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RADIATION, DIVERSITY, AND HOST-PLANT INTERACTIONS AMONG ISLAND AND CONTINENTAL LEGUME-FEEDING PSYLLIDS

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Abstract.—Island archipelagos and insect-plant associations have both independently provided many useful systems for evolutionary study. The arytainine psyllid (Sternorrhyncha: Hemiptera) radiation on broom (Fabaceae: Genisteae) in the Canary Island archipelago provides a discrete system for examining the speciation of highly host-specific phytophagous insects in an island context. Phylogenetic reconstructions based on three datasets (adult and nymph morphological characters, and two mitochondrial DNA regions: part of the small subunit rRNA, and part of cytochrome oxidase I, cytochrome oxidase II and the intervening tRNA leucine) are generally consistent. The combined molecular tree provides a well-supported estimate of psyllid relationships and shows that there have been several colonizations of the Macaronesian islands but that only one has resulted in a significant radiation. Psyllid diversification has apparently been constrained by the presence of suitable host groups within the genistoid legumes, and the diversity, distribution, and abundance of those groups. The phylogeny, by indicating pairs of sister species, allows putative mechanisms of speciation to be assessed. The most common conditions associated with psyllid speciation are geographical allopatry with a host switch to closely related hosts (six examples), or geographical allopatry on the same host (four examples). Where allopatric speciation involves a host switch, these have all been to related hosts. There is some evidence that switches between unrelated host plants may be more likely in sympatry. Only one sister pair (*Arytainilla cytisi* and *A. telonicola*) and the putative host races of *Arytinnis modica* are sympatric but on unrelated hosts, which may be a necessary condition for sympatric speciation in these insects. Where several psyllids share the same host, resources appear to be partitioned by ecological specialization and differing psyllid phenology.

Key words.—Biogeography, Fabaceae, host-plant specificity, insect-plant interactions, island colonization, island radiation, Psylloidea.

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Recent radiations of species in which many of the taxa are still extant can provide valuable information about the type and repetition of speciation mechanisms. Processes in adaptive radiations may be related to key innovations, opportunistic expansion in novel environments, changes in reproductive behavior, or a combination of multiple factors depending on the organisms and habitats (Wagner and Funk 1995; Givnish and Sytsma 1997; Grant 1998; Schluter 2000; Gillespie et al. 2001). Shared patterns of evolution in associated insects and plants have been explored in recent phylogenetic studies of phytophagous insects (e.g. Becerra 1997; Farrell 2001; Janz et al. 2001). However, it is often difficult to determine how processes of insect diversification are linked to processes of diversification in their host plants (Mitter and Farrell 1991; Futuyma and Mitter 1996; Becerra and Venable 1999), and the interpretation of historical insect-plant associations, historical host shifts, and ancestral host preferences has proved particularly challenging (Janz and Nylin 1998; von Dohlen and Moran 2000; Ronquist and Liljeblad 2001; Sequeira and Farrell 2001). The study of complex insect-plant interactions on islands has many advantages for better understanding the role of these interactions in speciation. For instance, multiple colonization and speciation events within island systems provide natural replicates for testing ideas about host shifts.

The detection of species radiations may require multiple approaches because of problems arising from either pronounced morphological convergence or divergence (Givnish 1997; Gillespie et al. 2001) or insufficient molecular divergence if the evolution of species was rapid (Brower 1994; Richardson et al. 2001; Malcomber 2002). Phylogenetic studies that combine analyses of environmental factors, species interactions, ecology, biogeography, and geological history may better estimate the conditions that could have promoted an increase in speciation and diversity at the time of radiation (Thorpe et al. 1994, 1995; Orr and Smith 1998; Roderick and Gillespie 1998). In this study, I interpret observed patterns by extrapolating from morphological, molecular, geographical, and ecological data.

Archipelagos are productive environments for studying radiations, and an increasing number of studies are using these ''natural laboratories'' to investigate speciation in various biological groups (reviewed in Roderick and Gillespie 1998; Juan et al. 2000; Emerson 2002; Gillespie and Roderick 2002). However, research in both Pacific and Atlantic island archipelagos has mainly focused on plant and animal groups independently. The interactions between plants and animals are the subject of far fewer studies (Kambysellis and Craddock 1997; Percy and Cronk 1997; Barrett 1998; Givnish 1998; Nogales et al. 2001). Research on islands has only rarely focused on herbivorous insects and their host plants, and these studies have mainly been undertaken in Pacific islands (e.g. Asquith 1995; Gagné 1997, and Roderick 1997). In the central Macaronesian islands (Madeira and Canary Islands, Fig. 1), there are many recent independent evolutionary studies of plants and insects (e.g. Francisco-Ortega et al. 1996; Mes and 'T Hart 1996; Pinto et al. 1997; Brunton and Hurst 1998; Emerson et al. 2000), but only one study, using a predominantly continental phytophagous beetle group, has addressed the question of island colonization in

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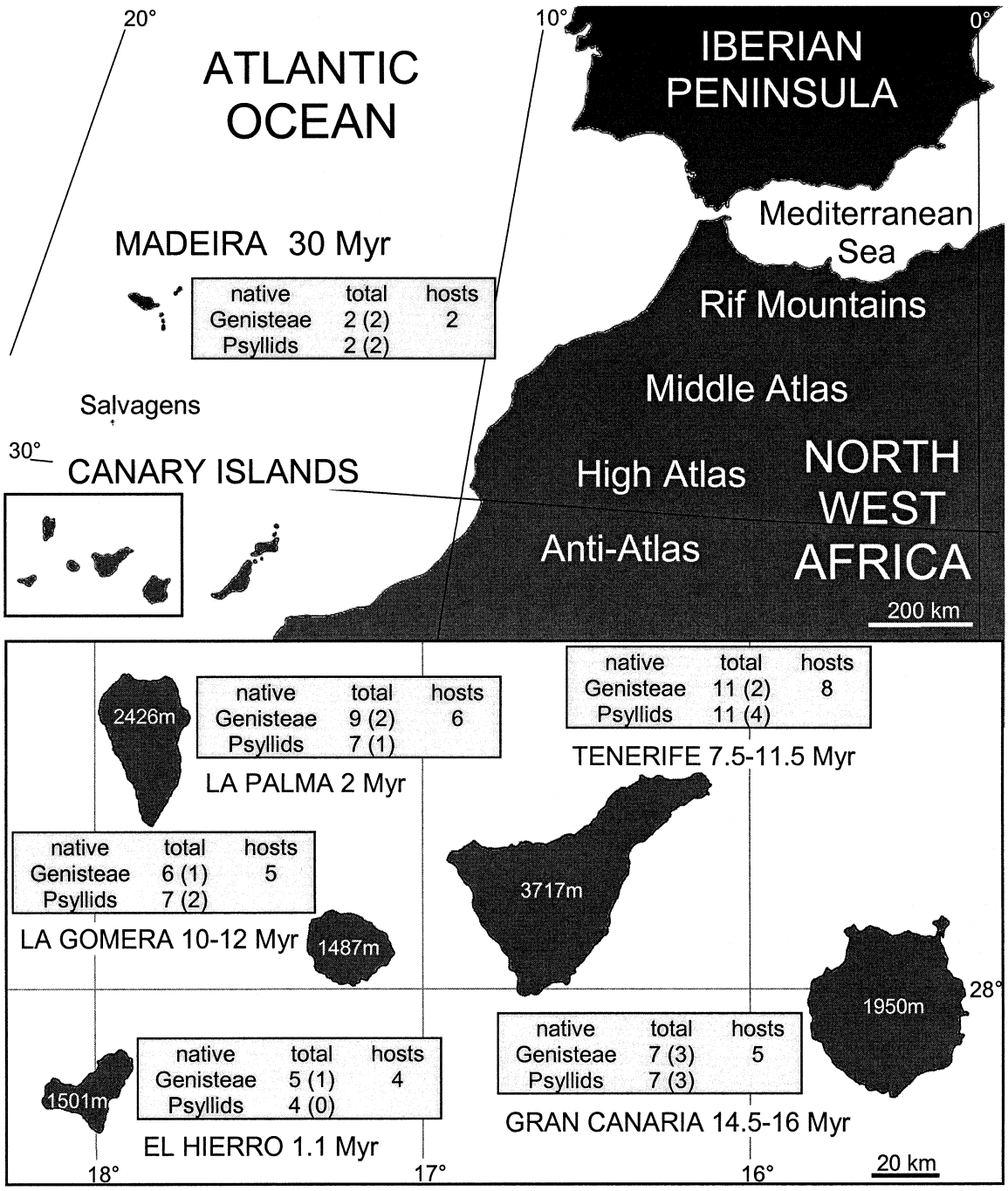

FIG. 1. Map of the Macaronesian islands and adjacent continental areas surveyed for this study. Boxes give the number of native legume species (Genisteae) and psyllids (Arytainainae) on Madeira and each of the central and western Canary Islands (number of endemic species in parenthesis), and the number of Genisteae species on which psyllids are found. The Appendix indicates specific collection locations for each taxon. The Canary Islands are probably derived from an oceanic hot spot (Carracedo et al. 1998) and have established geological ages (Ancochea et al. 1990; Ancochea et al. 1994; Guillou et al. 1996, 1998; Carracedo et al. 1999).

conjunction with host-plant selection (Garin et al. 1999). This study of legume-feeding psyllids represents the first use of phylogenetic analyses to examine evolution in a highly host-specific group of phytophagous insects in the Atlantic Macaronesian islands.

