

Dinosaur Tracks as Paleogeographic Constraints: New Scenarios for the Cretaceous Geography of the Periadriatic Region

**Umberto Nicosia, Fabio Massimo Petti, Gianluca Perugini,
Simone D’Orazi Porchetti, Eva Sacchi, Maria Alessandra Conti, and
Nino Mariotti**

Dipartimento di Scienze della Terra, Università “La Sapienza,” Roma, Italy

Annalisa Zarattini

MBBAACC—Soprintendenza per i Beni Archeologici del Lazio, Roma, Italy

A really unexpected finding of sauropod and theropod footprints in southern Latium raises to four the number of the trampled levels recognized in central and southern Italy. After the recent findings in Latest Jurassic and Early, mid and Late Cretaceous carbonate platform deposits of the Periadriatic region, dinosaur footprints seem to provide very important paleogeographic constraints for reconstructing the geodynamic history of the Mediterranean area. The presence of a varied ichnoassociation makes acceptance of the current paleogeographic models concerning the relative and absolute position of the Laziale-Abruzzese-Campano and of Apulian-Dinaric domains during the Late Cretaceous more and more problematic. Dinosaur footprints, combined with other paleontological data, demonstrate that these areas were never completely pulled apart by deep seaways, while frequent or continuous links between them, and to southern and northern mainlands, probably persisted. These data also allowed us to improve our understanding of the timing of the Mesozoic plate motion in this segment of the Western Tethys.

Keywords: Theropod, Sauropod, Footprints, Cenomanian, Mediterranean paleogeography

INTRODUCTION

More than 200 dinosaur footprints were found on three bedding surfaces in an abandoned quarry (Cava Petrianni) near the town of Sezze (Latina, central Italy), about 70 km south of Rome, at the westernmost foot of the Lepini Mts. (Sheet 159 “Frosinone” of the Geological Map of Italy on a scale 1:100.000; Accordi et al., 1967). The footprints were found in rocks that, in the notes of the Geological Map,

Address correspondence to Umberto Nicosia, Dipartimento di Scienze della Terra, “Università la Sapienza,” Ple A. Moro, 5-00185 Roma, Italy. E-mail: umberto.nicosia@uniroma1.it

are related to an Upper Cretaceous-Lower Paleocene time interval (Fig. 1). The Mesozoic carbonate platform deposits, forming the southern portion of the Central Apennines, are subdivided into a series of at least five minor structural units overtrusting each other eastward from the Tyrrhenian Sea to the Adriatic foreland (Cipollari et al., 1999). The westernmost unit, the “Lepini-Ausoni-Aurunci Unit,” in which footprints were uncovered, is bordered on the west by the deposits of the deeper Umbro-Marchean-Sabino domain (Parotto and Praturlon, 1975).

The ichnological material mainly consists of a trackway of a large quadruped and many trackways and isolated tridactyl and tetradactyl footprints of bipedal trackmakers. The subsequent study allowed us to infer the presence of theropods and sauropods among the trackmakers. The presence of these dinosaur footprints was really unexpected because the current paleogeographic models draw the Laziale-Abruzzese-Campana carbonate platform as a relatively small island inside the western portion of the Neotethys Ocean, throughout Mesozoic time (Stampfli and Borel, 2004). The study of this outcrop was thus immediately considered extremely important for its paleogeographic inferences. Ultimately, the results of the study integrated to already known and undervalued palaeontological and paleoenvironmental data, suggest a paleogeographic hypothesis quite radically different from the previous models.

GEOLOGICAL SETTING

At the Sezze outcrop footprints are preserved on three different partially cleaned, bedding surfaces in a sequence gently dipping north-eastward (7° – 10°), and cropping out, due to old quarry work. The footprint-rich levels crop out at the base of a 250 meters thick sequence pertaining to the so-called

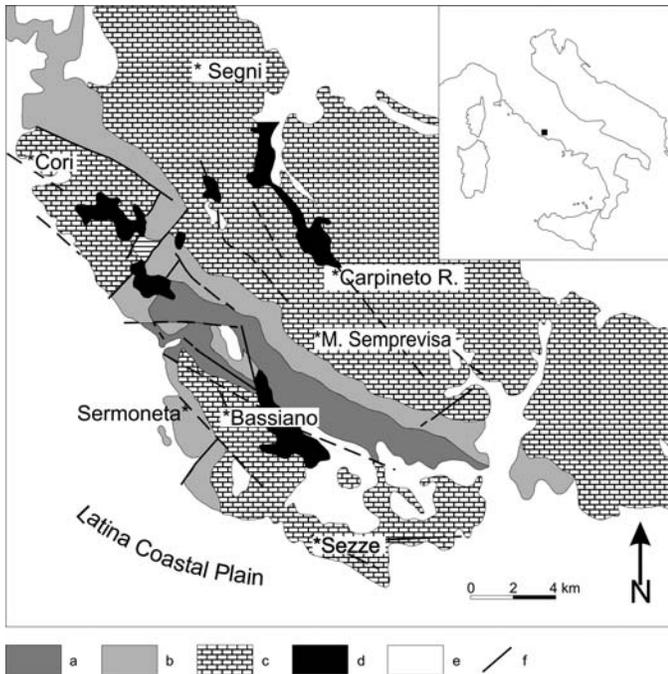


FIG. 1. Location map and geological setting of the Sezze tracksite. a) Jurassic limestones and dolostones; b) Neocomian to Cenomanian limestone and dolostones; c) Cenomanian to Danian limestones; d) Pleistocene volcanics; e) Recent deposits of the Latina coastal plain; f) fault (after Gallo et al., 1988, redrawn and simplified).

“Laziale-Abruzzese-Campano domain” (Parotto and Pratlurion, 2004) within the Apennine chain (LAC hereafter).

The Mesozoic portion of the LAC succession was deposited on a persistent carbonate platform, ranging from Late Triassic to Late Cretaceous, and shows a complete sequence of all the main types of sediments typical of that environment, varying from inner lagoonal mudstones to marginal oolitic grainstones and framestones (Accordi and Carbone, 1988). In detail, the sequence cropping out in the western portion of the Lepini Mountains (Gallo et al., 1988) better shows the peritidal deposits with a lithofacies association of inner lagoon mudstones and nearshore wackestones and packstones (Carbone, 1984). The studied outcrop consists of succession nearly 120 meters thick, slightly disturbed by many E-W trending, subvertical normal faults, with a throw from 10 to 200 cm. Due to this geological setting, which is not so favorable for footprint research, and due to the old quarry exploitation system, creating nearly vertical walls, only examination of the small basal portion of the sequence was possible.

The Petrianni Quarry Stratigraphy

The analyzed section is exposed along the Sezze Scalo-Sezze road just at the base of the Mesozoic sequence that abruptly crops out from the thick cover of Late Cenozoic sediments of the Latina coastal plain due to a marginal fault system. A careful analysis of a less than 10 meter thick portion of the sequence,

including the track-bearing levels, revealed repeated changes of the depositional environment, from subtidal to supratidal (Fig. 2). Frequent and repeated emersion events are evidenced by sedimentary structures (desiccation cracks) and footprints, intercalated into tidal flat or inner lagoon deposits.

The base of the measured section was chosen at the base of a bed, 1 m thick, made of white dolomitized wackestone with scattered centimeter-scale mud-chips and small fenestrae in its upper part. The upper surface shows a net of desiccation cracks on a 20–25 cm diameter scale. In thin section algal laminations are clearly distinguishable as well as very small serpulids and bioturbation. Above this unit a quarry road covers the section for a thickness of 55 cm.

A 90 cm thick wackestone bed follows with centimeter-scale dolomitized laminae in its upper part. It is characterized by a desiccation-cracked upper surface with polygon diameter of nearly 25 cm.

The following interval, 90–95 cm thick, is subdivided in three layers of a diagenetically formed pseudo-breccia, each nearly 20 cm thick, and a few thinner carbonate sand layers for the remaining 30 cm. Some pockets are present filled with peloids. Within the pseudo-breccias scattered white undisturbed algae are embedded in a partially silicified dark grey sandy matrix, (Fig. 3).

Higher in the section, at 345 cm from the base, the first track-bearing level crops out, consisting of a strongly dolomitized wackestone-mudstone bed of a thickness of 25 cm, in which footprints are up to 10 cm deep (Fig. 4). Footprints are filled with a wackestone whose thickness varies from 3 to 15 cm, showing submillimeter-scale microbial films, locally organized in dome-like structures ranging from a few mm up to 3–5 cm in diameter.

A white to light grey 60 cm thick bed follows, organized in two 26–28 cm thick, upward-fining sequences ranging from fine- to coarse-grained grainstones. Up section, 24 cm of tidal sediments follow with fenestrae in the lower 3 cm and in the upper 12 cm. Once again, at 5 cm from the top of the bed, tepee structures with cracks filled with a white mudstone testify to further subaerial exposure (Fig. 5). On the top surface durophagous fish teeth were found (Fig. 6).

After the interposition of 25 cm of well-sorted grainstone, a 2 m thick, locally dolomitized bed follows, including variable thickness of a breccia with centimeter- to millimeter-scale white clasts in a light grey matrix. The brecciate body shows neither clear boundaries nor internal organization. Higher up, 50 cm of tidal deposits with very small fenestrae are characterized by a 12 cm thick alternation of greenish and whitish centimeter-thick levels. The white levels represent early hardened carbonate crusts, detached from the base and showing once again incipient fractures or desiccation cracks. Fractures are filled with microbreccias and grainstone levels. At the top surface of this interval the second track-bearing level occurs (642 cm from the base); the whole surface is characterized by E-W trending fractures. Moreover the surface and the

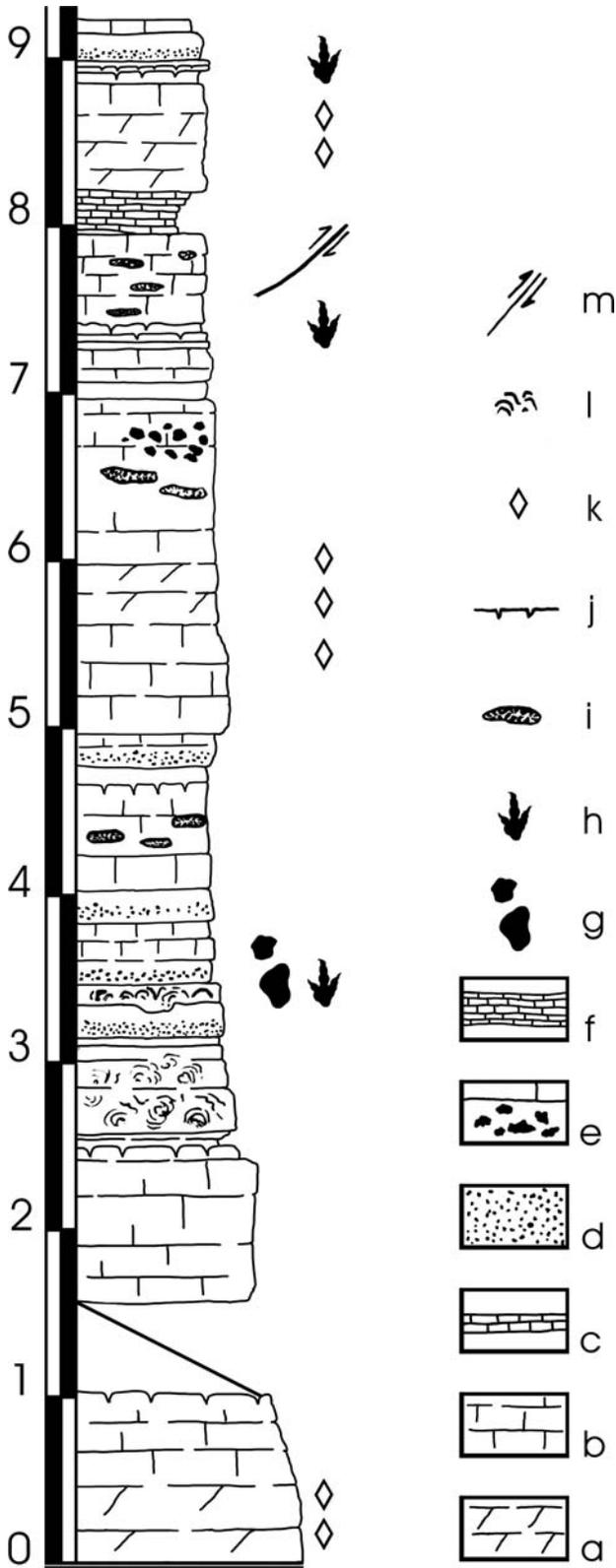


FIG. 2. Columnar section of the Petrianni quarry. a) Massive dolostone; b) thick bedded limestone; c) laminated intervals; d) fine-grained clastics; e) breccias; f) bedded marls; g) sauropod footprints; h) theropod footprints; i) fenestrae; j) mud-cracked surfaces; k) intense dolomitization phenomena; l) microbial mats; m) fault.

