

**BOOMERANGS OF BIODIVERSITY?: THE INTERCHANGE OF
BIODIVERSITY BETWEEN MAINLAND NORTH AFRICA AND THE
CANARY ISLANDS AS INFERRED FROM cpDNA RFLPs IN GENUS
ANDROCYMBIUM.**

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Palabras clave: *Androcymbium*, RFLPs de cpDNA, Islas Canarias, Africa, efecto boomerang, biogeografía

SUMMARY

Chloroplast DNA (cpDNA) restriction site (RFLP) data for 29 populations representing the distribution of *Androcymbium* in the Northern quarter of Africa were used to discuss the probable phylogeographical relationships of the two Canarian species (*A. psammophilum* and *A. hierrense*) with their closest extant mainland congener *A. wyssianum*. Although the topology of relationships obtained clearly points out that the origin of *A. psammophilum* and *A. hierrense* is best explained by a single colonization from a mainland ancestor in the eastern islands, our data cannot resolve among a Canarian or a mainland origin of the continental *A. wyssianum*. While a strictly parsimonious interpretation of the topology would favour the scenario that *A. wyssianum* derives from a mainland ancestor that may have survived the glaciations in refugia, the alternative of a Canarian origin of *A. wyssianum* is bolstered by two pieces of evidence. First, divergence time estimates show that the Canarian circumscription of *Androcymbium* originated some 5.8 ± 0.2 mya, more than twofold earlier than the estimated origin of *A. wyssianum* (2.6 ± 0.5 mya). Second, the topology of the clade of *A. wyssianum* places the Easternmost populations in a clearly derived position, thereby suggesting a settlement in a West-East sense. The hypothesis of a Canarian origin of the mainland *A. wyssianum* would entail a boomerang effect, whereby one lineage (the common mainland ancestor of the Canarian *Androcymbium* species) abandoned a climatically deteriorated area (Pliocene mainland North Africa) to found a population in a climatic refuge (the Canaries), from where a further founder event succeeded to settle in the mainland area of departure when its climatic conditions became more auspicious. Although we cannot decide between the two alternatives with the sampling and data available at present, this work has set forth the basic directions to address this problem in the future.

RESUMEN

Se discuten las probables relaciones filogeográficas de las dos especies canarias de *Androcymbium* (*A. psammophilum* y *A. hierrense*) con su congénere vivo más próximo *A. wyssianum* en base a datos de sitios de restricción (RFLPs) de DNA cloroplástico (cpDNA) para 29 poblaciones que representan la distribución del género en el cuarto norte del continente africano. Aunque la topología de relaciones obtenida apunta claramente a un origen de *A. psammophilum* y *A. hierrense* a partir de un solo evento

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colonizador desde el continente a las islas orientales, los datos no pueden discriminar entre un origen Canario o continental de la especie *A. wysianum*. Mientras una interpretación parsimoniosa de la topología favorece el escenario de que *A. wysianum* deriva de un antepasado continental que podría haber sobrevivido a las glaciaciones en refugios, la alternativa de un origen canario de esta especie se apoya en dos evidencias. En primer lugar, las estimaciones de tiempos de divergencia muestran que la circunscripción canaria de *Androcymbium* se originó hace unos 5.8 ± 0.2 mya y que es unas dos veces más antigua que el origen de *A. wysianum* (2.6 ± 0.5 mya). En segundo lugar, la topología del clado de *A. wysianum* sitúa a las poblaciones del este de África en una posición claramente derivada, lo cual sugiere un sentido de colonización oeste-este. La hipótesis de un posible origen canario de la especie continental *A. wysianum* implicaría un efecto boomerang, en virtud del cual un linaje (el ancestro común de las especies canarias de *Androcymbium*) habría abandonado un área deteriorada climáticamente (el África continental del Plioceno) para fundar una población en un refugio climático (las islas Canarias) desde donde un efecto fundador ulterior re-colonizó el área continental de partida cuando sus condiciones climáticas se volvieron más apropiadas. Aunque no podemos decidir entre estas dos alternativas con los datos y las muestras disponibles en la actualidad, este trabajo ha orientado las directrices básicas para abordar este problema

INTRODUCTION

A majority of molecular phylogenetic data associated with North African plant lineages that have a representation in the Canaries reconstruct the origin of the Canarian range by invoking a single introduction of a continental ancestor (usually in the easternmost islands), followed by a East-West inter-island colonization. Although it is probable that many groups may not follow this generalized colonization trend, there is only a single exception reported to date: the genus *Lavatera* Ray (Malvaceae), whose Canarian circumscription seems to have originated via multiple introductions (FUERTES-AGUILAR *et al.*, 2002).

The role played by the African continent in the flora of Macaronesia seems clear and is well studied. Chronologically, both the estimated geological ages of the Canaries (CARRACEDO, 1994) and fossil evidence of groups that are extant in the Canaries and extinct in the Mediterranean pinpoint the Tertiary as the geological sub-era where most of the colonization events happened (BRAMWELL, 1972; PANERO *et al.*, 1999). This geographic pattern has led to the generalized conception that Macaronesia acted as a receiver, preserver and (in many cases) amplifier of part of the plant biodiversity contained in mainland North Africa at that time.

