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A Review of the Eriococcid Genera (Hemiptera: Sternorrhyncha: Coccoidea) of South America

CHRIS HODGSON¹ & DUG MILLER²

¹Department of Biodiversity and Biological Systematics, The National Museum of Wales, Cardiff, CF10 3NP, Wales.

E-mail: hodgsoncj@cardiff.ac.uk

*²Systematic Entomology Laboratory, Beltsville Agricultural Research Center, U. S. Department of Agriculture, Beltsville, Maryland
20705 USA. E-mail: douglass.miller@ars.usda.gov*



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CHRIS HODGSON & DUG MILLER

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Abstract

This paper reviews the present status of all genera of Eriococcidae (Hemiptera: Sternorrhyncha: Coccoidea) known from South America and provides generic diagnoses based on the adult females of all available species for each genus. Redescriptions and illustrations are provided for the adult females of *Aculeococcus morrisoni* Lepage, *Apiococcus gregarius* Hempel, *Capulinia sallei* Signoret, *Carpochloroides viridis* Cockerell, *Macracanthopyga verganiana* Lizer y Trelles, *Pseudocapulinia lanosa* Hempel and *Tectococcus ovatus* Hempel, which are all type species of their respective genera. In addition, modified reproductions of original illustrations are provided for the adult females of the following species as representatives or type species of South American genera: *Acanthococcus aceris* Signoret, *Chilechiton lynnae* Hodgson & Miller, *Chilecoccus browni* Miller & González, *Coxicoccus foldi* Kozár & Konczné Benedicty, *Eriobalachowskya valenzualae* (Balachowsky), *Exallococcus laureliae* Miller & González, *Hempelicoccus paranaensis* (Foldi & Kozár), *Icelococcus nothofagi* Miller & González, *Intecticoccus viridis* Kondo, *Melzeria horni* Green, *Orafortis luma* Hardy, *Oregmomyga neglecta* (Cockerell), *Poliloculus stipae* González, *Pseudotectococcus anonae* Hempel and *Stibococcus cerinus* Miller & González. Descriptions and illustrations are also provided of the first-instar nymphs of: *Acanthococcus aceris* Signoret, *Aculeococcus morrisoni*, *Apiococcus gregarius*, *A. singularis* Hempel (which appears to be sexually dimorphic), *Capulinia sallei*, *Carpochloroides viridis*, *Chilechiton lynnae*, *Exallococcus laureliae*, *Hempelicoccus tucumanensis* (González & Granara de Willink), *Icelococcus lithrae* Miller & González, *Melzeria horni*, *Oregmomyga peruviana* Granara de Willink & Diaz, *Pseudocapulinia lanosa*, *Pseudotectococcus anonae* and *Tectococcus ovatus*. In addition, illustrated descriptions of the adult males of *Capulinia sallei*, *Carpochloroides viridis*, and *Tectococcus ovatus* are included. The first-instar nymphs and adult males of the other genera, where they are known, are also diagnosed and discussed. Based on the molecular studies of Cook & Gullan (2004), most species currently included in *Eriococcus* Targioni Tozzetti known from South America are considered to belong to the genus *Acanthococcus* Signoret, resulting in the following new combinations: *A. clapsae* (González) **n. comb.**, *A. cuneifoliae* (González) **n. comb.**, *A. divaricatae* (González) **n. comb.**, *A. pituilensis* (González) **n. comb.** and *A. lahillei* (Leonardi) **n. comb.** In addition, *Eriococcus pumuliae* González, *E. santiaguensis* González & Granara de Willink and *E. tucumanensis* González & Granara de Willink are transferred to *Hempelicoccus*, as *H. pumuliae* (González) **n. comb.**, *H. santiaguensis* (González & Granara de Willink) **n. comb.** and *H. tucumanensis* **n. comb.** (González & Granara de Willink). The status of *Opisthoscelis prosopidis* Kieffer & Jorgensen, the only species from the Neotropics currently included in *Opisthoscelis* Schrader, is discussed, and it is concluded that this species is unlikely to belong to this genus but is currently unrecognizable. Keys are provided for the identification of the 24 genera now known from South America based on the morphology of: (i) the adult females; (ii) the first-instar nymphs; and (iii) adult males, as far as these are known. In addition, Appendix 1 lists all Eriococcidae known from South America with their current generic placement, along with a brief summary of their host plants.

Key words: new combinations, taxonomy, Eriococcidae, *Acanthococcus*, Neotropical

Introduction

The family Eriococcidae has been demonstrated to be non-monophyletic using morphology of adult females (Cox & Williams, 1988) and adult males (Hodgson, 2002), and using molecular analysis (Cook *et al.*, 2002; Cook & Gullan, 2004). The latter works suggest the existence of three major lineages in the Eriococcidae *sensu lato* (Cook & Gullan, 2004), one of which is Gondwanan in distribution and encompasses species from Australia, New Zealand, and South America. The South American fauna also contains components of the more widespread acanthococcid clade (Cook & Gullan, 2004; Kondo *et al.*, 2006) but not the third clade which includes representatives of the Beesoniidae, Stictococcidae and *Eriococcus buxi* (Boyer de Fonscolombe) plus a few other eriococcid taxa.

