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A review of the genus *Capulinia* Signoret (Hemiptera: Coccoidea: Eriococcidae) with description of two new species

T. KONDO[1], P.J. GULLAN[2] & L.G. COOK[3]

[1]*Corporación Colombiana de Investigación Agropecuaria (CORPOICA), Centro de Investigación Palmira, Calle 23, Carrera 37, Continuo al Penal, Palmira, Valle, Colombia, E-mail: tkondo@corpoica.org.co*

[2]*Division of Evolution, Ecology & Genetics, Research School of Biology, The Australian National University, Canberra, Acton, A.C.T. 2601, Australia. E-mail: penelope.gullan@anu.edu.au*

[3]*School of Biological Sciences, The University of Queensland, Brisbane, Qld 4072, Australia. E-mail: l.cook@uq.edu.au*

Abstract

The eriococcid genus *Capulinia* Signoret currently comprises four Neotropical species (the type species *C. sallei* Signoret, *C. crateraformis* Hempel, *C. jaboticabae* Ihering and an undescribed species recognised in the literature) and one species from New Zealand (*C. orbiculata* Hoy). All species feed on plants in the family Myrtaceae and the undescribed species is a pest of guava, *Psidium guajava*, in Venezuela and Colombia. Here we describe the pest species based on the adult female and first-instar nymph and name it *Capulinia linarosae* Kondo & Gullan **sp. n.** We provide a summary of published information on the biology and pest status of *C. linarosae* by translating the Spanish literature. We also describe the adult female and first-instar nymph of a new Argentine species that we name as *C. luma* Kondo & Gullan **sp. n.** after its host *Luma apiculata*. In addition, we redescribe the adult female of *C. jaboticabae* and include notes on *C. crateraformis, C. orbiculata* and *C. sallei*. We provide a revised generic diagnosis and keys to all *Capulinia* species based on adult females and, where available, first-instar nymphs, as well as a revised key to South American eriococcid genera. Phylogenetic analyses of 18S rDNA place *Capulinia* within the "Gondwanan" clade of eriococcids, mostly likely within the Myrtaceae-feeding group.

Key words: Colombia, guava, insect pest, *Psidium*, Venezuela

Resumen

El género de eriocóccidos *Capulinia* Signoret comprende actualmente cuatro especies neotropicales (la especie tipo *C. sallei* Signoret, *C. crateraformis* Hempel, *C. jaboticabae* Ihering y una especie no descrita pero reconocida en la literatura científica), además de una especie de Nueva Zelanda (*C. orbiculata* Hoy). Todas las especies se alimentan de plantas de la familia Myrtaceae y la especie no descrita es una plaga de la guayaba, *Psidium guajava*, en Colombia y Venezuela. Se describe la especie plaga con base en la hembra adulta y la ninfa del primer estadio y se nombra *Capulinia linarosae* Kondo & Gullan **sp. n.** Se provee un resumen de la información publicada sobre la biología y el estado de plaga de *C. linarosae* con base en la literatura escrita en español. También se describe la hembra adulta y la ninfa del primer estadio de una nueva especie de la Argentina y se nombra *C. luma* Kondo & Gullan **sp. n.**, llevando el nombre de su planta hospedera *Luma apiculata*. También se redescribe la hembra adulta de *C. jaboticabae* y se incluyen notas sobre *C. crateraformis*, *C. orbiculata* y *C. sallei*. Se provee una diagnosis genérica y una clave taxonómica para todas las especies de *Capulinia* con base en hembras adultas y las ninfas de primer instar disponibles, así como una clave revisada para los géneros de eriocóccidos Sudamericanos. Análisis con base en el gen 18S rDNA ubican al género *Capulinia* dentro del clado "Gondwánico" de eriocóccidos, aparentemente en un grupo que se compone de especies que se alimentan de Myrtaceae.

Palabras clave: Colombia, guayaba, insecto plaga, *Psidium*, Venezuela

Introduction

The genus *Capulinia* Signoret has four named species and a fifth reported but undescribed species (García *et al*.,

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2016). All species feed on members of the Myrtaceae. Currently the genus includes: the type species *C. sallei* Signoret from Mexico, and perhaps Cuba, and probably restricted to *Eugenia* species (Signoret, 1875; Ferris, 1955; Hodgson & Miller, 2010) (see under the genus entry for further discussion of the host plant of this species); *C. crateraformis* Hempel from Brazil where it induces galls on *Plinia cauliflora* (in literature as *Eugenia jaboticaba*) (Hempel, 1900a); *C. jaboticabae* Ihering also from Brazil on *P. cauliflora*, but not inducing galls (Ihering, 1898; Townsend & Cockerell, 1898; Hempel, 1900a,b); *C. orbiculata* Hoy from New Zealand in the bark and cambium of *Metrosideros* (Hoy, 1958); and an unidentified species from Venezuela referred to in the applied entomology literature as *C*. sp. near *jaboticabae* (e.g., Cermeli & Geraud-Pouey, 1997; Camacho Molino *et al*., 2002; Chirinos *et al*., 2003, 2004) or *Capulinia* sp. (Chirinos *et al*., 2006, 2007) on *Psidium* species.

The species diversity of *Capulinia* probably has been underestimated, given the genus and species diversity of the family Myrtaceae in South America (Govaerts *et al*., 2008); for example, there may be 1000 myrtaceous species in Brazil alone (Landrum & Kawasaki, 1997). Furthermore, these insects seem only to be noticed when they occur on economically important plants and two distinct *Capulinia* species are known to occur on one host, *Plinia cauliflora* (in literature as *E. jaboticaba*).

Here we review *Capulinia* and formally describe and name two new species, one of which has been collected only once from a native forest in Argentina. The other new species described here has been recorded recently as a pest of guava or guayaba, *Psidium guajava* (Myrtaceae), in northern Colombia and is the same as the pest of *Psidium* reported in Venezuela as *C.* sp. near *jaboticabae*. This paper also discusses the relationships of *Capulinia* to other eriococcids based on nucleotide sequence data, provides an updated key to genera of South American eriococcids modified from the key of Hodgson & Miller (2010), and provides a revised generic diagnosis as well as keys to species of *Capulinia* based on adult females and first-instar nymphs.

Material, methods and terms

Specimens, morphological methods and depositories. Specimens were collected by the authors and placed in 75% and 100% ethanol in the field, or samples preserved in 75% ethanol were sent to the senior author (TK) for determination. Specimens were mounted one adult female per microscope slide but several nymphs per slide, as indicated in the descriptions, for example '2/15 first-instar nymphs' means two slides with a total of 15 nymphs. The slide-mounting method used was a modification from Kozarzhevskaya (1968) and Williams & Granara de Willink (1992) in which specimens were cleared by placing overnight in cold 10% KOH and then gently heated to 40°C for two hours before expressing the body contents in water to which a drop of detergent was added; then cuticles were stained for several hours in acid alcohol containing a few drops of acid fuchsin stain solution, prior to dehydration in a series of alcohol baths (including three final ones of 100% isopropyl alcohol, i.e. 2-propanol), and then transferred through three xylene baths prior to mounting in Canada balsam on microscope slides. Measurements were made using an ocular micrometer inserted in the eyepiece of either an Olympus or a Leica compound microscope. All measurements are maximum dimensions (e.g. body width and femur width were recorded at the widest points) and are expressed as the range. Tarsal length of nymphs excludes the claw. Spiracle length includes the muscle plate (apodeme). Setal lengths include the setal base. Measurements are based on the number of adult females specified in the descriptions and as many suitable quality nymphs as available for each species. The morphological terms for Eriococcidae follow those of Williams (1985) and Miller & McKenzie (1967). Illustrations were prepared with a drawing tube attached to an Olympus compound microscope and the Adobe program Photoshop CS4. Following the convention for scale insects, each figure displays the dorsal body surface on the left side of the page, and the ventral body surface on the right. Enlargements of diagnostic features are located around the margin of each main figure; the sizes of these structures are provided in the text.

A number of different host-plant names, including common names, occur in the literature on *Capulinia*, and many of these names are no longer accepted. For accepted plant names we used the world checklist of Myrtaceae by Govaerts *et al*. (2008).

Depositories of slide-mounted specimens are abbreviated as follows: **ANIC**: Australian National Insect Collection, CSIRO, Canberra, A.C.T., Australia; **CTNI**: Colección Taxonómica Nacional de Insectos "Luis María Murillo", Corpoica, C.I. Tibaitatá, Mosquera, Cundinamarca, Colombia. **IMLA**: Entomological Collection of the Instituto Miguel Lillo, Tucumán, Argentina; **MALUZ**: Museo de Artrópodos de la Universidad del Zulia, Facultad

de Agronomía, Universidad del Zulia, Maracaibo, Zulia, Venezuela; **UNCB**: Museo Entomológico, Facultad de Agronomía, Universidad Nacional de Colombia, Bogotá D.C., Colombia; **USNM**: National Museum of Natural History Entomological Collection, Washington, D.C., U.S.A. (Coccoidea collection held at USDA, Beltsville, Maryland).

The holotype and most paratypes of each of the new species are deposited in museums in the country of origin of the species. Slide-mounted DNA vouchers are deposited in the ANIC, where LGC's molecular vouchers are deposited. In addition to slide-mounted specimens prepared for this study, we examined Brazilian specimens of *C. jaboticabae* as well as Venezuelan specimens labelled as *C.* sp. near *jaboticabae* and held in the USNM.

We have registered the two new names published in this paper with the Official Registry of Zoological Nomenclature (ZooBank) and cite the Life Science Identifiers (LSIDs) after the heading for each new name as well as for the previously published *Capulinia* names. Each LSID is a globally unique identifier for the nomenclatural act of naming a new taxon.

Molecular methods. Eriococcidae, as it is currently recognised, is not monophyletic. In order to determine to which group *Capulinia* is most closely related, we sequenced the small subunit nuclear ribosomal RNA gene (SSU rRNA; 18S), which has been used in the phylogenetics of eriococcids previously (Cook & Gullan, 2004). DNA was non-destructively extracted from adult females of both new species as well as from *Tectococcus ovatus* Hempel, using a Bioline Isolate II Genomic DNA kit (cat. no. BIO-52067, Australia), with cuticles sterilely removed to 70% ethanol after the lysis and incubation step. 18S was amplified using primers 2880 (5'-CTGGTTGATCCTGCCAGTAG) and B- (Br) (5'-CCGCGGCTGCTGGCACCAGA) (von Dohlen & Moran, 1995), Mango Taq (Bioline Australia cat. no. BIO-21083), and an annealing temperature of 55°C. PCR products were cleaned with Antarctic Phosphatase and Exonuclease I (New England Biolabs, Australia) before being sequenced using the Sanger method at Macrogen Inc., Republic of Korea.

Sequence traces were checked and edited using Geneious R8 (Biomatters; available from http://www.geneious.com/) and aligned to the offset alignment used by Cook & Gullan (2004). To assess the impact of alignment assumptions, sequences from *Capulinia* were also aligned with those of other eriococcids using the E-INS-i algorithm in MAFFT (Katoh & Standley, 2013), which is better for sequences with multiple conserved regions and large variable regions, such as 18S in scale insects (Cook *et al*., 2002). The MAFFT alignment was adjusted manually for minor inaccuracies, and regions of alignment ambiguity were removed after visual inspection.

