

DIFFERENT FATES OF ISLAND BROOMS: CONTRASTING EVOLUTION IN *ADENOCARPUS*, *GENISTA*, AND *TELINE* (GENISTEAE, FABACEAE) IN THE CANARY ISLANDS AND MADEIRA¹

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Analysis of sequence data from the internal transcribed spacers (ITS) and 5.8S region of nuclear ribosomal DNA show that Canarian and Madeiran brooms (Genisteeae) of the genera *Teline*, *Adenocarpus*, and *Genista* are related to Mediterranean species and not to species from adjacent parts of Morocco. Each separate colonization of the islands has resulted in contrasting patterns of adaptation and radiation. The genus *Teline* is polyphyletic, with both groups (the “*T. monspessulana* group” and the “*T. linifolia* group”) separately nested within *Genista*. *Genista benehoavensis* (La Palma) and *G. tenera* (Madeira) form, with *G. tinctoria* of Europe, a single clade characterized by vestigially arillate seeds. The Canarian species of *Adenocarpus* have almost identical sequence to the Mediterranean *A. complicatus* and are likely to be the result of island speciation after a very recent colonization event. This Canarian/Mediterranean *A. complicatus* group is sister to the afro-tropical montane *A. mannii* which is probably derived from an earlier colonization from the Mediterranean, possibly via the Red Sea hills. The independent colonization and subsequent radiation of the two *Teline* groups in the Canary Islands make an interesting comparison: the phylogenies both show geographical structuring, each with a central and western island division of taxa. Within the “*T. monspessulana* group” there is some evidence that both continental and Madeiran taxa could be derived from the Canary Islands, although it is likely that near contemporaneous speciation occurred via rapid colonization of the mainland and islands. The finding of two groups within *Teline* also has implications for patterns of hybridization in those parts of the world where *Teline* species are invasive; in California members of the *T. monspessulana* group hybridize readily, but no hybrids have been recorded with *T. linifolia* which has been introduced in the same areas.

Key words: *Adenocarpus*; biogeography; Fabaceae; *Genista*; Genisteeae; island endemism; Macaronesia; molecular phylogeny; radiation; *Teline*.

The Genisteeae (brooms, gorse, and relatives) form a large (>450 spp.) and ecologically important group, distributed widely in both Old and New World regions (Polhill, 1976). They are notable for having a particularly confused generic taxonomy. There are several well-established genera, such as *Cytisus* and *Genista*, but little agreement as to which segregates of these genera are valid (Polhill, 1976; Bisby, 1981). Recent molecular studies have shown the Genisteeae to be

monophyletic (excluding *Melolobium* and *Argyrolobium uniflorum*; Käss and Wink, 1995, 1997), but further sampling is needed to resolve the generic classification.

The Genisteeae are well represented in the Canary Islands and Madeira, with 22 native species in six genera (see references in Table 1). In Madeira there are three endemic species (*Teline maderensis*, *T. paivae*, and *Genista tenera*) and one possibly native, nonendemic species (*Adenocarpus complicatus*). The situation is more complicated in the central and western Canary Islands (Fig. 1) where some groups appear to have undergone adaptive radiations. There are no native representatives on the dry, eastern islands (Fuerteventura and Lanzarote). The genus *Teline* is represented by ten endemic species and *Adenocarpus* by three endemic species (one of which, *A. ombriosus*, is considered to be close to extinction [Santos-Guerra, 1996]). The two common *Adenocarpus* species (local name is “codeso”) are ecologically important, in places forming the dominant vegetation. A good example is found in the “codesales” of high altitude areas of La Palma (*Genista benehoavensis-Adenocarpum spartioidis* A. Santos). *Teline canariensis* (the local name of which is “retamón”) is a prominent component of the fayal-brezal (*Myrica fayae-Ericion arboreae* Oberdorfer) vegetation on Tenerife, and *T. stenopetala* ssp. *stenopetala* (the local name of which is “gacia”) is cultivated in the islands for fodder (Pérez de Paz et al., 1986). *Genista*, however, is represented by a single endemic species (i.e., *G. benehoavensis*) reported as extremely rare in the 1970s

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TABLE 1. Present and former generic placement of Macaronesian Genisteae included in this study, after Gibbs (1967, 1974), Gibbs and Dingwall (1972), Santos-Guerra (1975), del Arco Aguilar, Acebes Ginovés, and Wildpret de la Torre (1978), del Arco Aguilar (1982, 1983, 1993), del Arco Aguilar and Acebes Ginovés (1982), Marrero and Suarez (1988). Dates of homotypic synonyms are given; heterotypic synonyms appear in brackets. (— indicates the species was never placed in these genera.)

Current name	Genus							
	<i>Adenocarpus</i>	<i>Convolvulus</i>	<i>Cytisus</i>	<i>Genista</i>	<i>Rivasgodaya</i>	<i>Spartium</i>	<i>Telinaria</i>	<i>Teline</i>
<i>Adenocarpus foliolosus</i>	1815	—	1789	—	—	—	—	—
<i>Adenocarpus ombriosus</i>	1947	—	—	—	—	—	—	—
<i>Adenocarpus viscosus</i>	1842	—	—	1802	—	—	—	—
<i>Genista tenera</i>	—	—	1784	1891	—	1798	—	—
<i>Genista benhoavensis</i>	—	1861	1954	1982	—	—	—	1975
<i>Teline canariensis</i>	—	—	1891	1753	—	(1801)	—	1842
<i>Teline gomerae</i>	—	—	—	—	—	—	—	1974
<i>Teline maderensis</i>	—	—	1881	1868	—	—	—	1842
<i>Teline microphylla</i>	—	—	(1878)	1825	—	—	—	1972
<i>Teline nervosa</i>	—	—	—	—	1973	—	—	1979
<i>Teline osyroides</i>	—	—	1949	(1891)	—	—	—	1974
<i>Teline paivae</i>	—	—	1881	1868	—	—	—	1972
<i>Teline pallida</i>	—	—	1881	(1819)	—	(1826)	—	1975
<i>Teline rosmarinifolia</i>	—	—	1881	—	—	—	1844	1842
<i>Teline salsoloides</i>	—	—	—	—	—	—	—	1982
<i>Teline splendens</i>	—	—	(1894)	1836	—	—	—	1983
<i>Teline stenopetala</i>	—	—	1887	1836	—	—	—	1842

(Santos-Guerra, 1975) but recently part of a successful conservation program in the high elevation zone of La Palma (Palomares Martínez, 1997). The remaining genera consist of *Spartocytisus* (an endemic genus with two species), *Chamaecytisus* (one variable endemic species), and *Retama* (a single, nonendemic species). The *Adenocarpus*, *Genista*, and *Teline* species have been the subject of much generic revision (see Table 1) and have been revised by Gibbs (1967, 1974), Gibbs and Dingwall (1972) and del Arco Aguilar (1982, 1983, 1993). These treatments, with minor modifications, have been followed here.