The aim of this study is to understand how processes of geographic and host-plant colonization affect speciation in psyllids. Both the plant and insect groups in this study (genistoid legumes and arytainine psyllids) reach their greatest diversity in the Mediterranean basin and the Macaronesian islands (Hodkinson and Hollis 1987; Cristofolini 1991; Percy 2002, 2003; Percy and Cronk 2002). I use the phylogenetic analyses to assess the monophyly of groups within the Genisteae-feeding psyllids, and to establish the number of times

the Macaronesian islands and different host groups were colonized by ayrtainine psyllids. One weakness that has been highlighted in evolutionary studies of phytophagous insects, particularly host-associated speciation processes, is the paucity of complete taxon sampling (Berlocher 1998). This study uses sister taxon comparisons in a species-rich, comprehensively sampled, monophyletic island group (Percy 2003). I compare island and continental patterns to infer processes involved in host selection and host switching. I examine how diversification in the host-plant group may have both constrained and promoted insect diversity, and I assess which factors (e.g. opportunism and ecological specialization) could have contributed to a species radiation.

As psyllids are predominantly monophagous (feeding on a single host plant), or sometimes oligophagous (feeding on a few closely related host plants; Hodkinson 1974, 1980), acceptance of a new host on colonization of a geographical region (such as an island) would test host specificity where the original host is absent. Host switches to distantly related hosts during geographic colonization events (i.e., allopatrically) would indicate an inherently broad host preference. If island species are only found on plants closely related to the hosts of continental sister taxa (or sister taxa on different islands) an inherently narrow host specificity might be assumed, with the success of geographical colonization ultimately dependent on the presence or absence of familiar plants in the new region. If constraints on host selection are strict, host switches between more distantly related plants might be expected only rarely when opportunities allowed for adaptations to new hosts to develop, such as increased contact with new hosts through sympatry and the formation of host races.

Materials and Methods

Selection of Ingroup/Outgroup Taxa and Data Sources

Psyllids, or ''jumping plant lice'' (Psylloidea) are one of four superfamilies in the monophyletic hemipteran suborder Sternorrhyncha (Campbell et al. 1995; Sorenson et al. 1995; von Dohlen and Moran 1995), all members of which are phytophagous sap-feeders. Psyllids are small (about 1–7 mm) insects that typically carry out their entire life cycle on a single host. Although all six psyllid families are cosmopolitan, many genera have restricted distributions (Hodkinson 1980; White and Hodkinson 1985; Burckhardt 1987a,b). The west Palearctic legume-feeding psyllids belong to two subfamilies (Acizziinae and Arytaininae) in the family Psyllidae (Hodkinson and Hollis 1987). Acizziinae is predominantly a southern hemisphere group (with only four native species in the west Palearctic), and the Arytaininae is predominantly a northern hemisphere group with six genera in the west Palearctic—*Arytaina*, *Arytainilla*, *Arytinnis*, *Livilla*, *Pseudacanthopsylla*, and *Cyamophila* (Hodkinson and Hollis 1987; Percy 2003). The first five of these genera are mostly restricted to the Mediterranean basin, and feed on papilionoid legume shrubs in the tribe Genisteae (e.g. brooms, gorse and relatives; Hodkinson and Hollis 1987; Burckhardt 1989; Conci et al. 1993; Percy 2002, 2003). There are no nongenistoid host records for these genera. The sixth genus, *Cyamophila*, is more widespread from Western Europe to central Asia and feeds on a much wider range of papilionoid legume tribes (Hodkinson and Hollis 1987).

The ingroup includes representatives of all Arytaininae genera that feed on legumes in the west Palearctic region (*Arytaina*, *Arytainilla*, *Arytinnis*, *Cyamophila*, *Livilla*, and *Pseudacanthopsylla*; see Appendix). Multiple individuals are included where species are found on different islands/continental regions and/or different host plants. Two subfamilies, Psyllinae and Acizziinae, were initially selected as possible outgroups for the subfamily Arytaininae. Members of Acizziinae feed on mimosoid legumes in the tribes Acaciae and Ingae, whereas members of Psyllinae feed on a wide variety of predominantly nonleguminous plant families. However, the Psyllinae species were found to be affiliated with *Cyamophila* (which is in the Arytaininae but is not Genisteae-feeding) in the early stages of the molecular analysis, when more distantly related members of the family Psyllidae, the family Triozidae and an aphid, were included. This indicated that the Psyllinae would be an unsuitable outgroup for the Arytaininae. Two species of Acizziinae were subsequently used as the outgroup: one species native to North Africa and the Middle East (*Acizzia hollisi*) and one Australian species (*Acizzia uncatoides*). The two Psyllinae species (*Cacopsylla alaterni*, *C. mali*) were included to analyze the monophyly of the Arytaininae, but not defined as an outgroup.

The datasets (morphological and molecular) in which each taxon is included are indicated in the Appendix. Morphological characters were obtained from alcohol-, slide-, and capillary-mounted material. A total of 67 characters, 43 derived from adults and 24 derived from fifth instar nymphs, were compiled for phylogenetic analysis using the program Nexus Data Editor (NDE; Page 2000). Seventeen (39%) of the adult characters and five (21%) of the nymphal characters were based on morphometric data. These data were partitioned into discrete character states by eye from graph-plotted data that incurred minimal polymorphism. The list of characters, character states, and notes on character scoring are available from the author, and online at http://taxonomy.zoology.gla.ac.uk/~dpercy/psyllids.htm. Two mitochondrial regions were sequenced: the more conserved small subunit rRNA (12S) region, and the more rapidly evolving cytochrome oxidase I (5′ end) plus cytochrome oxidase II (3′ end) and the intervening tRNA leucine (COI-tRNA-COII) region. The taxon sampling includes 84 individuals representing 62 taxa (61 species and one subspecies). A total of 46 taxa were sampled for the morphological analysis. For the two mitochondrial regions, 68 individuals from 61 taxa were sampled for the 12S region, and 73 individuals from 50 taxa for the COI-tRNA-COII region. Most of the samples were collected by the author during fieldwork from 1997 to 2000 in the Canary Islands, Madeira, and adjacent continental areas (material supplied by others is indicated in the Appendix). Insects were collected into 100% ethanol in the field and stored at −20°C.

Observations of psyllid ecology and distributions were made during June to July and December 1997, March to July 1998, March to May 1999, and July to August 2000 (Percy 2002, 2003). Geographical and host-preference ranges were determined by extensive sampling from different host populations and by sampling from the same population in dif-

ferent years and different times of the year. Each host-plant species was sampled between one and 34 times, with only the most rare species sampled once or twice. For each psyllid taxon, samples were collected from between one and 18 different localities. Details of field sampling procedures and localities are given in Percy (2002, 2003). The species delimitations follow current taxonomic accounts (Hodkinson and Hollis 1987; Burckhardt 1989; Conci et al. 1993; Percy 2002, 2003).

DNA Extraction, Amplification, and Sequencing

One to three insects (abdomens and wings removed and retained as vouchers) were either ground in 50 μl of 80% SDS lysis buffer and 20% Proteinase K (Qiagen, Crawley, U.K.) (10mg/ml); or alternatively whole insects were bisected and placed, with Proteinase K, in the buffer provided in the Qiagen DNeasy Tissue Kit (in which case, the whole insect was retained as a voucher after incubation). Specimens were incubated for 24 h at 55°C. The remainder of the extraction was performed with either the Geneclean II kit (Bio 101, Carlsbad, CA) in the first protocol, or the Qiagen DNeasy Tissue Kit in the second. Specimens collected by the author were processed within three years; however, dry mounted specimens and alcohol preserved material up to 20 years old (supplied by D. Burckhardt and I. Hodkinson) amplified successfully for the shorter 12S region (probably aided by highly conserved primers) but did not, or only poorly, amplified for the longer CO region.

The primers used to amplify 12S were SR-N-14588 and SR-J-14233 (Simon et al. 1994). The COI-tRNA-COII region was amplified for some taxa using primers UEA9 (Lunt et al. 1996) and C2-N-3389 (Simon et al. 1994). These CO primers amplified 68% of the taxa, and additional primers were designed to amplify the remaining taxa: DP1: 5′ GTT AGTAGTGGGTTATTAAGTTCRTC 3′ (positioned in COII and used as an antisense primer to UEA9); DP2: 5′ CGAT AATTTTAATTGTTAGTAGYGG 3′ (positioned in COII as an antisense primer to UEA9); UEA9-MOD: 5′ GGTATG CCTCGTCGTTATTCTAAYTAYC 3′ (positioned in COI and used as a sense primer to C2-N-3389).

Each PCR cycle comprised denaturation at 94°C for one min., 41 cycles of denaturation at 92°C for 30 sec, annealing at 45°C for 40 sec and an extension of 65°C for 90 sec, with a final extension of 72°C for 10 min. Amplified PCR products were either run on agarose gels and purified with a Qiagen QIAquick Gel Extraction Kit or were purified with a Qiagen QIAquick PCR Purification Kit, in both cases resuspension was in 30 μl of water for direct sequencing using an automated Perkin-Elmer ABI 377 sequencer with ABI Prism Dye Terminator Cycle Ready Reaction Kit (Applied Biosystems, Washington, U.K.) Sequences were aligned manually using the program Se-Al (ver. 1.0a1; Rambaut 1998). All the sequences referred to here have been deposited in GenBank: the 12S sequences under the accession numbers AF367776–AF36784, and the COI-tRNA-COII sequences under the accession numbers AY100373–AY100445. Both the aligned matrices are available from GenBank, and these matrices plus the morphological matrix, and trees (Figs. 2, 3) are available from TreeBASE (http://www.treebase.org/).

