



The Southern African orchid flora: composition, sources and endemism

H. P. Linder^{1*}, H. Kurzweil² and S. D. Johnson³

¹Institute of Systematic Botany, University of Zurich, Zurich, Switzerland, ²National Botanical Institute, Claremont, South Africa and ³School of Botany and Zoology, University of KwaZulu-Natal, Pietermaritzburg, South Africa

ABSTRACT

Aim The Southern African orchid flora is taxonomically well known, but the biogeographical and diversity patterns have not yet been analysed. In particular, we want to establish whether (a) it is, like the Southern African flora in general, more diverse than would be expected from its latitude and area; (b) it is an African flora, or whether it contains palaeoendemic relicts of a Gondwanan orchid flora; (c) the diversity and endemism in the orchid flora is concentrated in particular biomes and habitat types; and (d) the patterns of endemism in the flora can be accounted for by current environmental parameters, or whether we need to invoke historical explanations.

Location Southern Africa.

Methods We used the recent floristic account of the Southern African orchids, in conjunction with a data base of over 14,642 herbarium records, to assign the species and subspecies of Southern African orchids to biomes, habitats, and clades. We explored the relationship between the number and endemism of entities (species, subspecies and varieties) and the biomes and habitats. We compared the richness of this flora with that of 31 other regions from all continents and latitudes, to establish whether the Southern African orchid flora is richer or poorer than expected. We assigned the Southern African orchid species to 16 monophyletic clades and mapped the global distribution of these clades to establish the continental affinities of the flora.

Main conclusions The Southern African orchid flora is not any more diverse than could be expected from its latitude or area, while the two tropical African floras included were less diverse than expected. Latitude is an excellent predictor of regional orchid species richness; this might indicate that available habitat is more important for orchid diversity than gross area available, since latitude is probably correlated with the extent of suitable habitat. The Southern African orchid flora is clearly an African flora, since all clades are also found in tropical Africa, while many of them are absent from the Americas or Asia. Conversely, while most African orchid clades are also found in Southern Africa, both the Americas and Asia contain many clades absent from Africa. The distribution of orchid entities among the biomes in Southern Africa is very uneven, with two of the seven biomes totally devoid of orchids. Habitats and biomes that have no equivalent in tropical Africa are high in endemism, and habitats and biomes which are also well developed in tropical Africa are low in endemism. Endemism appears largely explained in terms of modern habitats. However, two patterns (the high endemism in the Succulent Karoo and the lack of endemism in the southern Cape among epiphytic orchids) may also be explained in terms of Quaternary climatic changes.

*Correspondence: H. P. Linder, Institute of Systematic Botany, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland.
E-mail: plinder@systbot.unizh.ch

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INTRODUCTION

The flora of Southern Africa (inclusive of South Africa, Namibia, Botswana, Lesotho and Swaziland), and in particular the Cape flora, is not only species-rich, but also dominated by several unusual families (Goldblatt, 1978; Takhtajan, 1986; Linder, 2003). It includes the Cape flora, which is possibly the most species-rich temperate flora (Cowling *et al.*, 1996) and is one of the world botanical hotspots (Myers *et al.*, 2000), almost 48% of the flora of sub-Saharan Africa is found in Southern Africa (Linder *et al.*, in press). The Southern African orchid flora appears to reflect this general pattern, and is remarkable for its peculiar composition, and the dominance of species of Disinae, Satyriinae and Coryciinae, which are morphologically very unusual (Dressler, 1993b; Linder & Kurzweil, 1999).

The Southern African orchid flora is relatively well known. The first Southern African orchids were described by Linnaeus in 1760, although the first collections of orchids from the Cape date to Hermann, who collected near the site of present-day Cape Town in 1672 (Schelpe, 1981). Over the past two centuries the orchid flora has had much taxonomic attention. The first comprehensive, illustrated account of the flora was by Bolus (1893–1896, 1911, 1913), this was shortly followed by an account by Rolfe in *Flora Capensis* (1912–1913), and recently by two books (Stewart *et al.*, 1982; Linder & Kurzweil, 1999). Most larger genera have also been monographed, some several times in the past century – for example the *Disa* group was studied by Kränzlin (1899–1900), Schlechter (1901) and Linder (1981a–f). Other large groups have also received detailed attention – for example *Eulophia* (Hall, 1965) and *Satyrium* (Hall, 1982). There have been a number of phylogenetic analyses of the orchids, both at generic and at species level (compiled in Linder & Kurzweil, 1999).

However, the larger-scale biogeographical patterns in the Southern African orchid flora have not yet been analysed. In particular, we want to establish whether (a) the orchid flora, as the Angiosperm flora in general, is richer than would be expected from its latitude and area; (b) whether the affinities of the orchid flora lie with the tropical Africa flora, or with one of the other southern continents [as in Proteaceae and Restionaceae (Johnson & Briggs, 1981; Linder, 1987)], or indeed with temperate northern floras (as in *Scabiosa*); (c) whether the diversity and endemism in the orchid flora is concentrated in particular biomes and habitat types; and finally, (d) whether some ecological or historical explanation could be found for the patterns of endemism in the flora.

MATERIALS AND METHODS**Phylogeny and taxonomy**

The taxonomy of Linder & Kurzweil (1999) is followed throughout this paper. We included all taxa – species, subspecies and varieties – to which we refer as ‘entities’ throughout the paper. This simplified the calculation of endemism, since there are a number of allopatric subspecies, with southern African and a south-central African subspecies separated by the Limpopo valley along the northern border of Southern Africa. In addition, we included a further three species recently recorded from Southern Africa: *Platycoryne mediocris* Summerh., *Eulophia arenicola* Schltr. and *E. kyimbilae* Schltr.

The global patterns of orchid diversity were compiled from a set of regional and local floras, selected to represent all continents, latitudes and a wide range of areas. The floras used are listed in the caption to Fig. 1. For each area the mean latitude and the area were determined, and the relationship between species richness, latitude and area was investigated with multiple linear regressions, as implemented in SPSS, version 11.5.0. Both species richness and area were log₁₀ transformed.

Affinities of the flora

In order to investigate the biogeographical elements in the Southern African orchid flora, the entities were grouped into monophyletic lineages (clades). Species are of little use in determining these biogeographical relationships, since most are endemic to Southern Africa. Genera are also unsuitable, since many may not be monophyletic. We grouped the genera into a tribal and subtribal classification, largely following Dressler (1993b). In view of recent proposals (Kores *et al.*, 1997; Cameron *et al.*, 1999), particularly regarding Spiranthoideae and Epidendroideae-Vanilleae, we do not follow Dressler’s (1993b) subfamily classification but that of Pridgeon *et al.* (1999, 2001, 2003). However, these taxa suffer from the twin problems that they are also often not monophyletic, and secondly may not be at a suitable rank. We, therefore, delimited clades that are reciprocally monophyletic, that is, no clade is nested within another clade. For this, phylogenetic analyses are required. The available cladograms at subtribal, tribal and family level account only for a very small proportion of the genera (e.g. Kores *et al.*, 1997; Cameron & Chase, 1999; Cameron *et al.*, 1999; Douzery *et al.*, 1999; Gravendeel *et al.*, 2001; Freudenstein *et al.*, 2004). These were taken to be