There currently are 72 species of described eriococcids in 24 genera (not counting “*Opisthoscelis*” *prosopidis* Kieffer & Jorgensen) in South America (see appendix 1). This fauna is relatively poorly known (Kondo *et al.*, 2006; Kozár & Konczné Benedicty, 2008) although there has been increased interest in the area in the last 10 or 15 years. Recent works include those of Kozár (2009), Foldi and Kozár (2007), González (2008a, 2008b, 2009), Granara de Willink and Diaz (2007), Hardy *et al.* (2008), Hodgson and Miller (2002), Hodgson *et al.* (2004), Kondo *et al.* (2006), and Kozár and Konczné Benedicty (2008). Some of the more important older works include those of Hempel (1900, 1900a, 1919, 1932, 1934, 1937), Miller and González (1975), and Morrison (1919). Most other descriptive research encompasses descriptions of single species.

Miller and González (1975) discussed similarities between New Zealand eriococcids and those from southern Chile. In a more recent paper, Kondo *et al.* (2006) provided an analysis of the eriococcids of southern South America using molecular data of 13 taxa; their phylogram shows a mixture of South American, New Zealand and Australian taxa within the Gondwanan lineage and a mixture of South American, New Zealand, and European taxa within the acanthococcid clade. The work of Hardy *et al.* (2008) demonstrated congeneric relationships among species of *Madarococcus* that occur in South America, New Zealand and Australia. Because knowledge of the South American fauna is cursory, it is difficult to reach definitive conclusions about the evolution and biogeography of the eriococcids, but it seems clear that Gondwanan affinities remain in the extant fauna. This was also the conclusion of Kozár (2009) in his zoogeographical analysis of the world's eriococcid fauna.

The purpose of this paper is to describe the adult females of the type species of the poorly known eriococcid genera from South America and provide generic diagnoses based on the adult females of all genera. A key to the adult females of the genera in the region is also included. In addition, we describe (or present generic diagnoses based on) first-instar nymphs and adult males of all genera where these are available. Keys are provided for the known first-instar nymphs and adult males.

Adult males of eriococcids have not been described for most species. Some important literature on the subject includes: Afifi (1968) (*Acanthococcus*, *Eriococcus*, *Gossyparia*, *Ovaticoccus* and *Pseudochermes*); Gullan *et al.* (2006) (*Calycicoccus*); Henderson & Hodgson (1995) (*Eriochiton*); Hodgson (2005) (*Eriococcus*); Hodgson *et al.* (2004) (*Pseudotectococcus*); Koteja (1988a) (*Kuenowicoccus*); Kozár *et al.* (2008) (*Pseudomontanococcus*); Miller and González (1975) (*Stibococcus*), Miller *et al.* (1992) (*Eriococcus*), Theron (1968) (*Apiomorpha* and *Opisthoscelis*); Wu (2000) (*Cryptococcus*).

Immature stages of eriococcids have also not been described for most species. Some important literature on the subject includes: Beardsley (1971) (*Gallacoccus*); Cook (2003) (*Apiomorpha*); Cook *et al.* (2000) (*Apiomorpha*); González (2009) (*Eriococcus*); González & Granara de Willink (2010) (*Eriococcus* = *Hempelicoccus*); Gullan (1999) (*Subcorticoccus*); Gullan & Jones (1989) (*Apiomorpha*); Gullan *et al.* (2006) (*Calycicoccus*); Hardy & Gullan (2007) (*Fragorbis*); Hardy *et al.* (2008) (*Madarococcus*); Henderson (2007) (*Affeldococcus*); Hodgson (1994) (*Eriochiton*); Hodgson & Miller (2002) (*Chilechiton*); Hodgson *et al.* (2004) (*Pseudotectococcus*); Kondo *et al.* (2004) (*Oregmopyga*); Koteja (1988b) (*Balticococcus*, *Jutlandicoccus*, *Gedanococcus*); Kozár *et al.* (2008) (*Pseudomontanococcus*); Marotta *et al.* (2001) (*Eriococcus*); Miller *et al.* (1992) (*Eriococcus*); Miller (1991) (eriococcids).

Material and methods

Terminology in the descriptions follows that of Hodgson and Miller (2002) and Hodgson *et al.* (2004). The term “cruciform pore” is used for oval secretory structures in which the centre appears either cruciform or bilocular, although some other authors refer to these structures as “bilocular pores”. Material examined is shown as (for example): 2/5 adff (= 2 slides with a total of 5 adult females). Depository abbreviations are National Museum of Natural History, Beltsville, Maryland, USA (USNM), The Natural History Museum, London, UK (BMNH) and Bohart Museum of Entomology, University of California, Davis, USA (BME).

Figure captions. The letters and abbreviations on the figures of the adult females and first-instar nymphs are given below each figure. The letters for each figure of an adult male are also given below each figure but the abbreviations are as follows (all on Fig. 11 unless otherwise stated): aas = ante-anal setae; ab = antennal bristle; ads = dorsal abdominal setae; aed = aedeagus; als (Fig. 44) = alar seta; amss = anterior metasternal setae; an = anus; as_{viii} = abdominal sternite VIII; at_{viii} = abdominal tergite VIII; avs = ventral abdominal setae; bra = basal rod of aedeagus; c (fig. 14) = claw; caps = capitate setae; cdt = claw digitules; cp = campaniform pore; cx (Fig. 14) = coxa; dhs = dorsal head setae; dmcr = dorsal midcranial ridge; dps = dorsal pleural setae; dse = dorsal simple eye; dss = dorsospiracular setae; epm₃ = metepimeron; eps₂ = mesepisternum; eps_{3,s} = postmetaspiracular setae; fs = fleshy seta; g = gena; gls = glandular pouch setae; gp = glandular pouch; gs = genal setae; gts = setae of genital segment; hs = hair-like setae; lpl = lateropleurite; lmcr (Fig. 14) = lateral

