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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.

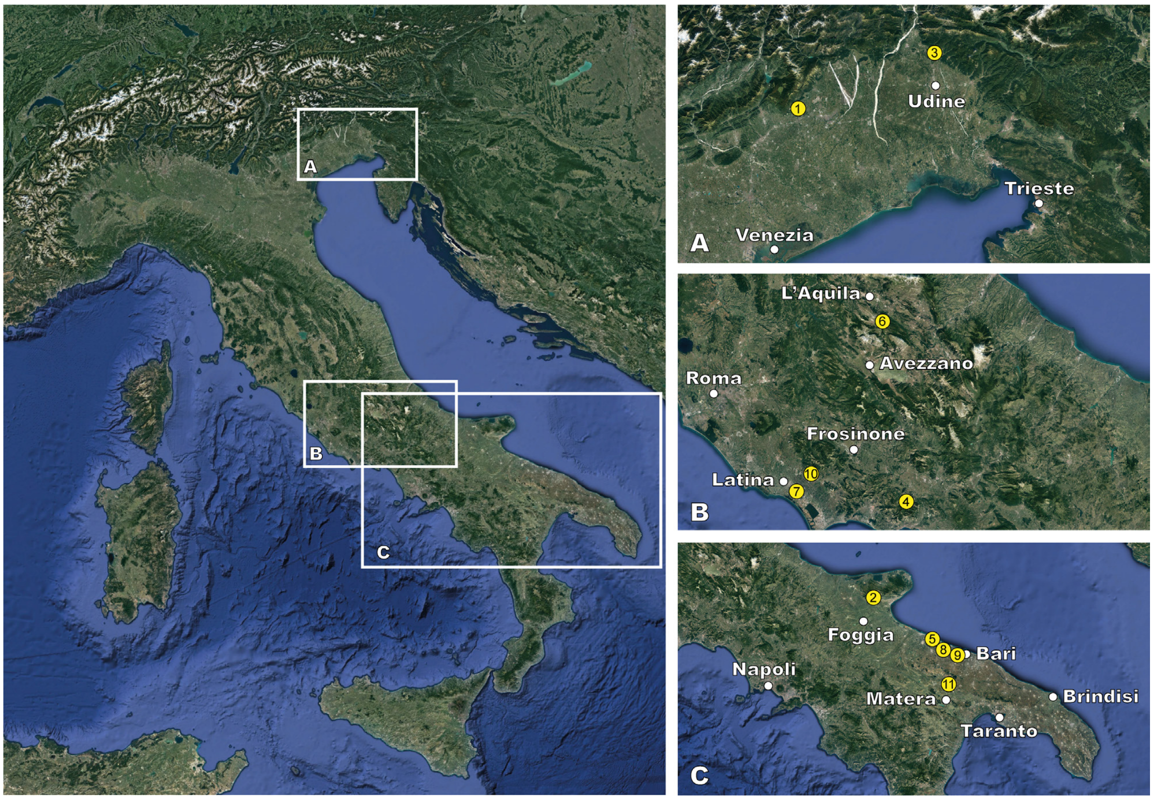

Fig. 1 - Location map of the Cretaceous dinosaur ichnosites from Friuli (A), central Apennines (B) and Apulia (C). 1) Sarone; 2) Borgo Celano; 3) Monte Bernadia; 4) Esperia; 5) Bisceglie; 6) Monte Cagno; 7) Rio Martino; 8) Molfetta; 9) Lama Balice; 10) Sezze; 11) Altamura.

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., 2018) 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

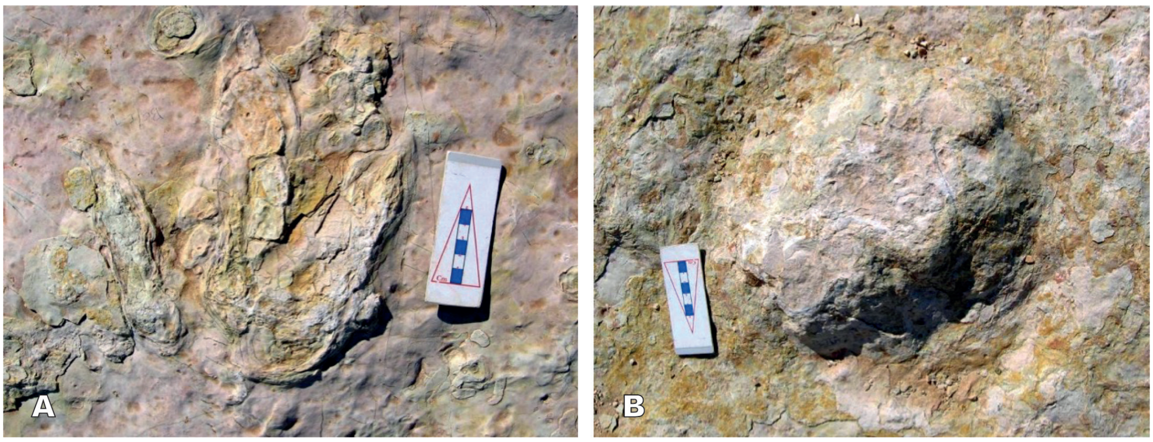

Fig. 2 - The Borgo Celano dinosaur footprints: A) tridactyl medium-sized theropod track; B) medium-sized ankylosaurian track. Scale bar 5 cm.

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-early Albian age was inferred on the basis of a benthic foraminiferal assemblage (Iannone et al., 2012; Fanti et al., 2014; Petruzzelli, 2017). The track-bearing surface is a wackestone of subtidal environment in which no sedimentological features are recognizable, probably due to subaerial exposure (Petti et al., 2018). The track-bearing surface represents the top of an intensively bioturbated wackestone bed (Fanti et al., 2014) and the occurrence of dinosaur footprints is the most convincing evidence of short subaerial exposure of this surface.

