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Historical biogeography of *Androcymbium* Willd. (Colchicaceae) in Africa: evidence from cpDNA RFLPs

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The cpDNA restriction variation in 39 populations representing a geographical sampling of 18 species of *Androcymbium* in southwestern and northern Africa was examined to assess the historical biogeography of the genus. The cpDNA phylogeny indicates that the disjunction between South and North Africa is best explained by the dispersal of southern African ancestors into North Africa. Divergence time estimates suggest that the geographic range of the genus may have extended considerably north (perhaps to Tanzania and Kenya) prior to the global desiccation of Africa in the Miocene. Further expansion of the genus northward was probably stalled until climatic changes in the late Miocene brought about the gradual replacement of a subtropical woodland savanna with the arid landscape that gave rise to the Sahara. Aridification of the northern quarter of the continent provided the ecological conditions for fostering the expansion of *Androcymbium* along the Mediterranean fringe (probably east to west) and its introduction into the Canary Islands. Unlike their South African congeners, the northern species have experienced expansions, fragmentations, and local extinctions in response to the severe climatic shifts in this area during the Pliocene-Pleistocene. According to our divergence time estimates, the arid track may have already existed as a continuous area connecting southern and northern Africa in the late Miocene.

ADDITIONAL KEY WORDS: African biogeography – arid track – dispersal – phylogeny.

INTRODUCTION

Androcymbium Willdenow (Colchicaceae) consists of about 50 species (Müller-Doblies & Müller-Doblies, 1998; Pedrola-Monfort *et al.*, 1999a,b, 2000; Membrives, 2000) of hermaphroditic geophytes that exhibit a disjunct distribution between northern and southern Africa. Four of the six North African species are distributed in the Mediterranean fringe: *Androcymbium gramineum* and *A. wyssianum* are widespread in north-west Africa, *A. palaestinum* has two populations in the Middle East and *A. rechingerii* occurs along the Libyan coast and in the Greek islet of Elafonisos. The other two are Canary Island endemics: *Androcymbium hierrense* occurs in the western islands of La Palma, El Hierro, and La Gomera, and *A. psammophilum* is found in the eastern islands of Lanzarote and Fuerteventura. Southern Africa is the centre of taxonomic diversity of the genus, with most of the species occurring throughout western South Africa and in some arid areas of Namibia, Angola, Zambia, northern Zimbabwe and Botswana. Only 11 taxa are found in the area comprising eastern South Africa, the Indian coast of Africa (Kenya and Tanzania), and Ethiopia (Müller-Doblies & Müller-Doblies, 1998).

All *Androcymbium* species pioneer open arid or semi-arid habitats. The four circummediterranean species

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and the South African *A. austrocapense*, *A. eghimocymbion*, and *A. capense* occur in strictly Mediterranean climates. The other South African species are found in a diverse array of edaphic conditions with Mediterranean-like, desert, or summer-concentrated rain regimes, in vegetation types ranging from the Fynbos to the arid Karoo (Acocks, 1988). Only two species are found at high elevations: *A. melanthioides*, on the Drakensberg mountains in Lesotho, and *A. striatum*, on Mt Kilimanjaro in Tanzania.

Because of its distribution, *Androcymbium* qualifies as a member of the arid track (Balinsky, 1962), an irregular sickle-shaped area in Africa where monthly rainfall is less than 10 mm (Fig. 1). The only representatives of the genus that do not fit within this area are the five taxa of the *A. melanthioides* complex, which are distributed in northern South Africa and along the Indian coast in eastern South Africa. Members of this complex, however, bear some morphological similarity with southeastern African species within the arid track (e.g. *A. decipiens*, *A. natalense*, *A. longipes*, *A. burkei*, and *A. leistneri*).

Until recently, all molecular evidence on *Androcymbium* was restricted to allozyme variability in the North African species (Pedrola-Monfort & Caujapé-Castells, 1994, 1996). A chloroplast DNA (cpDNA) restriction site phylogeny (Caujapé-Castells *et al.*, 1999) provided the first molecular phylogenetic framework to understand the relationships among the species of a genus distributed in the arid track. To our knowledge, the only other formal attempt to understand the distribution of a genus with a similar geographic distribution was a morphological cladistic analysis of *Lotononis* (Fabaceae) (Linder, Meadows & Cowling, 1992). A biogeographic hypothesis for *Androcymbium* based on molecular, morphological, and other biological evidence would provide a general model that can be tested using other important groups of plants with a similar distribution in Africa. De Winter (1971) lists eight genera and 41 species with disjunctions between arid areas in North and South Africa. Of these, *Lotononis* has a species diversity pattern similar to *Androcymbium*, with about 90 species in southern Africa and some 10 to 15 in northern Africa. Conversely, *Tetrapogon* (Poaceae) is represented by about five species in northern Africa and by only two in southern Africa. Other groups (Schnell, 1971) occur along the arid track without exhibiting an obvious discontinuity (e.g. Boraginaceae, Cupressaceae, or Ericaceae). Pollen (Pérez de Paz, 1993) and biogeographic (Bramwell, 1976, 1985) evidence for the *Echium–Lobostemon* complex (Boraginaceae) suggested a closer connection between *Lobostemon* from southwestern and southeastern Africa and the Canary Island species of *Echium* than between Mediterranean and Canarian *Echium* species.

The wide diversity of plant groups found throughout this dry area and their contrasting patterns of distribution suggest that the arid track may have played several roles in the biogeographic history of Africa. The region may have been a migration corridor from south to north (or vice versa) for some groups. It is also plausible that the region influenced the fragmentation of other organisms that were widespread before the desiccation of the continent in the late Miocene (Van Zinderen Bakker, 1975). The relationship between arid zones of North and South Africa is one of the more intriguing phenomena in plant distribution patterns (De Winter, 1971). Unfortunately, there is a paucity of molecular phylogenetic investigations of these important African groups. Thus, the role of the arid track in the biogeographical history of Africa is still poorly understood. The cpDNA data set for *Androcymbium* is relevant because it enables us to address previously unexplored and challenging topics. At present, the colonization sequence of the genus is perhaps one of the more interesting because it allows us to analyse critically the evolutionary and biogeographical history of a genus distributed in the arid track.

Our goal in this paper is to propose a hypothesis of the distribution of the genus *Androcymbium* in Africa based primarily on the information provided by cpDNA restriction site data.

