

On the origin of southern African subtropical thicket vegetation

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The origin and affinities of southern African subtropical thicket have been misunderstood and neglected. This formation was only recognised as a biome distinct from savanna and karoo in the mid 1990s. One hypothesis states that it is a young vegetation type, assembled from forest, savanna and karoo elements after Holocene climatic amelioration. Others have suggested an ancient history for thicket. Here we review fossil and phylogenetic data in order to provide a better assessment of the origins of thicket. Albeit patchy, the fossil data are suggestive of a Palaeogene origin for this formation. A review of molecular phylogenetic data of extant thicket lineages indicated three major patterns: (i) ancient Cretaceous elements, including *Encephalartos* and the Strelitziaceae, (ii) basally branching lineages — many of which dominate contemporary thicket — that evolved in the Eocene (e.g. in the Celastraceae, Sapindaceae, Didiereaceae,

Crassulaceae: Cotyledonoideae), and (iii) lineages derived from adjacent biomes that diversified in thicket in association with Neogene climatic deterioration (e.g. Aizoaceae, Asteraceae). We provide a narrative account of the evolution of thicket, which concludes that it is an ancient formation, extending back at least to the Eocene and derived initially from elements in the forest formations that prevailed in Upper Cretaceous and early Palaeogene times. As a biome, thicket is not uniquely southern African, being part of a formation that was globally widespread in the Eocene and which is extant in many parts of the world. Future research on the origins of thicket should focus on providing dates for major dichotomies as a complement to the rapid emergence of molecular phylogenies, as well as data on the genetic variation in populations of taxa categorised as ancient or young, and widespread or range-restricted.

Introduction

How old is southern African subtropical thicket vegetation? This question has received scant attention, possibly because of confusion regarding the phytogeographical affinities and ecological characteristics of this formation. Indeed, subtropical thicket was only recognised as a distinct southern African biome (Figure 1) relatively recently (Low and Rebelo 1996). The first published account on the origin of subtropical thicket is that of Cowling (1983), who suggested a Holocene origin: the formation was assembled from plants recruited from adjacent biomes — mainly forest, savanna and karoo — after climatic amelioration at the end of the Pleistocene. Vlok *et al.* (2003: 38) suspected 'that the endemic [thicket] flora will include ancient taxa, basal to clades that have diversified in adjacent vegetation types, as well as clusters of terminal taxa derived from karroid, fynbos, and forest relatives'. Recent phylogenetic data on Fabaceae endemic to extant thicket suggest that subtropical thicket is part of a semi-arid tropical biome that was widespread

across the globe in the early Tertiary, and was replete with basally-branching taxa that contributed lineages to vegetation formations that became established in the Neogene (Schrire *et al.* 2005). Thus, the question that we pose is an interesting one. Here we review available palaeontological and phylogenetic data in order to provide a preliminary assessment on the age and origins of subtropical thicket in southern Africa. First, however, we review the biogeography and ecology of subtropical thicket (hereafter termed thicket), and place it in an African and global context.

Floristics, Typology and Biogeography

Thicket is a dense formation of evergreen and weakly deciduous shrubs and low trees (2–5m), often spiny and festooned with vines. Drier forms harbour a large biomass and diversity of succulents, including arborescent forms of



Figure 1: Location of the thicket biome (dark shading) in southern Africa (including Swaziland and Lesotho) (Low and Rebelo 1996). Also shown are the boundaries of other biomes in the region and the distribution of vegetation types (after Low and Rebelo 1996) (light shading) that include thicket vegetation (mostly mosaics) mappable at the 1:100 000 scale. (Fo, forest; Fy, fynbos; Gr, grassland; Nk, Nama-karoo; Sa, savanna; Sk, succulent karoo)

Aloe and *Euphorbia*. Variants associated with wetter climates are transitional to dry forest (Vlok *et al.* 2003). However, although a suite of species that do not grow in most forms of thicket does distinguish it from forest floristically, the distinction between thicket and dry forest is often difficult to make, since many plants widespread in thicket have a tree habit under better soil moisture conditions.

Thicket is centred in the southeast of southern Africa, where it is the dominant formation in the central and eastern Little Karoo, and in the major river valleys coastwards of the Great Escarpment (Gamtoos, Sundays, Fish, Kei) (Vlok *et al.* 2003). However, thicket — as a mosaic with vegetation of other biomes (bush clumps and bontveld) — is widespread throughout the subcontinent (Figure 1). The climate of thicket's core area is semi-arid to subhumid (250–800mm yr⁻¹) and subtropical to warm-temperate (largely frost-free) (Acocks 1953, Low and Rebelo 1996). A distinguishing feature of thicket climates is bimodal rainfall, with peaks in spring and autumn, although copious rain may fall at any time of the year (Vlok *et al.* 2003). A hallmark of thicket is the absence or low cover of grass. Consequently, unlike

savanna, fire is not a component of the thicket disturbance regime, although thicket clumps in fire-prone matrices (thicket mosaics) are fire-affected (Trollope 1974, Manders *et al.* 1992, Cowling *et al.* 1997).

Thicket has a rich flora, conservatively estimated at about 1 600 species, 20% of which are endemic to the Subtropical Thicket Biome (Vlok *et al.* 2003). Plant families and genera well represented in thicket include:

Trees and shrubs: Anacardiaceae (*Heeria*, *Loxostylis*, *Rhus*), Apocynaceae (*Acokanthera*, *Carissa*), Araliaceae (*Cussonia*), Asteraceae (*Brachylaena*, *Euryops*, *Tarchonanthus*), Bignoniaceae (*Tecomaria*), Boraginaceae (*Ehretia*), Brassicaceae (*Boscia*, *Maerua*), Celastraceae (*Cassine*, *Elaeodendron*, *Gloveria*, *Gymnosporia*, *Lauridia*, *Maurocena*, *Maytenus*, *Mystroxydon*, *Pterocelastrus*, *Putterlickia*, *Robsonodendron*), Ebenaceae (*Diospyros*, *Euclea*), Fabaceae (*Acacia*, *Calpurnia*, *Indigofera*, *Schotia*, *Umtiza*), Flacourtiaceae (*Dovyalis*, *Scolopia*), Loganiaceae (*Strychnos*), Malvaceae (*Grewia*), Moraceae (*Ficus*), Meliaceae (*Nymania*), Myricaceae (*Myrica*), Myrsinaceae (*Myrsine*, *Rapanea*), Ochnaceae (*Ochna*), Oleaceae (*Olea*), Pittosporaceae (*Pittosporum*), Plumbaginaceae (*Plumbago*),

Polygalaceae (*Polygala*), Rhamnaceae (*Noltea*, *Rhamnus*), Rubiaceae (*Canthium*, *Psydrax*, *Xeromphis*), Rutaceae (*Clausena*, *Zanthoxylum*), Salvadoraceae (*Azima*), Santalaceae (*Rhoiacarpus*, *Osyris*), Sapindaceae (*Allophylus*, *Atalaya*, *Dodonaea*, *Hippobromus*, *Pappea*, *Smelophyllum*), Sapotaceae (*Sideroxylon*), Stilbaceae (*Nuxia*), Solanaceae (*Lycium*), Scrophulariaceae (*Buddleja*), Strelitziaceae (*Strelitzia*), Thymelaeaceae (*Dais*), Zamiaceae (*Encephalartos*);

Succulents: Aizoaceae (*Bergeranthus*, *Delosperma*, *Drosanthemum*, *Faucaria*, *Glottiphyllum*, *Ruschia*), Apocynaceae (*Ceropegia*, *Huernia*, *Orbea*, *Pachypodium*, *Stapelia*), Asphodelaceae (*Aloe*, *Bulbine*, *Gasteria*, *Haworthia*), Asteraceae (*Othonna*, *Senecio*), Crassulaceae (*Adromischus*, *Crassula*, *Cotyledon*, *Kalanchoe*), Didiereaceae (*Portulacaria*), Euphorbiaceae (*Euphorbia*), Geraniaceae (*Pelargonium*), Portulacaceae (*Anacampseros*), Zygophyllaceae (*Roepera*);

Vines: Apocynaceae (*Cynanchum*, *Sarcostemma*), Asparagaceae (*Asparagus*), Asteraceae (*Senecio*), Brassicaceae (*Capparis*), Geraniaceae (*Pelargonium*), Oleaceae (*Jasminum*), Rhamnaceae (*Scutia*), Vitaceae (*Cyphostemma*, *Rhoicissus*);

Understorey and margin soft shrubs: Acanthaceae (*Barleria*, *Hypoestes*, *Isoglossa*), Geraniaceae (*Pelargonium*), Lamiaceae (*Plectranthus*);

Geophytes: Amaryllidaceae (*Brunsvigia*, *Cyrtanthus*, *Clivia*, *Haemanthus*, *Scadoxus*), Hyacinthaceae (*Albuca*, *Drimia*, *Ornithogalum*), Iridaceae (*Tritonia*) Oxalidaceae (*Oxalis*).

Range-restricted thicket species are over-represented among succulents and, to a lesser extent, geophytes; they are strongly associated with a limited number of families, namely Aizoaceae, Asphodelaceae, Crassulaceae, Euphorbiaceae and Apocynaceae (Cowling 1983, Cowling and Holmes 1991, Hoffman and Cowling 1991, Johnson *et al.* 1999, Vlok *et al.* 2003). Most of the shrub and tree species have relatively wide distributions, often extending in satellite thicket patches beyond the boundary of the Subtropical Thicket Biome. An expanded phytochorological region, which includes outlying thicket enclaves on the subcontinent, would substantially increase the incidence of tree and shrub endemics. Local endemics are concentrated in zones of intermediate rainfall (Valley Thicket — see below) in the Gamtoos, Sundays and Fish River valleys (Hoffman and Cowling 1991, Vlok *et al.* 2003).

Thicket has puzzled plant ecologists and biogeographers. It has been termed karroid scrub (Bews 1925), valley bushveld, strandveld (Acocks 1953), mediterranean shrubland (Boucher and Moll 1980), savanna (Rutherford and Westfall 1986) and dry forest (Midgley *et al.* 1997). Only recently was it circumscribed as a distinctive biome (Low and Rebelo 1996), distinguished from forest on the presence of a single stratum of woody plants and lower overall canopy height, and from savanna on the absence of a well-developed grass component.

Tinley (1975) was the first ecologist to interpret southern African thicket as a part of a pan African thicket formation. White (1983) included much of southern Africa's eastern seaboard thicket in his African-wide 'thicket and bushland' concept. Cowling (1984) introduced the concept of

subtropical transitional thicket for the 'valley bushveld' and 'dune scrub' communities of the southwestern and southern Cape coastal forelands. This study divided thicket into succulent and non-succulent forms, the former showing strong floristic relationships to the Karoo-Namib phytochorion, the latter to the subtropical forests of the Tongaland-Pondoland phytochorion of the eastern seaboard. Ensuing phytosociological studies (Everard 1987, Palmer 1991) upheld these concepts and identified a further subdivision, namely a xeric form of succulent thicket that corresponds with Acocks' (1953) noorsveld and spekboomveld types.

The work of Vlok *et al.* (2003) was a major breakthrough in our understanding of thicket distribution and typology. They identified and mapped 112 thicket vegetation types in the core area of the Subtropical Thicket Biome (Gouritz to Kei Rivers). Their contributions can be summarised as follows: (i) the identification of a major division separating coastal (mainly growing on dunes) and inland types (Figure 2a); (ii) the development a four-tier typological hierarchy for thicket vegetation based on geography (mainly drainage basin), floristics, structure and grain (solid or mosaic); (iii) the expansion of the thicket concept, and its consequent distribution in the region through the recognition of mosaic forms, where thicket clumps occur in a matrix of non-thicket vegetation (Figures 2b and c). The structural types for the inland forms were arranged along a gradient of increasing moisture availability, from Arid Thicket (including noorsveld and spekboomveld) (Figure 2d), to Valley Thicket (typically with emergent *Euphorbia grandidens* and *E. tetragona*) (Figure 2e), to Thicket, the last-mentioned having a low overall abundance of succulents and showing affinities with drier forms of subtropical forest (Figure 2f).