Petti et al. (2018) preliminarily recognised tridactyl footprints making up different trackways of medium-sized theropods (Fig. 7), in association with incomplete quadrupedal trackways attributed to small- to medium-sized herbivorous dinosaurs. On the surface there is also a long, 'L-shaped' track showing meniscate structures and raised rims, that has been tentatively attributed to a large turtle (Petti et al., 2018).

The ichnological material of the disused San Leonardo quarry will be described in detail in a forthcoming paper.

3.8. LAMA BALICE ICHNOSITE

The Lama Balice tracksite is located in a disused quarry, opened in the Cretaceous limestones of the Calcare di Bari Formation. It is part of the Parco Naturale Regionale Lama Balice (Lama Balice Regional Natural Park), within the boundaries of the Metropolitan City of Bari, along the eastern flank of the Murge Plateau (Apulia, Southern Italy) (Fig. 1C). Several dinosaur footprints were discovered in 2013 by M. Petruzzelli on the bottom surface of the quarry. A research convention agreed to between the Park authority, the University of Bari and the Soprintendenza Archeologia, Belle Arti e Paesaggio per la Città Metropolitana di Bari, promoted study of the stratigraphic succession and the track-bearing surface (Petruzzelli et al., 2019). The quarry shows an approximately 20-m-thick section of upper Albian deposits. It represents a tidal flat repeatedly exposed subaerially. The ichnological analysis was performed through interpretative drawings and close-range photogrammetry. The best-preserved footprints are tridactyl and show well preserved digital pad impressions. They were attributed to small- to medium-sized theropods (Fig. 8A). On the track-bearing surface a *manus-pes* couple attributed to a medium-sized ankylosaur is clearly visible. The *pes* has a rounded heel and shows four short and stubby digit impressions; the *manus* is sub-circular (Fig. 8B). Other large footprints were detected in cross-section along the quarry walls. They are about 35 cm long and 10 cm deep, and show both displacement rims and distinct undertrack levels. They were tentatively attributed to medium-sized sauropods (Petruzzelli et al., 2019).

Fig. 7 - One of the theropod trackways of the Molfetta ichnosite.

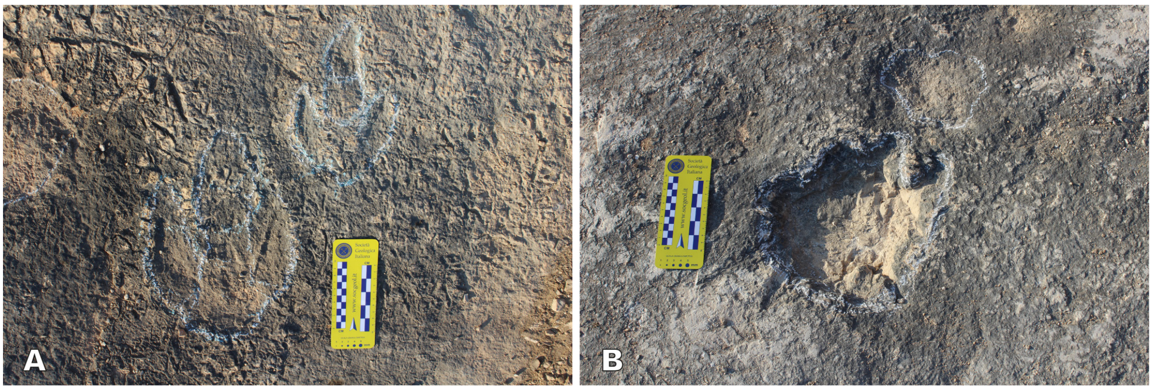

Fig. 8 - Lama Balice ichnosite: A) Small- and medium-sized theropod footprints; B) *manus-pes* couple attributed to an ankylosaur. Scale bar 10 cm.

4. LOWER TO MIDDLE CENOMANIAN

4.1. SEZZE ICHNOSITE

The Sezze ichnosite is to date the largest ichnosite of central Italy (Fig. 1B), preserving on three different surfaces of a disused quarry (Cava Petrianni) more than 200 dinosaur footprints, both organized in trackways and isolated singletons (Nicosia et al., 2007). The ichnosite is located in the westernmost sector of the Lepini Mts., within Sheet 159 'Frosinone' of the Geological Map of Italy on a scale 1:100,000 (Accordi et al., 1967). The carbonate succession exposed in the quarry belongs to the Lepini-Ausoni-Aurunci Unit, one of five structural units constituting the southern portion of the Central Apennines and overtrusting each other eastward from the Tyrrhenian Sea to the Adriatic foreland (Cipollari et al., 1999). The track-bearing surfaces lie at the base of a 250-m-thick succession attributed to the "Laziale-Abruzzese-Campano domain" (Parotto and Praturlon, 2004) within the Apennine chain, ranging in age between the Late Triassic and the Late Cretaceous in persistent carbonate platform settings (Accordi and Carbone, 1988).

The stratigraphic section shows repeated changes in the depositional environment, from subtidal to supratidal conditions to subaerial exposure (Nicosia et al., 2007). The oldest level bearing footprints lies on the surface of a 25-cm-thick bed, at 3.45 m from the base of the section and is composed of strongly dolomitized wackestone-mudstone preserving traces up to 10 cm deep. The second track surface occurs 6.42 m from the base of the section, at the top of 50 cm of tidal deposits characterised by very small fenestrae. The third track-bearing level occurs 8.80 m from the base of the section, and is characterised by a 10-cm-thick layer with faint traces and desiccation cracks. The microfaunal assemblage (Nicosia et al., 2007) includes *Cuneolina* gr. *pavonia*, *Nezzazata* sp., miliolids, and *Sellialveolina vialli*, a species whose range is restricted to the early Cenomanian (Berthou, 1984; Chiocchini et al., 1994) or latest Albian to middle Cenomanian (De Castro, 1985; Vicedo et al., 2011).

