A DIVERSE VERTEBRATE ICHNOFAUNA FROM A QUATERNARY EOLIAN OOLITE, RHODES, GREECE

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ABSTRACT: In coastal areas of the SW part of the island of Rhodes, Greece, eolian oolitic sediments represent the latest depositional phase, and are presumed to have a Late Pleistocene to Early Holocene age. The ooids have sand-size nuclei and are lightly cemented by vadose meniscus cement. In a road cut, supplemented by minor sections in small, ancient stone quarries nearby, the sedimentary architecture and trace fossils are visible. The dunes have ramp morphology and contain three horizons of paleosols that divide the eolian sediments into three units. The paleosols contain rhizoliths and poorly preserved invertebrate bioturbation. Vertical sections allowed representative measurements of 79 tracks and limited horizontal surfaces supplied four measured tracks. Five size classes of tracks are distinguished. The mode of preservation of the tracks is poor, probably on account of the oolitic nature of the substrate. The three smallest size classes are probably of artiodactyls. The largest class probably was produced by proboscidians. A bedding-plane view of one track indicates that the next-largest class may be the work of camels. If this is the case, and the bedding-plane specimen is convincing, it is the first record of Pleistocene or Early Holocene camels on Rhodes. The combination of size groups of tracks differs in the three units, demonstrating differences in faunal composition in the different periods of deposition of the oolite.

INTRODUCTION

In the coastal regions of the southwestern part of the island of Rhodes, Greece, are patches of carbonate eolianitic sediments resting on the Lower Oligocene Kattavia Flysch. The sediments rest on the deeply weathered erosion surface, locally preserving a deeply weathered paleosol. The upper surface of the eolianite unit is the present-day erosion surface and shows advanced weathering features that indicate subsoil karstification. Deforestation and soil loss has now exposed this surface to the atmosphere.

Owing to the heavy weathering of the carbonate sediments, natural surfaces show few remains of sedimentary structures, even in vertical sections along small watercourses. Possibly for these reasons, the unit does not appear to have been mentioned in the published literature. When the road around the island was widened about twenty years ago, a road cut was made through the eolianite west of Kattavia (Fig. 1), revealing reasonably well preserved sedimentary structures. The ichnological significance of this section (Fig. 2) went unnoticed until February 2004, when preliminary fieldwork was undertaken. We refer to the unit herein as the Kattavia eolianite. The fieldwork was completed in March 2005. Data were collected chiefly from the road cut but also from a few small quarries for building stone close by the cut. Mammal tracks, invertebrate burrows, and plant rooting structures are abundant. Owing to the generally poor quality of preservation of invertebrate trace fossils, particular attention was paid to the mammal tracks.

Fossil and subfossil animal tracks are most easily recognized when exposed on bedding planes representing the original tracking surface. But because tracks are three-dimensional structures deforming the original sedimentary fabric, commonly to a considerable depth below the original tracking surface, it is possible to recognize tracks in vertical sections or random erosional cuts through bedding (Loope 1986; Lea 1996; Allen 1997; Fornós et al. 2002).

Small surfaces of the original bedding planes were exposed in the bottom of the ditch running beside the road section and on loose slabs of carbonate grainstone, lying on the opposite side of the road. Four measurable tracks were found in bedding-plane view. In contrast, 79 tracks were measured in vertical section.

GEOLOGY

Recent work has demonstrated that eolian carbonate deposits in some cases can be virtually indistinguishable from subtidal marine deposits if macroscale sedimentary structures are not observed or are weakly developed (Guern and Davaud, 2005). Even though the sedimentary structures in the Kattavia eolianite are not that well preserved, steep slopes of the sedimentary foreset sheets, as well as their lateral continuity, clearly indicate an eolian origin. And in this case, the presence of numerous vertebrate tracks and plant roots further proves the eolian origin of the deposit.

Coastal eolian dune sands in the Mediterranean region are well described from the Valencia region and from the Balearic Islands in Spain, from Lebanon and from the northern and central coastal plain of Israel, from the northwestern coastal plain of Egypt, from Libya and Tunisia, and from the Mediterranean coast of Morocco (Brooke, 2001, and references therein; Clemmensen et al. 1997; Clemmensen et al. 2001). On the island of Rhodes, eolianites were mentioned by Hansen (2001) as common features on a wave-cut platform level, approximately 25–35 m above present sea level. They represent the youngest deposits, overlying Mesozoic and Tertiary basement rocks as well as marine Plio-Pleistocene sedi-

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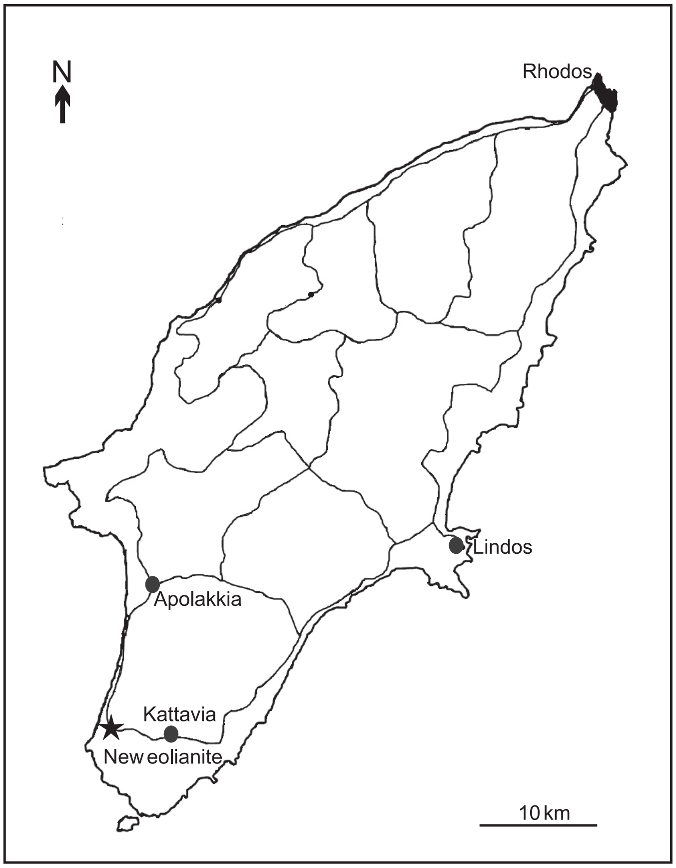

FIG. 1.—Location map of the island of Rhodes. The newly discovered Kattavia eolianite locality, marked by a star, is exposed in a road cut near the SW coast.

ments. Hansen (2001) distinguished throughout the island different dune shapes: coastal dunes, echo dunes, and dunes having ramp morphology. The sediment composition is variable and consists of reworked marine bioclasts (molluscs, red algae, bryozoans, etc.) and lithoclasts (calcite or quartz grains, dependent on the source areas of the hinterland). Commonly the dune sands are subdivided by soil horizons rich in rhizoliths. The stratigraphic position of the eolianites overlying Upper Pleistocene marine sediments at Cape Plimiri (observations by J.T.) and Pleistocene sediments in Lindos Bay (Hanken et al., 1996) suggest a Late Pleistocene to Early Holocene age for these eolianites.