Molecular techniques have been used to interpret the historical biogeography of island taxa by sampling putative sister

groups from different source areas (Böhle, Hilger, and Martin, 1996; Kim et al., 1996; Francisco-Ortega et al., 1997a; Panero et al., 1999; Vargas, Morton, and Jury, 1999; Helfgott et al., 2000). Biogeographic links for the Macaronesian flora are diverse. There is evidence for Eurosiberian (*Saxifraga* [Saxifragaceae]; Vargas, Morton, and Jury, 1999), Mediterranean (*Argyranthemum* [Asteraceae], *Bencomia* [Rosaceae]; Francisco-Ortega et al., 1997a; Helfgott et al., 2000), Southern African (*Phyllis* [Rubiaceae]; Sunding, 1979), North and East African (*Dracaena* [Agavaceae]; Sunding, 1979) and New World (*Pericallis* [Asteraceae]; Panero et al., 1999) origins, as well as Asian and Australasian disjunctions (*Apollonias* [Lauraceae], *Picconia* [Oleaceae]; Sunding, 1979). The ITS (internal transcribed spacers)-5.8S region often fails to provide adequate sequence divergence for phylogenetic resolution of rapid and recent speciation, with many examples for island groups (Böhle, Hilger, and Martin, 1996; Kim et al., 1996; Helfgott et al., 2000), and in particular the highly conserved 5.8S region is often uninformative in such studies.

The objectives of this study were: (1) to examine phylogenetic relationships of the Macaronesian Genisteae; (2) to determine whether the Canarian Genisteae share a common biogeographic origin (i.e., European, Mediterranean, or African); and (3) to investigate the biogeography of *Teline* within the Canary Islands. This study is part of an ongoing project concerning the biology of Canarian Genisteae; in a separate paper, one of us (Percy, in press) also reports some aspects of the ecological relationships of Macaronesian Genisteae and endemic species of plant feeding psyllids (Hemiptera). It is hoped that a robust phylogeny for the endemic legumes may shed light on patterns of speciation in their associated insects.

MATERIALS AND METHODS

Taxon sampling—Included in the analyses are 18 of the 22 endemic and native species of Genisteae in the Canary Islands and Madeira, which are considered to have ambiguous or unresolved ancestry. Excluded are the only native nonendemic species, *Retama monosperma* (L.) Boiss., a widespread and common species of less biogeographic interest, and three endemic species in *Spartocytisus* and *Chamaecytisus*, which have been shown by Käss and

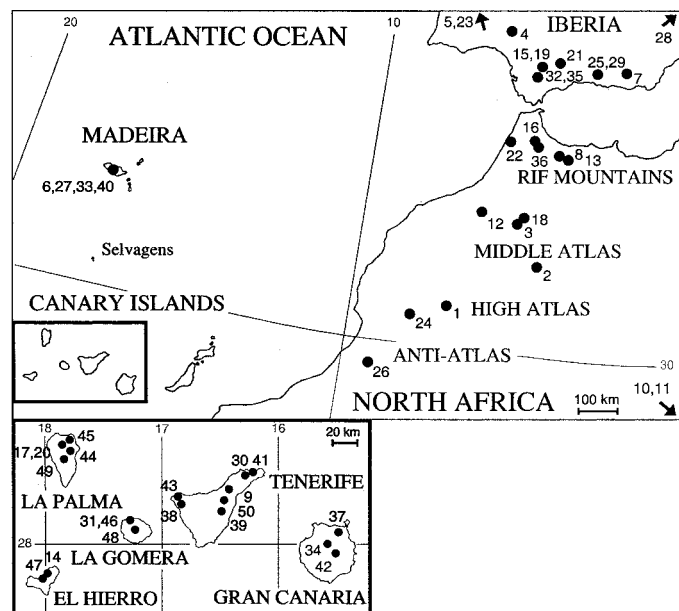


Fig. 1. Map indicating approximate localities of samples used for this study with inset showing the central and western Canary Islands (numbers refer to accession details listed at <http://ajbsupp.botany.org/v89/percy.doc>).

Wink (1997) to have originated from within the *Cytisus*-group. To shed further light on the origins of these species would require extensive sampling among the cytisoid legumes, which was beyond the scope of this study. Fourteen species of *Teline* were sampled, representing the entirety of the genus as usually circumscribed (section *Teline*) with the exception of the restricted endemic *T. osmariensis* (Coss.) P. E. Gibbs & Dingwall, from Morocco. This species, known only from two collections, is described as showing close affinity to *T. monspessulana* (Gibbs and Dingwall, 1972; Maire, 1987). Two Spanish species recently transferred (Talavera and Gibbs, 1999) from *Cytisus* to a separate section of *Teline* (section *Chronanthus*: *T. patens* (DC.) Talavera & P. E. Gibbs and *T. tribracteolata* (Webb) Talavera & P. E. Gibbs) are not considered to be closely related to the Macaronesian species and have not been included here. The majority of intraspecific taxa in the Canary Islands, including all five subspecies of *T. stenopetalata* (the most variable species), were also analyzed, the only exceptions being the very rare *T. rosmarinifolia* subsp. *eurifolia* del Arco and a recently described subspecies, *T. pallida* subsp. *silensis* del Arco (del Arco Aguilar, 2000). Eleven of the 15 *Adenocarpus* species, representing each of the three to five species groups delimited by Lems (1958), Gibbs (1967), and Maire (1987), were used to determine the affiliation of the Canarian taxa. The distinctive basal cytisoid plant, *Argyrocytisus battandieri*, which Talavera and Salgueiro (1999) have suggested should be placed in *Adenocarpus*, is also included. Finally, a number of *Genista* spp. (7 of about 80 spp.) from a wide geographical range in Africa and Europe, as well as different morphological types (unifoliolate and trifoliolate), were chosen to investigate the biogeographic origins and monophyly of the island species of *Genista* and *Teline* and to ascertain the specific affiliation of *G. benehoavensis* from the Canary Islands. Details of all the taxa sampled and location of voucher specimens have been archived at the Botanical Society of America website (<http://ajbsupp.botany.org/v89/>).

In order to provide rooting of the tree, we used a member of a related leguminous tribe (Thermopsidae) as the outgroup (*Anagyris foetida*). An unrooted analysis without *Anagyris* was used to check that this outgroup did not affect the topology of the ingroup, in view of the divergence of *Anagyris* from the ingroup.

Molecular procedures—A total of 50 individuals, representing 36 species, were sampled, mostly from field-collected leaf material (vouchers in GL = University of Glasgow Herbarium). However, herbarium material was used for *Adenocarpus mannii* (E = Royal Botanic Garden Edinburgh Herbarium), *A. ombriosus* (TFC = Herbario de la Universidad de La Laguna, Tenerife) and *Teline stenopetalata* subsp. *microphylla* (from La Gomera) (E). In addition, leaf material was obtained from a cultivated, wild-origin specimen of *Genista tinctoria* (RBGE = Royal Botanic Garden Edinburgh). DNA was extracted from silica-dried leaf material using a QIAGEN DNeasy Plant Mini Kit (Qiagen, Crawley, West Sussex, UK).

