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Late Cenozoic palaeoenvironments on the west coast of Southern Africa

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ABSTRACT. Evidence from sedimentary deposits and their biogenic component shows that aridity on the west coastal margins of southern Africa, south of 17°S, was established during the late Cenozoic. The parallel evolution of aridity in Australia suggests that the climatic changes were global. Age correlation relates these events to the history of the Southern Ocean and the Antarctic ice cap. In the Miocene, the vertebrate fauna was of a pan-African nature and the environment sclerophyllous woodland and grassland with summer rainfall. Middle to late Miocene molluscs with a low degree of latitudinal organization of species show that the coastal waters were undifferentiated. Extensive phosphorites indicate the existence of upwelling and a related subtropical anticyclone.

The earliest evidence of the modern semi-arid environment and winter rainfall in the southwestern Cape dates to the Pliocene. Invertebrate and vertebrate faunas show strong provinciality. Molluscs are indicative of cold upwelling offshore south of latitude 32°S; pollens are partly sclerophyllous fynbos (macchia) suggesting a trend towards winter rainfall. Full semi-arid conditions with winter rainfall were achieved in the southwest by the end-Pliocene or earliest Pleistocene. Vertebrate faunas of that age were predominantly of a browsing type.

Aridity in southern Africa was thus fully established in the Quaternary, but was affected by global climatic oscillations. Laterally-restricted late Pleistocene warm (hyperthermal) mollusc assemblages suggest a warm hydroclimate in the numerous lagoons and estuaries created by a marine transgression during a thermal maximum 120 000 years ago. A southward shift of the subtropical anticyclone and zone of upwelling is inferred. Evaporite deposits indicate arid conditions and a poleward contraction of the rain-bearing westerly flow.

Conversely, in the succeeding cold interval (hypothermal) there was a 5° equatorward shift of the climatic belts so that the winter rainfall area expanded. Ephemeral rivers on the Namaqualand coast were rejuvenated and palaeo-lakes filled during the later half of the last major sea level regression. The arid zone, including the Namib Desert, also moved equatorward. Atmospheric circulation, and probably aridity, was more intense in the arid core in the north about 20 000 years ago.

Introduction

Paleoclimatic reconstruction, involving the interpretation of diverse data, suggests that Cenozoic climate was marked by a long-

term cooling trend. In recent years, the most significant advances have resulted from the study of deep-sea cores, and the salient features of Cenozoic palaeoclimate are now emerging (Devereux, 1967; Denton *et al.*,

1971; Kennett *et al.*, 1975; Shackleton & Kennett, 1975a; Savin, Douglas & Stehli, 1975). A lowering of temperatures from the late Eocene until the late Oligocene was followed by a temperature rise through the early Miocene. The sudden divergence of middle Miocene high- and low-latitude oceanic temperatures accompanied the onset of major Antarctic glaciation and the development of the circum-Antarctic Current (Savin *et al.*, 1975).

Widespread aridity on the western coastal margins of southern Africa is related to the upwelling of cold subsurface water. Aridity becomes more intense northward, culminating in the Namib Desert (Fig. 1). But physical, chemical and biological attributes of Tertiary and Quaternary strata suggest that this aridity is youthful, and has developed progressively since the Miocene. The purpose of this paper

is to describe the development of desiccation on the west coast of southern Africa through the late Cenozoic, to show the comparative youthfulness of the Namib Desert system, and to show evidence of late Pleistocene climatic changes.

Climatic and oceanic setting of southern Africa

The present climate of the subcontinent, which becomes more arid in a westerly direction, is controlled by the behaviour of subtropical anticyclones over the South Atlantic and Indian Oceans (Schulze, 1965). The South Atlantic anticyclone lies relatively close to the west coast, and migrates 4° equatorward in winter from a summer position centred at 30°S (Fig. 2a). Persistent summer

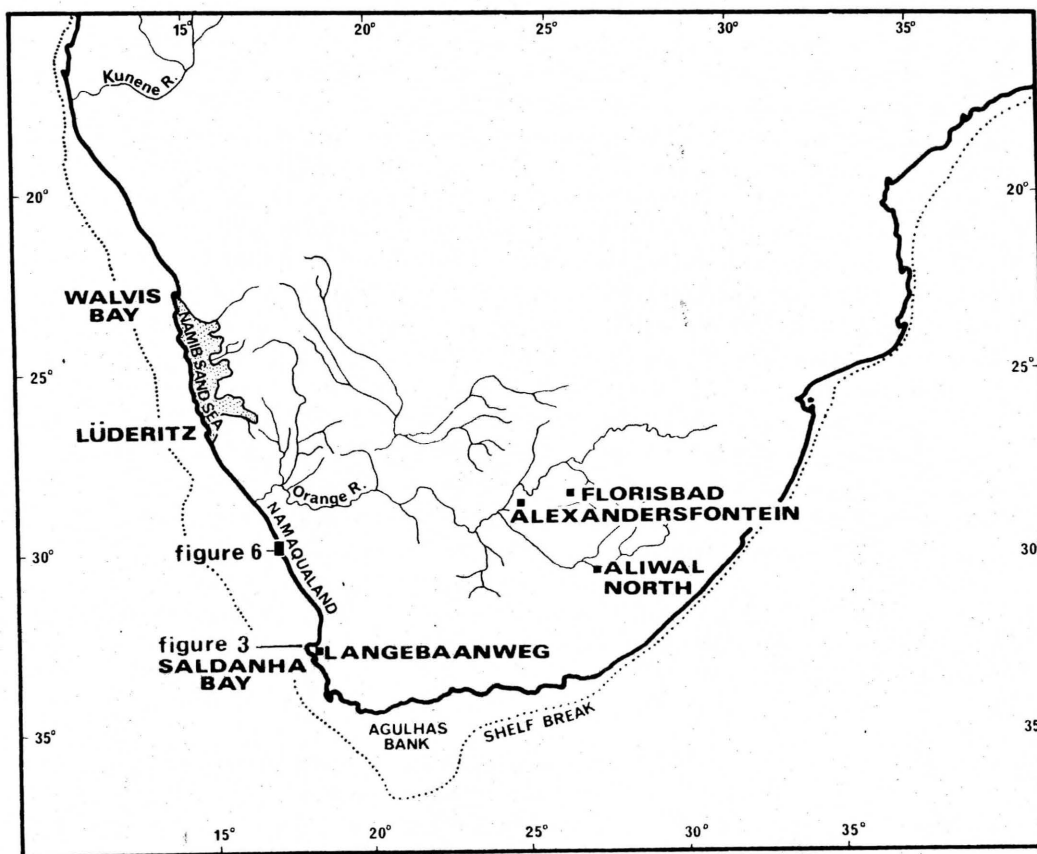


FIG. 1. Location map.

