A new look at *Crocodylopodus meijidei*: implications for crocodylomorph locomotion

DIEGO CASTANERA,[1*] CARLOS PASCUAL,[2] JOSÉ IGNACIO CANUDO,[3] and
EDUARDO PUÉRTOLAS-PASCUAL[4,5]

[1]Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, c/
Escola Industrial 23, 08201 Sabadell, Barcelona, Spain;
[2]C. Real 65, 42002 Soria, Spain, capascual-1@telefonica.net;
[3]Aragosaurus—IUCA, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, 50009
Zaragoza, Spain, jicanudo@unizar.es;
[4]GeoBioTec, Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa, Caparica,
Portugal, eduardo.puertolas@gmail.com;
[5] Museu da Lourinhã, Lourinhã, Portugal

RH: CASTANERA ET AL.— *CROCODYLOPODUS MEIJIDEI* AND LOCOMOTION IN FOSSIL CROCODYLOMORPHS

* Corresponding author. Email: diego.castanera@icp.cat; dcastanera@hotmail.es

Color versions of one or more of the figures in the article can be found online at www.tandfonline.come.ujvp.

ABSTRACT—A review of the type material of the crocodylomorph ichnotaxon *Crocodylopodus meijidei* Fuentes Vidarte and Meijide Calvo, 2001 from the Berriasian of Spain is carried out. The review allows a better characterization of this type ichnotaxon and provides interesting new data on the candidate trackmakers and especially on their locomotion. Three different size classes possibly related to different ontogenetic states or sexual dimorphism of the same small to medium-sized crocodylomorph trackmaker are distinguished. Morphological differences within the sample such as digital impression lengths might be a consequence of differences in allometric growth, assuming similarities with extant crocodylians. Other differences are a consequence of variation in the morphological quality and mode of preservation across the sample. Some trackway features (intermediate-gauge trackways with high pace angulation, absence of tail, belly or drag marks) indicate the trackmakers, presumed neosuchian crocodylomorphs, were walking in a "high-walk" mode with a semi-erect posture at a moderate speed. The trackmaker may have walked with more erect limb posture and with the center of mass located more anteriorly than occurs in extant species, albeit not as erect as quadrupedal animals such as mammals or other extinct archosaurs including trackmakers of other crocodylomorph ichnotaxa (e.g., *Batrachopus*).

SUPPLEMENTAL DATA— Supplemental materials are available for this article at www.tandfonline.com/XXXX.

INTRODUCTION

Crocodylomorphs were an abundant component of vertebrate assemblages throughout the Mesozoic. For more than 220 million years from the Late Triassic to the present, crocodylomorphs have occupied a variety of habitats. Some clades contained completely aquatic or marine forms (e.g. Thalattosuchia and Tethysuchia), and others were fully terrestrial (e.g. Notosuchia, Sphenosuchia and Protosuchia), whereas many others (mainly Neosuchia) had a freshwater, semi-aquatic mode of life (Benton and Clark, 1988; Brochu, 2003; Pol et al., 2009; Bronzati et al., 2015; Wilberg et al., 2019). The crocodylomorph track record is relatively scarce compared with the osteological record, and only a few ichnotaxa attributed to crocodylomorphs have been described. Hitchcock (1845) was first to identify crocodylomorph tracks (*Batrachopus*) in the Lower Jurassic of the USA.Since then, the description of new tracks of extinct crocodylomorphs has increased considerably (see Milàn et al., 2010; Lockley et al., 2020; Kim et al., 2020; Masrour et al., 2020 and references therein) including several reports in the Iberian Peninsula (Vila et al., 2015; Segura et al., 2016; Castanera et al., 2021). Crocodylomorph tracks are well known from the Lower Jurassic to the Cenozoic (Klein and Lucas, 2010; Lockley and Meyer, 2004; Lockley et al., 2010b) with three main crocodylomorph ichnotaxa being the most significant in terms of the number of reports: *Batrachopus* (mainly Lower Jurassic - Cretaceous), *Crocodylopodus* (mainly Upper Jurassic- Cretaceous) and *Hatcherichnus* (mainly Upper Jurassic-Cretaceous, see Lockley et al., 2020; Kim et al., 2020; Masrour et al., 2020 and references therein). The ichnotaxon *Crocodylopodus meijidei* from the Huérteles Formation (Soria, Spain) is the type of the ichnogenus *Crocodylopodus* and is thus a key ichnotaxa during the Mesozoic (Fuentes Vidarte and Meijide Calvo, 2001). Since its description, new materials related to *Crocodylopodus* have been described, especially from Middle–Upper Jurassic and Lower Cretaceous localities of Morocco, Spain, Korea and Iran (Avanzini et al., 2007, 2010; Abbassi et al., 2015; Klein et al., 2018; Lockley et al., 2020). Recent studies are providing excellent information that aids our understanding of how extant crocodylians move and can help us interpret the stance and gait of extinct crocodylomorphs (Houck et al., 2010; Farlow et al., 2018a, 2018b; Hutchinson et al., 2019). Two features seen in trackways assigned to *Batrachopus* and *Crocodylopodus* that differ from extant ones are their narrowness (autopods located close to the trackway midline) and the absence of tail traces (Masrour et al., 2020; Lockley et al., 2020 and references therein), suggesting differences in limb posture during the locomotion.

The Lower Cretaceous Huérteles Formation in Soria is one of the key Mesozoic formations to understand the crocodylomorph footprint record, since several sites with crocodylomorph tracks have been reported (e.g.: Pascual Arribas et al., 2005; Hernández Medrano et al., 2008). During a review of the *Crocodylopodus meijidei* collection in the Museo Numantino de Soria (Spain), we noticed certain ichnotaxonomic issues related with the original description of the type material. Furthermore, the collection includes undescribed materials. The aims of this paper are multiple. Firstly, to review and describe all the *Crocodylopodus meijidei* material housed in the Museo Nunmantino de Soria (Spain). Secondly, to resolve the ichnotaxonomic issues and emend the diagnosis for the type material through comparisons with other tracks assigned to *Crocodylopodus*, other extinct crocodylomorph ichnotaxa, and extant crocodylian footprints. Thirdly, to reconstruct limb posture of the trackmaker based on trackway parameters. Finally, to provide an overview of the candidate trackmakers for *Crocodylopodus meijidei*.

Institutional Abbreviations—MNS, Museo Numantino de Soria (Numantine Museum of Soria), Spain.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The type material of *Crocodylopodus meijidei* comes from a site close to the El Frontal and Fuente Lacorte tracksites (Fuentes Vidarte and Meijide Calvo, 2001; Razzolini et al., 2014) located in the village of Bretún (Fig. 1), which lies within the region of Tierras Altas in the northern part of the province of Soria (Spain). The area has been well known from an ichnological point of view since the 1980s and especially since the geotourism project “Ruta de las icnitas de Soria” (Ichnite Route of Soria) was launched (see Hernández Medrano et al., 2008; Castanera et al., 2018 and references therein). Geologically, the Tierras Altas region is part of the eastern Cameros Basin. A detailed description of the geological setting of the El Frontal tracksite can be seen in Razzolini et al. (2014). In summary, these tracksites belong to the Huérteles Formation (Fig. 1), which is included in the Oncala Group as a part of depositional sequence 3 of the infill of the Cameros Basin (Gómez-Fernández and Meléndez, 1994a; Quijada et al., 2013; Mas et al., 2019). This formation comprises mainly siliciclastic deposits and was deposited in broad, low-gradient tidal flats, traversed by meandering channels (Quijada et al., 2013; but see also Gómez-Fernández and Meléndez, 1994b). The age of the Huérteles Formation is Berriasian according to ostracods and charophytes (Gómez-Fernández and Meléndez, 1994a; Schudack and Schudack, 2009; Mas et al., 2019). The slabs that preserved the crocodylomorph tracks are siltstones to very fine-grained sandstones.

MATERIALS AND METHODS

The material is housed in the MNS. The *Crocodylopodus meijidei* collection comprises 10 slabs: 2002/96/2bis, 2002/96/3, 2002/96/4, 2002/96/5, 2002/96/6, 2002/96/7, 2002/96/8, 2002/96/10, 2002/96/12, 2003/92/8. The acronym MNS precedes the registration number and refers to the museum. The word "bis" after the number is used by the museum to distinguish among registration numbers. Slab 2002/96/12 preserves one set of coupled manual and pedal tracks and one trackway made by different trackmakers, which are hereafter referred to the registration number plus t1 and t2, respectively. Slab 2003/92/8 preserves two trackways at the upper and lower surface of the slab (but it is unkown which surface is the base and which one the top); these are here after referred to as 2003/92/8a and 2003/92/8b. 2002/96/7 and 2002/96/8 are part and counterpart, as possibly 2002/96/10 and MNS2003/92/8b are as well. Fuentes Vidarte and Meijide Calvo (2001) proposed three holotypes (trackways MNS2002/96/2bis, MNS2003/92/8a and MNS2002/96/4), and as paratypes they proposed the set of coupled manual and pedal tracks MNS2002/96/3 and the "isolated footprints in the tracksite" (see Remarks section for clarification within the context of the ICZN rules).

We reviewed all the material housed at the MNS and took photographs of each slab with a Sony Alpha 5100. From sets of 20-48 pictures we constructed photogrammetric 3D models of each slab using the software 3DF Zephyr Free version 4.530 (https://www.3dflow.net/3df-zephyr-free/) and Agisoft Metashape Standard Edition. Subsequently, the 3D models were processed in CloudCompare (v.2.7.0) in order to obtain false-color depth maps. The photogrammetric 3D model of the lectotype is available for download in the Supplemental data, following the recommendations of Falkingham et al. (2018).

Measurements for individual tracks were taken (Fig. 2, Table 1, S1) for the footprint length (FL), footprint width (FW), the length (LI, LII, LIII, LIV, LV) and width (WI, WII, WIII, WIV, WV) of the digital impressions, interdigital impression angles (I^II, II^III, III^IV, IV^V) and manual–pedal impression distance (Dm–p). The total interdigital divarication was judged to be either low (IA < 30º), medium (30º-60º) or high (IA > 60º) on the basis of the published data for crocodylomorph footprints (extant and extinct). Individual digital impressions are referred to as DI, DII, DIII, DIV and DV. Trackway parameters were measured for pace length (PL), stride length (SL), pace angulation (PA, center of the footprint; ANG, tip of the impression of digit III), footprint rotation (FR), outer width of the trackway (OW). Heteropody was determined on the basis of the heteropody index (HI), calculated as HI = FL x FW of the manual impression/ FL x FW of the pedal impression x 100. The heteropody was accordingly considered either pronounced (HI < 35%), medium (35-70%) or low (HI > 70%) on the basis of the published data for crocodylomorph tracks. Masrour et al. (2020) recently characterized trackway gauge in crocodylomorphs on the basis of Ar/FW, where Ar is the distance from center of the track to the midline. We have used here the following categories: narrow (Ar/FW < 0.5), intermediate Ar/FW (0.5-1) and wide (Ar/FW >1). Measurements were taken from the 3D models using the software ImageJ. The morphological preservation (MP) of each specimen was calculated according to Marchetti et al. (2019) and following their recommendations only tracks with its MP scale values higher than 2 were used for ichnotaxonomy. The letters m and p are used in the description of each specimen and in the tables to distinguish between the manual and pedal tracks. ML refers to the trackway midline. The glenoacetabular distance was estimated following Leonardi (1987) and Farlow et al. (2018b). A review of the main crocodylomorph tracks suggested the following size classes on the basis of footprint length: small < 5 cm; medium 5-10 cm; large 10-20 cm; and very large > 20 cm. Data for comparisons among ichnotaxa were taken or estimated from the descriptions and outline drawings in the original publications.

SYSTEMATIC PALEONTOLOGY

Ichnogenus *CROCODYLOPODUS* Fuentes Vidarte and Meijide Calvo, 2001

Emended Diagnosis—star-shaped pentadactyl manual prints with slender digital impressions whose lengths vary as follows: III⩾ IV=II> V=I. Pedal track with digital impressions with the following length variations DIII> DII≥ DIV>DI. DIII is clearly the longest and DI the shortest. Interdigital divarication varies from medium to high. Pronounced to medium heteropody (HI = 30-40%). Manual tracks are laterally rotated whereas the pedal tracks are slightly medially rotated. Intermediate-gauge trackway. Absence of tail, belly or any other drag marks.

CROCODYLOPODUS MEIJIDEI Fuentes Vidarte and Meijide Calvo, 2001

(Figs 3, 6)

Lectotype— MNS2002/96/2bis

Paralectotypes— MNS2003/92/8a; MNS2002/96/4 (see descriptions in Supplemental Data).

Referred Specimens— MNS2002/96/3, MNS2002/96/5, MNS2002/96/6, MNS2002/96/7, MNS2002/96/8, MNS2002/96/10, MNS2002/96/12, MNS2003/92/8b (see descriptions in Supplemental Data).

Locality, Horizon, and Age—Bretún, close to the El Frontal tracksite (Soria), Huérteles Formation (Berriasian).

Diagnosis—as for the ichnogenus

Description— *MNS2002/96/2bis*. This specimen is one of the holotypes (Trackway A, fig. 1 and fig. A in Fuentes Vidarte and Meijide Calvo (2001) and is the holotype according to Lockley and Meyer (2004). The specimen (Fig. 3) includes four sets of coupled manual and pedal tracks (Fuentes Vidarte and Meijide Calvo, 2001, also draw one isolated manual print partially preserved at the beginning of the trackway that is not clearly identified here). The tracks are preserved as true tracks (or very shallow undertracks). Digital pads cannot be recognized but other details such as claw marks are clearly discernible. Some tracks (e.g. 3m) still preserve part of the overlying layer inside them. The MP value is quite variable (1–2.5) along the trackway, with manual-pedal set 3 (Fig. 3D, 3E) showing the highest MP (2.5). This is a small- to medium-sized specimen (Pedal FL= 4.6–5.1 cm; Pedal FW = 3.3–3.9 cm). The manual prints are pentadactyl, star-shaped and wider than long (FL = 1.5–2.2 cm; FW = 2.5–3 cm; FL/FW ratio = 0.6–0.75). The digital impressions are noticeably thin (WI-WV 0.3–0.4 cm), with an apparent acuminate end in the fifth digital impressions (no clear differences between DI-DIII and DIV-DV). DIII is the longest (1.7–2.2 cm), DII and DIV are slightly shorter and similar (but variable) in length, whereas DI and DV are the shortest and also of similar length. I^II is the lowest angle (36–41º), the other angles (II^III, III^IV, IV^V) being higher and variable (43–66º). The total divarication in the manual track is high (IA = 209º–218º). Generally, DI-DII and DIV-DV are oriented medially/antermedially and laterally/posterolaterally respectively, and DIII has an anterior orientation. DI and DV are to a large extent point in opposite directions. These orientations are variable because of the variability of the footprint rotation, which is lateral (15º–36º outwards) in all the manual prints. No clear claw marks are identified in the manual tracks. The pedal tracks are tetradactyl, subtriangular in shape, and longer than wide (FL/FW ratio =1.3–1.42). The central digital impressions (DII and DIII) are longer than the lateral and medial ones. Specifically, DIII is the longest (4.6–5.1 cm); DII (4.5–4.7 cm) and DIV (4.1–4.2 cm) are slightly shorter, with DII clearly longer than the latter. DI is the shortest, being considerably shorter (3.2–3.5 cm). The digital impressions are thin and of variable width (WI-WIV = 0.3–0.6 cm). The four of them have an acuminate end, showing clear evidence of claw marks associated with the first three digits, DIV having a less acuminate end as seen in 2p and 3p (Fig. 3D, 3E). No evidence of the claws digging into the substrate. The orientation of the digital impressions is medial (DI and DII), anteromedial (DIII) and anterolateral (DIV), with an average total divarication of 56–57º. I^II (10–15º) is the lowest angle, II^III (21–24º) and III^IV (18–24º) being quite similar. The heel impression is oval to subtriangular and quite symmetric, and is shallower than the anterior part of the footprint. Pedal rotation is low (8–20º) and medial (inwards). No clear evidence for the presence of webbing in both manual and pedal tracks. The trackway is intermediate-gauge (Ar/FW = 0.58-0.62). The trackway shows an irregular gait, which might be associated with a slight change in the direction of travel or some sinusoidal movement as a consequence of swaying during the walk cycle. The manual–pedal impression distance is short 3.8–4.5 cm. PL shows few variations, with relatively similar values between the manual and pedal tracks (9.5–11.6 cm). SL is also similar for both the manual and pedal tracks (17–20 cm). Pace angulation is high but variable (PA = 118–137º and ANG = 116–137º for the pedal tracks; PA = 105–140º and ANG = 102–129º for the manual tracks). The heteropody varies from pronounced to medium values, with HI varying from 21–33%. The lower values are related to the lower MP value of some manual prints (1mMP = 1.5, showing slightly collapsed sediment). The manual-pedal track ratio is approximately 1:3. The manual prints are deeper than the main area of the pedal prints, especially in the first two manual-pedal sets, the anterior part of the digital impressions having similar depth. There is no evidence of overprinting of the manual impression or of tail or belly drag marks. The estimated glenoacetabular distances range from 11.5 to 14.2 cm.

Remarks—Lockley and Meyer (2004) noted that three holotypes (Rastro A, B and C = MNS2002/96/2bis, MNS2003/92/8a and MNS2002/96/4, respectively) were designated in the original description by Fuentes Vidarte and Meijide Calvo (2001) and that such a procedure is not permitted by the ICZN, so they selected “Rastro A” as the holotype and designated “Rastro B” and “Rastro C” as paratypes. According to the ICZN, however, the holotype “can only be fixed in the original publication and by the original author” (Article 73.1.3). The ICZN thus recommends the designation of “a lectotype rather than (assuming) a holotype” (Recommendation 73F). Accordingly, here we designate specimen MNS2002/96/2bis (Fig. 3) as a lectotype. On the other hand, an “author who designates a lectotype should clearly label other former syntypes as “paralectotypes” (Article 74F), and we thus designate specimens MNS2003/92/8a (Fig. 4A-C) and MNS2002/96/4 (Fig. 4D-F) as paralectotypes. In the original diagnosis proposed by Fuentes Vidarte and Meijide Calvo (2001) and the revised diagnosis proposed by Lockley and Meyer (2004), we have found some issues that have led us to propose an emended one. Although Fuentes Vidarte and Meijide Calvo (2001) proposed MNS2002/96/3 and the isolated tracks in the tracksite as paratypes, these are not considered here to be the paralectotypes. This is because they 1) show some features that are slightly different from the lectotype and paralectotypes; 2) the MP value is rather low; and 3) they are isolated manual prints.

Fuentes Vidarte and Meijide Calvo (2001) suggested that the *Crocodylopodus meijidei* material was different enough to define the new ichnofamily Crocodylopodidae. Lockley and Meyer (2004) also noted the differences between Batrachopodidae and Crocodylopodidae (slenderness of the digital impressions on both the manual and pedal tracks, divarication angles, especially in the pedal tracks, pace angulation and footprint rotation), but judged that there were not enough differences to define a new ichnofamily. Accordingly, they included *Crocodylopodus meijidei* in Batrachopodidae Lull, 1904 and synonymized Crocodylopodidae with Batrachopodidae (Lockley and Meyer, 2004:177). The authors criticized the fact that

Fuentes Vidarte and Meijide Calvo (2001) had made a tri-level monospecific diagnosis for ichnofamily, ichnogenus and ichnospecies. Although the procedure might be not correct, *Crocodylopodus meijidei* does not fit in the revised diagnosis of Batrachopodidae proposed by Lockley and Meyer (2004) since they differ in several features; in tracks assigned to ichnotaxa within Batrachopodidae, for example, the digital impression lengths II and IV in the pedal tracks are generally not subequal in length, the manual prints do not show lateral rotation and the pace angulation is considerably lower (and the trackway is narrower). Kim et al. (2020:5) recently proposed that differences between *Batrachopus* and *Crocodylopodus* “may be explained in part by differential preservation”. Thus, many of the differences between the two ichnotaxa are likely to be a consequence of differences relating to the different modes of locomotion of their respective trackmackers rather than just preservational factors.

DISCUSSION

Morphological Variations in the Type Material of *Crocodylopodus meijidei*

The sample shows some differences among the various specimens, which are related to divergent MP values (variation from 0.5 to 2.5) and the mode of preservation of the tracks (either as epireliefs or hyporeliefs). Differences in the size of various tracks across the sample suggest that they were produced by different individuals. The lectotype (MNS2002/96/2bis, Fig. 3) and paralectotypes (MNS2003/92/8a and MNS2002/96/4, Fig. 4) as well as MNS2003/92/8b and MNS2002/96/10 (Fig. 5D-I) and MNS2002/96/12t1 (Fig. 6A-C) are more or less similar in size and fall between the small and medium-sized categories. The similarities among the values of these specimens raise the hypothesis that some of them could even be parts of the same trackway or produced by the same individual. The former two have a pedal FL (see Table 1 and S1) of around 5 cm, whereas the latter four have lower pedal FL (close to 4 cm) but lack the preservation of the heel mark (so all of them can be considered medium-sized). This similar size is corroborated by a similar pedal FW (close to 4 cm) and similar FL (around 2 cm) and FW (between 2.5 and 3 cm) in the manual track among all the specimens. MNS2002/96/7 and MNS2002/96/8 (Fig. 6E–6F) also fall within this medium-sized category (manual FL around 2 cm). Since MNS2003/92/8a and MNS2003/92/8b are preserved in the same slab, they represent two different trackways (and slightly different stratigraphic levels). These data indicate that there are at least two different trackmakers that fall within the medium-sized category. MNS2002/96/3 (Fig. 5A-C) is the largest specimen (Pedal FL = 7 cm), whereas MNS2002/96/5 (Fig. 6D) is a manual print that is similar in size to the manual track of MNS2002/96/3. Thus, there is at least one other medium-sized (but larger) trackmaker. MNS2002/96/12t2, is the smallest track (Pedal FL = 2.5 cm) in the whole sample, and represents one trackmaker of the small-sized category. Accordingly, there were at least four different individuals: a small individual (MNS2002/96/12t2), at least two medium-sized individuals (MNS2002/96/2bis, MNS2003/92/8a, MNS2003/92/8b, MNS2002/96/10, MNS2002/96/4, MNS2002/96/12t1; MNS2002/96/7-MNS2002/96/8), and at least one medium-sized but larger individual (MNS2002/96/3 and MNS2002/96/5).

The lectotype (Fig. 3, MNS2002/96/2bis), one of the paralectotypes (Fig. 4A-C, MNS2003/92/8a), and the pedal impression in MNS2002/96/3 (Fig. 5A-C) are those with high MP values. Interestingly, the manual tracks generally have higher MP values than the pedal tracks and in many specimens are deeper (similar depth just to the anterior part of the pedal impression). MNS2002/96/3 is the only specimen that has a clearly deeper pedal than manual impression. Other major morphological differences among the specimens are related to the preservation, such as the presence/absence of a heel impression, slight variations in heteropody, variations in interdigital divarication angles (from medium to high), or the manual impression sometimes seeming tridactyl/tetradactyl instead of pentadactyl. Specimens preserved as natural casts have lower MP values; the claw marks are not clearly identified; the divarication angles are higher; and the length of DI and DIV in the pedal impressions are more similar, but this might be a consequence of the absence of the heel mark impression and thus it is difficult to measure correctly.

Other considerable differences among the specimens are the relative lengths of the digital impressions. Padian and Olsen (1984) warned of the possible allometric changes in footprints from ontogenetic and phylogenetic aspects. Possible differences due to allometric growth were proposed for *C. meijidei* by Lockley and Meyer (2004: 176), who, on the basis of the sketches by Fuentes Vidarte and Meijide Calvo (2001), calculated a lower heteropody for MNS2002/96/3 (the largest) and proposed “an allometric increase in the relative size of the pes during growth”. According to our data, the heteropody in specimen MNS2002/96/3 is dubious because of the low MP value of the manual print, but our estimated values are not very different from the lectotype (HI = 29% and 28–33%) or from the other specimens (see Table S1). What is more intriguing is that on MNS2002/96/3, the impression of digit IV is of similar length to the impression of digit II, a feature not apparent in the other medium-sized but smaller specimens. This specimen is slightly larger (2 cm longer in FL) than the others, but these differences among the specimens could be explained by possible ontogenetic differences as a consequence of allometric growth (cf. Lockley and Meyer, 2004). Notably, Farlow and Britton (2000:189) pointed out possible changes in autopodial lengths with body size in *Alligator mississippiensis* (“with increasing body size, hind limb and autopodial lengths become shorter relative to the shoulder-hip length and the pes become shorter”).

