

Intimations on the Tertiary vegetation of southern Africa

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ABSTRACT

Fossil pollen sequences from the Cape Peninsula and the Saldanha region indicate that sub tropical vegetation and climates existed in these regions during the Miocene. The pollen record from the Cape Peninsula may point to the extinction of some taxa by the terminal Miocene/Early Pliocene with the subsequent strong development of macchia. This major change can probably be related to the maximum build-up of the Antarctic ice-cap in the latest Miocene and the accompanying profound palaeoceanographic changes such as the major cooling of the Benguela current with its effect on the aridification of the Namib desert, and the global glacio-eustatic sea level drop.

Parallel palynological and lithological studies in the Saldanha region show that prominent Miocene vegetation shifts were linked to profound local changes in the palaeoenvironment associated with the northward migration of the Miocene Berg River. Such studies are of paramount importance for the possible assessment of the causes of changes in the palaeoenvironment and should first be carried out at many more sites over a wide region. It is to some extent premature to draw firm conclusions as to the origin and migration of some taxa in southern Africa. The record of very primitive angiosperms such as the *Clavatipollenites/Ascarina* complex and Winteraceae is of considerable phytogeographic interest.

RÉSUMÉ

INDICATIONS SUR LA VÉGÉTATION DU TERTIAIRE EN AFRIQUE AUSTRALE

Des séries de pollens fossiles de la Péninsule du Cap et de la région de Saldanha indiquent qu'une végétation et des climats tropicaux existaient dans ces régions durant le Miocène. Le recensement des pollens de la Péninsule du Cap peut démontrer l'extinction de certains taxa à la fin du Miocène/début du Pliocène avec un fort développement du maquis. Ce changement majeur peut probablement être mis en rapport avec le développement maximum de la calotte glaciaire de l'Antarctique à la fin du Miocène et avec les profonds changements paléocéanographiques qui l'ont accompagné, tel que le refroidissement important du courant du Benguela donnant son aridité au désert du Namib, et la chute globale glacio-eustatique du niveau de la mer.

Des études palynologiques et lithologiques parallèles dans la région de Saldanha montrent que les changements de végétation remarquables du milieu du Miocène étaient liés aux profonds changements locaux dans le paléo-environnement associés avec la migration vers le nord de la Berg River du Miocène. De telles études sont d'une importance primordiale en vue d'une évaluation possible des causes de changements dans le paléo-environnement et devraient d'abord être conduites dans beaucoup d'autres sites dans une vaste région. Dans une certaine mesure, il est prématuré de tirer des conclusions fermes quant à l'origine et à la migration de certains taxa d'Afrique australe. Le recensement d'angiospermes très primitifs tels que le complexe *Clavatipollenites/Ascarina* et les Winteraceae est d'un intérêt phytogéographique considérable.

INTRODUCTION

The immense present day diversity of the biota of southern Africa, their phylogenetic relationships and adaptations to different environments are manifestations of important palaeogeographic events since the separation of Africa from Gondwanaland between Mid-Jurassic and Mid-Cretaceous times. During the rafting of this continent to its present situation it not only experienced the long-term development of the post-Gondwana physiographic features (Du Toit, 1966; King, 1967, 1978; Haughton, 1969; Truswell, 1970), but also the major Tertiary palaeoceanographic events of the Southern Ocean which profoundly effected global climates and biogeography. These were further greatly modified by the waxing and waning of the Pleistocene glaciations of the Quaternary, the degree of influence depending on the locality. In this connection a model has been synthesized for the Quaternary climates for southern Africa, based on a wealth of well-dated information (Van Zinderen Bakker, 1976; 1983). However, going further back in time to the Tertiary of southern Africa it

becomes more difficult to reconstruct palaeoenvironments because of the lack of suitable fossil material or absolute dating. Palaeoecologies are also difficult to evaluate against the background of vastly different Tertiary climates compared to the present situation. Reconstructions of Tertiary vegetation on a palynological basis alone is not ideal but in recent years this discipline has become of immense significance in both the Northern and Southern Hemispheres. Although many palynomorphs of this period can be assigned to modern taxa (Muller, 1981), many of the microfloras of the rich and diverse assemblages may remain unidentified, often because of the extinction of the parent taxa. From a palaeoecological point of view difficulties also arise because some identifications can only be made to family level. Nevertheless the study of fossil pollen remains a very important source of information on past vegetation.

A recent synthesis on the Cretaceous and Tertiary vegetation history of southern Africa has been provided by Axelrod & Raven (1978) who have based their hypotheses on present phytogeographic distributions and a few inadequate fossil floras from Banke in Namaqualand (Kircheimer, 1932) and from the Knysna lignites (Thiergart *et al.* 1963).

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Recently, however, abundant microfossil evidence has become available from palynological investigations of a number of terrestrial deposits from different sites in the South-Western Cape which is now for the first time giving a picture of the Cainozoic vegetation and climatic history of at least the southernmost region of the subcontinent (Coetzee, 1978a, 1978b, 1980, 1981). They indicate the subtropical nature of the Tertiary vegetation of which some of the components, as in other Southern Hemisphere continents, have become extinct. The pollen sequences from the Langebaanweg area of the Saldanha region and from Noordhoek on the Atlantic coastline of the Cape Peninsula which have so far yielded the most interesting data, will form the basis of the present discussion (Fig. 1).



FIG. 1.—Locality map. From J. Rogers in Coetzee & Rogers (1982).