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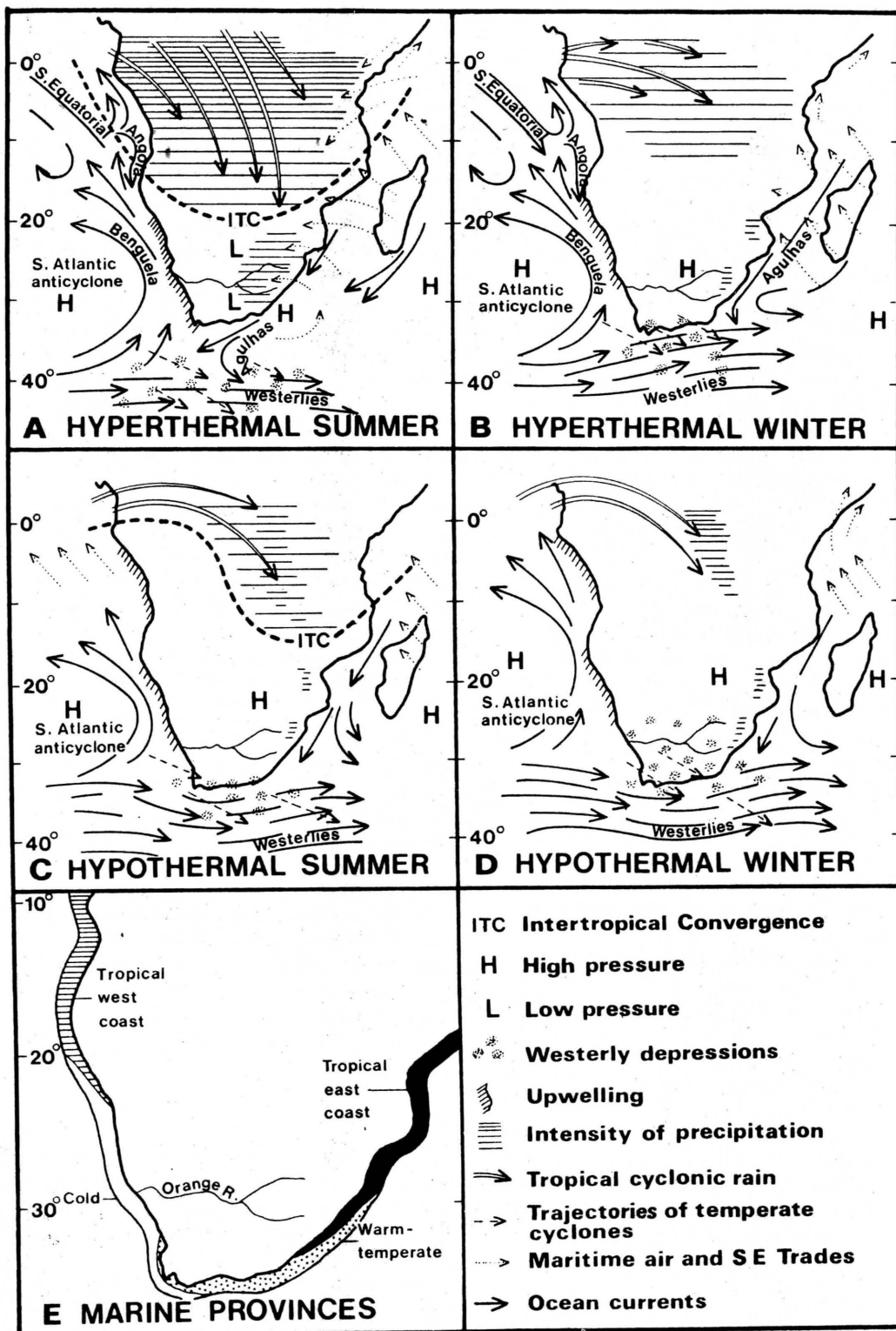


FIG. 2. Atmospheric and oceanic circulation patterns during hyperthermal (interglacial) and hypothermal (glacial) times (A-D) (modified after Van Zinderen Bakker, 1976). E, present distribution of marine provinces about southern Africa.

southerly winds are generated by the interaction of this anticyclone with a subsidiary anticyclone which lies off the south coast at 35°S. The frictional drag of southerly gales, combined with the rotation of the earth, causes a net displacement of surface water away from the coast. Cold Central Water, derived from the Southern Ocean, wells up nearshore as the Benguela Current to replace the warm, offshore-displaced surface water (Hart & Currie, 1960). The cold water has an aridifying effect on the adjacent coast by condensing moist sea air and forming coastal fog banks (Logan, 1960). The warm Angola Current flows poleward beside the coast, as far as 25°S at times, interacting with the northern decaying end of the Benguela Current (Moroshnikov, Bubnov & Butalov, 1970).

In summer, the Indian Ocean anticyclone is generally far from the east coast, permitting moist maritime air to penetrate inland and precipitate orographic rain over the headwaters of the Orange River. Summer droughts are associated with a close proximity of the Indian Ocean anticyclone to the coast. Tropical convectional rain also follows the Inter-tropical Convergence southward in summer, bringing rain to the northern catchments of the Orange River, and to the intermittent rivers which drain into the Namib Desert.

Mid-latitude westerlies are situated poleward of the two subtropical anticyclones, associated with a steep pressure gradient. The equatorward shifting of the westerlies brings cyclonic winter rain to the southwestern and southern coasts. These westerlies are more variable than the trades because they are affected by cells of low and high pressure which move eastwards within the basic wind system (Barry & Chorley, 1968, p. 127).

The warm Agulhas Current off the east and south coasts (Fig. 2), a southward extension of the Indian Ocean South Equatorial Current, is deflected by the Agulhas Bank (Clowes, 1950). Agulhas water only occasionally rounds the Cape Peninsula into the South Atlantic (Schell, 1969).

Tertiary history

The depositional history of the coastal margin of southern Africa is closely related to sea-level history. Eustatic transgressions in the

late Cretaceous, middle Eocene, and middle to late Miocene are commonly attributed to oceanic-ridge uplift, consequent upon increased spreading rates (Hallam, 1971; Flemming & Roberts, 1973; Rona, 1973). But on the west coast of southern Africa this history is complicated by local epeirogenesis. South of the Orange River, the only Tertiary transgression complexes are of middle to late Miocene and Pliocene age, the latter resulting from local transgression induced by downwarping during a time of worldwide regression (Tankard, 1975a). North of the Orange River, middle to late Eocene and Miocene transgressions are recorded (Kaiser, 1926; Haughton, 1963, p. 311).

Reconstruction of the palaeoclimates is based on interpretation of data derived from climatically-sensitive components of the transgression complexes, or from continental deposits of known age. A more thorough reconstruction of the palaeoclimate and palaeoenvironment awaits detailed study of the biologic components in particular, and more reliable dating of the stratigraphy.

Pre-Miocene

The only evidence of the nature of the pre-Miocene environment is comprised of pollen and leaf flora from a lacustrine deposit at Banke in Namaqualand, of probable late Eocene or Oligocene age (Estes, 1978). Banke was then near latitude 35°S (Axelrod & Raven, 1978). The flora includes *Podocarpus*, *Gunnera*, *Myrica*, *Ficus*, a proteaceous genus similar to *Brabeium*, and xerophilous-type leaves. An ectonal area between temperate rainforest and sclerophyllous vegetation, with relatively dry climate and summer rainfall is indicated.

Miocene

Evidence of moist conditions on land, and warmer waters offshore, is more abundant in deposits of Miocene age. Along the Namaqualand coast, this evidence consists of extensively buried fluvial deposits of Miocene-Pliocene age (Carrington & Kensley, 1969). The late early to middle Miocene vertebrate fauna of the Namib Desert region (Stromer, 1922) and Arrisdrift near the mouth of the Orange River (Corvinus & Hendley, 1978), are v

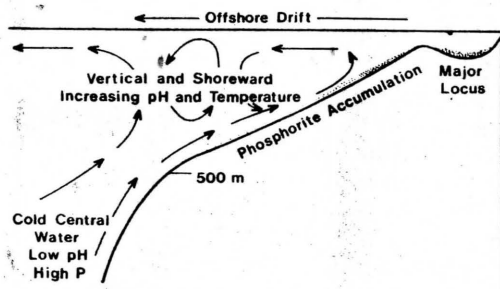


FIG. 3. Optimum conditions for formation of phosphorite. The major locus is an embayed coastline adjacent to an upwelling system (cf. Gulbrandsen, 1969).

similar to the contemporaneous fauna of east Africa. These elements formed part of a pan-African faunal province. Hopwood (1929) interpreted the presence of antelopes and jumping hares in the Miocene Namib Desert fauna as indicating wooded-grassland (savanna) conditions, while tragulid remains indicated riverine woodland. The slightly younger Arrisdrift assemblage, including rhinoceros and ruminants, also suggests the existence of a wooded-grassland environment (Corvinus & Hendey, 1978).

