

Adaptive radiation and genetic differentiation in the woody *Sonchus* alliance (*Asteraceae: Sonchinae*) in the Canary Islands

SEUNG-CHUL KIM, DANIEL J. CRAWFORD, JAVIER FRANCISCO-ORTEGA, and ARNOLDO SANTOS-GUERRA

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Abstract: The woody *Sonchus* alliance consists of 19 species of *Sonchus* subg. *Dendrosonchus*, one species of *Sonchus* subg. *Sonchus* and species of five genera (i.e. *Babcockia*, *Sventenia*, *Taeckholmia*, *Lactucosonchus*, *Prenanthes*), and is restricted primarily to the archipelago of the Canaries in the Macaronesian phytogeographical region. An enzyme electrophoretic study, including 13 loci, was conducted to assess genetic diversity within and divergence among species of the alliance. Nei's genetic identities (distances) between genera and/or subgenera range from 0.490 (0.714) to 0.980 (0.013), and pairwise comparisons of all populations show relatively high genetic identities, with a mean of 0.804. The high identities further support the genetic cohesiveness of the alliance and its single origin on the Macaronesian islands. Species in the alliance also show about 50% higher total genetic diversity (H_T) than the mean for other oceanic endemics. There is greater divergence between endemics or species on older islands compared to those on younger islands, which suggests that time is a factor for divergence at allozyme loci. Furthermore, populations on older islands have higher total genetic diversities and lower identities than conspecific populations on younger islands. These results imply early colonization, radiation, and divergence of the woody *Sonchus* alliance on older islands followed by subsequent colonization to younger islands. The taxonomic distribution of alleles in the alliance indicates lineage sorting also played a role in divergence among species. Lineage sorting may also produce nonconcordance with either taxonomic designation or the pattern of variation obtained from other molecular markers such as ITS sequences of nrDNA. Timing for the origin and radiation of the alliance agrees with the estimate based on ITS sequences, and suggests that the early divergence and rapid radiation took place during the Late Tertiary on either Gran Canaria or Tenerife.

The woody *Sonchus* alliance (*Asteraceae: Sonchinae*), endemic to the Macaronesian islands, is composed of 19 species of primarily woody members of *Sonchus* (subg. *Dendrosonchus*), seven species of *Taeckholmia*, one species of subg. *Sonchus*

(*S. tuberifer*), three monotypic genera *Babcockia*, *Lactucosonchus*, *Sventenia*, and one species of *Prenanthes*, *P. pendula* (KIM & al. 1996a, b). The alliance has been regarded as an outstanding example of adaptive radiation among angiosperms in Macaronesia (ALDRIDGE 1975, 1979). These taxa are all endemic to the Canary Islands (except three species of *Dendrosonchus* in Madeira and *S. daltonii* in the Cape Verde archipelago) and display extensive morphological, ecological, and anatomical diversity (ALDRIDGE 1977, 1978). Despite this diversity, all taxa have a uniform chromosome number (i.e. $n = 9$, $2n = 18$; ARDÉVOL GONZALES & al. 1993), and the high fertility of frequent interspecific and intergeneric hybrids suggests genetic cohesiveness within the alliance (ALDRIDGE 1976, PEREZ DE PAZ 1976, HANSEN & SUNDING 1985). DNA sequence data from the internal transcribed spacer region of nuclear ribosomal DNA (ITS of nrDNA) and noncoding region of chloroplast DNA (cpDNA) suggest that the considerable morphological and ecological diversity results from a single colonization event (KIM & al. 1996a, b, 1999). These previous studies also hypothesized that the radiation of the alliance took place in the Canary Islands during the late Miocene or early Pliocene.

The Canary archipelago, where most of the alliance occurs, is located in the Atlantic Ocean and consists of seven islands (Fig. 1). These islands are of volcanic origin and form an approximately linear chain (MCDUGALL & SCHMINCKE 1976–1977, BANDA & al. 1981). In contrast to several remote archipelagos in the Pacific, such as the Hawaiian, Galapagos, and Juan Fernandez Islands, the Canaries have

