

Dinosaur track sites in the upper Cenomanian (Late Cretaceous) of Istrian Peninsula (Croatia)

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ABSTRACT – Four late Cenomanian sites with dinosaur footprints are here reported from the Istrian coast (NW Croatia). Footprints are preserved in marine limestones of the Cretaceous Adriatic-Dinaric Carbonate Platform. The presence of dinosaurs suggests the existence of emergent areas on the carbonate platform despite the fact that the late Cenomanian is considered an interval of sea level highstand and the geologic evidence of emersion of the platform is very scarce in Istria. The most common dinosaurs are medium-sized bipeds, most probably theropods. Unusually small sauropods are also present in at least two sites. Absence of large predators and of large plant-eating dinosaurs could be due to an insular habitat by analogy with the presence of a similar association in the upper Albian of Istria and in agreement with the paleogeographic reconstructions of central Tethys.

RIASSUNTO – [Siti con impronte di dinosauri nel Cenomaniano superiore (Cretaceo superiore) della Penisola Istriana (Croazia)] – Quattro siti del Cenomaniano superiore con orme di dinosauro vengono segnalati nella costa Istriana (Croatia nord occidentale). Le orme sono conservate in calcari marini della piattaforma carbonatica Adriatica-Dinarica del Cretaceo. La presenza di dinosauri suggerisce l'esistenza nella piattaforma di aree emerse nonostante che il Cenomaniano superiore sia considerato un intervallo di alto stazionamento marino a livello globale. I dinosauri più comuni erano bipedi di medie dimensioni, molto probabilmente teropodi. Anche sauropodi di dimensioni particolarmente ridotte sono presenti in almeno due siti. L'assenza di grandi predatori e di grandi vegetariani potrebbe essere dovuta all'habitat insulare, in analogia con la presenza di una simile associazione nell'Albiano superiore dell'Istria e in accordo con le ricostruzioni paleogeografiche della Tetide centrale.

INTRODUCTION

Before the beginning of our field research in 1993, the only Cenomanian track site in the Istrian region (NW Croatia) reported in the literature was that of Fenoliga (known also as Fenolega), a small islet near the southern point of the Istrian peninsula. This site was mentioned for the first time in the literature by Gogala (1975) and was described by Gogala & Pavlovic (1978), Tišljarić *et al.* (1983), Leghissa & Leonardi (1990), and Pavlovic & Gogala (1993). However, none of these papers described the whole outcrop and all the dinosaur tracks actually preserved.

Here we describe in detail the Fenoliga site and other three sites, one new and two others which previously have been only briefly reported in the literature (Dalla Vecchia, 1998; Dalla Vecchia & Tarlaio, 1995; Dalla Vecchia & Venturini, 1996).

Dinosaur tracks have also been noted by occasional visitors on Unije island of Quarnaro (W Croatia), just south to the region here considered. This record was noted by Dalla Vecchia & Tarlaio (1995). F.M. Dalla Vecchia and A. Tarlaio visited Unije on September 1995. They surveyed the southeastern coast of the island without finding any dinosaur evidence. The northeastern coast of the island, which can be reached only by boat, was later surveyed by

Mrs M. Nikolić, inhabitant of the island, who sent us the photographs of every structure which was reminiscent of a tridactyl dinosaur footprint. Only one of the photographed structures could actually be a dinosaur footprint, possibly belonging to a medium-sized bipedal individual. Cross-sections of rudist shells can be recognized on the footprint-bearing surface and the surrounding layers contain the oyster-like bivalve *Chondrodonta*, which is particularly frequent in the middle-late Cenomanian.

This paper is the second contribution dedicated to a detailed description of the dinosaur ichnological record of Istria; the first was dedicated to two new Albian sites (Dalla Vecchia, Tarlaio, Tunis & Venturini, 2000).

F.M. Dalla Vecchia is responsible for the paleontological and paleogeographical part of this paper, S. Venturini and G. Tunis prepared the sedimentological-stratigraphical section, and A. Tarlaio discovered the sites and helped in the field work.

Sometimes we report two names for each locality because the part of the Istrian region where footprints are found is bilingual (Italian and Croatian).

Abbreviations: A = pace angulation, A° = interdigital angle, AWS = average walking speed, d = length of the part of digit III projecting beyond ends of II and IV, h = height at hip, L = footprint length,

Lm = length of manual print of quadrupedal trackmakers, Lp = length of pedal print of quadrupedal trackmakers, M = average value, R = length of the rear of the pedal print, SL = stride length, V = velocity, W = footprint width of tridactyl footprints, Wm = width of manual print of quadrupedal trackmakers, Wp = width of pedal print of quadrupedal trackmakers.

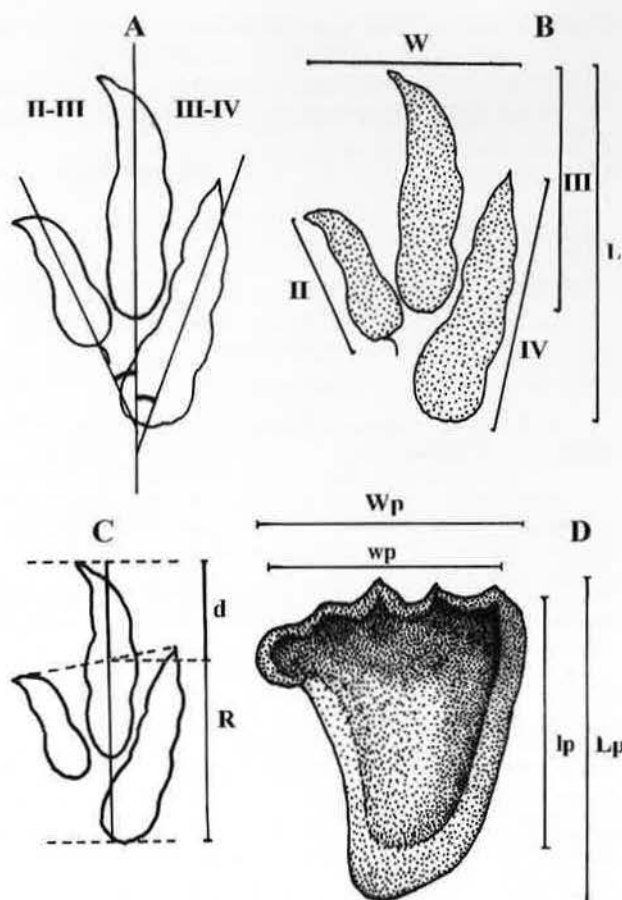
METHODOLOGY

The English terms concerning vertebrate paleoichnology mainly follow Farlow and Chapman (1997). According to W.A.S. Sarjeant (pers. comm., May 1998) "track" is a sequence of footprints and "trackway" is the area occupied by the tracks. We follow here this orthodox use, despite the fact that the term "track" is often used in the literature as a synonym of "footprint", and "trackway" is considered as a sequence of footprints. We use the terms "gait" and "trotting gait" in the sense of Thulborn (1990).

We do not use the words "continent" and "continental" in the geological sense of "continental crust" as opposed to "oceanic crust". "Continent" is intended in the geographical meaning of "wide emergent area" opposed to "island", a small emergent area.

All the surfaces with footprints were mapped. We outlined with chalk the margins of the footprint and all the other visible features, including the displacement rims, when the light was the best possible to identify them; then we made a copy on wide, transparent sheets of polyethylene stretched out on the footprint-bearing surface, using an indelible felt pen. In this way we obtained an exact reproduction of the structures we have recognized in the field and we were able to work on them and reproduce the footprint-bearing surface in the laboratory, when necessary. Then the map was reduced photographically and by computer to the final size for printing. The better preserved and the most interesting footprints were cast with silicon rubber or plastiline. Measurements were taken mainly on the tracings and on casts because of the always difficult logistic situation of the sites (bad illumination, weather problems, access problems, war hazards etc.). Drawings of the footprints were prepared by tracing photographs with the casts of the specimens at hand.

Here we will consider as "small bipedal dinosaur footprints" those with $L < 15$ cm and "mid-sized" those with $15 < L < 25$ cm. Thulborn (1990) used the category "small bipedal dinosaur" for those tridactyl prints with $L < 25$ cm, but we think it is useful to make a further distinction. The footprints belonging to a track often have different lengths. Therefore the height at hip (h) was calculated using the mean of L if footprints were not very deformed or not poorly preserved; the length of the less deformed or best preserved footprint was used if lengths of other footprints were not reliable. Height at hip is the size parameter for trackmakers and is used in speed estimates (see below).



Text-fig. 1 - A-C) Parameters of tridactyl footprints, D) parameters of sauropod pedal prints. Legend: II, III, IV = length of digit II, III, IV; II-III = interdigital angle II-III°; III-IV = interdigital angle III-IV°; d = length of the projecting part of digit III; L = footprint length (of tridactyl footprints); Lp = outer pedal print length; lp = bottom pedal print length; R = length of the rear of the pedal print (of tridactyl footprints); W = footprint width (of tridactyl footprints); Wp = outer pedal print width; wp = bottom pedal print width.

The interdigital angle is calculated as shown in Text-fig. 1A.

The relative projection of digit III (R/d) was obtained from measurements taken on footprints by the method shown in Text-fig. 1C. Because of the non-optimal preservation of the footprints, mainly the frequent absence of one or more of claw marks or/and the elongation of "heel" because the foot had slipped, the R/d ratio is just indicative.

The stride SL in the tracks of bipedal trackmakers is measured taking as reference point the proximal termination of digit III print, which is nearly always preserved and is usually the less ambiguously defined digital mark.

SL/h is indicative of the gait of the trackmaker. According to Thulborn (1990, p. 260) SL/h less than

2 indicates a walking gait, between 2 and 2.9 a trotting gait and greater than 2.9 a running gait.

Speed (V) is calculated by the equation of Alexander (1976) $V = 0.25 \times g \times 0.5 \times SL^{1.67} \times h^{-1.17}$. The critical parameter in this equation is the height at hip (h), because there are many different ways to estimate it. For the reasons explained in Dalla Vecchia & Tarlaio (2000, p. 230), we choose the morphometric ratios method ($h = 4.6L$, for small bipedal dinosaurs with $L < 25$ cm) for h estimates. This permits a better comparison with the AWS (see below), because the formula to calculate AWS is based on data from bipedal dinosaurs in general (Thulborn, 1990). For quadrupedal tracks $h = 4Lp$ according to Alexander (1976).

The mean of SL is used to calculate SL/h and V in short and long tracks. SL is highly variable in the latter; for this reason in two cases we plotted the variation in this parameter along the track.

The Average Walking Speed (AWS) is the speed that we would expect from a dinosaur with a height at hip h had it walked with the average gait expected for individuals of comparable size belonging to its taxonomic group ($SL/h - 1.29$ for bipedal tridactyl trackmakers, calculated on a sample of 400 tracks; see Thulborn, 1990, p. 293). AWS is useful to understand whether the trackmaker was going faster or not with respect to the expected walking speed on the basis of individuals of similar size in Thulborn's sample. AWS is calculated here by the equation 10.6 of Thulborn (1990) for bipedal tridactyl trackmakers and by his equation 10.8 for quadrupedal trackmakers.

The direction (D) of the tracks, of the footprint pair and of each single isolated footprint is measured as azimuthal angle and plotted to check whether there are preferential directions. Of course, what we measured are the directions with respect to the present day position of the north: they are not the original directions of the trackmakers, since Istria rotated counterclockwise about 50° , mainly after middle Eocene times (Marton *et al.*, 1995).

When the longitudinal axis of the footprint is directed inward or outward with respect to the midline of the trackway, we use respectively the term "inward rotation" and "outward rotation".

All the footprints are negative (concave) epireliefs.

We created acronyms for the tracks and single footprints with letters corresponding to the locality (for example, FEN = Fenoliga islet site, SLD = S. Lorenzo di Daila/Lovrečica site). This abbreviation, followed by a number, identifies a single tridactyl footprint (for example, SLD16). The letter T identifies a track (for example, SLD-T1), the letter S a sauropod footprint or track (for example, FEN-ST1). Letters p and m distinguish sauropod manual and pedal prints. For each footprint of a track there are a couple of numbers, the first indicating the track, the second the footprint (for example, FEN-T1-1) according to the direction of movement.

All the data are available at the Museo Paleontologico Cittadino di Monfalcone or from E. M. Dalla Vecchia (e-mail: fabdalla@tin.it).

AGE AND PALEOENVIRONMENT

The four sites here described are, from north to south, S. Lorenzo di Daila/Lovrečica, Carigador/Karigador, Grakalovac (reported in literature also as Promontore/Premantura site), and Fenoliga or Fenolega (Text-fig. 2). They occur in a thick sequence of Cretaceous marine carbonates outcropping along the Istrian coast (see for example, Tišljär *et al.*, 1983; Vlahović *et al.*, 1994; Velić *et al.*, 1995).

Their dating to the late Cenomanian is based on foraminiferal associations found in the sites. The foraminifers with biostratigraphic importance found in the samples from S. Lorenzo di Daila/Lovrečica site are *Vidalina* cf. *hispanica* Schlumberger, *V. cf. radoici-cae* Cherchi & Schroeder, *Broeckina* (*Pastrikella*) *bal-*



Text-fig. 2 - Late Cenomanian sites with dinosaur footprints in Istria. 1) S. Lorenzo di Daila/Lovrečica (Umag/Umag), 2) Carigador/Karigador, 3) Grakalovac (Promontore/Premantura), 4) Fenoliga islet.

canica Cherchi, Radoičić & Schroeder, *Chrysalidina gradata* d'Orbigny and *Biconcava bentori* Hamaoui & Saint-Marc. Among the foraminifers found in the samples from Carigador/Karigador there are *Broeckina balcanica*, *Vidalina* cf. *hispanica*, *V. radoicicae*, *Chrysalidina gradata* and *Biconcava bentori*. In the samples from Grakalovac site we found *Merlingina cretacea* Hamaoui & Saint-Marc, *Broeckina balcanica*, *Vidalina* sp., *Pseudorhipidionina* cf. *casertana* De Castro, *Pseudorhapydionina* cf. *dubia* (De Castro), *Chrysalidina gradata* and *Pseudolituonella* sp. The footprint-bearing level of Grakalovac can be correlated as approximately in the same stratigraphic position of that of Fenoliga, few kilometres away, also on the basis of a marker bed made of large bivalves (inoceramids?), found in the both outcrops. Finally, in the samples from Fenoliga site *Biplanata peneropliformes* Hamaoui & Saint-Marc, *Broeckina balcanica*, *Vidalina* cf. *hispanica*, *Pseudorhapydionina dubia*, *Chrysalidina gradata* and *Biconcava bentori* are present.

In the biozonation of the Cenomanian of NW Istria by Vlahović & Velić (1994) *Vidalina* cf. *hispanica* is found only at the very beginning of the assemblage zone CEN-5, i.e. at the base of the upper Cenomanian. The only other species of *Vidalina* (*V. radoicicae*) occurs only in CEN-5. *Broeckina balcanica* is found in the zones CEN-4 (upper part of the middle Cenomanian) and CEN-5, with an acme in the latter. *Biconcava bentori*, *Pseudorhapydionina dubia* and *Biplanata peneropliformes* occur from the middle of the CEN-4 to the end of CEN-5. *Chrysalidina gradata* is present in CEN-3 to CEN-5, i.e. in the whole middle-upper Cenomanian.

Therefore, the footprint-bearing sites are situated in the upper Cenomanian, probably at the base of the upper Cenomanian. The Fenoliga outcrop was dated as late Cenomanian on the basis of the foraminiferal content of the samples also by Leghissa and Leonardi (1990, p. 12) and as middle-late Cenomanian by Mezga & Bajraktarević (1999) on the basis of the presence of *Broeckina* cf. *balcanica*.

Cenomanian limestones outcrop like an elongated and nearly continuous band from the northwestern to the southwestern extremities of the peninsula (e.g. Tišljarić *et al.*, 1983; Vlahović *et al.*, 1994). Footprint sites are found where this band reaches the present-day coastline, i.e. at the extremities of the band.

The section containing the footprint-bearing layer of the S. Lorenzo di Daila/Lovrečica site is shown in Text-fig. 3A. The footprint-bearing layer is a rudstone with abundant muddy matrix, with rounded micritic-microsparitic clasts and a graded structure. The clasts sometimes include miliolids; desiccation structures and vadose silt are also observed. This suggests sedimentation caused by storms in an inter-supratidal environment. Storms eroded and transported mud clasts from the lagoon and clasts of partially altered sediments from supratidal settings. This situation resembles that of Grakalovac site (see below) where,

however, the sedimentation probably occurred in an intertidal-subtidal setting. There are mounds with radiolitic rudists and the oyster *Chondrodonta* just above the footprint-bearing layer of the S. Lorenzo di Daila/Lovrečica site. In the same section, stratigraphically few metres above the footprint-bearing layer, knoll-shaped stromatolites can be observed.

The upper part of the footprint-bearing layer of the Carigador/Karigador site differs from that of S. Lorenzo di Daila/Lovrečica. It is a fossiliferous wackestone with widespread evidence of desiccation, deposited in an open lagoonal environment sometimes subject to emersion. It is covered by a thin layer (1.5 cm) of irregular bands of wackestone-packstone-grainstone containing pellets, peloids and the algae *Thaumtoporella* sp.. The environment of deposition of this layer was probably a tidal-flat. Alternations between these two facies and, less common, floatstones with radiolitic rudists and *Chondrodonta* sp., characterize the whole investigated section (Text-fig. 3B). Just above the footprint-bearing layer there is a thinly bedded interval 20 cm thick; mud-cracks are observed about one metre above the latter.

