The Cape element in the Afrotropical flora: from Cape to Cairo?

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The build-up of biodiversity is the result of immigration and *in situ* speciation. We investigate these two processes for four lineages (*Disa*, Irideae p.p., the *Pentaschistis* clade and Restionaceae) that are widespread in the Afrotropical flora. These four lineages may be representative of the numerous clades which are species rich in the Cape and also occur in the highlands of tropical Africa. It is as yet unclear in which direction the lineages spread. Three hypotheses have been proposed: (i) a tropical origin with a southward migration towards the Cape, (ii) a Cape origin with a northward migration into tropical Africa, and (iii) vicariance. None of these hypotheses has been thoroughly tested. We reconstruct the historical biogeography of the four lineages using likelihood optimization onto molecular phylogenies. We find that tropical taxa are nested within a predominantly Cape clade. There is unidirectional migration from the Cape into the Drakensberg and from there northwards into tropical Africa. The amount of *in situ* diversification differs between areas and clades. Dating estimates show that the migration into tropical East Africa has occurred in the last 17 Myr, consistent with the Mio-Pliocene formation of the mountains in this area.

Keywords: historical biogeography; ancestral character reconstruction; phytogeography; molecular dating; Africa

1. INTRODUCTION

Local floras and faunas accumulate diversity by the recruitment of new lineages as well as by *in situ* speciation. The sourcing of lineages has long occupied biogeographers: historical biogeographers list the diverse ‘elements’ for a biota (Wulff 1950); panbiogeographers assemble ‘tracks’ showing the shared elements between biota (Craw *et al.* 1999); and cladistic biogeographers compile sets of ‘components’ or three-area statements (Nelson & Ladiges 1996; Humphries & Parenti 1999). The increasing availability of dated phylogenies has made it possible to understand how and when biomes were assembled (Crisp 2006). No region is isolated from immigration, consequently the relative roles of immigration and *in situ* diversification are more difficult to untangle for regions which share many lineages. Well sampled phylogenies are needed to determine whether an endemic species in a biota speciated locally or recruited from a ‘source area’.

Here, we explore the phytogeographical patterns in the Afrotropical region (Weimarck 1936; Wild 1964; Linder 1990). The region is an archipelago of isolated areas ranging from the highlands of Ethiopia in the northeast, to the southern tip of Africa and to the Fouta Djallon in Guinea in the west (White 1978). It combines the Afrotropical and Cape phytochoria of White (1983). These patches of temperate vegetation, often separated

by thousands of kilometres, can be grouped into three centres of endemism: the Cape region; the greater Drakensberg range; and the Afrotropical Centre (Linder 1990). Although the floristic affinities between these centres have frequently been explored (Weimarck 1941; Hedberg 1965; Wild 1968; Killick 1978; White 1978; Linder 1990), the historical biogeography remains enigmatic.

Many of the very diverse Cape clades (Linder 2003) also occur in the Afrotropical region (Cowling 1983; Carbutt & Edwards 2002) although their species richness decreases to the west and the north. Their contribution to the floras of these regions is substantial: Hilliard & Burtt (1987) considered an estimated 22% of the genera recorded in the southern Drakensberg as ‘centred in the Cape region’, while Hedberg (1965) showed that 4% of Afroalpine flora elements form a ‘Cape element’. These constitute part of the austral element in the Afrotropical flora and complement the boreal element which has more north temperate affinities.

Three main hypotheses for the origin and migration of these taxa have been postulated to explain their current distribution: (i) an origin in tropical Africa and migration through the Afrotropical region southwards into the Cape (Levyns 1938, 1952, 1964), (ii) an origin in the Cape and migration northwards into tropical Africa (Linder 1994), and (iii) vicariance, with the floras in each region representing relics from a once widespread African flora that has receded with climatic changes (Adamson 1958; Wild 1968; King 1978). Although the disjunctions are well documented and the historical processes have been discussed (Levyns 1952; Adamson 1958; Levyns 1962,

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1964; Wild 1968; King 1978; Van Zinderen Bakker 1978), few authors have tested these hypotheses. Linder (1994) rejected a north to south migration on the basis of a cladistic biogeographical analysis of Disinae (Orchidaceae) and Griswold (1991) found it difficult to reconcile a Pleistocene vicariance scenario with the current distribution of Afrotropical spiders. McGuire & Kron (2005) inferred a north to south migration for the Cape mega genus *Erica*, but did so on the basis of an under-sampled and poorly supported molecular phylogenetic tree.