branch of midcranial ridge; mc = median crest; mr = marginal ridge; mth = mouth; mts = metatergal setae; o = ocellus, ocs = ocular sclerite; pa (Fig. 14) = postalare; pcr₂ = mesoprecoxal ridge; pdc = pedicel; pepcv = proepisternum + cervical sclerite; pl_{1,s} = propleural seta; plr₃ = metapleural ridge; pms = postmesospiracular setae; pmss = posterior metasternal setae; pn₂ = mesopostnotum; pn₃ (Fig. 39) = metapostnotum; pna = postnotal apophysis; pnp (Fig. 14) = posterior notal wing process; pocr = postocular ridge; por = post occipital ridge; pra (Fig. 14) = prealare; prn = lateral pronotal sclerite; prnr = pronotal ridge; procr (Fig. 14) = preocular ridge; pror (Fig. 41) = preoral ridge; prsc = prescutum; prscs = prescutal setae; ps = penial sheath; pscs = prescutal suture; psp = penial sheath sensilla; pss = penial sheath setae; pscr (Fig. 14) = prescutal ridge; pt = post-tergite; scl = scutellum; scls (Fig. 14) = scutellar setae; scp = scape; sct = scutum; scts = scutal setae; ser = subepisternal ridge; sp₂ = anterior spiracle; sp₃ = posterior spiracle; stn₁ (Fig. 14) = prosternum; stn_{1,s} = prosternal setae; stn₂ = basisternum; stn_{2,s} (Fig. 14) = basisternal setae; stn₃ (Fig. 14) = metasternum; tar (Fig. 14) = tarsus; tars = tarsal spur; tdt = tarsal digitule; teg (Fig. 14) = tegula; tegs = tegular setae; tib (Fig. 14) = tibia; tibs = tibial spur; tp (Fig. 14) = triangular plate; tr (Fig. 14) = trochanter; vhs = ventral head setae; vmcr (Fig. 14) = ventral midcranial ridge; vmcrs = ventral midcranial ridge setae; vps = ventral pleural setae, and vse = ventral simple eye.

References. Only the basic references are given below. For a full list of references for each species, see either SCALENET or Miller & Gimpel (2000).

Acanthococcus Signoret

Acanthococcus Signoret 1875: 16; Williams 1985: 358–359. Type species *Acanthococcus aceris* Signoret 1875: 35–36.

Generic diagnosis. Adult female (Fig. 1). Surface covered in waxy ovisac. *Dorsum*. Derm membranous. Setae often enlarged and spinose but highly variable among species. Enlarged tubular ducts absent. Macrotubular ducts present throughout. Microtubular ducts present, of varied structure. Loculate pores rarely present. Cruciform pores absent. Anal lobes well developed and often sclerotised; frequently with teeth-like projections on inner margins. Median plate present. Anal ring well developed with pores and setae. *Margin*. Often clearly demarcated by a line of enlarged spinose setae. *Venter*. Setae often spinose near margin but hairlike elsewhere. Macrotubular ducts present, frequently of more than 1 type. Microducts, when present, usually restricted to near margins; similar to those on dorsum in structure. Loculate pores present, usually with 5 loculi. Cruciform pores usually present. Frontal lobes present; antennal tubercles absent. Antennae usually 6 or 7 segmented. Labium 3 segmented, basal segment with 2 pairs of setae. Legs well developed; claw and tarsal digitules with apical knobs; claw with denticle; hind legs usually with translucent pores. Vulva present between abdominal segments VII and VIII.

The species from the Neotropics currently included in this genus are found on a wide range of plant families.

Comment. Currently *Acanthococcus* has a world-wide distribution, but the identity and number of species that are closely related to the type species *A. aceris* will not be known until more detailed analyses are undertaken. Following the work of Cook & Gullan (2004), it is here considered that all species from the Neotropics currently placed in the genus *Eriococcus* are more appropriately placed in *Acanthococcus* (see Appendix 1) excluding those recently placed in *Eriobalachowskya* and *Hempelicoccus* (Kozár & Konczné Benedicty, 2008). However, because most South American species in *Eriococcus* were placed in *Acanthococcus* by Miller and Gimpel (2000) or Kozár & Konczné Benedicty (2008), new combinations are required only for *E. clapsae* González, *E. cuneifoliae* González, *E. divericatae* González, *E. pituilensis* González and *E. lahillei* (Leonardi) (González, 2009), which become *A. clapsae* (González) **n. comb.**, *A. cuneifoliae* (González) **n. comb.**, *A. divericatae* (González) **n. comb.**, *A. pituilensis* (González) **n. comb.** and *A. lahillei* (Leonardi) **n. comb.** There are currently 29 species of “*Acanthococcus*” known from this region (see Appendix 1) but this number is likely to be a considerable underestimate of the total fauna. For recent studies on the “*Acanthococcus*” species of the Neotropics, see Miller and González (1975), González (2008a,

2008b, 2009), Foldi and Kozár (2007), and Kozár and Konczné Benedict (2008). Based on recent molecular research, it is possible that none of the species currently placed in this genus from South America will remain there after careful analysis. None of the “*Acanthococcus*” species known from South America have been recorded as causing galls.

