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# *Crocuta dietrichi* from Meob, Namibia: implications for the age of the Tsondab Sandstone in the coastal part of the Namib Desert

## Crocuta dietrichi *de Meob, Namibia: Implicaciones sobre la edad de la Arenisca de Tsondab en la zona costera del desierto de Namibia*

J. Morales[1], B. Senut[2], M. Pickford[2, 3]

ABSTRACT

Palaeontological field work in the Namib Sand Sea, east of Meob, Namibia, has led to the discovery of the lower dentition of an Early Pliocene hyaenid. The same aeolianite series contains abundant carnivore footprints and coprolites compatible in size with the dental remains. The closest match for the teeth is with the extinct species *Crocuta dietrichi*, the type locality of which is the Upper Laetoli Beds, Tanzania, ca 3.5-3.8 Ma. Elsewhere the species is reported to range in age from ca 4.4 to 1.9 Ma. The primitive aspect of the teeth and their diminutive dimensions suggest that the fossils are closer in age to 4 Ma than to 2 Ma. This discovery provides the first evidence concerning the age of the Tsondab aeolianites in the Meob sector of the Namib Desert.

**Keywords:** Hyaenidae, Crocuta, Pliocene, Meob, Namib Desert, Namibia

RESUMEN

Los trabajos paleontológicos en el mar de arenas del desierto del Namib, al este de Meob, Namibia, nos han llevado al descubrimiento de una dentición inferior de hiénido. Las mismas series de eoleanitas contienen abundantes huellas y coprolitos de carnívoros, compatibles en tamaño con los restos dentarios. El parecido más cercano para dentición de Meob es la especie extinguida *Crocuta dietrichi*, cuya localidad tipo son las capas de Laetoli Superior, Tanzania, ca. 3,5-3,8 Ma. En otros lugares, la especie se distribuye en un rango de edad de entre ca. 4,4 a 1,9 Ma. El aspecto primitivo de la dentición y sus pequeñas dimensiones sugieren que los fósiles están más cerca en edad a 4 Ma que a 2 Ma. Este descubrimiento suministra la primera evidencia concerniente a la edad de las eoleanitas de Tsondab en el sector de Meob del desierto del Namib.

**Palabras clave:** Hyaenidae, Crocuta, Plioceno, Meob, desierto de Namib, Namibia

## Introduction

Meob lies on the Atlantic coast of Namibia (24°38'35"S: 14°44'15"E). Inland from the lightly vegetated coastal plain lies the Namib Sand Sea, a vast field of dunes. In the lee face of large pale yellow-grey barchanoid and seif (longitudinal) dunes, there are deflation depressions, occasionally deep enough to expose the underlying red indurated aeolianites of the Tsondab Sandstone Formation (Ward, 1988). There has been debate about the age of these aeolianites (Pickford, *et al.*, 1995; Senut *et al.*,

[1] Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal, 2. E-28006 Spain. Email : mcnm166@mncn.csic.es
[2] Département Histoire de la Terre, Muséum national d'Histoire naturelle, UMR 7207 du CNRS, Case Postale 38, 8, rue Buffon, F-75005, Paris. Email : bsenut@mnhn.fr
[3] Collège de France. Email : pickford@mnhn.fr

1994, Ward, 1988; Ward *et al*., 1983, 1990) but up to now there has been no direct evidence available from Meob to resolve the doubt. Elsewhere in the Namib, fossil struthious egg shells have been of immense value for determining the ages of the aeolianites (Pickford *et al*., 1995) but none have been found *in situ* at Meob.

Ward (1988, fig. 12) recorded the presence of burrows characteristic of the dune shark (*Eremitalpa*) in well bedded red aeolianites near Meob, but until 2009, no mammalian body fossils had been found. In April, 2009, Members of the Oranjemund Angling Club discovered the first fossil remains at a small exposure of aeolianite 2 km east of Meob Camp (fig. 1). Fossil footprints have been known to occur at this outcrop for many years. During a follow-up survey in 2010 to collect the fossils from Meob 1, a second exposure of aeolianite at Meob 2 was examined (fig. 1, 2), and it yielded a set of lower teeth of a diminutive hyaenid (first spotted by Dr André Oelofsen). During the survey carnivore coprolites were noted in the aeolianites, and judging from their dimensions, they could belong to the Meob hyaenid.

The aim of this note is to put on record the small hyaenid teeth, the carnivoran footprints and coprolites at Meob (Table 1), and to interpret the remains in terms of biogeography and biochronology.

