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FIRST RECORD OF DINOSAURS IN THE LATE JURASSIC OF THE ADRIATIC-DINARIDIC CARBONATE PLATFORM (CROATIA)

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ABSTRACT

All previously known dinosaur remains on the Adriatic-Dinaridic carbonate platform (ADCP) were described from Cretaceous deposits. A new trackbearing locality is late Tithonian in age and represents the oldest evidence of dinosaurs on the ADCP. The site is in an active quarry near the village of Kirmenjak in western Istria. Almost a thousand sauropod footprints including 23 single trackways have been found on the outcrop. Oval impressions represent pes prints, and horseshoe-shaped impressions represent manus prints; pes prints are 23 to 52 cm long. Calculated heights at the hip range from 153 to 306 cm. The main direction of dinosaur movement was toward the northeast, and some of the individuals were moving together. The trackways show a characteristic narrow gauge, and pace and stride lengths indicate a slow walk. The footprints are similar to *Parabrontopodus* ichnogenus, and the ichnocoenosis could be assigned to the *Brontopodus* ichnofacies. The presence of the sauropods on the Adriatic-Dinaridic carbonate platform during the Late Jurassic could be explained by connection with the African continent via its southern margins during emersion.

INTRODUCTION

All dinosaur remains on the Adriatic-Dinaridic carbonate platform (ADCP), which now outcrops along the eastern margin of the Adriatic Sea, are from Cretaceous sediments of the Istrian peninsula. Istria is located on the northwestern part of the Croatian coast, with an area of ~3000 km^2. Among those remains are numerous dinosaur footprints and bones. The oldest finds to date are sauropod footprints found in Hauterivian layers (Dalla Vecchia et al., 2000). Although the ADCP was formed as an independent paleogeographic unit during the Lower Jurassic (Vlahović et al., 2005), there are no dinosaur finds older than Hauterivian. The sauropod track records on the ADCP, besides the Hauterivian find, include numerous sites from upper Albian and upper Cenomanian sediments. When compared to other Cretaceous ichnites (Dalla Vecchia, 2002), the main feature of ADCP sauropods is their small size, with pes length rarely exceeding 40 cm. Only narrow- and medium-gauge sauropods have been recorded on the ADCP so far, with no evidence of gregarious behavior or parallel trackways.

A new locality with dinosaur footprints was discovered recently near the village of Kirmenjak in western Istria (Fig. 1). The locality is situated in Kirmenjak quarry, about 2 km south of the Sv.Lovreč-Poreč road, and represents the largest site with dinosaur tracks discovered on the ADCP so far. The outcrop with footprints is located on the formerly active quarry front (Fig. 2) and extended over an area of about 4000 m^2. Since the discovery of the site in the summer of 2001, about 50% of the primary outcrop has been moved away by quarry workers. Fortunately, further destruction of the site has stopped, and the locality is now under informal protection.

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GEOLOGICAL SETTING

Istria belongs to the northwestern part of the ADCP. It is formed mainly of shallow-water carbonates with a stratigraphic range from the Middle Jurassic–Eocene (Velić et al., 1995a), and to a lesser extent from Eocene siliciclastic rocks, flysch, and calcareous breccias. The Istrian succession can be divided into five sedimentary units or megasequences separated by important discontinuities: emersion surfaces of varying duration (Tišljar et al., 1998; Vlahović et al., 2005). Those megasequences are: (1) Bathonian–lowermost Kimmeridgian, (2) upper Tithonian–lower or upper Aptian, (3) upper Albian–upper Santonian, (4) Eocene, and (5) Quaternary.

The investigated area is situated in the Upper Jurassic deposits belonging to the second transgressive-regressive megasequence, which is characterized by peletal limestones and laterally linked hemispheroid (LLH) stromatolites, with sporadic occurrences of emersion breccias with clayey matrix in the Tithonian, Hauterivian, and Barremian, and early to late diagenetic dolomites. The megasequence began in the upper Tithonian with shallowing-upward cycles deposited in subtidal, intertidal, and supratidal environments (Tišljar et al., 1998); these limestones are known as the architectural building stone, Pietra d'Istria or Kirmenjak. The uppermost part of the upper Tithonian deposits is more or less late diagenetically dolomitized (Velić et al., 2003). The upper Tithonian deposits in western Istria are known as the Kirmenjak unit (Velić and Tišljar, 1988) and as the informal lithostratigraphic Poreč formation (Vlahović, 1999), which is composed of two members, the older Kirmenjak and the younger Zlatni rt Member. The deposits of the Kirmenjak Member represent alteration of shallowing-upward cycles, which are composed of black pebble breccias, stylolitic mudstones, fenestral mudstones, and fenestral grainstones (Velić and Tišljar, 1988).

Depositional Environments and Microfossil Assemblage

The locality probably belongs to the lower part of the Kirmenjak unit, i.e., to the lowermost part of the second Istrian megasequence, based on the presence of black pebble breccias (Velić and Tišljar, 1988). Several shallowing-upward cycles can be distinguished from 0.5 to 1.5 m in thickness (Fig. 3). The shallowing-upward cycles begin with black pebble breccia (in two cycles) or mudstones, followed by fenestral mudstone, and usually end with peloidal packstone–grainstones and grainstones.

Mudstones are massive in appearance, highly stylolitic (Fig. 4A), rarely laminated, and in places interbedded with lenses and layers of peloidal packstone to grainstone. Rare fossils include ostracodes, green algae, gastropods, small foraminifera, and in some of the mudstones, crustacean pellets. Because the mudstones were deposited in a subtidal environment, black pebbles in the base of the mudstones suggest reworking of marsh deposits during a sea level rise. Fenestral mudstones (Fig. 4B) are compositionally similar to the above-described mudstones without fenestrae, in places also interbedded with lenses and layers of peloidal packstone to grainstone with mm-scale muddy intraclasts. Fenestral voids are filled with sparite and are irregular in shape. Laminar fenestrae (sheet cracks) are also present but less abundant. In some of the fenestral mudstones, subvertical to irregular mm- to cm-scale desiccation- and dissolution-enlarged voids with geopetal infill are also present. The fenestral mud-

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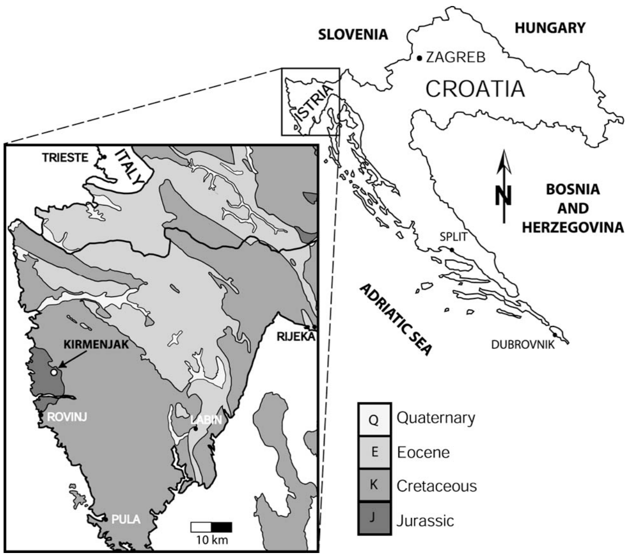

FIGURE 1—Geographic and geologic setting of the locality, showing the location of Kirmenjak, Istria (Croatia).

stones characterize restricted shallow subtidal to intertidal environments. Peloidal packstone–grainstones (Fig. 4C) and grainstones (Fig. 4D) are characterized by abundant irregular fenestrae filled with sparite and common intervals with mm-scale intraclasts. Rare fossils of the same types as those found in mudstones, darkened clasts (black pebbles), and mm- to cm-scale voids with geopetal infill (Fig. 4C) are also present. Peloidal packstone–grainstones and grainstones are also characterized by thin calcrete crusts and a cm-scale clay-rich cap. This type of limestone was deposited by high-energy storm waves and tides in an intertidal to supratidal environment and modified under subaerial exposure conditions, which produced recognizable shallowing-upward cycle tops. Dinosaur footprints occur on top of a shallowing-upward succession in intertidal fenestral mudstones, which are capped with a thin peloidal packstone–grainstone layer and overlain by subtidal mudstone. The formation and preservation of footprints were favored by a short exposure of the muddy sediment and its rapid burial beneath more mud.