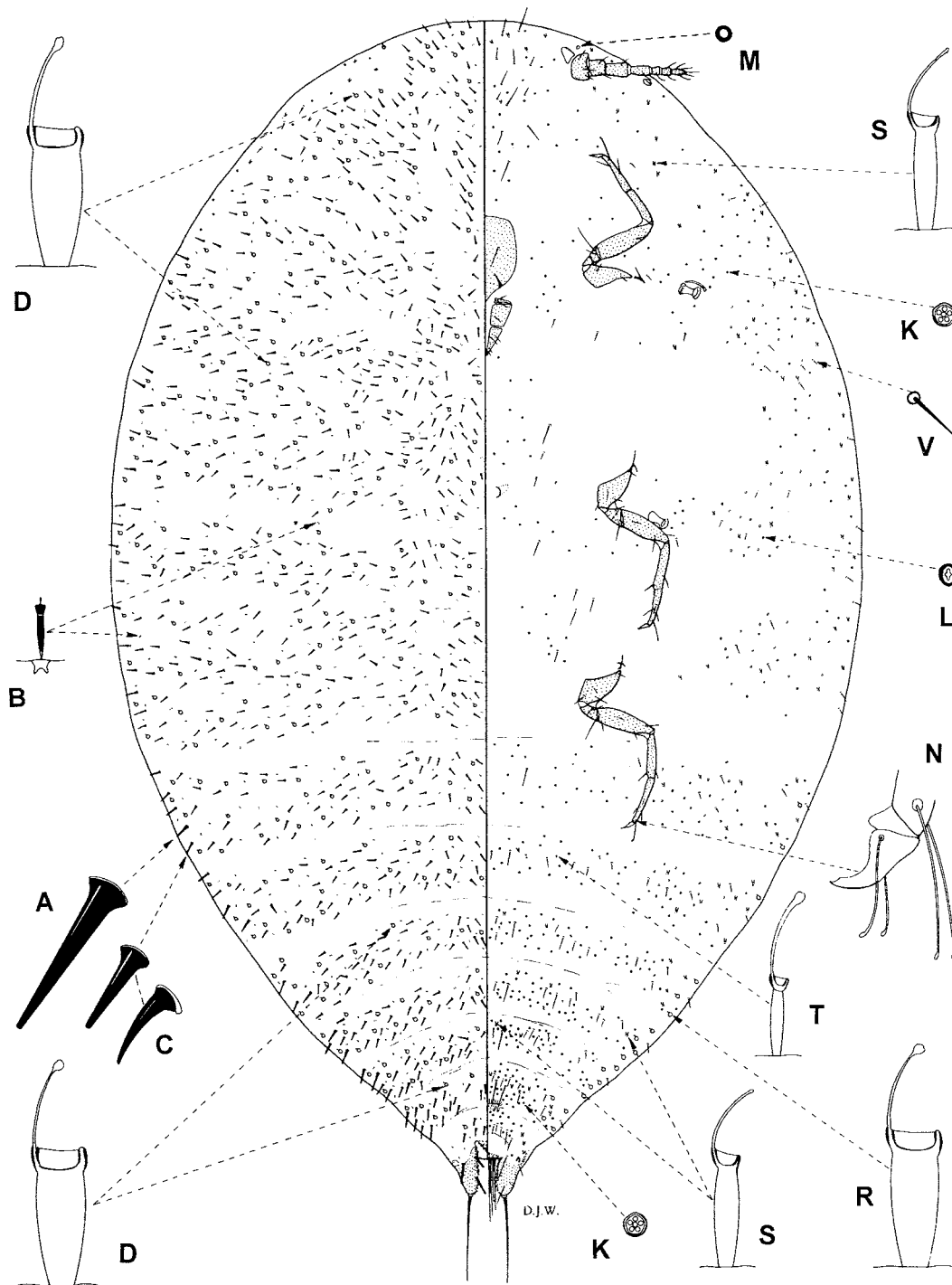


FIGURE 1. *Acanthococcus aceris* Signoret. Adult female, where A = marginal spinose seta; B = dorsal microtubular duct; C = dorsal spinose seta; D = dorsal macrotubular duct; K = ventral loculate pore; L = cruciform pore; M = frontal lobe; N = claw of metathoracic leg; R = larger ventral macrotubular duct; S = intermediate-sized macrotubular duct, T = small macrotubular duct; V = ventral seta (modified after Williams, 1985).

First-Instar Nymph (of *Acanthococcus aceris*, sex not determined) (Fig. 2)

Mounted material. Body oval, more pointed at posterior end. *Dorsum.* Dorsal setae of 1 type, in 2 submedial lines, 2 mediolateral lines and around margin. Macrotubular ducts absent. Microtubular ducts conspicuous, with a bifurcate dermal orifice, scattered. Anal lobes weakly sclerotised or unsclerotised, without a serrate inner margin. Median plate present, unsclerotised, inconspicuous. *Margin.* Delineated by band of spinose dorsal setae. *Venter.* Setae of 1 type: hairlike, arranged in 4 pairs of longitudinal lines. Macrotubular ducts absent. Microtubular ducts absent. Loculate pores, each with 3–5 loculi, present in a very sparse longitudinal line mediolaterally. Cruciform pores few, submarginal on thorax. Antennae 6 segmented. Small frontal lobe present. Labium 3 segmented, basal segment with 2 pairs of setae. Legs without pores; tarsus much longer than tibia; tarsal digitules capitate; claw with an inconspicuous denticle; claw digitules similar both with small capitate apices.