A complex suite of Neogene sediments is preserved at Langebaanweg (Fig. 1). There, Miocene strata comprise two peat-bearing cyclothem overlain by phosphorite. The lower peat is 3 mm thick and contains a broad-leaf flora. Wood remains have been identified as the mesic endemic *Curtisia dentata* (G. L. Hartwig, personal communication). *Curtisia* is a temperate rainforest tree which cannot tolerate arid conditions. It survives today as a relict in moist mountain valleys of the southwestern Cape.

The autochthonous phosphorites at Langebaanweg, of probable middle to late Miocene age, have been attributed to deposition in a marine embayment shallower than 100 m (Tankard, 1974a, 1975a). Although Pevear (1966) suggested that not all phosphorites need be associated with upwelling, most accounts follow Kazakov's (1937) model of direct precipitation of marine apatite from upwelled phosphate-rich waters (Fig. 3) (Sheldon, 1964; McKelvey, 1966; Gulbrandsen, 1969; Tooms, Summerhayes & Cronin, 1969; Blatt *et al.*, 1972, p. 551; Tankard, 1974b). The major locus of accumulation of the Langebaanweg Miocene phosphorites is

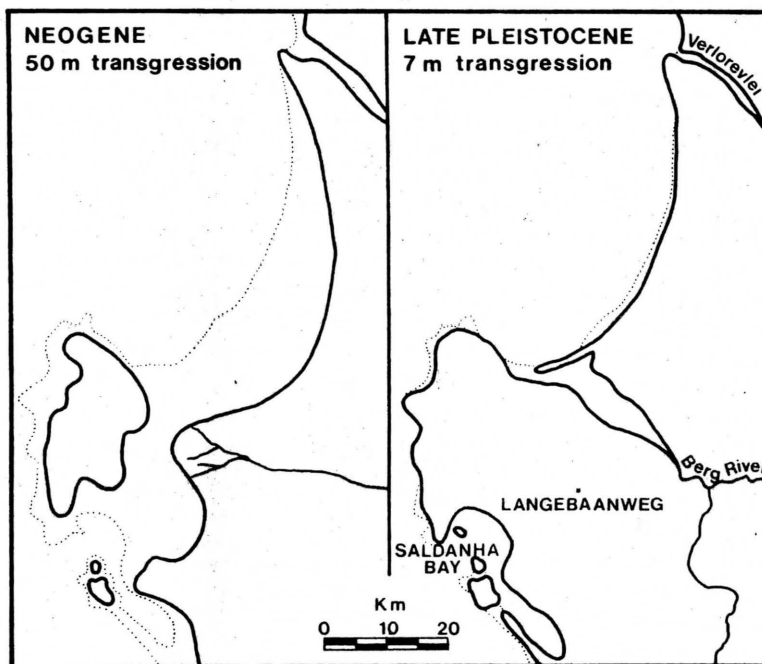


FIG. 4. Palaeogeography of the Saldanha region, related to 50 m and 7 m sea level rises, which influenced Neogene phosphogenesis and late Pleistocene mollusc distribution.

a shallow basin adjacent to a belt of active upwelling (Figs. 3 and 4), a common characteristic of emerged phosphorite accumulations (Riggs & Freas, 1965; Blatt, Middleton & Murray, 1972, p. 551).

The composition and distribution of Neogene mollusc assemblages from southern African marine deposits probably have climatic significance. The distribution of modern mollusc faunas about the present coastline is strongly provincial, and defines four provinces (Fig. 2e). The fauna from each of these provinces is distinctive, and there is a great diversity of species. In contrast, the Neogene mollusc assemblages are broadly cosmopolitan. Although there is a low degree of regional faunal organization, assemblages from Namaqualand to Algoa Bay (26°E) are characterized by *Glycymeris borgesii*, *Cardium edgari*, *Ostrea atherstonei*, *Scissodesma spengleri*, *Venus verrucosa*, *Lutraria lutraria*, *Dosinia lupinus*, and related species (Tankard, 1975b). A degree of provinciality is also shown by the restriction of *Pecten sapolwanaensis*, *Aequipecten uloa* and *Amusium umfolozianum* to the Zululand and Mozambique deposits, although these deposits also have *Glycymeris borgesii*, in common with the south and west coasts. King (1953) has shown that the Zululand Miocene molluscs have tropical affinities. Latitudinal diversity gradients possibly existed as today, but a poleward shift of the faunal provinces resulted in most of the Cape coastline having a warm temperate to subtropical molluscan fauna with little species diversity. Addicott (1970) has described a similar record from the late Tertiary deposits of California, which are also adjacent to a modern upwelling system.

To summarize, the marine phosphorites suggest that upwelling already influenced the Miocene coast, but that surface temperatures were probably considerably warmer than today. The coastline was also more embayed. Cosmopolitan molluscs indicate a less distinctive latitudinal faunal zonation, and considerably expanded limits of tropical water. Vertebrate fossils apparently belonged to a pan-African fauna and indicate a subtropical and more luxuriantly vegetated mesic subcontinent. A broad-leaf flora in the south suggests that temperate rainforest, summer rainfall conditions prevailed.

Pliocene

Marine molluscs associated with the Pliocene transgression complex sediments at Langebaanweg suggest the existence of shallow marine temperatures which were 3–5°C warmer than today (Tankard, 1974a, b). These molluscs include *Cellana capensis*, *Turbo sarmaticus*, *Barbatia obliquata* and *Ostrea atherstonei*. Also, an oyster bank containing stunted valves of *Striostrea margaritacea* occurs adjacent to the present open coast north of Saldanha. These taxa all inhabit the present warmer south coast of the Cape Province. Contemporaneous shallow marine deposits on the Namaqualand coast contain a mollusc assemblage of tropical west African affinities (Tankard, 1974b). Although the hydroclimate of the west coast appears to have been warmer than today in the Pliocene, no authigenic phosphorite was generated, suggesting a possible temperature drop from the Miocene high.

Carbonaceous sands and peats from estuarine deposits in the Langebaanweg transgression complex contain abundant pollen (Table 1). Van Zinderen Bakker comments (personal communication) that the presence of Restionaceae and *Cliffortia*, which are typical of the Cape Flora and winter rainfall suggests that this flora was already established at the time of sedimentation. It is interesting that only about half of the taxa which were distinguished could be identified. This could be the result of extinction, which would suggest that the flora was still very different from the present one. The spectrum includes *Podocarpus* and grass pollens. The dominant unidentified type (Table 1) is probably a member of the Aizoaceae.

