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CRETACEOUS DINOSAUR AND TURTLE TRACKS ON THE ISLAND OF VELI BRIJUN (ISTRIA, CROATIA)

ALEKSANDAR MEZGA and ZLATAN BAJRAKTAREVIĆ

Department of Geology and Paleontology, Faculty of Science, University of Zagreb, Zvonimirova 8, HR-10000 Zagreb, Croatia; amezga@geol.pmf.hr; zbajrak@geol.pmf.hr

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Abstract: The dinosaur footprints have been discovered on the island of Veli Brijun, Croatia at one Late Barremian site (Pogledalo) and three Late Albian sites (Ploče, Kamik/Plješivac, Trstike/Debela Glava). The Late Barremian ichnocoenosis contains tracks of large theropods in intertidal sediment. The footprints assigned to the large 'carnosaur'-type theropods predominate over a rare gracile form. Footprints of small to medium sized theropods, medium sized ornithopods and small ornithopods are present in Late Albian ichnocoenosis as well as possible chelonian footprints. They were formed in a lagoonal environment that was occasionally subaerially exposed. The parallel trackways could indicate gregarious behaviour among the small ornithopods. Footprints of an iguanodontid ornithopod represent the only such findings in the Istria. The speeds of individuals at all four localities indicate normal walk. A total of 145 dinosaur footprints and 75 possible chelonian prints have been mapped; 111 prints are arranged in 14 trackways.

Key words: Croatia, Late Barremian, Late Albian, ichnology, dinosaurs, turtles, theropods, ornithopods.

Introduction

Dinosaur footprints in Istria occur in well-bedded limestones of the Adriatic-Dinaric carbonate platform. Until recently the age of these footprints was regarded as Barremian–Albian but new findings and micropaleontological analyses have widened that range from Early Hauterivian (Dalla Vecchia et al. 2000) to Late Cenomanian (Mezga & Bajraktarević 1999; Dalla Vecchia et al. 2001). Research on the dinosaur footprints of the Brijuni Archipelago (Fig. 1) began in 1925 with the work of the Austrian industrialist Bachofen-Echt who has described two different types of footprints. He assigned small to large tridactyl tracks to the genus *Iguanodon* and circular footprints with visible traces of claws to turtles (Bachofen-Echt 1925a). The locality at which Bachofen-Echt discovered the footprints is described in his work as cape "Rocca", but such name does not exist on the maps of the Veli Brijun Island and the exact location of this outcrop cannot be precisely determined. Today it is presumed that the site on the Ploče promontory could be the site described by Bachofen-Echt (Dalla Vecchia et al. 1993, 2002). Footprints on the Plješivac promontory (Polšak 1965; distinguish two types of footprints) and Pogledalo (Velić & Tišljar 1987) were discovered during later investigations and described recently (Dalla Vecchia et al. 2002). Tridactyl footprints previously assigned to the genus *Iguanodon* (e.g. Polšak 1965; Velić & Tišljar 1987) have recently been identified as theropod footprints (Dalla Vecchia et al. 1993, 2002).

Geological setting

The Upper Barremian to Upper Albian carbonates lie flat on the Veli Brijun Island. The southern and northern parts of the island are composed of well-bedded limestones of Late Albian age, while the central and north-western parts are composed of Upper Barremian carbonate deposits (Velić & Tišljar 1987). These sediments were deposited in shallow marine carbonate platform environments, which changed from shallow subtidal to intertidal zones and experienced frequent emersions. Carbonate sediment layers with the dinosaur footprints on the Pogledalo locality (Fig. 2A) are of Late Barremian age. The age has been proved by the findings of the algae *Salpingoporella melitae* Radoičić, *S. genevensis* (Conrad) and *S. urlanadasi* Conrad et al. (Velić & Tišljar 1987). Dinosaur footprints occur on the upper bedding plane of a layer composed of fenestral micrite. The layer is sub-horizontal, with an exposed area of 43 × 5.5 m, and thickness of 130 mm. A thin-bedded, stromatolitic-pelletal limestone with a thickness of 100–200 mm is found above the track-bearing layer. Ripple marks indicate shallow water to intertidal environment. Thick-bedded, peritidal limestone breccias are found below the track-bearing layer. The footprints also occur in the Upper Albian carbonate layers at three different sites. At the Trstike/Debela Glava site (Fig. 2B) the layers are made up of white pelletal-peloidal wackestone–packstone, partly recrystallized. The microfossil assemblage includes numerous *Thaumatoporella* sp. algae, foraminifers like *Glomospira* cf. *urgoniana* Arnaud-Vanneau, *Istriloculina* cf. *granumtrici* Neagu, *Earlandia*? sp. and ostracods. Footprints occur on the upper bedding plane of a horizontal layer with exposed area of 41.5 × 31.5 m and bed thickness of 120 mm. The overlying limestone bed is about 300 mm thick, and the underlying limestone bed is about 150 mm thick. At the Kamik/Plješivac (Fig. 2C) and Ploče (Fig. 2D) locality limestone layers show somewhat different characteristics. The sediment is miliolid-peloid wackestone with the transition to miliolid packstone. On the Ploče locality there are numerous geopetal infillings

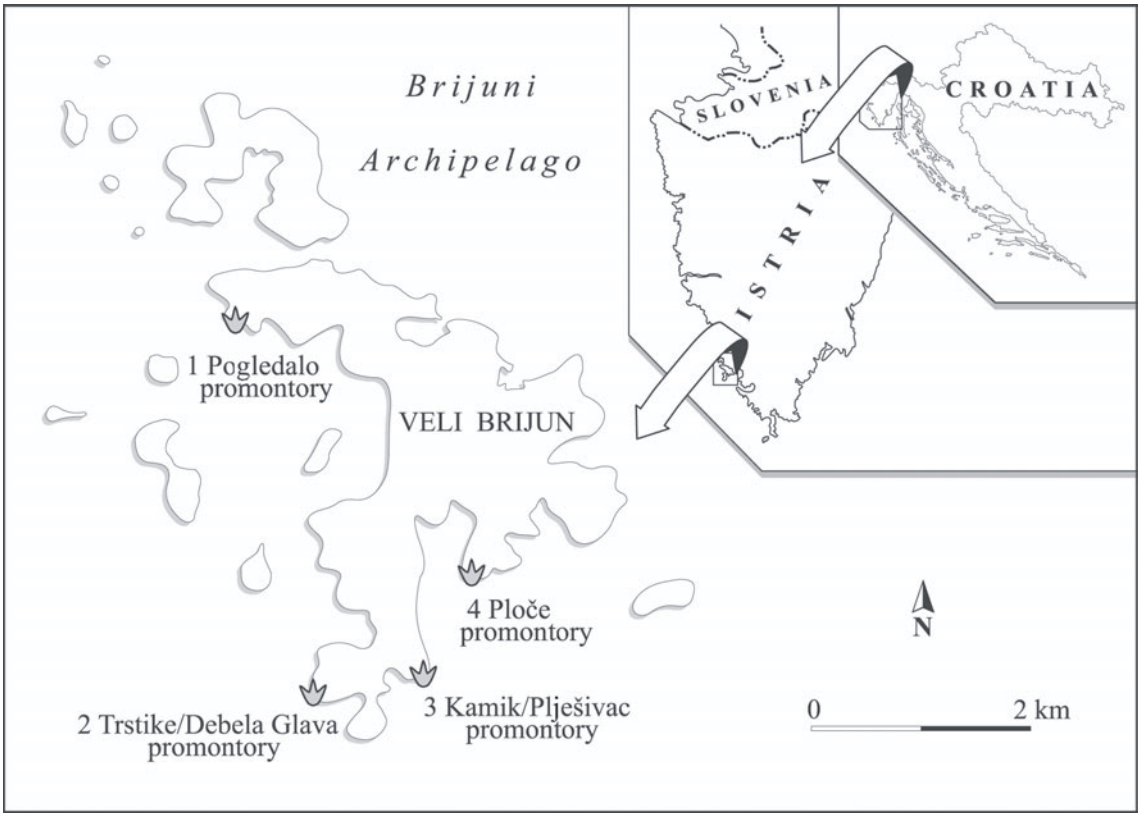

Fig. 1. Locality map with footprint localities indicated.

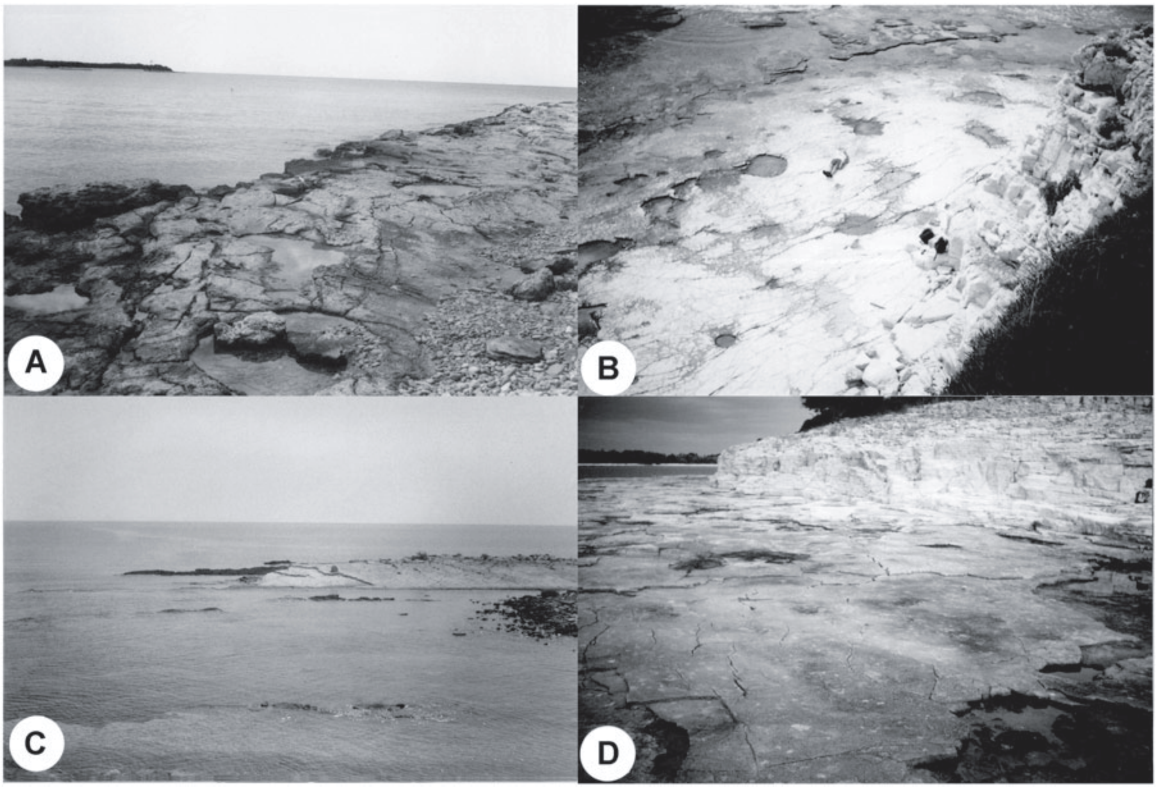

Fig. 2. The four track-bearing outcrops on the Veli Brijun Island. **A** — Pogledalo promontory; **B** — Trstike/Debela Glava promontory; **C** — Kamik/Plješivac promontory; **D** — Ploče promontory.