Subsequently, Farlow (2018) analyzed the proportions of pedal skeletons in alligators, suggesting that young alligators posess relatively longer digits and feet than adult specimens. Assuming proportional changes during growth similar to those of an extant species such as *Alligator mississippiensis*, the possibility of variations in digit proportions should be taken into account when analyzing *C. meijidei* material. A comparison of the foot proportions reveals the FL/FW ratio in the pedal impression of MNS2002/96/3 (1.25) to be slightly lower than in the lectotype (1.3–1.42) but within the range of variation seen in the paralectotype MNS2003/92/8a (1.19–1.3). Moreover, the other specimens with low MP values also show lower values for the FL/FW ratio. Thus, we consider that these differences in relative size are not very significant. A comparison of the relative lengths of the digital impressions in MNS2002/96/03 (DI, DII, DIII, DIV = 0.68, 0.9, 1, 0.88), the lectotype (3p; DI, DII, DIII, DIV = 0.62, 0.9, 1, 0.88) and the paralectotype (2p; DI, DII, DIII, DIV = 0.72, 0.9, 1, 0.8) shows the relative lengths of the digital impressions are very similar, except for the DI. The MP value of the smallest specimen (MNS2002/96/12t2) is rather low and DIV is not preserved, so a comparison of the FL/FW ratio and the fourth digital impression is not possible. However, the other three digital impressions (B1p; DI, DII, DIII = 0.6, 0.84, 1) show some difference in DI, although smaller in DII. These differences between lengths in digital impressions might be explained by allometry.

Another possible explanation for these differences between relative lengths of the digital impressions, especially between MNS2002/96/3, the lectotype (3p) and the paralectotype (2p), which are the specimens with the highest MP values, might be just preservational factors. Extant crocodylian pedal prints show claw marks in digits I, II and III that sometimes dig into the substrate, thus not reflecting real anatomical lengths (Farlow et al., 2018b). Furthermore, the absence of a claw mark in digit IV might also produce differences in relative digit lengths, since this digit may be less clearly marked in the sediment. Other possible differences could be associated with different kinematics and behavior during locomotion, but these are more difficult to analyse across the sample since there are only a few short trackways. For instance, there are slight variations in the trackway gauge (narrower in the lectotype than in the paralectotypes) that are common in other quadrupeds (e.g. Castanera et al., 2012). The narrownes of the lectotype might be caused by a slight change in direction or with the swaying as a consequence of the lateral movement (Carpenter, 2009) rather than by different speed, since the stride lengths are very similar in all three specimens. The manual-pedal distances are also similar among the specimens (3.5–4.5 cm), although in the largest specimen it is slightly larger (9 cm). An alternative explanation for the size classes might be sexual dimorphism since in extant crocodylians adult males can be 20–40% larger than adult females. This difference is more marked in larger than in smaller species where this difference is not as pronounced or even females can be slightly larger (Thorbjarnarson, 1994; Cox et al., 2007; Platt et al., 2009; Hone et al., 2020).

In summary, the *C. meijidei* type material shows a series of morphological differences among specimens that can be mainly explained in terms of two different factors: 1) different ontogenetic states (variations in lengths of the digital impressions and size differences); 2) differences in the preservation of the specimens (e.g., natural cast vs true tracks, absence/presence of heel mark impressions, absence/presence of claw marks, absence/presence of certain digital impressions associated with both the manual and pedal tracks). Besides, possible differences due to sexual dimorphism (size variations) and kinematics and behavior during locomotion (variations in certain features or parameters) may have also played a role.

Comparisons with Other Tracks Assigned to *Crocodylopodus*

A comparison of *C. meijidei* with other *Crocodylopodus* material is necessary to understand possible variations (Fig. 7, Table S2). The oldest *Crocodylopodus* reports are from the Middle Jurassic of Iran (Abbassi et al., 2015) and the Middle-?Upper Jurassic of Morocco (Klein et al., 2018). Abbassi et al. (2015) reported a small-sized trackway classified as *Crocodylopodus* isp. (Fig. 7B). This trackway differs from *C. meijidei* in a number of ways. Firstly, the manual morphology, which is tetradactyl with the four digital impressions anteriorly directed. Secondly, the pedal track differs in having a rounded heel impression. The trackway also preserves tail drag impressions. Klein et al. (2018) described medium-sized tracks assigned to *C. meijidei* (Fig. 7C) from the Middle-?Upper Jurassic of Morocco. They display considerable differences in the pedal impressions, such as widely divaricated digital impressions, an elongated heel, and differences in relative lengths of the digital impressions. The manual prints are also star-shaped, but DI and DV are not located as posteriorly as in the type of *C. meijidei*. Upper Jurassic beds of the Asturian basin of the Iberian Peninsula have also produced material related to *Crocodylopodus* (Avanzini et al., 2007; 2010). Among these tracks, MUJA 0101 is small-sized (Fig. 7F) and mainly differs from *C. meijidei* in the digitigrade pedal impression, with lower FL/FW ratio, lower interdigital divarication, evidence of drag marks or the absence of manual impression. MUJA 0102 is small in size (Fig. 7G–7H) and main differences include the preservation of phalangeal pads in the pedal impressions and the manual prints generally tridactyl, showing almost no rotation. *C. meijidei* bears some similarities to MUJA0038, a large-sized specimen (Fig. 7D) which pedal impression has digital impressions II and IV subequal in length (and shorter than DIII) and extremely widely divaricated. But the heteropody of this specimen is slightly lower. Avanzini et al. (2010: 243) also studied other specimens and considered that the Asturian samples "show similar characteristics, which are consistent with a substrate-related morphological variation within the *Crocodylopodus meijidei* ichnospecies”. Recently, Castanera et al. (2021) reported one isolated pedal track from the Upper Jurassic of the Lusitanian basin (Fig. 7E) assigned to *Crocodylopodus* isp. in which the differences from *C.meijidei* were in the lower FL/FW ratio and the wider digital divarication angle, and slightly differences in the length of the digital impressions.

To turn to the Cretaceous occurrences of tracks related to *Crocodylopodus*, Pascual Arribas et al. (2005) described a large-sized crocodylomorph trackway (Fig. 7I) from the same formation as *C. meijidei* that was subsequently classified as cf. *Crocodylopodus* by Lockley et al. (2010a) and ?*Crocodylopodus* by Lockley et al. (2020). The tracks show considerable differences in the pedal impressions, which have digital pads, lower FL/FW ratio, are laterally rotated, have slightly lower digital divarication, and DII and DIV are similar in length. No clear tail marks exist, although the authors describe some traces that could be tail marks. Another large sample of *Crocodylopodus* tracks has recently been described from the Lower Cretaceous (?Aptian) of Korea (Lockley et al., 2020). The authors describe several small to medium-sized trackways (Fig. 7J–7M) that show several features that are different from *C. meijidei* especially the FL/FW ratio (varies in the Korean specimens), the relative digital impression lengths and their orientation (more anteriorly oriented), heteropody (much lower in the Korean specimens), the lower pace angulation and wider-gauge trackway than in *C. meijidei*. These trackways also show no evidence of tail drag marks. Only two possible reports of *Crocodylopodus* tracks have been described in Upper Cretaceous deposits. Simpson et al. (2010) describe a single large-sized pedal track classified as cf. *Crocodylopodus* from the Upper Cretaceous Wahweap Formation of Utah. The authors suggest that the track is indistinguishable from *Crocodylopodus,* although they also note differences in robustness and consider the specimen to be reminiscent of *Hatcherichnus* as well. Recently, Lockley et al. (2020) have proposed that it could be assigned to *Hatcherichnus* or cf. *Hatcherichnus*. Noteworthy differences are the orientation of the digital impressions (more anterior), relative lengths in digital impressions and the rounded heel impression. Finally, Vila *et* al. (2015) report a single small-sized track (Fig. 7N) classified as cf. *Crocodylopodus* from the Upper Cretaceous of Spain. This is an isolated pedal track that shows similarities in the symmetrical and triangular heel impression but also shows differences in that DIV seems longer than DII and has a very lateral orientation thus showing high intedigital divariaction.

As expounded in the previous paragraphs and shown in the Table S2 there are considerable differences among the tracks assigned to *Crocodylopodus*. Main differences are in manual impression morphology (which varies from tridactyl to pentadactyl), in the pedal impressions (FL/FW ratio, the length of digital impressions, heel morphology or in digital divarication) and in heteropody (variation from pronounced to medium). Some of these morphological variations are a consequence of possible anatomical differences that might also be ontogenetically influenced, as noted above. Nonetheless, as specified by Avanzini et al. (2010), many differences can be related to the state of the substrate and the preservation, such as variations in digital impressions (e.g., slender or stout), absence of certain digital impressions, digital divarication (higher in soft substrates), the morphology of the heel mark impression (from rounded to triangular but sometimes absent) that affect variations in FL/FW ratio, and the absence/presence of scale marks. Finally, other characters are linked to the locomotion (see next sections). These are the narrowness/width of the trackway, absence/presence of tail drag marks, lateral/medial rotation of the footprints. Taking into account the differences set forth in this section, the influence of substrate, locomotion and anatomical differences, and given the variation seen in the type material of *C. meijidei* and in the other *Crocodylopodus* tracks, it is difficult to ascertain whether *C. meijidei* is a monospecific ichnotaxon, or whether some of the tracks referred to *Crocodylopodus* might be a different ichnospecies from that represented by type material. Thus, the variations seen among the samples and in many cases the poor morphological quality of the specimens or the absence of abundant material justifies previous asignments taken by other authors who have classified (see references in Table S2) some tracks either as cf. *Crocodylopodus* isp. or *Crocodylopodus* isp. It is noteworthy that no unequivocal reports of *Crocodylopodus* have been reported from the Upper Cretaceous (see Table S2) and that many of the specimens not classified to ichnospecies level are medium to large sized often with wide gauge trackways (Table S2). All the material assigned to *C. meijidei* is produced by small to medium-sized individuals, and are (with the exception of one report from Morocco, Klein et al. 2018) restricted to the Upper Jurassic and the Lower Cretaceous (Berriasian) of the Iberian Peninsula. Thus, there is the possibility that more than one ichnospecies may exist taking into account differences in size, FL/FW ratio, heteropody or type of trackway although currently there are not enough data (see discussion) to distinguish between them.

Comparisons with Other Crocodylomorph Ichnotaxa

Crocodylopodus is clearly distinct from the other crocodylomorph ichnotaxa. Kim et al. (2020) recently summarized which crocodylomorph ichnotaxa comprise walking traces and which comprise swimming traces. *Crocodylopodus* is clearly distinct from all the ichnotaxa that represent swimming traces (e.g.: *Hatcherichnus* Foster and Lockley, 1997; *Kuangyuanpus* and *Laiyangpus* Lockley et al., 2010a; *Albertasuchipes* McCrea et al., 2004; *Indosuchipes* Rajkumar et al., 2015 and *Anticusuchipes* Mustoe, 2019). Of all the crocodylomorph ichnotaxa, it is interesting that only *Batrachopus* and related ichnotaxa (e.g.: *Antipus* Coombs, 1996 and *Angolaichnus* Mateus et al. 2017), *Crocodylopodus* and *Mehliella* represent walking traces (Fig. 8). The main differences between *Batrachopus* (Fig. 8B) and *Crocodylopdus* are the lower heteropody, wider pedal impression, more slender and divergent digital impressions, lower lateral rotation of the pedal impressions and greater lateral rotation of the manual prints in *C. meijidei*. Besides, in *Batrachopus* the digital impressions are straight, and the interdigital divarication angles for the pedal tracks are very low (25º–30º in the type specimen). Another notable morphological difference is the mark of digit V (when present) in the pedal impression and generally narrower gauge trackway in *Batrachopus* (Olsen and Padian, 1986; Lockley and Meyer, 2004; Masrour et al. 2020). Olsen and Padian, (1986) considered *Antipus* a synonym of *Batrachopus*, although this view has not been adopted by other authors (Coombs, 1996; Lockley and Meyer, 2004). *C. meijidei* differs from *Antipus* (Fig. 8C) in the pedal (shorter DI impression and lower digital divarication in *Antipus*) and manual morphology (DI-DV medially/laterally in *Antipus*) and the lateral rotation of both manual (strongly rotated in *Antipus*) and pedal prints. *Angolaichnus* from the Lower Cretaceous of Angola (Mateus et al., 2017, Fig. 8D) is also different showing a manual impression that is functionally tetradactyl and plantigrade with extreme lateral rotation, and a pedal impression with different digital impression lengths, DIV being the shortest. It also has different interdigital divarication (lower in *Angolaichnus*), digit orientation (digits II and III being bent slightly lateral) and higher pace angulation. *C. meijidei* is also clearly different from *Mehliella* (Mehl, 1931; Lockley, 2010, Fig. 8G) which is characterized by tracks larger in size, the wider trackway, with a very low pace angulation (50º), and with clear tail or belly traces. Besides, it may also shows interdigital webbing traces.

Main differences among crocodylomorph ichnotaxa are in manual/pedal morphology, lengths of digital impressions in the pes, heteropody, footprint rotation or trackway gauge. Differences in certain features could be explained by substrate-related factors (e.g. slender and divergent digital impressions, digit orientation, absence/presence of webbing). Nonetheless, several differences among the ichnotaxa at the ichnogenus level are better explained by anatomical factors (heteropody, digit divarication, the presence/absence of digital impression V) and especially locomotor and behavior factors (rotation of the footprints, mode of locomotion, swimming/subaqueous behavior, low walk/slow high walk). Although Kim et al. (2020) note that differences between *Batrachopus* and *Crocodylopodus* might be preservation-related, we consider that major differences between them are related to different locomotor modes employed by their respective trackmakers reflected in, the trackway gauge, pace angulation and footprint rotation.

Comparisons with Tracks of Extant Crocodylians and notes on the Mode of Locomotion

Regarding the tracks of extant crocodylians there are considerable differences from *Crocodylopodus* tracks. A summary of trackway features in extant crocodylians is provided in Table S3 and sheds interesting light on the interpretation of certain features. In a general comparison it should be noted: manual imprints generally have DI and DV located more medially/laterally (lower interdigital divarication) with claw marks in DI-DIII, a feature not clearly seen in *C. meijidei* (preservation bias?). Pedal impressions show differences in the length of the digital impressions with the central digits (DII and DIII) being the longest but DI and DIV being more similar in length and slight variations in the orientation of the digital impressions. Besides, several extant species show lower interdigital divarication values than those of *C. meijidei*, these being more similar to members of Alligatoridae (higher values) than to Crocodylidae (Milàn and Hedegaard, 2010; see Table S3). These variations in interdigital divarication in both manual and pedal impressions might be related to the development of webbing between extant crocodylians and the trackmaker of *C. meijidei* (it would have reduced interdigital webbing) and may also explain the variations seen in

Crocodylopodus tracks from the different areas (Table S2). Trackways of extant crocodylians differs from that of *C. meijidei* in the presence of tail, belly and drag marks, wider-gauge trackways (with lower pace angulation), pedal prints deeper than the manual impressions, and overprinting of the manus by the pes.

Some of the differences are anatomical (e.g., interdigital divarication angles, DIV in the pes more laterally located, relative digital impression lengths, webbing development), whereas others might be just preservational (e.g., the presence/absence of scale prints and webbing, evidence of clear claw marks, the orientation of the digits). Many of the main differences are associated with locomotion and possible differences in gait (e.g., pedal impressions deeper than the manual, DI and heel deeper than the rest of the pedal impression, lower pace angulation and wider trackways, belly and tail drag marks). The locomotion of some extinct crocodylomorphs is different from that of extant taxa. For example, the earliest members of Crocodylomorpha walked with an erect limb posture that fits well with their terrestrial habits (Parrish, 1987; Salisbury and Frey, 2001; Molnar et al., 2015). On the other hand, extant crocodylians use a variety of gaits: the belly walk, the high walk, and galloping. Thus, in terms of locomotor posture, extant crocodylians fall between early sprawler reptiles and erect dinosaurs and birds (Zug, 1974; Parrish, 1987; Gatesy, 1991; Reilly and Elias, 1998; Hutchinson et al., 2019). Parrish (1987:396) suggested that the “sprawling stance used by extant crocodylians can be viewed as a secondary adaptation to an aquatic existence”. Reilly and Elias (1998:2559) pointed out that the crocodylian sprawl is not equivalent to the primitive sprawling (seen in other reptiles), being “a lower version of a high walk”. Accordingly, they named it “low walk” and suggested that crocodylomorphs do not change from “a primitive sprawling posture to an intermediate semi-erect posture”, arguing that “crocodilian low and high walk behaviors are not intermediate forms in the sprawling-to-erect continuum”. Houck et al. (2010) summarized the features that characterized high-walking and low-walking in extant crocodylian trackways. In the particular case of *Crocodylopodus* trackways, many of these show the features described in the high-walking trackways (see table 3 in Houck et al., 2010), although they also show some differences, such as a higher pace angulation, the absence of tail and foot drag marks, and infrequent pes/manus overprinting.

In recent years, advances have been made in studies of the limb posture and gait of extinct archosaurs by analyzing the pace angulation of both fossilized and recent trackways (Kubo and Benton, 2009; Kubo and Ozaki, 2009). Kubo and Benton (2009) argued that the erect limb posture likely evolved during the Early Triassic, as the average pace angulation value of the trackways underwent a major increase during this epoch. Kubo and Ozaki (2009) demonstrated how pace angulation can be used to estimate limb posture and its relation with the femoral abduction angle and pelvic rotation. Their analysis of locomotion in species of extant crocodylians and lizards provided them how to reconstruct the limb posture in extinct tetrapods. Differences in limb abduction are directly related to the pace angulation, which also reflects differences in stride length and trackway width. Accordingly, an erect animal would leave a trackway with a high pace angulation, whereas a sprawler would produce a trackway with a low pace angulation. Kubo and Ozaki (2009) thus suggested that femoral abduction has more influence on pace angulation than pelvic rotation does (high PA values cannot be explained only by pelvic rotation) and that speed has less significant influence, although the fact that only walking gaits were analyzed in that study may have affected the result. They reasoned that “a trackway with an average pace angulation value of 120° or more could not be produced by a trackmaker that is a true sprawler”. The authors also estimated that “at values of 108° the predicted range of the femoral abduction angle did not include 0” (Kubo and

Ozaki, 2009:58). This implies that a trackway with an average pace angulation value of 108º or less is unlikely to be produced by an animal with fully erect limbs in which the femoral abduction angle is 0º.

Interestingly, the pace angluation values for *Crocodylopodus* trackways are very close or higher than this threshold value of 108º (Tables 1, S1 and S2), an exception being the trackways from Korea (Lockley et al., 2020, see Fig. 7J–7M). Avanzini et al. (2007, 2010) already noted the high PA values for the tracks from Asturias and related them with different styles of walking, during which the pace angulation is higher (and the resultant trackway narrower) when speed increases. Tracks assigned to *Batrachopus* (Lockley et al., 2018; Kim et al., 2020; Masrour et al., 2020) or included in Batrachopodidae (e.g. *Angolaichnus,* Mateus et al., 2017) have even higher PA values than *Crocodylopodus* trackways. Regarding the data for extant species the PA values (Table S3) are generally lower (variation between 75º and 120º in different species) than in *Crocodylopodus* trackways, the values of most of the studied specimens being close to the upper range of the values of extant crocodylians. Variations in pace angulation can be influenced by a series of factors such as posture, speed, body sized and thus ontogeny and body mass or the hip and knee joint excursions or the lateral movement of the body (Kubo, 2008; Kubo and Benton 2009; Carpenter, 2009; Kubo 2010). Kubo and Benton (2009:1033) also suggested "body size could be an important factor in determining pace angulation since modern sprawlers are small and modern erect animals are generally relatively large". Notably, Salisbury and Frey (2001) indicated that the greater the mass of an animal, the more difficult sustained highwalking is likely to become. Thus, "large (>three metre) extant crocodilians often seem reluctant to carry their own weight on land, and sustained terrestrial locomotion appears to be a labour, only undertaken in moments of extreme urgency or alarm" (Salisbury and Frey 2001:120). Although there are several anatomical features that exert an influence but cannot be known directly from the trackways (e.g. lateral body movement, hip and knee joint excursions), the *Crocodylopodus* tracks were produced by small to medium-sized crocodylomorph trackmakers and ontogeny is not a factor influencing the PA data in the type material since the four reported trackways have similar pedal lengths, suggesting a small to medium-sized trackmaker. Despite the high PA values in *C. meijidei*, it should be borne in mind that they are far from the values of completely erect animals such as mammals, birds and other archosauromorphs, which have values generally higher than 140–150º including several trackways assigned to *Batrachopus* (see Kubo and Benton, 2009; Masrour et al., 2020). These variations in pace angulation are directly related with the variations seen in trackway gauge seen in extinct crocodylomorph ichnotaxa where *Crocodylopodus* trackways are characterized by intermediate-gauge trackways that are narrower than extant crocodylians and some extinct crocodylomorph ichnotaxa such as *Mehliella* but wider than *Batrachopus* (see Masrour et al., 2020). These data suggest different postures during locomotion among extinct crocodylomorphs.

As regards the absence/presence of tail marks in crocodylomorph trackways, their absence is noteworthy in all the *Crocodylopodus* trackways described in the literature (except the one described by Abbassi et al., (2015)). Avanzini et al. (2007:151) suggested that this absence of tail marks "suggests complete support of the whole-body during walking". Comparison with trackways of extant species reveals that many of the trackways described have tail marks (Fig. 8F, Table S3). McCrea et al. (2004) noted that the absence of tail drag marks could be a consequence of a variety of factors such as behavior, gait and the consistency of the substrate, as well as the possibility that the animal was walking or wading underwater (with floating tail). From a biomechanical point of view, tails provide semi-aquatic tetrapods with propulsion during swimming, although they can compromise terrestrial locomotion, as they have to be dragged. In extant crocodylians such as *Alligator mississippiensis* the tail weight represents 28% of the total body mass (Willey et al., 2004). In consequence, both the fore and hindlimbs have to counteract the tail's braking effect (Willey et al., 2004). The common presence of tail, belly and digital drag marks observed in extant crocodylian footprints (Table S3, Fig. 8F) is likely to be related to this awkward high-walking. On the other hand, there is no evidence of drag marks of any type (foot, claw, belly or tail) in *C. meijidei*.

Another difference between *Crocodylopodus* and some modern trackways is that in *Crocodylopodus* the manual tracks are deeper than the majority of the pedal impression area (with the exception of MNS2002/96/3) with the heel traces generally absent or poorly preserved (Fig. 7, Tables S2-S3). Lockley et al., (2020:5) suggested that this "raises questions of whether the trackmakers exerted more pressure on the substrate with manus than pes". A crucial factor underlying the aforementioned differences is likely to be a different center of mass between extant species and the trackmaker of *Crocodylopodus meijidei*. This would also be in accordance with the absence of tail marks in the latter. Thus, in the high-walking extant crocodylians the tail is dragged behind the body rather than elevated off the ground, so the long, heavy tail causes the center of mass to lie more caudally, just in front of the pelvis (Willey et al., 2004). Experiments with extant alligators have shown that body weight support is concentrated over the hindlimb (51%) during locomotion, while the forelimbs and tail support 37% and 12% of the remaining weight respectively (Willey et al., 2004; Grigg and Kirshner, 2015). Therefore, the fact that the deeper areas in the trackways are in the manual tracks and the anterior part of the pedal tracks seems to indicate that the producer of *C. meijidei* would have had its center of mass more anteriorly located. This anterior displacement of the center of mass could be explained by a reduction in the size of the tail (length or weight) or by an increase in the mass of the anterior region of the body (Fig. 9). Another possible factor that could cause a displacement of the center of mass is a different distribution of weight among the limbs due to different forelimb/hindlimb length proportions from those observed in extant crocodylians (see next section). In extant crocodylians and most fossil crocodylomorphs, the hindlimbs are longer than the forelimbs (Iijima et al., 2018). Another interesting feature of *C. meijidei* in comparison with extant crocodylian trackways is the near-absence of overprinting of the manual impressions by the pes (see Table S3). These overstepping is produced at moderate to higher speeds (Padian, 2003; Kubo, 2008; Milàn and Hedegaard, 2010).

The described extant crocodylian tracks (Table S3) can give us an idea of the size of the trackmaker of *C. meijidei*. These data give us an intimation of the total length of the trackmaker of *C. meijidei*, which is around 50–80 cm for the lectotype and slightly greater for the largest specimen, MNS2002/96/3 (Farlow et al. (2018b) proposed equations for predicting the length of *Crocodylus acutus* on the basis of manual and pedal length proxies. Though based on a different species, it will provide an indication of the total length and the shoulder-hip length of the *C. meijidei* trackmaker. Estimations for the lectotype yield a total length of 78.71 cm based on the pedal impression length, and 58.59 cm based on the manual impression length. The estimation for the largest specimen (MNS2002/96/3) would be 109.58 cm. On the basis of the hindfoot (HF), Hutton (1987) proposed a ratio for the length of the Nile crocodile of 1 : 14 where HF < 150 mm, and 1 : 13.5 where HF > 150 mm. Accordingly, *C. meijidei* (the lectotype) would be around 71.4 cm long, and MNS2002/96/3 would be 98 cm long. Farlow and Britton (2000) proposed that the total length is about four times the glenoacetabular distances that gives consistent, or slightly smaller size (46–56.8 cm) for the lectotype trackway.

In summary, the combination of PA data and the absence of tail and other drag marks plus the presence of almost no overprint in *Crocodylopodus meijidei* trackways suggests that the trackmaker was probably walking in a semi-erect posture in a high-walking mode and at moderate speed when it produced the trackways. Moreover, the trackmaker would have possibly had rather long forelimbs (at least in relation to the hindlimbs and the total length). These data suggests that the trackmaker of *C. meijidei* walked in an agile way compared to extant crocodylians (Fig. 9), possibly also on account of its small size and the fact that the trackmaker was not a crocodylian sensu stricto (next section).

