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Palynology and palaeo-environment of Pleistocene hyaena coprolites from an open-air site at Oyster Bay, Eastern Cape coast, South Africa

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Hyaena coprolites in a soil horizon at Oyster Bay, Eastern Cape coast, South Africa, were found associated with abundant, early Last Glacial vertebrate faunal remains that were apparently accumulated by brown hyaenas and prehistoric humans. Artefacts of the Howieson's Poort sub-stage of the Middle Stone Age occur in the same soil. Although direct association between the different finds cannot be demonstrated, there is evidence to suggest that they are broadly contemporaneous. Pollen assemblages in the coprolites were dominated by *Myrica* and, to a lesser extent, *Stoebe-Elytropappus* type and Poaceae. Comparison with the modern pollen spectrum suggests that the past environment differed markedly from the current. The presence of *Stoebe-Elytropappus*, in particular, is considered to indicate a displacement of vegetation zones to lower altitudes. Both fossil pollen and fauna suggest a landscape with a complex mosaic of vegetation indicative of overall cooler, more inland conditions than today.

Our understanding of the early Last Glacial environments in the southern and eastern Cape is almost entirely limited to the evidence from Klasies River[1–4] and Herolds Bay Cave.[5] At these sites animal remains and traces of past human activity comprise the bulk of palaeobiological evidence, and little is known of the palaeobotany of this period in this area. Here we report the results of a palynological investigation of fossil hyaena coprolites collected at an open-air site near Oyster Bay, Eastern Cape coast (Fig. 1). These remains derive from an ancient deflated soil horizon, which also contains a rich, well-preserved fossil fauna of vertebrates, and artefacts of the Howieson's Poort sub-stage[6] of the Middle Stone Age (MSA) (Fig. 2). Besides the light that the Oyster Bay coprolites shed on early Last Glacial environments in the Eastern Cape, the site is also significant as being the source of the first open-air Howieson's Poort occurrence known to us. The precise relationship between these archaeological and palaeontological finds is difficult to determine and the possibility that they are associated is discussed.

The Howieson's Poort sub-stage of the Middle Stone Age in the southern Cape[6] is taken to date to around 70 000 years BP, or slightly more. The Oyster Bay fauna shows agreement with early Last Glacial levels at Klasies River[7] and at Herolds Bay Cave[5] (Fig. 1), that are close to the Marine Isotope Stage 5a/4 boundary.[8] This interpretation of an early Last Glacial age for the fossil assemblage is corroborated by certain characteristics of the pollen spectra from the Oyster Bay hyaena coprolites, as will be explained below. These coprolites form part of a rich vertebrate fossil occurrence that seems to have had a complex history of formation, but reflecting a restricted time period. As is often the case at open-air sites, multiple primary agents of accumulation may have been responsible for the fossils, and at Oyster Bay it seems that evidence of human occupation of the Howieson's Poort sub-stage was overprinted by hyaena activities. This creates a problem of determining the stratigraphical relationship between the different components but we intend to show below that it is likely that the coprolites are all broadly contemporaneous with stone tools. In itself the recovery of fossil pollen from hyaena coprolites is of interest, as they often do not contain pollen grains. For example, specimens supplied by R.G. Klein (Stanford University) from Redcliff Cave, and by the late A.R. Hughes from the Cave of Hearths and Makapansgat, were barren, and not all coprolites from productive sites like Equus Cave contained pollen.[9]

The stratigraphical association of fauna, coprolites and artefacts

It seems that the Oyster Bay site is periodically exposed and covered over by wind action; at present the site is again covered by mobile dunes, which in turn are being stabilized by the spread of dune-covering vegetation, primarily by *Myrica cordifolia* and *Passerina rigida*. The materials on which the present study is based were collected over a period of two weeks in February 1993 by two of the authors (J.N.F.B. and J.S.B.).