(not mentioned in Dalla Vecchia et al. 2002) inside the miliolid wackestone which are clear indicators of subaerial exposure. There are also numerous coated grains inside miliolid packstone indicating a more agitated environment. The microfossil assemblage found in the thin sections is typical for the Late Albian environment of the Adriatic-Dinaric carbonate platform. Among the foraminifers the miliolids prevail, there are numerous *Scandonea* aff. *phoenissa* Saint-Marc, *Pseudonummoloculina heimi* (Bonet), *Istriloculina* cf. *granumtrici* Neagu, *Rumanoloculina* cf. *minima* (Tappan) and *Sigmoilina*? sp. *Nezzazata isabellae* Arnaud-Vanneau et Sliter and *Novalesia* cf. *angulosa* (Magniez) are also present as well as the algae *Salpingoporella*? sp. This microfossil assemblage is more detailed than the assemblage mentioned in Dalla Vecchia et al. (2002) and more clearly proves the Late Albian age of the sediment. At the Kamik/Plješivac locality, the structures and textural characteristics of the sediment do not indicate subaerial exposure, and it was probably formed in a shallow subtidal environment. The footprints occur on the upper bedding planes of the two concordant sub-horizontal layers. The lower bed has an exposed area of 14 × 9 m and thickness of 0.52 m with the preserved ripple-marks on the top of it. The upper bed covers a larger area of 29 × 10 m and is about 200 mm thick. Both layers are in direct contact with the sea and during high tides the footprints are partially submerged. At the Ploče locality footprints occur on the upper bedding planes of the two concordant layers; the lower (stratigraphically older) layer has a thickness of 40 mm, and the upper layer has a thickness of 450 mm. The underlying and overlying beds are 100 mm thick. The area of the outcrop on which the footprints occur is horizontal and 14.5 × 12.7 m in extent. All four footprint localities are now situated on the shoreline and are in permanent contact with the sea with corresponding adverse effects on footprint preservation.

Systematic description

Upper Barremian footprints (Pogledalo locality)

Sixty-one dinosaur footprints were discovered on the track-bearing surface and 16 of them form four trackways (I–IV) (Fig. 3). In the trackway III an irregularity of the footprints can be observed; some footprints are missing from the trackway. The other footprints are not arranged in trackways, but occur individually.

Our map of this locality as well as the maps of the other localities on the Brijuni Island differs somewhat from Dalla Vecchia et al. (2002). This is mainly due to the different interpretations of some prints and trackways. The different angle of the sunlight during the day could also be the limitating factor in the footprint recognition, especially because of the poor preservation of the most of the footprints.

Although the sediment consistency was the prevailing factor in the preservation of the footprints, in contrast to Dalla Vecchia et al. (2002) we distinguish two morphotypes of the

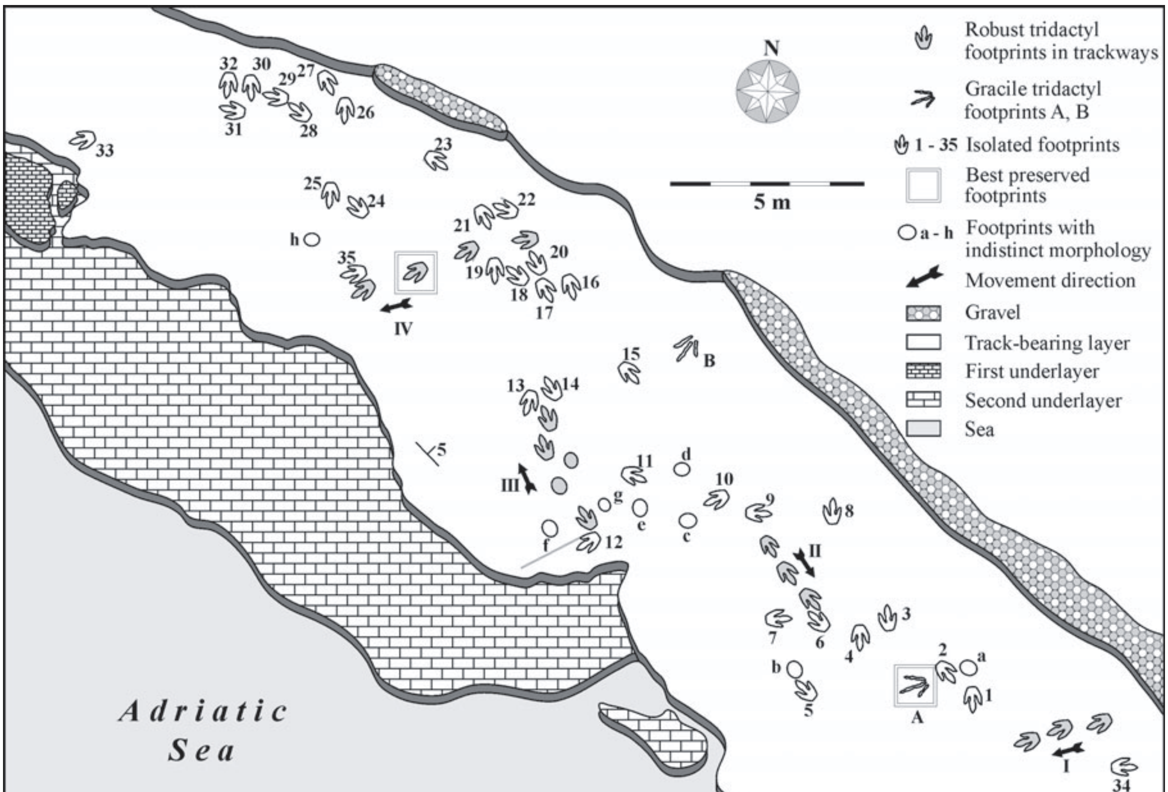

Fig. 3. Map of the Pogledalo locality.

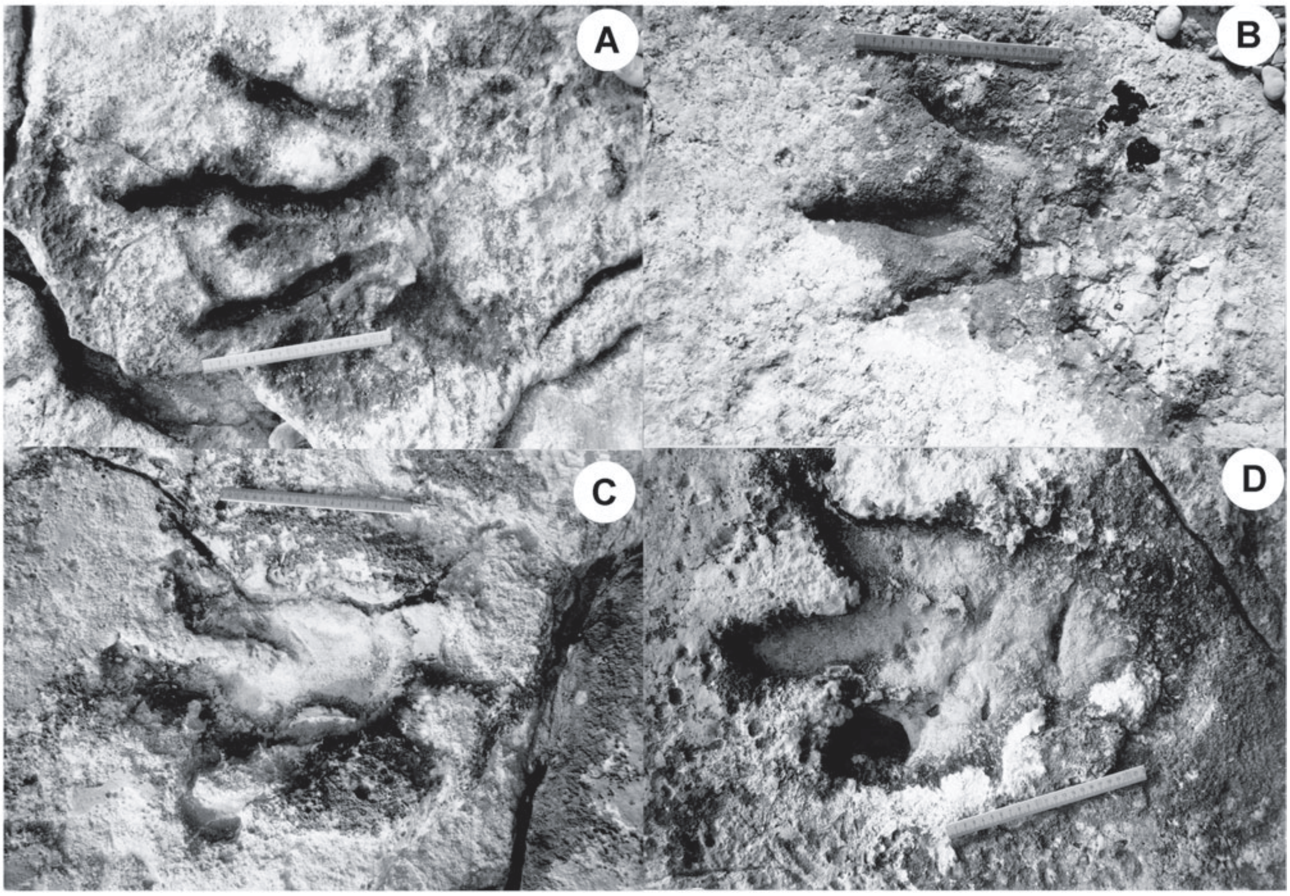

Fig. 4. Theropod footprints from the Pogledalo promontory. **A** — gracile type marked as A; **B** — gracile type marked as B; **C** — third footprint in trackway III, robust type; **D** — third footprint in trackway IV, robust type. Scale bar = 22 cm.

tridactyl footprints. The first type is a robust, stout, tridactyl form, arranged in four trackways (I, II, III and IV in Fig. 3) and 35 isolated footprints. The second type is a gracile, slender, tridactyl form (A, B in Fig. 3). Footprints marked with letters a–h represent dinosaur footprints, which are not distinct enough to be classified as either of the two types. Due to their specific morphology, the footprints marked with the letter A and IV3 (representing two different morphotypes) are described separately.

