A THEROPOD DOMINATED ICHNOCOENOSIS FROM LATE HAUTERIVIAN-EARLY BARREMIAN OF BORGO CELANO (GARGANO PROMONTORY, APULIA, SOUTHERN ITALY)

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Abstract. Several dinosaur footprints were discovered on three different levels cropping out in the CO.L.MAR quarry, south of the village of Borgo Celano in the Gargano Promontory (Apulia, southern Italy). The track-bearing levels belong to a carbonate inner platform succession referred to the Lower Cretaceous (upper Hauterivian-lower Barremian). This paper describes only the lowest dinoturbated bed, where footprints are preserved as natural cast. Forty footprints, mostly tridactyl, have been attributed to medium-sized theropods. Tridactyl tracks are similar to Kayentapus Welles, 1971 regarding ichnotaxonomy. Round shaped footprints, previously not described from this site, are found in association with tridactyl footprints and are related to ornitischian dinosaurs.

Riassunto. Numerose impronte di dinosauri sono state scoperte su tre distinti livelli nella cava CO.L.MAR., a sud di Borgo Celano nel Promontorio del Gargano (Puglia, Italia meridionale). I livelli ad impronte appartengono ad una successione carbonatica di piattaforma interna ascrivibile al Cretacico inferiore (Hauteriviano superiore-Barremiano inferiore). Nel presente lavoro è stato analizzato solamente il più antico dei tre livelli, in cui le orme sono preservate come controimpronte. Le orme studiate sono quaranta, prevalentemente bipedi e tridattile, attribuibili a teropodi di medie dimensioni. Queste ultime, da un punto di vista icnotassonomico, sono riferibili all'icnogenere Kayentapus Welles, 1971. Oltre alle impronte tridattile sono state rinvenute orme arrotondate, non descritte in precedenza, riferibili ad ornitischi.

Introduction

In Italy discoveries of dinosaur tracks have increased greatly in the last decade, especially in the Apu-

lia region (Andreassi et al. 1999; Dalla Vecchia 2000; Nicosia et al. 2000a, b, 2007; Gianolla et al. 2000a, b, 2001; Conti et al. 2005; Sacchi et al. 2006).

A research team of the University of Ferrara (A. Bosellini, P. Gianolla e M. Morsilli) discovered in June 2000 several dinosaur footprints in the CO.L.MAR quarry (41° 40′ 52″ N; 15° 39′ 23″ E), south of the village of Borgo Celano (Gargano Promontory, Apulia, southern Italy), allowing a first description of the material.

Footprints were found at three different stratigraphic levels in a carbonate sequence attributed to the Lower Cretaceous. A detailed ichnological analysis of the footprints started only two years ago owing to the delay caused by mining activity. Most of the footprints are tridactyl, somewhere arranged in trackways: some blocks also yielded round tracks in association with the tridactyls.

The aim of this paper is to describe all the recognized tracks, supplying comparisons with existing ichnotaxa. Trackmaker identification is based on well preserved anatomic features observed on some specimens. Palaebiogeographical significance of the Borgo Celano tracks, in the broader context of Italian dinosaur footprints, has been discussed in other papers (Bosellini 2002; Conti et al. 2003; Petti 2006; Sacchi et al. 2006; Nicosia et al. 2007).

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Geologic setting

The Gargano Promontory mainly consists of a thick carbonate succession ranging from Upper Jurassic to Eocene (Bosellini et al. 1993, 1999, 2000; Morsilli & Bosellini 1997; Morsilli 1998; Bosellini & Morsilli 2001), with minor scattered outcrops of Miocene and Pliocene (Fig. 1). The Borgo Celano ichnosite is located in the western sector of the Gargano Promontory, which is part of the Apulian foreland in the frame-work of the Southern Apennine orogenic system. The Gargano Promontory is a moderate to strong deformed area forming a broad gentle anticline oriented WNW-ESE. This general structure is intersected by several tectonic lineaments, including normal, reverse and strike-slip faults (Funiciello et al. 1992; Bertotti et al. 1999; Brankman & Aydin 2004; Borre et al. 2003; Tondi et al. 2005; Milano et al. 2005). The Gargano Promontory belongs to the Apulian Carbonate Platform (ACP), one of the main paleogeographic domains of the Tethys southern margin (D'Argenio 1976). The ACP is bounded to the east by pelagic deposits of the Ionian Basin, and to the north by the Umbria-Marche-Sabina basin and westward by basinal deposits of the Lagonegro-Molise domain (Zappaterra 1990, 1994).

As a whole the Gargano Promontory represented a complex platform-basin system during the Late Jurassic-Eocene interval, with various depositional environments and sub-environments (Luperto Sinni & Masse 1986, 1987; Bosellini et al. 1993, 1999; Bosellini & Morsilli 2001; Borgomano 2000; Morsilli et al. 2004) (Fig. 1).

The Jurassic-Cretaceous succession, mainly made by shallow-water deposits, reaches a thickness of 3000-3500 m, according to well data (Ricchetti et al. 1992; Bosellini et al. 1993).

Many geologic events have been recognized in the history of this platform. These events are responsible of the whole architecture of the platform, and have been used to distinguish large scale stratigraphic sequences (Bosellini et al. 1993, 1999; Morsilli & Bosellini 1997).

During the Valanginian and early Aptian the carbonate factory was shut down by two distinct platform drowning events (Bosellini & Morsilli 1997; Bosellini et al. 1999; Graziano 1999). At the end of the Albian a major change occurred along the whole ACP margin; huge megabreccia bodies onlap and cover the previous margin. Bosellini and co-workers (1993, 1999, 2000) suggest large-scale margin collapse and subsequent infill of the huge scar by slope to base-of-slope deposits. During the Turonian a widespread emersion phase interested the ACP platform facies (Crescenti & Vighi 1964; Mindszenty et al. 1995). After this event shallow-water deposition started again in the ACP, although Upper Cretaceous platform facies called "Altamura Limestone" crops out scantily in the Gargano Promontory (Laviano & Marino 1996; Luperto Sinni 1996). On the contrary this stratigraphic unit is widespread in the Murge area where thousand of dinosaur footprints have been discovered (Andreassi et al. 1999; Nicosia et al. 2000a, b).