In recent years much attention is being paid to biogeographic patterns in the Southern Hemisphere. In this connection it is interesting that abundant micro- and macrofossil evidence from most of the Gondwana segments shows great similarities in their Tertiary Floras. This phenomenon and present day distribution patterns are, however, not easy to evaluate against the background of the present controversies on the methods and philosophies of biogeographic analysis. The vicariance school

examines the vicariance of whole biotas as a result of continental drift and the subsequent postvicariance, as opposed to the fundamentally different view of long distance dispersal of individual components of biotas (Cracraft, 1980; McDowall, 1980). In this respect some of the palynomorphs from the Cape deposits which belong to the most primitive of angiosperms are of particular interest as the families to which they belong are extinct on this continent and have a disjunct distribution elsewhere.

PALAEOGEOGRAPHIC CONSIDERATIONS

Palaeoceanographic events

The well documented oceanographic events of the Tertiary in the Southern Ocean which have led up to the final glaciation of Antarctica have been of basic global biogeographical and palaeoenvironmental significance. This climatic evolution has been shown to be closely connected with plate tectonics, the far reaching effects of which have in recent years been described for the south-west Pacific by a number of authors such as Kemp (1978), Mildenhall (1980), Kennett (1980), Cracraft (1980), McDowall (1980), Coleman (1980) and others. From a biogeographical point of view as discussed for Australia (Kemp, 1978) it is also of great importance that the palaeolatitudes of the Gondwana segments and their concurrent positions in relation to the earth's pole of rotation have now been determined with some certainty from at least the Jurassic to the Late Miocene (Smith & Briden, 1977). Also of basic significance are the palaeotemperature curves for the Cainozoic estimated from oxygen isotope studies, for the bottom waters of the subantarctic (Shackleton & Kennett, 1975) and for the surface and bottom waters of the North Pacific (Savin, 1977 in: Frakes, 1979). Furthermore, the recent studies of global sea level cycles (Vail *et al.* 1977; Vail & Hardenbol, 1979) are receiving much attention in the explanation of palaeoenvironmental evidence.

As summarized by Kennett (1980), the main trend of Tertiary global climates is the general progressive climatic deterioration which was already initiated in the terminal Cretaceous. The underlying cause was the continuous breakdown of low latitude circulation and oceanic connections as a result of the progressive separation of the Gondwana segments until Antarctica finally became thermally isolated and situated across the pole. In this connection one of the most important events was the most precipitous drop (5°C) in temperature during the Cainozoic of the warm bottom ocean waters at the Eocene/Oligocene boundary (38 MY). This major change has been attributed to the progressive separation of Australia from Antarctica. Unrestricted flow of the Circum Antarctic Current set in after the final separation of these two continents by Mid-to Late Oligocene (30–25 MY) and the opening of the Drake Passage by 22 MY. It is significant that the largest relative fall in global sea level of the Cainozoic has been recorded for the Mid-Oligocene (30 MY) (Vail *et al.*, 1977; Vail & Hardenbol, 1979). It is also of importance that during this time the first weak spasmodic introduction of cold water into the Benguela Current has been recorded off the Walvis Ridge (Siesser, 1978).

The second profound climatic-glacial event was the development of the major ice-cap on East Antarctica and increased ice-rafting in the Middle Miocene (14–11 MY). It is significant in this regard that oceanographic studies off the Walvis Ridge indicate that the major cooling of the Benguela Current occurred in Late Miocene times with the subsequent rapid desiccation of the Namib Desert (Siesser, 1978). A marked increase in the ice volume of Antarctica occurred during the terminal Miocene (ca. 5 MY) which is estimated to have exceeded the present ice mass by about 50%. This was accompanied by a rapid northward migration of the Antarctic Convergence by 300 km and a marked global glacio-eustatic drop in sea level (200 m below the present sea level) (Vail *et al.*, 1977; Vail & Hardenbol, 1979; McKenzie *et al.*, 1979; Kennett, 1980). This important event which had far reaching biogeographical effects especially in coastal regions is considered to be partly responsible for the total isolation of the Mediterranean Basin and its salinity crisis (Messinian Stage) when it became tectonically closed off from the Atlantic inlet (McKenzie *et al.*, 1979). Evidence for this lowering of sea level has been recorded worldwide. These oceanographic changes have also been shown to be manifested in the cyclic transgressions and regressions of Miocene and Pliocene age in the southernmost parts of South Africa in the Saldanha region (Hendey, 1981a, 1981b; Coetzee & Rogers, 1982). These and other palaeogeographic events are basic to the explanation of the Tertiary biogeography of the south-western Cape.

Palaeotopography

Africa probably emerged from the Gondwana complex with segmented Gondwana biotas existing on a relatively flat Gondwana surface. Traces of the Great Escarpment of southern Africa were apparent at the close of the Karoo sedimentation in the Early or Mid-Jurassic and by Mid-Cretaceous it was already a prominent feature (King, 1967).

The subsequent evolution of the topographical features of the subcontinent has been described by King (1967, 1978) and it is important that by the end of the Tertiary 'the aspect of southern Africa was recognisably ancestral to the present' (King, 1978). Probably of particular interest with regard to the Tertiary vegetation of the Cape is the evolution of the Afromontane floristic Region (White, 1978; Axelrod & Raven, *l.c.*) along the eastern disjunct chain of mountains from Ethiopia along the Great eastern Escarpment to the southern Cape. From a phytogeographical point of view it is significant that the chain of high volcanoes in Ethiopia and East Africa are of early Miocene, Pliocene and Pleistocene age and could have afforded interrupted migration routes between the Northern and Southern Hemisphere during these periods (Axelrod & Raven, *l.c.*).

With regard to the south-western Cape, the topography is dominated by the Cape Folded Mountains of which the mountains of the Cape Peninsula are outliers. They are true orogenic mountains and are of Triassic age (Truswell, 1977).

