

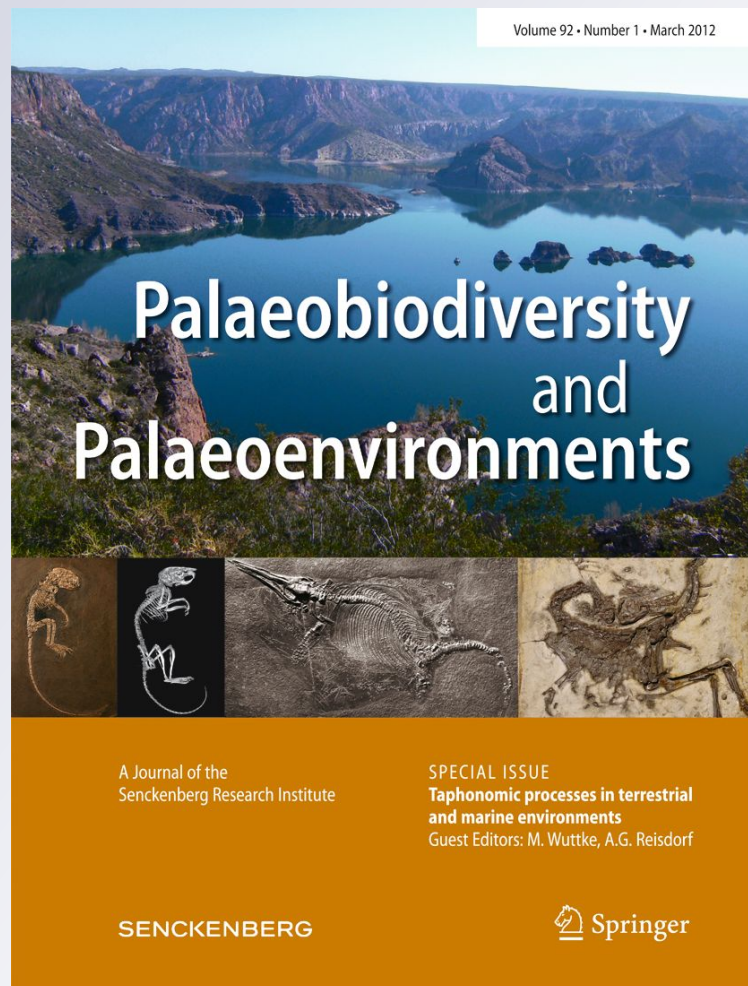
*First occurrence of carnivore footprint with
hyaenid affinities from the Late Miocene of
Crete (Greece)*

**George Iliopoulos, Socrates Roussiakis &
Charalampos Fassoulas**

**Palaeobiodiversity and
Palaeoenvironments**

ISSN 1867-1594

Palaeobio Palaeoenv
DOI 10.1007/s12549-012-0073-9



Your article is protected by copyright and all rights are held exclusively by Senckenberg, Gesellschaft für Naturforschung and Springer. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

First occurrence of carnivore footprint with hyaenid affinities from the Late Miocene of Crete (Greece)

George Iliopoulos · Socrates Roussiakis ·
Charalampos Fassoulas

Received: 25 October 2011 / Accepted: 2 February 2012
© Senckenberg Gesellschaft für Naturforschung and Springer 2012

Abstract Nine terrestrial mammal localities of Miocene age based on body fossils have been reported from the island of Crete to date. A new locality where footprints of terrestrial mammals were exposed has recently been discovered in western Crete. Platýlakkos, the locality, is situated near the village Vouves, west of the city of Chaniá. The ichnofossils come from lacustrine deposits that belong to the Chátzi Formation. The most impressive finding is a clearly defined footprint that might be referred to a large-sized hyaenid. The footprint impression, a convex hyporelief on a sandstone slab, is a natural cast of a left manus where the traces of the interdigital pad and all four digital pads, as well as their respective claw marks- are clearly visible. Based on nearby marine deposits of the Chátzi Formation, the age of the fossiliferous layer with the footprints can be considered to be early to middle Turolian (MN11–MN12) in terms of mammalian biochronology. To date, there is no certain record of Miocene large-sized hyaenid footprints worldwide, and

thus this isolated footprint might belong to a new ichnotaxon. However, in the absence of a trackway, the erection of a new ichnotaxon is avoided. The Platýlakkos findings are the first recorded case of fossil land mammal footprints from the Neogene of Crete, and Greece in general. They further the evidence for the presence of well-established terrestrial environments and faunas in the area of Crete during the Late Miocene.