Comment. The first-instar nymphs of this genus are similar to those of *Icelococcus* by having: (i) 3 pairs of longitudinal lines of dorsal spinose setae; (ii) similar microducts; (iii) submedial line of ventral loculate pores; (iv) median plate; (v) small frontal lobe; and (vi) cruciform pores restricted to thorax. These 2 genera differ as follows: *Acanthococcus* has (*Icelococcus* character states in parentheses): (i) weakly sclerotised or unsclerotised anal lobes, not plate-like (heavily sclerotized and plate-like); (ii) 4 pairs of longitudinal lines of ventral setae on abdomen (3 pairs); and (iii) loculate pores primarily with 5 loculi (3 loculi).

Aculeococcus Lepage

Aculeococcus Lepage, 1941: 141. Type species *Aculeococcus morrisoni* Lepage, 1941: 141–145.

Generic diagnosis. Adult female (Fig. 3). Induces elongate, pointed, conical galls on upper surface of leaves of host plant. Body approximately pear-shaped, venter becoming highly swollen anteriorly. *Dorsum.* Heavily sclerotised, forming a diamond-shaped area, which includes anterior part of head. Dorsal setae of 2 types: setose setae on thoracic and anterior abdominal segments, and strongly spinose setae on more posterior abdominal segments. Macrotubular ducts absent. Microtubular ducts probably present on abdominal segments II–IV. Loculate pores, each with 5 loculi, in broad bands across abdominal segments III–VII. Anal lobes forming rounded posterior edges to abdomen, with spinose setae. Anal ring with 6 setae. *Margin.* Indicated by edge of sclerotisation. *Venter.* Setae hairlike. Macrotubular ducts absent. Microtubular ducts very small with 8-shaped pore, sparse. Loculate pores as on dorsum, located near labium and each spiracle. Cruciform pores absent. Antennae 1 segmented, located on anterior end of sclerotised dorsum. Frontal lobes and antennal tubercles absent. Mouthparts with a pair of large apodemes arising from tentorial box in old specimens. Legs weakly developed; segmentation obscure; metacoxae large and heavily sclerotised; without translucent pores. Vulva not detected.

South American hosts unknown.

Comment. *Aculeococcus* currently includes 2 species, the type species from Brazil and *A. yongpingensis* Tang & Hao from Yunnan Province, China. We have examined specimens of both species and they appear to be congeneric. Lepage (1941) compared the adult females of *A. morrisoni* with those of *Calycicoccus merwei* Brain from South Africa, (recently redescribed by Gullan *et al.* (2006)). Whilst there are some superficial similarities, these 2 genera are clearly quite different and the similarities were considered to be convergent by Beardsley (1984) and Gullan *et al.* (2006). Adult females of *C. merwei* have none of the characters states of *A. morrisoni* listed below.

Adult females of *Aculeococcus* differ from all other eriococcid genera considered here in having the following combination of characters: (i) mouthparts with large apodemes arising from the tentorial box – although these may be absent or poorly developed in youngest adults and probably expand with age (also found in *Carpochloroides* and *Tectococcus*); (ii) heavily sclerotized, diamond-shaped area, mainly dorsal but also including antennae and eyes, (and which probably serves as a plug for the gall opening); (iii) greatly reduced legs; (iv) hind 2 pairs of legs and posterior spiracles separated from front legs and anterior spiracles by considerable distance; and (v) hind coxae greatly enlarged.