Vlok *et al.* (2003) assigned their thicket types to a Subtropical Thicket Biome, associated physiographically with the non-seasonal rainfall and largely frost-free zone between the Great Escarpment foothills and coast in southern and southeastern South Africa. Subtropical thicket extends eastwards into Kwazulu-Natal where it grows, usually as a mosaic with savanna and grassland, on fire-protected sites in deeply-incised valleys (Acocks 1953, Edwards 1967) (Figure 1). Elements of this biome are also found in the winter-rainfall region of the country, extending along the coastal forelands from Cape Agulhas to northern Namaqualand, as mosaics with fynbos and succulent karoo on coastal dunes (strandveld) (e.g. Boucher and Jarman 1977), and as mosaics with renosterveld (Boucher 1987). Fynbos-thicket mosaics are also widespread in rocky terrain (that affords fire protection) on the lower slopes of the north-trending Folded Belt (e.g. Taylor 1996), and thicket forms mosaics with succulent karoo and renosterveld in the Namaqualand uplands (the so-called Namaqualand Broken Veld of Acocks (1953) (Cowling and Pierce 1999). These winter-rainfall thickets are best placed within the Subtropical Thicket Biome since they have strong affinities with those to the east. However, they do include a number of endemic shrub and tree species such as *Heeria argentea*, *Ozoroa dispar*, *Rhus cuneifolia*, *R. stenophylla* (Anacardiaceae), *Maurocentia frangula*, *Maytenus oleoides* (Celastraceae), *Diospyros ramulosa*, *Euclea lancea*, *E. tomentosa*

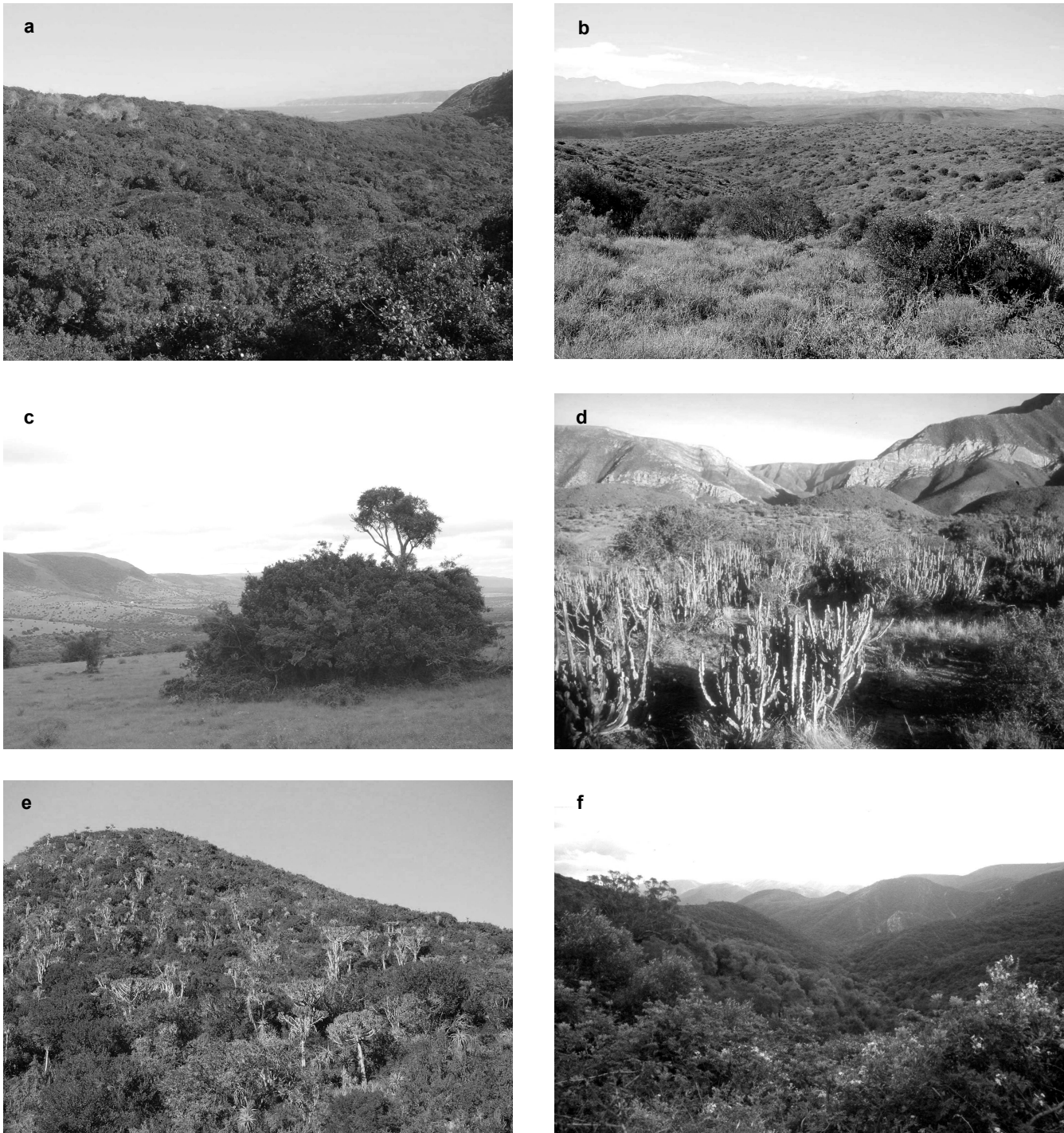


Figure 2: The major types of subtropical thicket in the core biome, after Vlok *et al.* (2003): a) Goukamma Dune Thicket near Sedgfield. Dominants include *Sideroxylon inerme*, *Pterocelastrus tricuspidatus* and *Euclea racemosa* (photo: JHJ Vlok); b) Bloosoms Karroid Thicket, south of Oudtshoorn in the Little Karoo. This is a mosaic of Arid Thicket and succulent karoo. Thicket elements include *Euclea undulata* and *Gloveria integrifolia*, while the matrix is dominated by *Pteronia* spp. and members of the Aizoaceae: Ruschioideae (photo: JHJ Vlok); c) Grahamstown Grassland Thicket east of Grahamstown. This is a mosaic of Thicket and grassland. Thicket elements include *Cussonia spicata*, *Diospyros dichrophylla* and *Rhus pallens*; the grassy matrix is dominated by *Themeda triandra* but also includes fynbos elements (*Erica maesta*, *Restio triticeus*) and a high diversity of range-restricted species, especially *Brachystelma* (Apocynaceae); d) Sundays Noorsveld, a form of Arid Thicket, near the Darlington Dam north of the Zuurberg hills. Dominants include *Euphorbia coerulescens*, *Boscia oleoides* and *Gymnosporia polyacantha* (photo: RM Cowling); e) Albany Spekboom Thicket, a form of Valley Thicket, near Alicedale. Dominants are *Euphorbia tetragona*, *Portulacaria afra*, *Euclea undulata*, *Pappea capensis* and *Aloe speciosa* (photo: JHJ Vlok); f) Sundays Thicket, a Thicket type on the Zuurberg hills above Addo. Dominants include *Tecomaria capensis*, *Allophylus decipiens*, *Canthium inerme*, *Ptaeroxylon obliquum* and *Schotia latifolia* (photo: RM Cowling)

(Ebenaceae), *Hyaenanche globosa* (Picrodendraceae), *Ficus ilicina* (Moraceae) and *Erythrophysa alata* (Sapindaceae). Vlok *et al.* (2003) alluded to the existence of temperate thicket, a mosaic formation associated with the karroid shrublands, grasslands and Afrotemperate forests of the frosty, interior plateau of southern Africa (O'Connor and Bredenkamp 1997). Characteristic species include *Aloe striatula*, *Buddleja auriculata*, *B. glomerata*, *B. corrugata*, *Cussonia paniculata*, *Gymnosporia buxifolia*, *G. karoocia*, *Leucosidea sericea*, *Myrsine africana*, *Olea europaea* ssp. *africana*, *Rhus burchellii*, *R. erosa*, *R. leptodictya* *R. krebsiana*, *R. magaliesmontana* and *R. montana*.

Vegetation that resembles southern African thicket structurally and functionally, being fire-intolerant and having a dense stratum of shrubs and low trees, a paucity of grass biomass, and the invariable presence of succulents — many large-bodied forms — is widespread throughout the tropics and subtropics of the New and Old Worlds where rainfall is relatively low, erratic or non-seasonal (Schrire *et al.* 2005). It is widespread in tropical and subtropical Africa, associated with the 'arid corridor' in fire-protected sites (such as rocky outcrops, riparian zones and termitaria) in savanna landscapes (De Winter 1971, Tinley 1975, Thulin 1994, Jürgens 1997) and lateritic African geo-surfaces (e.g. the Itigi-Sumbu thicket of Tanzania and Zambia (Burgess *et al.* 2004), and as an extensive zonal formation in the Somalia-Masai region (White 1983). Succulent thicket is also the dominant formation of southwestern Madagascar (Leroy 1978, Grubb 2003). Additional nodes are found from Arabia to west Asia and northwest India (Quézel 1978, White and Léonard 1991). In the Neotropics, this formation is represented by the succulent thickets of semi-arid tropical to subtropical Mexico, Central America and the Caribbean (Wolfe 1975, Lavin *et al.* 2001), the dry forest elements of the inter-Andean valleys of Ecuador and Peru, the Piedmont area of northwestern Argentina and central Bolivia, the Misiones region of northeastern Argentina and adjacent Paraguay, and the Caatinga of eastern Brazil (Prado and Gibbs 1993, Pennington *et al.* 2000).

Semi-evergreen vine thicket, described by Webb (1978), from eastern and northern Australia also bears a strong resemblance to southern African non-succulent thicket. Taxonomic affinities with thicket are surprisingly strong, with a high incidence of Sapindaceae (including *Atalaya* and *Dodonaea*), Rubiaceae (including *Canthium*), Apocynaceae (*Carissa*), Celastraceae (*Cassine*, *Maytenus*), Brassicaceae (*Capparis*), Oleaceae (*Jasminum*) and Boraginaceae (*Ehretia*) (e.g. Benson *et al.* 1996). Vegetation that also superficially resembles non-succulent thicket and associated mosaics is widespread in the Mediterranean Basin and Mediterranean-climate California and Chile. Component genera include *Olea*, *Osyris*, *Pistacia* in the Mediterranean Basin (Herrera 1992), *Heteromeles*, *Prunus*, *Rhamnus* in California (Keeley and Keeley 1988), and *Cryptocarya*, *Escallonia* and *Lithrea* in Chile (Arroyo *et al.* 1995). These taxa are functionally similar to dominant southern African thicket shrubs, having evergreen, sclerophyllous leaves, fleshy fruits dispersed by animals, very long lifespans, and an ability to sprout after disturbance. They are regarded as tropical 'phantoms' (Herrera 1992), being components of

early Neogene woodlands and thicket that persisted through the onset of cooler and drier Mediterranean-type climates in the Pliocene (Axelrod 1975, Herrera 1992, Valiente-Banuet *et al.* 1998, Verdú *et al.* 2003).

Ecology

In comparison to other southern African biomes, the ecology of thicket ecosystems is poorly understood (Midgley *et al.* 1997). However, recent research has provided sufficient information to sketch in broad outline the ecological processes that maintain thicket structure and composition. Below we briefly review aspects of thicket ecology salient to this paper.