Neighbour-joining (NJ) phylograms were generated in Geneious for each alignment using the Tamura-Nei genetic distance and support was assessed using 1000 bootstrap pseudoreplicates. Both alignments (OFFSET and MAFFT) were also analysed using MrBayes (Ronquist *et al*., 2012), applying a K2P+gamma model. Two runs, each of 10 million generations, were sampled every 1000 generations and checked for convergence using Bayes Factor comparisons based on harmonic means and checking the ESS values for each parameter. Samples from the burn-in period were discarded before constructing the consensus tree, and finding the maximum clade credibility tree using TreeAnnotator (available in the BEAST package; Drummond *et al*., 2012).

For comparison with the other phylogeny estimation methods, we also estimated phylogenies for each alignment using maximum parsimony (MP) with equal weights and the heuristic search algorithm in PAUP* (Swofford, 2003). We first used 1000 random-addition starts, saving only 10 MP trees per iteration. Trees saved during this search were then used as the staring trees for a search with no limits to the number of MP trees saved.

Systematics

Relationships within *Capulinia* and of *Capulinia* to other eriococcids. The adult female morphology of *C. sallei* and *C. orbiculata* differs from that of *C. jaboticabae* and the two new species described here. In particular, the hind legs of the latter three species are well developed with the coxa retractable into a membranous pocket and the body shape is ovoid, whereas *C. sallei* and *C. orbiculata* have tubercle-like hind legs with reduced segmentation with the coxa not in a pocket and the body is globular in shape. The morphology of the adult female of *C. crateraformis* is too poorly known for accurate comparison with the other five species, but it was described as having reduced hind legs. The antennae of *C. sallei* and *C. orbiculata* are reduced to tubercles with indistinct, if any, segmentation, whereas the antennae of the other four species are well developed with 4 to 6 segments. All species (except

unknown for *C. crateraformis*) have tubular and/or microtubular ducts on the dorsum and venter. Only the adult female of *C. sallei* has a band of tubular ducts surrounding the apex of the abdomen. The first-instar nymphs of *C. sallei* and *C. orbiculata* resemble each other more closely, particularly in the shape of the dorsal setae, than they resemble the nymphs of the two new species described here (nymphs unknown for *C. crateraformis* and *C. jaboticabae*).

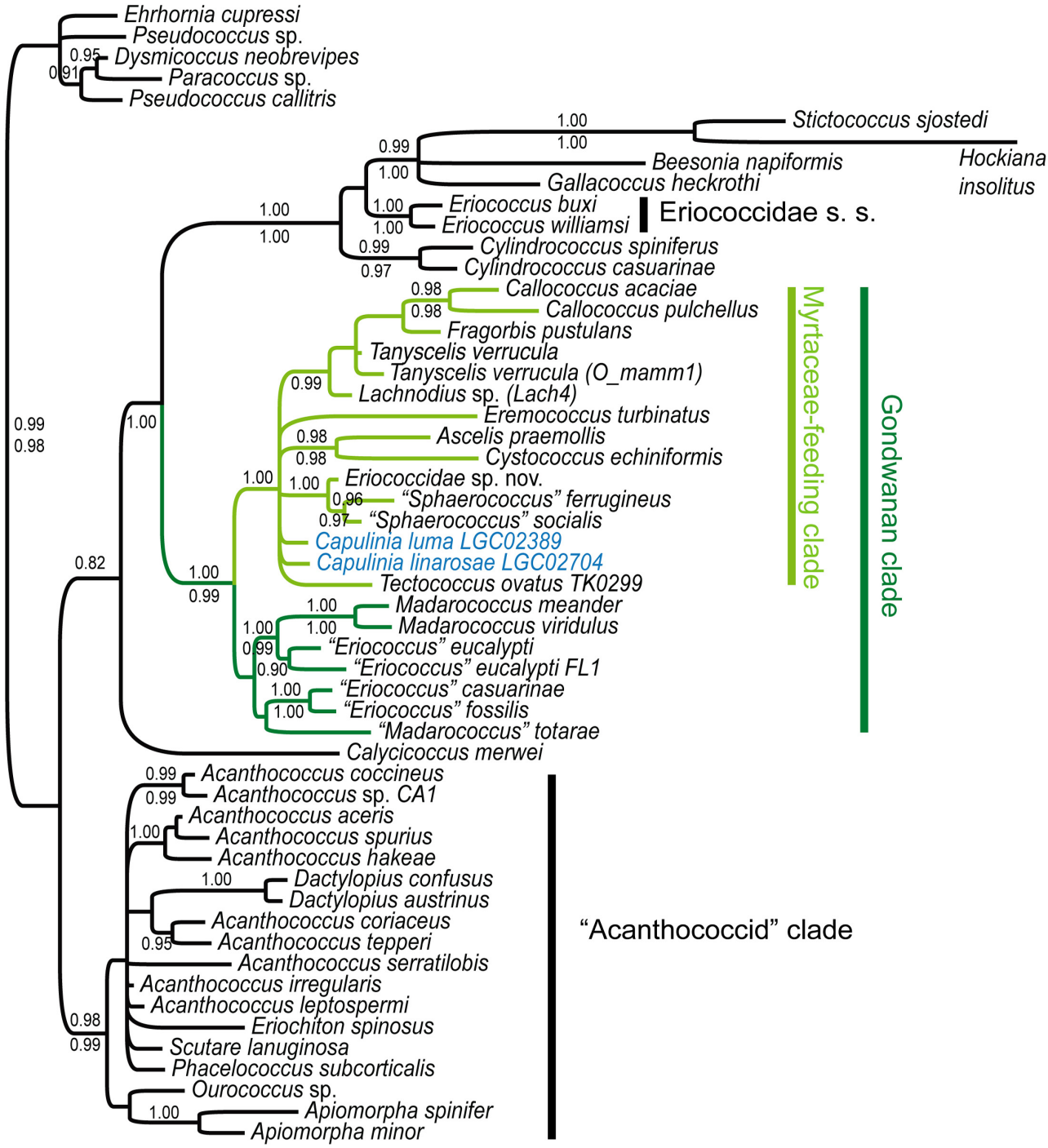

FIGURE 1. Bayesian consensus tree from analysis of the OFFSET alignment with posterior probability (PP) support values >0.90 shown above branches. PP > 0.90 from Bayesian analysis of the MAFFT alignment shown below branches. DNA sequences for all species except the two *Capulinia* species and *Tectococcus ovatus* were published previously by Cook & Gullan (2004).

Thus, as noted by Hodgson & Miller (2010), there are significant morphological differences between the type species, *C. sallei*, and other members of the genus. It is likely that most or all of the other species currently placed in *Capulinia* are not congeneric with *C. sallei*, making it is difficult to concisely diagnose the genus because of morphological variation among the species. Hodgson *et al*. (2004) and Hodgson & Miller (2010) provide a key to genera of Eriococcidae found in South America, but for *Capulinia* the distinguishing features are based on the type species *C. sallei* and so other species of *Capulinia* may not key out to this genus. Thus herein we have modified the generic key of Hodgson & Miller (2010) in order to accommodate all *Capulinia* species (see key below).

The morphology of adult males and DNA sequence data for *Capulinia* would help to elucidate relationships among the species, but would require much further specimen collection. At present, molecular data are available only for the two new species of *Capulinia*. Analyses of 18S rDNA show that these two species of *Capulinia* belong to the "Gondwanan" clade of Cook & Gullan (2004) (PP=0.99, BS=79; Fig. 1). This relationship was obtained irrespective of which alignment (OFFSET or MAFFT) or phylogeny estimation method (NJ, MP, MrBayes) was used. The Gondwanan clade of eriococcids comprises species from three of the landmasses once connected via Antarctica: Australia, New Zealand and South America. The relationships of *Capulinia* within the Gondwanan clade are less clear. In analyses of the OFFSET alignment using MrBayes, there was strong support for species of *Capulinia* being within or sister to the "Myrtaceae-feeding" clade (PP = 1.0; Fig. 1), the members of which are restricted to myrtaceous plants, as are species of *Capulinia*. This relationship was also recovered in analyses of the MAFTT alignment, and NJ and MP analyses of the OFFSET alignment, but with no support (BS<70; PP<0.90).

Only the NJ analysis of the OFFSET alignment recovered *Capulinia* as monophyletic, but without bootstrap support. In this analysis, *Capulinia* was sister to the other South American Myrtaceae-feeding eriococcid, *Tectococcus ovatus*, also without bootstrap support. In all other analyses, *Capulinia* was not recovered as monophyletic, but there was no support for non-monophyly. The lack of resolution and support for relationships of *Capulinia* within the Myrtaceae-feeding clade is likely due to low information content in the 18S gene. This is not due solely to lack of substitutions but most likely because of the loss of information in the hypervariable regions that cannot be unambiguously aligned between more distantly related taxa. To better test the relationships of *Capulinia*, and other members of the Gondwanan clade, many more nuclear-encoded genes are required for analysis.

The morphology of first-instar nymphs (Hodgson & Miller, 2010) supports the molecular findings in that the nymphs of *Capulinia* are most similar to the monotypic genera *Pseudocapulinia* Hempel and *Tectococcus* Hempel, which are gall-inducing taxa known only from Brazil. The adult females of these latter two genera share some features with *Capulinia* (see below) but the adult female of *Pseudocapulinia* lacks legs, whereas that of *Tectococcus* has all legs well developed but small relative to body size.

Key to the genera of the Eriococcidae of South America based on adult females

(modified from that of Hodgson & Miller (2010) to include all *Capulinia* species as well as three new genera described by Hodgson *et al*. (2011, 2013))

1	Legs present, sometimes greatly reduced or located near anal opening	5
-	Legs absent	2
2(1)	Conspicuously enlarged setae (excluding marginal setae) absent from dorsum	3
-	Conspicuously enlarged setae present on dorsum, either enlarged and narrow on posterior abdominal segments or cupolate-shaped and robust scattered over thorax and abdomen	4
3(2)	Antennae segmented; quinquelocular pores restricted to ventral thorax mostly near spiracles, absent from dorsum	*Pseudocapulinia* Hempel
-	Antennae each represented by an unsegmented knob; quinquelocular pores present on both body surfaces	*Carpochloroides* Cockerell
4(2)	Enlarged setae of 2 types present, cupolate-shaped setae on anterior abdomen, thorax, and head, and elongate setae on posterior abdominal segments	*Macracanthopyga* Lizer y Trelles
-	Enlarged setae cupolate-shaped only present, scattered over dorsum	*Apiococcus* Hempel
5(1)	All legs developed more-or-less equally although may be weak or distorted	7
-	First 2 pairs of legs absent, tubercle-like or weakly developed with segmentation sometimes obscure	6
6 (5)	Hind coxa greatly enlarged; dorsum sclerotised	*Aculeococcus* Lepage
-	Hind coxa not greatly enlarged but sometimes in a membranous pocket; dorsum not sclerotised	*Capulinia* Signoret
7(5)	Legs fully developed with normal segmentation; in gall or free-living	9
-	All legs weakly developed; living in a gall	8

