# DIVERSIFICATION OF LEGUME-FEEDING PSYLLIDS (HEMIPTERA, PSYLLOIDEA) AND THEIR HOST PLANTS (LEGUMINOSAE, GENISTEAE)

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A thesis submitted for the degree of Doctor of Philosophy to the
University of Glasgow

Division of Environmental and Evolutionary Biology
Institute of Biomedical and Life Sciences

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# Declaration

I declare that the work recorded in this thesis is entirely my own, unless otherwise stated, and that it is my own composition. No part of it has been submitted for any other degree to any institution.

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## Abstract

Psyllids ('jumping plant lice') are small phytophagous insects that are related to aphids, scales and whiteflies (Hemiptera, Sternorrhyncha). Psyllids are highly host specific, occurring on one or a few closely related hosts, and they predominantly feed on dicotyledonous angiosperms. In the subfamily Arytaininae (Psylloidea, Psyllinae) there are five psyllid genera that feed exclusively on shrubby legumes in the Genisteae (Leguminosae, Papilionoideae), and the species diversity for both plant and insect groups is highest in the Mediterranean. I made a detailed field survey of psyllids on Genisteae hosts in the western Mediterranean, including southern Iberia, NW Africa and two of the Macaronesian archipelagos (Canary Islands and Madeira). These collections (over 300) of both psyllids and legumes provided the basis for the taxonomic, phylogenetic and co-diversification analyses presented in this study.

I have reassessed the classification of the legume-feeding psyllids native to Macaronesia, and I have revised the taxonomy of one genus (*Arytainilla*). I present evidence that the largest Macaronesian group has a unique island origin distinct from the predominantly continental genera. This Macaronesian group, which also has three continental members, is described as a new genus in order to clarify the monophyly and placement of this group within the Arytaininae. Seventeen new psyllid species in four arytainine genera, discovered in continental and Macaronesian regions, are proposed.

I constructed phylogenies for both the arytainine psyllids and their legume host plants, in order to compare colonization, biogeographic patterns and island radiations. I present a phylogenetic study of the Palaearctic arytainine psyllids that incorporates both morphological data (adult and nymphal characters) and molecular data (mitochondrial genes: cytochrome oxidase I and II, including the intervening tRNA leucine; and the small ribosomal subunit rRNA). To investigate the evolution of the island legumes and to establish the relationships between continental and island host plants, a molecular phylogeny of part of the Genisteae was generated from sequences of the nuclear region: ITS1-5.8S-ITS2. The legume phylogeny shows a Mediterranean origin for the Canarian Genisteae (*Adenocarpus*, *Genista* and *Teline*), and a diphyletic origin for *Teline* – with two distinct island groups nested within *Genista*. The psyllid phylogeny shows that the two largest genera are paraphyletic, but there is some evidence that the Genisteae-feeders, as a whole, are monophyletic. The phylogenetic analyses for both psyllids and legumes highlight the problems of establishing host-parasite interactions using traditional morphological classifications alone. Colonization and biogeographic patterns among the island psyllid species implies a close correlation between the radiation of psyllids and the diversity of their host plants.

Psyllid and legume phylogenies are compared in order to establish the extent of phylogenetic congruence between the insects and their host plants. To test assumptions of cospeciation, an absolute time scale is applied to both plant and insect phylogenies. A comparison of psyllid and legume phylogenies suggests that, whilst rare cospeciation events may play a significant role in promoting diversification, historical reconstructions of psyllid-legume interactions are complicated by systemic host switching. Psyllids appear to be opportunistic specialists with host switching occurring when the plant lineage fluctuates in geographical abundance, population structure or through dispersal. However, preadaptation is evident in many cases where selection of a new host may be constrained by plant chemistry and architecture. Successful establishment by a psyllid colonist is more likely when available hosts are phylogenetically and ecologically related to the original host. A history of parallel cladogenesis between psyllid and legume lineages is rejected in favour of a fluctuating lineage model of co-diversification which presents a more realistic interpretation of the present day pattern of host associations.

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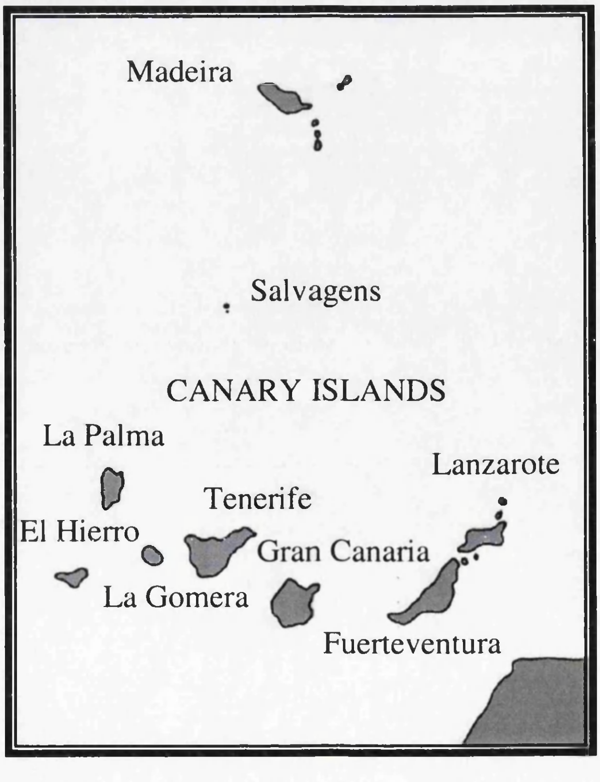


**Above:** The Macaronesian region showing the five archipelagos (north to south: Azores, Madeiras, Salvagens, Canaries, and Cape Verdes) which lie off the west coast of North Africa and southern Europe, between 15° and 40°N latitude. The geological ages of individual islands range from 1-30 Myr.

**Right:** The centrally positioned Canary Islands (27°-29°N) and Madeira (33°N) are the focus of this study. Only the five central and western Canary Islands (east to west: Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro) support the habitat type in which the insects and host plants in this study occur.

# CHAPTER ONE
# INTRODUCTION

## 1.1 Ocean island research

> 'By studying clusters of islands, biologists view a simpler microcosm of the seemingly infinite complexity of continental and oceanic biogeography ..... their very multiplicity, and variation in shape, size, degree of isolation, and ecology, provide the necessary replications in natural "experiments" by which evolutionary hypothesis can be tested.' (MacArthur & Wilson, 1967)

Island biogeography has influenced a broad range of biological investigation, including systematics, ecology and conservation (Grant, 1998). The science of island, or insular biogeography was made popular by MacArthur & Wilson (1967). It has since contributed significantly to the study of biotas on oceanic islands as well as those in habitat fragments on continents (Pickett & Thompson, 1978; Hanski & Gilpin, 1997). As MacArthur & Wilson (1967) pointed out, the inherent appeal of islands is the 'visibly discrete object that can be labelled with a name and its resident populations identified'.

Volcanic ocean archipelagos have presented biologists since Darwin and Wallace with natural laboratories in which to observe discreet and speciose systems. The most famous example is Darwin's Galapagos finches (Grant, 1986), but more recently the Hawaiian Drosophila with more than 1000 species (Kambysellis & Craddock, 1997) and island plant groups such as the woody composites of the Atlantic and Pacific archipelagos (Wagner & Funk, 1995; Givnish & Sytsma, 1997) have become model groups for the study of speciation processes. Understanding the mechanisms at work in ocean islands has been invaluable to a broader understanding of pattern and process in biogeography and evolution. Ideas that have germinated in the laboratories of ocean islands have proven applicable to continental land masses, where equivalent 'patchiness' in ecosystem patterns has resulted in equivalent 'island' dynamics or 'stepping stone' processes (e.g. the cichlid fish of Africa's Great Lakes, Rüber *et al.*, 1998), but these are often more subtle and less easily studied than those found on real islands (Wu & Levin, 1997; Holt & Keitt, 2000).

## 1.2 Insect-plant interactions

### 1.2.1 *Introduction*

Insect-plant interactions have played an important role in defining models of interactive evolution such as coevolution and cospeciation (Futuyma & Slatkin, 1983). Although stricter terms of coevolution may be appropriate for some insect pollination and floral syndromes (Thompson, 1994), it is widely believed that herbivorous insect speciation is sequential in relation to the host plant (Jermy, 1976; Menken, 1996). Once insect host specificity is established, close tracking of ecological, phenotypic and chemical changes in closely related host plants may result in phylogenies similar to those arising from cospeciation or parallel cladogenesis. Determining the history of insect-plant associations is crucial to evaluating the cause and extent of associated evolution. Comparing host associations on the mainland with those found on islands provides an insight into preadaptation and the changes in host association that result from island colonization, radiation and ecological specialization.

### 1.2.2 *The role of insect and plant taxonomy*

Different approaches to the concept of species in the taxonomic treatment of plants and insects can present difficulties when comparing host and parasite phylogenies. Psyllids or 'jumping plant-lice' (Hemiptera, Psylloidea) are small, phytophagous, phloem feeding insects that are typically monophagous or oligophagous (i.e. specific to one or a few closely related hosts). They feed on a wide variety of dicotyledonous and a few monocotyledonous plants. Within the Psylloidea, six families are recognized (Burckhardt, 1987; White & Hodkinson, 1985) and within all families, a high degree of host specificity is typical. This study focuses on psyllids that feed on legumes in the tribe Genisteae (Leguminosae), a tribe which includes the common broom, gorse and related shrubs. The Genisteae has a complex taxonomic history that is littered with synonomy as a result of numerous taxonomic revisions. In contrast, the genistoid-feeding psyllids have been investigated by fewer workers and have been the subject of a limited number of taxonomic revisions. In addition, the legume host classification has numerous intraspecific taxa, while there is only one subspecific taxon among the entire 96 species of Palaearctic arytainine psyllids.

All of the 12 native Leguminosae genera represented in the Canarian archipelago are in the subfamily Papilionoideae, which is considered more evolutionarily advanced than the other two subfamilies, Mimosoideae and Caesalpinoideae (Käss & Wink, 1996).

Six of the Canarian legume genera (50%) are in the tribe Genisteae, which is one of four tribes retained by Bisby (1981) or six tribes delimited by Hutchinson (1964), after the subdivision of the Genisteae *sensu lato* of Bentham (1865).

The Canary Islands, with a history of discovery possibly stretching as far back as Phoenecian navigation of the African coast in 610 BC (Krüss, 1976), experienced a boom of scientific exploration in the late 18th and 19th centuries. Floristically, Macaronesia (with the exception of the Cape Verde Islands) is associated with a circum-mediterranean flora that would have been familiar to the creators of our present system of plant classification. Modern botany took shape in Europe (Walters, 1961) and is largely based on Eurocentric plant distributions. Approximately two thirds of all the genera in Linnaeus's 'Species Plantarum' (1753) are European. These beginnings, it has been proposed, are the root of the artifice constraining current plant taxonomy within a psychological and historical framework resulting in the psychohistorical process of 'chaining' (Cronk, 1989). 'Chaining' arises when taxonomic groups named by Linnaeus, or associated with pre-Linnaeun Medieval classifications have acted as 'nuclei' or 'sinks' for subsequently discovered taxa. This results in falsely 'skewed', large heterogeneous groups such as the genera *Rosa* (Rosaceae) and *Cassia* (Caesalpinioideae), and the subsequent splitting off of small anamolous taxa that can no longer be satisfactorily circumscribed within the larger group (e.g. the Canary Island genera *Dendrosonchus*, *Teline* and *Spartocytisus*). The result is a pattern of a few very large groups and many small groups.

Within the Leguminosae, the three subfamilies recognised today were known to Linnaeus but each was given a very different treatment according to the number and distribution of species familiar to Linnaeus. Hence *Mimosa* (mainly tropical) was established as a single genus to incorporate all of the then known species (39) of today's Mimosoideae (c. 2,820 species); the Caesalpinoideae was created for 19 genera, with the majority of species in the single genus *Cassia*; while the remaining majority of species (378) were placed in 45 genera under the Papilionoideae.

The historical legacy of this early bias is that the Leguminosae contains 18,000 species in 650 genera, and nearly a third of these taxa are in just six genera: *Astragalus, Crotalaria, Indigofera* (Papilionoideae), *Mimosa, Acacia* (Mimosoideae), and *Cassia sensu lato* (Caesalpinoideae).

However, taxonomic artifice alone is not the sole cause of this pattern, which though distorted in shape by human classification, is nevertheless reflective of biological trends within the Leguminosae. Namely, 1) the Caesalpinoideae is an ancient group, primarily of relict species which have undergone little recent speciation, 2) the Mimosoideae are an ancient group which has undergone a massive bloom of recent speciation and 3) the Papilionoideae are a comparitively recently evolved group, resulting in large, poorly differentiated segregates with complex patterns of variation (Cronk, 1990).

The classification of the Canarian Leguminosae can be explained in the light of both taxonomic artifice and evolutionary trends in the Papilionoideae, with the additional component of adaptive radiation. Members of the Canarian Genisteae have all been incorporated in the large amorphous *Genista-Cytisus* generic group, probably due equally to the process of historical chaining, as to recent evolution in the Papilionoideae, resulting in poorly divisible genera. Both of these genera, *Genista* and *Cytisus* have acted as linked nuclei for a huge complex of species (c. 230 species). Amongst the Canary Island genera, two groups are an example of the budding off of morphologically anomalous taxa – *Teline* and *Spartocytisus* – which have been recognised by some but not all workers as distinct from the *Genista-Cytisus* group, but which molecular data have clearly shown, belong within one or other group (Käss & Wink, 1997; Chapter 4)

Compounding the problems of artifice in plant classification is the dilemma of regional research by many different workers (often lacking communication with one another), versus monographic work done by a few co-workers. This problem is evident in the tropics today and was faced by Linnaeus with access to only a part of the worlds floristic diversity. It is alluded to by Bentham (1875) in discussing Linnaeus's treatment of the Leguminosae 'a disproportionate treatment probably aggravated by the circumstances of the small number of botanists who have access to good working materials in *Cassia* and Mimoseae'. In assessing the amount of synonymy that accumulated during the 18th and 19th century exploration of Macaronesia, it is apparent that a certain degree of 'buccaneer' taxonomy by those working in isolation resulted in a somewhat lawless classification.

It is also possible to examine the reliability of the host plant taxonomy from the perspective of phytophagous insects. Incorporating phytophagous insect preferences into the systematic treatment of plants may prove to be useful, especially in the case of complex species groups. In the Canarian Genisteae, as might be expected, the phytophagous insect 'taxonomy' has tended to lump where human taxonomy has tended to split. The psyllid 'taxonomy' supports many of the species delimitations in the present classification but frequently does not recognise intraspecific taxa which are more likely to be a product of human artifice. The psyllid fauna supports the *Cytisus-Genista* split but suggests that *Adenocarpus* should be sister to the *Genista* group, which contradicts the placement of

*Adenocarpus* as an outlier of a monophyletic *Cytisus-Genista* group. However, using molecular data (Käss & Wink, 1997) there is insufficient resolution at the base of the Genisteae, to contradict or confirm either placement. In another example, psyllid preference appears to contradict all other data – according to the psyllid fauna, *Chamaecytisus* has an intermediate position between the *Cytisus* and *Genista* groups, but the morphological (Cristofolini, 1991) and molecular (Käss & Wink, 1997) data place this genus unequivocally in the *Cytisus* group. Characteristics determining host preference may not reflect phylogeny, i.e. convergences in chemistry and plant architecture, and the plasticity of such characters within the plant group is likely to determine the usefulness of phytophagous insects to plant taxonomy.

### 1.2.3 *Relative endemic diversity of native legume-feeding psyllids and their host plants*

Comparative numbers for endemic insect diversity in the Canary Islands indicate that psyllids (Psylloidea) have a relatively high endemic diversity when compared, either to the Homoptera as a whole (in which psyllids are included) or to other insect groups. Endemism is even higher (100%) for the native legume-feeding psyllids (Arytaininae) (Table 1). A similar comparison for the host plant group indicates that the genistoid legumes also have a high degree of endemism when compared to the angiosperms or dicotyledons as a whole (Table 2).

There is an association between the number of habitat zones per island and the diversity of native legume-feeding psyllids and genistoid legumes on each island (Tables 3, 4 & 5 and Table 1 Chapter 3). However, the number of endemic species is more closely associated with the proximity of the island to the African continent, although there is a need for caution in interpreting associations, given the small number of islands. The relative paucity of both legume-feeding psyllids and their hosts on Madeira is probably due to the more uniform habitat and climate on this island, and to the greater isolation of Madeira from large neighbouring islands or from a continental landmass (which could serve as sources of immigrants). The greater richness in psyllid fauna within the Canarian archipelago reflects the greater diversity of habitat, climate and variety of ecological niches, as well as greater diversity in host plant genera and species.

The isolation of Madeira increases the likelihood that species on this island will be endemic, and indeed endemism is 100% for the arytainine psyllids and their native hosts. Within the Canary Islands psyllid endemism is also 100% (all 21 species are endemic), but for each of the five islands endemism is consistently less than 50% (Gran Canaria 43%, Tenerife 36%, La Gomera 29%, La Palma 14%, and El Hierro 0%). This scale shows some

TABLE 1.

| | no. endemic sp. | % endemic | |
|---|---|---|---|
| Orthoptera | 31 | 37 | |
| Dermaptera | 16 | 66 | |
| Homoptera | 160 | 40 | |
| Heteroptera | 107 | 27 | |
| Coleoptera | 1160 | 59 | |
| Diptera | 331 | 31 | |
| Lepidoptera | 190 | 31 | |
| Hymenoptera | 194 | 23 | |
| **Psylloidea** | **25** | **62.5** | – all psyllids |
| **Arytaininae** | **21** | **100** | – native legume-feeding psyllids |

TABLE 2.

| | no. endemic sp. | % endemic | |
|---|---|---|---|
| Angiospermae | 519 | 27 | |
| Dicotyledonae | 497 | 31.4 | |
| **Genisteae** | **17** | **94.1** | – genistoid legumes |

Adapted in part from Báez *et al.* (2000) and Oromí & Báez (in press) association with the distance of each island from the African continent, and its geological age. The highest level of endemism is found on Gran Canaria which is the oldest (14.5-16 Myr) and closest island to the African continent (245 km), while there are no endemic species on El Hierro which is the youngest (1.1 Myr) and furthest island from the continent (489 km) (Table 3).

In comparison, species richness – the total number of psyllid species present on each island – shows some association with island area: 11 species on the largest island of Tenerife (2058 km$^2$), seven species each on the islands of Gran Canaria (1534 km$^2$), La Palma (728 km$^2$) and La Gomera (378 km$^2$), and four species on the smallest island of El Hierro (277 km$^2$) (see Table 1 Chapter 3). However, a simple regression analysis using data from the five central and western Canary Islands (Table 1 Chapter 3) indicates that only two components are significantly correlated with species richness per island: altitude (which also dictates the variety of ecological niches, $r^2 = 78.6\%$, $P = 0.045$, d.f. $\approx 4$) and the number of potential host plants in the Genisteae ($r^2 = 79.6\%$, $P = 0.042$, d.f. $\approx 4$). Yet, the latter component is not a functional correlate, as up to one third (17–33%) of potential host plants (i.e. host congenerics) on an island may not be utilized as hosts. When species richness in the host plant group is assessed using the same predictors, there is a significant correlation with altitude only ($r^2 = 92.8\%$, $P = 0.008$, d.f. = 4), implying that habitat diversity may operate independently on host plant and psyllid groups to promote speciation.

Classification of habitat zones which are primarily determined by altitude and leeward (southern) or windward (northern) locations:

1 – xerophytic lowland, 0-600 m, typically a southern zone
2 – lowland scrub and sabinar (*Juniperus phoenicea*), 100-600 m, northern regions
3 – laurel forest, 600-1000 m, northern regions
4 – fayal-brezal (*Erica arborea* and *Myrica faya*), 800-1200 m, northern regions
5 – pine forest, 600-1900 m
6 – sub-alpine 1900-3700 m

Opposite page:

HABITATS

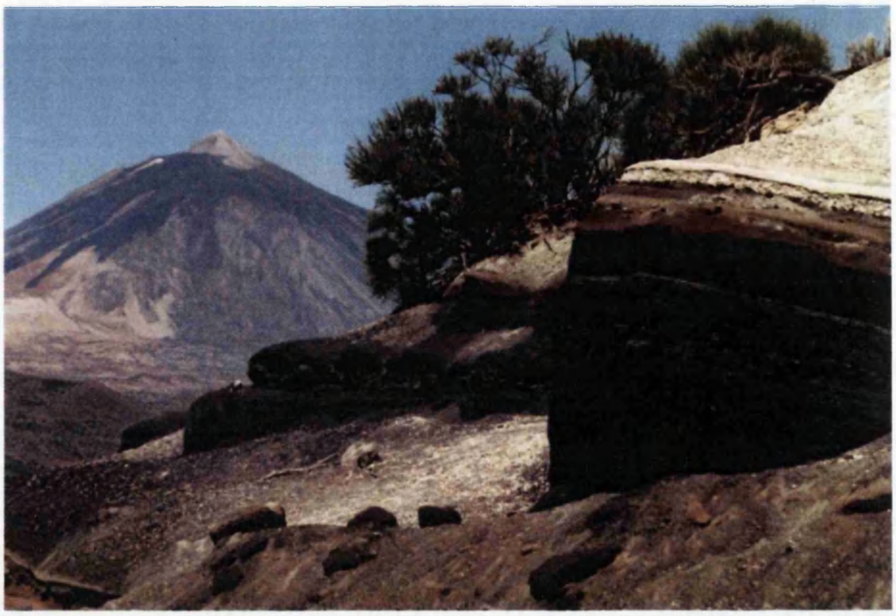
*Top* – high altitude subalpine zone on Tenerife, showing El Teide (3717m) in the background and the host plant *Spartocytisus supranubius* in the foreground.

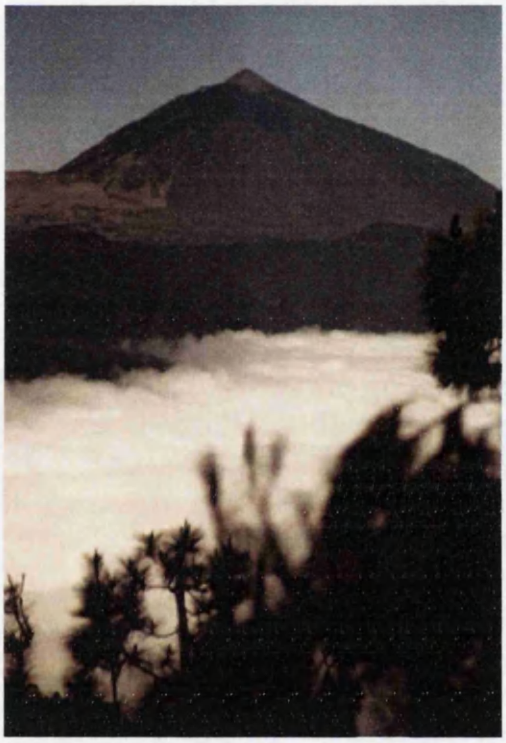
*Centre left* – cloud sea on the northern slopes of Tenerife

*Centre right* – pine forest on La Palma

*Bottom left* – mesic laurel forest on Madeira

*Bottom right* – lowland xeric scrub on Tenerife, with the host plant *Retama monosperma.*





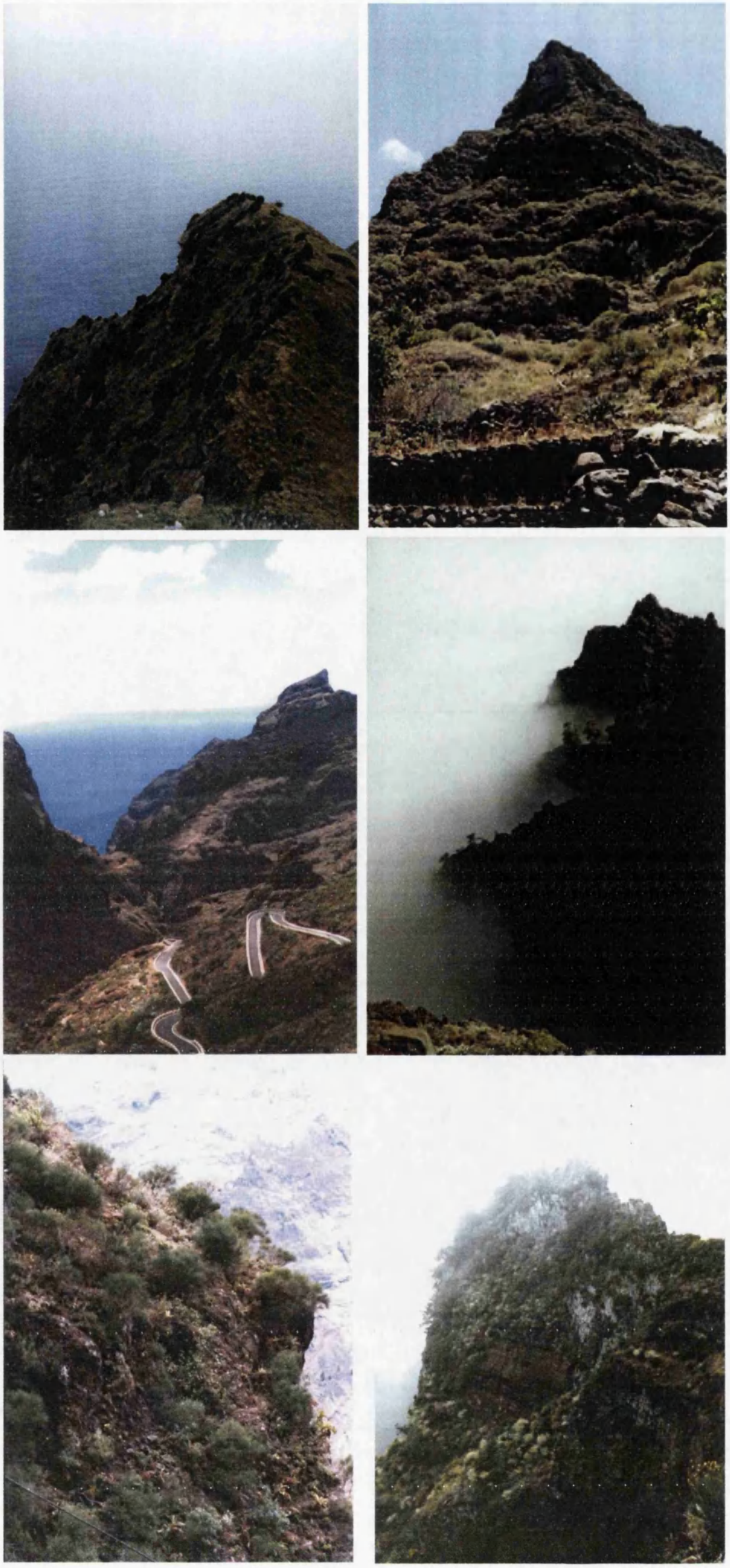
HOST PLANTS: *Teline splendens* (La Palma) and *Teline stenopetala* (La Gomera)

*Chamaecytisus proliferus*, flowers (Tenerife) and fruit (Gran Canaria)

*Cytisus grandiflorus* (Andalusía) and *Adenocarpus anagyrifolius* (Moroccan High Atlas)

PSYLLIDS: Adults are usually 2-4 mm in length, left, the largest Canary Island species, *Livilla monospermae* on the host plant *Retama monosperma*. Right, ovipositing female of *Arytinnis proboscidea* on the host *Adenocarpus viscosus*.

NYMPHAL FEEDING SITES: above left and below, eggs and nymphs are usually found on leaves and leaf buds of *Chamaecytisus proliferus*, but above right, nymphs of psyllid species feeding on *Teline* hosts are usually found on the flowers.



The terrain of volcanic islands is often steep and many of the places in which the host plants grow are difficult to access. *Top*: La Gomera. *Centre left*: Tenerife, *centre right*: La Palma. *Bottom left*: La Palma, *bottom right*: Madeira.

ANTHROPOGENIC EFFECTS: Cultivation of the native host plant *Chamaecytisus proliferus* increases host abundance (e.g. on El Hierro, top photo) and may promote psyllid abundance on cultivated and wild populations. Above, a large number of psyllids collected from a single wild individual.

*Genista benehoavensis* (top) and *Spartocytisus supranubius* (above) on La Palma where they are critically endangered from overgrazing by introduced rabbits and goats. In recent years, successful conservation programs have promoted the regeneration of these species in fenced off areas.

TABLE 3. Relative diversity of psyllids and legumes for each island:

| island | no. of habitat zones | no. of Genisteae sp. | no. of psyllid sp. | no. of endemic Genisteae | no. of endemic psyllids |
|---|---|---|---|---|---|
| Gran Canaria | 5 | 7 | 7 | 3 (43%) | 3 (43%) |
| Tenerife | 6 | 11 | 11 | 2 (18%) | 4 (36%) |
| La Gomera | 4 | 6 | 7 | 1 (17%) | 2 (29%) |
| La Palma | 6 | 9 | 7 | 2 (22%) | 1 (14%) |
| El Hierro | 5 | 5 | 4 | 1 (20%) | 0 |

TABLE 4. Distribution of legume plant species (Genisteae) per island:

| host plant genera | Gran Canaria | Tenerife | La Gomera | La Palma | El Hierro |
|---|---|---|---|---|---|
| *Genista* | 0 | 0 | 0 | 1 | 0 |
| *Retama* | 1 | 1 | 1 | 1 | 1 |
| *Teline* | 4 | 5 | 2 | 2 | 1 |
| *Chamaecytisus* | 1 | 1 | 1 | 1 | 1 |
| *Spartocytisus* | 0 | 2 | 1 | 2 | 1 |
| *Adenocarpus* | 1 | 2 | 1 | 2 | 1 |

TABLE 5. Distribution of psyllid species (Arytaininae) per island:

| psyllid genera | Gran Canaria | Tenerife | La Gomera | La Palma | El Hierro |
|---|---|---|---|---|---|
| *Arytainilla* | 0 | 0 | 0 | 1 | 0 |
| *Livilla* | 0 | 1 | 1 | 1 | 1 |
| *Arytaina* | 1 | 2 | 2 | 2 | 1 |
| *Arytinnis gen. nov.* | 6 | 8 | 4 | 3 | 2 |

### 1.2.4 *Host plant specificity*

Strict cospeciation (matching phylogenies) would predict a single psyllid species to be present on each legume species, and in fact the total number of psyllid species in the Canary Islands (21) is only marginally greater than the total number of Genisteae (18) and remains comparable when each island is taken separately (Table 3). However, as mentioned earlier, the number of species in each group are subject to different species concepts and different approaches to taxonomic treatments. The situation is further complicated by the presence of many psyllid species on some legumes, while other legumes do not appear to have a psyllid fauna. In some cases, where a single plant species appears to host many psyllids, these may be associated with intraspecific host taxa.

A more flexible and ultimately more realistic approach to the interactive evolution of plants and insects was championed by J. N. Thompson (1994) in his book 'The Coevolutionary Process'. Thompson (1994) challenged the conventional cospeciation model, pointing out that interactions between plants and insects may not result in prolonged historical associations that can then be mapped onto a phylogenetic tree; but instead there may be a shifting geographic mosaic of transient associations, as a result of differences in the physical environment and the local genetic and demographic structure of populations.

> "Differential speciation rates of interacting taxa, differential extinction rates, differences in geographic ranges among interacting species, novel mutations, and new ecological opportunities together prevent complete concordance in almost all comparisons. A run of parallel speciation is soon broken by a shift in one or more parasite populations onto a phylogenetically unrelated host. The larger the number of species in the group, the lower the chance of sustained phylogenetic tracking." (Thompson, 1994)

Thompson (1994) suggested that localized coevolution could take place within a shifting landscape, as part of the fluctuating nature of plant and insect metapopulations; and the history of these transient interactions would not be detected by a strict model of pairwise species for species coevolution.

Primitively, insects were probably saprophagous with a shift to the more complex lifestyle of herbivory, a secondary adaptation (Mitter, Farrell & Wiegmann, 1988). Psyllid fossils have been found from the early Permian before the angiosperms evolved. Thus, psyllids may have primitively fed on gymnosperms, or even lycopods (Hodkinson, 1980).

The explosive radiation of the angiosperms in the Cretaceous was paralleled by a massive radiation of associated insects, and many of the morphological and metabolic characters that the angiosperms exhibit may have evolved as defenses against herbivorous insects (Ehrlich & Raven, 1964; Jermy, 1984).

Allocation of resources in plants can vary seasonally, within an individual plant, between individuals, and from species to species. An example of this is evident in the phenological changes in chemical profile of flowers, leaves, stems, and fruit of the legume genus, *Adenocarpus* (Greinwald *et al.*, 1992) – a genus that is host to several Canarian and continental psyllid species. The changing character of an individual plant is a complex and challenging landscape to herbivorous insects (Wink, 1992). An insect that attains an adaptive peak on one plant species is likely to be in an adaptive trough on another species (Janzen, 1979).

## 1.3 The Macaronesian region

### 1.3.1 *Introduction*

Macaronesia encompasses the five Atlantic Ocean archipelagos of the Azores, Madeiras, Salvage Islands, Canary Islands and Cape Verde Islands, comprising aproximately 14,400 km$^2$ lying between 15°-40°N latitude. Of all the archipelagos, the most easterly point of the Canary Islands approaches closest to a continental landmass (only 115 km), with successively greater distances to the Salvage Islands (360 km), Cape Verde Islands (500 km), Madeira (630 km), with the Azores the most isolated at 1600 km from a continental landmass. A broad range of geological ages, from 1-30 Myr has been established for these islands (Table 6).

On oceanic islands the combination of altitude and climatic conditions are particularly important in the development of island biodiversity. A comparison of species richness and endemism for the flora of Macaronesia reflects the diversity of habitats in each archipelago (Table 7).

### 1.3.2 *The Canary Islands*

The Canary Islands occupies a central position within the Macaronesian region, extending over more than 500 km between 27°37' and 29°23'N, and 13°20' and 18°16'W. The Canaries are 1400 km north of the Cape Verdes and 170 km south of the Salvagens. These islands are exceptional in several respects: the greatest diversity of island ages, altitudes, habitat zones and species richness within Macaronesia are all to be found in the Canary Islands.

The two large, eastern islands, together with the small archipelago of La Graciosa, combine the largest land area in Macaronesia with the lowest altitudes (Table 10). This highly eroded profile and the geological dating of these land masses indicate a far greater age for the eastern islands than that extrapolated for the western islands, which some have taken to imply a continental origin and a rift from the bulge of Africa during the Cretaceous (Schmincke, 1976).

TABLE 6. Characteristics of the five archipelagos:

| archipelago | no. of islands | total km$^2$ | highest altitude (m) | latitude N | distance to mainland | distance to closest archipelago | origin Myr BP |
|---|---|---|---|---|---|---|---|
| Azores | 9 | 2235 | 2351 | 37° | 1600 | 900 | 4-8 |
| Madeiras | 3 | 796 | 1861 | 33° | 630 | 260 | 30 |
| Salvagens | 2 | 14 | 183 | 31° | 360 | 170 | 10 |
| Canaries | 7 | 7273 | 3718 | 28° | 115 | 170 | 1-21 |
| Cape Verdes | 10 | 4033 | 2829 | 16° | 500 | 1400 | 6-20 (45) |

TABLE 7. Data for angiosperms:

| archipelago | no. of endemic species | % endemic | no. of endemic genera |
|---|---|---|---|
| Azores | 44 | 5 | 0 |
| Madeiras | 120 | 11 | 1 |
| Salvagens | 1 | 1 | 0 |
| Canaries | 520 | 27 | 17 |
| Cape Verdes | 92 | 14 | 0 |

Adapted from Humphries (1979), Press & Short (1994), Báez, Martín & Oromí (2000).

## Geology

The geological origins of the Canaries are still unresolved with a number of contradictory hypothesis still under debate. Largely disputed now as a piece of 'parascience', which nevertheless was contested academically during the first half of the 20th century, is the 'Atlantis' or sunken continent theory. It was proposed that all five of the Macaronesian archipelagos were part of a single landmass – Plato's Atlantis – which, having sunk, left exposed only the tips of the mountain ranges as aerial islands. Remaining theories still contested seriously are discussed below, and due in part to the variety of questions and resolutions sought, none appear to convince all workers.

It was proposed by Raven & Axelrod (1974) that the break up of the Pangean landmass, approximately 180 Myr BP set in motion the tectonic forces that would eventually result in the formation of the Macaronesian islands. Within the framework of these macrogeological events, the real debate surrounds the source and temporal origin of the individual islands. It is now widely accepted that all the Atlantic islands, with the possible exception of the eastern Canary Islands, are oceanic in origin (Ancochea *et al.*, 1990; Carracedo *et al.*,1998). However, there remain some mystifying factors that would be explained more easily if some islands were fragments of the Old World's continental edges, which became isolated with the disappearance of earlier land-bridges and subsequent continental movements. Geologically it appears that the majority of the Macaronesian islands were formed *de novo* during ocean crust volcanism. Although this allows for no direct contact with neighbouring continents, current island size may not be equivalent with historical size. Islands may have been larger or smaller, sediment accumulation and uplifting may have resulted in inter-island or even mainland connections in the case of the eastern Canary Islands (Schmincke, 1976).

Several biological and palaeontological factors are at odds with the geological probabilities. These include the presence of fossil ostrich eggs of Miocene age in Lanzarote and fossils of terrestrial turtles of Pliocene and Pleistocene age in Tenerife. Biologists have found it difficult to come up with dispersal methods for flighless birds and giant land turtles required to explain their presence on ocean islands with no historic link to the mainland. Nor are the striking floristic and faunistic links between Macaronesia, the Mediterranean, Africa, Arabia and America easily explained by the evocation of long distance dispersal alone (Bramwell, 1976; Sunding, 1979).

The proximity of the eastern Canary Islands to the African Continent (only 111 km) (Table 10) combined with the shallowness of the intervening ocean shelf 1000-1500 m, as opposed to 1500-4000 m around the western Canaries, has favoured the hypothesis that the eastern islands of Fuerteventura and Lanzarote are continental in origin. This is supported by the phytogeographical evidence, with a major split in the floristic element between the eastern and western Canaries (Humphries, 1979). Seismic and gravimetric studies reveal the presence of oceanic crust in the west becoming transitional under Gran Canaria, and possibly continental farther east. It is extremely difficult to determine the origin of the basal crust and the accuracy of these results may be compromised by the accumulation of sediment, hence most studies have focused on the historical development and geodynamics of individual islands (Ancochea *et al.*, 1990; Guillou, Carracedo & Day, 1998; Carracedo *et al.*,1999) (Table 8).

There have been three volcanic eruptions this century – on Tenerife (1909) and on La Palma (1949 and 1971) (Table 9). The Canaries are the second most volcanically active archipelago in Macaronesia, and in the Atlantic Ocean region only Iceland and the Azores are more active. Volcanic activity produces stochastic environmental changes that are likely to have a critical influence on the evolution of the flora and fauna, effecting both extinction and creating new environments for colonization (Brown & Pestano, 1998; Emerson, Oromí & Hewitt, 1999).

The ocean floor around the Canaries is estimated to be around 180 Myr old, while the islands are considered to be much younger structures (1-21 Myr) (Table 10). The oldest sedimentary rocks are Cretaceous, from Fuerteventura. While some believe volcanic activity may have begun in the Canaries as early as the late Cretaceous, others believe there is no evidence for volcanism before the Oligocene (Schmincke, 1976).

The ‘Atlas structural trend’ or ‘African trend’ is thought to be associated with the orogenesis of the Atlas mountains, running NE-SW, which is reflected in the alignment of Fuerteventura and Lanzarote and the alignment of Hierro-Gomera-Tenerife. What is termed the ‘Atlantis fracture zone system’ or ‘Atlantic trend’, from which the islands may have arisen, runs NW-SE, and is reflected in the alignment of Gran Canaria-Tenerife-Palma (Schmincke, 1976). However, Carracedo *et al.* (1998) have proposed a ‘hot spot model’ unrelated to the Atlas tectonism, whereby the Canaries originated by an asthenospheric plume.

TABLE 8.

Ages of the shield-building lavas:

| island | date Myr BP |
|---|---|
| Fuerteventura | 12-17(20) |
| Lanzarote | 5-11(19) |
| Gran Canaria | 10-16 |
| La Gomera | 8-12 |
| Tenerife | 4-8 |
| La Palma | 0-2 |
| El Hierro | 1 |

TABLE 9.

Dates of volcanic eruptions in the Canaries:

| island | date |
|---|---|
| Fuerteventura | c. 3000 BP |
| Lanzarote | 1730, 1824 |
| Gran Canaria | c. 3075 BP |
| | |
| Tenerife | 1704, 1705, 1706, 1798, 1909 |
| La Palma | 1585, 1646, 1677, 1712, 1949, 1971 |
| El Hierro | c. 2900 BP |

Adapted from: Schmincke (1976), Ancochea *et al.* (1990), Carracedo *et al.* (1998).

TABLE 10. Characteristics of the Canary Islands:

| island | altitude m | area km$^2$ | distance from mainland | distance to closest island | origin Myr BP |
|---|---|---|---|---|---|
| Tenerife | 3717 | 2058 | 303 km | 27 km – Gomera | 7.5-11.5 |
| La Palma | 2426 | 728 | 489 km | 54 km – Gomera | 2 |
| Gran Canaria | 1950 | 1534 | 245 km | 57 km – Tenerife | 14.5-16 |
| El Hierro | 1501 | 277 | 489 km | 61 km – Gomera | 1-1.1 |
| La Gomera | 1487 | 378 | 417 km | 27 km – Tenerife | 10-12 |
| Fuerteventura | 807 | 1731 | 111 km | 11 km – Lanzarote | 16-20.6 |
| Lanzarote | 670 | 796 | 112 km | 11 km – Fuerteventura | 15.5-19 |

TABLE 11. Canary Island endemism

| group | no. endemic sp. | % endemic |
|---|---|---|
| Plants | 528 | 21.1 |
| Invertebrates | > 3,054 | 51 |
| Vertebrates | 20 | 16.1 |

Adapted from Humphries (1979), Báez *et al.* (2000) and Oromí & Báez (in press)

## History

There are several parallels between the anthropological history and the biogeographic history of other fauna and flora groups in the Canary Islands, such as repeated colonizations from the continent, patterns of inter-island colonization and genetically isolated island lineages. The arrival and settlement of humans on these islands is likely to have altered the ecology, with mostly negative effects on the biodiversity (especially the endemic element) evident today (Báez, 1988).

It is thought that the pre-hispanic, aboriginal Canary Island population stemmed from northwest Africa, but was early isolated through founder effect and genetic drift in small colonizing populations which then became distinct, both from the mainland and from populations on other islands. At least three waves of immigration have been proposed to account for the diversity of anthrolpological remains (Schwidetzky, 1976). The first wave of immigrants arrived around 2000 BC and the most recent in early Christian times, around the 1st century AD. Cultural differences between islands is explained by the failure of the most recent immigrants to reach all the islands. There is a distinct gradation from the oldest populations to the most recent, with La Gomera and Tenerife only inhabited by the oldest immigration group, the 'Guanches'. The patchy diaspora is established from skull characters with the extremes represented by the broad, prominent browed cromagnoid type found in La Gomera to the slim, gracile type found in the coastal regions of Gran Canaria. Prevailing winds and ocean currents from north to south combined with the levant winds from the Sahara would have made ocean travel from the continent to the islands far easier than the reverse journey from the islands back to the continent.

Scriptorially (the cave 'inscriptions' of El Hierro) and linguistically there are links to North Africa, with Berber, Egyptian and Libyc associations (Schwidetzky, 1976). Further cultural links are to be found in the ceramics, jewellery, leatherwork, obsidian knives and particularly the ancient Canarian custom of mummifying the dead. Despite associations with developing continental cultures, a lack of basic technological advancement has puzzled investigators. At the time of the Spanish Conquista in the 15th century, there was no use of metals. This led to the belief that the culture was neolithic and estimates of latest immigrations were much earlier than is believed today. Also puzzling is the lack of ship building in the archaeological record. This is strange in a people whose initial colonization must have been by boat, but contributes towards the explanation of the marked isolation of the different island populations.

A more tentative historical record can be found in ancient mythology. It has been suggested that several ancient names refer to the Canary Islands. The 'Elysian Fields' from Homer (c. 800 BC), the 'three Gorgones' and the 'three hesperides' from Hesiod (c. 800 BC), and the 'Atlantides' from Plato (c. 400 BC). It is thought unlikely that any of these authors knew of the Canary Islands, but it is certain that they were known of by Ptolemy (200 BC) as he placed his '0' meridian through the islands, and until the discovery of the New World, the Canaries were considered the most westerly point on earth. In later mythology, the Canaries were widely alluded to as the 'Happy Islands' due to the absence of snakes and abundance of wild fruit, wine and honey (Virgil, Horace and Pliny 70 BC-70 AD). The Phoenicians knew of the island of Madeira but it is still doubtfull as to whether they visited the Canarian archipelago in their navigation of the African coast (c. 610 BC). It has been suggested that they were responsible for locating Homer's 'Islands of the Cyclops' with the associated idea of barbarism somewhere in the Atlantic, possibly in the Canary Islands. The first incidence of the current archipelago name is 'Canariae Insulae' from Anobius (330 AD) (Krüss, 1976).

### Origin of the flora and fauna

The 'Macaronesian' concept was first introduced, not for a geographical or political region, but as a phytogeographical term by the botanist Philip Barker Webb in the 19th century. The diversity of habitats appears to be one of the main factors responsible for the rich Macaronesian flora, which includes c. 780 endemic species, while the diversity and endemism of the invertebrates is even more impressive (Table 11).

The Canary Island biota has the greatest affinity with the biotas of adjacent continental regions (Mediterranean and NW Africa) (Kunkel, 1976). However, there are several groups (both animal and plant) that show remarkable disjunctions, with the closest relatives of the island species found in Australasia, SE Asia, South Africa and South America (Bramwell, 1976; Báez, 1987). Fossil evidence indicates that the present day Macaronesian laurel forest was once the dominant element of a widespread subtropical Tertiary flora, remnants of which still survive around the Mediterranean as well as in southern Africa, Asia and the Americas (Bramwell, 1976; Sunding, 1979). The presence of species associated with the laurel forest ecology in Macaronesia suggests that these islands have acted as refugia, buffered by a relatively temperate oceanic climate, from the massive extinction and migration of plants and animals during periods of glaciation and desertification on the continent (Bramwell, 1976; Sunding, 1979). However, the relictual status of certain plant groups has been controversial. Bramwell (1976) argued that a number of woody island plant groups, based on cytological and morphological evidence, were relictual (e.g. *Bencomia*, *Echium*, and *Senecio*), but these have been shown by molecular analyses to be recently derived from herbaceous, Mediterranean ancestors (Kim *et al.*, 1996; Böhle, Hilger & Martin, 1996; Helfgot *et al.*, 2000). These neoendemic groups are examples of spectacular and speciose adaptive radiations, and partly for this reason have been preferentially selected for molecular studies. However, genuine palaeoendemic elements in the Canary Islands may be less amenable to molecular studies because of a lack of suitable outgroups still living today.

The uniqueness of island biotas is partly attributed to adaptations (or loss of adaptations) to features that are peculiar to islands, such as the absence of predators, competitors or specialist pollinators. The diversity of these adaptations may be preserved by the insularity of each island and reinforced following an adaptive reduction in dispersal mechanisms (Carlquist, 1974). However, islands, which are therefore a 'nursery' for evolution and diversity, have proven to be drastically susceptible to aggressive competition and predation from introduced continental elements. This has led to a stability paradox on islands – there is long term stability protecting the diversification and the survival of palaeoendemics, but there is extreme instability when confronted with foreign invasions from recently introduced elements (Cronk, 1997). Thus, isolation may be the cause of a rich and unusual diversity, but also of great vulnerability. As islands are avenues for evolution they can also be cul-de-sacs of extinction.

### Effects of seasonality and climate on the flora and fauna

Climate is one of the key features determining the floristic and faunistic character of the Canary Islands. As with other ocean archipelagos, the islands are subject to a relatively milder climate than the continental landmasses due to a temperate oceanic influence. However, the Canary Islands have a far from uniform climatic profile. There are certain prevailing conditions that result in a somewhat predictable pattern but the Canaries also come under the influence of more unpredictable weather systems.

The principle air masses blowing over the Canaries are associated with the Azores anticyclone over the North Atlantic region. Winds blowing outward and eastward from this region acquire a northeasterly direction as they turn towards the south under the influence of equatorial and continental low pressure zones. These winds from the north and northeast form the prevailing trade winds that blow throughout the year and are the most consistent influence of climatic factors in the Canaries (Fernandopullé, 1976).

The lower layer of the trades is thin, usually only 1000-1500 m, and humidity is acquired during traversion of the cool ocean waters resulting in a characteristic formation of extensive strato-cumulus clouds. These winds also attain the highest mean wind speeds, 27 km/hr (Lanzarote) to 14 km/hr (Tenerife) according to the shape and size of the geographic ‘wind break’ features.

Less prevalent winds blow from the NW, W and SW in association with winter depressions over the Atlantic. Anti-trade winds associated with hot, dry Saharan winds blow from the SE and sometimes E. The effect of the hot, dry anti-trades above the lower humidified trade layer results in a temperature inversion often forming at about 1000 m around the higher islands and resulting in the characteristic and dramatic cloud seas. The inversion layer shifts seasonally, being lower in summer and higher in winter. The winter cloud bank is therefore thicker but it is less persistent, while the summer cloud bank is permanent during the summer months of June and July.

Differences in climate between individual islands are determined primarily by the altitude of the island and by its proximity to the African continent. Mean monthly temperature varies with altitude from 27°C at sea level to 7.5°C above 3200 m. Local variation within islands becomes increasingly pronounced with altitude, and the higher islands rising above the inversion zone are subject to dramatic variation in temperature and precipitation between the northern (windward) slopes and the southern (leeward) slopes. Local land and sea breezes also effect the formation of the cloud banks. Clouds that are widespread over the sea, arrive on the windward side and pile up on the mountain slopes aided by sea breezes during the day, at night land breezes push the cloud bank offshore. In contrast, on the leeward slopes cloud banks may form 10-15 km offshore but do not form over land because of the heating effect produced by descent over the dry slopes (Fernandopullé, 1976).

Two forms of precipitation occur in the Canaries. Winter rains are the result of cyclonic depressions associated with North Atlantic air masses and northerly or north westerly polar maritimes. Occasional heavy precipitation results from humid tropical maritime air masses from the SW, and tropical cyclones originating over the African continent and arriving from the E. Sixty per cent of the yearly rainfall occurs between December-January, and in most cases the total annual precipitation occurs within 10-40 days of rainfall. The intensity of these rains is similar for northern and southern slopes but the number of rain days is higher in the north. Daily intensities vary with between 25-300 mm/24hr, indicating that 25-40% of the total yearly rainfall can occur in 24 hours. A second source of precipitation results from orographic uplift of the humid winds and horizontal precipitation from condensation by fog and mist associated with the cloud bank. Unlike the cyclonic winter rains, these forms of precipitation are exclusive to the northern slopes. Horizontal precipitation is believed by local people to be an important source of water and there is a famous story of the 'árbol de lluvia' or 'rain tree' of El Hierro. The story relates how large cisterns (of which remnants survive today) were carved out of rocks beneath the tree, and collected sufficient water dripping from the foliage to meet the needs of the local people. On arrival of the Spanish Conquista this valuable resource was kept secret. However, a local girl who was enamoured of a Spanish soldier was persuaded by her lover to give the secret away, for which she was condemned to death by the islanders (Bramwell & Bramwell, 1990).

Orographic factors are the most important general distributors of rain in the islands, and as these factors are a result of altitudinal gradients, low islands such as Lanzarote and Fuerteventura lack the high relief barriers to catch the humid winds. Islands of medium height (El Hierro and La Gomera) are high enough to accumulate a large amount of cloud cover over the whole island, while the high islands (Gran Canaria, Tenerife and La Palma) rising above the cloud layer act as barriers which result in dramatically different climatic zones above and below the inversion zone. Thus low islands (Lanzarote and Fuerteventura) near the African coast have a semi-desert climate, while the central and western islands range from semi-arid southern areas to sub-tropical northern areas, and sub-alpine peaks with snow caps of 30-40 cm recorded for El Teide (Tenerife).

The summer is relatively quiescent compared to winter weather systems. The dry season lasts from May to August and in the height of the summer during July and August, heat waves from the Sahara influence weather conditions in the Canaries for up to 20-25% of the time. There is a clear pattern of increasing rainfall in a westerly direction away from continental Africa (Table 12).

TABLE 12. Mean rainfall for the period 1949-1967:

| island | mean rainfall mm/yr |
|---|---|
| Lanzarote | 135 |
| Fuerteventura | 147 |
| Gran Canaria | 325 |
| Tenerife | 420 |
| La Gomera | 410 |
| El Hierro | 426 |
| La Palma | 586 |

Adapted from Fernandopullé (1976).

## 1.4 Genesis and rationale for this study

The initial aim of this study was to select a plant-insect system that could be investigated against the backdrop of island biogeography. Preferably, a highly host specific insect group that was associated with one of the famously speciose plant groups, arisen from a dramatic adaptive radiation. The Macaronesian region, and in particular the Canary Islands, was selected primarily because these islands had been the focus of a number of exciting evolutionary studies in the last decade, but also important was the element of a logistically feasible field site (i.e. travel, expense, and facilities).

There had been several phylogenetic studies of independent plant and insect groups from Macaronesia, but there were no studies dealing specifically with interactions between native plants and insects. Selecting the plant and insect groups was the first step. I had narrowed the possibilities down to a hemipteran insect group, but I had little idea of which group would be suitable until the end of my first week collecting in the Canary Islands (1997). I noticed the legume-feeding psyllids quickly because I always found a member of this group on every legume I sampled, while there appeared to be less consistency (to my inexperienced eye at least) in the mixed assemblage of insects gathered from other target plant groups. However, it was not until sorting through these collections under a microscope at the University of La Laguna, that I began to realize that each psyllid from the different legumes sampled was a different species. In fact, this was the first major hurdle – learning how to identify psyllids, predominantly by characters of the genitalia. By the end of my first visit to the Canary Islands, I was convinced I had the right system and I had begun to sample systematically from every legume species/subspecies and population I could find, in the five central and western islands. The collecting I did in this first year produced five of the 10 new species discovered on the Canary Islands. A broader and more detailed survey in my second year included the Canary Islands, Madeira and continental regions – especially the Moroccan Atlas mountain ranges; and an additional twelve new species were discovered. This brought the number of new species I would need to name and describe to 17.

Although the focus throughout this study has been predominantly on the Canary Islands, the sampling in adjacent regions has provided a vital phylogenetic and biogeographic framework in which to view the evolution of the Canary Island psyllids. By far the most detailed sampling was undertaken in the Canary Islands, including repeated sampling of the same host populations at different times of the year and in different years, in order to monitor fluctuations in psyllid populations. A series of pilot host transplant experiments in the field showed a high level of mortality among psyllids transplanted to foreign hosts, as well as an association in the rate and extent of mortality with the phylogenetic distance of the foreign host. Unfortunately, further research following up these preliminary hosts transplant experiments was beyond the scope of this PhD.

The taxonomy of the legume-feeding psyllids in this study was unsatisfactory when I started, and the need to describe and classify the new species I had collected led me undertake the revision of the genus *Arytainilla* presented in Chapter 2. As my work on the alpha taxonomy of the psyllid group progressed contemporaneously with the construction of the molecular phylogenies, I was able to cross reference between the two approaches, which I feel was advantageous to the interpretation and results of both. Molecular data provides an important contribution towards interpreting the monophyly or paraphyly of morphologically determined groups (particularly where there may be a high level of morphological homoplasy). Paraphyletic genera and taxonomic ambiguity in both insect and plant groups may reflect periods of rapid and, in some cases, recent diversification, resulting in poor differentiation of groups using either morphological or molecular data. In order to analyse the patterns of island and host plant colonization, I needed to resolve sister taxon relationships within groups. I determined that this would be best achieved by comparing and combining phylogenetic information from both morphological and molecular characters. In Chapter 3, I present the first phylogenetic analysis for the psyllid group. I compare and contrast molecular and morphological phylogenies, and I use both types of data to investigate the psyllid classification and evolutionary patterns in continental and island species.

An extremely confused taxonomy characterizes the legume classification (based on morphological data) and previous molecular phylogenies have inadequately sampled the major Canary Island host plant groups. Early on, it became apparent to me that accurate assessment of psyllid-legume interactions would be hindered without a detailed molecular phylogeny for the host plants. This led me to produce the molecular legume phylogeny, presented in Chapter 4, which has proved essential for interpreting the patterns of host preference and host switching in psyllids. For instance, the most polyphagous psyllid in the Canary Islands feeds on three legumes, but these three legume species have near identical sequences for the nuclear region sampled, suggesting that this psyllid, based on molecular evidence, is in fact monophagous. The construction of accurate phylogenies for both psyllids and legumes was the only way to address the question of cospeciation in Chapter 5, and to undertake the analyses required to test assumptions of parallel cladogenesis.

In many respects each aspect of this thesis, field surveys, taxonomy, morphological and molecular phylogenies as well as the combined synthesis, would all benefit from another three years study. However, in the past three years, I believe I have made some inroads into the complex and multilayered dimensions of insect-plant interactions. Perhaps my only regret is that I did not spend the entire three years of this study in the field, as there remains a great wealth of evidence to be gathered.

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# CHAPTER TWO

# THE LEGUME-FEEDING PSYLLIDS (HEMIPTERA, PSYLLOIDEA) OF THE CANARY ISLANDS, MADEIRA AND ADJACENT AREAS

[Part of this chapter has been submitted as a paper to the *Journal of Natural History*]

## Abstract

A detailed survey of the legume-feeding jumping plant-lice, or psyllids (subfamily Arytaininae) in the Canary Islands and Madeira indicates a high level of endemism and diversification in this region. An additional survey in possible continental source areas provides a comparison of continental and island species diversity. The taxonomy of the genus *Arytainilla* is revised to reflect a distinct origin for the predominantly Macaronesian group. The position of this island group is clarified in relation to the mainly continental *Arytainilla sensu stricto*. One new genus and 17 new species are described. Descriptions of previously undescribed 5th instar nymphal stages for 31 species are also included. Nine of the new species are described in ***Arytinnis* gen. nov.**, four in *Arytainilla*, three in *Livilla* and one new species in *Arytaina*. In addition, 14 new combinations are proposed including the transfer of *Psylla improvisa* to *Pseudacanthopsylla*. A high degree of host specificity is typical and information is given on host plant associations, biology and geographic distribution. Separate keys for adults and nymphs are provided for ***Arytinnis* gen. nov.**, *Arytainilla* and the remaining Canary Island species.

## 2.1 Introduction

The psyllid subfamily Arytaininae comprises 14 genera, five of which feed exclusively on genistoid legumes (Genisteae, Leguminosae). Hodkinson and Hollis (1987) examined two of the genistoid-feeding genera, *Arytaina* and *Livilla*, but observed that the genus *Arytainilla* was ‘certainly not a monophyletic group’ and required further collecting. A survey of genistoid hosts in the Canary Islands, Madeira, Southern Iberia and North Africa has provided additional material for a revision of *Arytainilla sensu* Loginova,1972. The predominantly Macaronesian species are here placed in a separate genus, *Arytinnis* gen. nov., to reflect the monophyly of this group and its origins as distinct from *Arytainilla sensu stricto* represented by the type species *Arytainilla delarbrei*. As defined here, *Arytainilla sensu stricto* returns to a concept closer to the original for this genus (*sensu* Ramírez Gómez, 1956) before the inclusion of the Macaronesian species by Loginova (1972). However, the present inclusion of *A. sulci*, *A. gredi* and *A. montivaga* sp. nov. in this genus is problematic, nevertheless it seems best to retain these species in *Arytainilla* until further work resolves their placement within Arytaininae.

None of the five genera of legume-feeding psyllids represented in the Canary Islands are exclusively endemic. However, all 21 Canary Island species in the four Arytaininae genera, *Arytaina*, *Arytainilla*, *Arytinnis* gen. nov. and *Livilla* are endemic, while a single *Acizzia* (Acizziinae) species is introduced. There are 21 species in *Arytinnis* gen. nov., 16 of which are endemic to the Canary Islands and half of these are newly described species. In addition, one *Arytinnis* species is described from Morocco. Of the remaining five non-Canarian species, two are endemic to Madeira, one to the Moroccan Anti-Atlas mountains, one to the Moroccan High Atlas mountains and one, *A. hakani*, is the only widespread species occurring throughout the western Mediterranean.

Within the Hemiptera the morphological transformation between immature and adult is particularly dramatic in the Psylloidea. The term 'larvae' for immature stages has been used to emphasise the absence of shared characteristics between nymph and adult, and indicates the importance of descriptions for both immature and adult stages. Previous descriptions of the last (5th instar) nymphal stage for *Arytinnis* gen. nov. have been limited to one species (*A. hakani*, Rapisarda, 1987). With the addition here of a further 19 descriptions of 5th instar nymphs, only one species remains with the nymph undescribed (*A. canariensis*). In contrast to the relative homogeneity of nymphal forms in *Arytinnis* gen. nov., differences in nymphal morphology are pronounced in the remaining *Arytainilla* species. This divergence reflects a similar heterogeneity in the adult form, perhaps indicating the greater age of this lineage and possibly extinct intermediates.

All native legume-feeding psyllids in the Canary Islands feed on hosts in the tribe Genisteae (Papilionoideae, Leguminosae). These papilionoid legume shrubs include the common brooms and gorse, and are most diverse in the Mediterranean and North African regions. Macaronesian representatives from the Canary Islands and Madeira have clear affinities to Mediterranean taxa. However, within the islands species affiliations have been controversial, particularly in the genus *Teline* (Gibbs & Dingwall, 1972; Gibbs, 1974; Arco Aguilar, 1983, 1993). Of the 16 species currently recognized for *Teline*, 10 are endemic to the

Canary Islands, one to Madeira and five species are continental, occurring in the Mediterranean and North Africa (Gibbs & Dingwall, 1972; Talavera & Gibbs, 1999). The extensive ecological radiation of this group in the Canary Islands contrasts with other genistoid genera present in the Canaries: *Chamaecytisus* and *Genista* are each represented by a single species, while *Adenocarpus* and *Spartocytisus* exhibit limited diversification with a high and low altitude species in each genus. The Genisteae are considered to be a monophyletic tribe but the delimitation of genera has proved problematic (Polhill, 1976; Bisby, 1981; Käss & Wink, 1997). There are three generally accepted groups: a *Genista* group, a *Cytisus* group and various outliers. Of the genera that occur in the Canary Islands, *Teline* and *Retama* are in the *Genista* group, *Chamaecytisus* and *Spartocytisus* are in the *Cytisus* group while *Adenocarpus* is considered an outlier. Although some members of *Arytinnis* gen. nov. feed on hosts in *Adenocarpus* (two species), *Genista* (three species) and *Chamaecytisus* (two species); *Teline*, on which 15 species feed, is the primary host group for this genus. In the Canary Islands there has been considerable diversification of the *Teline*-feeding psyllids that reflects the diversification in the host genus.

## 2.2 Materials, methods and terminology

Field collections were made during June-July and December 1997, March-July 1998, March-May 1999 and July-August 2000. Adults and nymphs were collected by sweeping host plants with a canvas net and stored in 100% ethanol. Host plant material was examined in the field and in the laboratory for presence and placement of eggs and 1st-2nd instar nymphs. Identifications were made from alcohol, slide mounted (method in Hodkinson & White, 1979) and capillary mounted (method in Ossiannilsson, 1992) material. Geographical and host preference ranges were determined by sampling from several different host populations and by sampling from the same populations in different years (details of hosts and host populations sampled in the Canary Islands are given in Appendices 1 & 2). Pressed plant specimens (deposited at Glasgow University Herbarium (GL) and Royal Botanic Garden Edinburgh (E)) were made of all host plants including intraspecific taxa for confirmation of host plant identification. The methods used to assess host specificity were a) the presence of nymphs – immature stages are mobile but typically sedentary, particularly in 1st-3rd instar stages, 4th-5th instars can move rapidly but are unlikely to travel far from feeding sites or to disperse from one plant to another; b) comparison of adult distribution in locations where the host plant is isolated, with locations where the host plant grows sympatrically with other genistoid legume species. In the latter situation transient adults are frequently found on legumes other than the host or, at high densities, on non-leguminous plants. Material was collected by the author unless otherwise stated. Terminology and measurements used in some adult characters are illustrated in Figs 1 and 2 and the treatment of setal placement in nymphal descriptions and keys is indicated in Fig. 2. All other terminology and measurements follow Hodkinson & White (1979) and White & Hodkinson (1982, 1985). In the type and other material examined the host plant is only listed when the species is oligophagous on more than one host plant or when adults, as transients, were collected from hosts other than the specified host plant for that species. The following abbreviations are used to indicate institutions in which type material is deposited: The Natural History Museum, London (BMNH); Departamento de Biología Animal (Zoología), Universidad de La Laguna, Tenerife (DZUL); Naturhistorisches Museum Basel (NHMB). Other material is in the collection of the author indicated by DP and a collection number. Numbers in parenthesis after new species names will represent that species in a current molecular analysis.

Abbreviations used in the descriptions are as follows (all measurements are recorded in mm):

Adults
WLPT = ratio forewing length : pterostigma length
ALHW = ratio antennal length : head width
GCVL = ratio genal cone length : vertex length
WLHW = ratio forewing length : head width
VLW = ratio vertex length : width
WLW = ratio forewing length : width
CUR = ratio forewing cell $cu_1$ width : height
MR = ratio forewing cell $m_2$ width : height
RMCU = ratio forewing wing vein Rs length : vein $M+Cu_1$ length
TLFL = ratio hind leg tibia length : femur length
TLHW = ratio hind leg tibia length : head width
SCHW = ratio mesoscutum width : head width
ATIB = ratio hind leg apical tarsus length : tibia length
MTIB = ratio hind leg metatarsus length : tibia length

PBHW = ratio distal proboscis segment length : head width
ATMT = ratio hind leg apical tarsus length : metatarsus length

Adult genitalia ♂
MP = proctiger length
PL = paramere length
AEL = distal aedeagus segment length
AEH = aedeagus hook length
MPHW = ratio proctiger length : head width
PLHW = ratio paramere length : head width
MPPL = ratio proctiger length : paramere length
AEPL = ratio distal aedeagus segment length : paramere length
MSLH = ratio subgenital plate length : height
AHS = ratio distal aedeagus segment length : aedeagus hook length
PLSH = ratio paramere length : subgenital plate height

Adult genitalia ♀
FP = proctiger length
FSP = subgenital plate length
RL = anal ring length
OV = ovipositor valvulae dorsalis length
EL = egg length
FPHW = ratio proctiger length : head width
FPSP = ratio proctiger length : subgenital plate length
FPCR = ratio proctiger length : anal ring length
OLSP = ratio ovipositor valvulae dorsalis length : subgenital plate length
FEOL = ratio mean egg length : mean ovipositor valvulae dorsalis length

Nymphs
BL = body length
BW = body width
WL = forewing pad length

CPL = caudal plate length
CPW = caudal plate width
RW = circumanal ring width
RL = circumanal ring length
HW = head width
AL = antennal length
AL3 = length of 3rd antennal segment
WBL = ratio body width : length
ALHW = ratio antennal length : head width
ALWL = ratio antennal length : forewing pad length
WLHW = ratio forewing pad length : head width
WCPL = ratio caudal plate width : caudal plate length
CPRW = ratio caudal plate width : circumanal ring width

## 2.3 Taxonomic treatment

[Figures, where appropriate, are referenced in the keys and presented at the end of the chapter. Terminology and measurements are illustrated in Figs 1 and 2]

**2.3.1** *Key to adults of the legume-feeding genera in the Canary Islands and Madeira.*

1 Body colour predominantly orange-brown; forewing membrane with apical, orange-brown pattern of clouds and spots, cell $m_2$ narrow and long (MR $< 0.37$) and cell $cu_1$ narrow and high (CUR $\leq 1.38$); antennae shorter than 1 mm; male paramere shorter than 0.25 mm; distal aedeagus segment ($< 0.22$ mm) appearing jointed, apex without a hook but with a sharp point and dorsal blade; male proctiger with a pronounced basal posterior lobe and subsidiary projection, the apical portion slender; male subgenital plate elongate, length greater than 1.55 x height; female genitalia truncated, proctiger ($< 0.5$ mm) shorter than 0.7 x head width, circumanal ring relatively long – proctiger length less than 2.6 x ring length, subgenital plate shorter than 0.3 mm; ovipositor valvulae dorsalis short ($< 0.12$ mm) and relatively high with a slender anterio-dorsal elongation at the base (Fig. 1D) ..................... ........................................................................................ *Acizzia* Heslop-Harrison

[a single introduced species, *Acizzia uncatoides* (Ferris & Klyver), on *Acacia* spp.]

— Body colour predominantly green or dark brown to grey; forewing membrane either clear, or more darkly pigmented (often towards the apex), or with distinct dark brown apical banding, cell $m_2$ broader and shorter (MR $> 0.37$) and cell $cu_1$ broader and lower (CUR $>

1.38); antennae longer than 1 mm; male paramere longer than 0.25 mm; distal aedeagus segment (> 0.22 mm) either straight or curved, apex with a hook or bluntly rounded; male proctiger either not, or only gradually becoming inflated posteriorly towards the base; male subgenital plate more orbicular, length less than 1.55 x height; female genitalia longer, proctiger (> 0.5 mm) greater than 0.7 x head width, circumanal ring relatively short – proctiger length greater than 2.6 x ring length, subgenital plate longer than 0.3 mm; ovipositor valvulae dorsalis relatively long (> 0.12 mm) and slender, without anterio-dorsal elongation at the base ........................................................................................ 2

2 Forewing membrane with distinct pattern of dark brown transverse bands and clouds, pterostigma rudimentary, vein Rs distinctly curved upwards at the apex towards the costal margin, vein M sinuous, cell $m_2$ almost as wide as long (MR > 0.8), surface spinules dense (> 100 per 0.1 $mm^2$); genal cones longer (> 0.3 mm) than the vertex; male subgenital plate dorsal posterior margin with a pair of long (more than half the length of the paramere) stout setae; metatarsal spur absent (Fig. 1K) ........................................................ *Livilla* Curtis

[a single species, *Livilla monospermae* Hodkinson, on *Retama monopserma*]

— Forewing membrane either clear or more darkly pigmented, often with darker patches in the apical cells, but without a distinct pattern, pterostigma either absent or long (about ¼ or greater the wing length), vein Rs not, or only weakly, curving upwards at the apex towards the costal margin, vein M evenly curved, cell $m_2$ significantly longer than wide (MR < 0.7), surface spinules less dense (< 100 per 0.1 $mm^2$); genal cones shorter (< 0.25 mm) than the vertex; male subgenital plate dorsal posterior margin without a pair of long, stout setae; one metatarsal spur (Figs 1I–J & L–N) ...................................................................................... 3

3 Forewing coriaceous, yellow-brown becoming darker at the margins, cell $r_1$ narrow with vein Rs running close to the costal margin, cell $cu_1$ broad and low (CUR > 2.3); hindwing costal margin straight; genal cones longer than 0.75 x vertex length; male paramere slender and sinuous, as long, or longer than 0.9 x head width; male proctiger slender, longer than 0.7 x head width; distal aedeagus segment longer than 0.45 mm, apex relatively small, less than 0.15 x segment length, and bluntly rounded without a hook; female genitalia robust, the proctiger apex arched and tip upturned; ovipositor massive, valvulae dorsalis longer (> 0.5 mm) than 0.5 x subgenital plate length (Figs 1F & 3) ................. *Arytainilla* Loginova

[a single species, ***Arytainilla serpentina sp. nov.***, on *Spartocytisus filipes*]

— Forewing not coriaceous, either clear or with darker patches in the apical cells, cell $r_1$ relatively wide, cell $cu_1$ relatively high (CUR < 2.3); hindwing costal margin concave;

genal cones shorter than 0.75 x vertex length; male paramere shorter than 0.9 x head width; male proctiger relatively broad and short, less than 0.6 x head width; distal aedeagus segment shorter than 0.45 mm, apex relatively large, greater than 0.2 x segment length, and with a shallow or well rounded hook; female genitalia more slender, the proctiger apex straight or slightly upturned; ovipositor slender, valvulae dorsalis shorter (< 0.3 mm) than 0.5 x subgenital plate length (Figs 1G–H) ........................................................................ 4

4 Body colour predominantly dark brown or grey (recently emerged adults may be green); forewing costal break and pterostigma absent; head not, or only weakly, deflexed downwards with genal cones in approximately the same plane as the vertex; male paramere shorter than the proctiger, length less than 0.4 x head width; distal aedeagus segment longer than 0.95 x paramere length ........................................................................ *Arytaina* Foerster

— Body colour predominantly green (mature adults sometimes develop brown colouration); forewing with costal break and long pterostigma; head deflexed downwards with genal cones directed downwards relative to the plane of the vertex; male paramere longer than the proctiger, length ≥ 0.4 x head width; distal aedeagus segment shorter than 0.95 x paramere length ........................................................................ ***Arytinnis* gen. nov.**

### **2.3.2** *Key to 5th instar nymphs of the legume-feeding genera in the Canary Islands and Madeira.*

1 Abdominal sectasetae either absent or if present, one or two pairs .................................... 2

— Abdominal sectasetae three or four pairs ........................................................................ 3

2 Antennae with nine segments (including scape and pedicel) and with a capitate seta on 3rd and 5th segments; anterior head and ocular setae distinctly capitate; total body length less than 1.5 mm; antennae shorter than 0.7 mm, less than 1.5 x forewing pad length, or 1.2 x head width; width of caudal plate greater than 1.7 x length, and greater than 5 x anal ring width (Fig. 29D) ........................................................................ *Acizzia* Heslop-Harrison [a single introduced species, *Acizzia uncatoides* (Ferris & Klyver), on *Acacia* spp.]

— Antennae with seven segments (including scape and pedicel) and with simple setae only; ocular seta simple and anterior head setae simple or narrowly capitate; total body length greater than 1.5 mm; antennae longer than 0.7 mm, greater than 1.5 x forewing pad length, or 1.2 x head width; width of caudal plate less than 1.7 x length, and less than 5 x anal ring width (Figs 24B–D) ........................................................................ *Arytaina* Foerster

3 Distinctly capitate setae present on anterior margin of the head, and distally on 3rd and 5th antennal segments; numerous small, pale, capitate setae present dorsally on the wing pad surfaces and thorax (Fig. 24A) .......... *Livilla* Curtis

[a single species, *Livilla monospermae* Hodkinson, on *Retama monopserma*]

— Anterior margin of the head with simple or narrowly capitate setae, antennae with simple setae only; wing pad surfaces usually without capitate setae or where present on the wing pads and thorax, long and darkly pigmented .......... 4

4 Forewing pad and abdomen acutely rounded apically; marginal abdominal setae (other than sectasetae) two pairs; wing pads with minute simple setae only; antennae shorter than forewing pad length, or head width; head width less than forewing pad length; forewing pad longer than 0.7 mm; caudal plate length (> 0.8 mm) greater than width (Fig. 22C) *Arytainilla* Loginova

[a single species, ***Arytainilla serpentina* sp. nov.**, on *Spartocytisus filipes*]

— Forewing pad and abdomen broadly rounded apically; marginal abdominal setae (other than sectasetae) one, three or four pairs; wing pads with one or more prominent setae; antennae longer than forewing pad length, or head width; head width as great or greater than forewing pad length; forewing pad shorter than 0.7 mm; caudal plate length (< 0.6 mm) less than width (Figs 25–29) .......... ***Arytinnis* gen. nov.**

## **2.3.3** SUBFAMILY ARYTAININAE

### Genus *Arytainilla* Loginova

*Spartina* Heslop-Harrison, 1951: 443; 1961a: 417. Type species *Psylla spartii* Guerin, by monotypy [Homonym of *Spartina* Harris and Burrows, 1891]

*Lindbergia* Heslop-Harrison, 1951: figures 2 a, b, nomen nudum [no included species] (nec *Lindbergia* Riedel, 1958)

*Lindbergiella* Heslop-Harrison, 1961b: 509, nomen nudum [type species not designated]

*Arytaina* subgenus *Arytainilla* Ramírez Gómez, 1956: 76, nomen nudum [type species not designated]

*Alloeoneura* subgenus *Hispaniola* Ramírez Gómez, 1956: 91, in part, nomen nudum [type species not designated]

*Arytainilla* Loginova, 1972: 17; 1977: 64. Type species: *Psylla delarbrei* Puton, designated by Loginova, 1972: 17

*Adult Description:* Variable in colour, from bright green or grey-green, to yellow or dark brown; lacking distinct forewing patterns. Forewing membrane may be transparent or opaque, or more rarely coriaceous and sometimes darkly pigmented; veins uniformly pigmented, pale or mid-brown. Forewing widest in the apical third with a broadly rounded apex, or in the middle third with a more acutely rounded apex; costal break and pterostigma present, pterostigma varying from rudimentary to long, typically less than one quarter the wing length; vein Rs may be slightly curved in the middle, but not, or only weakly curved at the apex, towards the costal margin. Hindwing costal margin straight. Antennae typically short, with eight or ten segments. Head deflexed downwards with genal cones directed downwards relative to the plane of the vertex; genal cones varying from short to long. Distal proboscis segment short to mid-length. Number of basal tibial spurs variable, typically four to five (2/3+1+1), though individuals may have as few as three; one metatarsal spur. Paramere longer or shorter than the proctiger, often slender, elongate and simple, or shorter and broader, with or without a small or more pronounced anteriorly directed hook at the apex. Female genitalia large to massive with a robust ovipositor, or smaller with a slender ovipositor.

*Nymphal Description:* Forewing pads and abdomen broadly or acutely rounded apically. Antennae with seven segments. Tergites varying from barely reduced to extensively reduced. Circumanal ring variable in shape, outer ring with a single, or multiple rows of pores; contiguous or not with the apical abdominal margin. Head and antennae with or without distinct capitate or club setae. Wing pads with or without prominent setae. Sectasetae absent or present (one to four pairs). Legs with or without capitate setae.

*Comment:* This is a heterogeneous group of 12 species. *Arytainilla sensu stricto* is a monophyletic group of 9 species that can be distinguished most notably by the large female genitalia and robust ovipositor. The three remaining species, *A. gredi*, *A. sulci* and *A. montivaga* sp. nov. are not included in this group and their correct placement within the Arytaininae is not clear. Thus, they are retained in *Arytainilla* for the present and are treated here as residual species. *Arytainilla* is a predominantly continental genus with only one species occurring in the Canary Islands. Useful biological notes for species occurring in Italy can be found in Conci, Rapisarda & Tamanini (1993, 1996).

Key to adults of *Arytainilla*.

1 Female ovipositor large (often with serrations or projections), valvulae dorsalis longer than 0.25 mm and greater than 0.5 x subgenital plate length, valvulae ventralis higher than valvulae dorsalis at least in part, valvulae dorsalis dorsally more or less straight (either slightly concave/convex, or bearing tooth-like processes) or markedly concave with an inflated base (Figs 1A & B) .......................................................................................... 2

— Female ovipositor small (not toothed or serrated), valvulae dorsalis shorter than 0.25 mm and less than 0.5 x subgenital plate length, valvulae ventralis slender, not higher than valvulae dorsalis, valvulae dorsalis dorsally convex and wedge shaped (Fig. 1C) ......... 11

2 Male paramere shorter than 0.5 x head width, in lateral view with a terminal blade present laterally exterior to the apex and the sclerotized apex with a large, anteriorly directed hook; aedeagus distal segment longer than 0.9 x paramere length, with a relatively large apical hook – the length about 0.25 x segment length; male subgenital plate dorsal profile raised anteriorly with a distinct step; female proctiger apex squarely truncated; ovipositor valvulae dorsalis concave dorsally and distinctly inflated anteriorly at the base; ovipositor valvulae ventralis relatively slender, apex rounded with minute serrations that extend along the ventral margin (on *Retama*; Continental) (Fig. 1B) .......................... *sulci* (Vondráček)

— Male paramere longer than 0.5 x head width, in lateral view without a terminal blade and the sclerotized apex with or without a small hook or projection; aedeagus distal segment shorter than 0.9 x paramere length, apex not developed into a hook or with a relatively small hook – the length less than 0.25 x segment length; male subgenital plate dorsal profile more or less straight or slightly curved, but without a distinct step; female proctiger apex bluntly rounded or acute; ovipositor valvulae dorsalis more or less straight dorsally (either slightly concave/convex or bearing tooth-like processes); ovipositor valvulae ventralis extremely robust, apex either round or square, ventral margin either smooth or with two small projections ........................................................................................ 3

3 Antennal segments eight (including scape and pedicel); head wider than 0.86 mm; distal proboscis segment longer ($\geq 0.14$ mm); male paramere (in lateral view) with lower part curvaceous, bulging rearward at the base and forward in the middle, but with the upper part straight and more or less parallel sided, interior surface with numerous stout setae on the lower part and densest on the anterior and posterior protrusions; aedeagus distal segment longer than 0.85 x paramere length; female subgenital plate ventral profile with pronounced, medial bulge (on *Cytisus*; Continental) .............................. *delarbrei* (Puton)

— Antennal segments ten (including scape and pedicel); head narrower than 0.86 mm; distal proboscis segment shorter (< 0.14 mm); male paramere (in lateral view) more slender, either curvaceous or straight, tapering or expanding towards the apex, interior surface either with fewer, slender setae, or with stout setae more evenly distributed; aedeagus distal segment shorter than 0.85 x paramere length; female subgenital plate ventral profile shallowly or more deeply curved, or angled medially ........................................ 4

4 Forewing coriaceous, long and narrow, length greater than 2.65 x width, with an acutely rounded apex, cell $r_1$ narrow with vein Rs running close to the costal margin; pterostigma long, about 0.25 x wing length; genal cones long (> 0.16 mm), longer than 0.75 x vertex length; male paramere and proctiger extremely long and slender – paramere (> 0.7 mm) longer than 0.85 x head width, proctiger (> 0.5 mm) longer than 0.7 x head width; aedeagus distal segment longer than 0.45 mm; female proctiger dorsal profile anteriorly more or less straight but with the apex arched and the tip upturned, proctiger longer than 1.12 mm; female subgenital plate ventral profile angled medially (on *Spartocytisus filipes*; La Palma) (Fig. 3) ........................................ ***serpentina* sp. nov.**

— Forewing not coriaceous and relatively short and broad, length less than 2.65 x width, with a broadly rounded apex, cell $r_1$ not narrow; pterostigma short or rudimentary; genal cones short (< 0.16 mm), equal to, or shorter than 0.75 x vertex length; male paramere and proctiger shorter – paramere (< 0.7 mm) shorter than 0.85 x head width, proctiger (< 0.5 mm) shorter than 0.7 x head width; aedeagus distal segment shorter than 0.45 mm; female proctiger dorsal profile anteriorly more or less straight, or slightly concave with the tip upturned, proctiger shorter than 1.12 mm; female subgenital plate ventral profile shallowly or more deeply curved ........................................ 5

5 Body colour bright green to grey green, forewing membrane clear or faintly yellow; female proctiger robust, dorsal profile more or less straight from anus to apex, apex blunt, circumanal ring length less than 0.25 x proctiger length, proctiger length not greater than 1.55 x subgenital plate length ........................................ 6

— Body colour yellow to brown (genitalia typically dark brown), forewing membrane with yellow-brown or brown pigmentation in part or all of the wing; female proctiger more slender, dorsal profile concave, the apex acute and upturned, circumanal ring length about 0.25 x proctiger length, proctiger longer than 1.55 x subgenital plate length .................. 8

6 Genal cones shorter, terminal setae often longer than the vertex; male paramere length ≤ 1.5 x subgenital plate height, in dorsal view lacking long stout seta on interior underside of

apex; female genitalia smaller – female proctiger shorter than 0.85 mm, less than 1.2 x head width and less than 1.35 x subgenital plate length; ovipositor valvulae dorsalis shorter than 0.43 mm, less than 0.65 x subgenital plate length, dorsally slightly concave, the base not extending downwards to overlap the valvulae ventralis (on *Cytisus albidus*; Continental) (Fig. 4) .......................................................................... ***atlantica* sp. nov.**

— Genal cones longer, terminal setae often shorter than the vertex; male paramere longer than 1.5 x subgenital plate height, in dorsal view with long stout seta on interior underside of apex; female genitalia larger – female proctiger longer than 0.85 mm, greater than 1.2 x head width and greater than 1.35 x subgenital plate length; ovipositor valvulae dorsalis longer than 0.43 mm, greater than 0.65 x subgenital plate length, dorsally slightly convex or with distinct tooth-like processes, the base extending downwards to overlap the valvulae ventralis ..................................................................................................................... 7

7 Antennal length $\geq$ 1.25 mm; male paramere longer (> 0.5 mm) and broader, greater than 0.7 x head width, interior surface with numerous stout setae; male proctiger longer than 0.4 mm, greater than 0.53 x head width, but less than 0.75 x paramere length; distal aedeagus segment longer than 0.35 mm, but less than 0.7 x paramere length; female proctiger longer (0.98-1.11 mm); ovipositor valvulae dorsalis longer than 0.5 mm, with distinct dorsal tooth-like processes (on *Calicotome*; Continental) ....................................... *cytisi* (Puton)

— Antennae shorter than 1.25 mm; male paramere relatively short (< 0.5 mm) and slender, less than 0.7 x head width, interior surface with fewer, slender setae; male proctiger shorter than 0.4 mm, less than 0.53 x head width, but greater than 0.75 x paramere length; distal aedeagus segment shorter than 0.35 mm, but greater than 0.7 x paramere length; female proctiger shorter (0.92-0.98 mm); ovipositor valvulae dorsalis shorter than 0.5 mm, without distinct dorsal tooth-like processes (on *Adenocarpus telonensis*; Continental) (Fig. 5) ...... .................................................................................................................. ***telonicola* sp. nov.**

8 Antennae shorter than 0.96 mm, $\leq$ 1.65 x head width; male paramere (in lateral view) slightly constricted medially, expanding into a bulbous apex with the sclerotized tip displaced to the rear of the top of the paramere and with a slight posterior projection; aedeagus distal segment strongly curved, apex blunt, not developed into a hook; ovipositor valvulae ventralis with two small projections ventrally towards the apex (on *Genista aetnensis*; Continental) ............................................................... *barbagalloi* Rapisarda

— Antennae longer than 0.96 mm, > 1.65 x head width; male paramere (in lateral view) simple, parallel sided or tapering towards the apex; aedeagus distal segment more or less straight, apex with a shallow hook; ovipositor valvulae ventralis without ventral projections ........................................................................................................................ 9

9 Forewing pterostigma rudimentary; aedeagus distal segment with a poorly developed hook; ovipositor valvulae dorsalis not, or only slightly tapering anteriorly at the base (on *Cytisus*; Continental) ........................................................................................ *spartiicola* (Šulc)

— Forewing pterostigma more developed but short; aedeagus distal segment with a more developed hook; ovipositor valvulae dorsalis triangular in shape, tapering both to the apex and anteriorly (Fig. 1A) ........................................................................................ 10

10 Male paramere longer (> 0.35 mm), greater than 1.3 x subgential plate height; aedeagus longer than 0.27 mm; female proctiger length less than 1.75 x subgenital plate length, apex more elongate; female subgenital plate ventral profile deeply curved (on *Cytisus*; Continental) ........................................................................................ *spartiophila* (Foerster)

— Male paramere shorter (< 0.35 mm), less than 1.3 x subgenital plate height; aedeagus shorter than 0.27 mm; female proctiger longer than 1.75 x subgenital plate length, apex less elongate; female subgenital plate ventral profile more shallowly curved (on *Cytisus*; Continental) ........................................................................................ *algeriensis* Burckhardt

11 Surface forewing spinules relatively dense (40-60 per $0.1\text{mm}^2$) with 50% or more coverage in all cells; pterostigma rudimentary; head narrower than 0.7 mm, genal cones long ($\geq 0.11$ mm), greater than 0.65 x vertex length; male paramere (in lateral view) slender and simple with more or less parallel sides, longer than 1.3 x subgential plate height, sclerotized apex dorsally rounded with a small, anteriorly and interiorly directed hook; aedeagus distal segment apex blunt, not developed into a hook and short (< 0.08 mm), less than 0.25 x segment length; male proctiger longer than 0.5 x head width; male subgenital plate longer than 1.3 x height; female proctiger length greater than head width, dorsal profile concave with an upturned, acute apex; female subgenital plate ventral profile with a slight medial bulge; ovipositor valvulae dorsalis longer than 0.2 mm (on *Genista*; Continental) (Fig. 1C) ........................................................................................ *gredi* (Ramírez Gómez)

— Surface forewing spinules sparse (less than 40 per $0.1\text{mm}^2$) and either absent or reduced coverage in most cells; pterostigma well developed; head wider than 0.7 mm, genal cones short ($\leq 0.11$ mm), less than 0.65 x vertex length; male paramere (in lateral view) broader and shorter than 1.3 x subgential plate height, with a shallow blade on the external anterior margin, sclerotized apex dorsally flattened with, or without, a slight anterior projection; aedeagus distal segment apex with a relatively large hook (> 0.08 mm), about 0.33 x segment length; male proctiger shorter than 0.5 x head width; male subgenital plate shorter than 1.3 x height; female proctiger length less than head width, dorsal profile more or less straight from anus to apex, or with a post anal depression, apex bluntly rounded; female subgenital plate ventral profile angled medially; ovipositor valvulae dorsalis shorter than 0.2 mm (on *Adenocarpus decorticans*; Continental) (Fig. 6) ............. ***montivaga* sp. nov.**

Key to 5th instar nymphs of *Arytainilla.*

1 Abdominal sectasetae either absent or with one apical pair with indistinct medial bisection; antennae longer than 0.8 mm ........................................................................................ 2

— Abdominal sectasetae three or four pairs; antennae shorter than 0.8 mm ......................... 3

2 Abdominal sectasetae absent; tergite structure extensively reduced on the thorax and typically, not extending to the lateral margin on the abdomen; circumanal ring broadly crescent-shaped with well rounded margins; ocular seta long; marginal abdominal capitate setae four pairs; tibiae with between two to five capitate setae; forewing pad shorter than 0.7 mm, anntenal length greater than 1.3 x wing pad length; caudal plate shorter than 0.5 mm (on *Adenocarpus decorticans*; Continental) (Fig. 23B) .............. ***montivaga* sp. nov.**

— Abdominal sectasetae one apical pair with indistinct medial bisection; tergite structure not extensively reduced on the thorax and extending to the lateral margin on the abdomen; circumanal ring narrowly crescent-shaped with lateral margins either straight or slightly concave; ocular seta absent or minute; marginal abdominal capitate setae numerous; tibiae with numerous capitate setae; forewing pad longer than 0.7 mm, antenal length less than 1.3 x wing pad length; caudal plate longer than 0.5 mm (on *Retama*; Continental) (Fig. 22B) .................................................................................................. *sulci* (Vondráček)

3 Abdominal sectasetae three pairs ........................................................................... 4

— Abdominal sectasetae four pairs (1st pair may be reduced) ............................................ 6

4 Total body length greater than 2.2 mm, body narrower than 0.55 x length; antennae, thorax, forewing and hindwing pads with minute simple setae only; marginal abdominal setae (other than sectasetae) two pairs, simple or slightly spathulate; legs with simple setae only; caudal plate length (> 0.8 mm) greater than width (on *Spartocytisus filipes*; La Palma) (Fig. 22C) .................................................................................................. ***serpentina* sp. nov.**

— Total body length less than 2.2 mm, body wider than 0.6 x length; head, antennae, thorax, forewing and hindwing pads with numerous, small, club-shaped setae; marginal abdominal setae (other than sectasetae) numerous small club setae, with 2-4 pairs more prominent;

legs with numerous, small, club-shaped setae; caudal plate length (< 0.8 mm) less than width .......... 5

5 General body colour bright green; larger species (total body length 1.6-2.11 mm); forewing pad longer than 0.6 mm; antennae longer (> 0.65 mm) than forewing pad length; circum-anal ring width ≥ 0.14 mm (on *Calicotome*; Continental) .......... *cytisi* (Puton)

— General body colour yellow and brown; smaller species (total body length 1.3-1.6 mm); forewing pad shorter than 0.6 mm; antennae shorter (< 0.55 mm) than forewing pad length; circum-anal ring narrower than 0.14 mm (on *Genista aetnensis*; Continental) .......... *barbagalloi* Rapisarda

6 Forewing pad and abdomen apically more acute; head, thorax, abdomen, wing pads and legs with numerous small club-shaped setae .......... 7

— Forewing pad and abdomen apically broadly rounded; head, thorax, abdomen, wing pads and legs with simple or longer capitate setae .......... 8

7 Caudal plate wider (> 0.7 mm) than 1.2 x length; circum-anal ring wider (0.14-0.19 mm) (on *Calicotome*; Continental) .......... *cytisi* (Puton)

— Caudal plate narrower (< 0.7 mm) than 1.2 x length; circum-anal ring narrower (0.12-0.14 mm) (on *Adenocarpus telonensis*; Continental) (Fig. 22D) .......... ***telonicola* sp. nov.**

8 Forewing pad and hindwing pads with numerous capitate setae on the surface and margins; arolium pad with a relatively long petiole; circumanal ring shape narrowly crescent-shaped, with acutely rounded anterior lobes; antennae with small capitate setae distally on 3rd and 5th segments; secondary post-ocular seta narrowly or distinctly capitate; capitate setae present on the foreleg tibia (on *Cytisus albidus*; Continental) (Fig. 22A) .......... ***atlantica* sp. nov.**

— Forewing and hindwing pads with capitate setae present only on the outer margins; arolium pad with a short petiole; circumanal ring shape broadly crescent-shaped, with well rounded anterior lobes; antennae without capitate setae; secondary post-ocular seta simple or indistinct; foreleg tibia without capitate setae .......... 9

9 Forewing pad with one prominent apical seta, or if more then five or less marginal setae, lacking distinct surface or proximal setae; circumanal outer ring not contiguous with the apical abdominal margin, outer ring with multiple rows of pores, width about 0.3-0.35 x caudal plate width; head with simple and distinctly capitate setae; primary post-ocular seta distinctly capitate; secondary post-ocular seta indistinct; dorsal abdominal pre-caudal tergites and caudal plate without prominent setae; marginal abdominal setae (other than

sectasetae) short, distinctly capitate; marginal abdominal pleurites with capitate setae only; hind tibia with more than two capitate setae (on *Cytisus*; Continental) ............................ ............................................................................................. *spartiophila* (Förtser) [also *algeriensis* Burckhardt and *spartiicola* (Šulc), the latter may be distinguished by the presence of more than one capitate seta on the forewing pad, but see Conci & Tamanini (1986)]

— Forewing pad with more than five prominent setae, and with a few distinct surface and proximal setae; circumanal outer ring contiguous with the apical abdominal margin, outer ring with a single row of pores, width less than 0.25 x caudal plate width; head setae simple; primary post-ocular seta simple or narrowly capitate; secondary post-ocular seta simple; dorsal abdominal pre-caudal prominent setae on all tergites and dorsal caudal plate prominent setae present; marginal abdominal setae (other than sectasetae) long and narrowly capitate; marginal abdominal pleurite setae paired simple or paired capitate and simple; hind tibia with one or two capitate setae (on *Genista*; Continental) (Fig. 23A) ...... ............................................................................................. *gredi* (Ramírez Gómez)

### *Arytainilla sensu stricto*

### *Arytainilla delarbrei* (Puton)

*Psylla delarbrei* Puton, 1873: 21

*Arytainilla delarbrei* (Puton) Ramírez Gómez, 1956: 77

*Arytainilla delarbrei* (Puton) Loginova, 1972: 17

*Adult Colour:* Generally dark grey to brown, abdominal intersegments green; forewing membrane dirty yellow, veins uniform light brown.

*Adult Description:* Ramírez Gómez (1956)

*Nymph* Unknown

*Host plant: Cytisus purgans.*

*Distribution:* Continental: Moroccan High Atlas north throughout the Iberian peninsula to southern France.

*Comment:* Although recorded as having a wide geographic distribution it is uncommon. A survey of the host plant in a previously recorded location for *A. delarbrei*, in the Middle Atlas (BMNH), was not successful in finding this species. The host plant was, as in other Moroccan locations severely over grazed with no individuals gaining more than half a metre of growth above ground level. An unusual species in the atypical number of adult antennal segments.

*Material examined:* PORTUGAL: 1♀, Serra da Estrela, btw Seia and Loriga, 40°15'N 7°45'W, c. 800 m, ex *Cytisus striatus*, 27.vi.1998 (DP 265.1). 1♂, 7♀, as for previous except, ex *Cytisus purgans* (DP 265.2). FRANCE: 2♂, 2♀ (BMNH).

### *Arytainilla spartiophila* (Foerster)

(Fig. 1A)

*Psylla spartiophila* Foerster, 1848: 75
*Psylla spartii* Guérin, 1843: 370, homonym of *Psylla spartii* Hartig, 1841
*Arytainilla spartii* (Guérin) Ramírez Gómez, 1956: 82
*Arytainilla spartiophila* (Foerster) Loginova, 1972: 17

*Adult Colour:* Brown or red-brown, to grey, with abdominal intersegment colour yellow-green; genitalia dark brown; forewing membrane pale yellow-brown, veins uniform light brown.
*Nymphal Colour:* 5th instars yellow-green with black tergites; other sclerites, wing pads, legs and terminal antennal segments darker brown.
*Adult and Nymphal Descriptions:* Ramírez Gómez (adult, 1956), Hodkinson & White (adult, 1979), White & Hodkinson (5th instar nymph, 1982), Conci & Tamanini (adult, 1986), Ossiannilsson (adult and 5th instar nymph, 1992).

*Host plant: Cytisus scoparius, C. striatus, C. grandiflorus (= Sarothamnus lusitanicus), Cytisus baeticus (= Cytisus arboreus, Sarothamnus baeticus), C. fontanesii (= Chronanthus biflorus).*
*Distribution:* Continental: Europe and North Africa.
*Notes:* Common and widespread on several *Cytisus* species, from the Moroccan High Atlas north throughout Europe (Conci & Tamanini, 1986). As with *Arytaina genisteae* and *Artyaina adenocarpi*, this species is somewhat polyphagous on several closely related host species. *A.*

*spartiophila* is sympatric throughout much of its distribution with *Arytaina genisteae* and the asynchronous development of these two species has been well documented (Watmough, 1968).
*Biology:* Up to five nymphs were found inside the anther tubes of individual flowers of *Cytisus grandiflorus*. The majority of these were 5th instars, suggesting that eggs are laid elsewhere with subsequent migration to feed on the developing ovary.
*Comment:* This species is similar to *A. spartiicola* and *A. algeriensis* in both adult and nymphal characteristics.

*Material examined:* MOROCCO: 1♂, 3♀, Middle Atlas, rd Khénifra to Azrou, N of Mrirt, 33°15'N 5°35'W, c. 1200 m, ex *Cytisus arboreus* ssp. *baeticus*, 29.iii.1998 (DP 147). 11♂, 9♀, Middle Atlas, btw Khénifra and Azrou, S of Mrirt, 33°00'N 5°45'W, c. 1000 m, ex *Cytisus arboreus* ssp. *catalaunicus*, 29.iii.1998 (DP 148). 5♂, 2♀, Central Rif Mountains, S of Ketama, 34°55'N 4°40'W, c. 1400 m, ex *Cytisus striatus*, 22.vi.1998 (DP 251). 60♂, 57♀, 6 nymphs, High Atlas, c. 8 km S of Asni, 31°02'N 8°10'W, c. 2000 m, ex *Cytisus fontanesii*, 1.v.1999 (DP 327). SPAIN: 19♂, 26♀, 10 nymphs, Andalusia, blw Otivar, rd up Rio Verde valley, 36°47'N 3°40'W, c. 400 m, ex *Cytisus malacitanus*, 20.iii.1998 (DP 121). 11♂, 9♀, as for previous except, c. 450 m, ex *Cytisus fontanesii* (DP 123). 11♂, 7♀, 59 nymphs, Andalusia, rd Atequera to Algodonales, W of Olvera, 36°54'N 5°16'W, c. 500 m, ex *Cytisus grandiflorus*, 23.iii.1998 (DP 133). 1♂, Andalusia, Parque Natural Sierra de Grazalema, 36°45'N 5°20'W, c. 600-700 m, ex *Cytisus arboreus* ssp. *baeticus*, 23.iii.1998 (DP 138). 4♂, 6♀, Andalusia, c. 5 km S of Ubrique, 36°37'N 5°25'W, c. 600-700 m, ex *Calicotome villosa*, 24.iii.1998 (DP 141). 1♀, Andalusia, Sierra del Pedroso, E of El Pedroso, 37°50'N 5°45'W, c. 450 m, ex *Cytisus striatus*, 15.vi.1998 (DP 231). PORTUGAL: 1♀, Coimbra, rd Coimbra to Viseu, at Santa Comba Dão, 40°15'N 8°15'W, c. 300 m, ex *Cytisus grandiflorus*, 26.vi.1998 (DP 261). 6♂, 4♀, Serra do Caramulo, N of Caramulo, 40°30'N 8°15'W, c. 900 m, ex *Cytisus striatus*, 26.vi.1998 (DP 263.1). 2♀, as for previous except, ex *Cytisus grandiflorus* (DP 263.2). 4♂, 13♀, Serra da Estrela, btw Seia and Loriga, 40°15'N 7°45'W, c. 800 m, ex *Cytisus striatus*, 27.vi.1998 (DP 265.1). 2♂, 5♀, as for previous except, ex *Cytisus purgans* (DP 265.2). 1♂, 5♀, 1 nymph, as for previous except, ex *Cytisus striatus* (DP 266.2).

### *Arytainilla spartiicola* (Šulc)

*Psylla spartiicola* Šulc, 1907: 5

*Arytainilla spartiicola* (Šulc) Loginova, 1972: 17

*Adult Colour:* Red-brown with darker brown markings; genitalia dark brown; forewing membrane distally yellow-brown, veins uniform light brown.
*Nymphal Colour:* Pale green with brown sclerites; antennae and legs darker brown.
*Adult and Nymphal Descriptions:* Šulc (adult, 1907), Conci & Tamanini (adult and 5th instar nymph, 1986).

*Host plant: Cytisus scoparius, C. decumbens.*
*Distribution:* Continental: France, Germany, Italy and Switzerland (Burckhardt, 1983).
*Comment:* An uncommon species similar in adult and nymphal characteristics to *A. spartiophila.*

No material was examined and the diagnostic characters used in the keys were extracted from descriptions in Conci & Tamanini (1986).

### *Arytainilla algeriensis* Burckhardt

*Arytainilla algeriensis* Burckhardt, 1989a: 406

*Adult Colour:* Brown or red-brown, to grey; genitalia dark brown; forewing cells with faint brown patches, veins uniform mid-brown.
*Adult Description:* Burckhardt (1989a).

*Nymph* Undescribed, 5th instars examined were very similar to *A. spartiophila.*

*Host plant: Cytisus baeticus* (= *Cytisus arboreus*, *Sarothamnus baeticus*)
*Distribution:* Continental: Algeria and Morocco.
*Comment:* A relatively uncommon species.

*Material examined:* MOROCCO: 5♂, 4♀, 14 nymphs, Col de Jerada, 45 km S of Oujda, c. 1150 m, ex *Cytisus baeticus*, 23.iv.1992 (BMNH).

### *Arytainilla barbagalloi* Rapisarda

*Arytainilla barbagalloi* Rapisarda,1989: 24

*Adult Colour:* Cream or yellow with brown markings, genitalia dark brown; forewing membrane yellow-brown, veins uniform light brown.

*Nymphal Colour:* Cream to yellow with brown sclerites; terminal antennal segments darker brown.

*Adult and Nymphal Descriptions:* Rapisarda (adult and 1st–5th instar nymphs, 1989).

*Host plant: Genista aetnensis.*

*Distribution:* Continental: Italy.

*Comment:* Known only from the island of Sicily where it is locally common. The adult form of this species shares characteristics, particularly in the female genitalia, with *A. spartiophila*; although it is unique in the presence of ventral tooth-like processes on the ovipositor. The nymph however, is more similar to *A. cytisi* and *A. telonensis* sp. nov. in body shape and chaetotaxy.

*Material examined:* Paratypes (slide mounted), ITALY. SICILY: 1♂, 3♀, Catánia, c. 15 km SW of Rondazzo, c. 900 m, 1.vi.1979 (BMNH). 2♂, 6 nymphs, Catánia, c. 15 km E of Rondazzo, c. 550 m, 3.vi.1979 (BMNH). 1♂, 2♀, Catánia, c. 2 km NE of Nicolosi on Mt Etna, c. 700 m, 4.vi.1979 (BMNH).

### *Arytainilla cytisi* (Puton)

*Psylla cytisi* Puton, 1876: 284

*Arytainilla cytisi* (Puton) Ramírez Gómez, 1956: 79

*Arytainilla cytisi* (Puton) Loginova, 1972: 17

*Adult Colour:* Bright green, sometimes with darker abdomens; forewing membrane clear or faintly yellow, veins uniformly pale or light brown.

*Nymphal Colour:* 1st-3rd instars orange with or without black tergites, 5th instars bright green to yellow-green; sclerites, wing pads, legs and antennae yellow-brown; terminal antennal segment darker brown.

*Adult and Nymphal Descriptions:* Šulc (adult, 1911), Rapisarda (adult and 1st-5th instar nymphs, 1990, 1991).

*Host plant: Calicotome spinosa, C. villosa.*

*Distribution:* Continental: Widespread from the Moroccan Middle Atlas and Algeria north throughout southern Europe and the eastern Mediterranean (Halperin, Hodkinson & Burckhardt, 1988; Burckhardt & Önuçar, 1993; Conci *et al.*, 1993; Zeidan-Gèze & Burckhardt, 1998).

*Biology:* Large nymphs (4th-5th instars) were found under the bracts of floral buds (see also Rapisarda,1990).

*Comment:* This species is most similar to *A. telonicola* sp. nov. in both adult and nymphal characteristics, but it is unique in the presence of dorsal tooth-like processes on the ovipositor.

*Material examined:* MOROCCO: 11 nymphs, Middle Atlas, nr Ifrane, 33°25'N 5°10'W, c. 1800 m, 31.iii.1999 (DP 316). 1♂, 1♀, 18 nymphs, Taza, c. 5 km S of Taza, Jbel Tazzeka, rd to Bab-Bou-Idir, 33°51'N 4°00'W, c. 1100 m, 31.iii.1999 (DP 317). 5♂, 1♀, 33 nymphs, Rif Mountains, rd Aknoul to Taza, c. 15 km N of Taza, 34°20'N 3°58'W, c. 800 m, 1.iv.1999 (DP 319). SPAIN: 1♀, 11 nymphs, Gerona, 3 km from La Bisbal on Calonge rd, 1.vi.1975 (BMNH). 1♂, as for previous except, 14.vi.1976 (BMNH). ITALY. SICILY: 1♂, 1♀, Messina, c. 5 km S of San Fratello, 650 m, 31.v.1979 (BMNH).

### ***Arytainilla serpentina* sp. nov.** (1)

(Figs 3, 22C, 1F & 1I)

*Adult*

*Colour:* Abdomen and head bright geen or yellow-green, thorax, genal cones and legs yellow; forewing membrane yellow-brown, becoming darker brown apically, veins uniformly pale.

*Structure:* Forewing coriaceous and narrow, margins more or less parallel or slightly wider in the middle third, with an acutely rounded apex; cells $cu_1$ and $m_2$ relatively broad and low and cell $r_1$ narrow with vein Rs running close to the costal margin; pterostigma well developed, up to one quarter the wing length; surface forewing spinules present in all cells but reduced in cell c+sc; distribution of spinules non-uniform, dense: 60-100 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$ but absent or occasionally few present in cell $r_2$. Antennae relatively short, with ten segments; genal cones long, commencing dorsally from more or less the same level as the vertex, terminal setae shorter than the vertex. Paramere long, in lateral view slender and simple, tapering towards the apex, sclerotized apex dorsally rounded with small, anteriorly and interiorly directed hook, in dorsal view contiguous anteriorly and rounded with an acute point; paramere longer than the proctiger; proctiger not inflated posteriorly towards the base; aedeagus distal segment bluntly rounded, not developed into a hook; male subgenital plate dorsal profile more or less straight and horizontal. Female proctiger dorsal profile anteriorly, more or less straight but the apex is darkly pigmented and arched with an upturned bluntly rounded tip; subgenital plate ventral profile angled medially; ovipositor valvulae ventralis robust, apex rounded and minutely serrated; height of valvulae dorsalis less than valvulae ventralis, dorsal margin more or less straight or slightly convex. Egg slender with stout pedicel at the base.

*Adult measurements and ratios:* (3♂, 4♀) total length: ♂ 3.24-3.56, ♀ 3.64-3.88; forewing: ♂ length 2.6-2.7 width 0.91-0.99, ♀ length 2.96-3.19 width 1.01-1.1; pterostigma length ♂ 0.58-0.67, ♀ 0.66-0.8; hindwing length ♂ 2.15-2.25, ♀ 2.48-2.68; head width: ♂ 0.76-0.8, ♀ 0.8-0.85; antennal length: 1.3-1.53; genal cone length: 0.18-0.2; distal proboscis segment length: 0.09-0.1. WLPT: 3.7-4.79; ALHW: 1.7-1.87; GCVL: 0.78-0.91; WLHW: 3.35-3.89; VLW: 0.43-0.49; WLW: 2.71-2.93; CUR: 2.33-2.71; MR: 0.47-0.69; RMCU: 5.96-8.26; TLFL: 1.02-1.09; TLHW: 0.63-0.71; SCHW: 0.85-0.94; ATIB: 0.33-0.37; MTIB: 0.29-0.33; PBHW: 0.12-0.13; ATMT: 1.06-1.19. *Adult genitalia* ♂: MP: 0.56-0.6; PL: 0.72-0.74; AEL: 0.5-0.51; AEH: 0.06-0.07. MPHW: 0.73-0.76; PLHW: 0.9-0.96; MPPL: 0.77-0.81; AEPL: 0.68-0.71; MSLH: 1.24-1.27; AHS: 0.13; PLSH: 1.74-1.76. ♀: FP: 1.13-1.28; FSP: 0.96-0.99; RL: 0.23-0.25; OV: 0.54; EL: 0.2-0.28. FPHW: 1.38-1.56; FPSP: 1.18-1.29; FPCR: 4.71-5.12; OLSP: 0.55-0.56; FEOL: 0.44.