However, partly due to the recentness of some of the studied diversification phenomena (that prevents the detection of informative polymorphism in molecular phylogenetic markers) and because the final research objective is not so much to assess the post-colonization fates of the involved groups as to infer their probable origin and inter-island colonization pattern, the role of the Canarian archipelago in the floristic makeup of mainland North Africa is still poorly understood. Recently, the cases of *Aeonium* (Crassulaceae) (MORT *et al.*, 2001) and *Tolpis* (Asteraceae) (MOORE *et al.*, 2002) have furnished the first consistent evidence that there may be some groups whose mainland distribution ranges are best explained by a back-colonization from Macaronesia.

Because its distribution in North Africa is not restricted to the Canaries, the genus *Androcymbium* (Fig. 1), offers one appropriate model system to study the interchange of biodiversity between this archipelago and the mainland. In the mainland, *Androcymbium* consists of four species that distribute in Southern Spain

and the Atlantic fringe of Morocco from Casablanca to Tan-Tan (*A. gramineum* Macbride), from Tunisia across Algeria and South Morocco to the coastal fringe of Mauritania (*A. wyssianum* Beauverd & Turrettini), all through the coast of Libya and in the Greek islet of Elafonisos (*A. rechingerii* Greuter), and in the Middle East (*A. palaestinum* Baker). In the Canaries, the genus has two endemic species: *A. hierrense* A. Santos (that occurs in the western islands of La Palma, El Hierro, and La Gomera), and *A. psammophilum* Svent. (in the eastern islands of Lanzarote and Fuerteventura).

Despite this apparent uniformity, the taxonomic relationships between the Canarian *Androcymbium* and their continental congeners have stirred considerable controversies ever since (BRAMWELL, 1976; KUNKEL, 1977; PEDROLA-MONFORT & CAUJAPÉ-CASTELLS, 1994, 1996). As discussed elsewhere (CAUJAPÉ-CASTELLS *et al.*, 1999), the taxonomic debate around northern African *Androcymbium* is undoubtedly linked to the absence of consistent morphological characters on which to base specific ascription. However, it is probable that this lack of consensus also reflects the complex vegetation history of the Northern quarter of Africa and the vagaries of biodiversity interchange between the mainland and the Canaries during the Plio-Pleistocene glaciations.

My objective in this paper is to use geographic distribution and chloroplast DNA (cpDNA) restriction site (RFLP) data (CAUJAPÉ-CASTELLS *et al.*, 1999, 2001) to discuss the probable phylogeographical relationships of the two Canarian species of *Androcymbium* with their closest extant mainland congener *A. wyssianum*.

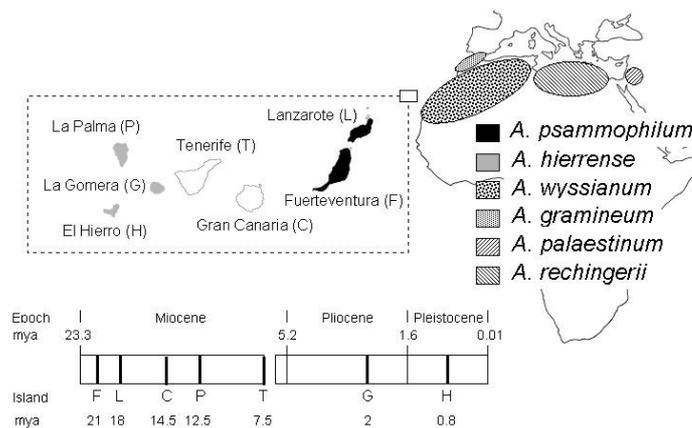


Figure 1.- Geographical distribution of the Northern African *Androcymbium* species and geological chronology with the respective estimated ages (in mya) of the Canary Islands according to CARRACEDO (1994).

MATERIAL AND METHODS

We will consider 29 populations of *Androcymbium* (Table 1) representing the geographic distribution of the mainland North African species *A. wyssianum* (9 populations), *A. gramineum* (13 populations), *A. rechingerii* (1 population), *A. palaestinum* (2 populations), and the Canarian endemics *A. hierrense* (3 populations) and *A. psammophilum* (1 population). DNA isolation, digestion with 21 restriction endonucleases, and filter hybridizations with *Oncidium excavatum* Lindl. (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 two populations of *Colchicum lusitanum* Brot. and one population of *Merendera pyrenaica* Auct. ex Steud as outgroups.

The g_1 statistic (HILLIS & HUELSENBECK, 1992) was calculated for 100,000 random trees to evaluate the amount of phylogenetic signal in the data. Parsimony analyses were performed using branch-and-bound searches with MULPARS and furthest addition sequence using Wagner (FARRIS, 1970) parsimony in PAUP* version 3.1.1 (SWOFFORD, 1998). Bootstrap values (FELSENSTEIN, 1985) were obtained from 100 branch-and-bound replicates.

Two-tailed Wilcoxon matched-pair signed rank tests (TEMPLETON, 1983) involving six independent branches in the consensus tree were carried out to test whether differences in rates of cpDNA evolution were significant. The amount of sequence divergence between selected pairwise combinations of populations was estimated following NEI & LI (1979). Divergence time estimates were derived from these values through computing the average value between a slow (0.07%) and a fast (0.1%) average divergence rate per million years, following PARKS & WENDEL (1990) and WENDEL & ALBERT (1992). We assessed the temporal sequence of diversification of the Canarian *Androcymbium* and *A. wyssianum* in five nodes that correspond to their common ancestor, to the origin of the Canarian circumscription of the genus, to the origin of *A. wyssianum*, and to two further diversification events in the islands.

