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H J Deacon, Q B Hendey and J J N Lambrechts (editors)

A report of the Soils and Geomorphology Study Group
of the Fynbos Biome Project

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO

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PREFACE

The impetus to prepare this collection of papers came from meetings of the Soils and Geomorphology Study Group, one of the study groups formed to encourage research on aspects related to fynbos ecology. The Fynbos Biome Project is one of several national scientific programmes within the National Programme for Environmental Sciences administered by the CSIR.

The interest of the Soils and Geomorphology Study Group is in palaeoecology and the history of the fynbos ecosystems. The aim of the papers is to provide a synthesis of what is currently known about the hard and soft rock geology, the distribution of soils, mammalian palaeontology, vegetation history and prehistoric human settlement in the fynbos region, defined here as the Cape Fold Mountains and adjacent coastal platform. Where reference is made in the report to the south-western Cape, the area west of the Hottentots Holland and ranges to the north is implied. Similarly, the term Overberg is used to refer to that part of the fynbos region between the Hottentots Holland mountains and the Gouritz River, and Outeniqualand refers to the area between the Gouritz and Storms rivers.

It is hoped that the papers will serve as an introduction and a source of references to the relevant literature as well as encouraging an interest in a historical perspective of the region. Although much of the research in the Fynbos Biome Project is directed towards studies in community ecology and management, the setting in an old landscape and the nature of fynbos and related ecosystems pose historical questions that can only be answered by palaeoecological research. These concern the age of the landscape and substrates, the origins of the biota, the scale of past changes in climate and the influence of human activities. The report shows how far such questions can be answered on the present state of knowledge and indicates what progress can be expected from future research.

A number of researchers not represented among the authors have contributed to the concept of this synthesis and among these special acknowledgement is due to D. C. Grey, R. R. Maud, J. Rogers, A. A. Theron and K. L. Tinley.

The copy editing, typing and preparation of photo-ready copy for this volume was undertaken by J. Deacon, and V. B. Geleijnse and C. Stevens assisted in the drafting of diagrams and preparation of tables.

We are grateful to B. J. Huntley, Manager (Terrestrial Ecosystems) of the Cooperative Scientific Programmes, M. L. Jarman, the coordinator of the Fynbos Biome Project, A. A. Theron, the Chairman, and members of the Steering Committee of the Fynbos Biome Project for their encouragement and help in many ways.

H. J. Deacon
Stellenbosch, 1983

ABSTRACT

Current knowledge of aspects of the geology, soils and palaeontology relevant to the study of the palaeoecology of the fynbos region, the southern margin of the African continent, is surveyed in nine essays and three introductory reviews. Precambrian sediments, granites and rocks of the early Phanerozoic Cape Supergroup, underlie the greater part of the region and the distribution of the main rock units is shown on an accompanying map. The main physiographic features were established by folding during the Cape orogeny (278-215 Myr) and by subsequent erosion and faulting, in part associated with the outlining of the continental margin at the end of the Jurassic (140 Myr). The Cenozoic deposits (0-65 Myr) are discussed in a synopsis of the evolution of the modern landscape. Soils as indicators of palaeoenvironments are reviewed and a description and maps of soils of the Cape coastal platform are included. The palaeontological record as known from the study of the late Tertiary vertebrates, Quaternary large and small mammals, Cretaceous and Cenozoic plant microfossils and macrofossils, is described and the palaeoenvironmental implications are reviewed. The history of human occupation of the region is put into perspective. It is clear that the fynbos region, an ancient landscape of high terrain diversity, showing varied substrate lithologies and a mosaic of eutrophic and dystrophic soils, has not been a constant environment over geological time. It is in this setting under conditions of dynamic environmental change that the composition of the modern biota has been determined and the specialized character of fynbos ecosystems has developed.

SAMEVATTING

Die huidige kennis rakende aspekte van die geologie, grondsoorte en paleontologie wat ter sake is by 'n studie van die paleo-ekologie van die fynbosstreek, die suidelike deel van die Afrika-kontinent, word in oënskou geneem in nege opstelle en drie inleidende samevattings. Voor-Kambriese sedimente, graniet en gesteentes van die vroeë Fanerosoïese Kaapse Supergroup vorm die onderlaag van die grootste deel van dié streek en die verspreiding van die vernaamste gesteente-eenhede word op die gepaardgaande kaart aangedui. Die vernaamste fisiografiese kenmerke is gevorm deur plooiing tydens die Kaapse-orogeen (278-215 Mj) en deur daaropvolgende erosie en skeuring, deels geassosieer met die vorming van die kuslyn ten die einde van die Jurastydperk (140 Mj). Die Senosoïese afsettings (0-65 Mj) word bespreek en 'n samevatting van die ontwikkeling van die hedendaagse landskap word gegee. Grondsoorte, as bewyse van paleo-omgewings word bespreek en 'n beskrywing en kaarte van die grondsoorte van die Kaapse kusplatform word ingesluit. Die paleontologiese rekord, soos bekend vanweë die studie van die laat-Tersiêre werweldiere, Kwaternêre groot en klein soogdiere en plantaardige mikro- en makrofossiele uit die Kryt en Senosoïese tydperk, word ook bespreek en die paleo-ongewingsimplikasies word in oënskou geneem. Die geskiedenis van die menslike bewoning van die streek word ook in perspektief geplaas. Dit blyk duidelik dat die fynbosstreek, 'n ou landskap met 'n hoë mate van fisiografiese verskeidenheid, wat deur verskeie gesteentes en 'n mosaïek van arm- sowel as voedingryke grondsoorte gekenmerk word, nie 'n konstante omveranderende omgewing tydens die verloop van geologiese tye was nie. Dit is teen hierdie agtergrond van dinamiese omgewingsverandering dat die samestelling van die hedendaagse biota geskied het en die gespesialiseerde kenmerke van fynbos-ekosisteme ontwikkel het.

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AN INTRODUCTION TO THE FYNBOS REGION, TIME SCALES AND PALAEOENVIRONMENTS

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INTRODUCTION

The concept of a fynbos region as used in this volume is as much physiographic as it is phytogeographical. The geographical focus is the landscape at the southern margin of the African continent that consists of the Cape Fold Mountains and the bordering coastal platform with its extension, the continental shelf, that has been variously exposed through changes in sea level in the past. Where appropriate the surrounding areas have also been considered. This physiographic entity corresponds in general terms to the Capensis region which is the main domain of the Cape Floral Kingdom (Takhtajan 1969; Good 1974; Taylor 1978) and that in which Cape fynbos and associated Cape transitional shrublands are important components of the natural vegetation (Taylor 1980). The concern is with the interpretation of the geological deposits and the fossils they contain and how these promote an understanding of aspects of the natural history of this region which Livingstone (1975) has suggested preserves possibly the most bizarre biota in the world today. The treatment is by no means exhaustive and many theoretical issues of biogeography and ecosystem evolution have still to be addressed. Theories of evolutionary mechanisms cannot be generated directly from palaeontological data alone but such data can be used to test predictions of the theories developed from the study of the modern biota (Eldredge & Gould 1972:93). There is a need to integrate processual and historical studies and herein lies the merit of attempting this synthesis of palaeoenvironmental and palaeoecological information for the fynbos region.

TIME SCALES: A FRAME OF REFERENCE FOR ENVIRONMENTAL HISTORY

The papers in this volume deal with geological time measured in thousands, millions and hundreds of millions of years. The time intervals are known with differing levels of precision. Some are known in a relative sense of one deposit or biological assemblage being older than another without a direct indication of the age difference. In other cases correlations with well dated events or faunas and floras afford greater precision. Chronometric age determinations, for example those based on radiometric

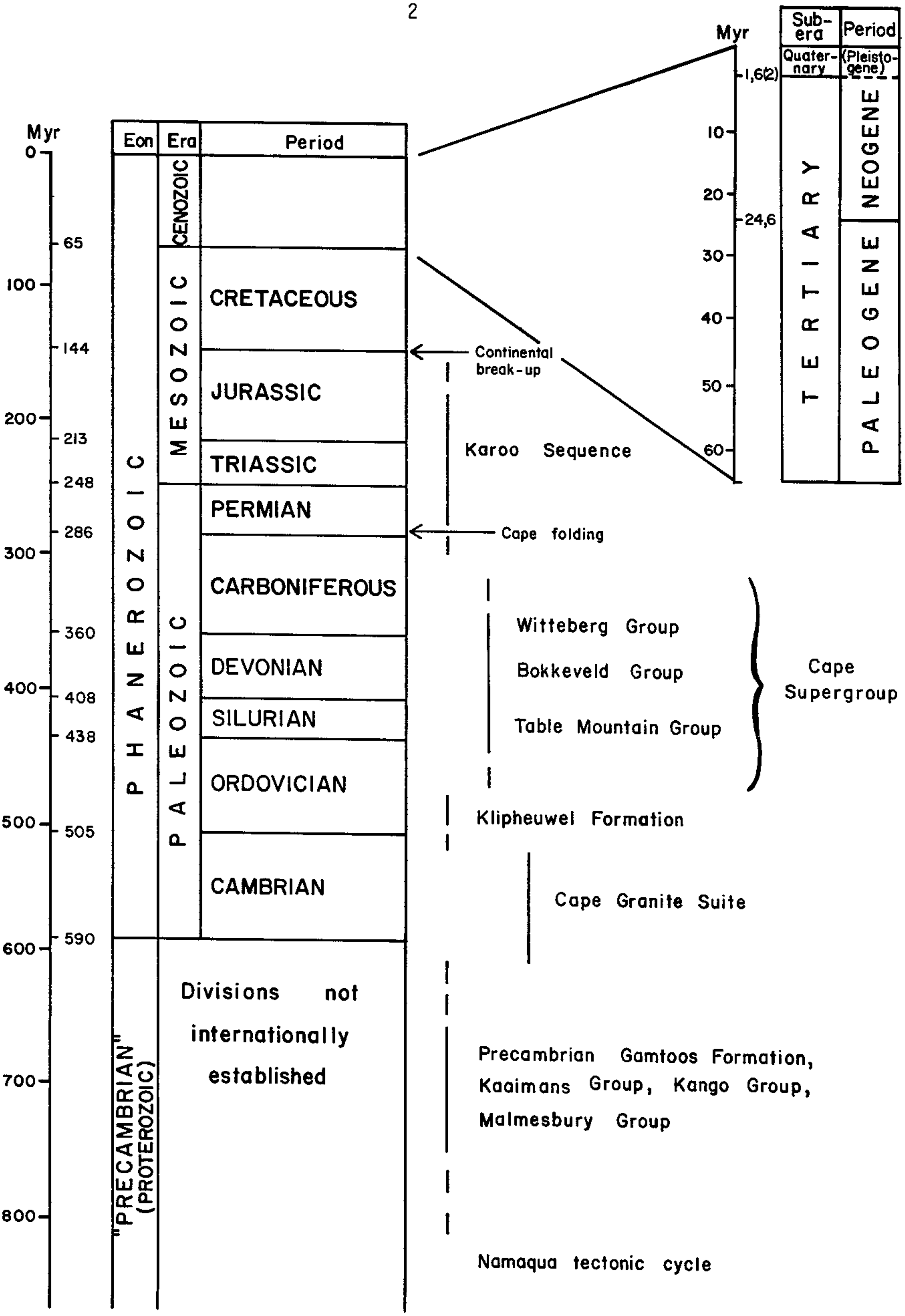

Table I. Geological time scales (after Harland et al.) and rock units (after S.A.C.S. 1980; Theron, this volume) in the fynbos region.

dating methods (where they can be applied), may provide relatively high resolution. Time scales are of fundamental importance as the framework for piecing together the sequence of events, linking isolated observations and measuring rates of change. In the accompanying tables the geological time scales follow those suggested by Harland et al. (1982).

The segment of geological time relevant to palaeoecological studies in the fynbos region spans almost the last 1 000 Myr (Table 1), the late Precambrian and the Phanerozoic Eon. There are inliers of Precambrian rocks that are evidence for the earliest period in the history of the region when sediments were accumulated in the Malmesbury-Kango geosyncline and were deformed by folding, shearing and intrusion by rocks of the Cape Granite Suite (Theron, this volume). The rocks of the Malmesbury Group are exposed over a significant area of the coast platform in the south-western Cape between Cape Town and north of Malmesbury and the shale, phyllite and other argillaceous members of this group are associated with economically important residual soils (Schloms et al., this volume). The occurrence of Precambrian rocks in the Overberg and Outeniqualand is less extensive. The largest is the Kango Group inlier with noteworthy phreatic cavern development in associated limestones and the Kaaiman's Group inlier on the coast near George is associated with red apedal soils (Schloms et al., this volume).

On the planed surface of these Precambrian strata, in a basin depository (Rust 1973) approximately conformable to the present continental margin, a maximum thickness of over 8 000 m (SACS 1980) of predominantly shallow-water marine sediments of the Cape Supergroup were laid down (Tankard et al. 1982; Theron, this volume). Sediment accumulation was initiated in the Ordovician and continued through the Silurian to the Carboniferous and was terminated with the displacement of the main centre of sedimentation northwards to the Karoo Basin (Table 1). Folding during the Cape orogeny gave positive relief to the rocks of the Cape Supergroup and this single phase, multiple event orogeny has been dated by 40Ar/39Ar step heating analysis to between the early Permian (278 Myr) and the late Triassic (215 Myr) (Halbich et al. 1983). In the process, a western zone of megafolds and monoclines trending north-north-west paralleling the south-western Cape coast and an eastern zone of northward verging folds paralleling the southern Cape coast in the Overberg and Outeniqualand were formed with the syntaxis in the surrounds of Caledon (Wellington 1955; Sohnge 1983). Although modified by subsequent faulting and reduced by erosion, the fold mountains that rose at this time determine the physiographic character of the region. Rocks of the Cape Supergroup comprising the Cape Fold Belt form the predominant substrates of the region with sandy, highly leached, nutrient-poor substrates largely associated with the quartz arenites of the Table Mountain and Witteberg groups making up the main mountain and ridge crests and argillaceous or clayey, nutrient-richer substrates associated with the intervening, less erosion resistant Bokkeveld Group found in intermontane valleys and in

Myr					
					Radiation of mammals
65–73	MESOZOIC	LATE CRETACEOUS	SENONIAN	MAASTRICHTIAN	Extinction of dinosaurs
73–83				CAMPANIAN	Recognition of microfloral provinces possible
83–87,5				SANTONIAN	Angiosperm pollens dominant
87,5–88,5				CONIACIAN	
88,5–91				TURONIAN	Appearance of a few modern plant taxa
91–97,5				CENOMANIAN	Diversification of the angiosperms
97,5–113		EARLY CRETACEOUS		ALBIAN	Final separation of Africa and South America
113–119				APTIAN	Undoubted pollen of angiosperms from the Cape Basin
119–125				BARREMIAN	
125–131			NEOCOMIAN	HAUTERIVIAN	Spore and conifer pollen assemblages from the Uitenhage Basin
131–138				VALANGINIAN	
138–144				BERRIASIAN	Southern continents begin to separate
		JURASSIC			

Table 2. The chronostratigraphy of the Cretaceous Period.

extended areas on the coastal platform as with rocks of the Malmesburg Group (Lambrechts 1979; Boucher & Moll 1981).

The Cape Fold Mountains provided a source of sediments for the Karoo sequence that accumulated on the northern margin and this sequence provides the first substantial terrestrial palaeontological record. The pre-angiospermous plants and reptilian fauna of Permian age in the Karoo sequence were similar to the biological communities of low diversity that existed in other parts of Gondwanaland at that time and Anderson (1977) suggests this indicates uniform climates and the absence of barriers to biological interchange. Such conditions appear to have persisted until the fragmentation of Gondwanaland in the Jurassic which culminated at the end of this period in the separation of the African and South American plates (Sclater et al. 1977). As a result of the process of shearing along a zone corresponding to the outer edge of the Agulhas Bank (Siesser et al. 1974), the southern continental margin was outlined in its essentially modern form. Penecontemporaneous and apparently related faulting with significant downthrows to the south, along the southern flanks of the mountains (Bishopp & Van Eeden 1971), established the relief of the region. This initiated renewed erosion of the uplands and the cutting of the coastal platform at the end of the Jurassic and at the beginning of the Cretaceous, some 140 Myr ago.

Early Cretaceous onshore deposition was limited to small fault-controlled basins (McLachlan & McMillan 1979; Theron, this volume) and the accumulated sediments provide evidence of a sporophyte and coniferophyte flora and the absence of undoubted angiosperms (Scott 1976; Table 2). The dispersal of the angiosperms took place in the mid-Cretaceous at a more advanced stage of continental separation and early angiosperm microfossils are recorded from this time in offshore sediments accumulated in the Cape-Argentine basin (McLachlan & Pieterse 1978).

The late Cretaceous was marked by the diversification of the angiosperms that preceded the end-Cretaceous extinction of the dinosaurs and the radiation of the mammals in the earlier Cenozoic. These periods are poorly represented in onshore deposits in the fynbos region because erosion and planation were the dominant processes and the depocentres lay offshore (Hendey, this volume). Thoday's comment (1925:198) that "The geological history of South Africa, moreover, reveals a land surface at least in part as old as the angiosperms", and again that "The folded belt . . . began to present topographic and geological features comparable in broad outline with those of the present quite early in the Tertiary" would find support in more recent studies.

The last 65 Myr of earth history, the Cenozoic Era, is divided into two periods, the Paleogene and Neogene. These terms have to an extent superceded the use of Tertiary and Quaternary although all are used in this volume. The Cenozoic is further divided into a number of epochs and the two most recent,

Myr	Era	Sub-era	Period	Epoch	
0,01	CENOZOIC	QUATERNARY	(Pleistogene)	HOLOCENE	Present interglacial
1				PLEISTOCENE	Last glacial maximum 18 000 years ago Glacial - Interglacial cycles with periodicity of about 100 000 years and warm interglacials lasting only 10 000 years
2 3 4 5		TERTIARY	Neogene	PLIOCENE	INCEPTION OF MEDITERRANEAN TYPE CLIMATES Continental glaciation in the northern hemisphere
6 7 8 9 10 20				MIOCENE	Marked expansion of Antarctic ice sheets Mid Miocene growth of Antarctic ice sheet Early Miocene relatively warm
30			Paleogene	OLIGOCENE	Initiation of circum - Antarctic deep-water circulation Marked cooling and start of cold bottom water oceanic circulation
40 50				EOCENE	Warm humid climates, ice-free globe
60 65				PALEOCENE	Separation of Australia and Antarctica

Table 3. The chronostratigraphy of the Cenozoic Era.

the Pleistocene and Holocene, which together comprise the Quaternary sub-era, are included in the Neogene rather than in a separate Pleistogene Period. The base of the Quaternary, the Pliocene-Pleistocene boundary, is variously defined as dating to 1,61, 1,8 and 2,0 Myr (Harland et al. 1982). The division of the Pleistocene followed here is lower Pleistocene, 2,0 (1,61) - 0,7 Myr; middle Pleistocene, 0,7 - 0,125 Myr; and late Pleistocene, 125 000 - 10 000 B.P. (years Before the Present). The Holocene represents the last 10 000 years (Table 3).

CENOZOIC CLIMATES

The Cenozoic Era is noteworthy not only as the time period important in the evolution of the mammals and the progressive modernization of the floras, but also for significant climatic trends. Palaeontological and oxygen isotope studies of deep sea sediments have provided a framework of global climatic changes that have taken place during the Cenozoic and have allowed the mapping of changes in ocean water masses and the estimation of past surface and bottom water temperatures for different latitudes. Temperatures show a stepped decline from the Paleocene through the Cenozoic (Shackleton & Kennett 1975), a gradual deterioration that contrasts with the uniformly mild climates of the preceding Mesozoic.

The temperatures of the earlier epochs of the Cenozoic, the Paleocene and Eocene (65 - 38 Myr), under conditions of an essentially ice-free globe, were only marginally higher than the present in the equatorial regions but were significantly higher than the present in the higher latitudes (Wilson & Hendy 1971). Wind strengths were lower as a consequence of a lower temperature gradient from equator to pole and the belt of the westerlies, a dominant element of atmospheric circulation, has been suggested to have been located at 60 - 80 degrees south in the southern hemisphere (Lamb 1972:119) and to the south of the then palaeolatitude of the Cape. Although a major feature of the Cenozoic record has been the equatorwards movement of the westerlies with important consequences for the contraction of the subtropical ocean gyre systems and reduced efficiency of meridional heat transfer (Frakes & Kemp 1973; Frakes 1979:197), the Cape did not lie within the belt of the westerlies at any stage during the Cenozoic. The palaeolatitude of the Cape at the time of the separation of Africa and South America has been given as 50 - 55 degrees south (McLachlan & McMillan 1979:168) and as 10 degrees south of the present position at the beginning of the Cenozoic (Axelrod & Raven 1978). The northward movement of the African plate was largely completed by the beginning of the Miocene. Warm and humid climates can be suggested for the latitude of the Cape in the early part of the Cenozoic and the imprint of these climates is to be seen in the deep chemical weathering, to depths of 50 m in places, of rocks in the fynbos region (Lambrechts, this volume).

In the isotope record, an abrupt cooling of the order of 5 degrees C in both surface and bottom waters is reported from the earliest Oligocene (38 Myr) in the low (Savin et al. 1975) and high latitudes (Shackleton & Kennett 1975) which Kennett & Shackleton (1976) relate to the onset of Antarctic bottom water formation. By the early Oligocene, the opening of the Atlantic had progressed to a point where the South Atlantic was open to Antarctic bottom waters (Sclater et al. 1977) and a cold current may have existed along the western Cape coast (Van Zinderen Bakker 1975) although not in its present form. A major global regression during the Oligocene, that on the evidence of the stable coast of Western Australia (Quilty 1977) represented a lowering of sea level of the order of 200 m, would have effectively exposed much of the continental shelf off the Cape (Siesser & Dingle 1981) and contributed to environmental change (Deacon 1983a; Hendey, this volume).

The early Miocene in the sub-Antarctic oxygen isotope record shows a recovery of temperatures which approached those of the later Eocene (Shackleton & Kennett 1975). This was followed by a major change in climates with the transition from what was in relative terms an unglaciated globe to one with a permanent south polar ice cap in the Miocene, between 16,5 and 13 Myr (Woodruff et al. 1981) with the West Antarctic ice sheet forming sometime after 9 Myr. There is clearer evidence of the existence of a proto-Benguela cold water current and upwelling system along the west coast (Siesser 1978, 1980) from this time (12 Myr), although it was only from the Plio-Pleistocene (circa 3 Myr) that the scale of upwelling reached modern proportions. The existence of a persistent upwelling system is evidence for the development of a trade wind and anticyclone circulation (Diester-Haas & Schrader 1979) and the intensification of this system along the western coast in the Plio-Pleistocene indicates a more fixed position of a stable South Atlantic high pressure cell. This upwelling system is reflecting global changes that came about with the closing of the mid-American sea way (Kennett 1978) and the restoration of the symmetry of zonal climates through the development of permanent sea ice in the Arctic (Flohn 1978). It was the equatorward movement of the westerlies accompanying the growth of polar ice caps in the Miocene and Pliocene that focused atmospheric subsidence in the present belt of sub-tropical high pressure cells. This is the fundamental cause of mid-latitude aridity and mediterranean-type climates bordering the arid belt. Thus although the season of precipitation is difficult to determine directly from land-based observation (Hendey, this volume) an approximate later Pliocene age can be given to the inception of summer-dry climates in the fynbos region. This would correspond to the dating of the equivalent event in the western Mediterranean (Michaux et al. 1979) at some time prior to 2,6 Myr. The modern climatic patterns of the fynbos region are thus a culmination of a trend through the Cenozoic towards lower temperatures and cooler oceans, and thus reduced evaporation and generally drier conditions.

A feature of the modern global climatic regimes initiated in the Pliocene and continuing through the Pleistocene has been the characteristic rhythm with a periodicity of about 100 000 years (linked to perturbations of the orbit of the earth relative to the sun [Hays et al. 1976]), of cooler climates (glacials) interrupted by short periods of warmer climates (interglacials). Appreciation of this periodicity has come from the study of continental loess deposits and deep sea sediments (Kukla 1977) and its most noteworthy effect on a global scale has been the alternate advance and retreat of northern hemisphere continental glaciers. The mountains of the Cape Fold Belt are not high enough to have been glaciated during the colder intervals although the scale of depression of mean annual temperature in the fynbos region was of the order of 5 degrees C less than the present day mean (Heaton 1981; Vogel 1983). This scale of temperature change between warmer intervals like the present Holocene and cool to cold intervals, however, has been significant and the response of large and small mammal populations and vegetation communities to this climatic forcing is a recurrent theme in this publication.

The best dating resolution of climatic changes is for the last 40 000 years, part of the late Pleistocene and the Holocene, for which a radiocarbon chronology is available. In the fynbos region the coldest interval of the late Pleistocene was between about 25-30 000 and 16 000 B.P. with the maximum cold and dryness, that is the most severe climatic conditions, apparently between 16 000 and 18 000 B.P. (Deacon 1983b). Prior to this interval climates were neither as cold nor as dry and there was a relatively rapid amelioration of climates after 16 000 B.P. which is consistent with the evidence from other southern continents (Salinger 1981) including Antarctica (Lorius et al. 1979). Although temperatures approximated to the present from about 12 000 B.P. and may have been slightly higher than the present in the beginning of the Holocene, lower amplitude yet significantly shorter-term climatic oscillations have continued up to the present (Tyson 1977).

CENOZOIC FOSSIL RECORD

The Cenozoic geology and palaeontology of the fynbos region are detailed in a series of papers in this volume. Marine and subaerial erosion initiated in the Cretaceous produced a remarkably bevelled coastal platform fringing the dissected mountains. Residual Cenozoic offshore deposits are thus restricted to thin veneers of older (Eocene) marine transgressions and to thicker sequences of younger (Neogene) marine, fluviatile and aeolian deposits associated with coastal embayments and river channels draining into them. Also of Cenozoic age are soils, duricrusts and colluvium capping erosion surfaces on the coastal platform and coarser scree materials, with some screes being deeply weathered and cemented and thus of high antiquity, and others relatively unweathered and subrecent (Hendey, this volume;

Lambrechts, this volume). The dating of these deposits is based primarily on the fossil content or the relationship to cycles of sea level changes. Lithological studies still have to be made of many deposits especially in the Overberg and Outeniqualand, and correlations need to be detailed on biostratigraphic grounds. There are thus some uncertainties in correlations and dating that stem from there being too few well studied fossiliferous localities and from having to rely on too few acceptable zone fossils. These uncertainties will be reduced in proportion to the future availability of exposures and drill cores for researchers to study and the degree to which the newer stratigraphic tools and dating techniques can be adapted to the solution of particular problems in the region. The dating of soils and duricrusts for example are difficult, not the least because some are the product of multiple cycles of weathering and reworking. Palaeomagnetic dating techniques are an obvious tool to use for the study of fossil duricrusts.

The age and stability of the landscape means that the physiographic character of the region has been maintained throughout the Cenozoic although transgressive and regressive seas have alternately inundated and exposed areas of the coastal platform and shelf (Hendey, this volume). Nutrient-poor substrates have been a consistent feature of the mountain zone and of parts of the coastal platform mantled by duricrusts even where underlain by argillaceous rocks. Erosion for example has reduced silcrete mesas on the coastal platform in the Overberg to small islands of acid substrates (Schloms et al., this volume). The acid sands and limestones associated with lowland fynbos, and calcareous sands associated with strandveld vegetation are Neogene, primarily Pliocene and Pleistocene to recent, in age. The coastal limestones in the Overberg are noteworthy in that they delimit a centre of neo-endemic plant species richness (Goldblatt 1978; Taylor 1978).

The trend through the Cenozoic has been towards the development of more diverse environments and more regionally distinctive plant and animal associations. The present-day character of the biota of the fynbos region is a product of this trend. For the earlier Cenozoic it is possible and indeed necessary at the present stage of research to draw on palaeontological observations from a wider area to supplement the fossil record from the region. Thus the only well studied Paleogene microflora is from Bushmanland (Scholtz in press; Coetzee et al., this volume). The presence of families like the Proteaceae, Restionaceae and Ericaceae in association with gymnosperms and taxa of present-day tropical affinities is particularly relevant. Some sclerophyllous families which are prominent in the modern vegetation have a long history on the margin of the fynbos region and might be expected to have an equally long history within the region. The Miocene vegetation record, and in particular the valuable record from Noordhoek on the Cape Peninsula (Coetzee 1978, 1980, 1981; Coetzee & Muller 1983), suggests that a diverse forest vegetation including numbers of archaic elements occupied significant areas of the fynbos region. This would seem to be supported by widely occurring disjunct forest relicts (Levyns 1962:8). The fragmentation of the Miocene forest in the Mio-Pliocene can be suggested as a consequence of progressive climatic deterioration in the later Cenozoic (Coetzee et al., this volume for discussion and references).

A complementary picture is given by the vertebrate fossil record. Early- to mid-Miocene localities in the Namib and importantly at Arrisdrift on the Orange River (Hendey 1978) suggest a fauna of woodland and forested habitats in what is now a hyperarid region. It can be assumed that under the less zonal climates of the earlier Miocene suitable habitats existed in the fynbos region for some of the same mammalian species. The richest vertebrate palaeontological locality from the fynbos region is "E" Quarry, Langebaanweg (Hendey, this volume). This early Pliocene occurrence provides a securely dated reference point against which to measure changes in environments and animal and plant communities in the south-western Cape lowlands between the Miocene and the later Plio-Pleistocene. The succession in the Varswater Formation at Langebaanweg (Hendey 1981) is also of wider significance in providing a framework for the correlation of the Neogene deposits in embayments along the Cape coast. The diverse but archaic mammalian fauna from the deposits of the lower course of the proto-Berg River in the early Pliocene suggests suitable habitats for browsers as well as grazers and relatively warm, seasonal, but not summer-dry climates are inferred from the evidence (Hendey, this volume).

In the Langebaan area, the age relationship of the Pliocene main vertebrate fossiliferous Varswater Formation to the underlying Elandsfontyn Formation, which preserves plant microfossils, has still to be conclusively established. Hendey (this volume) has noted the possibility that the Elandsfontyn Formation may belong to the same transgressive cycle as the Varswater Formation and thus also date to the Pliocene. This short chronology is in conflict with the suggested mid-Miocene age accepted for the Elandsfontyn Formation by Coetzee & Rogers (1982) in their study of the S1 borehole drilled at Langebaanweg. The microfossil horizons in the S1 borehole are altitudinally higher and thus younger than the oldest horizons sampled at Noordhoek, but again these probably represent different stages in the same transgressive cycle. The longer chronology would argue for an age of up to 10 Myr older than that suggested by the short chronology for the Elandsfontyn Formation. This is a problem for further investigation and it does have an important bearing on the time scale of change from forested to more open environments.

The record from the late Pliocene and early Pleistocene is sparse but several middle Pleistocene archaeological and palaeontological sites are known, notably the rich faunal occurrence on the farm Elandsfontein near Hopefield in the south-western Cape, the find site of an archaic hominid (Drennan 1954). It is late Pleistocene and Holocene cave sequences, excavated in the course of archaeological investigations, that have built up our present knowledge of the climate, fauna (Avery, this volume; Klein, this volume), vegetation (Coetzee *et al*., this volume; Deacon *et al*., this volume) and human adaptations (Deacon, this volume) over the period coeval with the last interglacial, glacial and present interglacial. These studies show the response of the biota to climatic forcing during the most recent cool pulse of the Ice Age in the late Pleistocene.

The analysis of the late Pleistocene large mammal faunas shows that the prey species of human hunters and carnivores during the period coeval with the cooler glacial climate included numbers of grassland forms (Klein, this volume). This is an indication that grasses, possibly temperate grasses, were more prominent in the vegetation mosaic in the intermontane valleys, on the coastal forelands and on areas of exposed continental shelf. It is these areas that would have been most affected by lowered precipitation due to cooler oceans and in particular the intermontane valleys most prone to an increased incidence of frost through temperature inversions under cooler climates.

The analysis of charcoals from a dated series of stratified hearths in the Boomplaas Cave (Deacon *et al*., this volume) gives an indication of the succession in the woody components in the vegetation of the Cango Valley over some 40 000 years. Woodland with *Olea* prominent was present in the valley prior to 42 000 B.P. but between 32 000 and a time bracketed by dates of 18 000 and 14 000 B.P., taller shrubs and trees were largely absent. During this period which includes the coldest and driest part of the late Pleistocene, woody composites were the main source of fuel. Woodland associations are again evidenced prior to 14 000 B.P. with the composition of the woodland changing and *Acacia karroo* dominant in the modern woodland in the valley only becoming prominent in the last 5 000 years. Vegetation associations in the intermontane valleys as indicated by this evidence have undergone notable change in the Pleistocene. It is obviously a priority to obtain comparable information from montane areas. It can be suggested that fynbos communities on the mountain slopes which are at intermediate elevations may have been relatively less affected by this scale of climatic change (Deacon 1983a) as they occur above the frost zone and the mountains receive relatively higher precipitation. This however does not gainsay that significant changes in the ecology of the mountain fynbos occurred between cooler and warmer periods of the late Pleistocene.

The small mammals (Avery 1982 and this volume) are sensitive indicators of habitat conditions and provide a very similar picture of environmental change in the Cango Valley to that obtained from the analysis of charcoals. The Boomplaas sequence includes abundant micromammal remains deposited by owls roosting in the cave. The owls have effectively sampled the small mammal populations of the valley over the last 80 000 years. The diversity of small mammals was low during the coldest period of the late Pleistocene and increased rapidly with the amelioration of climates and has been highest in the Holocene. Changes in diversity can be suggested as reflecting the productivity of the environment and comparable trends in diversity are evident in the charcoal and pollen microfossils (A. Scholtz, pers. comm.) from the same sequence. It would seem that cooler periods of glacial-type climate were marked by geographically more uniform communities of plants and animals of lower diversity and that at these times productivity was lower. From all these studies it is evident that it is not possible to generalize even about the late Pleistocene, because environmental oscillations were relatively rapid and conditions were more severe at some times than at others. The consequence is that the distribution and composition of some animal and plant communities were established only at the end of the Pleistocene and they are transient.

BIOGEOGRAPHY AND PALAEOECOLOGY

The fynbos region is noted as an area of endemism for primitive invertebrates (Stuckenberg 1962) and lower vertebrates (Bigalke 1979; Cody _et al_. 1983) and it has been thought that it functioned as a mesic refugium for some relict groups of Gondwana age. Most noteworthy however are the high percentage of endemic plant genera and species (to some extent a feature of southern African as a whole), and the plant species richness in the fynbos region (Goldblatt 1978). By contrast there are few endemic mammalian species and mammalian species diversity is low (Bigalke 1979).

The nucleus of the biota of southern Africa, including that of the fynbos region, has been considered to be of Gondwana origin (Van Zinderen Bakker 1976), but it is apparent that the present day temperate biotas of southern Australia and southern South America are more closely related to each other than either is to that of southern Africa (Keast 1973). So-called southern disjuncts in the present day Cape flora, for example, are restricted to relatively few elements (Levyns 1964; Goldblatt 1978). The lower vertebrate faunas (freshwater species, amphibians and reptiles) of Africa and South America however show stronger links than between any other pairing of the southern continents but these involve mainly tropical taxa (Cracraft 1975).

Historical biogeography as a study is split between divergent views on the relative importance of dispersal and vicariance as explanations for plant and animal distributions (Nelson & Rosen 1981) and the dispute is compounded by controversy between practitioners of phylogenetic and evolutionary systematics and the debate in evolutionary theory over punctuated and gradual modes of evolution (_vide_ Stoddart 1981 for a review of this topic). Data from the fynbos region has contributed little to the ongoing debates in historical biogeography possibly because the focus of discussion has been on large-scale vicariant events and the separation of Africa from the other southern continents in the latitudes of the Cape was remote in time and biological relationships are distant.

Taylor (1978) has reviewed the different schools of thought on the origins of the Cape flora. Vicariance hypotheses that assumed the Cape flora is a long isolated segment of southern angiospermous temperate flora have received little support in recent writings because of the apparent discrepancy in the timing of the break-up of the southern continents and the appearance of undoubted angiosperm fossils in the geological record. The appreciation that the presumed austral element in the Cape flora is limited and that the main affinities are with the flora of tropical Africa, has favoured a more northerly African origin of the flora and subsequent dispersal southward (Levyns 1964). This hypothesis has been elaborated by Goldblatt (1978) through the proposal of multiple migrations along upland and highland pathways in Africa and long-distance dispersal between Australasia and Eurasia to account for what are assumed to be the components from different geographical areas making up the Cape flora. In a more recent paper, Taylor (1980) has made the suggestion that central Africa may have served only as a secondary centre of dispersal for the flora that originated in austral lands. This follows from a comment by Axelrod and Raven (1978) that dispersal of taxa between Africa and Australasia across a narrower Indian Ocean may have been possible into the late Cretaceous. Their comment, however, was offered to explain a small number of disjunct distributions between Australia and Africa rather than to suggest a major dispersal route. Axelrod and Raven (1978:113) themselves have linked the origins of the Cape flora to the evolution of a richer sclerophyllous flora in south-western Africa and suggest its derivative, the Cape flora, was "largely swept" into the present fynbos region in the later Pleistocene as a result of drying climates.

Nordenstam (1969) has remarked that the tendency to particularize the Cape flora as a discrete entity, and to designate genera with their main distribution in the fynbos region as Cape elements, is hampering not helping the understanding of the phytogeography of South Africa. He concluded that it is both unnecessary and impossible to attempt to divide southern Africa into floral regions and that the concept of discrete regions was incompatible with a historical and phylogenetic approach. In view of the divergent and speculative nature of explanations for the origins of the Cape flora that have been offered in scenarios invoking dispersal, Nordenstam's study and perceptive comments are important and are in line with the vicariance paradigm in biogeography. They offer a different and perhaps more productive perspective to the study of biogeographic problems in South Africa. The flora of the fynbos region for example would be seen as made up by the coincidental distribution of a number of taxa reflecting part of the ancestral African flora fragmented by the development of more diverse environments since the Cretaceous and evolving its special features in isolation in a mesic area of high terrain diversity and particular edaphic conditions.

A further biogeographical pattern that deserves comment is the occurrence of centres of plant species richness in the fynbos region. Species richness is not uniform in space, and centres described originally by Weimarck and redefined by Dahlgren (1963), Nordenstam (1969) and others, are not simply mesic refugia but are areas favouring the multiplication of species. Such centres are well attested biogeographic features and thus are not restricted to the fynbos region. The main centre of the fynbos region, the Caledon Centre of Nordenstam (1969) has been seen as the home of the Cape flora (Taylor 1980) and is different in degree rather than in kind from other centres of species richness that can be recognized in southern Africa (Nordenstam op. cit.). Pielou (1979) has provided a valuable discussion of centres of high taxon diversity or diversity islands of which the Caledon Centre is a notable example. She suggests (1979:91) that two factors that foster species richness are, firstly, the fragmentation of parent species-populations into a number of isolated demes, and secondly, the existence of many locally distinct optimum phenotypes which she equates with adaptive peaks. Consideration of a genus like Aspalathus which contributes notably to the species richness of the Caledon Centre and shows high within-species variability (Dahlgren 1963:454) suggests these factors may indeed be important in accounting for species richness in the fynbos region. Dahlgren (op. cit.) considered that external conditions, for example climatic change, may promote the fragmentation of variable species-populations.

Kruger and Taylor (1979) have discussed plant species diversity in what is effectively the Caledon Centre and concluded that while gamma diversity (the number of species in a large landscape unit) is very high, the delta diversity (the change in floras from one area to another) is anomalously high. They ascribe these patterns in diversity to the constraints of habitat (terrain) diversity and climatic change in what is effectively an island situation. The high delta diversity is seen as indicating that geographical (non-sympatric) speciation is of primary importance in the evolution of the flora with the advent of drying climates in dissected landscapes in the Mio-Pliocene and mediterranean-type climates in the Pleistocene. On the other hand the authors suggest that climatic change has not been on such a scale as to cause extinction rates to exceed speciation rates. It is also implied that mediterranean-type climates have been of 'primary importance' in the development of the flora. The origins and evolution of species richness in centres in the fynbos biome (vide Groves et al. 1983 and Tilman et al. 1983 for recent reviews) is a topic of considerable interest. Further progress in the study of this problem will only come from a better understanding of systematics of key taxa and the study of patterns of distribution and diversity in the present and, in as far as these can be reconstructed, in the past. It will not be furthered, however, by maintaining simplistic views about the nature and effects of past climatic changes.

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REFERENCES

ANDERSON, J. M. 1977. The biostratigraphy of the Permian and Triassic. Part 3. A review of Gondwana Permian palynology with particular reference to the northern Karoo basin, South Africa. *Memoirs of the Botanical Survey of South Africa.* 41.

AVERY, D. M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quaternary in the southern Cape Province, South Africa. *Annals of the South African Museum* 85:183-374.

AXELROD, D. I. & RAVEN, P. H. 1978. Late Cretaceous and Tertiary vegetation history of Africa. *In* Werger, M. J. A. *ed*. *Biogeography and ecology of southern Africa*: 77-130. The Hague: W. Junk.

BIGALKE, R. C. 1979. Aspects of vertebrate life in fynbos, South Africa. *In* Specht, R. L. *ed*. *Ecosystems of the world. Vol. 9. Heathlands and related shrublands: descriptive studies*: 81-95. Amsterdam: Elsevier.

BISHOPP, D. W. & VAN EEDEN, O. R. 1971. Explanatory text for the tectonic map of Africa: areas co-ordinated by the southern group. *Tectonics of Africa*. Paris: UNESCO.

BOUCHER, C. & MOLL, E. J. 1981. South African mediterranean shrublands. *In* Di Castri, E., Goodall, D. W., & Specht, R. L. *eds* *Ecosystems of the world. Mediterranean-type shrublands*: 233-248. Amsterdam: Elsevier.

CODY, M. L., BREYTENBACH, G. J., FOX, B., NEWSOME, A. E., QUINN, R. D. & SIEGFRIED, W. R. 1983. Animal communities: diversity density and dynamics. *In* Day, J. A. *ed*. Mineral nutrients in mediterranean ecosystems. *South African National Scientific Programmes Report* 71:91-110.

COETZEE, J. A. 1978. Late Cenozoic palaeoenvironments of southern Africa. *In* Van Zinderen Bakker, E. M. *ed*. *Antarctic glacial history and world palaeoenvironments*: 115-127. Rotterdam: Balkema.

COETZEE, J. A. 1980. Tertiary environmental changes along the south-western African coast. *Palaeontologia Africana* 23:197-203.

COETZEE, J. A. 1981. A palynological record of very primitive angiosperms in Tertiary deposits of the south-western Cape Province, South Africa. *South*

African Journal of Science 77:341-343.

COETZEE, J. A. & MULLER, J. 1983. The phytogeographic significance of some extinct Gondwana pollen types from the Tertiary of the southwestern Cape (South Africa). Annals of the Missouri Botanical Gardens. In press.

COETZEE, J. A. & ROGERS, J. 1982. Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa). Palaeogeography Palaeoclimatology Palaeoecology 39:71-85.

CRACRAFT, J. 1975. Historical biogeography and earth history: perspectives for a future synthesis. Annals of the Missouri Botanical Gardens 62:227-250.

DAHLGREN, R. 1963. Studies on Aspalathus: phytogeographical aspects. Botaniska Notiser 116:431-472.

DEACON, H. J. 1983a. The comparative evolution of mediterranean-type ecosystems: a southern perspective. In Kruger, F. J., Mitchell, D. T. & Jarvis, J. U. M. eds Mediterranean-type ecosystems. The role of nutrients: 3-40. Berlin: Springer-Verlag.

DEACON, H. J. 1983b. Another look at the Pleistocene climates of South Africa. South African Journal of Science 79:325-328.

DIESTER-HAAS, L. & SCHRADER, H. J. 1979. Neogene coastal upwelling history off northwest and southwest Africa. Marine Geology 29:39-53.

DRENNAN, M. R. 1954. Saldanha man and his associations. American Anthropologist 56:879-884.

ELDREDGE, N. & GOULD, S. J. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In Schopf, T. J. M. ed. Models in Paleobiology: 82-115. San Francisco- Freeman.

FLOHN, H. 1978. Comparison of Antarctic and Arctic climate and its relevances to climatic evolution. In Van Zinderen Bakker, E. M. ed. Antarctic glacial history and world palaeoenvironments: 3-23. Rotterdam: Balkema.

FRAKES, L. A. 1979. Climates through geologic time. Amsterdam: Elsevier.

FRAKES, L. A. & KEMP, E. M. 1973. Paleogene continental positions and evolution of climate. In Tarling, D. G. & Runcorn, S. K. eds Implications of continental drift to the earth sciences. London: Academic Press.

GOLDBLATT, P. 1978. An analysis of the flora of southern Africa: its characteristics, relationship and origins. Annals of the Missouri Botanical Gardens 65:369-436.

GOOD, R. 1974. The geography of the flowering plants. London: Longmans.

GROVES, R. H., BEARD, J. S., DEACON, H. J., LAMBRECHTS, J. J. N., RABINOVITCH-VIN, A., SPECHT, R. L. & STOCK, W. D. 1983. Introduction: the origins and characteristics of mediterranean ecosystems. In Day, J. A. ed. Mineral nutrients in mediterranean ecosystems. South African National Scientific Programmes Report 71:1-17.

HALBICH, I. W., FITCH, F. J. & MILLER, J. A. 1983. Dating the Cape orogeny.

Geological Society of South Africa Special Publication 12:149-164.

HARLAND, W. B., COX, A. V., LLEWELLYN, P. G., PICKTON, C. A. G., SMITH, A. G. & WALTERS, R. 1982. *A geologic time scale*. Cambridge: Cambridge University Press.

HAYS, J. D., IMBRIE, J. & SHACKLETON, N. J. 1976. Variations in the earth's orbit: pacemaker of the ice ages. *Science* 194:1121-1132.

HEATON, T. H. E. 1981. Dissolved gases: some applications to groundwater research. *Transactions of the Geological Society of South Africa* 84:91-97.

HENDEY, Q. B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Annals of the South African Museum* 76:1-41.

HENDEY, Q. B. 1981. Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa and a re-interpretation of their geological context. *Annals of the South African Museum* 84:1-104.

KEAST, A. 1973. Contemporary biotas and the separation sequence of the southern continents. *In* Tarling, D. H. & Runcorn, S. K. *eds* *Implications of continental drift to the Earth Sciences*: 309-343. New York: Academic Press.

KENNETT, J. P. 1978. The development of planktonic biogeography in the southern ocean during the Cenozoic. *Marine Micropalaeontology* 3:301-345.

KENNETT, J. P. & SHACKLETON, N. J. 1976. Oxygen isotopic evidence for the development of the psychrosphere 38 m.y. ago. *Nature* 260:513-515.

KRUGER, F. J. & TALYOR, H. C. 1979. Plant species diversity in Cape fynbos: gamma and delta diversity. *Vegetatio* 41:85-93.

KUKLA, G. J. 1977. Pleistocene land-sea correlations. 1: Europe. *Earth Science Reviews* 13:307-374.

LAMB, H. H. 1972. *Climate: present, past and future. I*. London: Methuen.

LAMBRECHTS, J. J. N. 1979. Geology, geomorphology and soils. *In* Day, J., Siegfried, W. R., Louw, G. N. & Jarman, M. L. *eds* Fynbos ecology: a preliminary synthesis. *South African National Scientific Programmes Report* 40:16-26.

LEVYNS, M. R. 1962. Past plant migrations in South Africa. *Annals of the Cape Provincial Museums* 2:7-10.

LEVYNS, M. R. 1964. Migrations and origin of the Cape flora. *Transactions of the Royal Society of South Africa* 37:85-107.

LIVINGSTONE, D. A. 1975. Late Quaternary climatic change in Africa. *Annual Review of Ecology and Systematics* 6:249-280.

LORIUS, C., MERLIVAT, L., JOUZEL, J. & POURCHET, M. 1979. A 30 000-yr isotope climate record from Antarctic ice. *Nature* 180:644-648.

McLACHLAN, I. R. & McMILLAN, I. K. 1979. Microfaunal biostratigraphy, chronostratigraphy and history of Mesozoic and Cenozoic deposits on the coastal margin of South Africa. *Geokongres 77: Geological Society of South Africa Special Publication* 6:161-181.

McLACHLAN, I. R. & PIETERSE, E. 1978. Preliminary palynological results: site 361, leg 40. Deep Sea Drilling Project. *Initial Reports of the Deep Sea Drilling Project* 4:857-881.

MICHAUX, J., SUE, J. P. & VERNET, J. L. 1979. Climatic inferences from the history of the Taxodiaceae during the Pliocene and early Pleistocene in western Europe. *Review of Palaeobotany and Palynology* 27:185-191.

NELSON, G. & ROSEN, D. E. 1981. *Vicariance biogeography: a critique*. New York: Columbia University Press.

NORDENSTAM, B. 1969. Phytogeography of the genus *Euryops* (Compositae). *Opera Botanica* 23:1-77.

PIELOU, E. C. 1979. *Biogeography*. New York: John Wiley.

QUILTY, P. C. 1977. Cenozoic sedimentation cycles in Western Australia. *Geology* 5:336-340.

SACS, SOUTH AFRICAN COMMITTEE FOR STRATIGRAPHY. 1980. Stratigraphy of South Africa, Part 1. Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophuthatswana, Transkei and Venda. *Geological Survey of South Africa Handbook* 8. Pretoria: Government Printer.

SALINGER, M. J. 1981. Palaeoclimates north and south. *Nature* 291:106-107.

SAVIN, S. M., DOUGLAS, R. G. & STEHLI, F. G. 1975. Tertiary marine palaeotemperatures. *Geological Society of America Bulletin* 86:1499-1510.

SCHOLTZ, A. in press. The palynology of the upper lacustrine sediments of the Arnot pipe, Banke, Namaqualand. *Annals of the South African Museum*.

SCLATER, J. C., HELLINGER, S. & TAPSCOTT, C. 1977. The palaeobathymetry of the Atlantic ocean from the Jurassic to the present. *Journal of Geology* 85:509-552.

SCOTT, L. 1976. Preliminary palynological results from the Alexandersfontein Basin near Kimberley. *Annals of the South African Museum* 71:173-189.

SHACKLETON, N. J. & KENNETT, J. P. 1975. Palaeotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analyses in DSDP sites 277, 279 and 281. *Initial Reports of the Deep Sea Drilling Project* 29:743-755.

SIESSER, W. G. 1978. Aridification of the Namib Desert: evidence from oceanic cores. *In* Van Zinderen Bakker, E. M. *ed*. *Antarctic glacial history and world palaeoenvironments*: 105-113. Rotterdam: Balkema

SIESSER, W. G. 1980. Late Miocene origin of the Benguela upwelling system off northern Namibia. *Science* 208:283-285.

SIESSER, W. G. & DINGLE, R. V. 1981. Tertiary sea-level movements around southern Africa. *Journal of Geology* 89:89-96.

SIESSER, W. G., SCRUTTON, R. A. & SIMPSON, E. S. W. 1974. Atlantic and Indian Ocean margins of southern Africa. *In* Burk, C. A. & Drake, C. L. *eds* *The geology of continental margins*: 641-654. New York: Springer-Verlag.

SOHNGE, A. P. C. 1983. The Cape Fold Belt - perspective. *Geological Society* of South Africa Special Publication 12:1-6.

STODDART, D. R. 1981. Biogeography: dispersal and drift. Progress in Physical Geography 5:575-590.

STUCKENBERG, B. R. 1962. The distribution of the montane palaeogenic elements in the South African fauna. Annals of the Cape Provincial Museums 2:190-205.

TAKHTAJAN, A. 1969. Flowering plants, origin and dispersal. Washington D.C.: Smithsonian Institution Press.

TANKARD, A. J., JACKSON, M. P. A., ERIKSSON, K. A., HOBDAY, D. K., HUNTER, D. R. & MINTER, W. E. L. 1982. Crustal evolution of southern Africa: 3.8 billion years of earth history. New York: Springer-Verlag.

TAYLOR, H. C. 1978. Capensis. In Werger, M. J. A. ed. Biogeography and ecology of southern Africa: 171-230. The Hague: W. Junk.

TAYLOR, H. C. 1980. Phytogeography of fyngos. Bothalia 13:231-235.

THODAY, D. 1925. The geographical distribution and ecology of Passerina. Annals of Botany 39:175-208.

TILMAN, D., BOND, W. J., CAMPBELL, B. M., KRUGER, F. J., LINDER, H. P., SCHOLTZ, A., TAYLOR, H. C. & WITTER, M. 1983. Origin and maintenance of plant species diversity. In Day, J. ed. Mineral nutrients in mediterranean ecosystems. South African National Scientific Programmes Report 71:125-135.

TYSON, P. D. 1977. The enigma of changing world climates. South African Geographical Journal 59:77-116.

VAN ZINDEREN BAKKER, E. M. 1975. The origin and palaeoenvironment of the Namib desert biome. Journal of Biogeography 2:65-74.

VAN ZINDEREN BAKKER, E. M. 1976. The evolution of late Quaternary palaeoclimates of southern Africa. Palaeoecology of Africa 9:160-202.

VOGEL, J. C. 1983. Isotopic evidence for past climates and vegetation of South Africa. Bothalia in press.

WELLINGTON, J. H. 1955. South Africa, a geographical study. London: Cambridge University Press.

WILSON, A. T. & HENDY, C. H. 1971. Past wind strengths from isotope studies. Nature 234:344-345.

WOODRUFF, F., SAVIN, S. M. & DOUGLAS, R. G. 1981. Miocene stable isotope record: a detailed deep Pacific Ocean study and its paleoclimatic implications. Science 212:665-668.

GEOLOGICAL SETTING OF THE FYNBOS

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PRE-CAPE SUCCESSION

The final phases of the Namaqua tectonic cycle at about 950 Myr probably initiated sedimentation of the Malmesbury and Kango Groups and related pre-Cape successions in the south-western and southern Cape. Weathering of the varied granitoid basement supplied the terrigenous clastics to the adjacent Malmesburg/Kango Geosyncline. The sedimentary sequence is comprised of a wide variety of argillites, limestones and greywackes as well as more arenitic and conglomeratic entities. The Malmesbury succession is characterized by a larger percentage of argillaceous rocks than the Kango Group. The lithostratigraphic subdivisions of the Malmesbury, Kango, Gamtoos and Kaaimans Groups are given in Tables 1 and 2. Neither the base nor the top of the Groups are exposed and the total thickness of the entities is therefore unknown.

The Malmesbury Group represents a predominantly marine sedimentary assemblage with rocks giving clear evidence of turbidite sedimentation in the west (Tygerberg Formation) and marine shelf and possibly alluvial environments towards the east (Porterville, Piketberg and Brandwacht Formations). The field relationships and petrography indicate a deltaic complex encroaching onto the continental platform from the north (Hartnady *et al*. 1974; Beeson 1976).

A general miogeosynclinal sedimentary cycle is envisaged for the easterly Kango, Gamtoos and Kaaimans Groups (Gresse 1976; Stump 1976; Le Roux 1977). The Kango and Gamtoos Groups accumulated in an elongate plunging trough open to the ocean towards the south-east. The rocks indicate a granitoid/gneiss provenance to the west and deposition in an environmental setting varying from shallow shelf to tidal flat and supratidal (Matjies River Formation), to turbiditic flysch (Groenefontein and Huisrivier Formations), to braided alluvial-fan and alluvial-plain (Vaartwell, Uitvlugt and overlying Formations). The Gamtoos entities represent the genetically related distal shallow shelf, fluvial and fan-delta 'tapering wedges' (Stocken 1954; Stump 1976). The argillaceous Kaaimans sediments on the other hand closely resemble the westerly Malmesbury turbidites with the more arenitic entities reflecting shallowing and emergence. It seems plausible that the Kaaimans Group belongs to the same depositional cycle as the Kango and Gamtoos entities, representing the distal basin-ward sediments.

Table 1

STRATIGRAPHY OF THE MALMESBURY GROUP

South-western Tectonic Domain	Central Tectonic Domain	North-western Tectonic Domain
Tygerberg Formation	Mooreesburg Formation	Brandwacht Formation
	Porseleinberg Formation	Porterville Formation
	Klipplaat Formation	Piketberg Formation
	Berg River Formation	

During the late Precambrian Saldanian orogenic episode these rocks were deformed and metamorphosed. The Malmesbury succession displays tight upright folding along a north-west-trending axis with major differences in style and history of deformation between three tectonic domains. These domains are separated by two extensive linear zones of shearing and faulting. Late-syntectonic emplacement of the Cape granitoids is revealed owing to the shear zones transecting some of these intrusions. Regional metamorphic grade varies from nonmetamorphosed rocks that display only diagenesis, to rocks with a very low grade owing to burial metamorphism, to rocks metamorphosed to greenschist facies. The Kango and Gamtoos Groups are characterized by multiple phases of deformation, some even concomitant with deposition as evidenced by the hiatus between the Huisrivier and Vaartwell Formations. This deformation has resulted in local overturning of the strata and thrusts north and north-eastwards along tectonic slides. Deformation intensity attains greenschist facies. The successions in the Kango and in the Gamtoos Valley area are not intruded by granite. In contrast the Kaaimans Group was metamorphosed to lower amphibolite facies (sometimes, however, locally to upper amphibolite facies) during syntectonic granite intrusion. At least two periods of deformation can be recognized, firstly resulting in southward dipping schistosity and downdip lineation, followed by refoliation of the early syntectonic granitoids by crenulation cleavage or fracture cleavage and rotation of earlier folds to north-south trends (Krynauw & Gresse 1980).

Table 2

STRATIGRAPHY OF THE PRE-CAPE SUCCESSIONS IN THE SOUTHERN CAPE PROVINCE

Kango Group	Gamtoos Group	Kaaimans Group
Gezwinds Kraal Formation		Homtini Formation
Uitvlugt Formation	Arkosic sandstone with mudstone and limestone interbeds	Victoria Bay Formation
Vaartwell Formation		
	Limestone	Soetkraan Formation
Huisrivier Formation		
Groenefontein Formation	Phyllite and shale unit with coarse-grained thinly bedded arkose sandstone	Skaapkop Formation
		Sandkraal Formation
Matjies River	Dolomitic Limestone	Saasveld Formation
	Lower phyllite	Silver River Formation

Field evidence and radiometric dates clearly prove Saldanian deformation both before and after intrusion of the Cape Granite Suite. The latter orogenic episode on available isotopic evidence, ranged from about 610 Myr to about 500 Myr. The eastern multiphase granite batholith at George is characterized by east-west elongation and its gneissic nature clearly reflects extensive tectonic influence. The south-western granites display a north-westerly elongation and varying amounts of deformation. Two groups are recognized. The older generally coarse-grained megacrystic biotite to hornblende-biotite granite is partly foliated and characterized by magmatic differentiation and contamination from country rocks. The younger leucogranites, constituting less than 10% of the suite, evidently cooled rapidly at a high crustal level and show finer textures and relatively little contamination or differentiation.

Post-tectonic rise of the Gariep/Saldanian Province accompanied by intermittent reactivation of the major shear zones in the south-west yielded a complex intertonguing of red-brown conglomerates, feldspathic sandstones and shales. These typical terrestrial sediments of the Klipheuwel Formation contain intrabasinal clasts of both Malmesbury and granite origin and the entity forms a northward thinning wedge. It represents the culminating phase of the Saldanian orogenesis and was deposited as a series of coalescing and stacked alluvial-fan and interlobe deposits of southward-flowing braided fluvial systems (Visser 1967; Rust 1973; Vos & Tankard 1981). The oldest Klipheuwel beds have been affected by folding, thrusting and faulting, but the sequence becomes progressively less deformed northwards and upwards. In the east accumulation of similar molasse alluvial fans took place (Schoemans Poort Formation). All these molasse-type deposits unconformably overlie deformed Malmesbury and Kango metasediments and Cape granites.

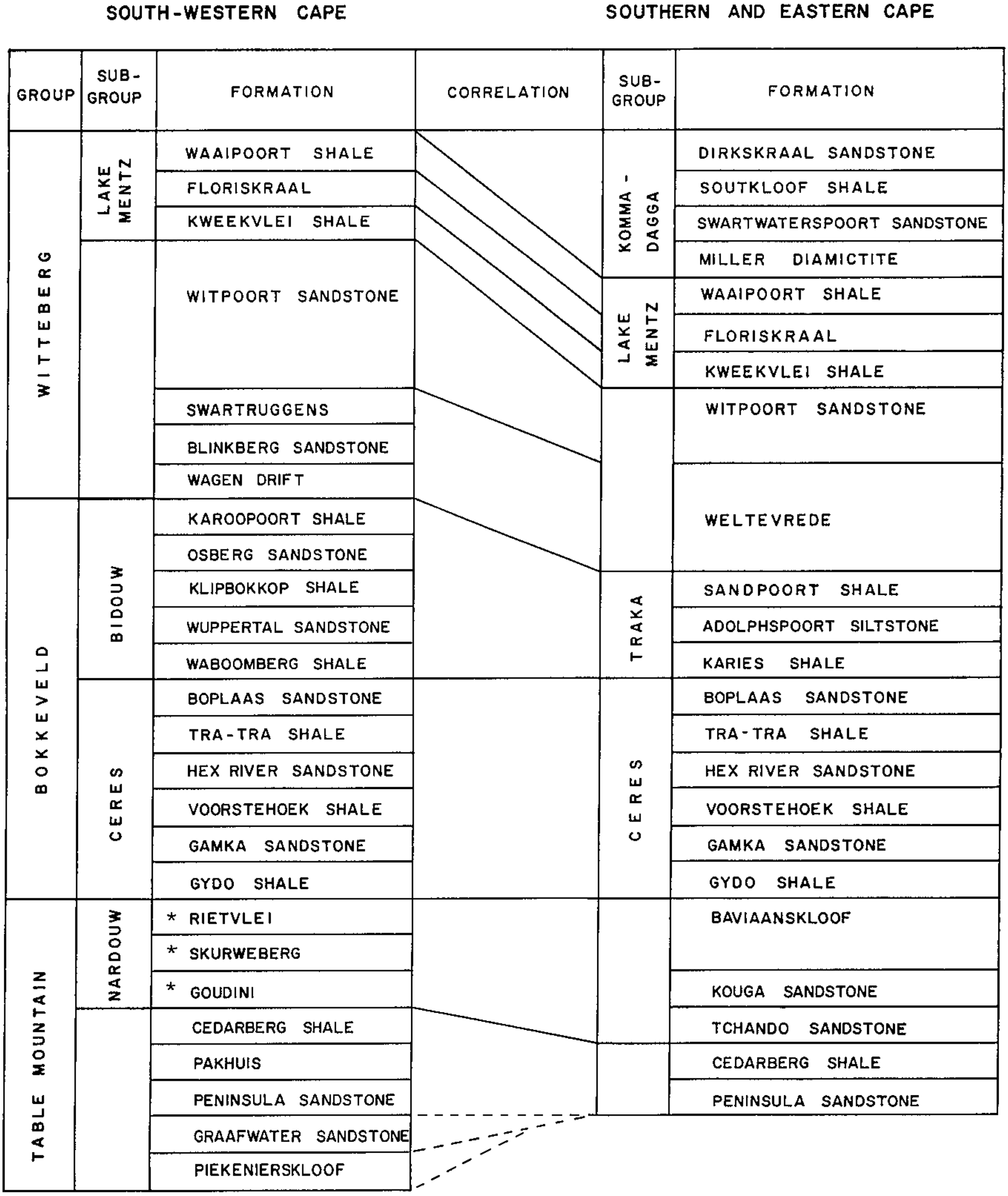
CAPE SUPERGROUP

At cessation of the Klipheuwel sedimentation (500 Myr) an extensive, fairly featureless peneplain covered most of the south-western Cape. Low rolling hills only bordered the braided alluvial coastal plain in the Piketberg/Worcester area.

Table Mountain Group.

Subsidence of the basement with a dominant southerly palaeoslope now paralleled the present coastline. A major fan-delta complex delivered sediment to a north-west-trending shallow embayment (basin) in the west. The supermature arenite and conglomerate beds of the Piekenier Formation suggests interplay of a braided alluvial complex with an energetic beach-type setting towards the south-east where the basin evidently opened to the sea. Reasonably energetic uplift of the western highlands delivered debris up to boulder size which was then redistributed through multiple channel-fill sequences. Downstream reduction of sediment size to sand in the overloaded streams resulted in a fan-delta being built into the shallow sea.

Less marked relief along the northern and western basinal margin (due to less active tectonic movement or as a result of the preceding extensive planation the area suffered), allowed northward marine encroachment and deposition of the overlying maroon-red mudstones, siltstones and medium-grained sandstones of the Graafwater Formation. Trace fossils as well as omnipresent primary structures indicative of subaerial exposure and red colouration, attest to a sheltered tidal flat and estuarine environment. Episodic subsidence of the basin allowed extensive multiple rapid northward transgressions of the shallow sea alternating with substantial fluvial



SOUTH-WESTERN CAPE

GROUP	SUB-GROUP	FORMATION
WITTEBERG	LAKE MENTZ	WAAIPOORT SHALE
		FLORISKRAAL
		KWEEKVLEI SHALE
		WITPOORT SANDSTONE
		SWARTRUGGENS
		BLINKBERG SANDSTONE
		WAGEN DRIFT
BOKKEVELD	BIDOUW	KAROOPOORT SHALE
		OSBERG SANDSTONE
		KLIPBOKKOP SHALE
		WUPPERTAL SANDSTONE
		WABOOMBERG SHALE
	CERES	BOPLAAS SANDSTONE
		TRA-TRA SHALE
		HEX RIVER SANDSTONE
		VOORSTEHOEK SHALE
		GAMKA SANDSTONE
		GYDO SHALE
TABLE MOUNTAIN	NARDOUW	* RIETVLEI
		* SKURWEBERG
		* GOUDINI
		CEDARBERG SHALE
		PAKHUIS
		PENINSULA SANDSTONE
		GRAAFWATER SANDSTONE
		PIEKENIERSKLOOF

SOUTHERN AND EASTERN CAPE

SUB-GROUP	FORMATION
KOMMA - DAGGA	DIRKSKRAAL SANDSTONE
	SOUTKLOOF SHALE
	SWARTWATERSPOORT SANDSTONE
	MILLER DIAMICTITE
LAKE MENTZ	WAAIPOORT SHALE
	FLORISKRAAL
	KWEEKVLEI SHALE
	WITPOORT SANDSTONE
	WELTEVREDE
TRAKA	SANDPOORT SHALE
	ADOLPHSPOORT SILTSTONE
	KARIES SHALE
CERES	BOPLAAS SANDSTONE
	TRA-TRA SHALE
	HEX RIVER SANDSTONE
	VOORSTEHOEK SHALE
	GAMKA SANDSTONE
	GYDO SHALE
	BAVIAANSKLOOF
	KOUGA SANDSTONE
	TCHANDO SANDSTONE
	CEDARBERG SHALE
	PENINSULA SANDSTONE

Table 3. Lithostratigraphy of the Cape Supergroup. (* formation names still to be approved by S.A.C.S.)

sediment influx. This estuarine tidal environment was bordered to the south by a barrier complex forming the major shoreline (basal Peninsula Formation).