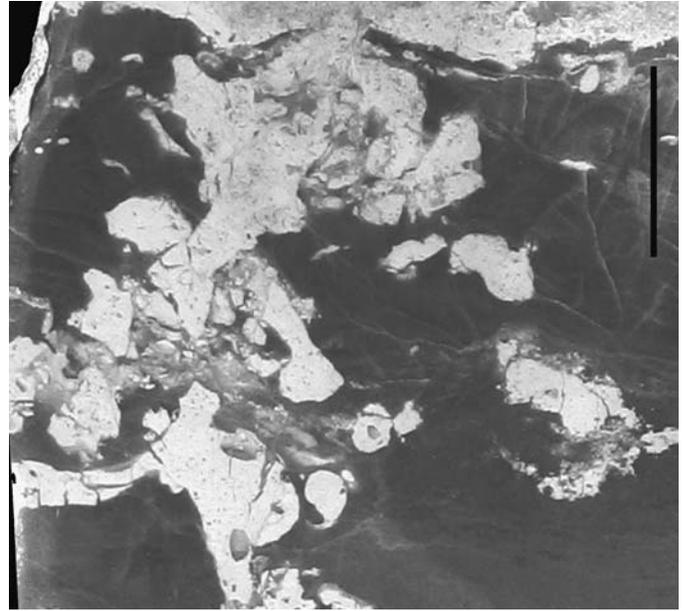


FIG. 3. Polished surface of the diagenetic pseudo-breccia. Scale bar 1 cm.

footprints are colored in greenish-grey by a very thin film of more muddy material, sometimes smeared and shiny due to interstratal movements. A small normal fault, with about 150 cm of vertical displacement, prevents direct observation of the section just above this level. Nevertheless, the section can be followed on a quarry wall, a few tens of meters away. After a thickness of nearly 156 cm, characterized by two reddish to dark brown laminated levels, the third track-bearing layer is reached (880 cm from the base). This is actually a compound level made by the surface of a 10 cm thick layer with weakly impressed footprints and desiccation cracks covered by a 2 mm thick crust



FIG. 4. Sauropod trackway (SCP I-1) on the lower track-bearing surface (SCP I). Hammer for scale (arrowed).



FIG. 5. Close-up of tepee structure at the top of a FU sequence. Scale bar 1 cm.

of fine mudstone which in turn is track-bearing and dessication cracked. On this layer the net of desiccation cracks is made up of very small polygons, rarely reaching 2 cm in diameter. Some very small and scattered invertebrate bioturbation is present as well as frequent millimeter-scale fish teeth. The two generations of desiccation cracks are thus evidence of different times of emersion that alternated with a short flooding event. Before and after that event, surfaces were trampled, dried and cracked. In the north eastern corner of the surface deeper traces and collapsed

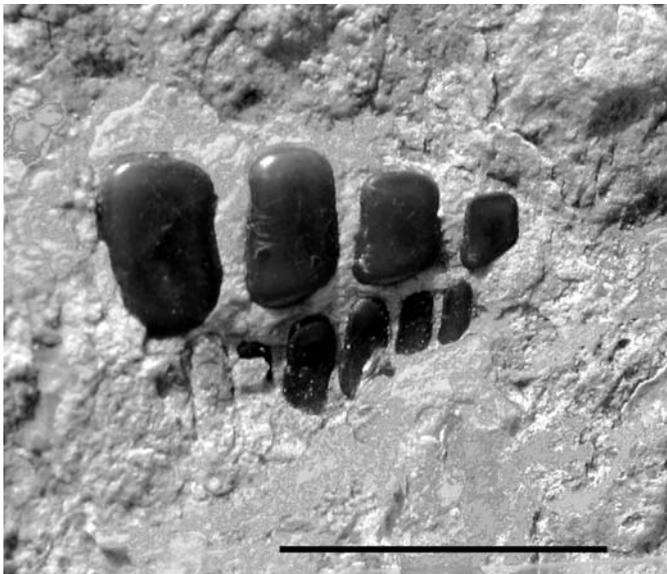


FIG. 6. A group of palatal teeth of an undetermined durofagous fish. Scale bar 1 cm.

footprints show the persistence of a wet mud area during the later desiccation phase. The rock sequence that it was possible to analyze without climbing, ends with a 25 cm thick limestone layer showing vertical granulometric variations from fine to very fine-grained grainstone.

In total, the section revealed at least eight emersion events in a short interval. Frequently rock bodies are organized in upward-fining sequences representing flooding events followed by decrease in energy and final deposition by settling out of the finest particles. The microfaunal association is composed of *Cuneolina* sp.,? *Cuneolina* gr. *pavonia*, *Nezzazata* sp., *Spiroloculina* sp., miliolaceans and frequent thin-shelled ostracods. *Sellialveolina vialli* Colalongo 1963 is present and is widespread in the whole perimediterranean area (Polsak et al., 1982; De Castro, 1988) in the Early Cenomanian (Berthou, 1984; Chiocchini et al., 1994), (Fig. 7). Thin sections revealed a low diversity microfauna, mostly represented by miliolaceans, Polymorphinidae and scattered algae. *Cuneolina* specimens, sometimes transported and eroded, are present as well as a poor (almost monotypic) thin-shelled ostracod microfauna. The reduced diversity of this fauna was related to unfavorable life conditions in a confined environment.

DINOSAUR FOOTPRINTS

As stated above, the tracksite consists of three track-bearing levels that were examined in detail for sedimentological and ichnological data. Each level was identified by the acronym SCP (Sezze Cava Petrianni) followed by a roman numeral: i.e., SCP I, SCP II and SCP III. A small track-bearing portion of SCP III, moved by a small fault, was identified as SCP IIIb. Surfaces SCP I and SCP III were completely mapped while the SCP II, being printed by less than twenty footprints, on a 150 m² surface, was studied so that the single prints were numbered, photographed and drawn.

The lowest surface (SCP I), cleaned for an area of nearly 30 m², is locally sculptured by frequent 2 cm wide unexplained circular depressions and cut by some E-W trending fractures. It revealed 44 footprints including a large quadruped trackway, consisting of 20 prints (SCP I-1) ascribed to a medium to large sized sauropod, two short theropod trackways, each made up of three consecutive prints, and 18 isolated footprints (SCP I-4 to -21) ascribed to small theropods. It is noteworthy that the large trackway is associated with small- to medium-sized theropod tracks that overlap the sauropod footprints in some places, testifying to subsequent trampling of theropods. The distribution of footprints on this surface is revealed to be non random; specifically, the largest number of tridactyl footprints is impressed either on the expulsion rims rising around the larger sauropod footprints or very close to them (Fig. 8). It suggests that the substrate was hardened early or was covered by microbial mats and did not easily allow the impression of the tracks of light animals. It was only after the passage of the heavy herbivore that the sediments were disturbed or softened by the

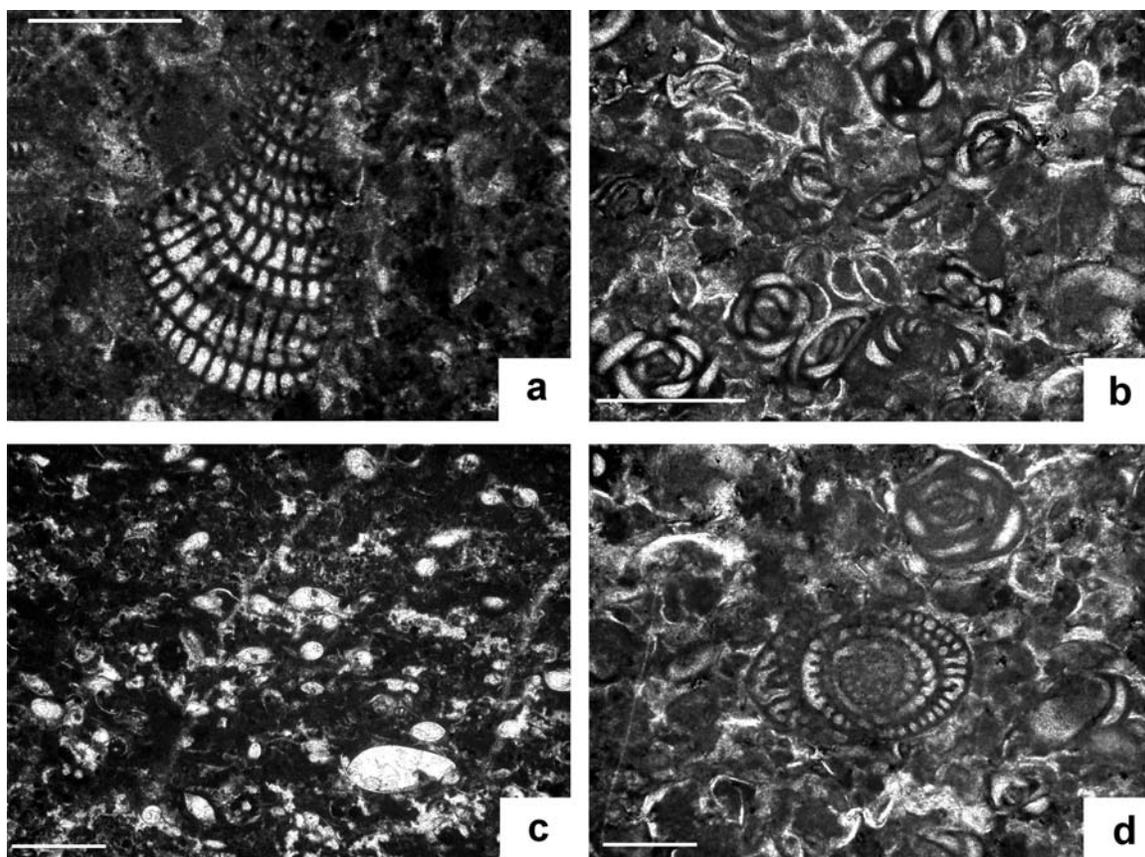


FIG. 7. Microfacies and microfauna. *a*) *Cuneolina pavonia ex grege. parva* Henson 1948: axial section. Scale bar 500 μm ; *b*) microfacies with miliolids and Polymorphinidae. Wackestone-packstone texture. Scale bar 500 μm ; *c*) microfacies with ostracods more or less isooriented. Wackestone texture made up of a mixture of peloids and clasts. Scale bar 1 mm; *d*) *Sellialveolina vialli* Colalongo 1963, subaxial section. Scale bar 500 μm .

upward expulsion of intergranular water which allowed the light theropod foot impression to be made (cf., Stanford et al., this volume).

The SCP II surface reveals scattered and weakly impressed footprints, less than 20 cm long all ascribed to medium-sized theropods (Fig. 9). The footprints are tridactyl, digitigrade, often with clear margins, while some are preserved as elongated, shapeless depressions. These last ones show an additional interesting feature. They are accompanied by the tilting of a small portion of the surface and by a suite of sub-concentric fractures (Fig. 10). These features and the style of the more normal light prints reveal that the surface layer was quite hard whereas the subsurface was still unconsolidated when dinosaurs passed there. All this speaks of a phase of early diagenesis and of the formation of a carbonate crust of a certain thickness soon after the lime mud dried.