Reproductively, thicket is dominated by trees and shrubs that fit Bond and Midgley's (2001) persistence niche concept. Plants are very long-lived and are capable of sprouting after defoliation from herbivores, frost and fire (Midgley and Cowling 1993, Cowling *et al.* 1997, Kruger *et al.* 1997). The mostly inconspicuous flowers and predominantly bird-dispersed propagules appear erratically throughout the year, although there is a weak tendency for reproductive phenology to peak in spring and autumn (Pierce and Cowling 1984, Sigwela 2004). In Arid and Valley types, shrub and tree seedlings are scarce, and recruitment is mainly via ramets (Midgley and Cowling 1993, Sigwela 2004); seedling recruitment is more important in the taller and more mesic Thicket types (Cowling *et al.* 1997, Kruger *et al.* 1997). Reproduction via seedlings is prevalent amongst the shorter-lived succulent component, including arborescent members of *Aloe* and *Euphorbia* (Midgley and Cowling 1993, Kamineth 2004), which are incapable of sprouting in response to herbivory (Cowling and Kerley 2002, Kamineth 2004).

Thicket supports a diverse mammal fauna, including 48 large and medium-sized species (>2kg) (Kerley *et al.* 1995). Amongst these are 28 herbivores, including large-bodied African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), African buffalo (*Syncerus caffer*), Burchell's zebra (*Equus burchelli*), kudu (*Tragelaphus strepsiceros*) and eland (*Taurotragus oryx*). Elephants — megaherbivores — were very abundant in thicket in pre-colonial times (Boshoff *et al.* 2002) and are regarded as a keystone species with regard to their impacts on ecosystem structure and functioning (Kerley *et al.* 1995, 2002). The same could be said of black rhinoceros. However, at their very high densities in the Addo Elephant National Park (up to 3.8 km⁻²), elephants have had a negative impact on the endemic biodiversity (mainly dwarf succulents and geophytes) of the park (Moolman and Cowling 1994, Lombard *et al.* 2001, Cowling and Kerley 2002), although overall structure and function is better maintained under this regime than goat browsing at equivalent stocking density (Stuart-Hill 1992, Moolman and Cowling 1994).

Thicket is unusual amongst African ecosystems in that — with the exception of mosaics with fire-prone matrices — herbivores alone are responsible for defoliation; drought, fire and gap-producing tree mortality are unimportant (Kerley *et al.* 1995). Most thicket plants are highly palatable (Aucamp *et al.* 1978), and many show morphological features that

enable them to cope with browsing, namely spines (e.g. *Gymnosporia*, *Putterlickia*, *Rhus*) that significantly slow browsing rates (Wilson and Kerley 2003), and a finely divaricating branch architecture (cf. McQueen 2000), especially of low-growing shrubs (e.g. *Azima*, *Ehretia*, *Rhus*). It would seem that there has been a long history of mammalian herbivory in thicket.

Biomass, litter fall and carbon storage in intact thicket are exceptionally high for a semi-arid ecosystem, exceeding by orders of magnitude values recorded for other semi-arid ecosystems and approaching values recorded for some forest ecosystems (Lechmere-Oertel *et al.* 2005a, Mills *et al.* 2005). It has been suggested that the unusually high biomass maintained in thicket ecosystems is a consequence of the accumulation of soil organic carbon (133t C ha^{-1} to a depth of 30cm at a rainfall of c. 300mm yr^{-1}) (Mills *et al.* 2005) beneath the densely shaded and relatively cool and dry canopy (Lechmere-Oertel *et al.* 2005a).

Overall, thicket is a stable but brittle formation. Excessive browsing by livestock — chiefly goats — results in its transformation to a pseudosavanna comprising isolated and highly stressed tree remnants, in a matrix of ephemerals and dwarf shrubs (Hoffman and Cowling 1990, Lechmere-Oertel *et al.* 2005a). Once the soil organic content is lost, ecosystem functioning is irreversibly impaired (Lechmere-Oertel *et al.* 2005a, 2005b), and active restoration — an extremely costly process — is the only option to regain ecosystem health (Mills and Cowling 2005).

Affinities and Origins

The absences of fossil data, well-resolved phylogenies, and dates for diversification have greatly constrained the development of hypotheses on the origins of thicket vegetation. Early work was based mainly on the biogeographical affinities of extant taxa, phylogenetic inferences derived from taxonomic monographs, and limited fossil data. We review these earlier studies below.

Both Bews (1925) and Acocks (1953) suggested a karroid origin for thicket, based on the abundance and diversity of taxa of Karoo-Namib affinity (*sensu* Werger 1978) that grow in the drier forms of this vegetation. Also invoked as evidence for this hypothesis was the gradation, via thicket-karoo mosaics, from solid thicket to karroid shrublands. Acocks (1953) also suggested a subtropical forest origin for the more mesic thickets, this being based on their smooth transition to dry forests on the southeastern coast. This was reinforced by Moll and White (1978) who, on the basis of the biogeographical affinities of thicket shrub and tree floras, characterised southern African thicket as a xeric expression of the eastern seaboard Tongaland-Pondoland forest flora. None of these early assessments attempted to explore the origin of thicket. Axelrod and Raven's (1978) account of the evolution of southern African vegetation did not identify thicket as a distinct formation; they postdicted a 'laurel forest' occupying the present-day Subtropical Thicket Biome.

Cowling (1983) hypothesised that subtropical thicket — at least in southeastern southern Africa — is a recent formation, assembled in the Holocene by recruiting species

from adjacent forest, karoo and savanna floras. Available palaeodata supported this assertion. At Boomplaas Cave in the Little Karoo, charcoal remains suggest a transition between Pleistocene and Holocene times from an asteraceous shrubland (renosterveld) to thicket (*Olea*, *Dodonea*, *Rhus*, *Buddleja*, *Acacia*, Ebenaceae) (Scholtz 1986). At Groenvlei, a coastal site south of Boomplaas that currently supports thicket-forest mosaic and patches of Afromontane forest, the onset of the Holocene saw the replacement of fynbos by forest and thicket taxa (Martin 1968). At both Nelson Bay Cave (east of Groenvlei) and Boomplaas, browsers replaced grazers in the mammal fauna at the start of the Holocene, suggestive of the establishment of woody vegetation (including thicket) at the expense of more open, grassier communities (Klein 1972, 1978).

Cowling's (1983) phytochorological analysis supported Moll and White's (1978) assertion that the strongest thicket affinities lay with the Tongaland-Pondoland forests of the eastern seaboard. He also observed that thicket endemics were over-represented among succulent lineages of 'karroid' affinity (Crassulaceae, Asphodelaceae, Aizoaceae) and inferred from this that the woody component invaded a widespread karoo formation after Holocene climatic amelioration. Hoffman and Cowling (1991) disagreed, citing evidence that many of these succulent endemics (e.g. *Crassula*, *Delosperma*, *Gasteria*, *Haworthia*) were biologically and geographically integrated with the dominant thicket shrubs, and that this was suggestive of a long history of coexistence.

In summary, by the mid 1990s, subtropical thicket was recognised as a formation in its own right that showed affinities with thicket formations elsewhere in Africa. Speculation on the origins of thicket suggested that it was a post-Pleistocene formation, assembled from taxa derived from adjacent biomes, principally the drier forests of the subtropical east coast, and that it replaced drier formations, mainly karroid shrublands, but also grasslands and asteraceous shrublands (renosterveld).

In the remainder of this paper, we delve further back in time — to the mid Cretaceous — in order to unravel the mysteries of thicket origins. At our disposal are new insights on the Cainozoic geomorphic and climatic history of southern Africa, 10 years of research on the molecular phylogenies of thicket lineages, and additional fossil data. Although the story is still patchy, there is compelling evidence that southern African thicket is part of an ancient, global formation — a xeric manifestation of an Upper Cretaceous–early Palaeogene warm temperate : subtropical forest flora.

Fossil record

Southern Africa is poorly endowed with Tertiary fossil data, and this greatly hampers the reconstruction of thicket origins. Moreover, there is considerable uncertainty regarding the dating of key fossil deposits, and this has greatly confused the vegetation history of the region. Another problem is the difficulty of distinguishing forest and thicket components of fossil assemblages, since many

supraspecific taxa (e.g. *Olea*, *Rhus*, Celastraceae, Sapindaceae) are shared between these two formations. However, given the close relationships between mesic thicket and dry forest, we have assumed that the presence of fossil floras of these taxa is indicative of thicket/dry forest occurrence.

Scarce as they are, mid Cretaceous deposits from southern Africa are indicative of mixed gymnosperm-angiosperm forests (Scott *et al.* 1997) consistent with the warm temperate and moist climate of that time (Scotese 2001). The terminal Cretaceous-Palaeocene (71–64Ma) pollen remains from the crater lake deposits in the Arnot kimberlite pipe at Banke in Namaqualand (Scholtz 1985) yielded abundant gymnosperms, particularly Araucariaceae, but also Podocarpaceae. However, angiosperms were well represented by many families, including Chloranthaceae, Restionaceae, Palmae, Ulmaceae, Casuarinaceae/Myricaceae, Proteaceae, Gunneraceae, Euphorbiaceae, Thymelaeaceae, Anacardiaceae, Cornaceae, Ericaceae and Fabaceae. Scholtz (1985) envisaged a dry forest with an understorey of 'Cape' elements (Restionaceae, Proteaceae, Ericaceae) consistent with the relatively dry conditions prevailing in south-central Africa at that time (Scotese 2001). An alternative reconstruction would be an australian woodland with patches of closed forest/thicket in a matrix of fynbos-like vegetation — a very early thicket mosaic.

There is a dearth of other fossil data for southern Africa for the Palaeogene and those that do exist are not dated unambiguously. Of interest is the fact that the 'Miocene' pollen deposits from Noordhoek on the Cape Peninsula (Coetzee 1978, Coetzee *et al.* 1983) and at Langebaanweg north of there (Coetzee and Rogers, 1982), which suggest a moist subtropical-austrotemperate forest vegetation (including many forms now extinct in Africa), are associated with sediments (the Elandsfontyn Formation) that are now dated as older than Middle Eocene (Dale and McMillan 1999, IK McMillan pers. comm.). The flora from shelf sediments at Noup on the Namaqualand coast, which is dominated by Asteraceae pollen and fern spores (Scott *et al.* 1997), is probably much younger than the Eocene age attributed to it. Recent evidence on the evolution of Asteraceae indicates that they reached Africa only in the late Oligocene or Miocene (Funk *et al.* 2005). Pollen, presumably of Palaeogene age, from channel fill deposits at Hondeklip Bay, also on the Namaqualand coast, is dominated by austral forest elements and palms (Arecaceae) (De Villiers and Cadman 1997). Other putatively Palaeogene deposits include macrofossils from the Fort Grey silcretes (near East London) (Adamson 1934) and the Knysna lignites (Thiegart *et al.* 1963): both include taxa that could be attributed to forest and thicket, while the lignites also include pollen of Restionaceae, Ericaceae and Proteaceae.

Global reconstruction of palaeoclimates postdict relatively dry and warm conditions in southern Africa in the Eocene-Palaeocene, and cool dry conditions during the Oligocene (Scotese 2001, Zachos *et al.* 2001). In this respect, it may be prudent to treat the suggestion of widespread Palaeogene forest vegetation (Coetzee 1993) with caution. A more realistic reconstruction might be an admixture of

forest and thicket formations, the former being associated with azonal, high-moisture sites.

Dry subtropical forest and woodland vegetation, possibly resembling thicket, has been inferred from Miocene fossil data from the lower Orange River Valley (Hendey 1983), Bushmanland (De Wit and Bamford 1993, Bamford 2000) and the Olifants River Valley (Western Cape) (Bamford 2000). Indications are that vegetation comprising an admixture of forest, thicket, fynbos and asteraceous shrubland was found in present-day Namaqualand during the Miocene (Scott 1995), although independent dates for the associated fossils are lacking.

From the Late Miocene onwards, the climate of southern Africa rapidly became colder and drier as a consequence of the growth of the Antarctic ice sheet and the development of the circum-Antarctic current in the Southern Ocean. By the end of the Pliocene, in the interior of the country, dense woodlands (or thicket) were replaced by more open savanna and grassland (Vrba 1985). The saw-tooth climatic fluctuations of the Pleistocene, where prolonged cold and dry conditions were interrupted by shorter warmer and wetter spells, resulted in the contraction (glacials) and expansion (interglacials) of thicket vegetation. Of interest is that thicket vegetation remained locally dominant (at Elands Bay, on the southwestern coast) through the last glacial (Cowling *et al.* 1999), whereas evidence from south coast sites indicates a post-glacial (Holocene) expansion (Scholtz 1986).

