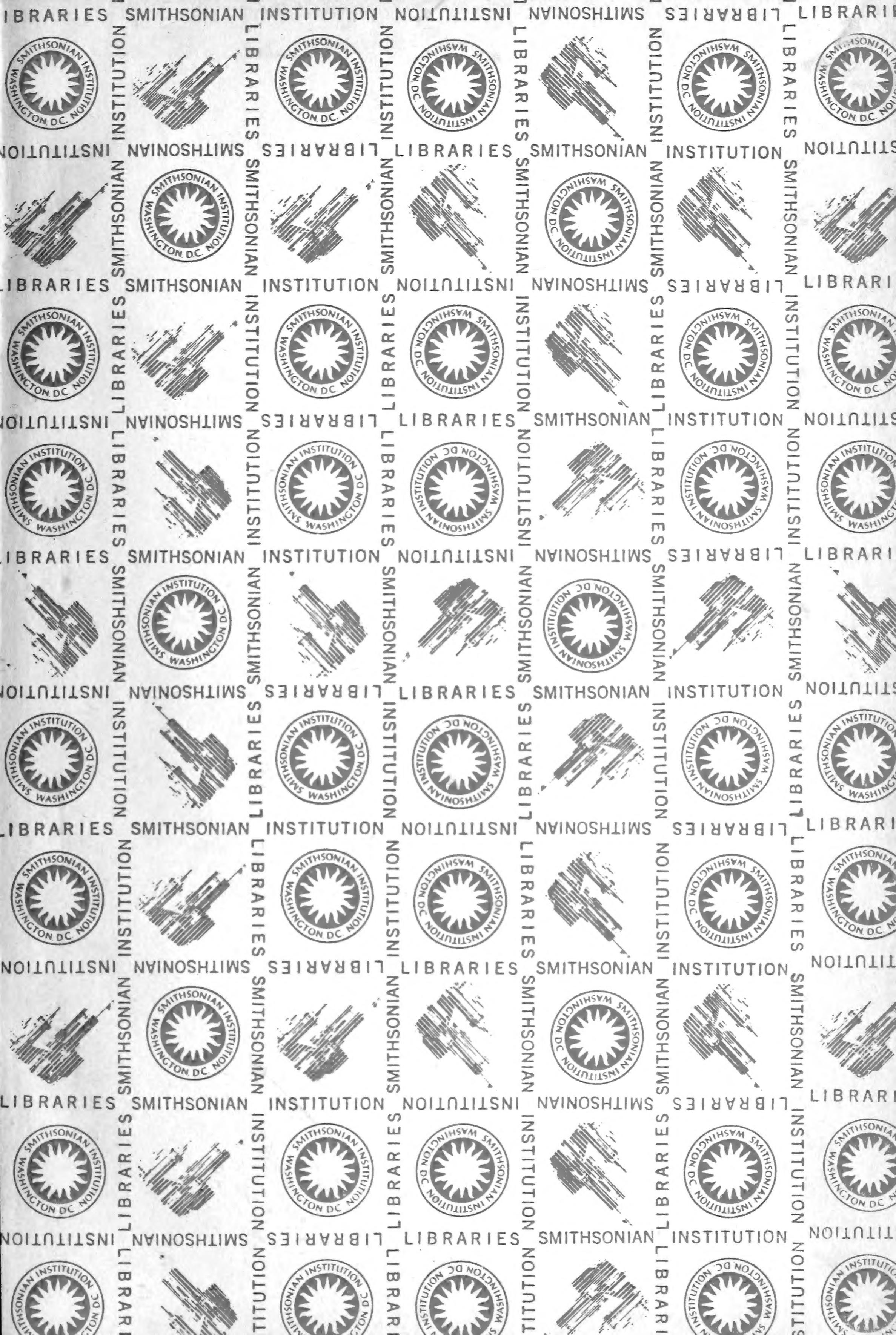
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THE LATE CENOZOIC CARNIVORA OF THE SOUTH-WESTERN CAPE PROVINCE

By

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Cape Town Kaapstad

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Q. B. Hendey

South African Museum, Cape Town

(With 78 figures and 91 tables)

(*MS accepted* 15 *March* 1973)

Contents

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General Introduction

The systematic investigation of the fossil Mammalia of South Africa was begun towards the end of the 19th century with the description of a new species of an extinct long-horned buffalo (Seeley 1891). This specimen, which had been found in 1839 by Andrew Geddes Bain and which is now housed in the South African Museum, came from the banks of the Modder River in the Orange Free State. The interior plateau of South Africa has remained the principal focus of local palaeomammalogical studies and numerous publications have appeared which deal with material recovered from gravels along the Vaal River, cave breccias in limestones and dolomites of the northern Cape Province and Transvaal, and from sites such as Cornelia and Florisbad in the Orange Free State. The Pleistocene mammal faunas of the interior of South Africa are now moderately well known (see Cooke 1963).

Until about the middle of the present century little was known of the fossil mammals of the coastal regions of the southern African subcontinent. Scott (1907) described a small assemblage of Pleistocene mammals from the Zululand coast, while series of fossils of late Tertiary age from the coasts of Namaqualand and South West Africa were described by Stromer (1926, 1931*a*, etc.) and Hopwood (1929). Broom (1909), in one of his earlier palaeontological contributions, described a new equine species from a specimen washed up on a beach near Cape Town, and this was the first description of a fossil mammal from the south-western Cape Province, the area under consideration in the present investigation. Following on this discovery was a period of about 40 years during which very little collecting of fossils was undertaken in this region.

In 1951 the prolific Pleistocene fossil occurrence on the farm Elandsfontein near Hopefield, which is about 90 km north-north-west of Cape Town, was visited by a scientist for the first time and its importance recognized (see Singer 1957). The discovery of the remains of a fossil hominid (the 'Saldanha skull') at Elandsfontein in 1952 led to considerable local and international interest in this site and thereafter a number of publications appeared which dealt with geological, palaeontological and archaeological aspects of the occurrence. These investigations were climaxed by a series of systematic excavations undertaken during 1965/6 (Singer & Wymer 1968).

Another major event in the south-western Cape was the discovery of vertebrate fossils in the phosphatic deposits at Langebaanweg, 105 km north-north-west of Cape Town (Singer & Hooijer 1958). The deposits at this locality have yielded the largest and most important assemblage of Pliocene vertebrates known from southern Africa.

Many other Quaternary vertebrate fossil occurrences are now recorded in this region (Hendey 1969), and the south-western Cape now features more prominently than before in the internationally-based investigations on the fossil Mammalia of Africa. Particular interest centres on Langebaanweg, which is the most prolific of the local sites and the best source of information on the nature of the Pliocene mammalian fauna of southern Africa.

The present widespread interest in the late Cenozoic of Africa is due largely to the fact that it was on this continent and during this period in time that important developments in the evolution of the Hominidae took place. Although the skull and mandible fragments from Elandsfontein are still the only important fossil hominid remains known from the south-western Cape, the study of other fossil mammals from local Pliocene, Pleistocene and Holocene occurrences are a significant part of the investigations into the life and events of the late Cenozoic of Africa as a whole.

The present report summarizes the existing knowledge of the fossil mammals of a geographical region which is limited in extent, and it deals in detail with the known remains of just one mammalian order, namely, the Carnivora. In general, carnivores tend to be less well represented in the fossil record than other orders and this does apply in the case of those from the south-western Cape. Nevertheless, the material available represents a significant assemblage of largely unstudied specimens made up of a wide variety of species.

Investigations on African fossil mammals are still essentially a matter of determining their systematics and it is the study of the relationships of the local Carnivora which make up the greater part of the present report. An appreciation of the taxonomy of the species represented does, however, allow for interpretive work of various kinds.

One of the most critical problems evident in southern African Cenozoic studies is the uncertainty which surrounds the relative and absolute age of many of the local occurrences which are relevant to these studies. At present only those which fall within the time limits of the radiocarbon dating technique are potentially datable in absolute terms. This means that most of the important fossil occurrences can only be dated in a relative sense and, although relative dating may be undertaken in a number of ways (see Oakley 1964), in dealing with fossil faunas it is usually most convenient to use the fauna itself as the basis for dating. Kurtén (1957*a*) has demonstrated the usefulness of the larger Carnivora in making temporal correlations between faunas in widely separated areas. Consequently, one of the aims of the present study was to determine the relative ages of the local assemblages on the basis of their carnivore faunas and other evidence and to make a temporal categorization of southern African fossil mammal faunas on a formal basis.

In addition to the determination of the age and phyletic relationships of the species described, account was taken of their past and present distributions. Viewed in relation to other mammals, some aspects of the evolution and dispersal of African Carnivora have become evident. Although the interpretation of the available factual evidence is necessarily subjective, there is the basis of an understanding of the evolutionary history of the carnivorous element in the African mammalian fauna.

Since predation and scavenging by carnivores may lead to bones being accumulated in certain areas and in certain ways, the possible relationships between carnivore activity and local fossil occurrences was also investigated.

The African Cenozoic fossil record is poor and, because of the nature of this record, account is taken only of the late Tertiary and Quaternary of the south-western Cape. It was during this period in time that the character and composition of the now declining modern fauna was developed and it is thus only the climax of the 'Age of Mammals' which can be investigated.

The South-Western Cape Province

The definition of geographical regions is frequently difficult and the final boundaries selected are often arbitrary. This is true of the south-western Cape Province and, although it is one of the most easily defined regions in southern Africa, its boundaries can be varied according to the nature of the study being undertaken.

In the present instance this region is taken to include that area between the coast from St. Helena Bay to Cape Hangklip and the Cape Folded Mountains, with the lower course of the Great Berg River forming its northern boundary. It may be subdivided as follows:

(1) Cape Peninsula—That area between Table Bay in the north and Cape Point in the south, and including Table Mountain and the mountains extending south from it.
(2) Coastal plain—The remainder of the region and including the areas known as the Cape Flats, the Sandveld and the Swartland (see Talbot 1947).

The maximum north–south extent of the region is about 190 km and the maximum east–west extent about 90 km (Fig. 1).

The regions adjacent to the south-western Cape (Fig. 2) and which will be referred to from time to time are as follows:

(1) West coast—The coastal plain north of the Great Berg River.
(2) Southern Cape—The southern coastal plain of the Cape Province stretching from Cape Hangklip in the west and Cape St. Francis in the east.
(3) Cape Folded Mountains—The mountains which separate the west coast, south-western Cape and southern Cape from the inland plateau (Karroo).

King (1951) has discussed the geomorphology of the south-western Cape and adjacent areas under the headings 'Cape Folded Belt' and 'Southern Coast'. The former is a complex system of mountain ranges which may be conveniently divided into two groups, namely, a group which trends north–south roughly paralleling the Atlantic coastline and those which trend east–west approximately parallel to the Indian Ocean coastline. The former group intersects the coastline in the south at Cape Hangklip, effectively separating the south-western Cape from the southern Cape. Since this group is parallel to the Atlantic Ocean, the west coast region is in the nature of an open corridor stretching northwards from the south-western Cape. The east–west group approaches the southern Cape coast at intervals so that the coastal plain is significantly narrowed for a distance of about 300 km west from Cape St. Francis.

In brief, the most southerly part of the African continent is made up of a complex system of mountain ranges and valleys fringed by a coastal plain, which in the south-western Cape has an average width of about 65 km. The physiography of the southern continental extremity is of considerable zoogeographic significance and will later be discussed again in this connection.

The geology of the south-western Cape is relatively simple. There are exposures of Archaeozoic and Proterozoic igneous and metamorphic rocks, mainly in the coastal plain, while the Cape Folded Mountains and Cape

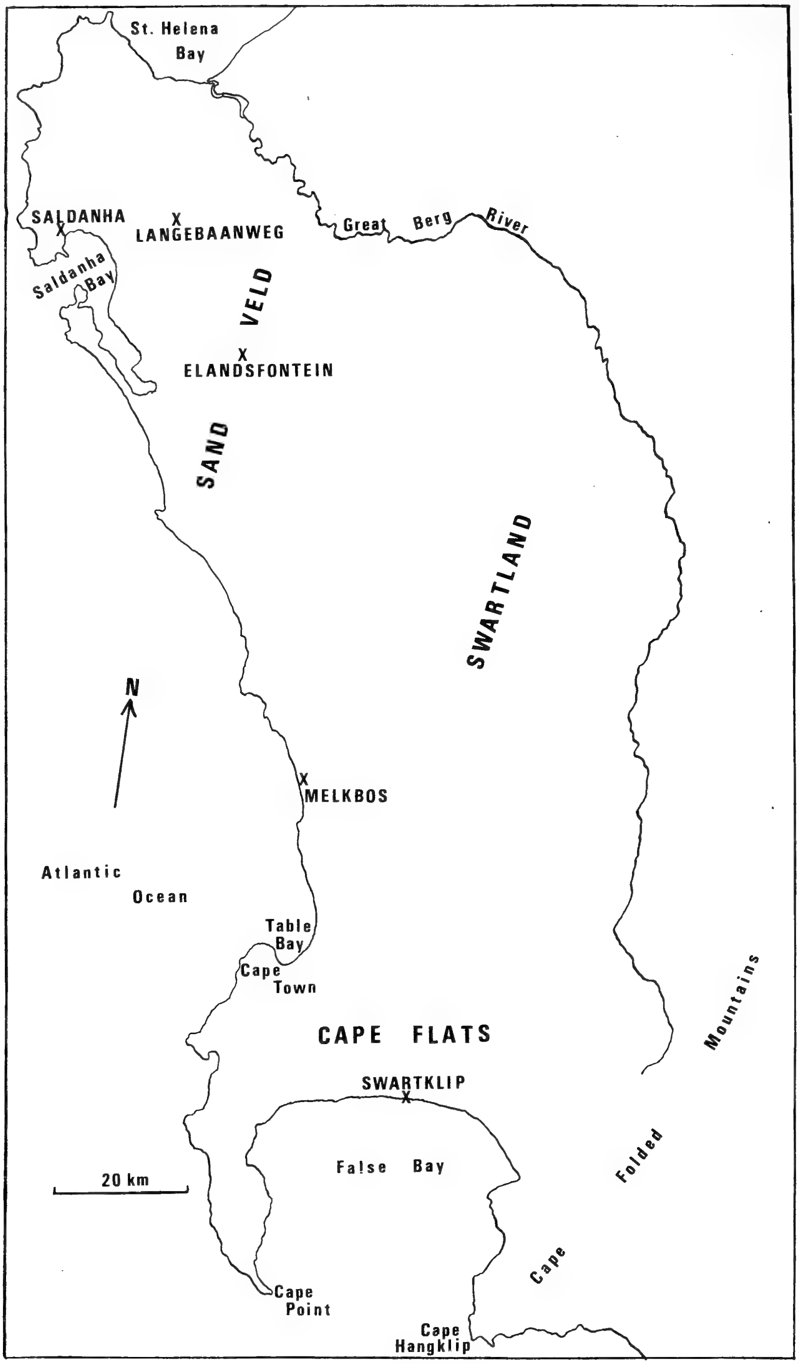

Fig. 1. The south-western Cape Province.

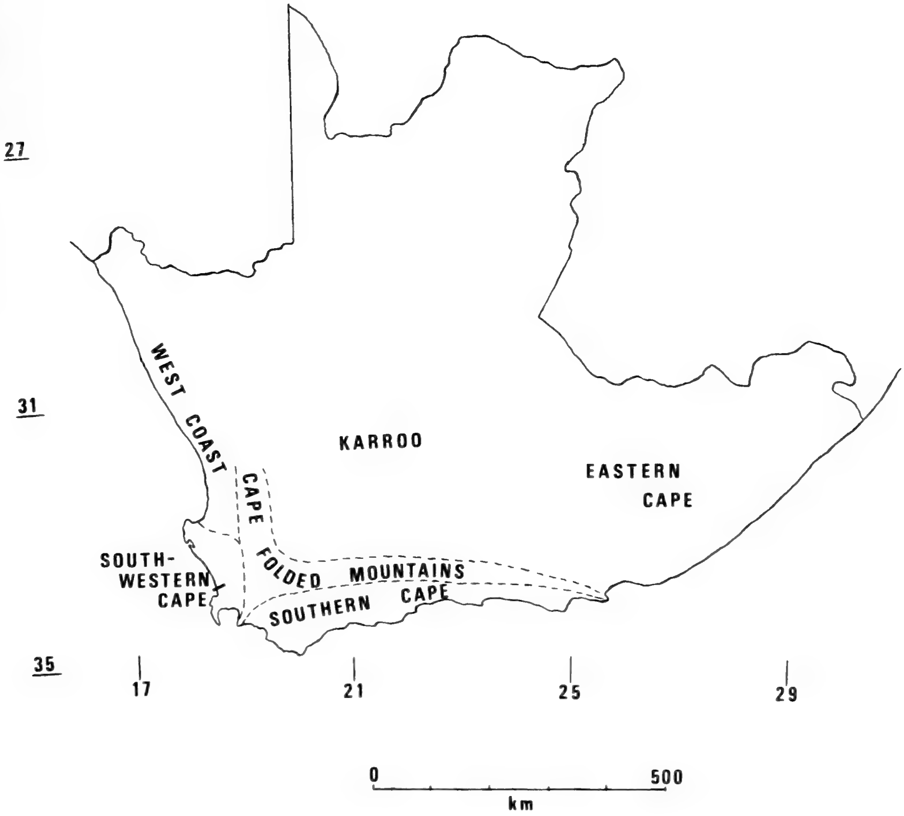

Fig. 2. The Cape Province, showing the regions referred to in the text.

Peninsula are made up principally of sedimentary and metamorphic rocks of the Cape System (Archaeozoic). The Cape Peninsula is connected to the mainland by an isthmus of largely unconsolidated late Cenozoic sediments, which extend along the coast to the northern limits of the region and beyond. Most of the Tertiary element of these deposits was apparently reworked during the Quaternary. Overlying some of the deposits of the coastal plain are unconsolidated aeolian sands which are probably largely Holocene in age.

The late Cenozoic deposits are significant because they contain the fossil occurrences dealt with in the present report. All the major, and most of the minor vertebrate fossil occurrences in the south-western Cape are located in either the Cape Flats or the Sandveld. In most instances the exposure of the fossiliferous deposits has resulted from the stripping of cover sands by erosion or human agency.

MODERN MAMMALS OF THE SOUTH-WESTERN CAPE PROVINCE

> *'In this Land of prester John ther was seene by our Men Lyons and monkeyes, Babownns a multid, with divers other Strange beastes as Antilops and many other deformed creattures verie strange to be Sene.'*
>
> Standish-Croft Journal, Cape of Good Hope, 23 June 1612.
> (Raven-Hart 1967: 59).

Like most of Africa, the south-western Cape Province is part of the Ethiopian faunal region and its mammalian fauna is unmistakably 'African' in character. It is an important part of this region since it was in this area that Europeans first encountered many of the mammals which characterize the Ethiopian fauna (Table 1).

By the time that the first permanent European settlement was established on the shores of Table Bay in 1652, ships of the great trading nations of Europe had already been calling at the Cape for more than 150 years and there are many log and journal references to the rich fauna of the region (see Raven-Hart 1967). Records such as that quoted above are, for the most part, brief and imprecise, although they indicate very clearly that the Cape had as rich a mammalian fauna as any other part of sub-Saharan Africa explored subsequently.

The indigenous inhabitants of the region were the beach-combing and pastoral Hottentots, whose presence apparently had little or no effect on the numbers and variety of mammals occupying the territory. The arrival of the European settlers, however, initiated the decline of both the indigenous people and animals. Hunting, wanton slaughter and destruction of natural habitats steadily escalated as the settlements grew and spread further afield and by the time that the first modern scientific records of fauna were being made in the 18th century, the fauna of the south-western Cape was already much depleted. Consequently, it is now impossible to make an accurate reconstruction of the nature and composition of the local mammalian fauna as it was early in the historic period.

The lists of local historic period mammals (Table 6, 89) were compiled on the basis of historical records, place names and such scientific accounts as are available and, although they are probably fairly comprehensive, they are of necessity provisional and subject to revision. The historical records are often vague, confusing and even fanciful, while the early scientific accounts also have their shortcomings. For example, the holotypes of some of the species listed in Table 1 were probably not from the south-western Cape region as it is here defined since locality records are vague. Most are simply recorded as being from the 'Cape of Good Hope' (see Ellerman *et al.* 1953), a term which is not necessarily synonymous with the south-western Cape. It is, however, probable that the holotypes of these species were representatives of populations which did, or still do, include the south-western Cape in their area of distribution.

TABLE 1

Some Ethiopian land mammals, the holotypes of which are from the south-western Cape Province or immediately adjacent regions.

*_Chrysochloris asiatica_ Linnaeus, 1758
*_Papio ursinus_ Kerr, 1792
*_Otocyon megalotis_ Desmarest, 1822
Canis mesomelas Schreber, 1775
*_Ictonyx striatus_ Perry, 1810
*_Mellivora capensis_ Schreber, 1776
*_Aonyx capensis_ Schinz, 1821
*_Genetta tigrina_ Schreber, 1776
*_Herpestes pulverulentus_ Wagner, 1839
Atilax paludinosus G. Cuvier, 1829
Hyaena brunnea Thunberg, 1820
Felis serval Schreber, 1776
*_Felis caracal_ Schreber, 1776
Orycteropus afer Pallas, 1766
*_Procavia capensis_ Pallas, 1766
Diceros bicornis Linnaeus, 1758
Equus zebra Linnaeus, 1758
Phacochoerus aethiopicus Pallas, 1766
*_Sylvicapra grimmia_ Linnaeus, 1758
*_Raphicerus campestris_ Thunberg, 1811
*_Raphicerus melanotis_ Thunberg, 1811
Oreotragus oreotragus Zimmermann, 1783
*_Pelea capreolus_ Forster, 1780
Taurotragus oryx Pallas, 1766
*_Lepus capensis_ Linnaeus, 1758
*_Bathyergus suillus_ Schreber, 1782
*_Georychus capensis_ Pallas, 1779
*_Cryptomys hottentotus_ Lesson, 1826
Pedetes capensis Forster, 1778
*_Praomys verreauxi_ A. Smith, 1834
*_Mus minutoides_ A. Smith, 1834
*_Acomys subspinosus_ Waterhouse, 1838
*_Otomys irroratus_ Brants, 1827
*_Tatera afra_ Gray, 1830

* Species of which indigenous populations still occur in the region.

During the 18th and 19th centuries, the European settlements spread beyond the confines of the south-western Cape and the destruction of flora and fauna became more widespread. By this time, however, scientific records were being made more frequently and specimens were being preserved in scientific institutions in Europe. Consequently, while the extinction of the blaauwbok (_Hippotragus leucophaeus_) in about 1790 passed unnoticed in South Africa, descriptions of this animal were already in existence and specimens were preserved in European museums. In addition, the 19th century saw the advent of the practice of wildlife conservation so that even in settled areas the preservation of species was assured. Unfortunately these developments came too late for the south-western Cape and by the end of the 19th century most of the larger mammals of this region were already extinct.

Such conservation as was undertaken in the Cape Province during the 19th century, and indeed for much of the present century as well, largely excluded the south-western Cape, at least in as far as the mammals were concerned. One hundred years ago there remained only the vestiges of the mammalian fauna which had flourished a scant 200 years earlier, and even this has continued to be depleted and disturbed.

Although the most obvious effect of human activities has been the reduction in the size of populations of locally occurring mammals, this is not a general rule. For example, in recent years there have been periodic plagues of gerbils (*Tatera afra*) in the grain-growing areas of the region, and it is the reduction or elimination of the natural enemies of this species which has largely contributed to this phenomenon.

Several of the mammals which had become extinct in the region have now been re-introduced, mainly into nature reserves, while other species not known to have occurred locally in historic times have also been introduced. The former category includes the eland (*Taurotragus oryx*), and the latter includes Burchell's zebra (*Equus burchelli*), the bontebok (*Damaliscus dorcas dorcas*) and springbok (*Antidorcas marsupialis*). Even exotic species have now become established locally. Apart from those species such as the brown rat (*Rattus norvegicus*) which have an almost world-wide distribution, there are the grey squirrel (*Sciurus carolinensis*), the fallow deer (*Dama dama*), the sambar deer (*Cervus unicolor*) and the Himalayan thar (*Hemitragus jemlahicus*).

In few other regions in sub-Saharan Africa has the natural pattern of the mammalian fauna been disturbed to the extent which is evident in the south-western Cape.

ZOOGEOGRAPHY OF THE SOUTH-WESTERN CAPE PROVINCE

INTRODUCTION

In the course of investigations into the fossil mammals of the south-western Cape it became evident that, in order to place these studies in perspective, account had to be taken of past and present patterns of distribution of African mammals. Pinniped distributions as they relate to the seal from Langebaanweg have already been discussed elsewhere (Hendey 1972*b*), and so the observations which follow concern only terrestrial species.

A study of late Cenozoic palaeozoogeography is necessarily based on an understanding of the modern biology and geography of the region in question, although even then a clear and unequivocal interpretation of past events is not always possible. This is at least partly due to the fact that there were marked changes in climate during this period in time and the nature and effects of such changes may be difficult to determine. The late Cenozoic climatic changes of southern Africa are not well documented or clearly understood and consequently many of the statements which follow are tentative and based on inadequate factual information. They could, however, provide a basis for future studies. As more becomes known of the fossil mammals of Africa and the nature of past climatic changes become better understood, the present conclusions may be tested and, when necessary, modified.

Darlington (1957: 420) summed up the basis of the present zoogeographic study by stating that it 'is only in the present that we can see exactly how animals really are distributed and how their distributions are related to space, climate, barriers, other organic factors, plant cover and each other'. The human activities and influences referred to earlier have, however, so altered the character of the modern flora and fauna of the south-western Cape that much of the information fundamental to the present investigation can now be obtained only by indirect methods. This is, of course, by no means a unique situation and many parts of the world are in a comparable or even worse state in this respect. Nevertheless, since sub-Saharan Africa includes large tracts of unspoilt countryside, it is as well to emphasize that this does not apply in the case of the south-western Cape.

This region differs from the rest of sub-Saharan Africa in other respects as well. It is the only part of the sub-continent to lie within a warm-temperate climatic zone and have a Mediterranean type of climate (*Cs* of Koeppen). Its climate is of considerable biological significance.

The rainfall, which is mostly cyclonic, falls mainly in the winter and the summers are long and dry. The precipitation varies considerably from place to place, the Cape Flats receiving only 400–500 mm per annum, while the annual total in the mountains only a few kilometres away may exceed 3 000 mm (Schulze 1965). The depressions which cause most of the precipitation pass from west to east in southern mid-latitudes and it is usually only in winter that they reach far enough north to affect the south-western Cape. There is a marked decrease in the rainfall northwards along the Cape west coast and north of the Orange River true desertic conditions prevail (the Namib Desert). The inland plateau is a summer-rainfall area and that part closest to the south-western Cape (the Karroo) is semi-arid. The southern Cape receives rain at all seasons, although in the western parts the totals are not high. Some of the higher mountains in these areas are snow-covered for short periods during winter.

The cold Benguela Current along the Cape west coast has a moderating effect on temperatures in the area. Cape Town has a mean annual temperature of 17°C and a relatively small mean annual range of 12,8° to 21,7°C. Frost is rare in the lower-lying areas and on the mountain slopes below 600 m.

The climate has been an important factor in the development of a unique vegetation in the region. As in other winter rainfall areas, evergreen bushes and shrubs with leathery or waxy leaves are predominant. The flora is very diverse and endemic species are abundant. This vegetation, which is usually referred to as 'Cape Macchia', may be subdivided into a number of groups, the distribution of which is largely dependent on the amount of rainfall. Forests are confined to well-watered and sheltered parts of mountain slopes, although most indigenous montaine forests have now been destroyed as a result of human activities. Grasses constitute a relatively insignificant element in the vegetation in all areas, but this applies particularly in the Sandveld and Cape Flats. The unique character of the local natural vegetation has attracted the interest of botanists for generations and there is an extensive literature on the subject. This vegetation is believed to have originated within the south-western Cape winter rainfall area (Levyns 1962).

The definition of the south-western Cape as a distinct geographical region is based principally on its climate and vegetation, and these in turn are determined by the latitude and physiography of the area.

PALAEOGEOGRAPHY

Brain & Meester (1964: 332) have pointed out that a 'fuller understanding of past climates will elucidate many of the problems concerning the distribution and systematic position of South African endemic (mammalian) species'. Unfortunately little generally acceptable work has been done on the late Cenozoic climatic changes of this country, although such changes undoubtedly occurred and, just as certainly, did influence the evolution and dispersal of local mammals.

There is evidence which shows that these climatic changes had a marked affect on the vegetation of the south-western Cape and adjacent areas. For example, the trunks of large trees have been found in excavations on the Cape Flats, an area which prior to the introduction of various exotic trees was covered by Cape Macchia and unvegetated sand dunes.

Much has been written about the Pleistocene climatic changes in South Africa and the principle of 'glacio/pluvial' correlations was once widely accepted. While it is now certain that such correlations are not generally applicable, it does seem likely that they have a certain validity in the case of the south-western Cape. At those times during the Pleistocene when there was a general lowering of world temperatures, there was apparently a shift towards the Equator of the world's climatic zones. In the south-western Cape the most obvious effect of such a shift would have been to bring the rain-bearing depressions into the area throughout the year, rather than just in winter as is presently the case. Van Zinderen Bakker (1967) has already suggested as much in a discussion on South African Pleistocene climates. If this was indeed the case, then the south-western Cape would have experienced a cool-temperate rather than warm-temperate climate and received rainfall throughout the year.

Butzer (1961) has stated as a general principle that the areas bordering the Mediterranean Sea experienced pluvial conditions synchronously with the higher latitude Pleistocene glaciations. He referred to these as 'Mediterranean pluvials' and concluded that they were 'Early Glacial' (Butzer 1961: 455). It is assumed that this principle applies for Mediterranean regions in the Southern Hemisphere as well.

The degree to which local climate changed during the colder phases of the Pleistocene has yet to be determined. Linton (1969) has recorded what he believed to be evidence of 'cryonival phenomena' in the south-western Cape. If his interpretation of the geological record is correct, it means that the lowering of temperatures in this region at certain times during the Pleistocene was sufficient to produce perennial snow cover on the mountains. Even today the higher peaks of the Cape Folded Mountains are snow-covered for short periods during winter and under colder conditions a snow cover for the duration of winter at least, is not difficult to visualize. Even without the perennial snows suggested by Linton, the presence of snow gathered for prolonged periods during winter would have had a marked effect on the local environment. For example, it would have served to keep local rivers and streams at higher levels during summer, in contrast to the position today when many local water-courses have a poor flow, or are completely dry during the largely rainless summer.

Thus, in theory at least, during those periods in the Pleistocene when the higher latitudes were glaciated, the south-western Cape is likely to have been far more verdant than at present. Conversely, the existing relatively dry phase would have been repeated during the Pleistocene 'interglacial' periods.

During the colder phases there was probably a northward expansion of the Cape flora and extensions to the areas covered by forest. Relict patches of such vegetation which are today found beyond the limits of their expected distribution (see Acocks 1953: 12) may thus be accounted for, although it is now difficult to distinguish between the effects of natural change and that induced by human influences.

It would be unrealistic to suppose that uniform changes in rainfall were experienced over the whole of the south-western Cape at any given time. Many local geographical factors would have to be taken into consideration and it is almost certainly impossible to reconstruct a detailed picture of climate and vegetation at various times during the late Cenozoic.

This region was probably never much more arid during the late Cenozoic than it is today, since many indigenous plant species would probably have become extinct if this was the case. Under more arid conditions moisture-demanding species may still have survived in isolated places where conditions remained favourable but, whereas major northward shifts of the flora were possible during wetter periods, the converse is not possible because of the situation of the south-western Cape at the southern continental extremity. This restricting influence, coupled with repeated climatic changes may have contributed to the extreme diversification of the local flora in which 'the majority of the species will vary from mountain to mountain' (Acocks 1953: 153).

The late Cenozoic climatic changes in the south-western Cape must have had a profound effect on the fauna of the region, perhaps most significantly in the limitation or otherwise of contacts between locally occurring populations and those further north (*vide infra*).

FAUNAL DISTRIBUTION IN THE SOUTH-WESTERN CAPE

In a discussion on the past and present dispersal of animals, Darlington (1957: 572) concluded that the 'South African fauna as a whole has evidently formed by southward movement (extension) of parts of the tropical African fauna. Replacements must have occurred both in the tropics and southward, but the absence of outright barriers has prevented the persistence of many relicts in South Africa. . . .'

Later he went on to qualify these remarks and in referring to the most southerly parts of the country he stated that 'climate has important effects on distribution of plants and animals in South Africa. Although the southern tip of Africa is not cold, it is climatically differentiated and also is isolated from the main part of the continent by a barrier of aridity that eventually retards southward dispersal of water-demanding organisms' (Darlington 1965: 110).

These quotations are relevant to many of the observations which follow and conveniently set the stage for a consideration of the south-western Cape fauna.

In an account of the biotic regions of southern Africa as indicated by the Amphibia, Poynton (1964: 206) commences his discussion on the pattern of amphibian distribution as follows:

'A cardinal feature of amphibian distribution in southern Africa is the north–east to south–west polarization of the fauna, there being one focal point in the Mozambique plain, *and another in the south-western Cape.*' The last part of his statement is emphasized here for obvious reasons.

In an earlier paper (Poynton 1960) he concluded that the south-western Cape amphibians are geographical equivalents of a north-temperate fauna and he regarded them as true south-temperate forms. In both papers he stresses the unusual character of the amphibian fauna of this region, which has 'a taxonomic bias quite different from that of the tropical fauna' (Poynton, 1964: 208).

While zoogeographic patterning is so marked in the Amphibia, Poynton (1964) found that this was little influenced by ecological factors and that similar habitats in the south-western Cape and south-east tropical Africa are occupied by completely different types of Amphibia. All these observations led to the conclusion that it is the aridity of the southern part of the central plateau which was the principal limiting factor in local amphibian distributions.

Although the south-western Cape is a significant and, in some ways, unique area in as far as the distribution and representation of one group of lower vertebrates is concerned, it does not necessarily follow that the mammals would exhibit the same degree of regionality of character. Nevertheless, the mammalian fauna does differ in certain respects from those of regions further north.

For example, a comparison between the modern mammals of the south-western Cape and those of south-eastern Kenya shows a considerable variation in the commonality of species in different orders (Table 2). Regional differences are most evident amongst small mammals (e.g. insectivores) and those which are highly selective as to habitat (e.g. primates). They are least evident in that group which is least dependent on environmental factors (i.e. the carnivores). Such differences as do exist amongst the carnivores are largely confined to the smaller species (viverrids), which might therefore be grouped with other small mammals for the purposes of accounting for observed regional differences. The larger herbivorous species (e.g. bovids) occupy a more or less intermediate position in respect of the species commonality of the two regions.

TABLE 2

Mammalian species occurring in south-eastern Kenya[1] and the south-western Cape Province.

	Insectivores and primates	Equids and bovids	Carnivores
South-western Cape species . . .	6	10	21
South-eastern Kenyan species . .	8	25	27
Species common to both areas . .	0	6	17
Index of resemblance (%)[2] . . .	0	60	81

[1] Based on records for the Tsavo National Park (Williams 1967) and supplemented from records given by Dorst & Dandelot (1970).
[2] Simpson 1967.

In dealing with the distribution of present-day species it is clear that the narrow definition of the south-western Cape given earlier is not the most convenient, but that in this instance the Cape Folded Mountains and southern

Cape regions should also be included. Meester's (1965) 'South-West Cape Biotic Zone' covers all these areas and it is here termed simply the 'Cape Biotic Zone', of which the south-western Cape is a subdivision.

The following small mammals are listed by Meester as being endemic to the Cape Biotic Zone:

Bathyergus suillus, *Praomys verreauxi*, *Acomys subspinosus* and *Tatera afra*.

Two endemic forms are included amongst the larger mammals, namely, the recently extinct blaauwbok (*Hippotragus leucophaeus*) and the bontebok (*Damaliscus dorcas dorcas*).

The blaauwbok was known in historic times only from the southern Cape, but it formerly occurred in the south-western Cape as well. Its status as a species distinct from the roan and sable antelopes (*H. equinus* and *H. niger*) has never been seriously questioned and it was either an autochthonous species, or, less probably in the light of available evidence, a more widespread species which survived later in the Cape Biotic Zone than elsewhere.

The bontebok was formerly given full species status (*D. pygargus*), but is now regarded only as a subspecies of *D. dorcas*. It is recorded in a natural state only in the western parts of the southern Cape, several hundred kilometres from the nearest record of its close relative, the blesbok (*D. d. phillipsi*) in the eastern Cape. This species presumably had a continuous distribution in the fairly recent past (? late Pleistocene) and the split between the two populations was probably the result of environmental changes which will be discussed later. *D. dorcas* is endemic to South Africa.

Another bovid which is largely confined to the Cape Biotic Zone is the grysbok (*Raphicerus melanotis*), although its range also extends into the eastern Cape where it is less common. By contrast, the mountain zebra (*Equus zebra*) occurs in the Cape Folded Mountains and also in parts of South West Africa. These two species are mentioned here as examples of mammals which, on the one hand, range from the Cape Biotic Zone into the comparatively well-watered south-east of the subcontinent and, on the other, range from the Cape Biotic Zone into the arid south-west.

Another significant feature of the distribution patterns of larger southern African mammals is that there are many essentially tropical species whose ranges extend into South Africa but stop short of the Cape Biotic Zone. These include the giraffe (*Giraffa camelopardalis*), the impala (*Aepyceros melampus*) and various species of waterbuck (*Kobus* spp.).

It is thus evident that the mammalian fauna of the most southerly parts of Africa is distinguishable from that of the subtropical and tropical parts of the continent, and that there is a distinct and significant patterning in the distribution of species. Some forms occur in the Cape Biotic Zone and elsewhere in the Ethiopian Region, some are endemic to this zone, some range from this zone into the arid south-west of the continent, others range into the south-east, and finally there is that group whose ranges do not extend into the Cape Biotic Zone. This zone might, therefore, be regarded as a focus and area of overlap of two distinct elements of the Ethiopian mammalian fauna, namely, that of the arid south-west and that of the well-watered south-east. These groups are superimposed on a third element, the endemic species of the region. On purely theoretical grounds it is possible that in the past the relative importance of each of these three elements may have changed in accordance with prevailing climatic and other factors.

Patterns of animal distribution are determined by geographical factors and are largely dependent upon the ease with which migrations can take place. In this connection Simpson (1967) has defined three categories under the heading of 'paths of faunal interchange', and although his work was based on inter-continental migrations of animals, the definitions can be applied equally well in a more restricted sense. They are as follows:

(1) Corridor route—'along which spread of many or most of the animals of one region to another is probable' (p. 87).
(2) Filter route—'across which spread of some animals is fairly probable but spread of others definitely improbable' (p. 87).
(3) Sweepstakes route—'across which spread is highly improbable for most or all animals but does occur for some' (p. 88).

Migrating mammals can approach the south-western Cape by any of three routes:

(1) From the north along the western coastal plain.
(2) From the interior plateau across the Cape Folded Mountains.
(3) From the east across the most south-westerly parts of the Cape Folded Mountains (the Hottentots Holland Mountains).

Each of these routes has its limitations and each could conceivably have had its character altered by past climatic and physiographic changes.

The northern route is the only one at present which might be regarded as a true 'corridor route' since there are no barriers of any significance along the Cape west coast and only the most southerly of the rivers traversing this route are perennial. Beyond the northerly limit of the Cape Folded Mountains the escarpment into the interior is low and discontinuous, so this route also offers easy access to the interior plateau. However, both forks of this route lead into arid (the Namib Desert) and semi-arid (the Karroo) regions and under existing climatic conditions it is likely to be used only by those animals which are adapted to dry conditions.

On the previously stated assumption that the most southerly parts of South Africa were never much more arid at any time during the late Cenozoic, it is concluded that the arid south-west element in the fauna of the extreme south was probably never much more prominent than it is today.

During those periods when the south-western Cape and immediately adjacent areas were wetter than at present, the northern route may have been used by animals originating in the interior plateau which had previously not been able to penetrate the semi-arid Karroo.

The alternative for such animals would have been to use the second of the access routes, namely, that across the Cape Folded Mountains, although even under the most favourable environmental conditions this was probably never more than a 'filter route' because of the obstacles presented by the mountains. There is a fairly easy route through the mountains from the Karroo into the southern Cape by way of the Hex and Breede River valleys, but passage into the south-western Cape would always necessitate the crossing of mountains.

The last of the access routes, that from the southern Cape, has a number of disadvantages and it is the one which would have had its character most altered by past climatic and physiographic changes. At present the Hottentots Holland Mountains form a barrier between the southern and south-western Cape which is probably sufficient to inhibit the free movement of some mammals. Consequently, it might now be regarded as a 'filter route'. The absence from the modern fauna of the south-western Cape of species such as the bontebok, blaauwbok, reedbuck (*Redunca arundinum*) and bushbuck (*Tragelaphus scriptus*) may in part be due to the presence of this mountain barrier.

At those times during the Pleistocene when the sea level was lower than at present, access to the south-western Cape around the southern tip of what is today Cape Hangklip must have been much easier. Such conditions probably did prevail during the late Pleistocene (the last glacial period) and both the blaauwbok and reedbuck were present in the south-western Cape at this time. Their extinction locally during the Holocene may have been due to a variety of factors, including the possibility that they failed to adapt to the changing environment. In this connection it is worth recording that bontebok introduced into the Cape Peninsula from the southern Cape have not adapted well to their new surroundings and remain in poor physical condition if left to the natural resources of the area.

The southern route also has disadvantages at its eastern end. Much of the southern Cape between Mossel Bay and Humansdorp, a distance of about 300 km, is an area of natural forest under existing climatic conditions, although little forest remains as a result of recent human activities in the area. This forested area, coupled with the relatively narrow coastal plain, must serve as a barrier to the free movement of many animals along this route.

This part of the southern route would, however, have changed character when sea level was lower than at present. The proof that this did indeed happen during the late Pleistocene and the effect it had on the local fauna was recently recorded by Klein (1972). He has suggested that the exposed continental shelf in the Plettenberg Bay area may have been a grassy plain about 75 km wide during the last glaciation, and that it was populated by an appropriate plains fauna drawn from the interior plateau. It may have been at this time that the distribution of *Damaliscus dorcas* was continuous between the areas occupied by the surviving populations of the bontebok and blesbok. With the rise in sea level again during the Holocene part of the late Pleistocene population of this species became cut off in the western part of the southern Cape. Here it survives as a relict population subspecifically distinct (*D. d. dorcas*) from the main body of the species (*D. d. phillipsi*) in the eastern Cape and interior.

If the wide, grassy coastal plain envisaged by Klein extended as far as the south-western Cape, and there is no reason to suppose that it did not, then it would have provided an ideal 'corridor route' between this region and the eastern Cape. Consequently, not only southern Cape mammals would have gained access to the south-western Cape as suggested earlier, but also species from still further afield.

While the situation in the late Pleistocene can be gauged with some confidence, it becomes progressively more difficult further back in time to determine the nature of both climatic and physiographic changes. Nevertheless, it is fairly certain that similar changes did take place earlier and that the character of fossil faunas was dependent upon the accessibility of the south-western Cape to the rest of the subcontinent.

One final point concerning the southern access route relates to the nature of the easterly outlet to the southern Cape. At present the semi-arid Karroo stretches almost as far as the east coast in the vicinity of Port Elizabeth, near to the easterly terminus of the Cape Folded Mountains. At any time when the rainfall in that area was lower than at present, the semi-arid barrier may have extended through to the Indian Ocean (see Cooke 1964: fig. 10). The Cape Biotic Zone would then have been completely sealed off from the north by desert and semi-desert stretching from the Atlantic to the Indian Oceans.

It may be concluded that while the south-western Cape was never completely isolated from the rest of the subcontinent in a zoogeographic sense, it is so situated that under certain conditions faunal interchange between it and adjacent regions may have been very limited. The south-western Cape has probably been occupied by at least some species endemic to the most southerly parts of Africa throughout that period covered by the fossil mammal record (late Pliocene to Holocene), while the arid south-west element of the Ethiopian fauna was never much more prominent than it is today, although the south-east African element probably has been more prominent on occasions.

FAUNAL DISTRIBUTION IN SOUTH AFRICA

Although a consideration of the zoogeography of South Africa as a whole is beyond the scope of the present report, some comments on this subject are appropriate.

During the Cenozoic the fauna of southern Africa can have changed its character in only two ways, namely, by evolution *in situ* and by the immigration of animals from the north. There is no evidence to suggest that this area has been a major centre of mammalian evolution in the late Cenozoic and not even the endemic mammalian genera are necessarily autochthonous. Almost all the recorded genera of the local late Cenozoic are also known from elsewhere in Africa, or even further afield and there are probably very few which had their origins in southern Africa. There are, however, possible exceptions. For example, the curious antelope, *Pelea*, is today confined to southern Africa and is also unknown as a fossil elsewhere. There are probably a number of exceptions amongst the smaller mammals as well (e.g. *Chrysochloris*, *Bathyergus*).

The contribution that the subcontinent has made to the Ethiopian mammalian fauna is most likely to have originated largely in the arid south-west, an area which includes the Kalahari and Namib Deserts. This is Africa's most extensive arid region south of the Sahara. The previous existence of an arid corridor between south-west and north-east Africa has been the subject of a number of investigations (see Van Zinderen Bakker 1969: 139), and the desertic faunas of these areas do have some mammalian species in common (e.g. *Oryx gazella*, *Madoqua kirki*). Such species could perhaps be southern African in origin.

It is likely that, for the most part, the mammals of the subcontinent had their origins elsewhere and that these were added to the local fauna by immigration from the north and that local differentiation of these forms was confined to lower taxonomic categories. Apart from the endemic bovid genera, *Pelea* and *Antidorcas*, larger mammals which are endemic to the sub-continent include *Hyaena brunnea*, *Connochaetes gnou* and *Damaliscus dorcas*, while recently extinct forms include the quagga (*Equus quagga*) and blaauwbok.

The last two are part of a category of extinct 'Cape' mammals, so named because they were largely confined to what is today the Cape Province. Certainly none is recorded from as far north as the Tropic of Capricorn. The Cape lion (*Panthera leo melanochaita*), the Cape warthog (*Phacochoerus aethiopicus*) (see Ewer 1957*a*) and the Cape hartebeest (*Alcelaphus buselaphus caama*) are other members of this category.

The suggestion has been made that the southern African fauna includes, or has included late survivors of species which are, or were already extinct elsewhere (e.g. Hendey 1969). There can be little doubt that this supposition has some validity, but locally endemic species are not necessarily primitive forms. For example, *Hyaena brunnea* is more specialized in certain respects than its East African counterpart, *Hyaena hyaena*.

On the other hand, the occurrence of a boselaphine and agriotheriine in the late Pliocene fauna from Langebaanweg when these two groups were apparently unrepresented elsewhere in sub-Saharan Africa, suggests that there was a tendency for certain species to persist for longer in the extreme south. In East Africa during the late Pliocene and early Pleistocene, the Bovidae were already represented exclusively by the genera which characterize the modern bovid fauna of the Ethiopian region, but in South Africa both boselaphines and ovibovines (*Makapania*) were still present. Southern Africa during this period in time may thus be regarded as a zoogeographic counterpart of the Indian subcontinent, with tropical Africa as a centrally situated region in which much of the development of the Ethiopian mammalian fauna took place. East Africa had an African bovid fauna at this time, but boselaphines and ovibovines survived in southern Africa and hippotragines, reduncines and alcelaphines survived in India.

In addition and based on purely negative evidence, the late Pliocene fauna of at least the extreme south of southern Africa had yet to be supplemented by mammals such as *Hippopotamus*, although they were already widespread in East Africa at the same time.

It is certainly not surprising that the fauna of an area situated at a continental extremity, with no possible access to other land masses, should develop certain unique characteristics. Similarly it is to be expected that the most southerly part of South Africa would itself have a fauna which differs in certain respects from that of the rest of the subcontinent, especially in view of the factors discussed earlier. Interpretation of the southern African fossil record, and that of the Cape Biotic Zone in particular, must, therefore, take zoogeographical factors into account.

Fossil Mammal Occurrences in the South-western Cape Province

General observations on the more important fossil occurrences in the south-western Cape have already been published (Hendey 1969), while a few more detailed accounts of some are also available (e.g. Singer 1957; Hendey 1968). Some earlier statements require revision in the light of more recent investigations and some occurrences not previously recorded will be mentioned in the course of the present report. An account is therefore given of those which are relevant.

A. QUATERNARY OCCURRENCES

1. *Coastal middens*

A large number of coastal hominid occupation sites dating from the Late Stone Age are recorded in the south-western Cape. All are Holocene in age and all those specimens from coastal middens which will be referred to are likely to date from the latter part of this epoch. The earliest date recorded for an excavated midden in the south-western Cape is 3220 ±55 B.P. (Van Noten 1967) and it is unlikely that any of the relevant specimens are older than this. They may in fact be much younger, since the local middens were still being added to early in the historic period (*post* 1500 A.D.).

Although the middens are a potentially useful source of dateable faunal material, such specimens as were available were acquired in a haphazard manner and are thus a poor reflection of the numbers and variety of mammalian remains represented in the middens. Only three carnivore species, namely, *Arctocephalus pusillus*, *Mirounga leonina* and *Canis mesomelas*, were represented in the South African Museum's collections from local middens and only the first-mentioned is common.

2. *Fish Hoek* (34° 7'S, 18° 25'E)

There are a number of sites of archaeological interest near Fish Hoek in the Cape Peninsula, notably Peer's or Skildegat Cave. Areas of wind erosion on the northern and southern slopes of the ridge which includes Peer's Cave have yielded archaeological and palaeontological material from time to time. Such material from the northern slope includes a leopard mandible which is described in this report. Although this specimen is regarded as Holocene in age, others from the same vicinity apparently date back to the Pleistocene. The latter include the fragmented skull of a *Megalotragus*, the giant alcelaphine which is not known to have survived into the Holocene. Although this specimen and the leopard mandible appear identical in preservation, they are not necessarily contemporaneous.

3. *Tygerfontein* (Approximately 33° 23'S, 18° 12'E)

This is one of the many localities in the region from which only a single specimen is recorded, in this instance an almost complete skull of *Mellivora capensis*, which was presented to the South African Museum in 1968. The farm Tygerfontein is situated on the coast approximately 65 km north of Cape Town, but nothing is known of the mode of occurrence of the skull and it was apparently without associations. It is regarded as being Holocene in age.

4. *Sea Harvest, Saldanha* (33°S, 17° 57′E)

This previously unrecorded locality is situated on the north-western shore of Saldanha Bay and has yielded a fairly large assemblage of fossils. They occur in small shelters in a limestone cliff immediately west of the Sea Harvest Corporation factory. The occurrences are strikingly similar to those at Swartklip (Hendey & Hendey 1968), except that the deposits incorporating the fossils are largely unconsolidated. The few that are in consolidated deposit are undoubtedly older than the remainder and they could date back to the Pleistocene, but they constitute an insignificant proportion of the available assemblage and none is included in the systematic descriptions of this report.

The nature of the occurrences suggests that, as at Swartklip, the fossils were accumulated in animal lairs. A feral cat has in fact been observed occupying one of the shelters and this animal may still be adding the remains of its prey to the bone accumulations. There are no indications that any of the fossils accumulated as a result of hominid activity and the shelters are small enough to preclude the possibility of hominid occupation. They may, however, have been larger before the cliff in which they are situated was eroded to the extent it is today. This appears to have been the case with one shelter near the north end of the cliff and which is now filled with partly consolidated deposit incorporating marine shells and stone artefacts. This shelter clearly was a hominid occupation site, but unlike the others it has produced no fossils other than the marine shells.

Both large and small mammals are included in the Sea Harvest assemblage, while non-mammalian remains are comparatively rare. Very large mammals, such as elephant and rhinoceros, are represented by skull parts of very young individuals, although medium- and small-sized mammals are represented by both adults and juveniles. In general the preservation of specimens is good, although cranial remains tend to be fragmentary. Postcranial bones are often complete in all respects.

Almost all the species recorded are known to have occurred in the south-western Cape in historic times. Exceptions are *Redunca*, *Connochaetes* and *Antidorcas*. Most species are apparently indistinguishable from their extant counterparts, although the Carnivora include varieties which are larger than the modern forms and the Perissodactyla include the extinct species, *Equus capensis*.

As at Swartklip, a wide variety of carnivores is represented and some, if not all of these species are likely to have been occupants of the shelters. Although much of the assemblage probably accumulated as a result of carnivore activity, other factors are undoubtedly involved. For example, a few of the fossils have been gnawed by porcupines and *Hystrix* is included in the assemblage. This species is also regarded as a likely one-time occupant, fossils having been added to the assemblage as a result of its bone collecting activities. In addition, some specimens almost certainly represent the remains of animals which died in the shelters.

Although the Sea Harvest and Swartklip assemblages are essentially similar in the variety of species represented, there are at least two striking differences in the nature of the assemblages.

Firstly, the Sea Harvest assemblage is characterized by an appreciably higher proportion of small mammals. These include large numbers of rodents (e.g. *Bathyergus*, *Georychus*, *Otomys*), a hare (*Lepus*) and dassie (*Procavia*). The latter is particularly common, but is not represented at Swartklip at all. The cranial remains of this species are very fragmented, which suggests that the animals were the prey of some carnivore and do not merely represent the result of natural fatalities in a dassie lair. Although the Sea Harvest and Swartklip sites are in essentially similar situations adjacent to the present coastline, the differences in the numbers and varieties of small mammals represented may be taken to indicate one or both of the following factors:

(1) The environment of the two localities differed at the time that their respective assemblages were accumulated and they cannot, therefore, be contemporaneous.
(2) The species responsible for adding to the two assemblages were not the same.

Confirmation of the first factor is afforded by the other major difference between the two assemblages. Both penguins (*Spheniscus*) and seals (*Arctocephalus*, *Lobodon*) are recorded from Sea Harvest, but no marine animals are known from Swartklip, indicating that the sea was close to the former site at the time when the fossils in the unconsolidated deposit were accumulated and that it was some distance away at the time that the Swartklip fossils were accumulated. There is a parallel to this situation in the faunal record of a single site in the southern Cape (Nelson Bay Cave), which was recently described by Klein (1972). There the advent of marine faunal remains in the succession was correlated with a rise in sea level from a late Pleistocene minimum to a level similar to that of the present early in the Holocene. On this basis the Sea Harvest fossils were tentatively regarded as Holocene in age, while those from Swartklip were regarded as late Pleistocene. This conclusion is supported by other faunal evidence, including the nature of some carnivore species represented (*vide infra*).

5. *Swartklip* (34° 5′S, 18° 41′E)

The occurrences at Swartklip on the False Bay coast have already been dealt with in some detail (Hendey & Hendey 1968), although a considerable number of additional specimens have since been recovered and some of the earlier statements about the fauna and its associations require revision. The Swartklip faunal list has, however, not been significantly altered. Previously unrecorded species include two carnivores (*Vulpes chama*, *Felis libyca*), which are described elsewhere in this report.

In the 1968 report a distinction was made between the material from Swartklip described by Singer & Fuller (1962) and Ewer (1962) and that from Sites 1 and 2. It was recently established that the 'Singer/Fuller Occurence' was actually a block of fossiliferous deposit which had fallen on to the present beach from Site 1 (i.e. that exposure from which the greater part of the Swartklip assemblage is derived). Almost all the specimens from this locality which are described in this report are from Site 1, the only exceptions being some belonging to *Canis mesomelas* and *Hyaena brunnea* which are from Site 2. The source of these specimens is indicated in the relevant specimen lists.

An additional point regarding the origin of at least a part of the Site 1 assemblage is that the porcupine must also have been involved in the bone-collecting at the site. A few of the Site 1 fossils have now been found to show porcupine gnaw-marks, so it is likely that at least a part of the assemblage resulted from the bone-collecting activities of this animal. The greater part of the assemblage is, however, still regarded as representing the results of carnivore activity and the remains of animals which died in the shelters.

The Swartklip fauna was reported in 1968 to be late Pleistocene or Holocene in age, but the latter alternative is now dismissed in the light of evidence discussed in connection with the Sea Harvest occurrence and the fact that ostrich eggshell from Site 1 has given a C14 date of more than 40 000 years (I-6840). In addition the geological context of the fossiliferous deposits suggests that they date from the earlier part of the last glacial (K. W. Butzer, pers. comm.). The statement that 'the lairs in which the fossils accumulated were (possibly) still being occupied after the arrival of the first settlers from Europe in 1652' (Hendey & Hendey 1968: 71) can no longer be accepted, although it is fairly certain that there was at least one hyaena lair in the area at some time during the historic period.

Of all the more important assemblages from the south-western Cape, that from Swartklip is the least problematical. The fauna has an essentially 'modern' character but the species represented are in many cases sufficiently different from their extant counterparts to indicate that the fauna must be pre-Holocene in age. This applies in the case of the carnivores which are to be described later. Some species are sufficiently well-represented to allow good definition of their dental and osteological characters and the Swartklip fauna provides a great deal of information on the nature and character of the local late Pleistocene mammalian fauna, exclusive of the very small species.

6. *Lime Quarry, Saldanha* (Approximately 33°S, 17° 57′E)

A number of specimens acquired by the South African Museum in 1918 and 1919 are recorded as being from a lime quarry, south of Hoedjies Bay, which is the old name for the town of Saldanha. Cooke (1955: 166) has already made reference to this assemblage, part of which is now lost.

This occurrence is clearly not the same as the Sea Harvest one, although the two must be in the same general area. The preservation of the Lime Quarry fossils suggests that they are older than those from Sea Harvest. The Lime Quarry assemblage also includes the seal, *Arctocephalus*, which indicates that it too must date from a period when relative sea level was similar or higher than at present. The Lime Quarry *Arctocephalus* is, however, a variety which is distinct from the extant *A. pusillus* and this suggests that it might be pre-Holocene in age. Unfortunately the characters which distinguish the Lime Quarry *Arctocephalus* from *A. pusillus* cannot be observed in the Sea Harvest material, so that the relative ages of the two faunas cannot be determined on these grounds. It is, however, tentatively concluded that the Lime Quarry fauna is earlier and that it probably dates from the latter part of the Pleistocene.

7. *Melkbos* (33° 40'S, 18° 26'E)

This occurrence has already been dealt with in detail (Hendey 1968) and little of significance has been added to the assemblage. One previously unrecorded species which was recently recognized is the giant alcelaphine, *Megalotragus*, and this lends support to the inferred Pleistocene age of the fauna from the site. The view that it probably predates the Swartklip assemblage is maintained.

The possibility that the fauna has Middle Stone Age associations requires further qualification since Early Stone Age artefacts have recently been found in surface association with the fossils. The cultural associations of the fossils can now be established with certainty only by controlled excavations at the site.

8. *Bloembos* (Approximately 33° 17'S, 18° 11'E)

Reference to this site has already been made by Cooke (1947, 1955) and nothing further can be added to his comments. No additional specimens have been acquired from this locality since 1906.

9. *Elandsfontein* (33° 7'S, 18° 14'E)

The fossil occurrences on the farm Elandsfontein near Hopefield are probably the best known in the region. Many of the species, and their geological and archaeological associations have already been described (see Singer & Wymer, 1968).

The age of the Elandsfontein fauna is more problematical than would appear from the various publications relating to the site. It is usually regarded as a single unit dating from the Vaal-Cornelia Faunal Span of the South African Quaternary (e.g. Cooke 1967), but it is evident that the specimens are not all contemporaneous, a fact which is clearly demonstrated by the carnivores which are described in this report. Artefacts from the Early, Middle and Late Stone Ages, as well as some dating from the historic period, have been recovered in surface association with fossils and the suggestion has been made that some elements of the fauna may be associated with each of these periods of hominid occupation (Hendey 1969). Most of the fossils are apparently contemporaneous or broadly contemporaneous with the Early Stone Age ('Final Acheulian') occupation and the only definitely recorded cultural/faunal association relates to this period in time (Singer & Wymer 1968).

In contrast to the other faunas already mentioned, that from Elandsfontein includes a number of extinct genera (e.g. *Simopithecus*, *Megantereon*, *Libytherium*), as well as a larger proportion of extinct species. Almost all the identified species have already been recorded elsewhere, but the Bovidae (A. W. Gentry & L. H. Wells, in preparation) and the Carnivora (*vide infra*) do include some apparently unique species.

The Elandsfontein carnivores have already been the subject of one detailed study (Ewer & Singer 1956), but many additional specimens are now available and a number of species not previously recorded at the site are known. Although most of the recorded carnivore specimens from Elandsfontein are described in this report, some specimens were not available as they are no longer in the South African Museum's collection.

8. *Elandsfontein Wes* (33° 7′S, 18° 13′E)

A few kilometres west of the Elandsfontein site is a smaller wind-eroded area from which a few fossils have been recovered. Such occurrences are not uncommon in the Sandveld and that at Elandsfontein Wes is included because *Hyaena brunnea* is represented in the assemblage. On the basis of its characteristics this material is concluded to be late Pleistocene in age.

B. LATE TERTIARY OCCURRENCES

There is only one late Tertiary occurrence relevant to the present report.

Langebaanweg (32° 58′S, 18° 9′E)

Since the first reported discovery of fossils in the phosphate quarries at Langebaanweg (Singer & Hooijer 1958), these quarries have become one of the most prolific sources of fossil vertebrates in South Africa. The remains of a large number of marine, fresh-water, terrestrial and flying vertebrates have been recovered, the fossils coming principally from the only quarry which is still being mined, namely, 'E' Quarry (Hendey 1970*a*). Some invertebrates, coprolites and fossil roots are also known. The fauna is significant not only because of its abundance and diversity, but also because it is the only one of Pliocene age being actively investigated in southern Africa (Hendey 1970*b*, 1972*c*, 1973*b*). It predates the more widely known South African australopithecine sites (Brain 1970), and is comparable in age to East African faunas such as Koobi Fora I (Maglio 1971) and Kanapoi (Patterson 1966).

Several phosphate occurrences are recorded in the south-western Cape (Du Toit 1917; Haughton 1932*a*), but those at Langebaanweg are the only ones being commercially exploited at present. Unpublished studies on the geology of the Langebaanweg area have been undertaken in addition to those referred to above (African Metals Corporation and Chemfos Limited records), and a further detailed study is in progress (A. J. Tankard, in preparation).

On the basis of the geological and palaeontological information presently available, the deposits at Langebaanweg are categorized as follows:

Varswater Formation—An occurrence of largely unconsolidated clastic sediments located on the farms Varswater and Langberg Suid and which are rich in phosphate. The deposits are made up mainly of marine, estuarine and terrestrial sands in which fossils of late Pliocene age are incorporated. The largest exposures of these deposits are at the scene of current mining operations ('E' Quarry), while those in an earlier open-cast mine ('C' Quarry) are now obscured by water and sand infill.

Unnamed deposits—Mined-out phosphate occurrences located on the farm Langberg, approximately 2 km east of the Varswater deposits which yielded fossils of late Pliocene age as well as some of apparently (? early) Pleistocene age. This mine (Baard's Quarry) has now been back-filled and the relationships of these deposits to the Varswater Formation are uncertain, although records suggest that those which contained the Pliocene fossils were fluviatile in origin. (Table 3)

TABLE 3

The stratigraphy of the Langebaanweg area.

Age	Varswater area ('E' Quarry)		Langberg area (Baard's Quarry)
Pleistocene/Holocene . . .	Surface bed		Surface bed
Pleistocene	—		Unnamed deposits
Pliocene	Varswater Formation	Bed 3b Bed 3a Bed 2 Bed 1	Unnamed deposits

The most significant palaeontological discoveries have been made in 'E' Quarry (Fig. 3). Although a detailed account of the geology of this site will be published elsewhere, observations made in the course of the fossil recovery program are summarized here.

DEPOSITS OF 'E' QUARRY (Table 4)

The exposed deposits consist largely of unconsolidated or partly consolidated medium-grade sands in which the commercially exploited granular phosphate occurs. These deposits are fossiliferous only in the lower levels. They are underlain by a clay of undetermined thickness and overlain by more recent aeolian sands which vary in depth from about 2 to over 40 metres. There are considerable differences in the appearance of the 'E' Quarry sediments both vertically and horizontally, and there are some important differences in the succession in the eastern and western parts of the quarry. The two areas are separated by a drainage channel ('Main Stream') which runs from near the north wall to the south-west, following the general dip of the deposits. In most parts of the quarry mining has extended below the level of the water-table, which has fallen as a result of dewatering of the mine. Main Stream has

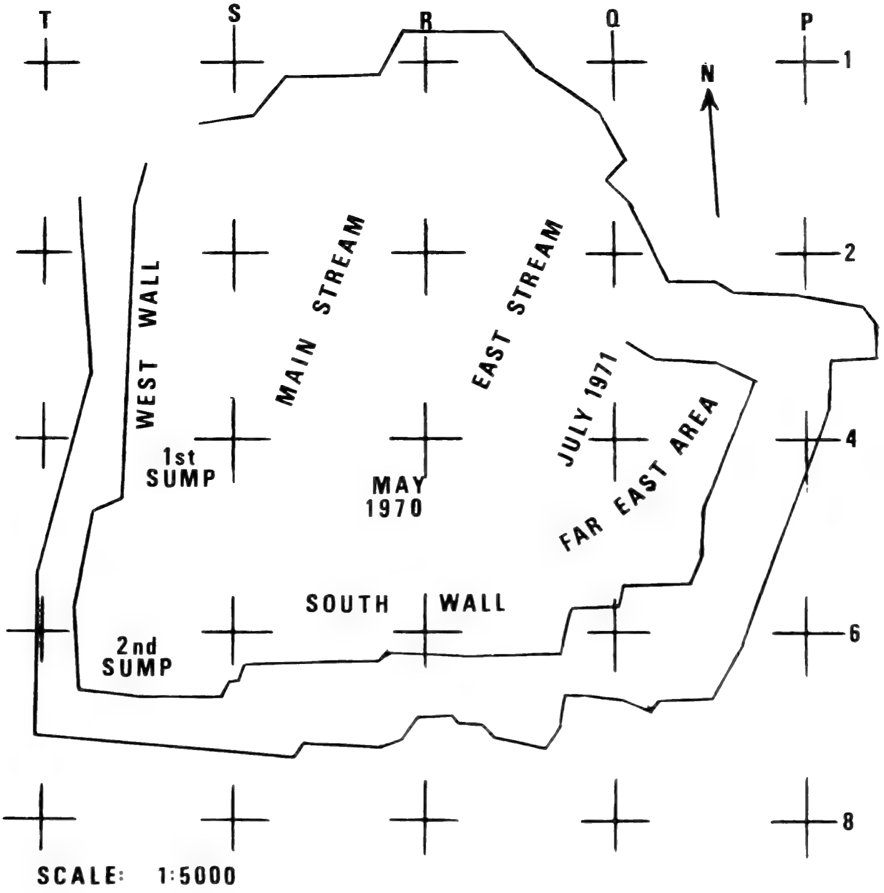

Fig. 3. Sketch plan of 'E' Quarry, Langebaanweg (July, 1972), showing collecting areas. The deposits exposed are as follows:

Bed 3a—West Wall
Bed 2 —All areas
Bed 1 —1st Sump, 2nd Sump, South Wall, Far East and July 1971 areas.

become progressively less active and is now ephemeral. It is, nevertheless, a significant feature, since apart from being the boundary between the east and west successions, the deposits of its bed and banks differ somewhat from those elsewhere in the quarry in that they are coarser-grained and completely unconsolidated. Main Stream may follow a drainage line of considerable antiquity.

Three stratigraphic units are recognized in the 'E' Quarry exposures of the Varswater Formation (Fig. 4).

Table 4

The stratigraphy of 'E' Quarry, Langebaanweg.

Age	Stratigraphic Unit		Lithology	Depositional Environments	Faunal Unit
Pleistocene/Holocene .	Surface bed		Sands, calcrete, etc.	Terrestrial	—
Pliocene	VARSWATER FORMATION	Bed 3b	Medium-grade sands (Phosphatic) 7,5 m	Estuarine	—
		Bed 3a			Estuarine Faunal Unit 2
		Bed 2	Medium-grade sands 2 m	Estuarine and Terrestrial	Estuarine Faunal Unit 1
		Bed 1	Sand with boulders, cobbles and pebbles of phosphate rock 1 m	Marine Littoral	Marine Faunal Units 1 and 2
?	—		Clay	?	—

Bed 1

The lowest horizon is characterized by the presence of phosphate rock. It was originally believed to underlie those deposits in which the bulk of the vertebrate fossils occur (Hendey 1970*a*), but subsequently it was thought to postdate and laterally truncate these deposits (Hendey 1970*b*). The original conclusion has now been shown to be correct, although it is still uncertain whether or not it underlies the whole of the next horizon in the succession.

In the absence of detailed petrographic studies it is difficult to interpret the origins and development of Bed 1, since it evidently had a complex history. However, at least two generations of phosphate rock are represented. The first is an extremely well-indurated rock, brown in colour, which occurs as large irregularly-shaped boulders with abraded surfaces, around which are scattered well-rounded cobbles and pebbles of the same material. Rare instances are known of embedded and unidentifiable bone fragments. The age and mode of origin of the rock is still conjectural.

Interspersed with this indurated phosphate rock is a partly cemented brown phosphate rock, which locally forms a matrix embedding elements of the older and more indurated rock. A suite of well-preserved marine invertebrates has been recovered from the second phosphate rock (Marine Faunal Unit 1) (Kensley 1972). The invertebrates included in this fauna represent both rocky and sandy shore species. Their presence indicates that a marine shoreline

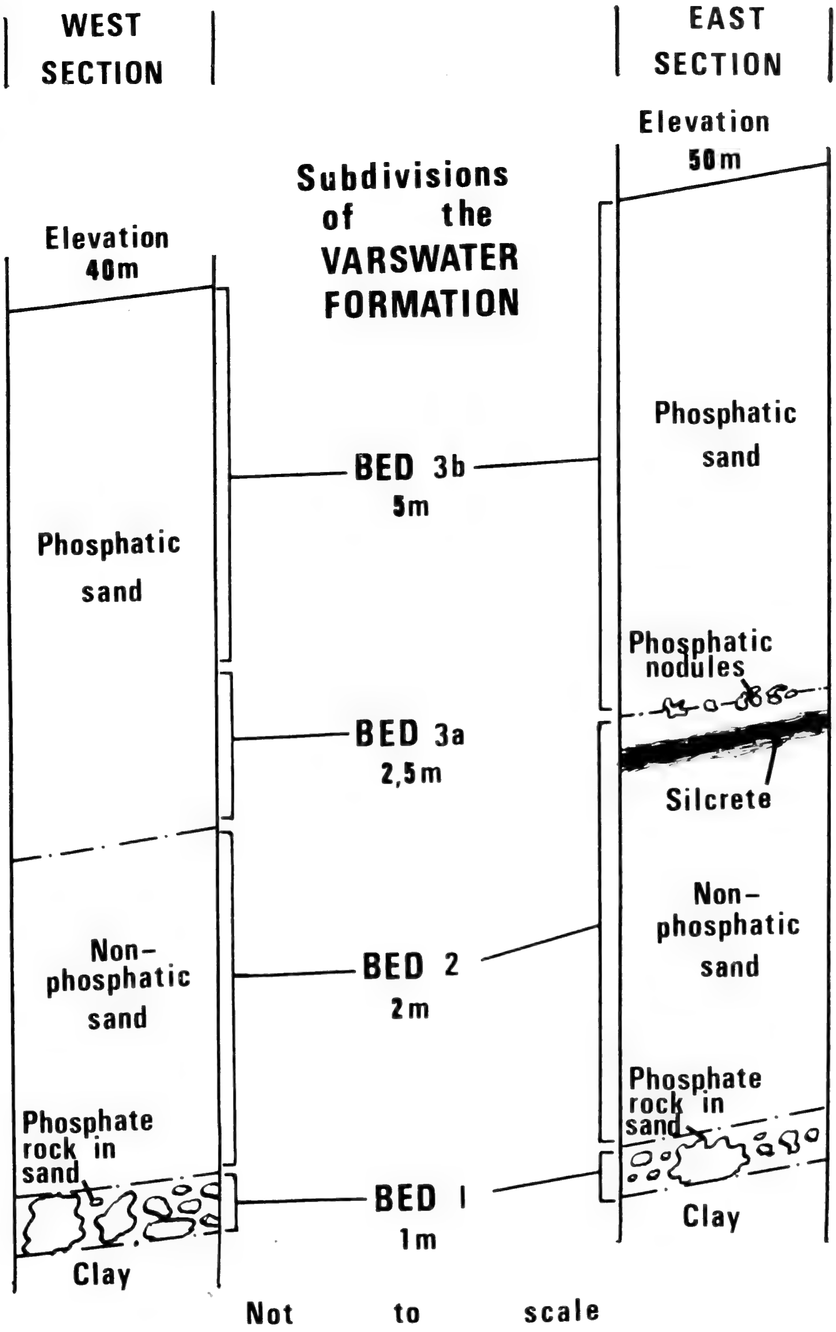

Fig. 4. The stratigraphy of 'E' Quarry, Langebaanweg.

existed in the area and that abrasion of the indurated phosphate rock was by wave action. The partly cemented phosphate rock has also been subjected to wave action, as shown by the abraded surfaces of infills of this material in Bed 1, and rounded fragments lie mixed with the cobbles and pebbles of the indurated rock. The abrasion of the second phosphate rock may be associated with a second period of marine erosion or with the later part of a single marine incursion. A wide variety of marine fossils (Marine Faunal Unit 2) is preserved in an unconsolidated, light-coloured and sandy matrix incorporating the two generations of abraded phosphate rock. Occasional remains of terrestrial vertebrates also occur and these are usually heavily rolled.

An exposure of Bed 1 east of Main Stream (BDT 1/1971) revealed that the rocky element is considerably less prominent than it is in more southerly exposures of this horizon. The BDT 1 exposure has cobbles and pebbles of both primary and secondary phosphate rock, the latter being more common, which is again in contrast to the more southerly exposures. In addition, rolled fragments of less consolidated and non-phosphatic sandstone were present.

Bed 2

The light-coloured, medium-grade sands of Bed 2, which are exposed over most of the floor of the quarry, are often not readily distinguishable from the unconsolidated matrix of the underlying bed. The sediments and fossils suggest that deposition was primarily in a relatively calm and shallow estuarine environment, but at least some of Bed 2 may have accumulated subaerially. In the vicinity of Main Stream, and sometimes also near the base of the horizon, coarse-grade sands suggest deposition by higher-velocity waters. Towards the eastern limit of the quarry, Bed 2 becomes very thin, no more than a capping on Bed 1, and perceptible mainly because of its fossil content.

Bed 2 is largely non-phosphatic and includes large numbers of non-marine vertebrate fossils, while marine vertebrates are rare (Estuarine Faunal Unit 1).

This horizon apparently began accumulating when a river, which had previously discharged into the sea elsewhere, altered its course and met the sea somewhere in the immediate vicinity of the present 'E' Quarry. This probably occurred during a period of marine transgression and Bed 2 is regarded simply as a facies change in the cycle of deposition which resulted in the marine erosion and deposition of Bed 1.

In the eastern part of 'E' Quarry the upper limit of Bed 2 is marked by a discontinuously-developed capping of phosphate nodules and phosphate rock. This rocky horizon was previously confused with Bed 1 and, although termed the 'basal marker' (Hendey 1970*b*), this name is appropriate only in that this horizon marks the lower limit of mining in this part of the quarry. Many of the nodules have built up around fossils and crushed and broken fossils at this level are often cemented together by a phosphatic matrix.

About 150 m east of Main Stream is a smaller and less well developed drainage course ('East Stream'). Between these two features and immediately below the phosphatic nodules is an extensive and well-developed zone of siliceous induration of the light-coloured sands of Bed 2. The origins of the nodules and 'silcrete' are not known, although the former may be connected with the deposition of the phosphatic sands which overlie Bed 2.

Beds 3a and 3b

The phosphatic nodules of Bed 2 are absent west of Main Stream and this bed is overlain by the brown, phosphatic and fossiliferous sands of Bed 3a.

Some of Bed 3a may have been laid down subaerially, but most of it was apparently deposited by faster-flowing water than was the case with the subaqueous element of Bed 2. Remains of both terrestrial and aquatic vertebrates tend to be concentrated towards the base of the bed and become progressively less common upwards. There are, however, several levels above the base of the bed where fossils occur in greater numbers and these levels, and the base of the bed, follow the general south-westerly dip of the deposits. They may represent old land surfaces over which successive periods of subaqueous deposition took place, perhaps at times when the river feeding the area was in flood. Even if such land surfaces existed, they were clearly not accessible to very large land mammals, which is a contrast to the situation prevailing at the time of the deposition of Bed 2, since such species are commonly represented in this horizon. The surfaces on which the Bed 3a fossils were apparently accumulated may actually have been subaqueous all the time and the land mammals represented in this bed may have been carried to their site of deposition by water.

Unweathered pebble-sized feldspar crystals, rolled feldspar and quartz pebbles and fragmentary fossils apparently derived from Bed 2 are included in the sedimentary suite of Bed 3a. Their presence indicates that at least some of Bed 3a was deposited by strongly flowing water. Bed 3a may have been laid down along the path of the periodically flooding 'Langebaanweg River' rather than in the backwaters of its estuary as is inferred for Bed 2. Bed 3a is far less extensive in area than Bed 2 and, although its distribution has yet to be finally determined, there is a suggestion that it has a linear north-east to south-west spread. If this can ultimately be demonstrated, it will be a further indication of deposition along or ahead of a river channel.

Bed 3a is presently regarded as a different facies of the estuarine sedimentation of the Varswater Formation and, although the *in situ* fossils cannot always be distinguished from those derived from Bed 2, its fauna is termed the 'Estuarine Faunal Unit 2'.

Overlying Bed 3a, or Bed 2 where 3a is absent, are the phosphatic sands of Bed 3b. This is by far the most extensive unit in the Varswater Formation and it is largely unfossiliferous. The only fossils ever recovered from it have been a few isolated giraffid limb bones. Along the west wall Bed 3b can be visually distinguished from Bed 3a only by the fact that it is apparently unfossiliferous and the subdivision of Bed 3 is made solely on these grounds. Evidently though, the environment of deposition of Bed 3b did differ from that of Bed 3a since animal remains were so rarely added to the accumulating sediments. Differences between the two units may be detected by detailed examinations of the sediments, although their lithology is superficially similar.

On the assumption that deposition of the Varswater Formation took place during a marine transgression, it is evident that a shift of the shoreline to the north-east with the rise in sea level would mean that the 'E' Quarry area was progressively further from the shoreline and no longer in an area of concentrated vertebrate activity. Consequently, although the Langebaanweg River was still discharging sediment into the area, very few vertebrate fossils were incorporated into the accumulating deposits.

Bed 3b is easily distinguished from the underlying deposits in the eastern part of the quarry (Bed 2), because it is non-fossiliferous and phosphatic, whereas Bed 2 is fossiliferous and non-phosphatic.

The upper limit of Bed 3 is marked by a variably developed zone of induration and it is always readily distinguishable from the overlying and non-phosphatic aeolian sands of what is informally termed the 'surface bed' (Hendey 1970*a*).

FAUNA OF 'E' QUARRY

Marine Faunal Unit 1

The fossil fauna of the partly consolidated phosphate rock of Bed 1 is known only from a single and very limited occurrence. The invertebrate remains are, however, very well preserved and have been described in detail elsewhere (Kensley 1972). A single shark's tooth is the only recorded vertebrate fossil in this faunal unit.

Marine Faunal Unit 2

The fossils from the unconsolidated matrix of Bed 1 represent a wide variety of invertebrate and vertebrate species.

The invertebrate fauna of this unit is represented only by internal casts and although they have been found at several places, most notably BDT 2/1972. several metres south of BDT 1, they are less well known than the invertebrates of Marine Faunal Unit 1.

By contrast, marine vertebrate remains are abundant. Shark's teeth are particularly common and an array of species similar to that recorded from 'C' Quarry is represented (see Hendey 1970*a*: 96). Sting-ray spines and denticles, eagle-ray tooth plates, skate denticles, vertebrae and teeth of bony fish, a variety of whale bones and a single seal femur have also been recovered from the unconsolidated matrix of Bed 1.

Some fragmentary and usually heavily rolled remains of terrestrial vertebrates occur in association with the marine fossils. Most frequently represented is a land tortoise and since this is also the most common fossil in Bed 2, it suggests that Beds 1 and 2 are broadly contemporaneous. A recently discovered *Hipparion* tooth from Bed 1 is a further indication that this faunal unit is indeed Pliocene in age.

Estuarine Faunal Unit 1

This faunal unit is characterized by the often very well-preserved remains of large terrestrial mammals. Smaller vertebrates are actually more commonly but less obviously represented.

The most common species is a land tortoise (*Chersina*) and even where the deposit is poorly fossiliferous, remains of this species are likely to occur Other non-mammalian vertebrates include sharks, bony fish, snakes, lizards, frogs and birds. Sharks and bony fish are rare and there was clearly not a concentration of the remains of these creatures by wave action as was the case in Bed 1. Birds are represented by a wide variety of species including ostrich, francolin, plover, penguin and cormorant, all of which are represented by modern counterparts in the immediate area or on the adjacent coast.

Small mammals are common and include insectivores, rodents, a lagomorph and small viverrids. Medium-sized herbivores are *Hipparion*, *Nyanzachoerus* and a variety of bovids. Large herbivores are *Mammuthus subplanifrons* (Maglio & Hendey 1970), a gomphothere, *Ceratotherium praecox* (Hooijer 1972), a sivathere and *Giraffa*. The larger carnivores include a machairodont, a viverrid and hyaenids, which are described elsewhere in this report. Also represented is a seal (Hendey & Repenning 1972).

The larger mammals of this unit are those on which the relative dating of the Varswater Formation is largely based. Comparisons with radiometrically dated East African faunas indicate a late Pliocene date for Bed 2 and an age of about 4 million B.P. is inferred (Hendey 1970*b*, 1972*c*).

A study of the fossil occurrences of Bed 2 (*vide infra*) has provided some information on the manner in which the fossils came to be accumulated and the nature of the environment at the time. Some fossils were clearly laid down on a land surface, with little disturbance subsequently by geomorphological agents. Damage to bone has resulted from both carnivore action and fires. Indications are that those fossils which were accumulated subaerially were subsequently inundated by relatively calm and shallow water and that subaqueous deposition of deposits and other fossils also took place.

Nothing certain is known of the vegetation of the area at the time that the fossils were being accumulated, but the abundance and variety of large herbivores suggests that it was more luxuriant than the present flora. The rainfall today averages about 250 mm per annum and falls mainly in winter. It is sufficient to support only a Mediterranean macchia vegetation without indigenous trees and little indigenous grass. The presence of *Giraffa* in the Bed 2 deposits indicates that trees must have been present during the late Pliocene, while the high-crowned teeth of the *Ceratotherium* and *Hipparion* suggest the presence of grassland as well.

The burnt bone in the deposits probably resulted from bush-fires and, since burnt bone is not uncommon and occurs at most levels, the fires must have been quite frequent, probably towards the end of a season which was long, hot and dry. On the other hand the inferred presence of trees and other more luxuriant vegetation points to a period of good rains as well. Together these factors indicate strong seasonality in precipitation and it follows that the Langebaanweg River is likely to have varied markedly in the volume of its flow according to the season.

The environment visualized on the basis of these facts and inferences is that of a coastal savanna crossed by a river flowing south-westwards and having its estuary surrounded by an area of low-lying sandy flats which were flooded during the rainy season. The marine environment is likely to have been fringed to the west by islands formed by granite outcrops in what is today the Saldanha/ St. Helena Bay area (see Hendey 1970*b*: fig. 4). Alternatively it may have been a north-east extension of the present Saldanha Bay, and in either case, a relatively sheltered area with low-energy waves.

A greater number of land mammals may have concentrated in the area during the dry season owing to the availability of fresh water in the river. The hypothetical floodplain may thus have been an area of intense terrestrial biotic activity during the dry season. Amongst other things predation and scavenging of terrestrial animals would have occurred, with the remains being buried beneath subaqueously deposited sediment during inundation of the floodplain in the succeeding rainy season. Judging from the dispersal of some of the fossils, the flooding must have been subdued rather than torrential in most of the area of Bed 2 which is now exposed in 'E' Quarry. This area may have had one or more perennial water courses and the present Main Stream may follow such a feature.

Estuarine Faunal Unit 2

The fauna of Bed 3a is not as well known as that from Bed 2 and it is problematical since it is not always possible to distinguish those fossils which are *in situ* from those that are derived from Bed 2. There are, however, some obvious differences between the two assemblages.

The large mammals which are so characteristic of Bed 2 are either not recorded from Bed 3a or are known only from very fragmentary remains, most or all of which may be derived from Bed 2. For example, *Ceratotherium praecox* is represented by occasional tooth fragments in Bed 3a, but in Bed 2 it is known from hundreds of complete teeth, partial and complete dentitions, parts of skulls and elements of the postcranial skeleton (see Hooijer 1972). The large pig, *Nyanzachoerus*, is not known from Bed 3a, although a miniature one, which is not known from Bed 2, is present. The most common of the Bed 2 bovids, a boselaphine, is not recorded from Bed 3a, where the two most common bovids are alcelaphines. They in turn are not definitely recorded from Bed 2. Each of the two estuarine faunal units has at least one hyaenid which is not recorded in the other. The seal, which is rare in Bed 2, is common in Bed 3a.

There are also differences in the nature of the fossil occurrences. Even amongst the *in situ* Bed 3a fossils, there is a greater proportion of fragmented bone and there have been fewer indications of close associations of different parts of single skeletons, although the latter feature may result from the smaller sample size.

There are probably a number of factors which could have caused the differences between the two estuarine faunal units. For example, it has already been suggested that the environment of deposition of Bed 3a differed from that of Bed 2 and this may have contributed to some of the observed differences. In addition, Bed 3a clearly postdates the underlying Bed 2 and, although the time difference may not have been very great, it may have been sufficient for changes to have taken place in the composition of the local fauna.

Unless otherwise stated all references in this report to the Langebaanweg vertebrate fauna relate to the 'E' Quarry occurrences.

DEPOSITS AND FAUNA OF 'C' QUARRY

The observations which have already been made on the 'C' Quarry occurrences (Hendey 1970*a*) have not been supplemented. The 'C' Quarry marine fossils apparently occur in deposits which are a westerly extension of the 'E' Quarry Bed 1, while the overlying deposits apparently include extensions of Beds 2 and/or 3. One puzzling feature of the 'C' Quarry succession is the occurrence of terrestrial vertebrate remains below deposits containing marine fossils (Hendey 1970*a*: fig. 4), a situation which has not been encountered in 'E' Quarry.

The actual relationships between the 'C' and 'E' Quarry deposits will only be determined as the area between them is mined away and exposures of the linking deposits become visible.

The few fragmentary carnivore remains from 'C' Quarry have already been referred to (Hendy 1970*a*: 97), and this material is not described in the present report since none of the pieces could be positively identified.

DEPOSITS AND FAUNA OF BAARD'S QUARRY

As with 'C' Quarry, no further progress has been made with investigations into the geology of the Baard's Quarry area. It is, however, clear that fossils of Pleistocene age are included in the Baard's Quarry assemblage (Hendey 1972*c*), although most may be contemporaneous with those from the Varswater Formation, and the earlier element in the Baard's Quarry succession is tentatively regarded as a fluviatile facies of the Varswater Formation.

The few specimens from Baard's Quarry which are included in the systematic section of this report are regarded as belonging with the Pleistocene element of the fauna from this site.

Fossil Mammals of the South-western Cape Province

The late Cenozoic fossil mammal record of the south-western Cape is potentially good, but at present only the faunas of the latter part of the Quaternary are comparatively well known. The Pleistocene element of the Baard's Quarry assemblage apparently dates from the earlier part of this epoch, but there are so many uncertainties relating to this occurrence and only a limited number of poorly represented species are involved, which means that they constitute a largely insignificant addition to the record. The Tertiary is known only from the late Pliocene Langebaanweg occurrences. The record is, therefore, far from complete and an additional disadvantage is that many of the available fossils have yet to be studied in detail.

In the account which follows, the record as it is presently known is reviewed. The Carnivora are excluded as they will be dealt with in detail later and of the remaining orders some are better known than others (Tables 5, 6). For example, the Chiroptera are completely unrepresented as fossils, whereas the Artiodactyla are ubiquitous and often abundantly represented.

The mammalian microfaunal remains are still largely unstudied, but a cursory examination of the available material has revealed nothing which is obviously out of character with the modern fauna.

The Chrysochloridae, which are endemic to Africa and which still occur commonly in the south-western Cape, are represented locally as fossils only at Langebaanweg. Apparently only a single species occurs and its remains are common in both Bed 2 and Bed 3a. The fossorial habits of this animal probably contributed to its preservation in these deposits. The fact that it is not recorded at other local sites is almost certainly due to the nature of the collecting which has been undertaken, since Langebaanweg is the only local occurrence where a determined effort has been made to recover microfaunal remains.

The Macroscelididae are another group which are endemic to Africa and they are also quite common at Langebaanweg but unrepresented in the Pleistocene. Once again there is apparently only one species represented at Langebaanweg and it occurs in both Bed 2 and Bed 3a.

The relative abundance of chrysochlorids and macroscelidids in the south-western Cape Pliocene is of special interest in view of the exclusively African distribution of these groups and the fact that neither has a good fossil record. Miocene, Pliocene and Pleistocene macroscelidids are known (Patterson 1965), while chrysochlorids are recorded from the Miocene of East Africa (Butler & Hopwood 1957; Butler, 1969) and the Pleistocene of South Africa (see De Graaf 1960). The Langebaanweg material includes both skull and postcranial remains and the large number of specimens available should allow for confident definition of the species represented. Both groups are, however, taxonomically complicated and the Langebaanweg species are unlikely to add much to the understanding of their phylogenies.

Soricidae are poorly represented as fossils in the south-western Cape and once again Langebaanweg is the only site from which they are recorded.

Table 5

The late Pliocene mammalian fauna from 'E' Quarry, Langebaanweg (May, 1972).*

	Marine Faunal Unit 2 (Bed 1)	Estuarine Faunal Unit 1 (Bed 2)	Estuarine Faunal Unit 2 (Bed 3a)	Faunal Unit unknown
ORDERS MENOTYPHLA AND LYPOTYPHLA (INSECTIVORA)				
Elephantulus sp.		×	×	
Soricidae (2 species)		×	×	
Chrysochloris sp.		×	×	
ORDER PRIMATES				
cf. Cercopithecidae		×		
ORDER PHOLIDOTA				
cf. *Manis* sp.		×		
ORDER TUBULIDENTATA				
Orycteropus sp.		×		
ORDER PROBOSCIDEA				
Gomphotheriidae		×		
Mammuthus subplanifrons		×		
ORDER HYRACOIDEA				
cf. *Procavia antiqua*			×	
ORDER PERISSODACTYLA				
Ceratotherium praecox		×	?	
Hipparion albertense baardi		×	×	
ORDER ARTIODACTYLA				
Nyanzachoerus sp.		×		
Suidae Species B (aff. *Diamantohyus*)			×	
Libytherium olduvaiense		×	?	
Giraffa cf. *gracilis*		×		
Tragelaphus sp.		×		
Bovini (aff. *Pelorovis*)		×		
Boselaphini (aff. *Tragoportax*)		×		
Reduncini				×
Alcelaphini Species A			×	
Alcelaphini Species B			×	
Neotragini (aff. *Raphicerus*)		×		
Gazella aff. *vanhoepeni*				×
Incertae sedis		×		
ORDER LAGOMORPHA				
Incertae sedis		×	×	
ORDER RODENTIA				
Bathyergidae (2 species)		×	×	
Muridae and perhaps others (several species)		×	×	
ORDER CETACEA				
Incertae sedis	×			

* Excluding Carnivora.

TABLE 6

The Quaternary mammalian fauna of the south-western Cape Province (May, 1972).[1]

	Baard's Quarry, Langebaanweg[2]	Elandsfontein	Melkbos	Swartklip	Sea Harvest, Saldanha	Historic Period
ORDER PRIMATES						
Simopithecus oswaldi hopefieldensis		×				
Papio ursinus						×
Homo sapiens rhodesiensis		×				
Homo sapiens					×	
ORDER PHOLIDOTA						
Manis sp.		×				
ORDER TUBULIDENTATA						
Orycteropus afer						×
ORDER PROBOSCIDEA						
'*Stegodon*' sp.	×					
Loxodonta atlantica		×				
Loxodonta africana			×		×	×
ORDER HYRACOIDEA						
Procavia capensis					×	×
ORDER PERISSODACTYLA						
Diceros bicornis	×	×	×		×	×
Ceratotherium simum		×	×	×		
Equus cf. *capensis*	×	×	×	×	×	
Equus cf. *plicatus*		×				
Equus zebra					cf.	×
ORDER ARTIODACTYLA						
Potamochoerus porcus						?
Mesochoerus paiceae *Mesochoerus lategani* } Probably conspecific		×				
Phacochoerus aethiopicus					?	?
Tapinochoerus meadowsi		×				
Hippopotamus amphibius		×	×	×	×	×
Libytherium olduvaiense	?	×				
Tragelaphus cf. *strepsiceros*		×	×			
Taurotragus oryx		×	×	×	×	×
Pelorovis sp.		×				
Syncerus sp.			×			
Syncerus caffer		cf.				
Redunca arundinum subspp.		×	×	×	×	
Hippotragus gigas		×				
Hippotragus leucophaeus		×	×	×	?	
? *Beatragus* sp.		×				
Damaliscus niro		×				
'*Rabaticeras*' *arambourgi*		×				
Megalotragus sp.		×	×			
Connochaetes sp(p).		×	×	×	×	
Alcelaphus buselaphus caama					cf.	×
Sylvicapra grimmia						×
Raphicerus sp(p).		×	×	×	×	
Raphicerus campestris						×
Raphicerus melanotis						×
Oreotragus oreotragus					×	×

TABLE 6 (*continued*)

	Baard's Quarry, Langebaanweg[2]	Elandsfontein	Melkbos	Swartklip	Sea Harvest, Saldanha	Historic Period
ORDER ARTIODACTYLA (*continued*)						
Gazella sp.		×				
Antidorcas recki		×				
Antidorcas australis		×	×	×	?	
Pelea capreolus		×			×	
Bovidae *incertae sedis* (2 species)		×				
ORDER LAGOMORPHA						
Lepus sp.		×			×	
Lepus capensis						×
Lepus saxatilis						×
ORDER RODENTIA						
Bathyergus suillus		×	×	×	×	×
Georychus capensis					×	×
Hystrix africae-australis		×		×[3]	×	×
Others		×		×	×	×

ADDITIONAL SPECIES:
Elephas transvaalensis (=*iolensis*) from near Melkbos
Giraffa camelopardalis from Bloembos

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[1] Excluding Insectivora, Chiroptera, Carnivora and Cetacea.
[2] Pleistocene species only.
[3] Indirect evidence only.

Compared to the chrysochlorids and macroscelidids the amount of material which is available is limited, but in this instance at least two and possibly more species are represented. Soricids are not uncommon as fossils elsewhere and a detailed study of the Langebaanweg specimens should complement the studies on those from the early Pleistocene of the Transvaal (see Meester 1955).

Rodents are more commonly represented as fossils than the insectivores and, although especially abundant at Langebaanweg, they are also known from local Quaternary occurrences.

About a dozen species are known from Langebaanweg and the most commonly occurring forms are Bathyergidae, a family with an essentially African distribution. As with the chrysochlorids, it is probably their fossorial habits which has led to their being more commonly preserved as fossils than other contemporary small mammals. Bathyergids are also known from all the more important Quaternary occurrences of the south-western Cape, their relatively large size and abundance probably having contributed to their discovery.

Their fossorial habits raises the possibility that they may sometimes become accidentally associated with fossils already buried in the ground, a situation which may easily arise because most of the local occurrences are in unconsolidated deposits in areas where bathyergids still occur. This possibility has already been mentioned in the case of the Melkbos bathyergid (Hendey 1968: 112), and also applies particularly in the case of the specimens from Elandsfontein. Owing to the cliff-side situation of the Swartklip and Sea Harvest sites, and the consolidated deposits of the former, there is less likelihood of non-contemporary bathyergids being associated with the rest of the fauna. It is also unlikely that the Langebaanweg bathyergids are later intrusive fossils since the levels at which they occur have been deeply buried ever since deposition of the Varswater Formation ceased. In addition, the species represented evidently differ from those of the Quaternary and there is no reason to believe that they are inconsistent with the Pliocene age of the deposits.

One of the Langebaanweg species is apparently a small form of *Bathyergus*, while the other, which is much less common, is tentatively referred to *Georychus*. Both these genera are still commonly represented in the south-western Cape today, and both are recorded from the local Quaternary occurrences.

The other small rodents from sites in the south-western Cape are, for the most part, unclassified. *Otomys* is recorded from some of the Quaternary occurrences and still occurs in the region today. It is, however, not known from Langebaanweg, which is surprising in view of the nature of the environment at the time of the deposition of the Varswater Formation.

Another notable absentee from the Langebaanweg fauna is the porcupine, *Hystrix*. This is a rodent of particular significance in local palaeontological investigations, since its bone collecting habit has resulted in it being at least partly responsible for some of the important fossil accumulations (e.g. Elandsfontein, Swartklip, Sea Harvest). Even when skeletal remains of this animal are not recorded in an assemblage, its presence may be deduced from the very characteristic gnaw-marks it leaves on the bones which it has collected. The fact that not a single one of the many thousands of bones recovered at Langebaanweg shows any signs of porcupine gnaw-marks suggests that this animal did not occur in the immediate vicinity in late Pliocene times. By contrast, porcupine gnaw-marks are a not uncommon feature of the fossils from Elandsfontein (Singer 1956), one of the few local sites from which porcupine skeletal remains have also been recovered.

Several recent porcupine lairs have provided an invaluable record of the historic period fauna of the Cape Folded Mountains and southern Cape regions, but no significant assemblages of such material from the south-western Cape was available in the course of the present study.

The Lagomorpha are another group of small mammals which are, as yet, unstudied. They are not particularly well represented locally and even in recent times they appear to have been a relatively insignificant element in the small mammal fauna.

One of the more remarkable features of the fossil and modern faunas of the south-western Cape is the small number of primate species and specimens which are represented. The only primates, other than *Homo*, which are definitely recorded locally are baboons.

Papio ursinus still occurs in the region today, but no *Papio* has been recorded locally as a fossil and the only fossil baboon which is known is the Elandsfontein *Simopithecus oswaldi* (Singer 1962). This giant cercopithecoid was almost certainly not arboreal and consequently its association with the remains of other terrestrial mammals is not surprising. Remains of this species are comparatively rare, although specimens in addition to those already described have been found. Cranial remains of nine and possibly ten individuals are now known (Q. B. Hendey, unpublished manuscript), but the additional specimens are no longer in the South African Museum's collections. The Elandsfontein *Simopithecus* was described as a distinct subspecies and it is apparently the most recently occurring representative of the genus in South Africa. A few isolated teeth from Langebaanweg are tentatively identified as belonging to a small cercopithecid.

If arboreal primates were ever present in the south-western Cape, it is highly unlikely that their remains would be found at the more important fossil sites. Such species are in any case rare as fossils and in the south-western Cape it is probable that wooded areas would always have been confined to more mountainous parts, away from the areas in which the principal fossil occurrences are located. Palynological evidence from Elandsfontein suggests that trees might have grown there in the past (Singer & Wymer 1968), while the presence of *Giraffa* at Bloembos and Langebaanweg suggests the presence of trees in these areas as well. However, this does not necessarily indicate suitable habitats for arboreal primates.

Both orders of Old World 'edentates', the Pholidota and Tubulidentata, are represented in the south-western Cape fossil record. The former are known from a braincase from Elandsfontein and some postcranial bones from Langebaanweg, while the latter are represented by a single cheektooth from Langebaanweg. Neither of these groups has a good fossil record and the local specimens are of little significance, except in as far as past distributions are concerned. Pangolins are not recorded in the historic period fauna of the south-western Cape, but aardvarks still occurred locally until fairly recently.

Hyracoidea are known from several local fossil sites. *Procavia capensis* is well represented in the Sea Harvest assemblage and is also known from the Saldanha Lime Quarry site, while a few isolated teeth, tentatively referred to *Procavia antiqua*, are recorded from Langebaanweg. It is unlikely that the Langebaanweg species can be positively identified on the basis of the material presently available, but it is in no way inconsistent with *P. antiqua* as defined by Churcher (1965). This would be the earliest record of an otherwise Pleistocene species, but its presence is not unexpected if Churcher's phylogeny for the group is taken into consideration.

Fossil Proboscidea, which have proved so useful in many parts of the world for relative dating purposes, are not particularly well represented in the south-western Cape. During the Pliocene and Pleistocene the Elephantidae arose and diversified in Africa, giving rise ultimately to the African elephant (*Loxodonta africana*), the Asiatic elephant (*Elephas maximus*) and the woolly mammoth

(*Mammuthus primigenius*) (Maglio 1970*a*). All three lineages are represented in the south-western Cape and, in addition, gomphotheres are recorded from Langebaanweg and from Milnerton, near Cape Town.

The Langebaanweg gomphothere has been referred to the genus *Anancus* (Hendey 1970*a*), but its relationships are actually uncertain, as are those of the Milnerton species. The latter is known only from a single tooth fragment, while the Langebaanweg species is represented by a number of complete teeth and several tooth and tusk fragments.

The Langebaanweg elephant is a primitive form of *Mammuthus subplanifrons* (Maglio & Hendey 1970), and is one of the earliest recorded members of the *Mammuthus* lineage. Its identification contributed towards the recognition of the Pliocene age of the Langebaanweg fauna. The Langebaanweg species was identified largely on the basis of the remains of a single individual, of which the mandible, an isolated upper molar and a number of elements of the postcranial skeleton are now known. Although this material is superior in some respects to previously recorded *M. subplanifrons* specimens, the skull is unknown and 'the reference of the Langebaanweg elephant to *Mammuthus subplanifrons* is more a matter of necessity than one of direct evidence' (Maglio & Hendey 1970: 87).

This additional record of *M. subplanifrons* lends support to the observation that it is an essentially southern African species (Maglio 1970*a*), while *Loxodonta adaurora* was the 'dominant elephant during the late Pliocene and early Pleistocene of east Africa' (Maglio 1970*b*: 19, 20). The latter was subsequently replaced in East Africa by *Elephas recki*, while the apparent derivative of *M. subplanifrons* was the North African *M. africanavus*.

By the Pleistocene *Elephas* had also appeared in South Africa and there is a single record of this genus in the south-western Cape, namely, *E. transvaalensis* (=*iolensis*; see Cooke & Maglio 1972) from near Melkbos (Hendey 1967). The actual age and associations of the Melkbos specimen are unknown, although it is unquestionably a Pleistocene species.

The elephant remains from Elandsfontein have been the subject of a number of unpublished studies, but the status of this material is still uncertain. The accompanying faunal list (Table 6) reflects the view that only one species, namely, *Loxodonta atlantica*, is represented (Cooke & Maglio 1972).

With a single exception, all other elephant fossils from the south-western Cape have been referred to *Loxodonta africana*, a species also recorded in the area in historic times. The exception is a tooth from Baard's Quarry which has been identified as belonging to *Stegodon* (see Hendey 1970*a*: 94).

As with most other important fossil sites in Africa, those from the south-western Cape have their assemblages dominated by the remains of ungulates. Both perissodactyls and artiodactyls are represented and, as is also usual in Africa, the latter are predominant.

The black and white rhinoceroses (*Diceros bicornis* and *Ceratotherium simum*) are both recorded as fossils in this region, although only the former survived into the historic period. This conservative group of mammals has been represented by the extant species for most, if not all, of the Pleistocene and the only extinct rhinoceros species presently recorded in southern Africa is that from Langebaanweg. This species, which is close to the dichotomy of the *Diceros* and *Ceratotherium* lineages, is actually an early form of the latter and is referred to the species *C. praecox* (Hooijer 1972).