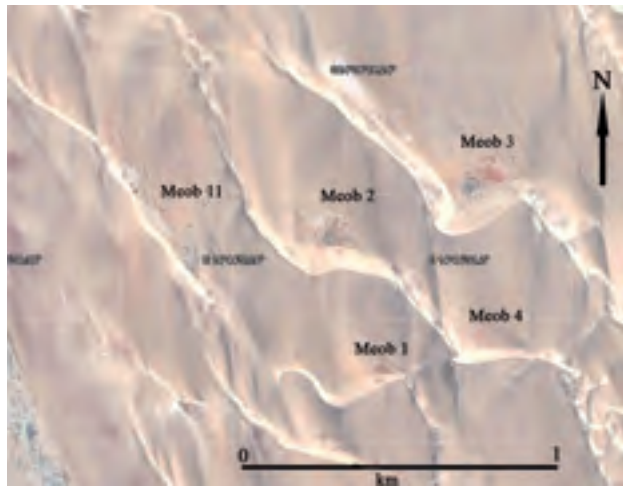


Fig. 1.—Part of the Namib Desert close to Meob, showing the distribution of fossiliferous aeolianites of the Tsondab Sandstone unconformably underlying unindurated dunes of the Namib Sand Sea (image modified from Google Earth).

## Systematic description

Family Hyaenidae Gray, 1821
Genus *Crocuta* Kaup, 1828
Species *Crocuta dietrichi* Petter & Howell, 1989

*Material*.- left and right i/2, left and right i/3, left lower canine, right lower canine root and part of crown apex, left p/2, rear half of right p/2, right p/3, mesial half of left p/3, left p/4, right m/1, mesial part of paraconid of left m/1.

*Locality*.- Meob 2, Namib Desert, Namibia

*Age*.- Early Pliocene

### *Description*

*Incisors*: The left and right second and third incisors are preserved (Fig. 3A). Their morphology is close to that of extant *Crocuta crocuta*. The i/3 has a convex labial wall, a strong distal accessory cusplet, and the lingual wall is bordered by a medium sized v-shaped cingulum. In the i/2 the lingual cingulum is weak and there is a central lingual ridge.

*Canine*: There is a fragment of root of the right canine, and the complete crown of the left canine (Fig. 3B). It is a robust tooth, with an oval transverse section. There is a distal cristid from which the enamel has flaked off; it was originally probably quite strong. The lingual cristid is weak but distinct, and terminates near the cervix in a small tubercle. There is an apical wear facet that exposes dentine, and a buccal facet descending about half the height of the tooth but not exposing dentine.

*Second premolar*: The left p/2 is small, with a low crown (Fig. 3C). There is a main cusp which occupies two thirds of the surface of the tooth, and there is a mesial stylid in the mesio-lingual corner of the tooth. The distal cusplet is low and extends slightly lingually. Wear facets have exposed dentine at the apices of the main cusp and the distal cusplet. This tooth has a single large root angled distally, with a relict of the mesial root fused to it anteriorly. The distal half of the right p/2 is preserved.

*Third premolar*: The right p/3 is a single cusped tooth, which is taller and more robust than the p/4, with the main cusp occupying almost the entire tooth (Fig. 3D). There is a small mesial stylid similar to the one in the p/4. Distally, there is a small talonid formed of a tall and strong cingulum, at the apex of which is a small cusplet which contacts the distal cristid of the main cusp. The basal cingula are weak, slightly more pronounced lingually than buccally. There is a prominent apical wear facet that extends slightly down the distal cristid. A second wear facet exposes dentine at the apex of the mesial stylid and upwards onto the cristid above it. The mesial half of the left p/3 is preserved.

*Fourth premolar*: The left p/4 is a robust tooth in which the main cusp occupies about two thirds of the surface of the crown (Fig. 3E). It lacks a small chip of enamel apically. There is no mesial cusplet, only a small stylid at the junction between the mesial cristid of the main cusp and the mesio-lingual cingulum, which is low and smooth. There is a well developed distal cusplet joined to the distal cingulum, which is partly worn and missing a small patch of enamel. This disto-lingual cingulum is strongly developed, extending lingually as far as the separation between the main cusp and the distal cusplet, bordering an inclined platform of moderate size. The buccal cingulum is

Fig. 2.—Meob 2, hyaenid site, showing Tsondab Sandstone exposure, surrounded by active dunes of the Namib Sand Sea. The star in the left image locates the site which yielded the hyaenid teeth described in this paper. The right hand image shows screening activity aimed at recovering fragments of the dentition.