The road-cut exposure studied herein has a length of 210 m and a maximum height of 8 m (Fig. 2A). No wave-cut platform level as mentioned by Hansen (2001) is developed at this part of the island, possibly owing to the lesser resistance of the Kattavia Flysch to erosive processes than many other basement rocks on the island and the lack at this locality of Plio-Pleistocene carbonate deposits. However, the Kattavia eolianite occurs at an altitude, between 17 and 41 m above present-day sea level, comparable to that of the dune sands described by Hansen (2001), and represents a ramp-shaped dune.

The Kattavia eolianite can be subdivided into three units by tracing reddish soil horizons that are rich in rhizolith traces and shells of land snails (Fig. 2B). The sediment differs significantly in its composition from the eolianites known from the rest of the island owing to the presence of ooids as the dominant sediment component.

The ooids enclose large sand-size cores consisting of fragments of red algae, bryozoans, serpulids, foraminiferans, quartz grains, and lithoclasts (Fig. 3). The cores and individual layers of the ooids have been subject to variable degrees of dissolution; cementation is weak and dominated by miniscus cements, clearly due to exposure to a vadose meteoric diagenetic environment. A detailed description of the sedimentology of the Kattavia eolianite is in preparation by J. Titschack and colleagues.

Ooids occur as a dominant sediment component in many tropical carbonate settings. The occurrence of ooids on Rhodes represents one of the few known examples where ooids have formed in a nontropical environment. Other occurrences are known from southern Tunisia and Libya (Fabricius and Berdau, 1970), from the southern Peloponnes, Greece (Richter, 1976), and from Turkey (but the Turkish occurrence may have been transported there in historic times by humans; see El-Sammak and Tucker, 2002).

The age of the Kattavia eolianite is difficult to estimate, but we consider it to be Late Pleistocene to Holocene in age on the basis of the following criteria. (1) The presence of metastable carbonate phases such as aragonitic bioclasts; (2) retention of their color banding in some of the snail shells; (3) the weak cementation, and (4), the altitude above sea level comparable to that of the east-coast eolianites on Rhodes. However, McKee and Ward (1983) pointed out that preservation and degree of lithification are variable in both Holocene and Pleistocene dune sands. While McKee and Ward (1983) considered drops in sea level, attributed to the start of glacial phases, as a condition favorable for eolianite development, Brooke (2001) favored a highstand condition for their formation. However, there are multiple reports of dune formation during glacial periods (McKee and Ward, 1983), also in the Mediterranean region (Frechen et al., 2001).

We suggest, therefore, as a preliminary working model, that the dunes of the Kattavia eoliante were formed during glacial intervals and that the soil formation occurred during interglacials. Further, we envision the following scenario: (1) The ooids were formed off the coast of Rhodes during the warm interglacial periods. (2) During sea-level lowstands of the cold glacial periods, the ooids became aerially exposed on the shelf around the island and were reworked and transported inland as eolian dune sands. (3) During the subsequent warm interglacial, sea level rose again, and flooding of the island shelf cut off the source of ooids. The wetter and warmer climate favored soil formation in the dune sands. However, this preliminary model for the formation and timing of the Kattavia eolianites is so far only speculative and must be proved or disproved by precise dating of the eolianite.

VERTEBRATE TRACE FOSSILS

Terminology

The original sedimentary surface in which the tracks were emplaced is termed the "tracking surface" *sensu* Fornós et al. (2002), and the animal responsible for the track is the trackmaker. The tracks formed in the tracking surface are termed "true tracks" and represent the direct impression of the trackmaker's foot (Lockley, 1991). The weight of the trackmaker is transferred via the foot radially outward into the sediment, causing deformation not only of the tracking surface, but also of subjacent layers (Allen, 1989, 1997). The deformation structures formed in the layers subjacent to the true track are termed "undertracks" (Lockley, 1991). Undertracks preserve less detail than true tracks, and they become successively shallower and wider, and preserve fewer anatomical features downward, layer by layer (Milàn and Bromley, 2006). The radial pressure of the foot