Paleoenvironmental conditions during the deposition of the Kirmenjak unit were not optimal for high biotic productivity. Microfossil remains include only some taxa of calcareous algae, while benthic foraminifera are very rare. According to the present state of knowledge, the microfossil assemblage of the Kirmenjak unit consists of: (1) green algae belonging

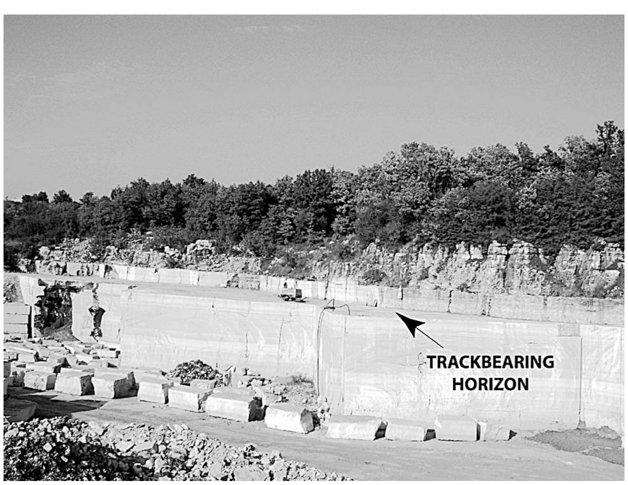

FIGURE 2—Panoramic view of Kirmenjak quarry and trackbearing horizon.

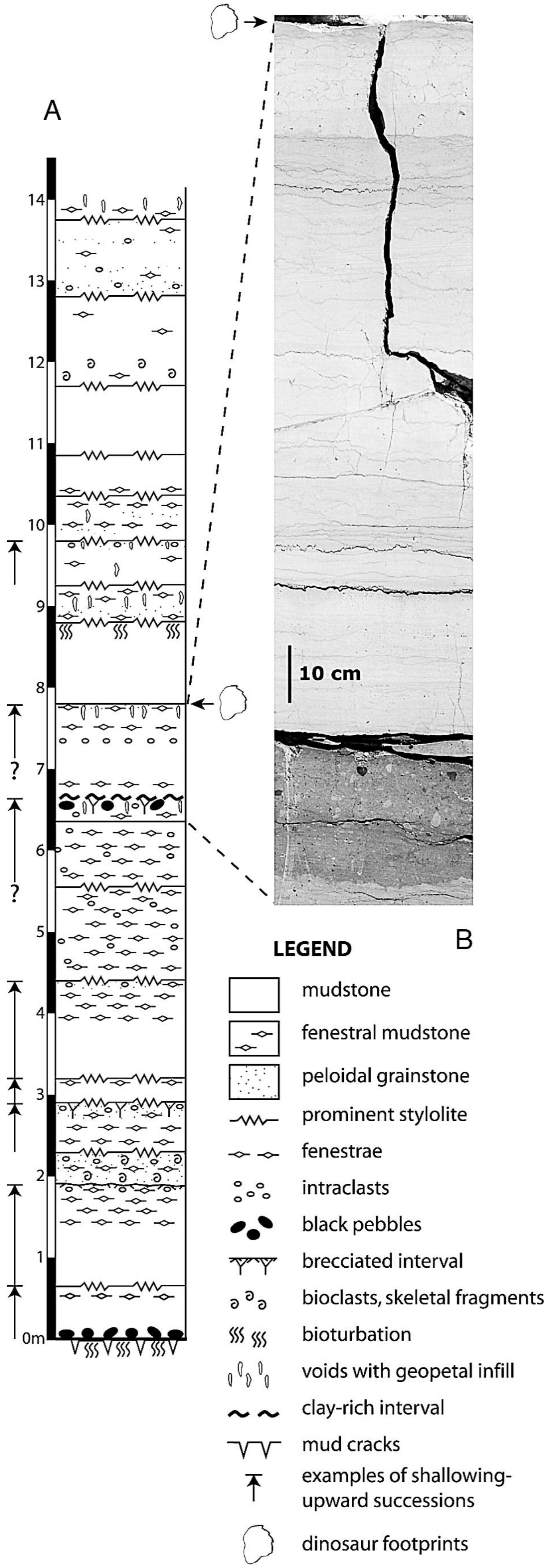

FIGURE 3—Detailed lithologic column from Kirmenjak quarry (A) with one of numerous shallowing upward cycles that begins with black pebble breccia and ends with trackbearing layer (B).

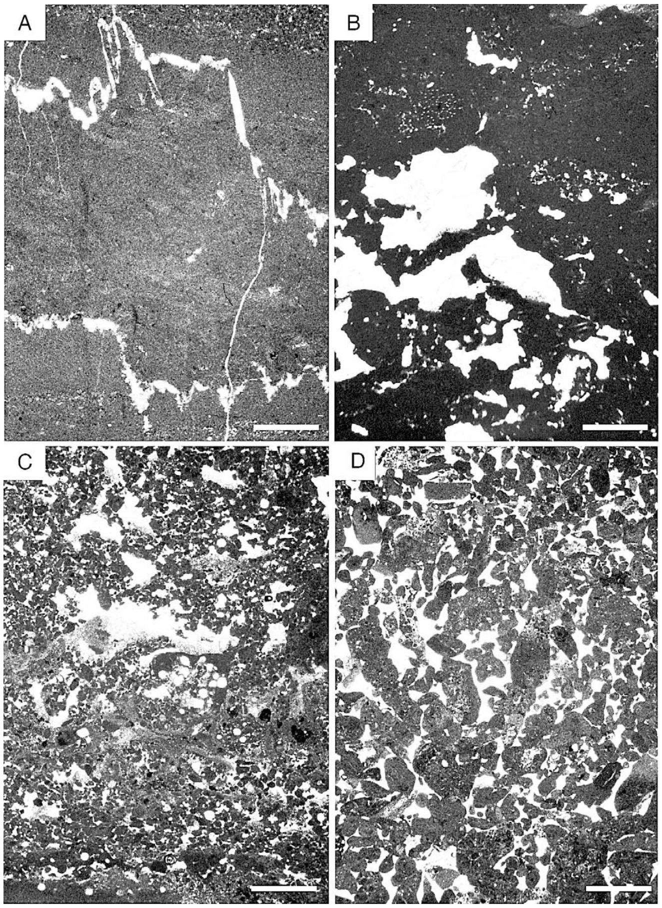

FIGURE 4—Microfacies types that represent shallowing-upward members of lower part of Kirmenjak unit, Kirmenjak quarry. Scale bar = 1 mm. A) Stylolitized mudstone, sample KI10. B) Fenestral mudstone with *Favreina* sp., sample KI7.75. C) Peloidal-intraclastic-fenestral packstone or grainstone with geopetal infill, sample KI4.3. D) Peloidal-intraclastic grainstone, sample KI5.4.

to *Clypeina jurassica* Favre, *Campbelliella striata* (Carozzi), *Salpingoporella annulata* Carozzi, and *S. grudii* (Radoičić); (2) crustacean pellets of *Favreina* cf. *fendiensis* Brönnimann & Zaninetti and *F. guinichoensis* Brönnimann; and (3) the hydrozoan *Cladocoropsis mirabilis* Felix (Velić et al., 1995b). This assemblage belongs to the *Campbelliella striata* taxon-range zone (Velić et al., 1995b), which would correspond to the late Tithonian in the Istrian area (Velić et al., 1995b). Microfossils recovered from the current locality include *C. striata* (Figs. 5A–C), *S. annulata* (Figs. 5D–5F), and *Favreina* spp. (Figs. 5G–H). Other undetermined foraminiferans, gastropods, ostracodes, and echinoids are present. This assemblage closely resembles the typical assemblage of the Kirmenjak unit and indicates a late Tithonian age.

The beginning of the Kirmenjak unit is marked by an oscillatory transgression over the emerged relief. The lowermost parts of paleorelief indicate early freshwater conditions, followed by a transition to a brackish environment (Vlahović, 1999). Deposits in the lower part of the Kirmenjak unit indicate the presence of marsh environments that represent the source for the black pebble breccias (Vlahović, 1999). Marshes were gradually replaced by shallow, protected lagoonal environments surrounded by wide tidal flats. It is on these tidal flats that the dinosaurs left their footprints.

ICHNOLOGY

The footprints were measured as follows: length was measured from the anterior to the posterior part of the print along its axis and width as a maximum perpendicular to the length. On prints with pronounced expulsion rims, measurements were taken only of the inner part of the prints (excluding the expulsion rims). Depth was measured in the center of the prints. On prints without expulsion rims, measurements were taken from the beginning of the depression margin. Data for footprints without expulsion rims should be regarded with caution due to the erosion and corrosion of the sediment, so the possibility of sedimentological magnification cannot be excluded. The angle of sunlight is a crucial factor in the recognition and measurement of footprints, so they were measured and analyzed between 1700 and 1800 hours each day. This is the optimal time for study in the Kirmenjak quarry during the summer. A detailed ichnological map of the outcrop was created by a relatively simple, but reliable grid method. A 5 × 5 m grid (with 1 × 1 m quadrants) was moved across the trackbearing horizon and each quadrant was photographed with a digital camera on a stand. The pictures were joined together in a map created using Adobe Illustrator®.