In Tertiary times they could have probably afforded some degree of altitudinal zonation or provincialism of vegetation especially in connection with the forests while the coastal lowlands probably harboured other ecosystems which must have been greatly influenced during the major Tertiary transgressions and regressions. The relationship between the geology and the present dominant macchia vegetation has been described by Lambrechts (1979).

PRESENT VEGETATION OF THE SOUTH-WESTERN CAPE

The present macchia (fynbos) vegetation in this area is unique and is one of the most interesting floras of the world. Because of its richness in species, the high degree of endemism (Goldblatt, 1978) and disjunct taxa, this floristic region, now known as Capensis (Werger, 1978; Taylor, 1978) has been regarded as one of six floral kingdoms of the earth. Many profound physical and climatic changes have contributed to the evolution of the remarkable diversity of this sclerophyllous vegetation in which restioid, ericoid and proteoid elements are characteristic. A detailed description of the vegetation including the marshes in the Saldanha region under discussion has been provided by Boucher & Jarman (1977).

Although it is considered to be a 'Mediterranean' flora, Capensis is distinct from other 'Mediterranean' floristic counterparts in many ways (Goldblatt, 1978). The area occupied by this floral Region has been variously delimited (Acocks, 1953; Levyns, 1964; Taylor, 1978; Goldblatt, 1978). Roughly it extends from the vicinity of Port Elizabeth, which receives all the year round precipitation, to the extreme south-western parts of the sub-continent where the climate at present is characterized by cyclonic winter rainfall and summer aridity under the influence of the Atlantic high pressure system and the cold upwelling of the Benguela Current. The interior of southern Africa receives summer rain and is dry in winter.

This vegetation is not confined to the south-western Cape, but has interesting outliers at increasing altitudes to the north in the mountains of the Karoo and Namaqualand and also in the north-east along the eastern disjunct chain of mountains of Africa as far as Ethiopia (Levyns, 1964; White, 1978; Killick, 1978). In agreement with Acocks (1953) and Goldblatt (*l.c.*) and contra Taylor (*l.c.*) and White (*l.c.*), Capensis is here considered to include the temperate forest elements which survive in the Cape in moist ravines and sheltered niches. This forest flora is related to the mesophytic forests of the Afromontane Region (White, *l.c.*) and according to the present palynological record are certainly relics of the ancient Tertiary forests which covered this area millions of years ago (Coetzee, *l.c.*). Also included in Capensis (Goldblatt, *l.c.*) in the drier valleys are elements of the Karoo Namib Region.

Recent accounts such as those of Axelrod & Raven (*l.c.*); Goldblatt (*l.c.*) and Werger (*l.c.*) have

given extensive reviews and discussions on the questions of the affinities, diversity, migrations and phytogeographical relationships of Capensis. The origin and age of this flora have been intriguing problems and conclusions have mostly been speculative. However, the recent palynological record indicates that the present vegetation of this floristic Region in the now mediterranean climate is of relatively recent origin and possibly owes its evolution primarily to the glacial history of Antarctica (Coetzee, 1978a, 1978b). The later vicissitudes of the Pleistocene epoch are probably responsible for the species richness and high degree of endemism (van Zinderen Bakker, 1976).

LITHOSTRATIGRAPHY AND AGE OF THE DEPOSITS

The only relative date for the palyniferous deposits at the sites under discussion is from the Langebaanweg area of the Saldanha region. Here the S1 borehole studied is south of the Varswater Quarry (Fig. 1), which is well known for its phosphate deposits and for the Early Pliocene Varswater Formation containing the richest fossil vertebrate assemblages of this age in Africa (Hendey, 1981a, 1981b). A definite age for the underlying Gravel Member of the 'Saldanha' Formation, also represented in the borehole, is not yet available at present although it had previously been assigned a Late Miocene age (Hendey, 1981). This latter Formation overlies the Elandsfontyn Formation which contains the palyniferous peat of the S1 borehole (Coetzee & Rogers, 1982; Hendey, 1981a). A firm age, for the Elandsfontyn Formation is, therefore, still problematical. The pollen assemblages of the peat including continuous representation of Compositae, however, suggest a Late Miocene to Pliocene age range. In this connection it is interesting that *Aglaoreidia qualumis*, one of the pollen taxa present, has not been recorded as young as Late Miocene in Australia (A. Partridge, pers. comm.), where it was first described.

In the Noordhoek area the pollen sequences were analysed from the continuous S.20 core and parts of the O-core from boreholes drilled in a pocket of terrestrial sediments of Tertiary to Quaternary age (Fig. 1). At this site the palyniferous Elandsfontyn Formation is at present well below sea-level (−21 m to −50 m) (Rogers, 1980). Components of the rich and diverse pollen assemblages suggest an age younger than the Late Oligocene/Early Miocene boundary (Coetzee, 1978a) for this Formation at Noordhoek. Basic to this contention is the absence of Compositae pollen in the deepest levels and their rare occurrence in the upper levels of the cores from this Formation. In this connection, it is also significant that the pollen of the *Clavatipollenites/Ascarina* complex is abundant in the deeper levels of the Noordhoek deposits (−45 to −32.4 m) and for the most part very rare in the upper levels (−32 to −20 m). In the Saldanha deposits no pollen of this group has so far been recorded. As some of the species of *Ascarina* are coastal plants, it is likely that they could also have existed at Saldanha and would have been recorded if the deposits were older.

Support for an age not older than the Late Oligocene/Early Miocene for the Noordhoek deposits comes from evidence of a major regression around southern Africa during the whole of the Oligocene and Early Miocene exposing much of the continental shelf to erosion (Siesser & Dingle, 1981).