Keywords Palaeoichnology · Footprint · Carnivores · Late Miocene · Crete · Greece

Introduction

The island of Crete is well known for its Quaternary unbalanced endemic land mammalian faunas, consisting mainly of dwarf elephants, deer and hippos, and endemic micro-mammals, indicating that, during Quaternary times, Crete was an island. More than 100 localities with such endemic faunas are known, mainly from the northern coast of the island (Dermitzakis 1977; Iliopoulos et al. 2010a; Lax 1996). By contrast, only 10 Miocene land mammal localities are known in Crete: nine body fossil localities and the new Platýlakkos ichnofossil locality described here (Fig. 1). Their age spans from Middle to Late Miocene and their faunas exhibit clear mainland affinities, indicating that during that epoch Crete was still connected to the continental mainland.

In Lassithi prefecture (eastern Crete), five localities are known, namely Petrás, Aghia Photiá, Maroniá, Géla, and Zákros. Petrás locality has yielded only a suid tooth (Leinders and Meulenkamp 1978). It was referred subsequently to *Microstonyx cf. major* by van der Made (1996), who considered that the most likely age of Petrás is Late

This article is a contribution to the special issue “Proceedings of the 9th EAVP Meeting, Heraklion 2011”

G. Iliopoulos (✉)
Department of Geology, University of Patras,
26500 Rio-Patras, Greece
e-mail: iliopoulosg@upatras.gr

S. Roussiakis
Department of Historical Geology and Palaeontology, Faculty of
Geology and Geoenvironment, National and Kapodistrian
University of Athens,
Panepistimiopolis,
15784 Athens, Greece
e-mail: srousiak@geol.uoa.gr

C. Fassoulas
Natural History Museum of Crete, University of Crete,
71409 Heraklion, Greece
e-mail: fassoulas@nhmc.uoc.gr



Fig. 1 The island of Crete showing the distribution of the terrestrial Miocene mammal localities. 1 Platýlakkos, 2 VrýsSES, 3 Plakiás, 4 Melámbes, 5 Kastéllios Hill, 6 Maroniá, 7 Petrás, 8 Aghia Photiá, 9 Géla, 10 Zákros. Data according to Athanassiou (2004), Benda et al.

(1970), Bonneau and Ginsburg (1974), de Bruijn and Meulenkamp (1972), de Bruijn and Zachariasse (1979), de Bruijn et al. (1971), Fassoulas and Iliopoulos (2011), Kuss (1976), Leinders and Meulenkamp (1978), Poulakakis et al. (2005), and personal observations

Miocene and more specifically late Vallesian (MN10) or early Turolian (MN11). Additional suid remains from Aghia Photiá were also referred to *Microstonyx* cf. *major* by Fassoulas and Iliopoulos (2011). Maroniá has yielded a lower molar of *Deinotherium giganteum* which is considered to be of Late Miocene age (Athanassiou 2004). Further *D. giganteum* remains were found in Géla which are considered of late Vallesian (MN10) or early Turolian age (MN11), as well as in Zákros (Fassoulas and Iliopoulos 2011; Iliopoulos et al. *in press*; Poulakakis et al. 2005).

The most important and taxonomically diversified Miocene land mammal locality in Crete is the Kastéllios Hill locality in central Crete (Heráklion prefecture). Fossils of large mammals and micromammals were collected from four different stratigraphic levels, from the eastern slope of Kastéllios Hill, as well as from the surface (de Bruijn et al. 1971; de Bruijn and Zachariasse 1979). According to van der Made (1996), the large mammal fauna (collectively) includes *Hipparion* sp., cf. *Dorcabune anthracotheroides*, cf. *Pliocervus pentelici*, *Taucanamo?* / *Yunnanchoerus?* sp., Bovidae *indet.* and Carnivora *indet.* van der Made (1996) provided an age between late early Vallesian (late MN9) or early late Vallesian (early MN10) for the older Kastéllios faunas to probably Turolian for some Kastéllios specimens.

In Réthymnon prefecture, two Miocene land mammal localities are known, namely Melámbes and Plakiás. According to van der Made (1996), the Melámbes fauna contains *Dorcatherium nauai*, cf. *Prohyrax hendeyi*, and Bovidae *indet.* (but see also Bonneau and Ginsburg 1974; Fischer and Heizmann 1992; Kuss 1976). The locality was long considered to be of Vallesian age (Bonneau and Ginsburg 1974), but according to van der Made (1996, 1999) it could be older, probably early Astaracian (MN6) or early in MN7/8. The Plakiás mammal fauna contains mainly

micromammals, but a suid tooth referred to cf. *Propotamochoerus palaeochoerus* is also reported (de Bruijn and Meulenkamp 1972; van der Made 1996). According to van der Made (1996), the most likely age for Plakiás is late Astaracian (late MN7/8). Recently, however, de Bruijn et al. (2012) provided an early Vallesian age (MN9) for the locality, based on the study of the micromammals.