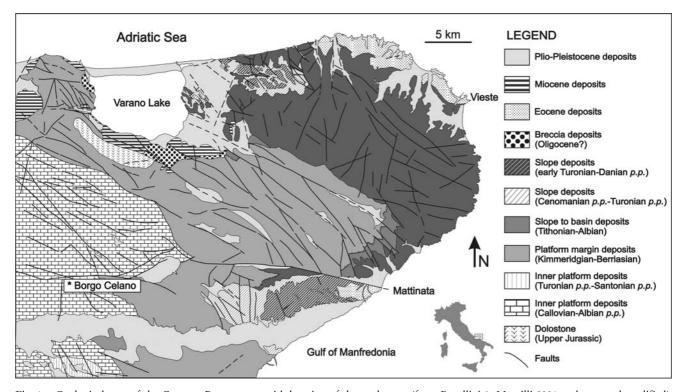


Fig. 1 - Geological map of the Gargano Promontory with location of the study area (from Bosellini & Morsilli 2001, redrawn and modified).

Sedimentology and stratigraphy

The trampled layers discovered in the CO.L.-MAR quarry belong to a carbonate succession representing an inner platform environment referred to the "S. Giovanni Rotondo formation" (Cremonini et al. 1971), also named as "Calcaires de S. Giovanni Rotondo" (Luperto Sinni & Masse 1986), "formazione dei Calcari di San Giovanni Rotondo" (Luperto Sinni 1996) and "S. Giovanni Rotondo Limestone" (Claps et al. 1996).

The succession exposed in the quarry (Fig. 2) (thickness 60 m) is part of a larger sequence (thickness 550 m) considered as the type-section of the formation (Luperto Sinni & Masse 1986; Claps et al. 1996), that crops out along the Borgo Celano-Foggia route (from km 1.5 to km 6.5). The sedimentologic and biostratigraphic characters of the "S. Giovanni Rotondo formation" have been thoroughly and repeatedly studied by different authors who defined its main stratigraphic-depositional elements (Luperto Sinni & Masse 1986; Masse & Luperto Sinni 1989; Luperto Sinni 1996; Claps et al. 1996). The "S. Giovanni Rotondo Limestone" has been subdivided by Claps et al. (1996) into three members, namely "Member 1", "Member 2" and "Member 3", partially corresponding to the ones formerly erected by Luperto Sinni & Masse (1986) ("Borgo Celano Member", "Loferitic Member" and "Requienidae Member"). "Member 1" is characterized by bioturbated wackestone to packstone, with peloids, bioclasts and oncoids of lagoon environment. "Member 2" shows a clear peritidal cyclicity, with high frequency cycles made of meter-scale shallowing upward sequences, as evidenced by the regular alternation of green clayey levels, stromatolites, and more rarely, by subaerial exposure surfaces associated with paleokarst. "Member 3" is represented by a heterogeneous group of facies; the lower portion consists of fine laminated calcarenites, while the upper displays cyclic alternations of mudstone

and stromatolite horizons, organized in shallowing upwards cycles (Claps et al. 1996). "Member 1" can be ascribed to a subtidal environment, "Member 2" is a peritidal sequence, while "Member 3" shows facies varying from sub- to supratidal (Claps et al. 1996).

The upper part of the "S. Giovanni Rotondo formation" ("calcari di Masseria Quadrone" sensu Merla et al. 1969; "calcare di S. Giovanni Rotondo 2" sensu Bosellini et al. 1999) consists of mudstone-wackestone alternated with peloidal packstone-grainstone.

Many authors (Luperto Sinni & Masse 1986; Ciaranfi et al. 1992; Bosellini et al. 1993; Spalluto et al. 2005), on the basis of facies analogy and age, suggested the correspondence of the "S. Giovanni Rotondo formation" to the Calcare di Bari formation (Valduga 1965; Delfrati et al. 2003 *cum bibl.*) cropping out in the Murge area, that recently yielded several dinosaur footprints (Sacchi et al. 2006).

The Borgo Celano type-section, previously referred to the Upper Jurassic-Lower Cretaceous interval (Cremonini et al. 1971), and successively to the Berriasian p.p.-Lower Aptian (Luperto Sinni 1996), has been more recently attributed by Claps et al. (1996) to the Valanginian-Aptian interval, on the basis of algal and foraminiferal biostratigraphy (Campanellula capuensis De Castro, Salpingoporella dinarica Radoicic, Praeorbitolina cormyi Schroeder, P. wienandsi Schroeder, Orbitolina lotzei Schroeder).

Dinosaur footprints

The Borgo Celano ichnosite yields three distinct dinoturbated levels (Gianolla et al. 2000a, b) and belongs to the "Member 2" of "San Giovanni Rotondo Limestone" (sensu Claps et al. 1996). Only the oldest level, a greenish clay alternating with peloidal wackestone-packstone (Fig. 3), has been studied (Fig. 4). This level represents an emergent event at the top of a shal-

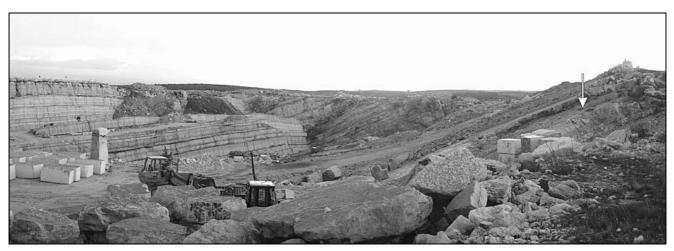


Fig. 2 - Panoramic view of the succession cropping out in the CO.L.MAR quarry. The arrow indicates the examined dinoturbated level.

