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A walk in the maze: Variation in Late Jurassic tridactyl dinosaur tracks - A case study from the Late Jurassic of the Swiss Jura Mountains (NW Switzerland)

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Background. Minute to medium-sized (FL less than 30 cm) tridactyl dinosaur tracks are the most abundant in the Late Jurassic tracksites of Highway A16 (Reuchenette Formation, Kimmeridgian) in the Jura Mountains (NW Switzerland). During excavations, two morphotypes, one gracile and one robust, were identified in the field. Furthermore, two large-sized theropod ichnospecies (*Megalosauripus transjuranicus* and *Jurabrontes curtedulensis*) and an ornithopod-like morphotype (Morphotype II) have recently been described at these sites. **Methods.** The quality of preservation (preservation grade), the depth of the footprint, the shape variation and the footprint proportions (FL/FW ratio and mesaxony) along the trackways have been analysed using 3D models and false-colour depth maps in order to determine the exact number of morphotypes present in the tracksites. **Results.** The study of the footprints (n = 93) collected during the excavations has made it possible to identify and characterize the two morphotypes distinguished in the field. The gracile morphotype is mainly characterized by a high footprint length/width ratio, high mesaxony, low divarication angles and clear, sharp claw marks and phalangeal pads (2-3-4). By contrast, the robust morphotype is characterized by a lower footprint length/width ratio, weaker mesaxony, slightly higher divarication angles and clear, sharp claw marks (when preserved), whereas the phalangeal pads are not clearly preserved although they might be present. **Discussion.** The analysis does not allow the two morphotypes to be associated within a morphological continuum. Thus, they cannot be a consequence of extramorphological variations on similar tracks produced by a similar/single trackmaker. Comparison of the two morphotypes with the larger morphotypes described in the formation (*Megalosauripus transjuranicus*, *Jurabrontes curtedulensis* and Morphotype II) and the spatio-temporal relationships of the trackways suggest that the smaller morphotypes cannot reliably be considered small individuals of the larger morphotypes. The morphometric data of some specimens of the robust morphotype (even lower values for the length/width ratio and mesaxony) suggest that more than one ichnotaxon might be represented within the robust morphotype. The features of the gracile morphotype (cf. *Kalohipus*) are typical of “grallatorid” ichnotaxa with low mesaxony whereas those of the robust morphotype (cf. *Therangospodus* and ?*Therangospodus*) are reminiscent of *Therangospodus pandemicus*. This work sheds new light on combining an analysis of variations in footprint morphology through 3D models and false-colour depth maps, with the study of possible ontogenetic variations and the identification of small-sized tridactyl ichnotaxa for the description of new dinosaur tracks.

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ABSTRACT

Background. Minute to medium-sized (FL less than 30 cm) tridactyl dinosaur tracks are the most abundant in the Late Jurassic tracksites of Highway A16 (Reuchenette Formation, Kimmeridgian) in the Jura Mountains (NW Switzerland). During excavations, two morphotypes, one gracile and one robust, were identified in the field. Furthermore, two large-sized theropod ichnospecies (*Megalosauripus transjuranicus* and *Jurabrontes curtedulensis*) and an ornithopod-like morphotype (Morphotype II) have recently been described at these sites.

Methods. The quality of preservation (preservation grade), the depth of the footprint, the shape variation and the footprint proportions (FL/FW ratio and mesaxony) along the trackways have been analysed using 3D models and false-colour depth maps in order to determine the exact number of morphotypes present in the tracksites.

Results. The study of the footprints (n = 93) collected during the excavations has made it possible to identify and characterize the two morphotypes distinguished in the field. The gracile morphotype is mainly characterized by a high footprint length/width ratio, high mesaxony, low divarication angles and clear, sharp claw marks and phalangeal pads (2-3-4). By contrast, the robust morphotype is characterized by a lower footprint length/width ratio, weaker mesaxony, slightly higher divarication angles and clear, sharp claw marks (when preserved), whereas the phalangeal pads are not clearly preserved although they might be present.

Discussion. The analysis does not allow the two morphotypes to be associated within a morphological continuum. Thus, they cannot be a consequence of extramorphological variations on similar tracks produced by a similar/single trackmaker. Comparison of the two morphotypes with the larger morphotypes described in the formation (*Megalosauripus transjuranicus*, *Jurabrontes curtedulensis* and Morphotype II) and the spatio-temporal relationships of the trackways suggest that the smaller morphotypes cannot reliably be considered small individuals of the larger morphotypes. The morphometric data of some specimens of the robust morphotype (even lower values for the length/width ratio and mesaxony) suggest that more than one ichnotaxon might be represented within the robust morphotype. The features of the gracile morphotype (cf. *Kalohipus*) are typical of “grallatorid” ichnotaxa with low mesaxony whereas those of the robust morphotype (cf. *Therangospodus* and ?*Therangospodus*) are reminiscent of *Therangospodus pandemicus*. This work sheds new light on combining an analysis of variations in footprint morphology through 3D models and false-colour depth maps, with the study of possible ontogenetic variations and the identification of small-sized tridactyl ichnotaxa for the description of new dinosaur tracks.

Keywords: Dinosaur ichnology, Theropods, Kimmeridgian, Reuchenette Formation

INTRODUCTION

Since the first reported sauropod tracks were found in the Lommiswil quarry (late Kimmeridgian, Canton Solothurn) in the Swiss Jura Mountains (Meyer, 1990), dinosaur track discoveries have increased considerably, and to date more than 25 tracksites have been documented in the cantons of Jura, Bern, Neuchâtel and Solothurn. Most of these tracksites belong to the Kimmeridgian Reuchenette Formation, and some of them to the Tithonian Twannbach Formation (Meyer & Thüring, 2003; Marty, 2008; Marty & Meyer, 2012; Marty et al., 2013). Between 2002 and 2011, six large tracksites were systematically excavated and documented by Palaeontology A16 prior to the construction of Highway A16. These tracksites covered a surface area of 18,500 m^2, and a total of 59 ichnoassemblages comprising over 14,000 tracks including 254 sauropod and 411 bipedal tridactyl dinosaur trackways were documented. Therefore, the Jura carbonate platform has today become a key area for Late Jurassic dinosaur palaeoichnology (Marty, 2008; Marty & Meyer, 2012).

Among the tridactyl dinosaur tracks, recent papers have described giant theropod tracks (*Jurabrontes curtedulensis*, Marty et al., 2017) and large theropod tracks (*Megalosauripus transjuranicus*, Razzolini et al., 2017), but most of the tridactyl tracks by far are the still largely undescribed minute, small and medium-sized tracks (footprint length < 30 cm). Marty (2008) described minute and small tridactyl tracks from the Chevenez—Combe Ronde tracksite and tentatively attributed some of these to *Carmelopodus*. Since then, however, many other tracksites and ichnoassemblages with minute to medium-sized tridactyl tracks have been discovered, including some very well-preserved tracks of different morphotypes and some very long trackways (up to 100 m).

In Europe, apart from the Swiss and French (Mazin, Hantzpergue & Pouech, 2016) Jura Mountains, the main Late Jurassic deposits that have yielded minute to medium-sized tridactyl dinosaur tracks are located in the Lusitanian Basin in Portugal (Antunes & Mateus, 2003; Santos, 2008), the Asturian Basin in Spain (Lockley et al., 2008; Piñuela, 2015), the Aquitanian Basin in France (Lange-Badré et al., 1996; Mazin et al., 1997; Moreau et al., 2017), the Lower Saxony Basin in NW Germany (Kaever & Lapparent, 1974; Diedrich, 2011; Lallensack et al., 2015), and several units in the Holy Cross Mountains in Poland (Gierliński, Niedźwiedzki & Nowacki, 2009). The units that date to around the Jurassic-Cretaceous boundary (Tithonian–Berriasian) in the Iberian Range in Spain (Santisteban et al., 2003; Castanera et al., 2013a; Alcalá et al., 2014; Campos-Soto et al., 2017) should also be mentioned. It is noteworthy that there is no corresponce between the high number of small to medium-sized tridactyl tracks (assigned to both theropods and ornithopods) described and the scarce number of ichnotaxa defined. Besides the tracks from the Combe Ronde tracksite tentatively assigned to *Carmelopodus* by Marty (2008), the main small to medium-sized tridactyl tracks identified have been from Spain (*Grallator* and *Anomoepus,* from several sites in Asturias, Lockley et al., 2008; Piñuela, 2015; Castanera, Piñuela & García-Ramos, 2016), France (*Carmelopodus*, Loulle tracksite, Mazin, Hantzpergue & Pouech, 2016), Poland (*Wildeichnus*, cf. *Jialingpus* and *Dineichnus*, different units in the Holy Cross Mountains, Gierliński, Niedźwiedzki & Nowacki, 2009), Germany (*Grallator*, Bergkirchen tracksite, Diedrich, 2011) and Portugal (*Dineichnus* and ?*Therangospodus*, Lockley et al., 1998a;

Lockley, Meyer & Moratalla, 2000). Other significant Late Jurassic areas with minute to medium-sized tridactyl dinosaur tracks are found in the USA (Foster & Lockley, 2006), Morocco (Belvedere, Mietto & Ishigaki, 2010), China (Xing, Harris & Gierliński, 2011; Xing et al., 2016), Yemen (Schulp & Al-Wosabi, 2012) and Turkmenistan (Lockley, Meyer & Santos, 2000; Fanti et al., 2013).

Several recent papers have examined the variability in track morphology along trackways (Razzolini et al., 2014, 2017; Lallensack, van Heteren, & Wings, 2016), showing how pronounced changes can occur along a given trackway. Thus, sometimes it can be very difficult to determine the exact number of ichnotaxa and clearly distinguish between them, especially when the tracks are morphologically similar. This should be borne in mind particularly when studying the material from Highway A16, where large theropod tracks have shown notable variations in shape along the same trackway, sometimes representing even two different morphotypes (Razzolini et al., 2017). In the case of the minute to medium-sized tridactyl tracks, two different morphotypes were identified at first glance during the documentation of the tracksites, one gracile and one more robust. The aim of this paper is to describe the minute to medium-sized tridactyl tracks collected in the Jura Mountains (NW Switzerland). In this description, special emphasis is put on the analysis of track morphology through 3D models and possible variations in footprint shape along trackways in order to discern whether or not the different morphotypes are a consequence of preservational variations. In addition, other factors such as possible ontogenetic variations in the larger ichnospecies described in the formation are also taken into account. Finally, we discuss the ichnotaxonomy of the tracks together with some palaeoecological implications.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The studied material comes from six different tracksites from Highway A16 and nearby areas (Fig. 1A): (1) Courtedoux—Bois de Sylleux (CTD–BSY), (2) Courtedoux—Tchâfouè (CTD–TCH), (3) Courtedoux—Béchat Bovais (CTD–BEB), (4) Courtedoux—Sur Combe Ronde (CTD–SCR), (5) Chevenez—Combe Ronde (CHE–CRO); and (6) Chevenez—La Combe (CHE–CHV). For the sake of simplicity BSY, TCH, BEB, SCR, CRO and CHV are used in the publication.

All the tracksites are located in the Ajoie district about 6-8 km to the west of Porrentruy (Canton Jura, NW Switzerland) and on the path of Swiss federal highway A16 except the Chevenez—La Combe tracksite, which is a quarry located near the village of Chevenez. The first five tracksites were systematically excavated level-by-level by the Palaeontology A16 (PALA16) from 2002 until 2011 (Marty et al., 2003; Marty et al., 2004; Marty et al., 2007; Marty, 2008).

Geologically, the study area belongs to the Tabular Jura Mountains and is located at the eastern end of the Rhine-Bresse transfer zone between the Folded Jura Mountains (South and East) and the Upper Rhine Graben and Vosges Mountains (North). The Upper Jurassic strata of the Swiss Jura Mountains are made up of shallow-marine carbonates deposited on the large and structurally complex Jura carbonate platform, which was located at the northern margin of the Tethys at a palaeolatitude of approximately 30° N (Thierry, 2000; Thierry et al., 2000; Stampfli & Borel, 2002).

The tracksites belong to the Kimmeridgian Reuchenette Formation, and the age is constrained by the presence of ammonites to the Cymodoce to Mutabilis (Boreal), and Divisum to Acanthicum (Tethyan) biozones (Comment et al., 2015). Accordingly, the age of the track-bearing levels is late early to early late Kimmeridgian (Gygi, 2000; Comment et al., 2015). This age is also confirmed by the presence of ostracods (Schudack et al., 2013). More information on the sedimentology and palaeoenvironment of the Highway A16 tracksites can be found in Marty (2008), Jank et al. (2006), Razzolini et al. (2017) and Marty et al. (2017).

Stratigraphically, the Highway A16 tracksites include three different track-bearing laminite intervals, separated by shallow marine limestones (Marty, 2008; Waite et al., 2008; Comment, Ayer & Becker, 2011; Comment et al., 2015). The three main track-bearing laminite intervals are referred to as the lower, intermediate and upper levels, respectively levels 500–550, 1000–1100, and 1500–1650 (Fig. 1B). Only tracks from the lower and intermediate track levels are included in the present study (Fig. 1B), and the studied tracks come from a total of 11 different ichnoassemblages (stratigraphic track levels). These are as follows: BEB500, CRO500, BSY1020, BSY1040, BSY1050, TCH1055, SCR1055, TCH1060, TCH1065, TCH1069 and CHV1000–1100 (precise level cannot be indicated).

MATERIAL AND METHODS

We analysed a total of 93 individual tracks (Table S1) that are housed in the track collection of PALA16 (Canton Jura), either as original specimens or as replicas. The track collection will be transferred to JURASSICA Muséum (Porrentruy, Canton Jura) in 2019. All the tracks are from the aforementioned tracksites, the largest samples coming from BEB500 (39 footprints), TCH1065 (15) and CRO500 (20). Each analysed track has two acronyms (Table S1): one represents the number of the slab within the collection, e.g.: TCH006-1100 denotes Tchâfouè tracksite, year 2006 (the year of discovery), slab 1100 (when the acronym has an “r” in front of the specimen number, this means that it is a replica and not an original specimen). In the case of the scanned footprints, these are referred to as “Laser-Scan”. A second acronym represents the level and number of the trackway and track, e.g.: TCH1055-T2-L1 denotes Tchâfouè tracksite, level 1055, trackway 2, track 1, left pes 1. The second acronym is used throughout the manuscript. As the track-bearing layers were excavated level-by-level there are no doubts about the preservation mode of the tracks. Thus, all the tracks were preserved as true tracks (concave epireliefs) and were produced in the tracking surface, with the only exception of TCH1060-E58, which was preserved as a natural cast (convex hyporelief).