The section containing the footprint-bearing layer of the Grakalovac site is shown in Text-fig. 3C. In this section the footprint-bearing layer appears as a packstone-rudstone with micritic clasts and foraminifers (Miliolidae, Ophthalmitidae, fragments of *Broeckina balcanica* and *Biconcava bentori*). There are mounds with radiolitic rudists and a thick bed of large bivalves (inoceramids?) a few metres below the layer.

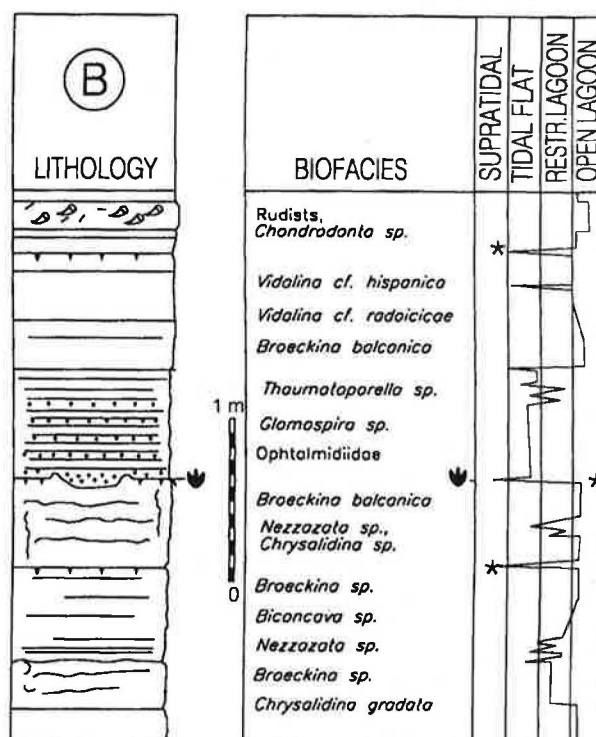
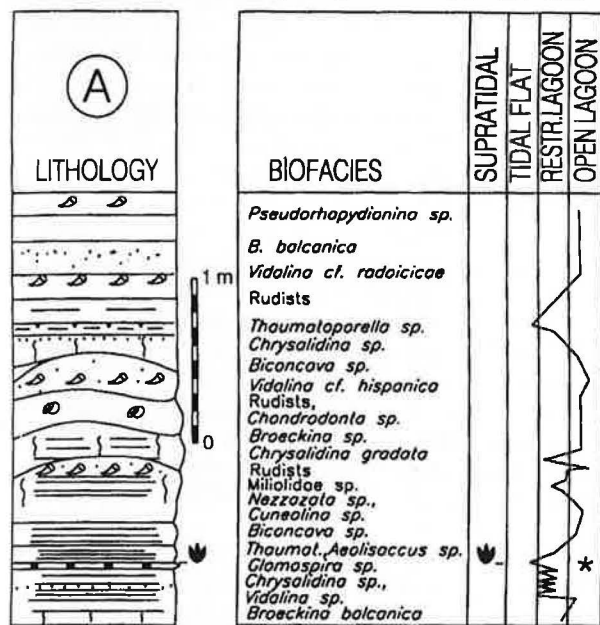
The section containing the footprint-bearing layer of the Fenoliga site is shown in Text-fig. 3D. The footprint-bearing layer is a bioclastic wackestone with fragments of rudist bivalves and foraminifers (Miliolidae, *Broeckina balcanica*, *Cuneolina* sp., etc.). Desiccation structures (microvacuities with sparry calcite, mud-cracks) and vadose silt are also observed. The footprint-bearing layer is covered by a slightly dolomitized mudstone with ostracods.

Summarizing, the segment of the sequence where the footprints are preserved is characterized by mounds with radiolitic rudists and *Chondrodonta*, and is dominated by floatstones with rudist bivalves, and bioclastic and fossiliferous wackestones and packstones. The environments are usually those of an open lagoon (subtidal) with generally rapid and short-lasting episodes of tidal flat deposition.

The identification of long-lasting emersions in Istria and in the Karst region during the middle-late Cenomanian is one of the objectives of our future research. No geological evidences of prolonged emersion of the carbonate platform (bauxites, fresh-water marl levels, pedogenetic breccias etc.) or long-lasting hiatus are found in the middle-upper Cenomanian of Istria (e.g. Velić *et al.*, 1995; Vlahović *et al.*, 1994; Vlahović & Velić, 1994). In contrast, they are relatively common in other segments of the carbonate platform sequence of the region (e.g. Dini *et al.*,

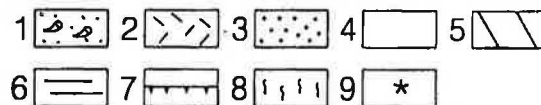
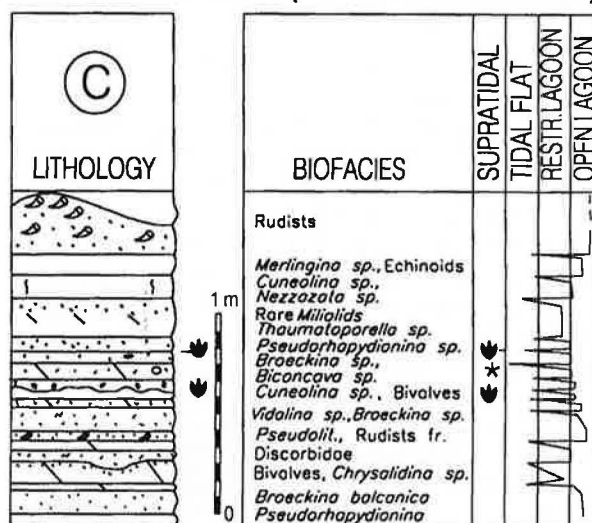
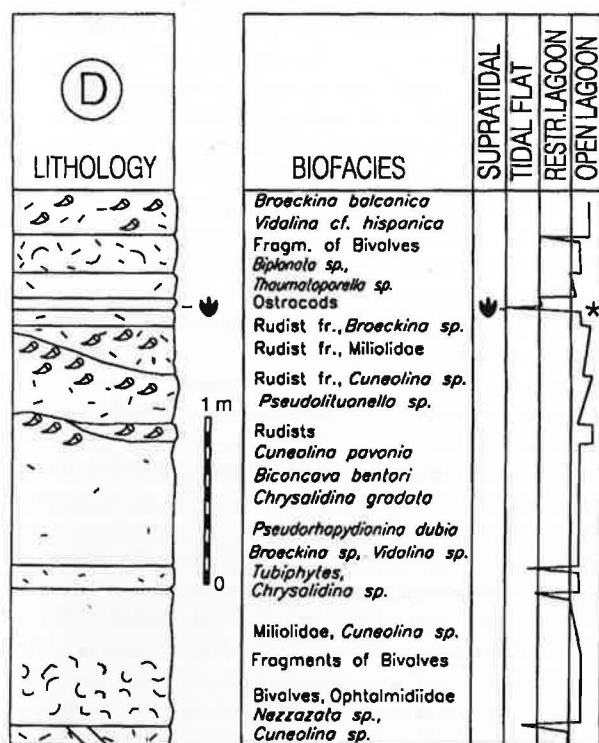
LOVREČICA - S. LORENZO DAILA

KARIGADOR-CARIGADOR



FENOLIGA ISLET

GRAKALOVAC (PROMONTORE)



Text-fig. 3 - Short stratigraphic columns of the sections containing the footprint-bearing levels: A) S. Lorenzo di Daila/Lovrečica, B) Carigador/Karigador, C) Grakalovac (Promontore/Premantura) and D) Fenoliga islet. Legend: 1) floatstone with rudists, 2) fossiliferous intraclastic packstone, 3) pelletiferous packstone, 4) wackestone/mudstone, 5) dolostone, 6) laminations, 7) mud cracks, 8) bioturbation, 9) desiccation microstructures.

1998; Dalla Vecchia *et al.*, 2000; Matičec *et al.*, 1996; Tunis & Venturini, 2000). Desiccation structures and vadose silt are usually found in the sections of the Cenomanian sites only in association with the footprint-bearing levels. The Cenomanian facies are decidedly more "open" (i.e. subtidal with rich and diversified foraminiferal associations) than those with footprints of the Hauterivian, upper Barremian and upper Albian.

THE SITES: S. LORENZO DI DAILA/ LOVREČICA (SLD)

A single footprint-bearing surface occurs in the site. The main exposure outcrops as a narrow band (see Pl. 1A and Text-fig. 4) along the coast just south of S. Lorenzo di Daila/Lovrečica (Umago/Umag; NW Istria). Another outcrop of the same surface is exposed a dozen of metres more to the south. This latter outcrop was not studied in detail since it bears only a few, badly preserved tridactyl footprints similar to those of the main outcrop.

PALEOICHOLOGICAL DESCRIPTION

Casts were taken of prints SLD-T1-1, 3, 5, 6, 9; SLD-T2-2, 3, 4, 5; SLD-T3-1; SLD-T4-1, 2; SLD-T5-1, 2; SLD-T6-1; SLD-T7-1; SLD-T9-1, 2; SLD-T10-1; SLD-T11-1; SLD-T12-1; SLD-T14-10; SLD-T15-1,7; SLD16, SLD18, SLD19. They are stored at the Museo Paleontologico Cittadino of Monfalcone.



Text-fig. 4 - The S. Lorenzo di Daila/Lovrečica site. A. Tarlao stands on the footprint-bearing surface (see Pl. 1A).

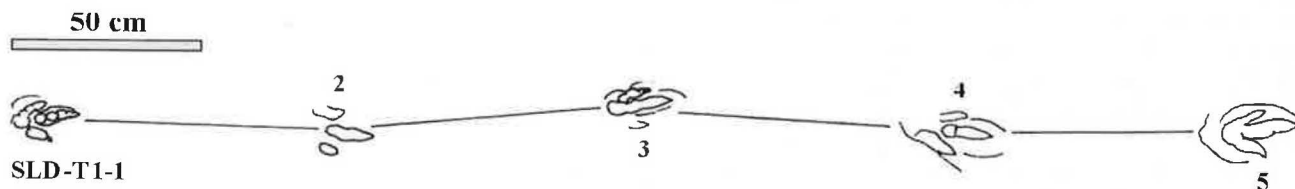
Because the footprint-bearing surface is exposed along the shore, it suffered marine corrosion (i.e. carbonate dissolution) and is usually flooded by the sea during storms. As a consequence, the state of preservation of the footprints is not good.

Five short tracks, seven probable but very incomplete tracks, three pairs of footprints, and four single footprints, for a total of 58 footprints, were identified on the main outcropping surface. All the footprints were impressed by functionally tridactyl mesaxonid feet of bipedal, small to medium-sized dinosaurs; only one reaches 25 cm in length. The footprints are rather shallow, some because they are still partly filled in by the original sediment. L ranges from 14.5 cm to 25 cm. Most of the L values are grouped in the interval 17.5-22.5 cm without a marked mode; only two smaller and two larger trackmaker are out of this group.

We briefly describe the five most complete track segments (Tab. 1).

SLD-T1 (Pl. 1A; Text-figs 5, 6, 7A1-5) is a segment with nine consecutive footprints; T1-8 cannot be identified. L ranges from 21.5-18.5 cm ($M = 20.4$ cm), W/L is rather constant (0.62-0.70; $M = 0.63$) and indicates rather slim, elongated footprints. A° ranges from 22° - 50° ($M = 39.6^\circ$; $N = 5$), R/d ranges from 1.05-1.50 ($M = 1.35$; $N = 4$). T1-5 is the most distinctive footprint, with a raised displacement rim, but it is still partly filled in (Text-fig. 6). The digit III print is much longer than the other two, as can be observed in T1-1 (Text-fig. 7A1), T1-5 (Text-fig. 7A3) and T1-9 (Text-fig. 7A5) (R/d is 1.40 in T1-5). Digit III is sigmoid and slightly wider midway along its length than proximally. The end of the digital print is triangular and pointed, but without a separated claw mark. Digit IV is slightly sigmoid in T1-1 and 5, and digit II is curved medially. Both are narrow distally, but no clear claw marks can be seen. In T1-5 the print of digit IV seems to be proximally fused to that of digit III, but this is not actually the case as can be seen in T1-1, 6 and 9. The track is directed straight to NW, and footprints show a clear outward rotation (Text-fig. 5). SL ranges from 162-170 cm ($M = 165.9$ cm), A 173° - 178° ($M = 175.2^\circ$). SL/h using M values is 1.77, indicative of a fast walking gait.

SLD-T2 (Pl. 1A; Text-figs 7J1-3) is a sequence of five consecutive footprints. L ranges from 14.5 to 16 cm ($M = 15.7$ cm), W/L from 0.58 to 0.65 ($M = 0.61$), A° ranges from 28° - 40° ($M = 34.7^\circ$), R/d is 1.24



Text-fig. 5 - Track SLD-T1, S. Lorenzo di Daila/Lovrečica site. Note the outward rotation. Scale bar = 50 cm.



Text-fig. 6 - The footprint SLD-T1-5. Scale bar = 10 cm.

and 1.40. The two better preserved footprints (SLD-T2-2 and 3; Text-fig. 7J1-2) differ slightly each other in the shape of digit IV, which is slightly sigmoid and narrow in T2-3 and wider and straight in T2-2. Digit III is decidedly longer than digit II and IV. In T2-2 digit III is wider in its middle portion and the distal end is triangular and sharply pointed, but without a claw mark separated from the preceding pad print. SLD-T2-5 (Text-fig. 7J3) has the prints of digits II and IV like those in PR-T1 and PR-T3 (see below) and has a digit III print which is narrower and more sigmoid than those of SLD-T2-2 and 3. The track is directed straight to the WSW, and footprints show a slight outward rotation. SL ranges from 117.5-121 cm ($M = 118.8$ cm), A from 171° - 174° ($M = 172.3^\circ$). SL/h using M values is 1.64 indicative of a fast walking gait.

SLD-T3 (Pl. 1A; Text-fig. 7I) is a segment of four consecutive footprints; T3-4 is only partly preserved. L ranges from 21 to 18 cm ($M = 19.3$ cm), W/L from 0.55 to 0.74 ($M = 0.62$), A° is 53° , R/d is rather high (about 1.80) in T3-1 (Text-fig. 7I), the best preserved footprint. This has a very slightly sigmoid digit III without a pointed end. The track is directed straight

to WNW and footprints show a very slight inward rotation. SL ranges from 139 to 145 cm ($M = 142$ cm), A is 163° - 167° . SL/h using M values is 1.60, indicative of a fast walking gait.

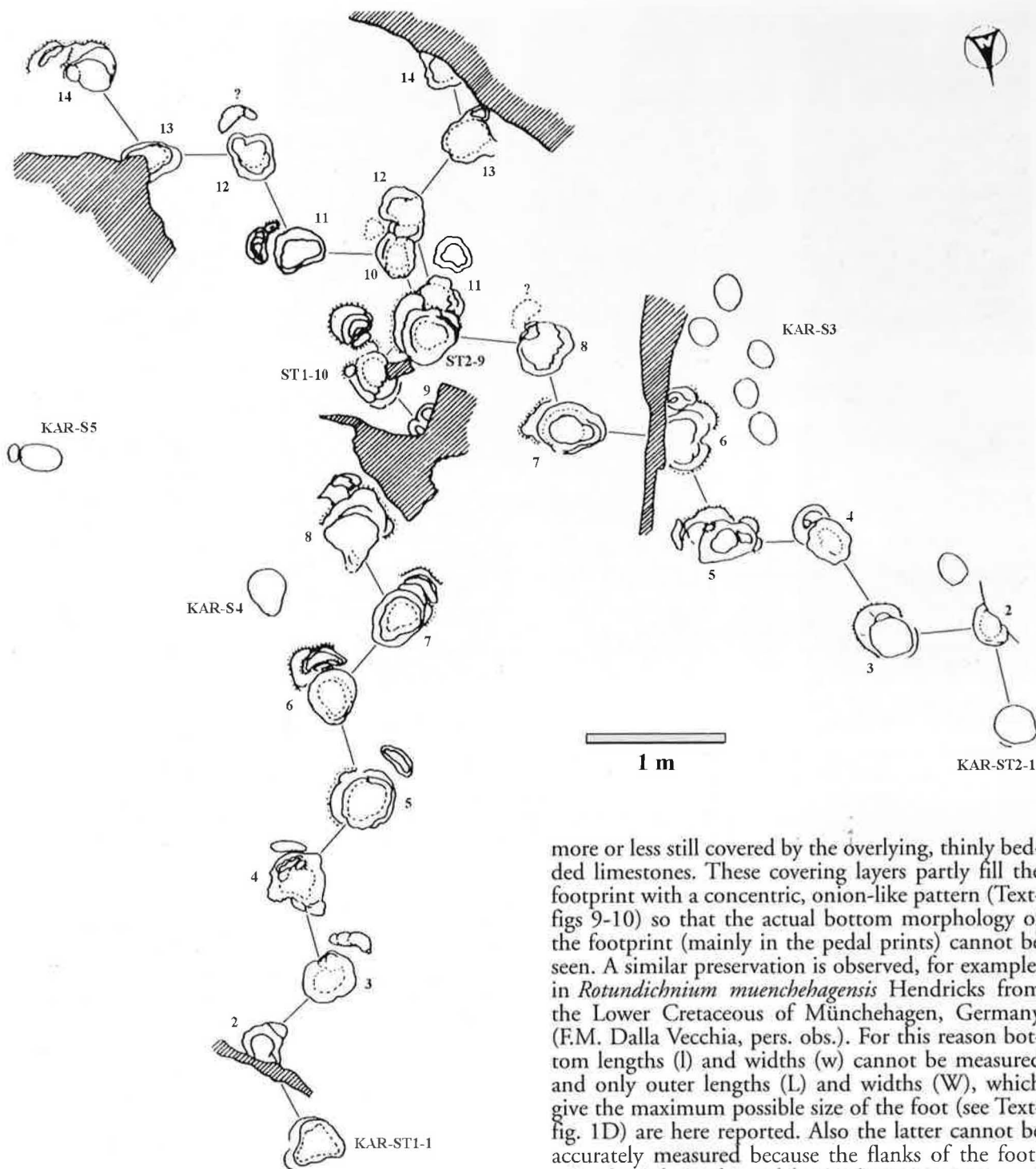
SLD-T4 (Pl. 1A; Text-figs 7B1-2) is a segment of four consecutive footprints. L ranges from 20.5-19.5 cm ($M = 20.1$ cm), W/L ranges from 0.56-0.73 ($M = 0.65$), A° is 30° and 36° , R/d is 1.26 and 1.47 respectively in T4-1 and T4-2. These are the best preserved footprints in the track and are rather similar to each other (Text-figs 7B1-2). Digit III is sigmoid in T4-2 and has a triangular point with a narrow claw mark in both footprints. The track is directed straight to SSW and footprints show a slight outward rotation. S ranges from 161.5-162 cm ($M = 161.7$ cm), A ranges from 170° - 173° . SL/h using M values is 1.75, indicative of a fast walking gait.