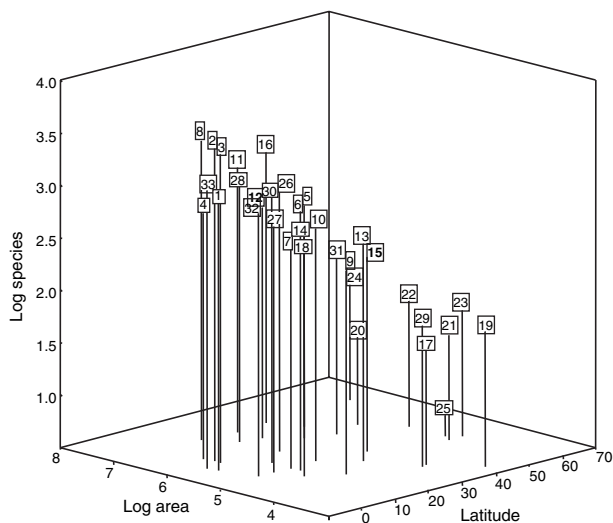


Figure 1 Relationship of species richness to area for selected orchid floras. 1, Sumatra (Comber, 2001); 2, Colombia (Escobar, 1990); 3, Papua New Guinea (Millar, 1978); 4, East Africa (Summerhayes, 1968; Cribb, 1984, 1990); 5, Costa Rica (Dressler, 1993a); 6, Panama (Williams & Allen, 1980); 7, Malawi (la Croix *et al.*, 1991); 8, Brazil (Pabst & Dungs, 1975); 9, Belize (McLeish *et al.*, 1995); 10, Guatemala + Belize (Ames & Correll, 1985); 11, Australia (Mark Clements, pers. comm.); 12, Southern Africa; 13, Bhutan (Pearce & Cribb, 2002); 14, SW-Australia (Hoffman & Brown, 1998); 15, Cape Floristic Region (South Africa); 16, China (Keng *et al.*, 1993); 17, Cyprus (Meikle, 1985); 18, Argentine (Correa, 1996); 19, Gargano (Italy) (Lorenz & Gembaradt, 1987); 20, Patagonia (Correa, 1969); 21, Netherlands (Weeda *et al.*, 1994); 22, Great Britain (Sell & Murrell, 1996); 23, Denmark (Rostrup & Jorgensen, 1961); 24, Siberia (Malyshev & Peschkova, 2001); 25, Tierra del Fuego (Moore, 1983); 26, Madagascar (Du Puy *et al.*, 1999); 27, Java (Comber, 1990); 28, India (Bose & Bhattacharjee, 1980); 29, Crete (Alibertis & Alibertis, 1989); 30, Philippines (Cootes, 1999); 31, Turkey (Kreuz, 1998); 32, Sarawak (Beaman *et al.*, 2001); 33, Borneo (Wood & Cribb, 1994). The two Southern African areas are in bold.

representative of clades (mostly more or less equivalent to Dressler's subtribes), and the classification of Dressler (1993b) used to assign the remaining genera to these clades, unless contrary information was available. The global distributions of the various clades was compiled from various sources (i.e. Dressler, 1993b; Mabberley, 1997).

Species diversity and endemism, biomes and habitats

The distributions of the Southern African orchids were taken from Linder & Kurzweil (1999), which were compiled from the herbarium collections at the Bolus Herbarium of the University of Cape Town (BOL) and the National Herbarium in Pretoria (PRE). Where additional information was available, this was also incorporated.

Southern Africa is divided into seven biomes (Rutherford & Westfall, 1986). These summarize climatic, edaphic and biotic data to produce broad descriptive entities. The Fynbos biome

has cold wet winters and dry summers, thus the main growing season is in spring and autumn. In general, the soils are oligotrophic and the vegetation slow-growing and burns on a 5–20 year cycle. The Succulent Karoo is also characterized by winter rainfall, but rainfall totals are less than 300 mm p.a., the soils are somewhat richer, and fire does not occur. The vegetation shows distinctive adaptations to drought. The Grassland biome receives almost all its rain in summer, and frost is frequent in winter, thus limiting tree growth, and the result is a steppe-like grassland. The Savanna Biome, like the Grassland Biome, is a summer rainfall area, but the winters are milder, and the vegetation is a woodland. Both Savanna and Grassland biome are burnt on a 1–4 year cycle. The Forest Biome is patchy and found mainly in areas with rain in summer, and with milder, often somewhat wetter winters. This, together with physical features such as cliff faces and rivers, might function to exclude fire. Entities were assigned to these biomes largely on the basis of their distributions, and to a lesser extent (especially the Forest biome) from habitat descriptions. The areas occupied by the various biomes were taken from Rutherford (1997).

Eleven habitats were recognized. Entities could be assigned to several categories, either because the entity is ecologically variable, or because several categories are needed to describe the habitat. Habitat assignments were based primarily on Linder & Kurzweil (1999), but were augmented with the personal field experience of the authors.

(1) Grassland habitats: damp to well-drained grassland, sometimes described as stony, at all altitudes. Although moisture, soil depth and altitude in grassland appears to be of some importance in differentiating between different grassland orchid species (e.g. Linder, 1981f), variation in these attributes is continuous, and no categorization seemed possible.

(2) Grassy woodland habitats: the typical habitat would be a savanna woodland, like 'miombo', with a sparse overstory of trees and a regularly burnt grassy understory. This is a common vegetation type in South-central Africa, but penetrates only into the northern parts of our territory. In the higher-rainfall areas of miombo the orchid flora is remarkably rich, made up of *Eulophia* and various genera of Orchideae (Williamson, 1977).

(3) Subalpine habitats: found above 2500 m in the Drakensberg, this area is characterized by severe frost in winter, and a temperate grassland (Pooid and Danthonioid species with C_3 -photosynthetic mode) and heathy patches (Killick, 1978a–c).

(4) Marsh habitats: areas that are either seasonally or perennially waterlogged. In most cases the marshes appear to be grassy, in some cases they may be heathlands (in the Western Cape Province) or forest (along the northern Indian Ocean coastline). There is no clear definition to separate marshy from non-marshy, and we have relied rather on the collectors indicating the habitat conditions.

(5) Scrub habitats: this describes a thicket vegetation, or short stunted trees. This is a common vegetation form along the coastline and along the margins of forest patches. Scrub is

distinct from forest in that there is no shady open area under the woody plants. Orchids either grow through the scrub, or in the half-shade along the margins of the scrub.

(6) Mature heath habitats: this is largely equivalent to 'fynbos' (Taylor, 1978). Species that only appear after fire in heathland were coded under the 'postfire' category. In arid areas the orchids grow between the widely spaced woody plants.

(7) Postfire habitats: this describes heathland in the first year after fire. Although both grassland and heathland burn regularly (van Wilgen, 1987), very few grassland species seem strongly linked to fire – at most they disappear if the grassland is not burnt for many years. In heathland the fires are much less frequent, and unburnt heathland is too dense and tall for orchids to compete directly with the woody vegetation. In this case many orchids flower only in the first year after fire, before the heath vegetation has been re-established.

(8) Stream-bank habitats: habitats along stream margins, often on bedrock or hanging over the water. Orchids may be avoiding competition from the taller vegetation by growing along stream banks, where the normal vegetation is inhibited. This is particularly common in the Cape flora, where the heathland can offer formidable competition to the low-growing orchids. It could also be that the moisture on stream banks during the dry summer months is important for the orchids, hence the stream-bank habitat might not be that important in the summer-rainfall area.

(9) Forest-floor habitats: all habitat on the forest floor. Most commonly this is in leaf-mould or leaf-litter, but can also include marshy habitat, or mossy stones.

(10) Epilithic habitats: growing on rock, or on shallow soil or mossbeds over rock. This includes a diversity of habitats: moss-covered rocks under a forest canopy, rock ledges facing moisture-bearing clouds, or shady cool rock ledges in arid areas. However, rocks along stream margins are not included under this category.

(11) Epiphytic habitats: growing on trees. We have assumed, except where we have direct evidence to the opposite, that epiphytes are shade plants, associated with forests. There are several species, though, that occur on isolated trees or shrubs that are in full sun, but might capture more cloud condensation.

RESULTS

Relative richness of the Southern African orchid flora

The most important correlate of orchid species diversity is latitude, and a regression of the log of species richness against latitude has negative linear relationship with $r^2 = 0.729$ (Fig. 1). Area is a much poorer predictor of species richness, with a positive linear relationship with $r^2 = 0.137$. Regressing both variables results in an r^2 of 0.83. The standardized partial regression coefficients show that latitude explains almost three times more of the variation than the area (Table 1). With 501 entities (469 species, and 32 subspecies or varieties) the Southern African orchid flora has more or less the diversity

Table 1 Multiple regression model for factors influencing orchid species richness, based on data for 33 regional floras (Fig. 1)

Dependent variable	Standardized partial regression coefficients		Model		
	Log ₁₀ area	Distance from equator	F	P-value	R ²
Species richness	0.318**	-0.825***	77.35	0.000	0.83

** $P < 0.01$; *** $P < 0.001$.

that can be expected from its latitudinal zone, while the orchid flora of the Cape Floristic Region (CFR, Goldblatt, 1978) is somewhat richer. The other two African areas included, Malawi and East Africa (Tanzania, Kenya, Uganda), have rather fewer than expected species; this might suggest that the Southern African orchid flora is somewhat richer than the other African orchid floras.

Affinities of the flora

The Southern African orchid flora can be grouped into 16 reciprocally monophyletic clades (Table 2). These represent three subfamilies (Vanilloideae, Orchidoideae, Epidendroideae). Several of the clades (such as Coryciinae) can also be further subdivided. The 16 'major' clades which we use in this paper are listed below.

Vanillinae

Vanillinae (Vanilloideae) is a sister clade to the monandrous orchids (Cameron & Chase, 1999; Cameron *et al.*, 1999; Freudenstein *et al.*, 2004). The clade is pantropical, only a single species (*Vanilla roscheri* Rchb.f.) is found in Southern Africa. It is known from a single collection in the north-eastern corner of the region, but the species is much more widespread in tropical Africa.

