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A new pupillarial scale insect (Hemiptera: Coccoidea: Eriococcidae) from *Angophora* in coastal New South Wales, Australia

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Abstract

A new scale insect, *Aolacoccus angophorae* **gen. nov.** and **sp. nov.** (Eriococcidae), is described from the bark of *Angophora* (Myrtaceae) growing in the Sydney area of New South Wales, Australia. These insects do not produce honeydew, are not ant-tended and probably feed on cortical parenchyma. The adult female is pupillarial as it is retained within the cuticle of the penultimate (second) instar. The crawlers (mobile first-instar nymphs) emerge via a flap or operculum at the posterior end of the abdomen of the second-instar exuviae. The adult and second-instar females, second-instar male and first-instar nymph, as well as salient features of the apterous adult male, are described and illustrated. The adult female of this new taxon has some morphological similarities to females of the non-pupillarial palm scale *Phoenicococcus marlatti* Cockerell (Phoenicococcidae), the pupillarial palm scales (Halimococcidae) and some pupillarial genera of armoured scales (Diaspididae), but is related to other Australian Myrtaceae-feeding eriococcids.

Key words: taxonomy, exuviae, Diaspididae, Halimococcidae

Introduction

Very few scale insects (Hemiptera: Coccoidea) have been collected from *Angophora* species (Myrtaceae) (García *et al.* 2016). The mealybug *Phenacoccus angophorae* Williams (Pseudococcidae) is known only from *Angophora* sp. at Cowan, New South Wales (NSW), Australia (Williams 1985a), and *Callipappus australis* (Maskell) (Callipappidae) was described from *Angophora* sp. at Sydney, NSW (Maskell 1890). However, it is quite likely that the host of *C. australis* is not *Angophora* because adult females of *Callipappus* Guérin-Méneville develop on roots in the soil and move to the aerial parts of any plant or vertical structure for oviposition, where they are most often collected (Gullan & Brookes 1998). Here we describe and discuss a new genus and species of scale insect collected from the trunks and branches of *Angophora* trees in coastal and near coastal areas of the Sydney region, NSW. These insects are very small (adult female less than 1 mm long) and each lives hidden under a thin layer of bark tissue (Fig. 1). The adult female is further protected by remaining inside the penultimate exuviae (moulted cuticle), which is lightly sclerotised. This type of development, in which the adult scale insect never leaves the preadult cuticle, is known as pupillarial, a term coined by Ferris (1937), and is relatively uncommon among scale insects. It seems that this condition has not been reported previously in the literature on eriococcids but occurs in the Beesoniidae (see below), a group that is nested inside the Eriococcidae *sensu lato* (Cook & Gullan 2007; Hodgson & Hardy 2013) and is sister to Eriococcidae *sensu stricto* (Cook & Gullan 2004).

For scale insect species that remain in the same position on the plant during development, the exuviae either (i) are pushed backwards and disintegrate over time (the most common condition), (ii) are incorporated into a protective cover (see below), or (iii) are used as the protective cover for the subsequent instar (the pupillarial condition, as in all species of the monophlebid genus *Mimosicerya* (Foldi & Gullan 2014) and found also in several other families, as explained below). In species that are mobile between instars, the newly moulted insect pulls itself out of the exuviae, which remain attached to the plant.

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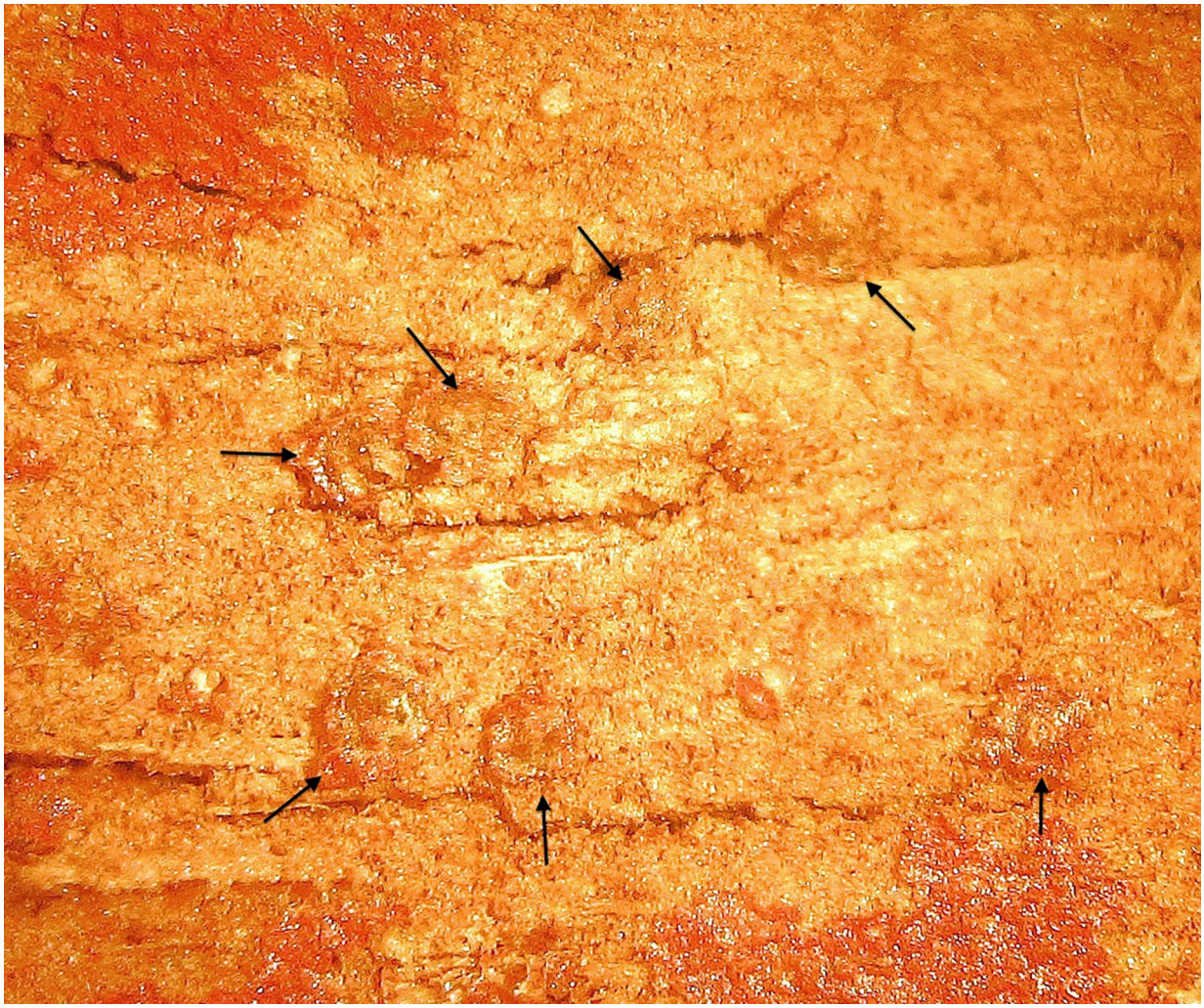

FIGURE 1. Underside of bark from trunk of *Angophora costata* showing seven bumps (indicated by arrows), each 0.7–0.8 mm across, and under each of which is a single female insect of *Aolacoccus angophorae* **sp. nov.** [Photograph by T. Kondo].