The footprint, marked with a letter A (Fig. 9B in Dalla Vecchia et al. 2002), representing the gracile type, is tridactyl, mesaxonic, with long and slender digits (Figs. 4A, 5). There is no hallux trace. This print is placed over another tridactyl print with different morphology; the individual that left the print passed over the track of the dinosaur, which crossed the same area earlier (see Fig. 4A; the V-shaped dent situated at the left side from the proximal part of the left digit is actually the distal part of digit III of the underlying track). It is characteristic of this footprint morphology that only digit prints are preserved while metapodium and "heel" impressions are absent. This could indicate that the dinosaur, which left this track, walked with an elevated digitigrade posture, but it may be a preservational factor. The three digit imprints are not connected at the rear of the print. Digit axes are straight, but the outer edges of each of the three digits are curved or winding. This is a product of the conspicuous digital pads on the phalanges of each of the three digits. The middle digit is the longest, while the outer left digit is longer than the right outer digit. The axis of the right digit describes with the axis of the middle digit a somewhat larger angle than the axis of the middle and left digit; 22.5° : 20° (interdigital angles were measured between digital axes representing lines of best fit; Fig. 4.5a in Thulborn 1990). On the basis of the interdigital angle measurement and the fact that the print of the left digit is shorter than the right one, it is concluded that this is a footprint of the left foot, with the right digit being digit II, middle digit III and left digit IV. Claw marks are well preserved on digits III and IV; the trace of the claw is sharp, V-shaped, and straight being coaxial with the digit. On digit II the claw impression is not clearly differentiated. Only a widened area, shallower than the rest of the digit, is present; it does not show the characteristic narrowing, but follows the line of the outer edge of digit II. Digit III is the widest, while the width of the outer digits is almost equal (generally speaking, all three digits are narrow in comparison to their length). The proximal ends of all three digits are in different planes. Impressions of two pads are noticeable on digit II. On digit IV there are three of them. The edges of digit III curve more than the edges of digits II and IV, but the impressions of at least three pads are visible (footprint dimensions are given in Table 1).

Table 1: Measurements of the footprints. All measurements in mm. Bold numbers are averages. Key to abbreviations: **TN** — trackway number (I, II, ...); **FM** — footprint mark (1, 2, ...; A, B, ...; a, b,...); **FL** — footprint length; **FW** — footprint width; **SI** — footprint size index; **FO** — footprint orientations; **DL II, DL III, DL IV** — length of digits II, III and IV; **DW II, DW III, DW IV** — width of digit II, III and IV; **TD** — total divarication.

TN/FM	FL	FW	FW/FL	SI	DL II	DL III	DL IV	DW II	DW III	DW IV	TD
Pogledalo											
I	**273**	**220**	**0.75**	**25.3**	**100**	**130**	**80**	**-**	**20**	**-**	**38°**
II	**345**	**280**	**0.81**	**31.1**	**120**	**170**	**115**	**60**	**70**	**70**	**44°**
III	**388**	**278**	**0.71**	**33.0**	**130**	**175**	**130**	**70**	**65**	**65**	**32°**
IV	**392**	**306**	**0.79**	**34.6**	**140**	**185**	**130**	**50**	**75**	**65**	**36°**
A	330	325	0.98	32.7	200	280	230	25	35	25	42.5°
B	280	240	0.85	25.9	100	155	110	25	40	30	44°
1–35	**324**	**265**	**0.80**	**29.2**	**128**	**179**	**133**	**52**	**60**	**54**	**43°**
a–h	**360**	**274**	**0.82**	**31.1**	–	–	–	–	–	–	–
Trstike/Debela Glava											
I	**153**	**140**	**0.93**	**13.7**	–	–	–	–	–	–	–
1–32	**141**	**141**	**1.03**	**14.0**	–	–	–	–	–	–	–
A	265	170	0.64	21.2	–	130	–	–	60	–	–
Kamik/Plješivac I											
I	**290**	**282**	**0.97**	**28.6**	**50**	**107**	**63**	**65**	**80**	**75**	**67.3°**
Kamik/Plješivac II											
II	**184**	**130**	**0.70**	**15.5**	**72**	**100**	**57**	**20**	**27**	**12**	**74°**
III	**185**	**145**	**0.78**	**16.4**	–	**105**	**70**	–	**45**	**35**	–
IV	**189**	**135**	**0.71**	**15.9**	–	**143**	–	–	**34**	–	–
Ploče											
I	**196**	**127**	**0.65**	**15.8**	**65**	**105**	**65**	**35**	**37**	**325**	**40°**
II	**198**	**140**	**0.71**	**16.6**	**57**	**110**	**30**	**27**	**40**	**20**	–
III	**228**	**141**	**0.62**	**17.9**	–	**100**	–	–	–	–	–
IV	**162**	**116**	**0.73**	**13.8**	–	**80**	–	–	**35**	–	–
V	**214**	**151**	**0.70**	**18.0**	**90**	**146**	**95**	**35**	**40**	**37**	**35°**
A	180	120	0.67	14.7	80	115	80	30	35	30	40°
B	235	180	0.76	20.6	55	95	45	40	45	40	41.5°
C	200	135	0.67	16.4	80	110	50	30	40	30	47.5°
D	190	130	0.66	15.9	80	120	70	35	40	30	45.5°
E	210	150	0.71	17.7	–	85	–	–	–	–	–
1–33	**87**	**111**	**1.28**	**9.83**	–	–	–	–	–	–	–
Ploče–Čamčarnica											
C1	320	250	0.78	28.3	100	160	180	65	45	50	–
C2	250	175	0.70	20.9	60	120	9	35	50	45	40°
C3	410	260	0.63	32.6	–	140	–	65	–	–	–
C4	430	250	0.58	32.8	90	160	65	55	60	60	44°

The footprint marked with IV3, representing the robust type, is the third in the row in the trackway IV (Figs. 4D, 5). The footprint is tridactyl, mesaxonic, with long and wide digits, 460 mm long and 320 mm wide. The middle digit is the largest (150 mm long and 70 mm wide) while the outer digits are of approximately the same size and are smaller than the middle digit (110 mm long and 50–80 mm wide). The middle digit is straight with parallel edges. It is widest at its proximal end (70 mm) and becomes gradually narrower toward its distal tip producing a V-like shape. The digit terminates with a V-shaped claw impression, which curves to the right side, in contrast to the digit itself. The right digit is curved to the right, but the curvature increases distally. The digit has a V-like shape and is widest in its proximal part. While the proximal part (2/3 of the digit length) is oriented in a straight line, the distal part (1/3 of the length) is sharply deflected to the right. A V-shaped claw impression is visible at the digit apex. The left digit is, in contrast to the other two, U-shaped, but also oriented in a straight line, and widest in the proximal part. The claw impression is not as conspicuous as on the other two digits. With respect to the middle digit, the axis of the left digit is oriented to the left. A hallux impression is not visible. The angle between the axes of the two outer digits is 30°, while their divergence with respect to the middle digit is about the same (15–16°). A characteristic of the footprint is the lack of well-defined creases separating the digital pad impressions. The impression of the distal part of the "heel" is visible. The heel impression is convex and has a gentle V-shape. The left margin of the heel impression is not connected in a straight line to the left outer edge of the left digit, but the characteristic indentation behind the left digit can be clearly seen. The right edge of the heel impression is continuously connected to the outer edge of the right digit, though the right digit appears separated from the footprint, because of a small indentation which can be noted at their junction. On the basis of the measured parameters, morphology and the position in the trackway, it was concluded that this is a footprint of the left foot, the right digit being digit II, the middle digit being digit III, and the left digit is digit IV.

