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Evolution of Endemic *Sideritis* (Lamiaceae) in Macaronesia: Insights from a Chloroplast DNA Restriction Site Analysis

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ABSTRACT. *Sideritis* L. subgenus *Marrubiastrum* (Lamiaceae) comprises 24 species of Macaronesian endemic perennials. The constituent taxa encompass a wide array of life forms that have exploited all ecological zones present in the Macaronesian archipelagos of Madeira and the Canary Islands. Though recently revised, an explicit phylogeny of the subgenus is still lacking. This group is especially intriguing because it exhibits the largest aneuploid series ever reported in oceanic island plants. The present study uses a chloroplast DNA restriction site analysis to elucidate the pattern of evolution within and among the islands. The insular taxa form a strongly supported monophyletic group, indicating a single colonization of Macaronesia. Monophyly of the sections is not supported. Integrating geographical and ecological distribution with the cpDNA phylogeny reveals a pattern of diversification within the islands consistent with adaptive radiation. Most other Macaronesian plant groups studied thus far have diversified by inter-island colonization between similar ecological zones. An analysis of chromosome number suggests a bimodal pattern of chromosomal change in the island subgenus, with one clade showing a decreasing aneuploid series and a second clade exhibiting aneuploid increase. The rate of change appears markedly amplified relative to that of the continental subgenus. This extreme level of chromosomal diversity stands in stark contrast to a general pattern of chromosomal stasis in island plants.

The Macaronesian biogeographic region comprises the five Atlantic Ocean archipelagos of the Azores, Madeira, Selvagens, Canary Islands, and Cape Verde Islands. Several unique features distinguish these islands from their generally younger, more remote Pacific counterparts, including a wider range of geologic ages (0.8 to 21 million years; Car-

racedo 1994) and distances from continental biotic source areas (100–1600 km). The influence of northeasterly trade winds combined with elevations ranging from sea level to over 3700 m has engendered a wide range of ecological diversity. This diversity has been partitioned by Macaronesian workers into five well-defined ecological zones

(Bramwell 1976; Francisco-Ortega et al. 1996). One of these, the lowland scrub zone, is frequently subdivided into northern and southern components to acknowledge the strong differentiation due to the presence or absence, respectively, of the humidifying trade winds. Some authors have suggested that the Macaronesian flora is a relict of the southern European-northern African Tertiary flora, which was extirpated on the continents by glaciation in Europe and desertification of northern Africa during the Quaternary (Bramwell 1972; Sunding 1979; Cronk 1992). This combination of distinctive features intimates the potential for patterns of colonization and speciation distinct from those described for Pacific island systems.

Sideritis L. subgenus *Marrubiastrum* (Moench) Mend.-Heuer (Lamiaceae) contains 24 suffrutescent to woody perennial species (Pérez de Paz and Negrin Sosa 1992) distributed among the 10 islands of the Canarian and Madeiran archipelagos, and constitutes one of the largest endemic groups in Macaronesia. Its continental congeners comprise the second, much larger subgenus *Sideritis*, containing approximately 125 species (Obón de Castro and Rivera-Núñez 1994) of both annual and perennial taxa with a center of distribution in Mediterranean Europe and northern Africa. The continental subgenus comprises four sections, two of which, *Hesiodia* and *Burgsdorffia*, are small groups containing only annual species distributed widely throughout the Mediterranean and central Asia. The remaining two continental sections, *Sideritis* and *Empedoclea*, contain suffrutescent perennials with centers of diversity in the western Mediterranean (especially the Iberian peninsula) and the eastern Mediterranean (Balkans, Turkey, Syria), respectively.

The Macaronesian subgenus *Marrubiastrum* was recently revised (Pérez de Paz and Negrin Sosa 1992) and divided into three sections, with circumscription of the taxa based on macromorphological and anatomical characters, pollen, chromosome number, and phytochemistry. While the morphology of the island taxa is well characterized, an explicit phylogeny for the group has not been proposed and monophyly of the sections is untested. The island endemics display a diverse array of life forms and are found in all ecological zones present in the two archipelagos. Most of the species have highly restricted distributions and small population sizes, and only four species occur on more than one island.

One of the most striking features of subgenus *Marrubiastrum* is its high level of chromosomal var-

iation (Marrero 1986, 1988, 1992). Aneuploid change in chromosome number is rare in perennial taxa in general (Levin and Wilson 1976; Kyhos and Carr 1994) and in island plants in particular (Carr and Kyhos 1981, 1986; Carr 1998; Stuessy and Crawford 1998). Prior reports of aneuploidy in island plants are restricted to the genus *Dubautia* (Asteraceae) of Hawaii (Carr and Kyhos 1981) and three genera, *Alpinia* (Zingiberaceae), *Callicarpa* (Verbenaceae) and *Malaxis* (Orchidaceae), in the Bonin Islands of Japan (Ono and Masuda 1981). None of these genera exhibit more than three different chromosome numbers. Marrero (1992) has documented nine different diploid numbers for the 24 island species of *Sideritis* (see Table 1), a range equal to that of the entire continental subgenus (9 diploid numbers in 125 species). Three species show intraspecific variation; for one of these (*S. dendro-chahorra*), five different diploid numbers are known.

In this study, we used a cpDNA restriction site approach to address questions about the evolution of *Sideritis* within Macaronesia. We wanted to determine whether *Sideritis* was introduced once into Macaronesia and to test the monophyly of the sections as currently circumscribed. We also wished to characterize the mode of diversification of the island taxa and to examine the pattern of chromosomal change within subgenus *Marrubiastrum*. Restriction site data often exhibit low levels of homoplasy (Palmer et al. 1988; Olmstead and Palmer 1994; Jansen et al. 1998) and such analyses have been used in many recent studies of island plants (Baldwin et al. 1990; Wendel and Percival 1990; Crawford et al. 1992; Givnish et al. 1995; Francisco-Ortega et al. 1996). Furthermore, restriction site analysis of the entire chloroplast genome often provides more phylogenetically informative characters than sequencing of single genes or DNA regions (Francisco-Ortega et al. 1997; Jansen et al. 1998).

