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Cretaceous tetrapod tracks from Italy: a treasure trove of exceptional biodiversity

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ABSTRACT - After about thirty years of investigation, the Cretaceous tetrapod track record from Italy has proved to be a 'Rosetta Stone' for improving understanding of the palaeogeographical and palaeoenvironmental evolution of the peri-Adriatic area. In the present contribution, we summarize current knowledge and different interpretations proposed on the basis of twelve ichnosites from northern, central and southern Italy. The tetrapod track record is represented by few ichnosites in the earliest Cretaceous, with the bulk of the record reported from carbonate platform deposits of the Aptian-Cenomanian interval and, in the Late Cretaceous, from a extensive-tracksite in Apulia preserving thousands of dinosaur footprints. On the whole, the ichnological diversity documented by the material indicates a high diversity of trackmakers, among which are sauropods, different kinds of theropods, ankylosaurs and hadrosaurs. The persistent occurrence of dinosaur footprints at different stratigraphic levels produced significant questions and constituted a dramatic constraint for the understanding of palaeogeographical and geodynamical evolution of the Mediterranean area during the Mesozoic, suggesting new and different interpretations that challenged previous reconstructions.

Keywords: dinosaur tracks; Lower Cretaceous; Upper Cretaceous; Apulian Carbonate Platform; Apennine Carbonate Platform; Adria; trackmakers.

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1. INTRODUCTION

Several Cretaceous dinosaur tracksites are known across the entire Italian territory. The first discovery dates back to the 1990s, when isolated theropod and sauropod footprints were found on a limestone block used to build the pier of Porto Corsini (Ravenna, northern Italy). The block was quarried close to Sarone (Pordenone, northeastern Italy), in Lower Cretaceous carbonate platform deposits belonging to the Friuli Platform (Fig. 1).

In 1999 the first *in situ* Cretaceous dinosaur footprints were found in southern Italy, with thousands of ornithischian tracks discovered in a disused quarry close to the town of Altamura; the quarry was mined in Upper Cretaceous shallow-water deposits of the Apulian Carbonate Platform (AP). Subsequently further discoveries of Cretaceous dinosaur tracksites in central and southern Italy were made on a fairly regular annual basis (Fig. 1). All the new ichnosites can be palaeogeographically referred to both the Apulian and Laziale-Abruzzese-Campana carbonate platforms. They span from the late Hauterivian to the early Campanian. Aptian-Albian ichnosites show broadly similar ichnoassemblages in both platforms, thus suggesting their possible geographical connection during this time interval. More generally, the Italian Cretaceous dinosaur footprints were used to question previous paleogeographic schemes that interpreted all the peri-Adriatic Carbonate Platforms as isolated from each other and far from the main emergent lands. The numerous dinosaur track finds warrant drawing a new palaeogeographic scenario of the Central Mediterranean area for the Cretaceous.