Slow but steady subsidence of the shelf resulted in northward transgression of a thick quartz arenite complex (Peninsula Formation) across the estuarine/tidal flats. A barrier-beach to shallow-shelf facies is indicated by the lithologically uniform medium- to coarse-grained sandstone with scattered quartz pebble washes. The great thickness (greater than 3 000 m), areal extent, maturity and medium- to large-scale cross-stratigraphic sets (generally 0,10 to 1,20 m thick) furthermore indicate predominantly high-energy current and storm winnowing processes (Rust 1967; Visser 1974). A regressive cycle terminated the Peninsula sedimentation and evidence of backbarrier sand shoal, barrier washover and tidal inlet environments are indicated (Hobday & Tankard 1978).

At this time a world-wide glacio-eustatic fall in sea level occurred, with the Cape basin bordering an extensive Gondwana ice sheet centered in central Africa. At least two major advances of the ice sheet separated by erosion and reworking of the tillites have been registered. A general southward palaeoslope is reflected and the basal massive pebbly arenitic diamictite (Pakhuis Formation) is associated with soft-sediment deformation of the underlying Peninsula Formation. Clasts are often polished, striated and faceted and consist of a wide variety of rock types. Subglacial deposition is envisaged, followed by proglacial reworking in part by marine processes. Renewed advance of the ice sheet was accompanied by extensive erosion and deposition of varicoloured tillites with erratics varying from pebbles to boulder-sized clasts displaying all the typical glacial structures. North of the basin margin extensive glacial striation characterizes the unconformity and thin dropstone varvites occur locally. This tillite attains a maximum thickness of about 120 m but thins rapidly basin-wards. A similar subglacial sedimentary setting is evidenced with varved shale sequences reflecting glaciolacustrine deposition in marginal proglacial environments. Gradual withdrawal of the ice sheet northwards on amelioration of climate was accompanied by glacio-eustatic rise of sea level and mainly clay was delivered to the basin. A 40 m thick laterally persistent sequence of thinly laminated shale with sporadic dropstone layers, some varvites and rare lenses of quartz arenite accumulated. In the western Cape then followed up to 100 m of mudstones and fine-grained sandstones which contain Lower Silurian invertebrate remains (Cedarberg Formation). The widespread distribution of these argillaceous proglacial and shallow marine deposits is ascribed to the isostatic depression of the basin (Table 3).

Rising sea level increased tidal circulation and current action. Deposition of coarser clastics now recurred and the Nardouw Subgroup reflects a return to the sedimentary setting prior to glaciation. The basin edge of this period had extended considerably further northward than in Peninsula time, either due to isostatic depression or perhaps increased rate of subsidence. The Goudini Formation consisting of 30-75 m of fine-grained sandstone beds alternating with purple siltstones, constitutes the basal zone and reflects increased current and tidal action. The overlying Skurweberg Formation, dominated by thicker bedded medium- to coarse-grained quartz arenites with ubiquitous pebble lag deposits and large-scale crossbedding, again reflect deposition in shallow-shelf and shore-zone environments. A gradual decrease of current activity caused deposition of thinner bedded sandstones, quartz arenites and mudstones in a shallower near shore environment (Rietvlei and Baviaanskloof Formations).

Bokkeveld Group

Bioturbation and extensive invertebrate-rich zones date these beds at about 380 Myr. The relatively stable steady downwarp of the basin and extensive reworking of the sediments as reflected in the Table Mountain Group, now became more erratic and the pulsatory nature and tectonic unrest of the basin are clearly reflected by the alternating arenitic and argillaceous entities of the Bokkeveld Group. The rate of subsidence in the eastern Cape was about double that towards the west and resulted in accumulation of about 3 200 m of sediment in the east. The four to five upward-coarsening clastic wedges which interpose southwards into a homogeneous mudstone-subgreywacke body, represent successive major progradations of lobate deltas onto the shallow shelf, affected by marine trans- and regressions. Large volumes of sediment were delivered to the coast by various rivers from actively rising provenance areas to the north and west of the basin. Initially the subsidence and sedimentary cycles of the western and eastern basins were reasonably in phase (Ceres Subgroup) and the various formations extend throughout the outcrop area. This did not however apply during deposition of the upper part of the Bokkeveld Group. In the western Cape the Bidouw Subgroup closely simulates the underlying Ceres Subgroup but this does not apply at all to the Traka Subgroup in the eastern Cape. Southwards the clastic wedges taper into prodelta slope and shelf deposits and northwards (especially in the west) are indicative of barrier washover sheet sand, backbarrier sand flat and tidal flat facies (Theron 1970; Tankard & Barwis 1982).

Early Devonian marine life teemed in the shallow epeiric sea as reflected by the abundant fossiliferous remains and feeding trails and tracks of infaunal bivalves, epifaunal brachiopods, some bryozoa, coral, crinozoa and placoderm fish. The earliest terrestrial plants had gradually evolved but as yet mainly bordered the many delta mouths and near-shore environment.

Witteberg Group

The imbalance in tectonic movement of the western and eastern depositories became more pronounced with the advent of the Witteberg sedimentary cycle.

Lithofacies in the west indicate a partial return to the sedimentary pattern of Table Mountain times, i.e. more extensive reworking of sediments and accumulation of thick mature arenitic beds (Blinkberg, Wittepoort and Swartruggens Formations). These barrier- and shelf-sands clearly indicate a decreased rate of subsidence here from Bokkeveld times, allowing more extensive marine reworking of the deltaic deposits. The same did not however apply in the east, where the numerous thin clastic wedges in a predominantly muddy succession indicate a complex history of numerous rapidly alternating regressions and transgressions. Marked shallowing is however apparent throughout the basin and bioturbation and plant fragments prove more common than invertebrate remains.

The first indications of a southerly border to the Cape basin as reflected during deposition of the Bidouw/Traka entities and reduction of the basinal dimensions, became more apparent during deposition of the extensive quartz arenites (850 m) composing the Wittepoort Formation and even more so in succeeding Lake Mentz and Kommadagga Subgroups. Transgressive reworking of the various delta lobes throughout the basin (Wittepoort Formation) indicate a reduced downwarp, extensive winnowing and the final Cape-Karoo basinal transition. The black fissile shale sequence of the Kweekvlei Formation probably represents shelf deposits of the final fluvial-barrier cycle (Floriskraal Formation) of the Cape Supergroup, prior to the advent of the first glaciogene sediments. It probably reflects a final overall spasmodic downwarp of the now narrow linear Cape basin. At this period with the approach of the Carboniferous palaeomagnetic South pole, valley glaciers had probably already been developing on the adjoining highlands to the north, west and south of the depo-centre and the first glaciogene sediments are reflected in the lacustrine and fluvial deposits of the Kommadagga Subgroup. Partial erosion of the tectonically active borders of the basin at this stage even involved Cape Supergroup sediments. Dropstones and englacial deformation (Bell 1981) furthermore reflect coalescence of the glaciers and overall growth of the ice mass during final Witteberg deposition.

KAROO SEQUENCE

As climate deteriorated with approach of the spreading centre an ice sheet engulfed the entire continent. Flow of the ice sheet was initially largely controlled by basement topography with major deposition therefore within the former Cape basin. Waxing and waning of the ice sheet caused numerous intermittent advances and retreats of the ice which is reflected in alternation of massive diamictite and stratified glacial outwash (Dwyka Formation) as well as numerous intra-formational striated pavements (Theron & Blignault 1975; Visser 1981). Both a floating and grounded ice shelf environment existed with water depth sufficient to accommodate floating ice shelves but grounding of advancing ice sheets. The inherited major depoaxis gradually moved northwards and a maximum thickness of glacials in excess of 1 000 m accumulated.

Ecca Group

The earlier uplift to the south in the distal portion of the Cape basin now intensified and a major reversal of the palaeoslope developed (280 Myr). The simultaneous gradual amelioration of climate as the area drifted out of polar latitudes resulted in deglaciation, abundant meltwater and deposition of transitional glaciolacustrine mud and silt beds (Prince Albert, Whitehill Formations) in a broad shallow epicontinental basin. Increased tectonic activity is reflected to the south by interspersed yellow tuff layers in the succeeding clastic deposits of the Ecca Group. Continued downwarping of the Karoo trough allowed accumulation of about 3 000 m of sediment in the west and almost 2 000 m towards the east. The basin rapidly deepened and interlayered muds and sands accumulated, which indicate the activity of turbidity currents (Kingsley 1979) during deposition (Vischkuil, Laingsburg, Ripon Formations).

The clastic grain size increased as extensive delta systems progressively encroached from the south and prodelta and delta front beds were deposited in the shallowing basin (Fort Brown, Waterford, Koedoesberg, etc.). Towards the western half of the Karoo basin more active progradation of the deltas is reflected by the coarse sheet-like sandstone units of the Waterford/Koedoesberg Formations which reflect low sinuosity fluvial channel deposition (Turner 1978). Deeper water evidently still existed towards the east.

Beaufort Group

Gradual reduction of fluvial activity, northward migration of the depoaxis and decrease of the Ecca sea eastwards characterized the overlying Beaufort sequence. Coarse grained arenitic wedges (most extensive in the eastern Cape) interbedded with massive mudstone sequences reflect orogenic pulses in the south. Episodes of maximum terrigenous influx were not in phase throughout the basin however, thus preventing correlation of individual stratigraphic units (Table 4). Mudstones and siltstones often red or purple in colour, predominate in the basal western Beaufort Group (Abrahamskraal) representing deposition on a floodplain criss-crossed by numerous meandering river channels. Levee, crevasse splay, proximal flood basin and distal flood basin depositional environments, each with a characteristic suite of vertebrate remains, are therefore common. The various cross-bedded arkosic sandstone bodies represent mainly channel-fill sandstones, point bar deposits, or crevasse splay sheets. The latter incorporate mudstone intraclasts, reworked nodules and bone and plant debris. Semi-arid to arid

GROUP	SUBGROUP	FORMATION	
		Southwest	Southeast
BEAUFORT		Clarens	
		Elliot	
		Molteno	
	Tarkastad		Burgersdorp
			Katberg
	Adelaide	Teekloof	Balfour
			Middleton
		Abrahamskraal	Koonap
ECCA		Waterford / * Koedoesberg	Waterford
		* Kookfontein / Skoorsteenberg	Fort Brown
		Laingsburg	Ripon
		Vischkuil / Tierberg	
		Collingham	
		Whitehill	
		Prince Albert	
		Dwyka	

Table 4. Stratigraphy of the Karoo sequence (*Not yet approved by S.A.C.S.)

conditions with vegetation mainly confined to belts along the main channel courses are envisaged (Keyser 1966; Smith 1978). The interfluvial lowlands were periodically briefly flooded, reverting to playa lakes intermittently (Stear 1979). Towards the east a major but rapidly dwindling intracratonic lake system existed.

The overlying 1 000 m predominantly mud and silt accumulation (Teekloof Formation) represents deposition in extensive flood basins, transected by only a few trunk channel systems in contrast to the Abrahamskraal cycle.

The corresponding beds of the Adelaide Subgroup in the eastern Cape (Koonap, Middleton and Balfour Formations) total about 5 000 m and consist essentially of greenish-grey and reddish mudstones, siltstones and thin, discontinuous sandstone units and represent shallow lacustrine deposits.

The succeeding units of the Tarkastad Subgroup and the Molteno, Elliot and Clarens Formations only accumulated north of the Cape orogenic belt, i.e. beyond the perimeter of the present distribution of the Fynbos and are therefore irrelevant to this discussion.

Karoo deposition terminated with increasingly more active volcanism, with the main episode between 200 and 190 Myr. Volcanic ash beds, brecciated lava flows and agglomerates attest to an initial explosive episode (exposed inter alia near Steytlerville and Kirkwood). This was followed by a monotonous succession of basaltic outpourings and contemporary dolerite intrusion which affected almost the entire Karoo basin.

CRETACEOUS SUCCESSIONS

Fragmentation of Gondwanaland extended from this period (190 Myr) until the Late Cretaceous (100 Myr). Numerous fault-controlled basins elongated parallel to the structural grain south of the Cape fold ranges thus developed. Synsedimentary boundary faulting influenced the accumulation of conglomerates (Enon Formation) and other terrigenous clastics. In some places basalts and pyroclastic rocks are also interbedded with the sediments (Algoa basin, Heidelberg/Riversdale area). The marine transgressions synchronous with the continental breakup and evolution of the southern Cape margin are only registered in the Algoa, Gamtoos, Plettenberg and Knysna basins. An overall maximum thickness of 4 000 m is attained in the Algoa basin.

The braided alluvial fans of the Enon Formation consist of poorly sorted conglomerate with subsidiary sandstone, siltstone and mudstone lenses, the whole of which tapers northward. Various fossiliferous remains, notably of wood and dinosaurs, have been found. The palaeocurrent data and imbrication of the clasts depict a low-sinuosity braided streams environment, with the Enon conglomerates representing longitudinal bars. The latter interfingered basinward with the 2 000 m-thick Kirkwood Formation consisting of alternating pebbly sandstone and mudstone containing plant, leaf and wood fossils. A fluvial plain environment is reflected by the extensive channel sandstone bodies. The thick (1 860 m) sequence of bioturbated and rooted red and green mudstones, siltstones and minor sandstone units (Sundays River Formation) represents estuarine-interdistributary bay deposits. Plant debris and diverse marine fossils occur, with the diversity and population density of the invertebrate faunas increasing south-eastwards. Typical braided fluvial and shoal-water deltaic processes are reflected.

In the landlocked basins of Oudtshoorn, Heidelberg, Worcester/Robertson/Swellendam areas the Enon is represented by thick alluvial fan conglomerates which change downslope to alluvial plain sandstones and playa lake mudstones (Lock 1978). Fossils include foliage, wood, dinosaur teeth and rare lignite layers. Upper Cretaceous deposition terminated during a major worldwide regression.

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REFERENCES

BEESON, R. 1976. Petrography of sediments of the Malmesbury Group in the Philadelphia area, Cape Province. Annals of the Geological Survey of South Africa 11:128-33.

BELL, C. M. 1981. Soft-sediment deformation of sandstone related to the Dwyka glaciation in South Africa. Sedimentology 28:321-9.

GRESSE, P. G. 1976. The structure and metamorphism of the pre-Cape rocks in the coastal strip south of George. Unpublished M.Sc. thesis: University of Stellenbosch.

HARTNADY, C. J. H., NEWTON, A. R. & THERON, J. N. 1974. Stratigraphy and structure of the Malmesbury Group in the south-western Cape. Bulletin of the Precambrian Research Unit of the University of Cape Town 15:193-213.

HOBDAY, D. K. & TANKARD, A. J. 1978. Transgressive barrier and shallow-shelf interpretation of the lower Paleozoic Peninsula Formation, South Africa. Geological Society of America Bulletin 89:1733-44.

KEYSER, A. W. 1966. Some indications of arid climate during deposition of the Beaufort Series. Annals of the Geological Survey of South Africa 5:77-9.

KINGSLEY, C. S. 1979. A composite turbidite-delta-fluvial model for Permian sedimentation in the Ecca and lower Beaufort of the eastern Cape Province:

a new link with Gondwanaland. Geological Society of South Africa 18th Congress Abstracts 1:96-112.

KRYNAUW, J. R. & GRESSE, P. G. 1980. The Kaaimans Group in the George area, Cape Province: a model for the origin of deformation and metamorphism in the Southern Cape Fold Belt. Transactions of the Geological Society of South Africa 83:23-38.

LE ROUX, J. P. 1977. The stratigraphy, sedimentology and structure of the Cango Group north of Oudtshoorn, C. P. Unpublished M.Sc. thesis: University of Stellenbosch.

LOCK, B. E. 1978. The Cape Fold Belt of South Africa: tectonic control of sedimentation. Geological Association Proceedings 89:263-81.

RUST, I. C. 1967. On the sedimentation of the Table Mountain Group in the western Cape Province. Unpublished D.Sc. thesis: University of Stellenbosch.

RUST, I. C. 1973. The evolution of the Palaeozoic Cape basin, southern margin of Africa. In Nairn, A. E. M. & Stehli, F. G. eds The ocean basins and margins. 1. The South Atlantic: 247-76. New York: Plenum.

SMITH, R. M. H. 1978. A study of the sedimentology and taphonomy of floodplain deposits of the lower Beaufort (Adelaide Subgroup) strata near Beaufort West, Cape Province. Annals of the Geological Survey of South Africa 12:37-68.

STEAR, W. M. 1979. Channel sandstone and bar morphology of the lower Beaufort Group uranium district near Beaufort West, Cape. Geological Society of South Africa 18th Congress Abstracts 2:132-5.

STOCKEN, C. G. 1954. The pre-Cape rocks of the central Cango. Unpublished Ph.D. thesis: University of Cape Town.

STUMP, E. 1976. On the Late Precambrian-Early Paleozoic meta-volcanic and metasedimentary rocks of the Queen Maud Mountains, Antarctica and a comparison with rocks of similar age from southern Africa. Institute for Polar Studies Ohio State University Report 62.

TANKARD, A. J. & BARWIS, J. H. 1982. Wave-dominated deltaic sedimentation in the Devonian Bokkeveld basin of South Africa. Journal of Sedimentary Petrology 52:

THERON, J. N. 1970. A stratigraphical study of the Bokkeveld Group (Series). Proceedings Papers of the 2nd Gondwana Symposium, South Africa: 197-204. Pretoria: C. S. I. R.

THERON, J. N. & BLIGNAULT, H. J. 1975. A model for sedimentation of the Dwyka glacials in the south-western Cape. In Campbell, K. S. W. ed. Gondwana geology, Proceedings and Papers of the 3rd Gondwana Symposium, Australia: 347-56. Canberra: Australian National University Press.

TURNER, B. R. 1978. Sedimentary patterns of uranium mineralization in the Beaufort Group of the southern Karoo (Gondwana) basin, South Africa. In Maill, A. D. ed. Fluvial sedimentology. Memoirs of the Canadian Society of Petrology Geology 5: 831-48.

VISSER, H. N. 1967. Verspreiding en korrelasie van die Formasie Klipheuwel in die Swartland en die Sandveld. Annals of the Geological Survey of South Africa 6:31-8.

VISSER, J. N. J. 1974. The Table Mountain Group: a study in the deposition of quartz arenites on a stable shelf. Transactions of the Geological Society of South Africa. 77:229-37.

VISSER, J. N. J. 1981. Carboniferous topography and glaciation in the north-western part of the Karoo basin, South Africa. Annals of the Geological Survey of South Africa 15:13-24.

VOS, R. G. & TANKARD, A. J. 1981. Braided fluvial sedimentation in the Lower Palaeozoic Cape basin, South Africa. Sedimentary Geology 29:171-93.

CENOZOIC GEOLOGY AND PALAEOGEOGRAPHY OF THE FYNBOS REGION

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INTRODUCTION

The fynbos region is situated on a passive continental margin that was developed during the Mesozoic fragmentation of the southern super-continent of Gondwanaland. Rifting commenced about 140 million years ago (Myr) during the late Jurassic, and by the mid-Cretaceous (ca 100 Myr) the region was fronted by open ocean (Gerrard & Smith 1980). Faulting along the subcontinental margin resulted in huge quantities of sediment being deposited in the widening ocean basins as rivers incised the pre-rift 'Gondwana surface'. For example, nearly 10 km depth of late Jurassic and Cretaceous sediment, much of it derived from the subcontinent, was deposited in the deepest part of the Orange Basin between the Olifants and Orange river mouths (Gerrard & Smith 1980).

By the beginning of the Cenozoic (65 Myr) relative stability of the subcontinent had been achieved and its form was essentially similar to that of the present, although some disturbance is indicated by vulcanism that occurred on the continental shelf, in Namaqualand and in Bushmanland early in the Cenozoic (Dingle et al. 1983). However, the mountains of the fynbos region (the Cape Fold Mountains and outliers such as the Cape Peninsula and Piketberg) have been in existence throughout the Cenozoic and, although subjected to continual subaerial erosion, their form has probably been little altered. Considerably less sediment was deposited offshore during the Cenozoic than during the comparable time span of the late Jurassic and Cretaceous. Cenozoic sediment off the west coast generally has a thickness of no more than 1,5 km, and then much of it is of biogenic rather than terrigenous origin. The suggestion that the Cape mountains underwent appreciable uplift on one or more occasions during the Cenozoic (e.g. King 1978) is discounted here. The thin acid soils of these mountains have provided an ancient and constant centre for the development of the sclerophyllous shrub vegetation that characterizes much of the fynbos region today.

By contrast, the extent, form and substrates of the coastal lowlands have not been constant. The lowlands were subject to fluctuations in sea-level that radically changed their areal extent, their form was affected by deposition and erosion that accompanied the sea-level changes, and substrates were altered in accordance with prevailing physiographic and climatic

EPOCHS	SOUTH-WESTERN CAPE	OVERBERG	OUTENIQUALAND
Holocene & Pleistocene	Cape Flats Formation (sands & clays with shelly horizons; mainly fluviatile) Bredasdorp Formation (calcareous sands with no primary phosphate; mainly non-marine)	Bredasdorp Formation (calcareous sands; marine & non-marine)	
Pliocene	↓ Varswater Formation (quartzose sands with primary phosphate; mainly marine) ? ↑		Formosa Formation (cobble gravels & angular talus, interbedded with clays & silts; mainly marine)
Miocene	Elandsfontyn Formation (angular quartzose sands with no primary phosphate; non-marine)	↓ ? (Analogue of Elandsfontyn Fm possibly present)	
Oligocene			
Eocene & Paleocene			Keurbooms Formation (boulder gravels, interbedded with clays & silts; mainly marine) Knysna Formation (sands & clays, including 'Knysna lignites'; non-marine)

Table 1. Principal lithostratigraphic units of the fynbos region.

conditions. The lowlands have therefore provided an insecure and changeable base on which a variety of vegetation types have waxed and waned.

The Cenozoic deposits of the coastal lowlands include onshore extensions of sediment bodies that occur on the continental shelf and slope (Dingle et al. 1983). The most important of the onshore centres of deposition are located in the Vanrhynsdorp Embayment (which includes the Knersvlakte), the Sandveld (including the Saldanha Embayment), the Cape Flats, the Bredasdorp and Albertinia Embayments, Outeniqualand, and the Algoa Embayment (Fig. 1). Sediments in these areas are largely or entirely of late Tertiary (Neogene) and Quaternary age, and are generally at elevations below 200 m. The principal lithostratigraphic units represented in these deposits are given in Table 1. Higher areas of the coastal lowlands include erosion surfaces, deeply-weathered soil profiles, duricrusts and other deposits dating back to the early Tertiary (Paleogene).

The geological history of the coastal lowlands is closely associated with the history of the adjacent oceans. The nature of the deposits, and of the weathering and erosion that has occurred, was determined by palaeo-ocean characteristics and palaeoclimates, factors that were closely related to sea-level changes, which in turn were largely controlled by plate tectonics.

PLATE TECTONICS AND PALAEOCEANOGRAPHY

Plate tectonics is the mechanism by which continental drift is effected and according to Cooper (1977:45) it "is the primary factor in our planetary evolution, governing not only the geology, geography, physiography and climatology, but also the patterns of biotic evolution and extinction." Consideration of the geological history and palaeoenvironments in the fynbos region must therefore take into account the influences of plate tectonics on this region.

The present size, shape and position of the world's continents and oceans has been determined by plate tectonics. It is the distribution of land and water masses that largely controls the nature of wind and oceanic circulation, and therefore also heat transference on the globe. It follows that plate tectonics has been of paramount importance in determining global climates. Furthermore, changes in the relative area of land and water, and in the relative positions of the continents, cause changes in both climates and the physical environment, and these factors in turn control the distribution and evolution of the biota.

The fragmentation of Gondwanaland that began during the Mesozoic has continued throughout the Cenozoic. The latter era has thus been characterized by pronounced climatic and environmental change, the origins of which can often be traced ultimately to plate tectonics, although astronomical factors played a role in the cyclical climatic changes during

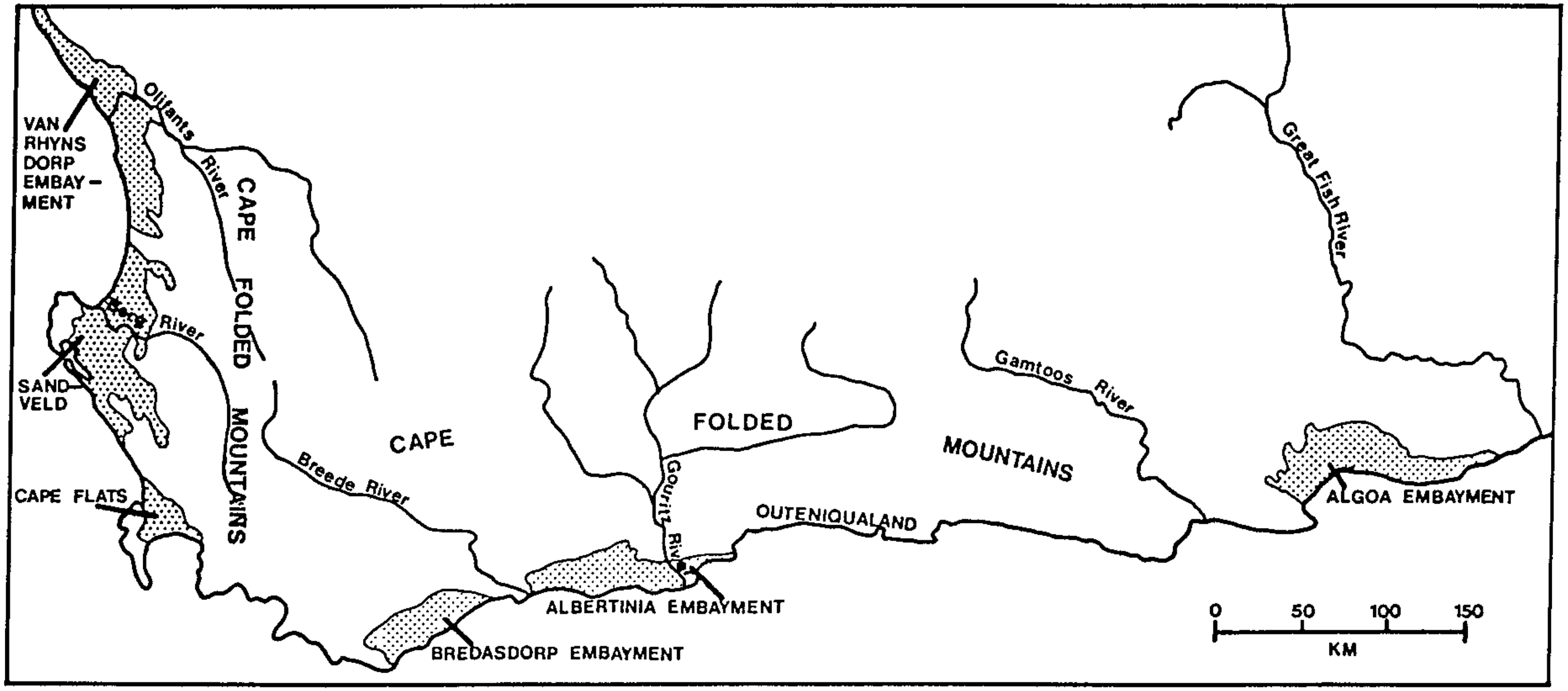

Fig. I Principal exposures of Cenozoic sediments on the coastal lowlands of the fynbos region. (Modified after Lambrechts 1979: fig. I) the latter part of this era.

Africa was an essentially stable continent that was entirely surrounded by oceans during the early Tertiary, and its isolation from other continents profoundly affected the nature of its biota. Unfortunately, the continent's fossil record for this period is poor. For example, the only notable early Tertiary vertebrate occurrences are in north Africa (Cooke 1978). The palaeobotanical record is little better and inference has played a large part in the reconstructions of early Tertiary vegetations (e.g. Axelrod & Raven 1978). However, it is evident that African plants and animals largely evolved in isolation during the early Tertiary and consequently developed a high degree of endemism. For example, over 50% of the plant taxa recorded from the Paleocene deposits at Banke in Namaqualand are endemics (Scholtz, in press). The situation changed radically early in the Miocene, with several events caused by plate tectonics influencing the continent's palaeoenvironments and the evolution of its biota.

Firstly, the northward-moving African/Arabian continental plate came into contact with south-western Asia, thus establishing the first direct land connection, and the first free biotic interchange, with another continent in 40 million years or more (Berggren & Van Couvering 1974; Maglio 1978). The greatest impact of this interchange was on the continent's fauna, especially the larger and more mobile mammals. The effects on the vegetation of the fynbos region at the southern continental extremity were indirect, but all African plant communities must have responded to the changes in the fauna, especially those involving the mammalian herbivores.

The collision between the African/Arabian and Eurasian plates also influenced the physiography of parts of Africa, and this too had an effect on the continent's environments and biota. Uplift occurred, notably in the Atlas region of north-western Africa, and in east Africa where it was accompanied by faulting and vulcanism associated with the developing rift system of this area. Significant changes in the ecosystems of these regions resulted from the transformation of generally uniform landscapes into ones of great diversity. Evidence for uplift in the fynbos region and elsewhere in southern Africa at this time is at best equivocal, but a ripple effect from changes in north and east Africa must have been experienced in the south.

Of greater significance to the fynbos region were developments stemming from the effects of plate tectonics in southern high latitudes. Early in the Cenozoic, South America, Antarctica and Australia still formed a single continent. By the Oligocene, Australia had separated from Antarctica, but the conjunction of Antarctica and South America maintained a warm-water circulation in the South Atlantic and adjacent Southern Ocean (Kvasov & Verbitsky 1981). Antarctica was finally separated from South America early in the Miocene, and the opening of the Drake Passage south of Tierra del Fuego allowed the first unrestricted flow of the Circum-Antarctic Current. This in turn led to the thermal isolation of Antarctica and large-scale glaciation of the continent, since warm tropical water and associated air masses could no longer penetrate to southern high latitudes (Kennett 1980). The Southern Ocean became frigid and cold water from this ocean was carried northwards along the west coast of southern African by the Benguela Current. A significant feature of this current is the upwelling of cold water caused by the strong southerly and south-easterly winds associated with the South Atlantic high pressure system. A sustained upwelling was established early in the late Miocene (ca 10 Myr) (Siesser 1980).

The glaciation of Antarctica and the related development of 'modern' wind and ocean circulation patterns in the Southern and South Atlantic oceans had a profound effect on southern African climates. For example, Siesser (1978, 1980) and Tankard & Rogers (1978) have discussed the development of the cold Benguela Current system in relation to the aridification of south-western Africa in general, and the Namib Desert in particular, while Deacon (1983) has indicated that it is the stability of the descending air masses of the South Atlantic high pressure system that is the prime cause of aridity.

Paradoxically, although the colder and drier climates that developed in southern mid-latitudes during the Miocene created harsher environments both on- and offshore, the biotas of both areas were enriched by the evolutionary changes that followed. The upwelled water of the Benguela Current system is rich in nutrients and the oceanic biota has therefore flourished. Onshore, the climatic changes were imposed on regions transitional between those with tropical and temperate climates and were more pronounced than those experienced in the more northerly parts of the subcontinent. Since climatic and environmental change provide a stimulus for evolutionary change, those elements of the biota with low mobility (i.e. plants, invertebrates and lower vertebrates) evolved a distinctive and diverse character.

Fynbos region palaeoenvironments were also influenced by developments in the Indian Ocean during the early Miocene. These included the closure of the eastern Tethys Sea through the meeting of the African/Arabian and Eurasian plates, the collision between the Indian plate and the Asian mainland, and the approach of the Australasian plate to south-eastern Asia and the consequent development of the Indonesian archipelago. The Indian Ocean was therefore taking on its present configuration, and its 'modern' wind and ocean circulation patterns were being developed. These patterns in the south-western Indian Ocean have an important bearing on the climates of the Overberg, Outeniqualand and eastern Cape. For example, it is the moist air advected across the warm Agulhas Current during summer that results in the relatively high rainfall in the eastern parts of southern Africa. Flow-paths of the Agulhas Current broadly similar to those of the present were established about 5 Myr (Martin 1981), which means that by the end of the Miocene, both the oceans fronting the fynbos region were essentially 'modern' in their characteristics.

Another aspect of palaeoceanography, namely sea-level changes, also had significant effects on the geology and palaeoenvironments of the fynbos region.

SEA-LEVEL CHANGES

Manifestations of plate tectonics include sea-floor spreading and mid-oceanic ridge development, factors that affect the capacity of ocean basins and, consequently, the level of the sea relative to the land (Russell 1968). The sea may either rise relative to the land (i.e. marine transgressions), or fall (regressions), and those movements caused by plate tectonics are on a global scale (eustatic). Such tectonically controlled eustatic sea-level changes were characteristic of the Cenozoic until the middle Miocene. Thereafter, the principal control was change in the volume of the polar ice-caps, which either withdrew from or added to the oceans large quantities of water. Glacio-eustatic sea-level changes were generally of lower amplitude than those that were tectonically controlled, but they occurred with greater frequency, with cycles during the Quaternary being as short as 10 000 years. It is worth noting that plate tectonics played a role in the development of both polar ice-caps, although their subsequent size fluctuations were due also to perturbations in solar radiation caused by oscillations in the earth's orbit (Frakes 1979).

Cooper's (1977:44) summary of the effect of sea-level changes on the terrestrial environment includes the following statements:

> On land, regressive episodes are characterized by climatic deterioration and increased aridity, together significantly modifying vegetation patterns and thus also trophic resources . . . Conversely, [during transgressions] the mild climate, increased rainfall [and] more luxuriant vegetation . . . would have provided a very favourable living environment . . .

Sea-level changes influence climate (temperature and rainfall) by altering the relative areas of the globe covered by water and land. Higher temperatures during transgressions are ascribed to greater absorption of incoming solar radiation due to an increase in the area covered by the oceans, water having a greater heat capacity than land (Frakes 1979). Higher temperatures lead to increased evaporation and, consequently, to increased precipitation. The reverse applies during regressions.

Other factors that affect climate during the contrasting sea-level states include the level of atmospheric CO_2 According to Fischer (1981), transgressions coincide with higher levels of atmospheric CO_2, the oceans having a high pelagic diversity with anaerobic conditions prevailing. This 'greenhouse' state contrasts with the 'icehouse' state during regressions, when CO_2 levels are lower, ice-caps are present (or enlarged), and ocean waters are well aerated. Thus, warmer conditions during transgressions are complemented by a 'greenhouse' effect in the atmosphere, while 'icehouse' conditions during regressions reinforce the prevailing cooler climates. Fischer's hypothesis was stated in reference to a major climatic cycle with a period of about 300 million years, but it presumably applies on a modified scale to the shorter sea-level cycles of the Cenozoic.

The continentality of climates is also influenced by sea-level changes (Cooper 1977). Since regressions increase the areas of continents, temperature ranges over wider areas of continental interiors increase accordingly, whereas during transgressions temperatures are more equable.

Vail et al. (1977) believe that falls in sea-level during tectono-eustatic regressions were rapid, whereas rises in sea-level during transgressive phases tended to be gradual. If this was indeed the case, then it follows that there would have been a rapid transition from the equable environmental conditions experienced during transgressions to the harsher conditions that prevailed during regressions, with subsequent climatic and environmental amelioration being more gradual. It is therefore likely that regressions had a more immediate and dramatic effect on the environment than transgressions.

In both sea-level states, the degree of climatic change, and its effects, would have been dependent on the magnitude of the change in sea-level. In addition, it should be noted that major climatic changes resulted from global sea-level fluctuations, and not ones resulting from local tectonism that affected only limited areas on coastal margins.

Sea-level changes also have significant effects on ocean environments (Cooper 1977), including the production of phosphate on continental margins, which is relevant here because of the occurrence of phosphorites on the western coastal lowlands of the fynbos region. Arthur & Jenkyns (1981) conclude that periods of transgression are most favourable for phosphate deposition, although regressions may rework and concentrate phosphatic sediment to form economic deposits of the mineral. They also suggest that conditions on land may contribute to phosphate deposition on the continental shelf and coastal margin. Evidently, the intense weathering associated with warm, humid and equable climates that accompany transgressions results in an increase in the phosphorous supply carried to the oceans by rivers.

These opinions are in accord with the nature of calcium phosphate deposits in the Saldanha Embayment (Hendey & Dingle, in press). For example, the only phosphate ore-body in this area that is currently being commercially exploited (a unit within the Varswater Formation at Langebaanweg), was laid down during the global transgression of the early Pliocene. Coincidentally, the aluminium phosphate deposits of the Saldanha Embayment also originated during a period of relatively high sea-level,

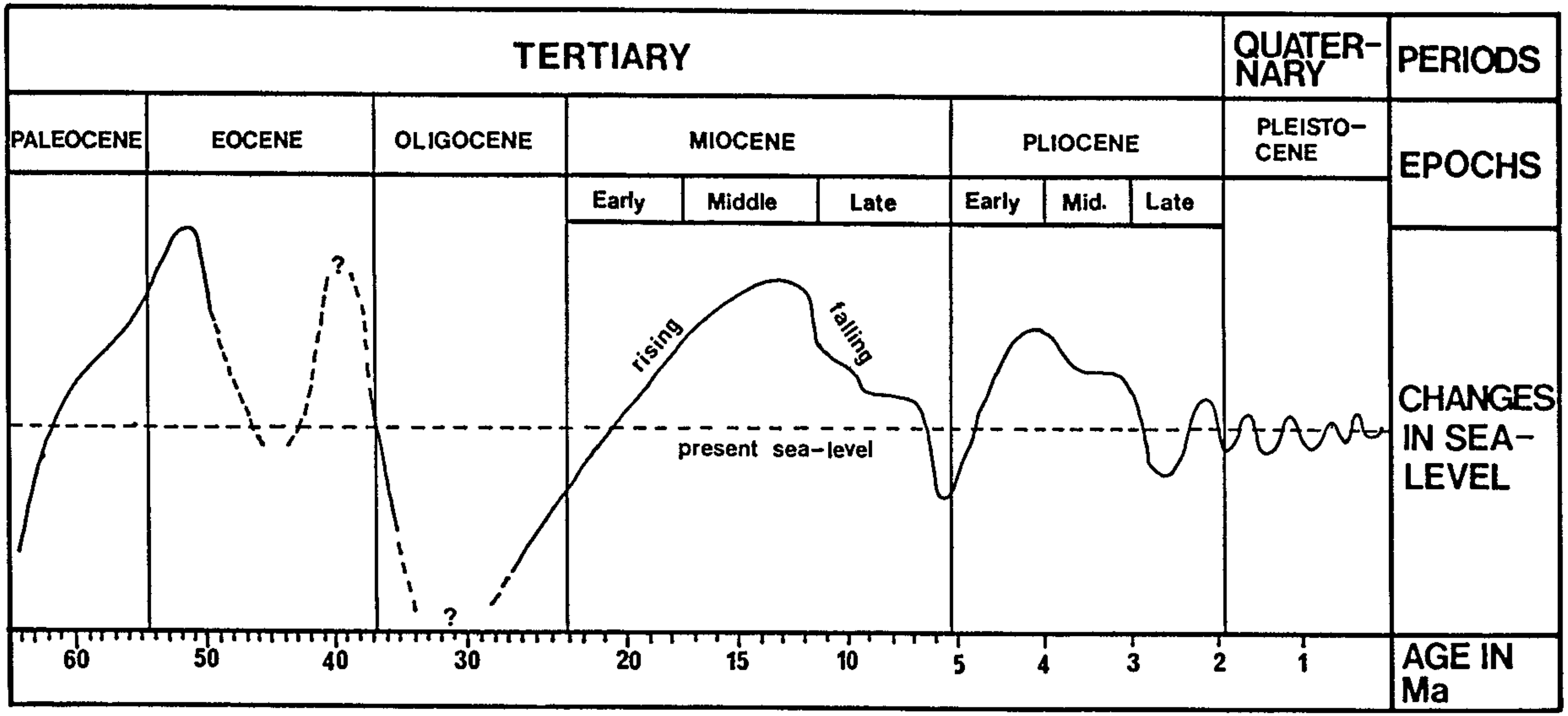

Fig. 2 Cenozoic time-scale and a diagrammatic representation of southern African sea-level changes during that era. (Modified after Dingle et al. 1983; Hendey 1982: p. 6) (Ma = millions of years ago.)

although by a process that differs from that described by Arthur & Jenkyns (1981). These deposits cap granite hills in the vicinity of Saldanha Bay and were laid down originally as guano derived from seabird colonies that occupied the hills when they were in the form of islands during one or more late Tertiary transgressions (early-middle Miocene and/or early Pliocene).

One of the principal requirements for phosphate production in the oceans is the presence of cold, nutrient-rich upwellings (Arthur & Jenkyns 1981), and such a system is present in the Benguela Current off the west coast of southern Africa (see above). Upwellings are more localized and less intense off the south coast (Schumann et al. 1982), which may account for the absence of phosphorites on the southern coastal lowlands of the fynbos region. Phosphorites are present on the adjacent Agulhas Bank, but these may have been formed by a process that is not necessarily associated with strong upwellings (Birch et al. 1983).

Southern African Tertiary sea-level changes have been documented by both on- and offshore evidence (Hendey 1981a; Siesser & Dingle 1981; Dingle et al. 1983) (Fig. 2). The effects of these changes on the subcontinent were formerly ascribed to continental tectonism, particularly uplift, but such earth movements probably played only a subordinate and perhaps insignificant role. Indications are that the coastal lowlands of the fynbos region preserve an essentially undisturbed record of Tertiary eustacy. Local Quaternary sea-level changes have been reviewed by Tankard (1975, 1976). Some of the sea-level events formerly dated as Pleistocene are now believed to be of Tertiary age, and the local Quaternary record reflects only the late Pleistocene and Holocene, the eustatic events of this period having obscured those earlier in the Pleistocene (Hendey 1981a).

The evidence for past high sea-levels in the fynbos region is generally fragmentary and the nature of the record varies from area to area according to the local geology and physiography (Hendey 1981a). A further difficulty is that direct evidence of age is limited and inference played a part in dating many of the ancient shorelines and associated erosion surfaces (Table 2). The terrestrial erosion surfaces are recorded between fairly constant altimetric limits that reflect past high sea-levels, and they are associated with characteristic soil profiles (vide Schloms et al. this volume).

The correlations between the shorelines and erosion surfaces are tentative since none of the latter have been dated by independent means. These correlations were based primarily on the assumption that the lowest of the surfaces on the western coastal lowlands (the Katarra surface - vide Schloms et al. this volume) dates from the middle to late Pliocene. This assumption stems from the fact that the Katarra surface in the Darling area is associated with the present valley of the Sout River, a feature that was developed after the early Pliocene transgression (100 m shoreline). The

EPOCHS	AGE in Myr	SHORELINES, RIVER TERRACES & EROSION SURFACES	SEDIMENTS & SOILS
Holocene & Pleistocene	1,7	6m & lower shorelines 6m river terrace	Bredasdorp Formation Calcareous coastal sands (mobile - A1) Cape Flats Formation Young alluvium (I1) Intermontane acid sands (B2)
Late Pliocene	3,8	20m shoreline 12m marine platform 15m river terrace	Bredasdorp Formation Calcareous coastal dunes (fixed - A2) Duplex soils (coastal plain; -30m - D1L)
Middle Pliocene	4,2	50m shoreline 45m river terrace Katarra surface (44-110m)	Bredasdorp Formation Coastal acid sands (70-110m - B1) Duplex soils (valley flats: 44-75m - D2S; 50-100m - D3S. upland plain: +100m - D4S)
Early Pliocene	5,2	100m shoreline 50-100m marine platform Lower Swartland surface (80-140m)	Varswater Formation Residual soils (80-140m - C1)
Late Miocene & Middle Miocene	15	30m shoreline ?120m shoreline	Gravel Member
Middle Miocene & Early Miocene	22	150m shoreline 80-140m marine platform Higher Swartland surface (150-200m)	Elandsfontyn Formation Residual soils (150-200m - C2)
Oligocene	37		
Eocene & Paleocene	65	150-200m marine platform	Red apedal soils (150-200m - F2) Red apedal soils (200-250m - F3)

Table 2. The age relationship of shorelines, river terraces, erosion surfaces, sediments and soils in the south-western Cape.

elevation of the Katarra surface in this area (44-75 m) is in keeping with post-early Pliocene high sea-levels (i.e. the 50 m and 20 m stands of the middle and late Pliocene, respectively). The higher erosion surfaces of the western coastal lowlands were correlated altimetrically with the higher and progressively older Tertiary transgressions. The lateritic soils of the higher erosion surfaces are a further indication that they are indeed of Tertiary rather than Quaternary age, since they are correlated with climates of the former period (see below).

Although not included in Table 2, the shorelines and erosion surfaces of the southern coastal lowlands may be correlated with those of the west on altimetric grounds. It is possible that the well developed 200-240 m 'coastal platform' of the southern coastal lowlands is a marine erosion surface contemporaneous with dated early Eocene deposits in the eastern Cape (Birbury, Needs Camp) that occur at elevations above 200 m (Siesser & Miles 1979). The Knysna Formation probably post-dates these deposits, the tenuous evidence combining to indicate an age for this formation of between middle Eocene and middle Miocene (Table 1) (vide Coetzee et al. this volume).

The most direct and immediate effect on the fynbos region of fluctuations in sea-level was change in the areal extent of the coastal lowlands. Sea-levels substantially lower than that of the present exposed wide areas of the continental shelf, particularly on the Agulhas Bank to the south of the Overberg and Outeniqualand. For example, the coastal plain south of the present mouth of the Breede River was widened from 50 to 200 km during the regression of the last glacial maximum when the sea fell about 120 m below its present level (Dingle & Rogers 1972). Comparable exposures of the continental shelf probably occurred during the earlier glacial maxima of the Pleistocene.

The magnitude of sea-level falls during the Tertiary are unknown or uncertain, although there is evidence that the Oligocene low stand was several hundred metres below present sea-level (Siesser & Dingle 1981; Dingle et al. 1983). This was the most substantial fall in sea-level during the entire Cenozoic, and much or all of the continental shelf was then exposed, with the area of the coastal lowlands being increased by 300% or more (Fig. 5).

During the interglacials of the Quaternary, including the present one, the sea stood at, or only slightly above, its present level, the maximum elevation attained being no more than about 6 m. Consequently, there were no significant decreases in the extent of the coastal lowlands during this period. This was not the case during the Tertiary. One of the recorded transgressions of the early Tertiary rose in excess of 200 m above present sea-level, inundating virtually the entire lowlands area. Thus in the 10 million years between the early Eocene and mid-Oligocene, the fynbos region lowlands were transformed from an area that hardly existed to one three times its present size. Large areas of the lowlands were also covered by the sea during the transgressions of the middle Miocene (150 m) and early Pliocene (100 m).

Sea-level changes had a pronounced effect on depositional and erosional processes on the coastal lowlands. During regressions at least some rivers incised their valleys causing extensive erosion, especially in their lower reaches. Erosion during the extreme low sea-level of the Oligocene was apparently particularly severe, since no deposits of early Tertiary age have been identified on the western coastal margin and in the Overberg. The only deposits that might be of this age are deeply-weathered rocks (saprolites) that occur in sheltered situations such as the Noordhoek valley and around Saldanha Bay (Glass 1977), although the possibility that they are of early-middle Miocene age cannot be excluded. This raises the question of the age of the oldest surviving sediments on the coastal margin of the south-western Cape other than the saprolites. These sediments are referred to the Elandsfontyn Formation and have generally been regarded as dating from the early-middle Miocene (e.g. Rogers 1980; Hendey 1981a; Coetzee & Rogers 1982). However, there is now some evidence to suggest that the Elandsfontyn Formation at Langebaanweg is of early Pliocene age. If this is indeed the case, then it means that at least in this area the erosive effects of the late Miocene regression must have been comparable to that of the Oligocene in removing virtually all pre-existing deposits resting on the local bedrock. The Elandsfontyn Formation in the Noordhoek valley may indeed date back to the early-middle Miocene (*vide* Coetzee *et al*. this volume). This serves as a reminder that litho- and chronostratigraphic units are not necessarily synonymous (see Table 1), although in the present instance the dating discrepancy has yet to be conclusively proven.

If sea-level falls during regressions were indeed precipitous, then valley incision and erosion must have been rapid and pronounced, with possibly catastrophic effects on the biota. The situation at such times would have been aggravated by the coincident decrease in rainfall, since this would have depleted the vegetation cover and left soils and other deposits even more susceptible to erosion. Since transgressions were supposedly more gradual, the transformation of the environment would have been less dramatic. Geological processes at such times would have involved the regrading of rivers through the build-up of channel-fill sediments, followed by the deposition of marine sediments in those areas inundated by the sea. The non-marine and marine elements in transgressive successions are usually separated by a complex of deposits characteristic of coastal environments (i.e. estuaries, lagoons, tidal flats, back-barrier marshes, and coastal dunes). A classic example of such a succession has been recorded at Langebaanweg in the Saldanha Embayment, where the non-marine Elandsfontyn Formation is overlain by the marine Varswater Formation

(Hendey 1981a; Hendey & Dingle, in press). There are similar successions on the Cape Flats (Rogers 1980), an area that also includes the late Quaternary paralic succession at Rietvlei, which represents the Cape Flats Formation (Schalke 1973). On the Cape Flats and in the Overberg, the marine elements in the succession are included in the Bredasdorp Formation (Table 1).

The amelioration of climates during transgressions would have improved the vegetation cover, thus reducing erosion even though the volume of water carried by rivers may have been substantially increased. On the other hand, chemical weathering of the bedrock would have been accelerated, especially during the Tertiary transgressions that preceded the glaciation of Antarctica, since both temperatures and rainfall were high. The products of this weathering survive today in various parts of the fynbos region as lateritic soil profiles and saprolites, the latter including economically important kaolin deposits, and which elsewhere were eroded to provide the angular clastic material that makes up much of the Elandsfontyn Formation.

Coastal dunes are an important and widespread feature of the lowlands, and their development and form can frequently be ascribed to sea-level changes. The sand constituting these dunes is a weathering product of the local pre-Cenozoic bedrock, and it was initially deposited either as fluviatile or marine sediment that was subsequently reworked by aeolian action. The exposure of coastal sand bodies during regressions provided an abundant source of material for dune development, this material being lime-enriched by the addition of the remains of marine organisms. The form of such dunes might then have been modified by subsequent transgressions. Given the sea-level history of the region, individual sand bodies may have a complex history of erosion and redeposition by marine, fluviatile and aeolian processes.

The coastal dunes are principally of two types. The most striking form on the west coast are the 'dune plumes' that extend inland from sandy beaches that lie obliquely to prevailing dry season winds (summer 'south-easters' under existing climatic conditions on the west coast) (Tankard & Rogers 1978; Rogers 1980). Dune plumes may be situated near river mouths, where the sediment discharge provides a regular source of sand to supplement that already on the beaches. There are invariably several generations of dunes constituting a single plume, and they are readily distinguished by the degree to which they are vegetated, the vegetation cover reflecting both the age and degree of consolidation of the substrate. The youngest consist of unconsolidated mobile dunes, usually with a barchanoid form, that are still active today. Older dunes are progressively more heavily vegetated and consolidated. Calcretized horizons are common since these dunes have a high lime content. The dunes flanking the present coast are of Quaternary age (Fig. 3).

Older plumes occur further inland, and since they have been subject to prolonged weathering and erosion, their form is usually indistinct. One such ancient dune plume exists west of Hopefield (Fig. 3), and its leached acid sands support a vegetation type (coastal fynbos) that is distinct from that on the younger calcareous dunes (coastal strandveld). Vestiges of another dune are located at Skurwerug, 2 km inland from the eastern shore of Saldanha Bay (Fig. 3). It overlies the 12 m late Pliocene marine platform and contains vertebrate fossils indicating an early Pleistocene age. The Hopefield plume is older, probably of middle-late Pliocene age since it clearly postdates the early Pliocene transgression.

Linear dunes that parallel the present and past coastlines occur on both the west and south coasts, and have been termed 'dune ridges', 'dune cordons' and 'barrier dunes'. Good examples are the series of dune cordons in Outeniqualand that increase in age away from the present coast (Martin 1962). Such dunes originate either offshore as submerged or emergent bars, or onshore as foredune ridges, the latter differing from dune plumes only in that they lack an inland extension. The coastal linear dunes may have a composite history when affected by sea-level changes, with offshore bars developing over drowned foredune ridges during transgressions, while offshore bars became foredune ridges during regressions.

One such barrier dune on the west coast is situated at Langebaanweg, and it has been studied in some detail (Tankard 1974; Hendey 1981a, b). It had its origins as a submerged bar when the early Pliocene transgression inundated the area 2 km west of the Langebaanweg railway station. Later during this transgression the bar became emergent, perhaps as a spit prograding from a line of granite hills to the south extended over it. This spit may eventually have reached another granite hill to the north of Langebaanweg, so forming a tombola enclosing a large bay to the east (Hendey 1981b: fig. 5). During the succeeding middle Pliocene regression, the barrier dune existed for a while as a foredune ridge, but this has since been progressively eroded away until all that survives today is a low hill (Anyskop), 10 km inland from Saldanha Bay (Fig. 3).

The core of Anyskop that was formed during the early Pliocene transgression is included in the Varswater Formation, but the deposits constituting the other coastal dunes in the south-western Cape and Overberg are included in the Bredasdorp Formation.

Duricrusts and certain other deposits represented in the fynbos region are of significance since they reflect climatic conditions that prevailed at the time of their formation, and they are therefore also an indirect reflection of past sea-level states.

One of the most significant effects of the relatively high temperatures and rainfall that accompanied transgressions was the increase in the rate of chemical weathering of bedrock. Deeply-weathered soil profiles with laterites are features of transgressive periods (e.g. Frakes 1979; McGowran

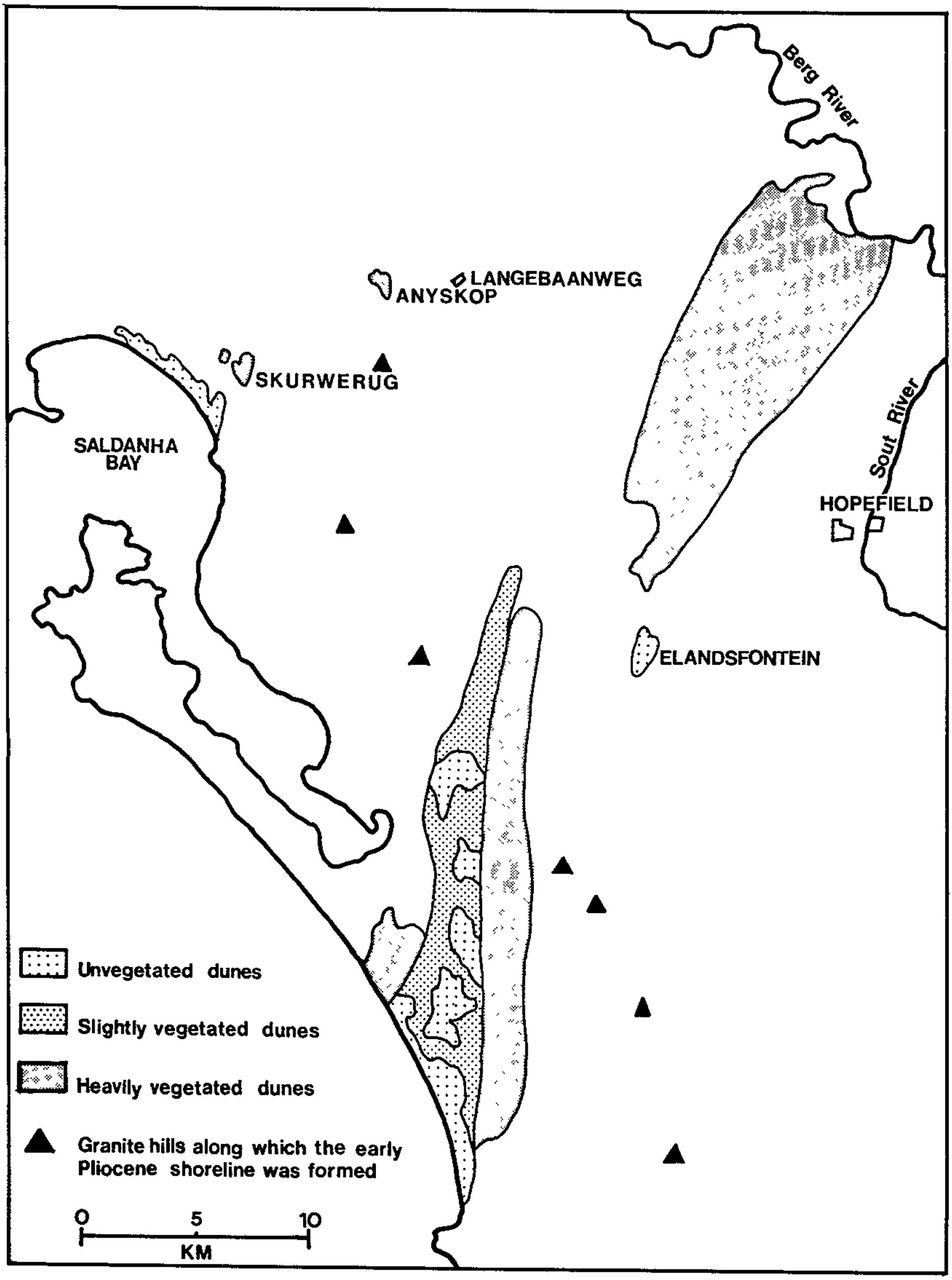

Fig. 3 Some late Tertiary and Quaternary dunes in the vicinity of Saldanha Bay, south-western Cape Province. (After Visser & Schoch 1973; Rogers 1980; Hendey 1981b.)

1979; Arthur & Jenkyns 1981). In addition, peats and lignites are often although not invariably associated with transgressions, since they represent the other end of the sedimentary spectrum from evaporites (Frakes 1979).

There are many recorded occurrences on the coastal lowlands of deep-weathering, laterites, peats and lignites that were developed at times in the remote past. Deeply-weathered profiles and laterites are widespread and are of interest since they are not being developed under existing interglacial (transgressive) climatic conditions, and nor could they have been formed during the colder (regressive) phases of the Pleistocene. They evidently date from warm and wet periods during the Tertiary, and they occur on certain of the higher and older erosion surfaces that are correlated with Tertiary transgressions (Table 2). The inception of colder climates during the late Miocene brought the formation of true laterites to an end, although soils with some laterite characteristics were developed during the Pliocene. These include the duplex soils associated with the Katarra erosion surface in the Darling district (vide Schloms et al. this volume), and the 'Brakkloof Soil' of Outeniqualand (Butzer & Helgren 1972).

Many of the peats recorded in the coastal lowlands were formed during transgressive periods. For example, although the peats of the Elandsfontyn Formation are of uncertain age, they were clearly formed during one or more of the late Tertiary transgressions. The peats of the Varswater Formation at Langebaanweg are definitely a product of the early Pliocene transgression. The Knysna lignites of Outeniqualand lack dating control, but they too are likely to be associated with a Tertiary transgression.

Calcretes are the most widespread and intensively studied of the duricrusts represented in the fynbos region (see Netterburg 1980 for references). It is generally agreed that they are indicative of relatively low rainfall, which is borne out by their distribution in southern Africa and the fact that most local calcretes are of post-Miocene age (Weinart 1976; Netterberg 1978). However, calcretes are a complex group of rocks that are difficult to date precisely, and individual occurrences must be treated on their own merits in determining the climatic regime that prevailed during formation. They are therefore not necessarily indicative of a particular sea-level state. However, Read (1974) noted that in the Shark Bay region of Western Australia calcrete horizons formed during regressions in marine limestones that had been laid down during preceding transgressions. Many of the calcareous sediments in the fynbos region were indeed deposited in marine environments during the transgressions of the late Tertiary and Quaternary, but calcareous coastal dunes were developed during the regressions of this period, and local calcretes may have formed at any time after the calcareous deposits were in place.

Silcretes are also widespread in the fynbos region and are characteristically associated with Tertiary erosion surfaces. Since they have undergone prolonged weathering and erosion, individual occurrences tend to be limited in extent. Although silcretes are undoubtedly of palaeoenvironmental significance, the conditions under which they were formed are still controversial. Some authors believe that silcretes are like laterites in requiring a warm and humid climate for formation (e.g. Wopfner 1978), whereas the more traditional view links silcrete with arid or semi-arid climates (Langford-Smith & Watts 1978). According to the former interpretation, local silcretes would correlate with the transgressive periods of the Tertiary, whereas the latter view would have silcretes formed during regressions (see McGowran 1979). Summerfield (1983) has recently suggested that the silcretes of the Cape coastal regions formed in well-vegetated areas under humid tropical and subtropical climates.

Silcretes have been most intensively studied in Australia, where most occurrences are of early Tertiary age, with only a few being as young as Pleistocene (Langford-Smith 1978). The situation in South Africa is similar, although at least in the case of the more conspicuous silcretes of the fynbos region, none are younger than Pliocene. It is clear that the climatic and other conditions required for silcrete formation no longer exist in this region. It is worth noting here that Fischer (1981:122) has described the present interglacial as "a comparatively mild episode within an icehouse state", with "the climate of the present world [being] far from representative of the Past as a whole." The latter statement also applies to the comparatively well known climates of the last glacial period of the late Pleistocene. Climates of the Holocene and late Pleistocene are at most representative only of the Quaternary, and pre-Quaternary climates were at least to some extent distinctive. On the subject of the requirements for the formation of the fynbos region silcretes, 'the present may <u>not</u> be the key to the past' simply because the necessary conditions no longer prevail in this region.

RIVER SYSTEMS OF THE FYNBOS REGION

Reference has already been made to the effects of sea-level and accompanying climatic changes on the river systems of the fynbos region. Gradient changes in valleys on the coastal lowlands in response to sea-level fluctuations, and the consequent erosional and depositional processes, coupled with the extensions of rivers onto the continental shelf during regressions, were amongst the most significant changes undergone by local rivers during the Cenozoic. In addition, sea-level fluctuations also caused changes in the direction of flow in the lower courses of rivers.

For example, it has been suggested that there was a progressive northward shift in the lower course of the Berg River between the Oligocene

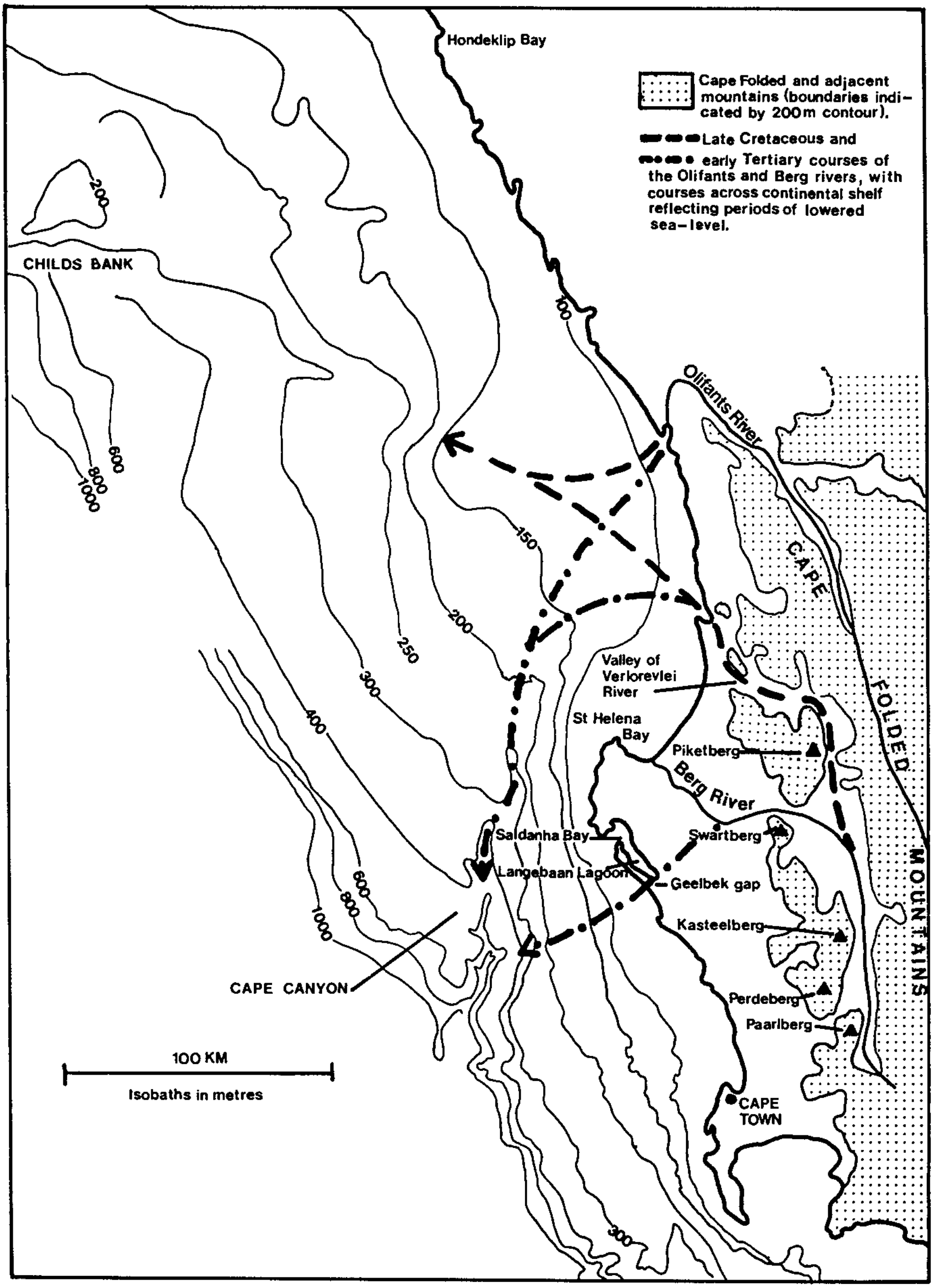

Fig. 4 The lower courses of the Berg and Olifants rivers during the late Cretaceous and early Tertiary.

and Pleistocene (Rogers 1980; Hendey 1981a). During the Oligocene the Berg River apparently flowed in a westerly direction through the 'Geelbek gap' south of Langebaan Lagoon, whereas during the Miocene and Pliocene its course was in the direction of Saldanha Bay, and it was only during the Pleistocene that it took up its present path into St Helena Bay (Fig. 4).

These were not the only course changes undergone by the Berg River. During the Cretaceous, and perhaps into the early Tertiary, it was apparently contained in a longitudinal valley that paralleled the Olifants River, its course passing east of Piketberg and then north-westwards to the coast via the valley presently occupied by the Verlorevlei River. During the major regressions of the Cretaceous and early Tertiary, the Berg and Olifants were probably joined into a single river system that discharged into the Orange Basin south of Childs Bank. Vestiges of the high ground that separated the middle course of the Berg River from the west coast remain today in Piketberg (maximum elevation, 1458 m), a series of low hills that includes Swartberg (479 m), Kasteelberg (946 m), Perdeberg (758 m) and Paarlberg (729 m) (Fig. 4). This watershed was breached south of Piketberg, perhaps at the time of the Oligocene low sea-level, and the Berg River took up its westerly path in the direction of Saldanha Bay.