*Nymph*

*Colour:* 5th instars bright green with thorax and head more yellow, wing pads and ventral abdomen pale orange, anal ring pale grey; terminal antennal segments darker brown.

*Structure:* Forewing pads and abdomen acute apically. Tergites extensively reduced on the thorax, typically not, or only posteriorly extending to the lateral margin on the abdomen. Arolium pad long, broadly expanded apically, with a distinct medial groove and short petiole.

Circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 4) BL: 2.3-2.63; BW: 1.23-1.3; WL: 0.81-0.85; CPL: 0.84-0.87; CPW: 0.75-0.85; RW: 0.18-0.18; RL: 0.09-0.1; HW: 0.72-0.76; AL: 0.65-0.69; AL3: 0.15-0.16. WBL: 0.47-0.54; ALHW: 0.9-0.91; ALWL: 0.8-0.84; WLHW: 1.11-1.13; WCPL: 0.89-0.99; CPRW: 4.17-4.72.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.05-0.06); antennal setae simple; ocular seta simple, small (max length 0.01); primary post-ocular seta simple or slightly spathulate (max length 0.07); secondary post-ocular seta indistinct. Dorsal thoracic setae very short simple (max length 0.02). Prominent wing pad setae absent; forewing and hindwing pads with minute simple setae only. Dorsal abdominal prominent pre-caudal and caudal plate setae absent (only minute simple); sectasetae three pairs; marginal abdominal setae (other than sectasetae) two pairs, simple, or slightly spathulate (max length 0.07-0.09); pleurite setae paired simple. Legs with simple setae only (max length 0.04).

*Host plant: Spartocytisus filipes.*

*Distribution:* Canary Islands: La Palma.

*Notes:* This is the only representative of *Arytainilla sensu stricto* in the Canary Islands. It is sympatric with *Arytaina vittata* sp. nov., but unlike the latter species it is restricted to the laurisilva habitat of the host, and in these locations on La Palma it was found to be more common than *A. vittata* sp. nov.

*Etymology:* Named for the long and sinuous male paramere.

*Comment:* This species is unique within *Arytainilla* in the narrow, coriaceous forewing and the shape of the genitalia, particularly in the female.

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. LA PALMA: NE, from El Granel to Barlovento and Roque Faro, 200-500 m, 19.v.1998 (BMNH). Paratypes 1♂, 2♀, 4 nymphs, as for holotype (BMNH). 1♂, 1♀, nr Los Galguitos, Barranco de la Fuente, 28°46'N 17°46'W, 350 m, 17.v.1998 (DZUL). 2♂, 1♀, as for previous (NHMB).

*Other material examined:* CANARY ISLANDS. LA PALMA: 7♂, 2♀, nr Los Galguitos, Barranco de la Fuente, 28°46'N 17°46'W, 350 m, 17.v.1998 (DP 191). 10♂, 6♀, as for holotype (DP 198).

## *Arytainilla atlantica* sp. nov. (2)

(Figs 4 & 22A)

*Adult*

*Colour:* Pale grey-green to blue-green, head, thorax and legs yellow or orange; forewing membrane clear or faintly yellow, veins uniform light brown.

*Structure:* Forewing widest in the middle third with more acutely rounded apex; pterostigma less than one quarter the wing length; surface forewing spinules present in all cells, but reduced in one or more cells; distribution of spinules non-uniform, density medium: 40-60 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent, or occasionally few present in cell $r_2$. Antennae short, with ten segments; genal cones very short, commencing ventrally relative to the vertex, with a distinct depression between the vertex and the genal cones, terminal setae as long as, or typically longer than the vertex. Paramere mid-length, in lateral view slender, simple, with sides tapering towards the apex, sclerotized apex dorsally rounded with small, anteriorly and interiorly directed hook, in dorsal view contiguous anteriorly, with inner margin straight edged; paramere longer than the proctiger; proctiger not inflated posteriorly towards the base; aedeagus distal segment with a shallow hook, tip of aedeagus hook acute; male subgenital plate dorsal profile more or less straight and horizontal. Female proctiger dorsal profile more or less straight from anus to apex, apex bluntly rounded; subgenital plate ventral profile shallowly curved, without a medial bulge; ovipositor valvulae ventralis robust, apex stepped with square tip; height of valvulae dorsalis less than valvulae ventralis, dorsal margin more or less straight or slightly concave.

*Adult measurements and ratios:* (3♂, 3♀) total length: ♂ 2.28-2.6, ♀ 2.56-2.92; forewing: ♂ length 1.76-1.9 width 0.72-0.76, ♀ length 2.1-2.26 width 0.87-0.93; pterostigma length ♂ 0.25-0.3, ♀ 0.3-0.35; hindwing length ♂ 1.4-1.53, ♀ 1.68-1.8; head width: ♂ 0.64-0.66, ♀ 0.68-0.7; antennal length: 0.99-1.16; genal cone length: 0.06-0.1; distal proboscis segment length: 0.1-0.11. WLPT: 6-7.6; ALHW: 1.55-1.81; GCVL: 0.3-0.53; WLHW: 2.75-3.23; VLW: 0.45-0.53; WLW: 2.41-2.52; CUR: 1.84-2.05; MR: 0.46-0.57; RMCU: 4.95-6.74; TLFL: 1.09-1.2; TLHW: 0.69-0.74; SCHW: 0.78-0.87; ATIB: 0.28-0.3; MTIB: 0.27-0.3; PBHW: 0.14-0.16; ATMT: 1-1.08. *Adult genitalia* ♂: MP: 0.38-0.41; PL: 0.5-0.51; AEL: 0.35-0.36; AEH: 0.07-0.09. MPHW: 0.59-0.62; PLHW: 0.77-0.78; MPPL: 0.76-0.8; AEPL: 0.69-0.72; MSLH: 1.21-1.26; AHS: 0.22-0.23; PLSH: 1.47-1.52. ♀: FP: 0.76-0.82; FSP: 0.62-0.64; RL: 0.16-0.18; OV:

0.39-0.41; EL: 0.19-0.23. FPHW: 1.09-1.17; FPSP: 1.23-1.28; FPCR: 4.33-5.13; OLSP: 0.62-0.64; FEOL: 0.53.

*Nymph*

*Colour:* 1st-3rd instars orange or red, 4th-5th instars pale grey-green or yellow with pale orange wing pads and thorax; sclerites, wing pads, legs and terminal antennal segments usually darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Tergites extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad long, broadly expanded apically with a slight medial groove and long petiole. Circumanal ring narrowly crescent-shaped with acutely rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 8) BL: 1.43-1.7; BW: 0.88-1.1; WL: 0.44-0.61; CPL: 0.44-0.55; CPW: 0.67-0.81; RW: 0.14-0.17; RL: 0.09-0.11; HW: 0.55-0.63; AL: 0.49-0.62; AL3: 0.1-0.15. WBL: 0.59-0.66; ALHW: 0.86-1.09; ALWL: 0.98-1.15; WLHW: 0.77-1.05; WCPL: 1.29-1.55; CPRW: 4.18-5.06.

*5th instar chaetotaxy:* Head setae simple and narrowly capitate (both present on anterior margin) (max length at anterior margin 0.09-0.1); antennal setae simple and capitate (small capitate present distally on 3rd and 5th segments); ocular seta simple, small, inconspicuous (max length 0.03-0.05); primary post-ocular seta distinctly capitate (max length 0.06-0.07); secondary post-ocular seta distinctly or narrowly capitate, rarely simple (max length 0.04-0.06). Dorsal thoracic setae short simple and capitate or rod (max length 0.03-0.04). Prominent wing pad setae max length 0.08-0.09; forewing and hindwing pads with capitate and minute simple setae; forewing pad prominent setae 8-9, distinctly capitate, surface and marginal (larger marginal, few smaller scattered on surface), proximal seta typically present, occasionally reduced or absent, narrowly or distinctly capitate; hindwing pad prominent setae 2-3, distinctly capitate, surface and marginal (larger apical, few smaller scattered on surface), proximal seta absent or if present, distinctly or narrowly capitate; small capitate and simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on all tergites, short simple and capitate (max length 0.05-0.06), prominent caudal plate setae present, 15-21 larger, with the most posterior centrally placed, distinctly capitate; sectasetae four pairs; marginal abdominal setae (other than sectasetae) four pairs, distinctly capitate (max length 0.1-0.12); pleurite setae paired capitate and simple or capitate only (anterior pleurites with three capitate). Legs with capitate setae present (max length 0.06-0.08); capitate foreleg setae present on femur and tibia, on the tibia 1-3 (1 proximal, 1-2 distal); capitate middle leg setae present on femur and tibia, on the tibia 3-5 (1 larger proximally and distally); capitate hind leg setae present on femur and tibia, on the tibia 5-6 (1 larger proximally and distally).

*Host plant: Cytisus albidus* (= *Chamaecytisus mollis*).

*Distribution:* Continental: Locally widespread in central Morocco, occurring on the lower slopes of the High Atlas and along the Atlantic coast.

*Notes:* It is typically sympatric with *Livilla blandula*, but probably developing earlier than the latter species, being both present and more common on the host in March, but absent from a collection made in June.

*Biology:* Nymphs (2nd-5th instars) were observed on leaf buds.

*Etymology:* Named for the geographic distribution in the lowland Atlas mountains and the Atlantic coast of Morocco.

*Comment:* The adult form is generally similar to *A. cytisi* and *A. telonicola* sp. nov., but the 5th instar nymph in body shape and chaetotaxy, is more similar to a *Livilla*-type.

*Type material:* Holotype ♂ (slide mounted), MOROCCO: Atlantic Coast, c. 15 km E of Azemmour, 33°12'N 8°18'W, c. 100 m, 2.iii.1999 (BMNH). Paratypes 3♂, 4♀, 10 nymphs, as for holotype (BMNH). 3♂, 3♀, as for holotype (NHMB). 6 nymphs, Atlantic Coast, c. 35 km S of Essaouira, just N of Smimou, 31°08'N 9°42'W, c. 100 m, 22.iii.1999 (BMNH). 8 nymphs, as for previous (NHMB).

*Other material examined:* MOROCCO: 15♂, 29♀, 3 nymphs, as for holotype (DP 296). 1♀, 2 nymphs, Atlantic Coast, c. 10 km SE of Essaouira, 31°31'N 9°37'W, c. 100 m, 22.iii.1999 (DP 298). 11♂, 10♀, 19 nymphs, Atlantic Coast, c. 35 km S of Essaouira, just N of Smimou, 31°08'N 9°42'W, c. 100 m, 22.iii.1999 (DP 300). 1♀, Atlantic Coast, Jbel Amsittene, c. 6 km on rd to Sebt-des-Ait-Daoud, 31°10'N 9°38'W, c. 850 m, 29.iv.1999 (DP 322). 28♂, 13♀, 1 nymph, High Atlas, c. 10 km N of Asni, 31°15'N 7°58'W, c. 1800 m, 1.v.1999 (DP 326). 1♀, High Atlas, S of Tizi n' Test, 30°45'N 8°30'W, c. 1500 m, 2.v.1999 (DP 330).

## *Arytainilla telonicola* sp. nov. (3)

(Figs 5 & 22D)

*Adult*

*Colour:* Bright green to yellow-green, genal cones and legs blue-green, head and thorax ochre; forewing membrane clear or faintly yellow, veins uniform light brown.

*Structure:* Forewing widest in the apical third with a broadly rounded apex; pterostigma less than one quarter the wing length; surface forewing spinules typically present in all cells but reduced in one or more cells, occasionally absent or few in cells $cu_1$, $m_2$ and c+sc; distribution of spinules both non-uniform and uniform, medium density: 40-60 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent, or occasionally few present in cell $r_2$. Antennae short, with ten segments; genal cones short, commencing ventrally relative to the vertex, with a distinct depression between the vertex and the genal cones, terminal setae typically shorter than the vertex, occasionally as long. Paramere mid-length, in lateral view slender, simple, tapering towards the apex, sclerotized apex dorsally rounded with small anteriorly and interiorly directed hook, in dorsal view contiguous anteriorly, with inner margin straight edged; paramere longer than the proctiger; proctiger slightly inflated posteriorly towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital dorsal profile more or less straight and horizontal. Female proctiger dorsal profile more or less straight from anus to apex, apex bluntly rounded; subgenital plate ventral profile shallowly curved, or slightly angled medially; ovipositor valvulae ventralis robust, apex stepped with square tip; height of valvulae dorsalis less than valvulae ventralis, dorsal margin more or less straight or slightly convex.

*Adult measurements and ratios:* (4♂, 4♀) total length: ♂ 2.28-2.6, ♀ 2.76-3; forewing: ♂ length 1.88-2 width 0.78-0.9, ♀ length 2.28-2.4 width 0.93-1.01; pterostigma length ♂ 0.28-0.35, ♀ 0.3-0.42; hindwing length ♂ 1.5-1.6, ♀ 1.85-1.9; head width: ♂ 0.68-0.7, ♀ 0.72-0.77; antennal length: 1.12-1.22; genal cone length: 0.09-0.12; distal proboscis segment length: 0.11-0.12. WLPT: 5.55-8; ALHW: 1.49-1.74; GCVL: 0.47-0.6; WLHW: 2.76-3.24; VLW: 0.42-0.51; WLW: 2.22-2.51; CUR: 1.83-2; MR: 0.51-0.63; RMCU: 4.12-6.5; TLFL: 1.13-1.23; TLHW: 0.72-0.78; SCHW: 0.79-0.88; ATIB: 0.26-0.31; MTIB: 0.26-0.29; PBHW: 0.15-0.16; ATMT: 1-1.07. *Adult genitalia* ♂: MP: 0.34-0.35; PL: 0.43-0.44; AEL: 0.32-0.34; AEH: 0.06-0.08. MPHW: 0.5-0.51; PLHW: 0.63-0.65; MPPL: 0.79-0.81; AEPL: 0.73-0.77; MSLH: 1.26-

1.35; AHS: 0.21-0.22; PLSH: 1.63-1.65. ♀: FP: 0.92-0.98; FSP: 0.63-0.7; RL: 0.15-0.2; OV: 0.45-0.49; EL: 0.19-0.23. FPHW: 1.23-1.32; FPSP: 1.4-1.51; FPCR: 4.75-6.13; OLSP: 0.68-0.73; FEOL: 0.45.

*Nymph*

*Colour:* 4th-5th instars bright blue-green to yellow-green; terminal antennal segment darker brown.

*Structure:* Forewing pads and abdomen apically acute. Tergite structure extensively reduced on the thorax, typically not, or only posteriorly extending to the lateral margin on the abdomen. Arolium pad short, expanded apically with slight medial groove and fairly short petiole. Circumanal ring narrowly crescent-shaped with acutely rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 3) BL: 1.75-1.78; BW: 1-1.13; WL: 0.63-0.66; CPL: 0.57-0.62; CPW: 0.62-0.68; RW: 0.12-0.14; RL: 0.08-0.09; HW: 0.62-0.68; AL: 0.7-0.75; AL3: 0.16-0.18. WBL: 0.53-0.63; ALHW: 1.09-1.15; ALWL: 1.06-1.19; WLHW: 0.93-1.03; WCPL: 1.03-1.12; CPRW: 4.43-5.33.

*5th instar chaetotaxy:* Head setae simple and club-shaped (max length at anterior margin 0.07-0.08); antennal setae simple and club-shaped (small club setae on 1st and 2nd segments and occasionally present distally on 3rd); ocular seta small rod (max length 0.01-0.02); primary post-ocular seta club-shaped (max length 0.03-0.04); secondary post-ocular seta indistinct. Dorsal thoracic setae short club-shaped (max length 0.02). Prominent wing pad setae max length 0.03-0.04; forewing and hindwing pads with club-shaped setae, each with one prominent seta apically and with numerous small club-shaped setae on the wing pad surfaces, proximal setae indistinct. Dorsal abdominal prominent pre-caudal setae present on all tergites, short club-shaped (max length 0.02), prominent caudal plate setae present, one club-shaped positioned centrally and posteriorly with numerous smaller club setae; sectasetae four pairs (1st reduced); marginal abdominal setae (other than sectasetae) four pairs (1st and 2nd reduced), club-shaped (max length 0.06-0.07); pleurite setae paired club and simple, or club only (anterior pleurites with three club setae). Legs with numerous small, club-shaped setae on the dorsal surface of femora and tibiae (max length 0.03-0.04).

*Host plant: Adenocarpus telonensis.*

*Distribution:* Continental: Spain, southern Andalusia.

*Notes:* Occurs sympatrically with *Arytaina adenocarpi*. *A. telonicola* sp. nov. appears to develop earlier than *Arytaina adenocarpi* judging from the greater abundance, particularly of nymphs, of this species in March and absence from collections made in June, when *Arytaina adenocarpi* was abundant.

*Etymology:* Named for the host plant.

*Comment:* This species is most similar to *A. cytisi* in both adult and nymphal characteristics, but notably lacks the dorsal tooth-like processes on the ovipositor of *A. cytisi.*

*Type material:* Holotype ♂ (slide mounted), SPAIN: Andalusia, N of Ronda on rd to Algodonales, S tip of Lake Zahara, 36°50'N 5°20'W, c. 500 m, 23.iii.1998 (BMNH). Paratypes 1♂, 2♀, as for holotype (BMNH). 1♂, as for holotype (NHMB). 2♂, 2♀, Andalusia, Parque Natural Sierra de Grazalema, 36°45'N 5°20'W, c. 600-700 m, 23.iii.1998 (BMNH). 1♂, 2♀, as for previous (NHMB). 5 nymphs, as for previous except, 36°45'N 5°18'W (BMNH). 4 nymphs, as for previous (NHMB).

*Other material examined:* SPAIN: 45♂, 25♀, as for holotype (DP 134). 1♂, 6♀, 31 nymphs, Andalusia, Parque Natural Sierra de Grazalema, 36°45'N 5°18'W, c. 600-700 m, 23.iii.1998 (DP 135). 8♂, 7♀, 32 nymphs, as for previous (DP 136). 19♂, 30♀, 61 nymphs, as for previous except, 36°45'N 5°20'W (DP 137). 6♂, 8♀, 1 nymph, Andalusia, c. 5 km S of Ubrique, 36°37'N 5°25'W, c. 600-700 m, 24.iii.1998 (DP 140).

## *Arytainilla* residual species

### *Arytainilla gredi* (Ramírez Gómez)

(Figs 1C & 23A)

*Alloeoneura* (subgenus *Hispaniola*) *gredi* Ramírez Gómez, 1956: 92
*Arytainilla gredi* (Ramírez Gómez) Hodkinson & Hollis, 1987: 42

*Adult Colour:* Yellow-green to yellow-brown, genitalia darker brown; forewing membrane dirty yellow, veins uniform light brown.

*Adult Description:* Ramírez Gómez (1956)

*Nymph*

*Colour:* 5th instars with sclerites, wing pads, legs and terminal antennal segments darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Tergites extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad short, expanded apically, without medial groove and with a short petiole. Circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 6) BL: 1.65-1.85; BW: 1.05-1.2; WL: 0.56-0.62; CPL: 0.45-0.53; CPW: 0.87-0.95; RW: 0.19-0.23; RL: 0.1-0.12; HW: 0.58-0.69; AL: 0.63-0.71; AL3: 0.15-0.17. WBL: 0.63-0.71; ALHW: 0.97-1.18; ALWL: 1.11-1.16; WLHW: 0.86-1.02; WCPL: 1.79-1.93; CPRW: 4.13-4.79.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.08-0.09); antennal setae simple; ocular seta simple, inconspicuous (max length 0.03); primary post-ocular seta simple or narrowly capitate (max length 0.08-0.11); secondary post-ocular seta simple (max length 0.04-0.07). Dorsal thoracic setae short and long simple (max length 0.05-0.06). Prominent wing pad setae max length 0.1-0.11; forewing and hindwing pads with simple and capitate setae; forewing pad with 10 prominent marginal setae, narrowly or distinctly capitate; hindwing pad prominent setae 2-4, distinctly capitate, marginal (2 apical and 0-2 on the outer margin, occasionally few more prominent setae on the surface); proximal setae simple (sometimes small); small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on all tergites, long simple and narrowly capitate (max length 0.07-0.12), prominent caudal plate setae present, ± 18, narrowly or distinctly capitate; sectasetae four pairs; marginal abdominal setae (other than sectasetae) four or more pairs, narrowly capitate (max length 0.19-0.22); pleurite setae paired simple, or paired narrowly capitate and simple. Legs with capitate setae present (often very narrow, max length 0.11-0.15); capitate foreleg setae absent; capitate middle leg setae present on femur and tibia, on the tibia 1-2 (typically 1 proximal and 1 distal, occasionally only distal present); capitate hind leg setae present on femur and tibia, on the tibia 1-2 (typically 1 proximal and 1 distal, occasionally only distal present).

*Host plant: Genista hispanica, G. florida, G.* cf. *pilosa.*

*Distribution:* Continental: Spain.

*Comment:* Apparently widespread in Spain but restricted to montane regions, this species has been recorded from the Sierra Nevada in the south to the Picos de Europa in the north. It is uncommon and was not collected by this author. There is a superficial similarity in the male and female genitalia to *A. spartiophila.* However, in many respects, notably the shape of the ovipositor and the nymph, this species is closer to a *Livilla*-type. The original description by Ramírez Gómez (1956) cites two basal metatarsal spurs. As all material examined has one spur there is the possibility that these specimens are not the same as the type species. However, no material from which the original description was made still exists, and so this discrepancy will likely remain unresolved.

*Material examined:* SPAIN:1 ♀, Huelva, 20 km S of Almonte, ex *Genista* sp., 13.vi.1977 (BMNH). 2♂,1 ♀, Sierra Nevada, Pico Veleta rd, 2500 m, ex *Cytisus purgans*?, 5.viii.1978 (BMNH). 3♂,3 ♀, 9 nymphs, Picos de Europa, Peña Romana, abv Santa Marina de Valdeón, 1700 m, ex *Genista* cf. *pilosa*, 9.viii.1993 (BMNH). 1♂,1 ♀, 2 nymphs, as for previous except, 1800 m, ex *Genista hispanica* (BMNH).

### *Arytainilla sulci* (Vondráček)

(Figs 1B & 22B)

*Psylla sulci* Vondráček, 1954: 81
*Arytainilla egena* Loginova, 1972: 18 [synonymized by Burckhardt, 1989b: 318]
*Arytainilla sulci* (Vondráček) Burckhardt, 1989b: 318

*Adult Colour:* Yellow-green to yellow-grey, sometimes with bright green or brown abdomen; legs ochraceous to brown; forewing membrane yellowish, veins uniformly pale.
*Adult Descriptions:* Vondráček (1954), Loginova (1972).

*Nymph*

*Colour:* Bright green to yellow-green, abdomens sometimes orange or wings and abdomen tinged with black; terminal antennal segments darker brown.
*Structure:* Forewing pads and abdomen broadly rounded apically. Tergites not extensively reduced on the thorax and extending to the lateral margin on the abdomen. Arolium pad short, expanded apically, without medial groove and with a long petiole. Circumanal ring narrowly

crescent-shaped with well rounded anterior lobes but with lateral margins either straight or slightly concave, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 10) BL: 2.2-2.53; BW: 1.48-1.6; WL: 0.72-0.81; CPL: 0.67-0.76; CPW: 0.97-1.1; RW: 0.16-0.2; RL: 0.11-0.12; HW: 0.83-0.92; AL: 0.85-0.95; AL3: 0.19-0.22. WBL: 0.62-0.66; ALHW: 0.98-1.09; ALWL: 1.09-1.22; WLHW: 0.85-0.9; WCPL: 1.36-1.52; CPRW: 5.21-6.56.

*5th instar chaetotaxy:* Head setae simple and narrowly capitate (anterior margin typically simple, occasionally capitate, max length at anterior margin 0.09-0.12); antennal setae simple and capitate (capitate setae typically present on all segments except 1st, 1-2 larger apically on the 3rd and 5th segments, smaller present on the remainder); ocular seta absent (possibly very small, but undetected in specimens examined); primary and secondary post-ocular seta distinctly, or occasionally narrowly capitate (max length 0.08-0.11). Dorsal thoracic setae short simple and long frequently narrowly capitate (max length 0.1-0.12). Prominent wing pad setae max length 0.1-0.12; forewing and hindwing pads with capitate setae only, prominent setae numerous, distinctly capitate, surface and marginal, proximal setae distinctly capitate. Dorsal abdominal prominent pre-caudal setae present on all tergites, long frequently narrowly capitate (max length 0.12), prominent caudal plate setae numerous, distinctly capitate; sectasetae one pair in the 4th position (as the medial bisection is indistinct these may appear as lanceolate setae); marginal abdominal setae (other than sectasetae) numerous, typically narrowly or distinctly capitate (apical pairs are longer and darkly pigmented, often narrowly capitate or simple) (max length 0.16-0.21); pleurite setae paired capitate and simple. Legs with capitate setae present on femora, tibiae and tarsi (max length 0.1-0.12), one distally on the femora and numerous on the tibiae.

*Host plant: Retama raetam.*

*Distribution:* Continental: Morocco, northern Libya, Israel and Jordan.

*Notes:* Occurs along the southern Atlantic coast and Anti-Atlas mountains of Morocco. It is sympatric with *Livilla retamae* and *Pseudacanthopsylla* spp. in Morocco and Jordan. *A. sulci* appears to develop earlier than either of these latter species in Morocco. It was the most abundant species on the host in March and was absent from collections made in June, when *Livilla retamae* and *Pseudacanthopsylla* (officially *Psylla improvisa*) were more common.

*Biology:* Nymphs were observed on the inner surface of the corolla.

*Comment:* Both adult and nymphal forms are unique within the Arytaininae.

*Material examined:* (ex *Retama raetam* unless otherwise stated) MOROCCO: 66♂, 46♀, 85 nymphs, Atlantic Coast, c. 15 km S of El Jadid, 32°55'N 8°35'W, c. 100 m, 21.iii.1999 (DP 297). 18♂, 19♀, 19 nymphs, Atlantic Coast, c. 10 km SE of Essaouira, 31°31'N 9°37'W, c. 100 m, 22.iii.1999 (DP 299). 3♂, 3♀, as for previous except, ex *Cytisus albidus* (DP 298). 2♂, 4♀, 4 nymphs, Southern Atlantic coast, E side of Agadir, 30°25'N 9°30'W, s.l. 23.iii.1999 (DP 301). 1♂, 1♀, as for previous except, 29.iv.1999 (DP 321).1♀, Anti-Atlas, SE slopes of Jbel Lekst, 29°42'N 9°05'W, c. 2000 m, 25.iii.1999 (DP 303). LIBYA: 4 nymphs, Fezzan, W of Fiqzah, 29.i.1982 (BMNH).

### ***Arytainilla montivaga*** **sp. nov.** (4)

(Figs 6 & 23B)

*Adult*

*Colour:* Generally bright green to mid-green or yellow-green, more mature specimens with darker abdomens; forewing membrane clear or faintly yellow, veins uniform light brown.

*Structure:* Forewing widest in the apical third with a broadly rounded apex; pterostigma less than one quarter the wing length (shorter in the Moroccan specimens – one half to two thirds as long as the Spanish specimens); surface forewing spinules present in all cells (or if absent, only from cell c+sc) but reduced, confined mostly to the margin of the wing; distribution of spinules uniform, density sparse: less than 40 per 0.1mm$^2$; apical spines in wing cells cu$_1$, m$_1$ and m$_2$, but absent, or occasionally few present in cell r$_2$. Antennae short, with ten segments; genal cones very short, commencing ventrally relative to the vertex, with a distinct depression between the vertex and the genal cones, terminal setae as long as, or typically longer than the vertex. Paramere mid-length, in lateral view simple with sides parallel, narrowing at the apex and with rudimentary development of an apical blade, sclerotized apex flattened dorsally with slight anterior projection, in dorsal view contiguous anteriorly with inner margin straight edged; paramere shorter or slightly longer than the proctiger; proctiger not inflated posteriorly towards the base; aedeagus distal segment with a flattened, shallow hook and, in Moroccan specimens, with a pronounced heel at the rear of the hook, tip of aedeagus hook acute; male subgenital plate dorsal profile more or less straight and horizontal or slightly raised anteriorly. Female proctiger dorsal profile more or less straight from anus to apex (Spanish specimens) or with a post-anal depression but subsequently more or less straight (Moroccan specimens), apex bluntly rounded; subgenital plate ventral profile angled medially, apex acute; ovipositor valvulae ventralis slender, apex acute; height of valvulae dorsalis greater than valvulae ventralis, dorsally convex, wedge-shaped and tapering to the apex. (The specimens from Morocco are in all respects considerably smaller than those from Spain.)

*Adult measurements and ratios:* (4♂, 6♀) total length: ♂ 2.44-3.12, ♀ 2.88-3.4; forewing: ♂ length 1.9-2.4 width 0.81-1.05, ♀ length 2.43-2.8 width 1.06-1.2; pterostigma length ♂ 0.33-0.5, ♀ 0.3-0.6; hindwing length ♂ 1.56-1.95, ♀ 1.98-2.21; head width: ♂ 0.73-0.8, ♀ 0.79-0.88; antennal length: 1.25-1.49; genal cone length: 0.09-0.11; distal proboscis segment length: 0.15-0.17. WLPT: 4.6-8.3; ALHW: 1.52-1.84; GCVL: 0.4-0.55; WLHW: 2.6-3.29; VLW: 0.4-0.46; WLW: 2.29-2.38; CUR: 1.5-1.76; MR: 0.46-0.63; RMCU: 4.5-6.22; TLFL: 1.16-1.25; TLHW: 0.76-0.88; SCHW: 0.89-1; ATIB: 0.23-0.3; MTIB: 0.26-0.3; PBHW: 0.19-0.22; ATMT: 0.83-1. *Adult genitalia* ♂: MP: 0.29-0.38; PL: 0.28-0.42; AEL: 0.23-0.3; AEH: 0.08-0.10. MPHW: 0.4-0.48; PLHW: 0.38-0.53; MPPL: 0.9-1.04; AEPL: 0.71-0.82; MSLH: 1.12-1.22; AHS: 0.32-0.37; PLSH: 1.17-1.24. ♀: FP: 0.66-0.79; FSP: 0.42-0.57; RL: 0.2-0.23; OV: 0.13-0.16; EL: 0.24-0.28. FPHW: 0.83-0.93; FPSP: 1.34-1.6; FPCR: 3.3-3.55; OLSP: 0.25-0.31; FEOL: 1.84.

*Nymph*

*Colour:* 1st-3rd instars cream and orange, 4th-5th instars bright mid- to light green or yellow-green, with or without black tergites; sclerites, wing pads, legs and terminal antennal segments darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Tergites extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad short, expanded apically, with slight medial groove and short petiole. Circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 6) BL: 1.28-2.03; BW: 0.95-1.28; WL: 0.49-0.62; CPL: 0.35-0.44; CPW: 0.61-0.74; RW: 0.15-0.17; RL: 0.1-0.12; HW: 0.62-0.79; AL: 0.81-0.84; AL3: 0.18-0.2. WBL: 0.61-0.74; ALHW: 1.06-1.34; ALWL: 1.35-1.65; WLHW: 0.74-0.92; WCPL: 1.39-1.97; CPRW: 4.06-4.63.

*5th instar chaetotaxy:* Head setae simple and distinctly capitate (simple anteriorly, with few capitate posteriorly, max length at anterior margin 0.11-0.16); antennal setae simple and capitate (1-2 capitate on the distal end of 3rd and 5th segments); ocular seta simple, long (max length 0.07-0.12); primary and secondary post-ocular seta distinctly capitate (primary max length 0.1-0.12, secondary max length 0.13-0.18). Dorsal thoracic setae long capitate (max length 0.13-0.17). Prominent wing pad setae max length 0.12-0.18; forewing pad with simple and capitate setae, prominent setae 12-16, distinctly capitate, surface and marginal (± 8 on the outer margin, 2-4 proximal, 2-4 surface) with small, simple setae scattered on the surface; hindwing pad with capitate setae only, prominent setae 5-7, distinctly capitate, surface and marginal (2 apical, 2 proximal, 1-3 surface); proximal setae distinctly capitate. Dorsal abdominal prominent pre-caudal setae present on all tergites, long capitate (max length 0.13-0.19), prominent caudal plate setae present, eight distinctly capitate; sectasetae absent (replaced by four pairs of small simple setae); marginal abdominal setae (other than sectasetae) four pairs, distinctly capitate (4th typically narrow) (max length 0.2-0.23); pleurite setae paired capitate and simple. Legs with capitate setae present (max length 0.12-0.13); capitate foreleg setae present on femur and tibia, on the tibia 2 (1 proximal, 1 distal); capitate middle leg setae present on femur and tibia, on the tibia 3 (2 proximal, 1 distal); capitate hind leg setae present on femur and tibia, on the tibia 3-5.

*Host plant: Adenocarpus decorticans.*

*Distribution:* Continental: Spain and Morocco.

*Notes:* Occurs in the mountain ranges of southern Andalusia and northern Morocco. *A. montivaga* is sympatric in the Andalusian mountains with *Livilla baetica* sp. nov.

*Biology:* Nymphs were observed on the base of young leaves, in leaf buds and on fruits.

*Etymology:* Named for the geographic distribution of this species in montane regions, the epithet is derived from the Latin for 'wandering over mountains'.

*Comment:* The host plant distribution illustrates the Tertiary links between southern Iberia and NW Africa (Valdés 1991). Populations of *A. montivaga* from these two regions are morphological distinct. However, although the Moroccan form is considerably smaller and differs in the shape of the male aedeagus and female proctiger, it otherwise shares sufficient similarity to the Spanish form for them to be treated as a single species. The 5th instar chaetotaxy exhibits some similarity with an *Arytaina*-type while and the short genal cones and well developed pterostigma of the adult suggest affinities with *Arytinnis* gen. nov. However, *A.*

*montivaga* lacks the full suite of characters of either of these genera and thus the placement of this taxon is uncertain.

*Type material:* Holotype ♂ (slide mounted), SPAIN: Andalusia, N slopes of Sierra de Baza, rd Caniles to Alba, 37°15'N 2°45'W, c. 1600 m, 22.iii.1998 (BMNH). Paratypes 2♀, 17 nymphs, as for holotype (BMNH). 2♂, 1♀, 10 nymphs, as for holotype (NHMB).

*Other material examined:* MOROCCO: 5♂, 5♀, Central Rif Mountains, S of Ketama, 34°55'N 4°40'W, c. 1300 m, 21.vi.1998 (DP 249). 2♂, 1♀, 22 nymphs, Western Rif Mountains btw Ketama and Chefchaouen, E of Bab Berret, 34°56'N 4°50'W, c. 1400 m, 22.vi.1998 (DP 253). 3♀, 50 nymphs, as for previous (DP 254). 4 nymphs, Taza, Jbel Tazzeka, 33°50'N 4°18'W, c. 1550 m, 31.iii.1999 (DP 318). SPAIN: 12♂, 12♀, 10 nymphs, Andalusia, N slopes of Sierra Nevada, rd Calaharra to Puerto de la Ragua, 37°05'N 3°02'W, c. 1850 m, 21.iii.1998 (DP 128). 21♂, 10♀, 30 nymphs, as for holotype (DP 129).

### Genus *Arytinnis* gen. nov.

*Arytainilla* Loginova, 1972: 17, in part; Hodkinson & Hollis, 1987:41, in part
Type species: *Arytainilla pileolata* Loginova, 1976: 26

*Adult Description:* Generally bright green to grey green (some species become brown with age), lacking distinct body and wing membrane patterns; terminal antennal segments brown; forewing cells either clear or faintly yellow throughout, with or without light brown apical patches, forewing veins either uniformly pigmented light to dark brown, or with distinct light and dark bands. Forewing widest in the apical third with a broadly rounded apex; costal break and pterostigma present, pterostigma long, one quarter or greater the length of the wing; vein Rs typically curved in the middle but not, or only weakly curved at the apex towards the costal margin; cells $cu_1$ and $m_2$ relatively high; costal margin of the hindwing slightly concave. Antennae with ten segments. Head deflexed downwards with genal cones directed downwards relative to the plane of the vertex; genal cones short, commencing ventrally relative to the vertex, with a distinct depression between the vertex and the genal cones; terminal setae as long as or typically longer than the vertex. Distal proboscis segment short to very long. Number of basal tibial spurs variable, typically five (3+1+1) though individuals may have as few as three; one metatarsal spur. Paramere longer than the proctiger, in lateral view either simple, tapering to the apex or with an apically thin neck above a medial blade or ridge, apex narrower than the base. Profile of female proctiger variable, apex bluntly rounded; subgenital plate shallowly curved or with a medial bulge, apex acute; ovipositor valvulae ventralis slender, apex acutely rounded with or without small dorsal projections at the tip; height of valvulae dorsalis typically as great or greater than valvulae ventralis, dorsally convex, wedge-shaped and tapering to the apex.

*Nymphal Description:* Variable in colour, generally with darker brown sclerites, wing pads, legs and terminal antennal segments; prominent setae pigmented light to dark brown. Forewing pads and abdomen broadly rounded apically. Antennal segments seven, eight or nine. Tergites extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad long, broadly expanded apically, usually with a distinct medial groove and long petiole. Circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores. Antennae and head without distinctly capitate setae. Eyes with a single ocular seta positioned towards the inner margin. Wing pads with prominent setae present, either capitate or simple. Abdomen with three to four pairs of marginal sectasetae. Legs with or without capitate setae.

*Etymology:* Named in part for the subfamily Arytaininae, 'Aryt-', together with the Gaelic for island, 'innis' in reference to the probable origin and extensive diversification of this group in Macaronesia. To be treated as a feminine noun.

*Comment:* The genus is defined by the combination of characters: short genal cones with long terminal setae; apically broad and well rounded forewing with an unpatterned membrane and a long, well developed pterostigma; ovipositor slender with small dorsal valvulae. The 5th instar nymphs have long antennae and three or more pairs of sectasetae. This is a homogeneous group of 21 species which appears to have radiated recently, mostly in the Macaronesian region and to a much lesser extent on the continent. Interspecific differentiation is based mainly on peculiarities of the male genitalia. Due to this overall similarity within the group there are only a few clear morphological synapomorphies such as banded forewing veins, elongate genitalia, and number of nymphal antennal segments. It may be easier to base an immediate identification using geographic region and host plant (although these aspects have not been used directly in the keys) but care must be taken in the Canary Islands where a number of species occur sympatrically on the same host or on hosts that grow in close association.

Key to adults of *Arytinnis*

1 Forewing veins with distinct light and dark banding ........................................................ 2

— Forewing veins uniformly coloured, pale to mid-brown ................................................. 3

2 Forewing veins with longer dark bands and fewer short, light bands; male paramere (in lateral view) with an apically thin neck above a broad, medially positioned blade produced on the external side and directed anteriorly, sclerotized apex with slight anterior and posterior projections; tip of aedeagus hook not upturned; male subgenital plate dorsal profile slightly raised anteriorly, usually without a distinct step (on *Adenocarpus*; Tenerife, La Palma) .......................................................................... *proboscidea* (Loginova)

— Forewing veins with light and dark bands of more or less equal frequency; male paramere (in lateral view) tapering towards the apex, without a medial blade, sclerotized apex with a pronounced anterior projection; tip of aedeagus hook slightly upturned; male subgenital plate dorsal profile markedly raised anteriorly with a distinct step (on *Adenocarpus foliolosus*; Gran Canaria, Tenerife, La Gomera) ......................... *nigralineata* (Loginova)

3 Males and females with strikingly large genitalia, female proctiger longer than 1.2 x head width; male paramere longer (> 0.5 mm) than 0.7 x head width ....................................... 4

— Male and female genitalia smaller, female proctiger shorter than 1.2 x head width, male paramere shorter (≤ 0.5 mm) than 0.7 x head width ....................................................... 7

4 Male paramere broad and female genitalia robust; male paramere with a medially positioned blade produced on the external side and directed anteriorly, sclerotized apex (in lateral view) dorsally flattened with a slight medial depression and broadly expanded with small anterior and posterior projections; in dorsal view, contiguous posteriorly with inner margins concave; tip of aedeagus hook acute, not, or only slightly upturned; surface forewing spinules dense (60-100 per 0.1mm$^2$) (on *Teline stenopetala*; Tenerife) (Fig. 10) ............................................................................................................ ***menceyata* sp. nov.**

— Male paramere and female genitalia slender and elongate; male paramere in the basal portion more or less parallel sided without a medial blade but with a prominent shoulder on the anterior margin towards the apex, above which the apex curves inwards, sclerotized apex (in lateral view) small, with small anterior projection, and displaced to the interior and posterior of the top of the paramere; in dorsal view, contiguous anteriorly with inner margins straight edged; tip of aedeagus hook blunt and markedly upturned; surface forewing spinules sparse (less than 40 per $0.1 mm^2$) ........................................................ 5

5 Larger species: (total length ♂ 2.96-3.72, ♀ 3-4.04) antennae longer than 1.5 mm; forewing longer than 2.4 mm; head wider than 0.75 mm; distal proboscis segment $\geq 0.15$ mm; male proctiger longer than 0.4 mm; distal aedeagus segment longer than 0.34 mm; female proctiger longer than 1 mm; female subgenital plate longer than 0.6 mm; male paramere (in lateral view) either with a sloping anterior shoulder produced about two thirds up from the base and with the apex (in dorsal view) strongly S-curved; or with a horizontal anterior shoulder close to the apex, about three quarters up from the base and with the apex (in dorsal view) not or only weakly curved ........................................................ 6

— Smaller species: (total length ♂ 2.6-2.84, ♀ 2.76-3.16) antennae shorter than 1.5 mm; forewing shorter than 2.4 mm; head narrower than 0.75 mm; distal proboscis segment $< 0.15$ mm; male proctiger shorter than 0.4 mm; distal aedeagus segment shorter than 0.34 mm; female proctiger shorter than 1 mm; female subgenital plate shorter than 0.6 mm; male paramere (in lateral view) with a horizontal anterior shoulder close to the apex, about three quarters up from the base and with the apex (in dorsal view) distinctly curved (on *Teline stenopetala*; La Gomera) (Figs 14 & 15C–D) ........................... ***hupalupa* sp. nov.**

6 Male paramere (in lateral view) with a posterior bulge at the base and with a sloping anterior shoulder produced about two thirds up from the base, the apex curving posteriorly and (in dorsal view) strongly S-curved and expanded towards the sclerotized tip (on *Chamaecytisus*; Gran Canaria, Tenerife, La Gomera) (Figs 15E–F) .. *dividens* (Loginova)

— Male paramere (in lateral view) without a posterior bulge at the base and with a sharper, horizontal anterior shoulder closer to the apex, about three quarters up from the base, the apex not or weakly curving posteriorly and (in dorsal view) not or weakly curved and tappering towards the sclerotized tip (on *Chamaecytisus* and *Teline stenopetala*; La Palma, El Hierro) (Figs 15A–B) ........................................................ *modica* (Loginova)

7 Male paramere (in lateral view) with an apically thin neck above a medially positioned blade (sometimes reduced to a shallow ridge) produced on the external side and directed anteriorly; sclerotized apex dorsally either slightly rounded or with a distinct bulge, and with slight anterior or posterior projections ........................................................ 8

— Male paramere (in lateral view) without a medial blade or ridge, either simple with sides tapering towards the apex or more parallel sided with a slight terminal blade present laterally exterior to the apex, and then with the sclerotized apex displaced either to the interior or posterior of the top of the paramere; sclerotized apex either dorsally rounded with or without small anteriorly and interiorly directed hook, or flattened with small anterior projection ........................................................................................................ 14

8 Male paramere longer than 0.4 mm ........................................................................ 9
(Continental and Madeira; *cognata*, *hakani*, *incuba*)

— Male paramere shorter than 0.4 mm ........................................................................ 11
(Continental and Canary Islands; *berber*, *canariensis*, *ochrita*, *pileolata*,)

9 Male paramere (in lateral view) with distinct medial blade, sclerotized apex dorsally with a slight medial depression and small anterior and posterior projections; male proctiger shorter (< 0.27 mm) than 0.6 x paramere length; female proctiger longer than 1.65 x length of subgential plate; female subgenital plate ventral profile usually with a medial bulge (on *Genista florida*; Morocco) ............................................................ *cognata* (Loginova)

— Male paramere (in lateral view) with shallow medial ridge, sclerotized apex dorsally flattened with a small anterior projection; male proctiger longer (≥ 0.27 mm) than 0.6 x paramere length; female proctiger length ≤ 1.65 x length of subgential plate; female subgenital plate ventral profile shallowly curved without a medial bulge ........................ 10

10 Male paramere shorter (< 0.45 mm) than 0.55 x head width, in lateral view the apical neck, above termination of the medial blade, longer and more slender; male proctiger length ≤ 0.3 mm; female proctiger shorter than 0.85 mm (on *Teline monspessulana*; Mediterranean) ........................................................................................................ *hakani* (Loginova)

— Male paramere longer (> 0.45 mm) than 0.55 x head width, in lateral view the apical neck, above termination of the medial blade, shorter and thicker; male proctiger longer than 0.3 mm; female proctiger length ≥ 0.85 mm (on *Teline maderensis*; Madeira) ........................ ........................................................................................................ *incuba* (Loginova)

11 Male paramere ≤ 1.25 x subgenital plate height, sclerotized apex (in lateral view) with slight anterior and posterior projections, and (in dorsal view) contiguous posteriorly; male proctiger longer than 0.75 x paramere length; head width ≥ 0.72 mm; distal aedeagus segment longer than 0.26 mm, hook larger (0.08-0.1 mm long) .................................... 12

— Male paramere > 1.25 x subgenital plate height, sclerotized apex (in lateral view) with small anterior projection, and (in dorsal view) contiguous anteriorly or contiguous more or less along entire inner margin; male proctiger length ≤ 0.75 x paramere length; head width ≤ 0.72 mm; distal aedeagus segment length ≤ 0.26 mm, hook small (≤ 0.08 mm long).. 13

12 Genal cones very short (< 0.09 mm), less than 0.5 x length of the vertex with the terminal setae darkly pigmented; distal proboscis segment long (≥ 0.2 mm); male paramere (in lateral view) with distinct medial blade supporting several long stout setae, sclerotized apex dorsally with a well rounded bulge; male proctiger longer (> 0.3 mm) than 0.85 x paramere length; tip of aedeagus hook blunt; hind leg tibia long, more than 0.9 x head width, metatarsus longer than apical tarsus (on *Teline canariensis*; Tenerife) (Figs 9 & 1M) ....... ........................................................................................................ ***canariensis* sp. nov.**

— Genal cones longer (> 0.09 mm), equal to or greater than 0.5 x length of the vertex with the terminal setae pale; distal proboscis segment shorter (< 0.2 mm); male paramere (in lateral view) with shallow medial ridge supporting several short, stout setae, sclerotized apex dorsally flattened; male proctiger length (≤ 0.3 mm) less than 0.85 x paramere length; tip of aedeagus hook acute; hind leg tibia relatively short, less than 0.9 x head width, metatarsus length equal to, or shorter than the apical tarsus (on *Teline*; Tenerife) ............................. ........................................................................................................ *pileolata* (Loginova)

13 Female proctiger length less than head width; surface forewing spinules sparse (less than 40 per 0.1mm$^2$); male paramere shorter (< 0.35 mm) than 0.55 x head width, or 1.4 x subgenital plate height, sclerotized apex (in dorsal view) contiguous anteriorly; tip of aedeagus hook blunt; male proctiger shorter (< 0.24 mm) than 0.35 x head width (on *Genista segonnei*; Morocco) (Fig. 16) ....................................................... ***berber* sp. nov.**

— Female proctiger length greater than head width; surface forewing spinules relatively dense (40-60 per 0.1mm$^2$); male paramere longer (> 0.35 mm) than 0.55 x head width, or 1.4 x subgenital plate height, sclerotized apex (in dorsal view) contiguous more or less along entire inner margin; tip of aedeagus hook acute; male proctiger longer (> 0.24 mm) than 0.35 x head width (on *Teline osyroides*; Tenerife) (Fig. 11) ..................... ***ochrita* sp. nov.**

14 Male paramere (in lateral view) more or less parallel sided with a slight terminal blade present laterally exterior to the apex, and with the sclerotized apex displaced either to the interior or posterior of the top of the paramere ........................................................ 15

— Male paramere (in lateral view) simple, either straight or more curvaceous, with sides tapering towards the apex ........................................................................................ 17

15 Surface forewing spinules sparse (less than 40 per 0.1mm$^2$); male paramere short and broad, length (< 0.35 mm) equal to, or less than the height of the subgenital plate; male proctiger inflated towards the base; male subgenital plate dorsal profile raised anteriorly with a distinct step; female proctiger dorsal profile without a post-anal depression but

concave with an upturned apex, shorter than 1.4 x length of subgenital plate; subgenital plate ventral profile with a pronounced medial bulge (on *Genista tenera*; Madeira) .......... ........................................................................................................ *umbonata* (Loginova)

— Surface forewing spinules relatively dense (40-100 per $0.1mm^2$); male paramere long and slender, length (> 0.35 mm) greater than the height of the subgenital plate; male proctiger not, or only slightly inflated towards the base; male subgenital plate dorsal profile more or less straight and horizontal, or slightly raised anteriorly; female proctiger dorsal profile either with a post-anal depression or more or less straight from anus to apex, length ≥ 1.4 x length of subgenital plate; subgenital plate ventral profile shallowly curved or with a slight medial bulge ........................................................................................................ 16

16 Genal cone terminal setae darkly pigmented; male paramere longer than 1.4 x height of subgenital plate, in lateral view apex not bent forwards, and with 3-4 stout setae at the top of the terminal blade, the sclerotized apex more or less triangular; sclerotized portion (in dorsal view) contiguous anteriorly with inner margins rounded; aedeagus hook small (≤ 0.08 mm), about 0.25 x length of distal segment, tip of hook acute and turning upwards; female proctiger dorsal profile with a post-anal depression, shorter than 1.5 x length of subgenital plate; female subgenital plate without pointed projections on the dorsal margins (on *Teline*; Gran Canaria, Tenerife) (Fig. 30C) ...................................... *diluta* (Loginova)

— Genal cone terminal setae pale; male paramere shorter than 1.4 x height of subgenital plate, in lateral view curving forwards towards the apex, the terminal blade and sclerotized apex with anterior projections; sclerotized portion (in dorsal view) contiguous posteriorly with inner margins straight edged; aedeagus hook longer (≥ 0.1 mm), about 0.33 x length of distal segment, tip of hook relatively blunt and not upturned; female proctiger dorsal profile more or less straight from anus to apex, longer than 1.5 x length of subgenital plate; female subgenital plate with pointed projections on the dorsal margins (on *Teline microphylla*; Gran Canaria) (Fig. 30D) ............................................................ *equitans* (Loginova)

17 Male paramere (in lateral view) S-curved with the posterior margin strongly curved forward medially and with an isolated, medial field of stout spines on the interior surface, sclerotized apex more or less flattened with slight anterior projection; aedeagus distal segment longer than 0.85 x paramere length (on *Teline stenopetala*; La Gomera) (Fig. 13) ........................................................................................................ ***gomerae* sp. nov.**

— Male paramere (in lateral view) with posterior margin more or less straight, if stout spines present on the interior surface, positioned and extending more towards the base of the paramere, sclerotized apex rounded with small anteriorly and interiorly directed hook, or small anterior projection; aedeagus distal segment shorter than 0.85 x paramere length .... ........................................................................................................................ 18

18 Surface forewing spinules sparse (less than 40 per $0.1mm^2$); antennae long (1.7-2.1 mm); male paramere interior surface with stout spines on the posterior and sometimes anterior sides of a medial ridge, sclerotized apex (in dorsal view) with inner margin concave; aedeagus distal segment apex with a well developed, curved hook; male subgenital plate dorsal profile slightly raised anteriorly (on *Teline stenopetala*; La Palma, El Hierro) (Figs 12 & 30E) ........................................................................................ ***occidentalis* sp. nov.**

— Surface forewing spinules relatively dense (40-60 per $0.1mm^2$); antennae shorter (1.1-1.71 mm); male paramere interior surface either lacking stout spines or with stout spines present anteriorly at the base, sclerotized apex (in dorsal view) with inner margin straight edged or rounded with an acute point; aedeagus distal segment apex with a somewhat flattened, shallow hook; male subgenital plate dorsal profile more or less straight and horizontal ..... ........................................................................................................................ 19

19 Male paramere longer than 1.3 x height of subgenital plate, sclerotized apex (in dorsal view) contiguous more or less along entire inner margin; aedeagus hook larger ($\geq 0.08$ mm) with an acute tip; male proctiger $\geq 0.4$ x head width; female proctiger length greater than the head width, with the circumanal ring shorter than 0.25 x proctiger length; female proctiger dorsal profile concave with a slightly upturned apex; female subgenital plate ventral profile with a medial bulge; ovipositor valvulae dorsalis longer than 0.15 mm (on *Teline microphylla*; Gran Canaria) .................................................. *prognata* (Loginova)

— Male paramere shorter than 1.3 x height of subgenital plate, sclerotized apex (in dorsal view) contiguous anteriorly; aedeagus hook small ($\leq 0.08$ mm) with a blunt tip; male proctiger shorter than 0.4 x head width; female proctiger length less than the head width, with the circumanal ring longer than 0.25 x proctiger length; female proctiger dorsal profile more or less straight from anus to apex; female subgenital plate ventral profile shallowly curved without a medial bulge; ovipositor valvulae dorsalis shorter than 0.15 mm ....... 20

20 Antennae longer than 1.5 mm, equal to, or greater than 2 x head width; genal cones larger; distal proboscis segment ($\leq 0.15$ mm) shorter than 0.2 x head width; male paramere interior surface with stout spines present anteriorly at the base, and several long slender spines on the anterior margin, sclerotized apex (in dorsal view) with inner margins straight edged;

hind leg tibia longer than 0.7 x head width (on *Teline splendens*; La Palma) (Figs 8 & 30F) ........................................................................................................ ***fortunata* sp. nov.**

— Antennae shorter than 1.3 mm, about 1.5 x head width; genal cones smaller; distal proboscis segment (> 0.15 mm) longer than 0.2 x head width; male paramere interior surface lacking stout spines, with the anterior margin supporting several short, slender spines, sclerotized apex (in dorsal view) with inner margins rounded to an acute point; hind leg tibia shorter than 0.7 x head width (on *Teline rosmarinifolia*; Gran Canaria) (Figs 7 & 1N) ........................................................................................ ***romeria* sp. nov.**

Key to 5th instar nymphs of *Arytinnis*. As the nymphs in this genus are structurally similar, the type and placement of setae becomes an important aid in species identification (see Fig. 2 for terminology).

1 Antennal segments nine ........................................................................................ 2

— Antennal segments eight ........................................................................................ 3

— Antennal segments seven ........................................................................................ 4

2 Forewing and hindwing pads with simple setae only; dorsal caudal plate with six prominent setae; marginal abdominal setae (other than sectasetae) simple or narrowly capitate (on *Adenocarpus*; Tenerife, La Palma) (Fig. 26D) ............................ *proboscidea* (Loginova)

— Forewing and hindwing pads with simple and capitate setae; dorsal caudal plate with four prominent setae; marginal abdominal setae (other than sectasetae) distinctly capitate (on *Adenocarpus foliolosus*; Gran Canaria, Tenerife, La Gomera) (Fig. 26C) .......................... ........................................................................................ *nigralineata* (Loginova)

3 Antennae shorter than 1 mm, less than 1.5 x head width; primary and secondary post ocular setae distinctly capitate; dorsal thoracic setae short simple and long capitate; proximal forewing and hindwing pad setae distinctly capitate; hindwing pad with two prominent capitate setae (apical and proximal) (on *Teline stenopetala*; La Gomera) (Fig. 28A) ......... ........................................................................................................ ***gomerae* sp. nov.**

— Antennae longer than1 mm, greater than 1.5 x head width; primary and secondary post-ocular setae simple or narrowly capitate; dorsal thoracic setae long simple; proximal forewing and hindwing pad setae simple or narrowly capitate; hindwing pad with one prominent capitate seta (apical) (on *Teline stenopetala*; La Palma, El Hierro) (Fig. 28B) .. .................................................................................................. ***occidentalis* sp. nov.**

4 Abdominal sectasetae three pairs ........................................................................ 5

— Abdominal sectasetae four pairs ........................................................................................ 10

5 Legs with one or more distinct capitate setae present (if only one on tibiae – positioned distally) ........................................................................................................................ 6

— Legs with simple setae only (one small rod or reduced capitate may be present proximally on the tibiae of *equitans*) .......................................................................................... 7

6 Wing pads each with one prominent apical seta, proximal setae indistinct; antennae shorter than 0.8 mm, less than 1.3 x head width, or 1.68 x forewing pad length; secondary post-ocular seta indistinct; thorax dorsally with very short simple setae; small capitate setae present in typical position of first sectasetal pair; middle and hind tibiae each with one captiate seta (on *Teline osyroides*; Tenerife) (Fig. 27D) .......................... ***ochrita* sp. nov.**

— Wing pads each with two prominent setae – apical and proximal; antennae longer than 0.8 mm, ≥ 1.3 x head width, and greater than 1.68 x forewing pad length; secondary post-ocular seta prominent; thorax dorsally with with short and long simple setae; middle and hind tibiae each with two or more captiate setae (on *Chamaecytisus*; Gran Canaria, Tenerife, La Gomera) (Fig. 27C) ...................................................... *dividens* (Loginova)

7 Prominent forewing pad setae two (apical and proximal) (on *Teline microphylla*; Gran Canaria) (Fig. 28D) ................................................................... *equitans* (Loginova)

— Prominent forewing pad setae more than five ............................................................. 8

8 Antennae typically longer, greater than 1.95 x forewing pad length; secondary post-ocular and prominent dorsal thoracic setae longer (max length greater than 0.1 mm), capitate (minute simple only); ocular seta long and conspicuous (on *Teline maderensis*; Madeira) (Fig. 25C) .................................................................................... *incuba* (Loginova)

— Antennae typically shorter, less than 1.95 x forewing pad length; secondary post-ocular and prominent dorsal thoracic setae shorter (max length 0.1 mm or less), not always capitate, thorax with short or longer simple as well as capitate setae; ocular seta usually shorter, less conspicuous ............................................................................................................ 9

9 Thorax dorsally with short simple setae anteriorly and longer capitate posteriorly; ocular seta always small; secondary post-ocular setae always simple (on *Genista tenera*; Madeira) (Fig. 25A) .............................................................................. *umbonata* (Loginova)

— Thorax dorsally with long simple and long capitate setae; size of ocular seta and type of secondary post-ocular setae variable (on *Teline monspessulana*; Mediterranean) ............... .................................................................................................. *hakani* (Loginova)

10 Legs with simple setae only ...................................................................................... 11

— Legs with one or more distinct capitate setae present ........................................ 14

11 Prominent marginal abdominal setae (other than sectasetae) one pair in 1st position (on *Teline microphylla*; Gran Canaria) (Fig. 26A) .................................. *prognata* (Loginova)

— Prominent marginal abdominal setae (other than sectasetae) four pairs ......................... 12

— Prominent marginal abdominal setae (other than sectasetae) three pairs (absent from 4th position) ........................................................................................................ 13

12 Antennae shorter than 0.9 mm; proximal wing pad setae indistinct; dorsal pre-caudal setae on posterior tergites; dorsal caudal plate with numerous prominent setae; marginal abdominal setae (other than sectasetae) simple (on *Teline*; Gran Canaria, Tenerife) (Fig. 26B) .......................................................................................... *diluta* (Loginova)

— Antennae longer than 0.9 mm; proximal wing pad setae prominent; dorsal pre-caudal setae on anterior tergites; dorsal caudal plate prominent setae absent or reduced; marginal abdominal setae (other than sectasetae) mostly capitate (on *Genista florida*; Morocco) (Fig. 25B) ........................................................................................ *cognata* (Loginova)

13 Antennae shorter than 0.9 mm; primary and secondary post-ocular setae distinctly capitate; proximal and outer margin forewing pad setae distinctly capitate; dorsal thoracic setae short simple and stout capitate; dorsal pre-caudal setae long capitate (on *Genista segonnei*; Morocco) (Fig. 25D) ......................................................................... ***berber*** **sp. nov.**

— Antennae longer than 0.9 mm; primary and secondary post-ocular setae simple or narrowly capitate; proximal and outer margin forewing pad setae simple; dorsal thoracic setae short simple; dorsal pre-caudal setae long simple (on *Genista florida*; Morocco) (Fig. 25B) ...... ........................................................................................................ *cognata* (Loginova)

14 Prominent marginal abdominal setae (other than sectasetae) four pairs ......................... 15

— Prominent marginal abdominal setae (other than sectasetae) three pairs (absent from 4th position) ........................................................................................................ 17

15 Forewing and hindwing pads each with more than five prominent setae on the surface and margin; dorsal pre-caudal setae on all tergites; dorsal caudal plate with numerous prominent setae, typically more than 20 (on *Teline stenopetala*; Tenerife) (Fig. 29C) ....... ....................................................................................................... ***menceyata*** **sp. nov.**

— Forewing and hindwing pads each with one or two prominent marginal setae; dorsal post-wing setae on anterior tergites, or indistinct; dorsal caudal plate prominent setae absent or if present 2-4 ............................................................................................................ 16

16 Forewing and hindwing pads each with one prominent capitate seta apically, proximal setae short simple or indistinct; dorsal pre-caudal setae short simple or indistinct; dorsal caudal plate prominent setae absent (on *Chamaecytisus* and *Teline stenopetala*; La Palma, El Hierro) (Fig. 27B) ........................................................................ *modica* (Loginova)

— Forewing and hindwing pads each with two prominent setae (apical and proximal), proximal setae prominent, simple or capitate; dorsal pre-caudal setae long simple or long capitate; dorsal caudal plate prominent setae present (on *Chamaecytisus*; Gran Canaria, Tenerife, La Gomera) (Fig. 27C) ....................................................... *dividens* (Loginova)

17 Forewing pad with two prominent setae (apical and proximal) (max length ≥ 0.1 mm) (on *Chamaecytisus*; Gran Canaria, Tenerife, La Gomera) (Fig. 27C) ....... *dividens* (Loginova)

— Forewing pad with one prominent seta apically (proximal seta short simple or indistinct) (max length less than 0.1 mm) ........................................................................................ 18

— Forewing pad with five or more prominent setae (max length ≥ 0.1 mm) ...................... 19

18 Apical forewing pad seta simple or narrowly capitate; marginal abdominal pleurite setae paired simple (on *Teline stenopetala*; La Gomera) (Fig. 27A) .............. ***hupalupa* sp. nov.**

— Apical forewing pad seta distinctly capitate; marginal abdominal pleurite setae paired capitate and simple (on *Chamaecytisus* and *Teline stenopetala*; La Palma, El Hierro) (Fig. 27B) ........................................................................................................ *modica* (Loginova)

19 Antennae shorter than 0.8 mm, less than 1.3 x head width, and ≤ 1.5 x forewing pad length; hindwing pad with one prominent seta apically paired with a small rod or simple seta, proximal seta indistinct; hind tibia with one capitate seta distally (on *Teline rosmarinifolia*; Gran Canaria) (Fig. 29B) .................................................................... ***romeria* sp. nov.**

— Antennae longer than 0.8 mm, ≥ 1.3 x head width, and greater than 1.5 x forewing pad length; hindwing pad with two or more prominent setae, apically with two paired capitate setae, proximal seta distinct; hind tibia with two or more capitate setae ........................ 20

20 Antennae shorter than 1.7 x forewing pad length; ocular seta small, inconspicuous (0.04-0.05 mm), secondary post-ocular seta simple; dorsal thoracic setae short simple (0.03-0.05 mm); dorsal pre-caudal setae short simple; forewing and hindwing pads with simple and capitate setae, proximal setae simple; prominent hindwing pad capitate setae two (apical); hind tibia with more than two capitate setae (on *Teline splendens*; La Palma) (Fig. 29A) .. ........................................................................................................ ***fortunata* sp. nov.**

— Antennae longer than 1.7 x forewing pad length; ocular seta long, conspicuous (0.08-0.1 mm); secondary post-ocular seta distinctly capitate; dorsal thoracic setae long (0.08-0.1

mm), only capitate, or with simple setae; dorsal pre-caudal setae long capitate; forewing and hindwing pads with capitate setae (minute rod or simple), proximal setae distinctly capitate; prominent hindwing pad capitate setae more than two (apical and proximal); hind tibia with two capitate setae (proximal and distal) (on *Teline*; Tenerife) (Fig. 28C) ........... ........................................................................................................ *pileolata* (Loginova)

*Arytinnis pileolata* (Loginova) **comb. nov.**

(Fig. 28C)

*Arytainilla pileolata* Loginova, 1976: 26

*Adult Colour:* Pale grey-green or yellow-green; forewing cells with faint brown patches apically, veins uniform light or dark brown.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 1st-3rd instars cream and black or orange-red, 4th-5th instars green with black tergites.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 4) BL: 1.53-1.8; BW: 0.98-1.03; WL: 0.49-0.55; CPL: 0.46-0.5; CPW: 0.63-0.72; RW: 0.19-0.2; RL: 0.11-0.12; HW: 0.64-0.68; AL: 0.91-0.96; AL3: 0.22-0.25. WBL: 0.58-0.67; ALHW: 1.4-1.48; ALWL: 1.73-1.96; WLHW: 0.72-0.86; WCPL: 1.37-1.53; CPRW: 3.15-3.79.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.13-0.16); ocular seta simple or occasionally narrowly capitate, dark, conspicuous (max length 0.08-0.1); primary and secondary post-ocular setae distinctly capitate (max length 0.08-0.1). Dorsal thoracic setae long, capitate only or with simple (max length 0.08-0.11). Prominent wing pad setae max length 0.11-0.13; forewing and hindwing pads with capitate setae only (minute simple or sometimes small rod setae on the wing pad surfaces), prominent forewing pad setae 6-9, distinctly capitate, marginal (4-5 larger, 1-3 smaller and 1 proximal); prominent hindwing pad setae 3-4, distinctly capitate, surface and marginal (1-2 apical, 1 surface, 1 proximal). Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long capitate (max length 0.12), prominent caudal plate setae absent or if present, two, distinctly capitate; sectasetae four pairs (1st pair sometimes reduced); marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.13-0.16); pleurite setae paired capitate and simple. Legs with capitate setae present (max length 0.08-0.09); capitate foreleg setae absent; capitate middle leg setae absent or if present, on tibia only, one (distal) with or without small rod proximally; capitate hind leg setae present on tibia only, 2-3 (1 proximal, 1-2 distal) with 4-5 small rod setae.

*Host plant: Teline canariensis*, *T. osyroides* ssp. *sericea*, *T. stenopetala* ssp. *spachiana.*
*Distribution:* Canary Islands: Tenerife.
*Notes:* This is the most polyphagous species in *Arytinnis* gen. nov., occurring on three species of host plant in the genus *Teline.* It is found throughout the range of the host plant, *Teline canariensis*, where other sympatric species are restricted to the relict laurisilva habitat of this host. It is sympatric with *A. menceyata* on *Teline stenopetala* ssp. *spachiana* in pine forest habitat, and it is the only species on *Teline osyroides* ssp. *sericea* in the southern xerophytic habitat.
*Biology:* Small nymphs (1st-2nd instars) were observed at the base of developing fruit under the persistent clayx, and in leaf buds.
*Comment:* This species is selected as the type for the genus as it possesses the more typical generic features: small female genitalia, male paramere with an anterior medial ridge and forewing veins uniformly pigmented.

*Material examined:* CANARY ISLANDS. TENERIFE: 1♂, 6♀, 7 nymphs, rd Buenavista to Santiago del Teide, N of turning to Los Carrizales, 28°19'N 16°50'30"W, 900 m, ex *Teline canariensis*, 28.vi.1997 (DP 21). 3♂, 2♀, just blw Aguamansa, 28°21'30"N 16°30'W, 950 m, ex *Teline stenopetala*, 29.vi.1997 (DP 23.1). 4♂, 4♀, 2 nymphs, Anaga, rd El Bailadero to Taganana, 28°32'30"N 16°12'W, 550 m, ex *Teline canariensis*, 30.vi.1997 (DP 30). 14♂, 12♀, 2 nymphs, Teno, 7 km S of Buenavista on rd to Santiago del Teide, 28°20'N 16°51'W, c. 800 m, ex *Teline canariensis*, 4.iv.1998 (DP 152). 14♂, 16♀, rd El Socorro to La Laguna, abv El Portezuelo, nr El Púlpito, 28°29'30"N 16°21'15"W, c. 600 m, ex *Teline canariensis*, 25.iv.1998 (DP 178). 4♂, 5♀, Anaga, E of Pico del Inglés, 28°32'15"N 16°16'30"W, c. 960 m, ex *Teline canariensis*, 25.iv.1998 (DP 179). 4♂, 4♀, 2 nymphs, Güímar, Caldera de Pedro Gil, 28°20'30"N 16°28'W, 1775 m, ex *Teline stenopetala*, 26.iv.1998 (DP 182). 10♂, 10♀, Anaga, E of El Bailadero, 28°33'15"N 16°10'30"W, c. 800 m, ex *Teline canariensis*, 1.v.1998 (DP 183). 39♂, 35♀, 14 nymphs, Barranco de Herques, 28°14'45"N 16°26'30"W, c. 500-600 m, ex *Teline* *osyroides*, 2.v.1998 (DP 184). 19♂, 11♀, 1 nymph, NW of Arona, Barranco del Rey, 28°06'30"N 16°41'30"W, c. 700 m, ex *Teline osyroides*, 10.v.1998 (DP 186). 2♂, 8♀, 2 nymphs, nr La Vega, 28°20'30"N 16°44'W, c. 800 m, ex *Teline stenopetala* and hybrids x *T. canariensis*, 31.v.1998 (DP 229).

### *Arytinnis nigralineata* (Loginova) **comb. nov.**

(Figs 26C, 1G, 1L & 30A)

*Arytainilla nigralineata* Loginova, 1976: 19

*Adult Colour:* Bright green, lacking the darker colouration in mature specimens characteristic of *A. proboscidea*; head and genal cones with darkly pigmented setae. Forewing cells with faint brown patches, veins with numerous short, light and dark bands.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 1st-2nd instars pale orange or cream, 3rd-5th instars pale green to bright green or orange and cream, with or without black tergites.

*Structure:* Antennal segments nine

*5th instar measurements and ratios:* (specimens 7) BL: 1.55-1.85; BW: 0.98-1.13; WL: 0.51-0.55; CPL: 0.46-0.51; CPW: 0.62-0.7; RW: 0.17-0.19; RL: 0.1-0.12; HW: 0.69-0.74; AL: 0.99-1.18; AL3: 0.25-0.29. WBL: 0.6-0.63; ALHW: 1.45-1.66; ALWL: 1.91-2.23; WLHW: 0.7-0.76; WCPL:1.35-1.4; CPRW: 3.44-3.82.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.13-0.18); ocular seta simple, dark, conspicuous (max length 0.04-0.09); primary post-ocular seta simple or narrowly capitate (max length 0.12-0.13); secondary post-ocular seta simple or narrowly capitate (max length 0.14-0.15). Dorsal thoracic setae long, simple and narrowly capitate (max length 0.12-0.14). Prominent wing pad setae max length 0.12-0.17; forewing and hindwing pads with simple and capitate setae; each pad with two prominent setae, simple or narrowly capitate, marginal (1 apical, 1 proximal); hindwing pad apical seta paired with small simple seta; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long simple and narrowly capitate (max length 0.14), prominent caudal plate setae present, usually four simple or narrowly capitate; sectasetae three pairs;

marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.14-0.18); pleurite setae paired simple or slightly capitate. Legs with simple setae only (max length 0.05-0.07).

*Host plant: Adenocarpus foliolosus.*

*Distribution:* Canary Islands: Gran Canaria, Tenerife, and La Gomera.

*Notes:* Occurs on the two central islands and one western island, where it is restricted to lower altitudes and more humid habitats than the other *Adenocarpus*-feeding species, *A. proboscidea.* It can also be found sympatrically with *A. proboscidea* in the extensive host hybrid zone between *Adenocarpus foliolosus* and *Adenocarpus viscosus* on Tenerife, and occasionally on *Adenocarpus viscosus* where this host is found at lower altitudes on the humid, northern pine forest slopes.

*Biology:* Eggs were found in inflorescences on the inner surface of bracts. Nymphs were frequently observed on inflorescences.

*Material examined:* (ex *Adenocarpus foliolosus* unless otherwise stated) CANARY ISLANDS. GRAN CANARIA: 26♂, 20♀, 50 nymphs, 1-2 km S of Cruz de Tejeda, 27°59'30"N 15°36'W, 1480 m, 5.vii.1997 (DP 36). 1♀, as for previous except, ex *Teline microphylla* (DP 35). 10♂, 7♀, 1 nymph, rd from Moya to Fontanales, 28°5'30"N 15°35'W, 800 m, 6.vii.1997 (DP 42). 9♂, 10♀, 1 nymph, just blw Pinos de Gáldar, 28°2'30"N 15°37'30"W, 1400 m, 6.vii.1997 (DP 43). 18♂, 25♀, 2 nymphs, c. 3.5 km NW of Cruz de Tejeda on rd to Pinos de Gáldar, 28°1'30"N 15°35'30"W, 1600 m, 7.vii.1997 (DP 46). 1♀, c. 5 km S of Moya on rd to San Bartolomé de Fontanales, 28°5'N 15°35'30"W, c. 800 m, ex *Teline stenopetala*, 15.iv.1998 (DP 158). 19♂, 14♀, rd Moya to San Bartolomé de Fontanales, 28°5'45"N 15°35'15"W, c. 700 m, 19.iv.1998 (DP 170). 1♂, rd Moya to St Bartolome de Fontanales, 28°5'30"N 15°35'W, c. 600 m, ex *Teline canariensis*, 19.iv.1998 (DP 171). 37♂, 34♀, 1 nymph, just N of Cruz de Tejeda, 28°30'N 15°35'30"W, c. 1500 m, 20.iv.1998 (DP 173). 4♂, 6♀, as for previous except, ex *Teline microphylla*, 20.iv.1998 (DP 172). 1♀, 1-2 km S of Cruz de Tejeda, 28°00'N 15°36'W, 1420 m, ex *Teline microphylla*, 20.iv.1998 (DP 175). TENERIFE: 5♂, 6♀, 1 nymph, rd from La Laguna to Parque Nacional del Teide, c. 5 km SW of Las Raíces, 28°26'N 16°22'30"W, 1190 m, 22.vi.1997 (DP 4). 2♂, 1♀, c.14 km south of Aguamansa, rd Aguamansa to El Teide, 28°19'N 16°33'30"W, 1200 m, ex *Adenocarpus viscosus*, 29.vi.1997 (DP 24). 5♂, 9♀, 2 nymphs, 5 km

NE of Las Canteras on rd to Anaga, 28°31'N 16°18'W, 700 m, 30.vi.1997 (DP 29). 7♂, 12♀, rd La Laguna to El Teide, Las Lagunetas, 28°25'N 16°25'W, 1400 m, 9.vii.1997 (DP 50). 4♂, 6♀, 3 nymphs, rd from La Laguna to El Teide, just abv Mirador de La Orotava, 28°24'N 16°25'30"W, 1590 m, 9.vii.1997 (DP 51). 4♂, rd La Laguna to El Teide, c.20 m before turning to Arafo, 28°23'30"N 16°26'30"W, 1650 m, ex *Adenocarpus* hybrids, *viscosus* x *foliolosus*, 9.vii.1997 (DP 52). 5♂, rd El Teide to Arafo 28°23'N 16°25'W, 1250 m, ex *Chamaecytisus proliferus*, 9.vii.1997 (DP 53). 31♂, 16♀, 8 nymphs, 3-5 km above Las Raíces, rd from La Laguna to Parque Nacional del Teide, 28°25'N 16°23'30"W, 1350 m, 11.iv.1998 (DP 156). 2♂, 2♀, Anaga, E of Pico del Inglés, 28°32'15"N 16°16'30"W, c. 960 m, ex *Teline canariensis*, 25.iv.1998 (DP 179). LA GOMERA: 112♂, 72♀, 30 nymphs, rd from Arure to Las Hayas, 28°7'30"N 17°18'30"W, 900 m, 13.vii.1997 (DP 67). 2♂, 3♀, as for previous except, ex *Chamaecytisus proliferus* (DP 68). 1♀, as for previous except, ex *Spartocytisus filipes* (DP 69). 1♂, 2♀, as for previous except, ex *Retama monosperma* (DP 70). 30♂, 30♀, 23 nymphs, N coast road, nr Tamagarda and Las Rosas, 28°11'30"N 17°13'30"W, c. 600 m, ex *Adenocarpus* hybrids, *viscosus* x *foliolosus*, 26.v.1998 (DP 223). 1♂, La Laguna Grande, Garajonay Park, 28°06'30"N 17°16'W, c. 1300 m, ex *Chamaecytisus proliferus*, 26.v.1998 (DP 224).

### *Arytinnis proboscidea* (Loginova) **comb. nov.**

(Fig. 26D)

*Arytainilla proboscidea* Loginova, 1976: 18

*Adult Colour:* Generally bright green to mid-green though more mature males and females, but particularly females, develope brown to black colouration on the legs, abdomen and thorax. The darkest specimens were collected from the subalpine zone on La Palma. Head and genal cones with darkly pigmented setae. Forewing cells with faint brown patches, veins with long dark and short light bands.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 1st-3rd instars cream and orange, 4th-5th instars bright green and orange, with or without black tergites.

*Structure:* Antennal segments nine.

*5th instar measurements and ratios:* (specimens 8) BL: 1.55-1.88; BW: 0.98-1.15; WL: 0.56-0.62; CPL: 0.5-0.54; CPW: 0.66-0.73; RW: 0.17-0.19; RL: 0.11-0.11; HW: 0.68-0.75; AL: 1.01-1.1; AL3: 0.23-0.26. WBL: 0.58-0.64; ALHW: 1.35-1.57; ALWL: 1.65-1.93; WLHW: 0.75-0.86; WCPL: 1.31-1.4; CPRW: 3.58-4.12.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.15-0.19); ocular seta simple, inconspicuous (max length 0.04-0.06); primary post-ocular seta simple (max length 0.12); secondary post-ocular seta simple (max length 0.14). Dorsal thoracic setae long simple (max length 0.1-0.15). Prominent wing pad setae max length 0.13-0.17; forewing and hindwing pads with simple setae, each pad with two prominent setae (occasionally slightly capitate), marginal (1 apical, 1 proximal); hindwing pad apical seta paired with small simple seta; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long simple (max length 0.15), prominent caudal plate plate setae present, six simple or narrowly capitate; sectasetae three pairs; marginal abdominal setae (other than sectasetae) three pairs, simple or narrowly capitate (max length 0.16-0.23); pleurite setae paired simple. Legs with simple setae only (max length 0.05).

*Host plant: Adenocarpus viscosus, A. foliolosus.*

*Distribution:* Canary Islands: Tenerife and La Palma.

*Notes:* Occurs on the two high islands, Tenerife and La Palma. On Tenerife it is restricted to the host plant *Adenocarpus viscosus* and also occurs on hybrids between *Adenocarpus viscosus* and *Adenocarpus foliolosus*. However, on La Palma it is the only species found on both *Adenocarpus* hosts, as the closely related *A. nigralineata* is absent from this island. It is extremely abundant in the high sub-alpine zone on La Palma where adults can often be collected from sympatric plants, both leguminous and non-leguminous. This abundance on La Palma is correlated with a population explosion in the host plant after the preferential grazing of goats on other native plants reduced several species typical of this zone to near extinction (Palomares Martínez, 1997).

*Biology:* Eggs were observed in developing inflorescences in small clusters on the inner surface of bracts and calices and on the corolla, as well as on the inner surface of petioles in developing leaf buds. From 35 to more than 300 (on La Palma) eggs were found in a single inflorescence, the majority of these were laid on the calyx (more than 60 eggs were found on a single calyx and more than 40 eggs on a single corolla). Nymphs ($1^{st}$-$5^{th}$ instars) were found in the same locations. Some nymphs migrate to the base of the flower or the pedicel, while others congregate on unopened inflorescences or at the base of the stylar tube inside mature flowers. *Comment:* This study did not survey the eastern Canary Islands (Fuerteventura and Lanzarote), where there are no recorded host plants in the Genisteae, yet one male was recorded from Fuerteventura by Loginova (1976). Neither did this study corroborate Loginova's distributions for La Gomera (one ♂ recorded) or Gran Canaria (one ♀ recorded). Loginova (1976) grouped this and the previous species (*A. nigralineata*) together with *A. dividens* and *A. modica* based on the extremely large, elongate female genitalia. However, in other respects the adult and nymphal forms in these two groups are distinct. *A. proboscidea* and *A. nigralineata* are the only *Adenocarpus*-feeding species in the Canary Islands and they share several unique features such as banded forewing veins, long distal proboscis segment and 5th instars nymphs with nine antennal segments.

*Material examined:* (ex *Adenocarpus viscosus* unless otherwise stated) CANARY ISLANDS. TENERIFE: 50♂, 50♀, 5 nymphs, rd to Parque Nacional del Teide, Miradores de la Cumbre, 28°23'30"N 16°26'W, 1800 m, 22.vi.1997 (DP 5). 36♂, 14♀, 17 nymphs, c.14 km S of Aguamansa, rd Aguamansa to El Teide, 28°19'N 16°33'30"W, 1200 m, 29.vi.1997 (DP 24). 56♂, 50♀, 18 nymphs, rd Parque Nacional del Teide to Santiago del Teide, 28°15'30"N 16°46'W, 1130 m, 29.vi.1997 (DP 27). 1♂, rd from La Laguna to El Teide, just abv Mirador de La Orotava, 28°24'N 16°25'30"W, 1590 m, ex *Adenocarpus foliolosus*, 9.vii.1997 (DP 51). 5♂, rd La Laguna to El Teide, c.20 m before turning to Arafo, 28°23'30"N 16°26'30"W, 1650 m, ex *Adenocarpus* hybrids, *viscosus* x *foliolosus*, 9.vii.1997 (DP 52). 14♂, 16♀, 12 nymphs, abv Roques Imoque and Brezo, nr Trevejos, rd from Arona to Vilaflor, 28°29'15"N 16°39'15"W, c. 1300 m, 10.v.1998 (DP 187). 2♂, 2♀, abv Vilaflor, 28°10'30"N 16°39'W, c. 1900 m, ex *Chamaecytisus proliferus*, 10.v.1998 (DP 188). LA PALMA: 4♂, 6♀, 1 nymph, SE rd Santa Cruz to La Caldera 28°43'N 17°46'W, 950 m, ex *Adenocarpus foliolosus*, 15.vii.1997 (DP 72). 36♂, 24♀, 47 nymphs, SE rd Santa Cruz to La Caldera, 28°43'N 17°47'30"W, 1500 m, 15.vii.1997 (DP 74). 11♂, 22♀, 2 nymphs, as for previous except, ex *Adenocarpus foliolosus* (DP 75). 17♂, 7♀, 108 nymphs, La Palma, Fuente de Olén, SE rd Santa Cruz to La Caldera, 28°43'30"N 17°48'W, 1730 m, 15.vii.1997 (DP 76). 5♂, 9♀, La Palma, SE rd Santa Cruz to La Caldera, 28°45'N 17°49'30"W, 1950 m, ex *Spartocytisus supranubius*, 16.vii.1997 (DP 80.1). 3♂, La Caldera, 2150 m, ex *Spartocytisus supranubius*, 16.vii.1997 (DP 80.2). 5♂, 16♀, La

Caldera, 28°45'N 17°50'30"W, 2250 m, ex *Genista benehoavensis*, 16.vii.1997 (DP 81). 2♂, 1♀, La Caldera, 28°46'N 17°50'30"W, 2280 m, ex *Spartocytisus supranubius*, 17.vii.1997 (DP 85). 8♂, 3♀, La Palma, La Caldera, 28°45'30"N 17°51'W, 2270 m, ex *Genista benehoavensis*, 17.vii.1997 (DP 86). 4♂, 5♀, 5 nymphs, NE, rd Barlovento to Garafía, nr Gallegos, 28°48'N 17°52'W, c. 600 m, ex *Adenocarpus viscosus* and hybrids with *A. foliolosus*, 19.v.1998 (DP 199). 1♂, NW rd from Llano Negro to La Caldera, 28°48'N 17°55'30"W, c. 1050 m, ex *Chamaecytisus proliferus*, 19.v.1998 (DP 201). 10♂, 18♀, Roque de los Muchachos, 28°45'30"N 17°53'W, c. 2300 m, ex *Genista benehoavensis*, 19.v.1998 (DP 202). 27♂, 15♀, 15 nymphs, La Palma, SE rd Santa Cruz to La Caldera, 28°43'N 17°47'15"W, c. 1100 m, ex *Adenocarpus foliolosus*, 20.v.1998 (DP 204). 3♂, 1♀, SE rd Santa Cruz to La Caldera, 28°43'30"N 17°48'30"W, c. 1700 m, ex *Chamaecytisus proliferus*, 20.v.1998 (DP 205). 5♂, 4♀, as for previous except, ex *Spartocytisus supranubius* (DP 206). 40♂, 40♀, La Caldera rim, NW of Pico de la Cruz, 28°45'30"N 17°51'W, c. 2200 m, 20.v.1998 (DP 209). 20♂, 15♀, as for previous except, ex *Genista benehoavensis* (DP 207). 7♂, 10♀, as for previous except, ex *Spartocytisus supranubius* (DP 208).

### *Arytinnis equitans* (Loginova) **comb. nov.**

(Figs 28D & 30D)

*Arytainilla equitans* Loginova, 1976: 25

*Adult Colour:* Pale grey-green, mature specimens becoming darker; forewing cells with faint brown patches apically, veins uniform mid-brown.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 1st-2nd instars orange-red with black tergites, 3rd-5th instars cream or green with black tergites.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 5) BL: 1.45-1.83; BW: 0.93-1.05; WL: 0.49-0.54; CPL: 0.42-0.47; CPW: 0.61-0.68; RW: 0.18-0.2; RL: 0.11-0.11; HW: 0.66-0.72; AL: 0.97-1.05; AL3: 0.22-0.26. WBL: 0.57-0.64; ALHW: 1.38-1.59; ALWL: 1.91-2.02; WLHW: 0.71-0.79; WCPL: 1.38-1.51; CPRW: 3.39-3.61.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.11-0.17); ocular seta simple, dark, conspicuous (max length 0.08-0.11); primary and secondary post-ocular setae simple or narrowly, to distinctly capitate (max length 0.09-0.12). Dorsal thoracic setae long, simple only or with capitate (max length 0.1-0.12). Prominent wing pad setae max length 0.12-0.15; forewing and hindwing pads with simple and capitate setae, prominent setae two on each pad, marginal (1 apical, 1 proximal) apical seta distinctly capitate, proximal seta distinctly capitate or simple; forewing pad with up to five smaller marginal simple or rod setae; hindwing pad apical seta paired with small simple seta; small simple or rod setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long capitate (max length 0.1-0.12), prominent caudal plate setae absent or if present, typically two distinctly capitate; sectasetae three pairs (small simple or lanceolate seta in 1st position); marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.12-0.16); pleurite setae paired capitate and simple. Legs with simple setae only or with capitate setae present (max length 0.03-0.07); capitate fore and middle leg setae absent (occasionally small rod setae proximally); capitate hind leg setae absent or if present, on tibia only, one (proximal) capitate or small rod.

*Host plant: Teline microphylla, T. canariensis.*

*Distribution:* Canary Islands: Gran Canaria.

*Notes:* Widespread throughout the distribution of the host plant, *Teline microphylla.* Two sympatric species, *A. diluta* and *A. prognata*, appear to be restricted to humid or more drier habitats respectively. During this study these two species were never found on the same host populations, however, Loginova (1975) records two locations (though no host details are given) where *A. diluta*, *A. prognata* and *A. equitans* were collected. A few adults and nymphs of *A. equitans* were also collected from relict individuals of the host plant, *Teline canariensis*, in the reduced laurisilva habitat on Gran Canaria. Host acquisition in this instance, may have been facilitated by hybridization which has been recorded between *Teline microphylla* and *Teline canariensis* on Gran Canaria (M. del Arco Aguilar pers. comm.).

*Biology:* Eggs were found on the outer surface of corolla segments. Small nymphs (1st-2nd instars) were observed on corollas, new leaves and developing fruit, usually under the persistent calyx and anther tube.

*Material examined:* CANARY ISLANDS. GRAN CANARIA: 45♂, 39♀, 18 nymphs, 1-2 km S of Cruz de Tejeda, 27°59'30"N 15°36'W, 1480 m, ex *Teline microphylla*, 5.vii.1997 (DP 35). 1♀, abv Fataga, 27°54'30"N 15°34'W, 800 m, ex *Teline microphylla*, 6.vii.1997 (DP 40). 3♂, 4♀, 2 nymphs, rd Moya to Fontanales, 28°5'30"N 15°35'W, c. 600 m, ex *Teline canariensis*, 6.vii.1997 (DP 41). 1♀, just blw Pinos de Gáldar, 28°2'30"N 15°37'30"W, 1400 m, ex *Teline microphylla*, 6.vii.1997 (DP 44). 1♂, 1♀, just abv Pinos de Gáldar, 28°2'N 15°37'W, 1500 m, ex *Teline microphylla*, 6.vii.1997 (DP 45). 1♀, 1 nymph, rd Ayacata to Tejeda, 27°57'30"N 15°38'S, 1370 m, ex *Teline microphylla*, 7.vii.1997 (DP 48). 6♂, 12♀, c. 5 km S of Moya on rd to San Bartolomé de Fontanales, 28°5'N 15°35'30"W, c. 800 m, ex *Teline stenopetala*, 15.iv.1998 (DP 158). 3♀, 1 nymph, abv Fataga, 27°54'N 15°34'W, c. 800 m, ex *Teline microphylla*, 16.iv.1998 (DP 160). 1♀, S of Risco Blanco, 27°56'N 15°33'30"W, c. 900 m, ex *Teline rosmarinifolia*, 16.iv.1998 (DP 162). 39♂, 55♀, 16 nymphs, rd to Risco Blanco, btw Agualatente and La Culata, 27°56'N 15°34'W, 1100 m, ex *Teline microphylla*, 16.iv.1998 (DP 163). 2♀, base of Risco Blanco, 27°56'N 15°33'30"W, 1150 m, ex *Teline rosmarinifolia*, 18.iv.1998 (DP 165). 1♀, rd Moya to St Bartolome de Fontanales, 28°5'30"N 15°35'W, c. 600 m, ex *Teline canariensis*, 19.iv.1998 (DP 171). 13♂, 22♀, 1 km N of Cruz de Tejeda, 28°30'N 15°35'30"W, c. 1500 m, ex *Teline microphylla*, 20.iv.1998 (DP 172). 47♂, 32♀, 2 nymphs, 1-2 km S of Cruz de Tejeda, 28°00'N 15°36'W, 1420 m, ex *Teline microphylla*, 20.iv.1998 (DP 175).

### *Arytinnis prognata* (Loginova) **comb. nov.**

(Fig. 26A)

*Arytainilla prognata* Loginova, 1976: 28

*Adult Colour:* Mid-green to yellow green; forewing clear, veins uniform light brown.
*Adult Description:* Loginova (1976).

*Nymph*
*Colour:* 1st-2nd instars orange-red with black tergites, 3rd-5th instars bright green, grey-green or cream, with or without black tergites.
*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 5) BL: 1.35-2.03; BW: 0.85-1.08; WL: 0.5-0.54; CPL: 0.42-0.49; CPW: 0.57-0.67; RW: 0.16-0.18; RL: 0.1-0.11; HW: 0.57-0.67; AL: 0.82-0.9; AL3: 0.19-0.22. WBL: 0.53-0.63; ALHW: 1.22-1.5; ALWL: 1.58-1.7; WLHW: 0.75-0.93; WCPL: 1.3-1.38; CPRW: 3.17-3.82.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.11-0.14); ocular seta simple, dark, conspicuous (max length 0.05-0.07); primary post-ocular seta narrowly or distinctly capitate (max length 0.08-0.09); secondary post-ocular seta simple (max length 0.03-0.06). Dorsal thoracic setae short with few long, simple (max length 0.07). Prominent wing pad setae max length 0.09-0.12; forewing and hindwing pads with simple and capitate setae; each pad with one prominent apical seta, distinctly capitate; hindwing pad apical seta paired with small simple seta; proximal setae indistinct from small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae on anterior tergites, long simple (max length 0.09), prominent caudal plate setae absent; sectasetae four pairs; marginal abdominal setae (other than sectasetae) one pair (1$^{st}$ position), distinctly capitate (max length 0.1-0.14); pleurite setae paired simple, occasionally slightly capitate. Legs with simple setae only (max length 0.05).

*Host plant: Teline microphylla.*

*Distribution:* Canary Islands: Gran Canaria.

*Notes:* In this study, *A. prognata* was found to be restricted to southern populations of the host plant where the habitat is xerophytic. In all cases it was found to be sympatric with *A.equitans* and in April, more abundant than this species on the most southerly host population sampled. However, it was absent from collections made from this same host population later in July, when only *A. equitans* was found. This suggests that these species may exhibit asynchronous development with *A. prognata* developing earlier than *A. equitans*.

*Biology:* Small nymphs were observed on the corolla and larger nymphs on the pedicel of developing flowers.

*Material examined:* CANARY ISLANDS. GRAN CANARIA: 14♂, 13♀, 19 nymphs, abv Fataga, 27°54'N 15°34'W, c. 800 m, ex *Teline microphylla*, 16.iv.1998 (DP 160). 2♂, 8 nymphs, rd to Risco Blanco, btw Agualente and La Culata, 27°56'N 15°34'W, 1100 m, ex

*Teline microphylla*, 16.iv.1998 (DP 163). 1♂, base of Risco Blanco, 27°56'N 15°33'30"W, 1150 m, ex *Teline rosmarinifolia*, 18.iv.1998 (DP 165).

*Arytinnis diluta* (Loginova) **comb. nov.**

(Figs 26B & 30C)

*Arytainilla diluta* Loginova, 1976: 24

*Adult Colour:* Yellow-green to yellow-brown, mature specimens become darker brown; genal cones with darkly pigmented setae. Forewing cells with faint brown patches apically, veins uniform mid- or dark brown.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 5th instars bright green to yellow or cream, with black tergites.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 2) BL: 1.5-1.68; BW: 1.03-1.08; WL: 0.5-0.52; CPL: 0.42-0.42; CPW: 0.61-0.67; RW: 0.14-0.15; HW: 0.64-0.66; AL: 0.84-0.86; AL3: 0.2-0.21. WBL: 0.64-0.69; ALHW: 1.27-1.34; ALWL: 1.62-1.72; WLHW: 0.78-0.79; WCPL: 1.45-1.6; CPRW: 4.36-4.47.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.15-0.16); ocular seta simple, dark, conspicuous (max length 0.05-0.08); primary and secondary post-ocular setae simple (max length 0.06-0.07). Dorsal thoracic setae short simple (max length 0.02-0.04). Prominent wing pad setae max length 0.12; forewing and hindwing pads with simple setae only, forewing pad with one prominent apical seta and up to eight smaller marginal setae; hindwing pad with one prominent apical seta (paired with one smaller); proximal setae indistinct from small simple setae on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on posterior tergites, long simple (max length 0.08-0.1), prominent caudal plate setae present, 6-8, simple; sectasetae four pairs; marginal abdominal setae (other than sectasetae) four pairs, simple (max length 0.15-0.19); pleurite setae paired simple. Legs with simple setae only (max length 0.05).

*Host plant: Teline microphylla, T. canariensis.*

*Distribution:* Canary Islands: Gran Canaria and Tenerife.

*Notes:* On Gran Canaria *A. diluta* was found to be restricted to northern populations of the host plant (*Teline microphylla*) where the habitat is more humid. In all cases it was found to be sympatric with *A. equitans* and in April, more abundant than this species on the most northerly host population sampled. However, it was absent from collections made from the same host population later in July when only *A. equitans* was found. This suggests that these two species may exhibit asynchronous development with *A. diluta* (as with *A. prognata*) developing earlier than *A. equitans*. On Tenerife *A. diluta* is symaptric with *A. pileolata*, but similarly found to be restricted to more humid habitats of the host plant (*Teline canariensis*) on the Anaga and Teno peninsulas. It also appears to develope earlier than A. *pileolata*, being absent or rare from collections made in June but common from the same locations in April-May.

*Biology:* Nymphs were observed on leaf buds.

*Material examined:* CANARY ISLANDS. GRAN CANARIA: 61♂, 50♀, 1 km N of Cruz de Tejeda, 28°30'N 15°35'30"W, c. 1500 m, ex *Teline microphylla*, 20.iv.1998 (DP 172). 9♂, 28♀, 1 nymph, 1-2 km S of Cruz de Tejeda, 28°00'N 15°36'W, 1420 m, ex *Teline microphylla*, 20.iv.1998 (DP 175). TENERIFE: 1♂, 1♀, 3 nymphs, rd Buenavista to Santiago del Teide, N of turning to Los Carrizales, 28°19'N 16°50'30"W, 900 m, ex *Teline canariensis*, 28.vi.1997 (DP 21). 13♂, 17♀, 1 nymph, Teno, 7 km S of Buenavista on rd to Santiago del Teide, 28°20'N 16°51'W, c. 800 m, ex *Teline canariensis*, 4.iv.1998 (DP 152). 1♂, 4♀, Anaga, E of Pico del Inglés, 28°32'15"N 16°16'30"W, c. 960 m, ex *Teline canariensis*, 25.iv.1998 (DP 179). 15♂, 15♀, Anaga, E of El Bailadero, 28°33'15"N 16°10'30"W, c. 800 m, ex *Teline canariensis*, 1.v.1998 (DP 183).

### ***Arytinnis romeria* sp. nov.** (5)

(Figs 7, 29B & 1N)

*Adult*

*Colour:* Yellow-green; forewing clear, veins uniform light brown.

*Structure:* Surface forewing spinules present in all cells but reduced in cell c+sc; distribution of spinules non-uniform, medium density: 40-60 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, and absent, or more typically few present in cell $r_2$. Antennae short; genal cones very short, terminal setae not darkly pigmented. Distal proboscis segment mid-length. Paramere short, in lateral view slender and simple, with sides tapering towards the apex, sclerotized apex dorsally rounded with small anteriorly and interiorly directed hook, in dorsal view contiguous anteriorly and rounded with an acute point; proctiger not inflated posteriorly towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile more or less straight and horizontal. Female proctiger dorsal profile more or less straight from anus to apex or with slight post anal depression; subgenital plate ventral profile shallowly curved.

*Adult measurements and ratios:* (4♂, 5♀) total length: ♂ 2.64-2.84, ♀ 2.96-3.16; forewing: ♂ length 2.2-2.25 width 0.89-0.93, ♀ length 2.25-2.45 width 0.93-0.99; pterostigma length ♂ 0.64-0.77, ♀ 0.7-0.85; hindwing length ♂ 1.78-1.8, ♀ 1.83-2; head width: ♂ 0.75-0.77, ♀ 0.77-0.81; antennal length: 1.1-1.27; genal cone length: 0.08-0.11; distal proboscis segment length: 0.16-0.18. WLPT: 2.84-3.36; ALHW: 1.47-1.62; GCVL: 0.4-0.58; WLHW: 2.86-3.18; VLW: 0.39-0.48; WLW: 2.37-2.53; CUR: 1.59-1.84; MR: 0.43-0.53; RMCU: 5-7.05; TLFL: 1.06-1.16; TLHW: 0.61-0.68; SCHW: 0.79-0.87; ATIB: 0.25-0.28; MTIB: 0.27-0.31; PBHW: 0.21-0.22; ATMT: 0.87-0.93. *Adult genitalia ♂*: MP: 0.22-0.23; PL: 0.3-0.31; AEL: 0.23-0.24; AEH: 0.06-0.07. MPHW: 0.29-0.31; PLHW: 0.4-0.41; MPPL: 0.71-0.77; AEPL: 0.74-0.8; MSLH: 1.21-1.31; AHS: 0.27-0.28; PLSH: 1.11-1.15. ♀: FP: 0.67-0.72; FSP: 0.42-0.49; RL: 0.18-0.21; OV: 0.13-0.14; EL: 0.25-0.29. FPHW: 0.87-0.94; FPSP: 1.47-1.6; FPCR: 3.43-3.74; OLSP: 0.27-0.31; FEOL: 2.01.

*Nymph*

*Colour:* 1st-3rd instars orange-red with black tergites, 4th-5th instars mid-green.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 4) BL: 1.35-1.63; BW: 0.93-1; WL: 0.52-0.53; CPL: 0.38-0.46; CPW: 0.63-0.67; RW: 0.16-0.19; RL: 0.11-0.11; HW: 0.61-0.64; AL: 0.72-0.78; AL3: 0.17-0.2. WBL: 0.61-0.7; ALHW: 1.16-1.28; ALWL: 1.38-1.5; WLHW: 0.83-0.85; WCPL: 1.46-1.66; CPRW: 3.5-4.06.

*5th instar chaetotaxy:* Head setae simple and narrowly capitate (max length at anterior margin 0.1-0.11); ocular seta simple, inconspicuous (max length 0.04-0.05); primary post-ocular seta distinctly capitate (max length 0.07); secondary post-ocular seta distinctly or narrowly capitate (max length 0.05-0.06). Dorsal thoracic setae short simple (max length 0.04-0.05). Prominent wing pad setae max length 0.1-0.11; forewing and hindwing pads with capitate setae only (minute simple setae scattered on the wing pad surfaces); forewing pad prominent setae 7-10, distinctly capitate, marginal (4-5 larger, 3-5 smaller), proximal seta short simple or narrowly capitate; hindwing pad with one prominent apical seta, distinctly capitate, paired with one small rod seta, proximal seta indistinct from simple surface setae. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, short simple and capitate (max length 0.05), prominent caudal plate setae absent; sectasetae four pairs; marginal abdominal setae (other than sectasetae) three pairs (4th may be reduced, simple or absent), distinctly capitate (max length 0.12-0.13); pleurite setae paired capitate and simple. Legs with capitate setae present (max length 0.1-0.11); capitate foreleg setae absent; capitate middle and hind leg setae present, on tibia only, one (distal).

*Host plant: Teline rosmarinifolia* ssp. *rosmarinifolia.*

*Distribution:* Canary Islands: Gran Canaria.

*Notes:* The host plant has a southern distribution on Gran Canaria and survives in small, isolated populations but was recently found to be more widespread than previously thought (Marrero, González-Artiles & González-Martín, 1995). Two subspecies of the host have been recognised but only one was sampled. *A. romeria* sp. nov. was found on only one of the two host populations sampled which suggests that size and fragmentation of host populations may effect this species' distribution.

*Biology:* Eggs were found scattered on the surface of fruits, at the base of leaflets and on the underside of leaves. Nymphs were observed on the corolla of developing flowers and on developing fruit under the persistent calyx and anther tube.

*Etymology:* Named both for the harvest festivals ('romería') celebrated at the time this species was discovered, and for the likeness of the foliage of the host plant (*Teline rosmarinifolia*) to 'rosemary' or 'romero' in Spanish.

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. GRAN CANARIA: base of Risco Blanco, 27°56'N 15°33'30"W, 1150 m, 18.iv.1998 (BMNH). Paratypes 2♂, 3♀, 6 nymphs, as for holotype (BMNH). 1♂, 1♀, as for holotype (DZUL). 2♂, 2♀, as for holotype (NHMB).

*Other material examined:* 12♂, 17♀, as for holotype (DP 165).

### *Arytinnis fortunata* **sp. nov.** (6)

(Figs 8, 29A & 30F)

*Adult*

*Colour:* Pale green to mid-green; forewing clear, veins uniform light brown.

*Structure:* Surface forewing spinules present throughout all cells, but reduced cell c+sc; distribution of spinules non-uniform, medium density: 40-60 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, and few present in cell $r_2$. Antennae mid-length; genal cones short, terminal setae not darkly pigmented. Distal proboscis segment mid-length. Paramere short, in lateral view slender and simple, with sides tapering towards the apex, sclerotized apex dorsally rounded with very small anteriorly directed hook, in dorsal view contiguous anteriorly, inner margin straight edged; proctiger not inflated towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile more or less straight and horizontal. Female proctiger dorsal profile more or less straight from anus to apex; subgenital plate ventral profile shallowly curved.

*Adult measurements and ratios:* (4♂, 5♀) total length: ♂ 2.92-3.12, ♀ 3-3.44; forewing: ♂ length 2.33-2.5 width 0.93-1.03, ♀ length 2.39-2.76 width 0.97-1.1; pterostigma length ♂ 0.82-0.89, ♀ 0.8-0.98; hindwing length ♂ 1.93-2, ♀ 1.95-2.25; head width: ♂ 0.77-0.79; ♀ 0.76-0.83; antennal length: 1.52-1.71; genal cone length: 0.1-0.13; distal proboscis segment length: 0.14-0.15. WLPT: 2.75-2.99; ALHW: 2-2.14; GCVL: 0.45-0.65; WLHW: 2.99-3.37; VLW: 0.4-0.49; WLW: 2.38-2.53; CUR: 1.79-1.93; MR: 0.47-0.54; RMCU: 4.83-6.21; TLFL: 1.13-1.21; TLHW: 0.72-0.77; SCHW: 0.79-0.85; ATIB: 0.25-0.29; MTIB: 0.27-0.29; PBHW: 0.18-0.19; ATMT: 0.94-1.06. *Adult genitalia* ♂: MP: 0.26-0.27; PL: 0.36-0.37; AEL: 0.24-0.25; AEH: 0.07-0.08. MPHW: 0.33-0.35; PLHW: 0.46-0.48; MPPL: 0.72-0.75; AEPL: 0.65-0.69; MSLH: 1.19-1.3; AHS: 0.3-0.31; PLSH: 1.13-1.2. ♀: FP: 0.61-0.72; FSP: 0.4-0.44; RL: 0.19-0.23; OV: 0.13-0.14; EL: 0.24-0.28. FPHW: 0.8-0.87; FPSP: 1.53-1.64; FPCR: 3.09-3.35; OLSP: 0.3-0.33; FEOL: 1.97.

*Nymph*

*Colour:* 1st-2nd instars orange and cream, 5th instars bright green.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* Specimens 4; BL: 1.5-1.98; BW: 1-1.18; WL: 0.56-0.6; CPL: 0.41-0.56; CPW: 0.64-0.73; RW: 0.18-0.19; RL: 0.11-0.11; HW: 0.65-0.71; AL: 0.9-0.94; AL3: 0.2-0.23. WBL: 0.6-0.69; ALHW: 1.3-1.42; ALWL: 1.55-1.64; WLHW: 0.83-0.9; WCPL: 1.3-1.56; CPRW: 3.56-3.84.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.12-0.13); ocular seta simple, inconspicuous (max length 0.04-0.05); primary post-ocular seta distinctly or occasionally narrowly capitate (max length 0.07-0.08); secondary post-ocular seta simple (max length 0.06). Dorsal thoracic setae short simple (max length 0.03-0.05). Prominent wing pad setae max length 0.1-0.12; forewing and hindwing pads with simple and capitate setae; forewing pad with 9-11 prominent setae, marginal, 3-5 larger distinctly capitate and up to 6 smaller narrowly capitate or simple; hindwing pad with two prominent apical setae, distinctly capitate; proximal setae short simple; small simple or rod setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, short simple (max length 0.06), prominent caudal plate setae absent; sectasetae four pairs; marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.13-0.15); pleurite setae paired capitate and simple. Legs with capitate setae present (max length 0.12-0.13); capitate foreleg setae absent; capitate middle leg setae present on tibia only, one (distal); capitate hind leg setae present on femur and tibia or tibia only (femur seta either capitate or simple), on the tibia 3 (1 larger distal, 2 smaller proximal and occasionally up to 2 small rod setae).

*Host plant: Teline splendens.*

*Distribution:* Canary Islands: La Palma.

*Notes:* The host plant distribution is restricted, found only locally in laurisilva habitat, however, *A. fortunata* sp. nov. was relatively abundant in all locations sampled. This is one of two occurrences where a single psyllid species is associated with a single host species, and both psyllid and host plant are endemic to a single island. The other is *A. romeria* sp. nov. on the host plant *T. rosmarinifolia* on Gran Canaria.

*Biology:* Eggs were found sparsely scattered on both sides of young leaves but mostly on the glaucous underside, and also scattered on fruit, towards the apex. Small nymphs ($1^{st}$-$2^{nd}$ instars) were observed on leaf buds and fruit usually under the persistent calyx. Large nymphs ($3^{rd}$-$5^{th}$ instars) were found in flowers, inside the anther tube on the developing ovary.

*Etymology:* Named for the ancient reference to the Canary Islands - Fortunatae Insulae - as the 'Fortunate Islands' and also because this species occurs on one of the most attractive species of *Teline*, *T. splendens*.

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. LA PALMA: SE rd Santa Cruz to La Caldera, 28°42'45"N 17°46'W, c. 600 m, 20.v.1998 (BMNH). Paratypes 2♂, 3♀, 10 nymphs, as for holotype (BMNH). 2♂, 1♀, 5 nymphs, as for holotype (DZUL). 3♂, 2♀, 5 nymphs, as for holotype (NHMB).

*Other material examined:* CANARY ISLANDS. LA PALMA: 22♂, 14♀, 25 nymphs, SE rd Santa Cruz to La Caldera 28°42'30"N 17°46'W, 790 m, 16.vii.1997 (DP 78). 52♂, 54♀, 31 nymphs, as for holotype (DP 203).

### ***Arytinnis canariensis* sp. nov.** (7)

(Figs 9 & 1M)

*Adult*

*Colour:* Mid-green to yellow-green, head and genal cones with darkly pigmented setae; forewing clear, veins uniform mid-brown.

*Structure:* Surface forewing spinules present but reduced in all cells, or if absent, only from cell c+sc; distribution of spinules uniform, sparse: less than 40 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, and in cell $r_2$ but not to the margin. Antennae mid-length; genal cones very short, terminal setae darkly pigmented. Distal proboscis segment long. Paramere short, in lateral view with an apically thin neck above a medially positioned blade produced on the external side and directed anteriorly, sclerotized apex dorsally rounded with slight anterior and posterior projections, in dorsal view contiguous posteriorly with the inner margin straight edged; proctiger not inflated towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile more or less straight and horizontal, or slightly raised anteriorly. Female proctiger dorsal profile more or less straight from anus to apex; subgenital plate ventral profile shallowly curved; egg with stout lateral pedicel at the base.

