

Distribution patterns and taxonomy of some legume-feeding psyllids (Hemiptera: Psylloidea) and their hosts from the Iberian Peninsula, Morocco and Macaronesia

DIANA M. PERCY

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Distribution patterns between continental and continental-island sister taxa are compared for some legume-feeding psyllids (Arytaininae, Psylloidea) and their host plants (Genisteae, Leguminosae). The host plant genera *Adenocarpus*, *Chamaecytisus*, *Retama* and *Teline* are characterized by distribution disjunctions, which sometimes match the disjunctions in the associated psyllids. Sister taxa pairs of *Retama*- and *Teline*-feeding psyllids from the continent and Macaronesian islands exhibit a similar geographic disjunction as their host plants, but this pattern is not found in *Adenocarpus*- or *Chamaecytisus*-feeding psyllids and their hosts. In addition, three closely related continental psyllids reflect the distribution of their *Adenocarpus* hosts in the montane regions of Morocco and Andalusía, but are not related to other *Adenocarpus*-feeding species. These examples suggest that among the Genisteae-feeding psyllids, shared distribution patterns with their hosts are localized rather than characteristic of the group as a whole. Six new species of psyllid, which feed on legume shrubs in the Genisteae, and are endemic to the Iberian Peninsula and Morocco, are described and illustrated. These species are in two taxonomically complex arytainine genera, *Arytainilla* and *Livilla*. Immature stages provide additional morphological characters useful for resolving taxonomic relationships within the Arytaininae, and the 5th instar nymphs of several species are described and illustrated. Genistoid-feeding psyllids are not known from all genera in the Genisteae but this may be due to incomplete sampling of rarer genistoid legumes. The majority of psyllids newly described here are narrow range endemics in either Andalusía or Morocco; one species occurs in both Andalusía and Morocco, and one species is more widespread in the Iberian Peninsula.

D. M. Percy, Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK. *Current address:* CSIRO Entomology, GPO Box 1700, Canberra, ACT 2601, Australia (diana.percy@csiro.au).

Introduction

Distributions of phytophagous insects rarely encompass the entire distribution of the host plant. Factors that may account for patchy or stochastic insect demographics include: temporary shifts in patterns of immigration and local extinctions with the formation of metapopulations (Thompson 1994; Hanski & Gilpin 1997); variation in microclimates and host quality (Bernays & Chapman 1994; Schoonhoven et al. 1998); and density of predators and competitors (Denno et al. 1995). If the host plant distribution is disjunct (possibly accompanied by divergence and speciation), such

as between islands and continents or adjacent mountain tops, then dispersal, colonization and establishment opportunities will determine the presence or absence of a similar disjunction in the associated insect fauna. This study gives examples of both the presence and absence of shared distribution patterns among sister taxa of legume-feeding psyllids and their host plants, and I discuss factors that may account for different degrees of coincident distributions.

The west Palaearctic legume-feeding psyllids in the subfamily Arytaininae are most diverse in the Mediterranean basin, NW Africa, and the central Macaronesian islands (Canary Islands and Ma-

deira) (Hodkinson & Hollis 1987; Percy in press). The majority of arytainine psyllids in this region feed on hosts in the legume tribe Genisteae (Papilionoideae). The Genisteae can be divided into the lupins (*Lupinus*, ca. 200 spp.) on which no psyllid species have been recorded, and the brooms (e.g. *Cytisus* and *Genista* groups, ca. 260 species in 20 genera) on which around 91 arytainine species are known. The absence of any psyllids on lupins may be due to differences in the phytochemical profile of *Lupinus* (Polhill 1976; Käss & Wink 1995). However, there are a number of shared chemical profiles between the lupins and the brooms (Käss & Wink 1995), and further collecting from lupins may yet reveal the presence of psyllids on this diverse plant genus.

Among the brooms, about half of the genera are recorded as supporting psyllids, and the apparent absence of psyllids from the remaining genera may be explained either by natural patterns of host colonizations such as constraints on intergeneric host switching, or by an artificial bias of sampling such as under-collecting from certain plants or regions. If a natural pattern, the asymmetrical distribution of psyllids on brooms could reflect either a lack of facility in psyllids to colonize particular hosts or a lack of opportunity to do so. About half of the genera on which psyllids are not recorded are monotypic (e.g. *Argyrocytiscus*, *Cytisophyllum*, *Hesperolaburnum*, *Petteria*, *Podocytiscus*). Although these legume genera may present sufficiently peculiar morphological or phytochemical landscapes to inhibit psyllid colonization, the lack of intrageneric diversity is frequently coupled with rarity or localized distributions, and this may significantly reduce opportunities for psyllids to encounter and colonize these species via a host switch from other brooms. The only monotypic genistoid host genus supporting a psyllid is *Spartium* (host to *Livilla spectabilis*). As *Spartium junceum* is a common and widely distributed species it appears, at least among the broom-feeding psyllids, that lack of opportunities to colonize particular hosts (host rarity) is more likely to predict the presence or absence of a psyllid fauna, than lack of facility (unpalatable or unfamiliar hosts). Another factor influencing the colonization of a legume by psyllids may be the presence of another psyllid species on that host. Host sharing between broom-feeding psyllids is common. However, in continental regions, this is nearly always between psyllids in different genera, suggesting a partitioning

of resources between less closely related species. The pattern in the Canary Islands is unusual, because of the number of congeneric species found on the same host (Percy in press), and the mechanisms by which host resources are partitioned among these taxa is the subject of an ongoing study.

Amongst those broom genera that host psyllids, there is a broad relationship between species diversity in the host and psyllid genera, with the greatest diversity of psyllids found on host genera with 30 or more species (*Cytisus*, *Chamaecytiscus* and *Genista*). This pattern of correlated diversification in legume and psyllid genera may reflect a process of co-diversification, or at least, host mediated diversification of the psyllid group. However, there may also be a tendency for collectors to sample from more commonly found plants, either by more frequent encounter or deliberately to target the more speciose plant genera as potential hosts. For example, there are several genistoid genera with between two to 20 species, which have no, or only few psyllids recorded from them. This study illustrates one example (the genus *Adenocarpus* with 15 species) where it appears that under-collecting, especially from geographically isolated host species (which are unlikely to be encountered by entomologists without specific botanical knowledge), may contribute to a biased interpretation of host preference within herbivorous insect groups. The genus *Adenocarpus* was previously thought to have been colonized rarely by psyllids, only three psyllid species (two in the Canary Islands and one continental) being previously known to feed on this genus (Hodkinson & Hollis 1987). I recently surveyed montane regions of north Africa and southern Iberia specifically targeting the diversity of localized *Adenocarpus* species and found a much more diverse psyllid fauna, including five of the six new species described here.

With the addition of five new *Adenocarpus*-feeding species (and the *Adenocarpus*-feeding habit established for *Livilla ima*), representatives of four broom-feeding psyllid genera are now known to feed on *Adenocarpus* (*Arytinnis*, *Arytainilla*, *Arytainilla* and *Livilla*). *Adenocarpus* is the only genus of brooms with a distribution extending into tropical Africa, with *Adenocarpus mannii* being found in montane regions from Nigeria to Malawi and Angola. Nearly half of the species of *Adenocarpus* are still unsampled, and a further

survey of the remaining species may reveal a greater psyllid diversity and contribute to our understanding of the biogeographic diversity in the broom-feeding Arytaininae.

The monophyly of the Arytaininae is doubtful (Hodkinson & Hollis 1987) and descriptions here of the nymphal morphology for a number of atypical species (*Arytainilla gredi*, *A. sulci*, *Livilla ima* and *Pseudacanthopsylla improvisa*) may contribute to an understanding of the evolution of this group. The nymphal morphology of *Pseudacanthopsylla* is particularly unusual within the subfamily and may provide evidence for the suggested link to South African taxa (Hodkinson & Hollis 1987). Species in the genus *Arytainilla* exhibit more infrageneric divergence in nymphal morphology than other broom-feeding genera, but the nymph of the type species, *Arytainilla delarbrei*, remains unknown.

Material, methods and terminology

Field collections were made during March–July 1998 and March–May 1999. Adults and nymphs were collected by sweeping host plants with a canvas net and stored in 100% ethanol. Host plant material was also examined 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. Pressed plant specimens, deposited at Glasgow University Herbarium (GL) and Royal Botanic Garden Edinburgh (E), were made of all host plants for confirmation of host identification. Presence of adults and nymphal instars was used to assess host specificity. Descriptive terminology follows Hodkinson & White (1979), White & Hodkinson (1982, 1985) and Percy (in press). The following abbreviations are used to indicate institutions in which type material is deposited: The Natural History Museum, London (BMNH); Naturhistorisches Museum Basel (NHMB). Other material is in the collection of the author indicated by DP and a collection number. Sister taxa relationships in the comparison of biogeographic patterns were established from morphological and molecular data for the legumes (Gibbs 1967; Cristofolini 1991; Fran-

cisco-Ortega et al. 1992; Käss & Wink 1997; Percy & Cronk 2002) and psyllids (Hodkinson 1990; Percy 2001).