Phylogenetic Analyses

Molecular and morphological phylogenies were constructed using PAUP* (ver. 4.0b3; Swofford 1999) and MrBayes (ver. 2.01; Huelsenbeck and Ronquist 2001). In PAUP*, the following heuristic search parameters were employed for the parsimony analyses: 100 random stepwise addition replicates with tree bisection-reconnection (TBR) branch swapping, saving multiple trees (MULTREES) and collapsing zero-length branches (COLLAPSE). For the analysis of the morphological data, characters were treated as unordered, with the exception of the morphometric characters, which were treated as ordered with multiple states as polymorphisms in order to preserve information on the relative similarity between taxa and overlapping states. Bootstrap analyses (2000 replicates) were performed using simple addition sequence of taxa with TBR branch swapping. Parameters and assumptions used in the maximum-likelihood (ML) searches were selected using program Modeltest (Posada and Crandall 1998) and based on the Akaike Information Criterion (AIC). The model selected for the 12S data was HKY85 with invariable sites and gamma distribution. The model selected for the CO data was general time-reversible (GTR) with invariable sites and gamma distribution. Maximum likelihood heuristic search parameters were simple addition sequence of taxa with TBR branch swapping, MULTREES, and COLLAPSE. Distance neighbor-joining (NJ) analyses were used to provide a comparison of topology and bootstrap. A ML analysis of the combined molecular data (12S and CO-tRNA) was performed using Bayesian methods and a GTR model in MrBayes. For this analysis four simultaneous Monte Carlo Markov chains (MCMC) were run for one million generations, saving a tree every 100 generations. The partition homogeneity test (ILD test of Farris et al. 1994) implemented in PAUP* was used to assess congruence between the different data sets (12S, CO-tRNA, and morphology). Biogeographic assumptions (i.e. derivation of continental species from the Macaronesian islands) in the genus *Arytinnis* were tested using constraint trees and the nonparametric Templeton's Wilcoxon signed-rank test implemented in PAUP*. Genistoid host-plant groups were optimized onto the combined molecular phylogeny using MacClade 3.07 (Maddison and Maddison 1992). Host-plant associations were treated as an unordered character with delayed and accelerated transformation (DELTRAN and ACCTRAN) optimization.

RESULTS

Phylogenetic Analyses

Molecular and morphological analyses recover the same major groups although significant incongruence was found between morphological and molecular data. The length of the 12S alignment is 342 characters (mean of 331 bp, 168 variable sites with 134 parsimony informative, and A + T content is 74–80%). The length of the COI-tRNA-COII alignment is 639 characters (mean of 618 bp, 352 variable sites with 297 parsimony informative, the tRNA is 65–71bp, and A + T content is 67–83%). The results of the partition homogeneity test implemented in PAUP* indicated that the two molecular datasets (12S and CO-tRNA) were compatible (*P*

= 0.99), but that the molecular and morphological data were significantly incongruent with one another ($P = 0.01$). Therefore, a maximum-parsimony (MP) tree for each of the three data sets (12S, CO-tRNA, and morphology) is presented independently (Fig. 2), and a combined molecular analysis (12S and CO-tRNA) is presented in Figure 3.

The MP search of the 12S data found 750 trees, and five islands of trees. The 12S tree presented in Figure 2A is one of the 750 MP trees, which was selected from the one island of trees with the most similar topology to that recovered after successive reweighting of the 12S data using the mean rescaled consistency index in PAUP*; the 22 nodes that collapse in a strict consensus of all 750 MP trees reveals the lack of resolution present in the 12S data. The MP search of the CO-tRNA data found a single island of six trees. The MP CO-tRNA tree presented in Figure 2B is one of the six trees that differs only in minor respects to the other five trees as shown by the three nodes in the genus *Arytinnis* that collapse in a strict consensus of all six trees. The MP search of the morphological data found a single island of 18 trees. The MP morphology tree presented in Figure 2C is one of the 18 trees, and as with the CO analysis, the five nodes that collapse in the strict consensus of all 18 trees are all within the morphologically homogeneous genus *Arytinnis*. The combined molecular phylogenies presented in Figure 3 are the strict consensus of eight trees derived from a MP analysis (large tree) and an ML Bayesian analysis (small tree), the topologies of which are very similar. A majority rule consensus of 9600 trees from the ML Bayesian analysis (the ln likelihood score stabilized after 4000 generations and therefore the first 400 trees were discarded) produced posterior probability values considerably higher for many of the same nodes than in either the MP or NJ bootstrap analyses (Fig. 3). The optimization of the host groups onto the tree (Fig. 3) differed between DELTRAN and ACCTRAN only at the base of the *Adenocarpus*-feeding *Livilla* plus *Pseudacanthopsylla* group.

Monophyly of Genisteae-Feeding Arytaininae and Genisteae-Feeding Genera

To assess patterns and directions of host-plant and geographical colonization it is important to establish whether the traditional classification is supported by the phylogenetic analysis. *Cyamophila* is the only non-Genisteae-feeding genus among the papilionoid legume feeders in the west Palearctic Arytaininae. The molecular analyses suggest that *Cyamophila* is distinct from the Genisteae feeders, and is more closely related to the subfamily Psyllinae (whose members feed on a wide variety of hosts including species in the Rosaceae, Rhamnaceae, Salicaceae, and the Caesalpinioideae) than to other Arytaininae. This placement suggests that papilionoid legumes may have been colonized at least twice within the west Palearctic region. The placement of the genus *Pseudacanthopsylla* has been considered problematic (Hodkinson and Hollis 1987). An outlying position for *Pseudacanthopsylla* is supported by the morphological data (Fig. 2C), and partly by the 12S data (ML analysis) and would imply two or more origins of the Genisteae-feeding habit. However, a NJ analysis of the 12S data, all analyses of the CO-tRNA data, and the combined molecular MP and ML analyses place *Pseudacanthopsylla* within the Genisteae-feeding Arytaininae. An inclusive position for *Pseudacanthopsylla* suggests a single evolution of the Genisteae-feeding habit and the MP strict consensus presents a monophyletic Genisteae-feeding group (Fig. 3). Nevertheless, the placement of *Pseudacanthopsylla* needs to be tested further, with additional sampling of Afrotropical genera considered related to this genus (Hodkinson and Hollis 1987).

The phylogenies in Figures 2 and 3 clearly show that three major generic clades are present in all analyses: AI (*Arytinnis*), an almost exclusively Macaronesian island genus with 16 endemic Canary Island species, two endemic Madeiran species, and three continental species (generic sampling is complete); AR (*Arytaina*), a genus of 14 species (five species including the type species, *Ar. genistae*, are sampled), three of which are endemic to the Canary Islands; L (main *Livilla* group), which, although representing the majority of *Livilla* species (about 32, of which 12 are included here), does not include the somewhat anomalous type species group (four species, represented in this analysis by *L. vicina*). This main group of *Livilla* includes neither the single endemic Canary Island species (*L. monospermae*) and its continental sister taxon (*L. retamae*), nor *L. nervosa*, nor a small group of exclusively *Adenocarpus*-feeding species. A fourth generic group, A (*Arytainilla* sensu stricto), is a group of nine species (six taxa including the type species, *A. delarbrei*, are sampled) which is characterized morphologically by a massive ovipositor; only one member of this group (*A. serpentina*) is endemic to the Canary Islands. *Arytainilla* sensu stricto is recovered as a monophyletic group in the CO-tRNA, morphological, and the combined molecular analyses, though not in the 12S analysis. All three datasets (12S, CO-tRNA, and morphology) suggest that the genera *Livilla* and *Arytainilla* sensu lato are paraphyletic as currently delimited, whereas *Arytinnis* and *Arytaina* are monophyletic genera.

Island and Continental Colonizations

The phylogenetic analyses can be used to infer the number and direction of geographic colonization events. There are 23 native legume-feeding psyllids in the Macaronesian islands, two in Madeira, and 21 in the Canary Islands, all of which are endemic (Loginova 1976; Percy 2003). The 21 Canary Island species are found on the five central and western islands (Fig. 1; there are no native genistoid legumes on the two much drier, eastern islands, Fuerteventura and Lanzarote). At least four, possibly five, independent colonizations of the Canary Islands are suggested by the data (Fig. 3): one colonization resulted in a radiation of 16 species in *Arytinnis*; two separate colonizations are each represented by single species in *Arytainilla* (*A. serpentina*), and *Livilla* (*L. monospermae*); and there have been at least one, possibly two, independent colonizations in the genus *Arytaina* (the ambiguity is due to the lack of support for the monophyly of the three Canary Island *Arytaina* species, *Ar. devia*, *Ar. nubivaga*, and *Ar. vittata*). The two endemic Madeiran species and three continental species form a well-supported subclade within *Arytinnis*. The possibility of one or two back colonizations to the continent (i.e., one colonization of the continent from the Canary Islands and one from Madeira; see