Table 1.—**Fossiliferous localities in the Meob area, Namib Desert, Namibia**

| Locality | Deposit | GPS co-ordinates (WGS 84) | Fossils |
|---|---|---|---|
| Meob 1 | Red aeolianite | 24°38'49.09"S: 14°44'22.27"E | Viverrid skeleton, many footprints |
| Meob 2 | Red aeolianite | 24°38'35.70"S: 14°44'15.51"E | Hyaenid teeth, many footprints |
| Meob 3 | Red aeolianite | 24°38'29.02"S: 14°44'35.36"E | Footprints and other ichnofossils |
| Meob 4 | Red aeolianite | 24°38'46.40"S: 14°44'39.14"E | Footprints |
| Meob 5 | Red aeolianite | 24°37'39.30"S: 14°44'02.94"E | Footprints |
| Meob 11 | Grey aeolianite | 24°38'37.42"S: 14°44'00.50"E | Many ichnofossils, rhizoliths |

moderate. There is an apical wear facet on the main cusp which is continuous with a facet down its distal cristid. A small apical facet occurs on the distal cusplet, separated from the main cusp by a deep incision. On the bucco-distal surfaces of the main cusp and distal cusplet there are vertical wear grooves in the enamel, which expose dentine on the distal cusplet but not on the main cusp.

*First Molar*: The right m/1 is reasonably well preserved but has lost some enamel in the mesial part of the paraconid, on the lingual wall of the protoconid and part of the talonid, but this damage does not prevent an accurate description of the tooth (Fig. 3F). The paraconid is large and robust, longer and broader than the protoconid. The metaconid has disappeared almost completely, leaving only a tiny fold of enamel on the distal cristid of the protoconid on which there is some dentine exposed. The postcristid of the protoconid is vertical. The talonid is low and reduced in dimensions, preserving enamel only on the lingual side, which shows a slightly raised border enclosing a shallow depression. The distal root is weak, whereas the mesial one is strongly developed and bucco-lingually compressed.

The buccal sides of the paraconid and protoconid are affected by a vertical wear facet which exposes dentine, beneath which the enamel is scored by parallel grooves caused by abrasion against the P4/. The wear facet on the talonid is almost horizontal.

A fragment of the paraconid of the left m/1 is preserved, which, unlike the right m/1, retains most of the enamel mesially. It preserves the remnant of a low mesial stylid.

## *Discussion*

The Meob hyaenid teeth (Table 2), in particular the premolars, fall into the small end of the range of variation of *Crocuta crocuta* (Fig. 6, 7) (Kurtén, 1956). The same observation applies to the teeth of *Crocuta dietrichi*, which is one reason why Turner (1990) considered that the species could be a synonym of *Crocuta crocuta*, a position supported by Werdelin & Solounias (1991), but later abandoned by Werdelin & Peigné (2010). Barry (1987) thought that the Laetoli specimens might belong to *Crocuta sivalensis* but detailed follow-up comparisons have yet to be made to confirm or refute the possibility.

The morphological differences between the material attributed to *C. dietrichi* (including the Meob fossils) indicates that it is indeed a taxon distinct from *Crocuta crocuta*, which possesses enlarged premolars and a distally slanting protoconid in the m/1 (the latter enhancing the sectorial action of the carnassial) compared to the teeth of *C. dietrichi*. We therefore concur with Petter & How-