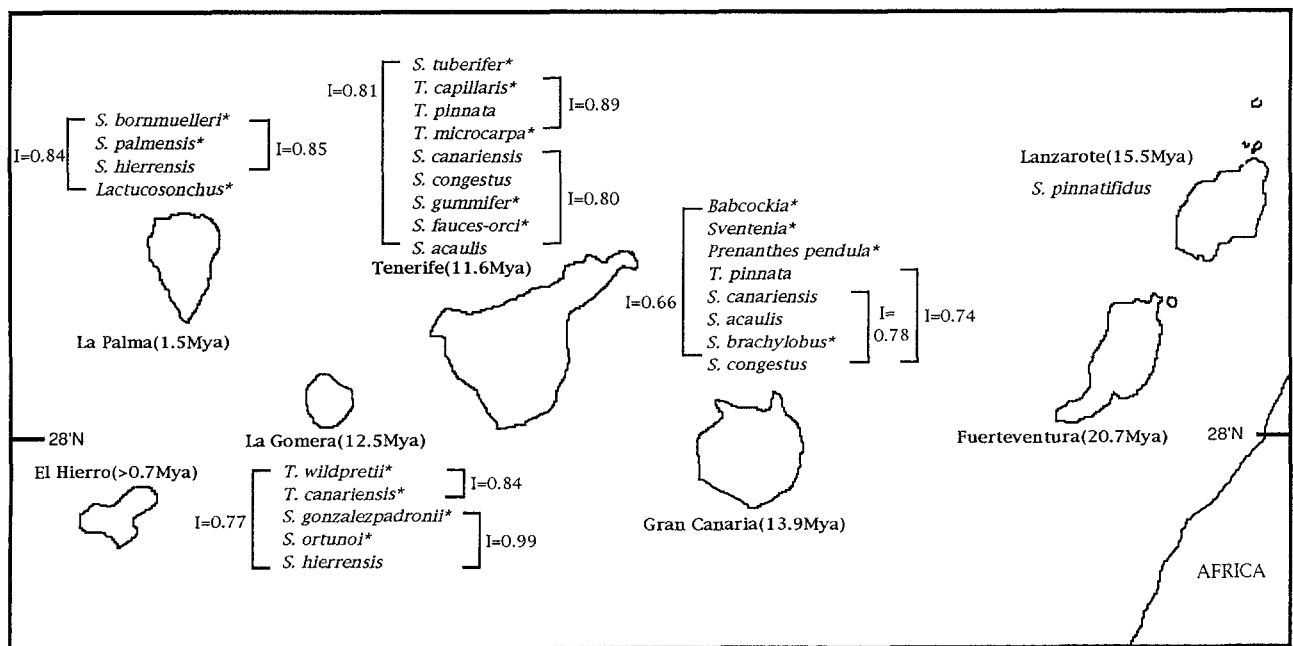


Fig. 1. The Canary archipelago and the woody *Sonchus* alliance taxa studied for isozymes. The oldest published radiometric ages from subaerial volcanoes of each island are indicated in parentheses (ABDEL-MONEN & al. 1971, 1972; MCDUGALL & SCHMINCKE 1976–1977; CANTAGREL & al. 1984; ANOCHEA & al. 1990, 1994; COELLO & al. 1992; FUSTER & al. 1993; CARRACEDO 1994). Average Nei's genetic identities are also shown in each island. Taxa with asterisk represent single island endemics

two unique features from a biogeographical perspective. The proximity of the islands to the African continent (i.e. the eastern most island, Fuerteventura, is only about 100 km distance from the west coast of Morocco) suggests that colonizers could reach the islands easily, and thus multiple introductions may have occurred for some closely related taxonomic groups. In addition, the broad range of geological ages of the archipelago, from 0.8 to 20 million years (Mya), raises the possibility that some elements of the Canarian flora are much older in origin than others (FERNANDEZ-PALACIOS & ANDERSON 1993, FUSTER & al. 1993, CARRACEDO 1994).

There are numerous studies concerning patterns of genetic variation in insular endemics from the Pacific islands using isozymes as markers: *Bidens* (HELENURM & GANDERS 1985), *Tetramolopium* (LOWREY & CRAWFORD 1985), and the silversword alliance (WITTER & CARR 1988) from the Hawaii; DENDROSERIS (CRAWFORD & al. 1987a) and *Robinsonia* (CRAWFORD & al. 1992) from the Juan Fernandez Islands; and *Gossypium* in Hawaii (WENDEL & PERCIVAL 1990) and the Galapagos (DE JOODE & WENDEL 1992). This previous work found generally low levels of genetic variation within and divergence between taxa, with the exception of certain species in the silversword alliance and *Robinsonia*. This low diversity within species may result from founder events associated with establishment of small populations in the islands. Low allozyme divergence among insular endemics has usually been attributed to the young age of most taxa (i.e. recent speciation) (HELENURM & GANDERS 1985, LOWREY & CRAWFORD 1985, CRAWFORD & al. 1987a; see also FRANKHAM 1997). These generalizations about isozymes in island plants have come almost exclusively from Pacific islands. Recent results from Macaronesia are similar in some but different in other respects from Pacific plants. For example, FRANCISCO-ORTEGA & al. (1996) found high genetic identities between taxa (average of 0.893) in *Argyranthemum* (*Asteraceae*), a result similar to many species endemic to Pacific islands. However, they detected 50% higher allozyme diversity within populations (0.098) in *Argyranthemum* than the mean total diversity ($H_T = 0.064$) for species endemic to other oceanic islands (DE JOODE & WENDEL 1992). Relatively high genetic diversity has also been reported for other Macaronesian endemics in *Avena* (*Poaceae*) (MORIKAWA & LEGGETT 1990), *Chamaecytisus* (*Fabaceae*) (FRANCISCO-ORTEGA & al. 1992), *Lolium* (*Poaceae*) (CHARMET & BALFOURIER 1994, OLIVEIRA & al. 1995), *Androcymbium* (*Colchicaceae*) (PEDROLA-MONFORT & CAUJAPE-CASTELLS 1994), *Dactylis* (*Poaceae*) (SAHUQUILLO & LUMARET 1995), *Lobularia* (*Brassicaceae*) (BORGEN 1996), and *Tolpis* (*Asteraceae*) (FRANCISCO-ORTEGA & al., unpubl.).

One purpose of the present study was to determine how the levels of isozyme variation within and divergence among species in the woody *Sonchus* alliance compare to results from other island endemics, both in the Pacific and Atlantic. Another objective of this study is to ascertain whether similarity among species at allozyme loci corresponds with proposed relationships based on morphological and ITS sequences of nrDNA.

Materials and methods

Plant material. A total of 478 plants representing 49 populations of the 22 species was examined (Table 1). All accessions, except *Sventenia*, were from wild populations. Three

Table 1. Populations and species of the woody *Sonchus* alliance studied for isozymes. Abbreviations of islands are as follows: *LA* Lanzarote, *FU* Fuerteventura, *GC* Gran Canaria, *TE* Tenerife, *GO* La Gomera, *PA* La Palma, *HI* El Hierro. *N* number of individuals per population; *species endemic to a single island

Taxon and population no.	N	Islands	Locality
<i>Babcockia platylepis</i> (WEBB) BOULOS*			
6	10	GC	Tejeda
54	10	GC	Ayacata
<i>Lactucosonchus webbii</i> (SCH. BIP.) SVEN.*			
	10	PA	San Antonio
<i>Prenanthes pendula</i> (WEBB) SCH. BIP.*			
9	10	GC	Fataga (south)
10	10	GC	Fataga (north)
<i>Sonchus</i> L.			
Subg. <i>Dendrosonchus</i> SCH. BIP. ex BOULOS			
<i>S. acaulis</i> DUM. – COURS.			
29	10	TE	Puerto de Erjos
30	9	TE	Articosa
31	9	GC	Valleseco
32	8	GC	Degollada Tasarte
<i>S. bornmuelleri</i> PITARD*			
43	12	PA	Bajamar cliffs
<i>S. brachylobus</i> WEBB & BERTH.*			
33	10	GC	Cuesta de Silva
34	7	GC	Anden Verde
119	6	GC	Cuesta de Silva
<i>S. canariensis</i> (SCH. BIP.) BOULOS			
38	18	TE	Carretera Chio-Boca
39	14	TE	Anaga
40	8	GC	Valleseco
41	8	TE	Puerto de Erjos
5	10	GC	Anden Verde
12	10	GC	San Nicolás
<i>S. congestus</i> WILLD.			
19	10	TE	Northern Free way exit 14
20	10	TE	Garachico
21	10	TE	Icod
22	5	TE	Anaga, El Bailadero
23	5	GC	Barranco de la Virgen
<i>S. fauces-orci</i> KNOCHE*			
7	10	TE	Masca
<i>S. gonzalezpadronii</i> SVENT.*			
4	10	GO	San Sebastián-Hermigua
48	5	GO	Hermigua
<i>S. gummifer</i> LINK*			
49	12	TE	Ladera de Güimar
51	8	TE	Punta de Teno
52	10	TE	Punta de Hidalgo

