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A new psyllid genus from Taiwan, *Danieliana* gen. nov. (Hemiptera: Psylloidea: Psyllidae)

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Abstract

A new genus, Danieliana gen. nov., in the subfamily Amorphicolinae (Psyllidae) is described, and one new species is described from Taiwan, D. manmiaoyangae sp. nov. The definition of the subfamily Amorphicolinae previously based solely on Amorphicola is broadened to incorporate characteristics of the new genus not shared with Amorphicola. Amorphicola with two species from North America and Danieliana gen. nov. from Taiwan, are strongly supported grouping together in Amorphicolinae based on mitogenome data. The morphological and molecular divergence between the two genera is reflected in the placement in separate tribes within the subfamily (Amorphicolini trib. nov. and Danielianini trib. nov.). The host plant of D. manmiaoyangae sp. nov. is Caesalpinia crista (Fabaceae), and the immatures are free-living with eggs found on emerging foliage. The genus name and species name honour entomologists, Daniel Burckhardt and Man-Miao Yang, who together have contributed enormously to the knowledge of the psyllid fauna of Taiwan, as well as to a wide breadth of research that has furthered our understanding of psyllids.

Key words: Amorphicolinae, Caesalpinia crista, Ciriacreminae, Fabaceae, Psyllidae

Introduction

The subfamily Amorphicolinae Burckhardt, Ouvrard & Percy, 2021 (Psyllidae) was erected by Burckhardt et al. (2021) to accommodate the genus Amorphicola Heslop-Harrison, 1961. Amorphicola is a genus of two species in North America that feed on the papilionoid legume genus, Amorpha L. (Fabaceae). Danieliana gen. nov. was included, as an undescribed genus/species, in the mitogenome analysis of Percy et al. (2018) where it grouped strongly with, yet deeply divergent from, Amorphicola amorphae (Mally, 1894). The majority of adult and immature characteristics used to define the subfamily Amorphicolinae by Burckhardt et al. (2021) are found in Danieliana gen. nov., but inclusion of both genera in Amorphicolinae requires a slightly broader definition of the subfamily. The inclusion of *Danieliana* gen. nov. in Amorphicolinae is well supported but to reflect both the morphological divergence and the deep molecular divergence between Amorphicola and Danieliana gen. nov., I introduce a tribal classification within the subfamily to accommodate these divergent genera. The majority of host plants for subfamilies Amorphicolinae and Ciriacreminae are in the plant family Fabaceae, and most of these are papilionoid and mimosoid legumes (e.g., Burckhardt 2021), with far fewer psyllids recorded from caesalpinoid legume hosts. The host plant of Danieliana gen. nov. is a caesalpinoid legume, Caesalpinia crista L. (Fabaceae). Caesalpinia crista is widely distributed in southeast Asia, Australasia and South Asia and is cultivated in a number of regions, including Africa (Zofou et al. 2013). Not surprisingly for such a widely occurring plant, it is used in numerous different medicinal practices depending on region (Kalauni et al. 2006; Upadhyay et al. 2019). Nearly all parts of the plant are used, including leaves, roots and fruit (Upadhyay et al. 2019), and toxins extracted from the seeds have been used as an insecticidal anti-feedant (Nathala & Dhingra 2006).

Methods

A single field collection was made in January 2010. Specimens were collected in the field into 90–95% ethanol and subsequently stored at -20°C. Ethanol-preserved material was macerated and cleared in 10% potassium hydroxide and clove oil, and then slide mounted in Canada balsam as described in Hodkinson & White (1979). Morphological terminology follows Burckhardt *et al.* (2021), Hodkinson & White (1979), Hollis (1984), White & Hodkinson (1985), and Percy (2003). Single whole specimens preserved in ethanol were used for DNA extraction and sequencing following protocols in Percy (2017) and Percy *et al.* (2018) and deposited in Genbank database. The genus/species described here was also included in the mitogenome analysis of Percy *et al.* (2018) (as "MERGE009_Psyllidae_Genus_sp") and listed in Table 3 as "Genus unnamed (Taiwan)". Specimens were imaged using a Zeiss Axio Scope A1 microscope with imaging software ZEN v2.6; HeliconFocus v8.2.2 and Inkscape v1.2 were used to prepare images for publication; measurements were made with ImageJ (Rasband 1997–2018). Type material is deposited in the Natural History Museum, London, UK (NHMUK), with additional material in my personal collection at the Biodiversity Research Centre, University of British Columbia (DMPC). In addition, recent material from a second collection made this year is included as a photographic record here from material held at the Department of Entomology, National Chung Hsing University (NCHU).