The fossil vertebrate site consists of an exposed and wind-eroded palaeosol in a series of linear dunes, which are still partly mobile (Fig. 3). These dunes cut into the palaeosol, which contains abundant evidence of prehistoric human activity, including stone artefacts (Fig. 2) of the Howieson's Poort sub-stage of the MSA[6] and vertebrate remains reflecting human bone-collecting. The stone artefacts were not systematically excavated, but collected from the surface as a random sample. There is hyaena damage to some bone specimens and this may indicate

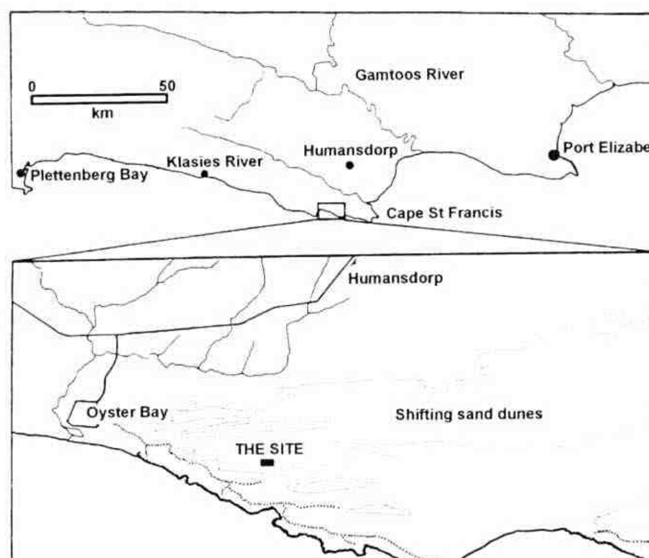

Fig. 1. Site location.

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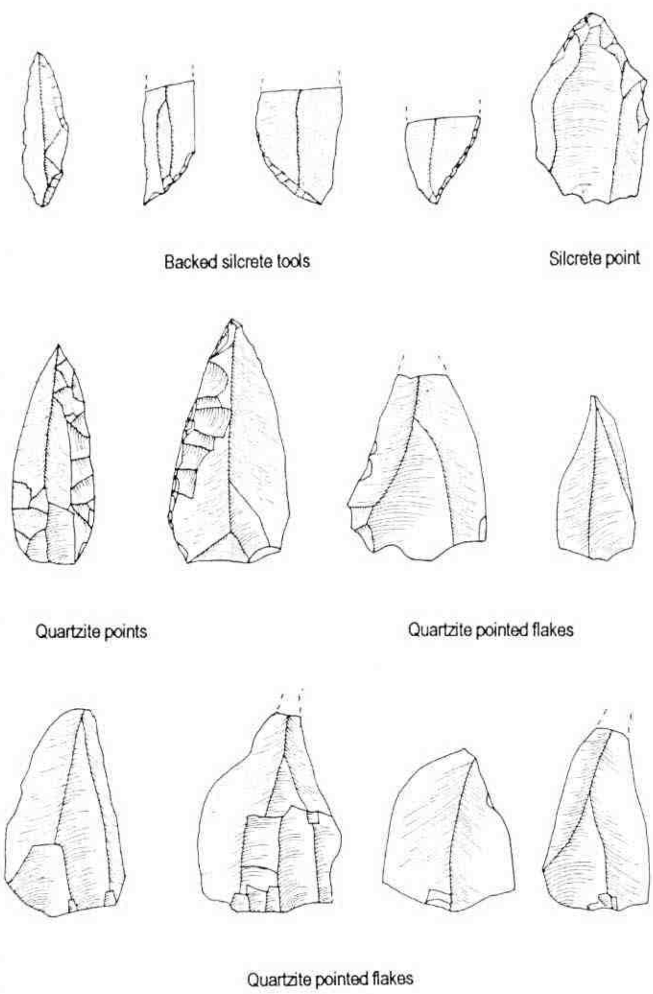

Fig. 2. Stone artefacts from the Oyster Bay site (55% natural size).

that these animals used the site soon after it was abandoned by humans. The presence of hyaena coprolites in localized patches seems to support this assumption. Thus, the apparent primary human-collected component of the fossil occurrence was preserved together with an overprint of hyaena bone modification and collecting activities. Dense surface clusters of bone and hyaena coprolites are interpreted as eroded and deflated hyaena burrows. In many instances *in situ* bone material, artefacts and even hyaena coprolites were visible in the palaeosol, but most of the material was collected as surface scatters.

