Early Cretaceous dinosaur footprints from the Molfetta tracksite (Apulia, southern Italy)

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Abstract

The track-bearing surface of the San Leonardo quarry (Molfetta, Apulia), early Albian in age, is characterised by more than 800 footprints, produced by both quadrupedal and bipedal dinosaurs. Six well-preserved bipedal trackways, composed by tridactyl footprints are attributed to medium- to large-sized theropod dinosaurs. Only one clear but poorly preserved trackway and numerous isolated manus-pes couples have been attributed to quadrupedal dinosaurs. The tridactyl ichnoassemblage, analysed using both traditional methods and close-range photogrammetry, is represented by weakly mesaxonic and robust specimens. Morphological comparison with Late Jurassic and Early Cretaceous theropod tracks from surrounding areas, supported by morphometric analyses, points out a highest affinity with the specimens from North Africa. Nevertheless, a set of unique characters appears to justify the establishment of a new ichnotaxon, *Cretabrontes melphicticus*. Additionally, the

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photogrammetric models of the quadrupedal trackway and four isolated manus-pes sets suggest they belong to the same morphotype, represented by asymmetrical tetradactyl *pes* and highly digitigrade tetra- or pentadactyl *manus*. These tracks share numerous morphological characters with both the ichnogenera *Tetrapodosaurus* and *Metatetrapodus* and thus can be attributed to a medium-sized ankylosaurian trackmaker.

1. Introduction

The Apulian Carbonate Platform is one of the most extensive Mesozoic-Cenozoic shallow water domains of the Tethyan ocean (Morsilli et al., 2017 and references therein). Its deposits crop out in the regions of Apulia (Gargano Promontory and Murge Plateau) and Abruzzo (Maiella Mountain) and extend beneath the Apennines foredeep to the west and offshore into the Adriatic Sea to the east (Morsilli et al., 2017 and references therein).

Since 1999, the year of discovery of the Altamura ichnosite (Nicosia et al., 2000a), the Cretaceous carbonate succession of the Apulia Carbonate Platform, cropping out in the Apulia region (Southern Italy), has proved to be a treasure trove for dinosaur footprints, and numerous new dinosaur tracksites have been discovered both in the Murge Plateau and on the Gargano promontory (Conti et al., 2005; Sacchi et al., 2009; Petti et al., 2008b; 2010, 2018; Petruzzelli et al., 2011, 2019). The so far studied tracksites range from the ?Late Jurassic (Kimmeridgian-Tithonian) to the Late Cretaceous (Campanian).

The discovered ichnoassemblages document a high biodiversity of trackmakers, testified by sauropod, theropod, ankylosaur and hadrosaur footprints (Nicosia et al., 2000a; 2000b; Conti et al., 2005; Sacchi et al., 2009; Petti et al., 2008b; 2010, 2018; 2020a; 2020b; Petruzzelli et al., 2011, 2019). The occurrence of dinosaur tracks from different stratigraphic horizons, both in the Apulian and in the other surrounding carbonate platforms of the Tethyan domain (Periadriatic Carbonate Platform *sensu* Zappaterra, 1990, 1994), led several authors to question all previous palaeogeographic reconstructions and propose new models to justify the contemporary presence of dinosaurs in

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different platforms and in distinct intervals of the Cretaceous period (Petti, 2006; Nicosia et al., 2007; Sacchi et al., 2009; Zarcone et al., 2010; Romano & Citton, 2017).

The aim of this paper is to describe and discuss the dinosaur ichnoassemblage discovered in 2005 on a working surface of the northern quarry, part of the San Leonardo quarry complex, close to the town of Molfetta. The complex opened at the beginning of 1900 is constituted by 3 pit shape quarries, in all of them there are trampled surfaces, but here reporting the most representative one. The dinosaur tracks herein preserved allowed to include the Molfetta ichnosite in the Geosite Census of the Apulia Region (CGP0137 in Mastronuzzi et al., 2015).

The tracksite has already been the subject of preliminary studies aimed at producing a geothematic map of the whole trampled surface that would highlight the ichnological record (Petti et al., 2018). To achieve this result Petti et al. (2018) applied aerial high-resolution digital photogrammetry by using two different UAVs (Unmanned Aerial Vehicles).

2. Geographic and geological setting

The studied ichnoassemblage lies on a bed surface of about 2700 m^2 exposed in a disused quarry (San Leonardo), located close to the town of Molfetta in the northern sector of the Murge area (Lat: 41,18125 N; Long: 16,57287 E, Apulia, southern Italy) (Fig. 1). The quarry was cultivated in a well-bedded lower Cretaceous carbonate succession dipping of 15°-20° to S-SW.

The Murge area is an autochthonous carbonate region and is considered as part of the extensive and only slightly deformed southern Apennine foreland area (Apulia foreland sensu Selli, 1962; D'Argenio et al., 1973; Ricchetti et al. 1988). The geologic structure of the area mainly consists of a S-SW dipping monocline of limestones and dolostones deformed by brittle structures (Festa, 2003). As a consequence of this tectonic setting, the oldest part of the Cretaceous succession crops out at the core of an anticline (M. Acuto Anticline) located to N, whereas the youngest one crops out to S (Fig. X). The backbone of the outcropping carbonate succession is made up of Cretaceous inner

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shelf limestones showing mud-supported facies associations formed in low-energy peritidal environments (Spalluto et al., 2008; Spalluto, 2012). In this shallow-water carbonate succession two formations were recognized (Ricchetti, 1975; Ciaranfi et al., 1988): the Calcare di Bari Fm (Valanginian p.p.- ?early Turonian), about 2000 m thick, and the Calcare di Altamura Fm (? late Turonian – Maastrichtian), 1000 m thick, separated by a Turonian unconformity, locally marked by bauxites and other continental deposits (Crescenti & Vighi, 1964).

The succession containing the track-bearing horizon belongs to the lower part of the Calcare di Bari Formation, and is part of the informal Bisceglie limestones member (*sensu* Luperto Sinni & Masse, 1992), whose age was referred to the Late Aptian based on the peculiar benthic foraminifera and green algae assemblages (Fig. Y). More recently, the litho- and bio-stratigraphic revision proposed for the Murge area by Spalluto et al. (2005) and Spalluto & Caffau (2010), allowed to extend the age of the informal Bisceglie limestones member to the late Aptian-early Albian interval. Accordingly, the age of the San Leonardo quarry has been preliminarily attributed to the late Aptian/early Albian (Iannone et al., 2012; Fanti et al., 2014; Petruzzelli, 2017).

~~The studied surface covers an area and is placed at the top of a highly bioturbated wackestone bed deposited in a shallow subtidal environment~~ (Petti et al., 2018). ~~The dinosaur footprints testify to temporary subaerial exposure of this surface.~~

3. Material and methods

During the repeated inspections and study phases that have taken place since the discovery, hundreds of dinosaur footprints were identified. They are mostly isolated and scattered over the whole surface even though some of them are arranged into distinct and randomly oriented trackways.

Petti et al. (2018) recognised and mapped six well preserved bipedal trackways likely produced by medium- to large-sized theropods, plus one incomplete quadrupedal trackway attributed to medium-sized herbivorous dinosaurs. It is worth mentioning the occurrence of a decametric 'L-shaped' trace, showing a central ridge, meniscate structures and raised rims. The enigmatic shape and

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the observed structure exclude a sedimentary origin and suggest a biological activity, such as the crossing of a large-bodied tetrapod.

The stratigraphic study was performed logging in detail the succession cropping out in the quarry, and collecting about 70 rock samples at a cm scale. Thin sections were made for each sample to perform the microfacies analysis and to determine the microfossiliferous assemblage.

The ichnological study was performed in the field on the trackways already mapped by Petti et al. (2018) by means of UAV photogrammetric surveys. All the studied material comes from the same stratigraphic horizon and was named using the acronym SL (San Leonardo quarry), followed by a number indicating the trackway. This latter is followed by a hyphen and another number to identify individual footprints within the trackway. All the material is still visible in the San Leonardo quarry. The recognised trackways were preliminarily surveyed and measured directly in the field using standard methods (Leonardi; 1987, Thulborn, 1990; Weems, 1992; Marty, 2008). Each footprint was outlined and interpreted using coloured chalks and the interpretative drawings were then traced on acetate overlays. Footprint parameters were taken using internal outlines gained directly in the field.

