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A new purported ankylosaur trackway in the Lower Cretaceous (lower Aptian) shallow-marine carbonate deposits of Puglia, southern Italy

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A B S T R A C T

The Apulian marine carbonate Platform, an unusual environment for terrestrial animals, has revealed a diverse ichnological record, especially for dinosaurs. Members of most higher taxa are present, including sauropods, theropods, ankylosaurs and ornithopods. Recently, a small outcrop of Aptian age referred to the Calcare di Bari near Bisceglie (Bari) has yielded a new quadrupedal trackway that we attribute to Ankylosauria. This new find enhances the record of Cretaceous ankylosaur footprints from the Apulian carbonate Platform, previously known from another site near Bisceglie (early Aptian), from Borgo Celano (late Hauterivian–early Barremian), and from Altamura (late Coniacian–early Santonian).

1. Introduction

In addition to the Bisceglie track site reported here dinosaur track sites are well documented in the Lower Cretaceous of the Murge area and the Gargano Promontory in Puglia (Petti et al., 2008; Sacchi et al., 2009). Five Cretaceous dinosaur track sites have been discovered so far on the Apulian carbonate Platform (Nicosia et al., 2000a,b; Conti et al., 2005; Petti et al., 2008, 2009; Sacchi et al., 2009), most of which are associated with the Lower Cretaceous deposits of the Calcare di Bari Fm. A diverse ichnocoenosis is recorded here: it includes sauropods, theropods, ornithopods and ankylosaurs.

Even if the Gargano Promontory footprints (Borgo Celano ichnosite; Petti et al., 2008) are ascribed to the late Hauterivian–early Barremian deposits of the San Giovanni Rotondo Fm, as recent stratigraphic studies suggest (Spalluto and Pieri, 2008), the latter formation is considered a synonym of the Calcare di Bari Formation, and the type area and type locality of the latter are on the Murge Plateau. The occurrence of dinosaur footprints on the Apulian carbonate Platform has lead us to re-examine the sedimentary evolution of this domain; in turn, this has provided important palaeontological constraints on how Cretaceous Western Tethyan palaeogeography can be interpreted (Sacchi et al., 2009).

This paper focuses on a new quadrupedal trackway produced by an ankylosaur, discovered at a site near Bisceglie (Bari, southern Italy) (Fig. 1). Footprints inferred to have been produced by ankylosaurs have previously been reported from the Lower Cretaceous carbonate deposits of the Gargano Promontory (Petti et al., 2008) and from a quarry near the town of Bisceglie (Sacchi et al., 2009), while isolated Upper Cretaceous ankylosaur tracks are known from Altamura (Dal Sasso, 2003; Petti, 2006) (see Fig. 2).

This study deals with a moderately well-preserved ankylosaur trackway from the Puglia region, made up of a sequence of nine consecutive manus–pes sets.

2. Stratigraphical and sedimentological setting

The Murge Plateau and the Gargano Promontory represent the Apulian foreland of the Apenninic orogenic system, developed since the Neogene as a consequence of the high subsidence rates related to the eastward rollback of the hinge of the west-dipping Apenninic subduction (Ricchetti et al., 1992; Doglioni et al., 1996). The Calcare di Bari Fm crops out extensively in the Murge area trending northwest–southeast, from Andria to the north down to Fasano to the south (Ciaranfi et al., 1992). It forms a thick pile of sediments (at least 2000 m) deposited on the Apulian carbonate Platform during the ?Callovian–Coniacian (for a review of the unit see also Delfrati et al., 2003 and Spalluto and Pieri, 2008). The unit has been analyzed in detail for stratigraphical purposes, and different informal lithostratigraphic subdivisions have been

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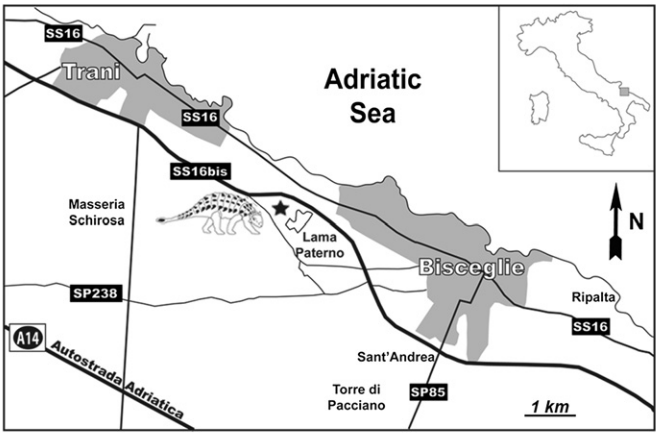