TERTIARY VEGETATION AND PALAEOENVIRONMENTS

Vegetation (Figs 2 & 3)

The Tertiary microfossil floras from the two different areas contain taxa which are comparable to fossil palynomorphs of southern Hemisphere continents like Australia, Ninetyeast Ridge and New Zealand (Kemp, 1976; Kemp & Harris, 1977; Couper, 1960; Stover & Partridge, 1973; Mildenhall & Crosbie, 1979; Mildenhall, 1980). The Tertiary pollen assemblages from Noordhoek appear to indicate a continuous record from probably Early/Middle Miocene to the Pliocene while those from Saldanha represent some period in the Middle or Late Miocene. The tentative pollen zones (Coetzee, 1978a, 1978b) for the Noordhoek area are at present being refined and can therefore not yet be firmly correlated with those erected for Saldanha (Coetzee & Rogers, 1982). However, pollen evidence shows that in both areas, particularly at Noordhoek, mixed coniferous forests with tropical elements including several different palms, were more prominent during certain times while palms became dominant during other periods. During other intervals local swamp was more evident. At Noordhoek the pollen sequences show that some of these Tertiary elements became finally extinct and that other subtropical taxa no longer continued to exist there. The disappearance of this type of vegetation in this area probably occurred in the Pliocene as suggested by the time ranges of certain pollen taxa in other Southern Hemisphere continents and by comparison with pollen assemblages from Saldanha (Tankard & Rogers, 1978). It has also been shown that in this latter region woodlands and grasslands existed during the Early Pliocene which supported long necked giraffes, grazers such as alcelaphine antelopes, *Hipparion*, rhinoceros and the remarkable woodland bear, *Agriotherium africanum* (Hendey, 1980, 1981a).

During the forested periods of the Tertiary the following were among the forest pollen taxa recorded ('extinct' refers to Africa): *Podocarpus* spp. (Podocarpaceae); *Microcachrydites* sp. cf. *M. antarcticus* (Podocarpaceae, extinct); *Widdringtonia* (Cupressaceae); *Cupanieidites* sp. cf. *C. orthoteichus* (Sapindaceae, Cupanieae, tropical to subtropical); *Haloragacidites* sp. cf. *H. harrisii* (Casuarinaceae, extinct); Myricaceae; *Echiperiporites*; *Croton* sp. (Euphorbiaceae, tropical-subtropical); Palmae (subtropical to tropical, partly extinct); Myrtaceae; *Alchornea* sp. (*Psilatricolporites operculatus*, Euphorbiaceae, tropical); *Rauvolfia* sp. (*Margocolporites rauvolfii*, Apocynaceae, tropical); *Cunonia* sp. (Cunoniaceae); Sapotaceae, Combretaceae/Melastomataceae-type (subtropical-tropical); *Celtis*