RESULTS

The g_1 statistic for 100,000 randomly generated trees was -2.136 , indicating that the data are skewed significantly from random ($P < 0.01$ for $g_1 = 500$ characters and ≥ 25 taxa); therefore, they contain considerable phylogenetic signal (HILLIS & HUELSENBECK, 1992). Parsimony analysis produced 30 equally parsimonious trees of 375 steps with a consistency index (CI) of 0.779, a homoplasy index (HI) of 0.221 and a retention index (RI) of 0.928 (excluding uninformative characters). The tree shown in Fig. 2 summarizes the phylogenetic relationships among the analysed populations based on cpDNA restriction site changes. Parsimony searches for the Canarian taxa and *A. wyssianum* generated 3 most parsimonious trees of 273 steps with a consistency index (CI) of 0.849, a homoplasy index (HI) of 0.151 and a retention index (RI) of 0.915 (excluding uninformative characters). In both analyses, the Ca-

Species/population	Code	Geographical area
CANARIAN POPULATIONS		
<i>A. psammophilum</i>		
Fuerteventura	FU	Eastern Canary Islands
<i>A. hierrense</i>		
La Gomera	GO	Western Canary Islands
La Palma	LP	Western Canary Islands
El Hierro	HI	Western Canary Islands
MAINLAND POPULATIONS		
<i>A. wyssianum</i>		
Ain Ouarka	AO	Algeria
Igli	IG	Algeria
Road from Taghit to Igli	TI	Algeria
Nefta 1	N1	Tunisia
Nefta 2	N2	Tunisia
Fonts Bleu de Meski	FB	South of Morocco
Road to Fonts Bleu de Meski	CF	South of Morocco
Er Rachidia	ER	South of Morocco
Erfoud	EF	South of Morocco
<i>A. gramineum</i>		
Los Molinos	LM	Almería (S of Spain)
Cortijar de Charco del lobo	CH	Almería (S of Spain)
Cerro de los lobos	CL	Almería (S of Spain)
Playa de Mónsul	PM	Almería (S of Spain)
Barranco de Curriá	BC	Almería (S of Spain)
El Barranquete	EB	Almería (S of Spain)
El Solanillo	ES	Almería (S of Spain)
Cerro de los peligros	CP	Almería (S of Spain)
Cerro de San Cristobal	CS	Almería (S of Spain)
Aïn Harrouda	AH	South of Morocco
Casablanca	CA	South of Morocco
Oualidia	OU	South of Morocco
Cap Beddouza	CB	South of Morocco
<i>A. palaestinum</i>		
Beit Shean	BS	Israel
Dimona Desert	DI	Israel
<i>A. rechingerii</i>		
Elafonisos	EL	Greece

Table 1.- Sampling details of the 29 populations of *Androcymbium* used in this study. Voucher specimens are deposited in the herbarium of the Marimurtra Botanical Garden.

narian taxa and the mainland *A. wyssianum* are grouped in two consistent sister sub-clades (supported by bootstrap values higher than 80%) that belong within a single clade holding maximum bootstrap support.

A molecular clock was not rejected in any of the 15 pair-wise comparisons involving six populations selected from independent branches of the clade of *A. wyssianum* and the Canarian species (Table 2). Therefore, it is safe to assume that molecular change has proceeded at the same rate for these populations.