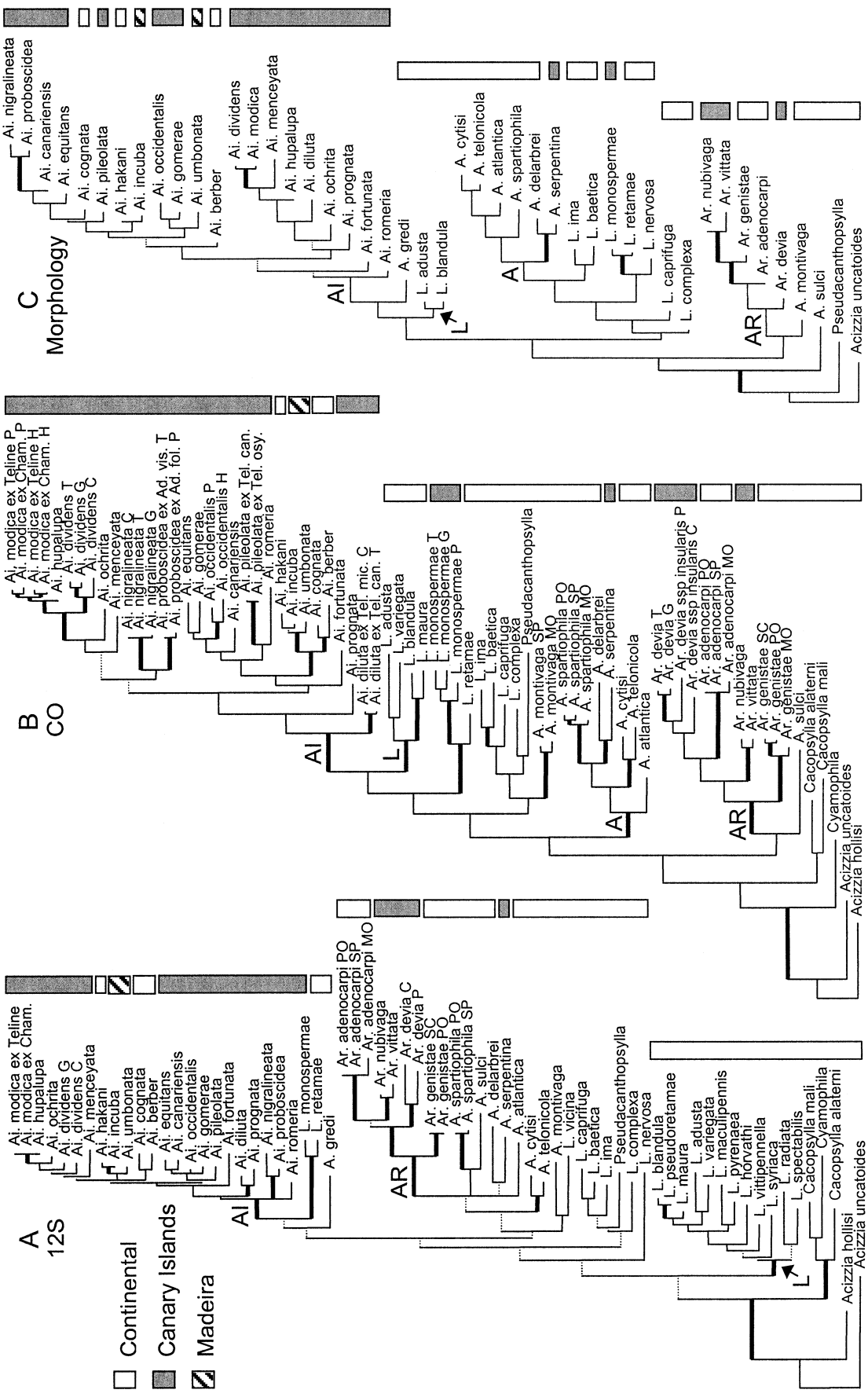

FIG. 2. Phylograms for each dataset. (A) 12S: one of the 750 maximum-parsimony (MP) trees based on 12S rRNA sequences (length 807, CI 0.32 excluding uninformative characters, RI 0.614); (B) CO: one of the six MP trees based on COI-tRNA leucine-COII sequences (length 2280, CI 0.248 excluding uninformative characters, RI 0.613); (C) Morphology: one of the 18 MP trees based on 67 morphological characters (length 554, CI 0.484 excluding a single uninformative character, RI 0.612). Thick branches indicate nodes with bootstrap values >75%, and dotted branches indicate the nodes that collapse in the strict consensus of all trees for each dataset. Labeled nodes: A, *Arytainilla* sensu stricto; AI, *Arytinnis*; AR, *Arytaina*; L, main *Livilla* group. Where taxa are sampled from different host plants, these have been indicated and abbreviated from host-plant names in the Appendix. Continental, Canary Island, and Madeiran distributions are shown. Abbreviated codes for sample origin (Figs. 2, 3): Canary Islands: C, Gran Canaria; T, Tenerife; G, La Gomera; P, La Palma; H, El Hierro; MAD, Madeira; MED, Mediterranean; MO, Morocco; PO, Portugal; SC, Scotland; SP, Spain.

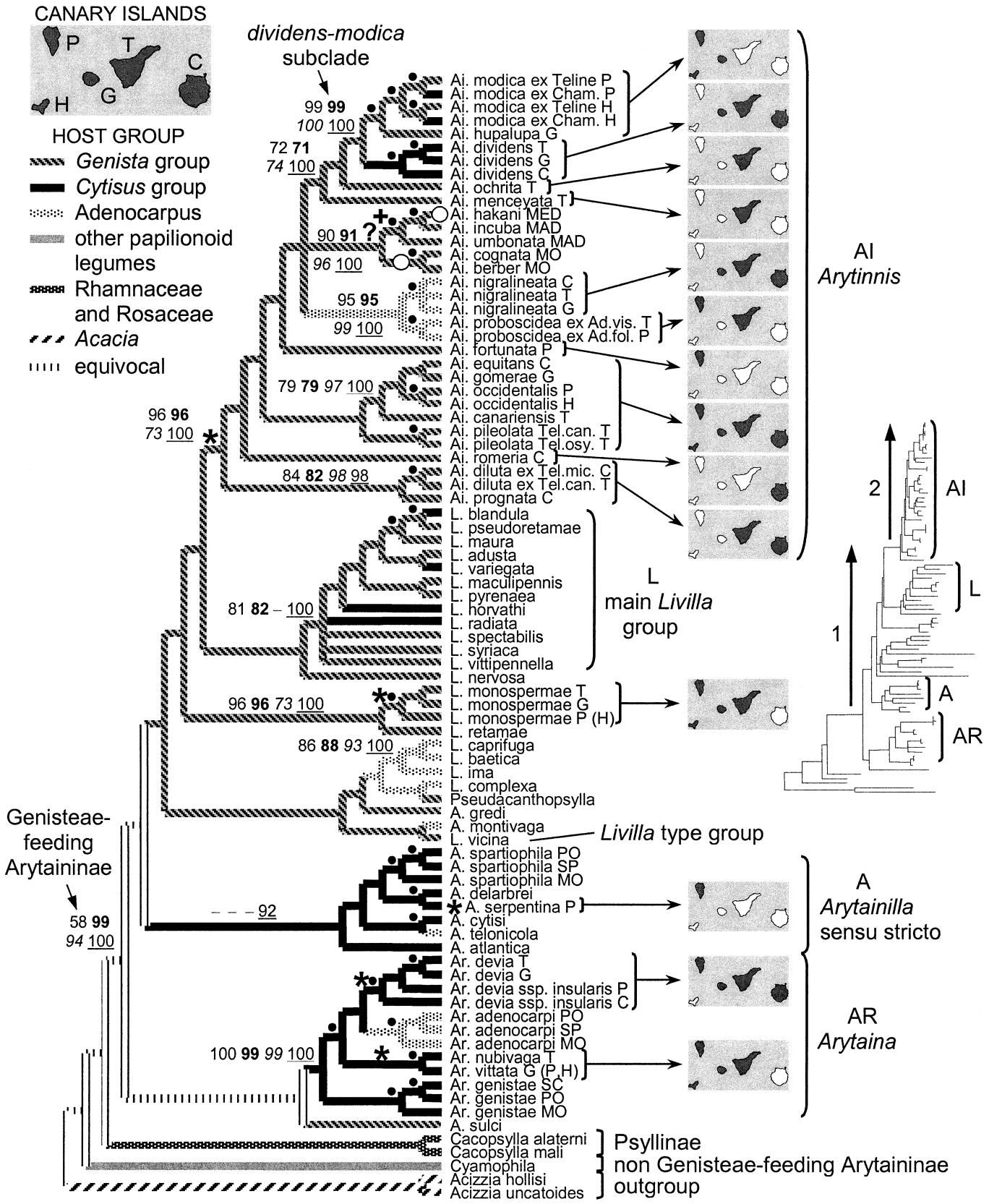

FIG. 3. Host-plant distributions, geographic locations, and tree architecture. The large tree is the strict consensus of the combined molecular maximum-parsimony (MP) analysis; numbers at nodes indicate support for major groups and subclades (left to right: MP bootstrap; MP bootstrap excluding the two *Acizzia* species, and with *Cacopsylla* and *Cyamophila* specified as the outgroup [bold]; NJ neigbor-joining bootstrap [italic]; maximum-likelihood (ML) Bayesian posterior probability value [underlined]; the remaining nodes with

Fig. 3) remains equivocal (indicated by a question mark) due to a nonsignificant ($P = 0.06$) additional tree length (10 steps) required to constrain the subclade of Madeiran and continental species as sister to the Canary Island species.

Only one colonization of the islands has resulted in a significant radiation (18 species in *Arytinnis*). In contrast, colonizations by *Arytaina*, *Arytainilla*, and *Livilla* have resulted in only one or two psyllid species after each colonization event. Among the island *Arytinnis*, the ''basal'' taxa, which may be ancestral in the island radiation (*Ai. diluta*, *Ai. prognata*, and *Ai. romeria*), are found on the oldest island (Gran Canaria), whereas some more recently derived taxa (e.g. *Ai. occidentalis* and *Ai. modica*) only exist on the youngest islands (La Palma and El Hierro). However, to determine whether colonization of the Canary Islands matches a ''stepping stone'' model, which is the case in some island groups (Roderick and Gillespie 1998; Juan et al. 2000), more intraspecific sampling and resolution within *Arytinnis* is needed.