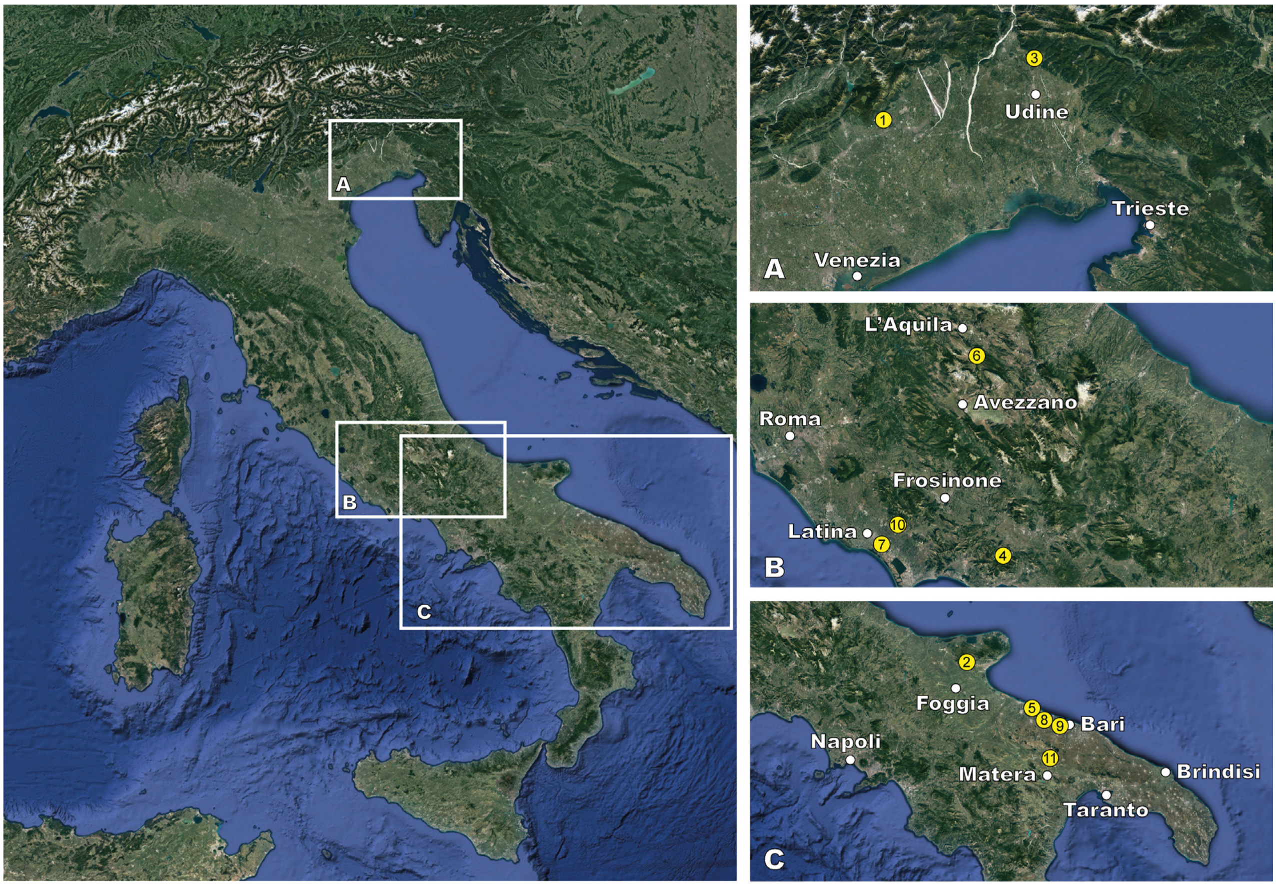

Fig. 1 - Location map of the Cretaceous dinosaur ichnosites from Friuli (A), central Apennines (B) and Apulia (C). 1) Sarone; 2) Borgo Celano; 3) Monte Bernadia; 4) Esperia; 5) Bisceglie; 6) Monte Cagno; 7) Rio Martino; 8) Molfetta; 9) Lama Balice; 10) Sezze; 11) Altamura.

2. LATE HAUTERIVIAN-EARLY BARREMIAN

2.1. ISOLATED BLOCK FROM PORTO CORSINI

Dalla Vecchia and Venturini (1995) described the first tridactyl Cretaceous dinosaur footprint from Italy. The footprint, preserved as a convex hyporelief, was found on a limestone block used to build the pier of Porto Corsini (Ravenna, northern Italy).

The block, about one meter thick and characterised by muddy facies with ostracods, shows a surface with intensive burrowing, pedogenic breccias and diffused mud cracks. The track filling is a wackestone with foraminifers and ostracods, likely indicating an intertidal environment (Dalla Vecchia and Venturini, 1995). Four years later, a second footprint was recognised and described by Dalla Vecchia (1999; see this paper for more information about the history of the finds) on the same block. The occurrence of the foraminifer *Orbitolinopsis capuensis* allowed the authors to determine the age of the block (Dalla Vecchia and Venturini, 1995; Dalla Vecchia, 1999). On the basis of both lithofacies and microfaunal content, Dalla Vecchia and Venturini (1995) traced the provenance of the block back to the Sarone quarry (Fig. 1A) and related this ichnological record to the southern flank of the Cansiglio Plateau, palaeogeographically belonging to the Friuli Platform that, in the Early Cretaceous, was connected to the Dinaric Platform (Sartorio, 1992; Adriatic-Dinaric Platform *sensu* Zappaterra, 1990).

The Porto Corsini tridactyl track is a poorly preserved left print, with faint digit tip traces. It is mesaxonic (*sensu* Romano et al., 2020) and 36 cm in total length (Dalla Vecchia and Venturini, 1995). The authors identified three digital pad impressions on digit III (the longest of the three toe marks), which is most clearly impressed in its proximal phalangeal portion. The digit II trace shows two pads and, like digit III, is characterized by a well-marked proximal phalangeal portion. The digit IV trace is the least detailed. The total digit divarication between digits II and IV is 28°. Despite poor preservation, distinct claw marks were recognised at the tips of digit II and digit III (Dalla Vecchia and Venturini, 1995). On the basis of the claw marks, coupled with a significantly longer digit III, the absence of *manus* impression, and the posterior indentation of the trace, Dalla Vecchia and Venturini (1995) attributed the footprint to a medium- to large-sized theropod (estimated hip height 181 cm, according to the equation of Thulborn, 1989). When compared to other theropod footprints of same size, the track from Porto Corsini is characterised by a marked and long digit II and quite stocky medial and outer digits (Dalla Vecchia and Venturini, 1995).

The second footprint preserved on the block lies on the same surface as the theropod footprint. According to Dalla Vecchia (1999), the footprint is as wide as long (30.5 cm in length and 31 cm in width) and is shallowly impressed (maximum depth of about 2.5 cm). Additionally, it is characterised by a double-crescent shape (see Farlow et al., 1989), with a larger anteriorly directed indentation, and smaller indentations along the medial and lateral sides, separating the anterior larger crescent portion from the posterior one (Dalla Vecchia, 1999). Based on the general morphology, Dalla Vecchia (1999) identified the track as the right *manus* impression of a sauropod dinosaur. The author suggested a similarity to the Early Cretaceous ichnogenus *Brontopodus*, in particular *Brontopodus birdi* described by Farlow et al. (1989) from the Glen Rose Limestone and related deposits of Texas and Arkansas; however, the footprint of Porto Corsini shows a markedly different morphology of digit I. Based on the general shape and rounded marks of the outer digits, the putative trackmaker should be sought within the Titanosauriformes, probably a basal member like *Brachiosaurus*, although taxa such as *Camarasaurus* or a member of the Diplodocidae cannot be ruled out, if a different interpretation of digit morphology is considered (Dalla Vecchia, 1999).

2.2. BORGO CELANO ICHNOSITE

In June 2000, a team from the University of Ferrara (A. Bosellini, P. Gianolla, and M. Morsilli) discovered a new ichnosite south of the village of Borgo Celano, in the Gargano Promontory (Fig. 1C; Apulia, southern Italy). Dinosaur footprints were recognised on three different stratigraphic levels exposed in the CO.L.MAR quarry, where a carbonate platform succession crops out. The best detailed footprints, preserved as natural casts, are imprinted on the lowest stratigraphic level and were first studied by Petti et al. (2008a).