Table 1 (continued)

Taxon and population no.	N	Islands	Locality
<i>S. hierrensis</i> (PITARD) BOULOS			
45	15	PA	Las Cabezas
46	1	GO	La Laguna Grande
<i>S. ortunoi</i> SVENT.*			
27	6	GO	Las Rosas
28	2	GO	Puerto de Hermigua
3	10	GO	Roques de Ojila
<i>S. palmensis</i> (SCH. BIP.) BOULOS*			
24	10	PA	Franceses
25	10	PA	San Bartolomé
26	10	PA	Las Cabezas
<i>S. pinnatifidus</i> CAV.			
36	10	LA	Famara
2	10	LA	Montaña Ganada
<i>S. wildpretii</i> U. & A. REIFENBERGER*			
	10	GO	Roque de Ojila
Subg. <i>Sonchus</i> L.			
<i>S. tuberifer</i> SVENT.*	10	TE	Masca
<i>Sventenia bupleuroides</i> FONT QUER.*			
	10	GC	Jardín Canario
<i>Taeckholmia</i> BOULOS			
<i>T. canariensis</i> BOULOS*	10	GO	El Camello
<i>T. capillaris</i> (SVENT.) BOULOS*			
	10	TE	Masca
<i>T. microcarpa</i> BOULOS*	10	TE	Malpaís de Güimar
<i>T. pinnata</i> (L. f.) BOULOS			
	15	GC	Cuesta de Silva
	17	TE	El Boquerón
	42	TE	El Boquerón

species of woody *Sonchus* from Madeira and *S. daltonii* from Cape Verde archipelago were not included because very few plants were available and they were not from natural populations. Young leaves were collected from natural populations, placed on ice, and returned to the laboratory of the Ohio State University. Seeds from several capitula from individual plants were also collected separately from natural populations, germinated, and grown in the greenhouse of the Ohio State University. One progeny (about three weeks old) from each individual plant in nature was subjected to enzyme electrophoresis. Voucher specimens are deposited at the Ohio State University Herbarium (OS).

Enzyme electrophoresis. Enzymes were extracted from young fresh leaves in a cold pestle and mortar using a buffer of 0.1 M tris-HCl (pH 7.5), 14 mM 2-mercaptoethanol, 1 mM EDTA (tetrasodium salt), 10 mM MgCl₂, 10 mM KCl, and 5–10 mg polyvinylpyrrolidone per 0.5 ml of buffer (GOTTLIEB 1981a). Three enzymes, glutamate dehydrogenase (GDH, E.C. 1.4.1.2), aspartate aminotransferase (AAT, E.C. 2.6.1.1), and alcohol dehydrogenase (ADH, E.C. 1.1.1.1), were resolved in polyacrylamide gels as described by CRAWFORD & al. (1987a). The following two buffer systems were employed to separate the remaining enzymes in 12% starch gels: (1) electrode buffer of 0.5 M tris, 0.65 M boric acid,

0.02 M EDTA, pH 8.0 diluted 1:9 for the gel buffer (phosphoglucomutase, PGM, E.C. 5.4.2.2; triose-phosphate isomerase, TPI, E.C. 5.3.1.1); (2) an electrode buffer of 0.04 M citric acid adjusted to pH 6.1 with N-(3-aminopropyl)-morpholine, the gel buffer a 1:19 dilution of the electrode buffer (malate dehydrogenase, MDH, E.C. 1.1.1.37; shikimate dehydrogenase, SKD, E.C. 1.1.1.25; phosphogluconate dehydrogenase, PGD, E.C. 1.1.1.44). Staining protocols for all enzymes followed WENDEL & WEEDEN (1989).

Data analysis. The genetic bases of the banding patterns were inferred from variation reported for other plants (reviewed by WEEDEN & WENDEL 1989). These include the active subunit composition of the enzymes and the minimal number of loci for each enzyme found in diploid plants. In all instances, only loci readily interpretable were scored, and the most conservative interpretation was used.

Allelic frequencies were determined for each population, and these frequencies were used to calculate genetic identities and standard genetic distances for populations of each species, and for pairwise comparisons of the taxa (NEI 1972). Polymorphism indices and gene diversity statistics were also calculated (NEI 1973, 1987). The GeneStat-PC 3.3 (LEWIS 1993) package was used to calculate these statistics. A tree based on Nei's distance was constructed by the UPGMA (unweighted pair-group method using arithmetic averages) of the Phylip package (version 3.52c, FELSENSTEIN 1986–1993).

Results

A total of 13 loci was resolved: *Aat-1*, *Aat-2*, *Adh-1*, *Adh-2*, *Gdh*, *Mdh-1*, *Mdh-2*, *Mdh-3*, *Pgd-1*, *Pgd-2*, *Pgm-1*, *Skd*, *Tpi*. In all instances, the number of isozymes detected and scored was the same or fewer than expected for diploid plants (GOTTLIEB 1982, WEEDEN & WENDEL 1989). Additional loci were expressed for most of the enzymes but were not included because of weak activity and/or poor resolution of bands; these included one locus for LAP, two loci for IDH, and one additional locus for PGM. Two of the loci, *Mdh-1* and *Mdh-2*, were monomorphic. The number of alleles per locus varied from one for *Mdh-1* and *Mdh-2* to seven for *Pgd-2*, with an average of 3.5. A table of allelic frequencies for all populations was generated and is available from the first author upon request.

