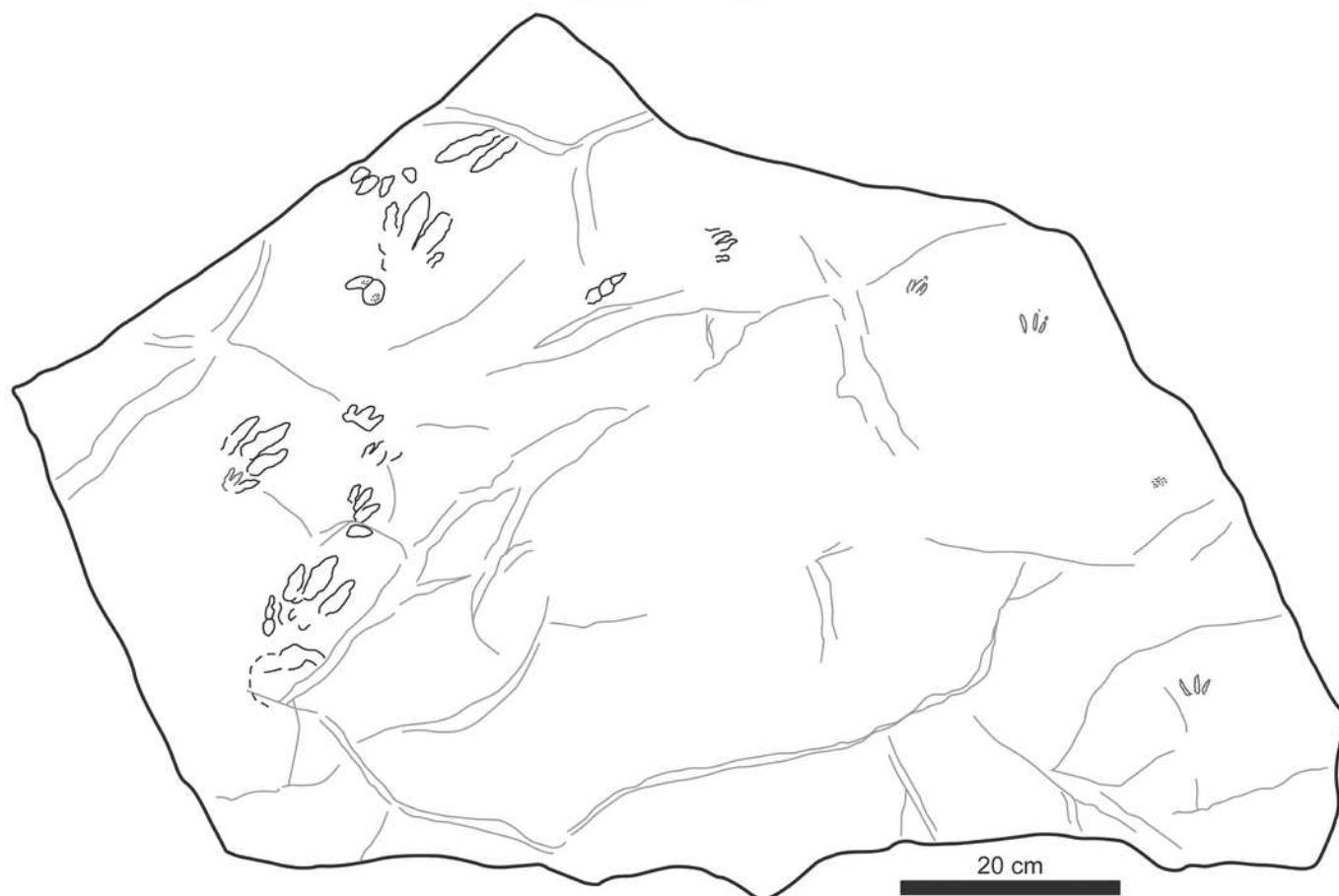
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Picture and sketch map of slab CS.DA.38