The ichnosite of Borgo Celano is located on the western sector of the Gargano Promontory, where a thick Upper Jurassic-Eocene succession crops out (Morsilli, 1998; Bosellini et al., 1999, 2000; Bosellini and Morsilli, 2001). It belongs to the Apulian foreland, within the framework of the Southern Apennine orogenic system. During the Early Cretaceous, the Gargano Promontory was part of the Apulian Carbonate Platform (AP), bounded to the north by the Umbria-Marche-Sabina Basin, to the west by the Lagonegro-Molise basinal deposits and to the east by the Ionian Basin pelagic deposits (Zappaterra, 1990, 1994).

With a maximum thickness of about 3,000-3,500 m based on well data (Ricchetti et al., 1992; Bosellini et al., 1993), the Gargano Promontory was a platform-basin system from the Late Jurassic to the Eocene, characterised by a broad range of depositional environments (e.g., Bosellini et al., 1999, 2000; Borgomano, 2000; Bosellini and Morsilli, 2001; Morsilli et al., 2004). The platform was affected by several major geological events (for a complete discussion see Petti et al., 2008a).

The track-bearing succession belongs to the S. Giovanni Rotondo Formation (Cremonini et al., 1971), possibly a synonym of the Calcare di Bari Formation of the Murge Plateau. Claps et al. (1996) subdivided the formation into ‘Member 1’, ‘Member 2’, and ‘Member 3’; the 60 m of section outcropping in the productive quarry can be referred to ‘Member 2’, characterised by marked peritidal cyclicity, with shallowing upwards sequences ending in emersion and karstified surfaces. The track surface indicates an emersion at the top of a shallowing upward cycle and is composed of greenish clay, alternating with peloidal wackestone-packstone; it overlies a stromatolitic interval and is followed by a strongly bioturbated interval (Bosellini et al., 2000; Gianolla et al., 2001). Based on the first occurrence of *Salpingoporella muehlbergii* and *S. biokovensis*, the track level was dated to the upper Hauterivian-lowermost Barremian (Petti et al., 2008a).

Petti et al. (2008a) described 40 dinosaur tracks preserved as natural casts and undertracks on ten different blocks (Fig. 2), constituting separate trackways. Most of the footprints are tridactyl, with a total length

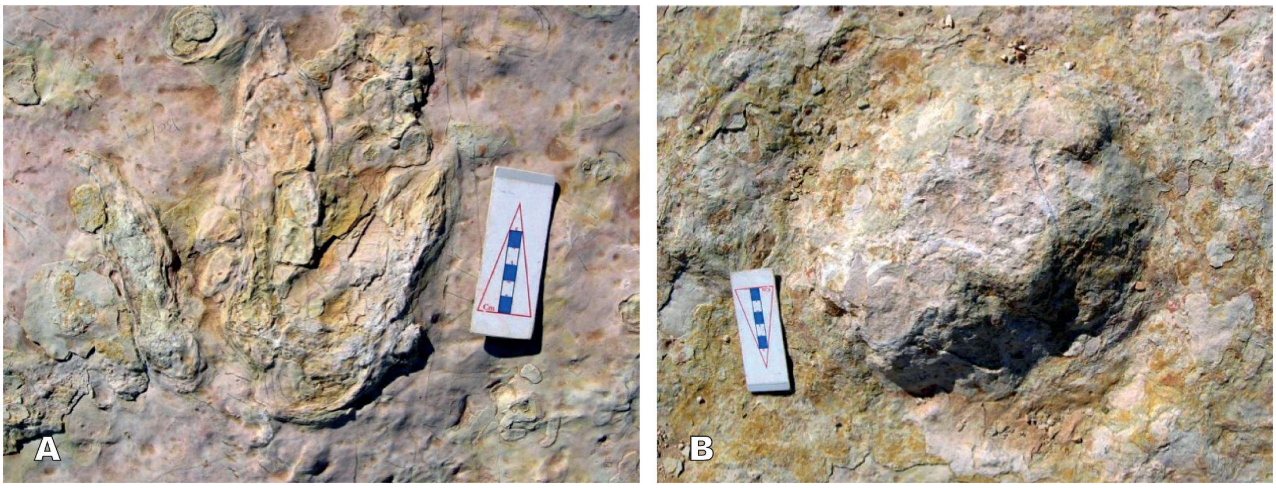

Fig. 2 - The Borgo Celano dinosaur footprints: A) tridactyl medium-sized theropod track; B) medium-sized ankylosaurian track. Scale bar 5 cm.

ranging from 21 to 56 cm (average length is about 33 cm); the higher values of footprint length are due to a metatarsal trace that, in some cases, characterises the footprint proximal portion. Elongated tracks have the largest interdigital angle between digits II and IV, up to a maximum of 106°, whereas the average divarication angle of the whole assemblage is ca. 75°. The FW/FL (Foot Width/Foot Length) ratio, calculated including the metatarsal trace, ranges from 0.61 to 0.75, or 0.77 and 1.30, excluding the proximal elongation. In digit III, the free portion is about 3/4 of the total length. In the best-preserved footprints, digit IV is slightly longer than digit II and claw marks, when preserved, are sharp; in general, two pads are recognised on digit II, three on digit III and three on digit IV. A total of eight footprints proximally show a V-shaped, elongated metatarsal impression, indicating a crouching posture for the trackmaker (Petti et al., 2008a).