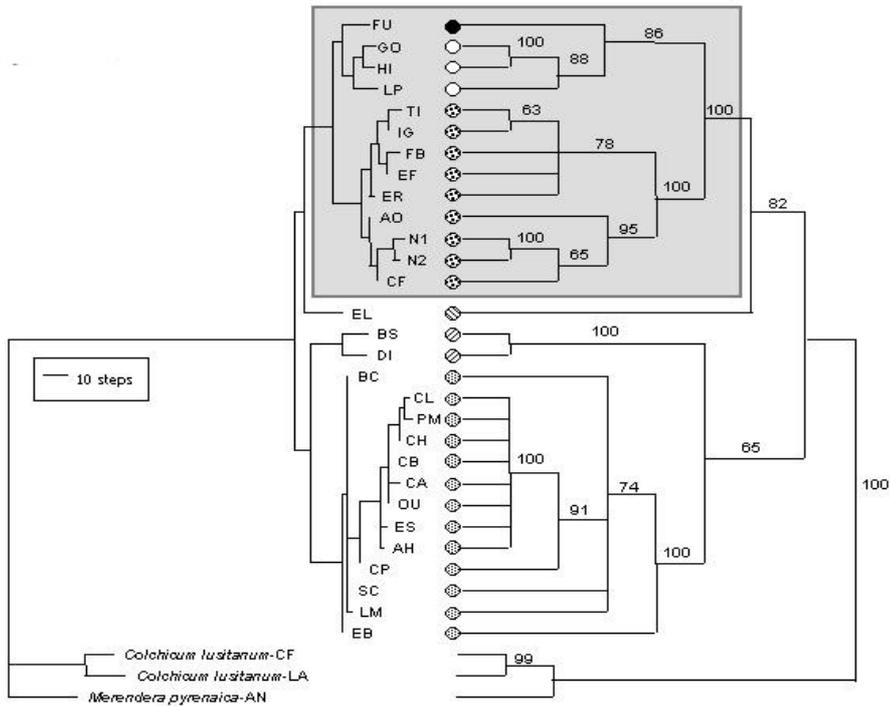


Figure 2.- Phylogram of one of 30 most parsimonious trees for the North African *Androcymbium* species (left) and strict consensus (right) with bootstrap values above the branches. The length gauge refers to the phylogram. The shadowed clade is the one that contains the populations of the Canarian taxa and *A. wyssianum*. Circle fillings are those used to label the distribution areas of these species in Fig. 1.

	1	2	3	4	5	6
1. FU	---					
2. LP	0.511	---				
3. GO	0.540	0.235	---			
4. HI	0.620	0.196	0.078	---		
5. N2	0.499	0.394	0.395	0.502	---	
6. FB	0.604	0.525	0.567	0.634	0.195	---

Table 2.- Sequence divergence values used to calculate divergence times at the five selected nodes of the phylogenetic tree. None of these 15 population pairs showed significant deviations from the hypothesis of a uniform molecular clock according to a Wilcoxon matched-pair signed rank test (TEMPLETON 1983). Population codes are those in Table 1.

The divergence times obtained from the sequence divergence values estimated the age of the common ancestor of the Canarian taxa and *A. wyssianum* (node 'a' in Fig. 3) at 6.3 ± 1.1 mya (late Miocene). The age of the more recent ancestor of the Canarian taxa was placed at the late Miocene-early Pliocene, roughly twofold that of the widespread mainland taxon *A. wyssianum*, which corresponds to the mid-late Pliocene (node 'd' in Fig. 3, 2.6 ± 0.5 mya). According to these estimates, inter-island colonization to the western Canary Islands dates back to the end of the Pliocene and the mid-Pleistocene (nodes 'c' and 'e', 2.7 ± 0.6 mya and 0.95 ± 0.2 mya, respectively).

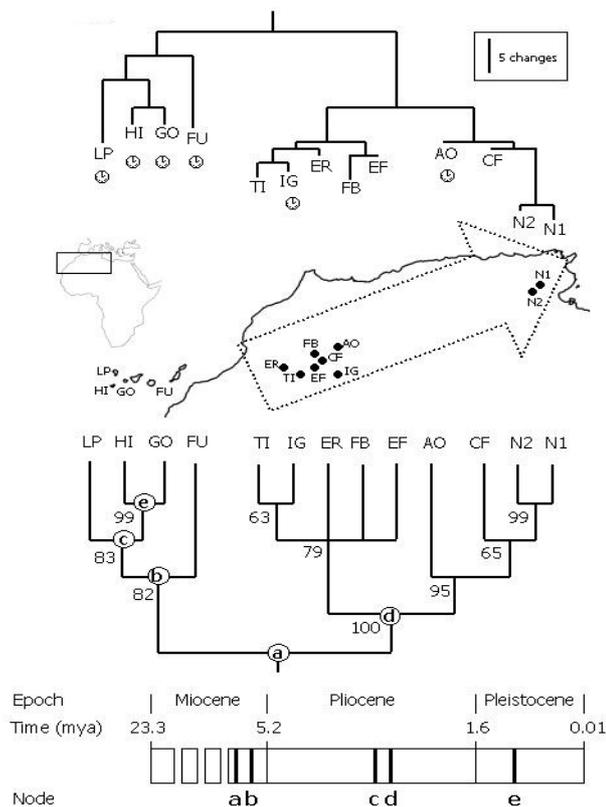


Figure 3.- Phylogram of one of the three most parsimonious trees for the populations of *A. psammophilum*, *A. hierrense* and *A. wyssianum* (above), map with the geographical distribution of populations (middle), and strict consensus tree with the estimated chronology of five nodes (below) (outgroups have been omitted). A watch below the population codes in the phylogram indicates that the corresponding population was used to test the hypothesis of a uniform molecular clock. Numbers to the left of the branches in the consensus tree are bootstrap support. The discontinuous arrow in the map indicates the hypothesized sense of *A. wyssianum*'s settlement as suggested by the topology and the chronology. Population codes correspond to Table 1.

DISCUSSION

The obtained topology of relationships for North African *Androcymbium* (Fig. 2) clearly points out that the origin of *A. psammophilum* and *A. hierrense* is best explained by a single colonization from a mainland ancestor also related to *A. wyssianum* that gave rise to *A. psammophilum* in the eastern islands. Subsequent inter-island colonization and differentiation westwards originated the populations of *A. hierrense* in the western islands of El Hierro, La Gomera and La Palma. This evidence refutes BRAMWELL'S (1976) and KUNKEL'S (1977) hypothesis with regard to the relationships between these Canarian species and their mainland congeners (these authors considered *A. psammophilum* closer to *A. gramineum* than to *A. wyssianum*), but is in agreement with their interpretation of the origin of the Canarian taxa via a single colonization event. Contrary-wise, the cpDNA data do not support PEDROLA-MONFORT & CAUJAPÉ-CASTELLS (1996) hypothesis of a double colonization of the Canaries from an ancestor related to *A. wyssianum*, but they do agree with a closer phylogenetic relatedness of *A. psammophilum* to this mainland taxon than to *A. gramineum*, as argued by these authors.