*Adult measurements and ratios:* (3♂, 3♀) total length: ♂ 2.64-2.92, ♀ 2.88-3.4; forewing: ♂ length 2.18-2.3 width 0.91-0.98, ♀ length 2.35-2.68 width 1.03-1.13; pterostigma length ♂

0.65-0.74, ♀ 0.73-0.94; hindwing length ♂ 1.8-1.85, ♀ 1.9-2.18; head width: ♂ 0.72-0.77, ♀ 0.77-0.82; antennal length: 1.5-1.65; genal cone length: 0.06-0.08; distal proboscis segment length: 0.2-0.25. WLPT: 2.85-3.35; ALHW: 2-2.17; GCVL: 0.3-0.42; WLHW: 2.92-3.31; VLW: 0.41-0.48; WLW: 2.28-2.4; CUR: 1.75-2.08; MR: 0.47-0.58; RMCU: 4.31-5.33; TLFL: 1.31-1.39; TLHW: 0.94-1.01; SCHW: 0.81-0.92; ATIB: 0.18-0.21; MTIB: 0.22-0.26; PBHW: 0.28-0.32; ATMT: 0.78-0.89. *Adult genitalia* ♂: MP: 0.33-0.35; PL: 0.38-0.39; AEL: 0.27-0.28; AEH: 0.09-0.10. MPHW: 0.43-0.47; PLHW: 0.5-0.53; MPPL: 0.87-0.9; AEPL: 0.69-0.74; MSLH: 1.15-1.26; AHS: 0.34-0.35; PLSH: 1.18-1.23. ♀: FP: 0.73-0.81; FSP: 0.48-0.55; RL: 0.19-0.23; OV: 0.15; EL: 0.25-0.29. FPHW: 0.95-0.99; FPSP: 1.47-1.52; FPCR: 3.3-3.84; OLSP: 0.27-0.31; FEOL: 1.8.

*Nymph* Unknown

*Host plant: Teline canariensis.*

*Distribution:* Canary Islands: Tenerife.

*Notes:* Known from only one location despite extensive sampling of the relatively widespread host plant. This species was discovered in the laurisilva habitat of the Anaga peninsula, occurring sympatrically with A. *pileolata*, *A. menceyata* sp. nov. and *A. diluta*, and was the most common species in this particular location.

*Etymology:* Named for the Canary Islands and for the host plant, *Teline canariensis.*

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. TENERIFE: Anaga, E of Pico del Inglés, 28°32'15"N 16°16'30"W, c. 960 m, 25.iv.1998 (BMNH). Paratypes 1♂, 1♀, as for holotype (BMNH). 1♂, 1♀, as for holotype (DZUL). 1♂, 1♀, as for holotype (NHMB).

*Other material examined:* 11♂, 9♀, as for holotype (DP 179).

### ***Arytinnis menceyata*** **sp. nov.** (8)

(Figs 10 & 29C)

*Adult*

*Colour:* Mid-green to yellow-green; forewing clear, veins uniform light brown.

*Structure:* Surface forewing spinules present in all cells but reduced in cell c+sc, distribution of spinules non-uniform, dense: 60-100 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent from cell $r_2$. Antennae short; genal cones very short, terminal setae not darkly pigmented. Distal proboscis segment mid-length. Paramere long, in lateral view with an apically thin neck above a medially positioned blade produced on the external side and directed anteriorly, sclerotized apex dorsally flattened, with slight anterior and posterior projections, in dorsal view contiguous posteriorly with inner margin concave; proctiger not inflated towards the base; aedeagus distal segment with a well developed, curved hook, tip of aedeagus hook acute, not, or only slightly turning upwards; male subgenital plate dorsal profile raised anteriorly with a distinct step. Female proctiger dorsal profile more or less straight from anus to apex; subgenital plate ventral profile shallowly curved.

*Adult measurements and ratios:* (3♂, 3♀) total length: ♂ 2.6-2.84, ♀ 2.8-3; forewing: ♂ length 2.13-2.2 width 0.88-0.93, ♀ length 2.35-2.4 width 0.98-1; pterostigma length ♂ 0.69-0.72, ♀ 0.8-0.86; hindwing length ♂ 1.8-1.85, ♀ 2-2.05; head width: ♂ 0.71-0.72, ♀ 0.73-0.75; antennal length: 1.23-1.35; genal cone length: 0.08-0.1; distal proboscis segment length: 0.16-0.17. WLPT: 2.73-3.14; ALHW: 1.66-1.88; GCVL: 0.38-0.56; WLHW: 2.99-3.24; VLW: 0.41-0.5; WLW: 2.37-2.42; CUR: 1.57-1.81; MR: 0.42-0.49; RMCU: 5.92-7.05; TLFL: 1.18-1.26; TLHW: 0.77-0.82; SCHW: 0.8-0.91; ATIB: 0.24-0.26; MTIB: 0.24-0.25; PBHW: 0.21-0.23; ATMT: 1-1.07. *Adult genitalia* ♂: MP: 0.33-0.37; PL: 0.58-0.59; AEL: 0.36; AEH: 0.08-0.09. MPHW: 0.46-0.51; PLHW: 0.82; MPPL: 0.57-0.63; AEPL: 0.61-0.62; MSLH: 1.33-1.4; AHS: 0.24; PLSH: 1.4-1.49. ♀: FP: 0.97-1; FSP: 0.6-0.63; RL: 0.15-0.19; OV: 0.24; EL: 0.24-0.27. FPHW: 1.33-1.34; FPSP: 1.54-1.65; FPCR: 5.26-6.6; OLSP: 0.38-0.4; FEOL: 1.06.

*Nymph*

*Colour:* 1st-2nd instars cream and orange with black tergites, 5th instars pale grey-green.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 3) BL: 1.48-1.8; BW: 1.05-1.1; WL: 0.52-0.56; CPL: 0.5-0.53; CPW: 0.7-0.72; RW: 0.16-0.17; HW: 0.62-0.63; AL: 0.75-0.77; AL3: 0.17-0.19. WBL: 0.6-0.61; ALHW: 1.19-1.24; ALWL: 1.38-1.44; WLHW: 0.83-0.87; WCPL: 1.34-1.41; CPRW: 4.12-4.5.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.14-0.16); ocular seta simple, typically dark and conspicuous (max length 0.07-0.08); primary post-ocular seta distinctly capitate (max length 0.1-0.11); secondary post-ocular seta simple or narrowly capitate (max length 0.09). Dorsal thoracic setae short simple and long capitate (max length 0.09-0.1). Prominent wing pad setae max length 0.11-0.12; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae 17-23, distinctly capitate, surface and marginal (10 marginal, 6-12 surface, 1 proximal); hindwing pad prominent setae 6-11, distinctly capitate, surface and marginal (2 apical, 3-8 surface, 1 proximal); proximal setae distinctly or narrowly capitate; numerous small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on all tergites, short simple and long narrowly capitate (max length 0.1), prominent caudal plate setae present, ± 25, distinctly capitate; sectasetae four pairs; marginal abdominal setae (other than sectasetae) four pairs, distinctly capitate (max length 0.15-0.17); pleurite setae paired capitate and simple. Legs with capitate setae present (max length 0.09-0.11); capitate foreleg setae present on tibia only, one (proximal, occasionally simple); capitate middle leg setae present on tibia only, two (1 proximal, 1 distal); capitate hind leg setae present on tibia only (femur seta typically simple or very slightly capitate), 3-4 (2 proximal, 2 distal).

*Host plant: Teline stenopetala* ssp. *spachiana*, *T. canariensis.*
*Distribution:* Canary Islands: Tenerife.
*Notes:* Occurs sympatrically with *A. pileolata.* It is much more abundant than *A. pileolata* on the host plant, *Teline stenopetala* ssp. *spachiana*, in pine forest habitat; while only a few adults were found on the host plant, *Teline canariensis*, in laurisilva habitat.
*Biology:* Small nymphs (1st-2nd instars) were observed in leaf buds and were found inside folded young leaves.
*Etymology:* Named for the discovery of this species in the 'Menceyato de Güímar', one of several seats of power for the Guanche people of Tenerife.

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. TENERIFE: Güímar, Caldera de Pedro Gil, 28°20'30"N 16°28'W, 1775 m, ex *Teline stenopetala*, 26.iv.1998 (BMNH). Paratypes 2♂, 2♀, as for holotype (BMNH). 2♂, 1♀, as for holotype (DZUL). 2♂, 2♀, as for holotype (NHMB).

*Other material examined:* CANARY ISLANDS. TENERIFE: 1♂, 3♀, Anaga, E of Pico del Inglés, 28°32'15"N 16°16'30"W, c. 960 m, ex *Teline canariensis*, 25.iv.1998 (DP 179). 24♂, 24♀, 3 nymphs, as for holotype (DP 182).

### *Arytinnis ochrita* **sp. nov.** (9)

(Figs 11 & 27D)

*Adult*

*Colour:* Pale yellow to ochre; forewing clear, veins uniform light brown.

*Structure:* Surface forewing spinules present throughout all cells, or reduced in one or more cells; distribution of spinules non-uniform, medium density: 40-60 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent, or occasionally few present in cell $r_2$. Antennae short; genal cones short, terminal setae not darkly pigmented. Distal proboscis segment short. Paramere short, in lateral view slender, with an apically thin neck above a reduced medially positioned ridge on the external side, and directed anteriorly, sclerotized apex dorsally rounded, with a slight anterior projection, in dorsal view contiguous more or less along entire inner margin, which is straight edged; proctiger not inflated towards the base; aedeagus distal segment with a shallow hook, tip of aedeagus hook acute, not turning upwards; male subgenital plate dorsal profile more or less straight and horizontal, or slightly raised anteriorly. Female proctiger dorsal profile more or less straight from anus to apex; subgenital plate ventral profile shallowly curved.

*Adult measurements and ratios:* (4♂, 4♀) total length: ♂ 2.2-2.52, ♀ 2.4-2.68; forewing: ♂ length 1.7-1.98 width 0.68-0.79, ♀ length 1.88-2.08 width 0.79-0.84; pterostigma length ♂ 0.6-0.71, ♀ 0.64-0.72; hindwing length ♂ 1.45-1.63, ♀ 1.53-1.73; head width: ♂ 0.63-0.66, ♀ 0.64-0.67; antennal length: 1.08-1.27; genal cone length: 0.08-0.11; distal proboscis segment length: 0.11-0.13. WLPT: 2.72-2.97; ALHW: 1.71-1.92; GCVL: 0.42-0.61; WLHW: 2.94-3.1; VLW: 0.44-0.53; WLW: 2.38-2.54; CUR: 1.65-2.09; MR: 0.44-0.53; RMCU: 4.91-5.72; TLFL: 1.17-1.24; TLHW: 0.68-0.76; SCHW: 0.78-0.87; ATIB: 0.27-0.3; MTIB: 0.24-0.28; PBHW: 0.17-0.2; ATMT: 1-1.17. *Adult genitalia* ♂: MP: 0.25-0.28; PL: 0.36-0.38; AEL: 0.24-0.26; AEH: 0.07-0.08. MPHW: 0.4-0.43; PLHW: 0.57-0.58; MPPL: 0.69-0.74; AEPL: 0.66-0.7; MSLH: 1.35-1.5; AHS: 0.29-0.31; PLSH: 1.46-1.57. ♀: FP: 0.67-0.72; FSP: 0.45-0.5; RL:

0.17-0.18; OV: 0.15-0.17; EL: 0.27-0.3. FPHW: 1.01-1.07; FPSP: 1.42-1.49; FPCR: 3.94-4.12; OLSP: 0.31-0.34; FEOL: 1.81.

*Nymph*

*Colour:* 3rd instars orange-yellow, 4th-5th instars yellow-green with black tergites.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 1) BL: 1.6-1.6; BW: 0.9-0.9; WL: 0.45-0.45; CPL: 0.39-0.39; CPW: 0.56-0.56; RW: 0.18-0.18; RL: 0.11-0.11; HW: 0.58-0.58; AL: 0.75-0.75; AL3: 0.19-0.19. WBL: 0.56; ALHW: 1.29; ALWL: 1.67; WLHW: 0.78; WCPL: 1.44; CPRW: 3.11.

*5th instar chaetotaxy:* Head setae simple and occasionally narrowly capitate (max length at anterior margin 0.09); ocular seta inconspicuous; primary post-ocular seta distinctly capitate (max length 0.07); secondary post-ocular seta, indistinct, small simple. Dorsal thoracic setae short simple (max length 0.02-0.03). Prominent wing pad setae max length 0.09; forewing pad with one prominent, distinctly capitate, apical seta; hindwing pad with simple and capitate setae, one prominent, distinctly capitate, apical seta, paired with small simple seta; proximal setae indistinct, minute simple setae scattered on wing pad surfaces. Dorsal abdominal prominent pre-caudal setae absent (small simple only), prominent caudal plate setae absent; sectasetae three pairs (small capitate seta in 1st position); marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.09); pleurite setae paired capitate and simple or small rod. Legs with capitate setae present (max length 0.08); capitate foreleg setae absent; capitate middle leg setae absent, or more probably, one distal; capitate hind leg setae present on tibia only, one (distal).

*Host plant: Teline osyroides* ssp. *osyroides.*

*Distribution:* Canary Islands: Tenerife.

*Notes:* Known from only one location where the host plant, *Teline osyroides* ssp, *osyroides*, survives in a population of circa 1000-2000 individuals around the Masca valley region of northwestern Tenerife. This is the smallest and possibly rarest species in *Arytinnis* gen. nov.

*Etymology:* Named for the small size and ochre colouration using the familiar diminutive form in Spanish.

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. TENERIFE: blw Masca, Barranco de Masca, 28°18'N 16°50'30"W, c. 600 m, 4.iv.1998 (BMNH). Paratypes 1♂, 2♀, 1 nymph, as for holotype (BMNH). 1♂, 1♀, as for holotype (DZUL). 1♂, 2♀, as for holotype (NHMB).

*Other material examined:* CANARY ISLANDS. TENERIFE: 2♀, blw Masca, Barranco de Masca, 28°18'N 16°50'30"W, 600 m, 2.vii.1997 (DP 33). 6♂, 3♀, as for holotype (DP 153).

### ***Arytinnis occidentalis* sp. nov. (10)**

(Figs 12, 28B & 30E)

*Adult*

*Colour:* Bright green or yellow-green; forewing clear, veins uniform mid-brown.

*Structure:* Surface forewing spinules present in all cells, but reduced in one or more cells, or if absent only from cell c+sc, where there are typically few present; distribution of spinules uniform, density sparse: less than 40 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent, or occasionally few present in cell $r_2$. Antennae long; genal cones short, terminal setae not darkly pigmented. Distal proboscis segment mid-length. Paramere short, in lateral view slender and simple, with sides tapering towards the apex, a medial ridge is present on the inner surface, sclerotized apex dorsally rounded with small, anteriorly directed hook, in dorsal view contiguous anteriorly with inner margin concave; proctiger slightly inflated posteriorly towards the base; aedeagus distal segment with a well developed, curved hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile slightly raised anteriorly. Female proctiger dorsal profile without a post anal depression, but slightly concave with an upturned apex; subgenital plate ventral profile shallowly curved; egg with stout lateral pedicel at the base.

*Adult measurements and ratios:* (6♂, 6♀) total length: ♂ 2.92-3.48, ♀ 3.08-3.88; forewing: ♂ length 2.4-2.72 width 0.96-1.1, ♀ length 2.55-3 width 1.03-1.23; pterostigma length ♂ 0.75-0.87, ♀ 0.78-0.96; hindwing length ♂ 1.94-2.2, ♀ 2.08-2.45; head width: ♂ 0.76-0.82, ♀ 0.8-0.89; antennal length: 1.7-2.1; genal cone length: 0.1-0.13; distal proboscis segment length: 0.14-0.19. WLPT: 2.83-3.33; ALHW: 2.12-2.51; GCVL: 0.46-0.57; WLHW: 3.1-3.37; VLW: 0.45-0.5; WLW: 2.38-2.58; CUR: 1.63-2.04; MR: 0.42-0.55; RMCU: 4.67-7.29; TLFL: 1.16-1.22; TLHW: 0.78-0.88; SCHW: 0.78-0.9; ATIB: 0.23-0.3; MTIB: 0.25-0.3; PBHW: 0.18-0.22; ATMT: 0.89-1.06. *Adult genitalia* ♂: MP: 0.24-0.27; PL: 0.35-0.4; AEL: 0.28-0.31; AEH:

0.08-0.10. MPHW: 0.31-0.36; PLHW: 0.46-0.49; MPPL: 0.68-0.77; AEPL: 0.75-0.84; MSLH: 1.17-1.29; AHS: 0.3-0.32; PLSH: 1.06-1.18. ♀: FP: 0.69-0.79; FSP: 0.47-0.56; RL: 0.21-0.24; OV: 0.15-0.17; EL: 0.23-0.28. FPHW: 0.86-0.91; FPSP: 1.41-1.53; FPCR: 3.13-3.41; OLSP: 0.3-0.34; FEOL: 1.56.

*Nymph*

*Colour:* 1st-3rd instars cream and orange-red, 4th-5th instars pale grey-green, blue-green or yellow-green, with or without black tergites.

*Structure:* Antennal segments eight.

*5th instar measurements and ratios:* (specimens 5) BL: 1.55-1.93; BW: 0.98-1.15; WL: 0.56-0.64; CPL: 0.47-0.51; CPW: 0.67-0.74; RW: 0.19-0.21; RL: 0.11-0.13; HW: 0.64-0.73; AL: 1.1-1.15; AL3: 0.27-0.29. WBL: 0.6-0.65; ALHW: 1.58-1.75; ALWL: 1.8-1.96; WLHW: 0.84-0.92; WCPL: 1.41-1.49; CPRW: 3.33-3.68.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.13-0.17); ocular seta simple, typically dark and conspicuous (max length 0.08-0.09); primary and secondary post-ocular setae simple or narrowly capitate (max length 0.08-0.1). Dorsal thoracic setae long simple (max length 0.08-0.1). Prominent wing pad setae max length 0.11-0.14; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae two, marginal (1 apical, 1 proximal), apical seta distinctly capitate, proximal seta simple or narrowly capitate; hindwing pad with one prominent apical seta, distinctly capitate, paired with small simple seta, proximal seta short simple; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long simple (max length 0.12), prominent caudal plate setae typically absent or if present, two simple or narrowly capitate; sectasetae four pairs; marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.14-0.17); pleurite setae paired capitate and simple. Legs with simple setae only (max length 0.04).

*Host plant: Teline stenopetala* ssp. *sericea*, ssp. *stenopetala* and ssp. *microphylla.*

*Distribution:* Canary Islands: La Palma and El Hierro.

*Notes:* Occurs on the two most westerly islands, sympatrically with *A. modica* on the host plant, *Teline stenopetala.* In May, it is less common than *A. modica* on the two host subspecies restricted to the humid laurisilva habitat, ssp. *stenopetala* and ssp. *microphylla*; but during the same period it is abundant on ssp. *sericea* in dry pine forest habitat, from which A. *modica* was absent. In July, *A. occidentalis* was found to be more common than A. *modica* on both ssp. *stenopetala* and ssp. *microphylla*, suggesting (as with sympatric species on the host plant *Teline microphylla*) asynchronous development and habitat preference.

*Biology:* Eggs were found singly scattered on the clayx, in small clusters under floral bracts or at the base of developing fruit under the persistent calyx. Small nymphs (1st-3rd instars) were observed on the corolla and base of the developing fruit, however, nymphs were more typically found on leaf buds and petioles. Larger nymphs (3rd-5th instars) and occasionally eggs were also found on the underside of mature leaves.

*Etymology:* Named for the geographic distribution of this species in the most westerly islands, La Palma and El Hierro.

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. LA PALMA: rd to La Cumbrecita, 3-4 km from El Paso rd, 28°41'15"N 17°51'30"W, 1250 m, 16.v.1998 (BMNH). Paratypes 1♂, 3♀, 6 nymphs, as for holotype (BMNH). 2♂, 1♀, 5 nymphs, as for holotype (DZUL). 1♂, 2♀, 5 nymphs, as for holotype (NHMB). EL HIERRO: 2♂, 2♀, 5 nymphs, El Golfo, rd to Frontera, 27°44'N 18°01'30"W, 1100 m, 22.v.1998 (BMNH). 1♀, as for previous (DZUL). 2♂, 1♀, as for previous (NHMB).

*Other material examined:* CANARY ISLANDS. LA PALMA: 6♂, 4♀, 2 nymphs, SE rd Santa Cruz to La Caldera, 28°43'N 17°46'W, 930 m, 15.vii.1997 (DP 73). 41♂, 38♀, 6 nymphs, as for holotype (DP 190). 2♂, 3♀, Los Tilos, Barranco del Agua, 28°47'30"N 17°47'45"W, c. 500 m, 17.v.1998 (DP 192). 2♂, 3♀, rd Barlovento to Garafía, c. 3 km E of Roque Faro, 28°48'15"N 17°52'30"W, c. 900 m, 19.v.1998 (DP 200). EL HIERRO: 8♂, 5♀, El Golfo, rd to Frontera, 27°43'30"N 18°1'30"W, 1070 m, 11.vii.1997 (DP 61). 3♂, 1♀, btw Mirador de la Peña and Mirador Jinama, 27°47'30"N 17°58'W, 960 m, 12.vii.1997 (DP 63.1). 2♂, 2♀, as for previous except, 900 m (DP 63.2). 59♂, 50♀, El Golfo, rd to Frontera, 27°44'N 18°01'30"W, 1100 m, 22.v.1998 (DP 212). 19♂, 7♀, nr Arbol Santo, 27°47'30"N 17°56'30"W, c. 1000 m, 23.v.1998 (DP 214).

### *Arytinnis gomerae* **sp. nov.** (11)

(Figs 13 & 28A)

*Adult*

*Colour:* Bright green to mid-green; forewing clear, veins uniform light brown.

*Structure:* Surface forewing spinules present in all cells, but reduced in one or more cells; distribution of spinules uniform, sparse: less than 40 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent, or occasionally few present in cell $r_2$. Antennae short; genal cones short, terminal setae not darkly pigmented. Distal proboscis segment short. Paramere short, in lateral view S-shaped with sides tapering towards the apex, sclerotized apex dorsally flattened, with slight anterior projection, in dorsal view contiguous anteriorly with inner margin concave; proctiger slightly inflated posteriorly towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile slightly raised anteriorly. Female proctiger dorsal profile without a post anal depression, but slightly concave with an upturned apex; subgenital plate ventral profile shallowly curved.

*Adult measurements and ratios:* (4♂, 4♀) total length: ♂ 2.32-2.76, ♀ 2.64-2.92; forewing: ♂ length 1.91-2.03 width 0.82-0.85, ♀ length 2.18-2.29 width 0.92-0.96; pterostigma length ♂ 0.6-0.75, ♀ 0.67-0.8; hindwing length ♂ 1.59-1.65, ♀ 1.8-1.86; head width: ♂ 0.69-0.73, ♀ 0.72-0.75; antennal length: 1.38-1.5; genal cone length: 0.09-0.12; distal proboscis segment length: 0.13-0.14. WLPT: 2.82-3.25; ALHW: 1.84-2.05; GCVL: 0.43-0.57; WLHW: 2.77-3.18; VLW: 0.43-0.51; WLW: 2.25-2.45; CUR: 1.58-1.77; MR: 0.43-0.52; RMCU: 5.13-6.75; TLFL: 1.13-1.22; TLHW: 0.71-0.76; SCHW: 0.77-0.89; ATIB: 0.25-0.29; MTIB: 0.25-0.28; PBHW: 0.17-0.2; ATMT: 1-1.07. *Adult genitalia* ♂: MP: 0.25-0.28; PL: 0.3; AEL: 0.26-0.27; AEH: 0.07-0.08. MPHW: 0.36-0.38; PLHW: 0.41-0.43; MPPL: 0.83-0.87; AEPL: 0.87-0.9; MSLH: 1.17-1.3; AHS: 0.28-0.29; PLSH: 1-1.11. ♀: FP: 0.62-0.67; FSP: 0.4-0.44; RL: 0.18-0.22; OV: 0.14-0.15; EL: 0.23-0.27. FPHW: 0.86-0.89; FPSP: 1.48-1.55; FPCR: 2.95-3.1; OLSP: 0.3-0.35; FEOL: 1.75.

*Nymph*

*Colour:* 1$^{st}$-2$^{nd}$ instars cream with red abdomens.

*Structure:* Antennal segments eight.

*5th instar measurements and ratios:* (specimens 4) BL: 1.4-1.75; BW: 0.88-1.03; WL: 0.48-0.51; CPL: 0.4-0.43; CPW: 0.6-0.64; RW: 0.17-0.19; RL: 0.1-0.11; HW: 0.59-0.64; AL: 0.82-0.88; AL3: 0.19-0.21. WBL: 0.53-0.66; ALHW: 1.28-1.49; ALWL: 1.63-1.8; WLHW: 0.75-0.83; WCPL:

1.43-1.55; CPRW: 3.26-3.76.

*5th instar chaetotaxy:* Head setae simple and occasionally narrowly capitate (max length at anterior margin 0.11-0.13); ocular seta simple, dark, conspicuous (max length 0.06-0.08); primary and secondary post-ocular setae distinctly capitate (max length 0.07-0.09). Dorsal thoracic setae short simple and long capitate (max length 0.05-0.09). Prominent wing pad setae max length 0.1-0.12; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae 2-6, distinctly capitate, marginal (1 apical, 1 proximal, 0-4 smaller marginal); hindwing pad prominent setae two, distinctly capitate, marginal (1 apical, 1 proximal), apical seta paired with small simple seta; proximal setae distinctly capitate; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long simple and capitate (max length 0.07), prominent caudal plate setae usually absent or if present, 1-4 distinctly capitate; sectasetae three or four pairs (1st may be reduced or simple-lanceolate); marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.12-0.14); pleurite setae paired capitate and simple. Legs with simple setae only, small rod seta sometimes present proximally on hind tibia (max length 0.02-0.03).

*Host plant: Teline stenopetala* ssp. *microphylla* and ssp. *pauciovulata.*

*Distribution:* Canary Islands: La Gomera.

*Notes:* Occurs sympatrically with *A. hupalupa* sp. nov. However, it is rare in collections made at higher altitudes in the laurisilva forest where *A. hupalupa* is abundant, and it is the only species found on the host in lower altitude habitats of dry sabinar or juniper scrub.

*Biology:* Eggs were found scattered on the surfaces of fruit and occasionally on leaf buds. 1st-2nd instar nymphs were found on fruit and 2nd-5th instars on leaf buds. Many nymphs were found on vegetative plants where they were attended by ants which were observed removing the excreted frass from the nymphs' abdomens.

*Etymology:* Named for the endemic status of this species on the island of La Gomera.

*Comment: A. gomerae* and *A. occidentalis* may represent an example of allopatric speciation as they occur on the same host plant but on different islands. Adult morphology and the unique feature of eight antennal segments in the 5th instar nymph supports a close relationship between these taxa.

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. LA GOMERA: blw Roque Cano, 28°11'N 17°15'30"W, 300-400 m, 26.v.1998 (BMNH). Paratypes 2♂, 2♀, 5 nymphs, as for holotype (BMNH). 1♂, 2♀, 5 nymphs, as for holotype (DZUL). 2♂, 2♀, 5 nymphs, as for holotype (NHMB).

*Other material examined:* CANARY ISLANDS. LA GOMERA: 3♂, 2♀, nr El Cedro, 28°7'30"N 17°14'W, 950 m, 14.vii.1997 (DP 71). 1♀, rd Hermigua to Monte del Cedro, 28°07'16"N 17°12'30"W, 700-1000 m, 25.v.1998 (DP 219). 21♂, 16♀, 26 nymphs, as for holotype (DP 221). 36♂, 32♀, Ermita de las Nieves, 28°06'30"N 17°11'W, c. 1000 m, 30.vii.2000 (DP 344). 25♂, 41♀, 10 nymphs, Roque Agando, 28°06'N 17°12'W, c. 1000 m, 31.vii.2000 (DP 345).

### ***Arytinnis hupalupa* sp. nov.** (12)

(Figs 14, 15C–D & 27A)

*Adult*

*Colour:* Grey-green or mid-green to yellow-green; forewing clear, veins uniform mid-brown.

*Structure:* Surface forewing spinules present in all cells, but reduced in one or more cells; distribution of spinules uniform, sparse: less than 40 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent, or occasionally few present in cell $r_2$. Antennae short; genal cones very short, terminal setae not darkly pigmented. Distal proboscis segment short. Paramere long, in lateral view slender, more or less parallel sided, with an apically thin neck above a ridge produced on the external side and directed anteriorly, sclerotized apex small, not hooked, but with a small anterior projection and displaced to the posterior of the top of the paramere, in dorsal view contiguous anteriorly, inner margin straight edged; proctiger not, or only sightly inflated posteriorly towards the base; aedeagus distal segment with a well developed, curved hook, tip of aedeagus hook blunt and turning upwards; male subgenital plate dorsal profile raised anteriorly. Female proctiger dorsal profile more or less straight from anus to apex, or with slight post anal depression; subgenital plate ventral profile shallowly curved.

*Adult measurements and ratios:* (3♂, 3♀) total length: ♂ 2.6-2.84, ♀ 2.76-3.16; forewing: ♂ length 2.1-2.21 width 0.86-0.87, ♀ length 2.35-2.38 width 0.91-0.97; pterostigma length ♂ 0.75-0.8, ♀ 0.73-0.8; hindwing length ♂ 1.73-1.8, ♀ 1.93-1.95; head width: ♂ 0.66-0.72, ♀ 0.72-0.74; antennal length: 1.31-1.47; genal cone length: 0.05-0.1; distal proboscis segment length: 0.12-0.14. WLPT: 2.75-3.26; ALHW: 1.77-2.16; GCVL: 0.31-0.5; WLHW: 2.92-3.33; VLW: 0.41-0.48; WLW: 2.41-2.59; CUR: 1.61-1.93; MR: 0.45-0.49; RMCU: 5.32-6.5; TLFL: 1.13-1.2; TLHW: 0.71-0.81; SCHW: 0.82-0.89; ATIB: 0.25-0.3; MTIB: 0.25-0.29; PBHW: 0.18-0.19; ATMT: 0.94-1.14. *Adult genitalia* ♂: MP: 0.32-0.35; PL: 0.56; AEL: 0.32-0.33; AEH: 0.08-0.09. MPHW: 0.44-0.53; PLHW: 0.78-0.85; MPPL: 0.57-0.63; AEPL: 0.57-0.59; MSLH: 1.31-1.47; AHS: 0.27-0.28; PLSH: 1.6-1.75. ♀: FP: 0.89-0.93; FSP: 0.56; RL: 0.17-0.2; OV: 0.2-0.21; EL: 0.18-0.26. FPHW: 1.24-1.26; FPSP: 1.59-1.66; FPCR: 4.65-5.24; OLSP: 0.36; FEOL: 1.08.

*Nymph*

*Colour:* 1st-2nd instars cream and orange, some with black tergites, 3rd-5th instars pale yellow or green with black tergites.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 5) BL: 1.45-1.9; BW: 0.93-1.13; WL: 0.54-0.61; CPL: 0.46-0.5; CPW: 0.62-0.66; RW: 0.16-0.17; RL: 0.1-0.1; HW: 0.59-0.62; AL: 0.75-0.82; AL3: 0.16-0.18. WBL: 0.59-0.64; ALHW: 1.15-1.33; ALWL: 1.3-1.41; WLHW: 0.86-1; WCPL: 1.3-1.43; CPRW: 3.65-4.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.1-0.14); ocular seta simple, inconspicuous (max length 0.02-0.04); primary post-ocular seta narrowly or distinctly capitate (max length 0.07); secondary post-ocular seta simple (max length 0.03-0.05). Dorsal thoracic setae short simple (max length 0.02-0.04). Prominent wing pad setae max length 0.07-0.08; forewing pad with simple and capitate or simple setae only, with one prominent apical seta simple or narrowly capitate; hindwing pad with simple and capitate setae, with one prominent apical seta distinctly or narrowly capitate, paired with small simple seta; proximal setae indistinct from small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae absent or if present on anterior tergites, short simple (max length 0.03-0.04), prominent caudal plate setae absent (numerous small simple); sectasetae four pairs; marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (4th small simple, or occasionally small capitate) (max length 0.09-0.11); pleurite setae typically paired simple, or longer simple with short, slightly capitate setae. Legs with capitate setae present (max length 0.04-0.08); capitate foreleg setae absent; capitate middle leg setae absent or if present on the tibia only, one (distal, or occasionally one small capitate seta present proximally); capitate hind leg setae present (but often narrow) on femur and tibia, or tibia only (small seta on femur capitate or simple), on the tibia 1-2 (1 larger distally, and typically 1 smaller proximally).

*Host plant: Teline stenopetala* ssp. *microphylla* and ssp. *pauciovulata.*
*Distribution:* Canary Islands: La Gomera.
*Notes:* It is occasionally sympatric with *A. gomerae* but is much more abundant in the humid laurisilva habitat than this species.
*Biology:* Small nymphs ($1^{st}$-$2^{nd}$ instars) were observed on leaf buds and developing fruit.
*Comment:* The shape of the male paramere is intermediate between *A. dividens* and *A. modica* (see Fig. 15). Otherwise *A. hupalupa* is very similar but considerably smaller than these species.
*Etymology:* The name is that of the pre-hispanic king of La Gomera.

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. LA GOMERA: rd Hermigua to Monte del Cedro, 28°07'16"N 17°12'30"W, 700-1000 m, 25.v.1998 (BMNH). Paratypes 3♂, 3♀, 8 nymphs, as for holotype (BMNH). 2♂, 3♀, 4 nymphs, as for holotype (DZUL). 3♂, 2♀, 5 nymphs, as for holotype (NHMB).
*Other material examined:* CANARY ISLANDS. LA GOMERA: 2♂, 4♀, nr El Cedro, 28°7'30"N 17°14'W, 950 m, 14.vii.1997 (DP 71). 72♂, 67♀, 30 nymphs, as for holotype (DP 219). 1♀, Ermita de las Nieves, 28°06'30"N 17°11'W, c. 1000 m, 30.vii.2000 (DP 344). 1♀, Roque Agando, 28°06'N 17°12'W, c. 1000 m, 31.vii.2000 (DP 345).

## *Arytinnis modica* (Loginova) **comb. nov.**

(Figs 15A–B & 27B)

*Arytainilla modica* Loginova, 1976: 23

*Adult Colour:* Mid-green to yellow-green or grey-green; forewing clear, veins uniform light or mid-brown.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 1st-2nd instars orange or cream, some with black tergites, 4th-5th instars pale green or yellow.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 4) BL: 1.6-1.75; BW: 1-1.03; WL: 0.57-0.65; CPL: 0.47-0.55; CPW: 0.61-0.7; RW: 0.17-0.18; RL: 0.1-0.1; HW: 0.61-0.69; AL: 0.88-1.08; AL3: 0.2-0.26. WBL: 0.57-0.63; ALHW: 1.44-1.59; ALWL: 1.52-1.72; WLHW: 0.84-0.97; WCPL:
1.27-1.47; CPRW: 3.59-4.12.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.12-0.17); ocular seta simple, inconspicuous (max length 0.03-0.05); primary post-ocular seta simple or narrowly capitate (max length 0.09); secondary post-ocular seta simple (max length 0.07). Dorsal thoracic setae short simple (max length 0.03-0.06). Prominent wing pad setae max length 0.07-0.09; forewing and hindwing pads with simple and capitate setae, each pad with one prominent apical seta, distinctly or narrowly capitate; hindwing pad apical seta paired with smaller simple seta; proximal setae if present simple, sometimes indistinct from small simple surface setae. Dorsal abdominal prominent pre-caudal setae absent, or present on anterior tergites, short simple (max length 0.04-0.05), prominent caudal plate setae absent (numerous small simple); sectasetae four pairs; marginal abdominal setae (other than sectasetae) three or four pairs (4th sometimes reduced or simple), distinctly capitate (max length 0.1-0.14); pleurite setae paired capitate and simple. Legs with capitate setae present (max length 0.06-0.1); capitate foreleg setae absent; capitate middle leg setae present on tibia only, two (1 proximal, 1 larger distal); capitate hind leg setae present on femur and tibia, on the tibia 2-3 (1-2 proximal, 1 larger distal).

*Host plant: Teline stenopetala* ssp. *stenopetala* and ssp. *microphylla*, *Chamaecytisus proliferus*.

*Distribution:* Canary Islands: La Palma and El Hierro.

*Notes:* This is the only species with bi-generic host preference in *Arytinnis* gen. nov. It occurs on the two most westerly islands where it replaces the closely related *A. dividens* on the host plant *Chamaecytisus proliferus*. It occurs sympatrically with *A. occidentalis* on *Teline stenopetala* ssp. *stenopetala* and ssp. *microphylla*, and sympatrically with *Arytaina devia* on *Chamaecytisus proliferus*.

*Biology:* Clusters of eggs and small nymphs ($1^{st}$-$2^{nd}$ instars) were found under floral bracts and petiolar bracts. Small nymphs were also observed on leaf buds and on fruit.

*Comment:* The colonization of host plants in two unrelated genera (i.e. from different host groups within the Genisteae) appears to originate from a recent host switch in the progenitor of *A. modica* (possibly *A. hupalupa* on La Gomera) from *Chamaecytisus* to *Teline*, and the subsequent retention of preference to both hosts with the colonization of El Hierro or La Palma. This evolutionary scenario and the genetic variation in these host races is currently being investigated in a molecular anaylsis.

*Material examined:* CANARY ISLANDS. LA PALMA: 3♂, 2♀, 1 nymph, SE rd Santa Cruz to La Caldera, 28°43'N 17°46'W, 930 m, ex *Teline stenopetala*, 15.vii.1997 (DP 73). 1♀, SE rd Santa Cruz to La Caldera, abv Fuente de Olén, 28°44'N 17°49'W, 1850 m, ex *Chamaecytisus proliferus*, 16.vii.1997 (DP 79). 1♂, 2♀, 1 nymph, E of tunnel under Cumbre Nueva, 28°39'N 17°49'W, 1020 m, ex *Teline stenopetala*, 17.vii.1997 (DP 82). 5♂, 1♀, rd to La Cumbrecita, c. 3-5 km N of El Paso rd, 28°39'30"N 17°50'45"W, c. 900 m, ex *Chamaecytisus proliferus*, 16.v.1998 (DP 189). 13♂, 16♀, 4 nymphs, Los Tilos, Barranco del Agua, 28°47'30"N 17°47'45"W, c. 500 m, ex *Teline stenopetala*, 17.v.1998 (DP 192). 30♂, 30♀, 12 nymphs, rd Barlovento to Garafía, c. 3 km E of Roque Faro, 28°48'15"N 17°52'30"W, c. 900 m, ex *Teline stenopetala*, 19.v.1998 (DP 200). 49♂, 26♀, 9 nymphs, NW rd from Llano Negro to La Caldera, 28°48'N 17°55'30"W, c. 1050 m, ex *Chamaecytisus proliferus*, 19.v.1998 (DP 201). 1♀, 6 nymphs, SE rd Santa Cruz to La Caldera, 28°43'30"N 17°48'30"W, c. 1700 m, ex *Chamaecytisus proliferus*, 20.v.1998 (DP 205). EL HIERRO: 1♂, rd Ermita de los Reyes to El Pinar, 27°43'30"N 18°1'30"W, 960 m, ex *Chamaecytisus proliferus*, 10.vii.1997 (DP 59). 3♀, El Golfo, rd to Frontera, 27°43'30"N 18°1'30"W, 1070 m, ex *Teline stenopetala*, 11.vii.1997 (DP 61). 1♀, btw Mirador de la Peña and Mirador Jinama, 27°47'30"N 17°58'W, 960 m, ex

*Teline stenopetala*, 12.vii.1997 (DP 63.1). 4♂, 1♀, as for previous except, 900 m (DP 63.2). 6 nymphs, as for previous except, 27°48'N 17°58'W, 860 m, ex *Chamaecytisus proliferus* (DP 64). 89♂, 56♀, 3 km W of San Andres, 27°45'30"N 17°58'30"W, 1250 m, ex *Chamaecytisus proliferus*, 22.v.1998 (DP 210). 6♂, 9♀, 1 nymph, El Golfo rim, nr Mirador del Golfo, 27°45'30"N 17°59'W, c. 1300 m, ex *Chamaecytisus proliferus*, 22.v.1998 (DP 211). 33♂, 28♀, 11 nymphs, El Golfo, rd to Frontera, 27°44'N 18°01'30"W, 1100 m, ex *Teline stenopetala*, 22.v.1998 (DP 212). 9♂, 9♀, nr Arbol Santo, 27°47'30"N 17°56'30"W, c. 1000 m, ex *Teline stenopetala*, 23.v.1998 (DP 214). 3♂, 1♀, El Golfo, blw Mirador de Jinama, 27°45'15"N 17°59'W, 1100 m, ex *Chamaecytisus proliferus*, 23.v.1998 (DP 215). 22♂, 27♀, rd N of Mirador de Jinama, 27°48'15"N 17°58'30"W, c. 900 m, ex *Chamaecytisus proliferus*, 23.v.1998 (DP 216).

### *Arytinnis dividens* (Loginova) **comb. nov.**

(Figs 15E–F & 27C)

*Arytainilla dividens* Loginova, 1976: 21

*Adult Colour:* Grey-green or mid-green to yellow-green, sometimes with parameres noticeable blue, mature specimens may be darker; forewing clear, veins uniform mid-brown.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 1st-3rd instars cream or orange, with black tergites, 4th-5th instars pale green or blue-grey, with or without black tergites.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 9) BL: 1.73-2.25; BW: 1.08-1.33; WL: 0.53-0.65; CPL: 0.49-0.59; CPW: 0.7-0.85; RW: 0.17-0.2; RL: 0.1-0.11; HW: 0.7-0.94; AL: 1-1.24; AL3: 0.23-0.31. WBL: 0.57-0.62; ALHW: 1.29-1.66; ALWL: 1.69-2.07; WLHW: 0.74-0.91; WCPL: 1.32-1.52; CPRW: 3.5-5.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.15-0.17); ocular seta simple, more or less inconspicuous (max length 0.04-0.07); primary and secondary post-ocular setae simple, narrowly or distinctly capitate (max length 0.09-0.12). Dorsal thoracic setae short and long simple, occasionally narrowly capitate (max length 0.06-0.08). Prominent wing pad setae max length 0.1-0.12; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae two, marginal (1 apical, 1 proximal, with numerous shorter simple setae on the outer margin) apical seta narrowly or distinctly capitate; hindwing pad prominent setae two, marginal (1 apical, 1 proximal) apical seta distinctly capitate, paired with small simple seta; proximal setae simple, narrowly or distinctly capitate; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, occasionally few on posterior tergites, long simple and capitate (max length 0.11), prominent caudal plate setae present, two or four, distinctly capitate; sectasetae three or four pairs (1st pair may be reduced or simple); marginal abdominal setae (other than sectasetae) three or four pairs (4th frequently reduced or simple), distinctly capitate (max length 0.13-0.16); pleurite setae paired capitate and simple. Legs with capitate setae present (max length 0.09-0.12); capitate foreleg setae absent (occasionally one proximally on the tibia); capitate middle leg setae present on femur and tibia, or tibia only, on the tibia 2-4 (2 larger and 2 small); capitate hind leg setae present on femur and tibia or tibia only, on the tibia 5-7.

*Host plant: Chamaecytisus proliferus*, on all three recognized subspecies (Acebes Ginovés, Arco Aguilar & Wildpret de la Torre, 1991).

*Distribution:* Canary Islands: Gran Canaria, Tenerife, and La Gomera.

*Notes:* Occurs sympatrically, on the two central islands and western island of La Gomera, with *Arytaina devia.* However, it is generally more common earlier in the year, and in more humid habitats, than the latter species. The host plant is a widespread and variable species, three subspecies and four varieties are recognized (Acebes Ginovés et al., 1991), but there is no apparent preference or specificity to intraspecific host taxa.

*Biology:* Eggs were observed in small clusters of three to five on the inner surface, typically along the midrib, of folded new leaves, and often towards the tips of the more mature leaves in developing leaf buds. In the latter instance, 1st instar nymphs on hatching migrate down into the bud to feed on the younger leaves (Fig. 31B). Eggs were also found singly, scattered on the surface of fruit. Small nymphs (1st-2nd instars) were observed on leaf buds, and (1st-5th instars) were observed at the base of fruit, beneath the persistent calyx.

*Comment:* One ♂ was recorded from La Palma by Loginova (1976) but this distribution has not been corroborated during this study.

*Material examined:* (ex *Chamaecytisus proliferus* unless otherwise stated) CANARY ISLANDS. GRAN CANARIA: 1♀, NE of Tejeda, rd to Cruz de Tejeda, 28°0'N 15°36'30"W, 1300 m, 5.vii.1997 (DP 38). 16♂, 13♀, c. 2-3 km S of Moya on rd to San Bartolomé de Fontanales, 28°5'45"N 15°35'15"W, 680 m, 15.iv.1998 (DP 157). 2♂, 5♀, c. 5 km S of Moya on rd to San Bartolomé de Fontanales, 28°5'N 15°35'30"W, c. 800 m, ex *Teline stenopetala*, 15.iv.1998 (DP 158). 14♂, 15♀, 42 nymphs, rd San Bartolomé de Tirajana to Fataga, 27°54'30"N 15°34'30"W, 920 m, 16.iv.1998 (DP 161). 7♂, 10♀, base of Risco Blanco, 27°56'N 15°33'30"W, 1150 m, ex *Teline rosmarinifolia*, 18.iv.1998 (DP 165). 10♂, 7♀, 17 nymphs, Barranco de Mogán, abv town of Mogán, 27°54'30"N 15°42'30"W, c. 500 m, 18.iv.1998 (DP 167). 61♂, 6♀, 28 nymphs, valley NE of Tejeda, btw Cruz de Tejeda and Tejeda, 27°59'30"N 15°35'W, 1300 m, 19.iv.1998 (DP 168). 29♂, 12♀, 2 nymphs, rd btw Moya and St Bartolome de Fontanales, 28°5'45"N 15°35'15"W, c. 700 m, 19.iv.1998 (DP 169). 4♂, 2♀, Gran Canaria, 1 km N of Cruz de Tejeda, 28°30'N 15°35'30"W, c. 1500 m, ex *Teline microphylla*, 20.iv.1998 (DP 172). 27♂, 22♀, 3 nymphs, just N of Cruz de Tejeda, rd Cruz de Tejeda to Valleseco, 28°30'N 15°35'30"W, c. 1500 m, 20.iv.1998 (DP 174). 47♂, 31♀, 21 nymphs, rd Cruz de Tejeda to San Mateo 28°00'N 15°34'30"W, c. 1220 m, 20.iv.1998 (DP 176). TENERIFE: 5♂, 2♀, 3 nymphs, rd to Parque Nacional del Teide, Miradores de la Cumbre, 28°23'30"N 16°26'W, 1800 m, 22.vi.1997 (DP 6). 3♂, 2♀, 3 nymphs, rd Buenavista to Santiago del Teide, N of turning to Los Carrizales, 28°19'N 16°50'30"W, 900 m, 28.vi.1997 (DP 19). 41♂, 37♀, 81 nymphs, as for previous (DP 20). 1♂, 2 nymphs, just N of Aguamansa, 28°21'30"N 16°30'W, 950 m, 29.vi.1997 (DP 23.2). 8♂, 11♀, mirador NW of Santiago del Teide, Barranco Seco, 28°18'30"N 16°49'30"W, 1000 m, 2.vii.1997 (DP 32). 3♂, 11♀, 29 nymphs, rd El Teide to Arafo 28°23'N 16°25'W, 1250 m, 9.vii.1997 (DP 53). 1♂, Teno, 7 km S of Buenavista on rd to Santiago del Teide, 28°20'N 16°51'W, c. 800 m, ex *Teline canariensis*, 4.iv.1998 (DP 152). 4♂, 5♀, 6 nymphs, blw Mirador de la Cumbre Norte, 28°22'30"N 16°27'30"W, c. 1850 m, 10.iv.1998 (DP 155). 6♂, 13♀, Barranco del Rey, NW of Arona, 28°06'30"N 16°41'30"W, c. 700 m, 10.v.1998 (DP 185). 5♂, 5♀, as for previous except, ex *Teline osyroides* (DP 186). 10♂, 9♀, 5 nymphs, N of Vilaflor, 28°10'30"N 16°39'W, c. 1900 m, 10.v.1998 (DP 188). LA GOMERA: 65♂, 53♀, 43 nymphs, rd Arure to Las Hayas, 28°7'30"N 17°18'30"W, 900 m, 13.vii.1997 (DP 68). 3♂, 2♀, as for previous except, ex *Spartocytisus filipes* (DP 69). 4♂, 4♀, as for previous except, ex *Retama monosperma* (DP 70). 36♂, 23♀, 24 nymphs, La Laguna

Grande, Garajonay Park, 28°06'30"N 17°16'W, c. 1300 m, 26.v.1998 (DP 224). 22♂, 30♀, blw Roque de Agando, 28°06'N 17°12'30"W, 900-1000 m, 27.v.1998 (DP 227). 8♂, 6♀, as for previous except, ex *Teline stenopetala* (DP 228).

### *Arytinnis umbonata* (Loginova) **comb. nov.**

(Fig. 25A)

*Arytainilla umbonata* Loginova, 1976: 30

*Adult Colour:* Grey-green to yellow-green with pale yellow or orange thorax; forewing cells with small brown patches apically, veins uniform mid- or dark brown.
*Adult Description:* Loginova (1976).

*Nymph*
*Colour:* 1st-3rd instars cream and orange, 4th-5th instars green or yellow with pink abdomens, with or without black tergites.
*Structure:* Antennal segments seven.
*5th instar measurements and ratios:* (specimens 6) BL: 1.45-1.75; BW: 0.95-1.1; WL: 0.56-0.6; CPL: 0.48-0.51; CPW: 0.65-0.7; RW: 0.16-0.19; RL: 0.11-0.12; HW: 0.61-0.68; AL: 0.95-1.07; AL3: 0.23-0.26. WBL: 0.62-0.66; ALHW: 1.42-1.72; ALWL: 1.58-1.88; WLHW: 0.84-0.94; WCPL: 1.3-1.46; CPRW: 3.53-4.06.
*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.12-0.14); ocular seta simple, inconspicuous, occasionally longer and darker (max length 0.04-0.05); primary post-ocular seta distinctly capitate (max length 0.08-0.1); secondary post-ocular seta narrowly or distinctly capitate (max length 0.05-0.09). Dorsal thoracic setae short simple and long capitate (max length 0.05-0.09). Prominent wing pad setae max length 0.1-0.14; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae 8-10, distinctly capitate, marginal (7-9 outer margin, 1 proximal); hindwing pad prominent setae distinctly capitate, 1-2 marginal (1 apical, 1 proximal), apical seta paired with small simple seta; proximal setae simple, narrowly or distinctly capitate; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long simple and capitate (max length 0.07-0.11), prominent caudal plate setae absent; sectasetae three pairs (occasionally reduced 4th pair present); marginal abdominal setae (other than sectasetae) three

pairs, distinctly capitate (max length 0.13-0.16); pleurite setae paired capitate and simple. Legs with simple setae only (max length 0.04-0.05).

*Host plant: Genista tenera.*

*Distribution:* Madeira.

*Notes:* Occurs throughout the host plant range from dry lowland to laurisilva habitat.

*Biology:* Eggs were found scattered on petioles and on the rim of floral bracts. Nymphs (1st-5th instars) observed on the clayx and corolla, and inside the flower on the stylar column.

*Comment:* Although the form of the adult genitalia is distinct, the 5th instar nymph is extremely similar to *A. incuba*, the only other Madeiran species, and to *A. hakani* from the Mediterranean.

*Material examined:* MADEIRA: 20♂, 20♀, 13 nymphs, Ribeiro Frio, Levada do Furado, W of Balcões, 900 m, 30.vi.1998 (DP 268). 12♂, 15♀, 7 nymphs, just N of Ribeira Brava, rd to Serra de Água, c. 100 m, 1.vii.1998 (DP 270). 15♂, 17♀, 3 nymphs, Pico do Gato, c. 1500 m, 2.vii.1998 (DP 272). 26♂, 23♀, 17 nymphs, Encumeada, path to Pico Ruivo, c. 1050 m, 3.vii.1998 (DP 273.1).

### *Arytinnis incuba* (Loginova) **comb. nov.**

(Fig. 25C)

*Arytainilla incuba* Loginova, 1976: 28

*Adult Colour:* mid-green to yellow-green, paler orange on the thorax, with some mature specimens darker; forewing clear, veins uniform mid- or dark brown.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 1st-3rd instars cream and orange, 4th-5th instars yellow-green or blue-green, with or without black tergites.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 5) BL: 1.6-1.95; BW: 1.03-1.15; WL: 0.6-0.61; CPL: 0.51-0.53; CPW: 0.68-0.8; RW: 0.19-0.21; RL: 0.11-0.13; HW: 0.68-0.73; AL: 1.18-1.22;

AL3: 0.26-0.29. WBL: 0.57-0.64; ALHW: 1.64-1.75; ALWL: 1.97-2; WLHW: 0.83-0.88; WCPL: 1.31-1.51; CPRW: 3.24-3.89.

*5th instar chaetotaxy:* Head setae simple and narrowly capitate (mostly simple anteriorly and capitate posteriorly) (max length at anterior margin 0.14-0.17); ocular seta simple, dark, conspicuous (max length 0.07-0.09); primary and secondary post-ocular setae distinctly capitate (max length 0.11-0.14). Dorsal thoracic setae long capitate with short or minute simple (max length 0.13-0.14). Prominent wing pad setae max length 0.12-0.14; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae 8-10, distinctly capitate, marginal (7-9 outer margin, 1 proximal); hindwing pad prominent setae two, distinctly capitate, marginal (1 apical, 1 proximal), apical seta paired with small simple seta; proximal setae distinctly capitate (or rarely simple); small simple or occasionally small capitate or rod setae on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long capitate (max length 0.11-0.15), prominent caudal plate setae typically absent or if present, two, distinctly capitate; sectasetae three pairs; marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.14-0.17); pleurite setae paired capitate and simple. Legs with simple setae only (max length 0.04-0.07).

*Host plant: Teline maderensis.*

*Distribution:* Madeira.

*Notes:* Occurs throughout the host plant range and on both subspecies recognized (Arco Aguilar 1983).

*Biology:* Eggs were found singly along the sericeous edges and midribs of mature leaves, or on petioles and stems. Clusters of eggs were also found under petiolar bracts and leaf bud bracts. Small nymphs ($1^{st}$-$2^{nd}$ instars) were also observed in these locations, and on the fruit. Many nymphs were collected from vegetative plants.

*Comment:* This species is extremely similar to the Mediterranean species *A. hakani*, and a record from Sicily (Conci et al. 1993) may be a misidentification of the latter species.

*Material examined:* MADEIRA: 25♂, 20♀, 20 nymphs, Ribeiro Frio, Levada do Furado, W of Balcões, 900 m, 30.vi.1998 (DP 267). 31♂, 15♀, 6 nymphs, Porto do Moniz, Levada da Central da Ribeira da Janela, 400 m, 1.vii.1998 (DP 271). 17♂, 11♀, 16 nymphs, W of

Encumeada, rd to Porto do Moniz, 1100 m, 3.vii.1998 (DP 274). 16♂, 9♀, 6 nymphs, Encumeada, Levada do Norte, 1000 m, 3.vii.1998 (DP 276).

### *Arytinnis hakani* (Loginova) **comb. nov.**

*Arytainilla hakani* Loginova, 1972: 21

*Adult Colour:* Bright green to mid-green or yellow-green; forewing clear, veins uniform light brown.

*Adult and Nymphal Descriptions:* Loginova (adult, 1972), Rapisarda (5th instar nymph, 1987).

*Nymph*al *Colour:* 4th-5th instars bright green or paler blue-green.

*Host plant: Teline monspessulana.*

*Distribution:* Continental: Mediterranean.

*Notes:* This species has the most widespread distribution of the three continental members of *Arytinnis* gen. nov. It is recorded from the western Mediterranean as far east as Algeria (Burckhardt, 1989a) and southern Italy (Conci et al., 1993); the host plant distribution, however, extends further east to Syria (Gibbs & Dingwall, 1972).

*Comment:* Both adult and 5th instar nymph are extremely similar to the Madeiran species, *A. incuba*, and these two species may represent disjunct host races which have undergone recent diversification.

*Material examined:* MOROCCO: 28♂, 16♀, 3 nymphs, Western Rif Mountains, rd Bab-Taza to Chefchaouen, W of Bab-Taza, 35°10'N 5°20'W, c. 1000 m, 29.iii.1998 (DP 146). 24♂, 23♀, Western Rif Mountains, btw Ketama and Chefchaouen, E of Bab Berret, 34°56'N 4°50'W, c. 1400 m, 22.vi.1998 (DP 256). 1♂, 7♀, as for previous except, ex *Adenocarpus decorticans* (DP 254). 4♂, 4♀, as for previous except, ex *Cytisus villosus* (DP 255). SPAIN: 12♂, 15♀, 8 nymphs, Andalusia, Parque Natural de los Alcornocales, W of Los Barrios to Alcalá de los Gazules rd, 36°15'N 5°37'W, c. 300 m, 25.xii.1997 (DP 118). 38♂, 23♀, 21 nymphs, Andalusia, c. 10 km S of Ubrique, rd to Puerto de Galis, 36°35'N 5°30'W, c. 600-700 m, 24.iii.1998 (DP 143). 2♂, as for previous except, c. 15 km S of Ubrique, 36°33'N 5°30'W, ex *Teline linifolia* (DP 144).

### *Arytinnis cognata* (Loginova) **comb. nov.**

(Fig. 25B)

*Arytainilla cognata* Loginova, 1972: 22

*Adult Colour:* Grey-green to yellow-green, mature specimens darker with abdominal intersegments yellow-green; forewing clear, veins uniform mid-brown.

*Adult Descriptions:* Loginova (1972, 1977).

*Nymph*

*Colour:* 5th instars bright green to blue-green or yellow-orange, with black tergites.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 7) BL: 1.45-1.98; BW: 0.95-1.2; WL: 0.54-0.64; CPL: 0.45-0.51; CPW: 0.62-0.74; RW: 0.17-0.19; RL: 0.1-0.11; HW: 0.62-0.74; AL: 0.91-0.99; AL3: 0.21-0.24. WBL: 0.59-0.66; ALHW: 1.28-1.6; ALWL: 1.44-1.83; WLHW: 0.83-0.92; WCPL: 1.35-1.55; CPRW: 3.44-4.06.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.11-0.13); ocular seta simple, inconspicuous (max length 0.04-0.06); primary post-ocular seta simple or narrowly capitate (max length 0.06-0.08); secondary post-ocular seta simple (max length 0.06-0.09). Dorsal thoracic setae short simple (max length 0.05-0.09). Prominent wing pad setae max length 0.08-0.11; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae 4-7, simple or distinctly capitate, marginal (1 apical seta capitate or simple, remainder simple); hindwing pad prominent setae two, simple or distinctly capitate, marginal (1 apical, 1 proximal), apical seta paired with small simple seta; proximal setae simple (sometimes reduced); small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long simple (max length 0.07-0.11), prominent caudal plate setae absent or if present, 4-7 simple (sometimes with one centrally and posteriorly placed); sectasetae four pairs; marginal abdominal setae (other than sectasetae) three or four pairs (4th frequently reduced), simple, narrowly or distinctly capitate (max length 0.1-0.14); pleurite setae paired simple (distal sometimes slightly capitate). Legs with simple setae only (max length 0.06).

*Host plant: Genista florida* var. *maroccana.*

*Distribution:* Continental: Morocco.

*Notes:* Occurs in the High Atlas mountains on a variety of *Genista florida* endemic to this region. The variety of *Genista florida* occurring in Portugal was found to host a *Livilla* species.

*Material examined:* MOROCCO: 44♂, 40♀, 10 nymphs, High Atlas, just north of Tizi n' Test pass, 30°50'N 8°30'W, c. 2080 m, 19.vi.1998 (DP 238). 3♂, 5♀, 3 nymphs, High Atlas, rd to Oukaïmeden, Vallée de l'Ourika, 31°10'N 7°45'W, c. 2000 m, 1.v.1999 (DP 324). 22♂, 29♀, 9n, High Atlas, c. 2 km blw Oukaïmeden, Vallée de l'Ourika, 31°08'N 7°40'W, c. 2600 m, 1.v.1999 (DP 325.1). 6♂, 3♀, High Atlas, just S of Tizi n' Test, 30°50'N 8°28'W, c. 2000 m, 2.v.1999 (DP 329).

## ***Arytinnis berber* sp. nov.** (13)

(Figs 16 & 25D)

*Adult*

*Colour:* Bright green or grey-green; forewing clear, veins uniform light brown.

*Structure:* Surface forewing spinules present in all cells, but reduced in one or more cells; distribution of spinules uniform, sparse: less than 40 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent, or occasionally few present in cell $r_2$. Antennae short; genal cones very short, terminal setae not darkly pigmented. Distal proboscis segment mid-length. Paramere short, in lateral view with an apically thin neck above a medially positioned blade produced on the external side and directed anteriorly, sclerotized apex dorsally rounded with slight anterior projection, in dorsal view contiguous anteriorly with inner margin straight edged; proctiger slightly inflated posteriorly towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile more or less straight and horizontal, or slightly raised anteriorly. Female proctiger dorsal profile more or less straight from anus to apex; subgenital plate ventral profile shallowly curved.

*Adult measurements and ratios:* (3♂, 2♀) total length: ♂ 2.52-2.6, ♀ 2.84; forewing: ♂ length 1.95-2.16 width 0.85-0.92, ♀ length 2.24-2.3 width 0.94-0.97; pterostigma length ♂ 0.53-0.62, ♀ 0.61-0.62; hindwing length ♂ 1.63-1.78, ♀ 1.8-1.88; head width: ♂ 0.66-0.7, ♀ 0.69-0.72; antennal length: 1.22-1.31; genal cone length: 0.06-0.1; distal proboscis segment length: 0.14-0.16. WLPT: 3.48-3.77; ALHW: 1.77-1.98; GCVL: 0.33-0.53; WLHW: 2.95-3.25; VLW: 0.45-0.5; WLW: 2.29-2.38; CUR: 1.47-1.76; MR: 0.48-0.6; RMCU: 5.12-6.48; TLFL: 1.14-

1.18; TLHW: 0.71-0.81; SCHW: 0.83-0.88; ATIB: 0.24-0.3; MTIB: 0.27-0.31; PBHW: 0.2-0.23; ATMT: 0.88-1.07. *Adult genitalia* ♂: MP: 0.22-0.23; PL: 0.33-0.34; AEL: 0.23-0.24; AEH: 0.07-0.08. MPHW: 0.33; PLHW: 0.49-0.5; MPPL: 0.67-0.68; AEPL: 0.68-0.73; MSLH: 1.19-1.36; AHS: 0.31-0.33; PLSH: 1.27-1.36. ♀: FP: 0.67-0.69; FSP: 0.43-0.44; RL: 0.17-0.19; OV: 0.15-0.16; EL: 0.27-0.3. FPHW: 0.96-0.97; FPSP: 1.52-1.6; FPCR: 3.63-3.94; OLSP: 0.34-0.37; FEOL: 1.84.

*Nymph*

*Colour:* 5th instars orange-yellow.

*Structure:* Antennal segments seven.

*5th instar measurements and ratios:* (specimens 4) BL: 1.25-1.48; BW: 0.83-0.95; WL: 0.47-0.5; CPL: 0.4-0.41; CPW: 0.57-0.62; RW: 0.16-0.17; RL: 0.1-0.11; HW: 0.54-0.57; AL: 0.77-0.8; AL3: 0.17-0.19. WBL: 0.64-0.71; ALHW: 1.38-1.48; ALWL: 1.6-1.68; WLHW: 0.86-0.89; WCPL: 1.39-1.53; CPRW: 3.41-3.88.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.11-0.13) ocular seta simple or narrowly capitate, dark, conspicuous (max length 0.05-0.07); primary and secondary post-ocular setae distinctly capitate (max length 0.05-0.1). Dorsal thoracic setae short simple and long, stout capitate (max length 0.07-0.1). Prominent wing pad setae max length 0.09-0.1; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae 3-7, distinctly capitate, marginal, proximal seta distinctly capitate or rarely indistinct; hindwing pad prominent setae 2-3, simple or distinctly capitate, marginal (1-2 apical, 1 proximal), proximal seta simple or distinctly capitate, apical seta paired with small capitate or small simple seta; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long capitate (max length 0.07-0.1), prominent caudal plate setae absent; sectasetae four pairs; marginal abdominal setae (other than sectasetae) three pairs, distinctly capitate (max length 0.11-0.12); pleurite setae paired simple or paired capitate and simple. Legs with simple setae only (max length 0.04).

*Host plant: Genista segonnei.*

*Distribution:* Continental: Morocco.

*Notes:* Occurs in the Anti-Atlas mountains. The host plant is locally common in isolated populations, but this species was not common in either of the locations sampled.

*Etymology:* Named for the Berber culture of the Anti-Atlas region.

*Type material:* Holotype ♂ (slide mounted), MOROCCO: Anti-Atlas, SE slopes of Jbel Lekst, blw Tagudicht Aitsmaon, 29°42'N 9°05'W, c. 1500 m, 3.v.1999 (BMNH). Paratypes 2♂, 1♀, 4 nymphs, as for holotype (BMNH). 1♂, 1♀, 4 nymphs, as for holotype (NHMB).

*Other material examined:* MOROCCO: 2♂, Anti-Atlas, just W of Col du Kerdous, 29°30'N 9°15'W, 1050 m, 23.iii.1999 (DP 302). 5♂, 1♀, as for holoptype (DP 332).

## Genus *Arytaina* Foerster

*Arytaina* Foerster, 1848: 69; Loginova, 1977: 66; Hodkinson and Hollis, 1987: 10. Type species: *Psylla spartii* Hartig, 1841 (= *Psylla genistae* Latreille, 1804), designated by Oshanin, 1912: 128

*Amblyrhina* Löw, 1879: 599; Loginova, 1977: 66. Type species: *Psylla torifrons* Flor, by monotypy; synonymized by Hodkinson and Hollis, 1987

*Psyllopa* Crawford, 1911: 628. Type species: Psyllopa magna Crawford, by original designation; synonymized by Crawford, 1914: 122

*Comment:* Two of the Canary Island species originally described in *Arytaina* (*A. devia* and *A. nubivaga*) by Loginova (1976) were transferred to *Arytainilla* by Hodkinson and Hollis (1987) based on forewing shape and the peculiar forms of the male paramere. However, these species are now returned to *Arytaina* based on the following characters: absence of a costal break or pterostigma, shape of the male proctiger and the female genitalia, and reduced number of sectasetae in 5th instar nymphs. The two larger species, *A. nubivaga* and *A. vittata* sp. nov. are most similar to *A. genistae* in general body and wing colouration, in the shape of the hindwing costal margin and the aedeagus hook, and in the relative segment lengths of the hind leg. In the same respects *A. devia* is more similar to *A. adenocarpi*. Any similarity in the paramere shape between *A. devia* and *A. nubivaga* may therefore be due to convergence.

Key to adults of the three Canary Island species of *Arytaina*.

1 Forewing short and broad, length less than 2.5 x width, widest in the apical third with a broadly rounded apex, veins and apical cells ($cu_1$, $m_1$ and $m_2$) with small dark patches at the margin of the wing; hindwing costal margin slightly concave, not darkly pigmented; antennae shorter than 1.9 mm; head width less than 0.9 mm; genal cones short (< 0.14 mm); distal proboscis segment longer, greater than 0.15 x head width; male paramere apex with a single anteriorly and interiorly directed hook; aedeagus distal segment with a more flattened, shallow hook; female proctiger equal to, or shorter than 0.9 mm; ovipositor valvulae dorsalis shorter than 0.2 mm; hind leg tibia longer than the femur, tibia length ≥ 0.75 x head width, apical and metatarsi relatively short, each about 0.25-0.35 x tibia length (on *Chamaecytisus*; Gran Canaria, Tenerife, La Gomera, La Palma) ........ *devia* Loginova

— Forewing long and narrow, length greater than 2.5 x width, margins more or less parallel, apex more acutely rounded, veins and apical cells without small dark patches at the wing margin, but with extensive brown patches in the apical half of the wing; hindwing costal margin markedly concave and darkly pigmented; antennae long (> 1.9 mm); head width greater than 1 mm; genal cones long (> 0.14 mm); distal proboscis segment short, less than 0.15 x head width; male paramere apex with an interiorly directed double claw; aedeagus distal segment with a well developed, curved hook; female proctiger longer than 0.9 mm; ovipositor valvulae dorsalis longer than 0.2 mm; hind leg tibia shorter than the femur, tibia length about 0.5 x head width, apical and metatarsi long, each about 0.5 x tibia length (Figs 1H & 1J) ........................................................................................................................ 2

2 Abdomen without dark, longitudinal dorsal stripe; male paramere shorter (< 0.33 mm) and broader, length less than 0.9 x subgenital plate height, and less than 0.32 x head width, interior medial ridge weakly developed and supporting relatively long setae (visible clearly only in posterior view) (on *Spartocytisus supranubius*; Tenerife) (Fig. 18B) ...................... ........................................................................................................... *nubivaga* Loginova

— Abdomen with dark, longitudinal dorsal stripe (more distinct in females); male paramere longer (> 0.33 mm) and narrower, length greater than 0.9 x subgenital plate height, and greater than 0.32 x head width, interior medial ridge extended inwards, such that inner margins of the ridge are virtually straight and nearly contiguous when parameres close, supporting short setae (visible clearly only in posterior view) (on *Spartocytisus*; La Gomera, La Palma, El Hierro) (Figs 17 & 18A) ........................................ ***vittata* sp. nov.**

Key to 5th instars nymphs of the three Canary Island species of *Arytaina.*

1 Antennae shorter than 1.1 mm; forewing pad shorter than 0.63 mm; primary and secondary post-ocular setae distinctly capitate; dorsal thoracic setae short simple and long capitate; forewing and hindwing pads with capitate setae only, each with five or more prominent capitate setae present on both wing pad surface and margins, proximal setae distinctly capitate; marginal abdominal pleurite setae paired capitate and simple; marginal abdominal capitate setae extremely long (max length 0.27-0.35); foreleg tibia with capitate setae present (on *Chamaecytisus*; Gran Canaria, Tenerife, La Gomera, La Palma) (Fig. 24B) .... ........................................ *devia* Loginova

— Antennae longer than 1.1 mm; forewing pad longer than 0.63 mm; primary and secondary post-ocular setae simple or narrowly capitate; dorsal thoracic setae short simple; forewing and hindwing pads with simple and capitate setae, typically each with one or two prominent capitate (occasionally simple) setae present on the wing pad margin, proximal setae small simple or indistinct; marginal abdominal pleurite setae paired simple; marginal abdominal capitate setae shorter (max length 0.14-0.22); foreleg tibia without capitate setae ........................................ 2

2 Abdominal sectasetae two pairs (in 3rd and 4th positions); forewing pad length (> 0.7 mm) greater than 0.87 x head width; circumanal ring width less than 0.25 x caudal plate width; ocular, thoracic and prominent leg setae longer; dorsal caudal plate with six prominent setae; middle and hind tibiae each with more than two capitate setae (on *Spartocytisus supranubius*; Tenerife) (Fig. 24D) ........................ *nubivaga* Loginova

— Abdominal sectasetae one pair (in 3rd position, apical pair small simple or rod setae); forewing pad length (< 0.7 mm) less than 0.87 x head width; circumanal ring width more than 0.25 x caudal plate width; ocular, thoracic and prominent leg setae shorter; dorsal caudal plate with two prominent setae; middle and hind tibiae each with one capitate seta distally (on *Spartocytisus*; La Gomera, La Palma, El Hierro) (Fig. 24C) ... ***vittata* sp. nov.**

### *Arytaina devia* Loginova **comb. rev.**

(Fig. 24B)

*Arytaina devia* Loginova, 1976: 14

*Arytainilla devia* (Loginova) Hodkinson & Hollis, 1987: 11

*Adult Colour:* Generally brown or dark grey, though females exhibit more colour variation than males and are frequently lighter coloured (recently emerged adults may be green). The abdominal intersegment colour is yellow-green, and the thorax is paler chestnut with dark bands. Forewing membrane without distinct pattern but apical cells have faint brown patches and small darker patches at the margin of cells $cu_1$, $m_1$ and $m_2$, forewing veins mid-brown with dark spots at the apices where the veins intersect the wing margin.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 5th pale grey-green or blue green with black tergites; terminal antennal segment darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Antennal segments seven. Tergites extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad long, broadly expanded apically, usually with a distinct medial groove and long petiole. Circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 7) BL: 1.6-1.9; BW: 1.08-1.23; WL: 0.57-0.6; CPL: 0.48-0.54; CPW: 0.7-0.76; RW: 0.16-0.17; RL: 0.1-0.11; HW: 0.66-0.77; AL: 0.93-1.02; AL3: 0.22-0.27. WBL: 0.59-0.68; ALHW: 1.32-1.44; ALWL: 1.58-1.76; WLHW: 0.8-0.91; WCPL: 1.37-1.58; CPRW: 4-4.59.

*5th instar chaetotaxy:* Head setae simple and narrowly capitate (max length at anterior margin 0.16-0.2); antennal setae simple; ocular seta simple, dark, conspicuous (max length 0.08-0.11); primary post-ocular seta distinctly capitate (max length 0.1-0.11); secondary post-ocular seta distinctly capitate (max length 0.13-0.18). Dorsal thoracic setae short simple and long capitate (max length 0.13-0.17). Prominent wing pad setae max length 0.14-0.17; forewing and hindwing pads with capitate and simple setae; forewing pad prominent setae 9-14, distinctly capitate, surface and marginal (typically 2-4 surface setae with the remainder marginal); hindwing pad prominent setae 5-6, distinctly capitate, surface and marginal; proximal setae distinctly capitate; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, long capitate (max length 0.14-0.17), prominent caudal plate setae present, four (Gran Canaria) - six (Tenerife, La Gomera and La Palma), distinctly capitate; sectasetae absent (Tenerife, La Gomera and La Palma) or if present, one pair (Gran Canaria); marginal abdominal setae (other than sectasetae) four pairs, distinctly capitate (max length 0.27-0.35); pleurite setae paired capitate and simple. Legs with capitate setae present (max length 0.14-0.18); capitate foreleg setae present on femur and tibia, on the tibia two (1 proximal, 1 distal); capitate middle leg setae present on femur and tibia, on the tibia 4-5; capitate hind leg setae present on femur and tibia, on the tibia 5-6.

*Host plant: Chamaecytisus proliferus*, on all three recognized subspecies (Acebes Ginovés et al., 1991).

*Distribution:* Canary Islands: Gran Canaria, Tenerife, La Gomera and La Palma.

*Notes:* Occurs on the two central and two of the western Canary Islands (apparently absent from El Hierro). It is sympatric with *A. dividens* on Gran Canaria, Tenerife and La Gomera and with *A. modica* on La Palma. No specificity or preference for intraspecific host taxa was detected.

*Biology:* Only a few large nymphs (5th instars) were found during April-May, when all of the smaller nymphs (1st-3rd instars) examined were those of the sympatric species *A. dividens* or *A. modica*. However, it was the only species collected from one location in late July when numerous 1st-5th instars were found on leaf buds, and eggs were found singly on the outer surface of young leaves. This suggests asynchronous development, as with other sympatric species, with *A. devia* developing later than either *A. dividens* or *A. modica*.

*Comment:* Loginova (1976) designated specimens from Gran Canaria and La Palma as ssp. *insularis*, citing the more slender and elongate paramere. I have retained this rank and since no type was published, I have designated the specimen - La Palma, El Paso, 26.v.1947, 1♂ - as a lectotype. 5th instar nymphs from Gran Canaria can be separated from those of the other three islands by the presence of sectasetae, suggesting a basal position for the Gran Canarian population in the colonization of the Canary Islands. Evidence that the reduction in number of sectasetae in this genus is derived is taken from a comparison with the ontogeny of this character in nymphs of the type species, *A. genistae*. The 5th instars of *A. genistae* have one or two pairs of sectasetae that may be either reduced or simple, however, 3rd instars have four pairs of well developed sectasetae and 4th instars have three pairs. Similarly, *A. adenocarpi* 4th instars have four pairs of sectasetae but 5th instars have only two pairs.

This study did not survey the eastern Canary Islands (Fuerteventura and Lanzarote), where there are no recorded host plants in the Genisteae, but one female was recorded from Fuerteventura by Loginova (1976).

*Material examined:* (ex *Chamaecytisus proliferus* unless otherwise stated) CANARY ISLANDS. GRAN CANARIA: 1♂, NE of Tejeda, rd to Cruz de Tejeda, 28°0'N 15°36'30"W, 1300 m, 5.vii.1997 (DP 38). 22♂, 23♀, 3 nymphs, rd San Bartolomé de Tirajana to Fataga, 27°54'30"N 15°34'30"W, 920 m, 16.iv.1998 (DP 161). 2♂, 3♀, base of Risco Blanco, 27°56'N 15°33'30"W, 1150 m, ex *Teline rosmarinifolia*, 18.iv.1998 (DP 165). 17♂, 19♀, 9 nymphs, Barranco de Mogán, abv town of Mogán, 27°54'30"N 15°42'30"W, c. 500 m, 18.iv.1998 (DP 167). 5♂, 2♀, 1 nymph, valley NE of Tejeda, btw Cruz de Tejeda and Tejeda, 27°59'30"N 15°35'W, 1300 m, 19.iv.1998 (DP 168). 4♂, 3♀, rd btw Moya and St Bartolome de Fontanales, 28°5'45"N 15°35'15"W, c. 700 m, 19.iv.1998 (DP 169). 1♂, 1♀, just N of Cruz de Tejeda, rd Cruz de Tejeda to Valleseco, 28°30'N 15°35'30"W, c. 1500 m, 20.iv.1998 (DP 174). 1♀, Gran Canaria, rd Cruz de Tejeda to San Mateo 28°00'N 15°34'30"W, c. 1220 m, 20.iv.1998 (DP 176). TENERIFE: 4♂, 5♀, rd to Parque Nacional del Teide, Miradores de la Cumbre, 28°23'30"N 16°26'W, 1800 m, 22.vi.1997 (DP 6). 1♀, just N of Aguamansa, 28°21'30"N 16°30'W, 950 m, 29.vi.1997 (DP 23.2). 1♀, mirador N of Santiago del Teide, Barranco Seco, 28°18'30"N 16°49'30"W, 1000 m, ex *Retama monosperma*, 2.vii.1997 (DP 31). 13♂, 12♀, mirador NW of Santiago del Teide, Barranco Seco, 28°18'30"N 16°49'30"W, 1000 m, 2.vii.1997 (DP 32). 14♂, 16♀, 1 nymph, rd El Teide to Arafo 28°23'N 16°25'W, 1250 m, 9.vii.1997 (DP 53). 1♂, 5 nymphs, blw Mirador de la Cumbre Norte, 28°22'30"N 16°27'30"W, c. 1850 m, 10.iv.1998 (DP 155). 3♂, 2♀, Barranco del Rey, NW of Arona, 28°06'30"N 16°41'30"W, c. 700 m, 10.v.1998 (DP 185). 1♀, as for previous except, ex *Teline osyroides* (DP 186). 5♂, 6♀, 1 nymph, abv Vilaflor, 28°10'30"N 16°39'W, c. 1900 m, 10.v.1998 (DP 188). 1♂, 2♀, 20 nymphs, rd Granadilla de Abona to Vilaflor, 28°08'N 16°37'W, < 1000 m, 28.vii.2000 (DP 342). LA GOMERA: 26♂, 30♀, 5 nymphs, rd Arure to Las Hayas, 28°7'30"N 17°18'30"W, 900 m, 13.vii.1997 (DP 68). 1♂, as for previous except, ex *Spartocytisus filipes* (DP 69). 4♂, 4♀, as for previous except, ex *Retama monosperma* (DP 70). LA PALMA: 2♂, 13 nymphs, SE rd

Santa Cruz to La Caldera, abv Fuente de Olén, 28°44'N 17°49'W, 1850 m, 16.vii.1997 (DP 79). 22♂, 26♀, rd to La Cumbrecita, c. 3-5 km N of El Paso rd, 28°39'30"N 17°50'45"W, c. 900 m, 16.v.1998 (DP 189). 10♂, 8♀, NW rd from Llano Negro to La Caldera, 28°48'N 17°55'30"W, c. 1050 m, 19.v.1998 (DP 201).

### *Arytaina nubivaga* Loginova **comb. rev.**

(Fig. 24D)

*Arytaina nubivaga* Loginova, 1976: 12

*Arytainilla nubivaga* (Loginova) Hodkinson & Hollis, 1987: 11

*Adult Colour:* Males generally dark brown, grey or chestnut, females with abdominal intersegment colour yellow-grey or green, thorax orange-red with grey bands. Genal cones, legs and proximal antennal segments yellow-grey, terminal antennal segments darker brown. Forewing cells with brown patches, veins uniform mid-brown; hindwing costal and claval margins darkly pigmented.

*Adult Description:* Loginova (1976).

*Nymph*

*Colour:* 4th-5th instars cream with black tergites. Sclerites, wing pads, legs and terminal antennal segments darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Antennal segments seven. Tergite structure extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad long, broadly expanded apically, usually with a distinct medial groove and long petiole. Circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 5) BL: 1.73-1.88; BW: 1.18-1.28; WL: 0.71-0.74; CPL: 0.6-0.63; CPW: 0.84-0.87; RW: 0.18-0.19; RL: 0.12-0.13; HW: 0.77-0.81; AL: 1.18-1.23; AL3: 0.29-0.3. WBL: 0.66-0.7; ALHW: 1.49-1.53; ALWL: 1.59-1.68; WLHW: 0.89-0.94; WCPL: 1.35-1.42; CPRW: 4.47-4.83.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.11-0.14); antennal setae simple; ocular seta simple, conspicuous (max length 0.06-0.07); primary post-ocular seta simple or narrowly capitate (max length 0.1-0.11); secondary post-ocular seta simple (max length 0.05-0.09). Dorsal thoracic setae short simple (max length 0.06-0.08). Prominent wing pad setae max length 0.14-0.15; forewing and hindwing pads with simple and capitate setae; forewing pad prominent setae 2-5, simple or narrowly capitate, surface and marginal; hindwing pad prominent setae surface and marginal with two apical, distinctly or narrowly capitate; proximal setae absent (indistinct from simple surface setae in 5th instars, more prominent in 3rd and 4th instars); numerous small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, short simple with long simple and capitate (frequently narrow, max length 0.12), prominent caudal plate setae present, six, narrowly or distinctly capitate; sectasetae two pairs; marginal abdominal setae (other than sectasetae) four pairs, narrowly or distinctly capitate (4th pair sometimes simple) (max length 0.17); pleurite setae paired simple. Legs with capitate setae present (max length 0.14-0.15); capitate foreleg setae present on femur only; capitate middle and hind leg setae present on femur and tibia, on the tibia three (1 large distal, 2 smaller proximal).

*Host plant: Spartocytisus supranubius.*

*Distribution:* Canary Islands: Tenerife.

*Notes:* Known only from Tenerife where the host plant is abundant in the sub-alpine zone. *A. nubivaga* is relatively common on Tenerife but is apparently absent from La Palma, the other high altitude island where the host occurs.

*Biology:* Eggs were found under the small floral bracts at the base of the clayx.

*Comment:* The host plant on La Palma is threatened by over grazing (less than 500 individuals recorded in 1988 (Palomares Martínez, 1997)). The dramatic reduction of *S. supranubius*, once considered to be widespread on La Palma, raises the possibility that *A. nubivaga* may have once been present but subsequently become extinct on this island with the demise of the host plant.

*Material examined:* CANARY ISLANDS. TENERIFE: 2♂, 6 nymphs, 12 km NE of Parque Nacional del Teide, 28°20'30"N 16°29'W, 2080 m, 23.vi.1997 (DP 7). 1♂, 2♀, 30 nymphs, 28°18'30"N 16°33'W, 2-3 km NE of Parque Nacional del Teide, 2070 m, 23.vi.1997 (DP 10). 17♂, 18♀, c. 2 km N of Observatory, Las Cañadas, 29°19'N 16°29'30"W, c. 2200 m, 5.iv.1998 (DP 154).

## *Arytaina vittata* sp. nov. (14)

(Figs 17, 24C, 1H & 1J)

*Adult*

*Colour:* Males generally darker than females, head and thorax brown or paler chesnut, thorax with grey bands, genal cones pale grey or blue-grey, legs grey to yellow-grey, abdomen bright green to yellow-green with distinctive dark brown to black dorsal stripe, male abdomens sometimes darker grey or chestnut. Apical forewing cells with brown patches, but these are less extensive than in *A. nubivaga*, forewing veins uniform mid- or dark brown; hindwing costal and claval margins darkly pigmented.

*Structure:* Forewing with margins more or less parallel, apex somewhat acute; costal break and pterostigma absent; the middle, but not the apex, of vein Rs is curved towards the costal wing margin; surface forewing spinules absent from cells c+sc and $r_1$, but usually present, though often reduced, in other cells, distribution uniform, sparse: less than 40 per $0.1mm^2$; apical spines in wing cells $cu_1$, $m_1$, $m_2$, and few in cell $r_2$; hindwing costal margin markedly concave. Antennae long, with ten segments; head not, or only weakly deflexed downwards with genal cones in approximately the same plane as the vertex; genal cones long, commencing ventrally relative to the vertex, with a distinct depression between the vertex and the genal cones, terminal setae typically shorter than the vertex, occasionally longer. Distal proboscis segment short. Tibia shorter than the femur, tarsi long; metatarsal spur one. Paramere short, in lateral view with a blade on the exterior-anterior margin, and with an internal medial ridge that, in posterior view is almost contiguous when the parameres are closed, sclerotized apex with a double claw, displaced to the interior and posterior of the top of the paramere, in dorsal view contiguous anteriorly, with the inner margin concave; paramere shorter than the proctiger; proctiger not inflated towards the base but with a pronounced posterior extension apically; aedeagus distal segment with a well developed, curved hook, tip of aedeagus hook acute; male subgenital plate dorsal profile more or less straight and horizontal. Female proctiger dorsal profile with a slight post anal depression, but subsequently more or less straight, apex bluntly rounded; subgenital plate ventral profile shallowly curved, apex acute; ovipositor valvulae ventralis slender, apex acute; height of valvulae dorsalis as great, or greater than valvulae ventralis, dorsally convex, wedge-shaped and tapering to the apex; eggs with a stout lateral pedicel.

*Adult measurements and ratios:* (5♂, 5♀) total length: ♂ 3.32-3.88, ♀ 3.68-4.33; forewing: ♂ length 2.7-2.88 width 0.98-1.05, ♀ length 3-3.2 width 1.03-1.13; hindwing length ♂ 2.2-2.38, ♀ 2.4-2.65; head width: ♂ 1.01-1.03, ♀ 1.08-1.13; antennal length: 2.15-2.41; genal cone length: 0.15-0.2; distal proboscis segment length: 0.13-0.14. ALHW: 2.07-2.31; GCVL: 0.57-0.71; WLHW: 2.67-2.87; VLW: 0.45-0.5; WLW: 2.68-2.91; CUR: 1.65-2.03; MR: 0.41-0.52; RMCU: 4.71-6.66; TLFL: 0.84-0.91; TLHW: 0.44-0.5; SCHW: 0.7-0.77; ATIB: 0.42-0.48; MTIB: 0.43-0.5; PBHW: 0.12-0.14; ATMT: 0.88-1.04. *Adult genitalia ♂*: MP: 0.46-0.49; PL: 0.34-0.36; AEL: 0.33-0.37; AEH: 0.08-0.09. MPHW: 0.46-0.48; PLHW: 0.33-0.35; MPPL: 1.31-1.44; AEPL: 0.97-1.03; MSLH: 1.25-1.4; AHS: 0.23-0.26; PLSH: 0.94-1.03. ♀: FP: 0.91-1.04; FSP: 0.6-0.7; RL: 0.25-0.29; OV: 0.2-0.22; EL: 0.25-0.33. FPHW: 0.84-0.92; FPSP: 1.48-1.52; FPCR: 3.56-4; OLSP: 0.31-0.33; FEOL: 1.41.

*Nymph*

*Colour:* 1st-2nd instars cream and orange or black, 3rd-5th instars cream and orange, pale yellow or blue-green, with black tergites. Sclerites, wing pads, legs and terminal antennal segments darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Antennal segments seven. Tergite structure extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad long, broadly expanded apically, usually with a distinct medial groove and long petiole. Circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 5) BL: 1.83-2.3; BW: 1.15-1.35; WL: 0.65-0.77; CPL: 0.57-0.65; CPW: 0.76-0.87; RW: 0.22-0.24; RL: 0.13-0.16; HW: 0.79-0.9; AL: 1.18-1.28; AL3: 0.28-0.3. WBL: 0.59-0.63; ALHW: 1.42-1.49; ALWL: 1.66-1.85; WLHW: 0.78-0.86; WCPL: 1.26-1.35; CPRW: 3.45-3.7.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.1-0.15); antennal setae simple; ocular seta simple, inconspicuous (max length 0.03-0.06); primary post-ocular seta simple or narrowly capitate (max length 0.07); secondary post-ocular seta absent or if present simple (max length 0.05). Dorsal thoracic setae short simple (max length 0.03-0.05). Prominent wing pad setae max length 0.1; forewing and hindwing pads with simple and capitate setae; forewing pad with one prominent apical seta, distinctly or narrowly capitate (occasionally reduced to small simple); hindwing pad with two prominent apical setae, distinctly capitate; proximal setae absent; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, short simple (or very slightly capitate, max length 0.05-0.09), two prominent caudal plate setae present, narrowly capitate; sectasetae one pair in the 3rd position (apical pair in the 4th position are small simple or rod setae); marginal abdominal setae (other than sectasetae) four pairs, distinctly capitate (4th pair sometimes simple) (max length 0.14.-0.22); pleurite setae paired simple. Legs with capitate setae present (max length 0.07-0.08); capitate foreleg setae absent; capitate middle leg setae present on femur and tibia, on the tibia one (distal); capitate hind leg setae present on femur and tibia, on the tibia one (distal).

*Host plant: Spartocytisus filipes, S. supranubius.*

*Distribution:* Canary Islands: La Gomera, La Palma, and El Hierro.

*Notes:* Occurs on the three most westerly islands. It is found throughout the host plant range, from dry lowland to sabinar and laurisilva habitat. On La Palma, it is sympatric with *Arytainilla serpentina* in the laurisilva habitat, where it is less common than the latter species.

*Biology:* Eggs, on *Spartocytisus filipes*, are laid in rows around the inside rim of the calyx, and in small clusters on the inner surfaces of corolla segments (Fig. 31A). Of 46 flowers examined, 35 were found to have between five, to more than 30 eggs per flower, the majority laid on the inner surface of the calyx which is persistent during development of the young fruit. In mid-May, small nymphs (1st-2nd instars) were observed in flowers on the corolla and clayx.

*Etymology:* Named for the dorsal, longitudinal stripe or 'vittae', particularly distinct in females, which makes this species easily recognisable in the field and distinguishes it from the closely related species, *A. nubivaga.*

*Comment: A. vittata* is very similar to *A. nubivaga*, and appears to represent a recent speciation event involving a host switch from the upland to the lowland *Spartocytisus* species. At present these two species do not occur on the same island. On La Palma *Spartocytisus supranubius* (the upland host) is rare and when sampled a few adults and nymphs of *A. vittata* were found. The lowland host, *Spartocytisus filipes*, is present but extremely rare on Tenerife, where no individuals were located for sampling. It is not apparent therefore, whether a host switch may have occurred on one island, or been coupled with colonization of a new island. *A. vittata* can be distinguished from *A. nubivaga* by the more slender paramere with an extended internal ridge which is shallow in *A. nubivaga*, also by the adult colour (i.e. dorsal vittae) and the 5th instar nymph which has a single pair of sectasetae in *A. vittata.*

*Type material:* Holotype ♂ (slide mounted), CANARY ISLANDS. LA PALMA: Barranco de las Angustias, 28°40'30"N 17°55'W, c. 300 m, 18.v.1998 (BMNH). Paratypes 1♂, as for holotype (BMNH). 1♂, 1♀, as for holotype (DZUL). 1♀, as for holotype (NHMB). 1♀, SE rd Santa Cruz to La Caldera, 28°45'N 17°49'30"W, 1950 m, ex *Spartocytisus supranubius*, 16.vii.1997 (BMNH). LA GOMERA: 2♂, 2♀, S of Hermigua, 28°08'30"N 17°12'W, 500-600 m, 25.v.1998 (BMNH). 3♂, 1♀, as for previous (NHMB). EL HIERRO: 5 nymphs, N coast btw Frontera and Sabinosa, 27°45'N 18°04'W, 300 m, 22.v.1998 (BMNH).

*Material examined:* (ex *Spartocytisus filipes* unless otherwise stated) CANARY ISLANDS. LA GOMERA: 8♂, 10♀, Barranco del Agua, abv El Retamal, Valle Gran Rey, 28°7'N 17°18'30"W, 550 m, 13.vii.1997 (DP 66). 17♂, 16♀, 7 nymphs, rd Arure to Las Hayas, 28°7'30"N 17°18'30"W, 900 m, 13.vii.1997 (DP 69). 21♂, 14♀, S of Hermigua, 28°08'30"N 17°12'W, 500-600 m, 25.v.1998 (DP 220). 2♂, 8♀, blw Roque Cano, 28°11'N 17°15'30"W, 300-400 m, 26.v.1998 (DP 222). LA PALMA: 1♀, SE rd Santa Cruz to La Caldera, 28°45'N 17°49'30"W, 1950 m, ex *Spartocytisus supranubius*, 16.vii.1997 (DP 80.1). 6♂, 23♀, Barranco de las Angustias, abv Los Llanos 28°41'N 17°53'30"W, 420 m, 17.vii.1997 (DP 83). 3 nymphs, La Caldera, 28°46'N 17°5'30"W, 2280 m, ex *Spartocytisus supranubius*, 17.vii.1997 (DP 85). 1♀, nr Los Galguitos, Barranco de la Fuente, 28°46'N 17°46'W, 350 m, 17.v.1998 (DP 191). 4♂, 53♀, 1 nymph, as for holotype (DP 193). 17♂, 15♀, Barranco de Jurado, S of Tijarafe, 28°42'15"N 17°56'45"W, c. 600 m, 18.v.1998 (DP 197). 1♂, 15♀, NE, from El Granel to Barlovento and Roque Faro, 200-500 m, 19.v.1998 (DP 198). EL HIERRO: 12♂, 11♀, c. 5 km W of Frontera on road to Sabinosa, 27°45'N 18°03'30"W, 230 m, 10.vii.1997 (DP 58). 27♂, 13♀, 13 nymphs, N coast btw Frontera and Sabinosa, 27°45'N 18°04'W, 300 m, 22.v.1998 (DP 213).

## Genus *Livilla* Curtis

*Livilla* Curtis, 1836: 625; Loginova, 1977: 67; Hodkinson and Hollis, 1987: 19. Type species: *Livilla ulicis* Curtis, by monotypy

*Floria*, Löw, 1879: 594; Loginova, 1977: 66. Type species: *Psylla pyrenaea* Mink, designated by Oshanin, 1912: 128; synonymized by Hodkinson and Hollis, 1987: 19

*Alloeoneura* Löw, 1879: 594; Loginova, 1977: 67. Type species: *Arytaina radiata* Foerster, by monotypy; synonymized by Hodkinson and Hollis, 1987: 19

*Floria* (*Floriella*) Ramírez Gómez, 1956: 87. Type species: *Psylla pyrenaea* Mink [objective synonym of *Floria*]

### *Livilla monospermae* Hodkinson

(Figs 24A, 1E & 1K)

*Livilla monospermae* Hodkinson, 1990: 29

*Adult Colour:* Green to yellow-green, thorax usually with dark bands, head and legs sometimes brown, femora, genal cones and terminal antennal segments darker brown; forewing membrane with distinct, dark brown transverse apical pattern, veins uniform light brown.

*Adult Description:* Hodkinson (1990).

*Nymph*

*Colour:* 1st-2nd instars cream with black tergites, 3rd-4th instars orange-brown with black tergites, 5th instars pale blue-green or yellow with black tergites. Sclerites, wing pads, legs and terminal antennal segments darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Antennal segments seven. Tergites extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad long, broadly expanded apically, usually with a distinct medial groove and long petiole. Circumanal ring shape broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 4) BL: 1.95-2.23; BW: 1.15-1.23; WL: 0.63-0.69; CPL: 0.56-0.59; CPW: 0.84-0.91; RW: 0.22-0.24; RL: 0.12-0.14; HW: 0.75-0.84; AL: 1.03-1.1; AL3: 0.25-0.28. WBL: 0.58-0.67; ALHW: 1.29-1.47; ALWL: 1.59-1.75; WLHW: 0.79-0.85; WCPL: 1.48-1.63; CPRW: 3.58-3.96.

*5th instar chaetotaxy:* Head setae simple and distinctly capitate (max length at anterior margin 0.09-0.1); antennal setae simple and capitate (small capitate on 1st, and distally on 3rd and 5th segments); ocular seta small, capitate (max length 0.01-0.05); primary post-ocular seta distinctly capitate (max length 0.08); secondary post-ocular seta distinctly capitate (max length 0.04-0.07). Dorsal thoracic setae short capitate (max length 0.03-0.04). Prominent wing pad setae max length 0.12-0.14; forewing and hindwing pads with capitate setae only; forewing pad prominent setae 8-12, distinctly capitate, surface and marginal (7-10 marginal, 1 proximal, remainder surface); hindwing pad prominent setae 4-7, distinctly capitate, surface and marginal (2 apical, 1 proximal, 1-4 surface); proximal setae distinctly capitate; numerous small capitate setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae present on anterior tergites, short capitate (max length 0.02), prominent caudal plate setae absent (numerous small capitate); sectasetae four pairs; marginal abdominal setae (other than sectasetae) four pairs, distinctly capitate (max length 0.23); pleurite setae paired capitate and simple or capitate only (anterior pleurites with 2-3 capitate setae). Legs with capitate setae present (max length 0.1-0.14); on all legs capitate setae present on femora, tibiae and tarsi, on the tibia 3-4 larger, with numerous smaller capitate setae.

*Host plant: Retama monosperma.*

*Distribution:* Canary Islands: Tenerife, La Gomera, La Palma, and El Hierro.

*Comment:* This is the only representative of *Livilla* in the Canary Islands. It is present on four of the five central and western Canary Islands, and the apparent absence from Gran Canaria may be due to the restricted host plant distribution on this island. It is closely related to the widespread continental, *Retama*-feeding species, *Livilla retamae.*

*Material examined:* CANARY ISLANDS. TENERIFE: 3♂, 13♀, 3 nymphs, c. 2 km S of Tamaimo, rd to Santiago del Teide, 28°15'N 16°48'30"W, 600 m, 29.vi.1997 (DP 28). 6♂, 13♀, 5 nymphs, mirador N of Santiago del Teide, Barranco Seco, 28°18'30"N 16°49'30"W, 1000 m, 2.vii.1997 (DP 31). 3♂, 3♀, blw Masca village, Barranco de Masca, 28°18'N 16°50'30"W, 550 m, 2.vii.1997 (DP 34). 2♂, 1♀, La Laguna University, 18.vii.1997 (DP 87). LA GOMERA: 15♂, 5♀, 3 nymphs, Barranco del Agua, abv El Retamal, Valle Gran Rey, 28°7'N 17°18'30"W, 550 m, 13.vii.1997 (DP 65). 66♂, 47♀, 1 nymph, rd Arure to Las Hayas, 28°7'30"N 17°18'30"W, 900 m, 13.vii.1997 (DP 70). LA PALMA: 4♂, 1♀, btw Las Nieves and Mirca, 28°42'N 17°46'30"W, 260 m, 16.vii.1997 (DP 77). 15♂, 9♀, 10 nymphs, Barranco de las Angustias, 28°40'N 17°55'30"W, c. 300 m, 17.vii.1997 (DP 84). 11♂, 9♀, 6 nymphs, Barranco de las Angustias, 28°40'15N 17°55'45"W, 350 m, 18.v.1998 (DP 196). EL HIERRO: 22♂, 12♀, 16 nymphs, c. 50 m blw Mirador de la Peña, E rim of El Golfo, 27°48'30"N 17°59'W, 560 m, 12.vii.1997 (DP 62).

### *Livilla ima* (Loginova) **comb. nov.**

(Fig. 23C)

*Arytainilla ima* Loginova, 1972: 19

*Adult Colour:* Bright or paler green, legs yellow, head and thorax sometimes brown or orange, mature specimens may be darker brown. Forewing membrane more or less opaque, yellow-brown, veins uniform light brown.

*Adult Description:* Loginova (1972).

*Nymph*

*Colour:* 1st-2nd instars orange, 4th-5th instars pale green or orange, with or without black tergites. Terminal antennal segment and sometimes sclerites and wing pads darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Antennal segments seven. Tergites extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad short, broadly expanded apically, usually with a distinct medial groove and short petiole. Circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 5) BL: 1.73-1.93; BW: 1.15-1.3; WL: 0.7-0.76; CPL: 0.57-0.59; CPW: 0.91-0.93; RW: 0.19-0.23; RL: 0.1-0.11; HW: 0.67-0.71; AL: 0.8-0.88; AL3: 0.22-0.23. WBL: 0.66-0.72; ALHW: 1.19-1.29; ALWL: 1.14-1.22; WLHW: 1.04-1.09; WCPL: 1.54-1.61; CPRW: 4.04-4.79.

*5th instar chaetotaxy:* Head setae simple (max length at anterior margin 0.1-0.15); antennal setae simple; ocular seta simple, inconspicuous (max length 0.02-0.04); primary post-ocular seta typically narrowly or distinctly capitate, sometimes simple (max length 0.05-0.08); secondary post-ocular seta absent or if present, short simple (max length 0.02-0.03). Dorsal thoracic setae short simple (max length 0.02-0.03). Prominent wing pad setae max length 0.05-0.12; forewing and hindwing pads with simple and capitate setae; each wing pad with one prominent apical seta, narrowly or distinctly capitate, hindwing apical seta paired with small simple seta; proximal setae absent; small simple setae scattered on the wing pad surfaces. Dorsal abdominal prominent pre-caudal setae absent (indistinct small simple), prominent caudal plate setae absent; sectasetae four pairs; marginal abdominal setae (other than sectasetae) three or four pairs, simple (occasionally slightly capitate, max length 0.18-0.2); pleurite setae paired simple. Legs with or without capitate setae (max length 0.06-0.08); capitate foreleg setae absent; capitate middle and hind leg setae absent or, if present on tibia only, one (distally, often narrow or simple).

*Host plant: Adenocarpus anagyrifolius.*

*Distribution:* Continental: Morocco.

*Notes:* Endemic to the High Atlas where this species and its host plant are locally common.

*Biology:* Clusters of eggs were found inside folded young leaves and under floral bracts or singly on the tips of petiolar bracts, and at the base and tips of young leaflets. Nymphs (1st-4th instars) were observed on leaf buds or in folded young leaves.

*Comment:* This species is removed from *Arytainilla* (Loginova, 1972) and placed in *Livilla* with the two following species (*L. caprifuga* sp. nov. and *L. baetica* sp. nov.) based on the reduced or absent pterostigma, slender genal cones, shape of the female genitalia and ovipositor, and similarities in paramere form such as thick setae at the base of the posterior margin. Together with *L. caprifuga* sp. nov. and *L. baetica* sp. nov., these species form an exclusively *Adenocarpus*-feeding group, which may also include *L. complexa* sp. nov.

*Material examined:* MOROCCO: 2♀, High Atlas, S of Tizi n' Test pass, 30°45'N 8°25'W, c. 2000 m, 19.vi.1998 (DP 236). 12♂, 13♀, as for previous except, c. 2030 m (DP 237). 22♂, 19♀, High Atlas, N of Tizi n' Test pass, 30°52'N 8°22'W, c. 2030 m, 19.vi.1998 (DP 239). 5♂, 13♀, 22 nymphs, High Atlas, just N of Taddert on Tizi n' Tichka rd, 31°20'N 7°25'W, 1650 m, 27.iii.1999 (DP 305). 2♂, 11♀, 2 nymphs, High Atlas, S of Taddert on Tizi n' Tichka rd, 31°18'N 7°25'W, 1650 m, 27.iii.1999 (DP 306). 8♂, 4♀, 13 nymphs, High Atlas, c. 13 km S of Ijoukak, Tizi n' Test rd, 30°50'N 8°28'W, c. 1800 m, 2.v.1999 (DP 328).

### ***Livilla caprifuga* sp. nov.** (15)

(Fig. 19)

*Adult*

*Colour:* Grey-green to grey-yellow, female abdomens more blue-grey; terminal antennal segments slightly darker brown. Forewing membrane somewhat opaque white, veins uniform yellow or light brown.

*Structure:* Forewing widest in the middle third with more acutely rounded apex; costal break absent (occasionally feint break discernible); pterostigma absent; vein Rs slightly curved in the middle and weakly curved at the apex, towards the costal margin; surface forewing spinules present throughout all cells, distribution non-uniform, very dense: more than 100 per $0.1mm^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent from cell $r_2$; hindwing costal margin straight. Antennae short, with ten segments; head deflexed downwards with genal cones directed downwards relative to the plane of the vertex; genal cones long, commencing dorsally from more or less the same level as the vertex, terminal setae shorter than the vertex. Distal proboscis segment mid-length. One metatarsal spur. Paramere mid-length, in lateral view slender, simple, with sides tapering towards the apex, sclerotized apex dorsally rounded with a pronounced anteriorly directed hook, in dorsal view contiguous anteriorly, the inner margin rounded with an acute point; paramere longer than the proctiger; proctiger slightly inflated posteriorly towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile raised anteriorly. Female proctiger dorsal profile more or less straight from anus to apex, or with slight post-anal depression, apex bluntly rounded; subgenital plate ventral profile shallowly curved, apex acute; ovipositor valvulae ventralis slender, apex acute; height of valvulae dorsalis as great, or greater than valvulae ventralis, dorsally convex, wedge-shaped and tapering to the apex.

*Adult measurements and ratios:* (4♂, 4♀) total length: ♂ 2.84-3.2, ♀ 3.16-3.4; forewing: ♂ length 2.35-2.38 width 0.96-1.03, ♀ length 2.54-2.82 width 1.13-1.24; pterostigma length ♂ 0.08-0.12, ♀ 0.05-0.15; hindwing length ♂ 1.93-2, ♀ 2.1-2.4; head width: ♂ 0.79-0.82, ♀ 0.81-0.93; antennal length: 1.13-1.29; genal cone length: 0.17-0.21; distal proboscis segment length: 0.14-0.17. ALHW: 1.31-1.58; GCVL: 0.68-0.87; WLHW: 2.9-3.22; VLW: 0.45-0.51; WLW: 2.24-2.48; CUR: 1.63-1.93; MR: 0.34-0.51; RMCU: 5.6-9.88; TLFL: 1.11-1.19; TLHW: 0.69-0.74; SCHW: 0.89-0.97; ATIB: 0.26-0.32; MTIB: 0.3-0.33; PBHW: 0.17-0.2; ATMT: 0.86-1.

*Adult genitalia* ♂: MP: 0.3-0.34; PL: 0.42-0.45; AEL: 0.34-0.36; AEH: 0.1-0.12. MPHW: 0.37-0.43; PLHW: 0.53-0.57; MPPL: 0.68-0.76; AEPL: 0.8-0.84; MSLH: 1.17-1.28; AHS: 0.31-0.32; PLSH: 1.25-1.31. ♀: FP: 0.95-0.98; FSP: 0.56-0.61; RL: 0.24-0.28; OV: 0.21-0.23; EL: 0.31-0.38. FPHW: 1.05-1.17; FPSP: 1.61-1.72; FPCR: 3.5-3.96; OLSP: 0.36-0.4; FEOL: 1.55.

*Nymph* Unknown

*Host plant: Adenocarpus bacquei.*

*Distribution:* Continental: Morocco.

*Notes:* The host plant occurs in isolated populations in the eastern High Atlas and Middle Atlas mountains of Morocco. *L. caprifuga* sp. nov. was not common in any of the locations sampled and many of the host plants showed signs of over grazing.

*Biology:* Eggs were found singly on the exterior of leaf buds.

*Etymology:* Named for the threat posed by large groups of grazing goats on the Middle Atlas plains, a likely cause of the host plant's rarity, now restricted to few isolated populations. The epithet is derived from the Latin 'capra' for goat, and 'fugo' to cause to flee.

*Type material:* Holotype ♂ (slide mounted), MOROCCO: Middle Atlas, c. 18 km E of Midelt, on rd to Rich, just S of Zebzate, 32°33'N 4°38'W, c. 1500 m, 29.iii.1999 (BMNH). Paratypes 2♂, 3♀, as for holotype (BMNH). 4♂, 2♀, as for holotype (NHMB). 1♂, 1♀, High Atlas, Ait-Toukhsine, Gorges du Dadès, c. 35 km N of Boulmalne-du-Dadès, 31°25'N 6°05'W,c. 1500 ♂, 28.iii.1999 (BMNH).

*Other material examined:* MOROCCO: 20♂, 15♀, as for holotype (DP 309). 4♂, 5♀, Middle Atlas, Ait Ou-fella, south of Col du Zad, rd Midelt to Azrou, 32°46'N 5°05'W, c. 1650 m, 29.iii.1999 (DP 310).

### ***Livilla baetica* sp. nov.** (16)

(Fig. 20)

*Adult*

*Colour:* Brown or dark grey, abdominal intersegment colour yellow, femora and terminal antennal segments darker brown, thorax with darker bands. Forewing membrane with brown pigmentation, veins uniform light or mid-brown.