A total of 971 footprints were registered (Figs. 6A–B). Among them, 161 constitute 23 trackways, while the others occur individually or in groups (Fig. 7). The potential of discovering new tracks is great as the quarry front progresses into the hillside and exposes new areas of the trackbearing horizon. The footprints are preserved as imprints (epichnia or negative epirelief), and there are two different types: larger circular-elliptic tracks and smaller semicircular, horseshoe-shaped ones. Since both types occur in the same trackways, it could be concluded that they belong to the same animals. An expulsion rim is visible on the majority of footprints, representing compressed, waterlogged sediment squeezed from the print by the weight of the dinosaur. Such rims are usually more prominent than the footprints themselves and serve to protect the prints from being obliterated by erosion. The footprints were marked (e.g., II 3) with a Roman numeral (II), indicating to which trackway the footprint belonged, and an Arabic numeral (3), indicating the position of the footprint in the trackway. These marks were given from the first print in the trackway (e.g., II 1) to the last (e.g., II 20), in the direction of animal movement. Footprints that could not be attributed with certainty to a particular trackway were numbered with Arabic numerals alone.

All the footprints at the site belong to the same type of dinosaur. The arrangement in the trackways and differences in footprint size and shape clearly indicate that the trackways were left by quadrupedal animals. The smaller, semicircular footprints represent manus prints and the larger circular ones, pes prints (Figs. 8A–B). The footprints are attributed to sauropod dinosaurs on the basis of their morphology (Fig. 9). In most cases the margin is clearly discernable because of the expulsion rims around the prints. The rims are more prominent at one side of the print, a possible result of the weight distribution on the sediment. Manus prints have more prominent rims along the anterior side, while on pes prints the expulsion rims are more prominent medially. The footprints are relatively shallow when compared to their overall dimensions. The bottom of the tracks are not flat, instead they show the same texture as the surrounding sediment. Although numerous, the state of footprint preservation is far from ideal. In fact it is difficult to find a footprint in which digit impressions are also recognizable. A large numbers of prints are infilled with sediment, further complicating the recognition of their morphology. When compared to the average size of Late Jurassic sauropod footprints (e.g., Farlow et al., 1989; Thulborn, 1990), the Kirmenjak footprints are relatively small, with an average length of 34.5 cm for pes prints (Supplementary Data 1[1]). One of the important features in the investigation of sauropod footprints is heteropody (Lockley et al., 1994a), i.e., the ratio between the manus-pes footprint areas. Heteropody is clearly pronounced among the Kirmenjak footprints. Manus prints are significantly smaller than pes prints; the area ratio varies from 1:3 to 1:4 (Figs. 9–10). Manus prints are semicircular to semilunate in shape, and wider than long, with the longer axis almost perpendicular to the midline of the trackway. The length of the manus ranges from 5.5 to 26.5 cm with an average of 14.2 cm; manus

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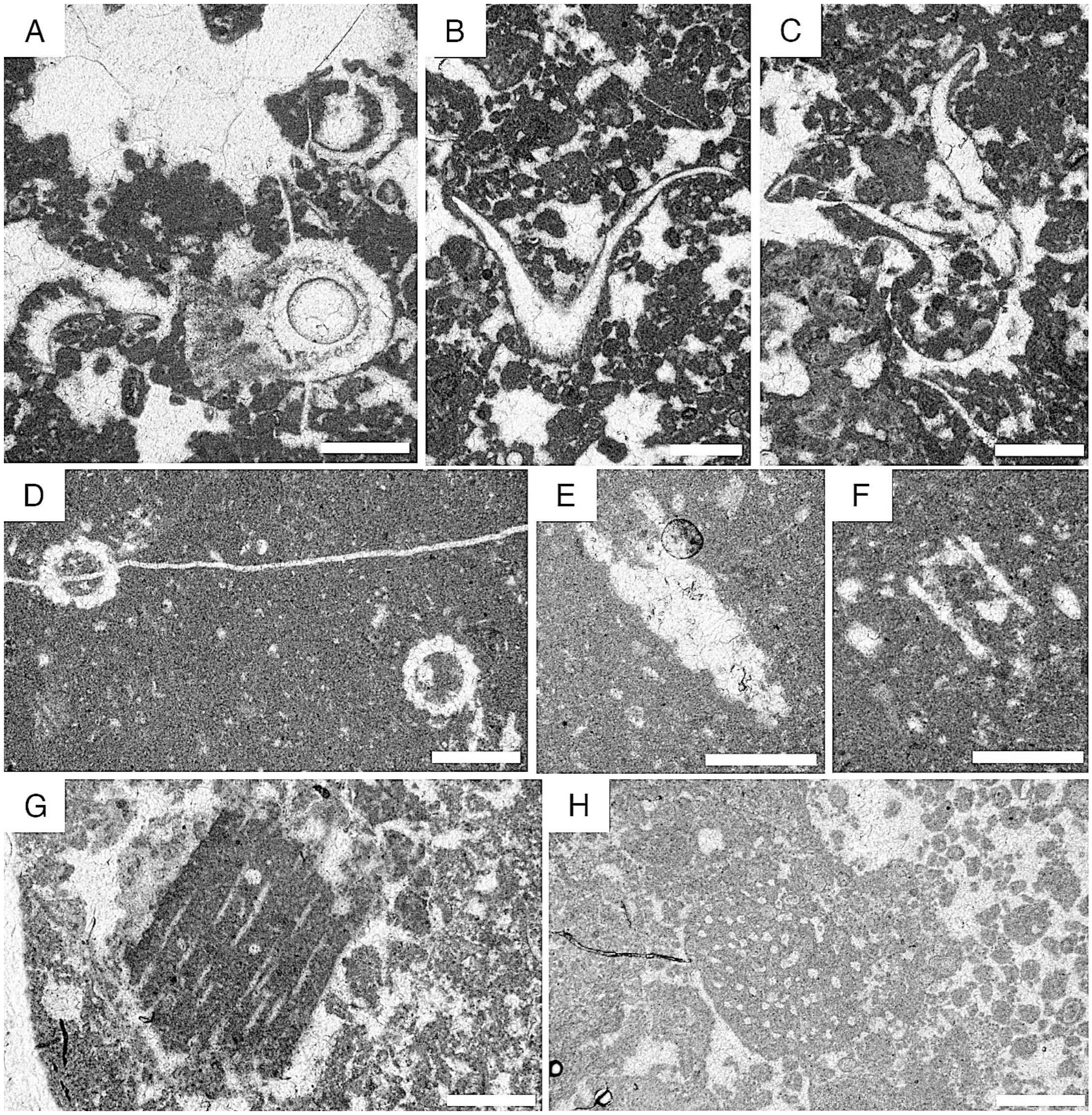

FIGURE 5—Microfossil assemblage of the Kirmenjak unit recognized in Kirmenjak quarry. Scale bars = 0.5 mm. A) Transverse sections of *Campbelliella striata*, sample KI2.25. B) Longitudinal section of *C. striata*, sample KI2.25. C) Near longitudinal section of *C. striata*, sample KI2.25. D) Algal mudstone with transverse sections of *Salpingoporella annulata*, sample KI11.8. E) Tangential-longitudinal section of *S. annulata*, sample KI11.8. F) Longitudinal section of *S. annulata*, sample KI11.8. G) Longitudinal section of *Favreina* sp., sample KI11. H) Transverse section of *Favreina* sp., sample KI5.

width ranges from 15 to 29 cm, averaging 21.5 cm (Supplementary Data 1[1]). Although the manus in sauropods is nearly concentric in shape, in most cases the prints are semicircular, semilunate, or horseshoe shaped. It is possible that the foot, during recovery from the mud, slips aside and deforms the print in this way, but it could also be that manus prints are deformed by complete or partial overlap by the pes prints. In most cases, however, manus prints are wider than long because of the collapse of the footprint margin, which occurs anteroposteriorly and causes deformation along its length. Due to poor preservation of the Kirmenjak prints, it is difficult to recognize impressions of single digits, but on some, the impression of digit I is faintly visible (Fig. 9) and gives the manus prints their characteristic horseshoe shape. Pes prints are oval or elliptical in shape, anteroposteriorly elongated with a somewhat narrower heel impression. The length of pes prints ranges from 23 to 52 cm (average = 34.5 cm), while their widths range from 18.5 to 43 cm (average = 29.1 cm; Supplementary Data 1[1]). None of the pedal prints bears clearly visible digit impressions.