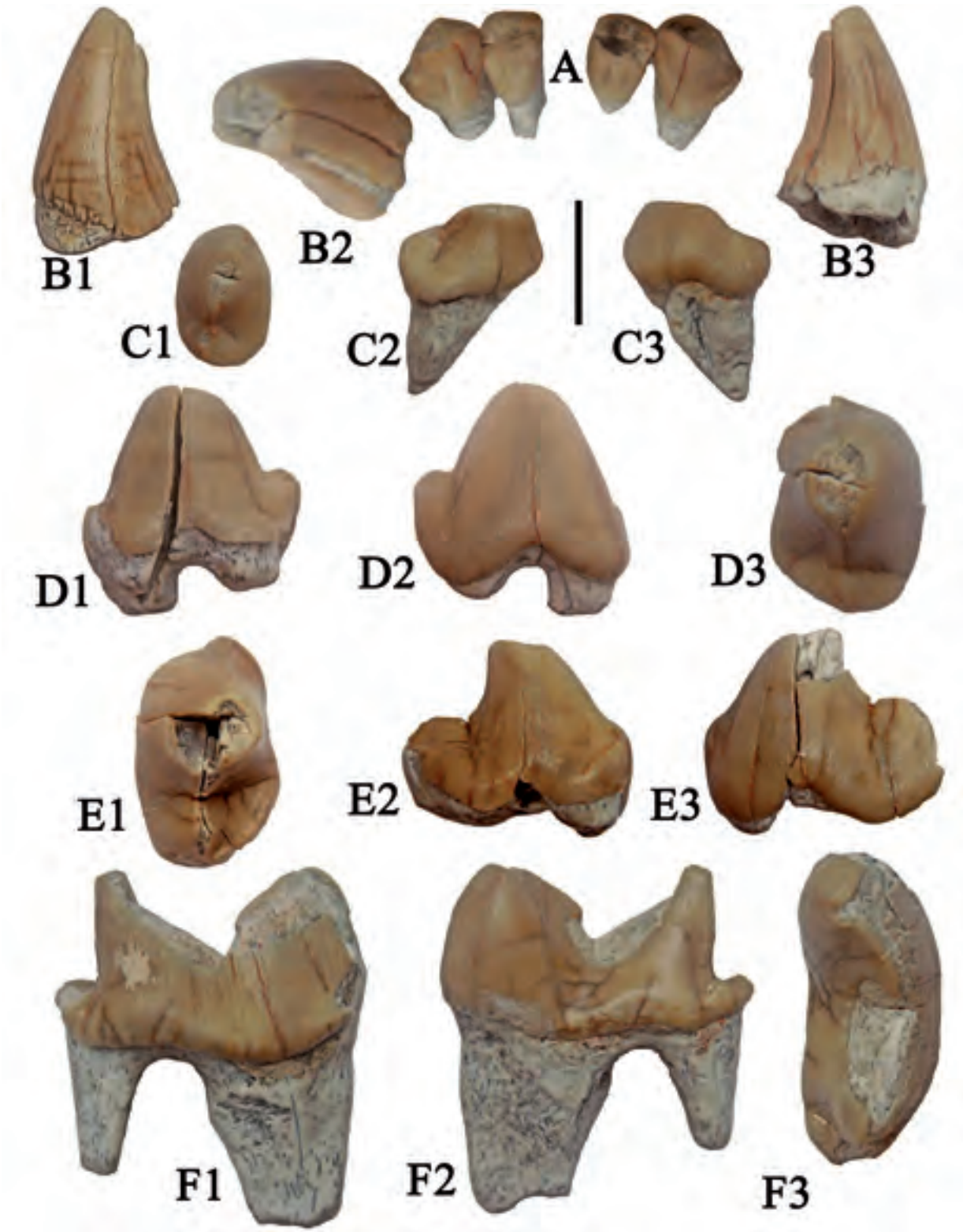


Fig. 3.—Lower dentition of *Crocuta dietrichi* from Meob 2, Namibia. A) right and left i/2-i/3, lingual view, B) left canine, B1 – buccal, B2 - oblique occlusal, and B3 - lingual views; C) left p/2, C1 – occlusal, C2 - lingual, C3 - buccal views; D) right p/3, D1 - lingual, D2 - buccal, D3 – occlusal views; E) left p/4, E1 – occlusal, E2 - lingual, E3 – buccal views; F) right m/1, F1 – buccal, F2 – lingual, and F3, occlusal views (scale: 10 mm).

Table 2.—**Length and breadth measurements (in mm) of the teeth of *Crocuta dietrichi* from Meob, Namibia**

| Tooth | Length | Breadth |
|---|---|---|
| i/2 left | 4.9 | 6.6 |
| i/2 right | 5 | 6.7 |
| i/3 left | 7.3 | 7.8 |
| i/3 right | 7.3 | 7.5 |
| c/1 left | 12.8 | 9.6 |
| p/2 left | 11.6 | 8 |
| p/2 right | — | 8.5 |
| p/3 left | — | 12 |
| p/3 right | 17.5 | 12 |
| p/4 left | 18.6 | 12 |
| m/1 right | 24.6 | 10.3 |