Single colonizations of the islands are the commonest pattern inferred from molecular phylogenies, and have also been inferred in the *Sonchus* L. alliance (KIM *et al.* 1996) and the genera *Argyranthemum* Sch. Bip. (FRANCISCO-ORTEGA *et al.*, 1997), *Bencomia* Webb & Berthel. (HELFGOTT *et al.*, 2000), or *Sideritis* L. (BARBER *et al.*, 2000). Only in a single instance have Canarian taxa been found to be the most likely result of multiple colonizations from the continent: *Lavatera* L. (Malvaceae) (FUERTES-AGUILAR *et al.*, 2002). However, it is certainly possible that the number of cases of multiple introductions grow as more molecular studies are conducted with other groups with a representation in the Canaries.

Although a single founder event suffices to construe the presence of the genus in the Canaries, a point of significant concern is the absence of populations of *Androcymbium* in Tenerife and Gran Canaria. This distributional gap is still more striking if we consider that these two islands have, respectively, the largest and the third largest physical areas in the archipelago, they are among the older ones (see Fig. 1), they are much closer to the eastern islands and to the mainland than the westernmost La Palma, El Hierro or La Gomera, and hold suitable ecological conditions to host xeric species like *Androcymbium*.

It is possible that the inter-island colonization sequence that explains the Canarian distribution of *Androcymbium* bypassed Gran Canaria and Tenerife or that floristic ignorance prevented us from including samples from these islands. However, it is also feasible that extinction played a significant role in generating this pattern. Gran Canaria underwent two volcanic ordeals subsequent to its origin some 14.5 mya: the sink and subsequent formation of the Caldera de Tejeda (ca. 14 mya) and the origin of the Roque Nublo volcano some 3-3.5 mya (PÉREZ-TORRADO, 1997). Following the estimates in MARRERO & FRANCISCO-ORTEGA (2001), if these events took place today, they would provoke the extinction of 80% and 50% of this island's flora, respectively.

In Tenerife, a period of substantial geological instability started about 3 mya that restructured the morphological facies of the island. Although it is still unclear whether this episode was related to outbursts of high explosivity (MARTÍ *et al.*, 1996) or caused by giant avalanches of lava (CARRACEDO, 1994), one of its consequences is bound to have been the extinction of a large contingent of the island's biodiversity. In the light of our time estimates (Fig. 3) it is possible that, if *Androcymbium* was present in these islands at the early Pliocene, it might have been extirpated by the action of the volcanic upheavals that took place in Gran Canaria and Tenerife at this epoch.

Can the RFLP data provide a hypothesis on the ancestor-descendant relationship between *A. wyssianum* and the Canarian species? The climatic stability in the northern quarter of mainland Africa was radically disrupted from the early Pliocene on (MONOD, 1957), and many of the constituents of its plant biodiversity were extirpated by the action of the glaciations that followed upon each other until the late Pleistocene (QUÉZEL, 1978). Although the influence of these recurrent climatic shifts sets forth important difficulties for historical reconstruction in *Androcymbium*, our molecular data may conform to two general historical settings.

Historical setting 1) Canarian origin of *A. wyssianum*. The boomerangs of biodiversity.

Paleobotanical and palinological evidence (LEBRUN, 1947; MALEY, 1980) bolster the hypothesis that the geographic situation of the Macaronesian archipelago sheltered its constituent islands from the climatic shifts underwent by mainland North Africa during the Pliocene and Pleistocene. Because of this fact and of their closer geographic proximity to the mainland than the Azores or Madeira, the Canaries are clearly the most important historical reservoir of part of the biodiversity contained in North Africa previous to the glaciations.

Under the historical setting of a Canarian origin of the mainland *A. wyssianum* (that we will refer to as *Hypothesis a*), the mainland ancestor of the Canarian taxa (node 'a' in Fig. 3) might have died off during the Plio-Pleistocene climatic events (once the Canarian circumscription of the genus was already founded), and then a back-colonization from the Canaries could have given rise to *A. wyssianum*, as schematised in Fig. 4a.

Arguably, this hypothesis is not the most parsimonious, as it would require one extra dispersal event respect to the topologically more plausible alternative of a single continental origin for both *A. wyssianum* and the Canarian taxa (see Fig. 4b and 4c and historical setting 2 below). However, it is bolstered by two pieces of evidence. First, divergence time estimates show that the closer ancestor of the Canarian taxa is almost twofold older than that of the mainland *A. wyssianum* (Fig. 3, below). Thus, a colonization from the Canaries to mainland Africa in the mid-late Pliocene is one chronologically cogent explanation for the present distribution of *A. wyssianum* (there are, however, other consistent explanations for this temporal leap, as discussed below). Second, the topology of the phylogenetic tree shows a trend toward a more derived condition of *A. wyssianum* populations Eastwards (Fig. 3, above). Thus, the extant populations closer to the Canaries are more ancient than those from Tunisia (N1 and N2), whose derived position is supported by a

100% bootstrap value (Fig 3, below). Constraining the Tunisian populations to appear in a basal position within the clade of *A. wyssianum* would require six extra steps on the most parsimonious tree (Fig. 5). Although these facts do not constitute compelling evidence (e. g., extinction in the mainland may have changed the original pattern), if the closest ancestor of *A. wyssianum* was of Canarian origin, we would have expected that the mainland populations closer to the Atlantic were more basal than those at the other extreme of the species' distribution range in the Mediterranean. This hypothesis suggests a "boomerang effect" because it entails a first founder event to the Canaries and then a back-colonization to the continent.