It was during the early Tertiary that the most significant drainage change affecting the fynbos region took place. This involved the diversion through the Vanrhynsdorp Embayment of the Upper Orange/Vaal river system, an event which caused drainage from most of the South African inland plateau to be directed into the southern Orange Basin off the south-western Cape (Dingle & Hendey, in press). This drainage pattern persisted for about 40 million years until the end of the Oligocene, the epoch during which the Upper Orange/Vaal cut the Cape Canyon on the continental shelf off the south-western Cape. During the low sea-levels of the early Tertiary, the Olifants River would have been a tributary of the large Upper Orange/Vaal system, a connection that accounts for similarities between the fish faunas of the modern Orange and Olifants rivers (Jubb 1964, 1965). The Berg River probably also formed part of this river system at these times (Fig. 5).

The effects on the environment of the addition to the western coastal lowlands of the large Upper Orange/Vaal river system are difficult to gauge, especially since the climates of the early Tertiary were very different from that of the present. However, there can be little doubt that the effects were significant. For example, this river system would have served as a pathway for the dispersal of both plants and animals from the central interior to the south-western coast. In addition, the south-western Cape would have been provided with a substantial source of fresh water during the relatively cool and dry regressive phases of the early Tertiary. The beneficial effects on the local environment and biota of the supply of fresh water in the lower Orange River under the more

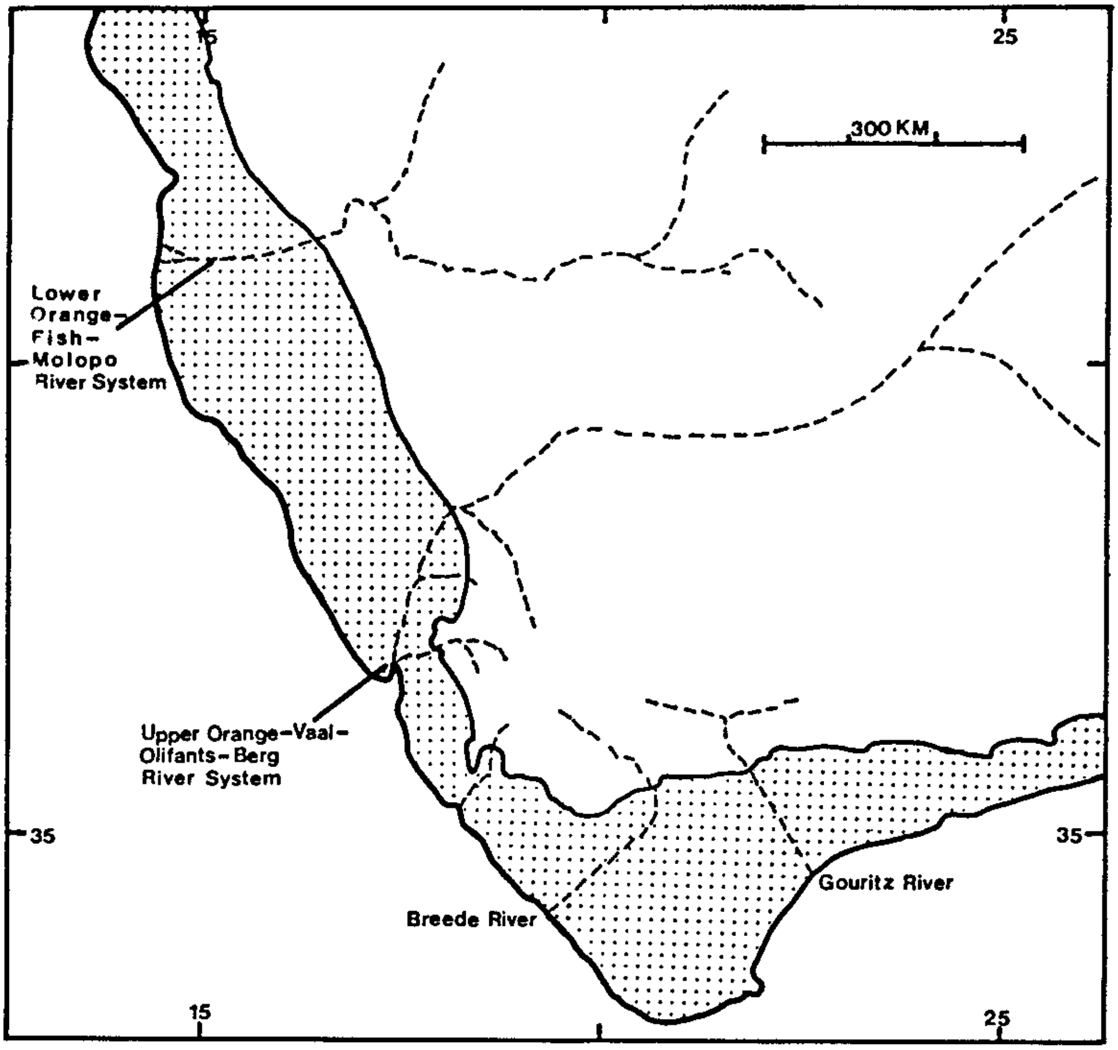

Fig. 5

Drainage systems in south-western Africa during the early Tertiary. The shoreline indicated is that which existed at the time of the maximum regression during the Oligocene. (Modified after Dingle & Hendey in press: fig. 3b.)

extreme conditions of the present are striking.

Changes in the river systems of the Overberg and Outeniqualand were probably less dramatic, since the large rivers of these areas are likely to have been confined to their present valleys throughout the Cenozoic. In contrast with the situation in the south-western Cape, the two largest rivers in the southern Cape (Breede and Gouritz) were not linked during periods of low sea-level, their courses across the continental shelf having been kept separate by the Agulhas Arch (Dingle et al. 1983). This separation is borne out by their distinctive fish faunas (see Farquharson 1962).

The elevated coastal topography in the southern Cape, especially in Outeniqualand, has resulted in the larger rivers being deeply entrenched in steep-sided valleys that were developed during marine regressions. These valleys sometimes contain thick unconsolidated boulder and cobble gravels, interbedded with finer-grained sediments (e.g. the Keurbooms and Formosa formations of Butzer & Helgren 1972). These deposits are usually referred to the Cretaceous (e.g. Dingle et al. 1983), although Helgren & Butzer (1977) dated them as early Tertiary to early Pleistocene. They are here regarded as being of early to late Tertiary age (Table 1). The gravels are derived from talus debris eroded by fluviatile and marine action, perhaps with some clasts having been reworked from pre-existing deposits. They are most likely to have been deposited in their present position during marine transgressions, and are analogous to the finer-grained channel-fill and overlying marine sediments.of the south-western Cape (Elandsfontyn and Varswater formations), and Overberg (Bredasdorp Formation).

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REFERENCES

ARTHUR, M. A. & JENKYNS, H. C. 1981. Phosphorites and paleoceanography. Oceanologica Acta 1981: 83-96.

AXELROD, D. I. & RAVEN, P. H. 1978. Late Cretaceous and Tertiary vegetation history of Africa. In Werger, M. J. A. ed. Biogeography and ecology of southern Africa: 77-130. The Hague: W. Junk.

BERGGREN, W. A. & VAN COUVERING, J. A. 1974. *The Late Neogene*. Amsterdam: Elsevier.

BIRCH, G. F., THOMSON, J., McARTHUR, J. M. & BURNETT, W. C. 1983. Pleistocene phosphorites off the west coast of South Africa. *Nature (Lond.)* 302: 601-3.

BUTZER, K. W. & HELGREN, D. M. 1972. Late Cenozoic evolution of the Cape coast between Knysna and Cape St Francis, South Africa. *Quaternary Research* 2:143-69.

COETZEE, J. A. & ROGERS, J. 1982. Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology* 39:71-85.

COOPER, M. R. 1977. Eustasy during the Cretaceous: its implications and importance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 22:1-60.

COOKE, H. B. S. 1978. Africa: the physical setting. *In* Maglio, V. J. & Cooke, H. B. S. *eds*. *Evolution of African mammals*: 17-45. Cambridge, Mass.: Harvard University Press.

DEACON, H. J. 1983. The comparative evolution of mediterranean-type ecosystems: a southern perspective. *In* Kruger, F. J., Mitchell, A. & Jarvis, J. U. M. *eds* *Mediterranean-type ecosystems. The role of nutrients*: Berlin: Springer-Verlag.

DINGLE, R. V. & HENDEY, Q. B. in press. Late Mesozoic and Tertiary sediment input to the eastern Cape Basin (S E Atlantic) and palaeo-drainage systems in southwestern Africa. *Marine Geology*.

DINGLE, R. V. & ROGERS, J. 1972. Pleistocene palaeogeography of the Agulhas Bank. *Transactions of the Royal Society of South Africa* 40:155-65.

DINGLE, R. V., SIESSER, W. G. & NEWTON, A. R. 1983. *Mesozoic and Tertiary geology of southern Africa*. Rotterdam: Balkema.

FARQUHARSON, F. L. 1962. The distribution of cyprinids in South Africa. *Annals of the Cape Provincial Museums* 2:233-51.

FISCHER, A. G. 1981. Climatic oscillations in the biosphere. *In* Nitecki, M. H. *ed*. *Biotic crises in ecological and evolutionary time*: 103-31. New York: Academic Press.

FRAKES, L. A. 1979. *Climates throughout geologic time*. Amsterdam: Elsevier.

GERRARD, I. & SMITH, G. C. 1980. *The post Palaeozoic succession and structure of the south-western African continental margin*. Johannesburg: SOEKOR.

GLASS, J. G. K. 1977. Deep weathering of the southwestern Cape Granite and Malmesburg Group: palaeoclimatic implications. *Technical Report of the Joint Geological Survey/University of Cape Town Marine Geoscience Group* 9:118-35.

HELGREN, D. M. & BUTZER, K. W. 1977. Paleosols of the southern Cape coast, South Africa: implications for laterite definition, genesis and age.

The Geographical Review 67:430-45.

HENDEY, Q. B. 1981a. Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum* 84:1-104.

HENDEY, Q. B. 1981b. Geological succession at Langebaanweg, Cape Province, and global events of the late Tertiary. *South African Journal of Science* 77:33-8.

HENDEY, Q. B. 1982. *Langebaanweg. A record of past life*. Cape Town: South African Museum.

HENDEY, Q. B. & DINGLE, R. V. in press. Onshore sedimentary phosphate deposits in south-western Africa. *In* Northolt, A. & Sheldon, R. P. *eds* *World phosphate rock resources*. Cambridge: Cambridge University Press.

JUBB, R. A. 1964. Freshwater fishes and drainage basins. *South African Journal of Science* 60:17-21.

JUBB, R. A. 1965. Freshwater fishes of the Cape Province. *Annals of the Cape Provincial Museums* 4:1-72.

KENNETT, J. P. 1980. Paleoceanographic and biogeographic evolution of the Southern Ocean during the Cenozoic, and Cenozoic microfossil datums. *Palaeogeography, Palaeoclimatology, Palaeoecology* 31:123-52.

KING, L. C. 1978. The geomorphology of central and southern Africa. *In* Werger, M. J. A. *ed*. *Biogeography and ecology of southern Africa*: 1-17. The Hague: W. Junk.

KVASOV, D. E. & VERBITSKY, M. Y. 1981. Causes of Antarctic glaciation in the Cenozoic. *Quaternary Research* 15:1-17.

LAMBRECHTS, J. J. N. 1979. Geology, geomorphology and soils. *In* Day, J., Siegfried, W. R., Louw, G. N. & Jarman, M. L. *eds* Fynbos ecology: a preliminary synthesis. *South African National Scientific Programmes Report* 40:16-26.

LANGFORD-SMITH, T. 1978. A select review of silcrete research in Australia. *In* Langford-Smith, T. *ed*. *Silcrete in Australia*: 1-11. Armidale: University of New England.

LANGFORD-SMITH, T. & WATTS, S. H. 1978. The significance of coexisting siliceous and ferruginous weathering products at select Australian localities. *In* Langford-Smith, T. *ed*. *Silcrete in Australia*: 143-65. Armidale: University of New England.

MAGLIO, V. J. 1978. Patterns of faunal evolution. *In* Maglio, V. J. & Cooke, H. B. S. *eds* *Evolution of African mammals*: 603-19. Cambridge, Mass.: Harvard University Press.

MARTIN, A. K. 1981. Evolution of the Agulhas Current and its palaeoecological implications. *South African Journal of Science* 77:547-54.

MARTIN, A. R. H. 1962. Evidence relating to the Quaternary history of the Wilderness Lakes. *Transactions of the Geological Society of South Africa* 65:19-42.

McGOWRAN, B. 1979. The Tertiary of Australia: foraminiferal overview. Marine Micropaleontology 4:235-64.

NETTERBERG, F. 1978. Dating and correlation of calcretes and other pedocretes. Transactions of the Geological Society of South Africa 81:379-91.

NETTERBERG, F. 1980. Geology of southern African calcretes: 1. Terminology, description, macrofeatures and classification. Transactions of the Geological Society of South Africa 83:255-83.

READ, J. F. 1974. Calcrete deposits and Quaternary sediments, Edel Province, Shark Bay, Western Australia. American Association of Petroleum Geologists Memoir 22:250-82.

ROGERS, J. 1980. First report on the Cenozoic sediments between Cape Town and Elands Bay. Report of the Geological Survey of South Africa 1980-165:1-64. (Open file.)

RUSSELL, K. L. 1968. Ocean ridges and eustatic changes in sea level. Nature (Lond.) 218:861-2.

SCHALKE, H. J. W. G. 1973. The Upper Quaternary of the Cape Flats area (Cape Province, South Africa). Scripta Geologica 15:1-57.

SCHOLTZ, A. in press. The palynology of the upper lacustrine sediments of the Arnot pipe, Banke, Namaqualand. Annals of the South African Museum.

SCHUMANN, E. H., PERRINS, L-A. & HUNTER, I. T. 1982. Upwelling along the south coast of the Cape Province, South Africa. South African Journal of Science 78:238-42.

SIESSER, W. G. 1978. Aridification of the Namib Desert: evidence from oceanic cores. In Van Zinderen Bakker, E. M. ed. Antarctic glacial history and world palaeoenvironments: 105-13. Rotterdam: Balkema.

SIESSER, W. G. 1980. Late Miocene origin of the Benguela upwelling system off northern Namibia. Science 208:283-5.

SIESSER, W. G. & DINGLE, R. V. 1981. Tertiary sea-level movements around southern Africa. Journal of Geology 89:83-96.

SIESSER, W. G. & MILES, G. A. 1979. Calcareous nannofossils and planktonic foraminifers in Tertiary limestones, Natal and eastern Cape, South Africa. Annals of the South African Museum 79:139-58.

SUMMERFIELD, M. A. 1983. Silcrete as a palaeoclimatic indicator: evidence from southern Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 41:65-79.

TANKARD, A. J. 1974. Varswater Formation of the Langebaanweg-Saldanha area, Cape Province. Transactions of the Geological Society of South Africa 77:265-83.

TANKARD, A. J. 1975. The late Cenozoic history and palaeoenvironments of the coastal margin of the south-western Cape Province, South Africa. Unpublished Ph.D. thesis: Rhodes University.

TANKARD, A. J. 1976. Cenozoic sea-level changes: a discussion. Annals of the South African Museum 71:1-17.

TANKARD, A. J. & ROGERS, J. 1978. Late Cenozoic palaeoenvironments on the west coast of southern Africa. Journal of Biogeography 5:319-37.

VAIL, P. R., MITCHUM, J. R. & THOMPSON, S. 1977. Seismic stratigraphy and global changes of sea-level. American Association of Petroleum Geologists Memoir 26:49-212.

VISSER, H. N. & SCHOCH, A. E. 1973. The geology and mineral resources of the Saldanha Bay area. Geological Survey of South Africa Memoir 63:1-150.

WEINART, H. H. 1976. Past climate derived from calcrete and N-value. Annals of the South African Museum 71:133-40.

WOPFNER, H. 1978. Silcretes of northern South Australia and adjacent regions. In Langford-Smith, T. ed. Silcrete in Australia: 93-141. Armidale: University of New England.

SOILS, SOIL PROCESSES AND SOIL DISTRIBUTION IN THE FYNBOS REGION: AN INTRODUCTION

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INTRODUCTION

In theory it is possible to have soils that are in equilibrium with the present environment. This implies that they have developed under conditions where parent material, climate, topography and biotic factors have been constant and they show no characteristics inherited from previous environmental conditions (Ruellan 1971). In practice most soils show some features which are relictual and not in phase with the present environment. This applies to the soils of the fynbos biome in a landscape of high antiquity as well as to younger landscapes. Relict features in themselves do not imply great age in absolute terms although they can be very old; rather their age is dependent on the tempo of soil evolution in a particular setting.

A palaeosol (Ruellan 1971) by contrast is a soil that is characterized largely by attributes that relate to past soil forming processes under environments different from the present. In such cases soil formation may have been interrupted by burial or the characteristics of the soil may be irreversible and persist unaltered through time. Erosion rather than deposition has characterized the fynbos landscape in the Cenozoic. Yet in coastal environments and locally inland, the substrates which are the product of deep weathering under more humid climates than the present, where not stripped by erosion, may be mantled by sands or younger soil materials. These preweathered substrates could not have formed under present-day conditions and are palaeofeatures. Some duricrusts which form noteworthy features in the fynbos landscape are also palaeosoil materials which may be of high antiquity. Their preservation is due to their resistance to both erosion and chemical alteration.

A number of factors have contributed to the evolution of the modern soils found in the fynbos landscape. Important amongst these have been climatic changes throughout the Cenozoic which have influenced the distribution and properties of soil and soil materials found in the region. Another factor has been the geomorphological history controlling the evolution of the landscape. The Cape Fold Mountains are ancient features of the landscape and were largely moulded in their present form by erosion in the Cretaceous or earlier times. Transgression and regression of sea levels during the Cenozoic have resulted in changes in stream erosion base levels and landscape dissection with the consequent stripping of older soils, exposure of preweathered materials and remodelling of earlier erosion surfaces. In this way new parent materials have been provided for ongoing soil forming processes. The soils of the fynbos region are both old and young and they are the products of dynamic changes. A challenge in their interpretation is to separate inherited or derived characteristics from those which are more clearly recent in their development. Although inherited characteristics have no relationship to modern conditions, they can provide important palaeoecological information. In this paper the palaeoecological value of studying soils and soil materials is highlighted. These materials provide an essential line of evidence on the history of the biome and evolution of the biota, because in the fynbos biome the importance of a range of plant taxa which are substrate specialists is particularly noteworthy. A general review of the soils of the fynbos is given elsewhere (Lambrechts 1979) and this paper should be consulted in conjunction with that contribution.

WEATHERING AND SOIL FORMATION IN THE EARLY CENOZOIC

The warm humid climates that prevailed at the Cape in the earlier Cenozoic led to weathering and soil formation similar to that of subtropical and tropical climates. Under such conditions and with free drainage on the coastal forelands, there was rapid ferrallitic chemical breakdown of primary silicates with feldspathic minerals weathering to kaolinitic clays and micaceous minerals changing to degraded mica clays, such as vermiculites but also mainly to kaolinite and residual oxides and hydroxides of iron and aluminium. An almost complete loss of basic cations, and to an extent silica, took place under appropriate conditions of internal drainage and leaching. The end result of this type of weathering was uniformly red or yellow-coloured, porous apedal soils with low base status.

With progressive weathering, the characteristic haematitic red and white mottling of the ferrallitic mottled zones (Mohr _et al_. 1972) was developed in depth below the soil solum. Under conditions of deep water tables pallid zones of varying thicknesses have developed. The thicknesses and uniformity of pallid zones in the fynbos landscape are however very variable and at times difficult to distinguish from the mottled zones. The total depth of saprolite (pallid and mottled zones) in places can exceed 50 m (Glass, pers. comm. 1973). The weathering front is very irregular depending as it does on the structure and lithology of the base rock. The weathering front in plutons of the Cape Granite Suite is very irregular and large dome-shaped bodies and small core stones of unweathered granite finger into the overlying kaolinitic saprolite. This is typical of the weathering processes in granites (Linton 1955). In the metamorphosed phyllites and schists of the Malmesbury Group, shales of the Bokkeveld Group and metasediments of the Kaaimans Group, the weathering front is less sharp, core stones are absent and the mottled and pallid zones can form a complex pattern. This kind of weathering is shown by substrates on the coastal platform where they have not been removed by subsequent erosion. These are fossil features and processes of pedogenesis in subsequent times and under different climates have modified these preweathered materials.

Due to the age of ferrallitic weathering profiles, the original landscapes in which they were developed have been variously modified by incision and stripping during subsequent erosion, and younger transported materials like marine clays and aeolian sands or locally derived materials like colluvial wash or soil creep may mantle the ferrallitic preweathered material. The result is that a considerable variety of soils may be found on different erosional surfaces in areas of ferrallitic preweathering (Fig. 1). Many soils may exhibit one or more relict features such as ferruginous grit lines, kaolinitic clay suites in the dry areas or haematitic mottled subsoils. Grit lines are a common feature of a number of soil units. They are particularly well developed in the residual soil unit (C2) in the south-western Cape and in the duplex soil unit (D5) in Outeniqualand.

DURICRUSTS

Soil materials cemented to varying degrees by iron or silica occur throughout the fynbos landscape and are generally referred to as duricrusts. Although not always exposed at the soil surface, duricrusts once formed can persist for great lengths of time because of their resistance to weathering and erosion and they are important in protecting the landscape from degradation. Thus duricrusts may be seen occupying top slope or crest positions in the landscape instead of the lower slope positions at which they were originally formed. This is known as slope or landscape inversion.

Iron crusts or ferricretes, although never extensive, are the most widespread duricrust type in the fynbos landscape. They vary greatly in morphology, degree of iron accumulation and mineralogy of the cement as a function of genetic environment and process. Under conditions of ferrallization, haematitic crusts develop as a result of residual accumulation of iron and loss of bases and silica (Alexander & Cady 1962). They have a vesicular appearance with red, yellow and white coloured mottles and seldom harden to the same degree as nodular or lamellar, goethitic iron crusts that develop as a result of absolute accumulation of iron and/or manganese under the influence of fluctuating ground water tables. Absolute iron accumulation crusts generally develop in concave foot slope positions at or near the upper boundary of perched water tables in sandy overburdens on

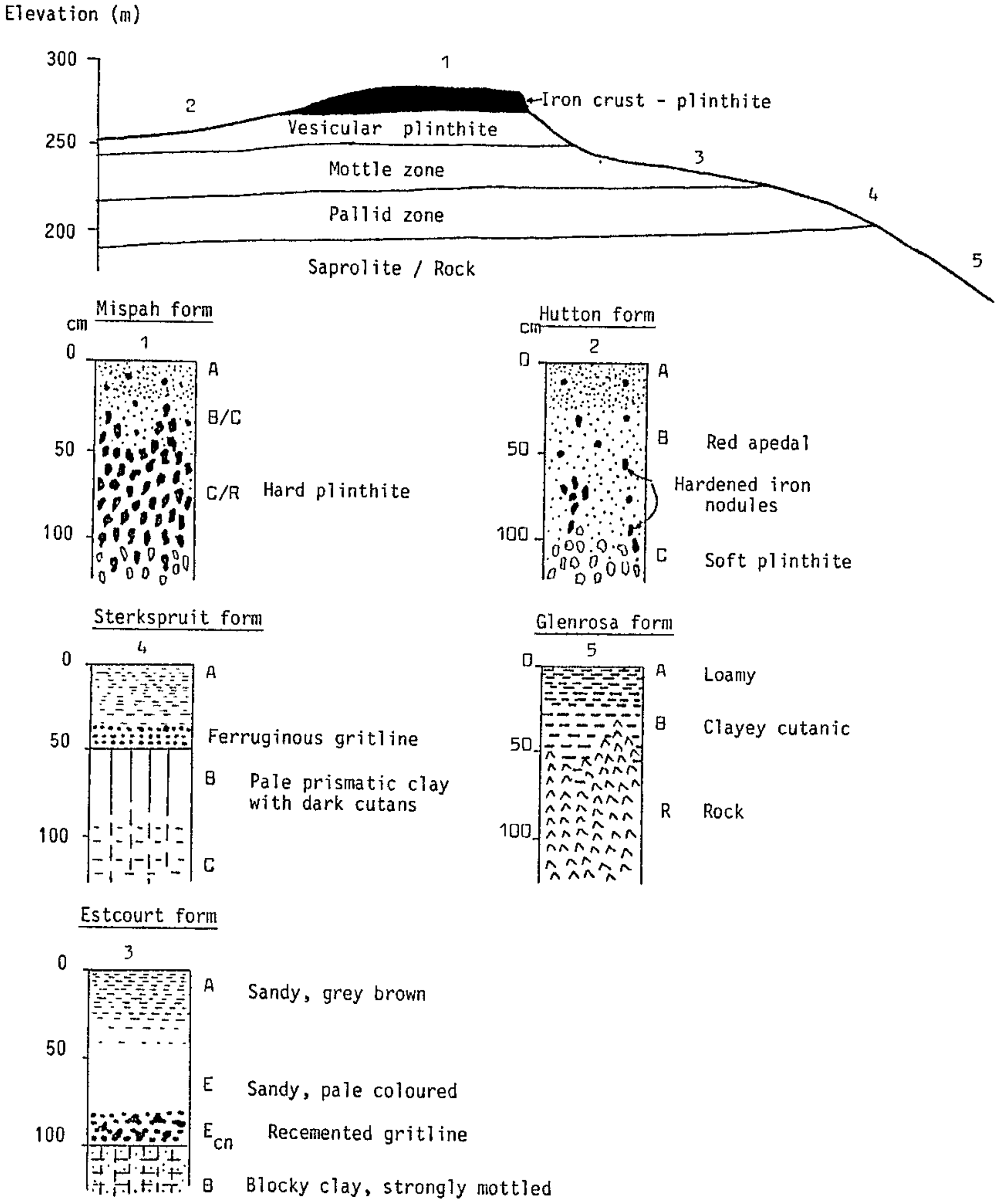

Fig. 1. A diagram showing the soils associated with an eroded and dissected pre-weathered granite landscape in the Stellenbosch surrounds.

relatively dense, impervious subsoil clays, saprolite or rock. In especially sandy or gravelly materials development can be rather rapid. Goethitic crusts can be very extensive as for example on the Katarra plain in the valley of the Sout River near Darling (vide Schloms et al., this volume).

Haematitic or upslope ferricretes, essentially from iron concentrated in the profile during ferrallitic weathering, can degrade rapidly because iron in this form is readily mobilized. In areas such as Paarl (Merryweather 1965) and Darling (Van Niekerk 1967), in situ ferricrete weathering has produced characteristic sandy loam red soils which are known as red apedal soils (vide Schloms et al., this volume). Stripping of the surficial apedal soils and upslope ferricretes through erosion and colluviation leads to deposition of iron-rich weathered materials in downslope positions where, under the influence of ground waters, they may become recemented by iron in the form of goethite. True haematitic ferricretes thus seldom form pronounced scarps. Goethitic ferricretes on the other hand have greater physical and chemical stability and may form relatively pronounced scarps in a dissected landscape.

Although not as widespread as ferricretes, silcretes give rise to spectacular landscape features such as the flat-topped mesas and ridges in the Heidelberg and Albertinia areas in the Overberg region (Ellis 1973) and silcrete plains near Oudepos, north of Malmesbury. Various forms of silcrete have been described by Ellis (1973) and Frankel (1952). In the Heidelberg area the silcretes occur on Bokkeveld shales, at an average elevation of 300 m above sea level and generally have a very coarse polygonal to prismatic structure at the surface which grades into a more massive to weakly lamellar structure deeper in the profile. Locally the upper zone appears conglomeritic with chemically precipitated silica nodules in an amorphous silica matrix. With depth the nodules are replaced by finely divided silica. Abruptly beneath this extremely hard grey silcrete, soft pale-coloured kaolinized shales occur. In localities where ochre is mined in kaolinized shales, the pallid zone is reddish to pinkish-coloured. The silcretes near Albertinia at elevations of between 250 and 330 m also exhibit the nodular structural features. The nodular layer may, however, occur below, above or in fine-grained massive cemented horizons, and more than one nodular layer may be present in any vertical sequence (Frankel 1952). Frankel also observed simple or multiple silcrete layers in clay on slopes with very little evidence of their persistence into the hillside.

In the Cretaceous basin at Heidelberg (Ellis 1973), the silcretes associated with Enon Conglomerate are composed of pebbles, cobbles and boulders of quartzite cemented by silica. The underlying pallid zone, as well as the silcrete itself, is more reddish probably due to the higher iron content of the parent rock. On the lower coastal plain at 140 - 150 m and at even lower altitudes, Ellis (1973) has described silcretes that are less compact and that show a lower degree of cementation than the 100 m silcretes.

Rounded silcrete fragments and quartzite gravels form the skeleton of these crusts.

Silcretes have a somewhat anomalous distribution occurring in Namaqualand, on the Cape coastal forelands, in the Little Karoo, between the Outeniquas and the Swartberg ranges, at high altitudes at Grahamstown, at Fort Grey near East London, and as far east as Kokstad (Frankel 1952; Ellis 1973; Maud, pers. comm.). They are apparently absent from Natal. In all cases they are associated with deep weathering although they may be developed in colluvial mantles. Summerfield (1983) has classified these as weathering profile silcretes, noteworthy for a relatively high TiO_2 content and suggested that their genesis is related to local mobilization and precipitation of silica as well as titanium under acid conditions. He considers silica replacement of clays in the weathered profile to have been important and that this type of silcrete formation is related to weathering under abundant vegetation and a humid subtropical to tropical climate. Since silcrete formation has been operative over a long time range, such climatic conditions could have existed in the fynbos region during its formation in the Cenozoic. The variability in silcrete petrology and the association of silcretes with different erosion surfaces however suggests that different stages and ages of silcrete formation may be present. They are however essentially fossil features in the landscape and are unrelated to weathering conditions that are found under mediterranean-type climates. All these silcretes are thus Pliocene and older.

EROSION AND SOIL CREEP

Changes in base levels of erosion during the Cenozoic due to relative changes in sea level have resulted in the stepped erosion or planation surfaces that characterize the coastal platform and incision of these surfaces. These changes in base level complicate the understanding of soil distribution in the fynbos landscape.

In palaeo-ferrallitic weathering environments, periods of accelerated erosion and dissection have variously led to the exposure of plinthite, mottle zones, pallid zones and unweathered bedrock as the parent materials for subsequent soil formations under more stable conditions. Under such conditions a particular slope sequence of soils may be found with soils with ferricrete horizons in the upper slope position followed by gleyed kaolinitic clays in the mid-slope positions and shallow soils on bedrock on the lower slope positions. This generalized sequence is rendered more complex where the ferrallitic weathering front has been highly irregular as in areas of granitic rocks. Where erosion has led to the development of a more uniform surface cut into preweathered profiles and the general depth of weathering was of the same order, there is widespread uniformity in soil types. A good example is the 100 m plus surface associated with duplex soils extending from Eendekuil, Hermon, Gouda and Agter Paarl to Lynedoch in the south-western Cape. The B horizons of these soils are residual, mottle zone materials of the fossil preweathered profiles.

Slow mass movement of soil and soil materials down slope under the influence of gravity is a normal process in a mature landscape with some relief and a competent vegetation even when erosion is not pronounced. These soil creep layers are generally separated from the in situ underlying soil material by grit lines composed of rounded ferruginous gravels, stones and even stone artefacts, essentially a lag deposit. This is a continuous process in upland areas and the soil creep or colluvial layers vary considerably in thickness and texture depending on the distance of transport, the source material itself and the slope angle and shape. A thick (0,5 m) coarse sandy creep layer forms the A and E horizons of the duplex soils on the extensive Katarra plain (vide Schloms et al., this volume) in the Darling and Stellenbosch areas. Colluviation of high-lying red ferrallitic materials has resulted in the occurrence of red apedal soils adjacent to duplex soils on lower surfaces. In the hills west of Darling colluvial red soils are found adjacent to unweathered granite with grit lines marking the contact.

THE PALAEOECOLOGICAL VALUE OF SOILS AND SOIL MATERIALS

The most obvious soil related feature indicating environmental conditions different from the present in the fynbos region is the occurrence of ferrallitic weathered profiles. Such deep weathering could only have developed under more humid Cenozoic climates. There is also a clear pattern of soils or pedological systems that can be recognized in the region that may provide more detailed palaeoecological information. These are suites of similar soils found associated with particular terrain types reflecting episodes of planation and dissection and to a degree parent materials. No soil or soil material on any terrain remnant can be older than the age of the surface and may be of any younger age. However, even with polycyclic soil development some inherited soil characteristics may survive. This seems to apply in the fynbos region where suites of red apedal soils, residual soils, duplex soils and other forms show a coherent pattern in the landscape. Thus in the south-western Cape red apedal soils are found on the older dissected foothill zone of the Cape Fold Mountains, residual and duplex soils are found on the planation surfaces informally known as the higher and lower Swartland and Katarra surfaces (vide Schloms et al., this volume) and different duplex soils are found associated with lower planation surfaces. The soils of the lowest and youngest land forms in the landscape are podzolic or calcareous and preweathering of the substrates is of no consequence.

There are obvious difficulties in interpreting the sequence of suites of soils in terms of simple palaeoecological parameters such as temperature and precipitation but the implications of the gross patterning are clear. Climates have become drier and pedogenesis less pronounced through the Cenozoic. Red apedal soils for example are not forming under the present climate; they are a legacy from weathering under more humid climates. Shallow residual soils on granite or shales are in balance with present day climate and the clay mineralogy of their B horizons will reflect the present weathering environment. For podzolic soils, however, it is difficult to determine their evolutionary stage. In the mountains and in high rainfall areas on the coastal platform brown fulvic stream waters are positive evidence of podzolization being active at present. Some podzolic features in these soils such as multiple ferrihumic horizons, thin iron or placic pans and bleaching of existing dark B horizons may be interpreted as evidence of palaeo-podzolization and more recent degradation. In the deep acid sands of the south-western Cape podzolic features are associated with low annual precipitation values and white waters. Can these soils still develop under these conditions, or are they palaeosols?

Although soils are of potential palaeoecological value, it is of importance to keep in mind that soil properties and distribution even in relatively uniform soil units (*vide* Schloms *et al*., this volume) may vary greatly depending on local variation in topography and parent materials. The interpretation of the palaeoecological significance of soils and soil materials needs to be approached with due caution because of the complexities of soil forming processes operating through time.

REFERENCES

ALEXANDER, L. T. & CADY, J. G. 1962. Genesis and hardening of laterite in soils. *Technical Bulletin* 1281. Washington DC: USDA.

ELLIS, F. 1973. Soil studies in the Duiwenhoks River catchment area. Unpublished M.Sc. thesis: University of Stellenbosch.

FRANKEL, J. J. 1952. Silcrete near Albertinia, Cape Province. *South African Journal of Science* 49:173-182.

LAMBRECHTS, J. J. N. 1979. Geology, geomorphology and soils. *In* Day, J., Siegfried, W. R., Louw, G. N. & Jarman, M. L. *eds* Fynbos ecology: a preliminary synthesis. *South African National Science Progress Report* 40:16-26.

LINTON, D. L. 1955. The problem of tors. *Geographical Journal* 71:470-486.

MERRYWEATHER, F. R. 1965. The soils of the Wellington-Paarl area. Unpublished M.Sc. thesis: University of Stellenbosch.

MOHR, L. C. J., VAN BAREN, F. A. & VAN SCHUYLENBORG, J. 1972. *Tropical soils*. The Hague: Mouton.

RUELLAN, A. 1971. The history of soils. *In* Yaalon, D. H. *ed*.

Paleopedology. Jerusalem: Israel University Press.

SUMMERFIELD, M. A. 1983. Silcrete as a palaeoclimate indicator: evidence from southern Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 41:65-79.

VAN NIEKERK, B. J. 1967. The soils of the Darling area. Unpublished M.Sc. thesis: University of Stellenbosch.

SOILS OF THE CAPE COASTAL PLATFORM

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INTRODUCTION

Periurban pedological surveys in the south-western Cape and land type surveys in the southern Cape area carried out by the staff of the Soil and Irrigation Research Institute over an extended period gave the impetus to this attempt to provide a description and maps of the soils of the Cape coastal platform between the Berg and the Storms rivers. It was apparent from the classification of soils on the basis of morphology and textures in the south-western Cape that a series of natural units could be defined that showed a consistent relationship to the terrain, parent material and altitude. These units of morphologically similar soils had obvious equivalents on the coastal platform to the east (Overberg and Outeniqualand) and this has allowed the preparation of a series of four maps at 1:250 000 which accompany this report, and which cover the three regions recognized here, the south-western Cape, the Overberg and Outeniqualand.

The soil forms and series associated with the units are given in brackets and follow the binomial system of soil classification in use in South Africa (Macvicar et al. 1977). Soil properties such as leaching status, texture, structure and impermeable subsoil clay horizons are implied in the classification of soil forms and series. The binomial system is a two-level classification where the soil form represents a specific sequence of diagnostic soil horizons. Altogether there are five topsoil and fifteen subsoil diagnostic horizons. The soil series is a subdivision of the soil form on the basis of clay content and sand fraction (fine to coarse) of the diagnostic horizon, leaching status, presence of free lime, pH and colour. These features enable a large number of soil use interpretations to be made.

A separate key to the maps is provided and suggestions are made in the key for colouring in the maps with standard coloured pencils. This paper provides a description of the 10 units and the numerous subunits in each region.

The units are defined as follows:

A. Calcareous coastal sands: these include mobile or stabilized calcareous sands forming coastal dunes.

B. Acid sands: these are either leached non-calcareous coastal sands or colluvial sands occurring in intermontane valleys.

C. Residual soils: these are soils formed by in situ weathering and can be recognized by the retention of characteristics of the underlying parent materials (Fig. 1) but excludes duplex soils as defined under unit D.

D. Duplex soils: refers to soils with a relatively permeable topsoil abruptly overlying a very slowly permeable diagnostic horizon which is not a hardpan. In the study area these soils are usually of binary character with the A-E horizons texturally and lithologically distinct from the clayey B horizons. They occur in relatively flat landscapes.

E. Silcretes: these are duricrusts associated with pallid zones that represent relicts of formerly more extensive sheets. They are palaeosol features.

F. Red apedal soils: these are red in colour and have weakly developed structure that is never prismatic or blocky. They are generally well drained.

G. Soils associated with upland gravels and screes: these are soils associated with old colluvial and fluviatile materials on the higher inland margin of the coastal platform.

H. Soils on sandstone benches: these are generally thin acid lithosols that are found on structural features like surf cut platforms close to the coast and joint controlled bevels in the upland mountain areas.

I. Soils of river valleys: these soils are found on the sides of valleys or on the flood plain alluvium.

J. Soils associated with mountains: these include a variety of shallow soils.

Subunits have been defined in the different regions for all units except the J unit, to take into account differences in degree of leaching and texture as well as differences in parent materials, relief and elevation. Some subunits are found in all three regions, others are more restricted in distribution. A region-by-region description of the soil morphology units and subunits is given below.

THE SOILS OF THE SOUTH-WESTERN CAPE

Along the western seaboard from False Bay to Elands Bay, shelly aeolian sands of Holocene and later Pleistocene age form patches or plumes of mobile dunes (A1) and more commonly low calcareous dunes stabilized by vegetation

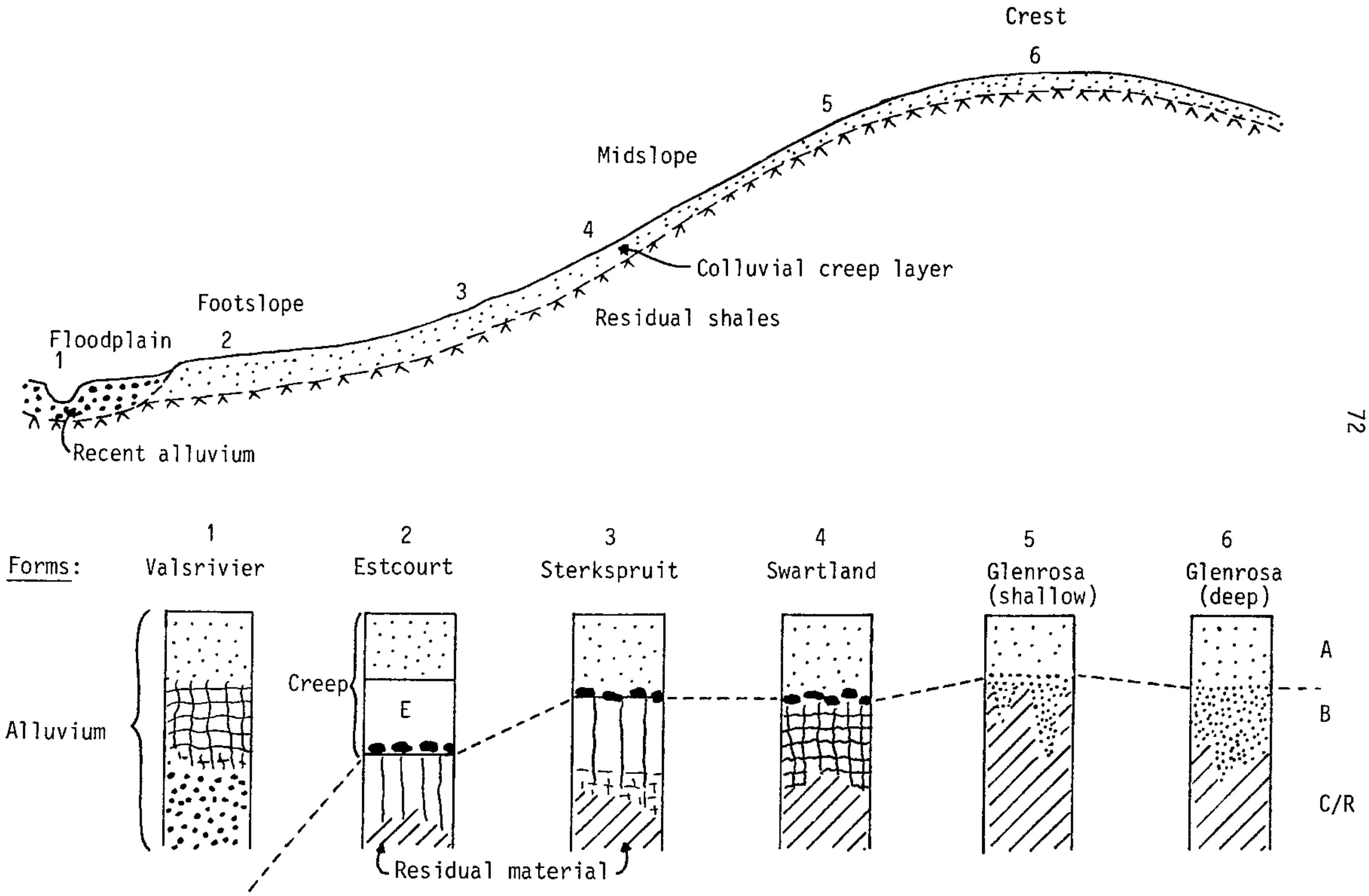

Fig. 1. Residual soils catena associated with undulating shale landscapes.

(A2). These dunes are found at elevations ranging from 0 - 200 m above sea level. The sands are deep (1 200 mm plus), slightly weathered and poorly leached due to their youth and the relatively low precipitation. The soils are mostly of the Fernwood (Fw 20, 21) form with the Mispah (Ms 22) form soils rare.

A parallel zone of acid sandy soils (B1) with a sharply defined boundary occurs inland of the calcareous sands. It is considered that these sands were originally calcareous and have become decalcified through leaching. The main source of the parent material appears to be sands accumulated in embayments along the coast during the Pliocene transgression (Rogers 1982; Hendey, this volume) with possible additional material contributed by dune plumes advancing inland. This sand mantle on the coastal platform forms a weakly undulating plain with an altitude of 70 - 110 m above sea level. Bleached podzolized soils of the Lamotte (Lt 11), Constantia (Ct 11) and acid series of the Fernwood (Fw 11) forms are dominant. Ground water ferricretes occur in patches to form Wasbank form soils. The soil profiles in the acid sands are deep (1 200 mm plus) and there are marked seasonal differences in the depth of the water tables. This subunit also extends locally up footslopes of hills as a relatively thin mantle of predominantly yellow coloured sands belonging to the Clovelly and Constantia soil forms. Haematitic ferricretes (R. W. Fitzpatrick, pers. comm. 1982) occur in these sands as relict features in upslope positions. The presence of red and yellow colours in the higher lying sands is an indication of an earlier stage of pedogenesis. Under conditions of hydromorphy and podzolization bleached sandy profiles have developed on the undulating plain.

Deep acid sands (B2) with similar physical and chemical properties to the B1 soils occur inland in the intermontane valleys. They are derived mainly from the quartzose members of the Cape Supergroup and their distribution has been controlled by fluvial and colluvial processes. These sands are also highly leached and podzolized and a similar catena to the B1 subunit, with yellow upslope soils grading through bleached podzolized soils to true podzol soils on the lower slopes, occurs.

The central plain of the south-western Cape where shales, phyllites and schists of the Malmesbury Group are the main preweathered parent substrates, residual soils occur in an undulating to rolling landscape. Two distinct erosion surfaces are distinguishable on the basis of their elevation and the relative degree of weathering of the substrates. On the lower surface (C1) at 80 - 140 m above sea level two groups of soils are found, both associated with thin loamy to gravelly surface creep layers. One group includes shallow Mispah (Ms 10) and Glenrosa (Gs 13) soil forms, found on convex slopes where most of the preweathered substrate has been removed. The other group includes duplex soils of the Swartland (Sw 31) and Sterkspruit (Ss 23) forms and these are found on plain remnants where some thickness of preweathered substrate is preserved. Silcretes and deflation pans are common on the plain

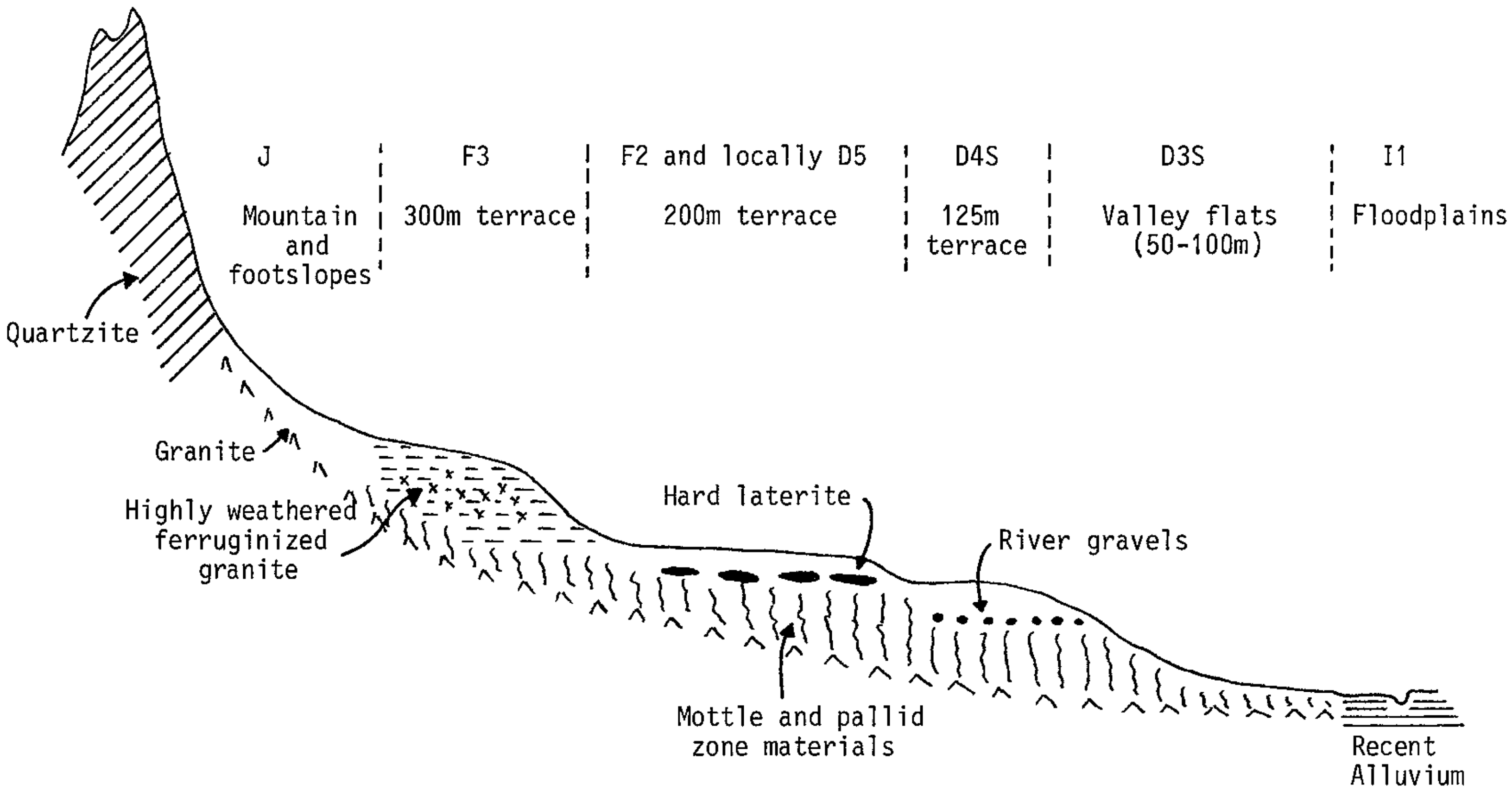

Fig. 2. A schematic section from Stellenbosch mountain to the Eerste River.

remnants and the soils are moderately to highly sodic or magnesic.

The higher surface (C2) at 150 - 200 m above sea level has similar soil forms associated with it, but because the underlying shales and phyllites show a higher degree of preweathering the soils are less sodic than those of subunit C1. No pans occur on the higher surface but true laterites with mottled saprolites and maghemitic grit lines (R. W. Fitzpatrick, pers. comm. 1982) are common.

Duplex soils of binary origin are found throughout the south-western Cape but different modes of deposition may be involved in the accumulation of the materials in which they are developed. In the Somerset West and Velddrift areas, the duplex soils occur on marine-cut benches at altitudes of about 30 m above sea level. These soils are grouped in the D1L subunit and are characterized by thin aeolian and colluvial fine to medium sandy loamy A horizons on marine and residual clays. The clays are generally sodic and salty. Hydromorphic green clays are common. Soils of the Estcourt (Es 33, 34) form are dominant with Kroonstad (Kd 21) and Sterkspruit (Ss 24) forms subdominant.

Further inland on the valley flats of the Sout, Berg, Diep and Papkuil rivers at 44 - 75 m altitude, sandy duplex soils (subunit D2S) consisting of aeolian sands of medium grade on fluvial and residual clays occur. Soils of the Kroonstad (Kd 21) and Estcourt (Es 41) forms are dominant. The subsoil clays are moderately sodic and stonelines are common at the sand-clay contact. In both subunits D1L and D2S the degree of weathering of the substrates is low.

At the headwaters of the Sout River (Darling) and lower Helderberg (Somerset West) at 50 - 100 m above sea level, coarse colluvial sand overlies highly preweathered clays which are low in sodium (subunit D3S). The dominant soils in these mature valley flats, commonly known as the Katarra flats in the Darling area, are Kroonstad (Kd 22) and Estcourt (Es 42) forms. Ferricretes and silcretes are widespread in this subunit. The boundary between the valley flats with duplex soils and the residual soils (C1) associated with the adjacent higher rolling Malmesbury shale landscape is abrupt and is a very characteristic feature in that part of the south-western Cape. The same soils are associated with the weakly dissected interfluves forming a plain at about 100-150 m in the Agter Paarl, Eendekuil, Hermon, Gouda and Lynedoch areas where coarse colluvial sands overlie residual clays and granites. Silcretes occur occasionally on this surface but sheet and concretionary ferricretes are widepsread and especially noteworthy in the Agter Paarl area.

Red apedal soils (F2 and F3) are widespread on high lying pediment plains and dissected footslopes in the south-western Cape (Fig. 2). Subunit F2 occurs as isolated patches in the Paarl, Agter Paardeberg, Malmesbury, Darling and Pools areas at 150 - 200 m altitude. The parent material consists of local creep or colluvium derived from adjacent ferrallitic environments and is moderately to highly preweathered. The overlying soils are red kaolinitic loams and clays with the Bontberg (Hu 25) and Msinga (Hu 26) series of the Hutton form dominant. Concretionary laterites are locally common and serve as parent material for present-day soils (Merryweather 1965).

Subunit F3 is associated with mountain or ridge footslopes (e.g. Helshoogte near Stellenbosch, and Rooihoogte near Malmesbury) and occur at 200 - 350 m altitude. The parent material on these dissected elevated pediments consists of highly weathered drift over preweathered saprolite and rock. Red kaolinitic clays are common with the Hutton (Hu 16) and Doveton (Hu 27) series of the Hutton form dominant. Stonelines on the boundary between the drift material and underlying saprolite and gravels are usually associated with these soils.

Sandstone benches (H1-H5) occur at various elevations ranging from 30 m (Betty's Bay) to 700 m (Piketberg mountain). The parent material consists of locally derived sandy colluvial or scree deposits of variable thickness on quartzitic bedrock. These materials are highly leached and the underlying rock is preweathered to varying degrees. Sandy podzolic and hydromorphic soils of the Houwhoek (Hh 30, 20), Cartref (Cf 30, 20) and Kroonstad (Kd 14) forms are common.

All river valleys and river terraces in the south-western Cape are grouped together in one subunit (I1). The parent material here is locally derived alluvial and fluvial deposits with a low degree of weathering. The soils are generally weakly developed and some are hydromorphic. Dominant soil forms are Dundee, Westleigh, Oakleaf and Valsrivier. Locally in lower lying areas they may be very saline.

All the mountains in the south-western Cape are grouped in unit J. They are the main physiographic feature and form the eastern boundary of the region. The parent material consists mainly of resistant quartzose sedimentary rock and granite which in some localities like Vredenberg show a very low degree of weathering. However, on higher-lying sections of the Du Toit's Kloof mountains the granite is deeply weathered. Highly leached, shallow sandy lithosols are found in these mountains. Dominant soil forms are Cartref (Cf 30, 20), Mispah (Ms 10) and Houwhoek (Hh 20, 30). The mountains together with the sandstone benches or flats and their associated fynbos shrubland vegetation make up an extensive area of the south-western Cape. Because of a low agricultural potential, the soils have been less disturbed by normal farming activity than the residual, red apedal and duplex soils.

THE SOILS OF THE OVERBERG

The coastal section of the Overberg area shows the same sequence of mobile

(A1) and stable calcareous (A2) sands as in the south-western Cape. These are bordered on the inland margin by older (Bredasdorp Formation) coastal limestones (A3) ranging from 50 - 250 m above sea level, formed in an embayment during the Pliocene transgression (Hendey, this volume). Whereas in the south-western Cape local blowouts and duneplume trails extending inland are a notable feature, in the Overberg region the mobile sands (A1) occur as more continuous fields of transverse dunes in a zone parallel to the coast. The distribution of the dune area is broken where mountains and sandstone benches extend to the coast. Found associated with the A1 and A2 subunits are sandy grey calcareous soils equivalent to those of the south-western Cape; however, Mispah (Ms 22) form soils and calcretes are more prominent. The A3 subunit exhibits more advanced pedogenesis and a wider spectrum of soils ranging from typical grey calcareous sands to red neutral loams of the Oakleaf (Oa 24) and Hutton (Hu 34) forms are found. The Mispah soil (Ms 22) form occurs on convex crest positions and on steep slopes.

Acid sands of aeolian origin (B1) are absent in the Overberg region and there are only restricted occurrences of acid colluvial sands (B2) on inland flats as in the Pearly Beach and Albertinia surrounds. These pediment-associated sands are heavily podzolized, Lamotte (Lt 11), Constantia (Ct 11) and Fernwood (Fw 11) soil forms being common. In the Albertinia area where a thin sand covering overlies clayey substrates, sandy hydromorphic duplex soils of the Kroonstad (Kd 21) form are found, and groundwater laterites are very common.

The residual soils in the Overberg region have been divided into four pedological subunits C1-C4. The first three are associated with rocks of the Bokkeveld Group and the last with Cretaceous conglomerates and clays. The C1 subunit occurs on an undulating plain, inland of the coastal sands, at altitudes of 110 - 140 m above sea level. Concretionary laterites and silcretes are present on remnants of an older plain and the soils range from shallow Glenrosa (Gs 13) on convex crests to duplex types like Swartland (Sw 31) and Sterkspruit (Ss 23) forms on the concave slopes. The degree of preweathering of the parent rock is moderate to low except under silcrete and laterite cappings where preweathered pallid and mottled zones are preserved. The C2 subunit is best developed on footslopes of the Kleinrivier, Bredasdorp and Potberg ranges which generally receive a higher rainfall. Due to the higher rainfall non-hydromorphic duplex soils of the Swartland (Sw 31) and Sterkspruit (Ss 23) forms are dominant with Glenrosa (Gs 13) rare. Maghemitic grit lines (R. W. Fitzpatrick, pers. comm. 1982) are found on the upper boundary of the residual clays in these soil profiles. The acid topsoils, thicker B horizons, and low plant nutrient levels, especially trace elements, are a result of higher precipitation. This subunit, C2, occurs at elevations from 150 - 200 m and the base material is moderately to highly preweathered. This is one of the few examples where fynbos shrublands are found on soils derived from Bokkeveld shales but disturbance through agricultural activities has largely resulted in the present dominance of renosterveld vegetation. Concretionary groundwater laterites are common throughout this subunit and are particularly well developed on the flats at Mierkraal, Bredasdorp.

The most extensive residual soil subunit (C3) occupying the central area of the Overberg and colloquially known as the Ruens, is a highly dissected landscape with relatively low rainfall. Aspect plays an important role in controlling soil moisture and temperature and consequently soil development. Shallow residual soils of the Glenrosa (Gs 13, 16) and Mispah (Ms 10) forms together with shale outcrops predominate on steep north-facing slopes and crests. Soils of the Swartland (Sw 31) form are rare and mainly restricted in occurrence to less steep, concave, cooler southern slopes. The rolling nature of the Ruens is indicative of intense dissection and stripping of surface materials. Silcretes, laterites and preweathered materials are consequently rare. Although the C1 and C2 subunits show a correspondence between the Overberg and south-western Cape subregion, the C3 subunit is absent from the latter (see description of E1 subunit).

Subunit C4 is restricted to Cretaceous conglomerates and clays which are highly susceptible to erosion and form a rolling landscape with terraced valleys. The parent material shows a low degree of pre-weathering and the soils, due to the high iron content (over 3% citrate-bicarbonate-dithionite extractable Fe), are generally reddish coloured. Red duplex soils of the Valsrivier form (Va 20, 21), generally sodic and saline in the lower slope positions, predominate. Brown and grey members of this form (Va 40, 41) with lime in the subsoil are found in the Hartebeeskuil area near Mossel Bay.

The duplex units (D) are restricted to featureless planed surfaces ranging from low elevations close to the coast to altitudes of up to 200 m further inland. In the west the D1L subunit is found on the Bredasdorp coastal plain at less than 30 m above sea level and further east it is associated with the flats adjacent to the Gouritz River. The soils of this subunit have developed from binary parent material consisting of fluvial-colluvial medium sands, overlying marine, fluvial or residual clays with a low degree of weathering. Sodic and calcareous variants of the Valsrivier (Va 40, 41), Sterkspruit (Ss 23, 24) and Estcourt (Es 33, 34) forms are most common on these materials. The low permeability of the swelling subsoil clays and the flatness of the topography makes the area covered by this subunit susceptible to flooding during heavy rains. Also included in the D1L subunit are Oakleaf form soils on recent alluvium in the Gouritz River valley.

The D2L subunit is restricted to the Wydgeleë and lower Heidelberg flats at elevations of 40 - 70 m and is found inland of the coastal limestones (A3) on flat to gently undulating valley plains. An exception is near Vleesbaai, where the soils are found in an area of deflation. The parent materials are limestones and marine clays which exhibit a low degree of weathering. The

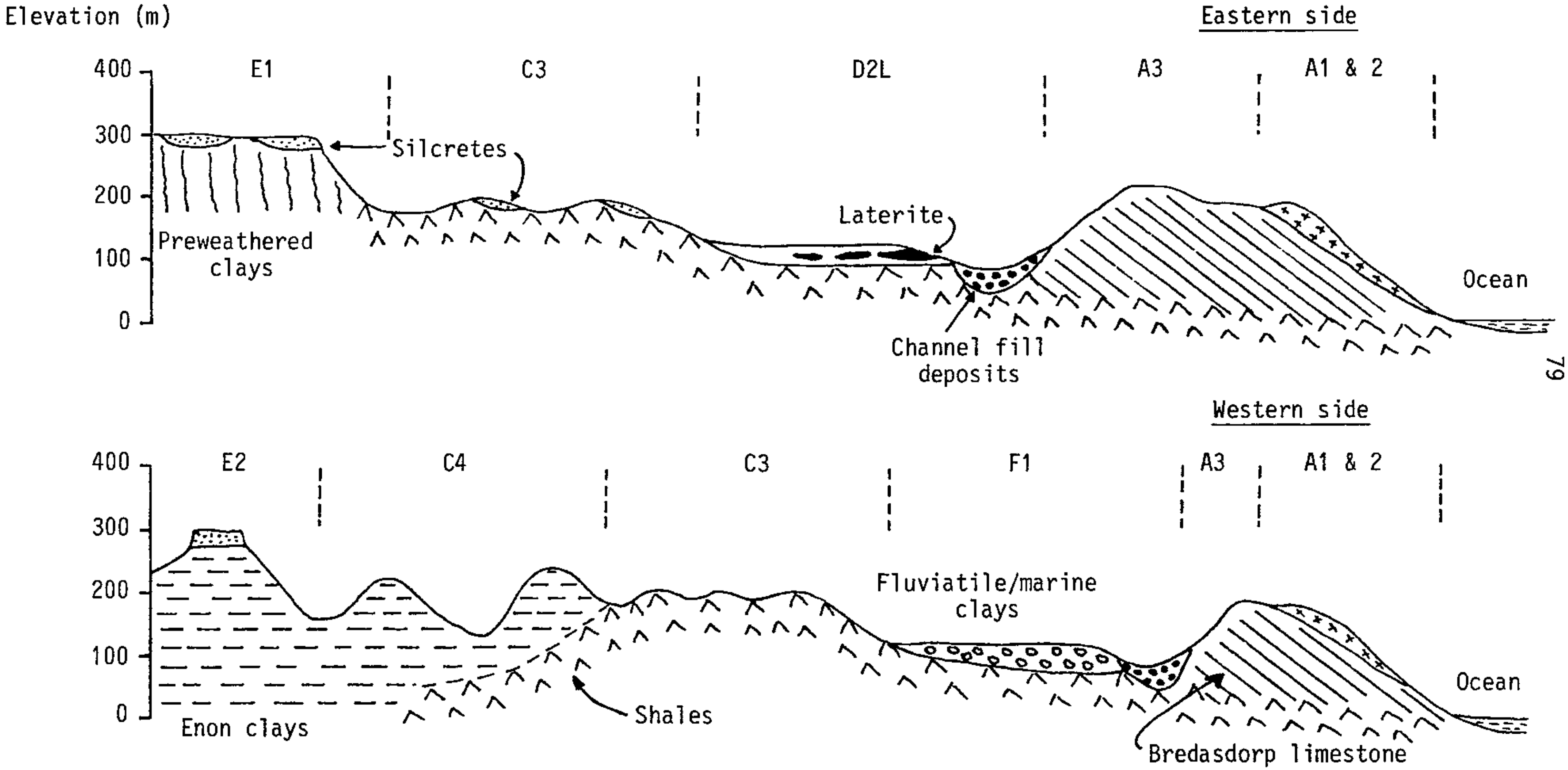

Fig. 3. Schematic north-south sections across the coastal platform in the Duivenhoks River catchment area, Heidelberg.

soils are generally shallow, dark coloured, calcareous loams of the Mispah (Ms 22) and Milkwood (Mw 20) forms, with well developed petrocalcic horizons (Ellis 1973). In weakly defined depressions saline, sodic duplex soils of the Valsrivier (Va 40) form occur. Piles of pale coloured petrocalcic blocks collected from ploughed fields are to be seen dotting this landscape. The soils associated with the 50 - 80 m high-lying Breede River terraces are grouped as subunit D2S. The parent materials are moderately weathered fluvial sands usually overlying residual clays. Quartzite cobbles are common in the sandy overburden. Estcourt (Es 41) and Kroonstad (Kd 21) are the main soil forms.

Extending from Swellendam in the west to Mossel Bay and Outeniqualand in the east, the D5L is associated with the dissected high level coastal platform at elevations of 200 - 250 m. This coastal platform is one of the most striking landscape features of the Overberg and Outeniqualand. The surficial cover is a thin loamy colluvial layer which in the west around Swellendam overlies residual moderately preweathered clays and to the east, in the neighbourhood of Mossel Bay, it overlies transported sodic calcareous clays probably of marine origin. Estcourt (Es 13, 33) and Sterkspruit (Ss 23) soils with maghemitic gravel lines are typical of this subunit. Between Albertinia and Mossel Bay, deflation pans are common and the surrounding areas are susceptible to episodic floods.

Amongst the oldest soil materials found in the whole landscape are silcretes, which cap mesas and overlie deep preweathered pallid zones (Fig. 3). These remnants represent a once more extensive occurrence of silcrete duricrusts. The E1 and E2 units occur at altitudes of 250 - 300 m but overlie different geological formations. Subunit E1 which extends from Bot River to Suurbraak occurs in a landscape similar to C3, namely a Bokkeveld shale rolling landscape. Prominent in this landscape are mesas of light coloured massive or polygonal silcretes with its associated whitish pallid zones. Well developed duplex soils such as Sterkspruit (Ss 23) and Estcourt (Es 33) occur on the highly preweathered pallid zone material. Laterites are commonly found in close relationship to silcretes generally below or at slightly lower positions and maghemitic gravel lines are invariably found in the duplex soils. The silcretes have provided some protection against erosion but where extensive stripping of the preweathered pallid material has occurred, weakly developed duplex and lithosols of the Swartland (Sw 31) and Glenrosa (Gs 13, 16) forms are found.