MATERIALS AND METHODS

We sampled 49 populations representing all Macaronesian taxa of *Sideritis* (Table 1). Taxa of widespread distribution or those occurring in more than one ecological zone were sampled multiple times. Leaves and seeds (if available) of all taxa were collected and preserved in silica gel. Fresh leaf material was obtained from plants grown from seed in the greenhouses at the University of Texas for five continental species of *Sideritis* that were used as outgroups. Total DNA was extracted using the

CTAB method (Doyle and Doyle 1987) and purified via cesium chloride and ethidium bromide gradients. The purified DNA was digested using 20 restriction enzymes having 4, 5, or 6 base pair (bp) recognition sequences. The enzymes used and their number of recognition sites in tobacco were: *AseI* (114), *AvaII* (60), *BclI* (54), *BglIII* (60), *BstnI* (128), *BstnI* (89), *ClaI* (59), *DraI* (64), *Eco0109I* (67), *EcoRI* (97), *HaeIII* (196), *HhaI* (89), *HincII* (57), *Hinfl* (718), *MspI* (214), *NciI* (113), *NsiI* (43), *RsaI* (286), *TaqI* (639), and *XmnI* (112). One of these (*Eco0109I*) was subsequently deleted from the analysis due to a lack of variation. DNA fragments were separated by gel electrophoresis and bidirectionally transferred to reusable nylon membranes. Nick translation and filter hybridization were performed as in Palmer (1986) using cloned fragments representing 80% of the tobacco chloroplast genome (Olmstead and Palmer 1992). We did not survey the inverted repeat because we did not expect to find significant variation within this highly conserved region (Jansen and Palmer 1987; Wolfe et al. 1987). Restriction site patterns were visualized and scored by exposing the filters to x-ray film.

Low levels of restriction site divergence and a low incidence of length variation permitted the interpretation of fragment patterns without having to construct restriction site maps (Jansen et al. 1998). If a site gain resulted in fragments too small to be observed, restriction site differences were scored by inferring the presence of small bands. In the few cases where fragment patterns did not permit unequivocal discrimination between restriction site differences and length variants, multiple digests of the same region of the chloroplast genome were compared to ensure against scoring a single length difference more than once.

We used five species representing all four sections (Table 1) of the continental subgenus *Sideritis* as outgroups for polarizing changes in restriction sites. Phylogenetic analyses were performed using PAUP* version 4.0b4a (Swofford 1999). The parsimony analysis used a heuristic search with 100 random replicates, TBR branch-swapping and MULPARS optimization. Support for groups was evaluated via bootstrap analysis (Felsenstein 1985) using simple addition sequence and 100 replicates, with the remaining parameters identical to those used in the parsimony analysis. Chromosome number evolution was reconstructed using MacClade version 3.08 (Maddison and Maddison 1999) with character states treated as unordered and state changes assigned equal weights.

RESULTS

A total of 432 restriction site changes was detected, of which 232 were phylogenetically informative. The data matrix has been deposited in TreeBASE (<http://www.herbaria.harvard.edu/treebase/>). The searches found 42 equally parsimonious trees with a length of 494 steps. The consistency index (CI) excluding uninformative characters was 0.78 and the retention index (RI) was 0.93. The g1 statistic for 100,000 randomly sampled trees was -1.05 ($p < 0.01$ for 250 characters and ≥ 25 taxa), indicating that the distribution of tree lengths is significantly skewed from random and that the dataset contains substantial phylogenetic signal (Hillis and Huelsenbeck 1992). Figure 1 shows one of the most parsimonious trees from this analysis; dashed lines indicate branches that collapse in the strict consensus tree. The island taxa are monophyletic and distinguished from their continental congeners by 51 steps; thus a single introduction to Macaronesia is strongly supported. Two major clades are identified within the island species. Monophyly of the sections within subgenus *Marrubiastrum* is not supported by the chloroplast data. Notably, while most multiple populations of species group together, there are several striking exceptions (e.g. *S. canariensis*, *S. cretica*, *S. gomerae*, *S. soluta*).

A more exhaustive parsimony analysis and bootstrap evaluation were performed on a reduced dataset after deleting multiple populations that grouped together in the previous analysis. This second analysis found 21 equally parsimonious trees with a length of 491 steps. The CI was the same as that of the full analysis; RI was 0.91 and the g1 statistic was -1.49 . Figure 2 shows one of the most parsimonious trees from this second analysis with island distribution and ecological zone mapped onto it. The topology of this tree is identical to that of the full analysis.

Chromosome number evolution was traced on all 21 trees of the abbreviated dataset, resulting in 14 reconstructions of 17 steps, and seven reconstructions requiring only 16 steps. We analyzed the pattern of chromosome number evolution within Macaronesia using these seven shortest reconstructions. All seven reconstructions unambiguously resolve an ancestral number of $2n=44$ for Clade 1, with a minimum of six aneuploid decreases in the terminal taxa. For Clade 2, variation in the basal topology of the seven shortest trees resulted in some ambiguity in the reconstructions. However,

TABLE 1. Source of material used in cpDNA analysis. Nomenclature follows Pérez de Paz and Negrin Sosa (1992). Chromosome numbers are from Marrero (1992). Numbers in parentheses following location indicate number of populations/accessions included in study. All vouchers are deposited in the University of Texas Herbarium (TEX) unless otherwise indicated. Abbreviations: CI = Canary Islands; MD = Madeira.