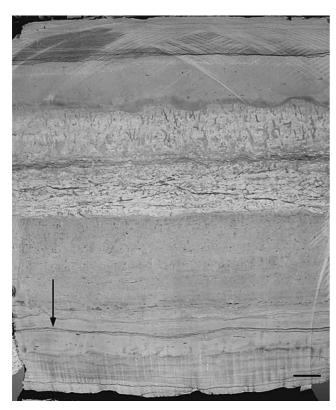


Fig. 3 - Sedimentologic features of the level containing the trampled horizon. The arrow indicates the trampled layer. The bioturbated interval lies in the mid-top of the block. Scale bar: 5 cm.

lowing upward cycle and lies over a stromatolitic interval and below strongly bioturbated limestones (Bosellini et al. 2000; Gianolla et al. 2001). The stratigraphic position of this level lies in the upper part of the "Interval B" of Claps et al. (1996), characterized by Campanellula capuensis De Castro, Vercorsella scarsellai (De Castro), Likanella? pejovici (Radoicic), Clypeina? solkani Conrad & Radoicic, Salpingoporella muehlbergii (Lorenz), S. biokovensis Sokac & Velic, Actinoporella podolica (Alth), Praturlonella danilovae (Radoicic) and Humiella teutae Sokac & Velic. As pointed out by Claps et al. (1996, p. 21), there are still some different view on the age of the Campanellula capuensis distribution, but the upper part of their "Interval B", starting from the first occurrence of Salpingoporella muehlbergii and S. biokovensis, is considered to be upper Hauterivian-lowermost Barremian.

The footprints are preserved as natural casts and undertracks on ten limestone blocks, preserved in the quarry deposit. Each block has been labelled with the acronym BC (Borgo Celano) followed by a roman numeral; footprints have been numbered sequentially. Each print was drawn on polyethylene films and analyzed *in situ*. Among 40 tracks, possible trackways have been identified, as well as other consecutive and isolated footprints. The recognized morphotypes, notwithstanding the modification related to the sub-

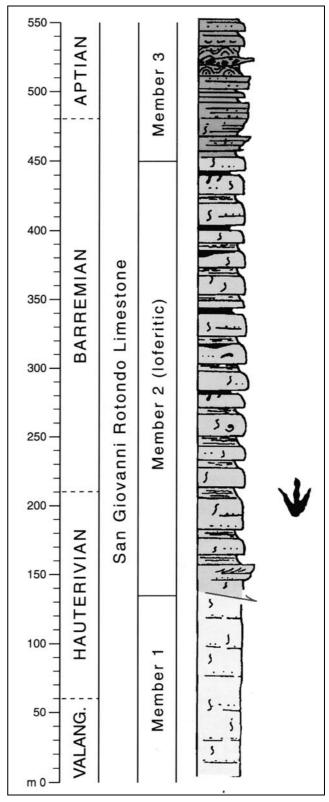


Fig. 4 - Stratigraphic log of the S. Giovanni Rotondo formation (from Bosellini & Morsilli 2001, redrawn and modified).

strate, show better anatomical features when preserved as natural cast than as undertracks. Natural casts are sometimes partially covered by clay laminae of the dinoturbated level, as well as by the underlying intervals (Fig. 5).

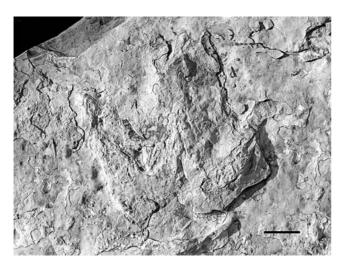


Fig. 5 - Close up of a tridactyl footprint (BC VII-4) showing the lamination of the trampled clay layer. Scale bar: 5 cm.

Footprint descriptions

The results of the ichnological analysis are reported in this section; all parameters have been measured based on the methods as defined in Leonardi (1987). Footprints are described block by block. In some cases numbering of digits was prevented owing to preservation bias. In such cases we refer to the left digit as "l" and right digit as "r" to indicate the position with respect to the digit III. Since footprints are preserved as natural casts actually digit positions are inverted. Some tracks are incomplete and not described in detail.

BC I block - The BC I block displays thirteen tridactyl footprints (Fig. 6), eight of which have been numbered and described.

BC I-1 is partially covered by older sediments. The distal portion of the footprint is well preserved, covered somewhere by greenish clay laminae. Footprint

length (FL) is about 27 cm, footprint width (FW) is 28 cm. Digit II, almost completely coated by older deposits, has a free portion of about 10 cm, claw trace included. The hypex between digit II and III is impressed. Digit III has a free portion of about 17 cm with one pad and the faint trace of the claw. Digit IV has a free portion of about 10 cm and shows two phalangeal pads and a claw mark. Total divarication (II^IV) is 65°, II^III = 26°, III^IV = 39°.

BC I-2 retains only digit III and a lateral digit (?IV). This faint footprint has a digit III length of about 19 cm with maximum width of 6 cm and shows two pads separated by a shallow groove. A hypex is visible although poorly preserved. The lateral digit (13 cm) tapers distally and has neither pads nor ungual traces.

BC I-3 is cut off proximally and shows the middle (III) and a lateral digit. This latter (11 cm long) becomes distally thicker and shows two pads and the shallow trace of a claw; digit III is partially preserved (13 cm long), has two pads and the claw trace.

In BC I-4 three isolated digit marks are preserved. Digit III length is 18 cm; digit IV, 19 cm long, displays three well defined phalangeal pads. Digit II is about 5 cm long.

BC I-5 is partially impressed with the trace of digit III and the distal portion of a lateral digit. FL is around 21 cm. The lateral digit has a phalangeal pad and a claw trace. The length of the free portion of digit III is about 12 cm.