The lowest surface preserving footprints (SCP I in Nicosia et al., 2007) has an area of 30 m^2 and shows a total of 44 dinosaur footprints, including a quadrupedal trackway consisting of 20 footprints (Fig. 9), two short trackways made by a bipedal dinosaur and 18 isolated footprints referred to small theropods. An interesting feature is that almost all the tridactyl footprints are impressed on the expulsion rims of the large quadrupedal footprints, thus indicating either a substrate already hardened or covered by microbial mats (see Nicosia et al., 2007 for

Fig. 9 - Sauropod trackway on the lower track-bearing surface (SCP I) of the Sezze ichnosite (hammer for scale).

a more complete discussion on track preservation). The quadrupedal trackway is about 7.5 m long, essentially straight, and consists of 9 *manus-pes* pairs for a total of 20 footprints. The SCP I-1 trackway has a large *manus* impression (FL=12 cm; FW=40 cm) relative to the size of the *pes* (FL=45 cm; FW=40 cm). All the traces are several centimetres deep and characterised by quite low expulsion rims. The *pes* outline ranges from sub-elliptical to sub-circular and, in some tracks, is characterised by sharp and short inward directed distal claw impressions. The *manus* outline is generally semi-circular, showing in some cases a peculiar indentation along the track's proximal border, and is clearly placed anterior to the *pes*, about half-way between two consecutive *pedes*, with the *pes* never overlapping the *manus*. The pace angulation is about 100°. According to Nicosia et al. (2007), the wide gauge of the trackway, the relatively large *manus* compared with the *pes* (heteropody index of about 1:2 taking into account footprint area), and the relative position of *manus-pes* couples in the trackway relative to the movement direction, permit possible attribution of the quadrupedal footprints to a titanosaurian sauropod (see Wilson and Sereno, 1998; Wilson and Carrano, 1999; Lockley et al., 2002; Bonnan, 2003).

The second surface (SCP II in Nicosia et al., 2007) preserves weakly impressed tridactyl digitigrade footprints, referable to medium-sized theropods, with an average foot total length of 24 cm, and a width of 13 cm. About 20 footprints preserved as concave epireliefs are observable on the surface: they are essentially tridactyl and never show the impression of the metatarsal or of digit I. The impression of digit III is the most clearly marked, with a proximal width of about 5 cm, and a digit III projection/footprint total length ratio of about 0.3. The observed digit divarication in the best-preserved footprints varies between 37° and 60°.

The third track surface (SCP III), 6 m long and 2.5 m wide, is characterised by the greatest concentration of footprints (more than 170) and can be considered as moderately trampled (following Lockley and Conrad, 1989). On the surface most of the traces are isolated, and only a few small trackways, represented by few consecutive tridactyl footprints, were recognised (Nicosia et al., 2007). Among the studied traces, about 10% are characterised by a clear proximal metatarsal trace and about 20% are more or less elongated. Nicosia et al. (2007) recognised up to ten different morphotypes, ranging from typical tridactyl digitigrade tracks to footprints characterised by a clear impression of digit I and of the metatarsal area, possibly indicating a crouching behaviour of the producers (Fig. 10). The characters of the different morphotypes detected by Nicosia et al. (2007) allowed them to refer all the footprints to *Kayentapus*-like footprints, following Lockley (2000). Variability among the different traces is interpreted as linked to varying conditions in sediment water content. In general, total digit divarication (II^IV) ranges from 57° to 85° (a maximum of 102°), and two pads are recognised on digit II, whereas usually three pads characterize digits III and IV (see Nicosia et al., 2007 for a detailed description). According to Nicosia et al. (2007), most tridactyl footprints preserved on the third surface can likely be referred to the same kind of trackmaker. Based on the retained digit I, with the metatarsal-phalangeal articulation of digit I distally placed along the metatarsus, Nicosia et al. (2007) considered the trackmaker most likely to be a theropod, possibly a basal form within the Ornithomimosaurs (*sensu* Makovicky et al., 2004) or a member of the Oviraptorosauria (*sensu* Osmólska et al., 2004). They found a closer match with the oviraptorosaurian foot skeleton, based on general digital proportions, the presence of digit I, and the narrow claw traces, comparable to the laterally compressed ungual of oviraptorosaurs (Nicosia et al., 2007).

The ichnocoenosis composition and paleobiogeographical inferences are discussed below.

5. SANTONIAN-EARLY CAMPANIAN

5.1. ALTAMURA ICHNOSITE

The Altamura ichnosite, discovered in June 1999, is located in the disused Pontrelli quarry, 4 km east of Altamura (Bari, southern Italy), along the road SS 171 to Santeramo (Nicosia et al., 1999a). About 30,000 dinosaur footprints were originally estimated to be preserved on a total area of about 15,000 m^2 (Nicosia et al., 1999a) (Fig.

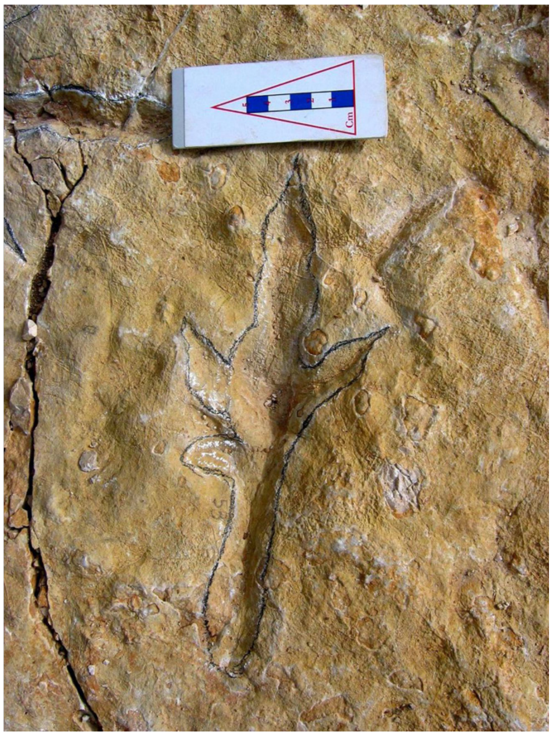

Fig. 10 - Tridactyl footprints showing digit I and metatarsal impressions, preserved on the SCP III surface of the Sezze ichnosite. Scale bar 5 cm.