Figure 4. Picture and sketch map of slab CS.DA.38



Picture and sketch map of slab CS.DA.39

Figure 5. Picture and sketch map of slab CS.DA.39

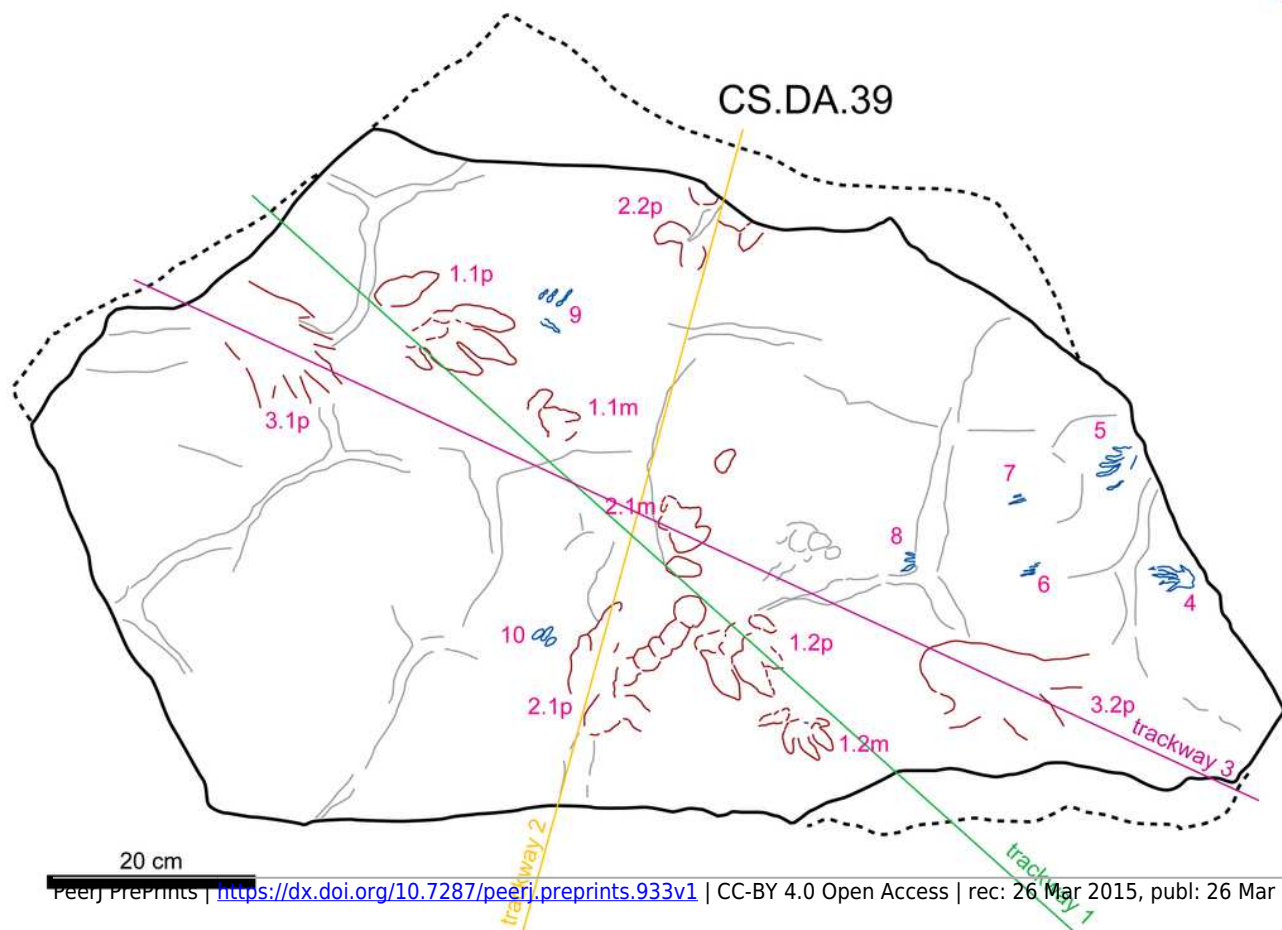
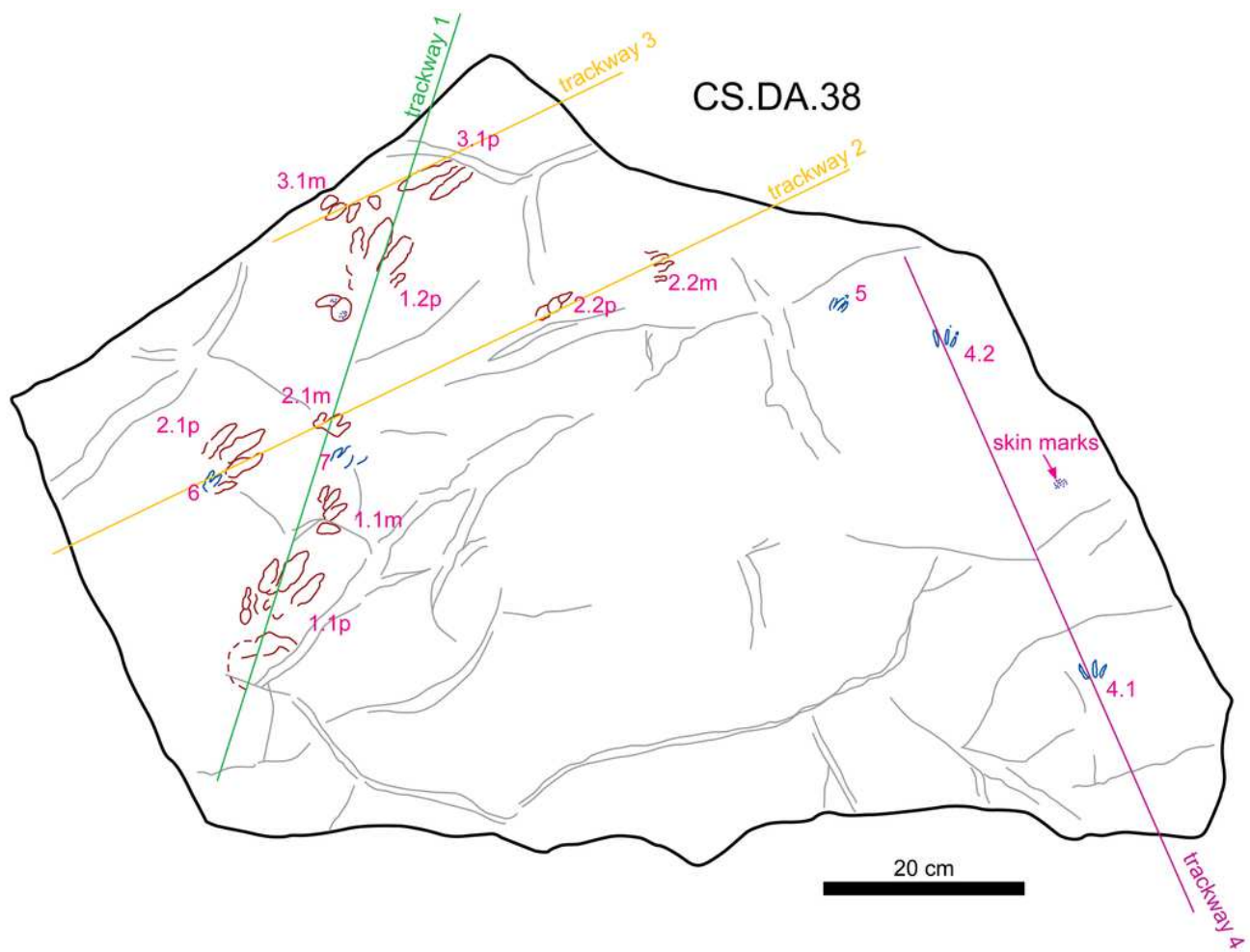