BC I-6 preserves three digits; digit III (digit length 16 cm, digit width 5 cm) shows two clear phalangeal pads and a pointed claw. On the lateral digit (digit length 10 cm) at least one phalangeal pad and a sharp claw are impressed.

BC I-7 (Pl. I, fig. a; FL and the FW are about 24 cm) displays a well preserved digit II (16 cm long; 4 cm

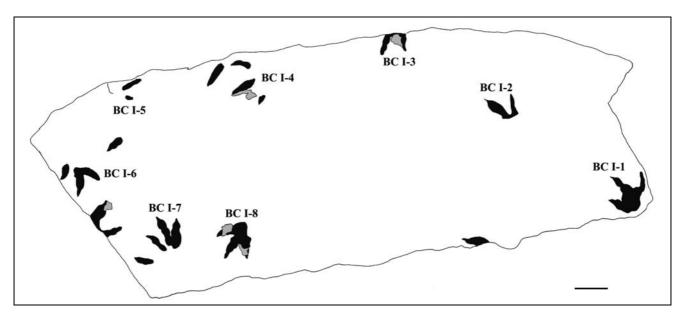


Fig. 6 - Map of BC I block. Scale bar: 20 cm.

wide), with two pads and a sharp claw mark, oriented outward. The claw is ogive-shaped. Digit III preserved three pads and a clear claw trace. It is about 20 cm long, and its maximum width is around 6 cm. The proximal and distal pad, and a claw mark parallel to the digit axis are visible on the digit IV (length 20 cm). Total divarication (II^IV) is 54°, II^III = 24°, III^IV = 30°.

BC I-8 preserves digit III with two phalangeal pads and a claw mark, heading to digit II (FL 27 cm, FW 25 cm). Lateral digits are partially covered by older sediments. The track has a V-shaped heel impression. Digit II shows the trace of the claw, outward oriented. The angles are II^IV = 74°, II^III = 38°, III^IV = 36°.

BC II block - The BC II block yielded eight tridactyl footprints (Fig. 7). Almost every footprint is covered by older sediments and, in some areas, by greenish clay laminae, actually the original trampled layer.

BC II-1 is posteriorly elongated, with a total length of 40 cm (digits length is about 28 cm) and a width of 27 cm. One lateral digit shows two pads and a claw trace in its distal part. Digit III tapers distally, showing two pads and a claw trace. Its width is about 6 cm. Total divarication (II^IV) is 83°, l^III = 38°, r^III = 45°.

In BC II-2 the metatarsal is partially impressed. Total length 36 cm (25 cm, metatarsal excluded), FW 22 cm. This footprint lacks claw marks and pads. Digits divarication (II^IV) is 73°, l^III = 32°, r^III = 41°.

BC II-3 is a posteriorly elongated tridactyl footprint. Digit impressions taper distally; the total length is about 35 cm (27 cm without metatarsal impressions) and a width of 26 cm (III^IV = 77°, l^III = 40°, r^III = 37°).

BC II-4 is a tridactyl footprint but the superimpression of the BC II-5 prevents the evaluation of linear and angular parameters.

BC II-5 is a tridactyl footprint posteriorly eroded. FL is about 26 cm, FW is 23 cm. A pad and a claw mark are preserved on a lateral digit. Total divarication (II^IV) is 63°, l^III = 27°, r^III = 36°.

BC II-6 is a badly preserved tridactyl track as long as wide (25 cm). Total divarication (II^IV) is 78°, l^III = 43°, r^III = 35°.

BC II-7 is an elongated track with the impression of metatarsal, totally covered by older sediments. Digits are more splayed if compared to the other footprints on the block. FL (with metatarsal impression) is 40 cm, without metatarsals about 23 cm. FW is 30 cm. Total divarication (II^IV) is 106°, l^III = 52°, r^III = 54°.

BC II-8 a partially preserved tridactyl footprint where digit III and a lateral digit are preserved. The trace of digit III has a maximum width of 7 cm. Estimated footprint length is 23 cm.

BC III block - The BC III block yields four rounded tracks and one tridactyl footprint (Fig. 8).

BC III-1 is a posteriorly elongated tridactyl footprint, with a total length of about 42 cm (30 cm if metatarsals are excluded). No pads are visible although a claw mark, pointing toward digit II, occurs at the end of digit III. Digit III maximum width is about 8 cm. Digits taper distally. Total divarication (II^IV) is 84°, l^III = 53°, r^III = 31°.

BC III-2 (Pl. I, fig. f) is rounded, 25 cm wide and 16 cm long, with four short and distally blunt digit marks. At least two hypices are visible. Anteriorly and posteriorly the footprint is bordered by two depressions, representing positive relieves on the original track surface and interpreted as expulsion rims. The anterior depression is crescent-shaped, the posterior one roughly half-rounded. Digits are 7 cm long and the anterior

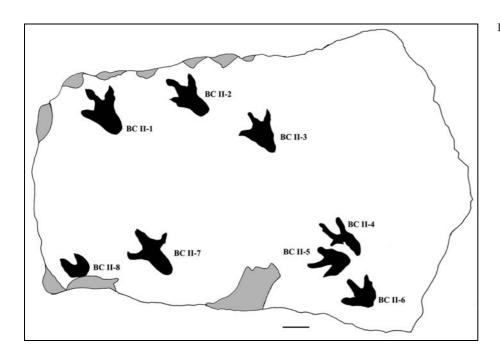


Fig. 7 - Map of BC II block. Scale bar: 20 cm.