Taxon	2n	Island	Location	Voucher/Accession #
SUBGENUS MARRUBIASTRUM				
Section <i>Marrubiastrum</i>				
<i>S. barbellata</i> Mend. - Heuer	44	CI: La Palma	Caldera de Taburiente Cueva de Belmaco Aldea de El Charco El Riachuelo, near La Cumbreci- ta	4310 (ORT) JB 261 JB 262 JB 263
<i>S. brevicaulis</i> Mend-Heuer	36	CI: Tenerife (2)	Barranco de Izcagua Degollada entre Palmar y Carri- zales	4299 (ORT) JB 226
<i>S. canariensis</i> L.	44	CI: Tenerife (1) La Palma (2)	Above Masca Carretera de Moquinal Breña Alta Cubo de la Galgo	JB 258 JB 227 JB 228 9014 (ORT)
<i>S. candicans</i> Aiton	38	MD: Madeira (1)	Talbano	JB 257
<i>S. cystosiphon</i> Svent.	44	CI: Tenerife (1)	Encumeada	JB 230
<i>S. dasygnaphala</i> (Webb et Berth.) Clos	36	CI: Gran Canaria (5)	Tamaimo Tamadaba Pico de las Nieves Peñones del Amo Amurga	JB 267 JB 279 18691 (LPA) JB 196 18690 (LPA)
<i>S. dendro-chahorra</i> Bolle	38, 39, 40, 41, 42	CI: Tenerife (1)	Barranco Pino Gordo Between Bailadero & Taganana	18674 (LPA) JB 224
<i>S. discolor</i> Bolle	36	CI: Gran Canaria (2)	Barranco Oscuro Barranco de los Tiles (Moya)	No voucher 8424 (ORT)
<i>S. eriocephala</i> Marr. ex Negr. et Pérez	34	CI: Tenerife (2)	Cañadas del Teide Topo de la Grieta	JB 266 33.959 (ORT)
<i>S. ferrensis</i> Pérez et Negr	44	CI: El Hierro (1)	Mocanal	JB 204
<i>S. infernalis</i> Bolle	40	CI: Tenerife (1)	Barranco del Infierno	JB 253
<i>S. kuegleriana</i> Bornm.	42	CI: Tenerife (1)	Barranco de Talavera	16767 (ORT)
<i>S. lotsyi</i> (Pit.) Bornm.	36	CI: La Gomera (2)	Carretera Garajonay Above Igualero	JB 259 2818 (ORT)
<i>S. nervosa</i> (Christ) Lind.	42	CI: Tenerife (1)	Punta de Teno	JB 265
<i>S. oroteneriffae</i> Negr. et Pérez var. <i>arayae</i>	44	CI: Tenerife (2)	Above Igueste de Candelaria Pine forest above Candelaria	JB 220 33.953 (ORT)
var. <i>oroteneriffae</i>		CI: Tenerife (1)	Montaña de Ayosa	JB 219
<i>S. pumila</i> (Christ) Mend.-Heuer	40	CI: Fuerteventura (1) Lanzarote (1)	Pico de la Zarza Peñas del Chache	22.226 (ORT) JB 278
<i>S. soluta</i> Clos				
subsp. <i>güeiimaris</i>	44	CI: Tenerife (1)	Barranco de Badajoz	JB 221
subsp. <i>soluta</i>		CI: Tenerife (2)	Between Topo de la Grieta & Llano de Maja	JB 217
<i>S. sp. nov.</i>	??	CI: La Gomera (1)	Pino Gordo, above Vilafior West of Inchareda, in laurisilva	JB 268 JB 281
<i>S. søentemii</i> (Kunkel) Mend.-Heuer	36	CI: Gran Canaria (1)	Ayagaures	JB 195

TABLE 1. Continued.

Taxon	2n	Island	Location	Voucher/Accession #
Section <i>Empedocleopsis</i>				
<i>S. gomerae</i> Bolle	44			
subsp. <i>gomerae</i>		CI: La Gomera (1)	Carretera betw. San Sebastian & Hermigua	JB 256
subsp. <i>perezii</i>		CI: La Gomera (1)	Road to Benchijigua	JB 269
<i>S. bolleana</i> Bornm.	(*)	CI: ?	*known only from type location	
<i>S. nutans</i> Svent.	44, 46	CI: La Gomera (2)	Barranco de Argaga El Santo	JB 285 JB 270
Section <i>Creticae</i>				
<i>S. cretica</i> L.				
subsp. <i>cretica</i>	34	CI: Tenerife (1)	Barranco de Talavera	JB 252
subsp. <i>spicata</i>	36	CI: La Gomera (1)	Carretera betw. San Sebastian & Hermigua	JB 255
<i>S. macrostachys</i> Poir.	36	CI: Tenerife (1)	Anaga, betw. Bailadero & Casa Forestal	JB 254
<i>S. marmorea</i> Bolle	36	CI: La Gomera (1)	Riscos de Puntallana	32073 (ORT)
SUBGENUS <i>SIDERITIS</i>				
Section <i>Burgsdorffia</i>				
<i>S. romana</i> L.	28	Italy (1)	San Bartolomeo al Mare, Imperia (seed from BG Hanbury, Genova)	JB 209
Section <i>Empedoclea</i>				
<i>S. scardica</i> Griseb.	32	Greece (1)	Thessalien, Nomos Larisis (seed from BG Dahlem, Berlin, Germany)	JB 211
<i>S. syriaca</i> L.	24	Greece (1)	Euboea, Mt. Dirfys (seed from BG Copenhagen, Denmark)	JB 210
Section <i>Hesiodia</i>				
<i>S. montana</i> L.	16	Provenance unknown (1)	Seed from BG Cluj-Napoca, Romania	JB 212
Section <i>Sideritis</i>				
<i>S. hyssopifolia</i>	30	Spain (1)	Picos de Asturias (seed from BG Dahlem, Berlin, Germany)	JB 202

since all reconstructions had the same number of steps, we chose the tree having the same topology as Fig. 2 to model chromosome number change (see Fig. 3). This reconstruction resolves an ancestral number of $2n=36$ for Clade 2, with a minimum of five aneuploid increases.

DISCUSSION

Taxonomic Implications. Taxonomic status of the Macaronesian species of *Sideritis* has been a matter of contention for over 150 years. Webb and Berthelot (1845) circumscribed the Macaronesian species as a distinct genus, *Leucophae*. In a study based on pollen characters, Huynh (1972) recombined the island taxa with the Mediterranean species of *Sideritis* and defined six sections. Kunkel (1973) proposed conservation of the generic name

Leucophae for the island taxa, but using morphological and phytochemical data respectively, Mendoza-Heuer (1977) and Fraga (1982) both concluded that generic recognition was not justified. Nevertheless, Mendoza-Heuer (1977) considered the Macaronesian taxa distinctive enough to assign them to their own subgenus, *Marrubiastrum*. Our study shows the Macaronesian species of *Sideritis* to be monophyletic and differentiated from their continental congeners by 51 restriction site changes. This degree of distinction may be an artifact of restricted sampling of continental taxa; thus, any re-evaluation of Kunkel's (1973) proposal will require increased sampling as well as confirmation from nuclear data. Monophyly of the established sections within subgenus *Marrubiastrum* is not supported by the cpDNA data (Fig. 1).