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

Adults

WL = wing length
 HW = head width
 AL = antennal length
 GC = genal cone length
 PB = distal proboscis segment length
 WLPT = ratio forewing length : pterostigma length
 GCVL = ratio genal cone length : vertex length
 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
 TLFL = ratio hind leg tibia length : femur length

Adult genitalia ♂

MP = proctiger length
 PL = paramere length
 AEL = distal aedeagus segment 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

Nymphs

BL = body length
 BW = body width
 WL = forewing pad length
 CPL = caudal plate length
 CPW = caudal plate width
 RW = circumanal ring width
 HW = head width
 AL = antennal length

Taxonomy

Subfamily ARYTAININAE

Genus *Arytainilla* Loginova

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

Comment. – The full synonymy of this genus is given in Hodkinson & Hollis (1987) and Percy (in press). This genus now includes 12 species after the removal of 18 Macaronesian island species and three continental taxa into the genus *Arytinis* Percy (Percy in press). Nine of these species (in-

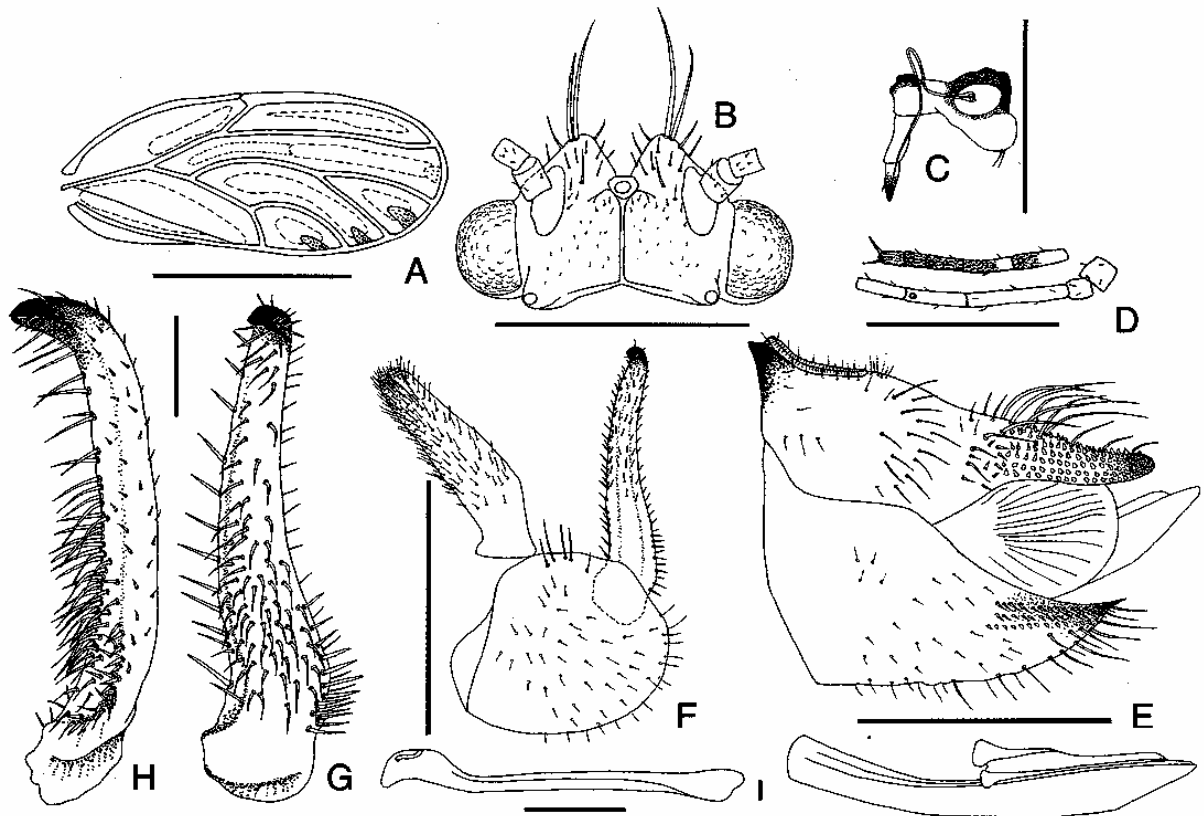


Figure 1. *Arytainilla atlantica* sp. n.: (A) forewing, (B) head, (C) proboscis and clypeus, (D) antenna, (E) ♀ genitalia and ovipositor, (F) ♂ genitalia, (G) ♂ paramere interior view, (H) ♂ paramere posterior view, (I) ♂ aedeagus. Scale bars: A = 1 mm, B-F = 0.5 mm, G-I = 0.1 mm.

cluding two described here: *A. atlantica* sp. n. and *A. telonicola* sp. n.), comprise *Arytainilla* s. str. and share characteristics with the type species (*A. delarbrei*), most notably the massive female genitalia and robust ovipositor. Three outlying species (*A. montivaga* sp. n., *A. gredi* and *A. sulci*) are not included in *Arytainilla* s.str., but remain in *Arytainilla* until further work resolves their correct placement in the evolution of the Arytaininae. These latter three species are atypical in both adult and nymphal morphology, and the 5th instar nymphs are described and illustrated here.

Arytainilla atlantica sp. n.

(Fig. 1, 7A)

Description. – **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, density medium: 40-60 per 0.1mm²; apical spines in wing cells cu₁, m₁ and m₂, but absent, or occasionally few present in cell r₂. Antennae short, with ten segments; genal cones very short, terminal setae as long as, or typically longer than the vertex. One metatarsal spur. Male genitalia as in Fig. 1F-I, paramere apex in dorsal view, contiguous anteriorly with inner margin straight. Female genitalia as in Fig. 1E, ovipositor valvulae ventralis robust, height of valvulae dorsalis less than valvulae ventralis, dorsal margin slightly concave.

Adult measurements and ratios. (3♂, 3♀) total length: ♂ 2.28-2.6, ♀ 2.56-2.92; WL: ♂ 1.76-1.9, ♀ 2.1-2.26; HW: ♂ 0.64-0.66, ♀ 0.68-0.7; AL: 0.99-1.16; GC: 0.06-0.1; PB: 0.1-0.11. WLPT: 6-7.6; GCVL: 0.3-0.53; VLW: 0.45-0.53; WLW: 2.41-2.52; CUR: 1.84-2.05; MR: 0.46-0.57; TLFL:

1.09-1.2. Adult genitalia ♂: MP: 0.38-0.41; PL: 0.5-0.51; AEL: 0.35-0.36; 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.

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 typically 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 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. (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; HW: 0.55-0.63; AL: 0.49-0.62.

5th instar chaetotaxy. Head setae simple and narrowly capitate (both present on anterior margin); antennal setae simple and capitate (small capitate present distally on 3rd and 5th segments); ocular seta simple, small, inconspicuous; primary post-ocular seta distinctly capitate; secondary post-ocular seta capitate, rarely simple. Dorsal thoracic setae short simple and capitate or rod. Forewing pad macrosetae 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 macrosetae 2-3, distinctly capitate, surface and marginal (larger apical, few smaller scattered on surface), proximal seta absent or capitate; capitate and simple microsetae scattered on the wing pad surfaces. Dorsal abdominal pre-caudal macrosetae present on all tergites, short simple and capitate, caudal plate macrosetae 15-21, with the most posterior centrally placed, distinctly capitate; sectasetae four pairs; marginal abdominal setae (other than sectasetae) four pairs, distinctly capitate; pleurite setae paired capitate and simple or capitate only (anterior pleurites with three capitate). Legs with capitate setae present on femora and tibiae; foreleg capitate setae on tibia 1-3 (1 proximal, 1-2 distal);

middle leg capitate setae on tibia 3-5 (1 larger proximally and distally); hind leg capitate setae on tibia 5-6 (1 larger proximally and distally).

Comment. – The adult form is generally similar to *Arytainilla cytisi* and *A. telonicola* sp. n., but the 5th instar nymph, in body shape and chaetotaxy, is more similar to some *Livilla* species.

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

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

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

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

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 18♂, 33♀, 13 nymphs, as for holotype (BMNH). 3♂, 3♀, as for holotype (NHMB). 6 nymphs, Atlantic Coast, c. 35 km S of Essaouira, 31°08'N 9°42'W, c. 100 m, 22.iii.1999 (BMNH). 8 nymphs, as for previous (NHMB).

Other material examined. – MOROCCO: 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, 31°08'N 9°42'W, c. 100 m, 22.iii.1999 (DP 300). 1♀, Atlantic Coast, Jbel Amsittene, 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. n.