The remains of Equidae occur quite commonly in the south-western Cape and most of the specimens belong to a large species of *Equus*. The numerous isolated teeth, partial dentitions and elements of the postcranial skeleton of this form appear to represent the same species as the mandible on which Broom (1909) based his description of *E. capensis*. Wells (1959) rejected this name, but subsequently Churcher (1970: 149) resurrected it and took '*E. capensis* to include *E. helmei*, *E. cawoodi*, *E. kuhni*, *E. zietsmani* and some of the teeth referred to *E. harrisi* and *E. plicatus*'. This array of names provides some indication of the confusion which has prevailed in the nomenclature of South African fossil Equidae and, while the final word in the controversy over the status of *E. capensis* may still be to come, Broom's name is retained in the present report since it seems likely that the *E. capensis* holotype is conspecific with other later Quaternary *Equus* specimens from the same region.

Clearly there was at least one species of now extinct equine of large size which was present in South Africa through most of the Pleistocene. *E. capensis* is recorded from the early Pleistocene Makapansgat assemblage (Churcher 1970), through a series of younger Pleistocene contexts in various parts of the country and it apparently survived into the Holocene of the south-western Cape.

The Baard's Quarry *Equus* was referred to the species *helmei* by Boné & Singer (1965) and in view of Churcher's synonomy it is here listed as *E. capensis* (Table 6). The single *Equus* tooth previously included with the 'E' Quarry assemblage (Hendey 1970*a*, 1970*b*) is now believed to have come from Baard's Quarry (Hendey 1972*c*).

At Elandsfontein the Equidae are represented by a large number of specimens, including one nearly complete skull. Singer & Inskeep (1961: 23) state that 'the majority of specimens . . . may be referred to *Equus plicatus*' and that some 'may belong to *E. helmei*' (i.e. *E. capensis*). In the absence of a detailed study these conclusions are regarded as tentative.

Apparently only two species are represented in the late Pleistocene and Holocene assemblages from the south-western Cape. The large *E. capensis* is most common and its most recent record is from the ? early Holocene Sea Harvest occurrence. The second species is a smaller one and is identified as *E. zebra*. No remains of *E. quagga* or *E. burchelli* have as yet been positively identified locally, although these species are commonly recorded as fossils elsewhere in South Africa. While it is fairly certain that *E. zebra* occurred in the south-western Cape in historic times, it is by no means certain that *E. quagga* was present, although it was very common in the adjacent Karroo and probably also in the west coast region.

Since *E. capensis* apparently did survive into the Holocene of the south-western Cape, it is possible that this species was the local equivalent of the plains-dwelling *E. quagga* and *E. burchelli*, while *E. zebra* occupied the intervening mountainous areas and also the mountainous parts of the south-western Cape itself. *E. zebra* may thus have formed a species barrier between *E. quagga* in the Karroo and *E. capensis* in the south-western Cape. A general mutually exclusive relationship between *E. capensis* and the plains zebras cannot, however, be concluded. Elsewhere in South Africa *E. capensis* has been recorded in association with both *E. quagga* and *E. burchelli* (see Churcher 1970: Table 8). A possible explanation of the available evidence is that *E. capensis* managed to survive fairly late in the south-western Cape because *E. quagga* did not extend its range into this region, but that elsewhere it had earlier failed in competition with both *E. quagga* and *E. burchelli*.

Yet another curious feature of the record of the South African Pleistocene zebras is the reported presence of both *E. burchelli* and *E. quagga* in the early Pleistocene of the Transvaal (Churcher 1970), even though the latter is often regarded as being no more than the most southerly variety of the plains zebra group. Even if it is accepted that *E. quagga* and *E. burchelli* are specifically distinct, it is difficult to accept that they were recognizably different and could have co-existed as far back as the early Pleistocene. Although this problem has no direct bearing on the present discussion, it is worth noting that if *E. quagga* did once extend its range as far north as the Transvaal, its absence from the fossil record of the south-western Cape is more unexpected than ever.

In spite of the fact that much has been written on the Pleistocene equines of South Africa and that their systematics have been reviewed several times (Haughton 1932*b*; Cooke 1950; Wells 1959), it is evident that there is still further scope for a further reappraisal of the available material. Until this has been done, interpretation of past patterns of distribution and determination of phyletic relationships of the recorded species will be difficult.

Apart from *Equus*, the only other equid known from the south-western Cape is *Hipparion albertense baardi* from Langebaanweg (Boné & Singer 1965). The described material was from 'C' and Baard's Quarries, but the species is best represented by the material from 'E' Quarry.

The relationships, if any, between the Langebaanweg species and *Notohipparion namaquense* (Haughton 1932*b*) and the South African Pleistocene *Hipparion steytleri* (Churcher 1970) have yet to be clearly demonstrated. Boné & Singer (1965: 389) included both *N. namaquense* and *H. steytleri* in the synonymy of *H. libycum*, although they stated that *N. namaquense* 'may prove to be a transitional form between the typical *Hipparion* and the more progressive *Hipparion* (*Stylohipparion*)'. The opinion held by the present author is that *N. namaquense* is earlier and perhaps ancestral to the Langebaanweg *H. albertense*, which is earlier and perhaps ancestral to *H. steytleri*. There is evidently scope for a further re-evaluation of African *Hipparion* as well as *Equus*.

The perissodactyls have not proved particularly useful for relative dating purposes in South Africa, although both the *Ceratotherium praecox* and *Hipparion albertense* from Langebaanweg have served to substantiate the inferred Pliocene age of the Varswater Formation, while the Baard's Quarry *Diceros bicornis* is one of the species which served to confirm that a Pleistocene element is included in the fauna, a conclusion originally based on the *Equus capensis* from this site. None of the perissodactyls can yet be used to indicate precise relative ages of Pleistocene faunas. The black and white rhinoceroses, *E. capensis* and the plains zebras apparently occurred through most of the South African Quaternary, while *Hipparion steytleri* persisted for most of the first half, or more, of this period. The perissodactyls are, however, potentially useful in palaeo-ecological studies.

The Artiodactyla are completely dominated in most of the fossil faunas of the south-western Cape by the Bovidae, although Suidae, Hippopotamidae and Giraffidae are also recorded locally.

The African late Cenozoic fossil record is remarkable for the variety of Suidae which are represented, but there are surprisingly few species of this family recorded in the south-western Cape. It is not even certain that the bushpig (*Potamochoerus porcus*) and the southern warthog (*Phacochoerus aethiopicus*) were present in the region during the historic period, although they were both widespread elsewhere in sub-Saharan Africa. The latter species is known from Sea Harvest by a single tusk fragment, which to date is the only suid fossil known from a local late Quaternary context.

At Elandsfontein three extinct species have been recorded, namely, *Mesochoerus paiceae*, *M. lategani* and *Tapinochoerus meadowsi* (Singer & Keen 1955; Keen & Singer 1956). It seems unlikely that there are indeed two species of *Mesochoerus* represented and the material thus identified may, at most, represent no more than two varieties of a single species. A reappraisal of the available material is required. The *Tapinochoerus* is very poorly represented.

The only other fossil suids recorded locally are from Langebaanweg. The most commonly represented is a species of *Nyanzachoerus* which was appreciably larger than the extant bushpig. The other is an extremely small and as yet unidentified species, comparable in size to the pygmy hog of India, *Sus salvanius*. It may have affinities with the small *Diamantohyus africanus* from the Miocene of South West Africa (Stromer 1926), a genus which is now also known from the Miocene of East Africa (Walker 1969), but has yet to be recorded from the Pliocene. The small species is poorly represented, but the *Nyanzachoerus* is comparatively well known. It differs in certain respects from the recorded East and North African species of *Nyanzachoerus* (H. B. S. Cooke, pers. comm.), but has yet to be studied in detail.

The Hippopotamidae are represented in the south-western Cape only by the extant species, *Hippopotamus amphibius*. The largest number of specimens are from Elandsfontein (Hooijer & Singer 1961), while other Quaternary occurrences have yielded only limited numbers of fragmentary specimens. This species is frequently mentioned in historical records and only became extinct in the region during the 19th century.

The absence of *Hippopotamus* at Langebaanweg has already been remarked upon elsewhere (Hendey 1970*a*: 98), and this remains one of the most remarkable absentees from the fauna of this site. Occurrences of comparable age in East Africa have yielded large numbers of hippopotamus specimens and the depositional environment at Langebaanweg in the late Pliocene was such that remains of this animal would have been preserved if it had been present. The negative evidence suggests that the Hippopotamidae had not penetrated to the southern continental extremity by the late Pliocene.

The extant giraffe, *Giraffa camelopardalis*, which was only recorded as far south as the Orange River area in historic times, is known locally from a single tooth from Bloembos (Cooke 1955). *Giraffa* is otherwise recorded only from Langebaanweg, where it is represented by a comparatively small species tentatively identified as *G. gracilis*.

The short-necked and large-horned Sivatheriinae are represented locally by what is apparently a single species, *Libytherium olduvaiense*, at both Langebaanweg and Elandsfontein (Singer & Boné 1960). Much more material has been recovered at Langebaanweg since 1960 and elements of both skull and postcranial skeleton are represented. With the exception of *Ceratotherium praecox*, *Libytherium* is the best represented large mammal from Bed 2 of the Varswater Formation.

As is, or was the case elsewhere in Africa, the Bovidae were once numerous in the south-western Cape and four antelope (*Raphicerus campestris*, *R. melanotis*, *Sylvicapra grimmia*, *Pelea capreolus*) are amongst the largest of the surviving indigenous mammals of the region. Bovidae are known from all the more important local fossil occurrences and, with the exception of the Cephalophini, all extant African bovid tribes, as well as representatives of nearly all the extant genera, are represented as fossils. In addition, the only South African representative of the Boselaphini, a tribe now restricted to southern Asia, is from the south-western Cape.

The Tragelaphini are represented by at least three species, one of which (*Taurotragus oryx*) still occurred in the region in historic times. The eland is, in fact, one of the more commonly represented fossil bovids and although all the known specimens are referred to *T. oryx*, the Elandsfontein assemblage apparently includes a more primitive variety of this species.

The kudu, *Tragelaphus strepsiceros*, is not known to have occurred in the region in historic times, but an extinct form, which is at least subspecifically distinct, is recorded from both Elandsfontein and Melkbos (Hendey 1968). This form has not been recorded elsewhere and it may warrant recognition as a distinct species, just as *Hippotragus leucophaeus* is recognized as a species distinct from *Hippotragus equinus*.

The small tragelaphine from Langebaanweg may be ancestral to the modern nyala (*Tragelaphus angasi*) (Gentry, in Hendey 1970*a*).

Bovini are well represented only in certain assemblages. Although abundant in the southern Cape during the historic period and often featuring in historical accounts of this region, the African buffalo, *Syncerus caffer*, was apparently rare in the south-western Cape. *S. caffer* has been certainly identified only by a single horn core from Ysterfontein, south of Saldanha Bay. This specimen does not appear to be very old. Some postcranial remains from Elandsfontein are tentatively referred to *S. caffer*. A large form of *Syncerus*, which might be specifically distinct from *S. caffer*, has been recorded from Melkbos (Hendey 1968).

Still larger are the long-horned buffaloes previously referred to *Homoioceras*, but which are now being included in *Pelorovis* (A. W. Gentry, pers. comm.). These belong on a lineage distinct from that of *Syncerus* and they are recorded locally from Elandsfontein and Bloembos. The Elandsfontein *Pelorovis* assemblage is probably the best of its kind in southern Africa.

The only other bovine recorded in the region is an as yet unnamed and poorly represented species from Langebaanweg. The only horn core fragments known suggest that it might be an early member of the *Pelorovis* lineage. A bovine of comparable age from East Africa is thought to be an ancestor of *Syncerus* (A. W. Gentry, pers. comm.), so the indications are that the two African bovine lineages were differentiated during the Pliocene. The latest recorded occurrence of *Pelorovis* in southern Africa is that from Nelson's Bay Cave in the southern Cape, which is dated at about 12 000 B.P. (Klein 1972). There is no comparable very late Pleistocene record from the south-western Cape.

The only South African record of a boselaphine is the Pliocene species recorded from Langebaanweg (Gentry, in Hendey 1970*a*). This species could perhaps derive from *Protragocerus labidotus* from the late Miocene from Fort Ternan in Kenya (Gentry 1970). The Langebaanweg species is considerably larger than *P. labidotus*, it differs from the Fort Ternan species in some morphological details as well and apparently has affinities with *Tragoportax* of the Dhok Pathan stage of the Siwaliks of India. The Boselaphini are an essentially Eurasiatic group and the available record suggests that only a single lineage, which is not known to have survived the Tertiary, was present in Africa.

The Reduncini are represented in the south-western Cape by at least three species. Curiously, this tribe was apparently not represented in the region in historic times, although *Redunca fulvorofula* may have occurred in the adjacent Cape Folded Mountains. The nearest recent record of this species, and of *R. arundinum*, is in the southern Cape. *R. arundinum*, or closely related forms, is one of the most commonly occurring bovids in the Pleistocene of the south-western Cape. It is well represented in the Elandsfontein, Melkbos and Swartklip assemblages and is also recorded from Sea Harvest. The Elandsfontein and Swartklip forms differ from another and both differ from modern *R. arundinum*. These three probably represent varieties of a single lineage, of which *R. darti* from the early Pleistocene of the Transvaal (Wells & Cooke 1956) may be a more primitive member.

Kobus is not recorded in the Quaternary of the south-western Cape, although it is not uncommon elsewhere in sub-Saharan Africa.

The other two reduncines recorded locally are from Langebaanweg, one from 'E' Quarry and the other from Baard's Quarry. The former is tentatively referred to *Kobus* and while that from Baard's Quarry was originally identified as *Redunca ancystrocera* (Gentry, in Hendey 1970*a*), its affinities are now uncertain.

No hippotragines were recorded in the south-western Cape in historic times, although the southern Cape was the last refuge of the recently extinct *Hippotragus leucophaeus*. This species is, however, recorded as a fossil in the south-western Cape. It was initially described as *H. problematicus* by Cooke (1947) on the basis of a specimen from Bloembos and has since been recorded from Swartklip (Hendey & Hendey 1968), Melkbos and Elandsfontein. Confirmation of the identity of the south-western Cape fossils has come from an increasing number of undoubted *H. leucophaeus* specimens from porcupine lairs and hominid occupation sites in the southern Cape. This species is of special interest since it was endemic to the most southerly parts of Africa and the available fossil material is currently being studied in detail (R. G. Klein, in preparation).

The only other locally occurring hippotragine is *H. gigas*, which is recorded from Elandsfontein where it is more commonly represented than *H. leucophaeus*. It apparently belongs in the earlier element of the Elandsfontein fauna, while *H. leucophaeus* is probably more recent.

The Alcelaphini are among the most diverse and abundant of the African Bovidae and are represented at all the more important south-western Cape fossil sites. Surprisingly, the wildebeest (*Connochaetes*) was not recorded in the region in historic times, although *C. gnou* was very common on the interior plateau and *C. taurinus* is still one of the most common bovids of the savannas further north. *Damaliscus* was also not recorded in the region in recent times, although *D. dorcas* still occurs in the southern Cape. The only alcelaphine which was definitely recorded locally was the southern hartebeest, *Alcelaphus buselaphus caama*. This species is also recorded from a number of Holocene occurrences such as Late Stone Age coastal middens, but is not known from a Pleistocene context. By contrast, both *Connochaetes* and *Damaliscus* are represented at Pleistocene occurrences.

The identification of alcelaphine species on the basis of relative tooth size is not always reliable. In most instances the local fossils were identified on the basis of horn cores and other skull characters, but the Swartklip *Connochaetes* and Sea Harvest *Alcelaphus* are represented only by teeth and their relationships are, therefore, not certain. Nevertheless, the present indications are that *Alcelaphus* replaced *Connochaetes* in the south-western Cape during the Holocene. Such replacements and the apparent local extinction of species such as *Ceratotherium simum* may well be related to environmental factors. It has already been suggested elsewhere that climatic conditions were more favourable in the south-western Cape during the late Pleistocene.

A number of now extinct alcelaphines are recorded locally. The spectacularly large *Megalotragus* is represented in both the Elandsfontein and Melkbos assemblages. Like *Pelorovis*, this giant bovid apparently became extinct in South Africa at the end of the Pleistocene (Klein 1972).

At least three other alcelaphines are known from Elandsfontein. One is tentatively referred to *Beatragus*, a genus now represented only in East Africa (*B. hunteri*), although its affinities may lie with the tsessebe, *Damaliscus lunatus*. The apparently recently extinct *D. niro* is represented by only a few specimens, which may belong in the later element of the Elandsfontein fauna. One of the most commonly represented bovids at the site is a form of '*Rabaticeras*', a genus which is otherwise known from Swartkrans (Vrba 1971), Olduvai Gorge (A. W. Gentry, pers. comm.) and Morocco (Ennouchi 1953).

Two medium-sized and as yet unnamed alcelaphines are represented at Langebaanweg. Both are primitive forms and at a stage of development not inconsistent with the inferred Pliocene age of the Langebaanweg deposits (A. W. Gentry, pers. comm.). One may be ancestral to '*Rabaticeras*', which in turn may be ancestral to *Alcelaphus*.

The Cephalophini, a group which is widespread in Africa, are not known as fossils in the south-western Cape, although the grey duiker, *Sylvicapra grimmia*, occurs in small numbers in the region today. It may be a relatively recent immigrant to the area.

By contrast, neotragines are common as fossils and are the most commonly occurring indigenous antelopes in the region today. Two of the three extant species of *Raphicerus* are represented locally, namely, the steenbok (*R. campestris*) and the grysbok (*R. melanotis*). Fossil specimens of these two species are usually difficult to distinguish from one another and no attempt has been made to identify the local fossil *Raphicerus* at the species level. There is clearly more than one variety represented in the Quaternary assemblages.

Two neotragines are represented at Langebaanweg, one from 'E' Quarry and the other from Baard's Quarry. Both are now tentatively referred to *Raphicerus*. The Baard's Quarry form is poorly known, but it apparently differs from the 'E' Quarry species, which in turn is clearly not conspecific with any extant species.

Another neotragine recorded locally is the klipspringer, *Oreotragus oreotragus*. It was formerly common on mountains in and adjacent to the south-western Cape and is known as a fossil only from Sea Harvest, where it is represented by a single metacarpal.

The only antilopine recorded from South Africa in recent times is the springbok, *Antidorcas marsupialis*. During the Pliocene and Pleistocene, however, several species of *Gazella*, a genus which still survives elsewhere in Africa and in Asia, were represented in the country. There are two extinct species of *Gazella* recorded from the south-western Cape, one from Langebaanweg and the other from Elandsfontein.

Although the modern springbok was not recorded in the south-western

Cape in historic times, *Antidorcas* is not uncommon as a fossil and at least two species are represented. The subspecies *A. marsupialis australis* (Hendey & Hendey 1968) is now regarded as a species distinct from *A. marsupialis* and it is also clearly distinct from the extinct species *A. recki*, which is locally recorded from Elandsfontein. The southern springbok is best known from Swartklip, but is also represented in the Elandsfontein and Melkbos assemblages and may also be present at Sea Harvest.

The horn cores of *A. recki* are more like those of *A. marsupialis* than are those of *A. australis*, which suggests that *A. marsupialis* could be a descendant of *A. recki* and that *A. australis* belongs on a distinct lineage. The latter species is so far known only from the south-western Cape, although fossil specimens from the southern Cape may also belong to this species. Like *Hippotragus leucophaeus*, it is regarded as a species which was endemic to the southern parts of the African continent.

A. recki is less well represented at Elandsfontein than *A. australis* and, if the former is indeed ancestral to *A. marsupialis*, its normal habitat may have been the inland plateau and its presence at Elandsfontein the result of penetration into this area of occasional groups of this plains species. Movements of the modern springbok into the Cape Folded Mountains and west coast region were recorded in historic times and it is not impossible that they also moved into the northern parts of the south-western Cape, that is, the area in which Elandsfontein is situated. *A. australis* is thus regarded as the locally enedmic springbok which occasionally may have met its plains counterpart near the northerly limits of its range.

The possibility that the Elandsfontein *A. recki* belongs to the early element of the fauna and was ancestral to *A. australis*, which would therefore belong in the later fauna, was considered but rejected. In all those instances where it is certain that early and late forms exist as, for example, amongst the Carnivora (*vide infra*), the former are more abundantly represented. Since *A. australis* is more common than *A. recki*, this would mean a reversal of the usual pattern in the case of the springboks. Furthermore, the possibility that certain specimens were not contemporaneous with others of the same or related species, was often suspected because of the nature of their preservation. The Elandsfontein *A. australis* assemblage includes at least one specimen which differs in preservation from the others, which suggests the possibility that early and late forms of the species are represented at the site.

The somewhat aberrant antelope, *Pelea capreolus*, which is endemic to southern Africa, still occurs in the south-western Cape today. Since it is a species which is largely confined to more mountainous areas, it would not be expected to occur in any of the more important local fossil occurrences. It is in fact extremely rare and is known only from a few fragmentary specimens from Elandsfontein and Sea Harvest.

In addition to those species already mentioned, there are two others from Elandsfontein and one from Langebaanweg which are unclassified. All three are moderately large forms and all are clearly not conspecific with any extant species.

Apart from the Carnivora, the only other mammals which are recorded locally as fossils are Cetacea. Holocene cetacean remains are not uncommon in hominid occupation sites and other deposits adjacent to the present coast and have also been recovered during building operations on Cape Town's reclaimed foreshore area. Heavily mineralized cetacean remains are frequently washed ashore on the beach at Milnerton near Cape Town, in association with other marine fossils and the remains of terrestrial mammals. The latter have included the gomphothere tooth fragment referred to earlier. Most of this material is in private collections and is unstudied. The cetacean remains from Langebaanweg (Hendey 1970*a*: 103), all of which are from Bed 1 of the Varswater Formation, are also unstudied.

The only extant orders of African mammals which are not represented in the fossil record of the south-western Cape are the Chiroptera and Sirenia. The former are well represented in the modern fauna of the region and although they may occur as fossils in caves, no such occurrence was investigated in the course of the present study. No sirenians have ever been recorded near the southerly parts of Africa in recent times and their absence from the local fossil record is, therefore, not surprising.

Non-mammalian Fossils from the South-western Cape Province

The invertebrate and non-mammalian vertebrate fossils from the south-western Cape form a significant part of the local fossil record. Although such fossils are recovered and studied only incidentally to current investigations on local fossil mammals, they have sometimes proved useful in interpreting the origins of the assemblages in which they occur, as well as giving indications of the nature of past environments. For example, the occurrence of marine invertebrates and vertebrates in Bed 1 of the Varswater Formation provided evidence that the Bed 1 deposits were laid down on a marine shoreline.

Most of the non-mammalian vertebrate fossils from this region have yet to be studied in detail, but some specimens have already been partly or completely classified.

Chondrichthyes are known locally in association with mammalian remains only from Langebaanweg and Milnerton, the latter being a littoral occurrence of little significance. In the Langebaanweg assemblage at least six species of shark are provisionally identified, as well as a skate, an eagle ray and a sting ray. The remains are very incomplete and mostly only isolated teeth or tooth-plates are found.

The only fossil mammal locality from which teleost remains have been recovered in any numbers is Langebaanweg, although Swartklip and Sea Harvest have produced a few isolated specimens. At Langebaanweg vertebrae have been most common, but occasional teeth are recorded from Bed 1 and catfish fin spines are known from Beds 2 and 3a.

Anuran remains are also quite common at Langebaanweg and have occasionally been found at Quaternary occurrences as well.

The remains of Reptilia are more common and Chelonia are almost ubiquitous. Skeletal elements of land tortoises occur at all the important south-western Cape sites and are also known from many of the less significant fossil occurrences. At Langebaanweg the individuals represented range from very small to moderately large and vast numbers of specimens are known. No attempt has ever been made to compute the number of individuals involved, but the figure must run into thousands. As far as is known, only one or possibly two species of land tortoises are represented in the Varswater Formation, while at Baard's Quarry a land tortoise and a water turtle are recorded.

Reptilia other than Chelonia are far less common, but both lizards and snakes are known and once again the largest assemblage is from Langebaanweg. A feature of the south-western Cape fauna, both modern and fossil, is the absence of crocodilians from the record. Elsewhere in Africa these reptiles are, or were common and it seems that, as with many mammalian species, they failed to penetrate to the more southerly parts of the continent.

With the exception of Langebaanweg, birds are not common as fossils in the south-western Cape, although the ostrich is known from all the more important occurrences. The Langebaanweg fauna includes a wide variety of smaller birds, of which only a penguin (*Spheniscus predemersus*) has been described

(Simpson 1971). Another penguin, apparently *Spheniscus demersus*, is known from Sea Harvest.

Relatively little attention has been paid to invertebrate fossils which occur in association with vertebrate remains. The shells of land snails are not uncommon at many of the Quaternary occurrences, but more significant are the records of marine invertebrates in Bed 1 of the Varswater Formation. They constitute the largest Pliocene invertebrate assemblage yet recorded from South Africa and have been described in detail elsewhere (Kensley 1972).

Late Cenozoic Mammal Ages in Southern Africa

The age of southern African fossil mammal faunas can be indicated in a number of ways. It is, of course, common to refer them to particular epochs, which may be subdivided into 'Lower', 'Middle' and 'Upper', or 'Early', 'Middle' and 'Late' stages. The practice thus far employed in the present report has been to use the latter alternative on an informal basis (e.g. late Pliocene), since there never has been an acceptable formal definition of subdivisions of the southern African Cenozoic epochs. References to the 'late Pliocene' and others such as 'Plio/Pleistocene' are not entirely satisfactory because the epochs themselves are poorly defined in southern Africa. European stage names such as 'Villafranchian' have been used as a substitute and with varying degrees of circumspection by various authors, but since this procedure is so obviously unsatisfactory, it is usually considered unacceptable.

It has long been the practice in other parts of the world to devise a system of local names to which are referred faunas dating from a particular period in time and with a particular character. This system has obvious advantages and at the Third Pan-African Congress on Prehistory (1955) it was recommended that the Pleistocene faunas of Africa be divided into four 'stages', namely, Omo-Kanam, Lower Olduvai, Upper Olduvai and Post Olduvai (Clark 1957: xxxi). This nomenclature never came into general use.

Cooke (1967: 179) has discussed in some detail the question of a formal stratigraphic nomenclature for the late Tertiary and Quaternary of Africa based on mammalian faunas and he concluded that, 'it is probably true to say that our knowledge is not yet adequate for the designation of Land-Mammal "Ages"'. His carefully considered justifications for the use of his own provisional terminology are undoubtedly sound, but his decision to regard the units as 'faunal spans' rather than 'stages' is questionable. This decision was based on the definition of a 'stage' as set out in the American Code of Stratigrophic Nomenclature (1961), and since on this basis his units did not rank as 'stages' he refrained from using '-an' and '-ian' endings for his 'stage' names.

The application of this code to a palaeontological rather than a geological problem can hardly be justified if it results in a clumsy and possibly confusing nomenclature. For example, it is now necessary to refer to the fauna from Makapansgat as a 'Sterkfontein faunal span fauna' rather than as a 'Sterkfonteinian fauna'. Any system of nomenclature, no matter how formal, must function as an aid to communication and no 'code of nomenclature' has been, or should be completely inflexible. While this is not intended as a plea for scientific anarchy, it is intended to convey the opinion that too rigid a control in such matters may ultimately lead to the very situation it is designed to avoid. Terms such as 'age' and 'stage' do have different connotations as any good dictionary will show and the former is used here to indicate a period of time characterized by a particular mammalian fauna, while 'stage' is recognized as a geological time-stratigraphic unit which is not applicable in the present instance.

The proposed series of age names (Table 7) are a modification of the current terminology applied to the Quaternary, with an additional two names to cover the known late Tertiary faunas. The use of these names, or subsequent modifications, will eliminate the necessity of using others defined and designed for use elsewhere and in other fields of study. It must be stressed that the proposed terminology is intended for use in reference to mammalian faunas only and its adaptation for use in other disciplines will inevitably lead to confusion.

TABLE 7

Mammal ages of southern Africa

Proposed names	Provisional terms of Cooke (1967)	Sites	Epochs
RECENT	'Recent'	Numerous cave and surface sites	Holocene
FLORISIAN	Florisbad-Vlakkraal Faunal Span	Elandsfontein (in part), Melkbos, Swartklip, Nelson Bay Cave (in part), Wonderwerk, Florisbad, Vlakkraal, Kalkbank and others	Pleistocene
CORNELIAN	Vaal-Cornelia Faunal Span	Elandsfontein (in part), Vaal River Younger Gravels, Cornelia, Cave of Hearths (in part)	
MAKAPANIAN	Swartkrans Faunal Span	Taung, Makapansgat, Sterkfontein, Swartkrans, Kromdraai, ?Langebaanweg (Baard's Quarry)	
	Sterkfontein Faunal Span		
LANGEBAANIAN		Langebaanweg, Kleinzee	Pliocene
NAMIBIAN		Elisabethfelder, Langental, Bohrloch	Miocene

A tentative correlation with European and North American ages is proposed (Table 8) but, to paraphrase Wood *et al.* (1941), although the supposed equivalence of the proposed names to the epochs and Northern Hemisphere ages is indicated, the new terms are emphatically not defined in relation to them. The precise limits of the ages is intended to be flexible and may be modified in the light of later discoveries.

The definitions which follow are based on the system employed by Wood *et al.* (1941). The faunal lists are by no means exhaustive and final and, bearing in mind the earlier comment by Cooke on our present inadequate knowledge of southern African fossil mammals, the definitions form only the foundations to which more secure and substantial information may be added from time to time.

FLORISIAN

Source of name: Florisbad, Orange Free State.

Includes the faunas from Elandsfontein (in part), Melkbos, Swartklip, Nelson Bay Cave (in part), Driefontein (Cradock), Wonderwerk, Florisbad, Vlakkraal, Kalkbank, Cave of Hearths (in part), Chelmer.

Cultural associations: Middle Stone Age and earlier part of Late Stone Age.

First appearance: Many modern species including *Homo sapiens sapiens*, *Papio ursinus*, *Loxodonta africana*.

Last appearance: *Pelorovis*, *Megalotragus*, *Damaliscus niro*, *Gazella*.

Comment: The fauna is composed essentially of modern species, many of which are characterized by individuals of larger size than their modern counterparts.

References: Cooke 1963; Wells 1970; Klein 1972; this report.

CORNELIAN

Source of name: Cornelia, Orange Free State.

Includes the faunas from Elandsfontein (in part), Vaal River Younger Gravels, Cornelia, Cave of Hearths (in part).

Cultural associations: Advanced Acheulian.

First appearance: *Homo sapiens rhodesiensis*, *Elephas transvaalensis*, *Loxodonta atlantica*, *Stylochoerus*, *Phacochoerus*.

Last appearance: *Simopithecus*, *Megantereon*, *Hipparion*, *Mesochoerus*, *Tapinochoerus*, *Libytherium*.

Comment: The modern element in the fauna is strong, although the forms represented are usually readily distinguishable from their extant counterparts. Some archaic elements are still present.

References: Cooke 1963; this report.

MAKAPANIAN

Source of name: Makapansgat (Limeworks), Transvaal.

Includes the faunas from Taung, Makapansgat, Sterkfontein, Swartkrans and Kromdraai.

Cultural associations: Earliest artefacts and Early Acheulian.

First appearance: *Australopithecus*, *Homo*, *Papio*, *Panthera*, *Megantereon*, *Crocuta*, *Diceros bicornis*, *Ceratotherium simum*, *Tapinochoerus*, *Hippopotamus*, *Connochaetes*, *Antidorcas*.

Last appearance: *Australopithecus*, *Homo erectus*, *Parapapio*, *Hyaenictis*, *Lycyaena*, *Dinofelis*, chalicothere, *Makapania*.

Comment: Archaic forms predominate, but modern genera appear in appreciable numbers.

References: Cooke 1963; this report.

LANGEBAANIAN

Source of name: Langebaanweg, Cape Province.

Includes the faunas from Langebaanweg and Kleinzee.

Cultural associations: None.

Characteristic fossils: *Prionodelphis*, *Agriotherium*, *Percrocuta*, *Machairodus*, *Enhydriodon*, *Mammuthus subplanifrons*, *Nyanzachoerus*, *Ceratotherium praecox*.

Comment: No extant species and many extinct genera.

References: Stromer 1931*a*, *b*; this report.

NAMIBIAN

Source of name: Namib Desert, South West Africa.

Includes the faunas from Elisabethfelder, Langental and Bohrloch.

Characteristic fossils: *Protypotheroides*, *Myohyrax*, *Pterodon*, *Diamantohyus*, *Propalaeoryx*, *Austrolagomys*, *Parapedetes*, *Bathyergoides*, *Diamantomys*.

Comment: No extant genera.

References: Stromer 1926; Hopwood 1929; Cooke 1968.

TABLE 8

Tentative correlation of mammal ages of southern Africa, Europe and North America

SOUTHERN AFRICA	EUROPE			NORTH AMERICA	Approximate age in millions of years
ETHIOPIAN REGION	PALAEARCTIC REGION			NEARCTIC REGION	
RECENT	RECENT			RECENT	0
FLORISIAN			PLEISTOCENE	RANCHOLABREAN	
CORNELIAN	CROMERIAN			IRVINGTONIAN	
MAKAPANIAN	VILLAFRANCHIAN			BLANCAN	2
LANGEBAANIAN	ASTIAN		PLIOCENE	REXROADIAN	4
	PONTIAN	PIKERMIAN		HEMPHILLIAN	8
		VALLESIAN		CLARENDONIAN	12
	TORTONIAN		MIOCENE	BARSTOVIAN	16
	HELVETIAN				
NAMIBIAN	BURDIGALIAN			HEMINGFORDIAN	20
				ARIKAREEAN	24
					28

Sources: Gabunia & Rubinstein 1968; Kurtén 1971.

The post-Langebaanian ages defined here differ only slightly in arrangement from the most recent of the subdivisions of the South African Pleistocene (Cooke 1967: Table 1). There is a precedent for this more simply defined threefold division since the Makapanian, Cornelian and Florisian correspond to the 'Ape-Man', 'Hand-Axe' and 'Middle Stone Age' faunas of Ewer & Cooke (1964). The definitions of these ages was based on the simple concept of the degree of similarity between the fossil faunas and the modern fauna of South Africa, with the latter being taken to have spanned the whole of the Holocene.

The most recent of the Pleistocene ages, the Florisian, is that in which the fauna was little different to that of the Holocene. Most of the species represented are still extant, although the varieties represented often differed in certain respects (e.g. size) from their extant counterparts. The only extinct genera recorded (*Pelorovis*, *Megalotragus*) are giant forms which are regarded as highly specialized rather than archaic in character. Their extinction may be linked with environmental and/or hominid activity factors rather than the rise of better adapted, ecologically related species.

The next oldest age, the Cornelian, was the one in which the modern character of the fauna became discernible, but in which the species represented were usually readily distinguishable from their modern counterparts by more than just size differences. Furthermore, some truly archaic genera appear for the last time. These include primates (*Simopithecus*), carnivores (*Megantereon*), perissodactyls (*Hipparion*) and artiodactyls (*Mesochoerus*, *Libytherium*), which were superseded by more advanced and better adapted forms. There was also at least one other important difference between the Cornelian and modern faunas. During the Cornelian the Suidae were represented by a wider variety of forms and the present almost total dominance by the Bovidae of the medium-sized herbivore fauna had yet to be achieved. The Cornelian is characterized by a fauna which bridges the gap between the essentially modern Florisian fauna and the first one to have a pronounced archaic character, namely, the Makapanian.

During the Makapanian there were few extant species represented amongst the larger mammals. Those that are conspecific with modern forms are either rather generalized representatives of their kind (e.g. *Canis mesomelas*, *Hyaena hyaena*) or specialized forms adapted to ecological niches in which they had no active competitors (e.g. *Hippopotamus amphibius*, *Ceratotherium simum*). Patterns in the representation of certain groups also differed from those in the Holocene fauna. Amongst the larger carnivores the dominance of the sympatric machairodonts and hyaenids was evident (see Ewer 1967: 120). The South African record of Makapanian Suidae is relatively poor, but judging from contemporaneous East African records this family was at about the peak of its late Cenozoic radiation in Africa (see Cooke & Maglio 1972: fig. 3). The fauna as a whole was, however, clearly 'African' in character and 'Eurasian' elements such as the ovibovine, *Makapania*, were exceptional.

The subdivision of the Makapanian into two or more units would mean that the whole basis for defining the Pleistocene ages would have to be altered. It would necessitate more involved and more precisely worded definitions and would probably serve no useful purpose. It should however be noted that in a recent review of the Pleistocene 'faunal spans' concept, Wells (1969: 94) suggested that 'Kromdraai should be dissociated from Swartkrans, and either included in the Cornelia span or made the type locality of an intermediate span'. The latter alternative would have resulted in the creation of five rather than four units. The present arrangement of only three units is an obvious reversal of at least one trend of thought.

The present definitions of the South African Pleistocene mammal ages are of some significance to anthropologists, since the local mammals include both *Australopithecus* and *Homo*. The Makapanian is characterized in part by the presence of both *Australopithecus* and *Homo erectus* and is, therefore, the age in which the genus *Homo* was differentiated. The only hominid recorded in the Cornelian is *Homo sapiens rhodesiensis*, which is included here on the basis of the Saldanha skull from Elandsfontein. *Homo sapiens sapiens* is not recorded until the Florisian. As a result, the ages can be broadly correlated with units of the local cultural succession.

The Tertiary mammal ages may also be considered in relation to the modern fauna of southern Africa, but the connections are more remote and would be largely meaningless for ages earlier than the Langebaanian. The Namibian and any other Tertiary ages which might be recognized in the future will have to be defined in relation to one another rather than in relation to the modern fauna.

The Langebaanian is differentiated from the Makapanian largely by the fact that no extant species of larger mammals are included. The fauna is definitely archaic in character and includes many extinct genera. Those genera which are still extant are conservative forms such as *Ceratotherium* or highly specialized and successful forms with long fossil histories such as *Felis*. In addition the 'Eurasian' element in the fauna is more marked than in the Makapanian and includes *Agriotherium*, *Percrocuta* and a boselaphine. The machairodont/hyaenid combination is similar to that of the Makapanian, but the Pantheriinae were evidently not yet present. The Suidae were apparently not yet diversified and the type fauna from Langebaanweg includes only two species. The Proboscidea recorded are a primitive elephantid and a gomphothere.

Although the proposed nomenclature is intended to be used instead of other systems, it is obviously desirable that the position of the ages relative to an absolute chronology and to the geological epochs be determined.

In terms of absolute age, the Pleistocene/Holocene boundary is here taken to be 12 000 B.P. There is evidence which indicates that at about this time there were significant changes in local environmental conditions which were associated with changes in the fauna and cultures (see Klein 1972). The South African Pleistocene/Holocene boundary may thus be defined to be more or less synchronous with that in other parts of the world.

The Plio/Pleistocene boundary is taken to date back 3,5 million years (see De Heinzelin 1969), although this is an arbitrary figure since there is at present no satisfactory basis on which this boundary can be defined in South Africa. A date of 3 million B.P. would be as convenient (see Savage & Curtis 1970), and other alternatives have been suggested so that the situation is still far from being resolved (see Flint 1971).

Similarly the Mio/Pliocene boundary is arbitrarily dated at 12 million B.P. In North America and Europe it is variously placed between 10 and 13 million B.P. (see Gabunia & Rubinstein 1968), to as little as 5 million B.P. (Van Couvering 1972).

Many East African late Cenozoic faunas have been dated by radiometric determinations on associated igneous rocks and this enables them to be related to the absolute chronology outlined above. Absolute age determinations in South Africa have only been possible for the late late Pleistocene and Holocene, so it is only by fixing the age of the local pre-Holocene faunas relative to those of East Africa that the mammal ages may be tentatively related to the absolute chronology.

The fauna of the Namibian is poorly known and comparisons with faunas. in East Africa have been inconclusive (Cooke 1968). It is, however, fairly certain that it does predate the 14 million-year-old Fort Ternan fauna and is probably broadly contemporaneous with those from sites such as Rusinga, Napak, Songhor and others. The Namibian is for the present regarded simply as a Miocene mammal age with undefined limits.

The Langebaanian type fauna has an inferred age of about 4,5 million years, so that this age is definitely in the Pliocene and clearly dates from the latter part of the epoch. On this basis it is concluded to be broadly equivalent to the Astian of Europe, the Dhok Pathan of India and the early Blancan (Rexroadian) of North America. The upper and lower limits of this age cannot be defined, but for the sake of convenience the former is taken to coincide with the Plio/Pleistocene boundary (i.e. 3,5 million B.P.).

The present indications are that the Namibian and Langebaanian may be separated by a time interval of 10 million years or more. This interval is without a significant recorded fossil history, although Namaqualand in the north-western Cape Province is an area with some potential in this respect. A previously unrecorded fossil mammal locality, Bosluispan near Gamoep, has yielded a limited and poorly preserved fauna in which the only identified specimen is a tooth of *Protanancus macinnesi* Arambourg, 1946. (Information supplied by the South African Geological Survey.) *Protanancus* is recorded from the 'Upper Miocene' of East Africa (Leakey 1967), and it thus seems likely that the Bosluispan fauna is intermediate in age between the Namibian and Langebaanian. Another fossil from Namaqualand which is apparently Pliocene in age and which apparently pre-dates the Langebaanian type fauna is the holotype of *Notohipparion namaquense* (Haughton 1932*b*). This specimen is from

Areb, which is about 80 km northwest of Bosluispan. On the basis of these two records it seems possible that a post-Namibian/pre-Langebaanian fauna, or faunas, may one day be recorded from Namaqualand.

The absolute ages of the upper and lower limits of the three Pleistocene mammal ages are also not certain, although the lower limit of the Makapanian and upper limit of the Florisian are taken to coincide respectively with the Plio/Pleistocene and Pleistocene/Holocene boundaries. The date of the Makapanian/Cornelian boundary is unknown. The faunas from Cornelia and Elandsfontein have been correlated with that of Olduvai Bed IV (see Cooke 1963), and recently the base of Bed IV was dated to about 0,7 million B.P. (Leakey 1971). The Makapanian/Cornelian boundary may therefore be somewhere between 0,5 and 1 million B.P. The Cornelian/Florisian boundary is also not fixed, but it may date back to something of the order of 100 000 years.

Although the dating of the mammal ages is so imprecise it is perfectly evident that those of the Pleistocene differ very considerably in the lengths of time which they cover. Even in the arrangement of 'faunal spans' discussed by Cooke (1967) the earlier units were clearly far longer than the later ones. This problem is by no means unique to the southern African systems and it does not necessarily detract from the value of defined mammal ages.

In a discussion on the geochronology of North America based on fossil mammals, Tedford (1970) pointed out the value, and shortcomings, of the system devised by Wood *et al.* (1941). There can be little doubt that were a comparable arrangement to come into general use in Africa, communications would be considerably facilitated. The present attempted emulation is certainly less satisfactory than the North American model and it would have been preferable for the nomenclature to have been based on the superior East African fossil record. Recently Coppens (1972) did indeed propose a subdivision of the African Pliocene and Pleistocene based on this record, although in this instance the two epochs were divided into 'Zones' (I to VIII in descending order of age). Coppens's nomenclatural system and that proposed here both have shortcomings and it is quite possible that neither will prove generally acceptable. However, it seems inevitable that agreement on a system for Africa will eventually be reached and although the American system is itself not faultless it does perhaps provide the best available model.

CARNIVORA OF THE PLIOCENE

The Carnivora from the late Pliocene deposits at Langebaanweg are treated as a unit separate from the Quaternary species since the two groups have little in common.

The study of the Langebaanweg material revealed that no extant species are represented, an entirely predictable conclusion in view of the age of the fossils. In the systematic accounts which follow, some of the fossils are compared with corresponding parts of modern species and it was intended that such comparisons should serve largely to clarify the descriptions of the fossils. The comparisons were not made in such a way as to prove that the fossils are taxonomically distinct from the modern species. In other words, no attempt was made to fully catalogue the differences between any two species dealt with in this fashion. The intention was rather that characters such as size of fossil species or of individual skeletal components might be referred to in terms of material which is more widely available and familiar.

In the case of the Quaternary fossils, references to modern comparative material had a greater significance, since in these instances the relationships between the modern and fossil species are far closer. Consequently, in order that the taxonomic status of the latter might be determined, the similarities and differences between them and the moderns had to be clearly established. The fact that inadequate modern osteological series limited the value of studies on certain of the Quaternary species did not alter the basic difference in approach to the treatment of the Pliocene and post-Pliocene fossil material.

The lack of direct access to relevant fossil specimens from outside the south-western Cape has undoubtedly had an adverse affect on the present study of the Langebaanweg Carnivora. However, it is hoped that by placing on record the material which is now available, future investigations on contemporaneous or related fossil species, especially those from East Africa, will be facilitated.

In all the systematic accounts which follow, the tooth cusp terminology illustrated in Figure 5 has been used. All original measurements under 130 mm were taken with the same pair of calipers and were corrected to one-tenth of a millimetre. Measurements over 130 mm were read off ortho-projections onto a plane surface using a ruler. The latter measurements are obviously less accurate and were corrected to the nearest millimetre.

All tooth measurements were taken across the longest and broadest points at, or near to the base of the crown. In the case of the canines, the dimensions are those taken at the base of the crown in line with the alveolar margin.

Unless otherwise stated, all specimen numbers are those in accession registers of the South African Museum, Cape Town. Modern specimens are distinguished from the fossils by the prefix 'SAM'. Specimens from collections in other institutions are distinguished as follows:

AMNH —American Museum of Natural History, New York.
BMNH —British Museum (Natural History), London.
GSI —Geological Survey of India.
NHMW—Natural History Museum, Vienna.

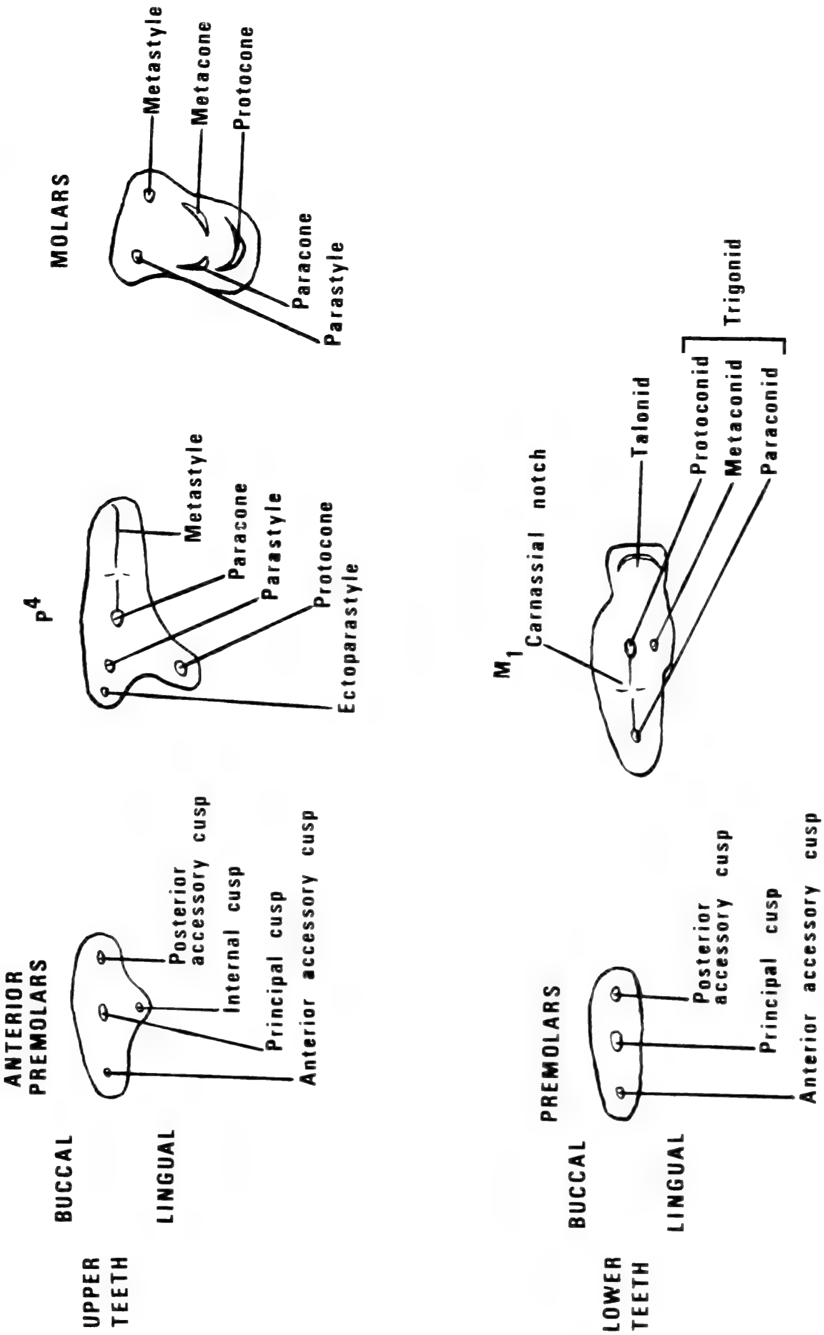

Fig. 5. Terminology applied to the teeth of carnivores.

During the late Pliocene, Langebaanweg was so situated in relation to marine, fluviatile and terrestrial environments that Carnivora from all three habitats were preserved as fossils. In this respect Langebaanweg is unique amongst the important late Cenozoic fossil sites of sub-Saharan Africa. The assemblage probably represents a very good cross-section of those carnivore species which inhabited the most southerly parts of Africa during the late Pliocene. More carnivore species are represented at Langebaanweg than in any other single occurrence in the south-western Cape.

Apart from the importance of this material as additional and new records in the African late Cenozoic fossil record, the carnivores evidently played a role in the addition of animal remains to the accumulating deposits. They are, therefore, an order of particular significance in the Langebaanweg assemblage as a whole.

Suborder PINNIPEDIA

Family **Phocidae**

Subfamily Monachinae

Prionodelphis capensis Hendey & Repenning, 1972

Discussion

The Langebaanweg pinniped, *Prionodelphis capensis*, has already been described in detail elsewhere (Hendey & Repenning 1972), and little additional material has since been recovered, none of which alters the conclusions already reached. The holotype and all the referred cranial remains are from Bed 3a and so is most of the postcranial material. Some postcranial bones are also known from Bed 2, while a single incomplete femur was recently recovered from the marine deposits of Bed 1.

This species has shed some additional light on the origins of the Antarctic monachines, a group which includes species that are still occasionally recorded as vagrants on the south-western Cape coast (*vide infra*), and it is a significant addition to the fossil record of the Monachinae in general (Hendey 1972*a*).

Recently *P. capensis* was tentatively identified at a second locality in South Africa. A canine (Q 1799), which is virtually indistinguishable from a Langebaanweg specimen (L 13152—see Hendey & Repenning 1972: pl. 9F), was found at Koingnaas near Hondeklip Bay on the Cape west coast about 250 km north of Langebaanweg. This specimen, together with a *Ceratotherium praecox* tooth found in the same area (Hooijer 1972), and the assemblage from Kleinzee a little further north (Stromer 1931*a*, 1931*b*), indicates that while the Langebaanweg occurrences are the most prolific of their kind yet recorded in the Cape Province, there are, or were other similar occurrences on the Cape west coast. All these occurrences are at, or near to, river mouths (Langebaanweg—Great Berg River; Koingnaas—Swartlintjies River; Kleinzee—Buffels River).

Suborder FISSIPEDIA
Family **Canidae**
Incertae sedis

Comment

Reference has already been made to two canid species in the Langebaanweg assemblage (Hendey 1970*a*), but this material has since been referred to the Viverridae (*vide infra*). There are, however, several recently discovered teeth which apparently do belong to a canid.

Material

L 15184B —Left P^4 and M$_1$, and right M^2.
L 15588B/C—Right M^1.
L 15526B ? Left P^2.
L 16120B ? Right M$_3$.

Locality and horizon

These specimens are from Bed 3a, 'E' Quarry, Langebaanweg.

Description

With the exception of the ? M$_3$, all the teeth are fairly worn and they may belong to a single individual. The ? M$_3$ still has an open root and is unworn. It definitely belongs to a second individual and may even belong to a different species. It is only provisionally grouped with the other specimens.

The worn teeth belong to a canid which was apparently comparable in size to modern *Vulpes vulpes*. The ? P^2 is a little larger than the P^2 of the two available *V. vulpes* specimens (Table 9), but it is otherwise similar. The P^4 differs from the comparative specimens in having a more prominent and more anteriorly situated protocone, while the anterior keel of the paracone is more lingually directed. The M^1 and M^2 of the two species are similar in morphology but in the fossil the lingual lobes have a greater transverse development and are relatively narrower antero-posteriorly.

TABLE 9

Dimensions of the canid teeth from Langebaanweg, compared with those of modern *Vulpes vulpes*.

	P^2		P^4		M^1		M^2		M$_1$		M$_3$	
	l	b	l	b	l	b	l	b	l	b	l	b
Fossil specimens .	9,7	3,2	*c.* 14,0	7,3	9,8	13,7	*c.* 6,5	*c.* 10,2	15,0	6,3	4,3	4,0
V. vulpes .	8,9 8,1	3,0 3,3	13,5 13,0	6,7 6,5	10,1 10,2	12,5 12,1	5,7 5,8	9,3 9,2	14,6 15,0	6,3 6,0	3,6 3,0	3,4 3,0

The lower carnassials of the two species are essentially similar to one another, but in the fossil specimen the trigonid is broader relative to the talonid and the metaconid is a little larger.

The problematical ? M_3 is a small, single-rooted tooth with a crown which is almost circular in occlusal view, while the occlusal surface is basin-shaped. It is far larger than the M_3 of the two *V. vulpes* specimens.

Discussion

The identification of this material is based principally on the fact that the M^1 and M^2 have protocones, which distinguishes them from the M^1 and/or M^2 of hyaenids and large viverrid which occur in the same deposits.

It is not clear from the material available to which canid genus the material belongs and comparisons with previously recorded fossil species were inconclusive.

Family **Ursidae**

Subfamily Agriotheriinae

Agriotherium africanum Hendey, 1972

Discussion

The Langebaanweg ursid has already been described and discussed elsewhere (Hendey 1972*b*), and the only additional specimen now known is another incomplete ulna. It is essentially similar to the one previously described.

Family **Mustelidae**

Subfamily Mellivorinae

Mellivora aff. *punjabiensis* Lydekker, 1884

(Fig. 6; also Hendey 1970*a*: pl. 2E)

Material

L 6385—Left mandibular fragment with P_4 and M_1.

Locality and horizon

This specimen is from 'E' Quarry, Langebaanweg.

Description

This specimen has already been mentioned and figured elsewhere (Hendey 1970*a*), although no conclusion as to its affinities was reached.

Except for some damage to the condyle, the specimen is complete as far forward as the anterior end of P_4. Both P_4 and M_1 are intact and this specimen belonged to a species or individual which lacked M_2. In size it compares with small individuals of the available modern *Mellivora capensis* assemblage ($n = 5$), this species being the largest of the extant African mustelids, excluding the otters. It is to the Mellivorinae that the fossil specimen evidently belongs, while the absence of M_2 suggests its affinities to the genus *Mellivora* itself. It does, however, differ from the modern species in certain significant details.

Both P_4 and M_1 are narrower than the corresponding teeth in the *M. capensis* comparative series (Table 51), and the talonid of M_1 is far smaller. The basic features of the modern and fossil teeth are, however, similar. The fossil P_4 has small anterior and posterior accessory cusps and around the latter is an expansion of the cingulum which makes the tooth broader posteriorly. The structure of the *M. capensis* P_4 is similar, although in this species the accessory cusps are more prominent and the development of the cingulum is more pronounced, especially postero-internally.

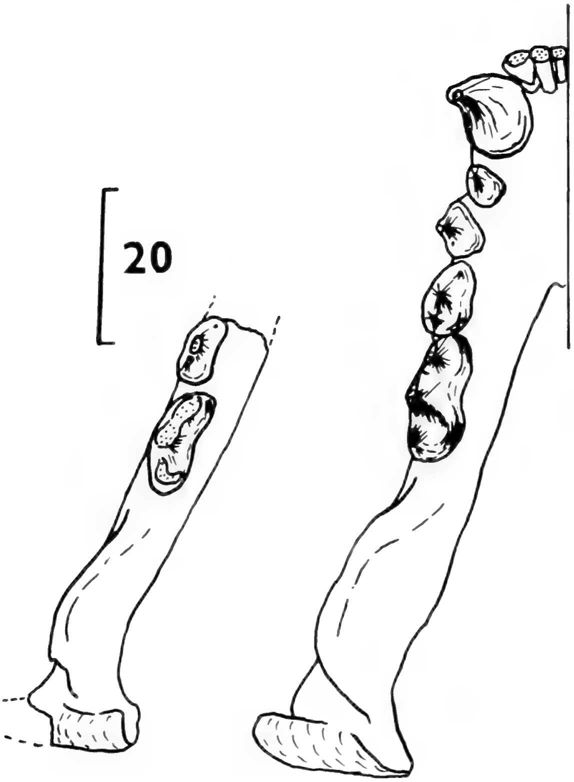

Fig. 6. Occlusal views of the *Mellivora* aff. *punjabiensis* mandible (L 6385) from Langebaanweg (left) and a modern *Mellivora capensis* specimen.

Although the M_1 of L 6385 is well worn, its characteristics are still evident. Except for being far larger, the tooth is not dissimilar to the M_1 of *Poecilogale*. The talonid is small and is narrower than the posterior end of the trigonid. In this respect it differs considerably from the M_1 of *M. capensis*, which has a relatively large and broad talonid. The trigonid of the fossil tooth, which lacks the metaconid, makes up about 75% of the total length of the tooth.

The inferior margin of the mandibular corpus of L 6385 is very slightly convex below the cheekteeth, whereas in the available *M. capensis* specimens it is slightly concave. Also in the modern species, the inferior margin is stepped upwards near the angle and, while there is a suggestion of this characteristic in the fossil, it is far less prominent. An apparently related feature in *M. capensis* is the fact that the dorsal surface of the condyle is above the level of the cheekteeth. In the fossil the lower pre-angular step goes with a less elevated condyle, the dorsal surface of which is level with the remaining cheekteeth.

The mental foramen of L 6385 is situated beneath the anterior end of P_4 and there are indications that the symphysis extended this far back as well.

Discussion

The differences between the mandibles of the Langebaanweg *Mellivora* and modern *M. capensis* have important functional implications which are suggested by the nature of the mandibles in other modern mustelids. In those species in which the carnassial shearing action is important (e.g. *Martes* spp., *Gulo luscus*), there is a tendency for little upward inflexion of the pre-angular inferior margin and for the condyle to be low in relation to the cheekteeth. On the other hand, in those species in which the posterior cheekteeth function as crushing agents (e.g. *Enhydra lutris*, *Aonyx capensis*), there is a sharp upward inflexion of the inferior margin towards the angle and the condyle is raised above the level of the cheekteeth.

The Langebaanweg mandible falls into the former category and *M. capensis* into the latter, although *M. capensis* does not show the extreme development of these characteristics which are evident in the highly specialized *Enhydra* and *Aonyx*. Similarly, the Langebaanweg *Mellivora* is not as extreme in the other direction. It may thus be regarded as showing the beginnings of a trend towards modification of the masticatory apparatus which culminated in the condition evident in modern *M. capensis*.

The similarities between the lower carnassials of L 6385 and *Poecilogale* might therefore be coincidental, the latter having retained the more primitive shearing dentition. *Poecilogale* is actually more progressive than most other mustelids in having lost both P_1 and P_2, and it is often without M_2 as well. It is possible that the Langebaanweg *Mellivora* and *Poecilogale* had a common ancestor some time fairly late in the Tertiary, although the former can itself probably be excluded as a possible ancestor of *Poecilogale*. Even if M_2 was sometimes present in the Langebaanweg species, just as it is sometimes present in *Poecilogale*, it is perhaps unlikely that a variable feature of this kind would have persisted for so long a period in time.

It is even less likely that there is any close relationship between the Langebaanweg *Mellivora* and the only other non-lutrine mustelid from southern Africa, *Ictonyx striatus*, since in this species M_2 is always present and its M_1

has a metaconid.

Having suggested a relationship between L 6385 and *M. capensis*, it is necessary to examine its possible affinities with extinct mellivorines such as *Eomellivora* Zdansky 1924, *Promellivora* Pilgrim 1932 and the early species of *Mellivora* itself.

Eomellivora can be excluded from consideration since one of the characteristics of this genus is the presence of M_2. The recorded species are also far larger than that from Langebaanweg.

Comparisons with *Promellivora* are not as simple owing to the fragmentary nature of the material referred to this genus. It is in fact known only from a single mandibular fragment from the Dhok Pathan stage of the Siwaliks (*Promellivora punjabiensis* Lydekker). Pilgrim (1932: 65) stated that this genus is distinguished from *Mellivora* 'by the presence of P_1, the shallower and more gradual symphysis, the length and compression of M_1 and the shorter and simpler premolars especially P_3 and P_2, and the larger canine'.

Lydekker (1884) had previously referred the Dhok Pathan mandible to *Mellivora* and Pilgrim's justification for erecting a new generic name was based on the principal of horizontal rather than vertical classification, although he recognized that 'it is not improbable that (*Promellivora punjabiensis, Mellivora sivalensis* and modern *Mellivora*) are on the same line of descent' (Pilgrim 1932: 66). Although it is inevitable that there will be differences of opinion in nomenclatural problems of this kind and that generic distinctions made within a single lineage are often arbitrary, it might be preferable, in view of the fragmentary nature of the *P. punjabiensis* holotype, to revert to the original generic designation rather than to accept a new name. The name '*Promellivora*' is here rejected and the Dhok Pathan mellivorine is once again identified as *Mellivora punjabiensis.*

Comparisons between the Langebaanweg *Mellivora* and both *M. punjabiensis* and the Pinjor *M. sivalensis* are inconslusive since the bases for comparison are limited. The three forms are comparable in size and, not surprisingly, each has certain characteristics which are more primitive than those of the extant *M. capensis.*

One of the characteristics of *M. punjabiensis* which is apparently shared by the Langebaanweg form is the long symphysis terminating below the anterior end of P_4. If the symphysis of L 6385 did indeed extend this far back, then this specimen may also have had the compressed anterior premolars characteristic of *M. punjabiensis.* Both forms have a slender M_1 and Pilgrim (1932: 66) stated that the M_1 talonid of *M. punjabiensis* 'could not have been expanded'. In addition, both have mental foramina below P_4. Other important characteristics such as the presence of P_1 and absence of M_2 are evident in only one specimen or the other. Although it is not possible to tell whether or not the two are conspecific, they do share certain characteristics and there are some grounds for believing that they are at the same stage in the evolutionary development of *Mellivora.*

Even less satisfactory are comparisons between the Langebaanweg form and *M. sivalensis*, since published descriptions of the latter deal mainly with skull characters (e.g. Matthew 1929). However, since *M. sivalensis* is younger and therefore probably more advanced than *M. punjabiensis*, the indications are that the relationship between the latter and L 6385 is closer than that between *M. sivalensis* and the Langebaanweg specimen. This opinion is reflected in the tentative identification of the Langebaanweg specimen.

As with several other carnivore species from Langebaanweg, the specific identity of the *Mellivora* is likely to be resolved only if additional specimens are recovered. The single available specimen is nevertheless important, since its observable characteristics are not inconsistent with a *Mellivora* of late Pliocene age and it is in character with the fauna as a whole.

Family **Mustelidae**

Subfamily Lutrinae

Enhydriodon africanus Stromer, 1931

(Fig 7)

Material

L 9138—Right mandibular fragment with part of P_4.

Locality and horizon

This specimen is from 'E' Quarry, Langebaanweg.

Description

The single positively identified lutrine fossil specimen from Langebaanweg, although not described in detail, has already been referred to the species *Enhydriodon africanus* (Hendey 1970*a*: 100). The Langebaanweg specimen is less complete than the *E. africanus* holotype, which is from Kleinzee in Namaqualand (Stromer 1931*a*), but, since both are right mandibular fragments, comparisons are facilitated.

The two specimens are similar in size (Table 10), although the mandibular corpus of that from Langebaanweg is slightly more robust. In this specimen only the posterior part of P_4 is preserved, but the alveoli and some of the roots of the other cheekteeth are present. Both the Langebaanweg and Kleinzee specimens have a small and single-rooted P_2, but in the former the alveoli margins are lost so the relative sizes of the two teeth cannot be determined. Both specimens have a double-rooted P_3 and these were apparently similar in size.

The P_4 of L 9138 is a little larger than that of the holotype, the size difference being in keeping with that of the mandibular corpora. These differences are, however, no greater than might be expected in a single species. As far as

Table 10

Dimensions of the teeth and mandible of the Langebaanweg *Enhydriodon*, compared with that of the *E. africanus* holotype.

		*Enhydriodon africanus**	L9138
Height of mandible below	M_1	27	30,1
Breadth of mandible below	M_1	14,8	17,7
$P_2 - M_2$	l	57	*c.* 55,0
$P_2 - P_4$	l	28	*c.* 25,5
$P_2 -$	l	*c.* 5,6	—
	b	—	—
$P_3 -$	l	6	—
	b	—	—
$P_4 -$	l	11,9	*c.* 13,0
	b	8,6	10,0
$M_1 -$	l	22,0	*c.* 22,0
	b	+12,0	*c.* 12,5

* Stromer 1931*a*.

can be judged, the P_4 morphology in the two specimens is similar. Both have a prominent cingulum and prominent posterior accessory cusp, although in L 9138 the accessory cusp is more widely separated from the principal cusp.

The lower molars of the two specimens were apparently similar in size.

The tooth-row lengths are also comparable, although the premolars of the Langebaanweg specimen are more crowded than those of the Kleinzee mandible.

The Langebaanweg mandible has four mental foramina, the largest of which is situated high up on the corpus below the posterior root of P_3. Only one mental foramen is visible in the illustration of the Kleinzee specimen (Stromer 1931*a*: fig. 1) and this is situated in the same position as the principal foramen of the Langebaanweg mandible.

Both specimens have the most posterior and inferior part of the symphysis projecting below the adjacent inferior margin of the corpus.

Discussion

Although there are minor differences between the Kleinzee and Langebaanweg *Enhydriodon* mandibles, there can be little doubt that the two specimens belong to the same species.

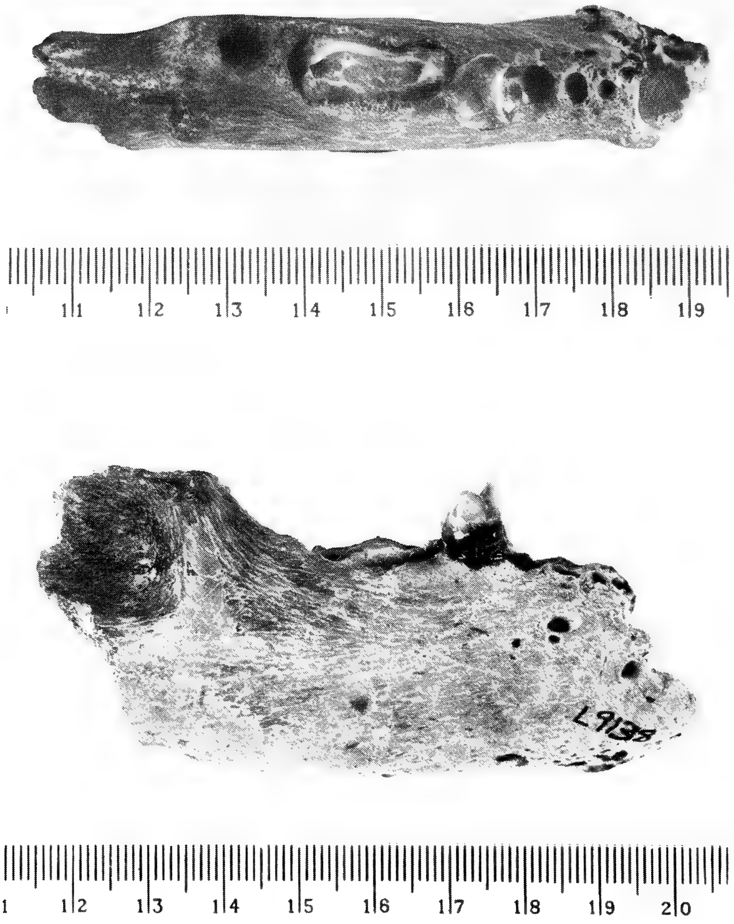

Fig. 7. Occlusal and buccal views of the *Enhydriodon africanus* mandible (L 9138) from Langebaanweg.

E. africanus is still regarded as a valid taxon, even though comparisons between it and previously described Eurasian species (see Pilgrim 1932: 82) are limited by the nature of the available material. Undescribed, but apparently specifically distinct material is now known from Omo in Ethiopia (F. C. Howell, pers. comm.), while the genus is also known from North America (Repenning 1967). The relationships between these various forms has yet to be determined. The widely dispersed records indicate that this was a very successful genus in the late Tertiary.

Family **Viverridae**

Subfamily Viverrinae

Viverra leakeyi Petter, 1963

(Figs 8, 9)

Comment

The material referred to this species may include two temporal variants of a single species and it is listed according to the stratigraphic unit from which it is derived.

Material from Bed 2, 'E' Quarry, Langebaanweg

L 12283—Isolated teeth comprising the dentition of a single individual and including:
Right $\underline{C}$, P^1, part of P^3, and $\underline{P}^4$ to M^2; left $\underline{C}$ and P^2 to M^2.
Right $\overline{C}$ and P_3 to M_2; left C, P_4 and M_1.

L 13097—Parts of the skull and skeleton of a single individual and including:
Posterior part of the braincase and right maxillary fragment with M^1.
Distal end of left humerus and proximal end of left ulna.

L 20253—Left maxillary fragment with P^4 and M^1.

The following are the remains of juveniles:

L 14459—Parts of a skull, including:
Left premaxilla and maxillary fragment with $d\underline{c}$, dp^2 and dp^3, with P^1 just erupting; right maxillary fragment with dp^3.
Right mandibular fragment with $d\overline{c}$, and dp_2 to dp_4, with P_1 just erupting; left mandibular fragment with P_1 and dp_2.

L 14460—Parts of a skull, including:
Right mandibular fragment with dp_3 and dp_4; left mandibular fragment with dp_2 to dp_4.

Material from Bed 3a, 'E' Quarry, Langebaanweg

The following specimens were recovered from the excavations LBW 1969/1 and 1970/1. The first six teeth listed apparently represent part of the dentition of one individual, while the last two may represent other individuals.

L 16240A—Left $\underline{C}$.
L 16224 —Left P^4.
L 16240C—Right M^1.
L 15174 —Right M^2.
L 16051 & L 16055A—Left M_1 and part of right M_1.
L 16197 —Right P^4.
L 16055J —? Right P_2.

Material from 'E' Quarry, but of unknown provenance

L 1700—Left mandibular fragment with M_1 and part of P_4.
L 2672—Right mandibular fragment with part of $\overline{C}$ and P_2 to P_4.

Judging from their preservation, it is likely that L 1700 is from Bed 2 and L 2672 from Bed 3a.

Description

These specimens belong to a viverrid of large size (Table 11) and although it is best represented in Bed 2, the Bed 3a material is described first.

The characteristics of the $\underline{\mathrm{C}}$ and P^4 to M^2 of the *Viverra leakeyi* holotype, which is from Laetolil in Tanzania (Petter 1963), are precisely those evident in the corresponding teeth of the Bed 3a sample. The P^4 protocone and supporting root are lost in the *V. leakeyi* holotype, but they are preserved in the Bed 3a specimens. Both the protocone and the root are large, the latter being larger even than the antero-external root. The long axis of the protocone and root projects antero-internally from the paracone and there is a marked indentation between the parastyle and protocone. The parastyle itself is very small and is situated at the base of the prominent paracone keel. It does not project as far anteriorly as the protocone. The buccal margins of both the Bed 3a specimens are more or less straight.

The lower teeth of *V. leakeyi* are unrecorded and comparisons with those from Langebaanweg are therefore not possible. The Bed 3a tooth tentatively identified as a P$_2$ is double-rooted, the crown is antero-posteriorly elongated and consists only of the principal cusp, the apex of which is directed slightly posteriorly. In lateral view the anterior and posterior keels of the principal cusp are slightly concave. The M$_1$ is a large tooth in which the talonid is much reduced relative to the trigonid. The paraconid is lower than the protoconid and it lies lingually relative to the protoconid, which results in the buccal surface of this portion of the tooth having a markedly convex outline in occlusal view. The metaconid is prominent, but is much smaller than the protoconid.

The mandible L 2672 belonged to a very aged individual, the remaining teeth are very worn and the specimen is poorly preserved. At least a part of M$_1$ must have been lost during life, since the alveolus of the anterior root is closed. The premolars appear to be essentially similar to the ? P$_2$ (L 16055J) in morphology and there is a progressive increase in size from P$_2$ to P$_4$. Although the M$_1$ is lost, it must have been about the same size as the Bed 3a M$_1$, L 16051. The M$_2$, which is also lost, was relatively small and single-rooted. The mandible is much larger than that of modern *V. civetta*, but its proportions are essentially similar.

In most respects the teeth from Bed 2 are similar to those from Bed 3a. The observed differences are not very marked and, since the assemblages are so small, their significance, if any, cannot be established at this stage.

The upper canine of L 12863 has pronounced grooves on both lingual and buccal surfaces and a not very prominent anterior keel. The nature of the anterior keel and the lingual grooves differentiates it from the Bed 3a canine, and apparently also that of the *V. leakeyi* holotype.

The P^1 is a small tooth with a rather conical crown and slightly bulbous

TABLE 11

Dimensions of teeth of the Langebaanweg *Viverra leakeyi*, compared with those of other Viverrinae.

		$\underline{C}$		P^1		P^2		P^3		P^4		M^1		M^2	
		l	l	l	b	l	b	l	b	l	b	l	b	l	b
Bed 2	L12863	9,3	7,0	4,6	3,6	10,4	4,4	13,2	5·7	17,4	11,1	8,9	14,4	4,3	7,2
	L13907	—	—	—	—	—	—	—	—	—	—	c. 9,3	15,2	c. 4,5	c. 7,0
	L20253	—	—	—	—	—	—	—	—	16,5	10,2	10,2	15,0	—	—
Bed 3a	Isolated teeth	(L16240A) c. 8,9	7,0	—	—	—	—	—	—	(L16224) 17,3	10,5	(L16240C) c. 9,0	14,0	(L15174) 5,7	8,3
	Viverra leakeyi[1]	8,5	—	—	—	—	—	12,0	5,9	17,2	—	10,1	14,5	5,0	8,0
	Vishnuictis durandi[2]	—	—	—	—	—	—	—	—	19,5	—	—	—	—	—

		$\overline{C}$			P_2		P_3		P_4		M_1		M_2	
		l	b		l	b	l	b	l	b	l	b	l	b
Bed 2	L12863	10,1	6,8		10,2	c. 4,2	—	c. 4,9	13,6	5,5	15,5	7,8	5,9	4,9
?Bed 2	L1700	—	—		—	—	—	—	—	c. 5,6	16,0	7,6	—	—
Bed 3a	Isolated teeth	—	—		(L16055J) 10,2	4,3	—	—	—	—	(L16051) 17,0	8,5	—	—
?Bed 3a	L2672	—	—		c. 10,2	c. 4,7	12,0	5,1	c. 13,8	6,2	c. 18,0	—	—	—

[1] Petter 1963.
[2] Pilgrim 1932.

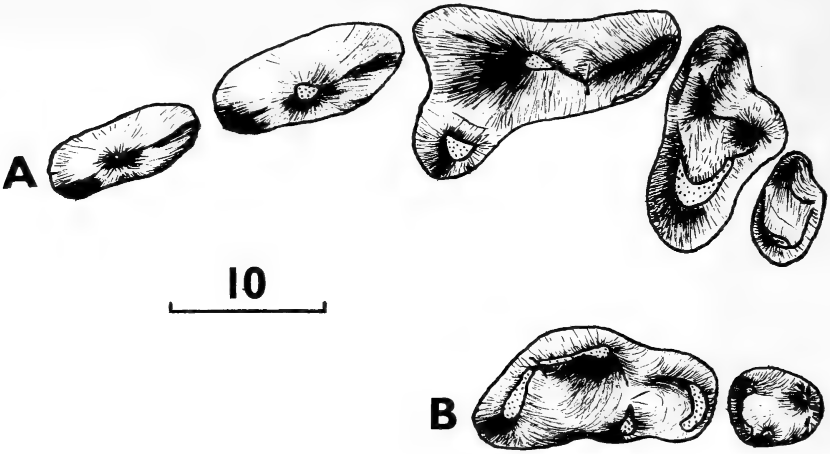

Fig. 8. Occlusal views of the left P^2 to M^2 (A) and right M_1 and M_2 (B) of the *Viverra leakeyi* from Langebaanweg.

root. The P^2 and P^3 are similar in structure to the ? P_2 from Bed 3a. The P^2 is much smaller than the P^3.

The P^4 of L 12863 differs from that of the Bed 3a form in certain respects. It lacks a parastyle, although there is a slight shelving where the parastyle would have been if present. The paracone lacks an anterior keel and the tooth is broader in the region of this cusp than in the Bed 3a specimens. The protocone is similar in size and situation to those of the Bed 3a specimens, but the indentation between the protocone and buccal cusps is not as sharply notched. The buccal margin of the L 12863 P^4 is markedly concave, rather than straight as in L 16197 and L 16224. The P^4 of L 20253 is similar to that of L 12863, except that it does have a small parastyle, in which respect it resembles the Bed 3a specimen, L 16224.

The M^1 is known from three specimens from Bed 2 and they are essentially similar to L 16240C from Bed 3a. There are, however, quite marked differences in the M^2 from the two beds. This tooth is lost in L 13097 and L 20253, but its alveolus is present in both specimens. These accommodate the M^2 of L 12863 quite well, so that at least in respect of size the M^2 of the three Bed 2 individuals are similar. The only known Bed 3a M^2 is appreciably larger and the individual features of the crown are more prominently developed than in the M^2 of L 12863. In L 13097 and L 20253 the buccal margins of M^1 and M^2 are at an angle of about 115° to the long axis of P^4 and their lingual limits form a line parallel to this axis.

The lower canine of L 12863 is similar in size to the upper canine, but lacks grooves on its lingual surface. Of the lower premolars of this individual, only P_2 and P_4 are reasonably intact and they are similar in morphology to P^2 and P^3. The P_4 of L 1700 does, however, differ from these teeth in that it has a prominent posterior accessory cusp, which is flanked posteriorly by a well-developed cingulum. This is the only premolar amongst all those which are referred to this species in which more than just the principal cusp is present.

On the other hand, the M_1 of L 1700 is virtually identical to that of L 12863. These teeth are in turn very similar to the M_1 of the Bed 3a form, except that their trigonids are less enlarged relative to the talonids. The overall size of the Bed 3a specimens is also greater and they have a more pronounced cingulum at the anterior end.

The M_2 of L 12863 is a small, single-rooted tooth, which is slightly elongated antero-posteriorly. There are two small cusps situated at the anterior and posterior ends of the buccal side of the tooth, while on the lingual side there are two cusps situated one behind the other at the anterior end. This tooth is accommodated quite well by the M_2 alveolus of L 1700. The M_2 of the Bed 3a form is not known, but judging from the size of the M_2 alveolus of L 2672, it was similar in size to that of L 12863.

The premolars of both Bed 2 and Bed 3a forms have markedly divergent anterior and posterior roots, which indicates that these teeth were well spaced in both mandible and maxilla. This is evident in both the mandibular fragments which are known (L 1700 & L 2672), even though the former is much more slender, comparing in size with that of modern *Canis mesomelas*.

The fragmentary braincase of L 13097 (Table 12) is a significant specimen, since, although it is so incomplete, it does exhibit some remarkable characteristics. The posterior constriction of the braincase is far more pronounced than in any modern viverrid species, while the posterior part of the sagittal crest is exceptionally high. The transverse compression of the posterior part of the skull is carried to such an extreme that the width across the occipital condyles is actually greater than the width of the occiput immediately above

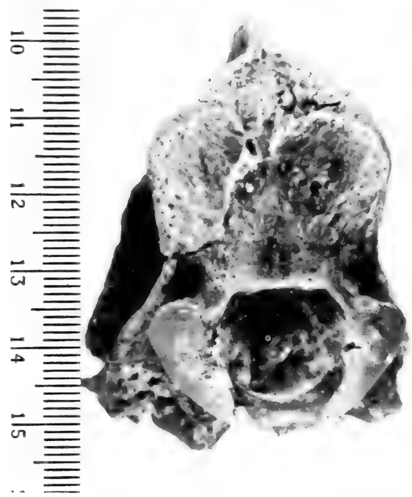

Fig. 9. Occipital view of the *Viverra leakeyi* braincase (L 13097) from Langebaanweg.

them (Fig. 9). In all extant viverrid species the reverse is true. In L 13097 the ratio of skull height (top of sagittal crest to inferior margin of condyles) to skull width (transverse diameter of occipital immediately above dorsal margin of foramen magnum) is 1,98:1, whereas in modern *V. civetta* (n = 1) it is 1,11:1 and in *Genetta* spp. (n = 11) it is 1,09:1.

TABLE 12

Dimensions of the skull, humerus and ulna of the Langebaanweg *Viverra leakeyi.*

Width across condyles	34,8
Skull height from base of condyles to top of sagittal crest	58,0
Transverse diameter of occipital immediately above foramen magnum	29,3
Greatest transverse diameter of distal articular end of humerus	26,1
Greatest antero-posterior diameter of ulna shaft	18,6

The skull of this species must, therefore, have been high, narrow and, judging from tooth size and mandible length, long.

The postcranial skeleton of this species is known only from the distal end of a humerus and the proximal end of an ulna (Table 12), which were found in association with the incomplete skull, L 13097. The humerus has already been mentioned elsewhere (Hendey 1973*a*) as being larger than that of a civet from the Kromdraai australopithecine site and much larger than that of modern *V. civetta*. The ulna is correspondingly large.

In respect of tooth and overall skull size, this species was apparently little different from modern *C. mesomelas*, but the humerus and ulna of *C. mesomelas* are only about half the size of corresponding parts of the fossil specimens. There are indications that the size discrepancy is considerably less in respect of the lengths of the bones, suggesting that the Langebaanweg *Viverra* was a stoutly-built and probably non-cursorial animal.

No deciduous teeth of modern or fossil civets were available for comparison with those from Bed 2. However, the dp_2 and dp_3 appear little different in structure to those of the East African early Pleistocene *Pseudocivetta ingens* (Petter 1967: Fig. 3), although the dp_3 of this species is lower crowned. The dimensions of the Bed 2 deciduous teeth are recorded here for future reference (Table 13).

Discussion

The principal differences between the teeth of the Bed 2 and Bed 3a forms of this species are as follows:

(1) The Bed 2 form has a smaller M^2.

TABLE 13

Dimensions of the deciduous teeth of the Langebaanweg *Viverra leakeyi*.

	dp^2		dp^3			dp_2		dp_3		dp_4	
	l	b	l	b		l	b	l	b	l	b
L 14459	7,1	2,2	13,0	6,6		7,2	2,3	10,5	3,4	12,8	4,4
L 14460	—	—	—	—		7,0	2,5	10,0	3,5	12,9	5,3

(2) The Bed 3a form has a larger M_1, with the talonid similar in absolute size to that of the Bed 2 form, while the trigonid is larger.

In addition, if the mandibles L 1700 and L 2672 are indeed from Bed 2 and Bed 3a respectively, then it is likely that the Bed 3a form was the larger of the two.

Even though the temporal difference between Bed 2 and Bed 3a may not be very great, Bed 3a is undoubtedly later and the differences between the civets from these two deposits may result from short-term intra-specific evolution. The Bed 3a form would, therefore, be the more advanced of the two. The larger M^2 of the Bed 3a form may represent the beginnings of the trend which led ultimately to the relatively large posterior crushing teeth of modern *V. civetta*. This speculation can only be tested if larger samples of the two forms become available.

There can be little doubt that the Langebaanweg *Viverra* is conspecific with the Laetolil *V. leakeyi* (Petter 1963). There are grounds for believing that an element of the Laetolil fauna is broadly contemporaneous with that from Langebaanweg and, consequently, the presence of *V. leakeyi* in the Langebaanweg fauna is not surprising (see Hendey 1970*b*: 123, 124).

In her discussion on the affinities of *V. leakeyi*, Petter considered its possible relationships to *Viverra* (*Viverra*) and *Viverra* (*Civettictis*). She found that *V. leakeyi*, *V. bakerii* Bose from the Siwaliks and *V.* (*Civettictis*) could, on morphological grounds, represent a phyletic series which derived from a *V.* (*Viverra*)-like ancestor. She concluded, however, that owing to uncertainty about the relative ages of the fossil species, an actual phyletic relationship of this kind could not be proven. In fact, since *V. bakerii* is recorded from the Upper Siwaliks (Pilgrim 1932) and is, therefore, almost certainly early Pleistocene in age, and since *V. leakeyi* is a late Pliocene species, such a phyletic series might indeed be possible. The only objection is that the series is geographically muddled, with the African *V. leakeyi* giving rise to the Asiatic *V. bakerii*, which in turn gave rise to the African *V. civetta*. The problem is, however, not serious since there might well have been a wide dispersal of civets of the *V. leakeyi* and *V. bakerii* types in Africa and southern Asia during the late Pliocene/early Pleistocene, with the lineage persisting only in Africa.

The Laetolil species was known only from teeth and the very curious braincase from Langebaanweg raises an additional complication to the question of civet relationships and phylogeny. Pilgrim (1932) defined a new viverrid genus from the Siwaliks, *Vishnuictis*, and this must now also be taken into account. This genus is characterized in part as follows:

> 'Viverrinae of medium to large size; . . . braincase exceptionally narrow; upper molars rather large; P^3 without internal cusp; premolar series rather spaced, premolars simple; mandible rather stout but shallow; M_1 with relatively long trigonid, relatively short talonid; M_2 rather large, oblong' (Pilgrim, 1932: 101).

The Langebaanweg species is accommodated quite well by this definition.

Pilgrim recorded two species of *Vishnuictis*, namely, *V. salmontanus* which is a smaller species from the Dhok Pathan, and *V. durandi* which is a very large species from the Upper Siwaliks. In respect of size and other characters, the Langebaanweg species is apparently most like *V. durandi*, a species characterized in part as follows:

> 'length of P^4 greater than united lengths of M^1 and M^2; angle between the axes of P^4 and the upper molars about 115°; outer borders of M^1 and M^2 continuous, their inner borders being in the same antero-posterior line' (Pilgrim 1932: 106).

The Langebaanweg species is, however, apparently not quite as large as *V. durandi* and, judging from the illustration of the holotype given by Matthew (1929), the size of the P^4 parastyle and the size of M^1 and M^2 relative to P^4, are greater even in the Bed 3a form of the Langebaanweg species. In these respects, *V. durandi* is the more advanced of the two species, which is in keeping with their inferred relative ages.

V. leakeyi is apparently not conspecific with either *Vishnuictis salmontanus* or *V. durandi*, but in view of the similarities which do exist between the three species, they should be regarded as congeneric. A simple and convenient solution to this taxonomic problem would be to regard *Vishnuictis* as a subgenus of *Viverra*, making it a third category within this genus, the others being *Viverra* (*Viverra*) and *V.* (*Civettictis*). Considering all the civets in terms of morphology, time and geography the relationships reflected in the tentative phylogeny presented here (Fig. 10) were concluded.

Viverra (*Viverra*) is regarded as the main lineage from which the others stemmed. During the Pliocene the first of the off-shoots, *Viverra* (*Vishnuictis*) was evolved and this was represented by an African lineage (*V. leakeyi*) and an Asian lineage (*V. salmontanus*—*V. durandi*), the latter persisting into the early Pleistocene. The African lineage is here regarded as the one which gave rise to the third group of civets, *Viverra* (*Civettictis*), which has culminated in the extant *V. civetta* of Africa, and which included an Asian off-shoot which is recorded only in the early Pleistocene (*V. bakerii*).

V. civetta has a poor Pleistocene record, but the Olduvai Bed 1 '*Pseudocivetta*' *ingens* (Petter 1967) is here regarded as an early representative of the

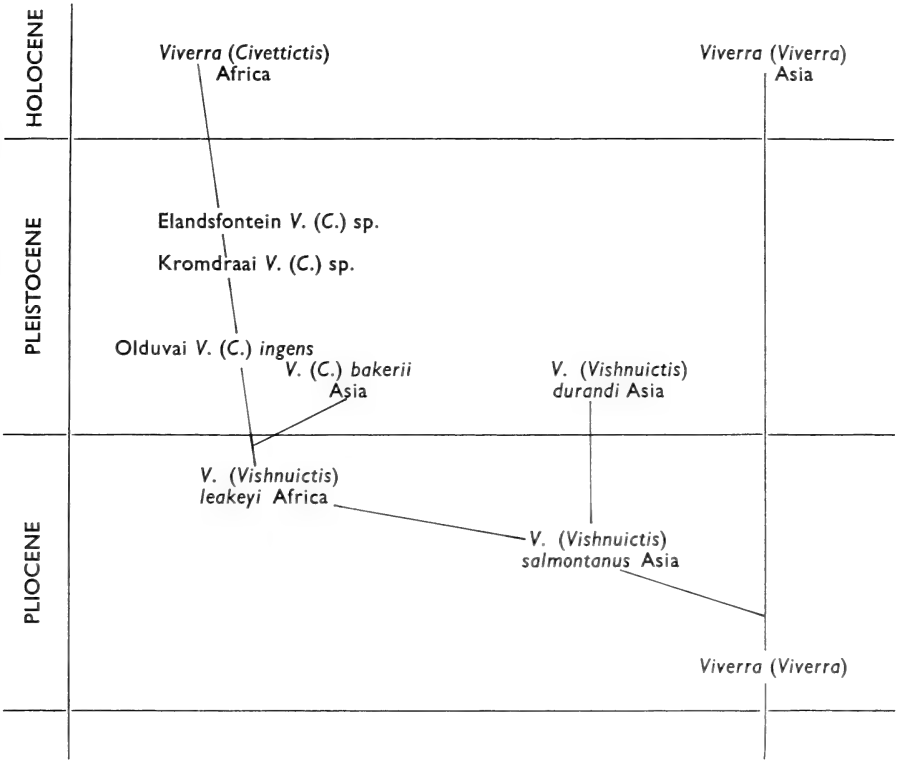

Fig. 10. Tentative phylogeny of the genus *Viverra*.

Viverra (*Civettictis*) group, while the Kromdraai and Elandsfontein civets (Hendey, 1973*a*; *vide infra*) are regarded as later members of the same group. The opinions concerning the relationships of the African Pleistocene civets are largely subjective owing to the nature of the recorded material, but it seems preferable to visualize a single lineage in which there was apparently a progressive decrease in body size from the Langebaanian to the Cornelian rather than to regard the isolated fossil records as representing distinct genera, as in the case of '*Pseudocivetta*'.

Family **Viverridae**
Subfamily Viverrinae
Genetta sp.
(Fig. 11)

Material

L 11191—Left mandibular fragment with P_2, P_3 and part of P_4.

Locality and horizon

This specimen is from Bed 2, 'E' Quarry, Langebaanweg.

Description

This specimen belongs to a very small viverrid. The mandibular corpus is relatively long and slender and the inferior margin is arched along its entire length (symphysis to below the anterior part of the masseteric fossa). The lower cheektooth row consisted of P_1 to M_2 and is approximately 20 mm long. The preserved premolars are narrow and sectorial. The P_2 has one posterior accessory cusp and the P_3 and P_4 have two.

Fig. 11. Buccal view of the *Genetta* sp. mandible (L 11191) from Langebaanweg.

Discussion

Apart from the fact that this specimen is about one-third smaller than corresponding parts of the mandible of modern *Genetta tigrina*, they are otherwise virtually indistinguishable. There can be little doubt that it belongs to a species of *Genetta*.

Stromer (1931*a*) has described a ? *Genetta* sp. from Kleinzee, but this is apparently not the same as that from Langebaanweg, since it is much larger. No other fossil *Genetta* from South Africa has yet been described. Petter (in Leakey 1965) mentions a *Genetta* of apparently small size from Olduvai Bed 1, but there is no description of this material.

The Langebaanweg *Genetta* probably belongs to a new species, but as this could only be poorly defined on the basis of the available material, it is left nameless.

Family **Viverridae**
Subfamily Herpestinae
Herpestes Species A

(Fig. 12)

Comment

As with the Langebaanweg *Viverra leakeyi*, the material assigned to this species is separated on the basis of its stratigraphic associations.

Material from Bed 2, 'E' Quarry, Langebaanweg

L 11847—Right mandibular fragment with part of P_2, and P_3 to M_1.
L 13040—Right mandibular fragment with M_1.
L 13053—Right maxillary fragment with P^3 to M^2; isolated left M^1.
L 13054—Right maxillary fragment with I^3, part of P^2, and P^3.

The following are the remains of juveniles:

L 14461—Right mandible with $d\bar{c}$, P_1, dp_4 and M_1, just erupting.
L 14462—Right mandible with $d\bar{c}$ and dp_2 to dp_4.

Material from Bed 3a, 'E' Quarry, Langebaanweg

L 15630B/1B—Right maxillary fragment with part of P^2.
L 15630B/1C—Left maxillary fragment with P^3.
L 15630B/1D—Part of left P^4.
L 16240F —Right $\underline{C}$.
L 16055D —Right mandibular fragment.
L 15630B/1A—Left mandibular fragment with M_1.
L 16177I —Part of right M_1.
L 15797B —Right $\bar{C}$.

Description

The Bed 2 material belongs to a species of *Herpestes* which is a little larger than the modern *H. pulverulentus* (Tables 14, 60, 61). Its dental formula is (?3).1.4.2/(?3).1.4.2.

The I^3 of L 13054 is appreciably larger than those of available *H. pulverulentus* specimens ($n = 14$) and, judging from the size of the alveolus, so was the canine. The pre-canine diastema is longer than in *H. pulverulentus*, which would be in keeping with a larger lower canine as well. The most anterior part of the snout of the fossil species was thus larger than in *H. pulverulentus* and the premaxilla projected further forward.

The cheekteeth are situated close to one another and the relative positions of these teeth, the infra-orbital foramen and the orbit are as in *H. pulverulentus*. The P^3 has a high principal cusp, a small posterior accessory cusp and a well-developed internal cusp. The P^3 of L 13054 lacks an anterior accessory cusp and in that of L 13053 there is a short horizontal shelf anteriorly from which projects a minute anterior accessory cusp. The P^4 is triangular in outline with the posterior surface of the protocone and the lingual surfaces of the paracone and metastyle in a straight line. The protocone is more anteriorly situated than that of *H. pulverulentus* and the parastyle is smaller relative to the paracone and metastyle. The M^1 is relatively broader internally than in *H. pulverulentus* and the M^2 is very small and relatively more reduced than in the modern species.

In general, the upper teeth of the fossil species are similar in structure to those of *H. pulverulentus*.

This applies also to the lower teeth, where the most obvious difference is

TABLE 14

Dimensions of the teeth and mandible of the Langebaanweg *Herpestes* Species A, compared with those of the ?*Herpestes* from Kleinzee.

			$\underline{C}$		I^3–$\underline{C}$	P^1–P^4	P^4		P_1–P_4	M_1–M_2	M_1		Height of corpus below M_1
			l (alveolus)	b	diastema	l	l	b	l	l	l	b	
Herpestes species A	Bed 2	L13054	4,8	3,3	2,6	c. 17,0	—	—	—	—	—	—	—
		L13053	—	—	—	—	8,0	5,4	—	—	—	—	—
		L 11847	—	—	—	—	—	—	c. 17,4	c. 9,3	6,7	—	9,5
		L13040	—	—	—	—	—	—	—	c. 9,2	6,8	3,6	9,5
	Bed 3a	L15630B/1A	—	—	—	—	—	—	—	c. 8,8	6,4	3,4	7,8
		L16177H	—	—	—	—	—	—	—	—	—	3,3	—
1930 X15a Kleinzee*			—	—	—	—	—	—	17,5	9,5	6,8	3,8	7,8

* Stromer 1931*a*.

Fig. 12. Buccal view of the *Herpestes* sp. A mandible (L 11847) from Langebaanweg.

that in the fossil the M_1 talonid is shorter relative to the trigonid. It also differs from *H. pulverulentus* in that P_1 is present. The mandibular corpus is more robust in the fossil and the masseteric fossa, especially that of L 13040, is much deeper.

The Bed 3a material is, as far as comparisons are possible, similar to that from Bed 2. The only observable difference is that the Bed 3a specimens are a little smaller than those from Bed 2. For example, the mandibular corpus and M_1 of L 15630B/1A are comparable in size to those of *H. pulverulentus* and are appreciably smaller than specimens from Bed 2.

Discussion

On the basis of the material presently available it seems probable that the Bed 2 and Bed 3a material is conspecific. There are certainly no major observable differences and the samples are so small that the significance, if any, of the size differences cannot be assessed.

Relatively little has been published on the smaller fossil viverrids of Africa, although this group is a significant element in the modern carnivore fauna of the continent and presumably the same applied during the late Tertiary and Pleistocene. None of the small viverrids described from the Transvaal caves (see Cooke 1963: Table 6) is relevant in the present instance, but it is likely that the Langebaanweg Species A is conspecific with the ? *Herpestes* sp. from Kleinzee (Stromer 1931*a*). The mandible L 11847 is virtually indistinguishable from the Kleinzee specimen which was described and figured by Stromer.

There is apparently no previously recorded fossil species to which this material can be referred and it is clearly not conspecific with any of the extant southern African species of *Herpestes*. As with the Langebaanweg *Genetta*, it probably represents a new species. It is, however, not named, since the present study of the smaller Viverridae was rather superficial and a meaningful diagnosis of a new species could probably not be given.

Family **Viverridae**
Subfamily Herpestinae
Herpestes Species B

(Fig. 13)

Comment

As with preceding species, the material from Bed 2 and Bed 3a is listed separately.

Material from Bed 2, 'E' Quarry, Langebaanweg

L 13055—Left maxillary fragment with P^1 to P^4, part of M^1, and M^2.

Material from Bed 3a, 'E' Quarry, Langebaanweg

L 16240P —Left maxillary fragment with P^3.
L 16055Q —Left M^1.
L 16177C —Right $\underline{C}$.
L 16177A, B—Right and left mandibular fragments, the former with C and P_2 to M_1.
L 15588B/B —Left mandibular fragment with P_4 and M_1.

Description

The Bed 2 maxilla belongs to a very small species of *Herpestes* (Table 15). It compares in size to corresponding parts of the skull of a modern *H. sanguineus zombae* specimen from Malawi (SAM 15797). Apart from the fact that it is

Fig. 13. Buccal view of the *Herpestes* sp. B mandible (L 16177A) from Langebaanweg.

much smaller it is essentially similar in detail to the *Herpestes* Species A from Langebaanweg.

The Bed 3a material is grouped with L 13055 since it also belongs to a very small *Herpestes* and there are no grounds for believing that the two samples are not conspecific. Apart from size, the only observable difference between this species and the larger *Herpestes* from 'E' Quarry is that the former lacks P_1.

Table 15

Dimensions of the teeth and mandible of the Langebaanweg *Herpestes* Species B.

		P^1–P^4	P^4		P_2–P_4	M_1		Height of corpus below M_1
		l	l	b	l	l	b	
Bed 2	L13055	13,8	5,3	3,6	—	—	—	—
Bed 3a	L16177A	—	—	—	10,0	4,3	2,3	—
	L15588B/B	—	—	—	—	4,2	2,4	*c.* 6,5

Discussion

There can be little doubt that this species and the larger Langebaanweg herpestine are congeneric, but because of the appreciable size difference between the two, they are clearly not conspecific.

The absence of P_1 is characteristic of some species of *Herpestes* (*Galerella*), and Species B may have affinities with this subgenus. No other conclusions as to its relationships were reached.

The specific identity of fossil forms of generalized small viverrids such as the two Langebaanweg *Herpestes* is a difficult problem to which there seems to be no immediate solution. If statistically significant samples of the fossil species were available, and in the present instance there is a good chance that this will eventually be the case, and these could be compared with large modern series, it does not necessarily follow that the fossil forms will be distinguishable from all modern species, in spite of the great time difference involved. For example, should it prove that Species B cannot be distinguished from the Malawian *H. sanguineus*, it does not logically follow that the two are conspecific.

The best way of making meaningful specific identifications of the fossil species would be by tracing their lineages to their conclusion. This is clearly an impossible task at present in view of the poor fossil record of the Herpestinae. In this respect it is as well to note that the major radiation of the Herpestinae, at least in Africa, apparently took place during the Pleistocene (*vide infra*), and the two Langebaanweg species could each be directly ancestral to more than one modern species, or genus, as well as other now extinct species. Consequently, even if the fossil record of this group was very much better known, it would probably still be difficult to establish a clear picture of relationships. The problem is compounded by the fact that during the Pleistocene many, if not all carnivore species underwent size changes. This may effectively eliminate an apparently useful method of distinguishing between generalized Herpestinae.

Since no other Pliocene Herpestinae have yet been named in Africa, a simple solution in the present instance would be to provide new names for the Langebaanweg species and to list all their observable characters in the diagnoses in the hope that some might prove genuinely useful in distinguishing them from other species. On the other hand, since it is almost certain that more material of both these species will become available, and since relevant material may yet be described from elsewhere in Africa, it is considered preferable at this stage to defer the naming of the species. It will almost certainly be more fruitful to consider this matter again at a later date and this may best be done without having to consider formal species names already in existence.

Family **Viverridae**

In addition to the material already listed, viverrid remains have also been recovered at sites 1/1968 and 12/1968 in 'E' Quarry (see Hendey 1970*a*: 81, 86–88). These occurrences are now regarded as belonging in Bed 2, but it is still considered preferable to consider these fossils separately for the time being.

The site 1/1968 viverrid specimens include a number of isolated teeth and two mandible fragments. One of the latter belongs almost certainly to *Herpestes* Species A, while the other is referred to the Bed 2 *Genetta* sp. A similar array of specimens was recovered from site 12/1968, although in this case a larger number of isolated teeth were recovered. Once again both *Herpestes* Species A and *Genetta* sp. were represented.

Family **Hyaenidae**

The Hyaenidae are the most commonly represented Carnivora in the deposits at Langebaanweg and they are in some respects the most problematical group in this order. Three species have been identified, while there are two other tentatively identified and informally named species. The latter may represent aberrant individuals of one or other of the three named species. Each of the three identified species, and one which was not formally named, is represented by cranial and associated postcranial remains of at least one individual of known provenance.

It was during the late Pliocene and early Pleistocene that the Hyaenidae reached the peak of their radiation and a large number of genera and species dating from this period in time have been recorded, principally from Eurasia. The importance of the Langebaanweg Hyaenidae lies chiefly in the fact that they are among the first African Pliocene representatives of this family to be described. Consequently, they provide information on hyaenids dating from a period in time during which significant evolutionary developments were taking place and they are from a continent which undoubtedly played an important role in the evolution of the family.

In the present report no mention is made of the as yet unpublished hyaenid material from the Pliocene of East Africa, although a few casts of relevant specimens were available. These specimens were, however, taken into account in reaching the conclusions on hyaenid phylogeny which are presented here. Hyaenid classification and phylogeny have been the subject of numerous studies and some of the conclusions of the present study are a departure from previously held opinions. They will almost certainly not be generally accepted, but the records of the Langebaanweg hyaenids themselves should prove useful in other accounts of the Hyaenidae which are still to come.

Family **Hyaenidae**

Subfamily Hyaeninae

Percrocuta australis n. sp.

(Figs 14, 15)

Holotype

L 14199—A crushed and incomplete skull, including the following teeth: Part of right P^3; left and right P^4; left I_1 to I_3, $\overline{C}$ and P_2 to M_1; right I_1 I_2, $\overline{C}$ and P_2 to M_1.

Referred Material

L 13033—Parts of the skull and skeleton of a single individual and including: Left and right $\underline{C}$; incomplete right mandible with P_4 and M_1.
Parts of at least seven vertebrae; three tarsal bones; parts of five metapodials; seven phalanges.

Locality and Horizon

These specimens are from Bed 2, 'E' Quarry, Langebaanweg.