11). Nicosia et al. (1999a) subdivided the track-bearing surface into three portions, the first relatively small and almost lacking traces, the second representing about one third of the total surface and preserving few trackways, and the third one characterised by a low to moderate degree of trampling *sensu* Lockley and Conrad (1989).

The surface containing the footprints belongs to the Altamura Limestone Formation (Azzaroli et al., 1968; Ciaranfi et al., 1988), consisting of carbonate platform deposits pertaining to the Apulian foreland structural unit, with a maximum thickness of 1000 m and an age ranging from the (?)upper Turonian to the Maastrichtian (Nicosia et al., 1999a). These deposits represent an inner shelf environment, with algae ('Loferitic member' of Luperto Sinni and Borgomano, 1989), benthic foraminifers, and rudists (Hippuritidae and Radiolitidae) (Ricchetti and Pieri, 1999). The formation paraconformably overlies the Calcari di Bari Formation; the boundary marker is a bauxitic layer that has been interpreted as reflecting a subaerial exposure episode (Maggiore et al., 1978a, 1978b; Iannone and Laviano, 1980; Luperto Sinni and Reina, 1996a, 1996b). Valduga (1965), Azzaroli et al. (1968) and Ricchetti (1975) defined the Salento and Murge Limestone Group as constituting the Calcare di Bari Formation and the Calcare di Altamura Formation. The age of the footprint-bearing part of the formation is most likely Santonian to early Campanian, based on strontium isotope stratigraphy and benthic foraminiferal assemblages (Perugini, 2006), whereas a preliminary late Coniacian-early Santonian age was inferred by Nicosia et al. (2007). A Santonian-early Campanian age is broadly supported by the occurrence of taxa such as *Murgeina apula*, *Rotalispira scarsellai*, *Scandonea samnitica*, *Moncharmontia apenninica*, and *Accordiella conica* throughout the section, and *Murciella* cf. *cuvillieri* in its upper part, about 18 m above the tracks (Perugini, 2006).

In the quarry, the carbonate platform deposits form a small anticline and are unconformably overlain by the Calcareniti di Gravina Formation of Plio-Pleistocene age (Ciaranfi et al., 1988). The site belongs to the Murge carbonate Plateau, parallel to the Bradanic Trough, with a NW-SE elongation; the plateau is bounded by the Salento Peninsula to the SE and the Tavoliere Plain to the NW.

Nicosia et al. (1999a) stressed the difficulty of studying and identifying the ichnotaxa and trackmakers due to the huge number of intersecting trackways. In any case, the authors preliminarily reported that the site appears dominated by footprints referable to different kinds of

Fig. 11 - Panoramic view of the Pontrelli quarry near Altamura, where thousands of dinosaur footprints are preserved on the same stratigraphic horizon.

quadrupedal dinosaurs of relatively small dimensions. No theropod tracks were recognised in this first phase of study.

Later, Nicosia et al. (1999b) described in detail the first quadrupedal dinosaur trackways from the Altamura ichnosite, introducing the new ichnotaxon *Apulosauripus federicianus*, after the Emperor Frederic II, who restored the town of Altamura (Fig. 12).

The trackway has an overall width of 80 cm, the *pes* total length is 67 cm, the *manus* length 74 cm, the stride for the *pes* is 105 cm and for the *manus* 103 cm; pace angulation ranges between 88° and 120° for the *pes*, and between 80° and 102° for the *manus*, with a calculated gleno-acetabular distance of about 125 cm. The *manus* is placed frontally and medially with respect to the *pes*. Both *manus* and *pes* are functionally tridactyl, with the *pes* oriented generally slightly outwardly and the *manus* essentially directed forward with respect to the trackway midline. The *manus* is broader than long, with digit III being the longest, and all digits terminate with bluntly rounded claw impressions. The *pes* is slightly broader than longer, mesaxonic and semiplantigrade, with an angle between digits II and III of about 99° and between digits III and IV of 71°. In general, digits are equal in length, with digit III slightly longer in some footprints; all digits terminate with the trace of rounded hooves.

Regarding the possible trackmaker, Nicosia et al. (1999b) reconstructed a total length for the dinosaur of about 5-6 m, with a height at the hip of about 140 cm (using the method of Thulborn, 1990) and a total weight ranging between 900 and 1,100 kg; based on formulas provided by Alexander (1976) and Thulborn (1990), the authors estimated a very slow gait and a possible speed respectively of 2 and 3 km/h (Nicosia et al., 1999b). After excluding theropods, sauropods and thyreophorans, the authors found a better match with an advanced quadrupedal, non-thyreophoran ornithischian, the most likely being an ornithopod in the family Hadrosauridae (Nicosia et al., 1999b). In contrast, Gierlinski et al. (2005) reinterpreted the footprints referred to *Apulosauripus federicianus* as suggesting an ankylosaurian origin, whereas Dalla Vecchia (2008) hypothesized a possible basal iguanodontian origin.