MATERIAL AND METHODS

TAXON SAMPLING

We sampled 39 populations of *Androcymbium* representing 18 of the approximately 50 species in the three main geographic regions where the genus is distributed (Fig. 1, Table 1). This includes most of the known populations of the six North African species and a geographic representation of their congeners in the centre of species diversity (i.e. the Atlantic coast and western mainland of South Africa). All North African species have a basic chromosome number of $2n = 18$, whereas the South African species exhibit an aneuploid series of $2n = 18$, 20 and 22 (Margelí, Pedrola-Monfort & Vallés-Xirau, 1999; Montserrat *et al.*, in prep.).

The limited representation of South African taxa requires some justification. Some populations from western South Africa could not be sampled because of insufficient floristic exploration of these regions. This factor is of concern for all *Androcymbium* taxa because the two biomes that they prefer in southwestern Africa (the Fynbos and the Karoo) are particularly under collected for Liliaceae (Milton *et al.*, 1997). Although the possible under-representation could be problematic, strict monophyly of all the species represented by more than one population in a previous cpDNA

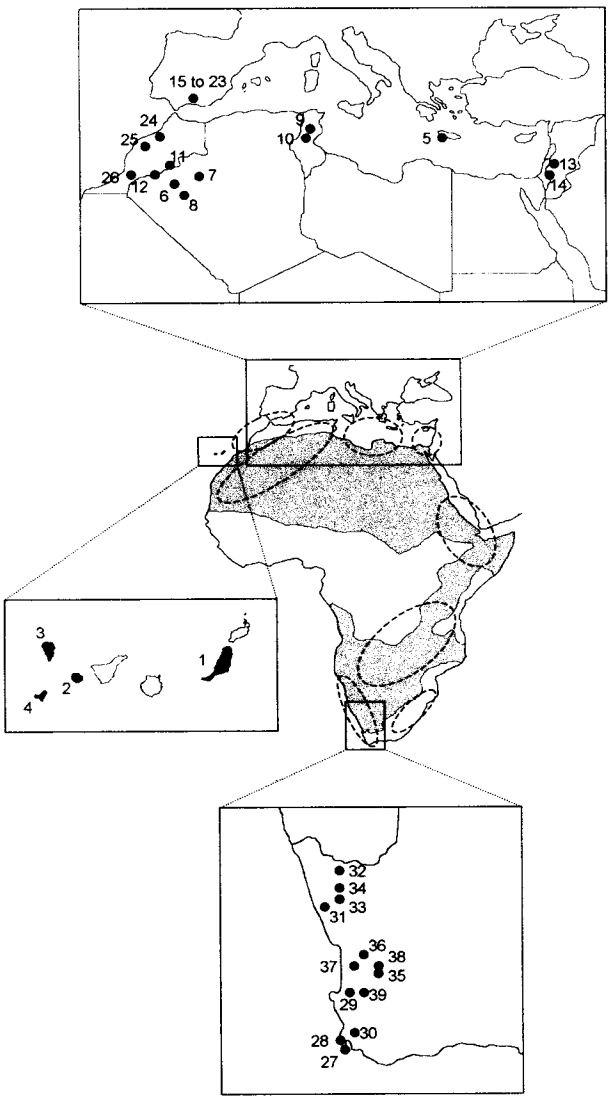

Figure 1. Geographic site map of the populations used in the analysis. Numerical codes correspond to those in Table 1. The shaded area corresponds to the arid track after Balinsky (1962). The dotted ellipses are the general distribution areas of *Androcymbium* in Africa.

phylogeny (Caujapé-Castells *et al.*, 1999) suggests that even a single population per taxon is sufficient.

Other southwestern African species are not represented at all. Despite their possible relevance, the impact of their absence is considerably diminished for two reasons. First, many of these species (e.g., *A. cruciatum*, *A. hughocymbion*, *A. huntleyi*, *A. kunkelianum*, *A. vanjaarsveldii* and *A. worsonense*) are very restricted geographically, and in most cases they are represented by a single population (Müller-Doblies & Müller-Doblies, 1998; Membrives, 2000). Second, our sampling design covers all the geographic areas of *Androcymbium* in southwestern Africa.

No representatives of the taxa from southeastern Africa could be included. These are important for a thorough understanding of the general patterns of diversification in *Androcymbium*. However, because their ranges are outside the arid track (Fig. 1), they are not particularly relevant to the discussion of the significance of the arid track in the biogeography of *Androcymbium*. Perhaps the only important weakness of our sampling is the absence of the two species in Tanzania and Kenya and of *A. roseum*, which is widespread from the Limpopo river at Messina (northern Province of South Africa) to arid zones of Angola, Zambia and Botswana. The latter species has been related directly to the North African taxa based on macromorphological (Krause, 1920; Roessler, 1974;

Table 1. Geographic distribution of the 39 populations of *Androcymbium* used in this study