Referred material which is probably from Bed 2:

L 6381—Left maxillary fragment with P^1 and P^2.
L 5355A, L 9140, L 12102, L 12333—Premolar fragments.

Diagnosis

A *Percrocuta* similar in size to *P. eximia* Roth & Wagner 1855, but differs in lacking P_1; P^2_2 and P^3 without anterior accessory cusps; premolars longer; M_1 metaconid very small or absent. Metacarpal I not as reduced as in modern Hyaeninae.

Etymology

From *australo* meaning 'southern', to indicate its geographical position in relation to other species of *Percrocuta*.

Description

The skull (Tables 16, 17)

The skull of the holotype is so badly crushed and so incomplete that little can be said of its characters. The post-glenoid process is not as stoutly developed as those of available modern *Crocuta crocuta* specimens ($n = 5$), a feature which is probably related to the less enlarged cheekteeth and weaker masticatory apparatus of the fossil. A very strong posterior buttress to the mandibular condyle is required by *C. crocuta* with its greatly enlarged cheekteeth and powerful muscles of mastication. In L 14199 the infra-orbital foramen is situated just above the antero-lateral root of P^4, rather than above the anterior root of P^3 as in the *C. crocuta* comparative series. In this respect it resembles the *P. eximia* specimen (BMNH M 4162) from Samos which was illustrated by Pilgrim (1931: pl. 1).

The maxillary fragment L 6381 has attached that portion of the premaxilla which separates the nasals from the maxilla. It is longer than corresponding parts of the premaxilla of the available *C. crocuta* specimens, and in lateral view it is visible along its entire length. In *C. crocuta* the most distal portion of the premaxilla curves into a horizontal position and in lateral view is partially obscured by the maxilla.

The nature of the M^1 of the fossil is not known.

The P^4 is comparable in length to that of *C. crocuta*, while the breadth is also similar, although the protocone of the fossil is somewhat reduced. The latter is a characteristic of the genus *Percrocuta* (Kurtén 1957*b*), although in the present instance the protocone reduction is not as marked as in species such as *P. tungurensis* and *P. grandis* and nor is it as posteriorly situated. In the P^4 of L 14199 the parastyle, paracone and metastyle are more or less equal in length, which is in contrast to the condition in *C. crocuta* where the parastyle is shorter than the paracone, which in turn is shorter than the metastyle.

Although only the posterior portion of the holotype P^3 is preserved, it is important since it also exhibits *Percrocuta* rather than *Crocuta* characteristics. The posterior accessory cusp is much more prominent than that of *Crocuta* and there is a well-developed cingulum which extends from the lingual surface opposite the principal cusp to behind the posterior accessory cusp. The fossil P^3 is also narrower and less high crowned than that of *Crocuta*.

The P^2 of L 6381 is much smaller than the P^3 of the holotype. The posterior portions of these two teeth are similar in morphology, except that the P^3 has a greater development of the posterior-internal region. The P^2 lacks an anterior accessory cusp but, like *C. crocuta*, it has a well-developed anterior keel on the principal cusp which terminates antero-internally at the cingulum.

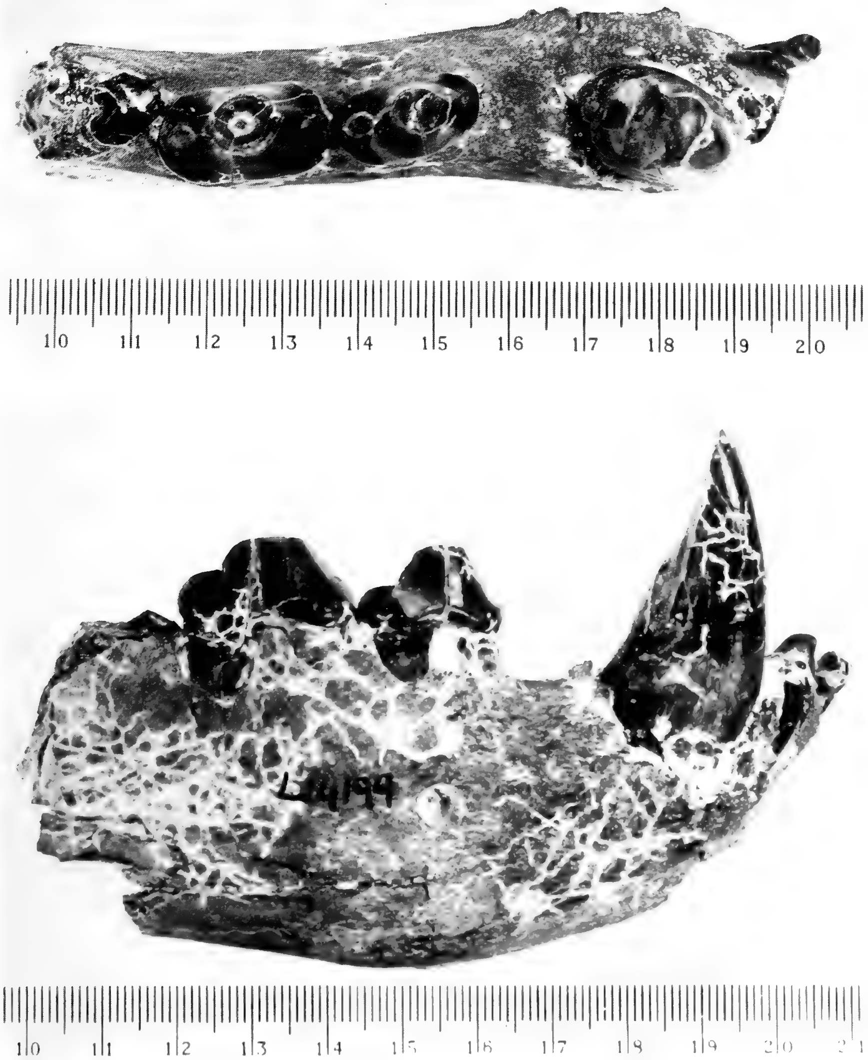

Fig. 14. Occlusal and buccal views of the *Percrocuta australis* mandible (L 14199) from Langebaanweg.

The P^1 of L 6381 is a relatively small tooth, which is similar in size and morphology to that of *C. crocuta*.

The upper canines of L 13033 are very worn, but it appears that, compared to those of *C. crocuta*, the crowns were small relative to the size of the roots. Although they belong to different individuals, the left canine of L 13033 fits

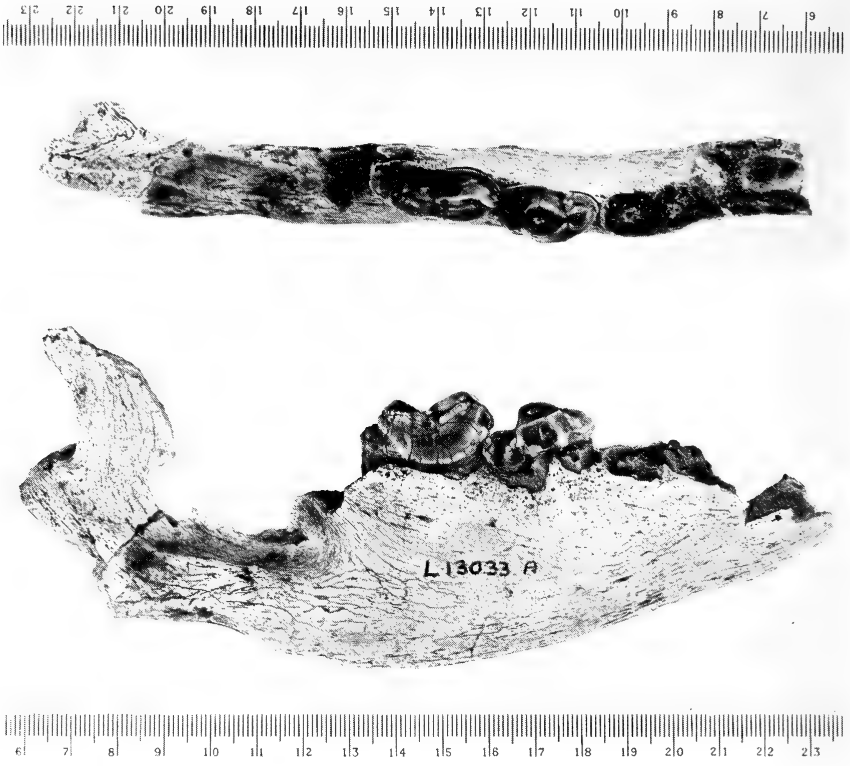

Fig. 15. Occlusal and buccal views of the *Percrocuta australis* mandible (L 13033) from Langebaanweg.

quite well into the canine alveolus of L 6381.

Although both halves of the mandibular corpora of the holotype are preserved, the posterior portions are detached, crushed and fused together by the phosphatic matrix which is characteristic of the upper levels of Bed 2 in the vicinity of East Stream. When articulated, the anterior parts of the corpora are V-shaped in ventral view, rather than being arched and almost U-shaped as in *C. crocuta*. The symphysis is similar in shape to that of *C. crocuta* and also terminates below the posterior root of P_2. It is, however, somewhat longer since the depth of the fossil corpora below P_2 is greater than in *C. crocuta*. The fossil mandibular corpora, especially in L 13033, are very robust and the overall length of the mandible is greater than those of the *C. crocuta* comparative series. The masseteric fossa of L 13033 is very deep and there is a horizontal ridge of bone along its inferior margin which is more or less parallel to the inferior margin of the mandible in this region. In *C. crocuta* this ridge and the inferior margin of the mandible towards the angle are inclined upwards, with the result that the condyle is higher relative to the cheekteeth than is the case with the fossil.

TABLE 16

Dimensions of the upper teeth of Hyaenidae from Langebaanweg, compared with those of some other hyaenid species.

		C		P^1		P^2		P^3		P^4		M^1		M^2	
		l	b	l	b	l	b	l	b	l	b	l	b	l	b
Percrocuta australis	L14199	—	—	—	—	—	—	—	15,5	38,4	20,0	—	—	—	—
	L6381	—	—	8,2	7,2	20,2	11,6	—	—	—	—	—	—	—	—
	l:b					1,74									
Hyaena abronia	L14186	12,3	9,8	5,4	5,0	14,9	8,2	19,8	12,1	28,0	16,2	9,5	15,4	4,0	4,3
	l:b					1,82		1,64							
Hyaena Species B	L12848	*c.* 14,2	10,5	—	—	*c.* 16,1	*c.* 10,0	20,8	13,2	29,8	17,8	10,5	17,9	—	—
	l:b					1,61		1,58							
Hyaenictis preforfex	L10055	—	—	*c.* 5,0	4,8	*c.* 14,5	8,1	*c.* 17,3	*c.* 10,8	*c.* 25,0	—	—	—	—	—
	l:b					1,79		1,60							
Hyaena hyaena makapani	Means[1]	12,9	9,1	6,2	5,8	14,6	9,4	19,4	12,8	28,7	17,2	5,8	12,8	—	—
	l:b					1,55		1,52							
Modern *Hyaena hyaena*	Means (n = 14)	—	—	6,1	5,7	15,8	9,7	20,4	13,3	30,1	18,2	—	—	—	—
	l:b					1,63		1,53							
Hyaenictis forfex[2]		—	—	5,7	5,7	16,4	10,4	21,8	14,0	31,4	19,2	—	—	—	—
	l:b					1,58		1,56							
Leecyaena lycyaenoides[3]		—	—	—	—	19,5	11,0	25,0	15,5	34,2	20,0	—	—	—	—
	l:b					1,77		1,61							

[1] Toerien 1952.
[2] Ewer 1955*a*
[3] Young & Liu 1948.

TABLE 17

Dimensions of the lower teeth of Hyaenidae from Langebaanweg, compared with those of some other hyaenid species.

		C		P_1		P_2		P_3		P_4		M_1		M_2	
		l	b	l	b	l	b	l	b	l	b	l	b	l	b
Percrocuta australis	L13033	c. 17,4	c. 12,8	—	—	—	—	—	—	24,7	c. 13,3	c. 29,4	c. 12,5	—	—
	L14199	18,1	13,4	—	—	19,4	10,5	23,2	12,6	c. 26,0	13,1	—	—	—	—
	l:b					1,85		1,84		1,98					
Hyaena abronia	L13167	—	—	—	—	—	—	—	—	—	—	20,9	10,4	—	—
	L14186	12,4	9,8	4,0	3,4	13,8	7,8	17,5	9,6	19,0	10,0	21,1	10,4	5,2	4,5
	l:b					1,77		1,82		1,90					
Hyaena Species B	L11206	—	—	—	—	—	—	—	—	—	—	c. 23,2	c. 11,2	—	—
	L12848	—	—	3,8	4,7	15,2	8,3	20,2	10,5	20,8	11,0	23,0	11,1	c. 5,6	—
	l:b					1,83		1,92		1,90					
Hyaenictis preforfex	L10055	—	—	—	—	c. 12,4	7,1	c. 15,1	9,4	c. 17,4	c. 9,0	c. 19,0	9,0	—	—
	l:b					1,75		1,61		1,93					
Hyaena hyaena makapani	Means[1]	13,4	10,3	—	—	13,4	7,8	17,8	10,7	19,2	10,9	20,0	9,9	—	—
	l:b					1,72		1,66		1,76					
Modern *Hyaena hyaena*	Means (n = 14)	—	—	—	—	13,9	8,5	19,0	11,4	20,5	11,5	20,9	10,5	—	—
	l:b					1,64		1,67		1,78					
Hyaenictis forfex[2]		—	—	—	—	—	—	19,7	12,8	22,5	11,9	24,7	12,5	—	—
		—	—	—	—	—	—	19,9	13,3	22,3	12,2	24,6	—	—	—
	l:b							1,54		1,89					
								1,50		1,83					
Leecyaena lycyaenoides[3]		—	—	—	—	16,7	10,0	22,8	13,4	24,0	13,6	25,0	12,3	—	—
	l:b					1,67		1,70		1,76					

[1] Toerien 1952.

[2] Ewer 1955*a*.

[3] Young & Liu 1948.

The lower incisors of the holotype are smaller than those of *C. crocuta*, but are similar in their relative proportions. The I_3 is also lower crowned and does not have such a prominent lateral projection.

The lower canines of the holotype are more transversely compressed than those of *C. crocuta* and also appear to have larger roots. The holotype canines are remarkable because they are worn in the way which is unusual in hyaenids. They lack horizontal wear facets and instead have vertical wear facets extending from the postero-external surfaces of the base of the crowns to the anterior surfaces near the original apices of the crowns. This is probably an individual peculiarity since the upper canines of L 13033 do have horizontally worn crowns in addition to wear facets on their anterior surfaces.

Both halves of the mandible of the holotype lack P_1 and the diastema is longer than in any of the *C. crocuta* comparative specimens. The anterior portion of the mandible of L 13033 is damaged, so it is not known whether or not P_1 was present in this individual.

The P_2 of the holotype is shorter and narrower than the P^2 of L 6381. It also narrows anteriorly and lacks the slight inflation of the postero-internal cingulum evident in the P^2. It lacks an anterior accessory cusp. The P_2 of *C. crocuta* is shorter, relatively much broader and lower crowned.

The holotype P_3 is appreciably larger than P_2 and, except that it is more or less rectangular in outline, it is otherwise similar to P_2 in morphology.

The P_4 resembles P_2 in that it also narrows anteriorly, but it differs from both P_2 and P_3 in having a fairly prominent anterior accessory cusp and a more pronounced postero-internal cingulum. This part of the cingulum also has a slight vertical component, so that there is a small postero-internal cusp flanking the posterior accessory cusp. This is less marked in L 13033 than it is in the holotype.

Although the P_2, P_3 and P_4 of *C. crocuta* differ quite considerably from the corresponding teeth of the fossil species, there are certain basic morphological similarities. The lower premolars of the two species have the same cusps represented, but there is a difference in their relative sizes. In both species broadening is most evident in P_3. The least dissimilar of the premolars is P_4 and it is really only the more rectangular outline and reduced anterior accessory cusp of the *C. crocuta* P_4 which differentiates it from the fossil.

Both lower carnassials of the holotype are crushed and incomplete. The talonid is short, although not as short as that in *C. crocuta*, and the paraconid is a little longer than the protoconid. The metaconid is present, but is very small. The M_1 of L 13033 is similar, except that the metaconid is apparently absent.

The holotype lacks M_2 and it is likely that this tooth was absent in L 13033 as well.

Postcranial skeleton (Tables 25, 26)

The only postcranial remains which are positively identified as belonging to this species are some vertebrae and parts of the right manus and left pes of L 13033. The individual skeletal elements are most readily distinguished from those of available skeletons of modern *C. crocuta* (n = 1) and *H. brunnea* (n = 2) by their larger size.

Of the seven vertebrae known, only one, the 7th cervical, is largely intact. This specimen is only slightly larger than the 7th cervicals of the modern comparative specimens, but the centrum of the fossil 2nd cervical is appreciably larger.

The manus is represented by a metacarpal I, the proximal end of metacarpal V and possibly some of the phalanges. The metacarpal I, a bone which is vestigial in modern *Hyaena* and *Crocuta*, resembles that of *Proteles cristatus* in morphology, but it is considerably larger. Its size relative to the remaining part of the metacarpal V is, however, similar to the relative sizes of these bones in *Proteles*. The metacarpal V is larger than those of the *Hyaena* and *Crocuta* comparative specimens, but is morphologically similar, although in dorsal view its proximal articular facet is slightly concave, rather than straight or slightly convex as in the modern specimens.

The tarsal bones of L 13033 which were recovered are a navicular, a cuboid and an internal cuneiform. They are much larger than those of the comparative specimens and although there is a basic morphological similarity between the navicular and cuboid of the modern and fossil specimens, there are some differences in detail. The navicular has a transverse diameter comparable to that of the available *C. crocuta* specimen, but it is broader than those of the two *H. brunnea*. Its antero-posterior diameter is greater than those of all three modern specimens. It also differs in that it lacks the deep median indentation at the posterior end of the proximal articular facet, while the medial facet of articulation with the cuboid is circular rather than antero-posteriorly elongated. The facets on the distal surface which articulate with the cuneiforms are more distinctly separated from one another than is the case in the modern specimens. There are comparable differences in size and in the nature of the articular facets in the cuboid. The internal cuneiform differs from those of the moderns only in its larger size.

The metatarsals II and V, which are intact, are similar to those of the comparative specimens, except again for their larger size. The metatarsal II has an abnormal growth of bone near the distal end of the shaft and the trochlea is inflected ventrally at a slight angle to the shaft. A similar pathological condition is evident in one of the 1st phalanges, while another is barely recognizable as a phalanx owing to a severe condition which has left the bone spongy, deformed and incomplete. The cause of the pathology is not known, but it might be the result of an old injury.

The phalanges are, in general, similar to those of the modern specimens, except for their larger size and the fact that the terminal phalanges are more strongly arched.

The relative sizes of fore- and hindlimbs of this species cannot be accurately assessed on the basis of the available material, but the relative sizes of the proximal ends of the metacarpal V and metatarsal V are not as disproportionate as those of extant hyaenids.

The postcranial material indicates that the fossil species was far larger than modern *C. crocuta* and since the known skull parts are only a little larger than corresponding elements in *C. crocuta*, it suggests that the fossil form was not as curiously proportioned an animal as *C. crocuta*.

Discussion

The affinities of the large hyaenid from Langebaanweg clearly lie with *Percrocuta* Kretzoi, 1938 rather than *Crocuta* Kaup, 1828. The former genus has been the subject of a critical study by Kurtén (1957*b*) who tentatively regarded it as a subgenus of *Crocuta*. Both Kurtén and Pilgrim (1932) suggested that there might be no direct phyletic connection between *Percrocuta* and *Crocuta* and Thenius (1966) subsequently indicated a major phyletic separation between them and allowed *Percrocuta* full generic status. Ficcarelli & Torre (1970) went a step further and recognized two genera within this group, namely, *Percrocuta* and *Adcrocuta* Kretzoi, 1938. It is, however, the arrangement of Thenius which is accepted here.

The Pliocene *Percrocuta* populations do fall into two groups, one culminating in the very large *P. gigantea*, Schlosser 1903, and the other in the smaller *P. eximia* of Eurasia. It is with the latter group that the Langebaanweg species apparently has its closest connections. The graphic representation of ratios devised by Simpson (1941) and used for cheektooth lengths by Kurtén (1957*b*) in his analysis of *Percrocuta*, gives a clear indication of the similarity between *P. eximia* and the Langebaanweg species (Fig. 16).

Kurtén (1957*b*: 399–400) recognized three subspecies of *P. eximia* and these range in age from early to mid Pliocene. In view of the late Pliocene age of the Langebaanweg species, it might be expected that it would be more advanced than the recorded subspecies of *P. eximia*. This is indeed the case and it is on these grounds that the specific separation is justified, while the wide geographic separation between *P. eximia* and the Langebaanweg species is intended to be suggested by the proposed new name for the latter, *P. australis*.

The most important observable differences between *P. australis* and *P. eximia* are that the former lacks P_1 and anterior accessory cusps on P^2_2 and P_3, while its premolars are more elongated than those of *P. eximia*. *P. australis* may well be a descendant of *P. eximia*, the ancestral form having been present in Africa earlier in the Pliocene when this species was at its peak and widely distributed in Eurasia as well.

Since the nature of the relationship, if any, between the late Tertiary *Percrocuta* and Quaternary *Crocuta* is obscure, and since *P. australis* is apparently the most recent of the smaller-sized *Percrocuta* group, it is of interest to consider the possibility of a relationship between the Langebaanweg species and *Crocuta*.

Kurtén (1957*b*) concluded that none of the *Percrocuta* species known at that time could be ancestral to *Crocuta* (*sensu stricto*). He regarded *C. sivalensis* Falconer & Cautley, 1868 as the earliest recorded direct ancestor of *C. crocuta*

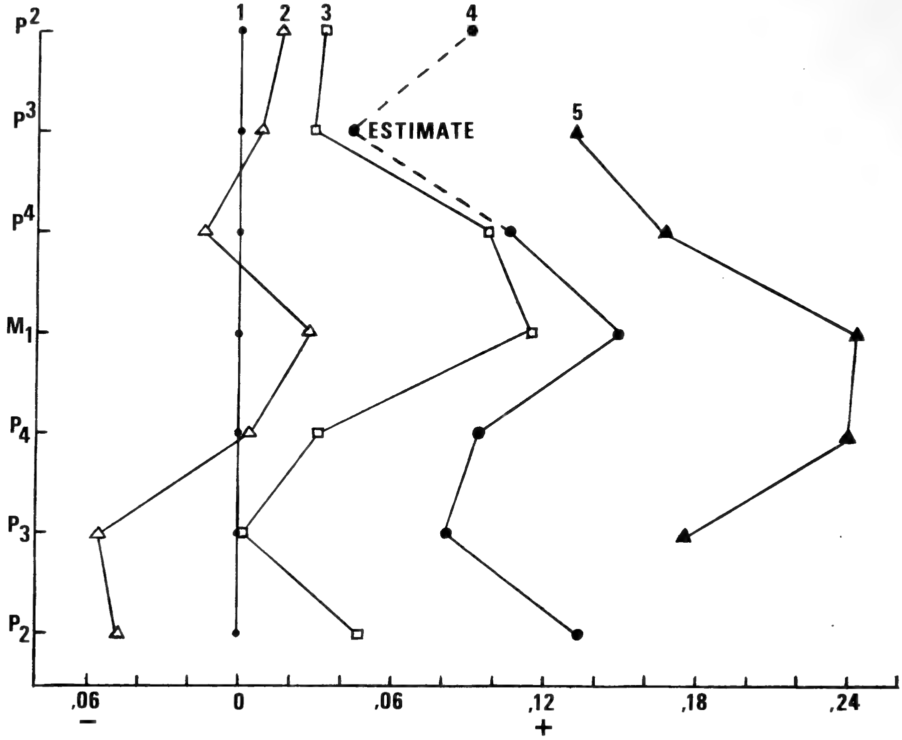

Fig. 16. Ratio diagram comparing relative lengths of the cheekteeth of *Percrocuta carnifex* (2), *P. eximia eximia* (3), *P. gigantea* (5) (Kurtén 1957*b*) and *P. australis* (4), with modern *Hyaena hyaena* (1) (Kurtén 1956) as a standard.

and visualized a hypothetical ancestor of the former species as having the following characteristics:

(1) M_1 metaconid well-developed.
(2) M_1 talonid long.
(3) Protocone of P^4 large.
(4) Anterior premolars heterodont.

Both Kurtén (1957*b*) and Thenius (1966) thought it likely that *Crocuta* was descended from *Lycyaena chaeretis* Gaudry, 1861. Since this species is a relatively primitive and rather generalized hyaenid dating from the earlier part of the Pliocene, there is little difficulty in regarding it as an ancestor of *Crocuta*. It is however, perhaps significant that later species of *Lycyaena* (e.g. *L. lunensis* from Europe and *L. nitidula* from South Africa) were 'non-scavenging fully predaceous forms in which the trend towards the development of heavy conical hammer-like premolars suitable for bone-crushing was reversed' (Ewer 1955*b*: 851). While it is not impossible that *L. chaeretis* also gave rise to a lineage in which the typical hyaenid trend was not reversed, it is curious that this is not reflected in the fossil record.

On the other hand, it is equally curious that the *Crocuta*-like *Percrocuta* group are essentially late Tertiary in age, while *Crocuta* itself is confined to the Quaternary, and that the apparently logical chronological succession has not been supported by the evidence of developing morphological characters. If it could be demonstrated that *P. australis* was more like early *Crocuta* than was *P. eximia*, then it might be accepted that a direct phyletic connection between *Percrocuta* and *Crocuta* did exist. However, this does not appear to be the case.

The four characteristics which were listed above and which were regarded by Kurtén as being likely in an ancestor of *C. sivalensis* are not convincingly evident in *P. australis*. In addition, there was apparently a trend towards the elongation of the premolars in the *P. eximia–P. australis* lineage and this would have had to be reversed if the latter was indeed ancestral to *C. crocuta* (Fig. 17).

Since *Percrocuta* has now been recorded from sub-Saharan Africa, there may yet be evidence forthcoming from the region which could substantiate a

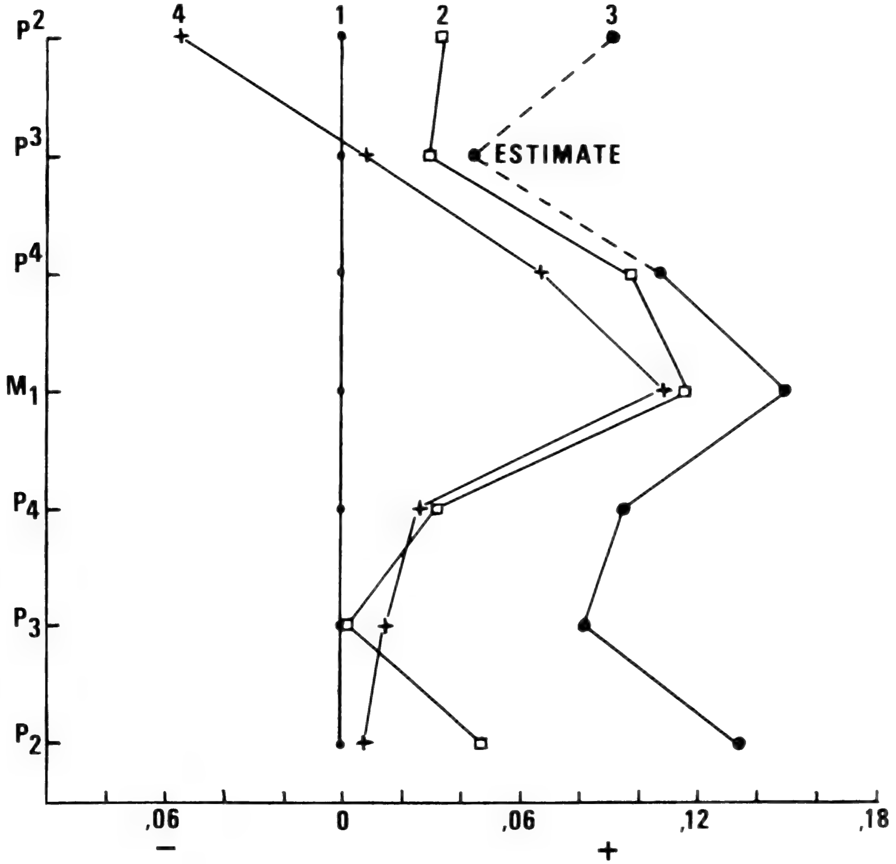

Fig. 17. Ratio diagram comparing relative lengths of the cheekteeth of *Percrocuta eximia eximia* (2), modern *Crocuta crocuta* (4) (Kurtén) 1957*b*, 1956) and *P. australis* (3), with modern *Hyaena hyaena* (1) (Kurtén 1956) as a standard.

direct relationship between *Percrocuta* and *Crocuta*.

Another opinion on the origins of *Crocuta* was recently expressed by Ficcarelli & Torre (1970), who concluded that this genus had an independent history dating back to the Miocene. This view is apparently at least partly based on the belief that *C. honanensis* Zdansky, 1924 from China is early Pliocene in age. No explanation is given of the otherwise complete absence of *Crocuta* in the Miocene and Pliocene, times when the fossil record of hyaenids is by no means poor.

Another African record of *Percrocuta* is *P. algeriensis*, which was described by Arambourg (1959) as a species of *Hyaena*. Ewer (1967) also regarded it as an *Hyaena*, and while Ficcarelli & Torre (1970) had doubts about its relationships, they refer to it as *Hyaena algeriensis* in their text. Thenius's (1966) grouping of this species with *Percrocuta* is accepted here (Fig. 18), since this is its most

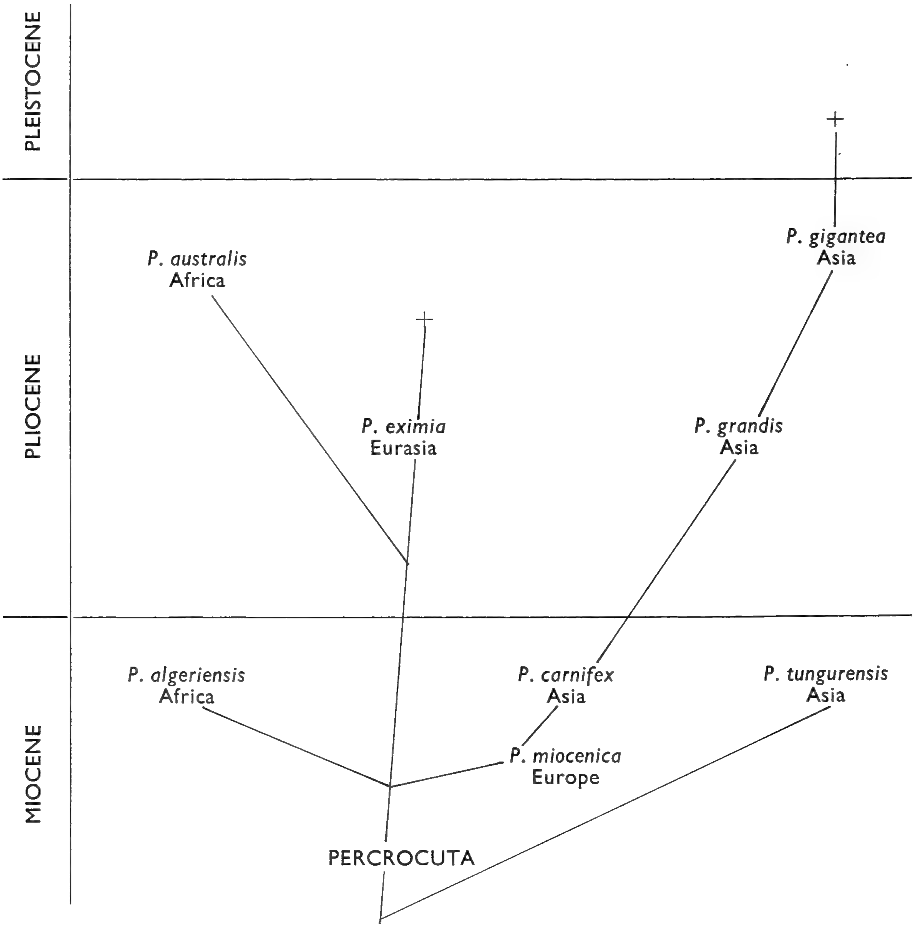

Fig. 18. Tentative phylogeny of the genus *Percrocuta*. (Adapted from Thenius 1966.)

likely phyletic position. *P. algeriensis* is apparently late Miocene in age and since *Hyaena* was probably descended from Pliocene *Ictitherium*, it is most unlikely that there can be any direct phyletic connection between *P. algeriensis* and *Hyaena*. This species is most likely to be comparable to *P. tungurensis*, which seems to have belonged in a monotypic and 'highly precocious phylum' that became extinct without issue (Kurtén 1957*b*: 401). The relationship between *P. australis* and *P. algeriensis* is probably no closer than that between *P. eximia* and *P. tungurensis*.

Family **Hyaenidae**

Subfamily Hyaeninae

Hyaena abronia n. sp.

(Figs 19, 20, 21)

Holotype

L 14186—A skull lacking only a few parts and an incomplete skeleton of which only the thorax is not represented.

Referred material

L 13167—Right mandibular fragment with M_1.

Locality and horizon

These specimens are from Bed 2, 'E' Quarry, Langebaanweg.

Diagnosis

A species of *Hyaena* comparable in size to *H. hyaena* Linnaeus. Braincase larger relative to face than in *H. hyaena*; post-orbital region broad and frontals not much inflated; premaxilla less protuberant than in *H. hyaena*; palate longer and broader. P_1, M_2 present; M^2 sometimes present; canines and anterior premolars are, in general, smaller and lower crowned relative to those of *H. hyaena*; P^2_2 lack anterior accessory cusps and these cusps are small in P^3_3; posterior accessory cusps of P^3_3 are small; P^4 protocone, parastyle and paracone reduced relative to those of *H. hyaena*; M^1 relatively large and triangular in outline. Fore- and hindlimbs more or less equally proportioned; metacarpal I approximately half the length of metacarpal II; tail long.

Etymology

From *abronia* meaning 'graceful', a reference to the body proportions of this species, which contrast with the more clumsy appearance of modern Hyaeninae.

Description

The holotype of this species is the most complete skeleton of any species ever recovered at Langebaanweg. The skull, some parts of which have been reconstructed, one half of the mandible, a few vertebrae and parts of all four limbs are known. The skeleton is that of a mature adult and the teeth are only moderately worn.

Skull (Tables 16, 17, 18, 19)

The skull with the mandible still articulated was damaged by a mechanical excavator, but relatively few parts were lost and it has been possible to almost completely restore the specimen. The upper dentition lacks only the left I^1. The left half of the mandible is largely intact and the dentition is complete. The right half of the mandible is represented only by the ascending ramus.

The skull is comparable in size to that of *H. hyaena*, but it differs from this species in certain details. The braincase of the fossil is larger relative to the face than those of three available *H. hyaena* skulls (Table 18). This is at least in part due to the greater development of the premolars in the modern species. The sagittal crest of L 14186 is slightly less prominent than is normally the case in *H. hyaena* and consequently the height of the fossil braincase is less. The sagittal crest of *H. hyaena* apparently usually terminates anteriorly at the contact between the parietals and frontals. Anteriorly from this point are two ridges of bone (temporal ridges), which may be parallel to one another for a short distance, but which then curve laterally terminating at the posterior edge of the post-orbital processes. There is a similar arrangement of these features in the *H. abronia* holotype, except that the bifurcation of the temporal ridges is already quite marked at the parietals/frontals contact and their actual divergence begins at this point. Related to this is the fact that the post-orbital region of the fossil is much more expanded than that of *H. hyaena*. On the other hand, the frontals on the dorsal surface between the orbits are less inflated. The post-orbital processes of the zygomata are much less prominent in the fossil and the rest of the zygomata have a lesser vertical development as well. The more prominent sagittal crest and stronger zygomata in *H. hyaena* indicate that the muscles of mastication are more powerfully developed in this species.

TABLE 18

Ratios of braincase to facial lengths in *Hyaena abronia* and *Hyaena hyaena*.

		(1) Facial length*	(2) Braincase length*	(1):(2)
Hyaena abronia	L 14186 . . .	104	*c.* 135	1:1,30
Modern *Hyaena hyaena*	BMNH 39.440 .	110	120	1:1,09
	BMNH 23.3.4.9 .	115	127	1:1,10
	SAM 36335 . .	103	122	1:1,18

* Point of division taken on midline of skull immediately posterior to the postorbital projections.

Differences between the posterior and ventral parts of the braincases of *H. abronia* and *H. hyaena* are more difficult to assess owing to the variation of features in these regions in the latter species. One apparently constant difference is that in the fossil the basi-occipital is broader between the anterior parts of the bullae, whereas in *H. hyaena* the broadest part is more posteriorly situated. There is also a greater development of the posterior part of the tympanic region in *H. abronia*.

The palate of *H. abronia* is longer than those of the fourteen *H. hyaena* skulls examined early on in this study (Table 19), and it is broader than those of the three *H. hyaena* skulls examined during the latter stages of the present investigation. On the other hand, the premaxilla of *H. hyaena* projects further forward than that of *H. abronia*, owing to the longer pre-canine diastema of the former. This longer diastema is directly related to the larger size of the lower canine in *H. hyaena*.

In *H. abronia* the infra-orbital foramen is situated slightly more posteriorly than in *H. hyaena* and the orbits themselves are smaller in the fossil species.

Taking into account the age disparity between the two species, there are remarkably few major differences in skull morphology.

The same applies in the case of the mandibles of the two species. They are comparable in size, but there are a few differences which are significant. The symphysis of *H. abronia* is shorter than those of three *H. hyaena* specimens and covers a smaller surface area. This suggests a weaker connection between the two halves of the mandible. The most marked differences are, however, in that region posterior to the cheekteeth, which is where the muscles of mastication attach. The fossil mandible has a very prominent subangular lobe, posterior to which the inferior margin at first inclines upwards and is then horizontal for a short distance anterior to the angular process. The angular process itself is bulbous in lateral view. In *H. hyaena* the subangular lobe is a less prominent feature and the inferior margin of the mandible below the ascending ramus continues to incline upwards to the very end of the angular process. This process is more elongated than that of *H. abronia* and in lateral view has a slight dorsally directed termination. The result of these differences is that in *H. hyaena* the condyle is more elevated relative to the cheekteeth. In *H. hyaena* specimens with teeth in a similar state of wear to those of the *H. abronia* holotype, a line drawn from the dorsal surface of the condyle to the top of the crown of I_3 passes well above the cheek teeth, whereas in L 14186 it intersects the crowns of M_1 and P_2.

It is likely that all the significant differences between the *H. abronia* and *H. hyaena* skulls and mandibles relate directly to the feeding habits of the two species, a conclusion which is supported by the differences in their dentitions.

In general, the teeth of *H. abronia* are a little smaller than those of *H. hyaena*, while the cheekteeth of the fossil are both more numerous and more evenly spaced. They are also smaller and much less specialized than those of *H. brunnea* and *Crocuta crocuta*.

TABLE 19

Dimensions of the skull of the Langebaanweg *Hyaena abronia*.

	Condylobasal length	Median length of nasals	Lateral length of nasals	Palate (Anterior incisors—posterior palatine incisure)	Width across canines	Zygomatic width	Inter-orbital width	Post-orbital width	Mastoid width	(Bulla—sagittal crest) Skull height	Skull height (Occipital condyle—sagittal crest)	Width across occipital condyles
L14186	217,0	51+	c. 67,0	c. 118,5	c. 50,0	c. 145,0	47,7	c. 45,0	78,1	87,3	78,3	43,3
*H. hyaena makapani**	210	—	—	—	—	138,0	44,8	—	—	—	—	—
H. hyaena (moderns)	211,0 (3)	47,5 (3)	64,0 (3)	111,9 (14)	50,2 (14)	c. 146,0 (3)	44,0 (3)	37,2 (14)	80,2 (14)	90,4 (2)	86,8 (13)	43,2 (14)

* Toerien 1952.

As an exception to the previously stated generalization, the I_1^1 and I_2^2 of *H. abronia* are a little larger than those in the *H. hyaena* comparative series. This applies also to I_3, but the I^3 of *H. hyaena* is larger, not in diameter, but in crown height. Much the same applies in the case of the canines, although in *H. abronia* these teeth are also a little shorter.

The P^1 of *H. abronia* differs from that of *H. hyaena* only in that it is slightly smaller. The fossil P^2 is also smaller and, in addition, it lacks an anterior accessory cusp. The P^3 is narrower, lower crowned and has a more prominent posterior accessory cusp.

The upper carnassial of *H. abronia* differs from that of *H. hyaena* in several respects. The protocone is smaller and more anteriorly situated and its posterior edge meets the lingual margin of the shearing blade at an obtuse angle. In the available comparative specimens this angle is nearer 90°. Also in *H. hyaena*, the parastyle and paracone are more or less equal in length, while the metastyle is shorter, whereas in the *H. abronia* P^4 it is the paracone and metastyle which are similar in length and the parastyle which is shorter. The *H. hyaena* P^4 is thus differentiated from that of *H. abronia* by a greater development of its three most anterior cusps.

In the upper dentition the most marked differences between the two species are in the post-carnassial teeth. The M^1 of *H. abronia* is larger than that of *H. hyaena* and is more or less triangular in outline, whereas in *H. hyaena* reduction of the postero-external part of M^1 has left it nearly oval in shape. In the *H. abronia* holotype there is an M^2 present on the right side. It is a small, single-rooted and almost circular tooth. There are no indications that the left M^2 was ever present in this individual. This tooth is apparently never present in *H. hyaena*. In the fossil the buccal margins of M^1 and M^2 make an angle of approximately 110° with the long axis of P^4 and both molars are partly visible in lateral view. In *H. hyaena* the M^1 is hidden behind P^4 in lateral view and the angle between its posterior margin and that of the long axis of P^4 is about 90°. The longer palate of *H. abronia* is at least in part due to the nature of the post-carnassial dentition.

The most striking feature of the lower dentition of *H. abronia* is that both P_1 and M_2 are present, a characteristic which distinguishes it from the extant hyaenid species.

The P_1 is a small, single-rooted and almost circular tooth, very much like a reduced version of P^1. It is situated a little forward from P_2 and the postcanine diastema of *H. abronia* is consequently shorter than that of *H. hyaena*. The fossil P_2 is similar to P^2, the principal difference being that it lacks a prominent internal cingulum. Unlike the P_2 of *H. hyaena*, it does not have an anterior accessory cusp. Morphologically P_3 is essentially similar to P_2, but differs in being broader anteriorly than it is posteriorly. There is a pronounced bulging of the cingulum at the most anterior end of the tooth which is almost distinct enough to be regarded as an anterior accessory cusp. It is smaller and lower-crowned than the P_3 of *H. hyaena*, a species which has a more distinct anterior

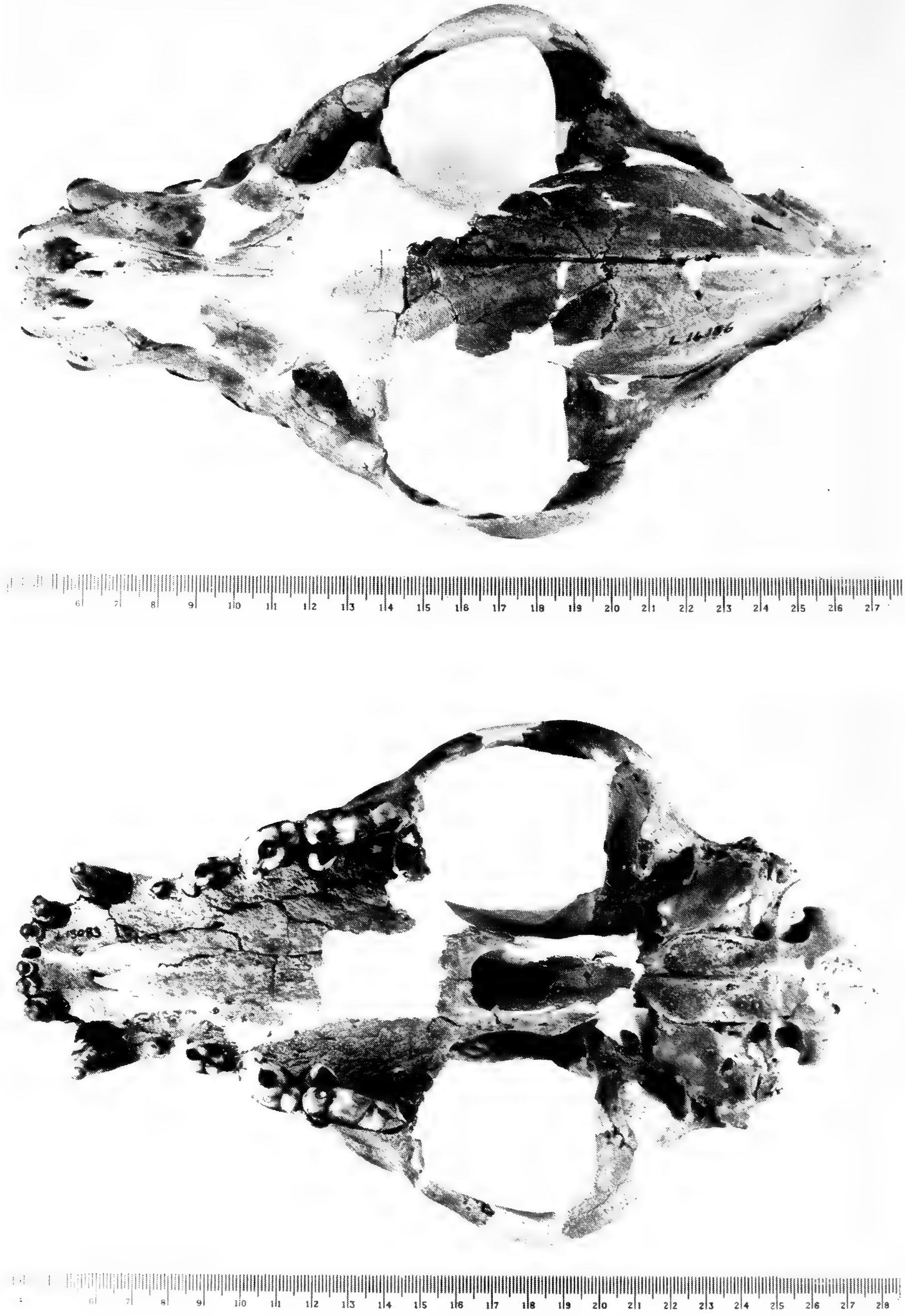

Fig. 19. Dorsal and ventral views of the *Hyaena abronia* skull (L 14186) from Langebaanweg.

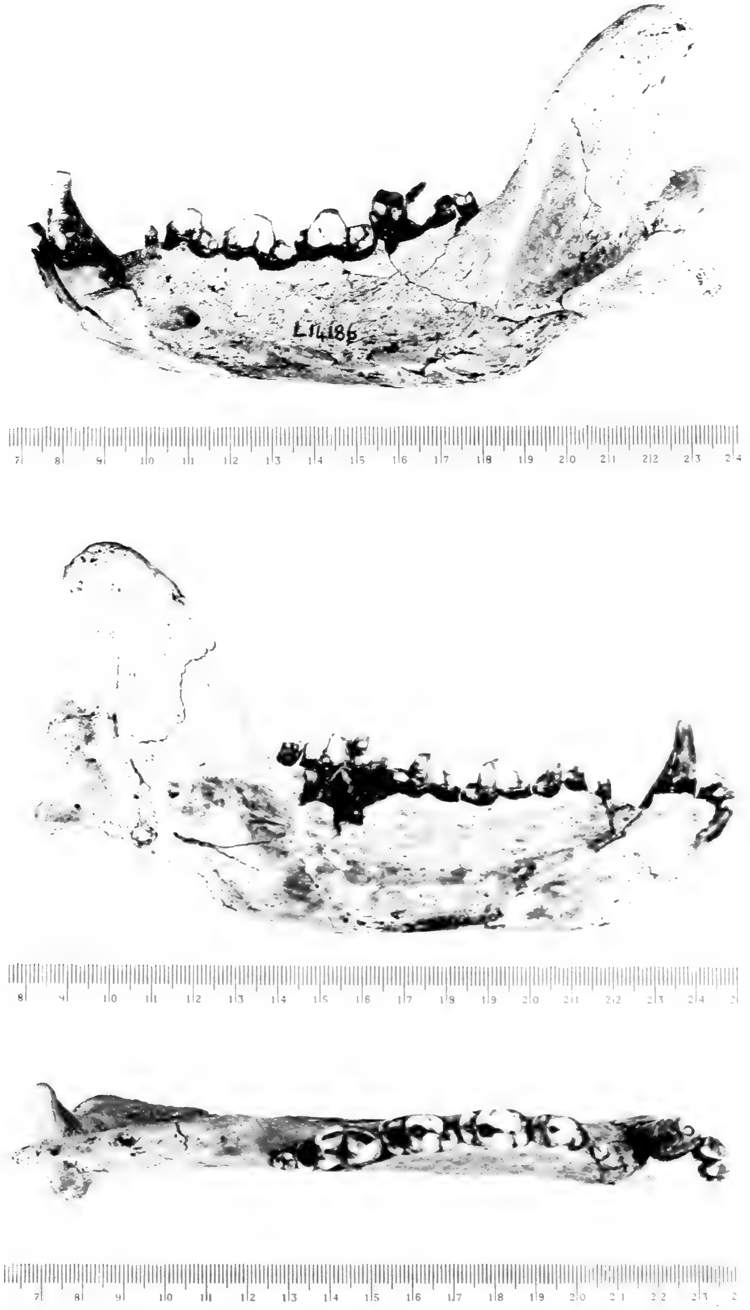

Fig. 20. Buccal, lingual and occlusal views of the *Hyaena abronia* mandible (L 14186) from Langebaanweg.

accessory cusp and a posterior accessory cusp which is relatively less prominent. In both species, the P_4 is essentially the same, although that of *H. hyaena* is larger and has a slightly more prominent anterior accessory cusp.

The lower carnassials of the two species are also similar, except that in *H. abronia* the talonid of this tooth is slightly longer, while the metaconid is a little more prominent.

The M_2 of *H. abronia* is small, single-rooted and slightly elongated. It is a little larger than P_1 and has a more complex crown made up of four tiny cusps, two situated lingually and two smaller and more closely set cusps situated buccally.

Postcranial skeleton (Tables 20 to 26)

The holotype of *H. abronia* is remarkable in comparison to many other early hyaenids since its postcranial skeleton is so well represented. Relatively little attention has previously been paid to the postcranial skeletons of fossil carnivores, probably because they are often not well represented and they are certainly less useful for taxonomic purposes than skulls.

Modern Hyaenidae are perhaps the most aberrant group of carnivores in respect of their body proportions and it is therefore appropriate that when opportunities arise to examine these proportions in ancestral forms, this should be done. In a classic study on animal locomotion, Howell (1944:51) referred to the Hyaenidae as follows:

> 'For carnivores of such size the hyaenas are rather slow, cumbersome beasts. Nevertheless, they are of very real interest in any study of locomotion because of the fact that the forequarters are much heavier than the hinder ones and the former are employed chiefly in progression, while the hind limbs are used chiefly to maintain balance, at least during the low speeds observed in captivity. The proportions of their limb segments are noteworthy among all the carnivores.'

In the present study, the functional aspects of the postcranial skeleton of *H. abronia* are touched upon, but attention is focused principally on the size of individual skeletal components relative to those of the two available skeletons of modern *H. brunnea*. In view of the conclusion on the relationships of *H. abronia*, it would have been more appropriate to make comparisons with the skeleton of *H. hyaena*, but such material was unfortunately not available. The study did little more than demonstrate that *H. abronia* had a skeleton very much as would be expected of an early form of *Hyaena*. However, the descriptions which follow may ultimately prove useful in studies aimed specifically at elucidating aspects of the evolution of the curious skeleton of modern hyaenids and the functional implications of changes in elements of the postcranial skeleton.

The postcranial material recovered in association with the skull L 14186 is as follows:

Vertebrae (Table 24)

Of the cervical vertebrae, only the 7th is known. It is similar in morphology to those of the available *H. brunnea* skeletons, but it is appreciably smaller, particularly in respect of the size of the neural arch. This is in keeping with the much greater development of the skull and neck muscles in *H. brunnea*.

A single slightly crushed and incomplete lumbar vertebra was recovered. Its position in the series is uncertain, but it was probably the 4th (second last). As far as can be judged, it is similar in size to that of *H. brunnea*, except that the transverse processes have a greater antero-posterior diameter.

The largely intact sacrum was also recovered. It is made up of three completely fused sacral vertebrae, the same number present in the *H. brunnea* comparative specimens, although Flower (1885) lists this species as having four sacral vertebrae. The fossil specimen is narrower than that of *H. brunnea* and the sacral foramina are smaller, but the total antero-posterior length of the centra is greater.

Five complete caudal vertebrae and the posterior half of a sixth are known. The incomplete specimen is probably the 10th in the series, while the others are the 11th to 15th. They are notable because they are about one-third longer than the corresponding ones of *H. brunnea*. This species has a tail length of about 300 mm (Fitzsimons 1919), and consequently the tail of *H. abronia* is likely to have been about 400 mm in length. This is considerably in excess of the tail length of 240–280 mm in *H. hyaena* (Harrison 1968).

Since the skull of the *H. abronia* holotype is smaller than that of *H. brunnea*, the size differences in cervical vertebrae are readily accounted for, but it is notable that the length of the centrum of the fossil 7th cervical is little different from that of *H. brunnea*. This apparently applies in the case of the lumbar vertebra as well. Consequently, it appears that the length of the spine from skull to pelvis was approximately the same in the two species. The fossil sacrum is longer and narrower than that of *H. brunnea*, while the tail of *H. abronia* was also appreciably longer. The latter is regarded as a primitive characteristic exhibited by this species and so too is the lesser development of the neck.

Forelimbs (Fig. 21; Table 25)

A large part of the right scapula and some parts of the left are known. The overall length of the fossil scapula is approximately the same as that of *H. brunnea*, but it has a smaller glenoid fossa, narrower neck and, apparently, less expanded blade.

The right humerus is largely intact. It is only a little shorter than those of the *H. brunnea* comparative specimens, but it is appreciably more slender. In spite of being more lightly built, the deltoid crest is very prominent and so is the projection where the medial ligament of the elbow joint attaches. In other respects the humeri of the two species are similar, although the articular surfaces are much larger in *H. brunnea*.

The left radius is intact and the right lacks only the distal end. The

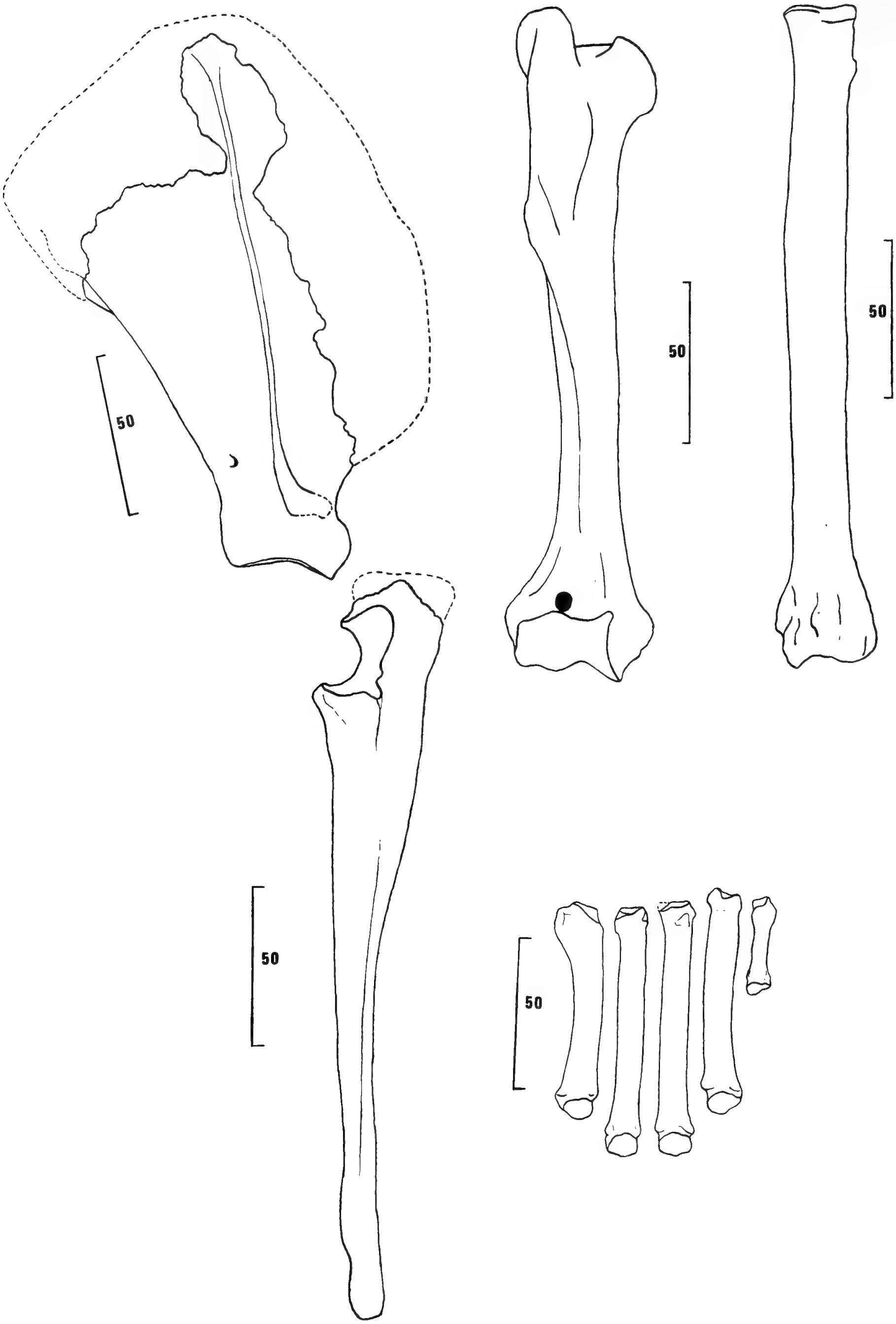

Fig. 21. Elements of the forelimb of the *Hyaena abronia* (L 14186) from Langebaanweg.

complete specimen is slightly shorter than that of *H. brunnea*, but it does have a somewhat stouter shaft. There is a very considerable difference in the sizes of the distal ends, that of *H. brunnea* being larger. There is a corresponding, but less pronounced difference in the sizes of the proximal articular facets. The fossil specimens are thus more evenly proportioned along their entire lengths.

The left ulna lacks only the most proximal part of the olecranon, while the right ulna lacks most of the olecranon and the distal end. The latter specimen apparently suffered an injury or fracture during life, approximately 45 mm from the distal end. The now missing distal part of this bone does not appear to have been properly knitted on to the shaft, where it is swollen and the bone is porous. The fossil specimens have stouter shafts than those of the comparative specimens, although the distal parts of the more complete specimen is actually more slender. The semi-lunar notch is smaller in the fossil and in keeping with the smaller size of the distal articular end of the humerus.

The manus of the fossil is represented by metacarpals II to V of both sides, the right metacarpal I, left scapho-lunar, pisiform, unciform, magnum and trapezoid, as well as several phalanges. In addition, a bone tentatively identified as the left radial sesamoid is known. The fossil carpal bones are all smaller than their counterparts in *H. brunnea*, but are otherwise similar in detail.

The radial sesamoids of the comparative specimens were lost, but in extant hyaenid species it is apparently a small and rather featureless bone. The articular facet for the radial sesamoid on the scapho-lunars of the *H. brunnea* specimens are similar in size to that on the fossil specimen, in spite of the fact that the latter is a much smaller bone. This suggests that the radial sesamoid was a relatively more prominent bone in the manus of *H. abronia*. The fossil bone tentatively identified as a radial sesamoid is approximately almond-shaped, with a more or less flat articular facet situated parallel to the long axis at the broadest end of the bone. It is actually not dissimilar to the vestigial metacarpal I of *H. brunnea*, although it is much larger. It is, however, clearly not a metacarpal I, since the articular facet is situated laterally rather than proximally and, in addition, the metacarpal I of *H. abronia* is known.

The metacarpal I is a significant bone, since its retention in a recognizable form is a primitive characteristic exhibited by *H. abronia*. It is a small bone, about half the length of metacarpal II and resembles that of *Proteles cristatus* in morphology. In *H. brunnea* this bone is much reduced and has no phalanges associated with it, but in *H. abronia* at least the 1st phalanx must still have been present as the metacarpal I has a distal articular facet.

The other metacarpals are shorter and their combined proximal articular surfaces are smaller than in *H. brunnea*. The metacarpals II and V are only slightly shorter than those of *H. brunnea* and are similarly proportioned, while the metacarpals III and IV are relatively and absolutely still shorter. Consequently, when the fossil metacarpals are articulated, III and IV do not project as far forward from II and V as is the case in *H. brunnea*.

The phalanges of the manus and pes of *H. brunnea* can be readily differentiated on the basis of their size, those of the manus being larger. This size differentiation is far less obvious in *H. abronia*, but the phalanges which were recovered could be separated into two categories. Of the twenty-one phalanges recovered, thirteen were identified as being from the manus (seven 1st, two 2nd and four 3rd). They are all smaller than their counterparts in *H. brunnea* and the size difference is especially marked in the case of the 3rd phalanges.

Hindlimbs (Table 26)

The greater parts of both innominates were recovered, although the symphyseal portions are missing and only the ilia and ischia are reasonably intact. The pelvis is similar in size and general morphology to that of *H. brunnea*, although the ischiatic spines are more prominently developed.

Both fossil femora were recovered, but both lack the greater trochanter and distal ends. They are similar in length to the femur of *H. brunnea*, they have slightly stouter shafts, but the heads are a little smaller. The lesser trochanter of the fossil and the ridges of bone on the shaft where muscles attach are more prominent.

The left and right tibiae were recovered and both lack their proximal ends, but in spite of this they are longer or nearly as long as the comparative specimens. Their estimated total lengths exceed that of the largest of the *H. brunnea* specimens by at least 5%. The shafts are appreciably stouter than those of the *H. brunnea* tibiae, but the distal articular ends are similar in size. This is in very marked contrast to the corresponding bone of the forelimb (i.e. the radius), in which the distal articular end was much smaller than that of *H. brunnea*.

Only the lateral malleoli and most distal parts of the shafts of the fibulae are known. They are similar to corresponding parts of the fibula of *H. brunnea*, but the fossil specimens are broader and what is visible of the shafts more robust.

The left pes is represented by the calcaneum, astragalus, navicular, external cuneiform, internal cuneiform and parts of metatarsals III, IV and V. The right pes is represented by the same tarsal bones, with the cuboid in addition, and by the complete metatarsals II to V. In addition three 1st, two 2nd and three 3rd phalanges were recovered.

Whereas the carpal bones of *H. abronia* were noticeably smaller than their counterparts in *H. brunnea*, the tarsal bones are not as simply differentiated. For example, the fossil and modern astragali are similar in size, the fossil cuboid is smaller and the fossil internal cuneiform is larger. If any generalization is warranted then it is that the proximal tarsal bones of the two species are similar in size, while those tarsals which articulate with the metatarsals are larger in *H. brunnea*, except for the internal cuneiform which is reduced. There are also some differences in the nature of the articular facets on the individual bones. For example, that facet on the cuboid which articulates with the external cuneiform has a figure-of-8 shape, whereas in the *H. brunnea* specimens it is more or less circular and, in addition, this facet is closer to the proximal end of the bone, whereas in *H. brunnea* it is nearer to the distal end.

The differences between the fossil and modern metatarsals are much less marked than those between the metacarpals. The metatarsals III and IV of the two species are similar in length, but the metatarsals II and V of the fossil are a little longer than those of *H. brunnea.* consequently, the articulated fossil metatarsals take on the same aspect as the metacarpals in that the two central ones do not project much further forward than those on either side.

The phalanges of the hindfeet of *H. abronia* are similar in all respects to those of *H. brunnea.*

Discussion

Of the extant species of Hyaenidae, *H. abronia* is undoubtedly most similar to *H. hyaena.* The similarity between the latter and another fossil hyaenid from South Africa, *H. makapani* Toerien, 1952, led Ewer (1967) to regard it simply as a sub-species of *H. hyaena.* It might therefore be expected that *H. abronia* and *H. h. makapani* are related and comparisons between these two fossil forms are necessary.

Some of the characteristics of *H. h. makapani* mentioned by Toerien (1952: 294) and which are relevant in the present instance are:

(1) 'the teeth . . . are on the whole a little smaller than the average for (*H. hyaena*).'
(2) 'The anterior cusp of the second premolar is practically absent. Only in one specimen is a trace of it present. In P^3 the anterior cusp is not as well developed as in *H. hyaena.*'
(3) 'In P_2 the anterior cusp is almost absent and in P_3 it is very feebly developed.'
(4) 'The anterior cusp of P_4 . . . (is) not well separated from the central cusp.'
(5) 'In the lower carnassial the inner cusp (metaconid) is better developed and more distinct than in *H. hyaena.*'

All these statements apply equally well to *H. abronia* and, consequently, in respect of these characters the Langebaanweg species differs as much from *H. hyaena* as *H. h. makapani.* The decision to distinguish the Langebaanweg form from *H. hyaena* at the species level is based principally on the fact that it retains P_1, M_2 and sometimes also M^2. The indications are that *H. abronia* is simply a more primitive version of *H. h. makapani*, which is in keeping with the inferred relative ages of the two forms, *H. abronia* dating from the Langebaanian and *H. h. makapani* dating from the Makapanian.

H. abronia, *H. h. makapani* and *H. hyaena* are here regarded as successive elements in a single lineage.

In his discussion of relationships within the genus *Hyaena*, Thenius (1966) took *H. pyrenaica* Depéret, 1890 (= *H. donnezani* Viret, 1954) to be the species from which all later forms of *Hyaena* arose. *H. pyrenaica* is an element of the French 'Perpignan fauna', which is dated as 'early middle Pliocene' by Bonifay (1969). Although the age of the Langebaanweg fauna relative to that from Perpignan is uncertain, it does seem likely that it is somewhat younger. Consequently, it might be expected that *H. abronia* was also a descendant of *H. pyrenaica*, but this is clearly impossible since in respect of the presence of P_1

and M_2, *H. abronia* is the more primitive of the two species. The only possible explanation of this fact is that they are early members of two distinct lineages (see Fig. 29).

It is now widely accepted that *Hyaena* stemmed from the *Viverra*-like ictitheres of the Pliocene. Kurtén (1971: 143) referred to this ancestral group as follows:

> 'The small *Ictitherium* was still rather like an overgrown civet, while the related *Palhyaena* comprises a number of species ranging in size from a fox to a wolf. The dentitions of these hyaenids suggest that they were highly predaceous.'

In view of the age of the Langebaanweg fauna, it might be expected that *H. abronia* would hold an approximately intermediate position between the ictitheres and *H. hyaena* in terms of morphology, and perhaps also habits. It does in fact resemble the ictitheres in the number of teeth in its dentition as it retains P_1, M_2 and M^2, but in tooth morphology there is a greater resemblance to *H. hyaena*, especially in the development of $P^2{}_2$, $P^3{}_3$ and P_4 into broad crushing teeth. It is also more like *H. hyaena* in respect of its overall size.

H. abronia is also intermediate between the ictitheres and extant hyaenids in respect of the development of its post-cranial skeleton. In his discussion on European Pontian *Ictitherium*, Pilgrim (1931) contrasted the limb proportions of the species he compared to *Ictitherium* by calculating the ratios between lengths of metatarsals and metacarpals. The same ratio was calculated for *H. abronia* and it was found that this species does indeed fall into an expected position in relation to *Ictitherium* and advanced hyaenids (Table 20).

TABLE 20

Length ratios of metacarpal IV and metatarsal IV in some carnivores.

	Mc IV : Mt IV
Viverra tangalunga	1,43 : 1
Ictitherium orbignyi	1,33 : 1
Ictitherium robustum	1,29 : 1
Ictitherium hipparionum	1,06 : 1
Hyaena abronia	1,03 : 1
Hyaena hyaena	0,96 : 1
Crocuta crocuta	0,93 : 1

Howell (1944) devised a series of indices which are useful in comparing limb proportions in animal species. The limb segment ratios of *H. abronia* are, in general, intermediate between those of a primitive aeluroid carnivore, represented here by *Viverra tangalunga*, and advanced hyaenids (Table 21). There was evidently very little change in the relative sizes of the humerus and radius in the *H. abronia—H. hyaena* lineage, but there was a reduction in the size of the tibia relative to the femur, as well a reduction in the size of both these bones relative to those of the forelimb. Consequently, the most marked differences between *H. abronia* and *H. hyaena* are in those ratios which contrast fore- and hindlimb elements (i.e. the femoro-humeral, tibio-radial and intermembral indices).

TABLE 21

Limb segment ratios in some carnivores.

	n	Humero-radial index	Femoro-humeral index	Femoro-tibial index	Tibio-radial index	Inter-membral index
Viverra tangalunga[1] . .	5	90,1	81,3	96,2	76,1	78,8
Hyaena abronia . . .	1	106,7	88,2	*c.* 90,9	*c.* 103,5	*c.* 95,5
Hyaena hyaena[2] . . .	3	106,8	95,7	88,9	115,0	104,8
Hyaena brunnea . . .	2	111,8	88,1	81,7	120,5	102,7

[1] Davis 1964.
[2] Kurtén 1956.

Limb segment ratios have also been expressed in other ways and some of the figures quoted by Pilgrim (1931: 89) are useful in the present instance, since *Ictitherium robustum* is included. This species probably represents, or at least resembles the archetype of the *H. abronia—H. hyaena* lineage. Comparisons between these three species (Table 22) show *H. abronia* to be more advanced than *I. robustum* in the development of both fore- and hindlimbs, while the *H. abronia* forelimb longbone elements are proportioned in a similar fashion to those of *H. hyaena* and those of the hindlimb are not as advanced.

TABLE 22

Limb segment ratios in some carnivores.

	Humerus : radius	Femur : tibia
Viverra tangalunga[1] . . .	1 : 1,09	1 : 0,97
Ictitherium robustum[1] . .	1 : 1,09	1 : *c.* 0,96
Hyaena abronia	1 : 1,07	1 : *c.* 0,91
Hyaena hyaena[2]	1 : 1,07	1 : 0,89

[1] Pilgrim 1931.
[2] Kurtén 1956.

The limb segment ratios of *H. brunnea* differ somewhat from those of *H. hyaena* (Table 21), and this has already been discussed by Kurtén (1956) in relation to the limb proportions of *Crocuta*. In *H. brunnea* the radius is enlarged relative to the humerus and the tibia reduced relative to the femur. Consequently, while the femoro-humeral index in *H. brunnea* is similar to that of *H. abronia*, the tibio-radial indices or these two species are appreciably different. Although the intermembral indices of *H. brunnea* and *H. hyaena* are similar, the indications from the other indices are that the two species achieved their present limb proportions in different ways. On the assumption that the few specimens whose limb segment ratios have been recorded here are indeed representative of their species, it follows that *H. brunnea* and *H. hyaena* may well have evolved along different lines for a long time, although ultimately they have ended up with essentially similar body proportions.

The limb segment ratios already discussed have not taken the extremities of the limbs into consideration, although some indication of relative sizes is gained by the figures recorded for the metapodials (Table 20). When the elements of the manus and pes of *H. abronia* are articulated, it is evident that the forefeet were a little broader than the hindfeet. This is, however, largely due to the presence of metacarpal I and since this digit was either non-functional or not fully functional, the effective widths of the fore- and hindfeet of *H. abronia* must have been much the same. This contrasts with the situation in modern hyaenids in which the forefeet are broader than the hindfeet, even though the pollex has been almost completely lost.

In respect of the development of its limbs, *H. abronia* is clearly much more advanced than its ictithere ancestor and is closer to, although not quite as advanced as *H. hyaena*. The same applies to its skull characters. With its more or less equally proportioned fore- and hindlimbs and its long tail, it must have been a less grotesque-looking animal than modern hyaenids, although its relatively large skull must have made it unmistakably hyaenid in appearance. It was perhaps more fleet-footed than modern hyaenids and may well have been more actively predaceous.

Family **Hyaenidae**

Subfamily Hyaeninae

Hyaena Species B

(Figs 22, 23)

Comment

Sufficient is known of this species to suggest that it belongs to a taxon distinct from other Langebaanweg Hyaenidae, although there is a possibility that the two individuals which are represented are large or otherwise aberrant forms of *Hyaena abronia*. Owing to this uncertainty the species is not formally named, although the description of the material is based on the belief that the first of the above alternatives is correct.

Material

L 12848—Parts of the skull and skeleton of a single individual, including the following:
Right maxillary fragment with $\underline{C}$, P^2 and P^3; left maxillary fragment with P^3, P^4 and M^1; right mandibular fragment with P_1 to M_1; left mandibular fragment with P_1 and P_2.
One cervical and one caudal vertebra.
Parts of one ulna, one radius and one tibia.
Twelve carpal and tarsal bones.
Parts of at least seven metapodials.
Five 1st, five 2nd and three 3rd phalanges.
Eight sesamoids.
L 11206—Incomplete left M_1.

Locality and horizon

These specimens are from Bed 2, 'E' Quarry, Langebaanweg.

Description

Although this species is less well represented than *H. abronia*, sufficient is known to allow for a fairly detailed analysis of its characteristics. The material L 12848 represents the remains of a young adult individual in which the permanent teeth are all fully erupted and, at most, only slightly worn, but in which the epiphyses of some elements of the postcranial skeleton are unfused.

Skull (Tables 16, 17)

The skull of L 12848 was badly damaged by a mechanical excavator and, while some repairs have been possible, it is still largely fragmentary and much is missing. Most of the teeth recovered were well preserved and intact. Of the skull itself, only parts of the occipital, the frontals and one nasal are in a condition which allows for examination of their characteristics.

The occipital condyles, foramen magnum and immediately adjacent parts are essentially similar to corresponding parts of the skulls of the *H. abronia* holotype and the *H. hyaena* comparative series, although the condyles are more elongated antero-posteriorly than in either of these species. The frontals are, as far as can be seen, similar to those of *H. hyaena*, but they differ from those of *H. abronia* in being more constricted in the post-orbital region. The preserved nasal is similar to those of *H. abronia* and *H. hyaena*.

The right mandible has been largely restored, except for parts of the ascending ramus which are missing. It is very like that of *H. abronia* in all observable respects. The subangular lobe is prominent and the curvature of the inferior margin posterior to this feature appears to be comparable to that of *H. abronia*, although the shape of the detached angular process is like that of *H. hyaena*. This process is, however, shorter than in the modern species. There is also a foreshortening in the anterior part of the mandible which is not evident in either *H. abronia* or *H. hyaena*.

This foreshortening of the anterior part of the snout is best illustrated by reference to tooth row lengths. Although the $\underline{\mathrm{C}}$ to P^3 of L 12848 are actually longer than the corresponding teeth in *H. abronia*, the total length of this part of the tooth row is actually less in L 12848 (55 mm as against 60 mm). There is a similar disparity in the corresponding teeth of the mandible, although the total lengths of the lower cheektooth rows of the two species are almost identical. The crowding of the anterior cheekteeth of L 12848 is at least in part due to this foreshortening, although the elongation of these teeth is another contributing factor.

It is the elongation of the cheekteeth and the fact that they are higher crowned that most readily distinguishes L 12848 from *H. abronia*. In general, the teeth are also longer than those of *H. hyaena*, but they are similar in breadth and crown height.

The upper canines of L 12848 and *H. hyaena* are similar in size. They differ in that the $\underline{\mathrm{C}}$ of the fossil does not have the distinct V-shaped projection from the anterior cingulum. The $\underline{\mathrm{C}}$ of *H. abronia* is similar to that of L 12848 in this respect.

The P^1 of L 12848 is lost, but judging from the size of its alveolus, it was similar in size to that of *H. hyaena* and larger than that of *H. abronia*. It was tightly sandwiched between the $\underline{\mathrm{C}}$ and P^2.

Only the right P^2 of L 12848 was recovered and this tooth is damaged. It is larger than that of *H. abronia* in all respects and apparently had a small but distinct anterior ancessory cusp. It differs from the P^2 of both *H. abronia* and *H. hyaena* in having the inflation of the internal cingulum more anteriorly situated.

Morphologically the P^3 of L 12848 resembles that of *H. abronia* more closely than that of *H. hyaena*, since the anterior accessory cusp is smaller and the posterior accessory cusp is larger than in the modern species. It is, however, more comparable in size to the P^3 of *H. hyaena*.

As with P^3, the P^4 is morphologically more like that of *H. abronia*, but is closer to that of *H. hyaena* in size. Both protocone and parastyle are reduced as in *H. abronia*. The metastyle is more strongly arched posteriorly than in *H. hyaena*, so at least in early wear the posterior part did not function as a shearing surface.

There are marked differences in the nature of the upper molars of the three species. The M^1 of Species B is appreciably larger than that of the *H. abronia* holotype and larger still than those of the *H. hyaena* comparative specimens. The posterior part of the maxilla of L 12848 is known from the left side only and although M^2 is lost, its alveolus is preserved. This tooth had at least two roots and was much larger than the single M^2 of the *H. abronia* holotype,

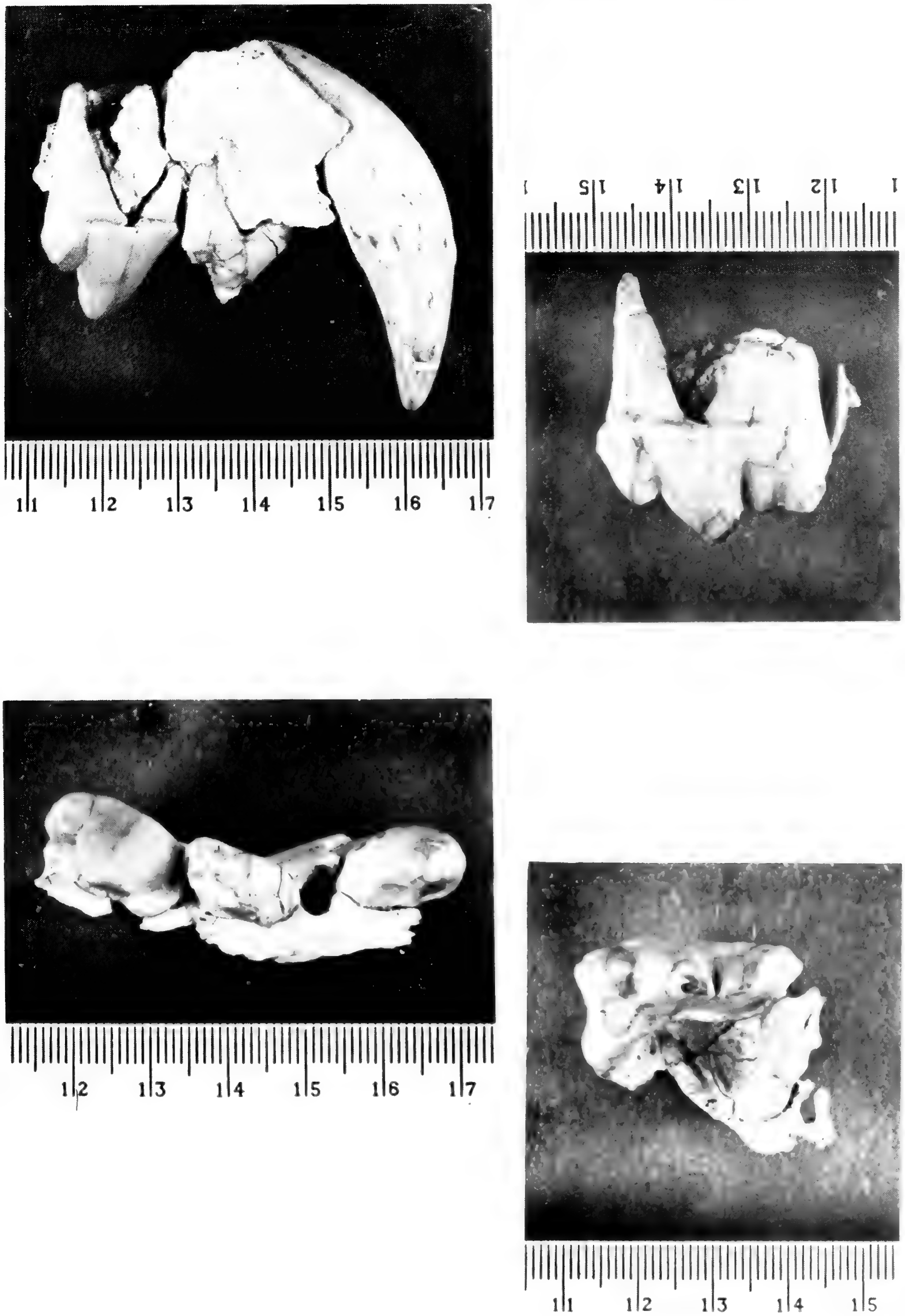

Fig. 22. Buccal and occlusal views of the *Hyaena* sp. B maxillary fragments (L 12848) from Langebaanweg.

Fig. 23. Occlusal and buccal views of the *Hyaena* sp. B mandible (L 12848) from Langebaanweg.

which is only single-rooted. The upper molars of L 12848 also differ from those of *H. abronia* in their positions relative to P^4. In the latter species the buccal surfaces of M^1 and M^2 make an angle of approximately 110° with the long axis of P^4, but in L 12848 this angle is about 100°, so that in lateral view the molars are, or were just visible behind P^4. Species B is intermediate between *H. abronia* and *H. hyaena* in this respect.

The P_1 of Species B is a little larger than that of *H. abronia*, but is otherwise similar. The other lower pre-molars are all more elongated and higher crowned than those of *H. abronia*, while in the P_3 the anterior accessory cusp is more clearly separated from the principal cusp.

Except for their larger size, the M_1 of L 12848 and the damaged specimen L 11206 are similar to that of *H. abronia*. The M_2 of L 12848 is damaged, but it also appears to have been similar to that of *H. abronia*.

Postcranial skeleton (Tables 23, 25, 26)

Little of the postcranial skeleton of L 12848 was recovered, but there is sufficient to indicate that this individual was a little larger than the *H. abronia* holotype, even though the animal itself was younger. There is also sufficient to suggest that Species B, like *H. abronia*, did not have the enlarged forelimbs characteristic of more advanced hyaenids.

Vertebrae

The preserved cervical vertebra, probably the 5th, is only a little smaller than those of the two available *H. brunnea* skeletons, while the caudal vertebra, probably the 10th or 11th, is appreciably longer than those of the comparative specimens. The latter is comparable to the 11th caudal vertebra of *H. abronia*, which indicates that Species B also had a relatively long tail. A few isolated epiphyses of vertebrae were also found.

Forelimb (Table 25)

The only significant observable feature in the fragmentary radius and ulna which were recovered, is that in the former the distal end is transversely expanded in a manner which is more comparable to the condition in the available *H. brunnea* specimens than in *H. abronia*. However, the distal epiphysis of the radius is lost and the distal end of the diaphysis is not fully ossified, so the character of this area of the radius may be due to the relative youth of the individual. This region of the radius of L 12848 actually has a greater transverse diameter than the distal end of the radius of the *H. abronia* holotype.

Corresponding to the enlarged distal end of the radius, the preserved elements of the manus of L 12848 are also large compared to those of *H. abronia*. The scapho-lunar and trapezoid are intermediate in size between those of *H. abronia* and the *H. brunnea* comparative specimens. The cuneiform of *H. abronia* is not known, but that of L 12848 actually has a greater transverse diameter than those of the *H. brunnea* specimens and, as it is not as high, the transverse elongation is very pronounced. The transverse diameter of the trapezium is also greater than in the *H. brunnea* specimens and the various articular facets on this bone are larger as well. The size of the distal facet indicates that the metacarpal I must have been a fairly substantial bone, perhaps being proportionately as large as those of *H. abronia* and *Percrocuta australis*.

The left metacarpal II and right metacarpal V are preserved intact, while the right metacarpal IV is represented only by the proximal half. They are comparable in size to those of *H. brunnea*, except that the two complete specimens are slightly shorter.

It is clear from the transverse dimensions of the various elements of the manus that the forefeet of Species B were broader than those of the *H. brunnea* comparative specimens, although in overall size they were not as large.

Hindlimb (Table 26)

Too little of the tibia of L 12848 is preserved to allow useful comments on its characteristics to be made.

Of the pes, the astragalus, navicular, all three cuneiforms, and parts of metatarsals III, IV and V are known. These bones are all a little larger than their counterparts in the *H. abronia* holotype and the two modern *H. brunnea* skeletons.

Phalanges of both manus and pes of L 12848 are apparently represented. The relative sizes differ to approximately the same extent evident in *H. abronia*.

Discussion

The overall impression gained from the comparisons between L 12848 and the holotype of *H. abronia* is that the two forms are little different, but that such differences as do exist are probably greater than would be expected of two individuals of the same species. They are here regarded as being specifically distinct and as having had a common ancestor not far removed from them in time. In respect of both size and the nature of the dentition, *H. abronia* is the species likely to have borne a closer resemblance to the hypothetical common ancestor, while Species B is the more specialized of the two. They are, however, equally primitive in that both retain P_1 and $M\frac{2}{2}$.

The specimens L 12848 and L 14186 were found about 100 metres apart at about the same level in Bed 2 and near each were the remains of a comparable array of other vertebrate species, so that there can be little doubt that they were contemporaries. The co-existence of two hyaenid species of comparable size may have been made possible by their occupying slightly different ecological niches. This possibility is lent some support by the nature of the dentition of the two forms, since the more slender and high crowned teeth of Species B suggest that it might have been an early member of a lineage in which the trend was towards more highly predaceous forms.

Since the forefeet of Species B are a little smaller than those of *H. brunnea* and the hindfeet a little larger, there was clearly not the disproportionate development of the forefeet that is evident in modern hyaenids and in this respect Species B resembles *H. abronia*. The general similarity in the size of fore- and hindlimbs in Species B cannot, however, be demonstrated in the same way as it was in *H. abronia*. Some additional indication of limb proportions was obtained by comparing the sizes of the proximal facets of the scapho-lunar and astragalus of the three species (Table 23). The size of these facets is a reflection of the size of the radius and tibia and the fossil species are closer to one another in this respect than either is to *H. brunnea*.

TABLE 23

The dimensions of the scapho-lunar and astragalus of some hyaenid species.

	(1) Greatest trans. diam. of radial facet of scapholunar	(2) Greatest trans. diam. of tibial facet of astragalus	(1) : (2)
Hyaena brunnea (n = 2)	26,30	18,55	1 : 0,71
Hyaena abronia	23,10	18,00	1 : 0,78
Hyaena Species B	25,20	20,10	1 : 0,80

The possibility does exist that L 12848, and the isolated carnassial L 11206, belong to large individuals of the species *H. abronia* and that the elongation of the teeth merely represent individual peculiarities. The situation would no doubt be resolved by the recovery of more specimens and since material is still being collected from Bed 2 in 'E' Quarry, there is a good chance that this might happen. Consequently, although the opinion expressed here is that the present material is specifically distinct from *H. abronia*, and apparently other previously recorded hyaenid species, some additional comment on this matter will have to be made in the future.

Family **Hyaenidae**

Subfamily Hyaeninae

Hyaenictis preforfex n. sp.

(Fig. 24)

Holotype

L 10055 and associated pieces—The skull and parts of the skeleton of a single individual, including:

Skull lacking parts of the braincase, palate, left nasal, right I^1 and left P^1.

Left and right mandibles lacking I_1, P_1, M_2 and I_1, I_2, P_1, M_2 respectively.

Several incomplete vertebrae.
Parts of both humeri, both radii, one ulna and both tibiae.
Five carpal and tarsal bones.
Parts of at least seven metapodials.
Seven 1st, two 2nd and four 3rd phalanges.

Locality and horizon

These specimens are from Bed 3a, 'E' Quarry, Langebaanweg.

Diagnosis

A small species of *Hyaenictis*; post-orbital processes long; nasals short, terminating anterior to the orbits; mandible long and slender; P_1 and M_2 present; P^2_2 and P_3 lack anterior accessory cusps; P_3 broader than P_4; M^1 large.

Limbs slender and relatively long; fore- and hindlimbs more or less equally proportioned.

Etymology

From *pre* meaning 'before' and *forfex*, the specific name of an hyaenid from Swartkrans in the Transvaal (Ewer 1955*a*).

Description

The holotype of this species is the incomplete skeleton of a very aged individual in which the teeth are extremely worn. The skull was largely intact when discovered, but was badly broken with bone fragments being held together in a sandy matrix. Attempts to restore the specimen have been made by several persons and it has been adversely affected by this attention. It is now in two parts, the face being detached from the braincase. Most of the post-cranial remains have suffered some post-mortem damage.

Skull (Tables 16, 17)

Owing to distortion of the face and braincase, the two parts of the skull can no longer be fitted together, but most of the skull characters can still be observed. The braincase lacks most of the occiput, the basi-cranium and the posterior portion of the sagittal crest. Apart from its smaller size, the braincase resembles those of *H. abronia* and the *H. hyaena* comparative specimens. The frontals show signs of disease or injury and are otherwise remarkable for the very elongated post-orbital projections. The facial portion of the skull is more complete than the braincase and the only really important part which is missing is the posterior palatal region. It differs from corresponding parts of the skulls of *H. abronia* and *H. hyaena* in its smaller size and the relatively shorter nasals, which terminate anterior to the orbits.

The mandible is long and slender and although it is not quite as elongated as those of available *Canis lupus* skulls, it is otherwise not dissimilar in proportions.

The subangular lobe is not as prominent as that in *H. abronia* and the inferior margin below the ascending ramus is more like that in *H. hyaena*, although the angular process is not as long. The condyle is not as high relative to the cheek-teeth as it is in *H. hyaena*, but it is higher than in *H. abronia*.

Although the remaining teeth of L 10055 are very worn and many of their characteristics are no longer evident, it is quite clear that they differ significantly from the teeth of other hyaenid species from Langebaanweg. As with *H. abronia* and Species B, P_1 and M_2 were still present in this species and in this respect it is equally primitive. On the other hand, P^2_2, P^3_3 and P_4 are relatively broader than those of the two *Hyaena* species from 'E' Quarry. In this respect

Fig. 24. Occlusal and buccal views of the *Hyaenictis preforfex* mandible (L 10056) from Langebaanweg.

the present species is the more highly specialized. The P^2_2 and P_3 lack anterior accessory cusps and the anterior keels of their principal cusps are not as prominent as in *H. abronia* and Species B. The broadening of the anterior cheekteeth is particularly noticeable in P^2 and P_3 and the latter is actually a little broader than P_4. It is also relatively broader than the P_3 of *H. hyaena.*

The carnassials and post-carnassial teeth are either very worn, damaged or lost. The P^4 protocone seems to have been fairly prominent and situated at right angles to the parastyle. The M^1 was apparently relatively large and at least as broad as that of Species B. In view of the relative sizes of these two species, the size of M^1 relative to the other cheekteeth must have been greater in the present species than in the *Hyaena* species from Langebaanweg. Since the posterior part of the palate is damaged, it is not known whether or not M^2 was present. The lower carnassials are very worn, but the proportions of these teeth appear to have been similar to those of the *H. abronia* lower carnassials. It is not known whether or not the M_1 metaconid was present. The M_2, like P_1, has been lost from both halves of the mandible, but whereas P_1 was lost during life, the loss of M_2 was post-mortem. Both these teeth were small and single-rooted.

Postcranial skeleton (Tables 24, 25, 26)

The postcranial skeleton of this species is less well known than that of *H. abronia*, but is better represented than that of Species B.

Vertebrae (Table 24)

The vertebrae recovered are, for the most part, very fragmentary. The cervical, thoracic and lumbar regions of the spine are represented and the most complete specimen is the 7th cervical. It is similar in morphology to that of *H. abronia*, but is appreciably smaller and is thus in keeping with the smaller skull size of the present species. It is a great deal smaller than the 7th cervical vertebrae of the *H. brunnea* comparative specimens and, although the other vertebral fragments are not identified as to their actual position in the spine, they too are all smaller than the vertebrae of *H. brunnea.*

Forelimb (Table 25)

The left humerus is largely intact and although only a little shorter than that of *H. abronia*, it is much more slender. The supratrochlea foramen is, however, larger than that of the *H. abronia* humerus.

The proximal end and shaft of the left radius and the distal end and part of the shaft of the right radius are preserved. Once again the estimated overall length of the bone is a little less than that of the radius of *H. abronia,* but it is much more slender. The same apparently applies in the case of the ulna, of which only the proximal part of the one from the right side is preserved.

The pes is represented by a scapho-lunar, both unciforms, a trapezoid, parts of both metacarpals II and III and part of one metacarpal IV. The carpal bones are similar in size to the corresponding bones in *H. abronia* and the metacarpals differ only in that they are more slender.

One of the 1st phalanges is much reduced in size and almost certainly belonged to the pollex, although a metacarpal I was not found. This bone may well have been similar to the metacarpals I of *Percrocuta australis* and *Hyaena abronia* and not reduced as in modern *Crocuta* and *Hyaena*.

The right metacarpals II and III and another of the 1st phalanges show signs of a severe pathological condition, the cause of which is not known, although it could well be connected to, or aggravated by the advanced age of the individual.

Hindlimb (Table 26)

The hindlimbs are less well represented. The tibia and metatarsal IV are approximately the same length as those of *H. abronia*. The only tarsal bones recovered were an incomplete calcaneum and navicular and both are smaller than the corresponding bones of *H. abronia*.

Discussion

In determining the affinities of this species, one of the most obvious possibilities to be considered is that group of Hyaenidae which are referred to the genus *Hyaenictis* Gaudry, 1861. Pilgrim (1931: 101) defined this genus as follows:

> 'Hyaenidae with moderately long, slender, rather shallow mandible and (by inference) with somewhat elongated facial region; M^1 large, triangular, almost at right angles to P^4; M^2 absent; P^4 with long posterior lobe and large protocone; M_1 short, hardly longer than P_4, without metaconid; M_2 small; P_1 present but with a tendency to be deciduous; P_2 with large posterior and small anterior cusps, P_3 with large posterior and small anterior cusps; P_4 with large anterior and posterior cusps.'

This definition is based on the type species, *H. graeca*, and it could, therefore, be modified to accommodate more advanced, but phylogenetically directly related forms, which postdate the Pikermi species. One such species is '*Hyaena*' *bosei*, which is probably from the Pinjor stage of the Siwaliks, and which was included in *Hyaenictis* by Pilgrim (1932). This later species differs from *H. graeca* in that its lower premolars lack anterior accessory cusps and P_1 is absent.

The Langebaanweg deposits postdate those at Pikermi, but are earlier than those of the Pinjor, and it might therefore be expected that if L 10055 is an *Hyaenictis*, it would be intermediate in character between *H. graeca* and *H. bosei*. This does in fact appear to be the case, although some of the features which characterize *Hyaenictis*, such as the absence of M^2 and presence of M_1 metaconid, are not evident in L 10055. *H. graeca* has anterior accessory cusps on the lower premolars, they are lacking in *H. bosei*, while in L 10055 they are absent in

P_2 and P_3. The first lower premolars of L 10055 were lost during life and this is taken as an indication that they had a 'tendency to be deciduous' as in *H. graeca*. They were, however, completely absent in *H. bosei.*

The Langebaanweg species also shares at least two striking characteristics with *H. bosei.* namely, very long post-orbital processes and nasals terminating anterior to the orbits (see Pilgrim 1932).

Although there is some justification for referring L 10055 to *Hyaenictis*, there is at least one other possibility to be considered. In her description of the Hyaenidae from Swartkrans, Ewer (1955*a*) assigned one of the species which had previously been referred to *Hyaenictis* to the genus *Leecyaena* Young & Liu, 1948. The reasons she dismissed an association between the Transvaal species and *Hyaenictis* were as follows:

(1) The Swartkrans species has a mandible which is heavy and fairly deep below M_1.
(2) The M_1 has a large metaconid. (It is, however, relatively small compared to that of *H. hyaena* and other species).
(3) The M^1 is broad from side to side, but short antero-posteriorly.
(4) The P^4 protocone is small.
(5) The skull does not have long post-orbital processes or nasals terminating anterior to the orbits.

Since the Swartkrans species is much more recent than the Pontian *H. graeca*, most of these factors could be dismissed on the grounds that the former is a more advanced species, but one which could nevertheless have derived from *H. graeca*. The most telling point against this interpretation is the fact that the Swartkrans species has an M_1 metaconid whereas *H. graeca* does not. However, even this does not totally preclude a relationship since Kurtén (1963*a*) has demonstrated that a 'lost' feature such as an M_1 metaconid can be regained in the course of the evolution of a single lineage.

One possible interpretation of the facts is that the Swartkrans '*Leecyaena*' *forfex* and the small Langebaanweg hyaenid are members of an African *Hyaenictis* lineage, or else were members of a lineage which paralleled but was independent of the Eurasian *Hyaenictis*. Before examining this possibility, it is necessary to examine the decision to refer the Swartkrans species to *Leecyaena.*

Subsequent to the description of '*L.*' *forfex*, Ewer (1967) expressed the opinion that it and the only other recorded species of *Leecyaena* (i.e. *L. lycyaenoides* from the late Pliocene of China) were probably not closely related. It seems likely that in view of their relative ages and the nature of their specialized characters (Ewer 1955*a*) the two species belong in separate lineages, so there is a real doubt that the Swartkrans species is a *Leecyaena.*

'*L.*' *forfex* differs from the small Langebaanweg hyaenid in the following respects:

(1) '*L.*' *forfex* is a little larger.
(2) The post-orbital processes are smaller and the nasals terminate more posteriorly.
(3) The premaxilla projects further forward.
(4) The premolars are broader.
(5) The mandible is more heavily built.

Since the Swartkrans fauna is younger than that from Langebaanweg, it follows that '*L.*' *forfex* must be the more advanced of the two species if they are indeed on the same lineage. In fact, all the observed differences between the two species could be accounted for in this manner. There was a trend in hyaenids towards increasing size; the nature of the post-orbital processes and nasals in the Langebaanweg species is shared by at least one species of *Ictitherium* (Pilgrim 1932: 123), and they could therefore be regarded as primitive characteristics;

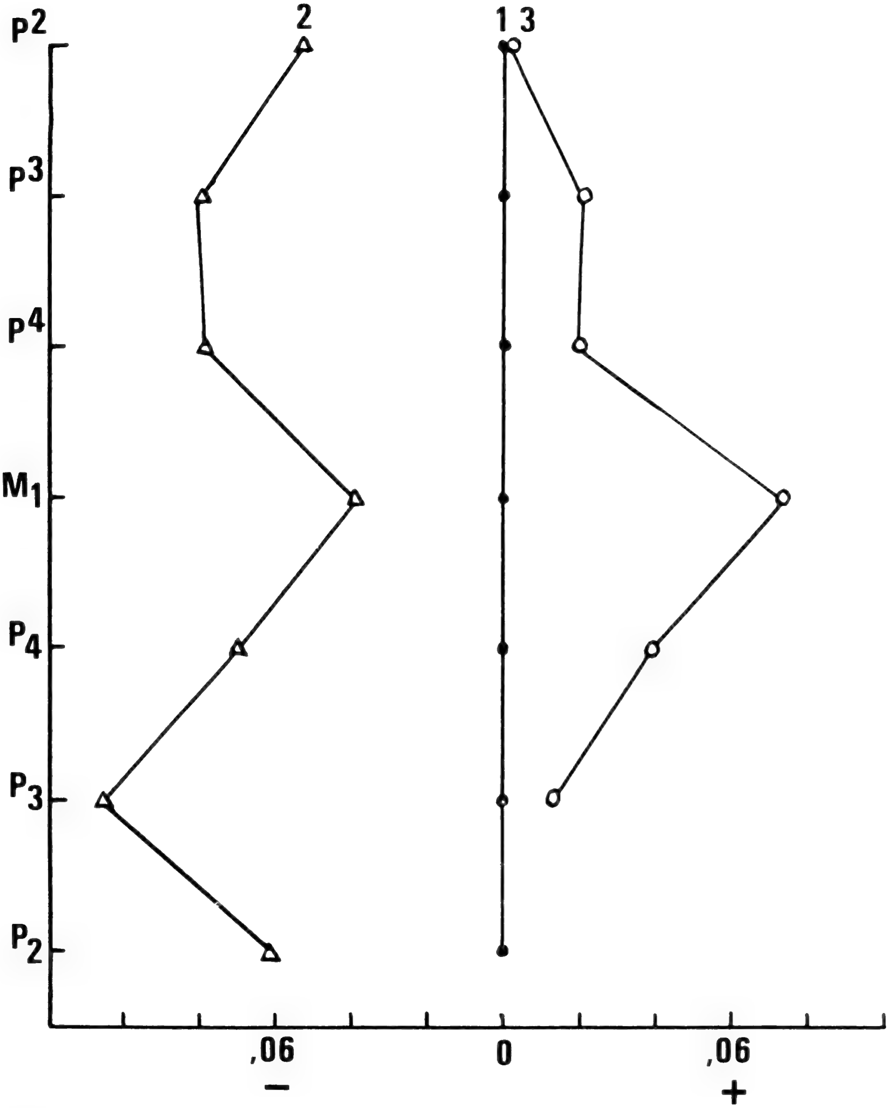

Fig. 25. Ratio diagram comparing relative lengths of the cheekteeth of *Hyaenictis preforfex* (2) and *H. forfex* (3) (Ewer 1955*a*), with modern *Hyaena hyaena* (1) (Kurtén 1956) as a standard.

the more prominent premaxilla of '*L.*' *forfex* is coupled with a longer pre-canine diastema and this in turn is determined by the larger size of the canines relative to those of L 10055; there was a trend in most hyaenid lineages for the premolars to broaden into crushing teeth; and the larger mandible of '*L.*' *forfex* is in keeping with the larger overall size of the species, coupled with the general enlargement of the cheekteeth (Fig. 25). The fact that the premolars of L 10055 are relatively broader than those of other contemporary hyaenids from Langebaanweg, indicates that it did indeed belong in a lineage where there was a trend for broadening of these teeth.

Perhaps even more significant than accounting for the differences between these two species are the characters which they have in common. In both species P^2_2 and P_3 lack anterior accessory cusps, P_3 is broader than P_4 and the premolars are generally comparable in morphology. Both species retain M_2 and in both the M^1 is large. The wear on the teeth indicates that they shared at least one important functional adaptation. The P_4 of L 10055 is extensively worn on its postero-lateral surface and is thus similar to that of '*L.*' *forfex* which 'is not a fully specialized exclusively crushing tooth, but still retains the shearing action typical of normal carnivore premolar occlusion' (Ewer 1955*a*: 820). In this respect the two species differ from *H. hyaena* and *H. brunnea* and parallel *Crocuta*.

The geographical proximity of the two species increases the likelihood that they are phyletically connected.

It is concluded that the Langebaanweg and Swartkrans species were members of the same lineage and are, therefore, congeneric. On balance it seems probable that their affinities lie with *Hyaenictis* and they are here referred to this genus. The specific name of the Langebaanweg *Hyaenictis preforfex* is given in the belief that it was ancestral to *Hyaenictis forfex*.

Since these two species are now included in *Hyaenictis*, the following revised statement concerning the genus is made:

Genus *Hyaenictis* Gaudry, 1861

Type species: *Hyaenictis graeca* Gaudry, 1861.

Diagnosis: Hyaenidae of small to medium size; M^1 large, almost at right angles to P^4; M^2 absent; P_1 sometimes present, but with a tendency to be shed; anterior accessory cusps of P^2_2 and P^3_3 present only in the earliest species; M_1 metaconid small or absent; M_2 small; mandible long and slender in early species, but more robust in later forms.

Stratigraphic range: Mid Pliocene to early Pleistocene of Eurasia and Africa.

Referred species: *Hyaenictis bosei* Matthew, 1929; *Hyaenictis forfex* Ewer, 1955; *Hyaenictis preforfex*, new species.