In most species of armoured scales (Diaspididae), following the final moult, the adult female incorporates the hardened first- and second-instar dorsal exuviae into a protective, secreted scale cover (Beardsley & Gonzalez 1975; Foldi 1990; Miller & Davidson 2005). However, after the final ecdysis in all genera of Halimococcidae (Stickney 1934; Köhler 1987) and some genera of the Diaspididae (Brown & McKenzie 1962; Howell & Tippins 1990) and Beesoniidae (Ferris 1950; Takagi 1992), the adult female remains inside the exuviae of the penultimate instar. Takagi (1992: 28) described how the adult females of the gall-inducing *Beesonia napiformis* (Kuwana) and *B. brevipes* Takagi (Beesoniidae) remain within the 'skins' (exuviae) of the previous nymphal stage, but he did not specifically mention pupillarity. In these beesoniids, the pupillarial condition may result from lack of space within the gall to remove exuviae. Köhler (1987) interpreted the strongly sclerotised 'shell' of the halimococcid *Colobopyga coperniciae* Ferris as a production of the adult female, but we believe that it is the sclerotised cuticle of the preadult (second-instar) female. In all of these taxa, the preadult exuviae become hard and afford protection for the adult female and any eggs or embryos. Mating does not seem to be hindered by the apparent inaccessibility of the hidden adult female. Adult females of some pupillarial diaspidids possess tooth-like apical lobes on the pygidium that probably rupture the second-instar exuviae to allow mating and egress of crawlers (Brown & McKenzie 1962; Beardsley & Gonzalez 1975) and a few others have long, finger-like processes at the posterior end of the abdomen (Williams & Miller 2010) that may act as a guide for the adult male. Also adult males of most diaspidids have elongate genitalia (Ghauri 1962) that allow mating with either a pupillarial adult female or one hidden under a scale cover (Beardsley & Gonzalez 1975). Similarly, where they are known, the adult males of halimococcids (e.g., *Colobopyga* Bréthes) have elongate genitalia (Stickney 1934), as do some but not all adult male beesoniids (Takagi 2001; Takagi & Hodgson 2005).

Material and methods

The slide-mounting method used was from Kozarzhevskaya (1968) and Williams & Granara de Willink (1992) or was a modification of their methods. Briefly, specimens were cleared by placing overnight in cold 10% potassium hydroxide in water and then gently heated to 40°C for a few 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 solution, prior to dehydration in a series of alcohol baths, and then transferred through either clove oil or three xylene baths prior to mounting in Canada balsam on microscope slides. Usually adult females were removed from the cuticle of the previous instar either prior to or during the slide-mounting procedure and were mounted on the same slide as the associated exuviae.

Measurements were made by PJG and taken from slide-mounted specimens using an ocular micrometer inserted in the eyepieces of an Olympus compound and a Leica compound microscope. All measurements are maximum dimensions (e.g. body width and apical segment width were recorded at the widest points) and are expressed as the range. Tarsal length of nymphs and the adult male excludes the claw. Spiracle length includes the muscle plate (apodeme). Setal lengths include the setal base. Stylet length was estimated by adding the length of the extended part to the estimated length of the coiled section, which was calculated based on the number of loops and their circumference estimated from their diameter.

The morphological terms follow those of Williams (1985b) and Miller & McKenzie (1967), and of Koteja (1980) for antennal sensilla. Illustrations were prepared by PJG by making a pencil outline sketch using a drawing tube attached to an Olympus compound microscope, then details were perfected by eye at higher magnifications and the final drawing was inked on tracing film placed over the pencil sketch. The Adobe program Photoshop CS6 was used for labelling the scanned illustrations. 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 each main figure; the sizes of these structures are provided in the text.

Depositories of slide-mounted specimens are abbreviated as follows: **ASCU:** Agricultural Scientific Collections Unit, Orange Agricultural Institute, New South Wales, Australia; **ANIC**: Australian National Insect Collection, CSIRO, Canberra, ACT, Australia; **BMNH**: The Natural History Museum, London, UK.

We have registered the new genus and new species 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. Each LSID is a globally unique identifier for the nomenclatural act of naming a new taxon.

Species concepts and relationships. We use only morphological evidence in recognising this new species and new genus, but we believe that sexual species are biologically distinct entities that are reproductively isolated from other similar entities (i.e., the biological species concept; Mayr 1942). No other scale insects closely resemble the species that is described here.

The adult female of our new species has some similarity to several Australian pupillarial species described by Brimblecombe (1959) from the bark either of *Acacia*, *Allocasuarina* or *Casuarina*, and currently placed in the armoured scale genus *Ancepaspis* Ferris (Diaspididae) (Ferris 1942; Brown & McKenzie 1962; García *et al*. 2016). The immature stages of Australian species of *Ancepaspis* are not known, but Stickney (1934) illustrated some immature and adult male features of the type species *A. tridentata* (Ferris) as well as three instars of *A. edentata* (Ferris), probably based on Ferris' type material from Arizona. Although the descriptions and drawings by Ferris (1919) and Brimblecombe (1959) are minimalist, Stickney's illustrations are excellent and it is clear that the new species from *Angophora* is not congeneric with the North American species of *Ancepaspis*. Among the palm scales, *Phoenicococcus marlatti* Cockerell (Phoenicococcidae) and a number of halimococcids (especially species of *Colobopyga* Bréthes and *Halimococcus* Cockerell (Stickney 1934; Ferris 1952; Deitz 1979)) share some female morphological features, such as adult and preadult body shape, antennal form and loss of legs, with the new taxon from *Angophora*. None of the above taxa (including *Ancepaspis*) have the group of pores and disc-like structures that surround the vulva of the adult female of our new taxon. Also, *Ph. marlatti* is not pupillarial (Stickney 1934; Brown & McKenzie 1962). However, similar to our new taxon, the adult males of all studied halimococcids, as well as *Ph. marlatti*, have antennae with a pedicellate base to the flagellum, which is an elongate club formed of several aggregated segments (Stickney 1934). The adult male of the eriococcid *Pseudochermes fraxini* (Kaltanbach) (Afifi 1968) has very similar antennae, and adult males of *Cystococcus* Fuller (Eriococcidae *sensu*

lato) have a pedicellate base to the antennal flagellum but most or all flagellar segments are fused (Semple *et al*. 2015). Also there are thick fleshy or peg-like setae on the antennae and posterior abdomen of adult males of both *Cystococcus* and the new taxon. Furthermore, the abdomen of the adult male of our new taxon is unlike those of adult males of *Ps. fraxini*, *Ph. marlatti*, halimococcids or diaspidids, but is similar to the abdomen of adult males of *Cystococcus* in that some segments are long and narrow and apparently telescopic (see description of the adult male below). *Ps. fraxini* is discussed further in the comments that follow the description of the adult male of our new taxon.

Nucleotide sequence data from the small subunit ribosomal RNA gene (18S) (L.G. Cook 2015, unpublished data) place our new taxon with the Myrtaceae-feeding group of eriococcids, as recognised by Cook & Gullan (2004), which includes *Cystococcus*, and not close to *Ps. fraxini*, which was sequenced by Gwiazdowski *et al.* (2006), nor to the Diaspididae. No molecular data are available for *Ancepaspis*, *Colobopyga* or *Halimococcus*. Some sequence data are available for *Ph. marlatti*, which is sister to Diaspididae in the analyses of Vea & Grimaldi (2016), and for the halimococcid *Thysanococcus pandani* Stickney, which is sister to all Diaspididae in the analyses of Andersen *et al.* (2010). *Thysanococcus* Stickney, however, shares more morphological features with armoured scales (see Stickney 1934) than with other halimococcids. All halimococcids and *Ph. marlatii* occur on various genera of palms (Arecaceae) and are considered morphologically specialised. The higher classification of these palm-feeding scales is uncertain and there have been no recent studies with adequate taxon sampling, although a relationship with Diaspididae is usually accepted. Currently *Ph. marlatti* is the sole species in the Phoenicococcidae (Miller *et al.* 2005; García *et al*. 2016), but previously this higher taxon was more broadly defined to include species and genera that now are placed in Halimococcidae (Stickney 1934; Ben-Dov 1990). Stickney (1934) placed these palm-feeding scales in his tribe Phoenicococcini of subfamily Phoenicoccinae of the diaspidid grouping. Brown & McKenzie (1962) first recognised the Halimococcidae for the genera, other than *Phoenicococcus,* treated by Stickney (1934).