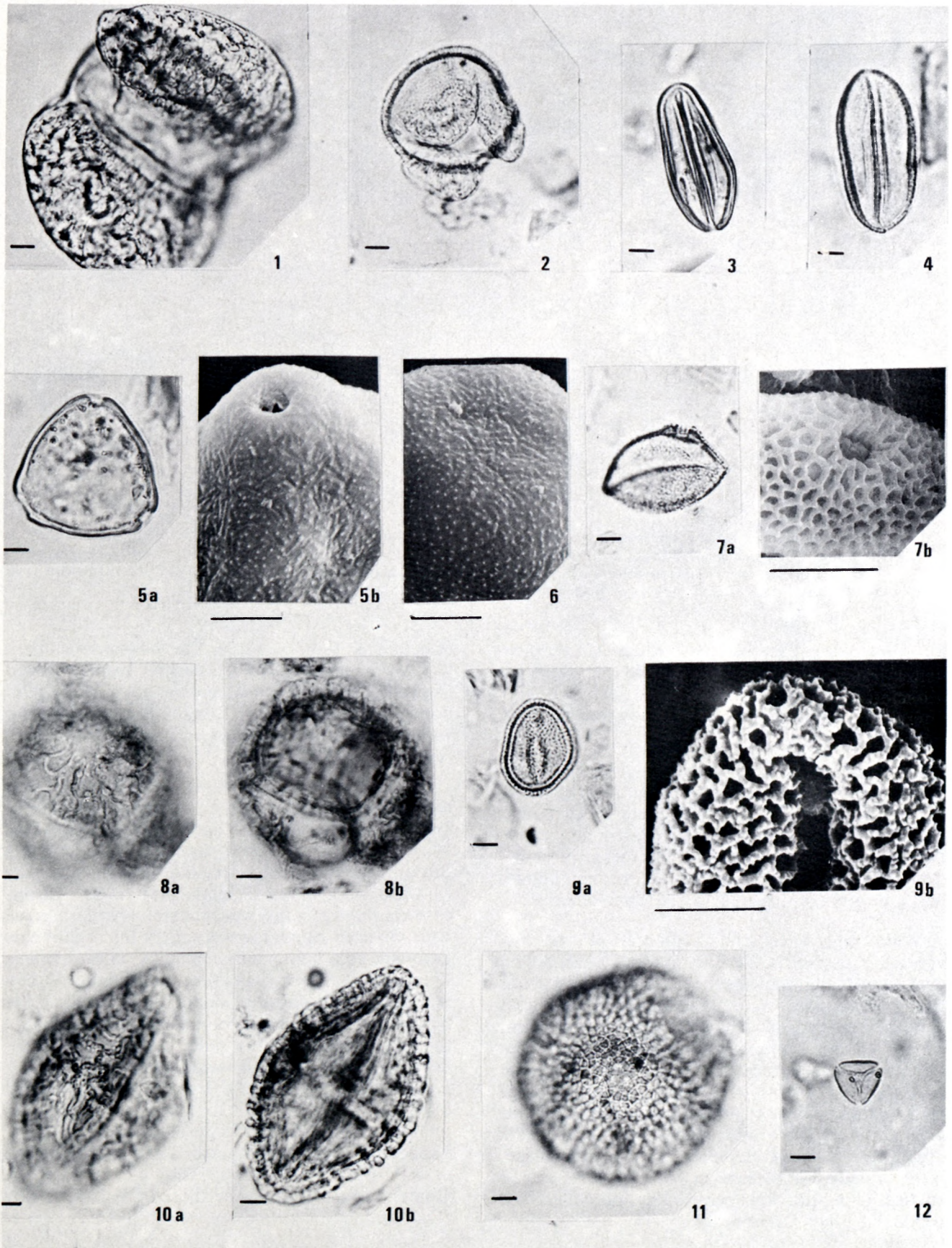


FIG. 2.—Fossil pollen of Miocene age from terrestrial deposits in the south-western Cape. Scale bars = 5 μ m. Noordhoek: 1, Podocarpaceae; 2, *Microcachrydites* sp. cf. *M. antarcticus*; 3, 4, Palmae; 5a, *Haloragacidites harrisii* (Casuarinaceae); 5b, scanning electron micrograph showing 'regularly spaced, minute grana borne on or at the intersections of vaguely defined linear elevations' (Kemp & Harris, 1977); 6, scanning electron micrograph of *Casuarina equisetifolia* (recent) revealing a similar surface configuration to 5b; 7a, *Aglaoeidia qualumis*, median focus showing annulus around the pore (see *A. qualumis* Partridge n. sp., Plate 20 figs. 8, 9, (Stover & Partridge, 1973)); 7b, scanning electron micrograph of the pore area; 8a, *Pseudowinterpollis* sp., tetrahedral tetrad, high focus showing the distal pore of a monad surrounded by the wavy reticulum; 8b, median focus showing clavate bacula; 9a, *Clavatipollenites/Ascarina* complex; 9b, scanning electron micrograph of colpus area; 10a, *Calodendrum* sp., high focus; 10b, median focus; 11, *Croton* sp., 12, *Cupanieidites* sp. cf. *C. orthoteichus*.

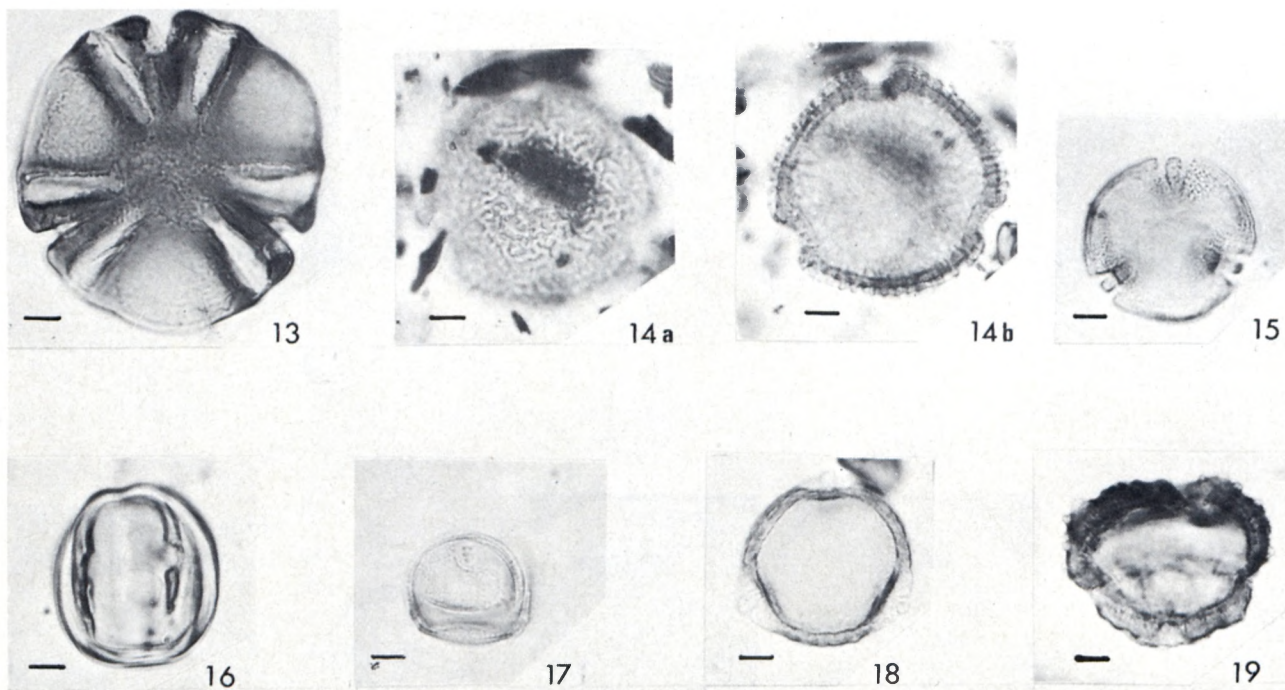


FIG 3.—Fossil pollen of Miocene age from terrestrial deposits in the south-western Cape. Scale bars = 5 μ m. Saldanha & Noordhoek: 13, *Rauvolfia* sp. (*Margocolporites rauvolfii*) (Saldanha); 14a, *Canthium* sp. (Saldanha), high focus; 14b, median focus; 15, *Alchornea* sp. (*Psilatricolporites operculatus*) (Saldanha); 16, Combretaceae/Melastomataceae type (Noordhoek); 17, *Celtis* sp. (Saldanha); 18, *Cliffortia* sp. (Saldanha); 19, Compositae (Saldanha).

sp. (Ulmaceae); Taxa such as the *Clavatipollenites/Ascarina* complex (Chloranthaceae, extinct), *Pseudowinterapollis* (Winteraceae, extinct) and *Calodendrum* (Rutaceae) were only recorded at Noordhoek.