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Sketch map of slabs CS.DA.38 and CS.DA.39 with the acronyms of each track

Figure 6. Sketch map of slabs CS.DA.38 and CS.DA.39 with the acronyms of each track



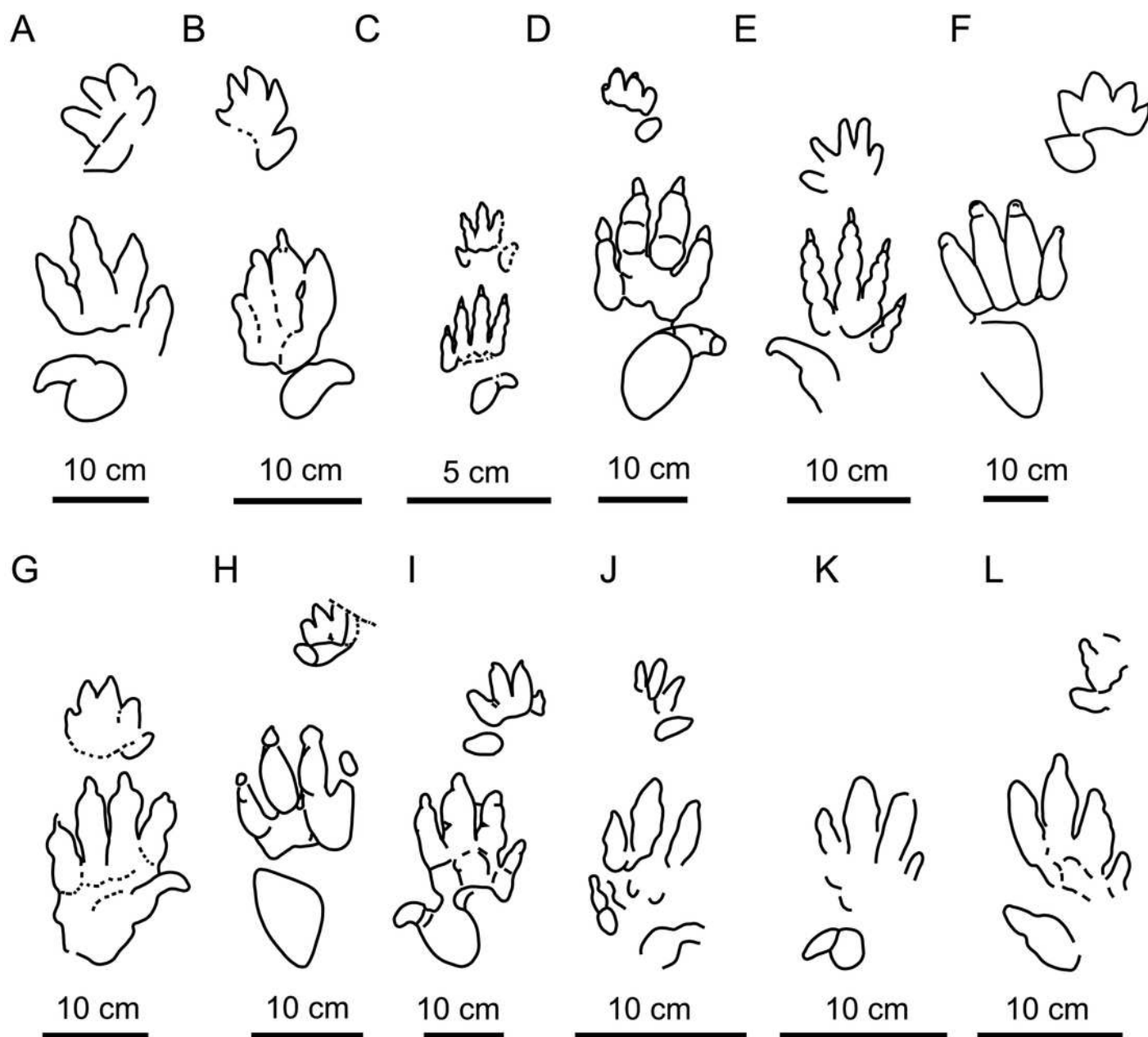
Pictures of the studied tracks assigned to *Chirotherium barthii*

Figure 7. Pictures of the studied tracks assigned to *Chirotherium barthii*. A: CS.DA.38.1.1p and CS.DA.38.1.1m. B: CS.DA.38.1.2p. C: CS.DA.39.1.1p. D: CS.DA.39.1.2m (see location in Fig.6).