The SCP III surface (2.5 m wide and about 6 m long) lies about 2 m above SCP II; it is the richest surface of the outcrop showing more than 170 footprints on the exposed portion (Fig. 11). The footprint/surface ratio lets us consider this level moderately trampled (Lockley and Conrad, 1989). Most of the footprints are isolated even if short trackways, made by

three or four consecutive tridactyl footprints, have been also identified on this surface; other trackways, represented only by pairs of consecutive footprints, can be easily inferred. All the footprints are small and most of them are oriented N-NE, as shown in the rose-diagram (Fig. 12). As already described the SCP III displays two discontinuous horizons separated by a 2 mm thick lamina; both surfaces show desiccation cracks testifying to repeated subaerial exposure (Fig. 13). The surfaces were trampled at different times but, as the horizons are so close together, the two events were considered as a single one. However, differences in water content of distinct portions of the surface caused different styles of footprint preservation. Deeper footprints located in a marginal portion of the surface, frequently show internal sediment back flow, probably due to a higher water content of sediments. The analyzed footprints are mainly tridactyl, but tetractyl morphotypes also occur. Several footprints are characterized by the impressions of the metatarsal area but a larger number are at least posteriorly elongated. From a total of 178 traces, 18 prints (nearly 10%) show clear impressions of metatarsals and 35 (20%) are elongate traces (elongate is here taken to include traces showing a triangular and well-developed "heel" frequently as long as the phalangeal

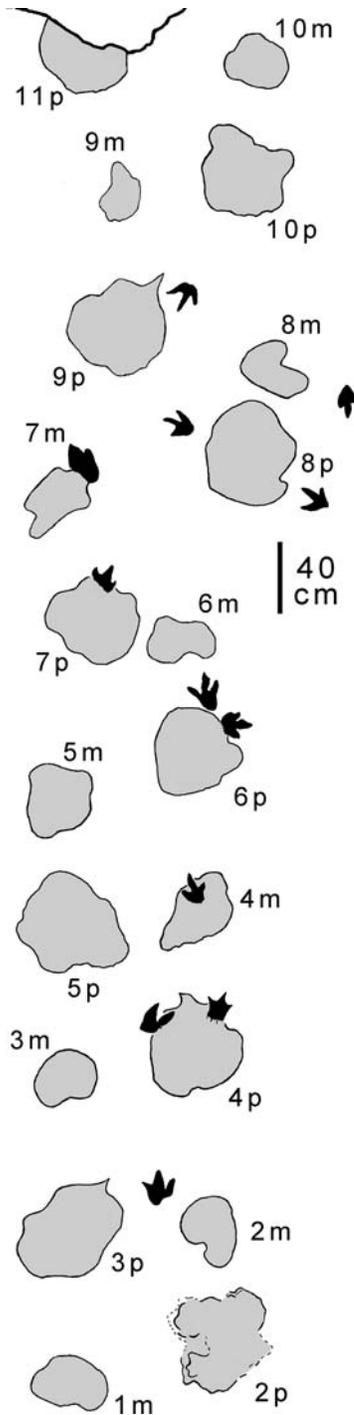


FIG. 8. Map of a portion of the SCP I surface. Notice the distribution of small theropod tracks around prints of the SCP I-1 trackway.

portion of the foot trace but lacking a well-defined posterior termination).

Elongate footprints are related either to the deep impression of large theropods (Lockley and Hunt, 1994; Gatesy et al., 1999; Lockley, 2000a) or to the unusual gait of stalking dinosaurs

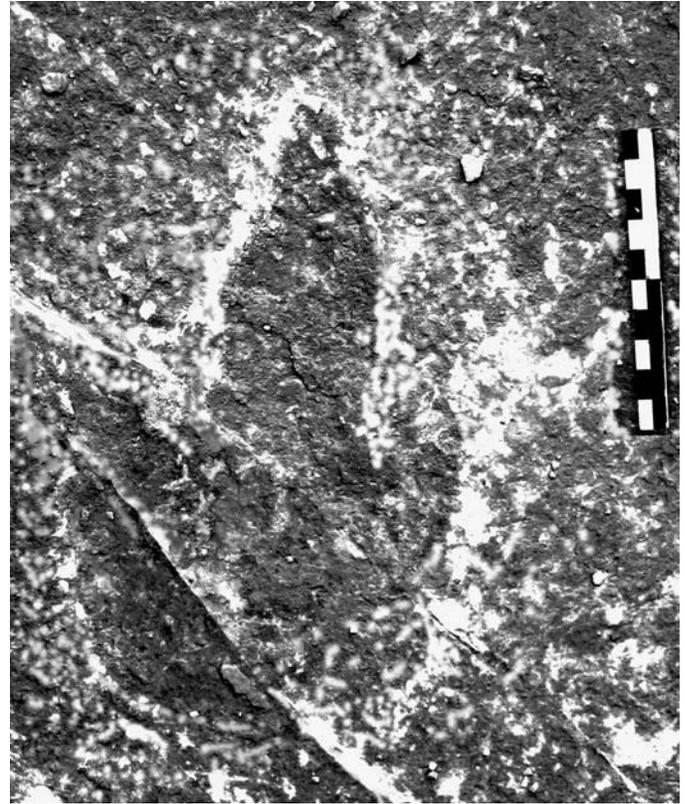


FIG. 9. Theropod footprint on the SCP II surface. Scale bar 10 cm.

(Kuban, 1989). On the SCP III surface all the footprints are small varying from 8 to 18 cm (excluding metatarsal impressions) and thus the large number of elongated footprints suggests a cautious walking-behavior on soft ground, as already suggested by Conti et al. (in press). In this case, the shallow impressions suggest firm grounds. Such behavior could be explained by invoking the presence of muddy water originally hiding the bottom.

Collectively the footprints of the Petrianni quarry can be attributed to sauropods and theropods. We describe these in an attempt to characterize the largest trackway (SCP I-1) and distinguish the principal morphotypes of theropod footprints.

The occurrence of saurischian (Sauropod and Theropod) tracks in carbonate platform deposits could be considered consistent with the *Brontopodus* ichnofacies concept (Lockley et al., 1994).

Sauropod Footprints

The trackway SCP I-1 is the first and, at the moment, the only sauropod track found in central and southern Italy. It is 7.5 m long, fairly straight, and oriented SSE. All the footprints are several centimeters deep and show relatively low expulsion rims. Some footprints are still partially or completely filled with sediments. The trackway consist of 20 footprints, 9 manus-pes pairs and two odd footprints, a manus and a pes, respectively at the beginning and at the end of the trackway. It is attributed to a

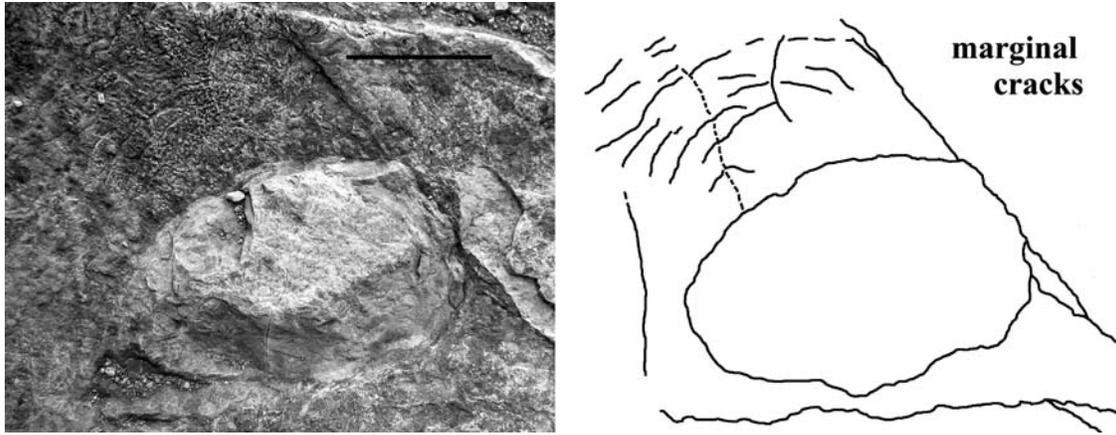


FIG. 10. Photograph and interpretative drawing of the break-down cracks of the superficially hardened portion at the SCP II surface. Scale bar 10 cm.

sauropod with manus about half the size of the pes. The trackway is rather regular with pes pace angulation of about 100° . The manus print lies exactly anterior to the pes at half-way between two consecutive pes prints. The pes never overlaps the manus impressions and the inner trackway width indicates quite a wide gauge posture.

Pes morphology is variable, ranging from sub-elliptical to sub-circular in outline. The most striking feature is the occurrence, in some pes footprints, of short and sharp claw impressions directed inward.

Manus impression morphology is also variable but it typically assumes a sub-circular or semicircular shape, sometimes showing an indentation in the middle of the posterior border of the footprint. In other cases it is also possible to observe an indentation in the lateral margin of the manus print.

Remarks: The SCP I-1 trackway has a large manus impression relative to the size of the pes (average ratio of about 1:2). If one looks closely through all the described sauropod trackways, the Sezze data on manus/pes area ratio differs from those noted for the Cretaceous sauropod tracks of Texas (1:3; Farlow et al., 1989) and from those of the Upper Jurassic of Colorado (1:4 or 1:5; Lockley et al., 1986) and Morocco (1:4 to 1:5; Ishigaki, 1989; Lockley and Rice, 1990). Furthermore, the heteropody index of the Sezze trackway is higher than that of the Toro Toro trackways (Bolivia; Leonardi, 1994) and of Fumanya (Spain; Schulp and Brox, 1999) which revealed a ratio of about 1:1. SCP I-1 heteropody best fits with the Middle Jurassic trackway of Portugal (Galinha Site, Bajocian-Bathonian; Santos et al., 1994) and with the Bolivian Late Cretaceous sauropod trackway of Cal Orcko and Humaca sites (Lockley et al., 2002).

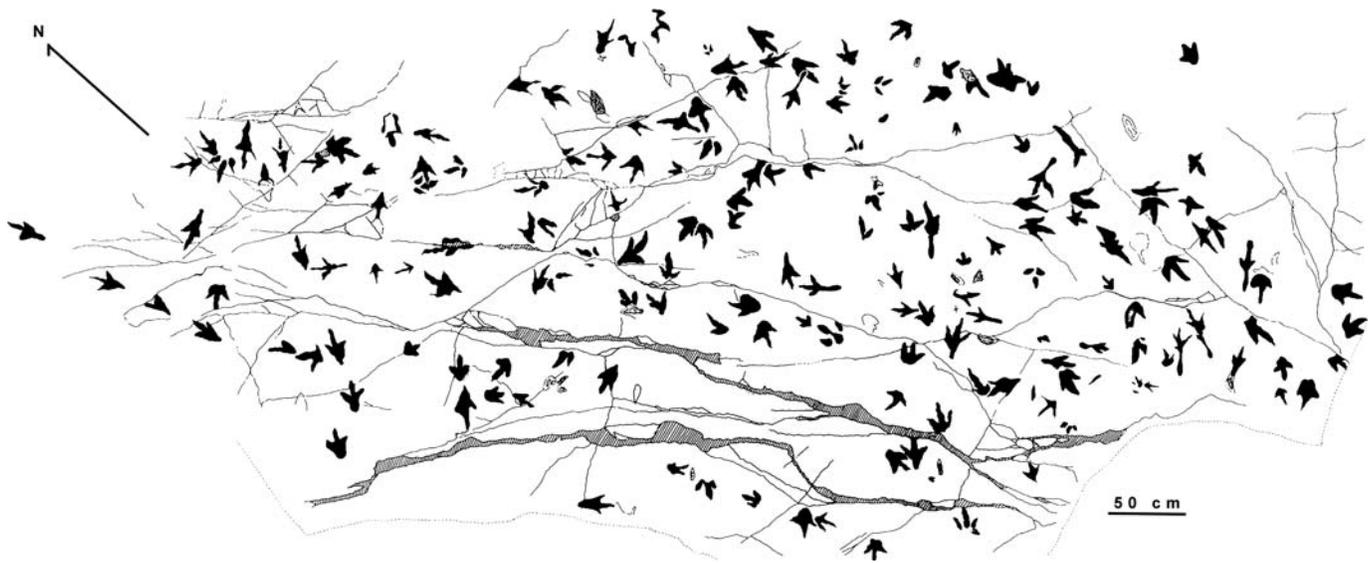


FIG. 11. Map of the third printed surface (SCP III).