Based on best-preserved footprint characters, Petti et al. (2008a) found a closer match with the ichnogenus *Kayentapus*, although the classical *Kayentapus*-like tracks (*sensu* Lockley, 2000) are known from Lower Jurassic deposits and are generally characterised by slender digits.

In spite of a conspicuous variation in the tracks, due to variable substrate conditions (especially water content), all the footprints can be reasonably ascribed to a single medium-sized theropod (Petti et al., 2008a). Petti et al. (2008a) also refined the trackmaker attribution, excluding the Troodontidae and Dromeosauridae because of their extreme specialization of digit II, and the Therizinosauroidea because of the long digit I and the strong narrow unguals on all digits. By inferring the absence of digit I in the producer's hindfoot, Petti et al. (2008a) also excluded Tyrannosauroidea, basal Tetanurae, Ceratosauria and Oviraptorosauria. In contrast, the absence of digit I impression, the digit relative lengths, and the MT/FL (Metatarsal trace/Foot Length) ratio, indicate a member of Ornithomimosaurs as the most likely producer of the tridactyl footprints from Borgo Celano (Petti et al., 2008a).

Along with tridactyl theropod footprints, Petti et al. (2008a) also recognised rounded traces with a total width of ca. 23 cm and an overall length of ca. 15 cm. These footprints are characterised by three to four short digit traces with blunt tips, interpreted by Petti et al. (2008a) either as putative ankylosaurian or ceratopsian footprints, but an ankylosaurian origin was tentatively preferred. In the history of dinosaur footprint discoveries in Italy, Borgo Celano was the first ichnosite in the Mesozoic of southern and central Italy recording the co-occurrence of both theropod and ornithischian dinosaurs.

2.3. MONTE CONERO ICHNOSITE

Natali et al. (2019) described a supposed tetrapod trackway in the Placche dei Gabbiani area (Conero National Park; Ancona, Marche). The alleged track surface belongs to the Maiolica formation and was dated to the Hauterivian-Barremian interval due to the absence of the genus *Calpionella* in the analysed samples. The supposed trackway is composed of eleven imprints, sub-circular or elliptical in shape. Foot length varies from 8 to 16 cm and foot width from 15 to 26 cm; the trackway is almost straight and is 5.20 meters in length. According to Natali et al. (2019), the tracks were produced on a deep seabed by the fore-paddles of a marine tetrapod, possibly an unknown reptile. This interpretation needs further research and remains speculative at this stage.

3. APTIAN-ALBIAN

3.1. PUTATIVE DINOSAUR TRACKS AT MONTE BERNADIA

Venturini (1995) reported some unusual load structures visible in cross-section within a succession of Lower Cretaceous carbonate deposits exposed along a road cut between the villages of Ramandolo and Chialminis (Valle del Cornappo, Monte Bernadia; Fig. 1A) in the Province of Udine (Friuli-Venezia Giulia). The structures were described as indentations on the upper surface of a 30-cm-thick greyish marl bed, rich in charophytes. The marl bed is covered by a limestone bed that fills in the observed indentations. The infilling itself is undisturbed and begins with a thin breccia level that covers the bottom of the indentations but does not extend beyond their bounding walls. These features were interpreted by Venturini (1995) as evidence that the depressions already existed at the time of the infilling and are not post-sedimentary deformations. The microfossil assemblage of the marl level points to a brackish or lagoonal environment. Its age was assessed as middle Aptian. Venturini (1995) provided neither illustrations nor any measurements of these structures. However, based on a comparison with similar structures described from North America by Nadon (1993) and Lockley and Hunt (1994), they were interpreted as dinosaur tracks viewed in section. Later, Dalla Vecchia and Venturini (1996) reinvestigated these structures, without providing unambiguous evidence for dinosaur tracks. Since then, no further research on this site has been published. If Venturini's (1995) interpretation is correct, this is one of the few sites in Italy where dinosaur tracks were recognised in a vertical section, without any available exposure of the track surface itself.

3.2. ESPERIA ICHNOSITE

In 2006, a dinosaur track-bearing surface was discovered by local hikers close to the town of Esperia, 30 km south of Frosinone (Latium, Central Italy). The ichnoassemblage was later investigated by a team from Sapienza University of Rome (M.A. Conti, U. Nicosia, F.M. Petti, S. D'Orazi Porchetti, and E. Sacchi). The Esperia ichnosite is located in the western Aurunci Mountains belonging to the Volsci Range (Cosentino et al., 2002; Centamore et al., 2007), a structural unit including the Lepini, Ausoni and Aurunci Mountains (Fig. 1B), and constituting the innermost sector of the Apennine Carbonate Platform (hereafter

ACP). The latter is bounded to the west by the basinal deposits of the Umbria-Marche-Sabina Basin, detected in wells (e.g. Parotto and Praturlon, 1975; Cippitelli, 2005).

In the area an Upper Triassic-Upper Cretaceous carbonate platform succession crops out, characterised mainly by recurrent tidal facies (Carannante et al., 1978; Accordi et al., 1988; Chiocchini et al., 1994; Centamore et al., 2007). Repeated subaerial exposure is indicated by several paleosols in the succession, mainly concentrated in the early Aptian-Cenomanian time interval (Accordi et al., 1967; Chiocchini and Mancinelli, 1977; Carannante et al., 1978; Chiocchini et al., 1994; Rossi et al., 2002; Centamore et al., 2007).