Here, we reconstruct ancestral distributions using likelihood optimization on phylogenetic hypotheses, for four clades with a classical Afrotropical distribution pattern, with the majority of their species restricted to the Cape. We test the directionality of migrations through Africa and address the following questions: (i) Is migration between the Cape and the regions north of the Limpopo River direct, or do we infer movement via the Drakensberg? (ii) How does the temporal sequence and dating of the migration events relate to the geological history of Africa? and (iii) Did taxa that are found outside the Cape speciate *in situ* or are they derived from separate migration events?

2. MATERIAL AND METHODS

(a) Phylogenetic trees

The phylogenetic hypotheses for the four study groups and sequence data for the dating were derived from the following sources: *Disa*, cpDNA and nrDNA (Bytebier *et al.* 2006); Irideae p.p., cpDNA (Goldblatt *et al.* 2002, fig. 3); the *Pentastichis* clade, cpDNA (Galley & Linder submitted, fig. 3); the African Restionaceae, cpDNA (Hardy *et al.* submitted). In the cases of *Disa* and the Restionaceae, the topology of the tree with the highest likelihood score from the set of Bayesian trees was used.

(b) Age estimations

Trees were made ultrametric and the ages of the disjunctions in the four study groups were estimated using a Bayesian relaxed clock (Renner 2005; Rutschmann 2006) as implemented in MULTIDIVTIME (Thorne & Kishino 2002). There are no fossils available for the study groups, so the crown node of each study group was constrained with a calibration point derived from a separate 'global analysis' which had four fossil calibration points. Details of the MULTIDIVTIME analysis and the global analysis can be found in the electronic supplementary material.

(c) Areas and taxon scoring

Taxa were scored as present or absent for six regions, shown in figure 1: the Greater Cape Floristic Region (hereafter referred to as the 'Cape'; Jürgens 1991; Born *et al.* 2006); the Drakensberg range comprising the Drakensberg escarpment (Partridge & Maud 1987), upland areas south to Elliot and north to Tzaneen (Carbutt & Edwards 2004); Zimbabwe overlap region between the Limpopo and the Zambesi rivers; South Central African centre including Mount Mulanje, the Nyika plateau and the southern Tanzanian highlands; 'Eastern Africa' including the Central and the East African uplands, as well as the Ethiopian plateau; and 'Western Africa' comprising the Cameroon highlands and the uplands westward to the Fouta Djallon. Other areas were also scored where applicable (Réunion, Madagascar, the Mediterranean and Amsterdam Island/St. Paul Island). Widespread taxa were coded as present

in all relevant areas. An exception to this is *Pentastichis natalensis* for which the three accessions (from Natal, Madagascar and South Central Africa) did not form a clade, consequently each accession was coded according to the area in which it was collected.

(d) Reconstruction of biogeographical history

The distribution ranges of ancestral nodes were reconstructed using likelihood optimization as implemented in MESQUITE v. 1.1 (Maddison & Maddison 2006) using the rate-corrected branch lengths. Each node was optimized as present versus absent for each of the six areas. A threshold value of 2 log-likelihood ($\ln L$) units was used to indicate statistical significance for the ancestral state optimization of each node (Mooers & Schluter 1999; Maddison & Maddison 2006). We compared the $\ln L$ scores of a two-rate (forward and backward rates independent) and a one-rate (forward and backward rates constrained to be equal) model for each character, for each taxon. The accuracy of parameter estimation depends on the amount of data available and the frequency of the minority character state, as well as model complexity (Mooers & Schluter 1999). All taxa had several characters for which the use of the two-rate model did not result in a significantly improved fit (sometimes a worse fit was obtained) and we therefore used the one-rate model for optimization. This handles trees with few transitions and an imbalance of character states better than the two-rate model (Schluter *et al.* 1997; Mooers & Schluter 1999).

To infer the ancestral distribution of a node, the optimization for each area was taken into account separately. The node was optimized as the area which was significantly 'present' at that node. In most cases, the node was optimized as 'absent' for all other areas and was thus optimized unambiguously. In a number of cases, a node was significantly optimized to more than one area. In nine cases, a node was optimized as absent to all areas except one for which support was not significant but above 0.75 proportional likelihood (see figure 2, also Figs. 1 and 2 of electronic supplementary material). In these cases we assigned this area to the node. Nodes that were not assigned any area were omitted from further calculations.