	Species (population)	Code	Location
1.	*A. psammophilum* (Fuerteventura)	PSA-FU	Eastern Canary Islands
2.	*A. hierrense* (La Gomera)	HIE-GO	Western Canary Islands
3.	*A. hierrense* (La Palma)	HIE-LP	Western Canary Islands
4.	*A. hierrense* (El Hierro)	HIE-HI	Western Canary Islands
5.	*A. rechingerii* (Elafonisos)	REC-EL	Greece
6.	*A. wyssianum* (Taghit-Igli)	WYS-TI	Algeria
7.	*A. wyssianum* (Ain Ouarka)	WYS-AO	Algeria
8.	*A. wyssianum* (Igli)	WYS-IG	Algeria
9.	*A. wyssianum* (Nefta 1)	WYS-N1	Tunisia
10.	*A. wyssianum* (Nefta 2)	WYS-N2	Tunisia
11.	*A. wyssianum* (Fonts Bleu de Meski)	WYS-FB	South of Morocco
12.	*A. wyssianum* (Er Rachidia)	WYS-ER	South of Morocco
13.	*A. palaestinum* (Beit Shean)	PAL-BS	Middle East
14.	*A. palaestinum* (Dimona)	PAL-DI	Middle East
15.	*A. gramineum* (Barranco de Curria)	GRA-BC	Almería (South of Spain)
16.	*A. gramineum* (Cerro de los lobos)	GRA-CL	Almería (South of Spain)
17.	*A. gramineum* (Playa de Monsul)	GRA-PM	Almería (South of Spain)
18.	*A. gramineum* (Charco del Lobo)	GRA-CH	Almería (South of Spain)
19.	*A. gramineum* (El Solanillo)	GRA-ES	Almería (South of Spain)
20.	*A. gramineum* (Cerro los Peligros)	GRA-CP	Almería (South of Spain)
21.	*A. gramineum* (San Cristóbal)	GRA-SC	Almería (South of Spain)
22.	*A. gramineum* (Los Molinos)	GRA-LM	Almería (South of Spain)
23.	*A. gramineum* (El Barranquete)	GRA-EB	Almería (South of Spain)
24.	*A. gramineum* (Cap Beddouza)	GRA-CB	North of Morocco
25.	*A. gramineum* (Casablanca)	GRA-CA	North of Morocco
26.	*A. gramineum* (Oualidia)	GRA-OU	North of Morocco
27.	*A. austrocapense* (Cape of Good Hope)	AUS-GH	Western South Africa
28.	*A. austrocapense* (Whale Point)	AUS-WP	Western South Africa
29.	*A. eghimocymbion* (Citrusdale)	EGH-CI	Western South Africa
30.	*A. burchellii* subsp. *burchelli* (Hexrivier)	BUR-HX	Western South Africa
31.	*A. walteri* (Steinkopf)	WAL-ST	Western South Africa
32.	*A. bellum* (Vioolsdrift)	BEL-VI	Western South Africa
33.	*A. poeltianum* (Concordia)	POE-CO	Western South Africa
34.	*A. circinatum* (Springbok)	CIR-SP	Western South Africa
35.	*A. cuspidatum* (Calvinia)	CUS-CA	Western South Africa
36.	*A. burchelli* subsp. *pulchrum* (Nieuwoudtville)	PUL-NI	Western South Africa
37.	*A. irroratum* (Vanrhynsdorp)	IRR-VP	Western South Africa
38.	*A. hantamense* (Calvinia)	HAN-CA	Western South Africa
39.	*A. albanense* subsp. *clanwilliamense* (Pakhuispass)	ALB-PK	Western South Africa

Pedrola-Monfort, 1993) and palynological data (Martín, Pedrola-Monfort & Caujapé-Castells, 1993).

Three outgroups from the Colchicaceae (two populations of *Colchicum lusitanicum* and one population of *Merendera pyrenaica*) were included in the analyses based on their close phylogenetic relationship to *Androcymbium* (Buxbaum, 1936; Nordenstam, 1982; Persson, 1993).

DNA EXTRACTION, DIGESTION AND HYBRIDIZATION

DNA isolation, digestion with 21 restriction endonucleases, and filter hybridizations with *Oncidium excavatum* (Orchidaceae) probes (Chase & Palmer, 1989) were carried out as described in Jansen & Palmer (1987) and Caujapé-Castells *et al.* (1999). Variable restriction sites were scored as present (1) or absent (0). Length changes were scored as the ancestral length (0) or derived length (1) using the outgroups.

PHYLOGENETIC ANALYSES

The g1 statistic (Hillis & Huelsenbeck, 1992) was calculated to evaluate the amount of phylogenetic signal present in the data. Most parsimonious trees were obtained after heuristic searches with 100 random

addition replicates using the TBR branch-swapping option in PAUP* version 4d64 (Swofford, 1998) with MULPARS. Bootstrap values (Felsenstein, 1985) were obtained after 100 replicates using heuristic search with random addition sequence of taxa, MULPARS, ACCTRAN optimization, and TBR branch swapping.

RATE HOMOGENEITY TESTS AND DIVERGENCE TIME ESTIMATES

Differences in rates of cpDNA evolution were evaluated by all possible pairwise comparisons involving 18 populations of *Androcymbium* (Fig. 2) representing independent branches of the phylogenetic tree and the outgroup *Merendera pyrenaica* using the two-tailed Wilcoxon matched-pair signed rank test (Templeton, 1983). Sequence divergence values between selected pairwise combinations of populations were calculated following Nei & Li (1979) and used to estimate divergence times based on a slow (0.07%) and a fast (0.1%) average divergence rate per million years (Parks & Wendel, 1990; Wendel & Albert, 1992). Divergence times were estimated for 15 nodes representing major diversification events in the phylogenetic tree (labelled 'a' to 'o' in Fig. 2) and compared with available palaeobotanical and geological evidence. Only the populations between which we could assume a uniform molecular clock rate according to Templeton's (1983) tests were used for the divergence time calculations (Table 2). Because this cpDNA data set is the first thorough molecular research in *Androcymbium*, the molecular clock could not be calibrated against independently derived estimates of divergence time. Although allozyme data for the genus are available (Caujapé-Castells, 1995; Membrives, 2000), we refrained from using these data for estimating divergence times because of the total lack of independent information about times of speciation and the enormous range of the rates from allozymes (Avise & Aquadro, 1982).

GEOGRAPHIC RELATIONSHIPS

The assessment of biogeographic relationships in *Androcymbium* was performed by replacing the terminal taxa in the cpDNA tree with their geographic distribution (Hennig, 1966; Brundin, 1966; Nelson, 1969). We evaluated the feasibility of the most parsimonious biogeographic hypothesis (Figs 2, 3) by taking into account diverse biological evidence and the available data on the biogeographic history of Africa (Quézel, 1978; Maley, 1980). While this approach assumes that biogeographic history proceeds parsimoniously and is deducible from phylogenetic history, there is no alternative testable methodological framework to undertake biogeographic reconstruction. Importantly, it is precisely the assumption of parsimony that allows us to falsify the favoured hypotheses by the addition of new data. We considered the four most general areas of distribution of *Androcymbium* (southwest Africa, northwest Africa, the Middle East and the Canary Islands).

RESULTS

The g1 statistic for 100 000 randomly generated trees is –0.489, indicating that the data are skewed significantly from random ($P<0.01$ for g1 = 500 characters and ≥ 25 taxa). Therefore, they contain considerable phylogenetic signal (Hillis & Huelsenbeck, 1992). The tree shown in Figure 2 summarizes the phylogenetic relationships among the 39 analysed populations based on cpDNA restriction site changes. Parsimony analysis produces 30 trees of 945 steps with a consistency index (CI) of 0.65 and a retention index (RI) of 0.90 (excluding uninformative characters). All South African species are basal and are divided into three well-supported clades (S1, S2 and S3 in Figs 2, 3). The North African taxa are monophyletic, occur in a derived position in the phylogeny, and share a common ancestor with the South African *A. austrocapense*.