The track-bearing succession is characterised by subtidal to supratidal facies that are cyclically repeated in a mainly inner carbonate platform environment with a predominance of sandy facies with respect to the muddy ones, likely indicating the effect of wave and tidal energy (Petti et al., 2008b). The track-bearing horizon is represented by an alternation of wackestone and grainstone, showing scattered fenestral fabric and miliolids. On the basis of the association of dasycladalean algae, abundant miliolids, nubeculariids, polymorphinids, cuneolinids, spiroplectamminids, hyperamminoidids, bagginids and nezzazatids, Petti et al. (2008b) dated the track-bearing level to the Aptian.

About 80 dinosaur footprints, preserved as concave hyporeliefs, were recognised on an original exposed surface of 40 m^2, with an orientation and disposition that did not allow recognition of trackways. Although footprints are poorly preserved, due to diagenetic and tectonic cleavage processes, Petti et al. (2008b) identified three tridactyl footprints left by bipedal dinosaurs and circular to sub-elliptic tracks referable to quadrupedal dinosaurs (Fig. 3).

The three tridactyl footprints are very similar in overall dimension, being about 18 cm in length and 13 in width, and total divarication (II^IV) of 58°, 48° and 58° respectively (average value about 54°). The best preserved tridactyl footprint (labeled ES 1) is mesaxonic, with a straight digit III trace that greatly protrudes beyond the tips of the medial and lateral digits (Petti et al., 2008b). One pad trace is observed on the anterior portion of all the digit traces. A feeble claw mark occurs on digit IV of footprint ES 3.

According to Petti et al. (2008b), the tridactyl footprints from Esperia differ from those from the Aptian Lama Paterno ichnosite (see below) and from the early-middle Cenomanian Sezze ichnosite (see below). In contrast, a better match exists with the tridactyl traces from Borgo Celano (see above), based on the affinity of digit IV and the amount of digit III protrusion.

Petti et al. (2008b) referred the tridactyl traces to a small-sized theropod, with a possible height at the hip of about 82.5 cm (based on the formula by Thulborn, 1990), a body length of 3.30 m (based on Paul, 1988) and a body mass around 60 kg (based on the formula by Thulborn, 1990).

The other footprint type is represented by tracks with an elliptical, or sub-rounded, external outline, lacking

Fig. 3 - The Esperia dinosaur track-bearing surface. Ranging rod for scale (1.40 m).

sufficiently preserved diagnostic features even tentatively to assign it to an existing ichnotaxon. Among the tracks, Petti et al. (2008b) recognised at least three putative *manus-pes* couples, with the *manus* in front or just lateral to the impression of the foot, interpreted as *manus-pes* sets left by a quadrupedal dinosaur. The *pes* impression is bigger (foot length around 40 cm) than the *manus* and characterised by an elongated shape (longer than wide), while the *manus* appears circular. Based on the footprint general morphology, disposition and heteropody, Petti et al. (2008b) considered an attribution to medium-sized sauropods as the most likely.

For a palaeoecological and palaeogeographical consideration and discussion of the site see the specific section below.

3.3. BISCEGLIE ICHNOSITE I

Sacchi et al. (2009) reported several track-bearing limestone blocks from the carbonate platform succession cropping out in the disused Lama Paterno quarry (Fig. 4A), close to the town of Bisceglie, about 35 km north-west of Bari (Apulia, southern Italy) (Fig. 1C). The blocks preserve both isolated footprints and short portions of trackways, referable to both bipedal and quadrupedal dinosaurs.

The outcrop has been referred to the Valanginian p.p. to Cenomanian or lower Turonian Calcare di Bari Formation, which has been subdivided into seven members (Delfrati et al., 2003; Spalluto et al., 2005). The section cropping out in the quarry was referred by Sacchi et al. (2009) to the lower Aptian “Corato member” (see Luperto Sinni and Masse, 1984, 1993).

The original stratigraphic provenance of the track-bearing blocks was obtained as information from the quarry workers, and by comparing sedimentological features observed in the blocks and the stratigraphic succession exposed in the quarry. At least three main track horizons were identified (Sacchi et al., 2009). The stratigraphic section is referred to a carbonate platform depositional environment in which subtidal-inner lagoon and supratidal facies alternate. The track-bearing blocks consist of mudstone/wackestone including miliolids, shell fragments and Requieniidae, alternating with grainstone containing gastropods and Requieniidae (Sacchi et al., 2009). The microfossil assemblage includes *Sabaudia minuta*, *Praechrysalidina* cf. *infracretacea*, *Debarina* cf. *hahounerensis*, *Spiroloculina* sp., *Cuneolina* sp., *Salpingoporella* spp., along with ostracods, miliolids, nubeculariids and unclassified calcareous algae.

According to Sacchi et al. (2009), footprint detail is sub-optimal due to mud-cracking prior to the impression of the dinosaur footprints, exacerbated by intense diagenetic pressure-solution that obliterated some track features. Nevertheless, Sacchi et al. (2009) were able to group the tracks into six morphotypes.

Morphotype 1 is represented by three *pes* impression associated with two *manus* traces, preserved as natural molds. The *pes*, with a total length of about 34 cm, is mesaxonic and preserves distally rounded digits outlines (FL/FW (Foot Length/Foot Width): 1; FL/ML (Foot Length/Manus Length): 4; FL/SL (Foot Length/Stride Length): 0.25; pace angulation: 40°). The small *manus* is placed anteriorly to the *pes* with a pattern referable to ornithopods adopting a quadrupedal gait (Thulborn, 1990; Lockley and Wright, 2001).