SLD-T5 (Pl. 1A; Text-figs 7L1-2) is a segment of five consecutive footprints; T5-4 cannot be identified. L ranges from 19.5-17 cm ($M = 18.3$ cm), W/L ranges from 0.61-0.78? ($M = 0.65$). A° and R/d cannot be measured because of the poor state of preservation. That of T5-2 is a case of a digit III particularly swollen in the middle-distal part (Text-fig. 7L2). The track is directed straight to the ESE and footprints show a slight outward rotation. SL ranges from 152-150 cm ($M = 84.2$ cm), A is 172° , SL/h using M values is 1.79, indicative of a fast walking gait.

A sigmoid digit III is found in SLD-T6-1 (Text-fig. 7G), SLD-T7-1 (Text-fig. 7H), SLD-T10-1 (Text-fig. 7C), SLD-T15-1 (Text-fig. 7P1), SLD16 (Text-fig. 7F) and SLD19 (Text-fig. 7E). SLD-T6-1 and SLD-T7-1 closely resemble SLD-T1-5. In SLD-T7-1 all digits show narrow and pointed claw marks. In SLD-T9-1 and T9-2 (Text-figs 7K1-2) the only pointed digit is the second; A° is 45° and 65° respectively, R/d is 1.46 in both footprints. In SLD-T10-1 (Text-fig. 7C) the end of digit III print is triangular and pointed, and the print of digit II is very short and curved medially, A° is 50° , R/d is 1.60. SLD-T14-10 (Text-fig. 7D), is the smallest ($L = 14.5$ cm), has a long, slightly sigmoid digit III, and a long curved claw mark, A° is 56° , and R/d is 1.43. Footprints of track SLD-T15 (T15-1 and T15-7; Text-figs 7P1-2)

Trackway	L	W/L	h	SL	SL/L	SL/h	V	AWS	V/AWS	D
SLD-T1	20.4	0.63	93.8	165.9	8.13	1.77	7.05	3.77	1.87	298
SLD-T2	15.7	0.61	72.2	118.8	7.57	1.64	5.47	3.38	1.62	247
SLD-T3	19.3	0.62	88.8	142	7.36	1.60	5.80	3.68	1.58	285
SLD-T4	20.1	0.65	92.5	161.7	8.05	1.75	6.86	3.75	1.83	210
SLD-T5	18.3	0.65	84.2	151	8.25	1.79	6.83	3.60	1.90	111

Tab. 1 - Data for the tridactyl tracks of S. Lorenzo di Daila/Lovrečica. The mean value of L and SL was used to calculate h, SL/L, SL/h, V and AWS. L, h and SL are in centimetres; V and AWS in km/hr, D in degrees.

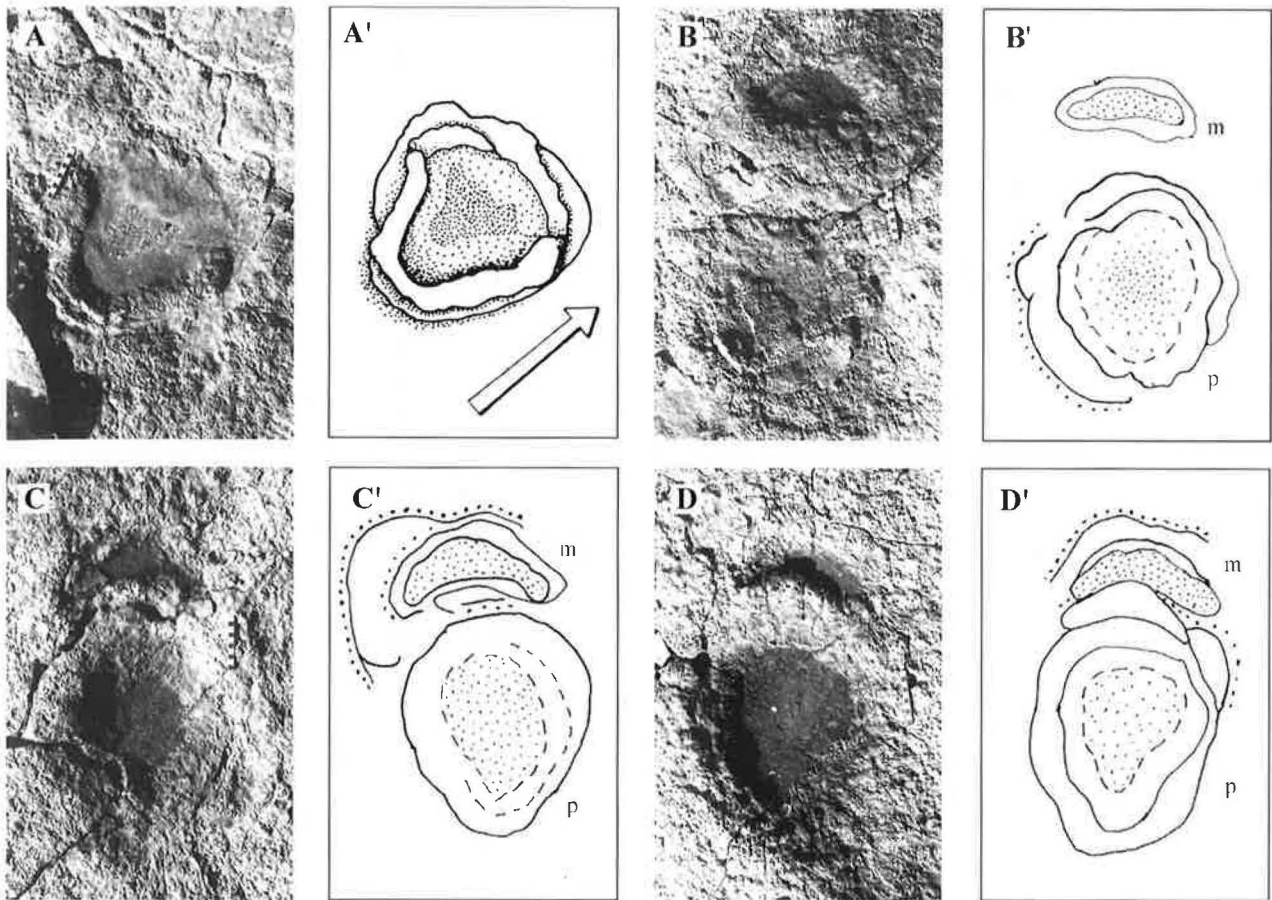


Text-fig. 8 - Map of the Carigador/Karigador site. Line with points in front identifies the anterior margin of the displacement rim. Scale bar = 1 m.

in ST1-3, 11 and 14 (Text-figs 8-11). Therefore, there is no doubt that the trackmaker was quadrupedal. The kind of preservation of the footprints is somewhat complex. The footprints are all

more or less still covered by the overlying, thinly bedded limestones. These covering layers partly fill the footprint with a concentric, onion-like pattern (Text-figs 9-10) so that the actual bottom morphology of the footprint (mainly in the pedal prints) cannot be seen. A similar preservation is observed, for example, in *Rotundichnium muenchehagensis* Hendricks from the Lower Cretaceous of Münchehagen, Germany (F.M. Dalla Vecchia, pers. obs.). For this reason bottom lengths (l) and widths (w) cannot be measured and only outer lengths (L) and widths (W), which give the maximum possible size of the foot (see Text-fig. 1D) are here reported. Also the latter cannot be accurately measured because the flanks of the footprint (mainly in the pedal prints) are not steep, and the border between footprint and surrounding undeformed layer surface cannot be easily distinguished. Sometimes, part of the margin of the pedal prints, and in some cases the whole manual print, are hardly distinguishable or masked at all, because the infilling layers have the same appearance of the printed layer and blend with it.

KAR-ST1-5 to ST1-8 (Text-figs 9-11) is the best preserved segment of the track and ST1-7 is the best



Text-fig. 9 - Saurpoid *manus-pes* couples of the KAR-ST1 track of Carigador/Karigador site. A-A') ST1-1, pedal print only, with the long axis inclined to the upper right corner of the photo (arrow); the footprint is still partly filled in by the overlying thin layers in an onion-like pattern; B-B') couple ST1-5 with the the pedal print still mostly filled in by the overlying thin layers, like ST1-1, C-C') couple ST1-6; D-D') couple ST1-7. Light is from the lower left side of the photos. Line with points in front identifies the anterior margin of the displacement rim. Legend: m = manual print, p = pedal print. Scale bar = 10 cm.

preserved *pes-manus* couple (Text-figs 9D-D') of the whole track. The pedal print is triangular to oval, wider anteriorly, without any trace of separate digital prints and claw marks. If developed claws had occurred in the trackmaker, their mark should be visible in the anterior margin of the footprint, not covered by the overlying layers. There is a faint lateral lobe which could be the print of the digit V if, as we hypothesize on p. 48, these are saurpoid footprints. Lp in ST1-6p and ST1-7p is about 40 cm and Wp is around 33 cm.

The manual print is placed in front the pedal print, slightly laterally to it (Text-figs 10-11). In most cases it is very narrow and crescent-shaped. In ST1-7 the distance between the middle point of the posterior margin of the manual print and the anterior margin of the pedal print is only 8 cm, and there is a raised displacement rim between the pedal and the manual print. There is no doubt that the displacement rim caused by the pedal impression strongly deformed the manual print. Lm in ST1-6m and ST1-7m is about

16 and 15 cm respectively and Wm is about 29 and 27 cm. The manual print of ST1-10 appears to be less deformed and less crescent-shaped than the others, with Lm about 20 cm and Wm 26 cm. In any case, no digital prints are recognizable.

The pedal prints show a marked outward rotation which is 30°, 20° and 27° respectively in KAR-ST1-5 to 7. The manual print has the same outward rotation as the pedal print.

The gleno-acetabular distance, estimated following Thulborn (1990, p. 238), is only 163 cm; obviously, this estimate depends on the gait of the animal and therefore is very approximate.

Pedal SL ranges from 123-136 cm (M = 128.15 cm; N = 10); SLp of ST1-4/6 is 134 cm, of ST1-5/7 is 135.5 cm and of ST1-6/8 is 123 cm. Manual SL is 129 and 130 cm respectively in ST1-5/7 and 6/8. Pedal A ranges from 105°-123° in the first eight footprints (M = 115.5°; N = 6); it can be calculated confidently only in the first part of the track, before the intersection with KAR-ST2. In the first five strides A



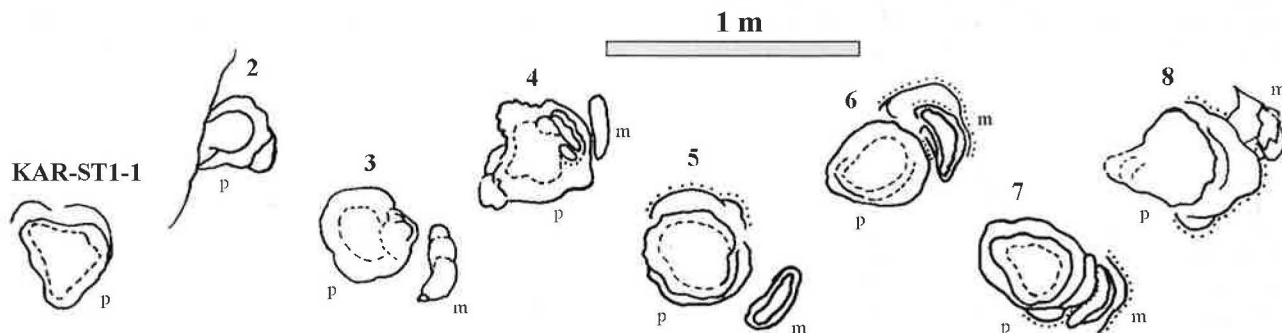
Text-fig. 10 - The track segment KAR-ST1-5 to 8, with in the upper-middle part of the figure the crossing of KAR-ST1 and KAR-ST2. Photograph in slightly perspective view; view to the SSW direction. Light is from the left side of the photo. Scale bar (center) = 10 cm.

increases (105° , 115° , 119° , 119° , 123°); the highest A value is measured in the best preserved footprints ST1-5/7. Manual A is lower than the pedal one: in ST1-5/7 is 90° .

Outer (external) width for the forefeet is 90 cm (ST1-5/7) and the corresponding for the hindfeet is 77 cm. The inner width in the segment ST1-4 to 8 is positive but rather narrow, not higher than few centimetres (Text-fig. 11). According to Farlow (1992, pp. 108-109) wide-gauge trackways are those in which the manual and pedal prints are "well away from the trackway midline" whereas those of narrow-gauge trackways "are close or even intersect the trackway midline". Therefore the gauge is neither narrow nor actually wide and this appears to be a case of medium-gauged track (cf. Meyer *et al.*, 1994, fig. 4). Direction is 200° and the trackmaker was moving on a straight line (Text-fig. 8).

Gait as indicated by SL/h (0.80), calculated with the mean of SL and h (160 cm) calculated as $4L_p$ using $L_p = 40$ cm, is a very slow walking (Tab. 2).

KAR-ST2 is a segment of track with 14 consecutive pedal prints (Text-fig. 8). The track was longer, but its NW portion was nearly completely weathered away; a pedal print with a clear anterior displacement rim can be identified about 3 m SW from KAR-ST2-1 but was not mapped. Manual prints are identifiable only in ST2-4, ST2-5, ST2-6, ST2-11 and ST2-14, perhaps also in ST2-8 and ST2-12 (where it appears to be filled in by the overlying layers). The absence of the manual print is probably due to the compression caused by the pedal displacement rim or by the amalgamation between the footprint-bearing layer and the overlying layers. The kind of preservation is the same as that of KAR-ST1, but here the state of preservation is generally worse. The overall pedal and manual morphology and size is the same as in KAR-ST1. KAR-ST2-8p, 9p, 10p and 12p and 8m and 12m are more or less still filled in by the overlying layers. The best preserved *manus-pes* couple is ST2-11, where, however, the pedal print is not filled in, but is strongly weathered and the manual print is deformed by the pedal one. L_p is about 40 cm and W_p is around 33 cm; L_m is about 16 cm and W_m 24 cm. In any case, no digital prints are clearly recognizable. The few pedal prints where the rotation can be measured, show a marked outward rotation (from 23° up to



Text-fig. 11 - Map of the track segment KAR-ST1-1 to 8. Line with points in front identifies the anterior margin of the displacement rim. Legend: m = manual print, p = pedal print. Scale bar = 1 m.

nearly 40°). Pedal SL ranges from 117-140 cm (M = 130.2 cm; N = 12) similar to KAR-ST1; manual SL is around 130 cm. Pedal A ranges from 112°-123° (M = 115.3°, the same as for KAR-ST1; N = 10) and is rather regular, with only the second stride markedly longer than the others. Manual A appears to be around 90°, decidedly lesser than the pedal A, like in KAR-ST1. Outer (external) width for the forefeet is 77-90 cm and the corresponding for the hindfeet is 65-75 cm (the variability is due to the poor preservation). The inner width is positive, but never higher than 8-10 cm. Therefore the gauge is neither narrow nor actually wide and this is another case of medium-gauged track. Direction is 140° and the trackmaker was moving on a straight line. It crossed the track KAR-ST1, and seems to overlap its footprints. Possibly, the trackmaker KAR-ST2 passed through the site after KAR-ST1. In fact, in the zone of intersection with KAR-ST1 the trackway KAR-ST2 appears less regular than before and after, so the crossing the other track possibly influenced the gait of the animal. Gait as indicated by SL/h (0.81), calculated with the mean of SL and h (160 cm) calculated as 4Lp using Lp = 40 cm, is a very slow walk and is nearly the same as that of the trackmaker of KAR-ST1 (Tab. 2).