A back-colonization from the Canaries to explain the current distribution of *A. wyssianum* is at odds with a majority of molecular phylogenetic studies, which converge to suggest that the Canarian taxa are derived respect to their mainland congeners. However, two cases have been found where the most probable direct ancestors of extant mainland species may be of Canarian origin: the genus *Aeonium* (Crassulaceae) (MES & HART, 1996; MORT *et al.*, 2001) and the genus *Tolpis* (Asteraceae: Lactuceae) (MOORE *et al.*, 2002). In *Tolpis*, the low number of restriction site changes obtained for the Canarian species prevented MOORE *et al.* (2002) from determining with certainty whether 1), this genus colonized Macaronesia in four occasions or 2), it dispersed to Madeira from the continent and then its mainland range was re-colonized from this island after being extirpated. These authors favour the second scenario based on a minimum geographic distance reconstruction method. The case for a Macaronesian origin of the eastern African *Aeonium leucoblepharum* seems much more robust, as this species appears in a highly supported derived position within the Canarian clade of the genus (MORT *et al.*, 2001).

Historical setting 2) mainland origin of *A. wyssianum*. Survival in refugia

Despite the severe action of glaciations in reducing the Miocene floristic richness of mainland northern Africa, some of the taxa distributed in this area are known to have survived these climatic changes in sheltered refugia (QUÉZEL, 1978). As the glaciations lasted for about 100,000 years and were followed by intervals of 10,000 years of post-glacial climatic stasis (HEWITT, 1999), many of the mainland taxa that have survived until present days were probably subjected to several stages of range contractions/expansions in response to the degree of climatic severity/auspiciousness, respectively.

If *A. wyssianum* survived the glaciations in refugia, there are two alternatives to explain the topology of Fig. 3 under a continental origin of this taxon. The first one, that we will note *Hypothesis b*, is that *A. wyssianum*'s current range represents a recent geographical expansion from a mainland climatic refugium where the older populations survived (Fig. 4b). Although this possibility conflicts with our divergence time estimates (that show that the most recent ancestor of *A. wyssianum* is noticeably younger than that of the Canarian species), there are two feasible explanations for this discrepancy: (I) the older populations of *A. wyssianum* might have gone extinct recently; and (II) the older populations of *A. wyssianum* may be still extant but remain unsampled because of floristic ignorance.

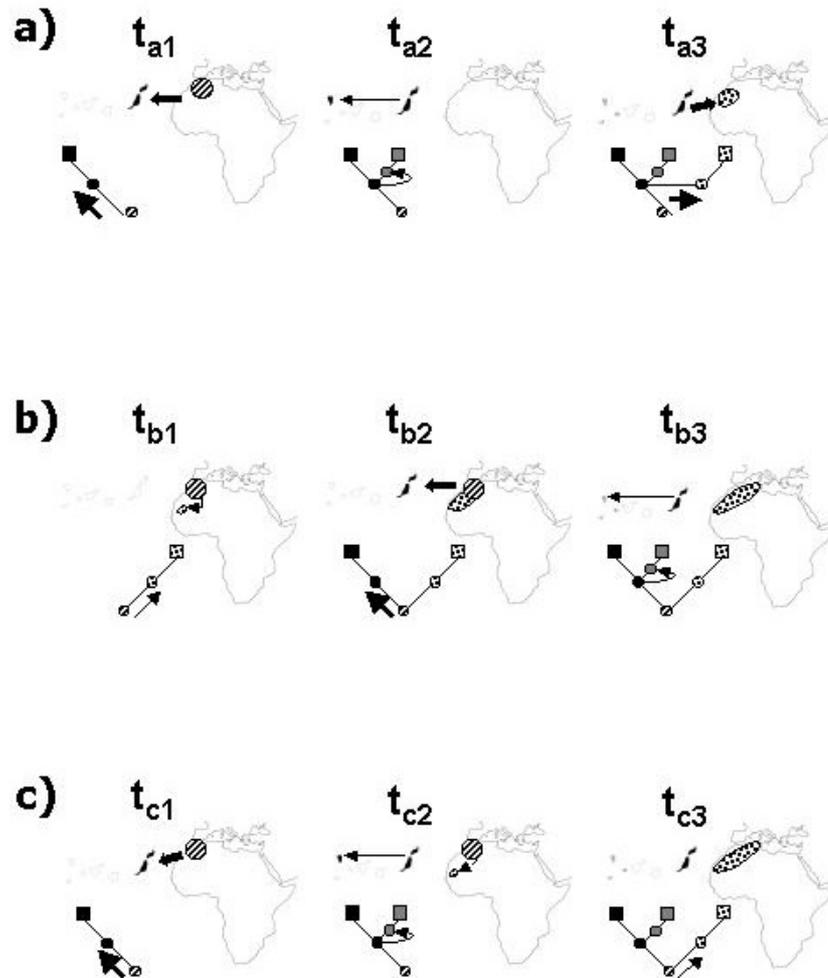


Figure 4.- Hypothetical sequence of events conducive to (a) a Canarian origin of *A. wyssianum* (historical setting 1) and to a mainland origin of this species according to Hypothesis *b* (b) and *c* (c) within historical setting 2. Circles symbolize hypothetical ancestors and squares represent current taxa (symbols correspond to those in Fig. 1). Thin arrows are hypothetical foundations among islands or within the mainland, and thick arrows stand for hypothetical island-mainland or mainland-island foundations.