Morphotype 2 (Fig. 4C) is represented by five tridactyl footprints ranging in total length between 15 and 20 cm (foot width: 13 cm; FL/FW: 1.3), with clearly impressed digits II and III, but digit IV trace less distinctly impressed and poorly defined. The trace of digit III is the longest and appears straight and pointed. Sacchi et al. (2009) referred these footprints to small-sized theropods, about 2 m tall and 4 m in total length following the formula provided by Paul (1988).

Morphotype 3 (Fig. 4B) is represented by three *manus-pes* couples composing a quadrupedal trackway, with a suboval *pes* (long axis essentially parallel to the trackway midline) of about 25 cm in average length (FL/FW: 1.5; FL/ML: 1.5; FL/SL: 0.25; pace angulation: 114°) and slightly smaller, almost rounded *manus* tracks, with a calculated heteropody index (the ratio between *pes* and *manus* areas; see Lockley et al., 1994) close to 1:1; the *manus* preserves the impression of bulky and short digit marks. Sacchi et al. (2009) attributed the morphotype to a medium-sized obligate quadruped dinosaur (60 cm tall at the hip, about 4-5 m in total length), characterised by a carriage (medium gauge) and heteropody consistent with a putative ankylosaurian trackmaker (McCrea et al., 2001).

Morphotype 4 is represented by several huge quadruped dinosaur tracks, preserved on four blocks both as concave hyporeliefs and as natural moulds. Among the material, two partial trackways were recognised, the first made of two *pedes* and a single *manus*, and a second represented by a further *manus-pes* set and a poorly preserved *pes*. The hindfoot print, sub-oval in outline, averages 55 cm in length and 48 cm in width, the *manus* 40 cm long and 44 cm wide. Based on tracks and general morphology, print arrangements in the set, and size, Sacchi et al. (2009) refer those footprints to a 10 m long sauropod trackmaker.

Morphotype 5 consists of four *pes* and two smaller *manus* arranged in a trackway. The *pes*, with an almost rounded outline, has an average total length of 26 cm and an average total width of 23 cm, whereas the *manus*, also sub-circular, is about 12.5 cm long and 9.5 cm wide; thus, the average foot area impression is three or four times larger than the *manus*. In the trackway, the *manus* is located nearly halfway between two successive *pedes*, the gauge is quite narrow (pace angulation between 115° and 127°), and the stride length is about 67 cm. Basing on the observed heteropody, Sacchi et al. (2009) referred the morphotype to a putative ornithischian trackmaker, with an estimated height at the hip of about 1.65 m and 4-5 m total length.

Morphotype 6 is represented by sub-triangular traces preserved on two blocks, with five footprints arranged in

Fig. 4 - A) Panoramic view of the Lama Paterno quarry (Bisceglie ichnosite I, Apulia); B) Bisceglie ichnosite I: the purported ankylosaur trackway partially preserved on block BLP 4. Desiccation cracks are widespread on the surface block (hammer for scale); C) Bisceglie ichnosite I: small-sized theropod footprints on BLP 3 block (hammer for scale). D) Bisceglie ichnosite II: the ankylosaur trackway made by a sequence of nine consecutive *manus-pes* couples (hammer for scale).

a trackway. The *pes* is characterised by an average length of 27 cm, average width around 24 cm, FL/SL ratio about 0.3, and a pace angulation of about 120°. According to Sacchi et al. (2009), the morphotype cannot be ascribed with confidence to any putative trackmaker.

3.4. BISCEGLIE ICHNOSITE II

Petti et al. (2010) described a second ichnosite about 1 km northwest of the Lama Paterno quarry, close to the town of Bisceglie (Bari, Apulia, southern Italy). The ichnosite is located between Via Crosta and the SS16 BIS national highway (Lat. 41,2522 N; Long. 16,4500 E), and is represented by a NNE dipping surface preserving a dinosaur trackway.

The surface belongs to the middle portion of the Calcare di Bari Formation (Luperto Sinni and Masse, 1993), a unit cropping out widely between Andria and Fasano (Ciaranfi et al., 1988) in the Murge area, deposited on the Apulian Carbonate Platform. The track-bearing surface is about 20 m^2 and is made by thick mudstone-wackestone with miliolids that, in the upper portion, passes to a bioclastic wackestone (with shell fragments of bivalves), and upward to a grainstone with fenestral fabrics (Petti et al., 2010). The general lithofacies, with a clear coarsening-upward succession, indicates an inner carbonate platform-back edge palaeoenvironment, also confirmed by the micropaleontological content, including *Salpingoporella (Hensonella) dinarica*, *Praechrysalidina infracretacea* and *Debarina hahounerensis*, referable to the *Salpingoporella dinarica* Zone *sensu* Chiocchini et al. (2008) and indicating an early Aptian age.

The trackway consists of a sequence of nine consecutive *manus-pes* sets, with a total length of 5.4 m and a calculated width of about 60 cm (Fig. 4D). *Pes* are longer than wide in average (30 cm in total length and between 23 cm and 29 cm in total width), and largely oriented in the direction of movement. *Manus* are always wider than long, with a general external outline ranging from sub-circular to crescentic. In some *manus*, five distally rounded digit impressions are observable; the axes of the central digits (II-IV) are always outwardly rotated, with respect to the trackway midline. The trackway has a narrow gauge and is generally straight, with a distance between *manus* and *pes* in the trackway varying between 6 and 16 cm; *pes* pace angulation ranges from 115° to 131°, whereas *manus* pace angulation ranges between 131° and 147°.