*Structure:* Forewing widest in the apical third with a broadly rounded apex; costal break and pterostigma present, pterostigma less than one quarter the wing length; vein Rs slightly curved in the middle and not, or only weakly curved at the apex towards the costal margin; surface forewing spinules present throughout all cells, distribution non-uniform, very dense: more than 100 per 0.1mm$^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$ but absent from cell $r_2$; hindwing costal margin straight. Antennae short, with ten segments; head deflexed downwards with genal

cones directed downwards relative to the plane of the vertex; genal cones long, commencing dorsally from more or less the same level as the vertex, terminal setae as long or longer than the vertex. Distal proboscis segment mid-length. One metatarsal spur. Paramere mid-length, in lateral view with anterior margin curving forward, sides tapering towards the constricted apex, sclerotized apex dorsally flattened with slight anterior projection, in dorsal view contiguous more or less along the entire straight edged, inner margin; paramere shorter than the proctiger; proctiger slightly inflated posteriorly towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile raised anteriorly with a distinct step. Female proctiger dorsal profile more or less straight from anus to apex, apex bluntly rounded; subgenital plate ventral profile angled medially, apex acute; ovipositor valvulae ventralis slender, apex acute; height of valvulae dorsalis as great, or greater than valvulae ventralis, dorsally convex, wedge-shaped and tapering to the apex.
*Adult measurements and ratios:* (3♂, 3♀) total length: ♂ 3.04-3.2, ♀ 3.36-3.68; forewing: ♂ length 2.35-2.58 width 1.02-1.08, ♀ length 2.66-2.84 width 1.1-1.18; pterostigma length ♂ 0.35-0.5, ♀ 0.35-0.45; hindwing length ♂ 1.85-2.05, ♀ 2.18-2.36; head width: ♂ 0.81-0.84, ♀ 0.83-0.88; antennal length: 1.34-1.48; genal cone length: 0.17-0.19; distal proboscis segment length: 0.14-0.15. WLPT: 5.16-7.77; ALHW: 1.52-1.76; GCVL: 0.72-0.76; WLHW: 2.9-3.23; VLW: 0.44-0.48; WLW: 2.3-2.47; CUR: 1.97-2.09; MR: 0.51-0.58; RMCU: 4.82-6.22; TLFL: 1.16-1.26; TLHW: 0.73-0.8; SCHW: 0.9-0.96; ATIB: 0.25-0.3; MTIB: 0.28-0.32; PBHW: 0.16-0.19; ATMT: 0.89-1. *Adult genitalia* ♂: MP: 0.46-0.51; PL: 0.41-0.43; AEL: 0.4-0.42; AEH: 0.14-0.15. MPHW: 0.57-0.61; PLHW: 0.51-0.54; MPPL: 1.09-1.19; AEPL: 0.95-0.98; MSLH: 1.1-1.25; AHS: 0.35-0.36; PLSH: 0.92-1.03. ♀: FP: 1.05-1.23; FSP: 0.74-0.79; RL: 0.22-0.29; OV: 0.24-0.25; EL: 0.29-0.35. FPHW: 1.27-1.4; FPSP: 1.42-1.56; FPCR: 4.24-4.77; OLSP: 0.32; FEOL: 1.3.

*Nymph* Unknown

*Host plant: Adenocarpus decorticans.*
*Distribution:* Continental: Spain.
*Notes:* Occurs sympatrically with *A. montivaga* sp. nov. on the host in the southern Andalusian mountains. It was far less common than the latter species in March, and probably develops later. *L. baetica* sp. nov. was absent from host populations sampled in Morocco.

*Etymology:* Named for the distribution in southern Spain.

*Type material:* Holotype ♂ (slide mounted), SPAIN: Andalusia, N slopes of Sierra de Baza, rd Caniles to Alba, 37°15'N 2°45'W, c. 1600 m, 22.iii.1998 (BMNH). Paratypes 1♂, 2♀, as for holotype (BMNH). 1♂, 2♀, as for holotype (NHMB).

*Other material examined:* SPAIN: 1♂, 1♀, Andalusia, N slopes of Sierra Nevada, rd Calaharra to Puerto de la Ragua, 37°05'N 3°02'W, c. 1850 m, 21.iii.1998 (DP 128). 2♂, 7♀, as for holotype (DP 129).

### ***Livilla complexa* sp. nov. (17)**

(Fig. 21)

*Adult*

*Colour:* Yellow-orange, femora and terminal antennal segments darker brown, with dark brown bands on the thorax. Forewing membrane coriaceous, yellow-brown becoming darker brown towards the apex and margins, veins uniform yellow or light brown.

*Structure:* Forewing widest in the middle third, with well rounded apex; costal break absent; reduced pterostigma present, less than one quarter the length of the wing; vein Rs more or less straight, not or only weakly curved towards the costal margin at the apex; surface forewing spinules present in all cells but confined to small patches at the margins of cells c+sc and $cu_2$, distribution non-uniform, increasingly dense towards the wing margin: more than 100 per $0.1mm^2$; apical spines in wing cells $cu_1$, $m_1$ and $m_2$, but absent, or occasionally few present in cell $r_2$; hindwing costal margin straight. Antennae short, with ten segments; head deflexed downwards with genal cones directed downwards relative to the plane of the vertex; genal cones long, terminal setae shorter than the vertex. Distal proboscis segment short. One metatarsal spur. Paramere short, in lateral view simple with sides tapering, sclerotized apex dorsally rounded with anteriorly directed hook, in dorsal view contiguous anteriorly; paramere shorter than the proctiger; proctiger not, or only slightly inflated posteriorly towards the base; aedeagus distal segment with a flattened, shallow hook, tip of aedeagus hook blunt; male subgenital plate dorsal profile more or less straight and horizontal. Female proctiger dorsal profile with a post anal depression, but subsequently straight, apex bluntly rounded; subgenital plate ventral profile shallowly curved, apex acute; ovipositor valvulae ventralis slender, apex acute; height of valvulae dorsalis as great, or greater than valvulae ventralis, dorsally convex, wedge-shaped and tapering to the apex.

*Adult measurements and ratios:* (2♂, 1♀) total length: ♂ 2.36-2.44, ♀ 2.76-2.88; forewing: ♂ length 1.83-1.93 width 0.9-0.94, ♀ length 2.13 width 1.02; pterostigma length ♂ 0.2-0.3, ♀ 0.15; hindwing length ♂ 1.53, ♀ 1.76; head width: ♂ 0.71-0.72, ♀ 0.74; antennal length: 1.13-1.22; genal cone length: 0.15-0.16; distal proboscis segment length: 0.13-0.15. WLPT: 6.43-14.2; ALHW: 1.57-1.72; GCVL: 0.65-0.73; WLHW: 2.54-2.88; VLW: 0.49-0.53; WLW: 2.03-2.09; CUR: 2.16-2.18; MR: 0.49-0.57; RMCU: 6.13-8.08; TLFL: 1.17-1.18; TLHW: 0.78-0.83; SCHW: 0.94-1; ATIB: 0.25-0.27; MTIB: 0.28-0.3; PBHW: 0.18-0.2; ATMT: 0.88.

*Adult genitalia* ♂: MP: 0.31-0.33; PL: 0.29; AEL: 0.27-0.28; AEH: 0.09-0.10. MPHW: 0.43-0.46; PLHW: 0.4-0.41; MPPL: 1.07-1.14; AEPL: 0.93-0.97; MSLH: 1.14-1.22; AHS: 0.34-0.35; PLSH: 1.04-1.07. ♀: FP: 0.69; FSP: 0.49; RL: 0.23; OV: 0.15; EL: 0.28-0.3. FPHW: 0.93; FPSP: 1.41; FPCR: 3; OLSP: 0.31; FEOL: 1.93.

*Nymph* Unknown

*Host plant: Adenocarpus complicatus.*

*Distribution:* Continental: Spain and Portugal.

*Notes:* The host plant is widespread but this species is known from only two locations in northern Andalusia and in central Portugal. Occurring sympatrically with *Arytaina adenocarpi*, it was not common in either of these locations. The host plant affiliation is not certain due to the small number of adults and absence of nymphs. However, the occurence of *L. complexa* sp. nov. on the same host from two distant locations, combined with the affinities of this species with the other *Adenocarpus*-feeding members of *Livilla* described here, provides evidence for the *Adenocarpus* affiliation.

*Etymology:* Named for the dual taxonomic complexity of both the host plant and the psyllid genus, *Livilla.*

*Comment:* Morphologically this species is closest to the *ulicis*-group, as defined by Hodkinson and Hollis (1987). It is similar to *Livilla vicina* and to the type species of *Livilla*, *L. ulicis*, in the short oval and coriaceous forewing, and in the shape of the head and genal cones.

*Type material:* Holotype ♂ (slide mounted), PORTUGAL: Serra da Estrela, nr Teixeira 40°15'N 7°45'W, c. 1000 m, 27.vi.1998 (BMNH). Paratypes 1♂, 1♀, as for holotype (BMNH).
*Other material examined:* SPAIN: 1♀, Andalusia, c. 7 km E of Aracena, 37°52'N 6°30'W, c. 400 m, 24.vi.1998 (DP 258). PORTUGAL: 3♀, as for holotype (DP 262.3).

### Genus *Pseudacanthopsylla* Samy

*Pseudacanthopsylla* Samy, 1972: 455
Type species *Pseudacanthopsylla retamae* Samy, 1972: 455

### *Pseudacanthopsylla improvisa* (Loginova) **comb. nov.**

(Figs 23D & 30B)

*Psylla improvisa* Loginova, 1972: 30

*Adult Colour:* Yellow-grey; forewing membrane clear or faintly yellow, veins uniformly pale.
*Adult Description:* Loginova (1972).

*Nymph*

*Colour:* Grey-green or more red; terminal antennal segment darker.
*Structure:* Forewing pads and abdomen acute apically. Antennal segments seven. Tergites extensively reduced on the thorax, typically not extending to the lateral margin on the abdomen. Arolium pad short, narrowly triangular, without medial groove and with a short petiole. Circumanal ring shape narrowly crescent-shaped with acutely rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.
*5th instar measurements and ratios:* (specimens 3) BL: 1.43-1.78; BW: 1.03-1.11; WL: 0.59-0.62; CPL: 0.45-0.46; CPW: 0.63-0.65; RW: 0.11-0.12; RL: 0.07; HW: 0.61-0.7; AL: 0.48-0.52; AL3: 0.11-0.12. WBL: 0.62-0.72; ALHW: 0.74-0.79; ALWL: 0.79-0.88; WLHW: 0.88-1; WCPL: 1.39-1.44; CPRW: 5.42-5.82.
*5th instar chaetotaxy:* Head with numerous sectasetae (few simple setae ventrally) (max length at anterior margin 0.03-0.04); antennae with two or more sectasetae on each segment; eyes with several small sectasetae dorsally (max length 0.02-0.03); primary post-ocular seta indistinct (of the numerous sectasetae, one in the equivalent position appears slightly larger); secondary post-ocular seta absent (indistinct from surrounding setae). Dorsal thorax with sectasetae (max

length 0.03-0.04). Prominent wing pad setae max length 0.04; forewing and hindwing pads with numerous sectasetae, surface and marginal, proximal setae indistinct from surface setae. Dorsal abdominal pre-caudal tergites and caudal plate with numerous sectasetae, including one larger positioned centrally and posteriorly; marginal abdominal sectasetae numerous; marginal abdominal setae (other than sectasetae) absent; pleurite setae paired simple. All legs with sectasetae present ventrally, on femora, tibiae and tarsi (max length 0.04).

*Host plant: Retama raetam.*

*Distribution:* Continental: Morocco.

*Notes:* This species occurs on populations of the host plant along the southern Atlantic coast of Morocco. It is found sympatrically with *Arytainilla sulci* and *Livilla retamae*, but it is less common than either of these species which also occur on inland host populations. The egg is particularly slender with a stout lateral pedicel at the base. Sculpturing is evident on the dorsal surface between the vitelline membrane and the egg shell in the chorion layer, implying a respiratory or insulatory function for this feature (Fig. 30B).

*Comment:* This species is transferred to *Pseudacanthopsylla* from *Psylla* (Loginova, 1972) based on the similarity in the form of both adult and nymph to *Pseudacanthopsylla retamae*. The nymphal form is uniquely peculiar within the Arytaininae. *P. retamae* is the only other congeneric species and occurs on populations of the same host plant in the eastern Mediterranean (Samy, 1972; Al-Khawaldeh, Katbeth-Bader & Burckhardt, 1997).

*Material examined:* MOROCCO: 4♂, 1♀, Southern Atlantic coast, E side of Agadir, 30°25'N 9°30'W, s.l., 19.vi.1998 (DP 234). 16♂, 10♀, as for previous except, 23.iii.1999 (DP 301). 11♂, 12♀, 7 nymphs, as for previous except, 29.iv.1999 (DP 321). 14♂, 9♀, Atlantic Coast, c. 15 km S of El Jadid, 32°55'N 8°35'W, c. 100 m, 21.iii.1999 (DP 297).

## **2.3.4** SUBFAMILY ACIZZIINAE

### Genus *Acizzia* Heslop-Harrison

*Neopsylla* Heslop-Harrison, 1949: 161

*Acizzia* Heslop-Harrison, 1961a: 417

Type species *Psylla acaciae* Maskell, 1894, by original designation

## *Acizzia uncatoides* (Ferris & Klyver)

(Figs 1D & 29D)

*Psylla uncatoides* Ferris & Klyver, 1932: 53

*Acizzia uncatoides* (Ferris & Klyver) Loginova, 1977: 577

*Adult Colour:* Orange-brown, sometimes with paler light green or yellow abdomens. Forewing membrane pale yellow with a pattern of orange or light brown clouds and spots in the apical portion and towards the margins, veins yellow or light brown.

*Adult Description:* Hodkinson & Hollis (1987).

*Nymph*

*Colour:* 1st-2nd instars cream and orange, 3rd-5th instars orange-brown with black tergites. Sclerites, wing pads, legs and terminal antennal segments darker brown.

*Structure:* Forewing pads and abdomen broadly rounded apically. Antennal segments nine. Tergites reduced on the thorax (though not as extensively as in other genera), typically not extending to the lateral margin on the abdomen. Arolium pad short, expanded apically with or without slight medial groove, and with a long petiole; circumanal ring broadly crescent-shaped with well rounded anterior lobes, outer ring not contiguous with the apical abdominal margin and with a single row of pores.

*5th instar measurements and ratios:* (specimens 4) BL: 1.13-1.28; BW: 0.86-0.94; WL: 0.48-0.49; CPL: 0.3-0.31; CPW: 0.55-0.6; RW: 0.1-0.11; RL: 0.06; HW: 0.52-0.58; AL: 0.52-0.54; AL3: 0.1-0.11. WBL: 0.73-0.77; ALHW: 0.9-1.02; ALWL: 1.06-1.13; WLHW: 0.83-0.94; WCPL: 1.83-2; CPRW: 5.18-6.

*5th instar chaetotaxy:* Head setae simple and distinctly capitate (capitate setae on the anterior margin, and short simple and longer capitate setae dorsally) (max length at anterior margin 0.07-0.08); antennal setae simple and capitate (capitate distally on 3rd and 5th segments); ocular seta capitate, dark, conspicuous (max length 0.05-0.06); primary post-ocular seta distinctly capitate (max length 0.06); secondary post-ocular seta indistinct (small simple). Dorsal thoracic setae short simple and long capitate (max length 0.07). Prominent wing pad setae max length 0.08-0.09; forewing and hindwing pads with capitate setae only; forewing pad prominent setae 13-16, distinctly capitate, surface and marginal (10-12 marginal, 3-4 surface); hindwing pad prominent setae 8, distinctly capitate, surface and marginal (2 apical, 2 marginal, ± 4 surface); proximal setae distinctly capitate; small rod or simple setae scattered on the wing pad surfaces.

Dorsal abdominal prominent pre-caudal setae present on all tergites, long capitate (max length 0.08), prominent caudal plate setae present, ± 21 (1 positioned centrally and posteriorly), distinctly capitate; sectasetae absent; marginal abdominal setae (other than sectasetae) four or more pairs, distinctly capitate (max length 0.09-0.1); pleurite setae paired simple or capitate (on anterior pleurites). Legs with capitate setae present (max length 0.06-0.07); capitate foreleg setae present on tibia only, 3-4; capitate middle and hind leg setae present on femur and tibia, on the tibia 4-7.

*Host plant: Acacia* spp.

*Distribution:* Canary Islands and Continental (introduced from Australia).

*Notes:* Recorded from Tenerife and La Palma, this introduced species is abundant on cultivated *Acacia* spp. and is likely to be present on all islands where the host has been introduced.

*Biology:* Nymphs were observed in inflorescences and on peduncles.

*Material examined:* CANARY ISLANDS. TENERIFE: 3♂, 3♀, La Laguna University, 18.vii.1997 (DP 87). LA PALMA: 50♂, 50♀, 20 nymphs, Barranco de las Angustias, 28°40'15"N 17°55'30"W, c. 300 m, 18.v.1998 (DP 194).

## 2.4 General notes on biology

All eggs examined with the exception of those of *Pseudacanthopsylla*, were smooth surfaced (Fig. 30A) and generally pale cream or yellow with an orange base and, in later development, black antennal spots and red eye spots were visible. The basal pedicel is frequently small but is more well developed in some species (Fig. 31B). Little variation in egg type was found. However, in the species comprising *Arytainilla sensu stricto* which are characterized by a massive ovipositor, the eggs are generally smaller and more slender. The dorsal part of the eggs of *Pseudacanthopsylla improvisa* are covered with a hexagonal sculpturing and the eggs are markedly elongate (Fig. 30B).

Parasitized 5th instar nymphs of three species *A. proboscidea*, *A. occidentalis* sp. nov. and *Livilla monospermae* were collected in the field and kept until parasitoids emerged after one to two weeks. All parasitoids were identified as Encyrtidae from the genera *Prionomitus*, *Pachyneuron* and *Trechnites* (J. Noyes pers. comm.). Mites were also common parasites and were found on a number of Macaronesian and continental species.

Mating between psyllids was frequently observed in the pooter and further observations were made in the laboratory. In all cases males were much more active than females. In field collections where more than one species was collected into the same vial (typically species that share the same host plant), mating was common but interspecific mating activity was never observed and only rarely was a male seen to approach a female of a different species.

## 2.5 Discussion

Among the Gensiteae-feeding species members of *Arytainilla* and *Arytaina* feed predominantly on host plants in the *Cytisus* group, while members of *Livilla* and *Arytinnis* gen. nov. feed predominantly on hosts in the *Genista* group. However, all genera include species feeding on *Cytisus*, *Genista* and *Adenocarpus* groups (Table 1). This implies that there are some constraints on host preference but that within these four genera switching between host groups does occur. It is sometimes difficult to assess from historical records whether single species feed on more than one host group, since identification of hosts, when present, is often doubtful or ambiguous. During this study only one species, *Arytinnis modica*, was found to feed sympatrically on 'unrelated' hosts, i.e. hosts from both *Cytisus* and *Genista* groups.

The diversity of *Arytinnis* gen. nov. in the Canary Islands is extraordinarily high for such a small area when compared to the continent. Much of this diversity appears to be linked to host plant diversity in the genus *Teline*. Speciation in other legume-feeding genera represented in the Canary Islands may therefore be constrained by the level of diversification undergone in the host genus. For instance, the host genus *Retama* is represented by a single widespread species which is host to a single psyllid species. The two host genera *Adenocarpus* and *Spartocytisus* are each represented by two ecologically specialized species, with each pair hosting two closely related psyllid species; and on Madeira there is one member of *Genista* and one member of *Teline*, each host to a single psyllid species. In these instances the one-to-one pattern suggests a possible history of parallel diversification in host and psyllid. However, the pattern is increasingly complex in the *Teline*-feeding group, where host sharing and switching may have been facilitated by host hybridization. Asynchronicity of development in species sharing the same host plant and close tracking of host plant phenology may partly explain the complex patterns of host associations. There is some evidence that abundance of psyllid species may be affected by fragmentation of habitat and host plant populations as well as by the cultivation of native legumes for fodder crops. In particular, the cultivation of 'tagasaste' (*Chamaecytisus proliferus* ssp. *proliferus* var *palmensis*) could account for the high densities of psyllids associated with this host, on both cultivated and natural populations of 'tagasaste' as well as on other intraspecific taxa.

More than a quarter of the new species described were collected from continental hosts in the genus *Adenocarpus*, but only a little over half the species in this genus were sampled. With several species endemic to montane regions in north Africa, in addition to being the only genus in the Genisteae with a distribution extending into tropical Africa (*A. mannii* is found in montane regions from Nigeria to Malawi and Angola), further extensive sampling of this host genus may reveal additional species that would contribute to the understanding of the phylogenetics of the Arytaininae, in particular the genus *Livilla sensu lato.*

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TABLE 1. Genera and taxa included in this treatment showing native distribution, host plant genus and host group affiliation within the Genisteae; CY – Cytisus group, GE – Genista group, OU – outlier.

| **species** | **native distribution** | **host plant genus and group** | |
|---|---|---|---|
| *ARYTAINILLA* | | | |
| ***Arytainilla sensu stricto*** | | | |
| *A. algeriensis* | N Africa | *Cytisus* | CY |
| *A. barbagalloi* | Italy | *Genista* | GE |
| *A. cytisi* | Europe, N Africa, Middle East | *Calicotome* | CY |
| *A. delarbrei* | W Europe, N Africa | *Cytisus* | CY |
| *A. spartiicola* | W Europe | *Cytisus* | CY |
| *A. spartiophila* | W Europe, N Africa | *Cytisus* | CY |
| *A. serpentina* | Canary Islands | *Spartocytisus* | CY |
| ***Arytainilla* residual species** | | | |
| *A. gredi* | Spain | *Genista* | GE |
| *A. montivaga* | Spain, Morocco | *Adenocarpus* | OU |
| *A. sulci* | N Africa, Middle East | *Retama* | GE |
| *ARYTINNIS* | | | |
| *A. berber* | Morocco | *Genista* | GE |
| *A. canariensis* | Canary Islands | *Teline* | GE |
| *A. cognata* | Morocco | *Genista* | GE |
| *A. diluta* | Canary Islands | *Teline* | GE |
| *A. dividens* | Canary Islands | *Chamaecytisus* | CY |
| *A. equitans* | Canary Islands | *Teline* | GE |
| *A. fortunata* | Canary Islands | *Teline* | GE |
| *A. gomerae* | Canary Islands | *Teline* | GE |
| *A. hakani* | Mediterranean | *Teline* | GE |
| *A. hupalupa* | Canary Islands | *Teline* | GE |
| *A. incuba* | Madeira | *Teline* | GE |
| *A. menceyata* | Canary Islands | *Teline* | GE |
| *A. modica* | Canary Islands | *Teline*, *Chamaecytisus* | GE + CY |
| *A. nigralineata* | Canary Islands | *Adenocarpus* | OU |
| *A. occidentalis* | Canary Islands | *Teline* | GE |

| | | | |
|---|---|---|---|
| *A. ochrita* | Canary Islands | *Teline* | GE |
| *A. pileolata* | Canary Islands | *Teline* | GE |
| *A. proboscidea* | Canary Islands | *Adenocarpus* | OU |
| *A. prognata* | Canary Islands | *Teline* | GE |
| *A. romeria* | Canary Islands | *Teline* | GE |
| *A. umbonata* | Madeira | *Genista* | GE |
| *ARYTAINA* | | | |
| *A. devia* | Canary Islands | *Chamaecytisus* | CY |
| *A. nubivaga* | Canary Islands | *Spartocytisus* | CY |
| *A. vittata* | Canary Islands | *Spartocytisus* | CY |
| *LIVILLA* | | | |
| *L. baetica* | Spain | *Adenocarpus* | OU |
| *L. caprifuga* | Morocco | *Adenocarpus* | OU |
| *L. complexa* | Spain, Portugal | *Adenocarpus* | OU |
| *L. ima* | Morocco | *Adenocarpus* | OU |
| *L. monospermae* | Canary Islands | *Retama* | GE |
| *PSEUDACANTHOPSYLLA* | | | |
| *P. improvisa* | Morocco | *Retama* | GE |
| *ACIZZIA* | | | |
| *A. uncatoides* | Australia | *Acacia* | — |

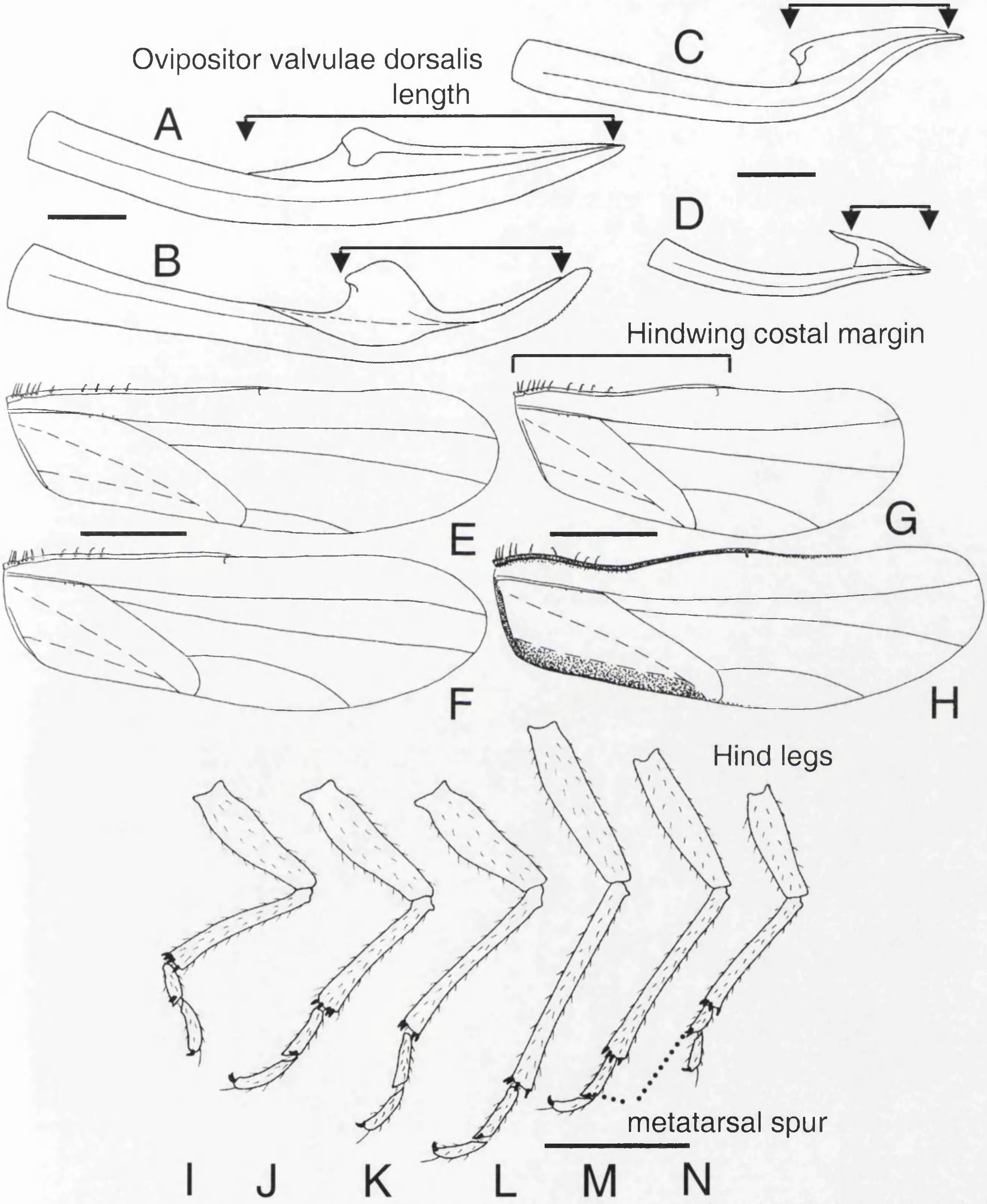

FIGURE 1. Examples of variation in adult ovipositors, hindwings and hind legs. A – *Arytainilla spartiophila*, B – *A. sulci*, C – *A. gredi*, D – *Acizzia uncatoides*, E – *Livilla monospermae*, F – ***Arytainilla serpentina*** **sp. nov.**, G – *Arytinnis nigralineata*, H – ***Arytaina vittata*** **sp. nov.**, I – ***Arytainilla serpentina*** **sp. nov.**, J – ***Arytaina vittata*** **sp. nov.**, K – *Livilla monospermae*, L – *Arytinnis nigralineata*, M – ***A. canariensis*** **sp. nov.**, N – ***A. romeria*** **sp. nov.** Scale bars: A–D = 0.1 mm, E–N = 0.5 mm.

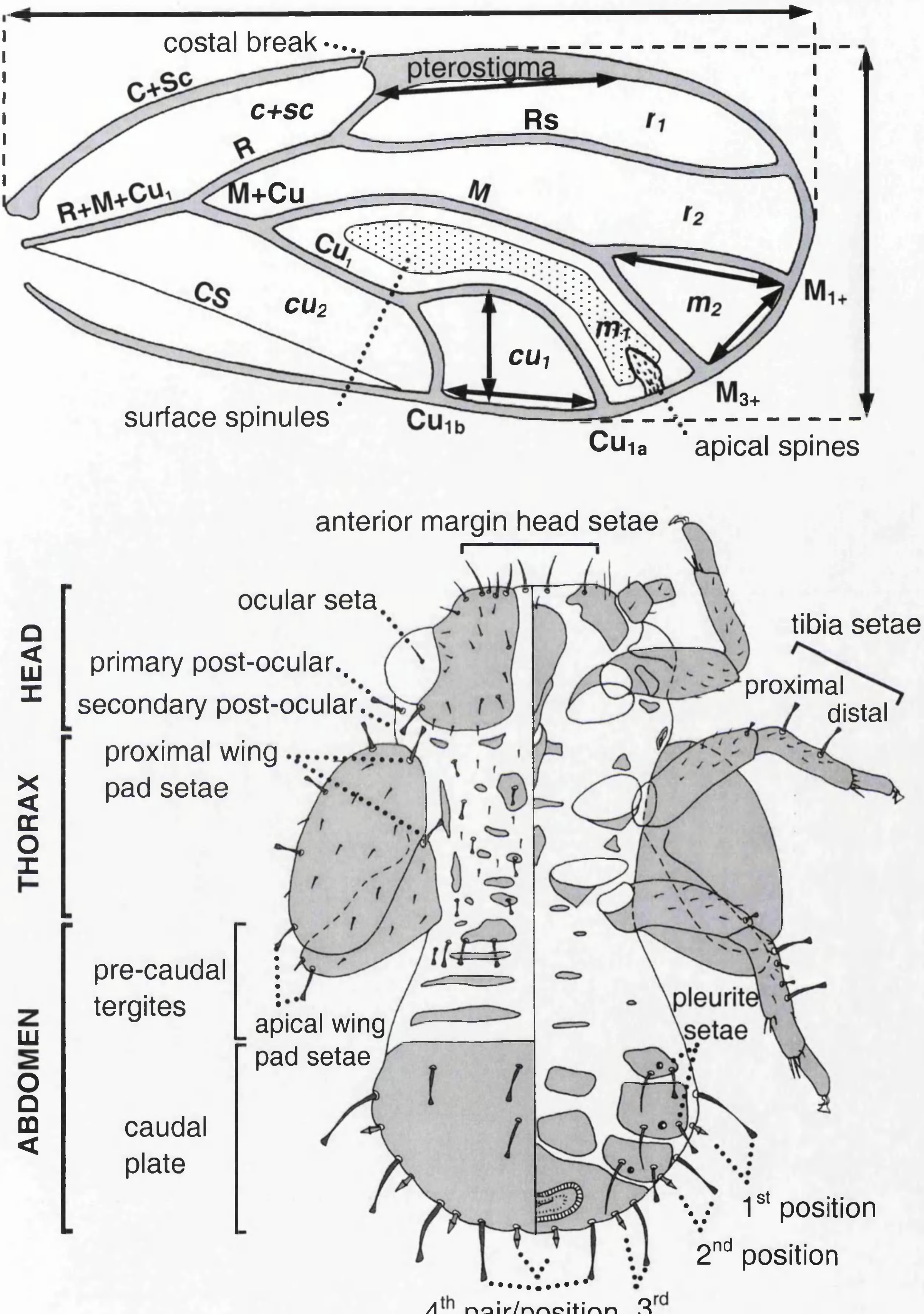

FIGURE 2. Adult forewing (above) and 5th instar nymph (below): guide to measurements, terminology and nymphal chaetotaxy. 5th instar nymphs can be distinguished from the preceeding four instars by the number of antennal segments and the differentiation of the tibia and tarsal segments.

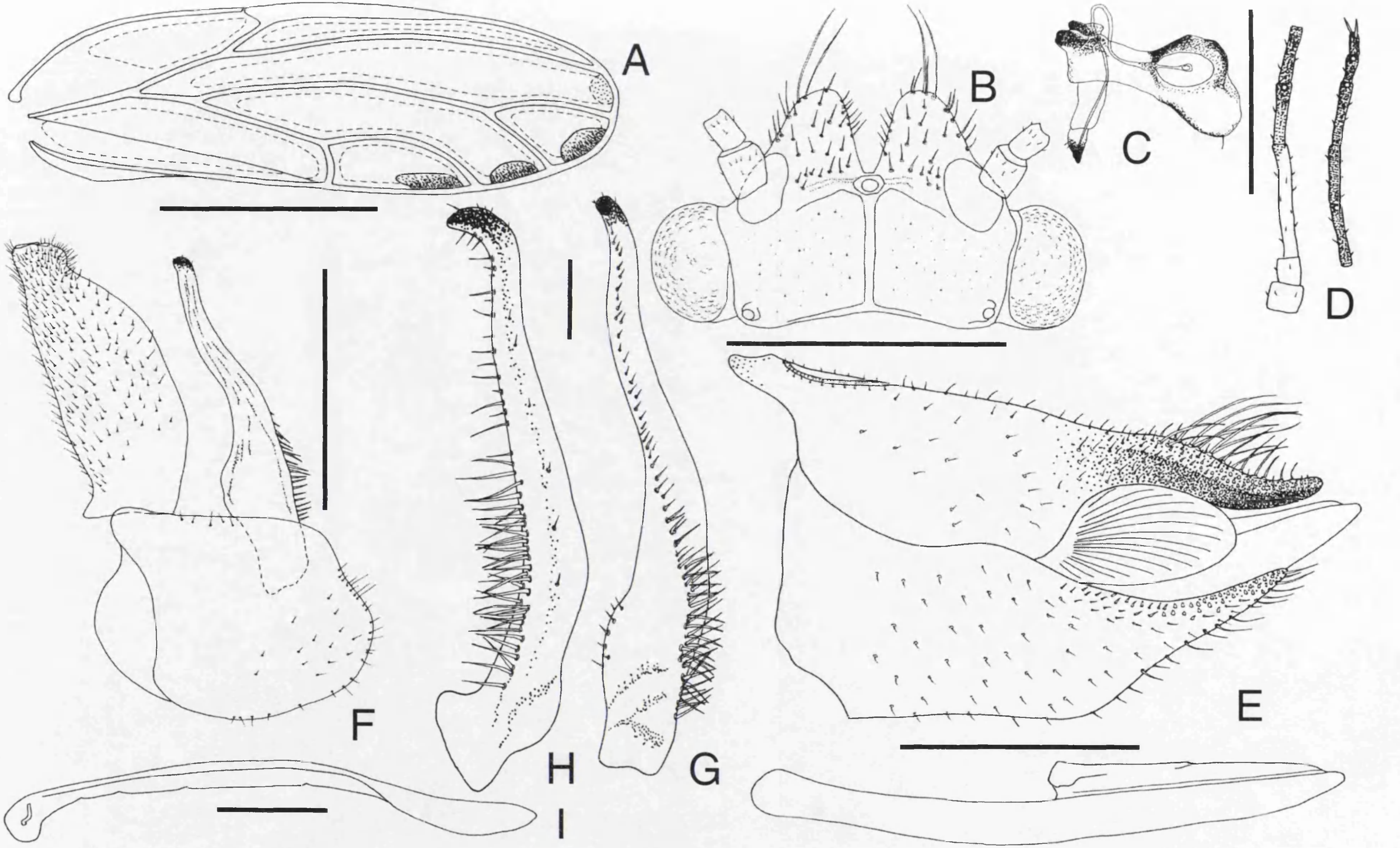

FIGURE 3. ***Arytainilla serpentina* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

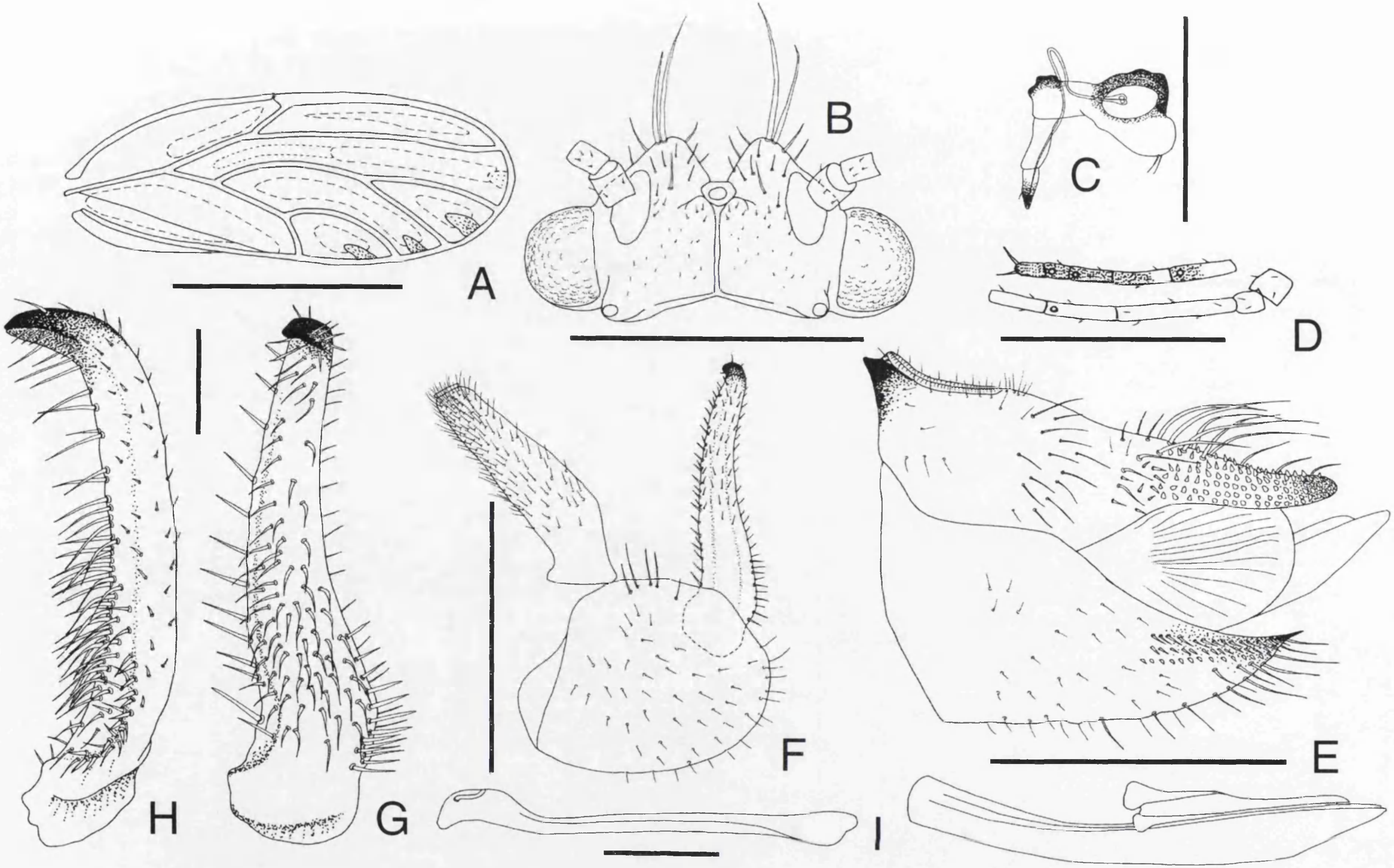

FIGURE 4. ***Arytainilla atlantica*** **sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

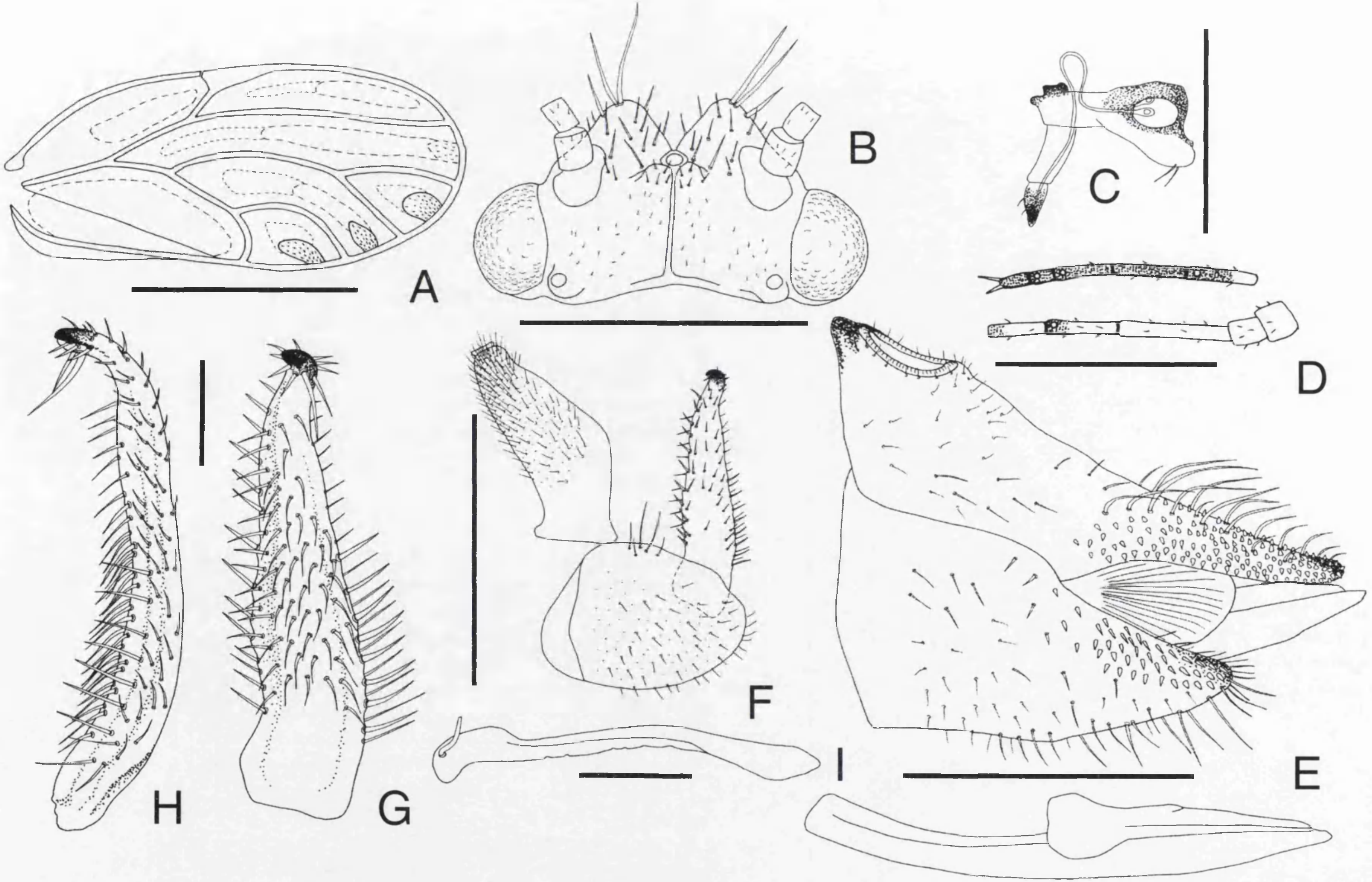

FIGURE 5. ***Arytainilla telonicola* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

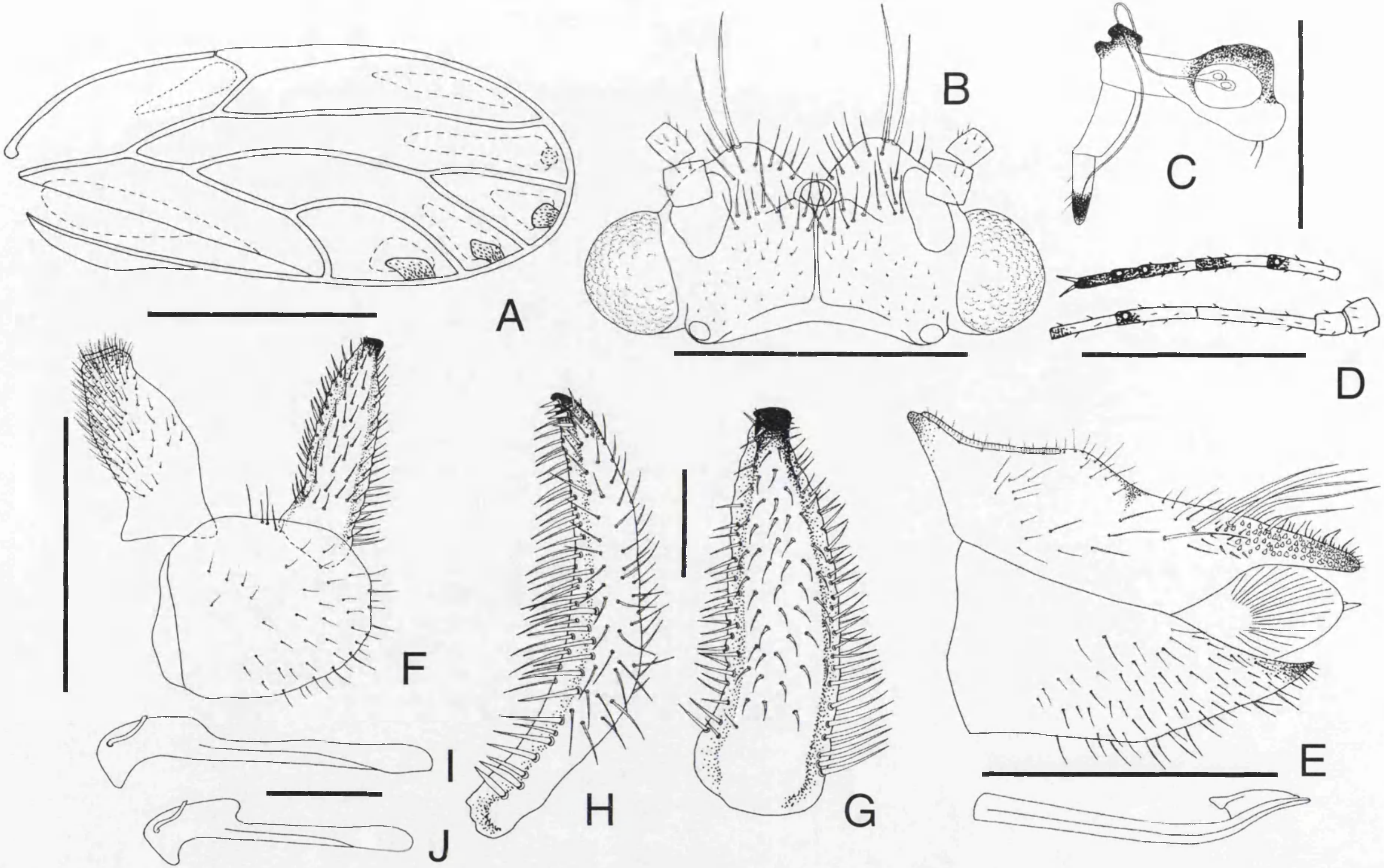

FIGURE 6. ***Arytainilla montivaga* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – aedeagus Spanish populations, J – aedeagus Moroccan populations. Scale bars: A = 1 mm. B–F = 0.5 mm. G–I = 0.1 mm.

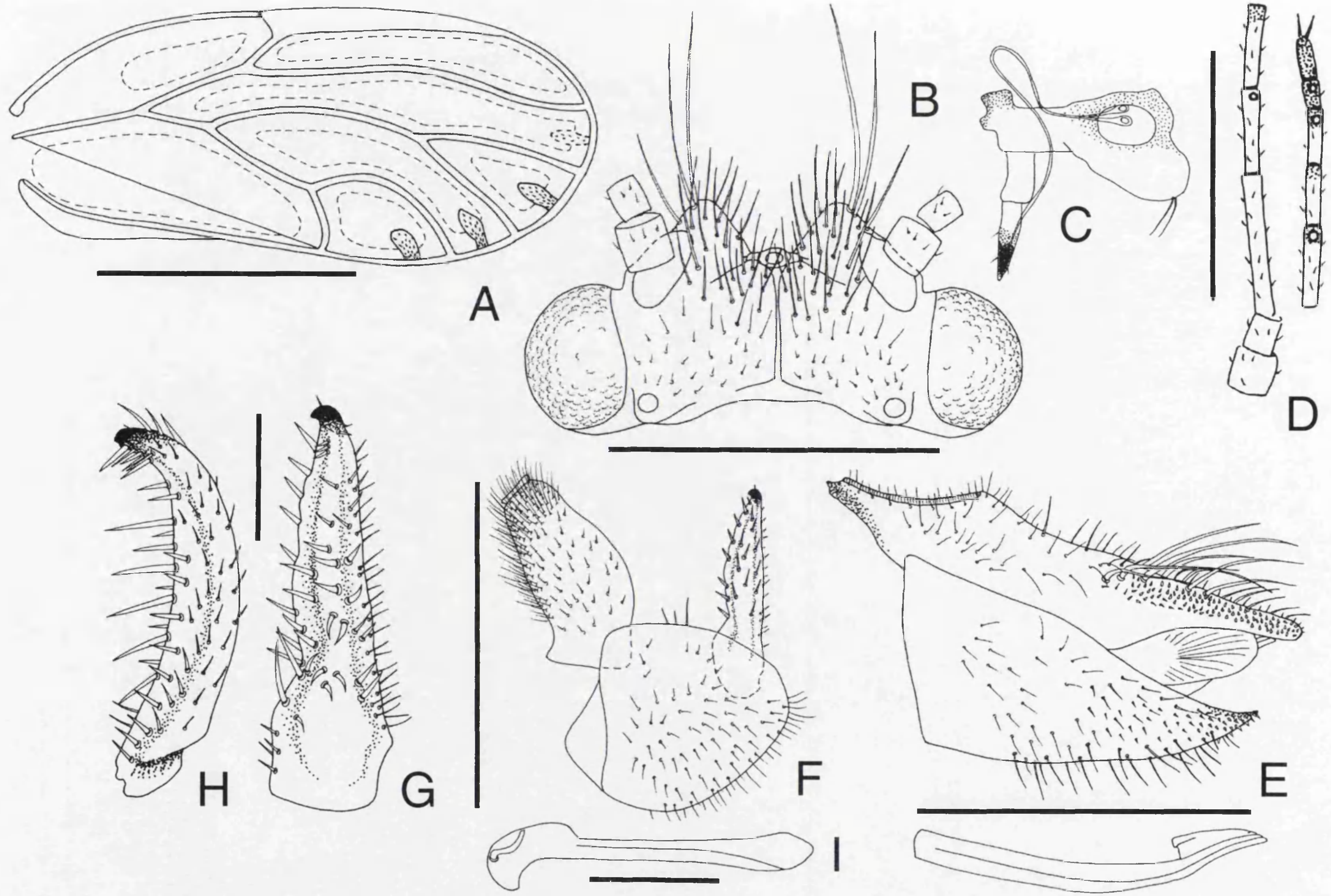

FIGURE 7. ***Arytinnis romeria* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

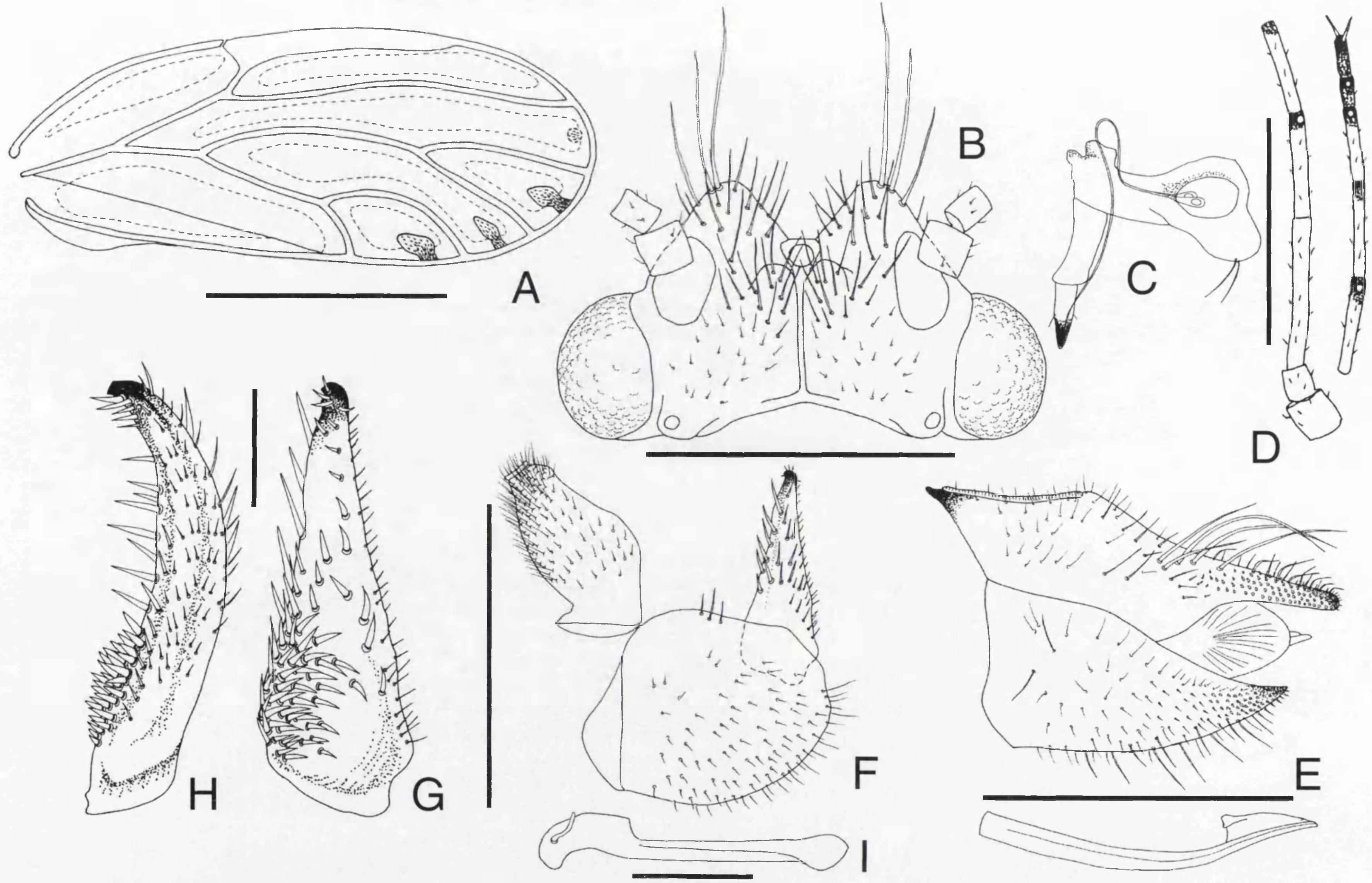

FIGURE 8. ***Arytinnis fortunata*** **sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

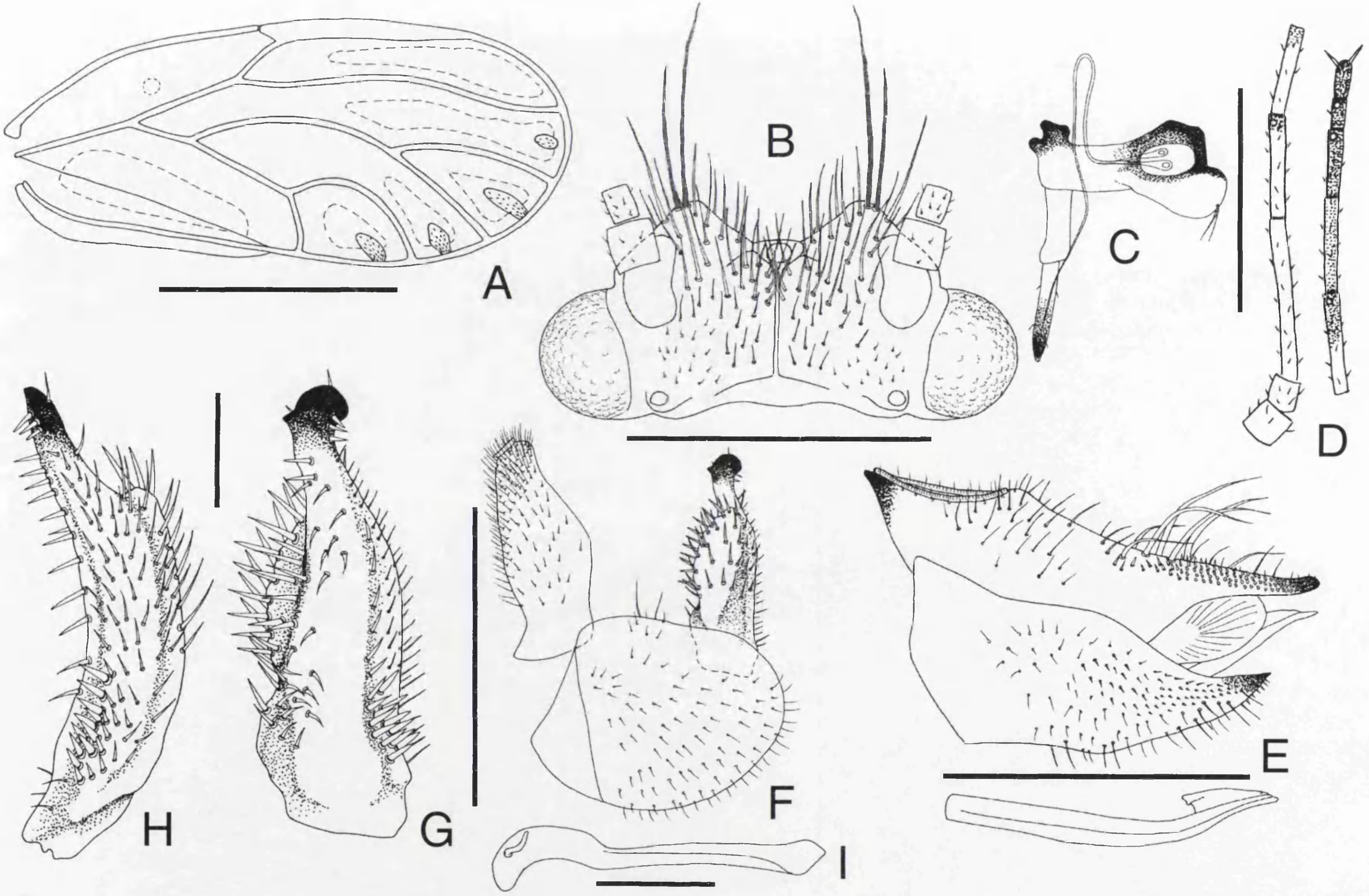

FIGURE 9. ***Arytinnis canariensis* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

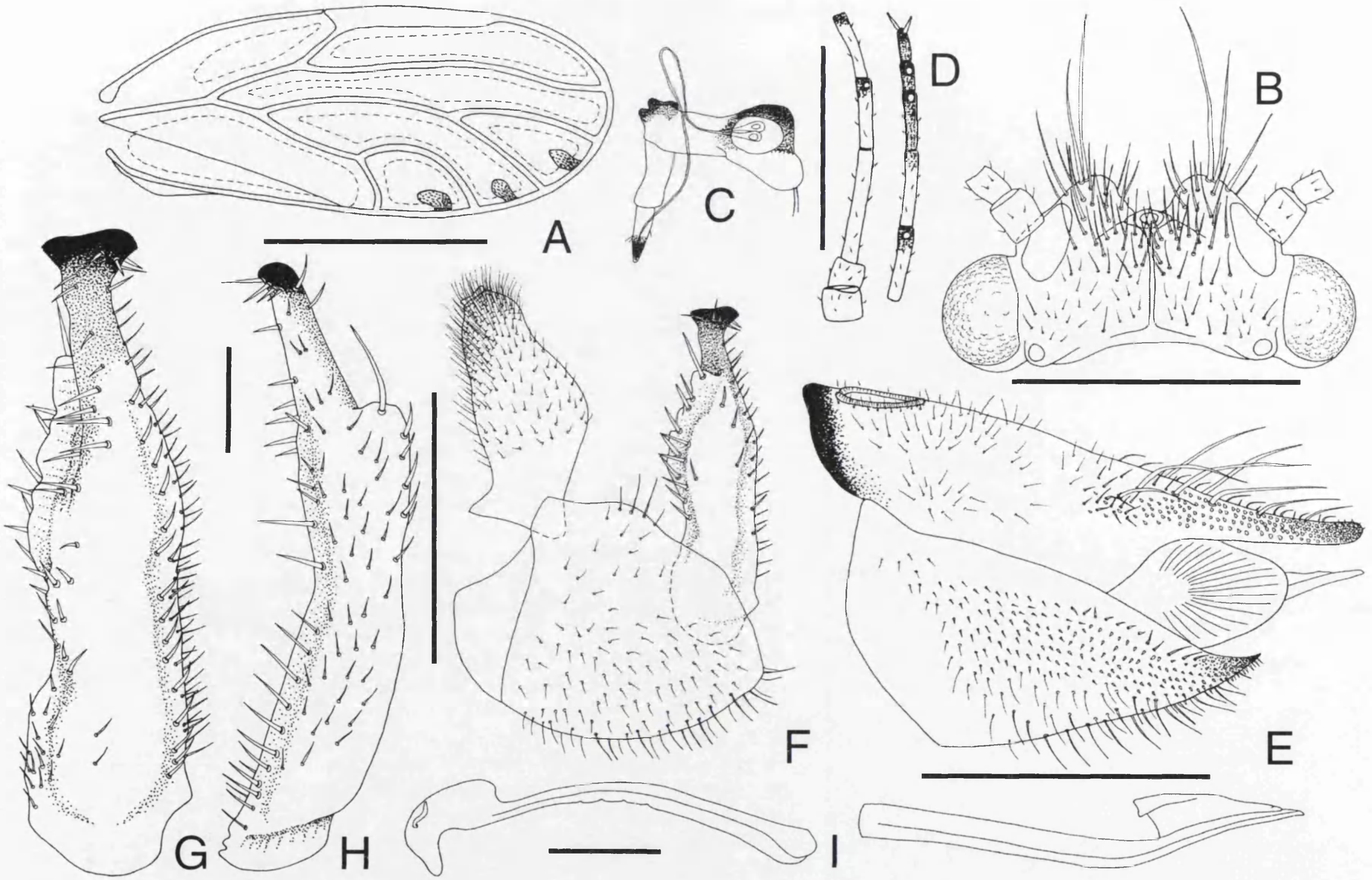

FIGURE 10. ***Arytinnis menceyata* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

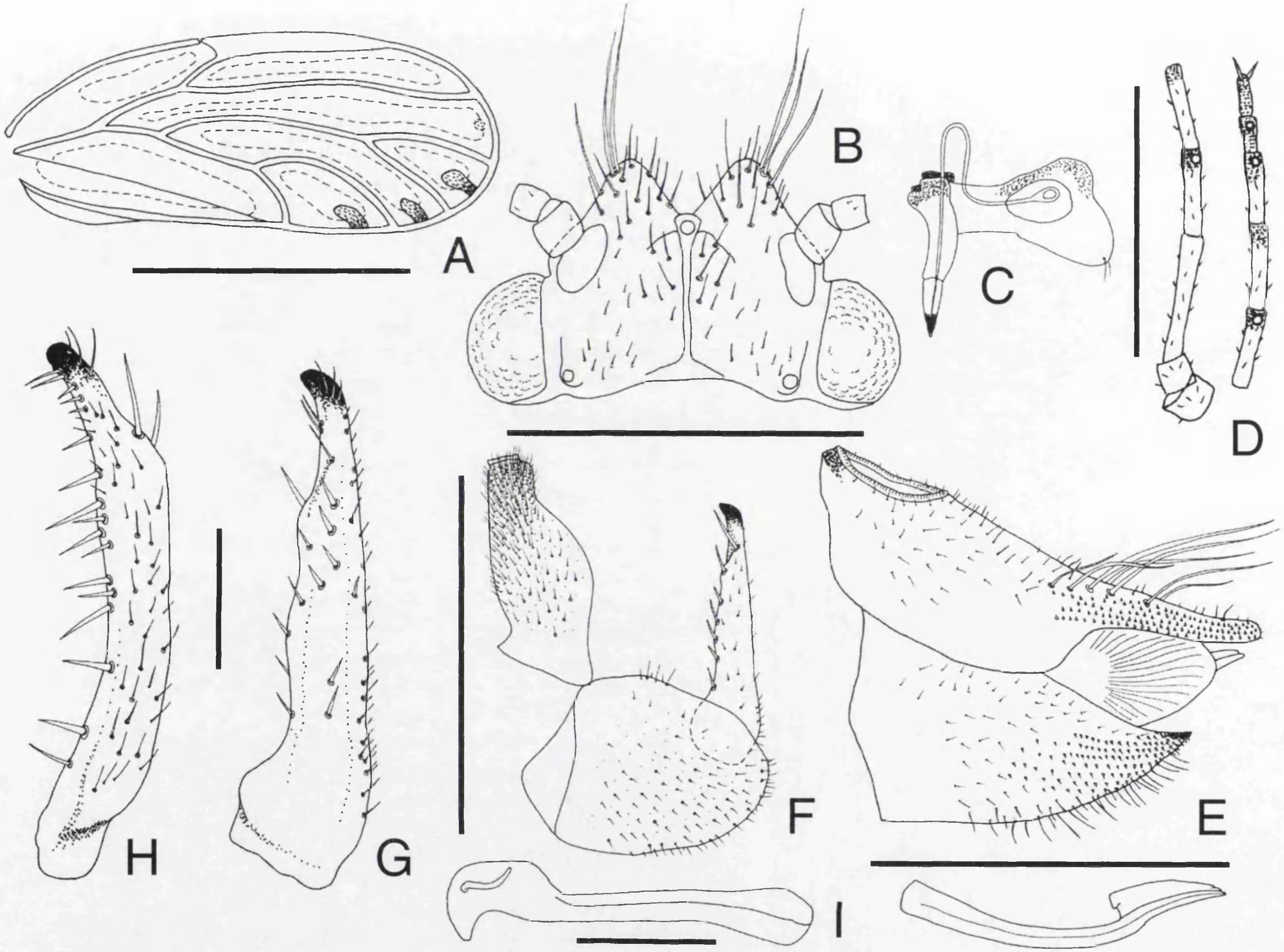

FIGURE 11. ***Arytinnis ochrita* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

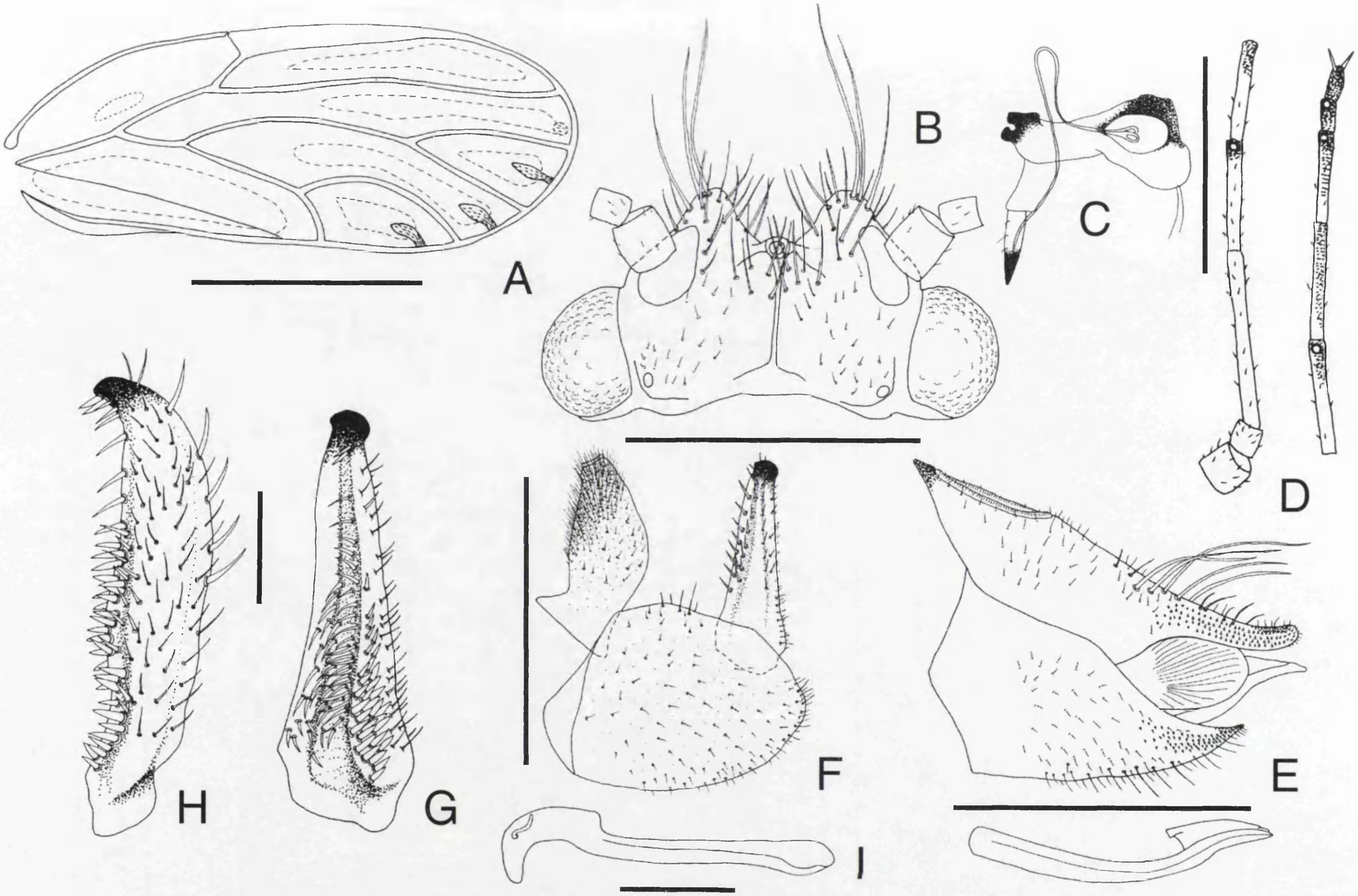

FIGURE 12. ***Arytinnis occidentalis* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

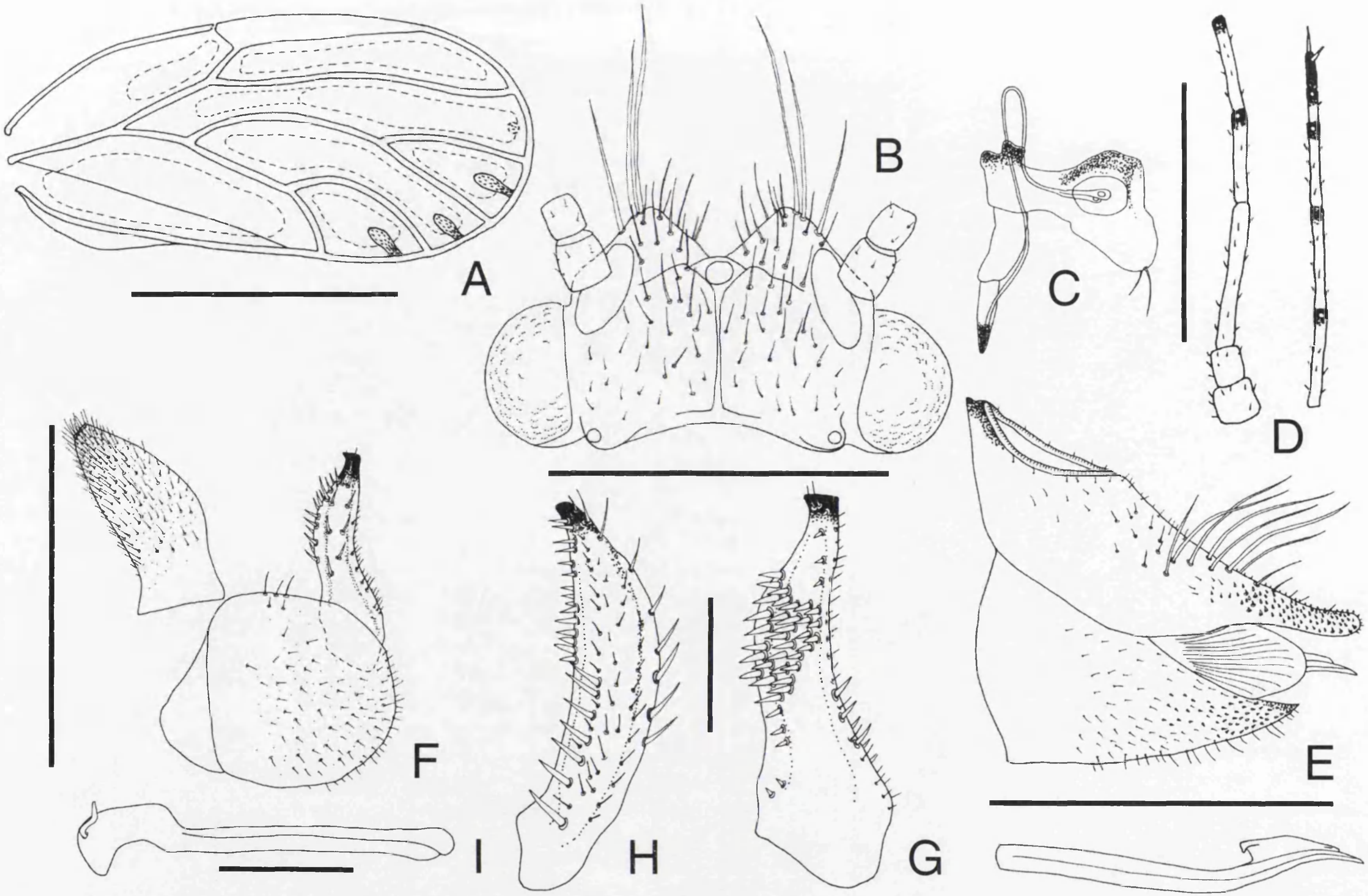

FIGURE 13. ***Arytinnis gomerae* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

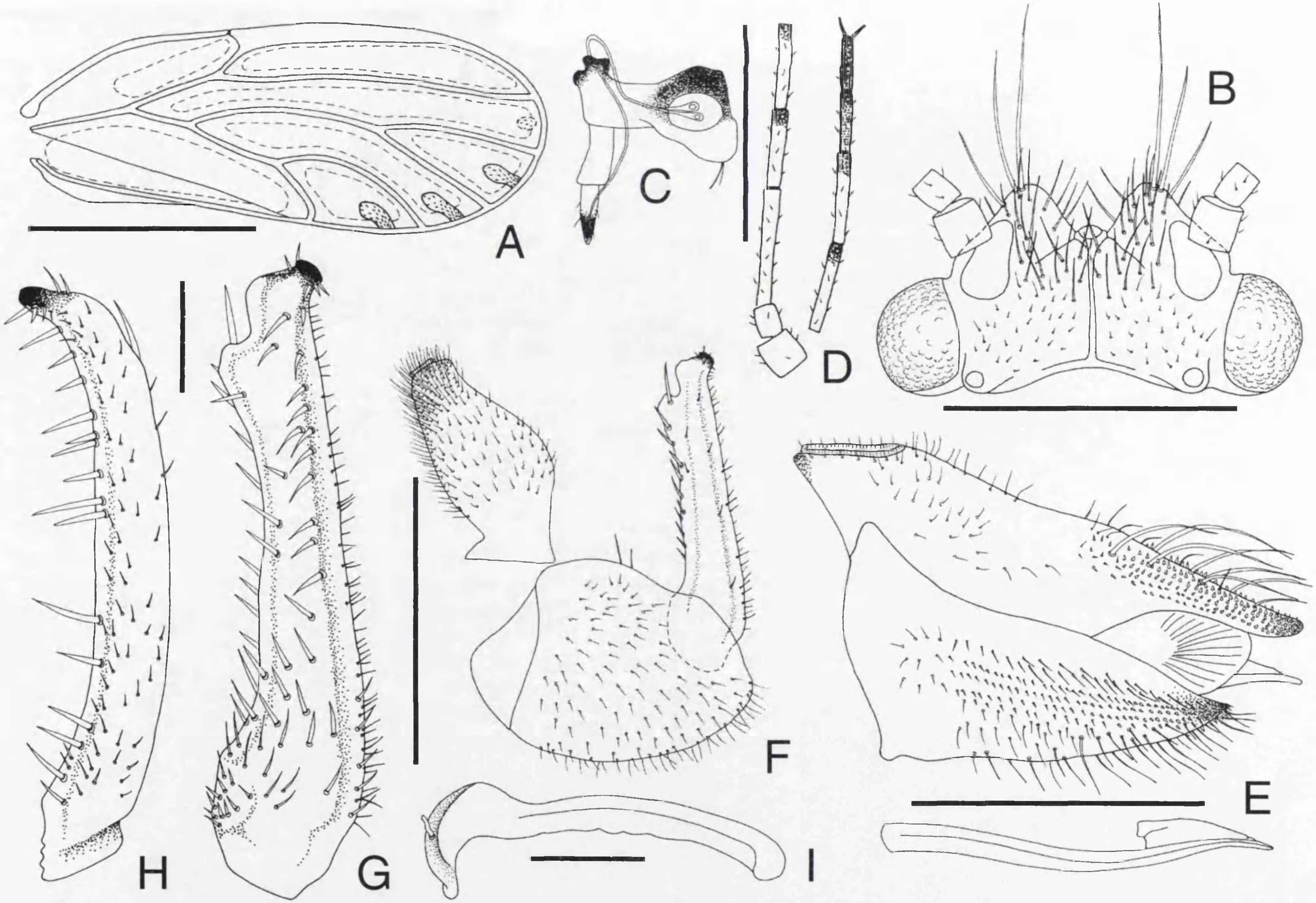

FIGURE 14. ***Arytinnis hupalupa* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

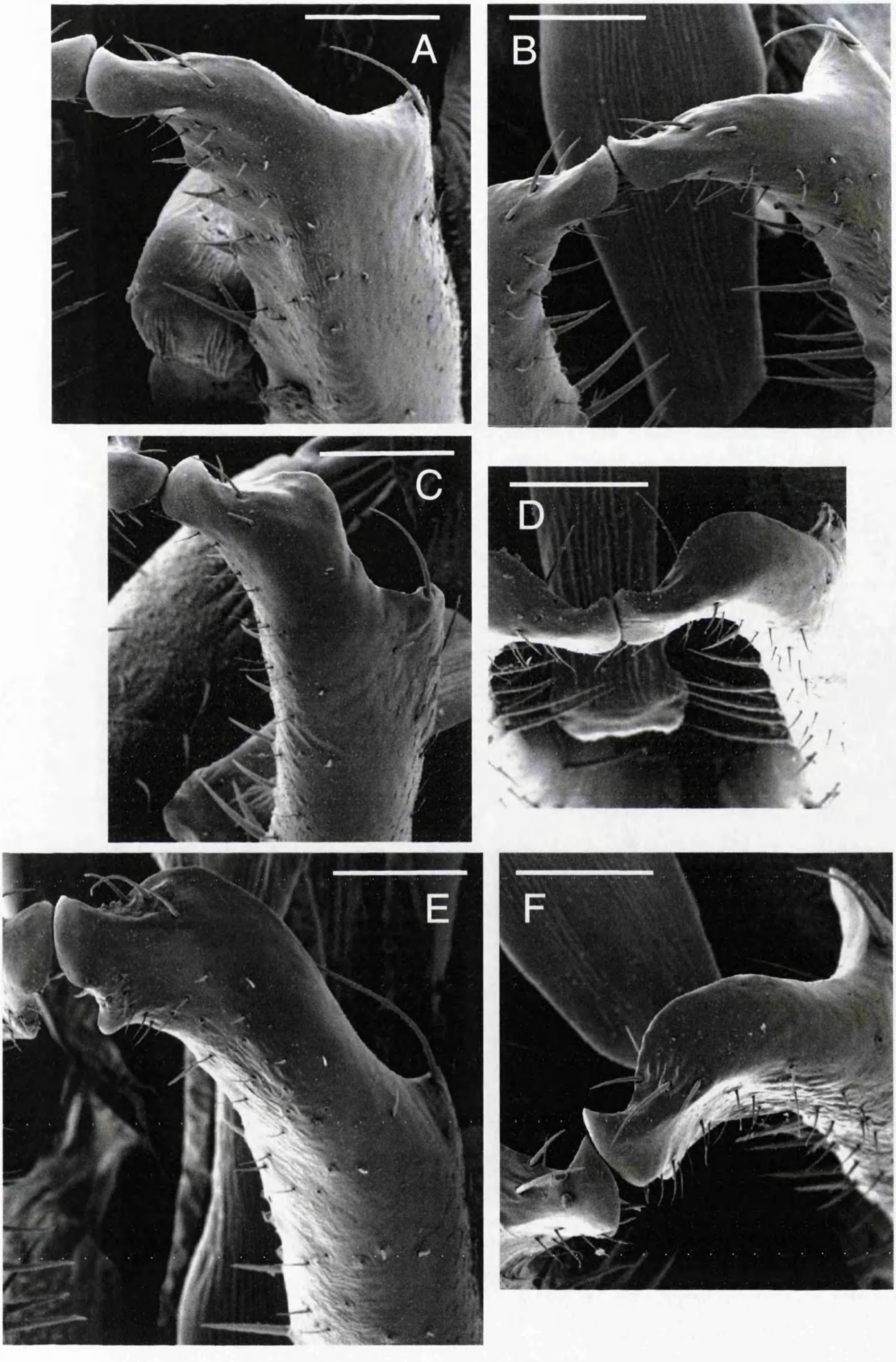

FIGURE 15. ♂ parameres in lateral and dorsal views, A–B *Arytinnis modica*, C–D ***A. hupalupa* sp. nov.**, E–F *A. dividens* (scale bars = 50 $\mu$m).

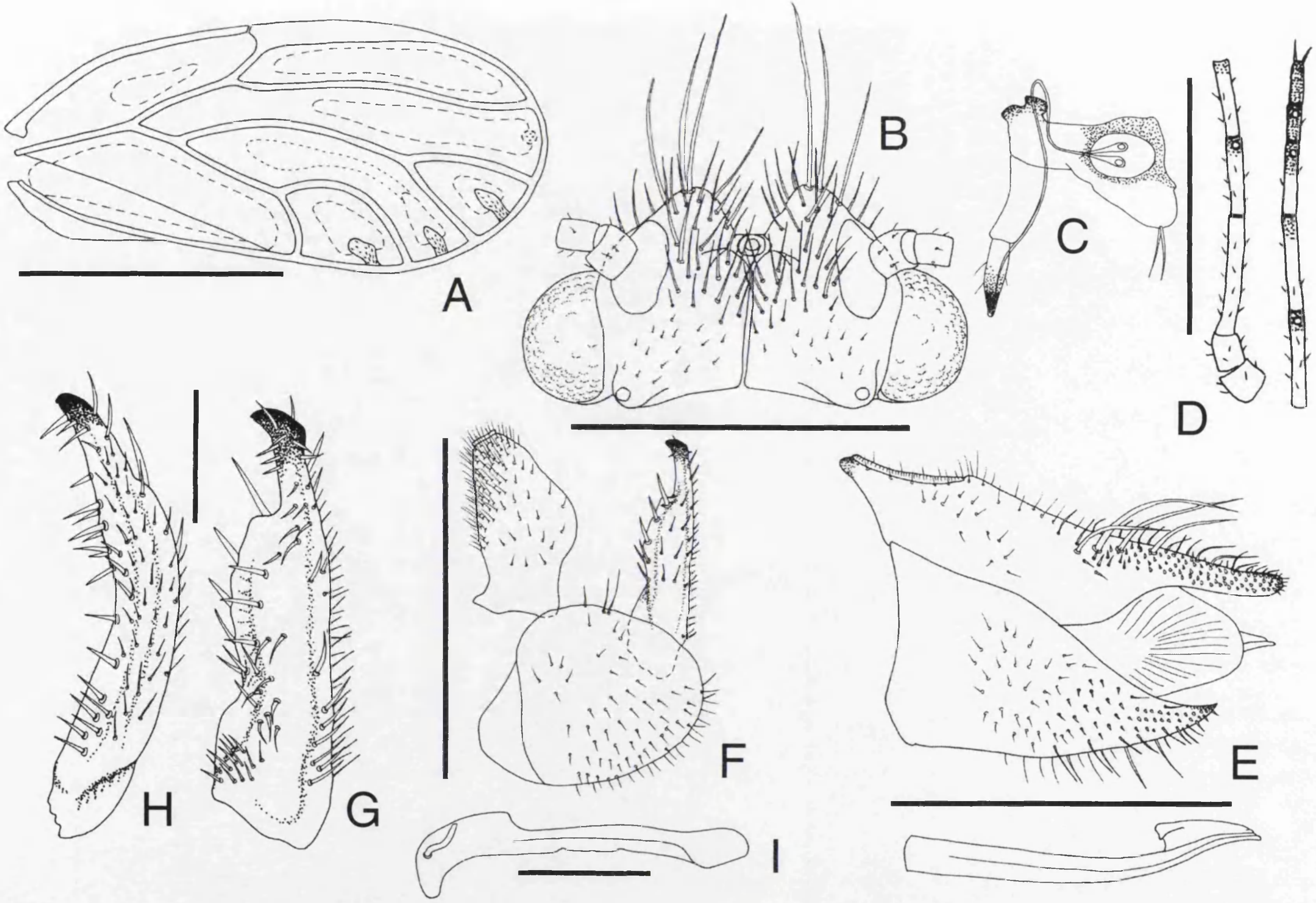

FIGURE 16. ***Arytinnis berber* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

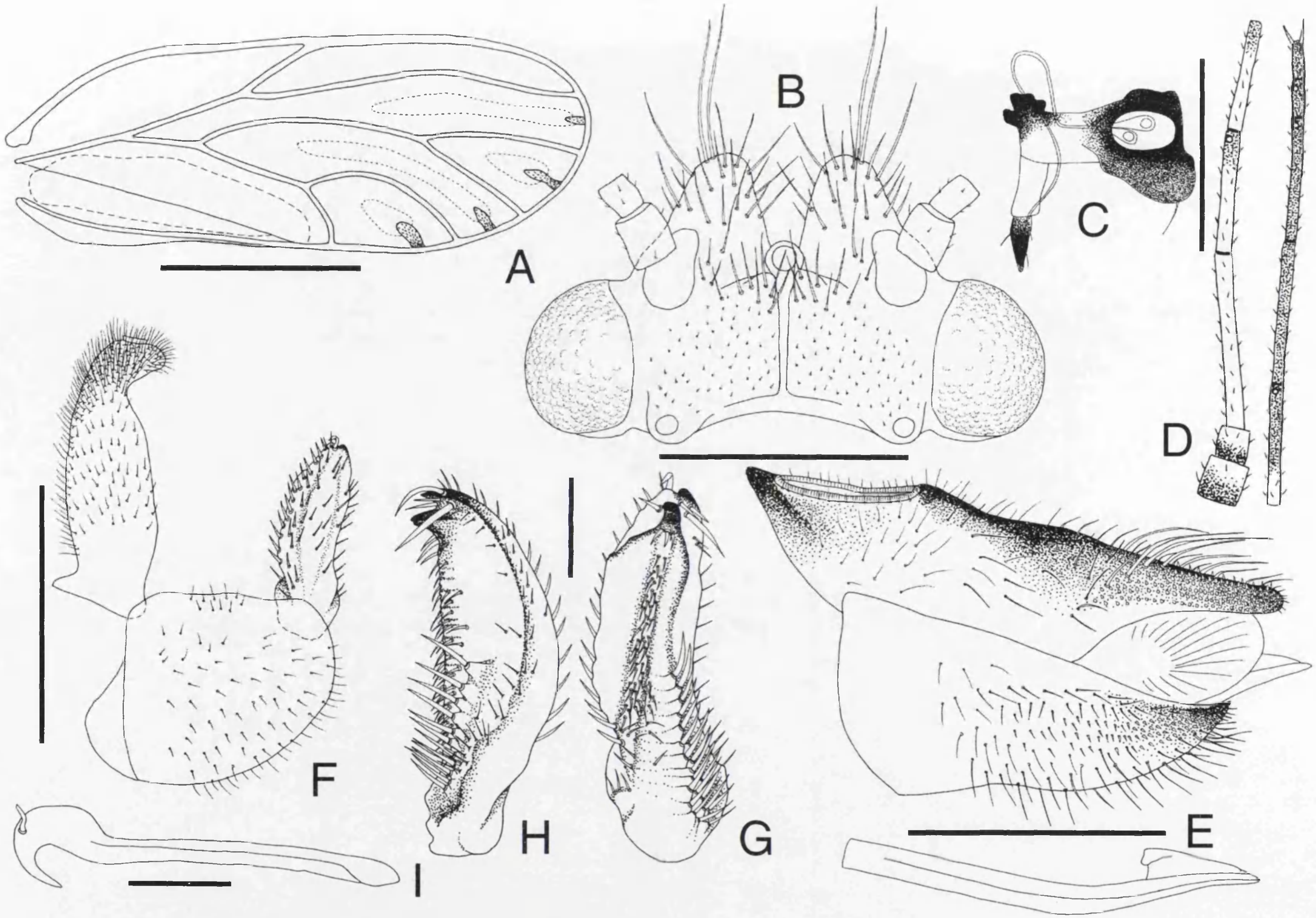

FIGURE 17. ***Arytaina vittata*** **sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

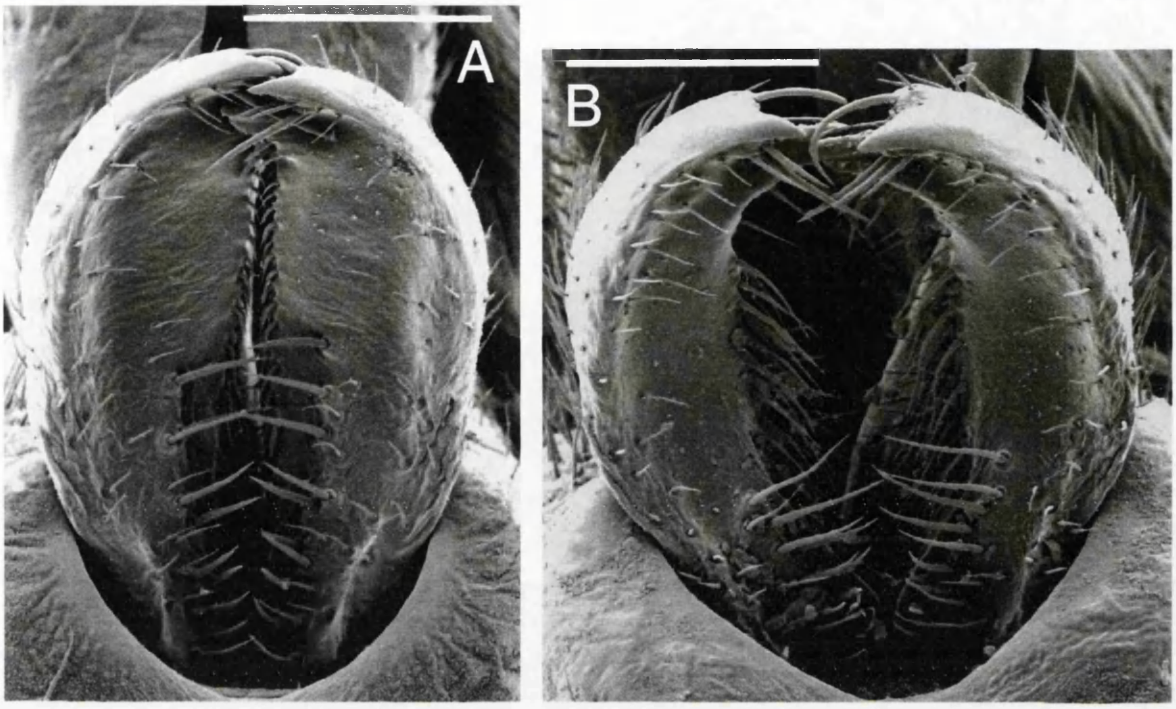

FIGURE 18. ♂ parameres in posterior view, A – ***Arytaina vittata* sp. nov.**, B – *A. nubivaga* (scale bars = 0.1 mm).

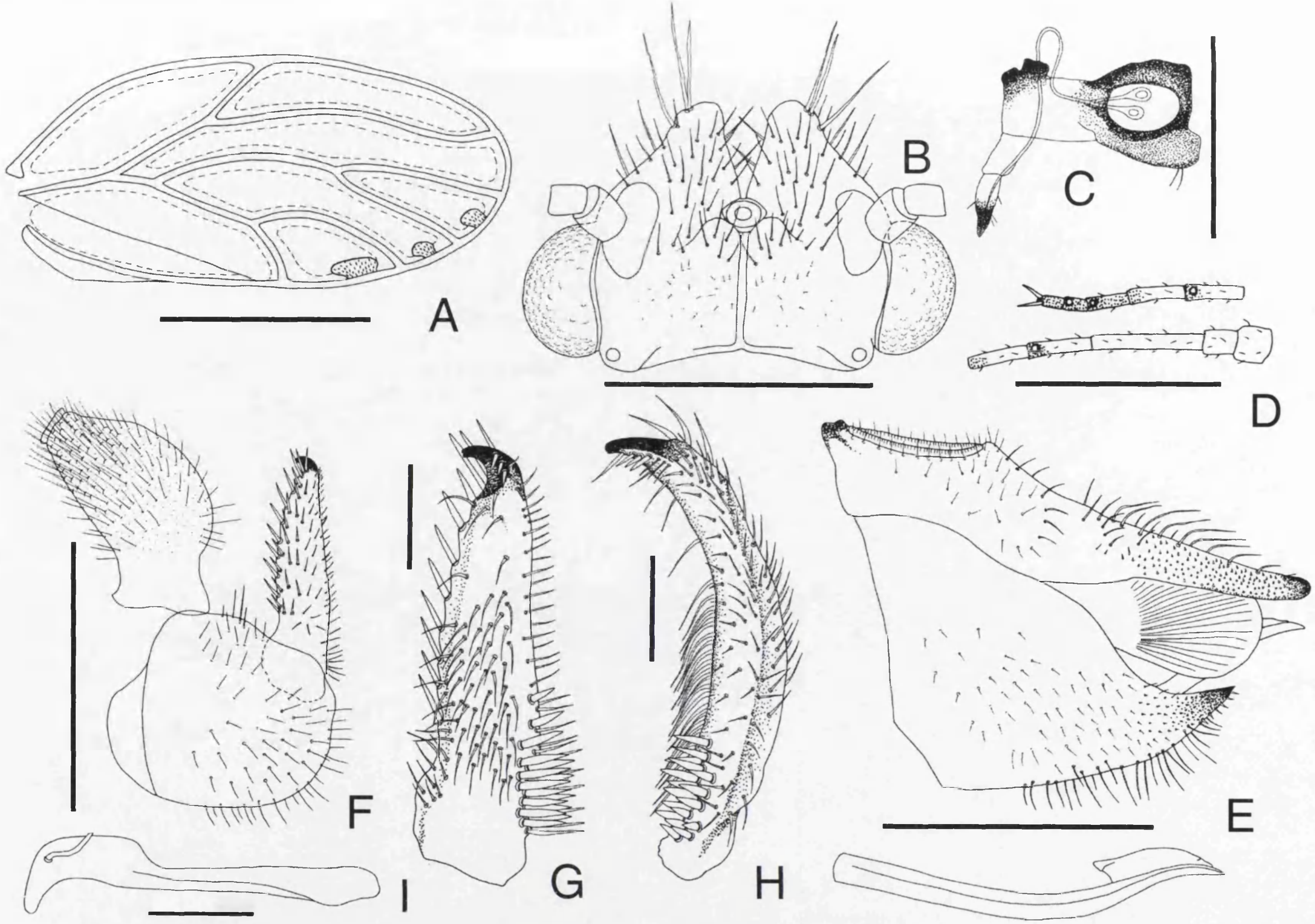

FIGURE 19. ***Livilla caprifuga* sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

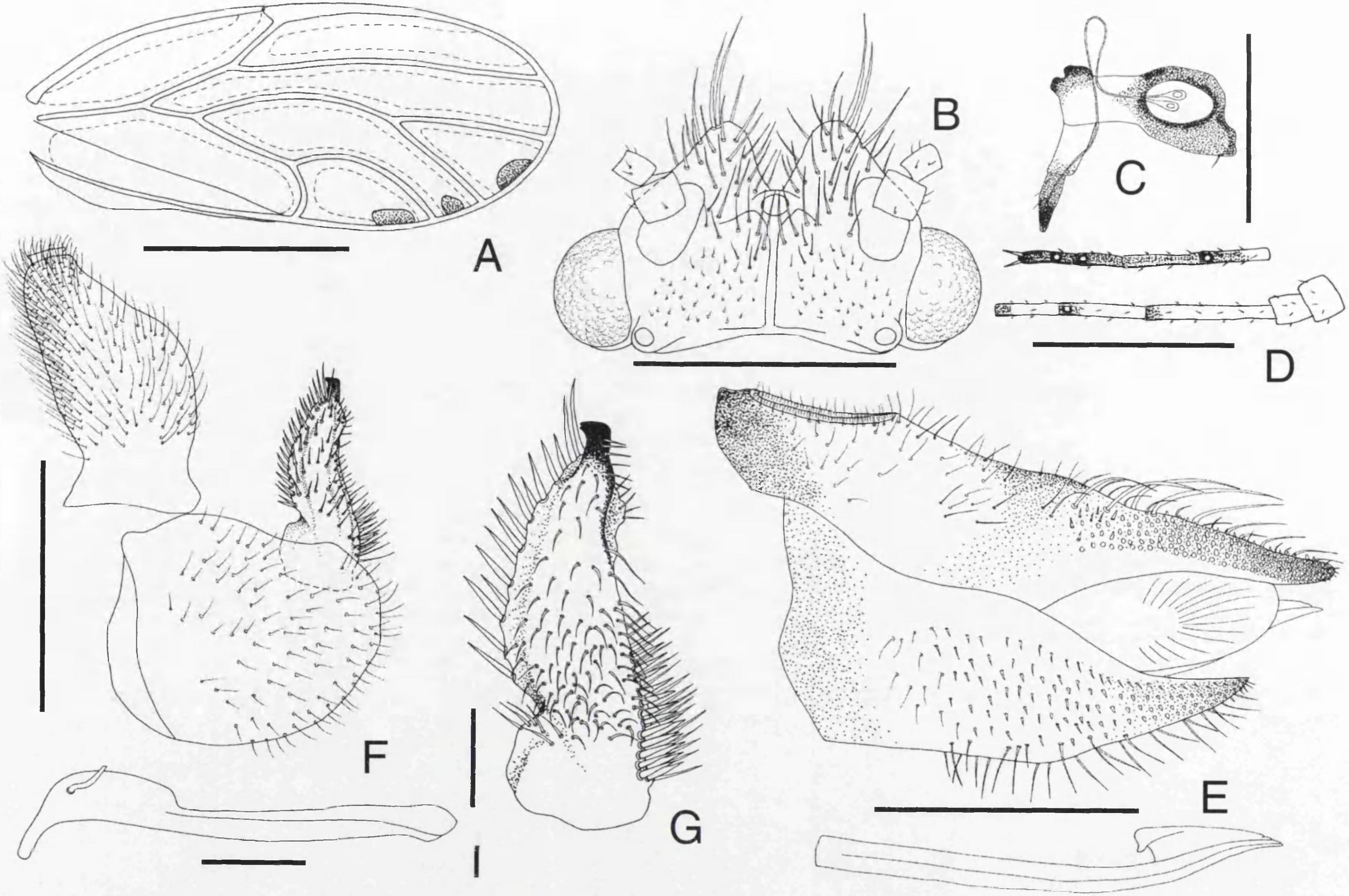

FIGURE 20. ***Livilla baetica*** **sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀ genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus. Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

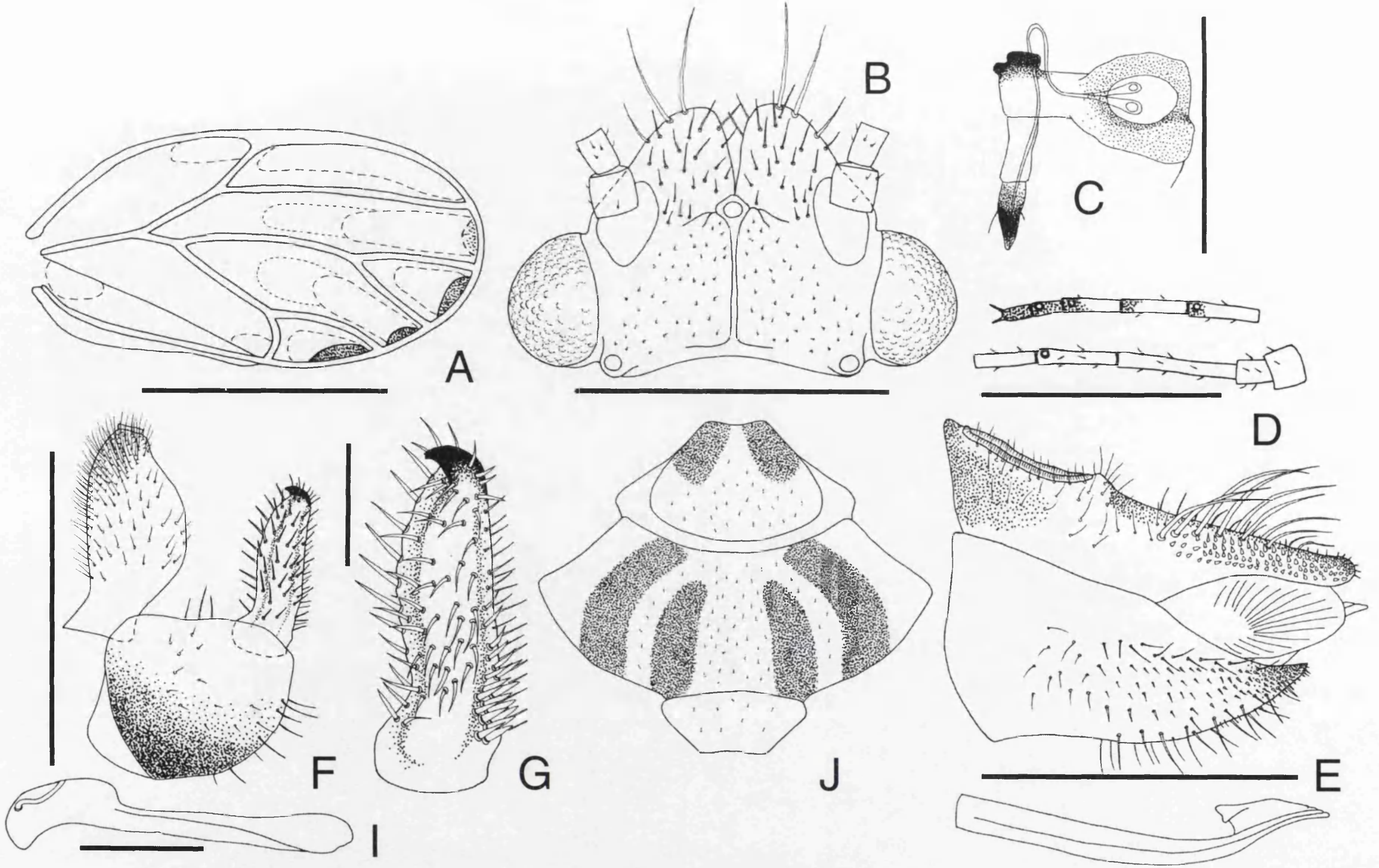

FIGURE 21. ***Livilla complexa*** **sp. nov.** A – forewing, B – head, C – proboscis and clypeus, D – antenna, E – ♀genitalia and ovipositor, F – ♂ genitalia, G – ♂ paramere interior view, H – ♂ paramere posterior view, I – ♂ aedeagus, J – thoracic tergal plates.

Scale bars: A = 1 mm, B–F = 0.5 mm, G–I = 0.1 mm.

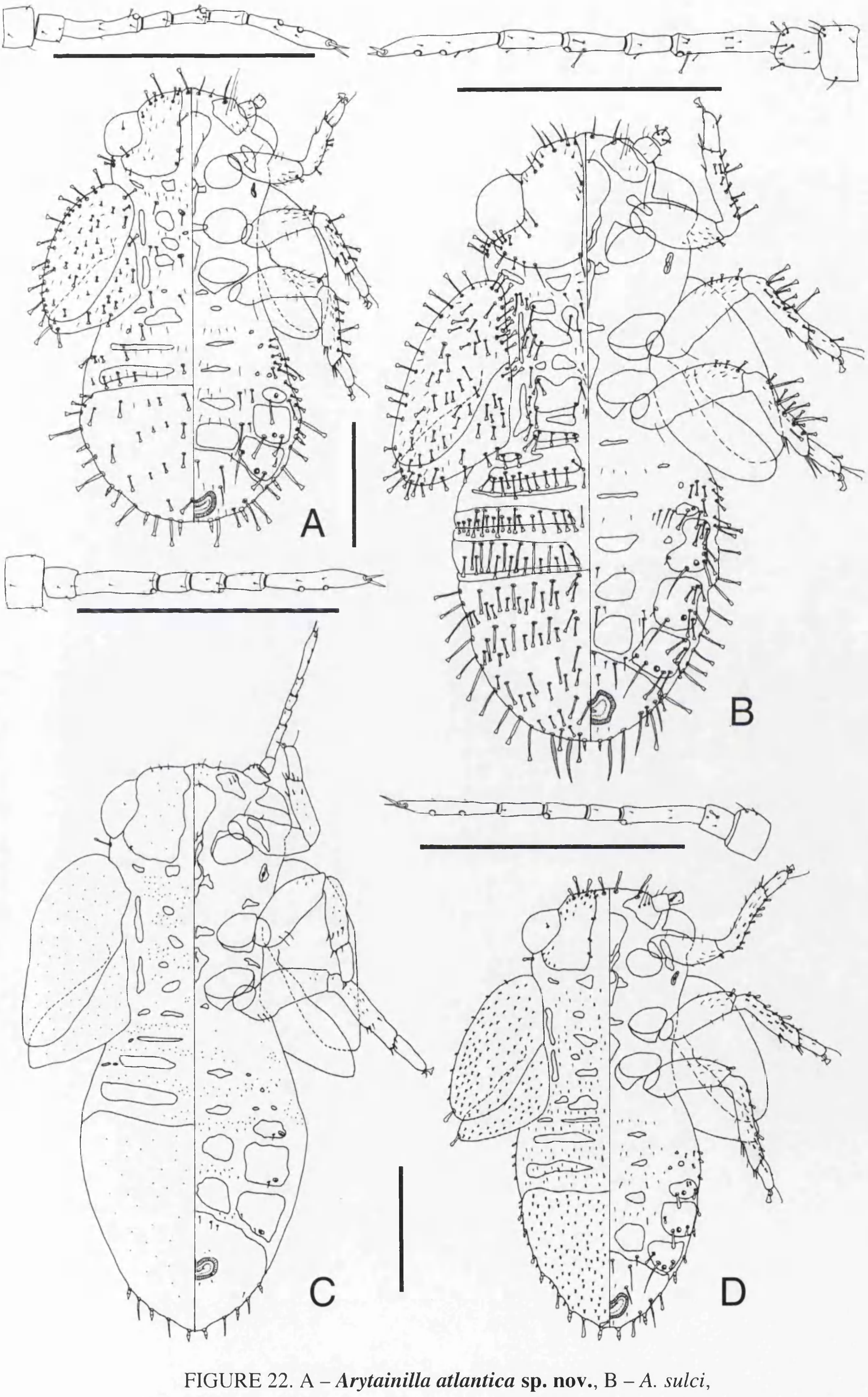

FIGURE 22. A – ***Arytainilla atlantica* sp. nov.**, B – *A. sulci*, C – ***A. serpentina* sp. nov.**, D – ***A. telonicola* sp. nov.** Scale bars = 0.5 mm.

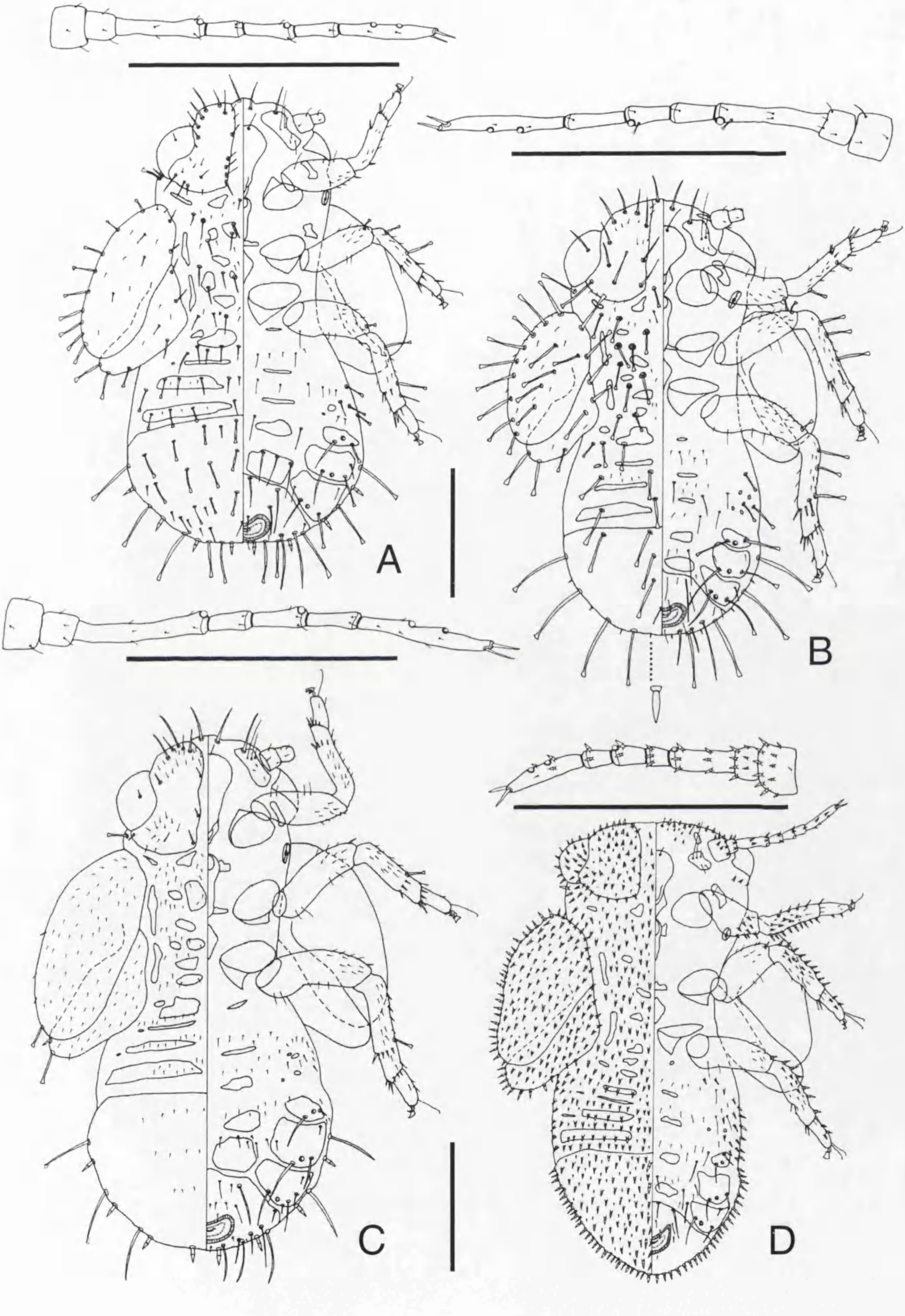

FIGURE 23. A – *Arytainilla gredi*, B – ***A. montivaga* sp. nov.**, C – *Livilla ima*, D – *Pseudacanthopsylla improvisa*. Scale bars = 0.5 mm.