A molecular clock is rejected in only 13 of the comparisons among *Androcymbium* populations (Table 2). None of these are between species from North African populations. Ten of the molecular clock rejections correspond to the population of *A. walteri* (WAL-ST) either with North African (ANHIE-LP, WYS-N2, GRA-CH, PAL-TA) or South African (AUS-WP, BEL-VI, CIR-SP, ALB-PK, HAN-CA, PUL-NI) populations. The other three rejections involve comparisons between PSA-FU and CIR-SP and PUL-NI, and between BEL-VI with ALB-PK. The divergence times estimated from the sequence divergence values given in Table 2 show that diversification of the genus in South Africa (nodes a–g in Fig. 2) proceeded continuously from the mid-late Eocene to the Miocene. In contrast, all major diversification events affecting the North African taxa (nodes h–l in Fig. 2) are within the late Miocene, between 12.1 ± 2.8 and 5.8 ± 0.2 million years ago (Mya). According to these estimates, the origin of *A. wyssianum* in the mid-late Pliocene (node n, 2.6 ± 0.5 Mya) and inter-island colonization in the western Canary Islands in the mid-Pleistocene (node o, 0.95 ± 0.2 Mya) represent the most recent events in the biogeographic history of *Androcymbium*.

All 30 most parsimonious trees show the same relationships among the geographic regions. If the cpDNA tree is an accurate representation of the phylogenetic relationships among species of *Androcymbium*, three dispersal events would be required to explain the present distribution by a northern origin. Only a single dispersal event is needed to explain their distribution under the assumption of a southern origin (Fig. 3).

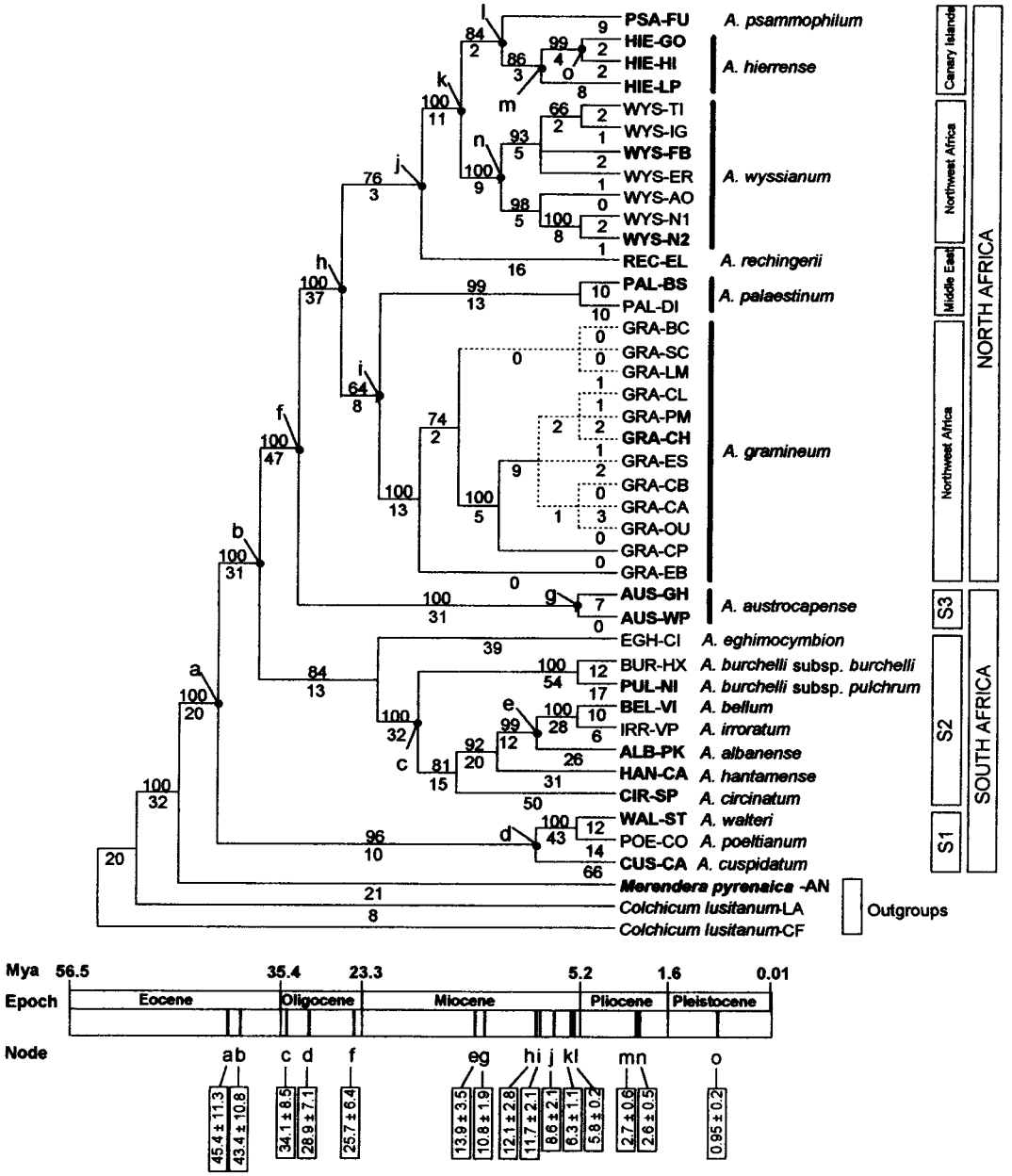

Figure 2. One of the 30 most parsimonious cpDNA trees showing the biogeographic relationships among the species of *Androcymbium* (right) and the chronological map of the diversification events represented by nodes 'a' to 'o' (below). Framed numbers below the chronology are the averaged divergence time estimates ± SD (in Myr). Numbers above the branches represent bootstrap support. Numbers below the branches indicate cpDNA restriction site changes. Branches drawn with a discontinuous line are those that collapse in the strict consensus tree. The codes of the populations selected to test the molecular clock hypothesis are in bold.