In summary, the fossil record is not particularly useful for elucidating the origin of thicket vegetation in southern Africa. However, throughout the Tertiary, taxa associated with contemporary thicket formations (e.g. *Rhus*, *Olea*, Capparaceae, Celastraceae, Ebenaceae, Sapindaceae) have been present in the region. Taxa that could be attributed to thicket (Anacardiaceae, Burseraceae, Celastraceae, Ebenaceae, Sapindaceae) have been located from Palaeogene and early Neogene deposits in present-day Sahara and Ethiopia (Dupéron-Laudoueneix and Dupéron 1995). It is not possible to say whether these fossil remains are indicative of formations similar to contemporary thicket. However, the representation among the Neogene fossils of taxa representative of several of today's biomes (forest, fynbos, karoo) — along with thicket taxa — suggest that thicket mosaics may have an ancient history in the region.

Phylogenetic perspective

In this section, we provide a brief review of phylogenetic patterns for lineages that are dominant in, or characteristic of, southern African thicket vegetation. Information on the general distribution of taxa and total species numbers is taken from Leistner (2000) and Germishuizen and Meyer (2003); the arrangement of plant taxa largely follows APG II (2003), and data on representation and dominance in thicket are based on Vlok *et al.* (2003). Although much of this section focuses on the generic level, genera are in many cases not monophyletic; therefore, biogeographical inferences may not be pertinent to the genera as such, but to certain clades or grades within them, or including them. Also, given the rapid changes in the understanding of plant

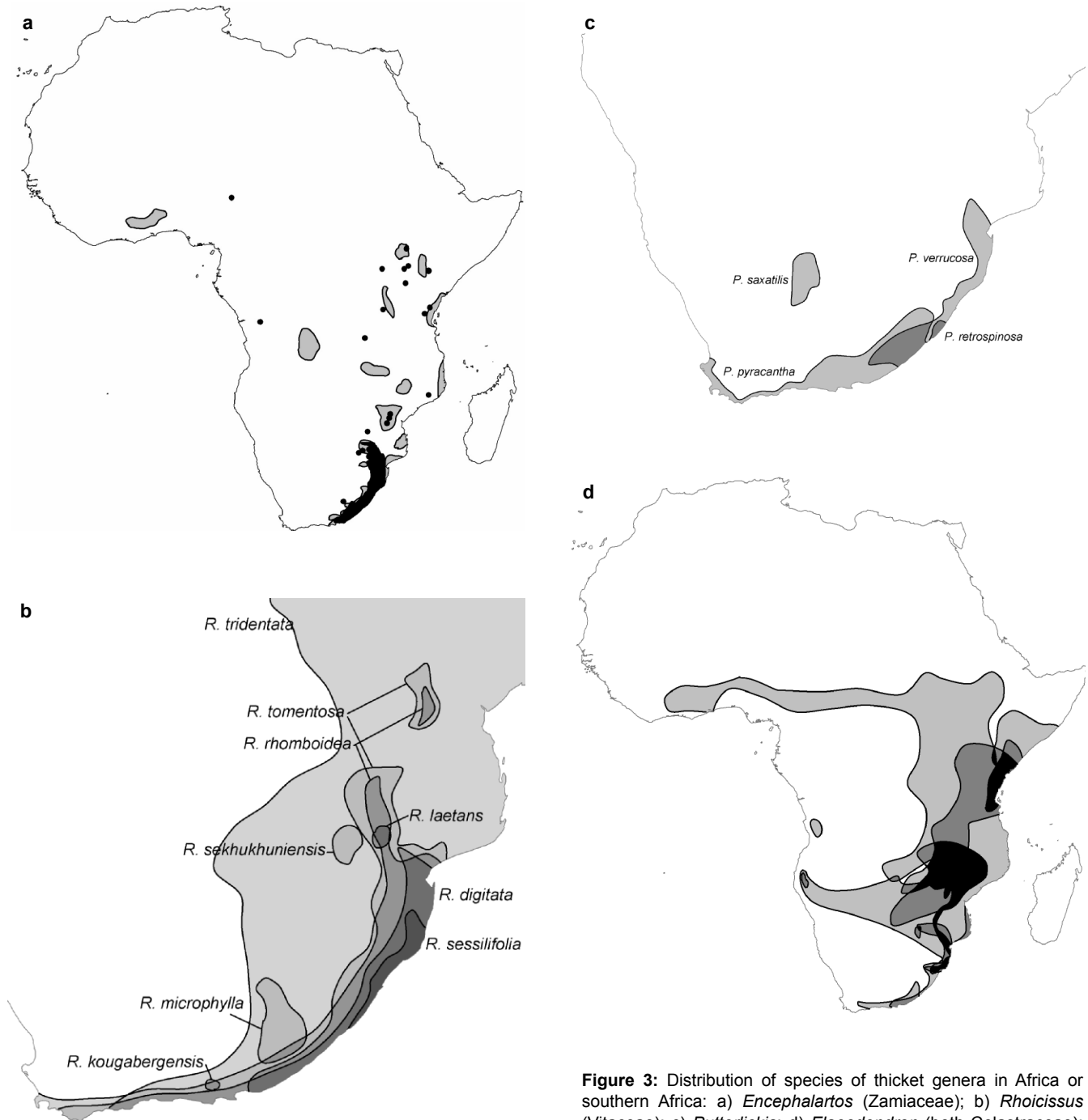
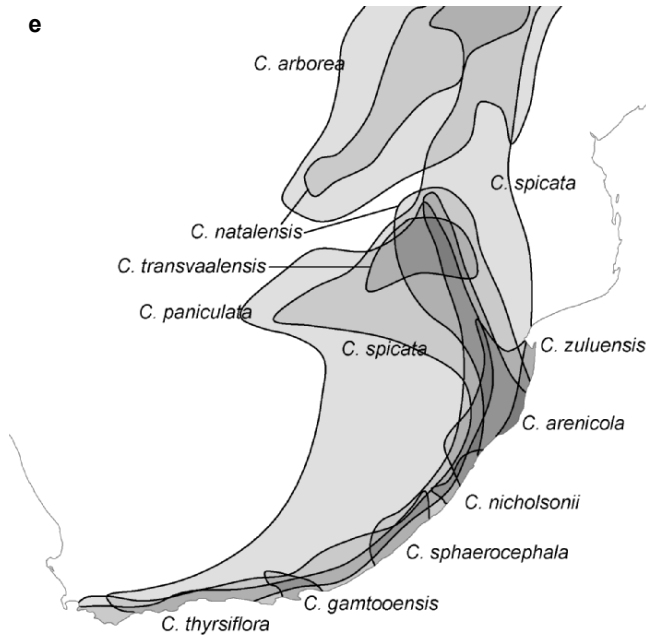


Figure 3: Distribution of species of thicket genera in Africa or southern Africa: a) *Encephalartos* (Zamiaceae); b) *Rhoicissus* (Vitaceae); c) *Putterlickia*; d) *Elaeodendron* (both Celastraceae); e) [opposite page] *Cussonia* (Araliaceae) (after Coates Palgrave 1977, Archer and Van Wyk 1998, Jordaan and Van Wyk 1998, Goode 2001, modified). Darker shades of grey indicate higher species diversity; dots represent point endemics

and animal phylogenies, some of the examples given here in a phylogeographic context may turn out to be inappropriate, as further molecular studies unfold. However, the general conclusions, based on multiple phylogenies and geographical distributions, are likely to hold. Unfortunately, in most cases there is no information available on the dates

when major intra-familial branching events occurred, and all inferences have to be made on the basis of broad diversification hypotheses (e.g. Davies *et al.* 2004 for angiosperms in general), which are themselves based on a limited numbers of calibration points.



Gymnosperms

Encephalartos, the most diverse African cycad genus, is most likely a Cretaceous relict, being most closely related to the Australian *Macrozamia* and *Ceratozamia* (Hill *et al.* 2003). Members of the genus occur mainly in rocky areas through much of the continent (Figure 3a). However, the vast majority of species are concentrated along the eastern escarpment of southern Africa, with two major diversity centres, one in the Eastern Cape, and one in KwaZulu-Natal–Limpopo (Goode 2001). Several distantly related clades of *Encephalartos* co-occur in the Eastern Cape, growing in a wide range of thicket types, but most species in this area belong to one of them (*E. altensteinii*, *E. arenarius*, *E. horridus*, *E. latifrons*, *E. lehmannii*, *E. longifolius*, *E. princeps*, *E. trispinosus*), in which diversification appears to have been relatively recent, and hybridisation frequently occurs (Van der Bank *et al.* 2001).

Monocotyledons

Another probably Cretaceous relict is the southern African endemic *Strelitzia* (Strelitziaceae), exhibiting a characteristic zingiberaceous growth form. The five species in this genus are distributed in sub-humid to semi-arid vegetation, from Zimbabwe to the southern Cape. The two species from drier environments, *S. reginae* and *S. juncea*, having a shrub rather than tree-like habit, occur in thicket. Considering the tall stature of the closest relatives (*Ravenala*, from Madagascar, and *Phenakospermum*, from South America) (Kress *et al.* 2001), it can be assumed that the lower stature in these two species is a derived character, representing an adaptation to a semi-arid climate.

In Iridaceae, the most plesiomorphic species in the genus *Dietes* — *D. iridoides* — is a dry forest-thicket species restricted to the Eastern Cape, while more derived species inhabit forest and thicket all along the eastern escarpment of

southern Africa (Goldblatt 1981, Donato *et al.* 2000). This genus is basal to a branch including the winter-rainfall genera *Bobartia*, *Ferraria* and *Moraea* (Goldblatt *et al.* 2005). In another branch of the family, the large winter-rainfall genus *Tritonia* appears to have thicket elements as the most basally branching species (P Goldblatt pers. comm.).

Much of the geophyte flora of African semi-arid areas — including thicket — belongs to two families: Amaryllidaceae and Hyacinthaceae. Among the Amaryllidaceae, the tribe Haemantheae is well represented in thicket, with the basal dichotomies in the genera *Clivia* and *Haemanthus* occurring between the western, winter-rainfall species, and those from the eastern parts of southern Africa (Conrad *et al.* 2003, Meerow and Clayton 2004). Both genera are centred in southern Africa; however, the diversity patterns they exhibit differ dramatically, *Haemanthus* having diversified mainly in the west in succulent karoo, and *Clivia* mainly in the east in forest and forest-thicket mosaics (Conrad *et al.* 2003, Procheş *et al.* 2004). Interestingly, *Clivia mirabilis*, the recently described, basally branching, winter-rainfall species (Rourke 2002), is associated with *Maytenus oleoides*–*Podocarpus elongata* thicket.

Several genera of Hyacinthaceae are fairly diverse in thicket, in particular *Drimia* and *Ledebouria* (both *sensu lato*, thus *Drimia* including *Tenicroa*, *Rhadamanthus*, *Sekanama*, *Charybdis*, *Urginavia*, *Fusifilum*, *Thuranthos*, *Boosia*, *Litanthus*, and *Ledebouria* including *Drimiopsis* and *Resnova*; see Manning *et al.* 2004). They represent two distinct branches in the family. *Drimia* show a remarkable degree of morphological plasticity and a broad Afro-Eurasian distribution, various clades having diversified in southwestern and southeastern Africa. *Drimia* is sister to another semi-arid clade, the unusual scrambler *Bowiea* (1–3 species, depending on treatment, distributed in southern and East Africa) (Manning *et al.* 2004). *Ledebouria* is similar in broad-scale distribution patterns, although most of the species are concentrated in more humid environments, and particularly in the Drakensberg region. A potentially early-branching *Ledebouria* clade occurs in southeastern Africa and Madagascar, and the most likely sister genus, *Schizocarphus*, occurs in southern and East Africa (see Wetschnig and Pfosser 2003). A third genus of Hyacinthaceae, *Veltheimia*, occurs in moister thicket types, and contains two species similar in distribution to the sister clades noted in both *Clivia* and *Haemanthus* (Amaryllidaceae), with which they probably share a common biogeographic history. The genus fits best in a clade with *Lachenalia* and *Massonia*, succulent-karoo-centred genera (Wetschnig and Pfosser 2003).