On the base of a gleno-acetabular distance of 85 cm, calculated following Leonardi (1987), Petti et al. (2010) reconstructed a possible total body length for the trackmaker of about 2.4 m. The reconstructed hip height, using the formula by Alexander (1976), is ca. 120 cm; an average speed of 3.10 km/h has been inferred based on the equation proposed by Thulborn (1990).

On the base of observed heteropody, trackways parameters and *manus* morphology, Petti et al. (2010) considered a thyreophoran, most probably an ankylosaur, as the most likely putative trackmaker, a hypothesis supported by the *manus* position, often internal to the *pes* position and/or crossing the trackway midline. The authors found a good fit between the gauge in the described material and that characterizing both *Metatetrapous valdensis* from the Bueckburg Formation of Germany (Lower Cretaceous, Berriasian; see Hornung and Reich, 2014 for a recent revision of the ichnospecies), and *M. gravis* originally described by Zakharov (1964) from the Lower Cretaceous of Tadjikistan (Shirabod Suite, Albian), even if the first ichnotaxon is characterised by a tridactyl *manus*, whereas the *manus* is not preserved in *M. gravis*. In addition, pace angulation and heteropody index show a great affinity with two quadrupedal trackways (namely BLP4 and BLP6) from the Lama Paterno quarry (Bisceglie ichnosite I), originally referred to an undetermined ornithischian and a medium-sized ankylosaur, respectively (Sacchi et al., 2009).

According to Petti et al. (2010), the new site represents further evidence for the presence of ankylosaurs on the Apulian platform during the Early Cretaceous.

3.5. MONTE CAGNO ICHNOSITE

The Monte Cagno ichnosite consists of a steeply inclined surface of about 300 m^2, one that is very difficult to access, exposed at about 1920 m a.s.l. on the eastern side of Monte Cagno (Fig. 1B), facing the town of Rocca di Cambio (L'Aquila, Abruzzo, Central Italy; Citton et al., 2017).

The outcrop falls within the geological map 1:100.000 Sheet 146 'Sulmona' (Reale Ufficio Geologico, 1942) and 1:50.000 Sheet 359 'L'Aquila' (Servizio Geologico d'Italia, 2006), and belongs to the ACP domain, represented by the Latium-Abruzzi and Campania platforms, regarded as a single palaeogeographic domain (Mostardini and Merlini, 1986; Pescatore et al., 1999) within Adria (Channell et al., 1979; Zarcone et al., 2010). The tracksite is referred to the informal unit 'Calcari ciclotemici a requienie', characterised by meter-scale peritidal cycles of brown to hazelnut mudstones, referred to the upper Aptian-lower Albian p.p. (Servizio Geologico d'Italia, 2006). The track-bearing surface consists of mudstone and wackestone, with a foraminiferal assemblage composed of *Haplophragmoides* cf. *globosus*, miliolids, and specimens tentatively referred to *Glomospira* cf. *urgoniana*, *Glomoinvolutina* cf. *apuliae*, and Nezzazatidae indet., whereas the microflora is represented by abundant *Salpingoporella dinarica* and rare *Thaumatoporella* sp., indicating an early Aptian age (Citton et al., 2017).

Due to the difficult accessibility to the track-bearing surface, in order to study the footprints a hexacopter drone was used to take images of the surface and build a three-dimensional model through high-resolution digital photogrammetry (see Citton et al., 2017 for further details).

Dinosaur tracks are preserved as concave epireliefs, and range mostly between 26 and 55 cm in overall length (Fig. 5). Different styles of track formation are represented on the surface. Most footprints are deep tracks likely produced by trackmakers sinking into soft mud (see Gatesy, 2003; Marty et al., 2009), making it difficult, in several cases, to detect diagnostic morphological features. The best-preserved trackway shows a width ranging between 65 and 85 cm, with a pace length between 120 and 135 cm and a pace angulation of about 160°, with a sequence essentially referable to a walking gait *sensu* Leonardi (1987). In general, tracks are poorly preserved, but a few footprints are better defined and characterised by complete metatarsal impressions. These specimens are parallel and arranged side-by-side and have been interpreted as an evidence of crouching behaviour during a resting phase (Citton et al., 2017). The authors attributed these footprints to a theropod trackmaker.

The overall length of the footprints with metatarsal impression is noteworthy; one footprint measures about 135 cm and represents, to date, the evidence of the largest theropod ever documented from the Mesozoic peri-Adriatic platforms of Italy, thus adding large-bodied, probably predatory theropods to this peculiar setting (Citton et al., 2017).

3.6. ISOLATED BLOCK OF PORTO CANALE-RIOMARTINO

The track-bearing block of Porto Canale-Riomartino (Latina, central Italy) was discovered in 2014 by B. Tamiozzo and S. Panigutti and brought to the attention of U. Nicosia (Sapienza University of Rome). It was excavated from a quarry close to the town of Terracina (Latium, Central Italy) and carried to Porto Canale-Riomartino for dock renovation (Fig. 1B).

The track-bearing block is 226 cm long and 210 cm wide and consists of hazel-coloured mudstone-wackestone. The microfauna recognised in thin section consists of *Cuneolina sliteri*, *Nezzazata isabellae* and *Arenobulimina* gr. *cochleata*, quite rare ostracods, and abundant shell fragments. Based on the occurrence of *Cuneolina sliteri* (Chiocchini et al., 2012), a late Aptian-?early Albian age was inferred (Citton et al., 2015). The succession exposed in the original quarry in the Ausoni mountains (Volsci range, see section 3.2.) records the evolution of the innermost portion of the ACP (Cosentino et al.,

Fig. 5 - Panoramic view of the Monte Cagno track-bearing surface.