DISCUSSION

ORIGIN OF *ANDROCYMBIUM*

Phylogenetic reconstructions are essential prerequisites for understanding historical biogeography. Cladistic biogeography postulates that positionally plesiomorphic areas are more likely to be the ancestral than positionally apomorphic areas (Platnick, 1981). This argument has been used extensively to infer dispersal and to locate ancestral areas (Nelson, 1969; Bremer, 1992; Ronquist, 1997; Liston & Kadereit, 1995). The application of this argument to the cpDNA

Table 2. Results of the Wilcoxon matched-pair signed rank test (Templeton, 1983) to evaluate the hypothesis of the molecular clock in the selected populations of *Androcymbium* (above the diagonal) and sequence divergence values (below the diagonal) used to calculate divergence times. Species' codes are those in Table 1. Symbols stand for non-significant differences (—) and significant differences at $P<0.05$ (*) and $P<0.01$ (**)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1.	PSA-FU		—	—	—	—	—	—	—	—	—	—	*	—	—	—	*	—	—	*
2.	HIE-LP	0.511		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*	*
3.	HIE-GO	0.540	0.235		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*
4.	HIE-HI	0.620	0.196	0.078		—	—	—	—	—	—	—	—	—	—	—	—	—	—	*
5.	WYS-N2	0.499	0.394	0.395	0.502		—	—	—	—	—	—	—	—	—	—	—	—	*	**
6.	WYS-FB	0.604	0.525	0.567	0.634	0.195		—	—	—	—	—	—	—	—	—	—	—	—	**
7.	REC-EL	0.780	0.567	0.717	0.704	0.757	0.889		—	—	—	—	—	—	—	—	—	—	—	**
8.	GRA-CH	1.210	1.088	1.091	1.162	1.036	1.183	0.922		—	—	—	—	—	—	—	—	—	*	**
9.	PAL-TA	0.945	0.689	0.758	0.786	0.854	1.000	0.797	0.966		—	—	—	—	—	—	—	—	*	**
10.	AUS-WP	2.680	2.217	2.134	2.075	2.297	2.479	2.170	2.672	2.566		—	—	—	—	—	—	—	*	**
11.	AUS-GH	2.032	1.761	1.680	1.622	1.839	2.048	1.804	2.262	1.748	0.889		—	—	—	—	—	—	—	**
12.	CIR-SP	3.873	3.531	3.397	3.352	3.621	3.711	3.641	4.125	3.698	2.425	2.840		—	—	—	—	—	**	**
13.	BEL-VI	3.737	3.245	3.130	3.099	3.301	3.455	3.448	3.928	3.543	2.797	3.161	1.855		**	—	—	—	**	**
14.	ALB-PK	3.550	3.306	3.122	3.128	3.363	3.518	3.415	3.829	3.549	2.657	3.159	1.766	1.155		—	—	—	**	**
15.	HAN-CA	4.007	4.168	3.962	3.982	4.129	4.278	4.081	4.484	4.256	2.605	3.645	3.900	3.718	1.346		—	—	**	**
16.	LAT-NI	4.013	3.672	3.503	3.528	3.763	3.987	3.783	4.245	3.823	3.310	3.335	2.281	2.378	2.631	3.935		—	**	**
17.	CUS-CA	3.947	4.047	3.809	3.862	4.008	4.166	3.961	4.360	4.134	3.412	3.659	3.912	3.796	3.770	0.236	3.770		—	**
18.	WAL-ST	4.013	4.008	3.849	3.896	4.035	4.094	3.988	4.286	3.962	3.247	3.554	3.589	3.448	3.607	2.527	3.562	2.389		**
19.	MPY-AN	0.653	3.510	3.613	3.652	3.600	3.822	3.299	3.850	3.724	3.120	3.234	4.122	3.698	3.601	2.736	3.816	2.536	2.680	

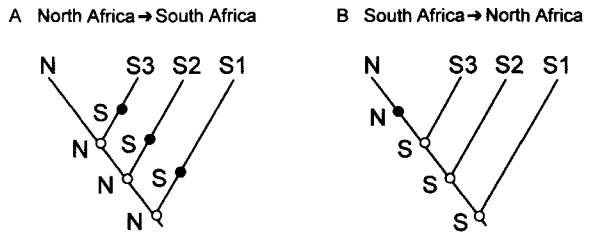

Figure 3. Assessment of the two possible biogeographic hypotheses on *Androcymbium*'s origin discussed in the text in a simplified phylogenetic tree. Under model A (North African origin) the phylogeny of *Androcymbium* is explained by three dispersal events to South Africa (S). Model B (South African origin) explains the phylogeny with a single dispersal event to North Africa (N). Hypothetical (○) geographical distributions of ancestors and (●) dispersal events.

phylogeny of *Androcymbium* suggests that South Africa is the more likely ancestral area of the genus (Fig. 3). The hypothesis of a South African origin is more parsimonious than a North African origin because the latter requires two extra dispersal events.

Biogeographical theory and karyological evidence provide additional support for a South African origin of *Androcymbium*. The criterion of main massing (Craw, 1985) states that the origin of a track for a particular group is in the region that has the highest species, genetic, or morphological diversity. Most species of *Androcymbium* (about 80%) occur in South Africa, and these are much more diverse morphologically than the six North African species (Membrives, 2000). Furthermore, the South African taxa have much higher levels of molecular divergence than their North African congeners both at the allozymic (Membrives, 2000) and at cpDNA restriction site levels (Fig. 2). An accelerated rate of evolution could also account for the much higher cpDNA sequence divergence in South Africa than in North Africa. If this were the case, we would expect to observe a considerable number of molecular rate inequities and many of these should be restricted to comparisons between North and South African species. Our relative rate tests indicate substantial rate uniformity between the southwestern and the northern ranges of *Androcymbium*. Only six rejections of a molecular clock involve one species from each zone, and approximately the same number of rejections are present in comparisons of southwestern African populations. Thus, the observed differences in levels of sequence divergence between the two regions cannot be attributed to rate inequities. In view of this remarkable rate homogeneity, it is likely that the much higher level of molecular divergence in the South African lineages of *Androcymbium* is due primarily to their antiquity relative to their North African congeners. *Androcymbium walteri* could be an exception because of the high proportion of molecular clock rejections in which it is involved (10 out of 13 total rejections). However, six of these correspond to comparisons with other South African species.