In Chaniá prefecture (western Crete), two Miocene mammal localities are known, VrýsSES and the Platýlakkos ichnofossil locality described here. The VrýsSES locality has yielded some proboscidean molar fragments (in fact, found in a lignite mine near the village of Mása). These were referred by Benda et al. (1970) to *Mastodon* sp., but they might be better referred to as Gomphotheriidae *indet.* The locality is considered of Late Miocene age by van der Made (1996). Zidianakis et al. (2007) described a leaf impression flora of late Tortonian-Messinian age (6–7.5 Ma) from a nearby locality. They considered the proboscidean remains from VrýsSES to be of about the same age, which according to the mammalian biostratigraphy would be from middle Turolian (MN12) to early late Turolian (early MN13). Finally, Platýlakkos is a recently discovered ichnofossil locality (2009). The first data concerning its faunal context were presented by Iliopoulos et al. (2010b, 2011). The findings include the carnivore footprint described here, as well as two artiodactyl footprints. Unfortunately, the latter are poorly preserved to be described adequately.

Geological setting

The Platýlakkos ichnofossil locality is situated 1 km southwest of the village of Voúves and about 22 km west of the city of Chaniá (Fig. 1). The actual locality is located at an artificial section which was revealed during earthworks that exposed

the local rocks and which separates two terraces with olive groves. The section reveals layers with a total thickness of 4 m that form a symmetrical, north plunging, gentle fold; the ichnofossils were traced on the east limb of the fold (Fig. 2). Geologically, the study area is located in the Neogene basin of Kastélli that covers the northwest part of the island. The fossiliferous layers belong to the Chátzi Formation (Freudenthal 1969), which can be separated into two units: a lower coarse clastic sequence consisting of conglomerates, marls and clays; and an upper finer one with silts, clays and sandstones, exposing locally on top gypsum deposits (Freudenthal 1969). The fossiliferous layers are found at the upper part of the formation several meters below the characteristic gypsum layer. The sediments of the section consist of alterations of cemented thick sandy layers and yellow silty clays without the presence of any obvious macrofossil findings (Figs. 2 and 3). The two lower clay beds contain horizons of thin platy lenses of cemented sands. The respective footprints were identified on the lower or the upper surface of these sands either with the form of natural casts (convex hyporeliefs) or moulds (concave epireliefs). Thus, based on the lithological characters, it is clear that the sediments were deposited in a lacustrine environment. Furthermore, the sedimentological regime indicates that during the deposition repeated cycles of sedimentation prevailed reflecting changes in the influx and grain size of the sediments due to periodic changes of the local environment.

Systematic palaeoichnology

Division Vertebratichnia Vialov, 1966

Class Mammalipedia Vialov, 1966

Order Carnivoripedida Vialov, 1966

Ichnogenus and ichnospecies *indet.*



Fig. 2 View of the fossiliferous locality at Platýlakkos (the arrow shows the fossiliferous layer)

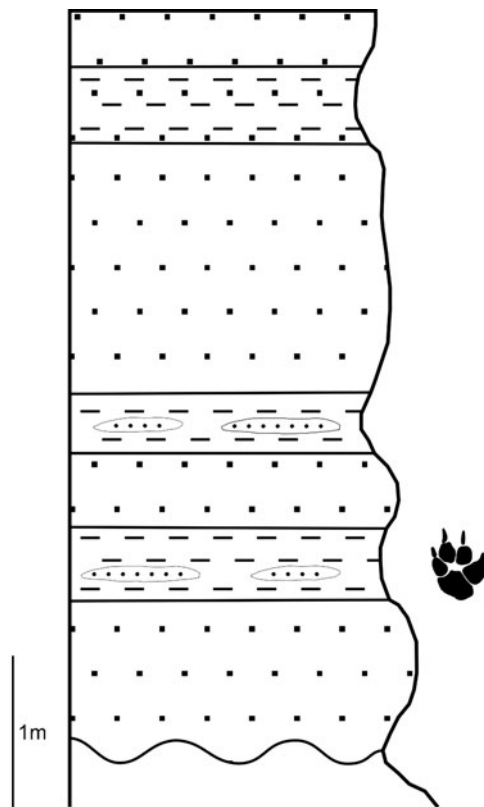


Fig. 3 Stratigraphic column of the section at Platýlakkos with the ichnofossil bearing layer. The dashed line depicts siltstone layers and the dotted lines sandstones. The footprint drawing pinpoints the fossiliferous layer

Material: NHMC 29.1.3.22. Isolated footprint impression preserved on a sandstone slab (Fig. 4). Specimen stored in the Natural History Museum of Crete.

Locality: Platýlakkos, near Voúves village, Prefecture of Chaniá, Eastern Crete.

Stratigraphic level: Chátzi Formation, Upper Miocene.