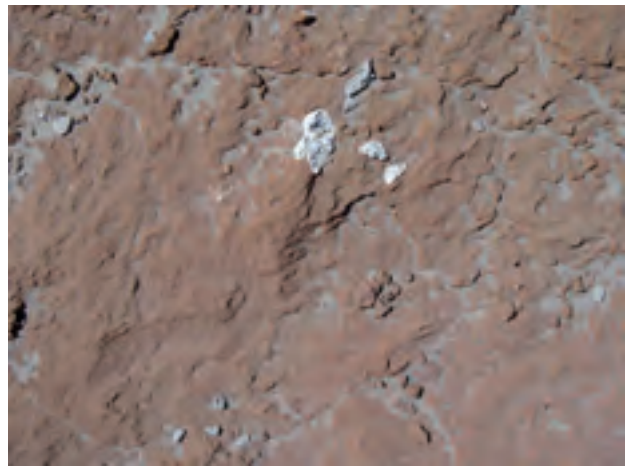

Fig. 4.—Calcium-rich coprolite in Tsondab Sandstone at Meob 2.

Fig. 5.—Carnivoran footprints in indurated interdune sands at Meob 1. Note the palaeodune outcrop to the left of the yellow pan and brush. Hammer provides the scale.

ell (1989) who erected the species *C. dietrichi* for these small, primitive, Early Pliocene *Crocuta* specimens.

## Coprolites

At several places in the Meob aeolianites there are white, chalky coprolites (Fig. 4), similar to those of hyaenids, but somewhat smaller than those of extant species of *Crocuta* and *Parahyaena*. The appearance of the coprolites likely indicates a diet high in calcium, suggesting that the maker was digesting bone. If so, then bone eating propensities may already have been established in the Early Pliocene.

## Ichnopalaeontology

The aeolianites cropping out east of Meob are well endowed with abundant and varied ichnofossils, ranging from plant pedotubules and rhizoliths to insect burrows, and traces made by mammals (Fig.

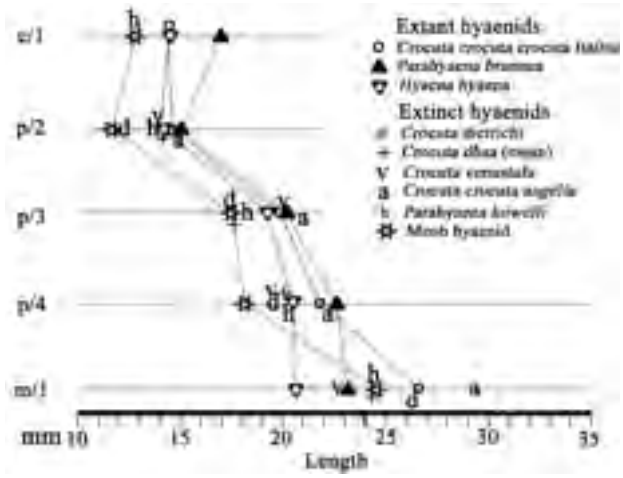


Fig. 6.—Lengths of c/1 – m/1 in extant and fossil hyaenids. The Meob specimen (hollow snow flake symbol) is similar in proportions to extinct *Crocuta dietrichi* (d symbol) and extant *Crocuta crocuta* (° symbol) and differs from the proportions seen in *Parahyaena howelli* (h symbol) which is of similar overall dimensions. (Data from Ewer, 1955a, b; Geraads, 1997; Kurtén, 1956; Petter & Howell, 1989; Werdelin, 2003). In the relative dimensions of the paraconid and protoconid of m/1, the Meob fossil is similar to *Crocuta*. However, it differs from the lower carnassial of *Crocuta crocuta* by possessing a vertical rear cristid of the protoconid, not overhanging the talonid as is usually the case in the extant spotted hyaena. In the extant species of *Crocuta*, the protoconid slants distally at a marked angle, and in unworn specimens protects the talonid from occlusal wear. In this respect, the Meob specimen accords with the species *Crocuta dietrichi*, first described from Laetoli, Tanzania (Barry, 1987; Petter & Howell, 1989) and subsequently reported from various Pliocene sites in East Africa (Werdelin & Peigné, 2010).