The Asphodelaceae, and the genus *Aloe* in particular, are conspicuous, leaf succulent components of thicket vegetation. A recent phylogeny (Treutlein *et al.* 2003) shows that *Gasteria*, *Haworthia*, *Poellnitzia*, *Astroloba* and *Chortolirion* are embedded in *Aloe*, all of these genera thus making up a formidable clade with more than 600 species, distributed throughout Africa, Madagascar and Arabia, but clearly most diverse in the drier regions of southern Africa (where all genera but *Aloe sensu stricto* are endemic). Sister to all other species in this clade are the larger tree aloes,

and although two of these occur in semi-desert and desert ecosystems of Namibia and the Northern Cape, the earliest branch is represented by the *A. barberae*, a species of dry forest and mesic thicket from the Eastern Cape to southern Mozambique. The earliest branching among the remaining sampled aloes is *A. ciliaris*, an Eastern Cape endemic that grows in thicket. From the same area is *Gasteria glomerata*, sister to all other gasterias in Treutlein *et al.*'s (2003) analysis. *Haworthia* is resolved as polyphyletic in the same study, but it is clear that much of the diversification in at least one of the clades is linked to thicket.

Asparagus is another hyper-diverse genus, comprising a variety of cladodineous vines and shrubs, many species of which occur in thicket. The general distribution includes Australia, Asia and southern Europe. However, diversity is highest in southern Africa, where two of the three subgenera occur, including the morphologically unusual *Myrsiphyllum*. The genus is associated with all types of southern African vegetation, from karoo to forest, but is most abundant and diverse in thicket. In the absence of a molecular phylogeny it is difficult to assess its origins. Much like *Asparagus* subgenus *Myrsiphyllum* in broad morphology, but unrelated, is *Behnia* (Agavaceae), occurring in forests and thicket from the southern Cape to Zimbabwe. The phylogenetic position of this monotypic genus has been long disputed (see Fay *et al.* 2000), suggesting ancient origins.

Dicotyledons

Three families in the orders Caryophyllales and Saxifragales contain the bulk of leaf-succulents in thicket. These are the Aizoaceae, Portulacaceae and Crassulaceae. In the Aizoaceae, the Ruschioideae form a recent (probably late Pliocene) and rapidly diversified clade, with diversity peaking in the winter-rainfall (western) parts of southern Africa (c. 1 500 species) (Klak *et al.* 2004). Several genera secondarily invaded thicket, *Delosperma* and *Drosantherum* being locally both abundant and diverse. A few other genera (*Bergeranthus*, *Orthopterum*, *Rhombophyllum*) are thicket endemics, but the phylogenetic status of these taxa is difficult to assess, as rapid diversification and possibly hybridisation obscure intergeneric relationships. The earliest-branching species in *Mesembryanthemum* (sister to all Ruschioideae) are western (Klak *et al.* 2004), suggesting a winter-rainfall origin for the entire group. Overall, however, Aizoaceae are important components of thicket, being the third most diverse family in this biome (Vlok *et al.* 2003).

The portulacoids are represented in subtropical thicket by a few, mostly herbaceous, species. Nevertheless, the only arborescent species of this formation (*Portulacaria afra* — spekboom) is dominant in more than 10 different types of Valley and Arid Thicket (Vlok *et al.* 2003). *P. afra*, together with an East African relative, is the sister clade to a branch including the other two *Portulacaria* species (lower shrubs associated with thicket-karoo mosaics in the Northern Cape and southern Namibia), as well as the genus *Ceraria* (from the same area). This dichotomy suggests an early disjunction between the western and eastern *Portulacaria* populations, the former diversifying into several species, while the latter became dominant over a large area. The

closest living relatives of the entire *Portulacaria*–*Ceraria* clade are the genus *Calyptrotheca*, from the Horn of Africa, and the Madagascan endemic Didiereaceae (Appelquist and Wallace 2000, 2001, Guralnick and Jackson 2001). The confirmation of these phylogenetic relationships led to the recent inclusion of *Portulacaria* and *Ceraria* in Didiereaceae (Appelquist and Wallace 2003), which thus represent an ancient Afro-Madagascan clade. It may well be true that *P. afra*, which is capable of switching between C3 and crassulacean acid metabolism (CAM) (Guralnick *et al.* 1984), is the earliest species amongst flowering plants exhibiting this photosynthetic pathway. The earliest unequivocal evidence for CAM photosynthesis dates back to only 40 000 years ago (Troughton *et al.* 1974); given the antiquity of *P. afra* — based on the phylogenetic evidence presented above — a much earlier (possibly mid-Tertiary) date for the appearance of CAM seems plausible.

Additionally, the order Caryophyllales includes the Plumbaginaceae, with *Plumbago auriculata* being locally dominant in thicket, and a few other species occurring in southern Africa. The genus *Plumbago* is widespread and it contains more than 20 species, several of them African; the sister genus appears to be *Dyerophytum* (three species), with an African-Arabian distribution (*D. africanum* reaching into the Northern Cape) (see Lledó *et al.* 2001).

Crassulaceae are the fourth largest family in thicket (Vlok *et al.* 2003), and locally are often the most common and diverse (Cowling 1983, Procheş and Cowling 2005). Three major clades can be distinguished in this family, two of them reaching peak diversity in southern Africa. The *Adromischus*–*Cotyledon*–*Tylecodon*–*Kalanchoe* branch represents yet another African–Madagascan xeric disjunction, in this case the only Madagascan genus (*Kalanchoe* incl. *Bryophyllum*) being clearly the more derived. In the southern African grade, the thicket-centred *Adromischus* diverged first, but with the winter-rainfall species *A. alstonii* being sister to the other sampled taxa; in *Cotyledon*, both of the major clades appear to be thicket-centred (see Tölken 1985, Van Ham and 't Hart 1998, Mort *et al.* 2001, M Mort pers. comm.). A phylogeny of *Crassula*, currently being compiled, is likely to provide important insights for diversification in thicket (M Mort pers. comm.).

Amongst the earliest rosids, the Vitaceae are of particular interest from a thicket perspective. The genus *Rhoicissus*, an African endemic today but previously more broadly distributed, forms, with *Ampelopsis* (found elsewhere, but also showing a relict distribution), the basal grade in Vitoideae. In its current distribution, *Rhoicissus* has its diversity centre in southern Africa, with seven of the 10 recognised species occurring in an area from the Eastern Cape to Limpopo (Figure 3b). The other four southern African genera, with less clear thicket affinities, are all embedded in the *Rhoicissus*–*Ampelopsis* grade (Ingrouille *et al.* 2002).

Pelargonium (Geraniaceae) is a large, predominantly southern African genus of a baffling morphological plasticity; among the thicket species alone there are annuals, perennial herbs, shrublets, geophytes and succulent vines. Numerous species are endemic to the thicket, and most of these belong to one, largely semi-arid clade, although some of the earliest-branching species in it are not southern

African thicket taxa, but grow in Namibia and East Africa (Bakker *et al.* 2004).

The newly segregated genus *Roepera* in Zygophyllaceae represents an Australian–southern African disjunction, probably resulting from long-distance dispersal (Beier *et al.* 2003); most African species are of karroid affinity, but *Roepera margsana* is locally dominant in thicket.

The Celastraceae are the most diverse family of woody thicket species. Their taxonomy has recently undergone major changes, indicating that a long and intricate evolutionary history, only now emerging, is masked by morphological uniformity. *Maytenus* (150 species worldwide, 11 occurring in southern Africa, mostly in thicket), together with the forest/thicket genus *Pterocelastrus* (three species, all southern African endemics), are distantly related to the other southern African genera. The main southern African radiation is associated with a second clade. The genus *Cassine* in its current definition (Archer and Van Wyk 1997) is a southern African endemic, with three species, two of which are restricted to the Western and Eastern Cape. The same clade includes *Allocassine* (monotypic, from Zimbabwe to the Eastern Cape); *Lauridia* (two species, from Limpopo to the Western Cape); the monotypic Cape endemic *Maurocenia*; *Lydenburgia* (two narrow endemic species, one from Limpopo, the other from the Eastern Cape); the monotypic *Catha* (the khat tree, of uncertain original distribution); *Putterlickia* (four southern African species, locally dominant in thicket) (Figure 3c); the closely-related genera *Empleuridium* and *Gloveria* (both Western/Northern Cape endemics); and *Gymnosporia* (with 80 species in Africa and Asia, 30 of which occur in southern Africa, indicating a radiation exceeded among woody thicket genera only by *Rhus*) (Islam *et al.* 2004). A third clade includes *Elaeodendron* (30 species, c. 10 African, mainly in thicket but occurring in savanna on termite mounds, three in southern Africa) (Figure 3d) and the mainly forest genera *Robsonodendron* (two species endemic to southern Africa), *Mystroxylon* (monotypic, *M. aethiopicum*, a typical thicket species from Africa and the Mascarenes), *Pleurostylia* (a few species in Africa, the Mascarenes and Australasia), *Pseudosalacia* (monotypic, endemic to the Pondoland centre), together with the Afro-Madagascan *Brexia*, previously placed in a family of its own (Islam *et al.* 2004). Finally, a fourth clade contains, amongst others, the genera *Salacia* and *Hippocratea* (the latter probably comprising several smaller genera), mainly from forest and woodland environments further north in Africa and elsewhere (Simmons *et al.* 2001, Islam *et al.* 2004). A calibrated phylogeny of the Celastraceae would provide important insights into the origin of thicket vegetation.

The legumes (Fabaceae) are under-represented in southern African thicket, relative to surrounding vegetation types, but there is at least one woody genus that is commonly present, namely *Schotia*, the most typical thicket species being *S. afra*. With a total of five species, *Schotia* is a southern African near-endemic, belonging to the basal Detarieae (Schrire *et al.* 2005). The basally-divergent clade in this tribe includes, besides *Schotia*, genera associated with semi-arid vegetation from tropical America and Madagascar. The Caesalpinieae include another subtropical thicket/dry forest genus, the narrow Eastern Cape endemic

Umtiza listeriana, most closely related to northern hemisphere *Gleditsia*. It has been suggested that in the Fabaceae, semi-arid thicket environments were of great importance in early lineage diversification, northern temperate, savanna and rainforest lineages having xeric ancestors, as shown for several world regions (Schrire *et al.* 2005). Besides the Detarieae and Caesalpinieae, examples are found in the Mimoseae, Acacieae, Swartzieae, Amorpheae, Indigofereae, Loteae and several others, although not particularly relevant in a southern African context. Indeed, legumes are dominant today in savanna ecosystems throughout the world and, prior to grass invasion, the same taxa (in some cases even the same species) were dominant in African dry forest ecosystems as far back as 46 million years ago (Herendeen and Jacobs 2000). In the tribe Podalyrieae, a predominantly Cape fynbos taxon, the basal genus is *Calpurnia*, an African genus of mesic thicket and forest-thicket mosaics (Käss and Wink 1997, Schutte and Van Wyk 1998).

Euphorbia, one of the largest and most morphologically diverse plant genera, has many diversity centres worldwide, yet few as rich as southern Africa. In particular, stem-succulent species are exceptionally well represented here, both in karroid and thicket environments. A recent phylogeny (Steinmann and Porter 2002) indicates that most of the subgenera and sections of *Euphorbia*, as previously defined, are polyphyletic. There is insufficient taxonomic coverage to infer relationships between the smaller karroid species and the tree-like species of thicket and savannas. Nevertheless, there is enough information to infer a Madagascan origin for the genus, with early southern African radiations. In two related families (until recently treated as Euphorbiaceae), *Hyaenanche* (Picrodendraceae, monotypic and restricted to fynbos-thicket mosaics in the Gifberg, Western Cape), *Lachnostylis* (Phyllanthaceae, comprising three thicket species endemic to the Western and Eastern Cape), and *Heywoodia* (also Phyllanthaceae, one species represented in two relictual metapopulations in dry forest in southern African and East Africa) probably represent ancient thicket/dry forest elements. *Hyaenanche* and *Heywoodia* are closely related to Madagascan and South American genera (Levin and Simpson 1994, Webster 1994).