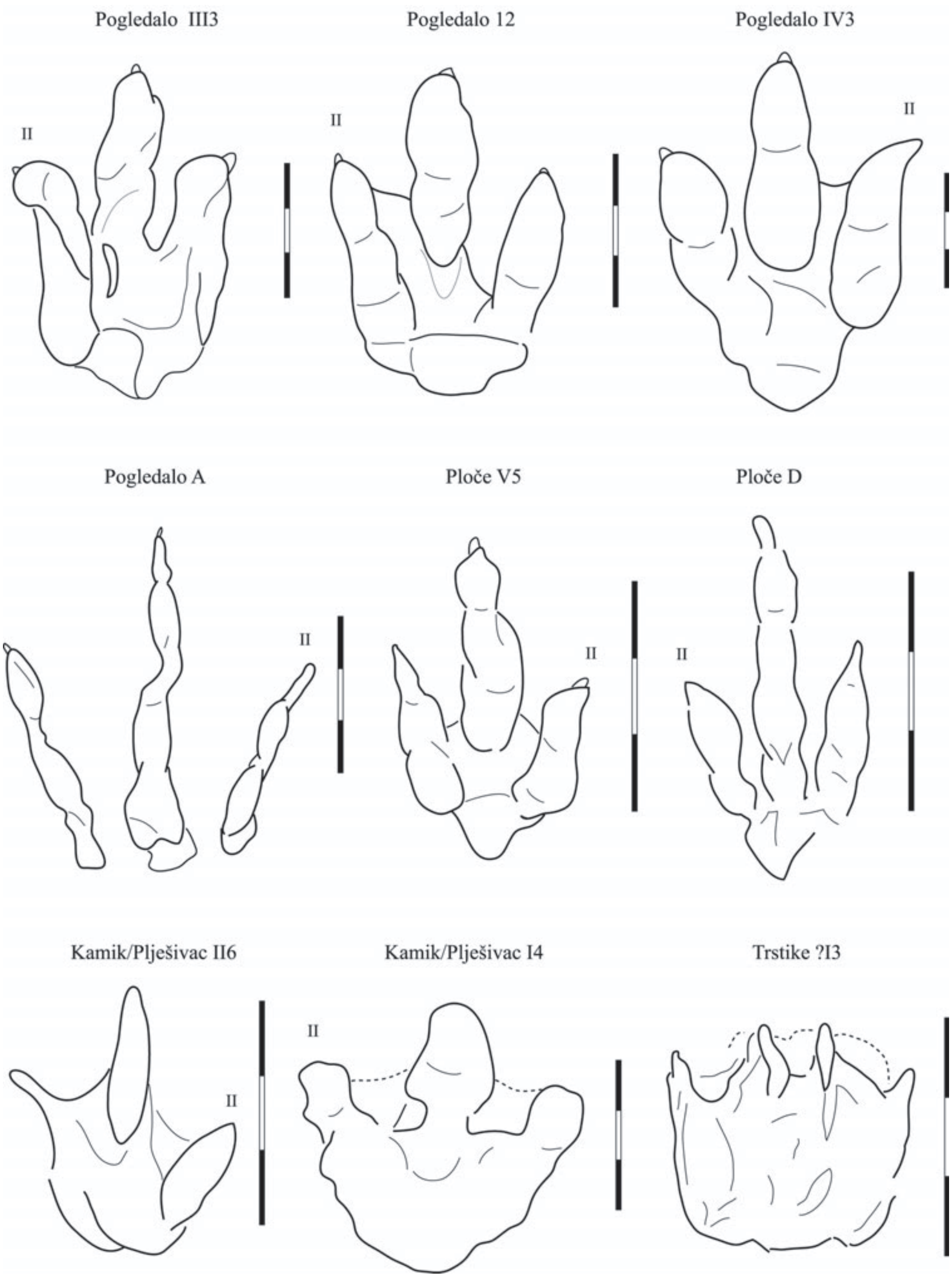

Fig. 5. Drawings of some footprints from the four localities on the Veli Brijun Island. Scale bar = 15 cm. The mark II indicates the position of digit II.

Upper Albian footprints (Kamik/Plješivac, Trstike/Debela Glava and Ploče localities)

Twenty consecutive dinosaur prints, discovered on the **Kamik/Plješivac I** layer surface, comprise trackway I (**Figs. 6, 7A**). The prints are tridactyl, very shallow, poorly preserved, and appear to have been produced by a bipedal dinosaur. The expulsion rims are visible. The pes morphology could still be recognized on two separate prints. The first is twelfth in a row in the trackway (Fig. 7B). It is tridactyl and mesaxonic with short blunt digits, 280 mm long and 300 mm wide. It is difficult to decide on the basis of the print itself whether it represents a left or a right foot. On the basis of its position in the trackway (it is on the right side of the trackway I central axis) we conclude that it is a print of the right pes. The left digit is consequently digit II, the middle digit is digit III, and the right digit IV. The left digit is not as well preserved as the other two. The outer digits have similar dimensions (40–45 mm long and 80–90 mm wide), are U-shaped and lack claw impressions. The middle digit is larger than the outer digits (105 mm long and 100 mm wide). The axes of all three digits are straight and the axes of the outer digits diverge substantially from the axis of the middle digit (37°). The total divergence is 73°. A heel impression is present, and is round-

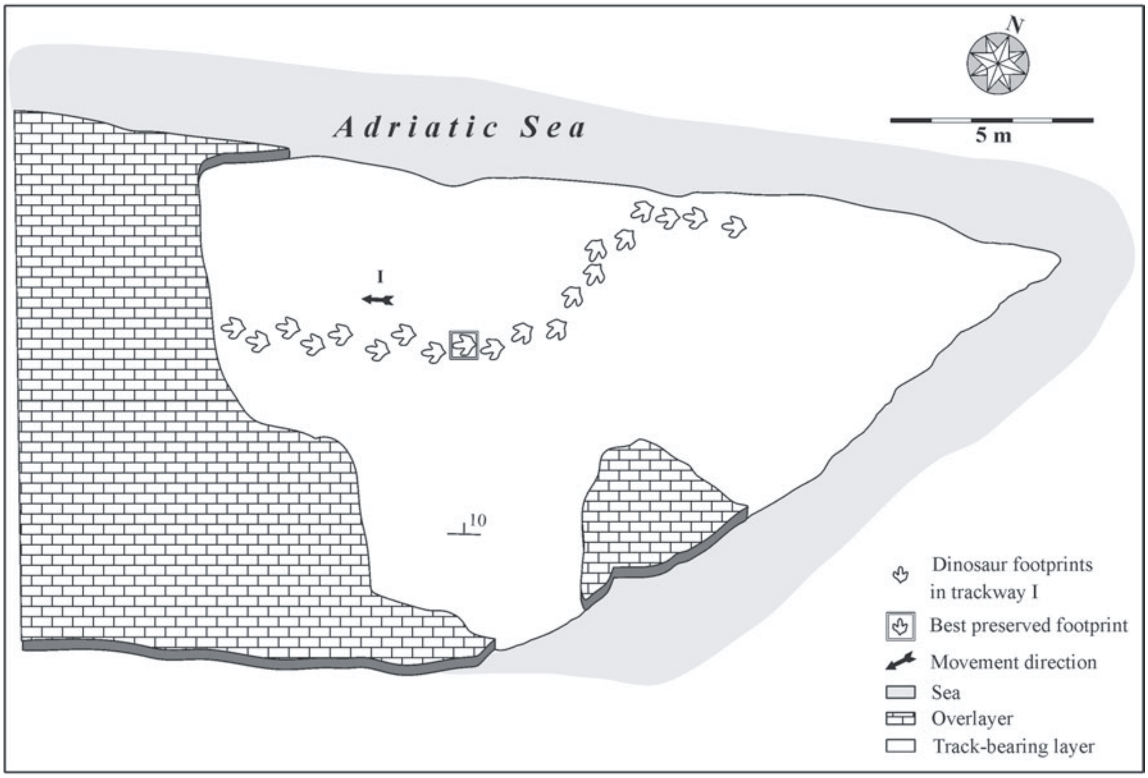

Fig. 6. Map of the Kamik/Plješivac I locality.

ed and convex, with a lunate shape. In fact, the whole footprint creates the impression of a semicircle with a single protuberance representing the print of the middle digit. The other print in the whole trackway in which the pes morphology can still be recognized is print I4 (Fig. 5). Its morphology corresponds to the description of the print I12, except that the middle digit has characteristically expanded tip (spade-shaped). The footprint has a length of 270 mm and width of 260 mm. The total divergence is 62°. Both footprints show a general morphology similar to the trefoil, which is a characteristic of the prints attributed to the pes of ornithopods (compare to Fig. 6.33 in Thulborn 1990; see also Dalla Vecchia et al. 2002).

Table 2: Measurements of trackways. All measurements in m. Key to abbreviations: **TN** — trackway number (I, II, ...); **TL** — trackway length; **TW** — trackway width; **TO** — trackway orientations (degrees); **PL** — pace length; **SL** — stride length; **SL/h** — relative stride length; **PA** — pace angulation (degrees); **h** — estimated hip height; **v1** — speed in m/s; **v2** — speed in km/h.

TN	TL	TW	TO	PL	SL	SL/h	PA	h	v1	v2
					Pogledalo					
I	2.12	0.28	256	0.84–1.03	**1.84**	**1.4**	176.9	**1.34**	**1.53**	**5.50**
II	2.34	0.42	151	1.04–1.06	**2.06**	**1.2**	160.7	**1.69**	**1.44**	**5.18**
III	3.11	0.36	340	1.10–1.46	**2.18**	**1.1**	88.1	**1.90**	**1.34**	**4.82**
IV	4.30	0.51	261	1.14–1.25	2.26–2.40	1.2–1.3	136.9–154.1	**1.92**	1.45–1.61	5.22–5.80
					Trstike/Debela Glava					
?I	1.30	0.99	229	0.50	–	–	–	?**0.61**	–	–
					Kamik/Plješivac I					
I	13.55	0.50–0.80	247	0.61–0.91	1.15–1.56	0.6–0.8	105.2–173.0	**1.71**	0.49–1.03	1.76–3.71
					Kamik/Plješivac II					
II	16.90	0.39	323	0.58–0.69	1.18–1.30	1.4–1.6	150.5–155.6	**0.86**	1.26–1.49	4.54–5.36
IV	13.80	0.37	339	0.65–0.68	**1.31**	**1.5**	160.1	**0.85**	**1.48**	**5.33**
					Ploče					
I	3.06	0.34	48	0.85–0.98	**1.58**		156.6	**0.88**	**1.99**	**7.16**
II	2.97	0.16	103	0.92–0.94	1.84–1.87	**2.1**	163.0–168.2	**0.89**	2.49–2.56	8.96–9.22
III	3.65	0.17	378	0.89–1.12	1.85–1.99	1.9–2.0	163.7	**1.03**	2.34–2.54	8.42–9.14
IV	2.06	0.18	91	0.62–0.76	1.28–1.51	1.6–2.2	135.9–166.8	**0.73**	1.51–2.42	5.44–8.71
V	2.93	0.30	36	0.69–0.73	1.34–1.38	1.4–1.5	137.0–160.6	**0.95**	1.34–1.43	4.82–5.14
VI	1.46	0.51	226	0.42	**0.85**	**2.7**	–	?**0.32**	**2.35**	**8.46**
VII	1.25	0.40	172	0.31–0.44	0.70–0.80	2.1–2.3	–	?**0.34**	1.67–1.77	6.01–6.37