8(7) Dorsum with sclerotised hump on thorax; dorsal and ventral setae small and slender. . . . *Dromedaricoccus* Hodgson & Miller
- Dorsum with sclerotised plate probably incorporating most of abdomen; most dorsal and some ventral setae spinose with broad base . . . . . *Bystracoccus* Hodgson
9(7) Antennae with 6 or more segments; almost exclusively free-living, but may be under a waxy or hard test or concealed on roots or under bark 13
- Antennae with 5 or fewer segments; living in a gall. 10
10(9) Enlarged setae not grouped in circular area on thorax and head. 11
- Enlarged setae grouped in circular area on thorax and head. . . . . *Neotectococcus* Hempel (in part)
11(10) Anal lobes protruding, heavily sclerotised . . . . . *Pseudotectococcus* Hempel
- Anal lobes absent or very small, unsclerotised 12
12(11) Body egg-shaped to turbinate and always membranous; dorsal setae slender spinose with blunt apices . . . . . *Tectococcus* Hempel (in part)
- Body globose with circular sclerotised area dorsally on mature females; dorsal setae hair-like with acute apices . . . . . *Eriogallococcus* Hodgson & Miller
13(9) Anal lobes absent or, if present (sclerotised or not), not protruding noticeably past posterior apex of abdomen 25
- Anal lobes present, clearly protruding from posterior apex of abdomen 14
14(13) Macrotubular ducts present on dorsum 18
- Macrotubular ducts absent from dorsum. 15
15(14) Antennae 6 segmented; without a cluster of spinose setae ventrally between mid and hind legs 16
- Antennae 8 segmented; with a cluster of spinose setae ventrally between mid and hind legs . . . . . *Eriobalachowskya* Kozár & Konczné Benedicty
16(12) Loculate pores absent from spiracular atria; anal ring with 8 setae and with a double row of pores 17
- Loculate pores present in spiracular atria; anal ring with 10 setae and with a single row of pores . . . . . *Poliloculus* González
17(16) Dorsal setae large, conspicuously spiniform; translucent pores on hind coxa either represented by large openings or absent . . . . . *Icelococcus* Miller & González
- Dorsal setae small, slightly spiniform; translucent pores on hind coxa represented by small dots . . . . . *Intecticoccus* Kondo
18(14) At least some macrotubular ducts on dorsum with a conspicuous rim surrounding dermal orifice 23
- Macrotubular ducts on dorsum without a conspicuous rim surrounding dermal orifice 19
19(18) Without groups of microducts on dorsum of thorax and anterior abdominal segments 20
- With conspicuous groups of microducts on dorsum of thorax and anterior abdominal segments . . . . . *Hempelicoccus* Kozár & Konczné Benedicty
20(19) Setae in medial areas of ventral abdomen with acute apices; translucent pores present on some, but not all, of hind coxa, femur and tibia 21
- Some setae in medial areas of ventral abdomen slightly capitate; translucent pores present on all of hind coxa, femur and tibia . . . . . *Coxicoccus* Kozár & Konczné Benedicty
21(20) Anal lobes conspicuous and sclerotised 22
- Anal lobes small and unsclerotised . . . . . *Oregmopyga* Hoy (in part)
22(21) Anal lobes plate-like, not protruding strongly . . . . . *Chilecoccus* Miller & González (in part)
- Anal lobes not plate-like, but protruding strongly . . . . . *Acanthococcus* Signoret and *Madarococcus* Hoy
23(18) Venter with tubular ducts; dorsum without simple pores; cruciform pores absent 24
- Venter without tubular ducts; dorsum with numerous simple pores; cruciform pores present on venter near body margin . . . . . *Exallococcus* Miller & González
24(23) Venter with large clusters of tubular ducts; posterior abdomen without sclerotised nodules; anal lobes unsclerotised. . . . . *Stibococcus* Miller & González (in part)
- Venter with tubular ducts scattered; posterior abdomen with sclerotised nodules; anal lobes heavily sclerotised . . . . . *Orafortis* Hardy
25(13) Anal lobes without conspicuous sclerotisation 27
- Anal lobes conspicuously sclerotised 26
26(25) Enlarged setae forming conspicuous band around body margin. . . . . *Chilechiton* Hodgson & Miller
- Enlarged setae not forming conspicuous band around body margin. . . . . *Chilecoccus* Miller & González (in part)
27(25) Enlarged setae absent or, if present, not grouped in circular area on dorsum of thorax and head 28
- Enlarged setae grouped in circular area on dorsum of thorax and head . . . . . *Neotectococcus* Hempel (in part)
28(27) Venter without large clusters of tubular ducts on abdomen 29
- Venter with large clusters of tubular ducts on abdomen . . . . . *Stibococcus* Miller & González (in part)
29(28) Largest dorsal macroducts without associated setae 30
- Largest dorsal macroducts with 1–3 associated setae . . . . . *Melzeria* Green
30(29) Some dorsal setae cupolate; without wing-like apodemes arising from mouthparts . . . . . *Oregmopyga* Hoy (in part)
- Dorsal setae not cupolate; with large wing-like apodemes attached to mouthparts.. . . . . *Tectococcus* Hempel (in part)

Taxonomy of *Capulinia*

Capulinia Signoret

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Capulinia Signoret, 1875: 27–28. Type species: *Capulinia sallei* Signoret, by monotypy.
Cupulinia; Signoret, 1875: 40. Misspelling of genus name.

This genus was described and named for *C. sallei* Signoret from Mexico (Signoret, 1875), but no specific collection location or scientific name for the host plant were given, although the host was called 'Capulino' by the local people. Today in Mexico, a capulin may refer to either a species of cherry, *Prunus salicifolia* (Rosaceae), or to *Eugenia capuli* (Myrtaceae), although Ferris (1955) suggested that this common name also was used for some species of figs, *Ficus* (Moraceae). The host of the type specimens of *C. sallei* is almost certainly a *Eugenia* species because subsequent collections of *Capulinia* all have been from species of Myrtaceae. The one record from Hoy (1963) of *C. sallei* from *Muntingia calabura* (Muntingiaceae) may have been based on a record from Ballou (1926), which also is cited by Mestre *at al*. (2011), but this host record is unsubstantiated and may be erroneous. Subsequent collections of *C. sallei* from Cuba have been from *Eugenia axillaris* and *Eugenia* sp. (Mestre *et al*., 2015b). Since the original description, most articles on *C. sallei* have referred to it as being on the leaves, which appears to be an error because this feeding location is not stated in Signoret (1875), who only says that the leaves and branches get covered in cottony wax. Furthermore, Mestre *et al*. (2015b) report *C. sallei* as being numerous on the branches and do not mention leaves.

With the exception of *C. orbiculata* from New Zealand, all species of *Capulinia* are from Central or South America. Hoy's (1958) descriptions and illustrations of the adult female and first-instar nymph of *C. orbiculata* are consistent with those of other species of *Capulinia* and most closely resemble those of *C. sallei* from Cuba. The most obvious differences in the adult female are the greater number of quinquelocular pores around each thoracic spiracle and the absence of a band of microtubular ducts encircling the abdomen in *C. orbiculata* compared with specimens from Cuba identified as *C. sallei*. Also the live female of *C. sallei* lives externally on its host plants and makes a long waxy ovisac, whereas *C. orbiculata* lives hidden in the bark of *Metrosideros* and produces only a small amount of powdery wax. *Capulinia orbiculata* appears to be native to New Zealand rather than an introduction from somewhere in the Americas (for discussion refer to entry on this species below), suggesting either great antiquity of the genus *Capulinia* or convergent evolution of a *Capulinia*-like species on Myrtaceae in New Zealand. Here we retain *C. orbiculata* in *Capulinia* and include it in the key to species below.

Generic diagnosis of *Capulinia.* On stems, branches or leaves of host, depending on species, sometimes inducing a gall or hidden beneath bark; adult female secreting white wax and eggs protected usually either by copious mass of wax or a long ovisac.

Adult female. Body globular to slightly turbinate; derm entirely membranous, segmentation either distinct or apparently absent; with ventral abdomen, and perhaps sometimes dorsal abdomen, small relative to thorax. ***Dorsum.*** Setae either hair-like to slender spinose and sparse (e.g., *C. sallei* and *C. orbiculata*), or slender spinose with mostly knobbed apices and moderately abundant (e.g., *C. jaboticabae*). Macrotubular ducts of typical eriococcid type absent. Microtubular ducts of 1–3, perhaps 4 types, depending on species. Loculate pores either absent, scattered uniformly and sparsely, or densely distributed marginally to submarginally and sparsely scattered elsewhere. Anal lobes either apparently absent or largely membranous and weakly developed. Median lobe absent. Anal ring partially sclerotised, lacking pores, sometimes with a pair of short setae on ring and sometimes setae around ring. ***Margin.*** Either undefined (*C. sallei* and *C. orbiculata*) or poorly defined by position of dorsal setae. ***Venter.*** Setae fine to robustly hair-like, shorter and finer than setae on dorsum. Macrotubular ducts of typical eriococcid type absent. Microtubular ducts of 1–3 types, similar to types on dorsum, scattered, sometimes sparse. Loculate pores with 4–6 (mainly 5) loculi, either restricted to laterad of each spiracle, or more widely distributed especially along margin and across abdominal segments as well as near spiracles. Antennae with 1–7 segments, either highly reduced or well developed, depending on species. Frontal lobes and antennal tubercles absent. Labium with 1 to perhaps 3 segments, segmentation poorly defined. Spiracles well developed and always associated with a group of mostly 5-locular (quinquelocular) pores; number of associated pores varies depending on species, from fewer than 6 to more than 50 pores. Fore and mid legs either absent or reduced to tubercles or membranous lobes. Hind legs either lobe-like with slight signs of segmentation and no setae or relatively well

developed with distinct segmentation and a few setae; translucent pores absent; claws often absent; legs positioned far posteriorly, and in at least 3 species coxa inside a membranous pocket. Vulva either well developed or not detected, depending on species.

Comments. Adult females of *Capulinia* can be separated from those of other South American eriococcids by the following combination of features: (i) derm entirely membranous with body margin weakly or not defined; (ii) anal ring simple, partially sclerotised, lacking pores; (iii) fore and mid legs absent or highly reduced; and (iv) hind legs either poorly developed with reduced segmentation, or well developed with coxa partly hidden in a membranous pocket.

First-instar nymph (based on *C. linarosae*, *C. luma*, *C. orbiculata* and *C. sallei*). Body outline oval, slightly more pointed posteriorly only in *C. sallei*; derm membranous, with segmentation distinct. ***Dorsum.*** Setae either spinose with a swollen base and rounded apex (*C. sallei*), conical spinose with a rounded apex (*C. orbiculata*) or short and broad with a rounded apex (other 2 species), distributed in 2 marginal rows along body and in 2 or 4 pairs of medial to submedial longitudinal rows on abdomen and usually with 2–4 setae medially to submedially on each segment of thorax and on head. Macrotubular ducts absent. Microtubular ducts present or absent. Loculate pores absent. Anal lobes poorly developed, each bearing long apical seta. Anal ring either very small or absent and lacking setae, or about equal to width of an anal lobe and with sclerotised ring and several associated setae (usually not on ring). ***Margin.*** Defined by 2 longitudinal marginal rows of robust setae on abdomen and either a single or double marginal row on head and thorax. ***Venter.*** Setae hair-like; with long setae in 3 pairs between antennae and 1 mesad of each mid and hind leg, abdomen with 1–3 pairs of setae across each segment except last. Macrotubular and microtubular ducts absent except for *C. sallei* with a few microtubular ducts present, mostly submarginally. Loculate pores absent. Antennae with 6 segments. Labium apparently without segmentation. Spiracles each with 1–3 loculate pores (probably always quinquelocular, i.e. with 5-loculi) associated with peritreme. All legs well developed, with hair-like setae, a long trochanteral seta, a pair of capitate tarsal digitules, a pair of capitate claw digitules and a well-developed claw either with small subapical denticle or lacking a denticle.