(Fig. 2, 7D)

Description. – *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 cu₁, m₂ and c+sc, medium density: 40-60 per

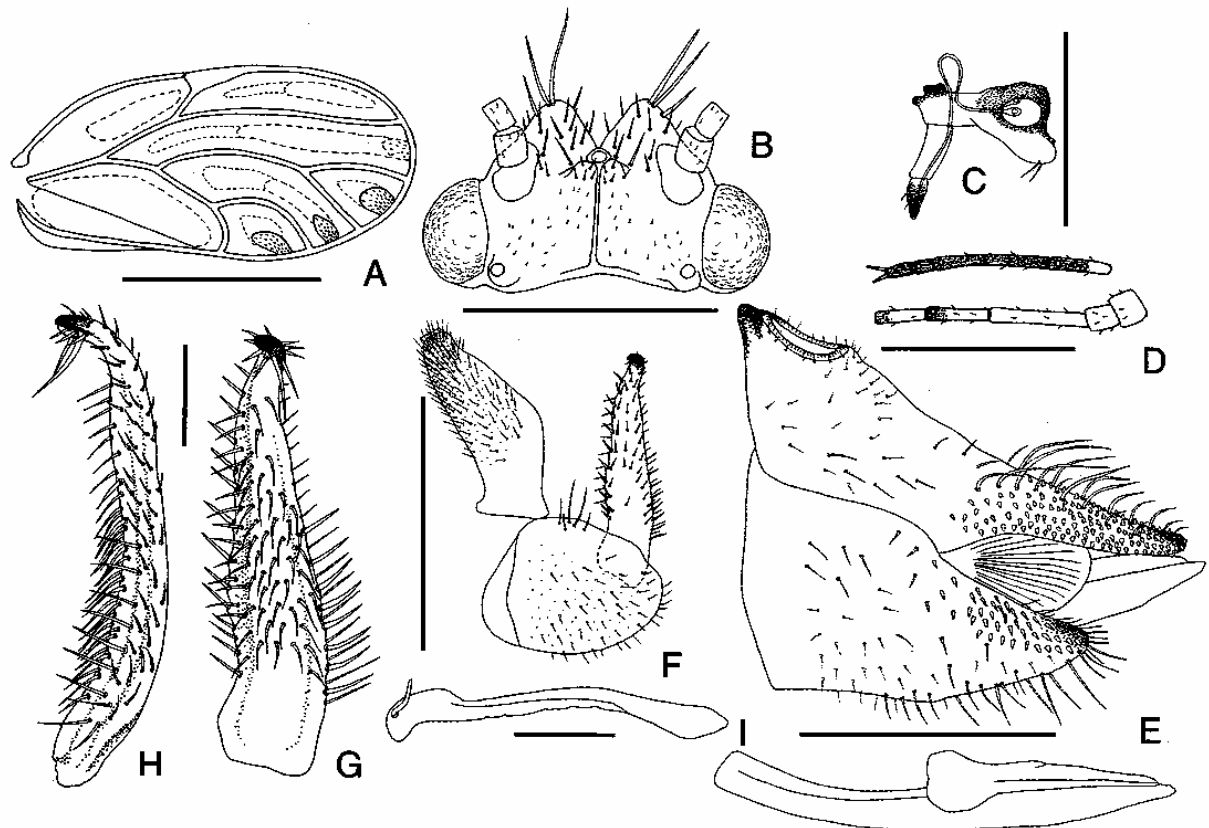


Figure 2. *Arytainilla telonicola* sp. n.: (A) forewing, (B) head, (C) proboscis and clypeus, (D) antenna, (E) ♀ genitalia and ovipositor, (F) ♂ genitalia, (G) ♂ paramere interior view, (H) ♂ paramere posterior view, (I) ♂ aedeagus. Scale bars: A = 1 mm, B-F = 0.5 mm, G-I = 0.1 mm.

0.1mm²; 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, terminal setae typically shorter than the vertex, occasionally as long. One metatarsal spur. Male genitalia as in Fig. 2F-I, paramere apex in dorsal view, contiguous anteriorly with inner margin straight. Female genitalia as in Fig. 2E, ovipositor valvulae ventralis robust; height of valvulae dorsalis less than valvulae ventralis, dorsal margin slightly convex.

Adult measurements and ratios. (4♂, 4♀) total length: ♂ 2.28-2.6, ♀ 2.76-3; WL: ♂ 1.88-2, ♀ 2.28-2.4; HW: ♂ 0.68-0.7, ♀ 0.72-0.77; AL: 1.12-1.22; GC: 0.09-0.12; PB length: 0.11-0.12. WLPT: 5.55-8; GCVL: 0.47-0.6; VLW: 0.42-0.51; WLW: 2.22-2.51; CUR: 1.83-2; MR: 0.51-0.63; TLFL: 1.13-1.23. Adult genitalia ♂: MP: 0.34-0.35; PL: 0.43-0.44; AEL: 0.32-0.34; 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.

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

Structure. Forewing pads and abdomen apically acute. Antennal segments seven. 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 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. (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; HW: 0.62-0.68; AL: 0.7-0.75.

5th instar chaetotaxy. Head and antennal setae simple and club-shaped (small club setae on 1st and 2nd antennal segments and occasionally present distally on 3rd); ocular seta small rod; primary post-ocular seta club-shaped; secondary post-ocular seta indistinct. Dorsal thoracic setae short club-shaped. Forewing and hindwing pads each with one club-shaped macroseta apically and with numerous club-shaped microsetae on the wing pad surfaces, proximal setae indistinct. Dorsal abdominal pre-caudal macrosetae present on all tergites, short club-shaped, caudal plate with one club-shaped macroseta positioned centrally and posteriorly and with numerous club microsetae; sectasetae four pairs (1st reduced); marginal abdominal setae (other than sectasetae) four pairs (1st and 2nd reduced), club-shaped; 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.

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

Host plant. – *Adenocarpus telonensis*.

Biology. – Occurs sympatrically with *Arytaina adenocarpi*. *A. telonicola* sp. n. 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.

Distribution. – Continental: Spain, southern Andalucía.

Etymology. – Named for the host plant.

Type material. – Holotype ♂ (slide mounted), SPAIN: Andalucía, S of Lake Zahara, 36°50'N 5°20'W, c. 500 m, 23.iii.1998 (BMNH). Paratypes 46♂, 27♀, as for holotype (BMNH). 1♂, as for holotype (NHMB). 2♂, 2♀, Andalucía, 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: 1♂, 6♀, 31 nymphs, Andalucía, 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, Andalucía, c. 5 km S of Ubrique, 36°37'N 5°25'W, c. 600-700 m, 24.iii.1998 (DP 140).

Arytainilla montivaga sp. n.

(Fig. 3, 7B)

Description. – *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; 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, density sparse: less than 40 per 0.1mm²; apical spines in wing cells cu₁, m₁ and m₂, but absent, or occasionally few present in cell r₂. Antennae short, with ten segments; genal cones very short, terminal setae typically longer than the vertex. One metatarsal spur. Male genitalia as in Fig. 3F-J, paramere apex in dorsal view, contiguous anteriorly with inner margin straight. Female genitalia as in Fig. 3E, proctiger dorsal profile more or less straight (Spanish specimens) or with a post-anal depression (Moroccan specimens); ovipositor valvulae ventralis slender; height of valvulae dorsalis greater than valvulae ventralis, dorsally convex, wedge-shaped and tapering to the apex. (Moroccan specimens are considerably smaller than those from Spain.)

Adult measurements and ratios. (4♂, 6♀) total length: ♂ 2.44-3.12, ♀ 2.88-3.4; WL: ♂ 1.9-2.4, ♀ 2.43-2.8; HW: ♂ 0.73-0.8, ♀ 0.79-0.88; AL: 1.25-1.49; GC: 0.09-0.11; PB: 0.15-0.17. WLPT: 4.6-8.3; GCVL: 0.4-0.55; VLW: 0.4-0.46; WLW: 2.29-2.38; CUR: 1.5-1.76; MR: 0.46-0.63; TLFL: 1.16-1.25.

Adult genitalia ♂: MP: 0.29-0.38; PL: 0.28-0.42; AEL: 0.23-0.3; 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.