Silcrete mesas and related preweathered materials found on Enon gravels and clays in the Heidelberg-Riversdale areas are grouped together in subunit E2. The ferritic and gravelly silcrete cappings contrast with the light coloured silcretes of E1 and the degree of preweathering in the underlying materials is somewhat lower. The latter materials are extensively mined for ochre. The soils of this area are structured red Valsrivier (Va 21) and red duplex Sterkspruit (Ss 16) forms with generally a low degree of preweathering but moderate to high preweathering where there is a more direct association with silcretes.

A small area of silcrete on the eastern footslope of Potberg caps quartzite colluvium and is the lowest altitudinal occurrence of silcretes in the region. The soils (E3) show a low degree of preweathering and weakly developed gravelly sands and sandy loams are found. The vegetation of the silcrete mesas of E1 and E2 is fynbos shrubland.

Red apedal soils (F1 to F3) are not as extensive as in the south-western Cape and they exhibit a lower degree of weathering and leaching, possibly indicative of a younger age or different parent material. On the Heidelberg flats and west of Wydgeleë and Vlees Bay at 80 - 110 m altitude, red loams and clays with lime (Hu 36, 43, 46) occur on high level plains or a marine-cut bench indicated by the occurrence of discoidal pebbles (F1). The origin of the parent material in which the soils have developed are diverse and include marine and fluvial deposited clays as well as <u>in situ</u> weathered shale material. Deflation pans are common on the Heidelberg flats.

Between Albertinia and Herbertsdale at approximately 200 m above sea level, red apedal soils are associated with a flat high level plain (F3) and with areas incised by the Gouritz River and its tributaries (F2). The soils of both the F2 and F3 subunits have developed in local drift and in saprolite on shales of the Bokkeveld Group. Lime is usually absent in the soils of F3 which are highly erodable and Hutton (Hu 36) and Swartland (Sw 21, 11) soil forms are characteristic of this subunit. The presence of lime, possibly derived from the Cretaceous-Tertiary calcareous deposits, is a distinguishing feature in the soils of F2 and it is reflected by the presence of the calcareous series of the Hutton (Hu 46) and Swartland (Sw 21) soil forms. These red apedal soils of F1-3 are well drained and except in abnormally dry years have a high agricultural potential.

Upland gravels found at 300 - 400 m altitude, associated with the highest, dissected parts of the coastal platform, are designated as subunits G1 and G3. On the southern footslopes of the Langeberg range and at Herbertsdale, thick colluvial gravels and screes composed of quartzitic materials are found. Up to 90% of the material is in the cobble and boulder grades and the matrix is medium sand while podzolic soils of the Lamotte (Lt 12) form predominate. Seepage laterites are widespread in this environment. In the Grabouw area, a thinner mantle of transported gravels consisting of ferruginized shale clasts in a more clayey matrix, overlies shales of the Bokkeveld Group which are highly preweathered (G3). Hydromorphic duplex soils of the Kroonstad (Kd 13, 16) and Pinedene (Pn 26) forms which have dark-coloured A horizons with goethitic pisoliths, are dominant. Recent ground water laterites are found on crest positions in this gently undulating plain.

Sandstone benches of the same form and altitudinal range as in the south-western Cape are found in the western part of the Overberg. The physical and chemical properties of the associated soils in the two regions are largely the same but some subunits in the Overberg region merit special mention. The H2 subunit in the Elim-Baardskeerdersbos area consists of a thick podzolized sand mantle and typically growing on this substrate are numerous fynbos shrubland taxa. The soils have low agricultural potential because of their sandy nature and low nutrient status and the area is only suitable for grazing. The H4 subunit in the Cooper Siding and Mossel Bay areas at 200 m, forming part of the coastal platform, is noteworthy for the occurrence of duplex soils similar to those in subunit D51. Podzolic soils usually associated with these benches are virtually absent here because of the presence of a thin cover of marine clays. Locally in areas where the clays have been removed by stripping, quartzite rock benches with Houwhoek (Hh 30, 20) soils occur. On the break in slope between units J and H4, silcretes similar to those in E3 are found and are noteworthy in being rich in titanium (A. R. Milnes, pers. comm. 1983).

The river valley and mountain units in the Overberg region are not markedly different from the equivalent units in the south-western Cape.

THE SOILS OF OUTENIQUALAND

In this region the coastal platform is relatively narrow and terminates at the coast in steep cliffs. There are rare embayments as for example at Mossel Bay-Glentana, the Wilderness and Plettenberg Bay. The proximity of the mountains to the coast in this region contributes to higher orographic rainfall and precipitation occurs in all seasons. The coastal fringe is so narrow that although mobile sand dunes occur in the embayments, the areas are too small to be mappable at a scale of 1:250 000.

Under these climatic conditions, dunes are rapidly stabilized by vegetation (A2) and only the outermost and youngest dunes are markedly calcareous (Fernwood form Fw 10, 20, 21). The leaching of lime, release of iron, and clay movement take place with stabilization of the sands resulting in the formation of soils of predominantly the Vilafontes (Vf 11, 21) form. In the Mossel Bay-Glentana embayment, soils of the Mispah (Ms 22) form are found in association with calcretes.

Two subunits of acid sands have been mapped. The B3 subunit, found between Wilderness and Knysna, represents older coastal dunes in which the solum has been decalcified and leached producing acid soils of the Fernwood (Fw 10, 11) and Vilafontes (Vf 11, 21) forms. Small patches of these soils are also found in the Glentana and Nature's Valley areas. Localized occurrences of Lamotte (Lt 11) soils are found in more sandy lithologies and are important because they are associated with forest. The second acid sand subunit (B4) is also predominantly of aeolian origin and forms an undulating cover on the coastal platform east of Knysna at elevations of 200 - 250 m above sea level. The parent materials are highly leached and preweathered with haematitic streaks and banding that has the appearance of an iron-rich mottled zone. The lithology is more variable than in B3 with clayey lenses present. On the more sandy facies, yellow and grey podzolic soils such as the Lamotte (Lt 10, 11, 20) and Constantia (Ct 13, 14) forms occur and on the more clayey facies, Constantia (Ct 23) and Valsrivier (Va 30).

The residual soils (C4) are poorly represented in Outeniqualand and are restricted to the Hartebeeskuil, Knysna and Plettenberg Bay areas associated with Cretaceous clays and conglomerates or materials derived from them. The Knysna and Plettenberg Bay occurrences are noteworthy for the more pronounced development of black organic clay cutans in the B horizons. Wetter conditions in the latter areas contribute to the marked development of E horizons and the presence of soils of the Estcourt (Es 13) form. In the drier Hartebeeskuil area, however, E horizons are absent and duplex loams of the Valsrivier (Va 20, 21, 30, 31) forms occur.

Duplex soils are the most widespread and extensive unit (D5) in the region. They occur on the weakly undulating coastal platform at altitudes of between 200 - 250 m and are an extension of the same subunit in the Overberg region. The substrates vary from granites to quartzites; locally lenses of transported clays of possibly marine and terrestrial origin overlie these substrates. Two subunits of duplex soils are recognized. The first is associated with the granitic substrates in the George-Knysna area (D5L). The duplex nature is the result of a colluvial fine sandy loam covering the residual or transported clays. Maghemitic grit lines mark the interface between the loams and clays and are also found within the transported clay lenses. Concretionary laterites are however rare. The clay minerals in the residual clays are generally kaolinite, vermiculite and degraded micas (illite) and in the transported clays sodic smectites are common. Magnesium is an important cation in these clays. The Estcourt (Es 13, 33) and Sterkspruit (Ss 23) forms found are similar in appearance to the duplex soils found in subunit C4, notably in the occurrence of black organic clay cutans and in the well developed E horizons in lower slope positions.

The second subunit (D5S) is underlain by quartzitic substrates generally mantled by transported clays with a medium to fine sand overburden. The area is flatter with upland vleis where peats and hydromorphic clays (Katspruit, Ka 10) are prominent, with steeply incised river gorges. The highest precipitation of the coastal platform occurs in the area of D5S and all the soils (Estcourt 40, Kroonstad 20, Longlands 10) show black cutans (weak podzolic in character) and prominent E horizons. Due to the sandy nature of the top soils of the duplex subunit and the high rainfall, vertical and lateral leaching have given rise to very low concentrations of basic cations, phosphorous, iron and other trace elements. The above-mentioned conditions explain the association of the D5S subunits with fynbos shrubland vegetation. Climax indigenous forest is not found on the duplex soils (Estcourt 13, 33, 40, Sterkspruit 23) with a B horizon shallower than 500 mm and it is doubtful if such soils ever provided a suitable environment for indigenous forest. The brown-coloured waters of streams draining this area are due to the high fraction of acid soluble organic material associated with the fynbos. Although in the natural state the A horizons are high in organic material (greater than 5%), the organic material is unstable and is rapidly mineralized under cultivation and fertilization.

A small area of subunit E1 is found in the Mossel Bay area and it is an extension of that described in the Overberg region. There are two localized occurrences of red apedal soils. The subunit F2 is found on the outer plateau margin at an altitude of 150 - 200 m between Herold's Bay and Wilderness associated with the Kaaiman's Group. The soils are deep, red apedal loams (Hutton 36) and structured red clays (Swartland 11), presently under-exploited for agriculture because of the absence of adequate irrigation water. Between the Varing and Great Brak rivers at altitudes of 200 m and higher, red apedal loams (Hutton 36) and red structured clays (Swartland 11, 21) have developed from local drift and residual phyllites.

The G2 subunit, covering the southern footslopes of the Outeniqua mountain range at elevations of 400 m and higher, is associated with prominent angular quartzitic screes. The terrain is highly dissected and the soils and parent materials show considerable variability. Slope position and aspect are important factors in soil distribution. At some localities the weathering of the coarse blocks of the scree is advanced to the point where the blocks are friable (high in gibbsite (R. W. Fitzpatrick, pers. comm. 1982)), and show red and yellow staining. Gibbsite is commonly formed. The dominant soil process operating is podzolization with the formation of Lamotte (Lt 11, 12) and Constantia (Ct 11, 12) forms. Other soils are of restricted occurrence. Remnants of degraded silcretes are found on convex crest positions and may represent some of the oldest silcretes in the southern Cape. Indigenous forests are widespread in this area.

The H5 subunit inland of Plettenberg Bay is a dissected intermontane quartzite bench at 400 - 700 m that is poorly defined. The soils are shallow residual Houwhoek (Hh 30, 20) and Cartref (Cf 30 20) forms with patches of high level gravels occurring on some convex crest and mid-slope positions. These soils have a low potential for afforestation (D. C. Gray, pers. comm. 1982) because of nutrient deficiencies and hydromorphy.

Broad river valleys (I1) have developed in the softer Cretaceous rocks of the Mossel Bay-Groot Brak and the Bitou River areas and in these valleys extensive terraces carry a range of saline alluvial soils. The steeper-sided valley systems (I2) are cut into granite and quartzites and are associated with shallow lithosols on the valley sides with flood plain soils absent. The rocky coastal cliff (Knysna to Storm's River) is also included in this subunit.

The mountain unit (J) covering the Outeniqua range forms the northern boundary of the mapped area. Shallow sandy lithosols of the Cartref (Cf 30, 20), Mispah (Ms 10) and Houwhoek (Hh 20, 30) forms with prominent organic rich A horizons are the most important soils found here.

CONCLUDING DISCUSSION

The four soil unit maps included in this volume show the spatial distribution of the different soil subunits and the relationships between the soils of the south-western Cape, the Overberg and the Outeniqua regions. If these maps are superimposed on the appropriate topocadastral maps it will be seen that the soil units correspond to and distinguish different erosion surfaces that can be recognized on the Cape coastal platform. The occurrence of scree deposits on the inner margin of the platform at altitudes of 400 m or more suggests that these are of the oldest deposits and the associated palaeosols are amongst the oldest soil materials found in the fynbos region. There is a notable association of silcretes, which are palaeosols associated with conditions of deep weathering, with the 300 m planation levels, suggesting that such planation relates to earlier Cenozoic climates very different from the present. In the south-western Cape there is a clear pattern of association of red apedal soils with topographic elevations of 200 - 250 m, residual soils with the higher Swartland bevel at 150 - 200 m and the lower Swartland bevel at 80 - 140 m, Katarra duplex soils with the 50 - 100 m mature valley profiles and again duplex loams with marine-cut benches at an altitude of 30 m. Equivalent units and subunits can be mapped in the other regions. The oldest deposits found on the Cape coastal platform may date to the Paleogene as may some of the palaeosols like the silcretes, but the bulk of the soils are Neogene in age. In particular, the planation of the 30 m bench and the Katarra surfaces can be related to Late Pliocene base levels (Hendey, this volume) and the soils can be no older and some are probably considerably younger.

The variety of soils found on the Cape coastal platform is a function of time as well as different pedological soil forming processes such as ferrallization, plinthite formation, podzolization, eluviation and illuviation (vide Lambrechts, this volume). Ferrallization is a process that was pronounced under earlier Cenozoic warm and humid climates and gave rise to the well-drained red apedal soils of the F unit. Plinthite formation is a process of secondary iron enrichment and localization in a zone of periodic water saturation to form high chroma mottles and concretions (Macvicar et al. 1977). This is associated with Westleigh and Longlands form soils in the I1 and D5S subunits. With time, such horizons can become indurated to form hardpans as for example in the Wasbank soils formed in subunit B1. Podzolization on the other hand is a process operative in acid sandy environments under fynbos-type vegetation where mobilization of iron, aluminium and organic matter from the topsoil horizons gives rise to ferrihumic B horizons over various substrates - unconsolidated and sometimes hydromorphic as in the Lamotte form or hard and saprolitic as in the Houwhoek form. Leaching and eluviation of soluble salts and clay have been important features in most soils.

The information on soils and landscape development contained in the accompanying maps may contribute to regional and agricultural planning, environmental and conservation studies, and to assessing the relationship between substrates and vegetion communities. The recognition of natural units of soils related to specific surfaces in the fynbos landscape will prove of value in geomorphological, palaeoecological and archaeological research.

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REFERENCES

ELLIS, F. 1973. Soil studies in the Duiwenhoks River catchment area. Unpublished M.Sc. Agric. thesis: University of Stellenbosch.

MACVICAR, C. N., DE VILLIERS, J. M., LOXTON, R. F., VERSTER, E., LAMBRECHTS, J. J. N., MERRYWEATHER, F. R., LE ROUX, J., VAN ROOYEN, T. H. & HARMSE, H. J. VON M. 1977. Soil classification: a binomial system for South Africa. Department of Agricultural Technical Services, Republic of South Africa, Science Bulletin 390: 1-150.

MERRYWEATHER, F. R. 1965. Soils of the Wellington and Malmesbury areas. Unpublished M.Sc. Agric. thesis: University of Stellenbosch.

ROGERS, J. 1982. Lithostratigraphy of Cenozoic sediments between Cape Town and Elands Bay. Palaeoecology of Africa 15:121-137.

PALAEONTOLOGY AND PALAEOECOLOGY OF THE FYNBOS REGION: AN INTRODUCTION

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INTRODUCTION

The composition and distribution of modern plant and animal communities in the fynbos region are a product of evolutionary processes that have been underway for many millions of years. Some of the living taxa have histories dating back to the late Cretaceous and early Tertiary, but the modern biota was largely developed during the late Tertiary and Quaternary, a period of about 20 million years. It is this part of the Cenozoic era that is best represented in the local geological record, but recorded fossil occurrences of this age are limited in number, widely scattered in the region, and are often insecurely dated. The only part of the late Cenozoic that is comparatively well represented by deposits and fossils is the late Pleistocene and Holocene, which covers little more than 0,004% of the time elapsed.

The intensity and quality of studies on individual fossil occurrences and taxonomic groups varies considerably. For example, few investigations on local terrestrial invertebrate and lower vertebrate fossils have been carried out, fossil plants (mainly pollens) and birds have only recently received sustained attention, and although fossil mammals have been studied in some detail for several decades, the various groups represented have received unequal treatment and much research on them remains to be done.

Interpretation of the origins and evolution of the fynbos region biota does not depend only on local fossil evidence, since fossils from further afield may be relevant. In addition, palaeontological evidence is complemented by palaeoclimatic data and the palaeoenvironmental implications of geological deposits and processes.

Although the data base has improved appreciably in recent years, it provides at most only a general outline of the history of the fynbos region biota, with the record being highlighted intermittently by details that reflect relatively short time intervals in restricted areas. Such details are often based on individual localities, and they may therefore represent local rather than regional situations, since the fynbos region is one of great geologic, physiographic and climatic diversity.

It is self-evident that the modern biota of the fynbos region differs in at least some respects from those that have existed in this region during the past. The state of nature in all its facets is so complex and so dynamic that the addition of even a short time component will be manifested by some change in an ecosystem. This is particularly true of those periods in geological time, including the late Cenozoic, when climatic and environmental changes have been both frequent and rapid. The tempo of change during the Tertiary accelerated progressively, and it culminated during the Quaternary when climatic cycles with periods of 100 000 years, 23 000 years, 10 000 years and even less (Frakes 1979; Fischer 1981) were accompanied by profound changes in the world's biota, especially in middle and high latitudes.

The task of documenting and interpreting the biotic history of the fynbos region is a complex one that is at least partly dependent on a clear understanding of the geology, geography and biology of the region as it is today. One of the basic principles of all studies that relate to the past is that of 'uniformitarianism', which simply stated is 'the present is the key to the past'. This principle is of particular relevance here since it is applied in the chapters which follow, on the grounds that the 'most basic method of interpreting environments from fossils is by assuming that their environmental requirements were the same as those of the most closely related living representatives and transferring this environmental information from the modern to the fossil' (Dodd & Stanton 1981:17).

In reality, the situation is often more complex, and there are many exceptions to this general rule. In the course of their evolution, plants and animals may adapt to environmental changes and living forms may have environmental tolerances and habitat preferences that differ from those of their extinct relatives. Although such adaptations will often be accompanied by morphological changes, this is not always the case, and all available evidence should be evaluated in instances where the palaeoenvironmental implications of a particular fossil is anomalous or in doubt. In addition, the greater the time interval separating a fossil from a related living form, the greater the circumspection required in applying the principle of uniformitarianism. For example, whereas the correlation of habitat preferences of late Pleistocene and living organisms is usually valid, related forms of Tertiary age may have had different requirements since conditions that prevailed then were generally distinct from those during the late Pleistocene and Holocene. This applies particularly in the case of vertebrates (Dodd & Stanton 1981).

Palaeoecological studies are fraught with even greater difficulties since they involve biotic communities rather than individual species of plants and animals. As communities evolve, their structure may change, and closely related fossil and living species need not necessarily be characteristic of similar communities. It is therefore desirable that palaeoecological studies be based on large fossil assemblages and that account be taken of sampling biases involved in both the deposition and recovery of these assemblages.

In spite of deficiencies in the local fossil record and the difficulties in interpreting available data, productive considerations of the palaeontology and palaeoecology of the fynbos region are possible. However, they are to a large extent dependent on a clear appreciation of the modern character and composition of its biota, a matter which is itself beset by problems.

THE MODERN BIOTA OF THE FYNBOS REGION

Much has already been written about the disturbed state of the flora and fauna of the fynbos region that has been caused by human activity (e.g. Moll 1982). This disturbance has been progressive and probably started as early as the middle Pleistocene, the period when man first occupied the region, culminating in the historic period (post-1652 A.D.) with the catastrophic impact of European settlement (vide Deacon, this volume). In spite of the existence of historical documents, and of museum and herbarium specimens and records, it is now impossible to reconstruct accurately the nature of the region's flora and fauna as it was early in the 17th century.

Indeed, even by that time the biota had already been modified to some extent by the 2 000-year occupation of indigenous pastoralists, and a far longer occupation by hunter-gatherers. The latter disturb ecosystems through their use of fire that either by accident or design (e.g. for driving game) add to the natural fire frequency and so affect the character of local vegetation. In addition, hunter-gatherers may over-exploit at least some of their preferred plant and animal foods, and they may contribute to the decline and extinction of species that are already under stress for other reasons. The situation in respect of prehistoric pastoralists is less equivocal and they undoubtedly had a detrimental affect on the fynbos region vegetation. They are known to have used fire to promote the growth of grass for their stock (Skead 1980), an activity that was to the detriment of shrubs and trees. In addition, a 1653 entry in Van Riebeeck's journal, quoted by Skead (1980:714), mentions the arrival near his settlement of an estimated 20 000 sheep and cattle, a high number which indicates that even primitive pastoralists had created the potential for overgrazing pastures. Thus, two key factors in modern agricultural mismanagement, fires and overstocking, were manifested in the fynbos region in prehistoric times.

Considerable efforts are now being directed towards conserving areas of the fynbos region that are 'undisturbed' by human activity, particular emphasis being placed on the preservation of the region's unique vegetation. These efforts are misguided in the sense that there is no area where this vegetation is undisturbed. Certain key elements in local ecosystems, notably the larger mammals, have been reduced or exterminated throughout the region, and even apparently undisturbed patches of vegetation are therefore no longer in a pristine state.

Although the effects of the elimination of large mammals from plant communities in the fynbos region cannot be specified in detail, and although these effects were less severe than those of urban development, agriculture, unnatural fire frequency, and the introduction of alien vegetation, it is certain that they were significant and are under-appreciated. The elimination of any element from an ecosystem will affect that system, and the greater the losses, the greater are the changes that will ensue. In the south-western Cape, all the herbivores larger than the grey duiker (*Sylvicapra grimmia*) have been exterminated, and of the larger carnivores only the leopard (*Panthera pardus*) survives in small numbers in remote mountain areas. The area has been profoundly affected by the loss of such large herbivores as the elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), mountain zebra (*Equus zebra*), hippopotamus (*Hippopotamus amphibius*), eland (*Taurotragus oryx*), and red hartebeest (*Alcelaphus buselaphus*). The situation in the southern Cape is essentially similar, although the original composition of the large mammal fauna in this part of the region differed from that in the south-western Cape (*vide* Klein, this volume).

The large mammals now missing from fynbos region ecosystems had the capacity to modify the vegetation mosaic in several ways. The browsers and mixed feeders (elephant, rhinoceros, eland) must have kept the shrub canopy more open than is the case today, a situation that would have promoted stands of grass sufficient to feed the grazers (zebra, hippopotamus, hartebeest). It has been noted elsewhere in Africa that a heavy concentration of large browsers (e.g. elephant) "can convert quite dense woodland into open grassland in a surprisingly short time" (Brown 1972:52). This need not necessarily have applied on a large scale anywhere in the fynbos region, but the example does indicate that even a single species of large mammal can modify vegetation patterns substantially.

Another notable example is the hippopotamus, a species that was formerly common in the lakes (vleis) and rivers of the region. Although opinions vary on the quantity of plants (mainly grasses) eaten by hippos, there is no doubt that even small groups consume prodigious amounts in the course of a year. Consequently, they are capable of modifying the character and composition of lake- and riverside vegetation very significantly. Kingdon (1979:264) records that because "they graze so close to the ground and alter the grass species composition there is no dead grass to catch fire so that small clumps of thickets become the focus for the expansion of dense woody growth." In addition, since all hippos except adult males habitually defecate in water, such water is considerably enriched by nutrients and is consequently biologically highly productive (Kingdon 1979). The loss of hippos from an ecosystem must therefore cause appreciable changes in that system.

Nutrient-enrichment of ecosystems by large mammals also applies on land where it is supplied in the form of both dung and carcass residues, and this may make a significant difference to biotic systems where soils are low in nutrients, which is the case in parts of the fynbos region. The role of large mammals in nutrient cycling is complex and involves more than providing natural fertilizer to soils, since an array of invertebrates (mainly micro-organisms) is involved in the processing of wastes. The loss of the primary waste-producer means that the plants consumed by them no longer reach the waste-processors in a form acceptable to them and an entire cycle is broken down.

Large mammals also play a role in seed dispersal. Seeds may be transported by becoming attached to the bodies of passing animals, a dispersal method that is common amongst grasses. Alternatively, they may be ingested and pass through the alimentary tract to be deposited elsewhere. In the latter instance, the process may be vital to the viability of seeds if successful germination requires thinning or removal of the seed cortex by stomach acids. Furthermore, the dung in which the ingested seeds are eventually deposited provides a nutrient-rich body on which germination and early growth is based. The fact that most seed dispersal in the fynbos region today is by wind, ants, birds and rodents may simply indicate the dominance achieved by the plants concerned since the loss of large mammals from the region led to the failure of plants with seeds that were dispersed by them.

It is likely that the subsidiary role of grasses in fynbos region vegetation mosaics is at least partly due to the extermination of large mammals in this region. Although the situation in respect of grass prominence in the mosaic may in reality have been extremely complex, a simple scenario is that browsers no longer keep the shrub canopy sufficiently open for grasses to flourish, and grazers no longer disperse their seeds. It is clear from well documented examples elsewhere in Africa that domestic stock is an inadequate replacement for the natural large mammal fauna. Indeed, the former tend to degrade further vegetation that has already been affected adversely by the loss of indigenous mammals that are adapted to it.

Even in remote mountain areas where grasses may never have been prominent and where little or no domestic stock has been introduced, the situation today is not as it was prior to European settlement. Indigenous herbivores such as the mountain reedbuck (Redunca fulvorufula), klipspringer (Oreotragus oreotragus), and vaal rhebok (Pelea capreolus), have been reduced in numbers or eliminated. The same applies to the main predator in these areas, the leopard. The reduction or loss of leopard populations has resulted in increases in the populations of baboons (Papio ursinus) and dassies (Procavia capensis), with the consequent over-exploitation of their preferred plant foods to the extent that these animals now eat plants that would not normally form part of their diet. Farmers have learnt to their cost that the elimination of one problem animal (the leopard) can result in the rise of new ones (baboons and dassies).

The same lesson is being learnt on the western coastal lowlands where reduced predation on gerbils (Tatera afra) through the elimination of their predator species (both mammalian carnivores and raptorial birds), has resulted in periodic population explosions of gerbils that have caused havoc in grain fields. While this problem may appear to be an agricultural one, such population imbalances must affect the natural vegetation as well.

Local ecosystems have been adversely affected not only by disturbance of indigenous mammal populations, but also by the introduction of exotic species. The most extreme example in this respect is the area of Table Mountain. Here fallow and sambar deer (Dama dama and Cervus unicolor), the Himalayan thar (Hemitragus jemlahicus) and grey squirrel (Sciurus carolinensis) have all played a role in disturbing the natural vegetation and terrain. The grey squirrel is often regarded as relatively harmless since it feeds off exotic trees such as pines (Pinus spp.) and oaks (Quercus spp.), although the taking of eggs from birds' nests is frequently cited as having had an adverse impact on the indigenous avifauna. However, less well known is the fact that it is a threat to natural stands of the silver tree (Leucadendron argenteum) since it feeds on the cones of this tree (Palmer & Pitman 1972).

Certain indigenous mammals provide a further indication that all is not well with the environment in the south-western Cape by having recently extended their ranges into this area from the semi-arid west coast and central interior. The species concerned are the bat-eared fox (Otocyon megalotis) and yellow mongoose (Cynictis penicillata), whose numbers have increased perceptibly since they were first observed a decade ago (Hendey 1974).

The implication of the preceding observations is, as indicated earlier, that the flora and fauna of the fynbos region today is everywhere disturbed to a greater or lesser extent. Consequently, if palaeontological investigations are to be based on the principle that 'the present is the key to the past', then circumspection is required in defining the data base for the 'present'. This can at least partly be corrected by reference to documentary and physical evidence from early in the historic period, especially as they apply to the mammalian fauna. The situation in respect of other elements in the biota is more equivocal, and a useful example that may be considered is of grasses in the vegetation of the south-western Cape.

Skead (1980) has made a comprehensive review of historical documents that refer to the mammalian fauna and flora of parts of the Cape Province. There are several references in Skead's monograph to abundant grass on the Cape Peninsula (op. cit.:710-718), good grass at Rietvlei (op. cit.:732), some grazing on the Cape Flats (op. cit.:735), fine pastures at Tygerberg op. cit.:736), and many others in a similar vein. There are instances where descriptions of grasslands appear exaggerated in the light of the nature of surviving patches of natural vegetation. For example, Francois Valentyn in the earlier 18th century wrote that "in all Africa there are no lovelier grass-fields" than those at Bottelary near Stellenbosch (quoted in Skead 1980:738). It is likely that these grasslands were at least to some extent the product of veld-burning by indigenous pastoralists and European settlers, although unnatural fire frequency may actually promote the growth of shrubs. For example, an important element in the coastal renosterveld, the renosterbos (Elytropappus rhinocerotis), has long been known to spread rapidly when fire frequency is increased (Levyns 1927). The protection of vegetation communities from fires may also affect them adversely.

Heydorn & Tinley (1980:30) have observed that the "mountain grasslands of the east Cape are being invaded by heath elements, particularly in response to overgrazing or, alternatively, through protection from fire over unnaturally long periods." While the situations in the fynbos region and the eastern Cape may not be entirely comparable, it is significant that human activity in the latter area has degraded it and allowed the spread of shrubland vegetation into what was previously grasslands. The shrublands of the fynbos region coastal lowlands must to some extent represent a parallel situation. In other words, the predominance of shrubs in the coastal vegetation communities is partly the result of human interference in local ecosystems. It is highly probable that grasses were previously more prominent in all the shrubland communities of the coastal lowlands under existing climatic conditions.

THE FYNBOS REGION DURING THE PAST

It is abundantly clear from the fossil record that the degrading of the fynbos region biota was not due solely to human activity. The latter has simply been an added factor to a natural process of long standing, although its impact has been of catastrophic proportions and has occurred extremely rapidly when measured in terms of geologic time. The Cenozoic era has been characterized by profound changes in physical environments and climates, and biotas have responded accordingly. As a general rule, these changes accelerated progressively during this era as the world passed into the current 'ice age', which is the third major 'ice age' of the Phanerozoic eon (Fischer 1981).

Virtually nothing is known of the fynbos region vertebrate fauna during the early Teritary, some from skeletons and fragmentary remains of other lower vertebrates from diatremes in Namaqualand and Bushmanland being the only fossils recorded from near this region. These diatremes also include plant remains and some useful information on the Paleocene vegetation of Bushmanland has emerged from studies on this material. In addition, the lignites of the Knysna Formation, which are believed to be of Eocene age, have provided some information on the early Tertiary vegetation of Outeniqualand (vide Coetzee et al., this volume). The poor early Tertiary fossil record in south-western Africa may be supplemented by fossil evidence elsewhere in Africa, and even on other continents, notably Australia, although inferences made on the basis of such evidence are inevitably very tentative. In addition, some assumptions about local palaeoenvironments and palaeoclimates during the early Tertiary may be made on the basis of non-biological evidence from a wide variety of sources and areas.

In general, climates in mid latitudes during the early Tertiary were warmer and wetter than those prevailing during the late Tertiary and Quaternary. However, the climates then were not constant, although periods of relative stability were longer, and major changes were less frequent than in later times. The Oligocene was the epoch when the most extreme deviation from the early Tertiary 'norm' occurred, but nothing definite is known of the climates that prevailed in the fynbos region at that time, or of its biota. Evidence from elsewhere suggests that although Oligocene climates were cooler and drier than at any other time during the early Tertiary, they were neither as cool nor as dry as subsequent climates. This is borne out by the fact that known Oligocene biotas had more in common with those of the Paleocene and Eocene than with biotas of post-Oligocene times.

Speculations on the character and composition of fynbos region vegetation during the early Tertiary serve little purpose at present, but as a broad generalization it is suggested that forests predominated on the coastal lowlands, whereas sclerophyllous shrublands were largely confined to the mountains. The situation in respect of the region's fauna is even more uncertain. The forests and wetlands are likely to have been inhabited by an array of vertebrates similar to those recorded from early Tertiary deposits in North Africa, including primitive primates, proboscideans and hyracoids (dassies) (Maglio & Cooke 1978).

The Miocene is an important epoch in the history of the fynbos region biota since it was then that the beginnings of the transition from the archaic world of the early Tertiary to the current 'ice age' were clearly manifested for the first time. Early in the Miocene, the climate became both warmer and wetter than it had been during much of the Oligocene, and conditions then were probably comparable to the early Tertiary 'norm'. Forests must have been widespread on the coastal lowlands, and the vertebrate fauna was probably little different from that of the late Oligocene. By the beginning of the middle Miocene, the situation had changed, and although palaeobotanical evidence for this change is lacking in the fynbos region itself, other evidence from further afield indicates unequivocally that climatic and environmental deterioration had set in.

The nature of the changes undergone by the fynbos region biota during the latter half of the Miocene have yet to be documented by direct evidence, but it is clear that by the end of this epoch both the flora and fauna already contained many of the elements that characterize the biota as we know it today. This is deduced largely on the basis of the early Pliocene fossil record, which is extremely good compared with that of earlier times. Both plants and animals are well represented for the first time in the Cenozoic fossil record, and data derived from the fossils are complemented by palaeoclimatic information derived from elsewhere.

The picture of the early Pliocene that emerges is one of relatively low temperatures and rainfall, the latter being strongly seasonal, with forests and woodlands probably confined to well-watered mountain slopes and river valleys, and with wide areas of more open country on the coastal lowlands. Plant types characteristic of vegetation communities found in the fynbos region today were well represented, although community compositions then were apparently still distinct from modern ones. In spite of the cooler and drier conditions during the early Pliocene, the local biota still included elements indicative of subtropical and tropical climates that were evidently relics of the warmer times during the Miocene. Some were to become extinct between the early Pliocene and the present, whereas others adapted to the changed conditions and still occur in the fynbos region today. Individual species developed wide environmental tolerances and now flourish in a variety of climatic regions. Although this applies particularly in the case of higher vertebrates (birds and mammals), even some plant species are included in this category. For example, the Outeniqua yellowwood (*Podocarpus falcatus*) that is so characteristic of the Afromontane forests of the southern coastal lowlands, is also found in tropical areas of the northern Transvaal and Mozambique (Palmer & Pitman 1972). The genus *Podocarpus* has an even wider distribution in Africa, occurring as far north as Ethiopia, as well as in so remote a region as Polynesia (Palmer & Pitman 1972). This illustrates the dangers inherent in using a single taxon as a palaeoenvironmental indicator.

The fossil record for the period between the early Pliocene and late Pleistocene is poor, and is inadeqate for documenting in any detail the changes that occurred in the fynbos region flora and fauna. It was evidently during this period that a summer dry/winter wet rainfall regime was experienced for the first time and when the cyclical climatic changes of the Quaternary were initiated. The nature of these changes and their effects on the biota, have been comparatively well documented for the late Pleistocene and Holocene, and this part of the record provides some indication of what transpired during the remainder of the Pleistocene. However, although the nature and timing of climatic changes during the late Pliocene, early Pleistocene and middle Pleistocene can be inferred on the basis of evidence derived from a variety of sources, this does not necessarily apply to the character and composition of the biota at any given time.

This is due to the fact that the biota was evolving at a relatively rapid rate during this period and the completion of any one climatic cycle did not return the biota to the state that it had been at the time of commencement of that cycle. For example, the large mammal fauna of the last interglacial is distinct from that of the present interglacial in several respects (*vide*

Klein, this volume). It is clear from the Pleistocene fossil mammal record that this group underwent significant changes, both locally and further afield. The representatives of some lineages changed markedly during this period, several taxa made their first appearance in the region, and many others became extinct. The situation in respect of the mammals is an indication that other elements in the biota also underwent changes. Finally, it was during the middle Pleistocene that man first settled in the fynbos region, and although his impact on the environment at that early stage may have been limited, it should not be underestimated. Sluiter & Kershaw (1982:220) found that during the late Quaternary in Australia "there was a massive expansion of open eucalypt vegetation at the expense of 'drier' rainforests and other sclerophyll communities in response to an increase in burning, most likely as a result of the activities of aboriginal man." Even primitive hunter gatherers have the potential to disturb the biota.

The study by Sluiter & Kershaw (1982) is of further interest here since they believe that in Australia the Pliocene vegetation pattern persisted until the disruption referred to above. Since there are many parallels in the evolution of environments in southern Africa and Australia, this observation is relevant here. Its implication for the fynbos region is that the late Pleistocene/Holocene vegetation patterns may in fact be even less representative of the rest of the Pleistocene than was indicated earlier. Available evidence from the western coastal lowlands suggests that during the Pliocene the local vegetation included gallery forests and extensive grasslands, with shrublands much less prominent than they are today. There is also some evidence to suggest that, as in Australia, the vegetation pattern established in the Pliocene did indeed persist well into the Pleistocene, although there were variations caused by climatic changes, the nature of which have yet to be documented.

The situation in respect of Pleistocene biotas in the fynbos region is one of extreme complexity, but a fact that does emerge repeatedly is that grasses were previously a more prominent element in the vegetation mosaic of the coastal lowlands than is the case today. A combination of large grazers that is characteristic of African mammalian faunas is that of zebras (Equus spp.), white rhinoceros (Ceratotherium simum), alcelaphine antelopes (Alcelaphus spp., Connochaetes spp., and others), and antilopines (Antidorcas spp., Gazella spp.). This combination is not found in the recorded Holocene faunas of the fynbos region, in which only Equus and Alcelaphus are represented in any numbers. Although it might be expected that the representation of grazers during the last interglacial would have been similar to that of the Holocene, this group is in fact more commonly represented (e.g. at Klasies River Mouth - see Klein, this volume). Indeed, the large grazers listed above, and others, are prominent in all the more important Pleistocene faunas recorded in the fynbos region. These faunas have been related to a variety of climates that have been identified as follows:

1. Cold and dry (e.g. Boomplaas - Avery, this volume).
2. Cool and wet (e.g. Swartklip - Klein, this volume).
3. Warm and wet (e.g. Elandsfontein - Klein, this volume).

The climates of the first two examples date to the glacial phase of the late Pleistocene. Evidence for the nature of the vegetation during the early-middle Pleistocene is limited, but it is perhaps significant that the climatic conditions inferred on the basis of the middle Pleistocene fauna from Elandsfontein (i.e. warm and wet) is without parallel in the late Pleistocene and Holocene. Since the climate was warm, it presumably dates from an interglacial phase, and one that differed from the present interglacial in being wetter. Insecurely dated small faunas of early-middle Pleistocene age include one from Bloembos and another from Skurwerug. The former includes the only Pleistocene record of a giraffe in the fynbos region, while the Skurwerug fauna includes a bushpig and two grazing antelopes. In both cases environments that are distinct from that of the Holocene are indicated, with trees and grasses evidently prominent in the vegetation mosaic.

Thus far interpretation of late Cenozoic climates and vegetations have been based largely on inferences drawn from the nature of mammalian faunas. Relevant palaeobotanical evidence has hitherto been more limited, although the amount available has been increased considerably by recent studies. The prominence of trees on the western coastal lowlands during the late Tertiary has been confirmed by palynological investigations (e.g. at Noordhoek and Langebaanweg - Coetzee et al., this volume), while fossil tree trunks and tree pollens on the Cape Flats that have been correlated with wetter periods during the late Pleistocene indicate the periodic recurrence of forests on the western lowlands during the Pleistocene. However, palaeobotanical evidence has been more significant in providing evidence of the prolonged presence in the local vegetation of plant types such as shrubs, annuals and geophytes that are so characteristic and prominent in the modern vegetation. It is clear that those taxa that have a long history during the Cenozoic (e.g. Proteaceae) formerly existed locally in environments that were very different from those of the present. Others (e.g. Compositae) made their first appearance during the late Tertiary, and only radiated after the onset of cooler and drier conditions during this period.

The distribution and relative prominence of these vegetation types has no doubt varied according to prevailing environmental conditions. The extreme diversity of the modern flora is largely due to the physical complexity of the fynbos region upon which have been imposed the marked climatic changes of the Cenozoic, and more particularly those of the late Tertiary and Quaternary. The potential in this region under changing climatic conditions for the isolation of vegetation communities in discrete areas is very great. The changing environmental conditions provided the stimulus for evolutionary change and the isolation of communities from one another created separate gene pools and thus greatly enhanced the potential for diversification of the flora. Further change would have allowed previously discrete 'islands' of vegetation to become united into more extensive communities spread over wider areas. Within these communities locally endemic taxa, some with extremely limited distributions, would reflect the discontinuities that had existed earlier. The repetition of these cycles of change over millions of years resulted in the diversity at lower taxonomic levels that has made the Flora Capensis so remarkable.

The present dominance of shrubs in the coastal lowlands of the fynbos region is probably at its extreme, a situation that is largely due to the disturbance of local ecosystems by human activity. It is worth noting that all the important fossil occurrences in the western coastal lowlands, and some of those in the southern lowlands, are located in areas that are today covered by coastal strandveld and coastal fynbos, which are the communities in which trees and grasses are least prominent. The implication is that during those periods when these elements were more prominent, they must have completely dominated areas where more fertile soils today support the coastal renosterveld vegetation.

CONCLUSION

Palaeontological evidence, coupled with documented and inferred information on the fynbos region biota during historic times, indicates that the present state of the flora and fauna is unlike any that has existed in this region previously. Even that period of the present interglacial that preceded European settlement differed from preceding interglacial phases of the Pleistocene in terms of the character and composition of the biota, and the situation differed even more during the much longer glacial phases of this epoch. The recording of past biotas and the changes that they underwent is still at an early stage, and a considerably increased effort is required if the history of one of the world's floral kingdoms and its associated fauna is to be understood.

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REFERENCES

BROWN, L. 1972. *The life of the African plains*. New York: McGraw-Hill.

DODD, J. R. & STANTON, R. J. 1981. *Paleoecology, concepts and applications*. New York: John Wiley & Sons.

FISCHER, A. G. 1981. Climatic oscillations in the biosphere. *In* Nitecki, M. H. *ed*. *Biotic crises in ecological and evolutionary time*: 103-31. New York: Academic Press.

FRAKES, L. A. 1979. *Climates throughout geologic time*. Amsterdam: Elsevier.

HENDEY, Q. B. 1974. The late Cenozoic Carnivora of the south-western Cape Province. *Annals of the South African Museum* 63:1-369.

HEYDORN, A. E. F. & TINLEY, K. L. 1980. *Estuaries of the Cape. Part 1. Synopsis of the Cape coast. Natural features, dynamics and utilization.* Stellenbosch: National Research Institute for Oceanology. CSIR Research Report 380.

KINGDON, J. 1979. *East African mammals*. Vol. 3, Part B. London: Academic Press.

LEVYNS, M. 1927. A preliminary note on the rhenoster bush (*Elytropappus rhinocerotis*) and the germination of its seed. *Transactions of the Royal Society of South Africa* 14:383-388.

MAGLIO, V. J. & COOKE, H. B. S. *eds*. 1978. *Evolution of African mammals*. Cambridge, Mass.: Harvard University Press.

MOLL, E. *ed*. 1982. *Proceedings of a symposium on coastal lowlands of the western Cape*. Bellville: University of the Western Cape.

PALMER, E. & PITMAN, N. 1972. *Trees of southern Africa*. Vol. 1. Cape Town: Balkema.

SKEAD, C. J. 1980. *Historical mammal incidence in the Cape Province*. Vol. 1. Cape Town: Department of Nature and Environmental Conservation.

SLUITER, I. R. & KERSHAW, A. P. 1982. The nature of the Late Tertiary vegetation in Australia. *Alcheringa* 6:211-222.

PALAEOENVIRONMENTAL IMPLICATIONS OF THE LATE TERTIARY VERTEBRATE FAUNA OF THE FYNBOS REGION

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INTRODUCTION

The record of late Tertiary vertebrates in the region that today constitutes the Fynbos Biome is extremely poor, with only one fossil occurrence of major significance known, namely, the early Pliocene Varswater Formation in 'E' Quarry at Langebaanweg (Fig. 1). The spectacularly rich fauna recorded from this locality, coupled with some plant fossils and a well exposed geological succession, has provided a wealth of palaeoenvironmental data that to some extent compensates for the lack of other important late Tertiary fossil occurrences in this region.

For reasons that will be explained below, the early Miocene and early middle Miocene vertebrate occurrences in the southern Namib Desert are included in the present study. They provide the only substantial evidence of the nature of southern African Miocene vertebrates. Some inferences concerning the likely composition of the fynbos region vertebrate faunas during the middle and late Miocene, and late Pliocene, are made on the basis of the fossil record elsewhere in Africa.

AFRICAN LATE TERTIARY VERTEBRATES AND VEGETATION

The best known and most complete record of African late Tertiary vertebrates is in East Africa, notably Kenya, but even there it is only the mammals that have been intensively studied (e.g. Maglio & Cooke 1978). It is also in East Africa that the only substantial work to date has been done on the palaeoenvironmental implications of late Tertiary vertebrates (e.g. Nesbit Evans *et al*. 1981). It is evident from the latter study, and other similar ones, that plant and animal communities in East Africa underwent very dramatic changes in the course of the Miocene and Pliocene. Van Couvering (1980) has summed up the vegetational changes by recording that the dominant equatorial rain forest community of the early Miocene had been replaced by the end of the Pliocene by dominant savanna-mosaic (i.e. woodland, wooded grassland, grassland and bushland).

Although the southern African late Tertiary fossil record is poor compared with that in East Africa, resemblances between the faunas of the two regions

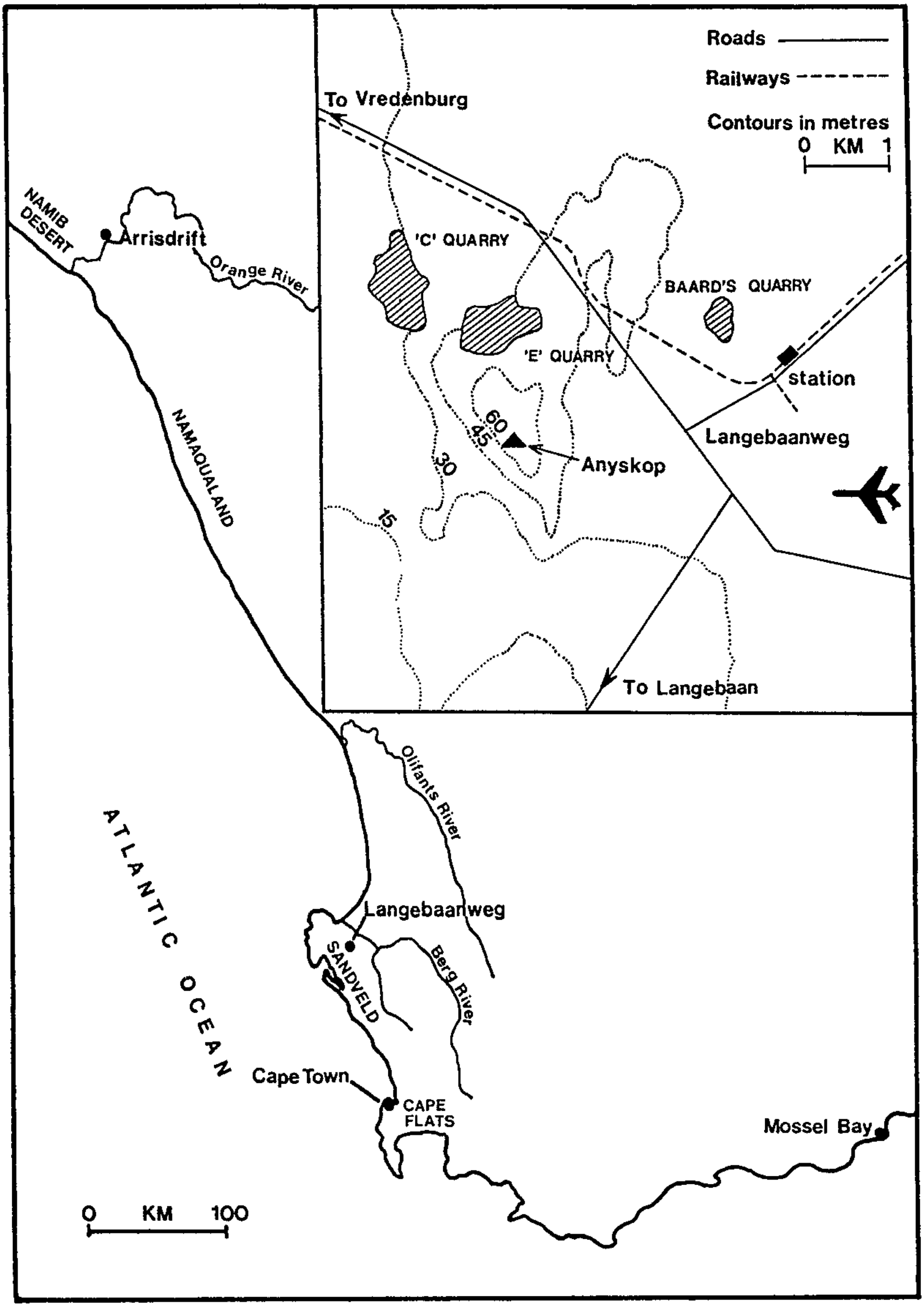

Fig. I South-western Africa, with an insert of the Langebaanweg area, showing localities referred to in the text.

suggest that palaeoenvironmental changes were broadly parallel. However, the changes in some elements of climate (e.g. temperatures, winds, season of rain) were more pronounced in the fynbos region and adjacent parts of south-western Africa than those experienced in East Africa, and thus provided a greater contrast between conditions that prevailed in the early Miocene and late Pliocene. The shrubland (= bushland) communities of the fynbos region owe their existence to the climatic changes that began in the late Tertiary, and their history goes back at least to the latter stages of this period, although their composition and distribution then remains unknown. What little evidence there is suggests that, at least in the coastal lowlands, shrubs did not predominate as they do today, and evidently this also applies to much of the succeeding Pleistocene epoch (Klein, this volume).

EARLY MIOCENE AND EARLY MIDDLE MIOCENE

The only vertebrate assemblages from the fynbos region that are possibly of Miocene age are comprised largely of marine fossils. They are therefore of little or no significance in indicating the nature of terrestrial environments during this epoch. Instead, account is taken here of assemblages from further afield, and the early Miocene and early middle Miocene (i.e. between about 20 and 14,5 Myr) are considered together, because the vertebrate faunas of these two periods are essentially similar in respect of their palaeoenvironmental implications.

While most African vertebrate localities of this age are in Kenya and Uganda (e.g. Rusinga, Koru, Maboko - see Pickford 1981), contemporary faunas elsewhere on the continent were essentially similar in terms of habitat preferences. Consequently, consideration is given here to faunas of this age from the southern Namib Desert, 400-500 km north of the present limits of the fynbos region. At that time, the cold Benguela Current upwelling system had not been initiated (Siesser 1980), and it is assumed that the climate, vegetation and fauna of the southern Namib and fynbos regions were similar.

Attention is focused on the comparatively rich early middle Miocene fauna from Arrisdrift (Hendey 1978a), since it provides the most substantial information on the likely palaeoenvironment of south-western Africa early in the Miocene. The smaller and apparently slightly earlier faunas from localities north of Arrisdrift (Hendey 1983: fig. 1) are essentially similar to that from Arrisdrift. The most useful palaeoenvironmental indicators in the latter fauna are the mammalian herbivores, and they fall into three categories.

Firstly, there are small mammals with hypsodont (high-crowned) cheekteeth. Such teeth are an adaptation to abrasive food, the most common being grasses, which are highly fibrous plants that contain hard siliceous phytoliths. Most grazers are of medium to large size, but there are also small forms, the best known and most widely distributed being the Lagomorpha (pikas, hares and rabbits). Small hypsodont herbivores are represented at Arrisdrift by the improbable combination of an elephant shrew (Myohyrax), a lagomorph (Kenyalagomys), and a springhare (Parapedetes). Myohyrax belongs to an aberrant group of extinct elephant shrews with lagomorph-like cheekteeth, while Kenyalagomys belongs to the pika family (Ochotonidae), a group that today inhabits cold mountainous regions in central Asia and North America.

Living pikas feed on a wide variety of vegetation types, including grasses (Walker 1964), an apparent response to the harsh environment where maximum use must be made of available food. Pikas survive only in relict populations, but were widespread in the Old World and North America during the Miocene. The fact that they are found today only in cold regions does not indicate that this was always the case. In fact, there is abundant evidence from other sources to the contrary and pikas are therefore an example of an animal that modified its habitat preference and feeding habits as climates changed during the late Tertiary.

Andrews & Van Couvering (1975:89) have suggested that East African Miocene springhares inhabited "open types of woodland and bushland", although they record (1975:84) that a similar "large burrowing and jumping rodent [Hypogeomys] inhabits the forests of western Madagascar." Hypogeomys has hypsodont cheekteeth (Petter 1971), and is said to be "the ecological equivalent of rabbits in Madagascar" (Walker 1964:827). It is of interest here in indicating that small mammals with an apparent grazing specialization (i.e.. hypsodont cheekteeth) are not necessarily confined to open country (grasslands). However, it is likely that the three hypsodont taxa at Arrisdrift did frequent a habitat where grasses were present. In view of conclusions given below concerning the nature of other vegetation types at Arrisdrift, it is suggested that the habitat of the small grazers was forest or woodland glades that were sufficiently open to allow grasses to grow.

The second category of herbivores in the Arrisdrift fauna comprises the small inhabitants of dense undergrowth that was probably largely confined to the banks of the river in which the fossils were deposited. They are a dassie (Prohyrax), two pigs (Lopholistriodon and an unidentified species), a tragulid (Dorcatherium), and an unidentified bovid. Thryonomyoid rodents may also be included in this category.

The latter dominated the early-middle Miocene rodent faunas of Africa, but today the only widespread members of the group are the cane-rats (Thryonomys spp.), which usually inhabit dense vegetation near marshes, rivers and lakes (Dorst & Dandelot 1970). It is possible that Miocene thryonomyoids had a similar habitat preference, and that their decline during the latter half of the Miocene coincided with the decline of this habitat due to increasing aridity.

The only living African tragulid, the water chevrotain (Hyemoschus aquaticus), is an inhabitant of dense riverside undergrowth, a characteristic it shares with its Asian relatives. There is no reason to believe that Miocene tragulids were any different in this respect. Indeed, the fact that tragulids were then a more widespread and diverse group is here regarded as evidence that this habitat type was very common in the Old World during the early-middle Miocene.

The small bovid and pigs from Arrisdrift are similar to the tragulid both in size and in their low-crowned dentitions, and they are likely to have had a similar habitat preference. The bovid has an analogue in the living forest duikers of Africa (Cephalophus spp.), although there are no small pigs still extant on this continent. The Arrisdrift bovid is poorly represented, but it does have some cephalophine-like characters in its dentition and it may be an early representative of this group.

The dassie (Prohyrax) was much larger than its living relatives, probably having been comparable in body weight to the tragulid, small bovid and pigs. It is the most commonly represented mammal at Arrisdrift. It has been suggested elsewhere to be a primitive pliohyracine, later members of this group having been amphibious forms of large size (Hendey 1978a). The fact that Prohyrax occurs so commonly in the fluviatile deposits at Arrisdrift suggests that it was a riparian species, although less adapted to an aquatic life than some of its later relatives (e.g. Pliohyrax, Kvabebihyrax). Living dassies are mixed feeders and the undergrowth along Miocene rivers no doubt provided an abundance of food for Prohyrax and sympatric herbivores.

The last of the palaeoenvironmentally significant categories amongst the Arrisdrift herbivores is that comprising medium- to large-sized forms. Of these, the medium-sized deer-like ruminant, Climacoceras, occurs most commonly. Other representatives of this group are a rhinoceros, a gomphothere and a deinothere (Prodeinotherium).

The Arrisdrift Climacoceras has low-crowned teeth, apparently straight and unbranched 'antlers', and relatively long legs, all characters that suggest it inhabited a forest or woodland environment. Low-crowned teeth are consistent with, and long legs are advantageous to, an animal with browsing habits. While the simple form of the 'antlers' may be a primitive characteristic of no palaeoenvironmental significance, they would have been of minimal impediment to movement through dense stands of trees, and therefore appropriate to a forest- or woodland-dweller.

The rhinoceros also had low-crowned teeth and relatively long legs, and was probably also an inhabitant of forests or woodlands.

Many early-middle Miocene faunas in Africa are characterized by the joint presence of a gomphothere and a deinothere. The feeding mechanisms and likely habitat preference of the latter have been investigated by Harris (1975:359), who concluded that "Prodeinotherium may have preferred a densely vegetated and even moist habitat." The same is likely to apply in the case of the gomphothere.

The general conclusion about the vegetation at Arrisdrift during the early middle Miocene is that it was made up of forests and woodlands, with some dense undergrowth and grassy glades.

The non-herbivorous mammals (carnivores and insectivores) are consistent with an environment of this type, while the abundant remains of a crocodile in the assemblage indicates that relatively high temperatures prevailed.

This faunal pattern is repeated in most, if not all, recorded African faunas of early and early middle Miocene age, including the few that are recorded elsewhere in the southern Namib region. Often, the forested nature of the environment is also indicated by the presence of a variety of primates and such specialists as 'flying squirrels' (Anomaluridae) (Van Couvering & Van Couvering 1976), although this does not apply in the case of the Namib localities. There appears to be no instance where open-country forms indicate anything other than restricted open areas such as glades and swamps.

The present interpretation of the early middle Miocene environment at Arrisdrift is supported by the fact that in East Africa better known and more diverse faunas of comparable age, interpreted by more elaborate studies, have led to similar conclusions. For example, Nesbit Evans et al. (1981:99) state that during the early Miocene, East Africa "was predominantly covered by rainforest", while by the early part of the middle Miocene "thick woodlands, perhaps verging on forest" (1981:112) had been developed.

MIDDLE MIOCENE AND LATE MIOCENE

Virtually nothing is known of southern Africa's terrestrial vertebrate fauna for most of the middle and late Miocene (i.e. between about 15 and 5 Myr). The fossil record elsewhere in Africa is also comparatively poor, although there are a few localities, especially in Kenya, that reveal something of the dramatic environmental changes that the continent underwent during this period. The more important localities include Fort Ternan (14 Myr), Ngorora (12-10 Myr), and Lukeino, Mpesida and Lothagam (7,5-5,5 Myr) (e.g. Pickford 1981). The most significant changes undergone by African mammals were as follows:

(i) Certain groups declined in importance (e.g. Pongidae, Tragulidae), or became extinct (e.g. Creodonta, Amphicyonidae, Anthracotheriidae, Climacoceridae).

(ii) Some groups made their first appearance (e.g. Hominidae, Equidae, Hippopotamidae).

(iii) Other groups radiated and became important elements in the continent's fauna (e.g. Cercopithecidae, Giraffidae, Bovidae).

In East Africa, the vegetational changes indicated by the faunal record are from dominant woodlands, through open woodlands, to savannas, with gallery forests persisting throughout this period (Van Couvering 1980; Nesbit

Evans et al. 1981). It is evident from the contrasts between the early middle Miocene fauna from Arrisdrift and the early Pliocene fauna from Langebaanweg (see below), that a similar opening-up of vegetation took place in south-western Africa.

In the latter area, this change is correlated with a deterioration in the local climate (i.e. lower temperatures and rainfall), which was caused by the glaciation of Antarctica and consequent change in southern mid-latitude wind and ocean current systems (e.g. Siesser 1978, 1980; Tankard & Rogers 1978; Deacon 1983; Hendey 1983).

EARLY PLIOCENE

The early Pliocene Varswater Formation, exposed in a phosphate mine ('E' Quarry) near Langebaanweg, has been the source of some exceptionally large assemblages of trace, plant, invertebrate and vertebrate fossils, that were laid down in a variety of depositional environments at, and near, the coast during a period when the sea rose from 20 to more than 70 m above its present level (Hendey 1981a, 1981b, 1982, 1983). For part of this period, the palaeo-Berg River had its mouth in the vicinity of Langebaanweg. The Varswater Formation is underlain by the Elandsfontyn Formation, which includes highly polleniferous back-barrier or overbank deposits that are recorded as being of middle Miocene age (Coetzee & Rogers 1982), but which may in fact also date from the early Pliocene.

In the account which follows, attention is focused on the vertebrate fossils, particularly mammals, and only passing reference is made to the palaeobotanical record (Coetzee et al., this volume) and the invertebrates. A significant feature of the vertebrate fossils is that although they occur in a restricted area, they represent animals from a variety of habitats, both coastal and inland. Animals were evidently attracted to the palaeo-Berg River by its fresh water. Some animals died in the area now exposed in 'E' Quarry, while others that died upstream had their remains carried to the quarry area by the river. The estuary itself was an area of high biological activity, and this also added a quantity of fossils to the deposits.

There are significant differences between the vertebrate faunas of Arrisdrift and Langebaanweg, which is not surprising in view of their 10 million-year age difference, with the Langebaanweg taxa being more advanced in an evolutionary sense. This can largely be ascribed to the profound environmental changes that took place in south-western Africa, and further afield, during the middle and late Miocene.

In contrast to the situation at Arrisdrift, the small grazer element in the Langebaanweg fauna is much less prominent. Only one such species is represented, namely a small hare, Pronolagus. The living species, P. crassicaudatus, includes forest fringes in its preferred habitats (Dorst &

Dandelot 1970), and in view of other evidence on the nature of the vegetation at Langebaanweg during the early Pliocene, this was its likely habitat then.

The Langebaanweg rodents are largely unstudied, but they are for the most part small species whose living relatives are not, or are not necessarily, found in forested habitats. Possible exceptions are a dormouse (*Graphiurus*) and a climbing mouse (*Dendromus*). The most commonly occurring rodent is a rodent mole (*Bathyergus*), whose presence indicates an abundance of geophytes in the vegetation, which is still a characteristic of the strandveld vegetation in the Langebaanweg area today. No thryonomyoids are recorded, and this is significant in illustrating the more 'modern African' character of the Langebaanweg fauna, compared with the 'archaic' character of the Miocene faunas in the Namib region.

Also in contrast to the latter faunas, is that small herbivores that might have inhabited dense forest undergrowth are an almost inconspicuous element in the Langebaanweg fauna. One candidate for this role is a small peccary (*Pecarichoerus*? *africanus*), that might have occupied the same ecological niche as the small pigs of the early-middle Miocene. Other small herbivores include two porcupines (Gen. & spp. indet.), a dassie (*Procavia* cf. *antiqua*), and two bovids (*Raphicerus paralius* and *Gazella* sp.). The latter, at least, were probably open-country forms, whereas the porcupines and dassie may have preferred either open or closed habitats.

The medium-sized herbivores from Langebaanweg are a more diverse group than that from Arrisdrift, and both open- and closed-country forms are represented. Perhaps the most significant of the former is the three-toed horse, *Hipparion*, a grazer whose rapid dispersal through the Old World at about 12 Myr indicates a wide distribution of grasslands at that time. Janis (1982) has suggested that the appearance of *Hipparion*, with the ability to deal with taller, coarser grass, opened the grazing niche to bovids that can deal with only higher quality grasses at lower levels in grassland vegetation. This distinction is due to the fact that *Hipparion*, and the later *Equus*, has incisors in both upper and lower jaws, as well as extremely hypsodont cheekteeth, whereas bovids have incisors only in the lower jaw and less hypsodont cheekteeth. There are also basic differences in the digestive systems of equids and bovids that reflect the nature of their diets (Janis 1982).

Although *Hipparion* already had a long history in Africa by the beginning of the Pliocene, the grazing bovids of that period were still relatively unspecialized. The Langebaanweg fauna provides some of the best evidence yet on the character and composition of an early bovid grazing fauna (Gentry 1980). Large, medium and small species are represented. They are a buffalo (*Simatherium demissum*), two alcelaphines (*Damalacra neanica* and *D. acalla*), two ovibovines (Gen. & spp. indet.), a steenbok (*Raphicerus paralius*) and a gazelle (*Gazella* sp.). Remains of these animals occur most commonly in fluviatile deposits, and it is likely that they were washed in to the

Langebaanweg area from upstream habitats.

Closed-country forms amongst the medium-sized herbivores are two bushpigs (*Nyanzachoerus* spp.), two nyala-like bovids (*Tragelaphus* spp.), a boselaphine (*Mesembriportax acrae*), and two waterbuck (*Kobus subdolus* and *Kobus* sp.). One of the bushpigs and the boselaphine are common in floodplain deposits accumulated near the river estuary, and indicate the presence nearby of forest or woodland. The other taxa occur more commonly in fluviatile deposits and suggest that the wooded habitats extended up the river as well.

The large herbivores are mainly closed-country forms, although one species, a rhinoceros (*Ceratotherium praecox*), is an early ancestor of Africa's grazing rhinoceros (*C. simum*). The Langebaanweg rhinoceros is especially common in the estuarine floodplain deposits, and it may have inhabited grasslands on the forest/woodland fringes. The proboscideans (*Anancus* sp., *Mammuthus subplanifrons*), and three giraffids (*Giraffa* sp., *Sivatherium hendeyi*, *Palaeotragus* sp.) indicate the presence of trees in the probable associations of open woodland, woodland and forest. Most of the remains of these animals are from the fluviatile deposits, which also include another large herbivore, a hippopotamus. The dentition of the hippopotamus is similar to that of the living *Hippopotamus amphibius*, which includes substantial quantities of riverside grasses in its diet. This, together with the presence of the rhinoceros in estuarine floodplain deposits, is evidence for extensive stands of grass in that environment.

Non-herbivorous mammals, other vertebrates, and invertebrates from deposits at Langebaanweg are less informative about the nature of the local and regional vegetation in early Pliocene times. However, none are inconsistent with the evidence provided by the herbivores.

The deposits themselves provide some indirect evidence about the early Pliocene vegetation at Langebaanweg. The presence of carbonaceous sands and clays ('peats'), and their situation relative to other deposits, reflect the existence adjacent to the estuary of a salt marsh. Pollens from these deposits represent plants that grew in the immediate vicinity and further afield. They include one or more marsh plants, grass, trees (including *Podocarpus*) and fynbos vegetation types (E.M. van Zinderen Bakker, pers. comm., *in* Tankard 1975). Pollens from the underlying Elandsfontyn Formation peats, which may also be of early Pliocene age, represent forests with a subtropical-tropical component and marsh plants, with fynbos taxa also present (Coetzee & Rogers 1982).

Although the available palynological data are limited, and equivocal in respect of the age of the Elandsfontyn Formation, the vegetation indicated agrees with that inferred on the basis of the mammalian herbivores. The major terrestrial habitats recognized are as follows:

(i) Open-country fringing the palaeo-Berg River estuary, with vegetation that included Chenopodiaceae, Gramineae, Restionaceae, geophytes and Compositae.

(ii) Coastal forest merging with gallery forest inland, and passing laterally through woodlands into more open country in which grasses were a significant element. The trees certainly included Podocarpus. The composition of the Elandsfontyn Formation forests is given by Coetzee & Rogers (1982) (vide Coetzee et al., this volume).

The early Pliocene vegetation at Langebaanweg contrasts with that inferred for the early-middle Miocene and that of the present, and represents something approaching an intermediate state. Forests and woodlands were no longer ubiquitous, while the open country was dominated by grassland rather than shrubland.

The Langebaanweg fauna also provides some evidence of palaeotemperatures. Deposits that are certainly of early Pliocene age include taxa (molluscs, seabirds, seal) which suggest sea temperatures then were similar to those of the present (i.e. a relatively cold 8-14 degrees C). On the other hand, the terrestrial fauna includes taxa that are today confined to subtropical and tropical regions of Africa. They include a freshwater snail (Ceratophallus natalensis), parrots (Gen. & spp. indet.), the giraffids and the waterbuck. However, some 'tropical indicators' that might be expected in a warmer-than-present climate are either absent (e.g. crocodiles) or rare (e.g. primates).