A migration event on a branch was counted when the daughter node optimized to a different area than that of the parent node. Three types of migration were recognized: range expansion, when a node or taxon is present in the same area as its parent node, but occurs in an additional area; vicariance, when a parent node is optimized to two areas but the two daughter nodes each to only one of these; and dispersal, when the parent and the daughter nodes optimize to different areas.

(e) Calculations

We calculated the age of the dispersal events by estimating the age of the ancestral node of the branch which has the change in distribution. This assumes that the migration accompanied speciation. The same method was used to date range expansions (migration without accompanied speciation). Since no speciation accompanied range expansions, they cannot be dated precisely; the date could be any time between the node subtending the taxon and the present. This approach therefore estimates a maximum age.

Migration is a function of movement from an area plus persistence, the former of which is related to the number of species in the source area. This needs to be taken into account to test for unidirectionality of migration and we divided the

Figure 1. Map indicating areas used in analysis. 'Western Africa' including: A the Fouta Djallon in Guinea and B Mount Cameroon; 'Eastern Africa' including: C Ethiopian highlands, D Virunga and Rwenzori mountains and E North Tanzanian/West and Central Kenyan/East Ugandan mountains; 'South Central African centre' including: F Nyika Plateau and southern Tanzanian highlands and G Mount Mulanje; 'Zimbabwe overlap region' including: H Chimanimani Mountains and Nyanga Plateau; the 'Drakensberg range' I; and the Greater Cape Floristic Region J. Areas north of the Limpopo from White (1978). Map adapted from (Linder 1990).

number of migration events by the number of (sampled) species in the source area.

3. RESULTS

The ancestral node of each of the four clades (*Disa*, Irideae p.p., the *Pentaschistis* clade and Restionaceae) optimizes to the Cape and to no other area. Approximately 94% of the nodes in the four clades can be optimized unambiguously. Most of these optimize to single areas (see electronic supplementary material Fig. 1, 2 and 3) and in two clades (Irideae p.p. and *Disa*) there are four nodes which optimize unambiguously to multiple areas. A minimum of 31 dispersal events have been documented (see table 1). Where range expansion has occurred without speciation, the precise route of migration cannot be known from a species-level study. Only unambiguous migrations are considered further, but detailed descriptions of the optimizations and migrations inferred for each clade are given in the electronic supplementary material. In all clades, most dispersal events out of the Cape are to the Drakensberg range (five events in *Disa*, three events in Irideae p.p., five events in the *Pentaschistis* clade and five or six events in Restionaceae), although there are two

dispersals (in Irideae p.p.) directly to areas north of the Limpopo River. From the Drakensberg range there are 12 events to north of the Limpopo River, meaning that the predominant source of the flora north of the Limpopo River is the Drakensberg range, rather than the Cape (see figure 3). There are only two dispersals into the Cape from the Drakensberg range (in *Disa*), demonstrating that most of the species diversity in the Cape is derived from a single lineage for each clade. In *Disa* and Irideae p.p., there has been diversification in the Drakensberg range but in the *Pentaschistis* clade and the Restionaceae all species in the Drakensberg range have their sister species in the Cape, indicating that they have migrated into the region. *Disa* and Irideae p.p. have species sampled in the Zimbabwe overlap region. With one exception in the Irideae p.p., all of these species have their sister species in other areas, indicating that the rate of local diversification has also been very low there. The migration events from the Cape to the Drakensberg range are more frequent than in the opposite direction, even if the number of taxa in the source area is taken into account (table 2, Wilcoxon sign ranks test: Cape to Drakensberg range versus Drakensberg range to Cape: $p=0.068$).

To reconstruct historical biogeography and biome assembly, it is essential to know the source and the

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Table 1. Summary table of migrations inferred from ancestral state reconstruction, showing the age estimation of migration events. (*, migration without speciation, therefore the event may be between the date range given and the present. Where a range of nodes and thus age estimates is used, the credibility interval (CrI) shown represents the upper and lower extremes.)