Candidate Trackmakers

It is difficult to assign the *Crocodylopodus meijidei* tracks to a concrete group of crocodylomorphs since a synapomorphy-based approach (Carrano and Wilson, 2001) cannot be pursued with confidence. This is because of the conservative morphology of autopods through crocodylomorph history. Geological provenance and body size can also help to infer trackmakers (Carrano and Wilson, 2001) but osteological fossils are almost absent from the Berriasian Huérteles Fm. (Hernández Medrano et al., 2008; Castanera et al., 2018). Indeed, the osteological crocodylomorph record of the Iberian Peninsula is almost absent in the Berriasian.

Crocodylomorphs identified of the Berriasian are goniopholidids, bernissartiids, pholidosaurids and “atoposaurids”. Berriasian crocodylomorph specimens of Europe mainly come from the Purbeck Limestone Group in England (see Salisbury, 2002; Andrade et al., 2011 and references therein); Cherves-de-Cognac and Angeac-Charente in France (Pouech et al., 2014; Martin et al., 2016; Rozada et al. 2020); the Rabekke Formation in Scandinavia (Schwarz et al., 2009); and the Obernkirchen Sandstone in Germany (Salisbury et al., 1999; Andrade and Hornung, 2011). Although there is no record in the Berriasian of Europe, possible representatives of a clade of small crocodylomorphs, Gobiosuchidae, have been recovered in the Kimmeridgian-Tithonian of Portugal (Buscalioni et al., 1996; Schwarz and Fechner 2004, 2008) and in the Barremian of Spain (Buscalioni 2017), so their presence in the Berriasian cannot be ruled out. However, aside from age, the extremely small size (less than 35 cm in total lenght) of these gobiosuchids (Buscalioni 2017) would dismiss them as the putative trackmakers. Pholidosaurids are unlikely to be the producers of *C. meijidei*. They were usually large-sized marine or freshwater aquatic animals with open, sagittally segmented paravertebral shield and amphicoelous vertebrae; therefore, they probably had lower or no capacity for sustained high-walking (Salisbury and Frey, 2001). Among the candidates, despite bernissartiids also have a similarly open dorsal shield, their small body mass, within the size range (60 cm estimated for *B. fagesii*) of *C. meijidei*, could have allowed them a sustained high-walking and a terrestrial locomotor behaviour (Salisbury and Frey, 2001; Martin et al., 2020). Goniopholidids and atoposaurids had much more rigid dorsal shields than that of extant crocodylians and the other neosuchians. These shields would have restricted the lateral flexion of the trunk in favour of greater stabilization of the vertebral column during terrestrial locomotion. The relative length of the limbs is directly related with locomotor functions and terrestrial locomotor capabilities (Iijima et al., 2018). Generally, atoposaurids have relatively longer hindlimbs than extant crocodylians whereas some goniopholidids have forelimbs that are longer than their hindlimbs (measurements from Tennant et al., 2016; Iijima et al., 2018; Ijima and Kubo, 2019). Several atoposaurid species were probably too small to have produced *Crocodylopodus meijidei* although some of them could have reached lengths that fit the size range such as *Alligatorellus* with a body length 42 to 55 cm (Schwarz-Wings et al., 2011). *Theriosuchus* is thought to be possible terrestrial taxa with a small size of around 50 cm total length and relatively long limbs (Schwarz and Salisbury, 2005; Schwarz et al. 2017), and *T. pusillus* is a Berriasian species. Goniopholidids are also good candidate trackmakers for *C. meijidei*. However, if the producers of *C. meijidei* were members of Goniopholididae, they would be juvenile individuals or belong to a small unknown species (Puértolas-Pascual and Mateus, 2020), so they would have greater ease walking on land. As we have already mentioned, one of the most remarkable characteristics of *C. meijidei* is the absence of tail marks (Fig.9). From an anatomical point of view, this could be explained by several factors or a combination of them such as the presence of a shorter or lighter tail or a stiffer tail base to keep it elevated. Regarding length, in most of the aforementioned candidate taxa the relationship between total body length and tail length cannot be compared due to the incompleteness of the fossil record. Some of the most complete specimens (e.g., *Alligatorellus* and *Atoposaurus*), do not seem to have a particularly shorter tail (see measurements from Tennant et al., 2016), with the length of the tail about half the total length of the body, a similar condition to that observed in extant crocodylians (see measurements from O'Brien et al., 2019). There is also no evidence of the lightness or rigidity of the tails of these taxa; therefore, the reason for the absence of tail marks in *C. meijidei* remains unclear until more complete fossils are found. Taking into account the paleogeographic and geochronological context of *C. meijidei,* only some non-eusuchian neosuchian taxa are the candidate of the trackmaker since the oldest eusuchian *Hylaeochampsa* is from the Barremian of England (Clark and Norell, 1992); and there is no record of protosuchians, notosuchians, gobiosuchids or sphenosuchians during the Berriasian of Europe. As a consequence, the producer of *C. meijidei* was most likely a small non-eusuchian neosuchian crocodylomorph such as goniopholidid, atoposaurid or bernissartid.

CONCLUSIONS

Little attention has been paid to extant crocodylomorph footprints until very recently, despite the fact that this is one of the few groups where we can directly compare living and extinct taxa. New descriptions in recent years have provided an excellent database to shed light on the reasons of morphological variations among the extinct ichnotaxa. Our review of the type material of *Crocodylopodus meijidei* has revealed the existence of new material and provides new data for the characterization of this type ichnotaxon. The *C. meijidei* collection shows at least three different size classes, which might reflect different ontogenetic stages and/or sexual dimorphism. Our analysis of the sample, plus comparison with other tracks assigned to *Crocodylopodus,* shows high morphological variation within this ichnogenus, but it is difficult to interpret whether these differences are anatomical, substrate- and preservation-related or locomotion/behavior-related. Comparisons with other crocodylomorph ichnogenera highlight that the main differences between them relate to trackway features and therefore different locomotor patterns/behaviors (either swimming tracks or walking traces with different lomotor patterns) or different body plan of the trackmakers. Several trackway parameters of the *C. meijidei*, such as its intermediate-gauge trackway, its relatively high pace angulation (values higher than 108º), the absence of tail and other drag marks and overprinting of manual prints by the pes, and manual tracks and anterior part of the pedal tracks deeper than the posterior part, point to a style of locomotion different from extant crocodylians and from the other walking tracks of extinct crocodylomorphs (e.g., *Batrachopus* and *Mehliella*). The trackmaker was a small (probably no larger than 1.10 m for the largest specimens) non-eusuchian neosuchian crocodylomorph presumably a goniopholidid, an atoposaurid or a bernissartid, and walked possibly with its center of mass more anteriorly located and with a more erect limb posture than exhibited by extant crocodylomorphs. Thus, the trackmaker was possibly better adapted for terrestrial locomotion than modern crocodylians.

ACKNOWLEDGMENTS

DC was funded by the Alexander von Humboldt Foundation and by the Beatriu de Pinós postdoctoral programme (BP2017-00195) of the Government of Catalonia's Secretariat for Universities and Research of the Ministry of Economy and Knowledge. EPP is supported by postdoctoral grants and projects funded by the Fundação para a Ciência e a Tecnologia, Portugal (SFRH/BPD/116759/2016 and Geobiotec UIDB/04035/2020). This study was subsidized in part by Project CGL2017-85038-P of the Spanish Ministerio de Economía y Competitividad-ERDF, as well as by the Aragón Regional Government ("grupo de Referencia Aragosaurus: reconstrucciones paleoambientales y recursos geológicos"). M.A. Arlegui Sánchez, B. Martínez, M. L. Revilla Andía, J. L. García and D. Diez Corral (Museo Numantino de Soria) are gratefully acknowledged for their help with the collections housed in the Museo Numantino de Soria. L. Piñuela (MUJA) provided valuable information on the Late Jurassic Asturian fossils; M. Belvedere (Università degli studi di Firenze) provided significant help with the use of the CloudCompare software and I. Díaz-Martínez provided valuable discussion on ichnotaxonomy. R. Glasgow (Zaragoza, Spain) revised the English grammar of a previous version of the manuscript. The comments of the reviewers, J.O. Farlow and T. Kubo, and the editor S.W. Salisbury have helped to improve the manuscript and are greatly appreciated.

LITERATURE CITED

Abbassi, N., S. D. O. Porchetti, A. Wagensommer, and M. G. Dehnavi. 2015. Dinosaur and crocodylomorph footprints from the Hojedk Formation (Bajocian, Middle Jurassic) of north Kerman, central Iran. Italian Journal of Geosciences 134(1):86–94.

Andrade, M. B., and J. J. Hornung. 2011. A new look into the periorbital morphology of Goniopholis (Mesoeucrocodylia: Neosuchia) and related forms. Journal of Vertebrate Paleontology 31(2):352–368.

Andrade, M. B., J. J. Hornung, R. Edmonds, M. J. Benton, and R. Schouten. 2011. A new Berriasian species of *Goniopholis* (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. Zoological Journal of the Linnean Society 163(1):S66–S108.

Avanzini, M., J. C. García-Ramos, J. Lires, L. Piñuela, and M. G. Lockley. 2007. Crocodylomorph tracks from the Late Jurassic of Asturias (Spain). Ichnos 14:143–153.

Avanzini, M., J. C. García-Ramos, J. Lires, L. Piñuela, and M. G. Lockley. 2010. Preservational morphotypes of *Crocodylopodus* from the Late Jurassic of Asturias (Spain). New Mexico Museum of Natural History and Science Bulletin 51: 239–244.

Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia; pp. 295–338 in M. J. Benton (ed.), The phylogeny and classification of the tetrapods. Volume 1, Systematics Association Special Volume no 35A Amphibians, reptiles, birds. Clarendon Press, Oxford, UK.

Brochu, C. A. 2003. Phylogenetic approaches toward crocodylian history. Annual Review of Earth and Planetary Sciences 31(1):357–397.

Bronzati, M., F. C. Montefeltro, and M. C. Langer. 2015. Diversification events and the effects of mass extinctions on Crocodyliformes evolutionary history. Royal Society Open Science 2(5):140385.

Buscalioni, A. D. 2017. The Gobiosuchidae in the early evolution of Crocodyliformes. Journal of Vertebrate Paleontology 37(3): e1324459.

Buscalioni, A. D., F. Ortega, B. P. Pérez-Moreno, and S. Evans E. 1996. The Upper Jurassic maniraptoran theropod *Lisboasaurus estesi* (Guimarota, Portugal) reinterpreted as a crocodylomorph. Journal of Vertebrate Paleontology 16(2):358–362.

Carrano, M. T., and J. A. Wilson. 2001. Taxon distributions and the tetrapod track record. Paleobiology 27(3):564–582.

Carpenter, K. 2009. Role of lateral body bending in crocodylian track making, Ichnos 16:202–207.

Castanera, D., C. Pascual, J. I. Canudo, and J. L. Barco. 2018. Bringing together research, geoconservation and reaching a broad public in the form of a geotourism project: the Ichnite Route of Soria (Spain). Geoheritage 10(3):393–403.

Castanera, D., C. Pascual, J. I. Canudo, N. Hernandez, and J. L. Barco, 2012. Ethological variations in gauge in sauropod trackways from the Berriasian of Spain. Lethaia, 45(4) :476–489.

Castanera, D., E. Malafaia, B. C. Silva, V. F. Santos, and M. Belvedere. 2021. New dinosaur, crocodylomorph and swim tracks from the Late Jurassic of the Lusitanian Basin: implications for ichnodiversity. Lethaia, 54(2), 271–287.

Clark, J. M., and M. Norell. 1992. The Early Cretaceous crocodylomorph *Hylaeochampsa vectiana* from the wealden of the Isle of Wight. American Museum novitiates 3032:1–19.

Carpenter, K. 2009. Role of lateral body bending in crocodylian track making. Ichnos, 16(3):202–207.

Cox, R. M., M. A. Butler, and H. B. John-Alder. 2007. The evolution of sexual size dimorphism in reptiles; pp. 38–49 in W.U., Blanckenhorn, T., Székely and D.J., Fairbairn (eds.), Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford, UK.

Coombs, W. P. 1996. Redescription of the ichnospecies *Antipus flexiloquus* Hitchcock, from the Early Jurassic of the Connecticut Valley. Journal of Paleontology 70(2):327–331.

Falkingham, P. L., K. T. Bates, M. Avanzini, M. Bennett, E. M. Bordy, B. H. Breithaupt, D. Castanera, P. Citton, I. Díaz-Martínez, J.O. Farlow, A.R. Fiorillo, S.M. Gatesy, P. Getty, K.G. Hatala, J.J. Hornung, J.A. Hyatt, H. Klein, J.N. Lallensack, A.J. Martin, D. Marty, N.A. Matthews, C.A. Meyer, J. Milàn, N.J. Minter, N.L. Razzolini, A. Romilio, S.S. Salisbury, L. Sciscio, I. Tanaka, A.L.A.Wiseman, L. D. Xing, and M. Belvedere. 2018. A standard protocol for documenting modern and fossil ichnological data. Palaeontology 61(4):469–480.

Farlow, J.O. (ed.). 2018. Noah's ravens: Interpreting the makers of tridactyl dinosaur footprints. Indiana University Press, Bloomington, Indiana, 636 pp.

Farlow, J.O., and Britton, A. 2000. Size and body proportions in *Alligator mississippiensis*: implications for archosaurian ichnology. Paleontological Society of Korea Special Publication 4:189–206.

Farlow, J.O., N. J. Robinson, M. L.Turner, J. Black, and S. M. Gatesy. 2018a. Footfall pattern of a bottom-walking crocodile (*Crocodylus acutus*). Palaios 33(9):406–413.

Farlow, J.O., N. J. Robinson, C. J. Kumagai, F. V. Paladino, P. L. Falkingham, R. M. Elsey, and A. J. Martin. 2018b. Trackways of the American crocodile (*Crocodylus acutus*) in northwestern Costa Rica: implications for crocodylian ichnology. Ichnos 25(1):30–65.

Foster, J. R., and M. G. Lockley. 1997. Probable crocodilian tracks and traces from the Morrison Formation (Upper Jurassic) of eastern Utah. Ichnos 5(2):121–129.

Fuentes Vidarte, C., and M. Meijide Calvo. 2001. Primeras huellas de cocodrilo en el Weald de Cameros (Soria, España). Nueva familia: Crocodylopodidae, nuevo icnogénero: *Crocodylopodus*, nueva icnoespecie: *C. meijidei*; pp. 329–335 in Colectivo Arqueológico-Paleontológico de Salas (eds.), Actas de las I Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, Salas de los Infantes, Burgos, Spain.

Gatesy, S. M. 1991. Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. Journal of Zoology, 224(4):577 –588.

Gómez Fernández, J. C., and N. Meléndez. 1994a. Estratigrafía de la "Cuenca de los Cameros" (Cordillera Ibérica Noroccidental, N de España) durante el tránsito Jurásico-Cretácico. Revista de la Sociedad Geológica de España 7(1-2):121–139.

Gómez Fernández, J. C., and N. Meléndez. 1994b. Climatic control on Lower Cretaceous sedimentation in a playa-lake system of a tectonically active basin (Huérteles Alloformation, Eastern Cameros Basin, North-Central Spain). Journal of Paleolimnology 11(1):91–107.

Grigg, G., and D. Kirshner, (eds.). 2015. Biology and evolution of crocodylians. Csiro Publishing, Clayton South, Victoria, Australia 672 pp.

Hitchcock, E. 1845. An attempt to name, classify, and describe the animals that made the fossil footmarks of New England. Proceedings of the 6th Annual Meeting of the Association of American Geologists and Naturalists 6:23–25.

Hernández Medrano, N., C. Pacual Arribas, P. Latorre Macarron, and E. Sanz Pérez. 2008. Contribución de los yacimientos de icnitas sorianos al registro general de Cameros. Zubía 23-24:79–120.

Hone, D., J. C. Mallon, P. Hennessey, and L. M. Witmer. 2020. Ontogeny of a sexually selected structure in an extant archosaur *Gavialis gangeticus* (Pseudosuchia: Crocodylia) with implications for sexual dimorphism in dinosaurs. PeerJ 8:e9134.

Houck, K., M. G. Lockley, M. Caldwell, and B. Clark. 2010. A crocodile trackway from the Dakota Group (Cretaceous) of the Golden Area, Colorado. New Mexico Museum of Natural History and Science Bulletin 51:115–120.

Hutchinson, J. R., D. Felkler, K. Houston, Y. M. Chang, J. Brueggen, D. Kledzik, and K. A. Vliet. 2019. Divergent evolution of terrestrial locomotor abilities in extant Crocodylia. Scientific Reports 9(1):1–11.

Hutton, J. M. 1987. Morphometrics and field estimation of the size of the Nile crocodile. African Journal of Ecology 25(4):225–230.

ICZN 1999. International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, UK. 306 pp.

Iijima, M., and T. Kubo. 2019. Comparative morphology of presacral vertebrae in extant crocodylians: taxonomic, functional and ecological implications. Zoological Journal of the Linnean Society 186(4):1006–1025.

Iijima, M., T. Kubo, and Y. Kobayashi. 2018. Comparative limb proportions reveal differential locomotor morphofunctions of alligatoroids and crocodyloids. Royal Society Open Science 5(3):171774.

Kim, K. S., M. G. Lockley, J. D. Lim, S. M. Bae, and A. Romilio. 2020. Trackway evidence for large bipedal crocodylomorphs from the Cretaceous of Korea. Scientific Reports 10(1):1–13.

Klein, H., and S. G. Lucas. 2010. The Triassic footprint record of crocodylomorphs–a critical re-evaluation. New Mexico Museum of Natural History and Science Bulletin 51:55–60.

Klein, H., A. Lagnaoui, G. D. Gierliński, H. Saber, J. N. Lallensack, M. Oukassou, and A. Charrière. 2018. Crocodylomorph, turtle and mammal tracks in dinosaur-dominated Middle–? Upper Jurassic and mid-Cretaceous ichnoassemblages of Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology 498:39–52.

Kubo, T. 2008. In quest of the *Pteraichnus* trackmaker: comparisons to modern crocodilians. Acta Palaeontologica Polonica 53(3):405–412.

Kubo, T. 2010. Variation in modern crocodylian limb kinematics and its effect on trackways. Crocodyle Tracks and Traces. New Mexico Museum of Natural History and Science Bulletin 51:51–53.

Kubo, T., and M. J. Benton. 2009. Tetrapod postural shift estimated from Permian and Triassic trackways. Palaeontology 52(5):1029–1037.

Kubo, T., and M. Ozaki. 2009. Does pace angulation correlate with limb posture?. Palaeogeography, Palaeoclimatology, Palaeoecology 275(1-4):54–58.

Leonardi, G. (ed.). 1987. Glossary and manual of tetrapod footprint palaeoichnology. Conselho Nacional de Desenvolvimento Cientifico e Tecnologico – Brasil.

Lockley, M. G. 2010. A solution to the *Mehliella* mystery: tracking, naming, identifying and measuring the first crocodylian trackway reported from the Cretaceous (Dakota Group, Colorado). New Mexico Museum of Natural History and Science Bulletin 51:157–164.

Lockley, M. G., and C. Meyer. 2004. Crocodylomorph trackways from the Jurassic to Early Cretaceous of North America and Europe: implications for ichnotaxonomy. Ichnos 11(1-2): 167–178.

Lockley, M. G., R. Li, M. Matsukawa, and J. Li. 2010a. Tracking Chinese crocodilians: *Kuangyuanpus*, *Laiyangpus* and implications for naming crocodylian and crocodylianlike tracks and associated ichnofacies. New Mexico Museum of Natural History and Science Bulletin 51:99–108.

Lockley, M. G., K. Cart, J. Foster, and S. G. Lucas. 2018. Early Jurassic *Batrachopus*-rich track assemblages from interdune deposits in the Wingate Sandstone, Dolores Valley, Colorado, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 491:185–195.

Lockley, M. G., S. Lucas, J. Milàn, J. Harris, M. Avanzini, J. R. Foster and J. Spielmann. 2010b. The fossil record of crocodylian tracks and traces: an overview. New Mexico Museum of Natural History and Science Bulletin 51:1–14.

Lockley, M. G., J. D. Lim, H. D. Park, A. Romilio, J. S.Yoo, J. W. Choi, K. S. Kim, S.-H. Kang, D.H. Kim, and T. H. Kim. 2020. First reports of *Crocodylopodus* from Asia: implications for the paleoecology of the Lower Cretaceous. Cretaceous Research 104441.

Lull, R.S. 1904. Fossil footprints of the Jura–Trias of North America. Boston Society of Natural History 5:461–557.

Marchetti, L., M. Belvedere, S.Voigt, H. Klein, D. Castanera, I. Díaz-Martínez, D. Marty, L. Xing, S. Feola, R.N. Melchor, and J. O. Farlow. 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.

Martin, J. E., J. Raslan-Loubatié, and J. M. Mazin. 2016. Cranial anatomy of *Pholidosaurus purbeckensis* from the Lower Cretaceous of France and its bearing on pholidosaurid affinities. Cretaceous Research 66:43–59.

Martin, J. E., T. Smith, C. Salaviale, J. Adrien, and M. Delfino. 2020. Virtual reconstruction of the skull of *Bernissartia fagesii* and current understanding of the neosuchian–

eusuchian transition. Journal of Systematic Palaeontology 18(13):1079–1101.

Mas, R., M.I. Benito, J. Arribas, S. Omodeo-Salé, P. Suárez-González, I.E. Quijada, J. Guimerà, L.González-Acebrón, and M.E. Arribas. 2019. The Cameros basin; pp. 205–214 in C.Quesada and J.T. Oliveira (eds.), The Geology of Iberia: A Geodynamic Approach. Volume 3: The Alpine Cycle. Springer, Berlin, Germany.

Masrour, M., M. Boutakiout, J. Herrero Gascón, J. L. S. R. De Zuazo, R. O. Martínez, and F. Pérez-Lorente. 2020. Footprints of *Batrachopus* isp. From the Imilchil megatracksite. Middle?-Upper Jurassic, central High Atlas (Morocco). Journal of African Earth Sciences, 172, 103980.

Mateus, O., M. Marzola, A. S. Schulp, L. L. Jacobs, M. J. Polcyn, V. Pervov, A. O. Gonçalves, and M. L. Morais. 2017. Angolan ichnosite in a diamond mine shows the presence of a large terrestrial mammaliamorph, a crocodylomorph, and sauropod dinosaurs in the Early Cretaceous of Africa. Palaeogeography, palaeoclimatology, palaeoecology 471:220–232.

Mazin, J. M., J. P. Billon-Bruyat, P. Hantzpergue, and G. Lafaurie. 2003. Ichnological evidence for quadrupedal locomotion in pterodactyloid pterosaurs: trackways from the Late Jurassic of Crayssac (southwestern France). Geological Society, London, Special Publications 217(1):283–296.

McCrea, R. T., S. G. Pemberton, and P. J. Currie. 2004. New ichnotaxa of mammal and reptile tracks from the Upper Paleocene of Alberta. Ichnos 11(3-4): 323–339.

Mehl, M.G. 1931. Additions to the vertebrate record of the Dakota Sandstone. The American Journal of Science 21:441–452.

Milàn, J., and R. Hedegaard. 2010. Interspecific variation in tracks and trackways from extant crocodylians. New Mexico Museum of Natural History and Science Bulletin 51:15–

29.

Milàn, J., S. G. Lucas, M. G. Lockley, and J. A. Spielmann. 2010. Crocodyle tracks and traces. New Mexico Museum of Natural History and Science Bulletin 51.

Molnar, J. L., S. E. Pierce, B. A. S. Bhullar, A. H. Turner, and J. R. Hutchinson. 2015. Morphological and functional changes in the vertebral column with increasing aquatic adaptation in crocodylomorphs. Royal Society Open Science 2(11): 150439.

Mustoe, G. E. 2019. Lower Eocene Footprints from Northwest Washington, USA. Part 1: Reptile Tracks. Geosciences 9 (321):1–19.

O'Brien, H. D., L. M. Lynch, K. A. Vliet, J. Brueggen, G. M. Erickson, and P. M. Gignac. 2019. Crocodylian head width allometry and phylogenetic prediction of body size in extinct crocodyliforms. Integrative Organismal Biology, 1(1), obz006.

Olsen, P. E., and K. Padian. 1986. Earliest records of *Batrachopus* from the southwestern United States, and a revision of some Early Mesozoic crocodylomorph ichnogenera; pp. 259–273 in K. Padian (ed.), The beginning of the age of Dinosaurs, faunal change across the Triassic-Jurassic boundary. Cambridge University Press, New York, USA.

Padian, K. 2003. Pterosaur stance and gait and the interpretation of trackways. Ichnos 10(2-4): 115–126.

Padian, K., and P.E. Olsen. 1984. The fossil trackway *Pteraichnus*: Not pterosaurian, but crocodilian. Journal of Paleontology 58:178–184.

Parrish, J. M. 1987. The origin of crocodilian locomotion. Paleobiology 13(4): 396–414.