The postcranial skeleton of *H. preforfex* is of interest since comparisons with that of the contemporaneous *Hyaena abronia* show that these two hyaenids were very different in their body proportions. The indications are that *H. preforfex* was only a little shorter at the shoulder and that the two had hindlimbs of comparable length. The limbs of the *Hyaenictis* were, however, much more slender and the head and neck less enlarged relative to the rest of the body. The implications are that it was more cursorial than the contemporary species of *Hyaena*. This is of interest because of the suggestion that the long-limbed 'hunting hyaena', *Euryboas*, was descended from *Hyaenictis graeca* (Thenius 1966). Pliocene *Hyaenictis* may thus have been a group of long-limbed forms which evolved in two directions, one branch becoming increasingly cursorial and actively predaceous (*Euryboas*), and the other paralleling *Hyaena* and *Crocuta* (*H. bosei*, *H. forfex*, *H. preforfex*).

TABLE 24

Dimensions of the vertebrae of *Hyaena abronia* and *Hyaenictis preforfex* from Langebaanweg, compared with those of modern *Hyaena brunnea*

7th cervical vertebra	*Hyaena abronia* L14186	*Hyaenictis preforfex* L10055	*Hyaena brunnea* SAM 36150	*Hyaena brunnea* SAM 17238
Length of centrum	35,5	31,0	37,7	40,9
Length from anterior zygopophysis to posterior zygopophysis	43,3	36,4	45,5	46,0
Transverse diameter of posterior epiphysis	24,3	20,0	27,8	27,8
Width across anterior zygopophyses	49,8	42,9	60,2	60,1

Sacrum	*Hyaena abronia* L14186	*Hyaena brunnea* SAM 36150	*Hyaena brunnea* SAM 17238
Antero-posterior diameter of centrum	55,0	54,5	52,5

Caudal vertebrae (lengths)	11th	12th	13th	14th	15th
Hyaena abronia L14186	22,7	21,4	21,1	19,3	17,7
Hyaena brunnea SAM 17238	16,3	16,2	16,1	14,7	13,5
Difference in %	39	32	31	31	31

TABLE 25

Dimensions of forelimb elements of Langebaanweg Hyaenidae, compared with those of *Hyaena brunnea*.

	Percrocuta australis L13033	*Hyaena abronia* L14186	*Hyaena* Species B L12848	*Hyaenictis preforfex* L10055	*Hyaena brunnea*	
					S.A.M. 17238	S.A.M. 36150
SCAPULA						
Greatest antero posterior diameter at proximal end	—	40,4	—	—	45,8	47,1
Antero-posterior diameter of neck	—	35,2	—	—	38,8	36,3
Antero-posterior diameter of glenoid fossa	—	31,3	—	—	37,1	38,7
Transverse diameter of glenoid fossa	—	24,3	—	—	27,3	—
HUMERUS						
Overall length	—	202,0	—	—	220,0	206,0
Length between proximal and distal articular surfaces	—	194,0	—	c. 185,0	206,0	194,0
Maximum transverse diameter at distal end	—	46,0	—	—	49,2	47,9
Maximum antero-posterior diameter at distal end	—	35,7	—	—	39,8	38,9
Minimum transverse diameter of shaft	—	16,9	—	13,6	16,4	14,8
Minimum antero-posterior diameter of shaft	—	18,9	—	15,4	22,3	20,7
RADIUS						
Overall length	—	207,0	—	c. 195,0	232,0	215,0
Maximum transverse diameter at distal end	—	31,3	—	—	38,9	38,7
Maximum antero-posterior diameter at distal end	—	20,3	—	—	22,9	22,4
Maximum transverse diameter at proximal end	—	22,5	—	c. 21,1	25,5	24,8
Maximum antero-posterior diameter at proximal end	—	15,2	—	14,3	17,5	18,4
Minimum transverse diameter of shaft	—	16,8	—	13,9	17,4	16,1
Minimum antero-posterior diameter of shaft	—	8,7	—	8,5	11,1	10,5
ULNA						
Overall length	—	c. 237,0	—	—	263,0	245,0
Maximum antero-posterior diameter of styloid process	—	11,9	—	—	14,2	14,0
Maximum transverse diameter of styloid process	—	9,2	—	—	9,5	9,2
Minimum antero-posterior diameter of shaft	—	10,2	—	—	13,6	10,8
Minimum transverse diameter of shaft	—	10,9	—	—	8,0	7,6
Antero-posterior diameter at coronoid process	—	35,7	—	c. 29,0	36,7	37,5
Minimum antero-posterior diameter at semi-lunar notch	—	23,2	—	—	22,2	21,2
CARPALS						
Scapho-lunar Maximum transverse diameter	—	26,2	28,1	26,3	32,6	32,6
Maximum antero-posterior diameter	—	17,9	—	18,5	22,8	22,7
Cuneiform Maximum transverse diameter	—	—	19,0	—	18,7	17,0
Maximum antero-posterior diameter	—	—	c. 10,0	—	10,9	11,6

CARPALS (*continued*)							
Unciform	Maximum transverse diameter	—	13,2	—	13,4	16,3	16,6
	Maximum antero-posterior diameter	—	17,7	—	16,3	19,1	18,9
Magnum	Maximum transverse diameter	—	10,0	—	—	11,5	11,5
	Maximum antero-posterior diameter	—	18,5	—	—	20,5	20,5
Trapezoid	Maximum transverse diameter	—	11,9	12,8	10,0	13,0	13,9
	Maximum antero-posterior diameter	—	9,0	11,0	8,8	10,7	11,1
Trapezium	Maximum transverse diameter	—	—	9,3	—	6,9	—
Pisiform	Overall length	—	30,2	—	—	31,9	31,1
	Transverse diameter at proximal end	—	11,6	—	—	11,7	10,9
?Radial sesamoid	Overall length	—	25,2	—	—	—	—
	Transverse diameter at proximal end	—	7,4	—	—	—	—
METACARPALS							
Mc I	Overall length	42,0	32,7	—	—	—	11,0
	Maximum antero-posterior diameter at proximal end	9,3	7,2	—	—	—	6,3
	Maximum transverse diameter at proximal end	6,9	7,7	—	—	—	4,5
	Maximum antero-posterior diameter at distal end	9,7	7,3	—	—	—	—
	Maximum transverse diameter at distal end	9,3	7,4	—	—	—	—
Mc II	Overall length	—	73,8	75,6	72,0	81,9	82,5
	Maximum antero-posterior diameter at proximal end	—	14,3	15,8	14,2	15,8	16,0
	Maximum transverse diameter at proximal end	—	10,2	11,7	10,0	12,2	12,4
	Maximum antero-posterior diameter at distal end	—	12,0	—	10,2	12,6	12,6
	Maximum transverse diameter at distal end	—	11,4	11,9	—	11,9	11,9
Mc III	Overall length	—	84,2	—	—	94,7	97,0
	Maximum antero-posterior diameter at proximal end	—	15,8	—	14,1	16,7	16,1
	Maximum transverse diameter at proximal end	—	11,4	—	10,8	11,9	12,2
	Maximum antero-posterior diameter at distal end	—	12,7	—	—	13,1	13,2
	Maximum transverse diameter at distal end	—	10,0	—	—	10,9	11,1
Mc IV	Overall length	—	82,6	—	—	92,8	94,5
	Maximum antero-posterior diameter at proximal end	—	14,9	15,6	15,1	15,0	15,8
	Maximum transverse diameter at proximal end	—	9,9	10,8	9,5	11,3	11,7
	Maximum antero-posterior diameter at distal end	—	12,6	—	—	12,7	12,9
	Maximum transverse diameter at distal end	—	9,9	—	—	10,6	10,6
Mc V	Overall length	—	72,0	74,1	—	79,3	79,6
	Maximum antero-posterior diameter at proximal end	19,3	15,0	14,4	—	14,5	15,1
	Maximum transverse diameter at proximal end	16,1	15,3	15,9	—	15,0	15,7
	Maximum antero-posterior diameter at distal end	—	12,0	13,1	—	12,0	12,6
	Maximum transverse diameter at distal end	—	11,9	11,9	—	11,7	12,2

TABLE 26

Dimensions of the hindlimb elements of Langebaanweg Hyaenidae, compared with those of *Hyaena brunnea*.

		Percrocuta australis L13033	*Hyaena abronia* L14186	*Hyaena* Species B L12848	*Hyaenictis preforfex* L10055	*Hyaena brunnea* S.A.M. 17238	*Hyaena brunnea* S.A.M. 36150
INNOMINATE							
	Minimum dorso-ventral diameter of ilium anterior to acetabulum	—	27,0	—	—	26,2	25,4
	Minimum dorso-ventral diameter of ischium posterior to acetabulum	—	14,0	—	—	13,6	13,4
	Antero-posterior diameter of acetabulum	—	25,6	—	—	27,0	27,3
FEMUR							
	Overall length	—	*c.* 220,0	—	—	233,0	221,0
	Maximum dorso-ventral diameter of head	—	21,5	—	—	21,5	23,4
	Maximum antero-posterior diameter of head	—	22,8	—	—	24,0	24,5
	Minimum antero-posterior diameter of shaft	—	16,2	—	—	15,3	13,7
	Minimum transverse diameter of shaft	—	15,0	—	—	18,0	15,6
TIBIA							
	Overall length	—	*c.* 200,0	—	*c.* 200,0	192,0	179,0
	Maximum antero-posterior diameter of distal end	—	22,7	—	18,9	25,5	25,0
	Maximum transverse diameter of distal end	—	29,2	—	27,2	29,4	29,4
	Minimum antero-posterior diameter of shaft	—	14,8	—	14,2	14,8	14,3
	Minimum transverse diameter of shaft	—	16,0	—	13,7	15,3	14,6
FIBULA							
	Maximum antero-posterior diameter of distal end	—	13,9	—	—	14,2	14,0
	Maximum transverse diameter of distal end	—	10,3	—	—	9,8	8,5
TARSALS							
Calcaneum	Overall length	—	49,0	—	—	47,6	47,8
	Maximum antero-posterior diameter	—	23,0	—	—	21,3	21,8
	Maximum transverse diameter	—	21,2	—	—	21,0	21,8
Astragalus	Overall length	—	29,2	31,2	—	29,2	30,2
	Maximum antero-posterior diameter	—	16,4	—	—	15,0	16,7
	Maximum transverse diameter	—	20,2	*c.* 22,5	—	20,6	22,8
Navicular	Maximum antero-posterior diameter	30,3	20,2	20,7	—	20,0	20,3
	Maximum transverse diameter	21,4	16,1	17,4	—	17,0	16,7

TARSALS (*continued*)							
Cuboid	Overall length	23,3	19,0	—	—	20,7	21,8
	Maximum antero-posterior diameter	22,5	15,2	—	—	13,8	14,4
	Maximum transverse diameter	19,6	15,0	—	—	15,0	15,9
External cuneiform	Overall length	—	13,0	15,4	—	13,2	13,7
	Maximum antero-posterior diameter	—	21,3	c. 22,0	—	21,0	—
	Maximum transverse diameter	—	11,4	12,3	—	10,5	—
Middle cuneiform	Overall length	—	—	8,6	—	7,4	—
	Maximum antero-posterior diameter	—	—	7,8	—	6,7	—
	Maximum transverse diameter	—	—	11,6	—	9,7	—
Internal cuneiform	Overall length	23,3	16,5	19,2	—	—	17,4
	Maximum antero-posterior diameter	11,1	9,6	10,0	—	—	7,9
METATARSALS							
Mt II	Overall length	87,3	79,2	—	—	77,3	—
	Maximum antero-posterior diameter of proximal end	17,9	13,9	—	—	12,6	—
	Maximum transverse diameter of proximal end	14,8	10,5	—	—	10,8	—
	Maximum antero-posterior diameter of distal end	13,6	10,6	—	—	10,8	—
	Maximum transverse diameter of distal end	13,9	10,0	—	—	9,4	—
Mt III	Overall length	—	85,7	c. 88,0	—	85,8	—
	Maximum antero-posterior diameter of proximal end	—	17,4	18,2	—	17,3	—
	Maximum transverse diameter of proximal end	—	11,9	12,1	—	11,7	—
	Maximum antero-posterior diameter of distal end	—	11,7	12,4	—	11,2	—
	Maximum transverse diameter of distal end	—	9,7	—	—	9,2	—
Mt IV	Overall length	—	85,5	—	—	84,3	—
	Maximum antero-posterior diameter of proximal end	—	14,0	—	—	14,5	—
	Maximum transverse diameter of proximal end	—	8,1	—	—	8,7	—
	Maximum antero-posterior diameter of distal end	—	11,3	—	10,2	10,4	—
	Maximum transverse diameter of distal end	—	8,9	—	8,5	8,2	—
Mt V	Overall length	91,4	77,0	—	—	74,4	—
	Maximum antero-posterior diameter of proximal end	14,7	12,3	—	—	12,0	—
	Maximum transverse diameter of proximal end	13,2	8,8	—	—	8,2	—
	Maximum antero-posterior diameter of distal end	13,4	10,1	11,5	—	9,8	—
	Maximum transverse diameter of distal end	11,9	8,7	c. 10,2	—	8,6	—

Family **Hyaenidae**
Subfamily Hyaeninae
Species E
(Fig. 26)

Material

L 2673—Right mandibular fragment with P_2 and P_3.

Locality and horizon

This specimen is from 'E' Quarry, Langebaanweg, and is probably from Bed 3a.

Description

This fragmentary specimen belongs to an immature individual of a species which is comparable in size to *H. abronia*. The permanent canine is unerupted and is visible through damaged portions of the alveoli of the third incisor and

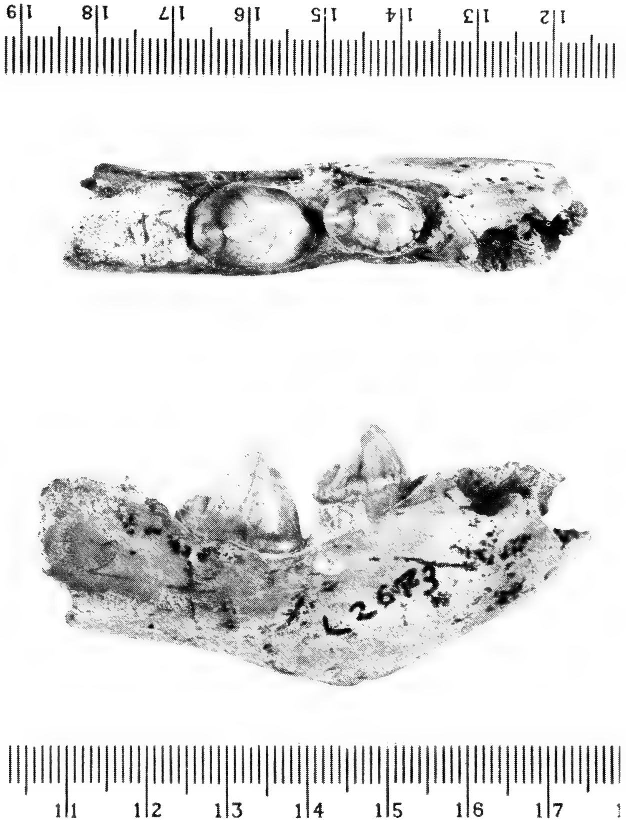

Fig. 26. Occlusal and buccal views of the hyaenid species E (L 2673) from Langebaanweg.

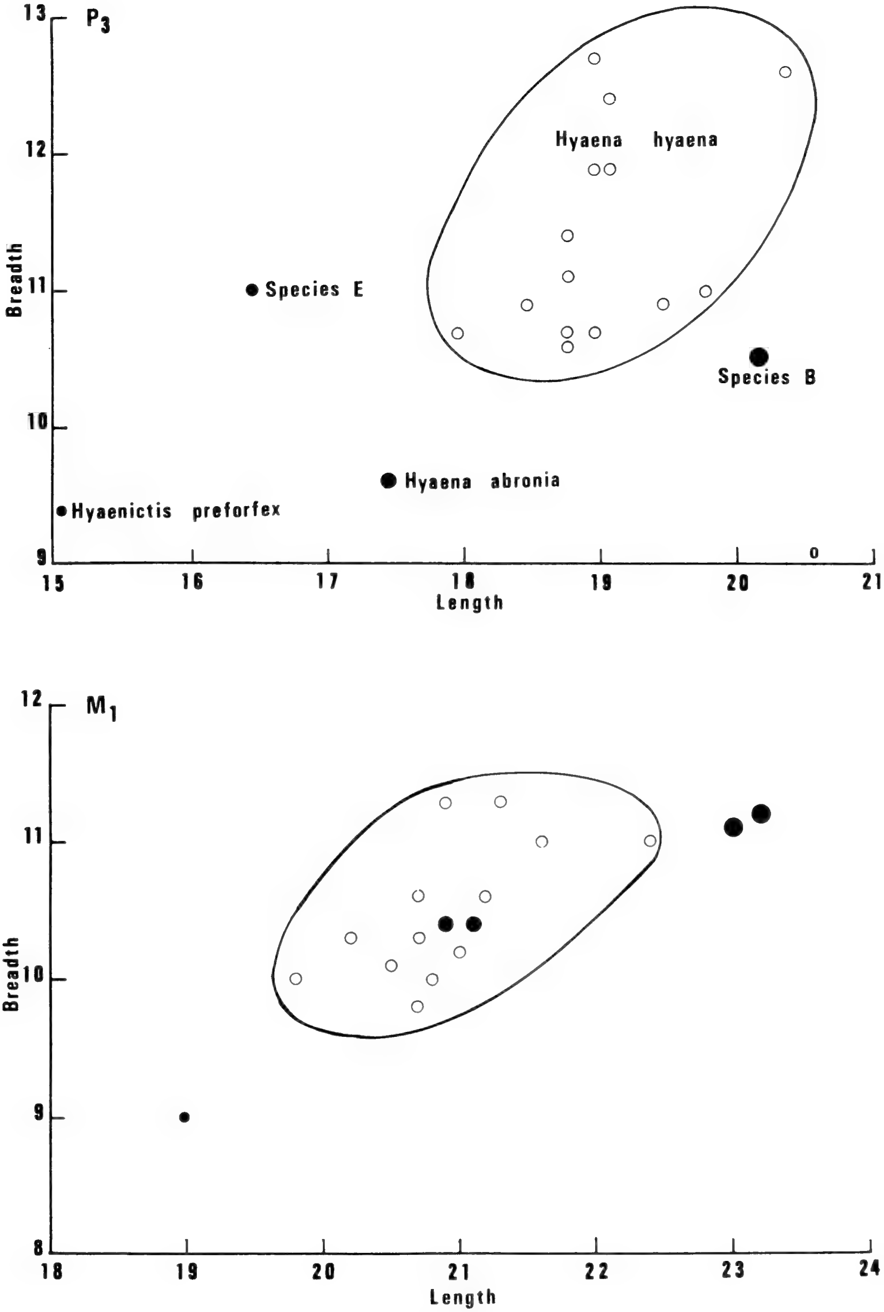

Fig. 27a. Dimensions of the P_3 and M_1 of Hyaenidae from Langebaanweg, compared with those of a series of modern *Hyaena hyaena*.

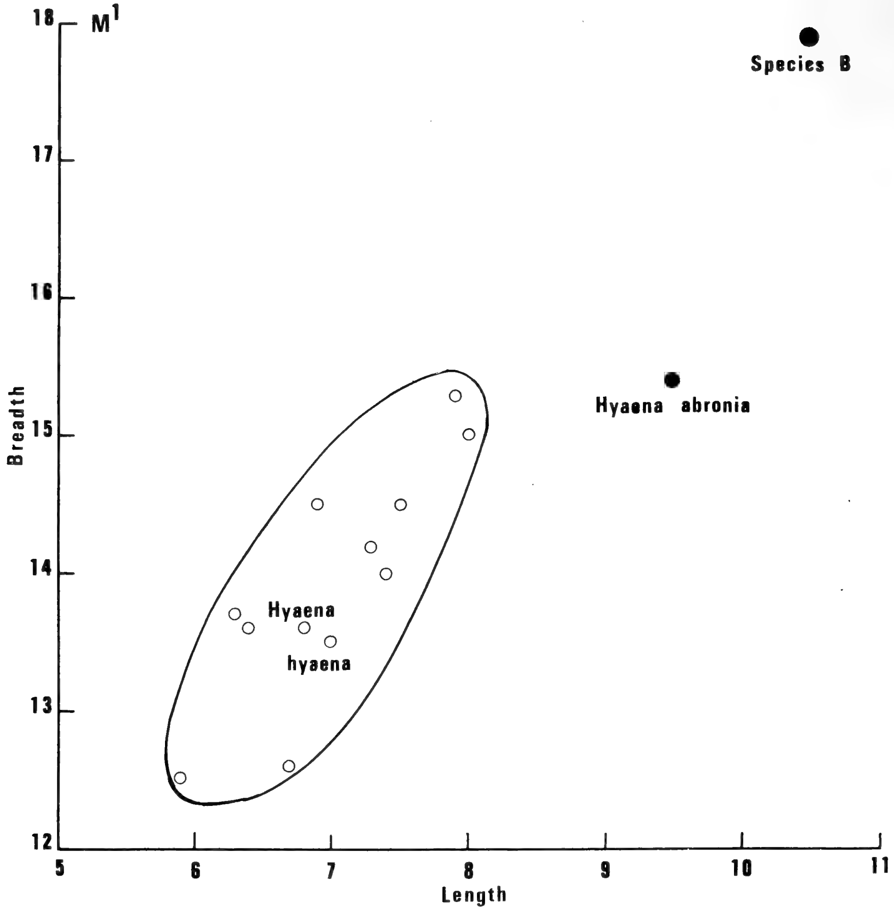

Fig. 27b. Dimensions of the M^1 of Hyaenidae from Langebaanweg, compared with those of a series of modern *Hyaena hyaena*.

deciduous canine. There are no indications that P_1 is, or was ever present. The P_2 and P_3 are only partly erupted. The mandible is broken posterior to P_3 and the nature of the other lower cheekteeth is unknown.

The P_2, which measures 12,9 by 8,8 mm, differs from those of other Langebaanweg Hyaenidae in that there is no trace of an anterior accessory cusp and no swelling of the cingulum at the anterior end of the tooth. In addition, although a posterior accessory cusp is present, it is much smaller than those of the other species. The tooth has prominent anterior and posterior keels and it is relatively broader than those of other Langebaanweg hyaenids. Both buccal and lingual cingular margins are markedly convex, in contrast to the other species in which these margins are more or less straight.

The P_3 (c 16,5 × 11,0) is morphologically very similar to P_2, but is larger and relatively broader. The posterior accessory cusp is almost identical in size

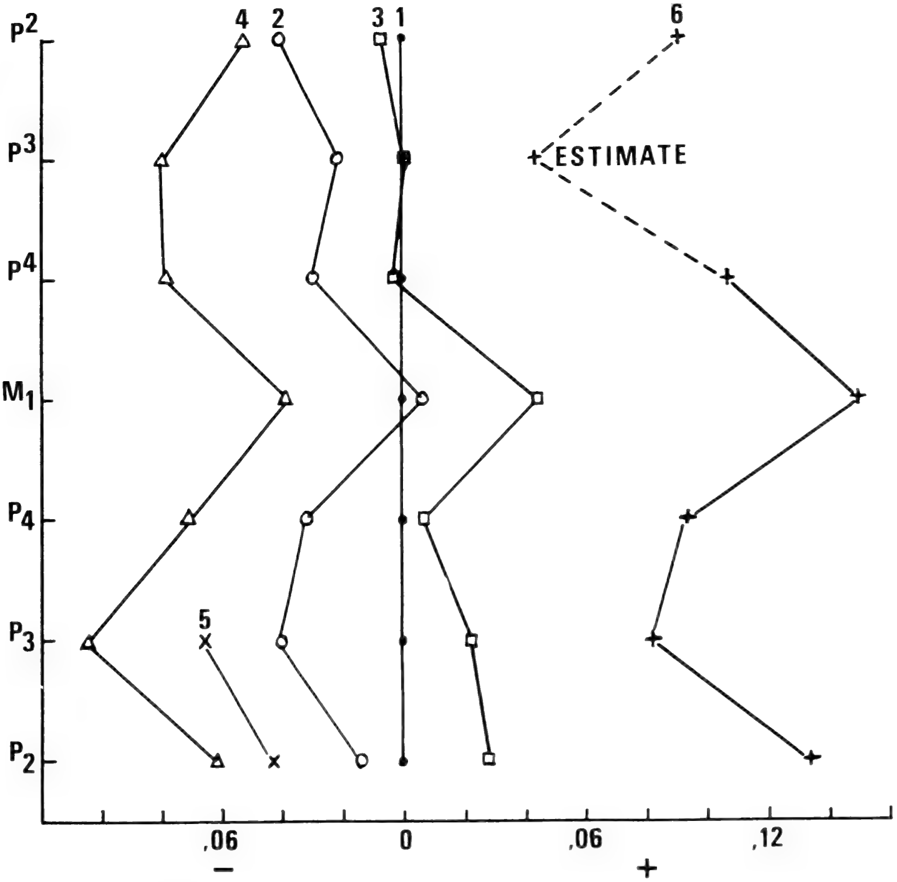

Fig. 28. Ratio diagram comparing relative lengths of the cheekteeth of Hyaenidae from Langebaanweg (*Hyaena abronia* (2), Species B (3), *Hyaenictis preforfex* (4), Species E (5), *Percrocuta australis* (6)), with modern *Hyaena hyaena* (1) (Kurtén 1956) as a standard.

to that of P_2 and is thus a relatively smaller and less significant feature of the tooth.

Discussion

The lack of P_1 and the broader, almost conical P_2 and P_3, which lack anterior accessory cusps and have very small posterior accessory cusps, readily distinguishes L 2673 from the other Langebaanweg hyaenids as well as other species previously recorded from South Africa. Its characteristics cannot be attributed to the ontogenetic age of the individual, since other specimens from Langebaanweg which belong to individuals of comparable age (e.g. 5/1966/1, *vide infra*) have unerupted cheekteeth which are morphologically comparable to those of adults.

Since this species is so poorly represented, and since its affinities were not determined, it is not classified below the subfamily level. For the purposes of convenience it is designated Langebaanweg hyaenid 'Species E'.

Family **Hyaenidae**
Subfamily Hyaeninae
Incertae sedis
(Hendey, 1970*a*: pl. 2A, B)

Material

(1) The following specimens are from Bed 2, 'E' Quarry:
   L9139—Right premaxilla with I^1 to I^3 and associated left $\underline{C}$.
   L 12499/500—Right I^3 and M^1.
   L 12850—Mandibular fragments with right $\overline{C}$ and left P_2.
   L 12868—Mandibular fragments with incomplete P_4.
   L 13042—Left P_3.

(2) The following specimens are from Bed 3a, 'E' Quarry:
   (i) Excavation LBW 1966/1:
      5/1966/1 and associated pieces—Parts of the skull and postcranial skeleton of a single individual, including:
         Right and left maxillary fragments with $\underline{C}$ and P^2 to M^1.
         Right mandibular fragment with P_4 and M_1; left mandibular fragment with $\overline{C}$ and P_3.
         Parts of one humerus and one ulna.
         Two tarsal bones.
         Parts of four metapodials.
         One 1st phalanx.
   (ii) Excavation LBW 1966/2:
      L 10566 to L 10569—P^4, M^1, P^1 and I^3.
      L 10802 to L 10804 and L 10806 to L 10808—M^1, M_1, P_3, P_4, P_2 and I^3.
   (iii) Excavations LBW 1969/1 and LBW 1970/1:
      A series of teeth probably belonging to a single individual:
      L 15742—Right dp^3, P^3 and P^4.
      L 15797A, L 15592, L 15896A, L 15897—Right C, P_3, P_4, M_1.
      L 15610, L 15896B, L 15898, L 15715—Left dp_4, P_2, P_3, P_4.
      Other isolated teeth:
      L 16055K—Right M^1.
      L 15824 —Left P^4.
      L 15588B/A—Left I^3.
      L 15784, L 15596, L 16240B, L 16260—Right $\overline{C}$, P_2, P_3, P_4.
      L 16055B, L 15854, L 16246—Left P_4 (two), M_1.

(3) The following specimens are from 'E' Quarry, provenance unknown:
   L 2055—Left mandibular fragment with P_4.
   L 5731—Right mandibular fragment with ?P_4.

L 6378—Right mandibular fragment with parts of P_2 to M_1.
L 6379—Right mandibular fragment with P_3 to M_1.
L 6380—Left mandibular fragment with M_1 and M_2.
L 10746 to L 10748—Premolars.
L 11822, L 11891, L 12101, L 12423B—Canines.
L 2054—Part of M_1.
Seven premolar fragments, one maxillary fragment and two mandibular fragments.

Discussion

Owing to certain similarities between the material assigned to *Hyaena abronia*, Species B and *Hyaenictis preforfex*, and to the poor definition of the characters of Species E, difficulty was experienced in identifying the material listed above, although it almost certainly does belong to one or other of these species.

Bed 2 material (Tables 27, 28)

Those specimens from Bed 2 could belong to either *H. abronia* or Species B. For example, although the P_3, L 13042, is very similar to that of the *H. abronia* holotype, it is an unerupted tooth belonging to a very young individual and, when fully developed, might conceivably have taken on the characters of the P_3 of Species B. It would serve no useful purpose at present to make tentative identifications of the Bed 2 specimens.

Bed 3a material (Tables 27, 28)

The material recovered from excavations in Bed 3a is more important since a large number of specimens, some relatively well represented, are involved. Probably most of the specimens should be referred to *H. abronia* (a Bed 2 species), but at least one exception is the P_4, L 16055B, which is virtually indistinguishable from the P_4 of *Hyaenictis preforfex* (a Bed 3a species). Many of the unclassified Bed 3a specimens belong to immature individuals and although in size such teeth are equally close to those of the *H. abronia* and *H. preforfex* holotypes, they are morphologically more similar to the former. Some of the isolated teeth other than P_2 and P_3 could perhaps belong to Species E.

The best represented of the unclassified Bed 3a specimens is the series from the excavation LBW 1966/1. These represent the remains of an immature individual of about the same ontogenetic age as the specimen referred to Species E. The deciduous dentition is not represented, but only the molars are fully erupted. The epiphyses of the preserved elements of the postcranial skeleton were not yet fused. The teeth of this individual are similar enough in size and morphology to those of the *H. abronia* holotype to suggest that the two are conspecific, although there is a somewhat ambiguous situation in respect of the M^2 of these two individuals.

Table 27

Dimensions of unclassified hyaenid upper teeth from Langebaanweg.

	P^2		P^3		P^4		M^1	
	l	b	l	b	l	b	l	b
5/1966/1 . . .	14,5	8,2	18,1	11,3	25,9	15,3	8,3	13,0
L15824 . . .	—	—	—	—	27,7	15,6	—	—
L10567 . . .	—	—	—	—	—	—	7,3	12,7
L10802 . . .	—	—	—	—	—	—	7,6	12,7
L16055K. . .	—	—	—	—	—	—	7,6	14,2
L12500 . . .	—	—	—	—	—	—	8,5	15,6

Table 28

Dimensions of unclassified hyaenid lower teeth from Langebaanweg.

	P_3		P_4		M_1	
	l	b	l	b	l	b
5/1966/1 . . .	17,2	9,2	17,9	9,4	20,2	9,2
L10803/6/4 . .	16,2	9,3	17,8	9,6	19,1	9,5
L6379	*c.* 16,5	9,8	*c.* 17,8	*c.* 9,7	19,8	9,8
L15592	17.0	9,1	—	—	—	—
L5731	19,2	11,1	—	—	—	—
L13042	17,7	10,0	—	—	—	—
L16246/60 . . .	—	—	*c.* 19,6	10,2	21,9	10,6
L15854	—	—	19,0	10,2	—	—
L16055B . . .	—	—	17,5	9,5	—	—
L15896A . . .	—	—	18,4	9,3	—	—
L2055	—	—	18,6	10,6	—	—
L15897	—	—	—	—	21,6	9,5
L9137	—	—	—	—	21,8	10,5

The M^1 of 5/1966/1 is virtually identical to two other specimens from Bed 3a (L 10567, L 10802), while another (L 16055K) is more or less intermediate in size and morphology between that of 5/1966/1 and the M^1 of the *H. abronia* holotype. The M^2 of the *H. abronia* holotype is present on the right side only and is a small, single-rooted tooth. In 5/1966/1 it was present on both sides and these teeth, which are unfortunately lost, had at least two, and possibly three roots. Since Bed 3a is later than Bed 2, the situation in respect of the M^2 of 5/1966/1 and L 14186 is the reverse of what might have been expected. If these two specimens are indeed conspecific, the explanation may simply be that the M^2, although becoming vestigial, was still very variably developed in the species during that period in time involved in the deposition of Bed 2 and Bed 3a. The significance attached to the differences in the M^2 of the *Viverra leakeyi* from these beds (*vide supra*) might therefore be unwarranted.

It is tentatively concluded that the unclassified Bed 3a hyaenid material represents at least two species and that these are probably *Hyaena abronia* and *Hyaenictis preforfex*.

Unprovenanced material (Tables 27, 28)

The unprovenanced material from 'E' Quarry apparently also includes specimens belonging to more than one species.

Judging from the preservation of the mandibular fragments and the dates of their discovery, these specimens are most likely to have come from Bed 3a. Consequently, they too might be expected to represent *H. abronia* and *H. preforfex*, while in some cases at least, Species E is another possibility.

An example of the difficulties encountered in identifying this material is offered by the mandibular fragments L 2055, L 6378 and L 6380. These specimens belonged to adult individuals and are, therefore, comparable to the holotypes of *H. abronia* and *H. preforfex* in this respect. L 6380 is much more robustly developed than the mandible of the former, but the differences are such that they might be accounted for by individual intraspecific variation. This would be still easier to accept if the Bed 3a *H. abronia* was a larger variety of the species than that represented in Bed 2. The M_1 and M_2 of L 6380 are very worn, but they are clearly appreciably smaller than the corresponding teeth of *Hyaena* Species B. Comparisons with Species E are completely inconclusive owing to the nature of the single specimen referred to this species.

The problem becomes more complex when L 6378 is taken into consideration. This specimen is still larger than L 6380 and it seems unlikely to be conspecific with *H. abronia* because of its size, although on the basis of the fragmentary teeth of L 6378, this possibility cannot be excluded. This would be the most reasonable identification if the Bed 3a variety of *H. abronia* was larger than that from Bed 2. In the case of L 6378, the nature of the cheekteeth precludes the possibility of it being identified with Species B or Species E.

The mandibular fragment L 2055 compounds the uncertainty because in this instance the corpus is actually a little more slender than that of the *H.*

abronia holotype, although it is still larger than that of the *H. preforfex* holotype. It is almost inconceivable that L 2055 and L 6378 could be conspecific, unless there was in this species a far greater size range of variation than those observed in modern hyaenid species in the course of the present study.

This appears to be yet another situation which will only be satisfactorily resolved by the recovery of additional material and there seems little point in making provisional identifications of the unprovenanced material at present.

General Discussion on the Langebaanweg Hyaenidae

On the basis of the specimens presently available, the following grouping of the Langebaanweg Hyaenidae is proposed:

SPECIES	SIZE	PROVENANCE
Percrocuta australis	Large	Bed 2
Hyaena abronia	Medium	Bed 2
Hyaena Species B	Medium	Bed 2
Hyaena cf. *abronia*	Medium	Bed 3a
Species E	Medium	?Bed 3a
Hyaenictis preforfex	Small	Bed 3a

The unclassified material probably belongs to one or other of the listed species.

Although there are obvious differences between the various species (e.g. see Figs 27, 28), the presence of unclassified material raises the question of whether or not the various species which have been named are adequately defined. There is no real problem with *Percrocuta australis* as the large size and specialized dentition of this species makes it easy to recognize. The difficulties lie with the medium- and small-sized species, which have rather generalized, primitive hyaenid dentitions.

On purely theoretical grounds it might have been predicted that it would be difficult to classify the Langebaanweg hyaenids, since this family was diversifying during the late Pliocene and early members of new lineages would exhibit only slight differences from the archetypes. By the Pleistocene those hyaenids which are known from South Africa were well advanced on their particular lineages and, consequently, they can be more readily distinguished from one another.

The evolutionary history of *Hyaena* and *Hyaenictis* as it relates to species recorded from South Africa (Fig. 29) is visualized as follows:

(1) The late Pliocene *H. abronia* from Langebaanweg and the mid Pliocene *H. pyrenaica* from Europe are regarded as the earliest recorded representatives of the *H. hyaena* and *H. brunnea* lineages respectively.
The *H. hyaena* lineage, which includes *H. h. makapani* from the Transvaal, was a conservative one which underwent comparatively little change from the late Pliocene onwards. The differentiation of this lineage might well have taken place in Africa.
An ancestor of *H. brunnea* probably entered Africa from the north during the Pliocene. It is first recorded in South Africa during the Makapanian (Swartkrans) and it apparently replaced *H. hyaena*, which is last recorded earlier in the age (Makapansgat). *H. bellax*, another Makapanian species, is probably an off-shoot of the *H. brunnea* lineage.

(2) Species B probably arose from an immediate ancestor of *H. abronia*. The problematical *H. namaquensis* from Kleinzee (see Ewer 1967) may be related to Species B.
(3) Another lineage which must have had its beginnings during the Pliocene is that which includes *Hyaenictis preforfex* and *H. forfex*. It is not known to have survived the Makapanian.
(4) Species E is a problematical form whose affinities are not known.

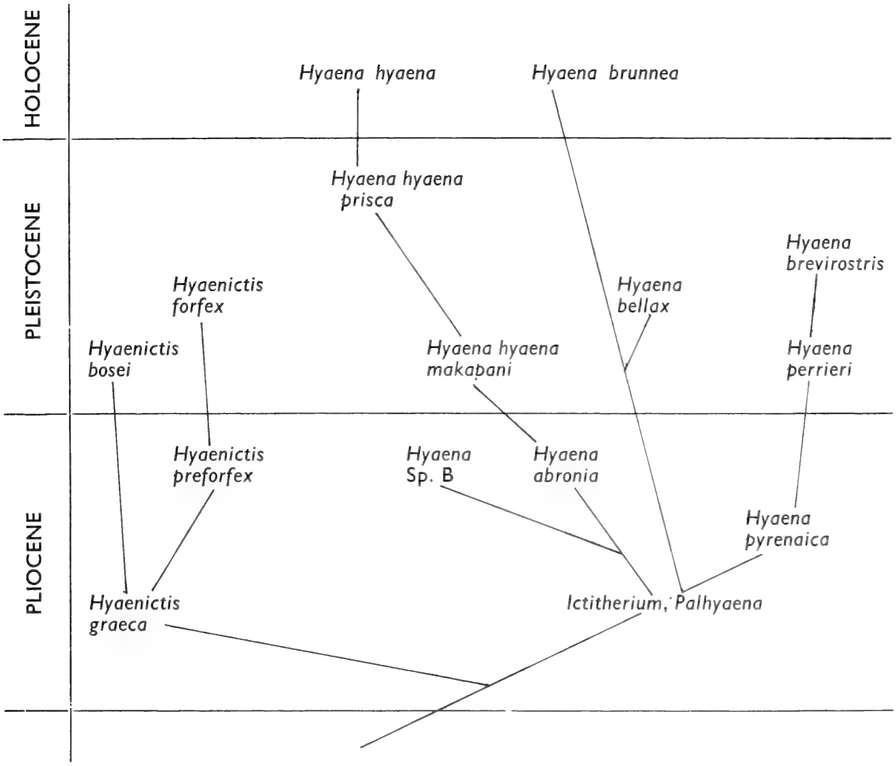

Fig. 29. Tentative phylogeny of some Hyaenidae.

The recorded late Pliocene Hyaenidae of South Africa thus include one species belonging to a lineage which is still extant (*H. abronia*), one species which has a Pleistocene descendant (*H. preforfex*), two which apparently became extinct without issue (*Hyaena* Species B and *Percrocuta australis*), and two of uncertain affinities (*H. namaquensis* and Species E).

This apparently complex association of hyaenids is not unique. Kurtén (1953) has investigated Chinese Pontian hyaenids and at a single occurrence (Loc. 49) the following species were recorded:
Ictitherium gaudryi, *I.* '*sinense*', *I. wongii*, *I. hyaenoides*, *? Lycyaena dubia* and *Crocuta variabilis*.

Kurtén's (1953) reassessment of this material led to the conclusion that *I.* '*sinense*' is probably a slightly aberrant *I. gaudryi* and ? *L. dubia* is an aberrant *I. hyaenoides*. *C. variabilis* was subsequently referred to *Percrocuta* (Kurtén 1957*b*). The Loc. 49 hyaenids thus comprise a *Percrocuta* and three species of *Ictitherium*, the latter including two aberrant specimens previously referred to other species. This is a remarkable match for the *Percrocuta*, three smaller hyaenid species and two problematical specimens from the South African Langebaanian. It is probably expecting too much to suppose that *H. namaquensis* and Species E can be disposed of as satisfactorily as the Loc. 49 *I.* '*sinense*' and ? *L. dubia*, but the important point is that there are precedents for an association of hyaenids such as that recorded for the Langebaanian and at Langebaanweg in particular. While this does not in itself validate the conclusions reached here, it does mean that the variety of species represented at Langebaanweg is not unexpected.

Although it is usually accepted that *Hyaena* arose from the ictitheres during the Pliocene, there is as yet no unanimity as to which, if any, of the recorded species is likely to have been the actual ancestor. Thenius (1966) concluded that *Hyaena* was derived from *I. robustum*, while Kurtén (1971 : 144) states that, 'The modern genus (*Hyaena*) presumably evolved from a *Palhyaena* ancestor'. By *Palhyaena* he presumably means '*I.*' *hipparionum* of the European Pontian and '*I.*' *wongii* of the Chinese Pontian.

In an earlier study on the ictitheres, Kurtén (1954) tentatively concluded that the recorded species could be grouped as follows:

(1) *I. wongii*, *I. hipparionum*
(2) *I. robustum*, *I. gaudryi*, *I. tauricum*
(3) *I. sivalense*, *I. hyaenoides*, ?*I. indicum*
(Not mentioned: *I. orbignyi*, a small species occupying a somewhat isolated position.)

Kurtén has thus apparently favoured derivation of *Hyaena* from group (1), while Thenius thought the genus derived from group (2). Perhaps both were right and *Hyaena* is polyphyletic rather than monophyletic in origin. It has already been suggested that the early ancestors of *H. hyaena* and *H. brunnea* were differentiated by the mid Pliocene and that the former may have arisen in Africa and the latter in Europe, or at least Eurasia. The mid Pliocene was also the time when the ictitheres were at the peak of their radiation and, although they have yet to be recorded in Africa, it is probably safe to assume that they were present on this continent as well. Consequently, there does seem to be a reasonable possibility that *H. hyaena* and *H. brunnea* did evolve from two different ictithere species. The common ancestor of the two species may thus date back to the Miocene, and the characteristics which they share might be the result of parallel evolution rather than a close phyletic relationship.

In recognition of their long independent history, it is proposed that the *H. hyaena* and *H. brunnea* lineages be differentiated by giving their members separate subgeneric status.

Subgenus *Hyaena*

Type species: Hyaena hyaena Linnaeus, 1758.

Diagnosis: Hyaenidae usually of medium size; P_1 and M^2_2 retained in late Pliocene forms; anterior premolars only moderately enlarged even the most advanced forms; M_1 metaconid large.

Stratigraphic range: Mid Pliocene to Holocene of Africa and Eurasia.

Referred species: Hyaena abronia (*H. makapani* Toerien and *H. prisca* De Serres included as subspecies of *H. hyaena*)

Subgenus *Parahyaena*

Type species: Hyaena brunnea Thunberg, 1820.

Diagnosis: Hyaenidae of medium to large size; P_1 and M_2^2 lost by the late Pliocene; anterior premolars much enlarged in the Pleistocene species; M_1 metaconid often small or absent.

Stratigraphic range: Mid Pliocene to Holocene of Eurasia and Africa.

Referred species: Hyaena bellax Ewer; *H. brevirostris* Aymard; *H. perrieri* Croizet & Jobert; *H. pyrenaica* Depéret.

Family **Felidae**

Subfamily Machairodontinae

Machairodus sp.

(Figs 30, 31, 32, 38)

Material

L 20505—Parts of the skull of a single individual, including: Isolated ? $I^{1 \text{ or } 2}$; right maxillary fragment with $\underline{C}$ and P^3 to M^1; left maxillary fragment with P^3 and P^4. Right mandibular fragment with part of M_1; left mandibular fragment with M_1.

Tentatively referred material

L 11890—? Left I^3.
L 6386 —Right mandibular fragment.
L 12641—Right mandibular fragment with incomplete P_4 and M_1.

Locality and horizon

These specimens are from Bed 2, 'E' Quarry, Langebaanweg.

Description

The fragmentary skull (L 20505) belongs to a relatively primitive and moderately large machairodont, the primitive character being suggested principally by the presence of P^2. Both the left and the right P^2 of this specimen have been lost, but their alveoli are preserved. The left alveolus (4 × 4 mm) indicates that the tooth was small, circular and single-rooted, while the right P^2 was evidently a little larger, antero-posteriorly elongated and double-rooted, the alveolus measuring 6 × 4,5 mm.

The isolated incisor of L 20505 is a worn and rather nondescript tooth and only because of its direct association with the remainder of the skull is it identified with this species.

The right C̲ is largely intact, except for some slight damage to the root. It is a relatively large tooth (Table 29), the overall length along the anterior curve behind about 120 mm. The root and crown make up approximately equal parts of the tooth. The root is somewhat bulbous and its contact with the neck is therefore clearly defined. The crown is transversely compressed and has a diametrical index of only 0,46. There are prominent anterior and posterior keels and these are finely serrated. The anterior serrations are less distinct and, unlike those on the posterior keel, they are absent for about 3 mm from the apex of the tooth. The posterior keel is rectilinear, but the anterior one curves lingually towards the base of the crown.

TABLE 29

Dimensions of the upper teeth of Machairodontinae from Langebaanweg, compared with those of a specimen from Makapansgat.

		Langebaanweg			Makapansgat
		Machairodus L20505	cf. *Machairodus* L11890	cf. *Homotherium* L11846	*Homotherium* M8280*
?$I^{1 \text{ or } 2}$	l	*c.* 6,2	—	—	—
	b	8,5	—	—	—
?I^3	l	—	8,2	—	—
	b	—	8,8	—	—
C̲	l	24,2	—	35,0	34,3
	b	11,1	—	13,5	14,0
	b : l	0,46	—	0,39	0,41
P^3	l	*c.* 15,6	—	—	10,8
	b	7,0	—	—	5,7
P^4	l	37,4	—	—	53,2
	b	*c.* 12,1	—	—	8,9
M^1	trans. diam.	6,3	—	—	—
	Ant-post-diam.	4,5	—	—	5,7
C̲–P^4	l	89,0	—	—	—

* Collings 1972.

The right P^3 is damaged, but the left is intact, except for the apex of the principal cusp which is lost. It has prominent anterior and posterior accessory cusps, the latter being the larger of the two, while there is an additional small

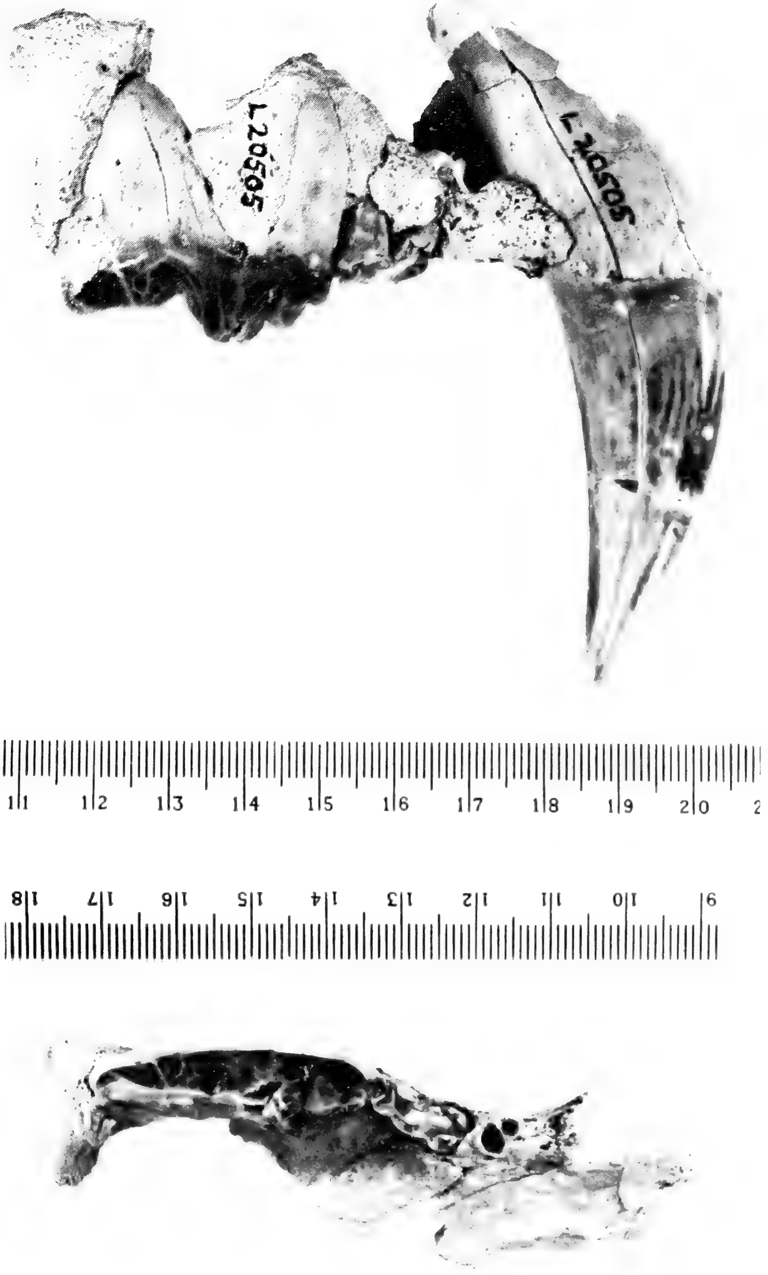

Fig. 30a. Buccal and occlusal views of the right maxilla (L 20505) of the *Machairodus* sp. from Langebaanweg.

Fig. 30b. Buccal and occlusal views of the left maxilla (L 20505) of the *Machairodus* sp. from Langebaanweg.

cusp situated at the posterior end of the tooth. This cusp is in close contact with P^4 and the pressure brought about by this contact has resulted in damage to its enamel surface. The same applies in the case of the right P^3. These teeth are relatively long and narrow.

Both the left and the right P^4 are complete. They are also long and narrow, with the protocones much reduced in size. They have prominent ectoparastyles, which are, however, much smaller than the parastyles. The ectoparastyle, parastyle and paracone of the left P^4 are about 20,5 mm in length, while the metastyle, which is the longest of the cusps, measures 16,5 mm. The roots

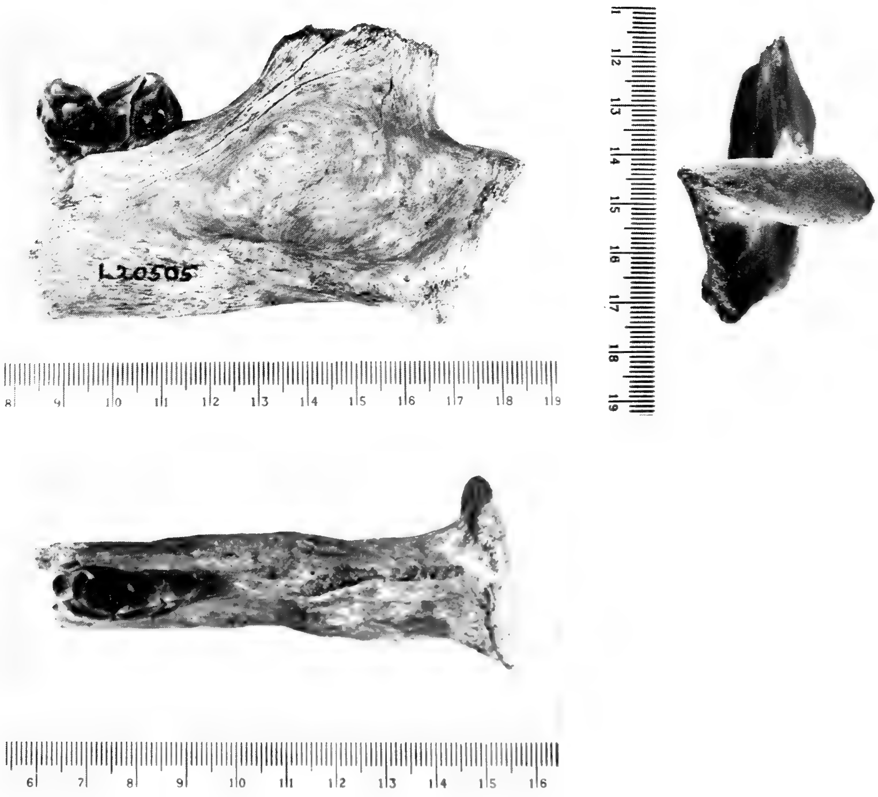

Fig. 31. Buccal, occlusal and posterior views of the *Machairodus* sp. mandible (L 20505) from Langebaanweg.

supporting the protocones are anteriorly directed, their dorsoventral axes being in line with the apices of the paracones. Although the C̲ and P^3 of this specimen show no obvious signs of wear, the shearing surfaces of the P^4 paracones and metastyles are heavily worn, while the protocones have been all but worn away. The lingual surfaces of the parastyles and ectoparastyles are also slightly worn.

The preserved right M^1 is also worn and little of the crown remains. It is single-rooted, but has a slight transverse elongation. The alveolus of the missing left M^1 shows vestiges of the more primitive double-rooted condition.

Little remains of the skull itself and the dorsal edges of the preserved parts are heavily abraded. The largest piece of the skull which is preserved consists of that part of the basi-cranium which includes the glenoid regions and the intervening basi-sphenoid. The glenoid fossae are approximately 13 mm below the level of the basi-sphenoid, the relative positions of these features being characteristic of the machairodonts. In the modern feline skulls used for comparative purposes during the present study the glenoid fossae and basi-sphenoids were all more or less in the same planes. This characteristic of L 20505 is also illustrated by the fact that the inferior margin of the left post-glenoid process is about 25 mm below the level of the inferior margin of the external auditory meatus. In a young adult lioness skull of similar overall size (SAM 35115), the corresponding figure is about 15 mm.

Both halves of the mandible of L 20505 lack the dorsal margins of the coronoid processes and the corpora anterior to M_1. The characteristics of the fossil are clearly illustrated by comparisons with corresponding parts of the mandible of the modern lioness referred to above. The two specimens are similar in overall size (Table 30), but there are marked differences in individual characteristics. In the fossil the angular region is directed buccally, whereas in

TABLE 30

Dimensions of the lower teeth and mandibles of Machairodontinae from Langebaanweg, compared with those of a young adult *Panthera leo.*

		Machairodus L20505	cf. *Machairodus*		*Panthera leo* ♀ SAM35115
			L12641	L6386	
P_3 alveolus	l	—	12,3	*c.* 12,0	—
	b	—	5,5	—	—
P_4 alveolus	l	—	20,5	—	—
	b	—	9,5	—	—
M_1 alveolus	l	—	*c.* 28,0	—	—
	b	—	11,0	—	—
M_1	l	*c.* 29,0	—	—	—
	b	11,2	—	—	—
$\bar{C}$–M_1	l	—	*c.* 104,0	—	98,0
$\bar{C}$–P_3 diastema	.	—	*c.* 27,0	*c.* 30,0	15,0
Height of corpus anterior to P_3	.	—	*c.* 33,0	*c.* 37,0	40,4
Breadth of corpus anterior to P_3	.	—	20,0	22,0	18,4
Height of corpus below M_1 . .	.	36,5	35,9	—	35,3
Breadth of corpus below M_1 .	.	17,0	18,6	—	19,4
Trans. diameter of condyle . .	.	40,3	—	—	43,0
Distance between posterior ends of condyle and M_1	.	66,0	—	—	73,0

SAM 35115 it is directed posteriorly. The most striking differences are in the coronoid processes. Although both these processes are damaged in the fossil, it is evident from the configuration of the masseteric fossae that little of the most dorsal parts is in fact missing and, as is characteristic of all machairodonts, the processes are low relative to those of the lioness and, indeed, other felines as well. In addition, the anterior margin of the ascending ramus is more steeply inclined and the coronoid processes are broader antero-posteriorly.

The left M_1 is intact and the tooth is relatively long and narrow. Superficially it appears to consist only of a protoconid and paraconid, the former being about 20% longer than the latter. The cingulum of the most posterior part of the tooth is slightly bulbous, its outline in occlusal view not conforming with those parts anterior to it, while there is a barely discernable notch on the posterior keel dorsal to this region. The keel posterior to this notch and dorsal to the bulbous cingulum is very finely serrated, the serrations being smaller than those of the $\underline{C}$. This region of the tooth may in fact be the talonid which is in the phyletic process of being incorporated with the protoconid. Both the protoconid and the paraconid have well-developed shearing facets worn on them and there is an additional shear facet resulting from occlusion with M^1 worn on the buccal surface along the contact between the 'talonid' and protoconid. The carnassial notch is fairly prominent and there is a slight groove on the buccal surface ventral to it which extends almost to the base of the crown.

The right M_1 has lost the paraconid and supporting root. In this tooth the 'talonid' is not readily demarcated since the serrations and notch separating it from the protoconid are absent. The transverse fracturing of this tooth at the carnassial notch has revealed the presence of an additional root beneath the protoconid. This root is relatively small and is situated on the buccal side towards the midpoint of the tooth. It has a slight antero-buccal inclination and serves to anchor the M_1 very firmly in the mandible.

The isolated ? I^3 (L 11890) and the mandibular fragments (L 6386, L 12641) are only tentatively grouped with L 20505, since the nature of the specimens precludes conclusive comparisons.

The crown of the incisor consists of a high, rather conical cusp, the sides of which are keeled and serrated, the latter characteristic suggesting its machairodont affinities. There are two small projections from the cingulum situated just posterior to the keels. It is a slightly larger tooth than the isolated incisor of L 20505.

The more complete of the two mandibular fragments (L 12641) lacks the ascending ramus and angle and all the teeth are lost or damaged. The corpus is long and low, but is relatively broad. The inferior margin below the cheekteeth is rectilinear. The symphyseal region is high and broad and there is a small mental flange (crest), which arises from below the larger and most anterior of the two mental foramina.

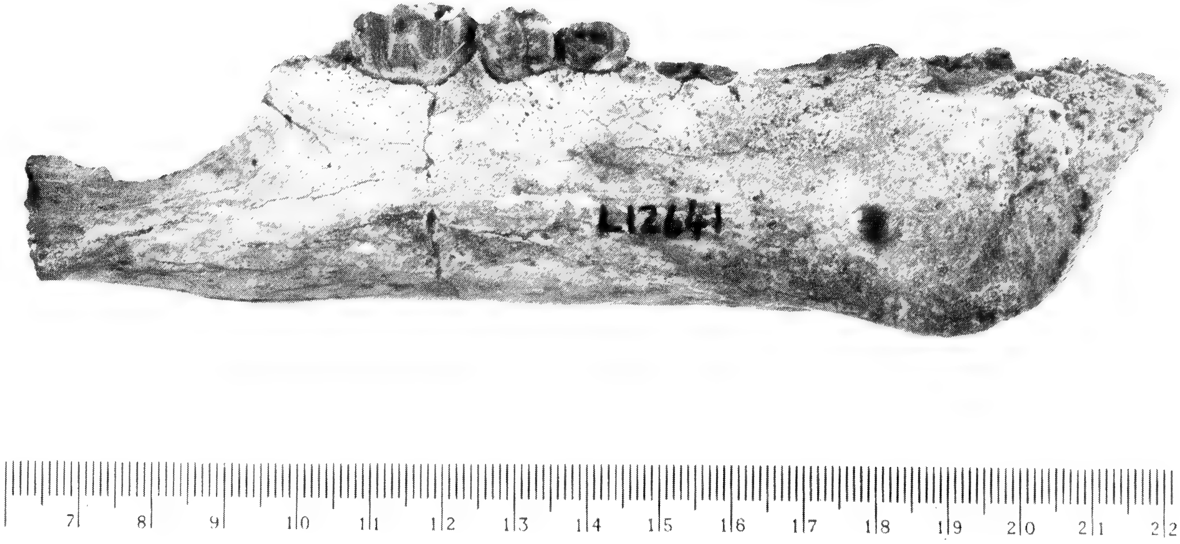

Fig. 32. Buccal view of the cf. *Machairodus* mandible (L 12641) from Langebaanweg.

The dorsal surface of the symphyseal region is damaged, but parts of the alveoli of I_3 and $\bar{C}$ are preserved. These two teeth were antero-posteriorly elongated and although their dimensions cannot be accurately measured, it is evident that the $\bar{C}$ was appreciably larger than I_3. It is also a little more posteriorly situated. Since their alveoli are not visible, it is probable that the I_1 and I_2 were much smaller than I_3. The alveolar margins of the symphyseal teeth must have been well above the level of those of the cheekteeth.

The postcanine diastema is long and at about its midpoint is a small alveolus (2,0 × 1,5 mm), which contains the root of a vestigial premolar. The P_3 has been broken off at the roots, but it was clearly a much smaller tooth than P_4. The P_4 itself is badly damaged, but it was apparently made up of a principal cusp, anterior and posterior accessory cusps and a smaller cusp projecting from the posterior cingulum. Of the M_1 only the anterior root and part of the crown which it supports is preserved. In addition to the post-mortem damage, this tooth was reduced to its present state by heavy wear during life. It lacks the additional small root beneath the protoconid which is visible in the right M_1 of L 20505.

In as far as comparisons between L 12641 and the mandibular fragments of L 20505 are possible, it appears that the specimens are essentially similar, although L 12641 has a broader corpus. This may, however, be accounted for by the fact that it belonged to a more aged individual, a judgment which is based on the more advanced wear on its M_1. A further indication that L 12641 belongs to a machairodont which was similar in size to L 20505 is the fact that the right maxilla of the latter specimen matches the referred mandible reasonably well. If the two specimens are indeed conspecific, then the $\underline{C}$ of this form must have projected outside the buccal cavity when the mouth was closed.

The second mandible fragment (L 6386) lacks part of the symphyseal region and those parts posterior to P_4. The damaged roots of the $\bar{C}$ and P_3 are still in place, while the lingual surface of the P_4 alveolus is still visible. This specimen is generally similar to corresponding parts of L 12641, although it is more robust, has larger mental foramina and does not have a vestigial premolar anterior to P_3. There is a very marked contrast in the relative robustness of the mandibular corpora of L 6386 and L 20505 and, although this does not necessarily preclude their being conspecific, it is possible that L 6386 and perhaps also L 12641 belong to a larger species. Such a species is recorded from Bed 3a (*vide infra*).

Discussion

There has been a considerable amount of confusion in the past concerning the taxonomy of the Machairodontinae and only five genera are recognized here. They are *Homotherium*, *Dinobastis*, *Megantereon* and *Smilodon*, which were all essentially confined to the Pleistocene, and the Pliocene genus *Machairodus* (see Kurtén 1963*b*; Thenius 1967).

The following characteristics were included in a diagnosis of *Machairodus* Kaup, 1833 by Pilgrim (1931: 128):

> 'Machairodontinae of large size . . . ; upper canine very large, stout, long, flattened; . . . mandible with deep symphysis; canines and incisors elevated considerably above the level of the back teeth, without mental process but with a prominent mental crest; . . . P^4 with protocone weak; paracone and parastyle well developed; with an extra cusp anterior to the parastyle (ectoparastyle); . . . M_1 with vestigial metaconid; . . .'

If the cusp referred to by Pilgrim as the 'metaconid' is the same as that tentatively identified here as the 'talonid', then the Bed 2 machairodont material is accommodated quite well by the above diagnosis.

In addition, the retention of P^2 in L 20505, and the relatively large size of P_3, the vestigial anterior premolar and the inferred relative sizes of the symphyseal teeth in L 12641, are all primitive characters in the Machairodontinae which are probably sufficient to distinguish the species from those referred to the four essentially Pleistocene machairodont genera.

The Bed 2 machairodont is therefore referred to the genus *Machairodus*, but its specific identity is uncertain. The $\underline{C}$ of L 20505 (24,2 × 11,1 mm) is similar in size and other respects to that of the Makapanian *Machairodus transvaalensis* from Bolt's Workings at Sterkfontein (24,5 × 12,1 mm) (Broom 1939). However, the isolated upper carnassial referred to this species by Broom has a much larger parastyle and shorter metastyle than those from Langebaanweg. There is no certainty that the Bolt's Workings P^4 and $\underline{C}$ do belong to the same species, but if this is so then the Langebaanweg *Machairodus* is clearly not *M. transvaalensis*, although it might be an ancestor of this species.

There are no other named machairodonts from South Africa to which the present material can be referred and comparisons to previously recorded Eurasian species were inconclusive. Since it may prove to be conspecific with one of the latter, it is for the present not identified at the species level.

Family **Felidae**

Subfamily Machairodontinae

cf. *Homotherium* sp.

(Fig. 38)

Material

L 11846—Incomplete left $\underline{C}$.

Locality and horizon

This specimen is from Bed 3a, 'E' Quarry, Langebaanweg.

Description

This canine, which belongs to a machairodont of large size, has lost part of the crown, but it has an estimated length along the anterior curve of about 200 mm, which is 80 mm longer than the $\underline{C}$ of the Bed 2 *Machairodus*. Even if the length of the restored part of the crown has been exaggerated, the overall length is most unlikely to have been less than 180 mm and the tooth is still appreciably larger than that of the *Machairodus* (Table 29). It is also very narrow and has a diametrical index of only 0,39. The anterior and posterior keels of the crown are serrated, the posterior serrations extending about 35 mm closer towards the root than those on the anterior keel. It differs from the canine of the Bed 2 species in this respect, since the anterior and posterior serrations of the $\underline{C}$ of L 20505 terminate in about the same horizontal plane. The canines of the two species also differ in that both keels of L 11846 are rectilinear, whereas the anterior keel of L 20505 curves lingually towards the base. As a result the anterior serrations of L 11846 are all visible in buccal view, while in the *Machairodus* they are all visible only in anterior and lingual view. There is no appreciable thickening of the root of L 11846 as is the case with L 20505.

Discussion

This specimen was previously tentatively referred to *Machairodus* (Hendey 1970*a*), but this identification is almost certainly incorrect.

Recently Collings (1972) described a machairodont from Makapansgat under the name of '*Megantereon problematicus*' and the right $\underline{C}$ of the holotype is similar in size to L 11846 (Table 29), and also has serrated keels. The Langebaanweg and Makapansgat species are probably congeneric and perhaps even conspecific, although the nature of the relationship cannot be concluded on the basis of the material presently available. In addition, the identity of '*Megantereon problematicus*' is open to question. The relatively short, serrated canines and the size of the teeth suggest that its affinities lie with *Homotherium* rather than *Megantereon*. Collings made no comparisons with previously recorded species of *Homotherium* and the specific identity of the Makapansgat specimen is therefore also not settled. It is concluded that it should for the present be listed as *Homotherium* sp. indet., while L 11846 is tentatively identified as belonging to a *Homotherium* as well.

The fact that the two 'E' Quarry machairodonts are recorded from different units in the stratigraphic succession suggests that they might not have occupied the area contemporaneously. These large predators are, however, very poorly represented at the site and this supposition is thus very insecurely based. Since the two species evidently differed considerably in size, it is likely that their preferred prey also differed so that their co-existence need not necessarily have been a problem. Taking this into account, together with the inferred broad contemporaneity of Beds 2 and 3a, it may yet prove that both species occurred in the area at the time of deposition of both beds.

Family **Felidae**

Subfamily Felinae

Felis aff. *issiodorensis* Croizet & Jobert, 1828

(Fig. 33)

Material

L 16055C—Left mandibular fragment with $\bar{C}$, parts of P_3 and P_4, and M_1.
L 3199 —Right mandibular fragment with M_1.
L 15608 —Right $\underline{C}$.
L 15788 —Left P^4.

Locality and horizon

All these specimens are from 'E' Quarry, Langebaanweg. L 3199 is of unknown provenance and the others are from Bed 3a.

Description

This material belongs to a felid which was similar in size to the modern lynxes.

The $\underline{C}$ is comparable in size to those of large individuals in the available series of modern *Felis caracal* (n = 19) (Table 31), but differs in that the groove on the buccal surface is longer and deeper, while the antero-internal keel is more prominent.

TABLE 31

Dimensions of teeth of the Langebaanweg *Felis* aff. *issiodorensis*, compared with those of some other lynxes.

		$\underline{C}$		P^4		M_1		$\bar{C}$–M_1	P_3–M_1
		l	b	l	b	l	b	l	l
Lange-baanweg	L15608, L15738	*c.* 8,8	7,0	17,6	8,4	—	—	—	—
	L16055C	—	—	—	—	15,3	*c.* 6,0	*c.* 56,0	*c.* 36,0
	L3199	—	—	—	—	12,9	5,9	—	—
F. issiodorensis (Means)*		—	—	20,2	9,5	14,7	—	—	36,8
Modern *F. caracal*	Mean	7,5	5,5	16,1	7,3	12,2	5,4	44,3	31,1
	Range	6,5– 9,0	4,8– 6,7	14,8– 17,8	6,4– 8,7	11,0– 14,0	4,9– 6,1	41,4– 50,5	29,0– 33,9
	n	17		19		19		19	7

* Saint-Vallier specimens (Viret 1954).

The P^4 is similar in all observable respects to the P^4 of large individuals in the *F. caracal* comparative series.

The more complete of the mandibular fragments (L 16055C) has a longer post-canine diastema than any specimen in the comparative series and, as a result, the $\bar{C}$ to M_1 length is also greater. The other specimen (L 3199) may belong to a female, since the M_1 is much smaller than that of L 16055C. However, even though this tooth is also smaller than those of males in the comparative series, that part of the mandibular corpus which remains is as large as corresponding parts of the mandibles of male *F. caracal.* This suggests that the fossil species was somewhat larger than the extant South African *F. caracal.*

The $\bar{C}$ has a larger root than any specimen in the comparative series and the groove on the buccal surface of the crown is more pronounced.

Although the P_3 and P_4 of L 16055C are damaged, they appear to be similar to the corresponding teeth of *F. caracal.*

In addition to the difference in their sizes, the two known lower carnassials also differ in that the smaller (L 3199) has a less prominent talonid. The M_1 of L 16055C has a very small metaconid, while in L 3199 there is just a trace of this cusp still visible. The former also has a slightly more prominently developed buccal cingulum. Both specimens have a wide and deep carnassial notch, which contrasts with *F. caracal* in which the notch is closed and terminates further from the cingulum.

Fig. 33. Buccal view of the *Felis* aff. *issiodorensis* mandible (L 16055) from Langebaanweg.

Although the provenance of L 3199 is not recorded, the preservation and adhering matrix suggests that it also came from Bed 3a. The observable differences between the lower carnassials of these two specimens are probably no greater than might be expected in a single species, while the size difference is certainly within reasonable limits (Table 31). There are, therefore, no grounds for believing that more than one species is represented by the material listed above.

Discussion

The modern felids of southern Africa range in size from the small *Felis nigripes*, through *F. libyca*, *F. serval*, *F. caracal*, *Panthera pardus*, *Acinonyx jubatus*, to the large *Panthera leo*. A similar range of species of differing size is recorded elsewhere in the world. Dental and osteological characters of certain species in any given area may be such that they can be most readily distinguished by their size. However, overlaps in the size range of variation in species can lead to great, or even insuperable problems in the classification of fragmentary remains. A further complication with fossil populations is that these may comprise individuals whose average size is greater or less than those of extant populations.

It is here assumed that the small feline from Langebaanweg is most closely related to the modern species which are closest to it in size, i.e. the lynxes. While it is here regarded as a lynx, it might alternatively or additionally have close phyletic links with the wild cat and serval groups. Lynxes are widely distributed in the Old and New Worlds and a distinction is made between the essentially Holarctic *Felis* (*Lynx*) and the essentially Ethiopian and Oriental *Felis* (*Caracal*). In view of the age of the Langebaanweg species, its possible relationships to both these groups must be considered.

F. caracal still occurs in the south-western Cape today, but in view of the temporal and observed morphological differences between it and the Langebaanweg form, it is very unlikely that they are conspecific. In the case of the extant species of *Felis* (*Lynx*) there is the additional factor of wide geographical separation which is applicable.

Kurtén (1968: 80) regards the European Villafranchian *F. issiodorensis* Croizet & Jobert and the possibly conspecific Chinese *F. shansius* Teilhard as being 'close to the starting point of the evolution of lynxes'. He also regards the earlier North American species, *F. rexroadensis* Stephens, as the possible ancestor of *F. issiodorensis*, and stated that, 'The Issoire lynx may well be ancestral to all the living Old World lynxes'. Since the Langebaanweg species is probably older by at least 0,5 million years than the earliest European record of *F. issiodorensis* (i.e. that from Etouaires), and is comparable in age to *F. rexroadensis*, it must be considered in relation to both these species.

One of the characteristics of the European *F. lynx* lineage is the regeneration in M_1 of a small metaconid and an increase in the size of the talonid (Kurtén 1963*a*). The Etouaires form of *F. issiodorensis* lacks a metaconid and has a rudimentary talonid and in these respects it resembles the M_1 of L 3199. On the other hand, the characters of the M_1 of L 16055C are more comparable to advanced *F. issiodorensis*. In view of the relative ages of these forms, that from Langebaanweg might be regarded as having retained in M_1 some of the characters evident in the ancestor of felines, namely, *Pseudaelurus*, but at the same time showing the trend towards reduction of metaconid and talonid, which in the *F.* (*Lynx*) lineage was climaxed in the Etouaires *F. issiodorensis*. Kurtén (1963*a*) states that in only 30% of modern *F. caracal* ($n = 23$) is the M_1 metaconid and talonid present. In 8 recent specimens from the Cape Province, the metaconid was not present at all, while the talonid was always very small.

The implications are that the Langebaanweg species could be ancestral to both *F. issiodorensis*, and therefore also *F. lynx*, as well as *F. caracal*. In the European *F. lynx* lineage there was a reversal of the trend toward reduction of the M_1 metaconid and talonid, but in the African *F. caracal* lineage this trend was apparently continued.

In general, the teeth and mandible of the Langebaanweg lynx are quite similar to those of *F. issiodorensis*. For example, the Saint-Vallier form of this species (Viret 1954) is comparable in size to the Langebaanweg lynx (Table 31), it also has the buccal surfaces of the canines deeply grooved, while the post-canine diastema of the mandible is equally long. However, the illustrated Saint-Vallier specimens, like modern lynxes, differ from the Langebaanweg form in that the M_1 carnassial notch is closed.

Unfortunately, the lower dentition of *F. rexroadensis* is unknown (Bjork, 1970), but the Langebaanweg P^4 differs from that of the American species in that the protocone is not as posteriorly situated (see Stephens 1959). It is more like *F. issiodorensis* in this respect. Another North American species, *F. lacustris* Gazin, is closely related to *F. rexroadensis* and is of comparable age (Bjork 1970). In this species the P^4 protocone is similarly situated to that of the Langebaanweg form. However, the M_1 of *F. lacustris* differs from the Langebaanweg specimens in that it lacks both metaconid and talonid (Gazin 1933). *F. lacustris* is also a larger species.

Although they all date from the late Pliocene, it is unlikely that there is any close connection between the Langebaanweg species and the two from North America. Apart from the wide geographical separation which must lessen the chances of direct phyletic links, Bjork (1970: 43, 44) concluded that although it is possible that the affinities of *F. rexroadensis* and *F. lacustris* lie with the '*Lynx* group', this 'must be considered with caution', and he 'would not assign [them] to *Lynx*'.

On the basis of the material presently available, the Langebaanweg species cannot be differentiated from *F. issiodorensis* and it probably represents an early stage in the development of this species. Since it is not certain that the two are conspecific, the Langebaanweg lynx can only be said to have affinities with *F. issiodorensis*.

The possible phyletic relationships of fossil and modern lynxes will be considered again following the description of the second feline from Langebaanweg (*vide infra*).

Family **Felidae**

Subfamily Felinae

Felis obscura n. sp.

(Fig. 34)

Holotype

L 10100—Left maxillary fragment with $\underline{C}$ to M^1, with parts of premaxilla and jugal attached.

Locality and horizon

This specimen is from Bed 3a, 'E' Quarry, Langebaanweg.

Diagnosis

A medium-sized feline with a short face; ascending ramus of premaxilla broad; P^2 absent; P^3 lacking anterior accessory cusp and with the posterior accessory cusp flanked posteriorly by a smaller cusp projecting from the cingulum; P^4 narrow, but with a prominent protocone linked to the paracone by a ridge of enamel; P^4 parastyle relatively small and a very small 'ectoparastyle' also present; P^4 paracone and metastyle approximately equal in length; M^1 double-rooted and nearly triangular in shape.

Etymology

The specific name indicates the doubt which exists about the relationships of the species.

Description

This specimen belongs to a felid which in some respects is comparable to small forms of modern *Panthera pardus*. It was initially compared and contrasted with a series of seven skulls of leopards from the south-western Cape and adjacent mountains, which represent a small variety of the species. Subsequently it was compared to other felines, including the *Felis caracal* series already referred to.

The pre-canine diastema is shorter than those of the available *P. pardus* specimens and the premaxilla does not project as far forward. The ascending ramus of the premaxilla is much broader in lateral view than in *P. pardus*.

The $\underline{C}$ of L 10100 is damaged, but it was evidently a fairly high crowned tooth. It is more transversely compressed and has a somewhat flatter lingual surface than the upper canines of the *P. pardus* series. The posterior keel was prominent, although its enamel has been lost either through wear or post-mortem damage.

The post-canine diastema is short, measuring only 5,5 mm, and P^1 and P^2 are absent.

The P^3 is slightly smaller than those of the *P. pardus* series (Table 32), but otherwise differs only in that the posterior accessory cusp is flanked by a more prominently developed posterior cingulum, the median part of which is in the form of an additional small cusp. In this respect it is more like the P^3 of available *Acinonyx jubatus* specimens, but it differs from this species in that it lacks an anterior accessory cusp.

TABLE 32

Dimensions of the teeth of the Langebaanweg *Felis obscura*, compared with those of *Sivafelis potens* from the Siwaliks and a series of modern *Panthera pardus*.

		P^3		P^4		M^1	
		l	b	l	b	l	b
L10100		14,0	6,3	*c.* 23,8	12,2	*c.* 5,6	7,4
*Sivafelis potens**		—	—	24,0	11,5	—	—
Modern	Mean	15,1	7,5	23,7	12,4	—	—
Panthera	Range	14,8– 15,7	6,7– 8,2	20,7– 24,9	10,4– 12,9	— —	— —
pardus	n	7		7		—	

* Pilgrim 1932.

The P^4 is similar in size to the smaller of the *P. pardus* specimens, but the shearing blade is more slender, the parastyle less prominent, while the protocone is more prominent. The apex of the protocone is situated opposite the notch between the parastyle and paracone and there is a ridge of enamel between it it and the apex of the paracone. There is a small hollow in the enamel surface between this ridge and the parastyle. The paracone is slightly longer than the metastyle, and both are longer than the parastyle. The anterior and posterior keels of the paracone are more or less mirror images of one another and this cusp resembles that of *Acinonyx*. In *P. pardus* and other extant South African felids, the anterior keel is more rectilinear than the other. There is a tiny cusp situated antero-externally from the parastyle. It would perhaps be more correct to regard it as a prominently developed part of the cingulum rather than as a true ectoparastyle such as that of the machairodonts. There is a similar but more obviously developed feature in the P^4 of the *Acinonyx* comparative series.

The M^1 has two roots and since the metastyle is still comparatively well developed, it is almost triangular in outline.

The distance between the P^4 alveolar margin and the inferior margin of the orbit is appreciably less than in P. *pardus,* while the infra-orbital foramen is slightly elongated dorso-ventrally rather than being circular in shape. In the

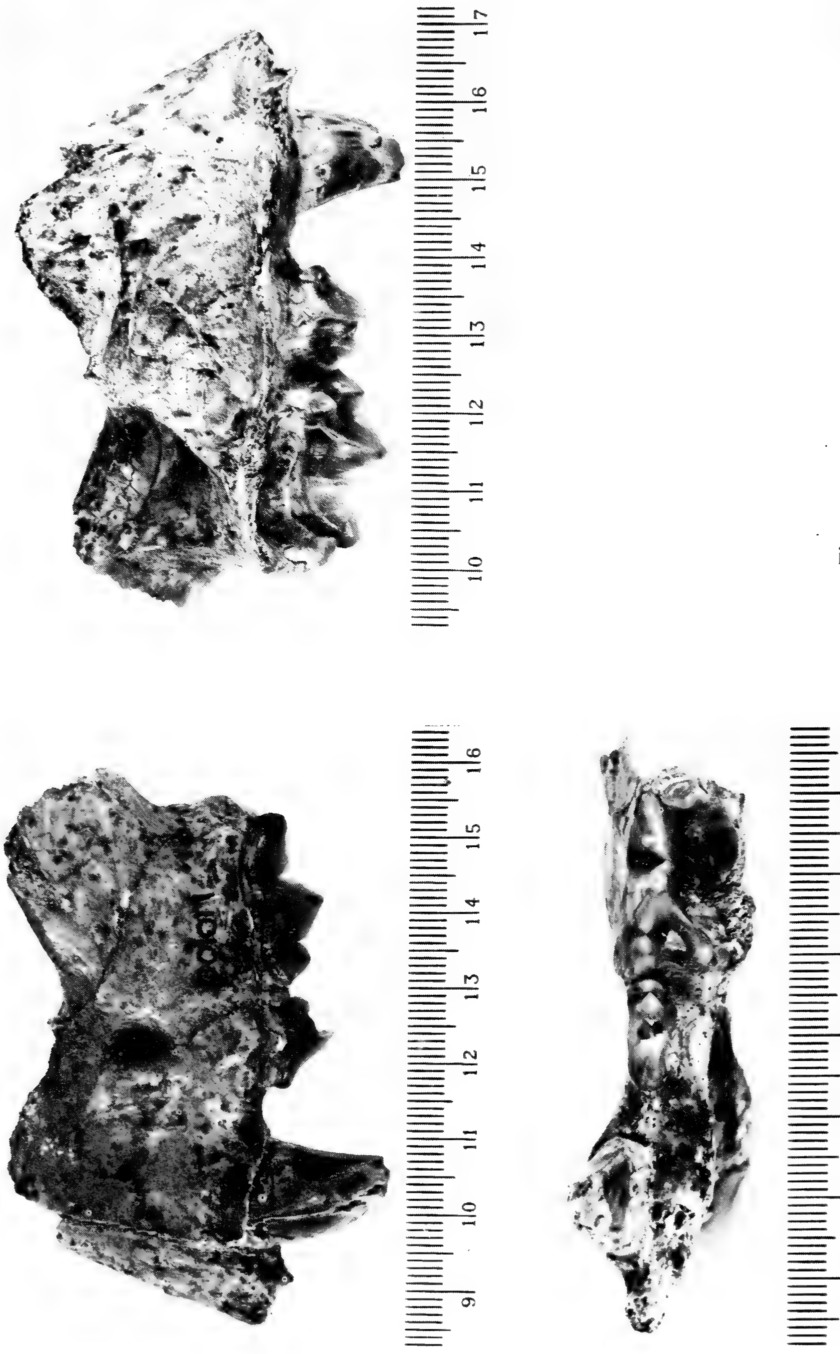

Fig. 34. Buccal, occlusal and lingual views of the *Felis obscura* maxilla (L 10100) from Langebaanweg.

fossil there is an additional very tiny foramen situated on the inferior margin of the infra-orbital foramen. A similar feature was observed in the available felid comparative material only in a skull of a North American *F. rufus*.

Discussion

Since this species lacks P^2 its affinities clearly do not lie with either *Panthera* or *Acinonyx*. In general, it probably resembles *Felis caracal* more closely than any other extant southern African felid.

It is similar to *F. caracal* in the following respects:

(1) Both species have a relatively broad ascending ramus of the premaxilla.
(2) The shape of the infra-orbital foramen and its position relative to the cheekteeth are similar in the two species.
(3) Both species lack P^2.
(4) Both have relatively short pre- and post-canine diastemas.
(5) The P^3 morphology of the two species is similar, although *F. caracal* may sometimes have a small anterior accessory cusp and the posterior cingulum cusp may be relatively less prominent.
(6) In general, the P^4 of the two species are similar, although the protocone of *F. caracal* is relatively reduced and in this species there is only occasionally a slight thickening of the cingulum antero-externally to the parastyle ('ectoparastyle').

The fossil and *F. caracal* definitely differ in the following respects:

(1) *F. caracal* is a much smaller species.
(2) In lateral view the jugal of *F. caracal* extends as far forward as the infra-orbital foramen, whereas in L 10100 it does not. In this respect the fossil resembles *P. pardus* and *Acinonyx*.
(3) The M^1 of *F. caracal* is relatively more reduced.

There is nothing which would preclude L 10100 belonging to a species which was directly ancestral to *F. caracal* and there is a good deal which suggests that such a relationship might be possible.

Of recorded fossil species, those referred to *Sivafelis* Pilgrim, 1932 are perhaps most likely to have affinities with L 10100. Pilgrim (1932) included three species in this genus, namely, *S. potens* Pilgrim and *S. brachygnathus* Lydekker, both of which are probably from the Pinjor stage of the Siwaliks, and *S. pleistocaenicus* Zdansky from China. The Langebaanweg species apparently predates the three Asiatic species and this reduces the likelihood of it being conspecific with any of them.

Unfortunately, the holotypes and most of the referred material of the Asiatic species are mandibles and comparisons with L 10100 are therefore unsatisfactory. Pilgrim (1932) has, however, referred a maxillary fragment with P^4 to *S. potens* and this tooth is similar to the P^4 of L 10100 in some respects. They are comparable in overall size, their protocones are similar in size and position and in both the protocones are linked to the paracones by a ridge of enamel. This ridge is separated from the parastyle by a small hollow in both species, while they also have a similarly shaped paracone. They differ in that the P^4 of *S. potens* has a longer metastyle, which may simply be a more advanced characteristic in this species. The relatively short mandible of *Sivafelis* is matched by the short maxilla of the Langebaanweg species.

There are, therefore, grounds for believing that L 10100 belongs to a species of *Sivafelis*, but one which is more primitive than the early Pleistocene *S. potens*.

In his discussion of *Sivafelis*, Pilgrim (1932) did not consider the possibility of its relationship to *F. caracal*. On the basis of size alone, such a relationship does at first sight seem rather improbable. There have, however, been some very marked size changes in other felid lineages and the size factor is not necessarily significant. It is thus possible that *F. caracal* stems from *Sivafelis* rather than from *F. issiodorensis* as was suggested earlier. The phyletic relationships of the lynxes, *Sivafelis* and L 10100 are therefore not altogether unequivocal and the Langebaanweg species is named accordingly.

A possible explanation of the available record is that the dichotomy of the *Felis* (*Caracal*) and *Felis* (*Lynx*) lineages took place earlier than the late Pliocene and the *Sivafelis* group was ancestral to *F.* (*Caracal*), while the true lynxes arose from *F. issiodorensis*, which is here taken to include the smallest of the Langebaanweg felines (Fig. 35).

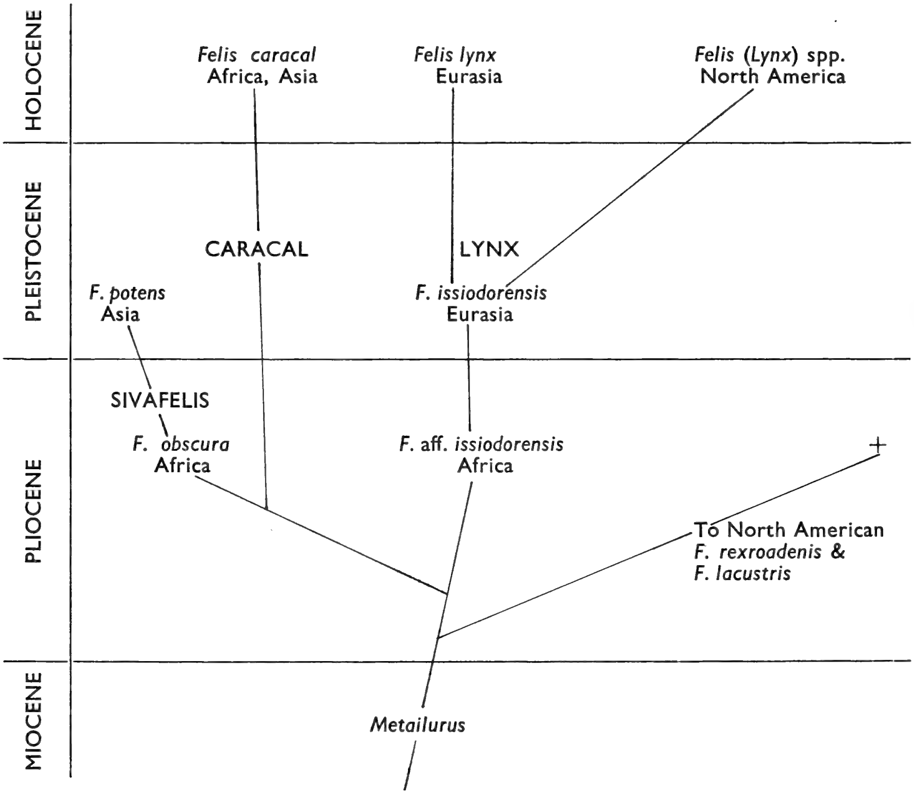

Fig. 35. Tentative phylogeny of some small- to medium-sized Felidae.

In the same way that the late Pliocene/early Pleistocene *Vishnuictis* was earlier suggested to be a subgenus of *Viverra*, so *Sivafelis* is here regarded as a contemporaneous subgenus of that group of felines commonly termed the lynxes. L 10100 is thus classified as *Felis* (*Sivafelis*) *obscura*.

Family **Felidae**

Subfamily Felinae

Dinofelis diastemata Astre, 1929

(Figs 36, 37, 38; Hendey 1970*a*: pl. 2D)

Material from Bed 2, 'E' Quarry, Langebaanweg

L 20284—Isolated right $\underline{C}$; left and right mandibles with $\overline{C}$ to M_1.

L 20685—Isolated left and right $\underline{C}$, right $\overline{C}$ and M_1; left mandible lacking incisors and P_3; associated with both clavicles, several ribs and vertebrae, some of which are intact, a few fragmentary long bones and a number of carpal and tarsal bones, metapodials and phalanges.

L 20702—Left $\underline{C}$.

Material from Bed 3a, 'E' Quarry, Langebaanweg

L 12237—Left mandibular fragment with P_4 and M_1.

Material from 'E' Quarry, but of unknown provenance

L 2674—Parts of a skull, including left maxillary fragment with $\underline{C}$ and right maxillary fragment with P^3 to M^1.

Description

This material belongs to a felid which is approximately the same size as the Langebaanweg *Machairodus*, and one which has some machairodont characteristics, although it is undoubtedly a feline.

Skull (Tables 33, 34)

The Bed 2 specimens L 20284, represent parts of a single skull. The isolated $\underline{C}$ is far larger than the canines of the mandible and superficially it bears a remarkable resemblance to the $\underline{C}$ of the Langebaanweg *Machairodus* (L 20505), differing only in that it is slightly broader and in lacking serrations on the prominently developed keels. It has a crown height of about 50 mm and the overall length of the tooth along its anterior curve is about 120 mm. By contrast, the crown height of the $\overline{C}$ is only 25 mm. Thus in respect of the development of its canines this species is comparable to machairodonts, although the diametrical index of the $\underline{C}$ (0,63), while being less than that of modern felines, is greater than that of most machairodonts (see Ewer 1955*c*: Table 3). The enamel of this tooth in the vicinity of the keels and on the buccal surface is finely rugose.

The $\underline{C}$, L 20702, is similar in all observable respects to that of L 20284, although it is less well preserved. The anterior and posterior keels were worn

Table 33

Dimensions of the upper teeth of the Langebaanweg *Dinofelis*, compared with those of *Dinofelis* from other localities.

		Dinofelis diastemata[1]	Langebaanweg				*Dinofelis barlowi*[2]		*Dinofelis piveteaui*[2]
			L2674	L20685	L20284	L20702			
$\underline{C}$	l	—	*c.* 19,0	19,6	20,8	*c.* 21,5	*c.* 24,0	24,4	20,5
	b	—	—	10,6	13,1	*c.* 13,2	*c.* 15,0	14,8	12,1
	l:b	1 :0,54	—	1 :0,54	1 :0,63	1 :0,61	1 :0,62	1 :0,61	1 :0,59
Postcanine diastema		—	4,5	—	—	—	9	—	—
P^3	l	21	19,5	—	—	—	21,5	*c.* 20,0	19,8
	b	—	*c.* 8,5	—	—	—	*c.* 11,3	—	10,0
P^4	l	29	*c.* 29,0	—	—	—	36,2	37,4	41,0
	b	—	*c.* 14,0	—	—	—	16,5	16,8	13,0
M^1	l	—	4,5+	—	—	—	6,8	—	alveolus 4,5
	b	—	9,0+	—	—	—	11,1	—	4,7

[1] Piveteau 1948.
[2] Ewer 1955.

during life, the apex of the crown is lost and the tooth is cracked longitudinally.

The right half of the mandible of L 20284 is the more complete and it lacks only the most posterior parts, including the angular process and condyle. The coronoid process is very high and typically feline in this respect, while in marked contrast to the condition in machairodonts. The symphyseal region of the mandible is, however, similar in structure to corresponding parts of the mandible of the Bed 2 machairodont. The post-canine diastema is relatively long and a small metal flange is present. The symphyseal regions of the mandibles of the two species differ mainly in that in the machairodont it is broader, higher and more stoutly developed.

The narrower mandibular symphysis in L 20284 is due to the fact that the incisors of this species were much smaller than those of the machairodont. Although these teeth have been lost, parts of the three alveoli are visible in the left half of the mandible and all were clearly far smaller than the $\bar{C}$. This species differs markedly from machairodonts in this respect.

The $\bar{C}$ of L 20284 is less transversely compressed than the $\underline{C}$ and, while it does have a prominent posterior keel, the anterior edge of the tooth is rounded. The 'anterior' keel is rotated on to the lingual surface, where it terminates in a bulge on the cingulum at about midway along the length of the tooth.

TABLE 34

Dimensions of the mandibles and lower teeth of the Langebaanweg *Dinofelis*, compared with those of *Dinofelis* from other localities.

		Dinofelis diastemata[1,2]	Langebaanweg			*Dinofelis barlowi*[3]		*Dinofelis piveteaui*[3]
			L20284	L20685	L12237			
$\overline{C}$	l	15,0	14,6	12,9	—	—	16,5	—
	b	10,5	11,1	9,5	—	—	10,0	—
Postcanine diastema		27,0	*c.* 27,0	*c.* 21,0	—	—	21,0	—
P_3	l	16,0	14,6	—	—	16,1	12,2	—
	b	—	7,2	—	—	8,7	7,1	—
P_4	l	23,0	22,4	20,6	20,7	24,7	21,4	23,7
	b	—	9,6	8,7	8,7	11,4	10,0	11,4
M_1	l	23/24	23,9	23,0	23,9	*c.* 26,0	25,9	27,7
	b	—	11,5	10,2	10,4	*c.* 14,0	11,6	16,9
P_3–M_1	l	60,0	58,9	*c.* 55,0	—	—	—	—
Max. height of ramus (coronoid process to inferior margin)		—	*c.* 88,5	73,5	—	—	—	—
Mandible height below M_1		—	*c.* 34,0	30,2	—	—	—	35,2
Mandible breadth below M_1		—	*c.* 18,5	16,5	—	—	—	18,7

[1] Astre 1929.
[2] Piveteau 1948.
[3] Ewer 1955.

The cheekteeth are typically feline in character. The P_3 is much smaller than P_4 and has a prominent principal cusp, a posterior accessory cusp flanked by a well developed posterior cingulum, while there is a shelving of the anterior end of the tooth where the anterior accessory cusp would have been situated if present. The P_4 is relatively long and narrow and, except for the presence of a prominent anterior accessory cusp, its structure is similar to that of P_3. The M_1 is the largest of the cheekteeth and is made up only of the paraconid and protoconid, although vestiges of a talonid are still evident. The paraconid blade (6,5 mm) is far shorter than the protoconid blade (12,3 mm).

The specimens L 20685 belong to an individual which was appreciably smaller than that represented by L 20284, the size difference perhaps reflecting sexual dimorphism in the species. Otherwise the material is essentially similar

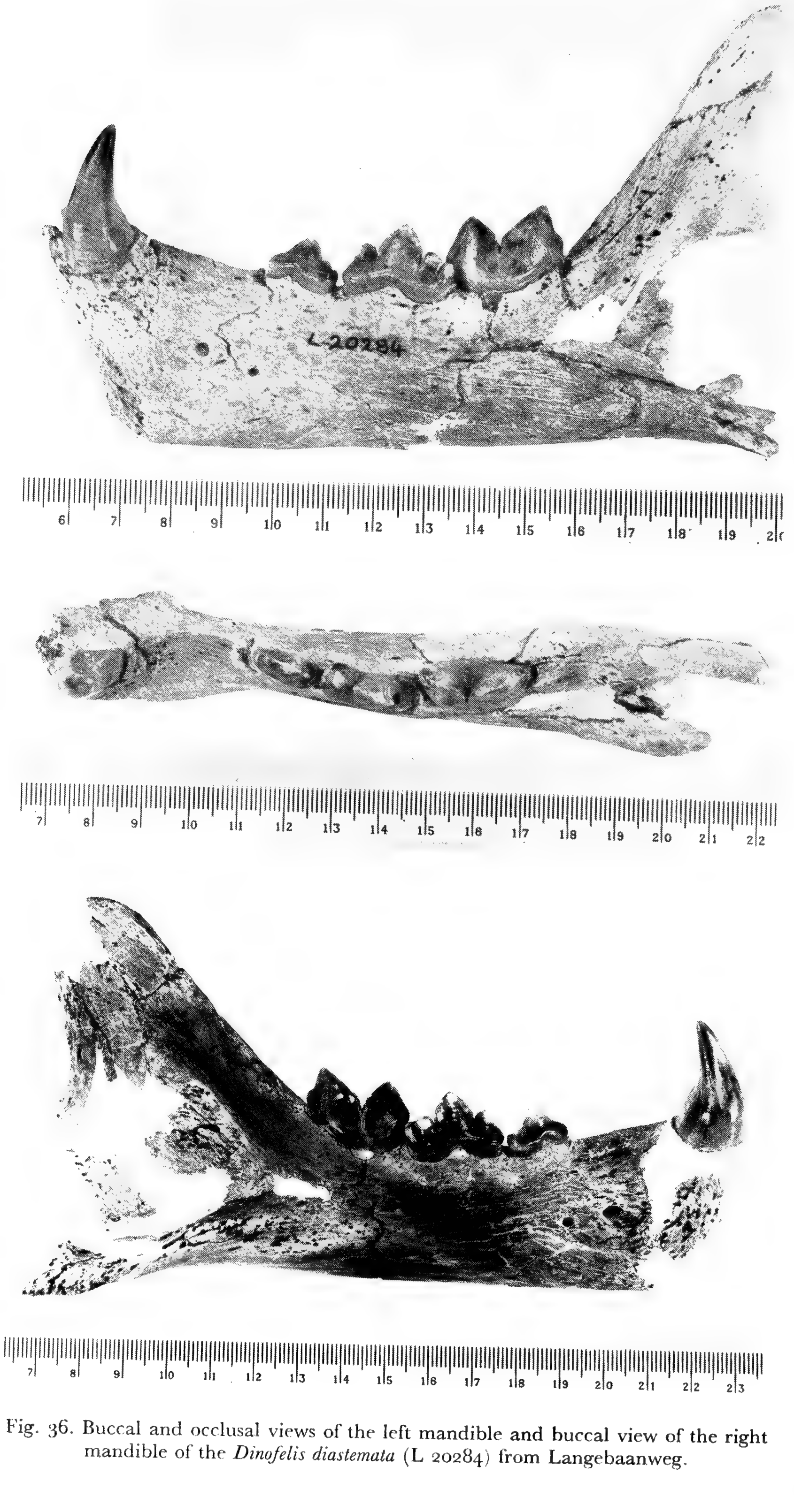

Fig. 36. Buccal and occlusal views of the left mandible and buccal view of the right mandible of the *Dinofelis diastemata* (L 20284) from Langebaanweg.

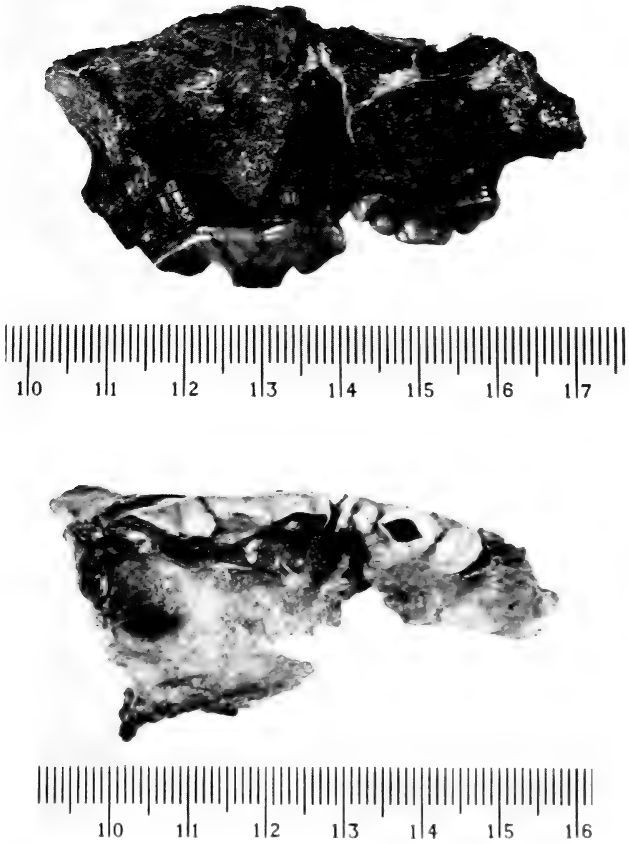

Fig 37. Buccal and occlusal views of the *Dinofelis diastemata* maxilla (L 2674) from Langebaanweg.

in all observable respects to that already described, although the $\underline{C}$ has a lower diametrical index than either of the other two specimens.

The Bed 3a mandibular fragment (L 12237) is similar to corresponding parts of the mandibles from Bed 2 and compares most closely in size with L 20685. This specimen lacks P_3, but the bone surface anterior to P_4 is scarred, which suggests that P_3 was lost during life. The P_3 of the preserved left half of the mandible of L 20685 is also missing, although in this instance the alveolus is still open. There are, however, indications of periodontal disease at the site of P_3 with alveolar recession and an overgrowth of bone on the buccal surface of the mandible. Consequently, this tooth might also have been lost during life even though there are no indications of alveolar resorption.

The unprovenanced material (L 2674) belongs to an aged individual and

Fig. 38. Buccal view of the upper canines of *Dinofelis diastemata* (L 20284), *Machairodus* sp. (L 20505) and cf. *Homotherium* sp. (L 11846) from Langebaanweg.

is very fragmentary. The preserved $\underline{C}$ is incomplete and is crushed so that its dimensions cannot be accurately measured. The post-canine diastema is very short and both P^1 and P^2 are absent. The P^3 is similar in morphology to the P_4 of the Bed 2 and Bed 3a mandibles.

Detailed observations on the characteristics of the P^4 of L 2674 are hampered by the fact that this tooth is very worn. The apices of all cusps have been worn away and the buccal surface of the paracone is damaged. The paracone is the most prominent of the cusps and is a little longer than the metastyle, which in turn is a little longer than the parastyle. A small 'ectoparastyle' is present and in relative size and position it resembles that of the *Felis obscura* holotype. The protocone is largely worn away, but it was evidently a fairly prominent cusp situated adjacent to the notch between the parastyle and paracone.

The crown of M^1 is completely worn away, the wear facet being oval in shape with its long axis at right angles to that of P^4. The single, transversely elongated root bifurcates near its base.