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. Antennal segments seven. 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. Cir-

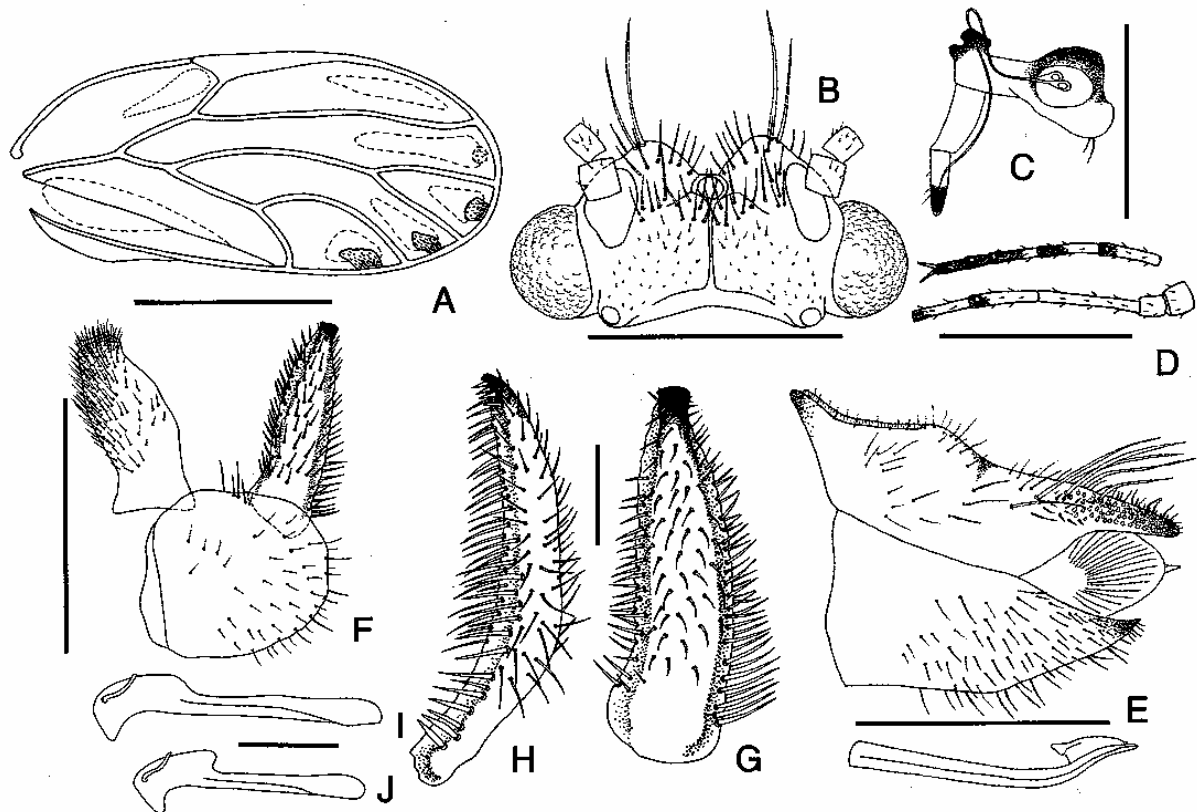


Figure 3. *Arytainilla montivaga* sp. n.: (A) forewing, (B) head, (C) proboscis and clypeus, (D) antenna, (E) ♀ genitalia and ovipositor, (F) ♂ genitalia, (G) ♂ paramere interior view, (H) ♂ paramere posterior view, (I) ♂ aedeagus Spanish populations, (J) aedeagus Moroccan populations. Scale bars: A = 1 mm, B-F = 0.5 mm, G-I = 0.1 mm.

cumanal 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. (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; HW: 0.62-0.79; AL: 0.81-0.84.

5th instar chaetotaxy. Head setae simple and distinctly capitate (simple anteriorly, with few capitate posteriorly; antennal setae simple and capitate (1-2 capitate on the distal end of 3rd and 5th segments); ocular seta simple, long; primary and secondary post-ocular seta distinctly capitate. Dorsal thoracic setae long capitate. Forewing pad macrosetae 12-16, distinctly capitate, surface and marginal (± 8 on the outer margin, 2-4 proximal, 2-4 surface) with simple microsetae scattered on the surface; hindwing pad macrosetae 5-7, distinctly capitate, surface and marginal (2 apical, 2 proximal, 1-3 surface); proximal setae distinctly

capitate. Dorsal abdominal pre-caudal macrosetae present on all tergites, long capitate, caudal plate macrosetae eight distinctly capitate; sectasetae absent (replaced by small simple setae); four pairs of marginal abdominal capitate setae; pleurite setae paired capitate and simple. Legs with capitate setae present on femora and tibiae; foreleg capitate setae on tibia 2 (1 proximal, 1 distal); middle leg capitate setae on tibia 3 (2 proximal, 1 distal); hind leg capitate setae on tibia 3-5.

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 distinct in some aspects of adult morphology. However, although the Moroccan form is smaller in overall size and the shape of the male aedeagus and female proctiger differ slightly, it otherwise shares sufficient similarity to the Spanish form for them to be treated as a single species. The 5th instar chaetotaxy is simi-

lar to *Arytaina* species, while the short genal cones and well developed pterostigma of the adult suggest affinities with *Arytainilla*. However, *A. montivaga* lacks the full suite of characters of either of these genera and thus the placement of this taxon is uncertain.

Host plant. – *Adenocarpus decorticans*.

Biology. – Nymphs were observed on the base of young leaves, in leaf buds and on fruits. Occurs in the mountain ranges of southern Andalusia and northern Morocco. *A. montivaga* is sympatric in the Andalusian mountains with *Livilla baetica* sp. n.

Distribution. – Continental: Spain and Morocco.

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

Type material. – Holotype ♂ (slide mounted), SPAIN: Andalusia, N Sierra de Baza, 37°15'N 2°45'W, c. 1600 m, 22.iii.1998 (BMNH). Paratypes 21♂, 12♀, 47 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, 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 Sierra Nevada, 37°05'N 3°02'W, c. 1850 m, 21.iii.1998 (DP 128).

Arytainilla gredi (Ramírez Gómez)

(Fig. 8B)

Alloeoneura (*Hispaniola*) *gredi* Ramírez Gómez 1956: 92.

Arytainilla gredi (Ramírez Gómez); Hodkinson & Hollis 1987: 42.

Description. – *Adult:* Ramírez Gómez (1956).

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

Nymph: *Colour.* 5th instars with sclerites, wing pads, legs and terminal antennal segments dark 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, 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 and antennal setae simple; ocular seta simple, inconspicuous; primary post-ocular seta simple or narrowly capitate; secondary post-ocular seta simple. Dorsal thoracic setae short and long simple. Forewing pad macrosetae 10, narrowly or distinctly capitate, marginal; hindwing pad macrosetae 2-4, distinctly capitate, marginal (2 apical and 0-2 on the outer margin, occasionally few on the surface); proximal setae simple (sometimes micro); simple microsetae scattered on the wing pad surfaces. Dorsal abdominal pre-caudal macrosetae present on all tergites, long simple and narrowly capitate, caudal plate macrosetae ± 18, narrowly or distinctly capitate; sectasetae four pairs; marginal abdominal setae (other than sectasetae) four or more pairs, narrowly capitate; pleurite setae paired simple, or paired narrowly capitate and simple. Legs with or without capitate setae (often very narrow); foreleg without capitate setae; middle and hind leg capitate setae on femora and tibiae, on middle tibia 1-2 (typically 1 proximal and 1 distal, occasionally only distal present); on hind tibia 1-2 (typically 1 proximal and 1 distal, occasionally only distal present).

Comment. – There is a superficial similarity in the male and female genitalia to *A. spartiophila*. However, in many respects, notably the smaller size and shape of the ovipositor, and the nymphal morphology, 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 it is possible that these specimens are not the same as the type species. However, no material from which the original description was made exists, and this discrepancy will remain unresolved until further collections provide more evidence.

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

Distribution. – Continental: Spain. 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, but it is uncommon.

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)**

(Fig. 8C)

Psylla sulci Vondráček 1954: 81.

Arytainilla egena Loginova 1972: 18 [synonymized by Burckhardt 1989: 318].

Arytainilla sulci (Vondráček); Burckhardt 1989: 318.

Description. – *Adult*: Vondráček (1954), Loginova (1972).

Colour. Yellow-green to yellow-grey, sometimes with bright green or brown abdomen; legs ochraceous to brown; forewing membrane yellowish, veins uniformly pale.

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. Antennal segments seven. 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); 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. Dorsal thoracic setae short simple and long frequently narrowly capitate. Forewing and hindwing pads with numerous distinctly capitate macrosetae, surface, marginal and proximal. Dorsal abdominal pre-caudal macrosetae present on all tergites, long frequently narrowly capitate, caudal plate macrosetae 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); pleurite setae paired capitate and simple. Legs with capitate setae present on femora, tibiae and tarsi, one distally on the femora and numerous on the tibiae.

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

Host plant. – *Retama raetam*, and possibly *Retama monosperma*.

Biology. – Nymphs were observed on the inner surface of the corolla. *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 improvisa* were more common.

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

Material examined. – MOROCCO (ex *Retama raetam* unless otherwise stated): 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).

Genus *Livilla* Curtis

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

Comment. – The full synonymy of this genus is given in Hodkinson & Hollis (1987) and Percy (in press). This is the largest Genisteae-feeding arytainine genus, with 43 species (including those described here). Although *Livilla* was revised by Hodkinson & Hollis (1987) it remains paraphyletic with an anomalous type species group and a number of *Adenocarpus*-feeding species (described below), which are distinct from the remaining *Livilla* species (Percy 2001).

Livilla ima (Loginova), stat. n.

(Fig. 7C)

Arytainilla ima Loginova 1972: 19.

Description. – *Adult*: Loginova (1972).

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.

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. (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; HW: 0.67-0.71; AL: 0.8-0.88.