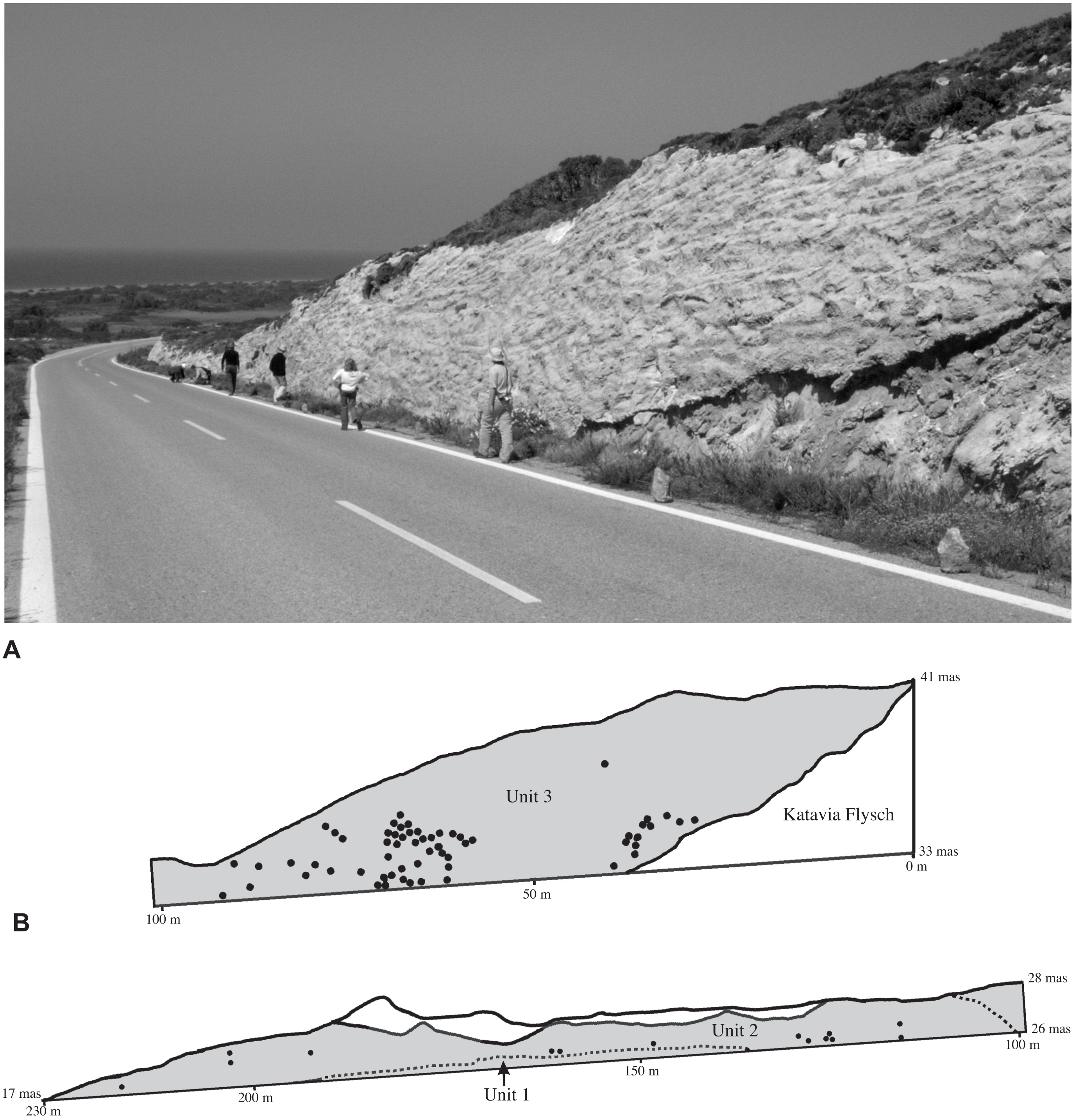

FIG. 2.—Schematic section of the Kattavia eolianite. **A)** Photo of the section viewed from the southeast. The section dips on average at 4 degrees toward NW. The highest point of the section is located 41 m above present-day sea level (mas), and the lowest part exposed is 17 mas. The contact between the eolianite and the Kattavia Flysch is exposed in the lower right corner of the photo. The persons on the photo are spaced at 10 m intervals. **B)** Sketch of the total section. The exposed eolianite is divided into three units separated by well-developed soil horizons, indicated by dotted lines. Recorded footprints are represented by black dots.

further creates a "marginal ridge" of displaced sediment around the tracks (Fig. 4A).

In soft or loose tracking substrates, the trackmaker's foot can plunge to a considerable depth, creating vertical or inclined walls from the bottom of the true track to the tracking surface. The vertical parts of the track are termed "trackwalls" (Brown, 1999) or "shaft" (Allen, 1997). In cases where the trackwalls are inclined, the track at the surface appears wider than the true track

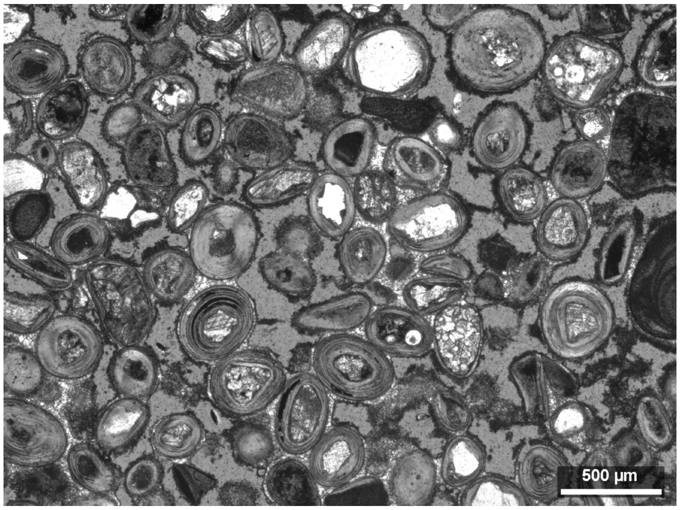

FIG. 3.—Thin section of the ooid grainstone of the Kattavia eolianite. The ooids show large nuclei composed of quartz grains, lithoclasts, and bioclasts. The ooidal coating is thin, and laminae are partially dissolved. Cementation is weak to moderate and of meniscus type. Plane-polarized light.

at the bottom of the track and is termed the "overall track" (Brown, 1999). When tracks are emplaced in dry, loose sediments, the trackwalls collapse after removal of the foot, destroying the shape of the true track and in extreme cases leaving only a bowl-shaped depression on the sediment surface. In this case the overall track is the only information available about the size of the trackmakers foot (Fig. 4B), and it is important to bear in mind that the overall track can appear significantly larger than the true track (Milàn, 2006). If the track subsequently is covered by several thinner layers of sediment, the layers drape the contours of the track and can form a shallowing-upward stacked sequence of "ghost tracks" *sensu* Fornós et al. (2002). If observed on horizontal surfaces, these ghost tracks may be misinterpreted as undertracks (Fig. 4C).

Tracks Exposed in Vertical Section

In the road cut, 74 footprints exposed in cross section were measured, and an additional five footprints seen in cross section were measured in a small quarry on the other side of the road. The footprints ranged in size from 4 to 37 cm in cross section (Fig. 5). All tracks appear as steep-walled, flat-bottomed depressions in the sediment surfaces. With very few exceptions they lack any preserved morphologic details of the feet, such as division into digits or hooves.

The sediment layers around and below the flat-bottomed tracks have been deformed by the impression of the feet, clearly leaving distinct undertracks below all the recorded specimens (Fig. 6). In several specimens the filling of the tracks is layered, causing the formation of several distinct ghost tracks above the true track (Fig. 6A, B).

Tracks on Horizontal Surfaces

Because the eolianite is exposed as a road cut, morphologic variation of the tracks as expressed in horizontal view is limited. Only a few surfaces representing the original bedding planes are exposed, but in the bottom of the ditch along the road, tracks in several surfaces were exposed in horizontal view. Two of these were complete enough to record, and, in addition, a slab containing two footprints was found in a loose block on the other side of the road.

The first is a small, circular track 7 cm in diameter, partly filled by sediment. The exposed parts of the track show no internal structures or indications of the trackmaker's anatomy owing to secondary collapse and filling of the footprint. A prominent pressure pad (*sensu* Fornós et al. 2002) of sediment displaced by the trackmaker's foot is developed on the downslope side of the footprint, and several sets of concentric fractures in the sediment are visible out to 6 cm down the paleoslope of the dune in which the track was emplaced. Radiating fractures in the sediment around the track are formed in the lower right side of the track (Fig. 7A).

A less well preserved and heavily weathered track is approximately 18 cm in diameter. The eroded state of the track makes it hard to identify whether it is a true track, an undertrack, or a ghost track. But the vague remains of a raised margin around the track makes it most likely that it is indeed a true track altered by erosion. The upper part reveals the remains of a weak division into two hooves (Fig. 7B).