Karyological investigations of *Androcymbium* indicate that all North African species are $2n=18$ (Angulo, 1954; Borgen, 1970; Bramwell *et al.*, 1971; Margelí *et al.*, 1995), whereas the South African taxa exhibit an aneuploid series of $2n=18$, 20 and 22 (Margelí *et al.*, 1999; Montserrat *et al.*, in prep.). Most importantly, species with $2n=20$ or 22 show a much more symmetrical karyotype than those with $2n=18$ (Margelí *et al.*, 1999; Montserrat *et al.*, in prep.). The karyological data have implications for our biogeographical hypotheses. Stebbins (1971) suggested that there is an evolutionary trend toward karyotype asymmetry in plants and this view is now widely accepted (Stace, 1989). Margelí *et al.* (1999) used this trend to suggest that the North African species of *Androcymbium* are probably derived from their South African congeners with $2n=20$ through descending dysploidy (i.e. a progressive loss of chromosomes through time). In the absence of evidence to refute Stebbins' (1971) hypothesis, karyological data indicate that species of *Androcymbium* with asymmetrical karyotypes (i.e. North African taxa) are more recent than their congeners.

The problems associated with the application of basal repetition of nodes for biogeographical inference were pointed out by Nelson (1975), who realized that this procedure may lead to erroneous conclusions if alternative hypotheses are not considered. In *Androcymbium*, there are at least two alternative biogeographic hypotheses other than a South African origin that would result in a basal position of the South African species in the cpDNA tree (Fig. 2). First, an ancestral species may have been distributed widely throughout North and South Africa and the first speciation events may have been restricted entirely to the south. When the areas eventually separated, this could have resulted in one more speciation event, which would place North African species in a much more derived position on the tree. In this case, a single ancestral area in South Africa would be inferred, even though vicariance would also be consistent with the topology. Second, if the initial area cladogram was ((S1, N1), ((S2, N2), (S3, N3))) and extinction occurred in N1 and N2, this would generate the current area cladogram (S1, (S2, (S3, N))).

How likely is the hypothesis that *Androcymbium* had a pan-African distribution in the geological past? Diverse palaeobotanical data suggest that southern Africa (including Zaire) was dominated by dry and at times even totally arid conditions since before the

Miocene (Maley, 1980). The uniformity of arid conditions in this area must have permitted the origin of a xerophytic flora, which was first hypothesized by Christ (Quézel, 1978) and named the "Rand Flora" by Lebrun (1947). Although many taxonomic uncertainties remain regarding the Rand Flora, it is likely that it was widespread in the southern part of Africa in the Eocene and expanded into the Namibian desert, which is estimated to have originated within the early Oligocene (Van Zinderen Bakker, 1975). During the Oligocene–Miocene, the displacement of the equator southwards coincided with the stabilization of climates and the establishment of the different types of vegetation in southern Africa (Axelrod & Raven, 1978).

In contrast, northern Africa was occupied by a subtropical woodland savanna with a sclerophyllous evergreen forest in the area of the present Mediterranean region until the late Miocene (Quézel, 1978; Maley, 1980). Although aridification of central and meridional Sahara was only episodic in the late Miocene–early Pliocene (Berggren & van Couvering, 1974), the appearance of considerable relief in this period (Quézel, 1978) should have multiplied biotypes favourable to the expansion of a xerophytic flora. During the Pliocene, the accentuated increase in moisture south of the Sahara established a latitudinal climatic gradient (Monod, 1957). The acquisition of typically desert climatic features north of this area probably began at least 5–6 Mya and increased up to the first pluvial phases of the Pleistocene (Quézel, 1978). The southern Sahara, however, was predominantly linked to the inter-tropical front rain regimes. This climatic contrast led Monod (1957) to suggest the existence of two Saharas: a palaeoartic one (in the north) and a palaeotropical one (in the south). Although it is not clear when the arid track (Fig. 1) connecting the Sahara–Arabian and the Namibian deserts was first established, there is no reason why it could not have existed as a continuous area during the later Miocene and Pliocene.

This palaeobotanical context and our divergence time estimates (Fig. 2) provide a valuable background to discuss the diversification of *Androcymbium* in Africa. However, it is important to keep in mind that chronological predictions for *Androcymbium* must be interpreted with caution, because our estimates of divergence times are based on a single molecular marker. Furthermore, we do not know whether the speciation events were directly related to the historical events being considered. Biological and geological hypotheses have been termed 'reciprocal illuminators' (Rosen, 1978) because they enhance but do not test one another. In the context of *Androcymbium*, this means that we cannot use the palaeobotanical evidence to assess the validity of the molecular clock based on cpDNA restriction site data. Yet, considering that the species of *Androcymbium* are closely related and do not exhibit differences in growth habit, our divergence time estimates can be used confidently to exclude some unlikely biogeographical scenarios. Rates of evolution among species with similar metabolic rates and generation times are likely to be stable (Li, 1993).

The cpDNA data indicate that the ancestor of the North African species (node h in Fig. 2) dates back to 12.1 ± 2.8 Mya, suggesting that *Androcymbium* may have already extended considerably north (maybe to Kenya and Tanzania) in the mid-late Miocene. Palaeobotanical evidence indicate that it is unlikely that the colonization of the northern quarter of Africa started earlier than the late Miocene, when the incipient aridification of the Sahara began to settle biotypes favourable to the expansion of a xerophytic flora. Our divergence time estimates support this interpretation by framing the expansion of *Androcymbium* into mainland North Africa (nodes i–k in Fig. 2) between 11.7 ± 2.1 Mya (common ancestor of *A. gramineum* and *A. palaestinum*) and 5.8 ± 0.2 Mya (ancestor of the Canary Island species).

The most parsimonious hypothesis based on biogeographical, karyological, and cpDNA data suggests that *Androcymbium* originated in southern Africa in the mid-late Eocene (Fig. 2) or earlier. Diversification in this area was probably aided by the antiquity of the edaphic mosaic, the arid conditions that prevailed there since the early Miocene, and the absence of catastrophic changes associated with Pliocene–Pleistocenic climatic cycles (Scott, Anderson & Anderson, 1997). In contrast, the origin of the northern distribution of the genus dates back to the late Miocene (some 12.1 ± 2.8 Mya at most) and was presumably a response to the progressive replacement of a subtropical woodland savanna with the arid landscape that gave rise to the Sahara. Although parsimony is not necessarily how patterns of geographic distribution develop in space and time, alternative explanations involving the existence of a hypothetical North African enclave of *Androcymbium* that underwent extinction prior to the late Miocene seem highly unlikely.