Diversity among Island and Continental Species

A comparison of sequence divergence with morphological divergence and geographic distributions can provide an indication of dispersal patterns and gene flow. Sequence divergence (estimated using uncorrected pairwise distances from the CO-tRNA data) between individuals from different geographic regions or hosts provides a comparative measure of intraspecific divergence in continental and island taxa. Three continental species (*Ar. adenocarpi*, *Ar. genistae*, and *A. spartiophila*) are widespread, found on several closely related host species in different geographical regions. Individuals of these taxa were sampled from Morocco, Spain, Portugal, and Scotland (Figs. 2, 3, and Appendix). Among the island species, individuals were sampled from populations that were found either on different islands and/or different host plants. Intraspecific genetic divergence was greatest within the four Canary Island species that existed on different islands but on the same host plant (*L. monospermae* from three islands, 4–5%; *Ar. devia* from four islands, 1–10%; *Ai. dividens* from three islands, 1–4%; and *Ai. occidentalis* from two islands, 5%). Divergence within the widespread continental species that were sampled from different hosts was less than 3%, and in each case divergence between Moroccan and European samples was double or more than double the divergence within Europe (e.g. *Ar. genistae* from Portugal and Scotland showed 0.8% sequence divergence, but 2.8% divergence from the Moroccan individual). This pattern could result either from greater gene flow on the continent than between islands, or by the establishment of recent continental distributions. Extensive continental gene flow is probably unlikely, whereas both northern Africa and the Canary Islands may have provided glacial refugia, with more recent dispersal through Europe in the continental species. In the Canary Islands, nine of the 21 species (43%) inhabit more than one island (*L. monospermae*, *Ar. devia*, *Ar. vittata*, *Ai. dividens*, *Ai. diluta*, *Ai. modica*, *Ai. nigralineata*, *Ai. proboscidea*, and *Ai. occidentalis*). All but one (*Ai. modica*) of these species is specific to a single host plant, or feeds on two closely related hosts. There is no evidence of major host switches coinciding with interisland colonizations. About half of these species on multiple islands shows low intraspecific molecular divergence (maximum 0.02–2.0%), suggesting recent interisland dispersal, but four species (all specific to a single host) show considerably greater divergence (maximum 4–10%), which can be compared to the maximum divergence in the genus *Arytinnis* (13%) as a whole. Sequence divergence is therefore not always related to the morphological divergence on which the species delimitations are based, and appears to be greatest (possibly via a process of drift) in putatively older populations that have been isolated on different islands but have not undergone ecological or host shifts.

Host Switching by the Genisteae Feeders

The mapping of host preference onto the phylogenetic analysis provides an indication of the frequency of host switching and can be used to infer whether, and under what conditions, host switching is related to speciation. When the host genera are mapped onto the psyllid tree, four of the five colonizations of the Canary Islands and two continental and Madeiran colonizations coincide with a host switch to a different genistoid genus. Only one Canary Island species (*L. monospermae*) and one Madeiran species (*Ai. incuba*) are found on the same host genus as their continental sister taxa (*L. retamae* and *Ai. hakani* respectively). However, when the host genera are categorized according to affiliations within the Genisteae (genistoid groups from Polhill 1976; Bisby 1981; Käss and Wink 1997), host switches between genera that coincide with geographical colonization events are all switches to related genera within the same major genistoid groups (Fig. 3). In addition, the majority of species within each of the well-supported psyllid genera or clades, are found on related hosts in the same genistoid group. Of the 18 island *Arytinnis* species, 13 feed on *Teline*, two on *Adenocarpus*, one on *Chamaecytisus*, one on both *Teline* and *Chamaecytisus*, and one on *Genista* (Table 1). In the genus *Arytinnis*, *Teline* appears to be the ancestral island host group with switching to other host genera occurring within the islands. The legume genera *Adenocarpus*, *Chamaecytisus*, *Genista*, *Retama*, and *Spartocytisus* each have one or two island species. The colonization of these legumes by *Arytinnis* (one species on *Genista*, two species on *Adenocarpus*), *Arytaina* (one species on *Chamae-*

←

bootstrap values >75% in either, but usually both, the MP or NJ analyses are indicated by a black dot; host groups are mapped as an unordered character using ACCTRAN optimization; colonizations of the Canary Islands are indicated by an asterisk; equivocal colonizations (question mark) of Madeira and the continent, from the Canary Islands, are indicated by a cross (Madeira), and open circles (continent; see text); distributions for the Canary Island taxa and subclades are indicated with island codes (abbreviated as for Fig. 2) and maps; island letters in parenthesis indicate taxon distribution that was unsampled. The *dividens-modica* subclade of *Arytinnis* is explored further in Figure 4. The small tree is the single ML Bayesian tree with the best ln score; this shows the short internal branches along the backbone of the tree, which suggest an initial radiation (1) when the Genisteae were first colonized, and a second radiation (2) when the Canary Islands were colonized by *Arytinnis*.

cytisus, two species on *Spartocytisus*), *Arytainilla* (one species on *Spartocytisus*), and *Livilla* (one species on *Retama*), with only one or two psyllid species derived from each colonization, reflects the low diversity of the hosts.

A comparison of host-plant associations and geographical distributions in sister species pairs (Table 2) indicates that the majority (seven pairs) are found on the same or related hosts, but on different islands/geographical regions, whereas one species pair and the putative host races of *Ai. modica* are sympatric but on unrelated hosts. The remaining two pairs exist on the same island, in one case on the same host (*Ai. diluta* and *prognata*) and in the other case on sister host taxa (*Ai. nigralineata* and *proboscidea*), but these taxa exist in different localities and habitats, and may have diverged through ecological shifts (discussed below). In addition, relationships within six well-supported subclades of psyllids also indicate that where taxa are sympatric the host plants are unrelated (e.g. *Ai. dividens* and *hupalupa* on *Chamaecytisus* and *Teline*) or moderately closely related (e.g. *Ai. incuba* and *umbonata* on *Teline* and *Genista*), and that where hosts are closely related, taxa are allopatric (e.g. *Ai. equitans*, *gomerae*, *occidentalis*, and *canariensis*, which are all found on a subgroup of hosts in the genus *Teline*, but on separate islands; and *L. baetica*, *caprifuga*, and *ima* on a subgroup of *Adenocarpus* hosts in different mountain ranges of Morocco and southern Spain).

TABLE 1. Summary of distribution and host associations for the 23 Macaronesian island taxa (abbreviated psyllid genera and island codes are given in the Fig. 2 caption). Multiple psyllids on a single host often occur on different host subspecies (e.g. the five subspecies of *Teline stenopetala*; Percy 2003). Hybrids between host plants are indicated where these have been recorded (Lems 1958; Arco Aguilar 1983; Suárez Rodgríguez 1991).

Maximum no. of hosts	Psyllid	Island	Host plant
1	*A. serpentina*	P	
2	*Ar. vittata*	G P H	*Spartocytisus filipes*
		P	
1	*Ar. nubivaga*	T	*Spartocytisus supranubius*
2	*Ai. proboscidea*	T P	*Adenocarpus viscosus*
		P	hybrids
1	*Ai. nigralineata*	C T G	*Adenocarpus foliolosus*
1	*Ar. devia*	C T G P	
1	*Ai. dividens*	C T G	*Chamaecytisus proliferus*
2	*Ai. modica*	P H	
1	*Ai. hupalupa*	G	
1	*Ai. occidentalis*	P H	*Teline stenopetala*
1	*Ai. gomerae*	G	hybrids
2	*Ai. menceyata*	T	
3	*Ai. pileolata*	T	*Teline osyroides*
1	*Ai. canariensis*	T	hybrids
1	*Ai. ochrita*	T	*Teline canariensis*
2	*Ai. equitans*	C	hybrids
2	*Ai. diluta*	T	
		C	*Teline microphylla*
1	*Ai. prognata*	C	
1	*Ai. romeria*	C	*Teline rosmarinifolia*
1	*Ai. fortunata*	P	*Teline splendens*
1	*Ai. incuba*	MAD	*Teline maderensis*
1	*Ai. umbonata*	MAD	*Genista tenera*
1	*L. monospermae*	T G P H	*Retama monosperma*

DISCUSSION

Causes of Radiation

The psyllid phylogeny suggests two periods of radiation: (1) when the Genisteae were first colonized, and (2) when the Canary Islands were colonized by *Arytinnis* (Fig. 3). In the first case, a key innovation may have allowed for the initial exploitation of genistoid hosts (e.g. tolerance of quinolizidine alkaloids). In the second case, colonization of a novel geographical region with a high diversity of hosts and habitats appears to have been important in promoting psyllid diversity. Both the breach of plant chemical defenses and the exploitation of unoccupied niches may precipitate an ecological release in phytophagous insects (Ehrlich and Raven 1964; Gillespie and Roderick 2002). Recent studies in the Canary Islands have found factors such as proximity to a continental landmass, geological chronology of island formation, and the exploitation of ecological opportunities to be important in determining the character of the insular fauna and flora (Juan et al. 2000; Emerson 2002). There have been multiple colonizations of the Canary Islands by psyllids, but the presence or absence of radiation in each of the island psyllid genera is apparently determined by three factors: (1) constraints on host acceptance, (2) the diversity of the host group and, (3) abundance and distribution of the host group. Island size (both elevation and area) is indicative of the variety of habitats, and better predicts legume diversity than psyllid diversity, whereas psyllid diversity is more closely related to legume diversity than to either island size or number of habitats per island.

(1) Constraints on host acceptance are evident in the Genisteae-feeding psyllids and appear to result from an inherently narrow host preference that effectively limits the possibilities of establishment and radiation in regions where there are no, or few, familiar plants. Similar constraints are apparent in some Canary Island colonizing leaf beetles (Garin et al. 1999), but in studies of Hawaiian hoppers, unexpected host shifts appear to have taken place in conjunction with island colonization (Roderick 1997; Roderick and Gillespie 1998).