Twenty-three trackways are recognized on the outcrop (Supplementary Data 2[1]). There are also numerous groups of footprints on the site in which trackways of several individuals overlap, but the precise allocation of single prints to a specific individual in these cases is difficult. Trackways marked with numbers XVII, XVIII, XIX, XX, and XXI are especially interesting because they are closely spaced, parallel to each other, and have nearly identical orientation (Fig. 7). These trackways are better preserved than the other trackways and also have a greater depth. Fifty-eight single footprints found on the north side of the outcrop (including prints #145–147) have nearly the same orientation as the trackways (Fig. 7). This could indicate that the number of individuals that passed through this area was even greater but because of high track density it is difficult to ascertain the total number of trackways. Trackway XIX was left by the largest individual; average pes length is 49.44 cm (Figs. 7, 11). Trackway XXI was left by one of the smallest individuals; pes length averaged 28.75 cm (Figs. 7, 12). Trackway XX is the best preserved trackway (Figs. 7, 13, 14). Trackways XXII and XXIII (Figs. 7, 15A–B) overlap and represent the corridors through which several individuals passed, moving one behind the other. An animal that passed through later has

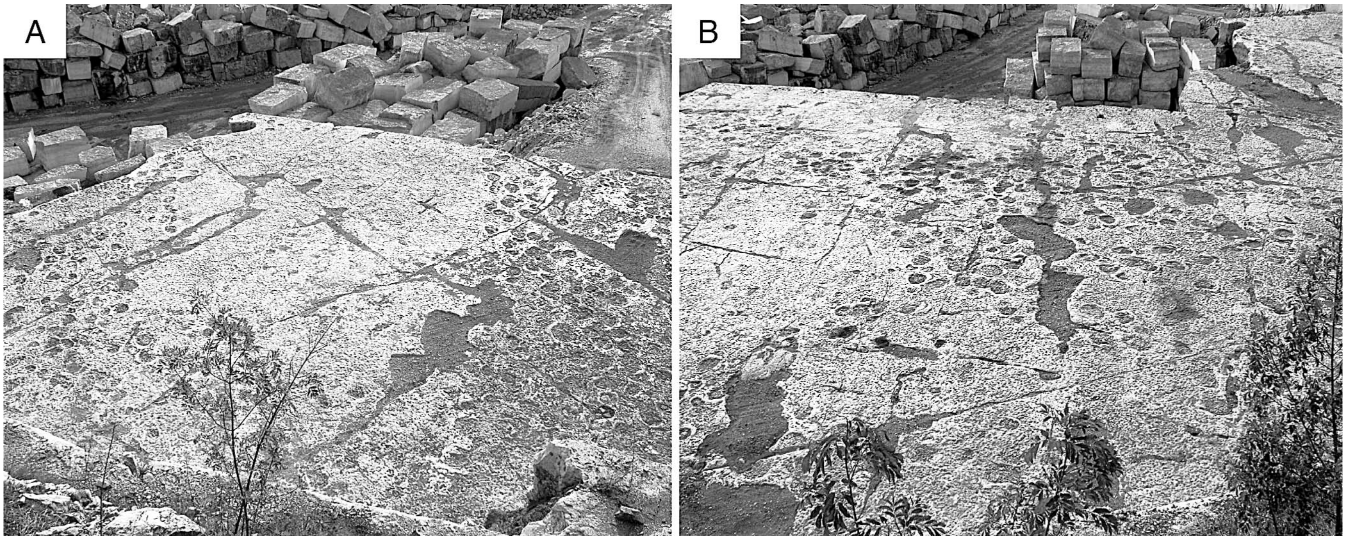

FIGURE 6—Trackbearing horizon. A) Central part of site. B) Northern part of site.

deformed the tracks of the individual that passed earlier. Because of the same state of preservation and the same direction, it could be assumed that the individuals moved through those corridors in a small time span or even together. All the trackways in Kirmenjak quarry are of the narrow-gauge type, where the internal trackway width rarely exceeds 10 cm and often has a negative value (Supplementary Data 2[1]; Figs. 11–13, 16). This excludes titanosaurians but not diplodocoids as possible track makers (Farlow et al., 1989; Lockley et al., 1994a; Wilson and Carrano, 1999). Footprints in the trackways are rotated outwardly from the trackway midline. Track density is so high in some parts of the outcrop that it is impossible to determine which footprint belongs to which individual. The sediment surface is completely trampled by sauropod feet and is a

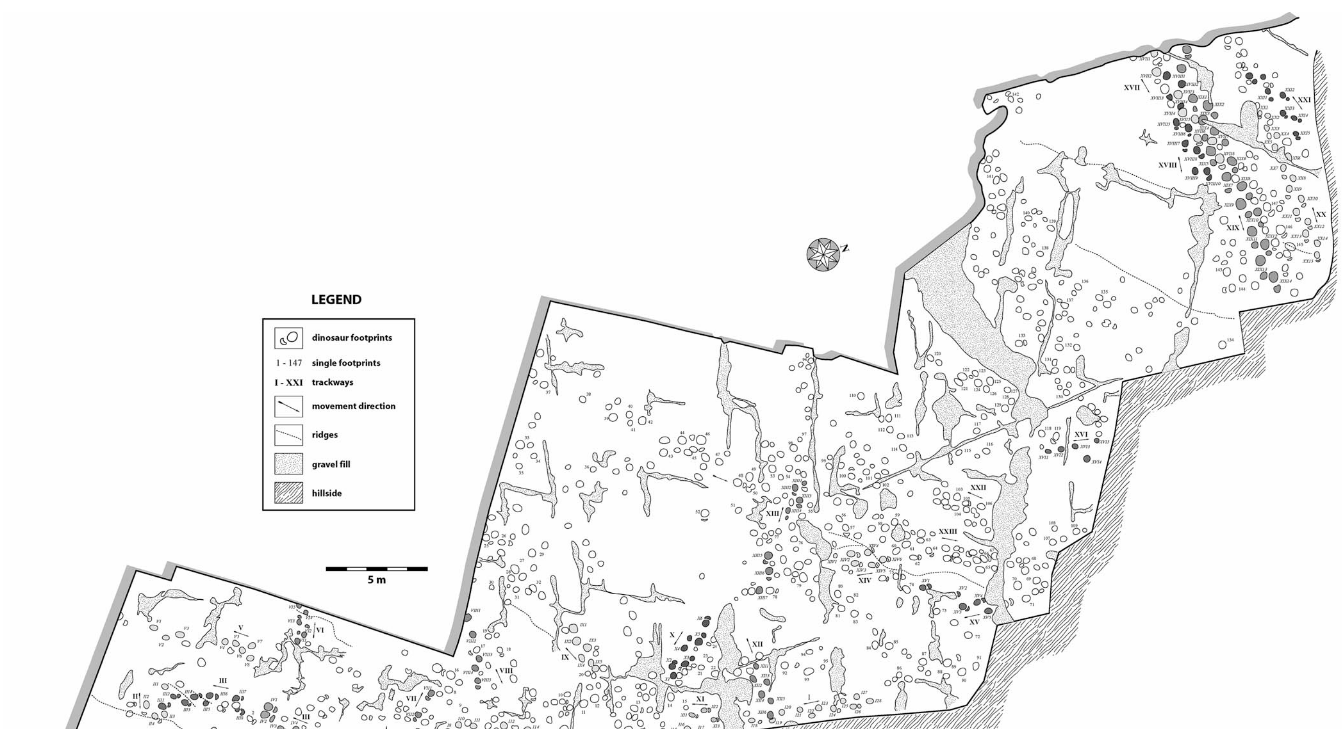

FIGURE 7—Detailed map of dinosaur tracksite in Kirmenjak quarry.

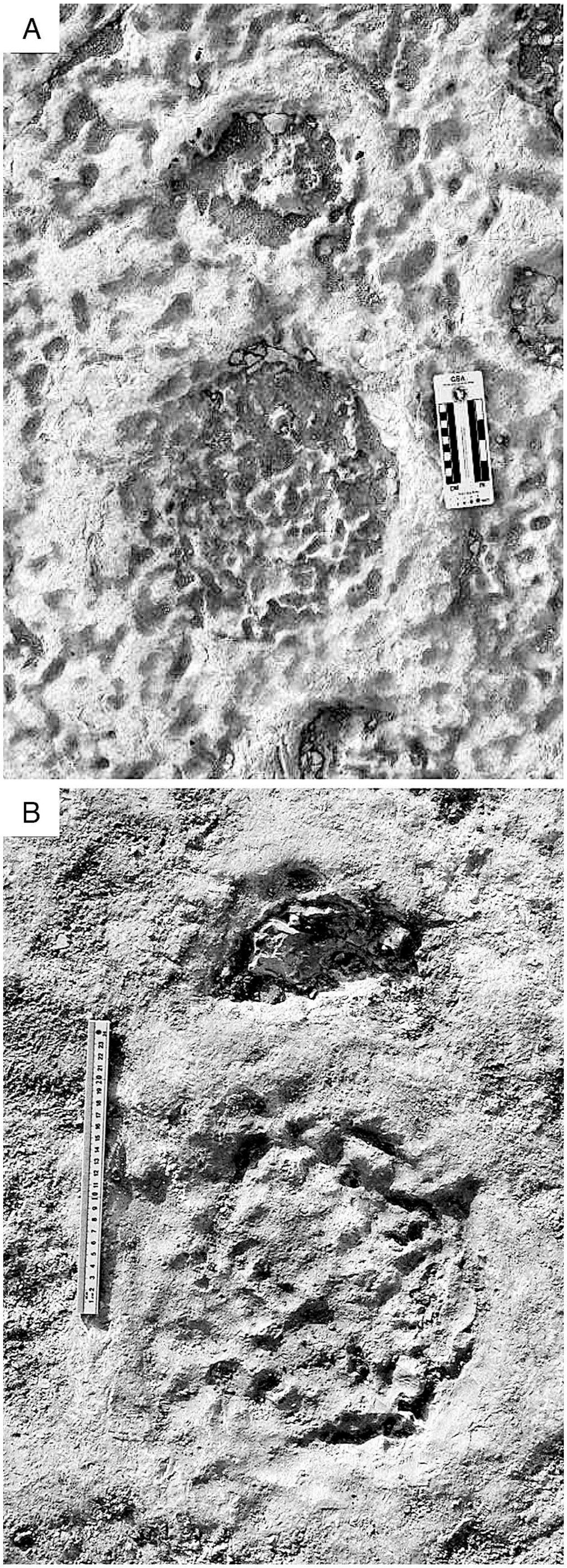

FIGURE 8—Manus and pes prints of sauropod from Kirmenjak. A) Footprint X 5. B) Footprint III 6.