Goodyerinae

Goodyerinae are represented in Southern Africa by three species from three genera. All three species are quite widespread in tropical Africa, and are found generally in damp litter under a forest canopy, or in swampy areas.

Habenariinae (Orchidinae)

Douzery *et al.* (1999) grouped representatives of *Brachycorythis*, *Holothrix*, *Habenaria*, *Bonatea*, *Cynorkis* and *Stenoglottis* under the very poorly supported Habenariinae. The implications for this, in conjunction with the more extensively sampled studies of Pridgeon *et al.* (1997) is that Orchidinae might be restricted to the Northern Hemisphere, and in this paper the term 'Habenariinae' is therefore used for the clade of all Southern African Orchideae sensu Dressler (1993b).

Table 2 Summary of the Southern African clades and their diversity values. The clades and genera are listed in presumed phylogenetic sequence

Clade	Genera	Number of entities	Number of endemic entities	Percentage of endemic entities
Vanillinae	<i>Vanilla</i>	1	0	0
Goodyerinae	<i>Platylepis</i> , <i>Cheirostylis</i> , <i>Zeuxine</i>	3	0	0
Disinae	<i>Disa</i> , <i>Schizodium</i>	148	133	90
Coryciinae	<i>Brownleea</i> , <i>Huttonaena</i> , <i>Disperis</i> , <i>Corycium</i> , <i>Pterygodium</i> , <i>Evetella</i> , <i>Ceratandra</i>	80	67	84
Satyriinae	<i>Satyrium</i> , <i>Pachites</i>	44	38	86
Habenariinae	<i>Habenaria</i> , <i>Bonatea</i> , <i>Centrostigma</i> , <i>Cynorkis</i> , <i>Platycoryne</i> , <i>Stenoglottis</i> , <i>Brachycorythis</i> , <i>Neobolusia</i> , <i>Dracomonticola</i> , <i>Schizochilus</i> , <i>Bartholina</i> , <i>Holothrix</i>	99	57	58
Nervilieae	<i>Nervilia</i>	5	0	0
Tropidieae	<i>Corymborkis</i>	1	0	0
Gastrodiinae	<i>Gastrodia</i> , <i>Didymoplexis</i>	2	1	50
<i>Calanthe</i>	<i>Calanthe</i>	1	0	0
Malaxideae	<i>Liparis</i> , <i>Oberonia</i>	5	2	40
Bulbophyllinae	<i>Bulbophyllum</i>	4	0	0
Vandaeae	<i>Acampe</i> , <i>Angraecum</i> , <i>Jumellea</i> , <i>Aerangis</i> , <i>Bolusiella</i> , <i>Cyrtorchis</i> , <i>Diaphananthe</i> , <i>Microcoelia</i> , <i>Mystacidium</i> , <i>Rangaeris</i> , <i>Solenangis</i> , <i>Tridactyle</i> , <i>Ypsilopus</i>	38	10	26
Polystachyinae	<i>Polystachya</i>	11	2	18
Cyrtopodiinae	<i>Acrolophia</i> , <i>Ansellia</i>	8	7	88
Eulophiinae	<i>Eulophia</i> , <i>Oeceoclades</i>	51	20	39
Total taxa		501	337	67

However, there are a number of problems with this interpretation. Firstly, the African genera of Orchidinae *sensu* Dressler and Habenariinae have been sampled very inadequately, and a more detailed sampling could result in changes in the tree topology. Secondly, the ITS sequence data used for his interpretation are not very informative, and the bootstrap support levels for the various suggested arrangements vary from weak to non-existent. This is clearly an area that needs extensive sampling and investigation. In the absence of contrary evidence, we will use the Douzery *et al.* (1999) interpretations here.

Several clusters of genera can be recognized in the Southern African Habenariinae: the *Brachycorythis* group (*Brachycorythis*, *Schizochilus*, *Neobolusia* and *Dracomonticola*); the *Holothrix* group (*Holothrix*, *Bartholina*), and the *Habenaria* group (*Habenaria*, *Bonatea*, *Centrostigma*, *Cynorkis*, *Platycoryne*, *Stenoglottis*). However, there is severe doubt about the monophyly of *Habenaria*, and in the available analyses species of *Habenaria* are often associated with some of these subclades. In the absence of even a morphologically based phylogeny of the African Habenariinae, we do not subdivide this clade further.

The generic limits in the *Brachycorythis* clade have not been evaluated, and it is possible that only one genus should be recognized (Linder & Kurzweil, 1999). This clade includes 47 species, of which 17 are found in Southern Africa. While *Brachycorythis* is found throughout tropical Africa, mostly in

grasslands (Summerhayes, 1955), the other three smaller genera are restricted to southern and south-central Africa (reaching to Malawi and Tanzania in the north), and are generally (but not exclusively) associated with grasslands at higher altitudes, reaching to the summit of the Drakensberg at 3000 m. Only one species (*Brachycorythis macowaniana*) is found in the heathy vegetation of the CFR. Endemism is variable in the group: in *Brachycorythis* only one species and one subspecies of the seven species are endemic. The situation is different in *Neobolusia*, *Dracomonticola* and *Schizochilus*, where all 11 indigenous entities are endemic to Southern Africa. Particularly in *Schizochilus* there has been a radiation into the available grassland habitats of the wetter summer-rainfall areas of Southern Africa (Linder, 1980).

The *Holothrix* clade is the most arid-adapted group of Southern African orchids, and species of *Holothrix* and *Bartholina* dominate the sparse orchid flora of the arid Richtersveld near the mouth of the Orange River (Bruyns, 1989). In wetter areas the species are often found on rock ledges and other seasonally dry habitats. However, some species are found in cool, damp forest understory habitats. This habitat range may have been enabled by the presence of water-storing upper leaf epidermal cells. The monophyly of *Holothrix* relative to *Bartholina* has not yet been investigated, it remains possible that the latter genus is embedded in *Holothrix*. Levels of endemism are high, and although more

than half of the species of *Holothrix* are tropical African, 20 of the 24 indigenous entities are endemic to Southern Africa. This is the opposite pattern from *Brachycorythis*, in which most of the species are also found outside Southern Africa, but the Southern African endemism is very low.

The *Habenaria* clade is more like the *Brachycorythis* clade, with 55 indigenous entities, of which only 21 are endemic. Ecologically, too, there are similarities, with the species found mostly in tropical and often upland grassland. But several genera are also associated with forest patches, shaded habitats, and rock ledges. As with the previous groups, the generic delimitations are confounded by the mega-genus *Habenaria*, which includes over 800 species. Many of the other genera in the group could be specialised elements embedded within *Habenaria*, and the clade is in need of a detailed investigation (Kurzweil & Weber, 1992). While *Habenaria*, the largest representative of this clade in Southern Africa, with 35 species, is largely restricted to grassland, the remarkable genus *Bonatea* is found mostly in bushland and scrub-forest. It is characterized by large flowers with very long spurs. Most of the species have very limited distribution ranges, and appear to be rare within these distribution ranges. Of the 10 species in Southern Africa, five are endemic to this region. *Stenoglottis*, with only four species (Stewart, 1989), is largely endemic to Southern Africa (outliers in Zimbabwe, Malawi and southern Tanzania). At least two of the species are associated with mossy habitats in the forest understory, thus under shady conditions. *Cynorkis*, with two species, is found in similar habitats, while *Centrostigma*, with a single non-endemic species, occurs in marshes.

Satyriinae

Diseae, comprising Satyriinae, Disinae, Coryciinae, Huttonaeinae and Brownleeinae, has long been recognized on the basis of the reflexed anther (e.g. Linder & Kurzweil, 1994). DNA sequences of ITS (Douzery *et al.*, 1999), the *rbcL* gene (Kores *et al.*, 1997; Cameron *et al.*, 1999) and the combination of *rbcL* and *matK* (Freudenstein *et al.*, 2004), however, do not support the monophyly of Diseae, consequently we use the subtribes here.

Satyriinae include two genera: the widespread genus *Satyrium*, with c. 88 species, and the remarkable *Pachites*, restricted to the Western Cape Province and including only two species. Morphologically the subtribe is distinct by non-resupinate flowers, a gynostemium with a long column-part, and a usually galeate and double-spurred lip. The extra-Southern African distribution extends throughout the cooler upland parts of Africa, from Ethiopia to West Africa, as well as into the Himalayan region as far as China, and Madagascar. All species grow in full sunlight, or in light shade under *Brachystegia* woodland. There are 42 entities in Southern Africa of which 36 are endemic to the region. All analyses suggest that *Satyrium* is monophyletic (Kurzweil, 1996; Kurzweil & Linder, 1998).