When the palms were dominant very few forest pollen taxa, of low diversity, were recorded and when marsh conditions were more evident the extinct *Aglaoreidia qualumis* Partridge, from Australia and Restionaceae were variously abundant. The affinity of the former taxon is not known but it is probably related to the Sparganiaceae.

With regard to the evidence of macchia vegetation during the Tertiary in these areas, pollen data indicate that some elements like the Proteaceae and Restionaceae were consistently present and variously abundant. In the Noordhoek area, Thymelaeaceae, Gramineae and Ericaceae were extremely sparsely recorded from a time before the first appearance of the Compositae, whereas *Cliffortia* and *Stoebe* (Compositae) appeared sporadically at respective later stages. In the Saldanha area these macchia elements, without Ericaceae, were already established in the Miocene period studied (but with low percentages of pollen and contained more Gramineae).

Palaeoenvironments

In an attempt to reconstruct the local Tertiary palaeoenvironments in connection with the above vegetation changes along these coastal areas, it is considered to be of paramount importance to carry out parallel detailed lithological and palynological studies. So far in the case of the Saldanha area this has been achieved with very interesting results

(Coetzee & Rogers, 1982). The pollen zones here indicate a retrogressive succession from a mixed tropical coniferous forest containing palms to palm dominated vegetation and finally to a local swamp with abundant *Aglaoreidia qualumis* and Restionaceae.

These vegetational changes are consistent with the lithological details from the Elandsfontyn Formation at the S1 site and the wider Saldanha-Hopefield region which indicate a fluctuating fluvial environment associated with a meandering Miocene Berg River (Rogers, 1980, 1982). In this case the tropical forest was probably riparian. As the river changed its course this gallery forest probably gave way to a dominant palm situation as drainage deteriorated (Moore, 1973) on a proximal developed floodplain. Further flooding, as a result of the S1 site becoming a distal floodplain, probably caused the deterioration of the palm vegetation and the development of a fresh water swamp (Coetzee & Rogers, 1982). The Berg River which is the most important river in the south-western Cape has gradually migrated from its palaeovalley south of the Langebaan Lagoon (Rogers, 1980), to a Pliocene estuary near the S1 site (Hendey, 1981a) to its Quaternary position on the shore of St Helena Bay (Fig. 1).

PHYTOGEOGRAPHICAL CONSIDERATIONS

Theories of the phytogeographical distribution of the flora of Capensis have suggested that the taxa of this floristic Region have arrived there from different Southern Hemisphere sources in ancient times, whereas others originated relatively recently from tropical African elements. (Levy, 1964;

Goldblatt, 1978; Johnson & Briggs, 1975; Axelrod & Raven, 1978). With the present knowledge of continental drift, palaeolatitudes of continents and the extensive palynological evidence now available from all the Southern Hemisphere continents, it may be possible to shed some light on these problems although much more evidence and multidisciplinary research from more localities are required.

The wide distribution of similar Tertiary floras especially in the southern Hemisphere is significant in connection with the vegetation of this period in southern Africa as this continent was the first to leave Gondwanaland, although direct austral biological links between Africa and Australasia existed via South America until Senonian times (Jardine *et al.*, 1974). It has been suggested (Levyns, 1964; Axelrod & Raven, 1978; Goldblatt, 1978) that some taxa reached Africa by long distance dispersal across a narrower Indian Ocean from Australasia via Ninetyeast Ridge (emergent in the Palaeocene) and the Mascarene Plateau including India, in the early Tertiary. In the Palaeocene Southern Africa with its long history as an island continent was, however, already situated at 15° further south than now, and India, according to the Palaeocene map of Smith & Briden (1977), was well separated from the southern continents. According to Leroy (1978), direct migrations between India-Madagascar and Australia had already become more difficult by Mid-Cretaceous times [Madagascar separated from Africa about Mid-Cretaceous (*ibid*)].

The phytogeographical aspects of some of the most significant pollen taxa of the Tertiary flora now extinct in the south-western Cape such as *Palmae*, *Casuarinaceae*, *Clavatipollenites* sp. and *Pseudowinterapollis* sp. have already been alluded to (Coetzee, 1978a, 1981). With more data available some of these taxa will be further digressed on in the following discussion.

As a consequence of its former position in the Gondwana complex, the early vegetation that covered these southern lands must to some extent have been shared by southern Africa although some provincialism of vegetation must have existed over the huge former land mass. Until at least Eocene times southern Africa situated at 50°S, like Southern Australia (Smith & Briden, 1977), must have experienced the high humidity and warmth of the early Palaeogene climate (Kemp, 1978; Frakes, 1979). This kind of climate could have maintained floras in southern Africa that were similar to those of the other Gondwana segments.

Ancient Angiosperms

It is of particular interest that pollen of the most ancient of Angiosperms, the *Clavatipollenites/Ascarina* complex and *Pseudowinterapollis* sp., another primitive angiosperm has been documented in the Noordhoek deposits (Coetzee, 1981).

(a) *Clavatipollenites/Ascarina* complex. The most recent discussion on the distribution, range and taxonomy of this palynomorph has been provided by Muller (1981). The microfossil *Clavatipollenites hughesii* Couper, first described from the Barremian

of England, has been considered to belong to the most ancient of angiosperms. In the Southern Hemisphere it has mainly been referred to as *Clavatipollenites* sp. cf. *C. hughesii* (Kemp & Harris, 1977). A strong affinity, however, exists between this pollen type and that of *Ascarina* (Chloranthaceae) which ranges from the Upper Cretaceous to the present in New Zealand (Mildenhall, 1980). This similarity has been the subject of continuous debate and in his consideration of the problem Muller (1981) agrees with Kemp & Harris (1977) to 'restrict the record for *Ascarina* to the Tertiary and indicate the possible identity of *Clavatipollenites hughesii* as Chloranthaceae with the oldest record as Aptian and to indicate it as *Ascarina* type'. According to the available records and ranges, Muller (*l.c.*) has demonstrated the continuity between *Clavatipollenites* sensu stricto and *Ascarina* and concludes that the Chloranthaceae or the ancestral group dates back to the Aptian and was dominant in the lower Cretaceous. Indications are that they were coastal plants.