taxon	from where	to where	age estimate (mean)	95% CrI
<i>Moraea albicuspa</i> clade	Cape	DR	9.11	4.06, 16.37
<i>M. inclinata</i>	Cape	DR	25.65	17.25, 34.80
<i>M. alpina</i> clade	Cape	DR	18.33	11.06, 26.84
<i>M. verdickii</i> grade	Cape	SCA	14.98	8.19, 23.32
<i>M. sisyrinchium</i>	Cape	Mediterranean	13.56	7.04, 21.80
<i>M. alticola</i> clade	SCA	DR	8.26	3.68, 14.80
<i>M. carsonii</i>	Cape	ZOR, SCA, EA	7.69	2.87, 15.20
<i>M. spathulata</i> / <i>M. muddii</i> clade	DR	ZOR	4.68	1.50, 9.69
<i>M. spathulata</i>	DR, ZOR	Cape	2.73*	0.28, 6.95
<i>Dietes</i>	Cape	EA, SCA, ZOR, DR	51.45*	46.05, 54.78
<i>M. schimperi</i>	SCA	ZOR, EA	10.07*	4.59, 17.31
<i>M. natalensis</i> / <i>M. elliotii</i> clade	DR	SCA	12.03*	5.78, 20.15
<i>M. natalensis</i>	DR, SCA	ZOR	4.28*	0.58, 10.43
<i>Disa tripetaloides</i>	Cape	DR	1.37*	0.14, 3.50
<i>D. bracteata</i>	Cape	DR	2.71*	1.16, 5.01
<i>D. sagittalis</i> and <i>D. zimbabweensis</i>	Cape	DR, ZOR	15.19	11.30, 19.44
<i>D. lugens</i> var. <i>lugens</i>	Cape	DR	1.7*	0.56, 3.65
<i>D. cephalotes</i> clade	Cape	DR	8.87	3.53, 12.92
clade 'z'	Cape	DR	17.88–15.39	21.41, 11.91
<i>D. baurii</i>	Cape	DR, ZOR, SCA	5.67	2.91, 9.30
<i>D. brevicornis</i>	Cape	DR, ZOR, SCA	0.82*	0.08, 1.67
<i>D. cornuta</i>	Cape	DR, ZOR	6.52*	3.84, 10.07
<i>D. borbonica</i>	Cape	Reunion Island	1.57	0.82, 1.99
<i>D. patula</i> var. <i>transvaalensis</i>	DR	ZOR	0.60*	0.03, 1.88
<i>D. woodii</i>	DR	ZOR	1.32*	0.18, 3.19
<i>D. rhodantha</i>	DR	ZOR	1.32*	0.18, 3.19
<i>D. versicolor</i>	DR	ZOR, SCA	0.61*	0.03, 1.91
<i>D. saxicola</i>	DR	ZOR, SCA	5.43*	2.69, 9.05
<i>D. fragrans</i> ssp. <i>fragrans</i>	DR	ZOR, SCA	4.87*	2.49, 8.18
<i>D. miniata</i> clade	DR	SCA	10.50–5.79	14.20, 3.00
<i>D. perplexa</i> clade	DR	SCA	10.61*	7.38, 14.28
<i>D. chrysostachya</i>	DR	Cape	2.67*	1.08, 5.14
<i>D. buchenaviana</i>	DR	Madagascar	8.23	5.36, 13.11
<i>D. caffra</i>	DR, SCA	Madagascar	2.38*	0.84, 4.73
<i>D. aconitoides</i> ssp. <i>aconitoides</i>	DR	Cape	9.05*	6.07, 12.67
<i>D. aconitoides</i> ssp. <i>goetzeana</i>	DR	EA	8.18	5.29, 11.70
<i>D. similis</i>	DR	SCA	8.18*	5.29, 11.70
<i>D. hircicornis</i>	DR, SCA	ZOR, EA, WA	2.38*	0.84, 4.73
<i>D. perplexa</i>	DR, SCA	ZOR, EA, WA	5.97*	3.38, 9.49
<i>D. zombica</i>	SCA	ZOR	2.45*	0.94, 4.83
<i>D. miniata</i>	SCA	ZOR	2.35*	0.78, 4.73
<i>D. ornithantha</i>	SCA	ZOR	2.30*	0.79, 4.61
<i>D. erubescens</i> ssp. <i>erubescens</i>	SCA	ZOR, EA	0.54*	0.03, 1.70
<i>D. ochrostachya</i>	SCA	EA, WA	2.35*	0.78, 4.73
<i>D. stairsii</i>	?	EA	5.79	3.00, 9.54
<i>Pentaschistis tysonii</i>	Cape	DR	9.95	7.75, 11.67
<i>P. basutorum</i>	Cape	DR	9.13	7.35, 11.37
<i>P. aurea</i> subsp. <i>pilosogluma</i>	Cape and/or DR	DR	1.75	0.25, 3.79
<i>P. exserta</i>	Cape	DR	5.35	3.76, 7.67
<i>P. chippindalliae</i>	Cape	DR	3.77	2.44, 5.47
<i>P. andringitrensis</i>	Cape	Madagascar	8.03	6.24, 10.27
the summer rainfall clade	Cape	?	5.29–6.14	3.66, 8.32
<i>P. insularis</i>	?	Amsterdam Islands	0.44	0.02, 1.29
<i>P. pictigluma</i> clade	?	EA	1.04	0.47, 1.88
<i>P. natalensis</i>	?	SCA/Madagascar	1.25–3.11*	0.20, 4.61
<i>Restio zuluensis</i>	Cape	DR	5.87	2.28, 11.89
<i>Ischyrolepis schoenoides</i>	Cape	DR	4.66	1.39, 10.30
<i>Calopsis paniculata</i>	Cape	DR	17.31	9.95, 29.44
<i>Re. sejunctus</i>	Cape	DR	5.35*	1.65, 11.59
<i>Rhodocoma fruticosa</i>	Cape	DR	1.25*	0.04, 4.45
<i>Re. galpinii</i>	?	DR	16.64	8.61, 29.22
<i>Re. mahonii</i> and <i>Re. mlanjiensis</i>	?	EA and SCA, SCA	16.64	8.61, 29.22