Fig. 1. Locality map showing the new dinosaur trackway near the town of Bisceglie. The star indicates the exact position of the outcrop.

proposed (Valduga, 1965; Ricchetti, 1969; Campobasso et al., 1972; Luperto Sinni and Masse, 1982, 1984, 1986, 1993; Luperto Sinni and Borgomano, 1989; Ciaranfi et al., 1992; Spalluto and Pieri, 2008).

The new ichnosite is located close to the town of Bisceglie (Bari, southern Italy), about 1 km northwest of the Lama Paterno quarry, where Sacchi et al. (2009) discovered and described an early Aptian dinosaur ichnocoenosis. The track-bearing layer crops out between Via Crosta and the SS16 BIS national highway (Fig. 1; GPS coord. Lat. 41,2522 N; Long. 16,4500 E), on an NNE dipping (about 10°) surface ascribed to the middle portion of the Calcare di Bari Fm (Luperto Sinni and Masse, 1993). The track-bearing level is 76 cm thick exposed over no more than 20 m^2. From the base to the top we recognized a basal portion characterized by a mudstone–wackestone with miliolids passing upward to a bioclastic wackestone with bivalve shell fragments, topped by a grainstone with fenestral fabrics. This coarsening-upward succession indicates a shallowing-upward cycle as confirmed by tracks occurrence.

Micropaleontological analysis revealed the occurrence of *Hensonella dinarica* (Radoičić, 1959), *Praechrysalidina infracretacea* Luperto Sinni 1979 and *Debarina hahounerensis* Fourcade et al., 1972, an assemblage referable to the *Salpingoporella dinarica* Zone (*sensu* Chiocchini et al., 2008) that constrains the age of the track-bearing bed to the early Aptian. The lithofacies and the micropaleontological assemblage clearly indicate an inner carbonate platform-back edge palaeoenvironment.

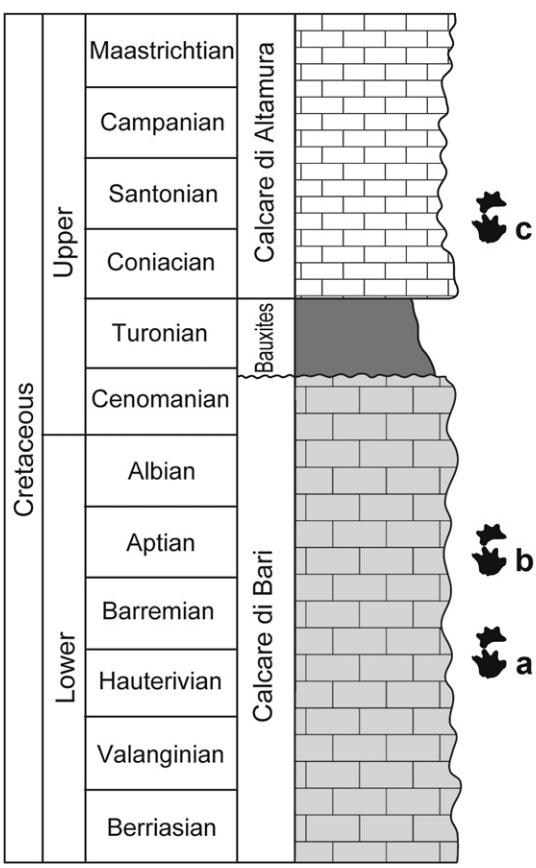

Fig. 2. Stratigraphic distribution of purported ankylosaur tracks in the Cretaceous platform deposits of Murge and Gargano Promontory (Puglia, southern Italy). (a) Borgo Celano; (b) Bisceglie; (c) Altamura. After Dal Sasso (2003), Petti et al. (2008) and Sacchi et al. (2009).

3. Material and methods

The material was photographed and traced on transparent acetate overlays but no molding of the surface has been performed. Unexpectedly, the trackway, found in a test quarry area, is no longer exposed, since a thick cover of filling material buried the site. In this paper we adopted the prefix BiC (Bisceglie, Via Crosta) to describe the trackway and single manus–pes couples.