Abbreviations used in the descriptions are as follows (all measurements are recorded in mm). Adults: WL, forewing length; WW, forewing width; HW, head width; AL, antennal length; PB, distal proboscis segment length; WL:WW, ratio forewing length:width; WL:RsL: ratio forewing length:vein Rs length; CUR, ratio forewing cell cu, width:height; MR, ratio forewing cell m, width:height; HM:HCU, ratio height forewing cells m,:cu,; HW:VW, ratio head width:vertex width; VL:VW, ratio vertex length:width; AL:HW ratio antennal length:head width; HW:HT ratio head width:hind tibia length; HT:HF, ratio hind tibia length:femur length. Adult male terminalia: MP, proctiger length; PL, paramere length; AEL, distal aedeagus segment length; PL:HW, ratio paramere length:head width; MP: PL, ratio proctiger length:paramere length; PL:AEL, ratio paramere length:distal aedeagus segment length; AEL: AELH, ratio distal aedeagus segment length:aedeagus apical head length; PL:SH, ratio paramere length:subgenital plate height. Adult female terminalia: FP, proctiger length; FSP, subgenital plate length; RL, anal ring length; OVH, ovipositor valvulae dorsalis height; EL, egg length; EW, egg width; FP:RL, ratio female proctiger: anal ring length; FP:HW, ratio female proctiger:head width; FP:SP: ratio female proctiger:subgenital plate length; EL:EW, ratio egg length:egg width. Immatures: BL, body length; BW, body width; WPL, forewing pad length; CPL, caudal plate length; CPW, caudal plate width; RW, circumanal ring width; HW, head width; AL, antennal length; BL:BW ratio body length: width; HW:AL ratio head width: antennal length; CPW:RW ratio caudal plate width: circumanal ring width.

Taxonomic treatment

Family PSYLLIDAE Latreille, 1807

Subfamily Amorphicolinae Burckhardt, Ouvrard & Percy, 2021

Comment. Burckhardt *et al.* (2021) erected a new subfamily, Amorphicolinae, for the genus *Amorphicola* based on the clade grouping and phylogenetic topology of the mitogenome analyses of Percy *et al.* (2018). The new genus described here was also included in the phylogenetic analyses of Percy *et al.* (2018), but the genus was not described at the time of the revised classification and the definition of subfamily Amorphicolinae was based solely on *Amorphicola*. Here, the subfamily definition is broadened to reflect characteristics of both genera in Amorphicolinae, as follows:

Adult. Amorphicola and Danieliana share head characteristics as described in Burckhardt et al. (2021) except the antenna length which is 1–1.5x head width in Amorphicola and longer, 1.5–1.6x head width, in Danieliana; in addition, there are differences in the relative lengths of the antennal segments which are either with segment 3 longer than segments 7 or 8 (in Amorphicola) or segment 3 shorter than segment 7, and segments 4–6 and 8 subequal (in Danieliana). Thorax and leg characters are as described in Burckhardt et al. (2021), except metatibia is either without (in Amorphicola) or with a small genual spine (in Danieliana), and metatibia apex either bearing

4 irregularly spaced, sclerotised, apical spurs (in *Amorphicola*) or 5 grouped (1+3+1) sclerotised apical spurs (in *Danieliana*). Forewing and hindwing as described in Burckhardt *et al.* (2021). Male proctiger as described in Burckhardt *et al.* (2021); paramere complex, in profile either axe or hammer-shaped with several sclerotised peg setae on the inner face (in *Amorphicola*) or long and sinuous with many long, extended setae on the inner face (in *Danieliana*).

Fifth instar immature. As described in Burckhardt *et al.* (2021).