Amplification of the ITS1–5.8S rDNA-ITS2 region was accomplished using forward primer ITS 5p: 5'-GGAAGGAGAAGTCGTAACAAG-3' (Möller and Cronk, 1997) and reverse primer ITS 4: 5'-TCCTCCGCTTATTGATATGC-3' (White et al., 1990). However, the amplification of *A. mannii* from herbarium sheets dated 1968 (Tanzania) and 1981 (Malawi) and *A. ombriosus* (specimen dated 1985) required the use of internal primers to sequence ITS1 and ITS2 independently. In this instance, ITS1 was amplified using primers ITS 5p and ITS 2p: 5'-GCTACGTTCTTCATCGATGC-3' (Möller and Cronk, 1997), and ITS2 was amplified with a forward primer we designed using sequences already obtained (ITS 2-LEG: 5'-GCAGAATCCCGTGAACCAT-3') and primer ITS 4. The primer ITS 2-LEG may also give improved amplification of the ITS2 region, over conventional primers, for other papilionoid legumes. Each polymerase chain reaction (PCR) cycle comprised denaturation at 94°C for 4 min, followed by 30 cycles of 94°C for 30 s, annealing at 58°C for 1 min, and an extension of 72°C for 1 min, with a final extension of 72°C for 10 min. Amplified PCR products were purified with a QIAGEN QIAquick PCR Purification Kit (Qiagen), and resuspended in 30 µL of H₂O for direct sequencing using an automated ABI 377 (Perkin-Elmer, Applied Biosystems, Warrington, UK). All the sequences referred to here have been deposited in GenBank database under the accession numbers GBAN-AF330637–GBAN-AF330686. (The prefix GBAN- has been added to these accession numbers

to link the online version of *American Journal of Botany* with GenBank but is not part of the actual accession number.)

Sequence analysis—Sequence boundaries for ITS1–5.8S–ITS2 regions were determined with reference to data for *Vicia faba* (Yokota et al., 1989) and previous sequences for the Genisteae (Käss and Wink, 1997). Alignment of sequences was straightforward and was done manually using the program SeAl (version 1.0a1; Rambaut, 1998). A single ambiguous region of 3 base pairs (bp) in ITS1 (position 219–221 of the aligned matrix) was excluded in a test analysis, but with no change of topology, so the final analysis was run on the complete matrix. The remaining insertion/deletion events (indels) were unambiguous and small (1–3 bp), with the exception of one notable 17-bp deletion in the ITS1 region of *Genista cinerea* and *G. ramosissima* (position 103–119 of the aligned matrix). The length range of ITS1 was 219–241 bp, and ITS2 was 217–221 bp, while 5.8S was uniformly 163 bp without gaps. Features of the aligned matrix are given in Table 2. The aligned matrix is available from GenBank and the aligned matrix and trees (Figs. 2 and 3) are available from TreeBASE (<http://www.herbbaria.harvard.edu/treebase/>).

Phylogenetic analyses were performed with PAUP* (version 4.0b3; Swoford, 1999). The following heuristic search parameters were employed for the maximum parsimony (MP) analysis: 1000 random stepwise addition replicates with tree bisection reconnection (TBR) branch swapping, MULTREES, and COLLAPSE. Bootstrap analyses were performed using 2000 simple addition replicates with TBR branch swapping, and decay indices (Bremer, 1988) were calculated using AutoDecay (version 4.0; Eriksson, 1998) and PAUP*. The analyses were run either with gaps coded as missing or treated as present/absent in a separate binary matrix using contiguous and simple indel coding (Simmons and Ochoterena, 2000). A maximum likelihood (ML) analysis was performed for a comparison to the maximum parsimony (MP) results. Parameters and assumptions used in the ML search were selected using program Modeltest (Posada and Crandall, 1998). The two models selected were Tamura-Nei with gamma distribution, and general time-reversible (GTR) with invariable sites and gamma distribution, the latter selected on the basis of the Akaike information criterion (AIC) (Akaike, 1974). Both these models produced the same tree but the GTR model had a slightly improved (lower) log-likelihood score. Maximum likelihood heuristic search parameters were simple addition sequence of taxa with TBR branch swapping, MULTREES, and COLLAPSE.

To examine the possible polyphyletic origin of *Teline*, MP and ML analyses were run with the monophyly of *Teline* constrained for (a) a monophyletic Macaronesian clade, (b) a monophyletic genus, and (c) a paraphyletic clade with the inclusion of *Genista segonnei*. The monophyly of an apparently paraphyletic *T. stenopetalata* (with and without subsp. *spachiana*) was also examined. The nonparametric Templeton's Wilcoxon signed-rank test, as implemented in PAUP*, and log-likelihood scores were used to assess these assumptions by testing significant length differences between constrained and unconstrained trees (Table 3).

RESULTS

Molecular evolution in island and continental Genisteae—A total of 637 sites with an average of 617 bp per species (excluding gaps) were used in the analyses; 453 sites were constant, 68 variable sites were parsimony-uninformative, and 116 were parsimony-informative. Further details of sequence characteristics are provided in Table 2. Sequences obtained using internal primers lacked between 38–107 bp of an invariable region of 5.8S. Sequence divergence for the ingroup was greater in ITS1 than in ITS2. The 5.8S region was generally conserved; however, there were seven variable sites (one at the 5' end and six toward the 3' end). Three of these 5.8S variable sites provided informative synapomorphies in *Adenocarpus* and *Teline* (these nodes are indicated in Fig. 2), and four variable sites were uninformative (three varying only between the ingroup and the outgroup, *Anagyris foetida*). In par-

TABLE 2. Sequence characteristics of ITS1, 5.8S, and ITS2 regions of 50 individuals representing 41 taxa (36 species) of Genisteae (Fabaceae). Sequence divergence was estimated using uncorrected pairwise distances.^a