5th instar chaetotaxy. Head and antennal setae simple; ocular seta simple, inconspicuous; primary post-ocular seta typically capitate, sometimes simple; secondary post-ocular seta absent or short simple. Dorsal thoracic setae short simple. Forewing and hindwing pads each with one apical macroseta, narrowly or distinctly capitate, on hindwing pad paired with small simple seta; prox-

imal setae indistinct; simple microsetae scattered on the wing pad surfaces. Dorsal abdominal pre-caudal macrosetae absent (indistinct small simple), caudal plate macrosetae absent; sectasetae four pairs; marginal abdominal setae (other than sectasetae) three or four pairs, simple (occasionally slightly capitate); pleurite setae paired simple. Legs with or without capitate setae; foreleg without capitate setae; middle and hind leg without capitate setae or one on tibia (distally, often narrow or simple).

Comment. – This species is removed from *Arytainilla* (Loginova 1972) and placed in *Livilla* with the two following species (*L. caprifuga* sp. n. and *L. baetica* sp. n.) based on: reduced or absent pterostigma, long 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. *L. ima* together with *L. caprifuga* sp. n., *L. baetica* sp. n. and *L. complexa* sp. n., form an exclusively *Adenocarpus*-feeding group.

Host plant. – *Adenocarpus anagyriifolius*.

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.

Distribution. – Continental: Morocco. Endemic to the High Atlas where this species and its host plant are locally common.

Material examined. – MOROCCO: 2♀, High Atlas, S of Tizi n' Test, 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, 30°52'N 8°22'W, c. 2030 m, 19.vi.1998 (DP 239). 5♂, 13♀, 22 nymphs, High Atlas, N of Taddert, 31°20'N 7°25'W, 1650 m, 27.iii.1999 (DP 305). 2♂, 11♀, 2 nymphs, High Atlas, S of Taddert, 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, 30°50'N 8°28'W, c. 1800 m, 2.v.1999 (DP 328).

Livilla caprifuga sp. n.

(Fig. 4)

Description. – *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

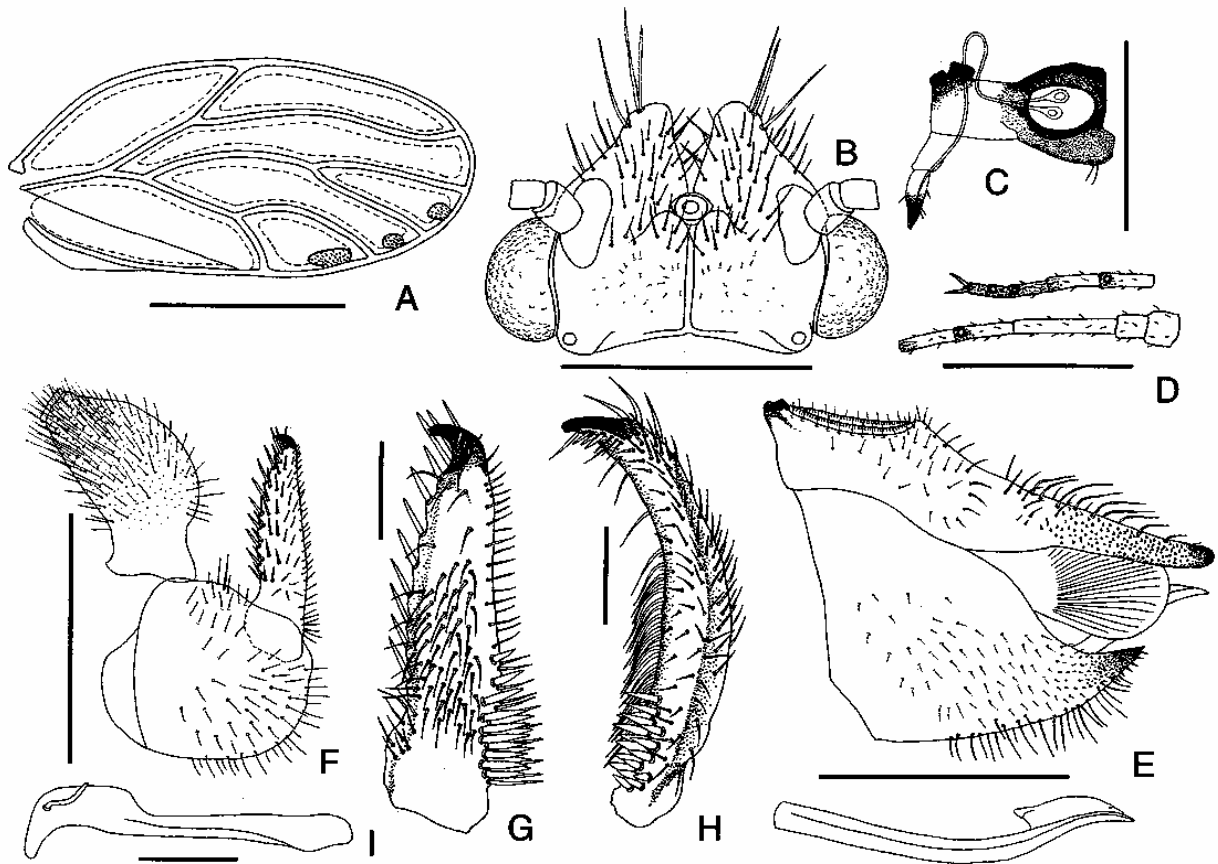


Figure 4. *Livilla caprifuga* sp. n.: (A) forewing, (B) head, (C) proboscis and clypeus, (D) antenna, (E) ♀ genitalia and ovipositor, (F) ♂ genitalia, (G) ♂ paramere interior view, (H) ♂ paramere posterior view, (I) ♂ aedeagus. Scale bars: A = 1 mm, B-F = 0.5 mm, G-I = 0.1 mm.

with more acutely rounded apex; costal break absent (occasionally faint break discernible); pterostigma absent; surface forewing spinules present throughout all cells, very dense: more than 100 per 0.1mm²; apical spines in wing cells cu₁, m₁ and m₂, but absent from cell r₂; hindwing costal margin straight. Antennae short, with ten segments; head deflexed downwards; genal cones long, terminal setae shorter than the vertex. One metatarsal spur. Male genitalia as in Fig. 4F-I, paramere apex in dorsal view, contiguous anteriorly, the inner margin rounded with an acute point. Female genitalia as in Fig. 4E.

Adult measurements and ratios. (4♂, 4♀) total length: ♂ 2.84-3.2, ♀ 3.16-3.4; WL: ♂ 2.35-2.38, ♀ 2.54-2.82; HW: ♂ 0.79-0.82, ♀ 0.81-0.93; AL: 1.13-1.29; GC: 0.17-0.21; PB: 0.14-0.17. GCVL: 0.68-0.87; VLW: 0.45-0.51; WLW: 2.24-2.48; CUR: 1.63-1.93; MR: 0.34-0.51; TLFL: 1.11-1.19.

Adult genitalia ♂: MP: 0.3-0.34; PL: 0.42-0.45; AEL: 0.34-0.36; 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.

Nymph: Unknown.

Host plant. – *Adenocarpus bacquei*.

Biology. – Eggs were found singly on the exterior of leaf buds. The host plant occurs in isolated populations in the eastern High Atlas and Middle Atlas mountains of Morocco. *L. caprifuga* sp. n. was not common in any of the locations sampled and many of the host plants showed signs of over grazing.

Distribution. – Continental: Morocco.

Etymology. – The name refers to the threat posed by large groups of grazing goats on the Middle Atlas plains,