Two families in Brassicales are important in thicket vegetation, being represented mainly by (often armed) shrubs. In the case of the Salvadoraceae, the entire family can be described as having semi-arid affinities, both larger genera (*Salvadora* and *Azima* with 4–5 species each) occurring in the drier parts of Africa and Asia. *Azima tetracantha* is locally dominant in subtropical thicket (see Verdoorn 1963). Also predominantly semi-arid thicket and savanna are the Capparoideae (Brassicaceae), Africa representing the main diversification centre for this tribe (Hall *et al.* 2002). Three of the genera (*Capparis*, *Maerua* and *Boscia*) occur as dominants in thicket.

The Anacardiaceae is a large family of woody plants, distributed globally. However, Africa and Madagascar are the most species-rich areas. The two subfamilies currently recognised (Pell 2004), the Anacardioidae and Spondioidae, are both well represented in southern Africa. By far the largest genus in the Anacardioidae is *Rhus*

(though re-circumscriptions may change this), with over 200 species, 75 of which occur in southern Africa, mostly in thicket. The genus is also well represented in the Americas. Recent phylogenies (Pell 2004) indicate that *Rhus* is not monophyletic, the broader *Rhus* clade also including *Smodingium* (one species endemic in southern Africa), *Ozoroa* (with 40 species throughout Africa, the Arabian Peninsula and Madagascar), the largely Madagascan *Protorhus* (20 species, one in southern Africa), as well as the monotypic *Loxostylis* (from thicket in KwaZulu-Natal and the Eastern Cape), *Laurophyllus* and *Heeria* (from thicket patches in the Western Cape) (Pell 2004). This clade show remarkably high species richness in KwaZulu-Natal, Mpumalanga and Limpopo, but with high species numbers in the Western and Eastern Cape as well; a few species are also Northern Cape or Namibian endemics. Most of the *Rhus* species are characteristic of semi-arid vegetation, many being dominant in subtropical thicket (e.g. *R. longispina*, *R. crenata*, *R. lucida*, *R. glauca*) or temperate thicket (e.g. *R. burchellii*, *R. erosa*), while others occur in savanna (*R. tenuinervis*, *R. lancea*). Nevertheless, the genus shows broad habitat tolerance, some species being restricted to fynbos (e.g. *R. rosmarinifolia*) or forest (*R. chirindensis*). At this stage, phylogenetic relationships within the broad *Rhus* clade are poorly defined, but it appears that *Smodingium* and *Loxostylis*, both monotypic genera from the eastern parts of southern Africa, are two of the earliest-branching sub-clades. In the core Spondioideae, the African elements are mainly widespread savanna trees (*Lannea*, *Sclerocarya*), but include one southern African endemic genus, the monotypic *Harpephyllum* that is a common component of forest and forest-thicket mosaics of South Africa's eastern seaboard (Pell 2004).

The sister family to the Anacardiaceae, the Burseraceae, includes the large genus *Commiphora* (close to 200 species, mostly African), which also appears to have been one of the components of early Tertiary African semi-arid vegetation (Dupéron-Laudoueneix and Dupéron 1995), although the genus is poorly represented in southern African thicket (see Van der Walt 1986).

In Sapindaceae, three genera deserve special mention. *Pappea* is a monotypic African endemic, presumably of ancient origin; it is dominant in several types of subtropical thicket (see Vlok *et al.* 2003), as well as in Namaqualand thicket patches and riverine, rock outcrop and termitaria thicket in savanna. *Hippobromus* and *Smellophyllum* are monotypic southern African endemics, both confined to thicket and dry forest formation in the eastern parts of the region, the latter locally so in the Eastern Cape.

The monotypic *Nymania*, although clearly embedded in the Meliaceae and closely related to the tropical African *Turraea* (Muellner *et al.* 2003), is so unusual morphologically that it had been previously described as a family of its own (see Verdoorn 1965). It occurs from Namibia to the Eastern Cape, and it is locally dominant in thicket-karoo mosaics (Vlok *et al.* 2003). The related Rutaceae are not particularly well represented in thicket, being represented by *Clausena* and *Zanthoxylum*. Of interest is the case of *Calodendrum capense* (the Cape chestnut), a monotypic genus occurring in southern and East African forest and mesic thicket, distantly related to

the diverse buchu clade of the Cape fynbos (Diosmeae). The plesiomorphic position of *Calodendrum* suggests that, in this case, fynbos elements are derived from a thicket/forest lineage (Chase *et al.* 1999, Trinder-Smith 2004).

Southern African Ebenaceae are largely associated with semi-arid vegetation. The cosmopolitan genus *Diospyros* (475 species worldwide) is represented by more than 100 species in Africa, and c. 20 in southern Africa, where the highest species diversity is reached in the eastern parts of the region. Some species (*D. dichrophylla*, *D. scabrida*) occur in subtropical thicket, while others (*D. austro-africana*) in temperate thicket. *Euclea* is an African endemic with 20 species, 16 of which occur in southern Africa, where they grow mainly in thicket and savanna. Both genera are more diverse in the east, but also include Namaqualand-Namibia endemics (De Winter 1963). Molecular phylogenies indicate that the earliest branching clade in Ebenaceae is one comprising the African *Diospyros* sections *Natalensis* and *Royena*, together with *Euclea* (which is thus phylogenetically contained within *Diospyros*) (Morton *et al.* 1996, Pyck *et al.* 2003). This suggests a possible southern African origin to the Ebenaceae, and supports the antiquity of the thicket elements in this genus.

At least three clades of Apocynaceae deserve attention from a thicket perspective. *Carissa*, a palaeotropical genus with some 20 species — five in southern Africa — is closest related to the largely African *Acokanthera* (five species) (Sennblad and Bremer 2002). Both genera are thicket components. The phylogeny of the Ceropegieae suggests a complex history of southern African–East African–Mediterranean migrations, *Ceropegia* itself being paraphyletic to a large and broadly-distributed clade with an entirely southern African subclade, in which the thicket genus *Ophionella* — endemic to the western part of the Eastern Cape — has a basal position (Potgieter and Albert 2001, Meve and Liede 2002). *Cynanchum* is a large cosmopolitan genus, comprising a variety of herbaceous and stem-succulent vines, the basal grade in this genus being African. Of particular interest in thicket is the stem-succulent clade, which apparently originated in Madagascar and includes *Sarcostemma* (with *S. viminalis* abundant in thicket) (Liede and Täuber 2000, Liede and Kunze 2002).

In Solanales, two shrubby genera from two distinct families represent important components of subtropical thicket: *Ehretia* (Boraginaceae) and *Lycium* (Solanaceae). Both are broadly distributed genera. While *Ehretia* appears to have an Old World origin (Gottschling and Hilger 2001), *Lycium* is centred in the Americas, with a monophyletic group of southern African species (of both karroid and thicket affinities), indicating diversification following a single long-distance dispersal event (Fukuda *et al.* 2001).

Olea (Oleaceae) is a major component of thickets and dry forests throughout Africa and the Mediterranean Basin, some species (*O. europaea*) being both broadly distributed and highly variable in morphology (Wallander and Albert 2000). Preliminary data suggest that peak genetic diversity in *O. europaea* is reached in East Africa (Guillaume Besnard, unpublished). In Bignoniaceae, *Tecomaria capensis* (a southern African thicket species), together with the only other species in the genus, *T. shirensis* from East

Africa, fit in the large paraphyletic tribe Tecomeae (the genus had been previously collapsed into *Tecoma*, but is in need of re-instatement) (Lohmann 2003).

In the Lamiales, *Nuxia* (formerly Buddlejaceae) and *Halleria* (formerly Scrophulariaceae), woody plants from thicket and forests respectively, are basal in the Stilbaceae, previously a fynbos endemic family (Oxelman *et al.* 1999, Olmstead *et al.* 2001). As is the case with Podalyrieae (Fabaceae) and Diosmeae (Rutaceae), this pattern suggests a thicket/forest origin for Cape fynbos lineages.

Among the Araliaceae, one ancient genus associated with African thicket and dry forest is *Cussonia* (25 species distributed in Africa and the Mascarenes, 10 of which occur in southern Africa) (Strey 1973, Reyneke 1981) (Figure 3e). Unfortunately no phylogenetic study for this genus has been undertaken. *Seemannaralia* is a monotypic genus occurring in thicket patches from KwaZulu-Natal to the Limpopo, and is presumably also an ancient element (Burt and Dickinson 1975).

The Asteraceae are the most species-rich plant family in thicket, although the proportion of endemics is lower than in adjacent biomes (Vlok *et al.* 2003). Thicket Asteraceae belong to a variety of lineages, of apparently different evolutionary ages. The one group that has been long associated with Afro-Madagascan semi-arid vegetation is the arborescent basal grade in Carduoideae, including the southern African endemic *Oldenburgia*. This genus comprises one tree species (*O. arbuscula*) of fynbos-thicket mosaics in the Zuurberg Mountains of the Eastern Cape, and three fynbos shrublets that grow in the Cape Fold Mountains of the Western Cape, a distribution pattern similar to *Portulacaria*. Also included in this grade is the Afro-Madagascan *Brachylaena–Tarchonanthus* clade, with *Tarchonanthus* fitting into the African *Brachylaena* clade (Kimball *et al.* 2004). The main diversification episodes in the Senecioneae in Africa seem to have occurred in arid and semi-arid vegetation, *Euryops* and several clades in the *Senecio–Kleinia–Delairea* group having clear thicket affinities (Knox and Palmer 1995, Pelsner *et al.* 2002, 2004). Southern Africa was equally important in the diversification of the Asteroideae; however, comparatively few taxa included here have thicket affinities: most are associated with fynbos and karoo. Some of the genera in this subfamily that are locally dominant in thicket (*Pteronia*, *Felicia*) are essentially of karroid affinity, and presumably secondary invaders in thicket (see Bayer *et al.* 2002).

Summary of plant patterns

The phylogenetic evidence for plants reveals a broad array of phylogeographic scenarios, corresponding to at least three major patterns:

1. Plants with unusual, primitive growth forms and belonging to lineages of Gondwanan distribution, such as *Encephalartos*, *Strelitzia* or the Araliaceae, are likely to represent Cretaceous or Paleocene relicts. In the case of *Strelitzia*, there are indications of a shift from mesic to xeric-adapted morphology, and the transition may have been Eocene or a more recent age. The drought-tolerant features of *Encephalartos* may be ancient, but the physical anti-herbivore defences are probably of recent origin (see Van der Bank *et al.* 2001).