We conclude that our new taxon is convergently similar to one or more instars of *Ps. fraxini*, *Ph. marlatti,* halimococcids and a few diaspidids. Some morphological convergence of small scale insects that live hidden on the bark of their host plant might be expected. Certainly, pupillarity has arisen independently in several families of scale insects and also multiple times in Diaspididae (Andersen *et al*. 2010). Here we place our new genus and new species into the Eriococcidae, although we recognise that this family, as currently circumscribed, is not monophyletic as shown by both morphological (e.g., Cox & Williams 1987; Hodgson & Hardy 2013) and molecular (e.g., Cook *et al*. 2002; Gullan & Cook 2007) data. Further molecular phylogenetic studies of eriococcids, diaspidids and their allies are needed to refine the higher-level classification.

Taxonomy

Aolacoccus gen. nov.

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Type species. *Aolacoccus angophorae* sp. nov., by present designation and monotypy.

Etymology. The genus is named after Dr Aola M. Richards, who first collected the species described here. Aola took a keen interest in scale insects when working at the Plant Diseases Division, Department of Scientific and Industrial Research, Auckland, New Zealand, before moving to the School of Zoology, University of New South Wales, Kensington, New South Wales, Australia. She was an excellent collector and published mainly on damage and control of scale insects. Her knowledge was much wider though, with other studies mostly on coccinellids, parasitoids and Orthoptera. After retiring, Aola settled in London where she still lives. The name *Aola* is combined with the genus name *Coccus* and is masculine.

Generic diagnosis. As the genus currently is monotypic, its description is the same as for the species description below and only a brief generic diagnosis based on the adult female is included here.

Adult female minute, <1 mm long, retained within the sclerotised cuticle of the second-instar female. In life, found on trunk and branches of *Angophora* trees, with each insect usually hidden under a thin layer of bark tissue. Body globular, margin not defined (lacking setae), with posterior of abdomen tapering to a rounded end. Derm

mostly membranous, with segmentation indistinct to absent. Most body setae minute (each about 2 µm long) and sparsely distributed, but setae longer on posterior of abdomen. Macrotubular and microtubular ducts absent. Loculate pores absent dorsally, all quinquelocular (5 loculi) ventrally and present only on derm around each spiracle and in a cluster around vulva. Small disc-like structures, perhaps cicatrices, in cluster posterior to vulva. Antennae each a small, unsegmented tubercle bearing several fleshy setae. Frontal lobes and antennal tubercles absent. Spiracles well developed, subequal in size, each with muscle plate (apodeme) expanded medially. Legs absent. Vulva well developed. Anal lobes absent. Anal ring small, apparently ventrally located and partially sclerotised.

Adult females of *Aolacoccus* can be identified using the key of Hardy *et al*. (2011) or Hardy & Gullan (2007) to genera of felt scales (Eriococcidae) found on *Eucalyptus* and *Corymbia* in Australia, but modified as follows for couplets 8 and 9 and with the addition of couplet 9a:

8. Anal ring invaginated, U-shaped, with numerous small pores and a pair of apodemes extending anterolaterally; pore plates (hind legs reduced to flattened plates bearing translucent pores) present; bilocular pores present; from bark of *Eucalyptus* . . . . undescribed genus A*
- Anal ring absent, or if present, circular or partial, not invaginated, without pores or apodemes; pore plates absent; bilocular pores absent 9
9. Body minute, <1 mm long; dorsum membranous, no part forming a sclerotic operculum; from bark of *Angophora* . . . . *Aolacoccus* gen. nov.
- Body almost always >1 mm in diameter or length and sometimes more than 1 cm long; part of dorsum forming a sclerotic operculum, either disc-like or button-like, that plugs gall orifice; ex galls on stems or leaves of *Corymbia*. . . . 9a
9a. Loculate disc pores absent but pore plates present, each with irregular rim and 3–40 rounded tubercles that appear as holes or 'pores'; each spiracle composed of broad, irregular atrium with tangled mass of radiating, sclerotic tracheal trunks; ex woody galls on stems of *Corymbia*. . . . *Cystococcus* Fuller
- Either small pore plates (as in *Cystococcus*) or loculate disc pores (mostly quinquelocular) present; spiracles either similar to those of *Cystococcus* or of typical eriococcid type; ex non-woody galls on leaves of *Corymbia* . . . . *Ascelis* Schrader

(*The use of this code name 'undescribed genus A' is not intended as a nomenclatural action.)

***Aolacoccus angophorae* sp. nov.**
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Etymology. The specific name is based on the genus name of the host plant, is in the Latin genitive singular and means "of *Angophora*".

Type material examined. Holotype: Adult female (body 740 µm long), on slide with its second-instar exuviae. **AUSTRALIA, New South Wales**: Sydney, Cremorne Point, under bark of *Angophora*, 15.x.1980, A.M. Richards, A12605, B3 (ANIC).

Paratypes: 5 slides, each with 1 adult female and 4 also with female's second-instar exuviae, 1 slide with 1 second-instar female exuviae and 5 embryos, 3 slides with 13, 10 or 2 first-instar nymphs respectively, 1 slide with 1 second-instar male and its first-instar exuviae, all with same data as holotype (8 slides in ANIC; 2 slides each with 1 adult female and its second-instar exuviae in ASCU); 4 slides, each with 1 adult female and its second-instar exuviae and 1 of these slides also with 1 first-instar nymph, 1 slide with 2 adult females and 3 second-instar exuviae, 1 slide with 16 embryos, all with same data as holotype except "B1" instead of "B3" (4 slides in ANIC; 2 slides each with 1 adult female and its second-instar exuviae in BMNH).

Other material examined: AUSTRALIA, New South Wales: 2 slides each with 1 male pupa (with pharate adult male in one pupa but broken in half), Bungwahl (misspelled on label as "Bungwalil") [N of Newcastle], ex *Angophora*, 16.v.1984, C. Ballard (ANIC); 1 slide with 5 second-instar males, Cowan [N of Sydney], under bark of *Angophora* sp., 2.x.1980, A.M. Richards, A12605, B2 (ANIC); 1 slide of adult male [poorly cleared], Hornsby Heights [N of Sydney], 29.v.1984, A.M. Richards (ANIC); 1 slide with 2 adult females, 1 slide with 1 adult female and its second-instar exuviae and 12 first-instar nymphs, 2 slides each with 1 adult female and its second-instar exuviae, 1 slide with 8 second-instar exuviae (4 with adult female inside), and 1 slide with 1 second-instar male, Sydney, Cronulla, Gunnamatta Park, roadside, ex trunk of *Angophora costata*, under small pieces of loose bark, 13.ii.2015, P.J. Gullan, P.S. Cranston & T. Kondo (ANIC).

Note: The second-instar male from the type collection was compared with those collected at other localities and they were identical. The pharate adult male from Bungwahl and the adult male from Hornsby Heights also

appeared identical and, although no associated female specimens are available for slide mounting, A.M. Richards said that females were present and she was certain that they were conspecific with specimens from Cremorne Point (pers. comm. to DJW).

Adult female (Figs 1, 2) **Unmounted material.** On trunk and branches of host trees, usually beneath bark; each adult female hidden beneath a thin layer of bark cells (Fig. 1) and pharate within sclerotised cuticle of penultimate instar.