Comments. The first-instar nymphs of *Capulinia* are most similar to those of *Pseudocapulinia lanosa* Hempel (described by Hodgson & Miller (2010)) with which they share the following features: (i) 6-segmented antenna; (ii) anal lobes not differentiated; (iii) dorsal body setae of one type; (iv) cruciform pores absent; and (v) loculate pores restricted to near each spiracle. They differ from the nymphs of *P. lanosa* in (i) the shape of the dorsal setae (pointed in *P. lanosa*). The first-instar nymphs of *Capulinia* also share some similarity with the first-instar nymph of *Tectococcus ovatus* Hempel (described by Hodgson & Miller (2010)), but can be separated by their (i) 6-segmented antennae (5-segmented in *T. ovatus*) and (ii) dorsal setae of one type (2 types in *T. ovatus*).

Key to species of *Capulinia* based on adult females

1. Antenna a small tubercle of 1–2 segments 2
- Antenna with 4–7 segments 3

2(1). Microtubular ducts abundant in a complete band around abdomen on about abdominal segment IV; quinquelocular pores either absent or in a small group of 4–6 lateral to each thoracic spiracle; feeding externally on host plant and producing a very long, pendant, white waxy filament; known from at least *Eugenia* in Mexico and Cuba . . . . . *C. sallei* Signoret
- Microtubular ducts not forming a band around abdomen; a group of 22–56 quinquelocular pores present lateral to each thoracic spiracle; feeding concealed in the bark and cambium of host plant and not producing a waxy filament; known only from *Metrosideros* in New Zealand . . . . . *C. orbiculata* Hoy

3(1). Hind legs atrophied and lacking segmentation; inducing a small crater-shaped gall on twigs and branches of jaboticaba (*Plinia cauliflora*) . . . . . *C. crateraformis* Hempel
- Hind leg with distinct coxa, trochanter-femur and fused tibiotarsus; not inducing galls but feeding externally on various host plants and producing copious white wax 4

4(3). Dorsum and margin of body with setae ≤ 40 µm long, with apex of all setae acute; antenna usually with 6 segments; eyespots represented by a finger-like invagination; known only from Argentina on *Luma apiculata* . . . . *C. luma* Kondo & Gullan **sp. n.**
- Dorsum and margin of body with at least some setae >50 µm long with apex of each seta capitate at least on abdomen; antenna with 4–5 segments; eyespots not invaginated, at most represented by a faint elevation 5

5(4). Hind leg tibia + tarsus (claw absent) 120–170 µm long; dorsal and marginal setae up to 55 µm long; known from Brazil on jaboticaba (*Plinia cauliflora*) . . . . . *C. jaboticabae* Ihering
- Hind leg tibia + tarsus + claw 230–340 µm long; dorsal and marginal setae up to 115 µm long; known from Colombia and Venezuela on *Psidium* species . . . . . *C. linarosae* Kondo & Gullan **sp. n.**

Key to species of *Capulinia* based on first-instar nymphs (known for 4 of 6 species)

1. Dorsal setae spinose, tapering to a rounded or bluntly pointed apex, with setal base much wider than apex 2
- Dorsal setae broad for full length with a rounded apex, and basal and apical widths usually subequal 3
2(1). Base of each dorsal seta swollen. . . . . *C. sallei* Signoret
- Base of each dorsal seta not swollen. . . . . *C. orbiculata* Hoy
3(1). Dorsal microtubular ducts present; 1 pore present immediately lateral to each peritreme . . . . . *C. linarosae* Kondo & Gullan **sp. n.**
- Dorsal microtubular ducts absent; 2 or 3 pores present immediately lateral to each peritreme . . . . . *C. luma* Kondo & Gullan **sp. n.**

Capulinia crateraformis Hempel

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Capulinia crateraformis Hempel, 1900a: 3–4.

Capulinia crateraformans; Hempel, 1900b: 397. Misspelling of species name; no explanation was given for the different spelling of the species epithet.

This species was described from small crater-shaped galls on the bark of *Plinia cauliflora* (given as *Eugenia jaboticaba*) from Sao Joao d'El Rei in the state of Minas Gerais in Brazil, collected by Mr Alvaro da Silveira (Hempel, 1900a). According to Miller & Gimpel (2000), type material is held in both the Museum fur Naturkunde der Humboldt Universitat zu Berlin, Germany, and in the USNM. We have not seen specimens of this species and cannot be certain that it is congeneric with *C. sallei*. Hempel (1900a) provides a table to distinguish the adult female of this species from those of *C. jaboticabae* and *C. sallei*. The following brief description of the gall and the adult female are summarised from Hempel (1900a, b).

The female induces small crater-shaped galls on the twigs and branches; each gall is about 1.5 mm high and consists of an outer circular ring from 1.0–1.5 mm in diameter enclosing a small cone that can be removed readily; the gall cavity has smooth walls lined with white powdery secretion. The live adult female is oval in outline, pink and dusted with white powdery secretion. After clearing the body contents in KOH, the adult female is about 0.96 mm long and 0.73 mm wide. It has small variable antennae, less than 100 µm long, of 5–6 segments, with apical segment bearing a terminal brush of coarse setae. The first and second pairs of legs are absent and the hind pair is atrophied without any visible segmentation and no claw; the hind legs are about 0.18 mm long and so near the posterior end of the body that half the length extends beyond the body margin. The mouthparts are large and well developed, with the labium apparently 2 segmented; the coiled stylet loop extends to the second pair of spiracles. The spiracles are well developed with 1–4 pores grouped around each one. The abdomen is segmented and ends in 2 short setae. The anal opening [referred to as the 'genital opening' by Hempel (1900a)] is surrounded by 4 small spines. The body margin and dorsal surface has scattered small spine-like setae.

This insect was recorded as causing much damage to the host tree (Hempel, 1900a). The same species has been reported from Itatiba in the state of São Paulo, Brazil (see footnote by Cockerell in Townsend & Cockerell, 1898), although it was misidentified as *C. jaboticabae* by Cockerell (Hempel, 1900a).

Capulinia jaboticabae Ihering

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Capulinia jaboticabae Ihering, 1898: 188. Type data: BRAZIL: on *Eugenia jaboticaba*. Type depositories: Washington: United States National Entomological Collection, U.S. National Museum of Natural History, District of Columbia, USA, and Berlin: Museum fur Naturkunde der Humboldt Universitat zu Berlin, Germany.

This species was described from jaboticaba (now *Plinia cauliflora*) from Capoeira Grande (Minas Gerais) in Brazil (Ihering, 1898) and subsequently was reported from a district of São Paulo, Brazil, on the same host (Hempel, 1900b). The USNM has one box of dry material marked "cotype" but we have not examined that material.

Material examined: BRAZIL: São Paulo, on *Eugenia jaboticaba* [now *P. cauliflora*], 20.vii.1962, S.W. Brown, #144, 1/1 adult female (USNM); São Paulo, Campinas, on *Myrciaria jaboticaba* [now *P. cauliflora*], 24.viii.1936, B.L. Ribeiro, 1/5 adult females (USNM).

Adult female. **Mounted material (**n=6). Body oval, becoming more rounded at maturity, 0.8–1.3 mm long, 0.5–1.1 mm wide. Segmentation apparent at least on abdomen.

Dorsum. Derm membranous, with a few scattered microtrichia medially to submedially. Dorsal setae spinose, usually with a slightly blunt apex and longer setae with a weakly capitate apex, each seta mostly either 5–12 µm long or 25–55 µm long, with longer setae more common on abdomen and body margins, but variable among specimens and setae often with broken apices; sparsely distributed in a row across each abdominal segment but more scattered on thorax and head. Macrotubular ducts absent. Microtubular ducts of 2 types, all scattered throughout: (i) a long thin microduct, each 12–17 µm long with a squarish, sclerotised distal apex 2 µm across, apparently with a very fine inner ductule (not always visible); (ii) a rarer, less obvious microduct, each perhaps 5 µm long, with a flat disc-like distal end up to 2 µm across, with an inner ductule. Loculate pores with 5 loculi, each pore 3–4 µm in diameter, present in a sparse row across each posterior abdominal segment and sparsely scattered elsewhere. Anal lobes not developed, but each long apical seta, up to 140 µm long, situated on a small membranous lobe with dorsal and ventral setae adjacent on body margin. Anal ring represented by a simple sclerotised ring, 15–20 µm wide, lacking pores; 4 setae on edge of anal ring, short and spinose, 5–9 µm long.

Margin. Weakly defined by an irregular row of dorsal setae similar in length and robustness to other long dorsal setae. Eyespots at most represented by a faint elevated area about 10 µm across, near margin anterolateral to antenna; usually apparently absent.

Venter. Derm membranous, with microtrichia at least medially to submedially on thorax and abdomen. Ventral setae slender to finely spinose, each 7–30 µm long, longest on abdomen posterior to legs; sparsely distributed in a row across each abdominal segment but shorter and scattered on head and thorax. Macrotubular ducts absent. Microtubular ducts of 2 types, similar in structure and distribution to ducts on dorsum except sometimes fewer microducts on posterior abdomen. Loculate pores with 5 loculi, each 3.0–4.5 µm in diameter, present in sparse marginal band, and usually in a sparse row on each posterior abdominal segment anterior to vulva, in a cluster of 9–16 pores anterolateral to each spiracle, and sparsely scattered elsewhere. Antennae apparently 4–5 segmented (segments usually poorly defined), each antenna 45–57 µm long, with 6 fleshy setae of varying lengths (10–20 µm) and thickness on antennal apex, with longest and thickest fleshy seta (about 25 µm long) positioned subapically, and 1 seta on basal segment. Clypeolabral shield 190–200 µm long, 140–150 µm wide. Labium 65–67 µm long, 63–90 µm wide, apparently 3 segmented with at least 4 pairs of setae on or near apex and 1 pair on first (membranous basal) segment and probably second segment. Spiracles subequal in size: length including muscle plate (apodeme) 40–49 µm; width across peritreme 18–21 µm. First 2 pairs of legs absent; hind legs well developed and lightly sclerotised, with distinct segmentation except tibia, tarsus and claw poorly formed with indistinct separation; leg setae apparently absent; coxa 33–53 µm long, partially hidden within a membranous pocket-like base with leg capable of being extended; trochanter + femur 57–65 µm long; tibia + tarsus 120–170 µm long; claw absent; tarsal and claw digitules present on only 1 leg of 1 specimen (perhaps broken off on other females), this leg with 3 capitate digitules 19–22 µm long and one hair-like digitule about 10 µm long; femur 30–35 µm wide; campaniform sensilla on trochanter either lacking or with single sensillum on ventral face; position of hind legs far posteriorly, apparently attached near anterior margin of segment III. Vulva well developed, with lightly sclerotised lips.

Comments. The description by Ihering (1898) is very brief, describing *C. jaboticabae* as lacking antennae and anterior legs, with just the last pair of legs present. Hempel (1900a) reported that there were 18 to 35 spinnerets (presumably loculate pores) around each spiracle. There were fewer than 18 pores near each spiracle of every specimen that we examined, and it is not clear whether this discrepancy is due to variation or to Hempel including marginal pores in his counts.