. Preservation was described accordingly to the scale of Belvedere and Farlow (2016). Analysis of track morphology was performed independently for each track; however, some tracks belong to trackways and so were also analysed with a view to establishing the variation in footprint morphology along a single trackway, thus trying to avoid over-identification of morphotypes. These trackways are: BEB500-T16 (3), BEB500-T17 (4), BEB500-T58 (6), BEB500-T73 (4), BEB500-T75 (2), BEB500-T78 (2), BEB-500-T82 (2), BEB-500-T93 (2), BEB500-T120 (4), CRO500-T10 (14), CRO500-T30BIS (5), TCH1055-T2 (2), TCH1065-T15 (2), TCH1065-T25 (2) and TCH1069-T2 (2). We analysed each individual track and made an evaluation of the quality of preservation according to the scale of Belvedere and Farlow (2016) (Table S1). As stated by Belvedere and Farlow (2016), "quantitative shape analyses need to be based on data of high quality, and comparisons are best made between tracks comparable in quality of preservation". Accordingly, only the tracks with a preservation grade equal to or higher than 2 were considered for measurement and analysis in this paper; field measurements exist for all the other tracks and are stored in the PALA16 database. The descriptions are based on identification of two different morphotypes, one gracile and one robust, during the documentation in the field. Thus, the footprint length (FL), footprint width (FW), length and width of digits II (LII, WII), III (LIII, WIII) and IV (LIV, WIV), divarication angles (II-III; III-IV) were measured (see Castanera, Piñuela & García-Ramos, 2016, fig. 2). Subsequently, the FL/FW ratio and the mesaxony were calculated. The latter was calculated on the basis of the anterior triangle length–width ratio (AT) following Lockley (2009). All these measurements were taken from perpendicular pictures with the software Image J. The tracks were classified according to different size classes (Marty, 2008) on the basis of pes length (FL) as: 1) minute, FL < 10 cm; 2) small, 10 cm < FL < 20 cm; 3) medium, 20 cm < FL < 30 cm; and 4) large, FL > 30 cm. The morphometric data of the studied tracks were compared in a bivariate plot (length/width ratio vs. mesaxony) with larger tracks (*Megalosauripus transjuranicus*, *Jurabrontes curtedulensis* and Morphotype II) described in the Reuchenette Formation (Razzolini et al., 2017; Marty et al., 2017). In addition, they were also compared with other theropod ichnotaxa using data from Castanera, Piñuela & García-Ramos (2016) which were mainly compiled after Lockley (2009) and Xing et al. (2014). Data were analysed with the software PAST v.2.14 (Hammer, Harper & Ryan, 2001). In addition, we analysed the maximum depth of all the tracks, in order to ascertain whether there is a relationship between this parameter, the preservation grade and the morphotype. The maximum depth was estimated using the false-colour map derived from the 3D-model in those tracks with a preservation grade generally higher than 0.5.

3D-photogrammetric models were generated from pictures taken with a Canon EOS 70D camera equipped with a Canon 10-18mm STL lens using Agisoft Photoscan (v. 1.3.2, www.agisoft.com) following the procedures of Mallison & Wings (2014) and Matthews, Noble & Breithaupt (2016). Within the BEB500 sample, 3D data of 10 footprints were obtained by laser-scanning carried out in the field in 2011 by Pöyry AG with a Faro hand-scanner, and most of these 10 footprints were destroyed with the construction of Highway A16. The scaled meshes were exported as Stanford PLY files (.ply) and then processed in CloudCompare (v.2.7.0, www.cloudcompare.com) in order to obtain accurate false-colour depth maps. All photogrammetric meshes used in this study are available for download here: https://figshare.com/s/faf59ba7c717e99fd146 (ca. 2.5 Gb).

DESCRIPTION OF THE TRACK MORPHOTYPES:

Gracile morphotype:

This morphotype was identified in all six tracksites. The footprints are small to medium-sized (15-21.2 cm) tridactyl tracks (Fig. 2), clearly longer than wide (FL/FW ratio = 1.50-1.90) (Table 1). The digits are slender with an acuminate end and clear claw marks preserved in the three digits in the majority of the tracks. Digit III is clearly longer and slightly wider than digits II and IV. Digits II and IV are similar in length and width. The mesaxony is variable but medium to high (AT =0.53-0.98), with a mean value of 0.77, although it is higher in most of the specimens (more than 0.8 in half of the sample). The divarication angles are relatively low, II-III generally being slightly higher (mean 25º) than III-IV (mean 22º). The hypices are quite symmetrical. The "heel" morphology is variable; some specimens have an oval to round heel pad connected with digit IV (BEB500-T16-R3, TCH1055-E53, TCH1055-T2-R1, TCH1069-T1-R2; see Fig.2), whereas in others it is not clearly preserved even when the preservation grade is high (e.g.: BSY1020-E2). Most of the specimens preserve a clear small medial notch located behind digit II, which with the rounded heel marks gives them an asymmetric shape. Well-defined digital pads can be discerned in some of the footprints. The tracks with the best quality of preservation suggest a phalangeal formula of 2-3-4 (including the metatarsophalangeal pad IV).

Robust morphotype:

This morphotype has mainly been identified on the track levels BEB500 and TCH1065 (Fig. 3). The footprints are small or medium-sized (17-21.8 cm) tridactyl tracks (Fig. 3), slightly longer than wide (FL/FW ratio = 1.13-1.46), (Table 1). The digits are relatively robust with an acuminate end and clear claw marks preserved in some of the tracks (e.g.: BEB500-T120-R5, TCH1065-T15-R1, TCH1065-T21-R1). Digit III is clearly longer and slightly wider than digits II and IV. Digits II and IV are similar in length and width. The mesaxony is variable but low-medium (AT =0.38-0.61), with a mean value of 0.49. The divarication angles are low, II-III (mean 26º) and III-IV (mean 27º) being quite similar. The hypices are quite symmetrical. The "heel" morphology is variable, ranging from subrounded to subtriangular. Only TCH1065-T21-R1 preserves a clear small medial notch located behind digit II, thus being slightly asymmetrical, whereas the other specimens are more symmetrical. Well-defined digital pads cannot be discerned in most of the footprints, although TCH1065-T21-R1 shows digital pads suggesting a possible phalangeal pad formula of 2-3-?4.

DESCRIPTION OF THE MORPHOLOGICAL VARIATIONS ALONG THE TRACKWAYS:

In this section we analyse the variations in footprint morphology (preservation grade and maximum depth) along some of the trackways.

BEB500-T16:

It is a long turning trackway (Fig. 4A) of the gracile morphotype, composed of 27 footprints. It is located in the northeastern part of the tracksite. Three consecutive footprints have been analysed. The variation in preservation grade is high, even within a single step/stride, ranging from 2.5 in

BEB500-T16-R3 to 0.5 in BEB500-T16-R4. On the other hand, the variation in maximum depth is only 1 cm between the three tracks (4.6 cm to 5.7 cm).

BEB500-T17

It is a very long, straight trackway (Fig. 4B) of the gracile morphotype, with 120 footprints documented. The trackway crosses the whole surface of the site from the SE to the NW. Four footprints were analysed. The preservation grade varies from 1 (BEB500-T17-L8) to 2 (BEB500-T17-R8) while the maximum depth varies slightly less than 3 cm among the footprints (4.2 cm to 7 cm). It is interesting to note that the left tracks analysed (BEB500-T17-L8 and BEB500-T17-L9) look more robust than the right ones (BEB500-T17-R8, BEB500-T17-R20), but on the other hand are shallower.

BEB500-T58:

It is a long trackway (Fig. 4C) of the gracile morphotype, composed of 53 footprints. It is located in the southeastern part of the tracksite and crosses through the middle of the site in a straight southerly direction. It crosses trackways BEB500-T17, BEB500-T78 and BEB500-T82. Analysis of six footprints suggests a variation in preservation grade from 0.5 (BEB500-T58-R22) to 1.5 (BEB500-T58-L22). The variation in maximum depth is around 2 cm (3.9 cm in BEB500-T58-L22 to 6.2 cm BEB500-T58-L23).

BEB500-T73:

It is a short turning trackway (Fig. 4D) of the gracile morphotype, located in the northeastern part of the site, and it runs in a NW/E direction. It crosses BEB500-T17 in the first part of the trackway. Analysis of four tracks suggests a variation in preservation grade from 1 (BEB500-T73-R4) to 2 (BEB500-T73-L5) and a variation in maximum depth of 2 cm (4.9 cm in BEB500-T73-R5 to 6.9 cm in BEB500-T73-L5).

BEB500-T75:

It is a very long trackway (Fig. 4E) of the robust morphotype, with 71 footprints documented. It is located in the southeastern part of the site, and crosses half of the site in a northerly direction. Analysis of BEB500-T75-R12 and BEB-500-T75-R15 suggests a preservation grade of 1.5 and a maximum depth of 3.3 cm in both tracks.

BEB500-T78:

It is a long trackway (Fig. 4F) of the gracile morphotype, composed of 24 footprints. It is located in the northeastern part of the site. It crosses through the middle of the site in a straight W-E direction. It crosses BEB500-T17 and BEB500-T82. Two footprints were analysed and the preservation grade is 1 in both of them. The variation in maximum depth is very low (5.7 cm in BEB500-T78-L5 and 6.2 cm in BEB500-T78-R3).

BEB500-T82:

It is a very long trackway (Fig. 4G) of the gracile morphotype, with 59 footprints documented. It is located in the northeastern part of the site, crossing trackway BEB500-T78 to which it is slightly subparallel. It also crosses BEB500-T17. It crosses almost the entire site running in a straight W-E direction. Analysis of BEB-500-T82-R9 and BEB-500-T82-R14 revealed a preservation grade of 1.5 and a variation in maximum depth of almost 2 cm (4.8 cm and 6.7 cm respectively).

BEB500-T93:

It is a very long trackway (Fig. 4I) of the gracile morphotype, with 64 footprints preserved. It is located in the northeastern part of the site and crosses the entire surface of the site in a straight W-E direction. Analysis of BEB-500-T93-L5 and BEB-500-T93-R6 suggests a preservation grade of 1 and a variation in maximum depth of less than 0.5 cm (5.7 cm and 6.1 cm respectively).

BEB500-T120:

It is a long trackway (Fig. 4H) of the robust morphotype, composed of 29 footprints. It is located in the southwestern part of the site and crosses half of the site in an almost straight W-E direction. Four tracks were analysed, the preservation grade varying from 0 (BEB500-T120-L6) to 2 (BEB500-T120-R5, BEB500-T120-R6). The variation in maximum depth is one of the highest, at almost 6 cm (4.2 cm in BEB500-T120-L5 to 10 cm in BEB500-T120-R6).

CRO500-T10:

It is a very long trackway (Fig. 5A) of the gracile morphotype (*Carmelopodus sensu* Marty, 2008), with 75 footprints documented. It crosses almost the entire surface of the site in a straight SW-NE direction, making a small turning to the north in the last part of the trackway. Analysis of 14 footprints suggests a high variation in the preservation grade of the footprints, ranging between 0 and 2 (CRO500-T10-L10). The variation in maximum depth is about 2 cm, ranging from 3.1 cm (CRO500-T10-R3) to 5.7 cm (CRO500-T10-L5).

CRO500-T30BIS:

It is a short trackway (Fig. 5B) of the gracile morphotype, composed of 11 footprints. It is located in the northeastern part of the site and crosses half of the site in an E-W direction. Analysis of five footprints also suggests a high variation in the preservation grade of the footprints, ranging between 0 (CRO500-T30BIS-L4) and 2 (CRO500-T30BIS-L5), even within a single stride. The variation in maximum depth is 4.7 cm (from 5.3 cm in CRO500-T30BIS-L5 to 10 cm in CRO500-T30BIS-R5), and is thus one of the highest. It is noteworthy that CRO500-T30BIS-R4 looks rather robust in comparison with the other tracks in the trackway, although this is not related with the maximum depth, as CRO500-T30BIS-R5 is the one with a maximum depth of 10 cm.

TCH1055-T2:

It is a short trackway (Fig. 5C) of the gracile morphotype, composed of four footprints and located in the northern part of the site. The trackway runs to the NW. Analysis of TCH1055-T2-L1 and TCH1055-T2-R1 suggests a high preservation grade of 2-2.5 and a maximum depth of 5.1 cm and 7.6 cm, respectively.

TCH1065-T15:

It is a very short trackway (Fig. 5D) of the robust morphotype, with just two footprints documented. It is located in the northern part of the site, and the trackway runs to the NW. Analysis of TCH1065-T15-L1 and TCH1065-T15-R1 suggests a high variation in preservation grade from 0.5 to 2, and a variation in maximum depth of 1.5 cm (6.8 cm and 8.3 cm respectively).

TCH1065-T25:

It is a short trackway (Fig. 5F) of the gracile morphotype, composed of four footprints. It is located in the northern part of the site, and the direction of the trackway is NW. Analysis of TCH1065-T25-L2 and TCH1065-T25-R2 shows a preservation grade of 2 and 1, respectively, and a high maximum depth of 10.2 cm and 12.9 cm, but not much variation (2.7 cm).

TCH1069-T2:

It is a short trackway (Fig. 5E) of the robust morphotype, with five footprints documented. It is located in the northern part of the site, and the direction of the trackway is NE. Analysis of TCH1069-T2-L2 and TCH1069-T2-R3 shows a preservation grade of 1 and 1.5 and a maximum depth of 9.6 cm and 7.8 cm, respectively.

DISCUSSION:

1) True ichnodiversity or variation due to substrate-foot interaction?