Although we cannot discard the possibility that part or all of the coprolites from Oyster Bay may have been produced by spotted hyaena (*Crocuta crocuta*), there are arguments for the likely involvement of the brown hyaena (*Hyaena brunnea*). First, the Oyster Bay coprolites vary between approximately 25 and 40 mm in length (Fig. 4), while spotted hyaena scats are generally larger (38–58 mm at Kebara Cave).[10] Secondly, the site contains bone remains of brown hyaena. Thirdly, the materials studied did not contain bone fragments, a feature common in spotted hyaena but rare in brown hyaena scats. According to studies on the present-day ecology and distribution of both species,[11] the brown hyaena's range includes savanna, highveld grassland, desert and coasts.[11,12]

The association of the fossil materials is uncertain, because of the apparent deflated nature of the occurrence. It is clear that there cannot be an exact stratigraphic resolution as is found in sealed cave deposits. It is unlikely that the hyaena coprolites and the Howieson's Poort stone artefacts are derived from the same

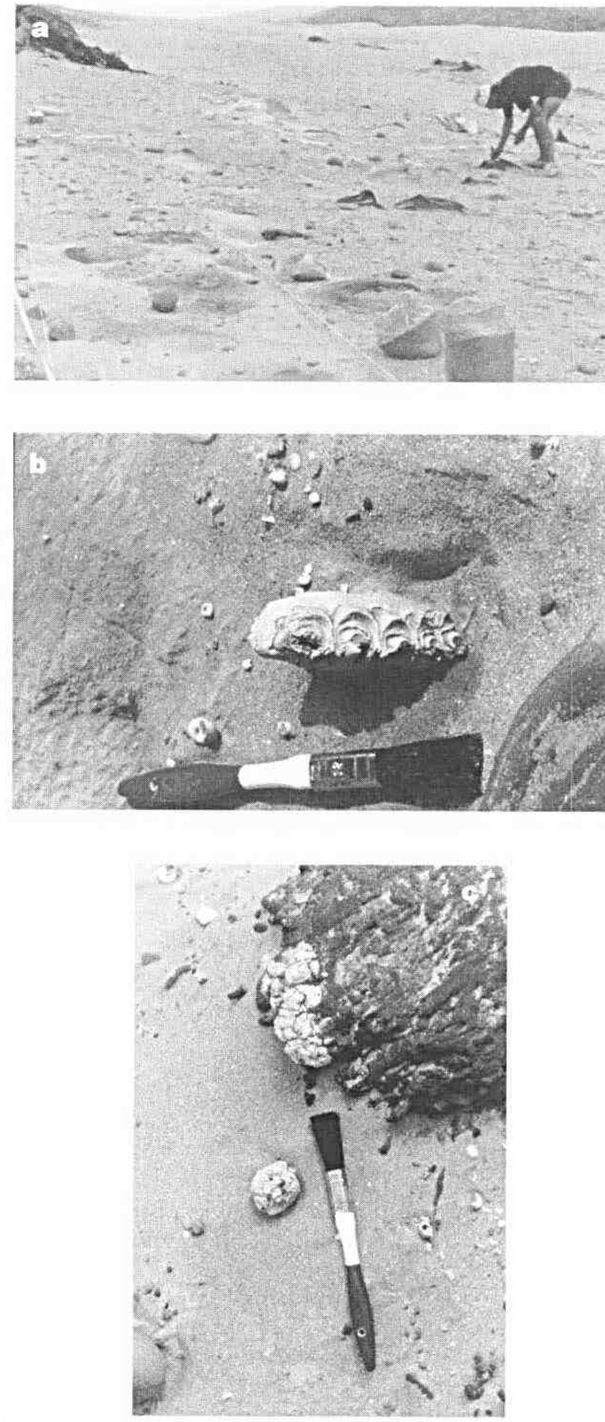

Fig. 3. An east-facing view of the landscape of the Oyster Bay fossil site (**a**), showing surface scatters of stone artefacts, fossil bones and fossil hyaena coprolites. The darker patches on the land surface represent areas where a dark-brown palaeosol protrudes through the overlying mobile sands. This palaeosol is the original sedimentary context of fossils, as is evident from *in situ* specimens, such as a lower jaw of the extinct bloubok, *Hippotragus leucophaeus* (**b**), and a hyaena coprolite (**c**).

taphonomic component, but this does not necessarily imply that the scats are not semi-contemporaneous with the other fossil materials. In the case of the Oyster Bay finds there is indeed evidence to suggest that human occupation, carnivore interference with the human collected bone material (and possible carnivore contribution to the fossil assemblage) and hyaena burrow occupation date from a relatively restricted period. This evidence is summarized as follows:

Fig. 4. Hyaena coprolites from Oyster Bay.

- Hyaena coprolites and fossil bone remains showing evidence of both carnivore teeth marks and human bone-breaking activities were found *in situ* in the same red-brown palaeosol (Fig. 3). MSA stone artefacts also derive from this palaeosol, although no typically backed pieces were found *in situ*. This may reflect the limited sampling of the palaeosol, since we did not conduct extensive excavations. The fact that we did not find *in situ* backed pieces is not unexpected, since they normally constitute a very small percentage of any stone artefact assemblage.