The trackway is 5.40 m long and on average 60 cm wide (Fig. 3). It consists of nine manus–pes couples with a regular heteropody index (about 1/2). Pes pace angulation varies slightly from 115° to 131°, but a range of manus pace angulations between 131° and 147°. Manus–pes distance ranges from 6 to 16 cm. The trackway is straight and narrow gauge for all its length, and represent a true tracking surface, as testified by displacement bulges surrounding several tracks (Fig. 4).

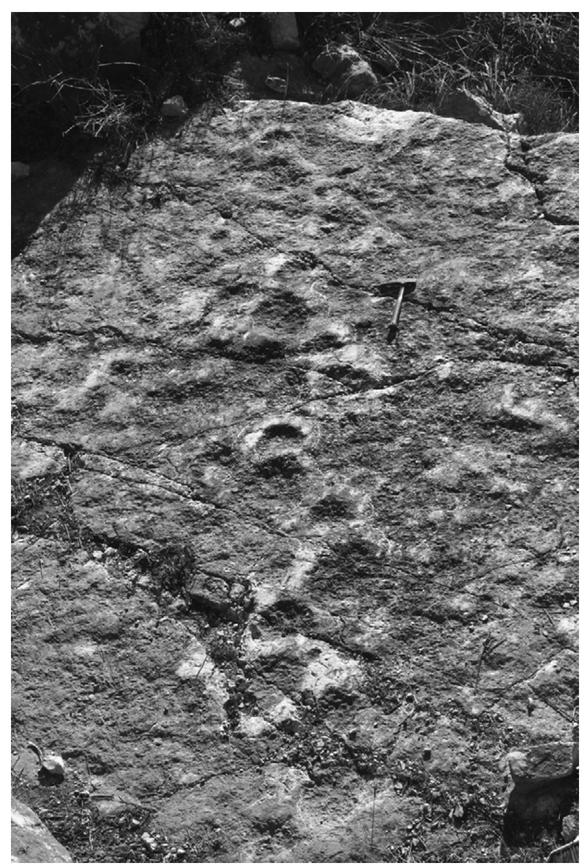

Fig. 3. Photograph of the BiC ankylosaur trackway. Hammer (33 cm) for scale.

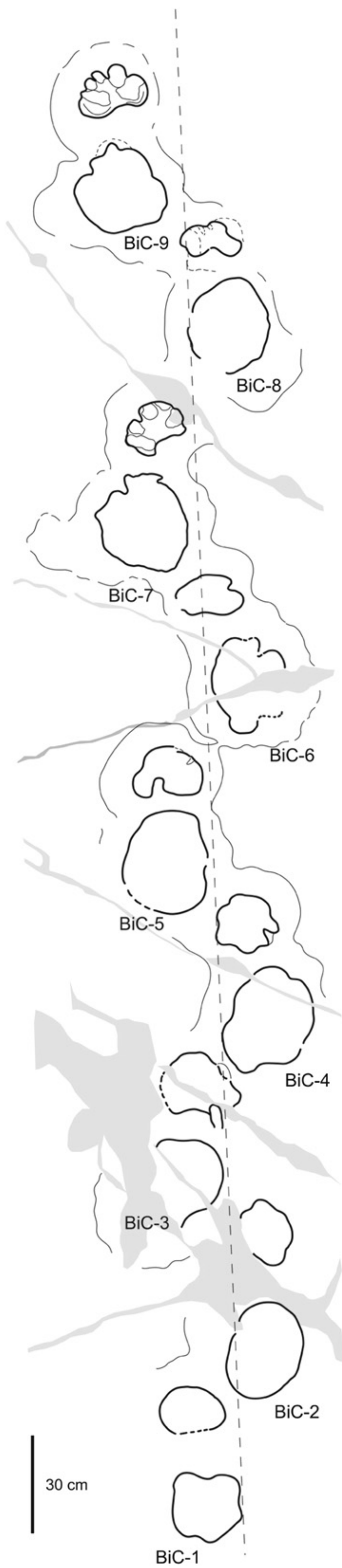

Fig. 4. Tracing of the BiC trackway sequence. Rock fractures are marked in pale grey.