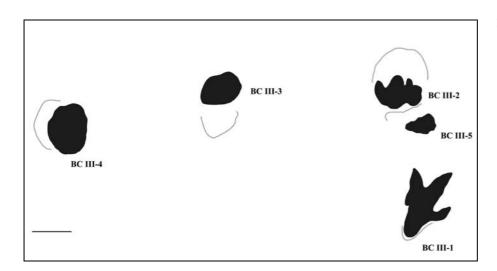


Fig. 8 - Map of BC III block. Scale bar: 20 cm.

footprint wall, between digit impressions and the expulsion rim, is steep.

BC III-3 is rounded, 16 cm long and 21 cm wide. No digits or claw marks are visible. Along one side an elongated depression has been observed, interpreted as an expulsion rim.

BC III-4 is an elliptic mark (FL 29 cm and FW 27 cm), with a crescent-like depression close to one long side.

BC III-5 is a rounded footprint where anatomical details are not recognizable.

BC IV block - The BC IV block bears only one tridactyl footprint (Pl. I, fig. c; BC IV-1) displaying the metatarsal impression which is less impressed than the digit marks. Total length 56 cm, 36 cm without metatarsal mark. FW is 36 cm. The right side of the footprint has less steep walls, and an expulsion rim borders the left side of digit III. Digits taper distally. Hypexes be-

tween digits II and III are well impressed. II^IV is 80°, II^III = 35°, III^IV = 45°.

BC V block - The BC V block reveals only one round footprint is preserved on this block (BC V-1), with a diameter of about 25 cm and an associated expulsion rim.

BC VI block - The BC VI block yielded at least four tridactyl footprints, preserved as undertracks.

BC VI-1 is a poor preserved elongated tridactyl footprint, with blunt digit-tips and without any pads or claw marks. Total length is 45 cm and the width is 32 cm. Total divarication (II^IV) is 69°, l^III = 33°, r^III = 36°.

BC VI-2 is elongated and reaches a total length of 44 cm (35 cm without metatarsal impression). Digits are faintly impressed, particularly in their proximal half.

In BC VI-3 digits are well impressed only in their distal portion. No claw marks or pads are preserved.

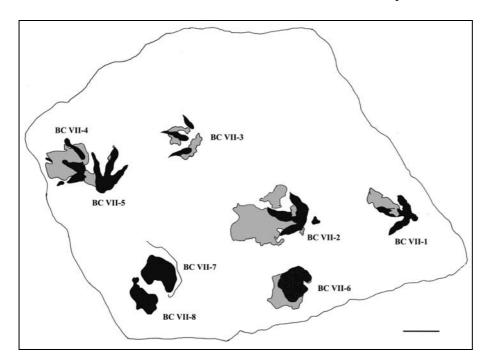


Fig. 9 - Map of BC VII block. Scale bar: 20 cm.

FW is 24 cm. Total divarication (II 1 IV) is 72 $^{\circ}$, 1^{1} III = 37 $^{\circ}$, 1^{1} III = 35 $^{\circ}$.

BC VI-4 has a FL of 35 cm and FW of 30 cm. II $^{\circ}$ IV is 60 $^{\circ}$, 1° III = 34 $^{\circ}$, 1° III = 26 $^{\circ}$.

BC VII block - The BC VII block is a slab with five tridactyl footprints associated with three round tracks (Fig. 9).

BC VII-1 is a natural cast of a tridactyl footprint which is less impressed in its proximal part (maximum length is 26 cm, width is 25 cm). Well preserved phalangeal pads are visible on all digits. Digit III is about 16 cm long. Total divarication (II^IV) is 83°, II^III = 37°, III^IV = 46°.

BC VII-2 (Pl. I, fig. b) is a tridactyl footprint which is better impressed distally (length is about 27 cm, width 26 cm). Both hypices are clearly visible although at different heights with respect to digit III. On digit III three pads and a claw trace are preserved. Maximum width of digit III is about 6 cm. Digit II displays a pad and a thin and pointed claw trace. Two pads and a claw trace are visible on digit IV. Total divarication (II^IV) is 70°, II^III = 35°, III^IV = 35°.

BC VII-3 (Pl. I, fig. e) has three digit marks separated from each other. The footprint is symmetric, digit impressions are pyriform (see also *Kayentapus* Welles, 1971) and sharp. Footprint width is 27 cm, digit III length 17 cm. On digit III three pads and a claw mark are visible. Digit II has two pads and the claw trace. No pad on digit IV, II^IV is 70°, II^III = 36°, IV^III = 34°.

BC VII-4 (Fig. 5) is a tridactyl symmetric footprint covered by older deposits, with neither pads nor claw marks. The rear half is wide, faintly impressed. Footprint is as long as wide (27 cm). Total divarication is 65°, l^III = 32°, r^III = 33°.

According to these interpretations BC VII-1, 3 and BC VII-2, 4 could represent two parallel trackways.

BC VII-5 (Pl. I, fig. d) is a tridactyl footprint with clearly impressed digits, less spread than BC VII-1-4. Hypices have different height with respect to digit III. The rear margin is feeble impressed. Digits taper distally, especially the lateral ones. Footprint length is 30 cm, width is 23 cm. All the digits show pads and claw marks. Digit III is about 20 cm long. Total divarication (II^IV) is 55°, II^III = 27°, III^IV = 28°.

BC VII-6 is a round footprint 22 cm wide and 18 cm long. One long side shows three or four lobes, interpreted as digit impressions. The rear margin shows a deep hollow.

BC VII-7 displays a less well preserved kidney-shaped track with four digit marks.

BC VII-8 has a widened outline with no morphological details and lies in front of the BC VII-7.

BC VIII block - The BC VIII block shows two tridactyl and one irregular round footprint.

BC VIII-1 is a poorly preserved tridactyl footprint as long as wide.

In BC VIII-2 only two digits are visible. A round footprint also occurs with irregular outline close to a depression along one side (BC VIII-3).

BC IX block - The BC IX block shows two tridactyl footprints (BC IX-1, 26 cm long and 24 cm wide).