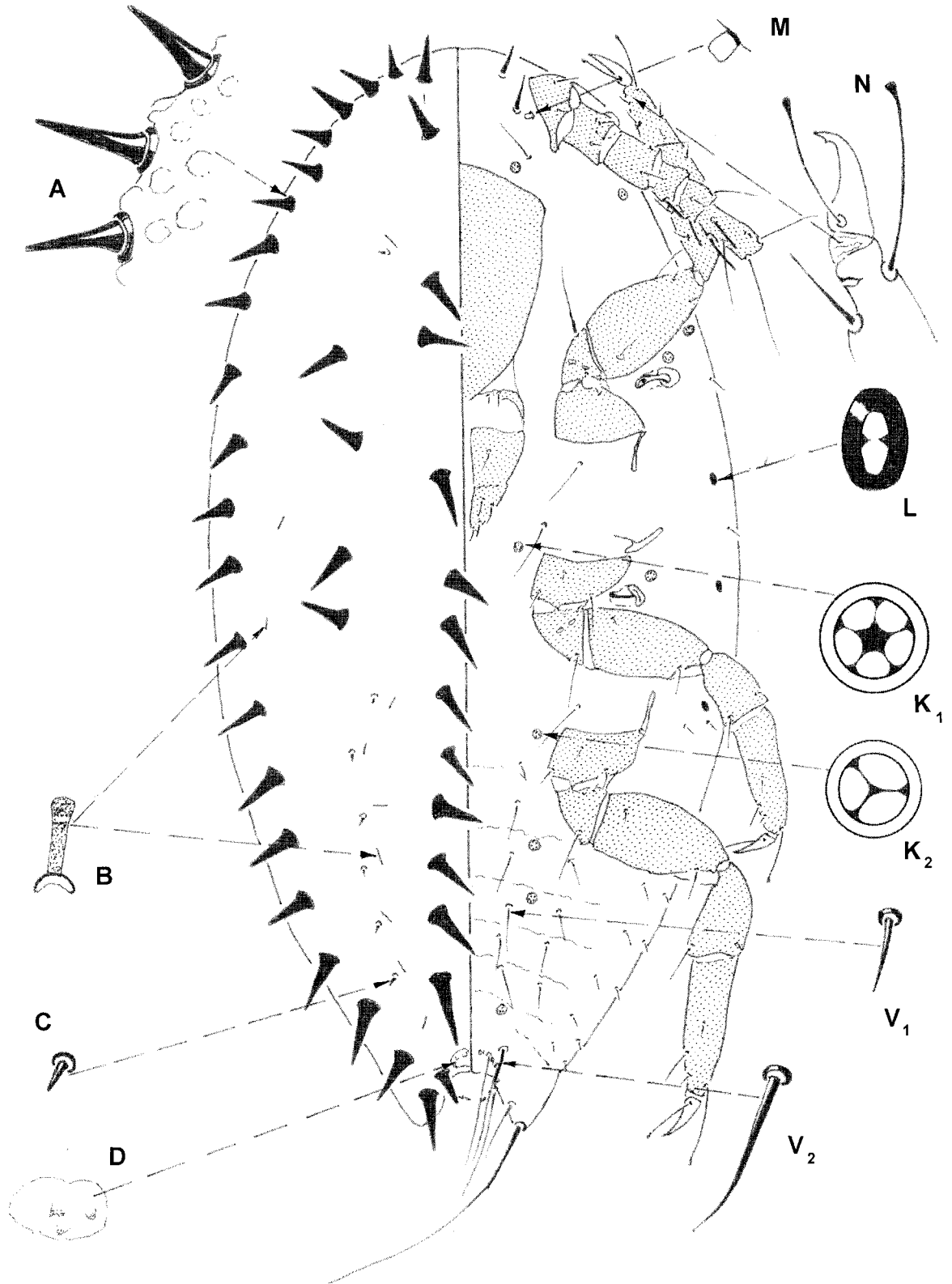


FIGURE 2. *Acanthococcus aceris* Signoret. First-instar nymph, where A = marginal spinose setae; B = dorsal microtubular duct; C = small spinose seta; D = median plate; K₁ = ventral loculate pore with 5 loculi; K₂ = ventral loculate pore with 3 loculi; L = cruciform pore; M = frontal lobe; N = claw of prothoracic leg; V₁ & V₂ = ventral setae