Pascual Arribas, C., N. Hernández Medrano, P. Latorre Macarrón, and E. Sanz Pérez. 2005. Nuevo rastro de icnitas de cocodrilo en la Aloformación Huérteles de la Cuenca de Cameros. Studia Geologica Salmanticensia 41:75–91.

Platt, S.G., T.R. Rainwater, J.B. Thorbjarnarson, A.G. Finger, T.A. Anderson, and S.T.

McMurry, 2009. Size estimation, morphometrics, sex ratio, sexual size dimorphism, and biomass of Morelet's crocodile in northern Belize. Caribbean Journal of Science 45(1):80–94.

Pol, D., A. H. Turner, and M. A. Norell. 2009. Morphology of the Late Cretaceous crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian phylogeny as related to the origin of Eusuchia. Bulletin of the American Museum of Natural History 324: 1–103.

Pouech, J., R. Amiot, C. Lécuyer, J. M. Mazin, F. Martineau, and F. Fourel. 2014. Oxygen isotope composition of vertebrate phosphates from Cherves-de-Cognac (Berriasian, France): environmental and ecological significance. Palaeogeography, Palaeoclimatology, Palaeoecology 410:290–299.

Puértolas-Pascual, E., and O. Mateus. 2020. A three-dimensional skeleton of Goniopholididae from the Late Jurassic of Portugal: implications for the Crocodylomorpha bracing system. Zoological Journal of the Linnean Society 189(2):521–548.

Quijada, I. E., P. Suárez González, M. I. Benito, and J. R. Mas. 2013. New insights on stratigraphy and sedimentology of the Oncala Group (eastern Cameros Basin): implications for the paleogeographic reconstruction of NE Iberia at Berriasian times. Journal of Iberian Geology 39(2): 313–334.

Rajkumar, H. S., G. E. Mustoe, K. S. Khaidem, and I. Soibam. 2015. Crocodylian Tracks from Lower Oligocene Flysch deposits of the Barail Group, Manipur, India. Ichnos 22(2): 122–131.

Razzolini, N. L., B.Vila, D. Castanera, P. L. Falkingham, J. L. Barco, J. I.Canudo, P.L. Manning, and A. Galobart. 2014. Intra-trackway morphological variations due to substrate consistency: the El Frontal dinosaur tracksite (Lower Cretaceous, Spain).

PloS ONE 9(4).

Reilly, S.M., and J.A. Elias, 1998. Locomotion in *Alligator mississippiensis*: kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. Journal of Experimental Biology 201:2559–2574

Rozada, L., R. Allain, R.Vullo, J. Goedert, D. Augier, A. Jean, J. Marchal, C. Peyre de Fabrègues, M. Qvarnstrom, and R. Royo-Torres. 2020. A Lower Cretaceous Lagerstätte from France: a taphonomic overview of the Angeac‐Charente vertebrate assemblage. Lethaia 54 (2): 141–165.

Salisbury, S. W. 2002. Crocodilians from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of Dorset, southern England. Special Papers in Palaeontology 68:121–144.

Salisbury, S. W., and E. Frey. 2001. A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodilians; pp. 85–134 in C.G. Grigg, F. Seebacher and C.E. Franklin (eds.), Crocodilian biology and evolution. Surrey Beatty and Sons, Chipping Norton, Australia.

Salisbury, S. W., P. M.Willis, S. Peitz, and P. M. Sander. 1999. The crocodilian *Goniopholis simus* from the Lower Cretaceous of north-western Germany. Special Papers in Palaeontology 60:121–148.

Schudack, U., and M. Schudack. 2009. Ostracod biostratigraphy in the Lower Cretaceous of the Iberian chain (eastern Spain). Journal of Iberian Geology 35(2):141–168.

Segura, M., F. Barroso-Barcenilla, M. Berrocal-Casero, D. Castanera, J. F. Garcia-Hidalgo, and V. F. Santos. 2016. A new Cenomanian vertebrate tracksite at Tamajón (Guadalajara, Spain): Palaeoichnology and palaeoenvironmental implications. Cretaceous Research 57: 508–518.

Schwarz, D., and R. Fechner. 2004. *Lusitanisuchus*, a new generic name for *Lisboasaurus mitracostatus* (Crocodylomorpha: Mesoeucrocodylia), with a description of new remains from the Upper Jurassic (Kimmeridgian) and Lower Cretaceous (Berriasian) of Portugal. Canadian Journal of Earth Sciences 41(10):1259–1271.

Schwarz, D., and S. W. Salisbury. 2005. A new species of *Theriosuchus* (Atoposauridae, Crocodylomorpha) from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal. Geobios 38(6):779–802.

Schwarz, D., and R. Fechner, 2008. The first dentary of *Lisboasaurus* (crocodylomorpha,? mesoeucrocodylia) from the Lower Cretaceous (Barremian) of Una, Cuenca Province, Spain. Journal of Vertebrate Paleontology 28(1):264–268.

Schwarz, D., J. Rees, and J. Lindgren. 2009. Lower Cretaceous mesoeucrocodylians from Scandinavia (Denmark and Sweden). Cretaceous Research 30(5):1345–1355.

Schwarz, D., M. Raddatz, and O.Wings. 2017. *Knoetschkesuchus langenbergensis* gen. nov. sp. nov., a new atoposaurid crocodyliform from the Upper Jurassic Langenberg Quarry (Lower Saxony, northwestern Germany), and its relationships to *Theriosuchus*. PLoS One 12(2):e0160617.

Schwarz-Wings, D., N. Klein, C. Neumann, and U. Resch. 2011. A new partial skeleton of *Alligatorellus* (Crocodyliformes) associated with echinoids from the Late Jurassic (Tithonian) lithographic limestone of Kelheim, S-Germany. Fossil Record 14(2):195–205.

Simpson, E. L., H.L. Hilbert-Wolf, M.C. Wizevich, S. G. Lucas, E. Tester, S.E. Tindall, and J. J. Bernard 2010. A crocodylomorph track in the upper cretaceous capping sandstone member of the Wahweap Formation, Grand Staircase-Escalante national monument, Utah, USA. New Mexico Museum of Natural History and Science Bulletin 51:165–

170.

Tennant, J. P., P. D. Mannion, and P. Upchurch. 2016. Evolutionary relationships and systematics of Atoposauridae (Crocodylomorpha: Neosuchia): implications for the rise of Eusuchia. Zoological Journal of the Linnean Society 177(4):854–936.

Thorbjarnarson, J.B. 1994. Reproductive ecology of the spectacled caiman (*Caiman crocodilus*) in the Venezuelan Llanos. Copeia, 4:907–919.

Vila, B., D. Castanera, J. Marmi, J. I. Canudo, and À. Galobart. 2015. Crocodile swim tracks from the latest Cretaceous of Europe. Lethaia 48(2):256–266.

Willey, J. S., A. R. Biknevicius, S. M. Reilly, and K. D. Earls. 2004. The tale of the tail: limb function and locomotor mechanics in *Alligator mississippiensis*. Journal of Experimental Biology 207(3):553–563.

Wilberg, E. W., A. H. Turner, and C. A. Brochu. 2019. Evolutionary structure and timing of major habitat shifts in Crocodylomorpha. Scientific reports 9(1):1–10.

Zug, G. R. 1974. Crocodilian galloping: an unique gait for reptiles. Copeia, 1974(2):550 – 552.

Submitted July 17, 2020; revisions received Month DD, YYYY; accepted Month DD, YYYY

Figure captions (Colour version)

FIGURE 1. Geographical and geological setting of the El Frontal tracksite. **A**, Geographical setting of the Ichnite Route of Soria (after Castanera et al., 2018). **B,** Geological setting of the area showing the outcrops of the Huérteles Formation (after Quijada et al., 2013). [Intended for page width]

FIGURE 2. Measurements taken on the *Crocodylopodus meijidei* specimens. **A**, trackway parameters in the pedal impressions; **B**, trackway parameters in the manual impressions; **C**, Estimation of the glenoacetabular distance; **D,** parameters in individual manus-pes set. PA = pace angulation from the center of the footprint; ANG, pace angulation from tip of the impression of digit III; SL = stride length; PL = pace length; FR = footprint rotation; OW = overall width; ML = trackway midline; Dm-p = manus-pes distance; FL = footprint length; FW = footprint width; LI, LII, LIII; LIV, LV = length of each digital impression; IA = interdigital divarication angle. [Intended for page width]

FIGURE 3. Lectotype of *Crocodylopodus meijidei*, specimen MNS2002/96/2bis. **A**, Picture of the trackway. **B**, False-colour depth map of the trackway. Purple colour indicating deeper parts of the slab. **C**, Outline drawing of the trackway. **D**, Close-up picture of manus-pes set 3mp. **E**, Close-up picture of manus-pes set 2mp. Note that both 2p and 3p only show evidence of claw mark in digital impressions I-III. Note that manual print 3m still has sediment inside the print. Scale bars equal 5 cm (A, B, C), 1 cm (D, E). [Intended for page width]

FIGURE 4. Paralectotypes of *Crocodylopodus meijidei*, specimens MNS2003/92/8a **(A-C**) and MNS2002/96/4 (D-F). **A**, Picture of the trackway. **B**, False-colour depth map of the trackway. Purple colours indicating deeper parts of the slab. **C**, Outline drawing of the trackway. **D**, Picture of the trackway. **E**, False-colour depth map of the trackway. Purple colours indicating shallower parts of the slab. **F**, Outline drawing of the trackway. Scale bars equal 5 cm. [Intended for page width]

FIGURE 5. Referred specimens of *Crocodylopodus meijidei,* specimens MNS2002/96/3 (A-C), MNS2003/92/8b (D-F) MNS2002/96/10 (G-I). **A**, Picture of the set of coupled manual and pedal tracks. **B**, False-colour depth map of the set. Purple colours indicating deeper parts of the slab. **C**, Outline drawing of the set. **D**, Picture of the trackway. **E**, False-colour depth map of the trackway. Purple colours indicating shallower parts of the slab. **F**, Outline drawing of the trackway **G**, Picture of two set of coupled manual and pedal tracks. **H**, False-colour depth map of the sets. Purple colours indicating deeper parts of the slab. **I**, Outline drawing of the trackway. Note that the latter two specimens are possibly part and counterpart (mold and true track of the same trackway). Scale bars equal 5 cm. [Intended for page width]

FIGURE 6. Referred specimens of *Crocodylopodus meijidei***, A-C,** Specimen MNS2002/96/12. A, Picture of the trackway. **B**, False-colour depth map of the trackway. Purple colours indicating shallower parts of the slab. **C**, Outline drawing of the trackway. **D**, Picture of specimen MNS2002/96/5, **E**, Picture of specimen MNS2002/96/7 and **F**, Picture of specimen MNS2002/96/8. Scale bars (and coin) equal 2.5 cm. [Intended for page width]

FIGURE 7. Comparison of the lectotype of *C.meijidei* with *Crocodylopodus* tracks described in other areas. **A**, Lectotype of *C.meijidei*. **B**, *Crocodylopodus* isp. from the Middle Jurassic of Iran (after Abbassi et al., 2015). **C,** *Crocodylopodus meijidei* from the Middle-?Upper Jurassic of Morocco (after Klein et al., 2018). **D, F, G**, **H,** *Crocodylopodus meijidei* tracks from the Upper Jurassic of Asturias, Spain (after Avanzini et al., 2007, 2010). **E,** *Crocodylopodus* isp. from the Upper Jurassic of Portugal (after Castaner et al., 2020). **I,** cf. *Crocodylopodus* from the Lower Cretaceous (Huérteles Formation) of Soria, Spain (after Pascual Arribas et al., 2005). **J, K, L**, **M,** *Crocodylopodus* isp. from the Lower Cretaceous of

Korea (after Lockley et al., 2020). **N**, cf. *Crocodylopodus* from the Upper Cretaceous of Spain (after Vila et al., 2015). Scale bars equal 1 cm (D, F, G, H), 3 cm (C), 5 cm (A, B, N), 10 cm (I, J, K, L, M). [Intended for page width]

FIGURE 8. Comparison of the lectotype of *C. meijidei* with walking trackways of extinct crocodylomorph ichnotaxa and a modern crocodylian trackway. **A**, Lectotype of *C. meijidei*. **B**, *Batrachopus deweyi* from the Lower Jurassic of the USA (after Padian and Olsen, 1986). **C**, *Antipus flexiloquus* from the Lower Jurassic of the USA (after Coombs, 1996). **D**, *Angolaichnus adamanticus* from the Lower Cretaceous of Angola (after Mateus et al., 2017). **E**, *Mehliella jeffersonensis* from the Cretaceous of the USA (after Mehl, 1931; Lockley 2010). **F**, Modern trackway of *Crocodylus niloticus* (after Mazin et al., 2003). Scale bars equal 3 cm (B), 5 cm (A, C), 10 cm (D, F) 50 cm (E). [Intended for page width]

FIGURE 9. Summary of anatomical features that may explain the trackway differences between the trackmaker of *C. meijidei* (an indeterminate neosuchian crocodylomorph) and an indeterminate extant crocodylian. Silhouettes of crocodylomorphs are not based on any particular species. Trackway in B modified from Milàn and Hedegaard (2010). Dark colours indicating depper parts of the footprints. [Intended for page width]

Figure captions (Black and white version)

FIGURE 1. Geographical and geological setting of the El Frontal tracksite. **A**, Geographical setting of the Ichnite Route of Soria (after Castanera et al., 2018). **B,** Geological setting of the

area showing the outcrops of the Huérteles Formation (after Quijada et al., 2013). [Intended for page width]

FIGURE 2. Measurements taken on the *Crocodylopodus meijidei* specimens. **A**, trackway parameters in the pedal impressions; **B**, trackway parameters in the manual impressions; **C**, Estimation of the glenoacetabular distance; **D,** parameters in individual manus-pes set. PA = pace angulation from the center of the footprint; ANG, pace angulation from tip of the impression of digit III; SL = stride length; PL = pace length; FR = footprint rotation; OW = overall width; ML = trackway midline; Dm-p = manus-pes distance; FL = footprint length; FW = footprint width; LI, LII, LIII; LIV, LV = length of each digital impression; IA = interdigital divarication angle. [Intended for page width]

FIGURE 3. Lectotype of *Crocodylopodus meijidei*, specimen MNS2002/96/2bis. **A**, Picture of the trackway. **B**, Solid three-dimensional model of the trackway. **C**, Outline drawing of the trackway. **D**, Close-up picture of manus-pes set 3mp. **E**, Close-up picture of manus-pes set 2mp. Note that both 2p and 3p only show evidence of claw mark in digital impressions I-III. Note that manual print 3m still has sediment inside the print. Scale bars = 5 cm (A, B, C), 1 cm (D, E). [Intended for page width]

FIGURE 4. Paralectotypes of *Crocodylopodus meijidei*, specimens MNS2003/92/8a **(A-C**) and MNS2002/96/4 (D-F). **A**, Picture of the trackway. **B**, Solid three-dimensional model of the trackway. **C**, Outline drawing of the trackway. **D**, Picture of the trackway. **E**, solid three-dimensional model of the trackway. **F**, Outline drawing of the trackway. Scale bars equal 5 cm. [Intended for page width]

FIGURE 5. Referred specimens of *Crocodylopodus meijidei,* specimens MNS2002/96/3 (A-C), MNS2003/92/8b (D-F) MNS2002/96/10 (G-I). **A**, Picture of the set of coupled manual and pedal tracks. **B**, Solid three-dimensional model of the set. **C**, Outline drawing of the set. **D**, Picture of the trackway. **E**, Solid three-dimensional model of the trackway. **F**, Outline drawing of the trackway **G**, Picture of two set of coupled manual and pedal tracks. **H**, Solid three-dimensional model of the sets. **I**, Outline drawing of the trackway. Note that the latter two specimens are possibly part and counterpart (mold and true track of the same trackway). Scale bars equal 5 cm. [Intended for page width]

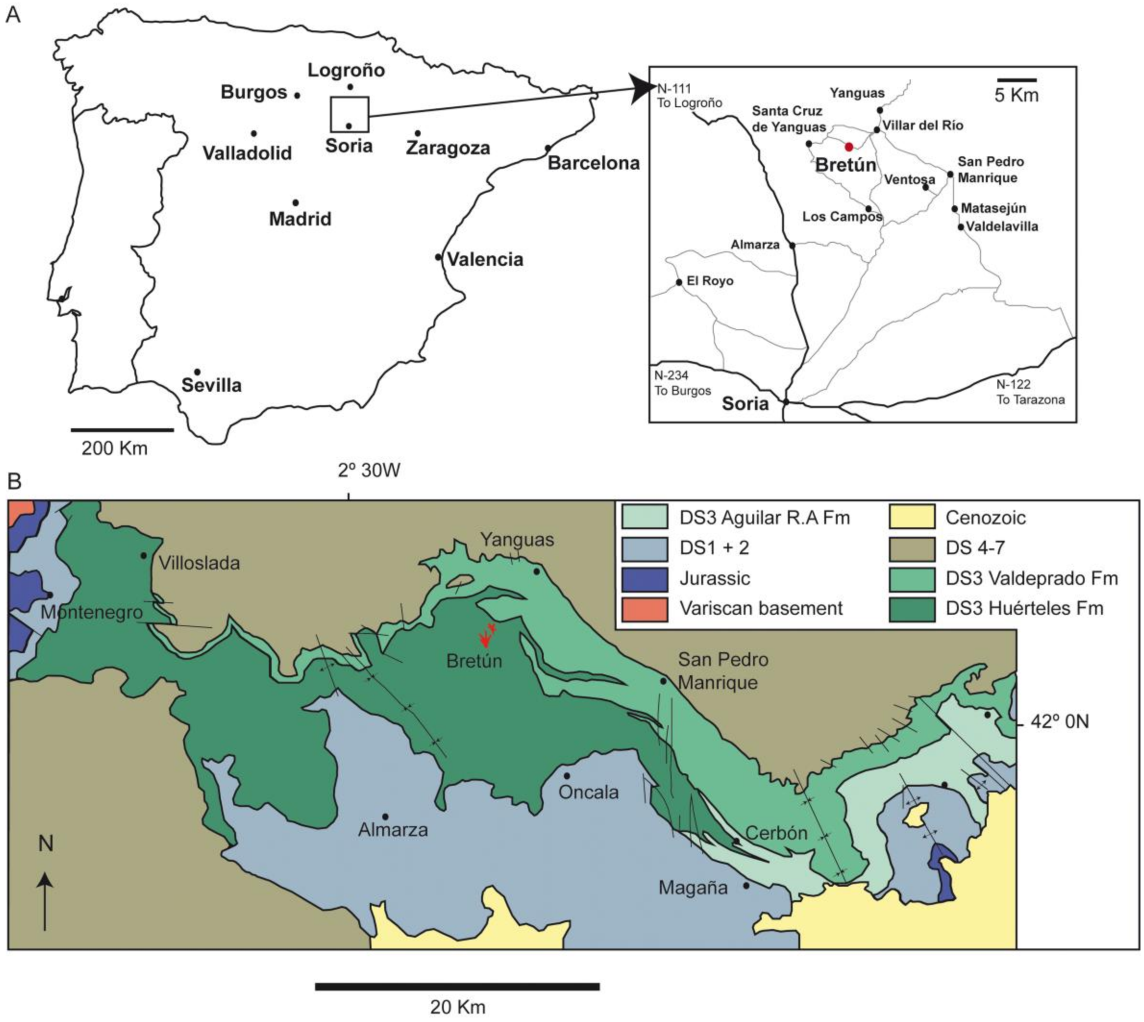
FIGURE 6. Referred specimens of *Crocodylopodus meijidei*. **A-C,** Specimen MNS2002/96/12. A, Picture of the tracks. **B**, Solid three-dimensional model of the tracks. **C**, Outtline drawing of the tracks. **D**, Picutre of specimen MNS2002/96/5, **E**, Picture of specimen MNS2002/96/7 and **F**, Picture of specimen MNS2002/96/8. Scale bars (and coin) equal 2.5 cm. [Intended for page width]

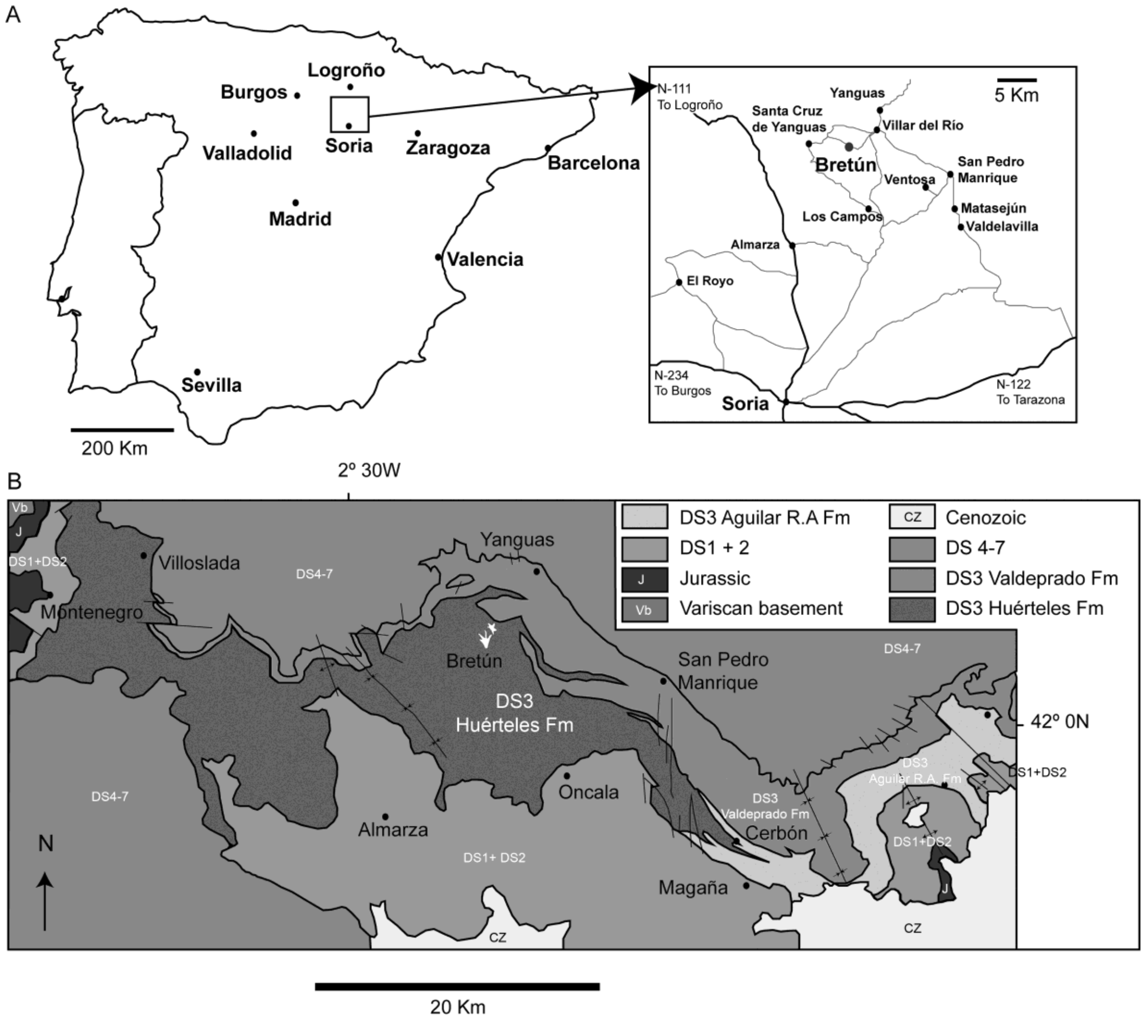
FIGURE 7. Comparison of the lectotype of *C.meijidei* with *Crocodylopodus* tracks described in other areas. **A**, Lectotype of *C.meijidei*. **B**, *Crocodylopodus* isp. from the Middle Jurassic of Iran (after Abbassi et al., 2015). **C,** *Crocodylopodus meijidei* from the Middle-?Upper Jurassic of Morocco (after Klein et al., 2018). **D, F, G**, **H,** *Crocodylopodus meijidei* tracks from the Upper Jurassic of Asturias, Spain (after Avanzini et al., 2007, 2010). **E,** *Crocodylopodus* isp. from the Upper Jurassic of Portugal (after Castaner et al., 2020). **I,** cf. *Crocodylopodus* from the Lower Cretaceous (Huérteles Formation) of Soria, Spain (after Pascual Arribas et al., 2005). **J, K, L**, **M,** *Crocodylopodus* isp. from the Lower Cretaceous of