Parameter	ITS1	5.8S	ITS2	Whole region
Total length range (bp)	219–241	163	217–221	600–624
Total length mean (bp)	235.7	163	217.9	616.6
Ingroup length range (bp)	219–241	—	217–220	600–622
Ingroup length mean (bp)	235.6	163	217.8	616.4
Outgroup length range (bp)	240	163	221	624
Aligned length (bp)	250	163	224	637
G + C content range (%)	57.1–66.4	51.3–60.9	56.5–64.7	56.2–64
G + C content mean (%)	61.9	53.1	61.7	59.3
Ingroup sequence divergence (%)	0–14	0–1.7	0–11.5	0–8.3
Ingroup/outgroup sequence divergence (%)	11.5–16.7	3.1–3.7	14.3–21.1	11.4–14.5
Number of indels (ingroup)	13	0	8	21
Number of indels (total)	18	0	9	27
Size of indels (ingroup)	1–17	—	1–2	1–17
Size of indels (total)	1–17	—	1–2	1–17
Number of variable sites (%)	89 (35.6)	7 (4.3)	88 (39.3)	184 (28.9)
Number of constant sites (%)	161 (64.4)	156 (95.7)	136 (60.7)	453 (71.1)
Number of informative sites (%)	60 (24)	3 (1.8)	53 (23.7)	116 (18.2)
Number of autapomorphic sites (%)	29 (11.6)	4 (2.5)	35 (15.6)	68 (10.7)
Transitions (minimum)	68	2	55	125
Transversions (minimum)	32	1	36	69
Transitions/transversions	2.1	2	1.53	1.8

Note: ^a Abbreviations: bp = base pairs; indel = insertions/deletions.

ticular, position 384 of the aligned matrix in the 5.8S region provided the single nucleotide change supporting the grouping of *T. maderensis* with *T. stenopetala* (subspecies from La Palma and El Hierro), which would not have been recovered with ITS alone. A number of species pairs/groups had identical sequences; these were (1) *A. foliolosus*, *A. ombriosus*, and *A. viscosus*; (2) *Genista cinerea* and *G. ramosissima*; (3) *T. nervosa* and *T. pallida* subsp. *pallida*; (4) *T. canariensis* and *T. osyroides*; and (5) *T. salsoloides* and *T. stenopetala* subsp. *spachiana*. Uncorrected pairwise distances within the *T. linifolia* group were 0–2.1% including both continental and island taxa, but only 0–0.8% between island taxa alone. Within the *T. monspessulana* group, distances were 0–2.1%, with greater distances between taxa within the Canary Islands (e.g., 1.6% divergence between subspecies of *T. stenopetala*) than between the Canary Island and continental or Madeiran taxa (and greater divergence [1.8%] occurs between Madeiran and Canary Island species than between continental and island species).

Phylogenetic results—A maximum parsimony analysis produced a single tree of length 318, a consistency index (CI) of 0.643 (excluding uninformative characters), and a retention index (RI) of 0.882, which had an identical topology to the tree recovered using ML analysis. Coding gaps as a separate binary matrix provided a single synapomorphy grouping *Teline salsoloides* with *T. stenopetala* subsp. *spachiana*, within an otherwise totally invariable *T. canariensis* clade. Another single indel grouped the three *Adenocarpus complicatus* samples in an otherwise invariable *complicatus*/Canary Island group. Two trees were recovered in an MP search without *Anagyris*. One of these differed from the tree presented, but only by a single change, which was the reverse placement of *Genista florida*-*G. tinctoria* in relation to the *G. segonnei*-*T. linifolia* group. Midpoint rooting gave the same root as that provided by *Anagyris*.

The ITS region provides sufficient resolution of the majority of continental species/group relationships but divergence is in-

sufficient to resolve with confidence the island species groups (Figs. 2 and 3). Nevertheless, the phylogeny provides 15 nodes (excluding intraspecific nodes) with bootstrap support $\geq 75\%$ and six nodes with decay indices ≥ 5 , from which a number of conclusions can be drawn on the relationships between island and continental taxa and relationships between island groups.

Genista—The molecular results support the transfer to *Genista* of *Cytisus benehoavensis* by del Arco Aguilar (1982), and moreover places this Canary Island species together with the Madeiran species, *G. tenera*, in section *Genista* with the type species, *G. tinctoria* (bootstrap = 96%). It is interesting that the members of this clade (*G. benehoavensis*, *G. tinctoria*, and *G. tenera*) all have a small or vestigial aril (Gibbs, 1974; del Arco Aguilar, 1982). The data also support the transfer to *Genista* of *Adenocarpus segonnei* (Gibbs, 1974) and strongly suggests (bootstrap = 93%) affinity within *Genista* to the *Teline linifolia* group.

Adenocarpus—The data analysis support the finding of Käss and Wink (1997) of the very close relationship between *A. foliolosus* and *A. viscosus* of the Canary Islands with the European *A. complicatus* (bootstrap = 93%). Our data further show that a third Canarian species not sampled by Käss and Wink (1997), *A. ombriosus*, has identical sequence to *A. foliolosus* and *A. viscosus*. Within *Adenocarpus* as a whole there appear to be three subgeneric groups (although the *anagyri-folius* group is not strongly supported; bootstrap = 55%). There is support (bootstrap = 78%) for a bracteate clade (species possessing distinct and persistent floral bracts) including *A. nainii*, *A. boudyi*, and *A. telonensis*. *Adenocarpus nainii* has previously been treated as a subspecies of the weakly bracteate *A. complicatus* (with narrow floral bracts, present when the inflorescence is in bud but rapidly caducous on maturation and extension of the inflorescence). *Adenocarpus mannii* occurs in montane regions of tropical Africa and is of biogeographic