Nei's genetic identities and distances for the genera of the woody *Sonchus* alliance are shown in Table 2, and those for all conspecific populations and among all the species are available from the first author upon request. Genetic diversity

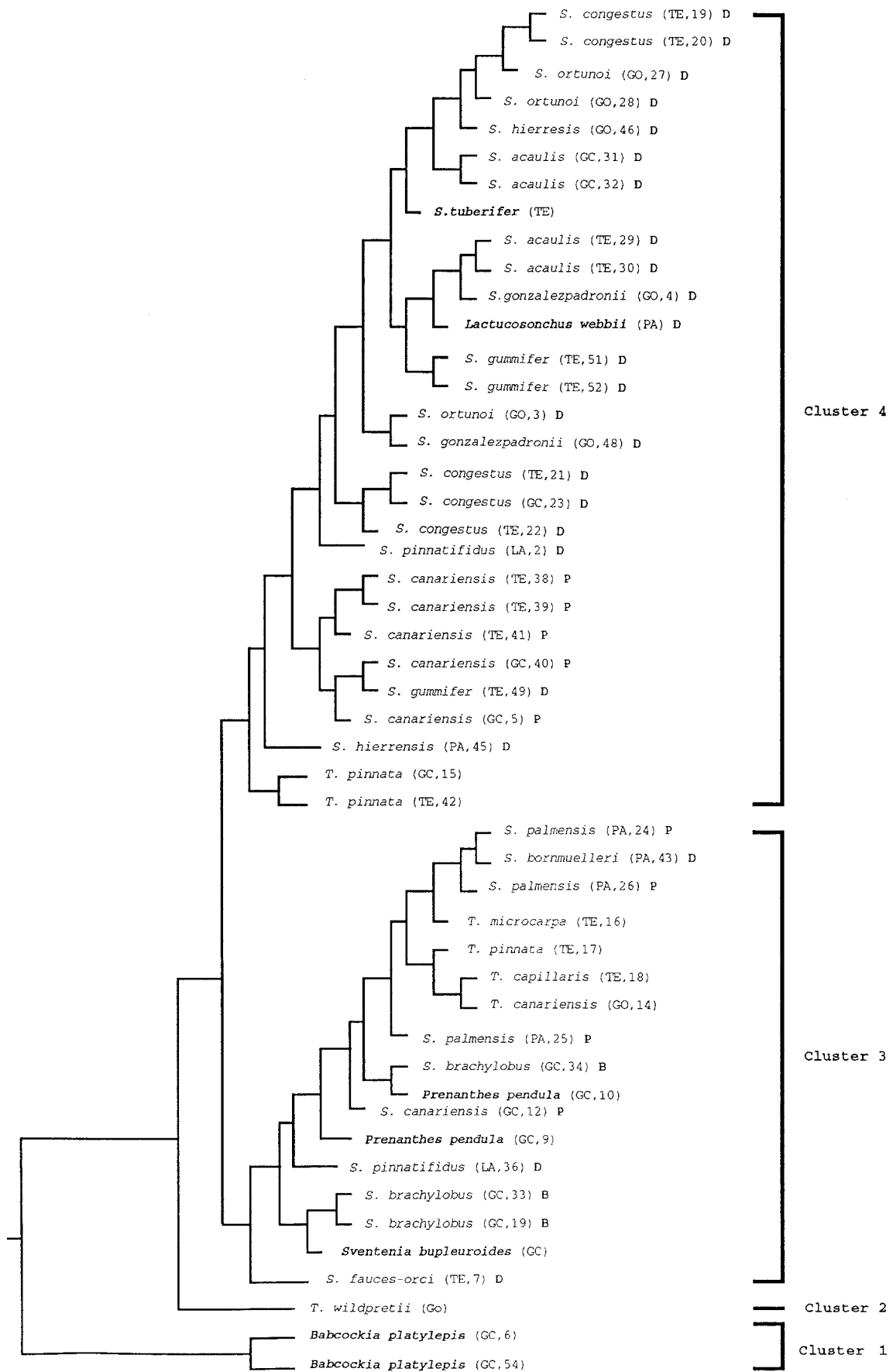
Table 2. Nei's genetic identities (upper right) and distances (lower left) for genera of the woody *Sonchus* alliance. Taxon abbreviations: *DENDR* subg. *Dendrosonchus*, *BABCO* *Babcockia platylepis*, *SVENT* *Sventenia bupleuroides*, *TUBER* *Sonchus tuberifer*, *PRENT* *Prenanthes pendula*, *LACTU* *Lactucosonchus webbia*, *TAECK* *Taekholmia*

	DENDR	BABCO	SVENT	TUBER	PRENT	LACTU	TAECK
DENDR		0.600	0.840	0.950	0.887	0.972	0.900
BABCO	0.511		0.490	0.494	0.495	0.508	0.503
SVENT	0.174	0.714		0.667	0.886	0.726	0.865
TUBER	0.054	0.706	0.405		0.711	0.988	0.745
PRENT	0.120	0.704	0.121	0.342		0.777	0.923
LACTU	0.028	0.678	0.320	0.013	0.252		0.894
TAECK	0.105	0.688	0.146	0.294	0.080	0.112	

Table 3. Gene diversity statistics for the woody *Sonchus* alliance. *N* number of populations examined; H_S diversity within populations; H_T total diversity; D_{ST} diversity among populations; G_{ST} proportion of total diversity among populations; *A* mean number of alleles per locus; A_p mean number of alleles per polymorphic locus; *P* proportion of polymorphic loci