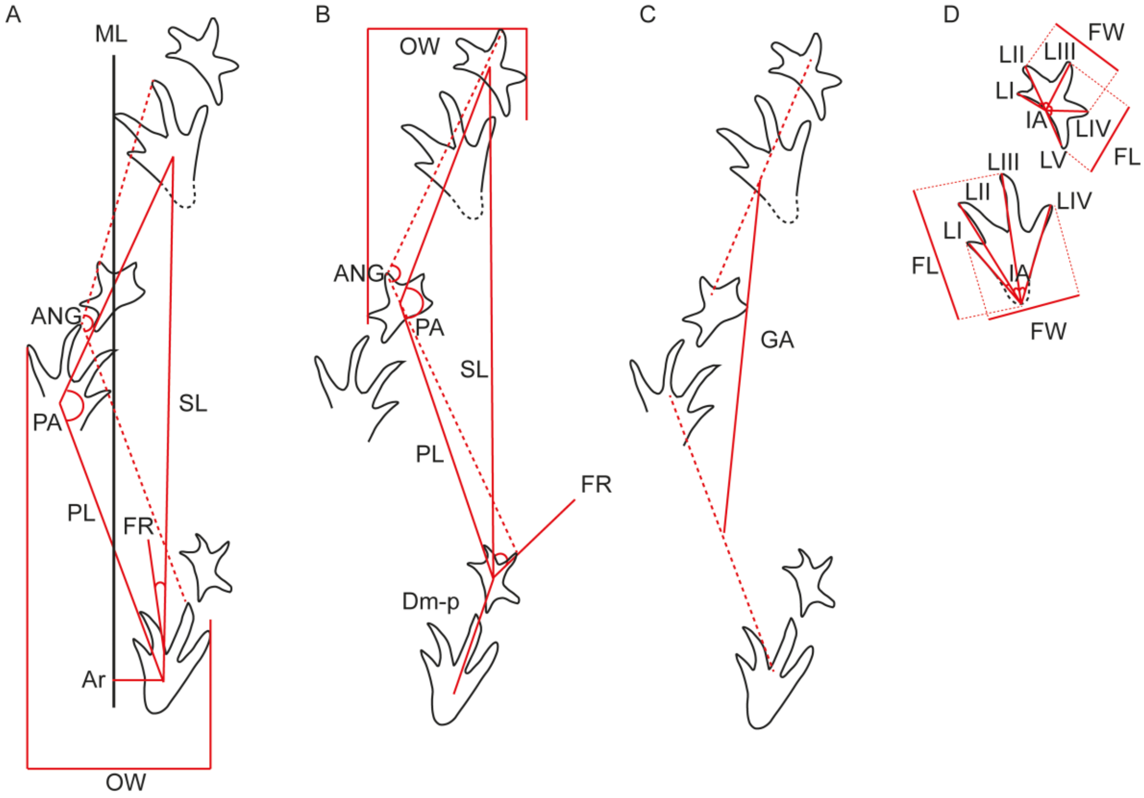
Korea (after Lockley et al., 2020). **N**, cf. *Crocodylopodus* from the Upper Cretaceous of Spain (after Vila et al., 2015). Scale bars equal 1 cm (D, F, G, H), 3 cm (C), 5 cm (A, B, N), 10 cm (I, J, K, L, M). [Intended for page width]

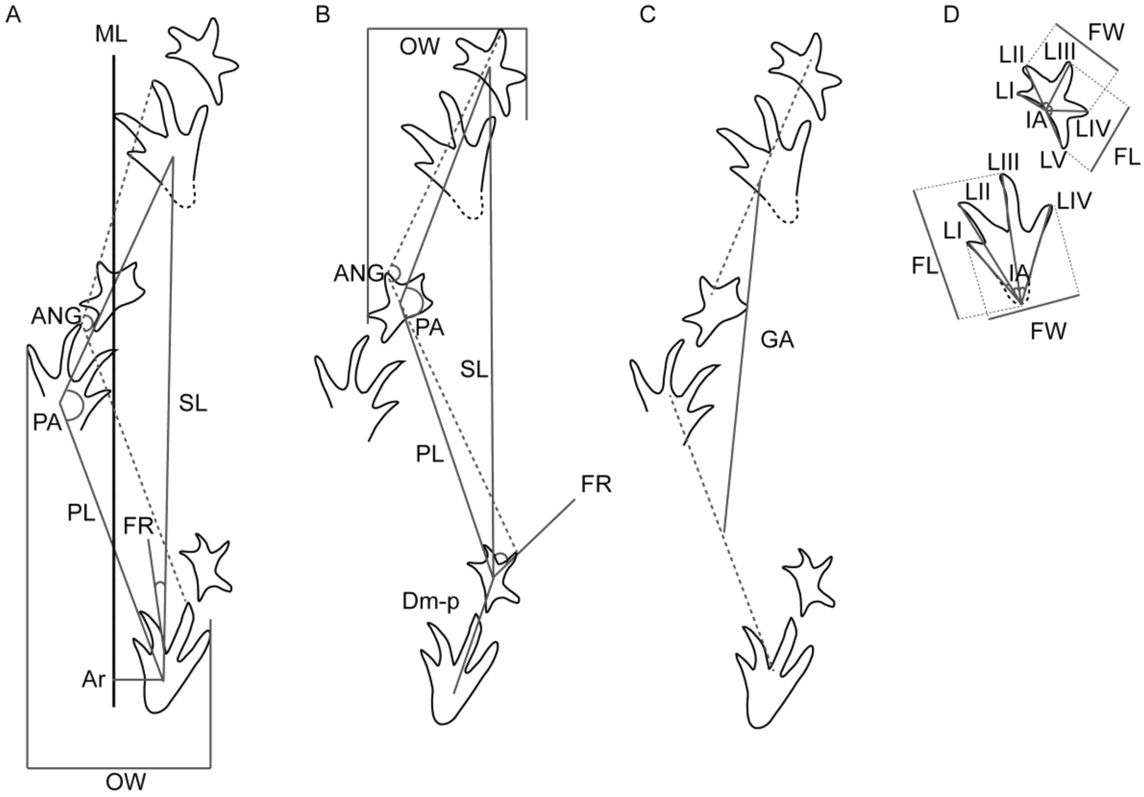
FIGURE 8. Comparison of the lectotype of *C. meijidei* with walking trackways of extinct crocodylomorph ichnotaxa and a modern crocodylian trackway. **A**, Lectotype of *C. meijidei*. **B**, *Batrachopus deweyi* from the Lower Jurassic of the USA (after Padian and Olsen, 1986). **C**, *Antipus flexiloquus* from the Lower Jurassic of the USA (after Coombs, 1996). **D**, *Angolaichnus adamanticus* from the Lower Cretaceous of Angola (after Mateus et al., 2017). **E**, *Mehliella jeffersonensis* from the Cretaceous of the USA (after Mehl, 1931; Lockley 2010). **F**, Modern trackway of *Crocodylus niloticus* (after Mazin et al., 2003). Scale bars equal 3 cm (B), 5 cm (A, C), 10 cm (D, F) 50 cm (E). [Intended for page width]

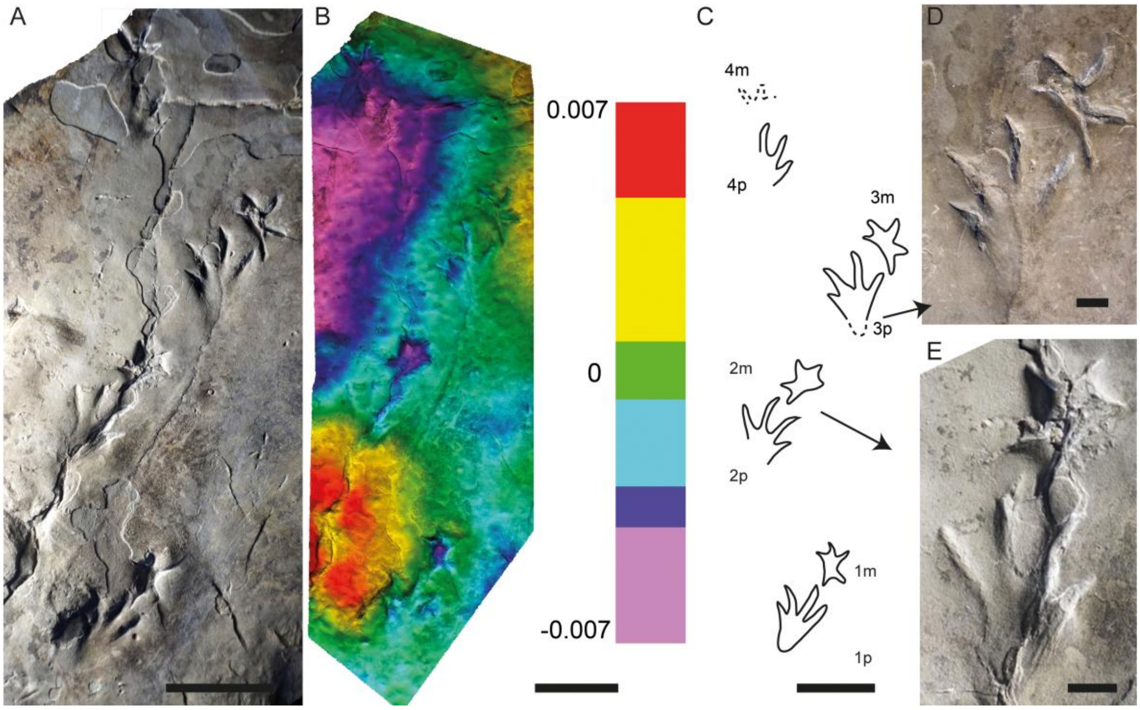
FIGURE 9. Summary of anatomical features that may explain the trackway differences between the trackmaker of *C. meijidei* (an indeterminate neosuchian crocodylomorph) and an indeterminate extant crocodylian. Silhouettes of crocodylomorphs are not based on any particular species. Trackway in B modified from Milàn and Hedegaard (2010). Dark colours indicating depper parts of the footprints. [Intended for page width]

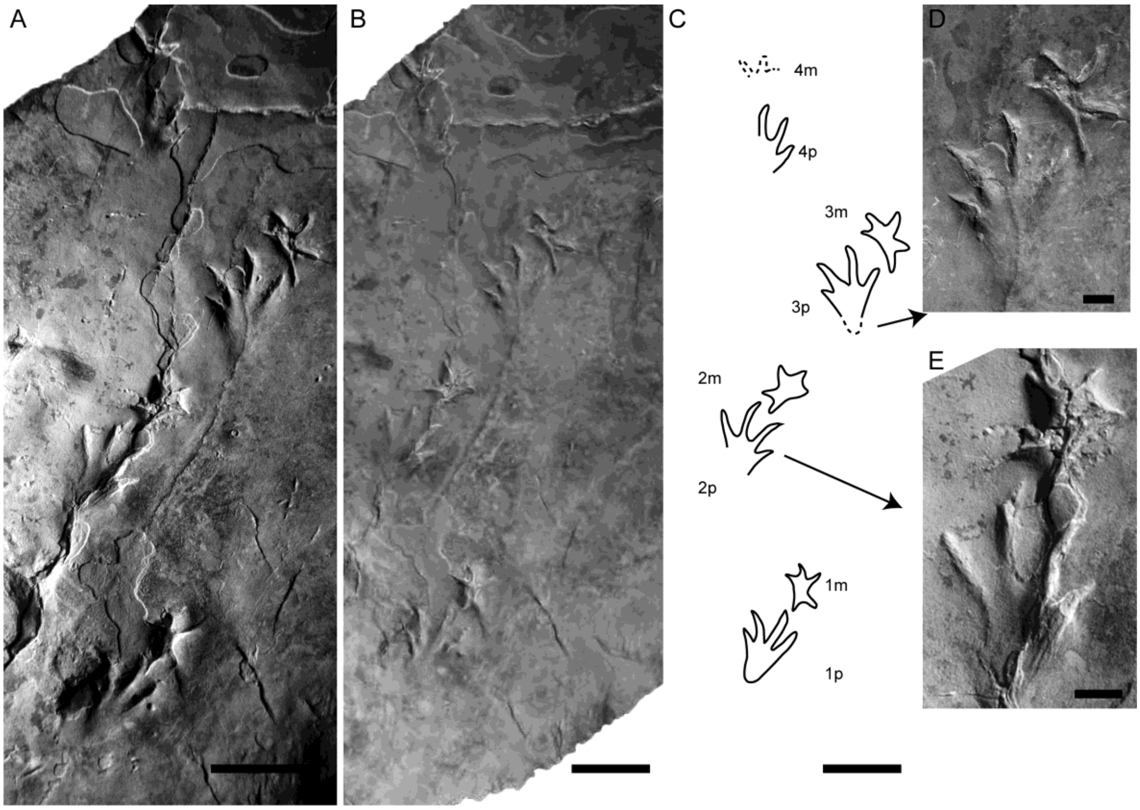

A
Logroño
Burgos
Valladolid
Soria
Zaragoza
Barcelona
Madrid
Valencia
Sevilla
200 Km
N-111
To Logroño
Yanguas
5 Km
Santa Cruz
de Yanguas
Villar del Río
Bretún
San Pedro
Manrique
Ventosa
Los Campos
Matasejún
Valdelavilla
Almarza
El Royo
N-234
To Burgos
Soria
N-122
To Tarazona
B
2º 30W
DS3 Aguilar R.A Fm
DS1 + 2
Jurassic
Variscan basement
Cenozoic
DS 4-7
DS3 Valdeprado Fm
DS3 Huérteles Fm
Yanguas
Villoslada
Montenegro
Bretún
San Pedro
Manrique
42º 0N
Oncala
Almarza
Cerbón
Magaña
N
20 Km

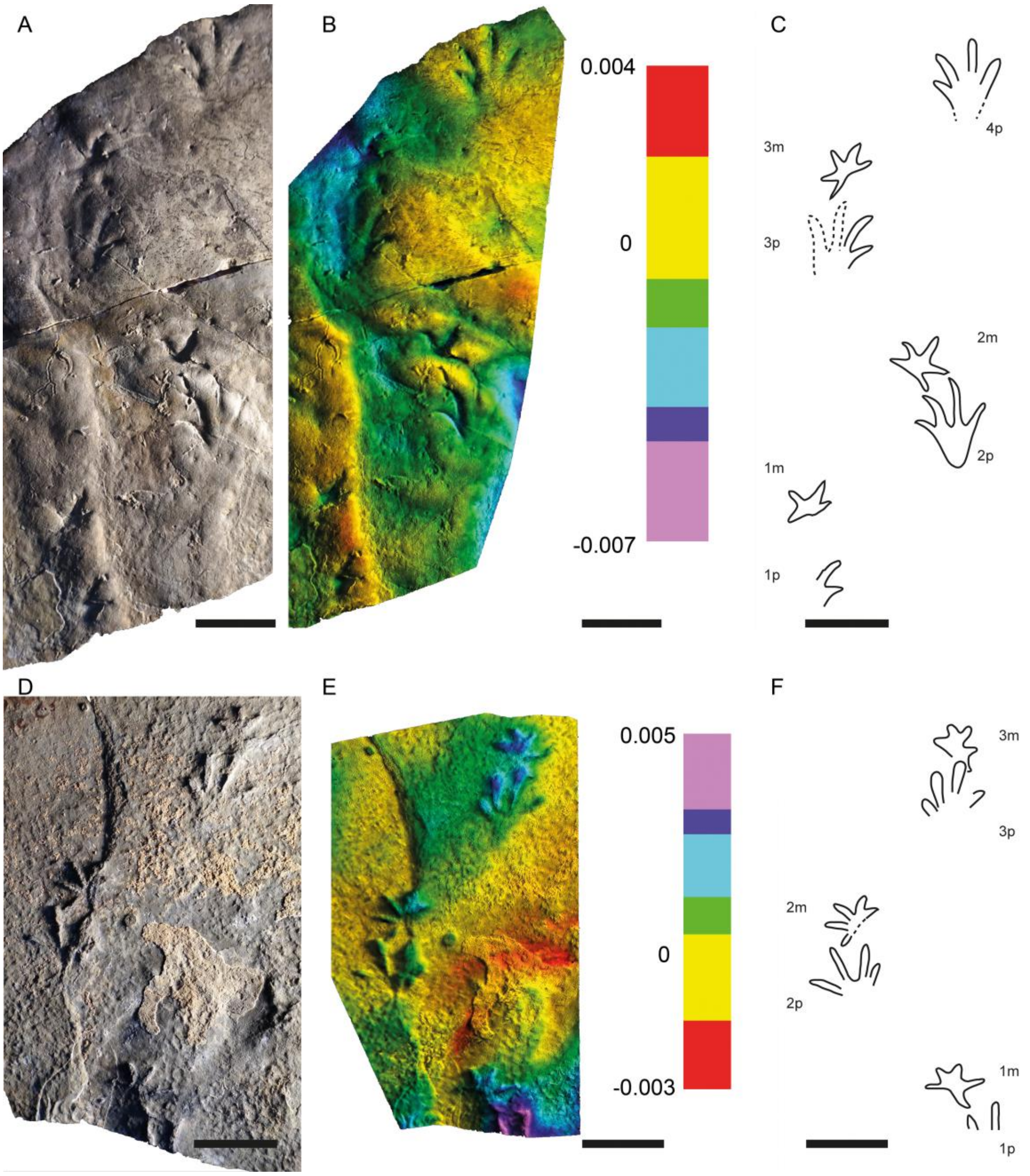

A
Logroño
Burgos
Valladolid
Soria
Zaragoza
Barcelona
Madrid
Valencia
Sevilla
200 Km
N-111
To Logroño
Yanguas
5 Km
Santa Cruz
de Yanguas
Villar del Río
Bretún
San Pedro
Manrique
Ventosa
Los Campos
Matasejún
Valdelavilla
Almarza
El Royo
N-234
To Burgos
Soria
N-122
To Tarazona
B
2º 30W
Vb
J
DS1+DS2
Villoslada
DS4-7
Yanguas
Montenegro
Bretún
DS3
Huérteles Fm
San Pedro
Manrique
DS4-7
42º 0N
DS3
Aguilar R.A. Fm
DS1+DS2
DS4-7
Almarza
Oncala
DS3
Valdeprado Fm
Cerbón
DS1+ DS2
DS1+DS2
J
Magaña
N
CZ
CZ
DS3 Aguilar R.A Fm
DS1 + 2
Jurassic
Variscan basement
Cenozoic
DS 4-7
DS3 Valdeprado Fm
DS3 Huérteles Fm
20 Km