A slab of grainstone found among loose blocks at the roadside opposite the cutting contained two tracks, one of which was well preserved. This track is 16 cm long, is almost circular in outline, and consists of two broad crescent-shaped impressions weakly divided anteriorly and posteriorly by a small wedge of sediment. The bottom of the track is flat, with a slightly raised area in the middle. The morphology of the two crescent-shaped hoof imprints is consistent with the foot morphology of an even-toed

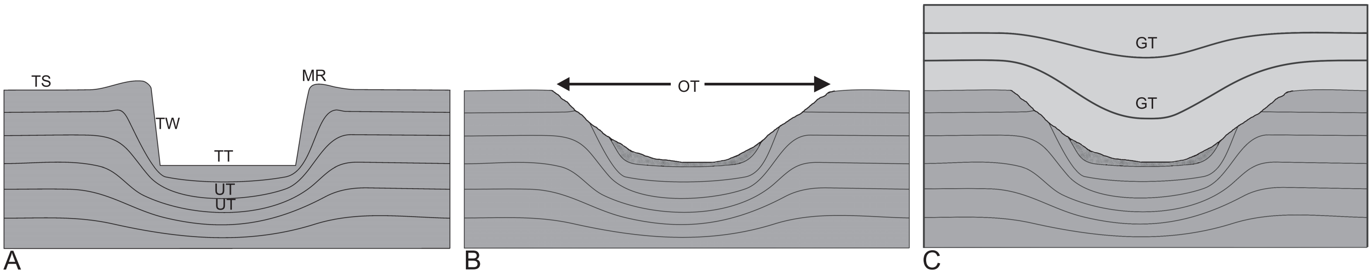

FIG. 4.—Schematic representation of track formation in dry sediments. **A)** The impression of the trackmaker's foot forms the true track, TT, in the tracking surface, TS, and a stacked succession of downward-shallowing undertracks, UT, deforms the subjacent layers. Vertical or nearly vertical trackwalls, TW, connect the tracking surface with the true track. A marginal ridge, MR, of laterally displaced sediment surrounds the track. **B)** After withdrawal of the foot, the trackwalls collapse, and the track appears as a bowl-shaped depression with an overall track, OT, with width significantly larger than the true track. **C)** Subsequent sedimentary covering creates a stacked succession of ghost tracks, GT.

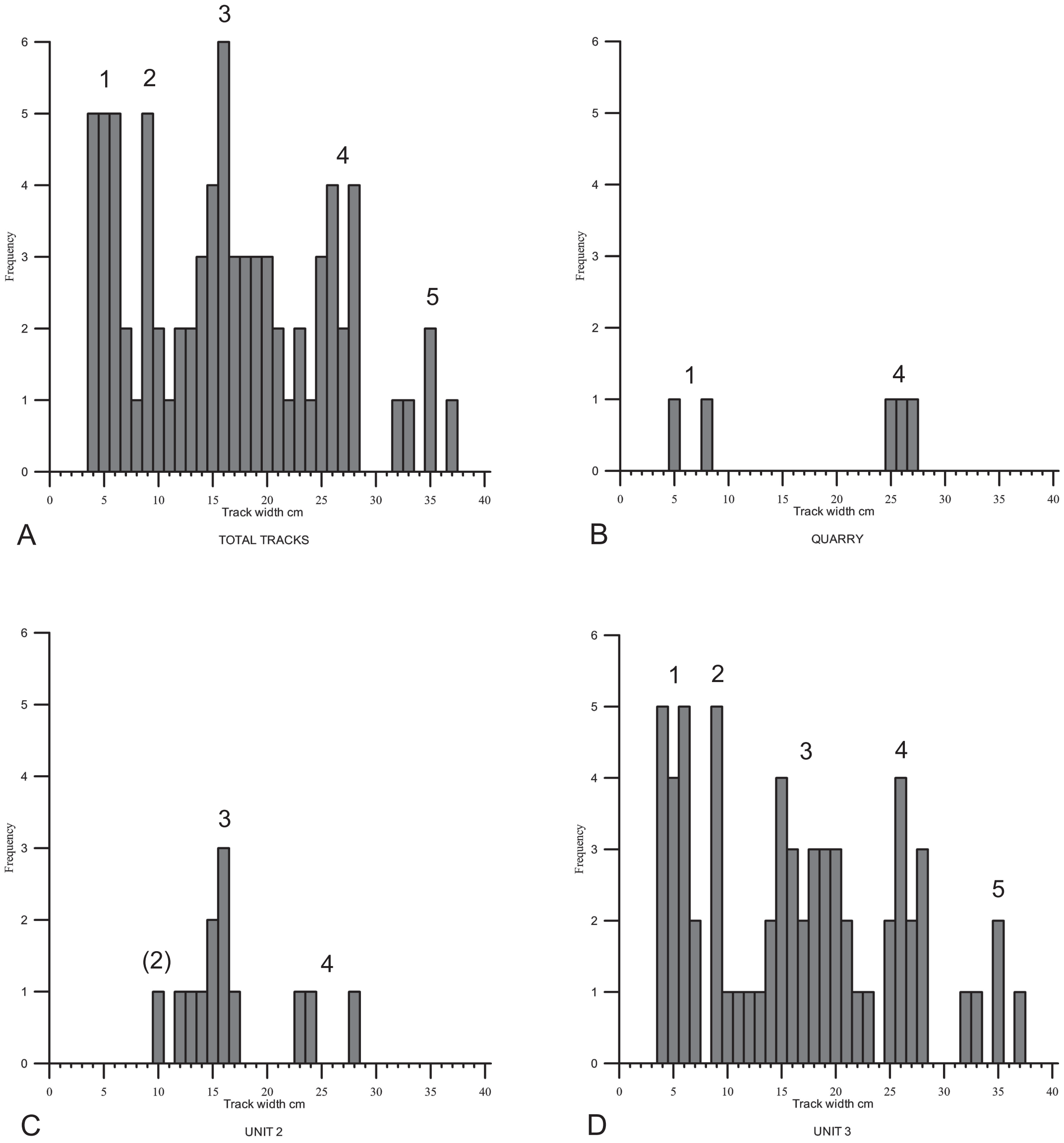

FIG. 5.—Size-frequency histogram of the 79 tracks recorded in vertical section. **A)** The histogram shows five distinct size groups: (1) small tracks from 4 to 8 cm in diameter, (2) tracks about 9 cm in diameter, (3) tracks from 12 to 22 cm in diameter, (4) tracks from 25 to 28 cm in diameter, and (5) large tracks with a diameter between 32 and 37 cm. **B)** The five tracks recorded in the small quarry fall into size groups 1 and 4. **C)** The tracks from unit 2 fall into size groups 3 and 4, and perhaps one track in group 2. **D)** The 61 tracks recorded from unit 3 include all five size groups.

trackmaker. Surrounding the track is a prominently raised rim of displaced sediment. The track walls are collapsed, giving the characteristic low-angle trackwalls of tracks emplaced in dry sand (Milàn, 2006). Beside the track, a less well preserved track is present, having a diameter of 12 cm. No anatomical details have been preserved, but a partly raised margin is present around the track (Fig. 7C).