Postcranial skeleton (Tables 35 to 38)

The postcranial remains of L 20685 were compared with corresponding parts of the skeletons of two modern leopards (*Panthera pardus*) and two cheetahs (*Acinonyx jubatus*). In general the fossil bones were larger than those of the leopards, although of similar proportions and therefore readily distinguishable from the bones of the cheetahs.

The preserved vertebrae include three thoracics and five caudals. The former are unremarkable being most similar to those of the cheetahs in size, but the caudal vertebrae are appreciably shorter than those of the comparative specimens. It was not possible to identify the positions of the fossil caudal vertebrae, but three of them correspond morphologically most closely to the 6th to 10th caudals of the comparative specimens. A comparison of the lengths of the available fossil and modern specimens shows that the former are only about 60% of the length of the leopard caudals and about 50% of those of the cheetah (Table 35).

TABLE 35

Lengths of the caudal vertebrae of the Langebaanweg *Dinofelis* compared with those of modern *Panthera pardus* and *Acinonyx jubatus*.

		a	b	c	Mean
Dinofelis	L20685	20,5	23,4	26,4	23,4

		6th	7th	8th	9th	10th	Mean
Modern *Panthera pardus*	SAM 36051	34,7	37,2	39,5	40,3	39,9	38,3
	SAM 36324	34,0	37,3	40,0	41,2	41,1	38,7
Modern *Acinonyx jubatus*	SAM 36703	45,3	49,2	51,4	51,6	51,2	49,7
	SAM 36704	43,0	46,5	48,6	50,0	49,8	47,6

Parts of at least nine ribs were recovered and of these three are largely intact, while both clavicles, one of which is complete, are preserved. Damage to ribs and vertebrae is largely of recent origin and resulted from plant growth in the area where the skeleton was buried. The completeness of these relatively delicate bones and of elements of the manus and pes is in marked contrast with the fragmentary condition of the long bones, some of which have been burnt.

Only the left ulna was recovered reasonably intact, although it is very poorly preserved, while the proximal end and part of the shaft of the right tibia and the complete right fibula were restored from a number of fragments found over an area of several square metres. These bones, and parts of both radii, are appreciably larger than corresponding elements in the two modern leopard skeletons. The articular surfaces of the fossil bones are, in some instances, similar in size to those of the cheetahs, although they are otherwise more stoutly proportioned. The few measurements possible on these bones are listed in Table 36.

TABLE 36

Dimensions of some elements of the postcranial skeleton of the Langebaanweg *Dinofelis* compared with those of modern *Panthera pardus* and *Acinonyx jubatus*.

		Radius		Tibia	Fibula			
		Ant.-Post. diam. prox. end	Trans. diam. prox. end	Trans. diam. prox. end	Overall length	Ant.-post. diam. prox. end	Ant.-post. diam. dist. end	Trans. diam. dist. end
Dinofelis	L20685	20,0	26,4	*c.* 53,8	*c.* 213,0	24,6	16,8	14,7
Modern *Panthera pardus*	SAM 36051	14,5	20,0	42,9	198,0	14,3	16,6	8,1
	SAM 36324	12,9	19,0	39,8	191,0	14,1	15,0	7,9
Modern *Acinonyx jubatus*	SAM 36703	16,7	21,7	51,8	280,0	19,9	17,5	9,2
	SAM 36704	16,7	22,3	51,5	270,0	20,5	19,0	9,6

Parts of all four feet were recovered and the various elements are mostly complete and well preserved. A few exhibit a pathological condition (osteitis). Apart from the fact that they are appreciably larger than the corresponding bones of the leopards, they are otherwise similar in both morphology and proportions, although perhaps somewhat more stoutly built. In respect of their proportions they are clearly distinguishable from the generally elongated foot bones of the cheetah which have been adapted for cursorial locomotion. The dimensions of some of the elements of the manus and pes are given in Table 37.

The fossil species differs from both the leopard and cheetah in respect of the relative size of its fore- and hindfeet. This is illustrated by a comparison of the relative lengths of the metapodials II of the three species (Table 38).

The Langebaanweg *Dinofelis* was evidently a heavily built animal, with the fore- and hindfeet, and perhaps the limbs in general, being more equally proportioned than in either the leopard or cheetah, and possessing a relatively short tail. Its locomotion is likely to have been ambulatory. The indications are thus that it had paralleled the developments in the Machairodontinae in its postcranial skeleton as well as the skull.

TABLE 37

Dimensions of elements of the manus and pes of the Langebaanweg *Dinofelis* (L20685).

	Metacarpal I	Metacarpal II	Metacarpal III	Metacarpal V	Metatarsal II	Metatarsal IV	Metatarsal V
Overall length	25,8	70,5	78,4	60,2	80,9	90,8	80,8
Max. ant. post. diam. at prox. end	13,2	18,4	16,3	14,9	18,0	19,3	12,2
Max. trans. diam. at prox. end	16,9	14,0	16,0	12,5	10,5	15,8	16,0
Max. ant. post. diam. at distal end	13,7	14,3	14,3	13,8	14,3	14,3	13,1
Max. trans. diam. at distal end	15,4	12,6	13,4	12,8	13,1	12,7	12,0

	Calcaneum	Astragalus	Navicular	Cuboid
Overall length	70,9	37,2	—	19,6
Max. dorso-ventral diam.	30,8	21,3	26,5	18,3
Max. trans. diam.	33,2	33,4	19,3	17,8

TABLE 38

Length ratios of metacarpal II and metatarsal II of the Langebaanweg *Dinofelis* compared with those of modern *Panthera pardus* and *Acinonyx jubatus*.

		Mc II length	Mt II length	Mc II : Mt II
Dinofelis	L20685	70,5	80,9	1 : 1,15
Modern *Panthera pardus*	SAM 36051	56,3	71,8	1 : 1,28
	SAM 36324	57,5	70,6	1 : 1,23
Modern *Acinonyx jubatus*	SAM 36703	79,4	106,8	1 : 1,35
	SAM 36704	76,4	102,6	1 : 1,34

Discussion

These specimens clearly belong to a 'false sabre-toothed cat' in that group of felids referred to *Dinofelis* Zdansky by Hemmer (1965). Included in this group are three species which were previously referred to the genus *Therailurus* Piveteau, namely, the European *D. diastemata* Astre, 1929, *D. barlowi* Broom, 1937 from Sterkfontein and *D. piveteaui* Ewer, 1955 from Kromdraai.

In the study of this group, Hemmer (1965: 75) arrived at the following conclusions:

> 'The most primitive species concerning the specialization of the teeth is *Dinofelis diastemata* (Astre 1929), the most evolved is *Dinofelis piveteaui* (Ewer 1955) and by parallel evolution *Dinofelis abeli* Zdansky 1924. *D. diastemata—D. barlowi—D. piveteaui* form a connected succession whilst *D. abeli* takes a more isolated place.'

The Langebaanweg *Dinofelis* evidently has its affinities with the *D. diastemata—D. piveteaui* series.

The European species is Astian in age and is, therefore, broadly contemporaneous with the Langebaanweg material, while the two recorded South African species date from the Makapanian. Consequently, because of geographical factors, it might be expected that the Langebaanweg species would have close phyletic links with *D. barlowi* and *D. piveteaui*, but because of its age it would be at a stage in evolutionary development comparable to *D. diastemata*. This hypothesis was found to conform quite well with the nature of the various specimens available.

Ewer (1955*c*: 598) expressed doubts as to whether *D. piveteaui* could have been directly descended from *D. diastemata* because of the low $\underline{C}$ diametrical index of the European species, although in other respects '(*Dinofelis*) *piveteaui* is considerably more advanced than (*D.*) *diastemata*.' As Ewer was dealing with only one specimen from each population no account could be taken of the possible range of variation in this particular character. In fact the range of the diametrical indices of the three specimens from Langebaanweg (0,54 to 0,63) actually exceeds that observed in the four specimens of the three previously recorded species (0,54 to 0,62). Possibly when larger samples of the three species become available, it will be found that their mean diametrical indices do differ, but this is clearly not a reliable differentiating characteristic at present and it cannot be used as a basis for determining phyletic relationships.

In all other observable respects the Langebaanweg *Dinofelis* is apparently more similar to *D. diastemata* than to the Transvaal species. Probably the most obvious character which differentiates the Pliocene specimens from those of the Pleistocene is the relative sizes of their carnassials. These teeth are longest in *D. piveteaui*, the most recent of the species, a little shorter in *D. barlowi*, and shortest in the Langebaanweg *Dinofelis* and *D. diastemata* from Europe.

There are actually no grounds for believing that the Langebaanweg *Dinefelis* and the European *D. diastemata* are not conspecific and consequently the former is identified accordingly. The suggested phyletic relationships of the various species are illustrated in Figure 39.

The characteristics of *Dinofelis* are yet another indication of the felid propensity for developing the 'sabre-tooth' condition. Although the *Dinofelis* experiment in this direction was not carried to the extreme evident in the three sabre-toothed cat subfamilies (Hoplophoneinae, Nimravinae, Machairodontinae—see Thenius 1967), it too was ultimately unsuccessful. The development of 'sabre' canines by a member of the subfamily Felinae is not confined to *Dinofelis,* since a similar development is evident in the extant clouded leopard of Asia (*Neofelis nebulosa*).

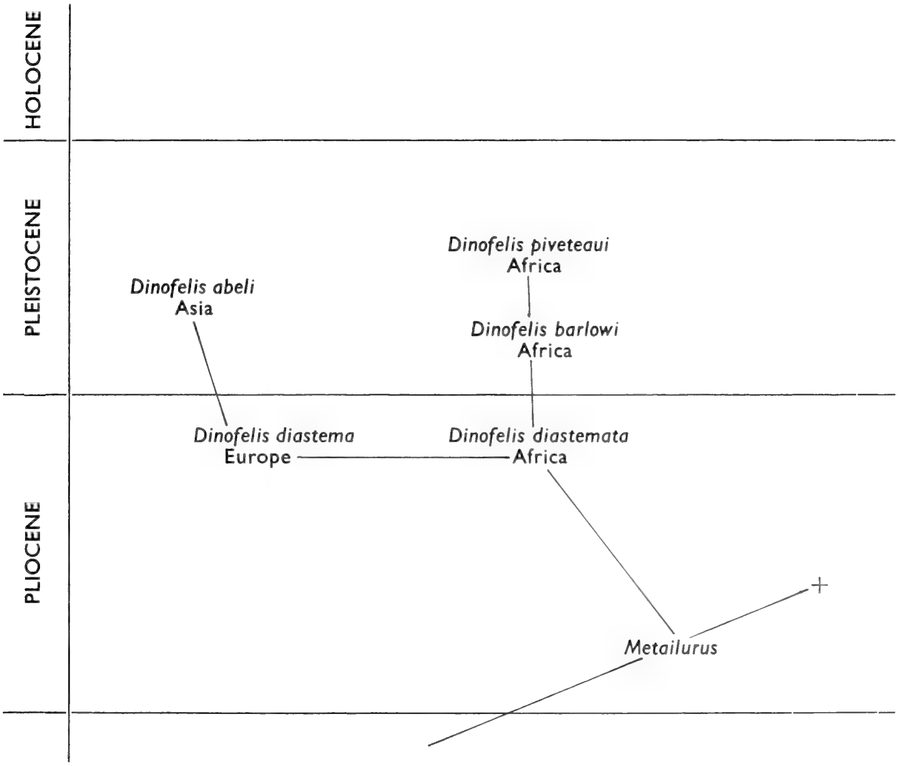

Fig. 39. Tentative phylogeny of the genus *Dinofelis*.

Suborder FISSIPEDIA
Incertae sedis
(Fig. 40)

Material

L 11752—Right maxillary fragment with $\underline{C}$ and two premolars (? P^1 and P^2).
L 12273—Left maxillary fragment belonging almost certainly to the same individual as L 11752.

Locality and horizon

These specimens are from Bed 2, 'E' Quarry, Langebaanweg.

Description

The specimen L 11752 comprises the most anterior part of a right maxilla to which part of the premaxilla is fused. The alveoli of I^2 and I^3 are present, the $\underline{C}$ is damaged and the first two premolars are preserved intact. The anterior rim of the orbit is damaged. The second specimen is only a small part of the left maxilla in which the anterior part of the orbit and immediately adjacent areas are preserved. The preservation of the two specimens is identical and they are essentially similar in the features which are observable. Although they were not found at the same time, it is probable that they do belong to the same individual.

The species concerned is of large size, the canine being comparable to that of modern *Crocuta*, but the snout is extremely short and the two premolars much reduced in size (Table 39). Although only two incisor alveoli are preserved, this species almost certainly had I^1 as well. Nothing is known of the nature of the posterior cheekteeth.

TABLE 39

Dimensions of the upper teeth and facial region of the unclassified fissiped carnivore from Langebaanweg (L 11752).

I^3 (alveolus)		$\underline{C}$		?P^1		?P^2	
l	b	l	b	l	b	l	b
c. 13,8	*c.* 7,9	*c.* 20,0	12,4	6,2	6,0	6,0	*c.* 5,3

Distance between I^3 anterior alveolar margin and infra-orbital foramen—*c.* 50,0

The infra-orbital foramina are unusual in that both are divided into two more or less equally sized parts. In the right maxilla there are two distinct foramina, but in the left there is a single external opening which divides internally. In the fairly comprehensive collection of skulls of modern Carnivora examined in the course of the present study, the only species in which a comparable development of the infra-orbital foramen was observed was *Proteles cristatus*. In a series of six *Proteles* skulls, two had both infra-orbital foramina as single openings, two had one single and one double opening, and two had both as double openings.

Discussion

The large canine and reduced anterior premolars of this species are reminiscent of the condition in many ursids, but the snout of the fossil is even shorter than that of such short-faced forms as *Helarctos malayanus*. Furthermore, the P^4 of the fossil must have been situated posterior to the infra-orbital foramen, whereas in the ursids this tooth is always situated anterior to the foramen. The fossil is almost certainly not an ursid and the specimens definitely do not belong to the Langebaanweg *Agriotherium africanum.*

The nature of the infra-orbital foramina and reduced cheekteeth suggested that the fossil might represent a primitive form of *Proteles*. L 11752 is, however, far larger than corresponding parts of the skull of modern *P. cristatus* and the premolars are more complex than the simple peg-like cheekteeth of *P. cristatus*, being more circular in shape with a more prominent internal cingulum flanking a lower and blunter principal cusp. In addition, the ? P^2 is a little smaller than the ? P^1, whereas in *P. cristatus* the second postcanine is larger than the first. On the other hand, the fossil premolars are not dissimilar to the P^1 of Hyaeninae and since *Proteles* is evidently descended from an early hyaenid, it was thought possible that the premolars of L 11752 might represent an early stage in the development of *Proteles* cheekteeth. Had L 11752 been found without the second reduced premolar, and if the greatly foreshortened snout had not been evident, then it might well have been identified as belonging to a hyaenid.

Although the structure of the infra-orbital foramina of *Proteles* and the fossil is similar, in the former this foramen is situated above or slightly posterior to the third postcanine, whereas in the fossil it is a little posterior to the ? P^1. The snout of the fossil is, therefore, relatively much shorter than that of *Proteles*.

Apart from the obvious size and morphological differences between the fossil and *Proteles*, a relationship between the two might also be doubted on purely theoretical grounds. *Proteles* has an extremely poor fossil record, but it is known from the Makapanian, being represented by a single mandibular fragment from Kromdraai, which differs from the moderns in only a few respects. The implication is that for much of the Pleistocene at least, *Proteles* was represented by forms which were not very different from that which is still extant (Hendey 1973*a*). It would therefore be surprising if the Makapanian *Proteles* was descended from so large a Langebaanian species as that represented by L 11752. Its derivation from a small form such as the Pontian *Ictitherium orbignyi* (see Thenius 1966) is far more likely.

Another carnivore family with which the fossil was compared was the Mustelidae. A shortened face and reduced anterior cheekteeth are characteristics of the Lutrinae and since a large otter, *Enhydriodon africanus*, is included in the 'E' Quarry assemblage, L 11752 was first compared with this species. The *E. africanus* mandible (L 9138) has very crowded anterior cheekteeth, whereas L 11752 has a postcanine diastema of 8 mm and gaps of 2 mm and 3 mm between the first three cheekteeth. The two specimens are clearly not conspecific and judging from the size of the $\underline{C}$, L 11752 belonged to a species even larger than *E. africanus*. The modern Lutrinae, *Aonyx*, *Enhydra* and *Lutra*, also have crowded anterior cheekteeth and are very much smaller even than *E. africanus*, so that there is clearly not a close relationship between them and L 11752 either.

Fig. 40. Occlusal and buccal views of the unidentified fissiped carnivore maxilla (L 11752) from Langebaanweg.

Although it seemed unlikely that the fossil species was an otter, Pilgrim (1932: 80, 81; pl. 17) has described a maxillary fragment from the Dhok Pathan stage of the Siwaliks (GSI D 207) which is similar to L 11752 in some respects, and which he believed belonged 'to an animal of Lutrine lineage which had specialized earlier than *Enhydriodon*, but along somewhat similar lines'. According to Pilgrim it had 'obviously remained closer to *Potamotherium*'.

Unfortunately the premaxilla, orbit and infra-orbital foramen of the Indian specimen are lost, but it is similar to L 11752 in that it has 'an exceptionally large' canine and its 'P^2 has a circular crown due to the presence of a marked internal cingulum'. It differs from L 11752 in that it lacks P^1 and has a very short postcanine diastema. The $\underline{C}$ of the Indian specimen is smaller (16,8 × 10,5 mm) than that from Langebaanweg, but the P^2 (6,2 × 5,7) is similar in size. The P^3 of D 207 is a fairly large tooth (13,4 × 7,7 mm). It is possible that the two premolars of L 11752 are in fact P^2 and P^3 and, if so, it could represent a more advanced form of the unnamed Dhok Pathan species in which P^3 was much reduced in size. Alternatively, it might be a representative of an African lineage which had an ancestor in common with that which includes the Dhok Pathan species.

It is unlikely that L 11752 and D 207 are conspecific, but they could be congeneric. Certainly of all the recorded late Cenozoic Carnivora, D 207 appears to be the one which is most likely to be related to the problematical Langebaanweg species.

Particular interest is attached to L 11752 and the companion specimen, since if they are lutrine, it means that there are two large otters represented in the Langebaanweg assemblage and not just *Enhydriodon.* In addition, these specimens probably belong to a genus which is as yet unnamed and if more specimens can be found which would determine conclusively the relationships of this animal, it would be another significant addition to the late Cenozoic fossil record.

All that can be said of the specimens at present is that they belong to a poorly known species, which may belong in a group of otters descended from *Potamotherium.*

Suborder FISSIPEDIA

Unclassified specimens

The Langebaanweg assemblage, including that from 'C' Quarry, includes carnivore specimens in addition to those already listed. Most of this material, which is made up of relatively few specimens, is at least classified to the family level and it is likely that most, if not all the specimens belong to species already listed. Cranial remains make up only a small proportion of the unclassified material and consist mostly of tooth fragments. Carnivore postcranial remains from Langebaanweg are usually found dissociated from more readily identifiable skull parts. In the case of the pinniped no problem in identification has arisen as there is evidently only one species represented, but the same does not apply to the fissiped postcranial remains.

The only fissiped species which has had elements of the postcranial skeleton positively identified even though they were not found associated with skull parts in *Agriotherium africanum.* This species is readily distinguished from others by its very large size. Viverrid, hyaenid and felid postcranial bones are not uncommon and although some have been identified with particular species, they were excluded from the relevant specimen lists because such identifications were not positive. There is no point at this stage in possibly confusing the issue on the nature of the postcranial skeletons of certain species. As more definite associations of skull and postcranial bones are discovered, it should become possible to positively identify unassociated postcranial remains and their description can be left to some future date. The same attitude was adopted in the case of the Quaternary Carnivora.

Reference has already been made to pathological conditions evident in some of the carnivore skeletal remains from Langebaanweg and there are other such examples amongst the unclassified material. Although past palaeopathological studies have been largely confined to hominid remains, there is a growing interest in this subject as it relates to other mammals as well. For this reason, and also because bone pathology is apparently more common amongst the Carnivora than it is in other mammals from Langebaanweg, some account was taken of those bones which show obvious indications of abnormal conditions. Only two such conditions were recognized, namely, osteitis and osteo-arthritis, the latter indicating diseases of the joints and the former indicating all other bone inflammations (see Brothwell 1963). Specimens not already mentioned include:

L 6388 —Right tibia (? *Machairodus*). Osteitis, mainly near the proximal end. Osteo-arthritis at the proximal end, with severe eburnation of the lateral articular facet and lipping of the bone (Fig. 41).
L 6422 & L 6425—Left and right calcanea (? *Machairodus*). Osteitis on lateral surfaces anterior to distal extremity.
L 6430 —Metapodial (? *Machairodus*). Osteitis on dorsal surface. Osteo-arthritis (eburnation) of distal articular facet.

The above four specimens may belong to a single individual.

L 9868 & L 9869—Proximal end of left ulna and distal end of left humerus (? *Machairodus*). Severe osteitis on lateral and medial sides of ulna and a less extensive but similar condition on the humerus, particularly the arch enclosing the entepicondylar foramen (Fig. 41).
L 6391 —Distal end of right tibia (? *Machairodus*). Severe osteitis on the shaft.
L 6409 —Proximal end of left humerus (? *Machairodus*). Extensive osteitis.
L 6403 —Distal end of left humerus (Hyaenidae). Osteitis of the supratrochlear fossa.
L 9884 —Left radius lacking distal epiphysis (? *Machairodus*, immature). Severe osteitis on the shaft.
L 12642—Metapodial (? *Agriotherium*). Osteitis, possibly resulting from a fracture. The shaft is bowed and thickened, the inflammation being largely confined to the thickened part.

Pathological conditions in the postcranial skeletons of the *Hyaenictis preforfex* holotype and the *Percrocuta australis* specimen, L 13033, have already been mentioned and in both these instances the conditions may relate to the advanced age of the individuals concerned.

Fig. 41. Pathological conditions in carnivore postcranial bones from Langebaanweg. Tibia (L 6388) showing eburnation and bony lipping (osteo-arthritis) of the proximal end. Ulna (L 9868) showing osteitis at the proximal end and on the shaft.

There are two points worth noting about the specimens listed above. Firstly, although relatively few individuals are represented, most of the specimens are tentatively identified as belonging to a machairodont. Secondly, both immature individuals and adults of this species are afflicted by osteitis, indicating that it was not necessarily an age-related condition. On the other hand, the osteo-arthritis may well have been related to advanced age.

Carnivora of the Pleistocene and Holocene

Although there are more carnivore species recorded from the Quaternary of the south-western Cape than from the Pliocene, none of the individual fossil assemblages matches that from 'E' Quarry in the variety of species represented. The most prolific of the local Quaternary occurrences is Elandsfontein and it is also this site which has yielded the largest number of carnivore species, namely, fifteen, as against twenty from Langebaanweg. The list of Quaternary species is lengthened by those which have been recorded during the historic period, but which are not known locally as fossils.

The Quaternary carnivores are less problematical than those from Langebaanweg since, with few exceptions, they are closely related to species which are still extant, and their identification was facilitated by comparisons with available osteological material belonging to modern species. In most instances, however, the modern comparative series were small and some of the observations made in respect of the characteristics of certain species may be incorrect.

The local record of Pleistocene mammals is far from complete. Those few species from Baard's Quarry which are regarded as Pleistocene in age, probably date from the earlier part of this epoch. Otherwise it is the Elandsfontein fauna which includes the earliest of the local Pleistocene mammal fossils. The record for the later Pleistocene and Holocene is comparatively good. In other words, the Makapanian fauna is known only from the almost insignificant Baard's Quarry occurrence, the Cornelian is known from one reasonably large assemblage, while only the Florisian and Holocene faunas are quite well known.

Since the early element in the Elandsfontein fauna may date back no more than 0,5 million years (*vide supra*), and the Plio/Pleistocene boundary is here taken at 3,5 million B.P., it means that only about one-seventh of the Pleistocene is represented in the local fossil record by assemblages including appreciable numbers of specimens. It also means that the Pliocene species from Langebaanweg predate the next oldest of the larger local assemblages by perhaps 3,5 million years and it is, therefore, not surprising that the Langebaanweg Carnivora have so little in common with those from the local Pleistocene.

Suborder PINNIPEDIA

Family **Phocidae**

Subfamily Monachinae

Hydrurga leptonyx Blainville, 1820

The leopard seal is an Antarctic species which normally lives on the outer fringes of the pack-ice, but which occasionally strays to the more southerly parts of South America, Africa and Australasia (King 1964). It is not known as a fossil in South Africa, but Roberts (1951) records the landing of a female on the coast about 40 miles north of East London in September, 1946. The only other South African record of this species is from the south-western Cape.

An immature female was found alive on the beach at Hout Bay near Cape Town in October 1969. It subsequently died in a local zoo and its skeleton is preserved in the South African Museum (SAM 35796).

It may be significant that these two specimens reached South Africa during the same season (i.e. the southern Spring). Scheffer (1958) has reported that leopard seals migrate northwards to ice-free islands during Winter and it is possible that in the return migration the following Spring some individuals become disorientated and land as strays far from their normal habitat.

Family **Phocidae**

Subfamily Monachinae

Lobodon carcinophagus Hombron & Jacquinot, 1842

Present status

The crabeater seal is an Antarctic species, but occasional stray individuals have been recorded on other southern continents in recent times.

Material

Sea Harvest, Saldanha

S 1004—Fragment of a right tympanic bulla.

Description

This specimen consists of the greater part of the ectotympanic and lacks only parts of the lateral, posterior and postero-medial margins. It is thick-walled and inflated in a manner which is characteristic of the phocid seals and obviously belongs to a member of this family.

It was compared with the bullae of several extant phocine and all extant monachine genera and in size and its general configuration it is most similar to that of *Lobodon*. The bulla of this, and other southern monachines, does exhibit individual variations in detail and although the fossil differs slightly from the bullae of all the available *L. carcinophagus* specimens ($n = 7$), these differences are no greater than might be expected within a single species.

Discussion

The tympanic bullae of the various phocid genera and, in the present instance, those of the Antarctic monachines in particular, are sufficiently distinct from one another to allow S 1004 to be confidently identified with *L. carcinophagus*. This species, which is the most commonly occurring seal in the Antarctic, has been recorded on the South African coast in recent years. The only two records from the south-western Cape are that of an immature male which came ashore at Gordon's Bay near Cape Town in December 1971 and another which was found nearby at Kalk Bay a month later. The skins and skeletons of these individuals are preserved in the South African Museum (SAM 36357, SAM 36358). Such vagrants are probably more common than the record suggests, since there is little careful reporting of seals landing on the South African coast. Nevertheless, it may be only in certain years that vagrants move as far north as South Africa and the number of individuals concerned is probably never very great.

The Sea Harvest specimen may represent the remains of such a stray, but since the chances of the natural preservation of the modern vagrants is extremely remote, it is possible that the species was more common locally at times in the past when sea temperatures were lower. This possibility is supported by the South African fossil records of two sub-Antarctic seals (*vide infra*).

The inferred early Holocene age of the Sea Harvest fossils suggests that S 1004 might indeed date from a period in time when conditions were colder than at present, or, if not actually colder, when influences of the preceding colder phase (latest Pleistocene) were still in operation. Since relative sea level in the very late Pleistocene was lower than at present, the coastal environments of that time are now all submerged so that there is no record of the locally occurring pinnipeds and the relative numbers of the different species which might have been present cannot be determined. Consequently, it is only the early Holocene record which may give an indication of what pinnipeds did occur locally during the more recent colder phases of the Pleistocene. The Sea Harvest *Lobodon* does suggest that this southern monachine was more commonly represented in the region than it is today and it was possibly still more common during the colder phases of the Pleistocene.

Family **Phocidae**

Subfamily Monachinae

Mirounga leonina Linnaeus, 1758

Present status

The southern elephant seal is a sub-Antarctic species, but occasional stray individuals have been recorded on the South African coast in recent times.

Material

Coastal midden at Ysterfontein (Approximately 33° 21'S, 18° 9'E)

Q 1801A—Edentulous right maxilla.

Description

This specimen is indistinguishable in all observable respects from the maxilla of adult male *Mirounga leonina* from sub-Antarctic regions.

Discussion

Since this species has a more northerly distribution than either the leopard and crabeater seals, it has been more frequently recorded on the South African coast than either of the Antarctic species (see Ross 1969).

Although the age of the Ysterfontein maxilla is not known, it has Late Stone Age associations and because of the nature of the local coastal middens it is most likely to date from the latter half of the Holocene (*vide supra*). Remains of elephant seals are also known from an early Holocene context on the southern Cape coast (Klein 1972), and this occurrence is more important because it is securely dated and the material is more abundant. *M. leonina* still has breeding colonies on the South American mainland (King 1964), and it is possible that there were also permanent colonies on the South African coast during the late Pleistocene and early Holocene. It has already been suggested elsewhere that the decline in the range of *M. leonina* during the Holocene may have at least in part been due to the warming of conditions during this epoch (Hendey 1972*a*).

Family **Otariidae**

Arctocephalus pusillus Schreber, 1776

(Fig. 42)

Present status

The Cape fur seal is still common along the coast of the south-western Cape Province, although its numbers have declined appreciably during the historic period.

Material

(1) *Lime Quarry, Saldanha*

5293A—Left mandible lacking only I_1.
Isolated $\underline{C}$ and three postcanines.
5293B—Right maxilla with $\underline{C}$ and pc^5.
5294 —Left humerus lacking proximal epiphysis.
Right femur lacking both epiphyses.

(2) *Sea Harvest, Saldanha*

S 19, S 259 to S 263, S 1009—Isolated postcanines.
S 214, S 1007, S 1008—Isolated canines.
S 1005—Skull fragment.
S 257 —Left femur lacking both epiphyses.
S 258 —Distal epiphysis of femur (not belonging to S 257).
S 1006—Metapodial lacking proximal epiphysis.

Tentatively referred material

Melkbos

Mb 546—Incomplete distal end of a humerus.

Comment

Reference has already been made to the Melkbos specimen (Hendey 1968), and nothing further can be added to these comments. Cooke (1955: 166) mentioned the Lime Quarry specimens as apparently being 'the first record of the Cape sea lion in the fossil state', but gave no detailed descriptions of this material.

Description

All the specimens listed, with the exception of the Lime Quarry mandible (5293A), are indistinguishable from corresponding parts of the skeleton of extant *Arctocephalus pusillus*.

Apart from the fact that the Lime Quarry mandible differs from that of modern *A. pusillus* in certain respects, it is remarkable because it is so complete. The missing incisor was apparently lost only recently and when it was first discovered this specimen must have been complete in all respects.

Judging from the condition of the teeth and the character of the mandible in general, it probably belonged to a mature adult male. For this reason comparisons were confined to a series of mandibles of adult males of the modern species. The comparative series was made up of 37 specimens, all of which belonged to individuals which had been grouped by Rand (1956) into his categories G, H, J, K, and L (i.e. 'bulls'). These individuals ranged in age from young to very aged adults.

In size and morphology the teeth of the fossil fell within the range of variation observed in the moderns, although the root of the canine was rather large. The same applies in the case of the isolated canine and postcanines from this locality.

The mandibular corpus, although robust, was also within the size range of variation observed in the modern species. There was, however, a consistent difference in the nature of the symphyseal region of the fossil and modern specimens. The former has a prominent 'chin', whereas in the moderns the anterior margin of the symphysis was generally receding. In this respect the fossil most resembled a few aged individuals in the comparative series, but even these specimens differed in that the margin of the symphysis posterior to the 'chin' was longer than in the fossil. The symphysis of 5293A is rather rectangular in outline, but in the moderns it tends to be oval in shape. The presence of a 'chin' in the fossil also has the effect of increasing the surface area covered by the symphysis, so that it is relatively and absolutely greater than in any of the modern specimens. These differences are not clearly reflected by linear measurements, although the fossil symphysis is a little longer than any observed in the moderns (Table 40).

A feature of the mandible of modern *A. pusillus* which is apparently related to the symphysis is an area of rugosity in the bone towards the inferior margin of the corpus immediately posterior to the symphysis. This is presumably the insertional area of a ligament attachment between the two mandibular corpora. It is absent in the fossil. Possibly the larger surface area of the fossil symphysis meant that the additional post-symphyseal attachment which is apparently present in modern *A. pusillus* was not required.

Table 40

Dimensions of the canine and mandible of the Lime Quarry *Arctocephalus pusillus*, compared with a series of modern specimens.

		$\overline{C}$		Length of postcanine row	Overall length of mandible	Overall height of mandible	Height of corpus posterior to pc 5	Transverse diameter of condyle	Symphysis length	Symphysis height
		l	b							
Lime Quarry	5293	*c.* 14,5	10,9	50,4	201	96,5	38,5	50,3	34,0	49,0
Modern *Arctocephalus pusillus*	Mean	14,0	10,4	50,4	191,7	82,3	34,9	42,8	29,0	48,3
	Range	12,5–17,0	9,0–13,0	48,0–54,5	178–206	73,5–94,0	31,6–39,8	39,5–47,1	22,6–33,6	38,5–56,5
	n	28		37	37	37	37	36	37	37

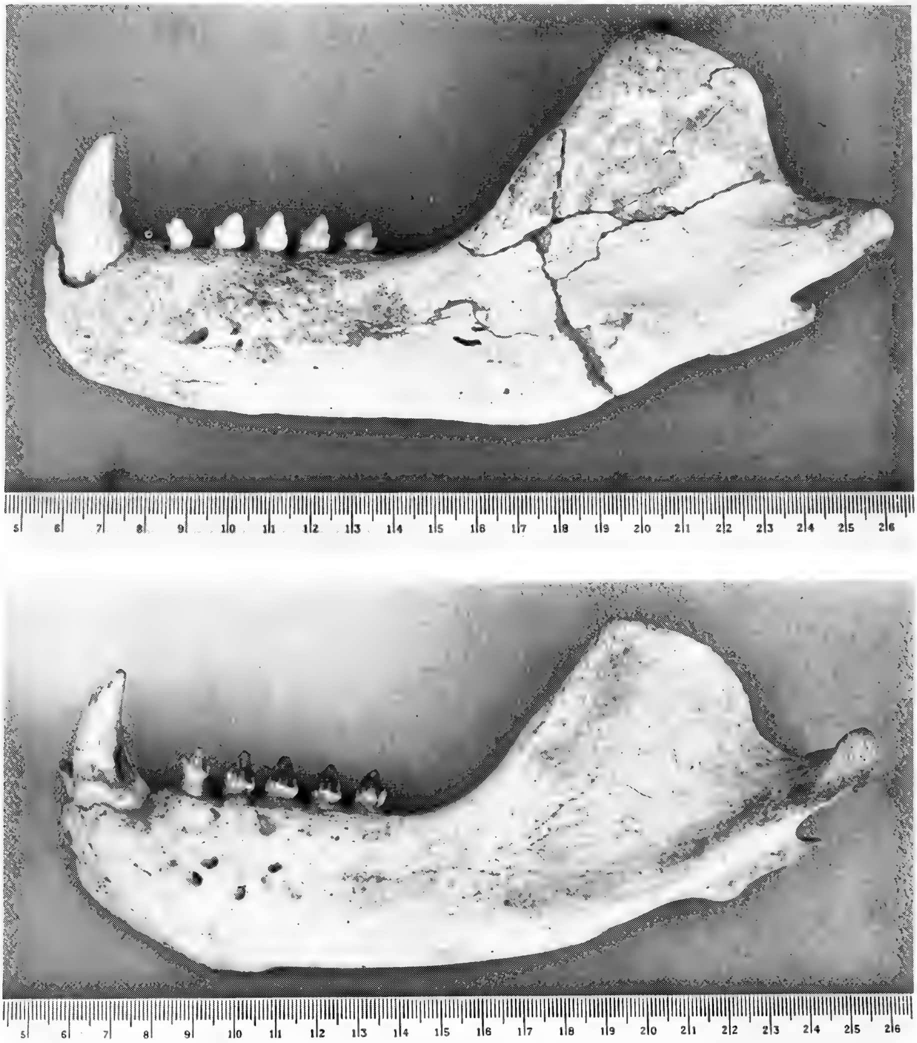

Fig. 42. Buccal views of the *Arctocephalus pusillus* mandible from Lime Quarry, Saldanha (5293A) and a modern specimen (SAM 34640).

The most striking difference between the fossil and modern specimens is in the greater development of the ascending ramus of the former. This is reflected in the greater overall height of the fossil mandible (Fig. 43) and the larger size of the condyle (Fig. 44). The general configuration of the ascending ramus of the fossil is similar to that of *A. pusillus* and the coronoid process is relatively broad and low. However, it resembles *A. australis* in having a deep pterygoid process (see Repenning *et al.* 1971: Fig. 7).

The degree of difference between the fossil mandible and that of modern

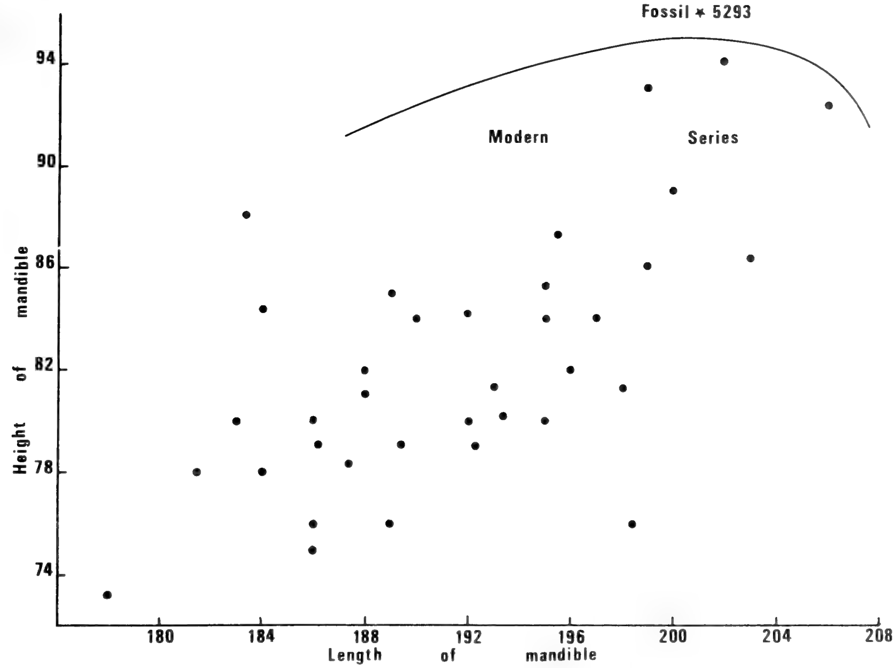

Fig. 43. The dimensions of the mandible of the *Arctocephalus pusillus* from Lime Quarry, Saldanha, compared with those of a series of modern specimens.

A. pusillus is actually greater than is reflected in the metrical data presented here, since the modern specimens to which the fossil is most similar in size are the oldest individuals in the comparative series. Individuals from this series which were judged on the basis of tooth wear and the thickening of tooth roots to be ontogenetically comparable to the fossil specimen are all appreciably smaller (Fig. 42).

The Lime Quarry maxilla (5293B) is evidently that of a female, since it is comparable in size to corresponding parts of the skulls of modern *A. pusillus* females.

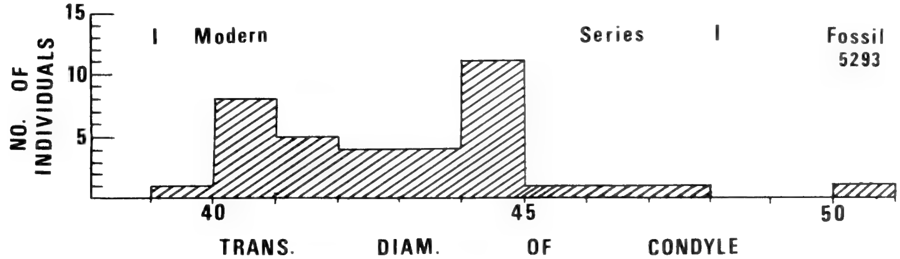

Fig. 44. The transverse diameter of the mandibular condyle of the *Arctocephalus pusillus* from Lime Quarry, Saldanha, compared with those of a series of modern specimens.

The postcranial material belongs to juveniles and so gives no indication of whether or not the individuals were exceptional in size.

The Sea Harvest specimens are similar in all observable respects to modern *A. pusillus*.

Discussion

There can be little doubt that the Sea Harvest and Lime Quarry specimens should be referred to *Arctocephalus pusillus*, although only in the case of the mandible from the latter occurrence need the identification be qualified in any way.

This specimen belonged either to an unusually large individual or to a more or less typical bull of a population in which the average size was greater than that of the moderns. The latter alternative is favoured since it also applied in the case of many other species investigated in the course of the present study.

Although relative size is one of the characters used in distinguishing the modern species of *Arctocephalus* (Repenning *et al.* 1971: 31), it is not a particularly useful criterion when applied to individuals owing to the considerable range of variation in size within any one species. *A. pusillus* is in fact the largest of the modern species and the Lime Quarry *Arctocephalus* is likely to be simply a large temporal variant of the extant species. As such it would at most warrant distinction at the subspecies level.

The problem of whether or not new subspecific names should be applied in the case of large variants of extant species was one which recurred in the present study and it will be discussed in greater detail later. The final decision in this respect is anticipated here and the Lime Quarry material is simply referred to *A. pusillus* without a subspecific distinction being made. The Lime Quarry fauna is regarded as being late Pleistocene in age (*vide supra*), and the seal is distinguished in a provisional manner by being referred to as the 'Florisian *A. pusillus*'.

Arctocephalus is very abundantly represented in local Holocene coastal middens. Those specimens which are in the collections of the South African Museum were acquired as a result of unsystematic collecting and they represent but a small part of what has been, or for that matter, still is available. The specimens which have already been collected were not studied in detail and they are, therefore, not listed.

Family **Otariidae**

Arctocephalus gazella Peters, 1875
&
Arctocephalus tropicalis Gray, 1872

The taxonomy of the fur seals from islands near the Antarctic Convergence has long been problematical and there is still a diversity of opinion as to whether one or two species should be recognized (Repenning *et al.* 1971; Nel 1971).

The importance of these seals in as far as the present study is concerned is that, like other Antarctic and sub-Antarctic species, they have been recorded in South Africa in recent times (Nel 1971) and as post-Pleistocene fossils (Klein 1972). It is largely immaterial in the present instance whether these records are of one species or the other, since they are all from regions beyond the confines of the south-western Cape. However, since sub-Antarctic *Arctocephalus* has been recorded on the South African coast, it is most unlikely that representatives of the group have never landed in the south-western Cape itself.

The fact that they have not been reported locally in recent times may be due to the fact that they would be easily confused with the indigenous *A. pusillus* by casual observation. The *Arctocephalus* remains from local coastal middens have not been critically examined, so it is possible that this material may include species other than *A. pusillus*. It is on these grounds that *A. gazella* and *A. tropicalis* are tentatively listed with the pinnipeds which did, and perhaps still do occur in the south-western Cape.

Suborder FISSIPEDIA

Family **Canidae**

Subfamily Caninae

? *Canis* sp.

Material

Baard's Quarry, Langebaanweg

L 1478—Left mandibular fragment with P_3.

Description

This very incomplete specimen includes the intact P_3 and the alveoli, some with roots of P_1, P_2 and P_4. Only those parts of the mandibular corpus immediately adjacent to the roots of these teeth are preserved. The P_1 to P_4 alveolar length is about 37,5 mm. The P_3 is made up only of the principal cusp and measures 9,9 by 3,9 mm. It falls within the size range of variation of modern *Canis mesomelas* (Table 42), and is essentially similar to the P_3 of this species in other respects as well.

Discussion

Since this specimen is virtually indistinguishable from corresponding parts of the mandible of modern *C. mesomelas*, its identification with the Canidae is reasonably secure and it may in fact be conspecific with this species. However, the positive identification of fragmentary canid remains of this kind is difficult, if not impossible.

Although this specimen may be conspecific with the poorly known canid from 'E' Quarry, it is considered more likely to belong with the Pleistocene element of the Baard's Quarry fauna and it is listed accordingly.

Family **Canidae**

Subfamily Caninae

Canis mesomelas Schreber, 1775

(Figs 47, 49)

Present status

The black-backed jackal is now extinct in the south-western Cape, but it was apparently still common in the region during the nineteenth century.

Material

(1) *Elandsfontein*

(a) Previously described specimens (Ewer & Singer 1956):

EC 18 to 20, 24 to 27 and 30—Incomplete mandibular fragments.
EC 31—M_1.
EC 32—P_4.
EC 21—Maxillary fragment with M^1 and M^2.

(b) Additional specimens:

(i) Skull and postcranial remains found in association and including:

17026—Part of a braincase and maxillary fragments with right I^2, I^3, P^1 to M^2, and left I^1 to I^3 and P^4 to M^2.
17022—Left and right maxillary fragments with P^3 to M^2.
17000—Left and right mandibles lacking only incisors, left P_1 and right M_3.
17001—Right mandible lacking incisors, P_1 and M_3.
17021—Left mandibular fragment with P_3 to M_2.
16867—Parts of a right mandible lacking only I_1, and M_3, and associated with isolated left and right P^4, M^1 and M^2.

(ii) A number of partial dentitions and isolated teeth found in association and including:

15833—Left maxillary fragment with P^1 to P^3.
Five right mandibular fragments with teeth as follows:
$\bar{C}$, P_2 to P_4; P_2 to M_1; P_3 and P_4; P_1 and P_3; P_1 and P_2.
Four left mandibular fragments with teeth as follows:
$\bar{C}$, P_2 to M_2; P_3, M_1 and M_2; P_2 to M_2; M_1 and M_2.
Isolated carnassials and molars as follows:
P^4—two; M^1—four; M^2—eight; M_1—two; M_2—one.

(iii) Parts of the skull of a single individual, including:

17213—Braincase; left maxillary fragment with P^1 to M^2.
17214—Right mandible with $\bar{C}$ and P_2 to M_3.

(iv) Maxillary fragments with teeth as follows:

3361 —Left M^1 and M^2.
5051 —Left M^1 and M^2.

5305 —Right P^3 and P^4 (both incomplete) and M^1; left P^4 to M^2.
5353 —Right P^1 to M^2; left I^3 and P^2 to M^2.
5448/9—Right P^4 to M^2.
5467 —Right M^1 and M^2.
6890 —Right M^1 and M^2.
6891 —Right P^4 to M^2; left P^4 and M^1; left M^1 and M^2.
6892 —Right P^4 to M^2; left P^4.
$$\left.\begin{array}{l}\text{7030 —Right } P^3 \text{ and } P^4\\ \text{7526 —Left } P^3 \text{ and } P^4\end{array}\right\}\text{Possibly one individual.}$$
8067 —Left M^1 and M^2.
8077 —Left M^1.
8093 —Left P^4 to M^2.
8110 —Right P^3 to M^2.
9994 —Right P^4 and M^1.
15609 —Right P^3 to M^1.

(v) Mandibular fragments with teeth as follows:

3363 —Left M_1 and M_2.
5305 —Right P_2 to M_1; left M_1 and M_2.
5478 —Right P_4 to M_2.
5481 —Left M_2.
5483 —Right P_3.
6217 —Left P_4 and M_1.
6863 —Right P_2 to M_1.
6865 —Left M_1 and M_2.
6871 —Right P_4 to M_2.
6878 —Right P_4 to M_2.
7027 —Left M_2.
7506 —Left P_3 to M_1.
7525 —Left M_1.
9491 —Right P_1 to M_2 (P_3 incomplete).
9507 —Right P_2, part of P_4, and M_1.
11159—Left P_1 to M_2.
11450—Right M_1 and M_2.
15613—Right M_1 and M_2.
15614—Left P_2, P_4 and M_1.
16622—Left M_1.
20511—Right P_2 to P_4.
20817—Right M_1.
20999—Right P_3 (incomplete) and M_1.
21005—Right P_3.

(vi) Isolated carnassials and molars as follows:

P^4—three; M^1—seven; M^2—five; M_1—four; M_2—one.

(2) *Melkbos*

Mb 556—Right M_1.

(3) *Swartklip*

ZW 1952—An almost complete skull, with mandible and first four cervical vertebrae found in articulation; lacking part of the left side, but with right side intact.
ZW 1999—Parts of a skull with upper dentition lacking only left and right I^1 and I^2, and with canines damaged.
ZW 2650—Part of a skull with right P^1 to M^2 and left P^3 to M^2.
ZW 1998—Part of a skull with right P^4 to M^2 and left P^4 and M^1.
ZW 102/3—Part of a skull with right $\underline{C}$ and P^1 and left I^2 to P^2; associated mandible with right dentition complete and left I_2 to P_4.

Maxillary fragments with teeth as follows:
ZW 2953 —Right $\underline{C}$ and P^2 to M^2.
ZW 104/5—Right P^4 to M^2.
ZW 1856 —Right M^1.
ZW 1858 —Left P^4 and M^1.
ZW 3243 —Right P^4 and M^1.
ZW 3071 —Right P^1 to P^3.
ZW 2952 —Left P^4 to M^2.
ZW 3781 —Right M^1 and M^2.
ZW 1314 —Left P^4 and M^1 (SITE 2).

Right mandibular fragments with teeth as follows:
ZW 3778—$\underline{I_2}$ to M_2.
ZW 2954—$\overline{C}$ to M_3.
ZW 1471—Part of $\overline{C}$, and P_1 to M_3.
ZW 2998—Part of $\overline{C}$, and P_1 to M_2.
ZW 2000—P_3 to M_2.
ZW 2635—Part of P_4, M_1 and M_2.
ZW 346 —P_1 to P_4.
ZW 2636—P_4 and M_1.
ZW 114 —P_2 and P_3.
ZW 3779—P_2 and P_3.
ZW 2315—M_2.

Left mandibular fragments with teeth as follows:
ZW 393 —P_2 to M_2.
ZW 2316—P_3 to M_2.
ZW 1471—P_4 and M_1.
ZW 1954—P_4 to M_2.
ZW 347 —M_1 and M_2.
ZW 107 —M_1.
ZW 2318—Part of P_4, M_1 and M_2.

ZW 3254—Part of $\bar{C}$ and P_1.
ZW 115 —M_2.

Isolated carnassials as follows:
P^4—four; M_1—two.

(4) *Lime Quarry, Saldanha*

5308B—Left maxillary fragment with part of P^4 and M^1.
5308D—Incomplete right M_1.
Some of the *Canis mesomelas* specimens from this site have been lost.

(5) *Sea Harvest, Saldanha*

S 224 and S 225—Skull fragments.
Right mandibular fragments with teeth as follows:
S 197—P_1, P_2 and P_4 to M_2.
S 135—P_4.
S 728—M_1 and M_2.

Left mandibular fragments with teeth as follows:
S 14 —$\bar{C}$ and P_2 to P_4 just erupting, M_1 and M_2.
S 15 —Part of M_1 and M_2.
S 198—M_2.
S 199—P_2.
S 726—Edentulous.

Isolated carnassials and molars as follows:
P^4—four; M^1—one; M^2—one; M_2—one.

(6) *Coastal middens*

(a) *Slangkop, Cape Peninsula* (34° 9′S; 18° 19′E)

Q 1803A—Parts of a skull, including:
Left premaxilla and maxilla with P^4 and M^1; left mandible with I_2 to M_3; right mandible with $\bar{C}$, P_1 and P_4 to M_2.

(b) *Melkbosstrand* (33° 44′S, 18° 27′E)

Q 1802A—Left mandibular fragment with P_3 to M_3.

(c) *Ysterfontein* (Approximately 33° 21′S, 18° 9′E)

Q 1801B—Skull lacking zygomata, nasals, left I^1 to P^3 and M^2, right I^1 to P^3, and the mandible.

Comment

Canis mesomelas is the best represented carnivore in the Quaternary fossil assemblages from the south-western Cape and it is also the species for which the largest comparative collection was available. Consequently, the examination of this species was in the nature of a pilot study and some later conclusions were based on observations made in this section of the report.

There are two extant species of jackal in southern Africa, namely, *C.*

mesomelas and *C. adustus*, and their dental characteristics have been discussed by Ewer (1956*b*). The classification of the south-western Cape material was based on the diagnostic criteria determined by Ewer and by making use of statistical data obtained in an independent comparative study. The two extant species are most readily differentiated by their 'carnassial:molar' ratios (see Fig. 45). Sixteen *C. adustus* skulls were examined in the course of the present study, while

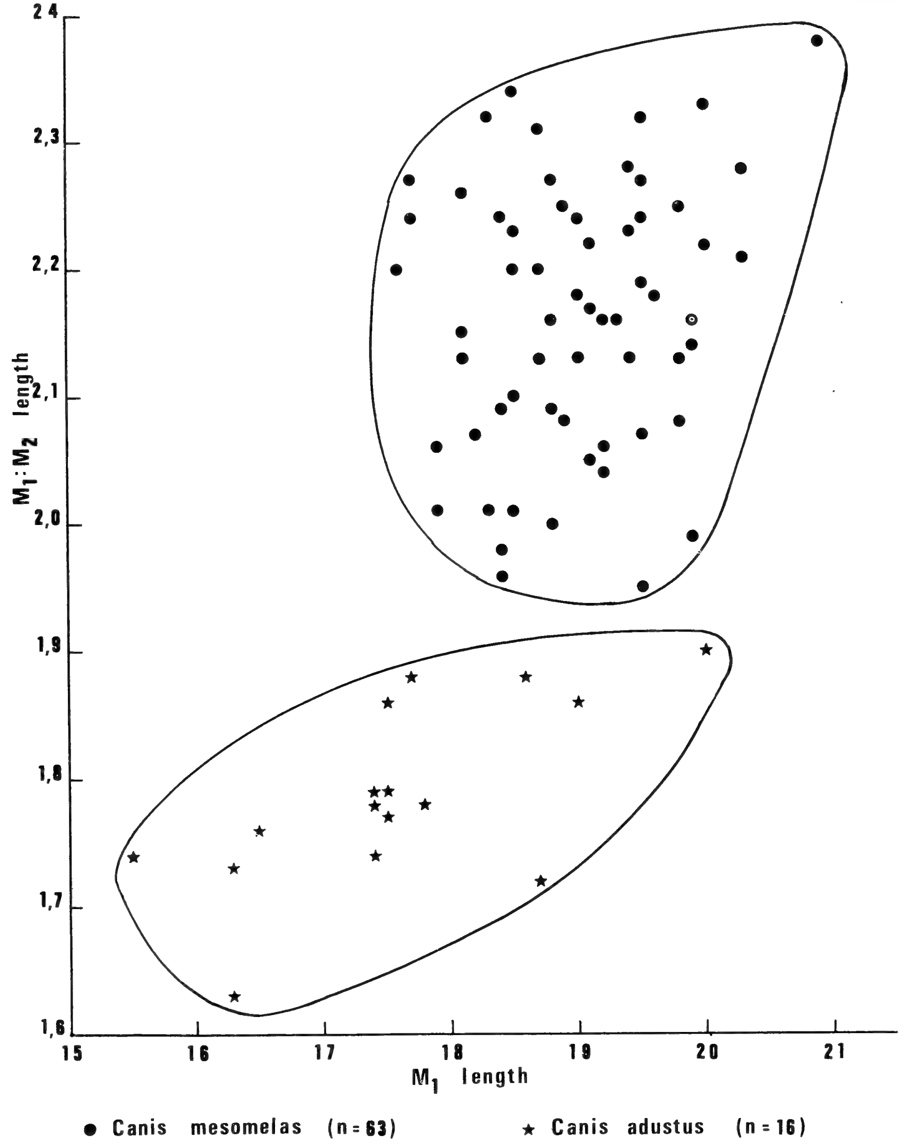

Fig. 45a. Lower carnassial: molar ratios of modern *Canis mesomelas* and *C. adustus* plotted against the lower carnassial length.

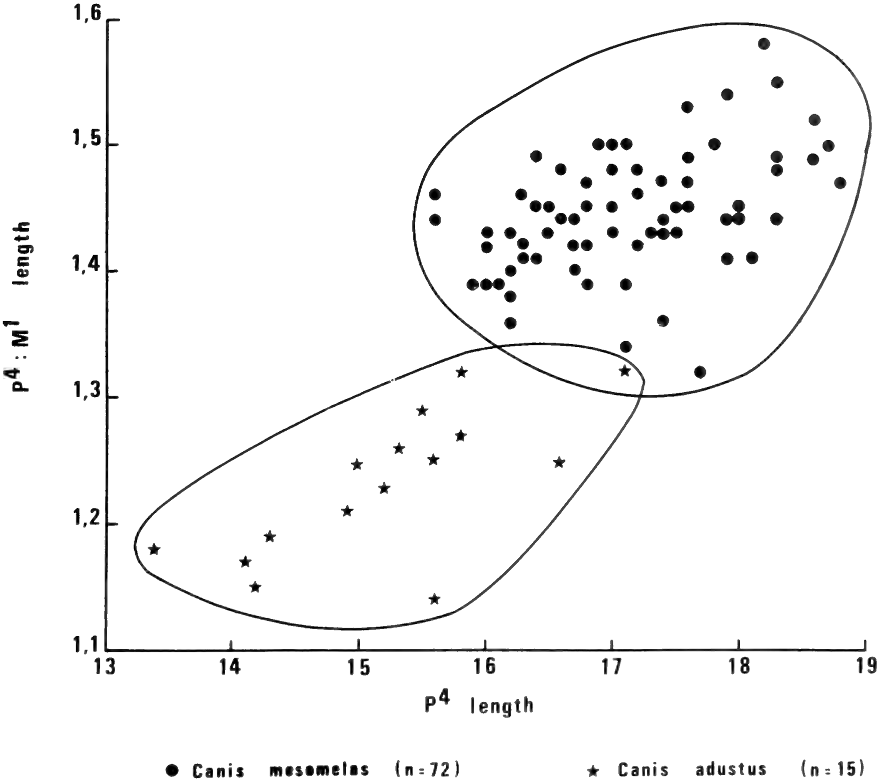

Fig. 45b. Upper carnassial: molar ratios of modern *Canis mesomelas* and *C. adustus* plotted against the upper carnassial length.

sixty *C. mesomelas* skulls from the Cape Province and thirteen from the northern part of South West Africa were also available. No significant difference between the two *C. mesomelas* series were observed and the two samples were treated as a single unit. The comparative series included both males and females, with ages ranging from young adult to aged individuals.

Description and Discussion

Owing to differences between the material from the various occurrences, it is convenient to consider the fossil samples in descending order of age.

Coastal middens

Since the midden material almost certainly dates from the latter part of the Holocene, it probably represents that form of *C. mesomelas* which inhabited the area in historic times. None of the modern comparative specimens came from the south-western Cape, although many were from immediately adjacent regions. Although specimens of the locally occurring form might be preserved in institutions other than the South African Museum, it is most probable that its osteological characteristics will have to be determined from fossil material such as that from the middens.

In respect of the carnassial:molar ratios the midden specimens are well within the ranges of variation observed in the *C. mesomelas* comparative series. The most northerly of the specimens, the Ysterfontein skull, is virtually indistinguishable from the skulls of the moderns in other respects as well. The Melkbosstrand specimen differs from the moderns only in having a more prominent subangular lobe. In this respect it resembles the mandible from Slangkop, which is the most southerly of the midden records and which also has a stouter mandibular corpus than most of the moderns.

One of the characters investigated in respect of the local Florisian *C. mesomelas* was the relative breadth of the lower premolars, notably P_4 (*vide infra*). This was found to be very variable in modern *C. mesomelas*, but there was an apparent tendency for the Florisian form to have the P_4 broader relative to that of the moderns. Although it is not necessarily significant, it is worth noting that the Slangkop P_4 is exceeded in relative breadth by only one of the 72 modern specimens measured. In this respect, and also in its robust mandibular corpus and prominent subangular lobe, the Slangkop specimen is reminiscent of the Florisian *C. mesomelas*.

In itself this is hardly sufficient evidence to suggest the existence of a locally endemic post-Pleistocene *C. mesomelas* population and one which was then replaced late in the Holocene from the north or north-east by a population which is still extant in those regions. There is, however, some evidence to indicate that this might have been the case with the local *Panthera leo* and *Hyaena brunnea*. The possibility is mentioned here in connection with *C. mesomelas* as something which can be borne in mind until further evidence in this regard is forthcoming.

Sea Harvest

The Sea Harvest specimens are essentially similar to modern *C. mesomelas*, although some of the teeth are larger than those of the comparative series (Tables 41, 42). It may be significant that the teeth of those specimens which have a less aged appearance (e.g. S 14) are comparable in size to those of the moderns, while the older looking specimens (e.g. S 197) are larger and more comparable to the specimens of Florisian age. On the other hand, the assemblage as a whole occupies a position intermediate between those of Florisian age and the moderns in certain respects (Fig. 46) and this may be taken as an indication that the total assemblage is of intermediate age. Since the Sea Harvest specimens were all derived from the same shallow unconsolidated deposits, the latter alternative is favoured.

In respect of the development of the subangular lobe of the mandible, one Sea Harvest specimen (S 198) is comparable to the moderns and another (S 15) is more like the Slangkop and Florisian specimens. The other mandibles belong

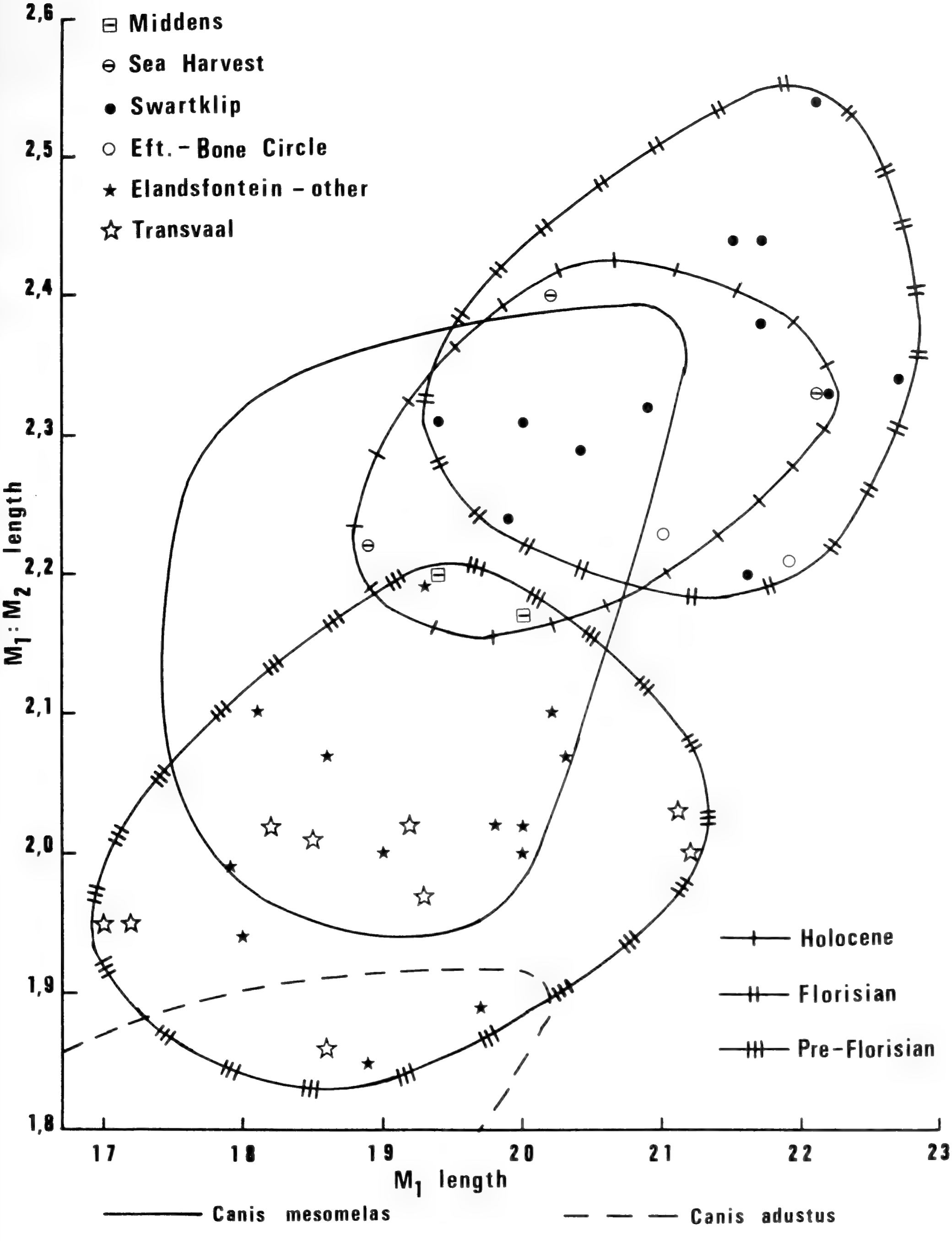

Fig. 46. Lower carnassial:molar ratios of fossil *Canis mesomelas* compared with those of modern *C. mesomelas* and *C. adustus*.

TABLE 41

Dimensions of the upper teeth of fossil *Canis mesomelas* from the south-western Cape Province compared with a series of modern specimens.

		P^3		P^4		M^1		M^2		P^4:M^1l
		l	b	l	b	l	b	l	b	
Modern *Canis mesomelas*	Mean	9,6	3,9	17,1	8,1	11,8	15,2	6,9	10,6	1,45:1
	Range	8,2–10,8	3,4–5,0	15,6–18,8	7,1–9,1	10,7–13,4	14,0–16,7	5,7–8,0	9,2–11,8	1,32:1–1,58:1
	n	69		72	71	72		70		72
Coastal middens	Q1801B	9,6	3,6	16,8	8,7	11,9	14,0	6,5	9,6	1,41:1
	Q1803A	—	—	17,4	8,1	12,5	15,1	—	—	1,39:1
Sea Harvest	S210, S219, S17	—	—	18,4	9,1	11,8	—	6,5	10,2	—
	S206, S137	—	—	19,2	—	12,3	—	—	—	—
Swartklip	Mean	10,0	4,3	18,9	9,2	12,3	16,3	7,2	10,8	1,54:1
	Range	9,2–10,4	3,6–5,0	17,4–20,2	8,1–9,8	11,8–13,3	15,2–17,8	6,8–7,5	10,3–11,6	1,47:1–1,68:1
	n	6		10		9		7		8
Elandsfontein (?Holocene)	5353	9,5	3,8	16,3	7,5	10,9	14,0	7,0	9,7	1,50:1
Elandsfontein (Bone Circle)	15833	—	—	19,1	9,6	12,9	16,2	7,2	10,8	1,48:1
	15833	—	—	—	—	c.12,5	16,8	7,6	11,0	—
	15833	—	—	—	—	13,2	16,8	7,3	10,3	—
Elandsfontein (Cornelian)	Mean	10,4	4,0	17,9	8,9	12,9	16,3	8,1	11,6	1,38:1
	Range	9,8–10,8	3,5–4,4	16,7–19,9	7,8–9,9	11,5–14,4	15,0–17,9	7,2–8,8	10,5–12,0	1,33:1–1,46:1
	n	7		14	13	20		13		12

TABLE 42

Dimensions of the lower teeth and mandibles of the fossil *Canis mesomelas* from the south-western Cape Province compared with a series of modern specimens.

		P_3		P_4			M_1		M_2				Height of corpus below M_1	Breadth of corpus below M_1
		l	b	l	l	l:b	l	b	l	b	P_4:M_1l	M_1:M_2l		
Modern *Canis mesomelas*	Mean	8,8	3,8	10,3	4,5	2,30:1	19,0	7,5	8,8	6,7	1:1,84	2,16:1	17,0	8,1
	Range	7,2–10,5	3,4–4,5	9,0–11,4	4,0–5,3	2,05:1–2,56:1	17,6–20,9	6,9–8,7	7,8–10,0	5,8–7,5	1:1,70–1:2,05	1,95:1–2,38:1	13,6–19,7	7,1–9,5
	n	69	71	71			68		63	61	67	63	69	69
Coastal middens	Q1802A	—	—	11,2	4,7	2,38:1	20,0	8,2	9,2	6,5	1:1,79	2,17:1	18,0	8,2
	Q1803A	9,0	4,0	10,3	5,0	2,06:1	19,4	7,8	8,8	6,1	1:1,88	2,20:1	19,2	8,8
Sea Harvest	Mean	—	—	11,6	5,5	2,10:1	20,4	8,1	8,7	6,6	1:1,86	2,32:1	—	—
	Range	—	—	11,2–11,9	5,4–5,6	2,00:1–2,20:1	18,9–22,1	7,2–9,0	8,4–9,5	6,3–7,2	—	2,22:1–2,40:1	—	—
	n	—		2			3		5		—	3	—	—
Swartklip	Mean	9,6	4,4	11,2	5,2	2,15:1	21,1	8,7	9,0	7,0	1:1,89	2,35:1	19,4	9,2
	Range	9,0–10,1	4,1–4,8	10,6–11,7	4,9–5,7	2,07:1–2,17:1	19,4–22,1	8,2–9,4	8,4–9,8	6,6–7,4	1:1,83–1:2,01	2,20:1–2,54:1	17,3–20,8	8,7–9,9
	n	10		10			16		12		10	12	10	9
Melkbos	Mb556	—	—	—	—	—	21,0	9,7	—	—	—	—	—	—
Elandsfontein (Bone Circle and other Florisian elements)	Mean	9,6	4,1	11,2	5,3	2,11:1	21,2	8,5	9,5	7,0	1:1,93	2,22:1	20,7	9,6
	Range	9,3–10,2	3,8–4,5	10,8–11,6	5,0–5,6	2,08:1–2,21:1	20,3–22,1	7,9–9,8	9,1–9,9	6,7–7,5	1:1,89–1:1,96	2,21:1–2,23;1	— —	— —
	n	6		3			10	9	3		3	2	1	1
Elandsfontein (Cornelian)	Mean	9,3	3,9	10,8	4,8	2,23:1	19,0	7,9	9,5	7,1	1:1,78	2,02:1	18,9	9,0
	Range	7,9–10,7	3,3–4,6	9,1–12,0	4,0–5,6	2,02:1–2,46:1	17,3–20,4	7,1–8,7	8,6–10,6	6,2–7,9	1:1,60–1:1,88	1,85:1–2,19:1	17,3–21,2	8,1–10,2
	n	14		19			30		19		15	14	16	16

either to immature individuals or are incomplete, so the character of their subangular lobes could not be determined.

Two specimens (S 197, S 135) have P_4 fully erupted and both these teeth are broader than most of the modern specimens and compare with those of Florisian age (Table 42). However, the incompletely erupted P_4 of S 14 has a length:breadth ratio of 2,40:1 and is much narrower than the other specimens. It is excluded from Table 42 since its dimensions may be determined by the ontogenetic age of the individual and all the other specimens recorded are fully grown adults.

Swartklip

The Swartklip *C. mesomelas* is taken to represent the typical local Florisian form and reference has already been made elsewhere to its relatively large size (Hendey & Hendey 1968). Since 1968 a large number of additional specimens have been recovered and the assemblage as a whole confirms that the Swartklip jackal was a little larger than the moderns in most respects, although there are overlaps in the observed size ranges of variation in the fossil and modern samples. The lower premolars of the fossil form are generally broader than those of the moderns and the subangular lobes of the mandibles tend to be more prominent. In other respects the Swartklip specimens are indistinguishable from the moderns.

Saldanha Lime Quarry and Melkbos

The comparatively large size of the single Melkbos tooth has already been mentioned (Hendey 1968). This specimen is taken to represent the local Florisian form of *C. mesomelas* partly because of its size, but largely because other faunal evidence suggests that the Melkbos fauna is Florisian in age.

Cooke (1955) mentioned the presence of *C. mesomelas* in the Lime Quarry assemblage. He gave no measurements of specimens and some of the material seen by him has been lost. The few remaining teeth compare in size to the larger Swartklip specimens and the Lime Quarry jackal is also taken to represent the local Florisian form of *C. mesomelas.*

Elandsfontein

In their original description of the Elandsfontein *C. mesomelas*, Ewer & Singer (1956) concluded that it was intermediate in character between the Makapanian *C. mesomelas pappos* (Ewer 1956*b*) and the modern form. Many more specimens from this site are now available and the new material, together with that from other local sites, necessitates a re-evaluation of the assemblage as a whole.

The size ranges of variation exhibited by the Elandsfontein teeth are, in general, greater than those recorded for the modern comparative series (Tables 41, 42), while the M_1:M_2 length ratios overlap with the ranges observed in both *C. adustus* and *C. mesomelas* (Fig. 46). This suggests the possibility that more than one form is represented by the specimens here referred to *C. mesomelas.*

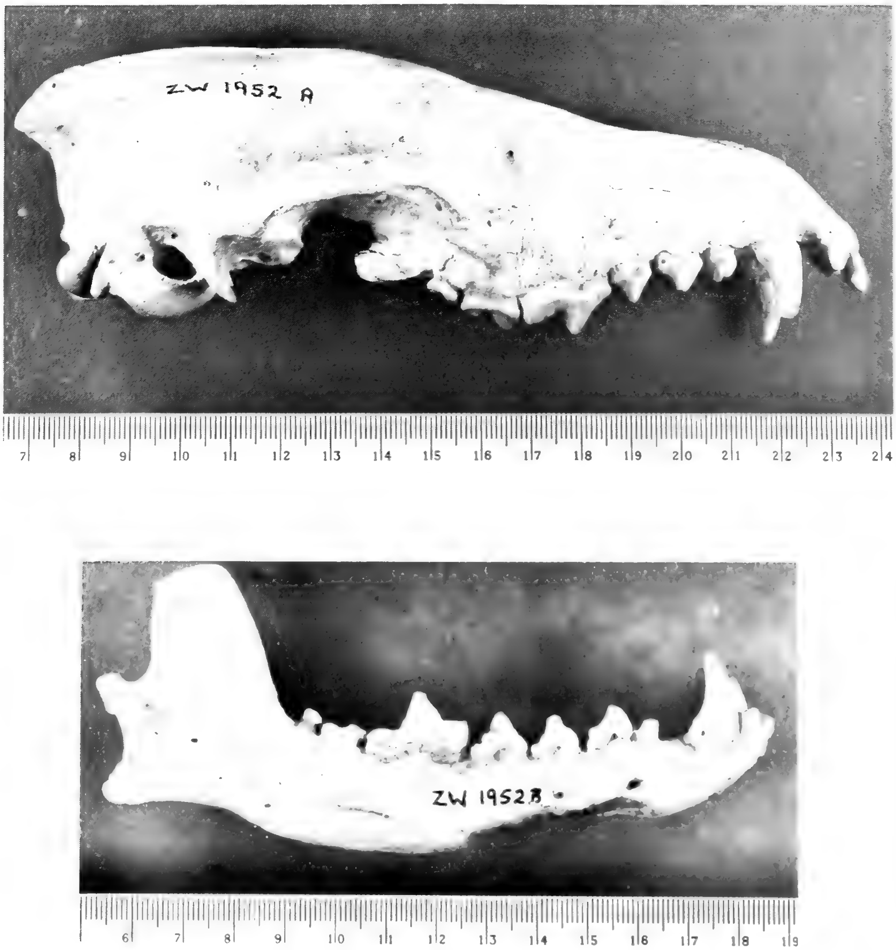

Fig. 47. Lateral view of the *Canis mesomelas* skull and mandible (ZW 1952) from Swartklip.

It has long been suspected that the Elandsfontein fossils are not all contemporaneous and that Cornelian, Florisian and perhaps even post-Florisian elements might be represented (Hendey 1969). It is also possible that the earlier material is itself not homogeneous, but was accumulated over a relatively long period of time. Consequently, the *C. mesomelas* assemblage was examined with a view to establishing whether or not temporal variants within a single species could be distinguished, since this could account for the apparent heterogeneity of the *C. mesomelas* sample and perhaps also assist in the analysis of other species represented at the site.

No constant morphological differences between the teeth in the modern and fossil series were observed and it was evident that if the fossils were to be separated into categories, this would have to be done on the basis of metrical data.

Initially a detailed analysis was undertaken of the lower carnassials in the various *C. mesomelas* samples since this tooth is easily identifiable, it is one of the most commonly represented of the fossil teeth and its relatively large size facilitates an assessment of dimensional characters and their changes.

Variations in M_1 length in the two modern *C. mesomelas* samples were found to be similar, 43,6 % of those from the Cape Province having a length of between 19 and 20 mm, while the corresponding figure for the smaller South West African sample was 50%. Frequency histograms of M_1 lengths in the modern and Swartklip series show single peaks (Fig. 48a), although that of the Swartklip series is between 20 and 21 mm, one unit higher than the moderns. In all, about 82 % of the moderns had M_1 lengths of between 18 and 20 mm, while about 87 % of those from Swartklip were between 20 and 23 mm in length. There is, therefore, a very clear difference in the average lengths of the M_1 in the modern and Florisian forms of *C. mesomelas*, although there is an overlap in the observed ranges of variation and the pattern of the histograms is essentially similar.

By contrast, the frequency histogram of the Elandsfontein *C. mesomelas* M_1 lengths has two peaks and a more even distribution of measurements over a greater number of units. The one peak between 20 and 21 mm suggests that

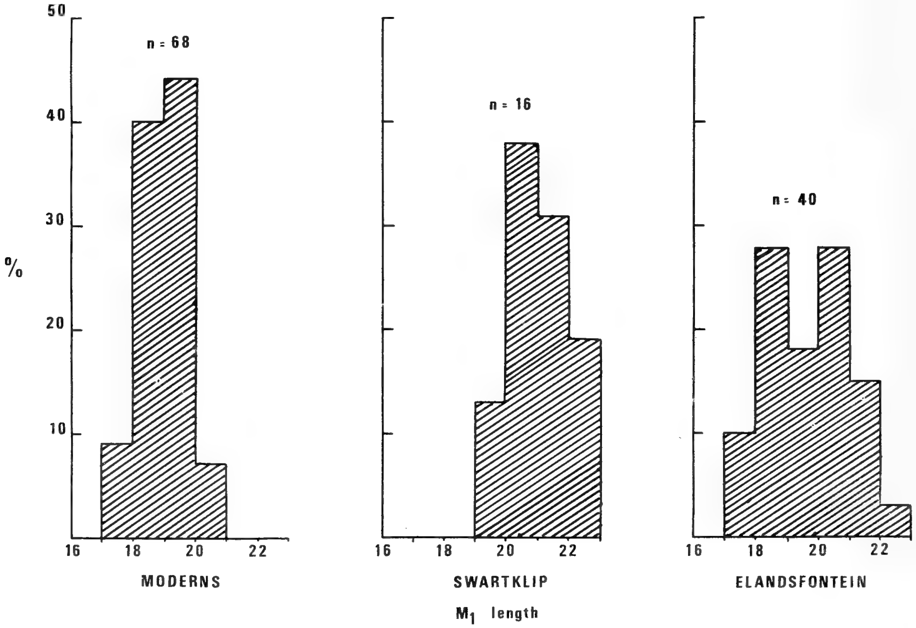

Fig. 48a. Frequency histograms of M_1 lengths of modern, Swartklip and Elandsfontein *Canis mesomelas*.

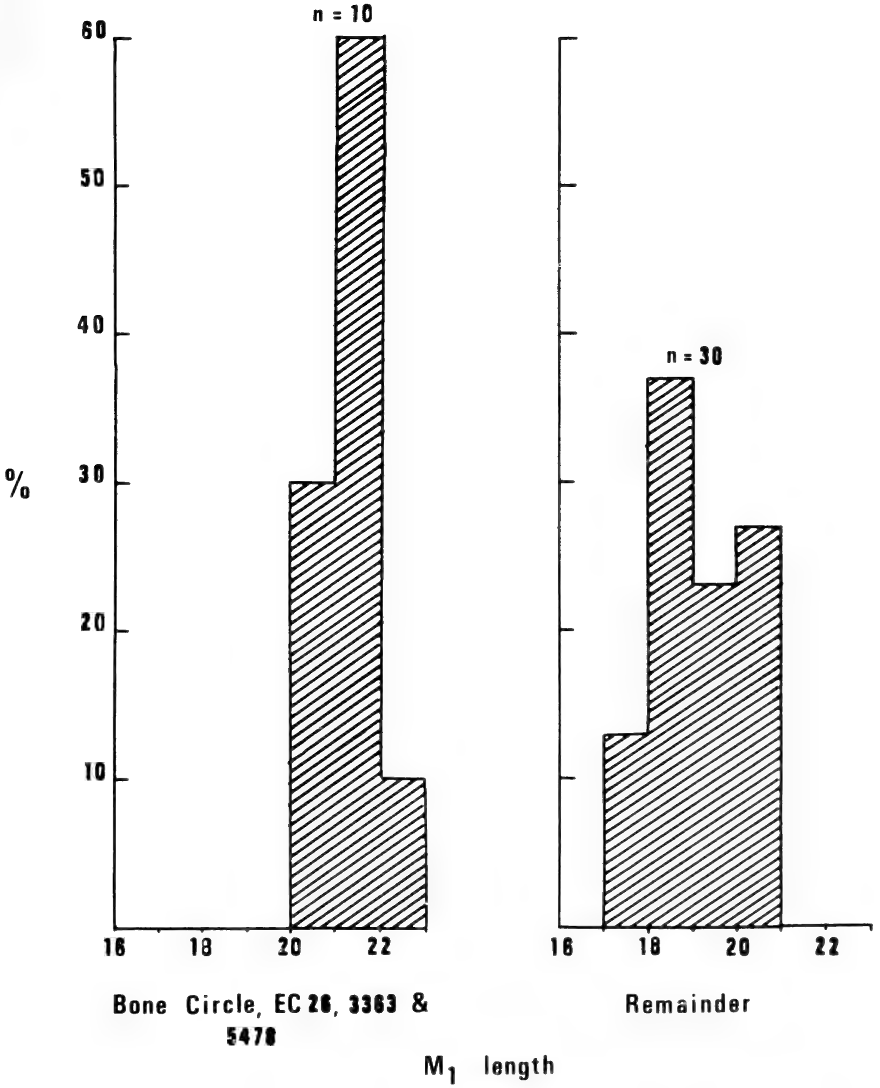

Fig. 48b. Frequency histograms of M_1 lengths of Elandsfontein *Canis mesomelas*.

a variety of *C. mesomelas* corresponding to that from Swartklip is included in the Elandsfontein assemblage, while the second peak between 18 and 19 mm suggests that a second form, similar to the moderns in respect of M_1 length, is also represented. The second peak is actually one unit lower than that of the moderns, indicating that this form is not identical with the extant species, a conclusion later confirmed by other evidence.

Included in the Elandsfontein *C. mesomelas* assemblage are a series of specimens (15833) from what is known as the 'Bone Circle' occurrence (Inskeep

& Hendey 1966). The preservation of the Bone Circle specimens differs from that of most other fossils from Elandsfontein and, in addition, this assemblage includes no extinct species. For these reasons it is thought to date from the Florisian. In respect of M_1 size, the Bone Circle specimens are larger than most others from Elandsfontein and are within the size range of variation observed in the Swartklip form (Fig. 46), which is a further indication that the Bone Circle occurrence is indeed Florisian in age.

A primary distinction was therefore made between those specimens from Elandsfontein which date from the Florisian and those which do not. Since the Elandsfontein fauna as a whole is clearly older than that from Swartklip, the common 'normal'-sized *C. mesomelas* was regarded as part of the earlier element of the fauna, although the possibility that it includes some post-Florisian elements was also recognized.

The separation of the *C. mesomelas* assemblage into categories on the basis of M_1 dimensions is complicated by the fact that the Florisian variety, as represented at Swartklip, has a size range of variation which overlaps with those of the 'normal'-sized moderns and the 'normal'-sized Elandsfontein specimens. Consequently, although three other unusually large specimens (EC 26, 3363, 5478) are tentatively assigned to the Florisian form, there might well be others which belong to it, but which are not recognized as such because their dimensions fall within the area of overlap of the various ranges of variation. 'Corrected' frequency histograms for the M_1 lengths of the Elandsfontein *C. mesomelas* (Fig. 48b) still show inconsistencies. Furthermore, since the M_1 of the earlier Elandsfontein form and the moderns are essentially similar in size, they cannot be separated from one another on this basis.

The same applies in the case of all other teeth and the Elandsfontein *C. mesomelas* can clearly not be categorized solely on the basis of individual tooth size.

One other point which emerged from the examination of the lower carnassials is that there has apparently been a fluctuation in the average size of this tooth through most, if not all of the Quaternary (Fig. 50). This was possibly accompanied by changes in actual body size as well.

The Makapanian *C. mesomelas pappos* was found to differ 'from living *C. mesomelas* in having the lower premolars and second lower molar longer in comparison with the length of the carnassial' (Ewer 1956*b*: 113). Ewer & Singer (1956: 342; Fig. 1) indicated that the Elandsfontein form is intermediate between the Makapanian and modern forms in this respect. They illustrated their contention by direct comparisons of mean cheektooth lengths. Carrying this reasoning further, it follows that the Swartklip form should be intermediate between the early Elandsfontein form and the moderns in respect of mean cheektooth lengths. However, it is found that this applies only in the case of M_2 and the Swartklip premolars are either closer or actually equivalent to those of *C. m. pappos* in length. Simple linear measurements are clearly misleading in this instance and, although the earlier Elandsfontein form should theoretically

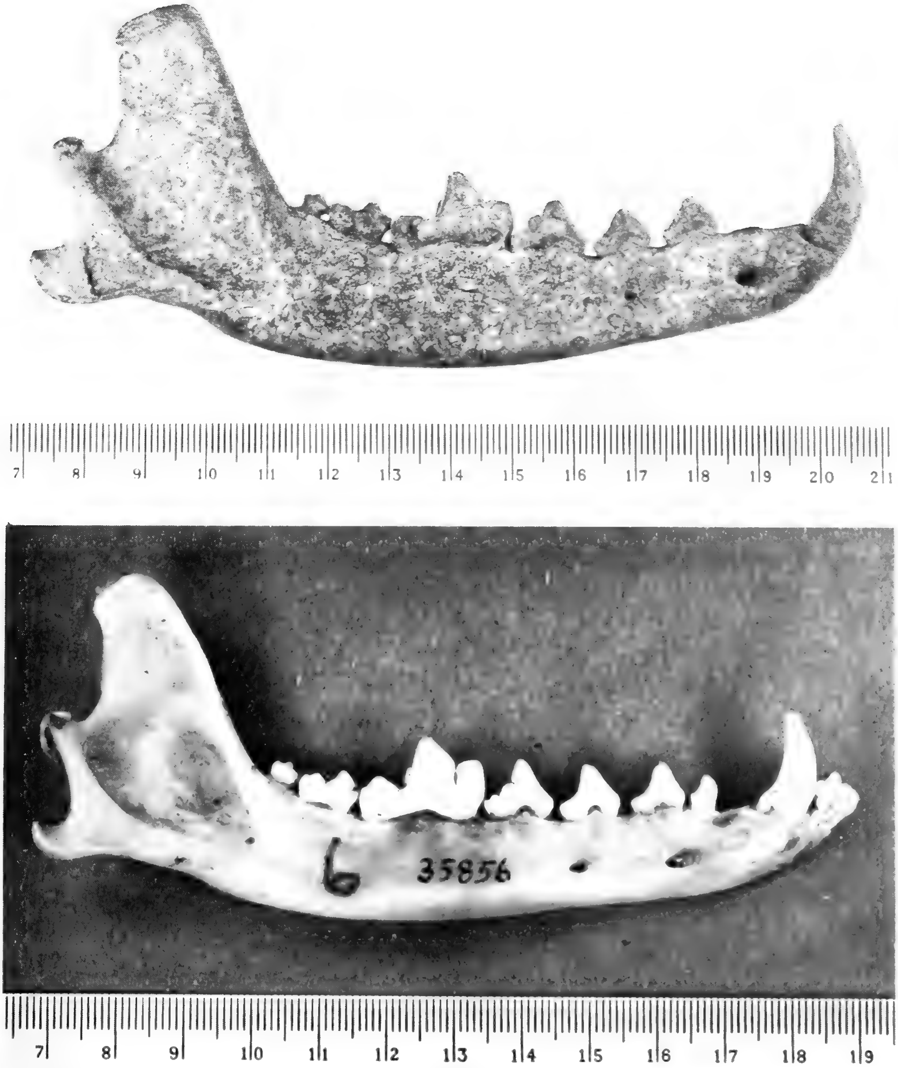

Fig. 49. Buccal views of a *Canis mesomelas* mandible from Elandsfontein (17214) and a modern specimen (SAM 35856).

occupy a position intermediate between *C. m. pappos* and the moderns, the evidence put forward in support of this by Ewer & Singer is unacceptable in the form in which it is presented.

A comparison between cheektooth lengths *relative* to the carnassial lengths gives a different, and somewhat surprising result. The M_1:M_2 length ratios of the early Elandsfontein form are actually essentially similar to those of *C. m.*

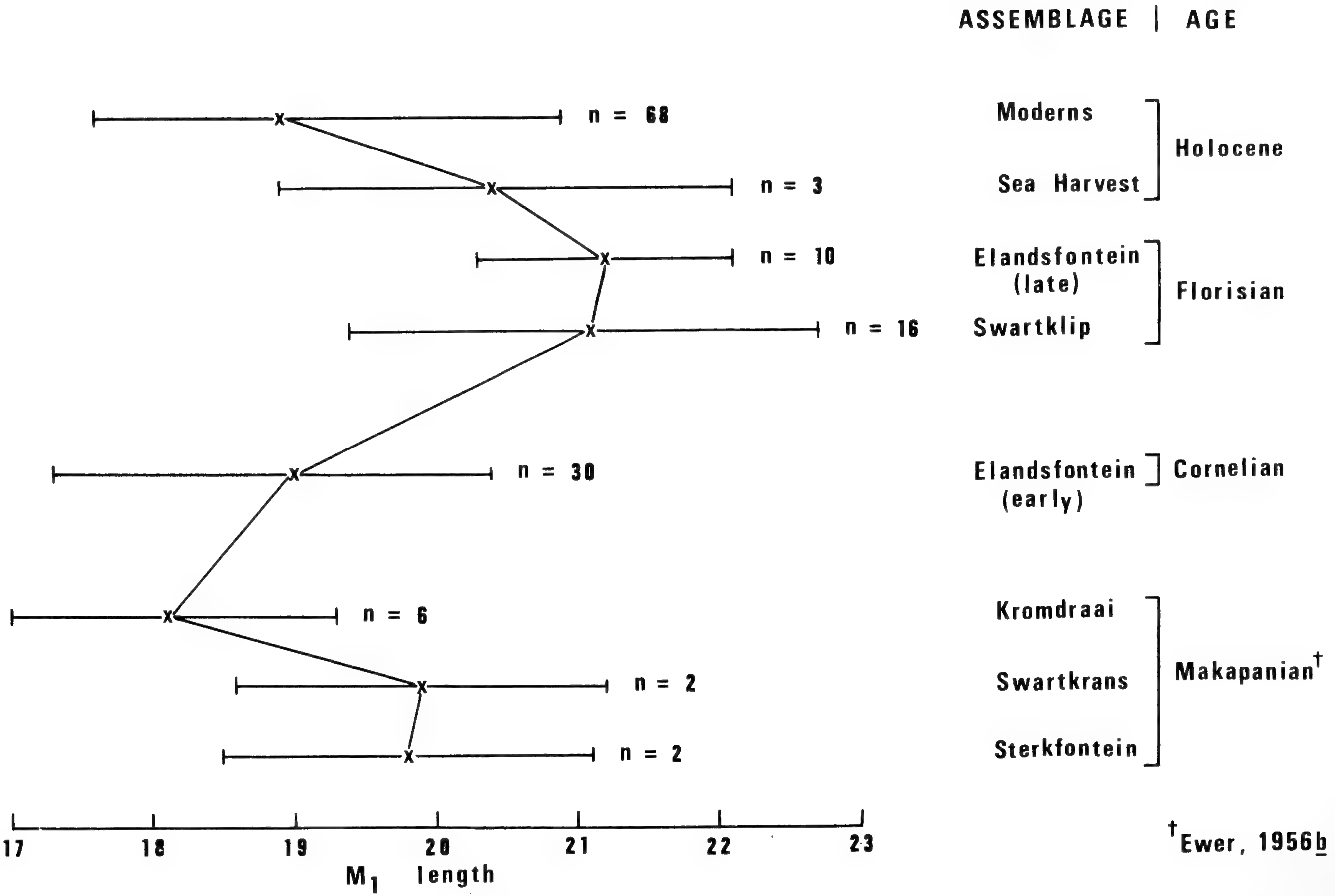

Fig. 50. The ranges and means of M_1 lengths of modern and fossil *Canis mesomelas*.

pappos (Fig. 46), indicating that the two forms are equally primitive in this respect.

The Elandsfontein and Transvaal samples overlap with the M_1:M_2 length ratios of both the modern *C. adustus* and *C. mesomelas* series, but not with the ratios of specimens from the Bone Circle, Swartklip and Sea Harvest. Consequently, a distinction between pre-Florisian and Florisian forms of *C. mesomelas* can be made on this basis, the earlier group having a ratio of 2,10 or less and the later one 2,20 or more. This distinction is not necessarily entirely reliable, since one of the Elandsfontein specimens (6865) has a ratio of 2,19 and could belong in either category, or may actually represent the post-Florisian form of the species.

The overlap with the *C. adustus* ratios does not necessarily indicate the presence of this species at Elandsfontein. It may simply be accounted for by the fact that *C. adustus* and *C. mesomelas* had a common ancestor and primitive forms of either species might be expected to exhibit characters which are intermediate between those of the modern forms. The specimen with the lowest M_1:M_2 length ratio (17021), which is therefore the one most like *C. adustus* in this respect, was found in direct association with others (16867, 17000, 17001) in which the ratio is well within the range observed in modern *C. mesomelas*. This is taken as an indication of a single population in which the M_1:M_2 length ratios overlap the ranges of the two modern species, rather than that both these species are represented.

Essentially the same pattern of similarities and differences was revealed by a comparison of P^4:M^1 length ratios. This ratio, which is less useful in distinguishing modern *C. adustus* from *C. mesomelas* (Fig. 45; Ewer 1956*b*), actually indicated the relationship between the fossil material and *C. mesomelas* more clearly than the M_1:M_2 length ratio. On the other hand, the distinction between the local pre-Florisian and Florisian forms is less clearly indicated, while the recorded *C. m. pappos* specimens overlap with the other forms of *C. mesomelas* in this respect. On the basis of the available specimens, the local Florisian form has a P^4:M^1 length ratio of more than 1,45, the pre-Florisian form has a ratio of less than 1,45, while the mean figure for *C. m. pappos* is 1,45.

The relatively broad lower premolars of the Florisian *C. mesomelas* have already been mentioned. The length:breadth ratios of the P_4 of the local forms, together with those of a series of Makapanian specimens from Kromdraai, indicate an apparently consistent broadening trend, which is only reversed in the modern form (Table 43). Although the P_4 length:breadth is very variable in the modern comparative series, the broadening of this tooth in the fossil populations is regarded as a real rather than apparent change, because a graphical representation of the change (Fig. 51) matches that of the change in M_1 lengths in the same populations (Fig. 50).

The relative breadths of P_4 also proved useful in demonstrating yet again the heterogeneity of the Elandsfontein *C. mesomelas* assemblage. It was suspected that the material included in the category 'Elandsfontein (excluding Bone

TABLE 43

Length:breadth ratios of P_4 of modern and fossil *Canis mesomelas* from southern Africa.

	n	P_4 l:b Mean	Range
Kromdraai	4	2,36:1	2,32–2,43
Elandsfontein (excl. Bone Circle) . .	19	2,23:1	2,02–2,46
Swartklip	10	2,15:1	2,07–2,17
Elandsfontein (Bone Circle) . . .	3	2,11:1	2,08–2,21
Sea Harvest	2	2,10:1	2,00–2,20
Slangkop coastal midden	1	2,06:1	—
Melkbosstrand coastal midden . . .	1	2,38:1	—
Moderns	71	2,30:1	2,05–2,56

Circle)' in Table 39 might include specimens of Florisian age, so the ratios of each individual P_4 were plotted on a frequency histogram and, as anticipated, there were two distinct peaks. The first, between 2,15 and 2,20, corresponds approximately to the mean figure of the Swartklip series, while the second, between 2,25 and 2,35, compares with the mean of the modern series. This is a parallel of the situation encountered when the M_1 lengths of the various series were compared. Once again it proved impossible to separate the Elandsfontein material into two distinct categories because of overlaps in the ranges of variation. It is, however, clear that the mean figure for the early Elandsfontein form, which is given as 2,23:1 in Table 43, is incorrect. The actual ratio for this form is probably closer to 2,30:1 and this alternative is indicated in Figure 51.

The possibility that some Elandsfontein specimens represent the modern form of *C. mesomelas* has already been mentioned and this seemed particularly likely in the case of the series of upper teeth, 5353. They not only occupy a somewhat isolated position in relation to the rest of the assemblage in respect of their dimensions (Table 41), but are also most unusual in the nature of their preservation. They differ most markedly from other Elandsfontein specimens in the relatively small size of the upper molars and this is reflected in the P^4:M^1 length ratio. Since pre-Florisian *C. mesomelas* is relatively primitive, the upper molars are generally larger than those of the moderns, but the M^1 of 5353 is actually near the lower size limit observed in the comparative series. It is clearly not conspecific with the second jackal from Elandsfontein (*vide infra*), although it might simply be an unusually small example of the pre-Florisian

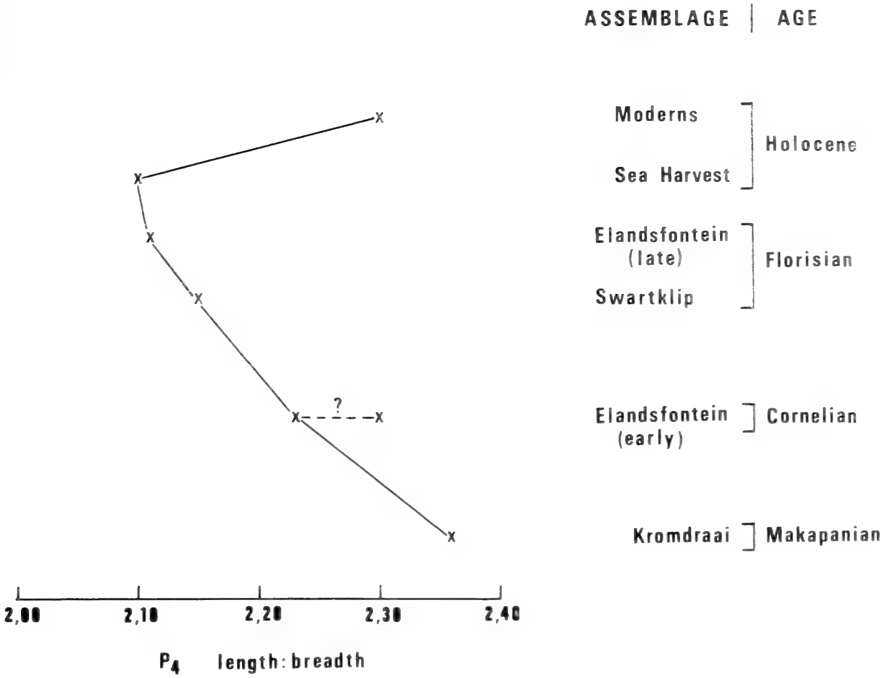

Fig. 51. The means of P_4 length:breadth ratios of modern and fossil *Canis mesomelas*.

C. mesomelas. On balance, the indications are that it probably does represent the Holocene form of the species.

Non-dental characters provide little useful information on the nature of the Elandsfontein *C. mesomelas*. The two braincases which are known apparently both represent the earlier form and they do not differ significantly from those of the moderns, although 17213 is larger and has a more prominent sagittal crest than any of the comparative specimens. The mandible of this specimen, and others belonging to the earlier form, all have more prominent subangular lobes than the moderns and, in general, are larger. Judging from the length of the cheektooth rows, the size of the mandibular corpora and the size of the braincase of 17213, the pre-Florisian *C. mesomelas* was probably comparable in overall size to the Florisian form and a little larger than the moderns. In this particular instance the size of the M_1 in relation to that of the modern form does not reflect the overall relative skull sizes of these two forms.

Summary

On the basis of metrical data the fossil *C. mesomelas* from the south-western Cape may be grouped into three main categories and these are for the present and for the sake of convenience correlated with the Cornelian, Florisian and

Holocene. The age of the pre-Florisian material will be discussed again later.

Depending upon the parts which are preserved, it is not always possible to assign material to one or other of the groups and categorization of the heterogeneous Elandsfontein assemblage is particularly difficult. Most of the Elandsfontein specimens are apparently Cornelian in age, but some, notably those from the Bone Circle occurrence, date from the Florisian, while a few may represent the Holocene *C. mesomelas*. It is also possible that the pre-Florisian assemblage includes early and late Cornelian elements or even pre-Cornelian specimens, while others intermediate in age between 'typical' Cornelian, Florisian and Holocene forms might also be represented.

The two Pleistocene categories which are presently recognized are most readily distinguished from one another on the basis of their carnassial:molar ratios. The M_1:M_2 length ratio of the Cornelian form is 2,10 or less and the P^4:M^1 length ratio is less than 1,45, while the corresponding figures for the Florisian form are 2,20 or more and more than 1,45.

The Melkbos, Swartklip and Saldanha Lime Quarry material, like that from the Bone Circle, represents the Florisian form of the species.

The Sea Harvest specimens are taken to be early Holocene in age and, viewed as a whole, this assemblage is intermediate in character between the typical Florisian form and the moderns. It may, however, actually be made up of specimens which are Florisian in age and others which are Holocene, so that the intermediate character results from a heterogeneous sample rather than from phylogenetic reasons.

The distinction between the Florisian and Holocene forms is principally a matter of a difference in the average size of individuals, the former being larger than the moderns.

The *C. mesomelas* from local Late Stone Age coastal middens represent the later Holocene form of *C. mesomelas*. The specimen from the most southerly of the middens relevant in the present instance (i.e. Slangkop) may belong to an endemic variety of the species.

The basic patterns in the nature and changes observed in the south-western Cape *C. mesomelas* were found to be repeated in a number of other locally occurring species.

Nomenclature

Although all the specimens listed earlier are referred to *C. mesomelas*, the different categories can be distinguished from one another to at least some extent. Consequently, the formal definition of distinct subspecies needs to be considered.

In respect of the M_1:M_2 length ratios the Elandsfontein Cornelian form is essentially similar to the Makapanian *C. m. pappos* and on these grounds alone the two forms could be regarded as belonging to the same subspecies. There is, however, not the same correspondence between P^4:M^1 length ratios. In addition, the indications are that the Elandsfontein assemblage is younger than any of those identified with the Makapanian. Finally, there is some doubt as to whether or not *C. m. pappos*, as it is presently defined, should be regarded as a valid subspecies.

Ewer (1956*b*: 111, 112) recognized that there was 'some heterogeneity of the sample' of *C. m. pappos* 'since the fossils came from several sites which, on the basis of other faunal evidence, are unlikely to be strictly contemporaneous'. She goes on to say that, 'The material may well include forms which are subspecifically distinct, or would be so regarded by a neontologist working with living material'. To add yet another series of specimens to this taxon, and one which is temporally and geographically removed from the *C. m. pappos* type material, would serve only to complicate it further and there seems no point and little justification for referring the early Elandsfontein material to this subspecies. On the other hand, osteological differences between it and *C. m. pappos* are such that a new subspecific name can hardly be supported by an adequate definition.

Similar difficulties are encountered in attempting to justify a new subspecific name for the local Florisian form, although in this instance the problems are mainly concerned with distinguishing it from the later Holocene form. In her discussion on the various *C. m. pappos* samples, Ewer (1956*a*: 112) stated that 'no useful purpose would be served by making a (taxonomic) separation which could be based only on an arbitrary decision as to size limits', and it is precisely this kind of decision which would have to be made in order to distinguish the Florisian *C. mesomelas* from the extant subspecies. However, since the extant *C. m. mesomelas* and *C. m. arenarum* are more similar to one another than either is to the Florisian form, this might be regarded as justification for affording the latter separate taxonomic status.