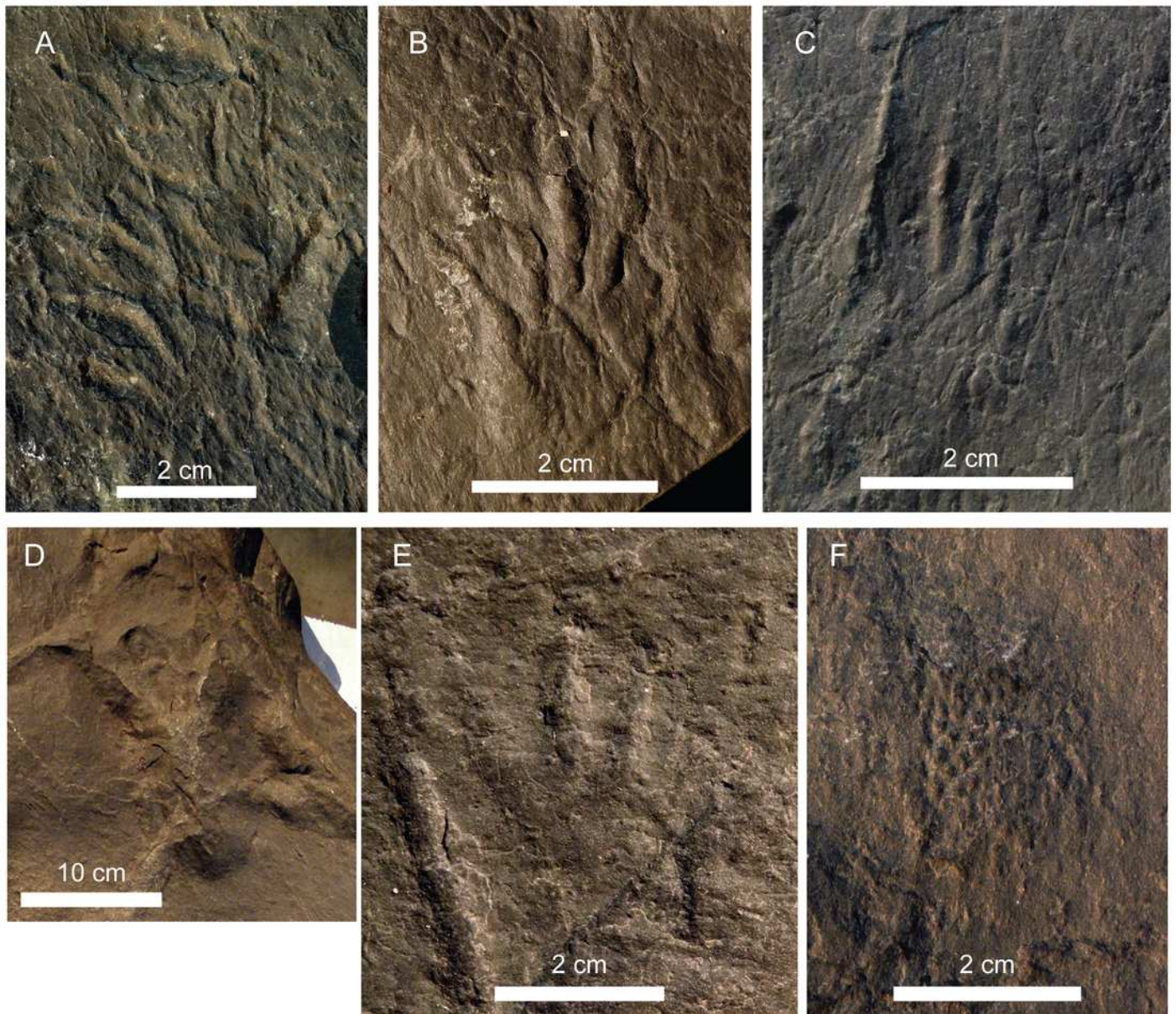
Main *Chirotherium* ichnospecies compared with the Navás site tracks.

Figure 8. Main *Chirotherium* ichnospecies compared with the Navás site tracks. A: *C. vorbachi* (redrawn from King et al., 2005). B: *C. sickleri* (redrawn from Haubold, 1971). C: *C. lulli* (redrawn from Baird, 1954). D: *C. lomas*i (redrawn from Baird, 1957). E: *C. storetonense* (redrawn from King et al., 2005). F: *C. rex* (redrawn from Peabody, 1957). G: *C. wondrai* (redrawn from Haubold, 1971). H: *C. coureli* (redrawn from Demathieu, 1970). I: *C. barthii* (redrawn from Haubold, 1971). J: CS.DA.38.1.1p. K: CS.DA.38.1.2p. and L: CS.DA.39.1.1p.