Disjunction dynamics

Dispersal explains disjunct patterns of distribution by dispersal across pre-existing barriers, whereas vicariance explains them by the appearance of barriers that fragments the distribution of ancestral taxa. Both vicariance (Wild, 1964) and dispersalist arguments (Linder, 1994) have been advocated to explain disjunctions between arid zones of North and South Africa. The vicariance model suggests that the group was once widespread throughout the African continent and that the current distributions must be relictual. In contrast, the dispersalists explain disjunct patterns

by invoking range enhancement through either long-range or short-range dispersal. Under this scenario, current distributions in Africa must have originated at a particular geographic centre of origin and then dispersed outward. Palaeobotanical and cpDNA divergence estimates are consistent with dispersal from Southern Africa as the primary factor in the establishment of the disjunct pattern of distribution of *Androcymbium*.

The only other study of a genus with a similar geographic distribution was of *Lotononis* (Fabaceae) (Linder *et al.*, 1992). In this genus, there is a general relationship of the Cape Floristic Region with Namaqualand, the Drakensberg, tropical Africa, and the Mediterranean basin (listed in decreasing degree of phylogenetic closeness). Linder *et al.* (1992) argued that this pattern may reflect events in the Oligocene to Pliocene, when the dessication of Africa, the establishment of strong polar gradients, and the formation of tropical deserts led to the fragmentation of the pan-African distribution of *Lotononis*. Thus, in both *Androcymbium* and *Lotononis*, it is likely that part of the distribution already existed before the arid track was established. The morphological cladogram of *Leucas* (Lamiaceae) also allowed Ryding (1998) to suggest a similar connection between the South African *L. capensis* and the northern *L. abyssinica*.

Major disjunctions on continents (when part of a repeated pattern) are usually explained by short-distance dispersal with subsequent major disruption in the geographic distribution caused by catastrophic events, either geological or climatic (Thorne, 1996). Clarification of whether *Androcymbium* fits this general pattern or if it arose as a consequence of long-range dispersal requires the sampling of the widespread *A. roseum* and the eleven taxa distributed in eastern South Africa and along the Indian coast. If long-range dispersal was a factor in the distribution of *Androcymbium* before the desiccation of Africa, then we would expect that some of the species in eastern South Africa would be much more recent than their western South African and northern African congeners. Studies of reproductive biology (Membrives, 2000) indicate that many taxa have characteristics which would be adapted for successful long distance dispersal. *Androcymbium austrocapense, A. eghimocymbion, A. poeltianum, A. cuspidatum, A. irroratum, A. albanense* subsp. *clanwilliamense* and all of the North African species are self-compatible. Some of these (*A. albanense* subsp. *clanwilliamense, A. austrocapense* and *A. poeltianum*) and other species (*A. bellum, A. circinatum, A. hantamense* and *A. walteri*) show high levels of clonal reproduction. Finally, *A. bellum* and *A. irroratum* have variable degrees of seed dormancy. These reproductive features certainly would have facilitated the establishment of even a single individual following long distance dispersal. A similar explanation was hypothesized for the disjunction of *Cienfuegosia digitata* (Malvaceae) between eastern and western Africa (Fryxell, 1967). In contrast, if progressive range expansion is the explanation for the disjunction in *Androcymbium*, then we would expect a more or less continuous trend towards increasing divergence times as we move north, with the North African species being more recent than any of the southern African lineages.

THE NORTH AFRICAN SPECIES

Although the northern quarter of the African continent is well known floristically, its complex climatic history poses many problems for historical interpretation. Because our sampling includes most of the known populations of the North African species (except for *A. rechingerii* in mainland Libya), the cpDNA phylogeny (Fig. 2) may provide important insights into the biogeographic history of *Androcymbium*'s in this region. The North African species form a monophyletic group that is divided into two moderately supported subclades (*A. rechingerii/A. psammophilum/ A.hierrense/ A.wyssianum*) and (*A. palaestinum/A. gramineum*). The basal position of *A. rechingerii* and *A. palaestinum* in their respective subclades suggests that these taxa may be older and indicates that the spread of the genus in north Africa may have initiated in the eastern Mediterranean. It is noteworthy that the relationship of *A. rechingerii* to *A. wyssianum* and the Canarian species is weakly supported. Constraining the tree so that *A. rechingerii* is sister to *A. palaestinum* and *A. gramineum* requires only two additional steps. This low level of support is most likely due to sampling. It has not been possible to sample populations of *A. rechingerii* along the coast of Libya and in mainland Greece. The only population examined is from the Greek islet of Elafonisos, certainly a peripheral location. Thus, until populations from Libya can be sampled, the phylogenetic affinities of this taxon must be interpreted with caution.

Unlike their South African congeners, the history of the North African species of *Androcymbium* may have been tightly linked to the frequent climatic shifts during the Miocene and the Pliocene–Pleistocene. Palaeobotanical data indicate that the appearance of dry seasons in North Africa was somewhat irregular during the late Miocene, stabilized in the Pliocene, and accentuated during the Pleistocene. Maley (1980) argued that the desert climate started to establish in northern Africa in the Pleistocene (at least in the lower altitudinal zones) when temperatures were decreasing in the Mediterranean region (de Lumley, 1976). Various authors (Balinsky, 1962; Van Zinderen Bakker, 1975; Wickens, 1984) suggest that the origin of the arid track connecting southern and northern Africa was

concurrent with the origin of the present vegetation of the Sahara–Arabian desert in the Pleistocene. Our divergence time estimates disagree, and indicate that *Androcymbium* must have been widespread in mainland North Africa (nodes i–l in Fig. 2) in the late Miocene (between 11.7 ± 2.1 and 5.8 ± 0.2 Mya), when the desert climate was only beginning according to palaeobotanical data. This suggests that the arid track may have existed as a more or less continuous area linking South and North Africa during this epoch.

A series of glacial periods occurred in northern Africa through the Pliocene and the Pleistocene, and it is possible that populations of *Androcymbium* south of the Sahara were extirpated by the increasing rains during this epoch. Fossil data indicate a similar pattern in *Erica arborea* (Quézel, 1978). Survival of *Androcymbium* in northern Africa during this unfavourable period may have occurred in sheltered refugia (Quézel, 1978).