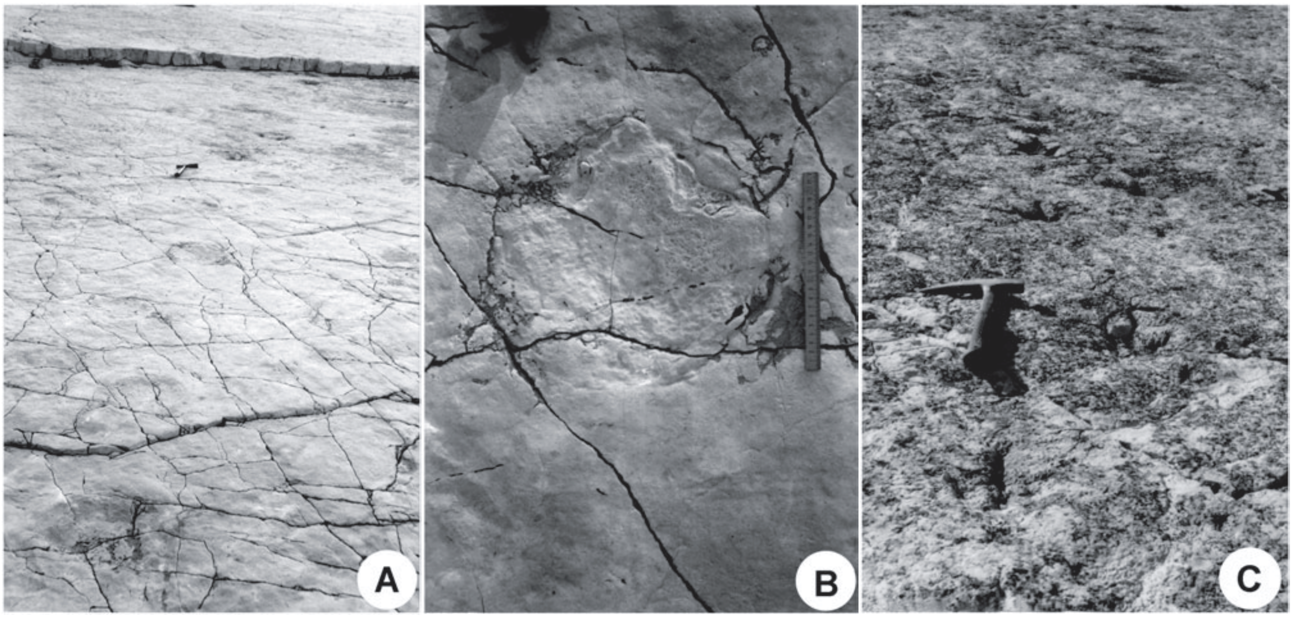

Fig. 7. Footprints from the Kamik/Plješivac promontory. **A** — ornithopod trackway I from the track-bearing underlayer; **B** — twelfth footprint in ornithopod trackway I; **C** — tridactyl trackway II from the track-bearing overlayer; **D** — second footprint in trackway II. Scale bar = 22 cm.

Fig. 7D. Second footprint in trackway II. Scale bar = 22 cm.

On the track-bearing layer **Kamik/Plješivac II** that overlies the above described bed (Kamik/Plješivac I outcrop), 36 dinosaur footprints have been found. These are arranged in three approximately parallel and closely spaced trackways. They are referred to here as trackways II–IV **(Fig. 8)**. Due to the intensive karstification, erosion by the sea and atmospheric conditions, the footprints are hard to recognize; they can be clearly seen only when the sun is low on the horizon. All three trackways have the same orientation (S-N); the westernmost trackway is several meters from the other two trackways (dimensions are given in the Table 2). The footprints in the trackways are not in a continuous succession, and interruptions occur in several places as some footprints are missing. The reason for that could be the non-preservation of the footprints due to the nature of the substrate itself (too soft), or the later destruction of the tracks due to erosion. The continuity (sequence) of the footprints is best seen in the first ten prints of trackway II. These are also the most conspicuous prints (Figs. 5, 7C,D). The prints are tridactyl, mesaxonic and with long, rounded digital prints. In the majority of the prints only two digits can be clearly discerned and, as a rule, these are the middle and the inner digits. The prints of the outer digits are visible, but are not well defined. This is probably the result of the fact that the animal, while walking, leaned more on the inner side of the foot and the foot on that side was consequently pressed more into the substrate. The digits are widest mid-way along their length and are narrower at the apex and at the base of the digit. The digit axes are straight. The total divergence is high and ranges from 61°–79°. Claw traces cannot be discerned, but this is probably a consequence of the poor preservation. The distal parts of the prints corresponding to the heel impressions are wide and rounded and often with a semicircular shape (dimensions of the prints are given in the Table 1).

The undefined prints found on the **Trstike/Debela Glava** locality in our opinion do not belong to dinosaurs but possible to chelonian reptiles. On the surface of the layer 42 undefined prints were found (identical to the prints discovered on the Ploče locality). The orientation of the ten prints in a line suggests the existence of a trackway (?I), while the remaining 32 prints occur individually (Fig. 9). The best preserved print has approximately a quadrangular shape and is wider than it is long (155 : 145 mm), tetradactyl and mesaxonic (Figs. 5, 10A). It seems to have a bilateral symmetry. Digit prints are of medium length when compared to print length (30–55 mm) and they are narrow (width is 5–10 mm). The digits are straight with their axes in a straight line. The digit furthest to the right has the greatest length and width. The length and the width of the digits decrease proportionally sinistrally. The digit further to the left is the smallest. All digits have a V-shape and become narrower distally. Claw impressions are most pronounced on the two middle digits. These impressions are also

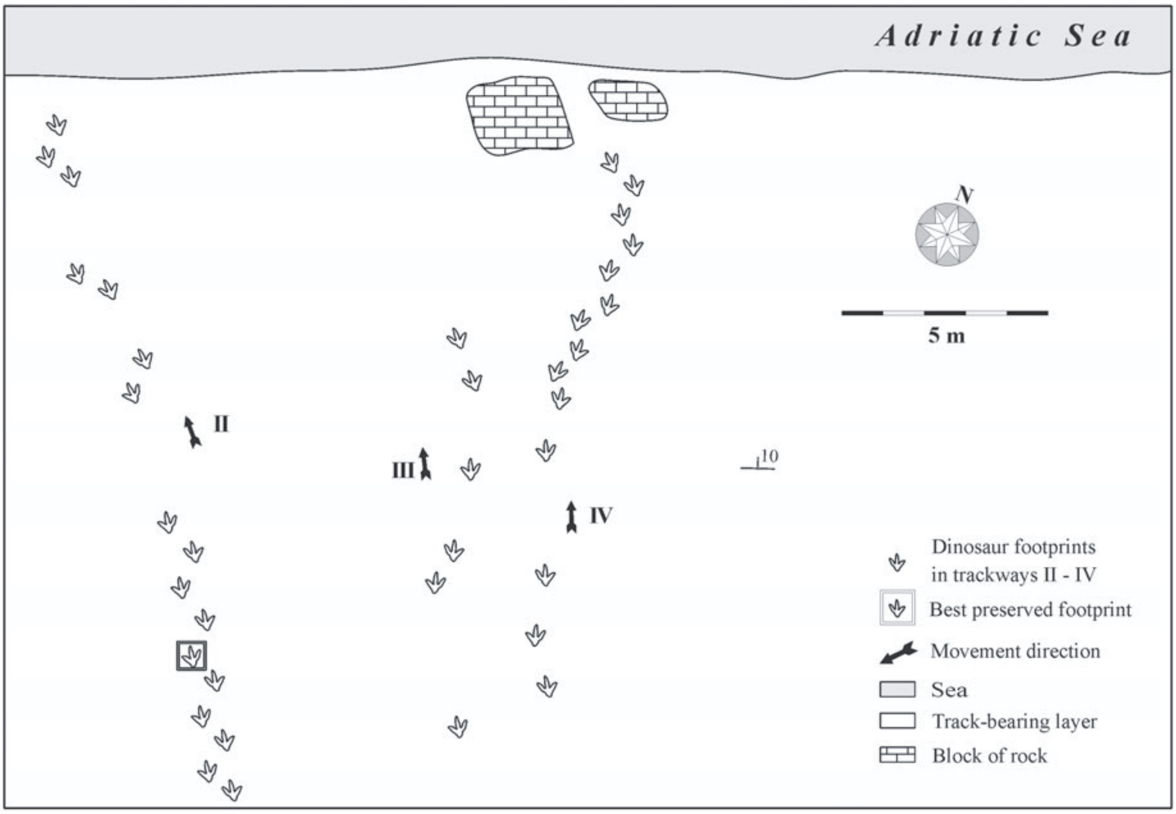

Fig. 8. Map of the Kamik/Plješivac II locality.

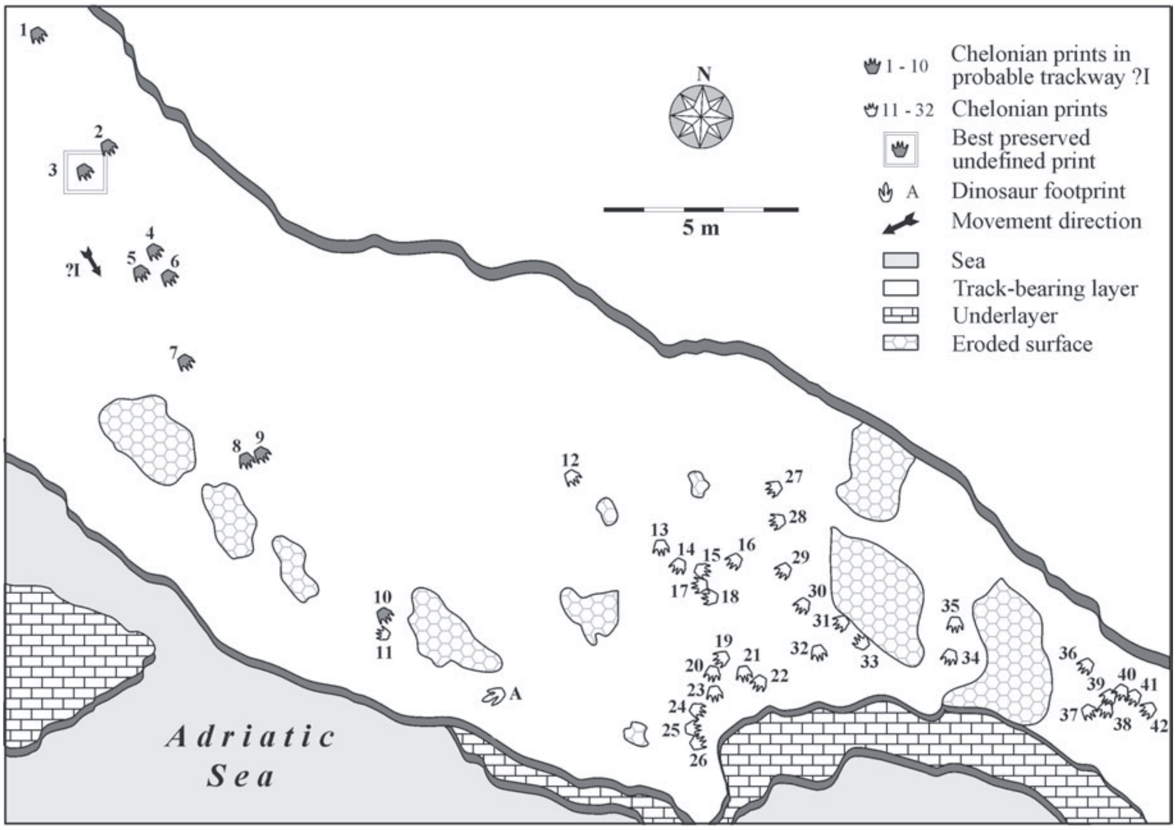

Fig. 9. Map of the Trstike/Debela Glava locality.