Taxa	N	H_S	H_T	D_{ST}	G_{ST}	<i>A</i>	A_p	<i>P</i>
<i>Babcockia</i>	2	0.059	0.127	0.068	0.538	1.128	2.000	0.182
<i>Lactucosonchus</i>	1	0.051	0.051	0.000	0.000	1.250	2.000	0.250
<i>Prenanthes</i>								
<i>P. pendula</i>	2	0.057	0.079	0.021	0.271	1.300	2.000	0.300
<i>Sonchus</i> subg. <i>Dendrosonchus</i>								
<i>S. acaulis</i>	4	0.030	0.030	0.000	0.009	1.385	2.667	0.231
<i>S. bornmuelleri</i>	1	0.000	0.000	0.000	NA	1.000	NA	0.000
<i>S. brachylobus</i>	3	0.059	0.126	0.068	0.535	1.500	2.200	0.417
<i>S. canariensis</i>	6	0.028	0.092	0.064	0.696	1.417	2.000	0.417
<i>S. congestus</i>	5	0.026	0.052	0.026	0.501	1.167	2.000	0.167
<i>S. fauses-orci</i>	1	0.184	0.184	0.000	0.000	1.500	2.000	0.500
<i>S. gonzalezpadroni</i>	2	0.056	0.079	0.023	0.294	1.300	2.000	0.300
<i>S. gummifer</i>	3	0.032	0.037	0.005	0.142	1.182	2.000	0.182
<i>S. hierrensis</i>	2	0.038	0.167	0.129	0.773	1.222	2.000	0.222
<i>S. ortunoi</i>	3	0.075	0.088	0.013	0.143	1.364	2.000	0.364
<i>S. palmensis</i>	3	0.052	0.087	0.035	0.401	1.182	2.000	0.182
<i>S. pinnatifidus</i>	2	0.253	0.415	0.163	0.392	2.111	2.111	1.000
<i>S. wildpretii</i>	1	0.000	0.000	0.000	NA	1.000	NA	0.000
<i>Sonchus</i> subg. <i>Sonchus</i>								
<i>S. tuberifer</i>	1	0.047	0.047	0.000	0.000	1.111	2.000	0.111
<i>Sventenia</i>	1	0.057	0.057	0.000	0.000	1.200	2.000	0.200
<i>Taackholmia</i>								
<i>T. canariensis</i>	1	0.068	0.068	0.000	0.000	1.273	2.500	0.182
<i>T. capillaris</i>	1	0.154	0.154	0.000	0.000	1.500	2.333	0.375
<i>T. microcarpa</i>	1	0.054	0.054	0.000	0.000	1.231	2.500	0.154
<i>T. pinnata</i>	3	0.095	0.204	0.110	0.536	1.692	2.125	0.615
Means		0.067	0.100			1.321		0.289
Island endemic means (DE JOODE & WENDEL 1992)			0.064			1.32		0.25
Endemics (HAMRICK & GODT 1990)		0.063	0.096			1.80		0.40

statistics, mean number of alleles per locus and per polymorphic locus, and proportion polymorphic loci are given in Table 3. Genetic identities (distances) between genera (or subgenera) of the alliance range from 0.490 (0.714) for *Babcockia* and *Sventenia* to 0.988 (0.013) for *Lactucosonchus* and *Sonchus tuberifer* (Table 2). About 70 % of them are above 0.70, and 50 % of the pairwise comparisons are higher than 0.80. The mean genetic identity for all populations of the alliance is 0.804. Mean genetic identities (distances) for conspecific populations of each species vary from 0.778 (0.265) for *Sonchus pinnatifidus* to



1.000 (0.000) for *S. acaulis*. Pairwise comparisons of genetic identities for all populations of *Sonchus*, subg. *Dendrosonchus*, range from 0.445 to 1.000, with an average of 0.824. The genus *Taeckholmia* shows slightly higher identities, ranging from 0.600 to 0.999, with a mean of 0.846.

Total genetic diversity (H_T) within species of the entire alliance varies from 0.000 in *Sonchus bornmuelleri* and *S. wildpretii* to 0.415 in *S. pinnatifidus*, with an average of 0.100. The diversity within populations (H_S) ranges from 0.000 in *S. bornmuelleri* and *S. wildpretii* to 0.253 in *S. pinnatifidus*, with a mean value of 0.067 for the entire alliance (Table 3). The total diversity (H_T) found for all populations of subg. *Dendrosonchus* and *Taeckholmia* is 0.206 and 0.165, respectively. The total diversity found for all populations of the alliance is 0.256. The number of unique alleles (u) found in subg. *Dendrosonchus* and *Taeckholmia* was nine and three, respectively. Only one unique allele was found in the monotypic genus *Babcockia*. Both *Sonchus brachylobus* and *S. pinnatifidus* have two unique alleles, while *S. congestus* and *Taeckholmia pinnata* each have one. G_{ST} values, which indicate proportion of total diversity among populations, range from 0.009 (*S. acaulis*) to 0.773 (*S. hierrensis*).

The allozyme phenogram of all populations based on Nei's distance and the UPGMA method is shown in Fig. 2. Four major groups may be recognized. Cluster 1 contains two populations of the monotypic genus *Babcockia*, endemic to Gran Canaria, whereas cluster 2 has only *Sonchus wildpretii* from La Gomera. The large cluster 3 contains several single island endemics, including *Sonchus palmensis*, *S. bornmuelleri*, *S. brachylobus*, *S. fauces-orci*, *Taeckholmia microcarpa*, *T. canariensis*, *T. capillaris*, *Prenanthes pendula*, and monotypic genus *Sventenia*. Also, cluster 3 includes one population of *S. canariensis* from Gran Canaria, *T. pinnata* from Tenerife, and one population of *S. pinnatifidus* from Lanzarote. The largest cluster 4 consists of the monotypic genus *Lactucosonchus*, *Sonchus tuberifer* (subg. *Sonchus*), and six species of subg. *Dendrosonchus* (i.e. *S. congestus*, *S. ortunoi*, *S. hierrensis*, *S. acaulis*, *S. gonzalezpadronii*, *S. gummifer*). This cluster also includes all but one population of *S. canariensis*, two populations of *T. pinnata* from Tenerife and Gran Canaria, and one population of *S. pinnatifidus* from Lanzarote.