Systematics. The majority of adult and all immature characteristics for Amorphicolinae given in Burckhardt *et al.* (2021) are shared by *Amorphicola* and *Danieliana*. The main shared characteristics are in the general structure of the adult head, thorax, legs, male proctiger, and elongate male subgenital plate, and in the immature structure and chaetotaxy. The main differences between the genera being antenna length, relative lengths of antennal segments, size of forewing cells cu₁ and m₁, presence/absence of a genual spine on metatibia and number of sclerotised apical metatibial spurs, and the shape of the paramere. Some of the morphological characters of *Danieliana* that differentiate it from *Amorphicola*, suggest an affiliation with Ciriacreminae Enderlein, 1910 (see comment under generic description below), particularly the genus *Isogonoceraia* Tuthill, 1964, which includes two species in South America (White & Hodkinson 1980; Burckhardt & Queiroz 2012) and one in Micronesia (Tuthill 1964). *Isogonoceraia* is also the only member of Ciriacreminae known to have caesalpinoid legume (referring to Caesalpinieae and Cassieae clades of Fabaceae) host plants (Ouvrard 2022), which is the same host plant group as *Danieliana*. Characteristics shared between some members of Amorphicolinae and Ciriacreminae may reflect shared ancestry (e.g., in the root of subfamilies Amorphicolinae, Ciriacreminae and Psyllinae Latreille, 1807), as the two subfamilies are phylogenetically close, or they may be homoplasious and converged in the two groups.

Adult key to genera (and tribes) of subfamily Amorphicolinae

Tribe Amorphicolini trib. nov.

Type genus: Amorphicola Heslop-Harrison, 1961

Morphological description as given in Burckhardt et al. (2021).

Included genus: Amorphicola Heslop-Harrison, 1961

Material examined. *Amorphicola amorphae*, 7 males, 6 females, 5 immatures, White Oak Conservation Park, ~30km north of Jacksonville, ex *Amorpha fruticosa*, 27 May 2005, coll. FL17-05, DM Percy leg. (DMPC).

Tribe Danielianini trib. nov.

Type genus: Danieliana gen. nov.

Included genus: Danieliana gen. nov.

Genus Danieliana gen. nov.

Type species: Danieliana manmiaoyangae sp. nov., by present designation.

Adult structure. Mid-sized psyllid. Head, in profile, moderately inclined at 30–45° from longitudinal body axis (Figs. 1H, 1M). Thorax moderately arched (Fig. 1M). Vertex longer than genae, separated from genae by transverse suture; genae forming diverging conical processes contiguous at base; coronal suture fully developed. Antenna 10-segmented, filiform, equal to or more than 1.5 times as long as head width, segment 3 shorter than segment 7, segments 4-6 and 8 subequal (Figs. 1I, 1J), a single subapical rhinarium on each of segments 4, 6, 8, and 9; terminal seta longer than segment 10 (Fig. 1G). Clypeus slightly flattened ventrally, hardly visible in lateral view, distal proboscis segment short, distinctly exceeding procoxae (Figs. 1F 1H). Thorax moderately arched (Figs. 1H, 1M), width subequal to head width; pronotum ribbon-shaped; mesopraescutum in longitudinal body axis about as long as mesoscutum; propleurites with subequal epimeron and episternum. Legs moderately long (Fig. 1M); metacoxa with moderately large, thorn-shaped meracanthus, length of metafemur and metatibia subequal, base of metatibia with short genual spine, apex bearing 5 (1+3+1) sclerotised apical spurs, basal metatarsus with 2 apical spurs and slightly shorter than apical metatarsus (Fig. 1K). Forewing widest in apical half, broadly rounded apically (Figs. 1A, 1C); membrane semitransparent, covered in densely spaced surface spinules in all cells, but with mostly spinule free areas bordering veins (Fig. 1L); three typical radular spine clusters, one each at apical margin of cells cu, m, and m,, and a fourth less prominent cluster at the apical margin of cell r, (Fig. 1L); costal break developed; pterostigma broad but short; vein R longer than M+Cu; anal break close to apex of vein Cu_{1b}. Hindwing ~0.8 times length of forewing, membranous, costal setae grouped, vein M+Cu developed. Male proctiger one segmented, more or less parallel sided (Fig. 2A); male subgenital plate elongate, about twice as long as high (Fig. 2A); paramere in lateral view simple, long, and slender (Figs. 2B, 2C), with long simple setae on the interior and posterior surfaces, and short simple setae on the exterior surface (Fig. 2C). Female terminalia short (Fig. 2K); proctiger apex acute in dorsal view (Fig. 2G), anal ring narrowly oval and composed of a double row of cells (Fig. 2J); subgenital plate shorter than proctiger, apex blunt in ventral view (Fig. 2H); ovipositor small with valvulae dorsalis low (Fig. 2I).