(2) The role of legume diversity in promoting or constraining psyllid diversification in the Canary Islands is evident in a comparison of the diversity of psyllids on *Teline* (the main host genus of *Arytinnis*) with the diversity of psyllids on other host genera. The legume genus *Teline* has undergone two separate radiations in the Canary Islands, resulting in 10 species (Percy and Cronk 2002), whereas the other five Canary Island genistoid legume genera have undergone little or no diversification. None of the psyllid genera that are associated only with these less diverse legumes has undergone a radiation. This shared diversity in island psyllids and legumes, together with the absence of host switches to unrelated genera during colonization of the islands and the greater number of in situ host switches to related hosts, suggests that narrow host specificity coupled with opportunistic host switching determines the observed patterns of psyllid diversity and host associations. Opportunistic host switching has clearly promoted diversification in Hawaiian Hemiptera (Asquith 1995; Gagné 1997), and it is central to ''escape and

TABLE 2. A comparison of host associations and geographic distributions in ten sister species pairs (and the putative host races of *Arytinnis modica*) with inferred modes of divergence. Each taxon pair is well supported in the combined molecular analysis (Fig. 3). The species pair *Ai. equitans* and *gomerae* is recovered in the combined molecular analysis, but an alternative pairing (indicated by an asterisk) of *Ai. gomerae* and *occidentalis*, though not recovered in the combined molecular and CO-tRNA analyses, is not inconsistent with the 12S data and is supported by a unique morphological synapomorphy (eight nymphal antennal segments). Positive/negative symbols indicate whether the taxa in each pair share/do not share host preferences and geographic distributions. The same host subspecies category is not applicable (NA) unless sister taxa are found on a single host that has been classified into subspecies. The majority of pairs (seven) are found on similar hosts but different geographical regions. Two species pairs are found on the same or closely related hosts on the same island. One species pair and the putative host races of *Ai. modica*, are sympatric but on unrelated hosts.

Species pair no.	Sister taxa	Same genistoid group	Same host genus	Same host species	Same host subspecies	Same island or geographical region	Same locality	Putative speciation/ divergence mode
	Ai. modica Cham. + *modica* Teline	−	−	−	NA	+	+	sympatric with switch to unrelated host
1	*Ai. hupalupa* + *modica*	+	+	+	−	−	−	allopatric without host switch
2	*Ai. hakani* + *incuba*	+	+	−	NA	−	−	allopatric with switch to related host
3	*Ai. berber* + *cognata*	+	+	−	NA	−	−	allopatric with switch to related host
4	*Ai. nigralineata* + *proboscidea*	+	+	+/−	−	+/−	−	allopatric? with switch to related host and ecological specialization
5	*Ai. equitans* + *gomerae*	+	+	−	NA	−	−	allopatric with switch to related host
	**Ai. gomerae* + *occidentalis*	+	+	+	+/−	−	−	allopatric without host switch
6	*Ai. diluta* + *prognata*	+	+	+	NA	+	−	allopatric? without host switch but with ecological specialization
7	*L. monospermae* + *retamae*	+	+	+	NA	−	−	allopatric without host switch
8	*A. delarbrei* + *serpentina*	+	−	−	NA	−	−	allopatric with switch to related host
9	*A. cytisi* + *telonicola*	−	−	−	NA	+	+	sympatric with switch to unrelated host
10	*Ar. nubivaga* + *vittata*	+	+	+/−	NA	−	−	allopatric with switch to related host

radiate'' models of evolution in plant-insect interactions (Ehrlich and Raven 1964; Thompson 1994).

(3) Nevertheless, a one-to-one psyllid-to-legume ratio is only evident in some groups and regions. Several psyllid species occupy localized habitats within a single widespread host range. This is consistent with increased colonization opportunities (via more frequent encounter) and a greater diversity of localized habitats provided by widespread and abundant hosts, as proposed by Opler (1974). Examples in this study include the legume *Teline stenopetala*, which has five subspecies on four islands and is host to six psyllid species; and, within a single island, *T. canariensis* (on Tenerife) and *T. microphylla* (on Gran Canaria) are widespread found in diverse ecological zones, and each host three to four psyllids (Table 1). In the Macaronesian islands there are more Genisteae-feeding psyllids than Genisteae (23 psyllids and 21 genistoid legumes), in contrast to the continent (about 230 species of Genisteae and only about 70 species of psyllid on these legumes). On Madeira there are two native genistoid legumes and two endemic psyllids (one on each legume), but in the Canary Islands, 21 psyllids occur on just 12 legumes. Furthermore, up to one third of the legumes (17–33%) per island in the Canary Islands do not host psyllids, and on each island there are multiple psyllids on at least one host. Thus, although host diversity is important, it is not the only determinant of psyllid diversity. Other factors, including the relative age of legume and psyllid groups (island groups may be more contemporaneous than continental groups), host abundance, habitat diversity, and the presence or absence of competitors and predators may also influence observed patterns of psyllid diversity.

Interestingly, this study encountered the highest within-species sequence divergence in island taxa that exist on different islands but the same host. In contrast, sequence divergence within continental species that are much more widespread and exist on several different but closely related hosts was considerably less. These results suggest there are different patterns of dispersal and gene flow among island and continental species, with perhaps more recent dispersal in continental areas (e.g. northward postglacial expansion), and more complete genetic isolation of island populations. In the Hawaiian Islands, similarly structured arthropod populations also display morphological stasis despite considerable genetic divergence (Roderick and Gillespie 1998).

In the Canary Islands and other archipelagos, the historical time frame provided by the geological formation of islands has been useful for interpreting island colonization sequences (e.g. Juan et al. 1995; Hormiga et al. 2003). This study sug-

gests only partial association between island age and colonization sequence (e.g. three putatively basal *Arytinnis* species are found on the older island of Gran Canaria, and some more recently derived taxa are only found on younger islands). Preliminary results from dating the legume and psyllid phylogenies suggest that, in both groups, initial colonization of the islands occurred well after most of the islands were already formed (D. M. Percy et al. 2004). In contrast, other island groups (e.g. flightless insects) may be older than the presently emerged islands on which they are found (Sequeira et al. 2000). For psyllids, which are moderately mobile, island distance to source populations may be more important in determining colonization patterns than island age. However, in the Canary Islands, patterns indicative of both processes may be found because older islands are nearer the continent than younger islands.

Host Specificity and Speciation

Host specificity is a dominant element in psyllid-legume interactions, but ecological specialization and host switching may be more important in promoting psyllid speciation. Of the 23 Macaronesian species, 16 (70%) are found on a single host plant, six species (26%) are found on two hosts, and one species is found on three hosts. A comparison of the psyllid phylogeny with host use and ecological and geographic patterns from field observations during 1997–2000 (Percy 2003) suggests that the majority of sister species are both ecologically and geographically allopatric. There is only one sister species pair that exists both on the same host and the same island (*Ai. diluta* and *prognata*). These species are separated ecologically, either on northern mesic or dry southern habitats of the widespread host, *Teline microphylla*, suggesting that there has been an ecological shift to different host habitats. Geographically separated sister taxa on different islands but on the same host sometimes show similar ecological specialization. For example, *Ai. occidentalis* and *gomerae* are more common on the xerically adapted host subspecies of *Teline stenopetala* on La Palma (ssp. *sericea*) and La Gomera (ssp. *pauciovulata*) respectively, whereas *Ai. modica* and *hupalupa* are more common on the mesically adapted host subspecies on each island (ssp. *stenopetala* and ssp. *microphylla*, respectively). However, ecological preferences may have shifted over time, so that observed preferences may not reflect historical preferences at the time of speciation.

The psyllid phylogeny also allows a comparison of the relationships between ecologically more specialized and more generalist taxa. A widespread legume exists in several types of habitat, and a widespread psyllid on this legume may therefore be considered an ecological generalist, whereas psyllids restricted to localized host habitats may be ecological specialists. On Tenerife, four psyllid species occur on *Teline canariensis*, but only one psyllid is found throughout the host range (*Ai. pileolata*), whereas the other species (*Ai. diluta*, *canariensis*, and *menceyata*) occur in localized regions or habitats. A similar pattern is found on Gran Canaria, where three psyllid species are found on *T. microphylla*, one widespread (*Ai. equitans*) and two localized species (*Ai. diluta* and *prognata*). The phylogeny suggests that on Tenerife, some of the localized species are more recently derived than the widespread species, but on Gran Canaria the widespread species appears to be more recently derived than the localized species. Notably, both widespread species develop later in the season than the localized species. This scenario agrees with studies that show ecological shifts between specialist and generalist to be bi-directional and not limited to unidirectional shifts from generalist to specialist (Gillespie and Roderick 2002).

In the Canary Islands, where it is common to find multiple psyllids on a single host, temporal divisions between closely related species that are sympatric could be an important mechanism to facilitate the sharing of host resources and avoidance of competition. There is also a temporal division in two unrelated species that are both widespread throughout the shared host range (*Ar. devia* develops later than *Ai. dividens* on *Chamaecytisus proliferus*). In addition, there is an example of apparently phenologically driven competitive exclusion in the two *Adenocarpus*-feeding species (*Ai. nigralineata* and *proboscidea*). Oviposition in these species is on the inflorescences of *Adenocarpus*. *Adenocarpus foliolosus* on two islands (Tenerife and La Palma) is found at lower altitudes and flowers earlier than *A. viscosus* at higher altitudes. Host phenology may therefore be the mechanism maintaining host specificity on Tenerife where sympatry could have resulted in competition between psyllids. On La Palma, only one of these psyllids occurs, but on this island host specificity is not maintained and the species is found throughout both host-plant ranges. Differences in host-plant phenology can result in reproductive barriers and lead to speciation in sympatric host races (Berlocher and Feder 2002), but whether host-plant phenology could have played a role in the speciation of these psyllid taxa is not yet determined.