Preservation: The Platýlakkos specimen is preserved as natural cast (convex hyporeliefs) in a sandstone slab (Fig. 4). The footprint represents a left manus paw-print of a large-sized carnivorous trackmaker. It exhibits the interdigital pad, four rather massive digital pads (corresponding to digits II–V), and four claw marks indicating non-retracted claws (Figs. 4 and 5). The casts of the digital pad II, digital pad III and its claw, and digital pad IV represent true prints. Claw cast of digit IV is broken, but its outline is clearly visible. The cast of the digital pad V and its claw, the cast of the interdigital pad, and the claw cast of digit II are “ghost prints”. It can be considered that the ghost prints are covered by a few deformed thin layers found below the level of the actual footprint.

Description: The overall paw-print is practically equal in length and width (Figs. 4 and 5). The claw casts of digits III and IV are elongated, transversely narrow, and directed

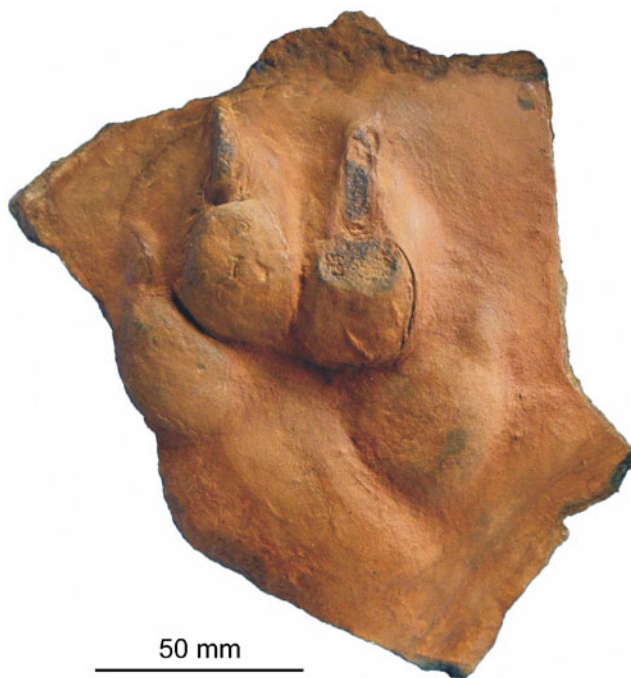
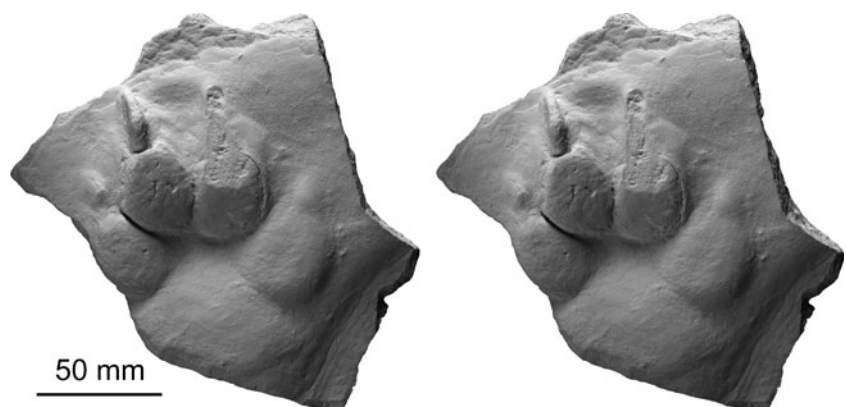


Fig. 4 Natural cast (convex hyporelief) of the carnivore manus footprint (NHMC 29.1.3.22) found in Platýlakkos (western Crete, Chaniá, prefecture)

rather forward. The claw casts of digits II and V are not well defined. The claw cast of digit III, which is well imprinted, is especially high.

The digital pads are close to each other. The outer digital pads (II and V) diverge strongly outwards and are also close to the interdigital pad, while the central digital pads (III and IV) diverge slightly relative to each another and are imprinted more anteriorly. Digital pad III extends anteriorly more than digital pad IV. Digital pad III impression is ovoidal and rather similar in size to the more quadrangular digital pad IV. Digital pad II is similar in length to digital pads III and IV, but narrower, and rather semicircular with slightly concave inner (antero-lateral) border. Digital pad V is the largest, in both length and width, and has a more trapezoidal outline with slightly concave inner (antero-

Fig. 5 Natural cast (convex hyporelief) of the carnivore manus footprint found in Platýlakkos (western Crete, Chaniá, prefecture). Stereopair views, based on a plaster cast of the original specimen



medial) border. The central digital pads (III and IV) are higher in relief than the outer pads (II and V) and the interdigital pad. Their longitudinal profile is slightly convex and symmetrical, but being higher toward the claws, they slope strongly posteriorly. Transversely, they are asymmetrical and medially higher. The relief of the digital pad II is similar, but less asymmetrical transversely. Digital pad V is slightly asymmetrical longitudinally and somewhat higher at its posterior third. Transversely, it appears strongly asymmetrical. It is higher outwards (laterally) and slopes strongly inwards (medially), where it appears rather flat.