The final shape of a footprint is determined by a combination of factors related to the anatomy of the trackmaker's autopodium, the kinematics and the substrate (Marty et al., 2009; Falkhingham, 2014); another important factor is the level in which the tracks were preserved (Milán & Bromley, 2006) , i.e. if they are preserved as undertracks. In the case of the tracksites of Highway A16, we can rule out this factor as the excavation was carried out level-by-level, so the footprints are true tracks (or natural casts). As the foot-substrate interaction is a major determinant of the final shape of a track, it is important to analyse variations in depth and shape along trackways to ascertain the morphological variation (e.g.: Razzolini et al., 2014). For this reason, we first analysed the individual footprint shape (Figs. 2, 3) and then looked at the variation along the trackway (Figs. 4, 5). The idea was to establish whether some of the described morphotypes represent variations produced by the same/similar trackmakers walking in a substrate with different properties (water content, thickness or cohesiveness). Previous researchers have described variations between two extremes of a morphological continuum or a gradational series

(Gatesy et al., 1999; Razzolini et al., 2014) to suggest that similar theropods traversed substrates of variable consistency. Only in such cases are the differences a consequence of foot-substrate interactions rather than anatomical differences in the foot morphology of the trackmaker. In the Swiss samples, clear evidence of intermediate morphologies is missing, supporting the presence of at least two different groups of tridactyl trackmakers. Where gradational series of theropod tracks have been reported (see refs above), these show a hallux, metatarsal marks, and distinctive displacement rims in the deepest tracks that are clearly extramorphological features. None of the morphotypes presented in this paper shows such evidence, even in the deepest tracks. This leads us to think that the sediment was relatively firm during the production of the tracks.

Generally, tracks with a preservation grade of 1 or more can be classified in one of the two described morphotypes: gracile or robust. There are just a few classification doubts regarding isolated footprints (e.g.: CRO500-T30BIS-R4). At the outset, one possible hypothesis was that the robust morphotype could be a variation on the gracile morphotype, produced by a similar trackmaker on a substrate with different rheological properties (e.g.: Gatesy et al., 1999; Razzolini et al., 2014, 2017). This hypothesis was especially appealing given the similar footprint dimensions of the two morphotypes. Thus, the reasoning would be that the deeper tracks would look more robust than the shallow ones, and the absence of clear phalangeal pad marks in most of the robust morphotype tracks might be a consequence of a softer substrate or of deeper penetration by the trackmaker foot. Indeed, according to our analysis of the maximum depth of the footprints, those classified as belonging to the robust morphotype show some of the higher values (e.g.: BEB500-T120-R5 = 6.1 cm; BEB500-T120-R6 = 10 cm; BEB500-E1 = 10.5 cm; TCH1065-E124 = 6.9 cm; TCH1065-E188 = 5.9 cm; TCH1065-T15-R1 = 8.3 cm; TCH1065-T21-R1 = 12.1 cm, see Table S1). Nonetheless, it is significant that the higher depth values for the robust morphotype occur in level TCH1065, where also the gracile tracks show their deeper values (TCH1065-E28 = 11.7 cm; TCH1065-T25-R2 = 12.9 cm; TCH1065-T25-L2 = 10.2 cm). Therefore, on this track level the presence of the two morphotypes cannot be associated with the depth of the footprints. In the case of BEB500 we see a similar scenario. In other words, some tracks/trackways from the same level (e.g.: BEB500-T16 and BEB500-T17/ BEB500-T120 and BEB500-E1) have similar depths, yet represent the gracile and robust morphotype, respectively.

The analysis of the morphological variation along the trackways shows that the gracile morphotype is quite consistent along the trackways, and no tracks classifiable as robust are found within these trackways. There are only a few cases, e.g. CRO500-T30BIS-R4 (Fig. 5B) and BEB500-T17-L8/ BEB500-T17-L9 (Fig. 4B), which might look more robust than the other tracks in the trackway, but here the features did not properly fit with the description of the robust morphotype. Regarding the robust morphotype, in the analysed trackways (BEB500-T120, TCH1065-T15 and TCH1069-T2) none of the tracks shows any feature of the gracile morphotype (noteworthy is the low preservation grade and the scarce data for TCH1065-T15 and TCH1069-T2). This suggests that, in our case, there is no clear correlation between the depth of the footprint and the morphotypes and that the intra-trackway variation is never significant enough to denote a shift between the morphotypes. Therefore, the present evidence indicates that there are *at least* (see following discussion) two different trackmakers of minute to small-sized theropods in the tidal flats of the Jura Mountains.

Analysis of the mesaxony and the FL/FW ratio supports the presence of *at least* the two morphotypes (Fig. 6). Some authors have used mesaxony (Weems, 1992; Lockley, 2009) as a good parameter to distinguish between tridactyl tracks. This parameter represents how far the projection of digit III extends with respect to digits II and IV. In the studied sample, this parameter is clearly lower in the robust morphotype than in the gracile one. The FL/FW ratio also shows a considerable difference between the morphotypes (likewise lower in the robust morphotype). A closer look at these two parameters within the robust morphotype (Fig. 6B) raises the question whether it represents a single ichnotaxon. The data for the two analysed tracks from BEB500-T120 show considerably lower data for the FL/FW ratio and weaker mesaxony than the tracks from TCH1065 (see also following discussion).

2) Morphotype variation due to ontogeny?

Another salient point relating to the number of morphotypes in the analysed sample is the possibility of variations due to different ontogenetic states. Few works have dealt with the relationship between dinosaur footprints and ontogeny (e.g.: Lockley, 1994; Matsukawa, Lockley & Hunt, 1999; Hornung et al., 2016). Ontogenetic variations have been suggested to explain morphological variation in the classical theropod ichnotaxa of the *Grallator*-*Eubrontes* plexus (Olsen, 1980; Olsen, Smith & McDonald, 1998; Moreau et al., 2012). Olsen, Smith & McDonald, (1998) proposed that the major proportional differences between *Grallator*, *Anchisauripus* and *Eubrontes* might be derived from the allometric growth of individuals of several related species. In these typical theropod tracks the large tracks (*Eubrontes*) are wider with weaker mesaxony than the smaller tracks (*Grallator*), showing a positive correlation between the elongation of the track and the elongation of the anterior triangle (Lockley, 2009). As this author suggested, the assumption of ontogenetic variation is thus based mainly on the assumption of a discernible allometric pattern. Nonetheless, little is known about how possible ontogenetic variations may have affected variations in footprint shape, and generally tracks that are similar in morphology but different in size are considered to belong to the same ichnotaxon (Thulborn, 1990; Lockley, 1994; Matsukawa, Lockley & Hunt, 1999; Clark, Ross & Booth, 2005; Pascual-Arribas & Hernández-Medrano, 2011). Demathieu (1990) also explored the use of ratios of length characters to reduce the influence of size when comparing footprints. For instance, Lockley, Mitchel & Odier (2007) assumed that small theropod tracks (*Carmelopodus*) from the Jurassic of North America represent adults of small species and not juveniles of larger species and suggested that "this inference is consistent with a model of rapid growth rates such as is typical of birds, which would have reduced the number of potential track making juveniles that could habitually make footprints". By contrast, Pascual Arribas and Hernández-Medrano (2011) considered minute theropod tracks from the Lower Cretaceous of Spain (subsequently assigned to *Kalohipus bretunensis* by Castanera et al., 2015) to belong to baby theropods because of the morphometric similarities with larger tracks from the same site and formation.

Different ontogenetic stages should also be considered in the interpretation of the Ajoie ichnofauna. In one case, there are the similarities between the gracile morphotype and the previously described *Carmelopodus* tracks from the Chevenez-Combe Ronde tracksite (CRO500-T8; CRO500-T10; CRO500-T16; CRO500-T21; CRO500-T26; CRO500-T41). According to the original description by Marty (2008), these tracks can be characterized as mesaxonic, slightly asymmetric, tridactyl tracks that are clearly longer than wide. Digit III is always the longest, digit IV being longer than digit II, which is shorter posteriorly. Claw impressions are present in the three digits, and there is a phalangeal pad formula of 2-3-3. There is a low total divarication angle, and divarication angles of the same order between digits II and III, and III and IV. It has a narrow-gauge trackway with small tracks with outward rotation. CRO500-T10-L10 is the track with the highest preservation grade recovered from level CRO500. Regarding the data taken from this footprint, it should be noted that the FL/FW ratio (1.69) falls within the range of the other gracile tracks, while the mesaxony is among the highest in the whole sample (0.96) but still within the range of the gracile morphotype (Fig. 6). The divarication angle is also low (32º-23º). Moreover, reanalysis of the tracks with the use of false-colour depth maps (Fig. 2F) allowed the fourth phalangeal pad in digit IV to be distinguished, suggesting a formula of 2-3-4, although this is not preserved in most of the tracks with a lower preservation grade (Fig. 5A). Accordingly, we consider that there are not enough data to interpret these tracks as a different morphotype and we regard them as part of the gracile morphotype. This result highlights the importance of analysing large samples and the variation in shape through the trackways.

A second hypothesis considers whether the gracile and the robust morphotype might be ontogenetic variations on the previously described larger ichnospecies (*Megalosauripus transjuranicus* and *Jurabrontes curtedulensis*) of the Jura Mountains (Razzolini et al., 2017; Marty et al., 2017). In fact, the two described ichnospecies represent large and more gracile (*Megalosauripus transjuranicus*) and giant and more robust (*Jurabrontes curtedulensis*) theropod tracks, respectively. In addition, a third large morphotype not assigned to any ichnotaxon and named Morphotype II has also been described (Razzolini et al., 2017). This morphotype is characterized by subsymmetric tracks that are generally slightly longer than wide (sometimes almost as wide as long), blunt digit impressions, with no evidence for discrete phalangeal pad and claw marks. These general features of the Morphotype II tracks are problematic because sometimes trackways assigned to *Megalosauripus* also show these features when tracks are poorly preserved. Thus, sometimes an extramorphological variation on *Megalosauripus* tracks could be assigned to Morphotype II. There are also some tracks that constantly exhibit these features through long trackways and that have been considered a third large unnamed ichnotaxon with probable ornithopod affinities. These long trackways are found in the very surfaces that many in the studied sample come from, such as BEB500 and CRO500 (Razzolini et al., 2017). Thus, the hypothesis that the gracile and the robust morphotypes might represent juvenile/subadult specimens of the larger tracks described in the tracksites must be explored.

Analysing footprint proportions, it should be noted that the FL/FW ratio of the gracile morphotype fits within the upper range of the tracks included in *Megalosauripus* (Fig. 6A) from the Reuchenette Formation; considering just the type material of *Megalosauripus transjuranicus*, it fits completely (Fig. 6B) (Razzolini et al., 2017). On the other hand, the mesaxony is substantially higher in the gracile morphotype than in the *Megalosauripus* tracks. In the case of the robust morphotype, the FL/FW ratio fits within the range of the *Jurabrontes curtedulensis* and Morphotype II tracks when analysing all the referred material (Fig. 6A) or just the type material of *Jurabrontes curtedulensis* and the best-preserved tracks of Morphotype II (BEB500-TR7-L2; BEB500-TR7-R2; BEB500-TR7-R7; BEB500-TR7-L10, Razzolini et al., 2017) (Fig. 6B). The robust morphotype has higher mesaxony than *Jurabrontes curtedulensis*, being more similar in this respect to the Morphotype II tracks. It is notable that the footprint proportions within the robust morphotype are quite variable between stratigraphic levels. For example, tracks from trackway BEB500-T120 have a lower FL/FW ratio and mesaxony, whereas tracks from track level TCH1065 have higher ratios. Thus, BEB500-T120 is closer to the ranges of *Jurabrontes curtedulensis* whereas the tracks from TCH1065 are closer to the ranges of *Megalosauripus transjuranicus* and especially the Morphotype II tracks (Fig. 6).

As we have discussed previously, the variations in mesaxony where larger tracks have lower mesaxony are well documented in theropod tracks (Weems, 1992; Olsen, Smith & McDonald, 1998; Lockley, 2009). Because there are some overlapping areas in the footprint proportions of the larger and the smaller tracks, it might be tempting to relate them according to these values; i.e. gracile with *M. transjuranicus*, robust from BEB500 with *Jurabrontes*, and robust from TCH1065 with Morphotype II. Nonetheless, the smaller morphotypes show other considerable morphological differences apart from size and mesaxony with respect to the larger morphotypes. The gracile morphotype differs from *M. transjuranicus* in key features of the diagnosis such as the sigmoidal impression of digit III (less sigmoidal), the divarication angle (less divaricated) and the digital pad of digit IV (proportionally smaller when preserved). The robust morphotype (from both BEB500 and TCH1065) differs from *Jurabrontes curtedulensis* in the absence of clear phalangeal pads (preservation bias?), the absence of the peculiar, isolated proximal pad PIII1 of digit III, and the interdigital divarication angles (asymmetric vs symmetric); it differs from the Morphotype II tracks in the absence of blunt digit impressions, possible evidence of a discrete phalangeal pad, and the presence of clear claw marks.