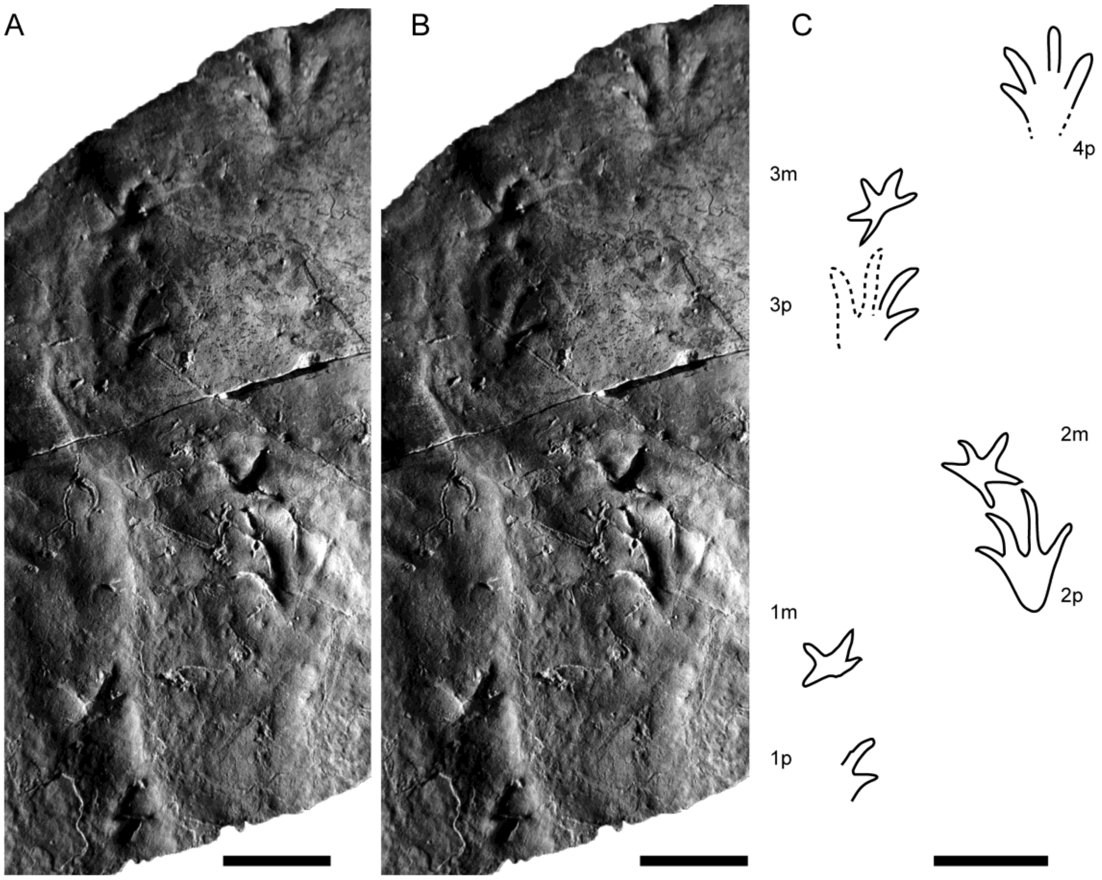

A
ML
ANG
PA
SL
PL
FR
Ar
OW
B
OW
ANG
PA
SL
PL
FR
Dm-p
C
GA
D
FW
LII
LIII
LI
IA
LIV
LV
FL
LIII
LII
LIV
LI
FL
IA
FW

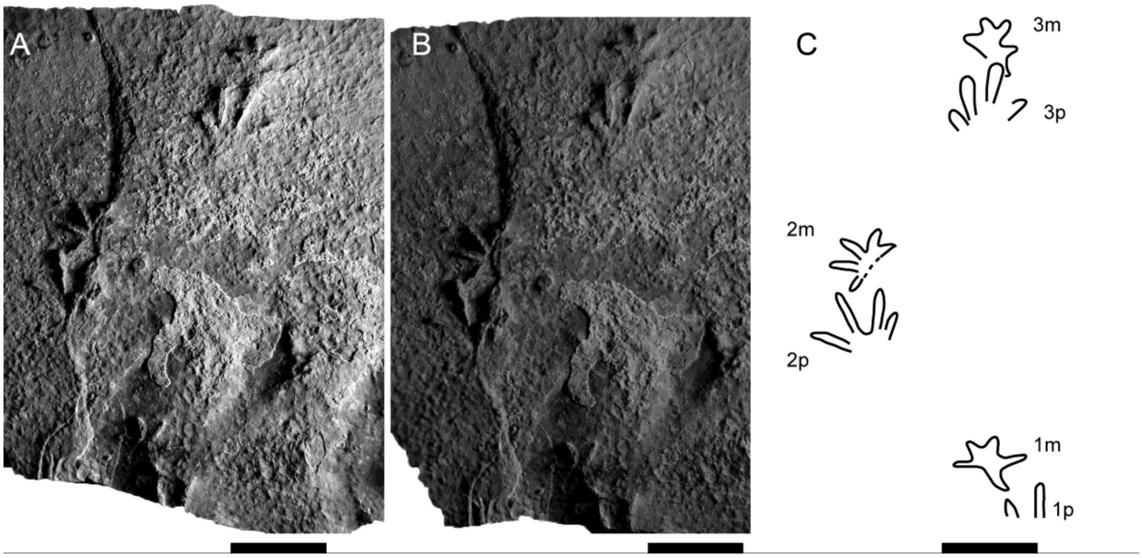

A
ML
ANG
PA
SL
PL
FR
Ar
OW
B
OW
ANG
PA
SL
PL
FR
Dm-p
C
GA
D
FW
LII
LIII
LI
IA
LIV
LV
FL
LIII
LII
LIV
LI
FL
IA
FW

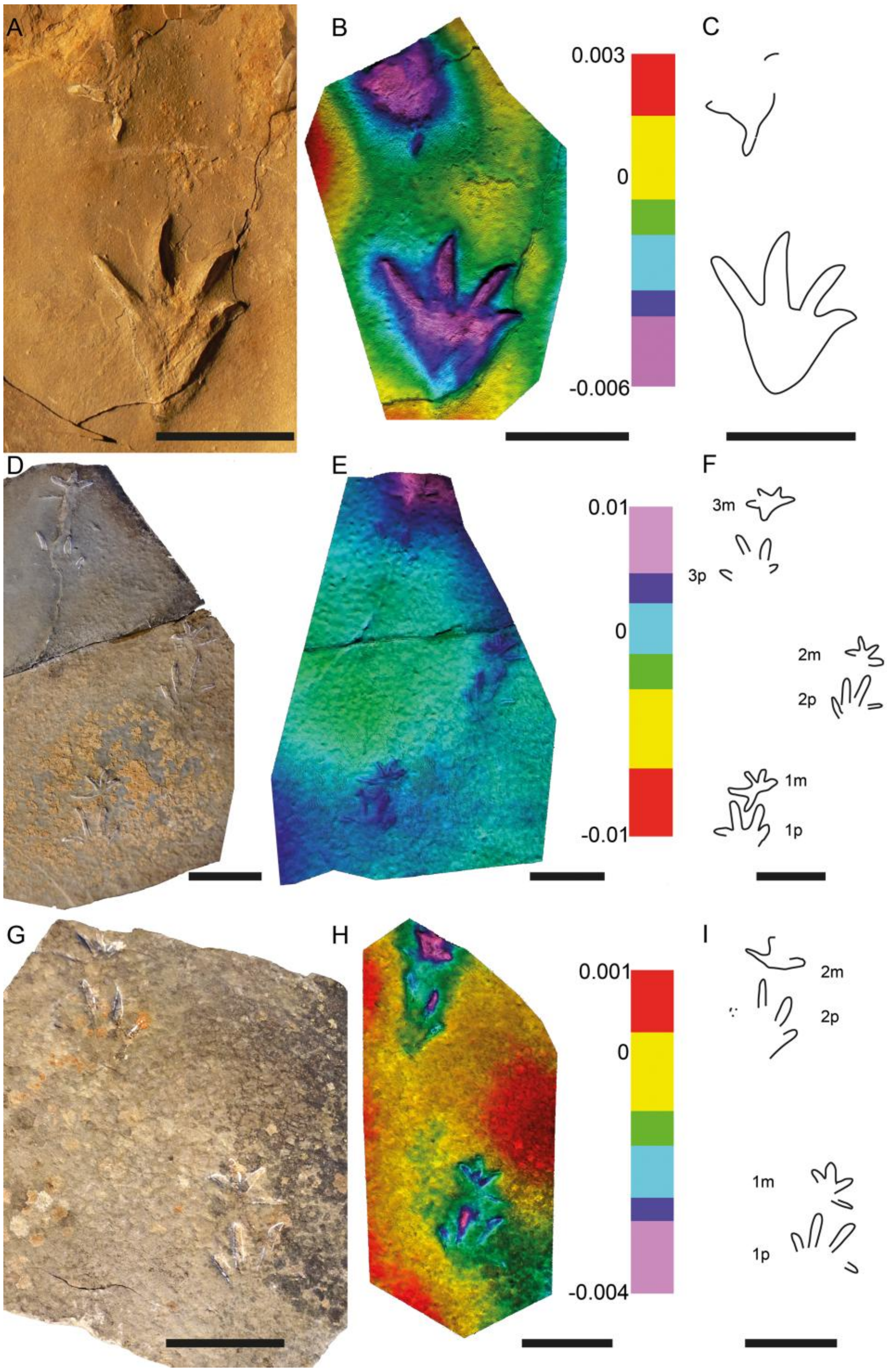

A
B
0.007
0
-0.007
C
4m
4p
3m
3p
2m
2p
1m
1p
D
E

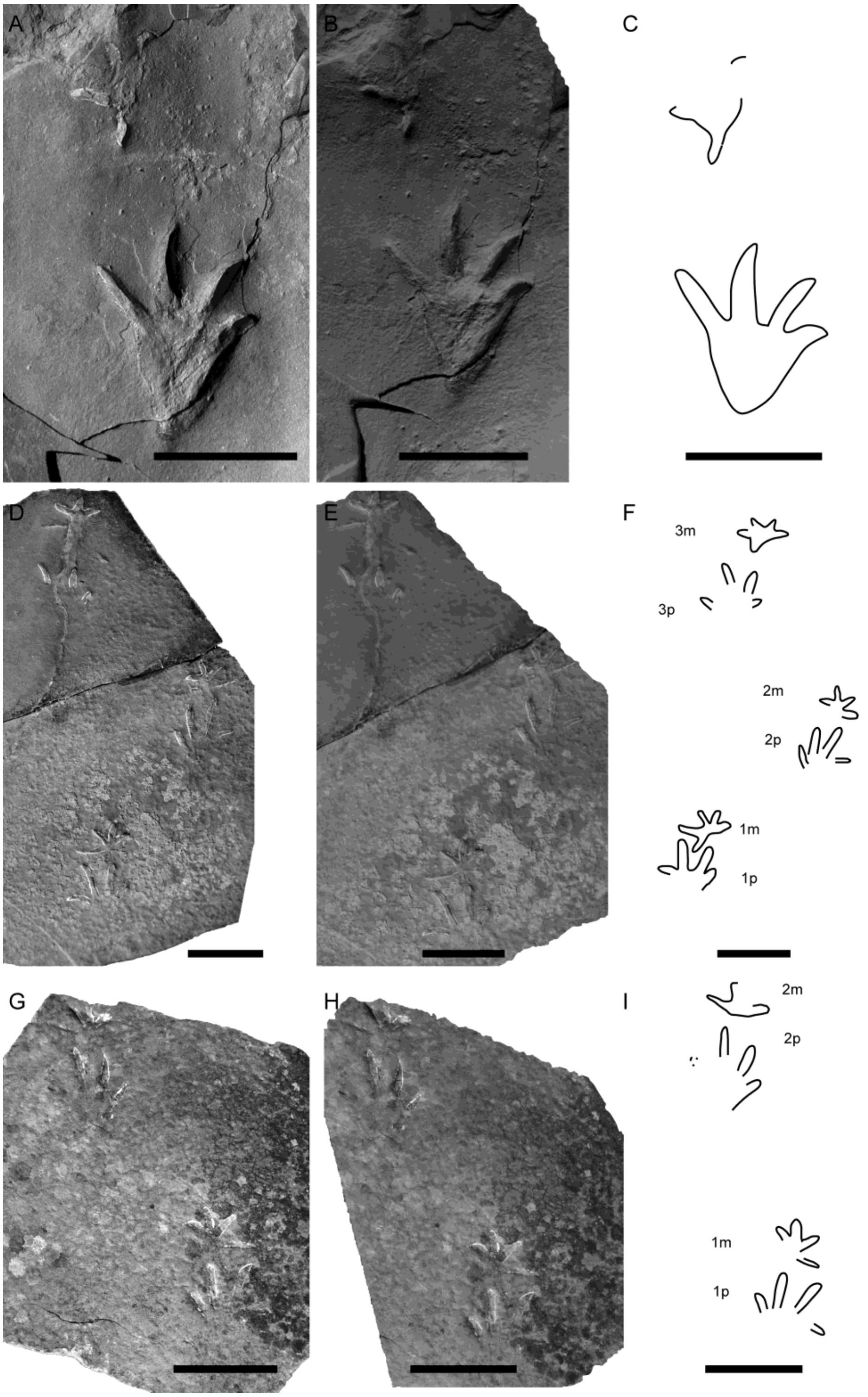

A
B
C
4m
4p
3m
3p
2m
2p
1m
1p
D
E

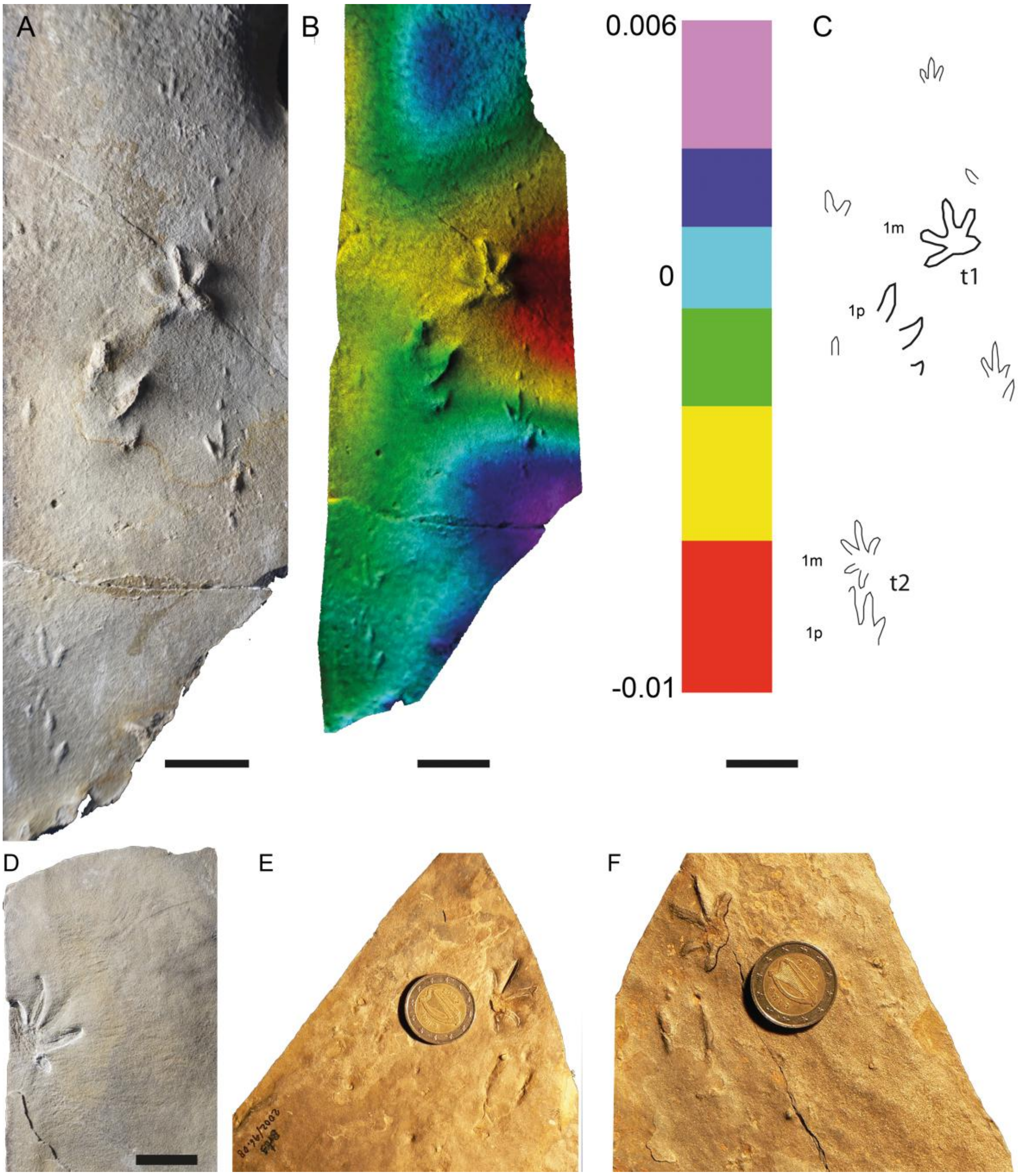

A
B
0.004
0
-0.007
C
4p
3m
3p
2m
2p
1m
1p
D
E
0.005
0
-0.003
F
3m
3p
2m
2p
1m
1p

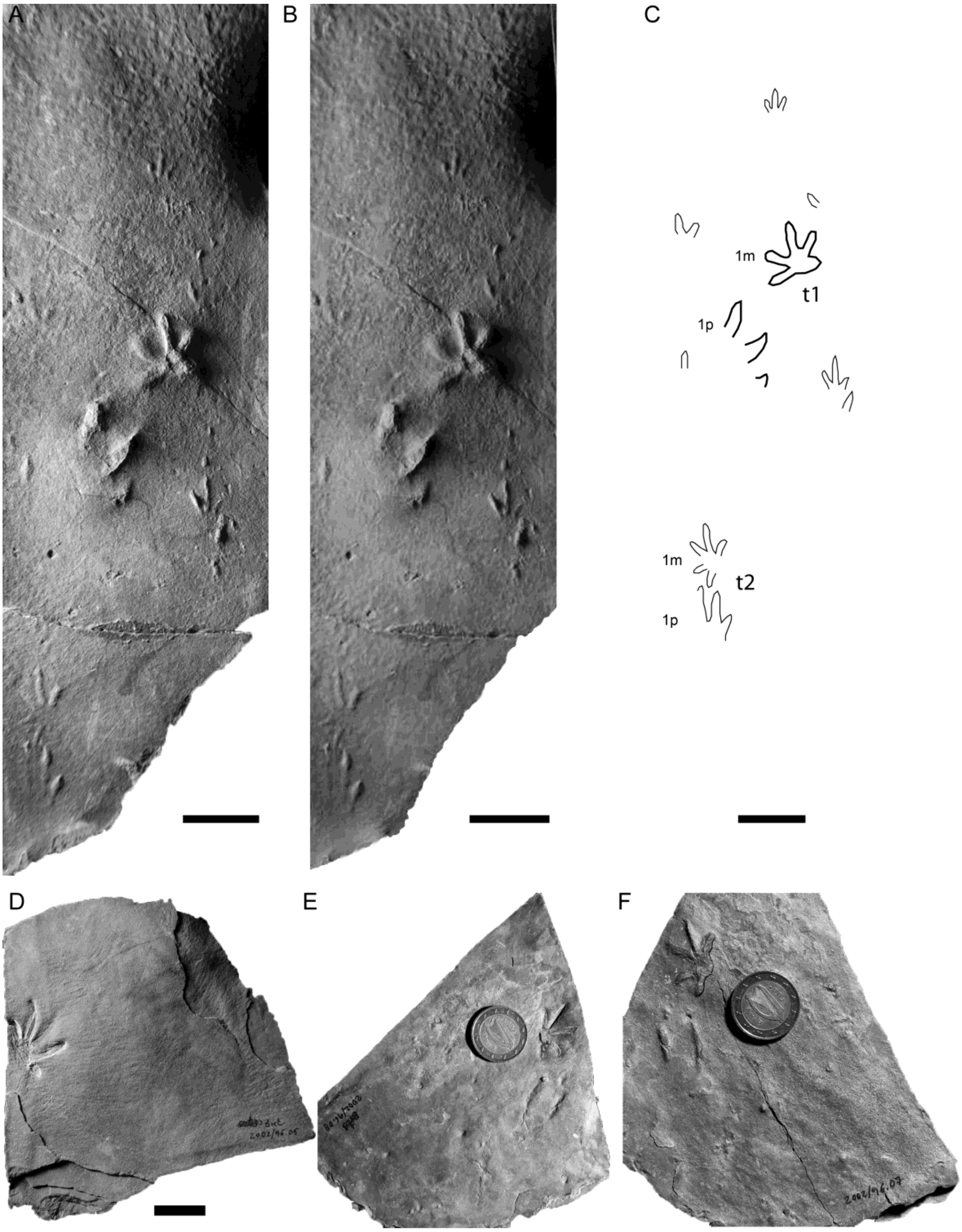

A
B
C
4p
3m
3p
2m
2p
1m
1p

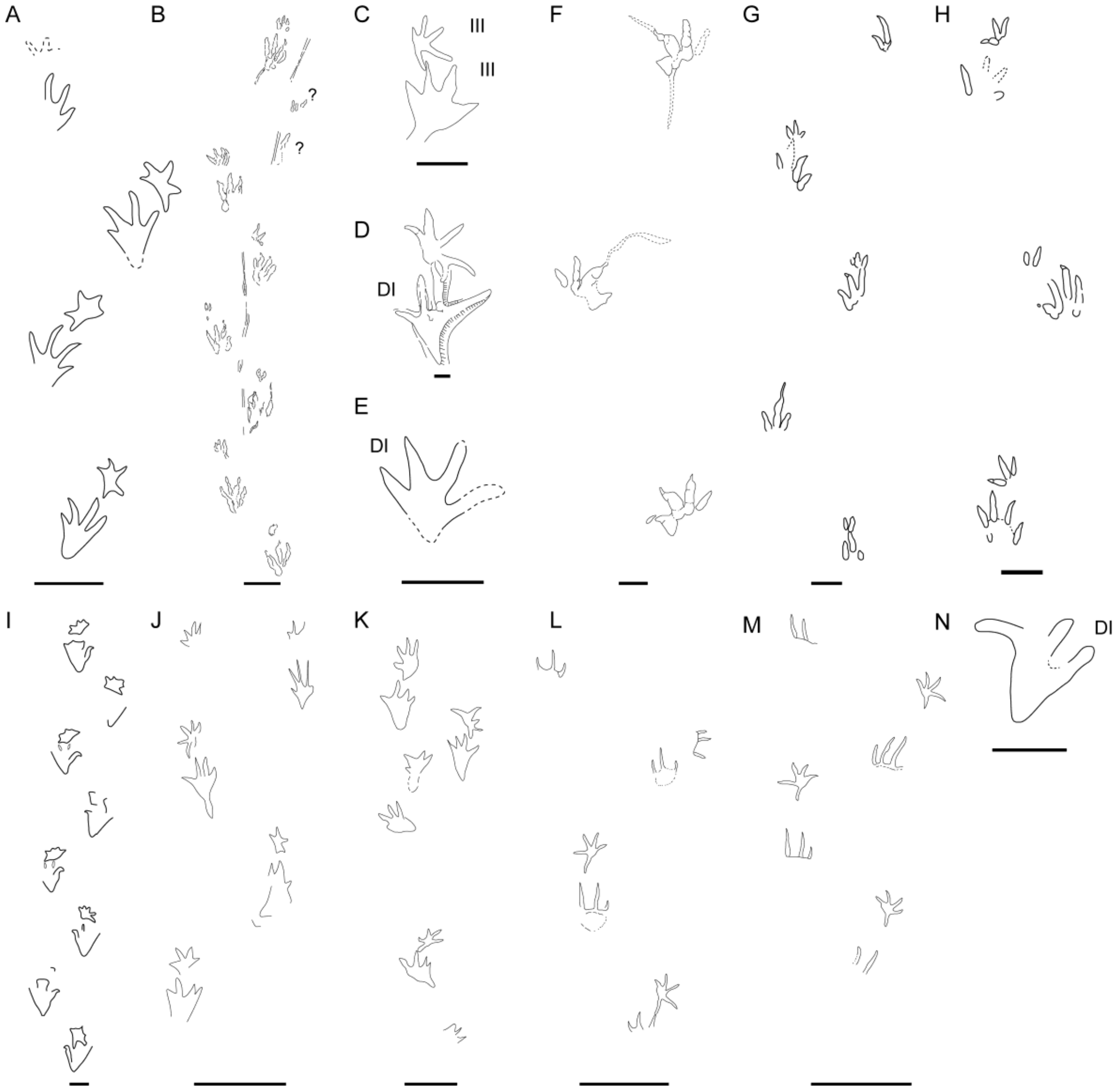

A
B
C
3m
3p
2m
2p
1m
1p

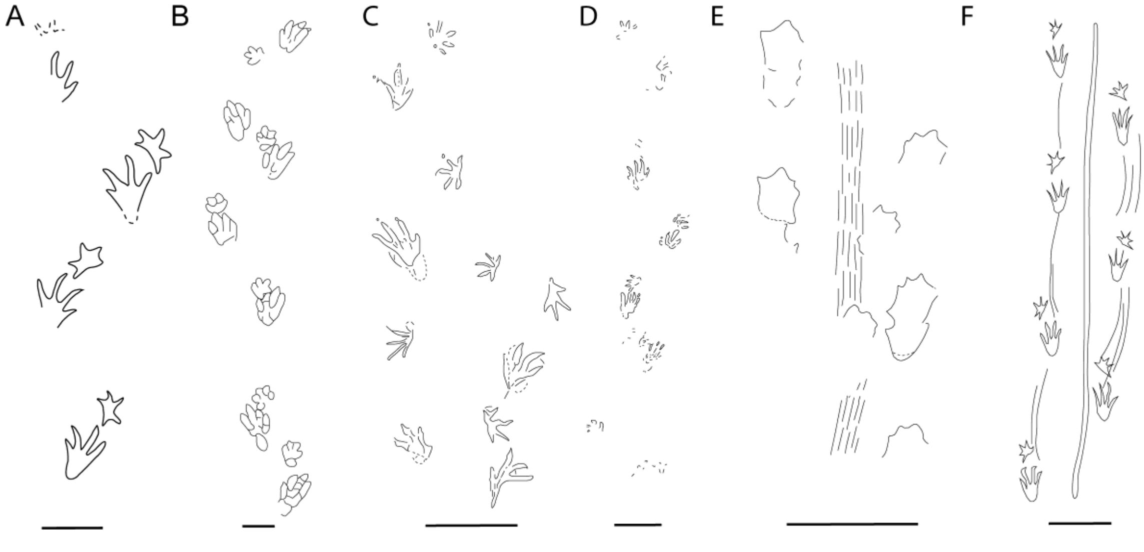

A
B
0.003
0
-0.006
C
D
E
0.01
0
-0.01
F
3m
3p
2m
2p
1m
1p
G
H
0.001
0
-0.004
I
2m
2p
1m
1p

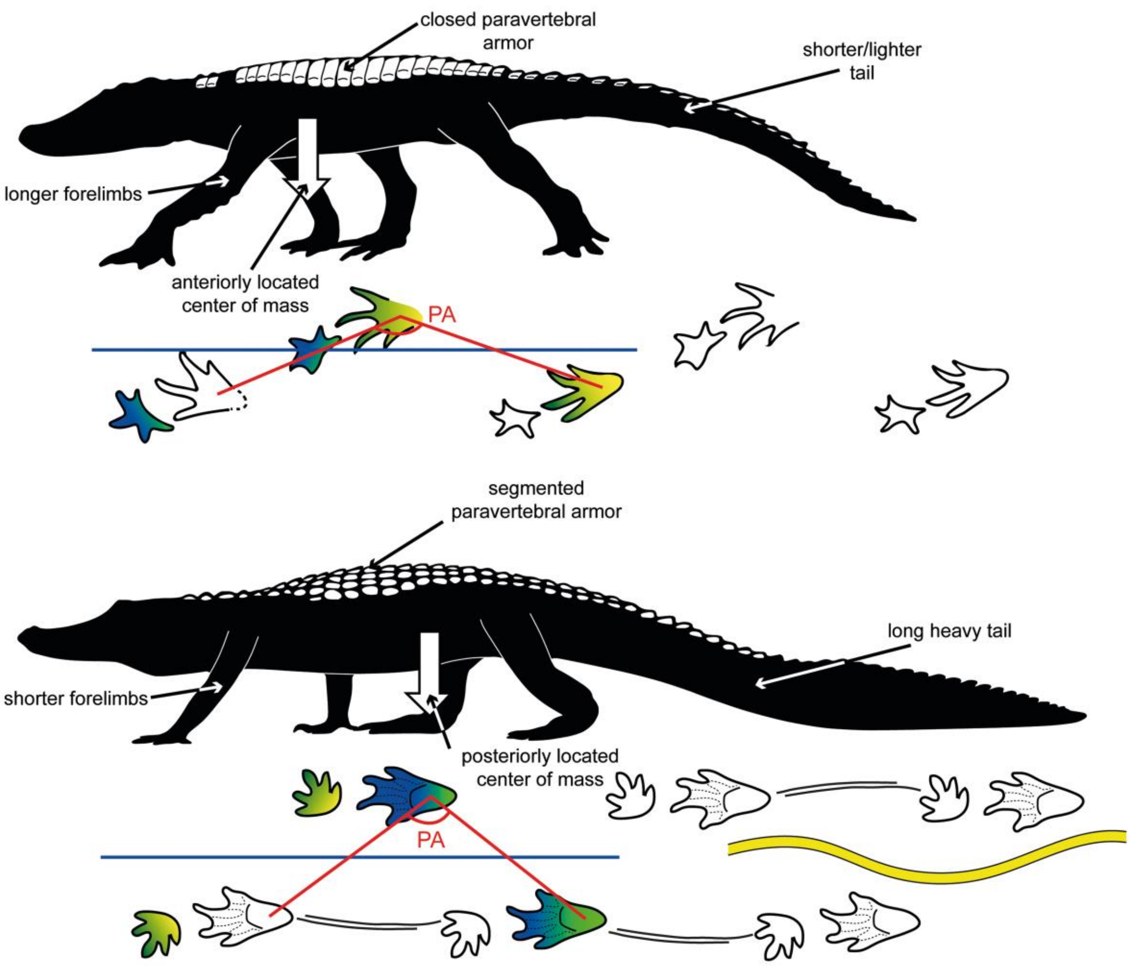

A
B
C
D
E
F
3m
3p
2m
2p
1m
1p
G
H
I
2m
2p
1m
1p


A
B
0.006
0
-0.01
C
1m
t1
1p
1m
t2
1p
D
E
F


A
B
C
1m
t1
1p
1m
t2
1p
D
Bnt.
2002/96.05
E
F
2002/96.07


A
B
?
?
C
III
III
D
DI
E
DI
F
G
H
I
J
K
L
M
N
DI


A
B
C
D
E
F


closed paravertebral armor
shorter/lighter tail
longer forelimbs
anteriorly located center of mass
PA
segmented paravertebral armor
long heavy tail
shorter forelimbs
posteriorly located center of mass
PA

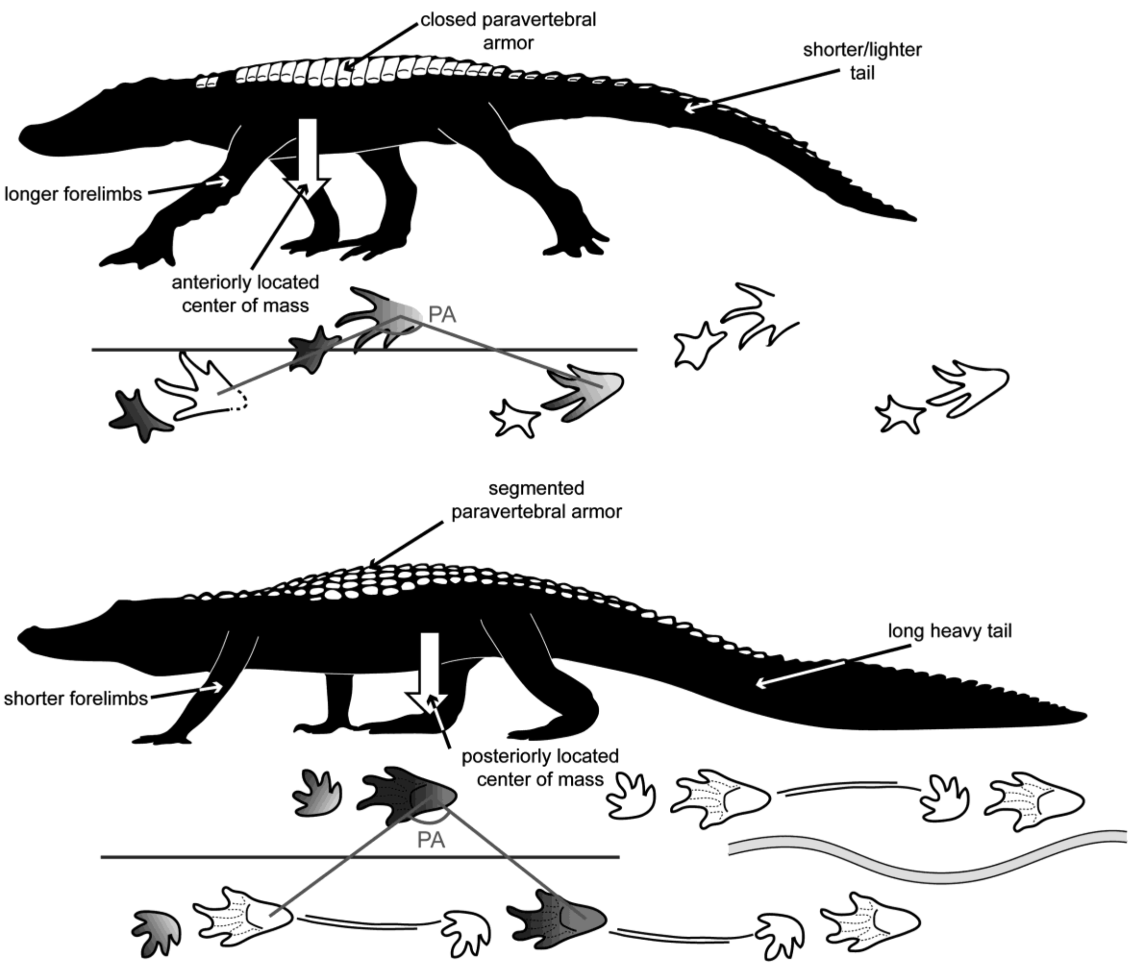

closed paravertebral armor
shorter/lighter tail
longer forelimbs
anteriorly located center of mass
PA
segmented paravertebral armor
long heavy tail
shorter forelimbs
posteriorly located center of mass
PA

TABLE 1: Measurements of the lectotype (MNS2002/96/2bis) of *Crocodylopodus meijidei*. **MP**, Morphological preservation value (Marchetti et al., 2019); **FL**, footprint length; **FW**, footprint width; **FL/FW**, footprint length/footprint width ratio; **LI, LII, LIII, LIV, LV**, digital impression length; **WI, WII, WIII, WIV, WV**, digital impression width; **I^II, II^III, III^IV, IV^V**, **Total IA**, interdigital divarication angles; **Dm–p**, manus-pes distance; **HI**, heteropody index; **PL**, pace length; **SL**, stride length; **PA/ANG**, pace angulation (**PA**, center of the footprint; **ANG**, tip of the impression of digit III); **FR**, footprint rotation; **OW** = overall width; **GA**, glenoacetabular distance. **Ar** = inner trackway width. FL, FW, LI, LII, LIII, LIV, LV, WI, WII,WIII, WIV, Dm-p, PL, SL, OW, GA, Ar in cm. I^II, II^III, III^IV, IV^V, Total IA, PA, ANG, FR in degrees (º). HI, PTR, MTR in %.