2. The vast majority of the plant lineages characteristic of thicket vegetation is probably of Eocene age, and these include woody plants, vines, succulents and geophytes. Some of these are limited in distribution, representing taxa endemic to southern Africa (*Hippobromus*, *Smelophyllum*, *Nymania*) or Africa (*Rhoicissus*, *Pappea*, the broader *Cassine* clade, *Tecomaria*). Disjunct patterns are represented by distributions that are Afro-Madagascan (Didiereaceae, Cotyledonoideae, *Brexia*, the stem-succulent clade in *Cynanchum*) or Afro-Mediterranean (several geophytes, Salvadoraceae, the central clade in *Olea*). Among the broadly distributed lineages, it is likely that some (e.g. *Plumbago*, Anacardiaceae, Ebenaceae, *Carissa*, Ceropogoniaceae) have originated in Africa. Others may have originated in other parts of the world, and invaded southern African during the Eocene or later (*Zygophyllum*, *Maytenus*, *Ehretia*, *Cordia*, *Lycium*). From this ancient semi-arid thicket cradle, some lineages have later (most often during the Pliocene) expanded into drier environments, represented in southern Africa by the Nama-karoo, succulent karoo and Namib Desert. This is probably true of *Haemanthus*, *Drimia*, *Aloe* sect. *dichotoma*, *Portulacaria*, and possibly *Haworthia*, *Veltheimia*, and some *Euphorbia* clades. Less common but even more interesting are the situations when thicket elements recolonised mesic and humid environments, as documented in several clades of Fabaceae; the same may be true of certain *Aloe* clades. Transitions from thicket and dry forest to fynbos, followed by rapid and extensive diversification there, happened in several groups (e.g. Iridaceae, *Calodendrum*, *Calpurnia*). Other thicket plant lineages did not radiate extensively into other vegetation types, but remain largely characteristic of thicket-like formations and forest margins worldwide (Vitoideae, Anacardiaceae, Cordioideae, Ehretioideae); many of these had broader distributions in the past than they have today (see Eocene records of *Ehretia* and *Rhoicissus* from Europe; Gottschling *et al.* 2002, Ingrouille *et al.* 2002).

3. Finally, *Mesembryanthemum* and the Ruschioideae, and some *Pelargonium* and Asteraceae lineages, represent recent invasions in thicket from other (generally more arid) environments, although secondary diversification in thicket is noted in some clades (e.g. *Drosanthemum*, *Pelargonium*). The distribution patterns of such groups are often indistinguishable from those of Eocene lineages (with both southern African endemics and African–Madagascan/African–Mediterranean disjunctions), and some of the lineages listed as Eocene may in fact be more recent. It is likely that in many cases there have been multiple transitions between thicket and other more arid and more mesic environments, resulting in the species enrichment of both thicket and surrounding vegetation types.

Insects

Ancient associates of thicket plants are evident amongst weevils (Coleoptera: Curculionoidea). Of particular interest is the relict family Oxycorynidae, one of the earliest branches of

Curculionoidea, the Neotropical species being associated with cycads (Oberprieler 1995). The African species has only been discovered relatively recently, and belongs to two genera. *Hispodes spicatus* was originally described from the Eastern Cape (Marshall 1955), and lives on *Rhoicissus*; an undescribed species occurs in Mpumalanga (RG Oberprieler pers. comm.). *Afrocorynus asparagi* (Oxycorynidae), from the Eastern Cape, lives on *Putterlickia pyracantha* (Celastraceae), while the host association of the second species in this genus is unknown. The Apionidae is a much larger and more successful family, with close to 2 000 described species worldwide and many more undescribed. *Antliarhinus* and *Platyperus*, associated with *Encephalartos* sporophylls, together comprise the earliest separated branch in this family, the latter genus being only known from southern Africa (Eastern Cape and KwaZulu-Natal) (Wanat 2001, but see Oberprieler 2000). In the tribe Ixapiini, the only African genus known to date occurs in Eastern Cape thicket on *Schotia afra*, and its closest relatives live on Melastomataceae in the Neotropics (Wanat and Procheş in prep.). Both *Strelitzia* and the Ebenaceae are hosts to species of Derolominae (Curculionidae), probably associated with these plants since the Cretaceous or early Tertiary (§P unpublished). It is expected that other host-specific insect herbivore groups mirror the patterns shown here in weevils, with multiple ancient associations between thicket plants and insects, but the data are still to be assembled.

Among herbivore generalists (usually of larger body size), vegetation type specificity is rare. In cicadas (Hemiptera: Cicadidae), *Xosopsaltria* is an Eastern Cape endemic, with at least two species (*X. thunbergi* and *X. annulata*) living in thicket vegetation, the latter apparently associated with *Plumbago auriculata*. Nevertheless, other species, characteristic of grasslands, are seen as ancestral in the genus. Closely-related genera also live in grasslands, indicating a recent origin for the thicket species (see Villet 1993, Villet and Captao 1996).

The newly-discovered order Manophasmatodea is most centred in the winter-rainfall region of southern Africa, but one species has been collected in East Africa, thus indicating an arid disjunction; no representatives of this group have been collected in the subtropical thicket as yet (Klass *et al.* 2002, Picker *et al.* 2002). Fossils are known from Europe — as in the case of several semi-arid plant groups now restricted to Africa.

A group that originally diversified in semi-arid and arid African vegetation, and subsequently colonised the entire world, are the advanced Caelifera (Orthoptera). Several families and subfamilies are African endemics, with some (Lentulidae, Acrididae: Euryphiminae) occurring in dry environments across East and southern Africa. The two superfamilies leading to hyper-diverse xeric-centred Acridoidea on the caeliferan tree (Pneumoroidea and Pyrgomorphoidea) are centred in Africa, the former occurring predominantly in humid, and the latter in xeric environments (Flook *et al.* 2000, Flook and Rowell 1997), thus suggesting that the transition to xerophily happened on this continent. Nevertheless, present-day caeliferan diversity in subtropical thicket is moderate (§P pers. obs.)

Mammals

Given the importance of mammalian herbivores in the structure and function of contemporary thicket (Kerley *et al.* 1995), the evolution of this component is of special interest. Elephant relatives (Proboscidea), together with dassies (Hyracoidea), and the now extinct anthracotheres and arsinotheres, represented the bulk of the mammalian herbivore communities in Eocene Africa, in assemblages that contained rabbit- to rhino-sized browsers (Kappelman *et al.* 2003). All of these represented branches of an earlier Afrotherian radiation that, according to molecular data, also includes sirenians, aardvarks, golden moles, tenrecs and otter shrews (Archibald 2003). Very few other placental lineages were able to cross into Africa at this time, owing to the Tethyan waters that separated it from Laurasia. With the land bridge that was formed during the Late Oligocene (c. 24Ma), a variety of other herbivores started crossing into Africa (Vrba 1995), these including the Antilopinae (Artiodactyla: Bovidae), which diversified here in separation from the originally Asian subfamily Bovinae (Hassanin and Douzery 1999). A similar scenario may have occurred in the case of the rhinos (Perissodactyla: Rhinocerotidae; see Tougaard *et al.* 2001). From the early to middle Miocene (10–20Ma) grass-dominated systems started expanding, and the newcomers were therefore able to fill the newly-established grazer niche. Additional grazers invaded Africa towards the end of the Miocene, in the form of equids (horse relatives) and the browser assemblages were also enriched with Tragelaphini (Bovinae; kudu relatives). At the beginning of the Pliocene, the herbivore fauna was already composed of equal proportions of grazers and browsers (Janis 1993). It is clear, however, that browsing by large mammals has been a selective force on woody plants in southern Africa since the Eocene.

General Discussion: Thicket Origin and Evolution

In this section we provide a narrative account of the origin and evolution of thicket vegetation in southern Africa. Our focus is on the macroevolution of thicket lineages and we do not consider mechanisms of speciation. It is based on the fossil and phylogenetic evidence presented in the preceding sections. Given the paucity of data, our narrative is undeniably speculative. However, we hope that this account will stimulate others to test the hypotheses that we have developed. We conclude this section by providing a preliminary list of further research questions.

Palaeogene (65–23Ma)

At the end of the Cretaceous, the overall configuration of southern Africa was similar to today, although the subcontinent was located about 10° further south. Sedimentation in offshore and onshore rift basins, the result of the fragmentation of Gondwana, was slowing down, and the region was tectonically stable (Partridge and Maud 1987, McMillan 2003). The African cycle of erosion was advanced, producing extensive pediplains above and below the Great Escarpment, this feature developing as a result of the new base levels established after the isolation of a relatively high

altitude (c. 2 000m) southern African land mass (Partridge and Maud 1987). Only the sandstone ridges of the Cape Fold Belt and parts of the Lesotho uplands — Gondwana surfaces — emerged above these vast pediplains, which were drained by sluggish, meandering rivers. As a result of this advanced planation, deep weathering and kaolinisation of underlying rocks was prevalent, as were surface duricrusts of ferricrete and silcrete (Partridge and Maud 1987). In short, the scenery of southern Africa at this time was considerably duller than present, as was the diversity of habitats for plants and animals.

The interval spanning the Palaeocene to middle Eocene (65–45Ma) was one of the warmest times in the Earth's history, and the globe was entirely ice-free. The climate of southern Africa during the Palaeocene was warm temperate and subhumid (Scotese 2001), and the vegetation of this and similar climatic zones in both hemispheres comprised a mixture of gymnosperms and angiosperms, the former including a predominance of Araucariaceae and Podocarpaceae in southern hemisphere localities (Willis and McElwain 2002). This reconstruction is consistent with the flora described by Scholtz (1985) from Banke in Namaqualand.

The early Eocene climate in southern Africa was subtropical, summer wet and sub-humid to semi-arid (Scotese 2001). The vegetation of the region has been grouped with a global formation termed paratropical forests (Wolfe 1985), widespread on the zones between warm temperate and tropical everwet forests on all continental landmasses (Willis and McElwain 2002). In the ice-free world of the time, this formation occurred at relatively high latitudes. Angiosperm families dominated fossil floras in northern hemisphere localities, and these included many that are now common in contemporary southern African thicket, namely Anacardiaceae, Sapindaceae, Vitaceae, Menispermaceae and Icacinaceae (Collinson 2000). It was at this time that thicket — dominated by woody plants (e.g. Anacardiaceae, Celastraceae, Ebenaceae, Sapindaceae) but also including vines (e.g. *Rhoicissus*), succulents (e.g. Didiereaceae, Cotyledonoideae) and geophytes (*Drimia*, *Haemanthus*) — began developing as a zonal vegetation type in southern Africa. At this early stage, primeval thickets were subject to browsing regimes associated with early mammal herbivores, some of which attained the size of contemporary megaherbivores (Kappelman *et al.* 2003).

From the middle Eocene, the world's climate began to deteriorate and, according to Schrire *et al.* (2005), it was at this time that semi-arid thicket vegetation began to develop globally, mainly along the margins of the Tethys Sea, but also in present-day Mexico, the Caribbean, middle Asia and southern Africa–Madagascar. It was in these seasonally dry thickets of the Tethyan Seaway that legumes began diversifying in earnest, later dispersing to other proto-thicket areas, including southern Africa (Schrire *et al.* 2005). This dispersal led to disjunct ranges, such as those noted in the Detarieae (Fabaceae), the basal genus *Schotia*, together with the more advanced *Umtiza* being stranded in southern Africa, with their relatives currently occurring in the Northern Hemisphere. Today the member of this latter monotypic genus is restricted to a forest-thicket mosaic on steeply-

incised valley walls in the southeastern Eastern Cape (Vlok *et al.* 2003); unfortunately, there are no reliable fossil deposits to provide any hint of the vegetation in which *Umtiza* originally grew. Precise dating for diversification in other thicket plant lineages is lacking; however, the available estimates (Davies *et al.* 2004) indicate that many families with strong succulent and geophytic contingents could have originated in the Eocene, this being the epoch of rapid splitting in both Asparagales and Caryophyllales. At the same time as the plants, the associated insect faunas migrated and were often forced to shift hosts; relicts such as the Afrocoryninae and Ixapiini are presumably of this age. Several groups of herbivore generalists also adapted to drier environments, the Eocene being the prime time for diversification in Acridoidea (Orthoptera), in both southern African and Tethyan regions (see Flook and Rowell 1997).

From the mid Eocene onwards, the climate of the world grew colder and drier, and by the mid-Oligocene (c. 30Ma), an ice sheet covered much of Antarctica (Scotese 2001). At this stage, southern African landscapes were senile and offshore sedimentation had ceased completely (Partridge and Maud 1987). Global reconstruction postdicts a warm temperate biome for the region (Willis and McElwain 2002), with climatic (but not topographical) conditions not dissimilar from those of today. However, given the lack of fossil data, we can only speculate on the vegetation cover of the time. This was most likely a mosaic of subtropical thicket and proto-fynbos on the duricrusts of the coastal pediplain, a heath-like proto-fynbos on residual peaks of the Cape Fold Belt, and temperate thicket (with fynbos elements) in the interior. It is notable that some Cape lineages began diversifying at this time (Linder 2003).