A "string" of six nearly rounded footprints, all with L of about 27 cm and mostly filled by the overlying layers, occurs just to the right side of KAR-ST2, between ST2-2 and ST2-6, and nearly parallel to it (D = 168°) (Text-fig. 8). They were probably made by a single trackmaker, but a clear organization in a track cannot be identified. In the map we indicate this possible track as KAR-S3.

Many other rounded to oval depressions, not clearly organized in tracks and poorly preserved, occur in the site. They have sizes similar or lower to those of the footprints of KAR-ST1 and ST2. Half a dozen are visible to the left of KAR-ST1. Only the better preserved are reported in the map (Text-fig. 8). KAR-S4 is an oval pedal print with Lp about 40 cm, Wp about 28 cm and D = 185°. KAR-S5 appears to be an isolated, shallow *manus-pes* couple. The pedal print is elliptical, about 32 cm long and about 24 cm wide, with D = 105°. The possible manual print is situated just in front of the pedal print and appears to be very small (Lm ~ 10 cm; Wm ~ 17 cm) and elliptical.

GRAKALOVAC PROMONTORY (PR)

The footprint-bearing surfaces are situated along the shore about 1.5 km SW of Premantura/Promontore (SW Istria). They are exposed in a narrow and elongated outcrop in the upper part of a cliff. Two short tracks with tridactyl footprints are preserved on a bed surface intensely bioturbated by invertebrates. Three other tridactyl footprints are visible in the same outcrop, but on a surface about five millimetres below. Both the footprint-bearing surfaces are covered by a microbreccia level few millimetres thick, which is partly preserved inside the footprints.

A few centimetres below the footprint-bearing surfaces, probable footprints in vertical cross-section are visible (Dalla Vecchia & Venturini, 1996) (Text-fig. 3C).

PALEOICHOLOGICAL DESCRIPTION

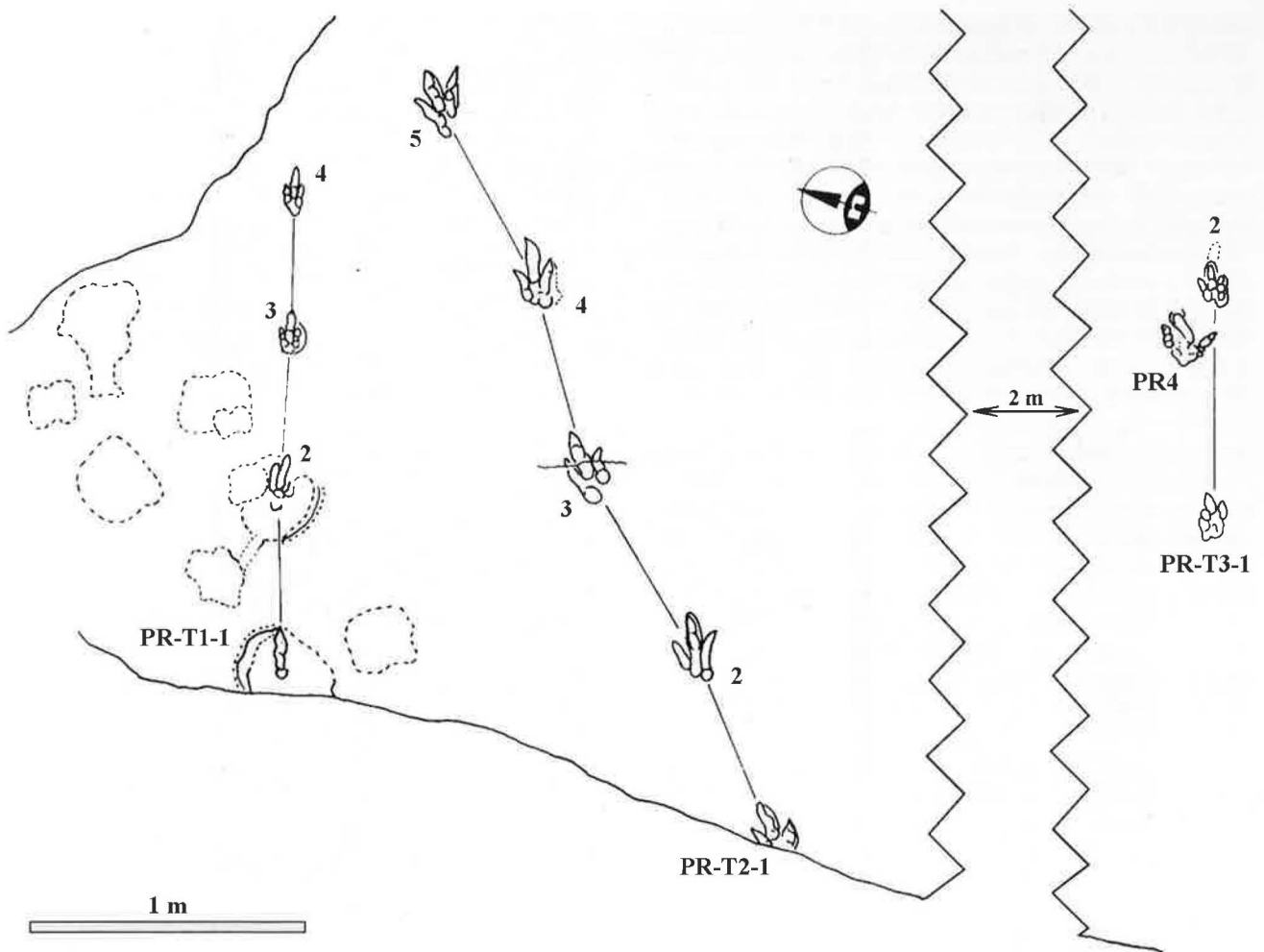
Two tracks (PR-T1 and PR-T2) are visible on the northern part of the outcrop, whereas another track (PR-T3) and a single footprint (PR4) are preserved in the southern part, on the lower surface (Text-fig. 12). PR-T1 and PR-T3 were impressed by animals of similar size while PR-T2 was made by a larger one. All are medium-sized, tridactyl mesaxonid footprints. The state of preservation is not good, the prints are rather shallow and difficult to be seen without low-angled light. Casts were taken of prints PR-T1-3 and 4, PR-T2-2, 4 and 5, PR-T3-2, and PR4. They are stored at the Museo Paleontologico Cittadino of Monfalcone.

PR-T1 is a track segment with four consecutive footprints (Text-figs 12, 13A1-2). Footprints are relatively small, with low A° and elongated digit III. L ranges from 16-18 cm (M = 17 cm), W/L 0.44-0.53 (M = 0.49), A° is low (24° and 17°), R/d is 1.33 and 1.52 respectively in T1-3 and 4. The track is directed straight to the ENE (75°). SL is 107-116.5 cm (M = 111.5 cm), A ranges from 173°-176° (M = 174.5°). SL/L using M values is 6.56, SL/h is 1.47, indicative of a walking gait.

PR-T2 is a track segment with five consecutive footprints (Text-figs. 12, 13C1-3). L ranges from 24.5-26 cm (M = 25.4 cm), W/L ranges from 0.54-0.68 (M = 0.59), A° ranges from 20°-50° (M =

Trackway	Lp	h	A	SL	SL/Lp	SL/h	V	AWS	V/AWS	D
KAR-ST1	~40	160	115.5	128.1	3.20	0.80	2.45	3.22	0.76	200
KAR-ST2	~40	160	115.3	130.2	3.25	0.81	2.51	3.22	0.78	140
KAR-S3	27	108	—	—	—	—	—	—	—	168
KAR-S4	39	156	—	—	—	—	—	—	—	185
KAR-S5	32	128	—	—	—	—	—	—	—	105

Tab. 2 - Measurements of the sauropod footprints and tracks of the Carigador/Karigador site. Lp, SL (pedal) and h are in centimetres, A in degrees, V and AWS in km/hr, D in degrees. In KAR-ST1 and 2 Lp, A and SL are mean measurements.



Text-fig. 12 - Map of the Grakalovac site. Line with points in front identifies the anterior margin of the displacement rim. Dashed lines identify the non-tridactyl footprints. Scale bar = 1 m.

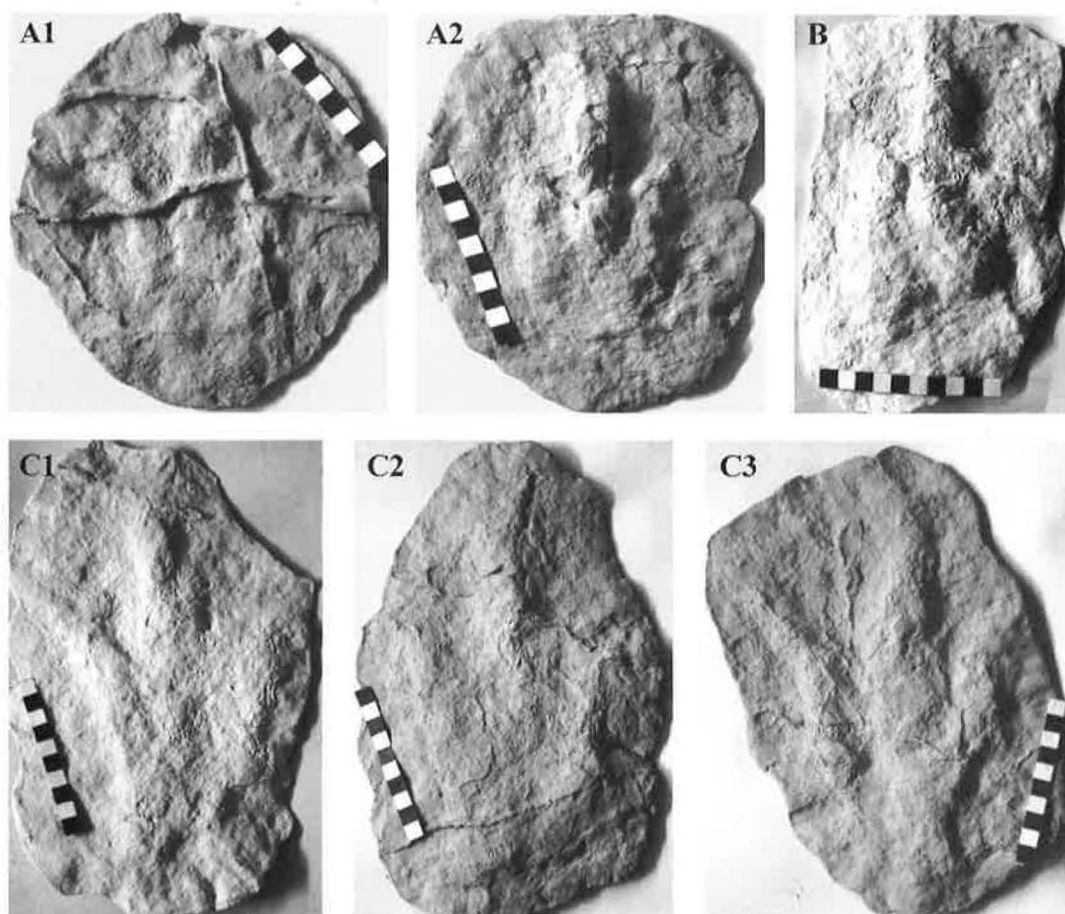
34.2°), R/d is very variable (1.48, 2.07, ~1.65). The best preserved footprint is T2-4 (Text-fig. 13C2). Narrow and pointed claw marks seem to occur on digit II and IV. These digital prints are narrow elongated, with larger, rounded proximal pads. Digit III is narrow, elongated and curved medially, mainly the distal segment, with a triangular and pointed termination. The distal half of the digital print is decidedly deeper than the proximal. Digit II is 105 mm long, digit III is 175 mm, digit IV is 125 mm, R/d is 1.48. This footprint is the most faithful to foot morphology because the others are more deformed. The variability in the morphology of the three cast footprints can be observed in Text-figs 13C1-3. The track is directed straight to the ENE (48°). SL ranges from 142-146.5 cm ($M = 144.7$ cm), A ranges from 164°-168° ($M = 166°$). SL/L using M values is 5.70, SL/h is 1.24, indicative of a relatively slow walking gait (Tab. 3).

PR-T3 is a track segment with a left-right pair of

consecutive footprints (Text-fig. 12), with the same ENE direction as PR-T1 (72°) and similar size ($L = 17$ cm). The better preserved footprint (T3-2; Text-fig. 13B) is narrow ($W/L = 0.59$), A° is 30° and R/d is 1.28. The prints of digit III and digit IV show triangular claw marks.

Footprints of PR-T1 and PR-T3 have similar size and morphology. A° is very low, digit II ends proximally before digit IV and both appear nearly parallel to digit III. The latter is narrow and straight, with the same width at the proximal end, in the middle and at the distal end. In the best preserved footprint PR-T1-3, triangular but not very narrow and sharp claw marks are visible on digits III and IV. The overall aspect of the "heel" plus digit II and digit IV is roughly rectangular because of low A° (see Text-figs 13A1-2, B).

PR4 is a single footprint of uncertain morphology, about 18.5 cm long. It is possibly a "composite" footprint made by the overlapping of two tridactyl footprints with the size of those of PR-T3.



Text-fig. 13 - A sample of the tridactyl footprints from the upper Cenomanian site of Grakalovac: A1) PR-T1-3, A2) T1- 4, B) PR-T3-2, C1) PR-T2-2, C2) T2-4, C3) T2-5. The photos are taken from the casts of the footprints. Lighting is from the left side. Scale bar = 10 cm.

Shallow, roughly circular to quadrangular depressions, 17 to 29 cm long, occur on the upper footprint-bearing surface of the outcrop and cross PR-T1 (Text-fig. 12). They are not clearly organized in a track, but form a "band" as is the case of similar depressions in the Fenoliga site (see below). They do not show a diagnostic morphology despite the fact that the outline of some of them could vaguely resemble that of sauropod manual prints.

FENOLIGA ISLET (FEN)

This site was the object of some preliminary and/or incomplete investigations on the part of several authors (Gogala, 1975; Gogala & Pavlovec, 1978; Tišljarić *et al.*, 1983; Leghissa & Leonardi, 1990; Pavlovec & Gogala, 1993), and was mentioned also in Dalla Vecchia (1994a,b; 1997a,b), Dalla Vecchia *et al.* (1993) and Dalla Vecchia & Tarlao (1995). A detailed description was published recently by Mezga & Bajraktarević (1999). We mapped in May 1997 the whole surface and all the footprints we identified are

Trackway	L	W/L	h	SL	SL/L	SL/h	V	AWS	V/AWS	D
PR-T1	17	0.54	78.2	111.5	6.56	1.47	4.49	3.49	1.29	75
PR-T2	25.4	0.59	116.7	144.7	5.70	1.24	4.34	4.13	1.05	48
PR-T3	17	0.59	78.2	—	—	—	—	—	—	72

Tab. 3 - Data for the tridactyl tracks of Grakalovac site. The mean value of L and SL was used to calculate h, SL/L, SL/h, V and AWS. L, h and SL are in centimetres; V and AWS in km/hr, D in degrees.



Text-fig. 14 - A segment of track FEN-T2, Fenoliga islet. The arrows point to the footprints. The scale bar is 10 centimetres.

reported here in the Pl. 1B. Our map differs somewhat from that published by Mezga & Bajraktarević (1999, fig. 3), mainly because we did not map the rounded depressions occurring in the very corroded N-NE part of the outcrop. We avoided this because the poorly preserved depressions appeared to us scarcely informative and the time accorded to map this site, very difficult to reach, was limited to just a day. Mezga & Bajraktarević (1999) interpreted these holes (group a-c and tracks V and VI in fig. 3) as sauropod footprints. We also found the tridactyl tracks to be slightly more complete, longer and linear, and the main sauropod track shorter, than those reported by Mezga & Bajraktarević (1999, fig. 3).

The wide footprint-bearing surface is exposed along the shore of the islet and is partly submerged by the sea during high tide and completely flooded during storms. Therefore, the surface suffered both strong erosion and corrosion (i.e. chemical dissolution of carbonates). As a consequence, the state of preservation of the footprints is in general very poor and is poorer in the part which is usually submerged.

