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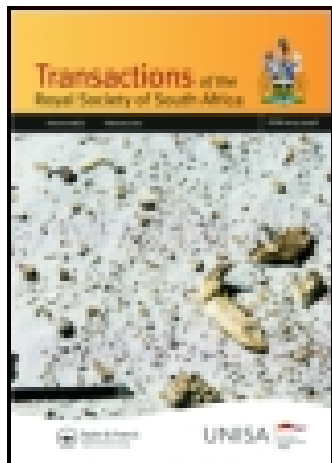
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Shaping of modern southern African biomes: Neogene vegetation and climate changes

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Long-term trends in climate, hydrology and geomorphology contributed to the formation of the current biomes of southern Africa. The Neogene terrestrial fossil record is patchy, due to the geomorphological evolution of the subcontinent and the restricted distribution of suitable sediment deposits. Here we review the hypotheses on the evolution of the topography and environment and concentrate on the fossil record, especially pollen, wood, charcoal, leaves and biomarkers. Tectonic studies suggest a lower relief landscape than at present at the onset of the Neogene. Southern Africa was drained by two river systems – the Kalahari and the Karoo Rivers – and was affected by an initially weak, cool Benguela current along the western coastline, gradually promoting an aridity trend along the southwestern coast. The Cape region during the Miocene, when the Great Escarpment began to evolve, was characterised by humid, subtropical forests not unlike those still occurring on the much wetter subtropical eastern shore of southern Africa. Southern Namibia (Sperrgebiet) was probably covered by a “proto-savanna”; hyper-aridity developed further north along the Namibian coast. Probably with more uplift, the hydrological regime changed *c.* 15 Ma when the palaeo Karoo and Koa Rivers were captured by the Kalahari/Orange River and drained western South Africa. Miocene fossil sites are missing in southeastern Africa. In southwestern Africa an enhanced aridity trend and the shift to a winter rainfall regime during the late Miocene-Pliocene was triggered by the development of the Westerly wind system and further strengthening of the cold Benguela current enhanced by the development of the Antarctic sheet and opening of the Drake passage. Eastern southern Africa was dominated by the Great Escarpment and relatively shorter deeply incised rivers and higher rainfall than the west. The Pliocene saw the evolution of the Fynbos and Succulent Karoo biomes including the further radiation of several drought adapted plant families encompassing the Asteraceae and Aizoaceae. At the transition towards the Pleistocene, the region around Sterkfontein in eastern central southern Africa, important for hominid evolution, experienced a shift from a woody environment towards more xeric, open conditions. The Savanna biome today stretches from northeastern South Africa as far north as East Africa; the Grassland and Fynbos biomes are unique and the more arid biomes are dominant in the western half of southern Africa.

Keywords: Neogene; biomes; vegetation history; southern Africa

INTRODUCTION

Southern Africa has a rich variety of biomes, which were for example mapped by Pole Evans (1936), Adamson (1938), Acocks (1953) and Rutherford & Westfall (1994) (Figure 1). These biomes stretch from the winter rainfall regions encompassing the Fynbos biome and the Succulent Karoo biome in the west to the summer rainfall region in the eastern and central interior incorporating the Grassland biome, unique to southern Africa, and the southernmost extension of the Savanna biome. The latter extends as far north as eastern Africa and has a prominent role in the evolution of early hominins (Mucina & Rutherford, 2006; Cerling *et al.*, 2011). The vegetation of southern Africa underwent profound changes during the Neogene, although some biomes might have a Palaeogene origin (e.g. Albany thicket, see Cowling *et al.*, 2005). Existing reviews are partly outdated (e.g. Scott, 1995;

Scott *et al.*, 1997) or focus on selected biomes or regions (e.g. Linder, 2003; Cowling *et al.*, 2005). Even rather recent reviews of global vegetation dynamics during the Neogene indicate that Neogene profiles in southern Africa are scarce and that dating is often problematic in comparison to other regions (e.g. Pound *et al.*, 2012). Additionally many Neogene profiles from southern Africa are presented in unpublished theses (e.g. Sciscio, 2011). Due to arid climate and the erosional character of the interior, most fossiliferous sediments accumulated along the coasts and offshore (Scott, 1995). The scarcity of terrestrial Neogene sites in southern Africa makes the study of marine records invaluable as this allows, at least to a limited degree, an indication of the vegetation onshore (e.g. van Zinderen Bakker, 1984; Dupont *et al.*, 2005; Udeze & Oboh-Ikuenobe, 2005; Hoetzel *et al.*, 2015). Although direct palaeobotanical evidence in Neogene terrestrial sites is often lacking,

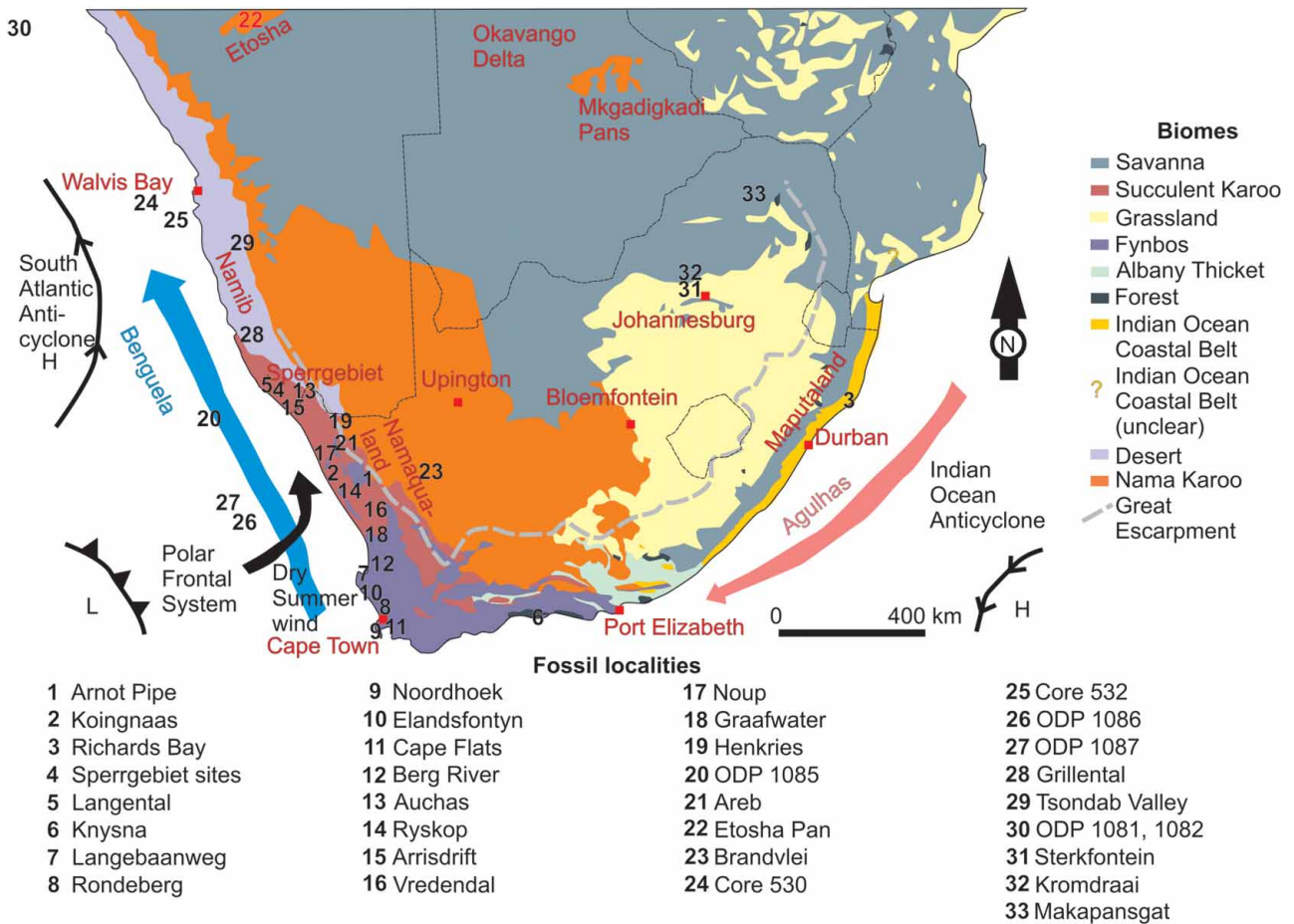


Figure 1. Major biomes of southern Africa: biome map modified after Russo *et al.* 2010 (Low & Rebelo, 1996; Mucina & Rutherford, 2006), wind systems and ocean currents after Roberts *et al.* (2013); Neogene and Palaeogene fossil sites mentioned in text are indicated by black numbers (see text for references), red: cities and landscapes.

geochemical approaches (e.g. studies of stable isotopes of speleothems [see Hopley *et al.*, 2007] or stable carbon and oxygen isotopic compositions of eggshells of Struthioniformes [see Ségalen *et al.*, 2006, Dupont *et al.*, 2013]) complete the knowledge of fossil environments. The Neogene changes of climate and vegetation are a consequence of several factors depicted in the sections below. Throughout the Neogene, the overall trend has been one of drying out; from the humid early and middle Miocene, with fluctuations, to today's arid to semi-arid western winter rainfall region, central sub-humid region and humid east coastal areas, the latter two characterised by summer rainfall.

SETTING

Palaeogeography, sea level changes and climatic trends

Compared with other continents Africa is topographically high, caused by an underlying superplume (Gough, 1973; Bond, 1979; Partridge & Maud, 1987) and by near-surface tectonics (Burke & Gunnell, 2008). After an initial period of uplift coinciding with the breakup of Gondwana *c.* 130 Ma, southern Africa was quiescent until *c.* 30 Ma (Burke & Gunnell, 2008) or until *c.* 20 Ma (Partridge, 1997a). During the quiescent period between *c.* 130 and 30 Myr, erosion prevailed and the "African Surface", that was first

recognised by King (1955, 1962), was formed and is still preserved in some major basins, such as the Kalahari, Congo and Chad Basins (Burke & Gunnell, 2008). During the Eocene (*c.* 56–34 Myr) the eastern continental margin of southern Africa was inundated; while in the subsequent Oligocene (34–23 Myr) a regression followed (Perissinotto *et al.*, 2013). Also, during the Oligocene the relatively higher elevation in the east resulted in three major river systems, one draining to the east and two to the west. The Limpopo River and many smaller, deeply incised rivers along the KwaZulu-Natal and Eastern Cape Coasts with the larger Sundays River in the southern Cape drained the interior and, *c.* 30 Ma, the escarpment along the eastern coast of southern Africa was formed by erosion and fostered high rainfall to the east (Hartnady, 1985; Thomas & Shaw, 1988; Botha & De Wit, 1996; Hattingh, 1996; Moore & Larkin, 2001; De Wit *et al.*, 2000). In addition, McCarthy *et al.* (1985), Malherbe *et al.* (1986), De Wit (1993) and de Wit *et al.* (2000) proposed two major westwards-flowing drainage systems during the Cretaceous (146–66 Myr) and Palaeogene/Neogene (66–2,6 Myr), the Kalahari and Koa Rivers that captured the waters to the north of the Griqualand-Transvaal Axis, exiting at the present day Orange River mouth, and a Karoo river that captured the drainage to the south of this axis, exiting at the present day Olifants River to the south.

In the early Miocene (23–16 Myr) the low-relief landscape was affected by the initiation of the still weak, cool Benguela current along the western coastline, slowly promoting an aridity trend along the southwestern coast. Siesser (1980), based on microfossils in a deep sea core, showed sustained upwelling from cold waters *c.* 10 Ma (Ward & Corbett, 1990; Pickford *et al.*, 2014b). Undisputedly, global palaeogeographical changes – for example the opening of the Drake passage between Antarctica and South America and the Tasmanian gateway between Australia and Antarctica (Wright *et al.*, 1991; Hassold *et al.*, 2009) – led to the establishment of the circum-Antarctic current, and consequently triggered the growth of the Antarctic ice sheet and Arctic glacial climates. The southern Ocean circulation and great Antarctic ice sheets were established by *c.* 34 Ma (Burke & Gunnell, 2008), the Drake passage opened *c.* 30 Ma (Barker & Burrell 1977; Barker & Thomas, 2004) or by *c.* 24 Ma (Pfuhl & McCave, 2005; Lyle *et al.*, 2007) and the circulation and icesheets were stabilised by *c.* 8.5 Ma (Hassold *et al.*, 2009).