The most restricted ranges for this pollen type are recorded in Brazil and Central Africa where the plants were eliminated in the Middle Cretaceous as a result of a drier climate (Muller, *l.c.*). In this connection it is significant that this microfossil, also recorded in off-shore sediments of Lower Cretaceous age (younger than Barremian) along the eastern and southern South African coasts (Scott, 1976; MacLachlan & Pieterse, 1978), is abundantly recorded in the Tertiary deposits at Noordhoek. It became extinct here, probably in the Late Miocene, before the last of the tropical Tertiary components of the vegetation disappeared. It was not recorded in the S1 borehole at Saldanha.

The Chloranthaceae do not occur in Africa today and the four genera have a very disjunct present distribution in the tropics. In this connection the presence of *Ascarina* today in Madagascar is an interesting phytogeographical phenomenon (Coetzee, 1981; Straka, 1966).

(b) *Pseudowinterapollis* (Winteraceae) is another interesting pollen taxon recovered from the Noordhoek deposits which probably became extinct in the Late Miocene/Early Pliocene (Coetzee, 1981). This family does not occur in Africa today but is confined to South America and the South Pacific and one species, *Takhtajania perrieri* occurs in Madagascar. This microfossil type, also recorded from the Upper Cretaceous and Tertiary of Australia and New Zealand (Stover & Partidge, 1973; Mildenhall & Crosbie, 1979; Mildenhall, 1980), is similar to the pollen of the extant *Drimys* (South America and Pacific). The only known fossil record of the Winteraceae from the Northern Hemisphere are the fossil leaves of *Drimys* from the upper Eocene from Oregon (Praglowksi, 1979). This record from the south-western Cape adds to the knowledge of the wider past distribution of this family.

The ancient forest

The Cretaceous and Palaeogene rain forests of most of the Southern Hemisphere continents show a

number of interesting similarities and give indications that Temperate Podocarp-Auracarean coniferous forests with *Nothofagus* spp. were mixed with tropical rain forest taxa (Cranwell, 1964; Kemp, 1978; Mildenhall, 1980). With regard to the important components of these forests it is, however, interesting that *Auracaria* that was still present in the Upper Cretaceous in the south-western Cape (McLachlan & Pieterse, 1978) probably became extinct before the beginning of the Palaeocene. It occurs, however, in the Palaeogene of India (Lakhanpal, 1970). *Nothofagus*, on the other hand has so far not been recorded in either the Cretaceous or Tertiary of southern Africa and is absent from deposits of this age in India and from Ninetyeast Ridge. This genus which seems to have had an Upper Cretaceous origin (Mildenhall, 1980) had probably not evolved by the time Africa and Greater India separated from Gondwanaland.

The Casuarinaceae, another Southern Hemisphere family, to which the form-genus *Haloragacidites harrisii* Couper has been assigned was an important constituent in the Tertiary forests of most of the Gondwana segments. The presence of this taxon in India has not been confirmed. This family does not occur in Africa today, but fossil pollen of this genus has been recorded at Noordhoek. Unconfirmed similar fossil pollen types have been recorded from Banke and the Knysna lignites. The possibility that this dispersed pollen belongs to the Casuarinaceae has already been discussed (Coetzee, 1978a). In this connection it is significant, as in other above mentioned cases, that *Casuarina equisetifolia* is indigenous to Madagascar (Straka, 1976). In Australia the Casuarinaceae were tropical components of the early rain forests and the megafossil records show that they belonged to the Division Gymnostomae which were the only type occurring before the separation of Australia from Antarctica. The fossil record from Patagonia supports a Gondwana distribution for these taxa. Casuarinaceae of the sclerophyllous Cryptostomae Division developed in Australia only after the separation of the two continents in the Eocene and during the progressive deterioration of the climate while the Gymnostomae became depleted (Christophel, 1980). It is possible that the microfossils assigned to the Casuarinaceae in southern Africa may have come from parent taxa of the Gymnostomae occurring in rainforests and that they became extinct in the south-western Cape at the end of the Miocene also perhaps as a result of the deterioration of the climate and progressive aridity. Macrofossil evidence, however would have to provide this information as the pollen from the two Divisions is difficult to distinguish.

Johnson & Briggs (1975) suggest that the Proteaceae of Australia and southernmost Africa originated in the Australian section of Gondwanaland in mixed mesothermic forests which became segmented with the separation of the complex. The first reliable microfossil evidence dates from Maestrichtian (Muller, 1981). Earlier occurrences are not yet certain (Dettman, 1981). According to Johnson & Briggs (*l.c.*) this family is probably derived from mesothermic tree forms and could

have arrived together with the gymnosperms, Podocarpaceae, *Widdringtonia* and other forest elements in Southern Africa. In this connection it is significant that *Proteacidites* has been recorded in the Cenomanian to Maestrichtian of the off-shore sediments in the south-western Cape (McLachlan & Pieterse, 1978). It must be pointed out, however, that *Proteacidites* does not necessarily include Proteaceae. Among the interesting components of these forests in southern Africa were probably Monimiaceae, fossil wood of which has been recorded from the Late Cretaceous of Pondoland, eastern Cape Province (Axelrod & Raven, 1978). The extant monotypic genus *Xymalos*, still occurring in these regions is also found today in Madagascar. Also recorded at Noordhoek is *Cupanieidites* sp. cf. *C. orthoteichus* a member of the Sapindaceae (Cupanieae) with a Gondwana distribution. The first occurrence of the Cupanieae dates from the Coniacian in the Late Cretaceous of Africa and India (Muller, 1981). *Calodendrum* of the primitive Diosmeae (Rutaceae) was also present among these Tertiary taxa at Noordhoek.