The existence of prolonged interglacial periods of aridity in northern Africa during the mid-Pliocene would have been conducive to the expansion of *Androcymbium* in circummediterranean Europe. Based on allozyme data, Pedrola-Monfort & Caujapé-Castells (1995) hypothesized that the present distribution of *A. gramineum* may be due to dispersal of this species from Spain to Morocco during the Messinian desiccation of the Mediterranean basin in the late Miocene, between 7.5–5.4 Mya (Hsü, Ryan & Cita, 1973). We do not have cpDNA divergence time estimates within the clade of *A. gramineum* to evaluate this hypothesis. However, the ancestor of the Moroccan populations of this species (GRA-CA, GRA-CB and GRA-OU) arose between 6.3 ± 1.1 Mya and 5.8 ± 0.2 Mya (nodes k and l in Fig. 2, respectively). The cpDNA phylogeny shows that all the Moroccan populations of *A. gramineum* are clearly derived and the Spanish populations are basal. This supports the hypothesized ancestral condition of the Spanish distribution. Pedrola-Monfort & Caujapé-Castells (1995) argued that the Pliocene flood of the Mediterranean basin subsequent to the Messinian desiccation may have caused the establishment of the current vicariant ranges of *A. gramineum* north and south of the straits of Gibraltar.

The origin of the Canary Island species, *A. psammophilum* and *A. hierrense*, can be explained by a single colonization in the late Miocene (5.7 ± 0.2 Mya, node k in Fig. 2) from an ancestor related to the mainland *A. wyssianum*. This introduction gave rise to *A. psammophilum* in the eastern island of Fuerteventura (Fig. 2). The cpDNA evidence dates the ancestor of the populations of *A. hierrense* in the western Islands (node m in Fig. 2) at 2.7 ± 0.6 Mya and the populations in La Gomera and El Hierro at 0.95 ± 0.2 Mya (node o in Fig. 2). There is substantial agreement between our divergence time estimates and the geological ages of the Canary Islands (Carracedo, 1994, 1996). The geologic ages are 21 Mya for Fuerteventura, 12.5 Mya for La Gomera, 2 Mya for La Palma, and 0.8 Mya for El Hierro. The population of *Androcymbium* from La Gomera is more recent than the one from La Palma, even though La Gomera is six times older. These results agree with the suggestion that some members of the endemic flora of the Canary Islands are relictual and related to the Mediterranean Tethyan–Tertiary Flora and the xerophytic flora from the east and south of Africa (Bramwell, 1976, 1990).

The distribution of the continental species of *Androcymbium* was disrupted considerably by the climatic upheavals in North Africa during the late Pliocene, especially the last glaciations in the Pleistocene (Maley, 1980). The most recent ancestor of the mainland species *A. wyssianum* (node n in Fig. 2, 2.6 ± 0.5 Mya) is approximately twice as young than that of the Canarian taxa (node l in Fig. 2, 5.8 ± 0.2 Mya). If the common ancestor of *A. wyssianum* and the Canarian species (node k in Fig. 2) was of continental origin and survived the Pliocene–Pleistocenic glaciations in sheltered refugia, then the distribution of *A. wyssianum* may have expanded from these refugia. In contrast, if that common ancestor went extinct in North Africa, then *A. wyssianum* may have originated via colonization from the Canary Islands. The hypothesis that the common ancestor of *A. wyssianum* and the Canarian species was from the Canary Islands is also plausible, although it involves one more dispersal event on the cpDNA phylogeny (Fig. 2). There are two other groups in which molecular phylogenies suggest that Canarian species are basal to continental taxa (*Lavatera*, Ray, 1995 in the Malvaceae and *Aeonium*, Mes, van Brederode & Hart, 1996 in the Crassulaceae). If this was the case for *Androcymbium*, a colonization from the Canaries to mainland Africa in the mid–late Pliocene is the more likely explanation for the present distribution of *A. wyssianum*.

CONCLUSIONS

The biogeographical interpretation of the cpDNA phylogeny of *Androcymbium* indicates that the disjunction between South and North Africa is best explained by the dispersal of southern African ancestors into North Africa. The combination of divergence time estimates, geological, and palaeobotanical evidence strongly suggests that the distribution of the genus may have extended considerably north previous to the global desiccation of Africa in the Miocene and the establishment of the arid track. Until the late Miocene, the existence of a woodland savanna in the region now occupied by the Sahara prevented the spread of the genus northward. Further establishment of the genus

in North Africa was probably affected by two opposing influences. First, the gradual desiccation that started in the late Miocene provided arid conditions that could facilitate expansion along the European and African Mediterranean fringe (probably east to west) during interglacial periods and introduction of the genus in the Canaries. Second, Pliocene–Pleistocene glaciations may have restricted a widespread mainland North African distribution of *Androcymbium* to a few refugia. The genus may have dispersed from these refugia when climatic conditions became more stable. An important implication of our divergence time estimates for the northern range is that the arid area known as the arid track may have already existed as a corridor linking South and North of Africa in the late Miocene.

According to Popper's concept of testability (Popper, 1972), this hypothesis can be corroborated or refuted by the addition of new data on *Androcymbium* and by evaluating the feasibility of the proposed dispersal scenario with other groups of taxa exhibiting the same geographic distribution. Our results suggest two future lines of research in *Androcymbium*. First, the sampling of *A. roseum* and of the eleven species from eastern South Africa, Kenya and Tanzania should be expanded. These samples may be critical for understanding whether the eastern African distribution range of the genus also existed previous to the settlement of the arid track or whether it arose afterwards, once the North African and southeastern African species began diversifying. Second, an assessment of the phylogenetic relationships using a nuclear DNA region is needed. This would result in independent divergence time estimates and provide a second molecular data set for assessing relationships among the species, especially the connections between the Middle-eastern taxa and the northwestern *A. gramineum* and *A. wyssianum*, and the relationship between *A. wyssianum* and the Canarian species.

Our cpDNA survey of *Androcymbium* represents the first molecular data that substantiate a causal explanation of the distribution of a genus in the arid track. The only other thorough assessment of a group whose distribution spans the arid track was in the genus *Lotononis* (Fabaceae) using morphological data (Linder *et al.*, 1992). These authors did not consider directionality along the track, but their results agree with ours in the interpretation that the distribution of these genera was widespread in the past and was fragmented after the desiccation of the African continent in the Miocene to Pliocene (Linder *et al.*, 1992). However, agreement of biogeographic patterns, tracks or range disjunctions does not guarantee that two or more taxa have similar biogeographic histories (Thorne, 1996). There are many other taxa that are either disjunct between North and South Africa (De Winter, 1971) or exhibit a more or less continuous distribution along the arid track (e.g. *Echium–Lobostemon–Echyostachys* complex or the genera *Olea* and *Micromeria*). Molecular and morphological studies for these groups would enable the testing of the general validity of the hypotheses proposed in this paper for *Androcymbium*. A thorough understanding of the significance of the arid track is needed to explain the distribution of many organisms in Africa.

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