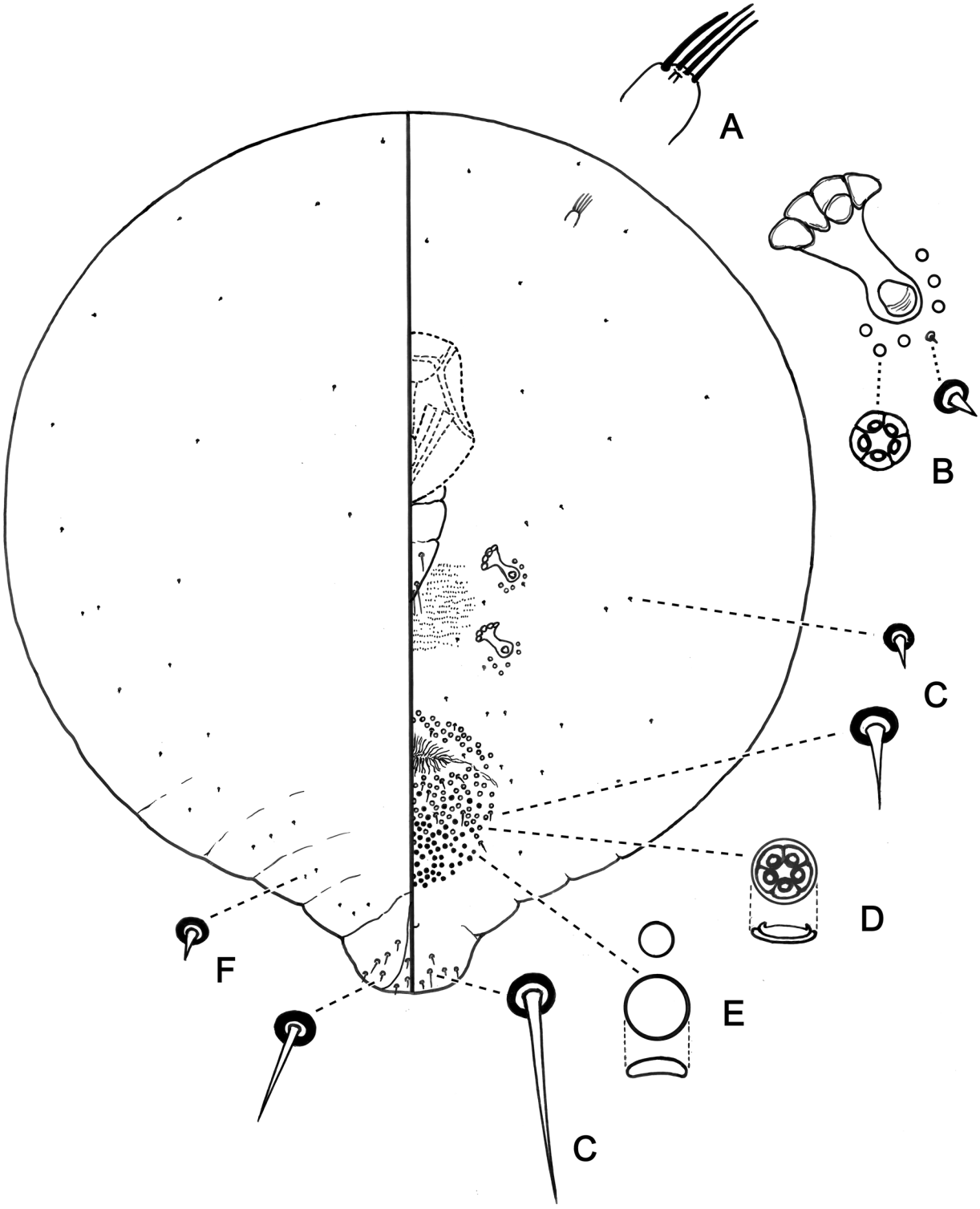

FIGURE 2. Adult female of *Aolacoccus angophorae* **sp. nov.** A, antenna; B, spiracle with enlargements of quinquelocular pore and minute seta; C, ventral setae; D, quinquelocular pore from near vulva; E, disc-like structure, perhaps a cicatrix; F, dorsal setae.

Mounted material (description based on 12 females). Body 400–760 μm long, 400–750 μm wide, rounded, almost circular when mature, with posterior of abdomen tapering to a rounded end with light sclerotisation for posteriormost 55–100 μm. Margin not defined, lacking setae. Derm membranous, except for posterior of abdomen and rows of minute microtrichia ventromedially between spiracles. Segmentation indistinct to absent.

Dorsum. Most setae (Fig. 2F) minute and sparsely distributed, each about 2 μm long and 2.0–2.5 μm across socket, except 8–15 longer setae, each 5–10 μm long, on posterior of abdomen. Macrotubular and microtubular ducts absent. Loculate pores absent. Anal lobes absent.

Venter. Setae (Fig. 2C) mostly minute and sparsely distributed as on dorsum, with 7–12 longer setae each 7–20 μm long on posterior of abdomen, and several setae each 5–10 μm long just posterior to vulva. Macrotubular and microtubular ducts absent. Loculate pores (Fig. 2D) all quinquelocular (5 loculi) (except for a single 9-locular pore detected on one female), restricted to 2 places: (i) 3–8 pores, each 3–4 μm in diameter, around atrial opening of each spiracle, and (ii) a dense cluster of 110–150 pores, each 4–5 μm in diameter, surrounding vulva. Small disc-like structures (Fig. 2E), each 2.5–5.0 μm in diameter, perhaps cicatrices, in cluster of about 90–110 posterior to vulva, partly intermixed with quinquelocular pores. Eyespots absent. Antennae (Fig. 2A) each a small unsegmented tubercle 12–23 μm long and 10–17 μm wide, bearing 4 or 5 fleshy setae, each seta 13–30 μm long. Frontal lobes and antennal tubercles absent. Clypeolabral shield 120–160 μm long, 90–120 μm wide. Labium 50–75 μm long, 45–60 μm wide, segmentation poorly defined, probably with 3 segments and 4 pairs of setae. Stylets 2000–2200 μm long (based on 2 females with intact stylets), coiled into about 4 loops when retracted. Spiracles (Fig. 2B) well developed, subequal in size, each with muscle plate expanded medially; length including muscle plate 25–40 μm; width across peritreme at atrial opening 10–15 μm and across widest part of muscle plate 16–26 μm; each peritreme surrounded by a group of quinquelocular pores (see above). Legs absent. Vulva well developed, its position marked by radiating wrinkles. Anal ring apparently ventral and represented by a small, partially sclerotised ring, lacking pores and setae.

Second-instar female (Fig. 3). **Mounted material** (description based on 8 females)**.** Body 550–1000 μm long, 500–900 μm wide, rounded, with posterior of abdomen tapering to a sclerotised and rounded knob, 65–90 μm long, that splits to become a hinged flap or operculum (Fig. 3D) to allow emergence of crawlers. Anal lobes absent and anus not detected. Margin not defined, lacking setae. Derm membranous when young, becoming sclerotised with age, and with 12–17 rows of minute microtrichia ventromedially between spiracles. Segmentation not discerned.

Dorsum. Setae absent on dorsal derm except for 8–12 short setae (Fig. 3G) on knob of posterior of abdomen, each seta 2–4 μm long and ~2 μm across socket. Macrotubular and microtubular ducts absent. Loculate pores absent except for several on posterior apex of abdomen on operculum (see below for venter).

Venter. Setae few and each mostly 1–2 μm long and 2 mm across socket, 1–3 pairs near spiracles, a few on posterior of abdomen and a pair of longer setae (Fig. 3E), each 10–13 μm long and 3 μm across socket, on posterior margin of abdomen (the latter may be apical setae). Macrotubular ducts and typical eriococcid microtubular ducts absent, but a sclerotised pore-like structure (Fig. 3B), 2 μm across widest dimension, possibly a bilocular microduct, sparsely distributed on abdomen. Loculate pores (Fig. 3F) all quinquelocular (5 loculi), each 2.5–3.0 μm in diameter, restricted to 2 places: (i) 2–6 pores around atrial opening of each spiracle, and (ii) a scattering of pores on abdomen posterior to spiracles with a denser grouping of 20–30 on posterior apex of abdomen, of which some may be dorsal. Eyespots absent. Antennae (Fig. 3A) each a small unsegmented tubercle 7.5–8.0 μm long and 8–10 μm wide, bearing 4–5 fleshy setae, each 7–16 μm long. Frontal lobes and antennal tubercles absent. Clypeolabral shield 75–100 μm long, 50–60 μm wide. Labium 35–45 μm long, 30–35 μm wide, segmentation poorly defined, probably with 3 segments and at least 3 pairs of setae. Stylets at least 1200 μm long (broken or missing on all but one specimen). Spiracles (Fig. 3C) small but well developed, subequal in size, each with muscle plate slightly expanded medially; length including muscle plate 18–24 μm; width across peritreme at atrial opening 5–7 μm and across widest part of muscle plate 8–10 μm; each peritreme surrounded by a small group of quinquelocular pores (see above). Legs absent.