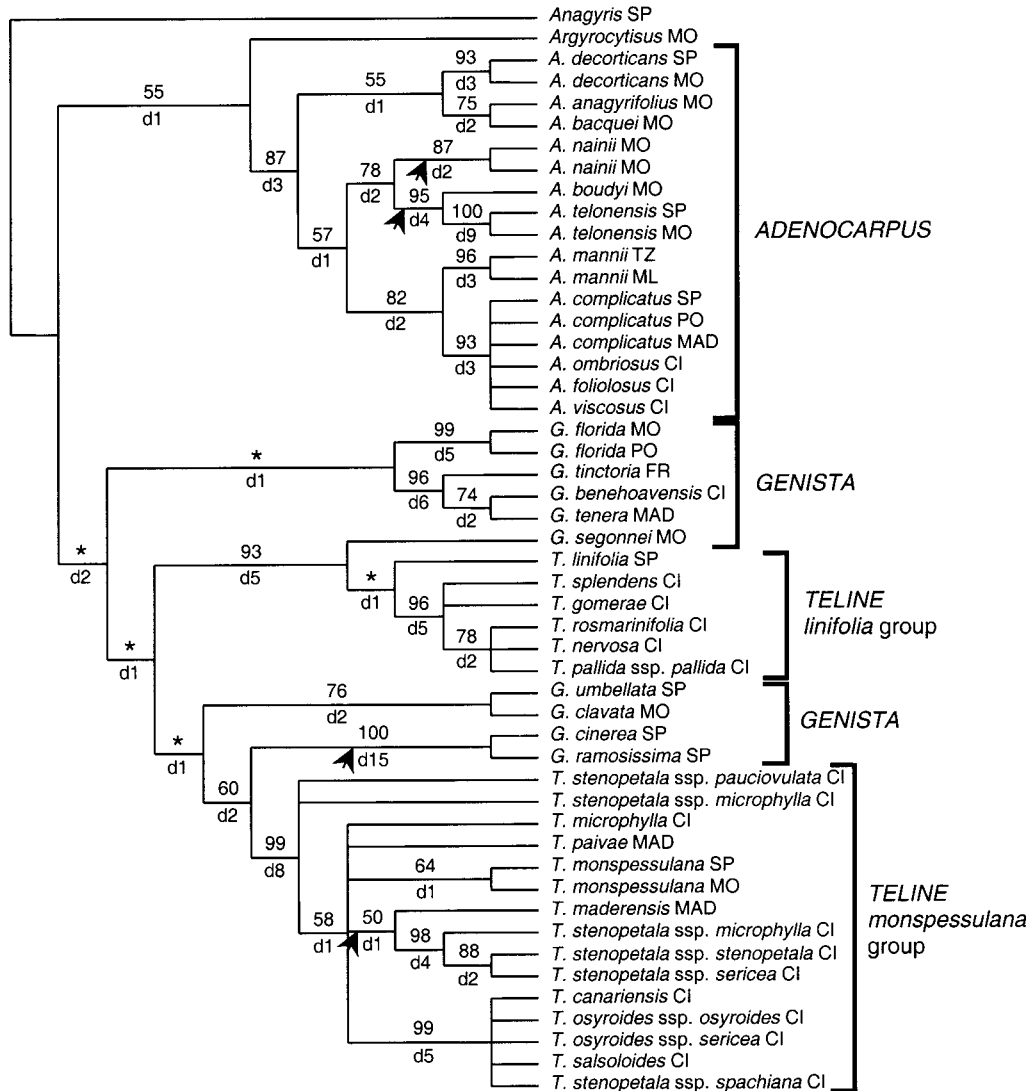


Fig. 2. Cladogram of the single most parsimonious tree (length = 318, consistency index = 0.643 excluding uninformative characters, retention index = 0.882, which has an identical topology to that recovered in the maximum likelihood analysis. Numbers above branches are percent bootstrap support (an asterisk indicates less than 50%) and decay values are given below. The branches supported by variable sites in the 5.8S region are indicated by arrows. Sample origin: CI = Canary Islands, FR = France, MAD = Madeira, ML = Malawi, MO = Morocco, PO = Portugal, SP = Spain, TZ = Tanzania.

interest as sister to the Mediterranean/Canarian *A. complicatus-viscosus-foliolosus* group (bootstrap = 82%).

Teline—Our data show that the genus *Teline* is polyphyletic, contrary to cpDNA (*rbcL*) results presented by Käss and Wink (1995), in which *Teline* is apparently monophyletic. With the more comprehensive sampling in this study, forcing *Teline* to be monophyletic results in an extra tree length of ten steps, a significantly longer topology ($P = 0.05$; Table 3). *Teline* has been considered of genistoid affinity (Polhill, 1976; Bisby, 1981; Norverto, González-Andrés, and Ortiz, 1994; González-Andrés and Ortiz, 1995) and we confirm that *Teline* is nested within *Genista*, as shown by Käss and Wink (1997). There therefore seems little reason, other than traditional taxonomic practice, to maintain the genus separate from *Genista*. Each of the two clades of *Teline* (“*linifolia* clade” and “*monspessulana* clade”) are monophyletic, with independent origins within the genus *Genista*, and each representing separate coloni-

zations of the Canary Islands. The continental species, *T. linifolia*, distributed in the western Mediterranean including northwest Africa, is the sister taxon to the island *linifolia* group. The more widespread continental species, *T. monspessulana*, which has a circum-Mediterranean distribution and occurs in the Azores, is possibly sister to the island *monspessulana* group (but see further discussion below on the biogeography of *Teline*). The Madeiran *Teline* species are in the “*monspessulana* clade.”

Within the island *linifolia* group, *T. pallida* from Tenerife is more closely related to *T. nervosa* and *T. rosmarinifolia* from Gran Canaria (bootstrap = 78%) than to the conspecific *T. pallida* ssp. *gomerae* (P. E. Gibbs & Dingwall) del Arco, from La Gomera. Within the island *monspessulana* group, one of the five subspecies of *T. stenopetala*, subsp. *spachiana*, is identical in sequence to *T. salsoloides* and differs from *T. canariensis* and *T. osyroides* by a single indel. The four Tenerifean taxa (*T. canariensis*, *T. osyroides*, *T. salsoloides*, and *T. sten-*