- The state of preservation of the fossil bone material found outside of sedimentary context and exposed by wind deflation, was homogeneous and similar (excluding recent wind abrasion) to that of those specimens found *in situ*. This suggests that the post-depositional history of both sets of fossil bone was similar, and thus derived from the same palaeosol.
- The character of the fauna presented in Table 1 is homogeneous and matches the Stage 4/5 time range as seen in the faunas of those sites mentioned in the text, for which there is good chronological control. It should be noted that the character of the Oyster Bay fossil assemblage is virtually entirely terrestrial, with only occasional marine indicators, such as seals. This is compatible with a reduced sea level, as would have been the case at the beginning of the Last Glacial. A further point of interest is that there were no elements in the fossil assemblage from Oyster Bay that would conflict with an early Glacial estimate of its age, when comparing it with Klasies River and Herolds Bay.

Even if individual coprolites and other fossil materials or artefacts were not deposited in the same season or year, broad contemporaneity seems likely in a setting where humans and hyaenas shared some of the resources.

A clear palaeo-environmental picture is provided by the vertebrate fauna (Table 1) and is complemented by the palaeobotanical analysis of the hyaena coprolites (Fig. 5). The fauna is remarkably diverse and indicative of an ecotone environment. Three ecological categories were identified, namely:

1. An open grassland habitat (*Equus quagga*, '*Pelorovis*' *antiquus*, *Connochaetes gnou*, *Alcelaphus buselaphus*, *Damaliscus dorcas*, and *Antidorcas* sp.).
2. A typically closed habitat (*Tragelaphus strepsiceros*, *T. scriptus*, *Raphicerus melanotis*).
3. A standing-water habitat (*Hippopotamus amphibius*, *Redunca arundinum*).

The association of typical grassland species with indicators of closed habitat compares well with the Howieson's Poort levels at Klasies River and the fauna of Herolds Bay Cave. The Herolds

Table 1. Taxonomic checklist of the vertebrate fossils collected at Oyster Bay.