At present, the site is part of the geosite census of the Apulia Region (CGP0137 in Mastronuzzi et al., 2015). In 2017 the Altamura municipality acquired the quarry and a research convention was negotiated involving the City of Altamura authority, the University of Bari and the Soprintendenza Archeologia, Belle Arti e Paesaggio per la Città Metropolitana di Bari, joined in a consortium with two private enterprises, COBAR, ENSU and CoopCulture. The whole track-bearing surface

Fig. 12 - A) *Apulosauripus federicianus* Nicosia et al., 1999b; ACDL 99/3. B-C) Close-up of two *manus-pes* couples of trackway ACDL 99/3 (ACDL 99/3-5 and ACDL 99/3-6).

was mapped by using small Unmanned Aerial Vehicles (UAVs) and about 26,000 tracks were surveyed, basically confirming the original estimate by Nicosia et al. (1999a). Twelve quadrupedal trackways were studied in detail, making use of close-range photogrammetry.

Work is still in progress and the results of the ichnological study will be described in forthcoming papers.

6. PALEOBIOLOGY *VS* PALEOGEOGRAPHY

The occurrence of dinosaur footprints in the carbonate platforms of the peri-Adriatic region immediately generated important interpretative questions, with inferred possible scenarios that may have a great impact on geodynamic reconstruction of the area during the Mesozoic.

The central portion of the Mediterranean area is represented by an assemblage of structural units, referable as a whole to the Adria microplate (Channell et al., 1979; Zarcone et al., 2010), where both shallow and deeper successions were deposited (Nicosia et al., 2007). The plate, originally pertaining to the African promontory according to Channell et al. (1979), was successively detached and pulled apart from the African continent by extension of the Tethys Ocean, to collide northward with the European foreland (Stampfli and Borel, 2004). For a long time, the traditionally accepted interpretation considered the Mesozoic shallow water and emergent areas of Adria as separated from both Laurasia to the north and Gondwana to the south, with oceanic areas surrounding the carbonate platforms, these being the Ligure-Piemontese, the Vardar and the Ionian oceans (Catalano et al., 2001; Passeri et al., 2005). As stressed by Bosellini (2002), the geodynamic setting of the eastern Mediterranean has been the subject of debate for at least three decades, in particular regarding: i) the interpretation of the Adria block as an independent microplate or alternatively as an African promontory, and ii) the interpretation of the Ionian basin of the eastern Mediterranean (e.g. Biju-Duval et al., 1976; Channell et al., 1979; Cloething et al., 1979; Farrugia and Panza, 1981; Finetti, 1982; Dercourt et al., 1986; Anderson, 1987; Casero and Roure, 1994; Finetti et al., 1996; Catalano et al., 2001; Wortmann et al., 2001; Bosellini, 2002). In particular, the occurrence of Middle Jurassic-Early Cretaceous ophiolites in the peri-Adriatic belt led several authors to conclude that Adria was detached from Europe and separated by an ocean; in contrast, little evidence exists for the putative connection to the south with the African plate (Bosellini, 2002). According to several authors, Adria was separated from the Africa continent by oceanic crust in the Ionian Sea (e.g. Dewey et al., 1973; Biju-Duval et al., 1976, 1977; Makris, 1981; Finetti, 1982, 1985; Dercourt et al., 1986, 1993; Ziegler, 1988; De Voogd et al., 1992; Finetti et al., 1996; Stampfli and Mosar, 1999). According to other authors Adria should be interpreted as a promontory of the African continent (Canavari, 1885; Argand, 1924; Staub, 1951; Stille, 1953; Caire, 1975; Channell, 1976; Channell et al., 1979), and the presence of oceanic crust in the Ionian abyssal plain is still controversial (e.g. Boccaletti et al., 1984; Sestini, 1984; Panza, 1987; Gealey, 1988; Hirsch et al., 1995; Ismail-Zadeh et al., 1998; Nicolich et al., 2000).

The discovery of several Cretaceous dinosaur track-bearing horizons has challenged the interpretation of isolated and restricted carbonate platforms for at least two main reasons: i) dinosaurs presumably could not swim for long distances, so a repeated connection with the mainland was necessary, along with a connection between the same carbonate platforms, to account for the track record; ii) in order to survive, especially huge herbivorous dinosaurs needed large vegetated areas, fresh water, and large stable nesting sites, with an environmental setting incompatible with the relatively small area of the isolated carbonate platforms.

Below we briefly summarize the palaeogeographic and geodynamic inferences provided in the two last decades by the existence of the Cretaceous dinosaur ichnosites reported above.

Dalla Vecchia (1994) stressed that the presence of sauropods on Mesozoic carbonate platforms, animals which needed a large amount of vegetation and fresh water, would indicate emergent areas larger than the very small tropical islands predicted by the classical geodynamic interpretation, with a larger extension during the low-stand phases, comparable to present-day Madagascar. According to Dalla Vecchia (1994), sea level fluctuations may have caused a restriction or total drowning as well as a total emersion of the platforms from Istria to the present northern Africa, leading to repeated migrations of dinosaurs from the African continent, as well as among the different portions of the Adria microplate. Dalla Vecchia (1994, 2008) also stressed that the relatively small dimensions of sauropods in the ?late Albian and the late Cenomanian could reflect insular adaptation (i.e. insular dwarfism), even if the sample is too small to make broader inferences.