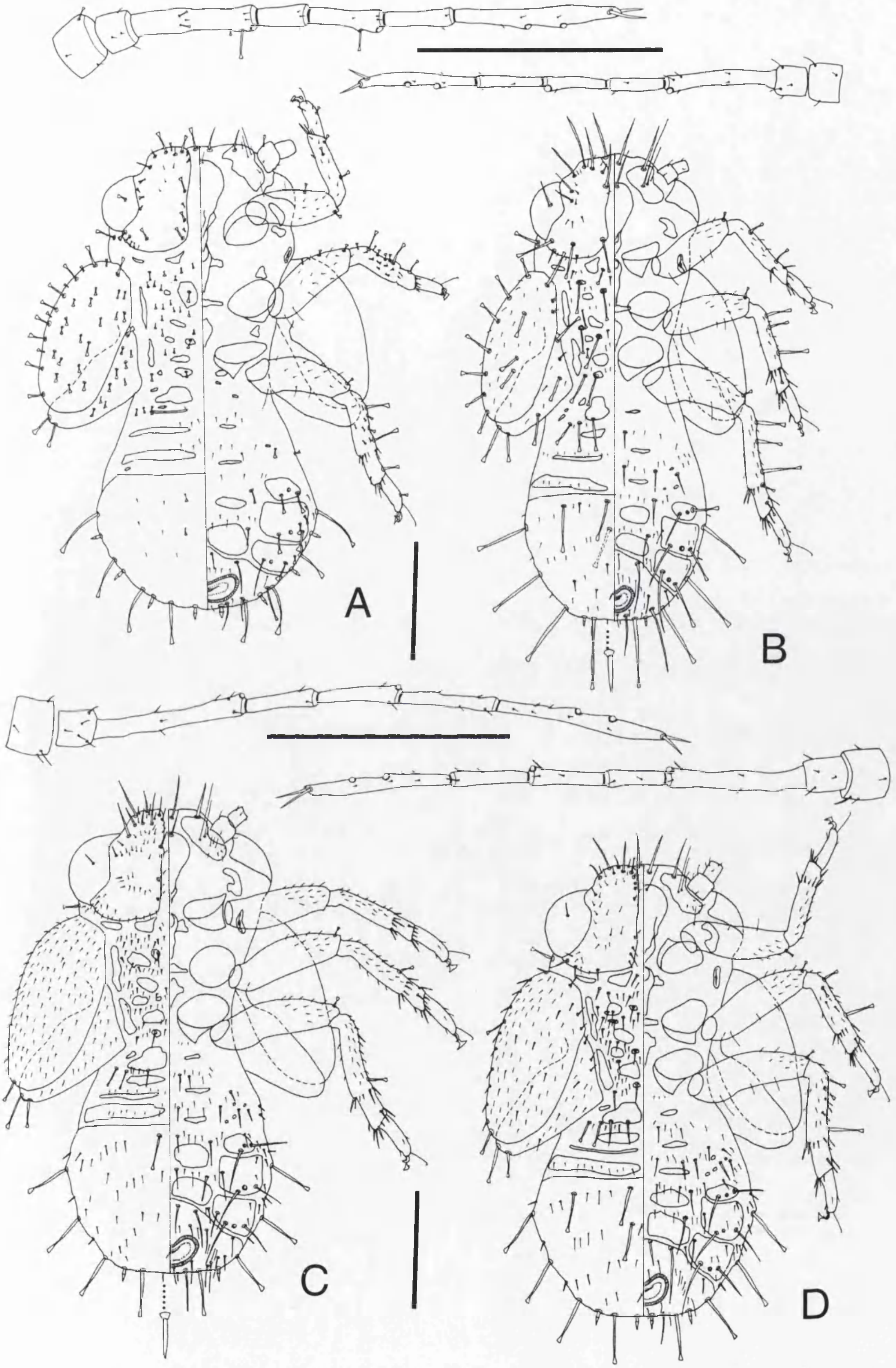

FIGURE 24. A – *Livilla monospermae*, B – *Arytaina devia* (Gran Canaria), C – **A. vittata sp. nov.**, D – *A. nubivaga*. Scale bars = 0.5 mm.

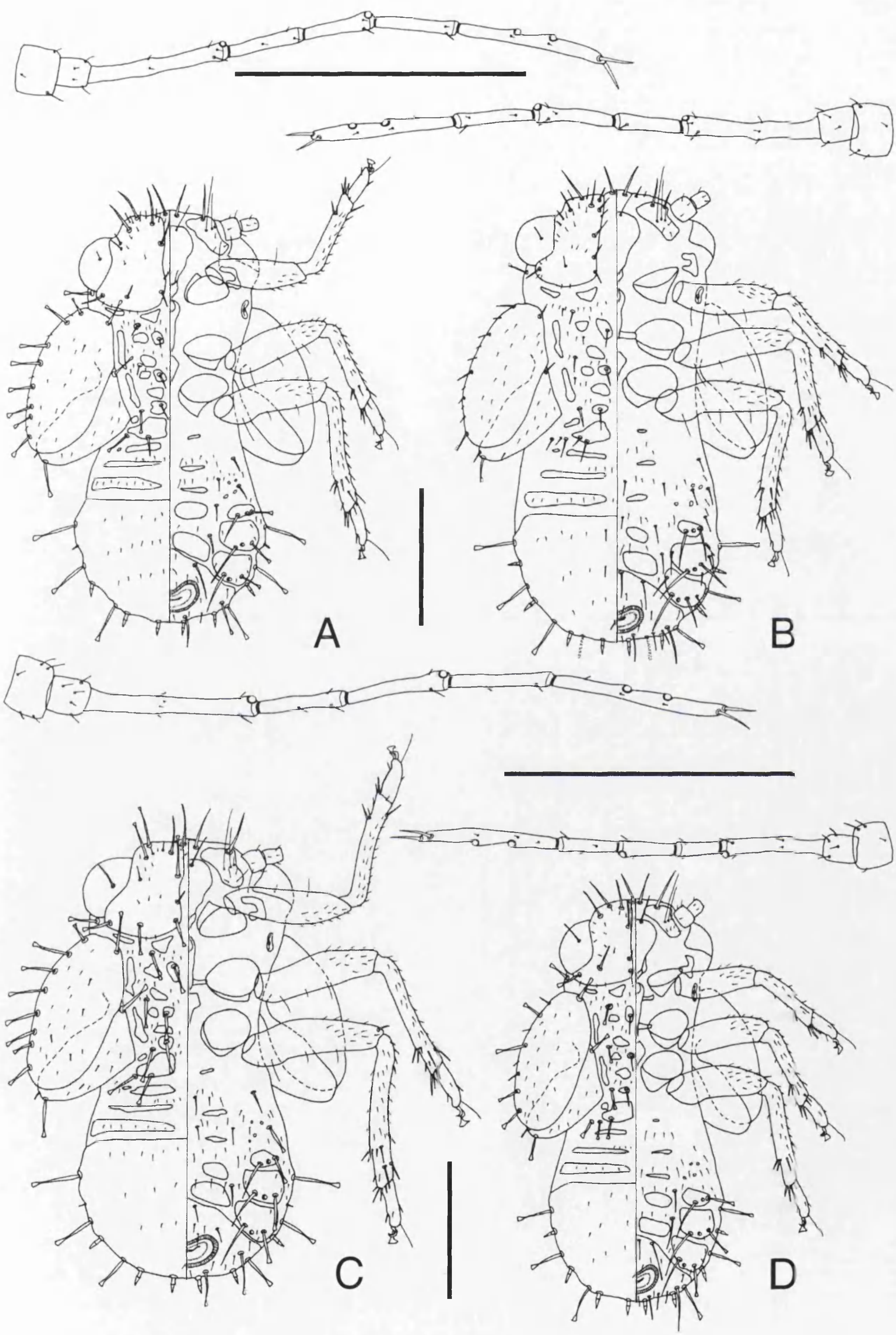

FIGURE 25. A – *Arytinnis umbonata*, B – *A. cognata*, C – *A. incuba*, D – ***A. berber* sp. nov.** Scale bars = 0.5 mm.

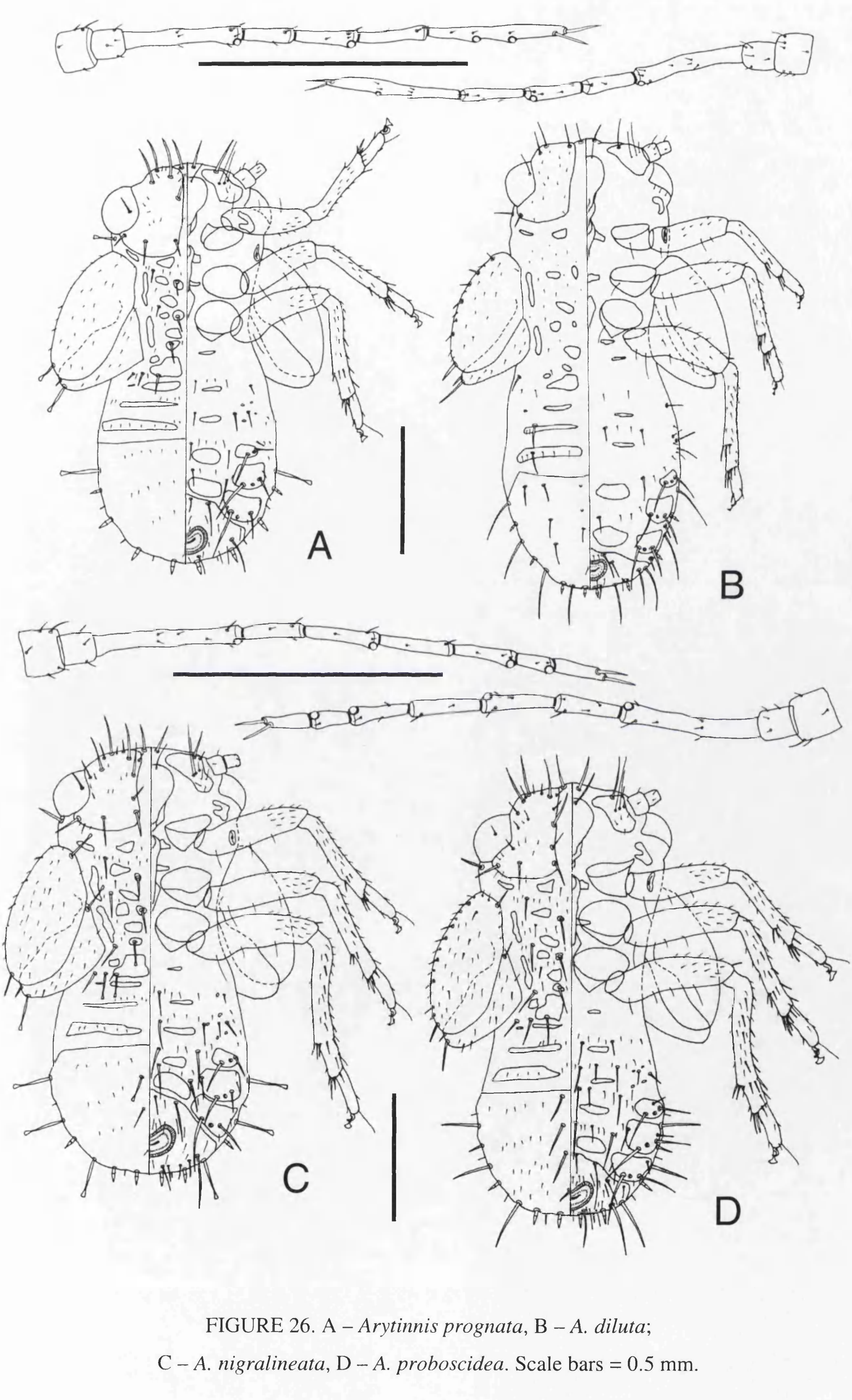

FIGURE 26. A – *Arytinnis prognata*, B – *A. diluta*; C – *A. nigralineata*, D – *A. proboscidea*. Scale bars = 0.5 mm.

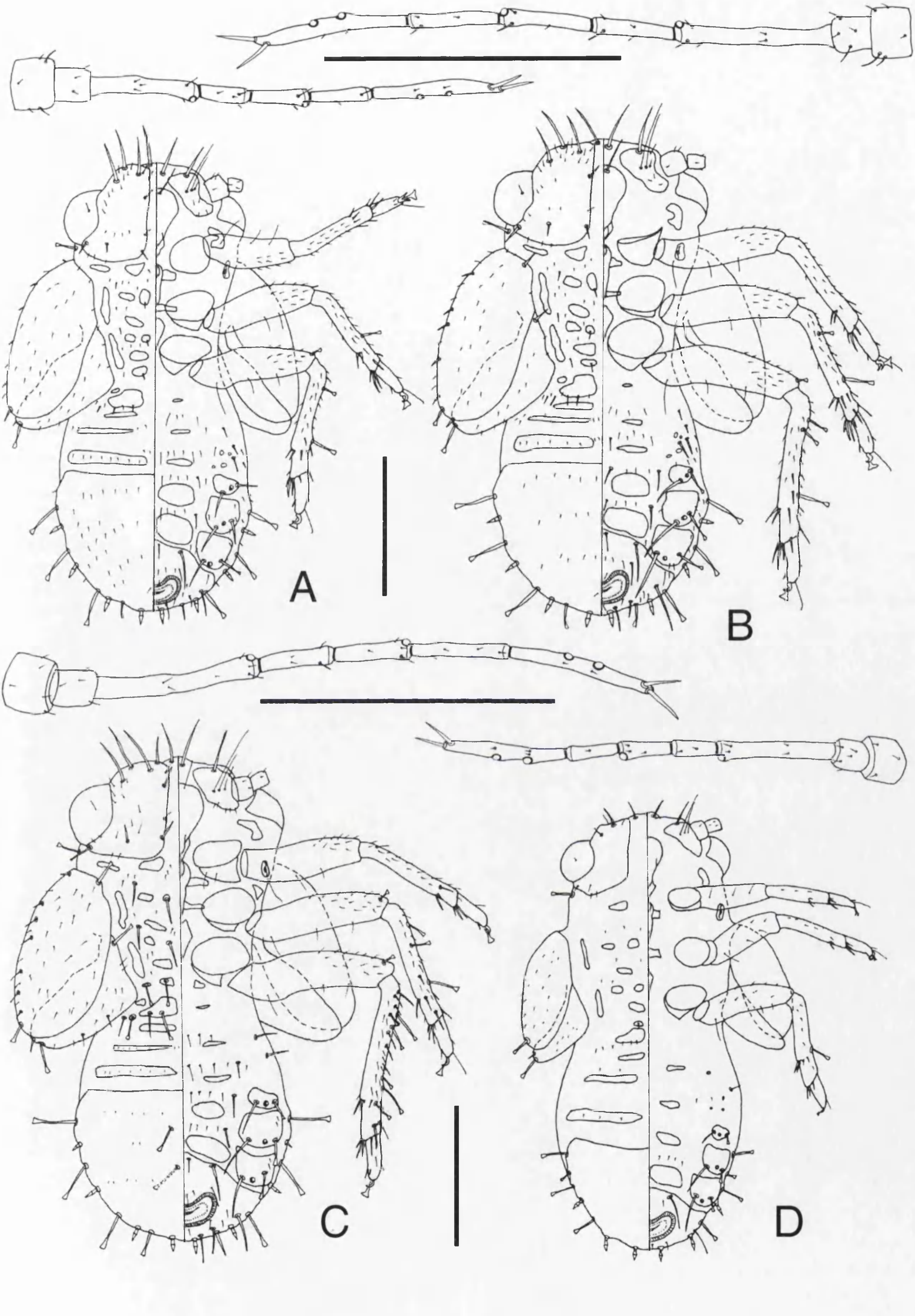

FIGURE 27. A – ***Arytinnis hupalupa* sp. nov.**, B – *A. modica*, C – *A. dividens*, D – ***A. ochrita* sp. nov.** Scale bars = 0.5 mm.

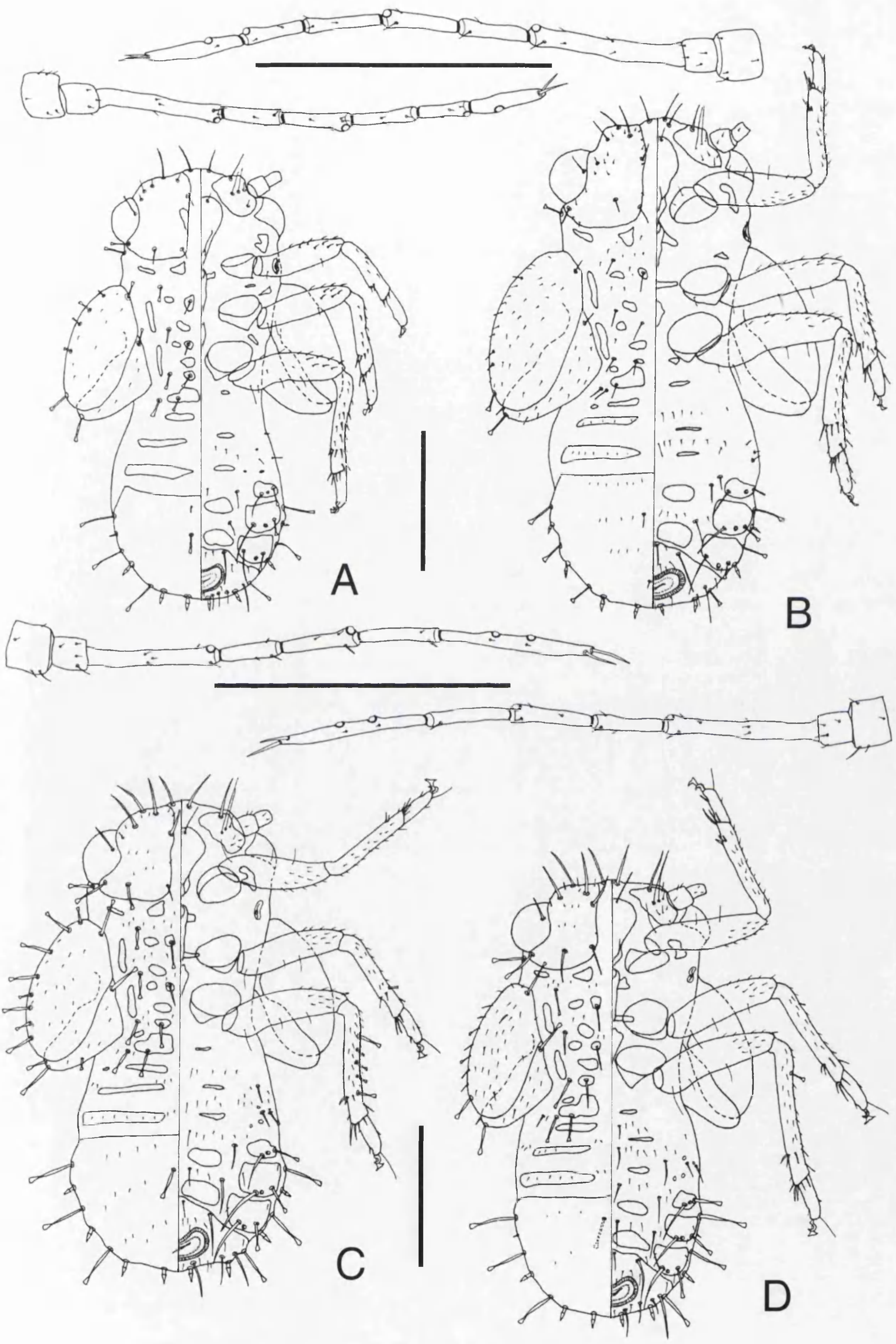

FIGURE 28. A – ***Arytinnis gomerae* sp. nov.**, B – ***A. occidentalis* sp. nov.**, C – *A. pileolata*, D – *A. equitans*. Scale bars = 0.5 mm.

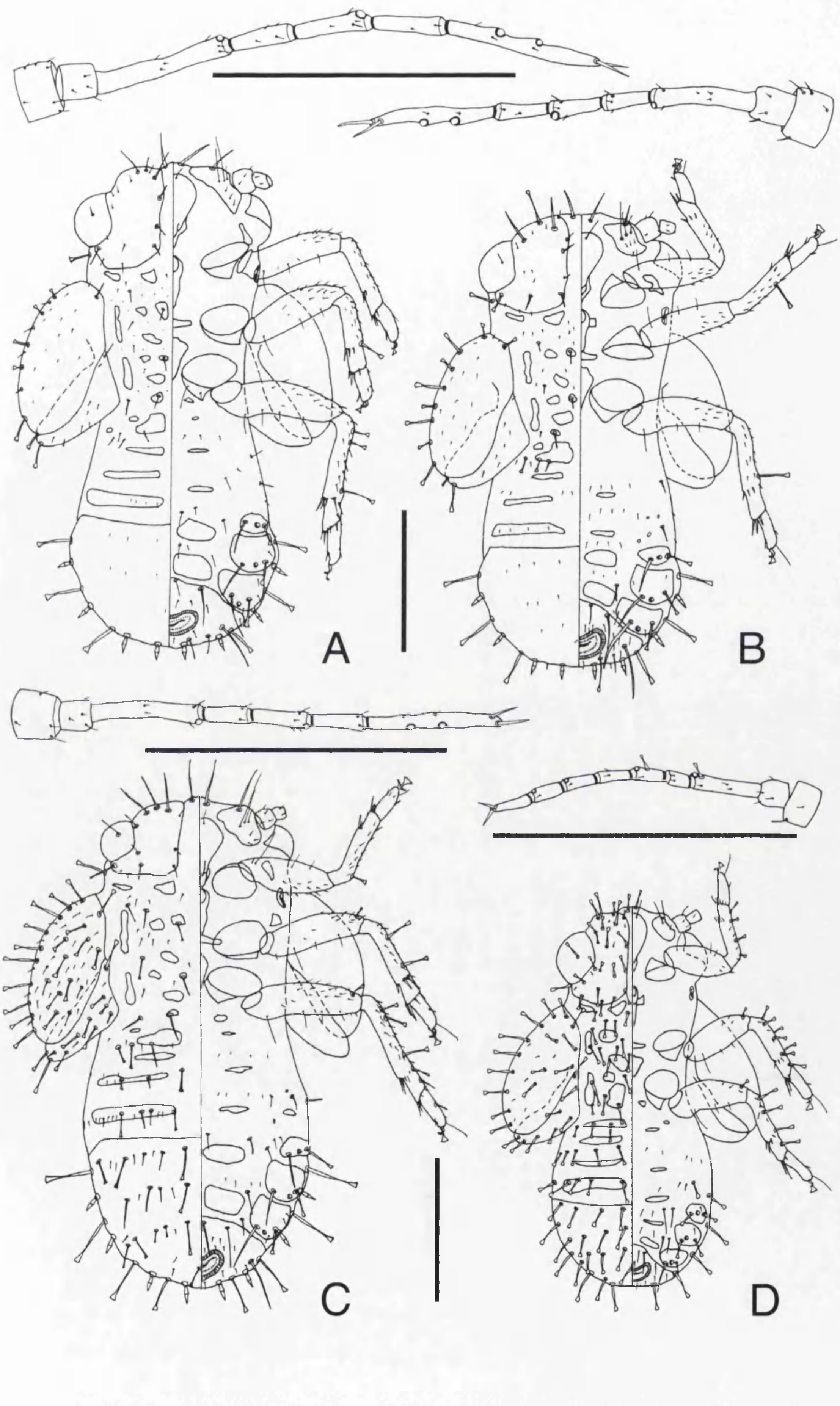

FIGURE 29. A – ***Arytinnis fortunata* sp. nov.**, B – ***A. romeria* sp. nov.**, C – ***A. menceyata* sp. nov.**, D – *Acizzia uncatoides*. Scale bars = 0.5 mm.

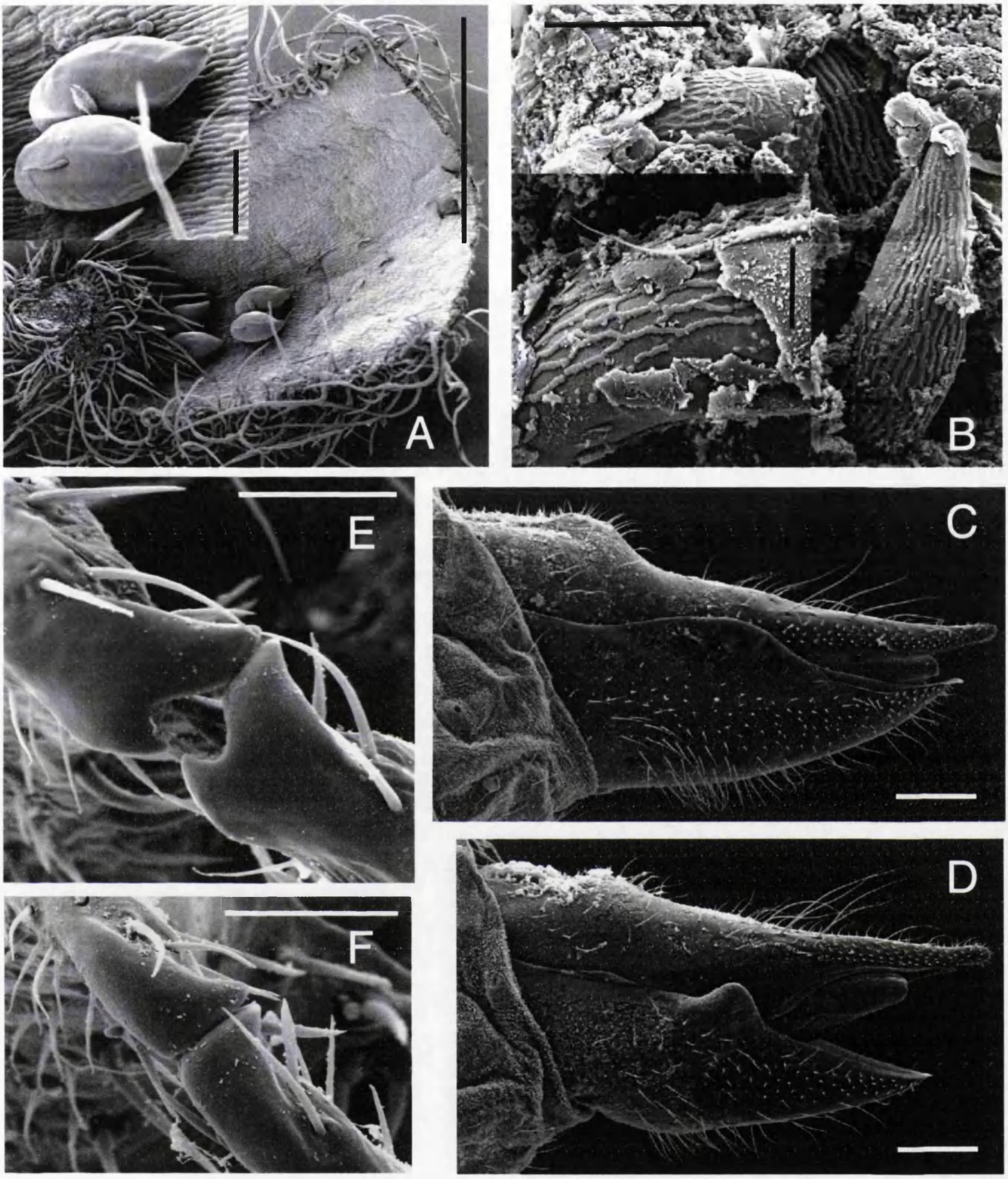

FIGURE 30. A – eggs of *Arytinnis nigralineata* laid on the inner surface of the floral bracts of *Adenocarpus foliolosus* (scale bar = 1 mm, inset = 0.1 mm), B – eggs of *Pseudacanthopsylla improvisa* embedded in the abdomen, showing sculpturing in the chorion layer (scale bar = 0.1 mm, inset = 30 μm), C–D ♀ genitalia, C – *Arytinnis diluta*, D – *A. equitans* (scale bars = 0.1 mm), E–F ♂ parameres in dorsal view, E – ***Arytinnis occidentalis*** **sp. nov.**, F – ***A. fortunata*** **sp. nov.** (scale bars = 30 μm).

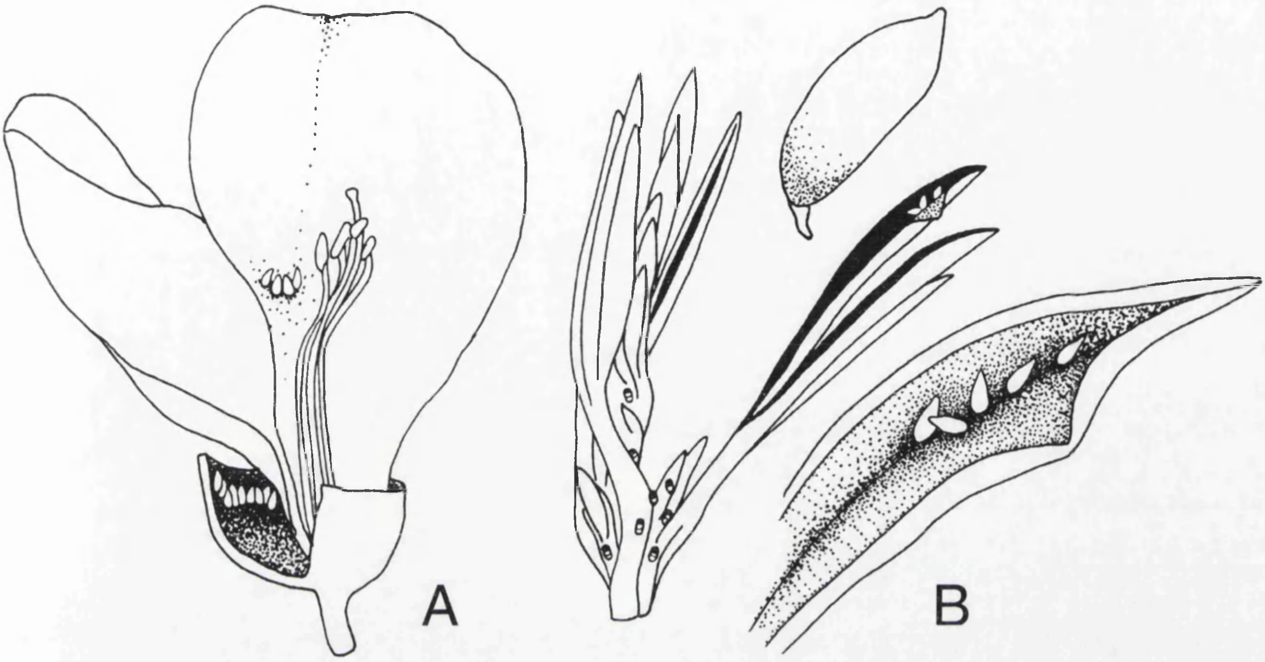

FIGURE 31. Egg placement, A – eggs of ***Arytaina vittata*** **sp. nov.** are laid around the inner rim of the calyx, and in small clusters on the corolla of *Spartocytisus filipes*, B – eggs of *Arytainilla dividens* are laid along the midrib, inside folded new leaves of *Chamaecytisus proliferus*, 1st-2nd instar nymphs then migrate down to feed on the leaf buds.

APPENDIX 1. Taxonomy of the Canarian plant genera in the Genisteae, showing taxon distribution and abundance; and indicating number of samples from each plant taxon and the psyllid fauna. Canary Islands: C – Gran Canaria, T – Tenerife, G – La Gomera, P – La Palma, H – El Hierro.

| Canarian Genisteae | plant distribution | plant abundance | no. samples 1997–2000 | psyllid fauna |
|---|---|---|---|---|
| *Genista benehoavensis* | P | rare | 4 | none |
| *Retama monosperma* | | | | |
| ssp. *rhodorrhizoides* | T, G, P | common | 7 | *Livilla monospermae* (T, G, P, H) |
| | C, H | uncommon | 3 | none (C) |
| ***T. monspessulana*** **group** | | | | |
| *Teline canariensis* | C | rare | 2 | *A. equitans* |
| | T | common | 7 | *A. diluta, A. pileolata, A. canariensis, A. menceyata* |
| *Teline microphylla* | C | abundant | 10 | *A. diluta, A. equitans, A. prognata* |
| *Teline osyroides* | | | | |
| ssp. *osyroides* | T | rare | 2 | *A. ochrita* |
| ssp. *sericea* | T | uncommon | 2 | *A. pileolata* |
| *Teline salsoloides* | T | rare | 1 | none |
| *Teline stenoptala* | | | | |
| ssp. *microphylla* | G, H | common | 9 | *A. gomerae* (G), *A. hupalupa* (G), *A. modica* (H), *A. occidentalis* (H) |
| ssp. *pauciovulata* | G | uncommon | 3 | *A. gomerae* (G), *A. hupalupa* (G) |
| ssp. *sericea* | P | uncommon | 1 | *A. occidentalis* |
| ssp. *spachiana* | T | uncommon | 1 | *A. menceyata, A. pileolata* |
| ssp. *stenopetala* | P [C, T, G] | common | 8 | *A. occidentalis* (P), *A. modica* (P) |

| | | | | |
|---|---|---|---|---|
| ***T. linifolia*** **group** | | | | |
| *Teline gomerae* | G | rare | 1 | none |
| *Teline nervosa* | C | rare | 1 | none |
| *Teline pallida* | | | | |
| ssp. *pallida* | T | rare | 1 | none |
| ssp. *silensis* | T | rare | | unsampled |
| *Teline rosmarinifolia* | | | | |
| ssp. *rosmarinifolia* | C | uncommon | 4 | *A. romeria* |
| ssp. *eurifolia* | C | rare | | unsampled |
| *Teline splendens* | P | uncommon | 2 | *A. fortunata* |
| *Chamaecytisus proliferus* | | | | |
| ssp. *angustifolius* | T, G | common | 9 | *A. dividens, Arytaina devia* |
| ssp. *meridionalis* | C | abundant | 4 | *A. dividens, Arytaina devia* |
| ssp. *proliferus* | | | | |
| var. *hierrensis* | H | rare | 3 | *A. dividens* |
| var. *calderae* | P | uncommon | 2 | *A. modica, Arytaina devia* |
| var. *canarieae* | C | common | 2 | *A. dividens, Arytaina devia* |
| var. *palmensis* | P [C, T, G, H] | abundant | 11 | *A. modica* (P), *A. dividens* (C, T), *Arytaina devia* (C, T) |
| var. *proliferus* | T | common | 2 | *A. dividens, A. devia* |
| *Spartocytisus filipes* | T | rare | | unsampled |
| | G, P, H | uncommon | 12 | *Arytaina vittata, Arytainilla serpentina* (P) |
| *Spartocytisus supranubius* | T | abundant | 4 | *Arytaina nubivaga* |
| | P | rare | 4 | *Arytaina vittata* |

| | | | | |
|---|---|---|---|---|
| *Adenocarpus foliolosus* | | | | |
| var. *foliolosus* | T, G, P | common | 9 | *A. nigralineata* (T, G), *A. proboscidea* (P) |
| var. *villosus* | C | common | 6 | *A. nigralineata* |
| *Adenocarpus ombriosus* | H | rare | | unsampled |
| *Adenocarpus viscosus* | | | | |
| ssp. *spartioides* | P | abundant | 4 | *A. proboscidea* |
| ssp. *viscosus* | T | abundant | 4 | *A. proboscidea* |

[ ] plant distribution non-native

APPENDIX 2. Population sampling of psyllids in the Canary Islands.

|  |  |  | no. of collections made |  |  |
|---|---|---|---|---|---|
| psyllid species | no. collections made from each island | host plant, with no. of host plant populations sampled and locations | June – July 1997 | April – May 1998 | July – August 2000 |
| *Arytaina devia* | C 7, T 8, G 1, P 3 | *Chamaecytisus proliferus*<br>C, 7, north – abv. Moya, abv. San Mateo, Cruz de Tejeda, south – abv. Tejeda, Risco Blanco, abv. Fataga, Bco. de Mogán<br>T, 7, north – Bco. Seco, abv. Arafo, Miradores de la Cumbre, Aguamansa, south – Bco. del Rey, nr. Vilaflor<br>G, 1, nr. Arure<br>P, 3, blw. La Cumbrecita, Fuente de Olén, abv. Llano Negro | 7 | 11 | 1 |
| *Arytaina nubivaga* | T,4 | *Spartocytisus supranubius*<br>T, 2, Las Cañadas | 2 | 2 | – |
| *Arytaina vittata* | G 4, P 5, H 2 | *Spartocytisus filipes*<br>G, 4, south – nr. Retamal, nr. Arure, north – nr. Hermigua, Roque Cano<br>P, 4, south – Bco. de las Angustias, Bco. de Jurado, north – Bco. de la Fuente, nr. Barlovento<br>H, 1, north nr. Sabinosa | 4 | 7 | – |
| *Arytainilla serpentina* | P 3 | *Spartocytisus filipes*<br>P, 2, north – Bco. de la Fuente, nr. Barlovento | – | 3 | – |
| *Arytinnis canariensis* | T 1 | *Teline canariensis*<br>T, 1, nr Pico del Inglés | – | 1 | – |
| *Arytinnis diluta* | C 2, T 4 | *Teline microphylla* | – | 2 | – |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
|  |  | C, 2, north and south of Cruz de Tejeda |  |  |  |
|  |  | *Teline canariensis*<br>T, 3, east – Teno region, west - Anaga, nr Pico del Inglés, nr. El Bailadero | 1 | 3 |  |
| *Arytinnis dividens* | C 10, T 12, G 6 | *Chamaecytisus proliferus*<br>C, 7, north – Cruz de Tejeda, abv. Moya, abv. San Mateo, south - abv. Tejeda, Risco Blanco, abv. Fataga, Bco. de Mogán<br>T, 7, north – Bco. Seco, abv. Arafo, Miradores de la Cumbre, Aguamansa, Teno region, south – Bco. del Rey, nr. Vilaflor<br>G, 4, nr. Arure, nr. Las Hayas, Roque de Agando, La Laguna Grande | 11 | 17 | – |
| *Arytinnis equitans* | C 13 | *Teline microphylla*<br>C, 6, south – abv. Fataga, Risco Blanco, abv. Tejeda, nr. Ayacata, north – Cruz de Tejeda, Pinos de Gáldar | 6 | 8 | – |
|  |  | *Teline canariensis*<br>C, 1, north nr. Moya | 1 | 1 |  |
| *Arytinnis fortunata* | P 3 | *Teline splendens*<br>P, 2, abv. Santa Cruz | 2 | 1 | – |
| *Arytinnis gomerae* | G 5 | *Teline stenopetala* (ssp. *microphylla* and ssp. *pauciovulata*)<br>G, 5, north – Roque Cano, El Cedro and abv. Hermigua, south – Roque de Agando, Ermita de Las Nieves | 1 | 2 | 2 |
| *Arytinnis hupalupa* | G 3 | *Teline stenopetala* (ssp. *microphylla* and ssp. *pauciovulata*)<br>G, 3, north – El Cedro, nr. Roque Blanco, south – Roque de Agando | 1 | 1 | 1 |
| *Arytinnis menceyata* | T 2 | *Teline stenopetala* ssp. *spachiana*<br>T, 1, Caldera de Pedro Gil | – | 2 | – |
|  |  | *Teline canariensis* |  |  |  |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
|  |  | T, 1, nr. Pico del Inglés |  |  |  |
| *Arytinnis modica* | P 7, H 10 | *Chamaecytisus proliferus* | 2 | 6 | – |
|  |  | P, 3, abv. Fuente de Olén, blw. La Cumbrecita, abv. Llano Negro |  |  |  |
|  |  | H, 5, Mirador del Golfo, nr. San Andres, nr. Mirador de la Peña, blw. Mirador de Jinama, nr. El Hermita de los Reyes |  |  |  |
|  |  | *Teline stenopetala* | 5 | 4 |  |
|  |  | P, 4, east of Cumbre Nuevas tunnel, abv. Santa Cruz, nr. Roque Faro, Los Tilos |  |  |  |
|  |  | H, 3, El Golfo, nr. Arbol Santo, nr. Las Montañetas |  |  |  |
| *Arytinnis nigralineata* | C 6, T 8, G 2 | *Adenocarpus foliolosus* | 11 | 4 | 1 |
|  |  | C, 5, north - abv. Moya, Cruz de Tejeda, west of Cruz de Tejeda, Pinos de Gáldar, south – abv. Tejeda |  |  |  |
|  |  | T, 7, abv. Las Raíces, Las Lagunetas, Mirador de La Orotava, abv. Las Canteras, nr. Pico del Inglés, abv. Aguamansa, abv. Arafo |  |  |  |
|  |  | G, 2, north – nr. Las Rosas, south – nr. Arure |  |  |  |
| *Arytinnis occidentalis* | P 4, H 5 | *Teline stenopetala* (ssp. *stenopetala* and ssp. *microphylla*) | 4 | 5 | – |
|  |  | P, 4, La Cumbrecita, abv. Santa Cruz, nr. Roque Faro, Los Tilos |  |  |  |
|  |  | H, 3, nr. Las Montañetas, El Golfo, nr. Arbol Santo |  |  |  |
| *Arytinnis ochrita* | T 2 | *Teline osyroides* ssp. *osyroides* | 1 | 1 | – |
|  |  | T, 1, Bco. de Masca |  |  |  |
| *Arytinnis pileolata* | T 10 | *Teline canariensis* | 2 | 5 | – |
|  |  | T, 5, abv. Vega, El Púlpito, abv. Los Carrizales, east of El Bailadero, nr. Pico del Inglés |  |  |  |
|  |  | *Teline osyroides* ssp. *sericea* | – | 2 |  |
|  |  | T, 2, Bco. de Herques, Bco. del Rey |  |  |  |

| | | | | | |
|---|---|---|---|---|---|
| | | *Teline stenopetala* ssp. *spachiana* | – | 1 | |
| | | T, 1, Caldera de Pedro Gil | | | |
| | | *Teline stenopetala* ssp. *stenopetala* and hybrids | 1 | 1 | |
| | | T, 2, abv. Vega, Aguamansa | | | |
| *Arytinnis proboscidea* | T 7, P 7 | *Adenocarpus viscosus* | 5 | 3 | – |
| | | T, 4, north – abv. Aguamansa, nr. Santiago del Teide, Miradores de la Cumbre, south - nr. Trevejos | | | |
| | | P, 4, north – nr. Gallegos, La Caldera rim, blw. Pico de la Nieve, Fuente de Olén | | | |
| | | *Adenocarpus foliolosus* and hybrids | | | |
| | | T, 2, Mirador de Oratava, abv. Arafo | 4 | 1 | 1 |
| | | P, 3, abv. Santa Cruz, nr. Gallegos | | | |
| *Arytinnis prognata* | C 2 | *Teline microphylla* | – | 2 | – |
| | | C, 2, nr. Risco Blanco, abv. Fataga | | | |
| *Arytinnis romeria* | C 1 | *Teline rosmarinifolia* | – | 1 | – |
| | | C, 2, Risco Blanco, abv. Fataga | | | |
| *Livilla monospermae* | T 5, G 2, P 3, H 1 | *Retama monosperma* | 9 | 2 | – |
| | | T, 4, nr. Retamar, Bco. Seco, Bco. de Masca | | | |
| | | G, 2, abv. El Retamal, nr. Arure | | | |
| | | P, 2, Bco. de las Angustias, abv. Santa Cruz | | | |
| | | H, 1, nr. Mirador de la Peña | | | |

# CHAPTER THREE

## ORIGINS AND BIOGEOGRAPHY OF MACARONESIAN LEGUME-FEEDING PSYLLIDS

### Abstract

This study presents the first phylogenetic analysis of a phytophagous insect group from Macaronesia. Molecular, morphological and ecological data are used to investigate the origins of the 23 species in the Macaronesian islands by reassessing the classification of the five Palaearctic legume-feeding psyllid genera in the Arytaininae. Molecular phylogenies generated from two mitochondrial regions: part of the small ribosomal subunit rRNA (12S), and a second region incorporating part of cytochrome oxidase I (COI) and cytochrome oxidase II (COII), are analyzed independently and in combination with the morphological data generated from adult and nymphal characters. These analyses confirm the paraphyly of the Arytaininae in relation to the Psyllinae, as well as the paraphyly of the two largest arytainine genera (*Arytainilla* and *Livilla*) – both of which are represented by anomalous taxa in the Canary Islands. The phylogenetic results suggest there have been five colonizations of the Canary Islands by arytainine psyllids, one or two colonizations of Madeira, and probably one or two back colonizations of the continent. Optimization of the host plant genera onto the psyllid phylogeny suggests that preadaptation is important in determining host plant selection when new regions or islands are colonized. The psyllid phylogeny together with ecological and biogeographic data provides evidence, in at least one case, for sympatric speciation on the same host plant, while the majority of cases involve allopatric speciation via host shifts and inter-island colonization. A surprising number of closely related psyllids in the Canary Islands are found on the same host plant and there is evidence that the sharing of host resources is facilitated by geographical segregation, ecological specialization and divergence in the timing of development. Human activity and habitat alteration are implicated in both the reduction and expansion of host plant distributions, as well as the promotion of host plant hybridization, all of which may affect psyllid host preferences and distributions. Habitat and host population fragmentation may reach a critical host plant abundance, below which a host specific psyllid fauna can not survive.

## 3.1 Introduction

Ocean islands have discrete boundaries and vary in their size and isolation from other islands and from the mainland. These elements have been greatly advantageous in the study of evolution (MacArthur & Wilson, 1967). In addition to the unique physical characteristics of islands, there is a spectacular diversity of species which is often in sharp contrast with the mainland, of which the most famous examples are Darwin's Galapagos finches (Grant, 1986), and the Hawaiian *Drosophila* with more than 1000 island species (Kaneshiro, Gillespie & Carson, 1995). Recent work using a combination of approaches – ecological, morphological and molecular – has addressed the mechanistic questions raised by the evolutionary fecundity of islands (Wagner & Funk, 1995; Givnish & Sytsma, 1997; Grant, 1998).

There are common patterns in biotas from different island systems, yet processes common to all of these – dispersal, colonization, isolation and adaptation – are also present in mainland areas. However, a primary difference between oceanic islands and continents is that islands provide a 'terra nullus' or virtually unoccupied territory, with low levels of immigration and establishment. The natural filters to immigration – isolation, surrounding ocean, small size of islands – limits the number of colonists. For those that do become successfully established, the low level of immigration is likely to reduce the number of competitors and/or predators, and allow the successful colonists to undergo an 'ecological release', which may take the form of an adaptive radiation into a variety of niches.

The age and size of islands are important determinants of species diversity: smaller and younger islands are likely to have accumulated fewer immigrants than larger, older islands; but as islands age they are increasingly eroded, resulting in loss of habitat and extinction (MacArthur & Wilson, 1967; Carson & Clague, 1995). An important structural aspect of island size is altitude which, together with the prevailing climatic zone, determines the number and quality of habitat types (high islands accommodate more habitat types than low islands). Thus, a high altitude, large sized island, that is middle-aged would be expected to have the greatest species diversity (e.g. the island of Tenerife in the Canaries, Fig 1 & Table 1). The Hawaiian archipelago has been the location for the most comprehensive research to date on the colonization and speciation processes of a progressively older island chain (Wagner & Funk, 1995), but recently research has also focussed on the flora and fauna of the archipelagos of Macaronesia (Francisco-Ortega, Jansen & Santos-Guerra, 1996; Mes & 'T Hart, 1996; Pinto *et al.*, 1997; Brunton & Hurst, 1998; Emerson, Oromí & Hewitt, 2000b; Juan *et al.*, 2000).

Macaronesia was originally circumscribed, not as a geographical or political region, but as a unique phytogeographical concept (Sunding, 1979). Macaronesia includes five Atlantic Ocean archipelagos (north to south: Azores, Madeiras, Salvagens, Canaries, and Cape Verdes) which lie off the west coast of North Africa and southern Europe, between 15° and 40°N latitude. The geological ages of individual islands range from 1-30 Myr. The centrally positioned Canary Islands (27°-29°N) have proven particularly rewarding for evolutionary studies because they provide the most extreme ranges of altitude, habitat types, size, and age of islands (Fig. 1 & Table 1).

Research in both Pacific and Atlantic archipelagos has mainly focussed on plant and animal groups independently. Some studies have addressed plant-pollinator systems or the endozoochorous dispersal of plants (Percy & Cronk, 1997; Barrett, 1998; Givnish, 1998), and there has been research into the plant substrate-mediated radiation in Hawaiian *Drosophila* (Kambysellis & Craddock, 1997). But only rarely has research focussed on herbivorous insects and their host plants, such as studies by Asquith (1995) and Roderick (1997) of Hawaiian Hemiptera.

This is the first Macaronesian study to examine island evolution in a highly host specific group of phytophagous insects. Related continental groups are included to determine the origin of the island species and to provide a comparison of species diversity between island and continental regions. The insects – psyllids – are a group of small, sap-sucking Hemiptera, and (in this study) the host plants – brooms – are shrubby papilionoid legumes (Genisteae). Psyllids (Psylloidea, also known as 'jumping plant lice') feed on a wide variety of dicotyledonous and a few monocotyledonous plants, but are generally less well known than the other hemipteroid groups of the Sternorrhyncha: aphids (Apidoidea), scales (Coccoidea) and whiteflies (Aleyrodoidea), due to the relatively low occurrence of psyllid pests. Habitat and host specialization in psyllids makes them an ideal group for investigating evolutionary patterns which are associated with habitat or host shifts, and geographic isolation. The psyllid group selected for this study (the Genisteae-feeding Arytaininae) combines continental species that are locally restricted or widespread across Europe and North Africa, with taxa that are isolated on two of the central Macaronesian archipelagos (Canary Islands and Madeira) (Fig.1). Among the island taxa, species may be endemic to a single island or more widespread on islands of different geological ages.

### 3.1.1 *The arytainine psyllids*

The psyllids that feed on papilionoid legumes in the Genisteae are all in the Arytaininae, a subfamily of the Psyllidae. The delimitation of the subfamily Arytaininae is unclear, particularly in relation to the subfamily Psyllinae (Heslop-Harrison, 1951, 1961; Loginova, 1976b, 1977; Hodkinson & Hollis, 1987). There are thirteen genera, distributed in both the Old and New World, that are considered to be in the Arytaininae; nine of these genera feed on host plants in the subfamily Papilionoideae (Leguminosae), and a further four, somewhat anomalous North American genera, feed on host plants in the families Rosaceae (two genera) and Rhamnaceae (two genera). Five of the genera are Palaearctic, all of them papilionoid legume-feeders, and four of these genera are confined to the west Palaearctic region and feed exclusively on host plants in the Genisteae. The Genisteae-feeding group will be the focus of this study. Diversification of the Genisteae in the Mediterranean basin, where these shrubs often form a dominant part of the vegetation, is likely to have been important in promoting the diversification of the associated psyllid group. There are around 96 arytainine species confined to this region and 91 of these feed on genistoid legumes. Represented in this study are all five Palaearctic arytainine psyllid genera – *Arytaina*, *Arytainilla*, *Livilla*, *Pseudacanthopsylla* (west Palaearctic, on genistoid legume hosts) and *Cyamophila* (Mediterranean to central Asia, on non-genistoid legumes). The monophyly of this Palaearctic group within the Arytaininae, is investigated in this study.

### 3.1.2 *The host plants*

The Genisteae (broom, gorse and relatives) is a monophyletic tribe of papilionoid legumes which has been the subject of a number of morphological revisions (Gibbs, 1967, 1974; Gibbs & Dingwall, 1972; Polhill, 1976; Bisby, 1981) and a recent molecular investigation (Käss and Wink, 1997). The lupins (*Lupinus*) are a large (c. 200 species), clearly delimited monophyletic group on which there are no recorded psyllid species. The remaining members of the Genisteae (c. 260 species in 20 genera) can be separated into three groups, a *Genista* group, a *Cytisus* group, and a number of generic 'outliers', and each of these groups has members that are psyllid hosts. However, about half of these genistoid genera do not have a psyllid fauna, which implies that there are constraints on intergeneric host switching.

The objectives of this study were: a) to test the monophyly of the Palaearctic psyllid genera in the subfamily Arytaininae, and in particular, the Genisteae-feeding subgroup; b) to investigate the taxonomic and biogeographic origin of the Macaronesian species; c) to investigate psyllid speciation using biogeographic patterns and host associations in the Macaronesian islands.

## 3.2 Materials and methods

### 3.2.1 *Ingroup selection*

The ingroup includes representatives of all Arytaininae genera that feed on legumes in the Palaearctic region (*Arytaina*, *Arytainilla*, *Cyamophila*, *Livilla* and *Pseudacanthopsylla*). All known species from the Macaronesian region were comprehensively sampled, and continental groups which were identified as possible sister groups to the island species were selectively sampled (Table 2, with additional details given in the Taxonomic Appendix). Multiple individuals are included where species occur on different islands/continental regions and/or different host plants. *Pseudacanthopsylla* is represented by a single species (= *Psylla improvisa*, see Taxonomic Appendix), and is a morphologically atypical arytainine genus that feeds on hosts in the Genisteae. *Pseudacanthopsylla* and *Cyamophila* (Arytaininae, but not Genisteae-feeding) are therefore included to test both the monophyletic origin of Genisteae-feeding and the monophyly of the Arytaininae. In addition, two species of *Cacopsylla* (Psyllinae) were included (but see discussion under outgroup selection).

### 3.2.2 *Outgroup selection*

Two subfamilies, Psyllinae and Acizziinae, were initially selected as possible outgroups for the subfamily Arytaininae, based on morphological affinity (Psyllinae) and host affinity (Acizziinae). Members of Acizziinae feed on mimosoid legumes in the tribes Acacieae and Ingae, while members of Psyllinae feed on a wide variety of predominantly non-leguminous plant families. Trial phylogentic analyses which included more distantly related taxa (e.g. *Psyllopsis*, *Livia* and *Trioza* spp., as well as *Schizaphis* (Aphididae)) using 12S rRNA data, indicated that the most suitable outgroup (based on topology and bootstrap values) for the Arytaininae was Acizziinae (*Acizzia*). These preliminary analyses affiliated the Psyllinae species with *Cyamophila* (Arytaininae) suggesting that the Psyllinae would be an unsuitable outgroup for the Arytaininae. Two species of Acizziinae were selected 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 analyse the monophyly of the Arytaininae, but not defined as an outgroup.

### 3.2.3 *DNA sampling and extraction*

Eighty-four individuals representing 62 taxa (61 species and one subspecies) are included in this study, and 17 of these species are undescribed, having been recently collected from Macaronesian and adjacent continental areas (these species are described and illustrated in Chapter 2). Based on the assessment of substitution rates within different cytochrome oxidase (CO) regions by Lunt *et al.* (1996) and Zhang & Hewitt (1997), faster evolving CO regions were selected to provide resolution between recently diverged species and intraspecific taxa (73 individuals from 50 species were sampled). The small subunit rRNA region (12S) was selected as a slower evolving region to resolve intergeneric and interspecific groups (68 individuals from 61 species were sampled). Fifty of the 61 species included are sampled for both molecular regions, but there are 11 continental species only sampled for 12S (10 *Livilla* spp. and *Arytainilla gredi*) (Table 2). Samples were collected during field work from 1997-2000 in the Canary Islands, Madeira and adjacent continental areas (except where indicated in Table 2). Insects were collected into 100% ethanol in the field and stored at -20°C. One to three insects (abdomens and wings removed and retained as vouchers) were either ground in 50µl of 80% SDS lysis buffer and 20% Proteinase 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 hr at 55°C. The remainder of the extraction was performed with either the Geneclean II kit (Bio 101) in the first protocol, or the QIAGEN DNeasy Tissue Kit in the second. In both cases extracts were resuspended in 35µl of sterile water and stored at -20°C; 1µl of this solution was used for each 25µl PCR reaction. 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 Daniel Burckhardt and Ian 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.

### 3.2.4 *PCR and sequencing*

Amplification of the small ribosomal subunit (12S rRNA) fragment was accomplished using primers 12Sai and 12Sbi (equivalent to SR-N-14588 and SR-J-14233 respectively, of Simon *et al.*, 1994). A single region incorporating the 3' end of COI, the tRNA leucine and the 5' end of COII was amplified for some taxa using primers UEA9 (Lunt *et al.*, 1996) and 'Marilyn' (equivalent to C2-N-3389 of Simon *et al.*, 1994). These CO primers amplified approximately 68% of the taxa. Additional primers were designed to amplify the remaining taxa for the CO regions – DP1: 5'–GTTAGTAGTGGGTTATTAAGTTCRTC–3' (positioned in COII, and used as an antisense primer to UEA9, amplified approximately 30% of the taxa); DP2: 5'–CGATAATTTTAATTGTTAGTAGYGG–3' (also positioned in COII as an antisense primer to UEA9, amplified *Pseudacanthopsylla*); UEA9-MOD: 5'–GGTATGCCTCGTCGTTATTCTAAYTAYC–3' (positioned in COI, and used as a sense primer to 'Marilyn', amplified approximately 10% of the taxa). Appendix 1 gives the primer combinations used for DNA amplification from each species.

Each PCR cycle comprised denaturation at 94°C for one minute, followed by 92°C for 30 seconds (41 cycles), annealing at 45°C for 40 seconds and an extension of 65°C for 90 seconds, with a final extension of 72°C for 10 minutes. 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 30μl of $H_2O$ for direct sequencing using an automated Perkin-Elmer ABI 377 sequencer with ABI Prism Dye Terminator Cycle Ready Reaction Kit. All the sequences referred to here will be deposited in GenBank database.

### 3.2.5 *Alignment and sequence analyses*

Sequences were aligned manually using the program Se-Al (version 1.0a1; Rambaut, 1998). The alignment of the CO regions was unambiguous, with the codon position assignment determined by comparison to other insect sequences from GenBank. The 12S fragment was generally easy to align, but three regions from 3-11bp in length were ambiguous (positions 152-154, 254-264 and 300-305 of the aligned matrix) and these were excluded from all analyses. Secondary structures of the tRNA and 12S genes were referred to for improved alignment. Sequence characteristics are given in Table 3. Appendices 2-3 give the aligned matrices, and the matrices and trees (Figs 3-5) are available from TreeBASE (http://www.herbaria.harvard.edu/treebase/).

### 3.2.6 *Morphological sampling and treatment*

Forty-six species were sampled for the morphological analysis. The Macaronesian taxa were comprehensively sampled and selected taxa from continental sister groups were included. The only groups present in the molecular data but not represented in the morphological phylogeny are the non-Genisteae-feeding genera (*Cacopsylla* and *Cyamophila*). Morphological characters were obtained from alcohol, slide and capillary mounted material. Sixty-seven characters were scored for phylogenetic analysis, of which 43 were derived from adults and 24 were derived from 5th instar nymphs. Seventeen (39%)

of the adult characters and five (21%) of the nymphal characters are based on continuous morphometric data. These were partitioned for discrete character states determined by eye from graph plotted data, which incurred minimal polymorphism. The data were compiled using the program NDE (Nexus Data Editor; Page, 2000). Appendices 4-5 give the list of characters/character states and the data matrix, which are also available from TreeBASE.

### 3.2.7 *Phylogenetic analyses*

Phylogenetic analyses were performed with PAUP* (version 4.0b3; Swofford, 1999). The following heuristic search parameters were employed for the parsimony analyses: 100 random stepwise addition replicates with tree bisection-reconnection (TBR) branch swapping, other options included saving multiple trees (MULTREES) and collapsing zero-length branches (COLLAPSE). For the analysis of the morphological data, all morphometric characters were treated as ordered and multiple states as polymorphisms, in order to preserve information on the relative similarity between taxa and overlapping states as a result of the somewhat arbitrary data partitions. Bootstrap analyses (2000 replicates) were performed using simple addition sequence of taxa with TBR branch swapping. Congruence between the different types of data (12S, CO and morphology) were tested using the partition homogeneity test implemented in PAUP*. Parameters and assumptions used in the maximum likelihood (ML) searches were selected using program Modeltest (Posada & Crandall, 1998) 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 with invariable sites and gamma distribution. ML heuristic search parameters included simple addition sequence of taxa with TBR branch swapping, MULTREES and COLLAPSE. Assumptions of monophyly (e.g. of the genera *Livilla* and *Arytainilla*), and particular biogeographic assumptions (i.e. continental versus island groups) in the ‘Macaronesian clade’, were tested using constraint trees and the nonparametric (Templeton’s Wilcoxon signed-rank) test implemented in PAUP*.

### 3.2.8 *Mapping host plant relationships*

Host plant relationships were mapped, as an unordered character, onto the combined molecular phylogeny of the Genisteae-feeding psyllids using MacClade 3.07 (Maddison & Maddison, 1992) with accelerated transformation (ACCTRAN) optimization. One taxon (*Livilla pseudoretamae*), for which the host plant is unknown, was excluded.

## 3.3 Results

### 3.3.1 *Molecular evolution of the 12S small subunit rRNA*

The total aligned length of the 12S matrix is 342bp (of the 322 included sites, 168 were variable, of which 134 were parsimony informative), with A+T content 74-80% (further sequence details are given in Table 3). The equally weighted maximum parsimony (MP) search found 750 trees on five islands (length 807, CI 0.32 excluding uninformative characters, RI 0.614).

The 12S region alone provides poor resolution at the base of the phylogeny, and this may be compounded by the short segment of sequence (c. 321bp) and large number of samples (68). The 12S and CO data both show saturation of transitions relative to transversions (Fig. 2). However, the 12S region is evolving more slowly, relative to the CO region, and periods of rapid speciation are likely to be the cause of the poor resolution. Extremely short branch lengths at the base of the phylogeny and at the base of several clades using maximum likelihood (ML) and neighbour-joining (NJ) analyses (not shown) suggest there has been rapid speciation during the evolution of the Arytaininae.

Three major clades have bootstrap support greater than 75% (*Arytaina* – AR, the 'Macaronesian clade' – M, and the 'core *Livilla*' group – L; see Fig. 3A). The 12S data are equivocal on the distinction between the Arytaininae and Psyllinae. The placement of the morphologically atypical genus *Pseudacanthopsylla* is the most variable between the different islands of MP trees: consensus trees for two of the five islands place this taxon within the Genisteae-feeding Arytaininae (i.e. a single evolution of the Genisteae-feeding habit), while consensus trees for the other three islands place *Pseudacanthopsylla* basal to the remaining ingroup taxa, with the Psyllinae nested within the Arytaininae (i.e. multiple evolution of the Genisteae-feeding habit). The MP 12S tree in Figure 3A shows the topology most similar to that recovered after weighting the 12S data using the mean rescaled consistency index in PAUP*. Excluding *Pseudacanthopsylla* from the analyses in order to assess whether the remaining Genisteae-feeding genera were a well supported monophyletic group resulted in a strict MP consensus with the Genisteae-feeding Arytaininae monophyletic (but with low bootstrap support: 66%) and sister to the Psyllinae. The application of distance and likelihood methods does not resolve this conflict. NJ analysis using the HKY85 model (see methods) supports the inclusion of *Pseudacanthopsylla* in a monophyletic Genisteae-feeding clade with NJ bootstrap > 80%. However, the ML analysis using the same model of nucleotide substitution places *Pseudacanthopsylla* basal to the remaining Arytaininae and Psyllinae.

### 3.3.2 *Molecular evolution of the COI-tRNA-COII region*

The combined COI-tRNA-COII matrix provides 639 characters when aligned (352 variable sites, of which 297 are parsimony informative), with A+T content 67-83% (further sequence details are given in Table 3). There are no gaps in COI or COII and sequence length differences are due to differences in the length of readable sequence obtained with various primer combinations. The tRNA leucine is 65-71bp in length, providing 79 characters when aligned (positions 263-341 of the aligned COI-tRNA-COII matrix, see Appendix 3). A MP search found a single island of six trees (length 2280, CI 0.248 excluding uninformative characters, RI 0.613), one of which is shown in Figure 3B.

When compared to the 12S data, the combined CO regions (including the tRNA leucine) provide improved resolution and bootstrap support in parts of the phylogeny. Interspecific genetic divergence is generally 30-50% higher in the CO than in the 12S region: 'Macaronesian clade' – CO: 2-13%, 12S: 0-9%; *Arytainilla sensu stricto* – CO: 6-14%, 12S: 3-11%; *Arytaina* – CO: 2-15%, 12S: 2-10%. As with the 12S data, the CO regions also show saturation, but there is a linear relation between transitions and transversions at low levels of divergence (Fig. 2), suggesting that the CO data is more appropriate for resolving groups that have recently speciated. However, there is variation in the grouping of taxa in the 'Macaronesian clade' using different analyses (MP, NJ and ML) possibly as a result of short branch lengths at the base of the clade. As with the 12S data, the low accumulation of substitutions in several parts of the CO phylogeny suggests periods of rapid speciation. *Pseudacanthopsylla* is placed in all analyses (MP, NJ, ML) within the Genisteae-feeding Arytaininae.

### 3.3.3 *Morphological evolution*

MP analysis found a single island of 18 most parsimonious trees (length 554, CI 0.484 excluding a single uninformative character, RI 0.612). The number of morphologically discrete characters that were applicable to all taxa was, to a certain extent, limited by a combination of many closely related taxa with little interspecific variation, and populations of widespread taxa isolated on islands or fragmented on the continent exhibiting considerable intraspecific morphological variation. In general, nymphal morphology was more plastic and incured greater polymorphism than adult characters. Few of the nodes in the morphological phylogeny are well supported (Fig. 3C), but excluding polymorphic characters, or the subset of morphometric (continuous) characters, resulted in a loss of resolution. (Appendix 6 shows the unambiguous character state changes mapped onto the morphological phylogeny.) Nevertheless, the morphological phylogeny recovers many of the groups present in molecular analysis – the 'Macaronesian clade' (M), *Arytaina* (AR) and *Arytainilla sensu stricto* (A), as well as similar paraphyletic groupings of *Livilla sensu lato*.

### 3.3.4 *Molecules and morphology combined*

The partition homogeneity test (ILD test of Farris *et al.*, 1994) indicated that the molecular data sets (12S and CO) were compatible ($P = 0.99$), but that the molecular and morphological data were significantly incongruent ($P = 0.01$) with one another. A combined molecular MP analysis (12S and CO), including all taxa sampled for one or both regions, found eight trees (length 3112, CI 0.265 excluding uninformative characters, RI 0.609), one of which is shown in Figure 4. Recent criticism of the ILD test suggests that the inclusion of small data sets with a relatively high degree of noise (e.g. the morphological data in this analysis) may give significant ILD test results even in the absence of systematic incongruence (Dolphin *et al.*, 2000). To investigate the presence of underlying similarities in the molecular (12S and CO) and morphological phylogenies, consensus trees (Strict and Adams) of the independent phylogenies were constructed (Fig. 5A & B). The lack of resolution in the strict consensus tree shows there is conflict in the MP topologies, but the Adams consensus is generally a more appropriate method for assessing underlying topological similarities, and it indicates considerable shared structure among the trees (Fig. 5B). Combining all three data sets in a total evidence MP analysis resulted in eight trees (length 2858, CI 0.342 excluding uninformative characters, RI 0.504), with the strict consensus showing clear delimitation and higher bootstrap support for several groups (e.g. *Livilla*, *Arytainilla sensu stricto*, and the Macaronesian *equitans* group) (Fig. 5C).

### 3.3.5 *The arytainine psyllids in the Canary Islands and Madeira*

The Macaronesian members of Arytaininae are from the Canary Islands and Madeira (Loginova, 1976a; Hodkinson, 1990). All the species from this region are endemic, and belong to three of the Genisteae-feeding genera (*Arytaina*, *Arytainilla* and *Livilla*). There are six genera of Genisteae on these islands, five of which host between one and 14 psyllid species. On the five central and western Canary Islands there are 21 arytainine species (four to 11 species per island). There are no native members of the host plant group on the dry, eastern islands of Fuerteventrua and Lanzarote. The island of Madeira (equivalent in area to La Palma, which has nine Genisteae species and seven arytainine psyllids) has only two arytainine psyllids and two native legumes in the Genisteae – the only Macaronesian island with a one-to-one legume to psyllid ratio (Fig. 1 & Table 1).

After recent sampling in the Macaronesian region, it is clear that a substantial radiation has resulted in a group which includes the two Madeiran taxa, 16 Canary Island species and three continental taxa referred to as the 'Macaronesian clade' due to the probable origination of this group in Macaronesia. This clade is by far the most speciose psyllid group in the Macaronesian region with no more than three species found in any other generic groups. All of the 'Macaronesian clade' species are presently in *Arytainilla* (Loginova, 1972, 1976a) but the evidence presented here distinguishes this clade as both morphologically and genetically distinct from the core *Arytainilla* (defined by the type species, *A. delarbrei*). This latter group, referred to as *Arytainilla sensu stricto*, is in fact only represented by a single species in the Canary Islands. Two additional genera present in the Canary Islands are *Livilla*, also represented by a single species (*L. monospermae*), and *Arytaina* (*sensu* Loginova, 1976a) represented by three species (*Ar. devia*, *Ar. nubivaga* and *Ar.* sp.14). Diversity and speciation within each genus in the Canary Islands appears mainly to be restricted by diversification in the host genus. The largest number of psyllids (13 species in the 'Macaronesian clade') occur on the most species rich host genus, *Teline* (ten species); and at the other end of the scale a single legume species representing the genus *Retama* is host to the one Canarian species of *Livilla*.

### **3.3.6** *Intergeneric host switching*

The number of host switches that have occurred between plant genera in the 'Macaronesian clade' is inferred by mapping the host genera onto the psyllid phylogeny (Fig. 6). The optimization of the host genera on the psyllid tree suggests that intergeneric host switches are less common than intrageneric host switching. The switches to *Adenocarpus*, *Chamaecytisus* and *Genista*, all appear to have been made by psyllids that were originally *Teline*-feeding (Fig. 6). There appears to have been a single host switch to *Adenocarpus* (indicated by a white bar, Fig. 6) which resulted in the evolution of two *Adenocarpus*-feeding species (*A. nigralineata* and *A. proboscidea*); and there appears to have been at least two, possibly three, host switches to *Chamaecytisus* (indicated by a black bar, Fig. 6). The three host switches to *Chamaecytisus* are required to explain the evolution of *A dividens* (one switch) and to explain the bi-generic host preference of *A. modica* (two switches). The samples of *A. modica* from *Chamaecytisus* and *Teline* hosts on two islands (La Palma and El Hierro) are segregated geographically (based on CO data) rather than by host affiliation. Therefore, it appears that *A. modica* made at least one host switch between *Chamaecytisus* and *Teline* on each island. *A. modica* is the only Macaronesian species found on more than one host genus and is a recently derived species on young islands (1-2 Myr). Further intraspecific sampling within islands, is required to determine whether members feeding on each plant genus have formed host races. Switching between *Genista* and *Teline* in the Madeira/continental subclade was equivocal, but when resolved using ACCTRAN optimization, shows a single switch to *Genista* (indicated by a black triangle, Fig. 6), followed by a switch back to *Teline* (indicated by a white triangle, Fig. 6).

### **3.3.7** *Continental versus island divergence*

The CO regions have been shown to evolve sufficiently rapidly to provide information on the phylogeographic patterns within species of Canarian beetles (Juan *et al.*, 1998; Emerson, Oromí & Hewitt, 2000a). Sequences of individuals from different populations in continental and Macaronesian taxa provided a comparative measure of intraspecific divergence. Three continental species (*Ar. adenocarpi*, *Ar. genistae* and *A. spartiophila*) are widespread occurring on several closely related host species. Individuals of these taxa were sampled from Morocco, Spain, Portugal and Scotland (Table 2 and Figs 3 & 4). Among the island species individuals were sampled from populations that either occurred on different islands and/or different host plants. Intraspecific genetic divergence (CO) was greatest within four Canary Island species that occurred on different islands but on the same host plant (*L. monospermae* from three islands, 4–5%; *Ar. devia* from four islands, 1–10%; *A. dividens* from three islands, 1–4%; and *A.* sp.10 from two islands, 5%). Divergence within the widespread continental species which 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 both samples showed 2.8% divergence from the Moroccan individual) (Figs 3 & 5). The same pattern in *Ar. adenocarpi* and *A. spartiophila* suggests that the Moroccan region may have provided glacial refugia, with rapid northward migration during inter-glacial periods, as has been shown for other invertebrates and mammals (Hewitt, 1996, 1999).

### **3.3.8** *Widespread taxa*

In the Canary Islands, nine of the 21 species (43%) occur on more than one island (*L. monospermae*, *Ar. devia*, *Ar.* sp.14, *A. dividens*, *A. diluta*, *A. modica*, *A. nigralineata*, *A. proboscidea* and *A.* sp.10). All but one of these are specific to a single host plant. About half of these species show low intraspecific molecular CO divergence (max 0.02-2%), suggesting recent inter-island dispersal; but four species (each specific to a single host) show considerably greater divergence (max 4-10%) (Figs 3 & 5). Specificity to a single host may be contributing to a lack of speciation (morphological stasis) in these taxa, particularly where host habitat and ecology are relatively uniform between islands. In other examples, where colonization of a new island is unaccompanied by a host switch but has resulted in speciation, the intraspecific host variation – distinct subspecies – may have promoted speciation. However, two of the widespread species occur on one of the most variable hosts, *Chamaecytisus proliferus* (3 subspecies, 4 varieties); and one these species (*Ar. devia*) was found to have almost as much intraspecific divergence (CO: 1-10%) as interspecific divergence found within the entire 'Macaronesian clade' (CO: 2-13%).

### 3.3.9 *Colonization patterns*

The 21 species of arytainine psyllid in the Canary Islands are probably derived from five independent colonizations of these islands (indicated by *, Fig. 6). Only one of these colonizations has resulted in a significant radiation (16 species in the 'Macaronesian clade'). Four of the colonizations have resulted in little or no radiation and are represented by one or two species in *Livilla*, *Arytainilla s.s.* and *Arytaina*. There has been one (ACCTRAN optimization), possibly two colonizations of Madeira (Fig. 6 shows the ACCTRAN optimization). The two Madeiran species (*A. incuba* and *A. umbonata*) form part of a group that includes the three continental species (*A. cognata*, *A. hakani* and *A.* sp.13) in the 'Macaronesian clade', and the derived position of this subclade within the 'Macaronesian clade' suggests one, or even two (with ACCTRAN optimization) possible back colonizations of the continent (i.e. one colonization of the continent from the Canary Islands and one from Madeira, Fig. 6 shows the ACCTRAN optimization). These continental recolonizations, however, may also be considered equivocal because the additional tree length (10 steps) required to exclude the Madeiran and continental species while constraining the Canary Island members of the 'Macaronesian clade' to be monophyletic, is not significant (Table 4).

The continental sister groups of the five Canary Island species not in the 'Macaronesian clade' (e.g. *Arytaina*, *Arytainilla s.s.* and *Livilla* spp.) are well resolved, and the continental sister taxa are all widespread and occur in the Iberian Peninsula and NW Africa. A comparison of host associations in the continental and island sister groups is used to assess the role of preadaptation to particular host plants in colonizing psyllids. In Figure 6, where the legume host genera of the island and continental sister taxa are mapped onto the psyllid tree, four of the five psyllid colonizations of the Canary Islands (indicated by *, Fig. 6) would also have required colonization of a novel host genus. The only example of an island psyllid occurring on the same host genus as its continental sister taxon, is *Livilla monospermae* on the host genus *Retama* (Fig. 6). However, the switches between host genera during island/continental colonization events, are all between host genera within the same host groups (e.g. the *Genista* group or the *Cytisus* group) within the Genisteae (Käss & Wink, 1997). Figure 7 presents these generic host groups mapped onto the psyllid phylogeny. Following dispersal, therefore, a psyllid may search among available hosts for recognizable features, and select the host as closely related to the original host as it can find, implying an important role for preadaptation to the selection process of particular types of available hosts.

## 3.4 Discussion

### 3.4.1 *Phylogeny of the Arytaininae*

The molecular analyses (Figs 3 & 4) confirm the reservations expressed by Hodkinson & Hollis (1987) concerning the monophyly of the Arytaininae. The current classification represents a paraphyletic group with respect to the Psyllinae (represented by *Cacopsylla*). Amongst the papilionoid legume-feeders, the genus *Cyamophila* whose members feed on the tribes Galegeae, Loteae, Phaseoleae, Soporeae and Loteae, are distinct from members feeding on the tribe Genisteae. *Cyamophila* appears to be 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 (Leguminosae). There is some evidence for a monophyletic Genisteae-feeding group (combined molecular analysis: MP bootstrap 59%, NJ bootstrap 92%, Fig. 4), but the inclusion of *Pseudacanthopsylla* in this group remains equivocal. Whether *Pseudacanthopsylla* unequivocally belongs to a monophyletic Genisteae-feeding group, may only be tested satisfactorily with additional sampling of Afro-tropical genera thought to be related to this genus (Hodkinson & Hollis, 1987).

The 'Macaronsian clade' ('M' in Figs 3-5) is a strongly supported monophyletic group, though the origin of this clade from within the Arytaininae remains ambiguous. The combined molecular analysis (12S and CO) suggests that it is nested within a paraphyletic *Livilla sensu lato*, and sister to the 'core *Livilla*' group ('L' in Figs 3-5). The three Macaronesian *Arytaina* species (*Ar. devia*, *Ar. nubivaga* and *Ar.* sp.14) do not appear to be a monophyletic group, but further intrageneric sampling is needed to confirm this. The single Macaronesian species of *Arytainilla s.s.* (*A.* sp.1) is strongly supported as grouping with the type species of this group (*A. delarbrei*), and the single Macaronesian species of *Livilla* (*L. monospermae*) is closely related to a continental outlying *Livilla* species (*L. retamae*) (Fig. 4). Further conclusions on the taxonomic implications of the phylogenetic analyses are given in the Taxonomic Appendix. Notably, there is good resolution and support for some major groups ('Macaronesain clade' – M, *Arytainilla s.s* – A, *Arytaina* – AR and the 'core *Livilla*' – L group), but among these groups, the relationships remain unsupported.

### 3.4.2 *Origins and colonization in Macaronesian Ayrtaininae*

Is there evidence to determine the sequence of colonization or to identify which of the Canary Islands was first colonized? The three basal species in the 'Macaronesian clade' (*A.* sp.5, *A. diluta* and *A. prognata*) occur on Gran Canaria (the geologically oldest and closest island to the African continent of the central islands). It is probable, therefore, that this island was the first island colonized, and the location of early diversification of the 'Macaronesian clade'.

Within the genus *Arytaina*, species or populations (*Ar.* sp.14 and *Ar. devia*) from geologically younger islands have 5th instar nymphs with fewer nymphal sectasetae on the abdomen. Optimization of this character on the psyllid phylogeny suggests that loss of sectasetae is derived in these taxa, which would reflect colonizations (east to west) from older to younger islands. However, a more extensive phylogeographic approach than the limited intraspecific sampling here, is required to test this interpretation, and would allow a comparison of the 'stepping stone' pattern of colonization found in other island invertebrate groups (Roderick & Gillespie, 1998; Juan *et al.*, 1998; Emerson *et al.*, 2000a). One common pattern that is evident in three species from different genera (*Ar. devia*, *A. dividens* and *L. monospermae*), is the close relationship between individuals sampled from the two closest islands, Tenerife and La Gomera (27 km apart). Further phylogeographic data for these taxa should be able to differentiate between a pattern of recent colonization (with markedly structured populations on each island) versus a pattern of gene flow between these geographically close islands, with distant islands more effectively isolated.

### 3.4.3 *Ecological and geographical patterns*

Host plant preference, ecology and geographical distribution in sister taxa, determined over three years of field surveys, are used to investigate the diversification of psyllids in Macaronesia. By combining field data with the psyllid phylogeny, three patterns of sister taxon relationships were inferred for the island Arytaininae. 1) the majority of sister taxa are ecologically and geographically allopatric, occurring both on different host plants and different islands or different regions within an island; 2) there are four cases of sister taxa occurring on the same host but different islands; 3) and there is only one case where sister taxa occur both on the same host and the same island (*A. diluta* and *A. prognata*). The latter may represent a case of sympatric speciation, however, there is evidence for a micro-allopatric adaptive shift, with each species restricted to either northern mesic habitats or dry southern habitats of the host. Geographical allopatry is the primary division when sister taxa occur on separate islands but on the same host, and furthermore, exhibit a shared preference for ecologically specialized subspecies of the host (*T. stenopetala*): sister taxa *A.* sp.10 and *A.* sp.11 are more common on the host's xerically adapted subspecies on La Palma (ssp. *sericea*) and La Gomera (ssp. *pauciovulata*); while *A. modica* and *A.* sp.12 are more common on the host's mesically adapted subspecies from the same islands (ssp. *stenopetala* and ssp. *microphylla*). These patterns suggest that, independently, ecological or geographical divergence may be sufficient to promote psyllid speciation, but both of these mechanisms are apparent in the majority of sister taxon relationships. The prevailing pattern that emerges is one of varying amounts of ecological and geographical shifts similar to other island invertebrate groups (Roderick & Gillespie, 1998).

A common feature of the Canarian Arytaininae is the presence of multiple (2-6) psyllid species on the same host (Table 5). The sharing of host resources may be facilitated by geographical segregation, ecological specialization and divergence in the timing of development. On Tenerife, *T. canariensis* is a widespread legume on which four psyllid species occur, but only one psyllid is found throughout the host range (*A. pileolata*) while the other species (*A. diluta, A.* sp.7 and *A.* sp.8) occur in particular regions or habitats. A similar pattern is found on Gran Canaria, where three psyllid species occur on *T. microphylla*, one widespread (*A. equitans*) and two localized species (*A. diluta* and *A. prognata*). As a widespread legume occurs in several types of habitat, a widespread psyllid species may be considered an ecological generalist, whereas psyllids restricted to local habitats types may be ecological specialists. Interestingly, the phylogeny suggests that, on Tenerife, the localized species are more derived, but this is reversed on Gran Canaria where the widespread species is more derived. In addition, both widespread species develop later in the season than the ecologically localized species, and this temporal division is also found in two widespread species which both occur throughout the host range (*Ar. devia* develops later than *A. dividens* on *Chamaecytisus proliferus*). These patterns suggest a degree of competitive displacement and/or exclusion is operating to partition the use of plant resources by psyllid species.

An example which supports a role for competitive exclusion is found in the two *Adenocarpus*-feeding species (*A. nigralineata* and *A. proboscidea*). On Tenerife both the psyllids are present and each psyllid is specific to one of two hosts (the hosts are divided altitudinally and ecologically). But on La Palma only one psyllid species is present, and this psyllid occurs throughout both host ranges. Oviposition in *Adenocarpus*-feeding species is on the flowers and inflorescence, and exclusivity on Tenerife may be driven by adaptation to phenological differences (*Adenocarpus foliolosus* flowers earlier than *A. viscosus*). The effects of phenology and altitudinal clines are therefore more likely to influence patterns of host specialization when the presence of another psyllid requires a competetive advantage. A study of willow psyllids found similar variation in resource exploitation along an altitudinal gradient (Hill, Hamer & Hodkinson, 1998).

### 3.4.4 *Anthropogenic effects on host populations and host hybridization*

The Genisteae species that were found to host psyllids were all estimated to have an abundance equal to, or greater than 2000 individuals. The rarest legume on which a psyllid was found is *T. osyroides* ssp. *osyroides* with a single population of c. 2000-3000 individuals in the Barranco de Masca. The Genisteae species which do not host psyllids (up to one third of the legumes (17-33%) per island) are all rare species with less than 2000 individuals, and in many cases these are rare because of human activity. Thus, there is a possibility that there were psyllids on these hosts in the past but these psyllids are now extinct. There may be a critical host plant abundance, below which a psyllid species may be unable to maintain a viable population. Fragmentation of host populations may also be critical: an uncommon legume (*T. rosmarinifolia*) occurs in several small, fragmented populations, and a rare psyllid species (*A.* sp.5) was found on only one of these populations. 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 (*Adenocarpus viscosus*) appears to have increased the abundance of psyllid species associated with these hosts.

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 occur on multiple hosts (*A. diluta*, *A.equitans*, *A. pileolata*, *A. proboscidea* and *A.* sp.8) and hybrids have also been recorded between these hosts (Table 5). On Tenerife, hybrids between three host species (*T. canariensis*, *T. stenopetala* and *T. osyroides*) occur around the Ladera de Güímar (Arco Aguilar, pers. comm.) – an area settled by the aboriginal Guanches; and the most polyphagous psyllid species in the Canary Islands (*A. pileolata* in the 'Macaronesian clade') is found on these three hosts. As hybrids are more likely to occur between closely related species, it is not clear, without mapping host and psyllid genotypes across hybrid zones, whether the host shifts occurred because of phylogenetic compatibility, or whether hybridization could have promoted the shift via a 'hybrid bridge' effect (Floate & Whitham, 1993; Roderick, 1997).

## 3.5 Taxonomic Appendix

### 3.5.1 *Arytainilla*

There are currently 34 species in this genus, but the genus is clearly paraphyletic (Table 4). The majority of the species (21) belong to the 'Macaronesian clade' discussed below. The remaining species can be divided into a small group which includes the type species (*Arytainilla sensu stricto*: nine species, of which six species are included in this study), and four residual and heterogeneous species that are morphologically atypical (*A. ima*, *A. sulci*, *A. gredi* and *A.* sp.4: *Arytainilla sensu lato*). *Arytainilla s.s.* is characterized by unusually large female genitalia and a massive ovipositor. This group (labelled 'A' in Figs 3-5) is supported as monophyletic in the CO phylogeny (bootstrap MP: 78%, Fig. 3B; NJ: 89%) and the combined morphological and molecular analysis (bootstrap MP: 87%, Fig. 5C) but appears paraphyletic in respect to the genus *Arytaina* in the 12S analysis using NJ and ML methods, and is unresolved in the MP 12S phylogeny (Fig. 3A). Hence the absence of support for *Arytainilla s.s.* in the MP combined molecular analysis (Fig. 4). There is a single species of *Arytainilla s.s.* in the Canary Islands (*A.* sp.1), which groups with the type species (*A. delarbrei*, MP bootstrap > 80% in the combined molecular (Fig. 4) and total evidence (Fig. 5C) phylogenies). The nymphal morphology of this group is extremely variable. *A. sulci* is unique within the Arytaininae in the tergal plates of the 5th instar nymph which are barely reduced. The combined molecular phylogeny (12S and CO, Fig. 4) suggests that *A. gredi* and *A.* sp.4 have closer affinities to *Livilla* than to *Arytainilla*, and that *A. sulci* is sister to *Arytaina*. *A. ima* belongs to a small, well supported group (MP bootstrap > 80% in both combined analyses, Figs 4 & 5) of outlying *Livilla* species that feed on the genus *Adenocarpus* (Fig. 7). Members of *Arytainilla s.s.* predominantly feed on host plants in, or allied to the genus *Cytisus* (*Cytisus* group) (Fig. 7).

### 3.5.2 The 'Macaronesian clade' of *Arytainilla*

This clade of 21 species is not exclusively Macaronesian, but appears to have evolved and diversified in Macaronesia. The clade (labelled 'M' in Figs 3-5) is unambiguously resolved in all molecular analyses and in the morphological analysis. Support for the monophyly of the clade is strong in the independent 12S and CO phylogenies (bootstrap MP: 79-99%,Fig. 3A & B; NJ: 91-100%); and although the clade lacks bootstrap support in the morphological phylogeny (Fig. 3C), the combined morphological and molecular data provide 99% MP bootstrap (Fig. 5C). Members of the 'Macaronesian clade' predominantly feed on host plants in, or allied to the genus *Genista* (*Genista* group) (Fig. 7).

### 3.5.3 *Arytaina*

There are 14 species in *Arytaina* of which five have been included in this study: three Macaronesian taxa which are endemic to the Canary Islands (*Ar. devia*, *Ar. nubivaga* and *Ar.* sp.14), and two continental species (*Ar. adenocarpi* and the genus type species, *Ar. genistae*). Although sampling is limited, the strong support for this group (labelled 'AR' in Figs 3-5), suggests that *Arytaina* is the only unambiguously monophyletic genus in the Genisteae-feeding Arytaininae (Figs 3-5). The Macaronesian taxa, although originally placed in this genus (Loginova, 1976a), were later removed and placed in *Arytainilla* based mainly on the peculiar morphology of the male genitalia (Hodkinson & Hollis, 1987). Nevertheless, there is strong support from both the morphological (MP booststrap 74%, Fig. 3C) and molecular (MP booststrap 89-100%, Fig. 3A & B) phylogenies for reverting to the original classification. Members of *Arytaina* predominantly feed on host plants in, or allied to the genus *Cytisus* (*Cytisus* group) (Fig. 7).

### 3.5.4 *Livilla*

This is the largest Genisteae-feeding genus and, like *Arytainilla*, it is clearly paraphyletic as indicated by the additional tree length required when the genus is constrained to be monophyletic (Table 4). There are 39 species, 19 of which are included in this study. The monophyly of a core group of *Livilla* species (labelled 'L' in Figs 3-5) is well supported (combined 12S and CO: MP bootstrap 81%, Fig. 4). Neither the single Macaronesian species (*L. monospermae*), nor the type-group as defined by Hodkinson & Hollis (1987) (represented in this study by *L. vicina*) is included in this 'core *Livilla*' group. However, constraining the 'core *Livilla*' species to be monophyletic with the inclusion of three of the outlying species (*L. nervosa*, *L. monospermae* and *L. retamae*) but not including *L. vicina* or the *Adenocarpus*-feeding species (*L.* sp.15, sp.16 and sp.17) does not require a significant increase in tree length (Table 4); and this group is recovered in the total evidence phylogeny (but with low bootstrap support, MP: 57%, Figs 5C). Members of this genus typically feed on hosts plants in, or allied to the genus *Genista* (*Genista* group, Fig. 7).

### 3.5.5 *Pseudacanthopsylla improvisa* comb. nov.

*Psylla improvisa* Loginova, 1972: 30

This genus, previously monotypic (a single species in the Middle East and NE Africa, *P.retamae*), is represented in this study by a second species (*Psylla impovisa*) from NW Africa, which is transferred to *Pseudacanthopsylla* based on the following generic features: unpatterned, parallel-sided forewing with well developed pterostigma, short robust genal cones, metatarsal spur absent, and a unique 'hedgehog' nymphal morphology with near entire coverage of sectasetae (Fig. 6B). *P. improvisa* differs from the type species (*P. retamae*, Samy, 1972: 455) in the narrower, more acutely rounded forewing apex, more slender genal cones, and the distinctive shape of the male and female genitalia (illustrated by Loginova, 1972). Both the species occur on the same widespread host plant (*Retama raetam*). The conflicting placement of this peculiar genus is discussed in the main body of the paper under the separate molecular analyses.

## 3.6 References

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TABLE 1. Physical characteristics of the Canary Islands and Madeira with diversity of host plant and psyllid species, and number of plants used as hosts.

| island | distance to mainland km | altitude m | area km$^2$ | age Myr | host plants (Genisteae) |  | psyllids (Arytaininae) |  | % Genisteae utilized as hosts (n) |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | native species | % endemic (n) | native species | % endemic (n) |  |
| Gran Canaria | 245 | 1950 | 1534 | 14.5-16 | 7 | 43 (3) | 7 | 43 (3) | 71 (5) |
| Tenerife | 303 | 3717 | 2058 | 7.5-11.5 | 11 | 18 (2) | 11 | 36 (4) | 73 (8) |
| La Gomera | 417 | 1487 | 378 | 10-12 | 6 | 17 (1) | 7 | 29 (2) | 83 (5) |
| La Palma | 489 | 2426 | 728 | 2 | 9 | 22 (2) | 7 | 14 (1) | 67 (6) |
| El Hierro | 489 | 1501 | 277 | 1.1 | 5 | 20 (1) | 4 | 0 | 80 (4) |
| Madeira | 630 | 1861 | 728 | 30 | 2 | 100 (2) | 2 | 100 (2) | 100 (2) |

TABLE 2. Distribution of taxa and location of 84 samples representing 62 taxa (61 species and one subspecies) included in this study. The data set in which each sample was included are indicated: 12S – small subunit rRNA; CO – cytochrome oxidase and tRNA leucine; M – morphological (adult and nymph), M* (adult only). Material supplied by Daniel Burckhardt (DB), David Hollis (DH) and Ian Hodkinson (IH) is indicated, all other material was collected by this author (see Chapter 2).

| data sets | taxon | origin of sample | plant species from which sample was collected [and host plant if different] | DNA voucher number |
|---|---|---|---|---|
| 12S CO | *Acizzia hollisi* | Morocco: High Atlas | *Genista florida* [*Acacia* spp.] | DP325.1B |
| 12S CO M | *Acizzia uncatoides* | Canary Islands: La Palma | *Acacia* spp. (cultivated) | DP194 |
| 12S CO M | *Arytaina adenocarpi* | Portugal: Coimbra | *Adenocarpus complicatus* | DP262.3A |
| 12S CO M | *Arytaina adenocarpi* | Spain: Málaga | *Adenocarpus telonensis* | DP233 |
| 12S CO M | *Arytaina adenocarpi* | Morocco: Middle Atlas | *Adenocarpus boudyi* | DP243 |
| CO M | *Arytaina devia* | Canary Islands: Tenerife | *Chamaecytisus proliferus* | DP188.1 |
| CO M | *Arytaina devia* | Canary Islands: La Gomera | *Chamaecytisus proliferus* | DP68 |
| 12S CO M | *Arytaina devia* ssp. *insularis* | Canary Islands: Gran Canaria | *Chamaecytisus proliferus* | DP161 |
| 12S CO M | *Arytaina devia* ssp. *insularis* | Canary Islands: La Palma | *Chamaecytisus proliferus* | DP189 |
| 12S CO M | *Arytaina genistae* | Scotland: Edinburgh | *Cytisus scoparius* | none |
| 12S CO M | *Arytaina genistae* | Portugal: Coimbra | *Cytisus striatus* | DP263 |
| CO M | *Arytaina genistae* | Morocco: High Atlas | *Cytisus grandiflorus* | DP325.2 |
| 12S CO M | *Arytaina nubivaga* | Canary Islands: Tenerife | *Spartocytisus supranubius* | DP154 |
| 12S CO M | *Arytaina* sp.14 (vittata) | Canary Islands: La Gomera | *Spartocytisus filipes* | DP69 + 220 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 12S | CO | M | *Arytainilla cognata* | Morocco: High Atlas | *Genista florida* | DP238 |
| 12S | CO | M | *Arytainilla cytisi* | Morocco: Rif mountains | *Calicotome villosa* | DP319 |
| 12S | CO | M* | *Arytainilla delarbrei* | Portugal: Coimbra | *Cytisus purgans* | DP265.2 |
| 12S | CO | M | *Arytainilla diluta* | Canary Islands: Gran Canaria | *Teline microphylla* | DP172 |
| | CO | M | *Arytainilla diluta* | Canary Islands: Tenerife | *Teline canariensis* | DP152 |
| 12S | CO | M | *Arytainilla dividens* | Canary Islands: Gran Canaria | *Chamaecytisus proliferus* | DP168 |
| | CO | M | *Arytainilla dividens* | Canary Islands: Tenerife | *Chamaecytisus proliferus* | DP188.2 |
| 12S | CO | M | *Arytainilla dividens* | Canary Islands: La Gomera | *Chamaecytisus proliferus* | DP244 |
| 12S | CO | M | *Arytainilla equitans* | Canary Islands: Gran Canaria | *Teline microphylla* | DP163 |
| 12S | | M | *Arytainilla gredi* DH | Spain: Picos de Europa | *Genista hispanica* | DH336 |
| 12S | CO | M | *Arytainilla hakani* | Morocco: Rif mountains | *Teline monspessulana* | DP256 |
| 12S | CO | M | *Arytainilla ima* | Morocco: High Atlas | *Adenocarpus anagyrifolius* | DP239 |
| 12S | CO | M | *Arytainilla incuba* | Madeira: Encumeada | *Teline maderensis* | DP271 + 274 |
| 12S | CO | M | *Arytainilla modica* | Canary Islands: La Palma | *Teline stenopetala* | DP192 |
| 12S | CO | M | *Arytainilla modica* | Canary Islands: La Palma | *Chamaecytisus proliferus* | DP201 |
| | CO | M | *Arytainilla modica* | Canary Islands: El Hierro | *Teline stenopetala* | DP212 |
| | CO | M | *Arytainilla modica* | Canary Islands: El Hierro | *Chamaecytisus proliferus* | DP211 |
| 12S | CO | M | *Arytainilla nigralineata* | Canary Islands: Gran Canaria | *Adenocarpus foliolosus* | DP173 |
| | CO | M | *Arytainilla nigralineata* | Canary Islands: Tenerife | *Adenocarpus foliolosus* | DP156 |
| | CO | M | *Arytainilla nigralineata* | Canary Islands: La Gomera | *Adenocarpus foliolosus* | DP67 |
| 12S | CO | M | *Arytainilla pileolata* | Canary Islands: Tenerife | *Teline canariensis* | DP178 |
| | CO | M | *Arytainilla pileolata* | Canary Islands: Tenerife | *Teline osyroides* | DP184 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 12S | CO | M | *Arytainilla proboscidea* | Canary Islands: Tenerife | *Adenocarpus viscosus* | DP5 |
| | CO | M | *Arytainilla proboscidea* | Canary Islands: La Palma | *Adenocarpus foliolosus* | DP204 |
| 12S | CO | M | *Arytainilla prognata* | Canary Islands: Gran Canaria | *Teline microphylla* | DP160 |
| 12S | CO | M | *Arytainilla spartiophila* | Portugal: Coimbra | *Cytisus striatus* | DP265 |
| 12S | CO | M | *Arytainilla spartiophila* | Spain: Málaga | *Cytisus grandiflorus* | DP133 |
| | CO | M | *Arytainilla spartiophila* | Morocco: High Atlas | *Cytisus fontanesii* | DP327 |
| 12S | CO | M | *Arytainilla sulci* | Morocco: SW coast | *Retama raetam* | DP297 |
| 12S | CO | M | *Arytainilla umbonata* | Madeira: Encumeada | *Genista tenera* | DP273 |
| 12S | CO | M | *Arytainilla* sp.1 (serpentina) | Canary Islands: La Palma | *Spartocytisus filipes* | DP198 |
| 12S | CO | M | *Arytainilla* sp.2 (atlantica) | Morocco: SW coast | *Cytisus albidus* | DP296 |
| 12S | CO | M | *Arytainilla* sp.3 (telonicola) | Spain: Málaga | *Adenocarpus telonensis* | DP134 |
| 12S | CO | M | *Arytainilla* sp.4 (montivaga) | Spain: Granada | *Adenocarpus decorticans* | DP128 |
| | CO | M | *Arytainilla* sp.4 (montivaga) | Morocco: Rif mountains | *Adenocarpus decorticans* | DP249 |
| 12S | CO | M | *Arytainilla* sp.5 (remeria) | Canary Islands: Gran Canaria | *Teline rosmarinifolia* | DP165 |
| 12S | CO | M | *Arytainilla* sp.6 (fortunata) | Canary Islands: La Palma | *Teline splendens* | DP203 |
| 12S | CO | M* | *Arytainilla* sp.7 (canariensis) | Canary Islands: Tenerife | *Teline canariensis* | DP179 |
| 12S | CO | M | *Arytainilla* sp.8 (menceyata) | Canary Islands: Tenerife | *Teline canariensis* | DP182 |
| 12S | CO | M | *Arytainilla* sp.9 (ochrita) | Canary Islands: Tenerife | *Teline osyroides* | DP153 |
| 12S | CO | M | *Arytainilla* sp.10 (occidentalis) | Canary Islands: La Palma | *Teline stenopetala* | DP190 |
| | CO | M | *Arytainilla* sp.10 (occidentalis) | Canary Islands: El Hierro | *Teline stenopetala* | DP214 |
| 12S | CO | M | *Arytainilla* sp.11 (gomerae) | Canary Islands: La Gomera | *Teline stenopetala* | DP221 |
| 12S | CO | M | *Arytainilla* sp.12 (hupalupa) | Canary Islands: La Gomera | *Teline stenopetala* | DP219 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 12S | CO | M | *Arytainilla* sp.13 (berber) | Morocco: Anti-Atlas | *Genista segonnei* | DP332 |
| 12S | CO | | *Cacopsylla alaterni* | Spain: Málaga | *Rhamnus alaternus* | DP112 |
| 12S | CO | | *Cacopsylla mali* | Scotland: Edinburgh | *Malus* sp. | DP293 |
| 12S | CO | | *Cyamophila prohaskai* DB | Switzerland: Aemsigén | Coniferae [*Anthyllis vulneraria*] | DB341 |
| 12S | CO | M* | *Livilla adusta* | Spain: Málaga | *Genista cinerea* | DP132 |
| 12S | CO | M | *Livilla blandula* | Morocco: SW coast | *Cytisus albidus* | DP296 |
| 12S | | | *Livilla horvathi* DB | Turkey: Kars | ? [*Chamaecytisus austriacus*] | DB1 |
| 12S | | | *Livilla maculipennis* IH | Algeria: El Gor | ? [*Genista* sp.] | IH8 |
| 12S | CO | | *Livilla maura* | Morocco: Rif mountains | *Chamaespartium tridentatum* | DP250 |
| 12S | CO | M | *Livilla monospermae* | Canary Islands: Tenerife | *Retama monosperma* | DP28 |
| | CO | M | *Livilla monospermae* | Canary Islands: La Gomera | *Retama monosperma* | DP70 |
| | CO | M | *Livilla monospermae* | Canary Islands: La Palma | *Retama monosperma* | DP196 |
| 12S | | M* | *Livilla nervosa* | Spain: Granada | *Genista umbellata* | DP124 |
| 12S | | | *Livilla pseudoretamae* IH | Algeria: Grand Kabylie | ? [host plant unknown] | IH7 |
| 12S | | | *Livilla pyrenaea* DB | Spain: Zaragoza | '*Genista scoparius*' [*Genista* sp.] | DB4 |
| 12S | | | *Livilla radiata* DB | Greece: Peloponnese | 'Genistae ?' [*Chamaecytisus* spp.] | DB6 |
| 12S | CO | M | *Livilla retamae* | Spain: Cádiz | *Retama monosperma* | DP94 |
| 12S | | | *Livilla spectabilis* IH | Italy: Liguria | *Spartium junceum* | IH6 |
| 12S | | | *Livilla syriaca* DB | Israel: Carmel | *Genista fasselata* | DB3 |
| 12S | CO | | *Livilla variegata* | Scotland: Glasgow | *Laburnum anagyroides* | DP337 |
| 12S | | | *Livilla vicina* DB | Switzerland: Vermala | *Genista radiata* | DB5 |
| 12S | | | *Livilla vittipennella* IH | Italy: Trentino | *Genista radiata* | IH5 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 12S | CO | M* | *Livilla* sp.15 (caprifuga) | Morocco: Middle Atlas | *Adenocarpus bacquei* | DP309 |
| 12S | CO | M* | *Livilla* sp.16 (baetica) | Spain: Granada | *Adenocarpus decorticans* | DP129 |
| 12S | CO | M* | *Livilla* sp.17 (complexa) | Portugal: Coimbra | *Adenocarpus complicatus* | DP262.3B |
| 12S | CO | M | *Pseudacanthopsylla improvisa comb. nov.* | Morocco: SW coast | *Retama raetam* | DP301 |

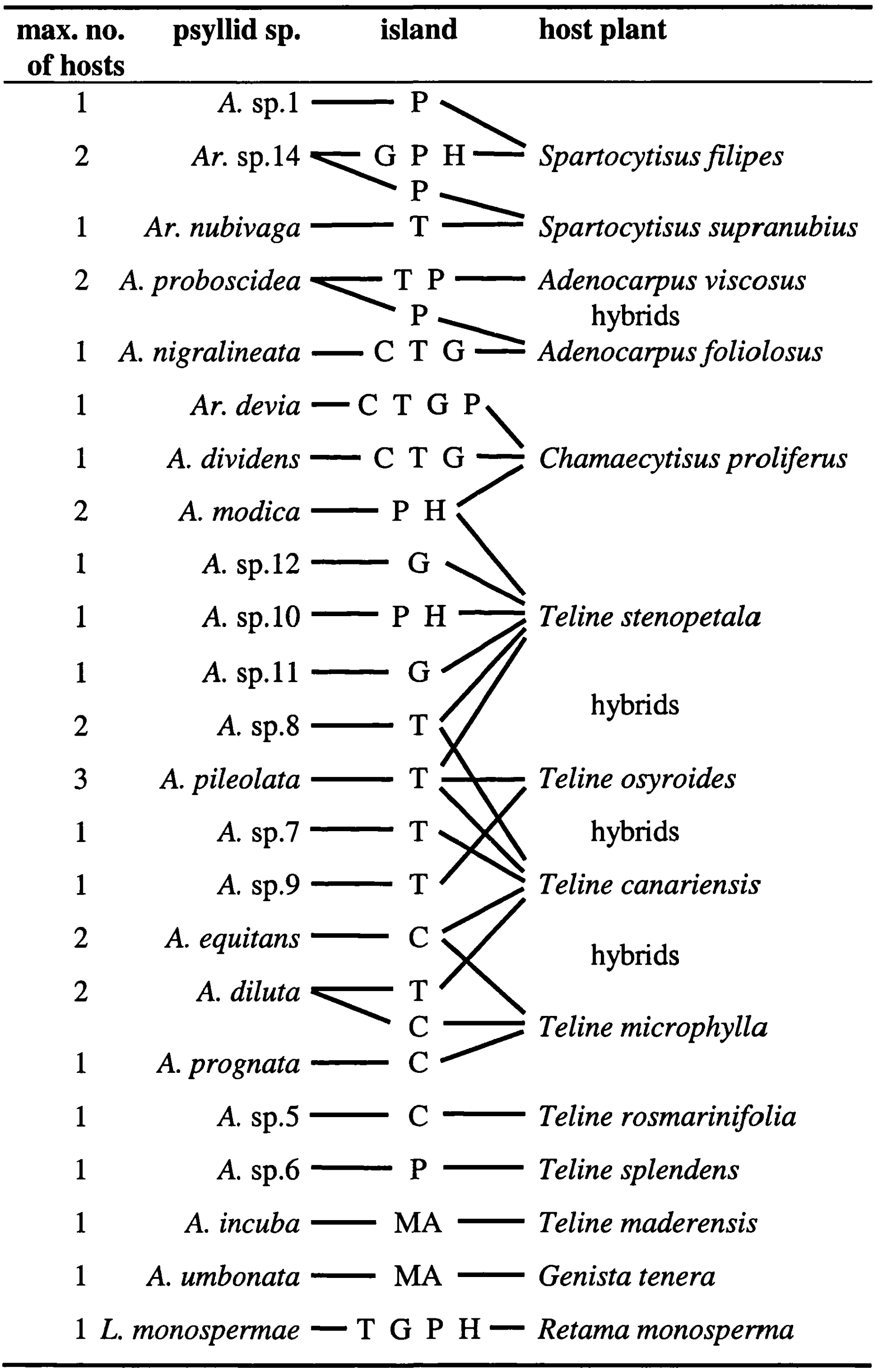
TABLE 3. Sequence characteristics of 12S, COI, tRNA leucine and COII regions of 62 taxa of Arytaininae (Psyllidae). Sequence divergence is estimated from uncorrected pairwise distances.

| parameter | 12S | COI | tRNA | COII | combined regions |
|---|---|---|---|---|---|
| length range (total) bp | 285-327 | 209-262 | 64-71 | 257-298 | 815-958 |
| length mean (total) bp | 321 | 255 | 67.5 | 285.2 | 927.7 |
| length range (ingroup) bp | 285-327 | 211-264 | 64-70 | 257-298 | 815-927 |
| length mean (ingroup) bp | 321 | 257 | 64.5 | 285.2 | 927.7 |
| length range (outgroup) bp | 307-323 | 262-265 | 65-71 | 298 | 932-954 |
| length mean (outgroup) bp | 315 | 263.5 | 66.5 | — | 943 |
| aligned length bp | 342 | 262 | 79 | 298 | 981 |
| A + T content range % | 74-80 | 67-77 | 72-83 | 71-80 | 67-83 |
| A + T content mean % | 77 | 72 | 78 | 76 | 76 |
| number of excluded sites (%) | 20 (5.9) | — | — | — | 20 (5.9) |
| sequence divergence (ingroup) % | 0-20 | 0-28 | 0-28 | 0-26 | 0-28 |
| sequence divergence (in/outgroup) % | 15-26 | 18-28 | 5-19 | 19-32 | 5-32 |
| number of indels (ingroup) | 15 | — | 7 | — | 22 |
| number of indels (total) | 17 | — | 7 | — | 24 |
| size of indels (ingroup) | 1-6 | — | 1-5 | — | 1-6 |
| size of indels (total) | 1-10 | — | 1-5 | — | 1-10 |
| number of sites after exclusion | 322 | — | — | — | 961 |
| number of variable sites (%) | 168 (52) | 150 (57) | 24 (32) | 178 (60) | 520 (53) |
| number of constant sites (%) | 154 (48) | 115 (43) | 52 (68) | 120 (40) | 441 (45) |
| number of informative sites (%) | 134 (42) | 131 (49) | 20 (26) | 146 (49) | 431 (44) |
| number of autapomorphic sites (%) | 34 (11) | 19 (7) | 4 (5) | 32 (11) | 89 (9) |
| transitions (minimum) | 380 | 485 | 40 | 500 | 1375 |
| transversions (minimum) | 271 | 240 | 43 | 290 | 861 |
| transitions/transversions | 1.4 | 2 | 0.9 | 1.7 | 1.6 |

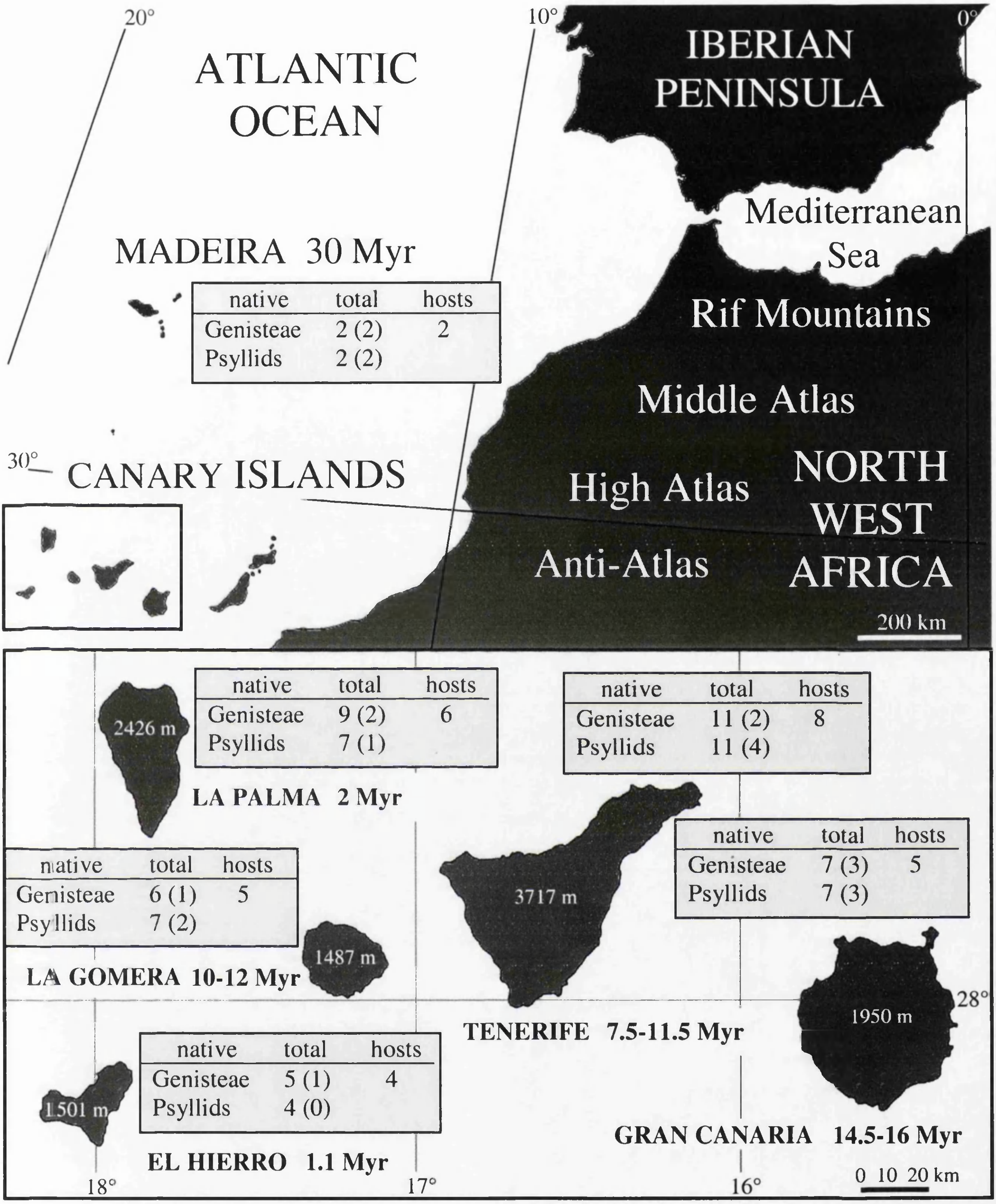
TABLE 4. Tests for monophyly in the genera *Arytainilla* and *Livilla*, and of biogeographic constraints within the 'Macaronesian clade'. Significant length difference ($P = < 0.05$) for constraints is indicated by *.

| constraint | no. of species | cost of monophyly: MP tree length difference | Templeton (Wilcoxon signed-rank) test |
|---|---|---|---|
| 1. monophyly of *Livilla* | 19 | 29 | $P = 0.0095$ * |
| 2. *Livilla* exc. type-group + *Adenocarpus*-feeding species | 15 | 4 | $P = 0.4328$ |
| 3. monophyly of *Arytainilla* | 31 | 34 | $P = 0.0065$ * |
| 'Macaronesian clade' | | | |
| 4. Macaronesian group excluding continental species | 18 | 33 | $P = < 0.0001$ * |
| 5. Canary Island group excluding continental and Madeiran species | 16 | 10 | $P = 0.0588$ |

TABLE 5. Macaronesian arytainine psyllid species showing the island distributions and host plant associations for each taxon in the three genera; host species between which hybrids have been recorded are indicated. (See Fig. 3 for island codes.)



| max. no. of hosts | psyllid sp. | island | host plant |
|---|---|---|---|
| 1 | *A.* sp.1 | P | |
| 2 | *Ar.* sp.14 | G P H | *Spartocytisus filipes* |
| | | P | |
| 1 | *Ar. nubivaga* | T | *Spartocytisus supranubius* |
| 2 | *A. proboscidea* | T P | *Adenocarpus viscosus* |
| | | P | hybrids |
| 1 | *A. nigralineata* | C T G | *Adenocarpus foliolosus* |
| 1 | *Ar. devia* | C T G P | |
| 1 | *A. dividens* | C T G | *Chamaecytisus proliferus* |
| 2 | *A. modica* | P H | |
| 1 | *A.* sp.12 | G | |
| 1 | *A.* sp.10 | P H | *Teline stenopetala* |
| 1 | *A.* sp.11 | G | hybrids |
| 2 | *A.* sp.8 | T | |
| 3 | *A. pileolata* | T | *Teline osyroides* |
| 1 | *A.* sp.7 | T | hybrids |
| 1 | *A.* sp.9 | T | *Teline canariensis* |
| 2 | *A. equitans* | C | hybrids |
| 2 | *A. diluta* | T | |
| | | C | *Teline microphylla* |
| 1 | *A. prognata* | C | |
| 1 | *A.* sp.5 | C | *Teline rosmarinifolia* |
| 1 | *A.* sp.6 | P | *Teline splendens* |
| 1 | *A. incuba* | MA | *Teline maderensis* |
| 1 | *A. umbonata* | MA | *Genista tenera* |
| 1 | *L. monospermae* | T G P H | *Retama monosperma* |



| native | total | hosts |
|---|---|---|
| Genisteae | 2 (2) | 2 |
| Psyllids | 2 (2) | |

| native | total | hosts |
|---|---|---|
| Genisteae | 9 (2) | 6 |
| Psyllids | 7 (1) | |

| native | total | hosts |
|---|---|---|
| Genisteae | 11 (2) | 8 |
| Psyllids | 11 (4) | |

| native | total | hosts |
|---|---|---|
| Genisteae | 7 (3) | 5 |
| Psyllids | 7 (3) | |

| native | total | hosts |
|---|---|---|
| Genisteae | 6 (1) | 5 |
| Psyllids | 7 (2) | |

| native | total | hosts |
|---|---|---|
| Genisteae | 5 (1) | 4 |
| Psyllids | 4 (0) | |

FIGURE 1. Map of the Macaronesian and adjacent continental areas surveyed for this study. Boxes give number of native host plant species (Genisteae) and psyllids for Madeira and each of the central and western Canary Islands (with number of endemic species in parenthesis).