Immature structure. Body elongate-oval in dorsal view with wing pads protruding (Fig. 3A). Antenna 7-segmented, with last segment showing numerous partial divisions, longest segment 7th, shortest segment 4th, single subapical rhinarium on 3rd and 5th segments, and two on the basal half of 7th segment, with small scattered simple setae and two long stout setae apical and subapical on terminal segment (Figs. 3C, 3D). Head and thorax with scattered long and shorter capitate setae and very short rod-like setae, and a single ocular capitate seta (Fig. 3B). Forewing pads lacking humeral lobes, both forewing and hindwing pads bearing long marginal capitate setae, and shorter capitate setae on the surface (Fig. 3H). Legs bearing capitate and simple setae (Fig. 3I), tarsal arolium longer than claws, fan-shaped with petiole and unguitractor, claws well developed (Fig. 3E). Caudal plate developed, semi-circular and rounded apically, with 4+4 marginal sectasetae and long capitate setae (Fig. 3F). Anus in ventral position, circumanal ring heart-shaped, consisting of a single row of pores (Fig. 3G).

Biology. Immatures are free living on young foliage.

Comment. Previously, Amorphicola, with two species, was the only genus in subfamily Amorphicolinae. Danieliana gen. nov. is sufficiently divergent from the North American Amorphicola based on both morphological and molecular data for these genera to be recognized as separate tribes within subfamily Amorphicolinae. Danieliana gen. nov. is similar to Amorphicola in general body and wing structure as given in Burckhardt et al. (2021). It differs from Amorphicola in having broader forewings with higher cells cu, and m, head with longer, upturned genae, longer antenna with a short 3rd segment (shorter than 7th and subequal to 4th, 5th, 6th and 8th), metatibia with a genual spine and 5 versus 4 apical spurs, paramere long and slender. Some of these differences suggest *Danieliana* gen. nov. shares traits characteristic of the related subfamily, Ciriacreminae (Burckhardt et al. 2021). Ciriacreminae includes 19 genera most of which occur on Fabaceae hosts (Ouvrard 2022). In particular, there is some resemblance to Isogonoceraia Tuthill, 1964, particularly Isogonoceraia venusta Tuthill, 1964 with which Danieliana shares the broad forewing, longer antenna with near equal length of most flagellar sections (Fig. 1J), large pterostigma (wide but short), presence of small genual spine, short female genitalia and somewhat in the shape of the female proctiger. It does not share the elongate vertex, contiguous genae, and peculiar shape of the aedeagus apex. Isogonoceraia includes two described species, with one species in Brazil and one species in the Mariana Islands (Micronesia). Isogonoceraia is also the only member of Ciriacreminae with caesalpinoid legume hosts, a trait also shared with Danieliana

Systematics. Danieliana gen. nov. was included, as an undescribed genus, in the mitogenome analysis of Percy et al. (2018) (referred to as "Genus unnamed (Taiwan)" in Table 3) where it was found to group strongly (97%) in Group U with Amorphicola Heslop-Harrison, 1961. Amorphicola includes two species, both distributed in North

America on hosts in the legume genus *Amorpha* (Fabaceae) (Tuthill 1943; Halbert & Burckhardt 2020; Ouvrard 2022). Group U was recognized as a new subfamily, Amorphicolinae, in Burckhardt *et al.* (2021) to accommodate *Amorphicola*, which is considered well characterised by its paramere morphology and by the *Amorpha* (Fabaceae) host associations. The phylogenetic placement and strong support grouping *Danieliana* gen. nov. with *Amorphicola* in Percy *et al.* (2018) implies it was tacitly assumed included in subfamily Amorphicolinae. The morphological differences between the two genera are also outlined in the revised subfamily definition (above) to accommodate *Danieliana* in subfamily Amorphicolinae.

Etymology. The genus name honours Daniel Burckhardt for his prodigious contribution to our knowledge of psyllids.

Note on species description. *Danieliana* **gen. nov.** is described as a monotypic genus. The species description below provides details of species-specific characteristics not supplied in the generic description above.

Danieliana manmiaoyangae sp. nov.