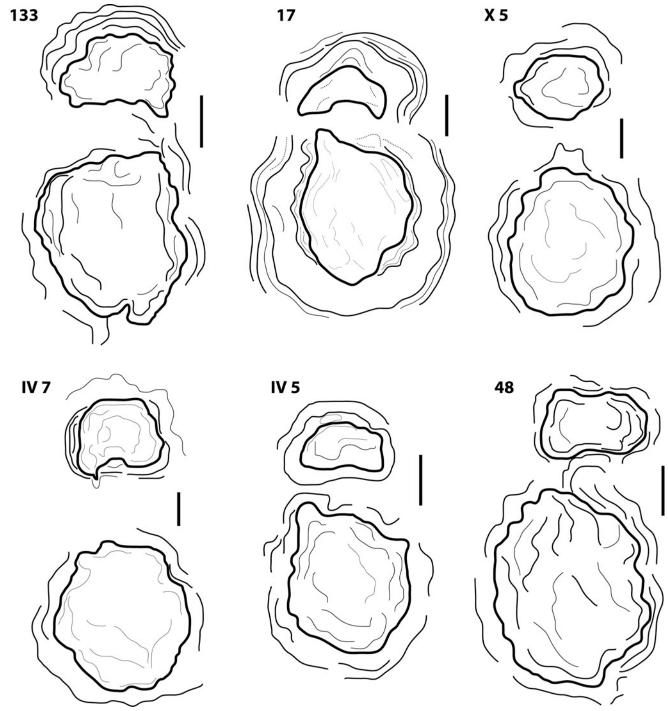

FIGURE 9—Drawing of some footprints (manus-pes) from the Kirmenjak site, with footprint numbers (see Fig. 7). Scale bars = 10 cm.

typical example of so-called dinoturbation. The index of dinoturbation is relatively high, about 60%, which is ranked as moderate to heavy dinoturbation *sensu* Lockley and Conrad (1989).

DISCUSSION

The footprints found in Kirmenjak quarry are, generally speaking, shallow for their dimensions (Supplementary Data 1[1]), which implies that the carbonate mud in which they were formed was rather solid and hard, with greater imprint resistance. Despite their overall shallowness and unpronounced morphology they are not preserved as undertracks. Clearly visible expulsion rims around the tracks verify their preservation as true tracks (Fig. 15C). Footprint depth varies greatly in relation to distance of the track from the waterline, as has been shown also in some recent examples (e.g., Cohen et al., 1993). Track depth is almost always related to the water saturation of the substrate. The deepest prints usually originate in substrate in which there is neither too much water nor too little (Cohen et al., 1993). The relatively shallow depth of Kirmenjak tracks does not necessarily mean that the substrate on which the dinosaurs walked was dry and exposed to the air; instead they could have been formed below water level where the sediment has greater water saturation. Footprint depths increase from the southern to the northern part of the outcrop in what could reflect different water saturation conditions in the substrate or a longer exposure to erosion. On the northern side of the outcrop footprints show a more pronounced morphology, which could indicate that the substrate was more pervious to the imprint of the foot. Obviously, all of the tracks at the outcrop were not formed at the same time. Those that were formed first are more eroded than the later-formed tracks.

To calculate the dimensions of sauropods from Kirmenjak we used the gleno-acetabular distance (GAD; Thulborn, 1990) and footprint length, and calculated hip height as 5.9 × foot length (FL) and 4 × FL (Alexander, 1989; Thulborn, 1990). The GAD was measured from the midpoint between a pair of hindfoot impressions to the midpoint between the next pair of forefoot impressions. There is a problem with this method

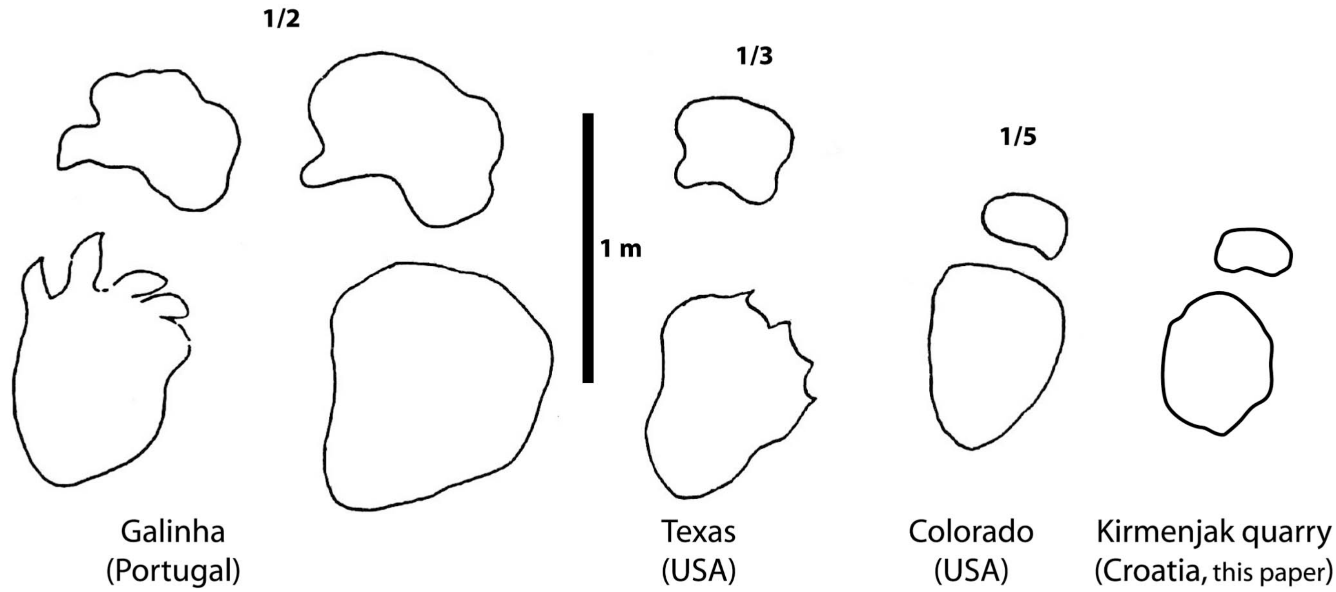

FIGURE 10—Heteropody of Kirmenjak footprints compared to other sauropod tracks (redrawn after Lockley et al., 1994a).

in that the distance is longer if the pace length becomes longer. Accordingly, a smaller dinosaur with longer steps would have a longer glenoacetabular distance and thereby distort its dimensions. Applying the minimal (107 cm in trackway XII) and maximal (192 cm in trackway XV) measured values of the GAD (Supplementary Data 2[1]) on the skeleton

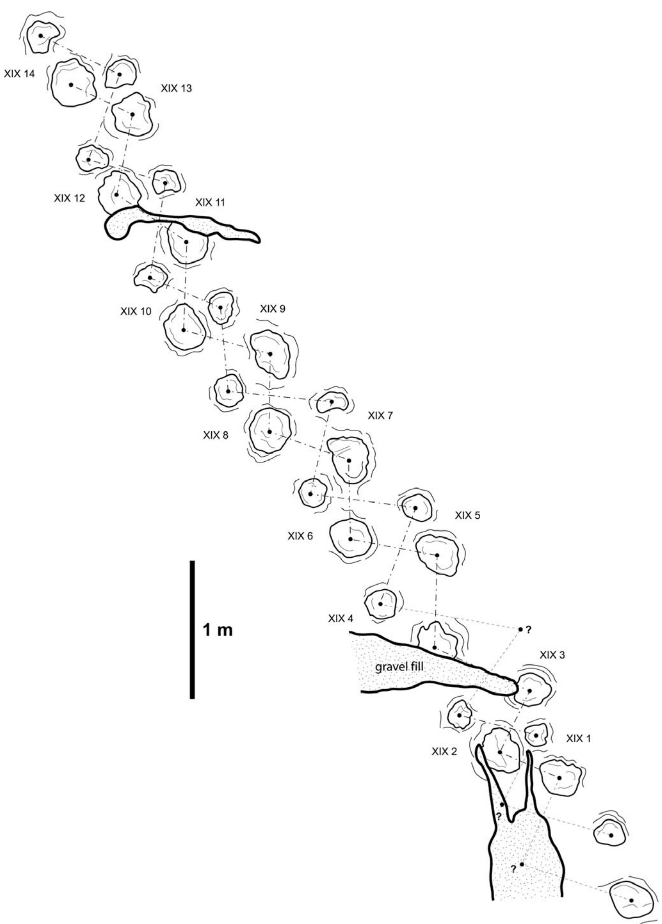

FIGURE 11—Trackway XIX. For position of the trackway, see Figure 7.

of *Dicraeosaurus*, we calculated the lengths of the animals as ranging from 7.5 m to 13.5 m. Using the calculation of hip height (Supplementary Data 2[1]) from footprint length and comparing it to *Dicraeosaurus*, body length ranges from 8.5 m to 17.5 m (h = 5.9FL) and 6 m to 12 m (h = 4FL). Such discrepancies come from the fact that Kirmenjak tracks do not belong to a single individual but to a number of individuals of varying size, based on the variation in footprint lengths. According to the calculated parameters, the smallest sauropods on the site were about 7.5 m in length, while the largest individuals attained some 14.5 m in length. As noted above, the size of the sauropods from Kirmenjak quarry was smaller than other Late Jurassic sauropod titans established from skeletal remains. This could be explained by the presence of new sauropod taxa or simply by the presence of relatively smaller species within a genus of large-bodied types, keeping in mind that all the species in a single genus were not of the same size.