First-instar nymph (Fig. 4). Mounted material (sex not determined; description based on 8 nymphs). Body 230–255 μm long, 110–135 μm wide, ovoid, with posterior of abdomen (Fig. 4C) rounded, lacking distinct anal lobes, anus located ventrally. Margin not defined by differentiated setae. Derm membranous; segmentation discernible only on abdomen.

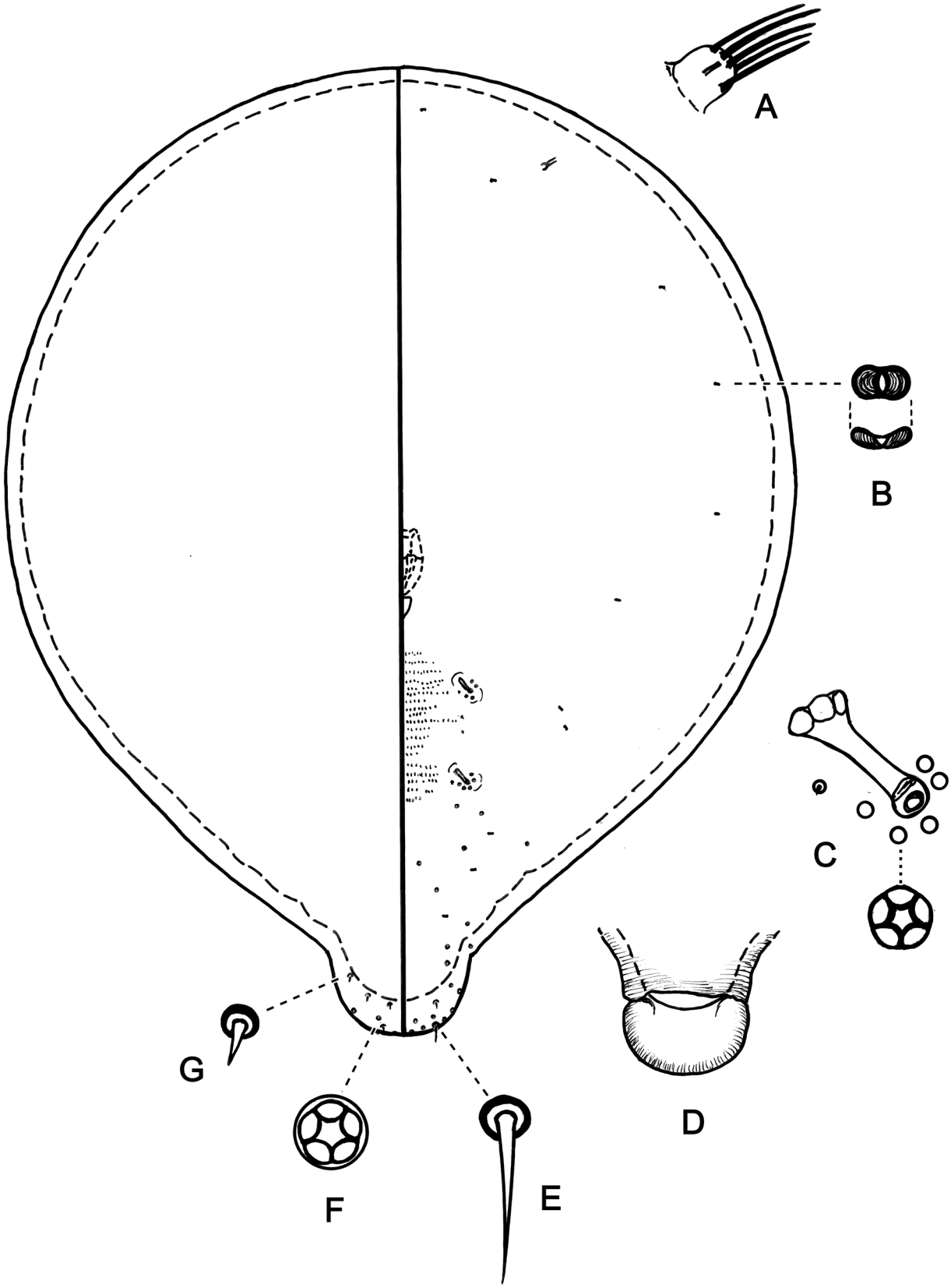

FIGURE 3. Second-instar female of *Aolacoccus angophorae* **sp. nov.** with body outline of adult female indicated by dashed line just inside body. A, antenna; B, pore-like structure, possibly opening of a microduct; C, spiracle with enlargement of quinquelocular pore; D, abdominal operculum; E, ventral seta; F, quinquelocular pores from operculum; G, dorsal seta.