Discussion

The woody *Sonchus* alliance shows quite high genetic identities despite the considerable morphological and ecological diversity. The mean genetic identity for all populations, 0.804, is still substantially higher than the mean of 0.65–0.70 reported for congeneric species of flowering plants as a whole (GOTTLIEB 1981b, CRAWFORD 1990). About 70 % of pairwise comparisons of genetic identities

←
 Fig. 2. UPGMA tree based on Nei's genetic distances for populations of the woody *Sonchus* alliance included in this study. Bolded taxa represent segregate genera of woody members of *Sonchus*. Abbreviations of sectional classification of subg. *Dendrosonchus* (also in bold) are as follows: D *Dendrosonchus*, B *Brachylobi*, P *Pinnati* (BOULOS 1972). Abbreviations of islands as in Table 1

between genera (or subgenera) are above 0.70 and 50 % of them are higher than 0.80. These high values for the woody *Sonchus* alliance further support the genetic cohesiveness of the group and its single origin on the Macaronesian islands. The results are congruent with the occurrence of natural and artificially produced interspecific and intergeneric hybrids within the alliance (ALDRIDGE 1976, PEREZ DE PAZ 1976, HANSEN & SUNDING 1985). Current results are also concordant with sequence data from ITS of nrDNA and noncoding region of chloroplast DNA, suggesting that the group has diverged from a single introduction (KIM & al. 1996a, b, 1999).

In general, island plant populations are less variable genetically than mainland ones (HAMRICK & al. 1979, DE JOODE & WENDEL 1992). Several studies from the Pacific, such as *Dendroseris*, *Tetramolopium*, and *Bidens*, showed low allozyme variation (HELENURM & GANDERS 1985, LOWREY & CRAWFORD 1985, CRAWFORD & al. 1987a), and this has been attributed to genetic bottlenecks associated with long distance dispersal and subsequent establishment on islands. Within an island archipelago, additional founder events and genetic drift in small populations could likewise reduce genetic variation by loss of alleles. Furthermore, inbreeding in small populations could also be an important factor involved in keeping diversity low. Species of the woody *Sonchus* alliance in the Macaronesian islands have approximately 50 % more genetic variation than the mean for insular endemics ($H_T = 0.064$), and the mean total diversity within each species of the alliance (i.e. 0.100) is similar to that of endemics overall ($H_T = 0.096$) (see Table 3; HAMRICK & GODT 1990, DE JOODE & WENDEL 1992). The total within-species diversity in the alliance is considerably higher than in other *Compositae* from the Pacific islands, such as *Bidens* ($H_T = 0.029$) (SUN 1986) and *Tetramolopium* ($H_T = 0.006$) (LOWREY & CRAWFORD 1985), but it is only slightly higher than that of the silversword alliance ($H_T = 0.075$) (WITTER & CARR 1988). The low genetic diversity in *Bidens* and *Tetramolopium* probably results from inbreeding in small populations with highly localized distributions (LOWREY 1986, CARR & al. 1986). Some species of the silversword alliance are self-incompatible, abundant, and ecologically dominant species in their communities, thus contributing to high genetic diversity (WITTER & CARR 1988).

The high overall genetic variation in *Sonchus* compared to endemics from the Pacific islands might at first glance be attributed to the large population sizes and relatively wide geographic distributions of several species. There is not, however, a constant correlation between population size and genetic variability in the alliance. For example, *Sonchus acaulis*, which is locally frequent in Gran Canaria and widespread in forest and xerophytic zones of Tenerife, has very low variation ($H_T = 0.030$) (Table 3). In contrast, *S. canariensis*, which is rare in both Tenerife and Gran Canaria, has relatively high genetic diversity ($H_T = 0.092$). In some cases, however, species with wide geographical distributions and large population sizes have high diversity. For example, *Taeckholmia pinnata*, which is very frequent with large population sizes in Tenerife and locally frequent in Gran Canaria, has high diversity ($H_T = 0.204$). It is also likely that self-incompatibility of the woody *Sonchus* alliance promotes high genetic diversity by obligate outcrossing (ALDRIDGE 1975). Total diversity in the alliance is comparable to that of *Argyranthemum*, which is an outbreeder and the largest endemic genus in the

Macaronesian islands (CUNNEEN 1995, FRANCISCO-ORTEGA & al. 1997). FRANCISCO-ORTEGA & al. (1996) found that average allozyme diversity within populations of *Argyranthemum* (0.098) is 50% higher than the mean total diversity (all populations) for species endemic to oceanic islands (0.064), and that the average total diversity for all populations of all species of *Argyranthemum* is 0.230, which is similar to that of the woody *Sonchus* alliance (0.256). High allozyme diversities have been reported for other Macaronesian endemics from a wide range of taxonomic families (including monocots and dicots) (MORIKAWA & LEGGETT 1990; FRANCISCO-ORTEGA & al. 1992; SAHUQUILLO & LUMARET 1995; FRANCISCO-ORTEGA & al., unpubl.). It is not known what factors promote high diversities in Macaronesian endemics compared to other oceanic endemics in general. Nevertheless, the woody *Sonchus* alliance displays the same pattern of high genetic diversities which is seemingly characteristic of Macaronesian endemics. Thus, the question of why the Macaronesian endemics have higher diversity than many endemics in other oceanic archipelagos should be addressed in future studies.

Pairwise comparisons of genetic variation for conspecific populations from geologically different islands demonstrate that time could be a factor promoting genetic diversity in populations. For example, several populations of *Sonchus canariensis* from Gran Canaria (ca. 14 Mya) have higher mean genetic variation ($H_T = 0.071$) than conspecific populations from the younger island of Tenerife (ca. 11 Mya) (i.e. $H_T = 0.051$). This trend can also be seen in other species of *Sonchus*, such as *S. acaulis*, which is one of the most abundant species in the Canaries. Populations on the older island of Gran Canaria have twice as much diversity ($H_T = 0.043$) as conspecific populations on the younger island of Tenerife ($H_T = 0.021$). Furthermore, Tenerife populations of *S. acaulis* have a subset of alleles found in Gran Canaria populations at the loci *Adh-1*, *Aat-1*, and *Aat-2* suggesting that Tenerife populations were colonized by geologically older Gran Canaria populations.