The best-preserved tracks were also digitally documented adopting close-range photogrammetry to produce 3D models. This technique is nowadays commonly used in tetrapod ichnology, providing detailed supplementary information (Breithaupt et al., 2004; Petti et al., 2008a; Remondino et al., 2010; Falkingham, 2012; Falkingham et al., 2014; McCrea et al., 2014; Mallison & Wings, 2014; Citton et al., 2015; Lallensack et al., 2015; Petti et al., 2015; Lallensack et al., 2016; Razzolini et al., 2016; Salisbury et al., 2016; Lallensack et al., 2017; Romilio et al., 2017; Avanzini et al., 2018). Close-range photogrammetry was performed using a 18.1 megapixel digital single-lens reflex camera (DSLR) Canon EOS 1200D, that mounts a 18.0 Megapixel CMOS (APS-C) image sensor. To obtain a 3D virtual model of each selected footprint about 60 photos were taken. They were acquired in three distinct photosets, from different points of view (ground level, camera dipping 30° and 60° and 90° with respect to the quarry surface) and turning around the footprints at 360°. A

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scale and three control points were used to scale the 3D models. The camera was set to autofocus with ISO on 100; shutter speed and aperture were set manually depending on lighting conditions. The photos were taken between 10 a.m. and 5 p.m. in order to catch adequate sunlight and were exported as JPEG files with 5184x3456 pixel resolution at 72 dpi. Data processing was carried out using a Dell Precision 7530, powered by CPU Intel Xeon E-2186M (2.90 GHz), with 32 GB RAM and graphics card Nvidia Quadro P3200. Three-dimensional models were obtained using Agisoft PhotoScan ® Professional v. 1.4.5 (www.agisoft.com) software and following the procedure established by Mallison & Wings (2014). The obtained dense cloud models were imported into Golden Software Surfer ® 16 (www.goldensoftware.com), where data points were interpolated using kriging algorithm method. The surface grids were therefore converted into colour-coded images with closely spaced contour lines and colour relief maps (see supplementary material for reports and details).

4. Depositional environments and microfossil assemblage

The carbonate succession cropping out in the San Leonardo quarry is about 9.5 m thick and can be split out in two distinct parts (Fig. XY): 1) the lower one (about 6 m thick) is dominated by coated bioclastic limestones showing a grain-supported fabric (packstones/grainstones); 2) the upper one (about 3.5 m thick) is mostly made up of biopeloidal limestones showing a mud-supported fabric (mudstones/wackestones). The track-bearing surface crops out at the top of the section (Fig. YX). More in detail, facies analysis showed that the lower part of the San Leonardo section consists of tabular cross-bedded packstones/grainstones made up of strongly micritized coated skeletal grains in association with rounded micritic intraclasts, benthic foraminifers, dasyclad green algae, and peloids. Coated bioclastic grains are mollusc shells (gastropods and bivalves), dasyclad green algae and benthic foraminifers. The grain-supported textures and the presence of high-energy sedimentary structures permit to interpret the lower part of the section as deposited in shallow wave- or current-agitated open lagoonal environments where migrating sandbars could form. The occurrence of a normal-marine and diversified benthic fauna also supports this interpretation. The upper part of the

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San Leonardo section consists of strongly burrowed biopeloidal mudstones and wackestones, and subordinately by microbial bindstones, with benthic foraminifers, ostracodes, oncoids, and peloids. Typically, biota show a very reduced diversity but with a high number of individuals. Two distinct horizons of few m-thick intraformational breccias showing a residual matrix also occur in this part of the section. This facies association may also show smaller fenestrae forming laminoid or irregularly distributed spheroidal spar-filled cavities. The mud-supported textures and the reduced benthic biota are diagnostic criteria of low-energy restricted peritidal environments subjected to ephemeral (fenestral limestones) or prolonged subaerial exposure (intraformation breccias). The studied surface is placed at the top of a burrowed fenestral wackestone bed (Petti et al., 2018), suggesting that dinosaur footprints were imprinted on shallow-subtidal limestones showing evidence of subaerial exposure.

Microfossil assemblage was characterized by the presence of the following index fossils: *Praechrysalidina infracretacica* Luperto Sinni (Fig. XYYA), *Debarina hahounerensis* Fourcade, Raoult & Vila (Fig. XYYB), *Pseudonummoloculina aurigerica* Calvez (Fig. XYYC), *Pseudonummoloculina heimi* (Bonet) (Fig. XYYD), *Vercorsella arenata* Arnaud-Vanneau, Vercorsella scarsellai (De Castro) (Fig. XYYE), *Cuneolina sliteri* Arnaud-V8anneau & Premoli Silva (Fig. XYYF), *Cuneolina pavonia* D'Orbigny (Fig. XYYG), *Nezzazatinella picardi* (Henson), and *Sabaudia minuta* (Hofker) (Fig. XYYH). According to Velic (2007), the most important fossils for determination of the boundary between Aptian and Albian is the first occurrence of species of Cuneolina which are certain indicators of the beginning of the Albian. Moreover, during the Early Albian *Pseudonummoloculina heimi* occur for the first time (Husinec and Sokac, 2006; Velic, 2007). Spalluto & Caffau (2010) demonstrated a good overlap in stratigraphic distribution of lower Cretaceous microfacies assemblages between the Adriatic Carbonate Platform and the Apulia Carbonate Platform. Following this evidence, the age of the track-bearing surface of the San Leonardo section, found at the top of the succession, is constrained to the lower part of the Early Albian.

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4. Description of tracks and trackways

The surface exposed in the San Leonardo quarry preserves about 800 tracks, likely representing different episodes of trampling. Preservation quality covers the entire range from poorly to finely preserved footprints with clear internal and external outlines, digit traces, phalangeal pad impressions and claw marks. Both bipedal and quadrupedal trackways are preserved and will be described hereafter.

4.1. Bipedal tracks

Six short trackways and two isolated tracks of bipedal dinosaurs have been identified in the San Leonardo Quarry tracksite, totalling 34 footprints.

Trackway SL1 (Fig. …….)

This is the longest and one of the best-preserved trackways and comprises nine consecutive tridactyl tracks. From SL1-8 an older surface positioned about 3 cm underneath the track bearing surface is exposed. The distal half of SL1-8 and the whole SL1-9 are indeed preserved as undertracks; SL1-9 is a roundish depression about 28 cm in diameter, with no recognizable digit impressions.

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Most of the tracks show phalangeal pad impressions and claw marks. All tracks are moderately deeply impressed (about 5 cm), with sub-vertical walls, displaying both internal and external outlines (*sensu* Marty, 2008).

On average, Footprint Length (FL) is about 30.8 cm whereas Footprint Width (FW) is 28.4 cm. Tracks are slightly longer than wide, with FL/FW ranging from 1.03 to 1.10 (mean = 1.08) and have a weak mesaxony (i.e., low prominence of digit III in relation to digits II–IV; see Lockley, 2009 for a discussion) as indicated by the average value of 0.33 for the te/FW ratio (min. 0,29; max 0,36), where te stands for “toe extension” (*sensu* Weems, 1992). Tracks can be considered as large-sized being the average footprint length slightly higher than 30 cm (Thulborn, 1990; Marty, 2008).

Digits are broad and robust and taper distally, culminating in most cases with a short and sub-triangular claw trace. Digit II is always rotated medially, digit III oriented straight forward or slightly rotated inward, whereas digit IV is always rotated outward. Digit II and III are clearly the deepest impressed, as evidenced by DEMs.

Distinct phalangeal pad impressions are clearly visible on the best-preserved tracks (SL1-1, SL1-2, SL1-3, SL1-4 and SL1-6, SL1-7), following the classical pattern for theropod tracks of four on digit IV, three on digit III and two on digit II. Pads on digit II are wider and stouter than those of digit IV; they are sub-elliptical in shape and equidimensional. On digit IV pads are about the same size and sub-circular with the exception of the distalmost one that could be slightly smaller. Digit III preserves three large sub-elliptical to sub-circular pads decreasing in size distally. A careful analysis of the 3D models allows, in some cases, to identify an additional and smaller proximal "pad" on digit III, likely due to the partial impression of the metatarsal-phalangeal portion.

The proximal portion of digit IV is backward positioned with respect to that of digit II and they are connected by an indentation typical for theropod tracks. The tip of digit II is always slightly forward positioned with respect to that of digit IV. The hypex between digits II and III is positioned forward or at the same height with respect to that between digits IV and III and lies approximately at the boundary between the proximal and medial pad of digit III.

SL 1-5 and likely SL 1-7 show a posterior v-shaped "heel" possibly due to the impression of the distal-most portion of the metatarsus.