2002; Centamore et al., 2007), bounded to the west by the pelagic deposits of the Umbria-Marche-Sabina Basin (Parotto and Praturlon, 1975).

On the block top surface, three clear tridactyl footprints (i.e., F1, F2, F3 in Citton et al., 2015) (Fig. 6A) with complete and semi-complete metatarsals impressions, are preserved as concave epireliefs, along with other undetermined traces (Citton et al., 2015). Footprints F1 and F2 are roughly parallel and arranged side-by-side, with a total length of about 38 cm (including metatarsal impression), whereas F3 is located ahead of the other two. Based on preservational features, Citton et al. (2015) consider F1 and F2 as 'modified true tracks' (*sensu* Marty et al., 2009), and F3 as a 'true track' (*sensu* Lockley, 1991; Marty et al., 2009). Footprint F3 is 40 cm long, asymmetric, mesaxonic, with an almost straight digit III (protruding about 6 cm beyond the tips of II and IV) and showing a terminal pointed claw mark. No trace of digit I is observed on the footprints' medial sides. The total digital divarication is about 41°, interdigital angle II^III 31° and III^IV 10°. Two phalangeal pad impressions were identified on digits III and IV, because these are more deeply impressed, whereas only one pad is observable in digit II. In all the digit traces, the depth of impression decreases anteriorly, as detected from the section obtained through the three-dimensional model. The ovoid area characterizing the portion of footprints behind digits III and IV was interpreted by Citton et al. (2015) as the impression of metatarsal-phalangeal fleshy pads.

Based on the preserved trace of the metatarsus, proportionally more elongated in theropods than in ornithopods ('morphodynamic rule' in Lockley et al., 2003; see also Thulborn, 1990), Citton et al. (2015) attributed the footprints to a medium-sized, non-avian theropod trackmaker. Based on the spatial relationship between the trace and the differential depth of impression, Citton et al. (2015) also provided a preliminary possible reconstruction of the peculiar trackmaker's locomotion. The theropod placed the right foot and then the left one on the ground before crouching, then crouched down into a resting position, impressing the metatarsus, ankle and, possibly, the ischial callosity. Then, after a resting pause, the theropod started to move again, still retaining a crouching posture for a single step forward, then finally returning to the typical upright posture (after the impression of trace F3). Citton et al. (2015) hypothesized that the greater impression depth characterizing the sub-circular portion of the metatarsal impression of F2 could be due to interference between two distinct movements.

Fig. 6 - Close-up of a theropod footprint from the Rio Martino ichnosite.

On this basis, they stressed how the interaction of multiple complex trackmaker movements could greatly affect the final three-dimensional geometry of a footprint (Citton et al., 2015).

Subsequently, Romano and Citton (2016) compared the tridactyl footprints from Porto Canale-Riomartino to known autopodial structures in major clades of theropods, in order to refine the trackmaker attribution. Based on the available material, the authors reconstructed two possible hypothetical pedal morphologies from the footprints, and chose four measurements (total length of the metatarsal impression, and lengths of the phalangeal portions of digits II–IV; see Romano and Citton, 2016) to characterize morphometrically the putative trackmaker foot. The same measures were calculated for thirty-seven theropod taxa, belonging to Abelisauridae, Allosauridae, Avialae, Coelophysoidea, Coelurosauria *incertae sedis*, Deinonychosauria, Neoceratosauria, Ornithomimosauria, Oviraptorosauria and Tyrannosauridae. The dataset, including the footprint and the theropod feet, was investigated by Principal Component Analysis and Cluster Analysis. The results show a close affinity between the studied tracks and the clade Ornithomimosauria, and especially *Struthiomimus*. The absence of a digit I trace in the footprints was considered to reflect a genuine character of the producer's foot anatomy, reinforcing the similarity to *Struthiomimus*, which is characterized, within Ornithomimosauria, by the derived absence of the first digit in the hindfoot autopodium. On this qualitative and quantitative evidence, Romano and Citton (2016) referred the footprint to an ornithomimosaurian trackmaker, close to *Struthiomimus*. On the basis of the complete articulated skeleton figured in Longrich (2008, Fig. 6, p. 985) for *Struthiomimus altus*, Romano and Citton (2016) reconstructed a possible hip height for the trackmaker of about 1.06 m and a total body length of ca. 2.8 m. Paleobiogeographical inferences about the occurrence of Ornithomimosauria in the peri-Adriatic platforms of Italy are discussed below.

3.7. MOLFETTA ICHNOSITE

The Molfetta tracksite was discovered in the disused San Leonardo quarry (Bari, Apulia, southern Italy) (Fig. 1C) (Petti et al., 2018), and has been recently included in the geosite census of the Apulia Region (CGP0137 in Mastronuzzi et al., 2015) due to the well-detailed dinosaur track record therein preserved. Petti et al. (2018) applied aerial high-resolution digital photogrammetry to map and geo-reference the ichnosite by using two different UAVs (unmanned aerial vehicles) and then compared the results (see Petti et al., 2018 for a thorough discussion of the methodology and broader application of the results).

The quarry surface has a total area of about 2700 m^2. In the quarry, a 15-m-thick carbonate succession of the Calcari di Bari Formation is exposed. A late Aptian-