The absence of crocodiles is regarded as particularly significant, since they are ubiquitous in African fluviatile deposits laid down under appropriately warm climatic conditions. Crocodiles are not recorded from the fynbos region in historic times, and they are not known from Pleistocene deposits either. The great rarity of primates suggests that the woodlands and forests were of a temperate rather than a tropical variety and could not remain productive in terms of primate food requirements throughout the year. This still applies to the Afromontane forests of the fynbos region today.

The implication of the palaeotemperature evidence is that temperate conditions prevailed during the early Pliocene, with some relicts of an earlier tropical biota still surviving in terrestrial habitats.

The condition of specimens and the nature of their occurrence provide some further clues as to the nature of the early Pliocene palaeoenvironment. Dental abnormalities in certain closed-country taxa (bushpig, giraffids, waterbuck) suggest that conditions prevailing in the forest/woodland habitats were not ideal. Also relevant here is the fairly common occurrence of burnt specimens amongst the fossils. Since such specimens occur at various levels in the deposits, fires must have been frequent. They would have been particularly detrimental to those animals dependent on vegetation types that recovered slowly after fires (e.g. trees). In addition, catastrophic mortality of some mammals, notably the giraffids, suggest floods of substantial proportions (Klein 1981).

The above evidence combines to suggest a climate that included a pronounced dry season during which fires were common, and which was terminated by heavy falls of rain that caused severe flooding. Lightning was the most likely cause of fires and since electrical storms are more characteristic of summer rainfall climates, it is possible that the present summer dry/winter wet rainfall pattern was not prevalent during the early Pliocene. Severe flooding is also not characteristic of the present climate.

Just as the vegetation at Langebaanweg during the early Pliocene was in a state intermediate between that of the early-middle Miocene and the present, so too was the climate. Temperatures had moderated from tropical to temperate, and rainfall had declined and become seasonal, but probably with a summer wet/winter dry pattern. There are no exact modern analogues to the nature of the early Pliocene flora, fauna and climate.

LATE PLIOCENE

The only fossil assemblages from the fynbos region that may include elements dating back to the late Pliocene are from Baard's Quarry and Anyskop near Langebaanweg (Hendey 1978b, 1981a, 1983). Apart from the uncertainty about their age, the assemblages are small and consist mostly of fragmentary material. However, they are significant in showing that by the late Pliocene/early Pleistocene forest or woodland species were still present (e.g. Proboscidea, *Sivatherium*), but that open-country grazers (e.g. Equidae, Alcelaphini, Antilopini) were relatively better represented than in the early Pliocene. The implication is that there had been a further opening-up of the vegetation, but in contrast to the present, grasses were still an important component of the lowland vegetation.

However, there is a notable addition to the fauna, namely the black rhinoceros (*Diceros bicornis*), a browsing species that occurred commonly in the south-western Cape and Overberg in early historic times, being well adapted to the shrubland communities of the fynbos region. While it is possible that the black rhinoceros reflects an expansion of shrublands by the late Pliocene/early Pleistocene, this species was also widespread elsewhere in Africa where abundant low-level, leafy vegetation was present.

A progression in the decline of forests and woodlands during the late Pliocene may also be inferred from the fossil record elsewhere in Africa. The grazing combination of zebras, wildebeest and springbok/gazelles that has characterized African grasslands during the Quaternary, was well established by the late Pliocene. Other grazers such as the white rhinoceros, buffaloes, reedbuck and hartebeests were also common, and it was during the late Pliocene that African savanna carnivores such as the lion, hunting dog and spotted hyaena made their appearance. All these animals, and others, are recorded from Pleistocene fossil localities in the fynbos region (Klein, this volume), and it is probably safe to assume that they also appeared in this region during the late Pliocene.

DISCUSSION

The fossil vertebrates from Arrisdrift and the Langebaanweg area, together with inferences drawn from fossil occurrences elsewhere, indicate a change in the climate of the fynbos region from tropical in the Miocene to temperate in the Pliocene. The moderation in temperatures was coupled with a decline in rainfall. The rainfall was initially perennial, but it had become distinctly seasonal by the early Pliocene. The dry season then was probably winter, and it was only later in the Pliocene that the present summer dry/winter wet rainfall pattern was experienced in the south-western Cape for the first time. A mediterranean-type climate in the south-western Cape, and other existing climates of the fynbos region were, however, atypical for this region during the late Tertiary, and could have prevailed for only a relatively short period (or periods) towards the end of its 20 million-year history. It is worth noting here that these climates were also atypical of the Quaternary, being experienced only during the relatively short interglacial phases, including the present one.

Vegetational changes during the late Tertiary took the form of a progressive replacement of forests and woodlands (early-middle Miocene) by savanna-mosaic with gallery forests (Pliocene). The African savanna-mosaic includes shrublands (= bushlands, see Van Couvering 1980), and localized sclerophyllous shrublands are likely to have been established on the coastal lowlands during this transition. They probably had a longer history on the shallow acid soils of the mountains.

Pollens from deposits at Langebaanweg prove that taxa characteristic of fynbos region shrublands were present on the coastal lowlands at least by the early Pliocene, but the faunal evidence indicates that trees and grasses predominated over shrubs in the local vegetation at that time. There can be no doubt that the relative proportions of trees, grasses and shrubs fluctuated in after early Pliocene times, but generally shrubs previously formed a less significant element in the lowland vegetation than is the case today. Of the three vegetation types presently represented in this area, the coastal fynbos is the only one which is treeless, and it also has the least conspicuous grass component (Boucher 1982). If a coastal fynbos vegetation existed at all during the Pliocene, it must have had a much more restricted distribution, since the leached acid sands on which it is found today in areas such as the Cape Flats and Sandveld were then recently exposed marine sediments that were almost certainly still lime-rich. The predominance of shrubs in the coastal plant communities was probably a progressive development during the interglacials of the Quaternary, while during the longer glacial phases they were prominent only on the mountains and in restricted areas of the coastal lowlands. The implication is that as far back as the Pliocene, the shrublands may have formed a relatively minor element in the coastal vegetation mosaic.

The fact that grasses were formerly more prominent in the coastal lowlands even under existing climatic conditions was indicated by Acocks (1979). According to Heydorn & Tinley (1980:29) "it is not generally appreciated that close to 80 acid grass species (Boucher 1978), mostly from the highveld and the tropical moist Savanna Biome, are hidden amongst the dwarf shrubs [of the south-western Cape fynbos]." Significant in this statement is the fact that the grasses are mainly types that characterize the moister eastern parts of southern Africa, rather than from the arid savanna and desert grasslands of the west. It is evident from the vertebrate fossil record that these grasses were even more prominent in the vegetation mosaic, during both the Pliocene and Pleistocene under climatic conditions that differed from those of the present.

Heydorn & Tinley (1980:29) continue with the statement: "The most common type of succession in fynbos is the in situ regrowth sequence following fire in which geophytes, restios and the grasses are most prominent in the early phases (Kruger 1979; Taylor, pers. comm.)." The suppression of shrubs by frequent burning was well known to indigenous herders and quickly learnt by early European settlers at the Cape (Skead 1980). Natural fires are rare in the coastal plain under existing climatic conditions (Kruger 1979). The natural fire frequency under these conditions is not known, but is probably in excess of 10 years (Kruger 1979). More frequent burning (e.g. annually) will obviously be disadvantageous to shrubs and promote the role of grasses in the vegetation mosaic. Thus, climatic conditions that increase fire frequency (e.g. through more lightning strikes) will increase the area under grass cover. Judging from the Langebaanweg evidence, such conditions prevailed during the early Pliocene. It is not known if the same applied to any subsequent period.

Fires are not the only factor that reduce the viability of shrubs in the fynbos region. Many fynbos taxa have a low tolerance to frost (Levyns 1962), and shrublands would consequently have been reduced in extent during periods colder than the present. Such conditions may have prevailed at least as far back as the late Miocene and thereafter were repeated during the colder (glacial) phases of the Pliocene and Pleistocene.

The lower temperatures necessary to produce frosts on a significant scale would inevitably have been accompanied by changes in rainfall, which themselves would have influenced the character and composition of vegetation communities in the fynbos region. The volume and pattern of rainfall in the region today is very variable. For example, the coastal strandveld ranges from Mossel Bay (ca 500 mm per annum, evenly spread through the year), westwards to the Cape Flats (ca 500 mm, mainly in winter), and northwards to Namaqualand (ca 50 mm, mainly in winter). The strandveld is distinguished principally by more common scrub forest patches on the south coast, and shorter bushes with a more open canopy in Namaqualand (Boucher 1982). The likely effects of rainfall changes using the Cape Flats as an example are considered.

A reduction in the amount, but not the season, of rainfall would do no more than create a Namaqualand variant of the strandveld on the Cape Flats. A similar volume of rainfall more evenly distributed through the year would create a south coast variant. An increase in evenly distributed rain would probably cause an expansion of scrub forest patches, and may even lead to the establishment of Afromontane forests such as those of the Cape Peninsula and Outeniqualand. It was perhaps this rainfall pattern that led to the two extensions of mixed Podocarpus forest on the Cape Flats that were recorded by Schalke (1973). The effects of a rainfall increase coupled with either a winter or summer maximum would no doubt be as significant. In the case of the latter alternative, a situation such as that which prevailed at Langebaanweg during the early Pliocene is possible. An increase in winter rain is likely to have favoured the growth of some plants at the expense of others, although the long-term results of this rainfall pattern are not known.

It is self-evident that high rainfall benefits the biota. Plant growth is stimulated and this promotes animal life in all taxonomic categories from protozoans to mammals. Even in areas of nutrient-deficient soils, a rich biota can be self-sustaining, with organically developed nutrients kept in cycle by the local ecosystem. Such a situation evidently prevailed in the fynbos region for much of the late Tertiary. The key factor in the replacement of the forests by shrublands and grasslands was that of increasing aridity. Self-sustaining ecosystems on barren substrates are delicately balanced, as is shown, for example, by the catastrophic consequences of the artificial destruction of areas within the Amazon Basin rainforest. In the case of the Miocene rainforests of the fynbos region it was a natural phenomenon, that of declining rainfall, that led either to their replacement over wide areas by more open vegetation, or to their degeneration into the vestigial patches of Afromontane forest that survive today.

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REFERENCES

ACOCKS, J. P. H. 1979. The flora that matched the fauna. Bothalia 12:673-709.

ANDREWS, P. & VAN COUVERING, J. A. H. 1975. Palaeoenvironments in the East African Miocene. Contributions to Primatology 5: 62-103.

BOUCHER, C. 1978. Cape Hangklip area: II. The vegetation. Bothalia 12: 455-97.

BOUCHER, C. 1982. Floristic and structural features of the coastal foreland vegetation south of the Berg River, western Cape Province. In Moll, E. ed. Proceedings of a symposium on coastal lowlands of the western Cape: 21-6. Bellville: University of the Western Cape.

COETZEE, J. A. & ROGERS, J. 1982. Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa). Palaeogeography, Palaeoclimatology, Palaeoecology 39: 71-85.

DEACON, H. J. 1983. The comparative evolution of mediterranean-type ecosystems: a southern perspective. In Kruger, F. J., Mitchell, D. T. & Jarvis, J. U. M. eds Mediterranean-type ecosystems. The role of nutrients: Berlin: Springer-Verlag.

DORST, J. & DANDELOT, P. 1970. A field guide to the larger mammals of Africa. London: Collins.

GENTRY, A. W. 1980. Fossil Bovidae (Mammalia) of Langebaanweg, South Africa. Annals of the South African Museum 79:213-337.

HARRIS, J. M. 1975. Evolution of feeding mechanisms in the family Deinotheriidae (Mammalia: Proboscidea). Zoological Journal of the Linnean Society 56:331-62.

HENDEY, Q. B. 1978a. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. Annals of the South African Museum 76:1-41.

HENDEY, Q. B. 1978b. The age of the fossils from Baard's Quarry, Langebaanweg, South Africa. Annals of the South African Museum 75:1-24.

HENDEY, Q. B. 1981a. Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. Annals of the South African Museum 84:1-104.

HENDEY, Q. B. 1981b. Geological succession at Langebaanweg, Cape Province, and global events of the late Tertiary. South African Journal of Science 77:33-8.

HENDEY, Q. B. 1982. Langebaanweg. A record of past life. Cape Town: South African Museum.

HENDEY, Q. B. 1983. Southern African late Tertiary vertebrates. In Klein, R. G. ed. Southern African prehistory and paleoenvironments: Rotterdam: Balkema.

HEYDORN, A. E. F. & TINLEY, K. L. 1980. Estuaries of the Cape. CSIR

Research Report 380:1-97.

JANIS, C. 1982. Evolution of horns in ungulates: ecology and paleoecology. Biological Reviews 57:261-318.

KLEIN, R. G. 1981. Ungulate mortality and sedimentary facies in the late Tertiary Varswater Formation, Langebaanweg, south-western Cape Province, South Africa. Annals of the South African Museum 84:233-54.

KRUGER, F. J. 1979. Fire. In Day, J., Siegfried, W. R., Louw, G. N. & Jarman, M. L. eds Fynbos ecology: a preliminary synthesis. South African National Scientific Programmes Report 40:43-57.

LEVYNS, M. R. 1962. Past plant migrations in South Africa. Annals of the Cape Provincial Museums 2:7-10.

MAGLIO, V. J. & COOKE, H. B. S. 1978. Evolution of African mammals. Cambridge, Mass.: Harvard University Press.

NESBIT EVANS, E. M., VAN COUVERING, J. A. H. & ANDREWS, P. 1981. Palaeoecology of Miocene sites in western Kenya. Journal of Human Evolution 10:99-116.

PETTER, F. 1971. Family Cricetidae, Subfamily Nesomyinae. In Meester, J. & Setzer, H. W. eds The mammals of Africa. An identification manual, Part 6.2. Washington: Smithsonian Institution.

PICKFORD, M. 1981. Preliminary Miocene mammalian biostratigraphy for western Kenya. Journal of Human Evolution 10:73-97.

SCHALKE, H. J. W. G. 1973. The Upper Quaternary of the Cape Flats area (Cape Province, South Africa). Scripta Geologica 15:1-57.

SIESSER, W. G. 1978. Aridification of the Namib Desert: evidence from oceanic cores. In Van Zinderen Bakker, E. M. ed. Antarctic glacial history and world palaeoenvironments: 105-13. Rotterdam: Balkema.

SIESSER, W. G. 1980. Late Miocene origin of the Benguela upwelling system off northern Namibia. Science 208:283-5.

SKEAD, C. J. 1980. Historical mammal incidence in the Cape Province. Vol. 1. Cape Town: Department of Nature and Environmental Conservation.

TANKARD, A. J. 1975. The late Cenozoic history and palaeoenvironments of the coastal margin of the south-western Cape Province, South Africa. Unpublished PhD. thesis: Rhodes University.

TANKARD, A. J. & ROGERS, J. 1978. Late Cenozoic palaeoenvironments on the west coast of southern Africa. Journal of Biogeography 5:319-37.

VAN COUVERING, J. A. H. 1980. Community evolution in East Africa during the late Cenozoic. In Behrensmeyer, A. K. & Hill, A. P. eds Fossils in the making: 272-98. Chicago: University of Chicago Press.

VAN COUVERING, J. A. H. & VAN COUVERING, J. A. 1976. Early Miocene mammal fossils from East Africa. In Isaac, G. & McCown, E. R. eds Human origins: 155-207. Menlo Park, California: W. A. Benjamin.

WALKER, E. P. 1964. Mammals of the World. Baltimore: John Hopkins Press.

PALAEOENVIRONMENTAL IMPLICATIONS OF QUATERNARY LARGE MAMMALS IN THE FYNBOS REGION

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INTRODUCTION

For the purposes of this paper, a large mammal is one in which adults exceed 0,75 kg. This is an arbitrary definition, but has a practical basis. It includes species that were probably introduced to sites by people or carnivores and excludes ones that were probably introduced by owls. The difference in bone collector is important for interpreting the palaeoenvironmental implications of a fossil fauna.

In general, large mammals are relatively insensitive to environmental change, particularly compared to plants. However, the Quaternary mammals of the fynbos zone are a partial exception. At least during the late Quaternary, beginning approximately 128 000 years ago, the large mammal fauna of the fynbos region changed systematically in response to climatic events that have been established both locally and globally. My purpose here is to summarize the evidence for the change.

HISTORIC LARGE MAMMALS OF THE FYNBOS REGION

The historic mammal fauna of the fynbos region provides a benchmark against which earlier faunas may be evaluated. At least in a general way, the historic fauna may be reconstructed from its surviving remnants and from an examination of early European settlers' and travellers' accounts, as collated most systematically by Skead (1980).

In terms of its large mammals, as well as of its climate and vegetation, the fynbos region can be divided into two major subregions, separated by a spur of the Cape Fold Mountains that reaches the sea at Cape Hangklip. The two subregions may be conveniently referred to as the 'south-western Cape', in which rainfall is largely restricted to the winter months, and the 'southern Cape' (Overberg and Outeniqualand), in which it is more evenly distributed throughout the year. In both subregions, browsers tended to dominate grazers in both species diversity and absolute numbers.

In the southern Cape, the principal browsers were bushpig (Potamochoerus porcus), bushbuck (Tragelaphus scriptus), blue duiker (Cephalophus monticola), grey duiker (Sylvicapra grimmia), Cape grysbok (Raphicerus *melanotis*), and black rhinoceros (*Diceros bicornis*). Among the grazers, only the Cape buffalo (*Syncerus caffer*) was common more or less throughout. Hartebeest (*Alcelaphus buselaphus*) was locally fairly numerous. Bontebok (*Damaliscus dorcas dorcas*) and blue antelope (*Hippotragus leucophaeus*), though entirely restricted (endemic) to this region, were rare, and the blue antelope became extinct about 1800 A.D. Roan antelope (*Hippotragus equinus*) occurred in small numbers in the forests of the south-east. Eland (*Taurotragus oryx*), steenbok (*Raphicerus campestris*), and elephant (*Loxodonta africana*) (all mixed feeders) occurred more or less throughout, though the steenbok was probably completely replaced by the grysbok in areas of dense fynbos, bush or forest. Vaalribbok (*Pelea capreolus*), mountain reedbuck (*Redunca fulvorufula*), and klipspringer (*Oreotragus oreotragus*) were common in suitably hilly locales, particularly in the flanking Cape mountains where they were joined by the mountain zebra (*Equus zebra*).

The most common non-ungulate herbivores were baboon (*Papio ursinus*), rock hyrax (*Procavia capensis*) (technically an ungulate *sensu lato*), porcupine (*Hystrix africaeaustralis*), and hares (*Lepus capensis* and others). On the west, a large endemic mole rat (*Bathyergus suillus*) was also abundant in sandy, mainly coastal areas. Among the large carnivores, lion (*Panthera leo*), leopard (*Panthera pardus*), caracal (*Felis caracal*), brown hyaena (*Hyaena brunnea*), ratel (*Mellivora capensis*), and black-backed jackal (*Canis mesomelas*) were well represented. Common smaller carnivores included the wildcat (*Felis libyca*), grey mongoose (*Herpestes pulverulentus*), Egyptian mongoose (*Herpestes ichneumon*), striped polecat (*Ictonyx striatus*), Cape fox (*Vulpes chama*), and bat-eared fox (*Otocyon megalotis*). Cape fur seal (*Arctocephalus pusillus*) was common in coastal waters, and rookeries even occurred on the mainland.

The fauna of the south-western Cape was similar, but notably impoverished, lacking bushpig, bushbuck, blue duiker, buffalo, mountain reedbuck, blue antelope, roan, bontebok, and perhaps other species found in the southern Cape. Grey duiker was relatively abundant and steenbok was generally more common than grysbok. As will become clear below, the southern and south-western Cape were much more similar in their large mammal faunas during Quaternary 'glacials', perhaps partly because faunal interchange was facilitated when lower sea levels exposed the continental shelf, but probably mainly because the two subregions were more similar climatically.

LATE QUATERNARY FAUNAL CHANGE

There are at least sixteen sites in the southern and south-western Cape that have provided mammal fossils dating from the last 5 000-3 000 years. In each case, neither the species represented nor their relative abundance in any way suggest an environment significantly different from the historic one.

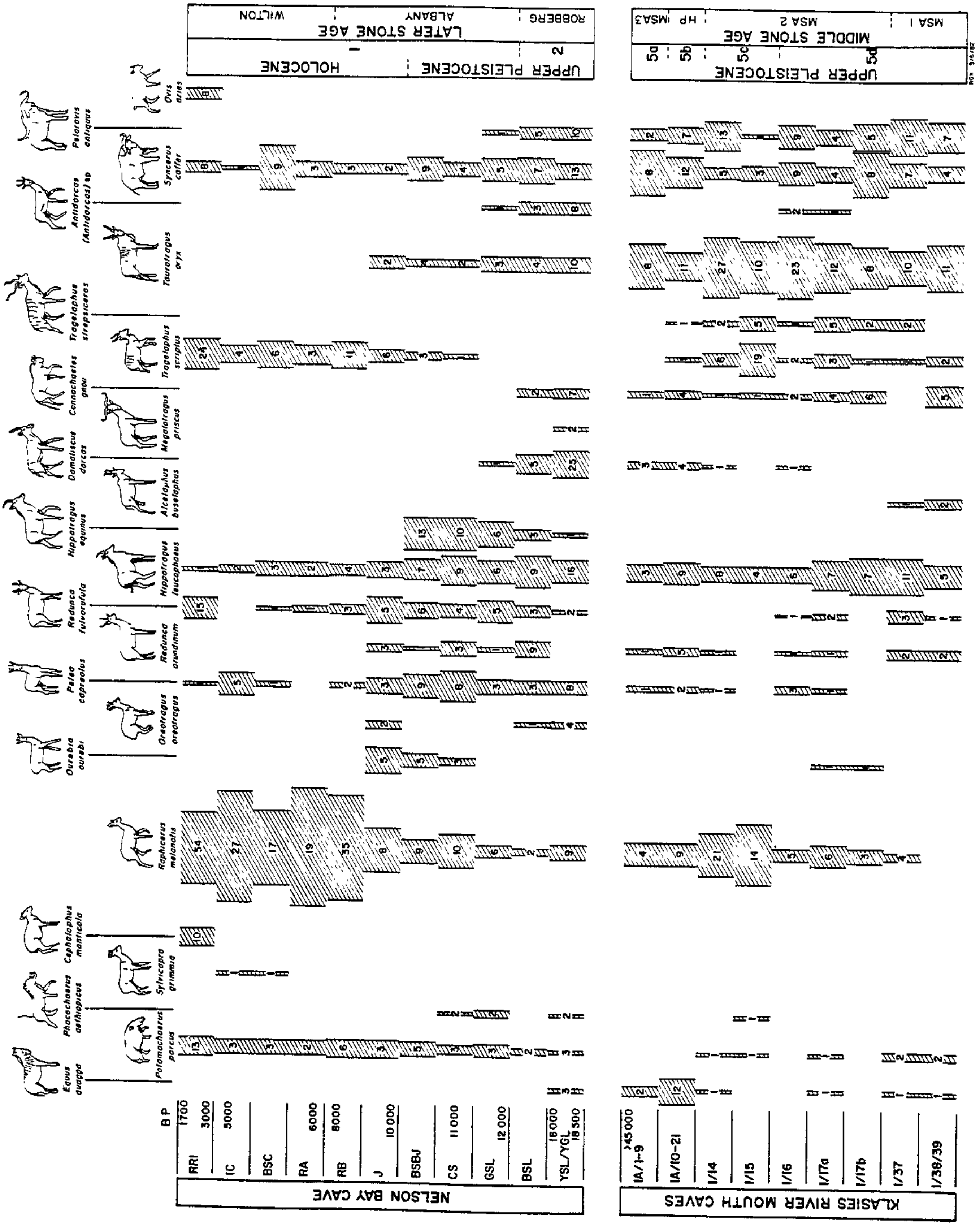
UPPER PLEISTOCENE
HOLOCENE
LATER STONE AGE
ROBBERG
ALBANY
WILTON
1
2
UPPER PLEISTOCENE
MIDDLE STONE AGE
MSA 1
MSA 2
HP
MSA 3
5a
5b
5c
5d
Ovis aries
Pelorovis antiquus
Syncerus caffer
Antidorcas (Antidorcas) sp
Taurotragus oryx
Tragelaphus strepsiceros
Tragelaphus scriptus
Connochaetes gnou
Megalotragus priscus
Damaliscus dorcas
Alcelaphus buselaphus
Hippotragus equinus
Hippotragus leucophaeus
Redunca fulvorufula
Redunca arundinum
Pelea capreolus
Oreotragus oreotragus
Ourebia ourebi
Raphicerus melanotis
Cephalophus monticola
Sylvicapra grimmia
Phacochoerus aethiopicus
Potamochoerus porcus
Equus quagga
BP
1700
3000
5000
6000
8000
10 000
11 000
12 000
16 000
18 500
RRI
IC
BSC
RA
RB
J
BSBJ
CS
GSL
BSL
YSL/YGL
NELSON BAY CAVE
>45 000
IA/1-9
IA/10-21
I/14
I/15
I/16
I/17a
I/17b
I/37
I/38/39
KLASIES RIVER MOUTH CAVES

Fig. 1

Fig. 1. The relative abundance of equid, suid and bovid species in different levels at Nelson Bay Cave (above) and in Klasies River Mouth caves 1 and 1A (below). Absolute abundance is measured by the minimum number of individuals (MNI) by which each species is represented in each level. The MNI numbers are presented inside hatched bars, while the bars are proportional to the percentage abundance of each species within each level. Levels are listed in descending order, from youngest to oldest, on the right hand side of the diagram. The numbers associated with the level designations are approximate radiocarbon ages B.P. (Before Present).

This is totally in keeping with regional and global evidence that the last 5 000-3 000 years was climatically broadly comparable to the present.

Yet earlier faunas, however, often point to a substantially different environment. The clearest example comes from Nelson Bay Cave located on the seaward edge of the Knysna Forest at Plettenberg Bay (Klein 1972). Bones were introduced to Nelson Bay primarily, if not exclusively, by Later Stone Age people. The fauna from levels dated by radiocarbon to between 18 500 and 16 000 years B.P. is comprised overwhelmingly of grazers, including quagga (Equus quagga), warthog (Phacochoerus aethiopicus), bontebok, black wildebeest (Connochaetes gnou), and springbok (Antidorcas cf. australis), none of which were recorded nearby historically. A similar fauna persisted, perhaps with interruptions, until about 12 000 years ago, when it was replaced by one in which historically dominant species (bushpig, grysbok, bushbuck, and buffalo) shared prominence with vaalribbok, mountain reedbuck and roan antelope. Only in deposits post-dating 5000 B.P. or so do the historic forms come to dominate completely (Fig. 1).

Global and local evidence for past temperatures and local (geomorphic/sedimentologic) evidence for past precipitation indicate that climate in the vicinity of Nelson Bay was cold and moist between 18 500 and 16 000 B.P., then cold and probably dry until 12 000-10 000 B.P., warm and dry from 10 000 to 5000-4000 B.P., and warm and moist (broadly like the present) after 5000-4000 B.P. (Butzer & Helgren 1972; Butzer 1973). The microfaunal bones accumulated by owls at Nelson Bay between 18 500 and 16 000 years ago confirm that local temperatures were significantly lower on average, and suggest that the vegetation nearby was more open than it was historically (Avery 1982), but do not confirm that climates were moist.

There is thus ample reason to conclude that climatic change was responsible for the faunal change observed at Nelson Bay, through the mediating influence of vegetation. From the large mammal fauna, it may be inferred that between 18 500 and 16 000 to 12 000 years ago, the surroundings of Nelson Bay were largely open grassland. In the 12 000-5000 year period,

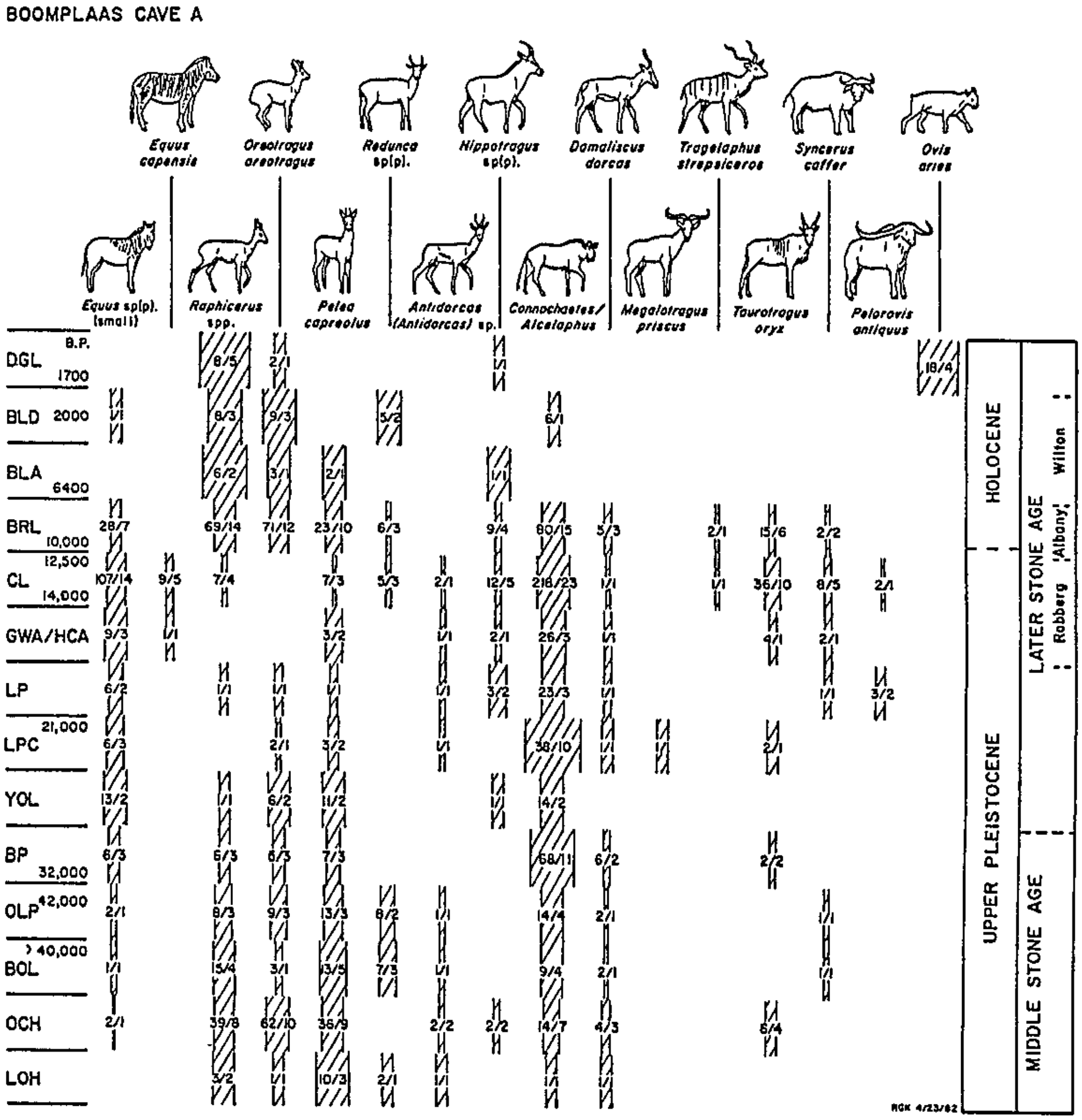

Fig. 2

The relative abundance of equid and bovid species in the main stratigraphic units of Boomplaas Cave A. For each unit and species "-/-" is the number of teeth or jaws/the minimum number of individuals (MNI) from which they must come. The hatched bars are proportional to the percentage of each species in each level as calculated from the MNI numbers. The figures associated with the stratigraphic units are approximate radiocarbon dates B.P. Because of the fragmentary nature of the teeth and jaws, some closely related species could not be consistently distinguished from one another. These include the grysbok (Raphicerus melanotis) and steenbok (R. campestris), the mountain reedbuck (Redunca fulvorufula) and southern reedbuck (R. arundinum), the blue antelope (Hippotragus leucophaeus) and roan antelope (H. equinus), and the black wildebeest (Connochaetes gnou) and Cape hartebeest (Alcelaphus buselaphus). Some of the isolated, late Pleistocene teeth assigned to the Connochaetes/Alcelaphus pair are very large and it is possible they come from the blue wildebeest (Connochaetes taurinus).

this was probably replaced by bushier vegetation with an important grass component. Only after 5000 B.P. or so did the present more or less complete bush and forest cover of the area become established. Both a pollen sequence developed by Martin (1968) at Groenvlei near Knysna and the changing geomorphic/pedologic environment (Butzer & Helgren 1972) may be read to support the kind of vegetational change the Nelson Bay fauna suggests for the 5000-4000 B.P. interval.

Broadly the same kind of vegetational change -- from a mosaic in which grasses were extremely prominent, if not dominant, to one in which they were progressively replaced by bush, forest or fynbos after 12 000-10 000 B.P. -- is implied by faunal changes at other Later Stone Age sites with deposits of appropriate age. These include Byneskranskop 1 (Schweitzer & Wilson 1982), Buffelskloof (Opperman 1978) and Boomplaas (Deacon 1979) within the fynbos zone proper, and Elands Bay Cave (Parkington 1979, 1981) and Melkhoutboom Cave (Deacon 1976) just beyond its north-western and south-eastern margins respectively.

The case of Boomplaas near Oudtshoorn is particularly clear, given the large samples involved (Fig. 2). The fauna from Boomplaas levels dated to between 22 000 and 12 000 B.P. is heavily dominated by equids (quagga, mountain zebra, or both) and alcelaphine antelope (wildebeest, hartebeest, or both). As at Nelson Bay, the indigenous ungulate species that dominated the local fauna historically -- grysbok, steenbok, klipspringer, and mountain reedbuck -- only dominate the fossil fauna after 6-5000 B.P. or so. In the period between perhaps 12 000 and 6-5000 B.P. the historically dominant species and the large grazers that dominated before 12 000 B.P. are about equally represented, suggesting a vegetation in which grasses were less common than before 12 000 B.P., but more common than after 6-5000 B.P. Taxonomic identifications of charcoals from the Boomplaas deposits confirm that the vegetation between 12-10 000 and 6-5000 B.P. was different from the vegetation both before and after (Deacon 1979), as do microfaunal bones accumulated by owls (Avery 1982).

At Boomplaas, the bottom-most units are believed to date from the 'last interglacial', and it is interesting that the fauna from these units is broadly similar in species composition and relative species abundance to the fauna from the topmost units, dating from the present interglacial or Holocene. This is true not only with respect to the frequencies of equids and bovids (Fig. 2), but also with regard to the frequencies of other species, especially baboon and hyrax (Fig. 3). It is tempting to conclude that the overall pattern of faunal change at Boomplaas reflects cyclical environmental change from 'interglacial' to 'glacial' and then back to 'interglacial' conditions, and this may well be true. However, there is evidence that many of the bones from the bottom of the sequence were collected by leopards, while the ones in the middle and top were collected by people. If so, this, rather than a similarity in environment, could explain

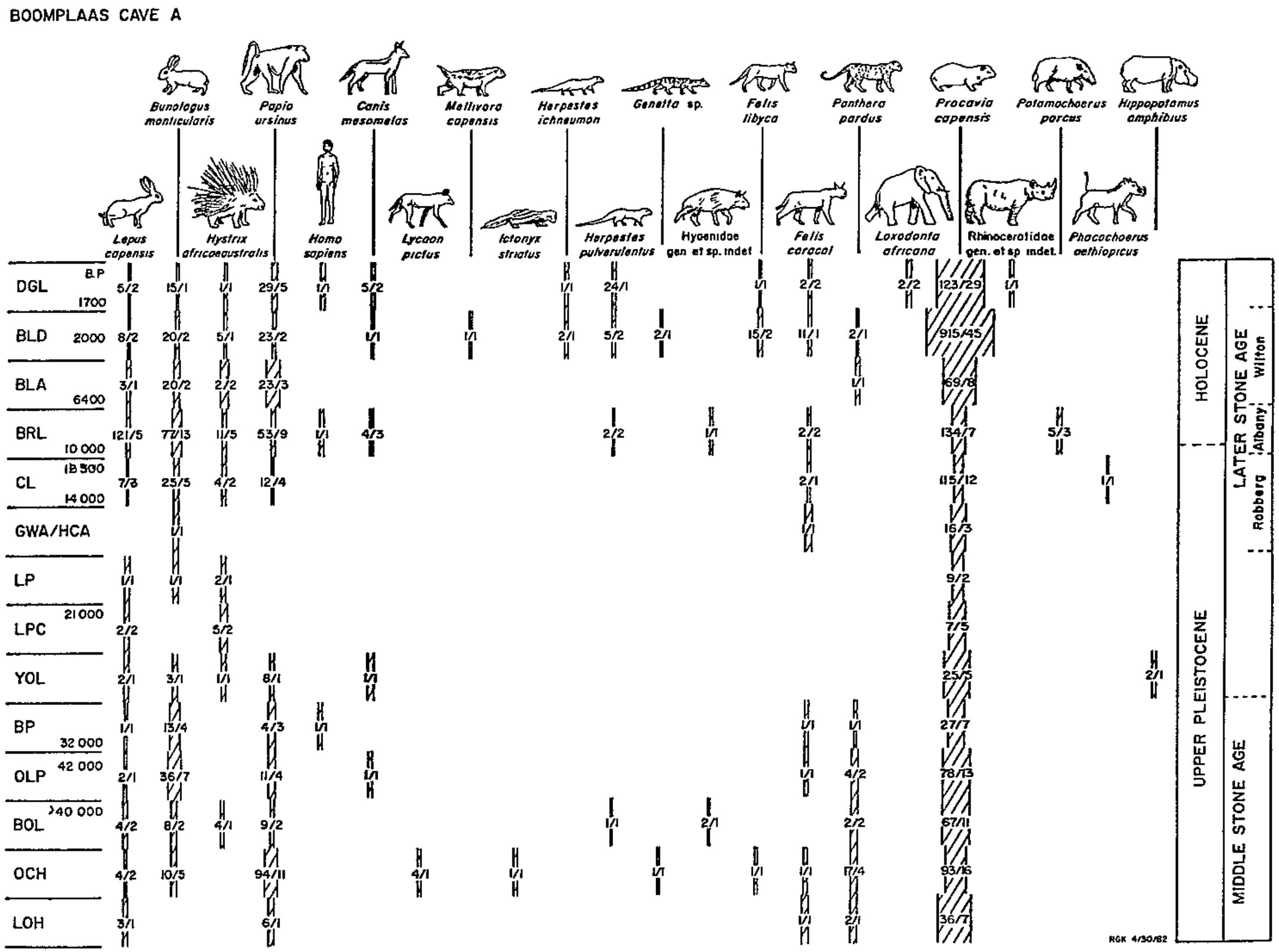

Fig. 3 The relative abundance of species besides equids and bovids in the main stratigraphic units of Boomplaas Cave A. For each unit and species, "-/-" is the number of bones/the minimum number of individuals from which they must come. Other features of the diagram are the same as for Fig. 2.

the abundance of hyraxes, baboons, and small ungulates at both the bottom and top.

The term 'last interglacial' as used here is synonymous with deep-sea oxygen-isotope stage 5, spanning the interval from approximately 128 000 years ago to about 75 000 years ago. The deep-sea record indicates that stage 5 was by no means uniformly warm, however (Shackleton & Opdyke 1973, 1976). It was interrupted by two pronounced cold intervals centred at about 109 000 and 92 000 B.P. These are known as substages 5d and 5b respectively. The preceding, intervening, and succeeding warm phases are known (from oldest to youngest) as 5e, 5c and 5a. Only 5e (from perhaps 128 000 to 118 000 B.P.) was as warm or warmer than the present interglacial (Holocene), and some specialists think that 5d to 5a are better regarded as the opening phases of the last glacial.

In addition to Boomplaas, other sites in the fynbos region that contain faunas dating from the time span of isotope stage 5 are the Klasies River Mouth caves near Humansdorp (Klein 1975b; Singer & Wymer 1982), Lake Pleasant (Groenvlei) near Knysna (Butzer & Helgren 1972), the Herolds Bay midden/bone occurrence (Brink & Deacon 1982), Linkerhandsgat-East near Stanford (Cooke 1955; Klein unpub.), Swartklip 1 on False Bay (Hendey & Hendey 1968; Klein 1975a), and Sea Harvest at Saldanha Bay (Hendey 1974; Klein unpub.). The Klasies River Mouth, Swartklip and Sea Harvest samples are particularly large and informative.

The bones in the Klasies River Mouth caves were accumulated primarily, if not exclusively, by Middle Stone Age people. Variation in sand grain size through the Klasies profile suggests sea level fluctuations nearby that can be correlated with substages of isotope stage 5 (Butzer in Singer & Wymer 1982). The correlations are supported by oxygen-isotope readings on Klasies marine shells that indicate that offshore waters were cooler during inferred periods of lower sea level (Shackleton in Singer & Wymer 1982). Fig. 1 shows that deposits formed at Klasies during isotope substages 5d and 5b are relatively richer in alcelaphine antelopes (wildebeest, hartebeest, and/or bontebok) and equids than are deposits correlated with the higher sea level of intervening substage 5c. In contrast, the deposits correlated with 5c are relatively richer in grysbok and bushbuck.

The pattern of faunal change from deposits correlated with 5d into ones correlated with 5c is in fact broadly reminiscent of the pattern of change in deposits formed during the climatically comparable transition from the last glacial to the present interglacial at nearby Nelson Bay Cave. (In terms of isotope stages, the transition at Nelson Bay would be from Stage 2 to Stage 1, about 12 000 years ago.) The fact that the two sites share a pattern of faunal change that coincides closely with a shared pattern of climatic change inferred from other evidence argues especially strongly that climatic change (not cultural change) was the ultimate cause of faunal change at both sites.

Besides broad similarities, the Klasies and Nelson Bay faunas that

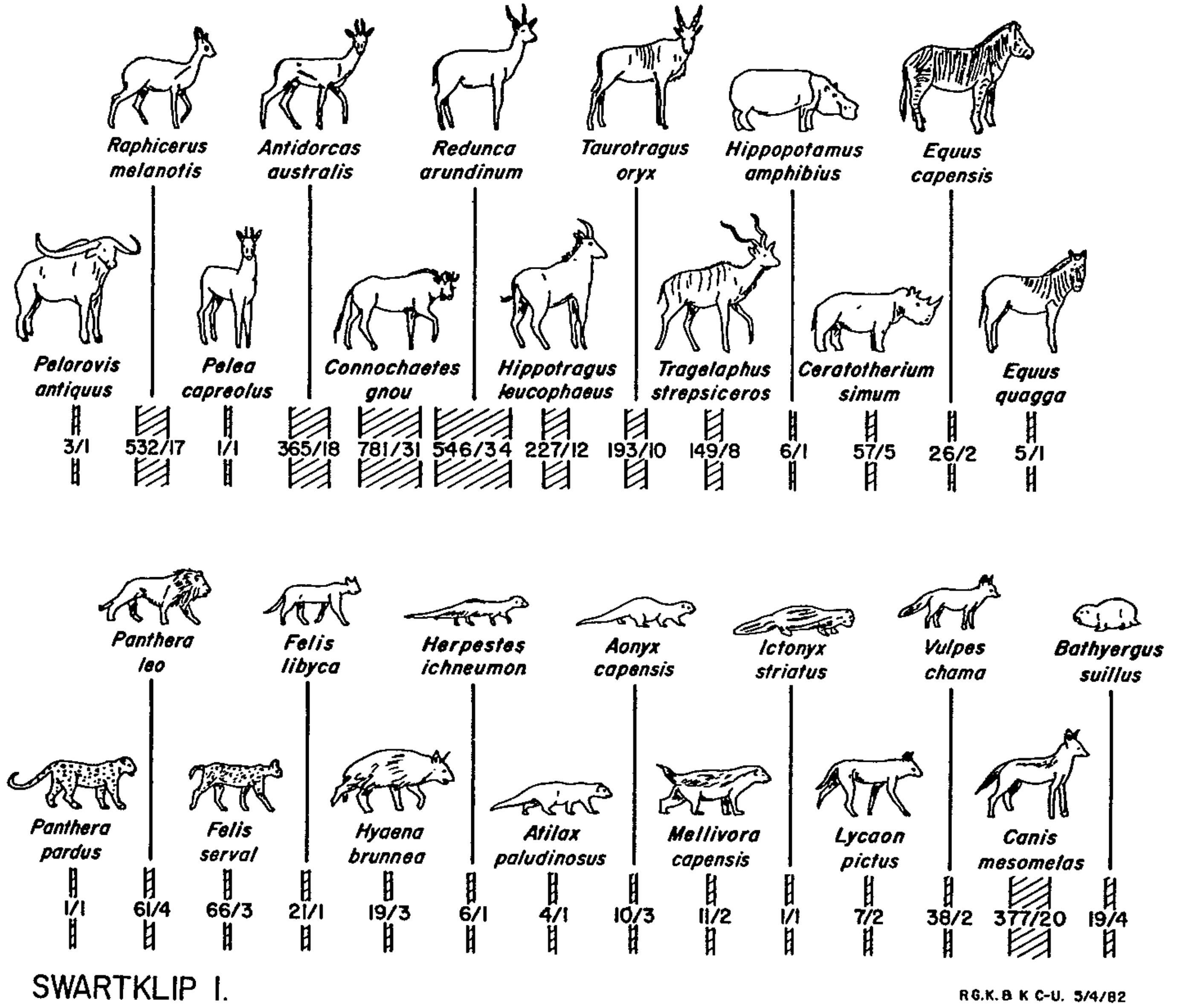

Fig. 4 The relative abundance of large mammal species in the fossil brown hyaena lair at Swartklip 1. "-/-" is the number of bones/minimum number of individuals (MNI) from which they must come. The hatched bars are proportional in breadth to the MNI's.

accumulated under broadly comparable ('interglacial') conditions exhibit some important differences. Especially striking is the great abundance of eland and giant buffalo (Pelorovis antiquus) at Klasies and the rarity of suids there. On analogy with Nelson Bay, at least the bushpig should be relatively common in those deposits where grysbok and bushbuck are well-represented.

It is possible that the abundance of eland and the rarity of suids at Klasies reflects the Klasies hunters' preference for relatively docile species (like eland) and the hunters' inability to obtain relatively dangerous ones (like bushpig). The (Middle Stone Age) artefacts made by the Klasies people are very different from the (Later Stone Age) ones made by the Nelson Bay people, and there is reason to suppose that only the Nelson Bay people possessed weapons like the bow and arrow that allowed hunters to attack dangerous prey from a distance.

Alternatively, it is possible that the local environment during substage 5c times differed from the present interglacial environment in ways that were especially favourable to eland and unfavourable to bushpig. Perhaps the same conditions were especially favourable to the giant buffalo, or perhaps the giant buffalo's grazing habits actually helped to create a special and distinctive environment that has no historic counterpart. The giant buffalo became extinct at the beginning of the present interglacial roughly 10 000 years ago, which itself constitutes an argument against strict comparability between the last interglacial and present interglacial environments near Nelson Bay and Klasies.

Finally, it is possible that eland were so abundant at Klasies because the cliffs nearby were ideal for driving eland to their death. Among the ungulates found at Klasies, eland were probably the ones most amenable to driving. Additionally, unlike the other ungulates at the site which are represented mainly by very young and by old individuals, the eland is well represented by prime-age adults (Klein 1979). The implication is that other ungulates were stalked individually and only the weakest, most vulnerable ones were usually obtained. In contrast, the high proportion of prime-age adult eland suggests hunting with a method that netted entire groups. The most likely method is driving. Unfortunately, the available evidence does not permit a clear choice among the alternative explanations for eland abundance at Klasies. It is similarly abundant in the much smaller Middle Stone Age sample from Die Kelders Cave 1 near Gansbaai, believed to date from the early part of the 'last glacial' (equivalent to isotope stage 4) (Klein 1975b,1976; Tankard & Schweitzer 1976). However, once again it is unclear if the reason is primarily environmental or cultural.

Geomorphic/sedimentologic data and methods similar to those employed in drawing palaeoenvironmental inferences from the Klasies River Mouth deposits indicate that the Swartklip fauna accumulated in the interval equivalent to isotope substage 5d, while the Sea Harvest fauna belongs to the broadly comparable, but more recent substage 5b (Butzer pers. comm.). In both cases,

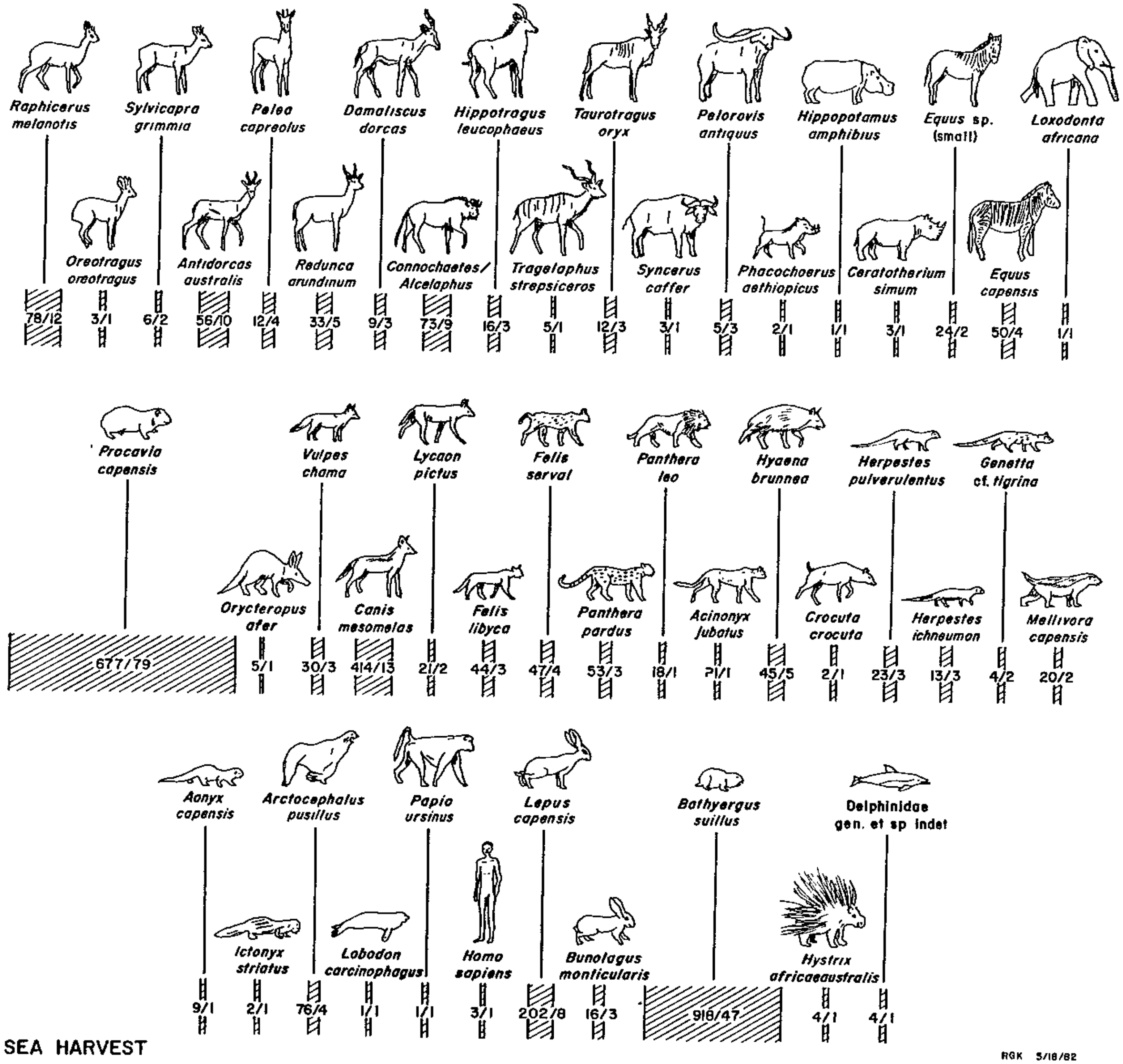

Fig. 5 The relative abundance of large mammal species in the Sea Harvest faunal locality, Saldanha Bay. For bovids, "-/-" is the number of teeth and jaws/minimum number of individuals (MNI) from which they must come. For other species "-/-" is the total number of bones/MNI. The hatched bars are proportional in breadth to the MNI's.

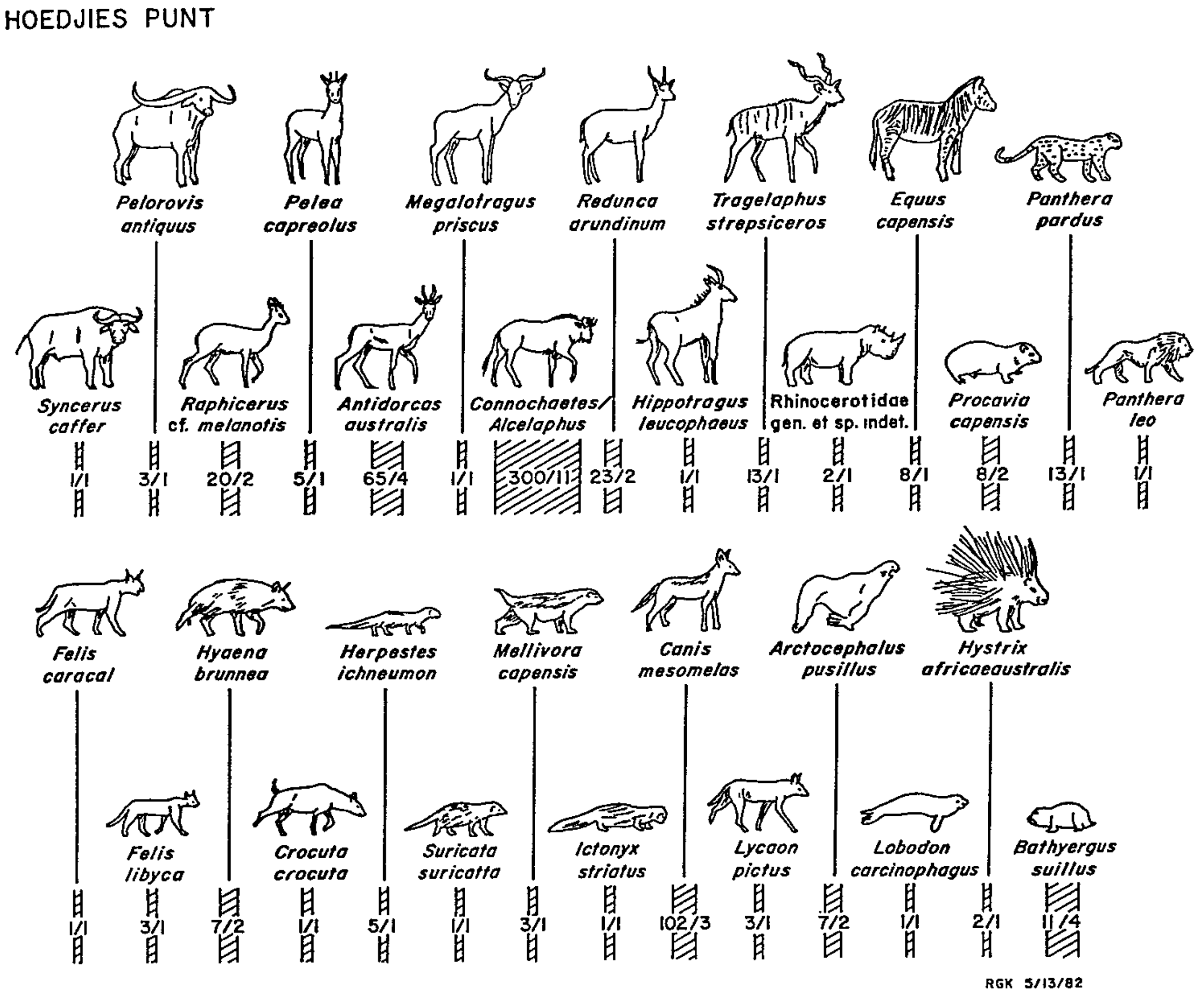

Fig. 6 The relative abundance of large mammal species in the Hoedjies Punt faunal occurrence, Saldanha Bay. "-/-" is the number of bones/the minimum number of individuals (MNI) from which they must come. The hatched bars are proportional in breadth to the MNI's.

the climatic conditions were essentially 'glacial', in spite of the 'last interglacial' (sensu lato) age assignment. In both fossil faunas, the most abundant ungulates are grazers that were rare or absent historically (Figs 4 and 5). This suggests once again that 'glacial' climatic conditions in the fynbos region favoured an expanded role for grasses in the regional vegetational mosaic.

Unlike the sites that have been discussed so far, neither Swartklip nor Sea Harvest is an archaeological occurrence. Instead, they represent places to which bones were brought by carnivores (probably the brown hyaena). In consequence of this, compared to archaeological faunas they are relatively rich in bones of carnivores, especially bones of black-backed jackals, probably killed by the hyaenas in contests for carrion. Sea Harvest is also very rich in bones of small mammals (hyrax, mole rats and hares), perhaps accumulated at the site by a small carnivore or owl. However, the fact that grazers dominate heavily among the ungulates at both Swartklip and Sea Harvest is a further strong argument that grazer abundance in archaeological sites dating from similar 'glacial' episodes reflects the genuine abundance of grazers nearby. The alternative -- that they are abundant in the archaeological sites because of a strong (and inexplicable) ancient human preference for rare species -- seems highly unlikely.

Several other late Quaternary carnivore sites in the fynbos zone have provided faunas basically similar to those from Swartklip and Sea Harvest in the high proportion of historically rare or absent grazers (e.g. Figs 6 and 7). So far, at most of these sites, there is no independent basis for determining what the environment was like at the time the bones accumulated, but it seems likely it was 'glacial' in the same sense that it was at Swartklip and Sea Harvest. The reason that 'glacial' faunas appear to be so much more common than 'interglacial' ones is probably that 'glacial' climatic conditions were far more common than 'interglacial' ones during the late Quaternary. At the same time, it is important to point out that with the exception of Boomplaas, there are no sites in the fynbos zone (and few in southern Africa as a whole) that have provided faunas clearly dating from the main part of the 'last glacial' (equivalent to isotope stage 3, between 64 000 and 32 000 years ago). The most probable reason is that hyperarid climate prevailed, reducing human and animal populations to levels with very low archaeological/palaeontological visibility.

EARLY AND MIDDLE QUATERNARY FAUNAS

Hendey (1978) has argued convincingly that the mammal fauna from the 'lower levels' of Baard's Quarry, Langebaanweg is of latest Pliocene or earliest Pleistocene (= early Quaternary) age. So far, no other early Quaternary faunas have been recovered in the fynbos region. Although the

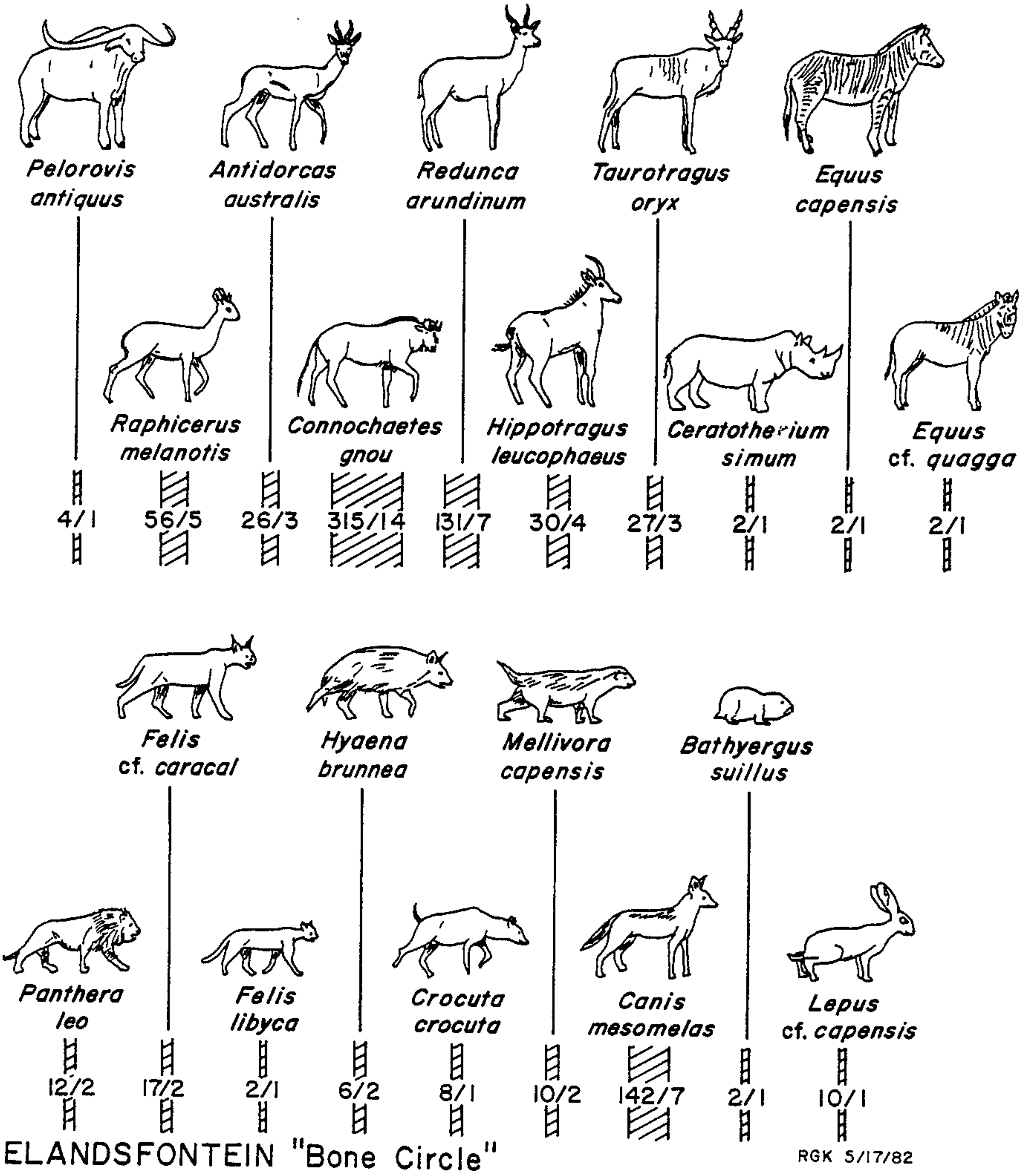

Fig. 7 The relative abundance of large mammal species in the Elandsfontein "Bone Circle". "-/-" is the number of bones/minimum number of individuals (MNI) from which they must come. The hatched bars are proportional to the MNI's.

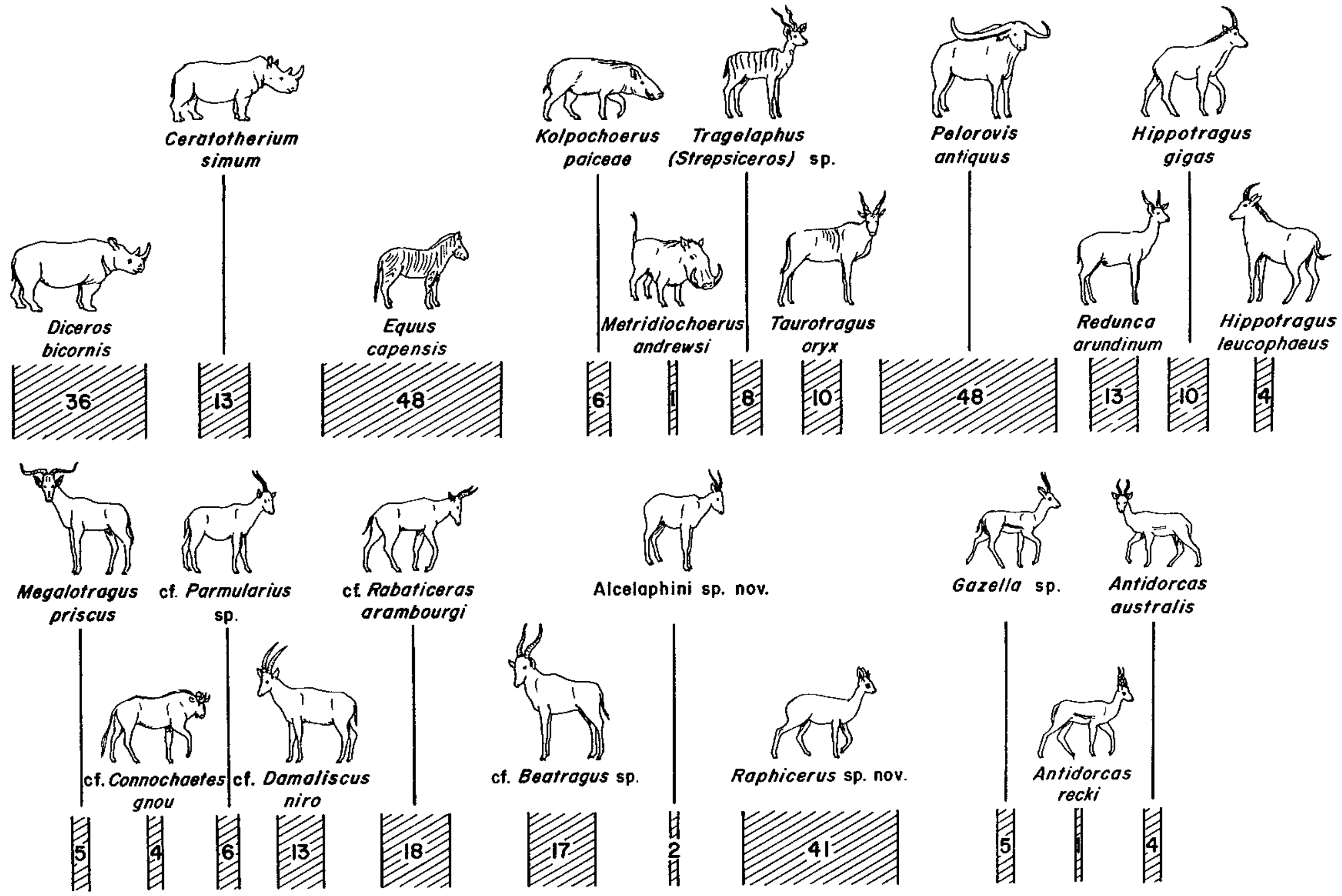

Fig. 8 The relative abundance of equid, suid and bovid species in the middle Quaternary fauna of Elandsfontein. Inside each hatched bar is the minimum number of individuals (MNI) by which each species is represented. The breadth of each bar is proportional to the MNI.

Baard's Quarry fauna is clearly much younger than the main ('E' Quarry = early Pliocene) fauna from Langebaanweg, there is nothing about it to suggest environmental conditions different from those that pertained at Langebaanweg earlier on, as discussed by Hendey (this volume).