During the middle Miocene (16–11 Myr) the Tethys Sea, controlling broadly zoned climates, was closed due to the collision of the African and Asian plate (Axelrod & Raven, 1978). The arid, followed by hyper-arid conditions along the West coast were present in the north by the early Miocene and in the south by the middle Miocene (Pickford *et al.*, 2014b; Guillocheau *et al.*, 2012, 2014). After the middle Miocene climatic optimum there was a period of decreasing temperatures (Coetzee, 1978; van Zinderen Bakker, 1984; Toggweiler & Bjornsson, 2000; Scotese, 2001; Cowling *et al.*, 2005; Hassold *et al.*, 2009; Majewski & Boharty, 2010).

Linder (2003) suggests a steeper climatic gradient from the equator to the poles from the middle Miocene onwards which globally led to the establishment of grasslands and savannas as well as pyrophytic vegetation. The Benguela current off the west coast of southern Africa, an upwelling system, cooled off from *c.* 12 Ma and again after 5 Ma (Jung *et al.*, 2014; Etourneau, 2014). The cool Benguela current led to winter rainfall and semi-arid conditions over much of the southwestern tip of South Africa (Deacon, *et al.*, 1992; Scott *et al.*, 1997; Roberts *et al.*, 2013). Seasonally fluctuating upwelling triggered high plankton biomass and large pelagic fish populations (Currie, 1953; Shannon 1985, Hutchings *et al.* 2009). In contrast the warm Agulhas current along the eastern shore of southern Africa was already in place throughout the Neogene, as indicated by strong erosional activity at the southern South African shelf which removed Oligocene to Quaternary sediments (Uenzelmann-Neben & Huhn, 2009). During the Pliocene the global climate cooled even more until a glacial period started in the Pleistocene (Hallam, 1994).

A possible two-phased Cainozoic uplift in southern Africa

The climate and vegetation history of southern Africa after the break-up of Gondwana *c.* 180 Ma is strongly related to geological aspects – for example, proposed Neogene uplift events since the last 20–30 Myr due to mantle convection – eventually leading to the elevation of the African surface (e.g. King, 1962; Partridge & Maud, 1987, 2000; Burke, 1996; Burke & Gunnell, 2008; Roberts & White, 2010; Jung *et al.*, 2014; Grab & Knight, 2015). It has been proposed that during the Pliocene from 5 to 3 Myr a second uplift occurred (Partridge & Maud, 1987; Partridge, 1997b; Moore *et al.*, 2009). The Neogene uplifts

resulted in enhanced erosion, the formation of new watersheds, new habitats, and the formation of a rainshadow desert creating the semi-arid Karoo and directly stimulating the diversification of southern African vegetation types (Desmet & Cowling, 1999; Cowling *et al.*, 2005). According to Jung *et al.* (2014), uplift in southwestern Africa might have triggered more intense coastal low-level winds, which led to an enhancement of the Benguela current upwelling (Seisser, 1980). The existence, the possible timing and cause of this second uplift remains a matter of debate. Flowers and Schoene (2010) suggest that the subcontinent might have been stable since the rifting in the Late Cretaceous. Rapid Pliocene uplift is questioned by Erlanger *et al.* (2012), who proposed, on the basis of isochron burial dating of terraces, persistent stability of the landscape during the last 4.5 Myr.

Palaeogene biomes of southern Africa

Most angiosperm families were in existence by the Palaeocene. The oldest Poaceae are from the Upper Cretaceous based on phylogenomics, pollen and phytoliths (Herendeen & Crane, 1995; Prasad, 2005; Jones *et al.*, 2014). The oldest grass macro-remains are from the late Palaeocene (*c.* 55 Ma, Jacobs *et al.*, 1999; Bremer, 2002). Ferns and gymnosperms are much older so most of the components of the modern vegetation were present, however the past diversity of angiosperms was probably lower. Palaeogene fossil records are rarer than Neogene records for South Africa but important to set the scene for the Neogene biomes.

Latest Cretaceous–Early Palaeocene vegetation is recorded in the crater-lake facies of the Arnot kimberlite pipe on the farm Banke in Bushmanland (no. 1, Figure 1). There are no direct dates for the flora but Scholtz (1985) inferred an age of *c.* 71–64 Myr based on the surrounding kimberlite pipes. Initially Rennie (1931), Adamson (1931) and Kirchheimer (1934) studied the leaves, wood and pollen respectively. This study was expanded by Scholtz (1985) who identified 64 types of pollen representing 28 plant families. Some of the main families are Proteaceae, Restionaceae, Ericaceae, Epacridaceae, Euphorbiaceae, Thymeliaceae, Chloranthaceae, Casuarinaceae, Cornaceae, Caesalpiniaceae, Anacardiaceae, Podocarpaceae and Araucariaceae. It is not possible to say to which biome this flora belonged as it has elements of the Fynbos, forest and woodland biomes but also has taxa which no longer grow in southern Africa, such as the Casuarinaceae and Araucariaceae. Most notably, several families and genera including *Nothofagus* sp., common in profiles from Australia or South America, are so far missing from the Arnot Pipe record and generally from Palaeogene, Neogene and Quaternary sediments in southern Africa. Few *Nothofagus* pollen specimens were recorded by Schalke (1973) from the Quaternary of the Cape Flats but interpreted as long distance transport from South America.

Along the west coast there are offshore and onshore terrigenous sediments. Fossil woods have yet to be described (Bamford, 2000) but some pollen samples have been analysed. Although the vegetation is consistent with relatively dry conditions in southern Africa at that time (Scotese, 2001), the large arboreal component is dissimilar to the desert asteraceous shrubland encountered in the region nowadays. Early Mutisiae-type Asteraceae with low spines evolved probably during the Palaeocene–Eocene (Koingnaas and Knysna, see below and compare Zavada & de Villiers, 2000; Scott *et al.*, 2006; Zavada & Lowrey, 2010), whereas during the Neogene

long spine Asteraceae pollen evolved (Scott *et al.*, 1997). Palynomorphs from Koingnaas, Namaqualand (no. 2, Figure 1), point to a forested temperate to subtropical environment with links to sites of the Cape floristic region (e.g. *Casuarinidites*, *Margocolporites*, *Cupaniedites*) and similarities to the Palaeocene Arnot Pipe pollen assemblage with Gondwana genera such as *Propylipollis*, *Podocarpidites*, *Cyathidites* (De Villiers & Cadman, 2001; no. 1 in Figure 1).

No other fossil plants are known from the Palaeocene in southeastern Africa but possibly Palaeocene lignites have been recorded near Richards Bay (Dingle *et al.*, 1983), but are of poor quality (no. 3, Figure 1).

Before the Bartonian (middle Eocene) the Sperrgebiet region (no. 4, Figure 1) in southernmost Namibia was humid and tropical and influenced by summer rainfall (Pickford *et al.*, 2014b). Based on phylogenetic data, Cowling *et al.* (2005) suggest that the Albany Thicket biome might have originated in the Eocene although some elements, e.g. *Cussonia*, *Encephalartos*, *Strelitzia*, might even reach as far back as the upper Cretaceous and Palaeocene (Cowling *et al.*, 2005). Former hypotheses, suggesting a Quaternary origin of the biome (Cowling, 1983), were shown to be incorrect and it was confirmed that thickets similar to the recent Albany Thicket Biome were part of a semi-arid tropical belt spanning the globe during the Palaeogene (Cowling *et al.*, 2005).

It is assumed that dry woodlands with a minor grassy component evolved in southwestern Africa during the Eocene and spread towards other regions in southern Africa when the climate became more arid (Axelrod, 1970, 1972).

An isolated terrestrial deposit of probably middle Eocene age with vertebrates and silicified woods occurs at Langental, near the coast in central Namibia (Ward & Corbett, 1990; Pether *et al.*, 2000; Bamford, 2000; Pickford & Senut, 2000; no. 5, Figure 1). The oldest of these sediments, the Blaubok Gravels (c. 55 Ma), contain some primitive woods with a distinctive arrangement of vessels in oblique flares, and some woods of the Combretaceae and Balanitaceae (Bamford & Ward, 2004). An isolated piece of gymnosperm wood has been recovered from the Buntfeldschuh Formation (upper Eocene). In contrast, Pickford *et al.* (2008) described a middle Eocene humid and tropical fauna from the Ystervark Carbonatite Formation in the Sperrgebiet (no. 4, Figure 1) and also re-dated these sites: the Langental Beds are considered to be early Miocene and the Blaubok deposits to be early Oligocene (Pickford *et al.*, 2011, 2014b).

Pollen and spores from the Koingnaas channel (no. 2, Figure 1), between Swartlinterijes and Buffels Rivers, indicate a forested temperate to subtropical environment, mostly unlike that of today, but with some families in common with the Cape Flora (de Villiers & Cadman, 1997, 2001). An Eocene age for these fluvial deposits along the west coast (Zavada & de Villiers, 2000) has been confirmed by foraminiferal ages (Scott *et al.*, 2006).

Clear evidence of Oligocene plant fossils from southern Africa is still missing. However, temperate Podocarpaceae-*Araucaria-Nothofagus* rainforest with austral (Gondwana) affinities is assumed along the southernmost coast of South Africa (inferred distribution of vegetation, Axelrod & Raven, 1978). Farther to the north, the Cape region c. 30–25 Myr (Rupelian-Chattian/Oligocene) was possibly characterised by rather humid, subtropical forests not unlike those still occurring on the much wetter subtropical eastern shore of southern Africa (inferred distribution of vegetation, Axelrod & Raven,

1978). During the Oligocene grasses, but not grasslands (Anderson, 1999), were already established, which might have been also true for southern Africa.

Along the Namaqualand coast there are a number of elevated fossiliferous marine packages with fluvial channels incising into them (Pether *et al.*, 2000). The fluvial sediments contain pollen which has been dated as Palaeogene to Neogene (de Villiers, 1997) and Cretaceous (Stevenson & McMillan, 2004). Since these channels have been re-incised these pollen dates point to a complex drainage history.

Many of the floral elements were present in parts of southern Africa before the Neogene but with the patchy record it is not possible to identify biomes or their distribution. The Miocene and younger records have much more data.

THE NEOGENE FORMATION OF THE MAJOR BIOMES OF SOUTH AFRICA

Fynbos biome

This biome (Figure 2) is restricted to the southwestern part of the sub-continent and affected by winter rainfall. Precipitation varies between 210 to 800 mm/year (Cowling *et al.*, 1997). It differs from the Succulent Karoo biome in climate, pedology and geology (Milton *et al.*, 1997). The Fynbos biome is arguably the most species rich temperate flora on the globe with >5000 species/10 000 km² (Barthlott *et al.*, 2007), has a high number of endemics and is characterised by families such as Ericaceae, Restionaceae and Proteaceae (Snijman, 2013; Linder, 2014).

Palynomorphs from probably middle Miocene lignites near Knysna in the Fynbos biome at the edge of the Forest biome on the southern coast of South Africa (Thiergart *et al.*, 1962; Thiergart, 1964; Carr *et al.*, 2010), point to wetland conditions and a mixed forest with sub-tropical affinity (no. 6, Figure 1; Figure 3). Pollen of palms, which are now extinct at the Cape, were identified along with *Podocarpus* pollen, Poaceae, Restionaceae, Proteaceae, Sapotaceae, Myricaceae and others (Thiergart *et al.*, 1962; Thiergart, 1964; Helgren & Butzer, 1977; Coetzee *et al.*, 1983; Carr *et al.*, 2010).