Digit IV is the longest (mean 21.9 cm), followed by digit III (mean 20.7 cm) and II (mean 17.8 cm). Total II^IV divarication ranges from 44° to 74° with a mean of 59.1°; interdigital angles III^IV are always wider (mean 34.4°) than those II^III (24.7°). The trackway is directed towards NNE. Pace length (PL) is in the range 90-109 cm, mean stride length is 195 cm. Pace angulation (PA) varies from 154° to 163°. (See Table 1 for more information about trackway measurements). The walking speed is estimated at about 5.2 km/h using the formula proposed by Alexander (1976), 3.7 km/h according to Weems (2006).

Trackway SL2 (Fig…….)

It consists of four consecutive footprints. The tracks in this sequence are less well defined than those of SL1. Only on SL2-1 three stout digits are recognisable, while pads and claw marks cannot be assessed with confidence. FL is 32.5 cm, FW is 29 cm, and thus the FL/FW ratio amounts to 1.12. Mesaxony is weak, as expressed by a te/FW ratio of 0.31. SL2-2 is largely covered by infilling sediment. Only the proximal portion of this track can be outlined and displays a rather broad "heel". SL2-3 is laterally compressed and shows an elongated "heel" in its proximal portion. The same is true for SL2-4. PL is around 78 cm and PA about 165° on average. The trackway is directed towards W. According to the formula of Alexander (1976), the walking speed would have been about 2.95 km/h, whereas it is 1.83 km/h using the formula of Weems (2006).

Trackway SL3 (Fig…….)

Trackway SL3 is made of seven footprints. Only three footprints (SL3-1, SL3-2 and SL3-5) are clear enough to be measured for further comparison, while SL3-6 allows at least to assess the footprint length. FL is in the range 29-32 cm (mean value 30.0 cm), while FW is 25-29 cm (average value 26.7 cm). FL/FW average values range from 1.03 to 1.16. Mesaxony is weak (average te/FW ratio is 0.36).

SL3-1 and SL3-2 show a posterior "heel" which can be confidently separated from the proximal end of the digits (measures of FL given herein are taken excluding the "heel"). SL3-3 has an even longer "heel" that extends about 20 cm backwards from the proximal end of the lateral digits. SL3-5 and SL3-6 display no "heel" and show the outlines of at least some phalangeal pads, although one of the lateral digits in SL3-6 is either covered by infilling sediment or has not been impressed at all. SL3-7 has unclear outlines and may include a partial posterior "heel". Total II^IV divarication ranges from 50° to 58° (average value: 54°). PL is 117.5 on average, PA ranges between 54° and 174°. The trackway is directed towards NNW. A walking speed ranging from 5.9 km/h (Weems, 2006) to 7.78 km/h (Alexander, 1976) is estimated.

Trackway SL4 (Fig……)

Trackway SL4 is composed of two segments (SL4a and SL4b) that share a similar orientation towards NNE but are separated by a gap of about twelve meters. We consider the two segments as pertaining to the same trackway because they are aligned and their footprints have comparable size and shape. Nevertheless, it cannot be excluded that they actually belong to distinct trackways. SL4a is made up of two consecutive footprints, while SL4b is composed of three tracks with one missing between SL4b-2 and SL4b-3.

Tracks are medium-sized, well-preserved and deeply impressed (up to 5 cm in SL4b-1), showing pad impressions and claw traces, especially in segment SL4b; segment SL4a is less well defined, because both of the tracks are still partially obliterated by sediment filling.

Footprints are slightly longer than wide, mean FL is 32.5 cm for SL4a and 30.3 cm for SL4b whereas mean FW is 31.0 cm for SL4a and 28.3 cm for SL4b. FL/FW mean values range from 1.05 to 1.07. Mesaxony is weak as evidenced by the mean value of the te/FW ratio (0.37 in segment SL4a and 0.38 in segment SL4b).

All the tracks show three well-separated digit traces, broad and massive. Subtriangular and blunt claw traces are evident on SL4a-2, SL4b-1, SL4b-2 and SL4b-3.

Digits II and III are always rotated inwardly, whereas digit IV is always rotated outward. Digit II and III are the deepest impressed. Discrete phalangeal pad traces are preserved on each digit of tracks SL4b-1, SL4b-2 and SL4b-3, in numbers of 2, 3 and 4 for digits II, III and IV respectively. Phalangeal pad traces on digit III are sub-elliptical and become gradually smaller distally. Pad impressions on digit II are larger and stouter than those observed on digit IV that are usually sub-circular in shape and about the same size.

The proximal margin of digit IV lies behind that of digit II, to which it is connected by an oblique, occasionally convex, line. The distal tips of these two digits lie at approximately the same height.

The hypices are nearly symmetrical but the hypex between digit IV and III is situated slightly forward, approximately at half the proximal pad of digit III.

Digit IV is the longest (mean 24.67 cm), followed by digit III (mean 23.00 cm) and II (mean 17.17 cm). Total divarication (II^IV) ranges from 50° to 68°; interdigital angles III^IV are always wider (mean 31.3) than those II^III (29.67°). The trackway is directed towards NE. Pace length (PL) is 95 for SL4a and 102 cm for SL4b, whereas stride length is 183 cm. (See Table 1 for more information about trackway measurements). By the method of Alexander (1976), a speed of 4.14 km/h is estimated, whereas following Weems (2006) it is about 3.3 km/h.

Trackway SL5 (Fig. …….)

Trackway SL5 is represented by three tridactyl footprints. They are preserved as very shallow imprints. Nevertheless, tracks are well preserved and 3D models allow to recognize phalangeal pads as well as internal and external outlines (*sensu* Marty, 2008). FL ranges from 29 to 32 cm (mean value is about 30.7 cm), whereas FW ranges from 26 to 28 cm (mean value is about 27 cm). The footprints are slightly longer than wide (FL/FW ratio is about 1.13 on average) and show a weak mesaxony (te/FW ranging from 0.37 to 0.46).

Three sturdy digits are well preserved in SL5-1 and SL5-2, while SL5-3 lacks a clear impression of digit IV. Digit II and III are medially directed while digit IV is laterally rotated. Each digit clearly shows small and pointed triangular claw traces. The print of digit III is the deepest, and the photogrammetric models suggest that digit II is more deeply impressed than digit IV, as evidenced by SL5-2.

Digit II is markedly stouter than digit IV and shows two large and sub-elliptical phalangeal pads, equidimensional in size. The four phalangeal pads on digit IV are smaller, sub-circular and sub-equal in size. On digit III three pads were recognised. Their shape is slightly sub-elliptical and their size decreases distally. On each track, DEM reveals a further impression in the proximal area of digit III, behind the first pad: as hypothesized for SL1, this likely represents the impression of the metatarsal-phalangeal portion. The proximal portion of digit IV is positioned further posteriorly than that of digit II, as well as the distal tip, slightly backward positioned with respect to that of digit II. Toe extension ranges from 9.5 to 13 cm, showing a weak mesaxony, as evidenced by the te/FW mean value of 0.41. The hypex between digits II and III is slightly forward positioned with respect to that between digits III and IV, lying within the proximal pad of digit III. Digit III and IV show approximately the same length (digit III is 21.5 cm long on average, whereas the mean value of digit IV is 21 cm) and digit II is the shortest (17 cm on average). Total divarication of the digits ranges around a mean value of 57°; the interdigital angle between digits II and III is averagely around 30°, whereas III^IV varies between 20° and 36°. The trackway is directed towards SSW. PL ranges from 86 to 90 cm, SL is 174 cm, while PA is about 170°. The estimated walking speed is 4.3 km/h applying the formula of Alexander (1976), and 2.92 km/h according to Weems (2006).

Trackway SL6 (Fig. …….)

Trackway SL6 is composed of four consecutive footprints. The preservation is very similar to trackway SL5, with shallowly impressed tracks and markedly preserved phalangeal pads. Both external and internal outlines are evidenced by DEMs.

FL has a mean value of 28.5 cm whereas FW is 26.6 cm on average. The tracks are slightly longer than wide, as evidenced by the low value of the FL/FW ratio (1.06 on average), and the weak mesaxony is confirmed by the te/FW value ranging from 0.37 to 0.42. Three wide and robust digits are clearly identifiable in SL6-2, the best-preserved footprint of the trackway; digit IV is only barely recognizable in SL6-1, completely missing in SL6-3 and partially filled by collapsed mud in SL 6-4. Digits II and III are well-preserved on each track, except for SL6-4 in which digit II is weakly impressed. Nevertheless, digit II and III impressions are deeper (up to 2 cm) than that of digit IV in SL6-1, SL6-2 and SL6-3. Small and pointed claw traces are appreciable, and the 3D models suggest that claw impressions are larger in digit II than on digit IV.