Capulinia jaboticabae is very similar morphologically to *C. linarosae*, but has smaller legs, generally shorter antennae, shorter and less robust setae, even though some specimens of *C. jaboticabae* that we examined were the same body size as those of *C. linarosae*. Also the larger (wider) of the two kinds of microducts has a squarish distal end on *C. jaboticabae* compared with a narrower asymmetrical end on *C. linarosae* (as examined with x100 objective and oil immersion).

***Capulinia linarosae* Kondo & Gullan sp. n.**
urn:lsid:zoobank.org:act:D24B8607-E2C7-418D-AE73-8E73C558454B

Capulinia sp. near *jaboticabae;* Cermeli & Geraud-Pouey, 1997: 115–123; Geraud-Pouey & Chirinos, 1999: 23–29; Geraud-Pouey *et al*., 2001: 21–27; 2001:165–171; Chirinos *et al*., 2000: 1–16; 2003: 7–20; 2004: 135–142.

García *et al*. (2016) list the name *Capulinia* sp. near *jaboticabae* in the database ScaleNet as an unavailable name. None of the authors (in several papers) who refer to this species as *Capulinia* sp. near *jaboticabae* were using this as a formal name (and it clearly is not in name format) and only were following an identification apparently made by D.R. Miller, as acknowledged in Cermeli & Geraud-Pouey (1997, page 115): "La especie fue determinada por el Dr. Douglas Miller como *Capulinia* sp. cercana a *jaboticabae* von Ihering 1898, posiblemente nueva especie (Coccoidea: Eriococcidae)."

Type material examined: HOLOTYPE: adult female, COLOMBIA, Departamento de Magdalena, Sevilla, Corpoica Caribia Research Station, on *Psidium guajava*, 20.viii.2014, coll. T. Kondo (UNCB). PARATYPES: same data as holotype, 32/32 adult females (11 slides, including DNA voucher LGC02704, ANIC; 3 slides CTNI; 6 slides MALUZ; 10 slides UNCB; 3 slides USNM), 2/15 first-instar nymphs (1 slide ANIC; 1 slide UNCB), 2/6 first- and second-instar nymphs (UNCB), 3/9 second-instar nymphs (male and female) (UNCB) & 1/1 prepupal male with its pharate pupa (UNCB); COLOMBIA, Departmento Bolivar, Clemencia, Honduras, El Higuerón (finca), on *P. guayava*, 12.xii.2013, S. Cervantes, 13/13 adult females (1 slide ANIC; 2 slides IMLA; 10 slides UNCB).

Other material examined: VENEZUELA: Maracay, San Vicente, on "Guyva (citrus)"[misspelling on label and probably refers to lemon guava = *Psidium guajava*], 9.ix.1994, M. Gemshi/Joly, Esc1, 94-11415, 4/17 adult females (USNM); on *Psidium guajava*, 15.v.1995, A. Ahmed, JFK-125408, 9706639, 1/1 adult female (USNM); Estado [state] Zulia, La Yaguara, on *P. guayava*, 13.vi.1994, F. Geraud & P. Corzo, 1/1 adult female (USNM).

Adult Female (Figs 2A–C, 3). **Unmounted material.** Occurs on the trunk, stems and foliage of its host; body light yellow, covered in a mass of loose white cottony wax (Fig. 2A–C).

Mounted material (n=14). Body oval, becoming more rounded at maturity, 0.8–1.9 mm long, 0.6–1.5 mm wide. Segmentation apparent on abdomen and usually on thorax.

Dorsum. Derm membranous, with a few scattered microtrichia medially to submedially. Dorsal setae slender spinose, longer ones mostly with a capitate or rounded apex, each 50–115 µm long, but some 27–40 µm long; shorter ones always with rounded apex, each 9–30 µm long, with longer setae more common on abdomen and near body margins; sparsely distributed in a row across each body segment. Macrotubular ducts absent. Microtubular ducts of 2 types, all scattered throughout: (i) a long thin microduct, each 10–17 µm long with a sclerotised, asymmetrical distal apex 3–4 µm across, apparently with a very fine inner ductule (not always visible); (ii) a slightly more slender microduct, each 10–18 µm long, with a smaller sclerotised, asymmetrical distal end up 2.0–2.5 µm across, with an inner ductule. Loculate pores with 5 loculi (very rarely 3, 6 or 7 loculi), each pore 3.5–5.0 µm in diameter, scattered. Anal lobes present but small and membranous to lightly sclerotised, each with about 6 dorsal setae, 11–73 µm long, and one long apical seta 83–175 (mostly 112–163) µm long. Anal ring represented by a simple sclerotised ring, 10–18 µm wide, lacking pores; usually 4 setae on or near ring, short and spinose, 5–15 µm long.

Margin. Defined by an irregular row of dorsal setae similar in length and robustness to other long dorsal setae, 50–120 (mostly 70–100) µm long, but apex of setae on anterior thorax and head usually rounded rather than capitate. Eyespots about 10 µm across; with circular lens and oval sclerotised rim, often poorly formed.

Venter. Derm membranous, with microtrichia medially to submedially on thorax and abdomen. Ventral setae finely spinose tapering to a rounded apex, each 6–50 µm long, longest on abdomen; sparsely distributed in a row across each abdominal segment but shorter and scattered on head and thorax. Macrotubular ducts absent. Microtubular ducts of 2 types, similar in structure and distribution to ducts on dorsum. Loculate pores with 5 loculi, each 3.8–5.0 µm in diameter, present in sparse marginal band, and usually in a sparse row on each posterior abdominal segment, in a cluster of 5–14 pores anterolateral to each spiracle, and sparsely scattered elsewhere but rare to absent around mouthparts and medially to submedially on thorax and anterior abdomen. Antennae 4 segmented, often second segment pseudosegmented, making antenna appear 5-segmented, each antenna 50–80 µm long; with a maximum of 5 fleshy setae of varying lengths (15–25 µm) and thickness on antennal apex; longest (22–27 µm) and thickest fleshy seta usually curved, positioned subapically, i.e. segment II; and 1 seta on basal

segment. Clypeolabral shield 205–265 µm long, 145–185 µm wide. Labium 68–108 µm long, 65–83 µm wide, apparently 3 segmented and with at least 4 pairs of setae on or near apex, and 1 pair on each of first (membranous basal) and second segments. Spiracles subequal in size: length including muscle plate (apodeme) 43–58 µm; width across peritreme 20–33 µm. First 2 pairs of legs absent; hind legs well developed and lightly sclerotised, with distinct segmentation except tibia, tarsus and claw poorly formed with indistinct separation; leg setae generally absent, some specimens with a short setae on ventral area of coxa, ca. 5 µm long; coxa 62–140 µm long, partially hidden within a membranous pocket-like base with leg capable of being extended; trochanter and femur fused, trochanter + femur 85–118 µm long; widest part of femur 35–60 µm; tibia + tarsus + claw 230–340 µm long; claw variably developed, often absent; tarsal and claw digitules absent; campaniform sensilla absent from trochanter; position of hind legs far posteriorly, apparently attached near anterior margin of segment III. Vulva well developed, with lightly sclerotised lips.

First-Instar Nymph (sex not determined) (Fig. 4A, Left). **Unmounted material.** Elongate oval, whitish just after hatching, becoming yellowish.

Mounted material (n=9). Body ovoid, 270–335 µm long, 160–170 µm wide.

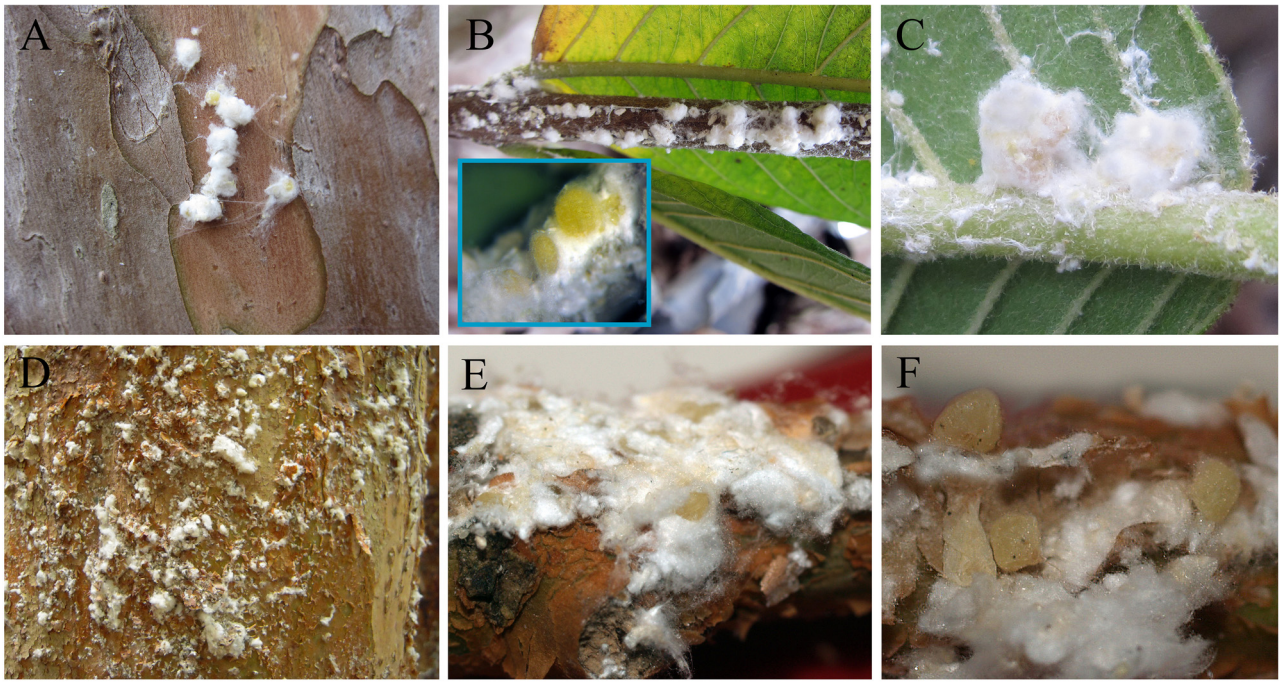

FIGURE 2. Habitat of two *Capulinia* species: **A–C.** Adult females of *Capulinia linarosae*: **A.** On bark of a guava tree; **B.** On a guava twig, with inset (light blue square) showing insects with their wax partially removed; **C.** Along leaf vein of guava tree. **D–F.** Adult females of *Capulinia luma*: **D.** On bark of *Luma apiculata*. **E.** On a twig of *L. apiculata*; **F.** A few females with their wax partially removed. All photos by T. Kondo.

Dorsum. Derm membranous, with microtrichia sparsely distributed in a band across each abdominal segment. Dorsal setae broad with a rounded apex, each 3–5 µm long, basal socket 3–4 µm wide, usually longest and more robust on posterior margins of abdomen; distributed as follows: on abdomen in a double marginal line (2 setae on each side of each segment) plus 2 medial to submedial longitudinal lines (1 on each side of midline); on thorax 2–3 marginal setae on each side of each segment plus usually 4 setae across each segment; head with about 16 setae from submedial area to margins. Microtubular ducts present around body margin and submedially on thorax, each 3–5 µm long, 1–2 µm wide. Loculate pores absent. Anal lobes small and rounded, membranous; each with a very long apical flagellate seta 175–233 µm long; marginally with 2 pairs of spinose setae, each 4–6 µm long, positioned between long apical setae. Anus circular, surrounded by a sclerotised ring, outer width of ring 10–12 µm, width of opening 6–7 µm; with 1 pair of setae posterior to ring, each seta about 5–6 µm long, plus 1 seta lateral to ring on each side, each 8–10 µm long.