Palaeontologists and neontologists may have a different basis for their classifications, even though they may be studying essentially the same taxonomic units, largely because of the nature of the evidence which they have to evaluate. In the present instance, subspecific distinctions would refer to a phylogenetic succession which culminated in a number of geographical variants, each of which is itself afforded subspecies status. A possible solution would be to name subspecies according to the age with which they are correlated, thus giving a separate name to the *C. mesomelas* of each of the three Pleistocene ages. The inherent difficulties in this procedure are manifest and its advantages are limited, since, to quote one example, 'Makapanian *C. mesomelas*' is as distinctive and more explicit than '*C. m. pappos*'.

Since the question of the definition of new subspecies has already arisen in connection with the Lime Quarry *Arctocephalus pusillus*, and since it will arise again in connection with other species, a standard approach to the problem was adopted during the present study. Quite simply, no new subspecific names are proposed and the way is left open for others who may feel that trinomens are justified and useful with some of the species described in this report.

Family **Canidae**

Subfamily Caninae

Canis terblanchei Broom, 1946/1948

(Fig. 52)

Present Status

Extinct.

Material

Elandsfontein

15605—Left and right maxillary fragments, the latter with P^1 to M^2.

Comment

The preservation of these specimens is atypical of the Elandsfontein assemblage as a whole. They are part of a small association of fossils which apparently occurred in a manner comparable to the Bone Circle association. They are, however, encrusted with a partly consolidated calcareous sand and have a more aged appearance than the Bone Circle fossils, although this does not necessarily prove that the two assemblages are not contemporaneous. A canid mandibular fragment from the same occurrence (15613) was earlier referred to *Canis mesomelas*. The dental characteristics of this specimen are those of *C. mesomelas*, but since the mandibular corpus shows signs of disease or severe injury, it is possible that the development of the teeth was also affected and that the specimen does in fact belong to a species other than *C. mesomelas*. Although 15613 clearly does not belong to the same individual as 15605, it may belong to the same species, namely, *C. terblanchei*.

Description

The right maxilla of 15605 is almost complete and all the cheekteeth are preserved intact. In respect of overall size (Table 44) and dental characteristics, this specimen is essentially similar to the holotype of *C. terblanchei* from the Makapanian of the Transvaal (Broom 1946, 1948; Ewer, 1956*b*).

The similarities between this species and the extant *C. adustus* were noted by Ewer (1956*b*). Although most of the characteristics which were said to distinguish *C. terblanchei* from *C. adustus* cannot be observed in 15605, the Elandsfontein specimen does have a relatively broad P^1, a character included in the diagnosis of the Transvaal species. The P^2 and P^3 of 15605 are also broader than those of *C. adustus* (Table 44) and, although the breadths of these teeth are not recorded for the Transvaal *C. terblanchei*, they too were probably relatively broad and in keeping with P^1 in this respect.

The premolars of 15605 are well spaced, as are those of the *C. terblanchei* holotype.

The P^4:M^1 length ratio of 15605 is a little less than those of the two previously recorded *C. terblanchei* specimens and, as with the holotype of this species, it falls within the range of variation observed in modern *C. adustus*

TABLE 44

Dimensions of the upper teeth of the Elandsfontein *Canis terblanchei*, compared with those of *C. terblanchei* from the Transvaal and modern *C. adustus*.

		P^1		P^2		P^3		P^4		M^1		M^2		P^3:P^4	P^4:M^1
		l	b	l	b	l	b	l	b	l	b	l	b		
Elandsfontein	15605	4,9	3,3	8,0	3,5	8,6	4,0	15,0	7,5	11,8	14,9	7,1	10,7	1:1,72	1,27:1
*Canis terblanchei**	Type	4,3	3,2	7,8	—	9,2	—	*c.* 14,5	—	11,1	—	7,8	11,7	1:1,58	1,31:1
	$K_2$83	—	—	—	—	—	—	15,0	7,3	11,0	13,1	7,7	10,8	—	1,36:1
Modern *Canis adustus*	Mean	4,4	2,7	8,4	3,0	9,6	3,4	15,2	7,8	12,4	14,7	8,4	10,9	1:1,60	1,23:1
	Range	3,8– 5,2	2·5– 3,0	7·3– 9,6	2,8– 3,4	8,1– 10,5	3,2– 3,7	13,4– 17,1	6,4– 9,3	11,4– 13,7	12,4– 16,4	7,8– 9,3	9,5– 12,6	1:1,48– 1:1,78	1,14:1– 1,32:1
	n	13		16	15	15		15		16		16		14	15

* Ewer 1956b.

(Table 44; Fig. 53). The referred specimen from the Transvaal has a P^4:M^1 length ratio which is a little beyond that of the *C. adustus* range of the available comparative series, but it is at the upper limit of the range for this species recorded by Ewer (1956*b*). It is this ratio which most clearly distinguishes 15605 from that material which was earlier referred to *C. mesomelas*.

Discussion

On the basis of the material presently available, there are no grounds for believing that 15605 and *C. terblanchei* are not conspecific. There are, however, grounds for doubting whether *C. terblanchei* warrants recognition as a species distinct from *C. adustus*. It may well be a primitive form of *C. adustus*, just as *C. mesomelas pappos* is a primitive form of the extant black-backed jackal.

The most striking characteristics of *C. terblanchei* are the prominent subangular lobe of the mandible and well-developed paramastoid process. Ewer (1956*b*) recognized these to be related features since the occipito-mandibularis muscle is inserted at the subangular lobe and originates at the paramastoid process, so the development of these osteological features is related to the development of this muscle.

Fig. 52. Occlusal view of the *Canis terblanchei* maxilla (15605) from Elandsfontein.

A prominent subangular lobe is a feature of extant canids such as the crab-eating fox (*Cerdocyon thous*), the bat-eared fox (*Otocyon megalotis*) and the raccoon dog (*Nyctereutes procyonoides*), that is, species which are somewhat atypical of the Canidae in dietary and other respects. On the other hand, it is also well developed in less remarkable species such as the New World grey fox (*Urocyon cineroargenteus*). In addition, it is a feature of the Cornelian and Florisian *C. mesomelas* and *Vulpes chama* from the south-western Cape. In none of the South African fossils is the subangular lobe quite as prominent or as posteriorly situated as it is in the modern species mentioned above. The development of this feature, and those directly related to it, in the fossil forms is regarded as a reflection of the differences between their dentitions and those of their modern counterparts and perhaps relate to size and/or dietary differences.

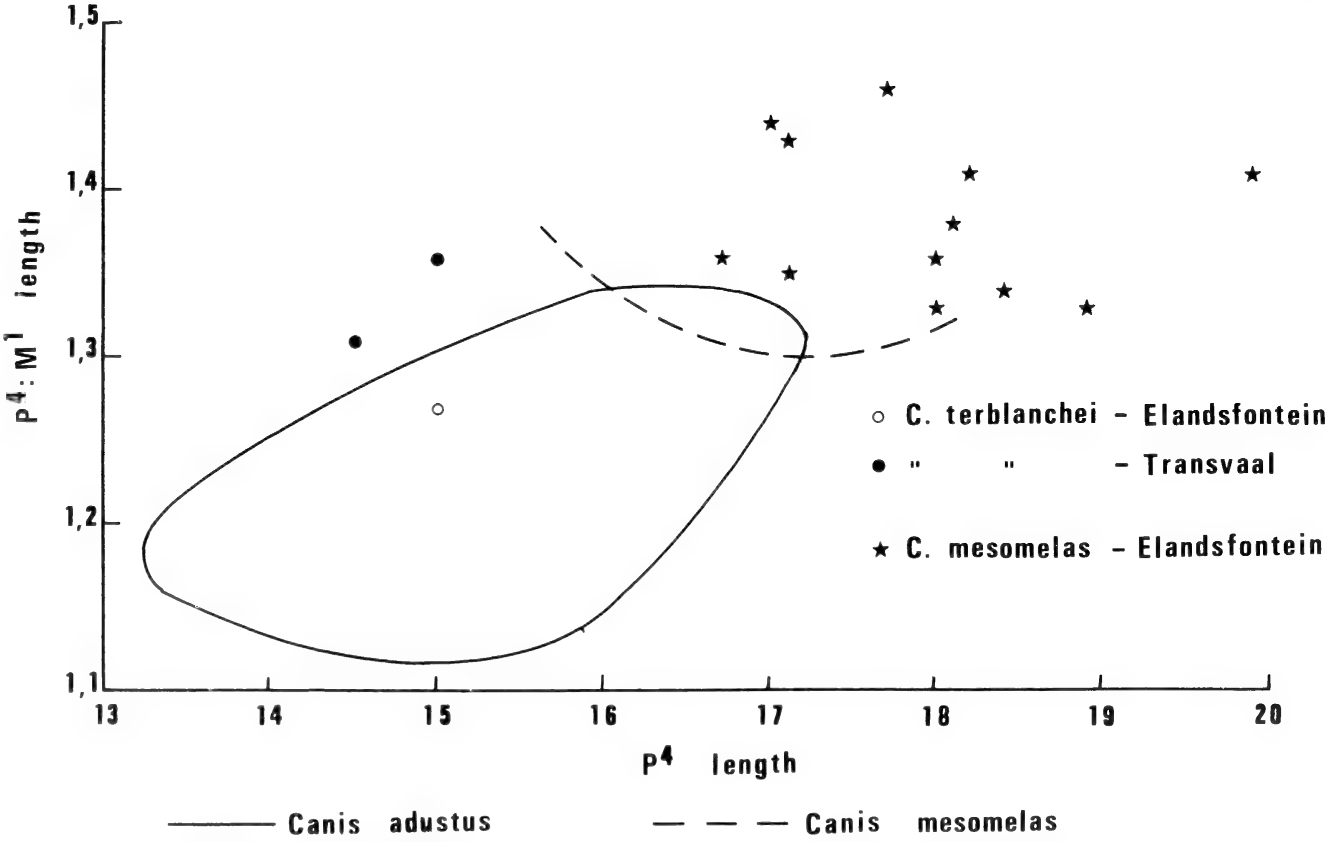

Fig. 53. Upper carnassial:molar ratios of the Elandsfontein *Canis terblanchei* and *C. mesomelas* compared with those of the *C. terblanchei* type material and modern *C. mesomelas* and *C. adustus*.

There apparently is a connection between the nature of the cheekteeth and the presence or absence of the subangular lobe in other groups of carnivores. For example, the Felidae with their highly specialized shearing dentition lack the subangular lobe, whereas the Hyaenidae with their broad and heavy crushing teeth have this feature well developed. In the fossil Canidae the subangular lobe may relate directly to broader lower premolars (e.g. Florisian *C. mesomelas*), broader upper premolars (e.g. *C. terblanchei*), relatively prominent posterior cheekteeth (e.g. Cornelian and Florisian *V. chama—vide infra*) and other such dental characteristics.

The analysis of the mammalian masticatory apparatus is a complex matter requiring detailed study (see Turnbull 1970) and the present speculations made in connection with the development of the subangular lobe are not necessarily desirable or useful. Nevertheless, the evidence of the local fossil record suggests that its development, and those of directly related features, could vary within a single lineage over relatively short periods in time and that its presence does not necessarily indicate only a distant phyletic connection to an otherwise similar form in which it is not developed.

Although *C. terblanchei* may be regarded simply as a less advanced form of *C. adustus*, its status as a separate species is retained. This is partly because *C. terblanchei* is relatively poorly known and its relationships are therefore more likely to be misinterpreted, and partly because it was found convenient to retain the names of two other Makapanian canid species (*Vulpes pattisoni*, *V. pulcher*) and for the sake of consistency *C. terblanchei* was treated in the same way. Ewer & Singer (1956: 345) state that the 'exact point (at) which progressive change is taken to be of sufficient importance to warrant nomenclatural recognition must be largely a matter of individual judgment.' *C. terblanchei* has been judged to merit separate species status and there is little point in suggesting a change based on another subjective opinion.

Referral of 15605 to *C. terblanchei* rather than the more advanced *C. adustus* is based largely on the relative breadths of P^1 to P^3, in which respect it is apparently similar to the *C. terblanchei* holotype and is definitely different to modern *C. adustus*.

The identification of a jackal in the Elandsfontein assemblage which has teeth resembling those of *C. adustus* raises yet another problem with that material referred to *C. mesomelas*. The teeth of the two modern species may be indistinguishable from one another (Ewer 1956*b*: 97, 98), and it is therefore possible that some of the specimens classified as *C. mesomelas* actually belong to *C. terblanchei*.

Relative age

It has already been indicated that the Transvaal *C. terblanchei* is Makapanian in age, but this is actually not certain. The holotype was originally reported to be from Kromdraai (Broom 1946), but apparently this is unlikely and its source is unknown (Ewer 1956*b*). The referred material was said to be from Coopers (Ewer 1956*b*), although subsequently Ewer (1956*c*: Table 2) did not list it as part of the carnivore fauna from this site. Whatever the actual source of the Transvaal specimens, they are almost certainly from the breccia deposits in the Krugersdorp area and they are most likely to be Makapanian in age.

Since there are no significant observable differences between 15605 and the type material, it follows that they might be broadly contemporaneous. The unusual preservation of 15605, and the specimens with which it was associated, may be an indication that this material differs in age from most other specimens from this site. The fauna associated with 15605 has not been investigated, but there is nothing obvious which would suggest it is of Makapanian age. The mandible from this occurrence earlier identified as belonging to *C. mesomelas* (15613) has dental characteristics which indicate that it could belong to either the Makapanian or Cornelian form of this species. Consequently, it is possible that some elements in the Elandsfontein assemblage predate the main Cornelian fauna. They could date from the Makapanian or perhaps from the earlier part of the Cornelian.

Taken in conjunction, the Elandsfontein jackals suggest that the fauna from this site is made up of elements aged as follows:

(1) A few specimens may be Makapanian or early Cornelian.
(2) The bulk are Cornelian.
(3) Some are Florisian.
(4) A few may be Holocene.

The only real departure from previously held opinions is that the fauna may include some specimens which are earlier than the main body of fossils. The evidence for this is very slender and it is probably preferable and certainly more convenient at this stage to regard all the early fossils as Cornelian in age. Until there is really convincing evidence to the contrary, the only age categories recognized in the Elandsfontein fauna are, in descending order of importance, Cornelian, Florisian and Holocene.

Family **Canidae**

Subfamily Caninae

Vulpes chama A. Smith, 1833

(Fig. 54)

Present status

The Cape or silver fox is now very rare in the south-western Cape Province, although it was formerly common.

Material

(1) *Elandsfontein*

21007—Parts of the skull and skeleton of a single individual, including:
Incomplete braincase; left maxillary fragment with P^3 to M^2; right mandible with $\overline{C}$ to M_2; left mandible with I_3 and P_2 to M_2.
Two vertebrae and parts of all four limbs.

5474, 5477, 5472—Right maxillary fragment with P^4; left maxillary with P^3 and P^4; isolated M^1.
5457, 5469—Right maxillary fragment with P^3, part of P^4, M^1 and M^2.
8073, 8114—Right and left M^2.

Mandibular fragments with teeth as follows:
5093 —Right P_4.
5453 —Right P_2 (incomplete), P_3, P_4 (incomplete) and M_1.
5455 —Right P_2 to M_1.
14244—Right M_1.
20022—Right M_1.
20023—Left M_1.

(2) *Swartklip*

ZW 1894—Left maxillary fragment with P^4.
ZW 2317—Right mandibular fragment with P_4 and M_1.

(3) *Sea Harvest, Saldanha*

S 39—Right P^4.

Comment

As with *Canis mesomelas*, the material here referred to *Vulpes chama* is heterogeneous and at least two forms are represented.

Description

Sea Harvest and Swartklip

The *Vulpes* specimens from these sites are too few and fragmentary to allow for adequate description of the form which they represent but, viewed in relation to the material previously referred to *C. mesomelas* and to other fossil and modern *Vulpes* specimens, their affinities are reasonably clear.

Of the four teeth represented, only one, the P_4 of ZW 2317, falls within the observed ranges of size of modern *V. chama* (Table 46). The M_1 of ZW 2317 is slightly broader than the broadest M_1 in the comparative series, while the upper carnassials from both sites are longer than any of those of the available *V. chama* specimens (Tables 45, 46).

Morphologically the fossil teeth are essentially similar to those of the moderns, although the Swartklip M_1 differs in having a relatively larger talonid. This tooth is broadest at about the midpoint of the talonid, rather than near the posterior end of the trigonid as in modern *V. chama*. The size of the M_2 alveolus indicates that this tooth was relatively large. The large M_2 together with the size of the M_1 talonid suggests that the upper molars of the Swartklip *Vulpes* must have been correspondingly larger than those of the modern species. This is indeed confirmed by the sizes of the M^1 and M^2 alveoli of ZW 1894.

Consequently, it appears that while the premolars of the Swartklip *Vulpes* were little or no different from those of modern *V. chama*, the carnassials and

TABLE 45

Dimensions of the upper teeth of fossil *Vulpes chama* from the south-western Cape, compared with those of *Canis terblanchei* and a series of modern *V. chama*.

		P^3		P^4		M^1		M^2		P^3:P^4	P^4:M^1
		l	b	l	b	l	b	l	b	l	l
Elandsfontein	21007	8,0	3,3	13,3	7,3	10,6	13,4	*c.* 6,4	*c.* 10,2	1:1,66	1,25:1
	5472/77	8,1	3,2	13,5	6,7	10,0	13,5	—	—	1:1,66	1,35:1
Swartklip	ZW 1894	—	—	11,8	6,0	—	—	—	—	—	—
Sea Harvest	S 39	—	—	11,1	6,1	—	—	—	—	—	—
Modern *Vulpes chama*	Mean	6,2	2,5	9,8	5,6	7,7	10,6	5,6	8,4	1:1,58	1,27:1
	Range	5,5–7,0	2,2–3,5	9,3–10,5	4,9–6,2	7,1–8,4	9,3–11,5	4,9–6,3	7,4–9,3	1:1,45–1:1,75	1,13:1–1,36:1
	n	23		23		22		21		23	22
*Canis terblanchei**	Type	9,2	—	*c.* 14,5	—	11,1	—	7,8	11,7	1:1,58	1,31:1
	$K_2$83	—	—	15,0	7,3	11,0	13,1	7,7	10,8	—	1,36:1

* Ewer 1956*b*.

TABLE 46

Dimensions of the lower teeth of the Elandsfontein and Swartklip *Vulpes chama* compared with those of *V. pulches* and *Canis terblanchei* from the Transvaal and a series of modern *V. chama*.

		P_1		P_2		P_3		P_4			M_1		M_2		P_4:M_1	M_1:M_2	P_1–P_4l
		l	b	l	b	l	b	l	b	l:b	l	b	l	b	l	l	
*Vulpes pulcher**	Swartkrans	3,0	1,6	6,2	2,3	6,8	2,4	7,4	3,2	2,31:1	12,1	4,6	6,0	4,7	1:1,64	2,01:1	26,6
	Kromdraai	3,7	1,9	7,1	2,4	8,0	2,5	8,4	3,2	2,63:1	14,0	5,0	7,1	—	1:1,66	1,97:1	29,1
Elandsfontein	21007	*c.* 3,5	2,3	*c.* 6,8	3,0	7,5	3,1	8,6	3,8	2,26:1	15,5	6,9	8,8	6,5	1:1,80	1,76:1	*c.* 27,4
	5455	—	—	7,0	3,1	7,6	3,3	8,4	3,8	2,21:1	15,3	6,2	—	—	1:1,82	—	*c.* 29,0
	20022	—	—	—	—	—	—	—	—	—	15,1	6,2	—	—	—	—	*c.* 28,5
	20023	—	—	—	—	—	—	—	—	—	14,4	6,4	—	—	—	—	—
	5093	—	—	—	—	—	—	8,9	4,0	2,23:1	—	—	—	—	—	—	—
Swartklip	ZW 2317	—	—	—	—	—	—	7,0	3,1	2,26:1	12,4	5,8	—	—	1:1,77	—	—
Modern *Vulpes chama*	Mean	2,7	1,7	5,5	2,2	6,2	2,5	7,1	3,2	2,21:1	11,5	4,8	6,4	4,7	1:1,61	1,80:1	25,7
	Range	2,4–3,1	1,5–1,9	5,2–6,4	2,0–2,5	5,7–6,9	2,2–2,9	6,5–8,1	2,9–3,6	1,91:1–2,45:1	10,9–12,6	4,3–5,6	5,6–7,0	4,0–5,2	1:1,48–1:1,72	1,64:1–1,98:1	23,9–27,6
	n	22		22		23		23		23	23		23		23	23	8
*Canis terblanchei**	Type	3,9	2,4	8,4	3,3	9,6	3,5	10,7	4,2	2,55:1	15,7	*c.* 6,7	9,1	7,2	1:1,47	1,73:1	39,1
	$K_2$82	—	—	—	—	—	—	—	—	—	15,8	6,8	8,9	6,7	—	1,77:1	—

* Ewer 1956*b*.

Fig. 54. Buccal view of the *Vulpes chama* mandible (21007) from Elandsfontein.

molars were appreciably larger. A possible exception is the M_3, the size of which is not known.

That part of the mandibular corpus of ZW 2317 which remains is poorly reserved, but it is clearly much more robust than the slender corpora of modern *V. chama*. In addition, it has a well-developed subangular lobe, which is in marked contrast to the mandible of the modern species.

The Swartklip and Sea Harvest *Vulpes* are evidently similar to the *C. mesomelas* from these sites in that they are larger than their modern counterpart. The Swartklip form also differs from the modern species in respect of the relative sizes of certain teeth, a fact that will be enlarged upon later. It has already been suggested that the Sea Harvest fauna is intermediate in age between that from Swartklip and the present, and interestingly the Sea Harvest P^4 is intermediate in size between that of ZW 1894 and those of the modern comparative series (Fig. 55). In view of the small number of specimens involved this is not necessarily significant, but at least the small size difference between the Swartklip and Sea Harvest upper carnassials is in the right order.

Elandsfontein

The Elandsfontein material belongs to a canid with a skull comparable in size to that of modern *V. vulpes*. Superficially it differs appreciably from both *V. vulpes* and *V. chama* and initially it was thought to belong to a small jackal rather than a large fox. The most important osteological character which distinguishes the skulls of jackals from those of foxes, the inflated frontal sinuses in the former (Huxley, 1880), cannot be observed in any of the specimens presently available and their relationships had, therefore, to be determined on other grounds.

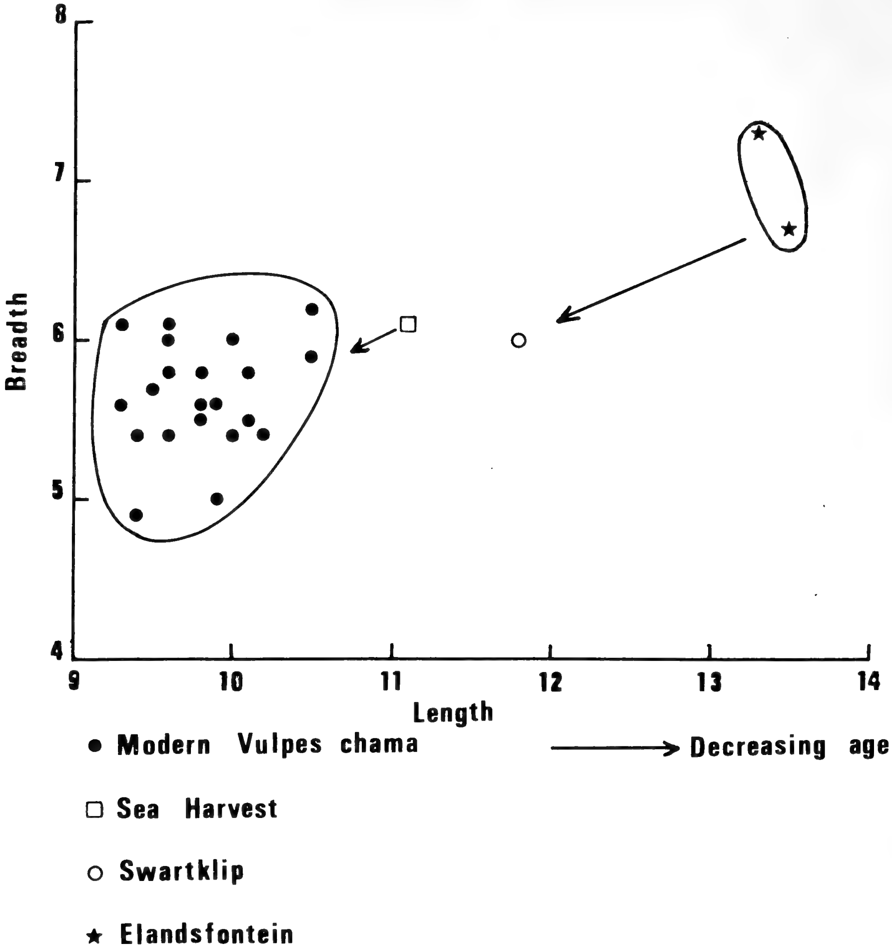

Fig. 55a. Dimensions of the P^4 of modern and fossil *Vulpes*.

Most of the observations which follow are based on the specimen 21007.

This form is clearly not conspecific with either of the canid species already described, although in respect of actual size of the posterior cheekteeth and the carnassial: molar ratios it is similar to *C. terblanchei*. The pre-carnassial teeth of 21007 are, however, appreciably smaller than any of the recorded fossil and modern jackals of southern Africa, a character best illustrated by the P_4:M_1 length ratio and P_1 to P_4 length. The contrast in the sizes of the anterior and posterior cheekteeth is reminiscent of the Swartklip *Vulpes*, although the actual size of the individual teeth of this form is appreciably less. In addition, the Elandsfontein *Vulpes* is smaller in overall size than any of the local jackals, but in this respect it is similar to fossil material from the Transvaal which is referred to a species of *Vulpes*, namely, *V. pulcher* from Kromdraai (Broom 1939).

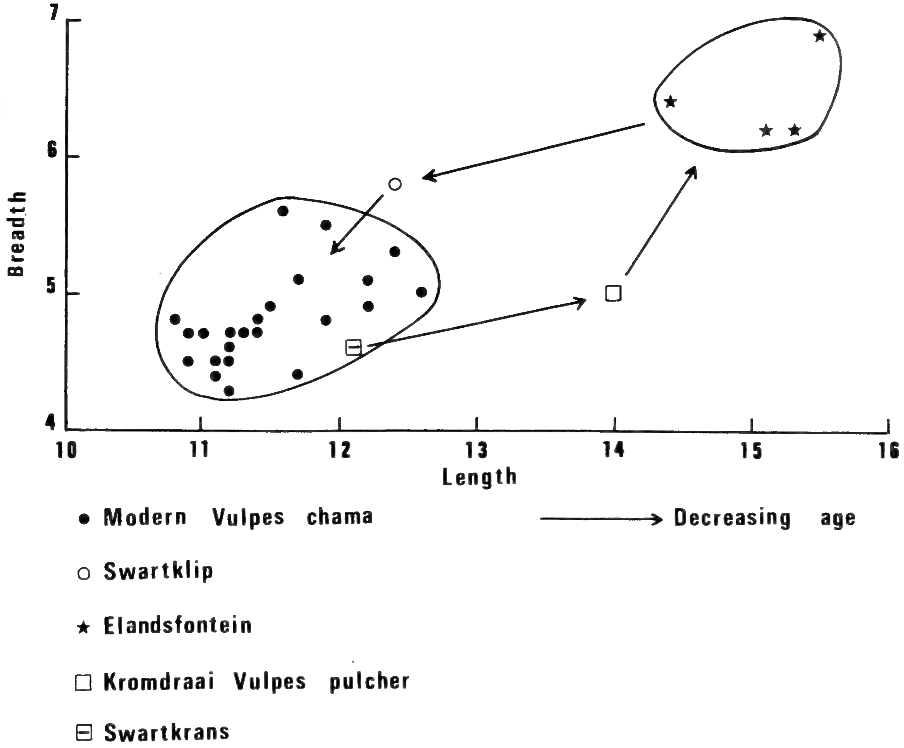

Fig. 55b. Dimensions of the M_1 of modern and fossil *Vulpes*.

The *Vulpes* which have been recorded from the South African Quaternary are, in descending order of age, as follows:

(1) *V. pattisoni* from Taung (Broom 1948), a small species comparable in size to modern *V. chama*. It is poorly known and largely excluded from the discussions which follow.
(2) A specimen from Swartkrans belonging to a species intermediate in size between *V. chama* and *V. vulpes* and which was referred by Ewer (1956*b*) to *V. pulcher*.
(3) The Kromdraai *V. pulcher*, which is in most respects a little larger than the Swartkrans form.
(4) Specimens which are Florisian in age and which are referred to *V. chama* (see Cooke 1963: Table 7), including those from Swartklip.
(5) Modern *V. chama*.

On the assumptions that these five units represent different stages of a single lineage and that the Elandsfontein specimens are Cornelian in age, it follows that 21007 should conform to the sequence in a position intermediate between the *V. pulcher* holotype and the Florisian *V. chama*, which is represented locally by the specimens from Swartklip. The characteristics of 21007 were investigated with this in mind.

There was apparently an increase in size with time in the Makapanian forms of *Vulpes* from the small *V. pattisoni* to the large *V. pulcher* holotype, with the Swartkrans specimen in an intermediate position. This was followed by a decrease in size with time with the Florisian form being intermediate between *V. pulcher* and modern *V. chama*. The length of the lower premolar row of 21007 is similar to that of the *V. pulcher* holotype, while the molars are longer. This indicates that the early Pleistocene size increase was continued in the Elandsfontein form at least in respect of the molars, and perhaps in overall size as well. It is, therefore, not out of place in the hypothetical phyletic series in respect of size.

The greater development of the molars relative to the premolars has already been mentioned in connection with the Elandsfontein and Swartklip specimens and, where possible, the P_4:M_1 length ratios were compared in order to determine the nature of changes in this respect. This ratio was found to be quite variable in the modern form, but, assuming that the fossil specimens represent fairly typical examples of their respective populations, it is apparent that there was a trend in the relative development of these two teeth which was consistent with the inferred overall size of individuals in the various populations (Table 46). The largest M_1 in both a relative and absolute sense is that of the Elandsfontein form.

The changes in the M_1:M_2 ratios of the fossil series also appear to be consistent, but in this instance the M_2 with the greatest relative length is apparently that of the Swartklip form. The estimated M_1:M_2 length ratio of ZW 2317 is calculated to be below 1,60:1 and is, therefore, less than the minimum observed in the modern comparative series. The trend towards the lengthening of M_2 thus appears to have been reversed in the Holocene.

In at least one respect the *V. pulcher* holotype is unlike any of the other specimens. The relatively narrow premolars of the Kromdraai specimen were remarked upon by Ewer (1956*b*) and its difference to the other forms in this respect is clearly illustrated by the P_4 length:breadth ratios recorded in Table 42. There is no detectable trend in the fossil series in the relative breadths of the premolars.

Upper dentitions are either unrepresented or less well represented in the fossil series, but they presumably underwent changes comparable to those in the lower teeth. The relative sizes of the Elandsfontein, Swartklip and modern upper carnassials are certainly similar to those of the lower carnassials and the same apparently applies in the case of the upper molars. However, the P^3:P^4 length ratio of 21007 does not differ from the moderns in the same way as the P_4:M_1 length ratio. As a general rule, the upper teeth of the Canidae appear to be less useful in distinguishing species than the lowers.

There are yet other indications of a relationship between the Elandsfontein and Swartklip specimens. The relatively large M_1 talonid of ZW 2317 was mentioned earlier and, although none of the lower carnassials from Elandsfontein has the talonid quite as prominent, in four of the five known specimens it is the broadest part of the tooth. This may indicate a development in the M_1 of the Elandsfontein form which is consistent with the trend in the fossils towards an increase in the size of grinding surfaces on the posterior cheekteeth.

Another feature of ZW 2317 is the prominent subangular lobe of the mandible. It is also well developed in the only three specimens from Elandsfontein in which the posterior part of the mandibular corpus is preserved. The three specimens belong to a young adult (20023), a mature adult (21007) and a very aged individual (5453). The nature of the subangular region in *V. pulcher* is not recorded.

The available evidence, limited as it is because of the small number of specimens involved, suggests that there are grounds for regarding the South African Quaternary *Vulpes* as belonging to a single lineage.

The fragmentary braincase of 21007 is comparable in size to corresponding parts of the skull of *V. vulpes* and it resembles this species in having a fairly prominent sagittal crest. It differs from the skull of modern *V. chama* in its larger size, more prominent sagittal crest and less inflated braincase.

The body size of the Elandsfontein *Vulpes* can be gauged from a comparison between limb bone dimensions of 21007, modern *V. chama* (1 male) and modern *C. mesomelas* (1 male, 1 female, 1 sex unknown) (Table 47). It was clearly a species which was much smaller than *C. mesomelas.* The individual limb bones of 21007 were even a little shorter than those of the *V. chama* skeleton, although the limb segment ratios are similar (Table 48). The fossil bones are, however, more stoutly proportioned, indicating that although it was comparable in stature to modern *V. chama,* it had a heavier body. The more robust body was coupled with a head which was larger than that of the modern species.

Discussion

Having suggested that those fossils from South Africa which are referred to *Vulpes* probably represent a single lineage, parallels can be drawn between the nomenclatural problems involving this group and those which were discussed in connection with the jackals.

Little can be said of *V. pattisoni* because it is so poorly known, but *V. pulcher* is like *C. mesomelas pappos* in that it includes material from more than one site and is a taxon comprised of samples which are heterogeneous in a temporal sense. The differences between *V. pulcher* and modern *V. chama* appear to be more marked than those between *C. mesomelas pappos* and modern *C. mesomelas.* This is largely due to the greater size of the *V. pulcher* specimens relative to the moderns, since other observable differences are probably no greater in the foxes than they are in the jackals. The fact that the fossil fox is afforded full species status and the jackal only subspecific status thus reflects an inconsistent approach to the problem of their taxonomy.

In respect of differences between the Elandsfontein *Vulpes* and modern *V. chama* much the same applies. In some features (e.g. the actual size of posterior cheekteeth; P_4:M_1 length ratio) they are even more different from modern *V. chama* specimens than is the material referred to *V. pulcher*, while in others (e.g. the P_4 length:breadth and M_1:M_2 length ratios) they are closer to the modern specimens. Once again, excluding differences in actual skull size,

TABLE 47

Dimensions of elements of the postcranial skeleton of the *Vulpes chama* from Elandsfontein compared with those of three modern *Canis mesomelas* and one modern *V. chama*.

		Humerus					Radius					Femur		Tibia			
		Overall length	Max. a–p diam. of prox. end	Max. trans. diam. of prox. end	Max. a–p diam. of dist. end	Max. trans. diam. of dist. end	Overall length	Max. a–p diam. of prox. end	Max. trans. diam. of prox. end	Max. a–p diam. of dist. end	Max. trans. diam. of dist. end	Max. a–p diam. of dist. end	Max. trans. diam. of dist. end	Overall length	Max. trans. diam. of prox. end	Max. a–p diam. of dist. end	Max. trans. diam. of dist. end
Elands-fontein	21007	105,0	22,3	18,3	15,1	19,8	101,7	6,9	10,3	7,5	14,0	22,2	19,2	116,0	20,6	10,0	13,2
Canis mesomelas	SAM 35823 ♂	135,0	30,2	21,1	17,0	22,6	140,0	8,5	12,5	9,3	16,7	26,3	21,9	158,0	23,1	11,5	15,7
	SAM 36252	129,3	27,2	24,3	18,1	24,3	132,1	8,9	12,9	9,1	18,0	29,7	22,5	151,0	25,0	11,2	15,7
	SAM 35824 ♀	123,5	28,4	22,6	17,3	22,8	131,6	8,6	13,0	8,8	17,2	25,8	21,8	145,0	24,9	11,5	15,8
Vulpes chama	SAM 35600	110,0	20,1	17,4	12,2	16,0	106,4	5,7	9,3	7,1	12,0	19,3	17,3	127,3	19,4	8,6	12,5

TABLE 48

Limb segment ratios of the *Vulpes chama* from Elandsfontein, compared with those of modern *V. chama* and *Canis mesomelas*.

	n	Humero-radial index	Tibio-radial index
Elandsfontein 21007 . . .	1	96,7	87,7
Vulpes chama	1	96,7	83,6
Canis mesomelas	3	104,1	89,0

the contrasts between the Elandsfontein *Vulpes* and modern *V. chama* are probably no greater than those between contemporary populations of *C. mesomelas*.

In the case of Cornelian and Florisian *C. mesomelas*, distinctions were made on the basis of relative tooth sizes (i.e. the P^4:M^1 and M_1:M_2 length ratios differ), but not actual skull size. The Cornelian and Florisian *Vulpes* are distinguished mainly by actual skull size and not relative tooth sizes (e.g. P_4:M_1 length ratios are essentially similar). The differences between Florisian and Holocene *C. mesomelas* were largely a matter of actual average size. Florisian and Holocene *Vulpes* also differ in this respect, but in addition there are differences in relative tooth sizes as well (e.g. P_4:M_1 length ratios).

The fossil *Vulpes* therefore contrasts with *C. mesomelas* in that it apparently underwent more marked changes in size, while the nature of the changes in the dentition were not the same. For example, a relatively long M_2 was a characteristic of early *C. mesomelas*, but developed to an extreme only in Florisian *Vulpes*. In addition, changes in dental characteristics were not synchronous in the jackals and foxes. A graded classification of fossil *C. mesomelas* could conveniently have distinguished between the Florisian and pre-Florisian forms, each group perhaps being given species status (i.e. *C. pappos* for the pre-Florisian group and *C. mesomelas* for the Florisian group). This would, however, have served no useful purpose because of the impossibility of distinguishing Holocene *C. mesomelas* from the two fossil categories.

By contrast, a graded classification based on the dental characteristics of fossil *Vulpes* could conveniently distinguish between the Makapanian forms (*V. pattisoni* and *V. pulcher*), a Cornelian/Florisian form (*Vulpes* n. sp.) and the Holocene *V. chama*. In this instance so few fossil specimens are involved that definition of the four categories would present no real difficulties, although the recovery of additional specimens could well render the definitions impracticable. One difficulty in this categorization is that when the actual size of individuals is taken into account, it is found that the Cornelian *Vulpes* is actually closer to *V. pulcher* rather than to the Florisian form. In other words, the most readily evident feature of the fossils (i.e. skull size) does not conform to a categorization based on dental characteristics.

If a new species name were to be given to the south-western Cape fossils, the definition would of necessity have to take into account the heterogeneous character of the Cornelian and Florisian specimens. Consequently, instead of defining a heterogeneous new species, it might be preferable to refer the fossil to an existing species and to extend its definition to include the characters of the Elandsfontein and Swartklip material. In this event, the local fossils could be referred to either *V. pulcher* or *V chama*. This material is in fact here referred to *V. chama* because the Swartklip specimens are closer to the modern species in morphology and time than the Elandsfontein specimens are to *V. pulcher*. In the final analysis, this decision is probably as subjective as any other in taxonomic problems of this kind.

The fossil populations of *C. mesomelas* were distinguished from one another by prefacing them with the age name to which they belong (e.g. Cornelian *C. mesomelas*), and this is also done in the case of the fossil *V. chama* from the south-western Cape. It serves to indicate that the Cornelian and Florisian forms differ from one another, that both differ from *V. chama*, but that all are part of the phyletic series which culminated in the extant silver fox.

While the naming of the local fossil *Vulpes* adopted here may not be an ideal solution to the problem of nomenclature, it is regarded as simple and convenient. Once again the way is left open for others who feel that new species and/or subspecies names are more desirable.

As with *C. mesomelas* and *C. terblanchei*, the existing names of the Makapanian forms are retained. In this connection it is worth noting that there is a precedent for distinguishing early Pleistocene foxes at the species level. In Europe each of the extant species is preceded by only one Pleistocene fossil species. *V. alopecoides* may be ancestral to both *V. vulpes* and *Alopex lagopus*, while *V. praecorsac* is ancestral to *V. corsac* (Kurtén 1968).

Family **Canidae**

Subfamily Simocyoninae

Lycaon pictus Temminck, 1820

(Fig. 56; also Ewer & Singer 1956: pls 30, 31)

Present status

The hunting dog is now extinct in the south-western Cape, but it apparently still occurred in the northern parts of the region in the eighteenth century.

Material

(1) *Elandsfontein*

(a) Previously described specimens (Ewer & Singer 1956):

EC 12—Right mandibular fragment with I_2, I_3 and $\overline{C}$. (Note: Number given as EC 121 in the original description.)

EC 13—Left mandibular fragment with P_1 to M_1 (Note: The M_1 was added to this specimen subsequent to its description.)
EC 30—Incomplete right M_1.

(b) Additional specimens:

EC 37—Right mandibular fragment with roots of cheekteeth.
6701 —Right mandibular fragment with parts of P_1 and P_2, P_3, part of P_4, and M_1.
17058 —Right mandibular fragment with part of M_2.
20439 —Right mandibular fragment with parts of $\bar{C}$, P_1, P_3 and P_4.
9194 —Part of right P^4.

(2) *Swartklip*

ZW 137 —Right I^2.
ZW 177 —Part of left I^3.
ZW 2320—Left M^1.
ZW 3070—Left I_3.
ZW 2314—Left mandibular fragment with part of $\bar{C}$.

Description

Elandsfontein

In their description of the *Lycaon* remains from Elandsfontein, Ewer & Singer (1956: 341) noted the following differences between the modern and fossil forms:

(1) 'the fossil jaw is considerably longer than that of the extant species'.
(2) 'the premolars are considerably longer, but not much broader'.
(3) 'the canine and I_3 are significantly larger in both dimensions while the significance of the slightly greater breadth of I_2 is less certain'.

On the basis of these differences the material was referred to a distinct subspecies, *Lycaon pictus magnus*.

The discovery of additional specimens of this species allows for amplification and modification of these observations.

Although it was stated that, 'Apart from their greater length the teeth differ in no way from those of the living *Lycaon pictus*' (Ewer & Singer, 1956: 341), there are other differences in some of the teeth. The most striking of these is the absence or small size of anterior accessory cusps on the P_2 to P_4 of the fossil. In the available modern *L. pictus* specimens ($n = 4$) the anterior and posterior accessory cusps are variably developed and are progressively less prominent from P_4 to P_2. They were, nevertheless, always present, although the anterior accessory cusp of P_2 was very small. In EC 13 this cusp is barely discernible on the P_3 and P_4, while it was not present at all on the P_2. The anterior portion of the P_2 of 6701 is lost, but in the P_3 the anterior accessory cusp is absent and in the P_4 it is very small.

L. p. magnus also differs from the modern form in having a relatively smaller M_1 metaconid. In addition, the three known lower carnassials of the

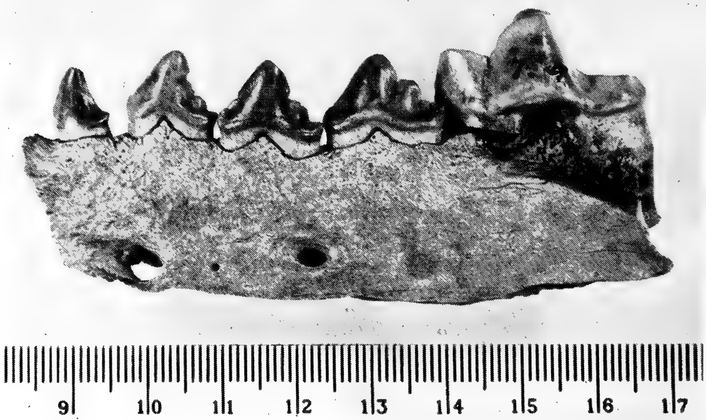

Fig. 56. Buccal view of the *Lycaon pictus* mandible (EC 13) from Elandsfontein.

fossil form have a small ridge on the lingual surface of the talonid which is not present in any of the available modern specimens.

There is a curious anomaly in the length/breadth ratios of the lower cheekteeth of the Elandsfontein *Lycaon*. The premolars of EC 13 are narrow relative to those of the moderns, but the carnassial is comparable in width (Table 49). The difference in the P_2 to P_4 of EC 13 is due largely to the lack of inflation of the postero-internal cingula of these teeth. This inflation is evident in the premolars of the available modern specimens as well as the fossil 6701. In the latter specimen it is the M_1 which is unusual, since it is relatively broader than the lower carnassials of EC 13 and the extant form. The modern species thus has premolars with length/breadth ratios comparable to 6701, but the M_1 length/breadth ratio is comparable to that of EC 13. Many more modern and fossil specimens are required before the significance of these similarities and differences can be assessed, but the earlier comment by Ewer & Singer on the breadth of the premolars of *L. p. magnus* is invalid in view of the nature of these teeth in 6701.

Standard measurements could not be taken on the incomplete P^4 (9194), which is the only known upper tooth of the Elandsfontein *Lycaon*, but it is appreciably larger than any in the comparative series.

Swartklip

The Swartklip mandibular fragment (ZW 2314) has a very slender corpus and probably belonged to an immature individual. The preserved canine and the alveoli of the cheekteeth compare in size to those of the available modern specimens.

The M_1 (ZW 2320) also falls within the size range of variation of the modern species. It measures 15,8 by 16,2 mm.

TABLE 49

Dimensions of the lower teeth of the Elandsfontein and Swartklip *Lycaon pictus* compared with those of a series of modern specimens.

		I_3		$\bar{C}$		P_1		P_2		P_3		P_4			M_1		
		l	b	l	b	l	b	l	b	l	b	l	b	l:b	l	b	l:b
Elandsfontein . . .	EC 12	7,7	6,5	12,9	9,1	—	—	—	—	—	—	—	—	—	—	—	—
	EC 13	—	—	—	—	8,1	5,2	12,4	5,6	14,2	6,2	16,4	7,4	2,22:1	28,7	10,6	2,71:1
	6701	—	—	—	—	—	*c.* 5,1	—	*c.* 6,6	13,7	7,0	*c.* 15,6	8,2	1,90:1	27,4	12,0	2,28:1
Swartklip	ZW 3070 ZW 2314	7,9	6,3	*c.* 12,0	7,7	—	—	—	—	—	—	—	—	—	—	—	—
Modern *Lycaon pictus* .	Mean	6,4	5,7	10,3	7,5	6,0	4,3	9,8	5,2	11,4	5,9	13,6	7,0	1,94:1	24,1	9,6	2,53:1
	Range	5,9–6,7	5,1–6,2	8,9–11,3	7,3–8,1	5,1–7,1	3,9–5,1	8,8–10,8	4,8–5,6	10,4–12,3	5,5–6,5	13,1–14,2	6,5–7,6	1,87:1–2,02:1	22,2–25,6	8,5–10,3	2,45:1–2,61:1
	n	4		4		4		4		4		4			4		

The only tooth in the *Lycaon* dentition which is common to the Elandsfontein and Swartklip assemblages is the I_3. The two fossil specimens (EC 12, ZW 3070) are similar in size and larger than the I_3 in the comparative series. The I^2 and I^3 from Swartklip (ZW 137, ZW 177) are also a little larger than the modern specimens, in spite of the statement to the contrary made about them earlier (Hendey & Hendey 1968: 64). ZW 137 measures 7,4 by 7,2 mm and ZW 177 measures 6,7 by 8,4 mm.

Discussion

The Elandsfontein *Lycaon pictus* material is apparently a homogeneous unit and represents a variety of this species which is appreciably larger than the moderns in most observable respects. It almost certainly belongs with the earlier (Cornelian) element of the Elandsfontein fauna.

The Swartklip *L. pictus* appears to be comparable to the moderns in size, although the incisors at least are more like those of the Elandsfontein form.

The available comparative series is obviously far too small to allow for an accurate assessment of size similarities and differences to be made, but it is not unexpected to find that the Swartklip *Lycaon* differs from that from Elandsfontein and is closer to but still different from the modern form. In keeping with the earlier decision to avoid the use of subspecific names, the local forms are categorized simply as 'Cornelian' and 'Florisian *Lycaon pictus*'.

In this instance, however, the former variety already has a subspecies name applied to it, and since its use may still be favoured by some, it is here redefined on the basis of the additional specimens which are now available.

Lycaon pictus magnus Ewer & Singer, 1956

A variety of *Lycaon pictus* which dates from the Cornelian age of the South African Pleistocene and which is presently recorded only from Elandsfontein in the Cape Province. It differs from the extant variety in its larger size, in the absence or near absence of anterior accessory cusps on the second to fourth lower premolars, and in having a relatively smaller metaconid on the lower carnassial.

Family **Canidae**

Subfamily Otocyoninae

Otocyon megalotis Desmarest, 1822

Although the bat-eared fox still occurs in the adjacent Cape west coast and Karroo regions, and was much more common in these areas in the past, there are no comparable records of this species in the south-western Cape. However, the presence of a family group in the vicinity of Paarl near Cape Town was recently reported by a local newspaper (*The Argus*, 29 December 1972) and the species is included here on the basis of this record.

There is no obvious reason why *Otocyon* should not have been common locally earlier in the historic period and before, although since it is essentially confined to the drier parts of sub-Saharan Africa it may well have found the environment of the south-western Cape unsuitable, especially at those times when it was cooler and wetter (e.g. the late Pleistocene). There are at least two other carnivores, namely, *Cynictis penicillata* and *Proteles cristatus*, which occur commonly in the adjacent more arid regions, that are known only from isolated recent records in the south-western Cape. Together with *Otocyon* they may have run counter to the general trend by actually extending their ranges into the south-western Cape comparatively recently. Their presence locally may thus be, or have been, dependent on the more arid conditions prevailing today and at other times earlier in the Quaternary.

Family **Mustelidae**

Subfamily Mustelinae

Ictonyx striatus Perry, 1810

(Fig. 57)

Present status

The striped polecat is one of the most commonly occurring fissiped carnivores in the south-western Cape today.

Material

Elandsfontein

9200—Braincase with associated right maxillary fragment which includes part of P^3.

Description

The fossil skull belongs to a small mustelid and is that of an aged individual, probably a male because of the presence of a well-developed sagittal crest. It is undoubtedly an *Ictonyx*, although it does differ in certain respects from the available skulls of modern *I. striatus* ($n = 6$).

The frontal region of 9200 is damaged and incomplete, and the right maxillary fragment is detached from the rest of the skull. The maxillary fragment is indistinguishable from corresponding parts of the modern specimens in all observable respects. The incomplete P^3 lacks most of its anterior half and the wear on the posterior keel indicates that the individual concerned was advanced in age. The posterior part of the $\underline{C}$ alveolus is preserved, as are the alveoli of P^2, P^4 and M^1. The teeth of the fossil were similar in arrangement, and apparently also in size to those of the modern species.

The remaining part of the frontal region of the fossil is, in general, similar to that of the comparative specimens, although the frontal sinuses are less inflated. Only a part of the left post-orbital process is preserved, but sufficient remains to indicate that it was more prominent than those of the modern specimens. Similarly the temporal ridges are well developed and clearly discernible. The post-orbital constriction is appreciably narrower than that of the moderns (Table 50).

TABLE 50

Dimensions of the skull of the Elandsfontein *Ictonyx* compared with those of a series of modern *I. striatus*.

		Braincase length from post-orbital constriction	Post-orbital constriction	Mastoid width	Width across occipital condyles	Trans. diam. of bulla at auditory meatus
Elandsfontein	9200	32,4	12,2	35,4	14,1	12,3
Modern *Ictonyx striatus*	Mean	35,9	14,6	33,5	15,9	11,9
	Range	32,8– 38,5	13,2– 16,2	30,7– 35,2	15,0– 16,8	10,5– 13,5
	n	6	6	6	6	6

The braincase is correspondingly narrowed and its lesser development is most evident when the specimen is viewed from the posterior, since the occipital almost completely obscures those parts of the braincase anterior to it. By contrast, the squamosals and parietals of the modern species are visible as an arch of bone over the occipital. The narrowing of the braincase is, however, confined to the more dorsal parts and the mastoid width is within the range of variation observed in the comparative series. The braincase is shorter even than that of the smallest female in the comparative series and is appreciably shorter than that of the largest male. The bone surface of the braincase is very rugose and while older individuals in the comparative series also exhibit such rugosity, in none was it developed to the same degree.

The width across the occipital condyles is less than in the modern specimens and the foramen magnum is correspondingly smaller. In all the modern specimens the occipital above the foramen magnum rises more or less vertically to the nuchal crest, but in the fossil there is a very prominent shelf of bone projecting over the dorsal margin of the foramen. The older of the modern specimens exhibit a similar feature, but in none is it as prominently developed.

The basicranium of the fossil is essentially similar to those of the moderns, except that the tympanic bullae are a little more inflated and there is a more pronounced ridging of bone along the midline of the basi-occipital.

Discussion

At least some of the characteristics of the fossil braincase are apparently due to the advanced age of the individual. Anderson (1970: 15, 16) mentions that with advancing age in *Martes*, the post-orbital constriction is narrowed, the gross size of the braincase decreases, the post-orbital processes are enlarged and a prominent sagittal crest is developed in males, while there is also 'an increase in the mass of the bone of the skull'. Presumably the same applies in the case of other mustelid genera.

Judging from the wear on the P^3 of 9200, this individual was older than any in the comparative series and since the ageing characteristics mentioned by Anderson are also the principal characters which distinguish the fossil from the moderns, the differences may be accounted for by this fact. An increase in the size of the brain cavity of 9200 would result in an inflation of the parietal/squamosal walls, widening of the post-orbital constriction, straightening of the occiput dorsal to the foramen magnum, increasing size of the foramen magnum itself and perhaps also an overall lengthening of the braincase. A reduction in the mass of the bone of the skull would reduce or eliminate the rugosity of the bone surface. These changes, coupled with a reduction of the post-orbital processes and sagittal crest would result in 9200 bearing a far closer resemblance to the available modern *I. striatus* specimens.

It is, however, likely that the fossil braincase would still be shorter than those of the males of the comparative series and that the bullae would still be more inflated. In addition, there might well be other differences between the modern and fossil specimens which cannot be determined on the basis of the available material. The differences do not, however, preclude the possibility

Fig. 57. Dorsal and ventral views of the *Ictonyx striatus* braincase (9200) from Elandsfontein.

of a close relationship between the fossil and *I. striatus*. Judging from its preservation, 9200 belongs in the Cornelian element of the Elandsfontein fauna and it is here regarded as representing a relatively primitive variety of the modern species.

I. striatus is the most widely distributed small mustelid in Africa today, but it has not previously been recorded as a fossil and nothing definite has been known of its origins and ancestry. The Elandsfontein record indicates that the species has undergone comparatively little change during the latter part of the Quaternary. *Ictonyx* has probably been a well-established member of the small carnivore fauna of Africa for much longer than that and it perhaps had its origins during the Pliocene when the Eurasian element in the African fauna was still well represented. It is remarkable that it should have remained so successful in spite of the radiation of the small viverrids in Africa.

Family **Mustelidae**

Subfamily Mellivorinae

Mellivora cf. *capensis* Schreber, 1776

Material

Baard's Quarry, Langebaanweg

L 179/12—Right mandibular fragment with parts of P_3 and P_4.

Description

This rather poorly preserved specimen has only the P_4 reasonably intact. The principal and posterior accessory cusps are damaged, but sufficient remains to show that in size (Table 51) and morphology it is indistinguishable from the corresponding tooth in the available modern *Mellivora capensis* series ($n = 5$). The less complete P_3 is apparently also similar to that of *M. capensis*. The roots of P_2 and the posterior part of the C alveolus are preserved and, at least in respect of size and relative positions, these teeth resembled their counterparts in the modern species. The M_1 is lost and the alveolar region of this part of the mandible is damaged, but it appears that this tooth was relatively longer than that of *M. capensis*.

The mandibular corpus resembles that of the modern species. There are two mental foramina below P_3, but the fossil differs from the available comparative specimens in having a shorter symphysis. This terminates below P_3 rather than below the anterior part of P_4.

Discussion

With the exception of the possibly longer M_1 and slightly shorter symphysis, there are no grounds for believing that this specimen should be referred to a species other than *M. capensis*. The reservation in the identification is made simply because the specimen is so incomplete. Its significance lies chiefly in the fact that it is clearly not conspecific with the 'E' Quarry *Mellivora*, and it is one of the species which indicates that the Baard's Quarry fauna includes a post-Langebaanian element.

TABLE 51

Dimensions of the teeth of the Langebaanweg 'E' Quarry *Mellivora*, compared with those of the Baard's Quarry *Mellivora* cf. *capensis* and modern *M. capensis.*

			P_4		$P_4b \times 100/l$	M_1		$M_1b \times 100/l$
			l	b		l	b	
Langebaanweg	'E' Quarry	L 6385	9,7	5,3	54,6	14,2	6,1	43,0
	Baard's Quarry	L 179/12	9,7	6,0	61,9	*c.* 16,0	—	—
Modern *Mellivora capensis*		Mean	10,2	6,4	62,8	14,7	7,0	47,3
		Range	9,7– 11,1	6,0– 7,6	59,2– 68,5	13,9– 16,4	6,4– 7,7	45,8– 50,0
		n	5		5	5		5

Family **Mustelidae**

Subfamily Mellivorinae

Mellivora capensis Schreber, 1776

(Fig. 58; also Ewer & Singer 1956: pl. 32)

Present status

The honey-badger or ratel may still occur in isolated areas in the south-western Cape, but it is certainly rare.

Material

(1) *Elandsfontein*

(a) Previously described specimen (Ewer & Singer 1956):

EC 14 —An almost complete skull lacking only the zygomata, right I^1 and $\underline{C}$, left I^1 to I^3 and mandible.

(b) Additional specimens:

EC 44 —Braincase.

8640 —Parts of the skull of a single individual, including: Incomplete braincase; right maxilla with $\underline{C}$ and P^2 to M^1; left I^3; left maxilla with $\underline{C}$ and P^2 to M^1; right mandible with $\overline{C}$ and P_2 to M_1; left mandible with C, P_4 and M_1.

15616/7—Maxillary and mandible fragments of a single individual with teeth as follows:
Right I^3, $\underline{C}$ and P^2 to M^1; left $\underline{C}$, P^3, P^4 and part of M^1; right $\overline{C}$, P_3 and P_4; left C, P_2, P_4 and part of M_1.

15833 —Parts of the skulls of at least two individuals, including:
Incomplete braincase; right I^3, P^3, part of P^4, and M^1; Left maxillary fragment with damaged P^4; left maxillary fragment with P^4 and M^1; right and left mandibles lacking incisors.

20021 —Braincase.

20887/8—Parts of a skull including:
Incomplete braincase; left maxillary fragment with P^3 and P^4.

20916 —Maxillary fragments with right P^2, P^3 and part of P^4, and left P^3 and P^4.

20981 —Parts of a skull including:
Braincase; left maxillary fragment with P^3 to M^1.

(2) *Swartklip*

Previously described specimens:

ZW 1 —An almost complete skull lacking only zygomata, left I^2 and I^3, right $\underline{C}$ and mandible (Singer & Fuller 1962).

ZW 142—Left maxillary fragment with P^2 (Hendey & Hendey 1968).

(3) *Tygerfontein*

Q 88—An almost complete skull lacking only zygomata, left and right I^1 and I^2, and mandible.

(4) *Sea Harvest, Saldanha*

S 787—Braincase.

Description

All the fossils are morphologically indistinguishable from modern *Mellivora capensis,* but the specimens were categorized according to relative size.

The Sea Harvest braincase (S 787) is that of an immature individual with all the skull sutures unfused. It compares in size to the braincase of modern *M. capensis* males (Table 52), and it is tentatively regarded as belonging to a young male of a population which was little or no different to that which is still extant.

The Tygerfontein specimen (Q 88) is virtually indistinguishable from the skulls of modern *M. capensis* males (Tables 52, 53), and it is also regarded as belonging to the Holocene variety of this species.

Both the Swartklip specimens have already been described (Singer & Fuller 1962; Hendey & Hendey 1968), and neither can be distinguished from modern *M. capensis.* However, Singer & Fuller (1962: 208) concluded that this *Mellivora* 'is phylogenetically intermediate between the (Elandsfontein) form and the extant honey-badger' because the skull (ZW 1) is rather small. Judging from the nature of the sagittal crest, this skull probably belonged to a young male and if this is indeed the case then it is smaller than the skulls of males in the available comparative series.

Singer & Fuller's statement does, however, require qualification, since the Elandsfontein assemblage includes two varieties of *M. capensis.* The specimens numbered 15833 are from the Florisian Bone Circle occurrence and although the braincase is as large as that of the modern males, it is identified as belonging to a female because of the presence of temporal ridges rather than a sagittal crest. It is concluded that the Bone Circle *Mellivora* is a Florisian variety of *M. capensis* which was larger than its modern counterpart.

The other Elandsfontein specimens, which apparently represent both males and females, probably belong with the Cornelian element of the fauna and they are smaller than the available modern *M. capensis* specimens. This was mentioned by Ewer & Singer (1956) in their description of the specimen EC 14, which is also distinguished from the modern variety by its shorter palate. Unfortunately, the palate is not complete in any of the additional specimens.

Discussion

All the material is referred to *Mellivora capensis* and four temporal variants are recognized.

The earliest (Cornelian) form was smaller than modern *M. capensis* and is represented by most of the specimens from Elandsfontein. There are apparently two varieties represented in the local Florisian assemblages. The first is that from Swartklip, which was a little larger than the Cornelian variety, but still smaller than the moderns. The second is that from the Elandsfontein Bone

TABLE 52

Dimensions of the skull of fossil *Mellivora capensis* from the Cape Province, compared with those of a series of modern specimens.

	Elandsfontein—early form										Modern *Mellivora capensis*				
	20021 ?♂	8640 ?♂	EC 14 ?♀	EC 44 ?♀	20887 ?♀	20981 ?♀	Swart-klip ZW1	Eft. Bone O 15833 ?♀	Tyger-fontein Q 88 ?♂	Sea Harvest S 787 juv.	SAM 35574 ♂	SAM 19940 ?♂	SAM 3325 ♀	SAM 3326 ♀	SAM 36132 ?♀
Braincase length*	64,0	62,0	64,5	58,0	60,5	59,0	*c.* 67,0	76,5	73,5	70,0	70,5	77,5	69,0	66,5	67,0
Braincase width	60,1	60,2	59,6	57,9	56,8	55,5	61,7	—	70,0	66,3	63,1	72,2	62,5	63,5	60,5
Mastoid width	74,8	*c.* 72,5	74,4	66,9	—	59,5	—	84,5	92,3	73,1	87,3	96,4	85,3	72,8	78,2
Occipital height	44,2	41,0	39,1	37,4	—	37,0	43,0	26,2	49,0	45,2	46,5	45,7	41,9	41,9	43,0
Post-orbital constriction	—	—	28,2	29,0	29,0	27,9	32,1	—	33,9	40,7	26,1	36,0	34,4	35,0	34,7

* Approximate.

Fig. 58. Dorsal views of the *Mellivora capensis* skulls from Elandsfontein (EC 14) and Tygerfontein (Q 88).

Table 53

Dimensions of the upper teeth of fossil *Mellivora capensis* from the south-western Cape, compared with those of modern specimens.

		$\underline{C}$		P^2		P^3		P^4			M^1	
		l	b	l	b	l	b	l	b	bl*	ll*	b
Elandsfontein early form	8640	7,6	5,9	5,1	3,4	7,7	5,3	11,7	*c.* 8,9	4,0	6,0	11,1
	EC 14	7,3	5,6	5,1	3,5	7,6	5,0	10,8	9,5	3,9	6,4	9,5
	20981	—	—	—	—	8,1	5,0	*c.* 10,8	*c.* 8,5	3,8	5,0	9,3
	20888	—	—	—	—	*c.* 7,7	5,5	*c.* 10,9	8,9	—	—	—
	15616	7,8	6,4	5,1	3,8	7,3	5,6	11,9	9,0	4,6	5,5	10,5
	20916	—	—	5,3	4,0	8,3	6,3	11,9	9,5	—	—	—
Elandsfontein Bone Circle	15833	—	—	—	—	—	—	12,5	10,6	*c.* 4,6	8,4	12,0
Swartklip	ZW 1	8,2	6,4	5,3	3,8	8,7	6,3	12,8	10,3	4,7	7,1	11,2
	ZW 142	—	—	6,3	4,4	—	—	—	—	—	—	—
Tygerfontein	Q 88	*c.* 9,0	*c.* 7,5	6,6	4,3	9,1	6,6	13,7	12,8	4,8	8,1	12,0
Modern *Mellivora capensis*	Mean	8,2	6,4	5,8	3,9	8,6	6,0	13,3	11,0	4,6	8,3	11,0
	Range	7,1–9,4	5,3–7,4	5,3–6,6	3,4–4,5	8,2–9,3	5,3–6,5	11,9–14,8	10,1–13,0	4,1–5,0	7,2–10,7	10,4–13,0
	n	4		5		5		5			5	

* bl—buccal length; ll—lingual length.

TABLE 54

Dimensions of the lower teeth of fossil *Mellivora capensis* from the south-western Cape, compared with those of a series of modern specimens.

		$\overline{C}$		P_2		P_3		P_4		M_1	
		l	b	l	b	l	b	l	b	l	b
Elandsfontein early form	8640	8,0	6,5	5,0	3,7	6,4	4,4	9,4	5,4	13,2	6,2
	15616	8,6	6,8	—	—	6,3	4,8	9,5	5,7	—	—
Elandsfontein Bone Circle	15833	10,2	8,0	5,8	4,5	6,8	5,4	9,4	6,8	15,4	7,1
Modern *Mellivora capensis*	Mean	8,9	7,1	5,4	3,9	7,2	5,2	10,2	6,4	14,7	7,0
	Range	7,8–10,1	6,0–8,5	5,0–5,9	3,5–4,6	7,0–7,7	4,8–5,9	9,7–11,1	6,0–7,6	13,9–16,4	6,4–7,7
	n	4		5		5		5		5	

Circle occurrence and this one was larger than the modern variety. The last of the temporal variants is the modern form itself and it is represented by the fossils from Sea Harvest and Tygerfontein, as well as being recorded in the historic period.

It was concluded earlier on the basis of the *Canis mesomelas* from the Bone Circle and Swartklip that these two occurrences were broadly contemporaneous and, while this probably is the case, the *M. capensis* remains suggest that the Swartklip fauna is closer to the Cornelian element of the Elandsfontein fauna than is that from the Bone Circle.

The south-western Cape *Mellivora* is, therefore, categorized as follows:

Cornelian *M. capensis*—Elandsfontein
'Early' Florisian *M. capensis*—Swartklip
'Late' Florisian *M. capensis*—Elandsfontein Bone Circle
Holocene *M. capensis*—Sea Harvest, Tygerfontein and modern fauna

The difficulties in categorizing specimens solely on the basis of size were discussed earlier and it is certain that if larger samples of the four groups of *M. capensis* were available, each would overlap in size characters with preceding and/or succeeding groups. Consequently, it might well prove impossible to categorize certain specimens of unknown age if they differ in size from the 'typical' examples of the categories which are recognized here. This taxonomically informal and flexible categorization has, therefore, a very restricted application and the arrangement is necessarily provisional.

Perhaps the only point of real significance to emerge from the present study of *M. capensis* was the suggestion that the Swartklip fauna predates that from the Elandsfontein Bone Circle.

Family **Mustelidae**

Subfamily Lutrinae

Aonyx capensis Schinz, 1821

(Fig. 59; also Ewer 1962: pl. 1)

Present status

The Cape clawless otter is now very rare in the south-western Cape, but it was formerly common.

Material

Swartklip

(a) Previously described specimen (Ewer 1962):

ZW 6a—Left M_1.

(b) Additional specimens:

ZW 2672A—A crushed and incomplete skull comprising the right half of the braincase and the most posterior part of the right maxilla with M^1.

ZW 2672B—A crushed and incomplete skull made up largely of the left half of the braincase.

ZW 2672C—Part of the right tympanic region of a skull, possibly belonging with ZW 2672B.

The above three specimens were recovered from a single block of matrix and they represent at least two individuals.

ZW 2930—Left maxillary fragment with P^4 and M^1.

ZW 3486—Right M_1.

Description

The specimen ZW 6a was described in detail by Ewer (1962), and she concluded that it belongs to a species other than *Aonyx capensis.*

The additional specimens also differ from the modern species in certain respects, although in this instance there is no doubt that the material should be referred to *A. capensis.*

Since the skull fragments are crushed and incomplete, they could only be measured in a few places (Table 55), but it is in any case evident that they are larger than corresponding parts of the few available skulls of the modern species ($n = 4$). The nuchal crest of ZW 2672A, and what little remains of the anterior part of the sagittal crest, are more strongly developed than in the modern *A. capensis* specimens, while the post-orbital process is more prominent. The tympanic bulla is less inflated than those of the moderns, but it has an appreciably greater transverse diameter. The difference between the antero-posterior diameters is less marked. Similarly, the glenoid fossa has a greater transverse diameter, but otherwise it and adjacent parts are similar to modern *A. capensis.*

Since the Swartklip canids are also larger than their modern counterparts, the size difference between the Swartklip otter and modern *A. capensis* is not unexpected. Unlike the canids, however, the otter teeth are less consistently larger than those of the modern form (Tables 55, 56). The upper teeth are either within the range of variation observed in the moderns, or are only slightly larger. They are morphologically indistinguishable from corresponding teeth of the comparative series.

The situation in respect of the known lower teeth, two carnassials, is more complex. One of the specimens, ZW 3486, is a little larger than any in the comparative series and its size is consistent with the upper teeth of the fossil form. It is essentially similar in size to the *A. capensis* M_1 from Florisbad (Ewer 1962), and it is accommodated quite well by the M_1 alveolus of an *Aonyx* mandible from a previously unrecorded locality in the southern Cape (Lake Pleasant). The Lake Pleasant occurrence is very similar to those at Swartklip and is also regarded as Florisian in age. The otter mandible (Q 1745) is appreciably larger than those of the moderns and, as far as can be judged, its size is consistent with that of the Swartklip skulls.

The previously described lower carnassial (ZW 6a) is very narrow compared with the other fossil specimens and also the M_1 of the moderns. It was this characteristic which prompted Ewer (1962) to suggest that it should not be referred to *A. capensis.* This specimen does not occlude well with the upper

TABLE 55

Dimensions of the upper teeth and skull of the Swartklip *Aonyx capensis* compared with those of a series of modern specimens.

		P^4		M^1		M^1	P^4:M^1	Trans. diam. of glenoid fossa	Trans. diam. of tympanic bulla	Ant.-post. diam. of tympanic bulla
		l	b	l	b	l:b	l			
Swartklip	ZW 2672A	—	—	14,0	15,7	0,89:1	—	32,0	29,3	*c.* 40,0
	ZW 2672B	—	—	—	—	—	—	—	29,2	41,0
	ZW 2930	14,4	13,7	13,7	16,7	0,82:1	1,05:1	—	—	—
Modern *Aonyx capensis*	Mean	13,3	13,5	13,4	17,2	0,78:1	1,00:1	26,9	25,1	37,4
	Range	12,5–13,8	13,0–13,8	12,6–13,8	16,3–18,3	0,75:1–0,80:1	0,96:1–1,02:1	25,5–28,1	24,7–25,5	37,0–37,6
	n	4		4		4	4	4	3	3

TABLE 56

Dimensions of the mandibles and lower teeth of modern and fossil *Aonyx capensis* from South Africa.

		$\bar{C}$		M_1		M_1	Overall length of mandible	Height of corpus below M_1	Breadth of corpus below M_1
		l	b	l	b	l:b			
Swartklip	ZW 6a	—	—	18,8	9,9	1,90:1	—	—	—
	ZW 3486	—	—	20,8	11,8	1,76:1	—	—	—
Lake Pleasant	Q 1745	10,8	8,3	*c.* 21,0	*c.* 12,5	*c.* 1,68:1	98,9	21,7	10,6
Florisbad	C 1490*	—	—	20,2	12,8	1,58:1	—	—	—
Modern *Aonyx capensis*	Mean	8,9	7,0	18,3	11,7	1,57:1	91,5	19,1	9,5
	Range	8,7–9,0	6,8–7,2	17,3–19,0	11,0–12,2	1,55:1–1,60:1	89,4–92,4	18,2–20,0	8,9–10,6
	n	3		4		4	4	4	4

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* Ewer 1962.

teeth from Swartklip and it is too small to fit the M_1 alveolus of the Lake Pleasant mandible. On the other hand, Ewer (1962: 275) stated that, 'The cusp pattern of the fossil tooth is the same as that of the extant species and its length falls within the range of a sample of 11 *A. capensis*' and concluded that it clearly belonged to the genus *Aonyx*.

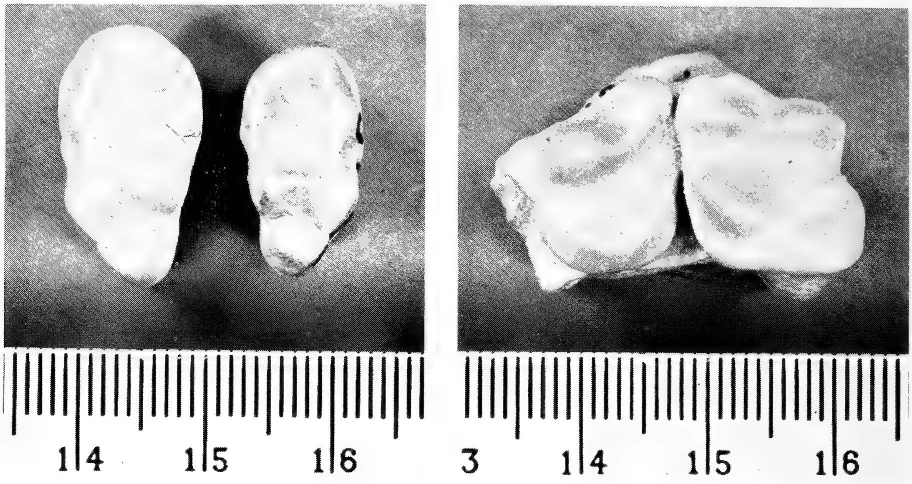

Fig. 59. Occlusal views of the *Aonyx capensis* lower carnassials (ZW 3486, ZW 6a) and maxilla (ZW 2930) from Swartklip.

Coetzee (1967: 14) gives one of the diagnostic characters of modern *A. capensis* the fact that the M_1 'measures over 16 × 10 mm'. The breadth of ZW 6a falls just short of Coetzee's minimum measurement, while its length is not inconsistent with that of the moderns. It is the length/breadth ratio of this tooth which really sets it apart from other specimens, both modern and fossil. In terms of its actual length and breadth, ZW 6a actually differs more markedly from the fossil specimens than the moderns.

Discussion

The Florisbad, Lake Pleasant and Swartklip material, exclusive of ZW 6a, evidently represents a Florisian form of *Aonyx capensis* which was larger than the extant variety. Ewer (1962: 276) suggested that ZW 6a belonged to 'a conservative, little modified descendant of the same stock as gave rise to the modern *Aonyx capensis*'.

These interpretations of the fossil evidence mean that not only were there two varieties of *Aonyx* present in the South African Florisian, but that both are represented in the Swartklip assemblage. While this possibility cannot be discounted, it is perhaps more likely that only a single variety is represented and that ZW 6a belonged to an aberrant individual. This specimen is now even more problematical than when it was first described and the situation will probably not be resolved until more Florisian *Aonyx* specimens are described.

Dreyer & Lyle (1931) referred the Florisbad otter specimens to a new species, *A. robustus*, but Ewer (1962: 276) concluded that they represent what is simply 'a rather large specimen of *A. capensis*'. She also stated that if 'the fossil teeth belong to an average-sized individual from a population whose mean tooth dimensions are significantly greater than those of the extant otter' then 'sub-specific separation would be warranted'. The Lake Pleasant and additional Swartklip specimens do indeed indicate that the Florisbad otter was not just an unusually large individual. Although the material is here categorized as 'Florisian *Aonyx capensis*', a name is available to those who prefer to recognize it as a distinct subspecies, that is *Aonyx capensis robustus* Dreyer & Lyle, 1931.

Family **Viverridae**

Subfamily Viverrinae

Viverra civetta Schreber, 1776

Present status

The African civet is largely confined to tropical Africa and has not been recorded in the Cape Province in historic times.

Material

Elandsfontein

15601/2—Right P_4 and part of right P^4.

Description

These two teeth evidently belong to a single individual. The P^4 is damaged and the protocone and parastyle are lost. That part which remains is indistinguishable from the P^4 of the only available modern *Viverra civetta* skull. The P_4 is intact and is similar in size (11,3 × 5,7 mm) and morphology to the corresponding tooth of the modern specimen, although the posterior cingular region is narrower and less crenellated.

Discussion

There can be no doubt that these specimens belong to a civet which, in respect of at least some teeth, was comparable in size to modern *V. civetta*. The less complex structure of the posterior cingulum of P_4 is what would be expected of a civet which was more primitive, but still closely related to *V. civetta*. The only other Pleistocene civet known from South Africa is that from the Kromdraai australopithecine site (Hendey 1973*a*), but since this is represented only by an incomplete humerus, it cannot be compared with the Elandsfontein form. It was, however, a large species.

On the basis of the material presently available, the Elandsfontein civet can only be referred to *Viverra* (*Civettictis*) *civetta* and, judging from the preservation of the teeth, it probably belongs with the Cornelian element of the Elandsfontein fauna. The indications are that there was a steady decrease in overall size in South African fossil civets from the Langebaanian *V. leakeyi*, through the Makapanian (Kromdraai) *Viverra* to the Cornelian *V. civetta*, and that they were representatives of a single lineage which culminated in the modern *V. civetta* (see Fig. 10).

The presence of this species in the Pleistocene of the south-western Cape is notable, because in recent times it has been recorded no closer than the northern coastal plain of Zululand (Shortridge 1934), which is about 1 500 km to the north-east. The failure of a number of herbivores to extend their ranges into, or to maintain their presence at the southern continental extremity was earlier attributed to environmental factors, but this control is far less likely to apply in the case of an essentially carnivorous omnivore such as *V. civetta*. The distribution and relative numbers of civets will be discussed in more detail later, but the indications are that they have become a progressively less significant element of the southern African fauna during the Pleistocene and Holocene.

Family **Viverridae**

Subfamily Viverrinae

Genetta genetta Linnaeus, 1758 & *Genetta tigrina* Schreber, 1776

Present status

The common and large-spotted genets still occur in the south-western Cape, but neither species is common.

Comment

Genets have a poor fossil record and only a single specimen belonging to this group has thus far been recorded from a Quaternary fossil occurrence in the south-western Cape. The taxonomy of the modern representatives of this group is complicated and about eleven species are currently recognized, with distinctions being based principally on external characters (see Coetzee 1967). Consequently the identification of fossil forms may be extremely difficult. In the present instance the fossil specimen was compared only with small series of the two species which still occur in the area and it is tentatively identified with one of them, i.e. *G. tigrina*.

Genetta cf. *tigrina*

(Fig. 60)

Material

Sea Harvest, Saldanha

S 1106—Right mandible lacking incisors and P_1.

Description

The mandibular corpus and ascending ramus of S 1106 are largely intact, although the angular process and immediately adjacent parts, together with a portion of the symphyseal region are missing. The mandible is appreciably larger than those of the available series of modern *Genetta genetta* (n = 4) and *G. tigrina* (n = 6) (Table 57), but it is otherwise similar to the comparative material. The modern specimens have two mental foramina in each half of the mandible and in *G. tigrina* the more posterior of these is situated below the anterior root of P_3, whereas in *G. genetta* it is more anteriorly situated, being either below the posterior root of P_2 or between the posterior root of P_2 and the anterior root of P_3. The fossil specimen has the posterior mental foramen situated as in *G. tigrina*.

Of those teeth remaining, only one, the M_2, compares in size with the corresponding tooth in one of the modern species (*G. genetta*). Otherwise the teeth are all larger than those of the comparative series and are thus in keeping with the overall larger size of the mandible.

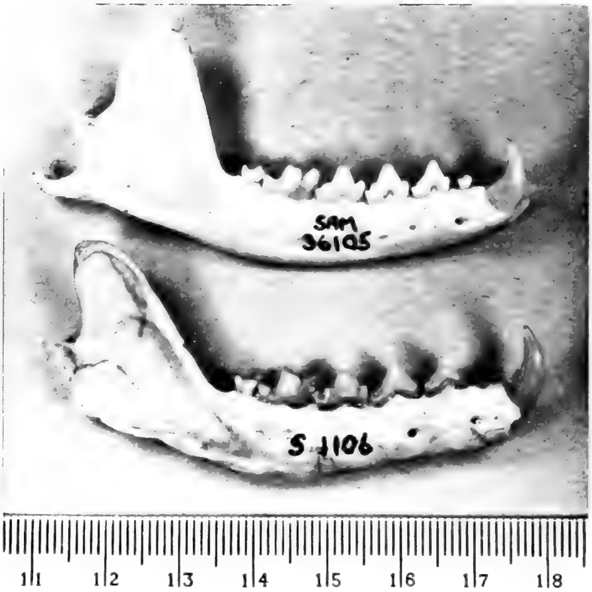

Fig. 60. Buccal views of the *Genetta* cf. *tigrina* mandible (S 1106) from Sea Harvest and a modern *G. tigrina* specimen (SAM 36105).

The lower dentitions of *G. genetta* and *G. tigrina* are not easily distinguished, but the most obvious distinguishing characteristics observed in the available comparative series are that *G. genetta* has a larger P_1 and higher crowned premolars than *G. tigrina*, while the M_2 was also usually larger. The P_1 of S 1106 is lost, but judging from the size of its alveolus it was proportionately as large as that of *G. tigrina* and smaller than that of *G. genetta*. Similarly the remaining premolars are less high crowned than those of *G. genetta* and more like those of

TABLE 57

Dimensions of the mandible and lower teeth of fossil *Genetta* from Sea Harvest, compared with those of a series of modern *G. genetta* and *G. tigrina*.

		$\overline{C}$		P_2		P_3		P_4	$P_3:P_4$	M_1		M_2		$M_1:M_2$	$\overline{C}$–M_2	Height of mandible below M_1	Breadth of mandible below M_1	Length of mandible ($\overline{C}$ to condyle)
		l	b	l	b	l	b	l	l	l	b	l	b	l	l			
	S1106	5,4	3,2	5,9	2,3	6,6	2,6	7,5 3,6	1:1,14	8,2	4,4	3,8	3,2	1:2,16	42,7	10,9	5,2	67,9
Modern *Genetta genetta*	Mean	3,8	2,5	5,7	2,0	6,4	2,3	6,6 2,8	1:1,04	7,6	3,8	3,8	3,0	1:2,01	37,8	8,3	3,8	59,9
	Range	3,6–3,9	2,4–2,6	5,5–6,0	1,9–2,2	6,2–6,5	2,2–2,3	6,5–6,7 2,7–2,8	1:1,02–1:1,06	7,4–7,7	3,7–3,9	3,6–4,0	2,9–3,1	1:1,93–1:2,14	36,0–40,2	7,9–8,7	3,6–4,1	56,9–63,4
	n	4		4		4		4	4	4		4		4	4	4	4	4
Modern *Genetta tigrina*	Mean	4,3	2,8	5,3	2,0	6,0	2,4	6,7 2,9	1:1,11	7,5	3,8	3,1	2,8	1:2,44	36,7	8,8	4,1	58,9
	Range	3,8–4,7	2,6–3,0	5,0–5,5	1,8–2,2	5,6–6,2	2,2–2,5	6,1–6,9 2,7–3,1	1:1,07–1:1,17	7,2–7,6	3,5–4,1	2,7–3,5	2,4–3,1	1:2,17–1:2,70	34,3–38,8	7,5–10,2	3,3–4,5	54,1–62,8
	n	5		6		6		6	6	6		6		6	6	6	6	6

G. tigrina. The relative lengths of the fossil P_3 and P_4 are also most similar to those of *G. tigrina*. In actual size the fossil M_2 corresponds with those of *G. genetta*, but in its length relative to that of M_1, it is intermediate between those of the two modern series.

Discussion

While the Sea Harvest genet was evidently a larger variety than either modern *G. genetta* and *G. tigrina*, its dentition most closely resembles that of the latter species and it is identified accordingly. The reservation in the identification is made because of the complexities in the taxonomy of the modern species, the fact that the present comparative study was inadequate and because the fossil variety is so poorly represented.

Family **Viverridae**

Subfamily Herpestinae

Herpestes ichneumon Linnaeus, 1758

(Fig. 61; also Hendey & Hendey 1968: pl. 7D)

Present status

The Egyptian mongoose is now extinct in the south-western Cape, but it still occurred in the region during the ninteenth century.

Material

(1) *Elandsfontein*

15833—Right P^4.
6867 —Right mandibular fragment with P_2 and P_3.
6880 —Left mandibular fragment with P_2 to P_4.
6885 —Left mandibular fragment with P_4.
8101 —Left M_1, possibly belonging to 6880.

(2) *Swartklip*

(a) Previously described specimen (Hendey & Hendey 1968):
ZW 111—A crushed skull lacking the braincase and mandible and with the following teeth missing:
Left I^1, P^1, P^4, M^1 and M^2; right I^1, part of P^4, and M^2.

(b) Additional specimens:
ZW 2647—Part of an occiput.
ZW 1627—Right mandibular fragments with $\bar{C}$ and M_1.
ZW 1845—Right mandibular fragment with P_3 and P_4.
ZW 2001—Left mandibular fragment with P_4.

(3) *Sea Harvest, Saldanha*

S 138—Left maxillary fragment with P^2 to M^1.
S 209—Right mandibular fragment.

Comment

The study of this material was hampered by the fact that only one skull of the modern species was available for comparative purposes. However, since the nature of the changes undergone by locally occurring fossil populations of this species is apparently essentially similar to those of other species (e.g. *Canis mesomelas*), the identification of this material and the observations made about it are probably secure.

Description

The maxillary fragment from Sea Harvest (S 138) is virtually indistinguishable from corresponding parts of the skull of a modern *Herpestes ichneumon* from Pondoland (SAM 1883) (Table 58). The same applies to the edentulous mandibular fragment (S 209), except that the corpus is a little broader and more heavily built (Table 59).

The incomplete skull from Swartklip (ZW 111) has already been described elsewhere (Hendey & Hendey 1968: 66). It is generally similar to the modern specimen, although the P^4 protocone is a little larger and the parastyle a little smaller. The Swartklip mandibular fragments do, however, differ quite appreciably from the modern and Sea Harvest specimens. The corpora are much more robust, the C is larger than that of the modern specimen and the cheekteeth are broader. The P_3 has a less distinct anterior accessory cusp and the protoconid of M_1 is only a little higher than the paraconid and metaconid, so that the trigonid is composed of three more or less equally sized cusps.

The only upper tooth recorded from Elandsfontein is an isolated P^4 (15833) from the Florisian Bone Circle occurrence. It resembles the Swartklip P^4 in having a smaller parastyle and larger protocone than the Sea Harvest and modern specimens.

The remainder of the Elandsfontein specimens probably belong with the Cornelian element of the fauna. The lower teeth are very similar to those of the modern specimen, but the mandibular corpora are more robust. There is a well-developed subangular lobe in 6885, which is the only specimen in which this region of the mandible is preserved. The Swartklip, Sea Harvest and modern specimens do not have subangular lobes. Judging from the size of the M_2 alveolus in 6885, this tooth was larger than in the later specimens.

Discussion

It has already been indicated that the south-western Cape fossil *Herpestes ichneumon* apparently differs from the modern variety in much the same way as the fossil *Canis mesomelas* differs from its extant counterpart. The characteristics may be summed up as follows:

(1) Sea Harvest—Specimens are essentially the same as the modern form.
(2) Swartklip—The fossil form is larger than the modern in most respects and there are also some minor differences in dental morphology.
(3) Elandsfontein—The Florisian form (i.e. that from the Bone Circle occurrence) resembles that from Swartklip.
The Cornelian form is similar in size to that from Swartklip and differs from the moderns in certain respects (e.g. presence of a subangular lobe; larger M_2).

TABLE 58

Dimensions of the upper teeth of fossil *Herpestes ichneumon* from the south-western Cape Province, compared with those of a modern specimen.

	$\underline{C}$		P^1		P^2		P^3		P^4		M^1	
	l	b	l	b	l	b	l	b	l	b	l	b
SAM 1883	5,2	3,6	2,3	2,4	5,8	3,2	7,0	4,5	10,9	7,0	5,7	9,9
Sea Harvest S 138	—	—	—	—	6,0	3,6	6,5	4,8	10,4	7,4	6,4	10,3
Swartklip ZW 111	5,4	3,8	2,6	—	6,0	3,1	7,2	4,5	—	7,3	5,6	9,8
Elandsfontein 15833	—	—	—	—	—	—	—	—	9,8	7,7	—	—

TABLE 59

Dimensions of the mandible and lower teeth of fossil *Herpestes ichneumon* from the south-western Cape Province, compared with those of a modern specimen.

		$\bar{C}$		P_2		P_3		P_4		M_1		Height of corpus below P_4	Breadth of corpus below P_4
		l	b	l	b	l	b	l	b	l	b		
	SAM 1883	6,9	3,8	5,5	2,7	6,8	3,0	8,6	3,7	9,6	5,1	10,4	5,4
Sea Harvest	S 209	—	—	—	—	—	—	—	—	—	—	10,9	6,3
Swartklip	ZW 1627	7,5	5,0	—	—	—	—	—	—	9,6	5,5	—	—
	ZW 1845	—	—	—	—	6,7	3,8	7,8	4,5	—	—	13,7	6,3
	ZW 2001	—	—	—	—	—	—	8,1	4,4	—	—	*c.* 13,5	6,2
Elandsfontein	6867	—	—	5,6	2,9	6,8	3,2	—	—	—	—	—	—
	6880	—	—	5,5	3,3	6,4	3,4	*c.* 7,8	4,0	—	—	12,3	6,2
	6885	—	—	—	—	—	—	*c.* 8,6	4,0	—	—	13,0	5,8
	8101	—	—	—	—	—	—	—	—	9,0	5,0	—	—

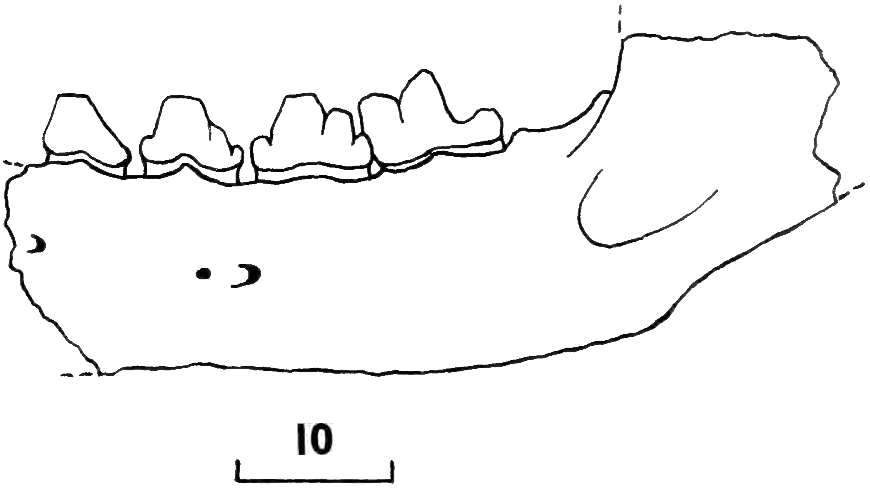

Fig. 61. The mandible of the *Herpestes ichneumon* from Elandsfontein reconstructed from the specimens 6880, 6885 and 8101.

H. ichneumon is recorded as a fossil from a number of localities in Africa (see Cooke 1963; Hopwood & Hollyfield 1954). It is still one of the most widely distributed of the African viverrids and is also recorded from Spain and Israel (Dorst & Dandelot 1970).

Family **Viverridae**

Subfamily Herpestinae

Herpestes pulverulentus Wagner, 1839

(Fig. 62)

Present status

The Cape grey mongoose is still common in the south-western Cape.

Material

Sea Harvest, Saldanha

S 786—Incomplete skull lacking most of the braincase and with the following teeth:
Right I^2 and I^3 and P^3 to M^1; left $\underline{C}$ to P^4.
S 2 —Right mandibular fragment with $\overline{C}$ to M_1.

Description

The mandible (S 2) is without P_1 and in this respect it is similar to the available *Herpestes pulverulentus* comparative series ($n = 14$). This tooth is often absent in *Herpestes* (*Galerella*), whereas in *Herpestes* (*Herpestes*) it is apparently always present. The other lower teeth of the fossil are morphologically indistinguishable from those of *H. pulverulentus* and, although they are relatively large, they fall within the size range of variation observed in this species.

The mandibular corpus is most clearly distinguishable from those of the comparative series in that it has a greater dorso-ventral diameter in the symphyseal region, but the post-symphyseal parts are also more robust than even the largest of the mandibles in the comparative series (Table 61).

The incomplete skull (S 786) evidently belongs to the same species as the mandible, but it is from a second individual. It differs from the skull of modern *H. pulverulentus* in its larger size (Table 60), and in having a more prominent post-orbital process.

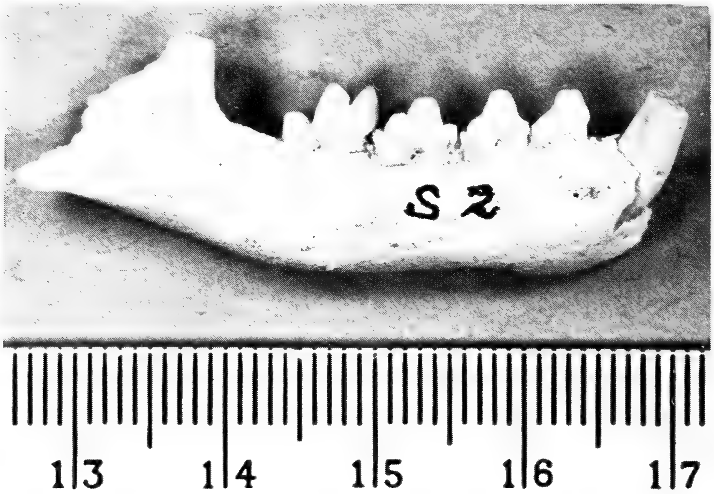

Fig. 62. Buccal view of the *Herpestes pulverulentus* mandible (S 2) from Sea Harvest.

Several of the teeth of this specimen are lost, but only I^1 and M^2 are not represented at all. The M^2 was a double-rooted tooth and, judging from the size of the alveoli, it may have been a little larger than any of those in the comparative series. The other upper teeth are generally similar to those of modern *H. pulverulentus*, although, like the lowers, they are relatively large. The $\underline{C}$ and P^3 are actually longer than any in the comparative series (Table 60). Both left and right P^1 of S 786 are absent and although the postcanine diastema is long enough to have accommodated this tooth, it seems that it was never present in this individual. Only one specimen in the comparative series had P^1 absent from both sides, while in two others it was present on one side only.

The right I^3 and $\underline{C}$ of S 786 were broken off during life, with the result that the right cheekteeth are more heavily worn than those on the left side.

TABLE 60

Dimensions of the skull and upper teeth of the Sea Harvest *Herpestes pulverulentus* compared with a series of modern specimens.

		C	P²	P³		P⁴		M¹		Width across post ends of P⁴	Median length of palate	Inter-orbital width	Post-orbital constriction
		l	b	l	b	l	b	l	b				
Sea Harvest	S 786	4,2	2,5	5,2	3,8	7,8	5,6	4,4	7,1	26,0	40,4	16,2	13,7
Modern *Herpestes pulverulentus*	Mean	3,4	2,1	4,7	3,4	7,3	5,2	4,1	6,8	23,2	36,1	14,4	13,3
	Range	2,9–3,8	1,8–2,5	4,4–5,0	3,0–3,8	6,8–8,0	5,0–5,6	3,7–4,5	5,4–7,4	21,8–24,6	33,5–39,3	12,4–15,9	11,4–15,0
	n	12	14	13		14		14		14	14	13	13

Table 61

Dimensions of the mandible and lower teeth of the Sea Harvest *Herpestes pulverulentus* compared with those of a series of modern specimens.

		$\overline{C}$		M_1		Height of mandible post. to M_1	Breadth of mandible post. to M_1
		l	b	l	b		
Sea Harvest	S2	4,1	2,7	6,5	3,8	8,5	4,3
Modern *Herpestes pulverulentus*	Mean	4,0	—	6,4	3,5	7,1	3,6
	Range	3,5– 4,3	— —	6,0– 6,8	3,2– 3,8	5,9– 8,1	3,0– 4,2
	n	12		14		14	14

Discussion

The small viverrid from Sea Harvest belongs to a species of *Herpestes* (*Galerella*) resembling *H. pulverulentus*, but one in which individuals were larger than those making up modern local populations of this species. The absence of P^1 and relatively large size of M^2 may prove to be more significant differentiating characteristics, but on the basis of the material presently available it is concluded that the two forms are conspecific.

This is apparently the first fossil record of the species. It is remarkable that it should be so rare as a fossil in a region where it still occurs quite commonly, whereas the larger *H. ichneumon* is more common as a fossil, but no longer occurs locally.

Family **Viverridae**

Subfamily Herpestinae

Atilax paludinosus G. Cuvier, 1829

The water mongoose still occurs in the mountains adjacent to the south-western Cape and it has been recorded from within the region in the past (Sclater 1900). It is also known locally from a Late Stone Age coastal midden (Van Noten 1967).

Family **Viverridae**

Subfamily Herpestinae

Cynictis penicillata G. Cuvier, 1829

In none of the standard textbooks on South African mammals (e.g. Sclater 1900; Roberts 1951; Ellerman *et al.* 1953) is the yellow mongoose recorded as occurring in the south-western Cape. Its presence locally was, however, recently recognized and as this species is a rabies vector it has been the subject of a detailed study (I. F. Zumpt, pers. comm.). This species is essentially confined to the drier western and central parts of the interior, where it is often found in association with *Suricata suricatta* and *Xerus inaurus*, two species which have not been recorded locally in recent times.

In view of the long standing and widespread human settlements in the south-western Cape, it is surprising that *C. penicillata* had not previously been recorded from this region and the possibility that it is a relatively recent immigrant cannot be dismissed (*vide supra*).

Family **Viverridae**

Subfamily Herpestinae

Suricata major n. sp.

(Figs 63, 64)

Holotype

8669—Parts of a braincase, a right maxillary fragment with P^4 and M^1 and left mandibular fragment with P_1 and P_2.

Referred material

EC 7, 6331, 9492—Incomplete braincases.
6873 —Right maxillary fragment with P^3 and P^4.
6893 —Left M^1.
16558—Right M^1.
17126—Left premaxillary and maxillary fragment with I^3, $\underline{C}$ and P^1.
9499 —Mandible lacking ascending rami and with right $\overline{C}$ to P_3; parts of left P_3 and P_4.
6884 —Right mandibular fragment with P_2 to P_4.
9197 —Right mandibular fragment with P_1 to P_3 and M_2.
6883 —Left mandibular fragment with P_1 to M_1.
8405 —Left mandibular fragment with $\overline{C}$ and P_2 to P_4.
8655 —Left mandibular fragment with P_3 to M_1.

Locality

Elandsfontein.

Age

Cornelian.

Diagnosis

A *Suricata* of large size; skull relatively long; sagittal and nuchal crests prominent; post-orbital process prominent but no post-orbital bar; transverse slot of ectotympanic continuously open and situated in a groove with well defined posterior and medial margins; external auditory meatus T-shaped in lateral view; P^1_1 present; P_4 without anterior accessory cusp; M_1 protoconid and metaconid approximately equal in size; M_2 paraconid and protoconid approximately equal in size and talonid equal in width to trigonid.

Etymology

The specific name serves to indicate the large size of this species relative to the extant *Suricata suricatta*.

Description

The fragmentary braincase EC 7 was referred to by Ewer & Singer (1956: 335) as follows:

> 'In size and general conformation the specimen closely resembles *Herpestes ichneumon* (Linn.), but in view of its incompleteness no detailed comparisons are possible.'

The reticence of these authors in giving further comment on this specimen has proved to be justified, since the more complete braincase 9492, which is almost identical with EC 7 in all observable respects, differs significantly from that of *H. ichneumon*. In dorsal and lateral view this braincase actually resembles that of *Cynictis* and differs from *H. ichneumon* in being more expanded and relatively shorter. In addition, the tympanic region is quite unlike that of *H. ichneumon* and of the extant viverrid genera it most resembles *Mungos* and *Suricata*.

The bulla of the fossil species is known from three specimens (the holotype, 6331, 9492), and it is one of the more important diagnostic features of this species. In general, it is more like that of *Mungos mungo* than any other viverrid species which occurs in southern Africa today. However, the bulla of *M. mungo* has a more inflated entotympanic, while the ectotympanic medial to the transverse slot is a little less inflated. The transverse slot of the fossil resembles that of *Suricata* in that it is relatively wide and continuously open, although it is open for a greater distance than is usually the case in *S. suricatta*. On the other hand, it is like *M. mungo* in that it is situated in a groove, which in the fossil has more clearly defined posterior and medial margins. This groove, or depression, has the effect in both the fossil and *M. mungo* of compressing the external auditory meatus dorso-ventrally. In the former the open transverse slot results in the meatus being T-shaped in lateral view. In *M. mungo* the slot is usually closed at the lateral margin so that the meatus is simply elongated antero-posteriorly. *Crossarchus*, which also has a discontinuous ectotympanic slot, has the meatus more or less circular in lateral view, as does *Suricata*.

Although the braincase of the fossil species resembles that of *Cynictis*, it differs from this genus, and *Suricata*, in that the post-orbital process is relatively shorter and does not form a post-orbital bar by linking up with the zygomatic arch. The fossil is similar to *Mungos* in this respect. The development of a post-orbital bar is an advanced characteristic in viverrids and is an ontogenetic feature. For example, it is completely developed in *Cynictis* only after the animal has reached the age of about one year (Zumpt 1969). Consequently, the fossil species is less advanced in respect of the development of its post-orbital process than *Cynictis* and *Suricata*. However, since this process is relatively more prominent in the fossil than it is in *Mungos*, the latter is the less advanced in this respect.

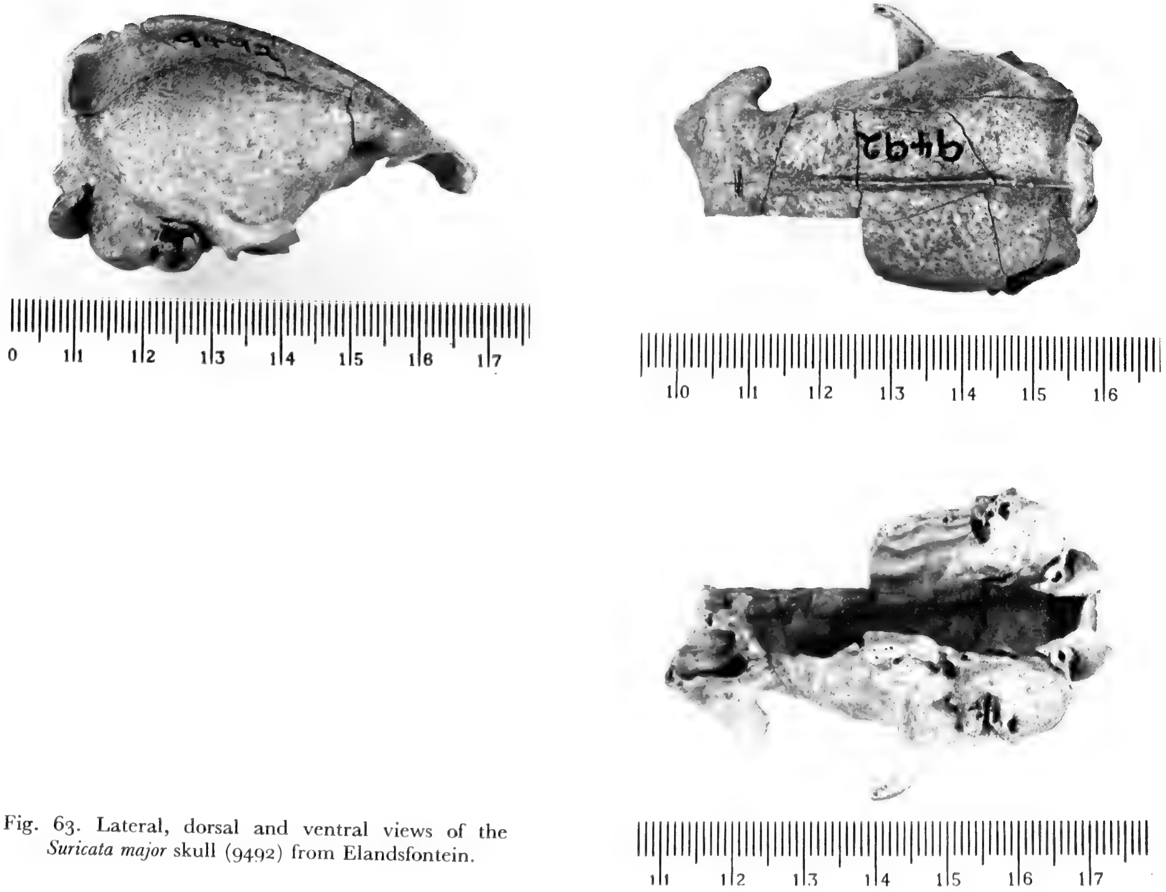

Fig. 63. Lateral, dorsal and ventral views of the *Suricata major* skull (9492) from Elandsfontein.