Digit II shows two wide and sub-elliptical phalangeal pads, nearly sub-equal in size, except in SL6-3, in which the first pad is larger than the second one. On digit III three pad impressions are recorded, the shape of which varies from sub-circular to sub-elliptical. The most proximal is the largest, and the others are nearly equal in size. As observed in other trackways, a deeper print is identifiable behind the proximal pad of digit III, possibly the impression of the metatarsal-phalangeal joint. Four sub-circular and equidimensional pads are preserved on digit IV, as evidenced by the DEM of SL 6-2. The backward position of the proximal pad of digit IV with respect to that of digit II leads to an asymmetrical morphology of the heel region, as observed in the other tridactyl tracks at the site. In SL6-2, the distal tips of digits II and IV lie at the same height, whereas the hypex between digits II and III is forward positioned with respect to that between digits III and IV. When measurable, digit IV is the longest (mean value 22.3 cm), followed by digit III (mean value 19.1 cm) and digit II (mean value 16.6 cm). Total divarication varies from 64° to 72°, and the interdigital angle III^IV is always greater (36.3° on average) than that between digits II and III (32.7° on average).

SL6 is oriented towards NNE. Pace Length is about 93 cm, Stride Length is 186 cm and Pace Angulation about 170°. The walking speed is estimated as ranging from 3.8 km/h (Weems, 2006) to 5.4 km/h (Alexander, 1976).

Isolated track SL7 (Fig. …….)

This is a shallowly impressed but neat footprint with clear phalangeal pads, thus resembling trackways SL5 and SL6 in its mode of preservation. FL is 28 cm, FW 18 cm. With a FL/FW ratio of 1.55, this track is appreciably more elongated than any of the tridactyl tracks belonging to trackways SL1-SL6. Protrusion of digit III beyond the tips of digits II and IV is higher, as shown by a te/FW ratio of 0.67. Total divarication II^IV is 50°. The track displays three elongated, oval shaped pads along digit III, which is the deepest impressed digit. Pads on digits II and IV are less evident but can be outlined in numbers of two on digit II and four on digit IV. The pads on digit II are oval shaped and comparable in size with those on digit III, while the pads on digit IV are roundish and smaller.

The proximal margin of digit IV lies behind that of digit II, giving the track an asymmetrical outline. The track is directed towards W.

Isolated track SL8 (Fig. …….)

This isolated footprint is located in the central area of the track-bearing surface. Although it is preserved as shallow imprint, the overall outline is clearly recognisable, and a moderate expulsion rim occurs around the distal portion of digit III.

It represents the largest tridactyl track of the ichnosite, slightly wider than long: FL is about 44 cm, FW is 44.5 cm, resulting in a FL/FW ratio of 0.99. The track is characterized by the weakest mesaxony (te/FW value of 0.28). The track lacks the proximal portion of digit IV and the whole heel region. Nevertheless, three broad and robust digits are clearly identifiable. Digit III is the most deeply impressed.

Digit II is stout and displays two wide and sub-circular phalangeal pads. Digit III is slimmer than lateral digits and characterized by three sub-elliptical to sub-circular pads. On digit IV, the 3D colour-coded model reveals three sub-elliptical impressions decreasing in size distally. The proximal tips of digits II and IV lie nearly at the same height, just like the distal tips. The digitigrade posture does not allow a clear identification of hypices, but the 3D model suggests that the hypex between digit II and III is positioned further ahead than that between digit III and IV. Digit III is the longest (36.5 cm) and digit IV (33 cm) is longer than digit II (27 cm). The interdigital angle between digit III and IV (30°) is wider than that between digit II and III (14°), resulting in a total divarication of 44°.

The large footprint points approximately towards W.

4.1.1. Systematic ichnology

Ichnogenus *Cretabrontes* ichnogen. nov. (Fig. …….)

Type species: *Cretabrontes melphicticus* ichnogen. et ichnosp. nov., described herein.

Derivatio nominis: In analogy to: i) *Eubrontes* Hitchcock, 1845, from the Early Jurassic of Connecticut (Massachusetts, USA); ii) *Jurabrontes* Marty et alii, 2018, representative member of the same ichnofamily in the Late Jurassic of Jura Mountains (Switzerland). "Creta" points to the Cretaceous chronological attribution of the tracks, whereas in Greek "brontes" means "thunder", thus suggesting the impressiveness of the stout theropod footprints.

Type locality: San Leonardo quarry, Molfetta ichnosite (Bari), Apulia, Southern Italy.

Type level: The track-bearing layer crops out at the top of a 15-m thick carbonate succession, belonging to the Calcare di Bari Fm.

Age: late Aptian-early Albian.

Diagnosis: Medium to large-sized theropod tracks (FL = 28-34 cm), slightly longer than wide (FL/FW comprised between 1.03 and 1.16 on average) and weakly mesaxonic (te/FW mean value between 0.29 and 0.46). Typical 2-3-4 phalangeal pad configuration on robust digits II, III and IV respectively, with occasionally the occurrence of a further proximal (metatarsal-phalangeal) impression on digit III. Short and sub-triangular and blunt claw traces recognizable on each digit. Digit length increasing from digit II to digit IV; digit II generally broader and more deeply impressed than digits III and IV. Slightly asymmetrical interdigital angles (generally, III^IV > II^III), with total divarication (II^IV) up to 74° (mean values between 50° and 60°). Proximal portion of digit IV backward positioned with respect to digit II, resulting in an asymmetrical and concave heel region. Some tracks are posteriorly elongated. Distal tip of digit II on the same line or slightly forward positioned compared to that of digit IV. Footprints antero-medially directed compared to the trackway axis. PA between 150° and 170°, SL ranging from 174 cm to 196 cm, correlated to a variable estimated speed ranging from 2,95 km/h to 6.48 km/h (using Alexander, 1976) or from 1.83 km/h to 4.76 km/h (using Weems, 2006).

Cretabrontes melphicticus ichnosp. nov. (Fig. …….)

Diagnosis: As for ichnogenus.

Derivatio nominis: from "Melphicta", the ancient Latin name of Molfetta.

Holotype: SL1-1 (Fig. ….), original specimen preserved in situ as concave epirelief. A cast (sigla calco Museo di Scienze della Terra of the University of Bari "Aldo Moro") was printed after the 3D-modelling of SL1-1 track. The 3D model is digitally stored in MorphoSource at the permanent link https://www.morphosource.org/.........

Paratypes: SL1-2 (Fig. ….), SL1-3 (Fig. ….), SL4b-1 (Fig. ….), and SL6-2 (Fig. ….), original specimens preserved in situ as concave epireliefs and recorded as photogrammetric models.

Other referred specimens: All the tridactyl footprints represented by the trackways SL1, SL2, SL3, SL4, SL5 and SL6. All tracks are preserved in situ and recorded as photogrammetric models (see Supplementary Material).

Age: late Aptian-early Albian.

Holotype: large-sized functionally tridactyl track, slightly longer than wide, showing weak mesaxony. Digits are broad and robust, with short and sub-triangular claw marks. Digit II is inward rotated, digit III is straight forward oriented, whereas digit IV is outward rotated. Digit II and III are broader than digit IV. The anatomical details reveal the typical configuration for theropod tracks: four phalangeal pads on digit IV, three on digit III and two on digit II. Furthermore, an additional proximal impression on digit III is recognizable, likely produced by the impression of the metatarsal-phalangeal portion. The backward positioned proximal portion of digit IV is connected to that of digit II by a convex indentation. Digit IV > digit III > digit II. Interdigital angle III^IV > II^III, resulting in a slightly asymmetrical shape.

Holotype morphometric parameters: FL = 31 cm, FW = 29 cm, FL/FW = 1.07; te = 9 cm, te/FW = 0.31, (FL-te)/FW = 0.76; digit II length = 18 cm, digit III length = 20.5 cm, digit IV length = 24 cm; II^III = 22°, III^IV = 28°, II^IV = 50°.

Discussion: theropod tracks are the most commonly reported kind of dinosaur footprints from the peri-Adriatic carbonate platforms (*sensu* Zappaterra, 1990, 1994). The morphometric parameters of each theropod track assemblage from primary literature were plotted on numerous diagrams (see Supplementary Material) enabling us to compare them to *C. melphicticus*.