Neogene (23–1.8Ma)

The Neogene is associated with three important phenomena, all of which had a profound influence on the evolution of southern Africa's biota.

1. The tectonic stability of the subcontinent was interrupted in the early Miocene (20Ma) by an uplift that was greatest in the eastern part of southern Africa where it approached 300m (Partridge and Maud 1987). A second, and much greater event — up to 900m in the southeast — was initiated during the Pliocene, 3–5Ma. As a result of these tectonic events, southern Africa's landscapes were rejuvenated as sediments were scoured from ancient fault basins; hardpans of silcrete and ferricrete, which covered the gently sloping plains, were consumed, and softer sediments and deeply-weathered soils were stripped away to reveal underlying lithologies. The creation of new suites of habitats as a result of these two Post African cycles of erosion must have been a great stimulus for the diversification of southern African plant lineages (Cowling and Procheş 2005).
2. Although a relatively short warm interval occurred in the middle Miocene (c. 20–15Ma), the remainder of the Neogene witnessed a decline in global temperatures, resulting in a major growth in the Antarctic ice sheet and the development of glacial climates in the Arctic (Scotese 2001). Towards the end of the Neogene, winter-rainfall

conditions were established in the southwestern part of the subcontinent (Deacon *et al.* 1992). Semi-arid conditions prevailed over much of southern Africa, especially on its western margin (Scott *et al.* 1997).

3. Grass-dominated ecosystems became established on a wide scale for the first time in the early to middle Miocene (20–10Ma) (Jacobs *et al.* 1999) and C₄ grass-dominated ecosystems appeared in the late Miocene (Cerling *et al.* 1997), probably in response to globally low levels of atmospheric CO₂ (Ehleringer *et al.* 1997). Two highly significant processes are associated with this: firstly, grasses would have greatly facilitated the spread of regular fires which, in turn, would have impacted on fire-intolerant thicket and forest vegetation (Bond *et al.* 2003); secondly, the evolution of grass-dominated ecosystems was the stimulus for the diversification of the bovid herbivore fauna (Vrba 1985), which — like fire — would have influenced the grass-tree ratio in the newly-emerging savanna ecosystems (Owen-Smith and Danckwerts 1997).

As a consequence of the above, the vegetation of southern Africa underwent profound changes during the Neogene. The massive diversification of many Cape and succulent karoo lineages occurred during the later Neogene (Linder 2003, Klak *et al.* 2004), a consequence of climatic deterioration, the development of winter-wet climates, and a greater incidence of fire (Cape fynbos only), which also led to the contraction of thicket and forest vegetation. However, the evolution of new edaphic surfaces and greater topographical diversity must also have played a key role in diversification (Cowling and Procheş 2005). In the interior, the combination of regular grass-fed fires would have shattered the widespread fire-intolerant thickets of the time, leaving only those species tolerant of this new regime to form the savanna tree component and stranding thicket remnants in fire-free sites such as rocky outcrops and riverine fringes. In this respect, it seems reasonable to interpret the savannas of Africa as 'transformed thicket'.

We suspect that the Miocene uplift was an important stimulus for thicket speciation when lineages such as *Rhus*, *Aloe*, *Euclea*, *Diospyros*, as well as the Celastraceae and Sapindaceae, diversified from basal elements that grew in Palaeogene thickets and dry forests. From the late Miocene onwards, these early thickets, now retreating in the face of expanding modern formations such as karoo, fynbos and savanna, would have incorporated many lineages that were evolving in these, especially from karoo (e.g. Asteraceae). They would also have come under the influence of a diversifying bovid-browsing fauna.

However, thicket also contributed species to these newly-emerging ecosystems. Schrire *et al.* (2005) have shown that Fabaceae clades associated with thicket vegetation worldwide are sister to clades that have diversified in grass-dominated and fire-prone vegetation, especially savannas. Among southern African thicket clades, the basally branching *Schotia* group is sister to numerous clades in African savannas (including *Colophospermum*) as well as rainforests in Madagascar and elsewhere. Thicket also contributed lineages that diversified in fynbos (e.g. Diosmeae, Podalyriaceae) and karoo (e.g. *Aloe sensu lato*, Didiereaceae).

By the end of the Pliocene, modern climatic conditions were established and thicket was banished to fire-free sites throughout most of southern Africa. It remained the predominant vegetation only on the southeastern coastal forelands, which experience bimodal rainfall, where large tracts persist in the deeply-incised river valleys (Vlok *et al.* 2003). Here it formed mosaics with a wide range of vegetation types, including grasslands, Nama-karoo, succulent karoo and fynbos. Indeed, much of the proteoid fynbos associated with colluvial slopes exposed after Pliocene tectonic uplift are probably derived from exposure of fynbos-thicket mosaics to increased fire frequencies attributed to modern humans and their Pleistocene ancestors. This extensive intermingling of thicket and other formations provided further opportunities for non-thicket lineages, such as the Aizoaceae and Asteraceae, to diversify in thicket environments, producing the rich assemblage of taxa and growth forms evident in contemporary forms (Cowling *et al.* 1994).

Quaternary (1.8–0Ma)

Quaternary environments in southern Africa and elsewhere are characterised by the saw tooth alternations of long (c. 100 000 yr) cold, dry conditions (glacials) and shorter (c. 10 000 yr) warmer and wetter interglacials (Deacon *et al.* 1992). Ongoing tectonic uplift, albeit at a reduced intensity, continued to create new edaphic surfaces, especially along the coast where uplift has exposed marine deposits, including the Bredasdorp Formation of the southwestern coast (Partridge and Maud 1987). Diversification of the southern African flora has maintained its tempo and many succulent karoo (Klak *et al.* 2004), fynbos (Linder 2003) and savanna (Schrire *et al.* 2005) species have originated during this period. The same is probably true of subtropical thicket, although conclusive data are lacking.

Colder glacial times must have been trying for subtropical (but not temperate) thicket, since most of the component species, especially the succulents, are frost-intolerant (RMC pers. obs.); they must also have been disruptive for plant-insect associations. However, the high diversity of contemporary communities suggest that relatively large areas of thicket persisted through these glacial periods, probably in frost-free areas, as they do today on the lower slopes of the Sneeuwberg portion of the Great Escarpment (Palmer 1991). The ability of subtropical thicket to persist — at biomass levels comparable to forest formations — under semi-arid (200–300mm yr⁻¹) conditions (Mills *et al.* 2005), has been attributed to its capacity to maintain exceptionally high levels of soil organic carbon, itself a consequence of a dense canopy that ameliorates ambient temperatures and prevents the penetration of rain (Lechmere-Oertel *et al.* 2005a). Consequently, we suspect that thicket was able to persist as a zonal formation — at least in southern and southeastern South Africa — throughout the climatic perturbations that characterise the Pleistocene.

In the last few decades of the Holocene, subtropical thicket has both contracted and expanded as a consequence of human impacts. Severe overgrazing of brittle Arid and Valley Thicket vegetation has resulted in the

total transformation of vast tracts (Hoffman and Cowling 1990, Lloyd *et al.* 2002, Lechmere-Oertel *et al.* 2005a). Owing to the dispersion of soil organic carbon, re-establishment is only feasible through active means, namely the establishment of truncheons of *Portulacaria afra* which is remarkably capable of restoring above- and below-ground carbon content within decades (Mills and Cowling 2005). However, under wetter conditions, especially where thicket forms mosaics with grassland or forest, thicket elements are expanding, usually via nuclei that form beneath *Acacia karoo*, an ubiquitous invader of grassland (Trollope 1974). Bond and Midgley (2000) implicate rising levels of CO₂ in this process. The consequences of these short-term, human-induced dynamics on the survival and persistence of thicket formations and species in their southern stronghold, is the subject of a major conservation initiative (Knight *et al.* 2003).

Conclusions and Research Questions

We conclude that southern African thicket is an ancient formation, extending at least to the mid Palaeogene. It probably emerged in the Eocene, derived initially from elements in the forest formations that prevailed on the subcontinent during Upper Cretaceous and early Palaeogene times. It includes many basally-branching clades, some entirely endemic, and others sister to those that have diversified in adjacent biomes, which became established as zonal entities from the middle Miocene onwards. In this sense, thicket could be regarded as the 'mother of southern African vegetation'. However, it also includes many species derived from lineages associated with adjacent biomes. There has been a two-way traffic of clades. Contemporary thicket includes a rich array of genetic material: ancient lineages as well as very recent ones. We suspect that measures of phylogenetic diversity of thicket will be substantially higher than those for vegetation from adjacent biomes.

We can conclude that southern African thicket is not a post-Pleistocene formation, as suggested by Cowling (1983). It has, in various forms, been a major component of southern African vegetation for a very long time. Although marked climatic deterioration from the Pliocene onwards has restricted its distribution, thicket elements are still widespread on the subcontinent.

Southern African thicket is part of a global tropical thicket formation that was once widespread during the Palaeogene (Schrire *et al.* 2005). Comparative research on the phylogenetic structure and ecological patterns and processes of the remnants of this formation would be of great interest (see Grubb 2003 for an interesting account of southwestern Madagascan thicket).

What are the outstanding research questions? The phylogenetic contribution to understanding thicket origins is emerging at a remarkable pace. Phylogenies of *Asparagus*, *Crassula*, Sapindaceae and additional studies in *Euphorbia*, Anacardiaceae and Ebenaceae will provide further insights. In particular, it will be of great interest to know the relationships of what we now presume to be monotypic palaeoendemics, such as *Hyaenanche*,

Smellophyllum and *Loxostylis*. It would also be interesting to ascertain, in the way that Schrire *et al.* (2005) have done for the Fabaceae, the existence of additional 'out of thicket' invasions into more modern formations, such as savanna, fynbos and forest.

On the other hand, data on the population genetics of thicket taxa are non-existent. While it seems clear that thicket has contracted and expanded repeatedly in response to Neogene and Quaternary climatic oscillations and has contributed lineages to, and incorporated them from, adjacent formations in the process, the rates at which these processes have occurred are poorly understood. The older woody lineages are long-lived and often reproduce clonally, while many of the younger lineages rely mainly on sexual reproduction for population persistence (Midgley and Cowling 1993). Research on the genetic architecture of populations of taxa attributed to these different ages would be instructive. This research would help assemble a molecular clock for dating the radiation of thicket lineages, and contribute to understanding geographical dynamics and speciation processes (cf. Gitzendanner and Soltis 2000, Dick *et al.* 2003). It would be particularly interesting to know to what extent morphological variation in widespread species such as *Pappea capensis* and *Rhoicissus tridentata* is due to genetic — as opposed to environmental — factors, and how this compares with genetic variability of localised endemics. Reconstructing speciation histories would be essential in building a picture of the past extent, patchiness and dynamics of thicket vegetation.

Unfortunately, advances in providing dates for the major dichotomies are not progressing at the same pace as the phylogenetic research. The major limitation is the poor fossil record available for thicket taxa. Pollen fossil data are not especially helpful, owing to the occurrence of similar pollen types in unrelated families and the fact that many thicket taxa are not prolific pollen producers, thereby biasing compositional reconstructions. Fossil woods are much more informative, but their availability, especially for the Palaeogene, is extremely limited. The succession for this period is entirely marine, and is dominated by carbonates or biogenic muds that accumulated on the sea floor in highly-oxidised conditions (IK McMillan pers. comm.). One promising exception is the Knysna lignites, which should be resampled and re-analysed as a matter of priority.

The ecology and evolution of southern African thicket has been misunderstood and ignored. This is unfortunate, since it is an intriguing formation, comprising — at least for this subcontinent — a unique admixture of lineages spanning an enormous range of ages. While some of the conclusions in the review may well prove to be wrong, we hope that this paper will encourage our colleagues to delve further into the origins and evolution of this fascinating vegetation type.

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