Margin. Marginal setae similar in shape and size to those on dorsum and about same size. Eyespots each 9–11 µm wide, situated on margin posterior to base of antenna.

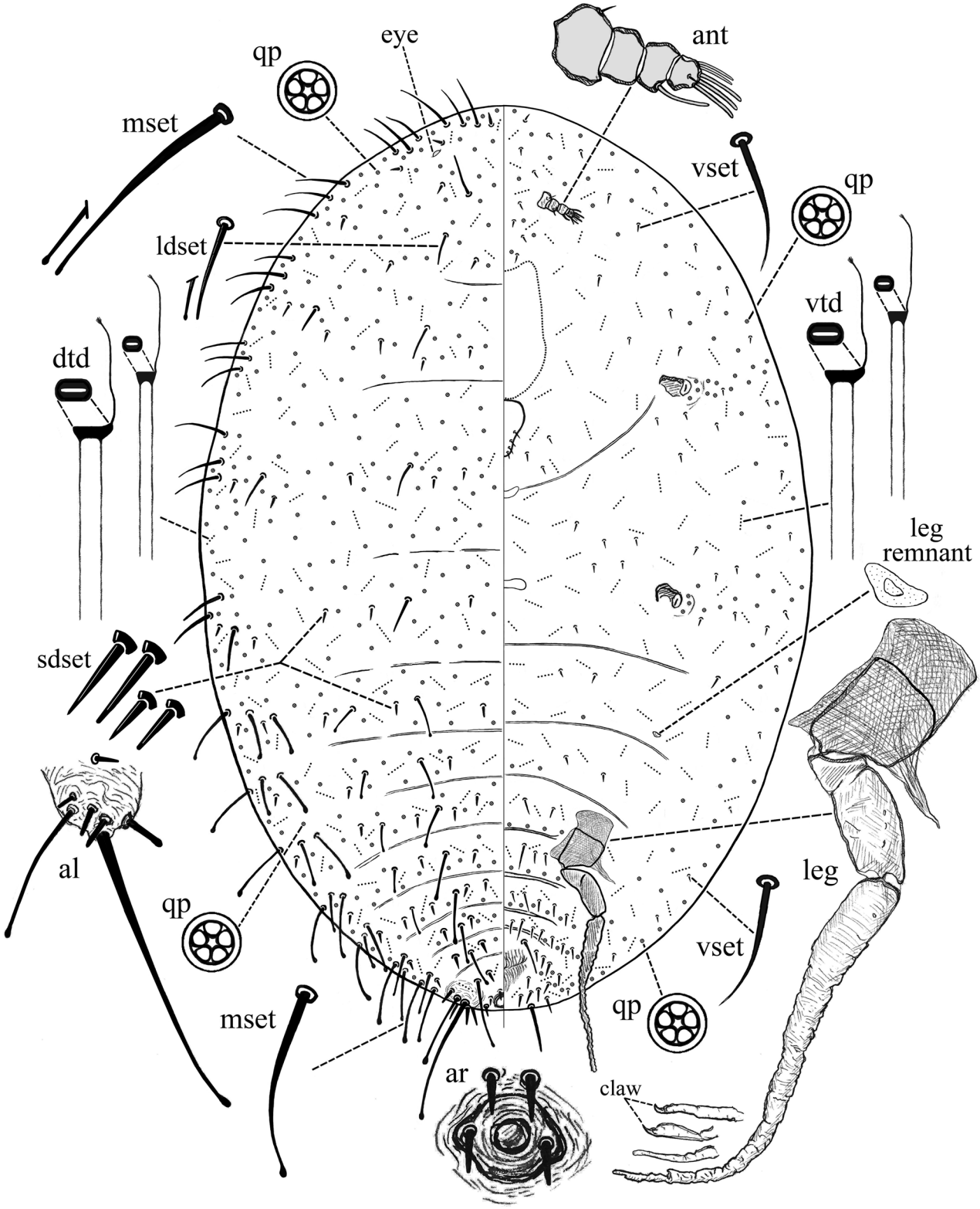

FIGURE 3. Adult female of *Capulinia linarosae* **sp. n.** Abbreviations: al = anal lobe; ant = antenna; ar = anal ring; dtd = dorsal tubular ducts; ldset = long dorsal seta; mset = marginal seta; qp = quinquelocular pore; sdset = small dorsal setae; vset = ventral seta; vtd = ventral tubular ducts.

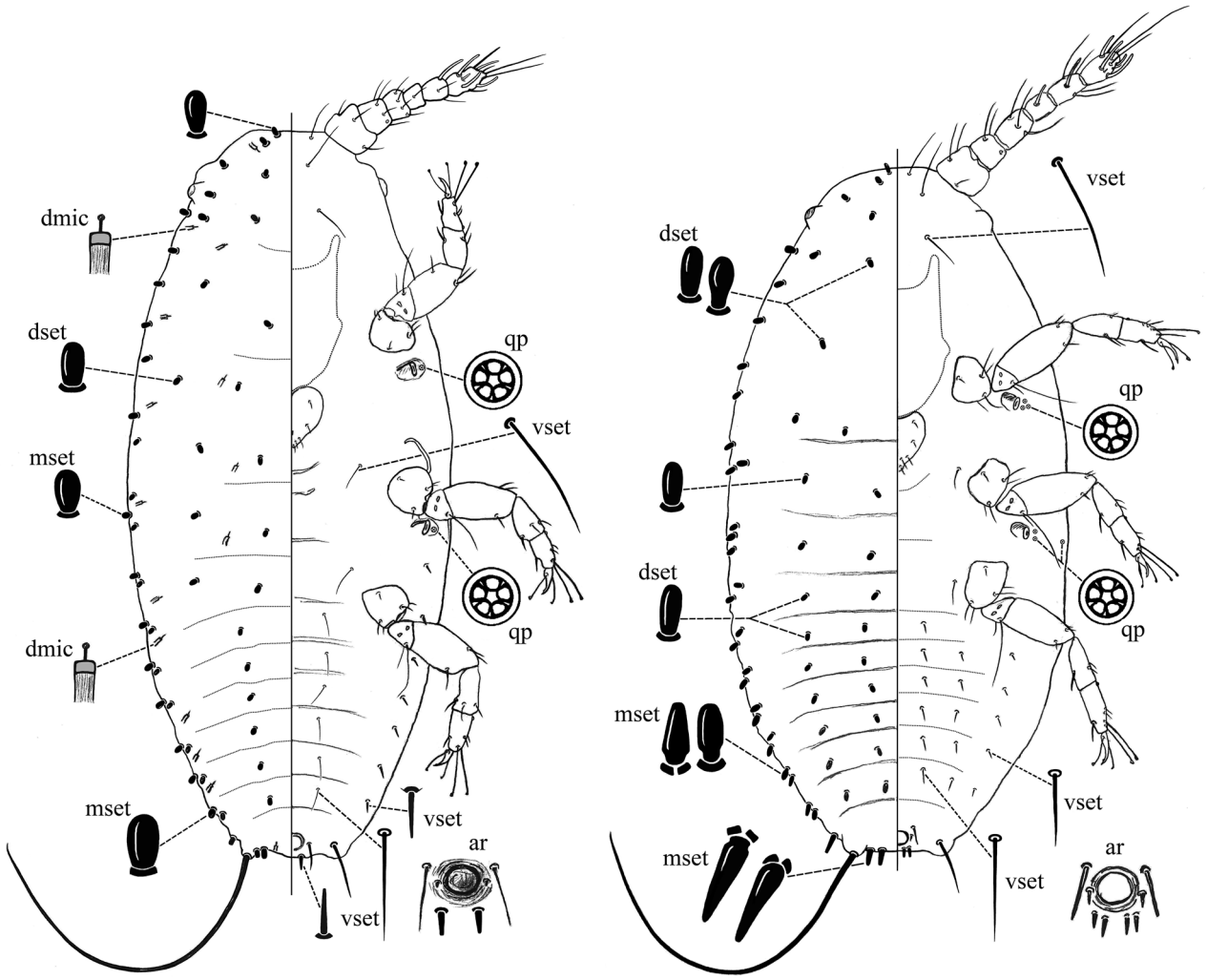

FIGURE 4. First-instar nymphs of: **Left.** *Capulinia linarosae* **sp. n. Right.** *Capulinia luma* **sp. n.** Abbreviations: ar = anal ring; dmic = dorsal microtubular duct; dset = dorsal seta; mset = marginal seta; qp = quinquelocular pore; vset = ventral seta.

Venter. Derm membranous, with microtrichia distributed in a band across middle of each abdominal and thoracic segment, denser than on dorsum. With 3 pairs of long setae between antennae, each 15–30 µm long, plus 1 seta mesad to each meso- and metacoxa (these setae long, each 15–25 µm); abdominal setae 7–10 µm long, in 2 submedial longitudinal lines (1 on each side of midline) present on abdominal segments II–VII. Macrotubular and microtubular ducts absent. Loculate pores with 5 loculi; with 1 pore present immediately lateral to each peritreme, none elsewhere. Antennae 6 segmented, each 77–88 µm long; setal distribution: scape: 3 setose seta; pedicel: 4 setose seta; segment III: 4 setose setae; IV: 1 setose setae; V: 2 setose setae + 1 fleshy seta; VI: 4 fleshy setae, about 3 short setose setae plus 3 long setae, length of longest about 40 µm. Clypeolabral shield 78–82 µm long, 42–53 µm wide; labium 1 segmented; about 26–31 µm long, 31–33 µm wide, with possibly 4 pairs of short setae + 1 pair rather long setae on apex. Spiracles small, 10–12 µm long (including muscle plate), width across peritreme 4–5 µm, each associated with a loculate pore (see above). Legs well developed; hind-leg lengths (in µm): coxa 21–25; trochanter + femur 52–57; tibia 23–26; tarsus 21–24; claw 17–19, with a small denticle; tibia generally subequal to tarsus. Setae on hind leg: coxa: 5 short setae, trochanter: 1 short and 1 long trochanter seta 30–40 µm long; femur: 3 short setae; tibia: 1 spur-like seta + 2 short setae; tarsus: 1 spur-like seta + 2 short setae; tarsal campaniform sensillum present; both tarsal digitules on all legs alike, 19–22 µm long, with capitate apex; claw digitules alike, 15–17 µm long, with capitate apex.

Comments. The first-instar nymphs of *C. linarosae* share the following morphological characteristics with the nymphs of *C. luma*, *C. orbiculata* and *C. sallei*: (i) 6-segmented antennae; (ii) dorsal setae all of one type, spinose with rounded to bluntly pointed apex, although varying in setal shape among species, (iii) marginal setae of same type and distributed several per segment on head and thorax and in a double line on the abdomen (i.e. a pair of setae

on each side of each segment); (iv) anal lobes poorly differentiated and not sclerotised; (v) loculate pores restricted to cavity laterad to each spiracle; (vi) paired claw and tarsal digitules similar to each other.