Theropod specimens are known from the deposits of the Apulian carbonate platform, from ?Kimmeridgian-Tithonian to late Albian. Numerous tridactyl tracks were described from the Mattinata ichnosite (?Late Jurassic, Apulia; Conti et al., 2005) and assigned to different morphotypes. Type 1 (cf. *Theroplantigrada* isp.) cannot be compared to the Molfetta specimens, due to the occurrence of the hallux and the slender morphologies. Type 2 is robust, weakly mesaxonic, but the lack of the metatarsal-phalangeal pad of digit IV suggests a more elongated shape (i.e., FL/FW > 1.18) if compared with *C. melphicticus*. Additionally, the total divarication is highly smaller (i.e., II^IV = 23°) than that of our specimens. Other footprints, compared to *Therangospodus* (Conti et al., 2005) for the lack of well-defined digital pads, show similar overall morphologies compared to *Cretabrontes*, such as the stout digits, the weakly elongated shape (i.e., FL/FW = 1.11) and the total divarication. Nevertheless, this morphotype shows a slightly higher mesaxony (i.e., te/FW up to 0.46) with respect to the specimens from Molfetta.

The tridactyl tracks from Borgo Celano (Hauterivian - Barremian, Apulia; Petti, 2006; Petti et al., 2008b) show several morphological and morphometrical affinities with the specimens from Molfetta, although they are generally slightly smaller: i) the weak mesaxony (i.e., te/FW between 0.30 and 0.43); ii) the robust morphologies; iii) the proportion with FL ≅ FW; iv) the relationship between digit lengths, with digit IV ≥ digit III > digit II. The Borgo Celano specimens have a total divarication slightly higher on average than that recorded in the theropod tracks of Molfetta, resulting in a more symmetrical shape of the footprints.

Five small-sized and elongated (FL/FW = 1.3) theropod footprints, preserved on a block from Bisceglie (Aptian, Apulia; Sacchi et al., 2009), are not enough defined to allow a reliable match. The preliminary reported tracks from the late Albian horizon of Lama Balice (Apulia; Petruzzelli et al., 2019) are neatly more elongated than *C. melphicticus* (FL/FW up to 1.57), also showing a higher mesaxony (te/FW up to 0.60).

Several theropod footprints are known from Latium (Sezze, Esperia and Riomartino ichnosites), referred to the Apenninic Carbonate Platform palaeogeographic domain (Petti, 2006; Nicosia et al., 2007; Petti et al., 2008c; Citton et al., 2015, 2017; Romano & Citton, 2017). They clearly differ from *C. melphicticus* mainly due to their much smaller size, the slender and elongated morphologies (e.g., FL/FW up to 1.41 in Esperia specimens, higher than 2 in Riomartino tracks and up to 1.80 for the footprints cropping out at the Sezze ichnosite) and the markedly higher mesaxony.

Theropod ichnoassemblages also occur in the Cretaceous record of the Adriatic-Dinaric Carbonate Platform. The best-preserved and most comparable specimens come from Friuli and Istria. The isolated specimen from the Sarone quarry (Hauterivian-Barremian, Cansiglio Plateau, Friuli; Dalla Vecchia & Venturini, 1995), despite similar broad morphologies, is more elongated and has a higher mesaxony if compared to the Molfetta specimens. Well-preserved tridactyl tracks were discovered from a Barremian surface at Pogledalo (Main Brioni Island, Croatia; Dalla Vecchia, 1998; Dalla Vecchia et al., 1993; 2002). Among the figured tracks, the best-preserved specimen (POG T24-3) displays morphological characters similar to *C. melphicticus*, such as the stubby digits and the weak mesaxony, although the impression of the heel region leads to a more elongated shape (i.e., FL/FW = 1.35). The slenderer morphology (with FL/FW next to 1.5 on average), the lower total divarication (mostly lower than 40°) and the similar length of digits II and IV allow to distinguish the theropod tracks of Pogledalo from those studied herein. Other well-preserved tridactyl tracks on the Adriatic-Dinaric Carbonate Platform are known from the two late Albian ichnosites of Puntizela and Solaris (Istrian peninsula; Dalla Vecchia & Tarlao, 2000; Mezga & Bajraktarevic, 2004), but they mainly differ from *C. melphicticus* due to their slenderer morphology (FL/FW up to 2,10 and 1,5 on average), the higher mesaxony (te/FW more than 0,46) and the lower total divarication (II^IV never more than 50°).

C. melphicticus from Molfetta shows well-defined morphological and morphometric features that also require a comparison with similar theropod tracks from the Upper Jurassic-Lower Cretaceous deposits of neighbouring areas, outside the peri-Adriatic region. *C. melphicticus* shows an overall affinity with Eurasian tracks from Switzerland (Razzolini et al., 2017; Marty et al., 2018), Germany (Troelsen & Wings, 2014; Lallensack et al. 2016), Spain (Moratalla et al., 2003; Cobos et al., 2014; Pérez-Lorente, 2015) and China (Li et al., 2006; Xing et al., 2014; Lockley et al., 2018).

Marty et al. (2018) describe *Jurabrontes curtedulensis* from three tracksites located between Courtedoux and Chevenez (Ajoie district, Canton Jura, NW Switzerland), belonging to the Reuchenette Formation (late Kimmeridgian). *Jurabrontes curtedulensis* is represented by giant tridactyl and weakly mesaxonic footprints (Marty et al., 2018). Despite the huge size, *J. curtedulensis* shares with *C. melphicticus* the weak mesaxony (te/FW = 0.34 in the holotype) and the occurrence of a peculiar isolated proximal pad on digit III. Nevertheless, some differences can be detected in *J. curtedulensis*, such as: i) the more elongated shape (FL/FW value between 1.11 and 1.50); ii) the generally greater (FL-te)/FW ratio (from 0.70 to 1.22); iii) different relative proportion of digit II and IV; iv) the lower total divarication, up to 37° and never exceeding 52°.

Another ichnospecies has recently been described from the same stratigraphic level as *Jurabrontes* in the Swiss Jura Mountains: *Megalosauripus transjuranicus* is definitely longer than wide, with slender and well separated digits (Razzolini et al., 2017). *C. melphicticus* has a comparable size and similar digit arrangement. However, *M. transjuranicus* clearly differs from *C. melphicticus* for: i) the elongated morphology, with FL/FW very higher (from 1.40 to 1.85); ii) the strong mesaxony (te/FW is 0.58 in the holotype); iii) the lower total divarication (i.e., II^IV < 52°); iv) the slender digits; v) the impression of a proximal pad on digit IV, very large and deep which form a rounded heel; vi) the sharp postero-medial notch separating digit II from the rest of the footprint.

Numerous dinosaur track-bearing levels were identified in the Wesling quarry in Münchehagen (Lower Saxony, Germany), belonging to the Obernkirchen Sandstone of the Bückeberg Group (Lower Cretaceous, Berriasian). Two theropod ichnotaxa are know from the Münchehagen tracksites (Troelsen & Wings, 2014): i) the large-sized *Bueckeburgichnus maximus* Kuhn 1958, characterized by the occurrence of a small hallux (Lockley, 2000); ii) the medium-sized *Megalosauripus* isp., characterized by strong mesaxony and slender digits. The most recently discovered theropod tracks, analysed by Troelsen & Wings (2014) and Lallensack et al. (2016), are preserved as natural casts. In the same ichnosite two additional morphotypes are identifiable: the T2 trackway, represented by medium-sized, slender and strongly mesaxonic footprints, and the T3 trackway composed by large-sized and weakly mesaxonic footprints. No ichnotaxonomic assignment was to date proposed for these latter tridactyl morphotypes. The smaller morphotype (referred specimen T2/4), although similar in size (FL around 30 cm), clearly differs from *C. melphicticus* for: i) the slenderer shape (FL/FW around 1.25); ii) the stronger mesaxony (te/FW is about 0.50); iii) the slimmer morphology of digits. The larger morphotype (FL = 34-38 cm in best-preserved tracks; referred specimen T3/18) shares numerous features with *C. melphicticus*, such as the weak mesaxony (te/FW = 0.30-0.44), the relative length of digits and their stout morphology. Nevertheless, some differences are evidenced: i) the T3 tracks are frequently slightly wider than long (FL/FW is comprised between 0.91 and 1.06); ii) the (FL-te)/FW ratio is lower in several specimens (up to a value of 0.57); iii) the phalangeal pads are not clearly identifiable on each digit, and no metatarsal-phalangeal impression occurs on digit III; iv) the interdigital angle III^IV is always wider than II^III if compared with *C. melphicticus* (in which some specimens have III^IV ≤ II^III).