PALEOICHOLOGICAL DESCRIPTION

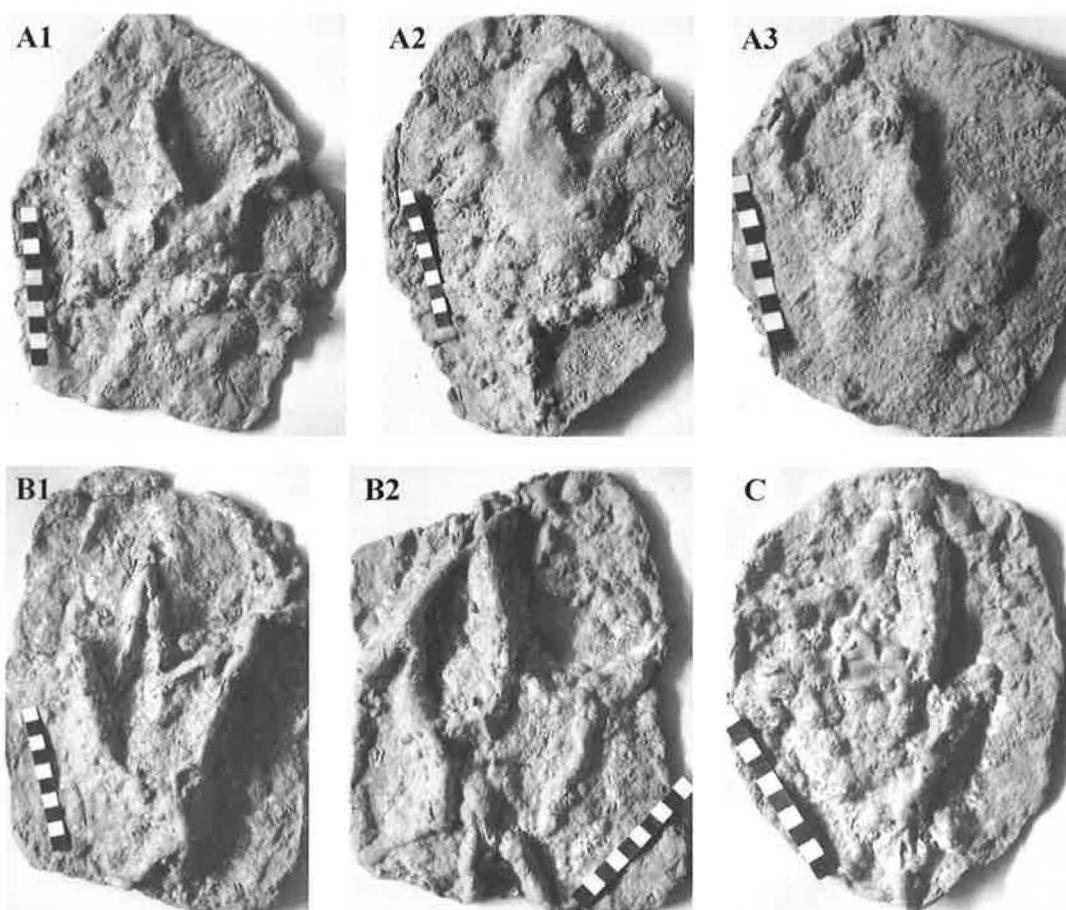
There are two long (FEN-T1 and FEN-T2; Text-fig. 14) and a shorter track (FEN-T3), all impressed by bipedal tridactyl trackmakers (Pl. 1B). FEN-T1, 20 m long, has 29 consecutive footprints; FEN-T2 shows 25 consecutive footprints; FEN-T3 shows five footprints. Casts were taken of prints FEN-T1-11, 13, 14, FEN-T2-7 and 8, FEN-T3-2. They are stored at the Museo Paleontologico Cittadino of Monfalcone.

The footprints, when the state of preservation permits to detect it, have a digit III decidedly longer than the other two, and which is narrow and pointed or tapering; the prints of digits II and IV are usually narrow.

The trackmakers were medium-sized, mean L in FEN-T1, FEN-T2, FEN-T3 being respectively 16.8 cm, 21.4 cm and 17.5 cm (Tab. 4).

A° ranges from 38° - 60° ($M = 48.3^\circ$) in the seven footprints of FEN-T1 where it can be measured; R/d ranges from 0.94-1.57 ($N = 7$; $M = 1.16$), but is about 1 in the best preserved print. The print of digit III is narrow and sinuous as can be seen in footprints T1-3, 11, 15 and 21. T1-13 and T1-14 are similar each other (Text-figs 15A2-3; FEN-T1-13 is probably the footprint of fig. 5C in Mezga & Bajraktarević, 1999), with relatively wide and unformed digital prints. The digit III print is curved in T1-13, but nearly straight in T1-14. T1-11 (Text-fig. 15A1) is different and resembles the footprints of FEN-T2 (see below); digit III is narrow, sigmoid and with a narrow claw mark. Some footprints still preserve the original infilling made by microbreccia with clasts 1-4 mm in diameter. A is variable but generally high, ranging from 160° - 178° ($M = 172.2^\circ$; $N = 17$). Sometimes a slight outward rotation occurred where the trackmaker slowed down and SL is less (e.g. between footprints T1-13/15). SL is very variable (Text-fig. 16A) ranging from 134 cm to 148 cm (possibly up to 152 cm), $M = 142.7$ cm ($N = 18$). SL/h calculated with the mean of L is 1.85 and would indicate a fast walking gait; V calculated with the mean of L is 6.87 km/hr (Tab. 4). The trackmaker of FEN-T1 was moving in a sinuous way with a SSW direction (154°).

A° ranges from 50° - 81° ($M = 58.2^\circ$; $N = 6$) in FEN-T2 and footprints have also a highly variable R/d ranging from 1.07-2.00 ($M = 1.65$; $N = 7$) because of the poor preservation. The print of digit III is long, but it is not very projecting because the "heel" print is relatively long. In the cast T2-7 and T2-8 (Text-figs 15B1-2; T2-7 is figured also in Mezga & Bajraktarević, 1999, fig. 5A) digit II ends proximally before digit IV and all digital prints are narrow and long. All digital prints are sinuous in T2-8, less sinuous in T2-7 where digit III is straight and tapering. The "heel" print appears to be wide in both specimens. The digital prints are clearly deepened by corrosion and they are extended beyond their actual



Text-fig. 15 - A sample of the tridactyl footprints from the upper Cenomanian site of Fenoliga: A1) FEN-T1-11, A2) T1-13, A3) T1-14, B1) FEN-T2-7, B2) T2-8, C) FEN-T3-2. The photos are taken from the casts of the footprints. Lighting is from the left side. Scale bar = 10 cm.

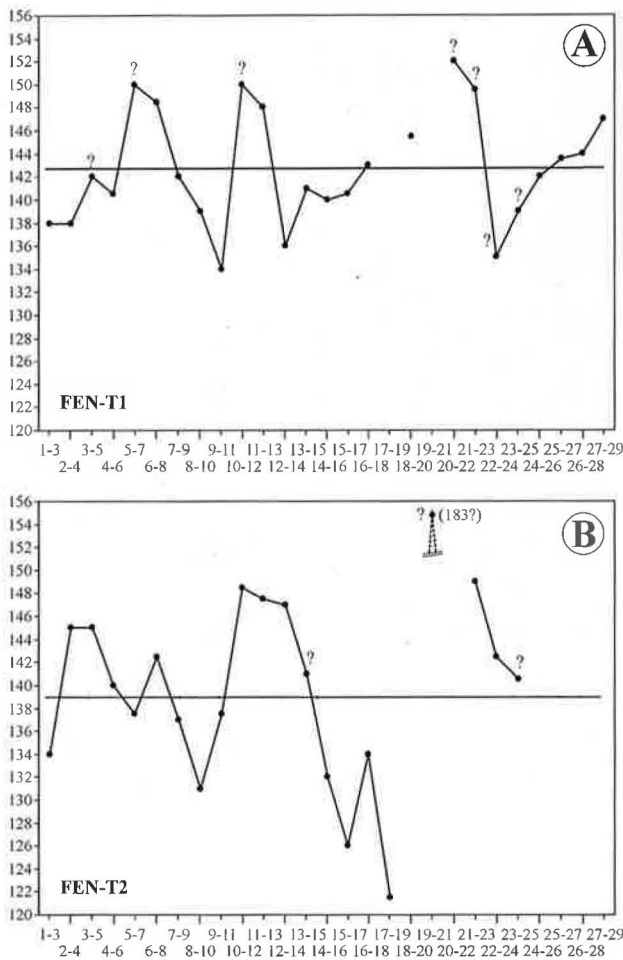
length as fractures in the limestone. It is possible that these fractures were originally mud-cracks set out on the digital prints (cf. Thulborn, 1990, fig. 5.19c). A is highly variable but generally low, ranging from 132° – 176° ($M = 154.3^{\circ}$; $N = 16$). Sometimes a slight outward rotation occurs (e.g. between footprints T2-5 to 8 and T2-17 to 18) just after a change of direction, but usually no rotation is evident. SL is very variable, ranging from 121.5 to 149 cm ($M = 139$ cm; $N = 18$) (Text-fig. 16B). SL/h calculated with the mean of L is 1.41 and would indicate a walking gait, V calculated with the mean of L is 4.96 km/hr (Tab. 4). The trackmaker of FEN-T2 was travelling with a sinuous gait like FEN-T1, but moving to the SW (208°).

FEN-T3 is a short, straight track segment. In the better preserved footprint (T3-2; Text-fig. 15C; also figured in Mezga & Bajraktarević, 1999, fig. 5D) A° is 63° and R/d is 0.93. The print of digit III is narrow. A slight outward rotation occurs and A is high, ranging from about 180° to 175° ($M = 177.3^{\circ}$; $N = 3$). Mean SL is 182 cm, SL/h is 2.78 and the gait, according to Thulborn (1990), is a fast trot. V is 9.84

km/hr and the direction is to SSW (167°), similar to the direction of FEN-T1.

A “band” of non-tridactyl, circular to oval to crescent-shaped depressions, is found in the zone where FEN-T1 crosses FEN-T2 and FEN-T3 crosses FEN-T2 (Pl. 1B). These relatively shallow depressions are most probably footprints and apparently belong to a non-tridactyl trackmaker. However, no other clear feature than peripheral outline is recognizable. They do not appear to us clearly organized in a track, but they are distributed on an elongated, trail-like band. Mezga & Bajraktarević, on the contrary, have identified this “band” as a sauropod track (Mezga & Bajraktarević, 1999; track III of fig. 3; fig. 4A).

On the southern part of the outcrop, a long and curved track (FEN-ST1, Pl. 1B, Text-fig. 17) is found which was described in detail by Leghissa & Leonardi (1990) and Mezga & Bajraktarević (1999). They identified this track as that of a sauropod moving roughly from SSE to NW, with a wide-gauge and with pedal prints completely or nearly completely overlapping manual prints.



Text-fig. 16 - Variation of SL (in centimetres, vertical scale) in FEN-T1 (A) and FEN-T2 (B) trackways. The horizontal line represents the mean SL value (respectively 142.7 cm and 139 cm), and the graph shows the oscillation around it. The question mark is used for uncertain measurements. The graph is interrupted due to missing values. The uncertain measurement FEN-T2-19/21 is actually outside the figure, but is reported inside, indicated with the dotted lines; values for 18/20 and 20-22 are missing).

We observed 32 consecutive footprints (FEN-ST1-9 to 40) that undoubtedly belong to the same track, but another eight footprints could belong to it and are here identified with a number and a question mark. Unfortunately, this part of the track is over-

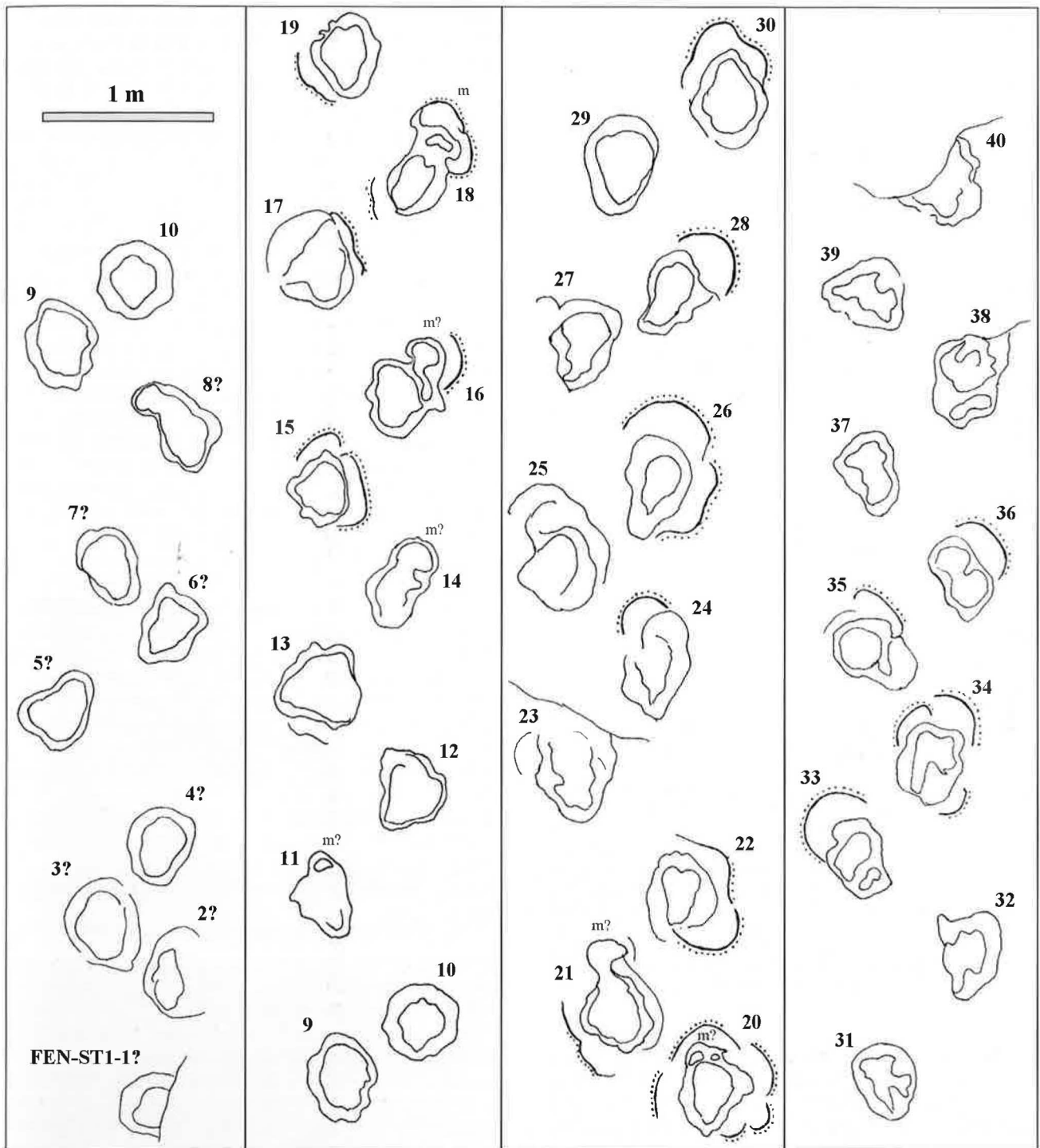
lapped by a "band" of other, similarly rounded to oval footprints, and the relationship among them cannot be clearly recognized (Pl. 1B). Mezga & Bajraktarević (1999) found 42 footprints as belonging to FEN-ST1, but do not report the overlapping "band".

The track is so poorly preserved that it is not easy to identify the actual direction of movement of the trackmaker. In our opinion, the previous identifications could be wrong, and in order to develop this argument we cannot avoid facing some ichnotaxonomic aspects. The displacement rims, which in sauropod prints are usually more developed in front and medial or lateral to the footprint than posteriorly (see Dalla Vecchia & Tarlo, 2000; Farlow *et al.*, 1989 and also the footprints of Carigador/Karigador), are found here on outer sides and on the "southern" side (actually from SE to SW) of the footprint (i.e. the supposed "posterior" one, Text-fig. 17), where they are sometimes huge (Text-figs 17, 18A, C). Furthermore, the footprints are often oval to triangular in shape, with the "southern" portion wider than the "northern" one (e.g. ST1-6?-7?, 11-12, 16, 19-20, 26, 28-29, 31-33; Text-fig. 17; see upside down fig. 2D of Mezga & Bajraktarević, 1999). This is the shape we would expect if the trackmaker was a sauropod directed to southern quadrants (see below). If so, many footprints show an outward rotation (see Text-fig. 17), which is the usual case of sauropod trackways (Thulborn, 1990). Leghissa & Leonardi (1990) noted in some cases the bypass of the pedal print over the manual one, which would be rather unusual for sauropods; in contrast, if the trackmaker was heading south, the manual print would be in the "normal" position, in front of the pedal print. Such possible manual prints are observed in front of pedal print ST1-8?, 11, 14, 16, 18, 20-21 and are often connected to the latter by structures caused by the strong dissolution of carbonates that occurred in recent times.

Leghissa & Leonardi (1990) were mistaken in their statement because of the presence of grooves in the footprints, which they interpreted as claw marks. Claws marks occur in the anterior part of the sauropod pedal prints, and so Leghissa & Leonardi (1990) identified the portion with the grooves as the anterior part of the Istrian footprints. These grooves are actually corrosion features caused by the action of the marine water on fractures of the rock, as was also concluded by Mezga & Bajraktarević (1999). This inter-

Trackway	L	W/L	h	SL	SL/L	SL/h	V	AWS	V/AWS	D
FEN-T1	16.8	0.67	77.3	142.7	8.49	1.85	6.87	3.48	1.97	154
FEN-T2	21.4	0.64	98.4	139	6.49	1.41	4.96	3.85	1.29	208
FEN-T3	17.5	0.51	80.5	182	10.68	2.26	9.84	3.54	2.78	167

Tab. 4 - Data for the tridactyl tracks of Fenoliga islet. The mean value of L and SL was used to calculate h, SL/L, SL/h, V and AWS. L, h and SL are in centimetres; V and AWS in km/hr, D in degrees.