Nicosia et al. (1999b) briefly discussed the palaeogeographical significance of dinosaur footprints and other Mesozoic terrestrial remains in their second paper on the Altamura ichnosite. In their view, the growing evidence of dinosaur occurrences in Italy, including tracksites from Northern Italy (Leonardi and Avanzini, 1994; Mietto and Roghi, 1993; Roghi, 1994), Tuscany and Liguria (Leonardi and Lockley, 1995; Sirigu and Nicosia, 1996), the compsognathid theropod *Scipionix samniticus* from near Benevento (Dal Sasso and Signore, 1998; Dal Sasso and Maganuco, 2011), and hadrosauroid remains found near Trieste (Dalla Vecchia, 2000, 2009), required a rethinking of the traditionally accepted model of isolated carbonate platforms of the Adria microplate. The unexpected abundance of dinosaurs was further increased by the Altamura ichnosite, extending to the south the occurrence of dinosaur footprints within the Adria region. According to Nicosia et al. (1999b), the evidence from the Late Triassic (Carnian to Norian), Early Jurassic (Hettangian to Toarcian), and Early, mid and Late Cretaceous (Hauterivian-Barremian, Albian, Cenomanian, Santonian), demonstrates a virtually continuous presence of dinosaurs in the Apulo-Adriatic-Dinaric region throughout the Mesozoic. In their interpretation, when considering the need for extensive emergent areas to produce a sufficient vegetal biomass for large herbivorous dinosaurs, and for the nesting of these oviparous animals, the geodynamic models accepted at the time needed a deep rethinking; additionally, the palaeogeographic maps published until then showed carbonate platform areas pulled apart by deeper basins (Dercourt et al., 1986, 1993), an interpretation rendered highly unrealistic by the presence of dinosaur footprint localities. The Altamura tracksite was thus interpreted as further evidence that a substantial change in palaeogeographic models was needed to account for the repeated migration and occurrence of dinosaurs in the Apulo-Adriatic-Dinaric region (Nicosia et al., 1999b).

Dalla Vecchia (2001, 2008) reviewed the occurrence of terrestrial vertebrate on the peri-Adriatic carbonate platforms during the Mesozoic, discussing the palaeoecological and palaeogeographical implications of the presence of dinosaurs, especially plant-eaters. He stressed that even if body fossils may be transported into the carbonate platform from a far continent by marine currents, footprints are autochthonous by definition. This in turn indicates that during the Mesozoic the peri-Adriatic carbonate platforms would necessarily have included emergent areas that were large enough to provide the fresh water and food resources sufficient to support resident populations of large vertebrates (Nicosia et al. 1999b). This issue, according to Dalla Vecchia (2001), was sufficient to necessitate a dramatic change in the interpretation of paleoenvironmental and paleogeographic reconstructions based only on geological data. According to Dalla Vecchia (2001), the carbonate platforms between Laurasia and Gondwana could have represented a bridge between Africa and Laurasia/Eurasia or, alternatively, a 'Noah's Ark', accepting the opening of an oceanic basin between them as proposed by Masse et al. (1993). Furthermore, Dalla Vecchia (2001) hypothesised: i) a possible connection of the peri-Adriatic carbonate platforms with Africa during the Hauterivian-Barremian based on a sauropod fauna showing Gondwanan affinities; ii) a period of isolation during the Albian-Cenomanian, and iii) a possible connection with the southern Asiatic margin of Eurasia during the early Senonian, indicated by the presence of late Santonian hadrosaurs.

Bosellini (2002) presented the first broad revision of the palaeotectonic and palaeogeographic scenario of the eastern Mediterranean area based on the growing evidence of dinosaur footprints from Italy; he integrated the ichnological evidence with geophysical and geological data on the Ionian Sea and the surrounding areas. According to Bosellini (2002), the evidence of large dinosaurs living on the Apulia carbonate platform represents an important constraint on the palaeotectonic and palaeogeographic history of the eastern Mediterranean area. In particular the Apulia Platform, formerly interpreted as an isolated carbonate bank at the southern margin of the Mesozoic Tethys ocean (generated by an Early Jurassic rifting; Eberli et al., 1993), according to Bosellini (2002) should be considered as a carbonate peninsula similar to present-day Florida and Yucatan, connected to the Cyrenaica spur of Africa during the Jurassic and Early Cretaceous. In this setting, the Apulia Platform may have subdivided the eastern Mediterranean region into a western Ionian basin and an eastern Levantine basin (Bosellini, 2002). As already pointed out by Nicosia et al. (1999b), Bosellini (2002) highlighted the problem of the limited area and thus the limited resources of water and food for a stable population of dinosaurs on the emergent carbonate platform environments. Based on the hierarchical organization of cycles in the platform carbonate sediments (20-100-400 ka periodicities of the Earth's orbital perturbations), the Mesozoic carbonate platforms of southern Italy should have been periodically exposed to subaerial conditions (for a duration of several thousands of years), thus generating large emergent areas that allowed dinosaurs to migrate (Bosellini, 2002). In light of this evidence, Bosellini (2002) maintained that dinosaurs from the peri-Adriatic carbonate platforms were not endemic to that region, but that the ichnological record suggests repeated migrations from a southern landmass, most likely corresponding to North Africa. Thus Bosellini (2002) denied the presence of oceanic crust in the Ionian abyssal plain and, following former interpretations (Panza, 1987; Hirsch et al., 1995; Ismail-Zadeh et al., 1998), considered the Ionian basin as "*a stretched, attenuated continental crust area*" (p. 230), generated by a Jurassic extensional phase related to the opening of the Ligurian Ocean (Western Tethys). According to this interpretation, Adria is considered again as a true African Promontory, following Channell (1976) and Channell et al. (1979).

Dalla Vecchia (2003) re-analysed biological and palaeocological implications of the presence of huge plant-eating dinosaurs on oceanic carbonate platforms. By using regression equations provided by Burness et al. (2001), which relate body mass of the biggest herbivores against landmass size, Dalla Vecchia (2003) found that the area of the emergent platform must have been much larger than reconstructed on the basis of geological evidence. According to Dalla Vecchia (2003), this result can be explained by assuming lower fodder consumption rates for the Italian sauropods than expected for modern endotherms of comparable size; alternatively, the Adriatic-Dinaric Platform may have possessed a bigger emergent area. Based on the paleogeographic reconstructions by Dercourt et al. (1993, 2000), who consider the subaerial portions of the peri-Adriatic carbonate platforms in post-Barremian times as islands, Dalla Vecchia and Tarlao (2000) and Dalla Vecchia (2001, 2002, 2003, 2008) interpreted the dinosaurs living on the oceanic carbonate platforms in the post-Barremian as insular dwarfs.