The interdigital pad is large, sub-triangular and asymmetrical in outline, with concave antero-lateral and antero-medial borders. While its posterior part is broken, it is adequately preserved postero-laterally, which suggests that there were no posterior lobes. It is equal in height to the outer digital pads. Its longitudinal profile is gently convex, but asymmetrical and higher at its posterior portion. Its transverse profile is also convex and asymmetrical. It is higher postero-laterally, behind the digital pad V impression.

Dimensions: Maximum print length: about 126 mm. Print length excluding the claws: about 98 mm. Maximum print width: 95 mm. Length of digits: II, 35 mm; III, 36 mm; IV, 34 mm; V, 38 mm. Width of digits: II, 25 mm; III, 28 mm; IV, 28 mm; V, 38 mm. Interdigital pad length: ≥ 54 mm. Interdigital pad width: about 68 mm. Observed claw length: II, about 17 mm; III, 26 mm; IV, 25 mm; V, about 17 mm.

Discussion

As mentioned above, the sediments of the section where the Platýlakkos fossiliferous layer was found belong to the Chátzi Formation. According to Freudenthal (1969), the age of the Chátzi Formation is Late Miocene and more specifically Tortonian–Messinian. The characteristic gypsum layer found in the vicinity of Platýlakkos is stratigraphically above the ichnofossil layer and its age has been determined as early Messinian (Freudenthal 1969; Frydas

and Keupp 1996). Thus, the age of the ichnofossil layer could plausibly be referred to as late Tortonian or earliest Messinian, and it could be correlated with the early Turolian–middle Turolian (MN11–MN12) in terms of mammalian biochronology.

Vertebrate palaeoichnology is a poorly explored palaeontological discipline in Greece. The only studied fossil vertebrate footprints from Greece to date come from the island of Rhodes. The findings include tracks of proboscideans and artiodactyls preserved in eolian deposits of Late Pleistocene to early Holocene age (Milàn et al. 2005; Milàn et al. 2007), and subfossil Holocene footprints of humans and cattle preserved in beachrocks (Bromley et al. 2009).

The described Platýlakkos fossil carnivore footprint (Fig. 4) represents the first unequivocal Miocene terrestrial mammal footprint recorded, not only in Crete but in Greece generally. On morphological grounds, it exhibits well-preserved claw marks that suggest non-retracted claws; rather massive and closely arranged digital pads; and an asymmetrical interdigital pad that, while not preserved in full, does not suggest the presence of lobes posteriorly (typical of extant felid footprints) (Fig. 6). Its morphology resembles that of footprints made by extant hyaenids (Fig. 6), while its size is comparable to that of the extant spotted hyaena, *Crocuta crocuta*. Footprints of fossil large-sized hyaenids are generally extremely rare, but known from

the Pliocene and Pleistocene of Africa and the Pleistocene of Europe (McDonald et al. 2007; Roberts 2008). Footprints with possible hyaenid affinities have been referred from the Late Miocene of Mushampa in Iran (Abbassi 2010) and the Early Miocene of Salinas de Añana in Spain (Anton et al. 2004), but generally the pre-Pliocene record of hyaenid footprints is questionable. The possible trackmakers of various carnivore footprints, referred to various ichnotaxa, remain of uncertain affinities, and a revision of the fossil carnivore footprints is strongly recommended. Carnivores are poorly represented in the Miocene fossil record of Crete. The only known specimens are some dental and mandibular fragments from Kastéllios Hill, but their fragmentary nature precludes any secure assignment even to family level. They are comparable in size (van der Made 1996) to the felid *Pseudaelurus quadridentatus* and the hyaenid *Protictitherium gaillardi*. However, both taxa represent rather small-sized carnivores and should be excluded as possible trackmakers of the Platýlakkos footprint. One could look for the Platýlakkos trackmaker among the large-sized hyaenids that have been recorded in other Greek Miocene localities. The most common of these large-sized hyaenids is *Adcrocuta eximia*. This species is known from many Greek Late Miocene localities (e.g. Pikérmi, Sámos, Ravin da la Pluie, Xirochóri-1), which span in age from late Vallesian (MN10) to middle Turolian (MN12) (Koufos 2003, 2006), as well as worldwide from Spain to China. Its skeleton is adequately known and comparable in size with that of the extant spotted hyaena, *C. crocuta* (Gaudry 1862–67; Pilgrim 1931). Unfortunately, the skeletons of other rather large-sized Late Miocene hyaenids recorded in Greece, such as *Hyaenictis* and *Chasmaporthetes*, are unknown. Neither *A. eximia* nor other large-sized hyaenids are known from the Miocene mammalian fossil record of Crete; hence, it would be premature to refer the hypothetical Platýlakkos trackmaker to any of these taxa. Nevertheless, the Platýlakkos footprint is of particular importance, given that fossil mammalian footprints are generally scarce. In fact, until recently, there were only about 60 such localities known around the world and fewer than 20 in Europe (Costeur et al. 2009). Thus, it is evident that footprint localities are extremely few compared to the thousands of body fossil localities known (Costeur et al. 2009). The Platýlakkos footprint could represent a new ichnotaxon. However, as at present there is only one footprint available and not a trackway, the erection of a new ichnotaxon should be avoided.