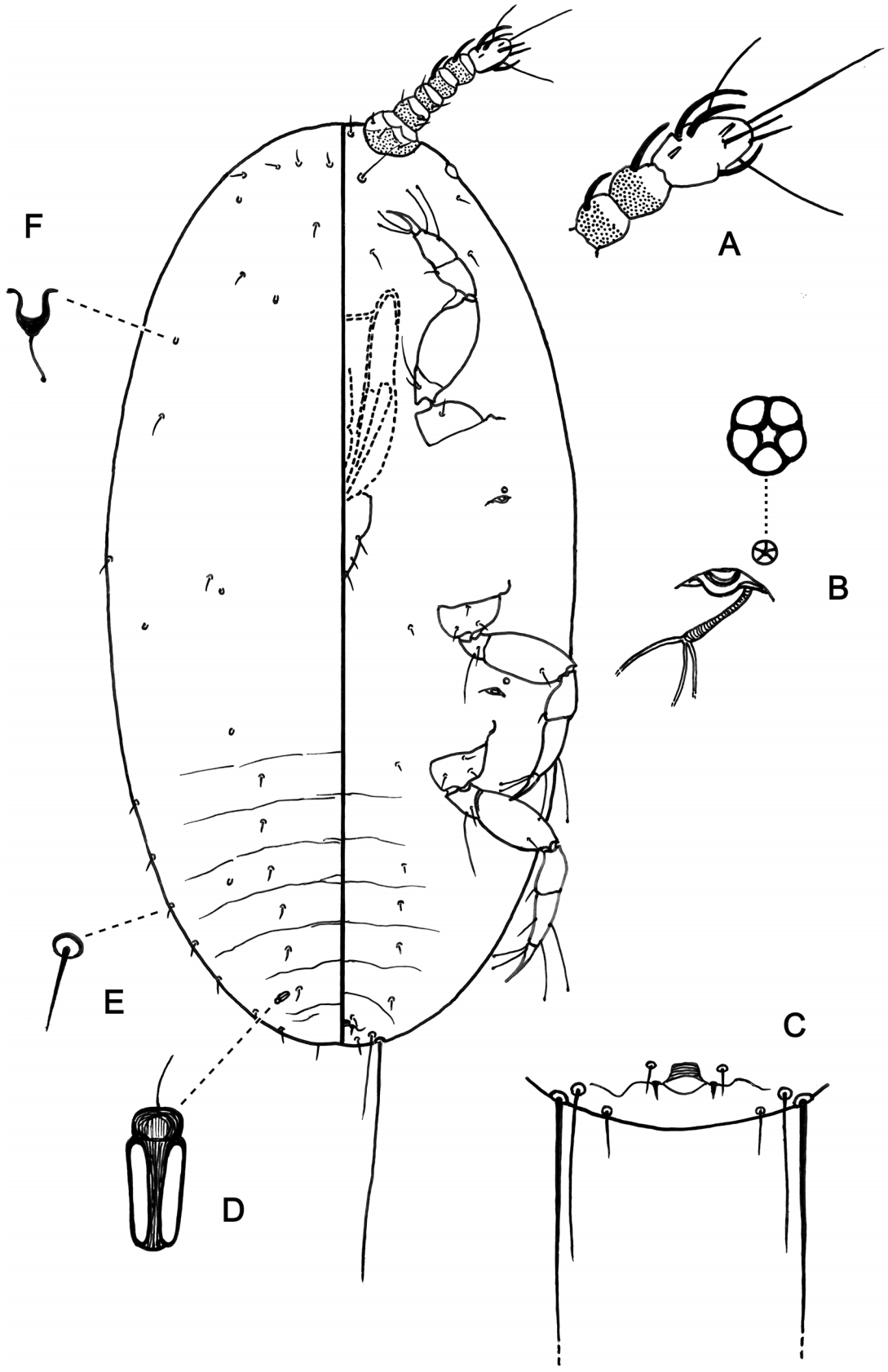

FIGURE 4. First-instar nymph of *Aolacoccus angophorae* **sp. nov.** A, apical antennal segments; B, spiracle with enlargement of quinquelocular pore; C, enlargement of ventral posterior of abdomen showing anal area; D, robust microtubular duct; E, dorsal seta; F, small microtubular duct.

Dorsum. Setae (Fig. 4E) minute hair-like, each 3–5 μm long, in marginal and submedial longitudinal rows on each side of abdomen, rare on thorax and scattered mostly anteriorly on head. Macrotubular ducts and loculate pores absent. Microtubular ducts of 2 kinds: (i) a single robust, sclerotised duct (Fig. 4D), 5.0–5.5 μm long and 2–3 μm wide, submarginally on each side of posterior of abdomen, and (ii) shallow, sclerotised ducts (Fig. 4F), 1.5–2.0 μm deep, mostly 1.5 μm wide, scattered, few in number (10–12 total).

Venter. Setae hair-like, each 2–4 μm long on abdomen and thorax, 5–12 μm long on head with longest situated submedially posterior to antennae; 1 pair of long flagellate apical setae, each 70–75 μm long, with a shorter apical seta, each 22–24 μm long, medial to each apical seta, and a pair of shorter setae, each 5–6 μm long, between 2 pairs of apical setae (Fig. 4C). Macrotubular and microtubular ducts absent. Loculate pores quinquelocular, each 2.0–2.5 μm in diameter, with 1 pore anterior to opening of each spiracle. Eyespot 8–10 μm in greatest dimension, situated on margin posterior to base of antenna. Antennae (Fig. 4A) each 43–53 μm long with 6 segments; segment I mostly lightly sclerotised and basal part of each of 5 distal segments with light sclerotisation; apical segment 13–15 μm long and 7.0–7.5 μm wide, bearing 3 curved fleshy setae each 8–11 μm long, 1 slender straight fleshy seta 6–9 μm long, 3 long hair-like setae each 16–26 μm long (apical one longest), 2 slender setae each 6–7 μm long, and 2 coeloconic sensilla; other antennal segments as follows: segment I with 3 or 4 hair-like setae; II with 2 hair-like setae and a campaniform sensillum; III with 2 or 3 hair-like setae; IV with 1 fleshy seta 5–6 μm long and no other setae; V with 1 fleshy seta 6–7 μm long and 2 or 3 hair-like setae. Frontal lobes and antennal tubercles absent. Clypeolabral shield 55–62 μm long, 30–35 μm wide. Labium 20–27 μm long, 18–20 μm wide, segmentation poorly defined, probably with 3 segments and 3 pairs of setae, with apical setae spike-like. Stylets 500–800 μm long, coiled into almost 2 loops when retracted. Spiracles (Fig. 4B) subequal in size, each with elongate sclerotised peritreme of length 7–8 μm, maximum width 2.0–2.5 μm; each spiracle associated with a quinquelocular pore (see above). Legs well developed; segment lengths (metathoracic leg (μm)): coxa 9–10; trochanter + femur 30–34; tibia 13–17; tarsus 12–15; claw 11–13; long trochanteral seta 14–17 μm long; a campaniform sensillum present at base of each tarsus (difficult to see); claw with a subapical denticle; both tarsal digitules on all legs capitate, with one digitule distal and other much more proximal, distal digitule 12–15 μm long, other digitule 14–19 μm long, with longest digitules on metathoracic legs; claw digitules alike, each 9–10 μm long, with small capitate apex. Anus represented by a sclerotised arc 2–3 μm across that may represent a partial anal ring; flanked by 2 pairs of setae, more distal pair spine-like and each 2–3 μm long, other pair hair-like and each ~4 μm long.

Second-instar male (Fig. 5). Unmounted material (only one live nymph seen)**.** On bark of host plant; in white waxy test of typical eriococcid type.

Mounted material (description based on 7 nymphs). Body 500–780 μm long, 300–455 μm wide, ovoid, with posterior of abdomen rounded, lacking distinct anal lobes and anus located ventrally. Margin not defined by differentiated setae. Derm membranous but with rows of minute microtrichia ventromedially between thoracic legs. Segmentation distinct dorsally, weakly indicated on ventral abdomen.

Dorsum. Setae (Fig. 5D) robust hair-like, each 10–17 μm long in a sparse row on each thoracic and abdominal segment; longer and sparsely scattered on head, each 25–30 μm. Macrotubular ducts (Fig. 5E) each with main duct and outer opening membranous (difficult to discern), up to 25 μm deep, with inner cup about 3.5 μm across and a membranous inner ductule 5–6 μm long; ducts sparsely distributed across all segments and with 1 duct opening on lateral margin of each side of each abdominal and thoracic segment and several opening on margin around head. Microtubular ducts absent. Loculate pores (Fig. 5B) all quinquelocular, each about 3 μm in diameter, sparsely scattered on every body segment.

Venter. Setae robust hair-like, each 10–30 μm long on abdomen, 15–38 μm long on thorax and laterally on head; but 6 or 7 (usually 7) setae, each 30–70 μm long, situated medially to submedially on head; one pair of long flagellate apical setae, each 85–90 μm long, with a pair of shorter setae, each 17–20 μm long, present between apical setae. Macrotubular and microtubular ducts absent. Loculate pores (Fig. 5B) all quinquelocular, each about 3 μm in diameter, sparsely scattered on every body segment but with a loose aggregation around each posterior spiracle and 2 or 3 pores anterolateral of atrial opening of each spiracle. Eyespots each 15–19 μm in greatest dimension, situated on margin posterior to base of antenna. Antennae (Fig. 5A) each 37–50 μm long with 6 segments; base of each of 5 distal segments with light sclerotisation but segment I entirely membranous; apical segment 10–15 μm long and 10–13 μm wide, bearing 3 subequal, curved fleshy setae, each 15–24 μm long, 6 hair-like setae, each 10–25 μm long, and a coeloconic sensillum; other antennal segments as follows: segment I with 3

or 4 hair-like setae; II with 2 hair-like setae and a campaniform sensillum; III with 2 or 3 hair-like setae; IV with 1 fleshy seta 12–15 µm long and no other setae; V with 1 fleshy seta 15–21 µm long and 4 hair-like setae. Frontal lobes and antennal tubercles absent. Clypeolabral shield 88–100 µm long, 70–80 µm wide. Labium 40–50 µm long, 30–40 µm wide, segmentation poorly defined, probably with 3 segments and 4 pairs of setae. Stylets 1000–1400 µm long. Spiracles elongate, subequal in size, each with muscle plate slightly expanded medially; length including muscle plate 20–26 µm; width across peritreme at atrial opening 4–5 µm and across widest part of muscle plate 7–10 µm; always associated with a few quinquelocular pores (see above). Legs well developed; segment lengths (metathoracic leg (µm)): coxa 40–50; trochanter + femur 58–70; tibia 35–42; tarsus 27–40; claw 12–15; long trochanteral seta 30–50 µm long; a campaniform sensillum present at base of each tarsus; claw with a subapical denticle; both tarsal digitules on all legs capitate and equal in size, each 17–20 µm long; claw digitules alike, each 10–12 µm long, with small capitate apex. Anus (Fig. 5C) represented by a sclerotised arc 5–7 µm across that may represent a partial anal ring; flanked on each side by a tiny sclerotised patch bearing a seta 7–8 µm long and with a slightly more anterolateral seta 10–12 µm long.