The second general framework to explain the origin of *A. wyssianum* under a mainland origin (Hypothesis *c*) is that the common mainland ancestor that it shares with the Canarian species gave rise to these island taxa much earlier (Fig. 4c).

Can we decide between the two general historical settings?

According to common phylogenetic practice, the cpDNA RFLP data for the extant populations sampled would favour the scenario proposed by Hypothesis **b** or **c** better, as these are the most parsimonious options. Accepting Hypothesis **a** (i. e. the ancestor of *A. wyssianum* was Canarian) would require one extra dispersal event from the islands to the mainland. However, the lesser conformance to parsimony criteria is insufficient to rule out Hypothesis **a**, as there is no way to test whether evolution proceeded parsimoniously. Given an adequate data set, parsimony offers an important criterion for the selection of hypotheses only in exchange for not allowing us to test it. Thus, we must conclude that the concerns raised by Historical setting 1 relate more to its untestability than to the intrinsic explanatory virtues of its alternative.

Epistemological nuances notwithstanding, there are important factors that stand in the way of a proper discrimination among these two sets of hypotheses. In the case of historical setting 1, the principal problem is that we cannot survey the populations of *Androcymbium* that might have died off because of the glaciations or in response to other historical contingencies. Although historical setting 2 is not devoid of limitations, these are less serious. Perhaps the most important one relates to the possibility that there may be extant populations of *Androcymbium* which were not sampled for this research project because of floristic ignorance. Including eventual unsampled populations of *A. wyssianum* in a more thorough molecular survey in the future would be important to help corroborate Hypothesis **b** or **c** if we found that some of these were more ancient than their Canarian congeners.

Conversely, failing to detect such a chronological leap in a thorough sampling of *A. wyssianum* would bestow some extra credibility on Hypothesis **a**, but without allowing for its testability. Finally, although historical settings 1 and 2 have been presented separately for the sake of clarity, these possibilities are not necessarily exclusive: survival of *A. wyssianum* or its ancestor in mainland refugia should not be incompatible with a back-colonization from the Canaries to a continental area near enough to make genetic interchange possible. Although we cannot decide between the two historical settings with the sampling and data available at present, this work has set forth the basic directions to address this problem in the future.

CONCLUSIONS

The case of *Androcymbium* provides one illustration that reconstructing phylogeographical sequences from only extant plant taxa is a difficult endeavour where historical ignorance overlaps with sampling incompleteness to hinder testability and, therefore, hypothesis' choice. In *Androcymbium*, the floristic link between continental Africa and the Canaries probably originated from a mainland ancestor that colonized the Eastern Canary islands once and started an inter-island colonization wave toward the West that originated *A. psammophilum* in the western islands of Fuerteventura and Lanzarote and *A. hierrense* in the Easternmost La Palma, El Hierro and La Gomera. This colonization might have

also founded populations in Gran Canaria and Tenerife (now presumably extinct), which would likely have performed as colonization stepping stones in this dispersal process.

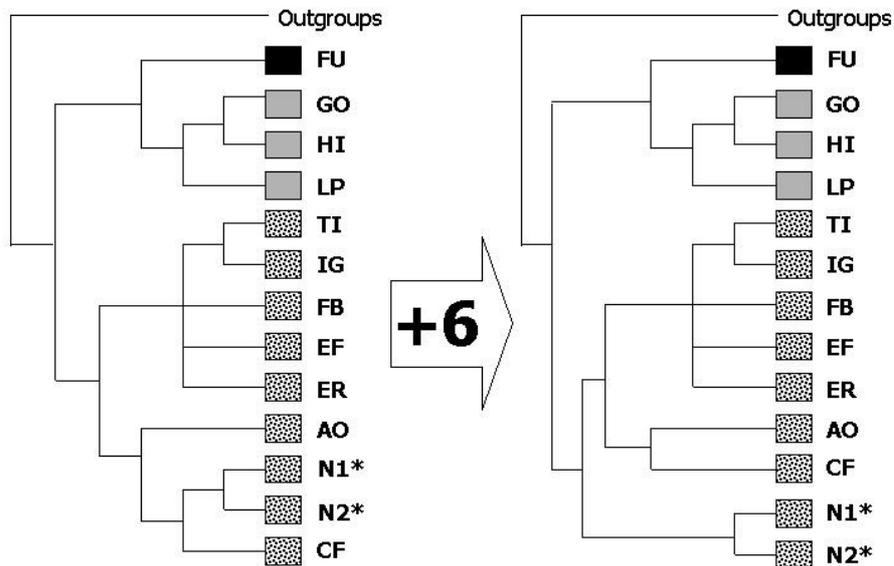


Figure 5.- Constraint of the topology of the clade of *A. wyssianum* and the Canarian taxa (left) so that the Tunisian populations of the former (labeled with an asterisk) appear basal (right) within the *A. wyssianum* sub-clade. This constraint would require six additional steps on the most parsimonious tree.