The habitat range of Satyriinae is wide, especially in the Western Cape, from quite arid conditions (e.g. *Satyrium pulchrum*), to rock ledges, heathlands, and grassland. Most

tropical species are associated with cool uplands, but with a few exceptions are not normally found in subalpine habitats.

Coryciinae

The monophyly of Coryciinae s.l. is not retrieved in a phylogeny based on ITS sequence data (Douzery *et al.*, 1999). Coryciinae s.l. is based on a number of peculiar morphological features: the stigma is constructed of the odd carpel apex, and the lateral carpel apices are strongly reduced (Kurzweil, 1991). Furthermore, the lip often develops remarkable outgrowths (Linder & Kurzweil, 1994, 1996). The signal in the ITS sequence data which is incongruent with the monophyly of Coryciinae is supported by only 43% bootstrap replicates, suggesting that it is not robust, and consequently we here follow the morphologically delimited Coryciinae s.l.

The delimitation of the genera *Disperis*, *Brownleea* and *Huttonaea* has never been questioned. However, the generic delimitations of *Corycium*, *Pterygodium*, *Ceratandra* and *Evotella* (here also referred to as Coryciinae s.s.) are more problematic. Linder & Kurzweil (1994) placed *Brownleea* and *Huttonaea* each in their own subtribe, because *Brownleea* showed the morphological attributes of both Coryciinae and Disinae, and on this basis the genus was interpreted to be of hybrid origin. It was therefore given the same rank as the two putative parental clades. Since *Huttonaea* was basal to *Brownleea* in the cladogram, it followed that it should also be given the subtribal rank.

Huttonaea, with its fimbriate petals and lips, is one of the more remarkable Southern African genera. The five species are endemic to the summer-rainfall areas of Southern Africa (this makes it the largest genus endemic to this area), where it is found in a wide range of habitats: from shady forest floor (*H. fimbriata*, *H. pulchra*), to alpine grassland and heathland (*H. woodii*, *H. oreophila*, *H. grandiflora*).

Brownleea has the reduced lip typical of Coryciinae, but the dorsal sepal is galeate and spurred, as is typical of Disinae. About half the species have a single-carpellate stigma (Linder & Kurzweil, 1996). Of the seven entities in the genus, six occur in Southern Africa, of which three are endemic to our area. *Brownleea coerulea* has an unusual disjunct distribution, being found in forest habitats in southern Africa and Madagascar. The ecological range of *Brownleea* is similar to *Huttonaea*, and the genus is also absent from the winter-rainfall areas (Linder, 1981e).

Disperis, with 74 species (H. Kurzweil, J.C. Manning, unpubl. data), has a similar distribution to *Satyrium*, except that there are more species in Madagascar (21), and to the east the genus reaches New Guinea. There are two lineages in the genus (Manning & Linder, 1992): of the largely tropical lineage, only three non-endemic species are found in Southern Africa, and these are restricted to forest floor habitats. The Southern African lineage includes 30 entities, of which eight are not endemic. The Southern African species are pollinated by oil-collecting *Rediviva* bees. The same syndrome is also found in Coryciinae s.s. (Steiner, 1989), and either results from, or dictates, a similar

flower morphology, with saccate lateral sepals from which the oil reward is gathered by the front legs of foraging bees. The ecological amplitude in the genus is large, ranging from karroid shrub to fynbos, forests, grassland, and from marshy to very dry habitats, from shade to full sun.

Coryciinae s.s., with 40 entities, is largely centred in the Western Cape with a secondary centre of diversity in the Drakensberg. Only one species is absent from Southern Africa (*Pterygodium ukingense*, from southern Tanzania), while only two of the 39 Southern African entities are not endemic. Despite the availability of the recent phylogeny based on morphological characters (Kurzweil *et al.*, 1991), the possibility remains that *Corycium* and/or *Pterygodium* may be paraphyletic.

Disinae

Disinae include c. 170 species, of which 137 are native to Southern Africa. The generic delimitations in this large clade are difficult, and the number of genera recognized has fluctuated between two (Schlechter, 1901) and seven (Rolfe, 1912–1913). We follow Linder and Kurzweil's recognition of only two genera (Linder & Kurzweil, 1999): a large genus *Disa*, and the small, largely Western Cape endemic genus *Schizodidium*. The most distinctive morphological feature in the subtribe is the galeate and usually spurred dorsal sepal, and the reduced but patent lip. As is indicated by the large number of genera recognised in the past, there is substantial variation in the clade. The phylogenetic structure within the clade is still not clear (Linder, 1986; Linder & Kurzweil, 1990; Bellstedt *et al.*, 2001). Endemism is high, and 133 of the 148 entities are restricted to Southern Africa. The pollination biology of the subtribe has received much attention, and the range of pollinators is remarkably broad (Johnson *et al.*, 1998b). Similar, the habitat range is very wide, and ranges from full sun habitats to partial shade, from semi-arid habitats to perennially wet stream banks.

Gastrodiinae

The phylogenetic position of tribe Gastrodieae is still unclear, since these saprophytic orchids lack a functional *rbcl* gene. There are only two genera in Southern Africa, both belonging to subtribe Gastrodiinae. *Didymoplexis* is represented by a single endemic species on the KwaZulu-Natal coast. In all, the genus includes some 20 species found in the tropical Old World, and eastwards to the Pacific islands. The second genus, *Gastrodia*, is represented by *G. sesamoides*, the only introduced orchid species in Southern Africa.

Nervilieae

The single genus in this tribe includes 65 species, widespread in tropical Asia, Australasia and Africa. None of the five species found in Southern Africa are endemic.

Tropidieae

Dressler (1993b) included the Tropidieae under Spiranthoideae, but several lines of evidence indicate that they are rather related to Epidendroideae (Cameron *et al.*, 1999). Of the Tropidieae, only *Corymborkis corymbis* is found in Southern Africa, and this species has a wide distribution in tropical Africa.

Malaxideae

This tribe of 960 species in six genera is represented in Southern Africa by *Liparis* with four species (two endemic) and *Oberonia*, with a single non-endemic species. *Liparis* is a large genus of 250 species, three of the Southern African species can be either terrestrial or epiphytic. *Liparis capensis* is found in the heathlands of the CFR, and shows remarkable convergence in growth form to the Orchidoideae. *Oberonia* is epiphytic, and is rare in the northern parts of South Africa.

Calanthe

The Blettiinae are represented by the very widespread *Calanthe sylvatica*, which reaches tropical Asia, and is found in shade under tropical and subtropical forests. Blettiinae are usually included in the Arethuseae, which appears to be polyphyletic (Cameron *et al.*, 1999). Since Blettiinae are also polyphyletic, we refer to this clade by the genus name.

Cyrtopodiinae

Tribe Cymbidieae, in the circumscription used by Dressler (1993b), is polyphyletic according to the phylogeny based on *rbcl* sequence data (Cameron *et al.*, 1999). There are four genera in Southern Africa, two placed in subtribe Cyrtopodiinae (*Acrolophia*, *Ansellia*) and two in subtribe Eulophiinae (*Eulophia*, *Oeceoclades*). While Cameron *et al.* (1999) show that Cyrtopodiinae are not monophyletic, *Acrolophia* was not included in their analysis, and in the absence of contrary evidence we assume that the two genera form a clade.

Ansellia is a monotypic tropical African genus, which is a fairly widespread epiphyte in the northern and eastern parts of Southern Africa and possibly the most drought-resistant epiphyte of the Southern African orchid flora. *Acrolophia* is remarkable in the Epidendroideae in that it is the only genus endemic to Southern Africa. Indeed, all seven species are found in the CFR, and only one has a few outlier populations to the north along the coastline of the Eastern Cape Province and KwaZulu-Natal, possibly restricted to outcrops of sandstone. The plants are evergreen and sclerophyllous, while the flowers are mostly very cryptically coloured.

Eulophiinae

Eulophia and *Oeceoclades* appear to be very closely related, and it is possible that *Oeceoclades* is nested in *Eulophia*. Both are

mostly terrestrial. *Eulophia* is pantropical, and includes c. 250 species, of which 44 are found in Southern Africa. There are 48 entities in Southern Africa, of which 20 are endemic. The Southern Africa species are generally sclerophyllous and capable of surviving relatively harsh grassland conditions. A few species have also adapted to the peculiar conditions in the CFR, with its oligotrophic soils and dry summers, but without any striking morphological adaptations. *Oeceoclades* is Afro-Madagascan and neotropical, and includes 31 species (Garay & Taylor, 1976). None of the three Southern African species are endemic. They are shade-loving and associated with leaf-mould and sandy soils.