BC IX-2 is a tridactyl footprint with a feebly impressed digit; footprint length is 32 cm, footprint width is 30 cm.

BC X block - The BC X block yielded two tridactyl and one sub-elliptic footprints.

BC X-1 is a poorly preserved natural cast of a tridactyl footprint, 34 cm long and about 35 cm wide. BC X-2 is also tridactyl (29 cm long and 24 wide), while BC X-3 is rounded, with the impression of three short and blunt digits. This track is truncated along one side and bordered by an expulsion rim.

Discussion

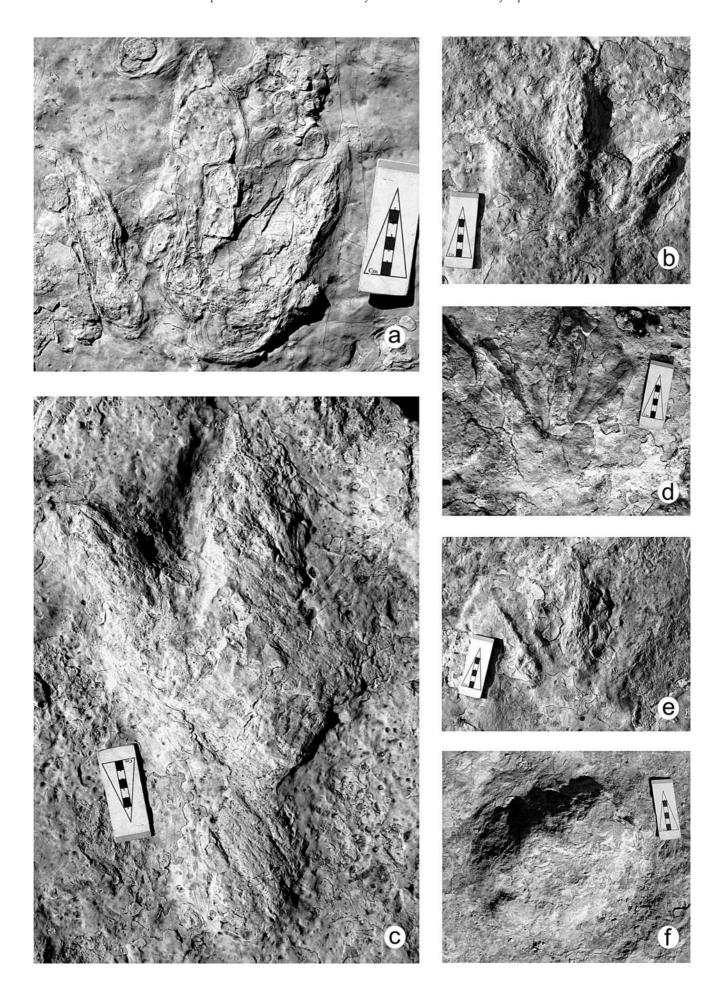
All the tridactyl footprints are digitigrade and mesaxonic. Foot length varies from a minimum of 23 cm to a maximum of 35 cm up to 56 cm when elongated by the metatarsal traces; the width varies from 23 cm to 36 cm (Tab. 1).

It is worth noting that the maximum values pertain to undertracks, which are therefore augmented in size with respect to the dimension of the actual footprints. The FW/FL ratio, including the elongation, varies from 0.61 to 0.75; without the metatarsal trace it varies from 0.77 to 1.30. Total divarication of the tridactyl footprints varies from 54° to 107° with an average of about 74°. Divarication II^III ranges from 26° to 39°, III^IV between 28° and 46° (Tab. 1).

No clear trace of digit I was observed. Claw marks are usually sharp. Digit II is slightly shorter than digit IV. Digit IV recognition was based on the presence of a notch in the rear margin of the footprint. The position of the hypex III^IV is sometime pulled slightly back compared to the hypex II^III. Digit III protrudes beyond the line connecting the tips of digits II and IV, no more than half of its total length. The free portion of digit III (e.g. BC I-7), is about 3/4 of its total length. Several footprints show large pads and their number can be generalised as follow: 2 pads on digit II, 3 pads on digit III, and 3 pads on digit IV. The heel of the footprint is V-shaped. In eight specimens (BC II-1, BC II-2,

PLATE 1

Photographs of tridactyl footprints from Borgo Celano. a) BC I-7; b) BC VII-2; c) BC IV-1; d) BC VII-5; e) BC VII-3; f) BC III-2. Scale bar: 5 cm.



	Foot	Foot				
	Lenght	Width	FW/FL	II^IV	l^III	r^III
	(FL)	(FW)				
BC I-1	27	28	1.04	65°	26°	39
BC I-7	24	24	1.00	54°	24°	30°
BC I-8	27	25	0.92	74°	38°	36°
BC II-1	28/40 [†]	27	0.96/0.67 [†]	83°	38°	45°
BC II-2	25/36 [†]	22	0.88/0.61 [†]	73°	32°	41°
BC II-3	27/35 [†]	26	0.96/0.74 [†]	77°	40°	37°
BC II-4	27/34 [†]	-				
BC II-5	26	23	0.88	63°	27°	36°
BC II-6	25	25	1.00	78°	43°	35°
BC II-7	23/40 [†]	30	1.30/0.75 [†]	106°	52°	54°
BC II-8	23					
BC III-1	30/42 [†]	30	1.00/0.71 [†]	84°	53°	31°
BC III-2*	16	25	1.56			
BC III-3*	16	21	1.31			
BC III-4*	20	27	1.35			
BC IV-1	36/56 [†]	36	1.00/0.64 [†]	80°	35°	45°
BC VI-1	36/45 [†]	32	0.88/0.71 [†]	69°	33°	36°
BC VI-2	44					
BC VI-3		24		72	37	35
BC VI-4	35	30	0.86	60°	34°	26°
BC VII-1	26	25	0.96	83°	46°	37°
BC VII-2	27	26	0.96	70°	35°	35°
BC VII-3		27		70°	36°	34°
BC VII-4	27	27	1	65°	32°	33°
BC VII-5	30	23	0.77	55°	28°	27°
BC VII-6*	18	22	1.22			
BC VIII-1	25	25	1	68°	42°	26°
BC VIII-2	24					
BC IX-1	26	24	0.92			
BC IX-2	32	30	0.94			
BC X-1	34	35	1.02	104°	79°	25°
BC X-II	29	24	0.83	72°	34°	38°

Tab. 1 - Morphometric parameters of the Borgo Celano footprints. l) left digit; r) right digit. (*) non-tridactyl footprints (†) elongated footprints.