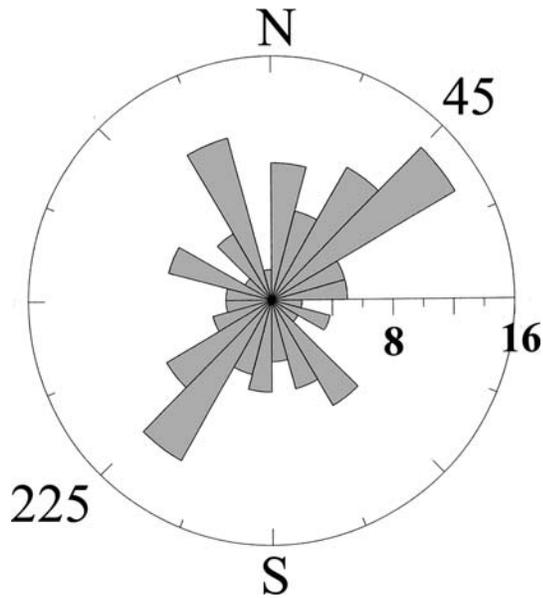


FIG. 12. Rose diagram of azimuth of the footprints at the SCP III surface. (See Color Plate II)

As previously indicated it could be attributed to a wide-gauge sauropod trackway. The SCP I-1 trackway morphology is distinct for some characters from all the ichnogenera and ichnospecies erected to date. Seven ichnotaxa, attributed to sauropods and referred to a time interval that spans the Late Jurassic to Early Cretaceous, were analyzed.

Trackway SCP I-1 differs from *Brontopodus birdi* Farlow, Pittman and Hawthorne 1989 (Aptian-Albian) mainly in that the gauge in the Sezze trackway is less wide; in *Brontopodus birdi* the pes axis is clearly rotated outward while in the LAC material, external rotation of the pes is not clearly discerned. The position of the manus with respect to the pes is similar in SCP I-1 and in *B. birdi*. The distance between manus and pes is also comparable. The manus of *B. birdi* has a double-crescent shape and a conspicuous forwardly directed indentation in the middle of the posterior margin (Farlow et al., 1989). The SCP I-1 manus has a double-crescent shape only in two cases (6 m and 7 m) and the indentation both in the rear and in the external margin is less pronounced. Manus footprints are also smaller than in *B. birdi* (manus width from 30 to 60 cm, manus length of approximately 50 cm). The pes in *B. birdi* is larger than the pes of SCP I-1 (pes length = 86.5 cm; pes width = 60–65 cm) with clear impression of digits I, II, III and outwardly directed claw marks.

Breviparopus taghbaloutensis Dutuit and Ouazzou 1980 (Late Jurassic-Early Cretaceous, Demnat, Morocco) differs from the Sezze trackway in the manus-pes set positions with respect to the midline, which are often directed outward (about 30°). In *B. taghbaloutensis* the manus has a crescent shape differing in this from all the manus impressions of the SCP I-1. The pes of the North African ichnotaxon is oval-shaped with clear digit and claw impressions directed forward or outward; however, the outline of the pes in *B. taghbaloutensis* is very

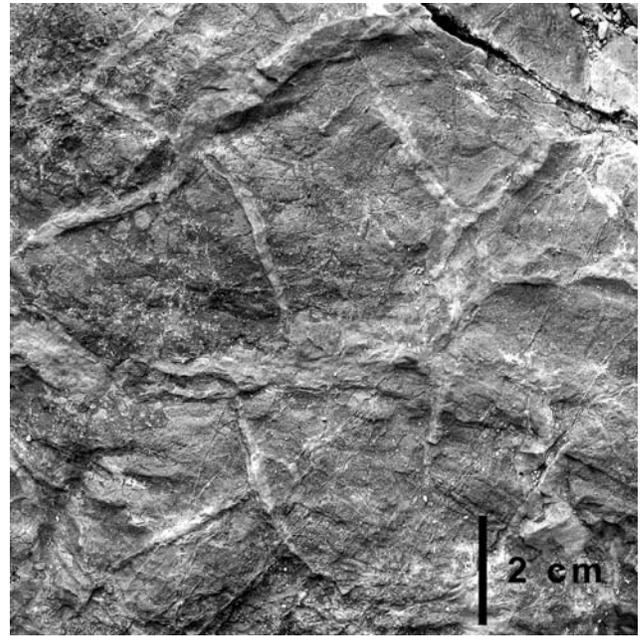


FIG. 13. Mudcracks at SCP III surface.

similar to some pes tracks observed in the SCP I-1 (4p and 6p), in having a small indentation on the lower portion of the outer margin. Nevertheless it is noteworthy that *B. taghbaloutensis* differs from the SCP I-1 footprints in the shorter distance between manus and pes impressions.

Parabrontopodus mcintoshi Lockley et al., 1994 (Late Jurassic, Colorado, USA) shows a lack of space between the inner margins of pes tracks (narrow gauge posture) compared to SCP I-1 where the inner trackway width ranges from 1/4 to about the same value as pes width. The manus of *P. mcintoshi* is quite a bit smaller than the pes. In *P. mcintoshi* manus impressions are semicircular (shorter than the manus of the Sezze ichnosite) wider than long and without any digit or claw impressions; furthermore, no indentation is present both in the rear and the external margin, as seen in the SCP I-1. Pes footprints are also different; in the North American ichnotaxon they are longer than wide, outwardly rotated and with claw impressions corresponding to digits I, II and III.

The trackway of *Polyonyx gomesi* Santos et al., 2004 (Pedreira de Galinha site, Middle Jurassic, Portugal; Santos et al., 1994; 2004) has a gauge that resembles that of the Sezze ichnosite. *P. gomesi* differs from the SCP I-1 trackway both in the constant outward rotation of the manus/pes pairs with respect to the midline and in the track morphology; the pes is longer than wide and shows impressions of digit I and II anteriorly directed and of digit III and IV medially directed. The manus track has a double-crescent shape, and is characterized by the impression of digit claw I, medially directed.

The trackway *Ophysthonyx portucalensis* Santos et al., 2004 belongs to a group of trackways that are markedly wide gauge. The characters that distinguish *O. portucalensis* from the tracks

of Sezze are the manus/pes pairs feebly outward directed and the occurrence in the manus of a digit I posteromedially directed.

Finally *Titanosaurimanus nana* Dalla Vecchia and Tarlo 2000 shows a pes-size comparable to those of SCP I-1 (approximately 50 cm long) but it has a manus size markedly smaller and characterized by the impression of fingers I, II, IV and V; the manus shows a double-crescent shape but it differs from the manus preserved in the Sezze ichnosite because the double-crescent shape is more marked and the indentation in the middle of the rear zone is deep enough to show evidence of the digit impressions.

Though ichnotaxonomic analysis is still in progress, the arrangement of the manus/pes pairs with respect to direction of movement, the wide gauge of the trackway, the large manus relative to the size of the pes (average ratio of about 1:2) and the absence of any digit marks in the manus, suggest that the trackway might be attributed to a titanosaur (Wilson and Sereno, 1998; Wilson and Carrano, 1999; Lockley et al., 2002; Bonnan, 2003).

Theropod Footprints

Because of the very derived morphology of the foot, theropod footprints are more difficult to attribute to ichnotaxa even if different morphotypes were distinguished.

More than twenty badly preserved tridactyl footprints are preserved on the SCP I surface, but their state of preservation prevents any attempt at deeper analysis.

The second surface (SCP II) bears about twenty footprints, all of them as concave epireliefs. The foot impressions are shallow, in a few cases showing feeble rims. The footprints under examination are tridactyl and neither traces of a digit I nor metatarsal impression have been found. Being as the impressions are quite faint, only the most visible traces, in natural light, have been reproduced by drawings and photographs. The average length is about 24 cm corresponding to a width of about 13 cm. Digit impressions are thick and they contact each other along most of their proximal part. Footprints are asymmetrical, and on initial consideration evoke the classical theropod shape; this is partly due to the presence of a notch at the base of digit IV that lies below the proximal end of the other digits. The free phalangeal portion of the digit is short, in particular for digits II and IV. The impression of digit III is the strongest with a basal width of about 5 cm, and it tapers distally to a small and pointed claw. Each side of the free phalangeal portion of digit III shows two indentations possibly related to the presence of pads covering the foot sole; the distal ends of digits II and IV lie about at the same level. The distal portion of both these digits is visible but it is not possible to outline a well-defined claw mark. Digit III projection (the portion projecting anteriorly of the line uniting the distal ends of digit II and IV) versus footprint total length is about 0.3. Where preservation allows a better analysis, digits II and IV were also found to have feeble pad impressions. Digit divarication ranges from 37° to 60°. To

date the taxonomic position of these footprints is still under examination, but worth noting is the resemblance of the SCP II traces with Early and Late Cretaceous footprints from the Istrian Peninsula. In fact, a close similarity was found with Late Albian footprints (Dalla Vecchia, 2001, Figs. 5–6, 7, 10, 12) described from Cervera/Črvar (Torre/Tar municipality, Istria, Croatia). Other similar footprints come from Upper Cenomanian layers cropping out near San Lorenzo di Daila/Lovrečica (Istria, Croatia) described by Dalla Vecchia (2001, Figs. 7, 8, 10, 17, 19). Tracks from SCP II can be only ascribed to a generalized theropod trackmaker due to the position of digit IV, with the base slightly pulled back in comparison with the base of digit II, due to digit divarication, and due to the small pointed claws.

Tracks printed on the SCP III surface were more difficult to study due to the peculiar characters of the substrate that caused many strange gaits and impressions. Moreover, trackways were hard to recognize due to the large number of footprints crossing the SCP III surface in all directions. The tracks represent ten different morphotypes or preservation expressions (Fig. 14) that vary from tridactyl digitigrade footprints to crouching traces with metatarsal impression and clear traces of the digit I.

Examination of single footprints, indicates that some footprints can be compared to different taxa known from the literature. As a whole SCP III footprints could be compared with several figurations of footprints quoted by Lockley (2000b, p. 291, Fig. 7) under the name of *Kayentapus*-like footprints.

A good match was found between *Carmelopodus* figured by Lockley et al. (1998) and SCP III-171 (Fig. 14B), SCP III-54 (Fig. 14E) and SCP III-64 (Fig. 14K). SCP III-171 and SCP III-54 closely resemble specimens shown by Lockley et al. (1998, Fig. 9 right), and a closer resemblance is noticeable between SCP III-64 and the specimen 184.21 figured by Lockley et al. (1998, Fig. 4).

Bressanichnus patagonicus Calvo 1991, from Albian-Cenomanian sediments of Argentina, is similar to SCP III-87 and -85, but differs from other footprints from SCP III.

SCP III footprints were also compared with Cretaceous tracks from Argentina described by Alonso and Marquillas (1986). *Yacoraitichnus avis* Alonso and Marquillas 1986, was attributed to an avian trackmaker due to the high value of digit divarication and to the thickness of the digits. *Yacoraitichnus*, even if smaller than SCP III tracks, shows similarities with SCP III-63, SCP III-171, SCP III-87, SCP III-48 and SCP III-54 (Fig. 14A–E) in relative digit length and thickness, in the protrusion of digit III over digits II and IV, and in II–IV digit divarication. Unfortunately, there is not a single published photograph of this taxon and the illustration shows little morphological detail (Alonso and Marquillas, 1986).