Figure 3. Diagram showing the number of migration events between the Greater Cape Floristic Region, the Drakensberg range and the north of the Limpopo River. Unambiguous migrations only were considered.

Table 2. The migration rate for each clade, calculated as the number of migrations per sampled taxon in the source area.

	Cape to DR	DR to Cape
<i>Disa</i>	0.0732	0.0435
Irideae p.p.	0.0526	0
the <i>Pentaschistis</i> clade	0.0806	0
Restionaceae	0.0174	0

(Schluter *et al.* 1997) or when optimizing more basal nodes (Mooers & Schluter 1999).

We used presence-only coding and binary optimization, rather than multistate coding and optimization, since currently available likelihood optimization software does not allow polymorphic character states at internal nodes, even if polymorphic states at the tips are accepted. Many of the species we investigated occur in more than one area (e.g. 19% of the *Disa* species occur in multiple areas) and we therefore assume that some internal nodes might also have had wider distributions. Such a scenario can only be reconstructed using binary optimization (Hardy & Linder 2005), since internal nodes can be optimized as polymorphic with statistical significance.

Topological uncertainty was not dealt with directly, except in the case of Irideae p.p., where the phylogenetic hypothesis contained polytomies (Goldblatt *et al.* 2002). In *Disa* and the *Pentaschistis* clade, there were several poorly supported nodes in areas of the topology where several distributional changes probably took place. However, there was also ambiguity in the optimization of these nodes (due both to this frequent change and to the short branch lengths involved). These ambiguous nodes were omitted from further analysis.

(b) Directionality and the sourcing of the Afrotropical flora in tropical Africa

The most recent common ancestor of all the four clades was unambiguously traced to the Cape. In total, 18 migrations from the Cape to the Drakensberg range and 12 from the Drakensberg to the rest of the Afrotropical region north of the Limpopo River are documented. There are two migrations from the Cape to the north of the Limpopo River. Migration events in the opposite directions are rare (figure 3). This pattern refutes the hypothesis that north to south has been the prevailing

direction of migration for taxa shared between the Cape and the Afrotropical floras (Levyns 1938, 1952, 1964; Axelrod & Raven 1978). Although neither the *Pentaschistis* clade nor *Disa* nor Irideae p.p. were mentioned explicitly, Levyns (1964) discussed many lineages that are similarly distributed within the Cape. Although she favoured a southern origin for a few taxa, such as Restionaceae and *Phyllaea*, the distribution of other lineages was postulated to be the result of north to south migration. This 'southward migratory stream' was based mainly on the widespread but scattered distribution of more 'primitive' relatives or members of the lineages in tropical Africa. These were seen as relics of a once more continuous vegetation. In contrast, more 'advanced' members of the lineages were found in the southwestern part of the Cape where, as 'youthful endemics' they usually have a narrower distribution.