Trackway MNS2002/96/2bis	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III
1p	2.5	5	3.5	1.42	3.2	4.5	5	4.2	none	0.5	0.5	0.5	0.6	none	13	21
1m	1.5	1.5	2.5	0.6	1.1	1.3	1.7	1.3	1	0.3?	0.3?	0.3?	0.3?	0.3?	38	53
2p*	2	4.6	3.3	1.39	3.5	4.5	4.6	4.1	none	0.5	0.5	0.4	0.4	none	15	24
2m	2	1.8	2.4	0.75	1.2	1.6	2	1.6	1	?	?	?	?	?	50	59

TABLE 1.

(Continued)

	2.5	5.1	3.9	1.3	3.2	4.7	5.1	4.2	none	0.3	0.4	0.4	0.5	none	10	23
3m	2.5	2.2	3	0.73	1.5	1.9	2.2	1.7	1.5	0.3	0.4	0.4	0.4	0.4	36	56
4p	1.5	?	?	?	1.8	3	3.3	?	none	0.4	0.4	0.4	?	?	?	?
4m	1	2?	2.9?	0.68?	?	?	?	?	?	?	?	?	?	?	?	?

	III^IV	IV^V	Total IA	Dm–p	FL x FW	HI	PL	SL	PA	ANG	FR	OW	GA	Ar	Ar/FW
1p	22	none	56	4.5	17.5	21	11.5	20	none	none	8-I	5.8	14.2	2.2	0.62
1m	66	61	218	4.5	3.75	21	11.5	20	none	none	36-O	6.3	14.2	none	none
2p*	18	none	57	4.4	15.18	28	10.5	17	137	137	20-I	7.5	11.5	2	0.6
2m	57	43	209	4.4	4.32	28	9.5	17	140	129	15-O	6	11.5	none	none
3p	24	none	57	3.8	19.89	33	10	none	118	116	none	8.7	?	2.3	0.58
3m	58	65	215	3.8	6.6	33	11.6	none	105	102	none	8.9	?	none	none

TABLE 1.

(Continued)

4p	?	?	?	4.3	?	?	?	?	?	?	?	7.7?	?	?	none
4m	?	?	?	4.3	?	?	?	?	?	?	?	8.8	?	none	none

Observations: * heel inferred

A new look at *Crocodylopodus meijidei*: implications for crocodylomorph locomotion

DIEGO CASTANERA[1*], CARLOS PASCUAL-ARRIBAS[2], JOSÉ IGNACIO CANUDO[3], EDUARDO PUÉRTOLAS-PASCUAL[3,4,5]

1: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, c/ Escola Industrial 23, 08201 Sabadell, Barcelona, Spain;

2: C. Real 65, 42002 Soria, Spain. capascual-1@telefonica.net;

3: Aragosaurus—IUCA, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, 50009 Zaragoza, Spain. jicanudo@unizar.es;

4: GeoBioTec, Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa, Caparica, Portugal. eduardo.puertolas@gmail.com;

5: Museu da Lourinhã, Lourinhã, Portugal;

* Corresponding author. Email: diego.castanera@icp.cat; dcastanera@hotmail.es

SUPPLEMENTAL DATA: DESCRIPTION OF THE PARATYPES AND REFERRED MATERIAL

MNS2003/92/8a. This specimen is one of the holotypes (Trackway B and fig. 2 in Fuentes Vidarte and Meijide Calvo, 2001) and one of the paratypes according to Lockley and Meyer (2004). The specimen (Fig. 4A-C) is composed of seven footprints, three manual-pedal sets, and one pedal print at the end of the trackway. The tracks are preserved as true tracks or very shallow undertracks. The MP value is high and quite constant (MP = 2–2.5), with the exception of the first manual-pedal set (MP = 1). It is a small- to medium-sized specimen (Pedal FL= 4.9–5.1 cm; Pedal FW = 3.9–4.1 cm). The manual prints are pentadactyl, star-shaped and wider than long (FL/FW ratio = 0.61–0.7). The digital impressions are thin with an acuminate end. DIII is the longest (1.9–2.1 cm), DII and DIV are similar and slightly shorter, whereas DI and DV are the shortest and also similar in length. The digital impressions are thin (WI-WV = 0.2–0.4 cm). I^II is the lowest angle (40–43º), the angles II^III (60–65º) and III^IV (61–67º) being higher and similar, whereas angle IV^V (42–59º) is slightly lower and variable. The total divarication in the manual impressions is high (IA = 203º–234º). Generally, digital impressions I-II and IV-V are oriented medially and laterally respectively, and digital impression III has an anterior-anterolateral orientation. DI and DV are slightly opposed. The manual prints are laterally rotated (28–40º). No clear claw marks are identified. The pedal impressions are tetradactyl, subtriangular in shape, and longer than wide (FL/FW ratio =1.19–1.3). The central digital impressions are longer than the lateral and medial ones. DIII is the longest (4.9–5.1 cm), DII (4.5–4.8 cm) and DIV (4–4.1 cm) are slightly shorter, but DII is clearly longer than DIV. DI is the shortest, being considerably shorter (3.3–3.7 cm). The digital impressions are noticeably thin (WI-WIV = 0.3–0.4 cm). The four of them have an acuminate end but only 2p shows clear evidence of claw marks in the first three digital impressions and a slightly rounded distal end in DIV. The orientation of the digital impressions is medial (DI and DII), anteromedial (DIII) and anterolateral (DIV), with a high total IA angle of 60–67º. I^II (16–19º) is the lowest angle, II^III (20–28º) and III^IV (23–25º) being relatively similar but variable. The heel area is shallow and poorly preserved in all the tracks but 2p possibly shows an oval to subtriangular symmetric morphology. Pedal rotation is low (6–20º) and medial. The manual-pedal distance is short (4.3–4.8 cm). PL is very similar for manual and pedal impressions (10.2–12.5 cm). SL is also very similar for both (19–19.5 cm). The trackway is intermediate-gauge (Ar/FW = 0.8-0.84). PA is medium-high, with values of 107–109° for the pedal impressions and 120º for the manual (ANG = 110º for both). The heteropody is medium, with HI of 29–31% suggesting that the manual-pedal ratio was around 1:3. There is not a great difference between the maximum depth of manual and pedal impressions, but in both limbs the anterior part is deeper; notably, digital impressions II-III-IV are deeper than I and V in the manual prints. There is no evidence of overprinting or of tail or belly drag marks. The estimated glenoacetabular distance is 14.2 cm.

MNS2002/96/4. This specimen is one of the holotypes (Trackway C and fig. 3 in Fuentes Vidarte and Meijide Calvo, 2001) and one of the paratypes according to Lockley and Meyer (2004). The specimen is composed of three manual-pedal sets although the first pedal print is not complete. The tracks (Fig. 4D-F) are preserved as a natural cast (the drawing in Fuentes Vidarte and Meijide Calvo (2001) is a mirror image of MNS2002/96/4). The three manual prints have a medium MP value (1.5-2), whereas the MP of the pedal prints is medium to low (0.5–1.5) since only the anterior part is well marked. It is a small-sized specimen (Pedal FL= 3.7–4.1 cm; Pedal FW = 3.8–3.6 cm). The manual prints are pentadactyl, star-shaped and wider than long (FL = 1.9–2.1 cm; FW = 2.6–2.7 cm; FL/FW ratio = 0.7–0.77). The digital impressions are thin and of variable width (WI-WV 0.2–0.5 cm), with an acuminate end. Manual print 3m has the widest digital impressions. DIII is the longest (1.9–2.1 cm), DII and DIV are slightly shorter, whereas DI and DV are the shortest and similar in length. I^II is the lowest interdigital angle (IA) but quite variable (35–56º), II^III (43–62º), III^IV (46–49º) and IV^V (57–59º) being higher and with similar values though also quite variable. The total divarication in the manual impression is high (IA = 200–206º). Generally, DI-DII and DIV-DV are oriented medially-anteromedially and laterally-posterolaterally, respectively; DIII has an anterior-anterolateral orientation. DI and DV are to a large extent opposed (e.g. 1m). The manual prints are laterally rotated (23º–43º). No clear claw marks are identified in the manual impressions. The pedal prints are tetradactyl and longer than wide (FL/FW ratio =0.97–1.33), although the heel is not preserved and the real lengths of the autopod cannot be calculated. DIII is the longest (3.7–4.1 cm), DII (3.6–3.7 cm) is slightly shorter, whereas DIV (2.8–3.1 cm) and DI are even shorter (2.5–2.8 cm). The digital impressions are thin, and the width varies (WI-WIV = 0.2–0.5 cm) among the different digits but also in different pedal impressions. The digital impressions have an acuminate end, with no clear evidence of claw marks. The orientation of the digital impressions is medial (DI), anteromedial (DII and DIII) and lateral (DIV), with a high (higher than the other specimens) total divarication angle of 71–89º. I^II (20–27º) is the lowest angle, II^III (22–31º) and III^IV (22–38º) being relatively similar but variable among the digital impressions. The heel area is not preserved (the total FL would be longer). Pedal rotation is very low (3–5º) and medial. The manual-pedal distance is short (3.5–4.2 cm). PL is very similar for manual and pedal impressions, with almost no variation between them (10.5–11.2 cm). SL is also very similar for the trackway (19.1–19.2 cm). The trackway is intermediate-gauge (Ar/FW = 0.68-0.88?). PA is medium-high, with 110°? for the pedal and 118º for the manual impressions (ANG =100º and 105º, respectively). The heteropody is medium, with an HI of 36–38% suggesting that the manual-pedal ratio was around 1:3. The manual prints are slightly deeper than the pedal prints although the anterior part of the pedal reaches a similar depth. There is evidence of overprinting in the third manual-pedal set, with the pedal partially overprinting DI of the manual impression. There is no evidence of tail or belly drag marks. The estimated glenoacetabular distance is 12.8 cm.

MNS2002/96/3. This specimen is an isolated manual-pedal set regarded by Fuentes Vidarte and Meijide Calvo (2001) as a paratype (fig. B in Fuentes Vidarte and Meijide Calvo, 2001). The tracks (Fig. 5A-C) are preserved as true tracks or very shallow undertracks, with the pedal showing a high MP value (2.5), but the manual has a low MP (0.5) and only some digital impressions can be distinguished. It is the largest specimen in the whole sample, being clearly medium-sized (Pedal FL= 7 cm; Pedal FW = 5.6 cm). The manual print morphology is not well preserved, but an FL of 2.8 cm and FW of 4.1 cm are estimated, making the print wider than long, with a FL/FW ratio of 0.68. The pedal impression is tetradactyl, subtriangular in shape, and longer than wide (FL/FW ratio = 1.25). DIII is the longest (7 cm), whereas DII and DIV are subequal in length (6.3 and 6.2 cm, respectively) and are considerably longer than DI (4.8 cm). The digital impressions are thicker than in the other specimens, WI and WII being slightly thinner than WIII and WIV (FW = 0.6 vs 0.8 cm). The four digital impressions have acuminate ends, the first three digital impressions being more acuminate than digit IV, indicating not well-preserved claw marks in DI-DIII and their absence in DIV. The orientation of the digits (taking into account the midline of the track) is medial (DI), anteromedial (DII), anterior (DIII) and anterolateral (DIV), with a high IA (61º) increasing from I to IV. I^II is the lowest angle (13º), then come II^III (21º) and III^IV (27º). The heel area is shallower than the anterior part of the footprint, but the morphology seems to be oval to subtriangular and quite symmetric. The manual-pedal distance is 9 cm, i.e. comparatively longer than previous specimens. The heteropody is pronounced, with an HI of 29% suggesting that the manual-pedal ratio was around 1:3. The pedal print is deeper than the manual print. Fuentes Vidarte and Meijide Calvo (2001) also described in this slab an isolated partial manual track, not clearly identified in this study.

MNS2003/92/8b. This trackway is preserved in the same slab as MNS2003/92/8a (Fig. 5D-F), but the tracks are preserved as natural casts. It is composed of three manual-pedal sets with a generally low-medium MP value (1–1.5), only 1m having a medium-high MP (2). It is a small-sized specimen (Pedal FL= 3.7–4.1 cm; Pedal FW = 3.4–4 cm). The manual prints are pentadactyl, star-shaped and wider than long (FL = 1.5? –1.8 cm; FW = 2.4–2.8 cm; FL/FW ratio = 0.6–0.7), but not all the digital impressions are clearly impressed. The digital impressions are thin and of similar width (0.3–0.4 cm), with an acuminate end. DIII (1.6–1.8 cm) and DIV (1.6–2.2? cm) are the longest, DII is slightly shorter (1.4–1.6 cm), and DI and DV are the shortest and similar in length (1.3–1.5 cm). The interdigital angle is quite variable. In 1m these are as follows: I^II (45º), II^III (51º) III^IV (55º) and IV^V (55º), the total IA being high (206º). DI is oriented medially, DII antermedially, DIII anteriorly, DIV laterally, and DV posterolaterally. DI and DV are in large measure opposed. The manual prints are laterally rotated (37–42º). No clear claw marks are identified in the manual impressions.

The pedal prints are tetradactyl and slightly longer than wide (FL/FW ratio =0.92–1.14) because the heel is not preserved and the real length of the autopod cannot be calculated. The central digital impressions (DII and DIII) are longer than the lateral and medial ones. DIII is the longest (3.7–4.1 cm) and DII (3.6–3.9 cm) is slightly shorter, whereas DIV (2.5–2.8 cm) and DI are even shorter (2.5–2.8 cm) and are similar in length. The digital impressions are thin, with widths varying (WI-WIV 0.2–0.5 cm) among the different impressions but also in different pedal prints. The digital impressions have an acuminate end with no clear evidence of claw marks. The orientation of the digital impressions is medial (DI), medial to anteromedial (DII), anterior to anterolateral (DIII), and lateral (DIV), with a high (higher than the other specimens) total IA of 72–95º. I^II (23–25º) and II^III (21–30º) are slightly lower than III^IV (28–40º). Pedal rotation is very low, almost 0 (0–4º) and medial. The trackway is intermediate-gauge (Ar/FW = 0.75-0.94). The manual-pedal distance is short (3.5–4.4 cm). PL is very similar for both manual and pedal impressions (11–12 cm). SL is also very similar for manual (19.5 cm) and pedal impressions (18.5 cm). PA is medium-high, with 106° for the pedal prints and 110º for the manual prints. The heteropody is pronounced to medium, with a heteropody index of 27–32% suggesting that the manual-pedal ratio was roughly 1:3. The manual prints are deeper than most of the pedal print, with the exception of the anterior part, the heel area being shallower than the anterior part of the footprint. There is no evidence of overprinting, or of tail or belly drag marks. The estimated glenoacetabular distance is 13 cm.

MNS2002/96/10. MNS2002/96/10 (Fig. 5G-I) is composed of two consecutive manual-pedal sets preserved as true tracks with a rather low-medium MP value (1–1.5). These two set of tracks correspond to the mold of the first two sets of the specimen

MNS2003/92/8b (part and counterpart). It is a small-sized specimen (Pedal FL= 3.8–4 cm; Pedal FW = 3.6 cm). The manual prints are star-shaped but not all the digital impressions can be distinguished, so the prints look tetradactyl. They are wider than long (FL = 1.4–1.8 cm; FW = 2.2–2.7 cm; FL/FW ratio = 0.63–0.66). The digital impressions are thin, with variable widths (0.2–0.4 cm) and an acuminate end. DIII (1.5–1.8 cm) and DIV (1.5–1.7 cm) are the longest, DII is similar or slightly shorter (1.3–1.8 cm), and DI and DV are the shortest and similar in length (1.3–1.5 cm). The digital divarication angles are quite variable: I^II (42º), II^III (55º), III^IV (38–63º) and IV^V (47–50º). The total IA is high (210º). DI is oriented medially, DII anteromedially, DIII anteriorly, DIV anterolaterally, and DV laterally. DI and DV are largely opposed (e.g. 1m). The manual prints seem laterally rotated. No clear claw marks are identified in the manual impressions. The pedal prints are tetradactyl and slightly longer than wide (FL/FW ratio =1.05–1.1) because the heel is not preserved and the real length of the autopod cannot be calculated. The central digital impressions (DII and DIII) are longer than the lateral and medial ones. DIII is the longest (3.8–4 cm), DII (3.6–3.7 cm) is slightly shorter, whereas DIV (2.4–3 cm) and DI are the shortest (2.6–2.9 cm) and are similar in length. The digital impressions are thin, with widths varying from 0.2–0.5 cm among them but also in different pedal impressions. The digital impressions have an acuminate end with no clear evidence of claw marks. The orientation of the digital impressions is medial (DI), anteromedial (DII), anterior to anterolateral (DIII), and lateral (DIV), with a high (relative to the other specimens) total divarication angle of 77º–99º: I^II (25–26º) and II^III (21–31º) are slightly lower than III^IV (31–42º). The heel area is not preserved, being shallower than the anterior part of the footprint. The manual-pedal distance is short (3.4–3.5 cm). The heteropody varies from pronounced to medium; a heteropody index of 21–35% suggests that the manual-pedal ratio was around 1:3. The manual prints are deeper than most of the pedal print, with the exception of the anterior part of the pedal impressions. There is no evidence of overprinting, or of tail or belly drag marks.

MNS2002/96/5. This specimen is an isolated manual track (Fig. 6D) preserved as a true track with a medium MP value (1.5). It is interpreted as a left manual impression and is a large-sized specimen (the largest manual track in the whole sample). It is pentadactyl, star-shaped and wider than long (FL = 2.9 cm; FW = 3.6; FL/FW ratio = 0.8). DIII (2.9 cm) and DIV (2.9–3.2 cm) are the longest digital impressions, DII is slightly shorter (2.6 cm), and DI and DV are the shortest and are slightly different in length (1.8 and 2.1 cm, respectively). The digital impressions are thin, with a width of 0.4 cm and with an acuminate end. The interdigital angles are quite variable, I^II (62º) being the highest, and the others roughly similar to one another: II^III (32º), III^IV (29º) and IV^V (30). The total IA is medium (153º), i.e. considerably lower than in the other specimens. DI and DV are not as opposed, showing a more medial/lateral orientation with respect to the footprint axis.

MNS2002/96/6. This specimen is an isolated manual-pedal set preserved as a natural cast with a very low MP value (0.5–1), so it is not described in detail.

MNS2002/96/7 and MNS2002/96/8. These specimens are part and counterpart (Fig. 6E–6F) of an isolated right manual-pedal set and are preserved as a natural casts (MNS2002/96/7) and true tracks (MNS2002/96/8), respectively. The manual impression has a medium-high MP value (2), whereas the pedal impression has a low MP (0.5) because only two digital impressions can be distinguished. The manual track is pentadactyl, star-shaped and wider than long (FL = 1.8 cm; FW = 2.4; FL/FW ratio = 0.75). DII and DIII are equal in length (1.8 cm), DIV being slightly shorter (1.5 cm), and DI and DV are the shortest and subequal in length (1.2–1.3. cm). III^IV is the highest interdigital angle (59º), whereas the others are more similar to one another: I^II (40º), II^III (41º), IV^V (50º). The total IA is high (190º), albeit lower than in many specimens. The pedal impression only shows marks of two digital impressions, possibly of digits III and IV considering their position, with DIII longer than DIV. The manual-pedal distance is short (about 3.9 cm).

MNS2002/96/12. This specimen (Fig. 6A-C) is composed of different tracks preserved as natural casts. MNS2002/96/12t1 is an isolated manual-pedal set and is a small-sized specimen (Pedal FL= 3.7). The manual impression has a medium MP value (1.5), whereas the pedal has a low MP (1). The manual print shows the typical pentadactyl star-shaped morphology. It is wider than long (FL = 1.8 cm; FW = 2.1 cm; FL/FW ratio = 0.85). DIII (1.8 cm) is the longest digital impression, DII and DIV are subequal in length and slightly shorter (1.4–1.5 cm), and DI and DV are the shortest (0.9 and 1.1). The digital impressions are thin (0.3 cm in width) with an acuminate end. The interdigital angles are quite variable, I^II (51º) and IV^V (60º) being considerably higher than II^III (35º) and III^IV (38º); the total IA is high (184º). DI and DV are slightly opposed. No clear claw marks are identified in the manual prints. Pedal tracks only shows the first three digital impressions. DIII (3.7 cm) is the longest, DII (3.4 cm) being slightly shorter and DI (2.1 cm) considerably shorter. The digital impressions are thin (W = 0.3–04 cm). DIV and the heel impression are not preserved. The digital impressions have an acuminate end, with possible evidence of claw marks (e.g. DII). The divarication angle would possibly be high, since I^III is 46º. The manual-pedal distance is 4.4 cm. The manual print is deep, indeed similar in depth to the anterior part of the pedal impression.

MNS2002/96/t2 is a manual-pedal set preserved as natural casts (B1p-B1m), with a low-medium MP value (1–1.5). The manual-pedal set is thought to be a right one, and is a very small-sized specimen (Pedal FL= 2.5 cm). The manual print is almost complete, pentadactyl, star-shaped and wider than long (FL = 1.4; FW = 1.8; FL/FW ratio = 0.77). In this case, DII is the longest digital impression, DIII being slightly shorter (1.4 cm), whereas DI, DIV and DV are shorter and similar to one another in length (1–1.1 cm). The digital impressions are thin and of similar width (0.2 cm), with an acuminate end. The interdigital angle is variable, I^II (30º) and II^III (36º) being considerably lower than III^IV (52º) and IV^V (58º); the total angle is high (176º). The manual track is laterally rotated with respect to the pedal print. The pedal print is partially preserved and shows three digital impressions. The central digital impressions (DII and DIII) are longer than the medial one, DIII (2.5 cm) being the longest, DII (2.1 cm) slightly shorter and DI (1.5 cm) the shortest. The digital impressions are very thin (W = 0.2–0.3 cm). The total divarication angle would have been low (I^III = 33º). The heel impression is not preserved. The manual-pedal distance is short (2.7 cm). The specimen also preserves other small tracks in the sample, which seem to be tridactyl tracks. They are possibly the impressions of two mani that left only three digits (DII-DIV). These impressions appear to be of roughly similar proportions to B1m, with DIII being longer than DII and DIV.