Polystachyinae

The probably polyphyletic Epidendreae (Cameron *et al.*, 1999) are also represented by a single genus, *Polystachya*. Of the 11 Southern African species, two and possibly three are endemic. This pantropical genus of c. 200 species is most diverse in Africa, where it is one of the most frequently found epiphytic orchids. *Polystachya ottoniana* is also found in forests in the winter-rainfall Western Cape region, and is one of the few epiphytes that can grow in this area, which appears otherwise to be very hostile to epiphytic orchids on account of the low humidity during summer.

Bulbophyllinae

The huge pantropical tribe Dendrobieae of c. 2263 species in 21 genera is represented in Southern Africa by four species in one genus, *Bulbophyllum*, and none of them is endemic.

Vandaeae

The monophyly of Vandaeae is strongly supported by *rbcL* sequence data (Cameron *et al.*, 1999). This large tribe includes almost 2000 species in 160 genera, and is pantropical, although the greatest diversity is in Australasia and Africa. It is by far the most important group of epiphytic orchids in Southern Africa, with 13 genera and 36 species, represented by 38 entities of which 10 are endemic. *Mystacidium* is the only genus centred in Southern Africa, where seven of its nine species are found, of which five are endemic. The remaining species in the Vandaeae are mostly southern-most extensions of otherwise widespread eastern African epiphytes. Many of the genera are represented in Southern Africa by a single species.

All 16 clades of Southern African orchids delimited above are also found in tropical Africa. Of these, nine are pantropical or cosmopolitan, five African with a few extra-African outliers, and two Afro-Asian. In addition, there are further orchid clades which are wholly absent from the Southern African orchid flora (Table 3). Of these clades, only Diceratostealeae, Neottieae and Podochileae are found in tropical Africa. Several major clades are restricted to the Americas or to Asia. African

orchids are found spread throughout the phylogeny of the orchids, except that the two basal clades (Apostasioideae and Cypripedioideae) are absent from the continent (Fig. 2).

Diversity and endemism in Southern Africa

Of the seven Southern African biomes, two lack orchids altogether – these are the Desert and the Nama-Karoo Biomes (this is a summer-rainfall semi-desert in the centre of the subcontinent). The orchid diversity in the other five biomes varies from a low 19 entities in the Succulent Karoo Biome (the winter-rainfall semi-desert along the West Coast) to a high of 207 entities in the Fynbos Biome (Table 4, Fig. 3), which is geographically more or less equivalent to the CFR of Goldblatt (1978). The percentage endemism varies from 100% for the Succulent Karoo, to 20% for the Forest Biome. Succulent Karoo and Fynbos, the two biomes that receive most of their rain in winter and have dry summers, have very high levels of endemism. Grasslands have a relatively high endemism at 67%, while the levels of endemism of Savannas and Forests are substantially lower, at 38% and 20%, respectively. It is evident that there is no relationship between the area of the biome and its orchid richness or endemism. The number of entities in each biome do not significantly predict the number of endemic entities [the square of the Pearson Product Moment correlation coefficient (r^2) of the relationship is 0.697, $P = 0.05$], and similarly there is no significant relationship between entity diversity and the proportion of endemic entities.

The distribution of the clades among the different biomes is also very unequal (Table 5), and of the 16 clades, three are restricted to the forest biome, although this has the second lowest number of species, and the lowest percentage endemism. One clade is restricted to the savanna biome, while the other biomes lack unique clades. The most even distribution of species among clades is also found in the forest biome, in which 12 of the 16 clades are found, and the most uneven distribution in the fynbos biome, with eight clades represented. Of the 207 entities in the Fynbos biome, 102 belong to Disinae, 42 to Coryciinae, and the rest to clades of less than 30 entities. A somewhat similar pattern is seen in the Grassland, but here the dominance is less clear, with Habenariinae with 55 entities, Disinae with 41, and Coryciinae with 31. Possibly the most even distribution of entities (except for the Forest Biome) is found in the Savanna biome, which is still dominated by Habenariinae (43 of 130 entities), but followed now by Eulophiinae (39 entities) and several clades with 12 or less entities. There is no relationship between the number of entities and the number of clades per biome. Some biomes, like the Forest biome, have many clades and few entities, while at the other extreme the Fynbos biome has few clades and many entities.

There is also a large variation in the number of entities of each clade in each habitat type. Many clades are absent from many of the habitats, while the biggest diversity is found in Habenariinae with 52 grassland entities (Table 6). Endemism also varies substantially among the different habitats, with the

Table 3 Major lineages of the orchids and their distribution (except where indicated by quotation marks lineages are suspected to be monophyletic; largely after Cameron *et al.*, 1999)

Lineages	Southern Africa	Tropical Africa	Global
Apostasioideae	–	–	Tropical Asia, Australasia
Cypripedioideae	–	–	America, Asia, Europe, Australasia
Vanilloideae	KZN: Vanillinae	Present	Pantropical
'Cranichideae'	KZN: Goodyerinae	Present	Pantropical
'Diurideae'	–	–	Southern South America, Australasia
Satyriinae	Widespread	Widespread	Africa ranging into Asia
Disinae	Widespread	Widespread	Africa
Coryciinae	Widespread	Widespread	Africa, tropical Asia (only <i>Disperis</i>)
'Orchideae'	Widespread: Habenariinae	Widespread	Cosmopolitan
Nervilieae	Summer-rainfall area	Widespread	Africa, Australasia, tropical Asia
Gastrodieae	Cape Town, KZN: Gastrodiinae	Widespread but scattered	Pantropical
Diceratostealeae	–	Tropical West Africa	Tropical West Africa
Triphoreae	–	–	Tropical and North America
Tropidieae	East coast	Widespread	Pantropical
Palmorchideae	–	–	Tropical America
Neottieae	–	Widespread	Northern Hemisphere, tropical Asia and Africa
Sobraliinae	–	–	Tropical America
'higher epidendroids'	Summer-rainfall area: <i>Calanthe</i>	Widespread	Mainly Asia
	Widespread: Malaxideae	Widespread	Cosmopolitan
	Summer-rainfall area: Bulbophyllinae	Widespread	Pantropical
	Mainly summer-rainfall area: Polystachyinae	Widespread	Pantropical but primarily African
	Mainly summer-rainfall area: Vandaeae	Widespread	Pantropical
	Widespread: Eulophiinae	Widespread	Pantropical
	Northern areas: <i>Ansellia</i>	Widespread	Africa
	Mainly CFR: <i>Acrolophia</i>	–	Southern Africa

In the highly diverse 'higher epidendroids' only lineages that are represented in southern Africa are listed while the majority of the clades are absent from Africa. Distribution data mainly from Dressler (1993b).

KZN, KwaZulu-Natal; CFR, Cape Floristic Region.

highest endemism in postfire habitats and heathland, associated with the winter-rainfall region (Table 7) in the Fynbos and Succulent Karoo biomes. Remarkably high, as well, is the endemism in lithophytes and stream-bank species. These are zonal, specialist habitats. The level of almost 83% endemism among the subalpine and alpine species is remarkably high. By contrast, species associated with forests (forest-floor habitats, epiphytes) have low endemism, between 22% and 24%. The lowest endemism is in grassy woodland species (14%). Despite this variation, there is a strong positive relationship between the number of entities in each habitat type, and the number of endemic entities ($r^2 = 0.966$, $P < 0.00$).

DISCUSSION

Relative richness of the Southern African orchid flora

Our results show that globally orchid diversity is remarkably well predicted by latitude, while there is no significant relationship between area and species richness. Although generally diversity is related to latitude (Pianka, 1966; Scheiner & Rey-Benayas, 1994; Rosenzweig, 1995; Mutke & Barthlott, 2000; Jansson & Dynesius, 2002), area should also play a major role in predicting diversity (Rosenzweig, 1995). The peculiar

pattern displayed by the Orchidaceae could be the result of the preferred habitats of orchids. The majority of the orchids world-wide are epiphytes, which do not survive harsh seasons, whether cold or dry, and this restricts them to rainforests and mistforests. These are almost restricted to the tropical areas. Terrestrial orchids are more able to survive dry or frosty seasons, and so are found in temperate areas as well as in the restricted parts of the tropics. However, they are almost completely absent from deserts. Thus latitude may be an excellent and better predictor of the amount of suitable habitat for orchids, than area.