Middle Quaternary mammals are considerably better known. There is a small sample recently recovered from Skurwerug at Saldanha Bay (Hendey, pers. comm.), small, probably late Middle Pleistocene, samples from Bloembos near Darling (Cooke 1955) and from Duinefontein 2 near Melkbosstrand (Klein 1976), and a very large sample from Elandsfontein near Hopefield (Hendey 1974). The Bloembos sample is notable because it has provided the sole Quaternary record of the giraffe (*Giraffa camelopardalis*) in the fynbos zone. This is direct evidence for the presence of trees in a local environment that was largely treeless historically. However, it is the large and diverse Elandsfontein sample which is potentially most informative from a palaeoenvironmental point of view.

Similar to many of the late Quaternary faunas discussed in the last section, the Elandsfontein middle Quaternary fauna is relatively rich in alcelaphine antelopes (at least six different species, including *Connochaetes gnou*, *Parmularius* sp., *Damaliscus niro*, *Rabaticeras arambourgi* and ?*Beatragus* sp.), equids and other grazers (Fig. 8). This implies that grasses played a more important role in the ancient environment than they did historically. However, the Elandsfontein fauna also contains a giraffid (*Sivatherium olduvaiense*) and a civet cat (*Viverra civetta*), indicating the grassland contained trees. With regard to rhinoceroses, both the black (which was present historically) and the white (*Ceratotherium simum*) (which was not) are represented, but the black is clearly more numerous, indicating that suitable browse was common in the vicinity. Suids are not common overall, but between the two that are present, *Kolpochoerus paiceae*, a probable browser, outnumbers *Metridiochoerus andrewsi*, a probable grazer. In sum, in contrast to the late Quaternary 'glacial' faunas which tend to suggest open grassland with relatively little bush or thicket, the Elandsfontein fauna suggests a vegetation in which grass and bush were more equally represented.

It is important to emphasize that Elandsfontein is a very different kind of site than any of the late Quaternary ones discussed previously. The middle Quaternary bones lie on one or more palaeosurfaces where they are currently being exposed by deflation. Associations of bones in anatomical order are common and many (?most) of the animals represented probably lie at or near the places where they died. Carnivore-gnawed bones and hyaena coprolites are probably more numerous than artefacts, and death was probably more often from 'natural' causes than from human action. Porcupine gnawing is also quite common, and many of the bones may have come from now-deflated porcupine lairs. The overwhelming majority of bones in the present sample were collected from the surface, without record of their associations or of their provenience within the site. This means that it is impossible to estimate how many may have come from semi-articulated skeletons, how many were associated with artefacts or coprolites, and so forth. Even with these problems in mind, however, the overall composition of the fauna still suggests an environment that was qualitatively different in important respects from any known late Quaternary one.

MEAN INDIVIDUAL SIZE AND CLIMATE

Mean individual size has been shown to vary with climate in a number of mammalian species, particularly carnivores and micromammals (small rodents and insectivores). Kurten (1959, 1965) has presented some examples and discussed the reasons for size variation, including Bergmann's Rule and so-called population density factors. Bergmann's Rule states that if all other things are equal, individuals of a species will be larger in colder climates. This is because as an animal grows, its volume, which produces heat, increases more rapidly than its skin area, which dissipates it.

Bergmann's Rule has been shown particularly to characterize carnivores, though there are many species that do not obey it. The reason is apparently that 'other things' are not always equal. Probably most important is the fact that individuals must be able to find sufficient food to maintain a larger body. It is in this context that 'population density factors' become important. In particular, increased body size will probably be selected against, if it reduces the number of individuals the environment can support below the critical level necessary for successful reproduction. Through its effect on food supply, a change in climate, even greater cold, might thus actually induce a reduction in mean individual body size.

Avery (1982) has shown that mean size in several southern African micromammal species is probably related to variation in temperature or precipitation, but otherwise very little research of this kind has been done in southern Africa. In a study designed to explore the possibility of a linkage between climate and size in somewhat larger mammals, I am currently compiling measurements on bones of black-backed jackal, Cape fox, brown hyaena, caracal, grey mongoose, rock hyrax, Cape mole rat and Cape grysbok. These are species which are abundant in sites of various ages within the fynbos region.

The study is incomplete, in that many more recent comparative specimens must be measured to confirm the patterns that appear to be emerging. The measurements compiled so far suggest that individual carnivore size generally varies with temperature in a way that would be predicted from Bergmann's Rule, that is, in the various carnivore species, mean individual size increases as mean annual temperature decreases. The pattern in the three herbivorous species is more complex, but appears to be broadly related to precipitation. In particular, at least within the fynbos zone, as precipitation increases, average hyrax size appears to decrease, while average mole rat and grysbok size appear to increase.

As an example of what is involved, Fig. 9 presents measurements on black-backed jackal first molar (M1) lengths. Average tooth size reflects average body size in most mammalian species, while jackal dentitions are common both in museum comparative collections and in fossil samples where the jackal itself is well represented. A further advantage to measuring the M1 is that it is readily identifiable to species, so there is no danger of confusing what is really a change in jackal species with a change in mean individual size within a single species.

Fig. 9 shows that Cape and Namibian jackals tend to be substantially larger than ones from Equatorial East Africa, as would be expected if Bergmann's Rule were operative. The figure also shows that modern Cape jackals tend to be significantly smaller than the ones represented at Swartklip 1. This is also in keeping with the operation of Bergmann's Rule, since geomorphic evidence indicates that the Swartklip fauna accumulated under very cool conditions. The Sea Harvest jackals were apparently intermediate in average size between modern Cape ones and the very large specimens from Swartklip. This is consistent with the fact that, unlike the Swartklip fauna, the Sea Harvest one contains some marine elements, suggesting accumulation at a time of somewhat higher sea level and less cool ambient temperatures.

The only jackals similar in size to the Swartklip ones are those from the 'Bone Circle' at Elandsfontein. This is an late Quaternary fossil hyaena lair in which the species representation is essentially identical to that at Swartklip (Inskeep & Hendey 1966; Klein unpub.) (compare Figs 5 and 7). The implication is that the 'Bone Circle' formed under climatic conditions very similar to those at Swartklip. Interestingly, the jackals associated with the middle Quaternary fauna at Elandsfontein (labelled 'other' in Fig. 9) are significantly smaller than the 'Bone Circle' ones. They are in fact similar in average size to modern Cape jackals. Together with the fact that the Elandsfontein middle Quaternary grysbok is very large, this may mean that the middle Quaternary fauna accumulated under relatively warm and wet conditions without parallel in the late Quaternary. As discussed in the last section, the taxonomic composition of the middle Quaternary fauna may be used to support the same conclusion. The relatively warm, wet conditions involved may be the ones that promoted the growth of yellowwood forests on the Cape Flats, as reported by Schalke (1973). Alternatively, it is possible these forests are much older than the middle Quaternary. Until recently, they were assigned to the late Quaternary on the basis of radiocarbon dates that are assumed to be finite, but which may well be infinite.

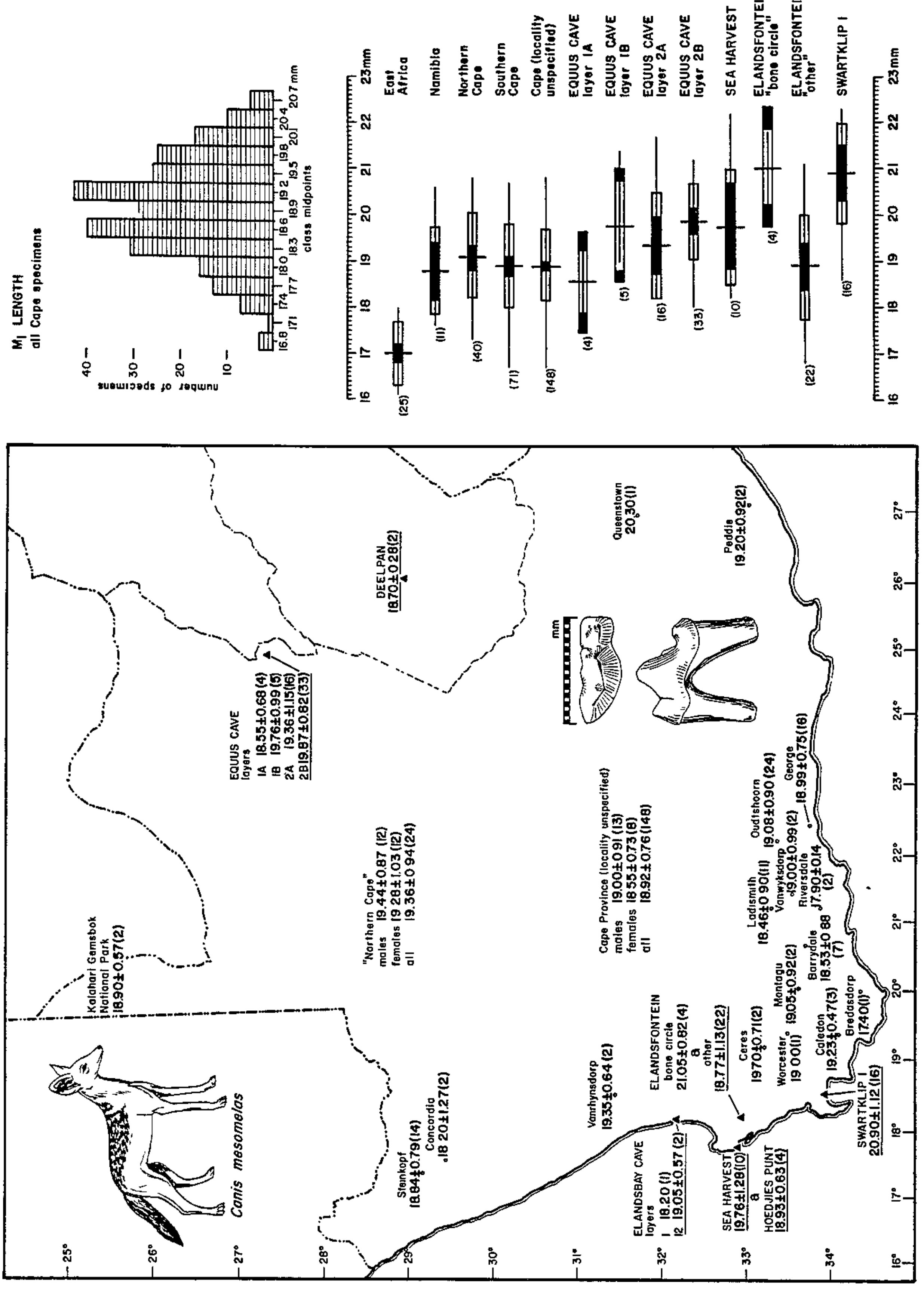
M1 LENGTH
all Cape specimens
number of specimens
40
30
20
10
16.8
171
174
177
180
183
186
189
192
195
198
201
204
207 mm
class midpoints
16
17
18
19
20
21
22
23mm
(25) East Africa
(11) Namibia
(40) Northern Cape
(71) Southern Cape
(148) Cape (locality unspecified)
(4) EQUUS CAVE layer 1A
(5) EQUUS CAVE layer 1B
(16) EQUUS CAVE layer 2A
(33) EQUUS CAVE layer 2B
(10) SEA HARVEST
(4) ELANDSFONTEIN "bone circle"
(22) ELANDSFONTEIN "other"
(16) SWARTKLIP I
Canis mesomelas
Kalahari Gemsbok National Park 18.90±0.57(2)
EQUUS CAVE layers
1A 18.55±0.68(4)
1B 19.76±0.99(5)
2A 19.36±1.15(16)
2B 19.87±0.82(33)
DEELPAN 18.70±0.28(2)
"Northern Cape"
males 19.44±0.87 (12)
females 19.28±1.03 (12)
all 19.36±0.94(24)
Steinkopf 18.84±0.79(14)
Concordia 18.20±1.27(2)
Vanrhynsdorp 19.35±0.64 (2)
ELANDSBAY CAVE layers
1 18.20 (1)
12 19.05±0.57 (2)
ELANDSFONTEIN bone circle 21.05±0.82(4)
& other 18.77±1.13(22)
SEA HARVEST 19.76±1.28(10)
& HOEDJIES PUNT 18.93±0.63(4)
Ceres 19.70±0.71(2)
Worcester 19.00(1)
Montagu 19.05±0.92(2)
Caledon 19.23±0.47(3)
Bredasdorp 17.40(1)
Barrydale 18.53±0.88 (7)
SWARTKLIP I 20.90±1.12(16)
Ladismith 18.46±0.90(11)
Vanwyksdorp 19.00±0.99(2)
Riversdale 17.90±0.14 (2)
Oudtshoorn 19.08±0.90 (24)
George 18.99±0.75(16)
Cape Province (locality unspecified)
males 19.00±0.91 (13)
females 18.55±0.73 (8)
all 18.92±0.76(148)
Queenstown 20.30(1)
Peddie 19.20±0.92(2)
mm
16°
17°
18°
19°
20°
21°
22°
23°
24°
25°
26°
27°
25°
26°
27°
28°
29°
30°
31°
32°
33°
34°

Fig. 9

Fig. 9. (Left). A map showing the provenience of recent and fossil samples of Cape Province black-backed jackals whose lower first molars (M1's) have been measured in an analysis of size change through time and space. Recent collection localities are in lower case and the approximate location of each is marked by a circle at the spot of a relevant administrative centre. The number before the "±" in each instance is the mean M1 length; the number immediately after the "±" is the standard deviation and the number in parentheses is the number of specimens measured. Numbers characterizing the fossil samples are underlined. Analysis of the numbers indicates that there is little, if any, significant variation among the recent Cape samples. This is the basis for lumping them for comparison with the fossil samples. (Right Upper): The frequency distribution of M1 lengths in the total sample of modern black-backed jackals from the Cape Province. The slight bimodality probably reflects slight sexual dimorphism in M1 length, which is more clearly indicated by the means calculated for the males and females separately. (Right Lower): The mean (vertical line), observed range (horizontal line), standard deviation (white bar), and 95% confidence limits for the mean (black bar) for M1 lengths in the black-backed jackal samples. The means for samples whose 95% confidence limits (black bars) do not overlap may be considered statistically different at the 0,05 level or below.

CONCLUSION

Fossil large mammals from the fynbos zone indicate conditions broadly like modern ones during the last 5-3000 years, preceded by distinctly different conditions during most of the late Quaternary. Conditions were especially different during the late Quaternary 'glacial' episodes, when large grazing ungulates greatly outnumbered the browsers and mixed feeders that dominated the fynbos fauna historically. The implication is that grasses played a much more prominent role in the regional vegetation during 'glacials' than they did historically.

The early and middle Quaternary large mammal fauna of the fynbos region is relatively poorly known, but limited evidence again suggests conditions different from historic ones and also a pattern of environmental change that differed from the late Quaternary pattern.

Judging by the large mammals, Quaternary environmental change was probably more dramatic in the fynbos zone than in any other part of Africa excepting the Sahara and the Maghreb (Klein 1980 and in press). Parallels with the Maghreb are particularly interesting, given its recent climatic and vegetational similarity to the fynbos zone. In the Maghreb, as in the fynbos region, late Quaternary 'glacial' faunas appear to have been dominated by stereotypic African grazing species, including wildebeest, zebra, warthog and white rhinoceros that were rare or absent in 'interglacial' times.

The large mammals suggest that conditions similar to recent ones in the fynbos region were relatively rare during the Quaternary. During much of the Quaternary the fynbos zone or biome would probably have been difficult to distinguish from adjacent zones on faunistic grounds. The precise implications for fynbos plant communities are unclear, but will probably emerge from the kind of palaeobotanical research reported elsewhere in this volume.

REFERENCES

AVERY, D. M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quaternary in the southern Cape Province, South Africa. Annals of the South African Museum 85:183-374.

BRINK, J. S. & DEACON, H. J. 1982. A study of a last interglacial shell midden and bone accumulation at Herolds Bay, Cape Province, South Africa. Palaeoecology of Africa 15:31-41.

BUTZER, K. W. 1973. Geology of Nelson Bay Cave, Robberg, South Africa. South African Archaeological Bulletin 28:97-110.

BUTZER, K. W. & HELGREN, D. M. 1972. Late Cenozoic evolution of the Cape coast between Knysna and Cape St Francis, South Africa. Quaternary Research 2:143-69.

COOKE, H. B. S. 1955. Some fossil mammals in the South African Museum collections. Annals of the South African Museum 42:161-8.

DEACON, H. J. 1976. Where hunters gathered. Claremont: South African Archaeological Society Monograph 1.

DEACON, H. J. 1979. Excavations at Boomplaas Cave: a sequence through the Upper Pleistocene and Holocene in South Africa. World Archaeology 10:241-57.

HENDEY, Q. B. 1974. The Late Cenozoic Carnivora of the south-western Cape Province. Annals of the South African Museum 63:1-369.

HENDEY, Q. B. 1978. The age of the fossils from Baard's Quarry, Langebaanweg, South Africa. Annals of the South African Museum 75:1-24.

HENDEY, Q. B. & HENDEY, H. 1968. New Quaternary fossil sites near Swartklip, Cape Province. Annals of the South African Museum 52:43-73.

INSKEEP, R. R. & HENDEY, Q. B. 1966. An interesting association of bones from the Elandsfontein fossil site. Actes du Ve Congres Panafricaine de Prehistoire et de l'etude du Quaternaire: 109:24. Tenerife: Museo Arqueologico de Tenerife.

KLEIN, R. G. 1972. The Late Quaternary mammal fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. Quaternary Research 2:135-42.

KLEIN, R. G. 1975a. Paleoanthropological implications of the non-archaeological bone assemblage from Swartklip 1, south-western Cape Province, South Africa. Quaternary Research 5:275-88.

KLEIN, R. G. 1975b. Middle Stone Age man-animal relationships in southern Africa: evidence from Die Kelders and Klasies River Mouth. Science 190:265-7.

KLEIN, R. G. 1976. A preliminary report on the 'Middle Stone Age' open-air site of Duinefontein 2 (Melkbosstrand, south-western Cape Province, South Africa). South African Archaeological Bulletin 31:12-20.

KLEIN, R. G. 1979. Stone Age exploitation of animals in southern Africa. American Scientist 67:151-60.

KLEIN, R. G. 1980. Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in southern Africa. Annals of the South African Museum 81:223-83.

KLEIN, R. G. in press. Mammalian extinctions and Stone Age people in Africa. In Martin, P. S. & Klein, R. G. eds Pleistocene extinctions. Tucson: University of Arizona Press.

KURTEN, B. 1959. Rates of evolution in fossil mammals. Cold Spring Harbor Symposia on Quantitative Biology 24:205-15.

KURTEN, B. 1965. The Carnivora of the Palestine Caves. Acta Zoologica Fennica 107:1-74.

MARTIN, A. R. H. 1968. Pollen analysis of Groenvlei Lake sediments, Knysna (South Africa). Review of Palaeobotany and Palynology 7:107-44.

OPPERMAN, H. 1978. Excavations in the Buffelskloof Rock Shelter, near Calitzdorp, southern Cape. South African Archaeological Bulletin 33:18-24.

PARKINGTON, J. E. 1979. Report on research in the Verlore Vlei 1976-9. Reports on research into the Late Stone Age of the Western Cape. University of Cape Town: Department of Archaeology.

PARKINGTON, J. E. 1981. The effects of environmental change on the scheduling of visits to Elands Bay Cave, Cape Province, South Africa. In Hodder, I., Isaac, G. & Hammond, N. eds Pattern in the Past: studies in honour of David Clarke: 341-59. Cambridge: Cambridge University Press.

SCHALKE, H. J. W. G. 1973. The Upper Quaternary of the Cape Flats area (Cape Province, South Africa). Scripta Geologica 15:1-57.

SCHWEITZER, F. R. & WILSON, M. L. 1982. Byneskranskop 1, a late Quaternary living site in the southern Cape Province, South Africa. Annals of the South African Museum 88:1-203.

SHACKLETON, N. J. & OPDYKE, N. D. 1973. Oxygen isotope and palaeomagnetic stratigraphy of Equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes on a 100 000 and 1 000 000 year scale. Quaternary Research 3:39-55.

SHACKLETON, N. J. & OPDYKE, N. D. 1976. Oxygen-isotope and paleomagnetic stratigraphy of Pacific Core V28-239. Late Pliocene to latest Pleistocene. Geological Society of America Memoir 145:449-64.

SINGER, R. & WYMER, J. 1982. The Middle Stone Age at Klasies River Mouth in South Africa. Chicago: University of Chicago Press.

SKEAD, C. J. 1980. Historical mammal incidence in the Cape Province. Vol. 1. The western and northern Cape. Cape Town: Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope.

TANKARD, A. J. & SCHWEITZER, F. R. 1976. Textural analysis of cave sediments: Die Kelders, Cape Province, South Africa. In Davidson, D. A. & Shackley, M. L. eds Geoarchaeology: 289-316. London: Duckworth.

PALAEOENVIRONMENTAL IMPLICATIONS OF THE SMALL QUATERNARY MAMMALS OF THE FYNBOS REGION

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INTRODUCTION

Animal communities may be seen as products of their environments. Therefore, the underlying assumption of palaeoenvironmental interpretation is that past communities may be used as indicators of the environment that produced them. Moreover, changes in various aspects of the community may provide insight into different facets of the environment of the community. The particular advantages of small mammals, here specifically rodents and insectivores (micromammals), in palaeoenvironmental interpretation are that their small size renders them particularly sensitive to environmental change and their rapid breeding reduces the time lag in adaptation to such change. Further, the evidence unquestionably refers to the locality in which the specimens were collected, and the relatively frequent occurrence of remains of large numbers of individuals facilitates the study of community change. Disadvantages have to do with the small size of the home range of micromammals and, consequently, the area to which the data refer. These can, however, be reduced in importance by increasing the number of areas sampled and by judicious extrapolation from the existing data. Interpretation is itself restricted by the amount of information available concerning the extant communities and populations of small mammals. This position can, however, only improve as more work is carried out by ecologists on the physiological tolerances and habitat requirements of living small mammals.

GENERAL

There has, in the past, been little work done on the ecology of the modern micromammalian fauna of the fynbos. Some recent studies (Bond *et al.* 1980; Nel *et al.* 1980; Rautenbach & Nel 1980) have, however, begun to provide some insight into the current position, at least in the mountain fynbos. Work on the coastal foreland will be hampered by the effects of intensive agriculture and consequent lack of natural vegetation. Remains from barn owl pellets (Avery 1977, 1982a,b and unpublished data) supplement the information available on the distribution of species. If some of the apparently more complete faunal lists are compared using the Faunal Resemblance Factor (FRF) discussed by Rautenbach (1978a, b), it appears that the micromammalian fauna endorses the vegetational divisions to a large extent. It may be, however, that in faunal terms the western Cape mountain region should be separated from the southern Cape mountain region.

THEORY AND METHODS

Theoretically, direct information on palaeoenvironments can be obtained from micromammals at the individual, population and community levels. At the individual level changes in the mean size may reflect changes in prevailing climatic conditions. This is based on Bergmann's rule which states that within a given species those members that live in colder climates will tend towards greater body mass (Coon 1962:59). Guilday (1971:252) has pointed out, however, that this rule is not universally applicable and, indeed, Schonlander (1955) has argued convincingly that climatic adaptation in homeotherms cannot be explained in this way. The precise climatic correlations have, therefore, yet to be established but it still seems that this line of investigation has potential. At the population level, identification of the main factor or factors governing distribution will allow correlation of the species with these parameters for purposes of interpretation. Moreover, changes in density of the species could be taken as indicative of changes in the parameter which the species may be said to represent. In general it appears that plant life-form and foliage density are of major importance (Rosenzweig & Winakur 1969; Bond et al. 1980). Even though abiotic factors such as nature of ground surface and substrate may be important on occasion (Nel & Rautenbach 1975) such factors will, in all probability, not have changed during the late Pleistocene and Holocene. They may therefore be discounted in any consideration of reasons for changes in small mammal population density. Population structure is another aspect that may prove useful but it has not yet been explored in any detail.

In fact, changes in population density will generally appear in the evidence as changes in community composition because it is the relative abundance of populations that is being monitored. It may be difficult to distinguish between direct independent reactions of different species to the same change in conditions and reactions in one species that are dependent on prior change in another species. In the final analysis, however, it is possible that a similar interpretation would emerge in either case. Changes in community structure constitute an allied line of approach, based on the proposition that those communities that occur in harsh climates, that is, under extreme and/or unpredictable conditions, will tend to exhibit less diversity than those occurring under more favourable conditions (Kowalski 1971).

The basic unit of information in all cases is the minimum number of individuals that the sample represents. There has been considerable discussion concerning the most accurate way of arriving at these counts (Avery 1982a). In this case, however, mandibles and maxillae were counted; the highest score for a particular element, such as the left mandible, constitutes the minimum number of individuals represented. Because many specimens are incomplete only those that include a certain frequently occurring feature are counted. In this way it is possible to avoid the possibility of counting the same mandible or maxilla twice. The resulting information has been examined with the aid of factor analysis, in the case of large samples, (Avery 1982a) and visually, using histograms.

Measurements of individuals of selected species were based where possible on those normally taken by taxonomists of extant material. Unfortunately, because of incompleteness, these measurements frequently have to be adapted (Avery 1982a, b). The coefficient of variability ($V = 100s/x$) can indicate which measurements are inherently homogeneous and therefore most likely to be useful for distinguishing populations. Significant differences between populations (established by Student's 't' test) can indicate periods of accelerated change if two samples are closely dated; over a longer period the extent of the change is indicated.

For the purposes of establishing changes in community structure, the Shannon index of general diversity has proved useful. This index is given as $H' = -\Sigma Pi \cdot \log Pi$ by Odum (1971:144), where Pi is the importance probability of each species and the base of the logarithms is at choice; natural logs have been used by the present author. This index appears most appropriate for general investigations but it may sometimes be important to establish whether species richness, dominance or evenness is the particular element that is varying. Dominance, for instance, may be an independently useful indicator of extreme physical conditions since these tend to be characterized by communities with a few dominant species (Odum 1971:145).

INTER-REGIONAL VARIATION

Examination of the FRF indices for samples representing different periods of the later Quaternary shows that the relationship of various areas within the fynbos region has not been static. For instance, when the modern Cango Valley sample is compared with the mid-Holocene samples from the Clanwilliam area the FRF indices are considerably higher than when the modern samples from both areas are compared. Conversely, there are also higher indices for the Cango Valley mid-Holocene sample and the modern Clanwilliam area samples and high indices when both sets of mid-Holocene samples are compared. This would suggest that a greater degree of similarity existed between the vegetation of the two areas during the mid-Holocene than is presently the case. Whether the divergence is due to natural causes or to the effects of

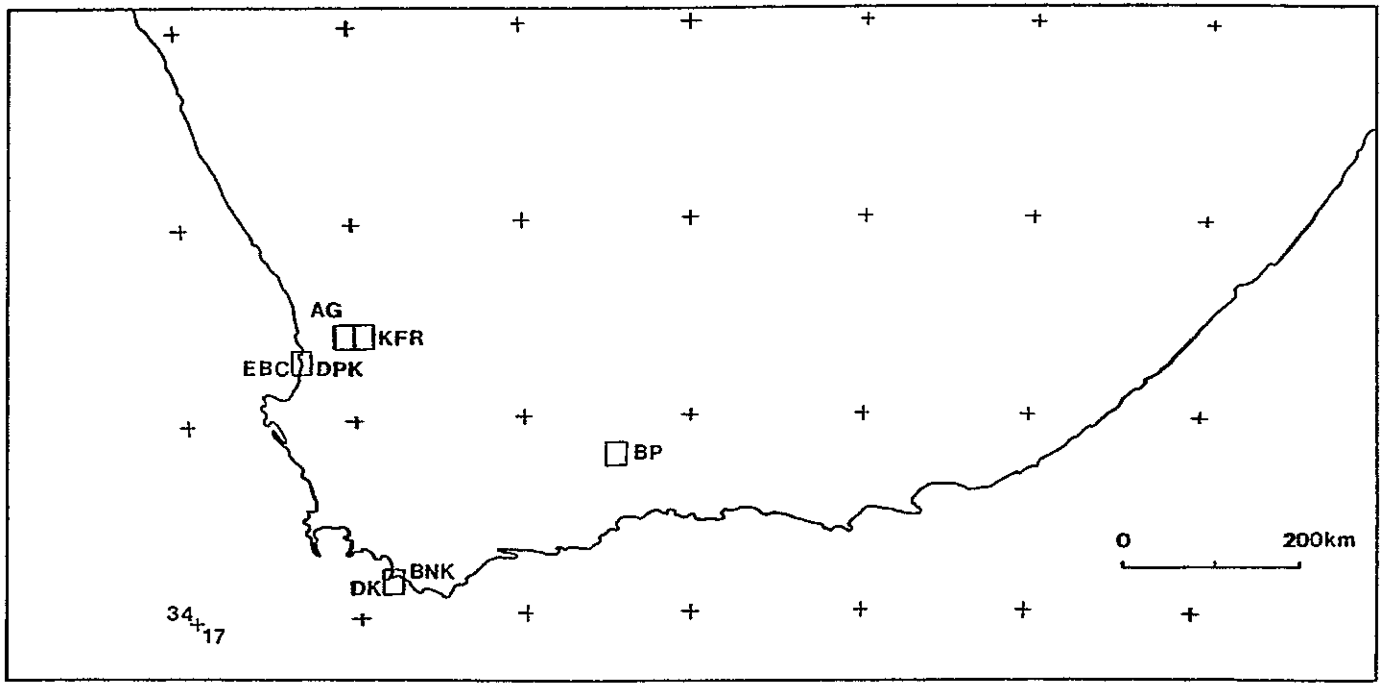

Fig. 1 Location of sites discussed in the text. AG = Andriesgrond; BNK = Byneskranskop; BP = Boomplaas; DK = Die Kelders; DPK = Diepkloof; EBC = Elands Bay Cave; KFR = Klipfonteinrand.

agriculture is not yet known. It is arguable, however, that there has been a real increase in the difference between the two regions because all FRF indices have not been reduced by a consistent amount. This is in spite of the fact that all areas have been subjected to agriculture, although it is possible that different types of farming may have varying effects. There is, however, still a relatively high FRF index for the Cango Valley and Overberg coast; in general the drop in indices within the western Cape, as well as within the southern Cape, has not been as noticeable as that between the western and southern regions. It is this discrepancy that prompts the suggestion that, at least faunally, the western and southern mountain (Overberg and Outeniqualand) regions should be considered discrete units in the same way that their associated areas of coastal foreland are distinguished vegetationally.

Sequences of samples from the Cango Valley (Outeniqualand) and the Overberg area (Fig. 1) provide evidence of differential rates of change in these two regions. Variation in mean size of individuals of Crocidura flavescens (red musk shrew) has been considerable both within and between sites. On average the means for the Cango Valley (Boomplaas Cave) are 9,57% higher than those for the Overberg (Byneskranskop 1) during the early postglacial period, about 12 000 years ago. Further, at that time the Cango Valley population was on average 10,3% greater in mean size than the modern population whereas the difference in the Overberg populations was only 5,36%. By about 4000 B.P., Cango Valley and Overberg mean sizes were both about 4,5% larger than those in the modern populations (Avery 1982a). There must, therefore, have been a much faster rate of change during that period in the Cango Valley than there was on the coast. The evidence from C. flavescens suggests that there was a differential rate of change in the climate, with initial amelioration on the coast followed by accelerated moderation inland until a status quo was achieved. The exact nature of the climatic change has not been determined since other evidence (Avery 1982b) indicates that it is not only temperature that is being monitored.

THE CAPE FOLDED MOUNTAINS

Southern branch (Outeniqualand)

The Cango Valley is situated in the foothills of the Swartberg mountains, inland of Oudtshoorn, at an altitude of about 600 m above sea level. It effectively represents the ecotone between mountain fynbos and the karroid broken veld (Acocks type 26) of the Little Karoo. Moffett & Deacon (1977) have noted the presence of four of Acocks's veld types in the Cango Valley, including both karroid broken veld and false macchia (A70), which is now included in the mountain fynbos (Kruger 1979). At present the natural vegetation comprises principally bush and dense shrubland, although grasses

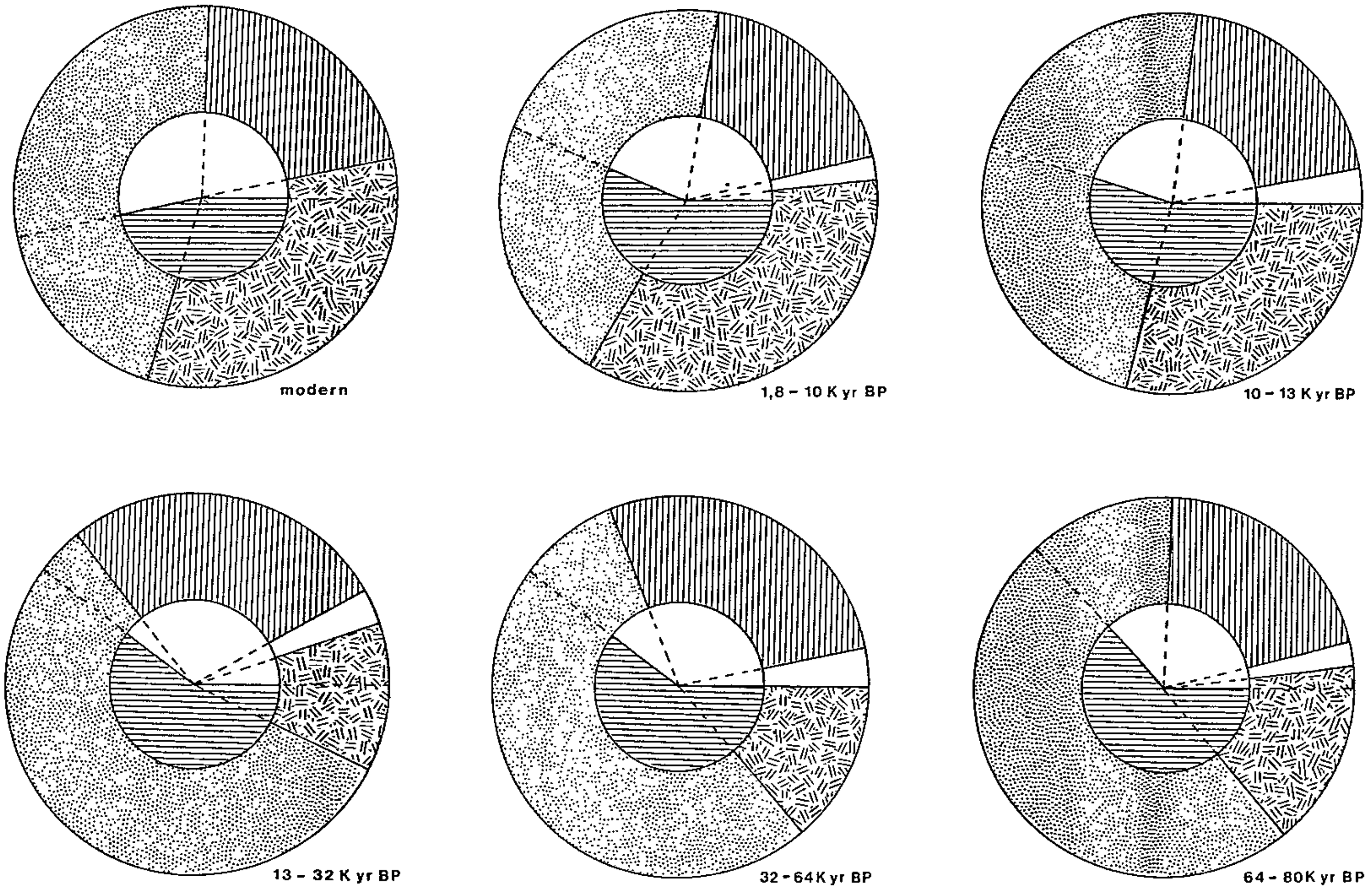

Fig. 2 Changes in proportions of vegetation types at Boomplaas in the Cango Valley during approximately the last 80 000 years. See Fig. 3 for key.

form an important component in all vegetation types (Moffett & Deacon 1977). The present vegetation also shows the effects of nearly 200 years of mixed farming and some 1 700 years of stock-keeping.

If the micromammalian fauna of today is compared with that occurring at different times in the past it is clear that conditions must have varied considerably during the approximately 80 000 years for which there is evidence in this area. During this time it is known, from various lines of evidence, that the last glacial occurred and the present interglacial came into effect. The last glacial has been divided into five phases, two colder pleniglacials alternating with three milder periods (Shackleton 1975). The micromammalian data have been examined to determine what detailed information they could provide concerning environmental conditions during these different episodes.

The evidence from community composition indicates that there were five major phases distinguishable in the sequence from Boomplaas Cave in the Cango Valley (Avery 1982a:315) (Fig. 2). The earliest of these palaeoenvironmental units (unit 5) has been equated with the relatively mild early glacial period and the subsequent colder lower pleniglacial, approximately 80 000 B.P. to 64 000 B.P. Relatively high proportions of Otomys unisulcatus suggest that during this cold period the vegetation was fairly open whereas intermediate proportions of Otomys irroratus and Myosorex varius indicate that there was a moderate amount of dense grass or reeds along the banks of the river in the valley bottom. Also on the valley floor there appears to have been some semi-arid shrubland (O. unisulcatus) as well as grass (Cryptomys hottentotus); a restioid or 'grassy' (sensu Bond et al. 1980) element apparently dominated the hillsides (Otomys saundersiae). It should be noted, incidentally, that here and elsewhere broad vegetation categories are indicated; specific vegetation or floristic types cannot be deduced directly from the micromammalian evidence. During the lower pleniglacial general climatic conditions were harsh according to the evidence of the community structure.

Palaeonenvironmental unit 4, approximately 64 000 B.P. to 30 000 B.P., apparently represents conditions intermediate between full glacial and full interglacial. The climate was probably moderate but with a certain amount of fluctuation. The open restioid or 'grassy' element appears to have continued to predominate on the hillsides, although there may have been some semi-arid scrub on the lower slopes. The dense vegetation of the valley floor seems to have been more extensive during this period than it was earlier.

Radiometric dating indicates that unit 3 lasted from about 30 000 B.P. to 15 000 B.P., during which time the coldest interval of the late Pleistocene occurred. The evidence (the same as, but more pronounced than, that for the lower pleniglacial in unit 5) confirms that the climate was severe, being relatively dry and cold, with either generally depressed temperatures or at least very cold winters. The vegetation on the hillsides continued to be restioid or 'grassy' and open, probably of a rather drier type than previously. Grass and semi-arid scrub seem to have predominated on the valley floor, with the dense riverine vegetation being reduced to a minimum. These data represent the extreme of conditions experienced in the Cango Valley during the last glacial.

The late glacial period was transitional between this extreme and the interglacial conditions that prevailed during the Holocene. At Boomplaas Cave palaeoenvironmental unit 2, covering the period approximately 15 000 B.P. to 11 000 B.P., represents this transition. Replacement of *Otomys saundersiae* by *O. irroratus* as the numerically dominant species indicates that dense vegetation greatly increased on the hillsides at the expense of the restioid or 'grassy' element that had occurred previously. Sparse semi-arid scrub seems to have disappeared from the valley floor, apparently becoming restricted to the hillsides, perhaps the presently drier western side of the valley. The expected increase in temperature is suggested by a reduction in the mean size of *Crocidura flavescens* and the climate appears generally to have been moderating during this period.

The earlier postglacial period is represented by unit 1 which indicates conditions similar to but not identical with those of the present day. Shrubland or bush, in some places sparse and semi-arid, in others dense and perhaps microphyllous, is indicated for the hillsides. On the valley floor relatively extensive dense riverine vegetation was flanked by open grass, possibly with some trees (*Steatomys krebsii* and *Saccostomus campestris*). There is evidence for fluctuations and accelerations in the general increase in temperature. Also, about 9000 B.P., the climate appears to have been rather drier than was general for the Holocene in this area.

Western branch

The western branch of the Cape Fold Mountains is represented by two sites in the Clanwilliam area. These provide some evidence of the conditions that existed on either side of the Cedarberg Mountains during the Holocene. The earlier of the two in Klipfonteinrand (Fig. 1) which is very close to Traveller's Rest, one of Shortridge's (1943) collecting stations, at about 200 m above sea level and some 30 km north-east of Clanwilliam in mountain fynbos. It would appear that in the mid-Holocene, perhaps about 5000 B.P., the vegetation of the area was predominantly fairly open scrub (*Otomys unisulcatus*, *Aethomys namaquensis*, *Gerbillurus paeba* and *Elephantulus edwardii*) but with a grassy and restioid element. The predominance of *Cryptomys hottentotus* suggests that there was probably also a high proportion of tuberous or bulbous plants such as the geophytes that are a feature of the fynbos today. By contrast, the present-day evidence suggests that conditions have probably become drier and that the open scrub has now extended its range on both the rocky and sandy substrates at the expense of the grassy/restioid and geophytic vegetation.

On the west side of the Olifants River valley just south of Clanwilliam, the site of Andriesgrond overlooks the Clanwilliam dam. About 1000 B.P. the vegetation was probably essentially similar to that described above for Klipfonteinrand. Fairly open scrub occurred on the rockier surfaces whereas on the sandy substrate or alluvium of the river margin grass and bulbous or tuberous plants grew. This is presumably the natural vegetation that occurred in the area before farming, the dam and roads changed the environment. Whether the vegetation would have been mountain fynbos or the succulent karoo (A31) that Acocks (1975) mapped for the Clanwilliam area in the Olifants River valley is not clear. This latter vegetation type includes bulbous plants as well as some grasses (Acocks 1975:70) and the type of vegetation that was present would almost certainly depend on the rainfall at the time in question. In this context it is interesting to note that Acocks (1975: map 1) has suggested that in about 1400 A.D. Clanwilliam would have been on the border between the macchia (= mountain fynbos) and bush-clump veld, and that the succulent karoo would have been considerably further north at the time.

THE COASTAL FORELAND

South coast

The two Overberg archaeological sites lie on and near the present coast between Hermanus and Cape Agulhas (Fig. 1). The late Pleistocene site of Die Kelders 1 is presently 8 m above sea level right on the coast. In the past, however, the position of the cave relative to the shoreline varied considerably as the sea level rose and fell during interglacial and glacial periods respectively (Tankard & Schweitzer 1976). The natural vegetation of the area is currently coastal fynbos. The fynbos on the limestone ridges has an upper proteoid stratum with ericoids and restioids below (Kruger 1979:106); on the sandstone hills restioids predominate (Schweitzer & Wilson 1978). There is also a greater proportion of grasses in coastal fynbos than there is in mountain fynbos. Patches of coastal shrubland (Taylor 1978:213) occur on the flats. The effects of agriculture and the invasion of alien vegetation have severely affected the natural vegetation.

It would appear from correlation of changing proportions of species (Avery 1982a:349) that palaeoenvironmental unit 3, the earliest at Die Kelders 1, represents conditions during the later part of the lower pleniglacial, around 65 000 B.P. It would thus correspond with the end of palaeoenvironmental unit 5 in the Cango Valley. Here too, relatively high proportions of *Otomys saundersiae* indicate open restioid 'grassy' vegetation on the hillsides (Fig. 3). The evidence of *Tatera afra* and *Mystromys albicaudatus* also suggests the existence of extensive grassland on the flat ground as well as a considerable amount of dense vegetation (*Otomys irroratus*). This latter vegetation may

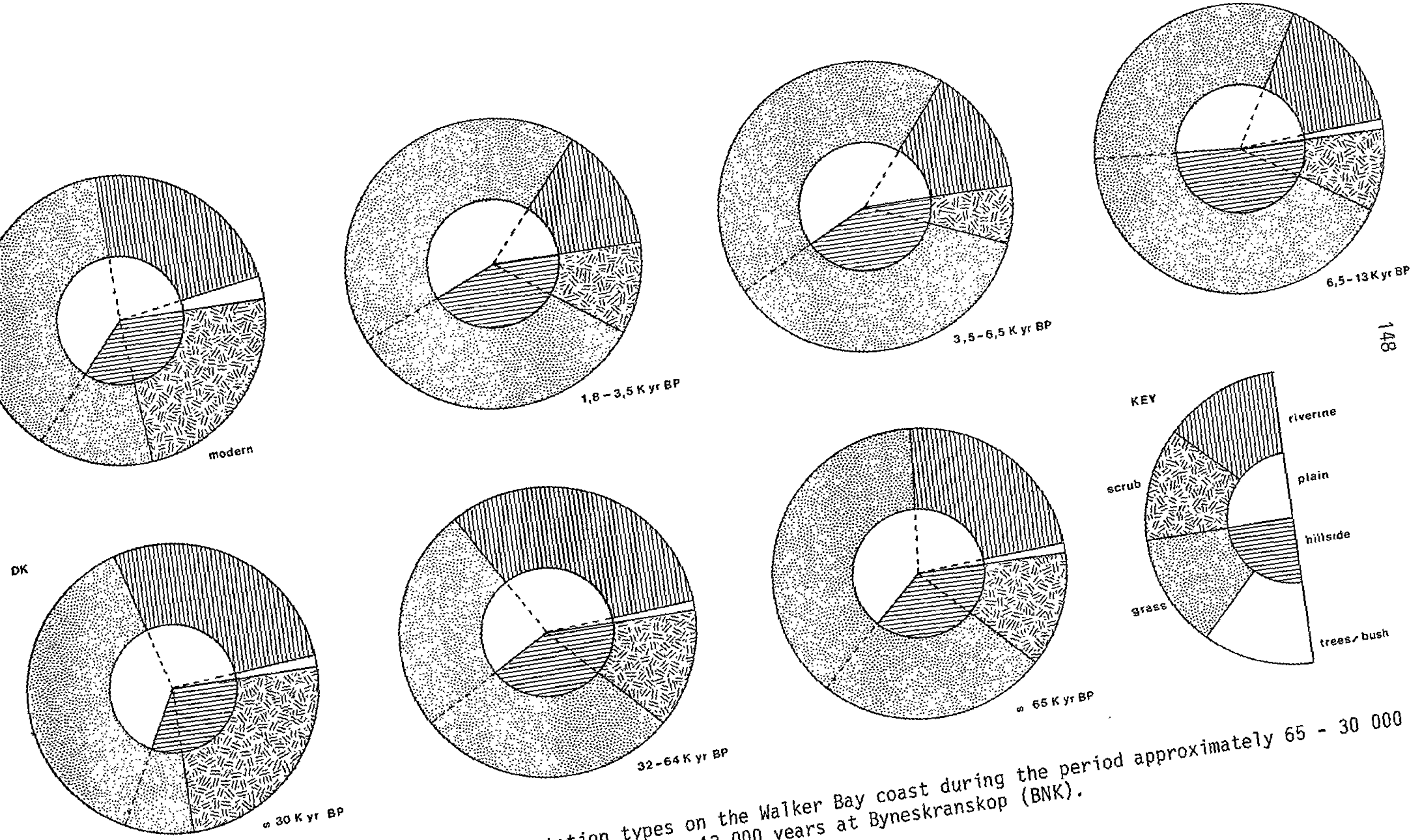

Fig. 3 Changes in proportions of vegetation types on the Walker Bay coast during the period approximately 65 - 30 000 years B.P. at Die Kelders (DK) and the last 13 000 years at Byneskranskop (BNK).

have bordered a lake or marsh which was situated below the cave and would therefore be below sea level now. A certain amount of the grassland probably also occurred on what is now the sea floor. The climate was probably rather wet and relatively cold.

Unit 2 corresponds with unit 4 in the Cango valley and refers to the slightly milder period between the two glacial maxima. An apparent reduction in both grass and dense vegetation on the flats without a compensatory increase in other vegetation forms suggests that the sea level was rather higher during this period; much of the land below the cave would thus have been inundated. The hillside vegetation remained essentially the same but was perhaps reduced in extent. A predominance of small micromammalian species such as Myosorex varius, Suncus varilla, Mus minutoides and Dendromus melanotis suggests that the vegetation was generally fairly open. The climate appears to have been drier and warmer than it was during the preceding period.

It is most likely that the uppermost palaeoenvironmental unit represents the onset of the coldest interval of the late Pleistocene around 30 000 B.P. An increase in grass (Tatera afra) and dense vegetation (Otomys irroratus) on the flats indicates a renewed lowering of the sea level. The vegetation on the hills seems to have changed from 'grassy' restioid to shrubland, the explanation for which is uncertain.

The height of the last glacial maximum is not represented in the Overberg area. It is not until the beginning of the late glacial about 13 000 B.P. that the evidence is resumed, this time at Byneskranskop 1. This site is about 9,5 km south-east of Die Kelders 1 and near a small river. It is presently 60 m above sea level and some 10 km inland. The lowest, third, palaeoenvironmental unit represents the late glacial and the first half of the Holocene, from about 13 000 B.P. to 6500 B.P. (Fig. 3). Extensive, possibly fairly closed grass (Tatera afra) and a certain amount of shrubland (Georychus capensis) covered the flats. There was also considerable dense vegetation along the river (Otomys irroratus) and perhaps on the lower hillsides (Crocidura flavescens). The restioid or 'grassy' element was prominent on the upper hillsides (Otomys saundersiae), although it is possible that there also existed a proteoid element (Otomys irroratus - see Avery 1982a:259) as there does today. There appears to have been a certain amount of fluctuation in the climate with perhaps rather milder conditions than general during the period approximately 8000 B.P. to 6500 B.P. on the evidence of the Shannon general diversity index (Avery 1982a:313).

After a period of change about 6500 B.P. the extensive grass on the flats apparently became more open and conditions were probably drier than they had been previously (Steatomys krebsii). Grass may have extended its range at the expense of the dense riverside vegetation. Shrubland appears to have invaded the hillsides to a certain extent, thereby reducing the 'grassy' restioid element. This shrubland was conceivably the proteoid element mentioned above. A general warming trend in the temperature seems to have continued into this period from the earlier one.

At the beginning of unit 1, about 3500 - 3200 B.P., the vegetation on the flats seems to have been similar to that occurring during unit 3, that is, denser and indicative of wetter conditions. On the hillsides, however, shrubland apparently continued to be as important as it was during the period of unit 2. By about 1800 B.P., when the sequence ends, the evidence suggests once more a return to more open vegetation on the flats.

West coast

On the west coast the strandveld region is represented by two sites on the south side of the Verlorevlei at Elands Bay. Elands Bay Cave is situated in Baboon Point, currently about 75 m above sea level and 1 km from the shoreline. The Holocene sequence from this site covers the period from about 8000 B.P. and after 3000 B.P. The vegetation was apparently predominantly fairly open shrubland (*Otomys unisulcatus*, *Aethomys namaquensis* and *Elephantulus edwardii*) throughout this period and, as such, similar to that of the present. There is, however, some suggestion that conditions were rather wetter about 3000 B.P. and that there was marginally more lush, probably vleiside, vegetation (*Steatomys krebsii*) than at other times. This accords with the evidence from the Overberg coast and would indicate that this was a general event, at least in the coastal zone. The most striking evidence to come from Elands Bay Cave is that relating to sea level changes. The great change in proportions of certain species of micromammals before and after the hiatus indicates that the sea level rose considerably during that time and that the coastal plain was much reduced (Fig. 4). Plains species *Otomys unisulcatus* was reduced in proportion by half whereas the proportion of hillside species such as *Aethomys namaquensis* increased greatly. The essential stability of proportions before and after this period suggests that there was not much change from approximately 11 000 B.P. to 8000 B.P. and that modern or near-modern sea level had been reached by about 3000 B.P. in this area.

Diepkloof is some 20 km inland of Elands Bay, overlooking Verlorevlei. The evidence allows contrast between presumably modern but pre-farming conditions (in a surface sample) and those existing perhaps 1 000 years ago. Comparison of the surface sample with a nearby owl pellet sample suggests some conclusions on the possible effects of agriculture. It is clear that there was considerable change in the vegetation during the last millennium. It seems likely, however, that the change was qualitative and possibly involved the plant species since two grassland animals (*Steatomys krebsii* and *Mystromys albicaudatus*) increased proportionately while two others (*Tatera afra* and *Dendromus melanotis*) decreased. Similarly, open shrubland species such as *Gerbillurus paeba* and *Aethomys namaquensis* increased where *Otomys unisulcatus* and *Elephantulus edwardii* decreased. Overall, the proportion of

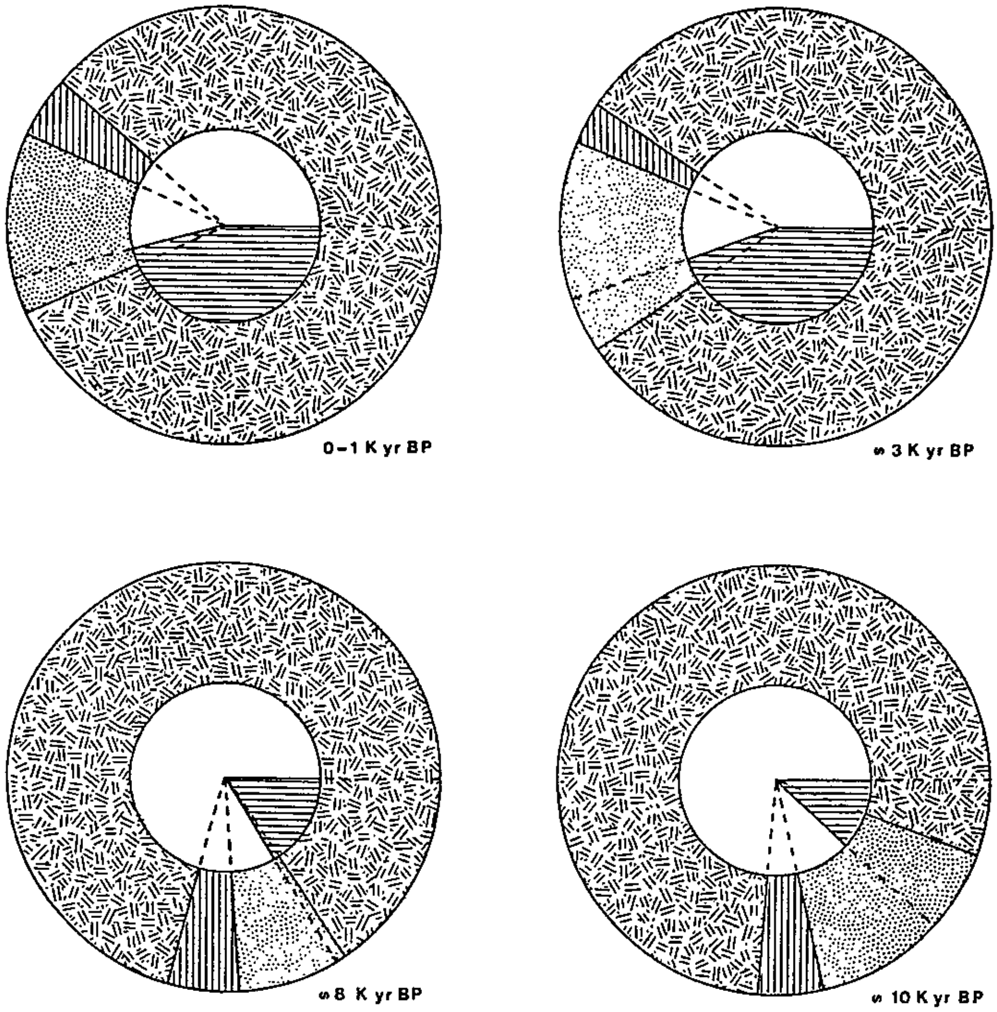

Fig. 4 Proportions of vegetation types at Elands Bay Cave during the last 1000 years compared with those occurring at approximately 3000, 8000 and 10 000 years B.P. See Fig. 3 for key.

shrubland appears to have increased and it may be that the other changes were consequent upon a certain decrease in precipitation. The owl pellet data, by comparison, indicate not only that the fauna is depauperate but that there has been a shift in the dominant species. Both facts are thought to have been due to disturbance of the vegetation during the course of farming operations. Tatera afra regularly occurs on farming land and Mus minutoides has consistently been found to be a dominant species in samples from agricultural areas (Avery 1977 and unpublished data). The surface sample from Diepkloof may perhaps suggest the natural vegetation that would exist in the area if there were not farming along the banks of the vlei.

DISCUSSION

Micromammals appear so far to have two main implications for Quaternary palaeoenvironments in the fynbos region. One is that while it is clear that there has been considerable change in the vegetation during that part of the Quaternary for which there is evidence, this change has apparently been in proportions rather than in kind. The other point is that changes have not necessarily been either regionally synchronous or comparable throughout the biome.

The micromammalian evidence refers to generalized vegetation categories, such as grass sensu lato and shrubland and has been interpreted in terms of changes in proportions of these categories. It does not, and never could, provide evidence of the plant species comprising the vegetation categories. It has also to be borne in mind that the changes are relative, because of factors relating to the accumulation of the samples, and that the proportions cannot be taken as those actually existing on the ground (see Avery 1982a for a more detailed discussion). It is also possible that the nature of the shrubland or other category may change, perhaps becoming more open or more xeric. Here the presence and proportions of particular species provide the more detailed evidence. In the present context the majority of species has been present throughout; it is this fact that suggests that the vegetation types have changed in relative proportion and perhaps in detail (as at Verlorevlei) rather than in nature. Under these circumstances one may, with a certain degree of confidence, translate general vegetational categories into the specific examples that exist in the biome today. Thus, for example, what is interpreted as grass in general terms may, in fact, be restioid vegetation in the context of the fynbos region, and shrubland may be specifically coastal fynbos, depending on the situation.

The fact that change has been variable within the region of the biome indicates that the present complexity of climate and vegetation is not new. It also emphasizes the need for caution in finding an acceptable and meaningful level of generalization or extrapolation from the evidence. The present evidence makes it clear, for instance, that the biome is too large a unit for such generalization because of the differential change within the biome. It seems likely, in fact, that homogeneous units will normally be based on physiographic elements (here mountain range or coastal foreland). Evidence from a site within such a unit may reasonably be taken as representative of that unit, at least until more data are available. The topography and associated edaphic features may, in a sense, be regarded as common denominators in the study of palaeoenvironmental change on the level being discussed here. During the period concerned they are essentially constants, whereas climate and vegetation are variables to be determined. In due course, when more evidence is accumulated, it may become possible to use the nature and amplitude of change in one area to predict the type of change likely in another area. At present, however, the patterns of change are not sufficiently well understood. Van Zinderen Bakker (1976) has already made major contributions on a subcontinental scale; what are needed now are details at the biome level in order to establish more precisely the nature of the relationship between the subregions of the biome. The micromammalian data have the potential for adding substantially to this detailed knowledge but the realization of this potential depends upon the acquisition of sufficient samples of suitable size from both palaeontological and modern contexts.

ACKNOWLEDGEMENTS

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REFERENCES

ACOCKS, J. P. H. 1953. Veld types of South Africa. Botanical Survey of South Africa Memoir 28.

AVERY, D. M. 1977. Past and present distribution of some rodent and insectivore species in the southern Cape Province, South Africa: new information. Annals of the South African Museum 74:201-9.

AVERY, D. M. 1982a. Micromammals as palaeonenvironmental indicators and an interpretation of the late Quaternary in the southern Cape Province, South Africa. Annals of the South African Museum 85:183-374.

AVERY, D. M. 1982b. The micromammalian fauna from Border Cave, KwaZulu, South Africa. Journal of Archaeological Science 9:187-204.

BOND, W., FERGUSON, M. & FORSYTH, G. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains.

South African Journal of Zoology 15:34-43.

COON, C. S. 1962. The origin of races. London: Jonathan Cape.

GUILDAY, J. E. 1971. The Pleistocene history of the Appalachian mammal fauna. In Holt, P. C. ed. The distributional history of the biota of the southern Appalachians. III: Vertebrates. Virgina Polytechnic Institute and State University Research Division Monograph 4:233-62.

KOWALSKI, K. 1971. The biostratigraphy and paleoecology of Late Cenozoic mammals of Europe and Asia. In Turekian, K. K. ed. The Late Cenozoic glacial ages: 465-77. New Haven: Yale University Press.

KRUGER, F. J. 1979. Plant ecology. In Day, J., Siegfried, W. R., Louw, G. N. & Jarman, M. L. eds Fynbos ecology: a preliminary synthesis. South African National Science Programme Report 40:88-126.

MOFFETT, R. O. & DEACON, H. J. 1977. The flora and vegetation in the surrounds of Boomplaas Cave, Cango Valley. South African Archaeological Bulletin 32:127-45.

NEL, J. A. J. & RAUTENBACH, I. L. 1975. Habitat use and community structure of rodents in the southern Kalahari. Mammalia 39:9-29.

NEL, J. A. J., RAUTENBACH, I. L. & BREYTENBACH, G. J. 1980. Mammals of the Kammanassie Mountains, southern Cape Province. South African Journal of Zoology 15:255-61.

ODUM, E. P. 1971. Fundamentals of ecology. Philadelphia: W. B. Saunders.

RAUTENBACH, I. L. 1978a. A numerical re-appraisal of the southern African biotic zones. In Schlitter, D. A. ed. Ecology and taxonomy of African small mammals. Bulletin of the Carnegie Museum of Natural History. 6:175-87.

RAUTENBACH, I. L. 1978b. Ecological distribution of the mammals of the Transvaal (Vertebrata: Mammalia). Annals of the Transvaal Museum 31:131-56.

RAUTENBACH, I. L. & NEL, J. A. J. 1980. Mammal diversity and ecology in the Cedarberg Wilderness Area, Cape Province. Annals of the Transvaal Museum 32:101-124.

ROSENZWEIG, M. L. & WINAKUR, J. 1969. Population ecology of desert communities: habitats and environmental complexity. Ecology 50:558-72.

SCHONLANDER, P. F. 1955. Evolution of climatic adaptation in homeotherms. Evolution 9:15-26.

SCHWEITZER, F. R. & WILSON, M. L. 1978. A preliminary report on excavations at Byneskranskop, Bredasdorp District, Cape. South African Archaeological Bulletin 33:134-40.

SHACKLETON, N. J. 1975. The stratigraphic record of deep-sea cores and its implications for the assessment of glacials, interglacials, stadials and interstadials in the mid-Pleistcene. In Butzer, K. W. & Isaac, G. Ll. eds After the australopithecines: 1-24. The Hague: Mouton.

SHORTRIDGE, G. C. 1943. Field notes on the first and second expeditions of the Cape museums' mammal survey of the Cape Province: descriptions of some new subgenera and subspecies. Annals of the South African Museum 36:27-100.

TANKARD, A. J. & SCHWEITZER, F. R. 1976. Textural analysis of cave sediments: Die Kelders Cave, Cape Province, South Africa. In Davidson, D. A. & Shackley, M. L. eds Geoarchaeology: 289-316. London: Duckworth.

TAYLOR, H. C. 1978. Capensis. In Werger, M. J. A. ed. The biogeography and ecology of southern Africa. Monographica Biologica 31:171-229.

VAN ZINDEREN BAKKER, E. M. 1976. The evolution of late Quaternary palaeoclimates of southern Africa. Palaeoecology of Africa 9:160-202.

PALYNOLOGICAL STUDIES AND THE VEGETATION HISTORY OF THE FYNBOS

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INTRODUCTION

The Cape floristic region, corresponding to the Cape Fold Belt and its attendant coast, is recognized as the distinctive Capensis floral kingdom. This species rich phytochorion, noteworthy for the high degree of endemism, is dominated by fynbos vegetation but also includes enclaves of Afromontane forest and Karoo vegetation (Taylor 1978). Problems of the age, origin and phytogeography of Capensis have been the subject of much debate. Adamson (1958) and Levyns (1964) have argued that the Cape flora is fundamentally African in origin and more recently Goldblatt (1978) has reviewed the question of the austral affinities of the forest elements, the tropical affinities of other components, and the evidence for floral links with Eurasia in this floristic region. In a more general synthesis of the Cretaceous and Tertiary vegetation history of the African continent, Axelrod and Raven (1978) have offered a reconstruction of the evolution of sclerophyllous vegetation from the stage of the development of xeromorphous adaptations at locally dry sites in the Cretaceous to the invasion of the present fynbos area, an event which they suggest occurred in the Pleistocene.

Hypotheses concerning the history of the Capensis flora must be tested in the fossil record. Hitherto this record has been meagre. Until recently the only evidence available from Tertiary sites for the fynbos region and its surrounds has been that from the Knysna Beds (Phillips 1927; Thiergart et al. 1963), Fort Grey near East London (Adamson 1934) and Arnot on the farm Banke in Namaqualand (Rennie 1931; Kirchheimer 1934). This paper surveys the information produced in recent palynological studies of offshore and onshore sites, dating primarily to the Cretaceous and Tertiary, including a reinvestigation of the Arnot microflora (Scholtz, in press) and the study of Neogene deposits in the south-western Cape (Coetzee 1978, 1980, 1981, 1983; Coetzee & Rogers 1982; Coetzee & Muller 1983) (Fig. 1).