The low levels of allozyme divergence among congeneric insular endemics despite morphological and ecological diversity have frequently been explained as the result of the combined effects of genetic bottlenecks associated with colonization, small population sizes, and recent speciation on the relatively young islands (HELENURM & GANDERS 1985; LOWREY & CRAWFORD 1985; CRAWFORD & al. 1987a, b). The accumulation of genetic differences between species can be explained by one or a combination of two processes: the first is the divergence in frequencies of alleles shared due to common ancestry, and the second is the accumulation of newly arisen mutations among independent lineages (WITTER & CARR 1988). The second process is presumably the slower of the two. If the ancestor(s) of insular endemics brought high allozyme diversity to the islands and little of it was lost during establishment, then divergence could occur through changes in allelic frequencies during lineage divergence and speciation. By contrast, if the ancestor carried very little allozyme diversity to the islands or it was lost subsequent to establishment, then divergence could occur only through mutation. WITTER & CARR (1988) argued that the accumulation of new mutations has been important in divergence observed at allozyme loci among species of the silversword alliance in the Hawaiian Islands because species in older islands show higher divergence, and this is what would be expected with the gradual

accumulation of mutations with time. For example, species of *Dubautia* on the oldest island of Kauai have lower genetic identities (mean of ca. 0.69) than those species on younger islands (0.95) in the archipelago. Therefore, the Hawaiian silversword alliance offers a clear illustration that allozyme divergence among genetically depauperate taxa depends on the slow accumulation of new genetic variation. However, this is not the case in the genus *Argyranthemum* in Macaronesia (FRANCISCO-ORTEGA & al. 1996). Given the much older ages of certain Macaronesian Islands compared to those in the Pacific, and their wide range of geological ages, it might be expected that some species, would be much older than others and, at least some of the taxa endemic to the older islands would be more divergent from taxa on younger islands. FRANCISCO-ORTEGA & al. (1996), however, did not find any evidence either of greater divergence between endemics on the older islands or between species on the older islands compared to those on younger islands. By contrast, the present study of *Sonchus* suggests early colonization, radiation and divergence on older islands followed by subsequent colonization to younger islands where speciation has been much more recent. For example, for those species of subg. *Dendrosonchus* sensu ALDRIDGE (including *Taeckholmia*; ALDRIDGE 1975) there is a correlation between the age of islands and genetic identities (Fig. 1). Those species endemic to the older island of Gran Canaria (ca. 14 Mya) have a mean genetic identity of 0.74, while the value is 0.77 for La Gomera (12.5 Mya), 0.81 for Tenerife (ca. 11 Mya), and 0.85 for La Palma (1.5 Mya). A similar correlation between island age and mean genetic identity is also revealed with other members of the woody *Sonchus* alliance. For example, several taxa from Gran Canaria, such as *Babcockia*, *Sventenia*, *Prenanthes pendula*, and *Sonchus* (including *Taeckholmia*), have the lowest mean identity of 0.66 for any island, while taxa from La Palma (i.e. *Sonchus* and *Lactucosonchus*) have the highest mean identity (0.84) for any island. Two island of intermediate age, La Gomera and Tenerife, show intermediate mean identities of 0.77 and 0.81, respectively (Fig. 1). Similar results were reported by FRANCISCO-ORTEGA & al. (1992) for *Chamaecytisus* who found that populations of Gran Canaria and Tenerife exhibited higher levels of genetic diversity and morphological differentiation than those of the younger islands (i.e. La Palma and El Hierro). This trend can also be seen in conspecific populations of *S. canariensis* and *S. acaulis*, which occur both in Gran Canaria and Tenerife. Several populations of *S. canariensis* from Gran Canaria have lower mean identity ($I=0.908$, range of 0.85–0.99) than conspecific populations from the younger island of Tenerife ($I=0.989$, range of 0.98–0.99). These results suggest that time is a factor for genetic differentiation during the radiation of the *Sonchus* alliance in Macaronesia. However, in the case of *S. acaulis*, there is almost no difference in mean identity: 0.99 and 1.00 in Gran Canaria and Tenerife, respectively.

In contrast to *Dubautia* and certain other insular endemics, the woody *Sonchus* alliance may not have diverged at allozyme loci simply by the accumulation of mutations. The taxonomic distribution of certain alleles suggests lineage sorting during radiation. For example, *Gdh^a* occurs in morphologically divergent taxa, such as most species of subg. *Dendrosonchus* sect. *Dendrosonchus*, the genera *Babcockia* and *Lactucosonchus*, and *Sonchus tuberifer* (a member of subg. *Sonchus*) (BOULOS 1972). In contrast, *Gdh^b* occurs in all species of subg.

Dendrosonchus sections *Pinnati* and *Brachylobi*, *Prenanthes pendula*, and most of *Taeckholmia*. All species of the alliance except two are fixed for *Adh-1^b*, while *Adh-1^a* is fixed in the two morphologically distinct taxa *Sonchus fauces-orci* and *Babcockia*. Furthermore, *Aat-1^b* occurs in most of the alliance, while *Aat-1^c* and *Aat-1^a* occur in morphologically distinct pairs of taxa *Sonchus brachylobus* and *Sventenia*, and *Babcockia* and *Prenanthes*, respectively. Lineage sorting could be responsible for these allelic distributions. The relatively high genetic identities (i.e. a mean of 0.804) and total diversity ($H_T = 0.100$) of the woody *Sonchus* alliance compared to other insular endemics together with the taxonomic distribution of alleles could be interpreted as evidence of ancestral allozyme polymorphisms in the alliance.

As indicated in the above discussion, there are several cases of nonconcordance between allozyme data and sectional assignment. For example, all but three species belonging to sect. *Dendrosonchus* of subg. *Dendrosonchus* are grouped in cluster 4 with two morphologically distinct species, *S. canariensis* (sect. *Pinnati*) and *Taeckholmia pinnata* (Fig. 2). Cluster 4 also includes two distinct elements of the alliance, *S. tuberifer* (subg. *Sonchus*) and *Lactucosonchus*, which are the only herbaceous perennials with tuberous roots. Cluster 3 contains all but two populations of *Taeckholmia*, the sole member of sect. *Brachylobi*, three species of sect. *Dendrosonchus*, and *S. palmensis* (sect. *Pinnati*) together with one population of *S. canariensis* (sect. *Pinnati*). This cluster also includes two Gran Canaria endemics, *Prenanthes pendula* and *Sventenia* (Fig. 2). Clearly, there is little concordance between allozyme similarity and sectional assignment in cluster 3. Noncongruence between the allozyme tree and the current morphological classification in sections of *Argyranthemum* have also been reported by FRANCISCO-ORTEGA & al. (1996) and these incongruences also extended to the cpDNA phylogeny (FRANCISCO-ORTEGA & al. 1997).