The pedal imprints are roughly longer than wide. They are on average about 30 cm long while width varies from a minimum of 23 cm to a maximum of 29 cm. Pedal prints are oriented in the direction of travel, nonetheless in BiC-4, BiC-6, BiC-7 and BiC-9 the pes morphology tapers proximally, close to the midline, suggesting a low outward rotation of the pes with respect to the midline (25°–39°). The trampled coarse-grained sediments affected the actual morphology of pedal prints, hiding the fine anatomy of the trackmaker's pes. The recent subaerial exposure and consequent weathering effects have contributed to worsen preservation. However in BiC-7 and BiC-9 three to four short and rounded lobes occur distally, here interpreted as digit traces.

Manus impressions always lie close to the midline, sometimes crossing it (BiC-3 and BiC-6). Manus prints are always wider than long and are smaller than pes traces. Manus morphology varies from sub-circular to crescentic with a concave indentation in the middle of the rear margin, as evidenced in BiC-5, BiC-8 and BiC-9. In BiC-8 and particularly in BiC-9 there are five rounded digit impressions. The inferred manus digit prints are arranged as follows: digits I and V are rounded and are similar in size while digits II–IV are short and stubby. Manual prints are more shallowly impressed posteriorly. The actual dimensions of the manus are easier to define in BiC-8, and the shallow area behind digits I and V in BiC-9 (Fig. 5) could be interpreted as the effect of faint sliding traces. The axes of digits II, III, and IV point slightly outward.

Pace and stride length and other morphometrical parameters are reported in Table 1.

The distance between the shoulder joint and the hip joint (GAD = gleno-acetabular distance), measured following the methodology of Leonardi (1987) is 85 cm, with an estimated body

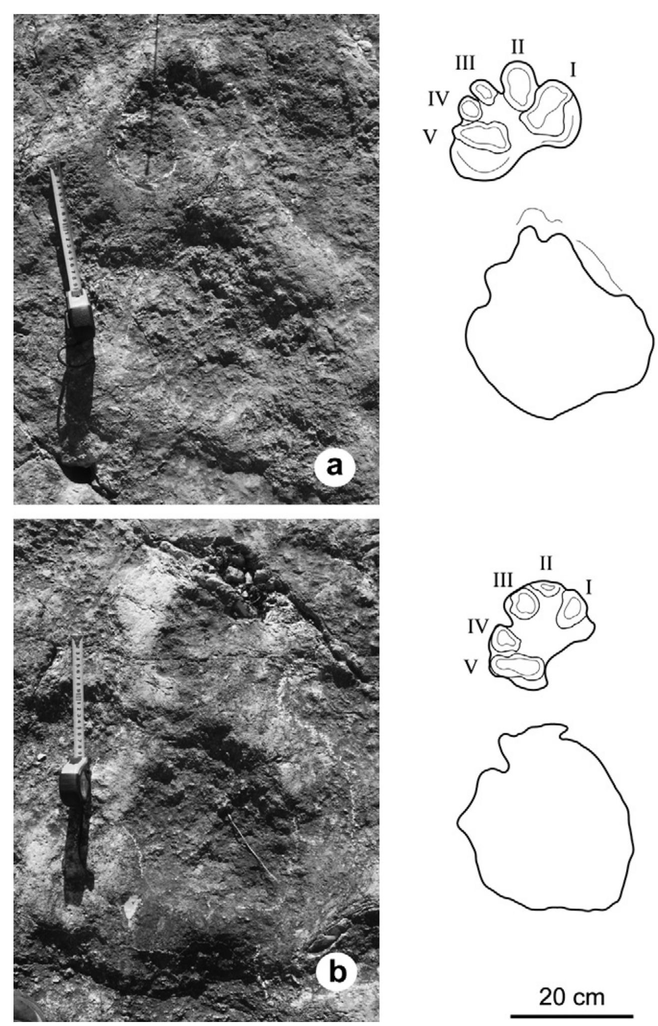

Fig. 5. Photographs and interpretive drawings of the best-preserved manus–pes sets (a: BiC-7 and b: BiC-9).

Table 1
Trackway parameters and their relationship; including pes length (PL), pes width (PW), pes length–pes width ratio (PL/PW), manus length (ML), manus width (MW), manus length–manus width ratio (ML/MW), manus–pes distance (M–P), pes pace (PP), pes stride (PS), manus pace (MP), manus stride (MS), pes pace angulation (PPA), manus pace angulation (MPA). All the measurements are expressed in cm and degrees.