Finally, we examine whether there is any spatiotemporal relationship between the larger and the smaller tracks from the Ajoie ichnoassemblages. Lockley (1994) warned that the track data "that most probably represent monospecific assemblages are those obtained for a single ichnotaxon from a single bedding plane". In this regard, it is interesting to note the scarcity of large theropod tracks in the ichnoassemblages where both the gracile and the robust morphotype have been identified, mainly levels BEB500, TCH1065 and CRO500. Level BEB500 (Fig. S2), the one with the highest number of studied tracks (n = 39), is mainly composed of sauropods (n = 17 trackways) and minute to small tridactyl (n = 158 trackways) tracks. No tracks assigned to *Jurabrontes curtedulensis* or *M. transjuranicus* have been documented in this level although it is the surface with the most Morphotype II tracks (n = 8 trackways) documented. Level TCH1065 (Fig. S3) (n = 15 studied tracks) is composed of 189 tracks, mainly of minute to small-sized theropods, and two parallel trackways (TCH1065-T26, TCH1065-T27) assigned to *Jurabrontes* have also been documented. In level CRO500 (Fig. S4), 16 sauropod trackways and 57 tridactyl trackways have been documented. One of the tridactyl trackways (CRO500-T43) has been assigned to Morphotype II (Razzolini et al., 2017). Thus, there are in the three cases a large track type (Morphotype II in BEB500 and CRO500, and *Jurabrontes* in TCH1065) and the robust and the gracile morphotypes in the same surface (Fig. S2-S4). Interestingly, no *Megalosauripus* tracks have been documented in any of the three levels. One way to confirm that some of the small tracks were juveniles of the larger ichnospecies would be to find some kind of relationship among them, such as gregarious behaviour (*sensu* Castanera et al., 2014). In BEB500 (Fig. S2), trackways TR1, TR3, TR4, TR5, TR6 and TR8 (Morphotype II) cross several trackways made by small trackmakers, but the orientations are completely different and do not show any kind of relationship. TR2 (Morphotype II) is subparallel with T34 (small track but unknown morphotype) at the beginning of the trackway but shows a significant change in direction, so this does not show any relationship either. Notably, TR7 (Morphotype II) is a long trackway that is subparallel to T120 (robust morphotype). Tracks T120-L10 and T120-R10 tread over tracks TR7-R8 and TR7-L9 but pass afterwards, so although they show some kind of relation there is no clear evidence of gregarious behaviour. In level TCH1065 (Fig. S3), the two parallel trackways (TCH1065-T26, TCH1065-T27) assigned to *Jurabrontes* do not show any evidence of a relationship with the smaller tracks either. Finally, in CRO500 (Fig. S4), T43 (Morphotype II) is slightly subparallel to T42 (small track but unknown morphotype), but there is no clear evidence to suggest that they were walking together. To sum up, generally the orientation of the large trackways does not seem to suggest any sort of relationship, with the possible exception of TR7 and T120. This single case might hint at the hypothesis that some tracks of the robust morphotype (BEB500-T120) might represent a juvenile of the producer of the tracks classified as Morphotype II. Nonetheless, BEB500-T120 is the very trackway that shows more morphometric similarities to *Jurabrontes* than to Morphotype II (Fig. 6). In the light of the previous discussion, the differences between the larger and the smaller morphotypes have thus led us to treat them as different ichnotaxa.

3) Ichnotaxonomy:

As noted by Marty (2008), small to medium-sized tridactyl tracks are generally not very common in the Late Jurassic and Early Cretaceous, and accordingly such tracks have only recently been the focus of ichnotaxonomic descriptions. Lockley, Meyer and Moratalla (2000) suggested that theropod track morphologies are much more variable through time than previously thought. These authors pointed out that “the perception of morphological conservatism and uniformity through time is, in part, a function of lack of study of adequately large samples of well-preserved material (Baird, 1957)”. In this sense, the studied tracks from the Ajoie ichnoassemblages represent a good sample of tridactyl dinosaur tracks in terms of the number of specimens (n = 93), with a considerable quality of preservation in many of them (n = 23 with a preservation grade greater than 2).

Although they are not very abundant in other European tracksites, small to medium-sized tridactyl trackways are the most abundant in the Ajoie ichnoassemblages. As mentioned above, the main small to medium-sized tridactyl dinosaur ichnotaxa that have been described from the Late Jurassic of Europe are (Fig. 7) *Grallator* (Fig. 7A) and *Anomoepus* (Fig. 7B) in Spain

(Lockley et al., 2008; Piñuela, 2015; Castanera, Piñuela & García-Ramos, 2016); *Carmelopodus* (Fig. 7C) and *Eubrontes* (Fig. 7D) in France (Mazin et al., 2000; Mazin, Hantzpergue & Pouech, 2016); *Wildeichnus* isp. (Fig. 7E), cf. *Jialingpus* (Fig. 7F) and *Dineichnus* (Fig. 7G) in Poland (Gierliński, Niedźwiedzki & Nowacki, 2009); *Dineichnus* (Fig. 7H) (Lockley et al., 1998a) and *Therangospodus*-like tracks (Fig. 7I) (Lockley, Meyer & Moratalla, 2000) in Portugal; and *Grallator* in Germany (Fig. 7J) (Diedrich, 2011). In addition, Conti et al. (2005) described medium-sized footprints (Fig. 7K) that "resemble *Therangospodus*" (their type 3) and another morphotype (their type 2, based on three specimens, Fig. 7L) that shares the same functional character with *Carmelopodus*, i.e., the lack of the fourth proximal pad on digit IV.

When compared with the type specimens of these ichnotaxa, the new data on the gracile morphotype of CRO500-T10 (Fig. 8N) (see previous sections) allow us to rule out the presence of *Carmelopodus untermannorum* (Fig. 8A) in the Ajoie, as previously discussed. Generally, the gracile morphotype (Fig. 8M-8O) does not fit with key features of the diagnosis of this ichnotaxon (Lockley et al., 1998b), differing in the phalangeal pad formula (2-3-4 rather than 2-3-3), symmetry, different length/width ratio, or the lower divarication. Among other theropod ichnotaxa, the gracile morphotype shows considerable differences with respect to *Wildeichnus navesi* (Fig. 8B, Casamiquela, 1964; Valais, 2011) from the Jurassic of Argentina (as well as larger size, a not subequal but lower divarication angle, larger claw marks, an unrounded digital phalangeal pad in digit IV, greater asymmetry, a generally higher length/width ratio); and with respect to *Therangospodus pandemicus* from the Late Jurassic of North America and Asia (Fig. 8C, smaller size, presence of clear phalangeal pads, higher mesaxony) (Lockley et al., 1998a; Fanti et al., 2013). The differences with respect to ornithopod ichnotaxa are noteworthy: it differs from *Anomoepus scambus* (Fig. 8D) in being less symmetric, having a metatarsal-phalangeal pad of digit IV not in line with the digit III axis, no hallux marks, higher mesaxony, and no manus prints present (see Olsen & Rainforth, 2003; Piñuela, 2015). It also differs notably with respect to *Dineichnus socialis* (Fig. 8E, higher FL/FW ratio, higher mesaxony, no quadripartite morphology, a different heel pad impression, lower digit divarication; see Lockley et al., 1998a).

The features of the gracile morphotype fit better with those of the tracks assigned to the smaller ichnotaxa of the *Grallator*-*Anchisauripus*-*Eubrontes* (Fig. 8F-8H) plexus (Olsen, 1980; Demathieu, 1990; Weems, 1992; Olsen, Smith & McDonald, 1998): small to medium-sized, well-defined digital pads, digits II and IV of similar length, digit III being longer and showing high mesaxony, an oval/subrounded "heel" and a low interdigital angle. Although these footprints have mainly been described from Late Triassic and Early-Middle Jurassic deposits, in recent years they have also been described from younger strata including the Late Jurassic of Europe (see Castanera, Piñuela & García-Ramos, 2016 and references therein). Regarding the use of the ichnotaxon *Anchisauripus*, Castanera, Piñuela & García-Ramos (2016) wrote a short review examining how different authors have considered *Grallator* and *Anchisauripus* as synonyms (Lucas et al., 2006; Lockley, 2009; Piñuela, 2015). The main sample of "grallatorid" tracks that has been described from Late Jurassic deposits in Europe comes from Asturias (Spain), and these have been assigned to *Grallator* (Castanera, Piñuela & García-Ramos, 2016). However, the gracile tracks from the Ajoie ichnoassemblages show some differences from those in Asturias, mainly regarding the digit proportions (FL/FW ratio) and mesaxony (Fig. 9). It should be noted that the Asturian sample shows a great variation in mesaxony (that does not correlate with size). Nonetheless, the gracile morphotype also shows great variations in mesaxony although the footprint proportions are less variable. Although Castanera, Piñuela & García-Ramos (2016) stated that mesaxony "should be used with caution in distinguishing between different ichnotaxa", we consider that the differences in mesaxony between the gracile morphotype and the *Grallator* tracks are great enough to do so. Furthermore, the FL/FW ratio is also considerably higher in the *Grallator* tracks than in the gracile morphotype. Regarding the *Grallator-Eubrontes* plexus, it is interesting to note the oversplitting that has occurred in some theropod ichnotaxa similar to this plexus. For example, Lockley et al. (2013) propose a great reduction in the Jurassic theropod ichnotaxa from Asia, arguing that many of them were subjective junior synonyms of *Grallator* and *Eubrontes*. Nonetheless, the authors retain the ichnotaxon *Jialingpus yuechiensis* (Fig. 8I) from the Late Jurassic-Early Cretaceous of China (Xing et al., 2014). On the basis of digit proportions (FL/FW ratio) and mesaxony, the gracile morphotype falls partially within the range of *Jialingpus* but also within the range of *Kalohipus bretunensis* (Fig. 8J) from the Lower Cretaceous (Berriasian) of Spain (Fuentes Vidarte & Meijide Calvo, 1998; Castanera et al., 2015). According to Xing et al. (2014), the main differences for distinguishing between *Jialingpus* and *Grallator* are the presence of a digit I trace and the large metatarsophalangeal area positioned in line with digit III, which are its main features. These features are absent in the gracile morphotype, so it cannot be assigned to *Jialingpus*. On the other hand, the diagnosis of *Kalohipus bretunensis* (Fuentes Vidarte & Meijide Calvo, 1998) clearly includes features that distinguish it from the gracile morphotype, such as its smaller size or robust digits, and as seen in Fig. 9, the footprint proportions and especially the mesaxony are also slightly different. As seen in the previous section, the morphology is also different from the larger ichnotaxa (*Jurabrontes curtedulensis*, Fig. 8K, and *Megalosauripus transjuranicus*, Fig. 8L) described in the formation.

To summarize, the gracile morphotype is quite similar to other grallatorid tracks (*Grallator*, *Anchisauripus, Kalohipus, Jialingpus*), the main differences being the digit proportions and mesaxony. Given the current state of knowledge, it is difficult to interpret how much variation between the aforementioned ichnotaxa is a consequence of variations in preservation, ontogeny or ichnodiversity. Taking into account the whole discussion, and bearing in mind the high variation in both the FL/FW ratio and mesaxony seen in tracks assigned to *Grallator,* we thus tentatively classify the gracile morphotype as cf. *Kalohipus*, as this is the ichnotaxon that is closest to it. Future studies should elucidate the similarities and differences between these grallatorid tracks, as some *Jialingpus* tracks have been described in the Late Jurassic/Early Cretaceous of Europe (Gierliński, Niedźwiedzki & Nowacki, 2009), and analysis of the differences between *Jialingpus* and other grallatorid tracks (including *Kalohipus*) is "pending" (Xing et al., 2014). In this regard it is interesting to note the differences in mesaxony between both *Kalohipus* and *Jialingpus* (low mesaxony) and *Grallator* (high mesaxony), the question being whether mesaxony is a good ichnotaxobase for discriminating between the three ichnotaxa. Also noteworthy are possible influences on preservation related to the composition of the substrates. For example, *Kalohipus bretunensis* and the main grallatorid ichnotaxa (Fig. 8) are preserved in siliciclastic materials whereas the Swiss Jura tracks cf. *Kalohipus* are preserved in carbonates.

Regarding the robust morphotype (Fig. 8P-8Q), a crucial question is whether it represents a single ichnotaxon. In this context, it should be noted that as well as the footprint proportions (Fig. 6B), the morphology of the tracks with a preservation grade of 2 or more such as those of trackway BEB500-T120 and the tracks from TCH1065 (TCH1065-T21-R1, TCH1065-E124 and TCH1065-E188) varies considerably. Whatever the case, the morphology of this morphotype *sensu lato* is completely different from that of the ichnotaxa mentioned for the gracile type, such as *Carmelopodus untermannorum* (Fig. 8A, size, phalangeal pad formula, digit divarication, well-developed claw marks), *Wildeichnus navesi* (Fig. 8B, size, gracility, symmetry, length/width ratio and mesaxony), *Anomoepus scambus* (Fig. 8D, size, absence of a manus impression, morphology of the metatarsal-phalangeal pad of digit IV) and *Dineichnus socialis* (Fig. 8E, no quadripartite morphology or circular heel pad impression). Obviously, it is also different from all the aforementioned grallatorid ichnotaxa *Grallator-Anchisauripus-Eubrontes*, plus *Jialingpus*, *Kalohipus* (Fig. 8F-J, mainly in the more robust morphology, footprint proportions, mesaxony, heel morphology, divarication) and the larger ichnotaxa (*Jurabrontes curtedulensis*, Fig. 8K, and *Megalosauripus transjuranicus*, Fig. 8L) described in the formation.

It is significant that, of all the known ichnotaxa, the one with most similarities to it is *Therangopodus pandemicus* (Fig. 8C, Lockley, Meyer & Moratalla, 2000), although the robust morphotype has higher digit divarication and probably higher mesaxony (unpublished data for this parameter). According to the original diagnosis, this ichnotaxon is a "medium sized, elongate, asymmetric theropod track with coalesced, elongate, oval digital pads, not separated into discrete phalangeal pads. Trackway narrow with little or no rotation of digit III long axis from trackway axis". The tracks from the Ajoie ichnoassemblages are slightly smaller in size than *Therangospodus pandemicus* (Lockley, Meyer & Moratalla, 2000; Fanti et al., 2013). According to these authors, and based on the original descriptions by Lockley, Meyer & Moratalla (2000), *Therangospodus* is characterized by: "1) oval digital pads not separated into discrete digital pads, 2) no rotation of digit III, 3) narrow trackway, and 4) relatively reduced size (<30 cm in average length)". Regarding the absence of discrete digital pads, Lockley, Meyer & Moratalla (2000) described in the type ichnospecies of *Therangospodus* the presence of "faint indentations at the margin of the pads" that sometimes reveal the location of the phalangeal pads, suggesting a 2-3-4 phalangeal pad formula. In this context, Razzolini et al. (2017) commented on the similar features of the tracks described as Morphotype II from the Ajoie ichnoasemblages compared to *Therangospodus* and the problems of assigning some of the tracks to this ichnotaxon. Razzolini et al. (2017) also pointed out the difficulties of distinguishing between *Therangospodus* and *Megalosauripus*, as discussed by other authors previously (Gierliński, Niedźwiedzki & Pieńkowski, 2001; Piñuela, 2015), suggesting that some of the diagnostic features might be extramorphological variations. It is notable that *Megalosauripus* and *Therangospodus* generally co-occur in the same sites (Meyer & Lockley, 1997; Lockley, Meyer & Moratalla, 2000; Lockley, Meyer & Santos, 2000; Xing, Harris & Gierliński, 2011; Fanti et al., 2013), which is relevant as the size and preservation could be the main differences between the two ichnotaxa. Interestingly, as we have seen in the previous section, the tracks described here as belonging to the robust morphotype do not co-occur with any *Megalosauripus* tracks, although some of them (BEB500-T120) co-occur with tracks described as Morphotype II. Even though the robust morphotype is reminiscent of *Therangospodus pandemicus*, it is not possible to assign it to this ichnospecies or to any of the described small-medium-sized ichnotaxa. The scarcity of specimens collected, the preservation grade (none of them as high as 2.5-3) and the doubts as to whether it might represent one or two ichnotaxa prevent us from erecting a new ichnotaxon. Taking into account that *Therangospodus pandemicus* is the closest ichnotaxon described, we thus tentatively classify the tracks from level TCH1065 as cf. *Therangospodus* and the tracks from BEB500 as ?*Therangospodus*. *Therangospodus pandemicus* tracks have been preserved in carbonate materials (Lockley, Meyer & Moratalla, 2000) like the Swiss material, so we can rule out the differences between this ichnotaxon and the robust morphotype being a consequence of this factor.