The speeds of Kirmenjak sauropods were estimated using Alexander's (1976) formula, $v = 0.25g^{0.5} \times SL^{1.67} \times h^{-1.17}$, where v = meters/second, SL = stride length, and h = hip height (Supplementary Data 2[1]). We did not use the average stride length and hip height of the single trackway; instead we calculated the speed for each segment of the trackway independently in order to obtain more relevant values. The speeds range from 0.5–2.5 km/h, which is comparable to the speeds estimated for sauropods in other localities (Thulborn, 1990; Lockley and Meyer, 1999). The average walking speed (AWS) for Kirmenjak sauropods was estimated (Supplementary Data 2[1]) using Thulborn's formula $v=1.675h^{0.129}$ (1990; his table 10.3). Values range from 3.21–3.50 km/h; an AWS of 3.50 km/h is similar to the predicted values for *Diplodocus* or *Apatosaurus* (3.45 and 3.51 km/h respectively; Thulborn, 1990). Almost all the measured speeds of Kirmenjak sauropods are one half or one third of their AWS, suggesting that the preferred gait of Kirmenjak sauropods was a very slow walk. The relationship between stride length and footprint length (SL/FL) as well as stride length and hip height (SL/h) was also calculated (Supplementary Data 2[1]). The average ratio of SL/FL for Kirmenjak sauropods is 3.24, significantly lower than the values obtained by Thulborn (7–8; 1990). Similarly, the SL/h ratio is 0.53, lower than the value predicted by Thulborn (0.95; 1990) for sauropods. Thus, Kirmenjak sauropods walked by taking relatively short strides. Furthermore, it is observed that the distance between the manus and pes prints in Kirmenjak trackways depends on the speed of the animal. The greater the speed, the longer the distance. In the case of the slow walk, overlap of prints occurs and the pes prints cover the manus prints. This

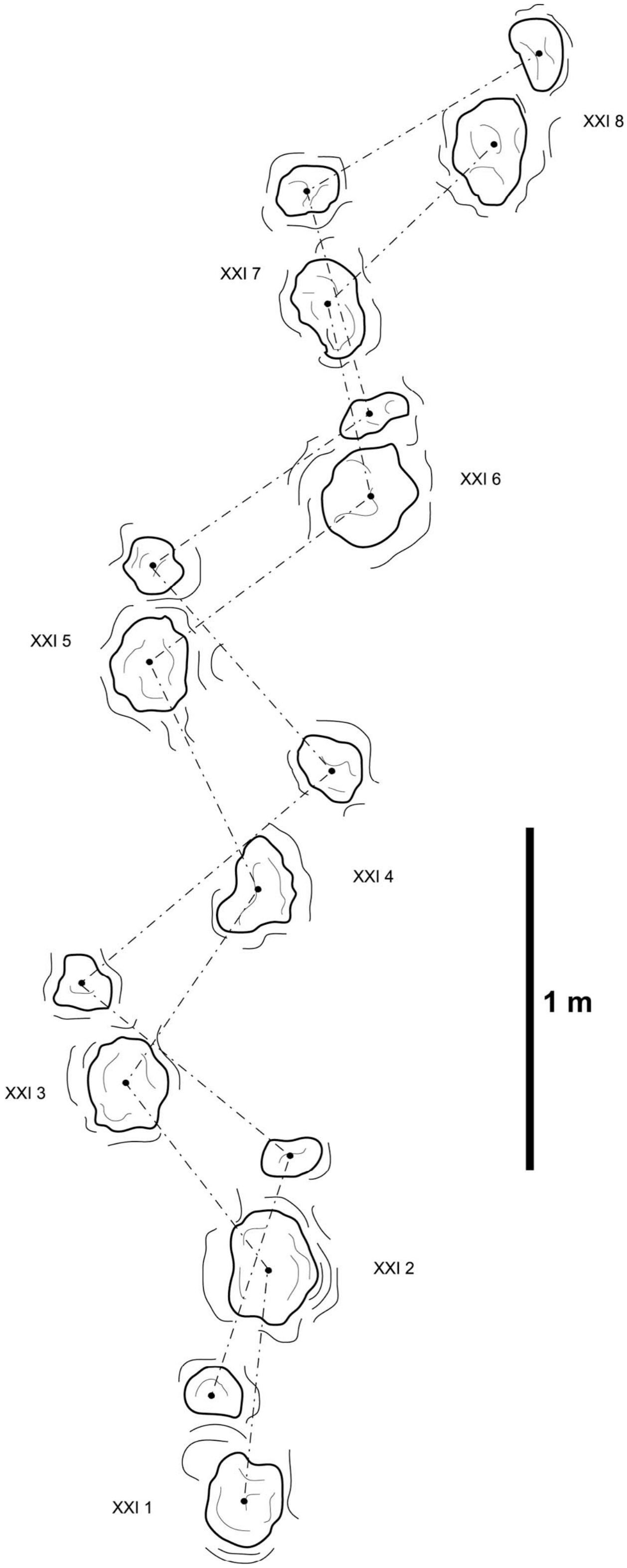

FIGURE 12—Trackway XXI. For position of the trackway, see Figure 7.

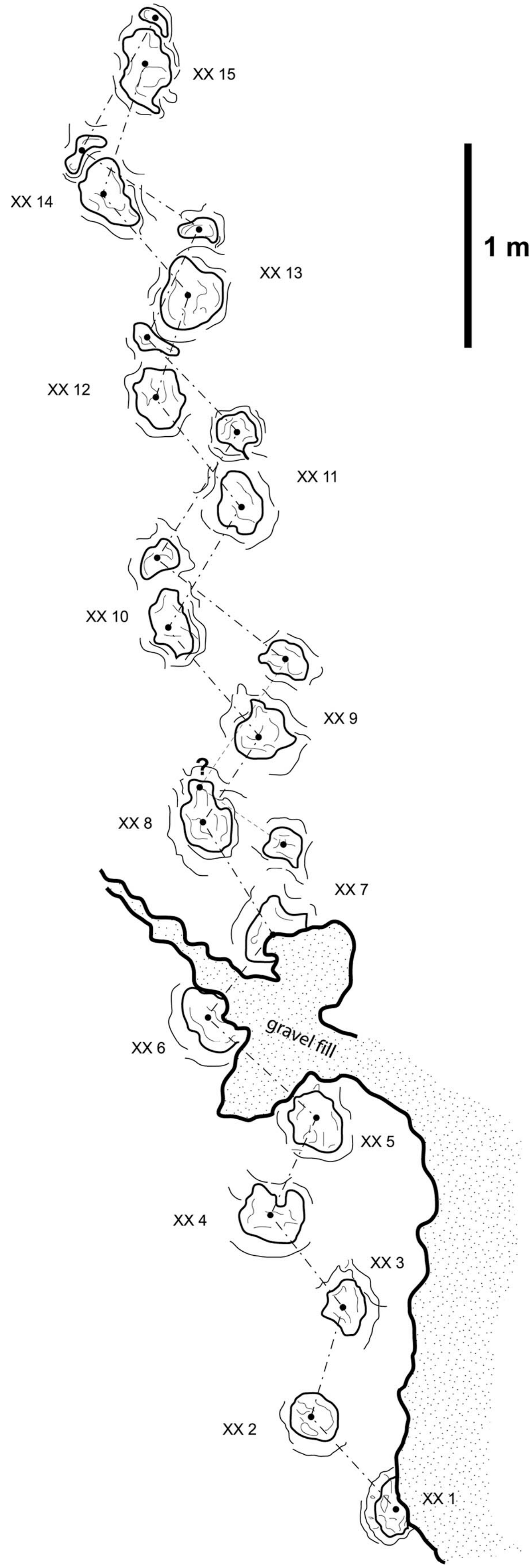

FIGURE 13—Trackway XX. For position of the trackway, see Figure 7.

feature indicates that the animals move their legs in pairs; e.g., front left foot–hind left foot, front right foot–hind right foot, similar to modern elephants (see also Alexander, 1989). This is further proof that the gait of sauropods resembled that of modern quadrupeds more than the gait of reptiles.