Text-fig. 17 - The track FEN-ST1, redrawn from the map (Pl. 1B), excluding some structures probably due to corrosion. Line with points in front identifies the anterior margin of the displacement rim. Legend: m = manual print. Scale bar = 1 m.

pretation is supported by the presence of up to seven very large, and more smaller grooves per footprint (Text-fig. 18B). Sauropods had at most only four clawed pedal digits (Farlow, 1992). According to our interpretation, these grooves are formed in the poste-

rior, shallower part of the footprint and cannot be claw marks also for this reason. They could have been created by the running waters flowing into the footprint by the sloping of the surface, the trap-effect of the deeper parts of the footprint and the barrier effect

of the displacement rims; they are actually enlarged fractures. In our opinion they are not collapse structures, as interpreted by Mezga & Bajraktarević (1999), because collapse structures in sauropod prints are concentric more than radial (Dalla Vecchia & Tarlao, 2000).

Parameters were measured on 32 footprints of track FEN-ST1 from footprint ST1-9 to 40. The track is curved, with the concavity to SW; the trackmaker was directed at the beginning of the curve to SE and at the end to SSW (Pl. 1B); the chord of the whole track is 160°.

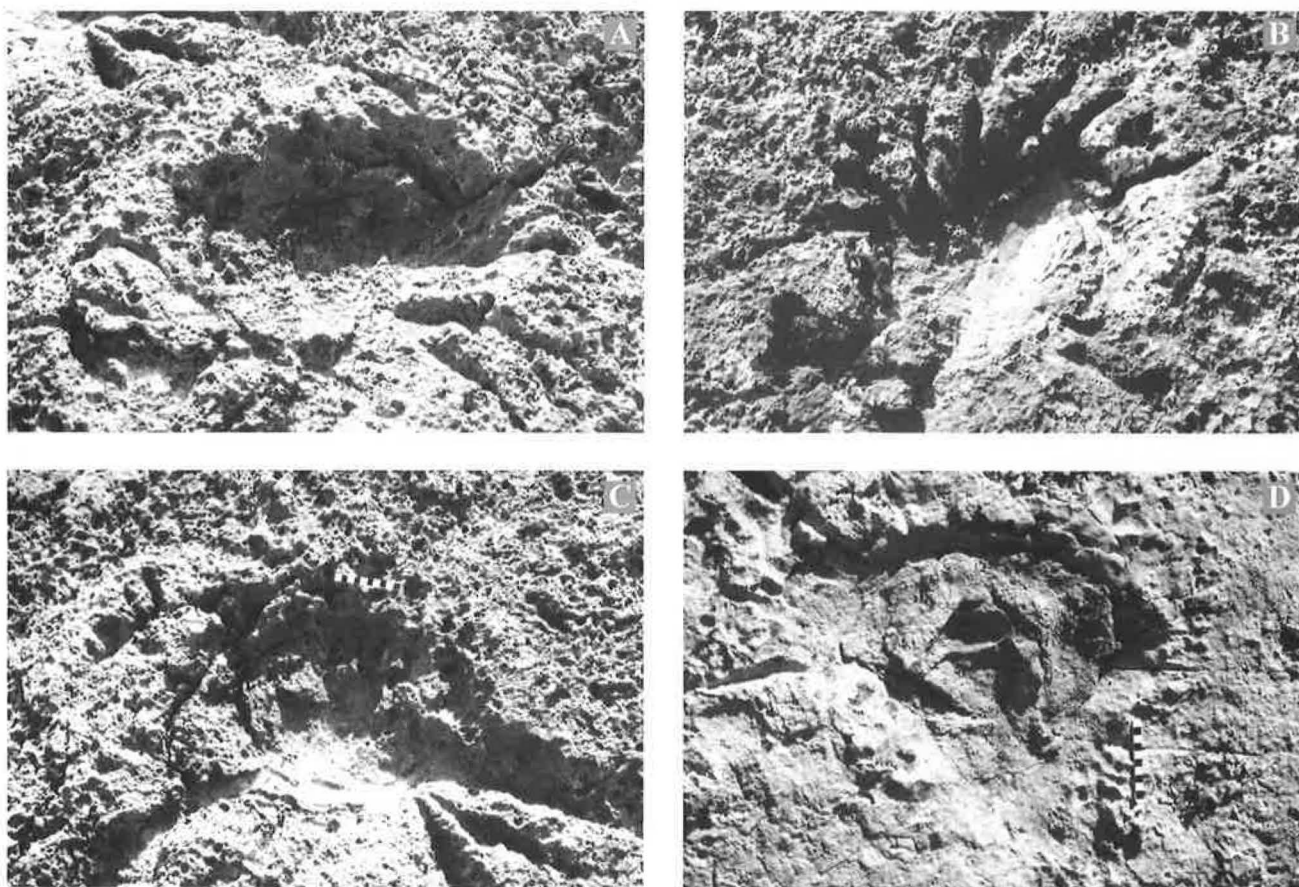
It must be emphasized again that the state of preservation is very poor (see Text-fig. 18 and Mezga & Bajraktarević, 1999, fig. 2B-D). Some footprints (ST1-3?, 5?, 9, 15, 17, 19, 22) still preserve part of the original infilling of rudist shell debris (Text-fig. 18D).

The disposition of the consecutive footprints appears that of a bipedal trackmaker, because in most cases no manual print is present or identifiable, and also the few possible manual prints are close to the corresponding pedal prints and connected to them by corrosion structures. Absence of manual print could

be original (i.e. the trackmaker was actually a biped), caused by the very poor state of preservation or by the overlap of other footprints. *Pes-manus* overlap, more or less total, suggested by Leonardi & Leghissa (1990) and subsequently also by Mezga & Bajraktarević (1999), is a plausible explanation, and was also observed in an Albian sauropod track of Istria (Dalla Vecchia & Tarlao, 2000). This will be developed further in the discussion.

It is extremely difficult to measure accurately Lp and Wp of these footprints. The pedal prints are basically misshapen depressions, roughly oval or circular, generally longer than wide (Text-fig. 17; Pl. 1B). Lp ranges from 42-53 cm (M = 47 cm; N = 29). Because of the corrosion which enlarged the footprints, Lp was originally lower than 47 cm, probably around 40 cm. This is the measurement independently reported by Mezga & Bajraktarević (1999) and, incidentally, is the length of the pedal prints successively found in Carigador/Karigador site.

Parameters of the trackway also cannot be precisely measured because the outline of the footprints is uncertain and heavily modified by corrosion. We



Text-fig. 18 - Footprints from the sauropod track FEN-ST1. A) ST1-25, anterior part to the left, note the still well-evident displacement rim; B) ST1-18, anterior part to the bottom of the figure, note the several "claw" marks; C) ST1-26, anterior part to the left upper corner, note the still well-evident displacement rim; D) ST1-5?, anterior part to the left, note the infilling of rudist debris. Photos are not taken exactly from above the footprints. Scale bar = 10 cm.

Lp	h	A	SL	SL/L	SL/h	V	AWS	V/AWS
~40	160	98.5	121.6	3.04	0.76	2.24	3.22	0.70

Tab. - 5 - Measurements of the sauropod trackway FEN-ST1, Fenoliga islet. Lp, h and SL are in centimetres, A in degrees, V and AWS in km/hr. Lp, A and SL are mean measurements.

choose the middle point of the depressions as the reference point. A, although inexact, is rather low and ranges from 86°-108° (N = 30, M = 98.5°). This is in agreement with the mean of 96° measured by Leghissa & Leonardi (1990, p. 15) and the mean of 97.73° of Mezga & Bajraktarević (1999).

SL is variable and in the segment FEN-ST1-8 to 40 ranges from 104.5-136.5 cm (M = 121.6 cm; N = 30). In the probable first segment of the track (FEN-ST1-1? to 8?) SL is even more variable, with a lowermost value of 89 cm and an uppermost 149 cm; however, including these seven more SL values, M does not change greatly (120.7 cm).

Gait as indicated by SL/h (0.76), calculated with the mean of SL and h (160 cm) calculated as 4Lp using Lp = 40 cm (Tab. 5), is a very slow walk, as suggested also by low A values.

Measuring the outer width and inner width is difficult because of the state of preservation and the curvature of the trackway. Measurements are inexact, because corrosion has enlarged the footprints. For an overview of these parameters see Text-fig. 17 and Mezga & Bajraktarević (1999).

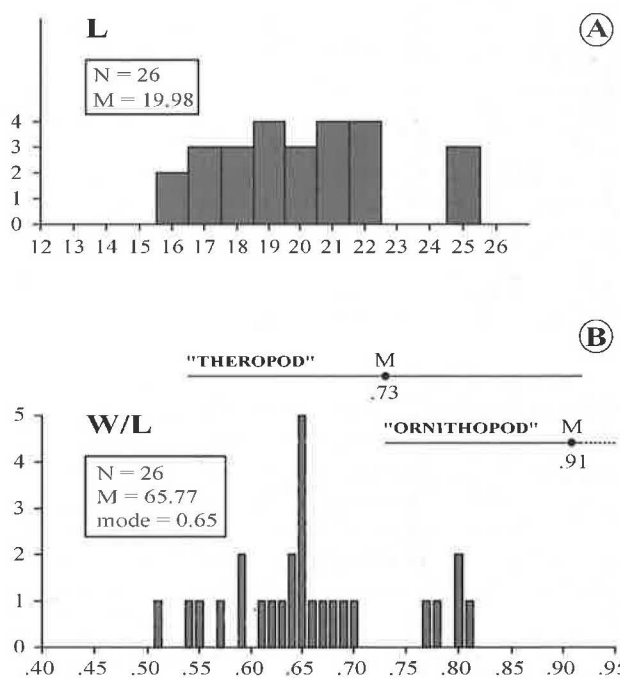
The gauge of FEN-ST1 was considered as wide by Mezga & Bajraktarević (1999). We observe that it is variable in the different segments (see Text-fig. 17), also because of curvature, and is most similar to the medium-gauge example in fig. 4 of Meyer *et al.* (1994) than to the wide-gauge example in the same figure and in fig. 1 of Wilson & Carrano (1999).

DISCUSSION

TRIDACTYL TRACKMAKERS

Size and determination - The whole sample shows a concentration of the L values around the interval 15.5-22.5 cm without a marked mode (Text-fig. 19A). Mean is 19.98 cm. A separated small group is found in the interval 24.5-25.5 cm. Therefore most of the trackmakers were medium-sized. The distribution in Text-fig. 19A is not significantly different from that reported in Dalla Vecchia, 1998, fig. 7, which was based on preliminary data. Footprint length in the late Albian sample of Solaris II site (N = 293) ranges from 11 and 26 cm, mode is 19 cm (class size 18.5-19.5 cm), and M is 18.16 cm (Dalla Vecchia & Tarlaio, 2000, fig. 11). The Cenomanian sample has a higher mean length value, but this could be partly due to the different state of preservation (corrosion and infilling).

In the sample of 26 values the footprint width/length ratio (W/L) shows a clear mode for 0.65 not very different from the mean (0.66) (Text-fig. 19B). There are two groups. Most of the values are grouped between 0.50 and 0.70 and show the prevalence of relatively narrow footprints. The second, much smaller, group is represented by wider footprints (W/L = 0.77-0.81), all from the site of S. Lorenzo di Daila/Lovrečica. There is not a clear relationship between L and W/L of the footprints; however the larger footprints (L > 21 cm) are always narrow (W/L < 0.70). W/L in the late Albian sample of Solaris II site based on 241 values, ranges from 0.41 to 0.93, but 81.3% of the values occur between 0.50-0.70, the mean is 0.61 and the mode is 0.55 and 0.58 (Dalla Vecchia & Tarlaio, 2000, fig. 12).



Text-fig. 19 - A) Distribution of length (L) of the tridactyl footprints (single, pairs and tracks) of the three sites (N = 26, measurements in centimetres). B) Distribution of width/length ratio (W/L) in a sample of tridactyl footprints from the three sites (N = 26). Also the range of values for "theropod" footprints and "ornithopod" footprints following Thulborn (1990) is reported for comparison.

Interdigital angles are rather variable, even among footprints of the same track (e.g. in SLD-T1 they range from 22°–50°, in PR-T2 they range from 20°–50°). However, measurements are rather low, even in the wider footprints. A° ranges from 20.5° to 63° ($M = 43.41^\circ$; $N = 15$) and falls in the field of “theropod” footprints (see Dalla Vecchia & Tarlaio, 2000, fig. 13). Mean A° is higher in the Fenoliga site ($M = 56.6^\circ$; $N = 3$), intermediate in S. Lorenzo di Daila/Lovrečica sample ($M = 45.5^\circ$; $N = 9$), and lower in the Grakalovac sample ($M = 28.2^\circ$; $N = 3$). The mean A° in the late Albian sample of Solaris II site is the same ($M = 43.4^\circ$; $N = 135$; Dalla Vecchia & Tarlaio, 2000, fig. 13A).

R/d is very variable, even in footprints of the same track: in SLD-T1 it ranges from 1.05–1.50, in PR-T2 from 1.48–2.07, in FEN-T1 from 0.94–1.57, in FEN-T2 from 1.07–2.00. The mean is 1.52 ($N = 9$), 1.40 ($N = 3$) and 1.25 ($N = 3$) respectively in the San Lorenzo di Daila/Lovrečica, Grakalovac and Fenoliga site; the mean for the Cenomanian sample is 1.39. R/d in the late Albian sample of Solaris II site ranges from 0.91–2.36 and $M = 1.36$ ($N = 89$) (Dalla Vecchia & Tarlaio, 2000, fig. 14). This suggests that in the Cenomanian footprints the length of the part of digit III projecting beyond ends of II and IV is comparatively shorter than the length of the rear of the pedal print with respect to the Albian sample, but this difference is not significant.

The problem of the identity of the medium to small-sized tridactyl trackmakers was discussed by Dalla Vecchia & Tarlaio (2000) in their study of the large upper Albian footprint sample of Istria, and to that paper we refer. Of course, medium to small-sized tridactyl footprints cannot be referred precisely to a theropod genus like *Coelurosaurus*, as Mezga & Bajraktarević (1999) do with regard to the footprints of Fenoliga (*ibidem*, p. 741: “...these footprints are assigned to a theropod dinosaur, i.e. *Coelurosaurus*”), also because *Coelurosaurus* does not exist (see Weishampel *et al.*, 1990).

The relative narrowness of the footprints (W/L), low interdigital angle, the elongation and narrowness of the digital prints, a digit III impression which is usually markedly longer than the others and projecting, digital prints which are curved, sigmoid and with pad prints, the digital print termination which is often pointed, sometimes with narrow claws marks, a digit II print which is shorter than the digit IV impression and the proximal indentation between the print of digit II and the “heel” print, observed in most of the footprints, and especially in the better preserved, suggest that most of them are “theropod” footprints in the ichnologic sense (see Dalla Vecchia & Tarlaio, 2000). At the state of the present knowledge of the skeletal structure of the feet and of the stratigraphic distribution of medium-size theropods and ornithopods, it seems most probable that they are actual theropod footprints (*ibidem*). However, the poor state of preservation cannot support this with the further data obtained from the Albian sample.