Although the 95% CIs of the age estimates are large, we date the migration of this flora to the tropical Afrotropical regions to between 0.54 (0.02–1.80 CrI) and 10.0 (4.59–17.31 CrI) Myr ago (see table 1). Such recent migrations into these areas are congruent with the recent formation of the uplands of tropical Africa, which dates to the Miocene, with further uplift in the Pliocene and the Pleistocene (Grove 1983; Partridge *et al.* 1985). Palynological evidence suggests that *Podocarpus* and *Juniperus* were not in the Turkana Basin, northern Kenya, before 25 Myr ago (Vincens *et al.* 2006), and that they were present in Fort Ternan, Kenya, at ca 14 Myr ago (Bonnefille *et al.* 2004). In contrast, the Cape Fold Mountains and the Lesotho highlands (within the Drakensberg range) precede the evolution of the Angiosperms and were partially preserved through the early African erosion cycle (King 1963; Grove 1983; Partridge & Maud 1987; Partridge 1998). There was important rejuvenation with two major periods of uplift in the early Miocene and the Pliocene especially in the Drakensberg (Partridge & Maud 1987; Partridge 1998; Partridge & Maud 2000). Stem lineages of members of the Cape clades date to the late Cretaceous and throughout the Tertiary (Galley & Linder 2006), consistent with the ancient Cape mountains. Migrations into the Drakensberg date to as early as 25.65 (17.25–34.80 CrI) Myr ago, and there is an increase in the number of events in the last 9 Myr, consistent with recent uplift in the area.

(c) The Drakensberg range in the spread of the Afrotropical flora

The Drakensberg range plays an important role as a 'stepping-stone' for plants between the Cape and the tropical Afrotropical region (figure 3). The close floristic affinity between the Cape and the Drakensberg range is well known (Weimarck 1941; Killick 1963, 1978; Hilliard & Burtt 1987; Carbutt & Edwards 2002). We demonstrate it to be the result of many migration events occurring over a wide time span and largely in one direction. This unidirectional migration cannot be explained simply by the number of taxa in the source area.

The Drakensberg range has been proposed to be the source of many of the Cape elements in the mountains of tropical Africa (Weimarck 1941). This has been demonstrated for *Aloe* (Holland 1978) and Coryciinae s.s. (Linder 1994). This stepping-stone role of the Drakensberg range in the spread of species through the Afrotropical

region is well supported by our data (figure 3). Although there are a few exceptions (*Moraea carsonii* and the *Moraea verdickii* grade, plus potential additional cases in *Restio* and *Pentaschistis*), direct migration from the Cape to the areas north of the Limpopo is not the norm. Furthermore, any extinction in the Drakensberg range would mask an indirect route. The Drakensberg range could also be the source of other Austral Afrotropical taxa also represented in the Cape, such as *Satyrium* (Orchidaceae), *Kniphofia* and *Aloe* (Asphodelaceae).

(d) Speciation outside of the Greater Cape Floristic Region

The Cape is known for its very high species richness (Levyns 1964; Goldblatt 1978; Goldblatt & Manning 2002; Linder 2003) concentrated in a relatively small number of clades (Levyns 1964; Goldblatt 1978; Linder 2003). It is unclear whether the high richness of the Cape relative to the other regions is the result of a more rapid diversification rate or simply of accumulation of species over a longer time period.

The wind-pollinated Restionaceae and *Pentaschistis* clades are represented by singleton species in the Drakensberg range, meaning that there has been no local diversification (i.e. speciation has not exceeded extinction). This cannot be explained by a lack of time to speciate since some of these migration events are very old (table 1), and in the *Pentaschistis* clade, for example, one Drakensberg species (*Pentaschistis basutorum*) is sister to a clade of at least 48 Cape species. Since all but one Drakensberg species from both clades have been sampled, we would not expect the pattern to change much with increased sampling. The biotically pollinated *Disa* and Irideae p.p. show a different pattern. *Disa* has reached the Drakensberg range at least 10 times and includes two clades that have subsequently radiated in the region, resulting in 12 and 26 taxa, respectively. Likewise Irideae p.p. has reached the Drakensberg at least six times and has speciated *in situ* resulting in three clades of three, five and seven taxa. The relative influence of pollinators and habitat diversity in the Cape and the Drakensberg range may have played an important role in the origin of differences between these two sets of clades and should be investigated.