Our analysis of the small to medium-sized footprints adds new data to the dinosaur palaeoecology of carbonate platforms. Generally, it has been thought that carbonate tidal flat deposits are dominated by saurischian assemblages (see Fanti et al., 2013; D'Orazi Porchetti et al., 2016). The gracile morphotype (cf. *Kalohipus*) has been related to the grallatorid ichnotaxa, which have generally been associated with theropod dinosaurs (Olsen, Smith & McDonald, 1998; Lockley, 2009; Fuentes Vidarte & Meijide Calvo, 1998; Xing et al., 2014; Castanera et al., 2015; Castanera, Piñuela & García-Ramos, 2016). Nonetheless, some authors have suggested that some grallatorid footprints might be attributed to ornithopod dinosaurs (Demathieu, 1990). Regarding the robust morphotype, *Therangospodus pandemicus* is also attributed to theropod dinosaurs (Lockley, Meyer & Moratalla, 2000). Determining whether small-medium-sized tridactyl tracks are attributed to theropods or ornithopods can be problematic. Some features (e.g.: manus impressions, generally low FL/FW ratios and mesaxony, clear sharp claw marks, short pace lengths) have been proposed to distinguish between them, clearly suggesting that the tracks were produced by ornithischians/ornithopods (Castanera et al., 2013a, 2013b and references therein). In the case of the Ajoie ichnoassemblages, there is no evidence of manus impressions and we can rule out a manus preservation bias (e.g.: Castanera et al., 2013a) as the tracks were excavated level-by-level. Only trackway BEB500-T120 has a FL/FW ratio and mesaxony that fall within the parameters of certain ornithopod ichnotaxa (Lockley, 2009; Castanera et al., 2013b, Fig. 9). Clear sharp claw marks have been distinguished in both the gracile and the robust morphotype, with the exception again of BEB500-T120. The pace lengths are reasonably long in all the trackways (Fig. S2). With the current data, the best candidates for producing the minute to small-sized tracks of the Ajoie ichnoassemblages are small-medium-sized theropods, for both the gracile and the robust morphotype (with the possible exception of BEB500-T120). The presence of at least two/three small-sized theropods reported in the present paper, plus the large (*Megalosauripus transjuranicus*, Razzolini et al., 2017) and the giant (*Jurabrontes curtedulensis*) theropod tracks, together with sauropod footprints (Marty, 2008; Marty et al., 2010), support previous assumptions that carbonate tidal flat ichnoassemblages are mainly dominated by saurischian (theropod+sauropod) dinosaurs (Fanti et al., 2013; D'Orazi Porchetti et al., 2016).

CONCLUSIONS

The minute to medium-sized tridactyl dinosaur tracks from the tracksites of Highway A16 in the Jura Mountains (NW Switzerland) represent one of the largest samples from the Late Jurassic worldwide. Analysis of the quality of preservation (preservation grade), the maximum depth, the shape variation along the trackway, and the footprint proportions (FL/FW ratio and mesaxony) opens a new window onto the interpretation of dinosaur track variations. The description and analysis of the material have made it possible to characterize in detail two different morphotypes, one gracile and one robust, that were already identified in the field. The new data allow us to rule out the notion that the two morphotypes represent a morphological continuum of extramorphological variations, or ontogenetic variations on the larger tracks described from the same sites. An ichnotaxonomical comparison with the main minute to medium-sized tridactyl ichnotaxa has not allowed the studied tracks to be assigned to any known ichnotaxon. On the one hand, the gracile morphotype (cf. *Kalohipus*), though similar to some grallatorid ichnotaxa, shows a number of morphometric differences; on the other hand, the robust morphotype (cf. *Therangospodus* and ?*Therangospodus*), though similar to *Therangospodus pandemicus*, also shows some differences with respect to the diagnosis of the type specimen. Further work is needed in order to understand the possible influence of the substrate composition on theropod ichnotaxonomy in general and the aforementioned ichnotaxa in particular. This study also highlights the difficulties of distinguishing between minute and medium-sized tridactyl dinosaur ichnotaxa and the importance of analysing different factors related to preservation and ontogeny before assigning a single track to a concrete ichnotaxon. The new data increase theropod ichnodiversity to 4/5? theropod ichnotaxa in the tidal flats of the Jura and support previous assumptions that carbonate tidal flats were mainly dominated by theropod and sauropod dinosaurs.

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FIGURE CAPTIONS:

Fig.1: Geographical and geological settings of the Highway 16 tracksites (modified from Razzolini et al., 2017; Marty et al., 2017). A) Geographical setting of the Ajoie district (NW

Switzerland) with the location of the tracksites (1- Courtedoux—Béchat Bovais, 2- Courtedoux—Bois de Sylleux, 3- Courtedoux—Tchâfouè, 4- Courtedoux—Sur Combe Ronde, 5- Chevenez—Combe Ronde, 6- Chevenez—La Combe) along Highway A16. B) Chrono-, bio- and lithostratigraphic setting of the Reuchenette Formation in the Ajoie district, Canton Jura, NW Switzerland (after Comment, Ayer & Becker, 2011, 2015).

Fig. 2: Pictures and false-colour depth maps of the tracks with a high preservation grade that belong to the gracile morphotype. A) BEB500-T16-R3; B) BEB500-T26-R5; C) BEB500-T73-L5; D) BSY1020-E2; E) CHV1000-E4; F) CRO500-T10-L10; G) SCR1055-T2-L2*; H) SCR1055-T3-L2*; I) TCH1055-E53; J) TCH1055-T2-L1; K) TCH1060-E58; L) TCH1065-E3; M) TCH1065-E177; N) TCH1065-T25-L2; O) TCH1069-T1-R2. *In these two cases, it is not a picture but a coloured mesh obtained from the 3D-model.

Fig. 3: Pictures and false-colour depth maps of the tracks with a high preservation grade that belong to the robust morphotype. A) BEB500-T120-R5; B) BEB500-T120-R6; C) TCH1065-T21-R1; D) TCH1065-E188; E) TCH1065-E124; TCH1065-T15-R1.

Fig. 4: Morphological variation in the footprint shape along the studied trackways from BEB500 tracksite. A) BEB500-T16 (gracile morphotype); B) BEB500-T17 (gracile morphotype); C) BEB500-T58 (gracile morphotype); D) BEB500-T73 (gracile morphotype); E) BEB500-T75 (gracile morphotype); F) BEB500-T78 (gracile morphotype); G) BEB500-T82 (gracile morphotype); H) BEB500-T120 (robust morphotype). I) BEB500-T93;

Fig.5: Morphological variation in the footprint shape along the studied trackways from the CRO500, TCH1055, TCH1065 and TCH1069 tracksites. A) CRO500-T10 (gracile morphotype); B) CRO500-T30BIS (gracile morphotype); C) TCH1055-T2 (gracile morphotype); D) TCH1065-T15 (robust morphotype); E) TCH1069-T2 (robust morphotype); F) TCH1065-T25 (gracile morphotype).

Fig. 6: Bivariate graph plotting the footprint length/footprint width ratio against the mesaxony (AT) of the studied tracks (gracile and robust morphotype) with the larger tracks described in the Reuchenette Formation. A) Gracile and robust morphotype compared with *Megalosauripus* tracks (including tracks classified as *Megalosauripus transjuranicus*, *Megalosauripus* cf. *transjuranicus* and *Megalosauripus* isp.), the Morphotype II tracks and *Jurabrontes curtedulensis* (after Razzolini et al., 2017; Marty et al., 2017). Note that in many cases the points represent tracks from the same trackway, so variation through the trackway is also represented. B) The studied tracks compared with just the holotype and paratype specimens of *Megalosauripus transjuranicus* and *Jurabrontes curtedulensis*, plus the best-preserved tracks of Morphotype II (BEB500-TR7). Outline drawings not to scale.

Fig. 7: Main small-medium-sized tridactyl dinosaur footprints described in the Late Jurassic of Europe. A) *Grallator* from Spain (S, after Castanera, Piñuela & García-Ramos, 2016); B) *Anomoepus* from Spain (S, after Piñuela, 2015); C) *Carmelopodus* from France (C, after Mazin, Hantzpergue & Pouech, 2016); D) *Eubrontes* from France (C, after Mazin et al., 2000); E) *Wildeichnus* from Poland (C, after Gierliński, Niedźwiedzki & Nowacki, 2009); F) *Jialingpus*

from Poland (C, after Gierliński, Niedźwiedzki & Nowacki, 2009). G) *Dineichnus* from Poland (C, after Gierliński, Niedźwiedzki & Nowacki, 2009); H) *Dineichnus* from Portugal (S, Lockley et al., 1998a); I) *Therangospodus*-like track from Portugal (S, after Lockley, Meyer & Moratalla, 2000; J) *Therangospodus*-like track from Italy (C, after Conti et al., 2005). K) *Carmelopodus*-like track from Italy (C, after Conti et al., 2005); L) *Grallator* from Germany (S, after Diedrich, 2011). Scale bar = 1cm (E), 5 cm (A, F, G), 10 cm (B, C, D, H, I, J, K, L). S and C refer to siliciclastic and carbonate substrate, respectively.

Fig. 8.: A) Outline drawing of the holotype of *Carmelopodus untermannorum* (S, redrawn after Lockley et al., 1998b); B) Outline drawing of the holotype of *Wildeichnus navesi* (V, redrawn after Lockley, Mitchel & Odier, 2007); C) Outline drawing of the topotype of *Therangospodus pandemicus* (S, after Lockley, Meyer & Moratalla, 2000); D) Outline drawing of of *Anomoepus scambus* (S, after Olsen & Rainforth, 2003); E) Outline drawing of the holotype of *Dineichnus socialis* (S, after Lockley et al., 1998a); F) Composite outline drawing of type trackway of *Grallator parallelus* (S, redrawn from Olsen, Smith & McDonald, 1998); G) Outline drawing of type specimen of *Anchisauripus sillimani* (S, redrawn from Olsen, Smith & McDonald, 1998); H) Outline drawing of type specimen of *Eubrontes giganteus* (S, redrawn from Olsen, Smith & McDonald, 1998). I) Outline drawing of type specimen of *Jialingpus yuechiensis* (S, redrawn from Lockley et al., 2013); J) Outline drawing of type specimen of *Kalohipus bretunensis* (S, redrawn from Fuentes Vidarte & Meijide Calvo, 1998). K) Outline drawing of type specimen of *Jurabrontes curtedulensis* (redrawn from Marty et al., 2017). L) Outline drawing of type specimen of *Megalosauripus transjuranicus* (redrawn from Razzolini et al., 2017). M) Outline drawing of specimen BSY1020-E2 (cf. *Kalohipus*). N) Outline drawing of specimen CRO500-T10-L10 (cf. *Kalohipus*). O) Outline drawing of specimen TCH-1060-E58 (cf. *Kalohipus*); P) Outline drawing of specimen TCH-1065-T21-R1 (cf. *Therangospodus*); Q) Outline drawing of specimen BEB500-T120-R5 (?*Therangospodus*). S, C and V refer to siliciclastic, carbonate and and volcanoclastic substrate, respectively. Scale bar = 2 cm (B, D), 5 cm (F,G, H, I, J), 10 cm (A, C, E, L, M-Q), 50 cm (K).

Fig. 9: Bivariate graph plotting the footprint length/footprint width ratio *vs* AT of the studied tracks (gracile and robust morphotype) with some of the main ichnotaxa mentioned in the text. Outline drawings not to scale.

Table 1: Measurements of the specimens with a high preservation grade: footprint length (FL), footprint width (FW), footprint length /footprint width ratio (FL/FW), digit length (LI, LII, LIII), digit width (WI, WII, WIII), divarication angles (II-III, III-IV), mesaxony (AT, anterior triangle ratio).

Supplemental information Table S1: List of the specimens analysed, their quality of preservation (preservation grade) and the maximum depth. Those with preservation grade 0-0.5 are not included in the figshare file. The tracks where the variation along the trackway has been analysed are in red.

Supplemental information Figure S2: Map of the Courtedoux—Béchat Bovais tracksite, level 500 (BEB500). In red (gracile) and blue (robust) the minute to medium-sized tridactyl tracks and in green, the larger morphtoype (Morphotype II).

Supplemental information Figure S3: Map of the Courtedoux—Tchâfouè tracksite, level 1065 (TCH1065). In red (gracile) and blue (robust) the minute to medium-sized tridactyl tracks and in green, the larger morphtoype (*Jurabrontes curtedulensis* see Marty et al., 2017).

Supplemental information Figure S4: Map of the Chevenez—Combe Ronde, level 500 (CRO500). In red (gracile) and blue (robust) the minute to medium-sized tridactyl tracks and in green, the larger morphtoype (Morphotype II).

Acknowledgements

We thank all technicians, photographers, geometers, drawers, collection managers, and preparators of the PALA16 that were involved during the excavation and documentation of the tracksites and during the set-up and organization of the track collection. We also thank the scientific staff of the PALA16 and JURASSICA Muséum for various stimulating discussions and valuable input. The authors also thank Laura Piñuela, Vanda Santos, Ignacio Díaz-Martínez, and Novella L. Razzolini for fruitful discussion on the topic of this manuscript. Rupert Glasgow revised the English grammar.