The similarity of the palynoflora of Knysna to that of other pollen sequences in the southwestern Cape- Langebaanweg, Rondeberg, Noordhoek (no. 7, 8, 9, Figure 1; Figure 3; Coetzee, 1978; Coetzee & Rogers, 1982; Coetzee *et al.*, 1983, Coetzee & Muller, 1984; Coetzee & Pragłowski, 1984; Scott, 1995; Sciscio *et al.*, 2013; Roberts *et al.*, 2013), points to a similar age which might post-date the middle Miocene according to Carr *et al.* (2010). In contrast, other references (Roberts *et al.*, 2011; 2013) suggest an early-middle Miocene age for the deposits at Langebaanweg, Noordhoek and Rondeberg. However, precise dating is not possible (see Scott *et al.*, 1997). Nonetheless all palynofloras from the southwestern Cape suggest a humid, subtropical climate (Scott *et al.*, 1997; Roberts *et al.*, 2013; Carr *et al.*, 2010). Also at Elandsfontein, from the Cape Flats and at Berg River, Miocene subtropical elements are reported (Rogers, 1980; Roberts *et al.*, 2013; no. 10, 11, 12, Figure 1; Figure 3). Regional Miocene vegetation changes were probably also linked to changes of the hydrological regime like the northwards shift of the Berg river (Coetzee, 1983). Several families, extinct in the Cape but still dwelling in Madagascar or Australia, for example Casuarinaceae, Chloranthaceae, Sarcocaulaceae and Winteraceae, exist in the palynological record up to the mid Miocene (Coetzee & Pragłowski, 1984; Coetzee & Muller, 1984; Goldblatt, 1996). At the end of the Miocene, as shown by phytoliths,



Figure 2. Fynbos biome, near Knysna/South Africa (photo: M. Bamford).

C_4 grasslands were spreading in the southwestern Cape whereas plants utilising the C_3 pathway (trees, shrubs, forbs, some grasses) were diminished (Rossouw *et al.*, 2009).

Major evolutionary steps within the Asteraceae took place from the Messinian (uppermost Miocene) until the Piacenzian (upper Pliocene), as supported by recent studies, placing the development of plant genera belonging to the daisy family within the last 6.9 Myr, probably influenced by the establishment of the winter rainfall conditions at the Cape (Bengtson *et al.*, 2015). Open Fynbos vegetation, already established during the early Pliocene, in association with subtropical C_3 vegetation, pointed to a more seasonal climate with a stronger Benguela current which was established at about 14 Ma (Hendey, 1984; Scott, 1995; Roberts *et al.*, 2011).

Succulent Karoo biome

The three dry biomes, the Succulent Karoo, the Desert biome and the Nama Karoo biome are distinct today based on distribution, floral composition and growth habits but during the Neogene they may not have been as distinctive. Here we discuss them as separate biomes but as will be seen there is an overlap in taxa, geographical distribution and climate.

The Succulent Karoo biome (Figure 4), part of the Greater Cape flora and a biodiversity hotspot “with the world’s richest semi-desert flora” (Linder, 2014), is defined as an oceanic semi-desert with a mild climate and winter rainfall in its western half whereas the eastern parts show either perennial or bimodal precipitation (Mucina *et al.*, 2006c). Fossil wood and pollen spectra from Namaqualand (van Zinderen Bakker, 1984; Scott *et al.*, 1997; Bamford, 2003) as well as faunal remains from the Sperrgebiet (Senut *et al.*, 2009; Senut and Ségalen, 2014; no. 4, fig. 1) also contribute to the knowledge about Neogene climate and vegetation development.

Fauna from the Sperrgebiet from 21–19 Myr (Aquitainian-Burdigalian, lower Miocene) indicates subtropical woodland conditions (Senut *et al.*, 2009) but during the Aquitainian winter rainfall predominated and aridity increased in the Sperrgebiet as suggested by Pickford *et al.* (2014b). The Burdigalian (c. 19 Ma, Pickford & Senut, 2002) silicified woods from the Auchas palaeo-channel on the Orange River (no. 13, Figure 1), draining the region since either c. 15 Ma (Burke & Gunnell, 2008), or 20–21 Myr (Pickford & Senut, 2003), include members of the Combretaceae and Burseraceae indicating a sub-humid climate (Pickford *et al.*, 1995; Bamford, 2003, Figure 3). Burseraceae and Combretaceae today typically grow in savanna environments which are normally influenced by summer rainfall (Coates-Palgrave, 2002). Bamford (2003) states that the fossil wood from Auchas points to a megathermal dry to mesic woodland or forest. We conclude that the middle Miocene environment might have been a “proto-savanna” (Figure 3, Pickford *et al.*, 1995).

Also during the Burdigalian, but slightly younger than Auchas (c. 18 Ma), terrestrial sediments from Ryskop (no. 14, Figure 1) revealed that the climate in Namaqualand was rather tropical/subtropical (Senut *et al.*, 1997, Figure 3). A more tropical and humid climate is suggested by Senut and Ségalen (2014) based on the presence of tortoises and crocodiles at Arrisdrift (no. 15, Figure 1; Corvinus & Hendey, 1978; Hendey, 1978) along the Orange River during the Burdigalian (c. 17.5 Ma), which might resemble a woody savanna (Figure 3). Fossil mammals from the same site point to a woody savanna flanked by gallery forest (Guérin, 2003; Pickford & Senut, 2002) which supports Pickford *et al.*’s (1995) assumption of an open woodland (Figure 3). Hendey (1984) reconstructed a dry, subtropical forest/woodland from Miocene fossil data of the Orange River. More Miocene

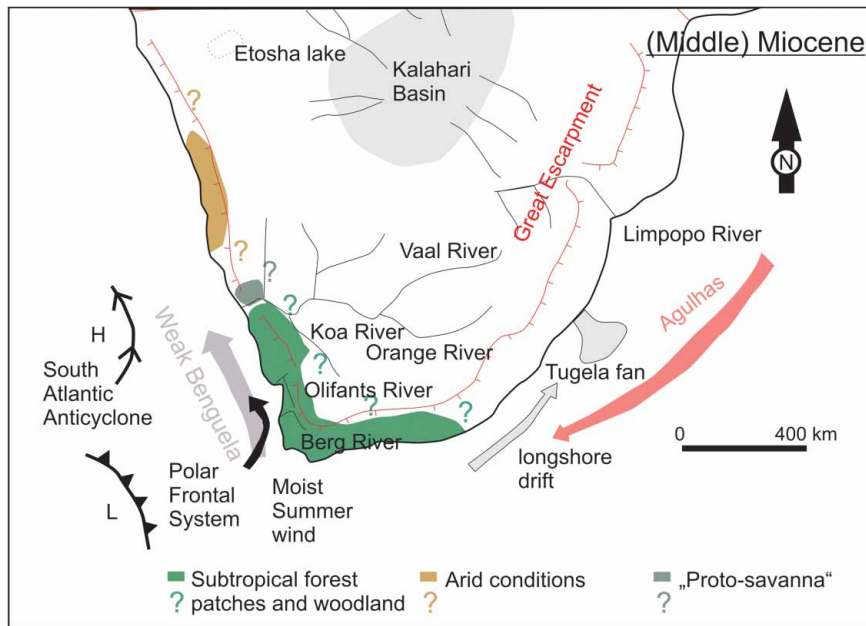


Figure 3. Schematic reconstruction of (middle) Miocene climate systems, vegetation patterns and palaeo-drainage systems modified and extended after Roberts *et al.* (2013), geomorphological features after Burke (1996), Dollar (1998), Burke and Gunnell (2008), wind systems and ocean currents after Roberts *et al.* (2013). Poleward migration of climate belts during the generally warmer Neogene and decreased southerly wind velocity weakened the Benguela System, with consequent increased monsoonal (summer) precipitation (Roberts *et al.*, 2013).

woods have been recovered from the Olifants River gravels near Vredendal (no. 16, Figure 1) and comprise members of the Meliaceae and Combretaceae with possible West African links. The dating is not precise but these woods represent mesic environments (Bamford, 1999a; 2000, Figure 3).

Miocene clays from sites in Namaqualand (Noup, Graafwater, Henkries, no. 17, 18, 19, Figure 1) show a transition

from humid woodland with *Olea* and *Podocarpus* and pollen spectra similar to the flora from the southwestern Cape, e.g. Langebaanweg, to open karroid vegetation where Fynbos elements also occur (Scott, 1995). Klak *et al.* (2004), on the basis of phylogenetic considerations, give an age of 8.7–3.8 Myr (Tortonian/upper Miocene-Zanclean/lower Pliocene) for the radiation of the mostly succulent Aizoaceae



Figure 4. Succulent Karoo biome, near Matjiesfontein/South Africa (photo: Marion Bamford).

which dominate the Succulent Karoo in terms of species diversity and coverage. The authors suggest that the onset of the winter rainfall regime has triggered this rapid diversification but also admit that Aizoaceae might have been present even during the Cretaceous since adjacent regions like the Namib were semiarid (with wet interludes) from that time. In contrast, a more recent estimate suggests that the radiation of the Aizoaceae occurred *c.* 17 Ma (Burdigalian, Arakaki *et al.*, 2011), showing that the dating of major plant lineages can be rather shaky and well-dated plant fossils from the region are in dire need.

The late Neogene evolution of the Succulent Karoo biome can also be reconstructed from marine cores along the southwestern African coast (Dupont *et al.*, 2005, 2011), although the Benguela current and winds might have mixed the signal which was moreover derived from a large region. Dupont *et al.* (2011) suggest a disappearance of *Podocarpus*-dominated Afromontane forest and subtropical coastal grasslands and thickets and a shift to succulent vegetation during the Tortonian and Messinian (upper Miocene) *c.* 11–4.7 Myr, prior to the assumed most recent uplift during the Pliocene.

An increase in summer-aridity might have been the main trigger for further vegetation changes during the Plio-Pleistocene, e.g. the strong increase of *Stoebe* and *Tarchonanthus* pollen in the marine core ODP 1085 (no. 20, Figure 1) offshore from the mouth of the Orange River (Dupont *et al.*, 2011). The north-western Kalahari including Namaqualand was more humid during the Pliocene than during the Pleistocene; at the Areb locality an equid, *Hipparion namaquense*, dwelled *c.* 6–4 Myr (Messinian-Zanclean, Pickford *et al.*, 1999, Figure 1, no. 21).

Nama-Karoo biome

The Nama-Karoo biome (Figure 5) is arid, continental and the annual rainfall varies between 70 mm in the north and 500 mm in the southeast (Mucina *et al.*, 2006b). In comparison to the neighbouring Succulent Karoo biome, the vegetation is less rich, centres of endemism are missing; it might well be the

least species rich biome on the sub-continent (Mucina *et al.*, 2006b). Several outliers exist in Botswana and Namibia, e.g. the Etosha pan (no. 22, Figure 1) and Makgadikgadi pans (Figure 1). Dominant families of the Nama-Karoo biome are Asteraceae, Fabaceae and Poaceae (Mucina *et al.*, 2006b).

The early and middle Miocene were characterised by subtropical and humid conditions with large trees, some up to 1.30 m in diameter occurring along the inland drainage of the Orange River, namely along the palaeo-Sak River near Brandvlei which was part of the palaeo-Kalahari River southern bank drainage (Bamford, 2000; no. 23, Figure 1; Figure 3). Based on the fauna and sedimentology from the old channels of the proto-Orange River there have been at least two pluvial phases in the Miocene and several phases of marine transgressions followed by regressions and river down-cutting into the filled channels (Pickford & Senut, 2003). The Miocene palaeo-Sak River (or Koa River) woods, also in the Brandvlei region (no. 23, Figure 1), belong to the Dipterocarpaceae, Myrtaceae, Oleaceae and Rutaceae, indicating a locally mesic environment. The Plio-Pleistocene wood has been identified as belonging to Polygalaceae (Bamford & De Wit, 1993).

The Etosha region experienced humid conditions until the middle Miocene, a shallow saline alkaline lake probably existed during the Oligocene, and since *c.* 16 Ma (Langhian) freshwater conditions (Lake Cunene) prevailed according to several authors (Buch, 1997; Hipondoka, 2005 and references therein; Dill *et al.* 2012; see no. 22, Figures 1 and 3). During the late Miocene fish and flamingo fossils as well as oncolites point to slightly alkaline lacustrine conditions (Miller *et al.*, 2010; Pickford *et al.*, 2014a; personal communications M. Pickford, 2015). Lake Cunene prevailed, with abundant freshwater gastropods, bivalves as well as findings of palms and unidentified dicotyledon trees during the Pliocene, but probably started to desiccate during the late Pliocene (Miller *et al.* 2010). At the end of the Neogene conditions were increasingly sub-humid to semi-arid (Pickford *et al.*, 2014a).



Figure 5. Nama Karoo biome, near Clanwilliam/South Africa (photo: Marion Bamford).



Figure 6. Desert biome, Gobabeb/Namibia (photo: Marion Bamford).