The large herbivore fossils from the Langebaanweg deposits suggests a more luxuriant

TABLE 1. Pollen flora identified from Pliocene carbonaceous sands, Langebaanweg (identified by Professor E. M. Van Zinderen Bakker)

Dominant unidentified type (?Aizoaceae)	~92%
Gramineae (grasses)	~3%
Restionaceae (reed)	~1.5
<i>Cliffortia</i> (bush)	~1.5
<i>Podocarpus</i> (tree)	<1%
<i>Myrica</i> (dry area shrub)	<1%
Chenopodiaceae-type (salt flat bush)	<1%
Compositae (flowers)	<1%
Other unidentified types (about eight)	~2%

vegetated environment, which was very different from the modern semi-arid sclerophyllous vegetation (Hendey, 1976). Long-necked giraffes (*Giraffa*) and the boselaphine and tragelaphine antelope (*Mesembriportax* and *Tragelaphus*) indicate the presence of woodlands, while the high-crowned teeth of the rhinoceros (*Ceratotherium*), the horse (*Hipparion*), and alcelaphine antelopes are indicative of grasslands. Hendey (1973) visualized an environment of this period characterized by riverine woodland flanked by grassland, with seasonal rainfall. This distinctive Pliocene fauna shows a trend towards regionalism, in contrast to the pan-African nature of the Miocene faunas (Q. B. Hendey, personal communication). *Ceratotherium* from the Namaqualand deposits indicates the presence of grassland in the Pliocene there too (Tankard, 1974b).

The pollen data, and the requirements of the herbivores, support the suggestion made by Axelrod & Raven (1978) that the Pliocene environment was characterized by sclerophyllous woodland and grassland with summer rainfall, but with a trend towards winter precipitation. Van Zinderen Bakker (1975) relates the sclerophyllous vegetation to the development of the modern upwelling system. Mollusc fossils (stunted *Striostrea margaritacea*) indicate the slightly warmer coastal waters, dominated by the vagaries of the northern decaying end of the cold Benguela Current.

Quaternary history

Since achieving its present extent and invulnerability to climatic change in the late Miocene, the Antarctic ice sheet has contributed little to major sea level changes (Shackleton & Kennett, 1975a). High Pleistocene sea levels are attributed to the combined effect of alternating glaciation and deglaciation in the northern hemisphere, tectono-eustatism, and local epeirogenesis (Tankard, 1976a). Shoreline deposits in southern Africa are important, however, because they can be equated with high-latitude interglacials, or hyperthermals.

Early Pleistocene

Sediments of probable basal Pleistocene, or latest Pliocene, age near Langebaanweg

(Baard's Quarry) contain a heterogeneous vertebrate fauna (Q. B. Hendey, personal communication). A few well-abraded elements are possibly contemporaneous with the nearby Pliocene fauna. But the more abundant, younger, and better preserved assemblage has affinities with the early faunas from the Makapansgat and Sterkfontein cave sites of the Transvaal, which provide the earliest evidence for human occupation of the subcontinent (Hendey & Deacon, 1977). In this, *Equus* remains suggest a Pleistocene rather than a Pliocene age, *Equus* being indicative of some grassland in the early Pleistocene. The rhinoceros has shown parallel evolution through the late Cenozoic, and at Langebaanweg the change from the Pliocene grazing type (*Ceratotherium praecox*) to the browsing type in the early Pleistocene (*Diceros bicornis*) further suggests a progressive desiccation from grassland to a more xerophilous vegetation (Axelrod & Raven, 1978). *Hippopotamus* remains suggest an abundance of surface water, leading Tankard (1974b) to suggest that the environment was fluvially dominated.

An absence of warm water taxa in the early Pleistocene marine deposits on the Saldanha coastline reflects oceanographic conditions which were similar to those of the present (Tankard, 1975c). On the other hand, the present geographic ranges of mollusc fossils from contemporaneous deposits on the Namaqualand coast indicate that early Pleistocene (possibly Milazzian) coastal waters there were considerably warmer (Carrington & Kensley, 1969). Most notable is the superabundance of the oyster *Striostrea margaritacea*, which forms the laterally extensive 'oyster line' (Haughton, 1931). Faunas from these two regions suggest that the southern part of the west coast was influenced by the upwelling of cold Central Water, while the Namaqualand coast was still north of the upwelling zone in the early Pleistocene.

Middle Pleistocene

Fossil molluscs associated with the middle Pleistocene 17m–21m transgression complex sediments on the Namaqualand coast, comprising mainly species which today inhabit the adjacent coast (Carrington & Kensley,

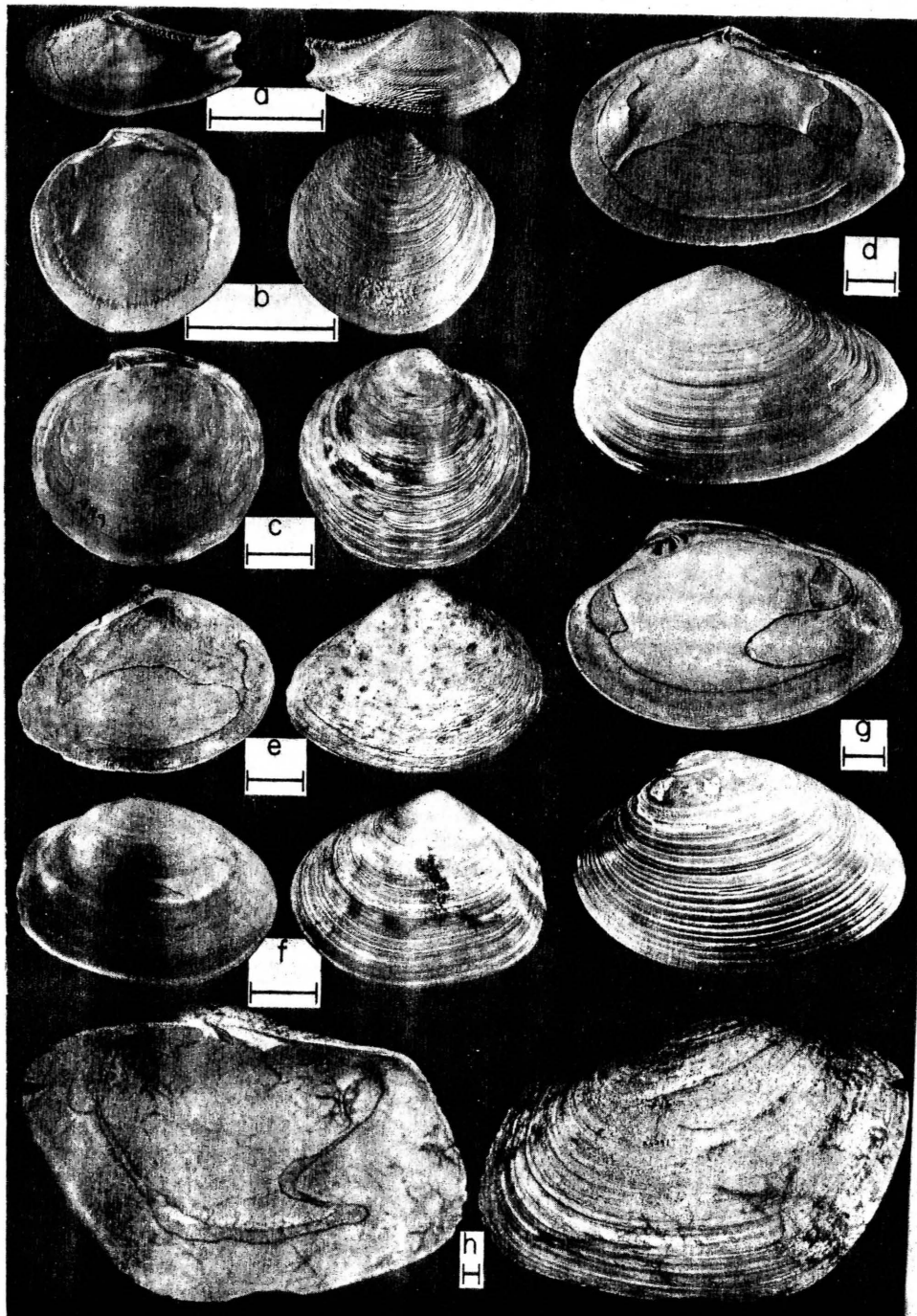


FIG. 5. Tropical west African bivalve species common in interglacial estuarine-lagoonal facies of southwestern Cape: (a) *Nuculana bicuspidata* (Gould); (b) *Loripes liratula* (Sowerby); (c) *Felania phana* (Gmelin); (d) *Tellina madagascariensis* (Gmelin); (e) *Macoma tricostata* (Römer); (f) *Leporim hanleyi* (Dunker); (g) *Venerupis dura* (Gmelin); (h) *Panopea glycymeris* (Born.). Scale = 1 cm.