Track	PL	PW	PL/PW	ML	MW	ML/MW	M–P	PP	PS	MP	MS	PPA	MPA
BiC-1	24	23	1.04	15	21	0.71	16	51	101	60	100	131°	132°
BiC-2	30	24	1.25	20	16	1.25	11	61	101	50	95	121°	138°
BiC-3	27	23	1.17	18	27	0.67	10	55	97	51	98	115°	136°
BiC-4	36	29	1.24	20	21	0.95	7	60	105	55	102	120°	139°
BiC-5	33	29	1.14	17	22	0.77	5	61	104	60	105	121°	147°
BiC-6	31	25	1.24	15	22	0.68	7	55	110	57	110	122°	145°
BiC-7	31	27	1.15	17	18	0.94	5	63	104	60	104	118°	131°
BiC-8	30	26	1.15	12	19	0.63	7	56		55			
BiC-9	29	28	1.03	18	22	0.81	12						

length of about 2.4 m. The gauge is narrow, and the trackmaker was a quadruped with a hip height of about 120 cm (Alexander, 1976). It seems to have been walking at an average speed of 3.10 km/h (following the equation in Thulborn, 1990).

4. Discussion

Fossil footprints preserved in the Apulian platform deposits are often poor in fine anatomical detail (Nicosia et al., 2000a, b; Conti et al., 2005; Petti et al., 2008; Sacchi et al., 2009) and the BiC material is also suboptimal. With the BiC trackway it is possible to identify a potential trackmaker to a high taxonomic rank. However, the preservation prevents ichnotaxonomic assignment of the specimen.

The trackmaker identification process is here based on the comparison of soft part traces with body fossil morphology. The tracks are complete enough to preserve important features of the autopodia.

Quadrupedalism was widely adopted by Cretaceous dinosaurs and – except for theropods and small ornithopods – all other groups shared this gait.

The forelimb traces of Cretaceous ornithopods are quite homogeneous and are usually no more than one-third the dimension of the foot (Thulborn, 1990). This ratio is smaller than BiC manual/pedal print ratios and therefore the group is excluded from potential trackmakers. Moreover the tridactyl pes is unlikely to have left a rounded print as found in the BiC trackway.

Quadrupedalism was obligatory for sauropods, and their fore- and hind-limbs have been extensively investigated as have their tracks (see Lockley et al., 1994; Wilson and Carrano, 1999). Remarkably, this group reached the largest dimensions ever seen in terrestrial animals: footprints which are larger than 1 m in length are exclusively referred to Sauropoda (Thulborn et al., 1994; Lockley et al., 2007). On the other hand smaller or dwarf forms (Sander et al., 2006) could have left footprints similar in gross shape and dimensions to the BiC tracks. Nevertheless features evident in the BiC trackway are inconsistent with known sauropod ichnogenera. Although the gauge could be attributed to a sauropod, the heteropody index and the pace angulation do not match with purported narrow-gauge sauropod trackways (*Parabrontopodus* isp., Lockley et al., 1994). Moreover, the BiC manual prints are always significantly different from the sauropod manual ichnites (Dutuit and Ouazzou, 1980; Farlow et al., 1989; Lockley et al., 1994, 2002; Santos et al., 2009) and particularly from those found in the Lower Cretaceous deposits of northern Italy (Dalla Vecchia, 1999) and Croatia (Dalla Vecchia and Tarlao, 2000). Sauropod manual prints are often wider than long but they display remarkably different characters such as the position and morphology of digit traces. All evidence, including ichnites and body fossils (Lockley et al., 1994; Apesteguía, 2005) shows that the manus of Cretaceous sauropods was embedded in a single pad, with no free digits, although in some cases a huge claw trace of digit I stands out as a remarkable feature (Santos et al., 2009). No evidence of this structure has been found in the Apulian trackway. Furthermore during the Aptian sauropods were essentially represented by macronarians (e.g. brachiosaurs and titanosaurs; Wilson and Sereno, 1998), showing little dimensional differences between the fore- and hind-limbs (Apesteguía, 2005). These differences are apparently reflected in tracks and trackways (Lockley et al., 1994) and macronarians seem to be more consistent with the large-manus and wide-gauge *Brontopodus*-like tracks common in the Lower Cretaceous deposits, and reported also from the Upper Cretaceous (Farlow, 1992; Lockley et al., 1994, 2002; Wilson and Carrano, 1999). Additionally, basal titanosauriform macronarians display lengthened metacarpals and extremely reduced phalanges, while in titanosaurs the long metacarpals were arranged vertically with the complete loss of all phalanges (Apesteguía, 2005). Consequently, manual digit traces should be absent in the latter group and the occurrence of digit marks in the best preserved manual prints of Bisceglie (BiC-8 and BiC-9) would seem to exclude titanosaurs as potential trackmakers.