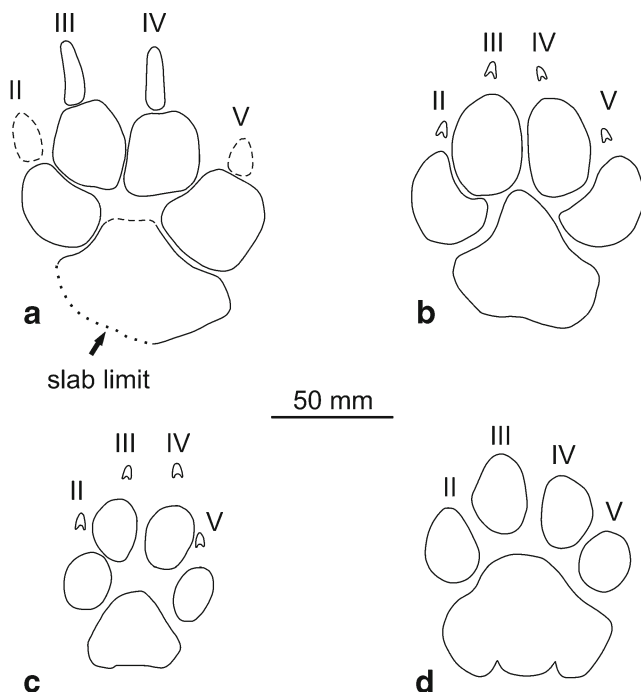


Fig. 6 Comparison of the Platýlakkos footprint with manus footprints of selected extant carnivores. **a** Platýlakkos footprint, **b** spotted hyaena, *Crocuta crocuta*, **c** wild dog, *Lycaon pictus*, **d** leopard, *Panthera pardus*. All figured as representing the right manus. **b–d** According to Stuart and Stuart (2000). Roman numerals indicate the digits. Dashed lines indicate indistinct outlines, dotted line indicates the slab limit

Palaeogeographical and palaeoecological implications

As mentioned above, the hyaenid footprint is not the only track found in the Platýlakkos locality. In addition, two footprints of artiodactyls have been discovered, but they are not sufficiently

well preserved to be described. However, their presence is important as it shows that the presence of the hyaenid footprint was not accidental, and it is possible that the area during the Late Miocene was part of a healthy ecosystem that maintained a balanced fauna. These, as well as other continental Late Miocene mammalian faunas of the island, indicate that at that time western Crete was connected by a land bridge to the mainland, presumably through Peloponnesus.

The sedimentological features of the fossiliferous layer of Platýlakkos indicate that the tracks were produced on fine-grained and laminated sandy clays near the shore of a lake. Such morphological definition indicates that the footprints were formed within the strandline of the lake where water-saturated sediments existed (Cohen et al. 1991). Exposed tracks are susceptible to destruction by physical and biological factors, hence the survivorship of tracks often does not exceed 1 week and in rare cases 2–3 weeks at most (Cohen et al. 1991). In the case of Platýlakkos, the preservation of the footprints should include quick burial, within a few days from their actual formation, possibly from a sudden flood that covered the shore and thus the tracks with sandy sediments, and formed the sandy lenses that are found in the fossiliferous layer. Palaeofloral data for the Late Miocene of western Crete and in particular for the composition of the Vrysses plant assemblage (about 40 km southeast of Platýlakkos) indicate a warm-temperate, humid climate for that time, with less pronounced seasonality than today (Zidianakis et al. 2007). As mentioned above, the footprints were formed in the vicinity of a water body, which facilitated their preservation. This is in agreement with the proposed humid climate for western Crete that would ensure the presence of water bodies and would facilitate the quick burial of footprints during flood events.