RODENTIA	*Bathyergus suillus* (dune molerat)
CARNIVORA	*Arctocephalus pusillus* (Cape fur seal)
	cf. Hyaena brunnea (brown hyaena)
PROBOSCIDEA	*Loxodonta africana* (African elephant)
PERISSODACTYLA	*Equus quagga* (plains zebra)
ARTIODACTYLA	*Hippopotamus amphibius* (hippopotamus)
	Taurotragus oryx (eland)
	Tragelaphus strepsiceros (kudu)
	T. scriptus (bushbuck)
	'Pelorovis' antiquus (extinct giant buffalo)
	Syncerus caffer (Cape buffalo)
	Redunca arundinum (reedbuck)
	Hippotragus leucophaeus (blue antelope)
	Connochaetes gnou (black wildebeest)
	Alcelaphus buselaphus (hartebeest)
	Damaliscus dorcas (bontebok/blesbok)
	Raphicerus melanotis (Cape grysbok)
	Antidorcas sp. (springbok)

Bay vertebrate fauna is dated to the terminal part of Marine Isotope Stage 5.[8] The overall environmental picture of the fauna and pollen from Oyster Bay differs greatly from the present.[13]

Coprolite palynology

Little is known about the history of the Fynbos Biome with its impressive species diversity,[14,15] despite the existence of several mountain valleys where sites for good pollen assemblages can potentially be found. The climate associated with the biome is differentiated from the 'grassland' and 'Nama karoo' biomes by a higher proportion of winter rainfall, from the 'succulent karoo' biome by lower summer aridity and from the forest biome by having higher summer aridity.[16]

Pollen from hyaena coprolites, especially those of brown hyaenas, has proved to be a valuable source of information about past environments in southern Africa, for instance, from Equus Cave (Taung, southern Kalahari).[8] The brown hyaena is an omnivore: it eats small prey of all kinds such as rodents, birds, eggs, reptiles, even insects, also young game animals, wounded big game and carrion.[11] On the coast it eats mussels, dead fish, squids, and stranded birds, seals and whales. Brown hyaenas feed on carrion a third of the time and another third on vegetable matter, which can include pods, seeds, fruits, leaves, grasses, and incidentally flowers. At some locations, such as the Kalahari Desert, they roam as much as 50 km away from their dens.[17] Pollen sources may, therefore, include airborne pollen from the surrounding vegetation, and pollen from plants they consume as well as that contained in stomachs of their prey. In addition, pollen can be incorporated into the coprolite through drinking-water.

Most pollen analyses done hitherto on brown hyaena scats show a predominance of grass pollen and a relatively high diversity of pollen taxa. Pollen composition in coprolite samples apparently is different from that obtained from sedimentary contexts,[9,18,19] because these materials differ as pollen traps. The dietary behaviour of the hyaenas must be taken into account in relation to the generally low pollen concentration, as well as the short time span during which pollen is incorporated into the faeces. Preservation appears to be generally poorer in sediment samples that do not seal pollen as effectively as coprolites. Even though hyaenas are mainly carnivorous, their droppings contain