The first-instar nymphs of *C. linarosae* can be distinguished from the nymphs of *C. luma* (characteristics of *C. luma* in parentheses) by having: (i) 2 longitudinal lines of robust spinose setae on the dorsal abdomen, excluding marginal rows (4 lines); (ii) 1 loculate pore present immediately lateral to each peritreme (2–3); (iii) 4 longitudinal lines of setae on ventral abdomen (6 lines); and (iv) microtubular ducts present on dorsum (absent). The nymphs of *C. linarosae* differ from those of *C. orbiculata* and Cuban specimens of *C. sallei* (characteristics of latter 2 species in parentheses) in having all dorsal setae broad for full length with a rounded apex (tapering to a rounded or bluntly pointed apex).

Notes on biology, natural enemies and control of *C. linarosae* in Venezuela. *Capulinia linarosae* (as *Capulinia* sp. nr. *jaboticabae* or as *Capulinia* sp.) has been reported as a pest of guava trees since 1993 in Venezuela, where it is considered as one of the most common pest species on guava (Cermeli & Geraud-Pouey, 1997; Paz, 1997; Geraud-Pouey & Chirinos, 1999; Chirinos-Torres *et al*., 2000; Geraud-Pouey *et al*., 2001a; Camacho-Molina *et al*., 2002). According to Cermeli & Geraud-Pouey (1997), the sudden appearance of *C. linarosae* in central and western Venezuela and how the problem was aggravated due to the lack of natural enemies, suggested that this eriococcid was introduced from a distant region. A personal communication cited by Cermeli & Geraud-Pouey (1997) points to the existence of infestations on guava with the same characteristics (cottony wax on tree trunk and branches) in the area of Puerto Ayacucho in the State of Amazonas for more than 20 years, thus suggesting that the insect came from the Amazonian region of Venezuela.

The population parameters of *C. linarosae* on three species of *Psidium*, namely *P. friedrichsthalianum*, *P. guajava* and *P. guineense*, were studied by Geraud-Pouey & Chirinos (1999) and Chirinos *et al*. (2003), who determined that survival was highest on guava, *P. guajava*. Chirinos *et al*. (2004) studied the species in the laboratory at 24–28°C and 72–86% RH, reported that the sex ratio was 1:1, that eggs hatched 8 days after laying, and that the growth stages each had the following durations: first-instar nymph 8.5 days, second-instar female 6.0 days, adult female 46.7 days, second-instar male 4.6 days, prepupa 2.0 days, pupa 3.7 days, and adult male only 1.1 days. This species had high fecundity with each adult female capable of laying about 2500 eggs.

A number of natural enemies of *C. linarosae* have been recorded in Venezuela. The encyrtid parasitoid *Metaphycus* sp. achieved parasitization levels of up to 40% (Geraud-Pouey *et al*., 2001b), with low levels of encapsulation of parasitoid eggs (Chirinos *et al*., 2006). Predators included *Curinus colombianus* Chapin, *Azia orbigera* Mulsant, *Pentilia egena* Mulsant and *Chilocorus cacti* (L.) (Coleoptera: Coccinellidae) (Cermeli & Geraud-Pouey, 1997), an undetermined chrysopid species (Cermeli & Geraud-Pouey, 1997), possibly of the genus *Chrysoperla* Steinmann (Neuroptera: Chrysopidae) (Chirinos-Torres *et al*., 2000), and an undetermined syrphid larva, possibly of the genus *Ocyptamus* Macquart (Cermeli & Geraud-Pouey, 1997). The fungi *Beauveria bassiana* Vuillemin and *Trichoderma harzianum* Persoon also were recorded (Zambrano & García, 2006).

Geraud-Pouey *et al*. (2001a) indicated that bark smoothness could constitute a source of resistance of guava plants to diminish the incidence and damage caused by *C. linarosae*, since survival of first-instar nymphs was significantly increased (>70%, $P \leq 0.05$) by the presence of exfoliations (bark peelings) where nymphs settled down to feed. Thus the removal of the tree bark may constitute a form of cultural control. Possibilities for chemical control have been discussed by Chirinos *et al*. (2007), Chirinos-Torres *et al*. (2000) and Zambrano & García (2006).

Etymology. The species is named after Lina Rosa Chirinos-Torres who was the first person who worked on this species when it became a problem in Venezuela in 1993. She worked on the biology and control of this species for her undergraduate thesis as part of her degree in agricultural engineering.

Capulinia luma Kondo & Gullan sp. n.

urn:lsid:zoobank.org:act:7E65D870-99D3-4C0C-8001-E3D3ECBBC029

Material examined. HOLOTYPE: adult female, ARGENTINA, Neuquén Province, near Villa de la Angustura, 40°51′28″S, 71°36′50″W, 780 m a.s.l., on *Luma apiculata* (Myrtaceae), 27.i.2010, P.J. Gullan (IMLA). PARATYPES: same data as holotype: 20/20 adult females (10 slides IMLA; 5 slides, including DNA voucher LGC02389, ANIC; 6 slides UNCB) & 5/55 1st-instar instar nymphs (2 slides IMLA; 2 slides ANIC; 1 slide UNCB).

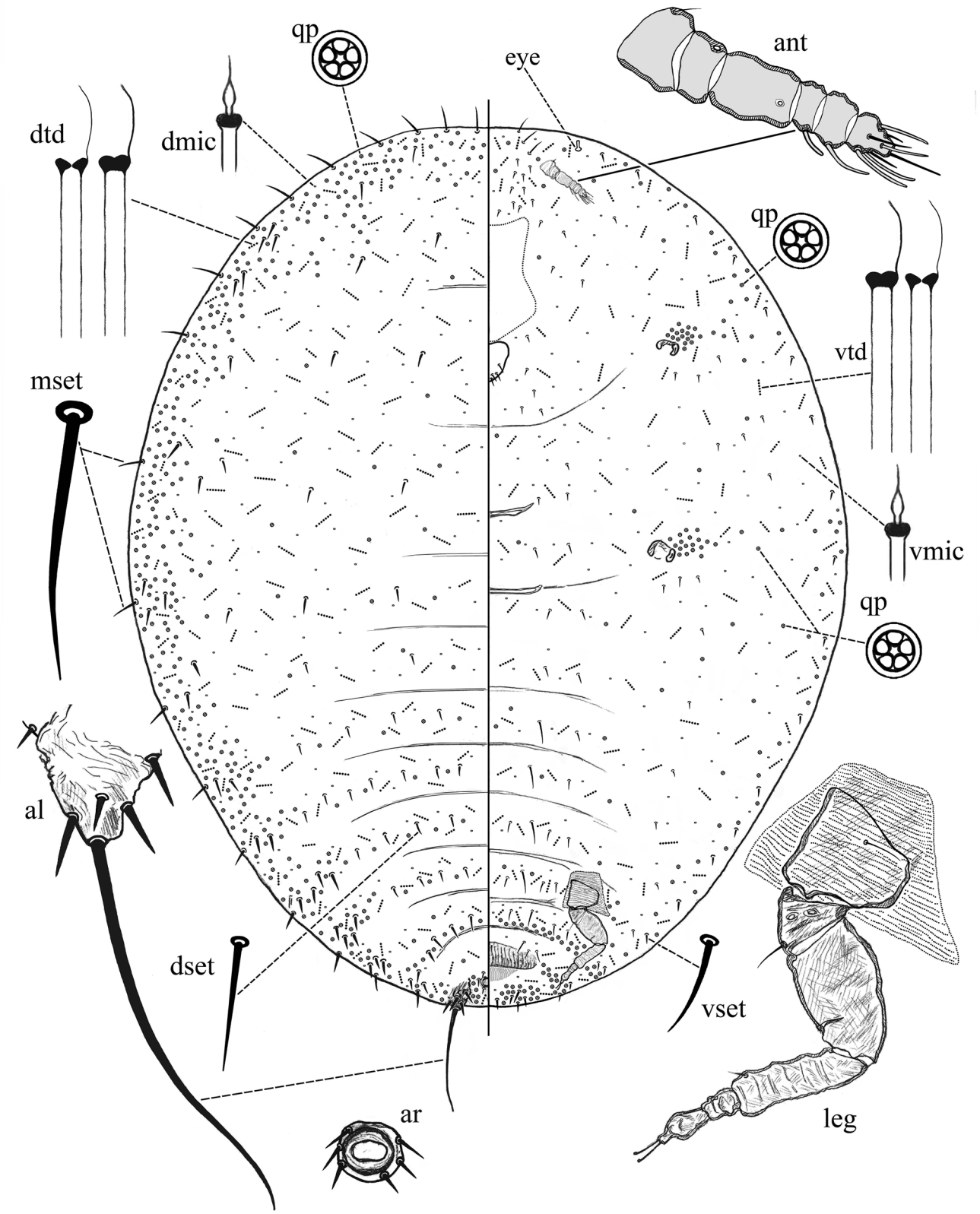

FIGURE 5. Adult female of *Capulinia luma* **sp. n.** Abbreviations: al = anal lobe; ant = antenna; ar = anal ring; dmic = dorsal microtubular duct; dset = dorsal seta; dtd = dorsal tubular ducts; mset = marginal seta; qp = quinquelocular pore; vmic = ventral microtubular duct; vset = ventral seta; vtd = ventral tubular ducts.

Adult Female (Figs 2D–F, 5). **Unmounted material.** Occurs on the trunk of its host (perhaps also on branches, but hard to reach to collect); body light yellow-brown, covered in a mass of loose white cottony wax, forming a large waxy mass when many females are close together (Fig. 2D–F).

Mounted material (n=12). Body apparently globular to slightly turbinate, depending on maturity, 1.6–2.2 mm long, 1.2–1.7 mm wide. Segmentation apparent at least medially to submedially on dorsum and venter.

Dorsum. Derm membranous, without microtrichia. Dorsal setae hair-like to finely spinose, tapering to a slightly rounded apex, each 7–40 µm long, those on margin, especially head and anterior thoracic margin, longest; sparsely distributed in a row across each abdominal segment, more irregular on thorax and head. Macrotubular ducts absent. Microtubular ducts of 3 types, all scattered throughout: (i) a long thin microduct, each about 16–21 µm long and 2.5–3.0 µm wide at opening, with a small and divided sclerotised distal apex, apparently with a very fine inner ductule (not always visible); (ii) a slightly broader microduct, of similar length as type (i), but with a more obvious sclerotised distal end, 3.0–3.5 µm wide at opening, with an inner ductule; (iii) a very small microduct, each about 5–7 µm long and 1.5–2.0 µm wide, with an inner ductule. Loculate pores with 3–6 but mostly 5 loculi, each pore 4–5 µm in diameter, present in a fairly dense marginal band and sparsely scattered elsewhere. Anal lobes distinct, lightly sclerotised, each with about 4 dorsal setae, each seta about 21–23 µm long, and one long apical seta 180–230 µm long. Anal ring represented by a simple sclerotised ring, 25–43 µm wide, lacking pores; usually 6 anal ring setae, short and spinose, each 12–22 µm long.

Margin. Weakly defined by a row of setae similar to other dorsal submarginal setae in being more robust than setae more medially on dorsum. Eyespots represented by a finger-like invagination, 7–12 µm in maximum width.