Adult male (Fig. 6). **Mounted material** (notes based on 2 adult males, one poorly cleared, other pharate in pupal cuticle and mostly poorly visible). Body ~800 µm long with abdomen ~430 µm long, with middle segments partially telescoped into each other. Head with 2 pairs of simple eyes and antennae each with 8 segments. Wings and hamulohalteres absent. Body with hair-like and peg-like setae; pores absent. Glandular pouches absent. Genital capsule only slightly longer than wide, tapered to a bluntly rounded apex.

Head. Broad conical with truncate anterior margin; head width across ocular sclerites ~120 µm; head ridges and most sclerites not apparent; width across each ocular sclerite 15–17 µm. Head setae: ventral surface with ~24 peg-like setae, each 3–4 µm long, and ~14 hair-like setae each 12–15 µm long; dorsal surface with ~6 peg-like setae, each 2–3 µm long, and ~12 hair-like setae each ~10 µm long. Antennae (Fig. 6A) each ~160 µm long, approximately twice length of head; scape and pedicel each about as long (~25 µm) as wide (25–30 µm); segment III pedicellate, 30–32 µm long, 20–23 µm wide at distal margin; distal 4 segments (V–VIII) forming an elongate club of maximum width 30 µm; apical segment rounded, 19 µm long, 20–22 µm wide, with 3 apical capitate hair-like setae each 23–25 µm long, 1 long antennal bristle 15 µm long, 2 basiconic sensilla each ≤3 µm long, and 4 fleshy setae each 12–16 µm long. Other segments of antennal club with several fleshy setae, each 6–7 µm long, and hair-like setae, each 15–23 µm long; more proximal antennal segments only with hair-like setae, each 12–20 µm long.

Thorax. Ridges and sclerites apparently degenerate although thoracic detail obscured by body contents; setae (as far as can be discerned): peg-like setae, each 4–5 µm long, on ventral and dorsal thoracic margins; dorsal hair-like setae in sparse transverse row across each thoracic segment (and abdominal segment I), each seta 7–9 µm long; ventral hair-like setae apparently represented by 1 pair between each pair of legs, each seta 13–15 µm long. Mesothoracic and metathoracic spiracles subequal in size, length including muscle plate 23–25 µm, width across peritreme 11–12 µm. Legs subequal in size; metathoracic legs with following segment lengths (in µm); coxa: 43–45; trochanter + femur: 100–103; tibia: 83–85; tarsus: 40; claw: 15–17, with subapical denticle; paired tarsal digitules capitate, 22–23 µm long; claw digitules capitate, longer than claw; long trochanteral seta ~25 µm long.

Abdomen. Segments I and II reasonably normal, but segments III–VII long and narrow with telescoping confounding estimate of their length relative to total body length; each of segments V and VI with fold where anterior part of segment telescopes into posterior part of preceding segment, or into anterior part of same segment for segment V. Tergites and sternites of segments I–VII considered absent. Abdominal segment VIII 43–46 µm long, with a pair of internal rod-like structures about the same length as segment. Caudal extensions, glandular pouches and glandular pouch setae absent. Abdominal setae of 2 types: hair-like, each 3–8 µm long, and peg-like, each 4–6 µm long. Genital segment with genital capsule (penial sheath) lightly sclerotised, 27–28 µm long, 18–22 µm wide at base; aedeagus 18–20 µm long, 4–5 µm wide at apex, parallel-sided; genital sensilla few: 3 pairs of stout fleshy setae (or bristles), one pair dorsal and 2 pairs marginal, each seta 6–8 µm long, plus one pair of ventral hair-like setae each 3–4 µm long, and a pair of subapical campaniform sensilla each 3 µm across.

Comments. The adult male of *A. angophorae* has the general body and antennal form of the apterous adult male of *Pseudochermes fraxini*, as illustrated by Afifi (1968), except that the posterior of the abdomen of *A. angophorae* is more elongate and is telescopic, whereas the legs are more typical of alate adult male eriococcids than those of *P. fraxini*. Presumably the resemblance of males of *A. angophorae* and *P. fraxini* is convergence due

to the adult males of both species being very small and wingless. The second-instar and adult females of the two taxa are extremely different in appearance (the first-instar nymph and the two female instars of *Ps. fraxini* are described and illustrated by Williams 1985b). We note that *Pseudochermes* Nitsche and *Cryptococcus* Douglas were placed in the family Cryptococcidae by Kozár *et al*. (2013) but current phylogenetic evidence (Gwiazdowski *et al*. 2006; Nan *et al*. 2013) does not support the recognition of a family just for these two genera of eriococcids *s.l.*

We also compared the adult male of *A. angophorae* with the adult males of *Apiomorpha* and *Opisthoscelis* (Theron 1968), *Callococcus* Ferris (Afifi & Kosztarab 1967 [therein as "*Sphaerococcus tomentosus* Fuller?"]; Coles *et al*. 1988), *Cystococcus* Fuller (Semple *et al*. 2015) and *Lobimargo* Hardy & Beardsley (formerly part of *Lachnodius*) (Hardy *et al*. 2011), which are all members of the eriococcid Myrtaceae-feeding clade of Cook & Gullan (2004). Only the adult males of *Cystococcus* species bore any resemblance to the male of *Aolacoccus*, as discussed above under "Species concepts and relationships".