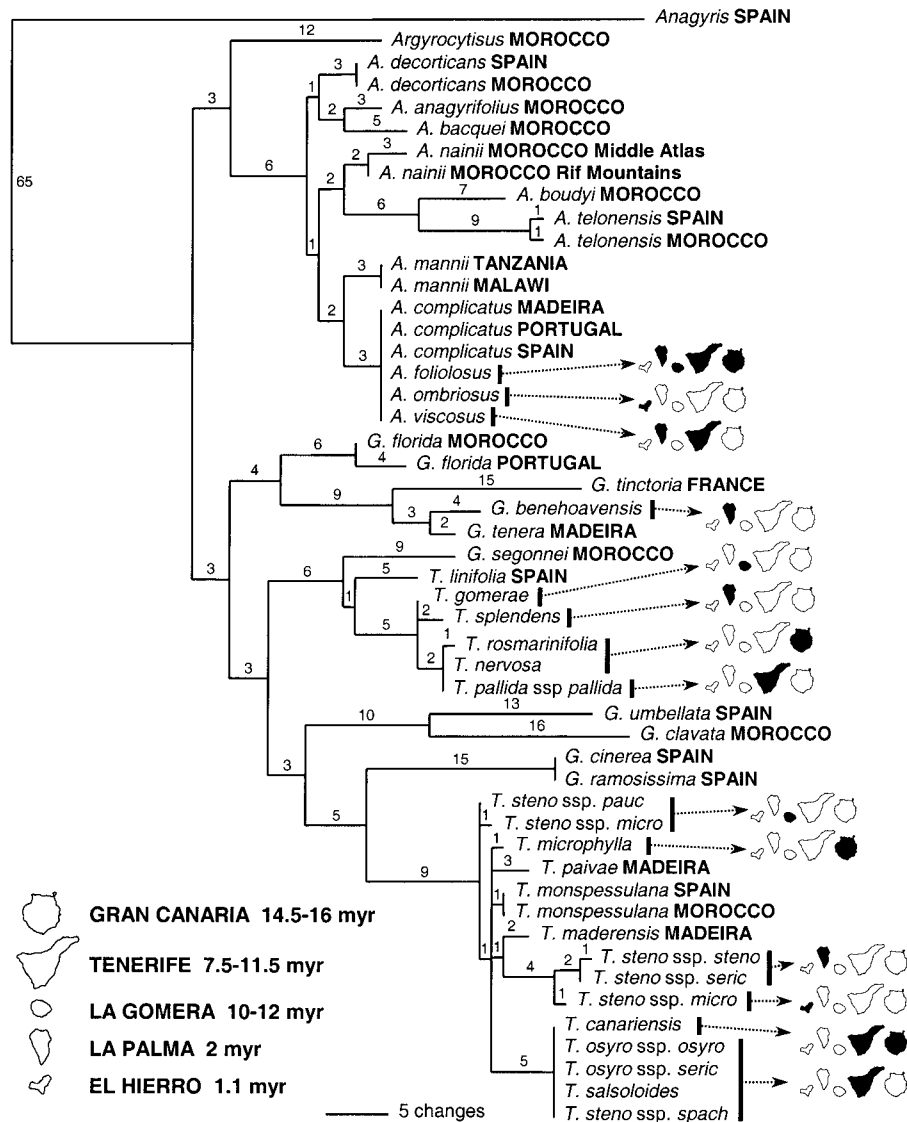


Fig. 3. Phylogram of the single most parsimonious tree with number of substitutions given above branches. Distributions for all Canary Island species are illustrated.

opetala subsp. *spachiana*) form the homogeneous *canariensis* group (bootstrap = 99%), which are distinct from the remaining four subspecies of *T. stenopetala*. Even excluding subsp. *spachiana*, *T. stenopetala* is paraphyletic in this analysis. However, constraining *T. stenopetala* to be monophyletic (ex-

cluding subsp. *spachiana*) requires an additional tree length of only two steps, which is not significant (Table 3). One should therefore interpret these results cautiously, as there is the possibility that gene flow in the “*monspessulana* clade” is confounding phylogenetic signal, and this risk is increased by the

TABLE 3. Tests for monophyly in the genus *Teline*. Significant tree length difference ($P < 0.05$) for constraints is indicated by an asterisk; MP = maximum parsimony.

Constraint	No. of species	Cost of monophyly, MP tree length difference	Templeton (Wilcoxon signed-rank) test, P	Cost of monophyly, log-likelihood difference
<i>T. stenopetala</i>	1 (5 subsp.)	7	0.0082*	35.180
<i>T. stenopetala</i> excl. subsp. <i>spachiana</i>	1 (4 subsp.)	2	0.1797	4.793
Macaronesian “ <i>monspessulana</i> group”	7	1	0.3173	2.763
Macaronesian clade	12	21	<0.0001*	69.445
Genus	14	10	0.0328*	26.140
Genus + <i>Genista segonnei</i>	15	4	0.1025	6.241

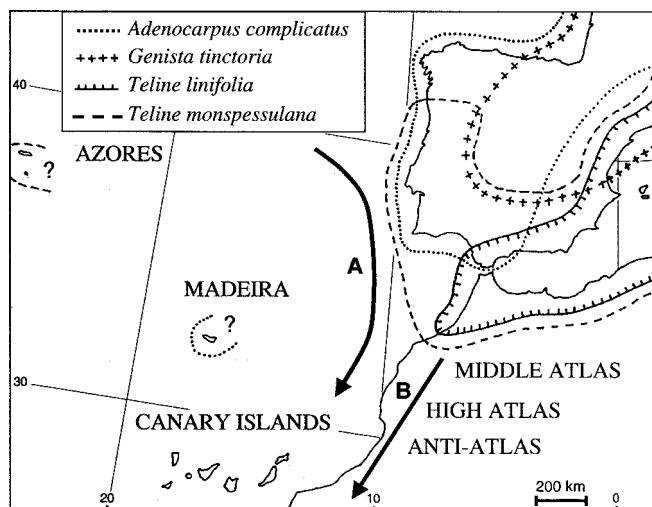


Fig. 4. Map showing disjunction between the Canary Islands and present distribution of putative progenitor species of Canarian *Adenocarpus*, *Genista* and *Teline* (see Fig. 2). A question mark indicates possible native distribution. There is a striking disjunction between the Canarian taxa and their putative sister taxa that are exclusively Mediterranean and do not occur in the Atlas mountains or on the southwestern Atlantic coast of Morocco, which is currently too dry. Arrow A shows the prevailing sea and wind currents, probably accentuated by meltwater currents during glacial periods (Rognon and Coudé-Gaussen, 1996), which may have been responsible for bringing propagules to the Canary Islands. Arrow B shows the Pleistocene southern range extension of Mediterranean taxa postulated by Quézal (see text for discussion) which would have narrowed the disjunction evident today.

human introduction and movement of species (Francisco-Ortega et al., 1997b; Clarke, Johnson, and Murray, 1998).

DISCUSSION

The Mediterranean element in the Canarian and Madeiran flora—The Canarian and Madeiran Genisteae have Mediterranean affinities in common with a large proportion of the Macaronesian flora (Bramwell, 1976; Sunding, 1979; Francisco-Ortega et al., 1997a; Helfgott et al., 2000). The most northern part of Morocco shares many floristic links with southern Europe (Valdés, 1991). However, this eu-Mediterranean element is currently almost completely absent from the northwestern part of Africa (southwestern Morocco) closest to the Canary Islands.

As the Canary Islands are oceanic in origin (Carracedo et al., 1998), long-distance dispersal is required. The Canarian Genisteae, which requires at least seven colonization events to account for 18 species (including the three genera not included in this study), have been relatively successful at distance dispersal. Quézal (1978) and Hooghiemstra et al. (1992) provide evidence for a southward extension of Pleistocene Mediterranean woodland along the northwest edge of Africa, which would have considerably lessened the present-day disjunction (arrow B in Fig. 4). Even so, seeds would still have needed to travel more than 200 km to reach suitable habitat on Gran Canaria. Wind, bird, and sea dispersal may all have been promoted by prevailing northeasterly trade winds and sea currents that were accentuated during the Pleistocene (Rognon and Coudé-Gaussen, 1996) (arrow A in Fig. 4). The Genisteae have an explosive dehiscence: seeds are ejected from the pod, which remains attached to the parent plant. These plants have no obvious adaptations to dispersal by air or water. Mature

seeds of all genera of Canarian brooms typically sink immediately in sea water (D. M. Percy, personal observation). Endozoochorous bird dispersal is a more likely means by which brooms of Mediterranean origin may have reached the Canary Islands. The endemic avifauna of the Canary Islands is predominantly Palearctic, with central European and Mediterranean affiliations (Bacallado, 1976), and European migrants occur as vagrants.