Figure 1

Geographical and geological settings of the Highway 16 tracksites (modified from Razzolini et al., 2017; Marty et al., 2017).

A) Geographical setting of the Ajoie district (NW Switzerland) with the location of the tracksites (1- Courtedoux—Béchat Bovais, 2- Courtedoux—Bois de Sylleux, 3- Courtedoux—Tchâfouè, 4- Courtedoux—Sur Combe Ronde, 5- Chevenez—Combe Ronde, 6- Chevenez—La Combe) along Highway A16. B) Chrono-, bio- and lithostratigraphic setting of the Reuchenette Formation in the Ajoie district, Canton Jura, NW Switzerland (after Comment, Ayer & Becker, 2011, 2015).

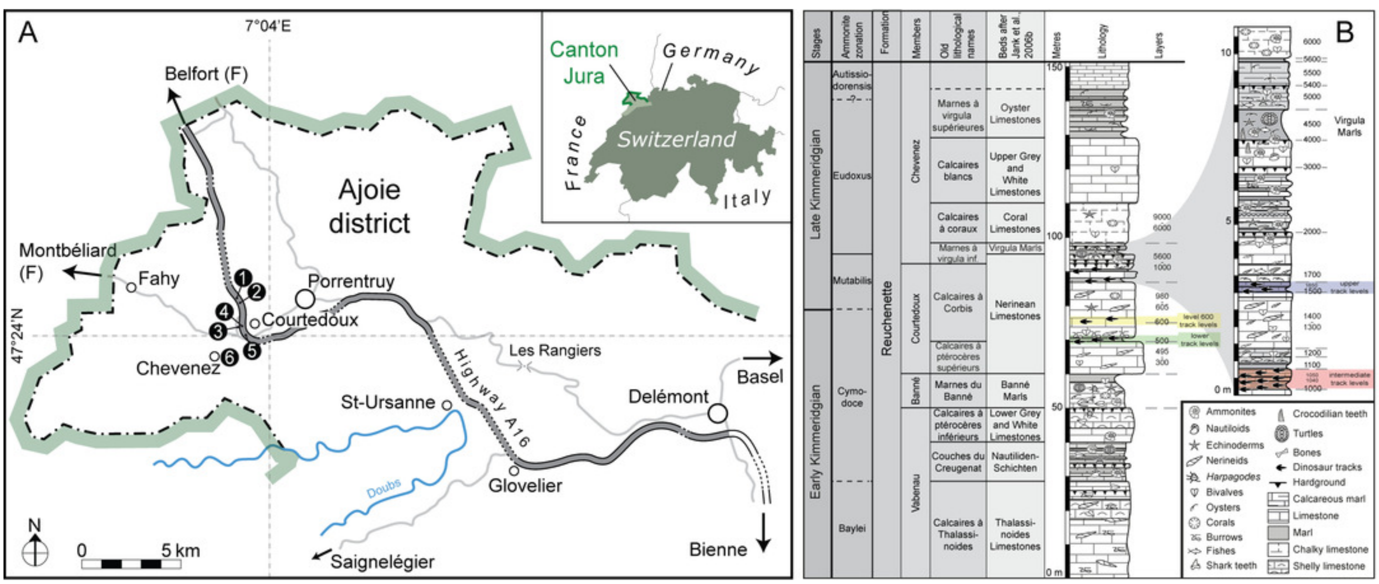

Figure 2

Pictures and false-colour depth maps of the tracks with a high preservation grade that belong to the gracile morphotype.

A) BEB500-T16-R3; B) BEB500-T26-R5; C) BEB500-T73-L5; D) BSY1020-E2; E) CHV1000-E4; F) CRO500-T10-L10; G) SCR1055-T2-L2*; H) SCR1055-T3-L2*; I) TCH1055-E53; J) TCH1055-T2-L1; K) TCH1060-E58; L) TCH1065-E3; M) TCH1065-E177; N) TCH1065-T25-L2; O) TCH1069-T1-R2. *In these two cases, it is not a picture but a coloured mesh obtained from the 3D-model.

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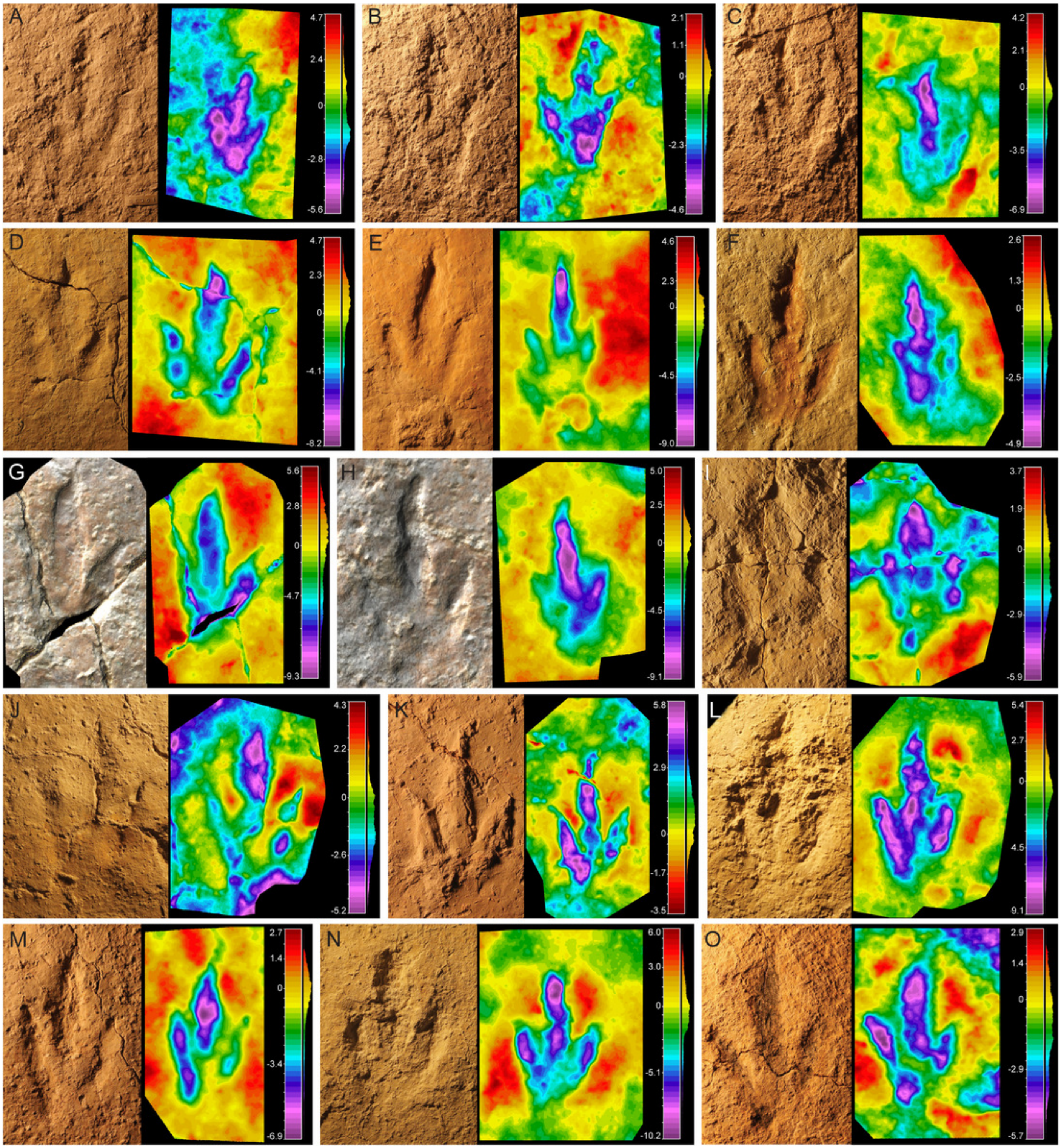
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0
-2.8
-5.6
B
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1.1
0
-2.3
-4.6
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2.1
0
-3.5
-6.9
D
4.7
2.3
0
-4.1
-8.2
E
4.6
2.3
0
-4.5
-9.0
F
2.6
1.3
0
-2.5
-4.9
G
5.6
2.8
0
-4.7
-9.3
H
5.0
2.5
0
-4.5
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I
3.7
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J
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K
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0
-1.7
-3.5
L
5.4
2.7
0
4.5
9.1
M
2.7
1.4
0
-3.4
-6.9
N
6.0
3.0
0
-5.1
-10.2
O
2.9
1.4
0
-2.9
-5.7

Figure 3

Pictures and false-colour depth maps of the tracks with a high preservation grade that belong to the robust morphotype.

A) BEB500-T120-R5; B) BEB500-T120-R6; C) TCH1065-T21-R1; D) TCH1065-E188; E) TCH1065-E124; TCH1065-T15-R1.

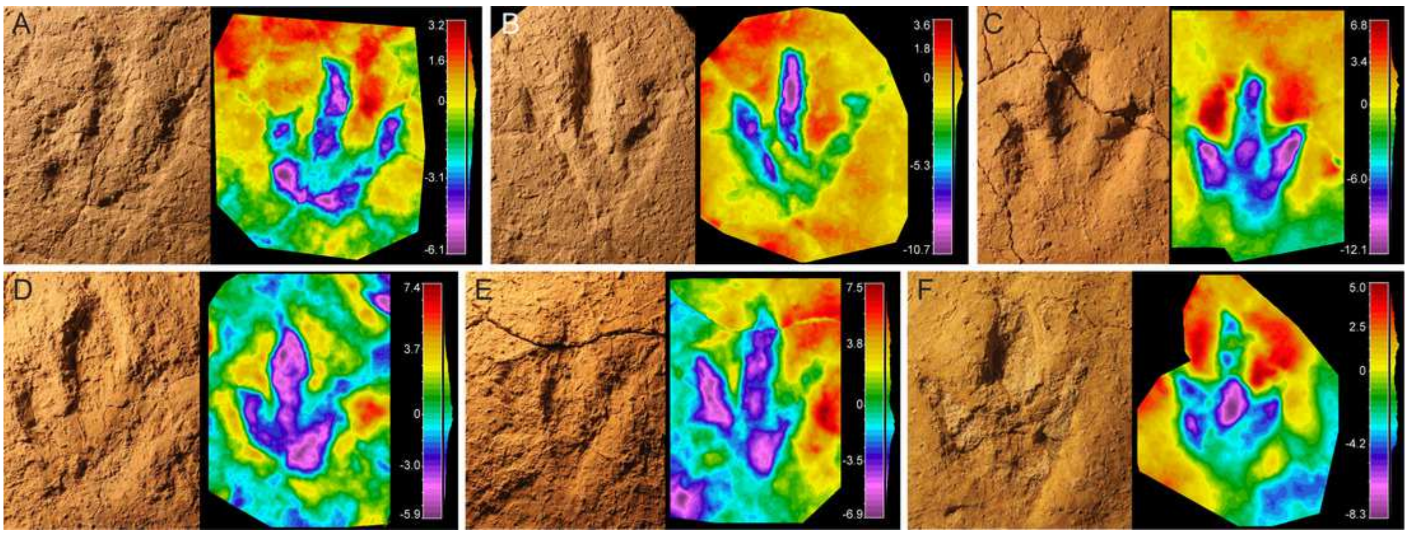
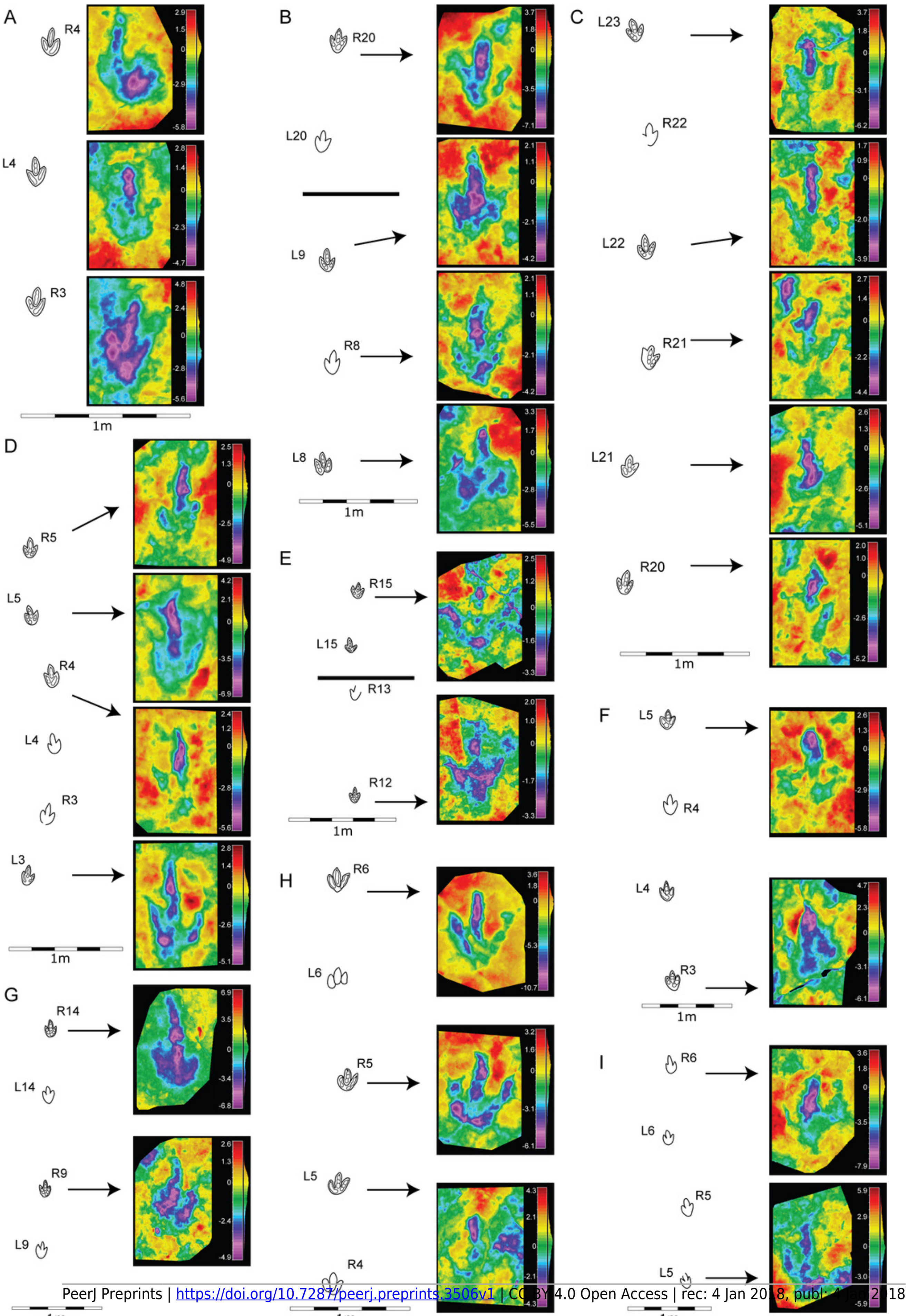


Figure 4

Morphological variation in the footprint shape along the studied trackways from BEB500 tracksite.