Conclusions

The Platýlakkos locality is the tenth Miocene land mammal locality in Crete, but the first based on footprints. It has provided footprints of artiodactyls and the footprint of a large-sized carnivore. These represent the first recorded cases of Miocene land mammal footprints discovered in Greece. The footprints come from lacustrine deposits that belong to the Chátzi Formation. Based on previously studied nearby marine sediments (Freudenthal 1969), the most likely age of the fossiliferous layer is early to middle Turolian (MN11–MN12). The carnivore footprint is referred to the order Carnivoripedia. Its morphology and size indicates that the trackmaker had hyaenid affinities and was similar in body size to the extant spotted hyaena, *C. crocuta*. Even though the hypothetical trackmaker can not be identified with certainty, its discovery is of particular significance since Neogene large-sized hyaenid footprints are extremely rare. The presence at the locality of both artiodactyl and

carnivore footprints indicates that during that time there was an ecosystem in western Crete that maintained a balanced fauna, which is in accordance with data from other Late Miocene mammalian and plant terrestrial localities in western Crete (Benda et al. 1970; Zidianakis et al. 2007). Furthermore, it provides additional evidence that, during the Late Miocene, western Crete was still connected to the mainland through Peloponnesus.

Acknowledgements We would like to thank the owner of the olive grove, Mr. Stylianos Perakis, who provided the information about the hyaenid footprint and allowed us to take samples from his property, as well as for his support in this study. We would also like to express our gratitude to the Chania Chamber of Commerce and Industry, and to its Chairman, Evangelos Spanoudakis, for funding the research project “Palaeontological survey of Chania Prefecture” (KA 2412) of the Natural History Museum of Crete of the University of Crete, which covered the fieldwork expenses of this study. Furthermore, the authors would like to thank the reviewers of this paper, Dr. Loïc Costeur (Naturhistorisches Museum Basel, Basel) and Dr. Martin Lockley (University of Colorado, Denver), for their useful comments and suggestions that improved the manuscript.

References

- Abbassi N (2010) Vertebrate footprints from the Miocene Upper Red Formation, Shokorch area, Zanjan Province, NW Iran. *Ichnos* 17:115–126
- Anton M, López G, Santamaria R (2004) Carnivore trackways from the Miocene site of Salinas de Añana (Alava, Spain). *Ichnos* 11:371–384
- Athanassiou A (2004) On a *Deinotherium* (Proboscidea) finding in the Neogene of Crete. *Carnets Géol Noteb Geol Lett* 5:1–7
- Benda L, Hiltermann H, Kuss SE, Symeonidis NK (1970) Der erste Mastodon-Fund der Insel Kreta. *Ann Géol Pays Hellén* 21:167–177
- Bonneau M, Ginsburg L (1974) Découverte de *Dorcatherium puyhauberti* Arambourg et Piveteau (Mammalia) dans les faciès continentaux de base de la molasse tertiaire de Crète (Grèce): Conséquences stratigraphiques et tectoniques. *C R Soc Geol Fr* 11–12
- Bromley RG, Milàn J, Uchman A, Hansen KS (2009) Rheotactic *Macaronichnus*, and human and cattle trackways in Holocene beachrock, Greece: reconstruction of palaeoshoreline orientation. *Ichnos* 16:103–117
- Cohen A, Lockley M, Halfpenny J, Michel AE (1991) Modern vertebrate track taphonomy at Lake Manyara, Tanzania. *Palaaios* 6:371–389
- Costeur L, Balme C, Legal S (2009) Early Oligocene mammal tracks from Southeastern France. *Ichnos* 16:257–267
- de Bruijn H, Meulenkamp JE (1972) Late Miocene rodents from the Pandanassa Formation (Prov. Rethymnon), Crete, Greece. *Proc Koninkl Nederl Akad Wetenschappen B* 75(1):54–60
- de Bruijn H, Zachariasse WJ (1979) The correlation of marine and continental biozones of Kastellios Hill reconsidered. *Ann Géol Pays Hell Sér* 1:219–226
- de Bruijn H, Sondaar PY, Zachariasse WJ (1971) Mammalia and foraminifera from the Neogene of Kastellios hill, (Crete), a correlation of continental and marine biozones. *Proc Koninkl Nederl Akad Wetenschappen B* 74(5):1–22