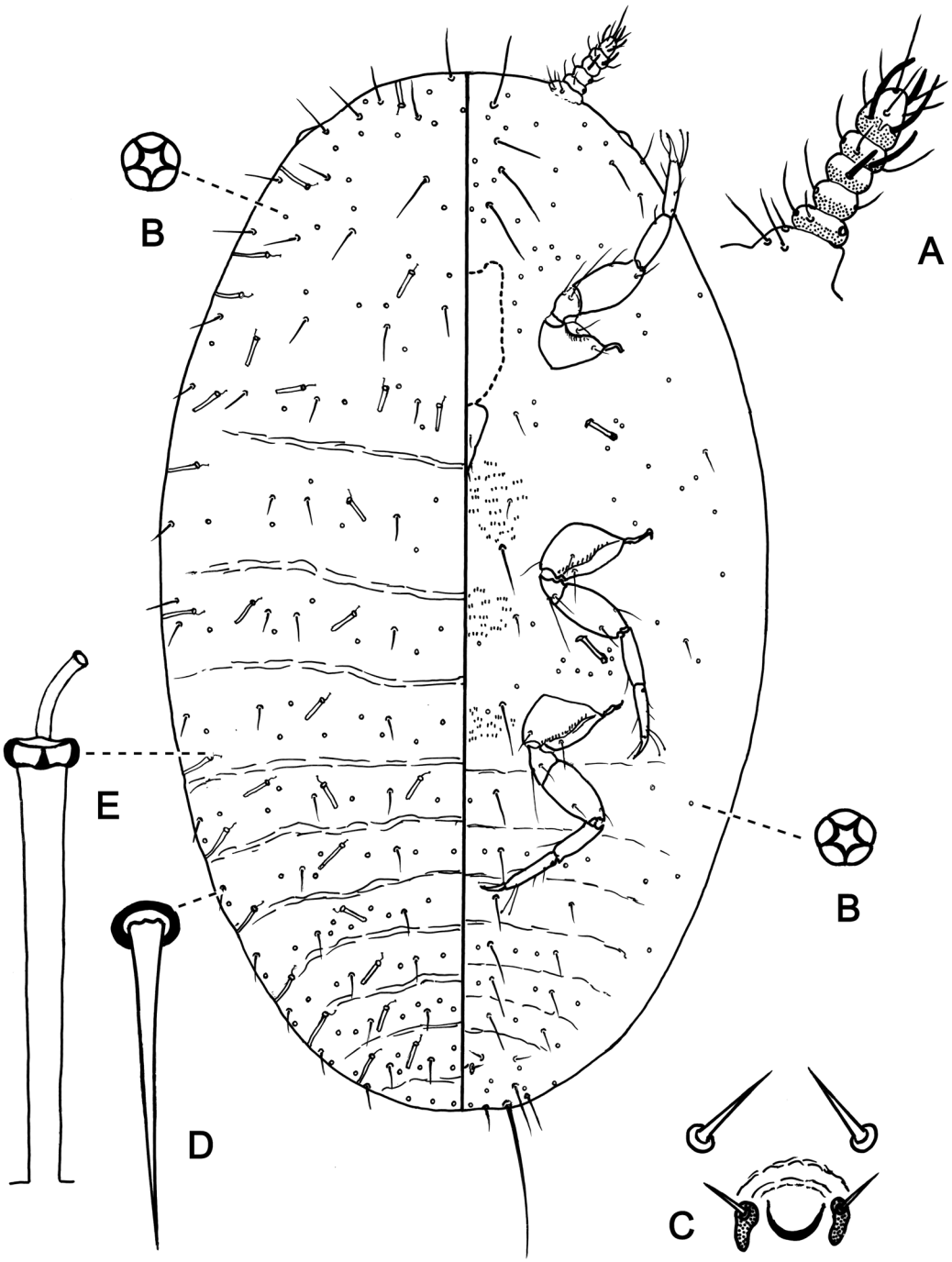

FIGURE 5. Second-instar male of *Aolacoccus angophorae* **sp. nov.** A, antenna; B, quinquelocular pores; C, anus and associated setae; D, dorsal seta; E, macrotubular duct.

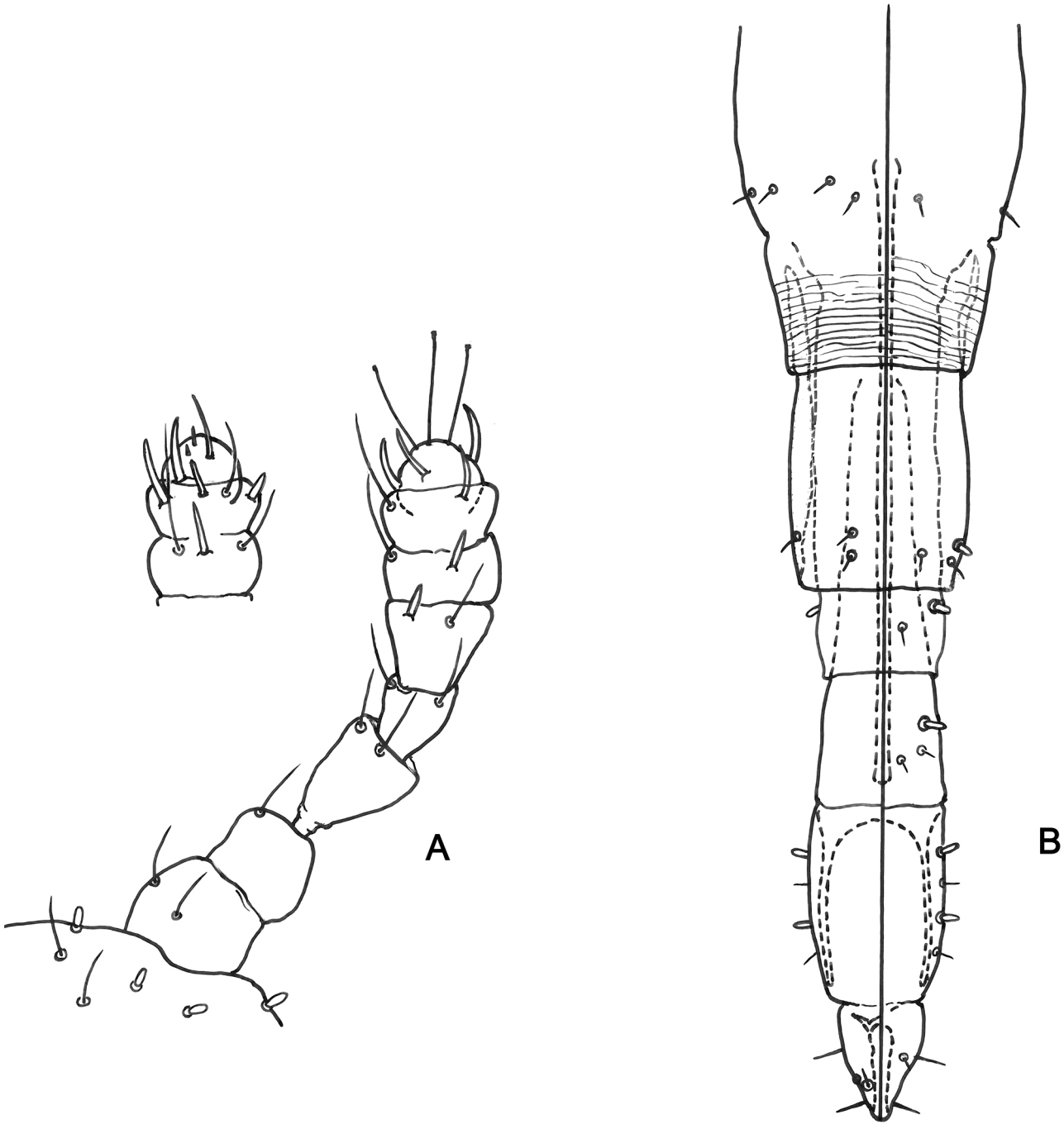

FIGURE 6. Adult male of *Aolacoccus angophorae* **sp. nov.** A, dorsal view of antenna with ventral view of apical segments on left; B, apical segments of abdomen.

Biology. Little is known of the biology of *A. angophorae*, although Dr A.M. Richards observed that the species was common on all *Angophora* trees around Sydney and she noticed two species of lady beetle (Coleoptera: Coccinellidae) present among infestations of the scale (pers. comm. to DJW). It appears that *A. angophorae* does not produce honeydew. Dr Richards never observed ant attendance even though ants were numerous and, in one case, were attending aphids on a nearby tree (pers. comm. to DJW). Each of the feeding stages (first instar, second instar of both sexes and adult female) has a highly reduced anus lacking a typical eriococcid anal ring and without wax-exuding pores (anus not definitely detected in the second-instar female), suggesting that no honeydew is produced. Similarly, in adult females of *Cystococcus*, the gut is blind-ended, the anus apparently non-functional and the short mouthpart stylets suggest that they do not access phloem tissue (Semple *et al*. 2015). Armoured scale insects, the diaspidids, produce no honeydew and have an unusual digestive system, but many are thought to

imbibe sap from phloem sieve tubes close to the cambium (Banks 1990). The tiny insects of *A. angophorae* must feed by accessing plant cells in the stems or trunk of their *Angophora* hosts and yet the body length of all life stages never exceeds 1 mm and for most it is much less. The fully extended feeding stylets of each instar are longer than the insect's body (e.g., about four times as long for some adult females) but even the adult female's 2 mm long stylets might not be able to reach the phloem on a main branch or trunk of an *Angophora* tree. The cortex lies below the epidermis on the stem or trunk of *Angophora* (Chattaway 1953; Bryant & Trueman 2015) and probably these insects feed from cortical parenchyma tissue.

The elongate abdomen of the adult male of *A. angophorae* presumably allows copulation with an adult female protected within its second-instar exuviae under the host-plant bark (Fig. 1). Similarly, the elongate abdomens and/or genitalia of the adult males of a number of gall-inducing eriococcid genera allow access to females hidden in galls, as discussed by Gullan *et al*. (2005).

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