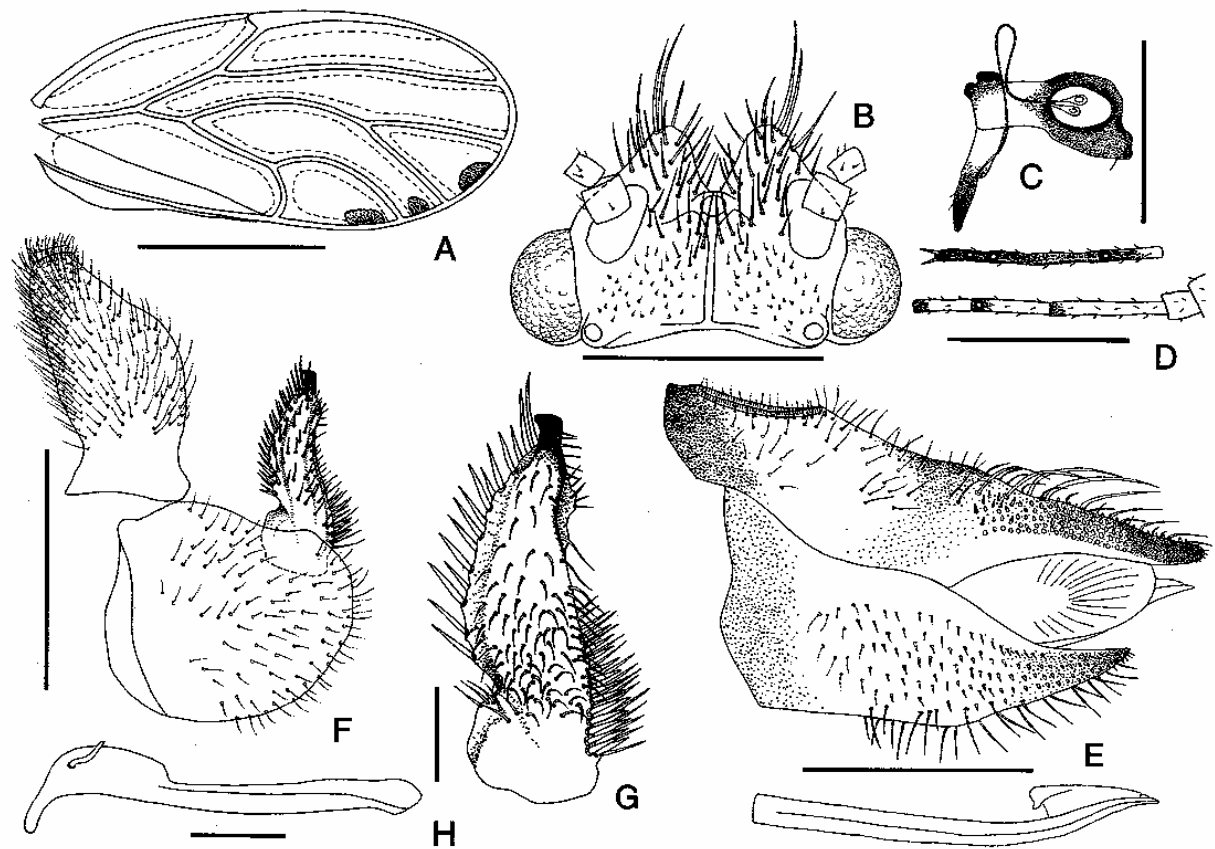


Figure 5. *Livilla baetica* sp. n.: (A) forewing, (B) head, (C) proboscis and clypeus, (D) antenna, (E) ♀ genitalia and ovipositor, (F) ♂ genitalia, (G) ♂ paramere interior view, (H) ♂ aedeagus. Scale bars: A = 1 mm, B-F = 0.5 mm, G-I = 0.1 mm.

which is 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 'fugere' to flee.

Type material. – Holotype ♂ (slide mounted), MOROCCO: Middle Atlas, c. 18 km E of Midelt, S of Zebzate, 32°33'N 4°38'W, c. 1500 m, 29.iii.1999 (BMNH). Paratypes 22♂, 18♀, 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 m, 28.iii.1999 (BMNH).

Other material examined. – MOROCCO: 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. n.**

(Fig. 5)

Description. – *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; surface forewing spinules present throughout all cells, very dense: more than 100 per 0.1mm²; apical spines in wing cells cu₁, m₁ and m₂ but absent from cell r₂; hindwing costal margin straight. Antennae short, with ten segments; head deflexed downwards; genal cones long, terminal setae as long or longer than the vertex. One metatarsal spur. Male genitalia as in Fig. 5F-H, paramere apex in dorsal view, contiguous along inner margin; male subgenital plate dorsal profile raised anteriorly with a distinct step. Female genitalia as in Fig. 5E.

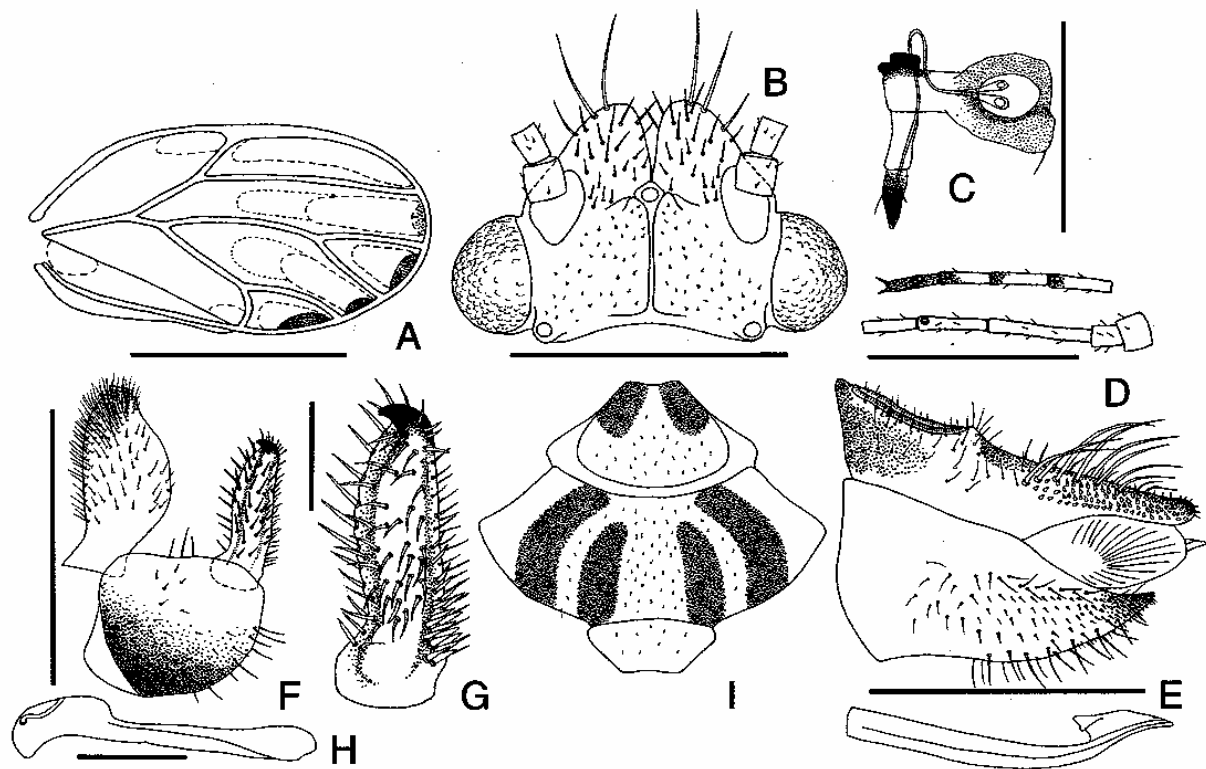


Figure 6. *Livilla complexa* sp. n.: (A) forewing, (B) head, (C) proboscis and clypeus, (D) antenna, (E) ♀ genitalia and ovipositor, (F) ♂ genitalia, (G) ♂ paramere interior view, (H) ♂ aedeagus, (I) thoracic tergal plates. Scale bars: A = 1 mm, B-F = 0.5 mm, G-I = 0.1 mm.

Adult measurements and ratios. (3♂, 3♀) total length: ♂ 3.04-3.2, ♀ 3.36-3.68; WL: ♂ 2.35-2.58, ♀ 2.66-2.84; HW: ♂ 0.81-0.84, ♀ 0.83-0.88; AL: 1.34-1.48; GC: 0.17-0.19; PB: 0.14-0.15. WLPT: 5.16-7.77; GCVL: 0.72-0.76; VLW: 0.44-0.48; WLW: 2.3-2.47; CUR: 1.97-2.09; MR: 0.51-0.58; TLFL: 1.16-1.26. Adult genitalia ♂: MP: 0.46-0.51; PL: 0.41-0.43; AEL: 0.4-0.42; 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.

Nymph: Unknown.

Host plant. – *Adenocarpus decorticans*.

Biology. – Occurs sympatrically with *Arytainilla montivaga* sp. n. 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. n. was absent from host populations sampled in Morocco.

Distribution. – Continental: Spain.

Etymology. – Named for the distribution in southern Spain.

Type material. – Holotype ♂ (slide mounted), SPAIN: Andalusía, N Sierra de Baza, 37°15'N 2°45'W, c. 1600 m, 22.iii.1998 (BMNH). Paratypes 3♂, 9♀, as for holotype (BMNH). 1♂, 2♀, as for holotype (NHMB).

Other material examined. – SPAIN: 1♂, 1♀, Andalusía, N Sierra Nevada, 37°05'N 3°02'W, c. 1850 m, 21.iii.1998 (DP 128).

Livilla complexa sp. n.

(Fig. 6)

Description. – *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; surface forewing spinules present in all cells but confined to small patches at the margins of cells $c+sc$ and cu_2 , 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; genal cones long, terminal setae shorter than the vertex. One metatarsal spur. Male genitalia as in Fig. 6F-H, paramere apex in dorsal view, contiguous anteriorly. Female genitalia as in Fig. 6E.

Adult measurements and ratios. (2♂, 1♀) total length: ♂ 2.36-2.44, ♀ 2.76-2.88; WL: ♂ 1.83-1.93, ♀ 2.13; HW: ♂ 0.71-0.72, ♀ 0.74; AL: 1.13-1.22; GC: 0.15-0.16; PB: 0.13-0.15. WLPT: 6.43-14.2; GCVL: 0.65-0.73; VLW: 0.49-0.53; WLW: 2.03-2.09; CUR: 2.16-2.18; MR: 0.49-0.57; TLFL: 1.17-1.18. Adult genitalia ♂: MP: 0.31-0.33; PL: 0.29; AEL: 0.27-0.28; 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.