Subsequently the implications and crucial importance as paleogeographic constraints of the numerous dinosaur tracksites from latest Jurassic and Early, mid and Late Cretaceous carbonate platform deposits of the peri-Adriatic region for the geodynamic history of the Mediterranean area were discussed by several authors (e.g., Petti, 2006; Nicosia et al., 2007; Petti et al., 2008b; Sacchi et al., 2009; Zarcone et al., 2010). Traditionally, the Laziale-Abruzzese-Campana carbonate platform (i.e., ACP) was considered in palaeogeographic models for the late Mesozoic as a quite small island within the western Neotethys Ocean (Stampfli and Borel, 2004). In general, classic palaeogeographic reconstructions interpret the peri-Adriatic region as a series of small, isolated carbonate platforms separated from the mainland by seaways represented by the Lagonegro trough and the Umbro-Marchean and the Ionian basin, generated essentially by the Early Jurassic phase of rifting in the western Tethys. Therefore, the peri-Adriatic carbonate platforms, along with smaller ones recognised in wells, were considered in previous paleogeographic interpretations as a sort of 'string of pearls' between the Gondwana and Laurasia mainlands (Nicosia et al., 2007). This general framework provided the basis for interpretation of some peculiar aspects of the fauna, defined as endemic dwarf or significantly smaller (Benton et al., 1997; Jianu and Weishampel, 1999; Dalla Vecchia et al., 2000; Dalla Vecchia, 2002, 2008), relict (Signore et al., 2001; Evans et al., 2004), endemic (Grigorescu et al., 1999) and depauperate (Benton et al., 1997). These biological properties, according to Nicosia et al. (2007), somehow seemed to confirm the arrangement of isolated platforms proposed in the accepted geodynamic setting.

In contrast, the tracksite from Sezze (Latina, central Italy) provided further evidence that the Laziale-Abruzzese-Campana and the Apulian-Dinaric domains were never completely separated by deep seaways and, as evidenced by dinosaur footprints (and other vertebrate and plant data), that a persistent and almost continuous link existed between them, and also with the southern and northern mainlands (Nicosia et al., 2007). The footprints from Sezze indeed indicate several kinds of both carnivorous and herbivorous dinosaurs, highlighting a quite structured and diverse dinosaur assemblage inhabiting the shores of the Cretaceous Tethys. A more complex issue, as highlighted by previous works, is the actual amount of landmass area for food supply, freshwater availability, and possible nesting sites in persistently emergent areas. According to Nicosia et al. (2007), the most parsimonious explanation to account for dinosaur survivors on the emergent platforms is to hypothesize a connection between small platform areas, thus increasing the total surface and possible sources of water and food, and also allowing inter-plate dispersal of dinosaurs. In fact, as stressed by Nicosia et al. (2007), a possible link between the ACP, the Apulian and the Dinarid-Gavrovo platforms could lead to a total emergent area of about 1000×600 km, quite close to the size of present-day Madagascar. This hypothesis was corroborated by the Aptian dinosaur tracks from Esperia (Petti et al., 2008b), the first evidence of Aptian dinosaurs in the ACP. The Esperia dinosaur assemblage has a similar composition to the coeval Bisceglie ichnoassemblage from the Apulian Carbonate Platform domain. Altogether, this evidence consistently suggests a geographical connection between the Apenninic and the Apulian platforms during the Aptian, as also indicated by geological and geophysical data (Fig. 13).

On the basis of all this evidence, including plant and body fossils as well as footprints, Petti (2006), Nicosia et al. (2007) and Zarcone et al. (2010) proposed the following chronological sequence for interpreting the palaeogeography of the peri-Adriatic region: i) an African connection among LAC, Apulian and Trieste areas from the Berriasian to Aptian to explain the theropod association of Sannicandro, S. Giovanni Rotondo and Pietraroia and the theropod-sauropod association characterizing the Istrian peninsula; ii) a pre-Cenomanian connection of LAC, Dinaric and Istrian domains with Africa and with each other, allowing the immigration of sauropod dinosaurs into the region; iii) an uplift and consequent diffuse emersion of large areas of the peri-Adriatic platforms during the Turonian and Coniacian; iv) a hadrosaur migration in pre-Santonian times from north or northeast to Istria and Apulia in order to explain the presence of this dinosaur clade in those areas; v) a connection in the pre-Campanian of Istria to southern Europe in order to allow the northward passage of hadrosaurs and titanosaurs. Based on this new model, a connection between Gondwana and the peri-Adriatic platforms is inferred at least from Late Jurassic to the Cenomanian, and a connection with the southern margin of Laurasia at least from the Coniacian to the Maastrichtian.

Romano and Citton (2016) discussed the paleobiogeographic significance of the proposed struthiomimid trackmaker inferred from the elongated footprints from Porto Canale-Riomartino (Latina, Central Italy). These footprints can be ascribed to a second association of the dinosaur track record of Italy (late Tithonian – late Cenomanian) proposed in the review by Citton et al. (2015). Within this framework, a dinosaur provenance from the north during the late Tithonian-late Cenomanian time interval can be ruled out by the presence of the large Vardar oceanic area (Channel and Kozur, 1997); similarly, a migration from the west and from the east is excluded based respectively on the presence of the deep Umbro-Marchean basin, and of the Ionian trough (Aubouin, 1959), the latter separating the Italian carbonate platforms from the Dinaric area. It follows that in mid-Cretaceous times dinosaurs could reach the ACP only by a migration path from Gondwana across Adria (Sacchi et al., 2009; Zarcone et al., 2010). In the light of this evidence, Romano and Citton (2016)