Macchia (Fynbos) elements

The Proteaceae and Restionaceae, [the latter also regarded by Johnson & Briggs (1981) as an old southern family] are well represented in the pollen assemblages of the Tertiary in the south-western Cape. These authors suggest that the evolution and diversification of ancestral sub-families of the Proteaceae had already taken place in the pre-Australian section of Gondwanaland. Comparison of the diversities of the early Tertiary form-genera of the south-western Cape and Australia remains to be evaluated. The Restionaceae, also of pre-Australian Gondwana origin, are first recorded from the Palaeocene and are considered to show a single ancient phytogeographic link with Africa (Johnson & Briggs, *l.c.*). It is also of interest that this family has a widespread Tertiary record in both hemispheres (Ladd, 1977).

Other Fynbos microfossil elements such as those belonging to the Compositae [with a late Tertiary appearance of *Stoebe*-type, Thymelaeaceae, *Cliffortia*, Graminae and Ericaceae (the latter not recorded at Saldanha)] were very sparsely represented until probably the Pliocene (as shown at Noordhoek) when the first strong development of Fynbos is evident from the pollen assemblages. By this time all traces of tropical Tertiary forest elements including the palms had disappeared (Coetzee, 1978a, 1978b). It has been suggested (Coetzee, *l.c.*) that this profound vegetation change is linked to the palaeoceanographic events associated with the maximum build-up of the Antarctic ice-sheet in the Terminal Miocene. However, according to Johnson & Briggs (1981) the present sclerophyllous communities of south-western Australia and the south-western Cape are rather the result of the progressive development of nutrient deficient soils than of the evolution of a mediterranean climate. They consider that these conditions already started in the Palaeogene in forests where nutrient deficiency at certain sites gave rise repeatedly to scleromorphic forms. This change could have been associated with

the deterioration of the climate, but under rainfall conditions permitting summer growth. The growth rhythm of the present Fynbos suggests an origin in summer rainfall conditions (Taylor, 1978). It is significant that at present macchia does not spread onto high nutrient soils in the mediterranean climates of either the Cape or Australia (Johnson & Briggs, *l.c.*).

It is not certain when the mediterranean type of climate set in in the south-western Cape as a consequence of the maximum Antarctic glaciation. Palaeontological evidence from the Saldanha area suggests that the transition from a probable monsoon climate to a mediterranean climate could have been in the early Pliocene. Precipitation must have been decreasing but a summer-wet/winter-dry climate was probably still prevailing. (Hendey, 1981b).

CONCLUDING REMARKS

Palynological evidence has indicated the existence of sub-tropical Tertiary vegetation in the south-western Cape from a period probably later than the early Miocene to possibly the early Pliocene. Many of the pollen taxa are similar to the Tertiary form-genera of other Southern Hemisphere continents. The continuous pollen sequence for this period from the Cape Peninsula suggests that most components of this type of vegetation had become eliminated by the early Pliocene. These extinctions and the dominant development of Fynbos vegetation are probably primarily related to major palaeoceanographic and palaeoenvironmental changes associated with the glacial evolution of Antarctica. In this connection the major cooling of the Benguela current and the aridification of the present Namib desert in the Late Oligocene must have initiated profound effects on the vegetation which continued into the Pliocene. According to Tankard & Rogers (1978) the progressive aridity of the subcontinent dates from the latter epoch. The pronounced sea level regression recorded on the South African continental shelf near the Miocene/Pliocene boundary (Siesser & Dingle, 1981) may have enhanced coastal dry conditions. Hendey (1981a) has correlated this event with the global glacio-eustatic sea level drop at 6,6–5,2 MY (Vail & Hardenbol, 1979). It is possible that these dry conditions could have affected extinctions of taxa like the *Clavatipollenites/Ascarina* complex.

It has, on the other hand, also been suggested that, as in south-western Australia, the dominant expansion of macchia in the Cape was due to the existence of nutrient deficient soils rather than to the change to a mediterranean climate. They consider this type of climate to have been superimposed on already pre-adapted scleromorphs. With regard to the origin and migration of the macchia vegetation much more palynological and lithological studies are essential before firm conclusions can be made.

The interpretation of local Tertiary shifts in vegetation as demonstrated by parallel lithological and palynological studies in the Saldanha region stresses the need for such detailed investigations at many more sites over a wide area before general

conclusions on regional vegetation changes during this epoch can be made. In the Saldanha region a monsoon climate (Hendey, 1981b) may have been responsible for the palaeoenvironmental changes. The possible high humidity of this period may be related to the global climatic optimum of the Miocene between 17 and 15,5 MY (Haq, 1980), the global high sea level of the Middle Miocene (Vail & Hardenbol, 1979) and the transgression of 16 MY along the S.W. African coast (Hendey, 1981b). A warm ocean and still warmer epicontinental seas could have contributed to the high humidity.

Many of the Tertiary vegetation elements including conifers, Palmae, Proteaceae, Restionaceae, the *Clavatipollenites/Ascarina* complex, Winteraceae and cf. Casuarinaceae could be of direct austral origin. The occurrence of these groups in the Tertiary of the south-western Cape and the disjunct distribution of some of these taxa in Madagascar could pose interesting problems in connection with vicariance and post vicariance biogeography.

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