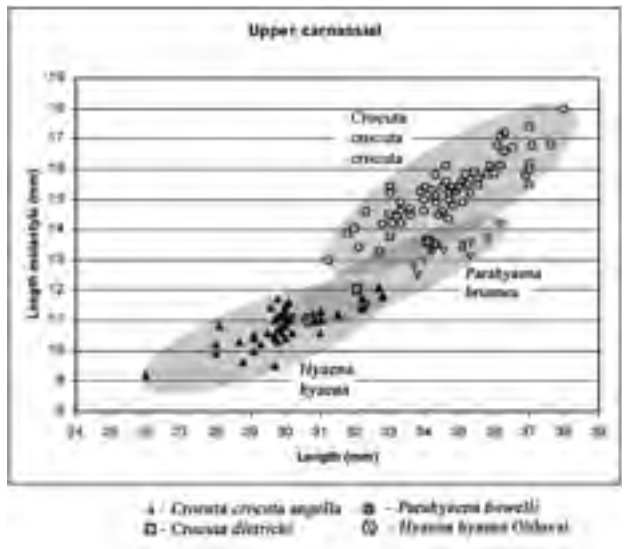


Fig. 7.—Length of P4/ versus the length of the metastyle in hyaenids. In the context of *Crocuta*, the P4/ attributed to *C. dietrichi* by Petter & Howell (1989) has a relatively short metastyle, more akin to the ratio seen in *Parahyaena*. Extant hyaenid data from Kurtén, 1956. Other data from Ewer, 1955a, b; Petter & Howell, 1989; Werdelin, 2003.

5). Among the known ichnofossils are burrowing traces attributed to the dune shark, *Eremitalpa* (Ward, 1988), but footprints made by mammals have long been known to occur in the region, although they have not yet reached the scientific literature.

At Meob 1, there is an interdune deposit covered with footprints of carnivores and ruminants. Similar traces occur at Meob 2, where the fossil hyaenid teeth were found, and they are also known from other exposures at Meob 3 and Meob 4. The richest and most instructive outcrops are at Meob 1 (Fig. 5) which show trails of footprints oriented in two main directions (predominantly easterly and westerly – i.e. away from, and towards the coast).

The dimensions of the footprints suggest an animal compatible in size with *Crocuta dietrichi*, and this is the species to which they are provisionally attributed. Further work is needed in order to document the stride, allure and other features of the trails, and to determine whether the front and hind prints can be distinguished from each other. Extant *Parahyaena brunnea*, which occurs in the region today, leaves foot print trails in the sand indicating a fore paw that is appreciably larger than the hind paw, making it easy to identify which is which. Preliminary impressions of the Meob fossil trails is that the hind and fore paw prints have almost the same dimensions, and are thus difficult to distinguish from each other, but further work may yield a better idea of the relative dimensions of the paws of the trail makers.

## General discussion

Werdelin & Lewis (2008) and Werdelin & Peigné (2010) indicated the distribution of *Crocuta dietrichi* and *Parahyaena howelli* as follows:

*Crocuta dietrichi* occurs in Ethiopia at Hadar/Sidi Hakoma, Hadar/Denen Dora, Omo/Usno, in Kenya at Koobi Fora/KBS, Lokochot, Upper Burgi, South Turkwel (cf), and West Turkana/Lower Lomekwi, and in Tanzania in the Laetoli/Upper Beds, and in Algeria at Ahl al Oughlam.

*Parahyaena howelli* occurs at Kanapoi and Allia Bay in Kenya, and at Laetoli/Lower Beds, Laetoli/Upper Beds in Tanzania.

Our metric analysis of the specimens attributed to these two species, reveals that they are similar to