Desert biome

The Desert biome (Figure 6) covers a strip along the Orange River and extends to the Namib Desert. Its origin is interwoven with the evolution of the cold Benguela current since the late Miocene (Dupont *et al.*, 2005), the South Atlantic Anticyclone and strong northwards blowing winds (e.g. Pickford & Senut, 2000; Senut & Ségalen, 2014). Summer rainfall is predominant, the variable annual precipitation is from 10 mm at the coast to 80 mm in the interior (Khavhagali, 2010). Important families are Aizoaceae, Crassulaceae, Zygophyllaceae, Fabaceae, Asteraceae, Acanthaceae, Poaceae; the flora has a high level of diversity and centres of endemism (Jürgens, 2006). The evolution of the Desert biome is partly also revealed in sediments of marine cores along the southwestern African coast (van Zinderen Bakker, 1984; cores 530, 532, no. 24, 25, Figure 1; Udeze & Oboh-Ikuenobe, 2005, cores ODP 1085, 1086, 1087, no. 20, 26, 27 in Figure 1). The flora of the biome is associated with the formation of the Namib Desert c. 15 Ma (Schneider & Marais, 2005), although Ward and Corbett (1990; proto-Namib in the Palaeogene, 55–20 Myr) and Senut and Ségalen (2014; maybe early Miocene) suggest an even older age.

Southern Namibia was characterised by semi-arid climate during the early Miocene as evidenced by fossil termite hives (Grillental, no. 28, Figure 1) and vertebrate fauna suggesting a certain amount of grasses (Senut & Ségalen, 2014). Also in the southern Namib, aeolianites dated to the early Miocene, indicating aridity (Senut *et al.*, 1994; Goudie & Viles, 2015). Ratite eggshells accompanied by hives attributed to the harvester termite (*Hodotermes*) from those aeolianites (location in Tsondab valley, no. 29, Figure 1) underline an arid to hyper arid climate under summer rainfall conditions with some grass cover and maybe even some trees in the

northern part of the proto-Namib desert (Pickford, 2014; compare Pickford *et al.*, 2014b). In contrast the southernmost part of the desert was maybe affected by a winter rainfall regime (Pickford, 2014). Along the west coast of southern Africa, as recorded by marine cores (Dupont *et al.*, 2005), an aridity trend is obvious since the late Miocene, attested to by the predominance of grasses, chenopods and Asteraceae, which point to a Karroid shrubland (compare Udeze & Oboh-Ikuenobe, 2005, who indicated sparse vegetation during the late middle Miocene) whereas a single sample from the late Miocene points to mesic conditions (Van Zinderen Bakker, 1984; Scott *et al.*, 1997).

An analysis of a marine core (ODP 1081, no. 30, Figure 1) off the coast of Namibia, involving pollen, microscopic charcoal and the stable isotopic composition of plant waxes, draws the picture of a late Miocene-Pliocene (c. 9–3 Myr) spread of C₄ grasses, probably more pronounced in the central than in the southern Namib (Ségalen *et al.*, 2006; 2007; Senut & Ségalen, 2014), in an environment of shrinking grasslands and expanding deserts (Hoetzel *et al.*, 2013). Hoetzel *et al.* (2015) distinguish three vegetation phases utilising ODP 1081: a wet phase during the Tortonian, a transitional Messinian period with a pronounced spread of grasses and a rather dry Pliocene period with desert plants. Another marine core close by (ODP 1082, no. 30, Figure 1) shows major vegetation changes 3,4–1,8 Myr but they also show developments in the eastern hinterland of the desert (Dupont, 2006).

Albany thicket biome

The vegetation of the Albany thicket (Figure 7) is characterised by dense, woody, thorny, semi-succulent vegetation with many species, e.g. from families such as Crassulaceae,



Figure 7. Albany thicket, near Grahamstown/South Africa; with *Portulacaria afra* on the left, front (photo: Marion Bamford).

Aizoaceae (Acocks, 1953). The subtropical Albany thicket is widespread in the semi-arid areas of the Eastern and Western Cape, especially the Little Karoo and features a bimodal precipitation curve (Vlok & Euston-Brown, 2002; Vlok *et al.*, 2003). The origins of the Albany thicket, only recognised as a biome in the mid-1990s and defined by its distinctive absence of grass (Low & Rebelo, 1996), were investigated by Cowling *et al.* (2005) on the basis of fossil pollen and phylogenetic data, pointing to a probably Eocene origin of the biome (see above). During the Neogene, when climate deteriorated, several succulents and geophytes migrated from the neighbouring Nama and Succulent Karoo biomes and diversified in the thicket biome, e.g. Aizoaceae and Asteraceae (Cowling *et al.*, 2005).

Grassland biome

The temperate Grassland biome (Figure 8) dominates the cold and dry Highveld region in the eastern centre of South Africa where summer rainfall and winter drought occur (Mucina *et al.*, 2006a). Rainfall is 400–2500 mm/year, frost is common (Mucina *et al.*, 2006a). Bredenkamp *et al.* (2002) underline that the southern African grasslands are not determined by droughts but by high altitude cool conditions which block a possible colonisation by trees that have in general a tropical origin in southern Africa. However, Mucina *et al.* (2006a) emphasize that this hypothesis still has to be proven either by phylogenetic analysis or experimental studies. The Afro-Alpine region, characterised by Killick (1978) and within the Drakensberg range above 1800m, is also part of the biome. The exceptionally high biodiversity of southern African temperate grasslands and the large quantity of endemics might point to a rather ancient origin of this biome (Bredenkamp *et al.*, 2002). Poaceae, that evolved during the upper Cretaceous

(see above), became prominent globally only during the Neogene (Mucina *et al.*, 2006a, and references within; Christin *et al.*, 2014). Globally, grassy ecosystems were spreading during the early-middle Miocene (20–10 Myr), in the late Miocene C₄ grasses evolved (Cerling *et al.*, 1997; Jacobs *et al.*, 1999). Grasslands had an effect on the fire regime (fire intolerant vegetation was pushed back) and the composition of the herbivore fauna (Vrba, 1985a; Bond *et al.*, 2003). At the end of the Miocene the southern African Highveld was probably elevated (see discussion above) and the Great Escarpment was formed (Partridge, 1997a; King, 1963; 1978; Gough, 1973; Newton, 1974 in Bredenkamp *et al.*, 2002). Palynological and palaeobotanical data from the interior of the sub-continent in the current grassland is sparse. The Sterkfontein region in Gauteng, where grasslands reach their northern most limit, but savanna patches in low-lying, frost protected areas can be found (Mucina *et al.*, 2006a), is of importance for human evolution (Scott & Bonnefille, 1986). Based on vertebrate fossils and pollen in caves (Sterkfontein, Kromdraai, no. 31, 32, Figure 1), some conclusions on the Neogene vegetation development have been drawn (see Scott & Bonnefille, 1986; Scott *et al.*, 1997). However, Scott (1995) questioned the palynological results suggesting that contamination by modern pollen might have played a role in those cave environments. Based on previous work by Vrba (1985b) it was suggested that at c. 2.5 Ma (Pliocene-Pleistocene boundary) vegetation changed from mesic, wooded to open, xeric environments. Pollen samples from Sterkfontein and Kromdraai at the Plio-Pleistocene boundary point to an open *Protea* savanna although pollen taphonomical problems might be implied (see above, Scott 1995). Fossil wood from Sterkfontein Member 4 (c. 2.8–2.6 Myr) in the Sterkfontein Cave shows a local gallery forest (Bamford, 1999b).



Figure 8. Grassland biome, Seekoeflei/South Africa (photo: Marion Bamford).

Savanna biome

The Savanna (Figure 9), the largest biome in southern Africa, is species poor and stretches up to the Congo basin and towards eastern Africa (Rutherford *et al.*, 2006; Linder, 2014). Main characteristics are the predominance of summer rainfall, C₄ grasses and the lack of frost (Rutherford *et al.*, 2006; Hoetzel *et al.*, 2013). A marine core from the Angola basin (not depicted in Figure 1) contains late Miocene pollen of savanna trees, e.g. *Bombacidites* sp. (botanical affinity: Bombacaceae), *Acaciapollenites myriosporites* (botanical affinity: *Acacia* sp.), *Margocolporites vanwijhei* (botanical affinity: Caesalpiniaceae) and others (Partridge, 1978). In eastern Africa, faunal communities typical for a savanna environment have appeared only since the latest Miocene (Leakey & Harris, 2003) with Poaceae only becoming dominant after 5 Ma (Feakins *et al.*, 2005). C₄ photosynthesis in grasses has probably developed c. 8.5 Ma during the Tortonian (Sage, 2004).

Pliocene records are often associated with hominin cave sites. Hopley *et al.* (2007), on the basis of high-resolution stable oxygen and carbon isotopes from speleothems from Makapansgat valley, concluded that C₄ grasses already were established c. 4–5 Myr whereas in the late Miocene C₃ vegetation (shrubs, trees) was predominant. Seemingly, C₄ grasses expanded later in southern Africa than globally, c. 8–6 Myr as documented by Cerling *et al.* (1997). In contrast Rayner *et al.* (1993), working on sediments from Makapansgat (no. 33, Figure 1), concluded that the hominid *Australopithecus africanus* developed c. 3 Ma in a still rather humid, subtropical environment defined by patches of forest and thicket rather than savanna. The marine core ODP 1082 (no. 30, Figure 1)

offshore of northern Namibia gives indirect evidence of the savanna 3.4–1.8 Myr (Dupont, 2006). Until c. 3 Ma, Poaceae-rich savanna with Mopane trees (*Colophospermum mopane*) was dominant probably in the eastern hinterland of the Namib Desert. In northern Botswana, which was largely occupied during the Pleistocene by the palaeo-mega lake Makgadikgadi, stretching from the current Makgadikgadi basin up to the Okavango delta (see Figure 1), the late Pliocene Alab dune fields point to rather dry conditions (Moore *et al.*, 2012; Podgorski *et al.*, 2013).

Forest biome

Afrotropical, subtropical and azonal forests in South Africa are evergreen, vary in height and composition and occur as scattered patches in the eastern and far southern parts of the country (Mucina & Geldenhuys, 2006) (Figure 10). There are 12 vegetation units and their distribution is affected by climate and fire but there are three hydrologic-edaphic azonal forest types. Many of the forests are confined to the steep slopes of hills and mountains and there usually is an abrupt transition between the forest and adjacent biomes. The palaeoecological history is not well known: species diversity of the forests may have been influenced by the past expansion and contraction of forests, caused by landscape and climatic change (Geldenhuys, 1997). The extent of the forest was probably also controlled by fire due to the formation of fire prone ecosystems since the late Miocene and Pliocene (Mucina & Geldenhuys, 2006). *Podocarpus* pollen, which certainly represents forest, has been recorded from a number of sites already discussed



Figure 9. Savanna biome; Lindani/South Africa; with *Acacia* spp., *Faurea saligna*, *Dombeya rotundifolia* (photo: Marion Bamford).

above, for example the Palaeocene Arnot pipe (Scholtz, 1985), Miocene southern Cape sites (Coetzee, 1978) and Knysna lignites (Carr *et al.*, 2010). Other typical forest elements such as *Ocotea bullata*, *Olea capensis*, *Cunonia capensis*, *Ilex mitis*,

Sideroxylon inerme, to mention but a few, are generally lacking or rare. Other forest elements are present in the Knysna lignites, e.g. Podocarpaceae (e.g. *Dacrycarpites africanus*), Myrtaceae, Leguminosae, Araliaceae, Sapotaceae



Figure 10. Afromontane forest, near Cathedral peak, Drakensberg/South Africa (photo: Marion Bamford).

(Thiergart *et al.*, 1962). Western Cape Vredendal fossil woods of Miocene age (Bamford, 1999a, no. 16, Figure 1) comprise some West African forest elements of the Combretaceae and Meliaceae. Today with the drier climate and winter rainfall there is no equivalent forest biome.