BC II-3, BC II-4, BC II-7, BC III-1, BC VI-1, BC VI-2) tridactyl footprints are elongated or have the entire metatarsal shaft touching the ground. This pattern is related to a plantigrade or crouching posture with metatarsal held at low angle or even in contact with the ground (Lockley et al. 2003). This posture widens the surface of the foot when in contact with the substrate providing a better stability on muddy and wet surfaces (Kuban 1989). Therefore the observed variability (occurrence of the heel and metatarsal impressions) is interpreted as the response to the different consistency of the substrate. This hypothesis could be validated by the concentration of elongated tracks on some blocks (e.g. BC II).

Round footprints (Pl. I, fig. f), although less wellpreserved than tridactyl ones, share features that allow us to include them under a single morphotype. These features are the latero-medial elongation of the footprint, the occurrence of a hollow along one side (BC III-2, BC VII-6 and BC VII-7) and lobes on the opposite one. Lobes are interpreted as digit marks, varying in number from three to four and are blunt, in some places joined to each other by well defined hypices. Average dimensions are 16 cm (FL) and 25 cm (FW).

Remarks

Our systematic analysis only deals with well preserved tridactyl tracks. BC I-7 has been adopted as the paradigm. Among the Cretaceous ichnogenera, Megalosauripus (sensu Lockley et al. 2000) is in some ways similar to the Borgo Celano tridactyl footprint morphotype. This ichnogenus is characterized by a larger anterior protrusion of digit III and larger posterior withdrawal of the proximal part of digit IV in comparison with the BC footprints (cfr. Lockley et al. 2000, fig. 8); moreover Megalosauripus is usually bigger. A better match was found with the Early Jurassic ichnogenus Kayentapus Welles, 1971 (see Lockley 2000, fig. 7), mainly for the relative digit length, protrusion of digit III, and total divarication. However the Kayentapuslike (sensu Lockley 2000) imprints have slender digits compared to the Italian material. Only BC VII-3 has digits slender enough to compare with Kayentapus. Otherwise, the BC material and Kayentapus shares the pattern of digit IV, but in general the outline of the former is more symmetric. Eubrontes Hitchcock, 1845 shows a higher protrusion of digit III and thicker digits with respect to the BC material. In Eubrontes digit II is closer to digit III and the base of digit IV is pulled posteriorly back to a higher degree. Grallator Hitchcock, 1858 and Anchisauripus Lull, 1904, which has digit III more anteriorly extended compared to Eubrontes, does not compare well with the BC tridactyl footprints. Ornithomimipus angustus Sternberg, 1926 and O. (Irenichnites) gracilis (Sternberg, 1932), has a metatarsal-phalangeal pad joining digits III and IV, leaving digit II slightly separated. This is also true for BC I-7, that otherwise differs from O. angustus for a lower protrusion of digit III and from O. gracilis for the strongly tapering digits. Irenesauripus mclearni Sternberg, 1932 has a general shaped resembling BC specimens, even if it has larger dimensions (FL = 38 cm, FW = 32 cm) and a larger protrusion of digit III.

On the basis of the FW/FL ratio, the position of digit IV, the claw morphology and the digit impression width, Borgo Celano material is comparable with some footprints from Ploce (late Albian, south-western Istria, Croatia; Dalla Vecchia et al. 2002). A good matching was found with footprints PLOII T2-1, PLOII T2-2, 23.5 cm long, with a FW/FL ratio of 0.75 and II^IV of 54° (Dalla Vecchia et al. 2002). The digit IV is sigmoidal as in BC I-7 and BC I-8. The posterior half of digit IV is similar to BC I-7 and BC I-8; however Ploce footprints

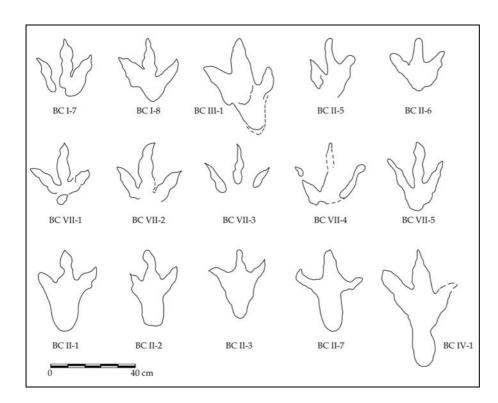


Fig. 10 - Interpretative drawing of the different morphotypes observed in the Borgo Celano ichnosite. The variability is linked to different water contents of the trampled substrates.

show a digit III usually more anteriorly projected than in Borgo Celano tridactyl tracks. These latter show a good match of relative digit dimensions, total dimensions of the footprints, as well as digit IV position, with footprints from ?Late Jurassic-?Early Cretaceous of Brazil (Leonardi 1994, fig. 3-3a). Tridactyl footprints from the ichnosite of Solaris (late Albian, Istria, Croatia; Dalla Vecchia & Tarlao 2000) have FW/FL values varying from 0.41 to 0.93, with 81.3% of the sample varying between 0.50 and 0.70. Although the Istrian tracks share some similarities with the Italian footprints (digit IV position and claw morphology), they differ in relative digit length and the larger protrusion of digit III for the Croatian ichnites.