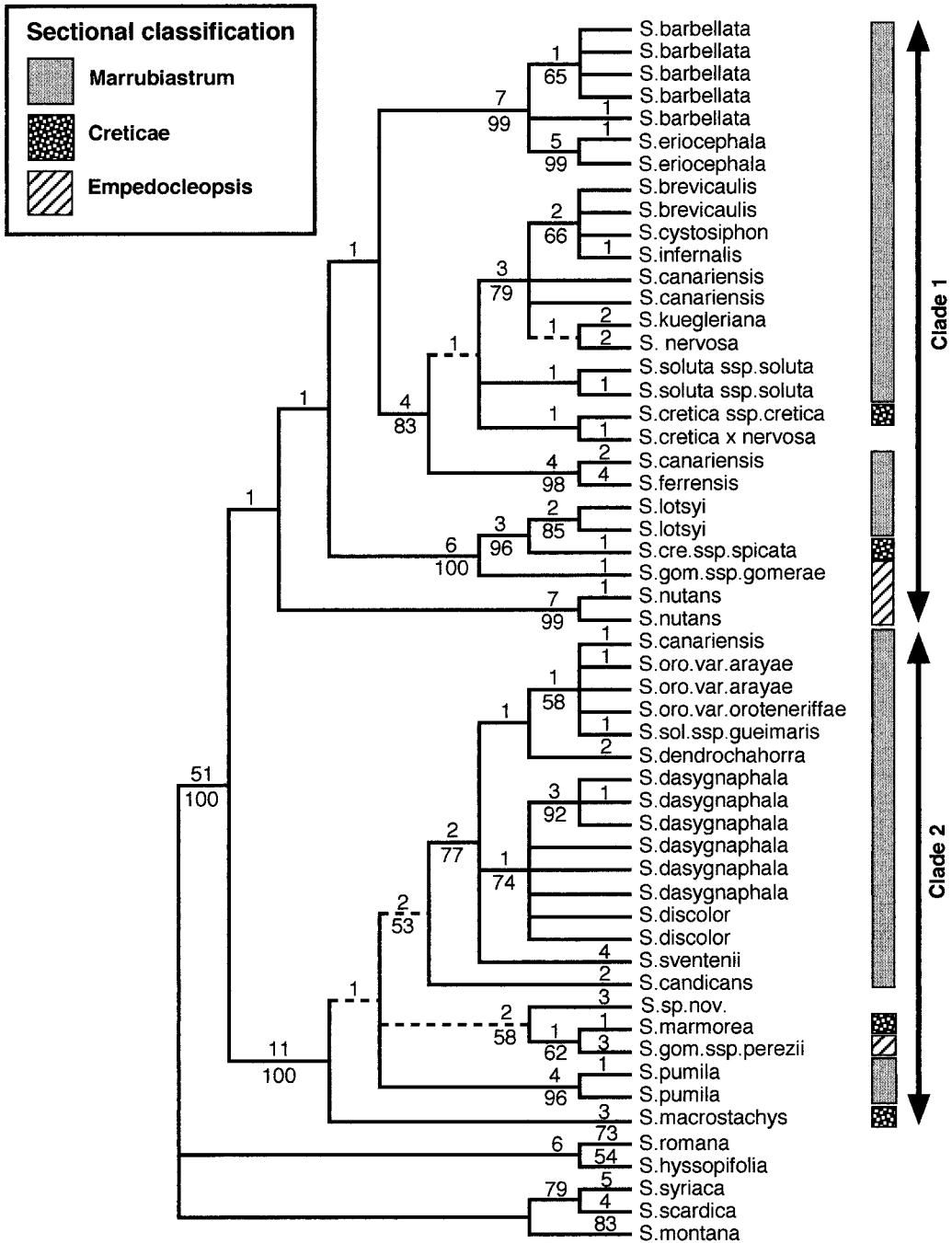


FIG. 1. One of 42 equally most parsimonious trees of 494 steps from the cpDNA restriction site analysis (CI=0.78, RI=0.93). Branch lengths appear above the nodes, with bootstrap values greater than 50% shown below. Dashed lines indicate clades that collapse in the strict consensus tree.