Indian Ocean Coastal Belt (IOCB) biome

The northern part of the biome (Figure 11) receives even rainfall. Towards the south, summer rainfall is more prominent, annual average rainfall in the region is 819–1272 mm/year (Mucina *et al.*, 2006d). Barthlott *et al.* (2007) mark the Maputaland-Pondoland region, largely part of the IOCB, as one of the global centres of vascular plant diversity. The Maputaland region was submerged during the Tortonian, *c.* 10 Ma. The Maputaland Group starts with Miocene-Pliocene beach and dune facies (Porat & Botha, 2008; Martini & Wanless, 2014). Unfortunately, terrigenous fossils are largely missing for this period, as during the Pliocene a regression followed (Porat & Botha, 2008). The suggested Neogene uplift resulted in former inundated land masses becoming dry land (Mucina *et al.*, 2006d). Although the erosion at the southern African shelf by the long-active Agulhas current hampers any study of Neogene climate variations along the eastern and southern coast of the sub-continent (Uenzelmann-Neben & Huhn, 2009), we tentatively suggest that the warm current created a warm, subtropical and humid climate at the coast of eastern South Africa not unlike the climate encountered there today.

SYNTHESES: MAJOR TRENDS IN THE DEVELOPMENT OF THE CURRENT BIOMES DURING THE NEOGENE

In our synthesis, where we also show connections to the vegetation developments outside southern Africa, we follow Linder (2014), who clusters all 45 000 Sub-Saharan African plant species into six biogeographical regions (Lowland forest, Savanna, Arid, Austro-temperate, Tropic-montane, Tropic-alpine) – all of which can be found in southern Africa where also the most species-rich temperate flora – the Cape flora – can be detected.

1. The Austro-temperate Flora, encompassing the Fynbos and Succulent Karoo biomes, but also the Drakensberg Alpine centre in the Grassland biome, seemingly has a fast diversification rate and a maximum radiation of its clades during the Miocene and Pliocene, when the winter rainfall regime established, although some lineages reach back to the Palaeogene (probably the Eocene: Dupont *et al.*, 2011; Linder, 2005; 2014). Partridge and Maud (2000) point out that an aridity gradient from east to west already existed during the Eocene, interestingly the biodiversity along the escarpment is generally extremely high (Linder, 2014) – maybe also linked to edaphic specialisation within the Cape Folded belt. The Succulent Karoo radiation seems closely connected to the evolution of the Benguela current (Dupont *et al.*, 2011).
2. Floristic links to the diversity poor tropical African Lowland forest, whose biodiversity peaks in the Guinean region, are restricted to the easternmost part



Figure 11. Indian Ocean Coastal belt biome, forest near Lake St Lucia, behind coastal sand dunes/South Africa (photo Marion Bamford).

of southern Africa (Linder, 2014), especially to the Indian Ocean Coastal Belt biome with its multitude of tropical tree species and extraordinarily high biodiversity (Mucina *et al.*, 2006d; Barthlott *et al.*, 2007). Lineages might date back to the Cretaceous when tropical, angiosperm dominated forest already existed around the Gulf of Guinea (Maley, 1996). Lowland forest might have been much more widespread during the Palaeogene, as supported by the few pollen studies, e.g. from Central Africa (Utescher & Mossbrugger, 2007; Linder, 2014), forming part of a pantropical hothouse (Rutschmann *et al.*, 2004). Linder (2014) argues that spreading C₄ grasslands and a change in the fire regime might have promoted low species richness.

3. The Tropic-montane forest, which has relations with the Lowland forest, stretches from eastern Africa towards the eastern and southern Cape and basically encompasses the regions where species like *Podocarpus* and *Cussonia*, but also several grassland elements can be found (Linder, 2014). This vegetation, also called "Afro-montane" by several authors (Chapman & White, 1970; White, 1978; 1981), might have tentatively evolved during the Miocene (Linder, 2014). Linder (2014) suggests that in southern Africa the Tropic-Montane forest might in fact be part of the greater Austro-temperate flora.
4. The Tropic-alpine or "Afro-Alpine" flora (White, 1983) probably has a late Miocene or even younger origin. In southern Africa this region is prominent in the high altitude Drakensberg region as part of the Grassland biome (Killick, 1978).
5. The Savanna flora evolved during the Miocene, when C₄ grasslands were spreading (Dupont *et al.*, 2013; Hoetzel *et al.*, 2013). Savannas are rather species poor, C₄ grasses are dominant and fires appear to increase in step with the evolution of savannas, suggesting a connection between C₄ grasses and fire frequency (Bond *et al.* 2005; Hoetzel *et al.*, 2013; Linder, 2014). Linder (2014) states that "C₄ grasslands might have driven a massive orgy of extinction (*of plant species*) during the late Miocene and Pliocene".
6. The Arid flora encompasses the Albany Thicket in southern Africa but excludes the Succulent Karoo which is regarded as part of the Austro-temperate region (Linder, 2014). White (1983) suggests a centre of the Arid flora in the Somalia region. An ancient origin, probably reaching back at least to the Palaeogene (Palaeocene: Linder, 2014) is suggested by Huber and Goldner (2012). The spread of C₄ grasses and therefore an increase in fire frequency might be responsible for the current restriction of the Albany Thicket biome (Linder, 2014).

CONCLUSIONS AND OUTLOOK

- During the Miocene the vegetation in the southwestern Cape northwards up to the Orange River was predominantly characterised by subtropical forest patches and woodland (Figure 3). The Sperrgebiet region in southern Namibia shows tendencies towards a "proto-savanna" vegetation whereas the coastal regions of central and

northern Namibia were already arid to hyper arid since the beginning of the Miocene.

- The Pliocene saw the further radiation of major plant groups (Asteraceae, Aizoaceae), signalling an adaptation towards aridity. The Fynbos and probably also the Succulent Karoo biomes developed. At the transition towards the Pleistocene the Sterkfontein region in the central eastern interior of southern Africa became more arid and open.
- Due to the connection between C₄ grasses and fire frequency, as pointed out for the Savanna flora and the Albany Thicket biome as part of the arid flora, those regions not affected by the spread of C₄ grasses like the Succulent Karoo and the Fynbos might function as relics of a much more diverse, now partly vanished, flora (Linder, 2014).
- To test the shifting biomes, particularly the expansion and contraction of the forests, future research will entail coring along altitudinal and latitudinal gradients in order to retrieve sequences which can be analysed geochemically, sedimentologically and palynologically.
- The chronological control of the fossil sites has to be improved, utilising new methods, e.g. dating by cosmogenic ¹⁰Be (compare Erlanger *et al.* 2012), in order to pinpoint major biome changes. Marine incursions are obvious at several sites in the Cape, e.g. Langebaanweg (Miocene Elandsfontein Formation), and shown by rare marine microfossils such as foraminiferal linings, dinoflagellates and silicoflagellates (Sciscio *et al.*, 2013). It is mandatory to compare and correlate the rare terrestrial records to archives from marine boreholes (e.g. Dupont *et al.*, 2005; Hoetzel *et al.*, 2013), where biostratigraphical dating is possible based on the abundant marine microfossils, especially foraminifera.

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REFERENCES

- ACOCKS, J.P.H. 1953. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 28: 1–192.
- ADAMSON, R.S., 1931. Note on some petrified wood from Banke, Namaqualand. *Transactions of the Royal Society of South Africa* 19: 255–258.
- ADAMSON, R.S. 1938. *The Vegetation of South Africa*. London, British Empire Vegetation Committee.
- ANDERSON, J. M. (Ed.) 1999. *Towards Gondwana Alive*. Pretoria, Gondwana Alive Society.
- ARAKAKI, M., CHRISTIN, P.-A., NYFFELER, R., LENDEL, A., EGGELI, U., OGBURN, R.M., SPRIGGS, E., MOORE, M.J. & EDWARDS, E.J. 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proceedings of the National Academy of Sciences* 108, 20: 8379–8384.
- AXELROD, D.I. 1970. Mesozoic palaeogeography and early angiosperm history. *Botanical Review* 36: 277–319.
- AXELROD, D.I. 1972. Edaphic aridity as a factor in angiosperm evolution. *American Naturalist* 106: 311–320.

- AXELROD, D.I. & RAVEN, P.H. 1978. Late Cretaceous and Tertiary vegetation history of Africa. In Werger, M.J.A. (Ed.), *Biogeography and Ecology of Southern Africa*. The Hague, W. Junk. pp. 77–130.
- BAMFORD, M.K. 1999a. Tertiary fossil woods from Vredendal, southwestern Cape, South Africa. *Annales Sciences Economiques* 25: 149–163.
- BAMFORD, M.K. 1999b. Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. *South African Journal of Science* 95: 231–237.
- BAMFORD, M.K. 2000. Cenozoic macro-plants. In Partridge, T.C. and Maud, R.R. (Eds), *Cenozoic of Southern Africa*. Oxford Monographs on Geology and Geophysics No. 40. Oxford, Oxford University Press. pp. 351–356.
- BAMFORD, M.K. 2003. Fossil woods from Auchas and their palaeoenvironment. Geology and palaeobiology of the central and southern Namib Desert, southwestern Africa. Volume 2: Palaeontology. *Geological Survey of Namibia, Memoirs* 19: 23–34.
- BAMFORD, M.K. & DE WIT, M.C.J. 1993. Taxonomic descriptions of fossil wood from Cainozoic Sak River terraces near Brandvlei, South Africa. *Palaeontologia africana* 30: 71–80.
- BAMFORD, M.K. & WARD, J.D. 2004. Eocene fossil woods from the Blaubok Gravels, Bogenfels, Namibia. International Symposium on Wood Sciences, CIRAD, Montpellier, France, 24–29 October 2004. *IAWA Journal* 25, 3: 385–389.
- BARKER, P.F. & BURRELL, J., 1977. The opening of Drake Passage. *Marine Geology* 25: 15–34.
- BARKER, P.F. & THOMAS, E., 2004. Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. *Earth-Science Reviews* 66: 143–162. doi: 10.1016/j.earscirev.2003.10.003.
- BARTHLOTT, W., HOSTERT, A., KIER, G., KUPER, W., KREFT, H., MUTKE, J., RAFIQPOOR, M.D. & SOMMER, J.H. 2007. Geographic patterns of vascular plant diversity at continental to global scales. *Erdkunde* 61, 4: 305–315.
- BENGTSON, A., NYLINDER, S., KARIS, P.O. & ANDERBERG, A.A. 2015. Evolution and diversification related to rainfall regimes: diversification patterns in the South African genus *Metalasia* (Asteraceae-Gnaphalieae). *Journal of Biogeography* 42: 121–131.
- BOND, G.C. 1979. Evidence for some uplifts of large magnitude in continental platforms. *Tectonophysics* 61: 285–305.
- BOND, W.J., MIDGLEY, G.F. & WOODWARD, F.I. 2003. What controls South African vegetation — climate or fire? *South African Journal of Botany* 69: 79–91.
- BOND, W.J., WOODWARD, F.I. & MIDGLEY, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–537.
- BOTHA, G.A. & DE WIT, M.C.J., 1996. Post-Gondwanan continental sedimentation, Limpopo region, southeastern Africa. *Journal of African Earth Sciences* 23: 163–187.
- BRENDENKAMP, G. J., SPADA, F. & KAZMIERCZAK, E. 2002. On the origin of northern and southern hemisphere grasslands. *Plant Ecology* 163: 209–229.
- BREMER, K. 2002. Gondwanan evolution of the grass alliance of families (Poales). *Evolution* 56: 1374–1387.
- BUCH, M.W., 1997. Etosha Pan – the largest lake in the world? *Madoqua* 20: 49–64.
- BURKE, K., 1996. The African Plate. *South African Journal of Geology* 99: 341–409.
- BURKE, K. & GUNNELL, Y. 2008. The African erosion surface: a continental-scale synthesis of geomorphology, tectonics, and environmental change over the past 180 million years. Boulder, CO, Geological Society of America, Memoir 201, 66 pp.
- CARR, A.S., BOOM, A. & CHASE, B.M. 2010. The potential of plant biomarker evidence derived from rock hyrax middens as an indicator of palaeoenvironmental change. *Palaeogeography, Palaeoclimatology, Palaeoecology* 285: 321–330.
- CERLING, T.E., HARRIS, J.M., MACFADDEN, B.J., LEAKEY, M.G., QUADE, J., EISENMANN, V. & EHLERINGER, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 153–158.
- CERLING, T.E., WYNN, J.G., ANDANJE, S.A., BIRD, M.L., KORIR, D.K., LEVIN, N. E., MACE, W., MACHARIA, A.N., QUADE, J. & REMIEN, *et al.*, 2011. Woody cover and hominin environments in the past 6 million years. *Nature* 476, 7358: 51–56.
- CHAPMAN, J.D. & WHITE, F. 1970. *The Evergreen Forests of Malawi*. Oxford, Commonwealth Forestry Institute.
- CHRISTIN, P.A., SPRIGGS, E., OSBORNE, C.P., STRÖMBERG, C.A.E., SALAMIN, N. & EDWARDS, E.J. 2014. Molecular dating, evolutionary rates, and the age of the grasses. *Systematic Biology* 63: 153–165.
- COATES-PALGRAVE, M. 2002. *Keith Coates-Palgrave Trees of Southern Africa*. Struik Publishers, Cape Town. 1212pp.
- COETZEE, J.A. 1978. Climatic and biological changes in southwestern Africa during the Late Cenozoic. *Palaeoecology of Africa and the Surrounding Islands* 10: 13–29.
- COETZEE, J.A. 1983. Intimations on the Tertiary vegetation of southern Africa. *Bothalia* 14: 345–354.
- COETZEE, J.A. & MULLER, J. 1984. The phytogeographic significance of some extinct Gondwana pollen types from the Tertiary of the south-western Cape (South Africa). *Annals of the Missouri Botanical Garden* 71: 1088–1099.
- COETZEE, J.A. & PRAGLOWSKI, J. 1984. Pollen evidence for the occurrence of *Casuarina* and *Myrica* in the Tertiary of South Africa. *Grana* 23: 23–41.
- COETZEE, J.A. & ROGERS, J. 1982. Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology* 39: 71–85.
- COETZEE, J.A., SCHOLTZ, A. & DEACON, H.J., 1983. Palynological studies and the vegetation history of the fynbos. In Deacon, H.J., Hendey Q. B., Lambrechts, J.J.N. (Eds), *Fynbos palaeoecology. A preliminary synthesis*. South African National Scientific Programmes Report 75. Pretoria CSIR, pp. 156–173.
- CORVINUS, G. & HENDEY, Q.B., 1978. A new Miocene vertebrate locality at Arrisdrift in Namibia (South West Africa). *Neues Jahrbuch für Geologie und Paläontologie* 1478: 193–205.
- COWLING, R.M. 1983. Phytochorology and vegetation history in the south-eastern Cape, South Africa. *Journal of Biogeography* 10: 393–419.
- COWLING, R.M., PROCHES, S.R. & VLOK, J.H.J. 2005. On the origin of southern African subtropical thicket vegetation. *South African Journal of Botany* 71: 1–23.
- COWLING, R.M., RICHARDSON, D.M. & MUSTART, P.J. 1997. Fynbos. In Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds), *Vegetation of Southern Africa*. Cambridge, Cambridge University Press.
- CURRIE, R. 1953. Upwelling in the Benguela Current. *Nature* 171: 497–500.
- DEACON, H.J., JURY, M.R. & ELLIS, F. 1992. Selective regime and time. In Cowling, R.M. (Ed.), *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Cape Town, Oxford University Press. pp. 6–22.
- DESMET, P.G. & COWLING, R.M. 1999. The climate of the Karoo – a functional approach. In Dean, W.R.J. and Milton, S.J. (Eds), *The Karoo – Ecological Patterns and Processes*. Cambridge, Cambridge University Press. pp. 3–16.
- DE VILLIERS, S.E. 1997. The palynology of Tertiary sediments from a palaeochannel in Namaqualand. Unpublished PhD thesis, University of Witwatersrand, Johannesburg, South Africa. 281 pp.
- DE VILLIERS, S.E. & CADMAN, A. 1997. The palynology of Tertiary sediments from a palaeochannel in Namaqualand, South Africa. *Palaeontologia africana* 34: 69–99.
- DE VILLIERS, S.E. & CADMAN, A. 2001. An analysis of the palynomorphs obtained from Tertiary sediments at Koingnaas, Namaqualand, South Africa. *Journal of African Earth Sciences* 33: 17–47.
- DE WIT, M.C.J. 1993. Cainozoic evolution of drainage systems in the north-western Cape. Unpublished PhD thesis, University of Cape Town, South Africa.
- DE WIT, M.C.J., MARSHALL, T.R. & PARTRIDGE, T.C. 2000. Fluvial deposits and drainage evolution. In Partridge, T.C. and Maud, R.R. (Eds), *The Cainozoic of Southern Africa*. Oxford, Oxford University Press. pp. 55–72.