Bioturbation and Root Traces

The eolianitic grainstone commonly shows a mottled or lumpy texture that may have resulted from animal burrows and plant roots. However, the degree of weathering precludes any detailed study. The paleosols, however, clearly have an ichnofabric indicating total bioturbation (Fig. 8A). Larger plant rooting structures are locally well preserved as rhizoconcretions (Fig. 8B–D) but, despite the good preservation of snail body fossils, smaller rooting structures and bioturbation were too poorly preserved for study on the weathered road-cut surface.

DISCUSSION

Among the tracks exposed in cross section, those that were considered "measurable" were those in which the true diameter could be estimated. Tangential sections were avoided, because these gave no clear idea of the true diameter of the track.

The width and depth of the 79 measurable tracks were determined and plotted in a set of size-frequency histograms, based on

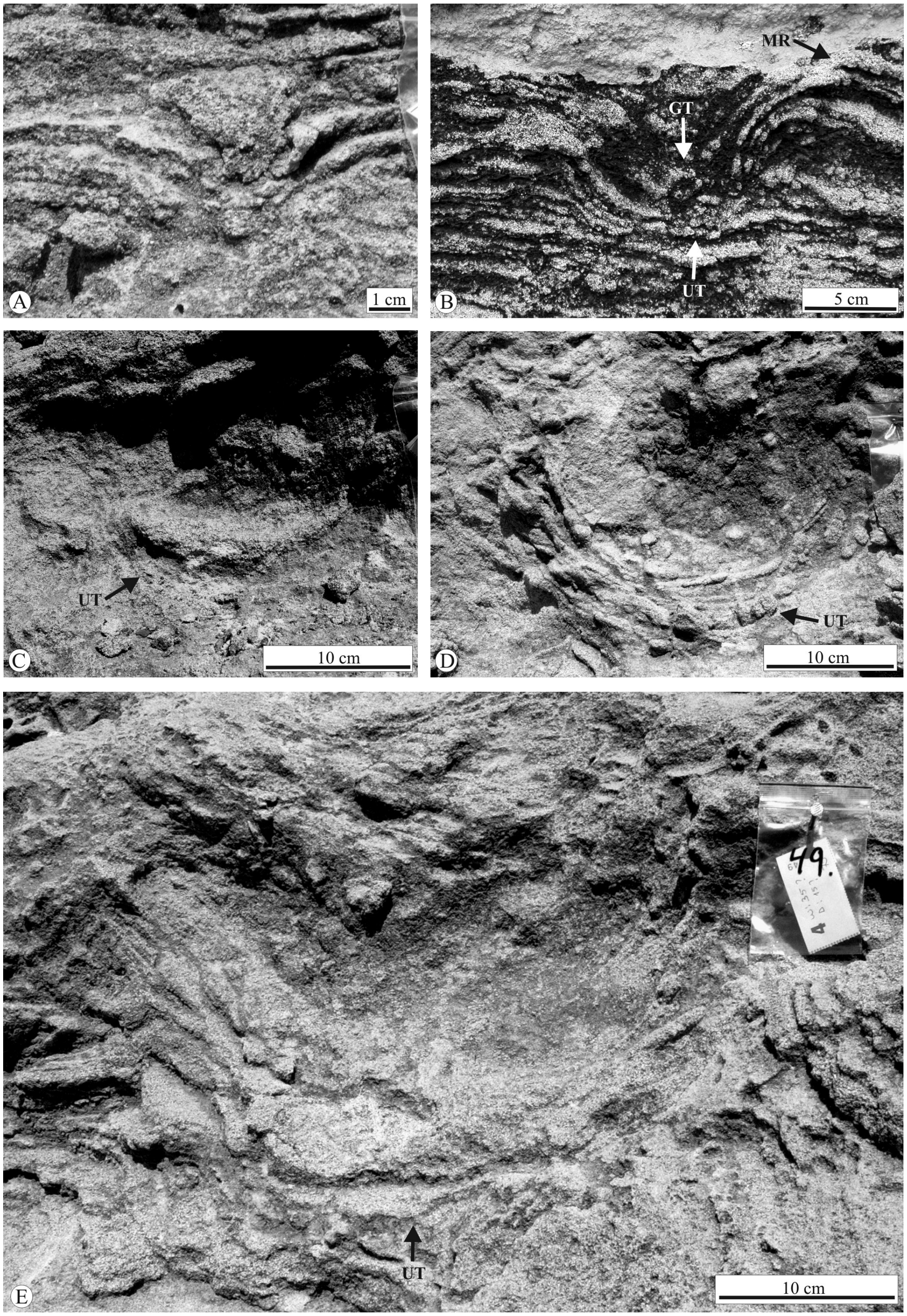

FIG. 6.—Five different sizes of tracks as they appear in the section. (Figures are not to the same scale.) **A)** Small track 4 cm wide. The smallest tracks appear mostly as V-shaped pinch structures protruding down from the tracking surface. **B)** The cross section through this track is 10 cm wide. Notice the well-developed undertracks (UT) in the subjacent horizons as well as the ghost tracks (GT) in the overlying layers created by gradual filling of the tracks. A prominent raised margin is seen on the right side of the track (arrows). **C)** Track 16 cm wide. The track is poorly preserved owing to little color contrast between the individual laminae. However, the shape of the track is defined by the undertracks (UT), indicated by arrows. **D)** Large bowl-shaped track 25 cm wide. Notice the well-developed succession of downward-shallowing undertracks (UT) below the track. No ghost tracks are formed above the track. **E)** One of the largest tracks recorded from the section, with a diameter of 35 cm. This and other large tracks are interpreted as proboscidean (elephant) tracks. The track appears more box-shaped than the smaller ones. Undertracks (UT) are present to a considerable depth below the track.