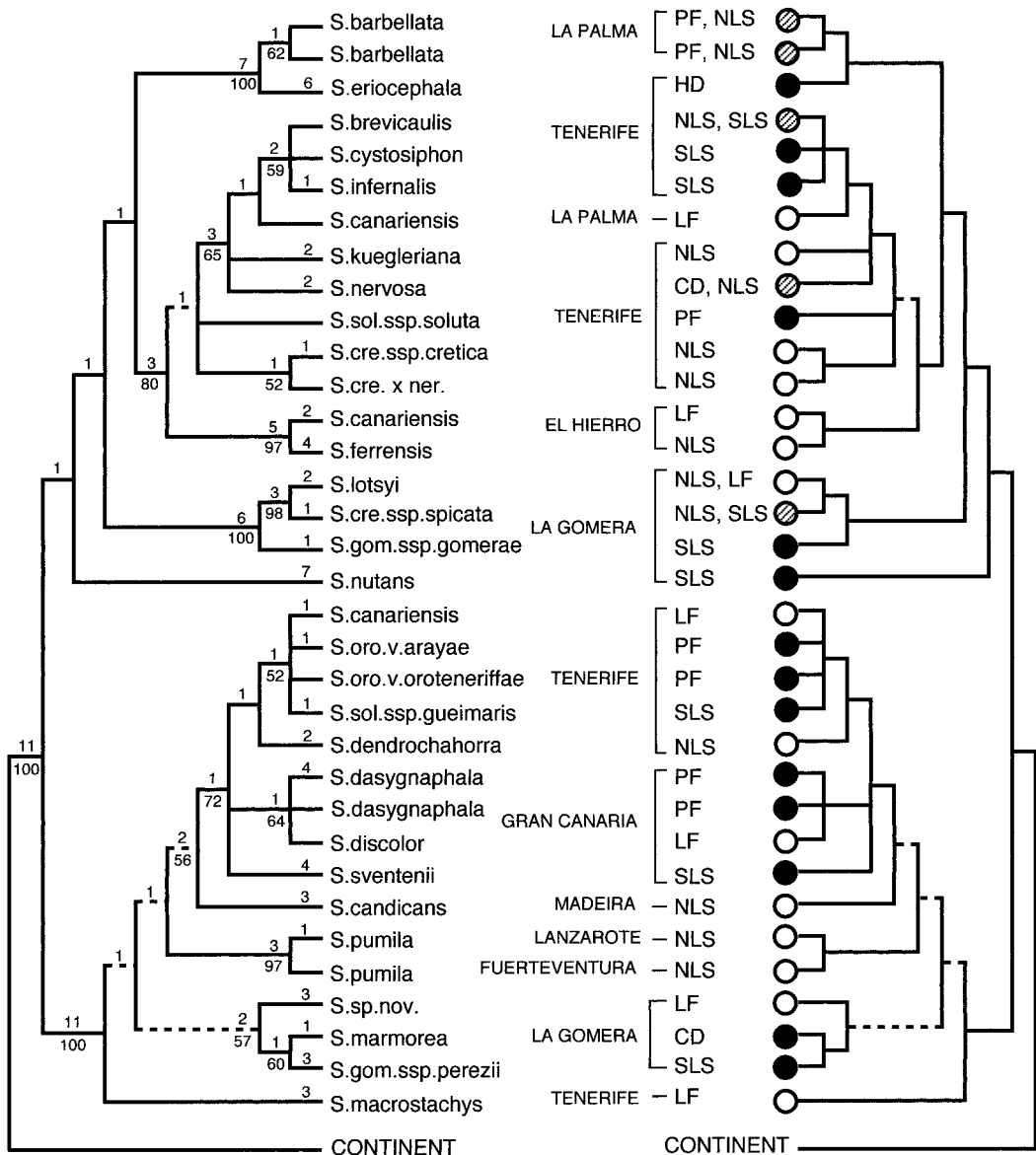


FIG. 2. Ecological zone and island distribution of Macaronesian *Sideritis* mapped onto one of 21 most parsimonious trees ($L = 491$) from the reduced dataset (see text for details). Ecological zone abbreviations as in Table 2. Open circles indicate ecological zones influenced by the humid northeastern tradewinds; solid circles denote arid zones not affected by the tradewinds. Hatched circles identify taxa found in both humid and arid climatic areas.

The position of several subspecific taxa in the chloroplast phylogeny suggests further taxonomic implications. *Sideritis cretica* subsp. *spicata* and *S. gomerae* subsp. *perezii* were earlier recognized as distinct species (*S. spicata* and *S. perezii*) by Marrero (1988; Bramwell and Bramwell 1990). Diploid chromosome number (see Table 1) also differentiates *S.*

cretica subsp. *spicata* ($2n=36$) from *S. cretica* subsp. *cretica* ($2n=34$). Nevertheless, in the most recent comprehensive revision of the subgenus, Pérez de Paz and Negrin Sosa (1992) reduced these taxa to subspecies of *S. cretica* and *S. gomerae*, respectively. Although the position of these taxa in the cpDNA tree (Fig. 2) appears to support their recognition at