A) BEB500-T16 (gracile morphotype); B) BEB500-T17 (gracile morphotype); C) BEB500-T58 (gracile morphotype); D) BEB500-T73 (gracile morphotype); E) BEB500-T75 (gracile morphotype); F) BEB500-T78 (gracile morphotype); G) BEB500-T82 (gracile morphotype); H) BEB500-T120 (robust morphotype). I) BEB500-T93.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R3
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B
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L9
R8
L8
1m
C
L23
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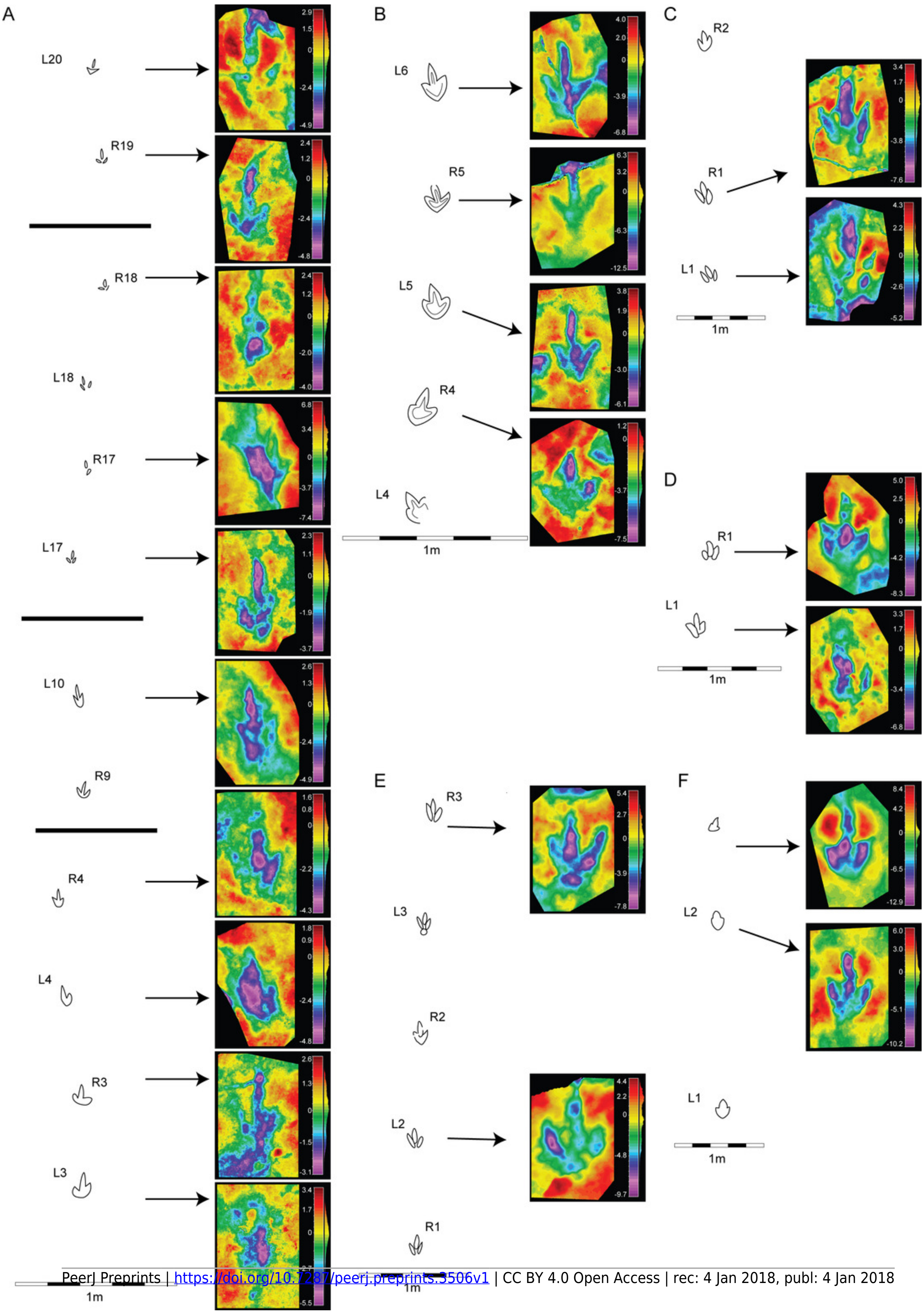
L22
R21
L21
R20
1m
D
R5
L5
R4
L4
R3
L3
1m
E
R15
L15
R13
R12
1m
F
L5
R4
L4
R3
1m
G
R14
L14
R9
L9
1m
H
R6
L6
R5
L5
R4
1m
I
R6
L6
R5
L5
1m

Figure 5

Morphological variation in the footprint shape along the studied trackways from the CRO500, TCH1055, TCH1065 and TCH1069 tracksites.

A) CRO500-T10 (gracile morphotype); B) CRO500-T30BIS (gracile morphotype); C) TCH1055-T2 (gracile morphotype); D) TCH1065-T15 (robust morphotype); E) TCH1069-T2 (robust morphotype); F) TCH1065-T25 (gracile morphotype).


A
L20
R19
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R17
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L10
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1m
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R5
L5
R4
L4
1m
C
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R1
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D
R1
L1
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R2
L2
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1m
F
L2
L1
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Figure 6

Bivariate graph plotting the footprint length/footprint width ratio against the mesaxony (AT) of the studied tracks (gracile and robust morphotype) with the larger tracks described in the Reuchenette Formation.

A) Gracile and robust morphotype compared with *Megalosauripus* tracks (including tracks classified as *Megalosauripus transjuranicus*, *Megalosauripus* cf. *transjuranicus* and *Megalosauripus* isp.), the Morphotype II tracks and *Jurabrontes curtedulensis* (after Razzolini et al., 2017; Marty et al., 2017). Note that in many cases the points represent tracks from the same trackway, so variation through the trackway is also represented. B) The studied tracks compared with just the holotype and paratype specimens of *Megalosauripus transjuranicus* and *Jurabrontes curtedulensis*, plus the best-preserved tracks of Morphotype II (BEB500-TR7). Outline drawings not to scale.

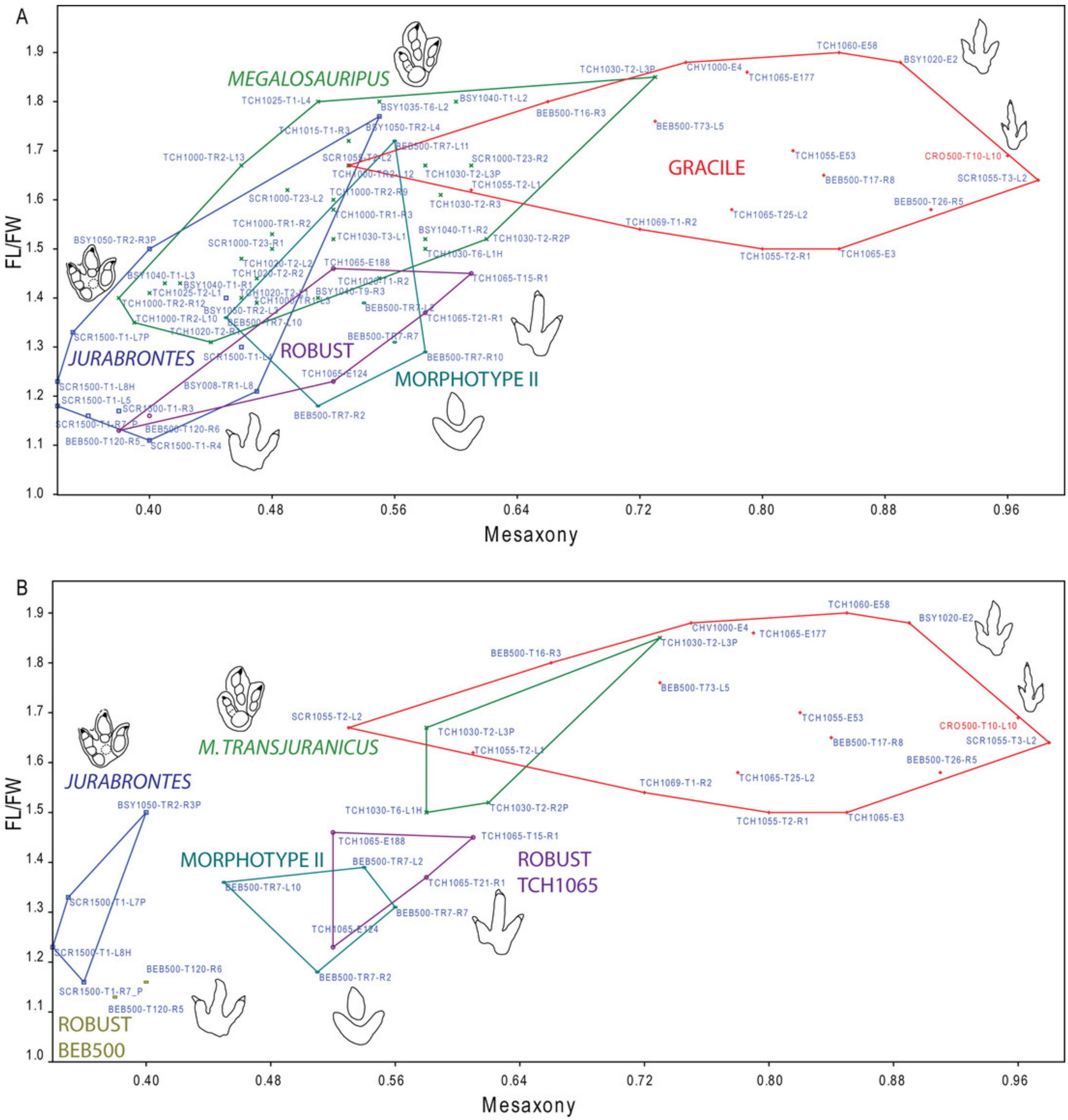

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Figure 7

Main small-medium-sized tridactyl dinosaur footprints described in the Late Jurassic of Europe.

A) *Grallator* from Spain (S, after Castanera, Piñuela & García-Ramos, 2016); B) *Anomoepus* from Spain (S, after Piñuela, 2015); C) *Carmelopodus* from France (C, after Mazin, Hantzpergue & Pouech, 2016); D) *Eubrontes* from France (C, after Mazin et al., 2000); E) *Wildeichnus* from Poland (C, after Gierliński, Niedźwiedzki & Nowacki, 2009); F) *Jialingpus* from Poland (C, after Gierliński, Niedźwiedzki & Nowacki, 2009). G) *Dineichnus* from Poland (C, after Gierliński, Niedźwiedzki & Nowacki, 2009); H) *Dineichnus* from Portugal (S, Lockley et al., 1998a); I) *Therangospodus*-like track from Portugal (S, after Lockley, Meyer & Moratalla, 2000; J) *Therangospodus*-like track from Italy (C, after Conti et al., 2005). K) *Carmelopodus*-like track from Italy (C, after Conti et al., 2005); L) *Grallator* from Germany (S, after Diedrich, 2011). Scale bar = 1cm (E), 5 cm (A, F, G), 10 cm (B, C, D, H, I, J, K, L). S and C refer to siliciclastic and carbonate substrate, respectively.

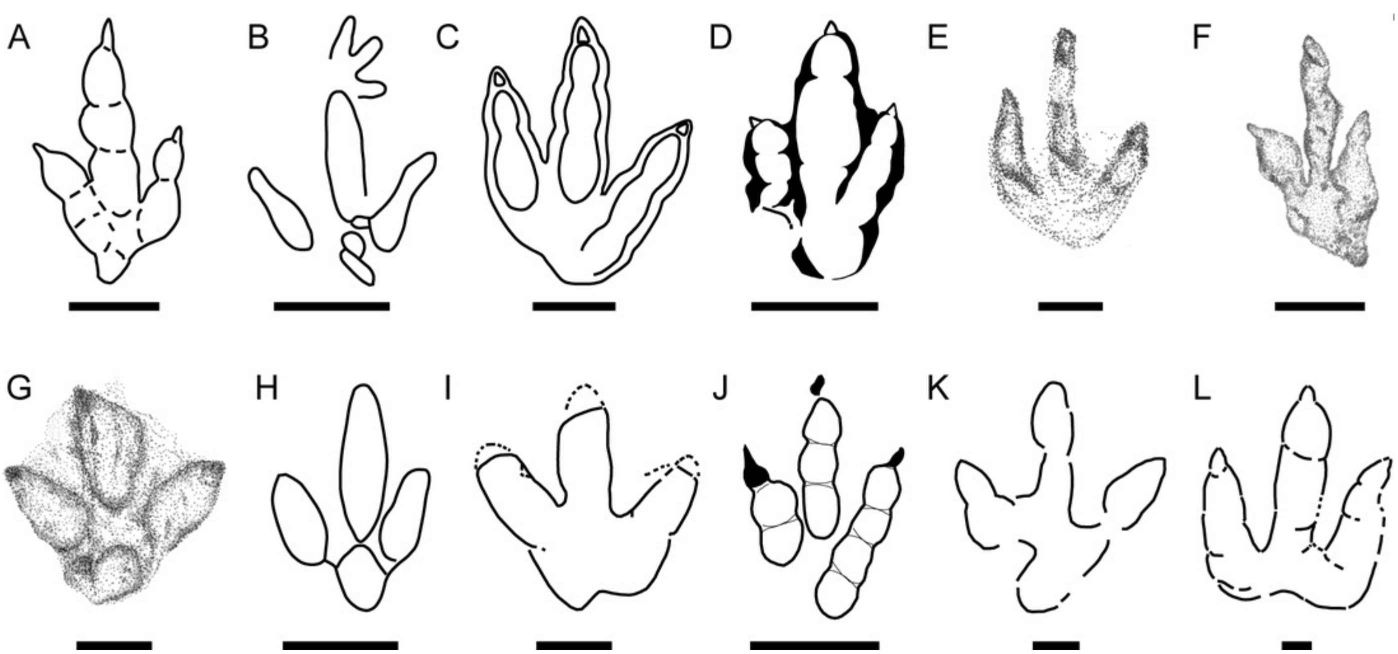

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Figure 8

Small-medium-sized tridactyl dinosaur ichnotaxa with affinities with the described morphotypes.