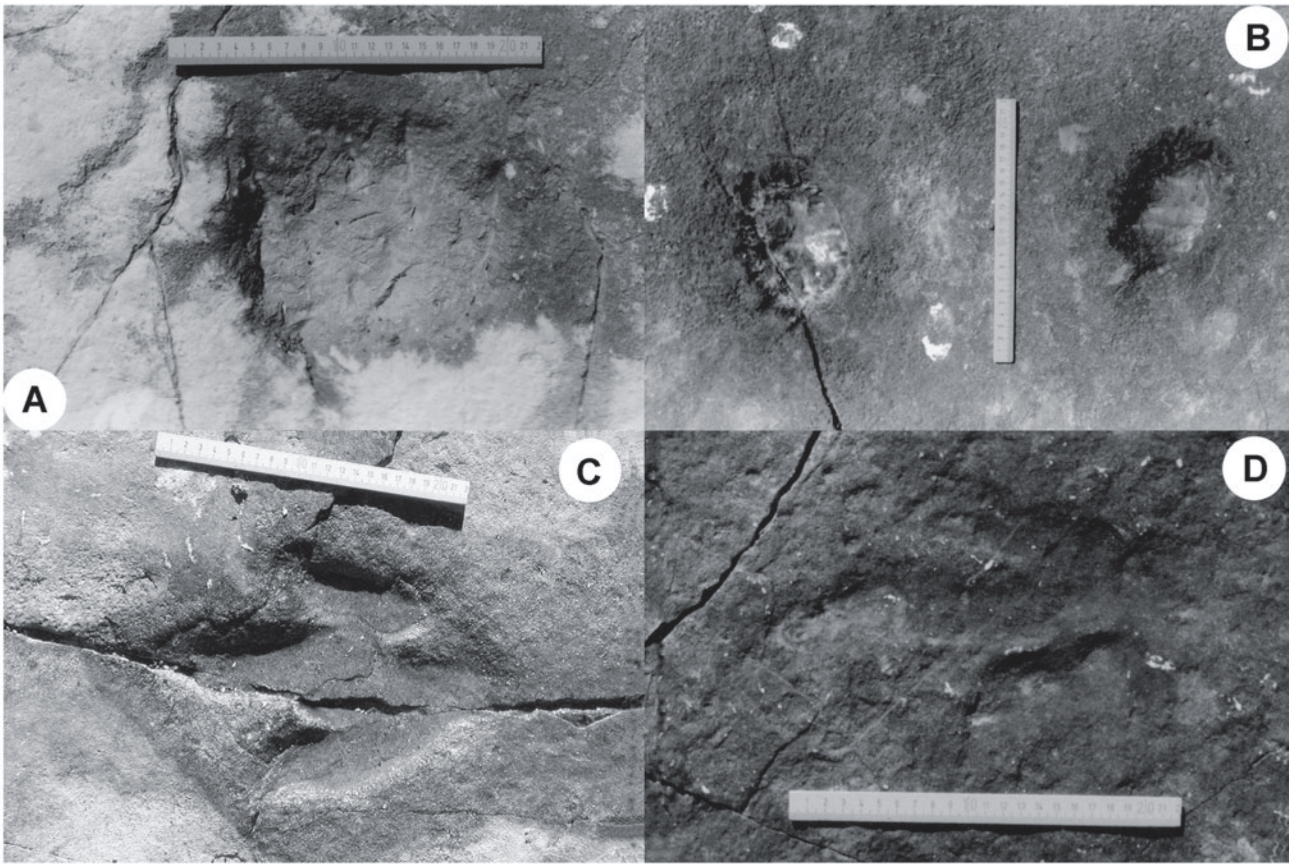

Fig. 10. Various footprints from the Trstike/Debela Glava and Ploče promontories. **A** — undetermined print from Trstike promontory; **B** — a pair of undetermined prints from Ploče promontory; **C** — second footprint in theropod trackway I at the Ploče promontory; **D** — theropod footprint marked with a letter D at the Ploče promontory. Scale bar = 22 cm.

sharply V-shaped, and are oriented in the same direction as the digit itself. The digits on the left side of the middle axis of the print diverge to the left, while those on the right side diverge to the right. The total divarication is 44.4°. The length of the digits is somewhat less than half of the print. The probable heel impression covers the remaining length of the print and is quadrate with well defined edges. Its proximal edge shows characteristic indentations (it describes a zigzag line). The left edge of the heel continuously passes in to the outer edge of the leftmost digit. A bulge can be seen along the right edge of the heel impression separating the pass (transition) into the outer edge of the rightmost digit, as seen on the left heel's edge. Most parts of the print are almost equally indented, though the digit prints are somewhat shallower. On the basis of the print position in respect to the prints I2 and I4, and in accordance with the morphology, it is concluded that this is a possible right pes print. The first left digit would be digit I, and the digit furthest to the right would be digit IV. An isolated tridactyl footprint was also discovered at the outcrop (Fig. 9A). Some morphological features, such as clearly separated digits with the middle digit longer than the outer digits, indicate a dinosaur origin of this track although it is poorly preserved.

Sixty footprints were recognized on the **Ploče** outcrop. Twenty-two tridactyl footprints are arranged in a sequence and they comprise five trackways (I–V), five tridactyl footprints are preserved individually (A–E), and 37 non-tridactyl prints occur individually (Fig. 11). Two types of footprints can be distinguished. The first type represents medium-sized, bipedal, tridactyl dinosaur pes prints, while the second type is non-tridactyl possibly chelonian prints, identical to the prints discovered at Trstike/Debela Glava. The typical example of tridactyl footprint is the second in the row in a couple of footprints C and D (Figs. 5, 10D). It is a tridactyl, mesaxonic print, 230 mm long and 123 mm wide. The print is shallow, with clearly separated, long and wide digits. The middle digit is the longest (164 mm) and the widest whereas the outer digits are of almost equal dimensions (100 × 30 mm). The axis of the middle digit is straight with parallel outer edges. The greatest width is in its middle part (41 mm) and it becomes narrower proximodistally. A clear rounded claw impression is present on the digit apex. The digit has three clearly pronounced digital pads. The right outer digit has a straight axis and a proximodistal narrowing; the outer margin is curved. A V-shaped trace of the claw is clearly visible. The left outer digit also has a straight axis, with two clearly pronounced impressions of flesh pads. The V-shaped claw mark is clearly visible on the digit apex. The angle that the axis of this digit closes with the axis of the middle digit (21°) is greater than the one between the axis of the middle and the right digit

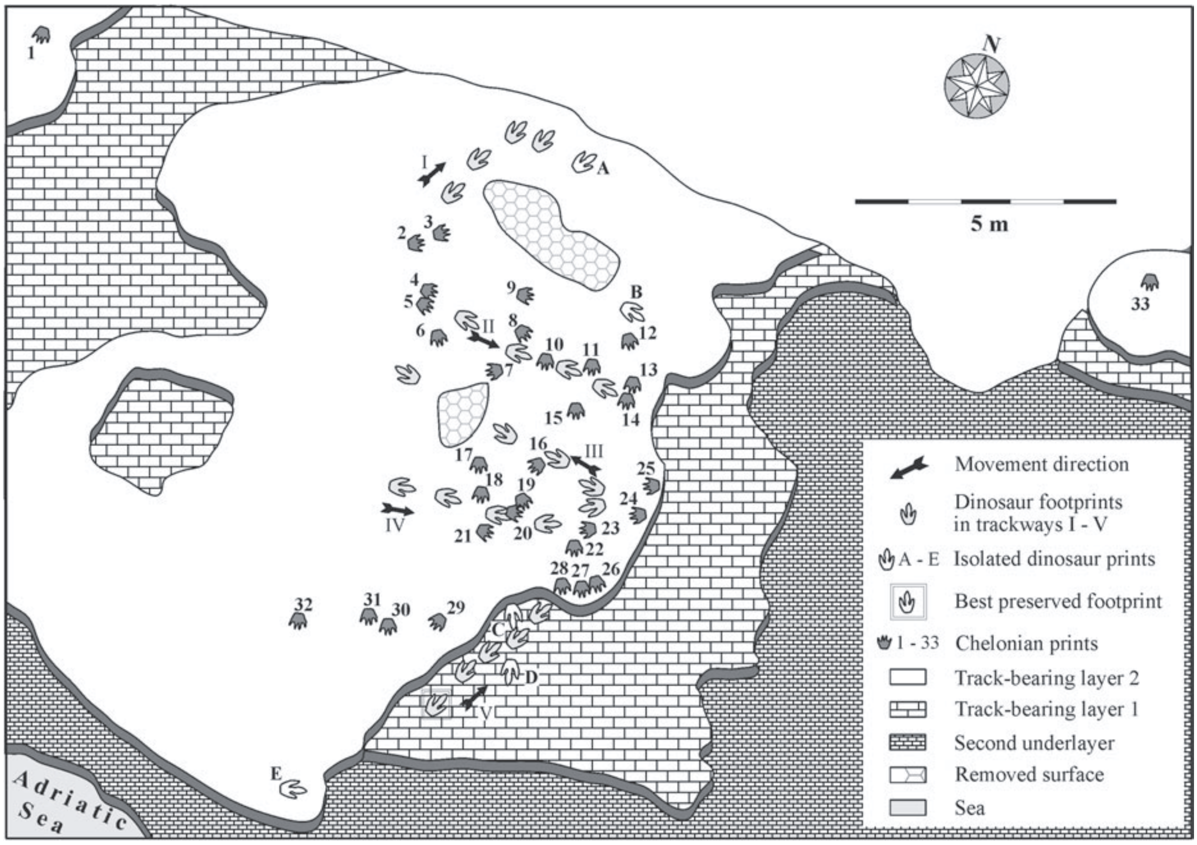

Fig. 11. Map of the Ploče locality.