FIGURE 2. Substitution rates shown as transitions/transversions for the 12S and CO regions.

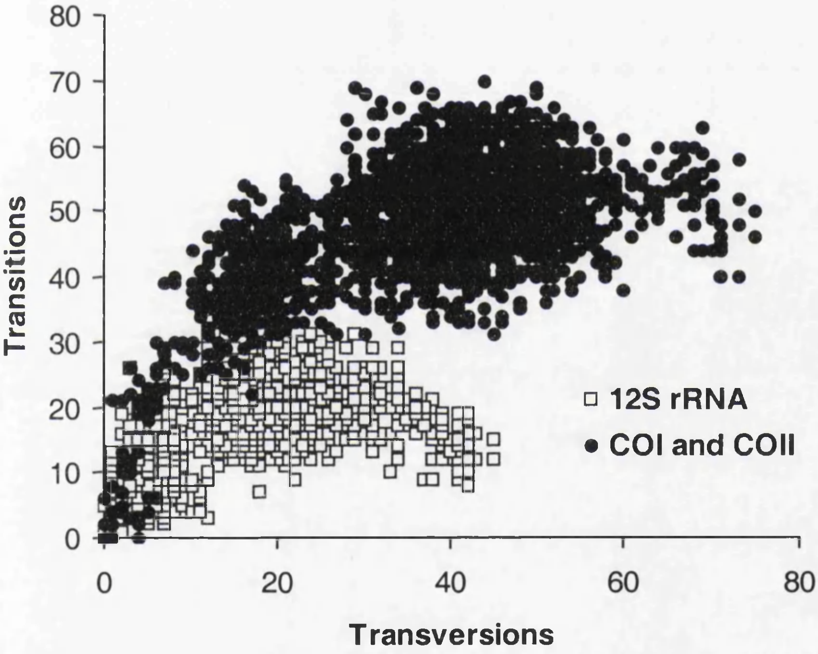


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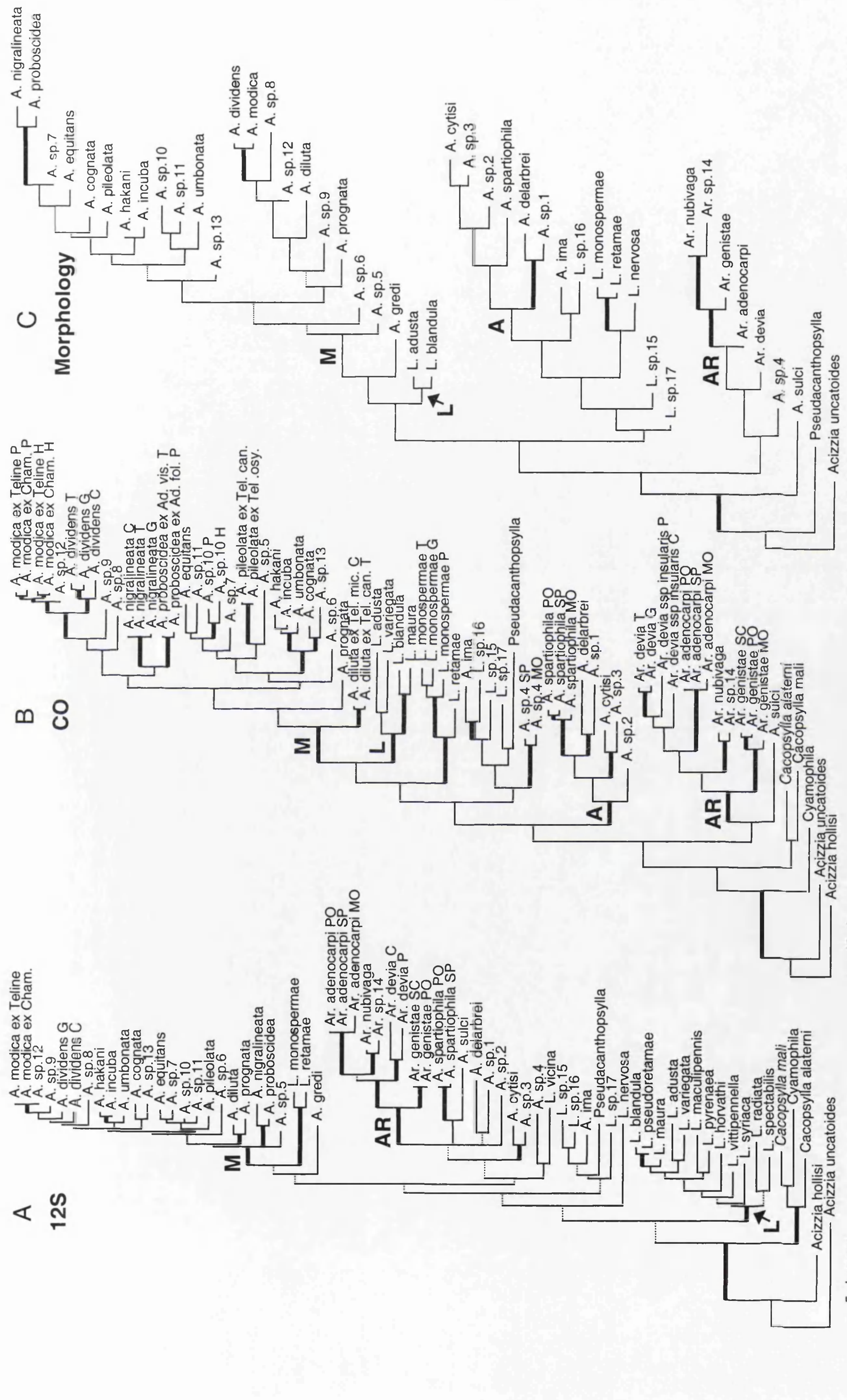
FIGURE 3.

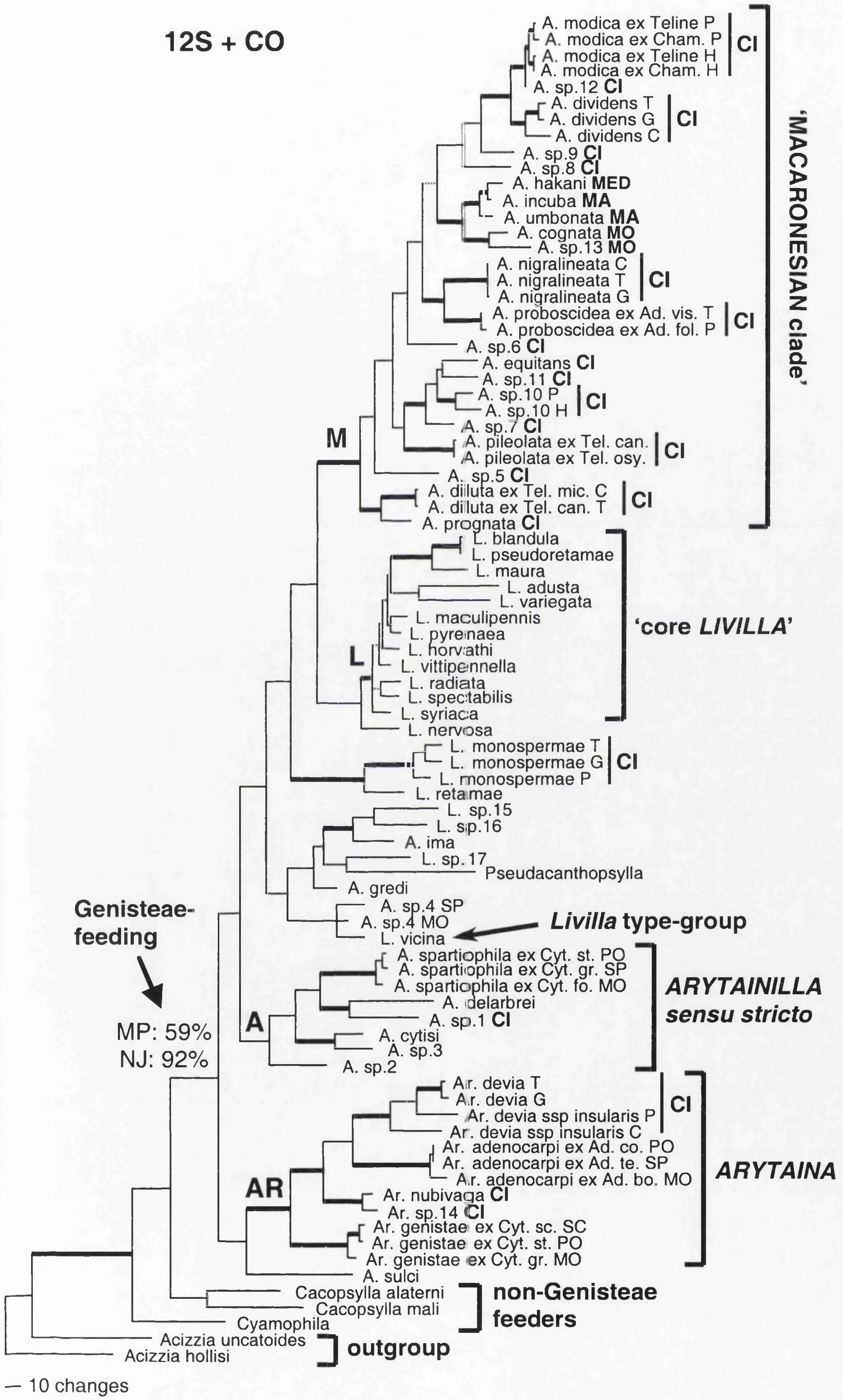
Phylograms of the three data sets in this study. A – 12S, one of the 750 MP trees based on 12S rRNA sequences (length 807, CI 0.32 excluding uninformative characters, RI 0.614); B – CO, one of the six MP trees based on COI-tRNA leucine-COII sequences (length 2280, CI 0.248 excluding uninformative characters, 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 nodes that collapse in the Strict consesus. Labelled nodes: A = *Arytainilla*, AR = *Arytaina*, L = 'core *Livilla*', M = 'Macaronesian clade'. Where samples occur on different host plants, these are indicated (abbreviated from Table 2). Abbreviated codes for sample origin and labelled nodes (Figs 3-5): Scotland – SC, Portugal – PO, Spain – SP, Morocco – MO, Madeira – MA, Canary Islands – CI: Gran Canaria – C, Tenerife – T, La Gomera – G, La Palma – P, El Hierro – H.


A
12S
A. modica ex Teline
A. modica ex Cham.
A. sp.12
A. sp.9
A. dividens G
A. dividens C
A. sp.8
A. hakani
A. incuba
A. umbonata
A. cognata
A. sp.13
A. equitans
A. sp.7
A. sp.10
A. sp.11
A. pileolata
A. sp.6
A. diluta
A. prognata
A. nigralineata
A. proboscidea
A. sp.5
L. monospermae
L. retamae
A. gredi
M
Ar. adenocarpi PO
Ar. adenocarpi SP
Ar. adenocarpi MO
Ar. nubivaga
Ar. sp.14
Ar. devia C
Ar. devia P
Ar. genistae SC
Ar. genistae PO
A. spartiophila PO
A. spartiophila SP
A. sulci
A. delarbrei
A. sp.1
A. sp.2
AR
A. cytisi
A. sp.3
A. sp.4
L. vicina
L. sp.15
L. sp.16
A. ima
Pseudacanthopsylla
L. sp.17
L. nervosa
L. blandula
L. pseudoretamae
L. maura
L. adusta
L. variegata
L. maculipennis
L. pyrenaea
L. horvathi
L. vittipennella
L. syriaca
L. radiata
L. spectabilis
Cacopsylla mali
Cyamophila
Cacopsylla alaterni
L
Acizzia hollisi
Acizzia uncatoides
5 changes
B
CO
A. modica ex Teline P
A. modica ex Cham. P
A. modica ex Teline H
A. modica ex Cham. H
A. sp.12
A. dividens T
A. dividens G
A. dividens C
A. sp.9
A. sp.8
A. nigralineata C
A. nigralineata T
A. nigralineata G
A. proboscidea ex Ad. vis. T
A. proboscidea ex Ad. fol. P
A. equitans
A. sp.11
A. sp.10 P
A. sp.10 H
A. sp.7
A. pileolata ex Tel. can.
A. pileolata ex Tel .osy.
A. sp.5
A. hakani
A. incuba
A. umbonata
A. cognata
A. sp.13
A. sp.6
A. prognata
A. diluta ex Tel. mic. C
A. diluta ex Tel. can. T
L. adusta
L. variegata
L. blandula
L. maura
L. monospermae T
L. monospermae G
L. monospermae P
L. retamae
M
L
A. ima
L. sp.16
L. sp.15
L. sp.17
Pseudacanthopsylla
A. sp.4 SP
A. sp.4 MO
A. spartiophila PO
A. spartiophila SP
A. spartiophila MO
A. delarbrei
A. sp.1
A. cytisi
A. sp.3
A. sp.2
A
Ar. devia T
Ar. devia G
Ar. devia ssp insularis P
Ar. devia ssp insularis C
Ar. adenocarpi PO
Ar. adenocarpi SP
Ar. adenocarpi MO
Ar. nubivaga
Ar. sp.14
Ar. genistae SC
Ar. genistae PO
Ar. genistae MO
A. sulci
AR
Cacopsylla alaterni
Cacopsylla mali
Cyamophila
Acizzia uncatoides
Acizzia hollisi
10 changes
C
Morphology
A. nigralineata
A. proboscidea
A. sp.7
A. equitans
A. cognata
A. pileolata
A. hakani
A. incuba
A. sp.10
A. sp.11
A. umbonata
A. sp.13
A. dividens
A. modica
A. sp.8
A. sp.12
A. diluta
A. sp.9
A. prognata
A. sp.6
A. sp.5
A. gredi
M
L. adusta
L. blandula
L
A. cytisi
A. sp.3
A. sp.2
A. spartiophila
A. delarbrei
A. sp.1
A. ima
L. sp.16
A
L. monospermae
L. retamae
L. nervosa
L. sp.15
L. sp.17
Ar. nubivaga
Ar. sp.14
Ar. genistae
Ar. adenocarpi
Ar. devia
AR
A. sp.4
A. sulci
Pseudacanthopsylla
Acizzia uncatoides
5 changes

Opposite page:

FIGURE 4.

One of the eight MP trees based on the combined 12S rRNA and COI-tRNA leucine-COII sequences (length 3112, CI 0.265 excluding uninformative characters, RI 0.609). Thick branches indicate nodes with bootstrap values > 75%, and dotted branches indicate nodes that collapse in the Strict consensus. Labelled nodes: A = *Arytainilla*, AR = *Arytaina*, L = 'core *Livilla*', M = 'Macaronesian clade'. MED – Mediterranean, see Figure 3 for other distribution codes. Note: as this analysis includes all individuals sampled for 12S and CO, branch lengths will be proportionally shorter for those taxa/individuals only represented in one data set (sampling is given in Table 2).


12S + CO
A. modica ex Teline P
A. modica ex Cham. P
A. modica ex Teline H
A. modica ex Cham. H
CI
A. sp.12 CI
A. dividens T
A. dividens G
A. dividens C
CI
A. sp.9 CI
A. sp.8 CI
A. hakani MED
A. incuba MA
A. umbonata MA
A. cognata MO
A. sp.13 MO
A. nigralineata C
A. nigralineata T
A. nigralineata G
CI
A. proboscidea ex Ad. vis. T
A. proboscidea ex Ad. fol. P
CI
A. sp.6 CI
A. equitans CI
A. sp.11 CI
A. sp.10 P
A. sp.10 H
CI
A. sp.7 CI
A. pileolata ex Tel. can.
A. pileolata ex Tel. osy.
CI
M
A. sp.5 CI
A. diluta ex Tel. mic. C
A. diluta ex Tel. can. T
CI
A. prognata CI
'MACARONESIAN clade'
L. blandula
L. pseudoretamae
L. maura
L. adusta
L. variegata
L. maculipennis
L. pyrenaea
L. horvathi
L. vittipennella
L. radiata
L. spectabilis
L. syriaca
L. nervosa
L
'core LIVILLA'
L. monospermae T
L. monospermae G
L. monospermae P
CI
L. retamae
L. sp.15
L. sp.16
A. ima
L. sp.17
Pseudacanthopsylla
A. gredi
A. sp.4 SP
A. sp.4 MO
L. vicina
Livilla type-group
Genisteae-feeding
MP: 59%
NJ: 92%
A. spartiophila ex Cyt. st. PO
A. spartiophila ex Cyt. gr. SP
A. spartiophila ex Cyt. fo. MO
A. delarbrei
A. sp.1 CI
A. cytisi
A. sp.3
A. sp.2
A
ARYTAINILLA sensu stricto
Ar. devia T
Ar. devia G
Ar. devia ssp insularis P
Ar. devia ssp insularis C
CI
Ar. adenocarpi ex Ad. co. PO
Ar. adenocarpi ex Ad. te. SP
Ar. adenocarpi ex Ad. bo. MO
Ar. nubivaga CI
Ar. sp.14 CI
Ar. genistae ex Cyt. sc. SC
Ar. genistae ex Cyt. st. PO
Ar. genistae ex Cyt. gr. MO
A. sulci
AR
ARYTAINA
Cacopsylla alaterni
Cacopsylla mali
Cyamophila
non-Genisteae feeders
Acizzia uncatoides
Acizzia hollisi
outgroup
— 10 changes

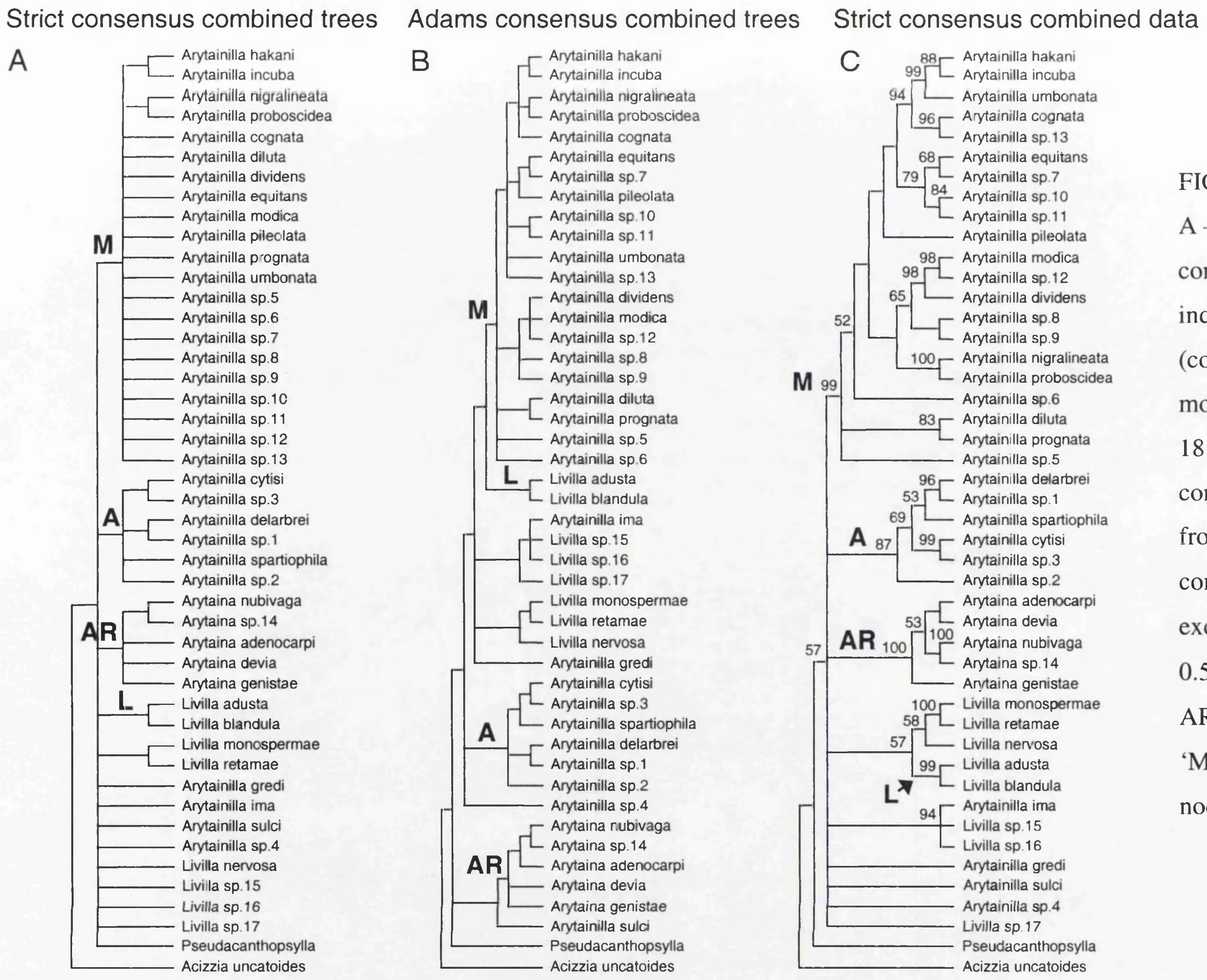


FIGURE 5.

A – Strict consensus, and B – Adams consensus of the 20 MP trees from independently constructed molecular (combined 12S and CO data; 2 trees) and morphological (adult and nymphal data; 18 trees) phylogenies; C – Strict consensus of the eight MP trees obtained from an analysis of all three data sets combined (length 2858, CI 0.342 excluding uninformative characters, RI 0.504). Labelled nodes: A = *Arytainilla*, AR = *Arytaina*, L = ‘core *Livilla*’, M = ‘Macaronesian clade’. Numbers above nodes indicate MP bootstrap support.

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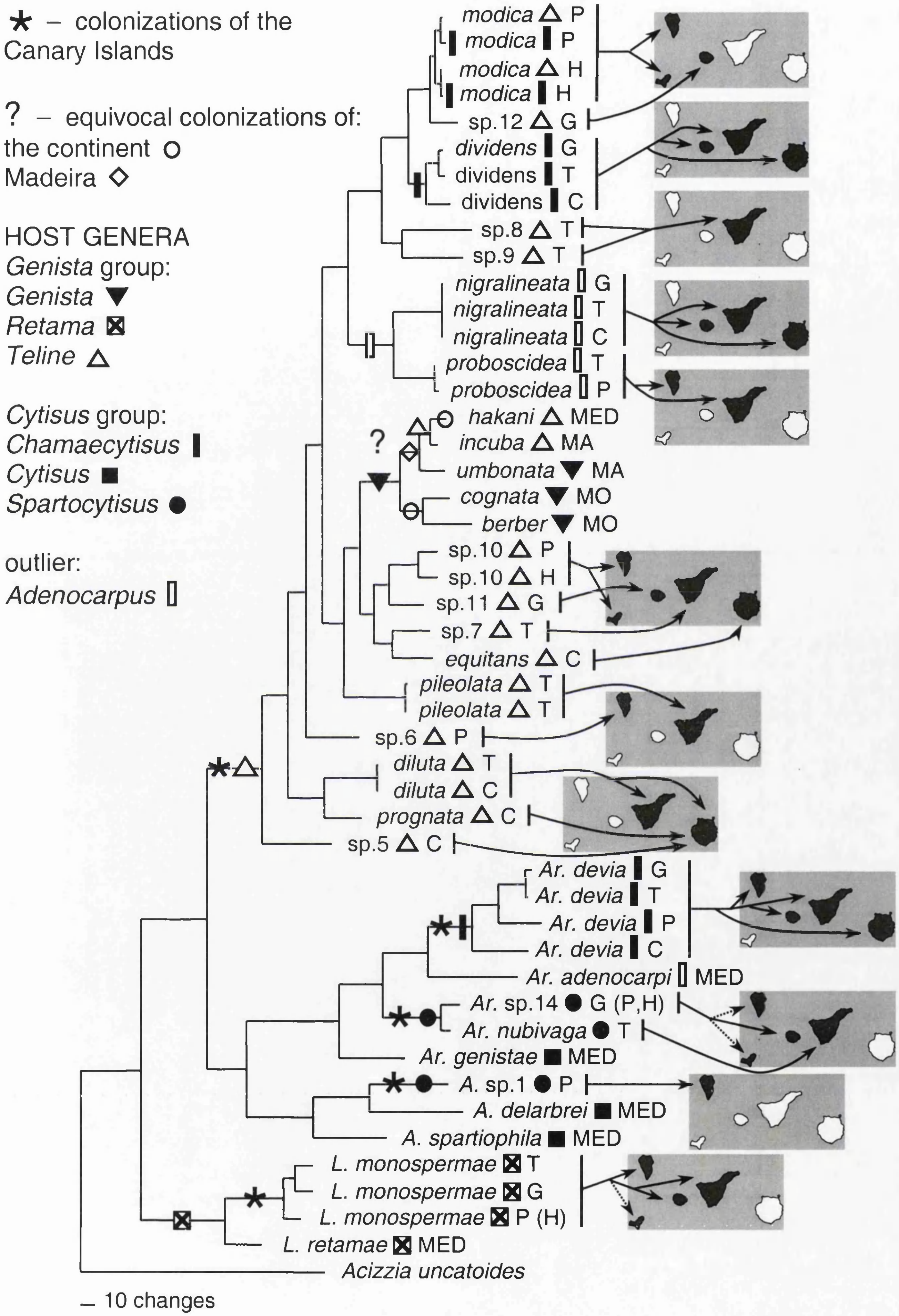
FIGURE 6.

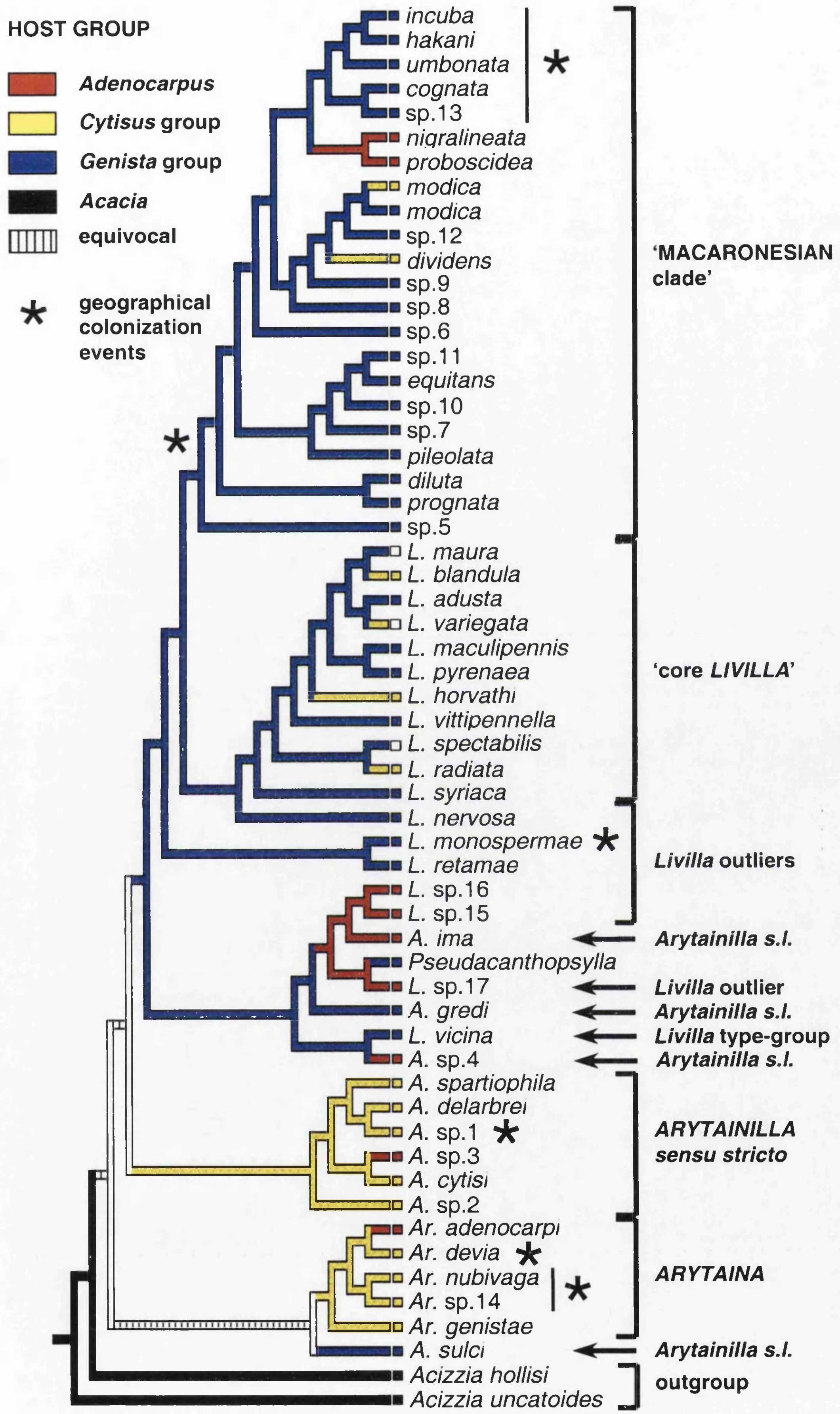
Phylogram of one of the eight MP trees from the total evidence analysis – combined molecular and morphological data, reduced to include all the Macaronesian taxa (plus intraspecific sampling) and selected continental sister taxa. Unequivocal colonizations of the Canary Islands, and equivocal colonizations of Madeira and the continent are mapped onto the tree, as are colonizations of host genera (using ACCTRAN optimization for the continental and Madeiran species). Distributions for all the Canary Island species are illustrated.


★ – colonizations of the Canary Islands
? – equivocal colonizations of:
the continent ○
Madeira ◇
HOST GENERA
Genista group:
Genista ▼
Retama ⊠
Teline △
Cytisus group:
Chamaecytisus ▮
Cytisus ■
Spartocytisus ●
outlier:
Adenocarpus ▯
modica △ P
modica ▮ P
modica △ H
modica ▮ H
sp.12 △ G
dividens ▮ G
dividens ▮ T
dividens ▮ C
sp.8 △ T
sp.9 △ T
nigralineata ▯ G
nigralineata ▯ T
nigralineata ▯ C
proboscidea ▯ T
proboscidea ▯ P
hakani △ MED
incuba △ MA
umbonata ▼ MA
cognata ▼ MO
berber ▼ MO
?
sp.10 △ P
sp.10 △ H
sp.11 △ G
sp.7 △ T
equitans △ C
pileolata △ T
pileolata △ T
sp.6 △ P
diluta △ T
diluta △ C
prognata △ C
sp.5 △ C
Ar. devia ▮ G
Ar. devia ▮ T
Ar. devia ▮ P
Ar. devia ▮ C
Ar. adenocarpi ▯ MED
Ar. sp.14 ● G (P,H)
Ar. nubivaga ● T
Ar. genistae ■ MED
A. sp.1 ● P
A. delarbrei ■ MED
A. spartiophila ■ MED
L. monospermae ⊠ T
L. monospermae ⊠ G
L. monospermae ⊠ P (H)
L. retamae ⊠ MED
Acizzia uncatoides
10 changes

Opposite page:

FIGURE 7.

Cladogram of the combined molecular analysis, including those species for which the host associations have been established. Host groups are mapped as an unordered character using ACCTRAN optimization. Major geographic colonization events in the psyllid group (i.e. between: Canary Islands/continent/Madeira; indicated by *) were apparently accompanied by selection of a host related to the original host (i.e. in the same major plant groups) suggesting an important role for preadaptation to particular hosts in colonizing psyllids. White branch tips indicate possible ambiguity in host group assignment for *Laburnum*: *Cytisus* group; and *Spartium* and *Chamaespartium tridentatum*: *Genista* group.


HOST GROUP
Adenocarpus
Cytisus group
Genista group
Acacia
equivocal
geographical colonization events
incuba
hakani
umbonata
cognata
sp.13
nigralineata
proboscidea
modica
modica
sp.12
dividens
sp.9
sp.8
sp.6
sp.11
equitans
sp.10
sp.7
pileolata
diluta
prognata
sp.5
L. maura
L. blandula
L. adusta
L. variegata
L. maculipennis
L. pyrenaea
L. horvathi
L. vittipennella
L. spectabilis
L. radiata
L. syriaca
L. nervosa
L. monospermae
L. retamae
L. sp.16
L. sp.15
A. ima
Pseudacanthopsylla
L. sp.17
A. gredi
L. vicina
A. sp.4
A. spartiophila
A. delarbrei
A. sp.1
A. sp.3
A. cytisi
A. sp.2
Ar. adenocarpi
Ar. devia
Ar. nubivaga
Ar. sp.14
Ar. genistae
A. sulci
Acizzia hollisi
Acizzia uncatoides
'MACARONESIAN clade'
'core LIVILLA'
Livilla outliers
Arytainilla s.l.
Livilla outlier
Arytainilla s.l.
Livilla type-group
Arytainilla s.l.
ARYTAINILLA sensu stricto
ARYTAINA
Arytainilla s.l.
outgroup

APPENDIX 1. Primer combinations used for DNA amplification from 73 individuals for the cytochrome oxidase region. The primer combination ‘UEA9-MOD + Marilyn’ was used to amplify DNA from five taxa that did not amplify well with ‘UEA9 + Marilyn’.

| taxa | primers |
|---|---|
| *Acizzia holisi*, *A. uncatoides* | UEA9 + Marilyn |
| *Arytaina adenocarpi*, *A. devia*, *A. genistae* | |
| *Arytainilla cytisi*, *A. equitans*, *A. hakani*, *A. ima*, *A. incuba*, *A. nigralineata*, *A. proboscidea*, *A. prognata*, *A. spartiophila* (MO), *A. sulci*, *A. umbonata*, *A.* sp.1, *A.* sp.2, *A.* sp.3, *A.* sp.4, *A.* sp.7, *A.* sp.11, *A.* sp.13 | |
| *Cacopsylla alaterni*, *C. mali* | |
| *Cyamophila prohaskai* | |
| *L. blandula*, *L. monospermae* (T, G), *L. maura*, *Livilla retamae*, *L. variegata*, *L.* sp.15, *L.* sp.16, *L.* sp.17 | |
| *Arytaina nubivaga*, *A.* sp.14 | UEA9 + DP1 |
| *Arytainilla cognata*, *A. delarbrei*, *A. diluta*, *A. dividens*, *A. modica*, *A. pileolata*, *A. spartiophila* (SP, PO), *A.* sp.5, *A.* sp.6, *A.* sp.8, *A.* sp.9, *A.* sp.10, *A.* sp.12 | |
| *Livilla monospermae* (P) | |
| *Pseudacanthopsylla* (*Psylla improvisa*) | UEA9 + DP2 |
| *Arytainilla atlantica*, *A. cytisi*, *A.* sp.4, *A. sulci* | UEA9-MOD + Marilyn |
| *Livilla* sp.15 | |

## **APPENDIX 2.** Aligned 12S matrix (342bp), ambiguous regions that were excluded from the anlyses are indicated by *.

```
[                                         10        20        30        40        50        60        70]
[                                          .         .         .         .         .         .         .]
                                 [12S rRNA start
Acizzia_hollisi                   GAGTAGTACAAGTTATTA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Acizzia_uncatoides                GAGTAGTAATAGTTATGG-TCTAGGAACTCAAAAAATTTGGCGGTATTTTATCTTATCAGAGGAACCTGT    [69]
Arytaina_adenocarpi_PO            GAGTAGTAAGAGTTATGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytaina_adenocarpi_SP            GAGTAGTAAGAGTTATGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytaina_adenocarpi_MO            GAGTAGTAGTAGTTATGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytaina_devia_ssp_insularis_C    GAGTAGTAAAAGTTATGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytaina_devia_ssp_insularis_P    GAGTAGTAAAAGTTATGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytaina_genistae_SC              GAGTAGTAAGAGTTAAGG-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytaina_genistae_PO              GAGTAGTAAGAGTTAAGG-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytaina_nubivaga                 GAGTAGTAAGAGTTATGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytaina_sp.14                    GAGTAGTAAGAGTTATGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytainilla_cognata               GAGTAGTAAAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_cytisi                GAGTAGTATAAGTTAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTTTTAGAGGAACCTGT    [69]
Arytainilla_delarbrei             GAGTAGTATCAGTTAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTGTTAGAGGAACCTGT    [69]
Arytainilla_diluta                GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Arytainilla_dividens_C            GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_dividens_G            GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_equitans              GAGTAGTAAAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_gredi                 GAGTAGTATAAGATATAA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Arytainilla_hakani                GAGTAGTATAAGATAAGA-TCTCGGAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_ima                   GAGTAGTAAAGGTTAAAATTCT-GAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Arytainilla_incuba                GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_modica_Teline_P       GAGTAGTACAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_modica_Cham._P        GAGTAGTACAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_nigralineata          GAGTAGTATTAGATACGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Arytainilla_pileolata             GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_proboscidea           GAGTAGTATTAGATAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Arytainilla_prognata              GAGTAGTATAAGATAGGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Arytainilla_spartiophila_PO       GAGTAGTAGTAGTTAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Arytainilla_spartiophila_SP       GAGTAGTAGTAGCTAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Arytainilla_sulci                 GAGTAGTAGAAGTTAAGG-TCTCAAAACTCAAAAAATTTGGCGGTACTTTATCTTATTAGAGGAACCTGT    [69]
Arytainilla_umbonata              GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_sp.1                  GAGTAGTACAAGTTAAGC-TCTTAAAACTCAAAAAATTTGGCGGTATTTTATCTTACTAGAGGAACCTGT    [69]
Arytainilla_sp.2                  GAGTAGTATCTGTTAAGA-TCATGAAACTCAAAAAATTTGGCGGTATTTTATCTAATTAGAGGAACCTGT    [69]
Arytainilla_sp.3                  GAGTAGTATAAGTTAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTTTTAGAGGAACCTGT    [69]
Arytainilla_sp.4                  GAGTAGTAAAAGTTAAAA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTCGTTAGAGGAACCTGT    [69]
Arytainilla_sp.5                  GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Arytainilla_sp.6                  GAGTAGTAAAAGATATGA-TCTCGAAACTCAAAAAATTTGGCGGTACTTTATCTTATCAGAGGAACCTGC    [69]
Arytainilla_sp.7                  GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_sp.8                  GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_sp.9                  GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_sp.10                 GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_sp.11                 GAGTAGTATAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_sp.12                 GAGTAGTACAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Arytainilla_sp.13                 GAGTAGTAAAAGATAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTAATCAGAGGAACCTGC    [69]
Cacopsylla_alaterni               GAGTAGTAAAAGTTAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Cacopsylla_mali                   GAGTAGTAGGAGTTAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTTTTAGAGGAACCTGT    [69]
Cyamophila_prohaskai              GAGTAGTAAGAGTTAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTATCAGAGGAACCTGT    [69]
Livilla_adusta                    GAGTAGTAGTAGATAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTGTTAGAGGAACCTGT    [69]
Livilla_blandula                  GAGTAGTAATAGATAAGA-TCTTCAAACTCAAAAAATTTGGCGGTATTTTATCTTGTTAGAGGAACCTGC    [69]
Livilla_horvathi                  GAGTAGTAAGAGTTAAGA-TCTTTAAACTCAAAAAATTTGGCGGTACTTTATCTTATTAGAGGAACCTGC    [69]
Livilla_maculipennis              GAGTAGTAGTAGATAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Livilla_maura                     GAGTAGTAATAGATAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTGTTAGAGGAACCTGC    [69]
Livilla_monospermae               GAGTAGTAAAAGGTAATA-TCTAGAAACTCAAAAGATTTGGCGGTATTTCATCTTATTAGAGGAACCTGC    [69]
Livilla_nervosa                   GAGTAGTAAGTGTTAAGG-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTTTTAGWGGWACCTGT    [69]
Livilla_pseudoretamae             GAGTAGTAATAGATAAGA-TCTTCAAACTCAAAAAATTTGGCGGTATTTTATCTTGTTAGAGGAACCTGC    [69]
Livilla_pyrenaea                  GAGTAGTAGTAGATAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Livilla_radiata                   GAGTAGTAAAAGGTAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Livilla_retamae                   GAGTAGTAAAAGGTAATA-TCTAGAAACTCAAAAGATTTGGCGGTATTTCATCTTATTAGAGGAACCTGC    [69]
Livilla_spectabilis               GAGTAGTATAAGTTATGA-TCTTTAAACTCAAAAAATTTGGCGGTACTTTATCTTATCAGAGGAACCTGC    [69]
Livilla_syriaca                   GAGTAGTAGGAGTTAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAATCTGC    [69]
Livilla_variegata                 GAGTAGTAAGAGGTAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTGTTAGAGGAACCTGC    [69]
Livilla_vicina                    GGGTAGTATAAGTTAAAA-TTTTTAAACTCAAAGGATTTGGCGGTATTTTATCTAATTAGAGGAACCTGT    [69]
Livilla_vittipennella             GAGTAGTAAGAGGTAAGA-TCTTTAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGC    [69]
Livilla_sp.15                     GAGTAGTATTAGCTAAAA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Livilla_sp.16                     GAGTAGTATAAGTTAATA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Livilla_sp.17                     GAGTAGTAAAAGTTAAGA-TCTCGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
Pseudacanthopsylla_improvisa      GAGTAGTAATAGTTAAGA-TCTTGAAACTCAAAAAATTTGGCGGTATTTTATCTTATTAGAGGAACCTGT    [69]
```

# APPENDIX 2 cont.

```
[                                          80        90        100       110       120       130       140]
[                                          .         .         .         .         .         .         .]

Acizzia_hollisi                   TTATTAATTGATAATCCACAACTTAAATTTACTTTTAAAATTAT--ATTTGTATACCGCTGTCATGAATC   [137]
Acizzia_uncatoides                TTAGTAATTGATATCCCACAACTTATATTTACTTTTATTATTAT--ATTTGTATACCGCCGTCATGAATC   [137]
Arytaina_adenocarpi_PO            TTATTAATTGATACTCCACAACTTAAATATATTTTCATTAGATT--ATTTGTATACCGTTGTCATGAATG   [137]
Arytaina_adenocarpi_SP            TTATTAATTGATACTCCACAACTTAAATATATTTTCATTAGATT--ATTTGTATACCGTTGTCATGAATG   [137]
Arytaina_adenocarpi_MO            TTATTAATTGATACTCCACAACTTAAATATATTTTCATTAAATT--ATTTGTATACCGTTGTCATGAATG   [137]
Arytaina_devia_ssp_insularis_C    TTATTAATGGATACTCCACAACTTTAATATACTTTTACTAGTTT--ACTTGTATATCGTTGTCATGAATG   [137]
Arytaina_devia_ssp_insularis_P    TTATTAATAGATACTCCACAACTTTAACTTACTTTCACTAGTTT--ATTTGTATATCGTTGTCATGAATG   [137]
Arytaina_genistae_SC              TTATTAATTGATATTCCACAACTTAAATATACTTTTATTAGTTT--ATTTGTATACCGTTGTCATGAATA   [137]
Arytaina_genistae_PO              TTATTAATTGATATTCCACAACTTAAATATACTTTTATTAGTTT--ATTTGTATACCGTTGTCATGAATA   [137]
Arytaina_nubivaga                 TTATTAATTGATATTCCACAACTTAAATGTATTTTCACTAGTTT--ATTTGTATACCGTTGTCATGAATG   [137]
Arytaina_sp.14                    TTATTAATTGATATTCCACAACTTAAATGTATTTTCACTAGTTT--ATTTGTATACCGTTGTCATGAATG   [137]
Arytainilla_cognata               TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_cytisi                TTATTAATTGATACTCCACAATTTTAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Arytainilla_delarbrei             TTATTAATTGATATCCCACAACTTAAATTTACTTTTTTAAAGTT--ATTTGTATACCGTTGTCATGAATC   [137]
Arytainilla_diluta                TTATTAATTGATATTCCACAACTTGAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_dividens_C            TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_dividens_G            TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_equitans              TTATTAATTGATATTCCACAACTTTAATTTACTTTTATTATTTT--ATTTGTATATCGTCGTCATGAATC   [137]
Arytainilla_gredi                 TTATTAATTGATACTCCACAACTTTAATTTACTTTTTTTATATT--ACTTGTATACCGTTGTCATGAATC   [137]
Arytainilla_hakani                TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_ima                   TTATTAATTGATATTCCACAACTTTAATTTACTTTTATTATGTT--ACTTGTATATCGTTGTCATGAATC   [137]
Arytainilla_incuba                TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_modica_Teline_P       TTATTAATTGATATTCCACAACTTAAACTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_modica_Cham._P        TTATTAATTGATATTCCACAACTTAAACTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_nigralineata          TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_pileolata             TTATTAATTGATATTCCACAACTTTAATTTACTTTTATTATTTT--ATTTGTATACCGTTGTCATGAATC   [137]
Arytainilla_proboscidea           TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_prognata              TTATTAATTGATATTCCACAACTTTAATTTACTTTTATTAATTT--ATTTGTATACCGTTGTCATGAATC   [137]
Arytainilla_spartiophila_PO       TTATTAATTGATATTCCACAACTTTAATTTACTTTTACTAAATT--ACTTGTATATCGTTGTCATGAATC   [137]
Arytainilla_spartiophila_SP       TTATTAATTGATATTCCACAACTTTAATTTACTTTTACTAAATT--ACTTGTATATCGTTGTCATGAATC   [137]
Arytainilla_sulci                 TTATTAATTGATAATCCACAACTTTAATTTACTTTTATTAATTT--ATTTGTATATCGTTGTCATGAATG   [137]
Arytainilla_umbonata              TTATTAATTGATATTCCACAACTTAGACTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_sp.1                  TTATTAATTGATAGTCCACAACTTTAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Arytainilla_sp.2                  TTATTAATTGATACTCCACAACTTAAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATGAGTC   [137]
Arytainilla_sp.3                  TTATTAATTGATATTCCACAATTTTAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Arytainilla_sp.4                  TTATTAATTGATATTCCACAACTCTAATTTACCTTTATTAAATT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_sp.5                  TTGTTAATTGATATTCCACAACTTTAATTTACTTTTATTAATTT--ATTTGTATATCGTCGTCATGAATC   [137]
Arytainilla_sp.6                  TTATTAATTGATATTCCACAACTTTAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_sp.7                  TTATTAATTGATATTCCACAACTTTAATTTACTTTTGTTATTTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_sp.8                  TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTTGTCATGAATC   [137]
Arytainilla_sp.9                  TTATTAATTGATATTCCACAACTTAAACTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_sp.10                 TTATTAATTGATATTCCACAACTTTAATTTACTTTTATTATTTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_sp.11                 TTATTAATTGATATTCCACAACTTTAATTTACTTTTATTATTTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_sp.12                 TTATTAATTGATATTCCACAACTTAAACTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Arytainilla_sp.13                 TTATTAATTGATATTCCACAACTTAAATTTACTTTTATTAATTT--ATTTGTATACCGTCGTCATGAATC   [137]
Cacopsylla_alaterni               TTATTAATTGATATTCCACAACTTACATTTACTTCTATTAAATT--ATTTGTATACCGCTGTCATGAATC   [137]
Cacopsylla_mali                   TTATTAATTGATATTCCACAACTTAAATATACTTTTACTAAGCT--ATTTGTATACCGCTGTCATGAATC   [137]
Cyamophila_prohaskai              TTATTAATTGATATTCCACAACTTTAATTTACCTTGACGAGATT--ATTTGTATACCGCTGTCATGAATC   [137]
Livilla_adusta                    CTATTAATTGATATTCCACGACTTTAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATAAATC   [137]
Livilla_blandula                  TTATTAATTGATATTCCACGACTTAAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATAAATA   [137]
Livilla_horvathi                  TTATTAATTGATATTCCACGACTTTACTTTACTTTTATTAAGTT--ATTTGTATACCGTTGTCATAAATC   [137]
Livilla_maculipennis              TTATTAATCGATACTCCACGACTTAAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATAAATC   [137]
Livilla_maura                     TTATTAATTGATATTCCACGACTTTAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATAAATA   [137]
Livilla_monospermae               TTATTAATTGATGTTCCACAACTTTAACTTACTTTTATGAGATT--ATTTGTATACCGTTGTCATGAATC   [137]
Livilla_nervosa                   TTATTAATTGATAATCCACAACTTTAATTTACTTTTTATTATTTTTACTTGTATACCGTTGTTATGAATT   [139]
Livilla_pseudoretamae             TTATTAATTGATATTCCACGACTTTAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATAAATA   [137]
Livilla_pyrenaea                  TTATTAATTGATATTCCACGACTTAAATTTACTTTTATTATATT--ATTTGTATACCGTTGTCATAAATC   [137]
Livilla_radiata                   TCATTAATTGATAATCCACAACTTTAATTTACTTTTATTAAATT--ACTTGTATACCGTTGTCATGAATC   [137]
Livilla_retamae                   TTATTAATTGATATTCCACAACTTAAATTTACTTTTATGAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Livilla_spectabilis               TTATTAATTGATGTTCCACAACTTTAACTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Livilla_syriaca                   CCATTAATTGATAATCCACAACTTTAATTTACTTTTATTAGATT--ATTTGTATACCGTTGTCATGAATC   [137]
Livilla_variegata                 TTATTAATTGATGTTCCACGACTTTAATTTACTTTTATTAAGTT--ATTTGTATACCGTTGTCATAAATC   [137]
Livilla_vicina                    TTAATAATTGATAATCCACAATTTAAACTTATTTCTATTAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Livilla_vittipennella             TTATTAATTGATATTCCACGACTTTAACTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Livilla_sp.15                     TTATTAATTGATGTTCCACAACTTTAATTTACTTTTATAAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Livilla_sp.16                     TTGTTAATTGATATTCCACAACTTTAATTTACTTTTATAAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
Livilla_sp.17                     TTATTAATTGATATTCCACAACTTTAATTTACTTTCATAAGATT--ATTTGTATACCGTTGTCATGAATC   [137]
Pseudacanthopsylla_improvisa      TTATTAATTGATATTCCACAACTTTAATTTACTTTTATTAAATT--ATTTGTATACCGTTGTCATGAATC   [137]
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## APPENDIX 2 cont.

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[                                         150       160       170       180       190       200       210]
[                                         .         .         .         .         .         .         .]
                                           ***

Acizzia_hollisi                   TATTAAGAAATTTTATTTTCTATCATTTAT-A-TAAAATTTATGTTAGGTCAAGGTGCAGTA-TTTAAAA   [204]
Acizzia_uncatoides                TATTAAAAAATTTAATTTTCCGTTATTCTT-A-TGGAATACATGTTAGGTCAAGGTGCAGTG-TGTAAAA   [204]
Arytaina_adenocarpi_PO            TACTAAAAAGTGT-ATTTTCAAGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTC-TGTGAGA   [203]
Arytaina_adenocarpi_SP            TACTAAAAAGTGT-ATTTTCAAGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTC-TGTGAGA   [203]
Arytaina_adenocarpi_MO            TACTAAAAAGTGT-ATTTTCAAGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTC-TGTGAGA   [203]
Arytaina_devia_ssp_insularis_C    TACTAAAAAGTG-AATTTTCAGGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTC-TGTGAAA   [203]
Arytaina_devia_ssp_insularis_P    TACTAAAAAGTG-AATTTTCAAGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TGTGAAA   [203]
Arytaina_genistae_SC              TACTAAAAAGT-AAATTTTCAAGATTTTTT-A-TGTAAATTATGTTAGATCAAGGTGCAGTT-TGTAAAA   [203]
Arytaina_genistae_PO              TACTAAAAAGT-AAATTTTCAAGATTTTTT-A-TGTAAATTATGTTAGATCAAGGTGCAGTT-TGTAAAA   [203]
Arytaina_nubivaga                 TACTAAAAAGTG-AATTTTCAAGATTTCCT-A-TATAGTTTATGTTAGATCAAGGTGCAGTT-TGTGAAA   [203]
Arytaina_sp.14                    TACTAAAAAGTG-AATTTTCAAG-ATTTCCTA-TATAGTTTATGTTAGATCAAGGTGCAGTT-TGTGAAA   [203]
Arytainilla_cognata               TACTAAAAAGTG--ACTTTCAGGGGTTTTT-A-TTTAATTTATGTTAGATCAAGGTGCAGTT-TGTAAAA   [202]
Arytainilla_cytisi                TACTGAAAAGT--AATTTTCGAGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TGTAAAA   [202]
Arytainilla_delarbrei             TACTAGAAAGT--AATTTTCAAGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TATGAAA   [202]
Arytainilla_diluta                TACTAAAAAGT--AATTTTCAGGAGTTTTT-A-TGTAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_dividens_C            TACTAAAAAGT--AATTTTCAAGGGTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_dividens_G            TACTAAAAAGT--AATTTTCAGGAGTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_equitans              TACTAAAAAGT--AATTTTCAAGAGTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TATAAAA   [202]
Arytainilla_gredi                 TACTAAAAAGTT--ATTTTCAGGAGTTTTT-A-TAAAGTTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_hakani                TACTAAAAAGT--AATTTTCAGGAGTTTTT-A-TGTAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_ima                   TATTAAAAAAT--AATTTTCAGAATTTTTT-A-TGGAATATATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_incuba                TACTAAAAAGTG--ATTTTCAGGAGTTTTT-A-TGTAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_modica_Teline_P       TACTAAAAAGT--AATTTTCAGGAGTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTT-TTTGAAA   [202]
Arytainilla_modica_Cham._P        TACTAAAAAGT--AATTTTCAGGAGTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTT-TTTGAAA   [202]
Arytainilla_nigralineata          TACTAGAAAGTT--ATTTTCAAGAGTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTG-TTTAAAA   [202]
Arytainilla_pileolata             TACTAAAAAGT--AATTTTCAGGATTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_proboscidea           TACTAGAAAGT--AATTTTCAGGAGTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_prognata              TATTAAAAAGT--AATTTTCAGAAGTTTTT-A-TGTAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_spartiophila_PO       TATTAAAAAGTG--ATTTTCAAGATTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTC-TGTAAAA   [202]
Arytainilla_spartiophila_SP       TATTAAAAAGTG--ATTTTCAAGATTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTC-TGTAAAA   [202]
Arytainilla_sulci                 TACTAAAAAGT--AATTTTCAAAATTTTTT-A-TAAAATTTATGTTAGATCAAGATGCAGTC-TATAAAA   [202]
Arytainilla_umbonata              TACTAAAAAGTG--ATTTTCAGGAGTTTTT-A-TGTAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_sp.1                  TATTAAAAAGT--AATTTTCAAGGTTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TATAGAA   [202]
Arytainilla_sp.2                  TACTCAAAAGT--AATTTTCAGAATTTTTT-A-TAGAATTTATGTTAGATCAAGGTGCAGTTATGTAAAA   [203]
Arytainilla_sp.3                  TACTAAAAAGT--AATTTTCAAGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TGTGAAA   [202]
Arytainilla_sp.4                  TACTAAAAAGT--AATTTTCAAGATTTCTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTA-TTTAAAG   [202]
Arytainilla_sp.5                  TACTAARAAGT--AATTTTCAGGAGTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_sp.6                  TACTAAAAAGT--AATTTTCAGGAGTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_sp.7                  TACTAAAAAGT--AATTTTCAAGAGTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TATAAAA   [202]
Arytainilla_sp.8                  TACTAAGAAGT--AATTTTCAGGAGTTTTT-A-TAAAATTTATGTTAAATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_sp.9                  TACTAAAAAGT--AATTTTCAGGAGTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_sp.10                 TACTAAAAAGT--AATTTTCAAGAGTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Arytainilla_sp.11                 TACTAAAAAGT--AATTTTCAAGATTTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TGTAAAA   [202]
Arytainilla_sp.12                 TACTAAAAAGT--AATTTTCAGGAGTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTT-TTTGAAA   [202]
Arytainilla_sp.13                 TATTAAGAAGTG--ATTTTCAGGGGTTTTT-A-TTTAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Cacopsylla_alaterni               TACTAAAAAGTTT-ATTTTCAAAATTTTTT-A-TGCAAGTTATGTTAGGTCAAGGTGTAGTA-TATAGAA   [203]
Cacopsylla_mali                   TACTTAGAAGTTT-ATTTTCAAGATTTTTT-A-TGTAATTTATGTTAGGTCAAGGTGCAGTA-TGTAGAC   [203]
Cyamophila_prohaskai              TACTTAAAAGT--AATTTTCGGGATTTTTT-A-TGAAAGTCATGTTAGGTCAAGGTGCAGTT-TGTGTTG   [202]
Livilla_adusta                    TACTAAAAGGTT-AATTTTTGAGGATTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAGAA   [203]
Livilla_blandula                  TACTAAAAAGT--AATTTTTAAGGATTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_horvathi                  TACTAAGAAGT--AATCTTTAAGAATTTTT-AATAGAATTCATGTTAAATCAAGGTGCAGTT-TTTAAAA   [203]
Livilla_maculipennis              TACTAAAAAGT--AACTTTTAAGCATTTTT-A-TGAAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_maura                     TACTAAAAAGT--AATTTTTAAGGATTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_monospermae               TACTAAAAAGT--AATTTTCGGGAGTTTAT-A-TAGAATTAATGTTAGATCAAGGTGCAGTA-TTTAAAA   [202]
Livilla_nervosa                   TACTAAAAAGTG-AA-TTTCAGGGAGTTTT-ATTATAATTTATGTTAGATCAAGGTGCAGTG-TTAAAAA   [205]
Livilla_pseudoretamae             TACTAAAAAGT--AATTTTTAAGGATTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_pyrenaea                  TACTAAGAAGT--AATTTTTAAGAATTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTC-TTTAAAA   [202]
Livilla_radiata                   TACTAGAAAGT--AATTTTTAAGGATTCTT-A-TTTAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_retamae                   TACTAAAAAGT--AATTTTCGGGAGTTTTT-A-TAGAATTCATGTTAGATCAAGGTGCAGTA-TTTAAAA   [202]
Livilla_spectabilis               TACTAAAAAGTT--ATTTTCAAGCATTTTT-A-TGTAATTTATGTTAGATCAAGGTGCAGTT-TTTGAAA   [202]
Livilla_syriaca                   TACTAAAAAGTT--ATTTTCAAGTATTTTT-A-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_variegata                 TACTAAAAAGT--AATTTTTGAGGATTTTT-A-TAGAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_vicina                    TACTAAAAAGT--AATTTTCAAGATTTTTT-A-TAAAATTTATGTTAGATCAAGGTGCAGTT-TTTAGAA   [202]
Livilla_vittipennella             TACTGAGAAGTG--ATTTTCAAGAATTTTT-G-TATAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_sp.15                     TATTAAAAAATG--ATTTTCAAAATTTTTT-A-TGAAATTTATGTTAGATCAAGGTGCAGTA-TTTAAAA   [202]
Livilla_sp.16                     TATTAAAAAAT--AATTTTCAAATTTTTTT-A-TGAAATTTATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
Livilla_sp.17                     TATTAAAAAAT--AATTTTCAGAGAGTTTT-A-TTTAATTTATGTTAGATCAAGGTGCAGTT-TTTGAAA   [202]
Pseudacanthopsylla_improvisa      TATTAAAAAAT--AATTTTCATATTTTTTT-A-TGGAATGCATGTTAGATCAAGGTGCAGTT-TTTAAAA   [202]
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## APPENDIX 2 cont.

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[                                          220       230       240       250       260       270       280]
[                                            .         .         .         .         .         .         .]
                                                                           ************

Acizzia_hollisi                   GTTTTA--ATGGGTTACTTTA-TTATAATGAATGGAAATTTAGATTT-GTTAT-TTTTTTTGAAAAAGGA   [269]
Acizzia_uncatoides                GTTATA-AATGGGTTACTTTAGTATC-ATGAATGAAATAAAATATAA-AAAA--CTGTTATGAAATAGGA   [269]
Arytaina_adenocarpi_PO            AAG-TAAAATGGGTTACAATATTTAATATGAATGGAAATTATTCTTA-GAAG--AATTTTAGAAAAAGGA   [269]
Arytaina_adenocarpi_SP            AAG-TAAAATGGGTTACAATATTTAATATGAATGGAAATTATTCTTA-GAAG--AATTTTAGAAAAAGGA   [269]
Arytaina_adenocarpi_MO            AAG-TAAAATGGGTTACAATATTTAATATGAATGAAAATTATTCTTA-AAAG--AATTTTAGAAAAAGGA   [269]
Arytaina_devia_ssp_insularis_C    GAA-CAAAATGGGTTACAATAATTAATATGAATGAAAAACATTCTTA-ATAT--AGTGTTAGAAAGAGGA   [269]
Arytaina_devia_ssp_insularis_P    GAA-TAAAATGGGTTACAATATTTAGTATGAATGGAAAGCATTTTTA-ATAT--TATGCTAGAAAAGGGA   [269]
Arytaina_genistae_SC              GTA-TAGAATGGGTTACAATATTTAATATGAATGGAAATTATTCTTA-AAAT--AATATTAGAAAAAGGA   [269]
Arytaina_genistae_PO              GTA-TAGAATGGGTTACAATATTTAATATGAATGGAAATTATTCTTA-AAAT--AATATTAGAAAAAGGA   [269]
Arytaina_nubivaga                 AAA-TAAAATGGGTTACAGTATTTAATATGAATGAAAAATATTTTTA-AAAG--AATGTTAGAAAAAGGA   [269]
Arytaina_sp.14                    AAA-TAAAATGGGTTACAGTATTTAGTATGAATGAAAAATATT-TTA-AAAG--AATGTTAGAAAAAGGA   [268]
Arytainilla_cognata               GAA-AAAAGTGGGTTACAATATTTAATATGAATGGAAATTATTGTTA-GATA--AATAAGGAAAATAGGA   [268]
Arytainilla_cytisi                GAA-AATAATGGGTTACATTAATTATTATGAATGAAAATTATTATT--GAAT--AATAACGGAAAAAGGA   [267]
Arytainilla_delarbrei             GTA-GAAAATGGGTTACATTAGTGAAGATGAATGAAAATTATTGTTA-GAA---AATAGTGGAAAAAGGA   [267]
Arytainilla_diluta                GAA-AAAAGTGGGTTACAATATTTAATATGAATGGAAATTATTATTA-GAGG--TATAATAGAAAGAGGA   [268]
Arytainilla_dividens_C            GAA-AAAAGTGGGTTACAATATTAAATATGAATGGAAATTATTGTTA-GATA--AATAATAGAAATAGGA   [268]
Arytainilla_dividens_G            GAA-AAAAGTGGGTTACAATATTTAGTATGAATGAAAATTATTGTTA-GGT---AATAATAGAAATAGGA   [267]
Arytainilla_equitans              GAA-AAAAGTGGGTTACAATATTTATTATGAATGGAAATTATTGTAA-GATA--AATGATAAAAATAGGA   [268]
Arytainilla_gredi                 GAA-AAAAATGGGTTACATTATTTATTATGAATGAAAATTATTACTA-AATT--AATAATGAAAATAGGA   [268]
Arytainilla_hakani                GAA-AAAAGTGGGTTACAATATTTAATATGAATGGAAGTTATTGTTA-GATA--AATAATAAAAATAGGA   [268]
Arytainilla_ima                   GAA-AAAAATGGGTTACATTATTTAGTATGAATGGAAATTATTGTTA-ATTT--ATTAATAGAAATAGGA   [268]
Arytainilla_incuba                GAA-AAAAGTGGGTTACAATATTTAATATGAATGGAAGTTATTGTTA-GATA--AATAATAAAAATAGGA   [268]
Arytainilla_modica_Teline_P       GAA-AAAAGTGGGTTACATTATTTAATATGAATGAAAATTATTGTTA-GATA--AATAATAGAAATAGGA   [268]
Arytainilla_modica_Cham._P        GAA-AAAAGTGGGTTACATTATTTAATATGAATGAAAATTATTGTTA-GATA--AATAATAGAAATAGGA   [268]
Arytainilla_nigralineata          GAA-AAAAGTGGGTTACATTATTTAATATGAATGAAAATTGTTGTTA-GATA--AACAATAGAAAAAGGA   [268]
Arytainilla_pileolata             GAA-AAAAGTGGGTTACAATATTTAATATGAATGGAAATTATTGTTA-GATA--AATA-TAGAAATAGGA   [267]
Arytainilla_proboscidea           GAA-AAAAGTGGGTTACAATATTTAGTATGAATGAAAATTGTTGTTA-GATA--AATAATAGAAAAAGGA   [268]
Arytainilla_prognata              GAA-AAAAGTGGGTTACAATATTTAATATGAATGGAAATTGTTGTTA-GATT--TATAATAGAAAGAGGA   [268]
Arytainilla_spartiophila_PO       GAA-AAAAATGGGTTACATTAGTTACTATGAATGAATATTATTATT--GGAA--AATATTGGAAAAGGGA   [267]
Arytainilla_spartiophila_SP       GAA-AAAAATGGGTTACATTAGTTACTATGAATGAATATTATTATT--GGAA--AATATTGGAAAAGGGA   [267]
Arytainilla_sulci                 GAA-AA-AATGGGTTACATTAGTTAATATGAATGAAAAATAAGTCTA-TAAA--ATTATTGAAAAGAGGA   [267]
Arytainilla_umbonata              GAA-AAAAGTGGGTTACAATATTTAATATGAATGGAAGTTATTGTTA-GATA--AATAATAAAAATAGGA   [268]
Arytainilla_sp.1                  GTA-AGAAATGGGTTACATTAGTTAAGATGTATGGAAGTTATTATTA-GAA---AATAATAGAAAAAGGA   [267]
Arytainilla_sp.2                  GAA-AAAAATGGGTTACATTAGTAACTATGAATGGAAATTATTGTTA-GAA---AATAATAAAAAAAGGA   [268]
Arytainilla_sp.3                  GAA-AATAATGGGTTACATTGATTATTATGAATGAAAATTATTATT--GAAT--AATAATAGAAAAAGGA   [267]
Arytainilla_sp.4                  GAA-AAGAATGGGTTACAATATTTAATATGAATGAAAATTACTAGA--AGAT--AGTTATGGAAATAGGA   [267]
Arytainilla_sp.5                  GAA-AA-AGTGGGTTACTATATTTAGTATGAATGAAAATTATTGTTA-GAAA--AATAATAGAAATAGGA   [267]
Arytainilla_sp.6                  GAA-AAAAGTGGGTTACAATATTTAGGATGTATGGAAGTTATTGTTA-GACA--AATTATAAAAATAGGA   [268]
Arytainilla_sp.7                  GAA-AAAAGTGGGTTACAATATTTATTATGAATGGAAGTTGTTGTTA-GATA--AATAATAAAAATAGGA   [268]
Arytainilla_sp.8                  GAA-AAGGGTGGGTTACAATATTTAGTATGAATGGAAATTATTGTTA-GATA--AATAATAAAAATAGAA   [268]
Arytainilla_sp.9                  GAA-AAAAGTGGGTTACACTGTTTAATATGAATGAAAATTATTGTTA-GATA--AATAATAAAAATAGGA   [268]
Arytainilla_sp.10                 GAA-AAAAGTGGGTTACAATATTTATTATGAATGAAAATTATTGTTA-GATA--AATAATAAAAATAGGA   [268]
Arytainilla_sp.11                 GAA-AAAAGTGGGTTACAATATTTATTATGAATGGAAATTATTGTTA-GATA--AATAATAAAAATAGGA   [268]
Arytainilla_sp.12                 GAA-AAAAGTGGGTTACATTATTTAATATGAATGAAAATTATTGTTA-GATA--AATAATAGAAATAGGA   [268]
Arytainilla_sp.13                 GAA-AAAAGTGGGTTACAGTATTAATTATGAATGGAAATTATTGTTA-GATA--AATAATAAAAATAGGA   [268]
Cacopsylla_alaterni               GAC-TAAAATGGGTTACAGTAATTATTATGAATGAATTACGCTATTA-GTGT--AGAGTATGAAAGAGGA   [269]
Cacopsylla_mali                   GAC-TAAAATGGGTTACATTATTTATTATGAATGGATTATTTTAATTAATATTTTAAATATGAAATAGGA   [272]
Cyamophila_prohaskai              GTT-CAAAATGGGTTACTTTATTTATTATGAATGGATTATTATTATT-GTT---AAATTATGAAAATGGA   [267]
Livilla_adusta                    GAA-TAAGGTGGGTTACATTTTTTATAATGAATGAAAATTATTGCTA-AAGG-TAATAATAGAAATGGGA   [270]
Livilla_blandula                  GAT-TAAAGTGGGTTACATTTTTTATAATGAATGAAAATTATTGTTA-GAGG--AATAGTGGAAATAGGA   [268]
Livilla_horvathi                  GGT-TAAAGTGGGTTACATTTTTTATAATGAATGAAAATTATTGTTG-AAAT--AATAGTATAAATAGGA   [269]
Livilla_maculipennis              GAT-TAAAGTGGGTTACATTTTTTATAATGAATGAAGCTTTTTATTA-AAAT--AATAATTGAAATAGGA   [268]
Livilla_maura                     GAT-TAAAGTGGGTTACATTTTTGATAATGAATGAAAATTATTGTTA-GAGC--AGTAGTAGAAATAGGA   [268]
Livilla_monospermae               GAA-AAAAGTGGGTTACATTATTTATTATGAATGAAATTTATGTGTA-GAT--AATTAAAGGAAATGGGA   [268]
Livilla_nervosa                   G-A-AAAAATGGGTTACACTATTTATTATAAATGGAAATTATCTATA-GTTT--GGTTATTAAAATAGGA   [270]
Livilla_pseudoretamae             GAT-TAAAGTGGGTTACATTTTTTATAATGAATGAAAATTATTGTTA-GAGC--AATAGTAGAAATAGGA   [268]
Livilla_pyrenaea                  GAT-TAAAGTGGGTTACATTTTTGATAATGAATGAAAATTATTACTA-AAAT--AATAATAGAAATAGGA   [268]
Livilla_radiata                   GAT-CAGAGTGGGTTACATTTTTTATAATGGATGGAAATTATTATTA-AAAT--AGTAATAGAAATGGGA   [268]
Livilla_retamae                   GAA-AAAAGTGGGTTACATTATTTATTATGGATGAAATTTATGTTTA-GAG--AATTAAAGGAAATGGGA   [268]
Livilla_spectabilis               GAT-TAAAGTGGGTTACATTTTTTATAATGGATGAAAATTATTAGTA-AAGT--AATAATGGAAACAGGA   [268]
Livilla_syriaca                   GAT-TGAGGTGGATTACATTTTTTATAATGAATGAAAATTATTGTTT-AACT--AATAATAGAAATAGGA   [268]
Livilla_variegata                 GAT-TAAAGTGGGTTACATTTTTTATAATGAATGAAAATTATTATTA-AAGT--AATAATGGAAATAGGA   [268]
Livilla_vicina                    GAA-AAAAATGGGTTACATTATTTATGATGAATGAAAGTTATTAAA--AAATT-AATAATGGAAAGAGGA   [268]
Livilla_vittipennella             GAT-TAAAGTGGGTTACATTTTTTATGATGAATGAAAATTATTGTTA-AATAT-AATAATAGAAACGGGA   [269]
Livilla_sp.15                     GAG-AAAAATGGGTTACATTATTTATTATGAATGAAAATTGTTATAA-ATTT--ATTAATGGAAATAGGA   [268]
Livilla_sp.16                     GAA-AAAGATGGGTTACATTATTTATTATGAATGAAAATTATTATTA-ATTT--ATTAATGGAAATAGGA   [268]
Livilla_sp.17                     GAA-AAAAATGGGTTACATTATTTATTATGAATGGAAATTACTAT-A-AAATT-AGTAATAGAAATAGGA   [268]
Pseudacanthopsylla_improvisa      GAA-AAAAATGGGTTACTATAGTTACAATGAATGAAAATTATAAAAATGGAAT-TATGATAGAAATAGGA   [270]
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## APPENDIX 2 cont.

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[                                        290       300       310       320       330       340]
[                                          .         .         .         .         .         . ]
                                                     ******                       12S rRNA end]
Acizzia_hollisi                   TTTAATAGTA---AAATAA----TTTTTAAGAAATAAAATGAATAT-AGATTCTAAAATATG   [323]
Acizzia_uncatoides                TTTGATAGTAAACTAATTT----------AGAGAATTAATGAAAAG-AT????????????   [320]
Arytaina_adenocarpi_PO            TTTAGCAGTA---AGTGAGA-ATTAATAAAGACTTTCTGTGAATTT-AGATTCTAAAATATG   [326]
Arytaina_adenocarpi_SP            TTTAGCAGTA---AGTGAGA-ATTAATAAAGACTTTCTGTGAATTT-AGATTCTAAAATATG   [326]
Arytaina_adenocarpi_MO            TTTAGTAGTA---AGTGAGA-ATTAATAAAGACTTTCTGTGAATTT-AGATWCTAAAATATG   [326]
Arytaina_devia_ssp_insularis_C    TTTAGAAGTAACCAGGAA----TTATTAAAGATTTTTATGAATAT-AGATWCTGAAATATG   [326]
Arytaina_devia_ssp_insularis_P    TTTAGAAGTAACCAGGGAT----TATTAAAGTTTTTCTATGAATTT-AGATTCTAAAATATG   [326]
Arytaina_genistae_SC              TTTAGAAGTAACCAAGAG----TTAATAAAGATTTCTTATGAATTT-AGATTCTAAAATATG   [326]
Arytaina_genistae_PO              TTTAGAAGTAACCAAGAG----TTAATAAAGATTTCTTATGAATTT-AGATTCTAAAATATG   [326]
Arytaina_nubivaga                 TTTAGAAGTAACCAGGAAA----TAGTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [326]
Arytaina_sp.14                    TTTAGAAGTAACCAGGAAAT----AGTAAAGATTTTTTATGAATTT-AGATWCTAAATT---   [322]
Arytainilla_cognata               TTTGAAAGTA---AAAAAA---TTATTAAAGATCTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_cytisi                TTTAAAAGTA---AAGGGAA-GTTATTAAAAATTTTTTATGAATTT-AGATTCTAAAATATG   [324]
Arytainilla_delarbrei             TTTAAAAGTA---AGGAGAA-ATTTGTAAAGATTTTTTATGAATAA-AGATTCTAAAATATG   [324]
Arytainilla_diluta                TTTAAAAGTA---AAAGAA---TTATTAAGGATTTTTTATGAATTY-AGATTCTAAAATAT?   [323]
Arytainilla_dividens_C            TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATT?????????   [323]
Arytainilla_dividens_G            TTTGAAAGTA---AACAAAA--TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_equitans              TTTGAAAGTA---AAAAAA---CTATTAAAGATTTTTTATGAATTT-AGATTCT???????   [323]
Arytainilla_gredi                 TTTAATAGTA---AAGGGAA--TTAA--AAGTGTTTTGATGAATTA-AGATTCTAAAATATG   [322]
Arytainilla_hakani                TTTGAAAGTA---AAAAAA---TTACTAAAGATTTTTTATGAATTT-AGATACTAAA-TAT?   [322]
Arytainilla_ima                   TTTAATAGTA---AATATAA----TTAAAAGATTTTTTATGAATAA-AGATTCTGAAATATG   [322]
Arytainilla_incuba                TTTGAAAGTA---AAAAAAA--TTACTAAAGATTTTTTATGAATTT-AGATACTAAA-TAT?   [323]
Arytainilla_modica_Teline_P       TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_modica_Cham._P        TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_nigralineata          TTTAAAAGTA---AAAGAA---ATATTAAAGATTTTTTATGAATTA-AGATACTAAAATA??   [323]
Arytainilla_pileolata             TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [322]
Arytainilla_proboscidea           TTTGAAAGTA---AAAAAA----TATTAAAGATTTTTTATGAATTT-AGATACTAAA-TA??   [321]
Arytainilla_prognata              TTTAAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_spartiophila_PO       TTTAAAAGTA---AAATAAA-ATTAATAAAGATTTTTCATGAATTT-AGATTCTAGAATATG   [324]
Arytainilla_spartiophila_SP       TTTAAAAGTA---AAATAAA-AT???????????????????????????????????????   [325]
Arytainilla_sulci                 TTTAAAAGTA---AAGAAAA-ATTAATAAAGATTTTTTATGAATTT-AGATTCTAAAGTATG   [324]
Arytainilla_umbonata              TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_sp.1                  TTTAAAAGTA---AAAGAA---TTAGTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [322]
Arytainilla_sp.2                  TTTAAAAGTA---AATAAG---TAAATAAAGATTTTTTATGAATATTAGATTCTAAAATATG   [324]
Arytainilla_sp.3                  TTTAAAAGTA---AAGGAAA-GTTATTAAA-ATTTTTTATGAATTT-AGATACTGAAATA??   [323]
Arytainilla_sp.4                  TTTAATAGTA---AATAAAATTTATTAGAGATTTTTTATGAATTT-AGATWCTAAAATAT?   [325]
Arytainilla_sp.5                  TTTAAAAGTA---AAAAAA----AATTAAAGATTTTATATGAATTT-AGATTCTAAAATATG   [321]
Arytainilla_sp.6                  TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAATAAT?   [323]
Arytainilla_sp.7                  TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_sp.8                  TTTGAAAGTA---AAAAAA----TATTAAAGATTTTT-ATGAATTT-AGATTCTAAAGTATG   [321]
Arytainilla_sp.9                  TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_sp.10                 TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_sp.11                 TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATWCTAAAATATG   [323]
Arytainilla_sp.12                 TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Arytainilla_sp.13                 TTTGAAAGTA---AAAAAA---TTATTAAAGATTTTTTATGAATTT-AGATTCTAAAATATG   [323]
Cacopsylla_alaterni               TTTATAAGTA---AAAAAA---TTGTTAAAGAATTTGTATGAATAT-AGATTCTAAAATATG   [324]
Cacopsylla_mali                   TTTATAAGTA---AAAAAG---TTATTAGAGATTTTATATGAATAG-AGATTCTAAAATATG   [327]
Cyamophila_prohaskai              TTTGTAAGTA---AAAAGA---TTATTAAAGATTTTATATGAATAA-AGATTCTAAAATATG   [322]
Livilla_adusta                    TTTAAGAGTA---AGGGAGA--TTATTAAAGACTTTATATGAATAA-AGATTCTAAAATATG   [326]
Livilla_blandula                  TTTAAAAGTA---AAAAAGA-ATTATTAAAGATTCTATATGAATAA-AGATTCTAAAATATG   [325]
Livilla_horvathi                  TTTAAAAGTA---AAGAAAA--TGATTAAAGATTTTACATGAATAT-AGATTCTAAAGTATG   [325]
Livilla_maculipennis              TTTAAGAGTA---AAGAAAG--TTATTAAAGATTTTATA?????????????????????   [325]
Livilla_maura                     TTTAAAAGTA---AAAAAAA--CTATTAAAGATTTTATATGAATAA-AGATTCTAAAGTATG   [324]
Livilla_monospermae               TTTAAAAGTA---AAACAGA-ATAATTAAAGATTTTTTATGAATAA-AGATTCTGAAATATG   [325]
Livilla_nervosa                   WTTAAAAGTG---TAAAAAA-A--ATTAAAGATTTTATATGAATAA-AGATWCTAAAATATG   [325]
Livilla_pseudoretamae             TTTAAAAGTA---AAAAAGA-ATTATTAAAGATTCTATATGAATAA-AGATTCTAAAATATG   [325]
Livilla_pyrenaea                  TTTAAAAGTA---AAAGGAA--TTATTAAAGATTC??????????????????????????   [325]
Livilla_radiata                   TTTAAAAGTA---AAGTGAA-CTTATTAAAGATTTTATATGAATTT-AGATTCTAAAGTATG   [325]
Livilla_retamae                   TTTAAAAGTA---AAATAGA-ATAATTAAAGATTTTGTATGAATTA-AGATTCTGAAATATG   [325]
Livilla_spectabilis               TTTGAAAGTA---AAGAGAG--TTATTAAAGATTTTACATGAATAT-AGATTCTAAAGTATG   [324]
Livilla_syriaca                   TTTAATAGTA---AAAGAAT???????????????????????????????????????????   [327]
Livilla_variegata                 TTTGAGAGTA---AGAGGAG--CTATTAAAGATTTTATATGAATAA-AGATTCTAAAGTATG   [324]
Livilla_vicina                    TTTAATAGTA---AAAGAAA-GTTAATAGAAATTTTTTATGAATTT-AGATTCTAAAATATG   [325]
Livilla_vittipennella             TTTAAAAGTA---AAAAGAA--TTATTAAAGATTTTATATGAATAT-AGATTCTAAAGTATG   [325]
Livilla_sp.15                     TTTGATAGTA---AATGTAA----TTTAAAGATTTTTTATGAATAA-AGATTCTAAAATATG   [322]
Livilla_sp.16                     TTTAACAGTA---AATATAA----TTAAAAGATTTTTTATGAATAA-AGATTCTAAAATATG   [322]
Livilla_sp.17                     TTTAATAGTA---AGTAAA------CTAAAGATTTTTTATGAATAG-AGATWCTAAAATATG   [320]
Pseudacanthopsylla_improvisa      TTTAACAGTA---AATAAA---TAAATAAAGAATTTTGATGAATAA-AGATTCTAAAATATG   [325]
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## **APPENDIX 3.** Aligned COI-tRNA-COII matrix (639bp), ambiguous regions in the tRNA leucine are indicated by *.

```
[                                        10        20        30        40        50        60        70]
[                                         .         .         .         .         .         .         .]
                                 [COI 262bp start
Acizzia_hollisi                  TCCTCAACATTTTCTAGGATTAATAGGAATACCTCGACGATACTCTAACTATCCAGATTTATTAATTTCA   [70]
Acizzia_uncatoides               TCCTCAACACTTTTTAGGATTAATAGGGATACCTCGACGATACTCAAACTACCCTGATCTTTTAATCTCT   [70]
Arytaina_adenocarpi_PO           TCCTCAACACTTCTTAGGACTTATAGGAATACCACGACGCTACTCTAATTACCCAGATTTACTTATCTTC   [70]
Arytaina_adenocarpi_SP           ?????????CTTCTTAGGACTTATAGGAATACCACGACGCTACTCTAATTACCCAGATTTACTTATCTTC   [70]
Arytaina_adenocarpi_MO           TCCTCAACACTTCTTAGGACTTATAGGAATACCACGACGCTACTCTAATTACCCAGATTTACTTATCTTC   [70]
Arytaina_devia_T                 ??????????????TTGGACTTATAGGAATACCTCGACGTTACTCAAACTACCCAGACCTCCTTATTTTT   [70]
Arytaina_devia_G                 ??????????????TTGGACTTATAGGAATACCTCGACGTTACTCAAACTACCCAGWCCTCCTTATTTTT   [70]
Arytaina_devia_ssp_insularis_C   ??????????CTCTTTGGACTCATAGGAATACCTCGACGTTACTCAAACTACCCTGATCTTCTTGTTTTT   [70]
Arytaina_devia_ssp_insularis_P   ??????????CTCTTTGGTCTTATAGGTATACCTCGTCGTTACTCAAATTACCCAGTCCTCCTTATTTTT   [70]
Arytaina_genistae_SC             ?????????????CTTGGTCTTATAGGAATGCCACGGCGTTACTCAAATTACCCAGGTTTACTCATTTTT   [70]
Arytaina_genistae_PO             ????????????TCTTGGTCTTATAGGAATGCCACGGCGTTACTCAAATTACCCAGATTTACTCATTTTT   [70]
Arytaina_genistae_MO             ???????????TCCTTGGTCTTATAGGAATACCACGGCGTTACTCAAATTATCCAGATTTACTCATTTTT   [70]
Arytaina_nubivaga                TCCTCAACACTTCCTTGGCCTTATAGGGATGCCACGACGCTACTCAAACTACCCAGATCTTCTTATTTTT   [70]
Arytaina_sp.14                   TCCTCAACACTTCCTTGGCCTTATAGGAATGCCACGACGTTACTCAAACTACCCAGATCTTCTTATTTTT   [70]
Arytainilla_cognata              ?????????CTTCTTAGGTCTCATAGGTATGCCACGCCGATATTCTAACTACCCTGACCTCCTAATTTCT   [70]
Arytainilla_cytisi               TCCTCAACATTTCTTGGACTTATAGGAATACCTCGACGATATTCTAATTACCCAGACCTTCTTATCTCT   [70]
Arytainilla_delarbrei            ???????????TCCTTGGCTTAATAGGAATACCGCGACGGTATTCTAACTACCCAGATCTTTTAACCTTT   [70]
Arytainilla_diluta_C             ?????????TTTCTTAGGTCTTATAGGAATACCACGCCGATACTCTAATTATCCTGACCTCCTAATTTCT   [70]
Arytainilla_diluta_T             ?????????TTTCTTAGGTCTTATAGGAATACCACGCCGATACTCTAATTATCCTGACCTCCTAATTTCT   [70]
Arytainilla_dividens_C           ?????????CTTCCTAGGCCTTATAGGTATGCCCCGCCGCTACTCTAATTACCCAGACCTTCTGATTTCC   [70]
Arytainilla_dividens_T           ?????????CTTCCTAGGTCTTATAGGWATGCCTCGCCGTTACTCTAATTATCCAGWTCTTCTAATTTCC   [70]
Arytainilla_dividens_G           ?????????CTTCCTAGGTCTTATAGGTATGCCTCGCCGTTACTCTAATTACCCAGACCTTCTAATTTCC   [70]
Arytainilla_equitans             ????????????TCTTGGCCTTATAGGAATACCTCGACGATATTCTAATTACCCTGATCTTCTAATTTCT   [70]
Arytainilla_hakani               ???????????????AGGGCTTATAGGTATACCACGTCGATACTCTAACTACCCCGACCTCCTCATCTCT   [70]
Arytainilla_ima                  ??????????????TAGGACTTATAGGAATGCCTCGACGCTATTCTAATTACCCTGATTTACTTATTTCT   [70]
Arytainilla_incuba               ????????????CTTAGGCCTTATAGGTATACCACGTCGATATTCTAACTACCCCGACCTCCTCATTTCT   [70]
Arytainilla_modica_Teline_P      TCCTCAACACTTCCTAGGCTTCATAGGCATGCCTCGCCGCTATTCTAATTACCCAGATCTTCTAATTTCC   [70]
Arytainilla_modica_Cham._P       ?????????CTTCCTAGGCCTCATAGGCATGCCTCGCCGCTATTCTAATTACCCAGNTCTTCTAATTTCC   [70]
Arytainilla_modica_Teline_H      TCCTCAACACTTCCTAGGCTTCATAGGCATGCCTCGCCGCTATTCTAATTACCCAGACCTTCTAATTTCC   [70]
Arytainilla_modica_Cham._H       ?????????CTTCCTAGGCCTCATAGGCATGCCTCGCCGCTATTCTAATTACCCAGACCTTCTAATTTCC   [70]
Arytainilla_nigralineata_C       TCCTCAACACTTCTTAGGTCTTATAGGTATGCCTCGCCGATATTCTAATTACCCCGACCTTTTAATTTCT   [70]
Arytainilla_nigralineata_T       TCCTCAACACTTCTTAGGTCTTATAGGTATGCCTCGCCGATATTCTAATTACCCCGACCTTTTAATTTCT   [70]
Arytainilla_nigralineata_G       ?????????CTTCTTAGGTCTTATAGGTATGCCTCGCCGATATTCTAATTACCCCGACCTTTTAATTTCT   [70]
Arytainilla_pileolata_T.can      ??????TCTCTCTGTAGGTCTTATAGGTATACCTCGCCGATATTCTAACTACCCTGACCTTTTAATTTCT   [70]
Arytainilla_pileolata_T.osy      ?????????CTCTGTAGGTCTTATAGGAATACCTCGCCGATATTCTAACTACCCTGACCTTTTAATTTCT   [70]
Arytainilla_proboscidea_A.vis_T  ??????TCTCTTCTTAGGTCTTATAGGAATACCGCGCCGATATTCTAATTATCCCGACCTTTTAATTTCT   [70]
Arytainilla_proboscidea_A.fol_P  ???????????TCTTAGGTCTTATAGGAATACCGCGCCGATATTCTAATTATCCCGACCTTTTAATTTCT   [70]
Arytainilla_prognata             ????????????TCTAGGTCTTATAGGAATACCTCGCCGATACTCTAATTATCCTGACCTTTTAATTTCT   [70]
Arytainilla_spartiophila_PO      TCCTCAACATTTCTTGGTCTAATAGGGATACCTCGACGATACTCTAATTATCCTGATCTTTTAACTTTT   [70]
Arytainilla_spartiophila_SP      TCCTCAACATTTCTTGGTCTAATAGGAATACCTCGACGATACTCTAATTATCCTGATCTTTTAACTTTT   [70]
Arytainilla_spartiophila_MO      ????????????TCTTGGTCTAATGGGAATACCTCGACGATACTCTAATTATCCTGATCTTTTAACTTTT   [70]
Arytainilla_sulci                ????????????TCTTGGCTTAATAGGAATACCTCGACGTTATTCCAATTACCCTGATCTTCTAATTTCC   [70]
Arytainilla_umbonata             ?????????CTTTGTAGGCCTTATAGGTATACCACGTCGATATTCTAACTACCCCGACCTCCTCATTTCT   [70]
Arytainilla_sp.1                 TCCTCAACATTTCTTGGTCTTATAGGAATACCTCGACGATATTCTAACTATCCAGATCTCCTTACCTTT   [70]
Arytainilla_sp.2                 ?????????????????????????????????????????????????????CTGATCTTCTAATTTTT   [70]
Arytainilla_sp.3                 ?????????????CTTGGACTTATAGGNATACCNCGACGWTACTCTAATTACCCAGACCTTCTTATTTCT   [70]
Arytainilla_sp.4_SP              TCCTCAACATTTTCTAGGATTAATAGGAATACCTCGACGATATTCAAATTACCCAGACTTACTTATTTCT   [70]
Arytainilla_sp.4_MO              TCCTCAACATTTTCTAGGATTAATAGGGATACCTCGACGATATTCAAATTACCCAGACTTACTTATTTCT   [70]
Arytainilla_sp.5                 ?????????CTTCCTAGGTCTTATAGGGATACCTCGCCGATACTCTAACTACCCTGATTTACTTATTTCT   [70]
Arytainilla_sp.6                 ?????????CTTCCTAGGTCTTATGGGGATACCTCGTCGATATTCTAATTACCCTGACCTTTTAATTTCT   [70]
Arytainilla_sp.7                 ?????????CTTCCTTGGTCTTATAGGGATACCTCGACGATACTCTAATTACCCAGATCTCCTAATTTCT   [70]
Arytainilla_sp.8                 ???????CTCGCTCTTGGGCTTATAGGCATACCTCGTCGCTATTCTAATTACCCCGATCTTTTAATTTCT   [70]
Arytainilla_sp.9                 ?????????CTTCCTAGGACTTATAGGAATACCTCGTCGCTATTCTAACTACCCCGACCTTTTAATTTCT   [70]
Arytainilla_sp.10_P              ?????????CTTCCTTGGTCTTATAGGTATGCCTCGACGTTATTCTAACTACCCTGATCTCCTAGTTTCT   [70]
Arytainilla_sp.10_H              TCCTCAACACTTCCTTGGTCTTATAGGGATGCCCCGACGATACTCTAACTACCCCGATCTTCTAGTTTCT   [70]
Arytainilla_sp.11                ?????????CTTCCTTGGCCTTATAGGAATACCCCGACGATATTCTAACTACCCCGATCTATTAATTTCT   [70]
Arytainilla_sp.12                ?????????CTTCCTAGGCCTCATAGGCATGCCTCGCCGCTATTCTAATTACCCAGACCTTCTAATTTCC   [70]
Arytainilla_sp.13                ?????????CTTCTTAGGTCTCATAGGCATACCACGTCGTTATTCTAACTACCCTGATCTCCTAATTTCT   [70]
Cacopsylla_alaterni              ?????????CTTCCTTGGACTTATAGGTATACCTCGACGTTACTCAAATTACCCTGATCTATTAATCTCT   [70]
Cacopsylla_mali                  TCCTCAACATTTCCTAGGCCTTATAGGGATACCCCGTCGATACTCCAATTACCCTGACTTATTAATTTCT   [70]
Cyamophila_prohaskai             TCCTCAACACTTCCTTGGCTTAATAGGAATACCTCGACGATATACAAATTACCCTGACCTTCTAGTATAT   [70]
Livilla_adusta                   TCCTCAACATTTTTTAGGCCTTATAGGAATACCTCGACGCTATTCTAACTACCCAGACCTTTTACTTTCA   [70]
Livilla_blandula                 TCCTCAACATTTCTTAGGTCTTATAGGAATACCTCGACGCTATTCCAACTACCCGGATCTTTTAATCTCA   [70]
Livilla_maura                    TCCTCAACATTTCTTAGGTCTTATAGGAATACCCCGGCGTTATTCCAACTATCCAGATCTTTTAATCTCA   [70]
Livilla_monospermae_T            TCCTCAACATTTCTTAGGTTTAATAGGAATACCTCGACGCTATTCCAATTACCCCGATCTTTTAATTTCC   [70]
Livilla_monospermae_G            TCCTCAACATTTCTTAGGTCTAATAGGAATACCTCGACGCTATTCCAATTACCCCGATCTTTTAATTTCC   [70]
Livilla_monospermae_P            TCCTCAACATTTCTTAGGTCTAATAGGAATGCCTCGACGCTACTCCAACTACCCCGATCTTTTAATTTCC   [70]
Livilla_retamae                  ???????????TCTTAGGTCTGATAGGCATGCCTCGACGCTACTCCAACTATCCCGATCTTTTAATTTCT   [70]
Livilla_variegata                ???????????TCCTAGGCCTCATAGGAATACCTCGACGATATTCTAACTATCCAGATCTTTTAATTTCA   [70]
Livilla_sp.15                    TCCTCAACATTTCTTAGGACTTATAGGTATGCCTCGACGATACTCAAACTATCCTGATCTATTAATTTCT   [70]
Livilla_sp.16                    TCCTCAACATTTTTTAGGACTTATAGGTATACCTCGACGTTATTCTAACTACCCTGATCTTCTTATTTCT   [70]
Livilla_sp.17                    TCCTCAACACTTCTTAGGACTAATAGGTATACCTCGACGATACTCAAATTATCCTGACTTATTAATTTCT   [70]
Pseudacanthopsylla_improvisa     ????????????????GGTCTAACAGGTATNNNNNGCCGACAATTAAATTACCCAGATTTACTAATTTCT   [70]
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# APPENDIX 3 cont.

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[                                      80        90        100       110       120       130       140]
[                                      .         .         .         .         .         .         .]

Acizzia_hollisi                        TGAAATGTAGTTTCATCAATTGGATCAATAATTTCATCATTTTCAATAATTTTATTTATAATTATTGTTT   [140]
Acizzia_uncatoides                     TGAAATATTGTATCATCATTAGGGTCAATAATTTCTTCGTTTTCTATGATTTTGTTTATAATTATTATTT   [140]
Arytaina_adenocarpi_PO                 TGAAATATTATTTCTTCAATTGGATCAATGATTTCAATATTTTCAGTTCTAATATTTGTAATTATTGTCT   [140]
Arytaina_adenocarpi_SP                 TGAAATATTATTTCTTCAATTGGATCAATGATTTCAATATTTTCAGTTCTAATATTTGTAATTATTGTCT   [140]
Arytaina_adenocarpi_MO                 TGAAATATTATTTCTTCAATTGGATCAATGATTTCAATATTTTCAGTTCTAATATTTGTAATTATTGTCT   [140]
Arytaina_devia_T                       TGAAATATTATTTCTTCTATTGGATCAATAATTTCTTTATTTTCAGTTCTTTTATTTGTAATTATTATTT   [140]
Arytaina_devia_G                       TGAAATATTATTTCTTCTATTGGATCAATAATTTCTTTATTTTCAGTTCTTTTATTTGTAATTATTATTT   [140]
Arytaina_devia_ssp_insularis_C         TGAAATATTGTTTCTTCTATTGGGTCTATAATTTCTTTATTTTCAGTACTTCTATTTGTAATTATTATTT   [140]
Arytaina_devia_ssp_insularis_P         TGTAATATTATTTCTTCTATTGGTTCAATAATTTCTTTATTCTCAGTTCTCCTATTTGTAATTATTATTT   [140]
Arytaina_genistae_SC                   TGAAATATTATTTCTTCTATTGGATCTATAATTTCTTTATTTTCAGTTCTTTTATTTATAATTATTGTTT   [140]
Arytaina_genistae_PO                   TGAAATATTATTTCTTCTATTGGATCTATAATTTCTTTATTTTCAGTTCTTTTATTTATAATTATTATTT   [140]
Arytaina_genistae_MO                   TGAAATATTATTTCTTCTATTGGATCTATAATTTCTTTATTTTCAGTTCTTTTATTTATAATTATTGTTT   [140]
Arytaina_nubivaga                      TGAAACATTATTTCTTCCATTGGATCAATGATTTCTTTATTTTCAGTACTTTTGTTTATAATTATTATTT   [140]
Arytaina_sp.14                         TGAAACATTATTTCTTCCATTGGATCAATGATTTCTTTATTTTCAGTACTTTTGTTTATAATTATTATTT   [140]
Arytainilla_cognata                    TGAAATATCGTCTCATCTCTTGGATCAATAATTTCTCTATTCTCAGTAATTTTATTTATTATTATTATTT   [140]
Arytainilla_cytisi                     TGAAATATTATATCTTCTGTTGGGTCAATAATTTCTCTTTTTTCAGTTATTTTATTTATTATTATTATTT   [140]
Arytainilla_delarbrei                  TGAAATGTAGTATCTTCTATTGGATCAGTAATTTCTCTTTTTTCAGTGATTTTGCTTGCTGTTATTATCT   [140]
Arytainilla_diluta_C                   TGAAACATTATCTCTTCTATTGGATCAATAATTTCTTTATTTTCAGTAATCTTATTTATTATTATTATTT   [140]
Arytainilla_diluta_T                   TGAAACATTATCTCTTCTATTGGATCAATAATTTCTTTATTTTCAGTAATCTTATTTATTATTATTATTT   [140]
Arytainilla_dividens_C                 TGAAATATTGTTTCATCTATTGGATCAATGATTTCTTTATTTTCAGTAATCCTATTTATCATTATTATTT   [140]
Arytainilla_dividens_T                 TGAAACATTATTTCATCTATTGGATCAATAATTTCTTTATTTTCAGTAATTCTATTTATCATTATTATTT   [140]
Arytainilla_dividens_G                 TGAAACATTATTTCATCTATTGGATCAATAATTTCTTTATTTTCAGTAATTCTATTTATCATTATTATTT   [140]
Arytainilla_equitans                   TGAAATATTATTTCCTCTATTGGATCAATAATTTCTTTATTTTCAGTAATTTTATTTATTATTATTATTT   [140]
Arytainilla_hakani                     TGAAATATTGTATCATCTATTGGGTCAATAATTTCTCTATTTTCAGTAATTCTATTTATTATTATTATTT   [140]
Arytainilla_ima                        TGAAATATTATTTCCTCAATTGGATCAATAATTTCGTTATTTTCAGTAATTATGCTTCTTATTATTATTT   [140]
Arytainilla_incuba                     TGAAATATTGTATCATCTATTGGATCAATAATTTCTCTATTTTCAGTAATTCTATTTATTATTATTATTT   [140]
Arytainilla_modica_Teline_P            TGAAACATTGTGTCATCTATTGGATCAATAATTTCTCTATTCTCAGTAATTCTATTTATCATTATTATTT   [140]
Arytainilla_modica_Cham._P             TGAAACATTGTGTCATCTATTGGATCAATAATTTCTCTATTCTCAGTAATTCTATTTATCATTATTATTT   [140]
Arytainilla_modica_Teline_H            TGAAACATTGTGTCATCTATTGGATCAATAATTTCGCTATTCTCAGTAATTCTATTTATAATTATTATTT   [140]
Arytainilla_modica_Cham._H             TGAAACATTGTGTCATCTATTGGATCAATAATTTCGCTATTCTCAGTAATTCTATTTATAATTATTATTT   [140]
Arytainilla_nigralineata_C             TGAAACATTTTATCTTCTATTGGATCAATAGTTTCTTTATTCTCAGTGATTTTATTTATTATCATTATTT   [140]
Arytainilla_nigralineata_T             TGAAACATTTTATCTTCTATTGGATCAATAGTTTCTTTATTCTCAGTGATTTTATTTATTATCATTATTT   [140]
Arytainilla_nigralineata_G             TGAAACATTTTATCTTCTATTGGATCAATAGTTTCTTTATTCTCAGTGATTTTATTTATTATCATTATTT   [140]
Arytainilla_pileolata_T.can            TGAAATATTGTTTCCTCCATTGGGTCAATAATTTCTTTATTTTCAGTGATCCTATTTATTATTATTATTT   [140]
Arytainilla_pileolata_T.osy            TGAAATATTGTTTCCTCCATTGGGTCAATAATTTCTTTATTTTCAGTGATCCTATTTATTATTATTATTT   [140]
Arytainilla_proboscidea_A.vis_T        TGAAACATTGTATCTTCTATTGGATCAATAATTTCTTTATTCTCCGTAATTCTATTTATTATTATTATTT   [140]
Arytainilla_proboscidea_A.fol_P        TGAAACATTGTATCTTCTATTGGATCAATAATTTCTTTATTCTCCGTAATTCTATTTATTATTATTATTT   [140]
Arytainilla_prognata                   TGAAACATTATTTCCTCTATTGGATCAATAATTTCCCTATTCTCAGTAATCTTATTTATTATTATTATCT   [140]
Arytainilla_spartiophila_PO            TGAAATATTGTATCTTCTATTGGATCTATAATTTCTCTTTTTTCAGTAATTTTATTTCTTATTATTATTT   [140]
Arytainilla_spartiophila_SP            TGAAATATTGTATCTTCTATTGGATCTATAATTTCTCTTTTTTCAGTAATTTTATTTCTTATTATTATTT   [140]
Arytainilla_spartiophila_MO            TGAAATATTGTATCTTCTATTGGATCTATAATTTCTCTTTTTTCAGTAATTTTATTTCTTATTATTATTT   [140]
Arytainilla_sulci                      TGAAACATTATTTCTTCTTTAGGATCAATAATTTCTACATTTTCAGTGATTTTATTTATAATCGTTATTT   [140]
Arytainilla_umbonata                   TGAAATATTGTATCATCTATTGGATCAATAATTTCTCTATTCTCAGTAATTCTATTTATTATTATTATTT   [140]
Arytainilla_sp.1                       TGAAATGTAGTATCTTCTATTGGATCAATAATTTCTCTTTTTTCAGTGATTTTGTTTATCATTATTATTT   [140]
Arytainilla_sp.2                       TGGAATATTATTTCTTCTATAGGATCAATAATTTCTCTTTTTTCAGTGATTTTCTTTATTATTATTATTT   [140]
Arytainilla_sp.3                       TGAAACATTATATCTTCTGTCGGATCAATAATTTCTCTTTTTTCAGTTATTTTATTTATTACTATTATTT   [140]
Arytainilla_sp.4_SP                    TGAAATATTATTTCTTCCATTGGTTCAATAATTTCTTTATTTTCTGTAATTATATTTATTATTATTATTT   [140]
Arytainilla_sp.4_MO                    TGGAATATTATTTCTTCCATTGGTTCAATAATTTCCTTATTTTCTGTAATTATATTTATTATTATTATTT   [140]
Arytainilla_sp.5                       TGAAATATTGTGTCTTCTATTGGATCAATAATTTCATTATTTTCAGTAATTTTATTTGTTATTATCATTT   [140]
Arytainilla_sp.6                       TGAAACATCATCTCCTCTATTGGATCAATAATCTCTCTATTTTCAGTAATTTTGTTTATAATTATTATTT   [140]
Arytainilla_sp.7                       TGAAATATTATCTCCTCTATTGGATCAATAATTTCCTTATTCTCAGTAATTTTATTTATTATTATTATTT   [140]
Arytainilla_sp.8                       TGAAATATTGTATCTTCTATTGGATCAATAATTTCTTTATTTTCAGTAATCTTGTTTATTATTATTATTT   [140]
Arytainilla_sp.9                       TGAAACATTGTATCTTCTATTGGATCAATAATTTCATTATTTTCAGTAATCTTATTTATCATTATTATTT   [140]
Arytainilla_sp.10_P                    TGAAATATTGTTTCCTCTATTGGATCAATAATTTCTTTATTCTCAGTAATTTTATTTATTATTATTATTT   [140]
Arytainilla_sp.10_H                    TGAAATATTGTTTCTTCTATTGGATCAATAATTTCTTTATTCTCAGTAATTTTATTTATTATTATTATTT   [140]
Arytainilla_sp.11                      TGAAATATTGTATCCTCTATTGGATCAATGATTTCTTTATTCTCAGTCATTTTATTTATTATTATTATTT   [140]
Arytainilla_sp.12                      TGAAACATTGTGTCATCTATTGGATCAATAATTTCTTTATTCTCAGTAATTCTATTTATCATTATTATTT   [140]
Arytainilla_sp.13                      TGAAACATCATTTCATCTCTTGGTTCAATAATTTCTCTATTCTCAGTAATTTTATTTATCATTATTATTT   [140]
Cacopsylla_alaterni                    TGAAATATTATTTCTTCAATTGGATCCATAATTTCTTTATTCTCAGTTATTTTATTTATAATTATTATCT   [140]
Cacopsylla_mali                        TGAAACATCATCTCATCTATTGGCTCAATAATTTCACTATTTTCAGTAATTCTATTTATAATTATTATCT   [140]
Cyamophila_prohaskai                   TGAAATATTATCTCTTCTCTTGGATCAATAATTTCTTTATTTTCAATAATCCTATTTATAATCATTATCT   [140]
Livilla_adusta                         TGAAATATTATTTCTTCTATTGGATCAATAATTTCCCTATTTTCAGTAATTTTATTTATACTAATTGTTT   [140]
Livilla_blandula                       TGAAATATTGTGTCATCTATTGGGTCAATAATCTCTTTATTTTCAGTAATTTTATTTATTGTAATTATTT   [140]
Livilla_maura                          TGAAATATCATATCATCTATTGGATCAATAATCTCTTTATTTTCAGTAATTTTATTTATTGTAATTATTT   [140]
Livilla_monospermae_T                  TGAAATATCATTTCTTCTATTGGATCAATAATTTCCCTTTTTTCAGTTATTTTATTTATTATCATTGTAT   [140]
Livilla_monospermae_G                  TGAAATATTGTTTCTTCTATTGGATCAATAATTTCCCTCTTTTCAGTTATCTTATTTATTATCATTGTAT   [140]
Livilla_monospermae_P                  TGAAATATCATTTCTTCTATCGGGTCAATAATTTCCCTCTTTTCAGTTATTTTATTTGTTATCATTGTAT   [140]
Livilla_retamae                        TGAAACATTATTTCTTCTATTGGATCTATAATTTCTCTCTTTTCAGTTATTTTATTTATTATTATTGTAT   [140]
Livilla_variegata                      TGAAATATTATTTCTTCTATTGGATCAATAATTTCTTTATTTTCAGTAGTTCTATTTGTCGTAATTATTT   [140]
Livilla_sp.15                          TGAAATATTGTTTCCTCAATTGGATCAATAATTTCATTATTTTCAATAATTTTAATTTTCATTATTATTT   [140]
Livilla_sp.16                          TGAAATATTATTTCTTCAATTGGATCAATAATTTCTTTATTTTCAGTAATTTTAATTTTTATTATTATTT   [140]
Livilla_sp.17                          TGAAATATTATTTCTTCAATTGGATCAATAATTTCTCTATTTTCAGTTATTTTGTTTATTACCATTATTT   [140]
Pseudacanthopsylla_improvisa           TGAAATATCATTTCATCTATTGGATCTATAATTTCTCTTTTTTCAATAATTTCTTTATTATTATTATGT   [140]
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# APPENDIX 3 cont.