Venter. Derm membranous, with microtrichia medially to submedially from posterior to mouthparts to anterior to vulva. Ventral setae hair-like, each 6–50 µm long, mostly 10–25 µm long; sparsely distributed in a row across each abdominal segment but scattered on head and thorax, longest setae near margins; without long setae medioventrally between antennae and mesad to coxae. Macrotubular ducts absent. Microtubular ducts of 3 types, similar in structure and distribution to types (i)–(iii) on dorsum. Loculate pores with 3–6 but mostly 5 loculi, each pore 4–5 µm in diameter, present in sparse marginal band, in a dense band on each posterior abdominal segment, in a cluster of 10–35 pores anterolateral to each spiracle, and sparsely scattered elsewhere. Antennae mostly 6 segmented (rarely with 5 or 7 segments), each antenna about 98–138 µm long, with about 4 fleshy setae and 4 long fine setae on apical segment, 1 fleshy seta on each of segments IV and V, and 1 seta on basal segment. Clypeolabral shield 220–290 µm long, 180–240 µm wide. Labium 73–101 µm long, 87–98 µm wide, apparently 3 segmented and with 5 pairs of setae on apical segment and 1 pair on each of first (basal) and second segments. Spiracles subequal in size: length including muscle plate (apodeme) usually 50–75 µm; width across peritreme 23–30 µm. First 2 pairs of legs absent; hind legs well developed and lightly sclerotised, with distinct segmentation except separation of tarsus and claw indistinct; setae few in number, usually 1 on coxa, 1 on trochanter and 1 or 2 on tibia; coxa 50–63 µm long, partially hidden within a membranous pocket-like base with leg capable of being extended; trochanter + femur 89–113 µm long; tibia 58–78 µm long; tarsus + claw 40–65 µm long; claw either present or absent; tarsal and claw digitules variously developed, sometimes none, mostly 2–3 usually capitate digitules 10–21 µm long; femur 40–50 µm wide; trochanter with 2 campaniform sensilla on each ventral face and dorsal face, those on dorsal face sometimes not easy to detect; position of hind legs far posterior, apparently attached near anterior margin of segment V. Vulva well developed, with lightly sclerotised lips.

First-Instar Nymph (sex not determined) (Fig. 4A, Right). **Unmounted material.** Elongate oval, whitish to cream-white in colour.

Mounted material (n=10). Body ovoid, 312–350 µm long, 162–190 µm wide.

Dorsum. Derm membranous, with microtrichia difficult to discern but apparently sparsely distributed in a band across each abdominal segment. Dorsal setae broad with a rounded apex, shorter setae each 4–5 µm long with basal socket 2.5 µm wide, longer setae each 6–7 µm long with basal socket 2.0 µm wide, usually longest on posterior margins of abdomen; distributed as follows: on abdomen in a double marginal line (2 setae on each side of each segment) plus 4 medial to submedial longitudinal lines (2 on each side of midline); on thorax 2–4 marginal setae on each side of each segment plus usually 4 setae across each segment; head with about 16 setae from submedial area to margins. Macrotubular and microtubular ducts absent. Loculate pores absent. Anal lobes small and rounded, membranous; each with a very long apical flagellate seta 175–215 µm long; marginally with 2 pairs of spinose setae between long apical setae, each 8–10 µm long. Anus circular, surrounded by a sclerotised ring, outer width of ring 12–13 µm, width of opening about 5–6 µm; with 2 pairs of setae on each side posterior to ring, each seta about 4–5 µm long, plus 1 pair of setae lateral to ring, one 4–5 µm long and other 7–8 µm long (latter perhaps anterior suranal setae).

Margin. Marginal setae similar in shape and size to those on dorsum and about same size except larger posteriorly, up to 10 µm long. Eyespots each 10–11 µm wide, situated on margin posterior to base of antenna.

Venter. Derm membranous, with microtrichia difficult to discern but probably in a band across middle of each abdominal and thoracic segment. With 3 pairs of long setae between antennae, each 15–18 µm long, plus 1 seta mesad to each meso- and metacoxa (these setae each 10–14 µm long); abdominal setae 5–16 µm long, in 6 longitudinal lines (3 each side of midline) present medially to submarginally on abdominal segments III–VII, abdominal segment II with 1 seta on each side. Macrotubular and microtubular ducts absent. Loculate pores with 5 loculi; with 2 or 3 pores immediately lateral to each peritreme, none elsewhere. Antennae 6 segmented, each 93–103 µm long; setal distribution: scape: 3 setose setae; pedicel: 3 setose setae; segment III: 3 setose setae; IV 1 fleshy seta; V: 4 setose setae + 1 fleshy seta; VI: 4 fleshy setae, about 3 short setose setae plus 3 long setae, length of longest about 50 µm. Clypeolabral shield 80–90 µm long, 48–59 µm wide; labium 1 segmented; about 27–31 µm long, 35–40 µm wide, with possibly 4 pairs of short setae + 1 pair rather long setae on apex. Spiracles small, 7–10 µm long (including muscle plate), width across peritreme 4–5 µm, each associated with loculate pores (see above). Legs well developed; hind-leg lengths (in µm): coxa 20–23; trochanter + femur 40–50; tibia 22–25; tarsus 20–25; claw about 12–15, with a denticle; tibia generally subequal to tarsus. Setae on hind leg: coxa: 5 short setae; trochanter: 1 short seta and 1 long trochanter seta 35–40 µm long; femur: 3 short setae; tibia: 1 spur-like + 2 short setae; tarsus: 1 spur-like + 2 short setae; tarsal campaniform sensillum present; both tarsal digitules on all legs alike, 17–19 µm long, with capitate apex; claw digitules alike, 12–15 µm long, with capitate apex.

Comments. The characteristics that the first-instar nymphs of *C. luma* share with the nymphs of *C. linarosae*, *C. orbiculata* and *C. sallei* are listed under the Comments section for *C. linarosae*. The first-instar nymphs of *C. luma* can be distinguished from the nymphs of *C. linarosae*, *C. orbiculata* and Cuban specimens of *C. sallei* by having: (i) 4 longitudinal lines of robust spinose setae on the dorsal abdomen, excluding the marginal lines (other species have 2 dorsal lines); (ii) 6 longitudinal lines of setae on ventral abdomen (other species have none or 4 lines of setae); and (iii) microtubular ducts absent on both dorsum and venter (*C. linarosae* has microtubular ducts on the dorsum only whereas Cuban specimens of *C. sallei* have microtubular ducts on both dorsum and venter; it is not known whether these ducts are present in *C. orbiculata*).

Capulinia orbiculata **Hoy**

urn:lsid:zoobank.org:act:5512EFBF-DFDB-4824-9285-E779372DDC72

Capulinia orbiculata Hoy, 1958: 190–191. Type data: NEW ZEALAND: North Island, Pohangina Valley, on *Metrosideros robusta*, 07/07/1955.

Hoy (1958) described this species after first collecting it during a 1955 survey of insects that might be associated with dieback of rata trees, *Metrosideros robusta* and *M. umbellata* (Myrtaceae), in New Zealand. Although high population levels of *C. orbiculata* appeared to be detrimental to rata trees, they were not considered a primary factor in large-scale rata mortality since these insects were present both where trees were dying and where they were not. The insects live in the bark and cambium of twigs and branches and their presence is not visible externally. Hoy reported that infestation appeared heaviest on branches above about 2 cm in diameter. He described the adult female and the first-instar nymph and compared them with South American species of *Capulinia*. Hoy's 16 localities for *C. orbiculata* were in native habitats and very widespread in New Zealand, occurring on both the North Island and the South Island including Stewart Island. Thus we consider *C. orbiculata* to be native to New Zealand.

For information on the morphology of *C. orbiculata* and its comparison with *C. sallei*, please refer to the text prior to the generic diagnosis of *Capulinia* earlier in this paper. The only other eriococcids described from *Metrosideros* in the Southern Hemisphere are several species of *Eriococcus* Targioni Tozzetti (often placed in *Acanthococcus* Signoret) from New Zealand (Hoy, 1962) and *Rhopalotococcus metrosideri* Williams from New Caledonia (Williams, 2007). The latter species induces leaf galls on an unidentified species of *Metrosideros* and the adult female has fully-developed legs and antennae.

***Capulinia sallei* Signoret**
urn:lsid:zoobank.org:act:E60F01CF-9930-410B-9587-6D91FD000F09

Capulinia sallei Signoret, 1875b: 28–29. Type data: MEXICO: on "Capulino". Syntypes, female. Type depository: Vienna: Naturhistorisches Museum Wien, Austria.

Signoret (1875) described the adult female and first-instar nymph and provided small, whole-body drawings of these two instars (venter for adult female and dorsum for the first-instar nymph). Signoret's type material has not been studied in detail by any subsequent author but it does exist because Miller & Gimpel (2000, p. 77) state that "Matile-Ferrero & Danzig visited the Naturhistorisches Museum, Vienna in June of 1997 and found dry type material as follows: two samples of stems, each with two labels: Mexico/sallei/ det. Signoret. Two vials containing dry material, each with two labels: Mexico/sallei/det. Signoret. Vial number one contains wax and vial number two contains five dried female specimens."

Stickney (1934) briefly described and illustrated some features of *C. sallei* and although he did not specify collection information for the specimens that he used, he was working in G.F. Ferris' laboratory at Stanford University and the large Ferris collection of Coccoidea is now in the Bohart Museum of Entomology (BME) at the University of California, Davis, USA. The BME online scale database lists only three collections of *C. sallei* and all are from Cuba. Subsequent redescriptions and illustrations of *C. sallei* (Ferris, 1955; Hodgson & Miller, 2010) also have been based entirely or largely on material from Cuba, rather than Mexico. For example, Hodgson & Miller (2010) redescribed and thoroughly illustrated this species based largely on Cuban specimens of the adult female and first-instar nymphs, but using Mexican material for the adult male. Signoret's description and drawing of the first-instar nymph of *C. sallei* from Mexico differs in dorsal setation from illustrations of this instar in Ferris (1955) and Hodgson & Miller (2010). Differences in body and leg size and leg differentiation of first-instar nymphs from Cuba and Mexico also were noted by Hodgson & Miller (2010). Furthermore, in Signoret's description of the adult female, the hind legs are said to each have a claw, whereas the Cuban specimens appears to lack claws on the hind legs, as pointed out by Hodgson & Miller (2010). We suspect that the Cuban specimens may represent another new species. To resolve this issue, it would be useful to make new collections in Mexico and Cuba for DNA analysis as well as to prepare and examine slide-mounts of a few specimens from the type material of *C. sallei*.

Since the original description, there have been several reports of *C. sallei* from Cuba (Houser, 1918; Ballou, 1926; Mestre *et al*., 2011, 2015a, b). Houser (1918) recorded *C. sallei* from Lagoona Castellana, Santiago de las Vegas, Cuba, but referred to the host plant as an unknown shrub. Mestre *et al*. (2011) cited specimens deposited in the zoological collection of Instituto de Ecología y Sistemática, La Habana, Cuba, collected at Taco Taco, Sierra de Rangel, Cuba, by S.C. Bruner, C.H. Ballou and J. Acuña, in 1922 on *Muntingia calabura*, which may be the collection recorded by Ballou (1926). Mestre *et al*. (2015a) listed *C. sallei* as occurring in Cuba by citing published literature, whereas Mestre *et al*. (2015b) reported specimens on *Eugenia axillaris* and *Eugenia* sp. collected from Topes de Collantes Natural Park, Alturas de Trinidad, in the mountains of Guamuhaya province of Sancti Spiritus, Cuba.

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