(10°). The left digit has a noticeably greater depth than the right and the middle digits. It is possible that this is the result of the animal leaning more on the left side of the foot. The total divergence is 31°. The heel impression is slightly visible and has a sharp V-shape. The hallux print is not visible. The axis of the left digit is at a greater distance from the axis of the middle digit than the axis of the right digit. On the basis of the general morphology, as well as the footprint position in the trackway (the footprint is positioned to the right from the middle axis of the trackway), it is concluded that this is a print of the right pes. The left digit is the digit II, the middle digit is the digit III, and the right digit is the digit IV. The typical example of the non-tridactyl print on the outcrop is tetradactyl, of approximately square size, with greater width than length (Fig. 10B). The print is bilaterally symmetrical. The digit prints are elongate and very narrow. The impressions of the two outer and two inner digits can clearly be discerned and the outer digits are positioned on the very edges of the print, while the inner ones are positioned directly along the left and right side of the middle axis of the print. All the digits are straight, oriented in a straight line and the angle of the axis of each digit with the middle axis of the print increases to the left and right of the middle axis. The angle of divergence between the middle axis of the print and the digits is small. All digits have a sharp V-shape, proximodistal narrowing, and leave the impression of the continuous transition into the claw prints. The claw prints are not visibly differentiated from the rest of the digit, but it seems, that each digit ends with a claw. The two outer digits are somewhat broader than the inner ones, but the inner digits are longer. The length of the digits itself comprises approximately 1/3 of the length of the entire print, the remaining length of the print comprising traces of the heel. The heel impression has a square shape with relatively sharp edges. The outer edges of the heel continuously pass into the prints of the outer digits. It is noticeable that the right part of the heel impression is somewhat shallower than the left part, especially along the right proximal edge. The proximal part of the print gives the impression of indentation (zigzag line). In the print region between the outer and the inner digits, two symmetrical V-shaped forms are visible, whose tips end in a line with the half of the inner digit length. It is possible that these are traces of the flesh pads. Due to the symmetry of the print, it is difficult to say to which foot it belongs, but since the print is positioned in a defined formation with two other prints to the right and in front of it, it can be concluded that this is a print of the left foot. From left to right, these would be the digits I–IV.

Discussion

Upper Barremian trackmakers

On the basis of the footprint morphology, their dimensions as well as trackway morphologies, we have decided to assign the robust tridactyl footprints from the Pogledalo promontory to a heavy, robust form of theropod dinosaur (sensu Thulborn 1990). This conclusion agrees with the statements made by Dalla Vecchia et al. (2002). Regarding their taxonomic determination, the following has been established: the non-existence of a hallux impression, the smaller length of the footprint, and the difference in the total divergence distinguishes them from large theropod footprints assigned to the ichnogenus *Bueckeburgichnus maximus* from the Lower Cretaceous basins of Germany (Kuhn 1958) and Spain (Moratalla 1993). The footprints from Pogledalo differ from the *Therangospodus* (Lockley et al. 1998b) by their larger size, more elongate prints, better defined digits and trackway parameters (footprint irregularities). The *Megalosauripus* (Lockley et al. 1998b) type are similar to the Pogledalo prints in having similar dimensions (see Table 1), footprint morphology (sensu Lockley et al. 1998a), and irregularity of the footprints in the trackways (although this could be a feature caused by the substrate conditions). One of the characteristics of *Megalosauripus* trackways is the great variability in the step length (Lockley & Meyer 1999). This characteristic can be noted in the majority of the trackways on the Pogledalo promontory (e.g. stride length of 114 to 126 m in trackway IV, or 110 to 156 in trackway III, Table 2). Although the *Megalosauripus–Therangospodus* assemblage was defined as being almost exclusively Upper Jurassic (Lockley et al. 1998b), it is possible that in Istria, due to its geographical isolation (e.g. Dercourt et al. 1993; Zappatera 1990), the dinosaurs which produced such tracks (similar to *Megalosauripus*) existed somewhat longer (at least to the end of Barremian). The difference between *Megalosauripus* and the footprints from Pogledalo is in the non-existence of the clearly visible digital pad impressions (though this is not the case with all *Megalosauripus* ichnospecies, e.g. *M. teutonicus*; Lockley et al. 1998a). The footprints from the Pogledalo promontory are most similar to the unnamed Lower Cretaceous footprints from the Koum Basin in Cameroon, Africa (Jacobs et al. 1989). The similarity is especially pronounced by comparing prints IV3 from Pogledalo and No. 3 from the KB3 locality, Cameroon (Fig. 38.2 in Jacobs et al. 1989). The footprints are of a similar size, have a very similar morphology (internal digit of each print is recurved), and similar trackway parameters. The single important difference is that the tracks from Cameroon were preserved in a "predominantly fluviatile sedimentary environment" (Jacobs et al. 1989, p. 350) and those on the Pogledalo promontory on a tidal flat.

On the basis of the morphology and size dimension (sensu Thulborn 1990), the gracile tridactyl footprints from Pogledalo locality are assigned to a gracile form of the large theropod dinosaur. Such a conclusion is in disagreement with Dalla Vecchia et al. (2002) who identified only one type of theropod footprint on this site. There are four ichnogenera with similar morphology and dimensions to the footprints described here. *Kayentapus hopii* (Welles 1971) from Lower Jurassic deposits of Arizona differs from the described form not only by the large time difference, but also by its wider angles of digit divarication (total divarication is 53°), broader digits and presence of a heel impression. *Schizograllator xiaobaensis* from the Lower Jurassic strata of China is similar to *Kayentapus* (after Zhen et al. 1989), and differs from Pogledalo footprint on the basis of the same characters mentioned above. The holotype of *Schizograllator* is even wider than long. The gracile footprints from the Pogledalo locality show most similarity and are closest in age to the footprints described as *Megalosauropus broomensis* from Lower Cretaceous complexes of Western Australia (Colbert & Merrilees 1967; illustration by Merrilees in Haubold 1971). Both footprints are of approximately identical length and width and have three slender digits with well pronounced digital pads. The reason for our proposal that the footprints from Pogledalo are a different ichnogenus is their smaller angle of total divergence (42.5° versus 59°) and the lack of a heel impression. Although a high density of the footprints has been established on the Pogledalo promontory, there are no preferred movement directions (Fig. 3); on the contrary, tracks go in almost every direction (except to the northeast, which could indicate the direction of the former shoreline). Footprints of several individuals are present at the locality, some of which overlap, which testifies that dinosaurs passed through that area repeatedly. Different levels of footprint preservation are also characteristic, being the result of differences in substrate consistency, which is especially evident on the last two footprints in trackway IV. The only skeletal remains of large theropods (more than 5 m long) in Lower Cretaceous deposits of Europe have been discovered in the Valanginian-Aptian strata of England: *Baryonyx walkeri*, *Valdoraptor oweni*, *Becklespinax altispinax*, *Neovenator salerii* and *Eotyrannus lengi* (Weishampel 1990; Hutt et al. 1996, 2001). Although Thulborn (1990, p. 147), states that gracile forms of large theropod footprints probably belong to dinosaurs such as *Megalosaurus* and Colbert & Merrilees (1967) assign footprints of *M. broomensis* to a megalosaurid dinosaur, we would not assign the gracile theropod footprints from the Pogledalo site to the megalosaurids. Not that we do not agree with their opinion, but we think that the presence of megalosaurids in the Cretaceous, based on their skeletal remains, is doubtful or at least unproven. The origin of the dinosaurs from the Adriatic-Dinaric carbonate platform is still not fully understood, and if we keep in mind paleogeographical reconstructions and interpretations of these areas during the Mesozoic (Channel et al. 1979; Zappaterra 1990; Dercourt et al. 1993), it seems very likely that Istrian populations originated on the African continent (see also Dalla Vecchia 1998). This opens a real possibility for identification of the trackmaker on the basis of skeletal remains from Africa. Gracile forms like *Afrovenator abakensis* (Hauterivian-Barremian basal tetanuran; Sereno et al. 1994) could be possible trackmakers for the gracile type of prints at Pogledalo.

Upper Albian trackmakers

In respect to their dimensions, morphology, SL/FL (5/1) ratio, and trackway parameters (see Tables 1, 2), the prints from Kamik/Plješivac I have been assigned to iguanodontid ornithopods (sensu Thulborn 1990). This statement is agreeable to conclusion made by Dalla Vecchia et al. (2002) earlier. The shallowness of the preservation, in respect to the footprint dimensions, and a diffuse outline are characteristic for this trackway. The footprints are very poorly preserved, which is probably the consequence of the firm consistency of the substrate in which the footprints were made. Therefore the possibility for the comparison with the other tracks of this type is limited. According to Lockley & Meyer (1999, p. 196) "in the lower Cretaceous of England and Europe, there are no large *Iguanodon*-sized ornithopods that were as abundant or as widespread as *Iguanodon*, so there is a high possibility that most tracks (regarding large ornithopods, author's remark) really were made by representatives of the genus *Iguanodon*". In the light of these statements, the footprints from Kamik/Plješivac I could be ascribed to *Iguanodon*. On the Adriatic-Dinaric carbonate platform no skeletal remains of iguanodontid dinosaurs have been found and as we mentioned earlier the connection of the platform with the African continent seems more plausible. The African iguanodontid genus *Ouranosaurus* could also be the possible trackmaker. Considering the problem of quadrupedalism vs. bipedalism in the ornithopods, we can only state that at the locality Kamik/Plješivac I prints corresponding to the manus were not observed, and therefore we conclude that iguanodontid on this site walked bipedally or overprinting its front footprints. However, it is also possible that manus prints were not preserved (even the pes prints are faintly recognizable or very shallow). These footprints represent the only find of the iguanodontid tracks on the Istrian Peninsula, although the prints from Ploče locality were identified as *Iguanodon* footprints by Bachofen-Echt (1925a,b).