(Figs. 1, 2, 3, 4)

Adult colour and structure. General body colour bright green, to yellow-green (Figs. 4A, 4C); forewing infused orange-yellow, in some individuals fuscous margins to apical cells. Antenna yellow-green with darker apices on segments 6-8, and segments 9-10 dark. Head and thorax structure as given in generic description, both with scattered short simple setae and longer simple setae on genae, surfaces rugose. Antenna structure as in generic description, with scattered simple setae. Forewing with vein Rs slightly to moderately sinuate (Figs. 1A, 1C). Male proctiger in lateral view, parallel sided with constriction only below apex (Fig. 2A). Male subgenital plate elongate, about twice as long as high, broader basally and tapering apically, in posterior view slightly vase-shaped, well rounded ventrally (Fig. 2E). Paramere in lateral view simple, long, slender and slightly sinuate (Figs. 2B, 2C), in dorsal view with interiorly directed ridge (Figs. 2E, 2F), with long simple setae on the interior and posterior surfaces, and short simple setae on the exterior surface, and one particularly long seta directed anteriorly from the apex (Fig. 2C). Proximal aedeagus segment inflated distally (Fig. 2A, 2D), distal aedeagus segment with bulbous, rounded apex bearing a posteriorly directed flange (Fig. 2D). Female terminalia short (Fig. 2K), in lateral view proctiger post anal ring concave, descending steeply to an upturned apex bearing long setae dorsally (Fig. 2L), apex acute in dorsal view (Fig. 2G), anal ring narrowly oval and composed of a double row of pores (Fig. 2J); ovipositor valvulae dorsalis small and low, with a single blunt serration on valvulae ventralis (Fig. 2I); subgenital plate short, apex blunt in ventral view (Fig. 2H).

Adult measurements (mm) and ratios. (7 males, 3 females). Males 2.7–3, females 3–3.4 (measured from apex of genae to wing apex). WL: 2.01–2.56; WW: 0.89–1.14; HW: 0.73–0.78; AL: 1.11–1.20; PB: 0.09–0.11; WL:WW: 2.12–2.34; WL:RsL: 1.63–1.72; CUR: 1.18–1.42; MR: 0.46–0.55; HM:HCU: 1.88–2.16; HW:VW: 1.63–1.76; VL: VW: 0.51–0.57; AL:HW: 1.49–1.59; HW:HT: 1.63–1.74; HT:HF: 0.98–1.07. Male terminalia: MP: 0.51–0.53; PL: 0.38–0.39; AEL: 0.24–0.26; PL:HW: 0.51–0.52; MP:PL: 1.31–1.37; PL:AEL: 1.50–1.63; AEL:AELH: 2.40–3.00; PL:SH: 1.63–1.90. Female terminalia: FP: 0.53–0.56; FSP: 0.32–0.33; RL: 0.21–0.23; OVH: 0.02–0.03; EL: 0.28; EW: 0.12; FP:RL: 2.43–2.52; FP:HW: 0.71–0.72; FP:SP: 1.7–1.75; EL:EW: 2.33.

Immature colour and structure. 5th instar yellow, green, or blue-green, typically with dark brown to black sclerites, caudal plate, wing pads, and notably, antennal segments 5th and 7th (Fig. 4B). Younger instars usually yellow or orange (Fig. 4A), some with darker sclerites. 5th instar structure and chaetotaxy as in generic description.

Immature measurements (mm) and ratios. 5th instar (n = 5): BL 1.69–1.99; BW 1.12–1.34; WPL 0.55–0.59; CPL 0.42–0.45; CPW 0.77–0.87; RW 0.20–0.21; HW 0.65–0.73; AL 0.89–0.93; BL:BW 1.31–1.60; HW:AL 0.73–0.80; CPW:RW 3.85–4.35.

Egg colour and structure. Orange-yellow (Fig. 4D), broadly ovoid, smooth, with no apparent surface sculpturing or patterning, with a short sub-basal pedicel on the underside, and a long tail (Fig. 2M).

Host plant. Caesalpinia crista (Fabaceae).

Biology. Immatures free-living, and the species is possibly multivoltine (see Discussion).

Note. Despite *Caesalpinia crista* (Fabaceae) being widespread and not uncommon in SE Asia, Australasia and South Asia, *Danieliana manmiaoyangae* is the first psyllid to be described from this plant.