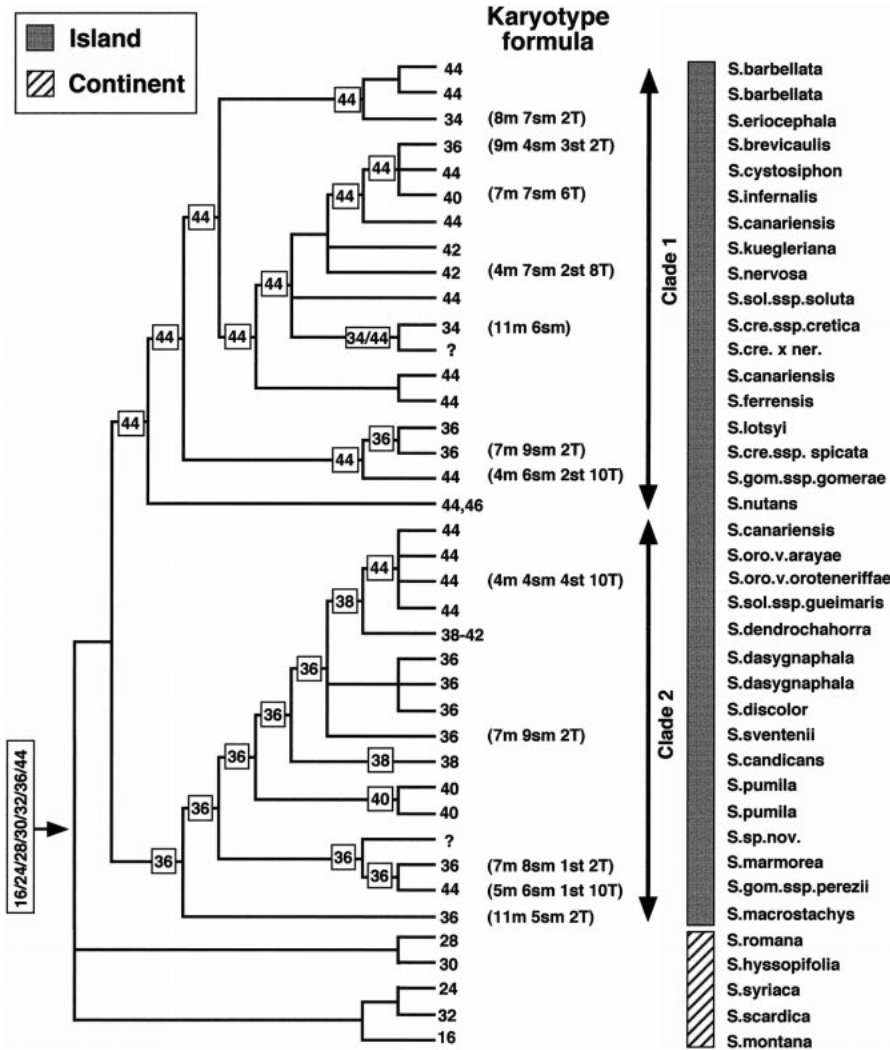


FIG. 3. Diploid chromosome number mapped onto one of 21 most parsimonious trees ($L = 491$) from the reduced dataset. Character states at nodes were reconstructed with MacClade 3.08 (see text for details). Karyotype formula determined by Marrero (1992) is shown for 12 taxa. Abbreviations are as follows: m=metacentric; sm=submetacentric; st=subtelocentric; t=telocentric.

the specific level, their placement could be due instead to confounding factors such as hybridization. *Sideritis soluta* is a third species whose infraspecific taxa do not have a sister relationship in the chloroplast phylogeny. *Sideritis soluta* ssp. *soluta* is diffusely distributed in pine forests in the barrancos on the south side of Tenerife, while *S. soluta* ssp. *gueimaris* is restricted to the barranco of Güimar at the northeastern limit of the species' distribution. This second subspecies is highly polymorphic and is easily confused (Negrin Sosa and Pérez de Paz

1988; Pérez de Paz and Negrin Sosa 1992) with *S. roteneriffae*, a species with which it overlaps in the upper reaches of its distribution. Resolution of these taxonomic issues will be aided by the construction of a phylogeny based on a nuclear marker.

Inter-island Colonization and Adaptive Radiation. The monophyly of the island taxa strongly supports a single introduction of *Sideritis* to Macaronesia. This is consistent with the pattern found in other Macaronesian plant groups (*Argyranthemum*, Francisco-Ortega et al. 1996; *Echium*, Böhle et

TABLE 2. Distribution of *Sideritis* in Macaronesia. Abbreviations for ecological zones are as follows: CD = coastal desert; SLS = southern (arid) lowland scrub; NLS = northern (humid) lowland scrub; LF = laurel forest; PF = pine forest; HD = high altitude desert. A dash (—) indicates ecological zone is not present on that island. Table adapted from Francisco-Ortega et al. (1996).

Island	Age (Myr)	Elevation (m)	Area (km ²)	Number of taxa per ecological zone					
				CD	SLS	NLS	LF	PF	HD
Canary Islands									
El Hierro	0.8	1520	307	0	0	1	1	0	—
La Palma	2.0	2423	789	0	0	1	1	1	0
La Gomera	12.5	1484	425	1	1	4	1	—	—
Tenerife	12.0	3714	2355	1	3	6	2	2	1
Gran Canaria	14.0	1950	1625	0	1	0	1	1	—
Fuerteventura	21.0	807	1717	0	0	1	—	—	—
Lanzarote	15.5	670	717	0	0	1	—	—	—
Madeira									
Madeira	13.0–18.0	1861	730	0	1	1	0	—	—
Porto Santo	5.5	515	44	0	0	1	—	—	—
Deserta Grande	2.8–5.4	479	20	0	1	—	—	—	—
Total by zone				2	7	16	6	4	1

al. 1996; *Sonchus* alliance, Kim et al. 1996; *Pericallis*, Panero et al. 1999; *Aeonium*, Mes et al. 1996). In fact, despite the close proximity of the African continent, which implies at least the potential for multiple colonizations, only two plant groups examined thus far in rigorous phylogenetic analyses (*Lavatera*, Ray 1995; *Hedera*, Vargas et al. 1999) have been explicitly shown to have experienced multiple introductions.

Two major clades are identified (Fig. 1) in the cpDNA tree. Although Clade 1 is weakly supported at the lower nodes, several of the terminal groupings have high bootstrap values. Conversely, Clade 2 has 100% bootstrap support for the clade as a whole, but support is low for many of the terminal groups. This may reflect differing rates of radiation within the two clades. Clade 1 may have experienced a rapid initial radiation, followed by a decrease in the rate of speciation, while Clade 2 may have had a slow initial radiation with a subsequent increase in speciation rate. Clade 1 comprises taxa from the four westernmost Canary Islands (Tenerife, La Gomera, La Palma and El Hierro); these islands range in age from 0.8 to 12.5 My. Geographically, Clade 2 is less clearly defined. It includes taxa from three western islands (La Gomera, Tenerife, and Gran Canaria) as well as the two easternmost islands (Lanzarote and Fuerteventura); the age range for these islands is from 12 to 21 My. The single species from Madeira is included in Clade 2, but its position does not permit us to make any clear inference about the direction of colonization

between the two archipelagos. The much greater diversity of the genus in the Canary Islands suggests that *Sideritis* was introduced to Madeira from the Canarian archipelago, but the direction of this introduction may seem counterintuitive given the relative positions of the two archipelagos and the prevailing northeasterly trade winds. Moreover, in at least two other groups with taxa in both archipelagos (*Argyranthemum*, Francisco-Ortega et al. 1996; *Aeonium*, Mes and 't Hart 1996) colonization has occurred in the opposite direction, from Madeira to the Canaries. However, a Canary Islands-to-Madeira pattern is believed to have occurred in at least three other Macaronesian plant groups: *Echium* (Böhle et al. 1996), the woody *Sonchus* alliance (Kim et al. 1996), and *Pericallis* (Panero et al. 1999).

Several factors influence the diversity of *Sideritis* on individual islands within Macaronesia. Most important of these are size of island and number of ecological zones (Table 2). The number of ecological zones on an island is in turn largely a product of the interaction of island size and altitude, as well as the influence of the trade winds. Age of island appears to have little or no influence. Lanzarote and Fuerteventura, the two oldest islands, harbor only a single species between them. These islands, while relatively large, are also low and thus have only three ecological zones. The youngest island, El Hierro, contains two species. It is smaller than either of the two easternmost islands, but is ecologically more diverse due to its greater elevation. Tenerife, with a median age of 12 My, has the highest

diversity of *Sideritis*, with 12 species. Tenerife is also the largest Macaronesian island, with an area of 2355 km² and an elevation of 3714 m, and contains all ecological zones described for the region.