While the Drakensberg range represents a source area for the more northerly part of the Afrotropical region, the Zimbabwe overlap region acts more like a sink. *Disa* and Irideae p.p. reached the Zimbabwe overlap region at least 15 and 4 times, respectively, but we document only one instance of local speciation. However, unlike *Pentaschistis* and Restionaceae in the Drakensberg range, these migrations are on average among the youngest events (table 1). Weimarck (1941) viewed the Inyangani subcentre (=Zimbabwe overlap region) as a 'relic', but although the habitats in these areas may be old, many of the species are clearly relatively recent additions. It is possible that the small surface area of the uplands in this region (approx. 1600 km², Timberlake & Muller 1994) may be linked to a higher probability of local extinction (Gaston 2003). A consequence would be that the contemporary taxa are relative newcomers to the area. *Disa* and Irideae p.p. in the Zimbabwe overlap region have been sourced from both the north (South Central Africa) and the south (the Cape or the Drakensberg range), and this mixed sourcing of the flora is consistent with the

suggestions of Weimarck (1941) and Van Wyk & Smith (2001). Four species of Irideae p.p., one of *Disa* and one of Restionaceae are endemic to the Zimbabwe overlap region but were not sampled here. Although this makes our figure an underestimation, including these would not alter our conclusions that this region has a low diversification rate and that there are multiple sources to its flora.

All the four lineages have species in South Central and Eastern Africa. For three of these (Restionaceae, *Pentaschistis* clade and *Disa*), we know that *in situ* speciation has contributed at least half of the species. One of the two species of Restionaceae evolved in South Central Africa. The five *Pentaschistis* taxa in Eastern Africa form a clade, showing a radiation from a single immigration to the area. *Disa* is represented by 45 species in South Central and Eastern Africa, of which 22 are included in our analysis. This indicates two radiations, one with two species and the other with 11 or 12 taxa. However, morphological data indicate that the first radiation includes 8, and the second includes 20 species. There are possibly more radiations but species sampling would need to be extended to test these. Unfortunately our sampling of the Irideae p.p. of South Central and Eastern Africa is not adequate for a conclusive biogeographical optimization. The *in situ* diversification in South Central and Eastern Africa contrasts with the situation in the Zimbabwe overlap zone, where there has been almost no diversification. Furthermore, in tropical Africa, the Restionaceae and the *Pentaschistis* clade also speciated unlike in the Drakensberg range. Overall, it seems that there has been more speciation in the geographically much more extensive and fragmented Afrotropical flora of South Central and Eastern Africa than in the Drakensberg range.

5. CONCLUSION

Biota comprise independent lineages that react differently to barriers, changes in climate, vegetation and pollinators. The biogeographical histories of their components are therefore not necessarily the same even if they occur in the same area. Using well-sampled phylogenies, the source areas of biota can be identified and the use of molecular clocks further allows us to put these events into a temporal framework. The Cape elements that we investigated occur in the tropical African mountains as a result of migration from the Cape or Drakensberg and also as a result of *in situ* speciation. This is similar to the situation in the Andes, where for the clades investigated the diversity is largely the result of recent and rapid *in situ* speciation (Hughes & Eastwood 2006). We also demonstrate a unidirectional migration in the Afrotropical flora. In contrast, migration across the Tasman Sea between New Zealand and Australia is bidirectional (Winkworth et al. 2002).

We do not attempt to provide a hypothesis for the origin of the complete Afrotropical flora, but rather for what is referred to as the Cape element, which nonetheless forms a substantial part of this flora. There has been a lot of migration throughout the region. In some areas, this immigration is the only source of diversity, whereas for other areas *in situ* diversification has been very important. These findings are however lineage dependant. We present overwhelming support for south to north migration for all clades and show that the Cape element in the Afrotropical flora is, at least in part, Cape derived. The Drakensberg

range has played an important role as a stepping-stone in the spread of the flora through this region. Clades such as *Stoebe*, *Oxalis*, *Cineraria*, *Felicia*, *Ursinia*, *Lobelia*, *Cyphia*, *Cliffortia*, *Pelargonium* and *Phyliceae* have, like our study groups, their greatest species richness in the Cape and probably show a similar pattern. In contrast, *Satyrium*, *Aloe* and *Kniphofia* have most species in the tropical mountains and may show a different pattern. A critical evaluation of the last set of genera would constitute an appropriate test of the generality of our Cape to Cairo hypothesis.

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