Comment. This is the only species currently known for the genus.

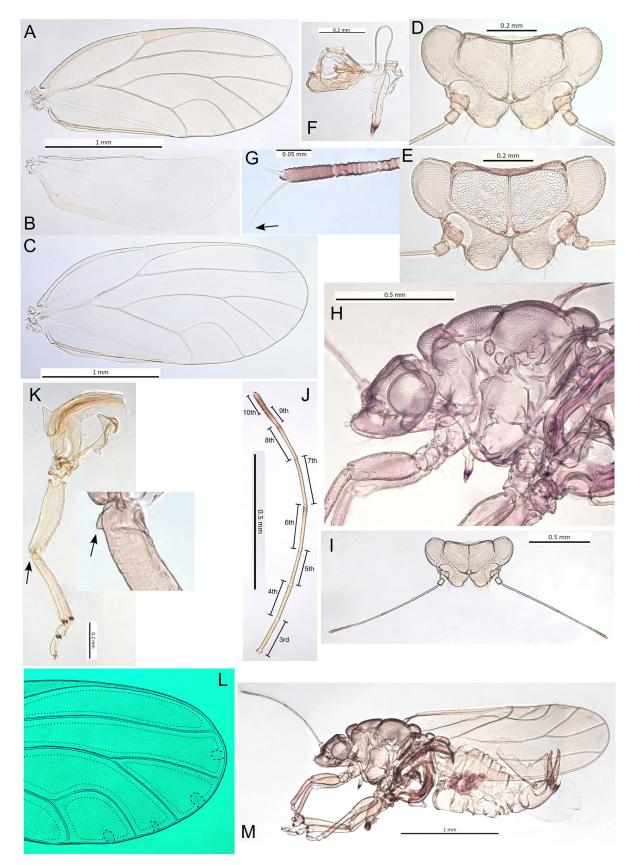


FIGURE 1. Danieliana manmiaoyangae. A, forewing (male); B, hindwing (male); C, forewing (female); D, head (male); E, head (female); F, proboscis; G, detail terminal antennal segments, arrow indicating long subapical seta; H, head and thorax (lateral view, male); I, head and antennae (male); J, antenna indicating segment and relative lengths; K, hind leg with inset detail of genual spine at base of metatibia; L, detail of forewing apex with outlines indicating distribution extent of surface spinules within cells, and position of marginal radular spine clusters; M male (lateral view).

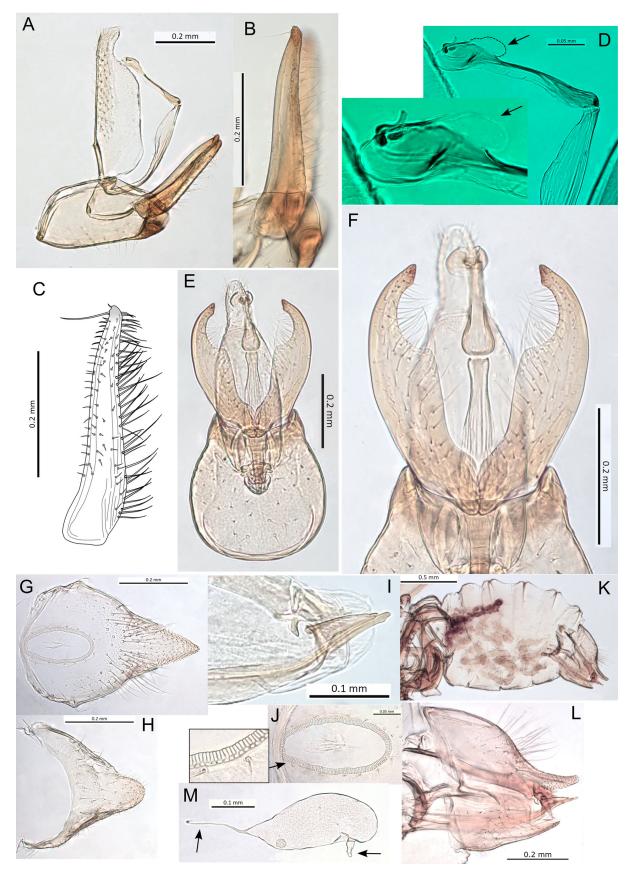


FIGURE 2. Danieliana manmiaoyangae. A, male terminalia; B, paramere; C, paramere illustrating setae; D, distal aedeagus segment with inset detail of posterior flange at the apex (arrowed and outlined); E, male terminalia (posterior view); F, parameres (posterior view); G, female proctiger (dorsal view); H, female subgenital plate (ventral view); I, ovipositor; J, anal ring with inset detail of pores; K, female abdomen; L, female terminalia; M, egg with arrows indicating pedicel and tail.