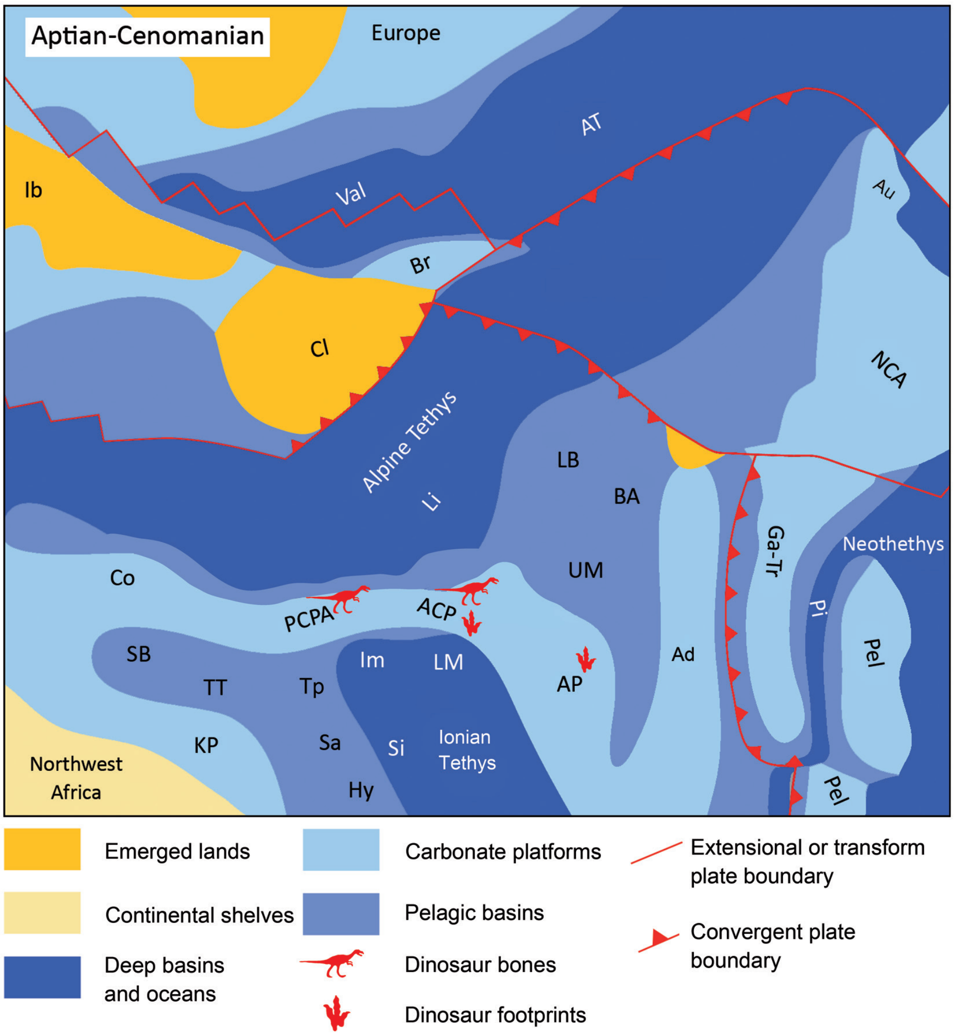

Fig. 13 - Palaeogeographic map of the Central Mediterranean area during the Aptian–Cenomanian interval, from Zarcone et al. (2010). Ad=Adriatic–Dinaric Carbonate Platform; ACP=Apenninic Carbonate Platform; AP=Apulian Platform; AT=Alpine Tethys Ocean; Au=Australpine; BA=Bagnolo Carbonate Platform; Br=Briançonnais; Cl=Calabria; Co=Constantine Platform; Ga-Tr=Gavrovo-Tripoliza; Hy=Hyblean Platform; Ib=Iberia; Im=Imerese Basin; KP=Kasserine Platform; LB=Lombard Basin; Li=Ligure-Piemontese Ocean; LM=Lagonegro-Molise Basin; NCA=Northern Calcareous Alps; PCPA=Panormide Carbonate Platform; Pel=Pelagonian; Pi=Pindos; Sa=Saccense Pelagic Plateau; SB=Sellaoua Basin; Si=Sicanian Basin; Tp=Trapanese Pelagic Plateau; TT=Tellian Trough; U-M=Umbria-Marche Basin; Val=Valais Ocean.

hypothesized that the footprints from Porto Canale-Riomartino suggest the unexpected occurrence in Gondwana of an ornithomimosaur, a clade known at the time essentially from Central Asia, North America, and Spain (Makovicky et al., 2004), except for the remains of *Nqwebasaurus thwazi* from South Africa (Kirkwood Formation, Lower Cretaceous), considered by Choiniere et al. (2012) as the basalmost known ornithomimosaur.

7. CONCLUDING REMARKS

Since the first discovery in the early 1990s, the Cretaceous dinosaur track record of Italy has continuously grown and, to date, more than ten tracksites and a plethora of footprints have been described. The record spans the late Hauterivian-early Barremian to the early Campanian, and presents a rich ichnological diversity, in turn reflecting a high diversity of the dinosaur trackmakers who dwelt on the emergent parts of the carbonate platforms of the Mediterranean area. Footprints are recorded from different carbonate platform facies that were generally affected by tidal cyclicity, characterizing inner carbonate platform environments, associated with subaerial exposure events, especially during the Aptian-Cenomanian time interval. A most intriguing contribution of the Cretaceous dinosaur track record from the peri-Adriatic region, intimately linked to the autochthony of tetrapod footprints, has been to challenge the interpretation of the Mediterranean area as a compound of small, isolated carbonate platforms. Over the years, the record has stimulated numerous questions leading to new palaeogeographical interpretations with the potential of greatly changing geodynamic reconstructions of the peri-Adriatic area during the later Mesozoic.

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