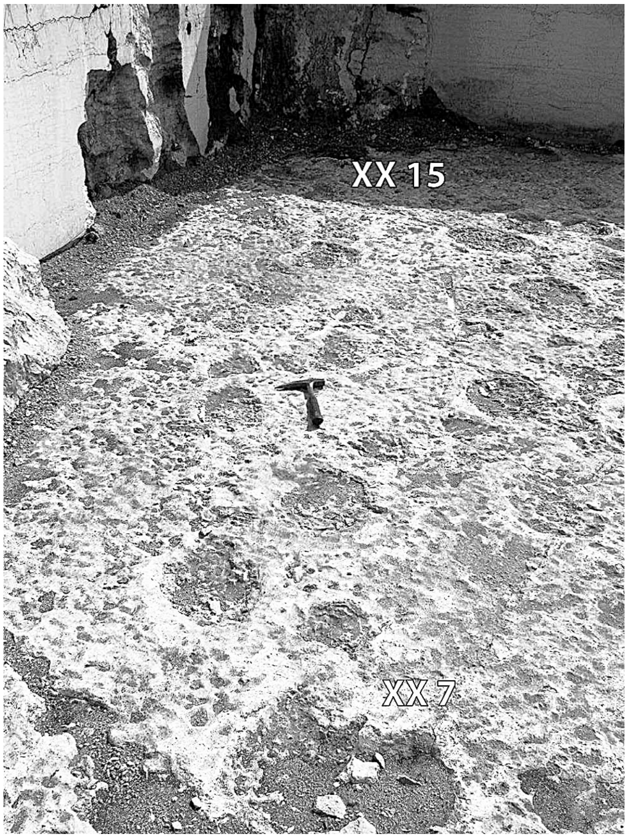

FIGURE 14—Eastern part of trackway XX (footprints XX 7–XX 15). For position of trackway, see Figure 7.

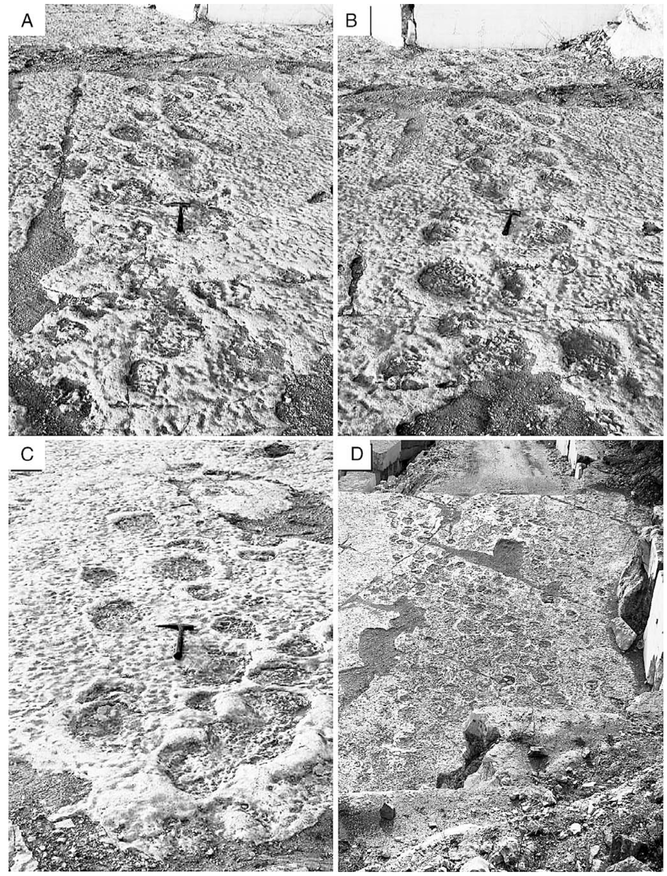

FIGURE 15—Sauropod trackways from Kirmenjak quarry. A) Trackway XXII. B) Trackway XXIII. C) Trackway X. D) Northern part of outcrop with four parallel trackways.

The orientation of the footprints on the outcrop usually depends upon some topographic or behavioral character. The direction of sauropod movement along the shoreline is a common case (Thulborn, 1990; Lockley and Meyer, 1999). Kirmenjak sauropods tended to walk north, northeast, and east, as indicated by measured trackway orientations (Fig. 17), so the former shoreline could have had a NE-SW direction. Analysis of pes print length (PL) and manus print width (MW) distribution allows interpretation of the composition of the ichnocoenosis. The distribution of the PL and MW among the Kirmenjak tracks indicates three distinct size categories (Fig. 18). The first category is the modal class of 28 cm pes length, second is the class of 33–35 cm, and third is the class of 40 cm upward. Such a grouping of footprint sizes suggests the presence of three sauropod taxa or three different age sizes of the same species (adult, subadult, and juvenile). They could indicate the presence of a sauropod herd composed of individuals of different ages (i.e., sizes), especially given the similar states of preservation of some trackways. The northern part of the site is especially interesting because four parallel trackways (XVII, XVIII, XIX, and XX; Fig. 7) and numerous individual footprints with the same orientation have been found (Fig. 15D). They most probably represent the footprints of the same generation because similar preservation suggests that they were produced at the same time. Because the trackways are so closely spaced and sometimes overlap, it could be assumed that those sauropods moved together, but not parallel to each other; instead they walked one behind the other.

Late Jurassic sauropod footprints are known in Europe from Portugal and Switzerland (Lockley and Meyer, 1999). The Cabo Espichel site in Portugal is similar to Kirmenjak in age and environment of deposition, but the footprints are of the wide-gauge type and have been ascribed to ichnogenus *Brontopodus* (Lockley et al., 1994b). The footprints at Avelino, Portugal, are of similar size, gauge, and type as the Kirmenjak tracks but are Kimmeridgian in age (Lockley and Santos, 1993). The Lommiswil and Moutier sites in Switzerland (Meyer, 1993) are also Kimmeridgian in age; here the tracks represent wide-gauge, *Brontopodus* type. Although the Kirmenjak footprints lack distinctive morphologic features, their narrow-gauge, strong heteropody (small manus), and outwardly rotated manus are characteristic of the sauropod ichnogenus,

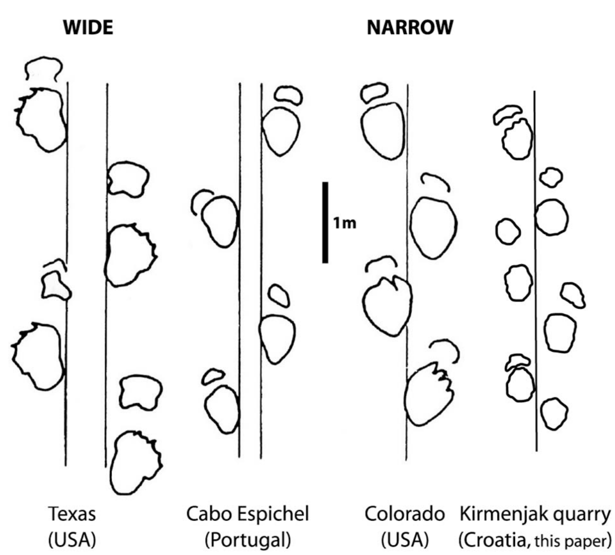

FIGURE 16—Kirmenjak quarry trackway compared to wide- and narrow-gauge types of sauropod trackways (redrawn after Lockley et al., 1994a).

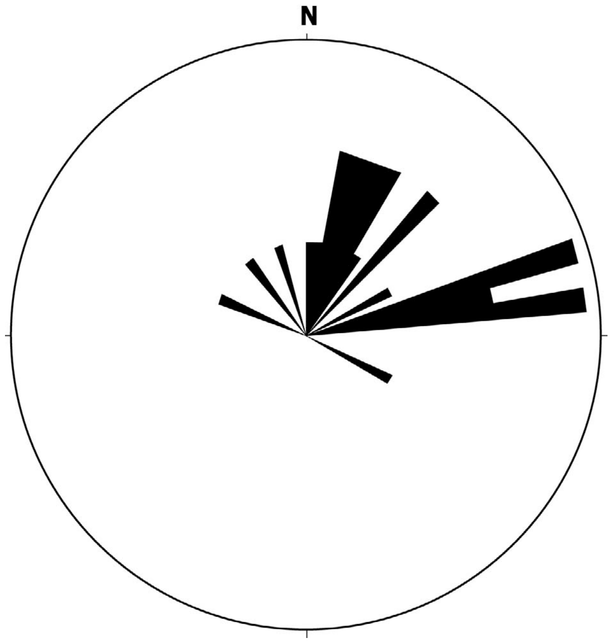

FIGURE 17—Rose diagram of movement direction distribution of Kirmenjak sauropods.