Although a strictly parsimonious interpretation of the phylogeny obtained would favour a continental origin of the widespread mainland *A. wyssianum*, there are several facts that, albeit not compelling, do lend support to the hypothesis that a back-colonization from the Canaries to mainland North Africa might have given rise to this taxon (Fig. 4a). *Androcymbium's* Hypothesis a converges with recently published evidence for other genera (MORT *et al.*, 2001; MOORE *et al.*, 2002) to suggest that the Canaries might not only have acted as receivers, preservers and enhancers of part of the continental Tertiary biodiversity, but could also have returned some of this biodiversity to the continent. The cases of *Tolpis*, *Aeonium* and *Androcymbium* suggest the concept of the boomerang effect as related to the genetics of plant diversification: a two-way founder event that starts when propagules from one donor population (A) give rise to a founded population (B) which, after a given time, acts as a donor to the area where A is (was) distributed.

In the case of Northern African *Androcymbium*, a boomerang effect could be interpreted as a strategy of conservation in time, whereby one lineage (the

common mainland ancestor of the Canarian *Androcymbium* species) abandoned a climatically deteriorated area (Pliocene mainland North Africa) to found a population in a climatic refuge (the Canaries), from where a further founder event succeeded to settle in the mainland area of departure when its climatic conditions became more auspicious. It is probable that similar biodiversity boomerangs have affected other North African plant lineages with a contingent in the Canaries, and that boomerang effects are common in other geographical contexts. In a more general framework, a diversity of population genetic entailments may follow from a boomerang effect depending on the levels of genetic variation in the population of origin, the post-colonization diversification subsequent to the first founder event, and the fate of the population of origin during the time window between the boomerang's departure and its return. These population genetic aspects will be discussed in a forthcoming paper (CAUJAPÉ-CASTELLS, in prep.).

GÖDEL'S (1931) incompleteness theorem demonstrates mathematically that all formal systems unavoidably come across a resolution threshold beyond which the correctness of theories becomes undecidable. Specifically, his proposition XI states that the consistency of any formal deductive system (if consistent!) is neither provable nor disprovable within the system. The science of phylogenetics does not escape this universal rule; rather, its tight dependance on historical contingencies (either unknown or unknowable), makes it especially prone to be affected by undecidability than totally non-historical sciences as mathematics. Phylogenetic resolution will always be smothered by historical ignorance and by the very biased sampling (in the dimensions of time, space and data sources) upon which most hypotheses are based. Of particular relevance to the discussion of whether historical setting one offers a more accurate picture of *Androcymbium*'s phylogeographic relationships, Gödel (1931) showed that there are true theories than cannot be proven.

In *Androcymbium*, obtaining phylogenies based on several independent sources of data for an enhanced geographical sampling is important to discard unlikely hypotheses regarding the relationships of its mainland and island taxa. Ongoing work in this direction (DEL HOYO, in prep.) is expected to provide new outlooks to assess the hypotheses on the diversification of the genus that have been proposed until 2004, whose molecular aspects have been addressed under my scientific (and, in the case of RFLPs, also financial) responsibility.

However, *Androcymbium* is just one case, and understanding the complexity of the relationships between island and mainland floras from the northern quarter of Africa requires the comparative study of more representative patterns of distribution that should also include plant groups that do not endemize in the islands. Although the exceptions to the mainland-to-island colonization pattern are scarce, their sole existence reveals that the role played by the Canaries in the floristic makeup of the African continent is still far from being understood. Part of the difficulty of exploring this problem with taxa that have undergone a long history of isolation in the Canaries is that their closest congeners are often unknown, either because the group has not been deeply studied or sampled (floristic ignorance) or because of the extinctions associated with the action of Plio-Pleistocene glaciations (QUÉZEL, 1978; PANERO *et al.*, 2002; HEWITT, 2001) in the biota of nearby mainland areas (historic ignorance). Maybe because of this

facts, the detection of (presumable) boomerang effects restricts to a few endemic genera for which sampling and data have been especially favourable.

The groups endemic to Macaronesia can only give incomplete evidence about a process (endemisation) that is in fact a continuous one. All in all, understanding the relationships of biodiversity interchange between the Canaries and the mainland can only be gained through the investigation of relatively modern groups, where the warping influences of a long divergence time, floristic ignorance and historical ignorance have a much minor impact. With these considerations in mind, we have initiated the investigation of genus *Matthiola* (Brassicaceae) at the molecular population genetic (SÁNCHEZ *et al.*, 2004, within project Pi 2003/032 funded by the Gobierno de Canarias) and phylogenetic (project REN 2003-07592, funded by the MCYT) levels. We expect this new model to afford meaningful insight in the study of incipient diversification in oceanic islands and provide consistent hypotheses on this extremely determinant (and altogether, sheer unknown) stage to understand the evolution and conservation of the Canarian endemic flora.

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