On the basis of the orientation and relative length of digits II and IV, it was possible to recognize some resemblances between SCP III-48 and SCP III-54 (Fig. 14D, E) and *Hopiichnus shingi* Welles 1971, established on material from Lower Jurassic strata of Arizona (Welles, 1971) which, according to Lockley and Hunt

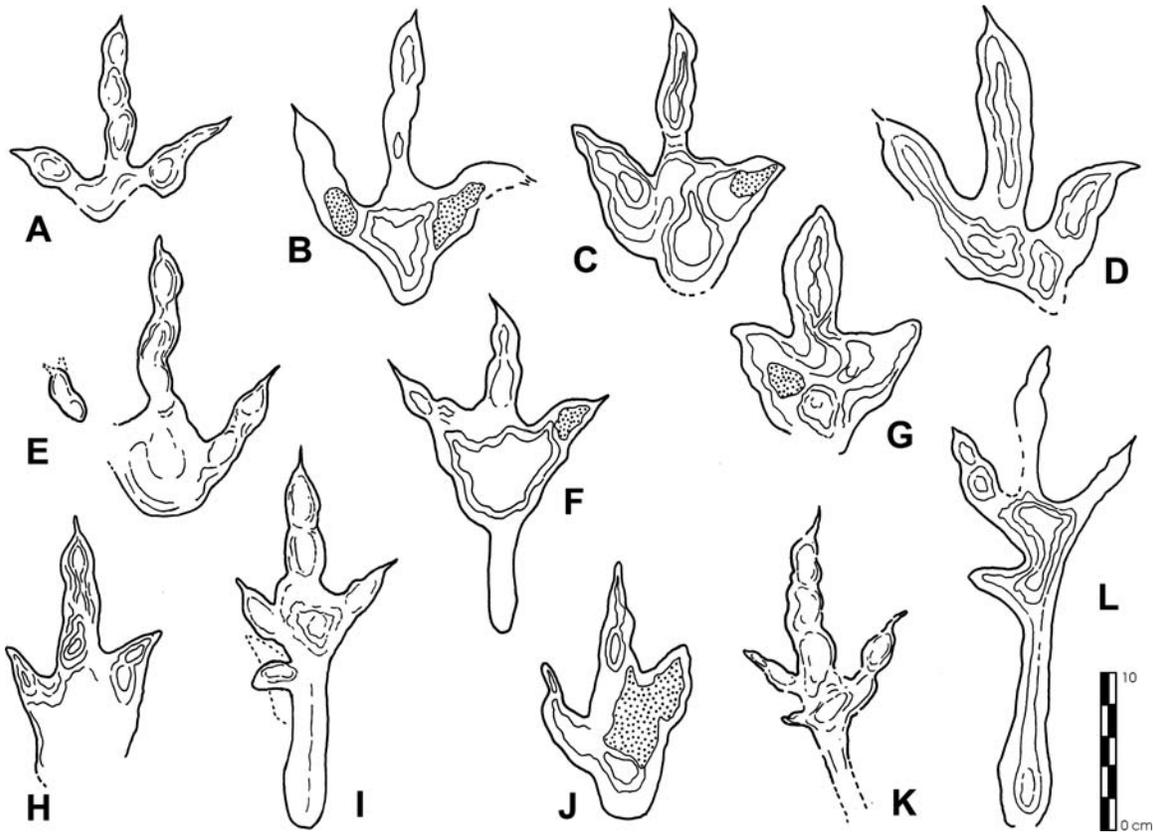


FIG. 14. Principal morphotypes of theropod related footprints on SCP III surface. a) SCP III 63; b) SCP III 171; c) SCP III 87; d) SCP III 48; e) SCP III 54; f) SCP III 177; g) SCP III b; h) SCP III 105; i) SCP III 53; j) SCP III 85; k) SCP III 64; l) SCP III 11.

(1995), is probably an example of *Anomoepus*. This footprint is slightly smaller than the SCP III morphotypes.

Unnamed footprints from the Cretaceous of Israel, described by Avnimelech (1966) have digit thickness, relative length and total divarications similar to SCP III footprints. It is possible to point out a stronger resemblance with SCP III-171, SCP III-87, and SCP III-85 (Fig. 14B, C, J) while similarities with other footprints are less clear.

A single footprint comparable to SCP III footprints is known from the Cretaceous of Istria (Dalla Vecchia, 2000a p. 358, fig. E).

Sternberg (1926) erected *Ornithomimipus angustus* from the Upper Cretaceous strata of Alberta (Canada). As the name suggests, it was attributed to Ornithomimid dinosaurs. The most important feature of this track is the presence of a metatarsal-phalangeal pad that closely joins digits III and IV, leaving digit II slightly separated. However, this form is more symmetric than the SCP III morphotypes; in particular the base of the foot is less wide in *O. angustus*. Another difference between the Italian and Canadian forms is the separation between digit II and the digit group III–IV, which is characteristic of *O. angustus* but missing in the Italian forms.

After the above-mentioned comparisons, we recognized that the continuous footprint variability resulted from differences

in sediment water content; where it was more fluid, digit impressions widened, giving rise to thicker digit impressions, with lateral walls less steeply inclined and a lower number of recognizable diagnostic features. Drier and slightly firmer sediment was capable of better reproducing of the original foot morphology. After cross-checking based on the above mentioned assumption (a back-stepping process based on the isolation of characters linked to a lesser extent to sediment constraints), it becomes evident that most of the footprints on SCP III surface were printed by a single type of trackmakers.

Considered as a single variable taxon, the SCP III footprints can be described as follows: tridactyl footprints with digit III extending beyond the line joining the tips of digits II and IV by a variable amount, which is linked to the degree of divergence in digits II–IV; however, this percentage never goes below 50% of the free portion of digit III. The shape of the footprint in the digitigrade position is asymmetric with an interdigital angle between digits II and III smaller than the one between digits III–IV. This is also noticeable when observing differences in the hypex morphology, with that of digit II–III being more closed and acute. The proximal end of digit IV lays slightly posterior to the base of digits II and III, but it is always slightly displaced with respect to the axis of digit III. Total divarication II–IV varies from 57° to 85°, with a maximum of 102° for footprint SCP III

63. Digit II bears two pads, while digit III is usually covered by three clear pads. Three pads cover the sole of digit IV. The toes are tipped with small claw impressions, which in digits II and IV are parallel to the digit axis, while in digit III claw marks are usually bent inward. The general outline of SCP III footprints is characterized by a wide base, where the proximal end of digit IV is only slightly pulled back with respect to the base of digits II–III, and quite divergent lateral digits. Toe impressions are thin and straight. A common extramorphological pattern, linked to the substrate consistency, is the collapse of the mud wall of digit prints that leaves a distinctive suture line.

Digitigrade impressions never show the presence of digit I which appears instead in the squatting traces, just beneath the base of digit II. Digit I left a triangular impression that diverges medially straight from the metatarsal, at an angle of about 90°. The base is wide, while the overall morphology is conical. Its length is less than a half the length of digit II.

Footprints with metatarsal impressions are quite commonly reported in the literature as isolated specimens, whereas trackways seem to be less common. The pioneer work of Kuban (1989) on tracks with metatarsal impressions was published more than a decade ago; since then several other outcrops bearing elongate tracks were described (Lockley et al., 2003). The importance of those kind of impressions is in the behavioral information and partly in the improved chance that they offer in the recognition of the trackmaker. At SCP III, metatarsal impressions are narrow. Their length varies from a minimum of 1.3 of the length of the free phalangeal portion of digit III, as in footprints SCP III-53, measured from the proximal end of digit IV, to twice the length of digit IV in SCP III-11 (Fig. 14I, L).

In conclusion, despite the possible comparisons with many different tracks, after a cross-check, all the footprints were ascribed to a single type of track-maker. This result points to difficulties in ichnosystematics related to diagenesis of *Kayentapus* and *Carmelopoduss*. It seems that each theropod track lacking the impression of the proximal portion of digit IV could be ascribed to the latter ichnotaxon; for the former an unclear taxonomic status led to misunderstanding of this form so that different authors refer different forms to this ichnotaxon (Piubelli et al., 2005). Moreover, in both cases it seems that the stratigraphical distribution is considered as an important character. This approach endangers footprint usefulness and must be avoided if it can be shown that there really are no clear morphological differences.

It is evident that in some cases it seems easier to attempt to refer tracks to trackmakers than to ascribe specimens to ichnotaxa. In this case, even if the attribution to an ichnotaxon is at the moment impossible, research into the trackmaker can at least be attempted. Indeed, some characters highlighted in the tracks and linked to osteological patterns, (the length of the metatarsal in comparison to the digit length, the presence, the position and the orientation of digit I, the position of digit IV especially in its proximal part as well as the morphology

of the unguals) can confidently allow us to exclude some theropod groups as the possible trackmakers of Sezze SCP III footprints.

Based on these arguments the trackmaker must be confined to a group of theropods retaining digit I, with the metatarsal-phalangeal junction of digit I very close to the ground; the metatarsal-phalangeal junctions of the three central digits are more or less equally anteriorly-situated and digit III is quite a bit longer with respect to the lateral ones. Consequently some theropod groups can be directly excluded, such as Therizinosauroida (*sensu* Clark et al., 2004). Troodontidae (*sensu* Makovicky and Norell, 2004) shows a specialized digit II that bears a trenchant claw as well as a shortened metatarsal II with respect to metatarsal III and IV, thus their foot skeleton does not fit the SCP III footprints. Dromaeosauridae (*sensu* Norrell and Makovicky, 2004) are excluded on the base of their functionally didactyl pes. Inside the Ceratosauria clade (*sensu* Tykoski and Rowe, 2004) foot morphology of Cretaceous forms such as the Neoceratosauria, is known to a lesser extent; eventually, the generalized large dimension reached by neoceratosaurians endorse their exclusion as possible trackmakers. Avialae, with their basal forms (*sensu* Padian, 2004) are excluded on the basis of a reversed hallux, whose presence has not been noted on SCP III tracks. Basal Tetanurae (*sensu* Holtz et al., 2004b) are a large group encompassing a large range of foot morphology and dimension. In general this group might be excluded on the basis of the position of digit I, usually contacting at midshaft metatarsal II, thus too far back to fit the trace of digit I in SCP III.

In conclusion, Ornithomimosauria (*sensu* Makovicky et al., 2004) and Oviraptorosauria (*sensu* Osmólska et al., 2004) are the best candidates as authors of SCP III. Inside Ornithomimosauria at least two forms retain the first digit, *Garudimimus* Barsbold 1981 and *Harpymimus* Barsbold and Perle 1984, while all the other forms (Ornithomimidae) lost this digit. Digit I position, as well as metatarsal/foot length ratio, and the digit relative length fall inside the field observed in SCP III prints. A better matching can be recognized with the Oviraptorosauria foot skeleton. This is based on several features such as digit proportion and the presence of digit I, whose position is close to the distal end of metatarsal II, as well as the claw morphology.

In particular, the narrow trace of a claw, which is more easily referred to a laterally compressed ungual (oviraptorosaurs) than to one that is flat ventrally and triangular in cross-section (ornithomimids), better supports the hypothesis of Oviraptorosaurs as the trackmaker of SCP III.

Even if age and distribution are not ichnotaxonomic characters, it is possible to compare the resulting attribution hypothesis with chronological and paleogeographic data. Oviraptorosauria are known from Barremian to Maastrichtian thus their stratigraphic occurrence fits the SCP III data well. On the contrary their geographical distribution suggests some problems; at present, Oviraptorosaur remains occur in China, Mongolia and North America, and in one site in Uzbekistan. All these sites

were quite geographically and geologically disjunct from the perimediterranean region.

These data are inconsistent with our findings and can be explained either by assuming that theropod geographical distribution is still incompletely known or that the Sezze footprints have to be ascribed to a still unknown dinosaur, perhaps a derived, endemic form.