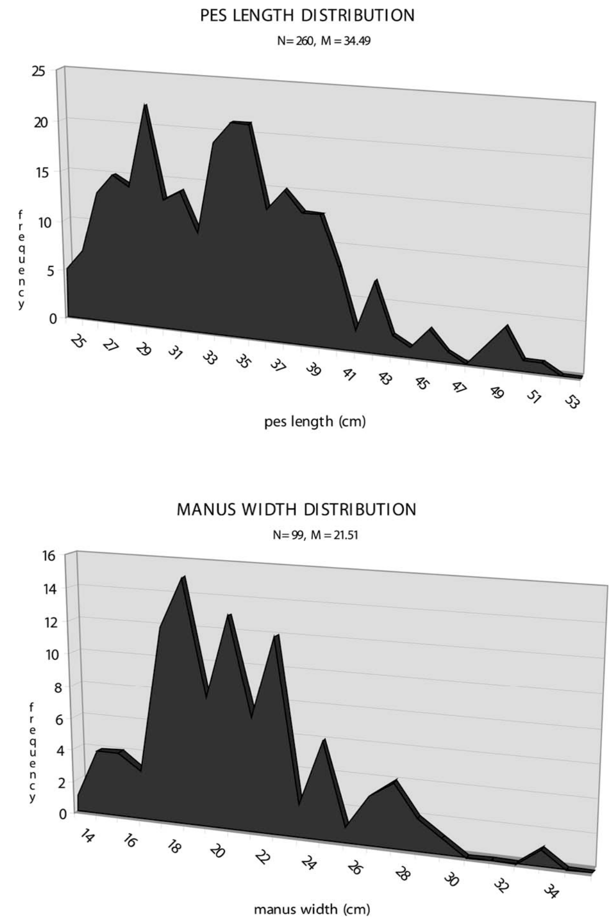

FIGURE 18—Pes length and manus width distribution of Kirmenjak sauropods.

Parabrontopodus (Lockley et al., 1994a; Lockley and Meyer, 1999). *Parabrontopodus* manus prints are wider than long, semicircular in shape, significantly smaller in size than the pes prints, and lack clearly visible digit impressions (Lockley et al., 1994a). *Parabrontopodus* pes prints are longer than wide with the longer axis rotated outward from the trackway midline (Lockley et al., 1994a). The Kirmenjak footprints most resemble those from the Courtedoux track site in Switzerland (Marty et al., 2003). These tracks are of the *Parabrontopodus* type, narrow gauge and similar dimensions, but are Kimmeridgian in age (Marty et al., 2003). Since the sauropod tracks from the Kirmenjak site are found in the carbonate environment of the ADCP, this ichnocoenosis could be assigned to *Brontopodus* ichnofacies *sensu* Lockley et al. (1994c), which is defined as a sauropod footprint ichnocoenosis in carbonate facies related to a carbonate platform environment. This ichnocoenosis occurs in the Late Jurassic and Cretaceous from numerous localities (United States, South Korea, Switzerland, Portugal, Morocco, and Bolivia). Similar cases of sauropod tracks in a carbonate platform environment have been described from the Paluxy River site in the Glen Rose Formation, Texas (Albian; Pittman, 1989) and from the Cabo Espichel site in Portugal (Late Jurassic; Lockley and Meyer, 1999). The main differences between these two sites and Kirmenjak is the fact that the Glen Rose Formation was deposited on an epeiric platform (Pittman, 1989), and both of these sites show minor siliciclastic content indicating terrigenous influx. Kirmenjak sediments, on the other hand, were deposited on a more-or-less isolated carbonate platform with no terrigenous influx.

The African sauropod fauna from the Late Jurassic is more diverse than the European fauna (Weishampel et al., 2004), and the only find of sauropod bones on the ADCP (Lower Cretaceous of Bale, Istria) shows African affinities (Dalla Vecchia, 1998a). In Africa, a rich dinosaur fauna is known from the Mkoawa Mtwara locality in Tanzania (Weishampel et al., 2004). The locality belongs to the Kimmeridgian Tendaguru Formation and includes: Diplodocoidea: *Dicraeosaurus hansemanni* Janensch, *D. sattleri* Janensch, *Tornieria africanus* (Fraas), and *Barosaurus gracilis* Janensch; Brachiosauridae: *Brachiosaurus brancai* Janensch; Titanosauria: *Janenschia robusta* (Fraas); and Sauropoda incertae sedis: *Tendaguria tanzaniensis* Bonaparte, Heinrich, & Wild (Weishampel et al., 2004). The sauropods from Kirmenjak quarry are more similar to *Dicraeosaurus* than to the other African taxa (Upchurch et al., 2004), in their smaller size (compared to the so-called titans of Late Jurassic age) and the diplodocoid nature of their tracks.

During the Late Jurassic the ADCP was one of the peri-Adriatic platforms oriented approximately NW-SE and was surrounded by deep marine basins on its western, northern, and eastern sides, partly analogous to the Bahaman archipelago in size, form, and internal structure (D'Argenio et al., 1975). The ADCP represented the northern tip of the Central Mediterranean Carbonate Platform (Vlahović et al., 2005), a larger paleogeographic unit that was also elongated in a NW-SE direction. According to Dercourt et al. (1993) this unit was separated from Laurasia and Gondwana by deep marine trenches. Dalla Vecchia (1998b) suggested that the ADCP was connected with the Apulian, Apenninic, and Trento platforms during the Cretaceous and via those platforms with the African continent as well, although it was a hundred kilometers from the so-called true land. This would make the ADCP a unique example of dinosaurs living on an isolated carbonate platform. The other Mesozoic carbonate platforms with dinocoenoses (Texas and Portugal) represent pericontinental platforms with carbonate prograding landward into siliciclastic shore and continental sediments. During the Late Jurassic the ADCP was characterized by shallow-water carbonate sedimentation (Vlahović et al., 2005). The occurrences of Middle Jurassic–Lower Cretaceous ophiolite in the peri-Adriatic region indicate the separation of the ADCP from the Eurasian continent by an ocean (Bosellini, 2002); however there is no unequivocal evidence of the ADCP southern connection with the African continent. There is still no sedimentary record on the ADCP other than the one that implies continuous shallow-water carbonate deposition; terrestrial deposits have not been found (Vlahović et al., 2005). The discoveries of dinosaurs within ADCP sediments are therefore extremely valuable, because they provide evidence of the existence of land and connection of the platform with the continent. All the available geological and sedimentological data reconstruct the ADCP as a flattened area surrounded by tidal flats and shallow lagoons. There is no direct evidence of any developed relief with forest cover and fresh water, crucial conditions for the survival of hundreds of large herbivores. Dinosaurs could not actually live on the carbonate platform itself, which was *sensu stricto* a few meters under water and characterized by tidal flats, channels, lagoons, and islets. There had to be a large terrestrial area nearby with lush vegetation and a well-developed river system in order to sustain such large animals. The entire ADCP area, as reconstructed earlier (e.g., Dercourt et al., 1993; Blakey, 2004), does not represent an environment in which the sauropods could have had survived. Some interpretations, however, have envisaged the full terrestrialization of Istria during shorter or longer time periods of the Mesozoic (Matičec et al., 1996; Veseli, 1999). Comparing the ADCP with the Bahamas-type platform would be risky with regard to dinosaur finds, as the ADCP was not an isolated platform during the Late Jurassic, according to the presence of sauropod tracks. The fact that there is still no record of terrestrial sediments in the Late Jurassic of ADCP does not prove that there was no land. The lacustrine sediments in the Lower Cretaceous of Bale, Istria, are filled with dinosaur bones (Dalla Vecchia, 1998a) and are proof that there was a widespread terrestrial area, at least during the Early Cretaceous. The Kirmenjak tracks are preserved in shallow marine sediments, not of an isolated platform but of a more coastal environment. During the Late Jurassic the sauropods may have migrated from the African continent onto ADCP across the wide corridors of shallow water environments that were formed during emersions. During this time the ADCP may have been less like the Bahamas platform and more fully terrestrialized, even similar to the Florida peninsula (Bosellini, 2002).

CONCLUSIONS

Dinosaur footprints from a new, late Tithonian locality near the village of Kirmenjak in western Istria, Croatia represent the oldest evidence to date of the presence of dinosaurs on the Adriatic-Dinaridic carbonate platform. Nearly 1000 single footprints and 23 trackways, most of which are oriented northeast, have been registered at the site. Footprints are shallow, oval or horseshoe shaped, lacking visible digit impressions, and are interpreted as belonging to sauropod dinosaurs. The numerous parallel trackways suggest that some of the individuals were moving together in herd. Trackways are narrow gauge; footprints are similar to the *Parabrontopodus* ichnogenus. The presence of large sauropod dinosaurs on the ADCP during the Late Jurassic could be explained by a connection with the African continent on the southern side. It also suggests that dinosaurs could have migrated onto the ADCP during phases when the platform was emerged.

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