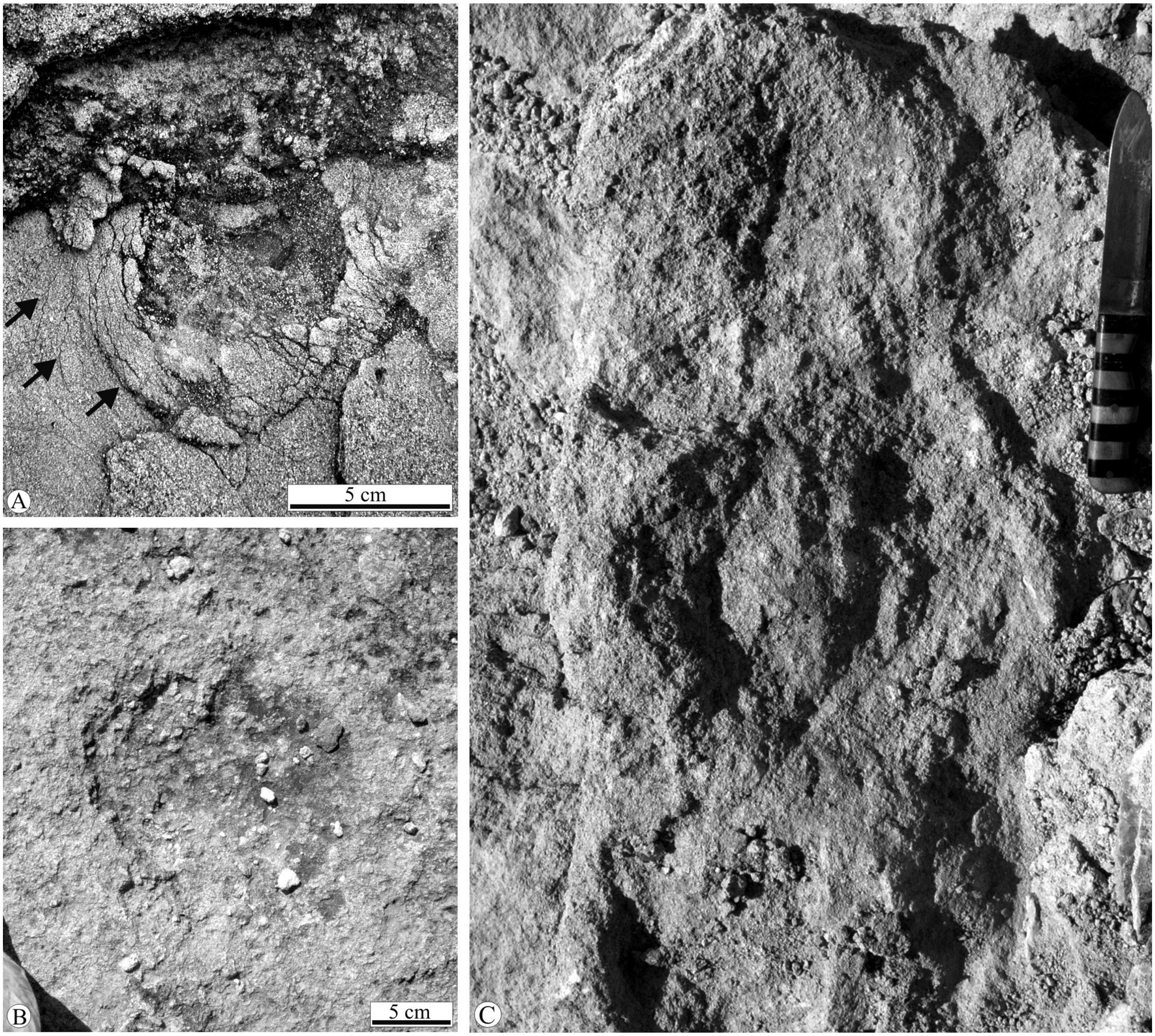

FIG. 7.—Four tracks were found exposed in horizontal view. Photos are not to scale. **A)** Track 7 cm wide. The track itself is partly filled with sediment and shows few morphologic details. The sediment surrounding the track was damp at the time of track formation, allowing the preservation of a series of concentric rings of displaced sediment and radiating fractures to be preserved around the track (arrows). **B)** Heavily weathered track 18 cm wide. The track shows no anatomical details, except for a vague division into two broad hooves, owing to the erosion of the grainstone. **C)** Slab containing two tracks. The first (middle of the picture) is 16 cm in diameter, divided into two distinct weakly divided crescent-shaped hoof impressions, which forms an almost flat bottom in the track. A prominent marginal ridge of displaced sediment is present surrounding the track. This track is interpreted as a camel track. The other track (below) is 12 cm wide, preserving no anatomical details. A partly preserved marginal ridge is present around the track.

diameter, to show the distribution of track sizes. The histograms show groupings of tracks indicating five distinct size classes: (1) small tracks from 4 to 7 cm in diameter; (2) a distinctive group having a diameter of 9 cm; (3) tracks 14–21 cm across; (4) a group of larger tracks 25–28 cm; and (5) some very large tracks ranging from 32 to 37 cm (Fig. 5A).

In contrast, an attempt to plot the diameter against depth of the tracks showed no sign of the size classes, indicating that diameter and depth of tracks were unrelated. Depth of a track is related to the weight of the trackmaker, the mode of progress and the presence, absence, and degree of erosion prior to burial of the track, but especially the consistency of the substrate. Eolian sediments, especially if dry, are far from an optimal medium for track preservation. A track formed in totally dry sand collapses immediately after lifting of the foot, leaving only a hole vaguely resembling the outline of the foot, whereas even