ENVIRONMENT AND FAUNAL ASSOCIATION INTERPRETAION

Facies analysis of the examined interval reveals continuous changes from subtidal to supratidal. The presence of a reduced and oligotypic ostracod fauna in some levels seems to indicate deposition in an innermost lagoonal area that was frequently restricted. When present, the microbial mats at the top of some layers seem to be the best indices of very shallow water. The flat and parallel bedding as well as the lack in any trace of tempestite layers can also be interpreted as evidence that the platform coast or the open marine water were far enough away that even exceptional energetic events were not registered in that innermost region. The distance from a margin could be inferred by the lack of tidal channels and in large bivalve associations, usually present in the marginal facies of the LAC succession. Frequent desiccation cracks show that each flooding event rapidly ended with a return to exposure and desiccation. Dolomitization phenomena, with widespread small dolomite crystals can also indicates early diagenesis as well as the preservation of footprints. An early superficial hardening is indicated by the peculiar distribution of footprints on the SCP I surface while the presence of a thick superficial crust is indicated at SCP II. All these data suggest a large and flat region, well inside the platform, frequently flooded by slow water-sheets and almost immediately dried.

The occurrence on different surfaces, very close to each other, of the footprints of herbivorous and carnivorous dinosaurs, is the evidence that at least three different types of trackmakers were contemporaneously present in the LAC platform during the Early Cenomanian. In particular the 180 small theropod footprints on the SCP III surface testify that this nearshore environment was usually inhabited by these animals. The many trackways and multiple, crossing orientation suggest much local activity in the area. Considering the relative food richness of such environments one can imagine that small sized theropods were searching among beached algae for marine invertebrate or stranded fish, after the sea receded, as happens today with shore-birds. Probably, they were adapted to come and go with each tidal cycle. This implies a long term adaptation. Though the ichnotaxonomic analysis of the three surfaces is still in progress, it is evident that the ichnoassociations of the SCP I, SCP II and SCP III are different.

The three track-bearing levels are so close to each other, both from a physical and stratigraphical point of view, that a stratigraphically controlled differentiation must be rejected.

Thus the recognized differences were interpreted as the results of the activity of different dinosaurs in slightly different subenvironments perhaps more or less distant from the platform margins. The examined footprints witness the presence of a diverse and structured dinosaur association dwelling on the shores of the Cretaceous Tethys.

The real importance of these data can only be evaluated when considered in the complete, regional-scale, framework of the geology of the periadriatic area.

PALEOGEOGRAPHICAL INFERENCES

In the following section the meaning of the new dinosaur footprints as paleogeographical constraints will be examined. As a preliminary step it is important to underline a simple fact, often forgotten in the interpretation of paleontological data: an animal (and its fossil traces) cannot be considered as a singularity. Animals do not live alone and isolated from the environment; only the popular "Nessie" can do this (even if some people seem to believe this was possible also for Mesozoic vertebrates). A geoscientist must be well aware that most paleontological data, have to be considered small windows with dirty glass, giving only a symplified idea of an enormously complex reality. Indeed, the smallest paleobiological datum represents the scanty evidence of balanced animal associations that, nevertheless let us infer the related food chain and all the near or remote causes influencing the physical and ecological space in which the animals could live. Consequently, when examining paleontological data related inferences have to be considered with the same weight as the data themselves.

In the case under examination, some dinosaur footprints (representing an association and their related food and freshwater supply) can help shed light on the paleogeography of central and southern Italy and of the neighboring regions. The central Mediterranean region is a complex puzzle of different small units, most of them included in the so called Adria microplate. This plate, on which both shallow and deeper water successions were deposited, was in origin an African promontory (Channel et al., 1979); it was pulled apart from the mainland by the extension of the Tethys Ocean and pushed up northwestward to collide with the European foreland (Stampfli and Borel, 2004). For a long time oceanic areas bordered the plate, as the Ligure-Piemontese, the Vardar and the Ionian Oceans (Catalano et al., 2001; Passeri et al., 2005; but see Bosellini, 2002 for a partially contrasting hypothesis). Consequently, in most of the geodynamical models, the Mesozoic shallow water and emerged areas of Adria are considered as having been separated from both the mainland of Laurasia to the north and from Gondwana to the south by deep sea areas from the Pliensbachian until the Coniacian—a long interval of about 130 My.

Moreover, the main shallow water successions (carbonate platform deposits) of the Periadriatic region are ascribed to different structural units: the LAC domain pertaining to the overthrust Apennine chain and the Apulian domain, interpreted

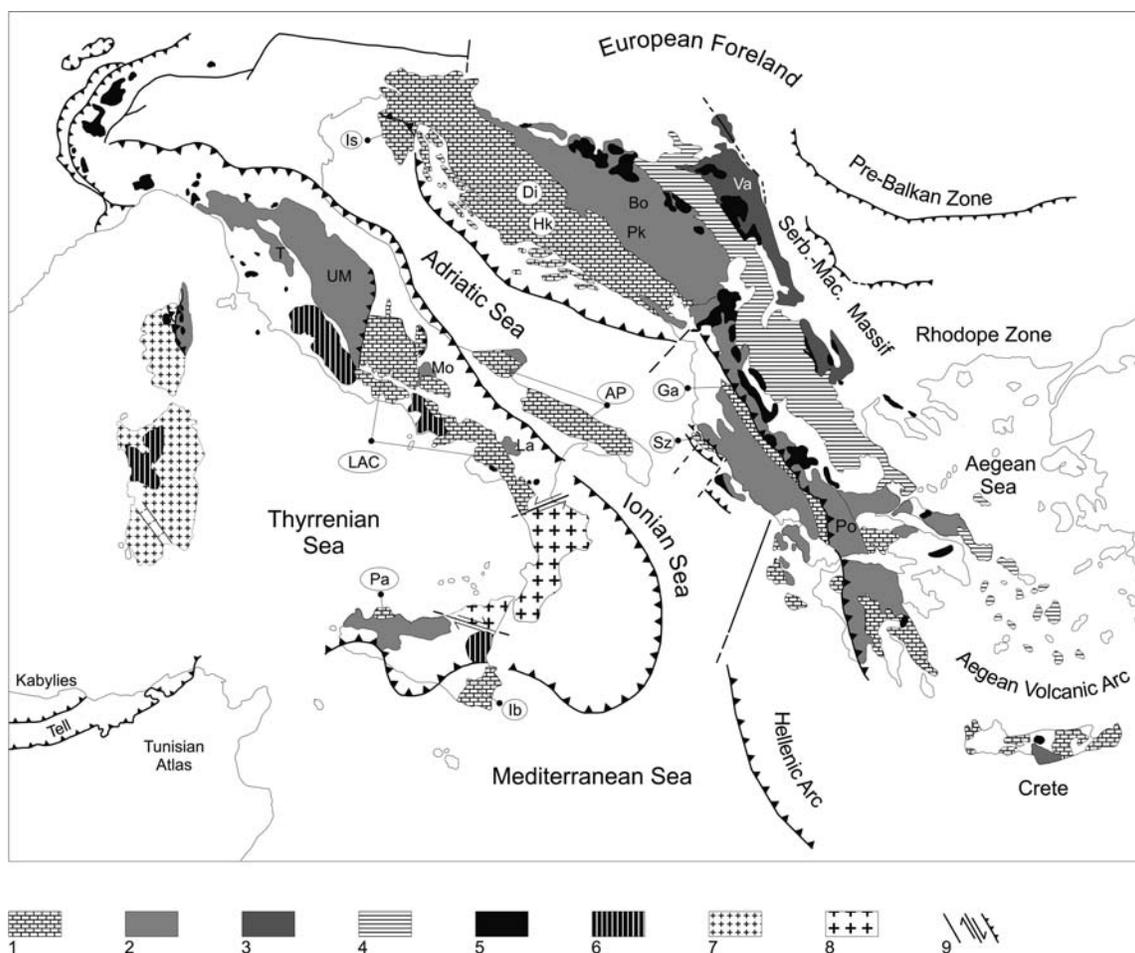


FIG. 15. Simplified structural map and principal domains of the periadriatic region. 1) Mesozoic carbonate platforms; 2) Mesozoic basins; 3) Vardar Zone; 4) Pelagonian Zone; 5) Ophiolites; 6) Volcanic rocks; 7) Variscan metamorphic basement and granitoids; 8) Pre-Alpine basement. AP Apulian carbonate platform; LAC Lazio-Abruzzi-Campania carbonate platform; Ga Gavrovo (Kruja, Tripolitsa carbonate platforms); Is Istrian carbonate platform; Sz Sazani carbonate platform; Pa Panormide carbonate platform; Iblean carbonate platform; UM Umbria-Marche basin; T Tuscan basin; Po Pindos Olonos Zone; Pk Pre-Karst Zone; Hk High Karst Zone; Bo Bosniac Zone; Di Dinarids (after various authors).

as its foreland on the western side of the Adriatic Sea (Fig. 15). On the eastern side of the Adriatic Sea, an almost mosaic framework comprised of the Slovenian, Albanian and Greek units (Dinaric-Kruja-Gavrovo carbonate platform domains) overthrusting westward, while the small Sazani unit and some portions of the Ionian islands are also related to the Apulian foreland. The Istrian peninsula is included in the Apulian foreland, even if paleogeographically it was tightly connected to the Dinaric platform. In some models the latter is separated by the small (persistent or ephemeral) Tolmino trough (Cati et al., 1989; Zappaterra, 1990).

Different paleogeographic interpretations exist for the area under examination (Dercourt et al., 1993; Yilmaz et al., 1996; Dercourt et al., 2000), most of them drawing various small carbonate platforms (and smaller islands) separated by deep seaways, such as the Lagonegro trough, the Umbro-Marchean and the Ionian basins. Most of the deeper sea areas originated by extensional movements, mainly from the late Early Jurassic

phase of western Tethys rifting; earlier movements, Triassic in age, are also known (Ciarapica and Passeri, 1998).

The LAC platform was thus frequently described as a Mesozoic shallow water area within an archipelago (Dalla Vecchia, 2003a) that also included some larger carbonate platforms (Apulian, Dinaric-Gavrovo) and by a number of smaller ones mostly recognized underground in wells drilled for oil research. Consistently, during most of the Late Mesozoic, a variable number of more or less small ephemeral islands, including the periadriatic and some more northern platforms, are hypothesized in a 'string of pearls' arrangement between the Gondwana and Laurasia mainlands (Fig. 16). These islands were also considered stepping stones for crossing the seaway that separated the two continents.

This scenario was often the basis for explaining some peculiar features of vertebrate faunas found in those regions. The faunas were described as depauperate (Benton et al., 1997), relict (Signore et al., 2001; Evans et al., 2004), endemic (Grigorescu