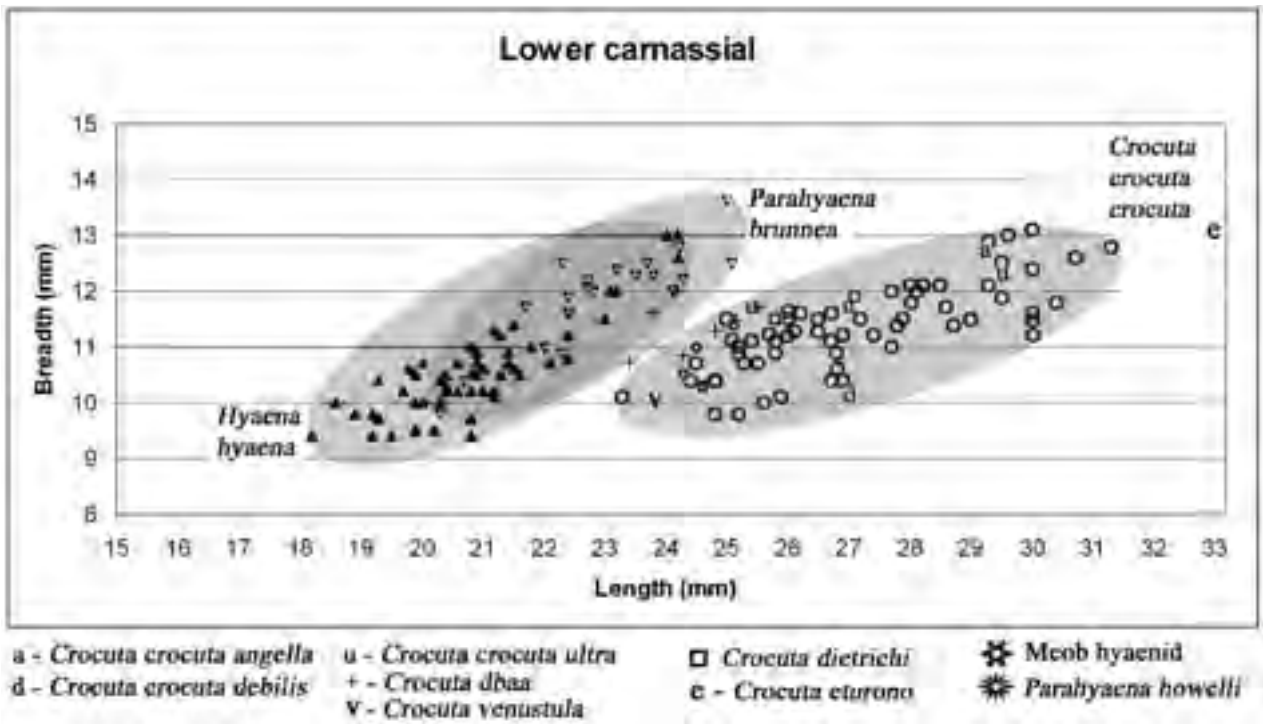


Fig. 8.—Bivariate length/breadth plot of lower carnassials of extant hyaenas and some Plio-Pleistocene African species. The Meob specimen plots within the low end of the range of variation of *Crocuta crocuta*, but its vertical protoconid represents a specific difference, also noted in *Crocuta dbaa* from Ahl al-Oughlam, Algeria. Extant hyaena data from Kurtén, 1956. Other data from Ewer, 1955a, b; Geraads, 1997; Kurtén, 1965; Petter & Howell, 1989; Werdelin, 2003; Werdelin & Lewis, 2008.