Several studies of Macaronesian plant groups have found a correlation between phylogeny and ecology, describing a pattern of diversification via inter-island colonization between similar ecological zones. The best examples of this uniquely Macaronesian pattern include *Argyranthemum* (Francisco-Ortega et al. 1996), *Aeonium* (Mes and 't Hart 1996), and the *Sonchus* alliance (Kim et al. 1996). In addition, Kim et al. (1996) note that diversification of the *Sonchus* alliance in Macaronesia has been accompanied by a number of ecological shifts, but in general, these shifts occur between, rather than within, islands. This is not the case for Macaronesian *Sideritis*. Our results support a predominant pattern of adaptive radiation by the island taxa. In general, taxa group together by island and within an island are found in diverse ecological zones (Fig. 2), suggesting that ecological shifts have accompanied speciation. This pattern is similar to that found in the Hawaiian silversword alliance (Baldwin and Robichaux 1995) and other plant groups of Pacific Island archipelagos (Hawaii: *Tetramolopium*, Lowrey 1995; *Cyanea*, Givnish et al. 1995; *Bidens*, Helenurm and Ganders 1985; Juan Fernandez: *Dendroseris*, Sang et al. 1994; *Robinsonia*, Crawford et al. 1993).

Complementing the correlation between phylogeny and habitat, Francisco-Ortega et al. (1996) found an additional relationship between phylogeny and climatic zone in *Argyranthemum*. Their study resolved two distinct clades within the Canary Islands, one of which was correlated with an arid climate zone not affected by the northeastern trade winds, and a second correlated with a climate zone subject to the trade winds' humidifying effects. Such a relationship is absent in *Sideritis* (see Fig. 2). Multiple introductions have occurred on several of the islands: the cpDNA phylogeny suggests that there have been two independent introductions each on La Gomera and La Palma, and at least four on Tenerife.

Evidence for Hybridization. Although hybridization is common in at least one section of the continental subgenus (Obón de Castro and Rivera Nuñez (1994), it has not been recognized by most workers as an important factor in the evolution of the insular taxa. Bornmüller (1924) reported a hybrid between cultivated individuals of *S. macrostachys* and *S. oroteneriffae* in the botanic garden in Berlin, but not until Sventenius' (1968) treatise on

Macaronesian *Sideritis* was hybridization noted within the islands. In their revision of the island taxa, Pérez de Paz and Negrin Sosa (1992) described six new hybrids; nevertheless, they noted that hybridization is a still-infrequent phenomenon of relative recency. They suggest that increased hybridization in the group may be due to anthropogenic disturbance, which has in turn led to the breakdown of ecological barriers that in the past maintained the respective taxa in isolation.

The chloroplast phylogeny of the present study contains several instances that imply hybridization. Three species have infraspecific taxa that do not show a sister relationship in the tree (Fig. 2): *S. soluta* (Tenerife), *S. gomerae* (La Gomera); and *S. cretica* (Tenerife and La Gomera; see discussion under Taxonomic Implications). The strongest evidence of hybridization is provided by *S. canariensis*, a laurel forest species that occurs on the islands of Tenerife, La Palma and El Hierro. Populations from all three islands are morphologically indistinguishable, yet they are not sister taxa in the cpDNA tree. Two of the populations (La Palma, El Hierro) group into Clade 1, while the third (Tenerife) is in Clade 2 (Fig. 2). The cpDNA data place the El Hierro population of *S. canariensis* sister to *S. ferrensis*, the only other species of *Sideritis* present on that island. We interpret this as evidence of chloroplast capture. Interestingly, *S. canariensis* is named as a progenitor in three of the six newly described hybrids in the recent revision (Pérez de Paz and Negrin Sosa 1992).

An alternative explanation for the relationships shown by *S. canariensis* in the cpDNA phylogeny is lineage sorting. We consider this alternative unlikely for several reasons. The strongly supported monophyly of Macaronesian *Sideritis* implies dispersal of a single propagule to the islands; cpDNA polymorphism in this founder is highly unlikely. Subsequent bottlenecks caused by radiation into new habitats and dispersal to new islands (Baldwin et al. 1998) argue against the amount of time necessary for the proliferation of cpDNA polymorphisms in situ and the subsequent extinction of many of them which would yield the confounding pattern typical of either lineage sorting or hybridization. The slow rate of cpDNA evolution (Wendel and Doyle 1998) and the relative youth of the Canarian and Madeiran archipelagos further reduce the likelihood of lineage sorting as an explanation for the placement of *S. canariensis* populations in the cpDNA phylogeny. Hybridization remains the most

parsimonious explanation; however, resolution of this issue requires data from a nuclear marker.

If hybridization is responsible for the placement of these taxa in the cpDNA phylogeny, patterns of island colonization and chromosome number change may differ from our interpretation here. In particular, estimates of change in chromosome number (see below) could be inflated.

Chromosome Number Evolution. The high level of aneuploid chromosome variation in Macaronesian *Sideritis* is unparalleled in Pacific island plant groups. In Hawaii, there have been a few occurrences of autochthonous polyploidy (Carr 1998) but only a single documented case of aneuploid change, in the silversword alliance (Asteraceae; Carr and Kyhos 1981). Within that group of three genera, only *Dubautia* exhibits aneuploidy, with haploid numbers of $n=13$ and $n=14$. No chromosome number variation has been reported for plants of the Juan Fernandez or Galapagos Islands (Stuessy and Crawford 1998). In the Bonin Islands of Japan, aneuploidy has been reported in three genera: *Alpinia* (Zingiberaceae), *Malaxis* (Orchidaceae), and *Callicarpa* (Verbenaceae). The first two of these genera each have two different haploid numbers, while *Callicarpa* has three (Ono and Masuda 1981).