Nymph. Unknown.

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.

Host plant. – *Adenocarpus complicatus*.

Biology. – 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 adenocarpis*, it was not common in either of these locations. Although the host plant affiliation can not be certain due to the small number of adults and absence of nymphs, the occurrence of *L. complexa* sp. n. on the same host from two fairly distant geographic regions supports the evidence for an *Adenocarpus*-feeding habit.

Distribution. – Continental: Spain and Portugal.

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

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♂, 4♀, 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).

Genus *Pseudacanthopsylla* Samy

Pseudacanthopsylla Samy 1972: 455. Type species
Pseudacanthopsylla retamae Samy 1972: 455.

Comment. – *Pseudacanthopsylla* was previously a monotypic genus, prior to the transfer of *P. improvisa*. However, though not officially transferred until now, *P. improvisa* has long been recognized as the sister taxon of *P. retamae* (D. Hollis pers. comm.). The generic features include: 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. 8D).

Pseudacanthopsylla improvisa (Loginova), stat. n.

(Fig. 8A, 8D)

Psylla improvisa Loginova 1972: 30.

Description. – *Adult:* Loginova (1972).

Colour. Yellow-grey; forewing membrane clear or faintly yellow, veins uniformly pale.

Nymph: Colour. Grey-green or red; terminal antennal segment brown.

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); antennae with two or more sectasetae on each segment; eyes with several small sectasetae dorsally; primary post-

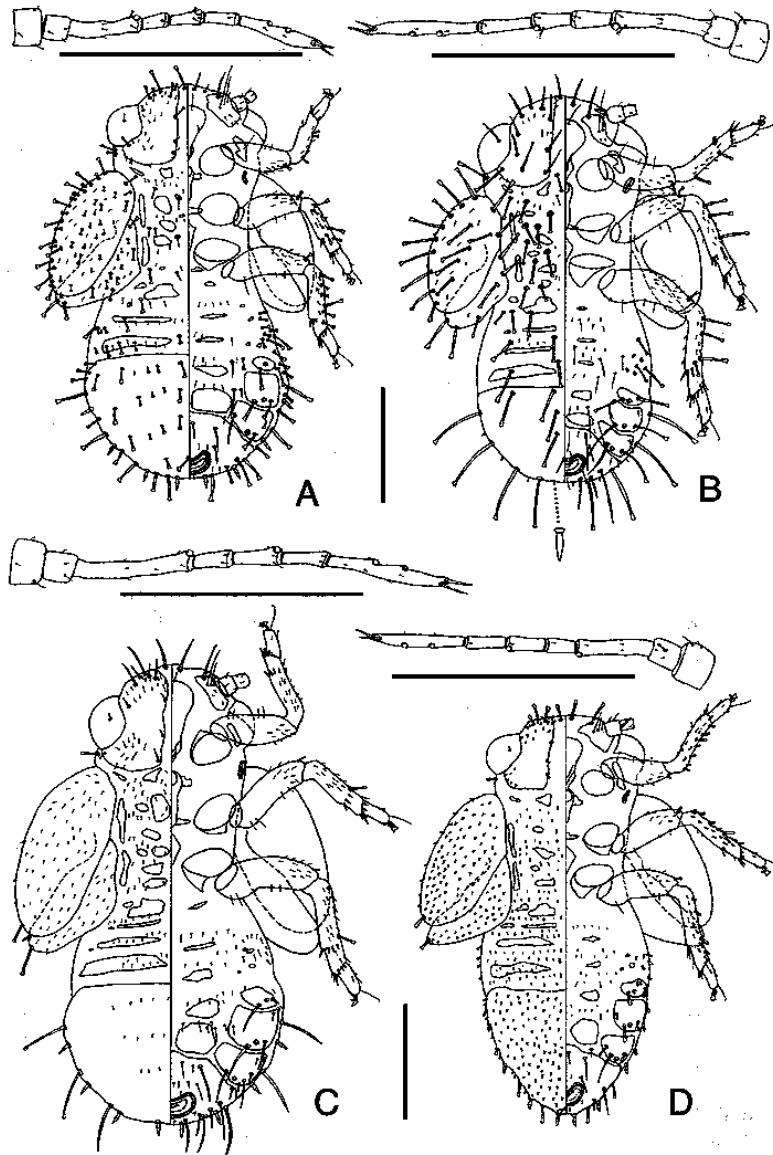


Figure 7. 5th instar nymphs: (A) *Arytainilla atlantica* sp. n., (B) *A. montivaga* sp. n., (C) *Livilla ima*, (D) *A. telonicola* sp. n. Scale bars = 0.5 mm.

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. 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.

Comment. – This species is transferred from *Psylla* (Loginova 1972) to *Pseudacanthopsylla* based on similarities in both adult and nymphal form to *P. retamae* (see the generic features mentioned above). *P. improvisa* differs from *P. retamae* 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). *P. retamae* occurs

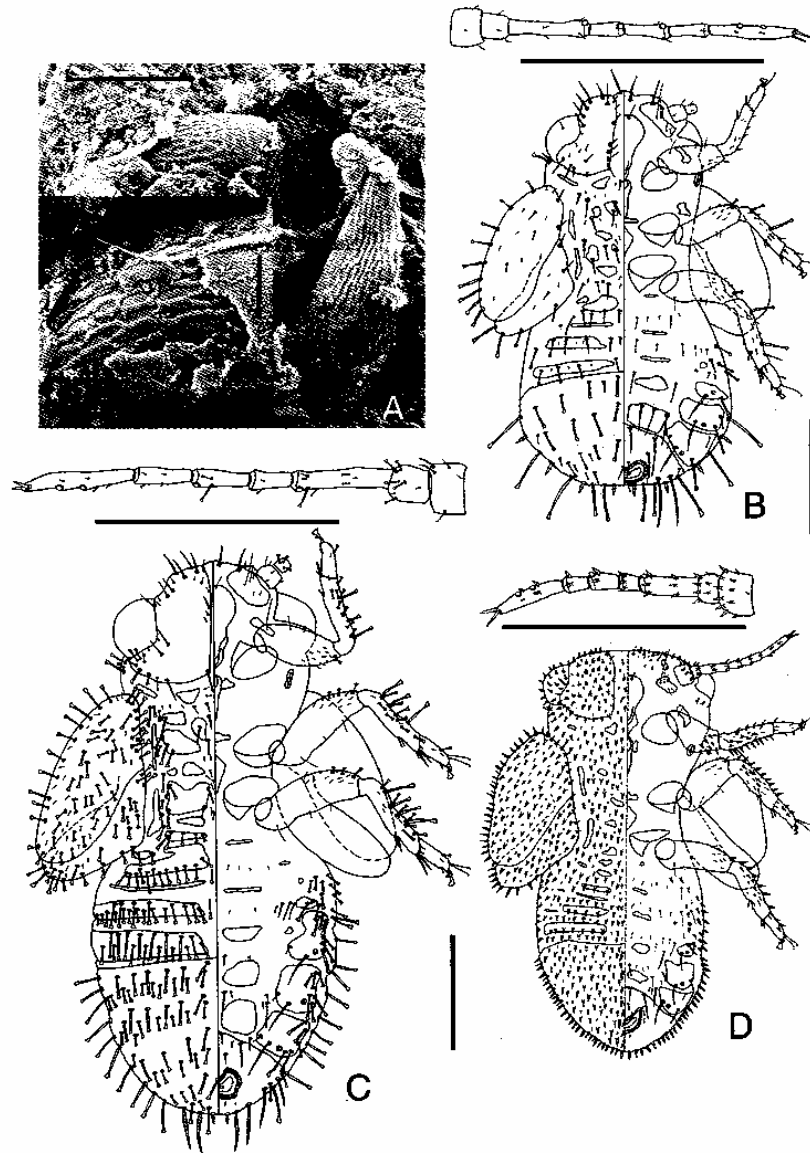


Figure 8. (A) Eggs of *Pseudacanthopsylla improvisa* embedded in the abdomen, showing sculpturing in the chorion layer (scale bar = 0.1 mm, inset = 30 μ m); eggs of all other *Arytaininae* examined were smooth surfaced. (B-D) 5th instar nymphs: (B) *Arytainilla gredi*, (C) *A. sulci*, (D) *Pseudacanthopsylla improvisa*. Scale bars = 0.5 mm.

on populations of the same host plant (*R. raetam*) in the eastern Mediterranean (Samy 1972; Al-Khawaldeh et al. 1997).

Host plant. – *Retama raetam*, and possibly *Retama monosperma*.

Biology. – 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 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 of the egg only, between the vitelline membrane and the egg shell in the chorion layer, suggesting a respiratory or insulatory function for this feature (Fig. 8A).

Distribution. – Continental: Morocco.