Cobos et al. (2014) established the ichnospecies *Iberosauripus grandis*, describing a trackway, composed by large tridactyl tracks, from the Villar del Arzobispo Formation (Upper Jurassic-Lower Cretaceous; Tithonian-Berriasian) of El Castellar (Teruel, Spain). The giant theropod footprints are slightly longer than wide and weakly mesaxonic. They share some characters with *C. melphicticus*, such as the low mesaxony (te/FW ≅ 0.30) and the relative proportion of digits (LIV ≅ LIII > LII), but differ in: i) the huge size (i.e., *Iberosauripus* is 54-58 cm long); ii) the lower total divarication (i.e., II^IV around 25°); iii) the elongated shape (i.e., FL/FW between 1.26 and 1.29); iv) the low protrusion of digit III.

As for the tracksites from La Rioja province (Lower Cretaceous; NE Spain), the most similar theropod tracks occur in Los Cayos (site A, Cameros Basin, lower Albian; Pérez-Lorente, 2015 and references therein). Although they have been recently interpreted as undertracks (Pérez-Lorente, 2015), the Los Cayos tridactyl footprints (e.g., trackway LCA-R3; Moratalla et al., 2003) show enough well-preserved characters to be compared with *C. melphicticus*. They are slightly larger (i.e., FL around 40 cm), but have the same FL/FW range (i.e., up to 1.14). Digits are similarly broad, recording a weak mesaxony (i.e., te/FW between 0.36 and 0.48). The main differences of Los Cayos A specimens are the wider total divarication (i.e., higher than 70°, with II^III ≅ III^IV) and the occurrence of the hallux in some specimens possibly due to the plantigrade posture of the trackmaker.

Eubrontes-like tridactyl tracks similar to *C. melphicticus* are known from the Lower Cretaceous of Chabu area (Inner Mongolia, China). They were classified as *Asianopodus robustus* and *Chapus lockleyi* (Li et al., 2006; Xing et al., 2014; Lockley et al., 2018) and are represented by medium- to large-sized and robust footprints. Although they have similar digit proportions and total divarication, *A. robustus* and *C. lockleyi* appear slimmer than *C. melphicticus*, differing mainly for their more elongated shape (i.e., FL/FW around 1.30), the stronger mesaxony (te/FW value around 0.40), and the large trace of a separated metatarsal-phalangeal pad behind digit IV, quite similar to that observed in *M. transjuranicus*.

The palaeogeographic position of the peri-Adriatic region close to the northern Gondwana margin suggests a comparison between the Molfetta specimens and those known from Northern Africa. Several theropod tracks were reported from Upper Jurassic to Upper Cretaceous deposits of Morocco (Boutakiout et al., 2009; Belvedere et al., 2010, 2013, 2019; Nouri et al., 2011; Masrour et al., 2013; Ibrahim et al., 2014, 2020) and Algeria (Bensalah et al., 2005; Mahboubi et al., 2007; Bessedik et al., 2008; Chabou et al., 2015; Mammeri, 2018).

Several dinosaur tracks are known from the Iouaridène Fm. (Central High Atlas, Morocco), dated ?Oxfordian-Kimmeridgian. Boutakiout et al. (2009) and Belvedere et al. (2010) described giant theropod footprints (FL > 50 cm; type specimen: 23IGR1.7). Although track elongation is comparable to that observed in Molfetta specimens (i.e., FL/FW ranging from 1.06 to 1.28), the poor preservation does not allow to accurately match these tracks to *C. melphicticus.* Belvedere et al. (2010) also describe the morphotype 2C, assigned to *Megalosauripus* isp., and represented by large and asymmetric tridactyl footprints. The type specimen Deio CXXVIII/16 is just slightly larger than the herein studied material, but it is neatly more elongated (i.e., FL/FW = 1.36) and with a higher mesaxony. Digits show a similar pattern to those of *C. melphicticus* (phalangeal pads geometry, relationship between proximal and distal tips), but they are clearly slimmer. Furthermore, *Megalosauripus* isp. from the Iouaridène Fm. shows a lower total divarication. The good overlap with the holotype of *Megalosauripus transjuranicus* (Razzolini et al., 2017) leads Belvedere et al. (2019) to assign the large specimen Deio CXXVIII/16 to *Megalosauripus* cf. *transjuranicus*. Nouri et al. (2011) describe a new theropod ichnotaxon from the Upper Jurassic Iouaridène Fm.: *Boutakioutichnium atlasicus*. It is represented by medium- to large-sized and tetradactyl tracks. *B. atlasicus* differs from *C. melphicticus* due to the clear occurrence of hallux, the elongated shape (i.e., FL/FW = 1.24 on average), the strong mesaxony and the lower total divarication.

Masrour et al. (2013) report eight theropod trackways from the Tazought Fm. (upper Barremian to lower Aptian) of Imi n'Tanout, south-west of Marrakesh (Western High Atlas, Morocco). Unfortunately, not enough data are available for a complete comparison with the Molfetta material, except that tracks are markedly more elongated (mean values of FL/FW are 1.45 for TML1 specimens, 1.67 for TML2 specimens).

Other theropod tracks in Morocco come from the Upper Unit of the Kem Kem beds (Cenomanian), coeval to the numerous body fossils discovered in the same Group (Ibrahim et al., 2020 and references therein). Belvedere et al. (2013) analyse several tetrapod natural casts (attributed to theropods, ornithopods and turtles) from Gara Sbaa (southern Morocco). Despite poorly preserved, the best-preserved tridactyl track (e.g., GSB 6 specimen) was classified as cf. *Megalosauripus*. The footprint is 30.6 cm long and 24.5 cm wide, and thus more elongated (i.e., FL/FW = 1.25) than *C. melphicticus*. Digit III is similarly robust and broad, but more projected beyond the slimmer digits II and IV, as evidenced by the diagram proposed by Weems (1992) and its mesaxony value. Ibrahim et al. (2014) describe numerous tridactyl tracks, preserved as natural casts, from different localities of the same region. No ichnotaxonomic assignment was provided because the tracks appear poorly defined. The best-preserved specimens are similar in length to *C. melphicticus* (i.e., FL around 30 cm on average), also showing a comparable mesaxony. Nevertheless, they are clearly slimmer (i.e., FL/FW about 1.3) and more symmetrical, with digits II and IV showing similar length and comparable interdigital angles with digit III.

More than twenty dinosaur tracksites are known from northern Algeria. They are clustered in five different localities in the Saharan Atlas (Bensalah et al., 2005; Bessedik et al., 2008; Chabou et al., 2015; Mammeri, 2018). Six ichnosites yielded theropod tracks similar to those from Molfetta: i) Site 1 (El Bayadh-El Grarij; Valanginian); ii) Site 2 (El Bayadh-El Mouilah; Valanginian); iii) Site 4 (Brezina-El Mezioued; Kimmeridgian-Valanginian); iv) Site 9 (Ouafeg-El Hamra; Barremian-Albian); v) Site 12 (Brezina-Mouilah El Fougani; Barremian-Albian); vi) Site 20 (Amoura-Gaada; late Albian-early Cenomanian). Several morphotypes have overall features closely resembling *C. melphicticus*, such as: i) weak mesaxony (i.e., te/FW is around 0.35 on average); ii) broad digits, among which digit II is often stouter than digit IV and digit IV is similar in length to digit III; iii) total divarication around 50°-55°, especially in Valanginian specimens; iv) asymmetrical shape linked to the backward position of the proximal margin of digit IV with respect to that of digit II; v) distal tips of digits II and IV lying at about the same height. But Algerian tracks also show remarkable differences. The morphotype “Ensemble 1” (Sites 1, 2 and 4), displaying close affinities with the ichnogenus *Megalosauripus* according to Bensalah et al. (2005), Bessedik et al., (2008), Mammeri (2018), is significantly larger than *C. melphicticus* (i.e., FL about 55 cm), despite a FL/FW ratio often very similar, and records slightly higher values of mesaxony (te/FW up to 0.50) and (FL-te)/FW ratio up to 1.03. The morphotype “Ensemble 2” (Site 4), comparable to the ichnogenus *Therangospodus* according to Mammeri (2018), by contrast is clearly more elongated with respect to the Molfetta tracks (i.e., FL/FW ≅ 1.3), despite a similar length. The morphotype “Ensemble A” (Site 20), related to the ichnogenera *Megalosauripus* and *Megalosauropus* (Bensalah et al., 2005; Bessedik et al., 2008; Mammeri, 2018), is considerably larger and shows a lower mesaxony (i.e., te is less than a third of FL-te). The morphotype “Ensemble B” (Sites 9 and 12), matched with *Megalosauropus* and

Therangospodus (Chabou et al., 2015; Mammeri, 2018), is slightly larger (i.e., FL ranging from 32 cm to 40 cm) and often more elongated than *C. melphicticus*. Digits II and IV could be similar in length in some specimens, and the total divarication is lower than that observed on Molfetta tracks. Finally, the tracks of “Ensemble B” are characterised by a weaker mesaxony.