TABLE S1: Measurements of the paratypes and referred specimens of *Crocodylopodus meijidei*. **MP**, Morphological preservation value (Marchetti et al., 2019); **FL**, footprint length; **FW**, footprint width; **FL/FW**, footprint length/footprint width ratio; **LI, LII, LIII, LIV, LV**, digital impression length; **WI, WII, WIII, WIV, WV**, digital impression width; **I^II, II^III, III^IV, IV^V**, **Total IA**, interdigital divarication angles; **Dm–p**, manus-pes distance; **HI**, heteropody index; **PL**, pace length; **SL**, stride length; **PA/ANG**, pace angulation (**PA**, center of the footprint; **ANG**, tip of the impression of digit III); **FR**, footprint rotation (I, inward; O, outward); **OW** = overall width; **GA**, glenoacetabular distance. **Ar** = distance from center of the track to the midline. FL, FW, LI, LII, LIII, LIV, LV, WI, WII,WIII, WIV, WV, Dm-p, PL, SL, OW, GA, Ar in cm. I^II, II^III, III^IV, IV^V, Total IA, PA, ANG, FR in degrees (º). HI, PTR, MTR in %.

Trackway MNS2003/92/8a	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III	III^IV	IV^V	Total IA	Dm–p	FL x FW	HI	PL	SL	PA	ANG	FR	OW	GA	Ar	Ar/FW
1p	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	4.8	?	?	12	19.5	?	?	10I?	?	14.2	?	?
1m	1	1.3	2.1	0.61	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	4.8	?	?	10.2	19	?	?	28O?	?	14.2	none	none
2p	2.5	5	4.1	1.21	3.6	4.5	5	4	none	0.4	0.4	0.3	0.3	none	19	21	25	none	65	4.3	20.5	29	12.5	19.5	107	110*	12I	10.6	?	3.3	0.8
2m	2.5	2.1	2.9	0.7	1.3	1.8	2.1	1.8	1.4	0.2	0.4	0.4	0.3	0.2	43	65	67	59	234	4.3	6.09	29	12	?	120	110?	33O?	8.2	?	none	none
3p*	2	5.1	3.9	1.3	3.7	4.8	5.1	4.1	none	0.3	0.4	0.4	0.4	none	17	20	23	none	60	4.6	19.89	31	11.5	?	109	110	20I	10.5	?	3.3	0.84
3m	2	2	3.1	0.64	1.6	2	1.9	1.7	1.5	0.3	0.3	0.3	0.3?	0.3	40	60	61	42	203	4.6	6.2	31	?	?	?	?	40O	8.7?	?	none	none
4p*	2	4.9	4.1	1.19	3.3	4.5	4.9	4.1	none	0.4	0.4	0.4	0.4	none	16	28	23	none	67	?	20.09	?	?	?	?	?	6I	10.8	?	3.3	0.8

Observations: * heel inferred. DIII estimated in 1p

Trackway MNS2002/96/4	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III	III^IV	IV^V	Total IA	Dm–p	FL x FW	HI	PL	SL	PA	ANG	FR	OW	GA	Ar	Ar/FW
1p*	0.5	?	?	?	?	0.9	1.5	?	none	?	0.4	0.4	?	none	?	?	?	?	?	4?	?	?	11	19.2	?	?	5I	?	12.8*	?	?
1m	2	1.9	2.7	0.7	1.2	1.6	1.9	2.2	1.5?	0.2	0.4	0.4	0.3	0.3	47	51	49	59	206	4?	5.13	?	10.5	19.1	?	?	23O	8.4	12.8*	none	none
2p	1.5	3.7	3.8	0.97	2.8	3.7	3.7	2.8	none	0.3	0.4	0.3	0.2	none	20	31	38	none	89	4.2	14.06	36	10.6	?	110?	100	?	11	?	2.6	0.68
2m	2	2	2.6	0.76	1.5	1.9	2	1.7	1.4	0.3	0.3	0.3	0.3	0.2	35	62	46	57	200	4.2	5.2	36	11.2	?	118	105	32O?	11	?	none	none
3p	1.5	4.1	3.6	1.13	2.5	3.6	4.1	3.1	none	0.5	0.5	0.4	0.4	none	27	22	22	none	71	3.5	14.76	38	?	?	?	?	3I	12.7	?	3.2?	0.88?
3m	1.5	2.1	2.7	0.77	1.5	1.8	2.1	1.8	1.4	0.2?	0.3	0.4	0.5	0.5	56	43	46	57	202	3.5	5.76	38	?	?	?	?	43O?	11.2	?	none	none

Observations: * 1p broken not complete 2p and 3p heel poorly preserved. Estimations.

Manus/pes set MNS2002/96/3	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III	III^IV	IV^V	Total IA	Dm–p	FL x FW	HI
1p	2.5	7	5.6	1.25	4.8	6.3	7	6.2	none	0.6	0.6	0.8	0.8	none	13	21	27	none	61	9	39.2	29?
1m	0.5	2.8?	4.1?	0.68	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	9	11.48	29?

Trackway MNS2003/92/8b	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III	III^IV	IV^V	Total IA	Dm–p	FL x FW	HI	PL	SL	PA	ANG	FR	OW	GA	Ar	Ar/FW
1p*	1.5	3.7	4	0.92	2.5	3.6	3.7	2.8	none	0.4	0.5	0.5	0.4	none	25	30	40	none	95	3.5	14.8	32	11	18.5	?	?	4I	10	13	3?	0.75
1m	2	1.7	2.8	0.6	1.3	1.6	1.7	2.2?	1.5	0.4	0.4	0.3	0.3	0.3	45	51	55	55	206	3.5	4.76	32	11.5	19.5	?	?	37O	10	13	none	none
2p	1.5	3.9?	3.4	1.14	2.6?	3.6?	3.9?	2.7?	none	0.3	0.4	0.4	0.3	none	23	21	28	none	72	3.8	13.26	27	12	?	106?	?	0	11.5	?	3.2	0.94
2m	1	1.5?	2.4	0.6	?	1.4	1.6	1.6	1.4	?	0.3	0.4	0.4	0.3	38?	48	51	43	180	3.8	3.6	27	12	?	110	105	42O	10.5	?	none	none
3p	1	4.1?	3.8	1.07	2.8	3.9	4.1?	2.5	none	0.4	0.5	0.4	0.2	none	23	28	37	none	88	4.4	15.58	28	?	?	?	?	3I	12.1	?	3.3	0.86
3m	1	1.8	2.5	0.7	1.4	1.4	1.8	1.9?	1.4?	0.3	0.4	0.4	0.3	0.3	51	59	61	50	221	4.4	4.5	28	?	?	?	?	42O	10.5	?	none	none

Observations: * heel inferred

Tracks MNS2002/96/10	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III	III^IV	IV^V	Total IA	Dm–p	FL x FW	HI
1p*	1	3.8	3.6	1.05	2.9	3.7	3.8	2.4	none	0.4	0.5	0.3	0.2	none	26	31	42	none	99	3.5	13.68	35
1m	1.5	1.8	2.7	0.66	1.5	1.8	1.8	1.7	1.3	0.4	0.4	0.3	0.2	0.2?	42	55	63	50	210	3.5	4.86	35
2p	1	4	3.6	1.1	2.6	3.6	4	3	none	0.3	0.4	0.3	0.2	none	25	21	31	none	77	3.4	14.4	21?
2m	1	1.4	2.2	0.63	?	1.3?	1.5?	1.5?	1.4	?	0.4?	0.3?	0.2?	0.2?	?	55?	38?	47?	?	3.4	3.08	21?

Observations: * heel inferred

Slab MNS2002/96/12	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III	III^IV	IV^V	Total IA	Dm–p	FL x FW	PL
t1.1p	1	3.7	?	?	2.1	3.4	3.7	?	None	0.3	0.3	0.4	?	None	23	23	?	none		4.4	?	none
t1.1m	1.5	1.8	2.1	0.85	0.9	1.5	1.8	1.4	1.1	0.3	0.3	0.3	0.3	0.3	51	35	38	60	184	4.4	3.78	none
t2.1p	1	2.5	?	?	1.5	2.1	2.5	?	None	0.3	0.2	0.2	?	None	19	14	?	none	?	2.7	?	?
t2.1m	1.5	1.4	1.8	0.77	1	1.6	1.4	1.1	1.1	0.2	0.2	0.2	0.2	0.2	30	36	52	58	176	2.7	2.52	8.1?

Track	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III	III^IV	IV^V	Total IA
MNS2002/96/5	1.5	2.9	3.6	0.8	1.8	2.6	2.9	2.9-3.2?	2.1	0.4	0.4	0.4	0.4	0.4	62	32	29	30	153

Manus/pes set MNS2002/96/7	MP	FL	FW	FL/FW	LI	LII	LIII	LIV	LV	WI	WII	WIII	WIV	WV	I^II	II^III	III^IV	IV^V	Total IA	Dm–p
1p	0.5	?	?	?	?	?	1.8	1.4	?	?	0.3	0.3	?	?	?	?	?	?	?	3.9
1m	2	1.8	2.4	0.75	1.2	1.8	1.8	1.5	1.3	0.3	0.3	0.3	0.3	0.3	40	41	59	50	190	3.9

TABLE S2. Comparison of the *Crocodylopodus* tracks described in the fossil record. **IA,** interdigital divarication angles (in degrees (º)). **HI**, heteropody index. Heteropody: pronounced (HI < 35%), medium (35-70%) or low (HI > 70%). **PA**, pace angulation. **Ar** = distance from the center of the track to the midline; **FW** = footprint width. Trackway gauge: narrow (Ar/FW < 0.5), intermediate Ar/FW (0.5-1) and wide (Ar/FW >1).*data estimated from the drawing.

Trackway	Age and Geological Formation	Previous Assignations	Size category	FL/FW ratio	Manual morphology	Digital impression lengths in pedal prints	IA	Heel morphology	Heteropody (HI)	PA	Trackway-gauge (Ar/FW)	Other different features	References
MNS2002/96/2bis Lectotype	Lower Cretaceous Huérteles Fm	*C.meijidei*	small-medium	1.37	pentadactyl	DIII> DII > DIV >DI	56	subtriangular	pronounced (30 %)	127	Intermediate (0.58-0.62)		This work
LBP-Type 1	Middle Jurassic Hojedk Fm.	*Crocodylopodus* isp.	small (4.8 cm)	1.3	tetradactyl	DIII> DII > DIV >DI	63	rounded	pronounced (32 %)	108	Intermediate (0.72)	tail present	Abbassi et al., 2015
CDUE 728	Middle-? Upper Jurassic Isli Fm.	*C.meijidei*	medium (6 cm)	1.3	pentadactyl	DIII> DIV > DII >DI	90	elongated	pronounced (22 %)	None	?	DI-DV in manual print more medially/laterally	Klein et al., 2018
MUJA 0101	Upper Jurassic Lastres Fm.	*C.meijidei*	small (2.8 cm)	0.96	not preserved	DIII> DII > DIV = DI	110	not preserved	unknown	126	Intermediate (0.85)	digitigrade pes; drag marks	Avanzini et al., 2007; 2010
MUJA 0102	Upper Jurassic Lastres Fm.	*C.meijidei*	small (2.1 cm)	1.3	tridactyl DI-DV not preserved	DIII> DII > DIV >DI	45	not preserved	medium (48%)	117-140	Intermediate (0.8-0.96)	Phalangeal pads in the pes.	Avanzini et al., 2007; 2010
MUJA0038	Upper Jurassic Lastres Fm.	*C.meijidei*	medium (8 cm)	1.23	pentadactyl	DIII> DII= DIV> DI	170	subtriangular	medium (40%)	?	?	DIV oriented very laterally	Avanzini et al., 2007
SHN.(JJS).ICNO.62	Upper Jurassic Alcobaça Fm.	*Crocodylopodus* isp	medium (7.5 cm)	0.88	not preserved	DII > DIII> DIV> DI	86	subtriangular	unknown	?	?		Castanera et al. 2021
VALD-NV-T2	Berriasian Huérteles Fm.	cf. *Crocodylopodus*	large (21.4 cm)	1.09	pentadactyl	DIII> DII= DIV> DI	48.5	oval	pronounced (29 %)	114	Intermediate (0.65)	digital pads; tail marks? Pes laterally rotated	Pascual et al., 2005

CUE E4 C001	Lower Cretaceous Jinju Fm.	*Crocodylopodus* isp.	medium (7.1 cm)	0.97	tridactyl to pentadactyl	DIII> DII= DIV> DI	42*	subtriangular to elongated	medium (36%)	89.3	wide (1.2)	DI-DIII anteriorly	Lockley et al., 2020
CUE Ji 3rd PCS001	Lower Cretaceous Jinju Fm.	*Crocodylopodus* isp.	medium (8.8 cm)	1.69	pentadactyl	DIII> DII= DIV> DI	45*	subtriangular to elongated	low (73%)	84	wide (1)	DI-DIII anteriorly	Lockley et al., 2020
CUE E100516-Cr001-1	Lower Cretaceous Jinju Fm.	*Crocodylopodus* isp.	small (3.6 cm)	1.1	pentadactyl	DIII> DII > DI	?	not preserved	low (89%)	106	Not calculated pes incomplete	DI-DIII anteriorly	Lockley et al., 2020
CUE E100516-Cr001-2	Lower Cretaceous Jinju Fm.	*Crocodylopodus* isp.	medium (5.4 cm)	1.74	pentadactyl	DII > DIII> DI	?	not well preserved	low (81%)	105	wide* (1.2 but variable)	DI-DIII anteriorly	Lockley et al., 2020
Wesses Canyon	Upper Cretaceous Wahweap	cf. *Crocodylopodus* *cf. Hatcherichnus*	large (14 cm)	1.4	not preserved	DIII> DII= DIV> DI	60	subrounded	unknown	?	?		Simpson et al., 2010; Lockley et al., 2020
Serraduy Norte	Upper Cretaceous Tremp Fm.	cf. *Crocodylopodus*	medium (7.1 cm)	1.2*	not preserved	DIV> DII > DI	70*	subtriangular	unknown	?	?	DIV oriented very laterally	Vila et al., 2015

LITERATURE CITED

Abbassi, N., S. D. O. Porchetti, A. Wagensommer, and M. G. Dehnavi. 2015. Dinosaur and crocodylomorph footprints from the Hojedk Formation (Bajocian, Middle Jurassic) of north Kerman, central Iran. Italian Journal of Geosciences 134(1):86–94.

Avanzini, M., J. C. García-Ramos, J. Lires, L. Piñuela, and M. G. Lockley. 2007. Crocodylomorph tracks from the Late Jurassic of Asturias (Spain). Ichnos 14:143–153.

Avanzini, M., J. C. García-Ramos, J. Lires, L. Piñuela, and M. G. Lockley. 2010. Preservational morphotypes of *Crocodylopodus* from the Late Jurassic of Asturias (Spain). New Mexico Museum of Natural History and Science Bulletin 51: 239–244.

Castanera, D., E. Malafaia, B. C. Silva, V. F. Santos, and M. Belvedere. 2021. New dinosaur, crocodylomorph and swim tracks from the Late Jurassic of the Lusitanian Basin: implications for ichnodiversity. Lethaia, 54(2), 271–287.

Klein, H., A. Lagnaoui, G. D. Gierliński, H. Saber, J. N. Lallensack, M. Oukassou, and A. Charrière. 2018. Crocodylomorph, turtle and mammal tracks in dinosaur-dominated Middle–? Upper Jurassic and mid-Cretaceous ichnoassemblages of Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology 498:39–52.

Lockley, M. G., J. D. Lim, H. D. Park, A. Romilio, J. S.Yoo, J. W. Choi, K. S. Kim, S.-H. Kang, D.H. Kim, and T. H. Kim. 2020. First reports of *Crocodylopodus* from Asia: implications for the paleoecology of the Lower Cretaceous. Cretaceous Research 104441.

Pascual Arribas, C., N. Hernández Medrano, P. Latorre Macarrón, and E. Sanz Pérez. 2005. Nuevo rastro de icnitas de cocodrilo en la Aloformación Huérteles de la Cuenca de Cameros. Studia Geologica Salmanticensia 41:75–91.

Simpson, E. L., H.L. Hilbert-Wolf, M.C. Wizevich, S. G. Lucas, E. Tester, S.E. Tindall, and J. J. Bernard 2010. A crocodylomorph track in the Upper Cretaceous Capping Sandstone Member of the Wahweap Formation, Grand Staircase-Escalante National Monument, Utah, USA. New Mexico Museum of Natural History and Science Bulletin 51:165–170.

Vila, B., D. Castanera, J. Marmi, J. I. Canudo, and À. Galobart. 2015. Crocodile swim tracks from the latest Cretaceous of Europe. Lethaia 48(2):256–266.

TABLE S3. Summary of the main footprint and trackway features in extant crocodylians. **FL,** Footprint length; **TL,** Total length; **IA,** interdigital divarication angles (in degrees (º)); **FR**, footprint rotation; **PA**, pace angulation; **Ml,** midline. * estimated from pictures. Note that some species names and ontogenetic states are abbreviated in the table (e.g.: *Pt* = *Paleosuchus trigonatus;* sa = subadult).

Species	Size category (FL and TL)	Manual morphology	Manual IA	Digital impression lengths in the pes	Pedal IA	Digital orientation in the pes	FR	PA	Trackway features	Other significant features	References
Paleosuchus trigonatus; Crocodylus porosus; Tomistoma schlegelii	small-medium sized 3.3–9.2 cm	tridactyl to pentadactyl claws in DI-DII-DIII	DI-DV more medially/laterally	DIV shallower DI-DIII deeper	20–55º	digit IV is curved anterolaterally	DII-DIII anterior in the pedal impressions	Pt: 94-97º Cp: 75-112º Ts: 76-89º	wide-gauge, tail marks (shallower than manus/pes)	scale impressions in manus and pes. pedal prints deeper than manual.	Kubo 2008
Crocodylus acutus	large to very large 15–24 cm	pentadactyl claw marks in DI-DIII	140º–160º DI-DV more medially/laterally webbing (especially DIV-DV)	DI-DIII with claw impressions. DII and DIII the longest, DI and DIV similar.	35-45º webbing (especially DII-DIV)	DI-DIII more anterior. DIV anterolaterally.	manual and pedal prints slightly lateral	about 90º (measured from DIII)	wide-gauge, drag and tail marks, overstepping manus-pes	DI and the heel deepest parts of the pedal print and pes deeper than the manus	Kumagai and Farlow (2010) Farlow et al. (2018)
Alligator mississippiensis	large 15.5–20 cm	pentadactyl claw marks in DI-DIII	180º DI-DV more medially/laterally	claw marks in DI to DIII	45-55º webbing especially (DIII-DIV)	DIV anterolaterally	manual laterally pedal parallel to midline	105º	wide-gauge, tail and belly drag marks	pes with interdigital webbing increases from DI to DIV (sometimes not registered)	Farlow and Esley, 2010
Paleosuchus palpebrosus	small (juvenile) large sized (adult) 4.8–13.6 cm 50 cm (j)–140 cm (a)	pentadactyl*	179º (j) 145º (a)	DI-DIV subequal in length*	86 (j) 72º (a)	DI-DII anterior-anterolaterally; DII-DIV anterolaterally*	manual laterally pedal parallel to midline*	87º (j)-102º (a)	wide-gauge, tail mark (j, a) Overprinting (a)		Milàn and Hedegaard (2010)

Species	**Size category (FL and TL)**	**Manual morphology**	**Manual IA**	**Digital impression lengths in the pes**	**Pedal IA**	**Digital orientation in the pes**	**FR**	**PA**	**Trackway features**	**Other significant features**	**References**
Caiman latirostris	medium (subadult) large sized (adult) 7.8–12.2 cm 70 cm (sa)–135 cm (a)	overprinted	overprinted	DI-DIV subequal in length*	82º (sa) 72º (a)	DI-DII anterior-anterolaterally; DIII-DIV anterolaterally*	pedal parallel to midline*	100º (sa) 96º (a)	overprinting, tail and claw marks. belly mark (a)		Milàn and Hedegaard (2010)
Alligator sinensis	medium-sized 14.7 cm 150 cm	overprinted	overprinted	not clear	60º	not clear	pedal parallel to midline*	93º	tail, belly and claw marks		Milàn and Hedegaard (2010)
Crocodylus johnstoni	medium-sized (subadult) 9.2 cm Large-sized (adult) 112 cm	overprinted	overprinted	not clear	46º (sa)	not clear	pedal parallel to midline*	99º (sa) 66º (a)	belly and claw dragmarks	scale marks (sa)	Milàn and Hedegaard (2010)
Crocodylus rhombifer	medium-sized (subadult) 5.1 cm 80 cm	overprinted	overprinted	DIV not impressed	?	?	?	100º	claw drag marks occasional tail mark		Milàn and Hedegaard (2010)
Crocodylus novaeguineae	large-sized (subadult) 12.5 cm 175 cm	overprinted	138º	DI-DIII subequal in length*	36º	anterolaterally*	manual strongly lateral, pedal slight lateral	86º	belly and claw dragmarks and faint tail mark		Milàn and Hedegaard (2010)
Crocodylus siamensis	large-sized (subadult) 12.1 cm 140 cm	tetradactyl	?	DII-DIII subequal; DI-DIV subequal*	47º	DI-DII anterior-anterolaterally; DIII-DIV anterolaterally*	manual laterally pes parallel to ml*	113º	narrow-gauge. tail and claw marks		Milàn and Hedegaard (2010)

Species	Size category (FL and TL)	Manual morphology	Manual IA	Digital impression lengths in the pes	Pedal IA	Digital orientation in the pes	FR	PA	Trackway features	Other significant features	References
Crocodylus cataphractus	large-sized (subadult) 12.5 cm 149 cm	overprinted	overprinted	?	51º	anterolaterally*	pedal slightly lateral	94º	wide gauge, tail, belly and claw marks		Milàn and Hedegaard (2010)
Osteolaemus tetraspis	medium (subadult) large sized (adult) 7.5–13.6 cm 79 cm (sa)–160 cm (a)	overprinted (a)	overprinted (a)	DI-DIII subequal in length*	42º (sa) 43º (a)	anterior-anterolateral*	manual lateral, pedal parallel* (sa) pedal parallel* (a)	110º (sa) 101 (a)	narrower (sa), wide (a) tail marks (a, sa) Belly and claw marks (a)		Milàn and Hedegaard (2010)
Crocodylus niloticus	medium sized (about 6 cm)	pentadactyl	DI-DV more medially	tetradactyl	47º*	DI-DII anteriorly; DIII-DIV anterolaterallly	manual laterally pedal parallel to midline	about 98º	tail and drag marks		Mazin et al., 2003 (estimated from drawing of Fig. 4a)
Caiman crocodilus	small sized 4.3 cm 48.6 cm	pentadactyl overprinted	overprinted	DII-DIII subequal; DI-DIV subequal*	45*	DI medially, DII-DIII anteriorly, DIV laterally	pedal parallel to midline	106º*	tail and drag marks		Padian and Olsen, 1984

LITERATURE CITED

Farlow, J. O. Elsey, R. 2010. Footprints and trackways of the American alligator, Rockefeller Wildlife Refuge, Louisiana. New Mexico Museum of Natural History and Science Bulletin 51: 31–40.

Farlow, J.O., N. J. Robinson, C. J. Kumagai, F. V. Paladino, P. L. Falkingham, R. M. Elsey, and A. J. Martin. 2018b. Trackways of the American crocodile (*Crocodylus acutus*) in northwestern Costa Rica: implications for crocodylian ichnology. Ichnos 25(1):30–65.

Kubo, T. 2008. In quest of the *Pteraichnus* trackmaker: comparisons to modern crocodilians. Acta Palaeontologica Polonica 53(3):405–412.

Kumagai, C. J., Farlow, J. O. 2010. Observations on traces of the American crocodile (*Crocodylus acutus*) from northwestern Costa Rica. New Mexico Museum of Natural History and Science Bulletin 51:41–49.

Mazin, J. M., J. P. Billon-Bruyat, P. Hantzpergue, and G. Lafaurie. 2003. Ichnological evidence for quadrupedal locomotion in pterodactyloid pterosaurs: trackways from the Late Jurassic of Crayssac (southwestern France). Geological Society, London, Special Publications 217(1):283–296.

Milàn, J., and R. Hedegaard. 2010. Interspecific variation in tracks and trackways from extant crocodylians. New Mexico Museum of Natural History and Science Bulletin 51:15–29.

Padian, K., and P.E. Olsen. 1984. The fossil trackway *Pteraichnus*: Not pterosaurian, but crocodilian. Journal of Paleontology 58:178–184.