The fossil braincase is relatively shorter and more bulbous than that of *M. mungo taenianotus*, the southern African subspecies. It is, however, similar in shape to that of the *M. mungo gothneh* specimen (AMNH 51112) from Central Africa illustrated by Allen (1925: Fig. 49), except for being slightly less inflated anteriorly. It is also about 50% larger. The fossil braincase is not as inflated as that of *S. suricatta* (Table 62).

TABLE 62

The dimensions of the braincase of *Suricata major* from Elandsfontein, compared with those of some extant Viverridae.

		Braincase length	Braincase breadth	l:b
Mungos mungo taenianotus	SAM 33329	42,8	28,1	1,52:1
	SAM 3484	41,5	28,2	1,47:1
Mungos mungo gothneh	AMNH 51112	(52,5)*	(40,0)*	1,31:1
Suricata major	9492	50,0	*c.* 38,0	1,32:1
Cynictis penicillata	SAM 17079	37,0	28,6	1,29:1
	SAM 4105	37,5	29,2	1,28:1
Suricata suricatta	SAM 19124	32,0	29,5	1,08:1
	SAM 36009	30,3	29,2	1,04:1

* Measured on fig. 49 of Allen (1925); scale × 3/2.

The nuchal crest is developed to about the same degree as in *M. mungo*, but the sagittal crest is more prominent.

The upper dentition of the fossil species is less well represented than the lower dentition. The specimen 17126, which includes I^3, $\underline{C}$ and P^1, agrees in its state of preservation and degree of wear on the teeth with the holotype and it may belong to the same individual. It is significant only because it shows that P^1, a small, single-rooted tooth, was still present in this species. This tooth has been lost in modern *Mungos* and *Suricata*.

The other upper cheekteeth differ from those of the two modern species in their larger size (Table 63) and in the relative sizes of certain cusps. The P^3 has an internal cusp which is proportionately similar in size to that of *Suricata*, but smaller than that of *M. mungo*. The P^4 differs from that of *Suricata* in having the parastyle and metastyle approximately equal in size and it resembles *M. mungo* in this respect. The fossil M^1 is represented by three very worn specimens and none exhibit any observable differences from the M^1 of the modern species.

Apart from their larger size (Table 64; Fig. 65), the most significant difference between the lower teeth of the fossil and modern species is the fact

Table 63

Dimensions of the upper teeth of *Suricata major* from Elandsfontein, compared with those of modern *S. suricatta* and *Mungos mungo*.

		P^3		P^4		M^1	
		l	b	l	b	l	b
Suricata major	8669	—	—	*c.* 7,0	8,0	*c.* 4,5	*c.* 8,5
	6873	5,9	*c.* 4,5	7,1	*c.* 7,5	—	—
	6893	—	—	—	—	4,2	8,2
	16558	—	—	—	—	4,7	7,6
Suricata suricatta	Mean	3,8	3,1	4,4	4,8	3,5	6,0
	Range	3,5–4,0	2,6–3,5	4,2–5,0	4,0–5,7	3,1–4,1	5,6–7,0
	n	8		8		8	
Mungos mungo	Mean	4,5	4,0	5,2	5,5	3,7	6,2
	Range	4,5–4,6	3,8–4,1	5,0–5,3	5,2–5,8	3,4–3,9	5,8–6,5
	n	3		3	2	3	2

that P_1 is present in the former. In only one of the seven hemi-mandibles represented is there no evidence of the presence of P_1, although this specimen (8655) may have lost the tooth during life. This was certainly the case with 6884, in which traces of the P_1 alveolus are still visible. The fossil P_1 is a simple, more or less conical tooth, which is very much smaller than P_2. Morphologically P_2 and P_3 resemble those of the modern species and are similar to *S. suricatta* and *M. mungo gothneh* (Allen 1925: Fig. 50) in that they are relatively high crowned. The P_4 differs from that of both modern species in lacking an anterior accessory cusp, although this cusp was also virtually absent in two of the thirteen modern *S. suricatta* specimens examined in the course of the present study.

In both modern species, the M_1 protoconid is a little larger than the metaconid, whereas in the fossil these cusps are approximately equal in size. They are also less divergent than in *M. mungo*. The fossil M_2 differs from the moderns in having the talonid as broad as the trigonid, while the paraconid and protoconid are more or less equal in size.

The lower cheekteeth are less crowded than those of *S. suricatta* and are spaced as in *M. mungo gothneh*.

The fossil mandibular corpora are much larger than those of the modern species, but they are similar in shape and have two mental foramina situated anteriorly and posteriorly of P_2 as in the moderns.

TABLE 64

Dimensions of the mandible and lower teeth of *Suricata major* from Elandsfontein, compared with those of modern *Suricata suricatta* and *Mungos mungo*.

		P_1		P_2		P_3		P_4		M_1		M_2		P_2–M_2	Height of corpus below M_1	Breadth of corpus below M_2
		l	b	l	b	l	b	l	b	l	b	l	b	l		
Suricata major	8669	—	—	—	—	—	—	—	—	—	—	—	—	—	11,3	6,0
	8655	—	—	4,8	3,0	5,2	3,4	6,5	4,3	6,2	4,5	—	—	*c.* 28,0	10,3	4,8
	6883	*c.* 2,3	*c.* 1,8	5,0	3,0	5,3	*c.* 3,4	6,4	4,2	6,3	4,6	—	—	—	9,9	5,8
	9499	—	—	—	—	—	—	—	—	—	—	—	—	*c.* 28,5	10,0	5,5
	9197	*c.* 2,2	*c.* 1,7	—	—	—	—	6,5	4,4	—	—	*c.* 5,0	3,7	*c.* 29,0	10,0	5,9
	8405	—	—	*c.* 4,5	2,9	4,9	3,1	6,2	*c.* 4,0	—	—	—	—	*c.* 27,7	9,0	5,4
	6884	—	—	5,1	3,3	—	—	6,7	4,7	—	—	—	—	—	—	—
Suricata suricatta	Mean			3,3	1,9	3,6	2,2	4,4	2,7	4,4	3,1	3,6	2,7	19,0	6,8	3,8
	Range			3,0–3,7	1,9–2,0	3,3–4,0	2,2–2,3	3,9–5,0	2,6–2,9	4,0–4,9	2,9 3,2	3,3–3,7	2,6–2,9	18,0–21,1	5,7–7,6	3,1–4,1
	n			7		7		7		7		7		8	8	8
Mungos mungo	Mean			3,7	2,3	4,3	2,6	4,9	3,1	4,7	3,3	4,0	2,8	21,5	6,8	3,5
	Range			3,6–3,8	2,1–2,4	4,0–4,5	2,4–2,8	4,8–5,2	2,8–3,2	4,5–4,9	3,2–3,4	3,5–4,6	2,7–3,0	20,5–22,5	6,1–7,7	3,4–3,6
	n			3		3		3		3		3		3	3	3

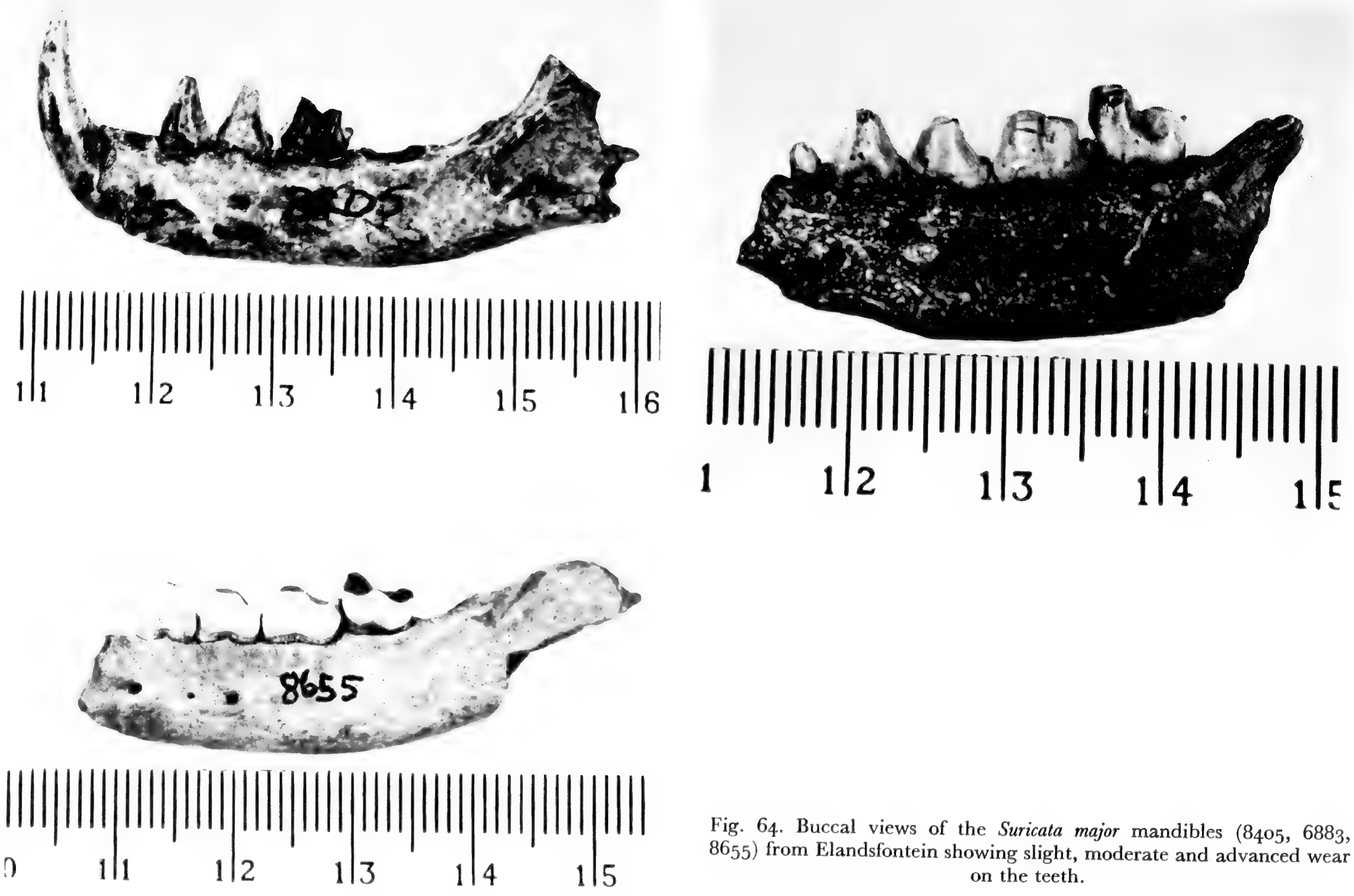

Fig. 64. Buccal views of the *Suricata major* mandibles (8405, 6883, 8655) from Elandsfontein showing slight, moderate and advanced wear on the teeth.

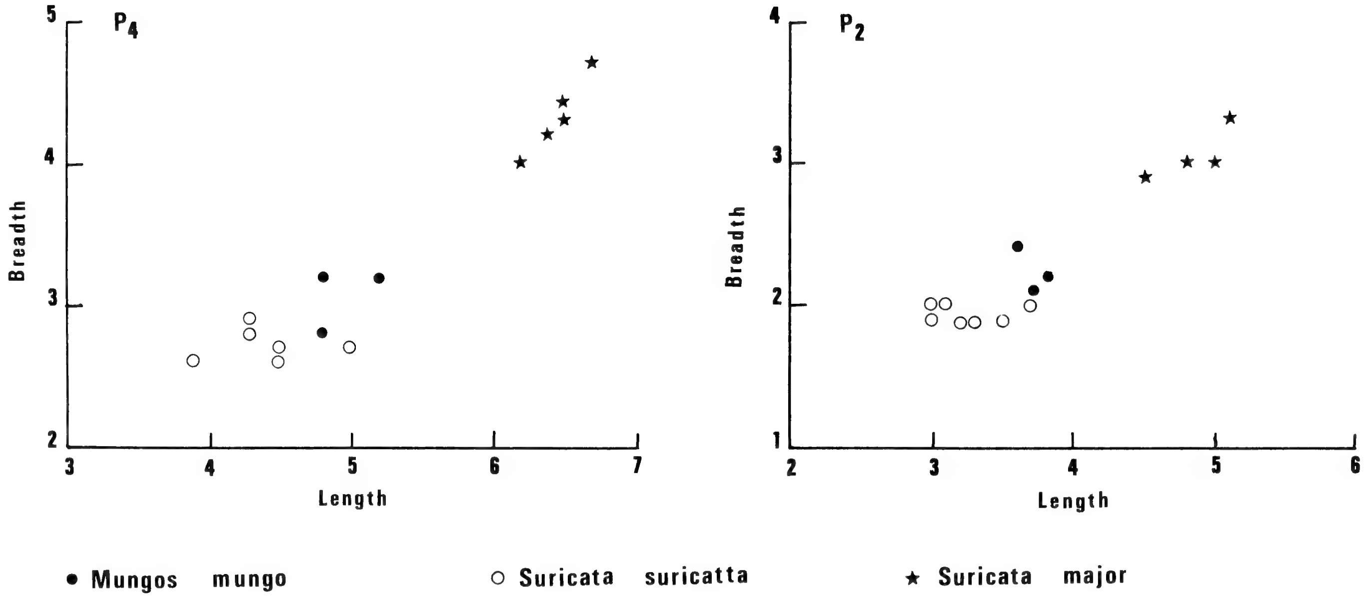

Fig. 65. Dimensions of the P_2 and P_4 of *Suricata major*, compared with those of modern *S. suricatta* and *Mungos mungo*.

Discussion

In their study of the mongooses, Gregory & Hellman (1939) recognized three groups, one of which included the genera *Mungos* and *Suricata*. It is with these genera that the fossil species evidently has its affinities. It also bears some resemblance to *Cynictis* (e.g. braincase shape, presence of P_1^1), a genus which Gregory & Hellman regarded as belonging in another group, but which had paralleled the evolution of *Suricata*. The dentition of the fossil is much more specialized than that of *Cynictis* and it is unlikely that there is any direct phyletic connection between the two.

Before considering the possible relationships of the fossil species to *Mungos* and *Suricata*, it is necessary to examine the differences between *M. mungo taenianotus* and *M. mungo gothneh*. In several respects the latter is the more specialized of the two subspecies and they were at one time recognized as separate species (e.g. Allen 1925). *M. m. gothneh* has a shorter and more bulbous braincase, a broader tympanic bulla, shorter tooth rows, while the P_2 and P_3 are higher crowned than in *M. m. taenianotus*. In these respects the Central African subspecies approaches *S. suricatta*, although in other osteological characters and in its external features it is clearly closer to *M. m. taenianotus*. The implication is that extant *M. mungo* includes a regional variant (i.e. *M. m. gothneh*) which has paralleled the development of some of the osteological and dental characters of *S. suricatta*.

The more important similarities and differences of the fossil to *M. m. taenianotus* and *S. suricatta* may be summed up as follows:

(1) The size of the fossil is appreciably greater than that of the modern species.
(2) The configuration of the braincase is intermediate between that of *M. m. taenianotus* and *S. suricatta*.
(3) The post-orbital processes are relatively longer than those of *M. m. taenianotus*, but are not as well developed as those of *S. suricatta*.
(4) The general morphology of the tympanic region resembles that of *M. m. taenianotus*, but the relative development of inflated parts of the bulla, and the nature of the transverse slot of the ectotympanic are more like *S. suricatta*.
(5) The dentition is a combination of characters evident in both modern species.

The fossil species is clearly not readily referable to one or other of the modern species and in several respects is actually intermediate between them. In respect of skull morphology and dentition, *M. m. taenianotus* is less advanced than *S. suricatta* while *M. m. gothneh* is advanced in the direction of *S. suricatta* to about the same degree as the fossil species. In view of the temporal and geographical separation between the fossil and *M. m. gothneh*, and the fact that they do differ in some observable respects, they cannot be regarded as conspecific.

It is concluded that the fossil species, although having some of the characteristics of *Mungos*, is actually an early member of the *Suricata* lineage and it is accordingly referred to this genus. *M. m. gothneh* is regarded as a product of parallel evolution, its characteristics having developed either at a slower rate, or after a later start.

In deciding upon the specific identity of the fossil form, account was first taken of *Mungos dietrichi* Petter, 1963 from Garussi (= Ngarusi) and Olduvai Bed I in Tanzania. The only specimen of this species which has been described is a mandibular fragment with a complete series of cheekteeth (Dietrich 1942; Petter 1963), although part of the upper dentition has also been figured (Petter 1969). The Elandsfontein species is a little larger than *M. dietrichi*, it has a higher crowned P_2 and P_3 and less widely spaced lower cheekteeth. It also has a smaller internal cusp on P^3, while the P^4 protocone is more anteriorly situated. In her illustrations of the *M. dietrichi* mandible, Petter (1963, 1969) does not show an anterior accessory cusp on P_4, but the original photograph of the specimen subsequently designated the holotype of the species (Dietrich 1942: pl. IV, 36) shows this cusp very distinctly. The two fossil species thus differ in this respect as well. They are, however, similar in that both retain P_1, and probably also P^1, and both have the M_2 talonid as broad as the trigonid.

Leakey (1967) gives the age of *M. dietrichi* as 'lower Pleistocene' and it is therefore probably appreciably older than the Elandsfontein species. The indications are that the two fossil forms are not conspecific. *M. dietrichi* might well be ancestral to the Elandsfontein species, or both might have an as yet unrecorded common ancestor further back in time. There is nothing in the *M. dietrichi* dentition which suggests that it belongs in the *Suricata* rather than *Mungos* lineage, and in most respects it is not dissimilar to *M. mungo taenianotus*. There can, therefore, be no doubt about its generic identity.

Fossil *Suricata* has previously been recorded from the Cave of Hearths in the Transvaal and this material was referred to the extant species (Cooke, in Mason 1962). In addition, Cooke (1955: 166) listed '*Suricata* sp. (or possibly *Cynictis*)' as part of the fauna from the Saldanha Lime Quarry occurrence. This material has been lost and its affinities remain unknown.

There is no other recorded species to which the Elandsfontein form can be referred and it is, therefore, given a new species name. The holotype is the only group of specimens presently known in which cranial and dental elements are associated, although since they are so fragmentary the description of the species was based principally on the various referred specimens.

The phyletic relationships of *Suricata major* which are suggested here (Fig. 66), conflict with the conclusion of Petter (1969) that *Suricata* was derived from *Herpestes* (*Galerella*). In the light of the preceding discussion and the fact that there is a far greater similarity between *Suricata* and *Mungos* than between *Suricata* and *Herpestes* (Gregory & Hellman, 1939), Petter's opinion seems largely insupportable.

There are further points which must be considered in respect of the taxonomy of *S. major*. The differences between it and modern *S. suricatta* are perhaps only a little more marked than those between the Cornelian *Vulpes chama* and modern *V. chama*. Consequently, for the sake of consistency, *S. major* should perhaps have been referred to as 'Cornelian *S. suricatta*' instead of having been given a new species name. The distinction between the taxonomy of the

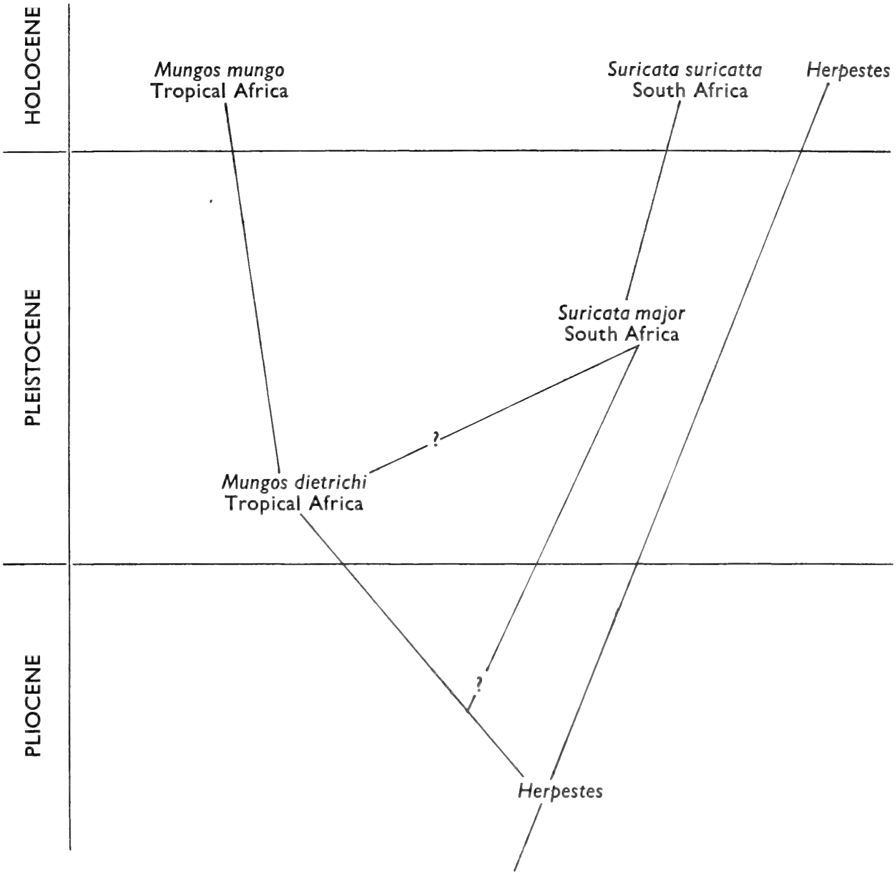

Fig. 66. Tentative phylogeny of some Viverridae.

Elandsfontein *Suricata* and *Vulpes* was made simply because a Florisian form of *V. chama* is known, whereas a Florisian *Suricata* has yet to be described. As a result, the phyletic relationship between Cornelian *V. chama* and its modern counterpart is more securely established than the suggested relationship between *S. major* and *S. suricatta*. In addition, the characteristics of the various fossil *V. chama* are such that it is difficult to make unequivocal definitions for the different forms. This is not the case with *S. major*. The time may well come when forms intermediate in age between *S. major* and *S. suricatta* are known and a situation comparable to that involving the post-Makapanian *V. chama* is encountered. For the present, however, a specific distinction seems warranted and supportable.

It is worth noting that although there is no certain record of *Suricata* in the south-western Cape in post-Cornelian times, *S. major* is the most commonly represented viverrid at Elandsfontein. This is attributed to the fact that *Suricata*, at least at the present, is a colonial animal which occupies subterranean lairs. The death of individuals in their lairs, coupled with a higher population density, creates a more favourable opportunity for the preservation of their remains than is the case with more solitary animals which spend most of their lives on the surface of the ground. It follows that other carnivore species which make use of subterranean lairs should also be relatively abundant as fossils at this site and this is indeed the case with *Mellivora capensis*, to quote but one example. The question of carnivore lairs at Elandsfontein will be discussed again later as this is regarded as an important factor relating to the origin of bone assemblages at the site.

The fact that neither *Cynictis* nor the ground squirrel, *Xerus*, both of which commonly occupy the same burrows as *Suricata* today, are not recorded from Elandsfontein, suggests that the association of these animals was not characteristic during the Cornelian in the south-western Cape. The significance of the disappearance of *Suricata* from this region is not known, but it may well relate to environmental factors.

Suricata is a genus endemic to the drier parts of southern Africa, while *Mungos* is an essentially tropical form, which is confined to the more humid subtropical east coast of South Africa in the most southerly part of its range. There is apparently no overlap in the distribution of *S. suricatta* and *M. mungo taenianotus*. The two modern species are not dissimilar in external appearances (see Dorst & Dandelot 1970: 124, 128; pl 18), and bearing in mind the more arid environment in which *S. suricatta* lives, its lighter coloration is not unexpected. *Mungos* and *Suricata* also share a number of habits. For example, both are very sociable and live in warrens, they are diurnal, very noisy and have a wide variety of calls, their diets are essentially similar and their mild disposition make them easy to tame (Dorst & Dandelot 1970). These habits, which could be regarded as heritage characteristics, add some substance to the theory that *M. mungo* and *S. suricatta* had a common ancestor in the relatively recent past. Possibly their separate identity was the result of evolution in different geographical environments.

The identification of *S. major* in the Elandsfontein assemblage lends support to Petter's (1969) conclusion that the diversification of the African viverrids took place comparatively recently.

The taxonomy of the Viverridae has long been problematical and controversial. It was earlier concluded that *Vishnuictis*, with its curiously modified skull, should rank only as a subgenus of *Viverra*, and there is a parallel with the inferred relationships of *Suricata* and *Mungos*. In this case, however, the question of whether or not *Suricata* should be regarded as a subgenus of *Mungos* could be additionally investigated by further studies on the anatomy of the modern species, as well as by further studies on non-anatomical aspects of the species. Such investigations are clearly beyond the scope of the present study and so no alteration to the presently accepted taxonomic status of *Suricata* is proposed, although the possibility for a future change is recognized.

Family **Hyaenidae**

Subfamily Hyaeninae

Hyaena cf. *bellax* Ewer, 1954

Material

Baard's Quarry, Langebaanweg

L 179/11 A–C—Right P^4 and part of $\underline{C}$; left I^3.

Discussion

These teeth were briefly described previously (Hendey 1970*a*) and tentatively referred to *Hyaena brunnea*. While they are superficially similar to the corresponding teeth of *H. brunnea*, the size of the P^4 (L 179/11C) and the proportions of its buccal cusps (Table 65), suggest that the material has affinities with *H. bellax* from Kromdraai (Ewer 1954). This is a Makapanian species which is apparently closely related to *H. brunnea* (Fig. 17). The Baard's Quarry P^4 lacks the protocone, but this cusp was perhaps more posteriorly situated and a little larger than that of the *H. bellax* holotype. Although this tooth is similar in length to the P^4 of the 'E' Quarry *Percrocuta*, it has a much larger parastyle and the two species are clearly not conspecific.

TABLE 65

Dimensions of the teeth of the Baard's Quarry *Hyaena* cf. *bellax*, compared with those of the *H. bellax* holotype and a series of modern *H. brunnea*.

		Langebaanweg	Kromdraai *Hyaena bellax**		Modern *Hyaena brunnea*		
		L 179/11	l	r	Mean	Range	n
I^3	l	12.0	11,2	11,5	11,4	11,0–12,1	4
	b	13,1	12,6	12,5	11,2	11,1–11,4	
C	l	16,5	19,2	19,8	15,2	13,9–15,9	9
	b	12,5	—	14,5	11,5	10,7–11,9	
P^4	l	*c.* 40,0	39,2	39,2	34,6	33,2–36,2	13
	l of parastyle	11,8	11,3	11,3	—	—	—
	l of paracone	13,6	13,3	13,1	—	—	—
	l of metastyle	*c.* 14,6	14,6	14,8	—	—	—
P^4 metastyle l × 100/P^4l		36,5	37,8		35,2*	—	15
P^4 parastyle l × 100/P^4 paracone + metastyle l		41,8	40,6		47,7*	—	15

* Ewer 1954.

The I^3 (L 179/11A), which is intact, is similar to those of both *H. brunnea* and *H. bellax*, although it has a very stout root which is perhaps more in keeping with the larger size of the latter species.

The $\underline{C}$ (L 179/11B), which lacks most of the root and part of the crown, is a little larger than those of the available modern *H. brunnea* series ($n = 9$), but smaller than that of the *H. bellax* holotype.

The Baard's Quarry hyaenid is evidently an *Hyaena* and, although the available material is too fragmentary for confident specific identification, it is tentatively referred to *H. bellax*.

Family **Hyaenidae**

Subfamily Hyaeninae

Hyaena brunnea Thunberg, 1820

(Fig. 67; also Hendey & Hendey 1968: pl. 6; Hendey 1968: pl. 9)

Present status

The brown hyaena is now extinct in the south-western Cape, but it apparently still occurred in the region during the nineteenth century.

Material

(1) *Elandsfontein*

(a) Previously described specimens (Ewer & Singer 1956):

EC 2, 3, 4, 6—Maxillary and mandibular fragments with teeth as follows: Right P^3, left P^3 to M^1; right I_3 to M_1; left $\overline{C}$ to M_1.

EC 11—Right maxillary fragment with dp^3 and dp^4.

(b) Additional specimens:

15833—Parts of the skull of a single individual, including: Incomplete brain-case; facial region with right I^3 and P^2 to P^4, and left I^2 to $\underline{C}$ and P^2; right mandible with P_2 to M_1; left mandible with $\overline{C}$ to M_1.

Maxillary fragments with teeth as follows:

EC 33/34—Right P^1 to M^1; left P^3 to M^1.

16669 —Right P^2.

Mandibular fragments with teeth as follows:

5307 —Left P_2 to P_4.

6870 —Left P_3 and P_4.

9562 —Right P_2 to P_4.

16584—Right P_2 to M_1.

16686—Incomplete $\overline{C}$, P_2 and parts of P_3 to M_1.

17125—Right P_3 to M_1.

20041—Right P_2 and P_3.

20081—Right $\overline{C}$ to M_1 (apparently associated with left P^1 and $\underline{C}$ numbered 20074/5).

Isolated teeth as follows:

$$\left.\begin{array}{l}\text{7785—Right } P^3\\ \text{6536—Right } P^4\end{array}\right\}\text{Probably one individual}$$

17128—Right P_4.

The following are the remains of juveniles:
3950 —Left mandibular fragment.
14153—Parts of the skulls of at least two individuals, including:
Left maxillary fragment with dp^3 and dp^4, and M_1 just erupting; two right mandibular fragments, one with dp_2 to dp_4 and the other with unerupted M_1.
16780, 20566 and others—Unerupted permanent teeth.

(2) *Elandsfontein Wes*

16317—Right mandibular fragment with $\overline{C}$ to P_3; left mandibular fragment with P_3 to M_1.

(3) *Melkbos*

Mb 116/7—Right mandibular and maxillary fragments with part of P_2, P_3 and P_4, and parts of P^2 to P^4.

(4) *Swartklip*

ZW 2659—Left maxillary fragment with P^2 to M^1.
ZW 394 —Right premaxillary fragment with I^2.
ZW 1836—Left mandibular fragment with incomplete $\overline{C}$ and P_3 to M_1.
ZW 3790—Right P^2.
The following are the remains of juveniles:
ZW 1311/3—An incomplete skull and mandible with teeth as follows:
Right dp^3, dp^4 and M^1 just erupting; left P^1, dp^2 to dp^4 and M^1 just erupting; right $d\bar{c}$, dp_2 to dp_4 and M_1 just erupting; left dp_4. (SITE 2)
ZW 141 —Right maxillary fragment with dp^3 and dp^4.
ZW 2662 —Right maxillary fragment with parts of dp^2 and dp^3.
ZW 2677 —Part of dp_4.

(5) *Sea Harvest, Saldanha*

S 13 —Right maxillary fragment with P^3 just erupting.
S 200 —Incomplete left $\underline{C}$.
S 133 —Right P^4.
S 722 —Right mandibular fragment with P_2 and P_3.
S 721 —Left mandibular fragment with P_4 and M_1.
S 724/5—Left $\overline{C}$.
S 134 —Left P_3.
S 36, S 207—Incomplete right M_1; left M_1.
S 37—Premolar fragment.

Description

Ewer & Singer (1956: 336) recorded some slight differences between the lower teeth of the Elandsfontein material available to them and those of modern *Hyaena brunnea*, but they considered it unnecessary 'to place the fossil specimens in a distinct subspecies'. Their observations were based on the dentition of a single adult individual (EC 2/6) and although some of the additional material apparently represents the same form, other specimens evidently belong to a second form which is itself slightly different to modern *H. brunnea*. The possibility of the existence of a second fossil variety of *H. brunnea* in the late Pleistocene of the south-western Cape has already been suggested (Hendey 1968).

The first form, which is regarded as the earlier of the two, and which includes the specimens EC 2/6, EC 33, 6096, 17125 and 20081, differs from modern *H. brunnea* in the following respects:

(1) The M^1 is larger (Table 66).
(2) The lower cheekteeth are generally smaller and relatively narrower (Table 67).
(3) The P_4 anterior accessory cusp is relatively prominent.
(4) The M_1 metaconid is relatively prominent.
(5) The mandible and probably also other skull parts are slightly larger.

The second form, which includes the material from the Bone Circle occurrence (15833), is larger than modern *H. brunnea* in most respects. For example, although some of the teeth of 15833 are within the size range of variation observed in the comparative series, the mandible and braincase are larger. The only convenient measurement which could be taken on the fragmented braincase to illustrate this point was the maximum occipital width (99,7 mm). This figure is appreciably greater than the mean of 13 modern *H. brunnea* skulls (90,6 mm) and is outside the observed range of variation (86,8–94,0 mm).

Other specimens which are assigned to the later (Florisian) variety are 6870, 9562, 16669 and 16686. They resemble the earlier (Cornelian) form in the size of the mandible, and probably also other skull parts, in having a fairly prominent P_4 anterior accessory cusp and in having a relatively narrow M_1 with a prominent metaconid. The lower premolars are, however, as broad as those of modern *H. brunnea*.

The criteria used in separating the two Elandsfontein forms are insufficient to allow for categorization of all specimens. The juvenile and poorly preserved or incomplete adult specimens were not categorized, although they clearly belong to *H. brunnea*. In addition, one of the mandibular fragments (20041), which is somewhat unusual in its preservation, was not referred to either of the two forms because of its exceptionally broad P_3. This specimen is more similar to corresponding parts of the mandible of modern *H. brunnea* than it is to other fossil specimens from the south-western Cape, although its P_3 is broader even than the broadest specimen in the modern comparative series (Table 67).

The specimens from Elandsfontein Wes, Melkbos, Swartklip and Sea Harvest also represent a form, or forms, of *H. brunnea* larger than the moderns in most respects. They are similar to the Elandsfontein Florisian variety in size, the relative breadths of the lower premolars and in the nature of P_4 and M_1.

Not all of these specimens can be distinguished from modern *H. brunnea*. For example, the Sea Harvest lower carnassial S 207 falls within the size range of variation observed in the moderns and has a reduced metaconid comparable to that of the modern form. It is, however, a little narrower than any M_1

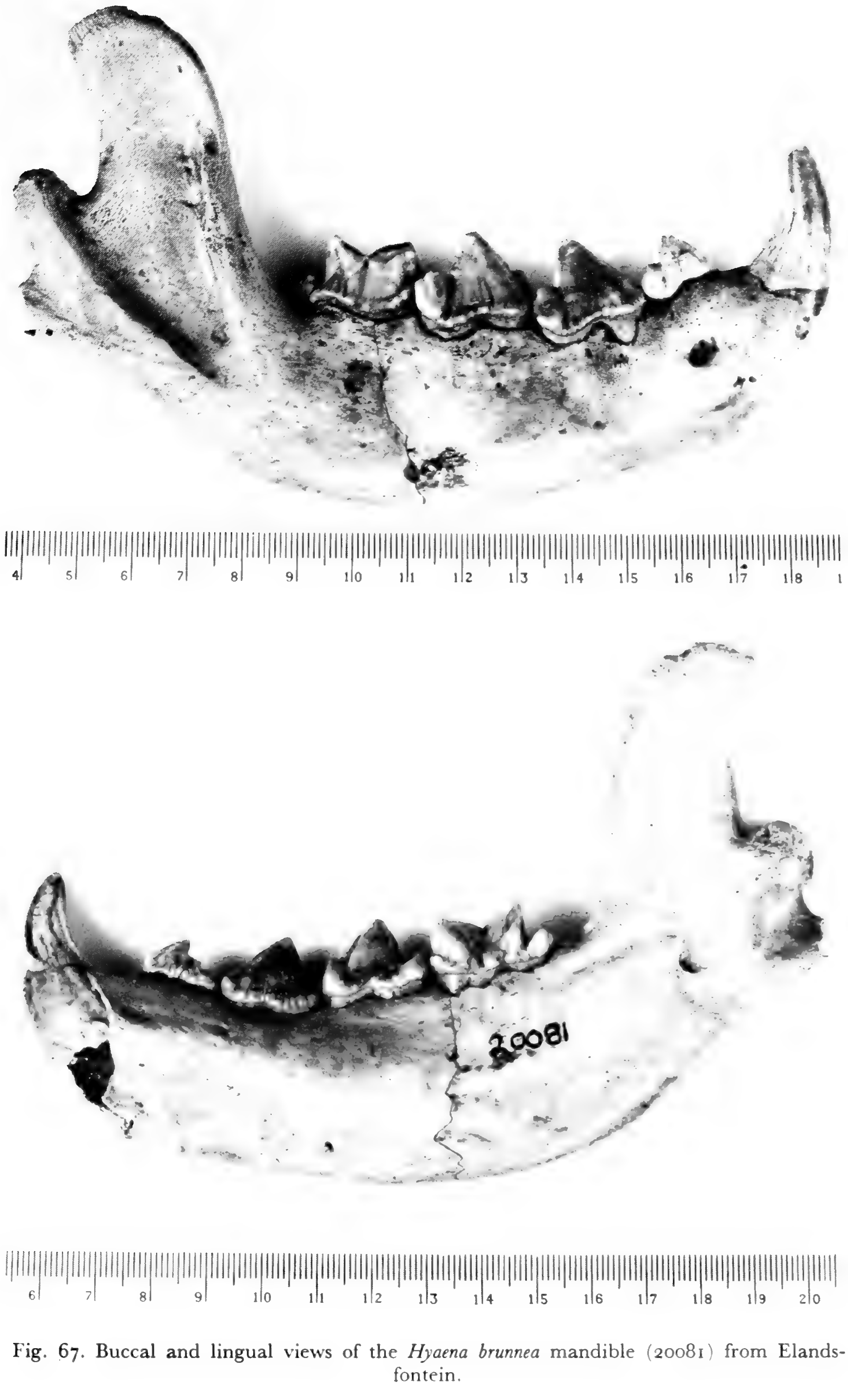

Fig. 67. Buccal and lingual views of the *Hyaena brunnea* mandible (20081) from Elandsfontein.

TABLE 66

Dimensions of the upper teeth of fossil *Hyaena brunnea* from the south-western Cape, compared with of a series of modern *H. brunnea*.

			C		P^1		P^2		P^3		P^4		M^1
			l	b	l	b	l	b	l	b	l	b	b
Modern *Hyaena brunnea*		Mean	15,2	11,5	6,6	7,2	16,9	11,5	22,5	16,1	34,6	21,4	12,1
		Range	13,9–15,9	10,7–11,9	5,5–8,3	6,6–8,2	16,1–17,7	10,5–13,2	21,6–24,4	14,8–18,3	33,2–36,2	20,4–22,6	10,8–12,9
		n	9		11		13		13		13		12
Sea Harvest		S 200, S 13*, S 133	16,5	12,3	—	—	—	—	24,0	17,9	34,9	21,3	—
Swartklip		ZW 2659	—	—	—	—	*c.* 18,5	*c.* 11,8	*c.* 24,5	—	*c.* 37,0	*c.* 22,8	13,2
		ZW 3790	—	—	—	—	18,2	12,3	—	—	—	—	—
Melkbos		Mb 116	—	—	—	—	—	—	22,9	15,5	—	—	—
Elandsfontein	Late form	15833	—	—	—	—	*c.* 16,2	*c.* 12,2	*c.* 21,8	*c.* 17,0	*c.* 34,5	21,4	—
		16669	—	—	—	—	19,0	13,1	—	—	—	—	—
	Early form	EC 2/6	—	—	—	—	—	—	23,1	15,9	35,8	21,0	14,4
		EC 33	—	—	6,2	6,5	17,0	12,2	23,4	16,0	32,9	20,9	13,1
		6096	—	—	—	—	—	—	23,9	16,6	—	—	—
		20074/5*	*c.* 15,5	*c.* 10,3	6,1	5,8	—	—	—	—	—	—	—

* Young Adults.

TABLE 67

Dimensions of the mandibles and lower teeth of fossil *Hyaena brunnea* from the south-western Cape, compared with those of a series of modern *H. brunnea*.

		C		P_2			P_3			P_4			M_1			Height of mandible below P_3	Height of mandible below M_1
		l	b	l	b	$\frac{b \times 100}{l}$	l	b	$\frac{b \times 100}{l}$	l	b	$\frac{b \times 100}{l}$	l	b	$\frac{b \times 100}{l}$		
Modern *Hyaena brunnea*	Mean	16,8	13,0	15,4	11,4	74,1	20,4	14,0	68,6	23,0	13,4	58,4	23,2	12,3	53,1	34,4	40,2
	Range	16,0–17,5	12,3–13,9	14,3–15,9	10,6–12,1	70,3–77,1	19,5–21,4	12,9–14,7	66,0–71,9	21,8–23,8	12,3–14,4	53,7–61,9	22,2–25,0	11,7–13,2	51,5–56,8	32,0–35,6	36,7–42,6
	n	10		11			13			13			12			5	13
Sea Harvest	S722	—	—	16,7	12,2	73,1	21,6	15,0	69,4	—	—	—	—	—	—	39,5	—
	S721*	—	—	—	—	—	—	—	—	25,9	16,0	61,8	26,4	13,8	52,3	—	—
	S36*	—	—	—	—	—	—	—	—	—	—	—	—	13,5	—	—	—
	S134*, S207	—	—	—	—	—	21,5	15,2	70,7	—	—	—	24,1	12,2	50,6	—	—
Swartklip	ZW1836*	17,5	—	—	—	—	21,5	15,0	69,8	23,6	14,1	59,7	24,4	12,3	50,4	—	—
Melkbos	Mb 117	19,6	12,6	—	—	—	21,0	c. 15,0	c. 71,4	c. 23,7	c. 13,7	c. 57,8	—	—	—	40,0	—
Elandsfontein Wes	16317	18,0	c. 12,3	16,5	11,5	69,7	22,7	15,2	67,0	c. 26,6	14,3	c. 60,6	25,0	12,7	50,8	c. 38,5	—
Elandsfontein ?	20041	—	—	15,3	10,9	71,2	19,5	14,5	74,4	—	—	—	—	—	—	31,5	—
Elandsfontein Late Form	15833	—	13,3	c. 15,0	c. 11,4	c. 76,0	c. 21,5	15,5	c. 72,1	23,0	13,9	60,4	c. 25,6	—	—	40,0	42,5
	16686	—	—	c. 18,0	c. 12,5	c. 69,4	22,2	c. 15,5	c. 69,8	c. 25,0	c. 14,8	c. 59,2	c. 25,0	c. 13,0	52,0	41,0	c. 48,0
	9562	—	—	c. 16,7	—	—	c. 22,0	c. 15,2	c. 69,1	23,5	13,9	59,1	—	—	—	c. 41,0	—
	6870	—	—	—	—	—	21,9	15,3	69,9	24,5	14,6	59,6	—	—	—	—	—
Elandsfontein Early Form	EC2/6	14,8	11,6	14,8	10,0	67,6	19,8	13,1	66,2	23,2	12,4	53,4	22,5	11,4	50,7	36,0	45,0
	17125	—	—	—	—	—	—	—	—	c. 22,5	—	—	22,3	—	—	—	44,5
	20081*	15,5	11,2	14,2	9,5	66,9	19,9	12,2	61,3	21,6	11,5	53,2	22,3	11,2	50,2	—	—

* Young adults.

in the comparative series and in this respect resembles most of the other fossils. By contrast, the specimen S 721 is as broad as the moderns, although it is larger in overall size and has a more prominent metaconid.

The upper dentitions of the fossil forms are less well represented and there are fewer observable differences between them and the moderns. While the larger size of the M^1 of the early Elandsfontein form is regarded as a primitive and possibly useful distinguishing characteristic, the slightly larger size of the M^1 of the Swartklip specimen, ZW 2659, is probably simply in keeping with the overall larger size of the individual to which it belongs. As with the *Canis mesomelas* from the site, overlaps in the tooth size ranges of variation of the modern and fossil forms limits the usefulness of size as a distinguishing criterion.

Discussion

Although local Cornelian and Florisian forms of *Hyaena brunnea* can be distinguished, and although both can be distinguished from that which is still extant, it is not possible to define the categories in such a way that all the available specimens can be classified. The differences between early and late specimens can be striking, but it is evident from the total assemblage that there is a gradation in characteristics from one extreme to the other. This point is clearly illustrated by the following examples.

The Sea Harvest specimen, S 721, and a mandible from Elandsfontein, 20081, belong to young adults of approximately the same ontogenetic age and can therefore be conveniently compared. The size differences between the P_4 and M_1 of these two specimens exceed the ranges observed in the modern comparative series, while the relative breadths of P_4 are almost the same as the two extremes in the comparative series. The Swartklip fauna, which is intermediate in age between the Elandsfontein Cornelian and the Sea Harvest faunas, includes the *H. brunnea* mandible, ZW 1836, which also belongs to a young adult. Theoretically, the P_4 and M_1 of this specimen should be intermediate in character between those of 20081 and S 721. It is in fact found that these teeth are intermediate in all dimensional respects (Table 68), although the teeth are not dissimilar morphologically.

Exactly the same applies in the case of the P_2 and P_3 of mature adults from Sea Harvest (S 722), Elandsfontein Wes (16317) and Elandsfontein (EC 2), although in this instance there are no other grounds for believing the Elandsfontein Wes specimen to be intermediate in chronometric age.

Owing to the variation encountered in all species, there obviously will be exceptions to this pattern and the problematical Elandsfontein specimen, 20041, is a case in point, but the general trend in the evolution of the later Quaternary *H. brunnea* of the south-western Cape is evident. There was apparently an increase in size, at least in some respects, from the early (Cornelian) form to a later (Florisian) form, which was eventually culminated in the Sea Harvest (? early Holocene) *H. brunnea*. The Cornelian variety is characterized by relatively narrow lower premolars and larger M^1, in which respects the later material is indistinguishable from the extant *H. brunnea*.

TABLE 68

Dimensions of the lower cheekteeth of typical examples of Cornelian, Florisian and ?early Holocene *Hyaena brunnea* from the south-western Cape, and mean dimensions of a series of modern specimens from elsewhere in southern Africa.

	P_2			P_3		
	l	b	$\frac{b \times 100}{l}$	l	b	$\frac{b \times 100}{l}$
M.A. Modern *Hyaena brunnea*	15,4	11,4	74,1	20,4	14,0	68,6
M.A. ?Early Holocene (S 722)	16,7	12,2	73,1	21,6	15,0	69,4
M.A. Florisian (16317)	16,5	11,5	69,7	22,7	15,2	67,0
M.A. Cornelian (EC 2)	14,8	10,0	67,6	19,8	13,1	66,2

	P_4			M_1		
	l	b	$\frac{b \times 100}{l}$	l	b	$\frac{b \times 100}{l}$
M.A. Modern *Hyaena brunnea*	23,0	13,4	58,4	23,2	12,3	53,1
Y.A. ?Early Holocene (S 721)	25,9	16,0	61,8	26,4	13,8	52,3
Y.A. Florisian (ZW 1836)	23,6	14,1	59,7	24,4	12,3	50,4
Y.A. Cornelian (20081)	21,6	11,5	53,2	22,3	11,2	50,2

M.A.—Mature adult. Y.A.—Young adult.

All the local fossils tend to differ from the modern form in the following respects:

(1) The M_1 is relatively narrow.
(2) The M_1 metaconid is relatively prominent.
(3) The P_4 anterior accessory cusp is relatively prominent.

Since no skulls of the *H. brunnea* which inhabited the south-western Cape in historic times were available, it is not known whether or not it also exhibited these characteristics in its P_4 and M_1. The local modern form was apparently no different in size to the more northerly variety which is still extant, so the large ? early Holocene Sea Harvest *H. brunnea* was apparently succeeded by one of 'normal' size comparatively recently.

The presence of a prominent M_1 metaconid and P_4 anterior accessory cusp are primitive characteristics evident also in *H. brunnea dispar* from Swartkrans (Ewer 1955*a*) and *H. bellax* from Kromdraai (Ewer 1954). The relative breadth of the M_1 in the former subspecies cannot be determined on the basis of the described material, but the M_1 of *H. bellax* is even narrower than those of the south-western Cape fossil *H. brunnea*.

The published records of other fossil *H. brunnea* from elsewhere in South Africa, namely, Florisbad (Dreyer & Lyle 1931) and Bolt's Workings (Toerien 1952), do not make it clear if these specimens also had the primitive characteristics of P_4 and M_1 evident in the south-western Cape fossils. However, judging from the illustration of the 'semi-fossilized' Bolt's Workings mandible (Toerien 1952: Fig. 4), this specimen is more like modern *H. brunnea* than, for example, the Sea Harvest specimen, S 721. Consequently, it is possible that modern *H. brunnea* derives from more northerly fossil populations, and that the south-western Cape late Pleistocene/early Holocene *H. brunnea* represented a locally endemic and recently extinct lineage.

Family **Hyaenidae**

Subfamily Hyaeninae

Crocuta crocuta Erxleben, 1777

(Fig. 68; also Ewer & Singer 1956: pl. 27–31)

Present status.

The spotted hyaena is now extinct in the south-western Cape, but it was apparently still common in the region during the eighteenth century.

Material

(1) *Elandsfontein*

(a) Previously described specimens (Ewer & Singer 1956):

EC 1—Braincase.
EC 5—Left maxillary fragment with P^3 and part of P^4.
EC 8—Left mandibular fragment with part of M_1.
EC 9—Right mandibular fragment with part of P_2, P_3 and P_4.

(b) Additional specimens:

15833—Parts of a skull, including:
Maxillary fragments with right I^3 to P^4 and left P^2, P^3 and part of P^4; mandibular fragments with right I_2 to M_1 and left P_2 and P_3.

(2) *Bloembos*

669—Braincase.

(3) *Sea Harvest, Saldanha*

S 203—Left P^3.

Description

In their original account of the Elandsfontein *Crocuta*, Ewer & Singer (1956) referred the material to *C. spelaea*, but in a subsequent reappraisal of South African fossil hyaenids, Ewer (1967: 113) concluded that 'there is no justification for regarding it as differing from the extant species'.

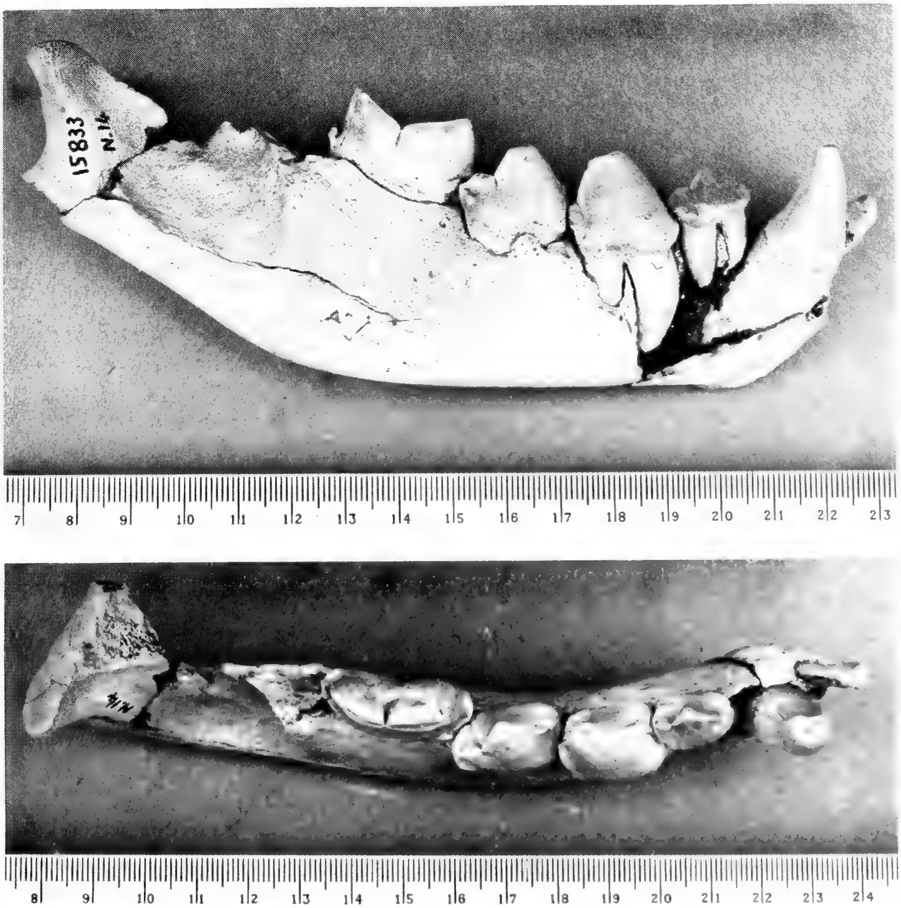

Fig. 68. Buccal and occlusal views of the *Crocuta crocuta* mandible (15833) from Elandsfontein.

Little can be added to the published description of the *Crocuta* from this site, although some of the incisors, the canines and the cheekteeth, with the exception of M^1, are now represented by complete specimens. None of the teeth differ from those of modern *C. crocuta* and, as in the modern form, the M^1 is small and only sometimes present. In 15833 the M^1 alveolus is preserved in the right maxillary fragment, but it is absent on the left side.

The preserved teeth of 15833 and the isolated P^3 from Sea Harvest (S 203) are similar in size to the moderns (Tables 69, 70), although S 203 and the P_2 of 15833 are slightly longer than those of the available comparative specimens. They resemble the premolars of EC 5 and EC 9 in this respect. Most of these teeth are, however, within the size range of variation observed in a large series of East African *C. crocuta* (Kurtén 1956). Since the southern African variety of *C. crocuta* is apparently a little larger than that from East Africa, it is probable

TABLE 69

Dimensions of the upper teeth of the fossil *Crocuta crocuta* from the south-western Cape Province, compared with those of a series of modern specimens.

		$\underline{C}$		P^1		P^2		P^3		P^4	
		l	b	l	b	l	b	l	b	l	b
Modern *Crocuta crocuta* (S. Africa)	Mean	16,6	11,8	8,1	7,0	16,2	12,1	22,9	17,1	37,2	20,3
	Range	16,0– 18,0	11,0– 12,8	7,1– 9,0	6,4– 7,6	14,9– 17,5	11,0– 13,3	21,7– 23,7	16,3– 17,9	35,5– 38,9	18,7– 22,1
	n	6		10		10		10		10	
Modern *Crocuta crocuta* (East Africa)*	Mean	—	—	—	—	14,4	—	21,1	—	35,0	—
	Range	—	—	—	—	11,7– 17,1	— —	18,2– 24,1	— —	29,7– 40,2	— —
	n	—		—		97	—	97	—	97	—
Sea Harvest	S 203	—	—	—	—	—	—	23,8	17,3	—	—
Elandsfontein	15833	*c.* 17,2	12,4	7,8	7,3	15,6	*c.* 11,5	23,4	17,5	36,4	*c.* 20,0
	EC 5	—	—	—	—	—	—	24,2	*c.* 17,4	*c.* 41,0	*c.* 22,0

* Kurtén 1956.

TABLE 70

Dimensions of the lower teeth of the Elandsfontein *Crocuta crocuta*, compared with those of a series of modern specimens.

		$\bar{C}$		P_2		P_3		P_4		M_1	
		l	b	l	b	l	b	l	b	l	b
Modern *Crocuta crocuta* (S. Africa)	Mean	15,6	12,6	15,4	11,0	21,2	15,3	22,9	13,2	29,3	12,1
	Range	15,2– 16,3	11,9– 13,6	14,0– 16,2	10,1– 11,9	20,3– 22,1	14,3– 15,8	21,8– 23,8	12,3– 14,0	28,1– 32,3	11,1– 12,7
	n	5		7		7		7		7	
Modern *Crocuta crocuta* (East Africa)*	Mean	—	—	14,5	—	19,9	—	21,7	—	26,7	—
	Range	—	—	11,8– 17,2	—	17,1– 22,6	—	18,5– 24,5	—	22,6– 30,7	—
	n	—		96	—	98	—	91	—	95	—
Elandsfontein	15833	*c.* 16,0	*c.* 12,7	16,3	10,9	20,7	15,4	21,5	13,3	30,1	12,4
	EC 8	—	—	—	—	—	—	—	—	*c.* 30,5	12,8
	EC 9	—	—	*c.* 18,0	—	22,6	15,1	*c.* 24,5	13,6	—	—

* Kurtén 1956.

that all the south-western Cape fossil teeth are actually within the size range of variation of the modern southern variety.

The Elandsfontein braincase has already been described in detail (Ewer & Singer 1956), and the specimen from Bloembos is essentially similar. Both specimens are comparable in size to the skulls in the available comparative series (Table 71).

TABLE 71

Dimensions of the skull of fossil *Crocuta crocuta* from the south-western Cape, compared with those of a series of modern specimens.

	Modern *Crocuta crocuta* (S. Africa)			Bloembos 669	Elandsfontein EC 1
	Mean	Range	n		
Occipital height (base of occip. cond. to top of sagittal crest)	100,6	93,7–106,1	5	*c.* 99,5	104,8
Maximum width of occiput	101,6	96,3–106,5	5	97,0	101,3
Maximum width across occipital condyles	52,4	49,9–53,9	5	52,0	47,0
Post-orbital constriction	48,4	46,9–50,4	5	49,8	—

Discussion

The fossil *Crocuta crocuta* from the south-western Cape is apparently indistinguishable from the extant southern African variety of this species, although it is perhaps slightly larger than the average size of the moderns. The original material from Elandsfontein may be Cornelian in age, 15833 is from the Florisian Bone Circle occurrence, the Bloembos skull is probably also Florisian in age and the Sea Harvest tooth is regarded as early Holocene. The age categories cannot be distinguished from one another on the basis of the specimens presently available.

Family **Hyaenidae**

Subfamily Protelinae

Proteles cristatus Sparrman, 1783

The aardwolf is not known as a fossil in the south-western Cape and until recently the only known local record of this species was that of a specimen from Stellenbosch referred to by Sclater (1900). During July, 1972 an adult female was killed on the main road 31 km south of Hopefield (SAM 36685). Since the aardwolf is a shy, nocturnal animal it may be more common locally than this meagre record suggests, but its numbers must in any case be very limited. The possibility that it is a recent immigrant to the region was mentioned earlier.

Family **Felidae**
Subfamily Machairodontinae
Megantereon sp.

Present status

Extinct

Material

Elandsfontein

3060 —Ascending ramus of a left mandible.
3058/9—Parts of the shafts of left and right humeri, probably belonging to the same individual as 3060.
6762 —Left humerus lacking proximal end.
5410, 277—Left femur and tibia belonging to one individual.
9486 C, D—Right tibia and left femur, probably belonging to one individual.
321 —Right femur lacking distal end.
3461 —Proximal end of right femur.

Comment

Casts of two parts of a right mandible, an unnumbered specimen no longer in the South African Museum's collections, were also examined. The teeth preserved are I_2 to $\bar{C}$, P_4 and M_1. These fragments may belong to the same individual as 3058/60.

Description

The ascending ramus (3060) has the reduced coronoid process characteristic of the machairodonts and is similar in size to that of the *Megantereon eurynodon* from Kromdraai (Ewer 1955*c*) (Table 72). The unnumbered mandible will presumably be described elsewhere, but judging from the available casts it was on the basis of this material that the Elandsfontein machairodont was identified as *Megantereon gracile* (see Boné & Singer 1965: Table 1), a species which resembles *M. eurynodon* (Ewer 1955*c*).

TABLE 72

Dimensions of the ascending ramus of the Elandsfontein *Megantereon*, compared with that of *M. eurynodon* from Kromdraai.

	Elandsfontein *Megantereon* 3060	*Megantereon eurynodon* TM Ka 64*
(1) Height of ramus from inferior margin to top of coronoid process	45,0	*c*. 51,0
(2) Height of coronoid process above condyle	21,5	*c*. 24,0
(3) (1):(2)	1:0,48	*c*. 1:0,47
(4) Transverse diameter of condyle	28,8	—

* From Ewer (1955*c*: pl. 2; fig. 2).

The fossil humeri are essentially similar to those of modern felines in morphology, but their proportions are different. The estimated overall length of the most complete specimen (6762) is only a little more than that of humeri of modern *Panthera pardus*, judging from two specimens of the small south-western Cape variety, but it is considerably more stoutly built (Table 73).

The femora and tibiae are referred to *Megantereon* since they too belong to a medium-sized felid with relatively short and heavy limbs. The femora are larger than those of the *P. pardus* comparative specimens, while the tibiae are approximately the same length as those of *P. pardus* although they are far stouter. In three of the four femora, the lesser trochanter is as large as those of available modern *P. leo* specimens (n = 7), although in overall size the fossil femora are much smaller.

Discussion

The Elandsfontein machairodont is a species which is comparable in size to *Megantereon gracile* from Sterkfontein (Broom 1948) and *M. eurynodon* from Kromdraai. Ewer (1955*c*: 608) thought it unlikely that these two forms could be conspecific, although the observable differences between them are slight. The suggestion has already been made that the Elandsfontein form is conspecific with *M. gracile* and on the basis of the material presently available, including the casts, there are no grounds for doubting that this is the case.

If it is assumed that only one *Megantereon* lineage was represented in South Africa, and once again there are no grounds for believing otherwise, then it would be expected that the Elandsfontein *Megantereon* would have greater affinities with the Kromdraai *M. eurynodon*, since this form would be the next oldest in the series. The relative age of *M. whitei* from Schurveberg (Broom 1937*a*) is not known.

The situation may be summed up by the statement that although the Elandsfontein *Megantereon* is phylogenetically closer to *M. eurynodon*, it is morphologically more like *M. gracile*. Since the fossil forms are so poorly represented, this statement cannot be substantiated. There is, however, a simple and convenient explanation of the available record and that is the three forms, and perhaps *M. whitei* as well, are conspecific and that their supposed distinguishing characters are no more than individual intra-specific variations. Just as temporal variants of a single species have already been recorded for other South African Carnivora, so the Schurveberg, Sterkfontein, Kromdraai and Elandsfontein *Megantereon* could be regarded as temporal variants of one species.

A re-examination of all the South African *Megantereon* specimens now available would no doubt resolve the question of their specific status and the identity of the Elandsfontein material is, for the present, left in abeyance.

According to Kurtén (1968: 75) the body of *Megantereon* is characterized by 'short but massive front legs and relatively feeble hindquarters'. The forelimb of the Elandsfontein *Megantereon* is known only from the humerus, which is

TABLE 73

Dimensions of the postcranial bones of the Elandsfontein *Megantereon*, compared with those of modern *Panthera pardus*.

HUMERUS	6762	3058			*P. pardus* SAM 36324 ?♀	*P. pardus* SAM 36051 ♂
Overall length	*c.* 230,0	—			192,0	202,0
Max. trans. diam. at dist. end	61,2	—			40,8	42,8
Max. ant.-post. diam. at dist. end	36,4	—			24,7	26,7
Min. trans. diam. of shaft	20,5	19,8			14,8	15,5
FEMUR	9486D	5410	321	3461		
Overall length	253,0	—	—	—	215,0	228,0
Max. trans. diam. at prox. end	70,6	—	74,6	70,1	40,0	44,8
Max. ant.-post. diam. of head	29,4	—	32,0	30,2	19,7	21,5
Max. trans. diam. at dist. end	50,9	51,4	—	—	37,4	40,3
Max. ant.-post. diam. at dist. end	*c.* 57,5	54,2	—	—	34,2	37,7
Min. trans. diam. of shaft	*c.* 24,0	24,9	24,5	—	14,6	16,7
TIBIA	9486C	277				
Overall length	194,0	203,0			202,0	210,0
Max. trans. diam. at prox. end	51,0	*c.* 51,5			39,1	41,8
Max. ant.-post. diam. at prox. end	61,8	53,8			41,8	45,4
Max. trans. diam. at dist. end	38,8	38,0			27,7	31,6
Max. ant.-post. diam. at dist. end	25,7	24,4			17,6	21,3
Min. trans. diam. of shaft	18,7	19,3			13,0	14,4
	6762:9486D, C					
Humerus: Femur length	*c.* 1:1,10				1:1,12	1:1,13
Femur: Tibia length	1:0,77				1:0,94	1:0,92

indeed relatively short and robustly proportioned. The hindlimb is represented by both femora and tibiae and, although they are stout, there evidently was some reduction in elements of the hindlimb relative to those of the forelimb. The humerus is slightly longer relative to the femur compared to those of *P. pardus*, while the tibia is appreciably shorter than the femur.

The femur and tibia, 5410 and 277, which evidently belong to the same individual, are of interest since they exhibit pathological conditions similar to those observed in the Langebaanweg *Machairodus*. There is osteitis of the distal and proximal ends of the femur and tibia respectively, and facets of eburnation which correspond to one another are worn on adjacent medial articular surfaces. Although the total number of machairodont limb bones from Langebaanweg and Elandsfontein is small, an appreciable proportion exhibit some sort of bone pathology.

Family **Felidae**

Subfamily Felinae

Felis libyca Forster, 1780

(Fig. 69; also Hendey & Hendey 1968: pl. 7C)

Present status

The African wildcat still occurs in the south-western Cape, but it is now rare.

Material

Swartklip

ZW 110 —Part of a skull comprising the braincase and posterior portion of the left maxilla with damaged P^4.
ZW 1841—Part of the facial region of a skull, the dentition of which lacks the right P^2, part of P^4, and M^1.
ZW 3487—Part of the facial region of a skull with incisors, canines, left P^2 and right P^3.
ZW 377 —Part of the facial region of a skull with right I^2 to $\underline{C}$, and left I^1 and I^2.
ZW 1843—Left maxillary fragment with P^3 and P^4.
ZW 183 —Left P^4.
ZW 178 —Left mandibular fragment with I_3, $\bar{C}$ and part of P_3.
ZW 3489—Right mandibular fragment with P_4 and part of M_1.

Comment

The difficulties which may be encountered in the identification of fossil felines were referred to earlier and two of the above specimens, ZW 110 and ZW 183, were previously tentatively identified as belonging to *Felis serval* (Hendey & Hendey 1968: 63). It is, however, evident that they belong to a large variety of the wildcat rather than to a small serval.

Description

The smallest felid from Swartklip differs from the extant southern African form of the wildcat, *Felis libyca cafra*, principally in its larger size and in the shape of the braincase. The fossil braincase ZW 110 is comparable to the 'narrow-waisted' type which characterizes the northern races of *F. libyca* (see Pocock 1951: Fig. 4). It is appreciably longer than the braincases of the available *F. libyca cafra* specimens (n = 6) (Table 74). In addition, the post-orbital processes are long and narrow, which is also a feature of the northern varieties such as *F. libyca ugandae*. The sagittal crest is well developed and extends anteriorly almost as far as the post-orbital constriction. It was much less prominent in the *F. libyca* skulls examined in the course of the present study (n = 7).

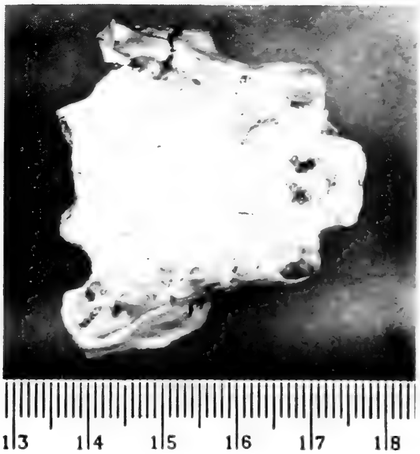

Fig. 69. Ventral view of the *Felis libyca* skull (ZW 1841) from Swartklip.

The facial region of the Swartklip wildcat is best represented by the specimen ZW 1841, which includes the complete dentition on the left side. The face of the fossil form is larger than that of modern *F. libyca* and this is indicated by the maximum width of the snout anterior to the infra-orbital foramina ('rostral width' of Table 74). Most of the upper teeth are also larger than those of the moderns (Table 75), although P^2 and M^1 were actually a little smaller than the means of the comparative series. Consequently, the small size of these teeth relative to P^3 and P^4 is more pronounced in the fossil form. In modern *F. libyca* P^2 is sometimes absent, but in those specimens in which the relevant part of the maxilla was preserved (ZW 377, ZW 1841, ZW 3487) the P^2, or its alveolus, was present. There are no differences in the morphology of the fossil and modern teeth and a similar variability in features was evident. For example, a small anterior accessory cusp is present on the left and right P^3 of ZW 1841 and in the P^3 of ZW 1843 it is represented by a trace, while in the available skulls of

TABLE 74

Dimensions of the skull of the Swartklip *Felis libyca*, compared with those of a series of modern specimens.

		Rostral width	Post-orbital constriction	Braincase length (from post-orbital constriction)	Maximum braincase width at squamosals	Mastoid width	Width across occip. condyles
Swartklip	ZW 110	—	30,5	60,0	52,0	*c.* 49,5	27,7
	ZW 1841	31,2	—	—	—	—	—
Modern *Felis libyca*	Mean	23,5	36,0	51,0	46,5	43,6	23,7
	Range	22,5–24,7	34,2–37,6	48,9–52,8	45,4–48,2	41,8–45,5	22,0–24,8
	n	5	6	5	5	5	5

TABLE 75

Dimensions of the upper teeth of the Swartklip *Felis libyca*, compared with those of a series of modern specimens.

		$\underline{C}$		P^2		P^3		P^4		M^1	$\underline{C}$–P^4
		l	b	l	b	l	b	l	b	trans. diam.	l
Swartklip	ZW 1841	5,0	4,0	2,6	1,8	7,8	3,9	12,3	5,8	3,1	32,4
	ZW 3487	5,3	4,5	2,1	1,6	8,0	4,4	—	—	—	—
	ZW 377	6,0	5,0	—	—	—	—	—	—	—	—
	ZW 1843	—	—	—	—	7,8	4,2	13,0	5,6	—	—
	ZW 183	—	—	—	—	—	—	14,0	6,1	—	—
Modern *Felis libyca*	Mean	4,8	3,7	2,7	1,9	7,0	3,7	11,5	5,6	3,8	30,4
	Range	4,5– 5,4	3,4– 4,0	2,3– 3,2	1,5– 2,2	6,4– 7,9	3,3– 4,2	10,7– 12,4	4,9– 6,4	3,2– 4,4	28,9– 32,1
	n	5		6		6		6		6	5

modern *F. libyca* it was absent in two specimens, represented by a trace in three and present in two.

The lower teeth of the fossil form are within the observed size range of variation of modern *F. libyca* (Table 76), but the mandibular corpus of ZW 3489 is larger than any of the moderns.

TABLE 76

Dimensions of the lower teeth of the Swartklip *Felis libyca*, compared with those of a series of modern specimens.

		$\bar{C}$		P_4	
		l	b	l	b
Swartklip	ZW 178	5,0	3,9	—	—
	ZW 3489	—	—	7,9	3,6
Modern *Felis libyca*	Mean	4,4	3,4	7,7	3,5
	Range	4,0–5,3	3,2–4,0	6,9–8,4	3,3–3,9
	n	5		6	

Discussion

The Swartklip wildcat is comparable to some of the other carnivores from this site in that it is larger than its modern counterpart. Otherwise differences between it and modern *F. libyca* are not marked, although the relatively small size of P^2 and M^1 may prove a significant differentiating characteristic.

The relatively elongated and 'narrow-waisted' braincase which it has in common with the more northerly varieties of *F. libyca* is perhaps a more primitive condition than the shorter and 'broad-waisted' braincase of the extant southern African subspecies (*F. l. cafra*, *F. l. griselda*, *F. l. mellandi*).

Although the Swartklip wildcat does differ in certain respects from the extant local variety, it is undoubtedly closely related and it is distinguished from the moderns by being termed 'Florisian *F. libyca*'.

Family **Felidae**

Subfamily Felinae

Felis serval Schreber, 1776

(Fig. 70)

Present status

The serval is now extinct in the south-western Cape, but it still occurred in the region during the nineteenth century.

Material

Swartklip

ZW 1480/1 — Parts of the skull of a single individual, including:
Right premaxilla and maxilla lacking only I^1 and P^2, found in articulation with a right mandible with I_2 to M_1; left maxillary fragment with P^3 and part of P^4, found in articulation with a left mandibular fragment with P_3 to M_1.
ZW 1448 — Left maxilla with P^3 and P^4.
ZW 1649 — Left $\underline{C}$.
ZW 2950 — Right mandibular fragment.
ZW 3438 — Right mandibular fragment with $\overline{C}$ to M_1.
ZW 3488 — Left mandibular fragment with P_4 and M_1.

Tentatively referred material

Sea Harvest, Saldanha

S 202 — Right mandibular fragment with P_3 to M_1.
S 1 — Left mandibular fragment with M_1.
S 216 — Left M_1.

Description

The material from Swartklip belongs to a felid which is comparable in size to the extant *Felis caracal*. This species is usually larger than *F. serval* in respect of skull and tooth size, although overlaps in the size ranges of variation were observed in the available series of modern comparative specimens (*F. caracal* n = 27; *F. serval* n = 13). The fossil teeth were all larger than those of the *F. serval* series (Tables 77, 78), and in most respects were within the ranges of variation observed in *F. caracal*. In other respects, however, the dentition of the fossil form is most similar to that of *F. serval*.

The most important *F. serval* characteristic exhibited by the Swartklip fossils is the presence of P^2. In ZW 1480 the root of this tooth is preserved, while in ZW 1481 and ZW1448 the P^2 alveoli are present. Judging from the available comparative material, P^2 is invariably present in *F. serval*, whereas in only 3 of the 27 skulls of *F. caracal* was it observed. In one of these specimens (BMNH 2.9.1.20a) the P^2 is comparable in size (3,2 × 1,9 mm) to that of *F. serval*, while in the others (SAM 35101, 36268) it is very small (1,5 × c1,2; 1,3 × 1,0). Judging from the P^2 alveoli of the fossil specimens, these teeth were comparable in size to those of modern *F. serval* and they occupied much of the space intervening between C and P^3. The P^2 alveolus of ZW 1480 measures 3,8 × 2,2 mm, while that of ZW 1448 measures c4,5 × 2,7 mm.

There are few other constant differences between the dentitions of *F. serval* and *F. caracal*. There is apparently a tendency for the posterior keel of the *F. serval* P_4 principal cusp to be more steeply angled than that of *F. caracal*, while the P_3 principal cusp of *F. serval* tends to be higher crowned. The anterior accessory cusps of these two teeth are a little more prominent in *F. serval*,

TABLE 77

Dimensions of the upper teeth of the Swartklip *Felis serval*, compared with those of modern *F. serval*.

		$\underline{C}$		P^2		P^3		P^4		M^1 Transverse diameter	$C-M^1$
		l	b	l	b	l	b	l	b		l
Swartklip	ZW 1480	7,9	6,5	—	—	9,9	5,2	16,2	7,7	6,0	41,7
	ZW 1448	—	—	—	—	10,0	5,3	*c.* 15,5	7,4	—	—
	ZW 1649	8,3	6,6	—	—	—	—	—	—	—	—
Felis serval[1]	SAM 36359	7,1	5,2	4,2	2,7	9,5	4,2	15,0	7,0	4,5	40,0
Felis serval[2]	BMNH 99.6.26.1	6,0	4,5	4,1	2,5	9,3	*c.* 4,5	15,1	6,8	5,4	38.6
Felis serval[3]	Mean	6,2	4,5	3,4	2,1	8,5	4,1	13,4	6,1	4,5	35,6
	Range	5,1–6,9	3,9–5,0	2,6–4,5	1,9–2,4	8,0–9,0	3,6–4,7	12,5–15,1	5,4–6,6	3,0–5,5	32,9–39,0
	n	13		13		12		13		13	13

[1] Somerset West, south-western Cape Province [2] Potchefstroom, Transvaal.

[3] Central and East Africa (specimens in British Museum (Natural History)).

TABLE 78

Dimensions of the mandibles and lower teeth of the Swartklip and Sea Harvest *Felis serval*, compared with those of modern *F. serval*.

		$\overline{C}$		P_3		P_4		M_1		$\overline{C}$–M_1	Height of corpus below M_1 (buccal surface)	Breadth of corpus below M_1	Post $\overline{C}$ diastema (between alveoli)
		l	b	l	b	l	b	l	b	l			
Swartklip	ZW1480	*c.* 7,5	*c.* 6,2	8,8	4,6	11,7	5,1	11,5	5,9	45,0	15,0	7,9	7,0
	ZW 3438	7,4	6,0	8,6	*c.* 4,2	11,0	4,6	11,5	5,3	—	—	—	8,2
	ZW 3488	—	—	—	—	11,6	4,5	11,4	5,5	—	12,8	7,0	—
	ZW 2950	—	—	—	—	—	—	—	—	—	15,0	8,4	—
Sea Harvest	S 202	—	—	9,7	4,2	10,8	4,9	12,3	5,3	—	14,9	7,7	7,2
	S 1	—	—	—	—	—	—	12,4	5,7	—	15,4	*c.* 8,3	—
	S 216	—	—	—	—	—	—	11,8	5,6	—	—	—	—
Felis serval[1]	SAM 36359	6,3	5,2	8,7	4,0	10,7	4,4	10,9	4,8	42,5	13,0	6,7	7,5
Felis serval[2]	BMNH 99.6.26.1	6,0	4,4	8,5	4,1	11,0	4,4	11,0	5,0	42,3	13,1	6,8	6,8
Felis serval[3]	Mean	6,1	4,4	7,5	3,6	9,4	4,0	10,2	4,5	38,1	11,9	6,5	5,8
	Range	5,0–6,8	3,6–5,0	6,8–8,3	3,3–4,0	8,8–10,3	3,7–4,5	9,0–11,4	4,2–4,8	35,5–43,1	10,5–14,3	5,7–7,4	4,2–8,8
	n	13		13		13		13		13	12	13	13

[1] Somerset West, south-western Cape Province.
[2] Potchefstroom, Transvaal.
[3] Central and East Africa (specimens in British Museum (Natural History)).

Fig. 70. Buccal and occlusal views of the *Felis serval* maxilla (ZW 1480) from Swartklip.

while the upper canine of this species is more deeply grooved on its buccal surface than that of *F. caracal*. In all these respects the Swartklip form resembles *F. serval* rather than *F. caracal*.

In the modern varieties of these species the proportions of the individual teeth are essentially similar, although there appears to be a fairly constant difference in the lengths of P_4 and M_1 relative to one another. In *F. serval* the tendency is for these teeth to be approximately equal in length, but in *F. caracal* M_1 is apparently always longer. The former condition is evident in the Swartklip fossils (Table 79).

The only other observable skull character which may be of significance in the present instance is in the nature of the external opening of the infra-orbital foramen. In modern *F. serval* and in the fossil that part of the maxilla which forms the lateral margin of the infra-orbital foramen projects further forward than in *F. caracal*.

The specimens from Sea Harvest belong to a felid which is comparable to that from Swartklip in almost all observable respects. A problem in identification does arise in connection with S 202, because the relative lengths of the

P_4 and M_1 are comparable to those of *F. caracal* rather than *F. serval*. On the other hand, the P_3 and P_4 of S 202 are similar to those of *F. serval* in respect of their morphology. The isolated lower carnassial, S 216, is an unusual tooth in that it has a small cusp projecting from the lingual cingulum at about the mid-point of the tooth opposite the carnassial notch. No such accessory cusp was observed in any of the other felid lower carnassials examined in the course of the present study, and it is probably an individual peculiarity which is of no real significance.

Discussion

Relatively few of the characteristics which distinguish the modern varieties of *F. serval* from *F. caracal* are observable in the Swartklip material. It is, however, really only in respect of size that the fossils resemble *F. caracal* rather than *F. serval* and the material is accordingly referred to the latter species. This is yet another species from Swartklip which is larger than its modern counterpart.

The Sea Harvest specimens are less certainly referred to *F. serval*. This reservation is based largely upon the relative lengths of the P_4 and M_1 of S 202. However, although it is usual for these teeth to be approximately equal in length in *F. serval*, there are individual exceptions. For example, in the specimen BMNH 99.10.23.3 the P_4:M_1 length ratio is 1:1,24, so that in this instance the M_1 is relatively longer even than that of S 202 (Table 79). Only when other cranial and dental characters of the Sea Harvest species become known will its identity be firmly established.

TABLE 79

Comparisons of the lengths of P_4 and M_1 of the Swartklip and Sea Harvest *Felis serval*, modern *F. serval* and modern *F. caracal*.

	lP_4	lM_1	lP_4:lM_1
Felis caracal (n = 19)	10,7	12,2	1:1,13
Sea Harvest *F. serval* (n = 1)	10,8	12,3	1:1,14
Felis serval (n = 13)	9,4	10,2	1:1,08
Swartklip *F. serval* (n = 3)	11,4	11,5	1:1,01

The record of *F. serval* from Swartklip and Sea Harvest indicates that this species was not uncommon locally during the Florisian and early Holocene. Since it was still present in the region until fairly recently, it is probably one of the many species which became extinct as a result of human activity. This is in curious contrast to the similar sized *F. caracal*, which has survived locally in spite of determined efforts aimed at its eradication. The serval apparently still occurs, but is rare, in the eastern Cape about 750 km east of the area under consideration. Its disappearance from the large tracts of un- and under-developed country in the southern Cape is also remarkable, since the caracal still occurs there in greater numbers than it does in the south-western Cape.

It is possible that the species was already in decline in the most southerly parts of South Africa and that human activity in the historic period merely hastened its extinction. There is, however, no real evidence to support this and as late as 1775, more than 100 years after the first European settlement at the Cape was established, Forster (1781:4) recorded the conspecific *F. capensis* near Cape Town, reporting that it still occurred in 'mountainous and woody tracts' near this city. As far as could be determined, the last local record of this species was a specimen from Somerset West near Cape Town which was acquired by the South African Museum in 1898 (SAM 36359).

A second possibility to account for the local disappearance of *F. serval* and its apparent absence from the southern Cape is that Forster's *F. 'capensis'* represented a relict population of *F. serval*, which survived for some time away from the main area of *F. serval* distribution in tropical Africa. There are no obvious differences between the Somerset West specimen and others from elsewhere in Africa, but detailed comparisons have yet to be undertaken.

At least one other extant carnivore species, namely, *Viverra civetta* did disappear from the south-western Cape and adjacent regions during the latter part of the Quaternary and there are certainly no indications of human involvement in this instance. There might well have been natural limiting factors operating in the case of *F. serval* as well.

Family **Felidae**

Subfamily Felinae

Felis caracal Schreber, 1776

Present status

The caracal still occurs in the south-western Cape, but it is classed as vermin and threatened with extinction.

Material

Elandsfontein

15833—Left mandibular fragment with $\bar{C}$ to M_1,; isolated right P_4 and M_1.
20072—Right mandibular fragment with P_3 to M_1.

Comment

The material 15833 is from the Florisian Bone Circle occurrence, while the other mandibular fragment, 20072, is in an unusual state of preservation and may also be post-Cornelian in age.

TABLE 80

The dimensions of the mandibles and lower teeth of *Felis caracal* from Elandsfontein compared with those of modern *F. caracal*.

		$\bar{C}$		P_3		P_4		M_1		Height of corpus below M_1 (buccal surface)	Breadth of corpus below M_1	Post-canine diastema
		l	b	l	b	l	b	l	b			
Elandsfontein	15833	7,7	5,7	9,0	4,8	12,4	5,4	13,3	5,7	*c.* 15,5	*c.* 9,5	5,8
Modern *F. caracal*	SAM 36072	8,3	6,1	9,3	4,5	12,4	5,5	14,0	5,6	15,0	9,5	6,8
Elandsfontein	20072	—	—	7,4	4,2	10,3	5,2	12,5	6,0	13,3	7,8	*c.* 7,3
Modern *F. caracal* (S. Africa)	Mean	6,9	5,1	8,2	4,0	10,9	5,0	12,4	5,5	14,0	8,5	6,4
	Range	6,2– 8,3	4,5– 6,1	7,4– 9,3	3,6– 4,5	10,0– 12,4	4,4– 5,5	11,0– 14,0	4,9– 6,1	12,2– 16,5	7,2– 10,0	4,3– 8,5
	n	12		15		15		15		15	15	15
Modern *F. caracal* (E. Africa)	Mean	6,7	5,1	7,5	3,9	10,2	4,7	11,8	5,3	13,1	8,4	6,7
	Range	5,8– 7,3	4,6– 5,4	6,6– 8,1	3,6– 4,2	9,8– 10,8	4,5– 4,9	11,4– 12,0	5,0– 5,4	12,5– 13,4	6,6– 9,4	6,0– 7,2
	n	4		4		4		4		4	4	4

Description

The Bone Circle specimens probably belong to a single individual and they are virtually indistinguishable from corresponding parts of the mandible of a large *Felis caracal* (SAM 36072) included in the available modern comparative series. Although they are also similar in size to the Swartklip *F. serval* specimens, they exhibit none of the features which characterize this form.

The specimen 20072 belongs to a smaller individual, which is comparable to average-sized specimens in the *F. caracal* comparative series (Table 80). The dentition is indistinguishable from that of *F. caracal.*

Discussion

Although the mandibles of *F. caracal* and *F. serval* are less easily distinguished from one another than the skulls of these species, the fossil specimens are so similar to *F. caracal* that their identification with this species is unavoidable.

Since the *Mellivora capensis* and *Canis mesomelas* from the Bone Circle are larger than their modern counterparts, it is possible that the same applies in the case of the *F. caracal.* Thus the recorded material may represent an average-sized individual of the fossil population, rather than an unusually large individual as was the case with SAM 36072, the modern specimen to which it compared most closely in size.

The smaller specimen, 20072, could be even younger than the Bone Circle material and since it belongs to an individual similar in all observable respects to an average-sized modern caracal, it might well be Holocene in age. The possibility that it predates the Bone Circle material cannot, however, be dismissed.

The absence of *F. caracal* from the Swartklip and Sea Harvest assemblages is surprising in view of the Elandsfontein and recent records of this species. As the Swartklip and Sea Harvest sites are both hillside animal lairs, the absence of *F. caracal* may simply indicate that this species did not make use of such lairs.

Family **Felidae**

Subfamily Felinae

Felis sp(p).

Material

Elandsfontein

Mandibular fragments with teeth as follows:
EC 38—None.
8402 —Right P_3 and P_4.
9198 —Incomplete right P_4.
11127—Incomplete left $\overline{C}$.

Isolated teeth as follows:
7086—Right M^1.
7527—Left $\underline{C}$.
7787—Left P_4.

Discussion

These specimens represent only a part of a larger assemblage of remains belonging to a caracal-sized felid, or felids. The remainder of the assemblage, which includes the specimens tentatively identified as *Felis serval* by Ewer & Singer (1956), is no longer in the South African Museum's collections and will presumably be described elsewhere.

At least one of the specimens listed above, 9198, differs in certain respects from those previously assigned to *F. serval* and *F. caracal*, while another, 8402, may belong to a large *F. caracal*.

Judging from their preservation, these specimens belong with the Cornelian element of the Elandsfontein fauna and since an assessment of this material could be better made in conjunction with the rest of the assemblage, it is not described in detail. The indications are, however, that there is at least one additional caracal-sized felid in the Elandsfontein assemblage. On the basis of the observations made on other Carnivora from this site, it is most likely that the present material represents Cornelian varieties of the serval and caracal.

Family **Felidae**

Subfamily Felinae

Panthera pardus Linnaeus, 1758

(Fig. 71)

Present status

The leopard became extinct in the south-western Cape during the nineteenth century, but small numbers still occur in the mountains adjacent to this region.

Material

(1) *Sea Harvest, Saldanha*

S 131—Right P^4.
S 132—Right M_1.
S 213—Premolar fragment.
S 32 —Femur lacking distal end.

(2) *Fish Hoek*

Q 1800—Right mandible with $\overline{C}$ to M_1.

Description

The Fish Hoek mandible is essentially similar to those of a series of leopards from the Cape Folded Mountains (n = 6), although the cheekteeth are rather narrow. (Table 81).

The Sea Harvest specimens are all appreciably larger than corresponding elements in the comparative series, but they are similar in all morphological details.

TABLE 81

Dimensions of the teeth and mandible of fossil *Panthera pardus* from the south-western Cape compared with those of a series of modern leopards from mountains adjacent to this region.

		P^4		$\overline{C}$		P_3		P_4		M_1		Overall length of mandible	Depth of mandible below M_1	Breadth of mandible below M_1
		l	b	l	b	l	b	l	b	l	b			
Sea Harvest	S 131, S 132	28,5	*c.* 15,5	—	—	—	—	—	—	*c.* 21,8	11,0	—	—	—
Fish Hoek	Q 1800	—	—	*c.* 11,0	8,5	11,8	5,3	16,7	7,0	16,6	7,2	*c.* 126,0	*c.* 22,0	10,5
Modern *Panthera pardus*	Mean	23,2	11,9	12,2	8,9	11,4	5,6	16,2	7,8	17,2	8,0	130,9	22,4	11,8
	Range	20,7–24,9	10,4–12,8	10,5–12,8	7,9–9,6	10,5–11,9	5,2–6,0	14,6–17,5	7,2–8,3	15,1–18,3	7,5–8,7	117,0–142,0	20,7–24,6	10,8–12,5
	n	6		4		5		6		6		6	6	6

Discussion

The Fish Hoek specimen, which might well be very recent in age, apparently represents the small variety of leopard which still occurs in the mountains adjacent to the south-western Cape.

By contrast, the ? early Holocene Sea Harvest material represents a very much larger variety.

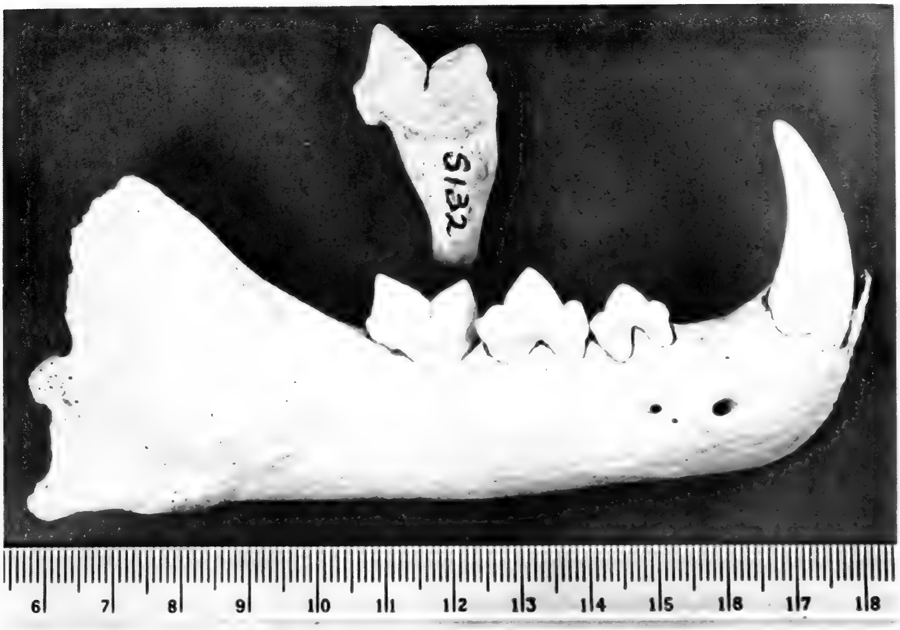

Fig. 71. Buccal views of the *Panthera pardus* M_1 (S 132) from Sea Harvest and the mandible (Q 1800) from Fish Hoek.

Panthera pardus is an exceptionally widely distributed mammalian species and a large number of subspecies have been named. Although the taxonomy proposed by Pocock (1932) has been modified by more recent work, the wide variation encountered within the species can be judged from Pocock's observations. Amongst the measurements of modern leopard skulls given by this author are the lengths of 112 upper carnassials and 102 lower carnassials. His figures represent both males and females from throughout Africa and all these specimens are exceeded in length by the Sea Harvest carnassials. Broom (1948) gives the length of the largest modern leopard P^4 recorded by him as 28,2 mm, which is still less than the 28,5 of the Sea Harvest specimen, S 131.

Smithers (1968: 12) discussed the taxonomy of modern *P. pardus* and observed that, 'In some cases attempts have been made to separate subspecies into larger and smaller types on skull and tooth measurements of comparatively few specimens, yet in some areas, e.g. Rhodesia, exceptionally large individuals do occur within populations of generally smaller size'. Since the Sea Harvest material may all belong to a single individual, it may simply be such an exceptionally large example of the species. However, other Sea Harvest Carnivora, such as *Hyaena brunnea* and *Herpestes pulverulentus*, are also larger than their modern counterparts in some respects, so it is more likely that the leopard material represents a large variety rather than just an exceptional individual.

The only other fossil leopard from South Africa which has been described is the Makapanian *P. pardus incurva* (Ewer 1956*a*), a variety which is probably a little smaller than the modern form from the Transvaal. The leopard is, therefore, yet another carnivore which underwent size changes during the Quaternary and, although their fossil record is poor, the Sea Harvest variety may well be one of the largest which occurred.

Family **Felidae**

Subfamily Felinae

Panthera leo Linnaeus, 1758

(Figs 72, 73, 74; also Hendey & Hendey 1968: pl. 7A, B; Hendey 1968: pl. 10)

Present status

The lion is now extinct in the south-western Cape Province, but it was still common in the region during the seventeenth century.

Material

(1) *Elandsfontein*

The only known cranial remains from this site, together with some associated postcranial bones, are no longer in the South African Museum's collections. A 2nd phalanx (9664) and parts of a radius (9054, 9632A), which apparently belong to the same individual, are still available, as are the following:

Fore- and hindlimb:

8487A–D—Metacarpal, metatarsal and restored femur and tibia of a single individual.

Forelimb:

16691A–C—Restored humerus, ulna and radius.

8377—Parts of left and right humeri, ulnae and radii.

20743—Radius and part of an ulna.

11202B, 12781—Humeri lacking proximal ends.

4331, 9115, 13715, 14763, 16670, 16795, 20216, 20217, 20416, 20422—Distal ends of humeri.

273, 11156, 11202A, 20429—Ulnae lacking distal ends.

270, 5684—Ulnae lacking distal ends and parts of proximal ends.

11154, 11155—Proximal and distal ends of a radius.

5845, 11510, 20040, 20641, 21010—Proximal ends of radii.
20430—Shaft of radius.
8869—Distal end of radius.
6510—Pisiform.
598, 3794, 8605, 9127—Metacarpals.

Hindlimb:
20284—Proximal end of femur.
105—Calcaneum.

(2) *Melkbos*

Mb 143—Left mandibular fragment with P_4 and M_1.
Mb 603—Right mandibular fragment with part of P_4.
Mb 561—Distal end of radius.
Mb 576, Mb 659—Incomplete metapodials.

(3) *Swartklip*

ZW 100 —Incomplete braincase.
ZW 101 —Incomplete braincase.
ZW 1447—Fragment of facial region with right I^2 and I^3, and left I^1 to I^3, part of $\underline{C}$, and P^2.
ZW 3789—Right maxillary fragment with P^3.
ZW 131 —Left maxillary fragment with dp^3, dp^4 and M^1 just erupting, and unerupted $\underline{C}$, P^3 and P^4.
ZW 106 —Left maxillary fragment with dp^2 and dp^3, and unerupted P^3.
ZW 122 —Left and right dp^4.
ZW 1872—Left dp_4.
ZW 1457 and others—Fragments of unerupted permanent teeth.
ZW 3492—Part of the shaft of a humerus.
ZW 2800—Ulna lacking distal end and part of proximal end.
ZW 350, ZW 526—Proximal and distal ends of a radius.
ZW 1040, ZW 1789, ZW 3240—Metacarpals or parts thereof.
ZW 3439—Distal end of a tibia.
ZW 2533—Incomplete metatarsal.
ZW 237, ZW 1775, ZW 2796, ZW 3276—1st phalanges.

(4) *Sea Harvest, Saldanha*

S 129—Right maxillary fragment with alveoli of $\underline{C}$, P^4 and M^1, and P^3 just erupting.
S 208—Incomplete right P_4.
S 237—Metacarpal.
S 230—Calcaneum.
S 130, S 234, S 715—Metatarsals.
S 241—2nd phalanx.

Description

The study of this material was hampered by the lack of adequate comparative material. Most of the cranial specimens belong to juveniles and only a single skull of a young modern lion was available, although 27 adult skulls were examined in the course of the study. Only seven complete skeletons were available, of which six belonged to zoo specimens which suffered from rickets. The seventh belonged to a large male from Botswana (SAM 3985).

Sea Harvest

The Sea Harvest maxillary fragment, S 129, belongs to an individual which was slightly older than that represented by the only juvenile skull in the comparative series (SAM 36663). The fossil dp³ had apparently just been shed, while that of the skull of SAM 36663 is still in position, but in the process of

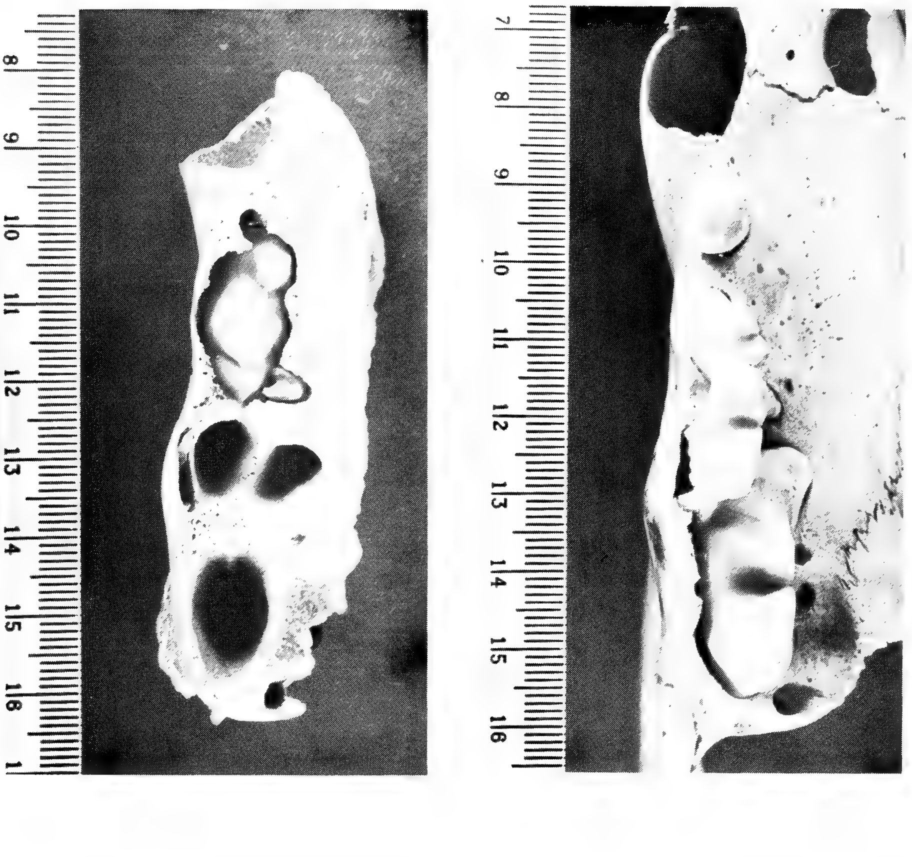

Fig. 72. Occlusal views of the *Panthera leo* maxilla (S 129) from Sea Harvest and a modern specimen (SAM 36663).

being forced out by the erupting P^4. The fossil is similar in size to corresponding parts of the modern specimen, but they differ in that the modern one has a fully erupted P^2, whereas in the fossil this tooth is completely absent. The fossil dp^2 is lost, its alveolus partly overlapping the erupting P^3. The post-canine diastema is very short. The P^3 is similar to that of modern *Panthera leo* in all observable respects and, judging from the size of the P^4 and M^1 alveoli, these teeth were comparable in size to those of the moderns.

Most of the Sea Harvest postcranial bones are similar in size to those of the large male from Botswana. The exceptions are a metatarsal II (S 715) and the 2nd phalanx (S 241), which are a little larger than the corresponding bones of SAM 3985.

On the basis of the few specimens available, it appears that the Sea Harvest lion was comparable in size to modern *P. leo*, but differed in lacking P^2. Although the Sea Harvest fossils are regarded as Holocene in age, the possibility that the lion from this site is the so-called 'Cape lion' (*P. leo melanochaita* H. Smith, 1842) was dismissed, since a well developed P^2 was present in this variety (*vide infra*).

Swartklip

Some of the Swartklip lion specimens have already been discussed (Hendey & Hendey 1968), and although it was concluded that they do not differ from the modern form, a more detailed examination has shown that this is not the case.

The two incomplete braincases, ZW 100 and ZW 101, belong to adults and are similar in overall size to corresponding parts of the skulls of modern females (Table 82). However, the more complete specimen, ZW 100, differs from the moderns in having a broader occiput dorsal to the occipital condyles. The occipital width expressed as a percentage of the braincase length is greater in the fossil than in both males and females of the comparative series. The post-orbital region is also relatively broad.

The snout fragment, ZW 1447, and the maxillary fragment, ZW 3789, evidently belong to mature adults, since both have worn teeth. ZW 1447 compares in size to corresponding parts of the skulls of modern males and is remarkable only because the P^2 is smaller than those of the comparative series (Table 84). This suggests the possibility that the Swartklip lion was ancestral to that from Sea Harvest, a variety in which P^2 is lost. These local fossils are regarded as belonging in a lineage distinct from other lions and one which is characterized by the reduction and eventual loss of P^2.

The P^3 of ZW 3789 is within the size range of variation observed in modern males, while the P^2 alveolus is similar in size to that of ZW 1447.

The juvenile maxillary fragment, ZW 131, is larger than those of the Sea Harvest specimen, S 129, and the modern juvenile, SAM 36663, although it belongs to an individual which was ontogenetically younger than both these specimens. The dp^4 is still in position and the P^4 is only just starting to erupt. The P^3, P^4 and M^1, although unerupted or only partly erupted, are larger than

TABLE 82

Dimensions of the braincase of the Swartklip *Panthera leo*, compared with those of a series of modern lions.

			(1) Length of braincase	(2) Width of occiput	(3) (2) × 100/(1)	(4) Mastoid width	(5) (4) × 100/(1)	(6) Post-orbital width	(7) (6) × 100/(1)	(8) Height of occiput	(9) Width across occiput condyles
Swartklip		ZW 100	148,0	76,3	51,6	*c.* 126,0	85,1	*c.* 72,0	48,6	*c.* 96,0	58,1
		ZW 101	—	—	—	*c.* 121,0	—	—	—	—	*c.* 60.0
Cape lion (*P. leo melanochaita*)		♀ SAM 7529	150,0	59,7	39,8	*c.* 115,0	*c.* 76,7	64,0	42,7	*c.* 92,5	—
		♀ SAM 35121	150,0	59,7	39,8	129,2	86,1	69,0	46,0	97,6	63,4
		♂ SAM 33425	170,0	63,9	37,6	*c.* 136,0	80,0	73,1	43,0	100,4	60,5
Modern *Panthera leo*	♀	Mean	143,8	61,5	42,5	118,9	82,7	64,2	44,9	93,1	56,6
		Range	134,0–152,0	57,2–65,0	41,1–44,8	117,8–136,0	77,5–86,7	59,3–73,1	40,9–48,1	85,7–100,4	52,4–63,4
		n	6	6	6	6	6	5	5	6	6
	♂	Mean	178,0	73,1	41,0	141,9	79,7	74,7	42,0	114,9	66,2
		Range	167,0–194,0	65,0–82,3	36,1–45,7	136,0–147,0	75,6–82,6	66,3–80,5	39,5–46,5	107,0–124,8	63,5–71,5
		n	8	8	8	7	7	8	8	6	7

TABLE 83

Dimensions of the deciduous teeth of the Swartklip *Panthera leo*, compared with those of a young modern lion

		dp^2		dp^3		dp^4		dp$_4$	
		l	b	l	b	l	b	l	b
Swartklip	ZW 131	—	—	26,8	15,5	8,0	14,7	—	—
	ZW 106	3,8	2,9	27,0	15,0	—	—	—	—
	ZW 122a	—	—	—	—	8,4	14,2	—	—
	ZW 1872	—	—	—	—	—	—	*c.* 20,1	8,0
Modern *P. leo*	SAM 36663	—	—	24,5	13,8	—	—	17,7	6,9

the corresponding teeth in the comparative series, while the dp^3 is larger than that of SAM 36663. The same applies in the case of the dp^3 of ZW 106 and the dp$_4$ of ZW 1872 (Table 83). Although ZW 106 belongs to a younger individual than S 129, it has a longer post-canine diastema and an unerupted P^2 in the maxilla, a further indication of the contrasting nature of this region of the skull of the Swartklip and Sea Harvest lions.