1969), indicate an upwelling of cold water offshore. No middle Pleistocene marine sediments are known south of Namaqualand.

A sedimentary complex at Elandsfontein, near Langebaanweg, contains a heterogeneous fauna with middle and late Pleistocene elements (Hendey & Deacon, 1977). The more primitive middle Pleistocene assemblage suggests an abundance of surface water (*Hippopotamus*), grassland (*Ceratotherium*, *Equus*, antelope and alcelaphine antelopes), and an absence of trees (no *Giraffa*), under hypothermal conditions. Although a xeric vegetation, and a semi-arid environment, were established in the southwestern Cape by the early Pleistocene, there were periodic incursions of grassland and temperate rain-forest during the Pleistocene pluvials which displaced the sclerophyllous vegetation (Axelrod & Raven, 1978).

Late Pleistocene hyperthermal

Mollusc fossils from marine sediments in the southern part of the study area show that during the late Pleistocene hyperthermal (the last interglacial), oceanic waters were warmer than today (Tankard, 1975d). The taxa are mostly extant and reflect shallow, predominantly intertidal conditions.

The faunal units from hyperthermal estuarine and lagoonal sediments are comprised mainly of species which today inhabit the adjacent coast, but also a significant proportion (> 30% of the individuals) of northern molluscs (Fig. 5), which lay far beyond their present-day geographic range end-points. The present-day southern range end-points of the tropical west African taxa are at

about 17°S, or the northern boundary of the Benguela Current (Table 2). In contrast, the hyperthermal deposits along the open coast contain no extra-limital species.

Further, tropical and subtropical west African taxa would have existed at least 16° south of their normal geographic ranges, by inhabiting relatively warm sheltered environments. The presence of all growth stages of these extra-limital species suggests that water temperatures were warm enough for spawning (Tankard, 1975d). A temperature minimum of about 5°C warmer than today has been suggested for the hyperthermal estuaries and lagoons which were then present. These thermally-anomalous mollusc assemblages are contemporaneous with the thermal maximum, and a marine transgression to 7m above present sea level, at about 120 000 years ago (Tankard, 1975c). The rise of sea level created an extensively-embayed coastline, and thus numerous habitats which suited the molluscs. But the warm water elements are mainly infaunal bivalves, to the exclusion of warm epifauna, suggesting the necessity of a sediment cover and an insulator. Thus water temperatures probably were not much higher than the minimum temperature tolerance of the extra-limital molluscs.

While the fossils from open-coast habitats demonstrate the prevalence of upwelling, extensive hyperthermal evaporite deposits are indicative of hot arid conditions. Evaporites are not forming extensively at present (Tankard, 1975c; Flemming, 1977).

Late Pleistocene hypothermal

The hypothermal climate of the western regions of the subcontinent reflects the

TABLE 2. Late Pleistocene warm-water taxa compared with their modern distribution

Species	Modern latitudinal range							
	35	30	25	20	15	10	5	0
<i>Nuculana bicuspidata</i>								
<i>Loripes liratula</i>					?			
<i>Felania diaphana</i>								
<i>Tellina madagascariensis</i>								
<i>Macoma tricostrata</i>							?	
<i>Leporimetis hanleyi</i>							?	
<i>Venerupis dura</i>								
<i>Panopea glycymeris</i>								
	Upwelling				Tropical			

influence of global refrigeration. The climate was cooler than formerly and, by inference, evapotranspiration rates were reduced. Cryoclastic debris in coastal caves on the south coast, at present a frost-free area, indicates a significant lowering of temperature during the early hypothermal (Tankard & Schweitzer, 1974; Tankard, 1976b). Butzer (1973) suggests a 10°C lowering of temperature at maximum. Red podzolic soils (Butzer & Helgren, 1972), and deposition into standing water at Die Kelders cave (34° 33' S, 19° 22' E) (Tankard & Schweitzer, 1974), could be attributed solely to reduced evapotranspiration. But a radiocarbon-dated pollen stratigraphy in the southwestern Cape records two invasions of temperate rainforest, and two wet intervals, between 33 000 and 45 000 years ago (Schalke, 1973). The rainforest, which included *Curtisia*, *Ilex* and *Podocarpus*, displaced the sclerophyllous vegetation. These mesic endemics are now largely restricted to those parts of the coastal Knysna region (23° E) which receive a mean annual rainfall of 860 mm with no seasonal maximum, i.e. a precipitation income double that of the southwestern Cape. Relict populations of Restionaceae, *Leucospermum*, *Aspalathus*, *Agathosma* and *Phyllica* in Namaqualand also strongly suggest a former moister hypothermal climate there (Rourke, 1972; and personal communication).

Locally coarse-grained aeolianite sequences may indicate an intensified atmospheric circulation, such as characterized the Australian hypothermal (Bowler, 1976). Karst weathering, *terra rossa* sediments, palaeosols, and colluvial deposits in the southern part of the study area all show that at times the environment was moister than formerly (Tankard, 1976b). Remains of grazing animals from the south-western Cape, including *Connochaetes* (wildebeest), *Antidorcas* (springbok), and *Ceratotherium* (white rhinoceros), suggest an expansion of grassland (Klein, 1974; 1975);