Evolution and biogeography of *Adenocarpus*—The three *Adenocarpus* groups recovered in the molecular phylogeny are also circumscribed geographically. First, there is a predominantly montane group with *A. anagyriifolius* (High Atlas Mountains), *A. bacquei* (High and Middle Atlas Mountains), and *A. decorticans* (montane regions of southern Spain and north Morocco). We also predict that this group includes *A. artemisiifolius* (High Atlas) and *A. hispanicus* (montane regions of central Iberia and north Morocco). It has been suggested by Gibbs (1967) that the latter four species form a group of vicariant species. Secondly, there is the bracteate group which is mainly confined to northwest Africa (Morocco and Algeria). The exception is *A. telonensis*, which has a range extending from northern Morocco to southern Iberia and France. The bracteate group is predicted to include three species additional to those sampled here: *A. cincinnatus*, *A. umbellatus*, and *A. faurei*, which share similar morphological traits (Gibbs, 1967).

The Canarian species belong to the third group, which is otherwise comprised of the polymorphic species *A. complicatus* (subsp. *complicatus* sensu Gibbs, 1967) and *A. mannii*, which occurs only in tropical and subtropical Africa. *Adenocarpus complicatus* is widespread across southern Europe to Turkey and Syria, localized in Algeria, and also present on Madeira. This species has a controversial taxonomic history with a number of separate species recognized by different authors (Castroviejo, 1999) as well as numerous intraspecific varieties (Rivas-Martínez and Belmonte, 1989). The lack of molecular divergence between the Canarian and European taxa implies a rapid and widespread expansion of this group, which contrasts with the relatively localized distributions and greater divergence in the other two *Adenocarpus* groups. The Canarian species are therefore considered part of a recent expansion of *A. complicatus* in southern Europe.

It is interesting that *A. mannii* also exhibits considerable morphological variation throughout its range but no sequence divergence was found between samples from Malawi and Tanzania. Two migration routes (arrows A and B in Fig. 5) have been suggested to explain the presence of European and Mediterranean elements in the montane tropical African flora (Quézal and Martínez, 1958–1959; Wickens, 1976; Quézal, 1978). The absence of *A. mannii* or *A. complicatus* in the Moroccan Atlas suggests that the Morocco-Sahara track (shown by Quézal and Martínez [1958–1959] to have had a Pleistocene extension of Mediterranean woodland; arrow A in Fig. 5) is not the route by which *A. mannii* reached central Africa. Instead, the close relationship with *A. complicatus* and the presence of the latter species around the eastern Mediterranean makes the Red Sea hills migration route (arrow B in Fig. 5) put forward by Wickens (1976) a reasonable alternative hypothesis. Subsequent migration of *A. mannii* to west Africa may have followed the southern migration route (arrow C in Fig. 5) proposed by White (1993).

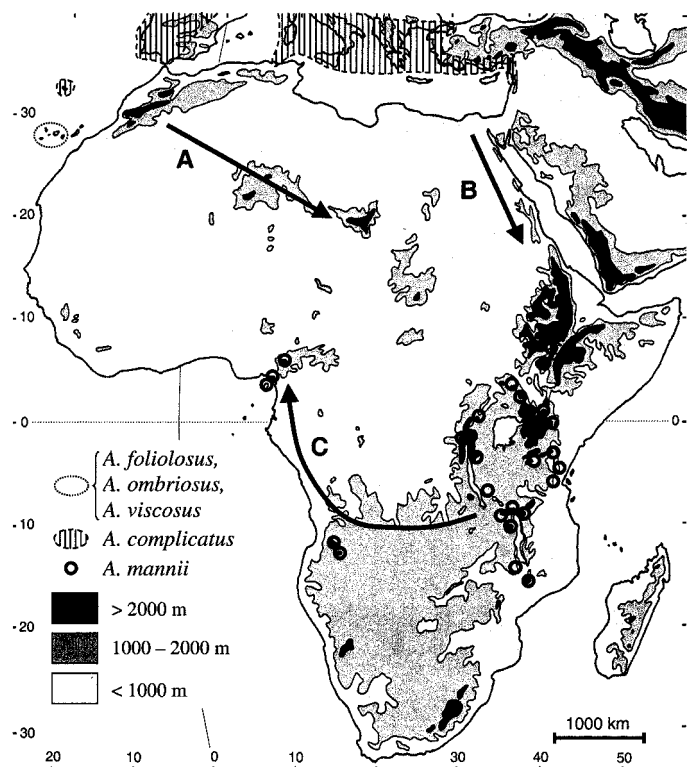


Fig. 5. Map of Africa (adapted from Wickens, 1976) indicating approximate distribution of *Adenocarpus mannii*, with the location of the Canary Island species and the southern extent of the distribution of *Adenocarpus complicatus*, also shown. (A) Incursion of Mediterranean vegetation into the central Sahara via the Ahaggar and Tibesti Mountains, from Quézel and Martinez (1958–59). (B) Eastern incursion of Mediterranean woodland vegetation via the Red Sea hills, from Wickens (1976). (C) Postulated southern migration route of White (1993).

Biogeography of *Teline*—The origin of the “*linifolia* clade” in the Canary Islands is unambiguous—there is a distinct monophyletic island group derived from a continental progenitor. In contrast, the ITS phylogeny for the “*monspessulana* clade” places both the continental and Madeiran species nested within the Canary Island taxa (which would require back-colonization of the continent from the islands). However, the possible derivation of the continental and Madeiran species from the Canary Islands is only weakly supported (bootstrap = 58%), and the additional tree length required to constrain a monophyletic Macaronesian group, excluding the continental *T. monspessulana*, is not significant (Table 3). It is therefore likely that near-contemporaneous speciation occurred via rapid colonization of mainland and islands.

A geographical division is evident in the phylogeny between the central and western island groups. This is particularly evident in the *T. linifolia* clade, which has a subclade of three species endemic to the central islands (Gran Canaria and Tenerife) while the remaining two species are restricted to the western islands (La Gomera and La Palma). In the *T. monspessulana* clade the situation is more complex, but the *T. canariensis* group and *T. microphylla* occur only on the central islands, while all the subspecies of *T. stenopetala* are native only on the western islands. One possible explanation for this east-west vicariance, that is consistent with the phylogeny presented here, is that (in both cases) an original colonization of the relatively old island of La Gomera, which is 10–12 million

years old (myr) was followed by two independent further colonizations from La Gomera of (1) the central islands and (2) the younger western islands (La Palma and El Hierro; 1–2 myr). This scenario would accord with the basal position of La Gomera species in both *Teline* clades.

Island evolution and different patterns of radiation—Each of the main groups of Canary Genisteae shows a different pattern of species diversification. These may be summarized as follows.

The *Teline monspessulana* clade—Geographical segregation within this clade indicates that interisland dispersal has been less frequent than diversification within islands. Diversification within islands is, in turn, linked to island size and habitat diversity. Thus, the most morphological diversity in *Teline* can be found on Tenerife (the most ecologically diverse island) between the five members of the *T. canariensis* group, but this morphological diversity is coupled with the least genetic divergence. The *T. canariensis* group may therefore represent a recent radiation on Tenerife after the main central volcanic and island building period, 1–2 mya (Ancochea et al., 1990). In contrast, *T. stenopetala* (excluding subsp. *spachiana*), which is probably a paraphyletic taxon, currently has four to five subspecies on three islands that exhibit greater genetic divergence but less morphological diversity than the *T. canariensis* group.