To sum up, the Swartklip lion is apparently characterized by a relatively short braincase and broad occiput, a reduced P^2, enlarged posterior cheekteeth, with a corresponding enlargement of the posterior part of the maxilla.

The postcranial skeleton is little different in size to that of the large modern male, SAM 3983, although the phalanges, a metacarpal V (ZW 1040) and the ulna (ZW 2800) are larger. If the larger specimens belonged to males and the others to females, it would indicate that the overall size of the Swartklip lion was greater than that of modern *P. leo*. This species would then have been like others from Swartklip in that it was larger than its modern counterpart.

Melkbos

The Melkbos specimens, with the exception of Mb 659, have already been described (Hendey 1968), and they too differ from the corresponding parts of modern *P. leo* in their larger size. The additional specimen, a metacarpal V, is also larger than that of the modern comparative specimens (Table 86).

Elandsfontein

The Elandsfontein skull, which will presumably be described in detail elsewhere, is appreciably larger than the skulls of modern lions and it has already been suggested that there might be a close relationship between this form and that from Melkbos (Hendey 1968).

TABLE 84

Dimensions of the teeth of fossil *Panthera leo* from the south-western Cape Province, compared with those of recent southern African lions.

		$\underline{C}$		P^2		P^3		P^4		M^1	$\overline{C}$		P_3		P_4		M_1		M_1 bx100/l
		l	b	l	b	l	b	l	b	b	l	b	l	b	l	b	l	b	
Sea Harvest	S129[1]	—	—	—	—	c. 24,6	—	c. 36,5	c. 19,3	c. 11,5	—	—	—	—	—	—	—	—	—
Swartklip	ZW1447	23,2	17,5	7,2	5,8	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	ZW 131[1]	—	—	—	—	c. 28,5	—	c. 43,0	c. 22,0	c. 16,3	—	—	—	—	—	—	—	—	—
	ZW3789	—	—	—	—	25,5	13,2	—	—	—	—	—	—	—	—	—	—	—	—
Cape Lion ♀	Murraysberg[2]	—	—	—	—	26,5	13,0	39,0	18,0	—	—	—	19,0	10,5	27,5	14,5	28,0	15,5	55,4
	SAM 35121	24,3	16,7	c. 10,0	7,3	22,6	11,8	34,6	17,4	9,8	c. 22,2	15,2	17,9	c. 9,0	24,9	13,2	26,5	14,5	54,7
Modern Panthera leo ♀	Mean	22,1	15,9	9,3	7,0	23,9	11,9	35,9	17,2	11,7	21,0	14,5	17,4	8,8	25,2	12,7	26,6	12,9	48,5
	Range	21,0–24,1	14,9–17,1	8,3–10,7	6,5–7,6	20,5–27,0	10,6–12,9	34,0–39,5	15,7–19,2	10,4–12,6	19,5–21,7	13,3–15,4	15,3–19,9	8,2–9,4	23,1–28,0	11,0–14,0	25,6–27,8	12,0–13,8	46,5–50,6
	n	7	6	7		8		8		6	5		6		6		6		6
Cape Lion ♂	NHMW 1422[3]	25,5	18,1	—	—	26,0	13,5	38,0	20,7	—	—	16,2	20,0	10,8	28,0	14,3	27,8	15,9	57,2
	SAM 33425	c. 28,0	20,2	9,5	7,6	26,0	c. 14,0	39,3	19,2	12,1	c. 28,6	c. 18,0	19,5	c. 11,2	29,0	15,1	29,4	16,1	54,8
Modern Panthera leo ♂	Mean	26,8	19,4	9,4	7,5	26,2	13,3	38,7	19,1	11,9	25,3	17,9	19,1	10,2	27,9	14,0	28,9	14,7	51,1
	Range	23,6–29,8	18,1–20,8	8,5–10,9	6,5–9,2	23,9–28,6	11,1–14,6	34,2–41,3	17,5–20,6	10,2–13,5	22,5–27,8	16,4–19,3	16,1–22,2	8,3–11,7	24,8–29,7	11,5–15,1	27,2–30,5	13,0–15,7	46,4–52,9
	n	8		11		11		11		8	8		10		10		10		10

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[1] Unerupted permanent teeth, or estimates based on size of alveoli.

[2] Lundholm 1952.

[3] Hemmer 1964.

In general, the postcranial bones from this site are as large or larger than those of the available modern *P. leo* specimens, although an appreciable size range of variation was observed in those skeletal elements which are represented by several specimens (i.e. humerus, ulna, radius). The best represented of the bones is the humerus and fifteen specimens belonging to at least thirteen individuals are known. The size difference between the smallest and the largest of the humeri appears to be rather more than would be expected in a single population, although, in view of the inadequate comparative series, this is a somewhat subjective judgement. However, the size difference between the humeri of the largest male and smallest female in the comparative series is only about 16%, while the difference between the largest and smallest humeri in the Elandsfontein series is about 33%, or twice as much. Consequently, it is possible that more than one form of the lion is represented at Elandsfontein as is the case with other species, although in this instance the nature of the preservation of the specimens did not suggest this. In fact, the preservation of one of the smallest specimens (16670) and the largest specimen (16795) would suggest that they both belong with the Cornelian element in the fauna.

The material may actually include some specimens which belong to a large felid other than the lion and some of the smaller bones approach those of the Langebaanweg ? *Machairodus* in size (Table 85). Large machairodonts are known from the Makapanian, namely the *Homotherium* sp. from Makapansgat (Collings 1972; *vide supra*), *Machairodus transvaalensis* from Bolt's Workings (Broom 1939) and ? *Epimachairodus* sp. (? = *Homotherium* sp.) from Kromdraai (Ewer 1955c), and one of these, probably a *Homotherium*, may have survived into the Cornelian. The absence of cranial remains of a machairodont larger than *Megantereon* is not necessarily significant, since the Elandsfontein *Megantereon* itself is apparently represented only by the incomplete mandible of one individual.

It is possibly significant that the relatively small humerus referred to earlier (16670) exhibits pathological conditions similar to those observed in other machairodont bones from the south-western Cape (*vide supra*). The pathology of 16670 includes osteoporosus in the region of the olecranon fossa, bony 'lipping' of the articular surface and eburnation. No similar pathology was observed in any of the other specimens referred to *P. leo*.

The identification of a large machairodont in the Elandsfontein assemblage can clearly not be substantiated on such slender evidence, but there is at least a possibility that a large machairodont was contemporary with the smaller *Megantereon*. This possibility is not reflected in the list of carnivores identified at Elandsfontein (Table 89), although a provisional listing might have been warranted.

In order to illustrate the degree to which the lion postcranial bones from the south-western Cape differ in size, measurements of one typical example, the metacarpal V, are given in Table 86.

Table 85

Dimensions of large felid humeri from Elandsfontein, compared with those of modern *Panthera leo* and the Langebaanweg *Machairodus*.

	Langebaanweg ?*Machairodus*		Modern *Panthera leo*			Elandsfontein Large felids		
	L 6399	L 9869	Mean	Range	n	Mean	Range	n
Max. trans. diam. at dist. end	73,1	71,0	87,7	79,5–94,0	7	94,7	74,9–114,4	9
Max. trans. diam. of dist. articulation	49,6	45,8	58,3	50,9–63,5	7	62,4	51,5–77,3	11
Max. ant.-post. diam. at dist. end	*c.* 45,5	43,7	57,6	51,4–61,1	7	62,9	53,4–75,0	10

TABLE 86

The dimensions of *Panthera leo* metacarpal V from the south-western Cape Province, compared with a series of modern specimens.

	Elands-fontein 598	Melkbos M 6659	Swartklip		Sea Harvest S 237	Modern *Panthera leo*		
			ZW 1040	ZW 1789		Mean	Range	n
Overall length	98,5	*c.* 102,0	—	90,5	93,2	90,4	83,3–95,3	7
Max. trans. diam. prox. end	28,7	28,0	26,7	25,0	24,0	23,7	21,5–25,9	7
Max. a.-p. diam. prox. end	28,9	27,6	26,9	24,4	22,5	23,9	21,4–25,7	7
Max. trans. diam. dist. end	22,2	*c.* 21,0	—	22,0	19,5	19,3	18,2–20,5	7
Max. a.–p. diam. dist. end	22,8	—	—	21,0	20,6	20,4	18,1–21,7	7

Discussion

Although all the fossil lion specimens from the south-western Cape are here referred to *Panthera leo*, it is evident that none of the forms represented is identical to the modern varieties of this species.

The Swartklip and Sea Harvest lions apparently belong in a lineage distinct from that which led to the modern South African *P. leo* and the large Elandsfontein form might also be a member of this southern lineage. This lineage may have become extinct quite early in the Holocene since it is last recorded in the Sea Harvest assemblage and the lion present in the area in historic times was apparently *P. leo melanochaita*, a skull of which is recorded from Betty's Bay in the vicinity of Cape Hangklip (Meester 1971).

An indication of the taxonomic status which should be afforded to a population of lions characterized by the reduction and eventual loss of a cheektooth is evident from a well-documented example of a similar development in modern *P. leo*. Todd (1966: 520), in his study of the only surviving population of Asiatic lions, found that the 'fusion of the roots of Pm3 is . . . a common trait in Gir lions . . . [and the] absence of this tooth appears for the first time in a skull of *c*. 1910 and appears to have increased in incidence among skulls of animals which died between approximately 1953–1963'. The craniological differences between the modern African and Gir lions are probably no greater than those between the Swartklip and Sea Harvest lions and their more northerly contemporaries. In order that the present study be consistent in respect of the taxonomic recognition given an apparently major difference such as the presence or absence of a cheektooth with the consequent recognition of a distinct lineage, the south-western Cape lion should be referred to a new species. The example of the Gir lions shows that such a step is not necessarily warranted. Furthermore, since the local fossil carnivores have not been given new subspecies names either, the lion material is all referred simply to *P. leo*.

Lions of Makapanian age are known in South Africa from Sterkfontein (*P. shawi* Broom, 1948), Swartkrans and Kromdraai (Ewer 1956*a*). All are poorly represented. The Sterkfontein lion is very large, that from Swartkrans is comparable in size to modern *P. leo*, while that from Kromdraai is larger. These size differences, coupled with those evident in the south-western Cape fossils, indicate that the lion, like *Canis mesomelas* and other species, underwent size changes through much, if not all of the Quaternary.

The Cape lion

Mention was made earlier of a number of species of 'Cape' mammals such as the quagga, Cape warthog and blaauwbok, the distributions of which were largely confined to the more southerly parts of the African continent and which became extinct during the historic period. The Cape lion, *Panthera leo melanochaita*, is the only carnivore included in this category of mammals and, as such, it is relevant to the present study.

Hamilton Smith (1842) described the Cape lion as follows:

> 'The species is of the largest size, with a bulldog head; the facial line is much depressed between the eyes; large pointed ears edged with black; a great mane of the same colour extending beyond the shoulders; a fringe of black hair under the belly; a very stout tail, and the structure in general proportions lower than in other lions.'

Since the Sea Harvest lion is supposedly Holocene in age, it seemed possible that it could perhaps have been the 'Cape lion' which is represented at the site. The known postcranial bones suggest that it was large and it thus conforms to the first of the statements in the diagnosis. In addition, the loss of P^2 and very short post-canine diastema may well have fore-shortened the snout so as to give it 'a bulldog head'. However, the Sea Harvest lion is definitely different from other specimens which are accepted as 'Cape lions'.

Mazak (1964) listed eight specimens preserved in various collections, while Meester (1971) described an additional skull and reviewed the craniological characters of the subspecies on the basis of the three recorded skulls, the other two having been described by Lundholm (1952) and Hemmer (1966). There are three skulls in the South African Museum's collections which must now be added to the list of specimens.

The first, SAM 35121, is the skull of a female which was removed from a mounted specimen in 1896. Its skin was destroyed. This specimen and another, a male, were acquired from the South African Literary and Scientific Institution when the collections of this organization were taken over by the newly founded South African Museum in 1855. They were apparently part of the collection made by Sir Andrew Smith prior to 1837 and are likely to have come from the Cape Province. Smith did collect specimens from north of the Orange River, but apparently none of these remained in South Africa. The possibility that these two specimens were Cape lions has long been recognized (South African Museum 1955), but the surviving skull has not hitherto been described. There is no record of the fate of the companion specimen, although it may have been destroyed before 1896.

This skull is largely intact and well preserved, although the left P^2 and some incisors are lost. At least three of the missing incisors were shed during life and this, taken in conjunction with tooth wear and suture closure, indicates that the skull belonged to a fairly aged individual. The braincase has been damaged by a bullet and there is an entry wound about 15 mm in diameter in the basi-sphenoid and an exit wound twice that size in the left parietal. It conforms quite well in size with the two previously recorded female Cape lion skulls (Table 87).

The second specimen, SAM 7529, also belongs to a female, but it is poorly preserved and lacks the mandible. It was found on the farm Bergplaats near Rooihoogte in the Beaufort West Division of the Cape Province and was presented to the South African Museum in 1903. It lacks the right zygomatic

TABLE 87

Dimensions of the skulls of Cape lions (*Panthera leo melanochaita*) compared with those series of other southern African lions.

		Greatest length	Condylobasal length	CBL × 100/GL	Base canine width	BCW × 100/GL	Mastoid width	MW × 100/GL	Zygomatic width	ZW × 100/GL	Inter-orbital width	IW × 100/GL
Cape lion ♀ . . .	Murraysberg[1]	307,0	291,0	94,8	92,0	30,0	120,0	39,1	202,0	65,8	61,0	19,9
	Betty's Bay[1]	310,0	281,0	90,7	90,0	29,0	126,2	40,7	200,0	64,5	62,9	20,3
	SAM 35121	328,0	292,0	89,0	94,4	28,8	129,2	39,4	242,0	72,8	67,2	20,5
	SAM 7529	*c.* 308,0	*c.* 289,0	*c.* 93,8	*c.* 88,0	*c.* 28,6	*c.* 115,0	*c.* 37,3	*c.* 212,0	*c.* 68,8	63,4	*c.* 20,6
Modern *Panthera leo* ♀ .	Mean	310,3	277,0	89,3	84,8	27,3	118,9	38,3	210,2	67,6	61,3	19,7
	Range	299,0–327,0	265,0–300,0	86,5–92,3	78,4–92,2	26,0–28,2	112,4–128,3	37,2–39,5	188,0–242,0	62,5–74,5	54,4–70,0	18,0–21,2
	n	6	6	6	6	6	6	6	5	5	6	6
Cape lion ♂ . . .	NHMW 1422[2]	355,0	330,5	93,1	99,0	27,9	132,0	37,2	241,0	67,9	57,0	16,1
	SAM 33425	*c.* 358,0	327,0	91,3	98,8	27,6	*c.* 136,0	38,0	246,0	68,7	74,4	20,8
Modern *Panthera leo* ♂ .	Mean	383,6	338,3	88,2	100,9	26,3	142,0	36,9	251,0	64,5	74,4	19,4
	Range	369,0–403,0	327,0–348,0	86,1–90,3	97,0–102,9	25,5–27,3	136,0–147,0	35,5–38,2	235,0–275,0	64,4–68,9	68,0–79,0	18,3–20,7
	n	7	7	7	7	7	6	6	7	7	7	7

[1] Meester 1971.

[2] Hemmer 1964.

arch and all the teeth, while the right maxillary, frontal and occipital regions are damaged. It is also similar in size to the previously recorded female Cape lion skulls.

The third skull, SAM 33425, is that of a male and was found in a cave near Studtis in the Willowmore district of the southern Cape Folded Mountains in 1948. It is remarkably well preserved and still has dried-out soft tissue adhering to it. This is not unexpected since Studtis is in an arid area and dry conditions in sheltered situations can result in the good preservation of animal remains through desiccation. The skull is that of a fairly aged individual. Parts of the nuchal crest and left mastoid process, the left $\underline{C}$ and right $\overline{C}$ are damaged, while the left P^2 and some incisors were lost during life. It is similar in size to the previously described male Cape lion skull and is larger than those of the females.

The last lions in the Cape Province were killed in the eastern Cape between 1842 and 1858 (Harper 1945). Sir Andrew Smith did his collecting in South Africa between 1821 and 1836, so that SAM 35121 must have been shot during this period. Both the Rooihoogte and Studtis specimens probably date from the early part of the nineteenth century as well, although this is by no means certain. Studtis is in a remote area in the southern Cape mountains and it is possible that some lions survived there later than elsewhere in the Cape Province. It is in these mountains that the last surviving population of *Equus zebra zebra* is found, which is an indication that the area offers the potential for late survivals.

Meester (1971: 28) examined the craniological characters which have been used to distinguish the Cape lion from those occurring further north and found that 'in view of the lack of agreement in skull features evident among the only three specimens known . . . the discovery of further material might still further complicate the task of diagnosis, and perhaps even render it altogether impossible'. The new specimens do not yet confirm Meester's fears and they too can be distinguished from the northern varieties.

Meester showed that the muzzle width (base canine width as a percentage of greatest length) is one of the more useful distinguishing characteristics of Cape lion skulls and this is substantiated by the new specimens (Table 87). The observed differences between the Cape lions and others are, however, very small, especially in view of the number of specimens involved. The least difference observed is only 0,6 % for females and 0,3 % for males.

The male skull also differs slightly in occipital length (condylobasal length as a percentage of greatest length), with the least difference being 1 %. The Rooihoogte female is also outside the range observed in the comparative series, but SAM 35121 is not.

In the study of the lion crania from Swartklip, standard skull measurements could not be taken owing to the incompleteness of the fossils. One of the ratios calculated was the occipital width expressed as a percentage of braincase length, and it was found that both the South African Museum's female Cape lion skulls differed from the modern females in this respect (Table 82). Four

Fig. 73. Ventral, dorsal and lateral views of the female *Panthera leo melanochaita* skull SAM 35121 (Scale approximately 300 mm).

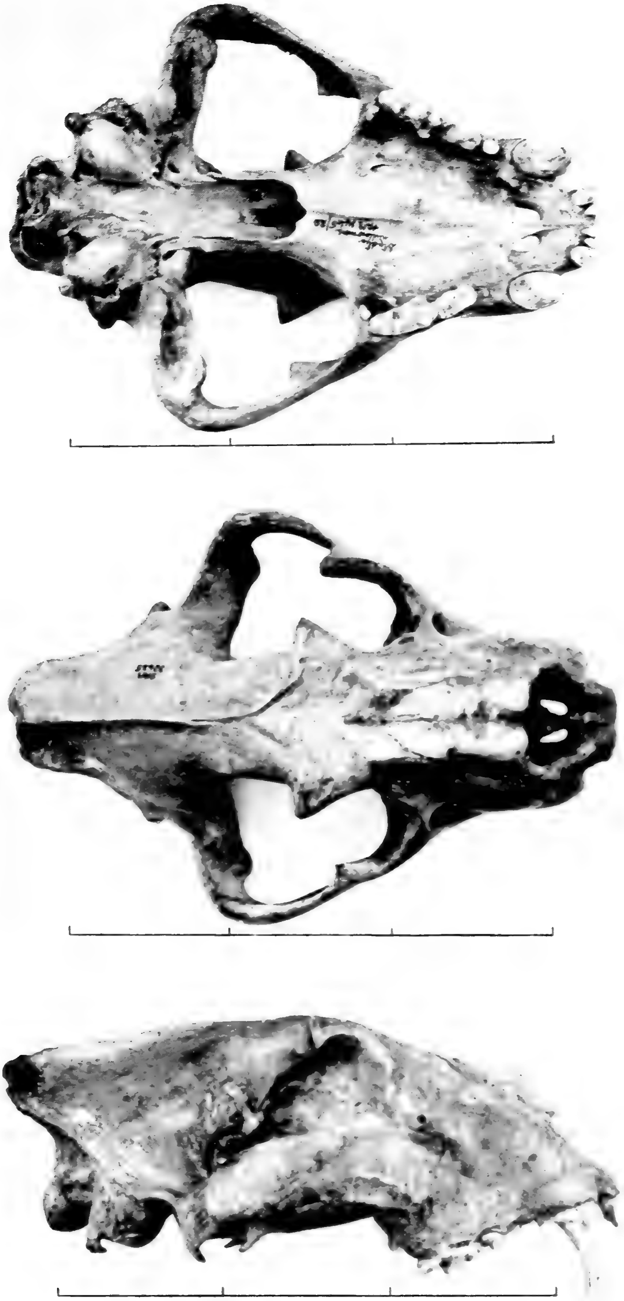

Fig. 74. Ventral, dorsal and lateral views of the male *Panthera leo melanochaita* skull SAM 33425 (Scale approximately 300 mm).

of the male skulls compared closely to both male and female Cape lions, but curiously they were the skulls of zoo specimens, while the skulls of the wild males differed from the Cape lions. This indicates that in the Cape lion the braincase is shorter relative to occiput width. This is probably just another way of illustrating the sometimes distinctive occipital length of the subspecies.

Hemmer (1966) emphasized the value of M_1 breadth in identifying Cape lions and these teeth in the new specimens are indeed broader than those of the comparative specimens (Table 84), the difference being especially marked in the case of the females.

Although Meester may ultimately be proved right and the Cape lion may be found to be not readily distinguishable from other varieties in respect of its skull characters, on the basis of the specimens presently known, the following characters may be said to be indicative of *P. leo melanochaita*:

(1) The muzzle is relatively broad.
(2) The occiput is relatively short and broad.
(3) The lower carnassials are relatively broad.

The Betty's Bay specimen described by Meester (1971) suggests that it was the Cape lion which inhabited the south-western Cape during the latter part of the Holocene, although since this specimen is from near the boundary, between the south-western and southern Cape regions, it is possible that the Cape lion was never present elsewhere in the former region. Neither the bontebok nor the blaauwbok are recorded from the south-western Cape late in the Holocene, so it is possible that the lion encountered locally by early European settlers was a descendant of the Sea Harvest variety and not the Cape lion at all.

The situation in respect of the characteristics of the local *Panthera leo*, *Felis serval*, *Hyaena brunnea* and *Canis mesomelas* populations will only be resolved as more specimens of these species are recovered. There are, however, some suggestions that locally endemic varieties were represented in the south-western Cape.

Suborder FISSIPEDIA

Unclassified specimens

As with the material of Pliocene age, there were a number of specimens in the Quaternary fossil assemblages which were not identified, although they clearly belong to fissiped carnivores. The unclassified specimens are mainly postcranial bones and fragmentary teeth and none suggested the presence of a species other than those already listed.

GENERAL DISCUSSION ON THE CARNIVORA

A striking feature of the fossil carnivore assemblages from the south-western Cape is the variety of species represented (Tables 88, 89). In no instance, however, is the number of species in any one assemblage in excess of the number which might be expected of a fauna in an African context. There are definite records of at least 25 carnivore species from the historic period of the south-western Cape and the most recorded in a fossil assemblage are the 20 from the Varswater Formation at Langebaanweg.

TABLE 88

The late Pliocene Carnivora of the Varswater Formation, Langebaanweg, Cape Province.

	Marine Faunal Unit 2 (Bed 1)	Estuarine Faunal Unit 1 (Bed 2)	Estuarine Faunal Unit 2 (Bed 3a)	Faunal Unit unknown
SUBORDER PINNIPEDIA				
Prionodelphis capensis	×	×	×	
SUBORDER FISSIPEDIA				
Canidae *incertae sedis*			×	
Agriotherium africanum			×	
Mellivora aff. *punjabiensis*				×
Enhydriodon africanus				×
Viverra leakeyi		×	×	
Genetta sp.		×		
Herpestes Species A		×	×	
Herpestes Species B		×	×	
Percrocuta australis		×		
Hyaena abronia		×	?	
Hyaena Species B		×		
Hyaenictis preforfex			×	
Hyaenidae Species E				×
Machairodus sp.		×		
cf. *Homotherium* sp.			×	
Felis aff. *issiodorensis*			×	
Felis obscura			×	
Dinofelis diastemata		×	×	
Carnivora *incertae sedis*		×		

All extant families of African Carnivora are represented locally, while the Ursidae are an addition to the list. Most of the extant African genera are recorded, the most notable exceptions being *Acinonyx* and a number of mustelids and viverrids. Although the absence of such forms may be due to inadequacies in the fossil and recent records, it is much more likely that they were never present locally.

The pattern of similarities and differences between the modern carnivores and the various fossil assemblages follows an entirely predictable pattern, with the resemblance at different taxonomic levels decreasing with the increasing

TABLE 89

The Quaternary Carnivora of the south-western Cape Province.

	Baard's Quarry, Langebaanweg*	Elandsfontein	Melkbos	Swartklip	Sea Harvest, Saldanha	Historic Period
SUBORDER PINNIPEDIA						
†*Hydrurga leptonyx*						×
Lobodon carcinophagus					×	×
Mirounga leonina						×
Arctocephalus pusillus			?		×	×
†*Arctocephalus gazella*						?
†*Arctocephalus tropicalis*						?
SUBORDER FISSIPEDIA						
?*Canis* sp.	×					
Canis mesomelas		×	×	×	×	×
Canis terblanchei		×				
Vulpes chama		×		×	×	×
Lycaon pictus		×		×		×
†*Otocyon megalotis*						×
Ictonyx striatus		×				×
Mellivora cf. *capensis*	×					
Mellivora capensis		×		×	×	×
Aonyx capensis				×		×
Viverra civetta		×				
†*Genetta genetta*						×
Genetta tigrina					×	×
Herpestes ichneumon		×		×	×	×
Herpestes pulverulentus					×	×
Atilax paludinosus						×
†*Cynictis penicillata*						×
Suricata major		×				
Hyaena cf. *bellax*	×					
Hyaena brunnea		×	×	×	×	×
Crocuta crocuta		×			×	×
†*Proteles cristatus*						×
Megantereon sp.		×				
Felis libyca				×		×
Felis serval				×	?	×
Felis caracal		×				×
Panthera pardus					×	×
Panthera leo		×	×	×	×	×

* Pleistocene species only. † Not known locally in a fossil state.

age of the assemblages (Table 90). About 50% of the genera recorded from the late Pliocene are now extinct, but only one of the 23 recorded Quaternary genera is extinct. The relative ages of the principal local fossil mammal occurrences were already established prior to the commencement of the present study and the carnivores have served to substantiate the earlier conclusions, while in the case of the Elandsfontein fauna they provided the first definite faunal evidence indicating that the assemblage is not homogeneous.

Table 90

Faunal resemblances* between the fossil and modern fissiped carnivore assemblages from the south-western Cape Province.

	Langebaanweg	Elandsfontein (Cornelian)	Swartklip	Moderns
Number of species . .	19	12	10	20
Number of genera . .	14	11	9	15
Number of families . .	6	5	5	5

	Langebaanweg/ Moderns	Elandsfontein/ Moderns	Swartklip/ Moderns
Species in common	0	8	10
Faunal resemblance (%) . . .	0	66	100
Genera in common	5	9	9
Faunal resemblance (%) . . .	36	82	100
Families in common	5	5	5
Faunal resemblance (%) . . .	100	100	100

Minimum number of genera and species are counted.
* Simpson 1967.

Before the significance of any element in a fossil mammal fauna can be assessed, it is necessary that the identity and phyletic relationships of the individual species be determined. In the case of most of the south-western Cape carnivores this basic requirement was established and their relationships are clear. In summing up the present state of knowledge of the local carnivores, it is convenient to consider the pinnipeds and each of the fissiped families individually.

PINNIPEDIA

The south-western Cape fossil record of the Pinnipedia is very incomplete and only the Langebaanian *Prionodelphis capensis* and the Holocene *Arctocephalus pusillus* are comparatively well represented. The local late Cenozoic history of this group has apparently centred on the replacement of the Phocidae by the Otariidae (Hendey 1972*a*). The former are now represented only by occasional stray individuals of Antarctic and sub-Antarctic species, but the Otariidae are represented by large permanent colonies of *Arctocephalus pusillus*, while individuals of sub-Antarctic species probably also stray onto the local coastline.

A. pusillus is known from a number of Holocene fossil occurrences, mainly Late Stone Age coastal middens, while there is at least one record, that from the Saldanha Lime Quarry, which may date back to the Pleistocene. There is a suggestion that species such as *Mirounga leonina* and *Lobodon carcinophagus*, which are today largely confined to higher latitudes, were more commonly represented earlier in the Holocene, and perhaps also the Pleistocene. The local presence of these species in greater numbers than at present may be related to the colder periods of the past.

The only phocid, and in fact the only pinniped other than *Arctocephalus* which still has permanent colonies on the coast of Africa is the Mediterranean monk seal, *Monachus monachus*, whose range also extends on to the west coast of North Africa. This is a declining species and may be a relict population descended from the generalized monachine which was probably ancestral to all other members of the subfamily (Hendey 1972*a*). The Langebaanweg *Prionodelphis* is in certain respects intermediate in character between *Monachus* and the other extant monachines *Leptonychotes*, *Ommatophoca*, *Hydrurga*, *Lobodon* and *Mirounga* (Hendey & Repenning 1972). Perhaps significantly the South African and Argentinian records of *Prionodelphis* are intermediate in age between the ancestral monachine of the European Miocene and the extant species, and they are intermediately situated between the surviving populations of *Monachus* in low latitudes and the main area of modern monachine distribution in southern high latitudes.

The successful radiation of the otariids at the expense of the phocids in southern mid-latitudes is one of the more remarkable aspects of pinniped evolution, since it was achieved in a relatively short space of time and it involved the decline of an extremely successful family, being the one which completely dominates the pinniped populations of the Northern Hemisphere and the high latitudes of the Southern Hemisphere.

CANIDAE

Although the Canidae are a morphologically conservative group of carnivores, they have been very successful and the only continent on which they have not become established in a natural state is Antarctica. In Africa today the most commonly occurring canids are the jackals (*Canis* spp.), while foxes (*Vulpes* spp., *Fennecus* sp., *Otocyon* sp.) and a hunting dog (*Lycaon* sp.) are, or were, also widespread. *Fennecus* and several *Canis* and *Vulpes* species are north or north-east African forms belonging in the Palaearctic region or only marginally in the Ethiopian Region.

Canis mesomelas is an essentially southern African jackal whose range extends also to East Africa, while *C. adustus* is a tropical species which only occurs in the more northerly parts of southern Africa. The Asiatic jackal, *C. aureus*, is found in Africa only in the north and north-east. These three species may have had their origins in South Africa, East Africa and Asia respectively.

C. mesomelas is an extremely successful species and its earliest records date back to the Makapanian. It manages to survive today even in areas where persistent efforts are made to bring about its eradication. In this respect it is similar to the North American coyote (*C. latrans*), a species which has actually extended its range in recent years (Cahalane 1961).

The pattern of distribution of the true foxes (*Vulpes* spp.) is essentially similar to that of the jackals. *V. vulpes* is a Palaearctic species with a limited distribution in North Africa, *V. pallida* and *V. rueppelli* are distributed in the more arid parts of tropical North Africa, while *V. chama* is a southern African species. The foxes have more restricted ranges than the jackals and there is no tropical equivalent of *C. adustus*. The absence of *Vulpes* from much of tropical Africa may be due to its ecological niche being occupied by *C. adustus*. The recorded distributions of *Vulpes* and *C. adustus* suggests that a mutually exclusive inter-relationship exists between them (see Dorst & Dandelot 1970).

The highly specialized, insectivorous *Otocyon megalotis* has a discontinuous distribution in sub-Saharan Africa, with one range centred in East Africa and the other in the arid south-western parts of the continent. It is one of the species whose distribution suggests the previous existence of a south-west to north-east arid corridor in Africa (*vide supra*).

Lycaon pictus was once widely distributed in Africa, but in common with other large predators its range has been considerably reduced as a result of human activities.

Three of the five canid genera represented in Africa are endemic to the continent (*Fennecus*, *Otocyon*, *Lycaon*), although *Lycaon* is also recorded in the Pleistocene of Europe (Kurtén 1968). Eleven canid species are still extant, of which only two (*Canis aureus*, *Vulpes vulpes*) are also recorded in Eurasia.

In general, the fossil record of the Canidae is good and this is essentially true of the south-western Cape late Cenozoic, although one of the curious features of the Langebaanweg fauna is the fact that this family is so poorly represented. The poor representation in a Pliocene fauna of a highly successful mammalian family which had its origins in the Eocene is obviously of some significance and a possible explanation is that the Langebaanweg *Viverra leakeyi* filled the ecological niche which was later to be occupied by the jackals in this and other areas. *V. leakeyi* was similar in size to the modern jackals and its dentition resembles that of *Canis*. In contrast to the Langebaanweg record, medium-sized canids are particularly well represented in the Quaternary of the south-western Cape, while *Viverra* is either extremely rare, as at Elandsfontein, or not represented at all.

Canis and *Vulpes* apparently had their origins early in the Pliocene of Eurasia and North America respectively, while *Viverra* was already established in Europe in the Miocene (Romer 1966). Consequently, it would not be surprising to find that *Viverra* was already established in Africa before either of the canid genera and that the latter only reached the most southerly parts of the continent late in the Pliocene.

The modern African civet, *Viverra civetta*, is apparently not an active competitor with canids of comparable size. It is an omnivorous species with a dentition modified accordingly, so that in this respect it is very different from

Canis and *Vulpes*, as well as from the Pliocene *V. leakeyi*. The survival of *Viverra* in Africa is therefore ascribed to the fact that it underwent a change in habits during the Pleistocene, so removing itself from competition with the canids.

It is worth noting that in southern Asia there is a civet with a dentition similar to that of *V. leakeyi*, namely, *V. zibetha*, which overlaps in its range with the jackal, *C. aureus*. In this instance the suggested competition between the civets and jackals must have been resolved in some other way, and it probably illustrates the point that challenges and responses in mammalian evolution are far more complex than would appear from the preceding speculations. Nevertheless, the hypothesis presented here to account for the nature of the local record of *Canis*, *Vulpes* and *Viverra* could offer at least the basis of an explanation.

The generic identity of the Langebaanweg canid is not known, but it is perhaps more likely to be *Canis* than *Vulpes*, partly because of its size and partly because *Vulpes* is much less commonly represented in the local Quaternary record. Both genera are recorded during the Makapanian, so both may also have been present in South Africa during the Langebaanian.

Lycaon is a genus which is apparently confined to the Quaternary. The absence of even an ancestral form at Langebaanweg may be the result of a faulty record, since these animals are rare as fossils. On the other hand, the suggestion was made earlier that the Langebaanweg Hyaenidae included cursorial and more actively predaceous forms (*Hyaena* Species B, *Hyaenictis preforfex*) and these species may have occupied the niche later taken over by *Lycaon*.

The Pleistocene canids of the south-western Cape are all representatives of genera recorded in the area in recent times, namely, *Canis*, *Vulpes* and *Lycaon*. The Elandsfontein *C. terblanchei* is the only extinct species recorded, but it may in fact simply be a primitive form of *C. adustus*. There is nothing, such as the Makapanian *C. brevirostris*, which is certainly without an extant counterpart. With the exception of the Elandsfontein *Vulpes chama*, none of the local fossil canids is obviously and strikingly different from their extant counterparts, although all the Pleistocene varieties do differ in some respects from those which are still extant.

The three most commonly represented local species, *V. chama*, *C. mesomelas* and *L. pictus*, form a complementary group in respect of size and habits. *V. chama* is the smallest and the modern form feeds on small mammals, birds and insects. *C. mesomelas* is a medium-sized canid and is capable of preying on small antelope and, in recent times, also sheep. Apart from its predatory habits, it will also scavenge the kills of other carnivores and its less discriminating diet may have contributed to its success as a species. The large *Lycaon* hunts in packs and preys on animals as large as the wildebeest and zebra. Although each of these species underwent size changes during the Quaternary, the relative sizes of the local fossil varieties remained the same.

The south-western Cape fossil canids shed little light on the evolution of the genera represented. Significant developments within this family took place largely during the Tertiary and the local record only reveals the later stages in the evolution of extant species.

URSIDAE

Prior to the discovery of *Agriotherium* at Langebaanweg, the Ursidae had not been recorded in sub-Saharan Africa, the only other members of this family on the continent being representatives of the *Ursus arctos* group, which are recorded from Pleistocene and Holocene contexts in North Africa (see Erdbrink 1953). The *U. arctos* group are, in general, north-temperate forms and they entered North Africa during the Pleistocene when conditions were more temperate than they are today, and when there existed a land link across what are today the Straits of Gibraltar in addition to that in the Suez region. Ursids were not the only Eurasian species to become established in North Africa and this region is part of the Palaearctic Region, with limited faunal affinities with sub-Saharan Africa. In spite of the fact that the Ursinae have proved a remarkably adaptable group, they were apparently unable to penetrate the arid barrier of the Sahara Desert.

The presence of *Agriotherium* in sub-Saharan Africa is not completely unexpected, since during the late Tertiary when the Agriotheriinae were radiating, there was far more faunal interchange between Africa and Eurasia than was the case subsequently. *Agriotherium* apparently had its origins in Eurasia in the mid Pliocene and it must have entered Africa at about this time. Since it is recorded from the late Pliocene of the extreme south of the continent, it must initially have been a widespread and successful immigrant.

It was suggested elsewhere that the principal cause of the extinction or limitation of the Agriotheriinae was their unsuccessful competition with the radiating Ursinae (Hendey 1972*b*). However, since *Agriotherium* was apparently a carnivorous rather than omnivorous ursid, its extinction cannot be accounted for in this way. *A. africanum* was a very large and apparently carnivorous species and if it was indeed actively predaceous, its prey is likely to have included the larger contemporary herbivores such as the giraffids, so it cannot have been the lack of suitable prey which led to the extinction of *Agriotherium* on this continent. Bourlière (1963: 51) has stated that, 'There is no doubt that *the African savannas represent an ideal type of habitat for any large-sized carnivore or omnivore with mainly carnivorous habits*'. This conclusion was based on studies of present mammal populations, but there is no reason to suppose that it would not have applied in the late Tertiary and Pleistocene as well.

While the extinction of a species may be caused by factors other than competition (e.g. climatic changes), it may simply be that the large and probably clumsy *Agriotherium* was unable to compete successfully with other contemporary carnivores such as 'lions' (*Panthera* spp.), which must have made their appearance in South Africa at about the time that *Agriotherium* became extinct.

Alternatively, *Agriotherium* may have been a scavenger which competed unsuccessfully with the radiating hyaenids of the late Pliocene, there having been more larger hyaenid species during this period in time than there were earlier in the Pliocene.

It is possible that in spite of the nature of its dentition, *Agriotherium* was omnivorous or herbivorous like most other ursids. If this was the case, then its extinction in other parts of the world could be ascribed to the rise of the Ursinae, but this would not apply in the case of sub-Saharan Africa. However, its extinction could have been caused by unsuccessful competition with an entirely unrelated mammalian group occupying the same ecological niche. In this instance the most reasonable possibility would have been the terrestrial Cercopithecoidea and/or Hominoidea, which were undergoing a radiation in Africa during the late Tertiary.

Since *Agriotherium* was successfully established in Africa during the Pliocene, it might be expected that the same would apply to the agriotheriine *Indarctos*, the genus from which *Agriotherium* was apparently derived and one which was also widespread during the Pliocene. Judging from its dentition, *Indarctos* was more like the Ursinae in its habits and the fact that it has not been recorded in Africa is not necessarily significant in view of the comparatively poor Pliocene record on this continent. If it was indeed present in Africa, then its extinction locally could also be ascribed to unsuccessful competition with the terrestrial primates.

MUSTELIDAE

The Mustelidae are an essentially Holarctic and Neotropical family and are not well represented in the Ethiopian Region. The extant genera recorded in southern Africa are *Ictonyx*, *Poecilogale*, *Mellivora*, *Aonyx* and *Lutra* and each is represented by only a single species. This family is also poorly represented in the African fossil record and the mustelids have apparently never been a significant element in the fauna of sub-Saharan Africa. The south-western Cape fossil record is not exceptional in respect of this family, but three of the extant genera, *Ictonyx*, *Mellivora* and *Aonyx*, are represented locally. In addition, there is at least one extinct genus recorded at Langebaanweg, namely, *Enhydriodon*, while there might also be a second, as yet unnamed giant otter represented at the site. Only *Mellivora* is comparatively common as a fossil and almost all the material is referred to the extant species, *M. capensis*. An extinct species which might be ancestral to *M. capensis* is known from Langebaanweg.

The 'badgers' (Mellivorinae and Melinae) are an unusual group of animals which have no parallel in other carnivore families, and the two subfamilies are themselves a remarkable example of parallel evolution. Judging from the fossil record, the Mellivorinae have been firmly established in Africa and southern Asia since the late Tertiary. They are not as diverse a group as the Holarctic Melinae and their evolution was apparently largely a matter of a change along one principal lineage from purely carnivorous forms to the more omnivorous *M. capensis*. The changes which were undergone are relatively minor and *Mellivora* has apparently remained virtually unchanged for much of the Quaternary.

The long-standing and widespread success of the mustelids as aquatic carnivores is one of the more notable aspects of this family. The Lutrinae are a more diverse subfamily than the Mellivorinae, but they are, nevertheless, by no means as diverse as some other carnivore groups. The Langebaanweg *Enhydriodon* has *Aonyx* as its local counterpart in the Quaternary, although the former was a much larger form. The other species from Langebaanweg which was tentatively identified as an otter is also a giant form and it has no counterpart recorded from the Quaternary.

There are two African viverrids, *Osbornictis piscivora* and *Atilax paludinosus*, which are adapted to life in or near water, but neither differs from other viverrids to the extent that the otters are differentiated from other mustelids. *Osbornictis* has only a very limited distribution in Central Africa, and while *Atilax* is more widespread it is not quite so tied to aquatic environments. The indications are that the mustelids adapted to aquatic habitats long before these two viverrids and the latter have so far been unable to establish themselves in this ecological niche as successfully as the otters.

While the success in Africa of the Mellivorinae and Lutrinae is readily explained by the nature of their specialized habits, this is not the case with the smaller and more generalized mustelids such as *Ictonyx*, which co-exists with the highly successful viverrids of comparable size and with comparable habits. With the Elandsfontein record of *Ictonyx*, it is now known that this genus has been a part of the African fauna at least since the Cornelian. Its local history is, however, probably far longer and, just as *Mellivora* has paralleled the evolution of the Melinae since the late Tertiary, so *Ictonyx* has paralleled the New World *Mephitinae*.

The co-existence of *Ictonyx striatus* and *Herpestes pulverulentus* in the south-western Cape may simply be explained by the fact that the former is essentially nocturnal, while the latter is diurnal. The same explanation may apply in other parts of Africa where *Ictonyx* is found in association with other herpestine species.

VIVERRIDAE

The Viverridae are the most diverse of the African carnivores and they are the dominant small carnivores of the Ethiopian and Oriental Regions, with about 80 extant species having been recorded (Morris 1965). Six species have been recorded in the south-western Cape in recent times, namely, *Genetta genetta*, *G. tigrina*, *Herpestes ichneumon*, *H. pulverulentus*, *Atilax paludinosus* and *Cynictis penicillata*. Only *H. pulverulentus* still survives in appreciable numbers. In addition to these smaller species, some of which are known locally as fossils, large civets have been recorded from Langebaanweg and Elandsfontein, although they are not known from a post-Cornelian context.

A feature of the South African Viverridae is that while the smaller Herpestinae apparently underwent a radiation during the Pleistocene, the larger

Viverrinae went into a decline. The latter development has already been accounted for by the suggestion that the civets gave way when they came into competition with canids of comparable size and that *Viverra civetta* survived by becoming progressively more omnivorous. Since this species now manages to survive elsewhere in Africa in the same areas as foxes and jackals, the apparent decline in its range in South Africa during the Pleistocene is still not accounted for, although mention was made earlier of possible environmental controls. Carnivores are not usually as influenced by environmental changes as herbivores, but since berries and fruits form part of the diet of *V. civetta* (Dorst & Dandelot 1970), it is possible that vegetation changes in parts of South Africa reduced the viability of the civet in these regions. In addition, there is little, if any, overlapping in the ranges of *V. civetta* and *Vulpes chama* and since these species probably do compete for certain foods such as insects and small vertebrates, they may well have a mutually exclusive relationship.

The apparently rather sudden radiation of the Herpestinae is also not readily accounted for, although it may be that the habitats presently occupied by the various species were simply unexploited in the late Tertiary. For example, the Makapanian form of *Atilax*, described by Ewer (1956*c*) as *Herpestes mesotes*, can only at that time have begun to exploit an environment (i.e. near water) which had obviously existed for far longer than the history of the family.

The local fossil record of the smaller Viverridae is not good, but apparently only *Genetta* and *Herpestes* were present in the south-western Cape during the Langebaanian. The first record of *Suricata* anywhere is that from the Cornelian element of the Elandsfontein fauna, so this is another genus which was most probably differentiated during the Pleistocene. The earliest record of *Cynictis* is that from Makapansgat (Ewer 1956*d*), so that this genus, and perhaps also *Paracynictis*, may well have had their beginnings in the Makapanian. The earliest record of *Mungos* is from the early Pleistocene of East Africa (Petter 1969), while *Crossarchus* is known from the Transvaal Makapanian (Broom 1937*b*). The other southern African herpestine genera (*Bdeogale*, *Helogale*, *Rhynchogale*, *Ichneumia*) have no local fossil record, but they too are likely to have originated during the Pleistocene (Petter 1969).

The north-temperate Mustelidae, which are ecological vicars of the Viverridae, apparently underwent a similar and comparatively recent radiation. For example, Anderson (1970) concludes that five of the seven extant species of *Martes* were derived from the 'early middle Pleistocene' *M. vetus*. The spread of *Martes* during the Pleistocene, and therefore also its taxonomic differentiation, was largely determined by the climatic changes of this epoch. Although such changes were not as extreme in Africa, they did influence the environment and may have made some contribution towards the diversification of the smaller viverrids as well.

HYAENIDAE

The diversification of the Hyaenidae during the late Tertiary and early Pleistocene and their subsequent decline is one of the more striking aspects of the Old World fossil carnivore record. As many as six hyaenid species are now definitely or tentatively recorded from the South African Langebaanian, while seven species are known from the Makapanian (Ewer 1967). This is in marked contrast to the two species which are still extant in South Africa today.

Ewer (1967: 120) has discussed this phenomenon and concluded that the rise and decline of the hyaenids was determined by its relationships with the machairodonts, since it was with these 'primary' predators that the 'niche for bone-crushing specialists (stood) invitingly wide open' and 'hyaenas and sabre-tooths . . . form an ideal . . . combination' with 'the existence of the latter . . . a precondition for the evolution of the former'.

At Langebaanweg the hyaenids were associated with two large machairodonts and the 'false sabre-tooth', *Dinofelis*. By the Makapanian the smaller machairodont, *Megantereon*, was also present, but so too were large felines (*Panthera* spp.) so that the Makapanian is the transitional age in respect of local hyaenid evolution. By the Cornelian the sabre-toothed cats are recorded for the last time and, judging from the Elandsfontein record, large felines (*Panthera leo*) became the dominant predators. The final disappearance of the machairodonts during the Cornelian 'corresponds with the shrinking of the hyaenid fauna to those few species which have succeeded in surviving today, in association with modern Felinae' (Ewer 1967: 121).

The South African Hyaenidae are, therefore, a group which began their decline during the Makapanian and by the Cornelian had stabilized at the two species which are still extant, namely, *Hyaena brunnea* and *Crocuta crocuta*.

The pattern of local hyaenid evolution is now so well documented that they have become important from the point of view of the relative dating of late Cenozoic faunas and deposits. Kurtén (1957*a*) indicated the possible usefulness of *Crocuta* for the purposes of dating South African and other fossil faunas and since then this, and other hyaenid genera have been similarly employed (see Ewer 1967). Relative dating using the hyaenids has not been without its problems and there are still crucial issues, such as the absolute dating of at least some hyaenid occurrences, which must be settled. It is in this respect that the East African hyaenid record is so important and if the situation is already promising, then it will become even more so as the East African material is studied.

The distribution of modern hyaenids bears some similarity to that of other carnivore families. One species, *C. crocuta*, is, or was widely distributed throughout sub-Saharan Africa and in this respect is similar to other large carnivores such as *Panthera leo* and *Lycaon pictus*. By contrast, *H. brunnea* is a southern African species, its distribution early in the historic period probably having been much like that of *Vulpes chama*. *H. hyaena* is an East and North African species whose range extends into Asia and is thus similar to that of *Canis aureus*.

FELIDAE

The modern fauna of the south-western Cape included five felid species ranging in size from the wildcat (*Felis libyca*) to the lion (*Panthera leo*). The felids are thus reminiscent of the canids, which were also represented by a series of species of differing sizes. Two felids which are recorded elsewhere in South Africa, the black-footed cat (*F. nigripes*) and cheetah (*Acinonyx jubatus*), were apparently never present in the south-western Cape. All the locally occurring modern species are recorded from Cornelian and/or Florisian contexts in the south-western Cape and it is likely that the whole series were represented from the Cornelian to early in the historic period.

Although there is no local record of Makapanian felids, inferences may be drawn from the local Langebaanian and Transvaal Makapanian records. During the Langebaanian the large felids were machairodonts and a false sabre-toothed cat, while smaller lynx-like felines were also present (*Felis* spp.). The representation of machairodonts continued throughout the Makapanian, but large felines (*Panthera* spp.) also appeared. The lynx-sized felines no doubt occurred during the Makapanian as well. It is by no means certain from the fossil record when the wildcat first appeared in the south-western Cape, but although it is first recorded from the Florisian, it is likely to have been present for far longer. The final change from the archaic to modern felid faunas was completed during the Cornelian and has already been referred to in connection with the Hyaenidae.

The felids are perhaps the most highly specialized and actively predaceous of the fissiped carnivores and the modern forms may be conveniently categorized according to their size and locomotory adaptations. The first category includes the smallest forms, of which *F. libyca* is the only local representative. The second includes *F. caracal* and *F. serval* and they may perhaps be distinguished by the former being an ambulatory and the latter a more cursorial form. This distinction is, however, not clear and both may be equally adaptable in as far as locomotion is concerned. A more definite distinction along the same lines is made in the third category, which includes *P. pardus* and *A. jubatus*. The former is an ambulatory form which is also well adapted to arboreal locomotion, while *A. jubatus* is a highly specialized cursorial form. The final category includes the largest of the extant felids and *P. leo* is the African representative. The felids are, therefore, so represented that the constituent species can prey on animals from very small to very large. In those categories in which there are two similar sized species, these may have distinct locomotory adaptations which enable them, if necessary, to favour different sorts of prey so that they need not be in active competition with one another.

Apart from their obvious dental specializations, the machairodonts also included locomotory adaptations not found in the felines mentioned above. The last definitely recorded South African machairodont, *Megantereon*, which had relatively short and heavy limbs, was evidently an ambulatory form quite distinct from the partly arboreal *P. pardus* and cursorial *A. jubatus* in respect of locomotion. While this should, theoretically, have enabled it to refrain from active competition with contemporary felids of similar size, it is obviously a disadvantage for a highly predaceous carnivore to be a relatively slow and cumbersome animal and this may have contributed to its ultimate extinction.

In an African context, the Suidae are perhaps the herbivores most likely to have been the preferred prey of a carnivore such as *Megantereon*. It may therefore be significant that the local decline of the machairodonts went together with the decline of the Suidae, which had undergone a relatively brief, but nevertheless spectacular radiation in Africa during the Makapanian and Cornelian.

These, and earlier speculations on the inter-relationships and habits of South African late Cenozoic carnivores give an insight into the enormously complex arrangement of the eco-systems of which these animals were a part. While any single statement on this topic would obviously oversimplify the realities of the situation, there are grounds for believing that the decline of the African Suidae in the face of competition with the Bovidae, contributed to the decline of the Machairodontinae, which in turn led to a decline in the Hyaenidae. At the same time the rise in the Bovidae favoured the success of their most common predators, the Felinae. Any one development in mammalian evolution is likely to have wide repercussions and there is ample scope for more detailed studies on the ecology of the local late Cenozoic Carnivora.

Although some aspects of the taxonomy, phylogeny and zoogeography of the south-western Cape Carnivora have been summarized, there are still two topics relating to this order which may be enlarged upon.

AGE AND RELATIVE DATING

Repeated references have been made to the age of the carnivore species dealt with in this report, and to the application in the relative dating of faunas and deposits. The use of the fossil carnivores in dating is directly dependent upon the extent to which their phyletic relationships are understood. It follows that some species are more useful than others in this respect, but no single species can yet be used as an entirely reliable age indicator on its own and the need to view a fauna as whole is an obvious necessity (see Ewer 1957*b*).

The accompanying illustrations (Fig. 75) summarize the recorded time spans of some of the species which have been described or referred to in this report. The carnivores are actually more useful for relative dating purposes than these text figures would suggest, because even though a single species may span most, or all of the Pleistocene ages, temporal variants are recognized. For example, comparisons between undated *Canis mesomelas* remains with those of the recorded Makapanian, Cornelian, Florisian and Holocene varieties could result in its identification with one of the forms and its age may be determined in this way. Clearly, the more material that is described, the more useful the age categorizations will become.

SIZE CHANGES

In most of the descriptions of the Quaternary fossil species mention was made of the size differences between them and their modern counterparts. Similar observations have previously been made in reference to a variety of

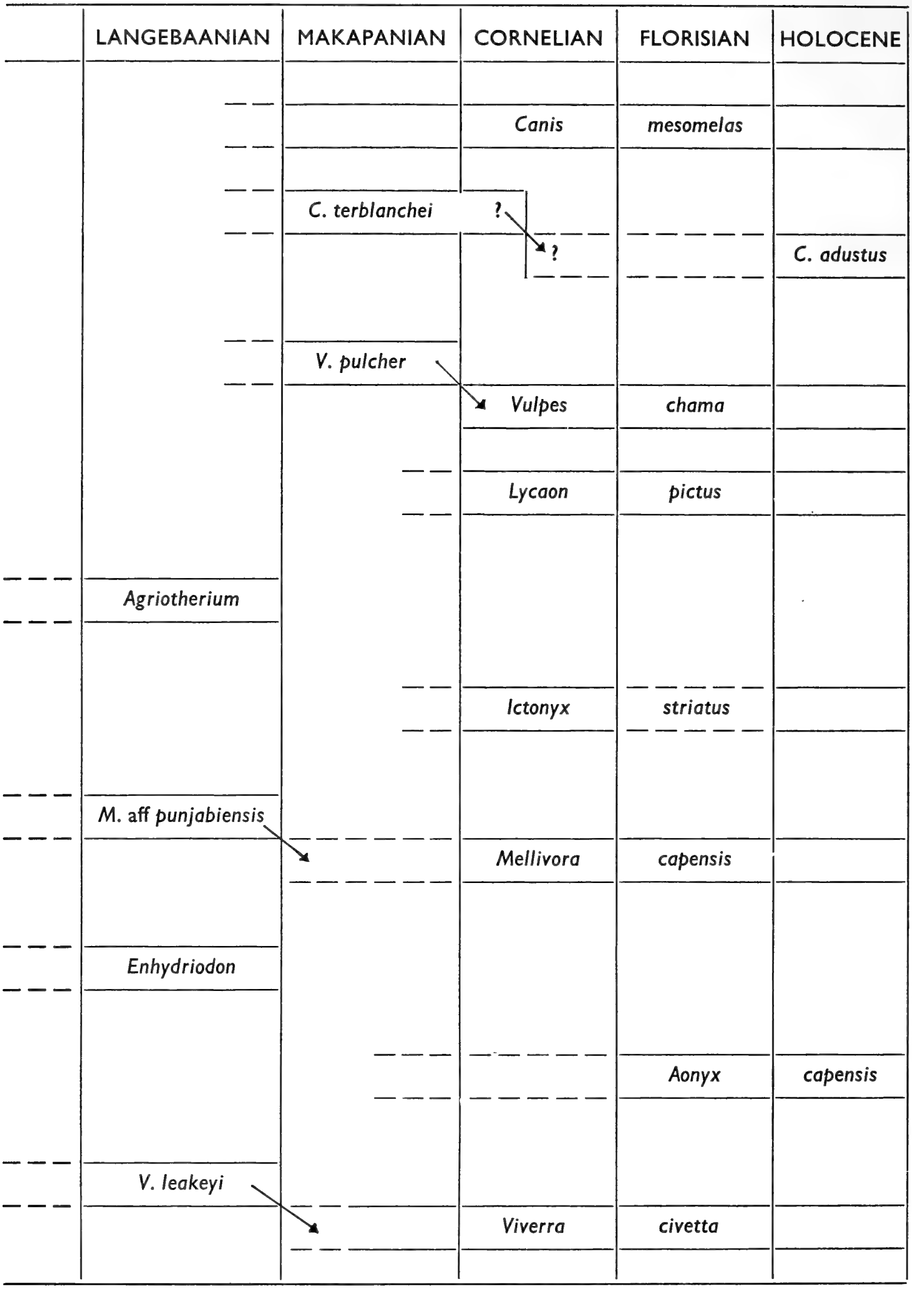

Fig. 75a. The recorded time spans of some South African Canidae, Ursidae, Mustelidae and Viverridae.

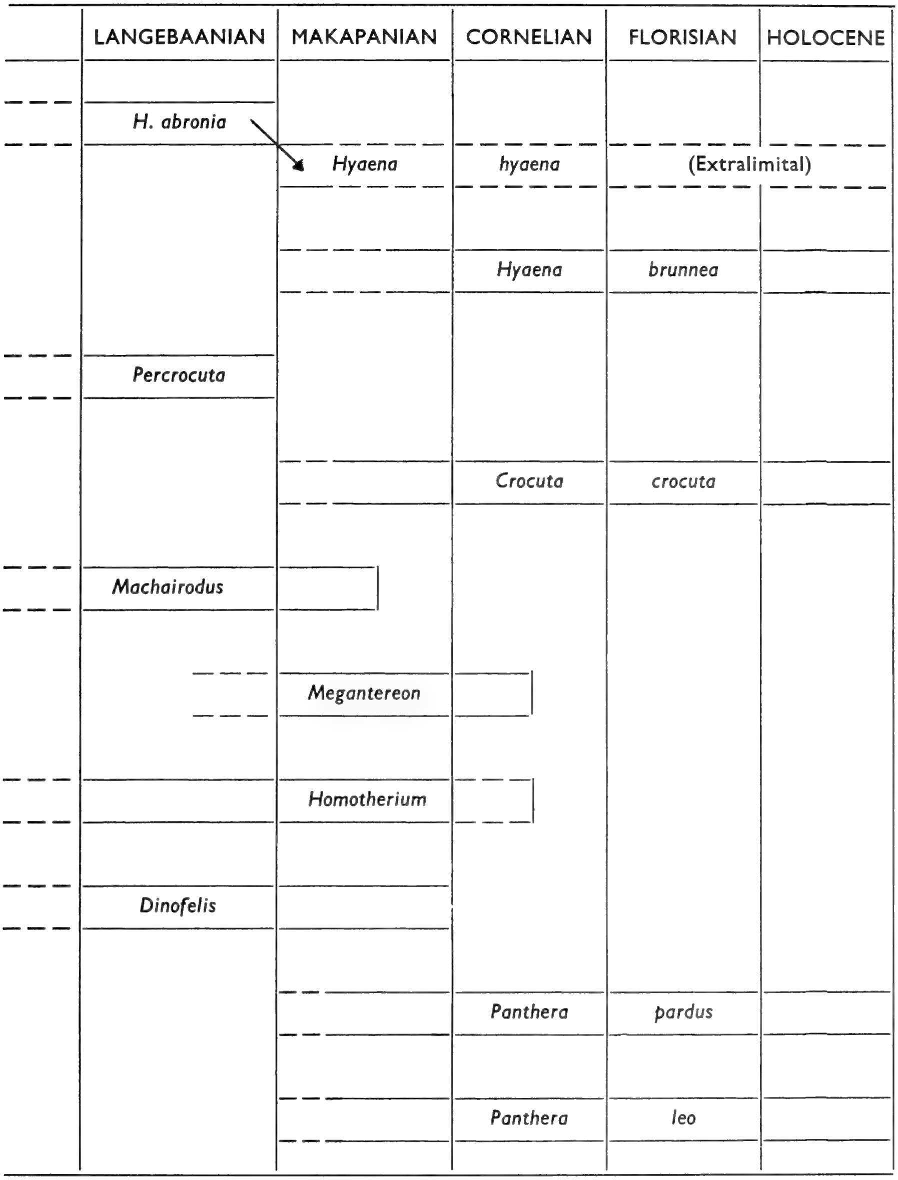

Fig 75b. The recorded time spans of some South African Hyaenidae and Felidae.

vertebrate species from many parts of the world.

More than twenty years ago, Hooijer (1950: 360) wrote: 'In current literature on Quaternary faunas, both in the Old and in the New World, we find quite a few scattered notes as to the large average size of a given fossil or subfossil relative to recent material of the same species used for comparison. It is, however, only during the last few years that statements as to this Quaternary size decrease apparently representing a general evolutionary trend appear in the literature. It is considered as probable by some authorities that this decrease in general size is to be correlated with the warming-up of the world's climates since the Ice Age, which would be the working of Bergmann's Principle in a temporal rather than a geographic way.' He continued, noting that, 'there can be no doubt that the fossil or subfossil animals are con-specific with the recent, and that we are consequently dealing with subspecific advances only. No extinction nor even migration is involved; it is evolution *in situ*. The means and modes of the various metrical characters are shifting in the course of time: we have temporal clines, chronoclines.'

More recently, Kurtén (1968: chapter 17) has discussed the question of Quaternary size changes and shown that they were not necessarily synchronous in carnivore species from the same parts of the world and that species in different parts of the world were not necessarily of uniform size at any given time. The latter is perhaps fairly obvious in view of the size differences between different populations of species which are still extant.

The reasons that species have undergone size changes in the course of their evolution are almost certainly complex and varied, but in the higher latitudes at least climatic fluctuations apparently played a significant role. Since Quaternary climatic changes in South Africa were probably not as extreme as those in the temperate latitudes of Europe, it is less likely that body size in relation to heat regulation (Kurtén, 1968: 245) was a significant mechanism influencing size changes. However, local environmental changes resulting from climatic fluctuations may have had some effect on the average size of individuals in the various species which occurred in the most southerly parts of Africa.

Apart from the problem of the causes of size changes, there are also difficulties in analysing the actual nature of the changes. For example, in South Africa there is an almost complete lack of chronometrically dated fossil faunas, so that even though their relative ages may be established, the absolute time differences between them are not. Consequently, rates of size change cannot be accurately determined. A second problem relates to the fact that size changes in different skeletal elements of a single species were not necessarily constant. This difficulty is clearly illustrated by the fossil *Vulpes chama* from the south-western Cape. The limb bones of the Cornelian variety were only a little longer than those of modern *V. chama*, but they were much stouter, while the skull was much larger. Some of the teeth of the two varieties were little different in size, but others, notably the posterior cheekteeth, were very much bigger in the Cornelian variety.

The species dealt with in this report are represented by a variety of skeletal remains which are not always directly comparable. In order that some comparison of the relative sizes of local Quaternary species be made, the mean lengths of upper and lower carnassials of some species are illustrated (Fig. 76). It is important to emphasize that the changes in the size of carnassial teeth do not necessarily reflect equivalent changes in other skeletal elements or overall body size. For example, it was shown that when the Cornelian *Canis mesomelas* from Elandsfontein is considered in relation to the modern form, the skull size is greater than would have been expected from the size of its lower carnassial.

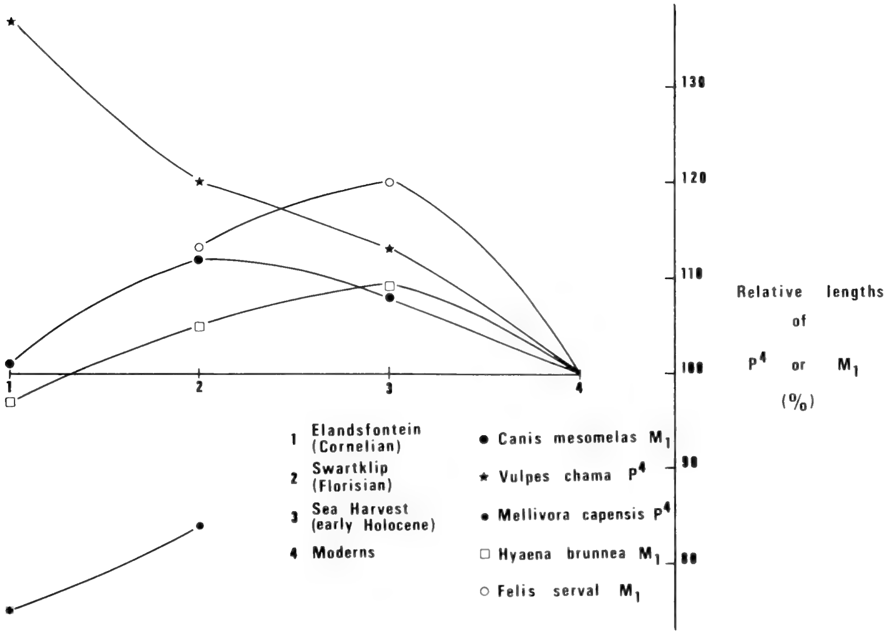

Fig. 76. The mean lengths of P^4 or M_1 of some South African Carnivora.

The selected examples show clearly that the size changes in the carnassials were not constant or synchronous in different species. In general, however, the largest sizes were attained in the Florisian and early Holocene. An apparent exception in the illustrated examples is *Mellivora capensis*, but the Elandsfontein Bone Circle representative of this species, which is not shown and which probably postdates that from Swartklip (*vide supra*), was in fact larger than the modern variety. A real exception to the general rule is *Vulpes chama*, the largest local representative being Cornelian in age. In this instance there is also a correlation between overall skull size and the size of the carnassials.

As far as actual body sizes are concerned, the situation is obscure. There are indications that some species such as *Vulpes chama* and *Panthera leo* underwent overall decreases in size between the Cornelian and the present. Most species probably did fluctuate in size, but generally the local fossil varieties appear to have been larger than their extant counterparts. The only species in which there might have been varieties which were appreciably smaller than the modern form is *Mellivora capensis*.

Perhaps the only confident statement which can be made at present on the subject of size changes in the Quaternary Carnivora of the south-western Cape is that such changes did take place and they were apparently of the same nature as those reported in other parts of the world.

The Role of Carnivora in the Origin of Bone Accumulations

In recent years there has been an increasing interest in the manner in which bones may become accumulated under natural conditions and as a result of the activities of animals, including man. The principal reason for this interest in Africa has been the controversy about the origin of the bone assemblages associated with early hominids (e.g. Dart 1957; Brain 1969). It is now evident that there has often been more than one factor involved in the accumulation of any single assemblage.

Animal activity is frequently the cause of bones being accumulated in particular areas and, since animal behaviour is so variable, it is inadvisable to generalize about the activities of a particular species in this regard. Each occurrence being investigated should be considered individually. For example, the contention that hyaenas are not 'bone collectors' (Dart 1956, 1957) has been shown to be erroneous (Sutcliffe 1970). While it might be expected that carnivores would be the mammals most likely to be responsible for bone accumulations because of their predatory and scavenging habits, herbivorous mammals may also be 'bone collectors'. In Africa the most obvious example of this kind is the porcupine (*Hystrix*), which is known to accumulate large quantities of bones and other hard materials in its lairs. The bones are gnawed by the porcupines to keep their constantly growing incisors sharpened and/or at the correct length, something which cannot be achieved by gnawing on its normally soft food. It is also possible that they derive some advantage from the pieces of bone which are ingested. As a result of the physical damage done to bones by porcupine gnawing, the association of this animal with bone accumulations is usually readily evident.

This may also be true of assemblages resulting from carnivore activity, since the teeth of carnivores may leave characteristic marks and fractures on bones. This has been clearly demonstrated by Brain (1969, 1970), who has shown that leopards were responsible for at least a part of the fossil accumulation at Swartkrans. Similarly, hominid activity may leave characteristic imprints on bone assemblages which represent food residue or raw materials for artefacts (e.g. Hendey & Singer 1965).

Two kinds of carnivores which have been responsible for bone accumulations have now been mentioned, namely, hyaenas and leopards. In each case the assemblages investigated differed in composition and situation. The spotted hyaenas (*Crocuta crocuta*) studied by Sutcliffe on the Serengeti Plain carried parts of carcasses which they had scavenged back to their lairs in order to avoid the loss of this food supply to other carnivores, notably the lion. Brain's example of the Swartkrans leopard (*Panthera pardus incurva*) is similar, although in this instance bones accumulated in a cavern fortuitously situated beneath trees into which the leopards had carried their prey.

The second example illustrates the fact that it is not necessary for carnivores to occupy a sheltered lair in order that they be responsible for the accumulation of bones. It is to be expected, however, that carnivores which do occupy such lairs are more likely to give rise to concentrations of bones. Consequently, although it is theoretically possible that any carnivore might be responsible for bone accumulations, in practise concentrations will only build up when a carnivore habitually returns to the same place with its kills and scavengings. Although a study of the habits of extant species will give an indication of those species which behave in this way, it does not necessarily follow that their extinct counterparts would have behaved in a similar fashion. For example, the modern lion is a free-ranging species and has not been reported to be responsible for any bone accumulations, but the extinct variety of the European Pleistocene (P. *leo spelaea*) apparently did occupy caves and might therefore have contributed some of the bones which are found in caves in Europe today.

Bone accumulations may also be only indirectly associated with the activities of carnivores. For example, predation and scavenging in any one area may be confined to a place where animals congregate for a special reason, such as at a waterhole. In these instances the remains of kills may accumulate in significant quantities and if they are fairly quickly covered by sediments and the conditions for bone preservation are good, then they will eventually appear as a relatively high concentration of fossils in a limited area.

Carnivore activity might also be only a primary factor contributing towards a bone accumulation. The remains of kills may be transported by some other agency and eventually be concentrated elsewhere. River transport is an obvious example of this kind and another is the concentration of fossils on wind deflated surfaces as a result of the removal of the deposit in which they were originally incorporated.

In the south-western Cape carnivore activity has apparently contributed towards the accumulation of some of the local fossil assemblages. This has already been suggested in the case of Swartklip (Hendey & Hendey 1968), while at Langebaanweg many of the fossils show signs of physical damage done by carnivores (Hendey & Repenning 1972). Langebaanweg differs from the situation at sites such as Swartkrans and Swartklip in that the carnivore kills were not concentrated in a limited area.

Since the south-western Cape assemblages differ in composition and origin, it is convenient to consider the more significant assemblages individually and to examine the evidence for and against carnivore activity in each instance.

There are three contrasting situations evident at the fossil sites of the south-western Cape, namely:

(1) Accumulation of bones in, or adjacent to, a river estuary (Langebaanweg).
(2) Accumulation in the vicinity of an inland water source (Elandsfontein).
(3) Accumulation in a rock shelter (Swartklip and Sea Harvest).

LANGEBAANWEG

Reference has already been made to the post-mortem damage to certain fossils recovered at Langebaanweg which results from their having been chewed by carnivores. Circular depressed fractures (punctate marks), striations on bone surfaces, spiral fractures of long bones and other signs of artificial interference (Fig. 77) are ascribed to activities of those predators and scavengers which are themselves part of the Langebaanweg assemblage. Some of the damage to bone is undoubtedly made by the teeth of carnivores. Other is in itself less convincingly so, but when it is associated with definite tooth marks it is also taken to be the result of carnivore activity.

In the current investigations at Langebaanweg particular attention is being paid to the condition of *in situ* fossils and also to their mode of occurrence. There is a great deal of accidental damage done to fossils in the course of the mining operations at the site, but it is clear that many of the fossils were damaged at or about the time they were incorporated in the accumulating sediments. It is well known that the remains of animals which die naturally, or which are killed by predators, are soon dispersed by the predators themselves, or by scavengers. The nature of the occurrence of many of the fossils at Langebaanweg suggest that they are the remnants of carcasses which have suffered in this manner. Incorporation into the sediments must have been at a variable rate, since the degree of bone destruction and dispersal of skeletal elements is itself variable.

Reference has already been made to the inferred nature of the environment at Langebaanweg at the time that the fossils were being accumulated (*vide supra*), and this has in part been determined by the nature of the fossil occurrences themselves. In order to illustrate this point, and also to indicate the manner in which some of the fossils came to be in their present condition and position, several contrasting examples are examined.

Fossil occurrences in Bed 2

Parts of a *Mammuthus subplanifrons* skeleton (L 12723) exposed at the north end of East Stream is a good example of the occurrence of a large mammal in Bed 2. An upper molar, mandible, some vertebrae, an innominate and some limb bones were found scattered over an area of several square metres. Although it is certain that some material was lost during mining operations, and that other bones might remain in unexcavated deposit, this specimen illustrates quite clearly than even skeletons of large mammals suffered post-mortem disturbance and were not necessarily preserved in their entirety. In this instance dismemberment of the skeleton was at least partly due to the activities of carnivores. A crushed but otherwise largely intact tibia has had parts of both extremities chewed away and there are marks left by large canine teeth on adjacent surfaces of the bone. The damage to this bone, and others from the same skeleton, was almost certainly done by hyaenas. *Hyaena abronia*, *Hyaena* Species B and *Percrocuta australis* remains are recorded from the same level of Bed 2, some in the immediate vicinity of East Stream.

The second example is that of a medium-sized herbivore, *Nyanzachoerus* (L 14429), the partial skeleton of which was exposed on the bed of East Stream about 70 metres south of the *Mammuthus* skeleton. The skull, vertebral column,

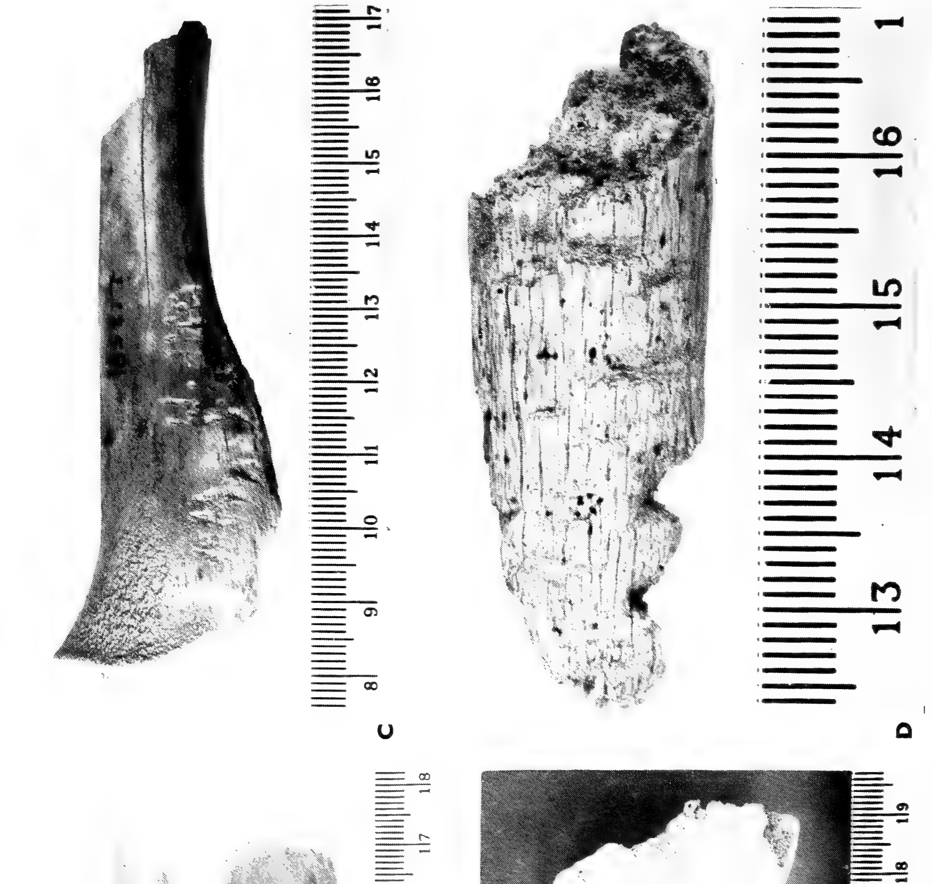

Fig. 77. Damage to bones from Langebaanweg resulting from the actions of carnivores.
A. Typical examples of bone fragments from Bed 3a recovered during the excavation LBW 1969/1.
B. Punctate marks on an innominate made by the canines of a carnivore.
C, D. Bone fragments showing carnivore tooth marks.

innominates and a hindlimb lacking only phalanges were recovered. The skull was badly fragmented before being incorporated into the deposits and there was no pattern to the distribution of individual skull parts, just as elements of the postcranial skeleton were completely disarticulated and disordered. Nevertheless, the fact that the remaining parts of this skeleton were found almost in their entirety over a limited area, indicates that after the loss of three of the limbs only minor post-mortem disturbance took place. A notable feature of this skeleton is that parts of the remaining hindlimb and adjacent skeletal elements are burnt. Fire damage to the sacrum, innominate and femur suggests that this could have occurred when these elements were still in articulation. However, damage to the distal extremity of the hindlimb is such that this could only have occurred after the individual elements had been disarticulated. The sequence of events must therefore have been the death of the animal, followed by at least partial dismemberment, then damage to the remains by fire, and finally incorporation in the accumulating sediments. Damage to some of the bones and the removal of three of the limbs may well have resulted from the actions of hyaenas. Following the fire there must have been little or no further disturbance, otherwise the bones would not have been found in so close an association. The implications are that this animal died on a land surface which must have been vegetated, the plant cover then having been burnt. The remains could not have been transported by water before being covered by sediment. Five other *Nyanzachoerus* individuals have so far been recorded in the vicinity of L 14429. The occurrence of the remains of fish in association with these specimens suggests that the land surface on which they occur was subsequently inundated and buried beneath subaqueously accumulated sediment.

A comparable example of another medium-sized herbivore is the partial skeleton of a boselaphine (L 13101) which was found near the northern end of Main Stream. As with the *Nyanzachoerus*, the skull was fragmented, the vertebral column was largely complete, but with this specimen only one scapula and part of one innominate was otherwise present. Only proximal parts of ribs were represented. No two elements of the skeleton were found in articulation, although the remaining parts were found over a very limited area. A large area was opened up around the skeleton, but no trace of the missing limbs was found. It is likely that L 13101 represents the remains of a carnivore kill and that after it had received the attentions of both predators and scavengers just about all that remained was the skull, vertebral column as far as the sacrum and the proximal parts of some ribs. A small part of the right innominate was found a little distance from the vertebrae and this shows very clear tooth marks left by a large carnivore (? hyaena). The dorsal spines of the thoracic vertebrae are scarred by the toothmarks of a small carnivore (? viverrid). In this instance none of the remaining bones had been burnt.

The skeleton of the *Hyaena abronia* holotype (L 14186) is unusually complete for a specimen from Langebaanweg. Since it was found only about 15 metres from the *Nyanzachoerus* discussed above, and since its occurrence contrasts in many ways with that of the pig, it is worth recording. The skull and about 80 bones of the postcranial skeleton were recovered, with the thorax the only part not represented. Most of the postcranial bones are complete, but some have suffered damage which is clearly not recent. For example, both femora lack their distal ends, both tibiae their proximal ends and the ulnae their olecranon processes. Neither of the patellae were found. The absence of the missing skeletal elements, and the damage referred to, could be explained if the newly-dead animal lay on its stomach with the back arched and the limbs drawn up. Partial burial leaving the now missing parts above ground surface would have left the exposed parts in a position to be removed or destroyed by scavengers, weathering or erosion. Thereafter there must have been some localized disturbance of the remains, since although they were found over an area of less than one square metre, the only parts still articulated were the skull and mandible, and the mandible was in fact slightly displaced.

It is possibly significant that quicksand conditions may develop in water-logged areas of 'E' Quarry, and if such conditions also existed at the time Bed 2 was being laid down, animals could have been trapped in such areas. This might have happened in the case of the *H. abronia* holotype.

There are no known examples of complete or partial skeletons of smaller vertebrates occurring in the Bed 2 deposits. This is possibly due to the fact that such skeletons are more readily dispersed by predators, scavengers and other agencies. Vertebrate microfauna is quite common in Bed 2, in which three small viverrid species are also recorded. It is likely that these small carnivores were responsible for the presence of at least some of the small vertebrate remains being added to the accumulating deposits, in the same way that the larger carnivores contributed to the presence of the preserved remains of large animals.

One of the most notable features of the deposits in certain areas of 'E' Quarry is the abundance of the remains of fossorial species. For example, in the vicinity of East Stream one chrysochlorid and two bathyergid species are represented in appreciable numbers. Their relative abundance can be explained by the fact that death of individuals underground virtually ensures preservation if soil conditions are favourable, and this was certainly the case with the Bed 2 deposits. The presence of these species is taken as a further indication that there was a land surface in the East Stream area at the time the deposits were being laid down.

In addition to the fish remains in the East Stream area mentioned earlier, a shark, frogs, a penguin and a seal are recorded in association with the remains of terrestrial vertebrates. They indicate the existence of an aquatic environment close to the East Stream land surface and the later inundation of this surface.

From the nature of the occurrences described above, it is deduced that at a certain time, or times, during the deposition of Bed 2, predation and scavenging of animals took place on the fringes of an estuary and that the activities of carnivores were a major factor involved in the mortality of the animals now preserved as fossils. In addition, the actual nature of the fossil occurrences was at least partly determined by the post-mortem disturbance of animal carcasses by carnivores. Although much of the damage to, and dismemberment of skeletons in this horizon can be attributed to hyaenas, other carnivores were also involved, as the evidence of toothmarks shows.

Another point of minor significance arises in this connection. Associated with a *Percrocuta* specimen from Bed 2 (L 13033) were a series of bone fragments the edges of which are apparently abraded. These specimens may owe their condition to erosion in the digestive tract of the *Percrocuta*, rather than having been transported by water or weathered on a land surface. The ability of hyaenas to crack and swallow bones is well known (see Dart 1956: 43), and the bone fragments which are swallowed are eventually completely reduced by digestion and the residue excreted. If the bone fragments associated with the *Percrocuta* were indeed stomach contents, then their digestion was obviously not far advanced. The significance of this particular discovery is that other, apparently water-rolled or surface weathered bone fragments may actually be stomach contents of hyaenas and possibly erroneous conclusions could be drawn from their presence in the deposits.

Fossil occurrences in Bed 3a

There appears to be a higher proportion of very fragmented bone in Bed 3a than is the case in Bed 2. As before, tooth marks indicate that fragmentation was caused by carnivores. Most often the broken edges are fresh and sharp, indicating that the fragments were never swallowed. In controlled excavations carried out in Bed 3a, it was noted that many of the bone fragments stand vertically, or near vertically in the deposits, which suggests that they were dropped or moved in soft waterlogged or subaqueous deposits. If they were transported by water, the movement must have been very limited because the edges of the fractures are still remarkably fresh in appearance.

Hyaenid remains are not uncommon in these deposits, so it is likely that once again they were to a large extent responsible for the condition of the *in situ* fossils of Bed 3a. However, seals are also very common in Bed 3a and perhaps they too played a role in the dismemberment and fragmentation of skeletons by scavenging floating or stranded carcasses of terrestrial mammals. No record could be located of this type of behaviour in seals, so that this opinion is pure speculation based only on the fact that the seal is perhaps the most commonly occurring carnivore in Bed 3a. It is perhaps more likely that the seal remains themselves owe their condition partly to the shoreline scavenging of hyaenids.

Ecology of the Langebaanweg Carnivora

Since the Langebaanweg Carnivora are the only local fossil series which differs appreciably from the modern carnivore fauna, it is of interest to consider their ecology in some more detail. In order to facilitate comparisons between the fossil and modern representatives of the group, they were categorized in the arbitrary manner illustrated in Figure 78.

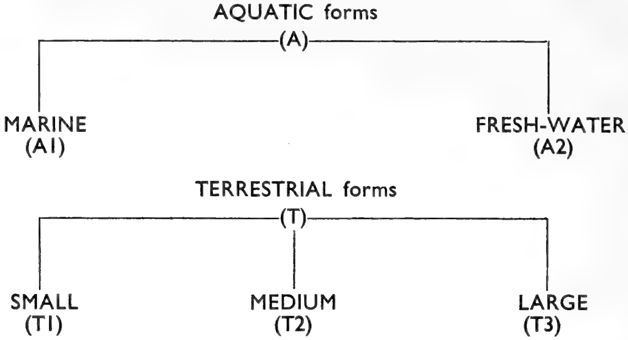

Fig. 78. Categories of Carnivora represented in the south-western Cape Province.

The marine aquatic group (A1) is the only one in which the Langebaanweg and modern faunas are directly comparable. A single resident pinniped species is represented in both faunas, the principal difference being that the Pliocene one is a monachine, while the modern species is an otariid. Although there is no certain evidence that the Langebaanweg *Prionodelphis* was not an exclusively piscatorial species, it has been suggested that it was an estuarine scavenger. Similar behaviour is not recorded for the extant *Arctocephalus pusillus*.

The fossil and modern representatives of the freshwater group (A2) differ in that the former includes one, and possibly two giant species, while there is only a single, relatively small otter in the modern fauna. Modern *Aonyx capensis* includes fish, frogs, crabs and molluscs in its diet. Although crabs have not been recorded from Langebaanweg, it is very likely that they were present, so the diet of the fossil otter(s) may have been essentially similar to that of the modern species. The size differences are, however, unexplained and it may well be that the Pliocene otters were different to modern *Aonyx* in their habits.

If the unclassified carnivore from Langebaanweg is indeed an otter, then it and not *Prionodelphis* may have fulfilled the role of an aquatic scavenger. The very large canine teeth of this species would have been admirably suited to tearing flesh from carcasses and its posterior cheekteeth, which are not known, may have been adapted for bone-crushing. Both it and the *Enhydriodon* may have contributed to the accumulation of terrestrial vertebrate bones in the Langebaanweg deposits.

There is a marked difference between the modern and fossil small terrestrial carnivores (group T1) in that the modern fauna includes a much wider variety of species. This group is comprised mainly of viverrids and it has already been indicated that their radiation was a feature of the Pleistocene. The rather generalized Langebaanweg *Genetta* and *Herpestes* species may have occupied a variety of ecological niches which are today filled by more specialized forms. The three small carnivores recorded from Langebaanweg were probably responsible for the accumulation of many of the vertebrate microfaunal bones at the site. The absence in the Langebaanweg fauna of a small felid comparable to *Felis libyca* may simply be due to an inadequacy in the fossil record.

There is a less marked difference in the number of species making up the group of medium-sized terrestrial carnivores (T2), although the highly specialized *Otocyon* and *Proteles* have no recorded counterparts in the Langebaanweg fauna. The early mellivorine from Langebaanweg is balanced by an advanced form in the modern fauna, although it is likely that the habits of the two species differed, modern *Mellivora capensis* being a more omnivorous form. The smaller of the Langebaanweg felids (*Felis* aff. *issiodorensis*, *F. obscura*) probably have the caracal and serval as their modern counterparts.

Comparisons between the modern and fossil faunas of group T3 can be made in three categories. Firstly, there are those species which prey on small vertebrates and scavenge from the kills of large predators. The fossil representatives are *Viverra leakeyi* and perhaps the unidentified canid, while *Canis mesomelas* is their modern counterpart. Secondly, there are the large predators which are represented at Langebaanweg by the two machairodonts and *Dinofelis* and in the modern fauna by *Panthera leo* and *P. pardus*. In addition, the modern fauna includes the cursorial *Lycaon pictus* which has no definite counterpart at Langebaanweg, while the giant *Agriotherium* has no modern counterpart. Finally there are the large scavengers, the Hyaenidae. They are well represented and complementary to the sabre-toothed cats in the Langebaanweg fauna and less diverse and complementary to the large predators of the modern fauna. *Hyaena* Species B and *Hyaenictis preforfex* may have been more actively predaceous than modern hyaenids. It is this group which was probably the most important contributor to the accumulation of fossils at Langebaanweg and whose activities determined the nature of many of the fossils which have been preserved.

On the basis of the available record, the following major changes were undergone by the south-western Cape carnivore fauna between the Langebaanian and the historic period:

(1) One family of seals was replaced by another, but in each instance only one resident species is represented.
(2) Giant fresh-water carnivores were replaced by a smaller form.
(3) There was a diversification among the smaller predators.
(4) Highly specialized insectivorous and omnivorous carnivores were evolved.
(5) There was a change in the representation of large terrestrial carnivores, including the replacement of a civet by a jackal, the replacement of sabre-toothed cats by ordinary forms, and a reduction in the variety of large scavengers represented.

To conclude the account of the Langebaanweg Carnivora, they are compared and contrasted with those of the North American Hagerman Local Fauna (Bjork 1970). The two assemblages are broadly contemporaneous and while that from Langebaanweg is from a coastal estuarine environment, 'the environment of deposition at Hagerman during the late Pliocene was a broad flood plain with trees and grassland adjacent to the tributary streams of Lake Idaho' (Bjork 1970: 51). The recorded vertebrate faunas from the two occurrences are essentially similar in composition (i.e. carnivores, herbivores, reptiles, birds, etc.), although the species represented are, of course, quite different.

The two assemblages include a similar number of fissiped carnivore species, but there is a taxonomic correspondence only at the family level (Table 91). Only one of the families represented at Langebaanweg, the Viverridae, is not recorded at Hagerman and this gap is filled by the Mustelidae, which make up 50% of the species recorded in the Hagerman carnivore fauna. At Langebaanweg the Mustelidae make up at most only 16% of the carnivore species represented, although the Mustelidae and Viverridae together make up about 45% of the total. Only one hyaenid is doubtfully recorded from Hagerman on the basis of a single deciduous tooth, whereas the five Langebaanweg species are represented by numerous specimens. There is, however, a large canid from Hagerman (*Borophagus*) which evidently fulfilled an hyaenid role in North America. Only in the case of the Felidae is there any marked resemblance in the nature of the species represented in the two assemblages.

TABLE 91

The representation of fissiped carnivores in the late Pliocene occurrences at Langebaanweg, compared with that of the Hagerman Local Fauna (Bjork 1970)

	Number of species	
	Langebaanweg	Hagerman
Canidae	1	2
Ursidae	1	2
Mustelidae	2 or 3	9
Viverridae	4	0
Hyaenidae	?5	?1
Felidae	5	4

	Langebaanweg	Hagerman
No. of species	19	18
No. of genera	*c.* 14	16
No. of families	6	4 or 5

	Langebaanweg/ Hagerman
Species in common	0
Faunal resemblance (%)	0
Genera in common	1
Faunal resemblance (%)	7
Families in common	4 or 5
Faunal resemblance (%)	100

It is remarkable that two carnivore faunas, which fulfil the same ecological role in essentially similar environments at the same period in time, should differ in so many ways. The indications are that even in the late Tertiary the faunas of South Africa and North America had long since been developing independently from one another.

ELANDSFONTEIN

The Elandsfontein fossil exposures are situated close to one of the few permanent waterholes anywhere in the Sandveld area of the south-western Cape. The river nearest to the site is the Sout, some 10 km distant, which under existing climatic conditions has water in it for only a few months each year and even then it is seldom, if ever flowing strongly. The water table in the Elandsfontein area is close to the surface and this, coupled with the presence of the existing waterhole, suggests that it might have been a local source of fresh water for a long time. Consequently, it is an area where animals are likely to have concentrated at least as far back as the Cornelian, to judge from the fossil record.

The situation is, therefore, one where there is likely to have been concentrated carnivore activity over prolonged periods and many of the fossils at the site probably represent the remains of carnivore kills. The Elandsfontein fossils have not been studied with the view to establishing evidence of carnivore activity in the same detail as those from Langebaanweg. In addition, there are some complicating factors which would have to be taken into consideration in any detailed analysis of the nature of the occurrences.

Many of the fossils from this site have been gnawed by porcupines (Singer 1956), and some of the recorded fossil concentrations may represent now exposed remnants of the subterranean lairs of these rodents. Porcupines still occupy such lairs in the area today, although none has been excavated and examined.

A second difficulty is that there has clearly been some contribution to the fossil occurrences as a result of hunting in the area by primitive man. For example, an Early Stone Age 'living floor' uncovered at the site revealed an association of artefacts with a variety of mammalian remains (Singer & Wymer 1968). Since there is evidence also of Middle Stone Age, Late Stone Age and historic period hominid activity, it follows that each of these periods of occupation may have added faunal remains to the deposits.

There are, however, some bone accumulations which might have resulted from the activities of carnivores. One of these is the Bone Circle occurrence, which was repeatedly referred to earlier in connection with the Florisian Carnivora from this site. Some accounts of this occurrence have previously been given elsewhere (Inskeep & Hendey 1966; Singer & Heltne 1966). The earlier opinions concerning the possible origin of this occurrence are here rejected.

There are marked similarities between the nature of this occurrence and those at Swartklip, the most obvious and perhaps also the most misleading difference between them being that whereas those at Swartklip are vertical exposures, the Bone Circle occurrence was a horizontal exposure. The Swartklip sites are more obviously in the form of subterranean animal lairs, but were they to have been exposed horizontally they might well have taken on the appearance of the Bone Circle occurrence. If it is assumed that carnivores such as *Canis mesomelas* made use of aardvark (*Orycteropus*) burrows, it follows that bones might become accumulated in the lair by its new occupants and might subsequently be exposed by the very active wind erosion which is prevalent at the site. *C. mesomelas* is quoted as an example because a number of specimens of this species were the only carnivore remains associated with a miniature 'bone circle' at the northern end of the site. The original Bone Circle also included *Hyaena*, *Crocuta* and *Mellivora* remains and in this instance these animals might also have been one-time occupants of the hypothetical lair. In neither of the two occurrences referred to was there evidence of porcupine activity.

It was suggested earlier in connection with the Elandsfontein *Suricata* that those carnivores which occupy subterranean lairs might be more commonly represented as fossils than those which do not. *Mellivora capensis* was mentioned as an obvious example in addition to the *Suricata*. The fact that *C. mesomelas*, and to a lesser extent also *Hyaena brunnea*, is so abundantly represented at Elandsfontein at least suggests the possibility that it did frequently, or habitually, occupy such lairs.

There is clearly a potential for a more thorough investigation of bone concentrations at the Elandsfontein site, but they are here regarded as the results of carnivore activity rather than 'some freak of deflation' (Singer & Wymer 1968: 64), although deflation is the mechanism by which they have been exposed.

There is other more direct evidence of carnivore activity at Elandsfontein. The machairodont humeri 3058/9 show signs of tooth marks which were definitely not made by porcupines, but which could have been made by a carnivore. More convincing still is the *Mellivora* braincase 20981, which has two circular holes 4 mm in diameter and 21 mm apart on its dorsal side and a similar hole in the basi-occipital. The spacing and size of these holes suggests that they were made by the canines of a carnivore of about the size of *Mellivora* itself, although the canines of *C. mesomelas* also fit them quite well. This specimen is reminiscent of the leopard-punctured australopithecine skull described by Brain (1970).

An aspect of the Elandsfontein fossil occurrences which might be an indication of carnivore activity is the fact that there are remarkably few recorded instances of skeletal elements having been found in articulation. This indicates a great deal of post-mortem disturbance and dispersal of skeletons of the kind which results from the actions of both predators and scavengers when animal remains are not fairly quickly buried. Exceptions to this general rule on skeletal dispersal are most commonly recorded in the 'bone circle' occurrences. Actual articulations are known, but more commonly individual skeletal elements were slightly separated from one another. This is also a feature of the Swartklip occurrences and in both instances it appears to be skulls and cervical vertebrae or the distal extremities of limbs which are found in the closest association.

One of the very few recorded instances of dispersal of a single individual outside of the 'bone circles' is that of a *Pelorovis* skeleton (16710). The almost complete skull was found ventral side uppermost a few metres away from both halves of the mandible and most of the anterior part of the vertebral column. There are no obvious tooth marks on any of the skeletal elements, but the disturbance of the skeleton is of the kind which might result from the actions of an hyaenid. On the other hand, this and other instances of disturbance might also be the result of butchering by hominids.

SWARTKLIP AND SEA HARVEST

Some evidence supporting the conclusion that the Swartklip assemblages accumulated in carnivore lairs has already been discussed elsewhere (Hendey & Hendey 1968: 48–51), but this may now be qualified and enlarged upon as a result of more recent observations.

Firstly, it was stated that the Swartklip assemblages did not include porcupine gnawed bones. These have in fact now been found at Site 1, but the numbers are so small that it is unlikely that the porcupine ever played a significant role in the accumulation of bones at these sites.

The presence of appreciable amounts of broken ostrich eggshell and at least two complete ostrich eggs was a problematical aspect of the assemblages, although it was suggested that these eggs formed part of the diet of one of the occupants of the lairs. Recently a photograph appeared in a Cape Town newspaper (*The Argus*, 19 April 1971) showing lionesses in a Kenyan wildlife park eating ostrich eggs and since it has been suggested that *Panthera leo* was one of the occupants of the Swartklip lairs, it is possible that this species was responsible for bringing in and breaking up the eggs found in the deposits. It was mentioned earlier that lions in Africa are not known to be occupants of caves and rock shelters, although this does not apply in the case of the Pleistocene lions of Europe. The Swartklip fossils date from the late Pleistocene when conditions in the south-western Cape were colder than they are today, so it is possible that the prevailing climate of that time prompted the local lions to make use of sheltered lairs, even though they do not do so today.

Just as porcupine gnawmarks on bones from Swartklip have now been recognized, so have tooth marks and fractures caused by carnivores. Bone fragments with spiral fractures and punctate marks, identical in appearance with those from Langebaanweg, have been recovered.

Although the Swartklip lairs were probably occupied by a variety of species over a period in time, the ones which are regarded as being responsible for most if not all of the bones introduced into the lairs are *Canis mesomelas*, *Hyaena brunnea*, *Panthera leo* and *Hystrix africaeaustralis*.

Essentially similar observations and conclusions apply in the case of the Sea Harvest site, although in this instance both *Crocuta crocuta* and *Panthera pardus* are added to the list of possible bone collectors.

Conclusion

For a region which is so limited in extent, the south-western Cape Province is providing a remarkable record of animal life during the late Cenozoic. The existing local record, taken in conjunction with that from the rest of southern Africa, has already given a fairly clear indication of the nature and evolution of higher forms of life in the subcontinent during this period in time. In general, the fossil occurrences of comparable age in East Africa are more significant than those to the south, but the records from the two areas are complementary to one another. The same applies in the case of the fossil faunas of the south-western Cape in relation to those from the rest of southern Africa. They are an integral part of the record as a whole and are, therefore, of more than just local interest.

In the present report the tendency was to emphasize the occurrences at Langebaanweg. This was done because the fauna from this locality is unique in so many ways and it is regarded as the most important of the local fossil faunas.

Many notable discoveries have already been made at Langebaanweg. For example, the fauna includes one of the earliest of the true elephants, an early ancestor of the white rhinoceros, the first fossil penguin recorded in Africa, the first bear from sub-Saharan Africa and what is perhaps the last of the African boselaphine antelopes. New or unusual records of this kind are of interest in themselves, but their real significance must be assessed against a broader background. Thus while the seal, *Prionodelphis capensis*, is only the second record of the genus and one which allows adequate definition of the genus for the first time, its significance lies chiefly in the additional insight it has given on the possible origin and evolution of the Antarctic seals. Previously little was known about this subject, even though surviving populations of these seals may be counted in millions and their area of distribution covers millions of square kilometres of the earth's surface.

In addition, the Langebaanweg fossils have given the first real indications of the nature of the local environment in late Pliocene times. It was evidently very different from that of the present and it is expected that geological and other studies stimulated by the palaeontological investigations at Langebaanweg will contribute more to the knowledge of the late Pliocene environment.

The local Quaternary record is of interest since it includes assemblages ranging in age from Cornelian to Holocene, which makes it possible to trace in some detail the final stages in the evolution of the modern fauna of the region. This part of the local fossil record is less remarkable than that from Langebaanweg, but this does not diminish its importance. Attempts to determine the character of the historic period fauna, which is now much depleted as a result of human activity, have been undertaken in conjunction with the Quaternary palaeontological investigations. One of the significant aspects of the recent fauna of the region is the fact that it was from the south-western Cape that many of the species which characterize the Ethiopian faunal region were first described.

Additional interest in the late Cenozoic fauna of the south-western Cape stems from the fact that this region is atypical of sub-Saharan Africa as a whole, since it is situated at the southern continental extremity and is climatically differentiated. The biological implications of its geographical location are significant in both palaeontological and neontological studies.

Although many investigations have already been carried out on the fossil mammals from the south-western Cape, the research potential in this field is still good. Boné & Singer (1965: Table 1) recorded 13 carnivore species from two sites in the south-western Cape, while the present report records at least 45 species from more than half a dozen occurrences. To a greater or lesser extent a species list increase can be expected in other mammalian orders as well.

It is striking how little information on the late Cenozoic mammals of Africa is included in a recent book on the fossil mammals of the world (Kurtén 1971), yet this was the time when the modern African fauna, which by any standard is exceptional in quantity and variety, went through the final stages in its development. In his review of the Pliocene, Kurtén (1971: 152) wrote that this epoch was 'something of a paradise lost, a climax of the Age of Mammals before the coming of the cold; a time when life was richer, more exuberant than ever before or after'. He goes on to say that conditions which prevailed at this climax are now found only in a few areas, and those are mainly in Africa. We are thus faced with the curious situation that the continent in which the modern mammals represent what may well be the acme of mammalian evolution is also the one in which the fossil mammal record is perhaps least well known.

The situation is, however, improving and the recent investigations into the origin and evolution of the Hominidae has brought about an increased, although still largely incidental interest in other African fossil mammals. It is probably true to say that some of the more significant advances in recent years in the field of palaeomammalogy have been made in Africa. The traditional view that Africa played a somewhat subsidiary role to Eurasia in the origins and evolution of its own fauna is now being modified. It had also become fashionable to regard Africa as a refuge for archaic forms and, while this is not without foundation, there has perhaps been a tendency to underemphasize the role this continent has played in the later history of mammals.

With these points in mind, it is hoped that the report is concluded on a note of expectation rather than achievement. There is much which has still to be done.

SUMMARY

A general account is given of the recorded fossil Mammalia of the south-western Cape Province and also of the more important late Cenozoic fossil occurrences in this region. A formal nomenclature for the Pliocene deposits at Langebaanweg is suggested and a new system of age names for the South

African late Cenozoic, based on fossil mammal faunas, is proposed.

A more detailed account is given of the species of Carnivora known from the local late Cenozoic and the following new species are described:

Percrocuta australis, *Hyaena abronia*, *Hyaenictis preforfex*, *Felis obscura* and *Suricata major*.

Promellivora Pilgrim, 1932 is rejected and the material identified as such is referred to *Mellivora*. *Vishnuictis* Pilgrim, 1932 is reduced to the status of a subgenus of *Viverra* and *Pseudocivetta* Petter, 1967 is included in *Viverra* (*Civettictis*). It is suggested that the *Hyaena hyaena* and *Hyaena brunnea* groups be subgenerically distinguished, with the new name, *Parahyaena*, being applied to the latter group. *Megantereon problematicus* Collings, 1972 is provisionally listed as *Homotherium* sp. indet. Three previously unrecorded skulls of the Cape lion, *Panthera leo melanochaita*, are described.

Some aspects of the zoogeography of local mammals are considered and the role of carnivores in the origin of bone accumulations is discussed. Brief comments on topics such as the local non-mammalian fossils and size changes in Quaternary carnivores are also included.

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INSTRUCTIONS TO AUTHORS

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For journal articles give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals.* 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination.

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To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a*, *b*; Liste: 11. Turton, 1932: 80.

Q. B. Hendey

THE LATE CENOZOIC CARNIVORA OF THE SOUTH-WESTERN CAPE PROVINCE