Palynological studies offer the best potential for learning about the

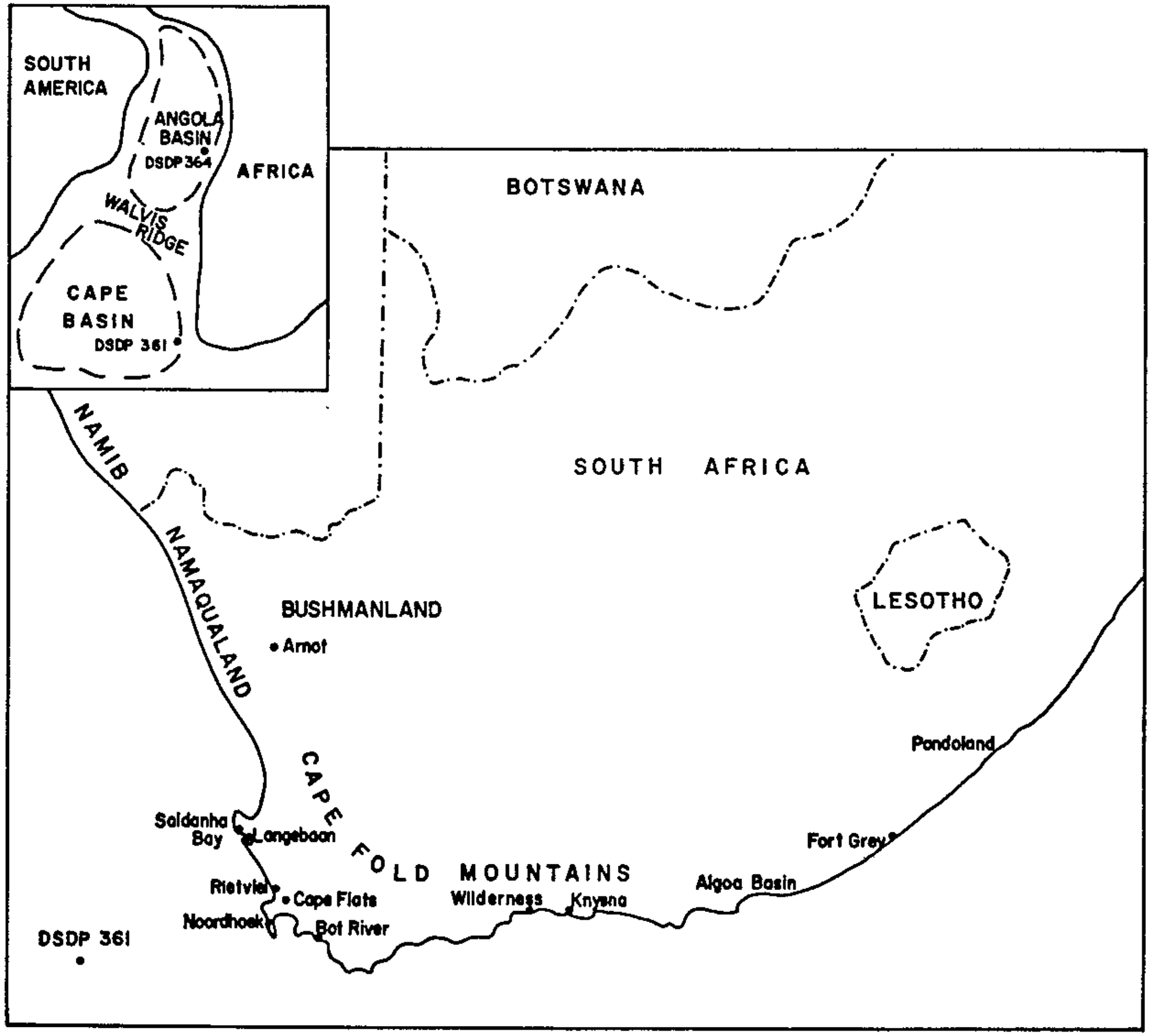

Fig. I Map of the fossil localities mentioned in the text. Inset: Mid-Cretaceous positioning of the Cape and Angola basins, after Morgan (1978).

evolutionary history of the main vegetation types associated with fynbos ecosystems. At the present stage of research undue weight has to be given to a few better studied localities that are widely separated in time and space and represent different modes of deposition. As has been pointed out by Truswell and Harris (1982) in the parallel case of Australian studies, the generalizations from such varied and isolated data must be made with caution. Studies currently being undertaken have, at this pioneering stage, to cope with tracing the modern affinities of well defined microfossil taxa, the description of unidentified extinct forms and the study of a large residue of form types which are produced by a wide range of families. Future research will improve the resolution of the fossil record but already important new insights into the vegetation history of the fynbos are emerging and are outlined in this paper.

CRETACEOUS

The separation of Africa and South America took place at the end of the Jurassic some 140 Myr ago (Theron, this volume) and thereafter land links with the other southern continents were indirect. The flora of the southern African subcontinent at the beginning of the Cretaceous was similar to middle and high latitude floras from Australia and South America and bisaccates were ubiquitous. In the lower palaeolatitudes Araucariaceae were more prominent. At that time many spore and conifer form genera had a worldwide distribution while others were already confined to Gondwanaland or Laurasia.

By the mid-Cretaceous, however, after the initial dispersal of the angiosperms, a number of authors (Brenner 1976; Srivastava 1978; Herngreen & Chlonova 1981) recognize distinct microfloral provinces in the Gondwanaland continents broadly equating with northern and southern Gondwanaland. Brenner has suggested that the northern Gondwana region enjoyed a warm arid climate while in the south of Gondwanaland the dominance of bisaccates of podocarpaceous affinity indicates a warm humid tropical/subtropical climate. The typical microfossil forms of the northerly mid-Cretaceous African/South American (ASA) floral province (Herngreen & Chlonova 1981) such as elatere bearing forms do not occur in assemblages of that time range from southern Africa where bi- and trisaccates of the Podocarpaceae still dominated. Other coniferous (e.g. Classopollis) and spore forms still have a wide distribution while some widely dispersed early angiosperm forms begin to enter the record.

By the late Cretaceous, with dominance of angiosperms established, it is clear from available evidence that southern Africa was not a part of the most southerly palaeofloral province, the Nothofagidites province recognized in Australia, South America and Antarctica and floral links with these regions were becoming more remote. The flora of southern Africa was, however, also distinct from that of lower African palaeolatitudes where a former dominance of ephedroid-types had given way to the establishment of a flora characterized by abundance of Palmae form genera. This is Herngreen and Chlonova's (1981) late Cretaceous Palmae Province. The southern African region may fall within Srivastava's (1981) Constantinisporis floral province and there are suggestions that the nominate species has a northern and southern middle latitude distribution in Africa and India.

It seems therefore that by the end of the Cretaceous the flora of southern Africa was already distinctive and the stage was set for the evolution in the sub-continent of a characteristic flora with the southern Gondwanaland floral inheritance enriched by a low latitude component.

Palynological sites containing typical lower Cretaceous microfloras are located in fault controlled basins along the southern Cape margin formed by the separation of the Falkland Plateau. These have been studied by A. R. H. Martin (1959), Scott (1976) and Stapleton & Beer (1977). In the Algoa Basin Sundays River Formation which is the best documented, Scott (1976) recorded 62 mostly gymnospermous forms common among which are Classopollis, Araucariacites and Microcachryidites as well as a diverse pteridophyte spore flora. The only published mid-Cretaceous record from near the Cape is the DSDP 361 borehole 180 km west-south-west of Cape Town. The gymnosperm flora is still dominant but the primitive angiosperm forms Liliacidites and Clavatipollenites are recorded for the first time in southern Africa.

Local evidence for the late Cretaceous is mainly from DSDP 361 (McLachlan & Pieterse 1978) where there is a marked increase in the range of angiosperm form types relative to the mid-Cretaceous record. These include Proteacidites, Cretacaeiporites and possibly Afropollis (Liliacidites peroreticulatus). A noteworthy occurrence is Constantinisporis. A wider perspective on the mid- to late Cretaceous microfloras of southern Africa is provided by assemblages from the Angola Basin and from Botswana. At DSDP 364 (Morgan 1978) in the Angola Basin elatere bearing forms, Hexaporotricolpites, and other tropical angiospermous forms absent from DSDP 361 are recorded. In Botswana (Scholtz & Deacon 1982) an interesting pollen sequence records the replacement of bisaccate dominated assemblages by assemblages in which Ephedripites, Araucariacites, Cretacaeiporites and Proteacidites are the most important forms.

The absence of Microcachryidites in the Angola Basin and Botswana and differences in abundance of Araucariacites at the various sites are an indication that some climatic gradient and corresponding zonation of vegetation existed in the subcontinent in the late Cretaceous.

In Table 1, a fossil wood occurrence in the Umzamba Beds, Pondoland, is included for completeness. Wood of the Monimiaceae and Euphorbiaceae has been identified from this occurrence (Muller-Stoll & Madel 1962).

Table 1. A fossil record of some prominent form genera and families from late Cretaceous to late Miocene sites in southern Africa.

Geological time	late Cretaceous			Paleocene	Eocene	early Miocene	late Miocene	Present
TAXON (mostly microfossil) M = Macrofossil	Botswana	Pondoland	DSDP 361	Arnot	Knysna Lignites	Noordhoek	Noordhoek Langebaan	Southern Africa
Inaperturopollenites	-	-	X	X	-	-	-	-
Zonalapollenites	-	-	X	X	-	-	-	-
Araucariacites	X	-	X	X	-	-	-	-
Podocarpidites	X	-	X	X	M	X	X	X
Podosporites (*Dacrycarpus*)	-	-	X	-	?	X	-	-
Microcachryidites	-	-	X	-	?	X	X	-
Phyllocladidites	-	-	X	-	-	?	-	-
Dacrydium cupressinum-type	-	-	-	X	?	?	-	-
Widdringtonia	-	-	?	-	M	X	X	X
Ephedripites	X	-	X	-	-	-	-	-
Constantinisporis	X	-	X	-	-	-	-	-
Hexaporotricolpites	X	-	-	-	-	-	-	-
Afropollis	?	-	X	-	?	-	-	-
Winteraceae	-	-	-	-	-	X	-	-
Monimiaceae	-	M	-	X	-	-	-	-
Chloranthaceae (*Clavatipollenites* spp.)	-	-	X	X	-	X	-	-
Ulmaceae (*Ulmus*-type)	-	-	-	X	-	-	-	-
(*Celtis*-type)	-	-	-	?	-	X	X	X
Casuarinaceae	-	-	-	X	X	X	X	-
Myricaceae	-	-	-	-	-	X	X	X
Ericaceae (*Ericipites*)	-	-	-	X	-	X	X	X
Sapotaceae (*Sideroxylon*-type)	-	-	-	-	-	X	X	X
Sarcolaenaceae	-	-	-	-	-	X	-	-

Table 1. (continued)

Euphorbiaceae	-	M	-	-	-	-	-	-
Klainanthus/Adenocline-type	-	-	-	X	-	X	X	X
Jatropha/Croton-type	-	-	-	-	X	X	X	-
Zimmermania-type	-	-	-	X	-	-	-	-
Alchornea-type	-	-	-	-	?	X	X	X
Thymelaeaceae	-	-	-	X	-	X	X	X
Rosaceae (*Cliffortia*-type)	-	-	-	-	X	X	X	X
Caesalpinaceae (*Bauhinia*-type)	-	-	-	X	-	-	-	X
Combretaceae/Melastomaceae	-	-	-	-	-	X	-	X
Myrtaceae	-	-	-	-	X	X	X	X
Gunneraceae	-	-	-	X	?	-	-	X
Anacardiaceae (*Rhus*-type)	-	-	-	X	X	X	X	X
Rutaceae (*Calodendrum*-type)	-	-	-	-	-	X	X	X
Sapindaceae, *Cupanieae* (*Cupanieidites*)	-	-	X	-	-	X	X	-
Cornaceae (*Curtisia*)	-	-	-	-	M	-	-	X
Alangiaceae	-	-	-	X	-	-	-	-
Icacinaceae?(*Echiperiporites*)	-	-	-	-	-	X	-	X
Celastraceae	-	-	-	-	-	X	X	X
Oleaceae	-	-	-	-	-	X	X	X
Proteaceae (Proteacidites)	X	-	X	X	X	X	X	X
Apocynaceae (*Rauvolfia*-type)	-	-	-	-	-	X	X	X
Gonioma	-	-	-	-	M	-	-	X
Rubiaceae (*Canthium*, *Anthospermum* and cf. *Randia*-types)	-	-	-	?	?	X	X	X
Compositae	-	-	-	-	-	X	X	X
Cyperaceae	-	-	-	-	-	X	X	X
Restionaceae								
Centrolepidoid type	-	-	-	X	-	X	X	X
Graminoid type	-	-	-	-	X	X	X	X
Transitional type	-	-	-	X	?	?	?	X
Gramineae	-	-	-	-	-	X	X	X
Palmae spp.	-	-	-	X	?	X	X	-
Nypa-type	-	-	-	-	?	?	-	-
Sparganiaceae	-	-	-	-	-	X	X	-

PALEOGENE

The beginning of the Tertiary was marked by a widespread extinction of older Cretaceous elements and a modernization of floras on a worldwide scale. The Paleogene, the first half of the Tertiary, saw the beginning of a trend towards cooler and drier climates. Several authors have considered the evidence of climatic change between the end Cretaceous and the Paleogene and have attempted to relate extinction at the end-Cretaceous to abrupt cooling (Salard-Cheboldaeff 1981; Muller pers. comm.).

Palynological evidence for the Paleogene is available from the sedimentary infillings of kimberlite pipes bordering on the fynbos region. The occurrence of amphibian remains and fossil leaves drew attention to the Arnot pipe on the farm Banke in southern Bushmanland, today an arid elevated plateau area lying between the mediterranean-type climate region of the Cape and the Namib Desert. Kirchheimer (1934) carried out a preliminary palynological analysis of sediments from the Arnot pipe and a more detailed study has been recently completed (Scholtz in press). This local basin depository is filled to a depth of at least 135 m (H. Jenner-Clarke pers. comm.) with claystones and samples have been analysed from the top 30 m. The radiometric dating of pipes in the area to between 64 and 71 Myr provides a maximum age for the deposit which is therefore end-Cretaceous to Paleocene in age. This dating is supported by the palynological evidence.

The Arnot microflora appears to represent a drier 'sub-tropical' type forest flora. The gymnosperm component includes a number of form types of Podocarpaceae as well as Araucariaceae and two tree fern form genera occur. Among the families with modern affinities that have been recorded are Anacardiaceae, Alangiaceae, Caesalpiniaceae, Casuarinaceae, Euphorbiaceae, Ulmaceae and possibly Rubiaceae, as well as palms and other monocotyledons. An important feature in relation to the origins of the Cape Flora is the occurrence of two to possibly five forms of Proteaceae and two form types each of Ericaceae and Restionaceae. These taxa may have formed an understorey in a relatively open forest.

There is a strong austral affinity in the gymnosperms and spores which represent an ancient Gondwana component. Casuarinaceae, Proteaceae, Gunneraceae, Ericaceae and its sister family the Epacridaceae, and Restionaceae are Paleogene taxa common to Australia and South Africa that are represented at Arnot. At a family level but not at the level of particular forms, there are obvious links to tropical Africa. These are shown by the Euphorbiaceae-Rubiaceae, Caesalpiniaceae, Anacardiaceae and Ulmaceae.

The Eocene Period that followed the Paleocene was characterized by warm humid climates and transgressive seas. The only onshore possible Eocene polleniferous locality known is the Knysna Beds (Rogers 1908). These sediments occur in channels cut into the coastal platform and comprise a sequence of 60 m of sands with lignite partings. The Knysna Beds appear to represent riverine facies. Macroscopic plant remains including Podocarpaceae, Widdringtonia and Cunoniaceae were reported by Phillips (1927) and a preliminary description of the microflora has been given by Thiergart et al. (1963). This flora represents a lowland wet site vegetation and new observations by the authors indicate the dominance of Casuarinaceae, a high diversity of Proteaceae and Restionaceae, the presence of Nypa type palm pollen and relatively very low percentages of Podocarpaceae. The absence of Ericaceae from the Knysna Beds has been remarked on by Levyns (1964).

NEOGENE

There are no Oligocene polleniferous deposits but the record from channel fill deposits in the south-western Cape is related to the subsequent transgressions of the Neogene. At Noordhoek on the Cape Peninsula in the centre of the fynbos region, in a steep channel, rimmed by mountains of the Cape Fold Belt and extending below modern sea-level, is a sequence of back-barrier and lagoonal deposits containing carbonaceous polleniferous clays. The age on geological and palynological grounds is considered to range from the early Miocene to the Plio-Pleistocene. The terms early and late Miocene are used informally and in a relative sense. Hendey (this volume) has discussed some of the problems of dating the Miocene-Pliocene deposits of the south-western Cape.

The early Miocene deposits at Noordhoek studied by Coetzee (1980) show pollen assemblages that differ in composition from associations dominated by mixed forest with gymnosperms and 'sub-tropical' or 'tropical' angiosperm components, to associations dominated by a lowland palm vegetation. There are also distinct assemblages representing swampy vegetation with Sparganiaceaepollenites barungensis and Restionaceae. These different assemblages represent changes in the depositional environment due to the transgressing shoreline and to other local edaphic factors. The bulk of the relevant deposits were formed during the transgression of sea level from -50 to -20 m.

The most important components of the early Miocene microflora from Noordhoek are a number of extinct Podocarpaceae including Microcachryidites antarcticus and amongst the angiosperms, Winteraceae (Bubbia and Drimys sect. Tasmannia), Cupanieidites, Casuarinaceae, Sarcolaenaceae (Xyloolaena-type), Ascarina (three morphological types), Sparganiaceaepollenites, and some palm species including rare Nypa pollen grains. Other types no longer found at the Cape are Euphorbiaceae of the Croton-type, Alchornea also of the Euphorbiaceae, Rauvolfia of the Apocynaceae and pollen of Combretaceae/Melastomataceae-type. In addition Widdringtonia, Myrica, Myrtaceae, Sapindaceae, Sapotaceae, Rutaceae (Calodendrum), Ulmaceae (Celtis), Oleaceae and Celastraceae are represented and are still found in

TAXON		MICROCACHRYS (Microcachryidites antarcticus) Podocarpaceae							
MODERN HABITAT		Temperate							
DISTRIBUTION		Africa	Madag.	Aust.	Pacific	Malaysia	India	S Amer.	N Amer.
RECENT				■					
TERTIARY	PLIOCENE			▨					
	MIOCENE	■▨		▨					
	OLIGOCENE			▨					
	EOCENE			▨					
	PALAEOCENE			▨					
CRETACEOUS	UPPER	▨		▨			▨		
	LOWER	▨	▨	▨			▨	▨	
JURASSIC				▨			▨		

TAXON		CUPANIOPSIS (Cupanieidites) Cupanieae Sapindaceae							
MODERN HABITAT		Subtropical-tropical							
DISTRIBUTION		Africa	Madag.	Aust.	Pacific	Malaysia	India	S.Amer.	N Amer
RECENT			■	■				■	■
TERTIARY	PLIOCENE								
	MIOCENE	■▨							
	OLIGOCENE								
	EOCENE			▨					
	PALAEOCENE	▨		▨					
CRETACEOUS	UPPER	▨					▨	▨	▨
	LOWER								
JURASSIC									

TAXON		CASUARINA (Haloragacidites cf. H. harrisii) Casuarinaceae							
MODERN HABITAT		Subtropical-tropical							
DISTRIBUTION		Africa	Madag	Aust	Pacific	Malaysia	India	S.Amer.	N Amer.
RECENT			■	■	■	■			
TERTIARY	PLIOCENE								
	MIOCENE	■▨		▨					
	OLIGOCENE			▨					
	EOCENE			▨					
	PALAEOCENE			▨				▨	
CRETACEOUS	UPPER								
	LOWER								
JURASSIC									

TAXON		ASCARINA CLAVATIPOLLENITES Chloranthaceae							
MODERN HABITAT		Subtropical tropical montane							
DISTRIBUTION		Africa	Madag	Aust.	Pacific	Malaysia	India	S.Amer	N Amer.
RECENT			■	■	■	■			
TERTIARY	PLIOCENE								
	MIOCENE	■▨							
	OLIGOCENE			▨					
	EOCENE			▨					
	PALAEOCENE			▨					
CRETACEOUS	UPPER	▨							
	LOWER	▨							
JURASSIC									

TAXON		Winteraceae							
MODERN HABITAT		Temperate and subtropical to tropical							
DISTRIBUTION		Africa	Madag	Aust	Pacific	Malaysia	India	S.Amer.	N.Amer.
RECENT			■	■	■	■		■	■
TERTIARY	PLIOCENE								
	MIOCENE	■▨		▨					
	OLIGOCENE			▨					
	EOCENE			▨					
	PALAEOCENE			▨					
CRETACEOUS	UPPER			▨					▨
	LOWER								
JURASSIC									

TAXON		XYLOOLAENA Sarcolaenaceae							
MODERN HABITAT		Subtropical to tropical montane							
DISTRIBUTION		Africa	Madag	Aust.	Pacific	Malaysia	India	S.Amer.	N.Amer
RECENT			■						
TERTIARY	PLIOCENE								
	MIOCENE	■▨							
	OLIGOCENE								
	EOCENE								
	PALAEOCENE								
CRETACEOUS	UPPER								
	LOWER								
JURASSIC									

TAXON		SPARGANIACEAE - POLLENITES Sparganiaceae							
MODERN HABITAT		Swamp							
DISTRIBUTION		Africa.	Madag	Aust.	Pacific	Malaysia	India	S.Amer	N.Amer.
RECENT									
TERTIARY	PLIOCENE								
	MIOCENE	■▨		▨					
	OLIGOCENE			▨					
	EOCENE			▨					
	PALAEOCENE							▨	
CRETACEOUS	UPPER								
	LOWER								
JURASSIC									

TABLE 2 A GENERALISED SURVEY OF THE FOSSIL RECORD OF EXTINCT TAXA AT NOORDHOEK AND THE PRESENT DISTRIBUTION OF THE TAXA.

■ = AT NOORDHOEK
AUST. = AUSTRALASIA

the biome (Table 1). In the early Miocene, Proteaceae and Restionaceae are well represented but many taxa now prominent in the Cape fynbos shrublands are rare or absent.

The overall aspect of the microflora is that of a mixed lowland and montane 'subtropical-tropical' rainforest. In its general character the early Miocene Noordhoek microflora contrasts with the less diverse, dry open 'subtropical' forest represented earlier on the margin of the fynbos region at Arnot and again with relatively impoverished forest surviving in the present in enclaves of the biome. A number of the extinct taxa show clear biogeographic connections with other southern continents (Table 2). Coetzee and Muller (1983) have suggested the existence of a common South American-Antarctic-African-Madagascan flora in the Cretaceous which became fragmented through plate movements and dispersed along tropical, subtropical or temperate routes among the Gondwana land masses. They consider that elements of this ancestral flora contributed to the early Miocene forest at Noordhoek and are prominent in the modern flora of the humid island refugium of Malagasy.

In the Saldanha embayment are channel fill deposits related to the proto-Berg River. These deposits investigated by Coetzee and Rogers (1982) include riverine, lagoonal and back-barrier facies and occur at altitudes of 2,95 - 12,65 m asl in the Langebaanweg area and are suggested as being of late Miocene age. There are similar aged deposits represented in the upper part of the Noordhoek sequence. In these later Miocene occurrences, taxa characteristic of the fynbos shrublands became more prominent. These include members of the families Compositae, Thymelaeaceae, Ericaceae and Rosaceae (Cliffortia spp.). In addition, in the Saldanha area, Gramineae are well represented. There is a clearer relationship to the modern vegetation of the fynbos region in the later Miocene and this relationship is even more strongly evidenced in the peaty deposits associated with the younger Pliocene Varswater Formation at Langebaanweg in the Saldanha area. A number of forest and swamp taxa that survive from the early Miocene into the late Miocene, however, become extinct in the Mio-Pliocene. The absence of Rauvolfia, Alchornea, Euphorbiaceae of the Croton-type, and Palmae, all taxa with 'subtropical-tropical' affinities in Pliocene deposits, suggests pronounced cooling and less equable climates at the end of the Tertiary.

In the Plio-Pleistocene some 3 Myr ago with both polar regions permanently glaciated, atmospheric circulation approximated to the present patterns and it is from this time that summer dry climates would have had their inception at the Cape. With the expansion and contraction of northern hemisphere continental ice sheets in the Plio-Pleistocene, climates were alternately cooler and drier than the present and as warm or warmer than the present (for discussion, see Deacon 1983). A record of the Plio-Pleistocene events is preserved in local sedimentary basins known from the Saldanha, Cape Flats, Bot River and Wilderness areas. The latter part of this time range is currently best known from studies such as those of A. R. H. Martin (1968) on the Wilderness Lakes, Schalke (1973) on the Rietvlei lagoon, and Scholtz (in prep.) on the peats of the George area. Although Schalke has suggested alternating periods of expansion of fynbos shrublands and forest in the Cape Flats, Van Zinderen Bakker (1976) has pointed out that the frequencies of Podocarpaceae and other forest pollen elements are too low to suggest forests growing near Rietvlei. One borehole on the Cape Flats near Langa however does show very high percentages of forest taxa but this may be older than the late Pleistocene. There is some evidence in Schalke's results that the terminal Pleistocene was characterized by higher percentages of Gramineae and this would be consistent with some of the palaeontological evidence (Klein, this volume). In the Wilderness embayment there is palynological evidence (A. R. H. Martin 1968) for a succession from drier shrubland vegetation to forest in the terminal Pleistocene-Holocene, in the last ca 10-20 000 years, and in this area and around George there is further evidence for a forest decline in the last ca 2 500-2 000 years, possibly due in part to anthropogenic factors. These more recent vegetation changes seen in the palynological record appear to reflect changes in plant communities in response to the amelioration of climates after the coldest interval of the late Pleistocene , penecontemporaneous with the last glacial maximum 18 000 years ago. It is in this time that modern vegetation communities have formed. In the study of these more recent periods, the palynological evidence is complemented by evidence from the study of charcoals from archaeological and geological sites as well as palaeontology (papers in this volume). Human activities have also played a role in the development of present-day plant communities and this is most obvious in the appearance of pollen of exotic invasives and weeds in spectra that mark the introduction of agriculture and large scale modification of the vegetation.

CONCLUDING DISCUSSION

The studies reported in this paper provide direct information on the vegetation history of the fynbos landscape and serve as a check on reconstructions of the past vegetation patterns and hypotheses that have been put forward to explain the origin and evolution of the Capensis flora. Modern biogeographic data are an important source of information for historical reconstructions but if a fuller appreciation of the dynamic evolution of the fynbos and related vegetation is to be gained, these data need to be complemented by fossil evidence. An effort is being made to locate potential sites for study and to improve the quality of the fossil record. Palynological approaches have been stressed in this paper because they currently offer the best opportunities for learning more about the vegetation history of the Cape, but there are also occurrences of macroscopic plant remains from various time ranges which merit attention.

The gymnosperms and pteridophytes which comprised the vegetation at the Cape at the time of the separation of the African and South American plates represent a truly ancient flora of wide southern hemisphere distribution that had existed under uniformly mild climates. The occurrence of the Podocarpaceae in the fynbos biome, and also in other southern continents, can be explained as an inheritance from these remote times. It is less easy to explain the occurrence of angiosperm elements which have a shared distribution between the southern continents, including the Cape, because plate movement was more advanced at the time of the mid-Cretaceous dispersion of the angiosperms. However land links between Africa and South America in the equatorial latitudes were only severed in the mid-Cretaceous, Aptian times (Förster 1978; Buffetaut & Taquet 1979) and there were opportunities for dispersal via Indian Ocean links to Australasia (Raven & Axelrod 1974) possibly until the late Cretaceous (75 Myr) (Schuster 1976). These are low latitude links and on our present knowledge of the history of the South Atlantic it is difficult to evaluate the importance of tracks for dispersal at higher latitudes that may have been offered by the Walvis-Rio Grande ridges and the Falkland Plateau in the Cretaceous. The most economical hypothesis is to assume that southern Africa derived its primary complement of angiosperms from tropical Africa, that is West Gondwana, sources as did the other austral lands. There was no barrier to the dispersal of angiosperms in Africa and their invasion of the southern austral forests, initiated in the mid-Cretaceous on the evidence from DSDP 361, had advanced significantly by the late Cretaceous.

In reviewing the evidence from the late Cretaceous it is apparent that already at this time some zonation of the vegetation existed in Africa south of the equator and the records of Podocarpaceae, *Cupanieidites*, *Clavatipollenites* and Proteaceae in the late Cretaceous deposits are links between the microfloras of the Cretaceous and those of the Tertiary. The end-Cretaceous is a crucial period in earth history and one that may be represented in some of the sedimentary infills in the craters of kimberlite pipes on the margin of the fynbos area. The single observation from Arnot in the succeeding Paleocene period indicates rapid modernization of the flora at the beginning of the Tertiary.

In spite of temporal differences it is possible to view the contrast between the microfloras of Arnot and Noordhoek as representing the differences in vegetation in the areas marginal to and within the fynbos landscape in the Tertiary (Table 1). The Noordhoek evidence documents the survival into the early Miocene of a warm humid rain forest (Table 2) with *Microcachrys* (*Microcachryidites antarcticus*), *Cupaniopsis* (*Cupanieidites*), *Casuarina* (*Triorites* (*Haloragacidites*) cf. *T. harrisii*), *Ascarinopsis* (*Clavatipollenites*), Winteraceae and Sarcolaenaceae as well as members of the Podocarpaceae, Cupressaceae (*Widdringtonia*), Palmae and a range of other angiosperms that had been added by recruitment through the Tertiary. On the basis of present knowledge, Sarcolaenaceae apart, these elements are comparable to taxa that were present during the Cretaceous and Tertiary of other southern hemisphere lands such as Australia, Ninetyeast Ridge and New Zealand (Couper 1960; Stover & Partridge 1973; Kemp 1976; H.A. Martin 1978; Mildenhall & Crosbie 1979; Mildenhall 1980). This Miocene alliance of a diverse range of elements whose modern representatives are found in tropical, subtropical and temperate habitats, is indicative of the uniformly favourable Miocene environment. The setting of Noordhoek is in many ways ideal in that the regional spectrum reflects both uplands and lowlands. The closest modern analogue that can be suggested for this Miocene rainforest, which is assumed to have occupied much of the fynbos landscape in the Tertiary, is the rainforests of Malagasy where some taxa like the Winteraceae, Sarcolaenaceae and Ascarinopsis, now extinct on the African mainland, are still found (Coetzee & Muller 1983). The more extended areas of the coastal platform on the evidence from Knysna and Noordhoek would have been occupied by a rich palm flora.

On the Arnot evidence the rainforests of the Cape Fold Mountains were bounded in the interior by drier forests which can be assumed to have persisted into the Miocene at least along rivercourses, progressively giving way to more open woodland. The western interior of South Africa has a long history of relative dryness, indicated not only in the Arnot microflora but also in the Ephedripites dominated late Cretaceous microflora of Botswana. Axelrod and Raven (1978) have argued that the drier interior margins of the fynbos region would have been an important region for the distribution of sclerophyllous taxa, pre-adapted under seasonal climates and available to occupy the fynbos region when summer dry climates developed. There are details of the Axelrod and Raven model for the origins of the fynbos vegetation, in particular the timing of the events and large scale displacement of vegetation, that can be questioned (Taylor 1980; Deacon 1983). For example, they propose that the fynbos was largely swept into its present areas as a result of drier climates at the end of the last pluvial 10 000 years ago, but the fossil evidence shows this vegetation has a very much longer history in the region. The Arnot evidence can be interpreted as supporting their general thesis of an early association of some taxa now prominent in the fynbos, with the drier vegetation types of the south-western interior, especially if it is assumed that the same taxa were not closely associated with the Noordhoek-type Tertiary rainforest vegetation. It is also possible, however, that similar drier vegetation associations existed from an equally early time in, for example, areas affected by rainshadow within the fynbos region.

A major change in the vegetation of the fynbos region is indicated from the end of the Miocene when the palynological evidence shows progressive impoverishment of the rainforest vegetation and significant increases in the pollen of Ericaceae, Compositae, Thymelaeaceae, Rosaceae (Cliffortia) and Gramineae. The dating suggests this evidence relates to the fragmentation of the distribution of rainforest and the spread of Cape fynbos shrublands in response to changes towards cooler and summer dry climates at the end of the Tertiary and in the Pleistocene. Although the nature and scale of this vegetation change is established, more observations are required to document details of the extinctions of old and the appearance of new taxa and to provide more precise dating. The composition of the Cape shrubland communities has been affected by the climatic pulses of the Plio-Pleistocene and their present status is a result of effects of the climatic changes, natural and man-made fires and recent agricultural activities.

The importance of the climatic changes in the history of the evolution of the fynbos since the early Miocene needs to be stressed and should be considered in relation to the physiography of the region. The area of highest terrain diversity is where the east-west and north-south trends of the Cape Fold Mountains cross in the south-western Cape. This is also the core area that enjoys a mediterranean-type climate (Aschmann 1973) in the present and shows the highest species richness (Taylor 1980). It corresponds to the Caledon centre as defined by Nordenstam (1969) and can be considered as essentially an island on which a complement of edaphic specialists have been isolated by the progressive trend towards drier climates in the later Tertiary and Quaternary. The noteworthy gamma diversity of the fynbos communities here and elsewhere (Kruger & Taylor 1979) can be accounted for by the terrain diversity. Levyns (1964) has pointed out that speciation in the fynbos is secondary in that it encompasses numbers of advanced forms, localized in their distribution and derived from more widely distributed generalist ancestors. She suggested an end-Tertiary age for speciation and linked it to the appearance of mediterranean-type climates. At the current stage of palynological research it would be premature to offer any conclusions on the timing, mode and tempo of speciation in the Capensis flora. The speciation in some families like the Proteaceae may be evident earlier in the Tertiary. It does seem however that the reduction in the areas of rainforest vegetation in the Mio-Pliocene linked to progressive climatic deterioration was an important factor in the evolution of features that characterize fynbos ecosystems. Further research is needed, however.

Some unexpected results have emerged from the present stage of palynological research in the fynbos region and its surrounds. These results are unexpected because they could not have been predicted from the present day phytogeography. A modern observer is impressed by the species richness of the Cape fynbos shrublands but from the perspective of the palynological evidence it can be appreciated that this richness has been achieved through extinctions, impoverishment and disruption of an older diverse forest flora. Enough palynological information is available now to outline some of the important features of the history of the major vegetation types found in the biome.

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REFERENCES

ADAMSON, R. S. 1934. Fossil plants from Fort Grey near East London. Annals of the South African Museum 31:67-96.

ADAMSON, R. S. 1958. The Cape as an ancient African flora. South African Journal of Science 58:118-127.

ASCHMANN, H. 1973. Distribution and peculiarity of mediterranean ecosystems. In Castri, D. I. & Mooney, H. A. eds Mediterranean type ecosystems: origin and structure: 11-19. Berlin: Springer-Verlag

AXELROD, D. I. & RAVEN, P. H. 1978. Late Cretaceous and Tertiary vegetation history of Africa. In Werger, M. J. A. ed. Biogeography and ecology of southern Africa: 77-130. The Hague: W. Junk.

BRENNER, G. J. 1976. Middle Cretaceous floral provinces and early migrations of Angiosperms. In Beck, C.B. ed. Origin and early evolution of angiosperms: 23-47. New York: Columbia University Press.

BUFFETAUT, E. & TAQUET, P. 1979. An early Cretaceous terrestrial crocodilian and the opening of the South Atlantic. Nature 280:486-487.

COETZEE, J. A. 1978. Late Cenozoic palaeoenvironments of southern Africa. In Van Zinderen Bakker, E. M. ed. Antarctic glacial history and world palaeo-environments: 115-127. Rotterdam: Balkema.

COETZEE, J. A. 1980. Tertiary environmental changes along the south-western African coast. Palaeontologia Africana 23:197-203.

COETZEE, J. A. 1981. A palynological record of very primitive angiosperms in Tertiary deposits of the south-western Cape Province, South Africa. South African Journal of Science 77:341-343.

COETZEE, J. A. 1983. Intimations on the history of the Tertiary floras and vegetation of southern Africa. Bothalia, in press.

COETZEE, J. A. & ROGERS, J. 1982. Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa).

Palaeogeography Palaeoclimatology Palaeoecology 39:71-85.

COETZEE, J. A. & MULLER, J. 1983. The phytogeographic significance of some extinct Gondwana pollen types from the Tertiary of the southwestern Cape (South Africa). Annals of the Missouri Botanical Gardens, in press.

COUPER, R. A. 1960. Southern hemisphere, Mesozoic and Tertiary Podocarpaceae and Fagaceae and their palaeogeographic significance. Proceedings of the Royal Society of London B 152:491-499.

DEACON, H. J. 1983. The comparative evolution of Mediterranean-type ecosystems: a southern perspective. In Kruger, F. J., Mitchell, D. T. & Jarvis, J. U. M. eds Mediterranean-type ecosystems: the role of nutrients. Berlin: Springer-Verlag.

FORSTER, R. 1978. Evidence for an open seaway between northern and southern proto-Atlantic in Albian times. Nature 272:158-159.

GOLDBLATT, P. 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. Annals of the Missouri Botanical Gardens 65:369-436.

HERNGREEN, G. W. F. & CHLONOVA, A. F. 1981. Cretaceous microfloral provinces. Pollen et Spores 23:441-555.

KEMP, E. M. 1976. Early Tertiary pollen from Napperby, central Australia. BMR Journal of Australian Geology and Geophysics 1:109-114.

KIRCHHEIMER, F. 1934. On pollen from the upper Cretaceous dysodil of Banke, Namaqualand (South Africa). Transactions of the Royal Society of South Africa 21:41-50.

KRUGER, F. J. & TAYLOR, H. C. 1979. Plant species diversity in Cape fynbos: gamma and delta diversity. Vegetatio 41:85-93.

LEVYNS, M. R. 1964. Migrations and origin of the Cape Flora. Transactions of the Royal Society of South Africa 37:85-107.

MARTIN, A. R. H. 1959. South African palynological studies 1. Statistical and morphological variations in the South African species of Podocarpus. Grana 2:40-53.

MARTIN, A. R. H. 1968. Pollen analysis of Groenvlei Lake sediments, Knysna (South Africa). Review of Palaeobotany and Palynology 7:107-144.

MARTIN, H. A. 1978. Evolution of the Australian flora and vegetation through the Tertiary: evidence from pollen. Alcheringa 2:181-202.

McLACHLAN, I. R. & PIETERSE, E. 1978. Preliminary palynological results: Site 361, leg 40. Deep Sea Drilling Project. Initial Reports of the Deep Sea Drilling Project 4:857-881.

MILDENHALL, D. C. 1980. New Zealand late Cretaceous and Cenozoic plant biogeography: a contribution. Palaeogeography Palaeoclimatology Palaeoecology 31:197-233.

MILDENHALL, D. C. & CROSBIE, Y. M. 1979. Some porate pollen from the upper Tertiary of New Zealand. New Zealand Journal of Geology and Geophysics 22:499-508.

MORGAN, R. 1978. Albian to Senonian palynology of Site 364, Angola Basin.

Initial Reports of the Deep Sea Drilling Project 40:915-951.

MULLER-STOLL, W. R. & MADEL, E. 1962. Fossil woods of Monimiaceae and Euphorbiaceae from the Upper Cretaceous Umzamba Beds of East Pondoland, Cape Province. Transactions of the Geological Society of South Africa 65:93-104.

NORDENSTAM, B. 1969. Phytogeography of the genus Euryops (Compositae): a contribution to the phytogeography of southern Africa. Opera Botanica 23:1-77.

PHILLIPS, J. F. V. 1927. Fossil Widdringtonia in lignite of the Knysna Series, with a note on fossil leaves of several other species. South African Journal of Science 24:188-197.

RAVEN, P. H. & AXELROD, D. I. 1974. Angiosperm biogeography and past continental movements. Annals of the Missouri Botanical Gardens 61:539-673.

RENNIE, J. V. L. 1931. Note on fossil leaves from the Banke clays. Transactions of the Royal Society of South Africa 19:251-253.

ROGERS, A. W. 1908. Notes on a journey to Knysna. Annual Report of the Geological Commission of the Cape of Good Hope 13:129-134.

SALARD-CHEBOLDAEFF, M. 1981. Palynologie Maestrichtienne et Tertiare du Cameroun. Resultats botaniques. Review of Palaeobotany and Palynology 32:401-439.

SCHALKE, H. J. W. G. 1973. The upper Quaternary of the Cape Flats area (Cape Province, South Africa). Scripta Geologica 15:1-57.

SCHOLTZ, A. in press. The palynology of the upper lacustrine sediments of the Arnot pipe, Banke, Namaqualand. Annals of the South African Museum.

SCHOLTZ, A. & DEACON, H. J. 1982. Report on fossil pollens from sediments associated with a group of kimberlite pipes in Botswana. Unpublished report.

SCHUSTER, R. M. 1976. Plate tectonics and its bearing on the geographical origin and dispersal of Angiosperms. In Beck, C. B. ed. Origin and early evolution of Angiosperms: 48-138. New York: Columbia University Press.

SCOTT, L. 1976. Palynology of Lower Cretaceous deposits from the Algoa Basin (Republic of South Africa). Pollen et Spores 18:563-609.

SRIVASTAVA, S. K. 1978. Cretaceous spore-pollen floras: a global evolution. Biological Memoirs 3:2-130.

SRIVASTAVA, S. K. 1981. Evolution of upper Cretaceous phyto-geoprovinces and their pollen flora. Review of Palaeobotany and Palynology 35:155-173.

STAPLETON, R. P. & BEER, E. M. 1977. Micropalaeontological age determination for the Brenton Beds. Geological Survey of South Africa Bulletin 60:1-9.

STOVER, L. E. & PARTRIDGE, A. G. 1973. Tertiary and Late Cretaceous spores and pollens from the Gippsland Basin, south-eastern Australia. Proceedings of the Royal Society of Victoria 85:327-286.

TAYLOR, H. C. 1978. Capensis. In Werger, M. J. A. ed. Biogeography and ecology of southern Africa. The Hague: W. Junk.

TAYLOR, H. C. 1980. Phytogeography of fynbos. Bothalia 13:231-235.

THIERGART, F., FRANTZ, U. & RAUKOPF, K. 1963. Palynologische untersuchungen von Tertiarkohlen und einer oberflachen probe nabe Knysna, Sud-Afrika. Advanc. Front. of Plant Science 4:151-178.

TRUSWELL, E. M. & HARRIS, W. K. 1982. The Cainozoic palaeobotanical record in arid Austalia: fossil evidence for the origins of an arid-adapted flora. In Barker, W. R. & Greenslade, P. J. M. eds Evolution of the flora and fauna of arid Australia. Adelaide: Peacock Publications.

VAN ZINDEREN BAKKER, E. M. 1976. The evolution of Late Quaternary palaeoclimates of southern Africa. Palaeoecology of Africa 9:160-202.

FOSSIL CHARCOALS AS A SOURCE OF PALAEOECOLOGICAL INFORMATION IN THE FYNBOS REGION

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INTRODUCTION

Charcoals, the carbonized remains of woody plants, are some of the most commonly preserved macroscopic plant remains found in younger Cenozoic archaeological and geological deposits. They are the product of man-made and natural fires and have been accumulated by human activities or by colluvial and fluviatile action. In this paper the results of studies of charcoal occurrences in archaeological deposits in caves in the foothills of the Swartberg, in particular Boomplaas Cave, and in soil colluvium in pits in the Knysna forest in Outeniqualand are reported. These are examples of an approach that has wider potential application in the study of past vegetation communities in other areas. Identification of fossil charcoals requires an appropriate comparative collection and can be made by the use of incident light and scanning electron microscopy.

THE CANGO VALLEY STUDY

The excavation of Boomplaas Cave in the foothills of the Swartberg some 4 km from the Cango Caves in the Oudtshoorn District was designed to provide a number of complementary lines of evidence on late Pleistocene and Holocene environments (Deacon 1979). This has entailed the recovery of faunal and floral remains as well as the study of sediments from the sequence of deposits, some 5 m deep, that accumulated in the cave during the last 80 000 years. Charcoals were routinely recovered by water flotation from discrete hearths and ashy lenses during the course of the excavation. Samples for analysis were drawn from each hearth and/or grid square in each stratigraphic member so that they would be representative of the multiple firewood collecting tasks carried out by the cave inhabitants over the period of accumulation of the member. Radiocarbon dates, run for the most part on charcoals, provide a chronology for the sequence.

A vegetation survey of the Cango Valley (Moffett & Deacon 1977) showed some 70 woody plants which could have been used as fuel. The woodland vegetation in the main valley and the side kloofs includes *Acacia karroo*, *Olea europaea africana*, *Rhus lucida* and *Maytenus heterophylla* which together may form a closed canopy, and in better watered sites Ilex mitis, Kiggelaria africana and Salix capensis are found. Euclea undulata, Dodonaea viscosa and Rhus undulata, shrubs up to 2 m high, and woody composites are noteworthy elements in the asteroid shrubland on the slopes immediately below the cave and Cussonia spp., Rhus lucida, Maytenus oleoides, Diospyros austro-africana, Tarchonanthus camphoratus and Rhus undulata occur in mixed bush at the foot of the steep cliffs above the cave.

Acacia karroo is widespread throughout the valley and is the preferred source of fuel in the present. Scattered trees occur on the edges of cultivated fields in the alluvial soils suggesting its abundance would have been more marked in the valley bottom prior to cultivation. This is confirmed by the dominance of Acacia in a strip of woodland growing along the margin of the valley below the cave. It was predicted that Acacia karroo, a hard wood with excellent charcoaling properties, would have been the main source of fuel for the cave inhabitants over the period when woodland in the valley was of essentially modern composition. This prediction was amenable to testing through the analysis of charcoal remains.

Olea europaea africana is another dense hardwood fuel that may have been subject to human selection. In the present however Olea is conserved as a source of fencing poles and is not usually used for firewood. Woodland in which Olea is dominant was recorded in a side kloof at Waenskloof, essentially a refuge situation, and it was predicted that Olea woodland may have been more widespread in the main valley under cooler climatic conditions of the late Pleistocene. The study then had the initial goal of tracing the relative dominance of Acacia and Olea in the stratigraphic succession. The predicted end-Pleistocene importance of Olea and the Holocene dominance of Acacia has proved to be essentially correct but different patterns emerge in earlier time ranges (Table 1).

The cave served as a stock post for herders from 1 700 years ago as evidenced by the capping layers of calcined dung with the remains of small stock. The possibility that the spread of Acacia karroo into the valley could be linked to the appearance of herders and overgrazing by their domestic stock can be rejected because charcoals of Acacia are dominant and make up 40% of the sample analysed from the most recent hunter-gatherer occupation preserved in the underlying BLD Member (acronym for brown loamy deposit) dated to some 2000 B.P. (Before the Present) (Table 1). In the next oldest member, the BLA dated to 6400 B.P., the representation of Acacia karroo is reduced to some 5% and charcoals of Acacia are absent from horizons older than 12 000 years. Supplementary samples were analysed from a rock shelter on the farm Buffelskloof near Calitzdorp some 25 km to the west. This site showed a similar significant increase in the representation of Acacia karroo bracketed by radiocarbon dates of 8000 and 4000 B.P. The absence of Acacia karroo charcoal in the Pleistocene levels of the site can be interpreted as due to this species not being represented in the woodland

DATING	2000 B.P.	6400 B.P.	9-10 000 B.P.	12-14 000 B.P.	18-21 000 B.P.	32 000 B.P.	42 000 B.P.
TAXA STRATIGRAPHY	BLD	BLA	BRL	CL	LP/LPC	BP	OLP
Salix cf. *mucronata*	-	-	-	9,09	4,90	0,40	1,82
Protea arborea	12,09	1,56	4,65	4,13	2,58	5,13	8,45
Other Proteaceae	-	-	-	4,13	-	6,33	3,65
Acacia karroo	38,60	4,69	6,98	-	-	-	-
Nymania capensis	4,65	1,56	-	-	-	-	-
Maytenus - Pterocelastrus	2,79	14,09	4,65	-	-	-	0,50
Rhus cf. *undulata*	4,65	3,13	-	1,65	-	-	-
Other *Rhus* spp.	6,05	9,38	23,26	23,14	-	-	0,63
cf. *Rhamnus*	-	-	2,33	2,48	5,09	0,53	-
Passerina spp.	2,79	-	-	-	-	-	3,53
cf. *Erica* spp.	-	1,56	-	5,78	15,72	34,52	6,30
Euclea/Diospyros	1,40	12,50	16,28	1,65	-	-	-
Olea group	3,26	15,63	18,60	38,86	-	-	33,69
cf. *Buddleia glomerata*	4,19	9,38	2,33	0,83	-	8,20	9,27
cf. *Buddleia salvifolia*	4,19	-	-	-	-	-	-
cf. *Lycium*	-	-	-	-	-	2,93	-
cf. *Nemesia fruticans*	-	-	-	-	0,72	3,26	2,52
Compositae	11,17	17,19	13,96	4,96	67,16	18,52	12,02
Type A	-	1,56	-	-	0,72	9,40	0,31
Other	4,20	7,81	6,98	3,31	3,47	11,25	16,56
Total number	215	64	43	121	129	217	185

Table 1. An analysis of fossil charcoals from Boomplaas Cave.

communities of the valley because human selection would favour its use had it been present. The dating evidence from Buffelskloof and Boomplaas suggests that after an initial spread into the Cango Valley in the early Holocene, *Acacia karroo* became a major component of the woodland only in the last 5 000 years. The extension of the geographic range of *Acacia karroo* with important ecological implications has been noted in grassland ecosystems in South Africa (Acocks 1953; Comins 1962) and this could be a process similarly initiated prior to the introduction of modern land use practices.

The sample sizes from the Holocene BLA and BRL members dated to 6400 B.P. and to between 9100 and 10 400 B.P. respectively are small but together indicate the importance of thicket taxa *Diospyros*/*Euclea* and *Maytenus*/*Pterocelastrus* in the earlier part of the Holocene. These horizons also show a trend towards increased representation of the *Rhus* and *Olea* groups that reaches a peak in the CL (acronym for carbonized loams) Member dated between 12 000 and 14 200 B.P. The *Rhus* group is represented by material referred to *R. undulata* and by two or more species possibly including *R. incisa* and *R. macowani*. The *Olea* group is predominantly *Olea* but included in this group in Table 1 are low percentages of the *Hermannia*/*Grewia* sub-group and possibly *Dodonaea*. In CL times, *Olea europaea africana* is some 35% and this suggests the existence of *Olea* woodland, possibly with a grass understorey of *Ehretia erecta* and *Myrsine africana* as occurs in Waenskloof (Moffett & Deacon 1977), was established in parts of the main valley below the cave. A parkland or open woodland environment with suitable grazing for herbivores would seem to be indicated by the large mammal fauna (Klein, this volume) from this member. The drier Compositae types are almost unrepresented in CL which can be interpreted as indicating more effective precipitation possibly as a result of lower temperatures relative to the beginning of the Holocene. *Salix*, a streambank species, becomes quite prominent in CL. A change in the position of the river channel or access to it could be indicated and it would seem that the river banks were a focus for collecting firewood possibly available as flood debris.

The interval that includes the coldest climates of the late Pleistocene dating between about 16 000 and 25 000 B.P. is represented in the Boomplaas sequence by the members GWA/HCA, LP, LPC and YOL. Counts from a combined sample from LP and LPC are given in Table 1 and in addition a further sample from GWA/HCA has been analysed. The charcoal samples from this time range are noteworthy because they show reduced diversity and the virtual absence of taller shrubs and trees in the collecting range of the cave. Composites make up almost 70% of the LP/LPC sample that dates to between 18 000 and 21 000 B.P. This pattern is interpreted as an indication of relatively extreme environmental conditions with significantly lower temperatures and precipitation.

The percentage of Compositae is very much lower in the BP Member, a layer of carbonized loams and ash that dates to 32 000 years ago. The dominant element with the noteworthy attributes of long parallel-sided rays and solitary vessels was originally designated Type H and two sub-groups can be distinguished in this material on the thickness of the fibre cell walls. It is not present in the reference sample of woody species occurring in the modern environs of the cave but supplementary collecting suggests it can be referred to *Erica* spp. An unknown labelled Type A which may be a legume (M. Tusenius, pers. comm.) makes up almost 10% of the BP sample. The importance in LP/LPC and BP of elements that are rare or absent in the modern vegetation suggests that at that time under very different environmental conditions there were plant communities present in the valley with no modern analogue.

The high representation of *Olea* in the sample from the OLP Member associated with a radiocarbon age of 42 000 B.P. is a link with the younger end-Pleistocene CL and the Holocene samples. Compositae percentages are relatively low but not as low as in CL and in this case as in BP, the minor elements, grouped under Other in Table 1, are mainly elements not matched in the modern reference collections. The diversity of woody species is relatively high and it is inferred that climates in the valley were not as dry or cold as during the period represented by GWA/HCA and LP/LPC. Some additional material from hearths in BOL dated to beyond the range of conventional radiocarbon dating has been analysed and pending further study this serves simply to indicate that *Olea* is prominent in this earlier horizon. *Olea* was an important taxon in the woodland associations in the Cango Valley both prior to and subsequent to the coldest interval of the late Pleistocene.

THE KNYSNA STUDY

Phillips (1931) recorded the occurrence of charcoal identified as the forest genera *Podocarpus*, *Trichocladus* and *Ocotea* in soils in stands of indigenous forest and in fynbos vegetation. He interpreted these observations as documenting an earlier extended distribution of forest. More recent soil pitting programmes undertaken by J. C. van Daalen and C. J. Geldenhuys of the Forest Research Institute, Saasveld, George, has confirmed the occurrence of charcoal-rich horizons in soils beneath forest and in fynbos islands in the forest. Several of these occurrences have been investigated and the potential does exist for more research.

A pit in indigenous forest on the Kaffirkop ridge east of Knysna yielded a charcoal sample composed of *Olea* cf. *capensis macrocarpa*, a forest species. The charcoal is buried 300 mm below the surface in a ferrihumic horizon and is partly mineralized. A radiocarbon date for the occurrence is given at 8000 B.P. (J. C. Vogel, pers. comm.) which is a *terminus post quem* for the dating of the fire and a minimum age for the forest at this locality. Although the charcoal from the sampled pit is of a single species, further pits in the immediate vicinity have also yielded charcoal (C. J. Geldenhuys, pers. comm.) but the extent of the fire has still to be established. Fire would not normally penetrate indigenous forest, but lightning strikes and the activities of honey hunters may account for isolated occurrences. In this context is is noteworthy that Martin (1968) mentions the presence of much charcoal in the sediments of the Holocene sequence at Groenvlei and fires in the general area were apparently not infrequent in historic times. J. C. van Daalen has sampled what is probably a recent occurrence of charcoal in an area of dry forest in the Gouna Forest which, as at Kaffirkop, consisted of a single species, in this case *Olinia cymosa*, and more sites are known.

At the Garden of Eden between Knysna and Plettenberg Bay, an excavation using flotation techniques was undertaken to sample charcoal in minor braided channels in a Dundee soil 0,6 m below the floor of the forest. The excavation was close to a 'white' water stream incised to a depth of 2 m and draining an area of forest. Apart from the remains of aquatics, the charcoals recovered consisted of *Platylophus trifoliatus* (C. P. Kromhout, pers. comm. to J. C. van Daalen) and the charcoal horizon was dated to 1000 B.P. (J. C. Vogel, pers. comm.). This evidence of alluviation and incision suggests at least local disturbance of a stand of forest in late prehistoric and possibly early historic times and similar evidence might be sought elsewhere.

Islands of fynbos in forest, the locally named 'eilande', may also reflect disturbance of forest in recent times. As a contribution to the problem of the origin of the islands, a sample of charcoal from the sub-surface level in a stand of 30-year old fynbos vegetation with *Virgilia oroboides* and *Protea* spp. dominant was analysed. Three taxa, *Canthium obovatum*, *Heteromorpha arborescens* and *Olea* cf. *europaea africana* were identified suggesting that a dry shrub rather than forest vegetation existed there in times prior to the fire event represented in the charcoal. The charcoal has not been dated but it can be assumed that the islands have a long and complex fire history.

CONCLUSIONS

Fossil charcoals have proved an instructive source of information on aspects of vegetation history in the fynbos region. In particular, the continuous and well-dated sequence in the Boomplaas Cave in the Cango Valley provides an outline of the scale and direction of vegetation change over the periods leading up to and subsequent to the coldest interval of the late Pleistocene, that is relevant in the general trends if not in specific details to the study of the vegetation history in the whole region. In the Cango Valley, woodland was replaced by treeless shrubland under the relatively extreme environmental conditions between about 25 000 and 16 000 B.P. and thereafter *Olea* woodland was re-established followed by the appearance of thicket species and finally by woodland in which Acacia karroo is dominant. The largest scale of change in vegetation communities can be suggested as occurring within the last 16 000 years and it is over this time range that the synthesis of modern communities has taken place.

The Boomplaas evidence is most pertinent to the influence of Pleistocene climate on vegetation in the intermontane valleys and to a lesser extent the coastal forelands where additional sites may be sought, and it is these habitats associated with generally richer substrates and occupied by more generalist species that may have been most affected by Pleistocene climatic changes (Deacon 1983). Habitats in the mountain zone, because of the high terrain diversity, higher rainfall and lower incidence of frost may have been somewhat less affected by the scale of Pleistocene climatic changes. It is reasonable to argue, however, as do Kruger and Taylor (1979), that even in this zone Pleistocene climatic changes would have created isolated subpopulations and been responsible for changes in community composition. As areas of erosion rather than deposition, the vegetation history of the mountains may always be less well known than that of the intermontane valleys and coastal lowlands.

It has been suggested that the Afromontane Knysna forest has had a more extended (Phillips 1931) and a more restricted (Martin 1968; Butzer & Helgren 1972) distribution in the past. In the Knysna area, forest occurs on the footslopes of the Outeniqua mountains and extends locally to the outer margins of the coastal platform and both climatic and edaphic factors (Schloms et al., this volume) control its distribution. The importance of orographic precipitation is indicated by the occurrence of forest on the southern slopes of the mountains. The exclusion of forest from soils subject to water stress either through seasonal waterlogging or through poor retention of soil moisture shows the importance of substrate conditions. On the coastal platform, fynbos communities are established on the sites edaphically unsuited to forest and there is little question that the fire frequency in the area is increased as a result of these inliers.

The extent of the Knysna forest may have been markedly reduced during the coldest interval of the late Pleistocene. The present distribution is a response to the general amelioration of climates thereafter and also to rising sea levels resulting in the movement of the coastline closer to the mountains and increased effectiveness of orographic rainfall. Sea levels rose by about 100 m in the last 16 000 years and the transgression of the coastline was of the order of 50-100 km (Dingle & Rogers 1972).

The palynological study of Hiller auger samples from Groenvlei (Martin 1968) showed one or more expansions of forest in the last 7 000 years and the existence of drier heath or asteroid shrubland vegetation in the Wilderness area prior to that time. The dating of the sequence rests on only two radiocarbon age determinations and these dates require confirmation and possible re-interpretation. The lower part of the Groenvlei sequence associated with shrubland is dated only by extrapolation to 8000 B.P. This may be an under-estimate and the occurrence of shrubland may date closer to 18 000 B.P. This is suggested by the charcoal data from Kaffirkop which indicate that forest was established on the outer margin of the coastal platform some time before 8000 B.P. Additional radiocarbon dates would be necessary to resolve the problem of the age of the replacement of shrubland by forest, a very significant vegetation change documented in the Wilderness embayment. Materials for dating, palynological and charcoal analyses could be obtained from a more extensive pitting programme and the drilling of long cores at selected sites in the lakes. Although costly, drilling in the Wilderness embayment would yield considerable palaeoecological information and Martin's initial study of the area needs to be extended.

The charcoal occurrences at Gouna, Garden of Eden and the fynbos islands point to fires having some frequency in the fynbos-forest mosaic on the coastal platform in the Holocene. More research needs to be done on the extent of these prehistoric and historic fires through pitting and the use of flotation to recover charcoals. Hitherto, charcoal samples have come from pits excavated to expose soil profiles and have been chance finds. The results of the initial studies completed so far point to significant disturbance of forest in the last 1 000 years or so that could be better documented.

Carbonized plant remains are relatively abundant in archaeological sites and they may be more common in colluvial and fluviatile deposits than has been generally appreciated. The studies at Boomplaas and Buffelskloof caves and in the Knysna forest enclave undertaken as part of the Fynbos Biome Project serve both as a test of some existing ideas on vegetation and fire history and as a starting point for further palaeoecological research.

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REFERENCES

ACOCKS, J. P. H. 1953. Veld types of South Africa. Botanical Survey of South Africa Memoir 28:1-192.

BUTZER, K. W. & HELGREN, D. M. 1972. Late Cenozoic evolution of the Cape coast between Knysna and Cape St Francis, South Africa. Quaternary Research 2:143-69.

COMINS, D. M. 1962. The vegetation of the districts of East London and King Williams Town, Cape Province. Botanical Survey of South Africa Memoir 33:

DEACON, H. J. 1979. Excavations at Boomplaas Cave - a sequence through the Upper Pleistocene and Holocene in South Africa. World Archaeology 10:241-57.

DEACON, H. J. 1983. The comparative evolution of mediterranean-type ecosystems: a southern perspective. In Kruger, F. J., Mitchell, D. T. & Jarvis, J. U. M. eds Mediterranean-type ecosystems. The role of nutrients. Berlin, Heidelberg, New York: Springer-Verlag.

DINGLE, R. V. & ROGERS, J. 1972. Pleistocene palaeogeography of the Agulhas Bank. Transactions of the Royal Society of South Africa 40:155-65.

KRUGER, F. J. & TAYLOR, H. C. 1979. Plant diversity in Cape fynbos: gamma and delta diversity. Vegetatio 41:85-93.

MARTIN, A. R. H. 1968. Pollen analysis of Groenvlei lake sediments, Knysna. Revue of Palaeobotany and Palynology 7:107-44.

MOFFETT, R. O. & DEACON, H. J. 1977. The flora and vegetation in the surrounds of Boomplaas Cave, Cango Valley, South Africa. South African Archaeological Bulletin 32:127-45.

PHILLIPS, J. F. V. 1931. Forest succession and ecology in the Knysna region. Botanical Survey of South Africa Memoir 14:1-327.

THE PEOPLING OF THE FYNBOS REGION

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INTRODUCTION

The earliest written record of peoples living at the Cape is of the people seen by Diaz and his mariners on their epic voyage undertaken between August 1487 and December 1488. His party landed at six points along the coast and recorded seeing people with cattle living at the Gouritz River mouth and Mossel Bay in early February 1488. Further east near Cape St Francis people were also observed and veld burning noted (Axelson 1973:108). The herders later became known as the Hottentots or Khoi. These observations are remarkable because they pose the questions of how long people with exotic domestic animals had been living at the Cape, and of who the earliest inhabitants were. Some answers to these questions about the prehistoric peoples in the fynbos region have been obtained by archaeological research.

The region has arguably the longest record of human habitation (Fig. 1) of all the mediterranean-type climate regions, rivalled only by the circum-Mediterranean region. These two Old World regions were inhabited for periods of hundreds of millennia before the present in contrast to the few tens of millennia that the New World mediterranean-type climate regions of California, Chile and Australia have been settled. Only the circum-Mediterranean region however has the dubious distinction of being adjacent to and part of a centre of early domestication of plants and animals and has paid the greater price for what Blair (1970) has said are man's mistakes: domesticating too few species and spreading them too widely, and domesticating the goat. Although animal husbandry of cattle and sheep, but not the goat, was practised at the Cape for more than a millennium prior to the Diaz voyage, here and in the New World regions mixed agriculture was introduced as recently as the colonial era. The practice of mixed agriculture implies a quantum increase in the human impact on natural ecosystems through the establishment of fixed settlements, the introduction of exotic cultigens and more intensive grazing by stock, but pre-agricultural peoples through their wide distribution, mobility and the control of fire, had the means to effect considerable modifications to their environments. For this reason the history of human activities in the fynbos region over the last 100 000 and more years is of interest and archaeology is the only source of information.

In the archaeological record people appear as generalists not specialists and the prehistoric people living in the fynbos landscape had the same basic behavioural norms and adaptations as peoples living elsewhere in southern Africa. In this sense they were not unique, although living in fynbos habitats and the use of a particular mix of local natural resources of this diverse environment contributed to small scale differences both within the region and between this and adjacent regions. The relatively large number of archaeological sites in the fynbos biome partly reflects the fact that this is one of the better studied areas archaeologically, but the frequency of sites (recognizable by concentrations of discarded artefacts, disused features and abandoned facilities) also reflects the fact that it was a generally favourable area for habitation in prehistory. There is no comprehensive survey of the total number of archaeological occurrences from all time ranges but these would number in the order of thousands, including open air surface and buried sites as well as a large number of rock shelters distributed between the coastal forelands, intermontane valleys and mountains. Preservation of finds and their context is generally good at the more recent Holocene sites but tends to be poorer at older Pleistocene ones because of the greater time lapse in which the normal processes of disturbance and decay of principally organic residues have been active. For this reason more detail can be learnt of the Holocene settlement but progress has also been made in the study of the earlier time ranges. These archaeological sites are a non-renewable cultural resource as much in need of scientific study and conservation as other attributes of the fynbos biome.

THE INITIAL SETTLEMENT

The Ethiopian Region contains the oldest hominid fossils and the oldest stone artefacts which are trace fossils of human presence (Behrensmeyer 1982). The initial dispersal of Homo in the savanna biomes of eastern and southern Africa did not, as far as is known, include the southernmost part of the continent. However, with the dispersal of Homo erectus beyond the confines of the tropics in the Middle Pleistocene, human populations became established in the fynbos region. Markers for this presence are characteristic Acheulian artefacts that include standardized bifacial tools like handaxes and cleavers in association with flakes, cores and other products of stone tool knapping.

It was the prolific finds of such artefacts in the plough zone of vineyards and in colluvium at Bosman's River crossing in Stellenbosch by Peringuey towards the close of the last century that led to the fuller appreciation of the antiquity of people in South Africa because the artefacts were typologically similar to the then oldest known artefacts from Europe. This was commemorated in the label 'Stellenbosch Culture', now superceded by the term 'Acheulian' that is used to denote the dominant assemblages of

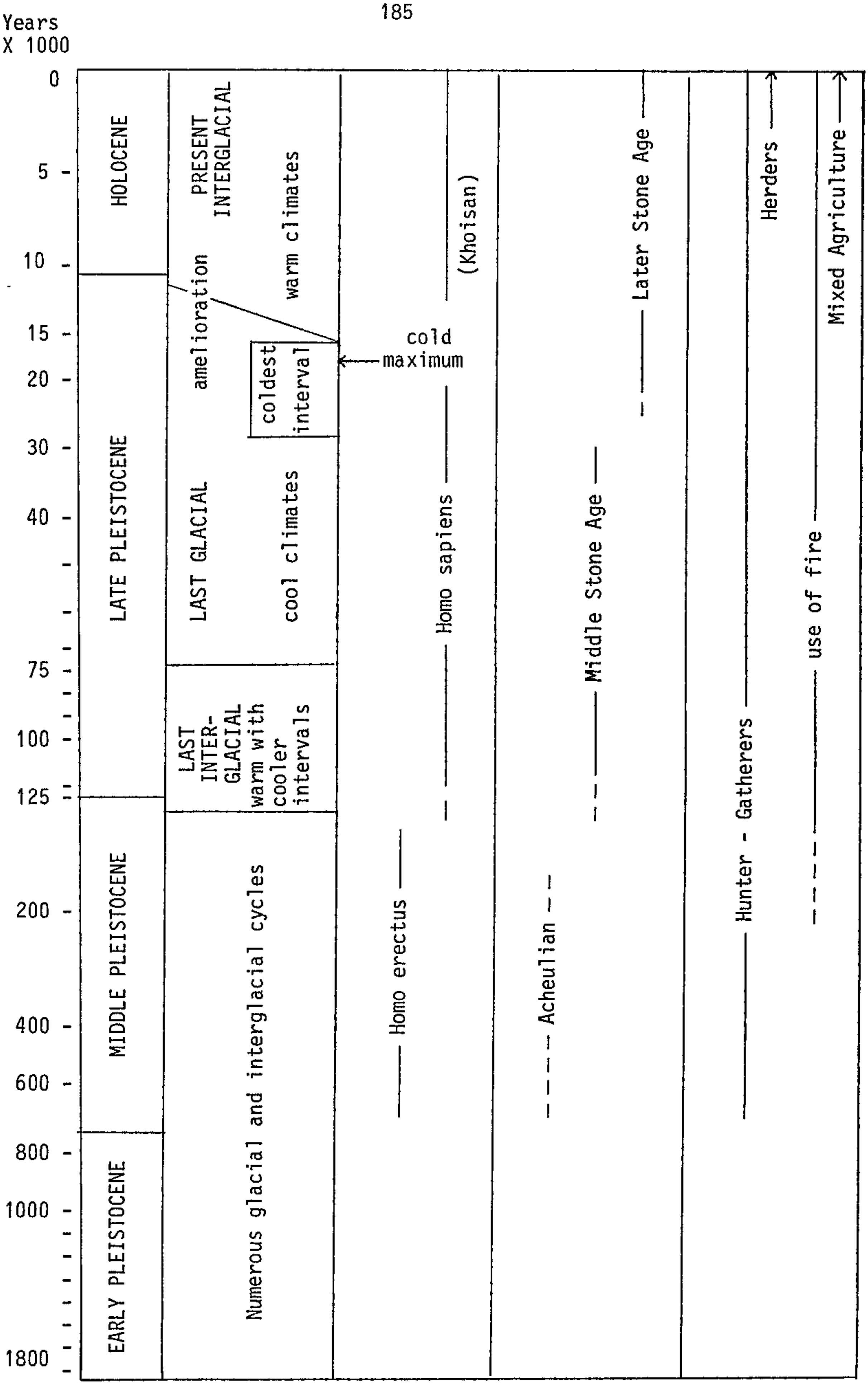

Fig. 1. Chronology of the peopling of the fynbos region.

artefacts that Goodwin & Van Riet Lowe (1929) group in the Earlier Stone Age of their tripartite technological-stage scheme. These pioneer researchers had no means of estimating the age of their Earlier Stone Age occurrences at Stellenbosch or elsewhere in the country and dating is still problematical. Comparable Acheulian industries are found widely in the whole African continent and available chronometric and relative dates suggest a time range between 1,5 Myr and 200 000 years before the present (B.P.) for such occurrences. This represents a long period of apparent technological stasis with only weakly developed stylistic variation in toolmaking apparent between sites distributed in space and time to provide some typological guide to chronological ordering (Deacon 1975).