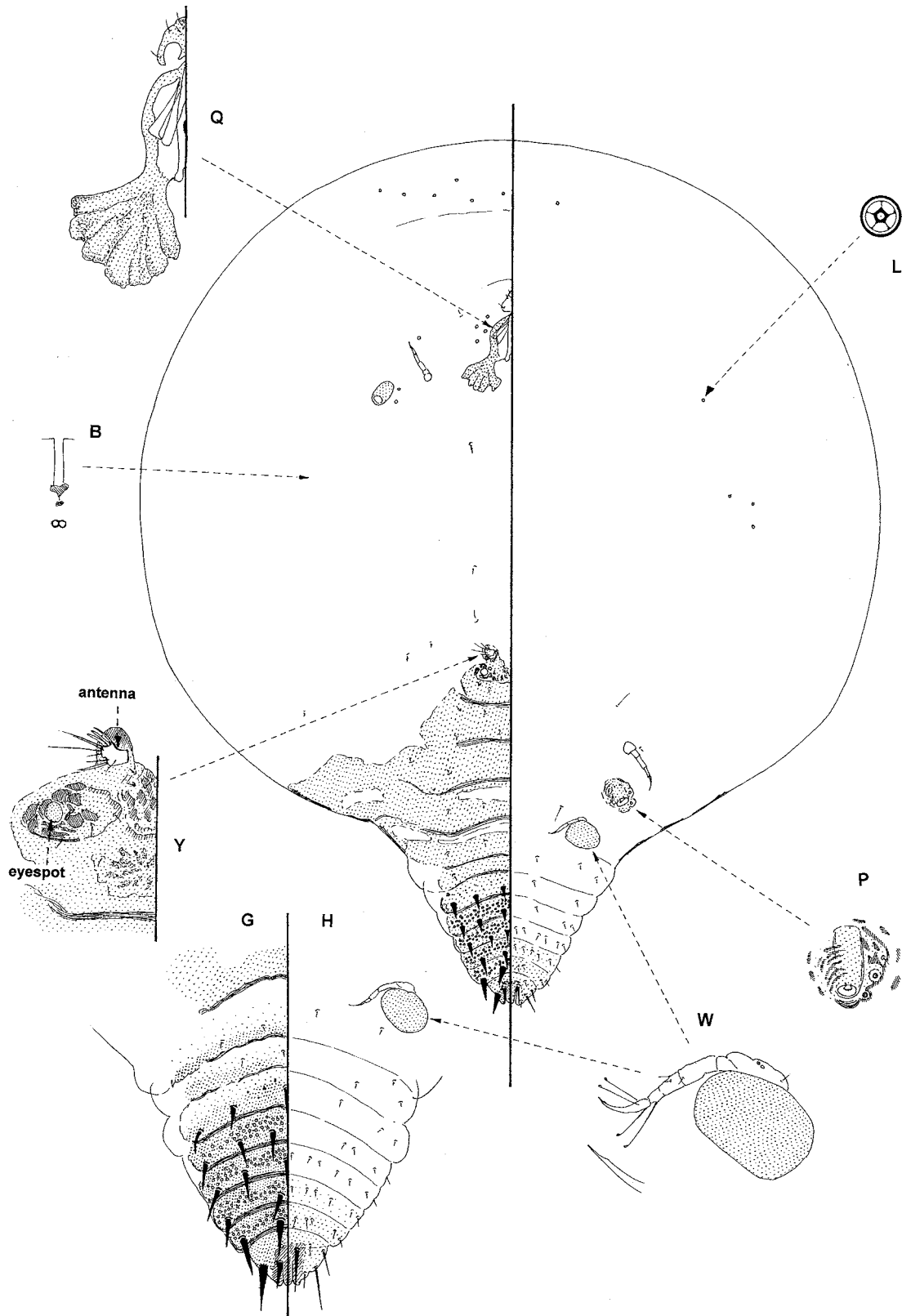


FIGURE 3. *Aculeococcus morrisoni* Lepage. Adult female, where B = ventral microtubular duct; G = dorsal view of abdomen; H = ventral view of abdomen; L = ventral loculate pore; P = posterior spiracle; Q = mouthparts with associated apodeme; W = metathoracic leg, and Y = head area showing antennae and eyespot.

Aculeococcus morrisoni Lepage

Aculeococcus morrisoni Lepage 1941: 141–145.

Material examined. No data: USNM: 1/4adff (in good condition) and 4 embryos (inside egg membranes, in fair condition) + 1/3 adff (in fair to good condition). The first slide lacks data except for a small label that has the date “24-VIII-3?” [the second number of the year is unclear but it does not look like a 9] and the number “61.” The second slide was sent to Morrison with a letter by Lepage dated February 2, 1939 with no data other than it was “No.1” from “Brazil” and was found “in galls on leaves.” In the letter, Lepage asked for assistance in identifying the species and suggested that it might be similar to the South African genus *Calycicoccus*. After considerable study, Morrison responded in a letter dated February 11, 1941, indicating that, although he could see several similarities with *Calycicoccus*, he found sufficient differences “to justify the erection of a distinct new genus.” It seems highly probable that at least the second slide is part of the type series. The identity of the host plant remains unknown.

Adult Female (Fig. 3)

Unmounted material. Females inducing elongate, pointed, conical galls on upper surface of leaves of host plant. Each gall with a small opening on lower surface of leaf, through which white waxy filaments extrude. Galls of perhaps 2 sizes, largest 2 mm wide at base and up to 17 mm long. Female lives within a cavity within gall, which it does not appear to fill completely. Body bulbous, becoming wider than long.

Mounted material. Body approximately pear shaped but anterior 2/3rds, becoming very swollen and membranous; division into head, thorax and abdomen complex. Head located dorsally in centre of dorsal surface, with labium pointing anteriorly and with antennae and eyespots at posterior end (see below); rest of membranous dorsal surface and all of swollen ventral surface representing thorax, with prothoracic legs and anterior spiracles located laterad to mouthparts on dorsal surface, and meso- and metathoracic legs and posterior spiracle located posteriorly on ventral surface. No indication of any segmentation on membranous areas. True dorsum represented by a diamond-shaped, heavily sclerotised, area located medially at posterior end of globular body. True dorsum showing distinct segmentation, including, at anterior end, a small area of sclerotisation with antennae and eyes, clearly representing dorsal surface of normal head. Dorsal surfaces of thoracic segments present immediately posterior to sclerotised part of head, while dorsal surface of abdomen forms posterior half of diamond, narrowing to pointed anal lobes; anterior end of abdomen quite narrow where it joins globular anterior section; thorax and abdomen therefore heavily sclerotised dorsally but both almost entirely membranous ventrally. Sclerotisation on dorsal surface probably becoming slightly more extensive on older specimens. Total body length 1.79–2.18 mm, width 1.6–1.86 mm.

Dorsum. True dorsum mainly heavily sclerotised, represented by a diamond-shaped area covering abdomen posteriorly and an equal area anteriorly, with a small part of head forming anterior point of diamond. Dorsal setae of 2 types: (i) setose setae, each 3–5 μm long, on thoracic segments and anterior 2 abdominal segments, possibly randomly distributed on thorax but with 1–4 on each segment; and (ii) strongly spinose setae on posterior 6 segments of abdomen, shortest on segment III (length 27–37 μm) and longest on segments VI and VII (length 39–67 μm); totals per segment as follows: III 5; IV 6; V 4 or 5; VI 3 or 4 and VII 4. Macrotubular ducts absent. Dorsal microtubular ducts possibly present on abdominal segments II–IV, indicated by minute pores in sclerotisation; structure unknown. Loculate pores with mainly 5 loculi, restricted to broad bands across abdominal segments III–VII, frequency per segment: III 0–6; IV 57–103; V 74–140; VI 63–96 and VII 37–69. Other pores absent. Eyespots each 16–19 μm wide, surrounded by an area of dimpled sclerotisation. Anal lobes strongly developed, outer margins of lateral lobes converging and with a long median lobe (length 23–32 μm long) medially. Anal lobe setae as follows: dorsally with larger spinose setae on lateral margin 46–67 μm long, and shorter setae on inner margin 20–23 μm long; ventrally with anterior suranal setae (laterad to anus) 18–26 μm long; setae along ventral outer margin: posterior seta 20 μm , middle seta 55–70 μm and anteriormost seta 27–42 μm long. Anal ring with 6 anal ring setae, each 62–70 μm long, situated beneath median lobe; with a denser area of sclerotisation around median lobe.