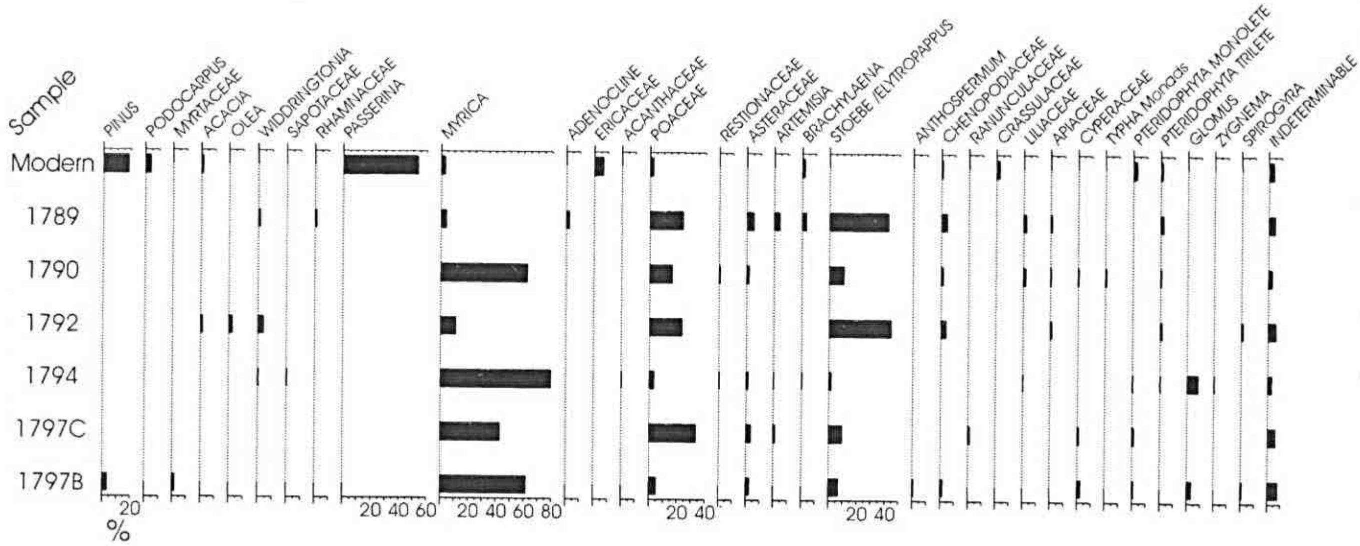

Fig. 5. Pollen diagram of hyaena coprolites from Oyster Bay compared to a surface pollen spectrum of the site.

well-dispersed atmospheric pollen from plants in the region. Pollen spectra in coprolites from Equus Cave sediments show relatively low arboreal pollen numbers that are typical of the wider surroundings.[9] In coprolites of spotted hyaena from spring vent structures at Florisbad,[19] which also reflect a regional environment, the proportion of grass pollen is high and that from aquatic and semi-aquatic plants is low.

Materials and method

Solid coprolites were initially washed to remove contamination. The laboratory procedure followed the conventional method of digesting successively in HCl, HF and KOH followed by mineral separation. Pollen concentration was determined by counting the grains observed in weighed samples. To compare with the present-day pollen signature, a surface sample consisting of several sand sub-samples at the study site was collected and analysed.

Results and discussion

All except one sample recorded fewer than 12 pollen grains per millilitre. The richest concentration was 56 grains per millilitre in sample 1794 (Table 2). Of the 12 coprolites analysed, only four provided pollen counts higher than 100. These did not come from any particular position in the collecting area. In Fig. 5 we show the pollen percentages of the six coprolites that yielded more than 80 pollen grains and compare them with a modern surface pollen signature from the site.

At least 32 pollen and spore types were identified. Pollen preservation was generally good, although an overall exine thinning was observed in most samples. Signs of present-century contamination appeared in two samples, two *Pinus* grains in 1791 and four in 1797B. Two Myrtaceae in the latter may represent either modern exotic *Eucalyptus* contamination or fossil *Syzygium*. The exotic grains are possibly modern contaminants in cracks in the coprolite surfaces that were not successfully removed by cleaning. The lack of obvious modern grains in most coprolites in comparison with the modern sample, however, and their characteristic composition, suggest that contamination is not significant.

The main pollen dominants in the coprolites were *Myrica* and, to a lesser extent, *Stoebe-Elytropappus* and Poaceae. Other common types were Asteraceae, Chenopodiaceae and ferns. Ecologically interesting pollen taxa such as *Acacia, Olea, Adenocline*, Acanthaceae, Restionaceae, *Artemisia*, Ericaceae, *Brachylaena*, and *Anthospermum* occurred in low numbers. Zygospores of Zygnemataceae were identified in samples 1792, 1794 and 1797B, suggesting ingestion of stagnant water by the hyaenas or their prey, especially in sample 1794, where other spores occurred which seemed to belong to cyanophyte and chlorophyte resting forms. *Glomus* chlamydospores were abundant in sample 1794;

Table 2. Coprolite samples and richness.