In terms of species richness the orchid flora of Southern Africa is quite unremarkable, with a more or less average number of species for its area and latitude. This is in contrast to the overall rather high richness of the Southern African flora. This poverty in orchids is well illustrated by a comparison with Australia, which has ca. 1100 orchid species (Mark Clements, personal communication) out of an Angiosperm flora of 17,590 species (Hnatiuk, 1990), compared with 469 species of a flora of 20,955 vascular species in the Southern African flora (Germishuizen & Meyer, 2003). The CFR orchid flora is amongst the richest for its latitude and area, and this is consistent with the general flora of the region, which is substantially richer than that of other temperate areas, not only

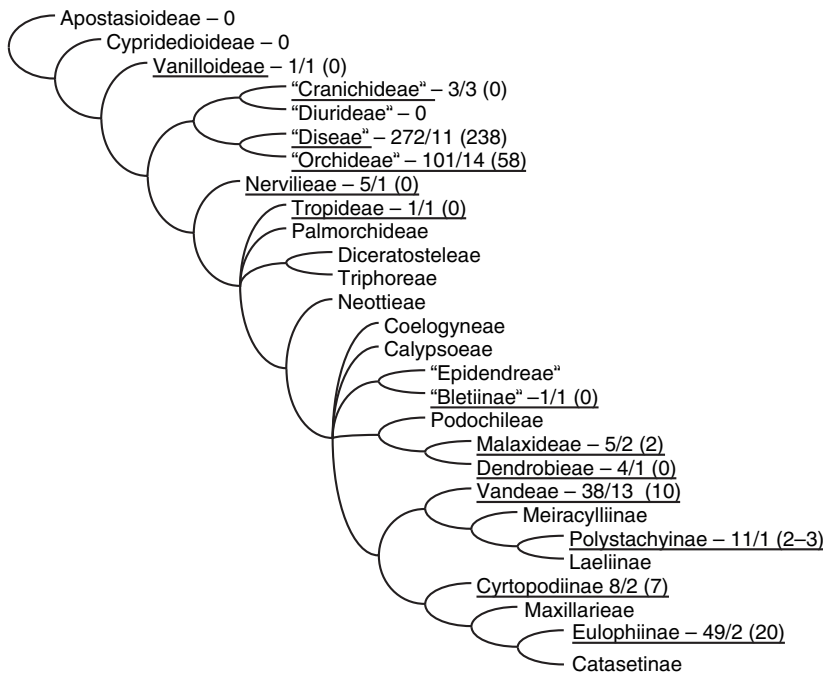


Figure 2 Simplified orchid phylogeny indicating the major clades. Underlined clades occur in Southern Africa, the first figure indicates the number of entities in Southern Africa, the second the number of genera, and the number of endemic entities are given in brackets. Taxa in quotations are most likely not monophyletic.

Table 4 Entity (species, subspecies or varieties) endemism by biome

Biome	Entity richness	Number			Number of clades
		endemic entities	% Endemic entities	Area (km ²)	
Desert	0	0	0	111,147	0
Grassland	161	108	67	349,174	7
Succulent Karoo	19	19	100	100,251	4
Forest	81	16	20	568	12
Nama Karoo	0	0	0	607,235	0
Savanna	130	49	38	1,435,713	10
Fynbos	207	202	98	71,337	8

in relationship to area (Barthlott *et al.*, 1996; Goldblatt & Manning, 2002; Linder, 2003), but also to latitude (Linder, 2003).

The steep latitudinal gradient in orchid richness observed in the Americas and in Asia is absent in Africa. East Africa, although straddling the equator, has only marginally more species than Southern Africa, and Malawi has somewhat fewer. As is evident from Fig. 1, both East Africa and Malawi are in a global comparison at the lower expected margin for species richness, Southern Africa as a whole average, and the CFR near the top of the range. This pattern is consistent with that observed in the African flora as whole, where Southern Africa includes over 48% of all sub-Saharan African species (Linder *et al.*, in press). The low tropical African orchid diversity is consistent with other observations that the African wet-tropical flora is species-poor (Brenan, 1978; Dransfield, 1988), leading to the label of Africa being the ‘odd man out’ among the tropical floras (Richards, 1973).

Affinities of the Southern African orchid flora

The Southern African orchid flora lacks many clades (subtribes, tribes and subfamilies) of orchids, that are striking because of their morphological peculiarity (e.g. Apostasioideae, Cypripedioideae), or because they dominate the orchid floras of other regions (e.g. ‘Diurideae’ in Australia, Maxillarieae, Laeliinae, and Catasetinae in South America, and Coelogyneae in Asia). The absence of clades could be explained either as the consequence of the necessary ecological conditions not being available, or because for historical reasons the clades could not reach the area.

Apostasioideae and Cypripedioideae are completely absent from Africa, although the former is found in the Asian tropics and Australasia, and the latter widespread in the Northern Hemisphere, as well as tropical America and Asia. These appear to be lineages that are absent from Southern Africa for historical, rather than ecological reasons. However, in this case it is unclear whether these two clades may have been present in Africa in the past, but were lost during palaeoclimatic changes, as has been suggested for palms (Dransfield, 1988).

Within the Orchidoideae an approximate division can be found, with ‘Diurideae’ centred in Australia, with a few genera found in southern South America, and a few reaching into tropical Asia, while ‘Orchideae’ and ‘Diseae’ are centred in Africa and the Northern Hemisphere, with a few species reaching the other continents (although the highest species number of *Habenaria* is found in Brazil). There are no diurids in Africa, but there is remarkable ecological similarity between the roles of the ‘Diurideae’ in Australia, and the ‘Orchideae’ – ‘Diseae’ in Southern Africa. This is illustrated by the observation that the introduced Cape orchid *Disa bracteata* is spreading in Australia. The phylogeny of Freudenstein *et al.*

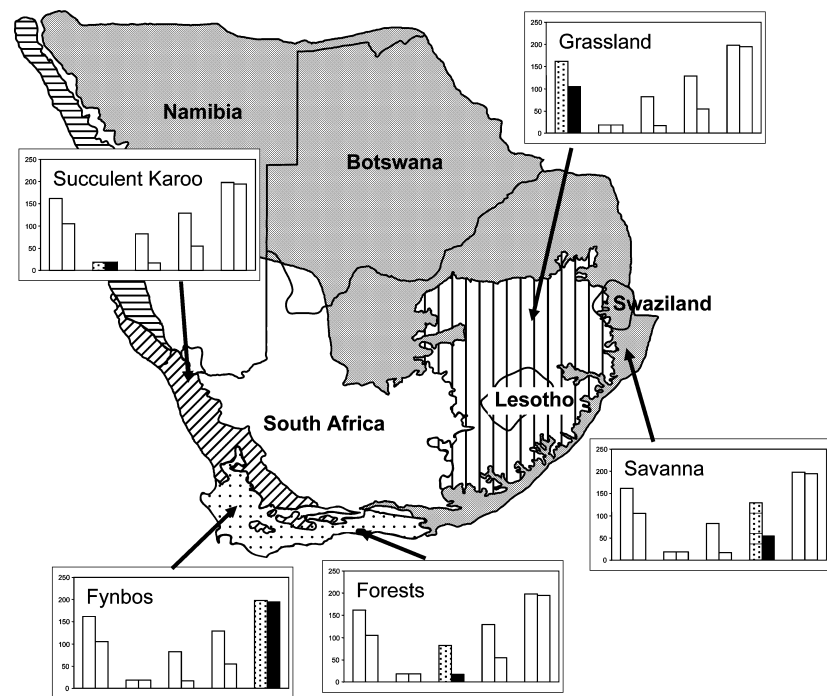


Figure 3 Biomes of Southern Africa, with graphs indicating the number of orchid species (dot-shaded column), and the number of endemic species (black-shaded) mapped onto them. Each bar-graph block contains the graphs for all biomes, but the relevant ones are the only shaded ones.

Table 5 Number of entities of each clade recorded from each biome

Clade	Grassland	Succulent Karoo	Forest	Savanna	Fynbos	Biome diversity
<i>Calanthe</i>	0	0	1	0	0	1
Cyrtopodiinae	0	0	0	3	7	2
Eulophiinae	18	0	4	39	4	4
Bulbophyllinae	0	0	4	0	0	1
Polystachyinae	1	0	10	2	0	3
Gastrodiinae	0	0	2	0	1	2
Malaxideae	0	0	4	0	1	2
Nervilieae	0	0	4	4	0	2
Tropidieae	0	0	1	0	0	1
Vandae	0	0	34	12	0	2
Goodyerinae	1	0	2	0	0	2
Coryciinae	31	4	9	5	42	5
Disinae	41	2	0	10	102	4
Satyriinae	14	5	0	11	29	4
Habenariinae	55	8	6	43	21	5
Vanillinae	0	0	0	1	0	1
Total entity richness	161	19	81	130	207	5

(2004) indicates that the sister-clade of the CFR-centred Disinae (Linder, 1994) and Coryciinae s.s. is *Disperis*, which is a more widespread African temperate genus, thus also corroborating the African affinities of the Disinae and Coryciinae.

Most of the larger clades absent from Southern Africa and also the rest of Africa are tropical American. Included among these are the Maxillarieae with *c.* 2600 species, the Laeliinae with *c.* 1500 species and the Pleurothallidinae with *c.* 3000 species.