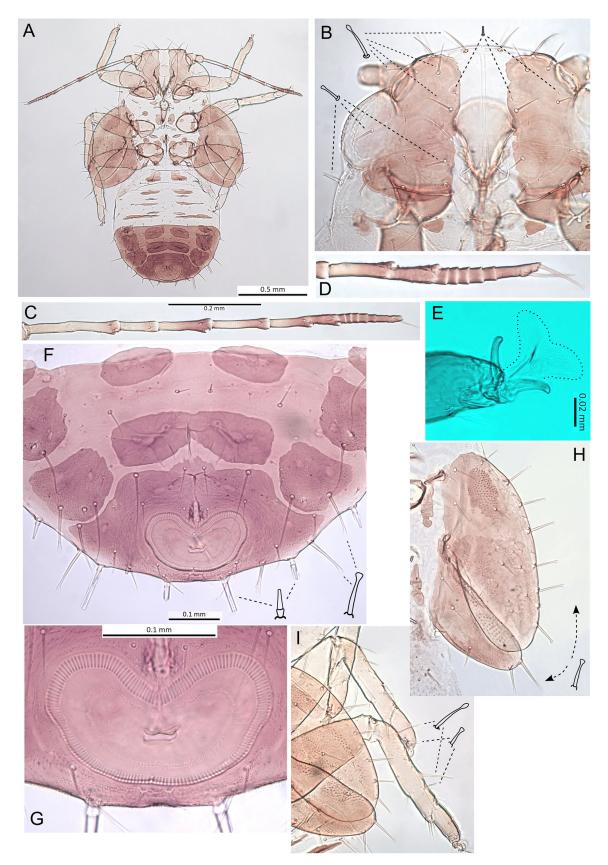


FIGURE 3. Danieliana manmiaoyangae. 5th instar immature. A, 5th instar; B, head detail indicating type and placements of long and short capitate setae (including single ocular seta), and short simple, rod-like setae; C, antenna; D, detail of 7th antennal segment; E, tarsal claws and tarsal arolium (outlined); F, detail of caudal plate indicating placements of long capitate and blunt sectasetae; G, circumanal ring; H, wing pad detail indicating distribution of marginal capitate setae; I, leg detail indicating placements of long and short capitate setae.



FIGURE 4. Danieliana manmiaoyangae on the host plant, Caesalpinia crista. A, Adult male and immatures; B, 5th instar immature, arrows indicating the darker coloured 5th and 7th antennal segments, and arrow indicating long waxy filaments produced from the abdominal sectasetae; C, adult female; D, eggs in and around emerging pinnae of young compound leaves of the host plant, Caesalpinia crista. All photo credits: Yi-Chang Liao.

Systematics. In the mitogenome analysis of Percy *et al.* (2018), this species is recovered in Group U (subfamily Amorphicolinae) as a strongly supported clade (97%) together with *Amorphicola amorphae*.

Genetic resources. Genbank: MG988747 (DPTAI79) for cytochrome oxidase 1 (COI), and MG989051 (DPTAI7910), OR886079 (DPTAI79) for cytochrome b (cytB).

Distribution. Only known from one area (Pingtung) in southern Taiwan.

Type material. Holotype male (slide mounted), Pingtung, Taiwan, N 21.95014, E 120.82314, 189 m, ex *Caesalpinia crista*, 30th January 2010, coll. DPTAI79-10, DM Percy leg. (NHMUK). Paratypes: 20 males (6 slide mounted, 14 in ethanol), 12 females (3 slide mounted, 9 in ethanol), 16 immatures (10 slide mounted, 6 in ethanol), as for holotype (NHMUK, DMPC).