Members of Marginocephalia and Thyreophora show comparatively homogeneous patterns in manual shape and arrangement. Five digits, with short and blunt claws and shortened phalanges, are common to stegosaurs, ceratopsians and ankylosaurs (Vickarous et al., 2004; Galton and Upchurch, 2004; Hailu and Dodson, 2004; Dodson et al., 2004). In contrast, pes morphology differs slightly among these groups.

Ceratopsians (basal Ceratopsia and Ceratopsidae) display a tetradactyl pes with four functional metatarsals (I–IV) (Hailu and Dodson, 2004; Dodson et al., 2004). Ceratopsians and their purported tracks are worth comparing to the Apulian material. The only purported ceratopsian ichnospecies, *Ceratopsipes goldenensis* Lockley and Hunt, 1995a, from the Maastrichtian of Colorado (Lockley and Hunt, 1995a), has a wider trackway gauge and its manus prints are clearly placed outward in relation to the position of the pes prints of the BiC trackway. The pes is also different from *C. goldenensis*, being as wide as long. Furthermore ceratopsian skeletal remains are mainly confined to the Upper Cretaceous deposits of United States and Canada, even if non-horned Asian ceratopsians were found in slightly earlier Cretaceous deposits (Dodson et al., 2004). To date no record of ceratopsians is known from northern Africa and only very recently few European ceratopsians - with Asian affinities - have been discovered (Ősi et al., 2010). Additionally some early representatives of ceratopsians, such as *Psittacosaurus*, were probably obligate bipeds (Hailu and Dodson, 2004; Senter, 2007).

Stegosaurs had essentially tridactyl pedes (Galton and Upchurch, 2004), even if some exceptions are recorded in Late Jurassic specimens (*Tuojiangosaurus*; Dong et al., 1977) which show four digits in the pes. Tracks probably attributed to stegosaurs were identified in various Middle-Upper Jurassic outcrops of England, Spain, Portugal and North America (Whyte et al., 2007; Lires et al., 2002; García-Ramos et al., 2008; Lockley et al., 2008; Mateus and Milàn, 2008, 2010; Milàn and Chiappe, 2009). Footprints named as *Deltapodus brodricki* Whyte and Romano 1994 seem to show the best fit for stegosaur pes anatomy (Whyte and Romano, 2001). This ichnospecies is characterized by crescent-shaped manus impression (wider than long), and by a triangular to subtriangular tridactyl pes (Whyte and Romano, 1994). It is therefore unlikely that the tracks described here can be attributed to stegosaurian dinosaurs.

Ankylosaur pedes are variable, being either pentadactyl (*Sauropelta*), tetradactyl (*Talarurus*) or tridactyl (*Euoplocephalus*) (Vickarous et al., 2004). The manus is usually pentadactyl slightly smaller than the pes and its stubby digits are arranged in a semicircular or radiating pattern (Thulborn, 1990). Late Cretaceous ankylosaur trackways show several similarities with our new finding, such as the heteropody, the gauge, and the overall dimensions. Potential ankylosaur tracks and trackways are known from more than a dozen of localities in Europe, North America, South America and Asia (Sternberg, 1932; Zakharov, 1964; Haubold, 1971; Lockley and Hunt, 1995b; Gangloff, 1998; Lockley et al., 1999, 2006; Lockley and Meyer, 2000; McCrea and Currie, 1998; McCrea and Sarjeant, 1999; McCrea, 2000; Meyer et al., 2001; Petti, 2006; Stanford et al., 2007; Petti et al., 2008; McCrea and Buckley, 2008; Sacchi et al., 2009; see also Thulborn, 1990 and McCrea et al., 2001 for a review of purported ankylosaur tracks). Probably only two out of five ichnospecies listed by McCrea et al. (2001) can be confidently attributed to ankylosaurs, namely *Tetrapodosaurus borealis* (Sternberg, 1932) from the Lower Cretaceous of Canada and *Metatetrapous valdensis* Haubold 1971 from the Lower Cretaceous of Germany. *Macropodosaurus gravis* Zakharov, 1964 from the Lower Cretaceous of Central Asia, considered by some authors (McCrea et al., 2001), as an ankylosaur track was recently reinterpreted as a probable therizinosaur ichnite (Sennikov, 2006; Gierliński, 2009; Gierliński and Lockley, in review).