- DILL, H.G., KAUFHOLD, S., LINDENMAIER, F., DOHRMANN, R., LUDWIG, R., BOTZ, R. 2012. Joint clay-heavy-light mineral analysis: a tool to investigate the hydrographic-hydraulic regime of the Late Cenozoic deltaic inland fans under changing climatic conditions (Cuvélai-Etoshá Basin, Namibia). *International Journal of Earth Sciences*, 102 (2012), 265–304.
- DINGLE, R.V., SEISSER, W.G. & NEWTON, A.R., 1983. *Mesozoic and Tertiary Geology of Southern Africa*. Balkema, Rotterdam.
- DOLLAR, E.S.J. 1998. Palaeofluvial geomorphology in southern Africa: a review. *Progress in Physical Geography* 22: 325–349.
- DUPONT, L.M. 2006. Late Pliocene vegetation and climate in Namibia (southern Africa) derived from palynology of ODP site 1082. *Geochemistry Geophysics Geosystems* 7, 5: doi: 10.1029/2005GC001208.
- DUPONT, L.M., DONNER, B., VIDAL, L., PEREZ, E.M. & WEFER, G. 2005. Linking desert evolution and coastal upwelling: Pliocene climate change in Namibia. *Geology* 33: 461–464.
- DUPONT, L.M., LINDER, H.P., ROMMERSKIRCHEN, F. & SCHEFUß, E. 2011. Climate-driven rampant speciation of the Cape flora. *Journal of Biogeography* 38: 1059–1068.
- DUPONT, L.M., ROMMERSKIRCHEN, F., MOLLENHAUER, G. & SCHEFUß, B. 2013. Miocene to Pliocene changes in South African hydrology and vegetation in relation to the expansion of C₄ plants. *Earth and Planetary Science Letters* 375: 408–417.
- ERLANGER, E.D., GRANGER, D.E. & GIBBON, R.J. 2012. Rock uplift rates in South Africa from isochron burial dating of fluvial and marine terraces. *Geology* 40: 1019–1022.
- ETOURNEAU, J. 2014. Tectonically driven upwelling. *Nature Geoscience* 7: 698–699.
- FEAKINS, S.J., DE MENOCAL, P.B. & EGLINGTON, T.I. 2005. Biomarker records of late Neogene changes in northeast African vegetation. *Geology* 33: 977–980.
- FLOWERS, R.M. & SCHOENE, B. 2010. (U–Th)/He thermochronometry constraints on unroofing of the eastern Kaapvaal craton and significance for uplift of the southern African Plateau. *Geology* 38: 827–830.
- GELDENHUYS, C.J. 1997. Composition and biogeography of forest patches in the inland mountains of the southern Cape. *Bothalia* 27: 57–74.
- GOLDBLATT, P. 1996. Floristic diversity in the Cape Flora of South Africa. *Biodiversity and Conservation* 6: 359–377.
- GOUDIE, A. & VILES, H. 2015. *Landscapes and Landforms of Namibia*. Dordrecht-Heidelberg-New York-London, Springer.
- GOUGH, D. I. 1973. Possible linear plume under southernmost Africa. *Nature Physical Sciences* 245: 93–94.
- GRAB, S. & KNIGHT, J. 2015. Landscapes and landforms of South Africa – an overview. In Grab, S. and Knight, J. (Eds.), *Landscapes and Landforms of South Africa*. Berlin, Springer International Publishers. pp. 1–9.
- GUÉRIN, C.A. 2003. Palaeoecological study of Arrisdrift mammals. *Geological Survey of Namibia Memoir* 19: 385–388.
- GUILLOCHEAU, F., ROUBY, D., ROBIN, C., HELM, C., ROLLAND, N., LE CARLIER DE VESLUDN, C. & BRANZ, J. 2012. Quantification and causes of the terrigenous sediment budget at the scale of a continental margin: a new method applied to the Namibia-South Africa margin. *Basin Research* 24: 3–30.
- GUILLOCHEAU, F., DATEUIL, O., BABY, G., PICKFORD, M. & SENUT, B., 2014. Timing of the Southern African Plate uplift: a couple landforms-margin study of southern Namibia. *Geophysical Research Abstracts* 16, EGU General Assembly 2014, id. 10728.
- HALLAM, A. 1994. *An Outline of Phanerozoic Biogeography*. Oxford, Oxford University Press.
- HARTNADY, C.J.H. 1985. Uplift faulting seismicity, thermal springs and possible incipient volcanic activity in the Lesotho-Natal Region, South Africa: the Quathlamba hotspot hypothesis. *Tectonics* 4: 371–377.
- HASSOLD, N.J.C., REA, D.K., VAN DER PLUIJM, B.A. & PARES, J.M. 2009. A physical record of the Antarctic Circumpolar Current: Late Miocene to recent slowing of abyssal circulation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 275: 28–36.
- HATTINGH, J. 1996. Late Cenozoic drainage evolution in the Algoa Basin with special reference to the Sundays River Valley. Unpublished PhD thesis, University of Port Elizabeth.
- HELIGREN, D. M. & BUTZER, K. W. 1977. Palaeosols of the Southern Cape coast, South Africa: implications for laterite definition, genesis and age. *Geographical Review* 67: 430–445.
- HENDEY, Q. B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Nature* 252: 576–577.
- HENDEY, Q.B. 1984. Southern African late Tertiary vertebrates. In Klein, R.G. (Ed.), *Southern African Prehistory and Palaeoenvironments*. Rotterdam, Balkema. pp. 81–106.
- HERENDEEN, P. S. & CRANE, P.R. 1995. The fossil history of the monocotyledons. In Rudall, P.J., Cribb, P., Cutler, D.F. & Humphries, C.J. (Eds.), *Monocotyledons: Systematics and evolution*. Kew, Royal Botanic Gardens. pp. 1–21.
- HIPONDOKA, M. 2005. The development and evolution of Etosha Pan, Namibia. Unpublished MSc thesis, University of Würzburg, Germany. 162 pp.
- HOETZEL, S., DUPONT, L., SCHEFUß, E., ROMMERSKIRCHEN, F. & WEFER, G. 2013. The role of fire in Miocene to Pliocene C₄ grassland and ecosystem evolution. *Nature Geoscience* 6: 1027–1030.
- HOETZEL, S., DUPONT, L.M. & WEFER, G. 2015. Miocene-Pliocene vegetation change in south-western Africa (ODP Site 1081, offshore Namibia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 423: 102–108.
- HOPLEY, P.J., MARSHALL, J.D., WEEDON, G.P., LATHAM, A.G., HERRIES, A.I.R. & KUYKENDALL, K.L. 2007. Orbital forcing and the spread of C₄ grasses in the late Neogene: stable isotope evidence from South African speleotherms. *Journal of Human Evolution* 53: 620–634.
- HUBER, M. & GOLDNER, A. 2012. Eocene monsoons. *Journal of Asian Earth Sciences* 44: 3–23.
- HUTCHINGS, L., VAN DER LINGEN, C.D., SHANNON, L.J., CRAWFORD, R.J.M., VERHEYE, H.M.S., BARTOLOMAE, C.H., VAN DER PLAS, A.K., LOUW, D., KREINER, A., OSTROWSKI, M., FIDEL, Q., BARLOW, R.G., LAMONT, T., COETZEE, J., SHILLINGTON, F., VEITCH, J., CURRIE, J.C., MONTEIRO, P.M.S., 2009. The Benguela Current: an ecosystem of four components. *Progress in Oceanography* 83: 15–32.
- JACOBS, B.F., KINGSTON, J.D. & JACOBS, L.L. 1999. The origin of grass dominated ecosystems. *Annals of the Missouri Botanical Garden* 86: 590–643.
- JONES, S.S., BURKE, S.V. & DUVAL, M.R., 2014. Phylogenomics, molecular evolution, and estimated ages of lineages from the deep phylogeny of Poaceae. *Plant Systematics and Evolution* 300: 1421–1436.
- JUNG, G., PRANGE, M. & SCHULZ, M. 2014. Uplift of Africa as a potential cause for Neogene intensification of the Benguela upwelling system. *Nature Geoscience* 7: 741–747.
- JÜRGENS, N. 2006. Desert Biome. In Mucina, L. and Rutherford, M.C. (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. Pretoria, South African National Biodiversity Institute. pp. 301–323.
- KHAVHAGALI, V.P. 2010. Importance, threats, status and conservation challenges of biodiversity in Northern Cape. *Grassroots* 10: 14–17.
- KILLICK, D.J.B. 1978. The Afro-alpine Region. In Werger, M.J.A. (Ed.), *Biogeography and Ecology of Southern Africa*. The Hague, W. Junk. pp. 515–560.
- KING, L.C., 1955. Pediplanation and isostasy: an example from South Africa. *Quarterly Journal of the Geological Society, London* 111: 535–539.
- KING, L.C. 1962. *The Morphology of the Earth: A study and synthesis of world scenery*. London, Oliver and Boyd.
- KING, L.C. 1963. *South African Scenery: A textbook of geomorphology*. 3rd edn. New York, Hafner.
- KING, L.C. 1978. The geomorphology of central and southern Africa. In Werger, W. M. A. (Ed.), *Biogeography and Ecology of Southern Africa*. The Hague, W. Junk. pp. 1–17.