Other material examined. Additional material collected in 2023 by Yi-Chang Liao is the subject of the photographs in Fig. 4, collection details as follows: 10 males, 11 females, 25 immatures; Pingtung Co., Hengchun; 21°57′11.9" N, 120°49′26.7" E; 19 Jan. 2023; YC Liao leg.; *Caesalpinia crista*; NCHU, dry mounted or stored in ethanol.

Etymology. The species name honours Man-Miao Yang in a tribute to her extraordinary contribution to our knowledge of psyllids.

Discussion

The host plant of *Danieliana manmiaoyangae*, *Caesalpinia crista* (Fabaceae), is widespread and not uncommon in southeast Asia, Australasia and South Asia. Due to the wide distribution of this host plant, as well as its use under cultivation in a number of these regions, I initially considered that *Danieliana manmiaoyangae* could be introduced to Taiwan from elsewhere. Moreover, although new psyllid species continue to be discovered and described from Taiwan (e.g., Liao *et al.* 2016; Cho *et al.*, 2020; Tung *et al.* 2020), the psyllid fauna is relatively well studied with more than 165 described species in more than 45 genera (Yang *et al.* 2009, 2013; Ouvrard 2022); it thus seemed less likely that there would be undescribed genera. However, no records of psyllids on *Caesalpinia crista* are known from Taiwan or elsewhere within the native distribution range of the host. Furthermore, the only region in Taiwan where *Danieliana* occurs is in natural forest habitat in the southern part of the island, this is despite the occurrence of *Caesalpinia crista* in other regions of the island. There is a disjunction in records of *Caesalpinia crista* in southern and northern parts of Taiwan (e.g., from iNaturalist observations), and this is possibly because northern records represent planted occurrences, particularly the records near urban and suburban areas.

Just prior to submission of this manuscript for publication, a second collection of *Danieliana manmiaoyangae* was made in the same forested region in southern Taiwan (close to the original collection site) by Yi-Chang Liao, and his collection is represented in the photos in Fig. 4. At the time of my original collection and also during Yi-Chang Liao's recent collection (pers. comm.), numerous adults and immatures were observed, mostly crowded on young foliage. Eggs are likely laid when leaves are in bud and these can be observed on the emerging leaflets (Fig. 4D). Immatures feed on the young foliage and produce copious amounts of honeydew in addition to the long waxy filaments from the abdominal sectasetae (Fig. 4B). In this southern, more tropical part of Taiwan, *Danieliana manmiaoyangae* may be multivoltine when there are multiple flushes of leaf growth per year. The density of individuals observed, together with production of honeydew suggests that this psyllid could have an adverse effect on host growth if it were introduced to regions where *Caesalpinia crista* is grown densely in cultivation. However, such a risk scenario is likely climate dependent as the absence in northern parts of Taiwan, despite the presence of the host plant, is assumed, at least in part, to be due to establishment limitations from unfavourable climatic conditions further north.

The Caesalpinia group is a large pantropical clade of more than 200 species (Gagnon et al. 2016), but only four other psyllid species have been described with host plants in the genus Caesalpinia Plum. ex L. All of these species are in family Psyllidae (Ouvrard 2022), otherwise nearly all the legume-feeders in this family are found on papilionoid and mimosoid legumes. One genus, Isogonoceraia in subfamily Ciriacreminae, occurs on caesalpinoid legumes, and this subfamily is close to Amorphicolinae (with the configuration Amorphicolinae sister to Ciriacreminae plus Psyllinae) (Percy et al. 2018, Burckhardt et al. 2021). Isogonoceraia has two species in Brazil (Burckhardt & Queiroz 2012), and another species found geographically closer to Taiwan in the Mariana Islands (Micronesia) in the western Pacific. The host plant of this latter species, Isogonoceraia venusta, is possibly Cynometra sp. L. (Fabaceae) (Tuthill 1964), also a caesalpinoid legume. Additional molecular systematic work is needed to both confirm the monophyly of South American and Pacific Isogonoceraia and determine if the host plant affiliation reflects a closer phylogenetic position, i.e., between Isogonoceraia and Amorphicolinae. Since subfamily Ciriacreminae is a somewhat heterogeneous group and only six of the genera were included in the molecular analyses of Percy et al. (2018), it may be that the host affiliations prove to be a more accurate systematic indicator than the current taxonomy, a scenario that has been found in a number of other instances (Percy et al. 2018; Burckhardt et al. 2021).

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