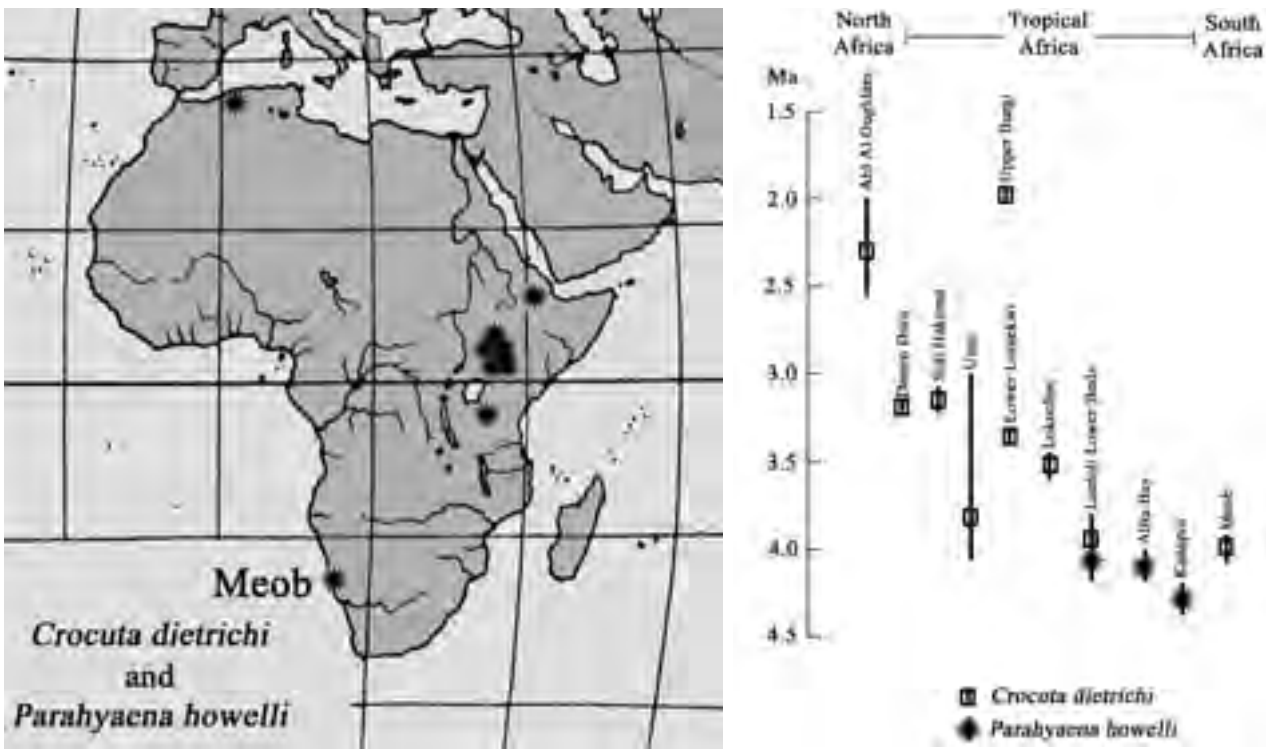


Fig. 9.—Geographic and stratigraphic distribution of Pliocene *Crocuta* and *Parahyaena* in Africa.

each other (Fig. 6-8) but they can be distinguished from each other by the relative dimensions of the paraconid and protoconid in the m/1. In *Crocuta* species, the paraconid is considerably longer than the protoconid, its length usually being as great as that of the protoconid and talonid combined. In *Parahyaena* species, in contrast, the paraconid and protoconid are subequal in length. There are other differences between the taxa, such as the tendency for *Parahyaena* to possess a metaconid in the m/1 (albeit variable in dimensions, sometimes being altogether absent (Hendey, 1974)).

*Crocuta dbaa*, from Ahl al-Oughlam, Algeria (Geraads, 1997) is similar to the Meob fossil in the form of the protoconid of m/1 and we are inclined to agree with Werdelin & Peigné (2010) that the North African species should be transferred to *Crocuta dietrichi*. This would make the distribution of the species pan-African (Fig. 9) which raises the question as to whether it might have relationships with Pliocene hyaenas in Europe.

*Pliocrocuta perrieri* (Croizet & Jobert, 1828) (= *Pliocrocuta pyrenaica* (Depéret, 1890) according to Werdelin & Solounias, 1991)) is reasonably close in morphology to *Crocuta dietrichi*, but it is a larger species. At present, there appears to be no record of the genus *Crocuta* outside Africa before the Pleistocene, although Prasad (1968) described a fragment of mandible containing two teeth from Hari Talyangar, India, (Late Miocene) which was subsequently attributed to *Crocuta sivalensis* by Werdelin & Solounias (1991). This record needs better substantiation before being accepted, as, if it is correct, then it would suggest that *Crocuta* was present in India during the Late Miocene and may then have spread to Africa during the Early Pliocene. If not, then the genus *Crocuta* would have an African origin, as postulated by Petter & Howell (1989). During the Pleistocene, however, *Crocuta* was extremely widespread throughout Europe and Asia, including India (Werdelin & Solounias, 1991) and Africa (Petter, 1973).

Werdelin & Peigné (2010) pointed out that there was a major turnover in the hyaenid fauna of Africa during the basal Pliocene, with several genera going extinct about 5 Ma, the only lineages which survived this phase being *Chasmaporthetes* and *Ikelohyaena*. In contrast, during the same period, the genera *Crocuta*, *Pliocrocuta*, *Pachycrocuta*, *Parahyaena* and *Hyaena* became established; of which only three genera (*Crocuta*, *Parahyaena* and *Hyaena*) survive to the present day. This turnover affected South Africa (Ewer, 1954, 1955a, 1955b; Hendey, 1974, 1978), North Africa (Geraads, 1997; Howell, 1987) as well as Central and East Africa (de Bonis *et al*., 2010; Haile-Selassie & Howell, 2009; Morales *et al*., 2005).

The demonstration of this Mio-Pliocene faunal turnover is important (Morales *et al*., 2005), not only for biogeography, but also for biochronology, as it provides constraints concerning the age of the Meob specimen of *Crocuta dietrichi*. It is unlikely to be older than about 4 Ma, but could be somewhat younger, perhaps, but unlikely, as young as the Plio-Pleistocene boundary (Fig. 9). We estimate an Early Pliocene age for the deposits at Meob on account of the small dimensions and primitive morphology (upright distal margin of the protoconid, small premolars with diminutive cristids and stylids) of the available teeth.

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