- KIRCHHEIMER, F. 1934. On pollen from the upper Cretaceous dysodil of Banke, Namaqualand (South Africa). *Transactions of the Royal Society of South Africa* 21: 41–50.
- KLAK, C., REEVES, G. & HEDDERSON, T. 2004. Unmatched tempo of evolution in Southern African semi-desert ice plants. *Nature* 427: 63–65.
- LEAKEY, M.G. & HARRIS, J.A. (Eds), 2003. *Lothagam: The Dawn of Humanity in Eastern Africa*. New York, Columbia University Press.
- LINDER, H.P. 2003. The radiation of the Cape flora, southern Africa. *Biological Reviews* 78: 597–638.
- LINDER, H.P. 2005. The evolution of diversity: the Cape flora. *Trends in Plant Science* 10: 536–541. doi: 10.1016/j.tplants.2005.09.006.
- LINDER, H.P. 2014. The evolution of African plant diversity. *Frontiers in Ecology and Evolution* 2: 1–14.
- LOW, A.B. & REBELO, A.G. 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Pretoria, Department of Environmental Affairs and Tourism.
- LYLE, M., GIBBS, S., MOORE, T.C. & REA, D.K., 2007. Late Oligocene initiation of the Antarctic Circumpolar Current: evidence from the South Pacific. *Geology* 35: 691–694. doi: 10.1130/23806A.1.
- MAJEWSKI, W. & BOHATY, S.M. 2010. Surface-water cooling and salinity decrease during the Middle Miocene climate transition at Southern Ocean ODP site 747 (Kerguelen Plateau). *Marine Micropaleontology* 74: 1–14.
- MALEY, J. 1996. The African rain forest—main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proceedings of the Royal Society of Edinburgh B* 104: 31–73.
- MALHERBE, S.J., KEYSER, A.W., BOTHA, B.J.V., CORNELISSEN, A., SLABBERT, M.J. & PRINSLOO, M.C. 1986. The Tertiary Koa River and the development of the Orange River drainage. *Annals of the Geological Survey of South Africa* 20: 13–23.
- MARTINI, P. & WANLESS, H.R. 2014. Sedimentary Coastal Zones from High to Low Latitudes: Similarities and Differences. Geological Society, London, Special Publications, 388 pp.
- MCCARTHY, T.S., MOON, B.E. & LEVIN, M., 1985. Geomorphology of the western Bushmanland plateau, Namaqualand, South Africa. *South African Geographical Journal* 67: 160–178.
- MILLER, R. MCG., PICKFORD, M. & SENUT, B., 2010. The geology, palaeontology and evolution of the Etosha Pan, Namibia. *South African Journal of Geology* 11: 307–334.
- MILTON, S.J., YEATON, R.L., DEAN, W.R.J. & VLOK, J.H.J. 1997. Succulent Karoo. In Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds), *Vegetation of Southern Africa*. Cambridge, Cambridge University Press. pp. 131–166.
- MOORE, A. & LARKIN, P. 2001. Drainage evolution in south-central Africa since the breakup of Gondwana. *South African Journal of Geology* 104: 47–68.
- MOORE, A., BLENKINSOP, T. & COTTERILL, F. 2009. Southern African topography and erosion history: plumes or plate tectonics? *Terra Nova* 21: 310–315.
- MOORE, A.E., COTTERILL, F.P.D. & ECKARDT, F.D. 2012. The evolution and ages of Makgadikgadi palaeo-lakes: Consilient evidence from Kalahari drainage evolution. *South African Journal of Geology* 115: 385–413.
- MUCINA, L. & GELDENHUYS, C.J. 2006. Afrotropical, subtropical and azonal forests. In Mucina, L. & Rutherford, M.C. (Eds), *The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia* 19. Pretoria, South African National Biodiversity Institute. pp. 607–608.
- MUCINA, L. & RUTHERFORD, M.C. (Eds). 2006. *The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia* 19. Pretoria, South African National Biodiversity Institute.
- MUCINA, L., HOARE, D.B., LOTTER, M.C., DU PREEZ, P.J., RUTHERFORD, M.C., SCOTT-SHAW, C.R., BREDENKAMP, G.J., POWRIE, L.W., SCOTT, L., CAMP, K.G.T., CILLIERS, S.S., BEZUIDENHOUT, H., MOSTERT, T.H., SIEBERT, S.J., WINTER, P.J.D., BURROWS, J.E., DOBSON, L., WARD, R.A., STALMANS, M., OLIVIER, E.G.H., SIEBERT, F., SCHMIDT, E., KOBISI, K. & KOSE, L. 2006a. Grassland Biome. In Mucina, L. & Rutherford, M.C. (Eds), *The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia* 19. Pretoria, South African National Biodiversity Institute. pp. 349–437.
- MUCINA, L., RUTHERFORD, M.C., PALMER, A.R., MILTON, L.S., LLOYD, J.W., VAN DER MERWE, B., HOARE, D.B., BEZUIDENHOUT, H., VLOK, J.H.J., EUSTON-BROWN, D.I.W., POWRIE, L.W. & DOLD, A.P. 2006b. Nama-Karoo Biome. In Mucina, L. & Rutherford, M.C. (Eds), *The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia* 19. South African National Biodiversity Institute, Pretoria. pp. 324–347.
- MUCINA, L., JÜRGENS, N., LE ROUX, A., RUTHERFORD, M.C., SCHMIEDEL, U., ESLER, K.J., POWRIE, L.W., DESMET, P.G. & MILTON, S.J. 2006c. Succulent Karoo Biome. In Mucina, L. & Rutherford, M.C. (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia* 19. Pretoria, South African National Biodiversity Institute. pp. 220–299.
- MUCINA, L., SCOTT-SHAW, C.R., RUTHERFORD, M.C., CAMP, K.G.T., MATTHEWS, W.S., POWRIE, L.W. & HOARE, D.B. 2006d. Indian Ocean Coastal Belt. In Mucina, L. & Rutherford, M.C. (Eds), *The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia* 19. Pretoria, South African National Biodiversity Institute. pp. 568–583.
- NEWTON, A.R. 1974. Nature of South Africa's Cape Fold Belt. *Nature* 248: 499–500.
- PARTRIDGE, A.D. 1978. Palynology of the Late tertiary Sequence at site 365 m, leg 40, Deep Sea Drilling Project. *Initial Reports of the Deep Sea Drilling Project* 40: 953–961.
- PARTRIDGE, T. C. 1997a. Evolution of landscapes. In Cowling, R. M., Richardson, D.M. and Pierce, S.M. (Eds.), *Vegetation of Southern Africa*. Cambridge, Cambridge University Press. pp. 5–20.
- PARTRIDGE, T.C. 1997b. Cainozoic environmental change in southern Africa, with special emphasis on the last 200 000 years. *Progress in Physical Geography* 21: 3–22.
- PARTRIDGE, T.C. & MAUD, R.R. 1987. Geomorphic evolution of southern Africa since the Mesozoic. *South African Journal of Geology* 90: 179–208.
- PARTRIDGE, T.C. & MAUD, R.R. 2000. Macro-scale geomorphic evolution of southern Africa. In Partridge, T.C. and Maud, R.R. (Eds.), *The Cenozoic of Southern Africa*. Oxford, Oxford University Press. pp. 3–18.
- PERISSINOTTO, R., STRETCH, D.D. & TAYLOR, R.H. (Eds) 2013. *Ecology and conservation of estuarine ecosystems: Lake St. Lucia as a global model*. Cambridge, Cambridge University Press.
- PETHER, J., ROBERTS, D.L. & WARD, J.D., 2000. Deposits of the Wet Coast. In Partridge, T.C. & Maud, R.R. (Eds.), *The Cenozoic of Southern Africa*. Oxford, Oxford University Press. pp. 33–54.
- PFUHL, H.A. & MCCAVE, I.N., 2005. Evidence for late Oligocene establishment of the Antarctic Circumpolar Current. *Earth and Planetary Science Letters* 235: 715–728.
- PICKFORD, M. 2014. New ratite eggshells from the Miocene of Namibia. *Communications of the Geological Survey of Namibia* 15: 70–90.
- PICKFORD, M. & SENUT, B. 2000. Geology and palaeobiology of the central and southern Namib Desert, southwestern Africa. Geological Survey of Namibia Memoir 18: 1–155.
- PICKFORD, M. & SENUT, B. 2002. *The Fossil Record of Namibia*. Geological Survey of Namibia, Windhoek, Namprint, 39 pp.
- PICKFORD, M. & SENUT, B. 2003. Miocene Palaeobiology of the Orange River Valley, Namibia. Geological Survey of Namibia Memoir 19: 1–22.
- PICKFORD, M., SENUT, B., MEIN, P., MORALES, J., SORIA, D., NIETO, M., WARD, J. & BAMFORD, M. 1995. The discovery of lower and middle Miocene vertebrates at Auchas, southern Namibia. *Comptes Rendus de l'Académie des Sciences, Paris* 322, série II a: 901–906.
- PICKFORD, M., EISENMANN, V. & SENUT, B. 1999. Timing of landscape development and calcrete genesis in northern Namaqualand, South Africa. *South African Journal of Science* 95: 357–359.
- PICKFORD, M. & SENUT, B. 2002. *The Fossil Record of Namibia*. Geological Survey of Namibia, Windhoek, Namprint, 39 pp.
- PICKFORD, M., SENUT, B., MORALES, J., MEIN, P. & SANCHEZ, I.M., 2008. Mammalia from the Lutetian of Namibia. Geological Survey of Namibia Memoir 20: 465–514.