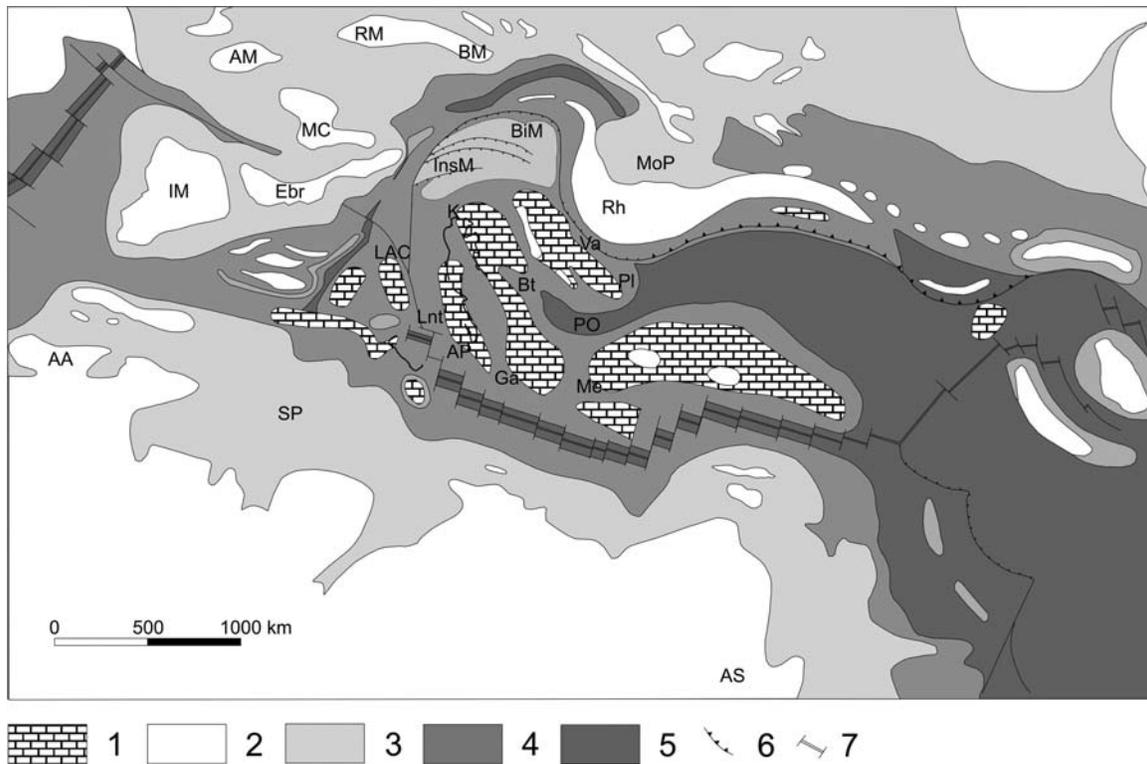


FIG. 16. Paleogeographical map of the periadriatic region in Cenomanian time. 1) Intraoceanic carbonate platforms; 2) exposed lands; 3) epicontinental seas and platforms; 4) slopes and basins; 5) oceanic basins; 6) subduction zones; 7) spreading zones. AA Anti Atlas; AM Aromorican Massif; AP Apulian Platform; AS Arabian Shelf; BIM Bihor Massif; BM Bohemian Massif; Bt Budva trough; Ebr Ebro Massif; Ga Gavrovo; IM Iberian Massif; InsM Insubrian Massif; K Karst; LAC Laziale Abruzzese Campana Platform; Lnt Lagonegro trough; MC Massif Central; Me Menderes; MoP Moesia Platform; PI Pelagonian Zone; PO Pindos Olonos; Rh Rhodope; RM Rhenish Massif; SP Saharian Platform; Va Vardar Zone (after Dercourt et al., 2000 redrawn and modified).

et al., 1999) and dwarf (Benton et al., 1997; Jianu and Weishampel, 1999; Dalla Vecchia et al., 2000; Dalla Vecchia, 2002). The presence of dwarf and endemic faunas was thus considered as further evidence of life in confined environments and of isolation. These characters were considered so important that some land vertebrate-rich outcrops were baptized as the “Hateg Island” (Jianu and Weishampel, 1999) and “Cornet Island” (Benton et al., 1997), thus supporting that scenario, even if contrasting interpretations were also suggested (Jianu and Boekschoten, 1999).

The above described traditional interpretations have already been challenged by the presence of the three dinosaur ichnoassemblages, different in age, found in the Apulian region (see also Dal Sasso, 2003). Since 1999 footprints have been recorded from the Altamura Limestone cropping out in two Early Santonian sites near Altamura town (southern Italy). They were ascribed to medium-sized Ornithischian (more probably to hadrosaurs, Nicosia et al., 2000a, b). Footprints with some characteristics of thyreophoran tracks are also present. Subsequently, theropod footprints were reported from the Hauterivian San Giovanni Rotondo Limestone near Borgo Celano (Gargano Promontory, southern Italy) (Bosellini et al., 2000; Gianolla et al., 2000) and from the Late Jurassic Sannicandro Formation (Gargano

Promontory, southern Italy; Conti et al., in press). The Cenomanian theropod-sauropod association of the Sezze outcrop thus raises to four the presently known track-bearing levels in central and southern Italy in a less than 80 My long time interval. Such overlooked palaeontological data dramatically question previous paleogeographic interpretations. A more or less similar situation was reported by Meyer et al. (2001) and by Meyer and Thuring (2003) for an almost similar situation from the Helvetic domain.

After the Sezze footprint finding a model was needed that would take into consideration the timing of the arrival of dinosaurs in central and southern Italy and their possible immigration route as well as the possibility for dinosaur assemblages to persist in confined areas; the same model had to include an explanation for dwarfing phenomena.

Indeed, dwarfing is not the main problem. It is related to reduced food availability or to the absence of predators and develops in peculiar environmental conditions, through selection pressure, in a population isolated from the bulk of the species at least for some generations. It is a short- or medium-term evolutionary phenomenon, starting to operate after a period ranging from thousands to tens of thousand years (Lister, 1989; Vartanyan et al., 1993). Populations show the

influence of these phenomena only after they lived in a confined space for relatively a long time interval, after that its members would have had breeding opportunities and offspring on which selection could be effective. Consistently a population does not show traces of endemism or dwarfing at the moment of its arrival in a confined area (nor when geographic barriers are established), but only after that the complex assemblage to which it pertains reaches new adaptations to the peculiar features and to the reduced energetic input of the changed environment (Raia et al., 2003).

From the opposite point of view, endemism-controlled dwarfing phenomena can be considered as the indices of an unexpectedly long persistence of a dinosaur or other animal association in a relatively small area, consequently the dinosaur traces evidently do not represent “passing dinosaurs” but the record of a relatively long lasting habitation of those animals within central Tethys areas. In this case one does not assume survivorship of a few individuals but adaptation to an extreme environment of balanced animal assemblages for a sufficient time to allow evolutionary changes. Thus, the survivorship of immigrants must be insured in terms of food and freshwater supply and nesting sites; that is of emerged areas persistent on geological time scales.

Alternatively the presence of long persistent islands during the Cretaceous of the LAC platforms is difficult to hypothesize due to the continuity of marine sediments. Gaps are frequent but, on the geological scale, they represent short time intervals. Thus only a small amount of the total platform area could be considered an emergent area available for land animals. Within the Cretaceous successions, in central and southern Italy, the most evident event that might be interpreted as the longest period of subaerial exposure, includes bauxite levels, gaps, paraconformities and unconformities around Turonian-Coniacian time. This was surely a significant episode but it is not sufficient to explain all the present data, because the events they represent, occurred either far earlier or much later.

The LAC succession is envisaged as having been laid down in a small platform ultimately surrounded by deeper basins beginning in the late Early Jurassic. The dimension of the platform during the Cretaceous did not exceed 250×200 km (also considering a largely accepted NE-SW retro-deformation of nearly 100 km) mainly in predominantly open marine environments with a smaller percentage of inner platform and tidal flat areas. Starting from these dimensions, and taking into account both the small percentage of vegetated areas within the carbonate platforms and the lack of well-established drainage systems, the supply of food and water for large herbivores is still puzzling as well as is the complex food-chain that has to be inferred by the presence of large sized carnivorous. In this geographic and environmental framework, the presence of land animals represents a problem in itself. However, it is mostly when taking into account the presence of large herbivores foraging and walking here and there through these areas, that the

stronger paleogeographic constraints came to light. The most striking problem that arises, when considering the presences of large herbivores in small islands (an enormous herd when considering the Altamura ornithischians), is represented by the quoted dimension of the emergent and vegetated areas needed for food and freshwater availability and by the need for nesting and egg deposition in persistently emergent areas.

In searching for an explanation of the presence of Early Jurassic dinosaurs in an area of the Trento platform (northern Italy), similar to the ones under examination, Leonardi (2000) suggested, among other explanations, an occasional presence on tidal-flat sediments of land animals coming from near emergent areas. Such an interpretation could be accepted as a scenario for platform areas during the Early Jurassic, when they still bordered continents in an early stage of Tethys rifting. When considered in the Cretaceous geographical framework, an occasional presence of sauropods and theropods seems much less probable, taking into account the progressive detachment of these areas from mainlands during the widening of the Tethys.

On the other hand, if the presences of dinosaurs is considered evidence of a long lasting and normal habitation, the number of constraints grows and suggests the need for different solutions.

A NEW HYPOTHESIS

In the described framework, the most parsimonious hypothesis for reaching the minimal dimension suitable to provide food and fresh water for plant-eating animals and to sustain the carnivorous food chain, is to enlarge the available areas linking some or all of the carbonate platforms; such links (continuous or very frequent) might also have allowed intraplate dispersal.

In particular, linking the LAC, the Apulian and the Dinarid-Gavrovo platforms would suggest a shallow water area of nearly 1000×600 km, thus approaching the present dimension of Madagascar. Considering the small percentage of emergent areas inside platforms these dimensions better fit the needs for large land animal habitation.

In light of the above mentioned hypothesis, data already known from different domains surrounding the present Adriatic Sea and frequently neglected become more significant and support the new interpretation of this segment of the Western Tethys. One must re-examine:

- The theropod footprints from the Late Jurassic Sannicandro Formation (Apulian Platform, Conti et al., in press) and from the Hauterivian San Giovanni Rotondo Limestone (Apulian Platform, Bosellini et al., 2000; Gianolla et al., 2000);
- The presence of thousands of ornithischian (probably hadrosaur) tracks in the Santonian Altamura Limestone (Apulian Platform, Nicosia et al., 2000 a, b);
- The presence of the small theropod *Scipionyx samniticus* Dal Sasso and Signore 1998 and of crocodiles, lepidosaurians and amphibians from Lower Albian

limestones at Pietrarroia (LAC, Dal Sasso and Signore, 1998; Signore et al., 2001)

- The so far undescribed hadrosaurs and crocodiles from Santonian-Campanian deposits of the Villaggio del Pescatore, Istria (Arbulla et al., 2001; Buffetaut et al., 2001);
- Theropod, sauropod and ornithopod bones and footprints of the Istria peninsula and of Karst (Hauterivian, Barremian, Aptian, Albian, Cenomanian, Santonian, Campanian, Maastrichtian; see Mezga and Bajraktarević, 1999 and Dalla Vecchia et al., 2000 for a review);
- Dinosaur footprints and bone remains from the Dinaric platform: Cenomanian theropod and titanosaur footprints from Hvar Island, Croatia (Smith, 2004) and Campanian (?Maastrichtian) crocodiles, ornithopods and theropods from Kozina, southwestern Slovenia (Debeljak et al., 2002);
- The presence of dinosaur footprints on the island of Crete (G. Gierlinski, pers. com.);
- The presence of the “Ruvo varanoid” (Varola, 1999) and of the Melissano reptiles (Medizza and Sorbini, 1980) on the Apulian Platform; both findings partial adaptation to marine environment even if the need of near emergent areas has to be hypothesized;
- The still imperfect marine adaptations ascribed to Agialosaurids of Comeno and from the Romano quarry in Istria (Dalla Vecchia, 2003c *cum bibl.*) allow us to hypothesize the need for beach heads;
- Characean-rich levels, indices of freshwater, are widespread throughout the western and eastern Adriatic platforms, mostly during the Aptian-Albian interval (Sirna, 1963; Tunis and Venturini, 2000);
- “Land plants” remains were recently reviewed (Dalla Vecchia, 2000b; Gomez et al., 2002) and revealed they are more widespread than previously believed. Plants are indicated from the Late Barremian to Aptian of the Friuli region (northern Italy) and from Early Aptian in the LAC (Dalla Vecchia, 2000b); from the Lower Albian at Pietrarroia (LAC, Bravi and Garassino, 1998b) and in the Albian sediments of the Alburni Mountains (LAC, Bravi and Garassino, 1998a). Some wide conifer trunks are reported from the Albian of the Trento plateau (Biondi, 1978). A silicified tree trunk was reported from the Aptian-Albian sediments in the Umbro-Marchean domain (central Italy, Deiana and Pieruccini, 1974). Albian-Cenomanian finds are known in the Friuli area (Gomez et al., 2002). Remains of “Sequoia” are recorded in Cenomanian limestone near Manduria in the southern Apulian Platform (Marinosci and Bortoletto, 2003). Late Cenomanian plants are known from near Brescia (northern Italy; Gomez et al., 2002). Cenomanian-Turonian remains are known from near Vicenza, Padova, Trento and

Treviso (northern Italy; Gomez et al., 2002) and from the Furlo area (central Italy; Gomez et al., 2002). Late Cretaceous (Cenomanian-Senonian) remains of land plants were mentioned from the Melissano limestone cropping out near Surbo (southern Italy; Meleleo et al., 1984). Coniacian-Santonian plants were recognized near Vernasso (northern Italy; Gomez et al., 2002). Conifers remains were reported in the Santonian near Polazzo (northern Italy) by Dalla Vecchia and Tentor (2004). Late Santonian plants come from the previously mentioned outcrop of Villaggio del Pescatore near Trieste (northern Italy; Dalla Vecchia, 2000b). Angiosperm, conifers and ferns were also collected from a Santonian outcrop near Apricena on the Apulian platform (Gargano promontory, southern Italy; Morsilli et al., 2002). Land plants are known from Campanian-Maastrichtian deposits at Vesole (LAC, Bravi et al., 1999) and in Late Maastrichtian sediments at Trebiciano (northern Italy; Dalla Vecchia, 2000b). Land plant remains were frequently undervalued, even though they are very interesting and their record is remarkably continuous in time. Most of them were found within very small outcrops both within lagoonal and basinal facies. In most cases they were transported but probably were derived from nearby areas. Moreover, their presence is strongly biased by preservation phenomena and, vice-versa, they were often preserved only within anoxic levels, thus they probably only partially record their continuous occurrence.