Acheulian occurrences are widespread on the coastal platform and intermontane valleys in the fynbos region. The majority are open air sites at which only the durable stone artefacts are preserved and through the incorporation of the artefacts in colluvial deposits the original context has been somewhat disturbed. This reduces the inferences that can be made on the activities of the Acheulian peoples but nonetheless the artefact finds mark the overall settlement pattern. There is the strong indication in the location of sites in valley bottoms, around springs or seepages and near vleis of the preferred settlement locations being close to watering points. An example is the excavated site of Amanzi springs near Port Elizabeth on the eastern margin of the region where occupation was directly adjacent to the spring eyes (Deacon 1970a). Only one cave in the region, Montagu Cave, has yielded evidence of Acheulian occupation (Keller 1973) and as caves in quartzite are long-lived features, it can be concluded that they were not preferred locations for habitation.

A site on the farm Elandsfontein near Hopefield in the south-western Cape lowlands has yielded a skull cap of an archaic form of Homo in apparent association with a late Acheulian industry and a fauna including a number of extinct mammal taxa (Drennan 1954; Singer 1955). Occupying some 300 ha, stone artefacts and bone material, the results of past activities of people, carnivores and natural mortality, have been incorporated in the top of an extensive sand mantle through the mobility of surface dunes. The water table has acted as the base level for deflation and the main Middle Pleistocene fossil fauna and Acheulian artefact horizon is a palimpsest of material accumulated at or lowered onto the level of the water table (Deacon 1975). In addition, sub-fossil fauna, some in circular concentrations (Inskeep & Hendey 1966) and linear burrows (G. Avery, pers. comm.) in sands overlying the main fossil horizon, leaf-shaped Middle Stone Age points and other post-Acheulian artefacts, pottery which would date to the last 2 000 years, and even Dutch clay pipes, have been found in the area. Modern deflation can scour down to the watertable forming inter-dune pools and at various times in the past such surface waters in the otherwise freely draining sandveld have provided a focus for both man and animals.

Typologically, some artefacts could relate to the Middle Acheulian while the bulk may be Late Acheulian in age (Singer & Crawford 1957; own observations). An interesting occurrence of a localized cluster of a biface-rich artefact assemblage was excavated from a cutting in the area (Singer & Wymer 1968). These very standardized bifaces are typical of the Late Acheulian (Deacon 1975) and may be of the order of several thousand years old rather than previous estimates where a dating of 50 000 years was assumed. The fauna, which has been incorporated into the main fossil horizon in various cycles of deflation, suggests a broadly Middle Pleistocene age (Hendey 1969; Klein 1973, this volume) for the main fossil horizon. This is some indication of the range of the large mammals which occurred on the coastal lowlands in the Middle Pleistocene and can be assumed to have been among the quarry of human hunters and scavengers. The fauna in including giraffids, suids, elephantids and a variety of herbivores and carnivores, is more diverse than would be expected in an area of coastal fynbos shrubland, the present vegetation of the site surrounds. This apparent anomaly can be explained by the acid sand substrates on which the fynbos vegetation grows being formed by pedogenesis subsequent to the accumulation of the elements found in the main fossil horizon. A brown sand, the B horizon of an acid podzol, caps the fossil occurrence. The implication is that more base-rich substrates supporting a vegetation with a higher carrying capacity existed in the area in the Middle Pleistocene. People may have played a role in the site-forming processes at Elandsfontein as it is in later Acheulian times that Oakley (1964:184) has suggested people in southern Africa learnt the art of making fire. Impairment of the stabilizing vegetation by fire would have triggered phases of dune mobility.

LATE PLEISTOCENE SETTLEMENT

By the beginning of the Late Pleistocene, 125 000 years ago, the Acheulian technology had been replaced by a characteristic flake blade Middle Stone Age technology. Middle Stone Age sites are more widespread than those of Acheulian times and occupations are recorded at open stations as well as in caves, some of which are at relatively high altitudes. That these people were less tied to obvious water sources may simply mean that they had an effective means of carrying it. Long sequences of accumulated debris from the episodic use of caves are particularly informative on the lifeways of the Middle Stone Age artificers. Conscious burial however was not apparently part of their behavioural repertoire and thus human skeletal remains found in undoubted association with Middle Stone Age artefacts are rare anywhere in southern Africa and come from only one site in the fynbos biome. Singer & Wymer (1982) consider that the fragmentary human remains from the Klasies River Mouth caves on the Humansdorp coast include material from the oldest horizon of the site, dating to more than 100 000 years, that can be referred to Homo sapiens sapiens. This material would be among the earliest remains of physically modern people from any part of the world.

Many Middle Stone Age occurrences date to beyond the resolution of radiocarbon dating and are probably largely of last interglacial age dating between 75 000 and 130 000 years ago. This is supported by the ionium dates available for Klasies River and Herolds Bay (Vogel, pers. comm.) and Shackleton's (1982) correlation of the base of the Klasies River sequence with stage 5e in the deep sea oxygen isotope record. An upper temporal limit is provided by the Boomplaas Cave sequence in the Cango Valley (Deacon 1979) where the most recent Middle Stone Age occupation is dated to 32 000 years ago. This suggests the Middle Stone Age persisted until the beginning of the coldest interval of the late Pleistocene.

The use of prepared cores for the production of standardized flakes, really flake blades and points, and the use of fine scalar flaking, backing and denticulation in retouching pieces as the hallmarks of Middle Stone Age technology was recognized by Goodwin and Van Riet Lowe (1929) in their original definition of this term. However, perhaps the most consistent attribute of this technological stage evident in both the Klasies River (Singer & Wymer 1982) and Boomplaas sequences, which together span much of this time range, is the production of short sections or segments, broken from parallel-sided flake blades. Although it is suggested that these and other design types (Mason 1962) were hafted, no complete hafts have survived and hafting is inferred from the care taken in standardization of the size and shape of pieces. There is an apparent absence of artefacts in bone from Middle Stone Age contexts, but it may be assumed that wood was an important raw material. The durable stone artefacts that are preserved at Middle Stone Age sites give a partial view of the technological competence of these people. Much of the lithic raw material used in the making of the stone artefacts is of a type that does not lend itself to use wear studies but, on morphological grounds, the armatures for relatively heavy spears, cutting, flensing and possibly wood working tools are indicated. In addition, the site locations suggest carrying devices for water and probably gathered foods as well. A consistent cultural feature at all Middle Stone Age occupations is the presence of ochre, but personal ornaments like beads are absent.

The subsistence ecology of the Middle Stone Age foragers is known from the study of better preserved cave deposits. Carbonized and humified horizons indicate that plant materials were gathered and returned to the living sites although preservation is not good enough for specific identifications in most instances. The remains of a variety of mammals, primarily bovids (Klein 1975, 1979), are found at Middle Stone Age sites and there is evidence for shellfish collecting at three sites along the coast, two of which are chronometrically dated to more than 80 000 years (Voigt 1973; Volman 1978; Brink & Deacon 1982). Klein (1979) has argued that the Middle Stone Age populations were less efficient in exploiting the available animal food resources than were succeeding Later Stone Age peoples, but whether this can be ascribed to poorer technology, lower population densities or to a less developed learning ability, or to all these factors, is not clear. However, the collapse of Middle Stone Age lifeways took place with the onset of the coldest period of the late Pleistocene beginning after 30 000 years ago and it would seem they were not able to cope effectively with what may have been a relatively abrupt lowering of diversity and productivity of their habitats.

Although in their low level of exploitation of plant and animal resources the Middle Stone Age people may not have been significant agents of ecological change, a consistent feature of all Middle Stone Age sites with reasonable preservation is the occurrence of domestic hearths. Such hearths which I have excavated in the Boomplaas sequence are normally shallow artificial depressions of the order of 400 mm in diameter, filled with ash and charcoal and commonly marked by a hearth stone as in the Later Stone Age. The numbers of hearths at these occupation sites is evidence of the ability to make fire at will. Control of fire may well have a longer history and, as noted, may have been widely practised by later Acheulian times and there is even the claim, admittedly not incontrovertible, that fire was used on an occupation floor at Chesowanja, Kenya, at 1,42 Myr (Gowlett et al. 1981). The use of fire in the systematic management of vegetation is well attested as a universal practice amongst hunter-gatherers in the ethnographic present (Mellars 1976) and in the context of Aboriginal Australia, Jones (1969) has referred to it as 'fire stick farming'. In activities like honey hunting, the improvement of game pastures and game driving and the 'farming' of geophytes, fire may have been as important in Middle Stone Age times as it was during the Later Stone Age (Deacon 1976). Even low density mobile populations with natural pyromaniacal tendencies would have caused a considerable increment in the number of fires over and above those expected under the natural fire regime. Two points are worth stressing here: firstly, 100 000 years is the minimum period that the vegetation of the biome has been subjected to some form of fire management and, secondly, the natural fire regime in the biome would have been somewhat different under glacial and interglacial conditions as a result of climatically induced vegetation changes.

The scale of human impact on the environment is affected by the population density. There is no direct means of making a census of extinct populations but some generalizations can be made from the archaeological record. Stone artefacts are relatively permanent markers of the location of people at specific times. Although the artefacts were made by individuals, the individuals themselves were part of a larger community of a size able to maintain itself. It would seem, on typological grounds, that the greater number of Middle Stone Age artefact assemblages date to the last interglacial and there is a low archaeological visibility of populations during much of the last glacial, between some 75 000 and 16 000 years ago. This appears to be supported by significant stratigraphic discontinuities that separate Middle Stone Age from Later Stone Age horizons in the majority of the excavated sequences and such discontinuities span most or all of this time interval. An example of a typical cave sequence in quartzite country rock would be Kangkara Cave (Deacon & Brooker 1976) in the Langkloof where the Middle Stone Age artefacts occur in a high density lag deposit that is heavily stained by iron humates and is disconformably overlain by end-Pleistocene and Holocene Later Stone Age deposits in which hearth features, stone and bone materials are preserved. The differential preservation in these deposits is a product of time and the action of acid ground waters. One of the few caves in limestone country rock in the region, Boomplaas Cave, gives a very much more expanded and continuous sequence through the last glacial and shows there was episodic human occupation during the period. Thus a nucleus of a Middle Stone Age population was maintained in the fynbos region over the period contemporary with the last glacial but densities can be suggested to have been low relative to the preceding and succeeding interglacials. Lower sea levels and an extended coastal plain bordering the Agulhas Bank may have provided an important refugium during the glacial. This pattern of demographic change is not unique to the fynbos area and seems to be repeated in other areas of southern Africa for which data are available. The implication however is that it was during the interglacials rather than the last glacial that people would have been more numerous and wide ranging and their activities like fire making would have been most significant.

END PLEISTOCENE AND HOLOCENE SETTLEMENT

Prior to 21 000 years ago, people with a Later Stone Age technology were occupying the fynbos region. The technological transition between the Middle and Later Stone Age stages needs to be studied in a wider geographical framework than the fynbos area but it represents a large scale change that may correlate with the appearance of new forms of social organizations and behaviour and even major genetic changes in the populations. Environmental shifts and resultant changes in productivity that can be suggested for the beginning of the coldest part of the late Pleistocene may have promoted the kind of population fragmentation and genetic isolation that led to the evolution of the Khoisan genotype from a generalized ancestral negroid population in southern Africa (Tobias 1978). Although the sample of well provenanced skeletal material from the fynbos region is limited and dates only to the Holocene (Rightmire 1977; Hausman 1982), it supports the association of the Later Stone Age with Hottentot and Bushman-like, i.e.

Khoisan, individuals.

It has long been recognized (Goodwin & Van Riet Lowe 1929) that there are fundamental differences between the Middle Stone Age and Later Stone Age technologies. The latter includes the miniaturization of flake blanks, the increase in design types of hafted stone tool bits and the introduction of formal bone tools and decorative objects. The better preserved Holocene sites yield artefacts in leather, wood, plant fibres, bone and shell in addition to stone, and show the use of the bow in hunting, net and skin bags in gathering, and fire sticks. Tortoiseshell bowls, engraved ostrich eggshell containers and shell ornaments, like beads and pendants, are preserved also in later Pleistocene contexts (Deacon 1983). These are objects that were used in a social context and reflect not only function but also style, symbolism and ritual with the latter perhaps most evident in the rock art (Lewis-Williams 1983).

The initial Later Stone Age settlement was at a time when charcoal and microfaunal evidence (Deacon et al., this volume; Avery 1982) from the Cango Valley indicates relatively severe environmental conditions and isotopic measurements of palaeotemperatures on speleothems from the Cango Valley (Vogel 1983) show a mean annual temperature depression of 5 degrees C. Few archaeological occupation sites date to this period but the numbers of dated sites increase very significantly after it ended 16 000 years ago. It would be too mechanistic to hold that the increase in sites after 16 000 years is simply a product of sea levels rising from a low of -120 m at the cold maximum (Dingle & Rogers 1972; Vogel & Visser 1981) to near present levels at the beginning of the Holocene and an important reason would have been that people became more numerous as productivity rose with the amelioration of climates.

Some indication of how the initial Later Stone Age people coped with living in these later Pleistocene environments comes from the foodwaste associated with traces of occupation. The most relevant observations are from the sites of Nelson Bay Cave on Robberg Peninsula and Boomplaas Cave. At these sites in different situations, one on the coastal platform and the other in an intermontane valley, the principal quarry of human hunters were herd animals, alcelaphines and equids and also eland (Klein 1980, this volume). In the Boomplaas sequence, the relevant horizons dating between 21 000 and 12 000 years are either rich in carbonized and humified organic remains or are massive leached ash lenses. The former by analogy to better preserved Holocene sites are likely to represent the inedible residues of plant foods. The ash accumulations by contrast may evidence a different activity such as meat drying and indeed the site may have functioned at times as a base camp when plant gathering was of some importance and at other times as a meat processing camp. The animal and plant remains carry different implications for the foraging behaviour of these people. The hunting of herd animals would have required the hunters to be mobile and wide ranging because of the need to spend time in searching for and tracking down the prey. Plant gathering by contrast is a more sedentary pursuit. The division of the labours of hunting and gathering between the sexes as is found in the ethnographic present would have been the obvious solution. It is not possible to gauge the relative importance of hunting to gathering in this time range but animals like wildebeest or zebra are large parcels of high quality food and would have been ranked higher as a resource than plant foods.

The most characteristic artefacts of the Robberg Industry associated with these later Pleistocene occupations are microbladelets of the order of 10-15 mm in length and about 2 mm in width. They may have been functionally related to hunting, underscoring the importance of this activity. Too small to be hand held, these standardized pieces were inserts in composite tools. A localized cluster of some 60 microbladelets from one level at Boomplaas suggests they were carried around in a container, like a skin bag, and used in quantity. A plausible hypothesis is that they served as the armatures for projectiles, spears rather than arrows, used in the hunting of relatively large animals. The raw materials used for making the microbladelets show strong patterning through time in the Boomplaas sequence and it appears that fewer exotic raw materials are associated with the more organic-rich horizons when it can also be suggested that more local food resources were being used. Such observations are sufficient to indicate something of the complexity of the behaviour and the variety of the responses of these Pleistocene Later Stone Age peoples to the potentials of their habitats. In part their success as the hunters of large herbivores may have been based on the awareness of the prominence of grasses in the post-fire succession in some ecosystems and the tendency of grazers like wildebeest to remain longer at recently burnt areas (Von Richter 1971). The potential and motivation existed to practise herd control by fire.

The pattern of hunting larger herbivores persisted until some 12 000 years ago although the amelioration of climates had been initiated some 3 000 years earlier and significant vegetation changes are documented at least for the Cango Valley during those 3 000 years (Deacon 1983). One contributory factor may have been that the coastline only approached its modern position about 12 000 years ago (Dingle & Rogers 1972) and the extended coastal plain had continued to provide a suitable habitat to maintain populations of grazers. By 12 000 years ago, however, temperatures in the southern hemisphere, on the evidence of ice cores from Antarctica (Lorius et al. 1979), had attained modern levels and since then have oscillated around the present day mean. The compound effects of rising sea levels, ameliorating climates and the synthesis of more modern shrubland and woodland vegetation communities led to the virtual disappearance of the niche for large herds of grazers and the creation of more heterogeneous or patchy habitats. In such changed circumstances new adaptations among hunter-gatherer groups might be expected and there is evidence for them. It would be an oversimplification to see these new adaptations as a direct response to or solely determined by local environmental changes. There are similar penecontemporaneous changes in the technology and subsistence ecology of people living in other biomes in southern Africa and this suggests a comparable scale of change in all these environments at the close of the Pleistocene and a gross uniformity in the responses of Later Stone Age peoples linked in a wider social and demographic network in southern Africa.

In the fynbos biome the overall foraging strategy that emerged at the end of the Pleistocene and in the Holocene was to increase diet breadth and to complement the gathering of clumped underground plant food resources like geophytes with the hunting of solitary territorial small browsers and ground game. This can be seen as a trend towards becoming more patch-bound in increasingly heterogeneous habitats with the patches providing both a reliable if low quality supply of plant foods and a supplement of higher quality more protein-rich food in the animals hunted, trapped or collected. Natural fields made up of clones of geophytes would have defined the core of patches, and food getting became a matter of knowing the location of the patches, when they could be exploited and then regulating movement between them in the seasonal round, as is the practice of the modern San hunter-gatherer groups in the Kalahari (Lee 1979). In the fynbos region it was possible to offset seasonal stress in plant food gathering by making use of coastal resources like fish and shellfish which would have provided important mineral trace elements in an environment otherwise poor in minerals. The hunting of non-gregarious antelope meant investing time in setting and maintaining traps and snares rather than in searching for and tracking herds. There are good ethnographic accounts of the social organization of foragers in patchy habitats (Lee 1972; Silberbauer 1972; Yellen & Harpending 1972) and the essential elements are flexible group size, small home ranges and rights of access to particular locations of resources. The potential existed within such a system or organization for the maintenance of higher population densities than in the Pleistocene Later Stone Age.

It has been suggested that the shift from foraging in habitats of relatively low diversity to foraging in more patchy heterogeneous habitats at the close of the Pleistocene was accomplished in two stages marked in the archaeological record by punctuated or abrupt changes in technology represented by the Albany and Wilton industries in the southern Cape (Deacon 1976), although more or less gradual technological change has also been argued (Parkington 1980). Changes in technology and subsistence are the archaeologically discernible results, the output of a complex interplay of social, demographic and environmental factors involved in the shift in the adaptations of Later Stone Age people between the Pleistocene and the Holocene.

Studies of the archaeological evidence of the subsistence ecology of Holocene people in the fynbos region were initiated in the 1930s by Hewitt (1931) and Goodwin (1938) but only received renewed emphasis from the early 1960s. The dry upper deposits of some rock shelters preserve macroscopic plant materials, several thousand years old, in a physical condition comparable to herbarium specimens. Samples have been analysed from sites like Scott's Cave (Wells 1965) and Melkhoutboom Cave (Deacon 1976) in the eastern Cape and De Hangen in the Cedarberg (Parkington & Poggenpoel 1971) and such deposits are a source of information on recent vegetation history. The best record is provided by Melkhoutboom Cave which shows the particular importance of a range of geophytes, notably Watsonia spp. and Hypoxis spp. in this example. A vegetation survey of the Cango Valley (Moffett & Deacon 1977) carried out in conjunction with the excavation of Boomplaas Cave showed that few plant food resources were locally available. The function of this site in the Holocene was not tied to plant food getting yet the remains of the only two plant food taxa found in the deposit are the same as those which are dominant at Melkhoutboom several hundred kilometres to the east. Some plant foods were widely exploited but given the high gamma diversity in the fynbos vegetation other plant foods selected reflect what was locally available and abundant.

From a study of the fauna associated with the Wilton Industry at the Wilton name site (Brain 1969) and Andrieskraal (Hendey & Singer 1965) it is evident that small bovids were a primary prey of Holocene hunters in the fynbos region and this is consistent with surveys of the modern fauna (Bigalke & Bateman 1962; Deacon 1972). Subsequent analyses from a wider range of sites (Klein 1980) have supported this conclusion. However, between the eastern margins of the fynbos area and the south-western Cape, a major protein supplement to plant foods was obtained from ground game like dassies and tortoises which became increasingly important relative to small bovids along this east-west gradient in the fynbos landscape.

Historical accounts in Van Riebeeck's journal (Thom 1952, 1954, 1958) refer to 'strandlopers' (beachcombers) living off coastal resources. The presence of such people is attested in the archaeological record by heaped accumulations of foodwaste comprising the shells of shellfish, the carapace of crustaceans and the bones of fish and marine mammals found all along the coast in association with artefactual remains, dating to the Holocene and the close of the Pleistocene. Shellfish remains have also been found in association with Middle Stone Age artefacts dating to the last interglacial when sea levels were relatively high, comparable to modern conditions. Any middens dating to the intervening period, contemporary with the last glacial (when sea levels would have been lower than at present), would now be located offshore and are thus inaccessible.

It would seem that the coastal middens which occur at rock shelter sites and more frequently at open stations strongly reflect resources available in the immediate vicinity (Deacon 1970b; Avery 1974; Parkington 1976; Robertshaw 1977, 1979). Rocky promontories with a higher diversity of species correlate with clusters of sites (Avery 1975) and at least in later Holocene times there is evidence for the near optimal use of such resources (Grindley 1967; Parkington 1976; Robertshaw 1977). The virtual absence of plant foods at coastal sites where conditions for their preservation are not a factor suggests that the gathering of shellfish and fishing served as an alternative resource to relieve stress in food gathering when plant foods were less available (Deacon 1972). The scheduling of movements to coincide with the seasonal availability of plant and marine resources in the Holocene is well documented in several studies (Parkington 1972, 1977; Avery 1975, 1976).

The Holocene gatherers were aware of the high underground productivity of fynbos ecosystems and the importance of geophytes in the plant food residues at archaeological sites implies that 'fire stick' farming was practised. Geophytes would be classed as a slowly renewing plant food resource, unlike cereal grasses, and success in using geophytes on any scale as a food resource would depend on taking advantage of the response such plants show to fire. A study of a natural field of Watsonia pyramidata at Jonkershoek, near Stellenbosch, illustrates the potential for fire management. An estimated one million plants of this species, commonly referred to as the 'bitter corm', are growing in a restricted area of 0,2 sq km. The corms have a mean mass of some 50 g and analysis of their nutritional value shows extremely high carbohydrate and low protein. An estimated 4-5% of the plants in the stand produce inflorescences in a normal year, but after fire this is an order of magnitude higher. Two buds are formed in each plant bearing an inflorescence and the buds rather than the seed produced are the important means of reproduction. It would seem that rather than playing with fire, Holocene gatherers in farming stands of Watsonia spp. with fire were involved in a more serious game of double or quits: quits if they harvested the plant, and doubles if they induced the plant to produce an inflorescence.

The strong reliance on gathered plant food resources in the Holocene implies that gatherers had a considerable knowledge of economic botany. A question arises as to why these people did not experiment with the domestication of some of the taxa that served as staples. The answer would seem to be that in an environment poor in nutrients with few annuals of economic importance, experiments in domestication were uneconomic. The best results in the maintenance of productivity of geophytes could be achieved by judiciously controlled veld burning. Similarly the absence of evidence for animal domestication can be explained because the main prey were species with territorial nocturnal and solitary habit and were not good candidates for domestication (Deacon 1972). The hunting and gathering way of life continued at the Cape into the late Holocene even after the herding of exotic domestic animals was introduced, but with the introduction of exotic cultigens after the period of European contact, much of the lore of food plants was lost

(Smith 1966). What survives into the present is primarily some knowledge of medicinal properties of some indigenous plants.

SETTLEMENT BY PASTORALISTS AND AGRICULTURALISTS

The discovery of the remains of sheep dated to between 1 500 and 2 000 years ago in a coastal shell midden deposit, in a cave at Die Kelders about 150 km east of Cape Town, was one of the more remarkable finds of the last few decades (Schweitzer & Scott 1973; Schweitzer 1974). This evidence for the herding of small stock at an early period has been since confirmed in excavations at a number of other sites but none have yielded undoubted remains of cattle. The absence of cattle may be more apparent than real, possibly being a reflection of the limited and fragmentary faunal samples available for study. Indirect evidence for the presence of cattle is provided by pottery. The oldest potsherds found at Die Kelders (Schweitzer 1979) suggest globular pot forms, but bag-shaped pots with lugs for suspension occur in deposits post-dating 450 A.D. One may infer that this style of pottery, typical of Cape coastal pottery (Rudner 1979), came into vogue when oxen were used for transport. At Die Kelders and elsewhere the faunal remains of domestic stock have come from archaeological horizons that do not differ in their other contents from hunter-gatherer horizons. This suggests a continuity of lifeways with herding as an added component (Deacon 1983). Indeed no large-scale immigration of physically different people accompanied the introduction of herding (Hausman 1982).

The origins of stock keeping at the Cape is an intriguing problem beyond the scope of this paper (for reviews, see Deacon et al. 1978; Robertshaw 1978). It is evident however that herder settlements were established over parts of the fynbos region in the early part of the last millennium and this pattern of settlement continued into historic times. Archaeological traces of herders are difficult to find because of the ephemeral nature of their encampments, poorer preservation at open stations and because their houses and belongings were designed to be transportable. Ethnoarchaeological studies of Khoi settlements in Namaqualand show that few traces of the basic unit of settlement which comprises a dwelling, a cooking shelter, ash heap and stock pen or kraal, survive more than a few years after abandonment (Webley 1982). At only one site in the fynbos region is evidence of a stock kraal preserved and this is a series of calcined dung layers with pottery and the remains of sheep in the top of the Boomplaas sequence dated to between 1 700 and 1 500 years ago. Abandoned Khoi stock kraals would have dotted the fynbos landscape in prehistoric times, and like 'heuweltjies' they would have been local points of nutrient enrichment. Domestic stock again would have been in competition with indigenous herbivores.

Historical sources from the time of European contact, both before

(Raven-Hart 1967) and after the establishment of permanent European settlements (for review see Elphick 1977) provide some information on the dispersal and density of Khoi and the numbers of stock they owned. Khoi 'tribes' (Maingard 1931) were located primarily along the coastal forelands and it is here that their settlement would have had the greatest impact. San hunter-gatherers on the other hand were more confined to the inland mountain zone but interacted with the Khoi at various levels, as antagonists and as clients. Van Riebeeck's journal gives accounts of the San or Soaquas, people living in the mountains of Africa (Cape Fold Mountains) who had no cattle and were mostly robbers (Thom 1958:281). The Khoi 'tribes' such as the Chochoquas living between the Berg River and Table Bay numbered an estimated 17-18 000 people and the Chainouquas located in the Cape Agulhas area were even more numerous (Thom 1958:253). The journal gives a glimpse of the impact Khoi settlement had on the environment. Large numbers of stock were concentrated in a limited area which was grazed bare in a matter of a few weeks and then the herds were moved on (Thom 1958:371). An example is an estimated 20 000 cattle as well as sheep which were driven into the Salt River area bordering Table Bay in the first half of December 1652 and were driven off again by the latter half of the month (Thom 1952:118, 1954:371). The arrival of these herds was apparent on the evening of the 2nd December when fires could be seen burning all over the country (Thom 1952:106). The implications are that at least in the south-western Cape, Khoi herding practices promoted a system of non-selective grazing at the cost of having to maintain high mobility.

The reluctance of the Khoi to trade cattle and sheep because the milk they provided was a staple food, is a common lament in the journal. Because of interest in potential trade, estimates were made of sizes of Khoi herds and herding groups. On the 23rd December 1652 after the main movement of Khoi away from Table Bay, it is recorded that two encampments of 8 and 9 huts respectively remained, housing a total of 70-80 pople who had 700 or 800 cattle and 1 500 sheep (Thom 1952:118), a ratio of 10 cattle per Khoi individual and double that ratio of sheep per individual. Another example is of a group which had lost cattle and sheep in clashes with other Khoi and San groups and were encamped in 30 huts on the Salt River in May 1655. This group possessed an estimated 600 cattle and a similar number of sheep (Thom 1952:314).

These observations show that substantial herds of cattle and sheep were maintained at the Cape at the time of contact. The archaeological evidence suggests that this had been the case for at least 1 000 years prior to contact. A rapid breakdown of Khoi social and economic systems followed after 1652, aided by the ravages of introduced endemic diseases, internecine conflicts and European expansion (De Kiewiet 1957). The Khoi had ceased to be a political force by 1689 (Walker 1959:70) and were progressively reduced to landless serfs. In the new order that emerged, however, elements of Khoi plant and animal lore, nomadism and veld management practices were integrated and greatly facilitated the rapidity of European expansion.

CONCLUDING REMARKS

Acocks (1953) provided a model of the vegetation of South Africa prior to European expansion that served to emphasize the dramatic changes that have taken place with the introduction of agriculture and permanent settlement. His model, based on the occurrence of relicts, telescopes the time depth of past vegetation changes due to causes like long term climatic oscillations and prehistoric human activities, although there is no question of the validity of his general thesis. The date of A.D. 1400? cited by Acocks should not be interpreted literally, as indeed the question mark implies. This model is a challenge to palaeoecologists to obtain more direct information on the evolution of fynbos and other ecosystems and the evolution of the dominant vegetation types associated with them. There is a long history of human settlement in the fynbos region and nearly an equally long record of the use of fire. The evidence of domestic hearths at archaeological sites is crucial because it shows the ability and the means to make fire at will. No great learning feat is involved in appreciating the value of fire as a tool for management and this would have been within the capabilities of Middle Stone Age peoples and certainly was within the capabilities of Later Stone Age people. The scale on which fire was used as an artefact is inferred from the kind of adaptations shown by prehistoric people and it is important to stress that the success of food-getting strategies in hunting and gathering would have depended on wise fire management. The inferences drawn are plausible by analogy to ethnographically known hunter-gatherers and are consistent with the archaeological data. Hunter-gatherers who survived in the region until the beginnings of written history had a considerable knowledge of fynbos ecology which unfortunately went unrecorded, and certainly they deserve better than to be remembered by the epithets of bandits and robbers accorded to them. One lesson that might be learnt from the past is that patch burning, which it can be suggested was practised by hunter-gatherers over millennia, is an effective programme for management of fynbos ecosystems. The burning of vegetation in larger blocks as a management technique does not have the same support in the prehistoric record.

The introduction of domestic stock in the last two thousand years can be singled out as another important aspect of human activities which would have had a marked impact on the ecology of the fynbos region. The same areas of the coastal forelands on which extensive areas of residual soils (Schloms _et al._, this volume) are found, and which are important agriculturally in the present, provided the focus for Khoi herders and their flocks. The Khoi with oxen as baggage animals, pots with lugs and collapsible mat houses were highly mobile. Historical sources suggest that in the south-western Cape region the stock was concentrated in large herds and was moved after a few weeks of heavily grazing an area. Although competition between groups for grazing and the need to provide protection for the herds against theft may have reinforced such a pattern in the more favourable grazing areas, this pattern of herding would also have been a sound ecological practice. The non-selective, heavy but intermittent grazing in small camps allows a higher carrying capacity and has less negative effects on the quality of the grazing (Acocks 1953). In areas of more broken terrain or drier areas with lower grazing potential such concentrations of stock would not have been possible and dispersal of herds amongst outlying stockposts would have been practised as is the case in Namaqualand today. Evaluation of the archaeological and historical evidence suggests near optimal use was made of the suitable habitats for herding in the fynbos region in later prehistoric time.

There is obviously considerable scope to extend the kind of archaeological and historical studies outlined here. Such studies are an essential part of palaeoecology and need to be integrated into programmes of research on the history of modern ecosystems. They offer a somewhat salutory perspective to the conservationist and planner. It was inconceivable for the Pleistocene hunter-gatherers to imagine their descendants would be living on the milk of exotic animals or for those Khoi herders to conceive of the urban developments that have taken place in areas where they grazed their stock. How does one plan for future changes in productivity due to long term trends in climatic change? The main result of human activities whether through the use of fire, grazing stock or practising agriculture has been to reduce diversity and to simplify the natural ecosystems (Harris 1969) thereby reducing their resilience. From the perspective of human ecology the conservation of the natural diversity of fynbos and related ecosystems at whatever cost is not an altruistic exercise but is a necessary investment for the continued wellbeing of people living here.

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REFERENCES

ACOCKS, J. P. H. 1953. Veld types of South Africa. *Memoir of the Botanical survey of South Africa*. 28.

AVERY, D. M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quaternary in the southern Cape Province, South Africa. *Annals of the South African Museum* 85:183-374.

AVERY, G. 1974. Open station shell midden sites and associated features from the Pearly Beach area, south-western Cape. *South African Archaeological Bulletin* 29:104-114.

AVERY, G. 1975. Discussion on the age and use of tidal fish-traps (visvywers). *South African Archaeological Bulletin* 30:105-113.

AVERY, G. 1976. A systematic investigation of open station shell midden sites along the south-western Cape coast. Unpublished M.A. thesis: University of Cape Town.

AXELSON, E. 1973. *Congo to Cape: early Portuguese explorers*. London: Faber and Faber.

BEHRENSMEYER, A. K. 1982. The geological context of human evolution. *Annual Review of Earth and Planetary Sciences* 10:39-60.

BIGALKE, R. C. & BATEMAN, J. A. 1962. On the status and distribution of ungulate mammals in the Cape Province, South Africa. *Annals of the Cape Provincial Museums* 2:85-100.

BLAIR, F. W. 1970. Protecting the human environment. *Optima* March 1970:9-15.

BRAIN, C. K. 1969. Faunal remains from the Wilton Large Rock Shelter, eastern Cape. *In* Deacon, J. Re-excavation and description of the Wilton type-site, Albany District, eastern Cape. Unpublished M.A. thesis: University of Cape Town.

BRINK, J. S. & DEACON, H. J. 1982. A study of a last interglacial shell midden and bone accumulation at Herolds Bay, Cape Province, South Africa. *Palaeoecology of Africa* 15:31-39.

DEACON, H. J. 1970a. The Acheulian occupation at Amanzi Springs, Uitenhage District, Cape Province. *Annals of the Cape Provincial Museums* 8:89-189.

DEACON, H. J. 1970b. Two shell midden occurrences in the Tsitsikama National Park, Cape Province: a contribution to the study of the ecology of the Strandlopers. *Koedoe* 13:37-49.

DEACON, H. J. 1972. A review of the post-Pleistocene in South Africa. *South African Archaeological Society Goodwin Series* 1:26-45.

DEACON, H. J. 1975. Demography, subsistence and culture during the Acheulian in southern Africa. *In* Butzer, K. W. & Isaac, G. Ll. *eds* *After the australopithecines*. The Hague: Mouton.

DEACON, H. J. 1976. *Where hunters gathered: a study of Holocene Stone Age people in the eastern Cape*. Claremont: South African Archaeological Society Monograph Series 1.

DEACON, H. J. 1979. Excavations at Boomplaas Cave - a sequence through the Upper Pleistocene and Holocene in South Africa. *World Archaeology* 10:241-259.

DEACON, H. J. & BROOKER, M. 1976. The Holocene and Upper Pleistocene sequence in the southern Cape. *Annals of the South African Museum* 71:203-214.

DEACON, H. J., DEACON, J., BROOKER, M. & WILSON, M. L. 1978. The evidence for herding at Boomplaas Cave in the southern Cape, South Africa. *South African Archaeological Bulletin* 33:39-65.

DEACON, J. 1983. Later Stone Age people and their descendants in southern Africa. *In* Klein, R. G. *ed.* *Southern African palaeoenvironments and prehistory*: in press. Rotterdam: Balkema.

DE KIEWIET, C. W. 1957. *A history of South Africa: social and economic*. London: Oxford University Press.

DINGLE, R. V. & ROGERS, J. 1972. Effects of sea-level changes on the Pleistocene palaeoecology of the Agulhas Bank. *Palaeoecology of Africa* 6:55-58.

DRENNAN, M. R. 1954. Saldanha man and his associations. *American Anthropologist* 56:879-884.

ELPHICK, R. 1977. *Kraal and Castle: Khoikhoi and the founding of white South Africa*. New Haven: Yale University Press.

GOODWIN, A. J. H. 1938. Archaeology of the Oakhurst shelter, George. *Transactions of the Royal Society of South Africa* 25:229-324.

GOODWIN, A. J. H. & VAN RIET LOWE, C. 1929. The Stone Age cultures of South Africa. *Annals of the South African Museum* 27:1-289.

GOWLETT, J. A. J., HARRIS, J. W. K., WALTON, D. & WOOD, B. A. 1981. Early archaeological sites, hominid remains and traces of fire from Chesowanja, Kenya. *Nature* 294:125-129.

GRINDLEY, J. R. 1967. The Cape rock lobster, *Jasus lalandii*, from the Bonteberg excavation. *South African Archaeological Bulletin* 22:94-102.

HARRIS, D. R. 1969. Agricultural systems, ecosystems and the origins of agriculture. *In* Ucko, P. J. & Dimbleby, G. W. *eds* *The domestication and exploitation of plants and animals*: 3-16. London: Duckworth.

HAUSMAN, A. J. 1982. The biocultural evolution of Khoisan populations of southern Africa. *American Journal of Physical Anthropology* 58:315-330.

HENDEY, Q. B. 1969. Quaternary vertebrate fossil sites in the south-western Cape Province. *South African Archaeological Bulletin* 24:96-105.

HENDEY, Q. B. & SINGER, R. 1965. The faunal assemblage from the Gamtoos Valley shelters. *South African Archaeological Bulletin* 20:206-213.

HEWITT, J. 1931. Artefacts from Melkhoutboom. *South African Journal of Science* 28:540-548.

INSKEEP, R. R. & HENDEY, Q. B. 1966. An interesting assemblage of bones from the Elandsfontein fossil site. *Actes du Ve Congrès Panafricaine de Préhistoire et de l'étude du Quaternaire*: 109-124. Tenerife.

JONES, R. 1969. Fire-stick farming. Australian Natural History 16:224-228.

KELLER, C. M. 1973. Montagu Cave in prehistory: a descriptive analysis. University of California Anthropological Records 28:1-98.

KLEIN, R. G. 1973. Geological antiquity of Rhodesian Man. Nature 244:311-312.

KLEIN, R. G. 1975. Middle Stone Age man-animal relationships in southern Africa: evidence from Die Kelders and Klasies River Mouth. Science 190:265-267.

KLEIN, R. G. 1979. Stone Age exploitation of animals in southern Africa. American Scientist 67:151-160.

KLEIN, R. G. 1980. Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in southern Africa. Annals of the South African Museum 81:223-283.

LEE, R. B. 1972. The !Kung Bushmen of Botswana. In Bicchieri, M. ed. Hunters and gatherers today: 327-368. New York: Holt, Rinehart & Winston.

LEE, R. B. 1979. The !Kung San: men, women and work in a foraging society. Cambridge: Cambridge University Press.

LEWIS-WILLIAMS, J. D. 1983. Introductory essay: Science and rock art. South African Archaeological Society Goodwin Series 4:3-13.

LORIUS, C., MERLIVAT, L., JOUZEL, J. & POURCHET, M. 1979. A 30 000-yr isotope climatic record from Antarctic ice. Nature 280:644-648.

MAINGARD, L. F. 1931. The lost tribes of the Cape. South African Journal of Science 28:487-504.

MASON, R. J. 1962. The prehistory of the Transvaal. Johannesburg: Witwatersrand University Press.

MELLARS, P. A. 1976. Fire ecology, animal populations and man: a study of some ecological relationships in prehistory. Proceedings of the Prehistoric Society 42:15-45.

MOFFETT, R. O. & DEACON, H. J. 1977. The flora and vegetation in the surrounds of Boomplaas Cave, Cango Valley. South African Archaeological Bulletin 32:127-145.

OAKLEY, K. P. 1964. Frameworks for dating fossil man. London: Weidenfeld & Nicholson.

PARKINGTON, J. E. 1972. Seasonal mobility in the Later Stone Age. African Studies 31:223-243.

PARKINGTON, J. E. 1976. Coastal settlement between the mouths of the Berg and Olifants rivers, Cape Province. South African Archaeological Bulletin 31:127-147.

PARKINGTON, J. E. 1977. Soaqua: hunter-fisher-gatherers of the Olifants River, western Cape. South African Archaeological Bulletin 32:150-157.

PARKINGTON, J. E. 1980. Time and place: some observations on spatial and temporal patterning in the Later Stone Age sequence in southern Africa. South African Archaeological Bulletin 35:73-83.

PARKINGTON, J. E. & POGGENPOEL, C. 1971. Excavations at De Hangen 1968. South African Archaeological Bulletin 26:3-36.

RAVEN-HART, R. 1967. Before Van Riebeeck. Cape Town: Struik.

RIGHTMIRE, G. P. 1977. Human skeletal remains from the southern Cape Province and their bearing on the Stone Age prehistory of South Africa. Quaternary Research 9:219-230.

ROBERTSHAW, P. T. 1977. Excavations at Paternoster, south-western Cape. South African Archaeological Bulletin 32:63-73.

ROBERTSHAW, P. T. 1978. The origin of pastoralism in the Cape. South African History Journal 10:117-133.

ROBERTSHAW, P. T. 1979. Excavations at Duiker Eiland, Vredenburg district, Cape Province. Annals of the Cape Provincial Museums (Human Sciences) 1:1-26.

RUDNER, J. 1979. The use of stone artefacts and pottery among the Khoisan peoples in historic and protohistoric times. South African Archaeological Bulletin 34:3-17.

SCHWEITZER, F. R. 1974. Archaeological evidence for sheep at the Cape. South African Archaeological Bulletin 29:75-82.

SCHWEITZER, F. R. 1979. Excavations at Die Kelders, Cape Province, South Africa: the Holocene deposits. Annals of the South African Museum 78:101-233.

SCHWEITZER, F. R. & SCOTT, K. J. 1973. Early occurrence of domestic sheep in sub-Saharan Africa. Nature 241:547.

SHACKLETON, N. J. 1982. Stratigraphy and chronology of the Klasies River Mouth deposits: oxygen isotope evidence. In Singer, R. & Wymer, J. eds The archaeology of the Klasies River Mouth Caves: 194-199. Chicago: Chicago University Press.

SILBERBAUER, G. 1972. The G/wi Bushmen. In Bicchieri, M. ed. Hunters and gatherers today: 271-325. New York: Holt, Rhinehart & Winston.

SINGER, R. 1955. Investigations at the Hopefield site. In Clark, J. Desmond ed. Proceedings of the 3rd Pan-African Congress on Prehistory, Livingstone 1955: 175-182. London: Chatto & Windus.

SINGER, R. & CRAWFORD, J. R. 1957. The significance of the archaeological discoveries at Hopefield, South Africa. Journal of the Royal Anthropological Institute 88:11-19.

SINGER, R. & WYMER, J. 1968. Archaeological investigations at the Saldanha skull site in South Africa. South African Archaeological Bulletin 25:63-74.

SINGER, R. & WYMER, J. 1982. The archaeology of the Klasies River Mouth Caves. Chicago: Chicago University Press.

SMITH, C. A. 1966. Common names of South African plants. Memoir of the Botanical Survey of South Africa 35:1-642.

THOM, H. B. ed. 1952. Journal of Jan van Riebeeck. Vol. 1. Cape Town: Balkema.

THOM, H. B. ed. 1954. Journal of Jan van Riebeeck. Vol. 2. Cape Town: Balkema.

THOM, H. B. ed. 1958. Journal of Jan van Riebeeck. Vol. 3. Cape Town: Balkema.

TOBIAS, P. V. 1978. The San: an evolutionary perspective. In Tobias, P. V. ed. The Bushman: San hunters and herders of southern Africa: 16-32. Cape Town: Human & Roussouw.

VOGEL, J. C. 1983. Isotopic evidence for past climates and vegetation of South Africa. Bothalia, in press.

VOGEL, J. C. & VISSER, E. 1981. Pretoria radiocarbon dates II. Radiocarbon 23:43-80.

VOIGT, E. A. 1973. Stone Age molluscan utilization at Klasies River Mouth Caves. South African Journal of Science 69:306-309.

VOLMAN, T. P. 1978. Early archaeological evidence for shellfish collecting. Science 201:911-913.

VON RICHTER, W. 1971. Observations on the biology and ecology of the black wildebeest (Connochaetes gnou). Journal of the Southern African Wildlife Association 1:3-16.

WALKER, E. A. 1959. A history of southern Africa. London: Longman, Green.

WEBLEY, L. E. 1982. Settlement studies among descendants of Nama herders: an ethno-archaeological approach. Khoisis 3:1-18.

WELLS, M. J. 1965. An analysis of plant remains from Scott's Cave in the Gamtoos Valley. South African Archaeological Bulletin 20:79-84.

YELLEN, J. E. & HARPENDING, H. 1972. Hunter-gatherer populations and archaeological inference. World Archaeology 4:244-253.

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SOUTH-WESTERN CAPE

KEY TO SOIL MAP

UNIT NAME	SUBUNIT SYMBOL	DISTRIBUTION	ELEVATION	TERRAIN TYPE	PARENT MATERIAL(S)	WEATHERING	SOILS
Calcareous coastal sands	A1	Coastal fringe from False Bay to Elands Bay; local isolated inland patches	0-45m+	Mobile dunes	Shelly aeolian sands	Unweathered	Grey calcareous sands: Fw20,21.
	A2	Coastal fringe and embayments extending inland to the north	0-200m	Low dunes	Calcareous aeolian sands	Low degree and poorly leached	Pale neutral to calcareous sands: Fw20, 21; Ms22.
Acid sands	B1	Inland north and east of calcareous sands	70-110m	Weakly undulating flats and extending up footslopes	Quartz rich cover sands of aeolian origin	Highly leached	Yellow and grey acid sands and podzols: Lt11; Ct11; Fw11; Cv21.
	B2	Inland valleys: Upper Berg River, Piketberg	100m+ variable	Intermontane valleys	Quartz rich sands derived from quartzose substrates by fluvial/colluvial redistribution	Highly leached	Grey acid sands and podzols: Lt11,12; Fw11,12; Ct11,12.
Residual soils	C1	Moorreesburg, Malmesbury, middle Berg River drainage system, Swartland agronomic region at lower elevations	80-140m	Undulating landscape with dissected plain remnants	Thin, loamy to gravelly creep layers on residual shales and phyllites	Moderate to poorly weathered	Poorly developed soils on convex slopes and duplex soils on plain remnants: Ms10; Gs13; Sw31; Ss23.
	C2	Koeberg, Stellenbosch, Agter Paarl, Malmesbury, Koringberg and Porterville. Swartland agronomic region at higher elevations	150-200m	Undulating to rolling	Thin, loamy creep layers on residual preweathered shales and phyllites	Highly preweathered	Poorly developed soils on convex slopes and duplex loams on concave midfootslopes: Ms10; Gs13; Sw31,11; Ss23.
Duplex soils	D1L	Velddrift, Somerset West	30m-	Marine cut Plio-Pleistocene surface	Thin aeolian-colluvial sandy cover on marine and residual clays	Low	Duplex soils with fine sand or loamy topsoils: Es33,34; Kd21; Ss24.
	D2S	Sout, Berg, Diep and Papkuil river valleys	44-75m	Valley flats	Aeolian sands on fluvial and residual clays	Low	Medium sand duplex soils: Kd21; Es41.
	D3S	Headwaters of Sout River (Darling) and lower Helderberg	50-100m	Valley flats	Coarse colluvial sands on residual clays	Highly preweathered	Coarse sand duplex soils: Kd22; Es42.
	D4S	Agter Paarl, Eendekuil, Hermon, Gouda and Lynedoch	100m+	Weakly dissected upland plain	Coarse colluvial sands on residual clays and granites	Highly preweathered	Coarse sand duplex soils: Kd22; Es42.

SOUTH-WESTERN CAPE

KEY TO SOIL MAP

UNIT NAME	SUBUNIT SYMBOL	DISTRIBUTION	ELEVATION	TERRAIN TYPE	PARENT MATERIAL(S)	WEATHERING	SOILS
Red apedal soils	F2	Relict patches through area at Paarl, Agter Paardeberg, Malmesbury, Darling, Pools	150-200m	Pediment plains and dissected footslopes	Local creep highly weathered transported drift	Highly to moderately preweathered	Red kaolinitic loams and clays: Hu26,25.
	F3	Associated with mountain footslopes. Helshoogte and Rooihoogte (Malmesbury)	200-350m	Dissected elevated pediments	Highly weathered drift over residual preweathered saprolite or rock	Moderate to highly preweathered	Red kaolinitic clays: Hu16,27.
Sandstone benches	H1	Kleinmond	30-50m	Surf cut bedrock benches along coast	Locally derived sand colluvial or scree deposits of variable thickness on quartzitic bedrock	Highly leached; variable degree of base rock preweathering	Sandy podzolic and hydromorphic soils: Hh30,20; Cf30,20; Kd14.
	H2	Cape Point, Pringle Bay	50-100m	Coastal			
	H4	Grabouw	200-250m	Intermontane			
	H5	Piketberg	400-700m	Intermontane			
River valleys	I1	Along major drainage lines	Variable?	Moderately wide valleys with river terraces and floodplains	Locally derived alluvium/ fluvial deposit	Low	Weakly developed soils dominant; generally hydromorphic: Du, We, Oa, Va.
Mountains	J	Eastern boundary	Variable; 700m+	Mountain ranges and high hills	Resistant quartzose rock	Low	Very shallow sandy lithosols: Ms10; Cf30,20; Hh30,20.

OVERBERG

KEY TO SOIL MAP

UNIT NAME	SUBUNIT SYMBOL	DISTRIBUTION	ELEVATION	TERRAIN TYPE	PARENT MATERIAL(S)	WEATHERING	SOILS
Calcareous coastal sands	A1	Sandy embayment	0-45m	Mobile dunes	Shelly aeolian sands	Unweathered	Grey calcareous sands: Fw20,21.
	A2	On coastal margin	0-200m	Low dunes; stabilized	Calcareous aeolian sands	Low degree and poorly leached	Calcareous sands and lithosols: Fw20,21; Ms22.
	A3	Heuningberg (Bredasdorp) to Gouritz River	50-250m	Dunal with secondary dissection and valley incision	Bredasdorp limestones and calcareous sands	Low	Grey calcareous sands, red-brown loams and lithosols: Fw21; Oa24; Ms22; Hu34.
Acid sands	B2	Albertinia flats and Pearly Beach	120-180m	Inland flats	Quartz rich sands locally derived with aeolian resorting	Highly leached	Red-yellow-grey acid sands, podzols and duplex soils: Fw11; Lt11; Ct11; Kd21.
Residual soils	C1	Along boundary between coastal sands and Rûens	110-140m	Undulating with plain remnants	Thin loamy to gravelly creep layers on residual shales	Moderate to low	Poorly developed soils on convex slopes and duplex loams on concave lower slope and plain remnants: Gs13; Sw31; Ss23.
	C2	Southern and eastern slopes of Klein River and Bredasdorp mountains	150-200m	Dissected footslopes pediments	Loamy creep layers on residual preweathered shale saprolite	Moderate to high	Duplex loams and poorly developed residual soils: Sw31; Ss23; Gs13,16.
	C3	Caledon, Heidelberg, Swellendam Rûens	200-300m	Highly dissected rolling landscape	Thin gravelly loam creep layers on residual shale	Low	Poorly developed residual soils: Ms10; Gs13,16; Sw31.
	C4	Heidelberg, Riversdale, Hartebeeskuil basins	variable	Rolling landscape with terraced valleys	Enon boulders and clays	Low	Red duplex loams: Va20,21, 40,41.
Duplex soils	D1L	Elim, Haasvlakte, De Hoop Gouritz River flood plain; inland of coastal dune cordon	30m-	Coastal flats and river flood plains	Loamy medium sand on marine or residual shale derived clay	Low	Duplex loams: Va40,41; Ss23,24; Es33,34; Oa43,46.
	D2L	Wydgeleë, Vlees Bay, Lower Heidelberg flats	40-70m	Flat valley plains; weakly undulating near rivers	Limestones and marine clays	Low	Shallow dark calcareous loams and duplex soils: Ms22; Mw20; Va40.
	D2s	Breede River terraces	50-80m	Flat, high level river terraces	Alluvium/fluvial sands and boulders on clay	Moderate	Duplex sands: Es41; Kd21.
	D5L	Mossel Bay	200-250m	Dissected high level coastal platform	Thin colluvial sandy loam layer on residual or transported clays	Moderate to high	Duplex sand and loams: Es13,33; Ss23.
Silcretes	E1	Central Overberg from Bot River to Suurbraak	250-300m crest heights	Rolling landscape with flat silcrete capped hill tops	Thin loamy or gravelly creep layer on residual shale derived clays	Low to moderate, but high associated with silcretes	Duplex soils on pallid zone materials associated with silcretes; poorly developed on dissected slopes: Ss23; Es33; Sw31; Gs13,16.

OVERBERG

KEY TO SOIL MAP

UNIT NAME	SUBUNIT SYMBOL	DISTRIBUTION	ELEVATION	TERRAIN TYPE	PARENT MATERIAL(S)	WEATHERING	SOILS
Silcretes	E2	Heidelberg, Riversdale	250-300m	Rolling landscape with flat silcrete capped hill topes	Enon gravels and clays	Low but moderate high associated with silcretes	Red structured and duplex soils: Va21; Ss16.
	E3	Potberg	100m	Flat footslope of Potberg mountain	Quartzitic colluvium	Low	Weakly developed gravelly sands and sandy loams.
Red apedal soils	F1	Heidelberg flats and west of Wydgeleë and Vlees Bay	80-110m	High valley plains or marine cut flats	Variable, fluviatile or marine deposits and shale derived clays	Low	Red loams and clays with lime: Hu36,43,46.
	F2	Herbertsdale	150-200m	Undulating	Local drift and residual on Bokkeveld shales	Moderate over preweathered materials	Red loams and clays neutral with lime common: Hu36,46; Sw11.
	F3	Herbertsdale, Albertinia	200m+	Flat high level plain with pans	Local drift and residual on Bokkeveld shales	Moderate	Red loams and clays, lime usually absent: Hu36; Sw21, 11.
Upland gravels	G1	Herbertsdale - Langeberg mountain footslopes	300-400 m crest heights	Dissected upland plateau	Colluvial gravels and screes	High	Podzolic soils: Lt12.
	G3	Grabouw	300-400m	Dissected upland plateau	Colluvial gravels	High	Hydromorphic duplex soils: Kd13,16; Pn26.
Sandstone benches	H1	Kleinmond, Bot River, Hermanus	30m+	Bedrock benches along coast	Locally derived sandy colluvial or scree deposits of variable thickness on quartzitic bedrock	Highly leached; variable degree of base rock preweathering	Sandy podzolic, hydromorphic and duplex soils: Hh30,20; Cf30,20; Kd14.
	H2	Elim	50-100m	Inland plain			
	H3	Bot River and Salmonsdam	100-200m	Intermontane			
	H4	Grabouw, Caledon, Cooper	200-250?	Inland plain and coastal platform			At Cooper duplex soils dominant: Ss23; Es13; Kd13.
	H5	Grabouw and Bredasdorp mountains	400-700m	Intermontane			
River valleys	I1	Along major drainage lines	Variable	Moderately wide valleys with river terraces and floodplains	Locally derived alluvium/fluvial deposits	Low	Weakly developed soils dominant, generally hydromorphic: Du, We, Oa, Va.
Mountains	J	Northern boundary and isolated ranges	Variable 700m+	Mountain ranges and high hills	Resistant quartzose rock	Low	Very shallow sandy lithosols: Cf30,20; Ms10; Hh30, 20.

OUTENIQUALAND

KEY TO SOIL MAP

UNIT NAME	SUBUNIT SYMBOL	DISTRIBUTION	ELEVATION	TERRAIN TYPE	PARENT MATERIAL(S)	WEATHERING	SOILS
Calcareous coastal sands	A2	Sandy embayments along coast	0-100m	Stable dunes	Shelly aeolian sands	Low	Calcareous sands: Fw20,21; lithosols Ms22 and argillic soils: Vf11.
Acid sands	B3	Rhenendal	150-200m	Undulating dunes banked against the coastal platform	Quartz sands	Highly leached	Grey podzolized soils: Fw10,11; Lt11 and argillic soils: Vf11,21.
	B4	Harkerville, Noetzie	200-250m	Undulating aeolianites on coastal platform	Quartz sands and loams	Highly leached and preweathered	Yellow and grey acid sands and podzols: Lt10,11,20; Ct13,14,23; duplex loams: Va30.
Residual soils	C4	Hartebeeskuil, Knysna, Plettenberg Bay	Variable	Rolling landscape with terraced valleys	Enon boulders and clays	Low	Rubified duplex loams on clays: Va20,21,30, 31 and other duplex soils: Es13.
Duplex soils	D5L	Mossel Bay to Knysna	200-250m	Dissected coastal plateau with prominent remnants	Drift material on weathered granite	Moderate to high	Duplex soils, fine sands on sodic smectitic clays Es13,33; Ss23.
	D5S	Knysna to Humansdorp	200-250m	Weakly dissected coastal platform	Transported material on weathered Cape Supergroup	Moderate	Duplex soils fine sands on clays, hydromorphic sands to clay loams: Es40; Kd20; Lo10; Ka10.
Silcretes	E1	As in Overberg					Ss23; Es13.
Red apedal soils	F2	Herolds Bay to Victoria Bay	150-200m	Outer plateau margin	Local drift and in situ materials of the Kaaimans Group	Moderate to low	Red apedal loams on saprolite: Hu36 and red structured clays: Sw11.
	F3	Between Varing-Grootbrak rivers	200m+	Undulating high level plain	Local drift and residual on shales	Moderate	Red loams and clays, lime usually absent: Hu36; Sw21,11.
Upland gravels and screes	G2	Along the margin of the Outeniqua mountains	400m+	Dissected footslope pediment of the mountains	Angular screes	High	Variable, podzolized: Lt11,12; Ct11,12.
Sandstones benches	H5	Bergplaas inland of Plettenberg Bay	400-700m	Dissected intermontane bench	Quartzite	Low	Shallow residual soils: Hh30,20; Cf30,20.
River valleys	I1	Mossel Bay, Bitou River, Groot Brak	Variable	Moderately wide valleys with river terraces and flood plains	Locally derived alluvial deposits	Low	Weakly developed soils; generally hydromorphic: Oa; Du; We; Va.
	I2	All along coastal platform	Variable	Deeply incised valleys	Shallow drift on bed rock	Low	Shallow creep on bedrock and saprolite: Gs15,13.
Mountains	J	Northern boundary	700m+	Mountain ranges	Resistant quartzose rocks	Low	Shallow sandy lithosols: Ms10; Cf30,20; Hh30,20.

NOTES

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SUGGESTED COLOUR CODES FOR MAPS
USING COLOURED PENCILS

Soil Maps

A Calcareous sands
  A1 light yellow
  A2 medium yellow
  A3 dark yellow

B Acid sands
  orange

C Residual soils
  C1 light green
  C2-3 medium green

D Duplex soils
  D1 light blue
  D2 dark greenish blue
  D3-4 medium blue
  D5 purple

E Silcretes
  medium brown

F Red apedal soils
  F1 light red
  F2 medium red
  F3 dark red

G Upland gravels and screes
  G1-2 light brown
  G3 reddish brown

H Sandstone benches
  hatching in pencil

I River valleys
  white

J Mountains
  black pencil

Geological Map

Q Cenozoic Groups: light yellow

K Cretaceous Groups: dark yellow

B-D Karoo Sequence: shades of green

W-P Cape Supergroup
W   Witteberg Group: light blue
T-C   Bokkeveld Group: medium blue
N-P   Table Mountain Group: dark blue

Z Klipheuwel Formation: dark brown

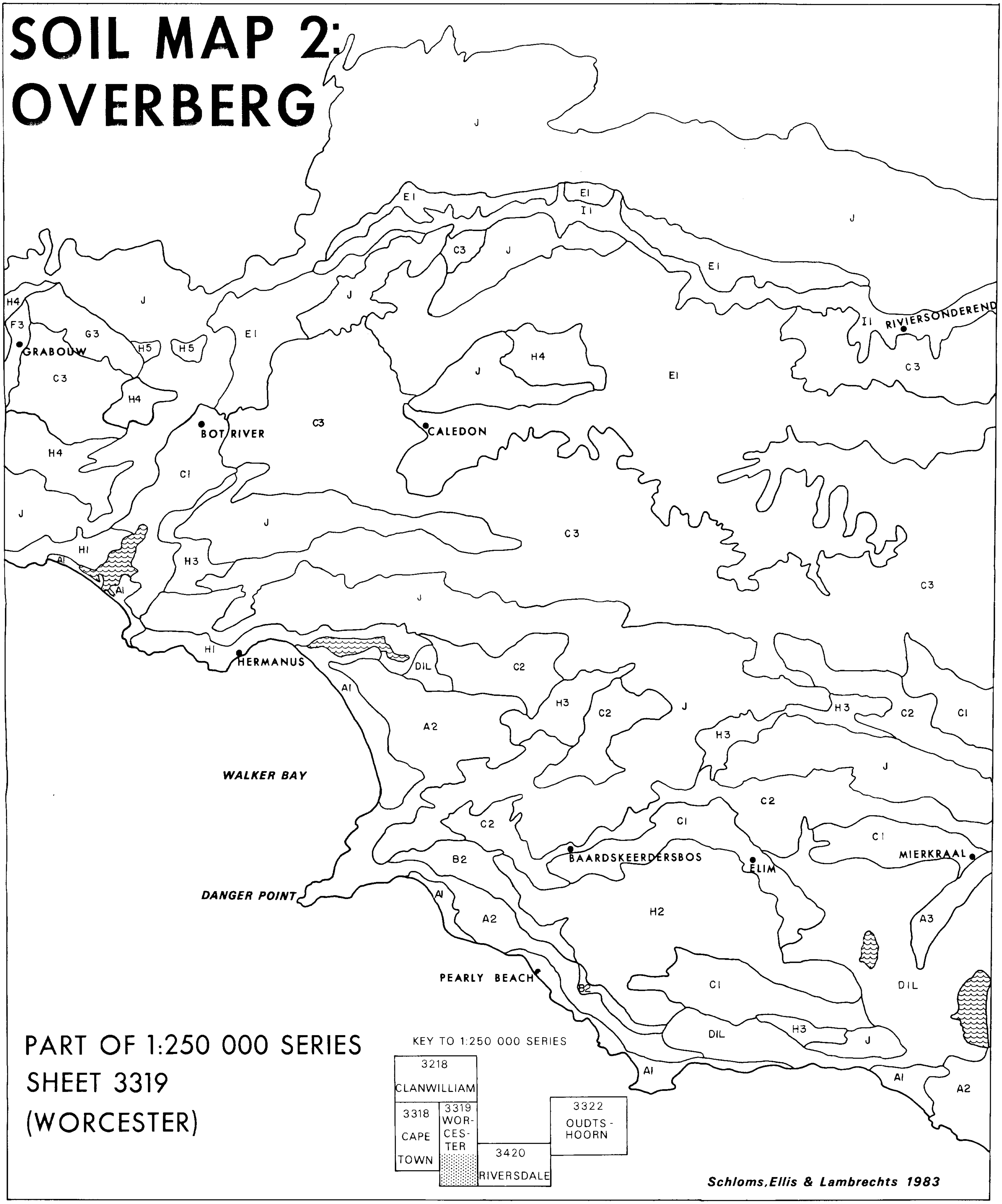
Y Nama Group: brownish orange

M Malmesbury Group, etc.: purple

G Cape Granite Suite: reddish pink

X Namaqualand Complexes: orange-red

SOIL MAP 2: OVERBERG



PART OF 1:250 000 SERIES
SHEET 3319
(WORCESTER)

Schloms, Ellis & Lambrechts 1983

SOIL MAP 3: OVERBERG

1:250 000 SERIES SHEET 3420 (RIVERSDALE)

Schloms, Ellis & Lambrechts 1983

SOIL MAP 4: OUTENIQUALAND

PART OF 1:250 000 SERIES SHEET 3322

(OUDTSHOORN)

Schloms, Ellis & Lambrechts 1983

GEOLOGICAL MAP OF THE FYNBOS REGION AND SURROUNDS

GEOLOGICAL LEGEND

Q	Cenozoic Groups		
K	Cretaceous Groups		
B	Beaufort Group	Karoo Sequence	
E	Ecca Group		
D	Dwyka Formation		
W	Witteberg Group		CAPE SUPER-GROUP
T	Bidouw and Traka Subgroups	Bokkeveld Group	
C	Ceres Subgroup		
N	Pakhuis and Cedarberg Formations; Nardouw Subgroup*	Table Mountain Group	
S	Peninsula Formation		
P	Piekenier and Graafwater Formations		
Z	Klipheuwel Formation		
Y	Nama Group		
M	Malmesbury, Kango, Gamtoos and Kaaimans Groups		
G	Cape Granite Suite		
X	Namaqualand Complexes		

* Provisional name not yet approved by SACS

J.N. Theron 1983

ADAPTED FROM PUBLISHED 1:1000 000 GEOLOGICAL MAP OF R.S.A

SOIL MAP 1: SOUTH WESTERN CAPE

1:250 000 SERIES SHEETS 3318 AND PART OF 3218 AND 3319

Schloms, Ellis & Lambrechts 1983