The Bisceglie trackway displays a step angle comparable with the value found in the ankylosaurian footprints of the Gething Formation (Grand Cache, Alberta, lower Albian; Sternberg, 1932) that is generally under 120°. In *T. borealis,* manual prints are about two thirds the length of the pes, whereas in the BiC trackway they are about half the length of the pes prints. It should be noted that the manus and pes prints of *T. borealis* have long digit traces. However, the manus morphology displays some analogies with the Apulian material; indeed the pentadactyl manus of *T. borealis* is characterized by a "backward" projection of digits I and V with respect to the direction of travel. The best-preserved manual prints of the new trackways (Fig. 5; BiC-8 and BiC-9) show a similar pattern although the digit traces are blunter with sub-circular traces of digits I and V, that are less obviously directed laterally and medially. The poor preservation of the pedal prints does not allow thorough comparison with North American material. The gauge of the BiC trackway fits well with both *Metatetrapous valdensis* Haubold 1971 from the Lower Cretaceous of Germany (Bueckburg Formation, Berriasian) and *M. gravis* Zakharov 1964 from the Lower Cretaceous of Tadjikistan (Shirabod Suite, Albian). The first ichnospecies differs from the Apulian material in having an apparently tridactyl manus. *M. gravis* has a similar pace angulation (145°) but it lacks manual prints, due to overprinting processes according to McCrea et al. (2001). A close match was found with the ankylosaurian manus prints from the Upper Cretaceous of Northeast British Columbia (Dunvengan Formation; Cenomanian; fig. 20.24b of McCrea et al., 2001) and Altamura (Apulia; upper Coniacian–lower Santonian; Dal Sasso, 2003; fig. 10 p. 54). *Apulosauripus federicianus* (Nicosia et al., 2000b), originally attributed to a medium-sized hadrosaurid, has been reinterpreted by Gierliński et al. (2005) as ankylosaurian in origin. Although some ankylosaurs may have tridactyl hands (possibly *Panoplosaurus*) while others may have tridactyl feet (*Euoplocephalus*) the combination of both characters has yet to be reported, thus excluding ankylosaurs from possible trackmakers.

The morphometric parameters measured in the BiC trackway (heteropody index and pace angulation) revealed also some affinities with the BLP4 and BLP6 quadruped trackways found in the Lama Paterno quarry (Bisceglie), and attributed respectively to an undetermined ornitischian and to a medium-sized ankylosaur (Sacchi et al., 2009). The hypothesis of ankylosaur as the most suitable trackmaker is somewhat corroborated by the manus position in the BiC trackway, often internal to the pes position and/or crossing the midline. Indeed, functional and morphological analyses of fore- and hind-limbs have demonstrated that ankylosaurs held the humerus posteroventrally oblique with respect to the long axis of the body while the femur was erect (Maryanska, 1977; Coombs, 1978a,b, 1979). Ankylosaurs have a global distribution, their fossils occurring in Europe, Australia, South America, Antarctica, North America and Asia. This new find endorses their presence on the Apulian platform during the Early Cretaceous.

5. Concluding remarks

The new discovery of a dinosaur trackway in the Aptian levels of the Calcare di Bari emphasizes the importance of this formation in attempts to reconstruct the abundance and diversity of Early Cretaceous dinosaurs in the Apulian carbonate Platform. It also highlights the high density of ankylosaur tracks in southern Italy. The track-bearing level belongs to a platform sequence typical of an inner carbonate platform-back edge palaeoenvironment and was subjected to reiterated subaerial exposure. Footprint morphologies and trackway parameters suggest that the trackway can be referred to a thyreophoran, most probably an ankylosaur. This inference is consistent with the known ichnological and body fossil records. This is the fourth discovery of thyreophoran tracks in the Cretaceous of Apulia, and compels palaeontologists to understand the dispersal pattern of this globally distributed dinosaur group.

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