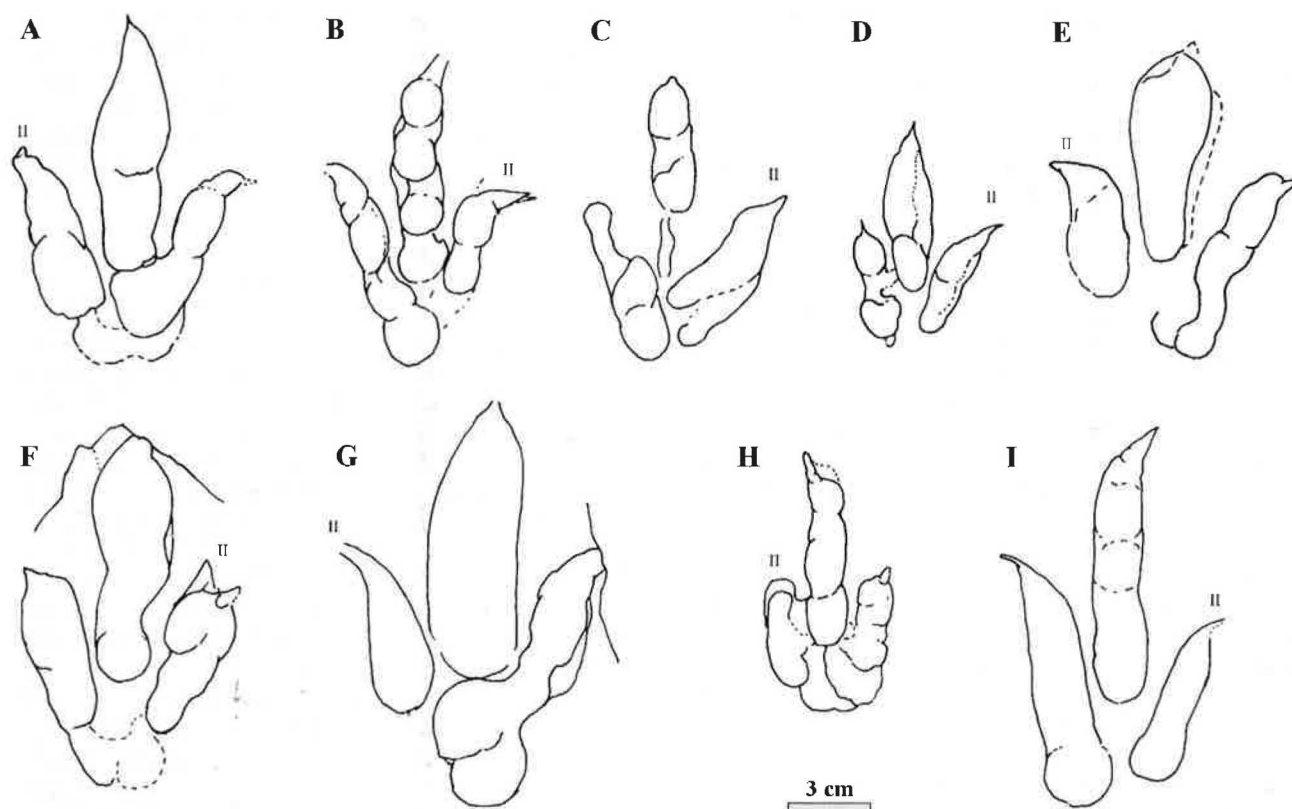
Some footprints from the S. Lorenzo di Daila/Lovrečica site differ from most of the other tridactyl footprints of similar size from both the upper Cenomanian and upper Albian of Istria (Dalla Vecchia & Tarlaio, 2000). They have a digit III print which is quite long, but also particularly swollen in the middle-distal part (e.g. SLD-T5-2; SLD-T11-1, SLD-T15-1 and 7; Text-figs 7L2, O, P1-2; 20E-F) and this is unusual in “theropod” footprints. This feature could be due to the substrate condition and in some cases is emphasized (e.g. in SLD-T1-5, see Text-fig. 6) by the still partly present infilling of the print (absent in the Albian footprints of the Solaris site). However, some footprints apparently without infilling also present this feature. The possibility that the author of these footprints could have been an ornithopod, or a theropod with a peculiar digit III, should be considered. However, an ornithopod trackmaker seems less probable because claw marks are present on some of these footprints (cf. SLD-T15-1 and SLD-T11-1), R/d is perhaps too low (e.g. it is less than 1.8 in SLD-T15-1 and 1.53 in SLD-T11-1) for ornithopod feet (Dalla Vecchia & Tarlaio, 2000) and footprints are decidedly asymmetrical.

The footprints SLD-T12-1 and SLD18 also have a wide digit III, but the maximum width is at the base or near it, and is constant or decreases gently distally, except in the terminal part where the print is triangular pointed (Text-figs 7M, N; 20G). In SLD-T12-1 this shape is probably related to the fact that the print of digit III is nearly completely filled in and its actual morphology is not visible.

An indication of the possible presence of two kinds of trackmaker in the S. Lorenzo di Daila/Lovrečica site is given by a group of distinctly wider footprints (Text-fig. 19B).

Ichnotaxonomic comparisons will be considered in another paper. However, we must comment on previous paleoichnological comparisons. Mezga & Bajraktarević (1999, p. 741) find their “type specimen B” of Fenoliga islet (here Text-fig. 15B1) “most similar to the ichnogenus *Ornithomimipus*”. Even if this ichnogenus would be based on unquestionable diagnostic characters, and we suspect that this is far to be certain, the comparison would be impossible because the very poor state of preservation of the Istrian specimen (see Text-fig. 15B1). The same is true for the other tridactyl footprints of the site, considered similar to *Eubrontes* and *Anchisauripus* (Mezga & Bajraktarević, 1999, p. 743). The only thing we feel comfortable to say is that, if the footprints were actually impressed by a theropod maker, as most likely, they all belong to a theropod with a plesiomorphic kind of foot, and not to the apomorphic-footed dromaeosaurids and troodontids.

Gait, speed and AWS – There is a high variability in the gaits of the tridactyl trackmakers among the different sites. Larger trackmakers (FEN-T2 and PR-T2; the latter was considered as a medium-sized individual



Text-fig. 20 - Different morphologies of tridactyl footprints in the late Cenomanian sites of Istria. A) SLD-T1-5, B) SLD16, C) SLD-T9-2, D) SLD-T2-2, E) SLD-T11-1, F) SLD-T15-1, G) SLD-T12-1, H) PR-T1-3, I) PR-T2-4. Drawings taken from the casts. Of course, the left-right symmetry in casts is reversed from actual footprints. Legend: II = print of digit II. Scale bar = 3 cm.

in the estimation of V even if L is slightly more than 25 cm) have a markedly slower gait with respect to the smaller ones (Tabs. 1, 3). In the long tracks of the Fenoliga islet site the stride was clearly oscillating as also the direction of movement, which is more or less undulating. The relatively high number of consecutive footprints in FEN-T1 and FEN-T2 allows us to test the change in the gait of the trackmaker by plotting the change of SL value (Text-fig. 16). Because V is proportional to SL, these variations reflect also speed variations. SL was markedly oscillating around the average value, therefore the gait was not a constant, relatively fast (mainly in FEN-T1) walking, as suggested by SL/h and V/AWS calculated with the mean of SL, but was a sequence of accelerations and slowing downs. This suggests a behaviour slightly more complex than a simple crossing the site, even if it is not exactly the behaviour of an animal randomly wandering. If we take a short segment of FEN-T1 and FEN-T2, it would appear straight and the gait would appear more or less constant. This suggests that the short segments of a track can give information only about the "instant" gait (speed) of the trackmaker and is uninformative about the actual, overall gait. Despite the changes of speed in the same track, it is clear that

FEN-T1 was moving comparatively faster than FEN-T2 and FEN-T3 was moving decidedly faster (with a trotting gait) than the other two.

The trackmakers of the Grakalovac site moved relatively slower if compared with those of S. Lorenzo di Daila/Lovrečica, and have V just slightly higher than AWS (see Tab. 3).

SL/h of the tracks of the S. Lorenzo di Daila/Lovrečica site points to a similar gait for all the five trackmakers (Tab. 4). They were fast walking and all moved in a straight line, at least in the short distance, with V decidedly higher than AWS (Tab. 4).

Directions – The relatively large track sample of S. Lorenzo di Daila/Lovrečica site shows us that the tridactyl trackmakers had preferential directions, with a bimodal distribution of the directions to ESE and WNW. This behaviour of the trackmakers also suggests that the animals were not randomly wandering.

In the Grakalovac site the two trackmakers of smaller size went nearly exactly in the same direction (ENE), even if they passed at different times, the footprints being on slightly different levels. The larger trackmaker is also ENE directed, but diagonally crossed the direction of the other tracks.

In the Fenoliga islet site two tridactyl trackmakers were moving SSE and one SSW. The maker of FEN-ST1 at the end of the track was moving to the SSW, too. According to Mezga & Bajraktarević (1999) the tracks in their Fenoligan sample show a preferential (non-random) direction (to NW, SSE and, lesser, SW), but these authors misunderstood the direction (verse) of the main track and the same could be true for other non-tridactyl tracks.

Preferential directions were also observed in the tridactyl footprint sample of the upper Albian Solaris site of Istria where they appear to be related to topographic constraints, like the coastline direction (Dalla Vecchia & Tarlao, 2000). This is most probably also the case of the upper Cenomanian samples, where the coastline direction could be responsible for the unimodal or bimodal distribution. However, unlike from the Albian sites, the Cenomanian ones do not show evidence of markers for local topography (e.g. ripple marks and drainage channels).

The influence of a common behaviour on this distribution of directions (i.e. individuals passing together at the same moment) cannot be excluded or confirmed because there is no way to clearly distinguish the resulting track pattern from that of single individuals passing at different moments along a band of wet sediment topographically constrained (i.e. bordered by the sea or a lagoon on one side, by lagoon, swamps, bushland or forest on the other).

QUADRUPEDAL TRACKMAKERS

Determination – KAR-ST1 and KAR-ST2 of the Carigador/Karigador site appear to have been impressed by the same kind of trackmaker. The morphology of the better preserved footprints (both manual and pedal) of KAR-ST1 perfectly matches with the footprints usually attributed to sauropods (cf. in particular, Thulborn, 1990, pp. 168-171; see also Farlow *et al.*, 1989; Ishigaki, 1989; Lockley, Farlow & Meyer, 1994; Meyer *et al.*, 1994; Pittman & Gillette, 1989). Also parameters of the track correspond. The outward pedal rotation is the same found in sauropod tracks (Thulborn, 1990), and the manus shows a distinct outward rotation (*ibidem*). Pedal A in the best preserved KAR-ST1 is the same as in *Brontopodus* Farlow, Pittman & Hawthorne (100°-120° in the Albian tracks of Texas according to Farlow *et al.*, 1989) as also SL/Lp (2-5 in *Brontopodus*; *ibidem*). Manual A is less than pedal A, in agreement with that reported by Thulborn (1990, p. 172) for sauropods.

The other footprints of the site also most probably belong to the same kind of trackmaker.

Although the manual prints are deformed by sediment pushed forward by pedal pressure, considering that probably they were originally as long as wide, like in the better preserved *Brontopodus* and *Titanosaurimanus* Dalla Vecchia & Tarlao prints, manual print width suggests that heteropody was not

very marked. However, this is not the case of KAR-S5 (and possibly also FEN-ST1), where the manual print appears to be rather small.

As reported above, the long track FEN-ST1 of the Fenoliga islet was interpreted by Leghissa & Leonardi (1990) as sauropodan, with complete or nearly complete *pes-manus* overlap. *Pes-manus* overlap is not common in sauropods but, for example, occurs in some tracks from the Albian Paluxy River site of Texas (Farlow, 1987) and in a track from the Albian of Istria (Dalla Vecchia & Tarlao, 2000). The interpretation by Leghissa & Leonardi (1990) was accepted by Lockley, Meyer *et al.* (1994) which considered FEN-ST1 as one of the few known Late Cretaceous sauropod tracks. However, the formal description by G. Leonardi was based on photographs and not on direct observations or accurate maps (Leghissa & Leonardi, 1990, p. 15). This led to some mistakes, some of which we mentioned above.

The size of the FEN-ST1 trackmaker could be consistent with that of a large ornithomimid (e.g. iguanodontid) or a large theropod dinosaur, not only of a sauropod. On the Main Brioni/Brijuni Island (SW Istria) a similar bipedal track with 20 consecutive footprint is found in the upper Albian (Dalla Vecchia, 1997a; Dalla Vecchia & Vlahović in progress). All the footprints are shallow, rounded or elliptical, about 30-35 cm long and the rather variable Δ is as low as 115°. Only one footprint on a total of 20 is without doubt tridactyl, with short, wide digital prints, absence of claw marks and a high Δ value, and shows that the trackmaker was most probably an ornithomimid. The case of FEN-ST1 could be similar and a deeper analysis is needed to confirm or disprove its sauropodan origin. The very poor preservation permits us only to say that there is no evidence that the footprints are tridactyl and that because of size and age the trackmaker was a dinosaur. No morphology can actually be recognized except that each print is a depression with a more or less circular-oval outline. Cretaceous dinosaurs with circular-oval, non-tridactyl pedal prints were all quadrupedal. Sometimes in FEN-ST1 there is a possible smaller print in front of the larger one (pedal), also suggesting that the trackmaker was quadrupedal. However, the most reliable feature suggesting an identification as a quadrupedal dinosaur is the regularly low pace angulation. Δ in the late Albian, bipedal track above mentioned is on average higher than in FEN-ST1, ranging from 115°-159° ($M = 135.6^\circ$; $N = 14$). Therefore, if the trackmaker was quadrupedal, in FEN-ST1 there was often a complete or nearly complete *pes-manus* overlap. Pace angulation in quadrupedal iguanodontians is clearly higher than in FEN-ST1 (Moratalla *et al.*, 1992, 1994; Thulborn, 1990). A of sauropod tracks is often in the range 120°-140° according to Thulborn (1990), but is 100°-120° in the Albian tracks of Texas according Farlow *et al.* (1989), as mentioned above; therefore the values in FEN-ST1 ($M =$

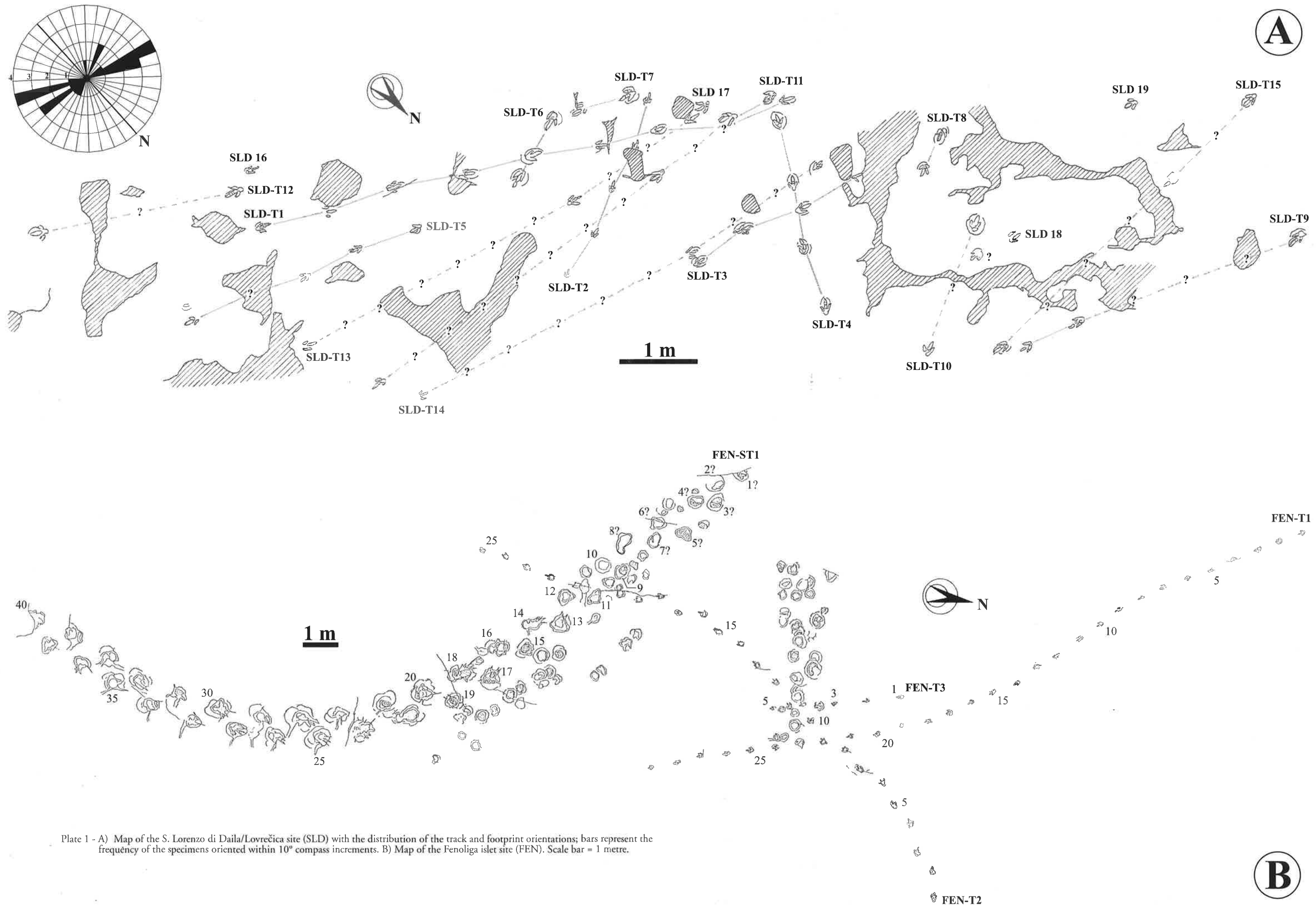


Plate 1 - A) Map of the S. Lorenzo di Daila/Lovrečica site (SLD) with the distribution of the track and footprint orientations; bars represent the frequency of the specimens oriented within 10° compass increments. B) Map of the Fenoliga islet site (FEN). Scale bar = 1 metre.

98.5°) are even lower than those usual for sauropods.

The trackmaker is more likely a sauropod than a neoceratopsian mainly because of the age of the site which excludes the latter. Neoceratopsians are found only in the Campanian-Maastrichtian of North America and east-central Asia (Dodson & Currie, 1990). However, on these grounds an ankylosaurian trackmaker cannot be excluded, because ankylosaurians were found in the continental Lower to Upper Cretaceous of Europe and Asia (Coombs & Maryanska, 1990). Both supposed neoceratopsian and ankylosaurian pedal prints are only slightly longer than wide or as wide as long (Thulborn, 1990). Ankylosaurian pedal prints, mainly in the Early Cretaceous *Tetrapodosaurus borealis* Sternberg, the best defined ichnotaxon attributed to this group, show four relatively long digital prints, and the hand has five short and divergent digital prints, without pedal overprint (Thulborn, 1990, fig. 6.41a). This suggests that the footprints of FEN-ST1 are not ankylosaurian. Sauropod tracks are much more common in the fossil record than those of ankylosaurians and neoceratopsians. Furthermore, sauropod footprints are common in carbonate platform settings (Lockley, Hunt & Meyer, 1994), whereas those of ankylosaurians and neoceratopsians are practically absent.