The Vanilloideae and many of the Epidendroideae in Southern Africa appear to be outliers of clades with a pan-tropical distribution. This applies particularly to Nervilieae,

Tropidieae, *Calanthe*, Malaxideae and Bulbophyllinae. These clades are represented in our region by a few species, and only by one or two genera, and are largely species-poor in tropical Africa [*Bulbophyllum* is a remarkable exception (Vermeulen, 1987)]. Other epidendroid clades are part of an Africa centre for the clade, even if the clade is also found on other continents. Typical of this pattern are the Vandae, Eulophiinae and Polystachyinae.

None of the 16 Southern African clades are endemic to Southern Africa. It is possible to divide the clades finer, and so to delimit Southern African endemic clades, but these in all cases have their closest relatives in tropical Africa. This is particularly evident in Disinae (Linder, 1983) and Coryciinae

Table 6 Clades and their entities in the various habitats

Clade	Stream												Habitat-diversity
	Shade	banks	Rocks	Postfire	Heath	Marshes	Scrub	Forestfloor	Grassland	Alpine	Woodland	Epiphytic	
<i>Calanthe</i>	1	0	0	0	0	0	0	1	0	0	0	0	1
Cyrtopodiinae	0	0	0	1	6	0	1	0	0	0	1	1	5
Eulophiinae	8	0	0	1	4	8	14	4	30	0	14	1	8
Bulbophyllinae	4	0	0	0	0	0	0	0	0	0	0	4	1
Polystachyinae	11	0	1	0	0	0	0	0	0	0	0	11	2
Gastrodiinae	2	0	0	0	0	0	0	2	0	0	0	0	1
Malaxideae	4	0	1	0	1	0	0	3	0	0	0	4	4
Nervilieae	5	0	0	0	0	0	0	4	2	0	4	0	3
Tropidieae	1	0	0	0	0	0	0	1	0	0	0	0	1
Vandae	38	0	2	0	0	0	0	0	0	0	0	38	2
Goodyerinae	3	0	0	0	0	2	0	2	0	0	0	0	2
Coryciinae	12	0	2	15	26	4	4	9	25	14	2	0	9
Disinae	2	8	24	41	49	17	1	0	44	10	0	0	8
Satyriinae	4	0	8	16	19	6	6	0	18	2	0	0	7
Habenariinae	22	1	17	5	12	14	12	13	52	9	7	0	10
Vanillinae	1	0	0	0	0	0	1	0	0	0	0	0	1
Totals of entities per habitat	118	9	55	79	117	51	39	39	171	35	28	59	11

Table 7 Habitats and endemism

	Entities	Endemic entities	% Endemic entities
Grassland	171	105	61.40
Grassy woodland	28	4	14.29
Subalpine	35	29	82.86
Marsh	51	23	45.10
Scrub	39	16	41.03
Mature heath	117	116	99.15
Postfire	79	79	100.00
Stream-bank	9	8	88.89
Forest-floor	39	9	23.08
Epilithic	55	48	87.27
Epiphytic	59	13	22.03

(Kurzweil *et al.*, 1991; Manning & Linder, 1992). Only the Southern African endemic *Acrolophia* (Epidendroideae) is still enigmatic, in that it is not clear to which extra-Southern African genus it is related.

However, three tropical African clades are absent from Southern Africa. *Diceratosteles gabonensis* remains an enigmatic taxon (Rasmussen & Rasmussen, 1979), which Dressler (1993b) placed in its own tribe. The Neottieae are represented by three species of *Epipactis* in East and Central Africa (including Congo, Rwanda and Burundi), and the 15 species of the African endemic genus *Stolzia* represent the Podochileae (assuming that the Dressler classification is correct), which are otherwise Asian and Australasian.

The Southern African orchid flora is thus a fully African flora, with no special relationship to the other southern continents. All the clades, with the exception of the introduced *Gastrodia sesamoides*, have their closest relatives in tropical Africa. Some of these clades have diversified enormously in

Southern Africa, and are represented in tropical Africa by only a few species (e.g. Disinae, Coryciinae excluding *Disperis*), while for others the situation is reversed (e.g. most of the epiphytic orchids including Vandae and Polystachyinae). In Habenariinae and Satyriinae the species richness is more or less the same in tropical and Southern Africa. The almost 68% endemism indicates that the Southern African orchid flora is a regionally differentiated African flora. This is consistent with the patterns suggested for the Cape flora in general (Adamson, 1958; Goldblatt, 1978; Linder *et al.*, 1992), and for numerous genera in particular. Although there have been no biogeographic studies relating the Southern African, rather than the Cape flora, to the African flora, this level of endemism in the Southern African orchids is of the same order of magnitude as the general endemism of the Southern African flora, estimated at 80% by Goldblatt (1978). This suggests that the orchids may be reflecting a general Southern African pattern.

It is not clear what the expected endemism in the Southern African orchid flora would be. Southern Africa is geographically isolated by the South Atlantic to the west (5900 km to South America), the South Indian Ocean to the east (8000 km to Australia), and the Southern Ocean to the south (4000 km to Antarctica). The absence of common species (and very few genera) between Southern Africa, South America and/or Australia indicates how effective this barrier is. Indeed, the success of *Gastrodia sesamoides*, introduced on the Cape Peninsula from Australia, supports the argument that the barrier is the geographical distance, not the habitat availability. The reciprocal 'accident', the introduction of *Disa bracteata* in Australia, and its success in the southern parts of Australia (Marchant *et al.*, 1987), also supports this argument. The only geographically accessible areas are to the north. Although there is a broad contact zone between southern and south-central

Africa, much of this region is inhospitable to orchids, the only corridor is along the eastern Indian Ocean coast and the adjacent uplands. This is in contrast to the situation in East or West Africa, where the orchid floras have a broader contact zone with other orchid-rich areas.

Biomes and available habitats – determining endemism

The absence of a correlation between endemism to the biomes and area of the biomes is unexpected, as it has been shown in a number of studies that the proportion of endemic species increases with the area (Major, 1988; Rosenzweig, 1995; Ribera, 2000). However, c. 31% of the surface area of Southern Africa is desert or semi-desert, and a further 53% rather arid savanna, and globally very few orchids are able to survive in these conditions. While the majority of the world's orchids are epiphytes, forests are very rare in Southern Africa (0.02% of the surface area).

Among the biomes, the highest endemism is associated with the Succulent Karoo and Fynbos Biomes, the Grassland Biome shows intermediate levels of endemism, and the Forest and Savanna Biomes have the lowest endemism. This variation in endemism could be an incidental result of the variation in species richness in these areas: if an area has more species than the surrounding areas (for whatever reason), then the number of endemic species, as well as the proportion of endemic species, would have to be higher. And indeed this fits the pattern in Southern Africa, except for the Succulent Karoo biome, which has the smallest flora (18 species) and 100% endemism. A second explanation is that endemism is more profound in 'refugial' areas, which have had little climatic change (Hamilton, 1976; Haffer, 1982). However, 'refugial' areas are usually recognized by the concentration of range-restricted endemics, consequently labelling endemism-rich areas as 'refugial' is circular.

Recently, it has been suggested that endemism-rich areas share two characteristics: they are ecologically different from the surrounding areas (ecological islands), and have probably been climatically stable. These criteria have been very effective at explaining patterns of bird endemism in East Africa (Johnson *et al.*, 1998a), as well as plant endemism in both arid and mesic habitats in East Africa and Ethiopia (Lovett & Friis, 1996). The unique habitat argument works well at biome level in Southern Africa. The heathland habitat of the Fynbos Biome is unique in Africa, the only other area that combines very oligotrophic soils with summer drought is found in south-western Australia (Milewski, 1983; Cowling & Witkowski, 1994). There is a small outlier of fynbos-like heathland in Eastern Zimbabwe [in a small area on the Chimanimani mountains (Phipps & Goodier, 1962)], but although the vegetation and soils are similar, the climate is not. The great distance from the Cape to Chimanimani, and the incomplete duplication of the habitat, should be reflected in the levels of endemism. Equally unique is the Succulent Karoo, a winter-rainfall semi-desert, that receives regular coastal fog

(Milton *et al.*, 1997). Most of the orchids are found on mountains with a cooler climate, and more substantial winter rains. The geographically nearest ecological equivalent is along the northern margins of the Sahara. Consequently, the high levels of endemism to these two biomes (Succulent Karoo and Fynbos Biomes) is not unexpected. This endemism in the orchid flora is also consistent with a general pattern of very high endemism to these floras (Goldblatt & Manning, 2002).