There are some Genisteae that apparently do not have any associated psyllids. In the Canary Islands, the Genisteae species that do not host psyllids are all rare species, and in many cases these are rare because of human disturbance. Fragmentation of host populations may also be critical. In contrast, cultivation of some native host plants for animal fodder (*Chamaecytisus proliferus* and *Teline stenopetala*) and the adaptation of other native hosts to disturbed or grazed landscapes (e.g., *Adenocarpus viscosus*) appears to have increased the abundance of psyllid species associated with these hosts (Percy 2003). Another effect of human disturbance is the breakdown of ecological barriers between plant species resulting in hybridization (Lems 1958; Francisco-Ortega et al. 2000). Several psyllid species (*Ai. diluta*, *equitans*, *pileolata*, *proboscidea*, and *menceyata*) are found on multiple hosts between which hybrids have been recorded (Table 1). On Tenerife, hybrids between three host species (*Teline canariensis*, *T. stenopetala*, and *T. osyroides*) are found around the Ladera de Güímar (Arco Aguilar 1983; M. Arco Aguilar, pers. comm. 1998), an area that was disturbed by early settlements of aboriginal Guanches. The most widespread psyllid on Tenerife (*Ai. pileolata*) is found on these three hosts. As hybrids are more likely to occur between closely related legumes, it is not clear whether the host range expansions occurred because the hosts were related (and therefore familiar), or whether hybridization could have promoted host shifts via a ''hybrid bridge'' effect (Floate and Whitham 1993; Roderick

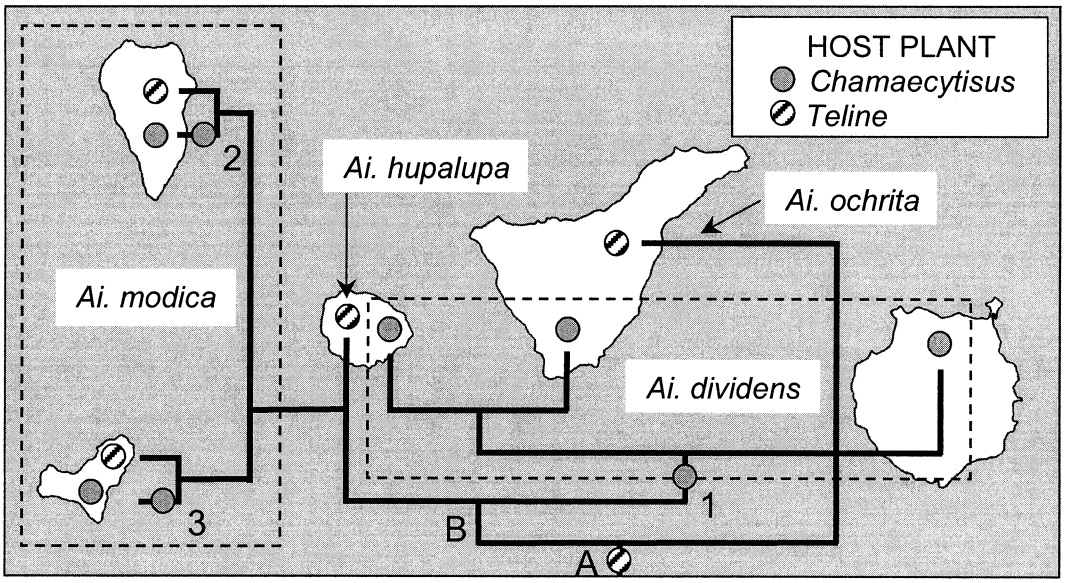

FIG. 4. Distributions and mapped host-plant associations in the *dividens-modica* subclade of *Arytinnis* (the uppermost clade in Fig. 3). The dashed boxes delimit *Ai. dividens* and *Ai. modica* based on a morphological analysis. Three independent colonizations of *Chamaecytisus* from *Teline* are numbered. The nodes marked A or B denote where possible ancestral polyphagy at the base of the subclade could account for a propensity to switch between the same unrelated hosts through the retention of dual host acceptance such as is evident in the repeated shift between *Teline* and *Chamaecytisus* in *Ai. modica* on La Palma and El Hierro.

1997). Recent molecular analysis of the host-plant group using the nuclear region ITS1–5.8S-ITS2 (Percy and Cronk 2002) found minimal genetic divergence between many of the Macaronesian host plants. Notably, the three host plants of *Ai. pileolata*, which are distinguished using morphological characters, had either identical ITS sequences or a single indel difference (Percy and Cronk 2002), and could therefore constitute a single species.

The host association patterns in the island groups, as with other phytophagous insects on islands (Roderick and Gillespie 1998), suggest that either ecological or geographical separation alone may be sufficient to promote psyllid speciation, but both mechanisms are apparent in the majority of sister species relationships.

Host Switches between Unrelated Hosts

Although there is evidence that preadaptation is operating on selection and acceptance of host plants during colonization of a new region, it remains to be answered how host switches have occurred between unrelated genera (in the Canary Islands these are between *Teline* in the *Genista* group and *Adenocarpus*, and *Teline* and *Chamaecytisus* in the *Cytisus* group). Because there are no apparent host switches to unrelated hosts during colonization events, successful colonization of a new region is apparently dependent on encountering familiar plants. Host switches between unrelated plant genera may therefore be facilitated by longer periods of contact, which allow acclimatization to novel plants and/or host race formation, as has been proposed to explain intergeneric host switching in host specific Hawaiian Hemiptera (Gagné 1997).

If the formation of host races subsequently leads to speciation via specialization on one or other host, observed specificity would have been derived from an initial condition of ancestral polyphagy. Similar unspecialized ''bridge species'' from which specialists evolve have been proposed for lepidopteran taxa (Menken and Roessingh 1998). Figure 4 illustrates an example where an atypical host switch between the same unrelated hosts (three independent colonizations of *Chamaecytisus*: *Cytisus* group, from *Teline*: *Genista* group) has apparently occurred repeatedly in a small subclade of closely related species (the *dividens-modica* subclade). The propensity to switch between *Chamaecytisus* and *Teline* in this subclade could reflect an earlier period of ancestral polyphagy, after which the formation of host races (which is possibly occurring in *Ai. modica*) may have led to specialization and speciation. This scenario is not inconsistent with the topology and current distributions. The retention of an ancestral host preference is present in a number of phytophagous insects (Keese 1998; Janz and Nylin 1998; Dobler and Farrell 1999; Janz et al. 2001), and could explain the repeated host switch between *Teline* and *Chamaecytisus* in *Ai. modica*. Despite a capacity for polyphagy, host specificity may maximize reproductive output because of the greater likelihood of finding conspecifics on the preferred host (Feder et al. 1997). Yet, retention of the capacity for polyphagy may be advantageous when fluctuations in the host lineage (long term) or host density (short term) favor survival on alternate hosts (Futuyma et al. 1995; Janz et al. 2001). Although retention of a historically broader host preference may remain in the ''memory bank'' of an insect lineage for a limited period of time (Futuyma et al. 1993, 1995), it could be an important evolutionary mechanism to the survival of an insect lineage.

Sympatric divergence is suggested by present day host distributions for one continental species pair (*A. cytisi* and

telonicola), and possibly *Ai. modica* if populations on different hosts are indeed diverging into distinct host races. However, it is also possible that changes in vegetation structure in the past (e.g. during the Pleistocene) resulted in initially allopatric divergence in the continental species. If unrelated hosts in sympatry do provide a mechanism for speciation, it may be that divergent selection pressures (caused by chemical or physical differences) are greater than between related hosts, providing a stronger barrier to gene flow between populations that are adapting to distinct hosts. The identification of distinct host races in *Ai. modica* could support this scenario but will require more extensive genetic sampling as well as ecological (e.g., host-transplant experiments) and behavioral studies (e.g., phenology and mating behavior).

The interpretations of speciation, colonization patterns, and host-plant shifts are dependent on correct estimates of phylogenetic relationships. In this study the molecular phylogenies are based on a single nonrecombining molecule (mtDNA). There are an increasing number of studies that have shown this to be a potentially unreliable means of estimating species relationships (Weinreich and Rand 2000), particularly in recently diverged groups (Giannasi et al. 2001; Shaw 2002). These studies emphasize the need to use nuclear markers as an alternative and independent estimate of phylogeny. The addition of nuclear data for the psyllids may also shed light on the apparent incongruence between the mitochondrial and morphological analyses.

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APPENDIX

Distribution of taxa and location of 84 samples from 62 taxa (61 species and one subspecies) included in this study. The datasets in which each sample was included are indicated: 12S, small subunit rRNA; CO, cytochrome oxidase I, tRNA leucine, and cytochrome oxidase II; M, morphological (adult and nymph; M* adult only). Material supplied by D. Burckhardt (DB), D. Hollis (DH), and I. Hodkinson (IH) is indicated, all other material was collected by D. Percy in 1997–2000.