As a whole the Borgo Celano footprints most closely resemble the material defined by Lockley (2000, fig. 7), as *Kayentapus*-like.

Attribution to trackmaker

The variability of the Borgo Celano footprints is evidently related to the different water content of the sediment. Furthermore undertracks and natural casts increased the morphological variability (Romano et al. 2004; Manning 2004). The metatarsal shaft was impressed where the sediment was muddier and more plastic; otherwise the metatarsal is not impressed and a larger number of morphological features are visible where the animal walked on firmer sediment. All the tridactyl footprints from Borgo Celano seems to belong to the same trackmaker type (Fig. 10). The observed morphologic features, namely sharp claws, three digits, relative digit dimensions (III>II; III>IV), and a

clear notch behind digit IV, is typical for theropod dinosaurs.

The attribution of theropod footprints at low taxonomic rank is usually considered a difficult task owing to the uniformity of the pes skeleton. However the length of metatarsals in the BC material (as long as digit III or slightly smaller), allows a further discrimination of the possible trackmaker.

The absence of the first digit impression in the "squatting" tracks of Borgo Celano could be linked to preservational patterns and not to the real absence of the digit (Milán 2006). On the other hand, the observed morphology (digit I not impressed) may not be assumed to be a preservational feature. Both hypotheses are tested below.

Troodontidae (sensu Makovicky & Norell 2004) and Dromeosauridae (sensu Norell & Makovicky 2004) are characterized by an extremely specialized digit II, with trenchant ungual related to a shortened metatarsal II in comparison to metatarsal III and IV. These features does not fit with the reconstructed pes morphology, the above groups can therefore be excluded from possible trackmakers. Therezinosauroidea (sensu Clark et al. 2004) shows a well developed digit I and all fingers have strong and narrow unguals. This latter feature and relative length of digits exclude inferring that Therizinosauroidea fit the Borgo Celano footprints. The exclusion of the two above mentioned groups is therefore justified.

Considering the absence of the first digit as a real anatomical feature, Tyrannosauroidea (sensu Holtz 2004), basal Tetanurae (sensu Holtz et al. 2004), Cerato-

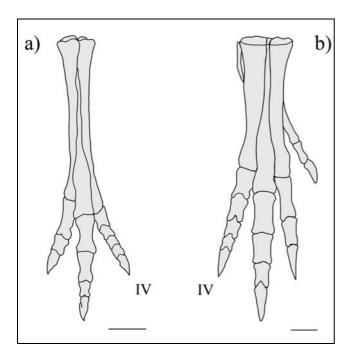


Fig. 11 - Pes skeletons of *Struthiomimus althus* (Ornithomimosauria)
(a) and *Albertosaurus* sp. (Tyrannosauroidea) (b). From Osborn 1917 (a) and Lambe 1917 (b) redrawn and modified. Scale bar: 5 cm.

sauria (sensu Tykoski & Rowe 2004) and Oviraptosauria (sensu Osmólska et al. 2004) can be excluded because they all show the presence of digit I. This is also true for Avialae (sensu Padian 2004) characterized by a retroversed hallux; the position of digit I, close to the distal end of metatarsal, the strongly curved claws as well as more spread fingers suggest the exclusion of this group.

Among Ornithomimosauria (sensu Makovicky et al. 2004) Garudimimus Barsbold, 1981 and Harpymimus Barsbold & Perle, 1984 retain a hallux and therefore can be excluded. The absence of digit I, the MT/FL ratio and the digit relative length of the pes of Ornithomimidae fits the tridactyl footprints from Borgo Celano quite well (Fig. 11a).

On the other hand, considering the absence of digit I impression as a preservational bias, many of the taxa excluded above could be considered as possible trackmakers (Fig. 11b).

The size of the BC material (FL from 24 to 35 cm, metatarsal impression excluded) indicates the largest observed Cretaceous Italian dinosaur footprints recorded to date. This value is comparable or even larger than the Cretaceous record of Adriatic-Dinaric Carbonate Platform (FL mean from 19 to 32 cm; Dalla Vecchia 2000) and also comparable to the mean value recorded from the Valanginian-Hauterivian of Spain (La

Rioja, Casanovas Cladellas et al. 1993) albeit this latter reaches higher maximum values (around 44 cm).

The above described morphological features of BC non-tridactyl footprints (i.e. three to four blunt, short and spread digit impressions, and an indentation in the rear margin) also allow some hypothesis concerning their origin. McCrea et al. (2001) reported many prints similar to the studied specimens. This kind of footprint is attributed to ankylosaurs on the basis of their congruence with the skeletal data. However, the above authors stated how difficult it is to discern between ankylosaurian and ceratopsian footprints when the material is not well preserved (McCrea et al. 2001, p. 414), as for the Borgo Celano footprints. For this reason the non-tridactyl Apulian footprints could be attributed to either ankylosaurs or ceratopsians. Nevertheless, the former group is more suitable on the basis of its stratigraphical distribution (McCrea et al. 2001 p. 419).

Conclusions

The Borgo Celano ichnocoenosis indicates to a diversified dinosaur fauna in the Apulian Carbonate Platform during the Early Cretaceous. In addition this is the first well documented report of the co-occurrence of theropod and ornitischian tracks in the Mesozoic of Central and Southern Italy. The theropod footprints display different morphotypes even if ichnological analysis reveals that all tridactyl tracks could be attributed to the same trackmaker type. Most of the footprints belong to theropods of intermediate size. The recognized morphotypes are comparable to Kayentapus, mainly for their relative digit length, protrusion of digit III and total divarication. The non-tridactyl footprints are considered of ornitischian origin. The preservation of these type of footprints prevent finer attribution between ceratopsians and ankylosaurs; nevertheless, the latter is preferred based on the stratigraphic distribution of the group.

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