The *Teline linifolia* clade—Radiation of this clade in the Canary Islands is less extensive than the “*monspessulana* clade.” Interisland dispersal has apparently been more frequent than diversification within islands, with all species endemic to a single island (typically localized or rare in distribution).

Adenocarpus—The two widespread taxa are distributed in similar altitudinal and ecological niches on different islands as opposed to the geographical/island circumscribed distribution in the *Teline* groups. *Adenocarpus viscosus* occurs only on the high islands (Tenerife and La Palma) in the subalpine zone and generally more xeric habitats, while *A. foliolosus* occupies a lower altitude, more mesic niche on four of the five islands with this habitat. There are also extensive hybrid zones that have developed in locations where these habitats intergrade and often in recently disturbed “hybrid habitats” (Lems, 1958).

Teline and *Adenocarpus* display a contrast between “single island lineages” (*Teline*) and interisland species or “horizontal lineages” (*Adenocarpus*) suggested for other groups (Francisco-Ortega et al., 1992; Francisco-Ortega, Jansen, and Santos-Guerra, 1996; Kim et al., 1996).

Genista—The monotypic island endemism of *Genista* contrasts with the *Teline* and *Adenocarpus* radiations. Neither *Genista* species in Madeira nor the Canary Islands has undergone any diversification or radiation.

Taxonomic implications—*Adenocarpus* as delimited here is clearly a monophyletic genus (bootstrap = 87%). The proximity of *Argyrocytissus battandieri* (a genus typically placed near *Cytisus*) in the tree topology suggests a more cytoid than genistoid affinity for *Adenocarpus* (Badr, Martin, and Jensen, 1994). However, a recent reclassification of *Argyrocytissus*

battandieri in *Adenocarpus* has been proposed due to the occasional presence of glandular papillae on the fruit surface (Talavera and Salgueiro, 1999). The limited sampling here, together with low bootstrap support (55%) grouping *Argyrocytisus* with *Adenocarpus*, does not allow us to confirm this classification, and the phylogenies presented by Käss and Wink (1997) do not provide an unambiguous placement of *Argyrocytisus battandieri*. Within *Adenocarpus* the molecular analysis shows that *A. nainii* is clearly distinct from European *A. complicatus*, and we therefore revert to former taxonomic treatments in recognizing this taxon at specific rank (Maire, 1922).

Teline maderensis has more recently been circumscribed to include *T. paivae* (del Arco Aguilar, 1983; Cannon and Turland, 1994), but as these two species appear to be distinct in the molecular analysis, we have reverted to recognizing two separate *Teline* species on Madeira. Similarly, it seems appropriate to revive the name *T. gomerae* (Kunkel, 1975) in place of *T. pallida* subsp. *gomerae*, due to the apparent polyphyly of the *Teline pallida* subspecies. *Teline stenopetala* subsp. *spachiana*, originally described as "*Genista (Teline) spachiana*" by Webb (1845), was later synonymized with *T. canariensis* by Gibbs and Dingwall (1972), who cited the intergradation of the two taxa. Furthermore, when del Arco Aguilar (1983) placed this taxon in *T. stenopetala*, he reported it as hybridizing with *T. canariensis*. Because of the difficulty of separating some *T. stenopetala* subsp. *spachiana* from *T. canariensis*, this plant is probably best treated as *T. canariensis* (*spachiana*-type). Interestingly, *T. stenopetala* subsp. *microphylla* from La Gomera and from El Hierro may not have the same origin (Fig. 3), which would support their independent treatment as advocated by Pitard and Proust (see Gibbs and Dingwall, 1972).

These taxonomic conclusions require further intraspecific sampling to assess the extent to which the retention of ancestral polymorphisms are affecting the observed pattern in this analysis.

Convergent morphologies in the Genisteeae—Morphological convergence between unrelated members of the island Genisteeae has led to some taxonomic confusion, such as the mistaken synonymization of *Genista tenera* with *Teline osyroides* (noted in Gibbs, 1974). It is also probable that morphological convergence within the "*monspessulana* clade" resulted in the misclassification of *T. stenopetala* subsp. *spachiana*. It is a member of the *T. canariensis* group but shares a number of characteristics (longer racemose inflorescences, larger leaves and flowers) with the morphologically circumscribed *T. stenopetala* group. At a higher level, the polyphyletic origin of *Teline* suggests that a number of the characters used to delimit the genus are convergent (e.g., strophiolate seeds and trifoliolate leaves). In the predominantly unifoliolate *Genista* sensu stricto, reversals to trifoliolate leaves may have occurred several times (e.g., the trifoliolate *G. clavata* in this analysis). Development of the seed aril appears to have independent origins in *Cytisus* and *Genista* and may also have independent origins in *Teline*. However, *G. segonnei*, which is both trifoliolate and possesses strophiolate (rim-aril) seeds, is morphologically similar to *Teline* (Maire, 1987), and constraining *Teline* to be monophyletic with the inclusion of *G. segonnei* does not require a significant increase in tree length (Table 3). Thus, there is a possibly monophyletic *Teline* + *G.*

segonnei group which may justify having a section *Teline* within *Genista*.

Hybridization and species boundaries—The facility with which island species hybridize when ecological barriers are removed has been addressed for a number of different plant groups (Francisco-Ortega et al., 2000). The introduction of several *Teline* species to North America provides a useful comparison to ecological behavior in the native range. It is notable that the one species reported as "a noxious weed" in California (McClintock, 1993), *T. monspessulana*, is the only widespread species within the genus' native distribution. Particularly revealing is the information on interspecific hybridization in California (McClintock, 1993). Five species of *Teline* have been introduced into cultivation in California and have become naturalized. Four of these introductions are members of the *monspessulana* clade, among which hybrids between *T. canariensis*, *T. monspessulana*, and *T. stenopetala* are recorded as "common." Hybrids are also known from Tenerife (and possibly Gran Canaria; Suárez Rodríguez, 1991) between *T. canariensis* and *T. stenopetala*, where the latter species is not native but cultivated. In contrast, *T. linifolia*, also naturalized in California, has not been reported forming hybrids with any of the *monspessulana* clade, and hybrids do not occur between the two *Teline* clades where these are sympatric in their native distributions. Also unrecorded are hybrids within the *linifolia* clade. However, contact between native species, which is frequent in the *monspessulana* clade, does not occur in the *linifolia* clade and no breeding experiments have been conducted to provide further data. These patterns of hybridization reflect the phylogenetic division in *Teline*. Further work is required to determine if hybridization in the *monspessulana* clade in the Canary Islands is contributing to genetic erosion via introgression and assimilation, as has been suggested for other groups (Francisco-Ortega et al., 2000).

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