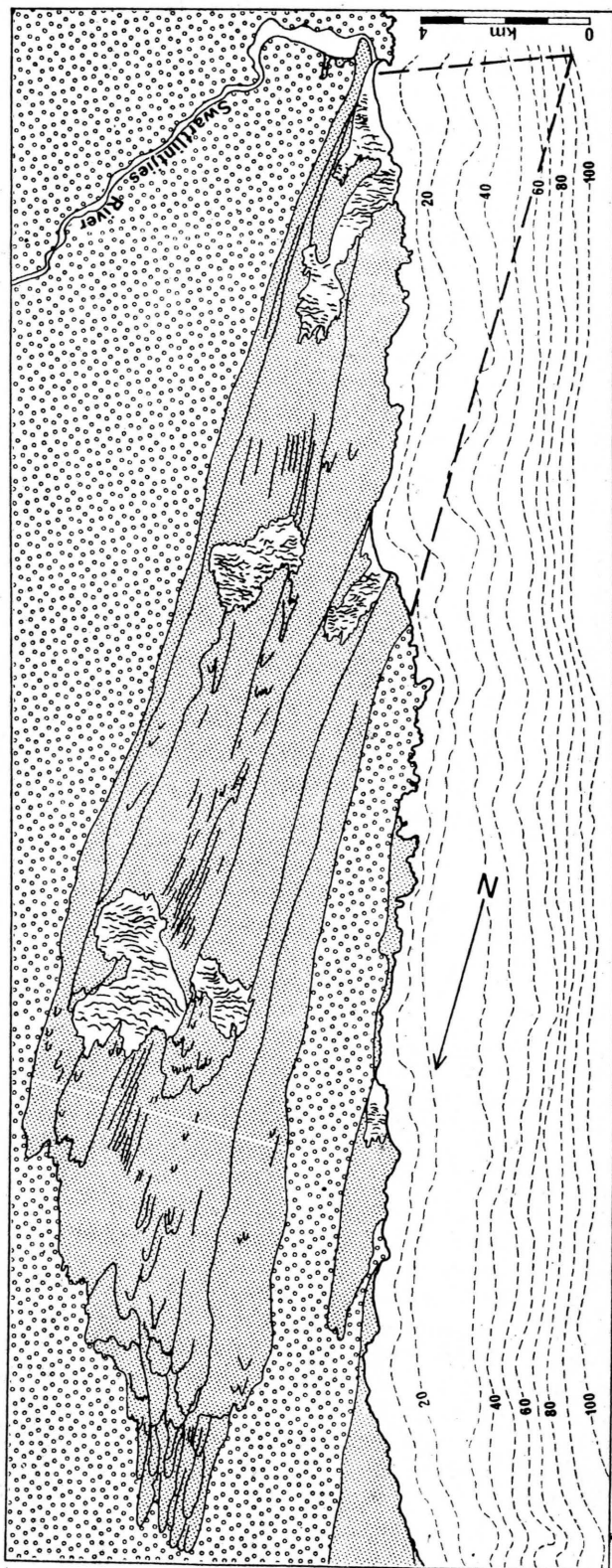
and a decrease in alcelphine antelopes, with an increase in *Tragelaphus* (bushbuck and kudu), indicates a concomitant expansion of forest vegetation. The expansion of rainforest limited the sclerophyllous fynbos, and displaced it northwards into the present semi-desert regions, where relict populations of it still exist (Axelrod & Raven, 1978). The sclerophyllous vegetation only returned southwards with climatic amelioration, between 12 000 and 9000 years ago (Klein, 1974).

The upper hypothermal climate of the continental interior was substantially cooler and wetter than today. Allowing for reduced potential evapotranspiration for an inferred temperature depression of 6°C, Butzer *et al.* (1973) have shown that the prevailing annual rainfall must have been double (880 mm) that of the present in order to fill a 19 m deep palaeo-lake at Alexandersfontein (Fig. 1). Pollen spectra in the Orange Free State support this view. Lower temperatures and/or a considerable increase in precipitation during the upper hypothermal is suggested by the grassland aspect of the Florisbad pollen record. Furthermore, the Aliwal North pollen record suggests that these conditions prevailed until about 12 000 years ago in the upper Orange River area (Coetzee, 1967). Moreover, the Alexandersfontein palaeo-lake was apparently coeval with the first of two periods of accelerated spring discharge in the southwestern Kalahari at 32 000 to 14 000 BP, and 9700 to 7600 BP (Butzer, 1976).

At the mouths of many ephemeral rivers on the west coast, dune plumes occur. For example, the plume of parabolic dunes north of the Swartlinter River at 30° S (Fig. 6) owes its present configuration to a movement of the river mouth sediment source, following the upper Würm sea-level lowering to point 5 km to the west and 110 m lower than today, and to the subsequent Flandrian transgression. The maximum lowering of ba

FIG. 6. Aerial photomosaic and interpretation of Quaternary dunes north of Swartlinter River (Fig. 1). The vegetated parabolic dune plume (stippled) accreted during movement of the river mouth sediment source with upper Würm sea level regression and transgression. Accretion took place over older degraded parabolic dunes (open circles). Modern unvegetated barchanoid dunes (clear) override the plume. Bathymetry in metres. (Extracts from aerial photographs reproduced under Government Printer's Copyright Authority 5723 of 4 August 1976.)

When were these hypothermal periods?



level coincides with the upper Würm sea level minimum of 17 000–18 000 years ago (Tankard, 1976a). Plume accretion is attributed to an increased sediment supply to the continental shelf as a result of stream rejuvenation, and the intensified hypothermal atmospheric circulation. The stream rejuvenation itself is attributed to the increased precipitation. Van Zinderen Bakker (1976) has estimated a 5° equatorward shift of the climatic belts during the hypothermal winter (Fig. 2d), and the expansion of the winter rainfall area to latitude 23°S (Walvis Bay). These Namaqualand plume patterns closely resemble others described from similar latitudes along the Californian coast (Cooper, 1967). The parabolic dunes, now stabilized by vegetation, display the extremely long and narrow 'hairpin' shape described by Cooper; however, they are now overridden by shifting, unvegetated barchanoid dunes which are fed by surf erosion of the older dunes at the coast.

With the equatorward contraction of the climatic zones in the hypothermal, the arid zone also migrated equatorward and expanded inland. The northern Kalahari thus was more arid at the height of the hypothermal (Van Zinderen Bakker, 1975). In the Congo Basin and Angola, Pleistocene dune fields, which are now forested, show the effects of this expansion of the arid zone into the equatorial tropics (Van Zinderen Bakker, 1976).

Discussion

Antarctic glaciation has substantially influenced oceanic circulation (Kennett *et al.*, 1975) and the climatic processes which controlled late Cenozoic desiccation in subtropical regions. Glaciation in Antarctica only reached sea level due to a major cooling close to the Eocene–Oligocene boundary (Shackleton & Kennett, 1975a). Glaciation persisted throughout the Oligocene, but with the ice sheet still considerably less extensive than today. It only developed to its present thickness between the early middle Miocene and early late Miocene. An even thicker ice sheet in the late Miocene to early Pliocene was associated with major regression and global marine cooling (Kennett *et al.*, 1975). By the late Miocene, the Antarctic ice cap had

achieved its present invulnerability to climatic change, and has existed in its present form since. In contrast, a substantial ice sheet only accumulated in the northern hemisphere about 2.6 million years ago (Shackleton & Kennet, 1975b).

The development of subtropical aridity, between the fortieth parallels, is dependent upon the genesis of a cold Southern Ocean. Although in the early Oligocene, Southern Ocean temperatures were similar to the present, the modern climatic and oceanic circulations date only to the late Oligocene, when the circum-Antarctic Current developed (Kennett *et al.*, 1975). Savin *et al.* (1975) have also attributed the sudden divergence of high- and low-latitude oceanic temperatures in the middle Miocene to development of the circum-Antarctic Current. Subtropical aridity could therefore not predate the late Oligocene.

The late Cenozoic climatic data for the western part of southern Africa, and the inferred climates, are summarized in Table 3. Axelrod & Raven (1978) have shown that desiccation has been progressive since the late Eocene, when temperate rainforest in Namaqualand was depleted, to become mixed with sclerophyllous vegetation. A mosaic of sclerophyllous woodland, grassland, and scrub vegetation, attributed to a dry climate with summer rainfall, persisted through the late Tertiary. The Miocene vertebrate fauna was typically pan-African.