Material examined. – MOROCCO: 4 σ , 1 ϕ , Southern Atlantic coast, E side of Agadir, 30°25'N 9°30'W, s.l., 19.vi.1998 (DP 234). 16 σ , 10 ϕ , as for previous except, 23.iii.1999 (DP 301). 11 σ , 12 ϕ , 7 nymphs, as for previous except, 29.iv.1999 (DP 321). 14 σ , 9 ϕ , Atlantic

Coast, c. 15 km S of El Jadid, 32°55'N 8°35'W, c. 100 m, 21.iii.1999 (DP 297).

Discussion

The new species described in this paper allow a comparison of distribution patterns in brooms and associated psyllids. A number of brooms (19 species in five genera) and broom-feeding psyllids (23 species in four genera) are endemic to the Canary Islands and Madeira (Hodkinson & Hollis 1987; Percy in press; Percy & Cronk 2002). In this study, psyllids from Moroccan and Iberian Genisteae, which are sister taxa to Macaronesian host plants, were sampled in order to identify whether sister psyllid taxa are found on sister host taxa exhibiting geographical disjunctions. A shared distribution between hosts and psyllids from the Macaronesian islands and adjacent continental regions is apparent for species of *Arytinnis* and *Livilla* on the host genera *Teline* and *Retama* respectively, but not for *Adenocarpus* or *Chamaecytisus*-feeding psyllids and their hosts.

The two pairs of island-continental psyllid sister taxa that share a similar distribution with their hosts are: *Livilla monospermae* (island) and *L. retamae* (continental) which both occur on *Retama monosperma* (Fig. 9A) (*L. retamae* also occurs on the sister legume taxon to *R. monosperma*, *R. rae-tam*); and *Arytinnis incuba* (island) and *A. hakani* (continental) on *Teline maderensis* and *T. monspessulana* respectively (Fig. 9B). In addition, a small continental *Adenocarpus*-feeding group (*Livilla ima*, *L. baetica* sp. n. and *L. caprifuga* sp. n.) from the Moroccan Atlas and Rif mountains, and the Sierra Nevada mountains of Andalusia, indicate a close link between psyllid and host distribution in this region (Fig. 9E). However, these three continental *Adenocarpus*-feeding species are not closely related to other *Adenocarpus*-feeding psyllids. Both *Adenocarpus* and *Chamaecytisus* (*Cytisus*, section *Tubocytisus* in Cristofolini 1991) have endemic members in the Canary Islands that are hosts to endemic psyllid species (Hodkinson & Hollis 1987; Percy in press). The closest continental relatives of the island plants are found in the Mediterranean in the case of *Adenocarpus* (*Adenocarpus complicatus*, see Käss & Wink 1997; Percy & Cronk 2002), and Morocco in the case of *Chamaecytisus* (*Cytisus albidus* = *Chamaecytisus mollis*, Cristofolini 1991; Francisco-Ortega et al. 1992). However, the psyllids found on island-con-

tinental sister taxa in *Adenocarpus* and *Chamaecytisus* are not closely related, and even belong to different genera (Fig. 9C, D).

These examples suggest that shared legume-psyllid distribution patterns are localized rather than prevalent among the Genisteae and its psyllid fauna as a whole. This patchiness in the extent of shared distributions may be indicative of insect-plant interactions in specialist herbivores generally. The presence or absence of similar distribution patterns between host plants and psyllids where the host distribution is disjunct, is determined by dispersal followed by location and establishment on suitable host plants. Within the broom-feeding Arytaininae there is unlikely to be much difference in dispersal ability, and dispersal (such as between continent and island) is probably related to chance events such as favourable weather conditions. Similarly, postdispersal location of suitable hosts may be due to chance arrival in suitable habitats, but establishment on hosts once located could depend on whether that host is already occupied by psyllids (i.e. available niches). Early dispersal events following soon after the dispersal of the hosts may therefore be more likely to encounter vacant niches, resulting in shared distributions between psyllids and hosts. With increased time after plant dispersal host niches may be filled by horizontal transfer from other hosts (i.e. opportunistic host switching). The timing of speciation events in associated pairs of legume and psyllid sister taxa then becomes critical to interpreting the processes underpinning shared distributions.

Molecular phylogenies for both legumes and psyllids, together with methods of dating these phylogenies, provide a means of investigating whether patterns of shared distributions are accompanied by contemporaneous or near contemporaneous dispersal/speciation events. A molecular study addressing these questions for the Genisteae-feeding psyllids has recently been completed (Percy 2001). This study suggests that the identification and comparison of associated pairs of sister taxa, particularly in recently derived groups of insects and their hosts, will be a valuable means of investigating patterns and mechanisms of cospeciation, sequential host tracking and host switching.

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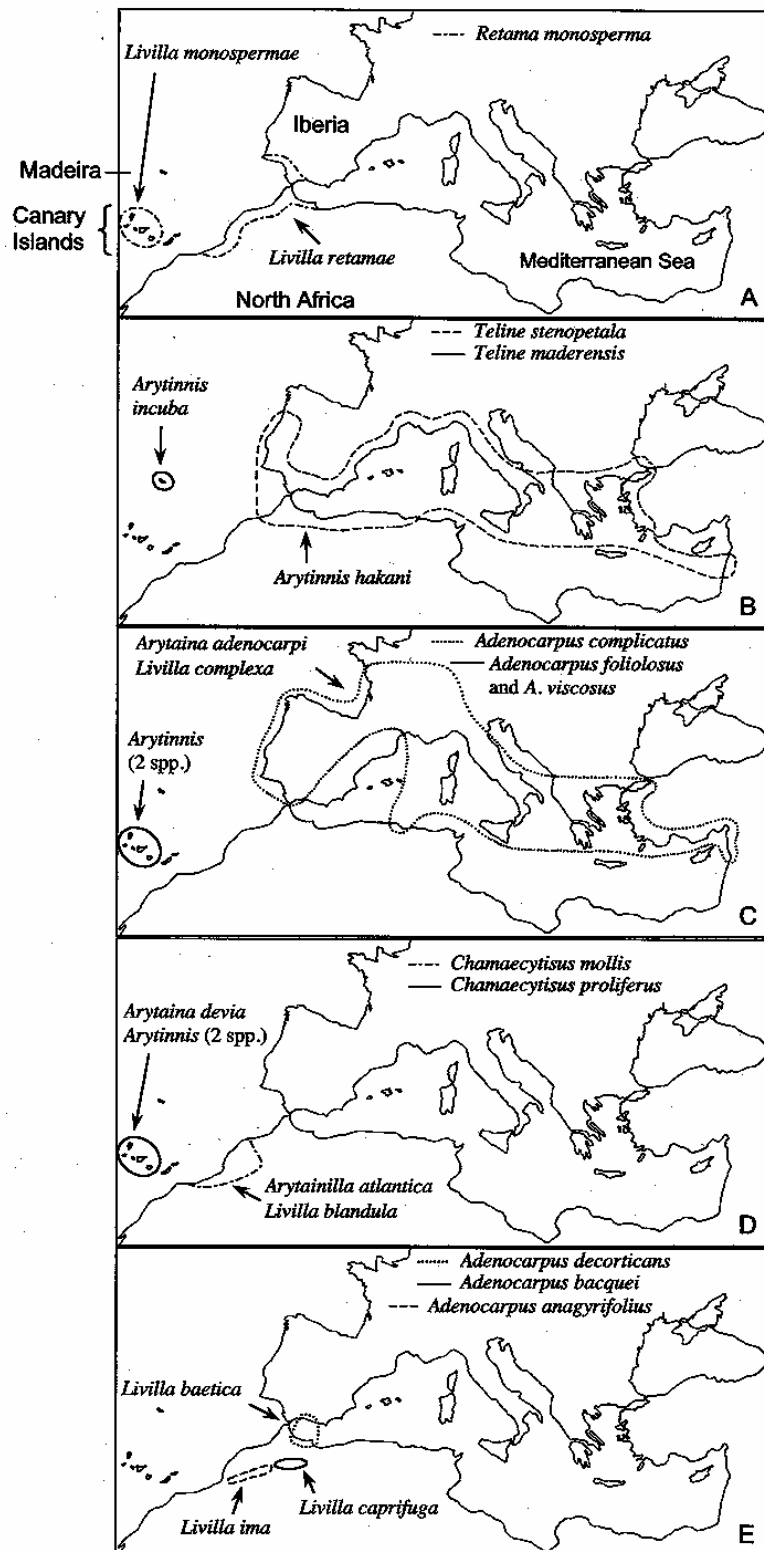


Figure 9. Distributions of sister taxa in legume hosts and psyllids: (A) Disjunction in host distribution is not accompanied by host speciation, as in examples B-E, although speciation has occurred in the psyllids. (B-D) Distributions of sister legume taxa, indicating the associated psyllids. (E) Distribution of a clade of three closely related *Adenocarpus* species restricted to different montane regions, indicating on which host three closely related psyllids are found. See text for discussion.

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