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[                                            150       160       170       180       190       200       210]
[                                              .         .         .         .         .         .         .]

Acizzia_hollisi                     GAGAAGCTTTAACTTCTAAACGTGTAATTATTTATAATTCTAATATTCACATAATTGAATGAATACAAAA   [210]
Acizzia_uncatoides                  GAGAAGCTTTAACTTCAAAACGAGTAGTCATTTTCAACTCAACTACTCACATGATCGAATGAATACAAAA   [210]
Arytaina_adenocarpi_PO              GAGAATCTCTACTTTCTAAGCGTTTAATAATTTTTAATACAACTTTTAATATAGTTGAGTGAATTCAAAA   [210]
Arytaina_adenocarpi_SP              GAGAATCTCTACTTTCTAAGCGTTTAATAATTTTTAATACAACTTTTAATATAGTTGAGTGAATTCAAAA   [210]
Arytaina_adenocarpi_MO              GAGAATCTATACTTTCTAAGCGTTTAATAATTTTTAATACAACTTTTAATATAGTTGAGTGAATTCAAAA   [210]
Arytaina_devia_T                    GAGAATCTTTATTATCTAAACGTCTCATAATTTTTAATAGAACTTTTACTATAATTGAATGAATTCAAAA   [210]
Arytaina_devia_G                    GAGAATCTTTATTATCTAAACGTCTCATAATTTTTAATAGAACTTTTACTATAATTGAATGAATTCAAAA   [210]
Arytaina_devia_ssp_insularis_C      GGGAATCTTTATTAGCAAAACGTATAATAATTTTTAATACAACTTTTACTATAATTGAATGAATTCAAAA   [210]
Arytaina_devia_ssp_insularis_P      GAGAATCTTTATTATCTAAACGGCTAATAATTTTTAATACAACTTTCACTATAATTGAATGAATTCAAAA   [210]
Arytaina_genistae_SC                GAGAATCCTTAGTATCTAAACGTTTTATACTCTTTAATACAACCTTTACTATAATTGAATGAATCCAAAA   [210]
Arytaina_genistae_PO                GAGAATCCTTAGTATCTAAACGTTTTATACTCTTTAATACAACCTTTACTATAATTGAATGAATCCAAAA   [210]
Arytaina_genistae_MO                GAGAATCCTTAGTATCTAAACGTTTTATACTCTTTAATACAACCTTTACTATAATTGAATGAATCCAAAA   [210]
Arytaina_nubivaga                   GAGAATCTTTATTATCTAAGCGTTTTATAATTTTTAATACAACTTTCACTATAATTGAATGAATTCAAAA   [210]
Arytaina_sp.14                      GAGAATCTTTATTATCTAAACGTTTTATAATTTTTAATACAACTTTCACTATAATTGAATGAATCCAAAA   [210]
Arytainilla_cognata                 GAGAATCCCTTATCTCTAAACGTTTATTAATCTTTAATACAACTTTTTCTATAATTGAATGAATCCAAAA   [210]
Arytainilla_cytisi                  GAGAATCCTTTTTAACTAAACGATTAATTATTTTTAATACTTCCTTTTTTATAATTGAATGAATTCAAAA   [210]
Arytainilla_delarbrei               GAGAATCACTAGTATCTAAACGATTAATTATTTTTAACACTCCCTTTTTCATAATTGAGTGAATCCAAAA   [210]
Arytainilla_diluta_C                GAGAATCCTTTGTGTCTAAACGATTCTTAATTTTTAATACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_diluta_T                GAGAATCCTTTGTGTCTAAACGATTCTTAATTTTTAATACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_dividens_C              GAGAATCATTTATAACAAAACGTTTATTAATTTTTAACACAACTTTTTCTATAATTGAATGAGTTCAAAA   [210]
Arytainilla_dividens_T              GAGAATCTCTTATAACAAAACGTTTATTAATTTTTAACACAACTTTTTCTATAATTGAATGAGTTCAAAA   [210]
Arytainilla_dividens_G              GAGAATCTCTTATAACAAAACGTTTATTAATTTTTAACACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_equitans                GAGAATCTTTAATTTCCAAACGTTTCATAATCTTTAATACAACTTTTTCTATAATTGAATGAATCCAAAA   [210]
Arytainilla_hakani                  GAGAATCCCTTGTCTCTAAACGGTTGTTAATCTTTAACACAACTTTTTCTATAATTGAATGAATCCAAAA   [210]
Arytainilla_ima                     GAGAAGCTTTAATTTCTAAACGTCTAATCATTTTTCATACAAATTTTTCTATAATTGAATGAATACAAAA   [210]
Arytainilla_incuba                  GAGAATCTCTTATTTCTAAACGTTTATTAATCTTTAACACAACTTTTTCTATAATTGAATGAATCCAAAA   [210]
Arytainilla_modica_Teline_P         GAGAATCTCTTGTAACAAAGCGTTTATTAATTTTTAACACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_modica_Cham._P          GAGAATCTCTTGTAACAAAGCGTTTATTAATTTTTAACACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_modica_Teline_H         GAGAATCTCTTGTAACAAAGCGTTTATTAATTTTTAACACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_modica_Cham._H          GAGAATCTCTTGTAACAAAGCGTTTATTAATTTTTAACACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_nigralineata_C          GAGAATCATTTATATCTAAACGATTATTAATTTTTAACACAAATTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_nigralineata_T          GAGAATCATTTATATCTAAACGATTATTAATTTTTAACACAAATTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_nigralineata_G          GAGAATCATTTATATCTAAACGTTTATTAATTTTTAACACAAATTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_pileolata_T.can         GAGAATCTTTTATATCCAAACGTTTATTAATCTTCAATACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_pileolata_T.osy         GAGAATCTTTTATATCCAAACGTTTATTAATCTTCAATACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_proboscidea_A.vis_T     GAGAATCCCTTGTATCTAAACGATTATTAATTTTCAACACAACTTTTTCTATAATTGAGTGAATTCAAAA   [210]
Arytainilla_proboscidea_A.fol_P     GAGAATCCCTTGTATCTAAACGATTATTAATTTTCAACACAACTTTTTCTATAATTGAGTGAATTCAAAA   [210]
Arytainilla_prognata                GAGAATCCCTTGTATCTAAACGATTATTAATTTTTAATACAACTTTTTCTATAATTGAATGAATCCAAAA   [210]
Arytainilla_spartiophila_PO         GAGAATCTTTTGTATGTAAACGATTACTTATTTTTAATACTTCTTTTTTTATAATTGAATGAATTCAAAA   [210]
Arytainilla_spartiophila_SP         GAGAATCTTTTGTATGTAAACGATTACTTATTTTTAATACTTCTTTTTTTATAATTGAATGAATTCAAAA   [210]
Arytainilla_spartiophila_MO         GAGAATCTTTTGTATATAAACGATTACTTATTTTTAATACTTCTTTTTTTATAATTGAATGAATTCAAAA   [210]
Arytainilla_sulci                   GGGAATCGTTATTACTAAAGCGTCTACTAATTTTTAATACAACTTTTACCATACTCGAATGAGTCCAAAA   [210]
Arytainilla_umbonata                GAGAATCTCTTATCTCTAAACGTTTATTAATCTTTAACACAACTTTTTCTATAATTGAATGAATCCAAAA   [210]
Arytainilla_sp.1                    GAGAATCTTTAGTGTCAAAACGATTAATTATTTTTAATACCCCCTTTTTTATAATTGAATGAATCCAAAA   [210]
Arytainilla_sp.2                    GAGAATCTTTTATATGTAAACGTTTACTTATTTTTAATACACCTTTTTTTATAATTGAATGAATCCAAAA   [210]
Arytainilla_sp.3                    GGGAATCCTTTATAGCCAAACGGCTAATTATTTTTAGTACTTCCTTTTTCATAATTGAATGAATCCAAAA   [210]
Arytainilla_sp.4_SP                 GAGAATCCTTAATATCTAAACGATTAATTATTTTTAATACAAATTTTTCTATAGTTGAATGAATTCAAAA   [210]
Arytainilla_sp.4_MO                 GAGAATCCTTAATGTCTAAACGATTAATTATTTTTAATACAAATTTTTCTATAGTTGAATGAATTCAAAA   [210]
Arytainilla_sp.5                    GAGAATCTTTTATATCTAAACGATTATTAATTTTTAATACAACTTACTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_sp.6                    GAGAATCTCTTATATCTAAACGATTATTAATCTTTAACACAACTTTCTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_sp.7                    GAGAATCCTTAATTTCTAAACGTTTAATAATCTTTAATACAACTTTCGCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_sp.8                    GAGAATCCTTAATAACAAAACGTTTAATAATTTTTAACACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_sp.9                    GAGAATCTCTTGTAACCAAACGTTTTATAATTTTTAACACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_sp.10_P                 GAGAATCCCTGATTTCCAAACGTTTAATAATCTTTAACACAACCTTTTCTATAATTGAATGAATCCAAAA   [210]
Arytainilla_sp.10_H                 GAGAATCCCTAGTTTCCAAACGTTTAATAATCTTTAATACAACCTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_sp.11                   GAGAATCCTTAATTTCAAAACGTTTAATAATCTTTAATACAACTTTCTCTATAATTGAATGAATCCAAAA   [210]
Arytainilla_sp.12                   GAGAATCTCTTGTAACAAAGCGTTTATTAATTTTTAACACAACTTTTTCTATAATTGAATGAATTCAAAA   [210]
Arytainilla_sp.13                   GAGAATCCCTTATCTCTAAACGTTTACTAATTTTTAATACAACTTTTTCTATAATTGAATGAATCCAAAA   [210]
Cacopsylla_alaterni                 GAGAATCTTTCACAGCAAAACGTATATTAATTTTTAACACAAACTTTGCAATAATTGAATGAATCCAAAA   [210]
Cacopsylla_mali                     GAGAATCCTTTATATGTAAACGTCTATTGATTTTCAATACAACATTCGCTATAATTGAGTGAATCCAAAA   [210]
Cyamophila_prohaskai                GAGAATCTTTAATTGTTAAACGTATCTTAATATTTAACACTAATTTTTCTATAATTGAATGAGCACAAAA   [210]
Livilla_adusta                      GAGAATCATTAATTTCTAAACGATTAATTGTTTTCAATATAAATTTTTCTATAATTGAATGAATTCAAAA   [210]
Livilla_blandula                    GAGAATCATTAACTTCGAAACGATTTGTTATCTTCAGTACAAATTTTTCTATAATTGAGTGATCTCAAAA   [210]
Livilla_maura                       GAGAATCATTAGCTTCGAAACGATTAGTTATCTTCACTACGAATTTTTCTATAATTGAGTGAGCCCAAAA   [210]
Livilla_monospermae_T               GAGAATCTTTACTCTCTAAACGACTCCTAATTTTCAATAGAACCTTTTCAATAATTGAATGAATTCAAAA   [210]
Livilla_monospermae_G               GAGAATCTTTACTCTCTAAACGGCTCCTAATTTTTAATAGAACCTTTTCAATAATTGAATGAATTCAAAA   [210]
Livilla_monospermae_P               GAGAATCTTTACTCTCTAAACGGCTCCTAATTTTCAATACAACCTTTTCAATAATTGAATGAATCCAAAA   [210]
Livilla_retamae                     GAGAATCTTTTGTTTCTAAACGACTCCTAATTTTCAATAGAACATTCTCAATAATCGAATGAATTCAAAA   [210]
Livilla_variegata                   GAGAATCATTAGTTTCTAAACGATCTATTATTTTCAGTACAAATTTTTCTATAGTTGAATGAGTCCAAAA   [210]
Livilla_sp.15                       GAGAAGCCTTAGTTTCCAAACGCTTAATTATTTTTAATACAAACTATTCTATAATTGAATGAATACAGAA   [210]
Livilla_sp.16                       GAGAAGCTTTAGTTTCTAAGCGTCTAATTATTTTTAATACAAACTTTTTTATAATTGAATGAATACAAAA   [210]
Livilla_sp.17                       GAGAAGCTCTTATCTCTAAACGATTAATTATTTTTAATACAAATTTTTCTATAATTGAATGAGCTCAAAA   [210]
Pseudacanthopsylla_improvisa        GAGAATCATTTATTTCCAAACGATTAATTTTATTTACAACGAATTTTTTTATAATTGAATGAGTCCAAAA   [210]
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## APPENDIX 3 cont.

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[                                           220       230       240       250       260       270       280]
[                                           .         .         .         .         .         .         .]
                                                                                COI 3’][tRNA leucine 5’
Acizzia_hollisi                    TTCCCCTCCATTAGAACACAGATACTCTGAAATCCCATCAATTTTAATTAAA----TACTATTGTGTCAG          [276]
Acizzia_uncatoides                 TTTCCCACCTATAGAACATAGTTATTCAGAAATTCCTTCTATCTTAATTAAATAAATACTAATGTGTCAG          [280]
Arytaina_adenocarpi_PO             CTTCCCCCCTATAGAACATAGTTATTCTGAAATCCCCACAATTTCAATTAAATA---ACTAATGTGTCAG          [277]
Arytaina_adenocarpi_SP             CTTCCCCCCTATAGAACATAGTTATTCTGAAATCCCCACAATTTCAATTAAATA---ACTAATGTGTCAG          [277]
Arytaina_adenocarpi_MO             CTTCCCCCCTATAGAACATAGTTATTCTGAAATCCCCACAATTTCAATTAAATA---ACTAATGTGTCAG          [277]
Arytaina_devia_T                   CTTTCCTCCTATAGAACATAGTTACTCTGAAATTCCTACAATTTCAATTAAATA---ACTAATGTGTCAG          [277]
Arytaina_devia_G                   CTTTCCTCCTATAGAACATAGTTACTCTGAAATTCCTACAATTTCAATTAAATA---ACTAATGTGTCAG          [277]
Arytaina_devia_ssp_insularis_C     TTTTCCTCCTATAGAACATAGTTATTCTGAAATCCCCACAATTTCAGTTAAATA---ACTAATGTGTCAG          [277]
Arytaina_devia_ssp_insularis_P     CTTCCCCCCCATAGAACATAGTTACTCTGAAATTCCCACAATTTCAATTAAATA---ACTAATGTGTCAG          [277]
Arytaina_genistae_SC               TTTTCCCCCCATAGAACATAGTTACTCTGAAATTCCCACAATTTTAGTTAAATA---ACTAATGTGTCAG          [277]
Arytaina_genistae_PO               TTTCCCCCCCATAGAACATAGTTACTCTGAAATTCCCACAATTTTAGTTAAATA---ACTAATGTGTCAG          [277]
Arytaina_genistae_MO               TTTTCCCCCCATAGAACATAGTTACTCTGAAATTCCCACAATTTTAGTTAAATA---ACTAATGTGTCAG          [277]
Arytaina_nubivaga                  CTTTCCACCCATAGAACATAGTTATTCTGAAATTCCCACAATTTCAATTAAATA---ACTAATGTGTCAG          [277]
Arytaina_sp.14                     CTTTCCCCCTATAGAACATAGTTATTCTGAAATTCCCACAATTTCAATTAAATA---ACTAATGTGTCAG          [277]
Arytainilla_cognata                TTTCCCCCCGATTGAACACAGATACTCTGAAATTCCCGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_cytisi                 TTTTCCTCCTATAGAACATAGTTATTCTGAGATTCCTGCAATTTTAATTAAATA---ACTAATGTGTCAG          [277]
Arytainilla_delarbrei              TTTCCCTCCCATAGAACATAGTTATTCTGAAATTCCTGCTATCTTAGTTAAATA---ACTAATGTGTCAG          [277]
Arytainilla_diluta_C               TTTTCCTCCTATCGAACACAGATACTCTGAAATTCCTACAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_diluta_T               TTTTCCTCCTATCGAACACAGATACTCTGAAATTCCTACAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_dividens_C             CTTCCCCCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_dividens_T             CTTTCCCCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_dividens_G             CTTTCCCCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_equitans               TTTTCCTCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_hakani                 TTTTCCTCCGATTGAACATAGATACTCTGAAATTCCCGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_ima                    TTTTCCTCCTACAGAACACAGTTACTCTGAAATTCCTACAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_incuba                 TTTTCCTCCGATTGAACATAGATACTCTGAAATTCCCGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_modica_Teline_P        CTTCCCCCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_modica_Cham._P         CTTCCCCCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_modica_Teline_H        CTTCCCCCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_modica_Cham._H         CTTCCCCCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_nigralineata_C         TTTTCCTCCGATTGAACACAGATACTCTGAAATTCCTGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_nigralineata_T         TTTTCCTCCGATTGAACACAGATACTCTGAAATTCCTGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_nigralineata_G         TTTTCCTCCGATTGAACACAGATACTCTGAAATTCCTGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_pileolata_T.can        TTTCCCCCCAATTGAACATAGATACTCTGAAATTCCAGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_pileolata_T.osy        TTTCCCCCCAATTGAACATAGATACTCTGAAATTCCAGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_proboscidea_A.vis_T    TTTTCCTCCAATTGAACATAGTTACTCTGAAATTCCTGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_proboscidea_A.fol_P    TTTTCCTCCAATTGAACATAGTTACTCTGAAATTCCTGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_prognata               TTTTCCTCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_spartiophila_PO        TTTTCCACCTGTTGAACACAGTTACTCTGAAATTCCCGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_spartiophila_SP        TTTTCCACCTGTTGAACACAGTTACTCTGAAATTCCCGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_spartiophila_MO        TTTTCCACCTGTTGAACACAGTTACTCTGAAATTCCCGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sulci                  TTTCCCCCCATTAGAACATAGTTACTCAGAAATTCCCATAATTTTAATTAAATA---ACTAATGTGTCAG          [277]
Arytainilla_umbonata               TTTTCCTCCGATTGAACATAGATACTCTGAAATTCCCGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.1                   TTTCCCTCCTGCTGAACATAGCTACTCTGAAATTCCTGCAATTTTAGTTAAATA---ACTAATGTGTCAG          [277]
Arytainilla_sp.2                   CTTTCCCCCAATAGAACATAGTTACTCTGAAATCCCTACGATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.3                   TTTTCCTCCCATAGAACATAGTTACTCTGAGATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.4_SP                TTACCCTCCTATTGAACATAGTTACTCTGAAATTCCTACAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.4_MO                TTATCCTCCTATTGAACATAGTTACTCTGAAATTCCTACAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.5                   TTTTCCTCCAATTGAACATAGATACTCTGAGATTCCTGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.6                   TTTTCCTCCTATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.7                   TTTTCCCCCAGTTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.8                   TTTTCCTCCCACTGAACATAGCTACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.9                   TTTTCCCCCAATTGAACATAGATACTCTGAAATTCCTACAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.10_P                TTTCCCTCCGATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.10_H                TTTCCCTCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.11                  CTTTCCTCCAATTGAACATAGATACTCTGAAATTCCCGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.12                  CTTCCCCCCAATTGAACATAGATACTCTGAAATTCCTGCAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Arytainilla_sp.13                  TTTCCCCCCAATTGAACACAGATACTCTGAAATCCCTGCAATTTTAGTTAAGTA---ACTAATGTGTCAG          [277]
Cacopsylla_alaterni                TTTTCCTCCTATCGAACATAGTTATTCTGAAATCCCCTCAATTTTAAGTAAATA---ACTAATGTGTCAG          [277]
Cacopsylla_mali                    CTTTCCTCCCACAGAACATAGTTATTCTGAGATCCCTTCAATCTTGAGTAAGTA---ACTAATGTGTCAG          [277]
Cyamophila_prohaskai               TTCTCCTCCCTCTGAACATAGTTATTCTGAAATCCCTTCAATTTTAACTAAATA---ACTAATGTGTCAG          [277]
Livilla_adusta                     TTTTCCTCCTGTTGAACATAGATACTCTGAAATTCCGACCATTTTAGTTAAATA---GCTAATGTGTCAG          [277]
Livilla_blandula                   TTTTCCCCCTATTGAACATAGTTACTCTGAAATTCCTACAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Livilla_maura                      TTTTCCTCCTATTGAACATAGTTACTCTGAAATTCCTACAATTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Livilla_monospermae_T              TTCCCCTCCTATTGAGCATAGTTACTCTGAGATTCCTGCAGTTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Livilla_monospermae_G              TTCCCCTCCTATTGAGCATAGTTACTCTGAGATCCCTGCAGTTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Livilla_monospermae_P              TTCTCCTCCTATTGAACATAGTTACTCTGAAATCCCTGCAGTTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Livilla_retamae                    TTCTCCCCCCATTGAACATAGTTACTCTGAGATCCCTGCAGTTTTAATTAAGTA---ACTAATGTGTCAG          [277]
Livilla_variegata                  TTTTCCTCCTATTGAACACAGTTACTCTGAGATTCCTGCAATCTTAATTAAGTA---ACTAATGTGTCAG          [277]
Livilla_sp.15                      TTTTCCTCCTATAGAACATAGTTACTCTGAAATTCCCGCAATTTTAGATAAGTA---ACTAATGTGTCAG          [277]
Livilla_sp.16                      TTTCCCACCAATTGAACATAGCTACTCTGAAATTCCCACAATTTTAGTTAAATA---ACTAATGTGTCAG          [277]
Livilla_sp.17                      TTTTCCCCCTATTGAACATAGTTACTCTGAAATTCCTGCAATTTTAGTTAAATA---ACTATTGTGTCAG          [277]
Pseudacanthopsylla_improvisa       TTTTCCTCCCATAGAACATAGATACTCAGAAATTCCAACAATTCTAATCAGGTA---ACTAATGTGTCAG          [277]
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# APPENDIX 3 cont.

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[                                           290       300       310       320       330       340       350]
[                                           .         .         .         .         .         .         .]
                                     *****                                *************** tRNA 3'][COII 5'
Acizzia_hollisi                    AGT---AATGTATTAAATTTAAGATTTGAAAATGAA--T--AAT-AA--GTTCCTTTAGTAATTGACTGA   [336]
Acizzia_uncatoides                 ATC-TAAATGTATTAAATTTAAGATTTAAATATGAA--T--TAC-TT--ATTCCTTTAGTAATTGACTGA   [342]
Arytaina_adenocarpi_PO             ACT-C-AATGTATTAAATTTAAGATTTAAGTATGAA----ATTT-TA---TTCCTTTAGTAATTGACTGA   [337]
Arytaina_adenocarpi_SP             ACT-C-AATGTATTAAATTTAAGATTTAAGTATGAA----ATTT-TA---TTCCTTTAGTAATTGACTGA   [337]
Arytaina_adenocarpi_MO             ACT-C-AATGTATTAAATTTAAGATTTAAGTATGAA----ATTT-TA---TTCCTTTAGTAATTGATTGA   [337]
Arytaina_devia_T                   ATT-T-AATGTATTAAATTTAAGATTTAGCTATGAG--T-TCCT-TT--ATTCCTTTAGTAATTGACTGA   [339]
Arytaina_devia_G                   ATT-T-AATGTATTAAATTTAAGATTTAGCTATGAG--T-TCCT-TT--ATTCCTTTAGTAATTGACTGA   [339]
Arytaina_devia_ssp_insularis_C     ATT-T-AATGTATTAAATTTAAGATTTAAATATGAA--T--TTT-TT--ATTCCTTTAGTAATTGACTGA   [338]
Arytaina_devia_ssp_insularis_P     ATT-T-AATGTATTAAATTTAAGATTTAACTATGAACCCCTTTT-A----TTCCTTTAGTAATTGACTGA   [340]
Arytaina_genistae_SC               ATC-T-AATGTATTAAATTTAAGATTTAAATATGAA-----AAT-TA---TTCCTTTAGTAATAGATTGA   [336]
Arytaina_genistae_PO               ATC-T-AATGTATTAAATTTAAGATTTAAATATGAA-----AAT-TA---TTCCTTTAGTAATAGATTGA   [336]
Arytaina_genistae_MO               ATC-T-AATGTATTAAATTTAAGATTTAAGTATGAA-----AAT-TA---TTCCTTTAGTAATAGACTGA   [336]
Arytaina_nubivaga                  ATC-T-AATGTATTAAATTTAAGATTTGAGTATGAA--AC-TTT-A----TTCCTTTAGTAATTGACTGA   [337]
Arytaina_sp.14                     ATC-T-AATGTATTAAATTTAAGATTTGAGTATGAA--AC-TTT-A----TTCCTTTAGTAATTGACTGA   [337]
Arytainilla_cognata                AGT-C-AATGTATTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_cytisi                 AAT-C-AATGTATTAAATTTAAGATTTAACTATGAA--A-TTTT-AT--ATTCCTTTAGTAATAGATTGA   [339]
Arytainilla_delarbrei              AAC-C-AATGTATTAAATTTAAGATTTAACCATGAA--A-TTTT-ATTACTTCCTTTAGTAATAGATTGA   [341]
Arytainilla_diluta_C               AGT-C-AATGTATTAAATTTAAGATTTACCTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_diluta_T               AGT-C-AATGTATTAAATTTAAGATTTACCTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_dividens_C             AGT-C-AATGTACTAAACTTAAGATTTAGCTATGAA---GTTTT-A----TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_dividens_T             AGT-C-AATGTACTAAACTTAAGATTTAGATATGAA---GTTTT-A----TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_dividens_G             AGT-C-AATGTACTAAACTTAAGATTTAGCTATGAA---GTTTT-A----TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_equitans               AGT-C-AATGTACTAAATTTAAGATTTAGATATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_hakani                 AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_ima                    ACC-T-AATGTATTAAATTTAAGATTTAATTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_incuba                 AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_modica_Teline_P        AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_modica_Cham._P         AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_modica_Teline_H        AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_modica_Cham._H         AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_nigralineata_C         AGT-C-AATGTACTAAATTTAAGATTTAGATATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_nigralineata_T         AGT-C-AATGTACTAAATTTAAGATTTAGATATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_nigralineata_G         AGT-C-AATGTACTAAATTTAAGATTTAGATATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_pileolata_T.can        AGT-C-AATGTACTAAATTTAAGATTTAGGTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_pileolata_T.osy        AGT-C-AATGTACTAAATTTAAGATTTAGGTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_proboscidea_A.vis_T    AGT-C-AATGTACTAAATTTAAGATTTAGATATGAA----AATT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_proboscidea_A.fol_P    AGT-C-AATGTACTAAATTTAAGATTTAGATATGAA----AATT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_prognata               AGT-C-AATGTATTAAATTTAAGATTTATCTATGAA--GTTTTT-A----TTCCTTTAGTAATAGACTGA   [338]
Arytainilla_spartiophila_PO        AAT-C-AATGTATTAAATTTAAGATTTAACTATGAA--A---TT-----TTTCCTTTAGTAATAGATTGA   [335]
Arytainilla_spartiophila_SP        AAT-C-AATGTATTAAATTTAAGATTTAACTATGAA--A---TT-----TTTCCTTTAGTAATAGATTGA   [335]
Arytainilla_spartiophila_MO        AAT-C-AATGTATTAAATTTAAGATTTAACTATGAA--A---TT-----TTTCCTTTAGTAATAGATTGA   [335]
Arytainilla_sulci                  ACC-C-AATGTATTAAATTTAAGATTTAAGTATGAA----AACC-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_umbonata               AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_sp.1                   AAT-C-AATGTATTAAATTTAAGATTTAATTATGAA--A-TTTT-TT--ATTCCTTTAGTAATAGACTGA   [339]
Arytainilla_sp.2                   AAATC-AATGTATTAAATTTAAGATTTAACTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [338]
Arytainilla_sp.3                   AAT-C-AATGTATTAAATTTAAGATTTAACTATGAA--A-TTTT-AT--ATTCCTTTAGTAATAGACTGA   [339]
Arytainilla_sp.4_SP                AAC-T-AATGTATTAAATTTAAGATTTAACTATGAA--A-TTTT-TT--ATTCCTTTAGTAATAGATTGA   [339]
Arytainilla_sp.4_MO                AAC-T-AATGTATTAAATTTAAGATTTAACTATGAA--A-TTTT-TT--ATTCCTTTAGTAATAGATTGA   [339]
Arytainilla_sp.5                   AGT-C-AATGTACTAAATTTAAGATTTAGATATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_sp.6                   AGT-C-AATGTATTAAATTTAAGATTTAGTTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_sp.7                   AGT-C-AATGTATTAAATTTAAGATTTAGTTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_sp.8                   AGT-C-AATGTACTAAATTTAAGATTTAACTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_sp.9                   AGT-C-AATGTATTAAATTTAAGATTTAAGTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_sp.10_P                AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTTTT--ATTCCTTTAGTAATAGACTGA   [339]
Arytainilla_sp.10_H                AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA--A-TTTT-TT--ATTCCTTTAGTAATAGACTGA   [339]
Arytainilla_sp.11                  AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Arytainilla_sp.12                  AGT-C-AATGTACTAAATTTAAGATTTAGCTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Arytainilla_sp.13                  AGT-C-AATGTACTAAATTTAAGATTTAGCCATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [337]
Cacopsylla_alaterni                AAA---AATGTATTAAATTTAAGATTTAAGTATGAA----ATTT-TA---TTCCTTTAGTAATAGATTGA   [336]
Cacopsylla_mali                    AAA-CAAATGTATTAAATTTAAGATTTAAGTATGAA--G-TCTT-TT--ATTCCTTTAGTAATAGACTGA   [340]
Cyamophila_prohaskai               AAA-C-AATGTATTAAATTTAAGATTTAAATATGAA----ATAT-TA---CTCCTTTAGTAATAGATTGA   [337]
Livilla_adusta                     AGT-C-AATGTATTAAATTTAAGATTTAGTTATGAA--A-AATT-TT--ATTCCTTTAGTAATAGACTGA   [339]
Livilla_blandula                   AAC-C-AATGTATTAAATTTAAGATTTAACTATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Livilla_maura                      AAC-C-AATGTATTAAATTTAAGATTTAACTATGAA--ATTTTT-A----TTCCTTTAGTAATAGACTGA   [338]
Livilla_monospermae_T              AAG-T-AATGTATTAAATTTAAGATTTAATTATGAA--ATTTTT-A----TTCCTTTAGTAATAGATTGA   [338]
Livilla_monospermae_G              AAG-T-AATGTATTAAATTTAAGATTTAATTATGAA--ATTTTT-A----TTCCTTTAGTAATAGATTGA   [338]
Livilla_monospermae_P              AAG-T-AATGTATTAAATTTAAGATTTAATTATGAA--ATTTTT-A----TTCCTTTAGTAATAGATTGA   [338]
Livilla_retamae                    AGA-T-AATGTATTAAATTTAAGATTTAACCATGAA----ATTA-TA---TTCCTTTAGTAATAGATTGA   [337]
Livilla_variegata                  AGT-T-AATGTATTAAATTTAAGATTTAAGTATGAA--AAAGTT-TT--ATTCCTTTAGTAATAGACTGA   [340]
Livilla_sp.15                      AAG-CAAATGTATTAAATTTAAGATTTAATTATGAA----ACCT-TA---TTCCTTTAGTAATAGACTGA   [338]
Livilla_sp.16                      AGC-T-AATGTATTAAATTTAAAATTTAAATATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Livilla_sp.17                      ACC-T-AATGTATTAAATTTAAGATTTAAATATGAA----ATTT-TA---TTCCTTTAGTAATAGACTGA   [337]
Pseudacanthopsylla_improvisa       ATT-C-AATGTATTAAATTTAAGATTTAATTATGAA----AACA-CTA--TTCCTTTAGTAATAGACTGA   [338]
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# APPENDIX 3 cont.

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[                                           360       370       380       390       400       410      420]
[                                             .         .         .         .         .         .        .]

Acizzia_hollisi                    ATAAAAGTATCTCTTTATGATAATGCCTCCCCTATTATAGAACAACTAATTTTATTTCATGATTATAGAA    [406]
Acizzia_uncatoides                 CTAAAATTTTCTCTATATGATAATGCTTCACCGATTATAGAACAACTTATTTTATTTCATGATTATAGAA    [412]
Arytaina_adenocarpi_PO             ATAAAAATTTCATTGTATGACAATGCATCACCAATTATAGAACAATTAACCCTATTCCATGATTACAGAA    [407]
Arytaina_adenocarpi_SP             ATAAAAATTTCATTGTATGACAATGCATCACCAATTATAGAACAATTAACCCTATTCCATGATTACAGAA    [407]
Arytaina_adenocarpi_MO             ATAAAAATTTCATTGTATGACAATGCATCACCAATTATAGAACAATTAACCCTATTCCATGATTACAGAA    [407]
Arytaina_devia_T                   ATAAAAATTTCATTATATGATAATGCATCTCCAATTATAGAACAATTAATCATATTTCATGACTATAGTA    [409]
Arytaina_devia_G                   ATAAAAATTTCATTATATGATAATGCATCTCCAATTATAGAACAATTAATCATATTTCATGACTATAGTA    [409]
Arytaina_devia_ssp_insularis_C     ATAAAAATTTCATTATACGATAATGCATCTCCAATTATAGAACAACTAATTTTATTTCATGATTATAGAA    [408]
Arytaina_devia_ssp_insularis_P     ATAAAAATTTCATTATATGATAATGCATCCCCAATTATAGAACAGTTAATTCTGTTCCATGATTATAGAA    [410]
Arytaina_genistae_SC               CTAAAAATTTCATTATATGATAATGCCTCTCCAATTATAGAACAATTAATTTTATTTCATGACTACAGAA    [406]
Arytaina_genistae_PO               CTAAAAATTTCATTATATGATAATGCCTCTCCAATTATAGAACAATTAATTTTATTTCATGACTACAGAA    [406]
Arytaina_genistae_MO               CTAAAAATTTCTTTATATGATAATGCCTCTCCAATTATAGAACAATTAATTTTATTCCATGACTACAGAA    [406]
Arytaina_nubivaga                  ATAAAAATTTCATTATATGATAATGCTTCCCCAATTATAGAGCAATTAACTCTATTTCATGATTATAGCA    [407]
Arytaina_sp.14                     ATAAAAATTTCATTGTATGATAATGCTTCCCCAATTATAGAACAATTAACTCTATTCCATGATTATAGTA    [407]
Arytainilla_cognata                ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACTTTATTCCATGATTACAGTA    [407]
Arytainilla_cytisi                 ATAAAAATTTCATTTCTTGATAATGCTTCTCCAATTATAGAACAATTAATTTTATTTCATGATTACAGTA    [409]
Arytainilla_delarbrei              ATAAAAATTTCACTTTTTGATAATGCTTCACCAATTATAGAACAATTAATTTTATTTCATGATTACAGTA    [411]
Arytainilla_diluta_C               ATAAAAATTTCGCTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACTTTATTTCATGATTATAGTA    [407]
Arytainilla_diluta_T               ATAAAAATTTCGCTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACTTTATTTCATGATTATAGTA    [407]
Arytainilla_dividens_C             ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTTCATGATTATAGTA    [407]
Arytainilla_dividens_T             ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTCCACGATTACAGCA    [407]
Arytainilla_dividens_G             ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTCCACGATTACAGCA    [407]
Arytainilla_equitans               ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTTCATGATTACAGTA    [407]
Arytainilla_hakani                 ATAAAAATTTCACTTTTTGACAATGCCTCCCCCATTATAGAACAATTAACCCTATTTCATGATTACAGTA    [407]
Arytainilla_ima                    ATAAAAATTTCTCTTTTTGATAATGCTTCTCCAATTATAGAACAATTAATTTTATTTCATGATTATAGTA    [407]
Arytainilla_incuba                 ATAAAAATTTCACTTTTTGACAATGCCTCCCCCATTATAGAACAATTAACCCTATTTCATGATTACAGTA    [407]
Arytainilla_modica_Teline_P        ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTTCATGATTACAGCA    [407]
Arytainilla_modica_Cham._P         ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTTCATGATTACAGCA    [407]
Arytainilla_modica_Teline_H        ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTTCATGATTACAGCA    [407]
Arytainilla_modica_Cham._H         ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTTCATGATTACAGCA    [407]
Arytainilla_nigralineata_C         ATAAAAATTTCACTTTTTGACAATGCTTCTCCCATTATAGAACAACTAACCTTATTTCACGATTACAGTA    [407]
Arytainilla_nigralineata_T         ATAAAAATTTCACTTTTTGACAATGCTTCTCCCATTATAGAACAACTAACCTTATTTCACGATTACAGTA    [407]
Arytainilla_nigralineata_G         ATAAAAATTTCACTTTTTGACAATGCTTCTCCCATTATAGAACAACTAACCTTATTTCACGATTACAGTA    [407]
Arytainilla_pileolata_T.can        ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACCTTATTCCATGATTATAGTA    [407]
Arytainilla_pileolata_T.osy        ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACCTTATTCCATGATTATAGTA    [407]
Arytainilla_proboscidea_A.vis_T    ATAAAAATTTCACTTTTTGATAATGCTTCCCCCATTATAGAACAATTAACCTTATTCCATGATTACAGTA    [407]
Arytainilla_proboscidea_A.fol_P    ATAAAAATTTCACTTTTTGATAATGCTTCCCCCATTATAGAACAATTAACCTTATTCCATGATTACAGTA    [407]
Arytainilla_prognata               ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACTTTATTTCATGATTATAGTA    [408]
Arytainilla_spartiophila_PO        ATAAAAATTTCATTTTTTGACCATGCTTCCCCTACTATAGAACAACTAATTTTATTTCACGACTATAGCA    [405]
Arytainilla_spartiophila_SP        ATAAAAATTTCATTTTTTGACCATGCTTCCCCTACTATAGAACAACTAATTTTATTTCACGACTATAGCA    [405]
Arytainilla_spartiophila_MO        ATAAAAATTTCATTTTTTGACCATGCTTCCCCTACTATAGAACAACTAATTTTATTTCACGACTATAGCA    [405]
Arytainilla_sulci                  CTAAAACTTTCACTTTACGATAATGCTTCCCCGATTATAGAACAACTCATTTTATTTCATGATTATAGTA    [407]
Arytainilla_umbonata               ATAAAAATTTCACTTTTTGACAATGCCTCCCCCATTATAGAACAATTAACTCTATTTCATGATTACAGTA    [407]
Arytainilla_sp.1                   ATAAAAATTTCATTATTTGATAATGCCTCTTCAATCATAGAACAACTAACTTTATTTCATGATTACAGTA    [409]
Arytainilla_sp.2                   ATAAAAATTTCACTTTTTGATACTGCTTCTCCAATTATAGAACAATTAACTTTGTTTCATGACTATAGTA    [408]
Arytainilla_sp.3                   ATAAAAATTTCATTTTTTGATAATGCTTCACCAATTATGGAACAATTAATTTTATTTCATGATTACAGTA    [409]
Arytainilla_sp.4_SP                ATAAAAATTTCACTTTCTGACAATGCATCACCTATTATAGAACAATTAATTTTATTTCATGATTACAGAA    [409]
Arytainilla_sp.4_MO                ATAAAAATTTCACTTTCTGACAATGCATCACCTATTATAGAACAATTAATTTTATTTCATGATTACAGAA    [409]
Arytainilla_sp.5                   ATAAAAATTTCGCTTTTTGACAATGCTTCTCCTATTATAGAACAATTAACCTTATTTCATGACTATAGAA    [407]
Arytainilla_sp.6                   ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACCTTATTTCATGACTACAGTA    [407]
Arytainilla_sp.7                   ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACCTTATTTCATGATTATAGTA    [407]
Arytainilla_sp.8                   ATAAAAATTTCACTTTTTGACAATGCCTCACCTATTATAGAACAATTAACATTATTTCATAATTATAGTA    [407]
Arytainilla_sp.9                   ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTTCACGATTACAGTA    [407]
Arytainilla_sp.10_P                ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACCTTATTTCATGATTATAGTA    [409]
Arytainilla_sp.10_H                ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACCTTATTTCATGATTATAGTA    [409]
Arytainilla_sp.11                  ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACCTTATTTCATGATTACAGTA    [407]
Arytainilla_sp.12                  ATAAAAATTTCACTTTTTGACAATGCTTCCCCCATTATAGAACAATTAACATTATTTCATGATTACAGTA    [407]
Arytainilla_sp.13                  ATAAAAATTTCACTTTTTGACAACGCTTCCCCCATTATAGAACAATTAACTTTATTTCATGATTACAGTA    [407]
Cacopsylla_alaterni                ATAAAAATTTCTCTTTACGACAATGCATCCCCAATTATAGAACAACTAATTCTATTTCATGATTACAGCA    [406]
Cacopsylla_mali                    TTAAAAATTTCGCTTTATGATAATGCCTCTCCAATTATAGAACAATTAATTCTATTTCATGATTATAGAA    [410]
Cyamophila_prohaskai               ATAAAAATTTCTCTTTACGACAGTGCCTCTCCAATTATAGAACAATTAATTTTATTTCATGATTACAGCA    [407]
Livilla_adusta                     ATAAAAATTTCTCTCTTTGATAATGCTTCCCCAATTATAGAACAACTAACTTTATTTCATAATTATACTA    [409]
Livilla_blandula                   ATAAAAATTTCTCTATTTGATAATGCCTCCCCAATTATAGAACAATTAACTTTATTTCACGATTATACTA    [407]
Livilla_maura                      ATAAAAATTTCTTTATTTGATAATGCCTCTCCAATTATAGAACAATTAACTTTATTTCATGATTATACTA    [408]
Livilla_monospermae_T              ATAAAAATTTCACTCTCTGACAATGCTTCACCAATTATAGAACAATTAATTCTGTTTCACGACTACAGTA    [408]
Livilla_monospermae_G              ATAAAGATTTCACTCTCTGACAATGCTTCCCCAATTATAGAACAATTAATTCTGTTTCACGACTACAGTA    [408]
Livilla_monospermae_P              ATAAAAATTTCACTCTCTGACAACGCTTCTCCAATTATAGAACAATTAATTCTGTTTCATGACTACAGTA    [408]
Livilla_retamae                    ATAAAAATTTCACTCTCTGACAATGCTTCCCCAATTATAGAACAATTAATTCTGTTTCATGATTATAGTA    [407]
Livilla_variegata                  ATAAAAATTTCACTTTCTGATAACGCTTCTCCTATTATAGAACAATTAATTTTATTTCATGATTACACTA    [410]
Livilla_sp.15                      ATAAAAATCTCTTTTTTTGATAATGCTTCTCCGATTATAGAACAATTAATTTTATTTCACGATTATGGAA    [408]
Livilla_sp.16                      ATAAAAATTTCTCTTTATGATAATGCTTCTCCAATTATAGAACAGCTAATTTTATTTCATGATTATACCA    [407]
Livilla_sp.17                      AAAAAAATTTCACTTTTTGATAATGCTTCACCTATTATAGAACAATTAATTTTATTTCATGACTACAGTA    [407]
Pseudacanthopsylla_improvisa       CTAAAAATTTCTCTTTTTGATAATGCTTCTCCCATTATAGAACAGCTAATTTTATTTCATAATTACAGTA    [408]
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# APPENDIX 3 cont.

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[                                            430       440       450       460       470       480       490]
[                                              .         .         .         .         .         .         .]

Acizzia_hollisi                     TATTAATTATTACAACAATTTTATCAGTAGTTTCTTTTTTTATATTTAAAATAATATTTAATAAATTTCT   [476]
Acizzia_uncatoides                  TACTGATTATTTCTACAACTCTCTCAGTAGTGTCATTTTTTATATTTAAAATAATAATTAATAAATTTTT   [482]
Arytaina_adenocarpi_PO              TATTAATTATCTCAAGCATTCTCTCTATTGTTTCATTCTTTATAATAAAAATAATTATAAGAACCTTTAC   [477]
Arytaina_adenocarpi_SP              TATTAATTATCTCAAGCATTCTCTCTATTGTTTCATTCTTTATAATAAAAATAATTATAAGAACCTTTAC   [477]
Arytaina_adenocarpi_MO              TATTAATTATCTCAAGCATTCTCTCTATTGTTTCGTTCTTTATAGTAAAAATAATTATAAGAACCTTTAC   [477]
Arytaina_devia_T                    TATTAATTATTTCAAGCATTCTTTCTATTGTATCTTTTTTTATAATAAAAATAATTATAAGAAAATTCAC   [479]
Arytaina_devia_G                    TATTAATTATTTCAAGCATTCTTTCTATTGTATCTTTTTTTATAATAAAAATAATTATAAGAAAATTCAC   [479]
Arytaina_devia_ssp_insularis_C      TATTAATTATTACAAGTATTCTCTCTATTGTATCTTTTTTTATAATAAAAATAATTACAAGAAAATTCAC   [478]
Arytaina_devia_ssp_insularis_P      TATTAATTATTTCAAGCATTCTTTCTATTGTCTCTTTTTTTATAATAAAAATAATCACAAGAAAATTCAC   [480]
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Arytaina_genistae_PO                TATTAATTATTTCAAGTATTCTCTCTATTGTCTCCTTTTTCATATTAAAAATAATTACAATAAAATTTAC   [476]
Arytaina_genistae_MO                TATTAATTATTTCAAGTATTCTCTCCATTGTATCCTTTTTCATATTAAAAATAATTACAATAAAATTTAC   [476]
Arytaina_nubivaga                   TACTTATTATTTCAAGTATTCTTTCTATTGTATCTTTTTTTATAGTAAAAATAATTATAAATAAATTTAC   [477]
Arytaina_sp.14                      TACTTATTATTTCAAGTATTCTTTCTATTGTATCTTTTTTTATAGTAAAAATAATTATAAATAAATTTAC   [477]
Arytainilla_cognata                 TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTTATTATAATTAAAATAGCTTTAAACAAATACAC   [477]
Arytainilla_cytisi                  TATTGATTATTTCTAGTATTTTATCCATTGTATCTTTCTTCATAATTAAAATAATTTAAATAAATTTAC   [479]
Arytainilla_delarbrei               TAATAATTATTTTCAGTATTTTATCTATTGTATCTTTTTTTATAATCAAAATAATTTAAATAAATTTAC   [481]
Arytainilla_diluta_C                TACTCATTATTTCTAGTATTTTATCTATTGTATCTTTCATTATAGTTAAAATAATTTAAACAACTATAC   [477]
Arytainilla_diluta_T                TACTCATTATTTCTAGTATTTTATCTATTGTATCTTTCATTATAGTTAAAATAATTTAAACAATTATAC   [477]
Arytainilla_dividens_C              TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATTATAATTAAAATAATCTTAAACAACTTTAC   [477]
Arytainilla_dividens_T              TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATCATAATTAAAATAATCTTAAACAACTTTAC   [477]
Arytainilla_dividens_G              TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATCATAATTAAAATAATCTTAAACAACTTTAC   [477]
Arytainilla_equitans                TACTAATTATTTCTAGAATTTTATCCATTGTATCTTTCATTATAATTAAAATAGCTTTAAACAGCTACAT   [477]
Arytainilla_hakani                  TATTAATTATTTCTAGTATTTTATCCATTGTATCTTTCATTATAATTAAAATAACTTTAAACAACTACAC   [477]
Arytainilla_ima                     TATTAATTATTTCAAGAATTTTATCTATTGTATCTTTTACTATAATAAAAATAATTTAAACAAATTTAC   [477]
Arytainilla_incuba                  TATTAATTATTTCTAGTATTTTATCCATTGTATCTTTCATTATAATTAAAATAGCTTTAAACAACTACAC   [477]
Arytainilla_modica_Teline_P         TACTAATTATTTCTAGTATTTTATCTATTGTCTCTTTCATCATAATTAAAATAATTTCAAACAAATTTAC   [477]
Arytainilla_modica_Cham._P          TACTAATTATTTCTAGTATTTTATCTATTGTCTCTTTCATCATAATTAAAATAATTTCAAACAAATTTAC   [477]
Arytainilla_modica_Teline_H         TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATCATAATTAAAATAATTTCAAACAATTTTAC   [477]
Arytainilla_modica_Cham._H          TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATCATAATTAAAATAATTTCAAACAATTTTAC   [477]
Arytainilla_nigralineata_C          TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATTATAATTAAAATAATTTAAACAACTACAT   [477]
Arytainilla_nigralineata_T          TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATTATAATTAAAATAATTTAAACAACTACAT   [477]
Arytainilla_nigralineata_G          TACTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATTATAATTAAAATAATTTAAACAACTACAT   [477]
Arytainilla_pileolata_T.can         TATTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATTATAATTAAAATAACCCTAAATAACTACAT   [477]
Arytainilla_pileolata_T.osy         TATTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATTATAATTAAAATAACCCTAAATAACTACAT   [477]
Arytainilla_proboscidea_A.vis_T     TATTAATCATTTCCAGTATTTTATCTATTGTATCTTTTATTATAATTAAGATAATTATAAACAACTACAC   [477]
Arytainilla_proboscidea_A.fol_P     TATTAATCATTTCCAGTATTTTATCTATTGTGTCTTTTATTATAATTAAGATAATTATAAACAACTACAC   [477]
Arytainilla_prognata                TACTCATTATTTCTAGAATCTTATCTATTGTATCTTTCATTATAATTAAAATAATTTTAAACAGTTACAC   [478]
Arytainilla_spartiophila_PO         TATTAATTATTTTTAGCATTTTATCTATTGTATCTTTTTTTATAATCAAAATAATTTAAATAAATTTAC   [475]
Arytainilla_spartiophila_SP         TATTAATTATTTTTAGCATTTTATCTATTGTATCTTTTTTTATAATCAAAATAATTTAAATAAACTTAC   [475]
Arytainilla_spartiophila_MO         TATTAATTATTTTTAGCATTTTATCTATTGTATCTTTTTTTATAATCAAAATAATTTAAATAAATTTAC   [475]
Arytainilla_sulci                   TACTTATTATTTTTACCATTCTCTCTATTGTAACTTTTTTTATAATAAAAATAATAACAAACAAATTTAC   [477]
Arytainilla_umbonata                TATTGATTATTTCTAGTATTTTATCCATTGTATCTTTCATTATAATTAAAATAGCTTTAAACAATTACAC   [477]
Arytainilla_sp.1                    TACTAATCATTTCTAGAATTATATCTATTGTATCTTTCTTTATAATTAAAATAATTTTTAATAAATTTAC   [479]
Arytainilla_sp.2                    TATTAATTATTTCTAATATTTTATCTATTGTATCTTTTTTTATAATCAAAATAATTTTGAACAAATTCAT   [478]
Arytainilla_sp.3                    TACTTATTATTTCTAGTATTTTATCTATTGTATCTTTTTTTATAATCAAAATAATTTAAATAAATTTAC   [479]
Arytainilla_sp.4_SP                 TATTAATTATCTCCAGAATTTTATCCATTGTATCTTTTTTTATAATTAAAATAATCCAAAACAAATTTAT   [479]
Arytainilla_sp.4_MO                 TACTAATTATCTCCAGAATTTTATCTATTGTATCTTTTTTTATAATTAAAATAATCCAAAACAAATTTAT   [479]
Arytainilla_sp.5                    TACTCATTATTACTAGAATTTTATCTATTGTATCTTTCATTATAACTAAAATAGCTTTAAACAATTTCAC   [477]
Arytainilla_sp.6                    TATTAATTATTTCTAGTATTTTATCTATTGTATCTTTTATTATAATTAAAATAATTTAAACAACTACAC   [477]
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Arytainilla_sp.8                    TATTAATTATTTCTAGTATTTTATCTATTGTATCTTTCATCATAATTAAAATAATCTTAAACAACTTCAC   [477]
Arytainilla_sp.9                    TACTAATTATCTCTAGTATTCTATCTATTGTATCTTTTATTATAATTAAAATAATTTAAACAACTTCAC   [477]
Arytainilla_sp.10_P                 TACTAATTATTTCTAGTATTTTATCCATTGTATCTTTCATTATAATTAAAATAGCCTTAAACAACTACAC   [479]
Arytainilla_sp.10_H                 TATTAATTATTTCTAGTATTTTATCCATTGTATCTTTCATTATAATTAAAATAGCTTTAAACAACTACAC   [479]
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Arytainilla_sp.13                   TACTAATTATTTCGAGTATTTTATCTATTGTATCTTTTATTATAATTAAAATAACTTTAAACAAATACAC   [477]
Cacopsylla_alaterni                 TACTTATTATTGTTACTATTTTATCAATTGTTTCTTTCTTTATAATTAAAATAATAATAAACAAATTTGT   [476]
Cacopsylla_mali                     TACTAATTATTGTCAGTATCTTATCAATTGTCTCTTTTTTTATAATTAAAATAATAATAAATAAATTTAT   [480]
Cyamophila_prohaskai                TATTAATTATTATAAGAATTCTTTCCATTGTATCCTTTTTTATAATTAAAATAATAAGAAATAAGTTTCT   [477]
Livilla_adusta                      TGTTAATTATTTGTACAATTTTATCTGTCGTTTCTTTCATCATAATAAAAATAATTCATAATAATTTTCT   [479]
Livilla_blandula                    TACTAATTATTTGCAGAATTCTTTCTGTTGTATCTTTTATTATAGTAAAAATAATTTTTAACAACTTCCT   [477]
Livilla_maura                       TACTAATTATTTGCAGAATCCTTTCTGTTGTCTCTTTCATTATAGTAAAAATAATTTTTAACAACTTCCT   [478]
Livilla_monospermae_T               TATTAATTATTACAAGAATTCTTTCTATTGTTTCTTTTTTCATAATTAAAATAATGTTTAACACCTTTAT   [478]
Livilla_monospermae_G               TATTAATCATTACCAGAATTCTTTCTATTGTTTCTTTTTTCATAGTTAAAATAATGTTTAGCACTTTTAT   [478]
Livilla_monospermae_P               TATTAATTATTACCAGAATTCTTTCTATTGTTTCTTTTTTCATAATTAAAATAATGTTTAGTACCTTTAT   [478]
Livilla_retamae                     TACTAATTATTTCAAGAATTCTTTCTATCGTCTCTTTTTTCATAATTAAAATAATCTTAAACACCTTTAT   [477]
Livilla_variegata                   TATTAATTATTTGCACAATTTTATCCGTAGTTTCTTCATTATAATAAAAATAATTTATAATAATCTTAT   [480]
Livilla_sp.15                       TATTAATTATTTCAAGAATTTTATCTATTGTATCTTTTACTATACTAAAAATAATTTTAAACAAATTTAC   [478]
Livilla_sp.16                       TAGTAGTTATTTCAAGAATTTTATCTATTGTATCTTTTACTATATTAAAAATAATCTTAAACAAATTTAC   [477]
Livilla_sp.17                       TACTTATTATTTCTAGAATTTTATCTATTGTATCTTTCATTATAATTAAAATAATTTAAATAAATTTAC   [477]
Pseudacanthopsylla_improvisa        TATTAATCATTGTTAGAGTAATATCTATCATTTCATTTTTTATAATTAAAATAATGATAAATAAATTTAT   [478]
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## APPENDIX 3 cont.

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[                                           500       510       520       530       540       550       560]
[                                           .         .         .         .         .         .         .]

Acizzia_hollisi                    CTCAAGAAGAATTCTCGAAAATCAAGTAATTGAAGTAATTTGAACTATAATCCCAACTCTAATTTTAAGA  [546]
Acizzia_uncatoides                 ATCAAGAAGAATCTTGGAAAACCAATTAATTGAAGTAATTTGAACCCTCATTCCTACTATTATCTTAAGA  [552]
Arytaina_adenocarpi_PO             TAGAAGTAAACTTCTTGAAAACCAATTAATTGAACTTGTATGAACATTAATTCCCACAATTATTTTAAGA  [547]
Arytaina_adenocarpi_SP             TAGAAGTAAACTTCTTGAAAACCAATTAATTGAACTTGTATGAACATTAATTCCCACAATTATTTTAAGA  [547]
Arytaina_adenocarpi_MO             CAGAAGTAAACTTCTTGAAAACCAATTAATTGAACTTGTATGAACCTTAATTCCCACAGTTATTTTAAGA  [547]
Arytaina_devia_T                   TAGAATAAAAATTCTAGAAAACCAATTAATTGAACTTGTATGAACTTTAATTCCTACAATTATTTTAAGA  [549]
Arytaina_devia_G                   TAGAATAAAAATTCTAGAAAACCAATTAATTGAACTTGTATGAACTTTAATTCCTACAATTATTTTAAGA  [549]
Arytaina_devia_ssp_insularis_C     TAGAATGAAAATTCTTGAAAATCAATTACTTGAACTTGTATGAACTTTAATTCCTACAGTTATTTTAAGA  [548]
Arytaina_devia_ssp_insularis_P     TAGAATAAAAATTCTTGAAAATCAGTTAATTGAACTTGTATGAACTTTAATTCCTACAATTATTTTAAGT  [550]
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Arytaina_genistae_PO               AAGAAGAAAAATTCTTGAAAATCAATTAATTGAAATTGTATGAACCCTAATTCCCACATTTATCTTAAGA  [546]
Arytaina_genistae_MO               AAGAAGAAAAATTCTTGAAAATCAATTAATTGAAATTGTGTGAACCTTAATTCCCACATTTATCTTAAGA  [546]
Arytaina_nubivaga                  CAGAAGAAAAATTCTTGAAAATCAACTTATTGAACTTGTATGAACACTAATTCCTACAATTATTTTAAGA  [547]
Arytaina_sp.14                     CAGAAGAAAAATTCTCGAAAATCAACTTATTGAACTTGTATGAACACTAATTCCAACAATTATTTTAAGA  [547]
Arytainilla_cognata                TAGCACAAAAATCCTTGAAAATCAAATAGTTGAACTTGTGTGAACTTTAATTCCCACAATTATTCTAAGA  [547]
Arytainilla_cytisi                 TAGAAGAAAAATTCTTGAAAATCAAATAATTGAACTTACATGAACACTTATTCCAACAGTTATTCTTAGT  [549]
Arytainilla_delarbrei              TAGAAATAACATTCTTGAGAATCAAATAATTGAACTCATATGAACACTTATTCCAACCATTATTCTTAGT  [551]
Arytainilla_diluta_C               TAGCACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTGTGAACCTTAATTCCCACAATTATTCTTAGA  [547]
Arytainilla_diluta_T               TAGCACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTGTGAACTTTAATTCCCACAATTATTCTTAGA  [547]
Arytainilla_dividens_C             TAGTACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTGTGAACCCTAATCCCCACAATTGTTCTGAGA  [547]
Arytainilla_dividens_T             TAGTACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTATGAACCCTAATCCCCACAATTGTTCTGAGA  [547]
Arytainilla_dividens_G             TAGTACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTATGAACCCTAANCCCCACAATTGTTCTGAGA  [547]
Arytainilla_equitans               TAGAACAAAAATTCTTGAAAATCAAATAGTTGAACTAGTATGAACATTGATCCCAACAATCATTCTTAGA  [547]
Arytainilla_hakani                 TAGAACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTATGAACTTTAATTCCCACAATTATTCTTAGA  [547]
Arytainilla_ima                    CAGAACAAAAATTCTTGAAAATCAAATAATTGAACTTGCATGAACCCTTATTCCTACTATTATTCTCAGA  [547]
Arytainilla_incuba                 TAGAACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTATGAACTTTAATTCCCACAATTATTCTTAGA  [547]
Arytainilla_modica_Teline_P        TAGTACAAAAATTCTTGAAAATCAAATAGTAGAACTTGTATGAACCTTAATCCCCACGATTGTTCTGAGA  [547]
Arytainilla_modica_Cham._P         TAGTACAAAAATTCTTGAAAATCAAATAGTAGAACTTGTATGAACCTTAATCCCCACGATTGTTCTGAGA  [547]
Arytainilla_modica_Teline_H        TAGTACAAAAATTCTTGAAAATCAAATAGTAGAACTTGTATGAACCTTAATCCCCACGATTGTTCTGAGA  [547]
Arytainilla_modica_Cham._H         TAGTACAAAAATTCTTGAAAATCAAATAGTAGAACTTGTATGAACCTTAATCCCCACAATTGTTCTGAGA  [547]
Arytainilla_nigralineata_C         TAGAACAAAAATTCTTGAAAATCAAATAATTGAACTTGTGTGAACTTTAATCCCAACAATTATTCTTAGA  [547]
Arytainilla_nigralineata_T         TAGAACAAAAATTCTTGAAAATCAAATAATTGAACTTGTGTGAACTTTAATCCCAACAATTATTCTTAGA  [547]
Arytainilla_nigralineata_G         TAGAACAAAAATTCTTGAAAATCAAATAATTGAACTTGTGTGAACTTTAATCCCAACAATTATTCTTAGA  [547]
Arytainilla_pileolata_T.can        TAGTACAAAAATTCTTGAAAATCAAATAGTTGAACTAGTTTGAACTCTAATCCCCACAATCATTCTTAGA  [547]
Arytainilla_pileolata_T.osy        TAGTACAAAAATTCTTGAAAATCAAATAGTTGAACTAGTTTGAACTCTAATCCCCACAATCATTCTTAGA  [547]
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Arytainilla_spartiophila_SP        TAGAACAAAAATCCTTGAAAATCAAACAATTGAACTTGTATGAACCTTTATCCCAACTATTATTCTTAGT  [545]
Arytainilla_spartiophila_MO        TAGAACAAAAATCCTTGAAAATCAAACAATTGAACTTGTATGAACCTTTATCCCAACTATTATTCTTAGT  [545]
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Arytainilla_umbonata               TAGAACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTATGAACTTTAATTCCCACAATTATTCTTAGA  [547]
Arytainilla_sp.1                   TAGAAACAAAATTCTTGAAAATCAAATAATTGAAATCGTATGAACCTTAATTCCAACTATTGTTCTTAGT  [549]
Arytainilla_sp.2                   TAGAAGAAAAATTCTTGAAAATCAAACAATTGAACTTTTATGAACATTAATTCCAACCGTTATTCTTAGT  [548]
Arytainilla_sp.3                   AAGAAGAAAAATTCTTGAAAATCAAGTAATTGAACTTACATGAACGCTTATTCCAACAGTTATACTTAGT  [549]
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Arytainilla_sp.4_MO                TAGAAAAAAAATTCTTGAAAATCAAATAATTGAATTAGTGTGAACCTTAATTCCTACTATTATTCTTAGA  [549]
Arytainilla_sp.5                   TAGTACAAAAATTCTTGAAAATCAAATAGTTGAACTCGTTTGAACTTTAATCCCTACTATTATCCTTAGA  [547]
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Arytainilla_sp.7                   TAGTACAAAAATTCTTGAAAATCAAATAGTTGAACTAGTATGAACTTTAATTCCCACAATCATTCTTAGA  [547]
Arytainilla_sp.8                   TAGCACAAAAATTCTTGAAAATCAAATAATTGAACTTGTATGAACTTTAATCCCCACAATCATTTTGAGA  [547]
Arytainilla_sp.9                   TAGCACAAAAATTCTTGAAAATCAAATAGTTGAACTTGTATGAACCTTAATCCCCACAGTTACTCTAAGA  [547]
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Arytainilla_sp.12                  TAGTACAAAAATTCTTGAAAATCAAATAGTAGAACTTGTATGAACCTTAATCCCCACGATTGTTCTGAGA  [547]
Arytainilla_sp.13                  TAGCACAAAAATCCTTGAAAACCAAATAGTTGAACTTGTATGAACTTTAGTTCCCACAATTATTCTTAGA  [547]
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Cacopsylla_mali                    TTCAAGAAAAATCCTTGAAAATCAAATAATTGAACTAGTATGAACTTTGATCCCTACAATCATCCTTAGA  [550]
Cyamophila_prohaskai               TTCAAGAAAAATTCTTGAAAATCAAATAATTGAATTAATTTGAACATTAATCCCCACAATTATTCTTAGA  [547]
Livilla_adusta                     TAGAACTAAAATTCTTGAAAATCAAATAGTTGAATTAGTATGAACTATAATTCCCACAATTATTCTAACA  [549]
Livilla_blandula                   TAGAACTAAAATTCTTGAAAATCAATTAGTTGAACTCATTTGAACTCTCATTCCTACAATTATTCTTACA  [547]
Livilla_maura                      TAGAACTAAAATTCTTGAAAATCAATTAGTTGAACTCATCTGAACTCTCATTCCTACAATTATTCTTACA  [548]
Livilla_monospermae_T              TAGAACAAAAATTCTTGAAAATCAAATAGTTGAACTCGTATGAACCCTTATTCCTACAATTATTCTTAGC  [548]
Livilla_monospermae_G              TAGAACAAAAATTATTGAAAATCAAATAGTTGAACTTGTATGAACCCTAATTCCTACAATCATTCTTAGC  [548]
Livilla_monospermae_P              TAGAACAAAAATTATTGAAAATCAAATAATTGAACTCGTATGAACCCTCATTCCTACAATCATTCTTAGC  [548]
Livilla_retamae                    TAGAACAAAAATTCTTGAAAATCAAATAATTGAACTTGTATGAACACTAATTCCTACAGTTATTCTTAGA  [547]
Livilla_variegata                  TAGAACTAAAATTCTTGAAAATCAAATAGTAGAACTTGTATGGACTCTAATTCCTACAATTATTCTCACA  [550]
Livilla_sp.15                      TAGAACTAAAATTCTTGAAAATCAAATAATTGAACTTATATGAACTCTCATTCCTACAATTATTCTTAGA  [548]
Livilla_sp.16                      TAGAACAAAAATTATTGAAAATCAAATAATTGAATTGATATGAACTCTTATTCCTACAATTATTCTTAGA  [547]
Livilla_sp.17                      TAGAAAAAAAATTCTAGAAAACCAAATAATTGAACTTATTTGAACTTTAATCCCTACAATTATTCTTAGA  [547]
Pseudacanthopsylla_improvisa       TAGAACAAAAATTTTAGAAAATCAAATAATTGAAATTATTTGAACTCTAGTTCCCACACTTATTCTAAGA  [548]
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## APPENDIX 3 cont.

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[                                            570       580       590       600       610       620       630]
[                                              .         .         .         .         .         .         .]

Acizzia_hollisi                           ATTATTGCCCTTCCGTCTCTTCATTTGCTATACTTAATAGATGAACTACTAAATCCTTTATTAACAATTA   [616]
Acizzia_uncatoides                        ATTATTGCACTGCCTTCCCTGCACTTACTCTATTTGATAGATGAGCTGCTCAATCCCATTTTAACTGTAA   [622]
Arytaina_adenocarpi_PO                    TTTATTGCTCTCCCATCCCTTCATCTTCTTTATTTAATAGATGAATTAAACAATCCCCTATTAACAATCA   [617]
Arytaina_adenocarpi_SP                    TTTATTGCTCTCCCATCCCTTCATCTTCTTTATTTAATAGATGAATTAAACAATCCCCTATTAACAATCA   [617]
Arytaina_adenocarpi_MO                    TTTATTGCTCTCCCATCCCTTCATCTTCTTTATTTAATAGATGAGTTAAACAATCCCCTATTAACAATCA   [617]
Arytaina_devia_T                          TTTATTGCTCTCCCCTCTCTTCATCTTCTTTATTTAATAGATGAATTAAATAATCCGTTATTAACAAGTA   [619]
Arytaina_devia_G                          TTTATTGCWCWCCCCACACTWCAACTACTTTATTTAATAGATGAATTAAATAAACCGTTATTAACAATTA   [619]
Arytaina_devia_ssp_insularis_C            TTTATTGCACTTCCTTCCCTTCAACTTCTTTACTTAATAGATGAACTAAATAAWCCGCTACTAACAATTA   [618]
Arytaina_devia_ssp_insularis_P            TTTATTGCCCTCCCTTCTCTTCACCTCCTTTACTTGATAGATGAATTAAATAATCCACTATTAACAATTA   [620]
Arytaina_genistae_SC                      TTTATTGCACTGCCTTCWCTTCAACTWCTGTACCTAATAGATGAACTAAATAACCCATTATTAACAATTA   [616]
Arytaina_genistae_PO                      TTTATTGCACTGCCTTCTCTTCATCTTCTGTACCTAATAGATGAACTAAATAACCCATTATTAACAATTA   [616]
Arytaina_genistae_MO                      TTTATTGCACTACCTTCTCTTCATCTTCTATACTTAATAGATGAACTAAATAACCCATTACTAACAATTA   [616]
Arytaina_nubivaga                         TTTATTGCACTTCCCTCCCTTCATCTTCTTTATTTAATAGACGAACTTAATAAC????????????????   [617]
Arytaina_sp.14                            TTTATTGCACTTCCCTCCCTTCATCTTCTTTATTTAATAGACGAACTTAATAACCCACTAC?????????   [617]
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Arytainilla_cytisi                        TTTATTGCACTCCCTTCACTTCATTTACTCTATCTTATAGATGAATTAAATAACCCCCTTTTAACAATTA   [619]
Arytainilla_delarbrei                     TTTATCGCTTTACCTTCTCTTCATATTCTTTATCTTATA???????????????????????????????   [621]
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Arytainilla_diluta_T                      TTCATTGCTCTACCATCACTTCACCTTTTATACCTTATA???????????????????????????????   [617]
Arytainilla_dividens_C                    TTTATTGCCCTACCGTCACTTCACCTTCTATATTTAATA???????????????????????????????   [617]
Arytainilla_dividens_T                    TTTATTGCCCTACCATCACTCCTTCTTCTATATTTAATA???????????????????????????????   [617]
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## APPENDIX 3 cont.