The early Miocene initiation of the Antarctic Convergence and increasing biogenic productivity (Kennett *et al.*, 1975), and the development of the major ice cap in the middle Miocene to late Miocene which caused mass extinctions of bottom-dwelling organisms (Hammond, 1976), favoured phosphorite formation on shallow shelves. The middle to late Miocene phosphogenesis can be attributed to a considerably embayed coastline (Fig. 4), warm surface water, the limited zonation of the water masses, and the dissolution of organisms following sudden mass extinctions which generated abnormal concentrations of phosphorus. A weaker pole-to-equator pressure gradient is inferred for this period prior to full development of the Antarctic ice cap, and less intense and less stationary subtropical anticyclones resulted from lower surface temperature contrasts between land and sea

TABLE 3. Summary of climatic indicators and interpretations for the Cenozoic of the west coastal margin of southern Africa

	Southwestern Cape	Namaqualand	South West Africa
Late Pleistocene hypothermal	Intensified atmospheric circulation (dunes); increased precipitation (cave record and vegetation change); invasion of grassland and rainforest (grazers, pollens); cold (cryoclastics); winter rain	Perennial rivers and intensified atmospheric circulation (dune plumes); increased precipitation (relict macchia vegetation); winter rainfall	Perennial rivers (archaeology and morphology); winter rainfall in south (Van Zinderen Bakker, 1975)
Late Pleistocene hyperthermal	Cold open coast with upwelling, and warm embayments (molluscs); arid (evaporites)	Arid (evaporites)	Arid (evaporites)
Middle Pleistocene	Pluvial grassland (grazers); ? winter rainfall	Cold open coast, upwelling (molluscs)	
Early Pleistocene	Cold open coast, upwelling (molluscs); sclerophyllous vegetation with reduced grassland (browsers); winter rainfall	Warm open coast, limited upwelling (molluscs); perennial rivers (fluvial sediments, peats); ? summer rainfall	
Pliocene	Open coast slightly warmer than today (molluscs); grassland (grazers); sclerophyllous vegetation (pollens); moist (perennial rivers, peats); mainly summer rainfall	Warm open coast, no upwelling (molluscs)	
		Perennial river drainage (extensive fluvial sediments)	
Middle to late Miocene	Warm open coast, upwelling (phosphorite, molluscs); little latitudinal zonation of the sea (cosmopolitan molluscs); grassland (grazers) and temperate rainforest (wood); summer rainfall	Warm open coast, some upwelling (phosphorite, molluscs); little latitudinal zonation of the sea (molluscs); summer rainfall	Wooded-grassland (rhinoceros and ruminants); summer rainfall
Early Miocene			Wooded-grassland (herbivores); riverine woodland (tragulid remains) summer rainfall
Oligocene		Ecotonal area between temperate rainforest and sclerophyllous vegetation (pollen and leaf flora); dry, summer rainfall	

in lower latitudes. Intermittent upwelling, warmer Central Water in the upwelling system, and an embayed coastline contributed to warmer coastal water on the west coast. The cosmopolitan molluscs therein showed only limited latitudinal zonation. Kennett *et al.* (1975) have suggested that the modern zonation of the water masses was only established in the late Miocene or early Pliocene, when there was a major increase in upwelling at the Antarctic Convergence. Cifelli (1976) has shown that a 10° poleward expansion of warm gyral water occurred in the North Atlantic in the Miocene. In the northern hemisphere, the equatorward retreat of the limits of the tropics is associated with the Miocene–Pliocene boundary.

Climatic change is a response to variations in the nature of atmospheric circulation due to changing thermal conditions. Aridity on the west coast of southern Africa is controlled by the cold Benguela Current. A nearly modern upwelling system could only be realized in the late Miocene or early Pliocene, with the full development of the Antarctic Convergence, and with the increasing intensity and stability of the sub-tropical anticyclonic circulation throughout the Neogene (Axelrod & Raven, 1978). Sedimentological, palaeontological and geochemical studies of deep sea cores from the Walvis Ridge Abutment show a marked intensification of upwelling on the west coast of southern Africa in the early Late Miocene (Siesser, 1978). In the south-western Cape, the Pliocene vertebrate fossils indicate grassland with summer rainfall, the sclerophyllous flora shows a trend towards a Mediterranean climate, and the molluscan evidence suggests an open coast influenced by the northern decaying end of a zone of cold upwelling. A relatively weak pressure gradient, and a more southerly position of the South Atlantic anticyclone, possibly induced weak and intermittent mid-latitude westerly depressions, while southerly extensions of the intertropical convergence brought summer cyclonic rains.

The fossil record and sedimentary facies show that semi-desert regions have spread mainly since the Pliocene, to replace the sclerophyllous woodland and grassland. The sclerophyllous vegetation was derived from taxa in the retreating vegetation that were

structurally pre-adapted to drought (Axelrod & Raven, 1978). An intensified pressure gradient, and a strong, persistent, and stable anticyclone off the west coast were established by the end of the Tertiary. With the consequent intensification of seasonal upwelling to present proportions, winter rainfall and desert climates then spread in southern Africa. Faunal and floral evidence show that semi-arid conditions were established in the south by the end-Pliocene or earliest Pleistocene, although cold upwelling had not fully influenced the Namaqualand coast then.

The Quaternary climates of southern Africa are related to the global climatic oscillations. The climatic and vegetation patterns were characterized by periodic incursions of grassland and temperate rain-forest during the pluvials, which displaced the sclerophyllous fynbos. Vertebrate fossil assemblages show an alternation between hypothermal grazer-dominated and hyperthermal browser-dominated assemblages.

In the late Pleistocene hyperthermal, a slight shift southward of the subtropical anticyclones effectively shortened the Benguela Current, and permitted a further southward flow of the warm inshore Angola Current (Fig. 2). This increased the likelihood of free-swimming tropical mollusc larvae being able to colonize the more numerous estuaries and lagoons created by marine transgression in the hyperthermal. Addicott & Emerson (1959) have shown that in California too, thermally anomalous mollusc populations thrived in last interglacial embayments far beyond their normal geographic ranges. Extensive evaporites along the west coast of South Africa imply more arid conditions there, and less frequent winter rainfall (Flemming, 1977), as a result of a corresponding southerly shift of the westerlies; a greater southward penetration of summer cyclonic rain in the northern regions was also possible. A weaker pressure gradient and less intense atmospheric circulation favoured lower evapotranspiration rates.

Ice age circulation is characterized by a greater mobility of the subtropical anticyclones and an intensified circulation of the westerly flow (Hays *et al.*, 1977). During the glacial maximum 18 000 years ago, significant changes in oceanic circulation affected south-

L. Pleist.
hyperthermal

ern Africa. In the South Atlantic, the Southern Polar Front shifted 10° northwards (Van Zinderen Bakker, 1976), the Benguela Current was colder and had a greater northward flow, and the east coast was less influenced by the Agulhas Current (CLIMAP Project Members, 1976).

Both Australia and southern Africa were affected by a 5° equatorward shift of the subtropical anticyclones in the late hypothermal (Van Zinderen Bakker, 1975; Bowler, 1976; Bowler *et al.*, 1976). Low hypothermal temperatures are conducive to the establishment of a greater intensity of the anticyclonic high pressure belt (Wyrwoll & Milton, 1976). The expansion of dunefields in Australia was encouraged by compression of the tracks of the anticyclones, which resulted in a greater frequency of influence of hot continental air masses, an intensified atmospheric circulation, and increased evapotranspiration rates in the vicinity of the anticyclones (Bowler, 1975, 1976). Furthermore, summer wind patterns then had a stronger westerly component than today. In Australia, the peak of aridity was 18 000–16 000 years ago, when lake levels fell. Aeolianites and dune plumes in southern Africa also show the consequences of an intensification of atmospheric circulation at this time; there was also a northward shift of the arid zone, so that northern Angola, the northern Kalahari, and the Congo Basin experienced greater aridity than formerly during the glacial maximum about 20 000 years ago (Grove, 1969; Butzer, 1976).