The Grassland Biome shows intermediate levels of endemism. Superficially it does not fit the pattern of isolation and uniqueness described above, as the Grassland Biome recurs north throughout Africa, mostly under climatic control as Afromontane grassland (White, 1978, 1983), but also under edaphic control (Vesey-Fitzgerald, 1963). However, the next nearest location of extensive grasslands to Southern Africa are the uplands of Zimbabwe, and in particular the Eastern Highlands at Inyanga, and these are separated from Southern Africa by the broad Limpopo valley, possible the largest interval in the distribution of grasslands in Africa south of the Sahara. Interestingly, there are several widespread tropical African grassland species (e.g. *Disa aconitoides*) with geographical subspecies separated by the Limpopo interval.

The very low level of endemism in the Forest biome is not surprising, and is shown by both forest-floor species (23%) and epiphytes (22%). The Southern African forests continue uninterrupted from northern KwaZulu-Natal into Mozambique, and indeed the intervals in the forest distribution within Southern Africa are rather more extensive than the intervals between the northern Southern African forests and the tropical African forests (Midgley *et al.*, 1997). Several epiphytic species are known from one or very few populations inside Southern Africa, while the distribution along the African East Coast is much more continuous. It is, therefore, hardly possible to talk about a distinctive Southern African forest orchid flora. This lack of endemism in forest species is not shared by other forest taxa, such as *Begonia* (Hilliard, 1976) or *Streptocarpus* (Hilliard & Burt, 1971), although the lack of endemism in Southern African forest tree species is quite striking (Midgley *et al.*, 1997).

The Savanna biome flora is a complex mixture of woodland (*Brachystegia*, *Acacia*, or *Burkea* woodland), grassland, marshy areas, and forest patches. It is, therefore, hard to interpret the endemism figures for the savannas, but they are higher than we had expected.

Curiously, there is a strong inverse relationship between clade diversity and the proportion of endemism in the biomes (Table 4). The Succulent Karoo contains only four clades, and has 100% endemism, while at the other extreme Forests include 12 clades, and have only 20% endemism. This is suggestive of autochthonous radiations in these biomes where few clades could thrive. This pattern is best developed in the CFR, with its heavy dominance of Disinae. This pattern is consistent with that described for many clades in the Cape flora (Linder, 2003), which have radiated extensively in the Region. This generated a general flora very rich in species and endemism at species level, but relatively poor in the diversity of higher clades (Linder *et al.*, 1992).

Habitat endemism shows a pattern similar to that of biome endemism. Habitats common in tropical Africa – marshes, forests, grassy woodland – show endemism figures of 16–45%. At the other extreme, habitats which are rare or absent in tropical Africa – postfire habitats, unburnt scrub- or heathland, alpine grass- or heathland – have endemism levels of 82–100%. Curiously, stream-bank and rock-ledge habitats, which are widespread in tropical Africa, also have a high endemism (89% and 87%, respectively). The explanation might be that stream banks as a unique habitat seem to have been largely exploited in the Fynbos biome, where the orchids compete with a shrubby vegetation. There are few opportunities for the herbaceous terrestrial orchids to compete successfully for light in this dense heathy vegetation, and the three most commonly exploited habitats are stream banks (the *Disa uniflora* group of species), rock ledges (several different groups) and the postfire habitat. Thus, although there are rock ledge or boulder species further north in the other biomes, they are numerically overshadowed by the Fynbos species. Grassland, which is also a common African habitat, also has a high level of endemism. This could be the result of the inclusion of the alpine flora, which has a much higher endemism than the general grassland flora (83% against 61%). Since most species in the ‘alpine’ habitat category were also scored for ‘grassland’, this would have inflated the endemism in the grassland. There are no other climatically equivalent areas in Africa south of the equator – all other areas over 3000 m are near the equator, and consequently have a tropic-alpine climate (Hedberg, 1964; Coe, 1967; Smith & Cleef, 1988). In Southern Africa, all alpine species occur in the Drakensberg, which has long been known to be a centre of endemism (Phillips, 1917; Hilliard & Burtt, 1987; Carbutt & Edwards, 2002). The overall levels of endemism to this mountain block are not yet known, since there has not been a complete evaluation of the geographical patterns of its flora.

The role of Quaternary climatic change

Variation in endemism is often related to past climatic changes. Although Southern Africa was not glaciated during the Quaternary climatic cycles, there is evidence of major changes in the extent of various vegetation types (Scott *et al.*, 1997). Grasslands expanded during the glacials at the cost of woody vegetation, caused by the lowering of the temperature. This would clearly have created more habitat for the alpine and grassland orchids. This is consistent with the rather high levels of endemism and high diversity in the modern orchid flora of these habitat types, and the lower diversity and particular endemicity of the savanna regions. Unfortunately there seems to be no direct evidence on the fate of the subtropical forests along the Indian Ocean coastline during the glacials, although it does appear as if forests may have been more extensive. There are various indications that the Afrotropical forests (dominated by *Podocarpus* and *Ocotea*) may have been much reduced. Currently, epiphytic orchids have an average level of diversity, but a low level of endemism. More striking is the

rapid tail-off in epiphytic diversity, and even more so in endemism, southwards, this could be a result of local extinctions during the glacial forest fluctuations. Meadows & Linder (1993) suggested that the southern forests, in the former Cape Province, were much reduced, and this would imply that the epiphytic orchids are only now expanding their ranges into these forests. It is also possible that the forest survived, but as ground-water forests. The epiphytic orchids do not appear to be able to survive a long dry period with low humidity in summer, and thus cannot survive in ground-water forests.

The climate of the Fynbos biome during the last glacial appears to have been colder and wetter in the west, and colder and drier in the south (Cowling *et al.*, 1999; Barrable *et al.*, 2002; Linder, 2003), and this implies that the modern habitats for terrestrial orchids, especially in the west, would have persisted during this period. However, in the southern Cape some habitat, and most likely the habitat of the epiphytic orchids, may have been lost. It is also possible that the Succulent Karoo was wetter during this period, and may have been largely replaced by fynbos during the glacials (Midgley *et al.*, 2001). If this is the case, the current orchid flora of the Succulent Karoo could be relictual from these wetter times. This is consistent with the high endemism and richness of the orchid floras of these areas.

CONCLUSIONS

Globally the species richness of Orchidaceae is strongly negatively correlated to the distance from the equator, possibly as this is correlated to the extent of habitat suitable to orchids. However, tropical Africa has fewer orchids than expected. Although the Southern African orchid floras are comparable with orchid floras elsewhere at similar latitudes, the orchids make up a much smaller proportion of the flora in southern Africa than they do in the Australian flora.

The major clades of the Southern African orchids (more or less equivalent to subtribes) are all typically African, showing that this orchid flora is essentially an African flora. However, the rank importance of these clades is very different, showing that the flora is dominated by different subtribes, or even tribes. Striking here is the dominance in Southern Africa of the Disinae and Satyriinae, morphologically peculiar taxa with their main centre in Southern Africa. This is indicative of a radiation at species level within this flora, and this can be interpreted as a regional specialization of an essentially African flora.

The patterns of endemism within the flora are quite variable, both by biome and by habitat. Very high levels of endemism are found in biomes and habitats not found outside Southern Africa, while biomes and habitats that are also found in South-central or Central Africa have lower levels of endemism. This analysis suggests that it may not be necessary to invoke hard-to-test historical explanations for the remarkably high endemism of Southern Africa. It may largely be the result of the peculiar habitats found in the subcontinent, especially associated with a Mediterranean type climate in the south and its

associated heathy vegetation, and the presence of montane-temperate climates along the eastern uplands. Nonetheless, the very high endemism of the Succulent Karoo orchid flora could indicate its relictual status, and the absence of endemism in the epiphytic orchid flora of the Southern Cape could indicate its recent status, occupying its modern range after the establishment of the mesic Holocene climate.

Thus, at a regional scale, available habitat appears to predict the species richness of orchid floras, and this is manifested by the strong relationship between latitude and species richness. The composition of the flora is determined by its continental position. And within Southern Africa, endemism to habitats and biomes is correlated to both the degree of uniqueness of habitats and biomes, and possibly to a lesser extent, Quaternary climatic changes.

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BIOSKETCHES

Peter Linder, previously from the Department of Botany at the University of Cape Town, is investigating the evolution of the Cape flora, with a particular emphasis on the Orchidaceae, Restionaceae and Poaceae of this very speciose and species-rich flora.

Steve Johnson is an Associate Professor in the School of Botany and Zoology at the University of KwaZulu-Natal, South Africa. He carries out research on the ecology and evolution of pollination systems, particularly those in the orchid family.

Hubert Kurzweil is primarily interested in the floral morphology and development of orchids, and has published extensively on the systematics and ontogeny of orchid flowers, and in particular of the Cape orchid groups. He is currently working on the succulent Mesembryanthema of Southern Africa.