- de Bruijn H, Doukas CS, van den Hoek Ostende LW, Zachariasse WJ (2012) New finds of rodents and insectivores from the Upper Miocene at Plakias (Crete, Greece). *Swiss J Palaeont* DOI: 10.1007/s13358-011-0030-7
- Dermitzakis MD (1977) The quaternary fossil mammals in the caves and karstic holes of Crete Island and their significance. *Bull Soc Spéleol Grèce* 14:152–190
- Fassoulas C, Iliopoulos G (2011) The excavations of *Deinotherium giganteum* from Siteia: life and environment in Crete during the Miocene. *Proc 10th Int Cretol Congr, Chania 1-8/10/2006, Vol A1*, pp 15–29
- Fischer MS, Heizmann EPJ (1992) Über neogene Hyracoiden (Mammalia). Die Gattung *Pliohyrax*. *N Jb Geol Paläont* 186(3):321–344
- Freudenthal T (1969) Stratigraphy of Neogene deposits in the Khania province, Crete, the special reference to foraminifera of the family Planorbulinidae and the genus *Heterostegina*. *Utrecht Micropal Bull vol 1*. Schotanus & Jens, Utrecht
- Frydas D, Keupp H (1996) Biostratigraphical results in Late Neogene Deposits of NW Crete, Greece, based on calcareous nannofossils. *Berliner Geowiss Abh E* 18:169–189
- Gaudry A (1862–67) *Animaux Fossiles et Géologie de l'Attique*. Savy, Paris
- Iliopoulos G, Eikamp H, Fassoulas C (2010a) A new Late Pleistocene mammal locality from western Crete. *Bull Geol Soc Greece, Proc 12th Int Congr Patras, May, 2010*, pp 1–7
- Iliopoulos G, Roussiakis S, Fassoulas C (2010b) Large mammal footprints from the Late Miocene of Western Crete. XIX Congress of the Carpatho-Balkan Geological Association, Thessaloniki, Greece. *Geol Balc* 39(1–2):164, Abstr Vol
- Iliopoulos G, Roussiakis S, Fassoulas C (2011) Hyaenid footprint from the Late Miocene of Western Crete. *European Association of Vertebrate Palaeontologists, 9th Annual Meeting, Heraklion, Crete, 14–19 June 2011, Abstracts*, pp 30–31
- Iliopoulos G, Fassoulas C, Lyberakis P, Poulakakis N (in press) A complete skeleton of *Deinotherium giganteum* (Proboscidea, Mammalia) from the Late Miocene of Siteia (Crete Island, Greece). *Proc 6th Eur Geoparks Meet, Lesvos Island 5-8/10/2005*
- Koufos GD (2003) Late Miocene mammal events and biostratigraphy in the Eastern Mediterranean. *Deinsea* 10:343–371
- Koufos GD (2006) The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. *Hell J Geosci* 41(1):183–214
- Kuss SE (1976) Ein erster Fund von *Pliohyrax* aus dem Vallesian von Kreta/Griechenland. *N Jb Geol Paläont, Mh* 3:157–162
- Lax EM (1996) A gazetteer of Cretan paleontological localities. In: Reese DS (ed) *Pleistocene and Holocene fauna of Crete and its first settlers*. Prehistory Press, Madison, pp 1–32
- Leinders JJM, Meulenkamp JE (1978) A *Microstonyx* tooth from eastern Crete; paleogeographical implications of Cretan Tortonian mammal associations. *Proc Koninkl Nederl Akad Wetenschappen B* 81(4):54–60
- McDonald HG, White RS, Lockley MG, Mustoe GE (2007) An indexed bibliography of Cenozoic vertebrate tracks. In: Lucas SG, Spielmann JA, Lockley MG (eds) *Cenozoic vertebrate tracks and traces*, *N M Mus Natl Hist Sci Bull* 42:275–302
- Milàn J, Bromley RG, Titschack J (2005) Vertebrate footprints from a new aeolian outcrop from Southern Rhodes, Greece. *International symposium on dinosaurs and other vertebrates palaeoichnology, Fumanya-St. Cornelt (Cercs, Barcelona) October 4-8th 2005, Abstracts*, p 81
- Milàn J, Bromley RG, Titschack J, Theodorou G (2007) A diverse vertebrate ichnofauna from a Quaternary eolian oolite, Rhodes, Greece. In: *Sediment–Organism Interactions: A Multifaceted Ich-nology*. SEPM Spec Publ No 88:333–343
- Pilgrim GE (1931) *Catalogue of the Pontian Carnivora of Europe in the Department of Geology*. British Museum (Natural History) Geology, London
- Poulakakis N, Lyberakis P, Fassoulas C (2005) *Deinotherium giganteum* (Proboscidea, Deinotheriidae) from the Late Miocene of Crete. *J Vertebr Paleontol* 25(3):732–736
- Roberts DL (2008) Last interglacial hominid and associated vertebrate fossil trackways in coastal eolianites, South Africa. *Ichnos* 15:190–207
- Stuart C, Stuart T (2000) *A field guide to the tracks and signs of Southern and East African wildlife*, 3rd edn. Struik, Cape Town
- van der Made J (1996) Pre-Pleistocene land mammals from Crete. In: Reese DS (ed) *Pleistocene and Holocene fauna of Crete and its first settlers*. Prehistory Press, Madison, pp 69–79
- van der Made J (1999) Intercontinental relationship Europe-Africa and the Indian subcontinent. In: Rössner GE, Heissig K (eds) *The Miocene land mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp 457–472
- Zidianakis G, Mohr BAR, Fassoulas C (2007) A late Miocene leaf assemblage from Vrysses, western Crete, Greece, and its paleoenvironmental and paleoclimatic interpretation. *Geodiversitas* 29:351–377