When the UPGMA phenogram based on allozyme data is compared to the cladogram generated from ITS sequences of nrDNA (KIM & al. 1996b: fig. 3; KIM & al., unpubl.), there are several major incongruences. For example, in the ITS phylogeny, *Lactucosonchus* diverges early in the alliance, and several other segregate genera such as *Sventenia*, *Babcockia*, *Prenanthes pendula*, and *Sonchus tuberifer*, represent early radiations and are closely related to each other. These genera are in turn sister groups to subg. *Dendrosonchus* sensu ALDRIDGE (including *Taeckholmia*), which represents a second radiation (fig. 3 of KIM & al. 1996b). However, the phenogram based on allozyme data shows *Babcockia* distantly related to the rest of the alliance (Fig. 2). It also suggests that *Sventenia* and *P. pendula* from Gran Canaria are more closely related to *S. brachylobus*, also from Gran Canaria. *Lactucosonchus* and *S. tuberifer* were grouped with other species from cluster 4 (Fig. 2). Also, in the ITS cladogram, two species of *Sonchus*, *S. ortunoii* and *S. gonzalezpadroni* from La Gomera (including *S. gummifer* from Tenerife in unpublished data, KIM & al.) clustered with most species of *Taeckholmia*, except *T. arborea*. This clade is rather strongly supported by both bootstrap (98%) and decay values (3). By contrast, in the allozyme phenogram, these three species are rather closely related to each other, but are not grouped closely with any other species of *Taeckholmia*. All but two populations of *Taeckholmia* are grouped in cluster 3 with two other species of *Sonchus*,

S. palmensis and *S. bornmuelleri*, which have morphological characteristics toward *Taeckholmia* (Fig. 2). However, in the ITS tree, the two *Sonchus* species clustered in another distinct lineage with most other species of *Sonchus* (KIM & al. 1996b; S.-C. KIM, unpubl.). These are some examples of nonconcordance between allozyme and other molecular data based on phenetic and cladistic approaches to the data analysis. The reasons are not known, however, several possibilities can be mentioned. First, as discussed above, populations in the *Sonchus* alliance have relatively high genetic identities, suggesting rather recent divergence between populations of the same and different taxa. Repeated genetic bottlenecks associated with the founding of new populations during radiation of the alliance may result in lineage sorting of ancestral allozyme polymorphisms. Therefore, populations of different taxa could be more similar to each other than to populations of the same taxa. This could also explain why species from the same island are sometimes more similar than populations of the same species from a different island. Second, we do not know how extensive hybridization was during radiation of the group, but based on field observations and previously reported occurrence of spontaneous interspecific and intergeneric hybrids, hybridization may well have been (and is) extensive (SVENTENIUS 1960, ALDRIDGE 1975, HANSEN & SUNDING 1985). It is also likely that this may cause nonconcordance among morphology, allozyme data, and ITS sequences. The nonconcordance between the allozyme and ITS sequence tree may partly also be due to different methods of the data analysis used, based on phenetics of allozyme frequencies and cladistics of ITS nucleotide sequences.

Timing the radiation of the alliance can be estimated based on allozyme data by using Nei's equation (1987) where time is equal to $D/2a$, with D the standard genetic distance and a the substitution rate per locus per year. If we assume the value of a is 10^{-7} , then t may be calculated as $(5 \times 10^6)D$ (CRAWFORD & al. 1992). The times for divergence for all pairwise comparisons of species pairs range between 0.06 million years (Mya) and 3.57 Mya. These estimated times postdate the origin of the Canary Islands, except for La Palma and El Hierro. The earliest divergence within the alliance can be estimated from taxa endemic to Gran Canaria and Tenerife (i.e. between 3.4 and 3.5 Mya) and this is long after the formation of the islands (14 Mya and 11.6 Mya in Gran Canaria and Tenerife, respectively; CARRACEDO 1994). These two islands are considered the center of diversity for woody members of *Sonchus* (subg. *Dendrosonchus*) including *Taeckholmia* (ALDRIDGE 1979). Therefore, initial divergence in the alliance probably started as early as 3.6 Mya ago when all the islands were formed, except La Palma and El Hierro, and rapid radiation apparently took place during Late Tertiary on Gran Canaria and Tenerife. The timing for the origin and radiation of the alliance agrees roughly with estimates based on ITS sequences; KIM & al. (1996b) suggested that the origin of the genera in the alliance may have occurred about 4.2 Mya or earlier (2.8 Mya or earlier when a faster rate of sequence divergence is assumed) on the Canary Islands, and the radiation of subg. *Dendrosonchus* accordingly took place between 4.2 and 3.6 Mya (2.8 and 2.3 Mya when a faster rate of ITS sequence evolution is assumed) ago on Gran Canaria or Tenerife. Furthermore, the estimated divergence and radiation times coincide closely with glaciation in the Northern Hemisphere (2.8 Mya; FLINT 1971) and beginning of Sahara desertification (2.5 Mya; WILLIAMS 1982). These events may have had an effect on the Canaries

and northwestern Africa and may have led to the extinction of some of the Canarian species providing open habitats, and allowed rapid speciation of the alliance.

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Addresses of authors: KIM SEUNG-CHUL*, DANIEL J. CRAWFORD, Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 1735 Neil Ave., Columbus, OH 43210, USA. *Present address: Department of Biology, Jordan Hall 425, Indiana University, Bloomington, IN 47405, USA. – JAVIER FRANCISCO-ORTEGA, ARNOLDO SANTOS-GUERRA, Jardín de Aclimatación de La Orotava, Calle Retama Num. 2, E-38400, Pureto de la Cruz, Tenerife, Canary Islands, Spain.

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