4.1.2. Undetermined track morphotypes

While the majority of tridactyl tracks preserved at the Molfetta ichnosite, and namely trackways SL1, SL2, SL3, SL4, SL 5 and SL6 are herein assigned to *Cretabrontes melphicticus*, each of the two isolated tracks SL7 and SL8 differs from all other tracks at the site by its morphology and thus SL7 and SL8 represent two more morphotypes. The elongated shape and stronger mesaxony of SL7 distinguishes this track from *C. melphicticus*, and probably hints at the presence of a second theropod trackmaker in the Molfetta ichnoassemblage. SL8 is distinguished by its large size, highly digitigrade posture and asymmetrical arrangement of interdigital angles. Its anatomical characters, such as the sharp claw traces, allow to assign SL8 to a large theropod. Despite the lack of the heel region, the morphometric parameters and the relative proportions are similar to those of *C. melphicticus*. The occurrence of only one and incomplete specimen does not allow a reliable assignment, leaving open the possibility that SL8 is just a large and partial *Cretabrontes* track.

4.2. Quadrupedal tracks

Several isolated *manus-pes* sets have been identified on the San Leonardo quarry surface, although only one quadrupedal trackway has been to date clearly recognised. The high degree of trampling and the possible coalescence of several tracks hinders the recognition of other trackways. The quadrupedal tracks usually show a poor preservation with respect to the bipedal ones but are often evidenced by the occurrence of raised rims. More detailed morphological features are observable from the photogrammetric models, mainly in some isolated tracks.

4.2.1. Material

Trackway SLH1 (Fig. …….)

Trackway SLH1 is composed of two segments (SLH1a and SLH1b) aligned towards NNW, with a gap of twelve meters due to the overlap of the L-shaped tetrapod trace. The two segments were likely produced by the same quadrupedal trackmaker due to their similar size and morphology.

SLH1a is composed of four *manus-pes* sets, while SLH1b is made by only two sets.

The tracks are wider than long: the manual prints are 17 cm to 24 cm long and 21 to 32 cm wide, whereas the pedal traces are 31 cm to 38 cm long and 35 cm to 41.5 cm wide. *Manus* is always smaller than *pes*: the heteropody index (*manus* area / *pes* area, according to Lockley et al., 1994) is variable, from 0.39 to 0.56, with a mean value of about 0.46.

The tracks are scarcely preserved as sub-circular to elliptical impressions, in which digit traces are barely recognisable. DEMs do not provide ultimate anatomical information but suggest the occurrence of four digit impressions in *pes* and possibly four to five in *manus*.

Both *manus* and *pes* appear slightly outward rotated with respect to the midline, with the manual impression forward positioned and generally in axis with the pedal print. The internal margin of *manus* lies on the midline, which is crossed by *pes*.

The trackway is clearly narrow gauge with a total width of 64 cm on average. It is quite straight but irregular, with the axis of segment SLH1b slightly counterclockwise rotated (about 12°) with respect to that of SLH1a. Stride Length and Pace Length are irregular too, with SLhigher in *manus* than in *pes* prints. PL of *pes* varies from 77 cm to 87.5 cm in SLH1a (87 cm in SLH1b), while in *manus* it varies from 76.5 cm to 103 cm in SLH1a (86 cm in SLH1b); SL of *pes* increases from 157.5 cm to 165 cm, while in *manus* it varies from 149 cm to 164 cm. *Manus-pes* distance ranges from 26 cm to 44 cm. PA is regular in *manus* (139-143°), whereas it decreases from 180° to 156° in *pes*.

The distance between the shoulder joint and the hip joint (gleno-acetabular distance) of the quadrupedal trackmaker is estimated in the range of 109-118 cm, while its hip height is estimated at

134 cm on average, using the methods described in Thulborn (1990). The walking speed is estimated at about 5.5 km/h (Alexander, 1976).

Isolated quadrupedal tracks (Figg. …….)

The San Leonardo quarry surface preserves numerous isolated *manus-pes* sets, some of which are better preserved than those belonging to trackway SLH1. The photogrammetric analysis performed on these tracks allowed to recognize more detailed morphologies that reflect the anatomical characters of the trackmaker. Both external and internal outlines are identifiable.

Specimens SLH2, SLH3, SLH4 and SLH5 (SLH2 is represented by two likely consecutive *manus-pes* sets) show morphological characters similar to SLH1. *Manus* is smaller than *pes* (the heteropody index varies from about 0.25 in SLH2 to 0.67 in SLH3). The manual impression is tetra- or more likely pentadactyl, highly digitigrade, wider than long (FL ranges from 11.5 cm to 18.5 cm; FW from 18.5 cm to 26.5 cm). Two or three central digits are forward projected, whereas external digits are laterally oriented. *Pes* is tetradactyl (showing a lower digitigrady with respect to associated *manus*), wider than long (FL between 23 cm and 30 cm; FW between 27.5 cm and 36.5 cm). Digits II and III are clearly recognisable and forward oriented, while digit I is slightly inward oriented (I^II from 25° to 35°) and digit IV is often laterally directed (III^IV up to 60°). *Manus-pes* distance varies from 20 cm to 35 cm. The manual print is generally slightly external and outward oriented with respect to the pedal impression (the angle between *pes* axis and *manus* axis is up to 35° wide). The two sets of SLH2 suggest a narrow gauge pattern (total width is 64 cm), with very short PL (34 cm for pedal impressions, 50 cm for manual prints). By the method of Thulborn (1990), a hip height ranging from 92 cm to 120 cm was estimated.

In the vicinity of trackway SLH1, numerous other impressions are distinguishable, on the field view apparently poorly defined and partially overlapping each other. Close-range photogrammetry allowed us to obtain a 3D model that reveals interesting morphological features about these tracks. We focused on two *manus-pes* sets (SLH6-1 and SLH6-2), heading NNW and thus subparallel to

SLH1, showing similar and peculiar characters not evidently observed in the other detected tracks. The two quadrupedal couples are oriented in the same direction and are quite symmetrical with respect to a hypothetical midline, suggesting they were produced by the same trackmaker. Both external and internal outlines and a weakly raised displacement rim are recognizable on DEMs.

Manus is slightly wider than long (FL = 15-20.5 cm; FW = 19.5-23 cm). The manual print of SLH6-1 is stubby and crescent-shaped, and four or five blunt impressions are identifiable. *Manus* of SLH6-2 also shows five weak impressions. *Pes* is longer than wide; FL is 38-40 cm, while FW is 31-32 cm. The hindlimb print is pear-shaped, narrower proximally and slightly concave internally. Three small impressions are recognizable in the distal part of SLH6-2, although four pointed and radially directed traces are observable in its internal outline. The *manus-pes* distance is around 43 cm. The manual impression is smaller, resulting in 0.24 or 0.38 the dimension of the associate pedal print. *Pes* is outward rotated with respect to the midline (20°-30°), and *manus* is slightly outward rotated with respect to *pes* (around 15°). The two couples are arranged in a narrow gauge configuration (the width between them is about 60 cm), with the hypothetical axis crossing the internal margin of the pedal prints. PL is 73 cm for the hindlimbs and 80.5 cm for the forelimbs. The estimated hip height is 152-160 cm (Thulborn, 1990).

4.2.2. Discussion

The scarce state of preservation of the quadrupedal tracks leads to a lack of numerous anatomical features, making it difficult to provide an ultimate ichnotaxonomic assignment. Nevertheless, data obtained from DEMs and trackway configuration allow to compare the quadrupedal specimens from Molfetta (i.e., the trackway SLH1 and the isolated sets SLH2, SLH3, SLH4, SLH5 and SLH6) with coeval ichnotaxa.

Quadrupedal gait was adopted by all main herbivorous dinosaur groups, including ornithopods, ceratopsians, thyreophorans and sauropods, widely distributed during the Late Jurassic and the Cretaceous. Ornithopod tracks (see the review of Díaz-Martínez et al., 2015 and references therein) clearly differ from the specimens from Molfetta, for which the 3D models reveal a tetradactyl *pes* and a tetra- or pentadactyl *manus*. Furthermore, the heteropody of trackway SLH1 is evidently lower than that observed in ornithopod tracks.