A) Outline drawing of the holotype of *Carmelopodus untermannorum* (S, redrawn after Lockley et al., 1998b); B) Outline drawing of the holotype of *Wildeichnus navesi* (V, redrawn after Lockley, Mitchel & Odier, 2007); C) Outline drawing of the topotype of *Therangospodus pandemicus* (S, after Lockley, Meyer & Moratalla, 2000); D) Outline drawing of of *Anomoepus scambus* (S, after Olsen & Rainforth, 2003); E) Outline drawing of the holotype of *Dineichnus socialis* (S, after Lockley et al., 1998a); F) Composite outline drawing of type trackway of *Grallator parallelus* (S, redrawn from Olsen, Smith & McDonald, 1998); G) Outline drawing of type specimen of *Anchisauripus sillimani* (S, redrawn from Olsen, Smith & McDonald, 1998); H) Outline drawing of type specimen of *Eubrontes giganteus* (S, redrawn from Olsen, Smith & McDonald, 1998). I) Outline drawing of type specimen of *Jialingpus yuechiensis* (S, redrawn from Lockley et al., 2013); J) Outline drawing of type specimen of *Kalohipus bretunensis* (S, redrawn from Fuentes Vidarte & Meijide Calvo, 1998). K) Outline drawing of type specimen of *Jurabrontes curtedulensis* (redrawn from Marty et al., 2017). L) Outline drawing of type specimen of *Megalosauripus transjuranicus* (redrawn from Razzolini et al., 2017). M) Outline drawing of specimen BSY1020-E2 (cf. *Kalohipus*). N) Outline drawing of specimen CRO500-T10-L10 (cf. *Kalohipus*). O) Outline drawing of specimen TCH-1060-E58 (cf. *Kalohipus*); P) Outline drawing of specimen TCH-1065-T21-R1 (cf. *Therangospodus*); Q) Outline drawing of specimen BEB500-T120-R5 (?*Therangospodus*). S, C and V refer to siliciclastic, carbonate and and volcanoclastic substrate, respectively. Scale bar = 2 cm (B, D), 5 cm (F,G, H, I, J), 10 cm (A, C, E, L, M-Q), 50 cm (K).

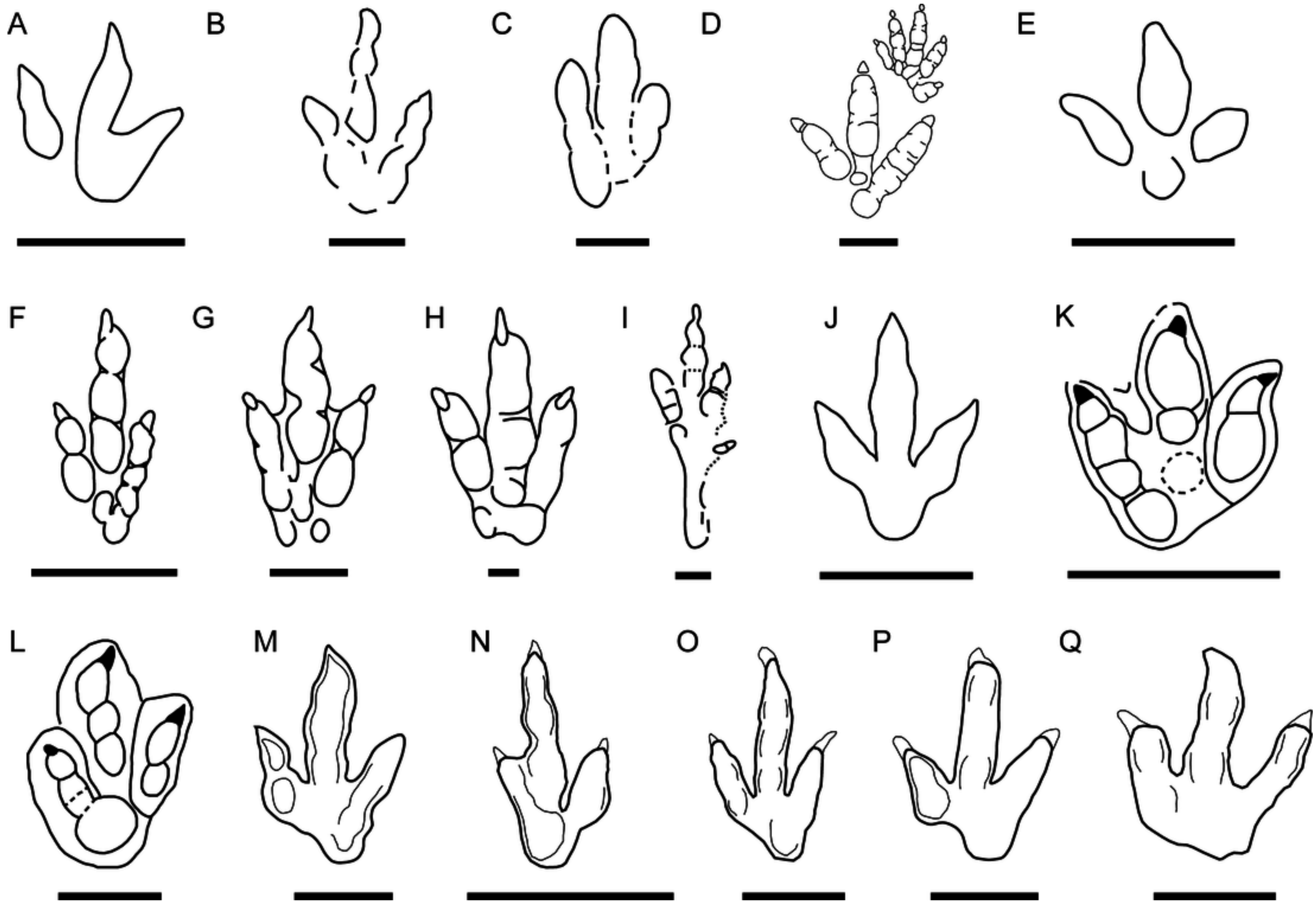
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Figure 9

Bivariate graph plotting the footprint length/footprint width ratio against AT of the studied tracks (gracile and robust morphotype) with some of the main ichnotaxa mentioned in the text.

Outline drawings not to scale.

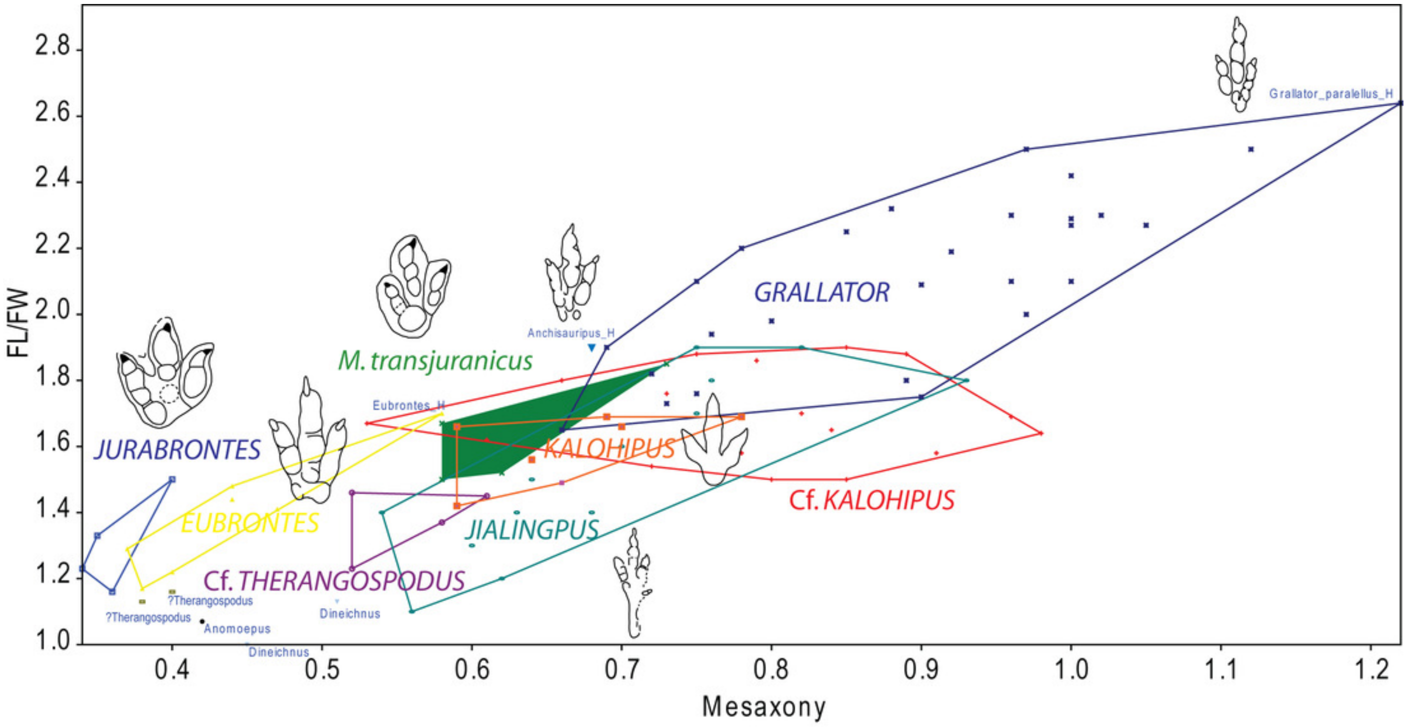

Table 1(on next page)

Measurements of the specimens with a high preservation grade:

footprint length (FL), footprint width (FW), footprint length /footprint width ratio (FL/FW), digit length (LI, LII, LIII), digit width (WI, WII, WIII), divarication angles (II-III, III-IV), mesaxony (AT, anterior triangle ratio).

Track	FL	FW	FL/FW	LII	LIII	LIV	WII	WIII	WIV	II^III	III^IV	ATw	Atl	AT
BEB500-T16-R3	18	10	1.8	13.5	18	13.8	2	1.9	1.8	22.5	17.5	8.8	5.8	0.66
BEB500-T17-R8	19	11.5	1.65	11	19	13	1.9	3.3	1.6	23	20	10.5	8.8	0.84
BEB500-T26-R5	19	12	1.58	13	19	14	2.2	3	2.9	32	26	10.3	9.4	0.91
BEB500-T73-L5	15	8.5	1.76	8.5	15	10	2.3	2.9	2.5	31	22	7.9	5.8	0.73
BSY1020-E2	22	11.7	1.88	15	22	13.5	3.6	3	2.7	21.5	24.5	9.5	8.5	0.89
TCH1055-E53	17.5	10.3	1.7	12.2	17.5	12	3	2.7	2.5	25	17.5	8.5	7	0.82
TCH1055-T2-L1	21.2	13.1	1.62	15.6	21.2	15	2.3	2.1	2.2	25	22	11.4	7	0.61
TCH1055-T2-R1	19.5	13	1.5	13.2	20.5	13.1	3.3	3.7	2.5	29	23	10.6	8.5	0.80
TCH1060-E58	20	10.5	1.90	20	13.5	12	3.4	3.1	2.9	27	22	8.8	7.5	0.85
TCH1065-E177	17.5	9.4	1.86	11.8	17.5	12.5	1.6	2.4	2	21	20	8.2	6.5	0.79
TCH1065-E3	18.4	12.3	1.5	12.3	18.4	11.7	3.3	3.8	2.3	30	24	9.14	7.8	0.85
TCH1065-T25-L2	19.3	12.2	1.58	14	19.3	12.3	3	3	2.7	25	21	10.3	8	0.78
TCH1069-T1-R2	20	13	1.54	14	20	13.5	2.1	2.7	2.1	24	29	11.5	8.3	0.72
SCR1055-T2-L2	20	12	1.67	15	20	16	2.7	2.9	2.5	25	18	11.4	6	0.53
SCR1055-T3-L2	18	11	1.64	12	18	12	2.3	2.1	1.8	26	26	8.5	8.3	0.98
CHV1000-E4	16	8.5	1.88	11	16	10	1.8	2.3	1.7	21	22	8.1	6.1	0.75
CRO500-T10-L10	11	6.5	1.69	6	11	7	1.4	1.8	1.5	32	23	5.6	5.4	0.96
BEB500-T120-R5	17	15	1.13	13.5	17	14.5	3.5	3.2	2.5	30.4	34	13	5	0.38
BEB500-T120-R6	18	15.5	1.16	14.5	18	15	2.5	3.1	3	22	27	14.2	5.7	0.40
TCH1065-E124	19	15.5	1.23	13.5	19	15	3.3	4.5	3.5	27.5	26.5	14.4	7.5	0.52
TCH1065-E188	18	12.3	1.46	13.3	18	13	3.2	3.7	3.3	25	27	10	5.2	0.52
TCH1065-T21-R1	19.8	14.5	1.37	14.4	19.8	14.8	3.5	3.7	3.5	27	27	11.8	6.9	0.58
TCH1065-T15-R1	21.8	15	1.45	15.7	21.8	17.2	2.7	3.4	3.1	29	25	12	7.3	0.61

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