Datasets	Taxon	Origin of sample	Plant species from which sample was collected [host plant if different]	DNA voucher number [collection no. if different]
12S CO	*Acizzia hollisi*	High Atlas, Morocco	*Genista florida* [*Acacia* spp.]	DP325.1B
12S CO M	*Acizzia uncatoides*	La Palma, Canary Islands	*Acacia* spp. (cultivated)	DP194
12S CO M	*Arytaina adenocarpi*	Coimbra, Portugal	*Adenocarpus complicatus*	DP262.3A
12S CO M	*Arytaina adenocarpi*	Málaga, Spain	*Adenocarpus telonensis*	DP233
12S CO M	*Arytaina adenocarpi*	Middle Atlas, Morocco	*Adenocarpus boudyi*	DP243
CO M	*Arytaina devia*	Tenerife, Canary Islands	*Chamaecytisus proliferus*	DP188.1
CO M	*Arytaina devia*	La Gomera, Canary Islands	*Chamaecytisus proliferus*	DP68
12S CO M	*Arytaina devia* ssp. *insularis*	Gran Canaria, Canary Islands	*Chamaecytisus proliferus*	DP161
12S CO M	*Arytaina devia* ssp. *insularis*	La Palma, Canary Islands	*Chamaecytisus proliferus*	DP189
12S CO M	*Arytaina genistae*	Edinburgh, Scotland	*Cytisus scoparius*	none [DP285]
12S CO M	*Arytaina genistae*	Coimbra, Portugal	*Cytisus striatus*	DP263
CO M	*Arytaina genistae*	High Atlas, Morocco	*Cytisus grandiflorus*	DP325.2
12S CO M	*Arytaina nubivaga*	Tenerife, Canary Islands	*Spartocytisus supranubius*	DP154
12S CO M	*Arytaina vittata*	La Gomera, Canary Islands	*Spartocytisus filipes*	DP69 + 220
12S CO M	*Arytainilla cytisi*	Rif mountains, Morocco	*Calicotome villosa*	DP319
12S CO M*	*Arytainilla delarbrei*	Coimbra, Portugal	*Cytisus purgans*	DP265.2
12S M	*Arytainilla gredi* DH	Picos de Europa, Spain	*Genista hispanica*	DH336
12S CO M	*Arytainilla ima*	High Atlas, Morocco	*Adenocarpus anagyrifolius*	DP239
12S CO M	*Arytainilla serpentina*	La Palma, Canary Islands	*Spartocytisus filipes*	DP198
12S CO M	*Arytainilla spartiophila*	Coimbra, Portugal	*Cytisus striatus*	DP265
12S CO M	*Arytainilla spartiophila*	Málaga, Spain	*Cytisus grandiflorus*	DP133
CO M	*Arytainilla spartiophila*	High Atlas, Morocco	*Cytisus fontanesii*	DP327
12S CO M	*Arytainilla sulci*	southwestern coast, Morocco	*Retama raetam*	DP297
12S CO M	*Arytainilla atlantica*	southwestern coast, Morocco	*Cytisus albidus*	DP296
12S CO M	*Arytainilla telonicola*	Málaga, Spain	*Adenocarpus telonensis*	DP134
12S CO M	*Arytainilla montivaga*	Granada, Spain	*Adenocarpus decorticans*	DP128
CO M	*Arytainilla montivaga*	Rif mountains, Morocco	*Adenocarpus decorticans*	DP249
12S CO M	*Arytinnis berber*	Anti-Atlas, Morocco	*Genista segonnei*	DP332
12S CO M*	*Arytinnis canariensis*	Tenerife, Canary Islands	*Teline canariensis*	DP179
12S CO M	*Arytinnis cognata*	High Atlas, Morocco	*Genista florida*	DP238
12S CO M	*Arytinnis diluta*	Gran Canaria, Canary Islands	*Teline microphylla*	DP172
CO M	*Arytinnis diluta*	Tenerife, Canary Islands	*Teline canariensis*	DP152
12S CO M	*Arytinnis dividens*	Gran Canaria, Canary Islands	*Chamaecytisus proliferus*	DP168
CO M	*Arytinnis dividens*	Tenerife, Canary Islands	*Chamaecytisus proliferus*	DP188.2
12S CO M	*Arytinnis dividens*	La Gomera, Canary Islands	*Chamaecytisus proliferus*	DP244
12S CO M	*Arytinnis equitans*	Gran Canaria, Canary Islands	*Teline microphylla*	DP163
12S CO M	*Arytinnis fortunata*	La Palma, Canary Islands	*Teline splendens*	DP203
12S CO M	*Arytinnis gomerae*	La Gomera, Canary Islands	*Teline stenopetala*	DP221
12S CO M	*Arytinnis hakani*	Rif mountains, Morocco	*Teline monspessulana*	DP256
12S CO M	*Arytinnis hupalupa*	La Gomera, Canary Islands	*Teline stenopetala*	DP219
12S CO M	*Arytinnis incuba*	Encumeada, Madeira	*Teline maderensis*	DP271 + 274
12S CO M	*Arytinnis menceyata*	Tenerife, Canary Islands	*Teline canariensis*	DP182
12S CO M	*Arytinnis modica*	La Palma, Canary Islands	*Teline stenopetala*	DP192
12S CO M	*Arytinnis modica*	La Palma, Canary Islands	*Chamaecytisus proliferus*	DP201
CO M	*Arytinnis modica*	El Hierro, Canary Islands	*Teline stenopetala*	DP212
CO M	*Arytinnis modica*	El Hierro, Canary Islands	*Chamaecytisus proliferus*	DP211
12S CO M	*Arytinnis nigralineata*	Gran Canaria, Canary Islands	*Adenocarpus foliolosus*	DP173
CO M	*Arytinnis nigralineata*	Tenerife, Canary Islands	*Adenocarpus foliolosus*	DP156
CO M	*Arytinnis nigralineata*	La Gomera, Canary Islands	*Adenocarpus foliolosus*	DP67
12S CO M	*Arytinnis ochrita*	Tenerife, Canary Islands	*Teline osyroides*	DP153
12S CO M	*Arytinnis occidentalis*	La Palma, Canary Islands	*Teline stenopetala*	DP190
CO M	*Arytinnis occidentalis*	El Hierro, Canary Islands	*Teline stenopetala*	DP214
12S CO M	*Arytinnis pileolata*	Tenerife, Canary Islands	*Teline canariensis*	DP178
CO M	*Arytinnis pileolata*	Tenerife, Canary Islands	*Teline osyroides*	DP184
12S CO M	*Arytinnis proboscidea*	Tenerife, Canary Islands	*Adenocarpus viscosus*	DP5
CO M	*Arytinnis proboscidea*	La Palma, Canary Islands	*Adenocarpus foliolosus*	DP204
12S CO M	*Arytinnis prognata*	Gran Canaria, Canary Islands	*Teline microphylla*	DP160
12S CO M	*Arytinnis romeria*	Gran Canaria, Canary Islands	*Teline rosmarinifolia*	DP165

APPENDIX. Continued.

Datasets	Taxon	Origin of sample	Plant species from which sample was collected [host plant if different]	DNA voucher number [collection no. if different]
12S CO M	*Arytinnis umbonata*	Encumeada, Madeira	*Genista tenera*	DP273
12S CO	*Cacopsylla alaterni*	Málaga, Spain	*Rhamnus alaternus*	DP112
12S CO	*Cacopsylla mali*	Edinburgh, Scotland	*Malus* sp.	DP293
12S CO	*Cyamophila prohaskai* DB	Aemsigén, Switzerland	Coniferae [Anthyllis vulneraria]	DB341
12S CO M*	*Livilla adusta*	Málaga, Spain	*Genista cinerea*	DP132
12S CO M	*Livilla blandula*	Southwestern coast, Morocco	*Cytisus albidus*	DP296
12S	*Livilla horvathi* DB	Kars, Turkey	? [*Chamaecytisus austriacus*]	DB1
12S	*Livilla maculipennis* IH	El Gor, Algeria	? [*Genista* sp.]	IH8
12S CO	*Livilla maura*	Rif mountains, Morocco	*Chamaespartium tridentatum*	DP250
12S CO M	*Livilla monospermae*	Tenerife, Canary Islands	*Retama monosperma*	DP28
CO M	*Livilla monospermae*	La Gomera, Canary Islands	*Retama monosperma*	DP70
CO M	*Livilla monospermae*	La Palma, Canary Islands	*Retama monosperma*	DP196
12S M*	*Livilla nervosa*	Granada, Spain	*Genista umbellata*	DP124
12S	*Livilla pseudoretamae* IH	Grand Kabylie, Algeria	? [host plant unknown]	IH7
12S	*Livilla pyrenaea* DB	Zaragoza, Spain	''*Genista scoparius*'' [*Genista* sp.]	DB4
12S	*Livilla radiata* DB	Peloponnese, Greece	''Genistae?'' [*Chamaecytisus* spp.]	DB6
12S CO M	*Livilla retamae*	Cádiz, Spain	*Retama monosperma*	DP94
12S	*Livilla spectabilis* IH	Liguria, Italy	*Spartium junceum*	IH6
12S	*Livilla syriaca* DB	Carmel, Israel	*Genista fasselata*	DB3
12S CO	*Livilla variegata*	Glasgow, Scotland	*Laburnum anagyroides*	DP337
12S	*Livilla vicina* DB	Vermala, Switzerland	*Genista radiata*	DB5
12S	*Livilla vittipennella* IH	Trentino, Italy	*Genista radiata*	IH5
12S CO M*	*Livilla caprifuga*	Middle Atlas, Morocco	*Adenocarpus bacquei*	DP309
12S CO M*	*Livilla baetica*	Granada, Spain	*Adenocarpus decorticans*	DP129
12S CO M*	*Livilla complexa*	Coimbra, Portugal	*Adenocarpus complicatus*	DP262.3B
12S CO M	*Pseudacanthopsylla improvisa*	southwestern coast, Morocco	*Retama raetam*	DP301