Locality	Pollen lab. No.	Actual pollen count	Sample volume (ml)	Pollen grains per ml
Modern soil	2155	237*	–	–
4	1788	26	20	1
18	1789	100*	15	7
27	1790	181*	20	9
28	1791	8	10	1
29	1792	81*	15	5
40	1793	8	10	1
Z3/n	1794	559*	10	56
Z3/W	1795	3	5	1
Z3/S1W	1796	7	20	–
Z3/R1	1797A	10	20	1
Z3/R1	1797C	84*	15	6
Z3/R1	1797B	115*	10	12

*Sample depicted in the pollen diagram (Fig. 5).

interpreting this record is difficult, since *Glomus* is a common soil microphyte and could have been introduced from many kinds of plant material, especially from roots.

Discussion

Although the pollen content was not sufficient to permit a detailed reconstruction of the vegetation associated with the scats, it has palaeobotanical and palaeo-environmental value. The modern pollen spectrum shows important differences from the coprolite results (Fig. 5). Moreover, the pollen evidence does not contradict the faunal interpretation, that they derive from the early Last Glacial. *Passerina, Pinus* and Ericaceae were dominant in the modern spectrum, with minor counts for *Myrica* and Poaceae and absence of *Stoebe-Elytropappus*. This evidence reflects the present-day local abundance of *Passerina rigida*, which also abounds in the regional coastal dune scrub together with *Myrica cordifolia, Anthospermum, Chrysanthemoides monilifera, Rhus crenata* and *Metalasia muricata*.[13]

A *Passerina* dominance is to be expected in the surface pollen spectrum in view of the vegetation. The fossil evidence with more *Myrica* grains can also be considered to be of a coastal origin or of a different inland species of *Myrica* associated with forest margins or streams, like *M. serrata*. The predominance of this genus together with *Brachylaena* and *Anthospermum* in the coprolites does not necessarily suggest very different local vegetation on the dunes, but the relatively higher occurrences of *Stoebe-Elytropappus* and Poaceae in the fossil spectra seem to indicate a changed regional environment. *Stoebe-Elytropappus* is characteristic of some present-day communities above 800 m in the Cape region[20] that corresponds to a relatively marked temperature decline during the time of coprolite deposition. The *Stoebe* type is generally much more prominent in fossil spectra of Pleistocene age, throughout southern Africa.[21] In the dune scrub, *Stoebe* behaves as a xerophyte, owing either to soil aridity or salinity.[13,14] Drier conditions inland are characterized by grass-dominated communities with abundant Asteraceae shrubs and Chenopodiaceae in the eastern Cape fynbos ecotones where rainfall is less.[22–24] The transition of fynbos to the succulent karroid shrubland along interior valleys is typically dominated by a renosterveld with asteraceous shrubs like *Elytropappus rhinocerotis* and grasses. The higher-lying, inland position of this vegetation suggests that the coprolites formed at a time of lower sea level when the coastline was farther south and therefore the site had more inland characteristics, lacking today's vegetation dominated by *Passerina*.

Although brown hyaenas are often reported from coastal areas, they have a very wide distribution including the highveld. A more inland occurrence of this species would therefore not have been unusual.

Today, between Mossel Bay and East London along the coast, an impressive diversity of vegetation types can be found, including afromontane forest, dune thicket, mountain fynbos, grassy fynbos, spekboom succulent thicket, xeric succulent thicket, eastern thorn bushveld, coastal grassland, subarid thorn bushveld and coastal forests. Towards the interior, vegetation is dominated by lower Karoo, eastern mixed Nama Karoo or mountain grasslands.[25] Local and regional vegetation therefore occurs in a complex mosaic.

Both the faunal and pollen evidence from Oyster Bay imply that at or near the time of Howieson's Poort occupation in the Eastern Cape, climatic and environmental conditions were different from today. These lines of evidence suggest a more complex palaeo-environment, which was cooler and more distant from the ocean.

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