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Arytaina_devia_G                   AAATTATTG   [628]
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Arytainilla_pileolata_T.can        ?????????   [626]
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Arytainilla_spartiophila_MO        ?????????   [624]
Arytainilla_sulci                  AAATTATTG   [626]
Arytainilla_umbonata               AAGTAATCG   [626]
Arytainilla_sp.1                   AAATCATTG   [628]
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Arytainilla_sp.10_H                ?????????   [628]
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Arytainilla_sp.12                  ?????????   [626]
Arytainilla_sp.13                  AAGTAATCG   [626]
Cacopsylla_alaterni                AAATTATTG   [625]
Cacopsylla_mali                    WAWTTTTCS   [629]
Cyamophila_prohaskai               AAATTATTG   [626]
Livilla_adusta                     ?????????   [628]
Livilla_blandula                   AGATTATTG   [626]
Livilla_maura                      AAATTATTG   [627]
Livilla_monospermae_T              AAATTATCG   [627]
Livilla_monospermae_G              AAATTATCG   [627]
Livilla_monospermae_P              ?????????   [627]
Livilla_retamae                    AAATTATCG   [626]
Livilla_variegata                  AAATTATTG   [629]
Livilla_sp.15                      AAATTAT??   [627]
Livilla_sp.16                      AAATCATTG   [626]
Livilla_sp.17                      AAATTATTG   [626]
Pseudacanthopsylla_improvisa       ?????????   [627]
```

**APPENDIX 4.** *List of 67 morphological characters and chararcter states.*

**Adult**

1. *Forewing shape*: **(0)** widest in the apical third with a broadly rounded apex; **(1)** widest in the middle third with more acutely rounded apex; **(2)** margins more or less parallel, apex broadly rounded or more acute.
2. *Forewing costal break*: **(0)** absent; **(1)** present.
3. *Forewing pterostigma*: **(0)** absent; **(1)** present.
4. *Forewing vein pigmentation*: **(0)** uniformly coloured; **(1)** with distinct light and dark banding; **(2)** with dark patches at the terminal apices.
5. *Termination of vein Rs at the forewing apex*: **(0)** strongly curved towards the wing margin; **(1)** not, or only weakly curved towards the wing margin.
6. *Surface forewing spinules density*: **(0)** sparse: less than 40 per 0.1 $mm^2$; **(1)** medium density: 40-60 per 0.1 $mm^2$; **(2)** dense: 60-100 per 0.1 $mm^2$; **(3)** very dense: more than 100 per 0.1 $mm^2$.
7. *Shape of hindwing costal margin*: **(0)** straight; **(1)** slightly concave; **(2)** markedly concave.
8. *Genal cones position*: **(0)** commencing dorsally from more or less the same level as the vertex; **(1)** commencing ventrally relative to the vertex, with a distinct depression between the vertex and the genal cones.
9. *Genal cones terminal setae length*: **(0)** as long as, or typically longer than the vertex; **(1)** typically shorter than the vertex, occasionally as long.
10. *Genal cones terminal setae colour*: **(0)** darkly pigmented; **(1)** not darkly pigmented.
11. *Metatarsal spur*: **(0)** absent; **(1)** one; **(2)** two.
12. *Male paramere shape*: **(0)** with an apically thin neck above a medially positioned blade or ridge produced on the external side and directed anteriorly; **(1)** apically thin neck typically absent or very short, without a medial blade but with a terminal ridge or blade present laterally exterior to the apex; **(2)** broad and parallel sided, lacking medial or apical blade; **(3)** slender, often simple with sides parrallel or tapering towards the apex, lacking medial or apical blade.
13. *Male paramere sclerotized apex in lateral view*: **(0)** rounded with small or more pronounced, anteriorly or interiorly directed hook; **(1)** flattened or more or less so, with slight or more pronounced anterior projection; **(2)** either flattened or with a well rounded bulge, and with slight anterior and posterior projections; **(3)** small, not hooked but sometimes with small anterior projection, and displaced either to the interior or posterior of

the top of the paramere.

14. *Male paramere sclerotized apex in dorsal view*: **(0)** contiguous anteriorly; **(1)** contiguous more or less along entire inner margin; **(2)** contiguous posteriorly.
15. *Male paramere sclerotized apex inner surface in dorsal view*: **(0)** straight edged; **(1)** concave; **(2)** rounded with an acute point.
16. *Male proctiger apex*: **(0)** with pronounced posterior extension apically; **(1)** without pronounced posterior extension apically.
17. *Male aedeagus distal segment apex*: **(0)** with a well developed, curved hook; **(1)** with a somewhat flattened, shallow hook; **(2)** not developed into a hook.
18. *Tip of male aedeagus hook*: **(0)** turning upwards; **(1)** not turning upwards.
19. *Male subgenital plate dorsal profile*: **(0)** more or less straight and horizontal; **(1)** raised anteriorly, either with or without a distinct step.
20. *Male subgenital plate dorsal posterior margin*: **(0)** with a pair of long (more than half the length of the paramere) stout setae; **(1)** without a pair of long stout setae.
21. *Female proctiger dorsal profile*: **(0)** more or less straight from anus to apex; **(1)** with a post anal depression, and subsequently more or less straight, or slightly concave or convex; **(2)** without a post anal depression, and concave with an upturned apex.
22. *Female proctiger apex*: **(0)** squarely truncated; **(1)** bluntly rounded; **(2)** acute.
23. *Female subgenital plate ventral profile*: **(0)** shallowly curved, without medial bulge but sometimes angled medially; **(1)** slight, or more pronounced medial bulge; **(2)** deeply curved, without medial bulge.
24. *Female ovipositor*: **(0)** valvulae ventralis slender, height of valvulae dorsalis typically as great or greater than valvulae ventralis; **(1)** valvulae ventralis robust, height of valvulae dorsalis less than valvulae ventralis.
25. *Female ovipositor valvulae dorsalis shape*: **(0)** dorsally convex, wedge-shaped and tapering to the apex; **(1)** dorsally concave, and distinctly inflated anteriorly; **(2)** more or less straight, with or without dorsal tooth-like processes; **(3)** triangular, tapering both to the apex and anteriorly.
26. *Female ovipositor valvulae ventralis apex*: **(0)** rounded, often acutely so, lacking any serration; **(1)** rounded with minute serrations that extend along the ventral margin; **(2)** stepped with square tip; **(3)** rounded with two small ventral processes near the tip.
27. *Forewing pterostigma length*: **(0)** short, less than one 20th the wing length (ratio wing length:pterostigma length equal to or more than 20); **(1)** medium, less than one quarter of

the wing length (ratio wing length:pterostigma length 4.5-20); **(2)** long, about one quarter of the wing length (ratio wing length:pterostigma length equal to or less than 4.5).

28. *Genal cone length*: **(0)** short to very short, 0.15 mm or less (up to half the length of the vertex); **(1)** long, 0.15 - 0.3 mm (roughly the same length as the vertex); **(2)** very long, more than 0.3 mm (about 1.5 times the length of the vertex).
29. *Antennal length*: **(0)** very short, less than 1 mm; **(1)** short, 1 to 1.5 mm; **(2)** medium, 1.5 - 2 mm; **(3)** long, more than 2 mm.
30. *Distal proboscis segment length*: **(0)** up to 0.14 mm; **(1)** 0.14 to 0.2 mm; **(2)** 0.2 to 0.3 mm; **(3)** 0.3 mm or more.
31. *Ratio forewing length to width*: **(0)** less than 2.2; **(1)** 2.2-2.6; **(2)** greater than 2.6.
32. *Ratio hind leg tibia length to femur length*: **(0)** up to 1; **(1)** 1 to 1.26; **(2)** 1.26 or more.
33. *Ratio hind leg apical tarsus to tibia length*: **(0)** up to 0.22; **(1)** 0.22 to 0.33; **(2)** 0.33 or more.
34. *Male proctiger length*: **(0)** 0.3 mm or less; **(1)** 0.3-0.4 mm; **(2)** 0.4-0.5 mm; **(3)** 0.5 mm or greater.
35. *Male paramere length*: **(0)** very short, less than 0.25 mm; **(1)** short, 0.25 to 0.4 mm; **(2)** mid-length, greater than 0.4 but less than 0.55 mm; **(3)** long, greater than 0.55 mm.
36. *Male aedeagus length*: **(0)** up to 0.26 mm; **(1)** 0.26 to 0.37 mm; **(2)** 0.37 to 0.47 mm; **(3)** 0.47 mm or more.
37. *Male aedeagus hook*: **(0)** small, 0.08 mm or less; **(1)** medium, 0.08-0.13 mm; **(2)** large, greater than 0.13 mm.
38. *Ratio male subgenital plate length to height*: **(0)** up to 1.3; **(1)** 1.3 to 1.55; **(2)** 1.55 or more.
39. *Ratio male paramere length to subgenital plate height*: **(0)** 1 or less; **(1)** 1 to 1.4; **(2)** 1.4 or greater.
40. *Female proctiger length*: **(0)** less than 0.5 mm; **(1)** 0.5 to 0.85 mm; **(2)** 0.85 to 1 mm; **(3)** 1 mm or greater.
41. *Female subgenital plate length*: **(0)** less than 0.35 mm; **(1)** 0.35 to 0.7 mm; **(2)** greater than 0.7 mm.
42. *Female ventral ovipositor valve length*: **(0)** up to 0.2 mm; **(1)** 0.2 to 0.35 mm; **(2)** 0.35 mm or more.
43. *Ratio female proctiger length to circumanal ring length*: **(0)** 4 or less; **(1)** greater than 4.

**5th instar nymph**

44. *Forewing pad and abdomen apically*: **(0)** acute; **(1)** broadly rounded.

45. *Antennal segments*: **(0)** seven; **(1)** eight; **(2)** nine.

46. *Circumanal ring shape*: **(0)** broadly crescent-shaped with well rounded anterior lobes; **(1)** narrowly crescent-shaped with well rounded anterior lobes, but with lateral margins either straight or slightly concave; **(2)** narrowly crescent-shaped with acutely rounded anterior lobes.

47. *Body length*: **(0)** up to 2 mm; **(1)** 2 mm or more.

48. *Antennal length*: **(0)** up to 0.63 mm; **(1)** 0.63 to 0.88 mm; **(2)** 0.88 to 1.18 mm; **(3)** 1.18 mm or more.

49. *Ratio forewing pad length to head width*: **(0)** 1 or less; **(1)** greater than 1.

50. *Ratio caudal plate width to length*: **(0)** less than 1.2; **(1)** greater than 1.2.

51. *Ratio caudal plate width to circumanal ring width*: **(0)** up to 4; **(1)** 4 to 5; **(2)** 5 or more.

52. *Head setae*: **(0)** simple, occasionally narrowly capitate; **(1)** simple and distinctly capitate; **(2)** simple and club-shaped; **(3)** simple and sectasetae.

53. *Antennal setae*: **(0)** simple; **(1)** simple and capitate; **(2)** simple and club-shaped; **(3)** sectasetae.

54. *Ocular seta*: **(0)** absent; **(1)** simple, or narrowly capitate or rod; **(2)** distinctly capitate; **(3)** sectasetae.

55. *Secondary post-ocular seta*: **(0)** absent or indistinct; **(1)** prominent, simple, sometimes narrowly capitate; **(2)** prominent, distinctly capitate, occasionally narrow.

56. *Dorsal thoracic setae*: **(0)** simple only; **(1)** capitate present; **(2)** club setae; **(3)** sectasetae.

57. *Dorsal prominent pre-caudal setae placement*: **(0)** absent or indistinct; **(1)** prominent, on anterior tergites; **(2)** prominent, on posterior tergites; **(3)** prominent, on all tergites.

58. *Forewing pad setae*: **(0)** simple only; **(1)** capitate only; **(2)** simple and capitate; **(3)** club-shaped; **(4)** sectasetae.

59. *Forewing pad prominent setae*: **(0)** marginal; **(1)** surface and marginal.

60. *Forewing pad prominent setae*: **(0)** one; **(1)** two; **(2)** more than two.

61. *Abdominal sectasetae*: **(0)** absent; **(1)** present.

62. *Abdominal sectasetae*: **(0)** one pair; **(1)** two pairs; **(2)** three pairs; **(3)** four pairs; **(4)** more than four pairs.

63. *Marginal abdominal setae (other than sectasetae)*: **(0)** absent; **(1)** one pair; **(2)** two pairs; **(3)** three or four pairs; **(4)** more than four pairs.

64. *Leg setal type*: **(0)** simple setae only; **(1)** capitate setae present; **(2)** club-shaped setae present; **(3)** sectasetae present.

65. *Foreleg tibia number of distinct setal type*: **(0)** one; **(1)** two; **(2)** more than two.

66. *Middle leg tibia number of distinct setal type*: **(0)** one; **(1)** two; **(2)** more than two.

67. *Hind leg tibia number of distinct setal type*: **(0)** one; **(1)** two; **(2)** more than two.

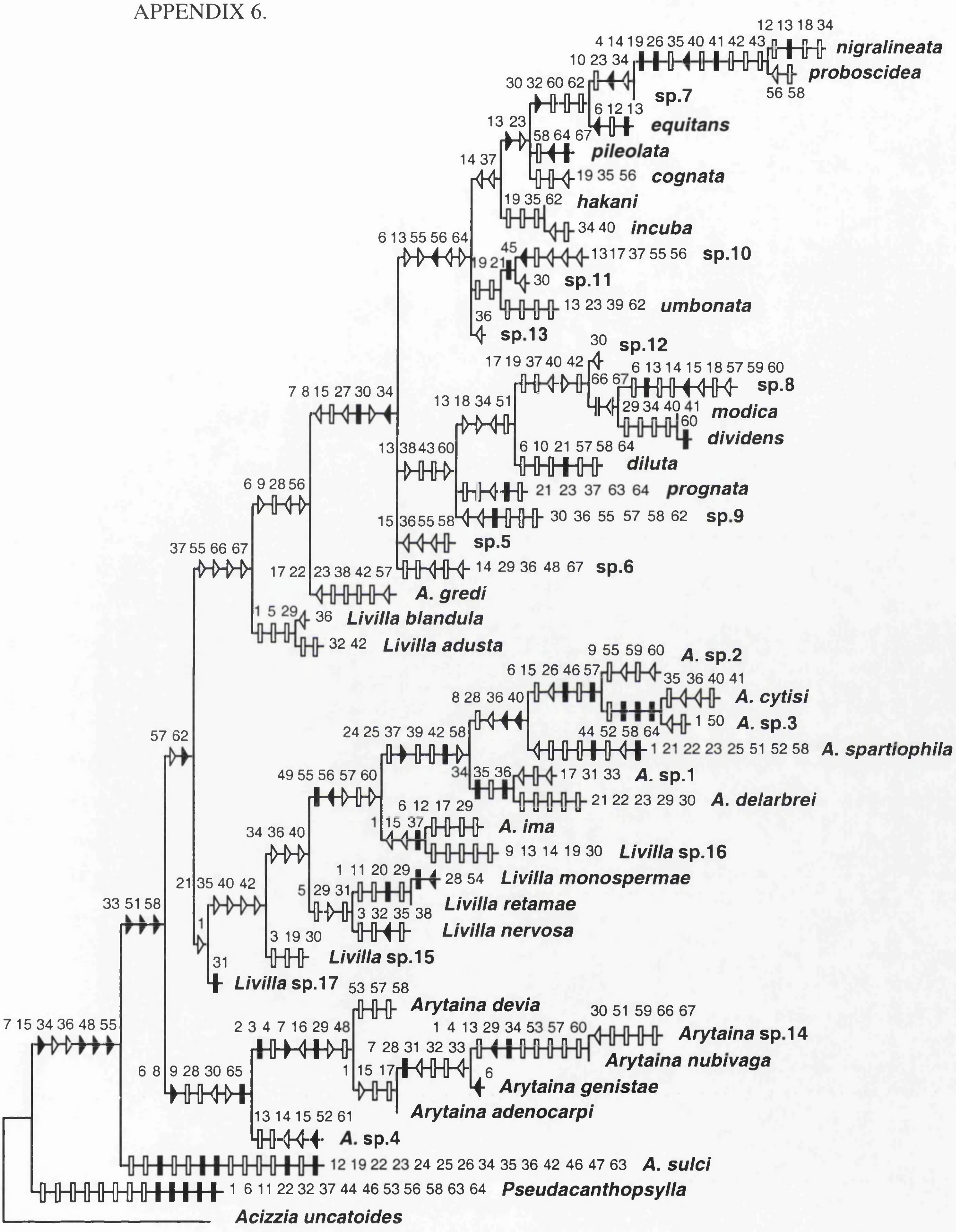
Opposite page:

## APPENDIX 5.

*Matrix of 67 morphological characters and character states.*
*Inapplicable or missing characters are indicated by '-' and '?' respectively.*

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acizzia uncatoides* | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 3 | 2 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 2 | 0 | 1 | 3 | 1 | 1 | 2 | 0 | - | 3 | 1 | 2 | 2 | 2 |
| *Arytaina adenocarpi* | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | - | 0 | 1/2 | 1 | 1 | 1 | 1 | 1/2 | 1 | 0/1 | 0 | 0/1 | 1 | 1/2 | 1 | 0/1 | 0 | 1 | 0 | 0 | 0/1 | 1/2 | 0 | 1 | 0/1 | 0 | 1 | 1 | 2 | 0/1 | 3 | 2 | 1 | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 |
| *Arytaina devia* | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | - | 0 | 2 | 1/2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0/1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0/1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 0/1 | 0 | 3 | 1 | 1 | 2 | 2 |
| *Arytaina genistae* | 1 | 0 | 0 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | - | 1 | 2 | 1 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0/1 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 1/2 | 0 | 3 | 2 | 1 | 2 | 0/1 | 0/1 | 3 | 1 | 1/2 | 2 | 2 |
| *Arytaina nubivaga* | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0/1 | 1 | 1 | 1 | 3 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | - | 1 | 3 | 1 | 2 | 0 | 2 | 2/3 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2/3 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 0/1 | 1 | 1 | 3 | 1 | - | 2 | 2 |
| *Arytaina* sp.14 | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0/1 | 1 | 1 | 1 | 3 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | - | 1 | 3 | 0 | 2 | 0 | 2 | 2 | 1 | 1 | 1 | 0/1 | 0/1 | 2/3 | 1 | 1 | 0 | 1 | 0 | 0 | 0/1 | 2/3 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 3 | 1 | - | 0 | 0 |
| *Arytainilla cognata* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0/1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 3 | 3 | 0 | - | - | - |
| *Arytainilla cytisi* | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 3 | 2 | 0 | 0 | 2 | 3 | 2 | 2 | 1 | 0 | 0 | 2 | 0/1 | 1 | 1 | 1 | 1/2 | 2 | 2 | 1 | 0 | 2 | 3 | 3 | 0 | 0 | 1 | 3 | 3 | 2 | 2 | 2 | 2 |
| *Arytainilla delarbrei* | 1 | 1 | 1 | 0 | 1 | 1/2 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | ? | 1 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 2 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 3 | 3 | 3 | 0 | 0 | 2 | 3 | 2 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Arytainilla diluta* | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0/1 | 1 | 1/2 | 0/1 | 1 | 2 | 1 | 0 | 0/1 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 3 | 3 | 0 | - | - | - |
| *Arytainilla dividens* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2/3 | 1/2 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 0/1 | 2 | 3 | 2 | 1 | 1 | 1 | 0 | 0 | 0/1 | 2/3 | 0 | 1 | 0/1/2 | 0 | 0 | 1 | 1/2 | 1 | 1 | 2 | 0 | 1 | 1 | 2/3 | 3 | 1 | - | 1/2 | 2 |
| *Arytainilla equitans* | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 2 | 2 | 1 | 2 | 0/1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1/2 | 1 | 1 | 2 | 0 | 1 | 1 | 2 | 3 | 0/1 | - | - | 0 |
| *Arytainilla gredi* | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 2 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0/1 | 0/1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 3 | 2 | 0 | 2 | 1 | 3 | 3 | 1 | - | 0/1 | 0/1 |
| *Arytainilla hakani* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 1/2 | 1 | 0 | 2 | 0/1 | 1 | 0 | 1 | 1 | 1 | 0 | 0/1 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1/2 | 1 | 1 | 2 | 0 | 2 | 1 | 2 | 3 | 0 | - | - | - |
| *Arytainilla ima* | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 0/1 | 1 | 3 | 1 | 1 | 0/1 | 1 | 0 | 0 | 0 | 1/2 | 1 | 1 | 1 | 0 | 0 | 1 | 0/1 | 0 | 0 | 2 | 0 | 0 | 1 | 3 | 3 | 1 | - | 0 | 0 |
| *Arytainilla incuba* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2/3 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 2 | 3 | 0 | - | - | - |
| *Arytainilla modica* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 3 | 1/2 | 1 | 1 | 2 | 3 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1/2 | 0 | 1 | 0/1 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 3 | 3 | 1 | - | 1 | 1/2 |
| *Arytainilla nigralineata* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 3 | 2 | 0 | 2/3 | 2/3 | 1 | 2 | 0 | 2 | 2 | 1/2 | 1 | 0 | 1 | 3 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 2/3 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 2 | 3 | 0 | - | - | - |
| *Arytainilla pileolata* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 1/2 | 1 | 1 | 1/2 | 1 | 0 | 1 | 1 | 1 | 0/1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 2 | 1 | 3 | 3 | 1 | - | 0 | 1 |
| *Arytainilla proboscidea* | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 3 | 2 | 0 | 2 | 3 | 1 | 2 | 0 | 1 | 2 | 1/2 | 1 | 0 | 1 | 3 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 2 | 0 | 1 | 0/1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 3 | 0 | - | - | - |
| *Arytainilla prognata* | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 3 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1/2 | 1 | 0/1 | 1 | 1 | 1 | 0/1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0/1 | 1/2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 3 | 1 | 0 | - | - | - |
| *Arytainilla spartiophila* | 0 | 1 | 1 | 0 | 1 | 3 | 0 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 2 | 2 | 2 | 1 | 3 | 0 | 1 | 0 | 1 | 0 | 1 | 1/2 | 1 | 1 | 2 | 1 | 0 | 0 | 1/2 | 1 | 1 | 2 | 0/1 | 1 | 0 | 0 | 0 | 0 | 0/1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3 | 3 | 1 | - | 2 | 2 |
| *Arytainilla sulci* | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1/2 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1/2 | 0 | 1 | 2 | 0 | 1 | 0 | 2 | 1 | 3 | 1 | 1 | 2 | 1 | 0 | 4 | 1 | 2 | 2 | 2 |
| *Arytainilla umbonata* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0/1 | 1 | 0/1 | 0 | 0/1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0/1 | 0 | 0 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 2 | 3 | 0 | - | - | - |
| *Arytainilla* sp.1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 1/2 | 1 | 1 | 0 | 2 | 1 | 2 | 3 | 3 | 3 | 0 | 0 | 2 | 3 | 2 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | - | - | 1 | 2 | 2 | 0 | - | - | - |
| *Arytainilla* sp.2 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1/2 | 2 | 1 | ? | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 0 | 0 | 0/1 | 1 | 1/2 | 0 | 1 | 1 | 2 | 1 | 3 | 0 | 1 | 2 | 1 | 3 | 3 | 1 | 1/2 | 2 | 2 |
| *Arytainilla* sp.3 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0/1 | 2 | 2 | 1 | 2 | 1 | 0 | 0 | 2 | 0 | 1 | 0/1 | 0 | 1/2 | 2 | 2 | 1 | 0 | 2 | 3 | 3 | 0 | 0 | 1 | 3 | 3 | 2 | 2 | 2 | 2 |
| *Arytainilla* sp.4 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 3 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0/1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1/2 | 0/1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0/1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 3 | 2 | 1 | 2 | 0 | - | 3 | 1 | 1 | 2 | 2 |
| *Arytainilla* sp.5 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0/1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0/1 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 2 | 1 | 3 | 3 | 1 | - | 0 | 0 |
| *Arytainilla* sp.6 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 3 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 2 | 1 | 3 | 3 | 1 | - | 0 | 2 |
| *Arytainilla* sp.7 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 2 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Arytainilla* sp.8 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 3 | 2 | 1 | 2 | 1 | 3 | 3 | 1 | 0 | 1 | 2 |
| *Arytainilla* sp.9 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 0/1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 3 | 1 | - | - | 0 |
| *Arytainilla* sp.10 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 3 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2/3 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 3 | 3 | 0 | - | - | - |
| *Arytainilla* sp.11 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 3 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1/2 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 2 | 0 | 1/2 | 1 | 2/3 | 3 | 0 | - | - | - |
| *Arytainilla* sp.12 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0/1 | 0 | 0 | 1 | 1 | 0 | 0/1 | 0/2 | 0 | 0 | 1 | 3 | 3 | 1 | - | 0 | 0/1 |
| *Arytainilla* sp.13 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0/1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 1 | 3 | 3 | 0 | - | - | - |
| *Livilla adusta* | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | ? | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Livilla blandula* | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0/1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0/1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 1 | 3 | 3 | 1 | - | 0/1 | 0/1 |
| *Livilla monospermae* | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 0 | 1 | 3 | 2 | 1 | 0 | 1 | 0 | 0 | 0/1 | 2 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 3 | 3 | 1 | 2 | 2 | 2 |
| *Livilla nervosa* | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | - | 1 | 2 | 0 | 2 | 2 | 1 | 2 | 1 | 1/2 | 1 | 1 | 1 | 3 | 2 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Livilla retamae* | 2 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0/1 | 1 | 3 | 0 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 0 | 1 | 3 | 2 | 1 | 0 | 1 | 0 | 0 | 0/1 | 2/3 | 0 | 1 | 0/1 | 1 | 1 | 1 | 1/2 | 1 | 1 | 1 | 0/1 | 2 | 1 | 3 | 3 | 1 | 0/1/2 | 2 | 2 |
| *Livilla* sp.15 | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | - | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Livilla* sp.16 | 0 | 1 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 3 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 0 | 1 | 3 | 2 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Livilla* sp.17 | 1 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0/1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| *Pseudacanthopsylla* | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 2 | 3 | 3 | 3 | 0 | 3 | 3 | 4 | 1 | 2 | 1 | 4 | 0 | 3 | 2 | 2 | 2 |

# APPENDIX 6.



Appendix 6. Phylogram of morphological data (strict consensus of 18 trees) showing unambiguous character state changes: black symbols = unique changes, white symbols = parallel changes; bars indicate apomorphic states, and arrows the direction of character change.

# CHAPTER FOUR

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

[This paper has been submitted to the *Botanical Journal of the Linnean Society*]

### Abstract

Analysis of sequence data from the internal transcribed spacers (ITS) and 5.8S region of nuclear ribosomal DNA show that Canarian and Madeiran brooms (Genisteae) 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 diphyletic 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 afrotropical 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 evidence that both continental and Madeiran taxa could be derived from the Canary 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.

## 4.1 Introduction

### 4.1.1 *The tribe Genisteae and its representatives in the Canaries and Madeira*

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

The Genisteae are well represented in the Canary Islands and Madeira with 22 native species in six genera. In Madeira there are three endemic species (*Teline maderensis*, *T. paivae* and *Genista tenera*) and one possibly native, non-endemic species (*Adenocarpus complicatus*). The situation is more complicated in the central and western Canary Islands (see map, 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 10 endemic species and *Adenocarpus* by three endemic species (one of which, *A. ombriosus*, may be close to extinction). The two common *Adenocarpus* species (local name: "codeso") are ecologically important, in places forming the dominant vegetation. *Teline canariensis* (local name: "retamón") is a prominent component of the fayal-brezal (*Myrica faya* and *Erica arborea*) vegetation on Tenerife, and *T. stenopetala* ssp. *stenopetala* (local name: "gacia") is cultivated in the islands for fodder (Pérez de Paz *et al.*, 1986). *Genista*, however, is represented by a single endemic species, reported as extremely rare in the 1970s (Santos-Guerra, 1975) but recently part of a successful conservation program in the sub-alpine 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, non-endemic 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 & Dingwall (1972) and Arco Aguilar (1982, 1983, 1993). These treatments, with minor modifications, have been followed here.

### **4.1.2** *Molecular approaches to plant biogeography in the Macaronesia flora*

Molecular techniques have been used to interpret the historical biogeography of island taxa by sampling putative continental progenitors in different source areas (Böhle, Hilger & Martin, 1996; Kim *et al.*, 1996; Francisco-Ortega *et al.*, 1997a; Vargas *et al.*, 1999; Panero *et al.*, 1999; Helfgott *et al.*, 2000). Biogeographic links for the Macaronesian flora are diverse. There is evidence for Eurosiberian (*Saxifraga*; Vargas *et al.*, 1999), Mediterranean (*Argyranthemum*, *Bencomia*; Francisco-Ortega *et al.*, 1997a; Helfgott *et al.*, 2000), Southern African (*Phyllis*; Sunding, 1979), North African (*Dracaena*; Sunding, 1979) and New World (*Pericallis*; Panero *et al.*, 1999) origins, as well as Asian and Australasian disjunctions (*Apollonias*, *Picconia*; Sunding, 1979). The ITS-5.8S region often fails to provide adequate sequence divergence for phylogenetic resolution of rapid speciation on islands (Böhle *et al.*, 1996, Kim *et al.*, 1996, Helfgott *et al.*, 2000), and in particular the highly conserved 5.8S region is often uninformative in such studies. However, in this analysis the three informative sites in the 5.8S region include a putative synapomorphy for a group otherwise not recovered with ITS alone (these nodes are indicated in Fig. 2).

The objectives of this study were: (1) to examine phylogenetic relationships of the Macaronesian species; (2) to determine whether the Canarian Genisteae share a common biogeographic origin (i.e. European, Mediterranean or African); (3) to investigate the biogeography of *Teline* within the Canary Islands. The Canarian Genisteae are host to 21 species of plant feeding endemic psyllids (Hemiptera). These are the subject of ongoing parallel studies by one of us (D.P.) and it is hoped that the answers to the above questions may shed light on patterns of speciation in the associated insects.

## 4.2 Materials and methods

### **4.2.1** *Taxon sampling*

*Ingroup selection*

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 non-endemic 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 & 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 circumscibed (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 & Dingwall, 1972; Maire, 1987). Two Spanish species recently transferred (Talavera & 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 *Teline stenopetala* (the most variable species) were also analysed, the only exceptions being the very rare *T. rosmarinifolia* ssp. *eurifolia* del Arco and a recently described subspecies, *T. pallida* ssp. *silensis* del Arco (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 & Salgueiro (1999) have suggested should be placed in *Adenocarpus* is also included. Finally, a selection of *Genista* spp. from Africa and Europe were chosen to investigate the biogeographic origins and monophyly of the island species of *Genista* and *Teline*, and to ascertain the specific affiliation of *Genista benehoavensis* from the Canary Islands. Details of all the taxa sampled are given in Table 2.

### *Outgroup selection*

In order to provide rooting of the tree I used a member of a related leguminous tribe (Thermopsideae) as the outgroup (*Anagyris foetida*). As *Anagyris* is highly divergent from the ingroup, an unrooted analysis without *Anagyris* was used as a check that this outgroup did not affect the topology.

## **4.2.2** *Molecular procedures*

### *DNA sampling and extraction*

A total of 50 individuals, representing 36 species, were sampled, mostly from field-collected leaf material (vouchers in GL). However, herbarium material was used for *Adenocarpus mannii* (E), *A. ombriosus* (TFC) and *Teline stenopetala* spp *microphylla* (from La Gomera) (E). In addition, leaf material was obtained from a cultivated, wild-origin specimen of *G. tinctoria* (RBGE). DNA was extracted from silica-dried leaf material using a QIAGEN DNeasy Plant Mini Kit. Extracts were eluted in 50μl of Buffer AE (included in the kit) and stored at -20°C. For PCR amplification 1µl of this solution was used for each reaction.

*PCR and sequencing*

Amplification of the ITS1-5.8S rDNA-ITS2 region was accomplished using forward primer ITS 5p: 5'–GGAAGGAGAAGTCGTAACAAG–3' (Möller & 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 & Cronk, 1997), and ITS2 was amplified with a forward primer I designed using sequences already obtained (ITS 2-LEG: 5'–GCAGAATCCCGTGAACCAT–3') and primer ITS 4. The primer ITS 2-LEG is likely to give better amplification of the ITS2 region than conventional primers for most papilionoid legumes. Each PCR cycle comprised denaturation at 94°C for four minutes, followed by 30 cycles of 94°C for 30 seconds, annealing at 58°C for one minute and an extension of 72°C for one minute, with a final extension of 72°C for 10 minutes. Amplified PCR products were purified with a QIAGEN QIAquick PCR Purification Kit, and resuspended in 30µl of $H_2O$ for direct sequencing using an automated ABI 377. All the sequences referred to here have been deposited in GenBank database under the accession numbers AF330637 – AF330686.

### 4.2.3 *Sequence analysis*

*Alignment*

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 & Wink, 1997). Alignment of sequences was straightforward and was done manually using the program Se-Al (version 1.0a1; Rambaut, 1998). A single ambiguous region of 3 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 217-221 bp, while 5.8S was uniformly 163 bp without gaps. Features of the aligned matrix are given in Table 3. The aligned matrix is given in Appendix 1 and is also available from GenBank; both the aligned matrix and trees (Figs 2 & 3) are available from TreeBASE (http://www.herbaria.harvard.edu/treebase/).

*Phylogenetic analyses*

Phylogenetic analyses were performed with PAUP* (version 4.0b3; Swofford, 1999). The following heuristic search parameters were employed: 1000 random stepwise addition replicates with TBR branch swapping, other options included 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 & Ochoterena, 2000). A maximum likelihood (ML) analysis was performed for a comparison to the MP results. Parameters and assumptions used in the ML search were selected using program Modeltest (Posada & Crandall, 1998). The model selected was Tamura-Nei with gamma distribution. An alternative model, general time-reversible with invariable sites and gamma distribution, selected on the basis of the Akaike Information Criterion (AIC), produced the same tree with slightly improved (lower) log-likelihood score. ML heuristic search parameters included simple addition sequence of taxa with TBR branch swapping, MULTREES and COLLAPSE.

To examine the possible diphyletic origin of *Teline*, three analyses were run with the monophyly of *Teline* constrained for: a) a monophyletic Macaronesian clade; b) a monophyletic genus; c) a paraphyletic clade with the inclusion of *Genista segonnei.* The monophyly of an apparently paraphyletic *Teline stenopetala* (with and without ssp. *spachiana*) was also examined. The Kishino-Hasegawa and nonparametric (Templeton's Wilcoxon signed-rank) tests, as implemented in PAUP*, were used to assess these assumptions by testing significant length differences between constrained and unconstrained trees (Table 4).

## 4.3 Results

### 4.3.1 *Molecular results*

*Molecular evolution in island and continental Genisteae*

A total of 637 sites with an average of 617bp 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 3. Sequences obtained using internal primers lacked between 38-107bp 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), four of these were uninformative (three varied only between the ingroup and the outgroup, *Anagyris foetida*) but three provided informative synamomophies in *Adenocarpus* and *Teline*. In particular, 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). A relatively high proportion of species pairs/groups had identical sequences, these were: (1) *A. foliolosus*, *A. ombriosus* and *A. viscosus*; (2) *Genista cinerea* and *G. ramosissima*; (3) *Teline nervosa* and *T. pallida* ssp. *pallida*; (4) *Teline canariensis* and *T. osyroides*; and (5) *T. salsoloides* and *T. stenopetala* spp. *spachiana*. Uncorrected pairwise distances within the *Teline linifolia* group were 0–2.1% including both continental and island taxa, but only 0–0.8% between island taxa alone. Within the *Teline 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 (with more divergence, 1.8%, between Madeiran and Canary Island species than between continental and island species).

*Results of phylogenetic analyses*

A maximum parsimony analysis produced a single tree (length 318, CI 0.643 excluding uninformative characters, RI 0.882). Coding gaps as a separate binary matrix provided a single synapomorphy grouping *Teline salsoloides* with *T. stenopetala* ssp. *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 a maximum parsimony search without *Anagyris*. One of these differed from the tree presented, but only by a single change (the reverse placement of the *Genista florida-G. tinctoria* and *G. segonnei-Teline linifolia* groups) and mid-point 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 insufficient to resolve with confidence the island species groups (Figs 2 & 3). Nevertheless, the phylogeny provides 15 nodes (excluding intraspecific nodes) with bootstrap support ≥ 75% and 6 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.

### 4.3.2 *Taxonomic results*

*Genista*

The molecular results confirm the transfer of *Cytisus benehoavensis* to *Genista* by Arco Aguilar (1982), and moreover places it 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*, *G. tenera*) all have a small, or vestigial aril (Gibbs, 1974, Arco Aguilar, 1982). The data also support the transfer to *Genista* of *Adenocarpus segonnei* (Gibbs, 1974), and strongly suggests (bootstrap 93%) affinity with the *Teline linifolia* group.

*Adenocarpus*

The data support the finding of Käss & 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, *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 *anagyrifolius* group is not strongly supported, bootstrap 55%). There is support (bootstrap 78%) for a bracteate clade (possessing distinct floral bracts that are persistent) including *A. nainii*, *A. boudyi* and *A. telonensis*. *A. nainii* has previously been treated as a subspecies of the weakly bracteate *A. complicatus* (with narrow, simple floral bracts, present when the inflorescence is in bud but rapidly caducous on maturation and extension of the inflorescence). However, *A. nainii* is clearly distinct from European *A. complicatus*, and I therefore revert to former taxonomic treatments in recognizing this taxon at specific rank (Maire, 1922). *Adenocarpus mannii* which occurs in montane regions of tropical Africa is of particular biogeographic interest, and is shown to be a sister group of the Mediterranean/Canarian *A. complicatus-viscosus-foliolosus* group (bootstrap 82%). *Adenocarpus* as delimited here is clearly a monophyletic genus (bootstrap 87%). The proximity of *Argyrocytisus battandieri* in the tree topology suggests a more cytisoid than genistoid affinity for *Adenocarpus* (Badr, Martin & Jensen, 1994). A reclassification of *Argyrocytisus battandieri* in *Adenocarpus* has recently been proposed due to the occasional presence of glandular papillae on the fruit surface (Talavera & Salgueiro, 1999). The limited sampling here does not allow us to contradict this classification, and the phylogenies presented by Käss & Wink (1997) do not provide an unambiguous placement of *A. battandieri.*

### *Teline*

Our data show that the genus *Teline* is diphyletic, contrary to cpDNA (rbcL) results presented by Käss & Wink (1995). Forcing *Teline* to be monophyletic results in an extra tree length of 10 steps, which is significant at $P = 0.05$ (Table 4). *Teline* has been considered of genistoid affinity (Polhill, 1976; Bisby, 1981; Norverto, González-Andrés & Ortiz, 1994; González-Andrés & Ortiz, 1995) and I confirm that *Teline* is nested within *Genista*, as shown by Käss & 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 represent two colonizations 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; and the more widespread continental species, *T. monspessulana*, which has a circum-Mediterranean distribution and also 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'. *T. maderensis* has more recently been circumscribed to include *T. paivae* (Arco Aguilar, 1983; Cannon & Turland, 1994), but as these two species appear to be distinct in the molecular analysis, I have reverted to recognizing two separate *Teline* species on Madeira.

Within the island *linifolia* group, *Teline 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). It accordingly seems appropriate to revive the name *Teline gomerae* (Kunkel, 1975). Within the island *monspessulana* group, one of the five subspecies of *Teline stenopetala* – ssp. *spachiana* – is identical in sequence to *T. salsoloides* and differs from *T. canariensis* and *T. osyroides* by a single indel. This taxon, originally described as '*Genista* (*Teline*) *spachiana*' by Webb (1845), was later synonomized with *T. canariensis* by Gibbs (1972), who cited the intergradation of the two taxa. Furthermore, when Arco Aguilar (1983) placed this taxon in *T. stenopetala*, he reported it as hybridizing with *T. canariensis.* The four Tenerifean taxa (*T. canariensis*, *T. osyroides*, *T. salsoloides*, *T. stenopetala* spp. *spachiana*) form the homogeneous *canariensis* group (bootstrap 99%), which are distinct from the remaining four subspecies of *T. stenopetala.* Because of the difficulty of separating some *T. stenopetala* ssp. *spachiana* from *T. canariensis*, this plant is probably best treated as *T. canariensis* (*spachiana*-type). Interestingly, ssp. *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 & Proust (see Gibbs & Dingwall, 1972). Even excluding ssp. *spachiana*, *T. stenopetala* is paraphyletic in this analysis. However, constraining *T. stenopetala* to be monophyletic (excluding ssp. *spachiana*) requires an additional tree length of only two steps which is not significant (Table 4). One should therefore interpret these results cautiously as the possibility that gene flow in the '*monspessulana* clade' is confounding phylogenetic signal is increased by the human introduction and movement of species (Francisco-Ortega *et al.*, 1997b; Clarke, Johnson & Murray, 1998).

## 4.4 Discussion

### 4.4.1 *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 (SW 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 – with seven colonization events accounting for 18 species in six genera – 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 (Fig. 4, arrow B). 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 & Coudé-Gaussen, 1996) (Fig. 4, arrow A). The Genisteae have an 'explosive dehiscence' – seeds are ejected from the pod, which remains attached to the parent plant, and have no obvious adaptations to dispersal by air or water. Mature seeds of all genera of Canarian brooms typically sink immediately in sea water (pers. obs.). 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 Palaearctic, with central European and Mediterranean affiliations (Bacallado, 1976), and European migrants occur as vagrants.

### **4.4.2** *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. anagyrifolius* (High Atlas), *A. bacquei* (High and Middle Atlas) and *A. decorticans* (montane regions of southern Spain and north Morocco). I 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 a single polymorphic species, *A. complicatus* (ssp. *complicatus sensu* Gibbs, 1967), and *A. mannii* which occurs only in tropical and subtropical Africa. *A. 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 & 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 (Fig. 5, arrows A & B) have been suggested to explain the presence of European and Mediterranean elements in the montane tropical African flora (Quézel & Martinez, 1958-59; Wickens, 1976; Quézel, 1978). The absence of *A. mannii* or *A. complicatus* in the Moroccan Atlas suggests that the Morocco-Sahara track (shown by Quézel & Martinez (1958-59) to have had a Pleistocene extension of

Mediterranean woodland, Fig. 5, arrow A) is not the route by which *A. mannii* reached central Africa. Instead, the close relationship with *A. complicatus* and the prescence of the latter species around the eastern Mediterranean makes the Red Sea hills migration route (Fig. 5, arrow B) put forward by Wickens (1976) a reasonable alternative hypothesis. Subsequent migration of *A. mannii* to west Africa may have followed the southern migration route (Fig. 5, arrow C) proposed by White (1993).

### 4.4.3 *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. 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 4).

A striking 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 (10-12 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.

### 4.4.4 *Island evolution and different patterns of radiation*

Each of the main groups of Canarian Genisteae shows a different pattern of species diversification. These may be summarized as follows:

(1) the *Teline monspessulana* clade: geographical segregation within this clade indicates that inter-island 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, and this 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 Myr ago (Ancochea *et al.*, 1990). In contrast, *T. stenopetala* (excluding ssp. *spachiana*), which has four to five subspecies on three islands, exhibits greater genetic divergence but less morphological diversity.

(2) the *Teline linifolia* clade: radiation of this clade in the Canary Islands is less extensive than the '*monspessulana* clade'. Inter-island dispersal has apparently been more frequent than diversification within islands, with all species endemic to a single island (typically localized or rare in distribution).

(3) *Adenocarpus*: the two widespread taxa are distributed in similar altitudinal and ecological niches on different islands. *A. 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. However, there are extensive hybrid zones that have developed in locations where habitats intergrade, and often in recently disturbed 'hybrid habitats' (Lems, 1958).

(4) *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, and *G. benehoavensis* and *G. tenera* may represent relict species.

These taxa thus display a contrast between 'single island lineages' (*Teline*) and inter-island colonization or 'horizontal lineages' (*Adenocarpus*) suggested for other groups (Sanchez-Yelamo *et al.*, 1995; Francisco-Ortega *et al.*, 1996; Kim *et al.*, 1996).

### **4.4.5** *Convergent morphologies in the Genisteae*

Morphological convergence between unrelated members of the island Genisteae 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* ssp. *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 *T. stenopetala* group. At a higher level, the diphyletic 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, *Genista 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 *Genista segonnei* does not require a significant increase in tree length (Table 4).

### 4.4.6 *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 behaviour 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 are members of the *monspessulana* clade and hybrids between *T. canariensis*, *T. monspessulana* and *T. stenopetala* are recorded as 'common'. Hybrids are also known from Tenerife (and possibly Gran Canaria; Suárez Rodgríguez, 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).

## 4.5 References

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TABLE 1. Former generic placement of Macaronesian Genisteae taxa included in this study, after Gibbs (1967), Gibbs & Dingwall (1972), Gibbs (1974), Santos-Guerra (1975), Arco Aguilar, Acebes Ginovés & Wildpret de la Torre (1978), Arco Aguilar (1982), Arco Aguilar & Acebes Ginovés (1982), Arco Aguilar (1983), Marrero & Suarez (1988), Arco Aguilar (1993). Dates of homotypic synonyms are given, heterotypic synonyms are in brackets.

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

TABLE 2. Distribution of taxa and location of samples included in this study. RBGE = Royal Botanic Garden Edinburgh, TFC = Herbario de la Universidad de La Laguna, Tenerife.

| no. | taxon | distribution | origin of sample | lat. long. | voucher no. |
|---|---|---|---|---|---|
| 1 | *Adenocarpus anagyrifolius* Coss. & Ball | Morocco: High Atlas | Tizi n' Tichka (1650 m) | 31°20'N<br>07°25'W | DP 305 |
| 2 | *Adenocarpus bacquei* Batt. & Pitard | Morocco: High and Middle Atlas | Midelt (1500 m) | 32°33'N<br>04°38'W | DP 309 |
| 3 | *Adenocarpus boudyi* Batt. & Maire | Morocco: Middle Atlas | Azrou, Forêt de Cèdres (1800 m) | 33°15'N<br>05°15'W | DP 243 |
| 4 | *Adenocarpus complicatus* (L.) J. Gay | S Europe, Madeira, E Mediterranean | Spain, Andalusia, Aracena (400 m) | 37°52'N<br>06°30'W | DP 258 |
| 5 | *Adenocarpus complicatus* (L.) J. Gay | | Portugal, Serra do Caramulo (500 m) | 40°30'N<br>08°15'W | DP 262.1 |
| 6 | *Adenocarpus complicatus* (L.) J. Gay | | Madeira, Funchal (1000 m) | 32°42'N<br>16°50'W | DP 269 |
| 7 | *Adenocarpus decorticans* Boiss. | S Spain, N Morocco | Spain, Andalusia, Sierra Nevada (1850 m) | 37°05'N<br>03°02'W | DP 128 |
| 8 | *Adenocarpus decorticans* Boiss. | | Morocco, W Rif Mountains (1400 m) | 34°56'N<br>04°50'W | DP 254 |
| 9 | *Adenocarpus foliolosus* (Aiton) DC. | Central and W Canary Islands (except El Hierro) | Tenerife, Las Raices (1350m) | 28°25'N<br>16°23'W | DP 156 |
| 10 | *Adenocarpus mannii* (Hook. fil.) Hook. fil. | Central and Southern Africa | N Malawi, Nyika Plateau (> 2000 m) | 10°40'S<br>33°50'E | Salubeni 3012 (RBGE) |

| | | | | | |
|---|---|---|---|---|---|
| 11 | *Adenocarpus mannii* (Hook. fil.) Hook. fil. | | N Tanzania, Shira Ridge, Kilimanjaro (3300 m) | 03°02'S<br>37°14'E | Carmichael 1469 (RBGE) |
| 12 | *Adenocarpus nainii* Maire | N Morocco | El Harcha (1000 m) | 33°25'N<br>06°18'W | DP 150 |
| 13 | *Adenocarpus nainii* Maire (*bracteatus*) | | Central Rif Mountains (1400 m) | 34°55'N<br>04°40'W | DP 252 |
| 14 | *Adenocarpus ombriosus* Ceballos & Ortuño | W Canary Islands: El Hierro | Fileba (1300 m) | 27°45'N<br>17°59'W | Pérez de Paz 24,625 (TFC) |
| 15 | *Adenocarpus telonensis* (Loisel.) DC. | S Europe, N Morocco | Spain, Andalusia, Algodonales (500 m) | 36°50'N<br>05°20'W | DP 134 |
| 16 | *Adenocarpus telonensis* (Loisel.) DC. | | N Morocco, W Rif Mountains (1800 m) | 35°10'N<br>05°23'W | DP 257 |
| 17 | *Adenocarpus viscosus* (Willd.) Webb & Berthel. | Central and W Canary Islands: Tenerife, La Palma | La Palma, La Caldera rim (2200 m) | 28°45'N<br>17°51'W | DP 209 |
| 18 | *Argyrocytisus battandieri* (Maire) Raynaud | Morocco: Middle Atlas, Rif Mountains | Azrou, Forêt de Cèdres (1800 m) | 33°15'N<br>05°15'W | DP 244 |
| 19 | *Anagyris foetida* L. | S Europe, E Mediterranean, N Africa | Spain, Andalusia, Zahara de la Sierra (1000 m) | 36°50'N<br>05°25'W | DP 108 |
| 20 | *Genista benehoavensis* (Bolle) del Arco | W Canary Islands: La Palma | La Caldera rim (2250 m) | 28°45'N<br>17°50'W | DP 81 |
| 21 | *Genista cinerea* (Vill.) DC. | SW Europe, NW Africa | Spain, Andalusia, Campillos (500 m) | 37°02'N<br>04°55'W | DP 132 |
| 22 | *Genista clavata* Poir. | N Morocco | Larache (30 m) | 35°23'N<br>06°08'W | DP 151 |
| 23 | *Genista florida* L. | Spain, Portugal, Morocco | Portugal, Serra da Estrela | 40°15'N | DP 266 |

| | | | | | |
|---|---|---|---|---|---|
| | | | (800 m) | 07°45'W | |
| 24 | *Genista florida* L. var. *maroccana* Ball | Morocco: High Atlas | Tizi n' Test (2080 m) | 30°50'N<br>08°30'W | DP 238 |
| 25 | *Genista ramosissima* (Desf.) Poir. | S Spain, NW Africa | Andalusia, Sierra del Chaparral (1100 m) | 36°55'N<br>03°43'W | DP 125 |
| 26 | *Genista segonnei* (Maire) P.E. Gibbs | Morocco: Anti-Atlas | Col du Kerdous (1050m) | 29°30'N<br>09°15'W | DP 302 |
| 27 | *Genista tenera* (Jacq. ex Murray) Kuntze | Madeira | Encumeada (1050 m) | 32°45'N<br>17°05'W | DP 273 |
| 28 | *Genista tinctoria* L. | Europe, E Mediterranean | France, Haute-Loire (1500 m) | 45°10'N<br>04°00'E | RBGE 1979 2627 |
| 29 | *Genista umbellata* (L'Hér.) Poir. | S Spain, NW Africa | Andalusia, Otivar (500 m) | 36°50'N<br>03°42'W | DP 124 |
| 30 | *Teline canariensis* (L.) Webb & Berthel. | Central and W Canary Islands: Tenerife | Anaga, Pico del Inglés (960 m) | 28°32'N<br>16°16'W | DP 179 |
| 31 | *Teline gomerae* (P.E. Gibbs & Dingwall) G. Kunkel | W Canary Islands: La Gomera | Tamargada (350 m) | 28°11'N<br>17°13'W | DP 218 |
| 32 | *Teline linifolia* (L.) Webb & Berthel. | SW Europe, NW Africa | Spain, Andalusia, Ubrique (650 m) | 36°37'N<br>05°25'W | DP 139 |
| 33 | *Teline maderensis* Webb & Berthel. | Madeira | Encumeada (1100 m) | 32°45'N<br>17°05'W | DP 274 |
| 34 | *Teline microphylla* (DC.) P.E. Gibbs & Dingwall | Central and W Canary Islands: Gran Canaria | Cruz de Tejeda (1500 m) | 28°00'N<br>15°35'W | DP 172 |
| 35 | *Teline monspessulana* (L.) Koch | S Europe, E Mediterranean, NW Africa | S Spain, Andalusia, Ubrique (650 m) | 36°35'N<br>05°30'W | DP 143 |

| | | | | | |
|---|---|---|---|---|---|
| 36 | *Teline monspessulana* (L.) Koch | | N Morocco, W Rif Mountains (1000 m) | 35°10'N<br>05°20'W | DP 146 |
| 37 | *Teline nervosa* (Esteve) Hansen & Sunding | Central Canary Islands: Gran Canaria | Riscos de Jimenez (500 m) | 28°05'N<br>15°31'W | DP 164 |
| 38 | *Teline osyroides* (Svent.) P.E. Gibbs & Dingwall ssp. *osyroides* | Central Canary Islands: Tenerife | Masca (700 m) | 28°18'N<br>16°50'W | DP 153 |
| 39 | *Teline osyroides* ssp. *sericea* (Kuntze) del Arco | Central Canary Islands: Tenerife | Fasnia, Barranco de Herques (550 m) | 28°15'N<br>16°26'W | DP 184 |
| 40 | *Teline paivae* (Lowe) P.E. Gibbs & Dingwall | Madeira | Ribeira da Janela (400 m) | 32°48'N<br>17°10'W | DP 271 |
| 41 | *Teline pallida* (Poir.) G. Kunkel ssp. *pallida* | Central Canary Islands: Tenerife | Anaga, Roque de Enmedio (300 m) | 28°31'N<br>16°12'W | DP 180 |
| 42 | *Teline rosmarinifolia* Webb & Berthel. | Central Canary Islands: Gran Canaria | Fataga (800 m) | 27°54'N<br>15°34'W | DP 159 |
| 43 | *Teline salsoloides* del Arco & Acebes | Central Canary Islands: Tenerife | Teno (200 m) | 28°21'N<br>16°53'W | DP 181 |
| 44 | *Teline splendens* (Webb & Berthel.) del Arco | W Canary Islands: La Palma | Santa Cruz, La Asomada Alta (600 m) | 28°43'N<br>17°46'W | DP 203 |
| 45 | *Teline stenopetala* (Webb & Berthel.) Webb & Berthel. ssp. *stenopetala* | W Canary Islands: La Palma | Los Tilos, Barranco del Agua (500 m) | 28°47'N<br>17°48'W | DP 192 |
| 46 | *Teline stenopetala* ssp. *microphylla* (Pit. & Proust) del Arco | W Canary Islands: La Gomera, El Hierro | La Gomera, Los Barranquillos de Vallehermoso (1000 m) | 28°09'N<br>17°18'W | Bramwell 2035 (RBGE) |
| 47 | *Teline stenopetala* ssp. *microphylla* (Pit. & Proust) del Arco | | El Hierro, El Golfo (1100 m) | 27°44'N<br>18°01'W | DP 212 |

| | | | | | |
|---|---|---|---|---|---|
| 48 | *Teline stenopetala* ssp. *pauciovulata* (del Arco) del Arco | W Canary Islands: La Gomera | Roque Agando (1000 m) | 28°6'N<br>17°11'W | DP 344 |
| 49 | *Teline stenopetala* ssp. *sericea* (Pit. & Proust) del Arco | W Canary Islands: La Palma | La Cumbrecita (1250 m) | 28°41'N<br>17°51'W | DP 190 |
| 50 | *Teline stenopetala* ssp. *spachiana* (Webb) del Arco | Central Canary Islands: Tenerife | Güímar, Caldera de Pedro Gil (1775 m) | 28°20'N<br>16°28'W | DP 182 |

TABLE 3. Sequence characteristics of ITS1, 5.8S and ITS2 regions of 50 individuals representing 41 taxa (36 species) of Genisteae (Leguminosae). Sequence divergence was estimated using uncorrected pairwise distances.

| parameter | ITS 1 | 5.8S | ITS 2 | whole region |
|---|---|---|---|---|
| length range (total) bp | 219-241 | 163 | 217-221 | 600-624 |
| length mean (total) bp | 235.7 | 163 | 217.9 | 616.6 |
| length range (ingroup) bp | 219-241 | — | 217-220 | 600-622 |
| length mean (ingroup) bp | 235.6 | 163 | 217.8 | 616.4 |
| length range (outgroup) 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 |
| sequence divergence (ingroup) % | 0-14 | 0-1.7 | 0-11.5 | 0-8.3 |
| sequence divergence (in/outgroup) % | 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 |

TABLE 4. Tests for monophyly in the genus *Teline*. Significant length difference ($P = < 0.05$) for constraints is indicated by *.

| constraint | no. of species | cost of monophyly: MP tree length difference | Templeton (Wilcoxon signed-rank) test | cost of monophyly: Log-likelihood difference | Kishino-Hasegawa likelihood ratio test |
|---|---|---|---|---|---|
| *T. stenopetala* | 1 (5 ssp.) | 7 | $P = 0.0082$ * | 35.180 | $P = 0.0035$ * |
| *T. stenopetala* excl. spp. *spachiana* | 1 (4 ssp.) | 2 | $P = 0.1797$ | 4.793 | $P = 0.2222$ |
| Macaronesian '*monspessulana* group' | 7 | 1 | $P = 0.3173$ | 2.763 | $P = 0.3129$ |
| Macaronesian clade | 12 | 21 | $P = < 0.0001$ * | 69.445 | $P = < 0.0001$ * |
| genus | 14 | 10 | $P = 0.0328$ * | 26.140 | $P = 0.0112$ * |
| genus + *Genista segonnei* | 15 | 4 | $P = 0.1025$ | 6.241 | $P = 0.1937$ |

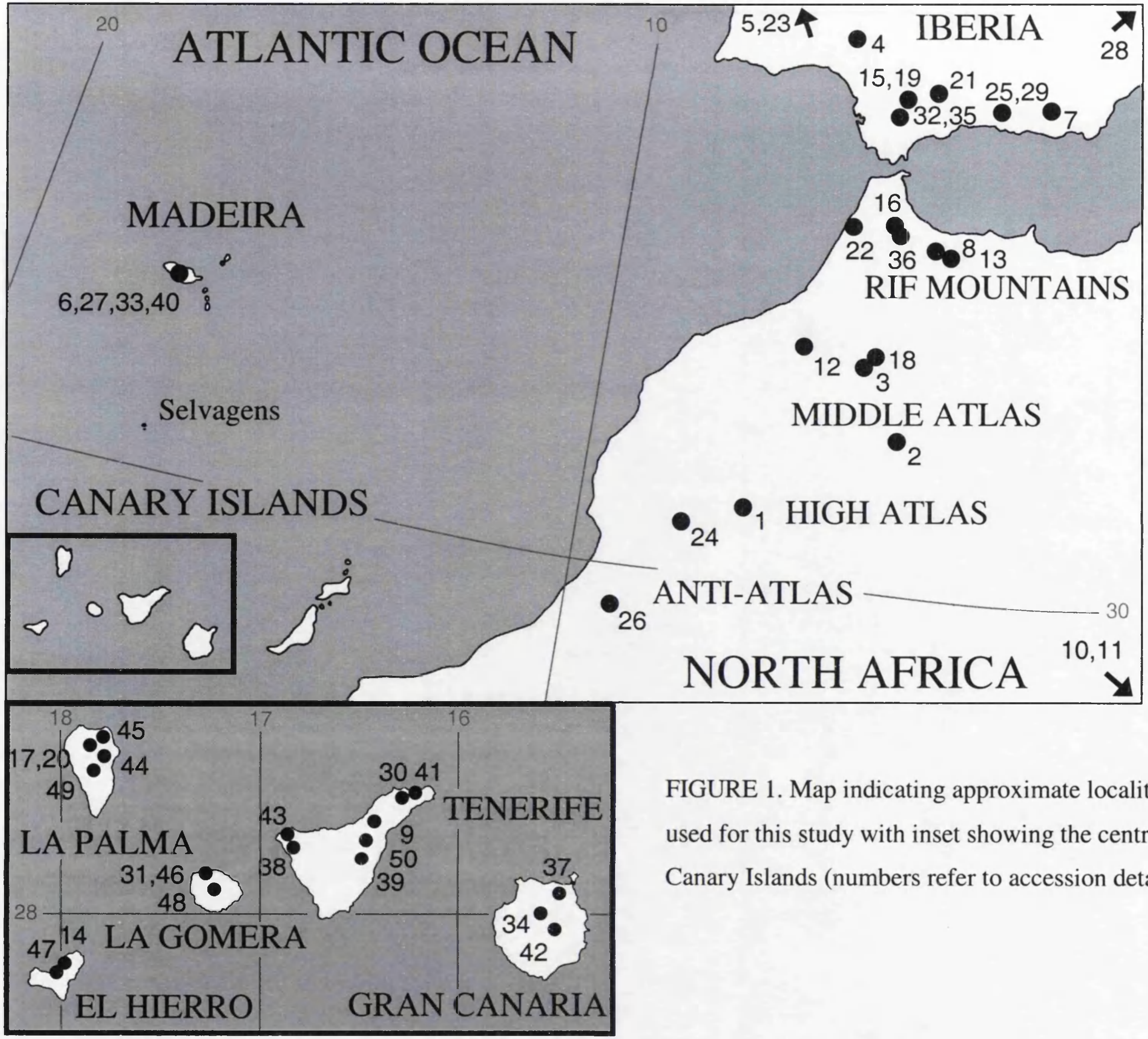


FIGURE 1. Map indicating approximate localities of samples used for this study with inset showing the central and western Canary Islands (numbers refer to accession details in Table 2).

FIGURE 2. Cladogram of the single most parsimonious tree (length 318, CI 0.643 excluding uninformative characters, RI 0.882) which has an identical topology to the maximum likelihood tree. Numbers above branches are % bootstrap support (* 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.

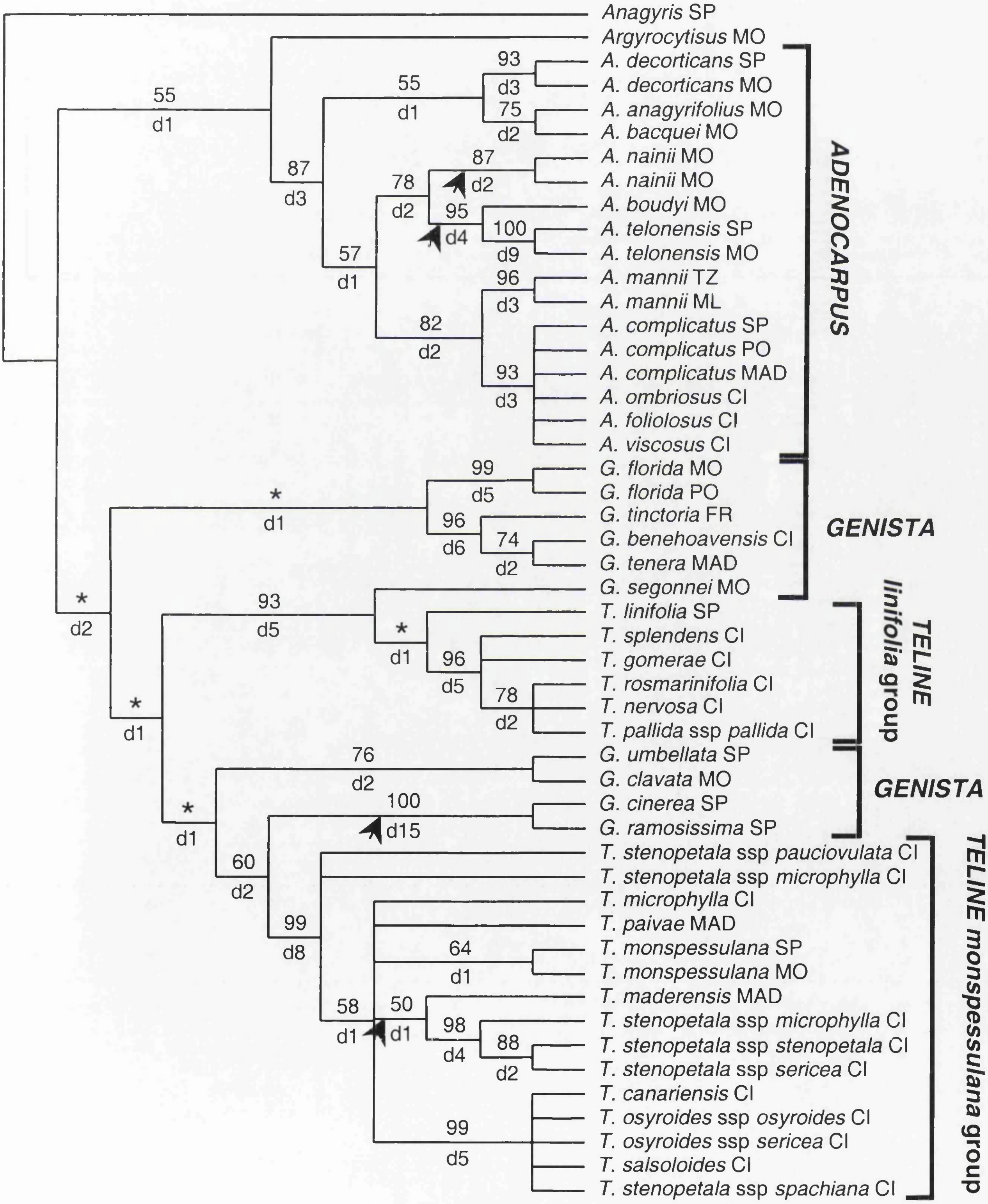
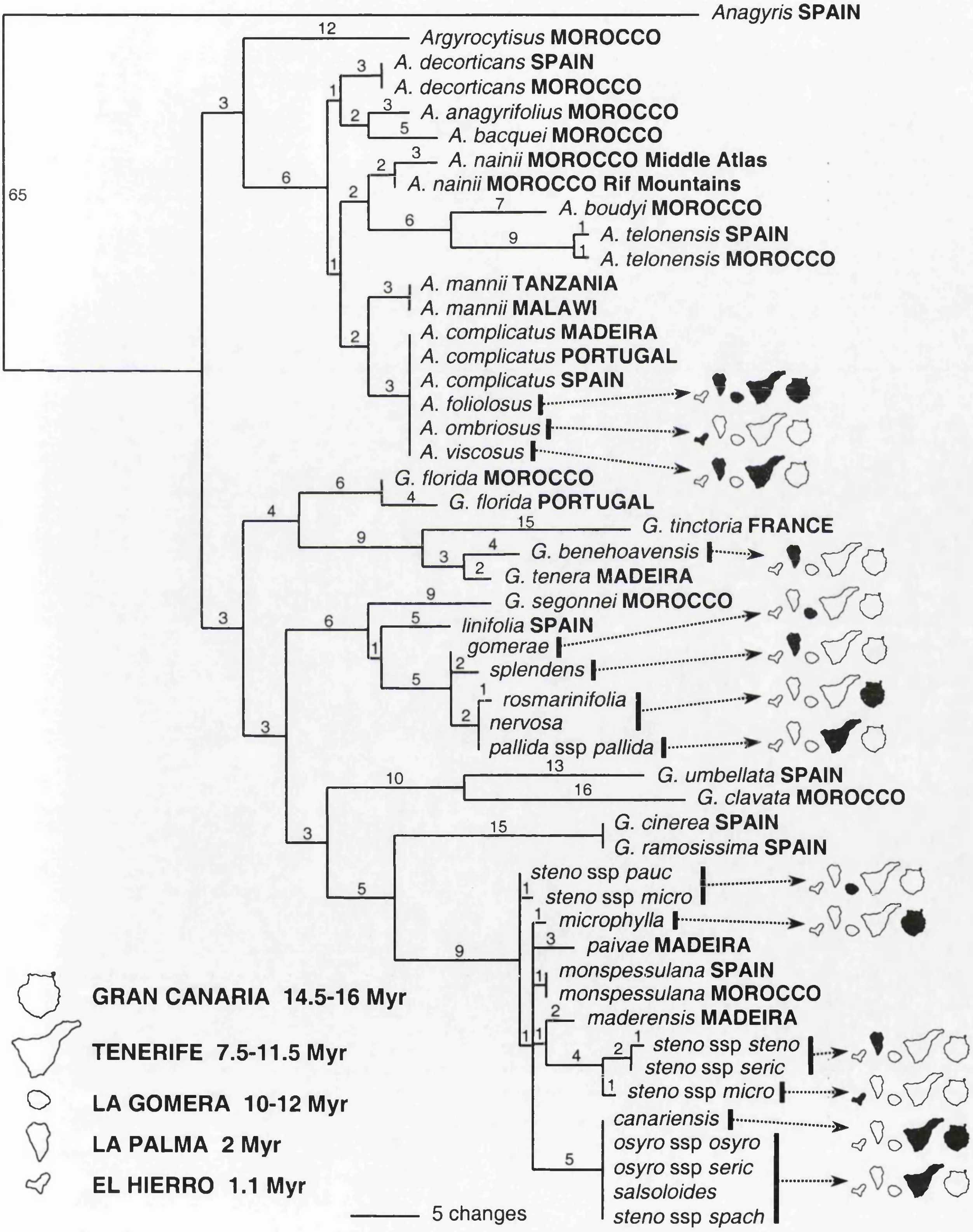


FIGURE 3. Phylogram of the single most parsimonious tree with number of substitutions given above branches. Distributions for all Canary Island species are illustrated.



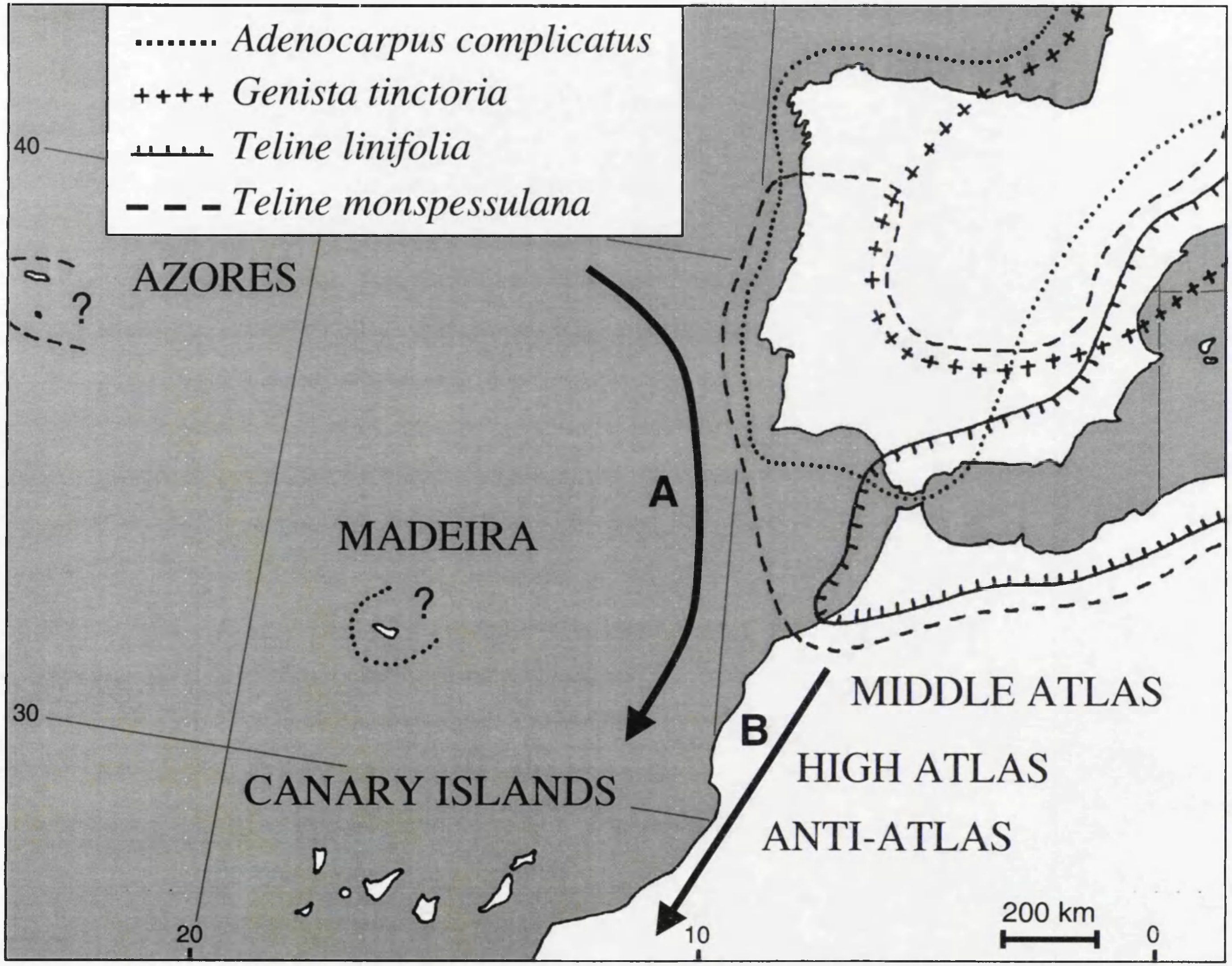
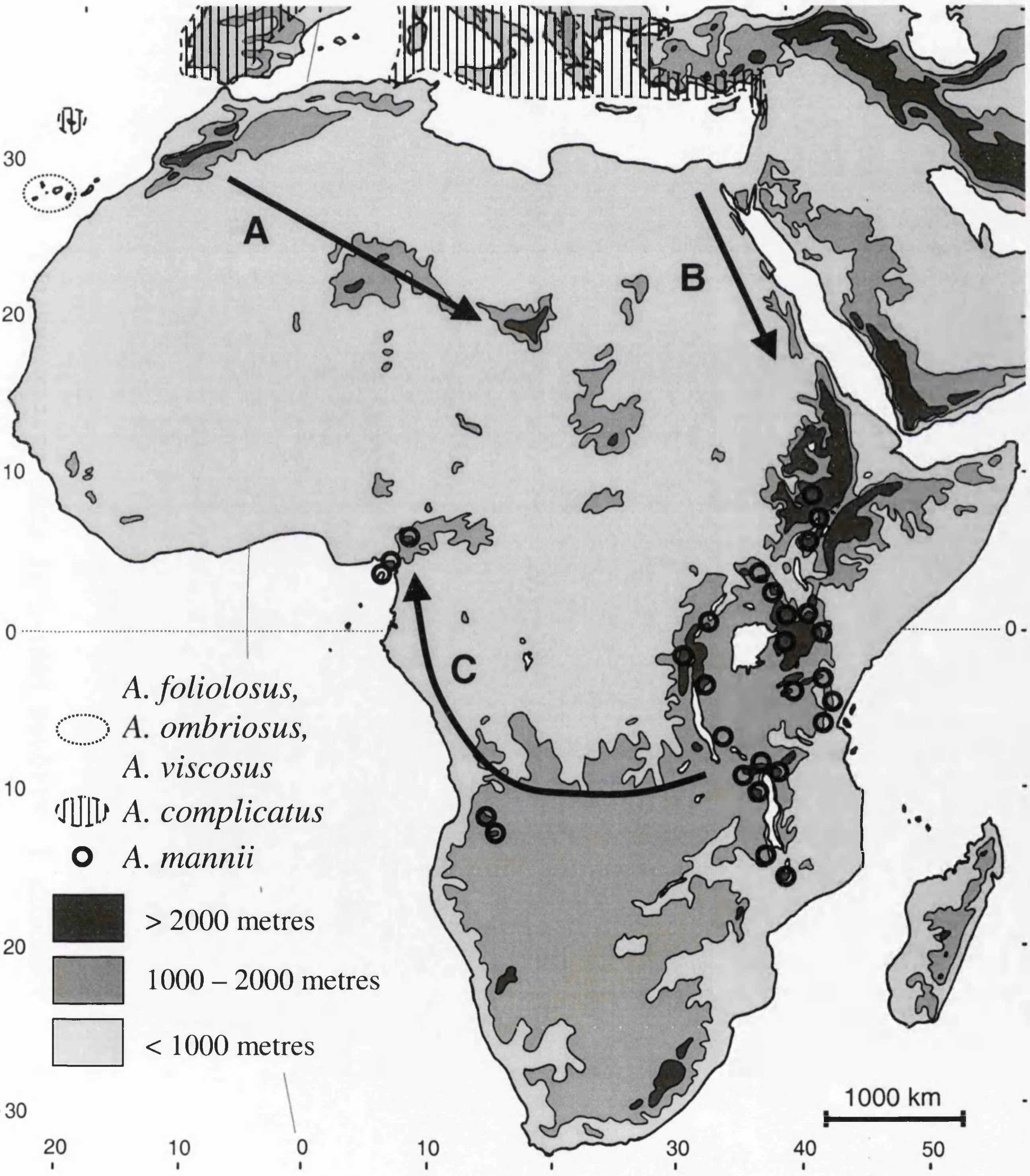


FIGURE 4. Map showing disjunction between the Canary Islands and present distribution of putative progenitor species of Canarian *Adenocarpus*, *Genista* and *Teline* (see Fig. 2). '?' indicates possible native distribution. There is a striking disjunction between the Canarian taxa and their putative sister taxa which are exclusively Mediterranean and do not occur in the Atlas mountains or on the SW 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 & 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.

FIGURE 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 & 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).



**APPENDIX 1.** Aligned ITS1-5.8S-ITS2 matrix (637bp), position of internal primers are shown.

```
[                                             10        20        30        40        50        60        70        80        90       100]
[                                              .         .         .         .         .         .         .         .         .         .]
                                      [ITS1 start
Anagyris_foetida                      TCGAAGCCTAACAAAGCAGTGCGACCC-GCGAATTTGTTTGACTACTCAGGGGAG---GCCAGAGGTGCTTG-GCACCTCGGTCCCCTCTTGTGTC-GGA   [94]
Argyrocytisus_battandieri             TCGAAGCCTCACAA-GCAGTGCGACCCTGTGAATTTGTTTGACTACTCAGGGGTG---ACTAGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_anagyrifolius             GCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_bacquei                   GCGAAGCATCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_boudyi                    TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTAAGGGGTG---GCTAGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_complicatus_SP            TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_complicatus_PO            TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_complicatus_MAD           TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_decorticans_SP            TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_decorticans_MO            TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_foliolosus                TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_mannii_ML                 TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_mannii_TZ                 TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_nainii_MA                 TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTAAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGT-CACCCTCGTGTCGGGA   [94]
Adenocarpus_nainii_RIF                TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTAAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_ombriosus                 TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Adenocarpus_telonensis_SP             TCGAAGCCTCACAA-GCAGTGCAACCCCGTGAATTTGTTTGACTACTAAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGT-CCCCCTCGGGTCGGGA   [94]
Adenocarpus_telonensis_MO             TCGAAGCCTCACAA-GCAGTGCAACCCTGTGAATTTGTTTGACTACTAAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGT-CCCCCTCGGGTCGGGA   [94]
Adenocarpus_viscosus                  TCGAAGCCTCACAA-GCAGTGCGACCCCGTGAATTTGTTTGACTACTCAGGGGTG---GCTGGAGGTGTTCG-GCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Genista_benehoavensis                 TCGAAGCCTCACAA-GCAATGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCCAGGGGTGTTCT-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Genista_cinerea                       TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Genista_clavata                       TCGAAGCCTCACAA-GTAGTGCGACCCTGTGAATTTGTTTGACTACTCAGGGGTGGCAGCTAGAGGTGTTCA-GCATCTCGGT-CCCCCTCGTGTCGGGA   [97]
Genista_florida_PO                    TCGAAGCCTCACAA-GCAGTGCAACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCT-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Genista_florida_MO                    TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCT-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Genista_ramosissima                   TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Genista_segonnei                      TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTATAGGTGTTCT-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Genista_tenera                        TCGAAGCCTCACAA-GCAATGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCCAGGGGTGTTCT-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Genista_tinctoria                     TCGAAGCCTCACAA-GCAATGCGACCC-GTGAATTTGTTTGACTACTCAGGGGCG---GCTCGAGGTGTTCCCACACCTTGGT-CCCCCTCGTGCCGGGA   [94]
Genista_umbellata                     TCGAAGCCTCACAA-GCAGTGCGACCACGTGAATTTGTTTGACTACTTAGGGGTG---GCTAGAGGTGTTTG-GCATCTCGGT-CCCCCTCGTGTCGGGA   [94]
Teline_canariensis                    TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_gomerae                        TCGAAGCCTCACAA-GCAGTGCGACCC-GAGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Teline_linifolia                      TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTAGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Teline_maderensis                     TCGAAGCCTCACAA-GCAGTGCAACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTTTGCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Teline_microphylla                    TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGCG---GCTAGAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_monspessulana_SP               TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_monspessulana_MO               TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_nervosa                        TCGAAGCCTCACAA-GCAGTGCGACCC-GAGAATTTGTTTGACTACTCAGGGGTG---GCTATAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Teline_osyroides_ssp_osyroides        TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_osyroides_ssp_sericea          TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_pallida_ssp_pallida            TCGAAGCCTCACAA-GCAGTGCGACCC-GAGAATTTGTTTGACTACTCAGGGGTG---GCTATAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Teline_paivae                         TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_rosmarinifolia                 TCGAAGCCTCACAA-GCAGTGCGACCC-GAGAATTTGTTTGACTACTCAGGGGTG---GCTATAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Teline_salsoloides                    TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTTTGCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Teline_splendens                      TCGAAGCCTCACAA-GCAGTGCGACCC-GAGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCG-GCACCTCGGT-CCCCCTCGTGTCGGGA   [93]
Teline_stenopetala_ssp_microphylla_G  TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_stenopetala_ssp_microphylla_H  TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATCTGTTTGACTACTCAGGGGTG---GCTATAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGTA   [93]
Teline_stenopetala_ssp_pauciovulata   TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTCT-GCACCTCGGC-CCCCCTCGTGTCGGGA   [93]
Teline_stenopetala_ssp_sericea        TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATCTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTT-GCACCTCGGC-CCCCCTCGTGTCGGTA   [93]
Teline_stenopetala_ssp_spachiana      TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATTTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTTTTTGCACCTCGGC-CCCCCTCGTGTCGGGA   [94]
Teline_stenopetala_ssp_stenopetala    TCGAAGCCTCACAA-GCAGTGCGACCC-GTGAATCTGTTTGACTACTCAGGGGTG---GCTAGAGGTGTCTT-GCACCTCGGC-CCCCCTCGTGTCGGTA   [93]
```

# APPENDIX 1 cont.

```
[                                       110       120       130       140       150       160       170       180       190       200]
[                                         .         .         .         .         .         .         .         .         .         .]

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Argyrocytisus_battandieri            GGCGCCCCACCCTGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAAGTGAAATCGTTTAGTGCGCCCCCGTC   [189]
Adenocarpus_anagyrifolius            GGCGCCCCGCCCAGCGTGG-TCTCCTCCTGGCCCAATAATAACAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [192]
Adenocarpus_bacquei                  GGTGCCCCGCCCAGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
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Adenocarpus_complicatus_SP           GGCCCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
Adenocarpus_complicatus_PO           GGCCCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
Adenocarpus_complicatus_MAD          GGCCCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
Adenocarpus_decorticans_SP           GGCGCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
Adenocarpus_decorticans_MO           GGCGCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
Adenocarpus_foliolosus               GGCCCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
Adenocarpus_mannii_ML                GGCGCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGATCAGTGCGCCCCCGTC   [189]
Adenocarpus_mannii_TZ                GGCGCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGATCAGTGCGCCCCCGTC   [189]
Adenocarpus_nainii_MA                GGCGCCGCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGTCCCCCTC   [189]
Adenocarpus_nainii_RIF               GGCGCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGTCCCCGTC   [189]
Adenocarpus_ombriosus                GGCCCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
Adenocarpus_telonensis_SP            GGTGCCCCGCCCCGCGTGG-TCCCATCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAACGTGTCCCCGTC   [189]
Adenocarpus_telonensis_MO            GGTGCCCCGCCCCGCGTGG-TCCCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAACGTGTCCCCGTC   [189]
Adenocarpus_viscosus                 GGCCCCCCGCCCCGCGTGG-TCTCCTCCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATTGTTCAGTGCGCCCCCGTC   [189]
Genista_benehoavensis                GGCGTCCCACCTCGTGTGG-TCTCCTTCTGGCCAAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCATC   [188]
Genista_cinerea                      GG------------------CCTCCTCCTGGCCAAATAA---CAAAAACCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTT   [172]
Genista_clavata                      GGCGCTCCACCTTGTGTGG-TGTCCTCCTGGCCCAATAA---CAAAA--CCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTACGCCCTCGTC   [191]
Genista_florida_PO                   GGCGTCCCACCTCGTGTG--TCTCCTCCTGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCTGCC   [187]
Genista_florida_MO                   GGCGTCCCACCTCGTGTG--TCTCCTCCTGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCTGTC   [187]
Genista_ramosissima                  GG------------------CCTCCTCCTGGCCAAATAA---CAAAAACCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTT   [172]
Genista_segonnei                     GGCGCCCCACCTTGCGTGG-TCTCCTCTTGGCCAAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTA   [188]
Genista_tenera                       GGTGTCCCACCTCGTGTGG-TCTCCTTCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTC   [188]
Genista_tinctoria                    GGCGTCCCACCTCGTGTGG-TCTCCTTCTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTC   [189]
Genista_umbellata                    GGTGCTCCACCTTGTGTGG-TGTCCTCTTGGCCCAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTC   [189]
Teline_canariensis                   GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGGTTAGTGCTCCCCCGTC   [188]
Teline_gomerae                       GGCGCCCCACCTTGCGTGG-TCTCCTCCGGGCCAAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTA   [188]
Teline_linifolia                     GGCGCCCCACCTTGCGTGG-TCTCCTCCTGGCCAAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCG-CCCCGTA   [187]
Teline_maderensis                    GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCTCCCCCGTC   [189]
Teline_microphylla                   GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCTCCCCCGTC   [188]
Teline_monspessulana_SP              GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAA--CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCTCCCCCGTC   [187]
Teline_monspessulana_MO              GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAA--CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCTCCCCCGTC   [187]
Teline_nervosa                       GGCGCCCCACCTTGCGTGG-TCTCCTCCGGGCCAAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTA   [188]
Teline_osyroides_ssp_osyroides       GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGGTTAGTGCTCCCCCGTC   [188]
Teline_osyroides_ssp_sericea         GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGGTTAGTGCTCCCCCGTC   [188]
Teline_pallida_ssp_pallida           GGCGCCCCACCTTGCGTGG-TCTCCTCCGGGCCAAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTA   [188]
Teline_paivae                        GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCTCCCCCGTC   [188]
Teline_rosmarinifolia                GGCGCCCCACCTAGCGTGG-TCTCCTCCGGGCCAAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTA   [188]
Teline_salsoloides                   GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGGTTAGTGCTCCCCCGTC   [189]
Teline_splendens                     GGCGCCCCACCTTGCGTGG-TCTCCTCCGGGCCAAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCGCCCCCGTA   [188]
Teline_stenopetala_ssp_microphylla_G GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCTCCCCCGTC   [188]
Teline_stenopetala_ssp_microphylla_H GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTCTAGTGCTCCCCCGTC   [188]
Teline_stenopetala_ssp_pauciovulata  GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTTTAGTGCTCCCCCGTC   [188]
Teline_stenopetala_ssp_sericea       GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTCTAGTGCTCCCCCGTC   [188]
Teline_stenopetala_ssp_spachiana     GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGGTTAGTGCTCCCCCGTC   [189]
Teline_stenopetala_ssp_stenopetala   GGTGCTCCACTTCGTGTGG-TCTCCTCTCGGCCTAATAA---CAAAA-CCCCGGCGCCGAACGCGCCAAGGAAATTGAAATCGTCTAGTGCTCCCCCGTC   [188]
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## APPENDIX 1 cont.

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[                                             210       220       230       240       250       260       270       280       290       300]
[                                             .         .         .         .         .         .         .         .         .         .]
                                                                              ITS1 end][5.8S start                    [← Primer ITS 2p
Anagyris_foetida                     GGCACCGGAGACGGTGTCGGTGCGGGCGGCGTTGTGACACACATATCCCAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [290]
Argyrocytisus_battandieri            GGC-CCGGAGACGGTGACCGTGCGGGTGGCGTTGCGACACGCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_anagyrifolius            GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACTCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [291]
Adenocarpus_bacquei                  GGC-CCGGAGACGGTGCCCGTGCGGGTGGCGTTGCGACACTCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_boudyi                   GGC-CCGGAGACGGTGCCCGTGCGGGAGTCGTTGCGACATGCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_complicatus_SP           GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACGCTTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_complicatus_PO           GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACGCTTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_complicatus_MAD          GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACGCTTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_decorticans_SP           GGC-CCGGAGACGGTGCCTGTGCGGGAGGCGTTGCGACACTCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_decorticans_MO           GGC-CCGGAGACGGTGCCTGTGCGGGAGGCGTTGCGACACTCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_foliolosus               GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACGCTTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_mannii_ML                GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACAAGCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCAT???????????????   [288]
Adenocarpus_mannii_TZ                GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACAAGCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCAT???????????????   [288]
Adenocarpus_nainii_MA                GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACGCGTATCCGAACGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_nainii_RIF               GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACGCGTATCCGAACGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_ombriosus                GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACGCTTATCCGAAAGACTCTCGGCAACGGATA??????????????????????????????   [288]
Adenocarpus_telonensis_SP            GGC-CCGGAGACGGTGCCCGTGCGGGAGTCGTTGCGACACGCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_telonensis_MO            GGC-CCGGAGACGGTGCCCGTGCGGGAGTCGTTGCGACACGCGTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Adenocarpus_viscosus                 GGC-CCGGAGACGGTGCCCGTGCGGGCGGCGTTGCGACACGCTTATCCGAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Genista_benehoavensis                GGC-CCGGAGACGGTGCC--TACGGGCGGTGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Genista_cinerea                      GGC-CCGGAGACGGTGCT--TGCGGGTGGCGTTACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [269]
Genista_clavata                      GGC-CCGGAGACGGTGCCCGTGCGAGCGGCGTTGCGACACGCGTATCCTAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [290]
Genista_florida_PO                   GGC-CCGGAGACGGTGCC--TGTGGGTGGCGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [284]
Genista_florida_MO                   GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [284]
Genista_ramosissima                  GGC-CCGGAGACGGTGCT--TGCGGGTGGCGTTACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [269]
Genista_segonnei                     GGC-CCGGAGACGGTGAC--TACGGGCGGCGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Genista_tenera                       GGC-CCGGAGACGGTGCC--TACGGGCGGTGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Genista_tinctoria                    GGC-CCGGAGACGGTGCC---TCGGG-GGTGTGTCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [284]
Genista_umbellata                    GGC-CCGGAGACGGTGCCCGTGCGGGCGGTGTTGCGACACGCATATCCTAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [288]
Teline_canariensis                   GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_gomerae                       GGC-CCGGAGACGGTCCC--TACGGGAGGCGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_linifolia                     GGC-CCGGAGACGGTGCC--TACGGGCGGCGTTGCGACACGCATATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [284]
Teline_maderensis                    GGC-CCGGAGACGGTGCC--TGTGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [286]
Teline_microphylla                   GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_monspessulana_SP              GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [284]
Teline_monspessulana_MO              GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [284]
Teline_nervosa                       GGC-CCGGAGACGGTCCCC--ACGGGAGGCGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_osyroides_ssp_osyroides       GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_osyroides_ssp_sericea         GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_pallida_ssp_pallida           GGC-CCGGAGACGGTCCCC--ACGGGAGGCGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_paivae                        GGC-CCGGAGACGGTGCT--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_rosmarinifolia                GGC-CCGGAGACGGTCCCC--ACGGGAGGCGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_salsoloides                   GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [286]
Teline_splendens                     GGC-CCGGAGACGGTCCC--TTCGGGAGGCGTTGCGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_stenopetala_ssp_microphylla_G GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_stenopetala_ssp_microphylla_H GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_stenopetala_ssp_pauciovulata  GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_stenopetala_ssp_sericea       GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
Teline_stenopetala_ssp_spachiana     GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [286]
Teline_stenopetala_ssp_stenopetala   GGC-CCGGAGACGGTGCC--TGCGGGTGGCGTCACGACACGCGTATCCAAAAGACTCTCGGCAACGGATATCTCGGCTCTTGCATCGATGAAGAACGTAG   [285]
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# APPENDIX 1 cont.

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[                                              310       320       330       340       350       360       370       380       390       400]
[                                                .         .         .         .         .         .         .         .         .         .]
                       ← Primer ITS 2p]                              [Primer ITS2-LEG →]
Anagyris_foetida                       CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCGTTGAACGCAAGTTGCGCCCGACGCCATCAGGTCGAGGGCACGCCTGCCT   [390]
Argyrocytisus_battandieri              CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_anagyrifolius              CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [391]
Adenocarpus_bacquei                    CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_boudyi                     CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGTTGAGGGCACGCCTGCCT   [388]
Adenocarpus_complicatus_SP             CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_complicatus_PO             CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_complicatus_MAD            CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_decorticans_SP             CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_decorticans_MO             CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_foliolosus                 CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_mannii_ML                  ????????????????????????TGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_mannii_TZ                  ????????????????????????TGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_nainii_MA                  CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_nainii_RIF                 CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_ombriosus                  ??????????????????????????????????????????????????????????????????????????????TAGGCTGAGGGCACGCCTGCCT   [388]
Adenocarpus_telonensis_SP              CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGTTGAGGGCACGCCTGCCT   [388]
Adenocarpus_telonensis_MO              CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGTTGAGGGCACGCCTGCCT   [388]
Adenocarpus_viscosus                   CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Genista_benehoavensis                  CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Genista_cinerea                        CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGCCTGCCT   [369]
Genista_clavata                        CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [390]
Genista_florida_PO                     CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [384]
Genista_florida_MO                     CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [384]
Genista_ramosissima                    CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGCCTGCCT   [369]
Genista_segonnei                       CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Genista_tenera                         CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Genista_tinctoria                      CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [384]
Genista_umbellata                      CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [388]
Teline_canariensis                     CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_gomerae                         CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_linifolia                       CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [384]
Teline_maderensis                      CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGCCTGCCT   [386]
Teline_microphylla                     CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_monspessulana_SP                CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [384]
Teline_monspessulana_MO                CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [384]
Teline_nervosa                         CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_osyroides_ssp_osyroides         CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_osyroides_ssp_sericea           CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_pallida_ssp_pallida             CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_paivae                          CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_rosmarinifolia                  CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_salsoloides                     CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [386]
Teline_splendens                       CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_stenopetala_ssp_microphylla_G   CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_stenopetala_ssp_microphylla_H   CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGCCTGCCT   [385]
Teline_stenopetala_ssp_pauciovulata    CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [385]
Teline_stenopetala_ssp_sericea         CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGCCTGCCT   [385]
Teline_stenopetala_ssp_spachiana       CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCTGAGGGCACGCCTGCCT   [386]
Teline_stenopetala_ssp_stenopetala     CGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGCCTGCCT   [385]
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# APPENDIX 1 cont.

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[                                           410       420       430       440       450       460       470       480       490       500]
[                                             .         .         .         .         .         .         .         .         .         .]
                                         5.8S end][ITS2 start
Anagyris_foetida                     GGGTGTCGCACATCGTTGCCCCCAATTCCTCAGCCTCGTGCTAGGCTTTGAGCGGGGCGAATGTTGGCTTCCCGCGAGCAAGGTCTCACGGTTGGTTGAA   [490]
Argyrocytisus_battandieri            GGGTGTTGCACATCGTTGCCCCC-GTGCCATGGCCACGTGCTAGGCACCGAGCGGGGCGAATGTTGGCTTCCCGTGAGCAGCGTCTCACGGTTGGTTGAA   [487]
Adenocarpus_anagyrifolius            GGGTGTTGCACATCGTTGCCCC-AGTGCCTTGGCCACGTGCTAGGCACCGAGCGGGGCGAATGTTGGCTTCCCGCGAGCATCGTCTCACGGTTGGTTGAA   [490]
Adenocarpus_bacquei                  GGGTGTTGCACATCGTTGCCCC-AGTGCCTTGGCCACGTGCTAGGCATCGAGCGGGGCGAATGTTGGCTTCCCGCGAGCAGCGTCTCACGGTTGGTTGAA   [487]
Adenocarpus_boudyi                   GGGTGTTGCACATCGTTGCCCT-AGTGCCTTGGCCATGTGCTAGGCACCGAGCGGGGCGAATGTTGGCTTCCCGCGAGCAGCGTCTCTCGGTTGGTTGAA   [487]
Adenocarpus_complicatus_SP           GGGTGTTGCACATCGTTGCCCC-TGTGCCTTGGCCACGTGCTAGGCACCGAGCGGGGCGAATGTTGGCTTCCCGCGAGCAGCGTCTCACGGTTGGTTGAA   [487]
Adenocarpus_complicatus_PO           GGGTGTTGCACATCGTTGCCCC-TGTGCCTTGGCCACGTGCTAGGCACCGAGCGGGGCGAATGTTGGCTTCCCGCGAGCAGCGTCTCACGGTTGGTTGAA   [487]
Adenocarpus_complicatus_MAD          GGGTGTTGCACATCGTTGCCCC-TGTGCCTTGGCCACGTGCTAGGCACCGAGCGGGGCGAATGTTGGCTTCCCGCGAGCAGCGTCTCACGGTTGGTTGAA   [487]
Adenocarpus_decorticans_SP           GGGTGTTGCACATCGTTGCCCC-AGTGCCTTGGCCACGTGCTAGGCACCGAGCGGGGCGAAAGTTGGCTTCCCGCGAGCAGCGTCTCACGGTTGGTTGAA   [487]
Adenocarpus_decorticans_MO           GGGTGTTGCACATCGTTGCCCC-AGTGCCTTGGCCACGTGCTAGGCACCGAGCGGGGCGAAAGTTGGCTTCCCGCGAGCAGCGTCTCACGGTTGGTTGAA   [487]
Adenocarpus_foliolosus               GGGTGTTGCACATCGTTGCCCC-TGTGCCTTGGCCACGTGCTAGGCACCGAGCGGGGCGAATGTTGGCTTCCCGCGAGCAGCGTCTCACGGTTGGTTGAA   [487]
Adenocarpus_mannii_ML                GGGTGTTGCACATCGTTGCCCC-AGTGCCTTGGCCACGTGCTAGGCACCGAGCGGGGCGAATGTTGGCTTCCCGCGAGCAGCGTCTCACGGTTGGTTGAA   [487]
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# APPENDIX 1 cont.

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## APPENDIX 1 cont.

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Teline_stenopetala_ssp_spachiana      GACCCATGGGGG-TCC-GTTGACCGCCCAAGACGGGA    [616]
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# CHAPTER FIVE

## LINEAGE CO-DIVERSIFICATION: ARYTAININE PSYLLIDS AND THEIR LEGUME HOSTS

### Abstract

To evaluate the extent of phylogenetic congruence between a group of phytophagous insects and their host plants, psyllid (Hemiptera) and legume (Leguminosae) phylogenies are compared. Inferred cospeciation events are tested by applying an absolute time scale to both the plant and insect phylogenies. The time scales are estimated using a nonparametric rate smoothing method, calibrated on the maximum geological age of the youngest Canary Islands (La Palma and El Hierro; 1-2 Myr). A comparison of the plant and psyllid phylogenies suggests that, whilst rare cospeciation events may play a significant role in promoting diversification, systemic host switching complicates historical reconstructions of psyllid-legume interactions. Psyllids appear to be opportunistic specialists with host switching occurring when the plant lineage fluctuates in geographical abundance, population structure or through dispersal. Although host switching may be frequent, psyllid preadaptation to particular hosts is evident in many cases, and selection of a new host may be constrained by plant chemistry and architecture. Thus, successful establishment by a psyllid colonist is likely to be more common when available hosts are phylogenetically and ecologically related to the original host. A history of parallel cladogenesis between psyllid and legume lineages is rejected in favour of a fluctuating lineage model of co-diversification which presents a more realistic interpretation of the present day pattern of host associations.

### 5.1 Introduction

It has frequently been noted that herbivorous insects may show strong patterns of taxonomic association with their hosts plants (Mitter, Farrell & Futuyma, 1991; Thompson, 1994). However, when cladograms of host and herbivore groups are compared the associations are frequently complicated and show relatively little cospeciation (parallel cladogenesis). The program TreeMap (Page, 1994a) which analyses host-parasite interactions, is designed to maximize cospeciation events when reconciling host and parasite trees. While this is appropriate for situations in which cospeciation is the dominant process, it may not be suitable for 'messy' data sets which have comparatively little cospeciation relative to other types of interaction between host and parasite lineages. Cospeciation is only one of the processes generating patterns of coevolutionary associations, and localized coevolution (both temporal and spatial) may take place between lineages despite historical incongruence (Thompson, 1994). Host switching onto related plants is another process that can possibly maintain taxonomic associations without parallel cladogenesis. I examine here the evidence that systemic host switching in a highly non-random fashion could be a mechanism which explains the observed patterns of strong taxonomic association in plant-herbivore interactions. A more realistic interpretation of the evolution of plant-herbivore associations may be addressed by a fluctuating lineage model described below.

### **5.1.1** *The psyllid-legume system*

Psyllids (Hemiptera, Sternorrhyncha) are sap-feeding insects which complete their life cycle on a single host. They are host specific and widespread on dicotyledonous angiosperms (a few species feed on monocotyledons, and over wintering adults can be found on gymnosperms). One subfamily of psyllids (Arytaininae) contains three closely related genera which are found exclusively on brooms (tribe Genisteae, Leguminosae). The Leguminosae (pea family) comprise one of the largest and most economically important families of flowering plants. Within the legumes, the Genisteae (brooms, gorse and relatives) are a group of, usually shrubby plants, particularly well represented in the Mediterranean.

The three genera of broom-feeding arytainine psyllid (*Arytaina*, *Arytainilla* and *Livilla*) are considered to be a monophyletic group (c. 90 known species) (Chapter 3) which appear to have diversified in parallel with the diversification of the genistoid legumes (c. 260 species). These three genera are only found on genistoid host plants and are most often restricted to a single host species. The Genisteae and their associated psyllids are well represented in the Canary Island archipelago. A detailed survey of the ecology and biogeography of the island species allows the evolution of host-parasite associations to be studied against a background of island radiation. These radiations can then be dated using the geological (K-Ar based) dates of the islands (Ancochea *et al.*, 1994; Guillou *et al.*,1996), as has been done in a study of diversity in Canary Island beetles (e.g. Emerson, Oromí & Hewitt, 2000).

## 5.2 Methods

### 5.2.1 *Tree construction*

Phylogenetic trees were produced using PAUP* (Swofford, 1999) from nuclear (ITS1-5.8S-ITS2) data for legumes and mitochondrial (12S rRNA, and cytochrome oxidase: COI-tRNA-COII) and morphological data for the psyllids, using the same methods as previously described (Chapters 3 & 4). For the legumes, 11 taxa were added from published GenBank sequences (accession numbers given in Table 1) to those previously obtained (Chapter 4). The equally weighted MP searches recovered three equally parsimonious psyllid trees and ten equally parsimonious legume trees. For each group (psyllid and legume) a single tree (identical to one of the equally weighted MP trees) was recovered on successive reweighting (using mean rescaled consistency indices), and these tree topologies were used in subsequent analyses. Although maximum likelihood (ML, molecular data only) for these data and the MP trees were not identical they were broadly congruent.

### 5.2.2 *Rate smoothing*

The reweighted parsimony topologies were used with the ML branch lengths estimated using a ML model, the parameters of which were determined by a nested hierarchical method using Modeltest (Posada & Crandall, 1998). The best model for both data sets, based on Akaike Information Criterion (AIC), was general time reversible with invariable sites and gamma distribution. The ITS branch lengths were used for the legumes and CO branch lengths were selected for the psyllids (see below). As the molecular clock was rejected for all data sets (based on the $\chi^2$ likelihood ratio test with and without the molecular clock enforced, i.e. evolutionary rates are variable across both legume and psyllid lineages), the branch lengths were rate-smoothed using the nonparametric (NPRS) method of Sanderson (1997) as implemented in TreeEdit (Rambaut & Charleston, 2000). The CO branch lengths were used in preference to the 12S branch lengths for the psyllid tree because the increased amount of data in the longer CO region improves the accuracy of the NPRS method (Sanderson, 1997). The rate smoothed trees were age-calibrated using geological dates for the islands of El Hierro and La Palma. These islands were used because they have a single estimated maximum age. The particular node selected for each tree was based on the presence of the most divergent taxon/clade endemic to La Palma or El Hierro. The selected node was assigned with the maximum age of the island (El Hierro, 1.1 Myr for the legumes; and La Palma, 2 Myr for the psyllids). Estimates of the error for the NPRS dates was established using 100 randomly weighted bootstrap replicates. For each bootstrap replicate the branch lengths were estimated for the given psyllid and legume trees, and the distribution of the resulting ages for each node and its standard deviation were calculated using the program r8s (Sanderson, 1997).

### 5.2.3 *Tanglegram*

In order to estimate the amount of cospeciation, the program TreeMap (Page, 1994a) was used to compare psyllid and legume phylogenies using reconciled trees (Page, 1994a, 1994b) (Fig. 1). A heuristic search (default settings) and the proportional-to-distinguishable randomization test (1000 randomizations) were implemented.

### 5.2.4 *Associated nodes*

Inspection of the trees indicated that individual nodes on the psyllid tree could be associated with nodes on the legume tree. In order to determine correspondence between psyllid and legume nodes, psyllid nodes were optimized onto the legume tree using the program MacClade (Maddison & Maddison, 1992) with an accelerated transformation (ACCTRAN). Each psyllid clade was mapped onto the legume tree and the legume node corresponding to this psyllid clade was then recorded (Fig. 2 and Table 2). However, where there is incongruence between psyllid and legume trees, it becomes more difficult to determine the corresponding nodes. I used a default optimization method which associated the psyllid node, with the basal legume node for the present day host or host clade. Where the psyllid node could be optimized to more than one legume node, the oldest legume node was selected. In some cases this led to a nonlinear sequence of legume node ages associated with a linear sequence of psyllid ages (Figs 2 & 4). The hypothetical chronology of psyllid and legume trees was determined by rate smoothing the molecular ML estimated branch lengths on the MP topology (Fig. 2). This allowed corresponding legume and psyllid nodes to be dated. The dates of the associated nodes are compared in Figure 3.

### 5.2.5 *Field observations*

Host specificity was determined by a wide geographical survey in which all relevant legume species in the Canary Islands and adjacent areas were examined for the presence of nymphs and adults (nymphs are apterous, and hence are good indicators of the correct host plant). In all, c. 315 legume populations were examined. Of these, c. 295 had associated psyllid populations. Egg placement and nymphal feeding sites were noted. In most cases samples were made across the geographical range of the host plant, and for many species sampling covered different times of the year in three consecutive years, in order to obtain information on seasonal fluctuations in psyllid populations (see Chapter 2).

## 5.3 Results

### 5.3.1 *Tanglegram*

The 'tanglegram' (Fig. 1) shows a complex pattern of host associations. Little parallel cladogenesis is apparent. However, the randomization test in TreeMap indicates that the 15 cospeciation events (suggested by TreeMap, and indicated by black circles on the nodes in Fig. 1) were significantly greater ($P = 0.005$) than the number expected by chance, and five additional cospeciation events (marked in red in Fig. 1) were recovered when secondary host associations were discounted. Secondary host associations may obscure cospeciation events if psyllids are present on a host only in the absence of the primary psyllid parasite. These results suggest that cospeciation is an important element of psyllid-legume interactions. It should, however, be noted that TreeMap maximizes cospeciation events by tracing the insect-host association back to the most recent ancestral node, and I detail below reasons why this method results in some of the 15 cospeciation events being spurious.

### 5.3.2 *Cospeciation and host switching*

There may be many possible reconstructions of the historical associations between host and parasite when there is incongruence between the phylogenies. Examining the pattern of host associations in terminal sister taxa may provide the best available evidence of historical evolutionary processes. At the tips of the tree there is good evidence for some cospeciation, where sister species of psyllid occur on sister host species (e.g. A, B on Fig. 1). However, many of the cospeciation events suggested by the TreeMap model appear to be spurious (e.g. C, D on Fig. 1). These are nodes in the psyllid phylogeny which represent relatively recent speciation events between psyllids that occur on phylogenetically divergent hosts (see Fig. 2). The reconciliation method implemented in TreeMap traces the host-parasite association back to the most recent common host ancestor, which, as the divergence of the hosts increases, will be mapped to increasingly deeper nodes in the host phylogeny (i.e. young psyllid nodes will map to much older legume nodes). It is more likely that recent host switching to relatively distant host species accounts for the incongruence between psyllid and legume phylogenies. The dynamics that precipitate host switching are interesting because the majority of host legumes are associated with a single psyllid species, if host switching is common one might expect multiple psyllids on a single host. Field data on the conditions under which host sharing by psyllids can occur is therefore important (see below).

### 5.3.3 *Optimization and dating of nodes*

Figure 3 indicates that the majority of the psyllid nodes are markedly younger than their associated legume nodes in this reconstruction (i.e. the majority of comparative points in Fig. 3 fall below the diagonal and are therefore not contemporaneous cospeciation events). The relatively younger psyllid nodes suggest that the general psyllid-host association pattern is not the result of cospeciation but that psyllid colonization is sequential to the origin of the legume hosts.

Where the phylogenies are incongruent the optimization of the psyllid nodes onto the legume tree may result in a nonlinear age sequence for the corresponding legume nodes. This occurs in the event of a host switch from a recently derived host to an evolutionarily older host, in which case the default optimization associates the psyllid node with the basal legume node of the present day host. A more realistic placement of the psyllid node on the legume lineage would be at some point in time further up the branch of the present day host, that would postdate the divergence of the host group on which the ancestral psyllid occurred (this is illustrated in Fig. 4 – B, C and D). Shifting the time of host colonization up the host branch is therefore required to linearize the age sequence of associated host nodes after host switching.

Another example of discordant age sequences between legume and psyllid nodes is evident where the divergence of the psyllid taxa appears to predate the divergence of their present day hosts. A markedly earlier divergence of psyllids relative to their legume hosts is only found in the 'Macaronesian clade' (Table 2, and Figs 2 & 3). The Canarian psyllids provide an isolated endemic group which has an estimated minimum colonization age of 4.8 Myr. The estimated minimum colonization age for the primary host group (*Teline*) in the Canaries is only 3.8 Myr. This age discrepancy (1 Myr) for the initial diversification of the island legume and psyllid lineages may not be significant as the standard deviation for the NPRS dates for all nodes in both psyllid and legume trees is 0.2-0.9 Myr. However, four additional examples in the 'Macaronesian clade' exhibit a greater discrepancy between an earlier psyllid evolution and later host evolution. Two of these examples involve psyllid species which are near the base of the 'Macaronesian clade' (*A.* sp.5 and *A.* sp.6, 2.2-4.6 Myr) but they occur on more recently evolved host species (0.7-2.4 Myr, Fig. 2, nodes 27 & 28; and Fig. 4C). The other two examples involve sister psyllid taxa which occur on sister host taxa (Fig. 2, nodes 35 & 36; and Fig. 4A), but the divergence between the psyllids is > 2 Myr, and the host taxa have identical sequences for the ITS region, giving 0 Myr for the time of host divergence.

As the occurrence of psyllid divergence prior to their host plants is only evident in the 'Macaronesian clade', there may be elements responsible for this pattern that are peculiar to the evolution of the island legume-psyllid associations. On the one hand the psyllids may have evolved and diverged prior to colonizing present day hosts, and then switched to the current hosts without speciating. The plausibility of this scenario depends on how closely related the ancestral hosts were to the present day hosts. If the current and ancestral hosts were distantly related (e.g. *Teline* and *Adenocarpus*), the absence of speciation during the switch to the current host is unlikely, based on the absence of such dual host associations in present day species. Moreover, the independent colonization by sister psyllid taxa of sister hosts would appear to be an unlikely coincidence. A second explanation involves the erosion of genetic divergence between the island host group due to hybridization and introgression, or via introduction of genetic material from more recent colonizations or human introduction. The presence of genetic exchange by these processes may be sufficient to obscure the original age of host divergence.

## 5.4 Discussion

### **5.4.1** *Determinants of host specificity in psyllids*

Evidence from field data, and from the psyllid and legume phylogenies, suggest that plant characteristics (most likely chemistry and surface properties) are important in restricting the host choice of psyllids. The *Adenocarpus* species are extremely abundant in the Canary Islands but have only been colonized by psyllids once. Their chemistry (presence of certain pyrrolizidine and biperidine alkaloids) and glandular surface make them unlike other Canarian legumes. *Chamaecytisus*, on the other hand, has a plant architecture that is superficially similar to *Teline*, and has been colonized four times (see Chapter 3). Three of the colonizations of *Chamaecytisus* were apparently from *Teline*, and were within the same small clade of psyllids which may have been preadapted to make this host switch. The extraordinarily high diversity to area ratio of psyllids in the Canary Islands may partly be explained by the creation of vacant niches each time a legume colonizes a new island. The pattern of psyllid distribution on *Adenocarpus* hosts provides evidence that the presence of a psyllid on a legume prevents colonization by other psyllids (presumably by competetive exclusion). The current distribution pattern is as follows: on Tenerife *A. nigralineata* is restricted to, and abundant on, *A. foliolosus*; whilst *A. proboscidea* is restricted to, and abundant on, *A. viscosus*. Under these conditions *A. proboscidea* is never found on *A. foliolosus* except in the extensive host hybrid zones. On La Palma, however, only one psyllid is present, *A. proboscidea*, and although it is more abundant on its primary host here, it can also be found on *A. foliolosus* (which, on La Palma, lacks its associated psyllid from Tenerife).

### 5.4.2 *Determining factors of psyllid occurrence on hosts*

Field survey data indicate that rare legumes (even from clades otherwise associated with psyllids) tend to lack psyllids. For instance, *Genista benehoavensis* is a rare species, presently with > 1000 individuals, but in the 1970s there were less than 50 individuals recorded (Santos-Guerra, 1975). *G. benehoavensis* lacks a psyllid but its sister taxon on Madeira, *G. tenera*, is a common species and has an associated psyllid which is part of a clade of *Teline*-feeding psyllids, which suggests that the phylogenetic switch from *Teline* to *Genista* is not prohibitive, but insufficient host abundance may have prevented *G. benehoavensis* from being colonized. In another example *Teline gomerae*, *T. nervosa* and *T. pallida* (< 2000 individuals each) lack psyllids, although this legume clade includes the host species *T. rosmarinifolia* and *T. splendens*, with > 3000 individuals each. No legume rarer than 2000 individuals has an associated psyllid, implying that psyllid extinction may occur if a host population drops below a certain level. However, population fragmentation may also be important, e.g. *T. rosmarinifolia*, which occurs in several small populations of c. 500-1000 individuals, and at the time of sampling the associated psyllid was a rare presence in only one of the two populations sampled. Conversely, extremely abundant hosts appear to be very favourable to psyllid association. On Tenerife, *T. canariensis* (with > 10,000 individuals) occurs in several habitats and climatic zones and has four associated psyllids – *A. pileolata* is abundant throughout the range of *T. canariensis*, but the other species tend to be geographically and ecologically restricted. Other common and widespread hosts in the Canary Islands with more than one psyllid are *Teline stenopetala* (with four psyllids) and *Chamaecytisus proliferus* (with three psyllids), and continental examples of the same pattern include *Adenocarpus complicatus* and *Cytisus scoparius* (each with two psyllids).

### 5.4.3 *Fluctuating lineage model*

Analysis of the phylogenetic trees as well as field data, indicate that host switching occurs throughout the diversification of the two groups (i.e. it is systemic). It is also non-random, with host switches to related hosts more typical. The situation in *Adenocarpus* indicates that host switching is unlikely if there is a psyllid already in residence on the host. However, a vacant niche may be exploited initially by a poorly adapted psyllid which gradually becomes selected to suit the host chemistry, phenology and surface characteristics. Evidence of how vacant niches may arise is taken from field data showing the absence of psyllids on rare hosts. If a legume species goes through a bottleneck (resulting in extinction of the psyllid fauna) or a population is established by long distance dispersal without its psyllid (as would be the case in island colonization), it may then recruit a host-switching psyllid when a population expands sufficiently to support a psyllid fauna. Thus, although a lineage may originate with an autochthonous (native) psyllid inherited from its ancestor, it may end up with an allochthonous (foreign) psyllid – though typically from a related legume lineage – thus breaking the parallel cladogenesis pattern.

The evidence presented here suggests that psyllids colonized the Genisteae early in the history of the group, so there is the potential for every broom to have a psyllid, inherited without host switching, from this ancestral association. However, the Genisteae lineage is clearly a fluctuating environment for psyllids and, where host numbers in a lineage drop below a certain level, its psyllid may be lost. If the lineage becomes common again it is an available niche for a psyllid, and can be colonized by a psyllid effecting a host switch. I call this the fluctuating lineage model of co-diversification. However, colonization of a new host is more likely to succeed if the switch occurs from a related host (preadaptation in the psyllid colonist). This model is shown diagrammatically in Figure 5, and may be a more realistic approach to the complex patterns of plant-herbivore associations. Further studies are needed to determine whether there is evidence for this model from other plant-herbivore associations (such as phytophagous lepidoptera; Menken, 1996).

### 5.4.4 *Concluding remarks*

Can historical associations be reconstructed given present distributions? If the hypothetical psyllid and host phylogenies derived from the reconstruction in Figure 5 are analyzed with TreeMap, the resulting TreeMap reconstructions under represents the number of host switches (maximum two host switches in TreeMap, but seven in Figure 5) and over represents the number of cospeciation, duplication (parasite speciation without host speciation) and sorting events (parasite extinction). However, a history of opportunistic host switching and stochastic extinction (such as that illustrated in Figure 5) may never be recoverable, and phylogenetic interpretations may remain susceptible to misinterpretation of the historical associations.

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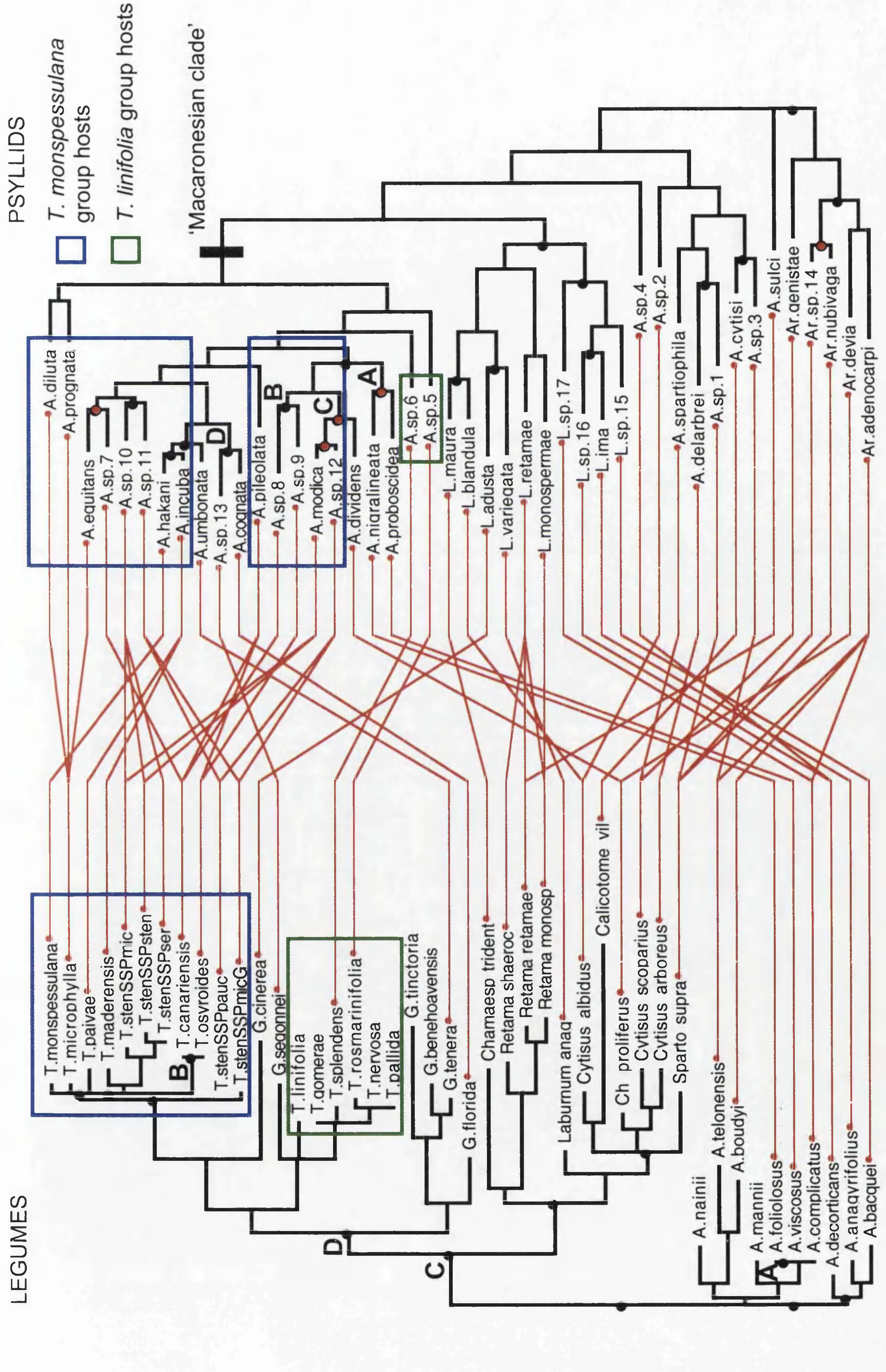
TABLE 1. Genbank accession numbers for 11 additional sequences used in this study.

| species | Genbank accession number | reference |
|---|---|---|
| *Calicotome villosa* | Z72252 + Z72253 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Chamaecytisus proliferus* | Z72234 + Z72235 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Chamaespartium tridentatum* | Z72280 + Z72281 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Cytisus albidus* | AF007472 (ITS1-5.8S-ITS2) | Aïnouche & Bayer, 1999 |
| (= *Chamaecytisus mollis*) | | |
| *Cytisus arboreus* | Z72240 + Z72241 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Cytisus scoparius* | Z72246 + Z72247 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Laburnum anagyroides* | Z72226 + Z72227 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Retama monosperma* | Z72302 + Z72303 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Retama raetam* | Z72304 +Z72305 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Retama sphaerocarpa* | Z72306 + Z72307 (ITS1 + ITS2) | Käss & Wink, 1997 |
| *Spartocytisus supranubius* | Z72250 + Z72251 (ITS1 + ITS2) | Käss & Wink, 1997 |

Opposite page:

FIGURE 1.
Tanglegram showing a complex pattern of host associations between psyllids and their legume hosts.


PSYLLIDS
T. monspessulana group hosts
T. linifolia group hosts
'Macaronesian clade'
A.diluta
A.prognata
A.equitans
A.sp.7
A.sp.10
A.sp.11
A.hakani
A.incuba
A.umbonata
A.sp.13
A.cognata
A.pileolata
A.sp.8
A.sp.9
A.modica
A.sp.12
A.dividens
A.nigralineata
A.proboscidea
A.sp.6
A.sp.5
L.maura
L.blandula
L.adusta
L.variegata
L.retamae
L.monospermae
L.sp.17
L.sp.16
L.ima
L.sp.15
A.sp.4
A.sp.2
A.spartiophila
A.delarbrei
A.sp.1
A.cytisi
A.sp.3
A.sulci
Ar.genistae
Ar.sp.14
Ar.nubivaga
Ar.devia
Ar.adenocarpi
A
B
C
D
LEGUMES
T.monspessulana
T.microphylla
T.paivae
T.maderensis
T.stenSSPmic
T.stenSSPsten
T.stenSSPser
T.canariensis
T.osyroides
T.stenSSPpauc
T.stenSSPmicG
G.cinerea
G.segonnei
T.linifolia
T.gomerae
T.splendens
T.rosmarinifolia
T.nervosa
T.pallida
G.tinctoria
G.benehoavensis
G.tenera
G.florida
Chamaesp trident
Retama shaeroc
Retama retamae
Retama monosp
Laburnum anag
Cytisus albidus
Calicotome vil
Ch proliferus
Cytisus scoparius
Cytisus arboreus
Sparto supra
A.nainii
A.telonensis
A.boudyi
A.mannii
A.foliolosus
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A.decorticans
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A.bacquei
A
B
C
D

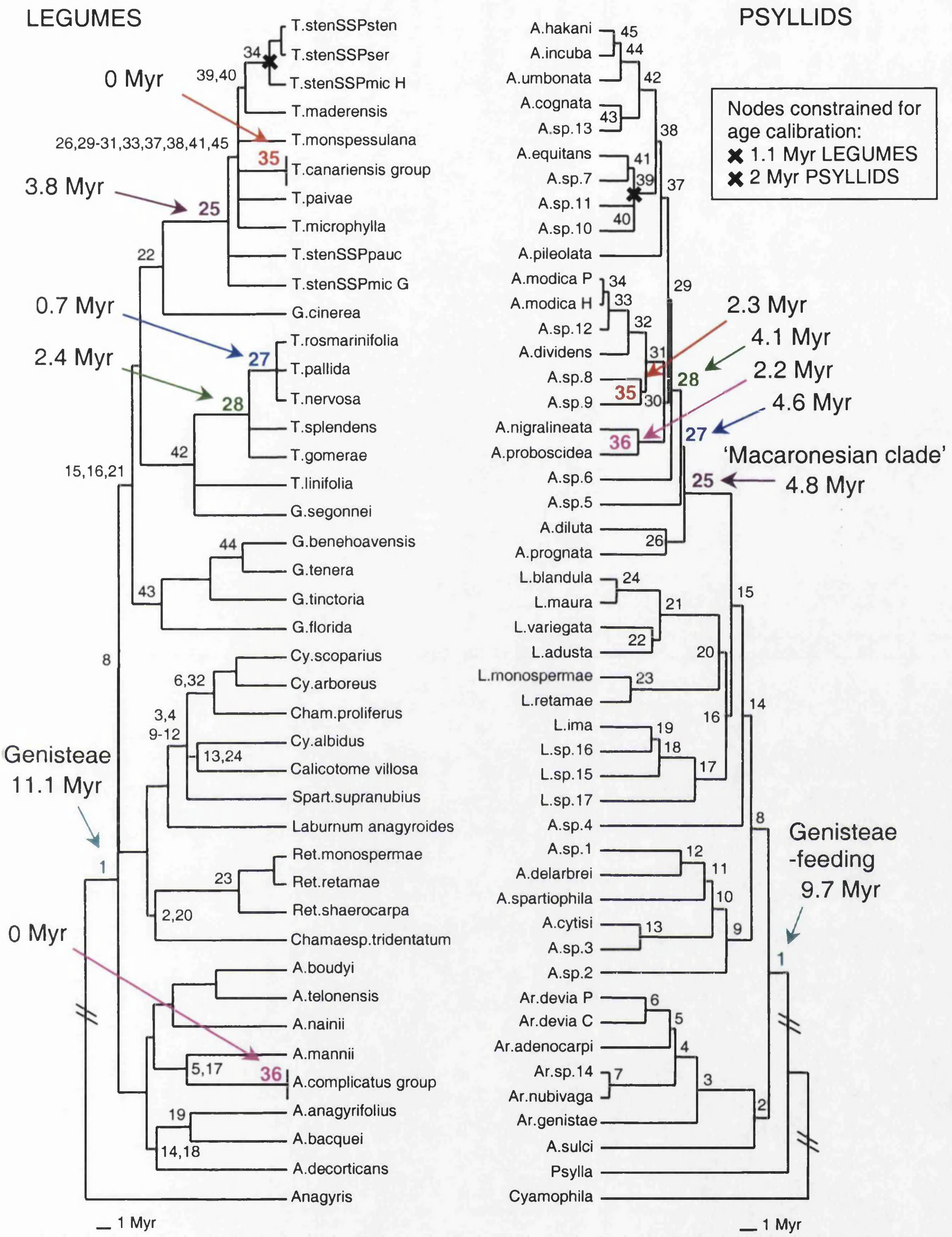
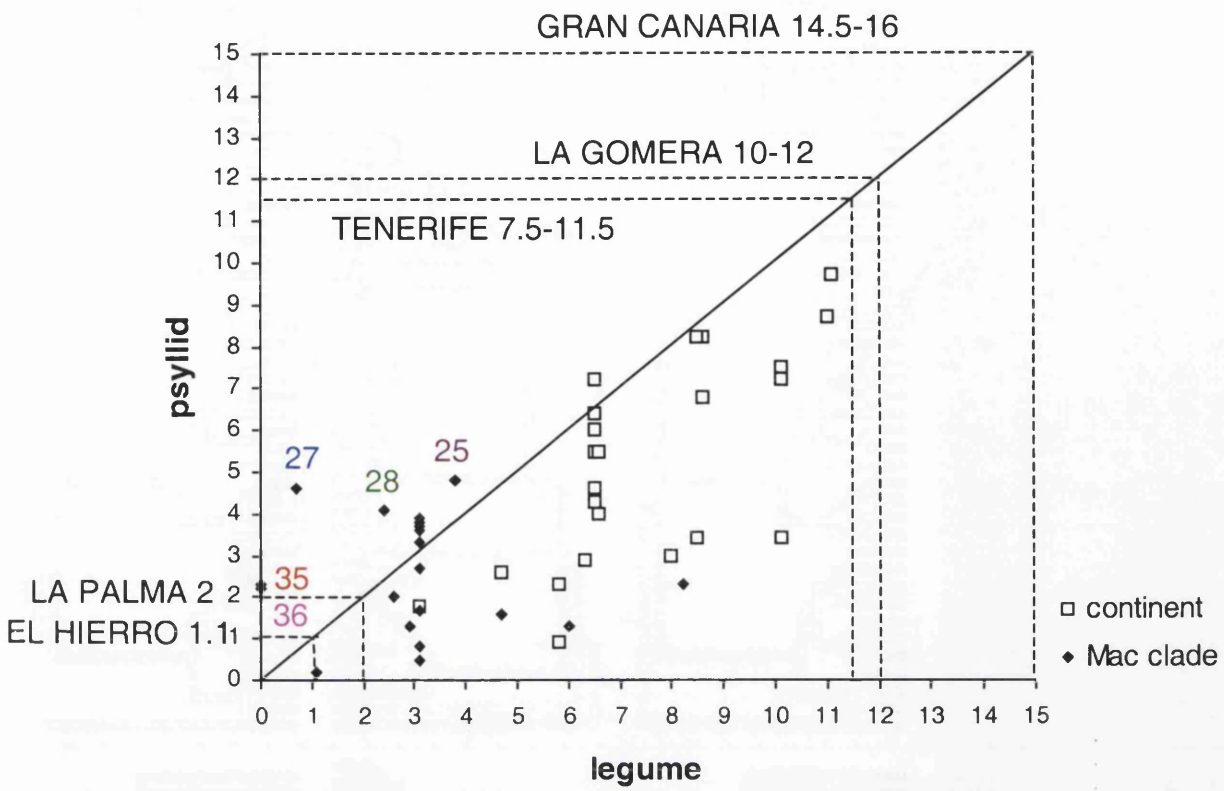


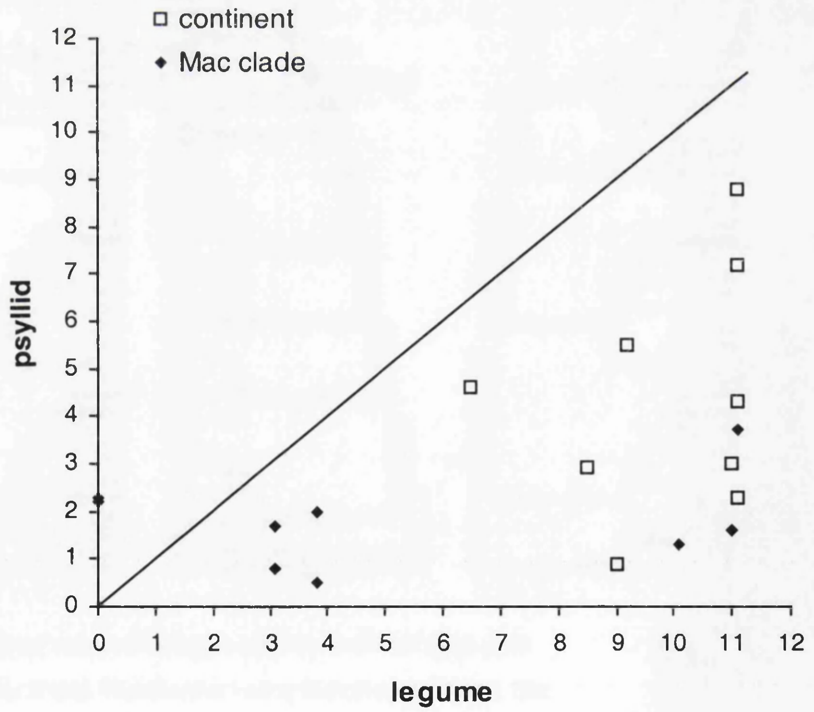
FIGURE 2. NPRS (nonparametric rate-smoothed) trees for the legume hosts and psyllids. Numbered nodes correspond to those in Table 2, and represent the psyllid nodes and the comparative host taxon/group node. The majority of the node ages on the psyllid tree are younger than the age of the corresponding node on the legume tree (i.e. sequential, see Figure 3), including 'node 1' which represents the initial diversification of the Genisteae and the Gensiteae-feeding psyllids. Several nodes (numbered) in the 'Macaronesian clade' of psyllids appear to predate the corresponding node in the legume tree and these are discussed in the text.

TABLE 2. Node number and corresponding ages of nodes in legume and psyllid phylogenies.

| node no. | age (Myr) of legume node | age (Myr) of psyllid node | |
|---|---|---|---|
| 1 | 11.1 | 9.7 | |
| 2 | 8.6 | 8.2 | |
| 3 | 6.5 | 5.5 | |
| 4 | 6.5 | 4.3 | |
| 5 | 6.6 | 4 | |
| 6 | 4.7 | 2.6 | |
| 7 | – | 0.5 | |
| 8 | 11 | 8.7 | |
| 9 | 6.5 | 7.2 | |
| 10 | 6.5 | 6.4 | |
| 11 | 6.5 | 6 | |
| 12 | 6.5 | 4.6 | |
| 13 | 5.8 | 2.3 | |
| 14 | 8.5 | 8.2 | |
| 15 | 10.1 | 7.5 | |
| 16 | 10.1 | 7.2 | |
| 17 | 6.6 | 5.5 | |
| 18 | 8.5 | 3.4 | |
| 19 | 6.3 | 2.9 | |
| 20 | 8.6 | 6.8 | |
| 21 | 10.1 | 3.4 | |
| 22 | 8 | 3 | |
| 23 | 3.1 | 1.8 | |
| 24 | 5.8 | 0.9 | |
| 25 | 3.8 | 4.8 | ↓ 'Macaronesian clade' |
| 26 | 3.1 | 3.8 | |
| 27 | 0.7 | 4.6 | |
| 28 | 2.4 | 4.1 | |
| 29 | 3.1 | 3.9 | |
| 30 | 3.1 | 3.7 | |
| 31 | 3.1 | 2.7 | |
| 32 | 4.7 | 1.6 | |
| 33 | 3.1 | 0.5 | |
| 34 | 1.1 | 0.2 | |
| 35 | 0 | 2.3 | |
| 36 | 0 | 2.2 | |
| 37 | 3.1 | 3.6 | |
| 38 | 3.1 | 3.3 | |
| 39 | 2.6 | 2 | |
| 40 | 2.6 | 2 | |
| 41 | 3.1 | 1.7 | |
| 42 | 8.2 | 2.3 | |
| 43 | 6 | 1.3 | |
| 44 | 2.9 | 1.3 | |
| 45 | 3.1 | 0.8 | |



Node age (Myr) for psyllid and legume phylogenies



Age (Myr) of 'cospeciation nodes' for psyllid and legume phylogenies

FIGURE 3. Comparative ages of psyllid and legume nodes are shown relative to island age. The majority of the node ages on the psyllid tree are younger than the age of the corresponding node on the legume tree (upper plot). Nodes which represent 'cospeciation events' when optimized in TreeMap are shown (lower plot). These would be expected to fall on, or near to the diagonal if they represented contemporaneous speciation events.

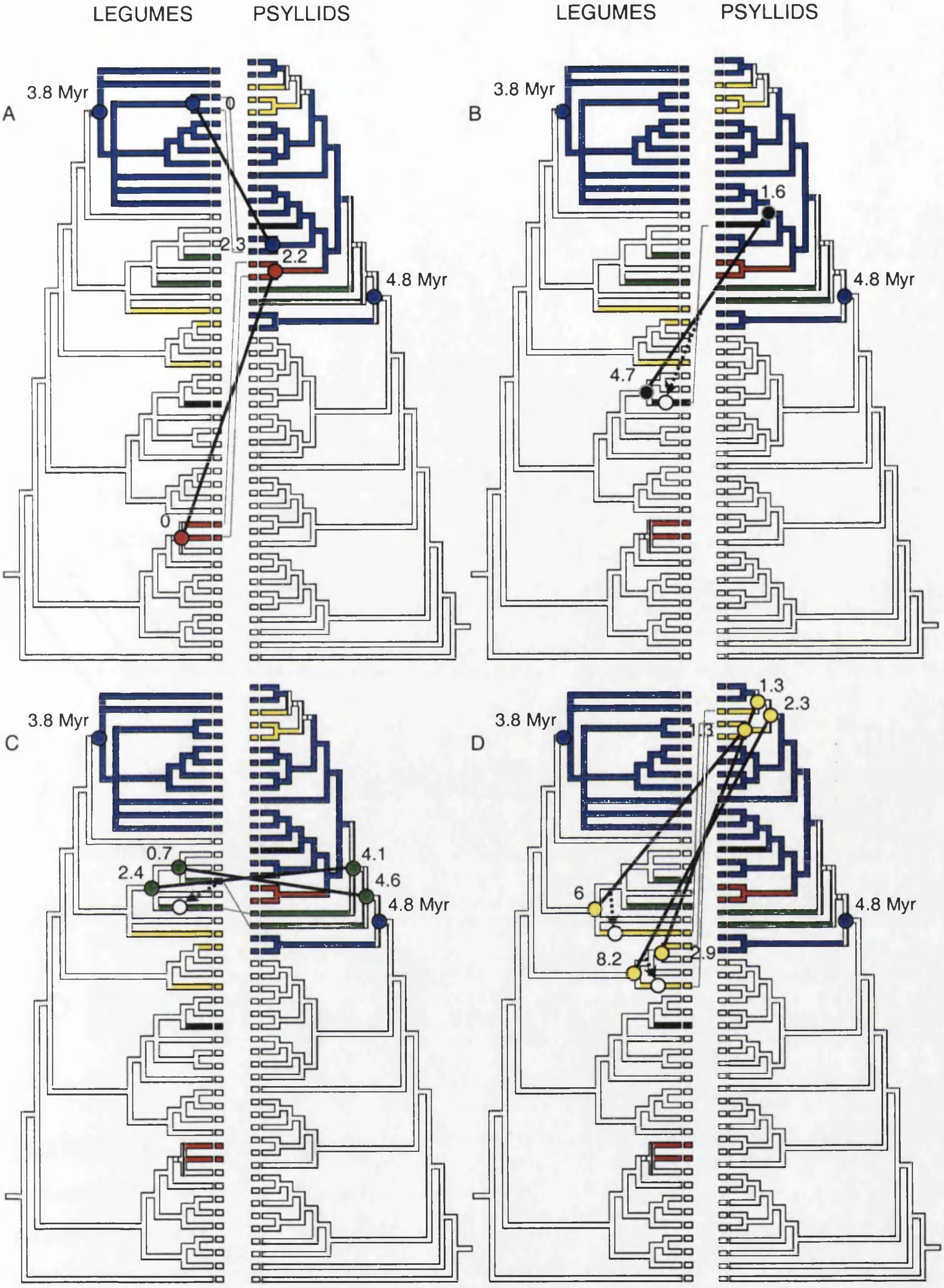


FIGURE 4. Illustration of methods used for associating psyllid nodes with host nodes. Numbers at nodes indicate age (Myr). See text for discussion of optimization methods and interpretation of nonlinear and noncontemporaneous node ages.

HOSTS

- 🟦 *T. monspessula* group
- 🟩 *T. linifolia* group
- 🟨 *Genista*
- 🟥 *Adenocarpus*
- ⬛ *Chamaecytisus*

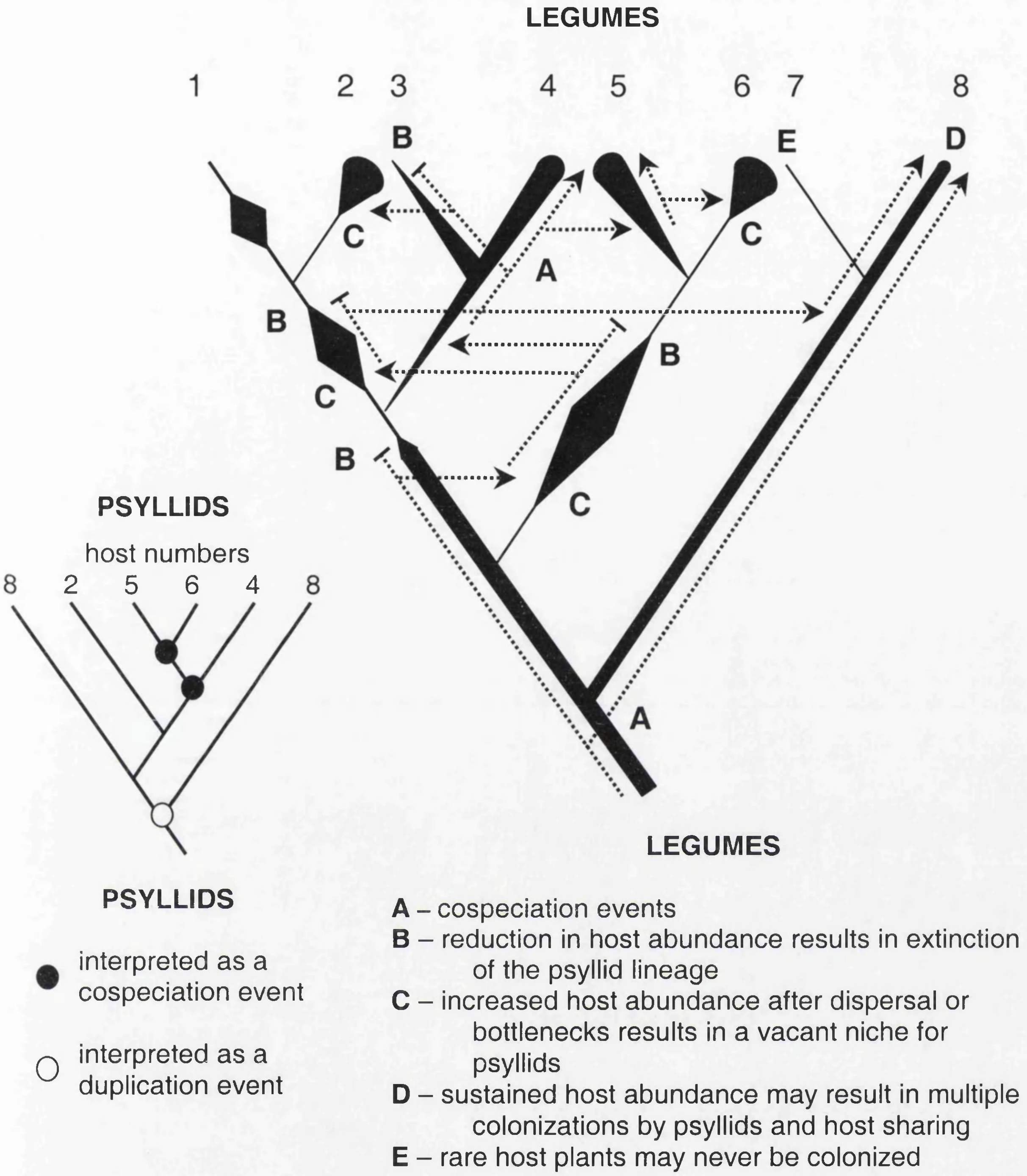


FIGURE 5. Hypothetical reconstruction of a fluctuating host lineage, and in response, opportunistic host switching by psyllids. There are some cospeciation events, but there is a greater degree of host switching, typically between closely related hosts. This history of host switching could not be reconstructed from the resultant psyllid phylogeny shown, and several misinterpretations of the historic associations may arise: such as the divergence of psyllids on hosts 4, 5 & 6, these could be interpreted as cospeciation events as they are sister taxa on sister hosts, but the reconstruction shows that the events are neither contemporaneous, nor is there sustained phylogenetic tracking (i.e. associaton by descent); another case for possible misinterpretation presents the cospeciation event at the base of the phylogeny as a duplication event which assumes sympatric speciation of psyllids on the same host (8) without host switching.

# CONCLUSIONS AND FUTURE WORK

This work highlights the need for concerted efforts towards documenting and describing, as yet unknown biodiversity - particularly those small sized organisms which are so easily overlooked. Several of the 17 new species of psyllid collected and described during this project are rare and their habitats are increasingly threatened. In other instances, psyllids previously recorded from sites - such as *Arytainilla delarbrei* in the Moroccan Middle Atlas - were no longer found in these locations. In the case of *A. delarbrei*, there has been severe overgrazing of the host plants in Morocco. Informed conservation using data on species numbers and distributions is critical to the preservation of biodiversity, which in this case implies knowledge of insects, host plants and host habitats.

Molecular techniques provide a valuable contribution, together with morphological and biological data, to the overall picture of speciation processes and genetic divergence. In particular, there is sometimes a surprising discrepancy between morphological and genetic divergence which emphasises the importance of a combined approach to biodiversity assessments. I would argue therefore, that a comprehensive approach, such as that taken in this study, is the best way forward for evolutionary studies.

Further work towards a broader phylogeny of the psyllids, including Southern African, American and Asian members of the Arytaininae, as well as a larger sampling of the sister subfamily Psyllinae, would help to clarify delimitations between the subfamilies, and to clarify the placement of outlying species/groups. In addition, using selected nuclear genes would provide a comparison to the mitochondrial genes used in this study. As for the host plant phylogeny, further sampling of legume species in, or allied to, the genus *Genista*, in particular, the two continental members of *Teline* section *Chronanthus*, would contribute to an understanding of the genesis of the two *Teline* groups.

Techniques for dating speciation events using molecular phylogenies are developing rapidly and these will be crucial to future analysis of coevolutionary histories of associated organisms. A broader sampling strategy for both legume and psyllid groups, combined with additional DNA data from mitochondrial and/or nuclear genes may result in more robust phylogenies which would facilitate a more accurate comparison of cladogenic patterns.