Macaronesian *Sideritis* make a striking contrast to this general picture of chromosomal stasis in insular settings. Nine different diploid numbers have been documented in the 24 species of this group (Marrero 1992), including three species with intra-specific variation (see Table 1). Carr (1998) and Stuessy and Crawford (1998) point out that chromosomal variation in insular endemics tends to reflect that of continental relatives, and this certainly holds true in *Sideritis*: an aneuploid series of nine different diploid numbers is present in the 125 continental species. However, the rate of chromosomal evolution appears to be accelerated in the insular species (nine diploid chromosome numbers in 24 species, or a ratio of 1:2.7) as compared to their continental congeners (nine diploid numbers in 125 species, or a ratio of 1:13.8). This accelerated rate may best be explained by the dynamics of evolution in an island setting. Bottlenecks caused by repeated colonizations of new ecological zones and/or islands would permit establishment of chromosomal variants that would not otherwise be expected to survive in a population (Kyhos and Carr 1994). Furthermore, nearly all insular species of *Sideritis* have small, isolated populations (Bramwell and Bramwell 1990; Pérez de Paz and Negrin Sosa 1992), contributing further to conditions favorable for estab-

lishing and maintaining such variants. Inbreeding could also contribute to chromosomal instability, particularly in small populations. The effects of inbreeding would be intensified if the plants were self-compatible. While protandry is very common within Lamiaceae (Zomlefer 1994; Proctor et al. 1996), the breeding system of *Sideritis* is unknown and self-compatibility in the genus has not been documented. Our observations suggest that the insular species, at least, are not self-fertile. Although we have grown nearly all the insular taxa in the greenhouse for several years, seed set has never been noted.

The pattern of chromosomal evolution in Macaronesian *Sideritis* is also unusual. In angiosperms, a descending mode of aneuploid evolution is more common than an ascending mode (Goldblatt and Johnston 1988; Kim 1994). In insular *Sideritis*, however, reconstruction of chromosome number evolution suggests a bimodal pattern of change (see Fig. 3). Clade 1 shows the more common decreasing mode of aneuploid change, but Clade 2 shows a contrasting pattern of aneuploid increase. Taxa that are sister in the tree generally share the same diploid chromosome number, strengthening the correlation between chromosome number and phylogeny.

There are no data on the mechanisms of chromosomal evolution in *Sideritis*. Marrero (1992) suggested that the variation present in the Macaronesian taxa could be due to changes in chromosome structure caused by centric fission or centric fusion (i.e., Robertsonian changes). In centric fission, a break within the centromere of a metacentric chromosome results in two telocentric chromosomes, thus increasing chromosome number while decreasing overall karyotype symmetry. Conversely, centric fusion occurs when two acro- or telocentric chromosomes join to form a single metacentric, resulting in a decrease in chromosome number and increased karyotype symmetry. Although karyotype data are scant, those that are available lend at least some credence to the possibility of such changes in Macaronesian *Sideritis* (Fig. 3). The clearest example is in Clade 2, which exhibits an increasing mode of aneuploid change. In the sister taxa *S. marmorea* ($2n=36$) and *S. gomeræ* subsp. *perezii* ($2n=44$), the taxon with the higher chromosome number has a less symmetrical karyotype, as would be expected if centric fission was the mechanism leading to an increase in chromosome number. In Clade 1, with its decreasing mode of aneuploidy, the closely related taxa *S. cretica* subsp. *spicata*

($2n=36$) and *S. gomerae* subsp. *gomerae* ($2n=44$) may illustrate the second mode of structural change. Here, the karyotype of the taxon with the lower chromosome number has a greater degree of symmetry, consistent with centric fusion. Both types of Robertsonian changes contribute to genetic variation via modified recombination and altered linkage relationships (Jones 1998). Nevertheless, while these mechanisms are important in karyotype evolution in animals (King 1993), particularly mammals (Holmquist and Dancis 1979), they are relatively rare in plants (see review by Jones 1998). Most reports of such structural changes in plants have come from monocots and gymnosperms, although there are several known cases in dicots, e.g. *Chaenactis* (Kyhos 1965) and *Pelargonium* (Gibby et al. 1996).

Though the mechanisms of chromosomal evolution in *Sideritis* are not known, the high level of chromosome number variation remains striking for oceanic island plants. Variation resulting from chromosomal lability could be of vital importance to the survival of small, isolated populations like those of *Sideritis* in Macaronesia. It has been suggested that in some plant groups (e.g., *Zamia*, slipper orchids), structural changes may be induced by selective pressures from ecological or environmental stresses (Caputo et al. 1996; Cox et al. 1998). Such stressful conditions are well-documented for oceanic island systems (Stoddart and Walsh 1992; Carson and Clague 1995; Whittaker 1995; Walker et al. 1996). Whether such structural changes have been operative in Macaronesian *Sideritis* will not be revealed until more extensive cytological studies are conducted.

Our cpDNA restriction site approach to reconstructing the phylogeny of Macaronesian *Sideritis* has elucidated important features of the evolution of subgenus *Marrubiastrum*. Like virtually every other plant group studied in Macaronesia, *Sideritis* has experienced a single introduction to the region, and monophyly of the island taxa is strongly supported. As in many plant groups that experience radiation in insular settings, the great morphological diversity within the group has resulted in non-monophyletic sectional circumscription. Most other Macaronesian plant groups studied thus far have diversified by inter-island colonization between similar ecological zones. In contrast, the pattern within Macaronesian *Sideritis* is primarily one of adaptive radiation, a pattern more common among Pacific island plant groups. Hybridization appears to be a relatively recent phenomenon within the

group, but one that may be increasing in importance due to the destruction of ecological barriers between formerly isolated taxa, many of which are classified as rare or endangered (Barreno 1984; Gómez-Campo 1996). The occurrence of hybridization has critical implications for rare taxa in insular settings because of the danger of extinction via introgression (Levin et al. 1996). Finally, the high level of aneuploid variation in Macaronesian *Sideritis* appears unique and stands in marked contrast to the general picture of chromosomal stasis in island plants.

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