All the above listed data can be interpreted as evidence of the persistence of relatively large emergent areas and of the presence of a rich vegetation during the Cretaceous (Fig. 17). It is not parsimonious, on the basis of footprints, to search for separate explanations for ephemeral passages between southern Greece and Apulia, between LAC and Apulia, between LAC and the Istria peninsula and between Istria and Apulia. On the contrary admitting that the periadriatic platforms were joined, provides a single explanation that is sufficient. Contemporaneously, the same explanation could justify intraplate migrations of terrestrial animals.

This seemingly more simple solution encouraged us to analyze the hypothesis of the junction of two or three of the main periadriatic platforms in a larger area to see if it could be consistently defended. The first obstacle to overcome before interpreting the data was to check if major structural obstacles can directly falsify the hypothesis: indeed the interpretation of the periadriatic platforms as a single plate was repeatedly stated (Cati et al., 1989; Schettino and Scotese, 2002; Stampfli and Borel, 2004) thus no obstacles exist from the geodynamic point of view. However, the dispersion of walking animals cannot be explained solely in terms of structural continuity. They also need true environmental stability. For demonstrating a persistent

Age \ Platform	LAC	AP	IP	Di	
Maastrichtian					
Campanian					
Santonian		 			
Coniacian					
Turonian					
Cenomanian	 		   	 	
Albian	  		    		
Aptian					
Barremian			 		
Hauterivian			   		
Valanginian					
Berriasian			 		
Tithonian					

FIG. 17. Scheme summarizing the data that suggest the presence of emergent land on the periadriatic platforms. LAC) Laziale-abruzzese-campana platform; AP) Apulian platform; I) Istrian peninsula; Di) Dinarids. 1) theropod footprints; 2) sauropod footprints; 3) theropod bone remains; 4) sauropod bone remains; 5) ornithopod footprints; 6) crocodyl bone remains; 7) land plants; 8) ornithopod bone remains.

environment other constraints have to be considered such as the type and the continuity of the deeper intraplate basins that bordered the carbonate platforms.

To validate the hypothesis these basins cannot be true persistent barriers but only discontinuous obstacles, at least sometimes easily crossable by land animals. Two secondary hypotheses could be considered: either such deeper areas could be overcome only periodically (e.g., during periods of lowering of water level) or some links were persistent.

According to the most recent data the maximum sea-level fall during the Cretaceous was around 200 m, too little to allow to the emergent passages through the basinal areas. Thus, temporary linking can be admitted only by hypothesizing either the formation of tectonically controlled ephemeral bridges or simultaneous sea-level changes and tectonic uplift. A Coniacian, tectonically controlled, marginal bulging of Adria plate is advocated by Mindszenty et al. (1995) to explain a general uplift and the related widespread occurrence of Turonian bauxite

horizons in the region (D'Argenio and Mindszenty, 1987). The bulging would have been caused by the northeastern collision of Adria after the closure of the Vardar Ocean. Even accepting this option, this event would have occurred too late to justify the presence of Early and lower Late Cretaceous dinosaurs. This solution is thus not sufficient to explain all the data.

The second possibility allows the existence of some "pedestrian passages" between the platforms, today buried and/or hidden by the following compressive tectonics. In this hypothesis the carbonate platforms would not have been separated by continuous basins, but would have been locally connected to each other.

Even if both solutions could explain most of the data concerning intraplate migrations, neither gives an explanation for the original provenance of the Cretaceous dinosaur found in central and southern Italy; thus a link with one or both the nearby mainlands has to be hypothesized. This complex situation was already examined by Dal Sasso (2003) and Dalla Vecchia (2003a, b). The former stated that large dinosaurs could only survive in terrestrial ecosystems and that periadriatic platforms acted as temporary continental bridges between Laurasia and Gondwana (Dal Sasso, 2003). Dalla Vecchia (2003 a, b) suggested for the Adriatic-Dinaric carbonate platform, an Early Cretaceous African connection and a more insular Late Cretaceous condition. Nevertheless some northern links would have allowed hadrosaur immigration in these areas during the Late Cretaceous (Dalla Vecchia, 2003 a, b).

Indeed, paleontological data can also be useful regarding this topic, even if a more complete analysis is needed to fully reveal their potential.

The skeleton of the Albian theropod *Scipionyx samniticus* Dal Sasso and Signore 1998, reveals both ancestral and derived characters. According to Dal Sasso (2003) this mix could be ascribed to isolation and genetic drift (the presence of more derived characters, shared with other forms, could have been reached by convergence). Accepting this hypothesis an immigration into southern Italy has to be considered, followed by a period of isolation long enough to justify such endemism-controlled evolutionary changes. From the same outcrop a suite of small terrestrial lepidosaurians and amphibians is known. Some European affinities were ascribed to these animals, and the fossil-bearing deposits were palaeogeographically set in an area that "... formed a small emergent carbonate platform that was a part of a longer arc close to the shores of Gondwana, although the recovered tetrapod fauna is primarily Laurasian in character." (Evans et al., 2004, p. 406). This cautious sentence is either evidence of a paleontological problem (too scattered findings or too few known outcrops) or it admits to a problematic Aptian connection northward to Europe. The last connection of the Adria plate to Laurasia, before their ultimate Late Cretaceous aggregation, was during the Bathonian (Schettino and Scotese, 2002) and persistence of an isolated fauna in a small island for more than 40 My seems at the best improbable. Thus an Aptian link of LAC with Africa is suggested.

Accepting the hypothesis of the presence of titanosaurs in the Cenomanian Sezze outcrop one also has to take into consideration the occurrence of titanosaurs on the Istria platform. There Barremian bone-rich deposits include titanosaurs bones ("...sauropods are the most common dinosaurs and Titanosauriformes appear to be the most common sauropods in the sample..."; Dalla Vecchia, 2003b) and Cenomanian footprints are ascribed to *Titanosaurimanus nana* Dalla Vecchia and Tarlao 2000. Moreover Cenomanian footprints ascribed to titanosaurs were recently reported from the Dinaric platform (Hvar Island, southern Croatia; Smith, 2004). Also worth mentioning are the data of Milner (reported in Skelton, 2003, p. 49) suggesting that titanosaurs moved from Africa to Europe in the Early and Late Cretaceous. Moreover Czerkas and Czerkas (1993) suggest a northward migration from Africa through the islands or tongues of emergent land that became the future terrain of Spain or Italy. Thus one can accept the hypothesis of a Cenomanian migration from Africa into central Italy. The hypothesis of an "African genesis" seems at the present the most probable for explaining the presence of such forms in the LAC domain. Titanosaurs are unknown in Europe until the Campanian (Upchurch et al., 2004). In this light a Cenomanian passage among Istrian, Dinaric and LAC platforms might be accepted and a connection to Gondwana has to be considered in pre-Cenomanian times. If the above mentioned hypotheses could be confirmed, and considering that the Iberian Massif was probably separated from Africa by the Jurassic ocean (Schettino and Scotese, 2002; Holtz et al., 2004a), a subsequent emigration from there toward Europe can also be hypothesized.

Furthermore, Dal Sasso (2003) on the basis of the presence, in the Santonian-Campanian hadrosaurs from the Villaggio del Pescatore (Trieste; northern Italy), of less derived characters in respect to the ones evident in the Campanian-Maastrichtian hadrosaurs from Transylvania, suggested that "... the ancestor of *Telmatosaurus* could have walked on dry land to the Hateg region via the Austro-Alpine block." (Dal Sasso, 2003 p. 59). Russell (1993) stated that basal hadrosaurs originated in Gondwana, and that some subsequently immigrated into Europe. Given that hadrosaurs are to date unknown in Africa and an immigration from Gondwana does not, therefore, seem justified, Horner et al. (2004) suggest an Early Cretaceous dispersal event from North America to Europe. In this case the presence of hadrosaurs in Istria could be better interpreted as evidence that there had been southward immigrations into the Adriatic platforms (from southern Europe?) in the pre-Santonian, and from there back to south-eastern Europe in pre-Campanian times. In this case one might also ascribe the presence of hadrosaurs in Apulia to the same dispersal event, thus suggesting a Santonian link between the Apulian region and the Istrian peninsula.

Following this analysis it is possible to interpret all these events as geographical constraints that can be arranged in chronological sequence as follows:

- African connections (repeated or continuous) during the Berriasian to Aptian with LAC, Apulian and Trieste areas are necessary to explain the theropod association of Sannicandro, S. Giovanni Rotondo and Pietraroia and the theropod-sauropod association of the Istrian peninsula;
- a pre-Cenomanian connection of Dinaric, Istrian and LAC domains with Africa and thus with each other, is necessary to allow the sauropod immigration into those areas;
- a Turonian and Coniacian uplift and widespread emergence of large areas of the periadriatic platforms;
- a pre-Santonian migration from north or northeast to Istria and Apulia is needed to justify hadrosaur presence in both regions; and
- a pre-Campanian link from Istria to southern Europe is needed to allow northward emigrations of hadrosaurs and titanosaurs.

Summarizing, in the light of the available data, an almost continuous link among the main perimediterranean Mesozoic carbonate platforms could be hypothesized as well as some long-lasting links between Adria and the Gondwana and Laurasia mainlands. Consistently, one is obliged to postulate a delay in the ultimate opening of the southern seaways at least until the earliest Cenomanian. This scenario also supports the hypotheses of Russel (1993) of an Afro-European filtering bridge during the Late Cretaceous and of Le Loeuff (1991) on Gondwana, influences on southern Europe faunas.

The younger northward link could be ascribed to an early collision (Coniacian) between the Adriatic platforms and southern Europe allowing basal hadrosaurs to immigrate from Asia during the Coniacian and to emigrate toward Europe (through Transylvania?) during the Late Campanian. If an African origin is confirmed for Early Maastrichtian titanosaurs characterizing European deposits, the same passage could also have been used by these sauropods.

In conclusion connections between Gondwana and the periadriatic platforms, might be accepted, at least from Late Jurassic to Cenomanian times and connections to the southern margin of Laurasia at least from Coniacian to Maastrichtian.

CONCLUSIONS

On the basis of paleontological data, mainly on dinosaur footprints, changes in the relative positions of some carbonate platforms during the Cretaceous in the perimediterranean segment of Western Tethys are suggested. For Cretaceous time, a scenario is depicted in which the main periadriatic carbonate platforms were almost continuously linked. In this hypothesis they were not subdivided by continuous shoestring-shaped basins. The deeper areas were probably just marginal embayments. Furthermore these platforms might have been frequently, or almost continuously, connected to southern (Gondwana) and, starting from Coniacian times, to northern

(Laurasia) mainlands. Consistently the timing of plate motion as well as the amount of extension should be reconsidered for this portion of the Tethys Ocean. This solution, explaining multiple effects with a single cause, corresponds well to the “Occam’s razor” principle, even though further data could falsify this scenario.

Irrespective, the above interpretation suggests that, in future paleogeographic modeling requires more attention to palaeobiological data.

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