Photographs of the new identified material assigned to *Rhynchosauroides*, *Chirotheriidae* indet., undetermined material and isolated set of skin impressions

Figure 9. Photographs of the new identified material assigned to *Rhynchosauroides*. A: CS.DA.39 .9. B: CS.DA.39 .4. C: CS.DA.39.5. D: *Chirotheriidae* indet. (CS.DA.39.3.2p). E: Undetermined material (Unnamed Morphotype, CS.DA.38.4.1). F: Isolated set of skin impressions from the slab CS.DA.38 (see location in Fig.6).



Stratigraphic distribution of tetrapod track ichnotaxa and form groups in the Triassic with the global biochrons compared with the Iberian record

Figure 10. Stratigraphic distribution of tetrapod track ichnotaxa and form groups in the Triassic with the global biochrons recognized by Klein & Haubold (2007) and Klein & Lucas (2010a). The red lines represent the Iberian record based on Table 4. Abbreviations: *Atr.*, *Atreipus*; *Grall.*, *Grallator*; *Coelurosau.*, *Coelurosaurichnus*; *Dicy.*, *Dicynodont* tracks; *Prot.*, *Protochirotherium*.

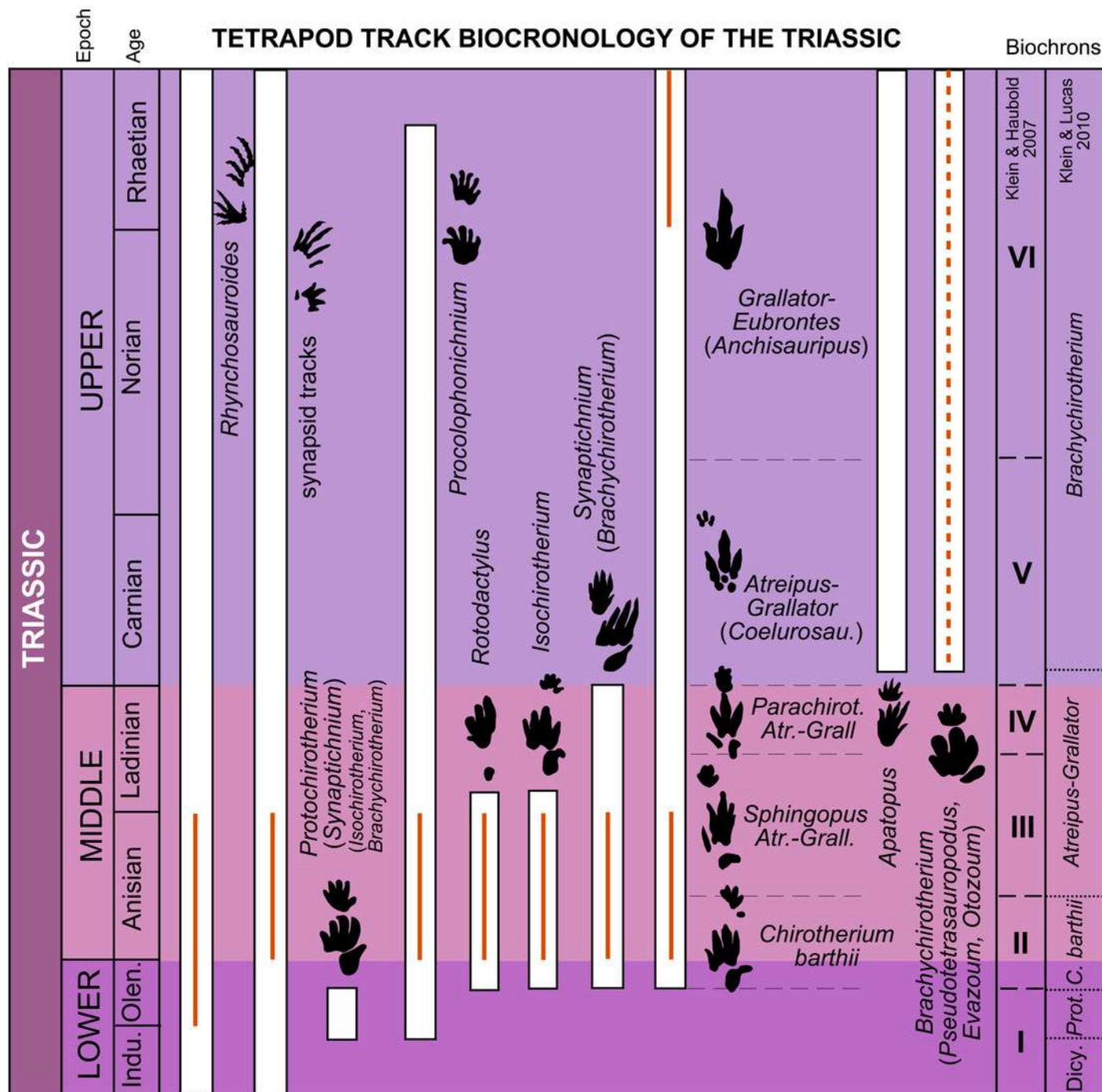


Table 1 (on next page)

Measurements of the *Chirotherium barthii* tracks from the Navás site.

Table 1. Measurements (in cm and degrees) of the *Chirotherium barthii* tracks from the Navás site. Abbreviations in Material and Methods.

	L	M	l	m	I	II	III	IV	V	t	t'	f	PL	pl	Apm	Dpm
38.1.1p	11.7	8	-	5.6	3.7	5.4	7.5	6.1	-	25	39	78	33.8	-	21	11.3
38.1.1m	4.7	3.3	-	-	-	1.4	2.3	2.8	2.3	45	-	-	-	-	-	-
38.1.2p	11.2	8	7.5	6.1	-	-	-	6.1	3.7	23	45	85	-	-	-	-
38.2.1p	-	-	-	-	-	3.7	5.2	4.2	-	20	28	-	35	-	30	11.8