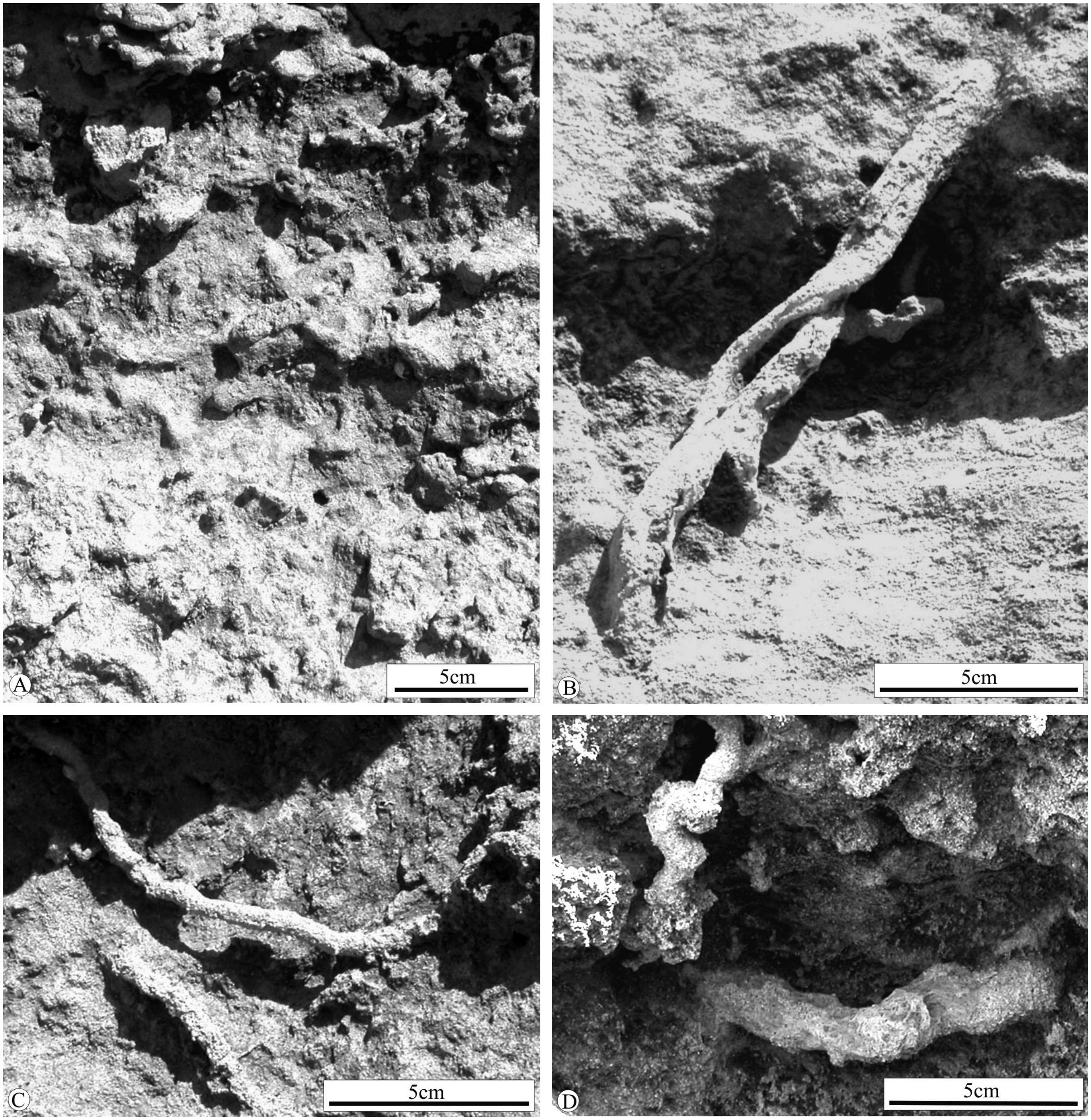

FIG. 8.—Root structures and possible invertebrate traces in the lowest paleosols. **A)** General total bioturbation of the paleosol. **B–D)** Various configurations of bush-size roots preserved as rhizoconcretions.

slightly damp sand can preserve well-defined tracks (Milàn, 2006). The problem is intensified by the dominance of ooids in the sediment, rendering it highly unstable. Clear preservation of the shaft is probably possible only in various states of dampness of the substrate.

It must be admitted that in weathered vertical section some inaccuracy is unavoidable in measurement of "diameter". It is usual that the orientation of the track is unknown and the width and length of the track are usually not the same. Nevertheless, the fact that distinctive size classes have indeed emerged from the measurement in hand indicates that the measurements are sufficiently accurate.

Because all the tracks, except for three, are exposed in vertical cross section, it is not possible to identify the trackmakers with any degree of accuracy on the basis of morphologic features in the tracks. However, the size and morphology of the bilobed track (Fig. 6C) bears resemblance to the morphology of purported Pleistocene camel tracks from New Mexico (Lucas et al. 2002) and the cameloid ichnogenus *Lamaichnium macropodium*, described from the Miocene of California (Sarjeant and Reynolds, 1999). Tracks and feet of a living camel was studied for comparison with the fossil track, and both the foot morphology and morphology of tracks emplaced in dry coarse sand closely resemble the specimen from the Kattavia Aeolinite (Fig. 9).

Although the main section is divided into three units by soil horizons (Fig. 2B), unit 1 is poorly exposed along only a short distance at the bottom of the section. The five tracks recorded from the small quarry on the other side of the road may belong to unit 1, but because the geometry of the dunes is complicated, this cannot be proved at this stage. Of the measurable five tracks from the quarry, the three are of similar size, 25 to 27 cm in diameter, and the two others respectively 5 and 8 cm (Fig. 5B). Unit 2 yielded 13 measurable tracks that seem to be randomly distributed all along the exposure. The tracks in unit 2 range in width from 10 to 28 cm, and of these, seven of the tracks are of relatively similar size, between 14 and 17 cm. Three tracks are smaller, having smaller cross sections between 10 and 13 cm, and the last three range from 23 to 28 cm in width (Fig. 5C).

Unit 3 contains 61 measurable tracks, the majority of tracks recorded. The diameters of the tracks range from 4 to 37 cm, and as a prominent difference from unit 2, a large number of the tracks (16) have a small cross section ranging between 4 and 7 cm. Five tracks peak out prominently with a diameter of 9 cm. Twenty-eight tracks fall between 10 and 23 cm, with the majority between 15 and 20 cm in diameter. The next grouping consists of 11 tracks between 25 and 28 cm, and last is the grouping of five large tracks from 32 to 37 cm in diameter (Fig. 5D).

The distribution of tracks in units 2 and 3 show two different patterns. The tracks in unit 2 are randomly distributed along the profile, whereas the tracks in unit 3 seem to cluster mainly in two groups in the section (Fig. 2B).

Because the vertical distribution of the tracks in the two groups is up to 4 m, the distribution cannot be explained as a single trampling event, but perhaps this stacked succession of tracks represents a preferred migration route or favorable topography, which was maintained even after new sands were deposited.

When comparing the size groups of tracks in the quarry, and the two track-bearing units, the tracks in the quarry indicate two different size groups of trackmakers, one having sizes about 25 to 27 cm and smaller trackmakers having sizes around 5 to 8 cm. Unit 2 bears evidence of two, perhaps three, distinct sizes of trackmakers, one group having sizes between 14 and 17 cm and a larger group having sizes between 23 and 28 cm; the three smallest tracks between 10 and 13 cm represent perhaps a third, smaller group of trackmakers. The composition of track sizes in unit 3 is more varied than in the quarry and in unit 2. Especially striking are the large number of small tracks less than 10 cm in diameter and the group of large tracks up to 37 cm in cross section.

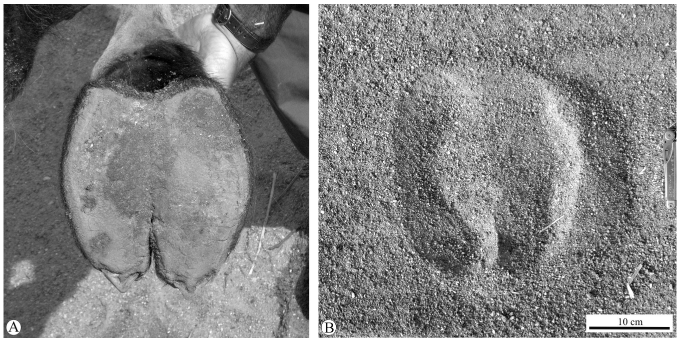

FIG. 9.—Foot and footprint of a living camel from the Zoological Gardens, Copenhagen. **A)** The camel foot consists of two broad, weakly divided digital pads, each terminating in short triangular claws. The foot has a subcircular outline. **B)** Track from the same foot emplaced in the coarse sand within the camel paddock. Even if the footprint is partly collapsed in the dry sand, it retains the distinctive shape of the two weakly divided digital pads and the almost flat bottom of the track; compare with Figure 7C.

Assuming from the preliminary sedimentologic investigations that the three eolian units represent three different time periods, a difference in faunal composition should be expected. The track fauna of unit 3 differs from that of unit 2 in that the size variation in the tracks is much larger. In unit 2 the tracks range from 10 to 28 cm in cross section, and the size range in unit 3 is from 4 to 37 cm in cross section. In particular, the whole group of small tracks having a cross section less than 10 cm is missing altogether in unit 2, as are also the very large tracks above 28 cm in cross section. On the basis of the recorded sizes of the tracks in the different units, it is evident that the size distribution of trackmakers, and thus animal diversity, was highest in the time period when unit 3 was deposited.