The morphological and morphometric characters, showing four digits quite radially oriented, rule out sauropods as possible trackmakers of the trackway SLH1 and the isolated specimens SLH2, SLH3, SLH4 and SLH5.

Thyreophoran and ceratopsian tracks generally show a similar pattern (McCrea et al., 2001). The main ichnotaxon to date referred to stegosaur trackmakers, *Deltapodus brodricki* (formerly attributed to sauropods by Whyte & Romano, 1994), does not match up with SLH1 and the isolated couples from Molfetta because of its elongated shape, the tridactyl *pes* and the wide gauge configuration. Most ankylosaur and ceratopsian tracks share the same features, such as a functionally tetradactyl *pes* (in which pedal digit I is shorter than the others) and a pentadactyl *manus*. The quadrupedal specimens from the San Leonardo quarry reflect similar morphologies.

Despite an overall homogeneous pattern, trackway SLH1 and the isolated tracks SLH2, SLH3, SLH4 and SLH5 seem to show a range of morphological details differently referable both to ceratopsians and ankylosaurs, although the poor preservation does not allow to clearly define them as true anatomical characters of the trackmaker. In trackway SLH1, *manus* is on average about half the size of the associated *pes* and follows an arcuate pattern, with inner and outer digits laterally or slightly backward oriented, similar to tracks referred to ankylosaurs. SLH2 displays a tetradactyl and quite symmetrical *pes*, similar to the pedal print of the ichnogenera *Ceratopsipes* (ceratopsian) and *Metatetrapodus* (ankylosaur); the heteropody index roughly equals 0.25, and the small manual print shows a general shape most similar to the ceratopsian *manus*. In SLH3 the asymmetrical shape of the hindlimb impression, the heteropody index of 0.67 and the arrangement of manual external digits clearly suggest an ankylosaurian trackmaker, but the unclear number of manual digits (four or five) does not allow a closer comparison with the ichnotaxa *Tetrapodosaurus* and *Metatetrapodus*. SLH4 shows enough characters to match it to ankylosaur features, such as the asymmetrical shape of *pes* (despite a sub-triangular shape of the heel, similar to ceratopsian tracks, according to McCrea et al., 2001) and the arrangement of manual digits (likely five in this specimen). SLH5 reveals longer and slightly more pointed digits than other specimens, attributable to an ankylosaur trackmaker according to McCrea et al. (2001).

No ceratopsian fossil record is to date known from Europe (except the small-sized *Ajkaceratops kozmai* Ősi et al., 2010 from the Santonian of Hungary) and Gondwana, whereas polacanthid and nodosaurid ankylosaurs have been reported from England (Pereda-Superbiola & Barrett, 1999), France (Garcia & Pereda-Superbiola, 2003), Spain (Pereda-Superbiola et al., 1995; Kirkland et al., 2013), Austria (Pereda-Superbiola & Galton, 2001), Romania (Nopcsa, 1915) and Hungary (Ősi, 2005). Poorly preserved tracks referred to ankylosaurs are reported in the Apulian record from: i) Borgo Celano (San Giovanni Rotondo Fm., late Hauterivian - early Barremian; Petti, 2006; Petti et al., 2008b); the isolated tracks are subcircular with faintly impressed digits and can be scarcely compared with the specimens described herein; ii) Bisceglie (Calcare di Bari Fm, Aptian; Sacchi et al., 2009; Petti et al., 2010), where two trackways closely match the quadrupedal tracks from Molfetta mainly for their narrow gauge, the similar heteropody, the overall shape of *manus* and the arrangement of the latter with respect to the trackway midline; iii) Lama Balice (Calcare di Bari Fm., upper Albian, Petruzzelli et al., 2019) where numerous specimens were attributed to an ankylosaurian trackmaker by preliminary researches (Petruzzelli et al., 2019). The best-preserved *manus-pes* set reveals morphologies (such as the tetradactyl and asymmetrical pedal print) very similar to the isolated quadrupedal tracks from Molfetta. Therefore, in the most parsimonious hypothesis, SLH1 and the isolated tracks SLH2, SLH3, SLH4 and SLH5 can be likely attributed to an ankylosaur trackmaker.

The two *manus-pes* sets of SLH6 are more problematic. The elongated and pear-shaped morphology of *pes* and the crescent-shaped *manus* print are reminiscent of sauropod tracks. On the other hand, we observe that all measured linear parameters (FL and FW of both *manus* and pes *prints*) are within the range seen in trackway SLH1 and in the isolated tracks SLH2, SLH3, SLH4 and SLH5.

The only obvious difference is a higher value for *pes* FL (38-40 cm, compared to an average of about 30 cm in all the other quadrupedal tracks discussed herein), which makes the *pes* longer than wide, as opposed to the wider than long *pes* of the remaining quadrupedal sample. However, FL varies significantly even among footprints belonging to the same trackway SLH1 (range: 31-38 cm) and is probably influenced by the original substrate conditions. The distance between the two *manus-pes* sets of SLH6-1/2 with respect to a hypothetical midline suggests a narrow-gauge configuration, comparable to that observed in SLH1. The *manus*/*pes* ratio of about 0.38 to 0.24 is at the lower end of the range observed in other quadrupedal tracks from Molfetta, implying a higher degree of heteropody which is, however, also found in tracks SLH1-2 and SLH2. The anterior half of the SLH6 *pes* displays no obvious morphological difference from the *pedes* of SLH1-SLH5, whereas the posterior (proximal) half of the *pes* track, besides adding to the total length, bears a lateral indentation that produces the overall "pear-like" outline of the track. Thus, all "sauropodan" characters observed in SLH6 (*pes* longer than wide and pear-shaped, high degree of heteropody) can be explained by a more plantigrade posture of the same trackmaker that produced trackways SLH1-SLH5. We consider this as the most parsimonious interpretation.

This case study shows that caution is always needed when interpreting tracks that are in a suboptimal state of preservation. Sauropods and thyreophorans have quite distinctively different *pes* morphologies that can easily be seen in well-preserved tracks. But it may prove hard to differentiate the two trackmakers based on gross trackway outlines or heteropody index alone.

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5. Conclusions

The dinosaur ichnoassemblage preserved at San Leonardo Quarry near Molfetta is composed of both quadrupedal (most probably ankylosaurian) and bipedal (theropod) tracks. Six different trackways and two isolated specimens are herein attributed to theropods, whereas only one trackway, but numerous isolated *manus-pes* sets were assigned to quadrupedal herbivorous dinosaurs. The 50 m long, L-shaped possible sliding trace preserved in the south-western sector of the quarry is provisionally assigned to a non-dinosaurian large tetrapod, pending a more in-depth study.

The theropod tracks can be divided into two morphotypes, among which only one (represented by six trackways) allows a reliable ichnotaxonomic assignment. It shows features comparable to the older tracks from other sites on the Apulian Carbonate Platform (Mattinata and Borgo Celano), but differs from them mainly for its larger size, the higher robustness and the lack of hallux impression. The large-sized, weakly mesaxonic and robust theropod footprints only partially match the specimens from the Late Jurassic-Early Cretaceous of Switzerland (Canton Jura), Germany (Münchehagen) and Spain (La Rioja), and show morphological affinities with the Early Cretaceous specimens from Northern Africa. For this reason, a new ichnotaxon, *Cretabrontes melphicticus*, is herein established, suggesting a Gondwanan affinity for the Molfetta theropods.

Furthermore, the ichnoassemblage of the San Leonardo quarry is enriched by the occurrence of two quadrupedal morphotypes, despite their scarce preservation. The first, represented by one trackway and numerous scattered sets, is attributed to medium-sized ankylosaurs, showing similar features to the Laurasian ichnogenera *Tetrapodosaurus* and *Metatetrapodus*, as well as other thyreophoran tracks from the Apulian Carbonate Platform. The second morphotype, identified from DEMs of only two *manus-pes* couples, is distinguished from the first by a more plantigrade *pes* posture, that lengthens the track and makes it vaguely reminiscent of a small sauropod footprint. Nevertheless, in our interpretation it is just a preservational variant of the main morphotype, which we refer to an ankylosaur trackmaker.

The ichnological researches at the Molfetta tracksite improve our knowledge of the Apulian Mesozoic ichnofauna, providing interesting information about dinosaur dispersal during the Late Jurassic-Early Cretaceous interval and suggesting an in-depth review of the peri-Adriatic region palaeogeography.

Acknowledgements

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