38.2.1m	-	-	-	-	-	1.4	1.8	-	-	30	-	-	-	36	-	-
38.2.2p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*11.8
38.2.2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
38.3.1p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	*11.8
38.3.1m	4.7	2.8	-	-	-	1.4	1.8	2.4	1.8	41	-	-	-	-	-	-
39.1.1p	14.5	8.9	8.9	7.5	-	7.9	9.4	7.4	5.2	29	43	79	42	-	-	14.1
39.1.1m	-	-	-	-	-	-	-	3.3	2.8	-	-	-	-	38.5	-	-
39.1.2p	13.1	8.9	7.9	7.9	2.8	6.1	7.5	6.6	4.7	18	42	85	-	-	14	11.8
39.1.2m	5.6	4.2	6.1	4.7	1.4	3.3	3.8	3.3	3.3	33	65	145	-	-	-	-
39.2.1p	13.1	-	-	-	-	-	-	-	-	-	-	-	45.1	-	-	16.4
39.2.1m	6.1	-	-	-	-	3.3	4.2	4.2	3.7	48	-	-	-	-	-	-
39.2.2p	-	-	-	-	-	-	-	-	5.2	-	-	86	-	-	-	-

Table 1. Measurements (in cm and degrees) of the *Chirotherium barthii* tracks from the Navás site. Abbreviations in Material and Methods.

Table 2 (on next page)

Measurements of the *Rhynchosauroides* tracks from the Navás site.

Table 2. Measurements (in cm and degrees) of the *Rhynchosauroides* tracks from the Navás site. Abbreviations in Material and Methods.

	L	I	II	III	IV	t	PL
38.4.1	2	2.8	1.7	1.8	1.5	48	37
38.4.2	2.4	2.5	1.7	1.9	1.8	35	-
38.5	2.3	1.6	1.4	1.9	1.4	18	-
38.6	2.3	-	1.4	1.6	-	-	-
38.7	2.4	-	1.7	1.7	-	-	-
39.11	2	2.2	1.4	1.8	1.4	12	-

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5 Table 3. Measurements (in cm and degrees) of the undetermined tracks from the Navás site.

6 Abbreviations in Material and Methods.

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Table 3(on next page)

Measurements of the undetermined tracks from the Navás site.