In respect to the poor preservation of the footprints at the Kamik/Plješivac II locality, some doubts about the identification of the trackmaker exist. The general morphology and the dimensions of the footprints indicate that a medium-sized bipedal dinosaur made the prints, but there is a doubt whether it was a small theropod or a small ornithopod. Guided by the principles of Thulborn (1990), we can say that the ratio between the stride and footprint length (7/1), the ratio between footprint width and footprint length (0.73), and the ratio between width and length of the digit III (0.31) suggest a medium-sized theropod origin. Support for a small ornithopod origin is found in the values of the pace angulation (150°–155°), total divarication (62°–79°), digit shapes, and rear margin of the footprints, which are rounded (U-shaped). When we compare pes skeleton in both, small theropods and small ornithopods (see Thulborn 1990) we could notice that the digit III is more projecting forward in the pes of theropods than ornithopods. If we keep that in mind we could say that the tracks on the Kamik/Plješivac II are more similar to ornithopod tracks than to theropods (compare the values in the Table 1 and Figs. 7D and 10D). Observing the width of the trackways at this locality, it is concluded that the footprints are far distant from each other in respect to their dimensions (wide-gauge trackway), which could indicate that the footprints were made by a dinosaur of a heavier, more robust form than the gracile theropods. Since the skeletal remains of mid-Cretaceous (Aptian–Cenomanian) small sized coelurosaurs from Europe or Africa are represented only by a rare forms like *Elaphrosaurus* and *Scipionyx* (Weishampel 1990; Dal Sasso & Signore 1998), while small ornithopod families like Hypsilophodontidae or Dryosauridae are relatively common in the mid-Cretaceous strata of both continents (Weishampel 1990), we are inclined to assign the footprints to small ornithopods similar to *Dryosaurus*. Such a conclusion differs from that made by Dalla Vecchia et al. (2002) where a theropod origin was stated. It should be noted that some tridactyl footprints of uncertain taxonomic position were also discovered in Upper Albian strata near the mouth of the Mirna River (NW Istria) (Dalla Vecchia et al. 1993). These are also poorly preserved but with similar morphology and dimensions as the Ploče prints and were assigned to theropods (Figs. 4B, 5, 6 in Dalla Vecchia et al. 1993). However, the high angle of divergence and the width of the outer digits, might suggest that these footprints could belong to a small bipedal ornithischian. On the basis of the almost identical trackway orientations (N–NW), speeds (about 5 km/h), and gaits (SL/h = 1.5), it could be possible to conclude that three small bipedal dinosaurs moved together in a 'pack'. These characteristics could indicate their gregarious behaviour, but they cannot prove it. Dalla Vecchia et al. (2002) already mentioned such a possibility although they also found no proof to confirm it.

On the basis of their morphology, dimensions, and trackway parameters (see Tables 1, 2), the tridactyl footprints from Ploče are assigned to a medium-sized theropod dinosaur (after Thulborn 1990). This is in accordance with the earlier statements that these are theropod prints (Haubold 1971; Dalla Vecchia et al. 2002) and not the prints of *Iguanodon,* as has been stated in the literature ever since the Bachofen-Echt (1925a,b), and for the number of years after (Polšak 1965; Velić & Tišljar 1987, also in all popular literature), but without supporting evidence. Dalla Vecchia et al. (2002) also stated that the Ploče tridactyl footprints show a feature of the ornithomimid foot. Theropod footprints of Albian age were also found in Istria at the Červar and Puntižela sites (Dalla Vecchia & Tarlao 2000). The tridactyl prints from these sites were assigned to medium-sized theropods and are similar to the tridactyl prints from Ploče (see Figs. 7, 8 in Dalla Vecchia & Tarlao 2000) although the sedimentological features are different. They have similar dimension and morphology; footprint lengths, angles of total divergence and the digit dimensions are within the same range of values, straight and slender digits, low divarication angles, sometimes visible pad impressions, digit III being the longest one. The trackway parameters correspond with similar pace length, stride length, and calculated speeds. On the basis of similar footprint dimensions, their morphology, parameters of the trackways as well as the similar age of the sediment in which they were found, it is concluded that the tridactyl footprints from Ploče correspond to those from Červar. Regarding the taxonomic classification of the tridactyl footprints from Ploče promontory, we support Haubold's (1971) conclusion regarding a theropod origin for these trackways, but not the establishment of the ichnospecies *Megalosauropus brionensis,* which he erected on the basis of Bachofen-Echt's (1925a,b) research. In this sense we agree with the statement of Lockley et al. (1998a) about the lack of demonstrated morphological match between the Ploče tracks and the *Megalosauropus* type material. In our opinion, there are no similarities between them, either in age or in morphology. Skeletal remains of middle Cretaceous small to medium sized theropods from the Adriatic-Dinaric platform and neighbouring areas (see Dercourt et al. 1993) are rare and fragmentary. Only the ceratosaur *Genusaurus sisterornis* (Accarie et al. 1995) discovered in the Lower Albian of southern France, and *Scipionyx samniticus* (Dal Sasso & Signore 1998) from the Lower Albian of southern Italy, are worth mentioning. For this reason it is difficult to assign the footprints from Ploče to a particular genus of mid-Cretaceous and medium-sized theropods. These footprints in fact represent the only proof of theropod presence on the platform during the mid-Cretaceous. Besides the footprints found *in situ* on the Ploče promontory, seven blocks with footprints were removed in the 1970's from the track-bearing level II. Five footprints were deposited in the so-called "Čamčarnica", a house on the southern side of the Veli Brijun main harbour, which was once a museum and is now deserted. All five prints are now in a very bad state, since the blocks with the footprints were broken during the extraction and transport and were later repaired with plaster. These are tridactyl footprints of theropod morphology (elongated prints, slender digits, low divarication angles), between 250 and 430 mm long (see Table 1 for dimensions). It is interesting that the extracted footprints have larger dimensions than those preserved *in situ* (see Table 1), which would suggest that some of them (e.g. C4, C5, see Table 1) belonged to another or larger type of the theropod dinosaur, as indicated by their morphology and dimensions (see also Dalla Vecchia et al. 2002). The possibility that the dimensions of the footprints were enlarged due to the influence of the seawater and atmospheric conditions on the sediment, should not be excluded either.

The majority of tracks found on the Veli Brijun Island localities are tridactyl footprints assigned to dinosaurs (Fig. 5). However, there are some prints at Trstike/Debela Glava and Ploče with a non-tridactyl morphology and an undetermined origin. If they are ichnofossils, then the problem of their identification arises. So far no dinosaur prints morphologically similar to these tracks have been found. Also, there is no dinosaur with a foot anatomy (skeletal construction) that corresponds to the prints from Trstike and Ploče. If we assume that this is not a new dinosaur species, possible alternative trackmakers could be turtles. Bachofen-Echt (1925b) also considered these prints to be turtle tracks. A successive series of footprints was found nowhere on the outcrops, which would indicate without doubt that they were made by a quadrupedal animal, although there are segments which could support such conclusions (e.g. trackway ?I on the Trstike locality). Conversely, it cannot be stated with confidence that the prints were made by a bipedal animal, since no well-preserved trackway can confirm this. Some specimens from these tracks are morphologically similar (tetradactyl, square-shaped, greater width than length) to forms like the Permian ichnogenus *Chelichnus* (McKeever & Haubold 1996) or the Upper Jurassic turtle ichnogenus *Chelonichnium* (Bernier et al. 1982). The irregular placement of the footprints might indicate swimming as well, but this option seems unlikely because, as Dalla Vecchia et al. (2002) already mentioned, they are deep impressed (deeper than the tridactyl prints). It is possible that these tracks were formed by human activities, like stone excavation (Dalla Vecchia 1997; Dalla Vecchia et al. 2002), since some quarries existed in the past in these areas. We agree with Dalla Vecchia et al. (2002) that some of the prints show forms that are similar to the marks made by tools, but it is possible that they are the results of the erosive process, caused by the sea and the atmospheric exposure.

Dimensions, speeds and ichnocoenoses

Considering the facts about the possible trackmakers, we can make some conclusions about the dimensions of the dinosaurs from the Veli Brijun Island. To obtain the lengths of the theropods from the Veli Brijun promontories, hip height calculations (Thulborn 1990; see Table 2) were used, and computed values were applied on the reconstructions of the mentioned dinosaurs. Large theropods from Pogledalo were 7.5–8 m long, small coelurosaur theropods from Ploče were 3–4 m long, medium-sized iguanodontid ornithopods from Kamik/Plješivac were between 6–6.5 m long and dryosaurid-like ornithopods or medium-sized theropods from Kamik/Plješivac promontory were around 3.5 m long. The speed at which the dinosaurs were travelling was estimated on the basis of equation $v = 0.25g^{0.5}\ SL^{1.67}\ h^{-1.17}$ where v = velocity, SL = stride length, h = hip height (Alexander 1976). Average velocities (see Table 2) are in general agreement with Dalla Vecchia et al. (2002) and for the large theropods from the Pogledalo locality were around 5 km/h (a little bit slower than calculated by Dalla Vecchia et al. 2002), for small theropods from Ploče around 7 km/h, while the average speed of movement for the ornithopods from Kamik/Plješivac was around 3 km/h for large and 5 km/h for small individuals. Such velocities indicate normal or fast walk of the individuals near the former seashore.

On Veli Brijun Island two distinct ichnocoenoses can be discerned: a Late Barremian one consisting of large theropods, and a Late Albian one of small theropod, medium and small sized ornithopod footprints. Both ichnocoenoses are related to the carbonate platform intertidal environment. According to Lockley et al. (1994) the *Brontopodus* ichnofacies is characteristic of carbonate platform environments dominated by sauropod footprints. Although there is an absence of sauropod footprints on the Veli Brijun localities, the Late Albian ichnocoenoses on the Veli Brijun Island could belong to a *Brontopodus* ichnofacies. They are associated with the same depositional environment and even the *Brontopodus* ichnofacies does not include all the footprint types (i.e. sauropods and theropods). The presence of the large theropods and the environment in which their tracks were formed, associates the Late Barremian ichnocoenosis with the *Brontopodus* ichnofacies. However, the absence of sauropod footprints and different age does not permit us to regard these two ichnofacies as the same.

Conclusions

Two distinct ichnocoenoses in the sediments on the Veli Brijun Island have been recognized. The Late Barremian ichnocoenosis found on the Pogledalo promontory is composed of footprints of large theropods among which large robust forms and gracile slender forms can be discerned. The Late Albian ichnocoenosis found on the Ploče, Trstike/Debela Glava and Kamik/Plješivac promontories is composed of the footprints of small theropods, small ornithopods, large ornithopods and of prints possible chelonian. A total of 220 footprints were discovered. 145 of them are of dinosaur origin while 75 are of possible chelonian origin. Some footprints suggest fragmentary trackways, while most occur separately. The velocities (5–9 km/h) and directions of movement, measured from trackways at all the four localities, indicate normal walking. The footprints were preserved in the limestones deposited in the intertidal to tidal flat zone. The ornithopod footprints represent the only such findings in the Upper Albian strata of Istria and the earliest record of the ornithopods on the Adriatic-Dinaric carbonate platform. Together with theropod and sauropod footprints, they increase our knowledge regarding the diversity of the dinosaur species that lived in this region during mid-Cretaceous times.

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