Further to the south, the zone of westerly depressions also moved northward in the hypothermal. Allowing for the cooler climate, and reduced evaporation over the oceans, the southern parts of South Africa experienced accordingly a greater year-round precipitation, with a winter maximum (Fig. 2d) (Butzer *et al.*, 1973; Van Zinderen Bakker, 1975; Tankard, 1976b). An invasion of temperate rainforest elements displaced the winter rainfall sclerophylls into the present Namib and western Karoo, where relict patches of them still exist (Rourke, 1972; Axelrod & Raven, 1978). The sclerophylls only returned with the subsequent expansion southward of the dry climate 12 000–9000 years ago (Klein, 1974). With the consequent reversion to

ephemeral river flow 9000 years ago, when sea level had nearly recovered (Tankard, 1976a; Tankard & Schweitzer, 1974), the mouths of Namaqualand rivers (Fig. 6) approximately assumed their present positions.

Although the climates of both Australia and southern Africa 18 000 years ago were characterized by an intensification of the arid zones and stronger westerly wind components in the south, the southern African climate departs from the Australian model in that the stronger westerlies also brought increased precipitation to the southern regions. This departure is attributed to the greater continentality of Australia, in which the strong westerly component would have originated in the arid interior (Bowler, 1975); in contrast, the westerly component of southern Africa would have originated over the Atlantic Ocean (Fig. 2). Modern differences in the climates of the two regions are emphasized by the fact that coastal western Australia is today not influenced by upwelling (Meigs, 1966). The climate of coastal California 12 000–17 000 years ago also was very similar to that of the southern parts of South Africa, and increased rainfall and runoff, and a more intense upwelling have also been attributed to an equatorward shift of the climatic belts there (Gorsline & Prenskey, 1975).

Available evidence suggests that the Namib Desert system was established in the Quaternary, although Acheulian archaeological remains (Korn & Martin, 1957), and the existence of dry river courses (Selby, 1976), indicate that the desert has at times been less arid than at present. The desert was, however, never eliminated, being shifted latitudinally in pluvials; and during the hypothermal, desiccation was intensified in the arid core.

Van Zinderen Bakker (1975) has suggested that the Namib Desert could have originated in the Oligocene, when cold Antarctic Central Water first moved northward. As evidence of the desert's antiquity, Koch (1960) and Van Zinderen Bakker (1975) both cite the degree of endemism of the desert biota, particularly the Tenebrionid beetles, which comprise thirty-four genera and 200 species. (Koch included within the Namib the semi-arid regions of the southwestern Kalahari and Namaqualand.) But M.-L. Penrith has com-

mented subsequently (personal communication) that the high degree of diversification in all ecotypes suggests that the Tenebrionidae probably evolved rapidly, in that their apterous form would make them strongly susceptible to the influence of isolation and would promote rapid evolution. Other groups within the Namib (e.g. Carabidae and Scarabaeidae) are much less diversified. Penrith (1977) believed that the Namib insects are largely derived from the northwestern Karroo, the Kalahari, and the Namaqualand areas. The Namib insects are all xerophilous, and their dominance in the present desert is likely to have been the result of desiccation eliminating the non-xerophilous insects, which must have existed in the original fauna; thus the original potential (pre-adaptation) is more important than the time factor involved in faunal selection. The present distribution of the beetles is apparently controlled more by the nature of the substrate than by climate, in that many of the insect groups which have specialized in the desert are adapted to a sandy substrate: they are adapted to survive drought, but do not necessarily depend upon it. S. Endrödy-Younga (personal communication) also stresses the importance of such a substrate to insect faunas: he suggests that the desert as a regional feature is of comparatively recent origin, and replaced a wooded-grassland ecosystem.

Leppik (1957) and Ehrlich & Raven (1964) have emphasized the importance of plant-herbivore insect (including beetles and bees) interactions in generating diversity. There is a close mutual evolutionary relationship between bee and flower according to Leppik. In the Namib Desert, a remarkable insect diversity, including many genera of beetles and bees, contrasts with an exceptionally low plant diversity. This again suggests a comparatively recent inequilibrium, and the youthful development of aridity.

One further indicator relating to the origins of aridity is the plant *Welwitschia mirabilis*, which is restricted to the Namib Desert and fringing areas in the north. Typical xerophytic characteristics including the thick cuticle, few and deeply sunken stomata, small or reduced leaves, and the ability to shed or roll them up to reduce surface area, are absent in *Welwitschia*. In fact, *Welwitschia*

has the longest-lived leaves in the plant kingdom, with enormous surface areas (Bornman, 1974). Germination in *Welwitschia* is controlled by an inhibitor, which is only leached by sufficient rain, and young plants are most abundant in the wetter regions north of the desert which receive summer cyclonic rain. The plant evolved the CAM syndrome (Crassulacean acid metabolism, i.e. the ability for photosynthetic carbon reduction of organic acids converted from nightly absorbed CO_2) as a secondary phenomenon in order to adapt to progressively developing aridity (Bornman, 1977). Succulent plants, many of which inhabit arid areas, are characterized by CAM photosynthesis. Bornman believes that the vortex of *Welwitschia* distribution is Welwitschia Flats, north of the Namib Sand Sea. He suggests that *Welwitschia* may have evolved in a more moderate temperate or tropical environment, and that the Namib Desert must be youthful: the succulents, and desert taxa in general, appear to have been derived by adaptation of woodland and savanna taxa to increasing drought.

Conclusions

The development of aridity on the west coastal margin of southern Africa, and the origin of the Namib Desert, are related to the development of a cold Southern Ocean, a circum-Antarctic circulation, a thick Antarctic ice cap, and intensified Antarctic Convergence and latitudinal zonation of the oceans.

Like the Australian model (Bowler, 1976), the development of aridity in southern Africa was progressive and comparatively youthful. Aridity was initiated in the late Tertiary, but only fully established in the Quaternary. The effect of Quaternary global climatic oscillations was to shift the climatic belts, including the arid zone, rather than to eliminate the latter.

In the late Pleistocene hyperthermal, the climatic belts expanded poleward, and tropical west African molluscs were able to populate the warm and more numerous estuaries and lagoons created by a 7 m sea-level rise. Greater aridity in the southwestern Cape at this time is attributed to the greater influence of trade winds and the poleward shift of the westerlies.

In the succeeding hypothermal, a 5° equatorward shift of anticyclone tracks and climatic belts enabled westerly winter rainfall to reach latitude 23°S. The arid core moved equatorward, and desiccation within it became more intense due to the intensified atmospheric circulation and increased evapotranspiration rates over the continents, and the decreased evaporation over the cooler oceans. The westerly wind component was stronger than today.

Acknowledgments

The writers would like to thank the following for helpful suggestions in preparation of the manuscript: D. I. Axelrod, C. H. Bornman, J. M. Bowler, R. V. Dingle, S. Endrödy-Younga, Q. B. Hendey, D. K. Hobday, R. G. Klein, M.-L. Penrith, J. P. Rourke, E. M. van Zinderen Bakker and V. Whitehead. Drafting was undertaken by Chrissie Coetzee. We are grateful to the Director of the Geological Survey of the Republic of South Africa and the Director of the South African Museum for permission to publish this paper, under the Government Printer's Copyright Authorization No. 5857, dated 23 February 1977.

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