Table 3. Measurements (in cm and degrees) of the undetermined tracks from the Navás site.

Abbreviations in Material and Methods.

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	L	I	m	I	II	III	IV	V	t	t'	f
39.4	4.6	2.7	2.4	1.6	2	2.5	2.8	0.8	10	50	78
39.5	-	-	-	0.9	1.7	2	2.6	-	15	30	-
39.6	-	-	-	-	-	-	-	-	-	-	-
39.7	-	-	-	-	-	-	-	-	-	-	-
39.8	-	-	-	-	-	-	-	-	-	-	-
39.10	4.6	-	-	-	1.3	1.7	2.3	2.2	13	-	-

3

4 Table 2. Measurements (in cm and degrees) of the *Rhynchosauroides* tracks from the Navás site.
5 Abbreviations in Material and Methods.

6

Table 4(on next page)

Summary of the published Triassic tracks from the Iberian Peninsula that are located in a concrete chronostratigraphic age.

Table 4. Summary of the published Triassic tracks from the Iberian Peninsula that are located in a concrete chronostratigraphic age. Only the most recent ichnotaxonomic determination is considered.

Iconotaxon	Age	Reference
<i>Dicynodontipus</i> isp.	Anisian	Valdiserri, Fortuny & Galobart (2009)
<i>Procolophonichnium</i> isp.	Anisian	Valdiserri, Fortuny & Galobart (2009)
<i>Rhynchosauroides</i> isp.	Anisian (Fortuny et al., 2012)	Calzada (1987)
<i>Rhynchosauroides</i> cf. <i>beasleyei</i>	Anisian (Fortuny et al., 2012)	Calzada (1987)
<i>Rhynchosauroides</i> isp.	Anisian	Valdiserri, Fortuny & Galobart (2009)
<i>Rhynchosauroides</i> isp.	Olenekian – Anisian	Gand et al. (2010)
<i>Rhynchosauroides</i> isp.	Anisian	Gand et al. (2010)
<i>Rhynchosauroides</i> isp.	Anisian	In this work
<i>Rotodactylus</i> sp.	Anisian	Valdiserri, Fortuny & Galobart (2009)
<i>Brachychirotherium</i> cf. <i>gallicum</i>	Upper Triassic?	Pérez-López (1993)
<i>Brachychirotherium gallicum</i>	Anisian	Gand et al. (2010)
<i>Brachychirotherium</i> isp.	Anisian	Gand et al. (2010)
<i>Chirtotherium barthii</i>	Anisian (in this work)	In this work
<i>Chirotheium barthii</i>	Anisian (Fortuny et al., 2012)	Calzada (1987)
<i>Chirotherium barthii</i>	Anisian	Valdiserri, Fortuny & Galobart (2009)
<i>Chirotherium barthii</i>	Anisian	Gand et al. (2010)
<i>Chirotherium</i> isp.	Anisian	Gand et al. (2010)
<i>Isochirotherium soergeli</i>	Anisian	Valdiserri, Fortuny & Galobart (2009)
<i>Isochirotherium</i> cf. <i>coureli</i>	Anisian	Gand et al. (2010)
<i>Synaptichnium</i> isp.	Anisian (Fortuny et al., 2012)	Calzada (1987)
<i>Synaptichnium</i> isp.	Anisian	Valdiserri, Fortuny & Galobart (2009)
Chirotheriid	Ladinian-early Carnian	Fortuny et al. (2012)
Chirotheriid	Ladinian	Meléndez & Moratalla (2014)
Chirotheriid	Anisian	In this work
<i>Eubrontes</i> isp.	Rhaetian	Pascual-Arribas & Latorre-Macarrón (2000)
<i>Anchisauripus</i> isp.	Rhaetian	Pascual-Arribas & Latorre-Macarrón (2000)
<i>Coelurosaurichnus perriauxi</i>	Anisian	Gand et al. (2010)
<i>Paratrisauropus latus</i>	Anisian	Gand et al. (2010)

Archosauria	Landian	Demathieu et al. (1999)
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Table 4. Summary of the published Triassic tracks from the Iberian Peninsula that are located in a concrete chronostratigraphic age. Only the most recent ichnotaxonomic determination is considered.