The sauropod tracks of Carigador/Karigador and Fenoliga sites were impressed by animals of similar size and with a similar slow gait. However, KAR-ST1 and ST2 have A values higher than FEN-ST1, and also SL and V are slightly higher in KAR-ST1 and ST2. The gauge is narrower in the tracks of Carigador/Karigador site. KAR-ST1 and FEN-ST1 differ also in the overlap of the *pes* and the *manus*.

If the other rounded-oval depressions identified by Mezga & Bajraktarević (1999) in the Fenoliga site are sauropod prints (actually Mezga & Bajraktarević do not prove with valid characters this attribution, but their identification as sauropodan is plausible), and the statement that there are nine groups of sauropod footprints ranging from 40–23 cm is correct, it would be the evidence that rather small sauropods (smaller than in the estimation by Mezga & Bajraktarević, 1999, p. 743) were common in this site. Also the rounded prints in Grakalovac site could be small sauropod prints and would confirm the relative abundance of small sauropods in the upper Cenomanian of Istria.

The sauropods represented in the late Cenomanian track sample had a size decidedly reduced in comparison with the sauropodan standards based on the osteological record (Dodson, 1990), a size comparable to that of the Albian sauropods of Istria represented by footprints (Tabs. 2, 5; cf. Dalla Vecchia & Tarlao, 2000). According to Thulborn (1990, p. 169) print lengths of sauropod hindfeet range from 50–150 cm, but are often about 90–100 cm. According to Farlow *et al.* (1989) pedal print length of

Brontopodus (Albian of Texas), the best known sauropodan ichnotaxon, ranges from 50 to over 100 cm. The late Cenomanian sauropod footprints of Istria are therefore unusually small.

The gauge of FEN-ST1 is wider than that of KAR-ST1 and ST2, but not as wide as usual in Cretaceous sauropod tracks (Wilson & Carrano, 1999). M. Lockley (pers. comm. in Dalla Vecchia & Tarlao, 2000) suggested that the relatively narrower gauge of the Albian sauropod track of the Solaris site could be due to the small size of the trackmaker. However, wide-gauge tracks of small sauropods are known in the Late Jurassic of Portugal (Lockley, Meyer & dos Santos, 1994). Furthermore, according to Wilson & Carrano (1999, p. 252) "lack of systematic size differences between footprint gauges argues against body-size-related influences".

Gait, speed and directions – The three sauropod trackmakers (KAR-ST1, KAR-ST2 and FEN-ST1) had all a slow walking gait and a V decidedly less than AWS ($V/AWS = 0.70\text{--}0.78$). Therefore, they were moving very slowly even for sauropod standards.

The sauropods of Carigador/Karigador site were all moving to the ESE-SSW, the same range of directions of the trackmakers at Fenoliga (bipedal and quadrupedal).

Comparisons – KAR-ST1 particularly resembles the sauropod track of fig. 6.15b of Thulborn (1990) labeled as "unnamed trackway from the Jurassic of Morocco".

The gauges of KAR-ST1 and ST2 resemble that of the Albian sauropod track at the Solaris II outcrop (Dalla Vecchia & Tarlao, 2000). The gauge of KAR-ST1 is decidedly narrower than in *Brontopodus* (see Farlow *et al.*, 1989; Lockley, Farlow & Meyer, 1994) and, according to the definition of narrow gauge (see p. 36), could be considered narrow, because footprints are "close to the trackway midline". Actually, as reported above, the gauge of the Istrian tracks is most reminiscent of the medium-gauge of Meyer *et al.* (1994, fig. 4). In KAR-ST1 the crescent-shaped manual print is placed in front of and lateral to the pedal one, that is pedal prints are closer to the midline than are manual prints. This is the condition in narrow-gauge trackways according to Wilson & Carrano (1999, p. 254), who also contend that all post-Aptian sauropod tracks are wide-gauged, and Titanosauria made only wide-gauged tracks because of skeletal constraints in the femur and hip. Following Wilson & Carrano (*ibidem*, fig. 6) the only sauropods during late Cenomanian times were Titanosauria. The ichnological record from the upper Cenomanian of Istria is not in agreement with such generalizations.

Besides the gauge, the best-known ichnogenus *Brontopodus* differs from KAR-ST1 and KAR-ST2 because, according to its diagnosis (Farlow *et al.*, 1989, pp. 391–392) it has 1) larger size, 2) a *manus*

print as wide as long and with impression of digits I, V and conjoined II-IV, 3) a pedal print with large, laterally directed claw marks at digits I-III, diminishing in size from I to III, 4) a *manus* print medial to a line through the *pes* print long axis, such that *manus* print centers are somewhat closer to the track midline than *pes* print centers, 5) outer limits of the track defined by the pedal print, 6) *manus-pes* distance 0.5-1.2 times *pes* print length.

A relative abundance of small sauropods and the absence of large ones was also observed in the late Albian outcrops of the Solaris site (Dalla Vecchia & Tarlao, 2000) where the maximum Lp is about 50 cm. Like the Albian Istrian ichnotaxon *Titanosaurimanus nana* Dalla Vecchia & Tarlao (Dalla Vecchia & Tarlao, 2000), the Cenomanian pedal prints do not show the large claw mark on digit I often found in sauropodan pedal prints (e.g. Farlow *et al.*, 1989; Lockley, Farlow & Meyer, 1994; Meyer *et al.*, 1994). In *Titanosaurimanus nana* the pedal claw marks are small, and in the Cenomanian footprints they are not found at all. Unfortunately, *Titanosaurimanus* is diagnosed mainly on manual characters, which indicate also a titanosaur affinity of the trackmaker, and manual print morphology is poorly preserved in the Cenomanian sample, also because of anteroposterior deformation caused by the sediment displacement on the part of the *pes*.

The gait was particularly slow in both the single late Albian and the three late Cenomanian tracks (cf. Dalla Vecchia & Tarlao, 2000, tab. 6), which all have a pace angulation lower than those indicated as most frequent for sauropods by Thulborn (1990, p. 169). In both the Albian track of Solaris II outcrop and the FEN-ST1 there is complete or nearly complete *manus-pes* overlap; however, this is not the case for KAR-ST1.

PALEOGEOGRAPHICAL REMARKS

The peri-Adriatic region, which basically corresponds to the present day Adriatic Sea and the surrounding mountain chains in Italy, Slovenia and Croatia, was an area of nearly exclusively carbonate sedimentation from the Late Triassic to the end of the Cretaceous (Zappaterra, 1990). The Istrian region was part of the northern point of the Adriatic-Dinaric carbonate platform. The Adriatic-Dinaric carbonate platform was a paleogeographic unit formed during the Jurassic that now outcrops mainly in northeastern Italy, Slovenia, Croatia, western Bosnia and western Montenegro. During Cenomanian times the platform was roughly N-S elongated and was bordered to the W, E and N by marine basinal areas (see Cati, Sartorio & Venturini, 1989; Zappaterra, 1990). It was one of the Cretaceous peri-Adriatic platforms "analogous to the Bahamas archipelago, not only in their carbonate facies, platform size and shape, and rate of subsidence...but also in the internal architecture" (Eberli *et al.*, 1993, p. 216). The paleogeographic relationships of the Adriatic-

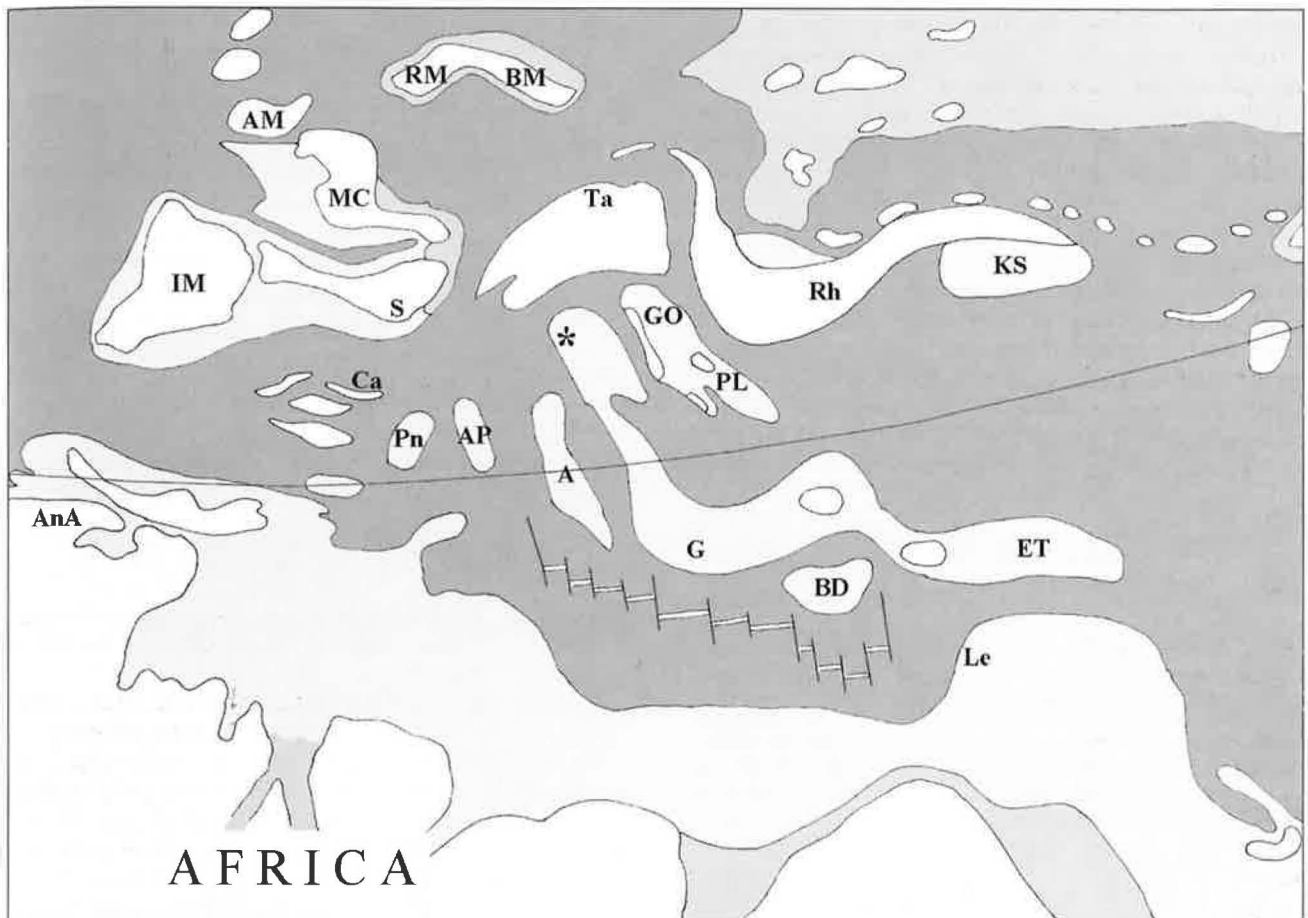
Dinaric carbonate platform with the other paleogeographic units of peri-Tethys, are shown in the late Cenomanian paleogeographic map of Philip *et al.* (1993) (here Text-fig. 21). Of course, the present day position of many paleogeographic units is different from that occupied during Cretaceous times. The Adriatic-Dinaric carbonate platform was the northern termination of a larger, narrow and NW to SE elongated, shallow marine paleogeographic unit made only of carbonate platforms in the reconstruction of these authors. According to the paleogeographic maps (see Dercourt *et al.*, 1993) it had been surrounded by deep marine troughs since Jurassic times, and it was somehow separated from both European and African-Arabian continents during the Cenomanian (see also Eberli *et al.*, 1993). According to Philip *et al.* (1993, p. 154 and map) the Apulian domain, and therefore also the unit under discussion, was separated from Africa by an oceanic trough during late Cenomanian (see Text-fig. 21).

As noted by Dalla Vecchia (1997b; 1998) and Dalla Vecchia & Tarlao (2000), the Cretaceous Adriatic-Dinaric carbonate platform was connected to other carbonate platforms, but was very far (hundreds of kilometres) from "land", the latter considered as a wide emergent area of sediment source, sediment bypass or with silicoclastic fluvial/lacustrine sedimentation. Furthermore, during Cenomanian times, deep marine basins completely surrounded this platform. Therefore, according to the paleogeographic reconstructions, we are dealing with the singular case of dinosaurs living on a carbonate platform practically separated from a continental area by deep marine basins. In fact, the other carbonate platforms where dinosaur ichnofaunas are found (e.g. Texas and Portugal) were pericontinental platforms (i.e. they bordered land margins) with carbonates grading landward into siliciclastic shore and continental sediments. In these pericontinental platforms the sauropods had the usual giant size and large theropods were common (Pittman, 1989; Dalla Vecchia & Tarlao, 2000).

This suggests the possibility that the Cenomanian dinosaurs were living on relatively small islands (as suggested also by the absence of widespread and prolonged emersions of the platform). This could have an important meaning for the understanding of dinosaur metabolism. The presence of only small-sized sauropods suggests, combined with the reduced size of the tridactyl trackmakers, that the insular conditions hypothesized for the late Albian, with dwarf sauropods and relatively small predators, continued during the late Cenomanian.

Presumably, the Cenomanian dinosaurs were the descendants of those living on the Istrian portion of the Adriatic-Dinaric platform during late Albian times (see Dalla Vecchia & Tarlao, 2000), at least 9.5 m.y. earlier according to Harland *et al.* (1982), as suggested by the overall similar ichnological association.

The late Cenomanian-early Turonian flooding of the platform (Polsak, 1979; Jenkyns, 1991; Gusić & Jelaska, 1993; Tentor *et al.*, 1993) probably led to the



Text-fig. 21 - Palaeogeography of central Tethys during the late Cenomanian (after Philip *et al.*, 1993, modified and redrawn). Legend: white = land, gray = terrigenous shelf and shallow terrigenous basin (shallow sea), light gray = carbonate platform (shallow sea), dark gray = deep sea (ocean, basin and slope, including the sea where the Chalk was depositing). The asterisk indicates the position of the northern part of the Adriatic-Dinaric Carbonate Platform and of the sites here described. The position of the Eastern Mediterranean Ocean is indicated by the stylized drawing of the crustal scar formed by the oceanic spreading. Abbreviations: AM = Armorican Massif (northwestern France), AnA = Anti-Atlas (Morocco), A = Apulia Carbonate Platform (southern Italy), AP = Lazio-Abruzzi-Campania Carbonate Platform (central-southern Italy), BD = Bey Dagları (Turkey), BM = Bohemian Massif (mainly Bohemia, Czech Republic), Ca = Calabria (southern Italy), ET = Eastern Taurus (Turkey), G = Gavrovo (Bulgaria), GO = Golija Massif (Montenegro), IM = Iberian Meseta (Spain), KS = Kırşehir (Turkey), Le = Lebanon, MC = Massif Central (France), PL = Pelagonian Massif (northern Greece), Pn = Panormides (Sicily, insular Italy), Rh = Rhodope Massif (southern Bulgaria), RM = Rhenish Massif (western Germany, partly Belgium, Luxemburg and N France), S = Sardinia (insular Italy), Ta = Tatra Mountains (Slovakia and southern Poland). The line crossing the figure is the parallel 20°N.

migration or extinction of the local dinosaur fauna. In fact, the successive dinosaurian evidence in the late Santonian (Italian Karst) and Campanian/Maastrichtian (Slovenian Karst) shows a different composition of the plant-eaters (primary consumers), which became dominated by hadrosaurs.

The Cenomanian track sites with footprints are limited to just a narrow band in the W Istria, where Cenomanian rocks outcrop, and where bed surfaces can be investigated because they are exposed. The dinosaurs very probably lived in other, emergent and vegetated parts of the platform and occasionally arrived on the tidal flats, the only places where they could leave evidence of their presence there.

Probably our knowledge of Mesozoic carbonate platforms, central Tethys paleogeography and dinosaur paleobiology is still inadequate to understand their reciprocal interactions.

CONCLUSIONS

We reported four sites with dinosaur footprints exposed along the Istrian coast in upper Cenomanian limestones. Dinosaur presence points to the existence of emergent areas of the carbonate platform despite the fact that marine limestones with rudists are prevalent and geological evidence of prolonged emersion very scarce in Istria. The land vertebrates lived on the

carbonate platform despite the fact that the late Cenomanian is universally considered a worldwide interval of sea level highstand (Haq *et al.*, 1987; Jenkyns, 1991; Philip *et al.*, 1993).

The most common dinosaurs were medium-sized bipeds, most probably theropods. Small sauropods are represented, too, and could have been relatively common; they are one of the rare ichnologic evidence of this group in the Upper Cretaceous (Lockley, Meyer *et al.*, 1994; Lockley & Meyer, 2000). Absence of large predators and large plant-eaters suggests that the insular habitat hypothesized for the late Albian Istrian dinosaurs (Dalla Vecchia & Tarlao, 2000) continued into the Cenomanian, in agreement with the palaeogeographic reconstructions of central Tethys.

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