- PICKFORD, M., SAWADA, Y. & SENUT, B. 2011. Geochronology and palaeontology of the Palaeogene deposits in the Sperrgebiet, Namibia. 22nd International Senckenberg Conference 2011. pp. 129–130.
- PICKFORD, M., SENUT, B., HIPONDOKA, M., PERSON, L., SEGALÉN, L., PLET, C., JOUSSE, H., MEIN, P., GUÉRIN, C., MORALES, J. & MOURER-CHAUVIRÉ, C. 2014a. Mio-Plio-Pleistocene geology and palaeobiology of Etosha Pan, Namibia. *Communications of the Geological Survey of Namibia* 14: 95–139.
- PICKFORD, M., SENUT, B., MOCKE, H., MOURER-CHAUVIRÉ, C., RAGE, J.C. & MEIN, P. 2014b. Eocene aridity in southwestern Africa: timing of onset and biological consequences. *Transactions of the Royal Society of South Africa* doi: 10.1080/0035919X.2014.933452.
- PODGORSKI, J.E., GREEN, A.G., KGOTLHANG, L., KINZELBACH, W.K.H., KALSCHUEER, K., AUKEN, E. & NGWISANYI, T. 2013. Paleo megalake and paleo megadelta in southern Africa. *Geology* G34735–1.
- POLE EVANS, I.B., 1936. A vegetation map of South Africa. *Memoirs of the Botanical Survey of South Africa* 15: 1–23.
- PORAT, N. & BOTHA, G.A. 2008. The luminescence chronology of dune development on the Maputaland coastal plain, southeast Africa. *Quaternary Science Reviews* 27: 1024–1046.
- POUND, M.J., HAYWOOD, A.M., SALZMANN, U. & RIDING, J.B. 2012. Global vegetation dynamics and latitudinal temperature gradients during the mid to Late Miocene (15.97–5.33 Ma). *Earth Science Reviews* 112: 1–22.
- PRASAD, V. 2005. Dinosaur coprolites and the early evolution of grasses and grazers. *Science* 310: 1177–1180.
- RAYNER, R., MOON, B. & MASTERS, J. 1993. The Makapansgat australopithecine environment. *Journal of Human Evolution* 24: 219–231.
- RENNIE, J.V.L., 1931. Note on fossil leaves from the Banke Clays. *Transactions of the Royal Society of South Africa* 19: 251–253.
- ROBERTS, D.L., MATTHEWS, T., HERRIES, A.I.R., BOULTER, C., SCOTT, L., MUSEKIWA, C., MTEMBI, P., BROWNING, C., SMITH, R.M.H., HAARHOEF, P. & BATEMAN, M.D. 2011. Regional and global context of the Late Cenozoic Langebaanweg (LBW) palaeontological site: West Coast of South Africa. *Earth Science Reviews* 106: 191–214.
- ROBERTS, D.L., SCISCIO, L., HERRIES, A.I.R., SCOTT, L., BAMFORD, M.K., MUSEKIWA, C. & TSIKOS, H. 2013. Miocene fluvial systems and palynofloras at the southwestern tip of Africa: implications for regional and global fluctuations in climate and ecosystems. *Earth Science Reviews* 124: 184–201.
- ROBERTS, G.G. & WHITE, N. 2010. Estimating uplift rates from river profiles using African examples. *Journal of Geophysical Research* 115: 1–24.
- ROGERS, J. 1980. First report on the Cenozoic sediments between Cape Town and Elands Bay. *Report for the Geological Survey of South Africa*. 165: 1–64.
- ROSSOUW, L., STYNDER, D.D. & HAARHOEF, P. 2009. Evidence for opal phytoolith preservation in the Langebaanweg 'E' Quarry Varswater Formation and its potential for palaeohabitat reconstruction. *South African Journal of Science* 105: 223–227.
- RUTHERFORD, M. & WESTFALL, R. 1994. Biomes of southern Africa: an objective categorisation. *Memoirs of the Botanical Survey of South Africa* 63: 1–94.
- RUTHERFORD, M.C., MUCINA, L., LOTTER, M.C., BREDEKAMP, G.J., SMIT, J.H. L., SCOTT-SHAW, C.R., HOARE, D.B., GOODMAN, P.S., BEZUIDENHOUT, H., SCOTT, L., ELLIS, F., POWRIE, L.W., SIEBERT, F., MOSTERT, T.H., HENNING, B.J., VENTER, C.E., CAMP, K.G.T., SIEBERT, S.J., MATTHEWS, W.S., BURROWS, J.E., DOBSON, L., VAN ROOYEN, N., SCHMIDT, E., WINTER, P.J.D., DU PREEZ, P.J., WARD, R.A., WILLIAMSON, S. & HURTER, P.J.H. 2006. Savanna biome. In Mucina, L. & Rutherford, M.C. (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia* 19. Pretoria, South African National Biodiversity Institute. pp. 438–539.
- Rutschmann, F., Eriksson, T., Schonenberger, J. & Conti, E. 2004. Did Crypteroniaceae really disperse out of India? Molecular dating evidence from *rbcl*, *ndhF* and *rpl16* intron sequences. *International Journal of Plant Sciences*, Supplement 165: S69–S83. doi: 10.1086/383335.
- SAGE, R.F. 2004. The evolution of C₄ photosynthesis. *New Phytologist* 161: 341–370.
- SCHALKE, H.J.W.G. 1973. The upper Quaternary of the Cape Flats Area (Cape Province, South Africa). *Scripta Geologica* 15: 1–57.
- SCHNEIDER, G. & MARAIS, C. 2005. *Passage through Time. The Fossils of Namibia*. Windhoek, Gamsberg Macmillan.
- SCHOLTZ, A. 1985. The palynology of the upper lacustrine sediments of the Arnot Pipe, Banke, Namaqualand. *Annals of the South African Museum* 95: 1–109.
- SCISCIO, L. 2011. Neogene deposits along the southwest coast of South Africa: understanding the palaeoclimate through proxies. Unpublished MSc dissertation, Rhodes University, Grahamstown, South Africa.
- SCISCIO, L., NEUMANN, F.H., ROBERTS, D., TSIKOS, H., SCOTT, L. & BAMFORD, M. 2013. Fluctuations in Miocene climate and sea levels along the south-western South African coast: inferences from biogeochemistry, palynology and sedimentology. *Palaeontologia africana* 48: 2–18.
- SCOTSE, C.R. 2001. *Atlas of Earth History, Vol. 1. Paleogeography*. Arlington, TX, PALEOMAP Project. 52pp. Available at <http://www.scotese.com>.
- SCOTT, L. 1995. Pollen evidence for vegetation and climatic change in southern Africa during the Neogene and Quaternary. In Vrba, E., Denton, G.H., Partridge, T.C. & Burckle L.H. (Eds), *Palaeoclimate and Evolution, with emphasis on human origins*. New Haven, CT, Yale University Press. pp. 64–193.
- SCOTT, L. & BONNEFILLE, R. 1986. A search for pollen from the hominid deposits of Kromdraai, Sterkfontein and Swartkrans: some problems and preliminary results. *South African Journal of Science* 82: 380–382.
- SCOTT, L., ANDERSON, H.M. & ANDERSON, J.M. 1997. Vegetation history. In Cowling, R.M., Richardson, D.M. & Pierce, S.M. (Eds), *Vegetation of Southern Africa*. Cambridge, Cambridge University Press. pp. 62–84.
- SCOTT, L., CADMAN, A., & MCMILLAN, I. 2006. Early history of Cainozoic Asteraceae along the Southern African west coast. *Review of Palaeobotany and Palynology* 142: 47–52.
- SÉGALEN, L., LEE-THORP, J.A. & CERLING, T. 2007. Timing of C₄ grass expansion across sub-Saharan Africa. *Journal of Human Evolution* 53: 549–559.
- SÉGALEN, L., RENARD, M., LEE-THORP, J.A., EMMANUEL, L., LE CALLONNEC, L., DE RAFELIS, M., SENUT, B., PICKFORD, M. & MELICE, J.L., 2006. Neogene climate change and emergence of C₄ grasses in the Namib, southwestern Africa, as reflected in ratite ¹³C and ¹⁸O. *Earth and Planetary Science Letters* 244: 725–734.
- SENUT, B., PICKFORD, M. & WARD, J. 1994. Biostratigraphie de éolianites néogènes du Sud de la Sperrgebiet (Désert de Namib, Namibie). *Comptes Rendus de l'Académie des Sciences* 318: 1001–1007.
- SENUT, B., PICKFORD, M. & WESSELS, D. 1997. Panafrican distribution of Lower Miocene Hominoidea. *Comptes Rendus de l'Académie des Sciences* 325: 741–746.
- SENUT, B., PICKFORD, M. & SEGALÉN, L. 2009. Neogene desertification of Africa. *Comptes Rendus, Geoscience* 341: 591–602.
- SENUT, B. & SEGALÉN, L. 2014. Neogene palaeoenvironments of the Namib Desert: a brief synthesis. *Transactions of the Royal Society of South Africa* 69: 205–211.
- SIESSER, W.G. 1980. Late Miocene origin of the Benguela upwelling system off northern Namibia. *Science* 208: 283–285.
- SHANNON, L.V., 1985. The Benguela ecosystem, Part 1. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology: An Annual Review* 23: 105–182.
- SNIJMAN, D.A. (Ed.) 2013. *Plants of the Great Cape Floristic Region. 2: The Extra Cape Flora*. Pretoria, South African National Biodiversity Institute.
- STEVENSON, I.R. & MCMILLAN, I.K., 2004. Incised valley fill stratigraphy of the Upper Cretaceous succession, proximal Orange Basin, Atlantic margin of southern Africa. *Journal of the Geological Society, London* 161: 85–208.

- THIERGART, F. 1964. Ein Vergleich der flözbildenden Elemente des niederrheinischen mit mehr oder weniger gleichaltrigen Südafrikas und Asiens auf Grund pollenanalytischer Untersuchungen. *Fortschritte der Geologie Rheinland und Westfalen* 12: 105–113.
- THIERGART, F., FRANTZ, U. & RAUKOPF, K. 1962. Palynologische Untersuchungen von Tertiärkohlen und einer Oberflächenprobe nahe Knysna, Südafrika. *Advancing Frontiers in Plant Science* 4: 151–178.
- THOMAS, D.S.G. & SHAW, P.A. 1988. Late Cainozoic drainage evolution in the Zambezi Basin: evidence from the Kalahari Rim. *Journal of African Earth Sciences* 7: 611–618.
- TOGGWEILER, J.R. & BJORNSSON, H. 2000. Drake Passage and paleoclimate. *Journal of Quaternary Science* 15: 319–328.
- UDEZE, C.U. & OBOH-IKUENOBÉ, F.E. 2005. Neogene palaeoceanographic and palaeoclimatic events inferred from palynological data: cape Basin off South Africa, ODP Leg 175. *Palaeogeography, Palaeoclimatology, Palaeoecology* 219: 199–223.
- UENZELMANN-NEBEN, G. & HUH, K. 2009. Sedimentary deposits on the South African continental margin: slumping versus non-deposition or erosion by oceanic currents?. *Marine Geology* 266: 65–79.
- UTESCHER, T. & MOSBRUGGER, V. 2007. Eocene vegetation patterns reconstructed from plant diversity – a global perspective. *Palaeogeography, Palaeoclimatology, Palaeoecology* 247: 243–271. doi: 10.1016/j.palaeo.2006.10.022.
- VAN ZINDEREN BAKKER, E.M. 1984. Palynological evidence for Late Cenozoic arid conditions along the Namibia coast from holes 532 and 530A, leg 57. Deep Sea Drilling Project. *Initial reports of the Deep Sea Drilling Project* 75: 763–768.
- VLOK, J.H.J. & EUSTON-BROWN, D.I.W. 2002. Subtropical Thicket Ecosystem Planning Project (STEP). Biological Survey Report (plants and birds). Terrestrial Ecology Research Unit Report, University of Port Elizabeth. www.zoo.upe.ac.za/step
- VLOK, J.H.J., EUSTON-BROWN, D.I.W. & COWLING, R.M. 2003. Acocks' Valley Bushveld 50 years on: new perspectives on the delimitation, characterisation and origin of subtropical thicket vegetation. *South African Journal of Botany* 69: 27–51.
- VRBA, E.S. 1985a. African Bovidae: evolutionary events since the Miocene. *South African Journal of Science* 81: 263–266.
- VRBA, E.S. 1985b. Early hominids in southern Africa: updated observations on chronological and ecological background. In Tobias, P.V. (Ed.), *Hominid Evolution*. New York, Alan R. Liss. pp. 195–200.
- WARD, J.D. & CORBETT, I. 1990. Towards an age for the Namib. In Seely, M. (Ed.), *Namib Ecology: 25 Years of Namib Research*. Pretoria, Transvaal Museum. pp. 17–26.
- WHITE, F. 1978. The afro-montane region. In Werger, M.J.A. (Ed.), *Biogeography and Ecology of Southern Africa*. The Hague, W. Junk. pp. 463–513.
- WHITE, F. 1981. The history of the Afro-montane archipelago and the scientific need for its conservation. *African Journal of Ecology* 19: 33–54. doi: 10.1111/j.1365-2028.1981.tb00651.x.
- WHITE, F. 1983. *The Vegetation of Africa*. Paris, UNESCO.
- WRIGHT, J.D., MILLER, K.G., FAIRBANKS, R.G., 1991. Evolution of modern deepwater circulation: evidence from the late Miocene Southern Ocean. *Paleoceanography* 6: 275–290.
- ZAVADA, M.S. & DE VILLIERS, S.E. 2000. Pollen of the Asteraceae from the Paleocene-Eocene of South Africa. *Grana* 39: 39–45.
- ZAVADA, M. & LOWREY, T.K. 2010. Comparative pollen morphology of *Brachylaena*, *tarchonanthus* and two species of *Tubulifloridites* (Asteraceae) from the Eocene, Knysna Lignite of South Africa. *Review of Palaeobotany and Palynology* 162: 183–192.