The camel track (Fig. 7C) is 16 cm in diameter, and tracks near that size are the dominant size in units 2 and 3 and are in total the most abundant track size (Fig. 5A). Interestingly, no track in "camel" size was observed in the quarry, but the exposure in the quarry is limited in extent and the five measurable tracks recorded there are probably not representative of the whole fauna of that unit.

No skeletal remains have been found associated with the footprints in the eolianite, but exposures of the Pliocene Apolakkia Formation in the basin south of Apolakkia (Fig. 1) have yielded an extensive mammal fauna (van de Weerd et al., 1982), while a balanced mainland fauna is known from Late Miocene and Pliocene localities of Rhodes (Desio, 1931; Boni, 1943; Meulenkamp et al., 1972), and according to Sondaar and Dermitzakis (1982) also from Early Pleistocene. The Damatria airport fauna includes a balanced fauna with *Equus* and *Leptobos*. This fauna should be placed in Pleistocene (Dermitzakis and Sondaar, 1978, p. 823). The Damatria formation is overlain by the Kritika formation, which is considered Upper Pliocene, in the sense of the marine Mediterranean stratigraphy (Meulenkamp et al., 1972; Dermitzakis and Sondaar, 1978). The mammal fauna from the Apolakkia Formation, described by van de Weerd et al. (1982), contains five genera of insectivores, one lagomorph species, and four genera of rodents. Large carnivores are represented by hyenas and canids, and in addition, Richter (1997) found a canine from a sabertooth cat. Ungulates are represented by *Hipparion*, *Cervus*, *Gazella*, and indeterminate species of Rhinoceratidea and Proboscidea (van de Weerd et al., 1982). The largest tracks, having a diameter from 32 to 37 cm, are considered to be of proboscidean origin, and abundant finds of skeletal material of Pliocene and Pleistocene proboscideans demonstrates their presence on the island (Kuss, 1975; Symeonidis et al., 1974; van de Weerd et al., 1982) and later finds of proboscidean material allowed the identification of *Anancus arvernensis* (Theodorou et al., 2000). The endemic elephant *Palaeoloxodon antiquus maidriensis* was discovered in 1974 at the Ladiko cave. At present, existing findings point to an average size of elephant of about 180 cm (Theodorou, 1983), but the available elephant material from Rhodes is not adequate to estimate the size variation among the elephants from Rhodes. This means that we can expect findings of both larger and smaller elephants than these already available, and thus expand the range of sizes of tracks expected to be of proboscidean origin.

The small- to medium-size tracks, 4–10 cm, occurring in the quarry and in unit 3 are comparable in size and shape to the Pleistocene caprine tracks described from eolian sediment in Mallorca (Fornós et al. 2002), and the presence of cervids and *Gazella* (Kuss, 1975; Symeonidis et al., 1974; van de Weerd et al., 1982) in the paleofauna makes them possible trackmakers, but, from the above mentioned, possibly only *Cervus* and the dwarf elephants have been documented for the Pleistocene of Rhodes. The balanced late Ruscinian fauna of Damatria airport became extinct during the Pleistocene when Rhodes became an island (Dermitzakis and Sondaar, 1978).

No camel remains have hitherto been described from Rhodes, but camel remains are known from the Upper Miocene of Turkey (van der Made et al., 2002); therefore, the possibility that another even-toed animal could be responsible for the tracks must be considered. Cervids have been found both from the Pleistocene fissure fillings at the Kritinia coast and from the Apolakkia Formation, deposited during the Pliocene (van de Weerd et al., 1982), and because both camels and deer (in the broad sense) are artiodactyls, their footprints all reflect the even-toed morphology of two hoofs. However, a number of differences distinguish cameloid footprints from deer footprints. The hoof of a deer is covered with horn, forming two distinct crescent-shaped impressions facing each other, with a prominent gap between the digits, which are preserved in the footprints as a raised ridge. Furthermore, the outline of a deer footprint is normally oval to pear shaped, and the individual hoof impressions have pointed tips. In contrast, the foot sole of a camel consists of two broad fleshy digital pads, which are almost grown together, and thus leaves footprints without a central raised ridge (Fig. 9). Only reindeer, *Rangifer tarandus*, has a footprint with a nearly circular outline, but their hoof impressions are widely crescent shaped and divided by a broad central ridge (Rezendes, 1999). The bottom of the footprint described herein is flat without indications of a prominent central ridge. The division of the two digital pads are indicated only in the ends of the footprint (Fig. 9).

In a deer, even where the footprint was emplaced in dry sand, which would collapse after removal of the foot, a raised ridge formed between the digit impressions would still be visible. A vertical section through a deer footprint, cut perpendicular to the walking direction, would show the bottom of the footprint to be W-shaped, and not flat-bottomed with sloping trackwalls as seen in both the fossil and the recent camel tracks (Fig. 9A, B). Furthermore, the shape of the track described herein is consistent with the shape of cameloid tracks described by Sarjeant and Reynolds (1999) and Lucas et al. (2002). All considered, this makes it most likely that a camel is the trackmaker of the footprint described herein. Future finds of either skeletal material or more tracks and trackways might either strengthen or weaken this identification.

A possibility for the occurrence of camel tracks on Rhodes is that they belong to camels introduced by humans. Camels have never been found in an unbalanced endemic fauna. Thus, they could represent a relict of an older, balanced, mainland population, or, much more probably, these tracks might belong to camels introduced on Rhodes by man. However, the last possibility would give a very young age for the deposits, which does not correspond with the scenario described herein for the deposition of the eolianite. Further studies by J. Titschack and colleagues may shed light on this problem when a definitive age of the Kattavia eolinite is determined.

The abundance of cross sections through tracks of size similar to those of the identified camel track indicates that camels were indeed present as part of the Pleistocene mammal fauna on Rhodes.

CONCLUSION

The new Kattavia eolianite is suggested to be of Late Pleistocene to Early Holocene age. It consists of three distinct units separated by soil horizons rich in rhizoliths and gastropod shells. The various units are considered to have been deposited during glacial periods, and the soil horizons formed during the warmer interglacials.

The eolianite contains ichnological evidence of a diverse vertebrate fauna, comprising footprints ranging from 4 to 37 cm in diametric cross section. The size range is largest in unit 3, suggesting a larger diversity in the vertebrate fauna during that period.

The largest of the tracks are interpreted to have been made by proboscideans, the medium-size endemic Pleistocene elephants of the island. One well-preserved footprint, exposed on a horizontal surface, is identified as a track from a camel, and this, together with abundant similar-size tracks exposed in cross section, represents the first evidence of camels on Rhodes.

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