Margin. Undefined on globose anterior portion of body but marked on abdomen by margins of sclerotisation. Marginal setae probably absent.

Venter. True venter making up probably at least 90% of body and almost entirely membranous, with segmentation apparent on abdomen. Setae on most of venter sparse and rather short, each 6–10 µm long; with a long seta associated with each meso- and metacoxa, each about 30–35 µm long and another long seta "anterior" to each antenna, each about 30 µm long; frequency in each abdominal segment as follows: II 2?, III 1–4, IV 1–6, V–VII 4–9; each abdominal segment with 2 setae on each side near "margin"; with about 3 pairs of short setae between antennae; other setae rather randomly placed. Macrotubular ducts absent. Ventral microtubular ducts very small, each 4–5 µm long, with 8-shaped inner sclerotisation; sparse, distribution uncertain. Loculate pores of similar structure to those on dorsum, restricted to thorax, with 2–5 associated with anterior spiracle and 0–2 with posterior spiracle; also with a few laterad to clypeolabral shield and "anteriorly and laterally" on thorax.

Antenna 1 segmented, each about 23 µm long, located close together at anterior end of sclerotised area, with some dimpled sclerotisation between; each with about 5 fleshy setae and 5 setose setae, 2 of latter quite long (39–45 µm long). Clypeolabral shield about 96–110 µm long, but with 2 large, rather wing-like, sclerotised apodemes, each 195–215 µm long and 125–143 µm wide arising from the tentorial box; labium 1 segmented, with 4 pairs of setae. Spiracles: width of peritremes 15–17 µm. Legs all very weak, with segmentation indistinct; lengths (metathoracic leg): coxa large, oval, heavily sclerotised, 70–90x53–70 µm (coxae very small on other legs); trochanter + femur indistinct; tibia + tarsus perhaps 35–49 µm long, claw 20–32 µm long, with a small denticle; setae very few; tarsal digitules well developed and longer than claw, claw digitules shorter than claw, capitate; without translucent pores on hind legs. Vulva not detected.

Comment. For a comparison of the adult female of *Aculeococcus* with other eriococcid genera see the "Comment" section after the generic diagnosis of *Aculeococcus*.

First-Instar Nymph (gender not determined) (Fig. 4)

Unmounted material. Yellow.

Mounted material. Body elliptical. Length about 305–350 µm, width 150–155 µm.

Dorsum. Derm membranous, without clear dermal spinules medially. Dorsal setae of 2 types: (i) spinose, broad, nipple-shaped, each about 5 µm wide and 5–6 µm long, with basal socket broader than base of seta: in 2 medial lines, with a pair on 1st abdominal segment plus pairs on pro-, meso- and metathorax and 2 pairs on head; also present submarginally on abdominal segments III, II and I, and on meta- and mesothorax, plus submedially on prothorax and posteriorly on head; and (ii) a conical seta, much narrower than type (i), each about 10 µm long, as follows: in 2 medial lines, on abdominal segments V–VII. Macrotubular ducts and loculate pores absent. Microtubular ducts long and narrow, each 5–6 µm long, with a lightly sclerotised dermal pore and a very short inner ductule; apparently distributed as follows: a pair submedially on abdominal segments VIII, V and II, plus on mesothorax; also submarginally on abdominal segment IV, pro-, meso- and metathorax and perhaps with 2 pairs on head. Anal lobes membranous, apparently present (only visible on 1 specimen not in egg membrane); possibly with a microtubular duct near base; each with a long apical flagellate seta about 150–170 µm long; with 2 pairs of spinose setae along inner margins, each slightly bent and 8–10 µm long; each anterior and posterior suranal seta 12–13 µm long. Median plate present between anal lobes, about 10 µm long and 5 µm wide. Anus appearing ventral, possibly with a narrow sclerotised anal ring with 3 pairs of setae.

Margin. Marginal setae spinose, similar in shape and size to type (i) on dorsum: with 8 between eyespots, 1 just dorsad to each eye, 5 on each side between eyes and point opposite anterior spiracles, 5 on each side laterally between anterior spiracles and abdomen and 1 on each side of abdominal segments I–VII. Eyespots large and oval, greatest width 16 µm, situated on margin posterior to base of antennae.

Venter. Derm membranous. With 3 pairs of long flagellate setae between antennae (each about 25 µm long); with a rather longer seta mesad to each meso- and metacoxa (about 33 µm long); none apparently near precoxae; also with a pair of setae medially on abdominal segments V, VI and VII, each 8–12 µm long. Submarginal setae minute, spinose (each about 3 µm long), with a seta on each side of abdominal segments I–VIII and 2 laterally between spiracles; none apparent on head. Macrotubular ducts absent. Microtubular ducts similar to those on dorsum, with 1 submarginally on each side along anterior margins of abdominal segments I–V, meta- and mesothorax and on head, just posterior to eyespot. Loculate pores with 5 loculi: with 1 pore immediately laterad of each peritreme.

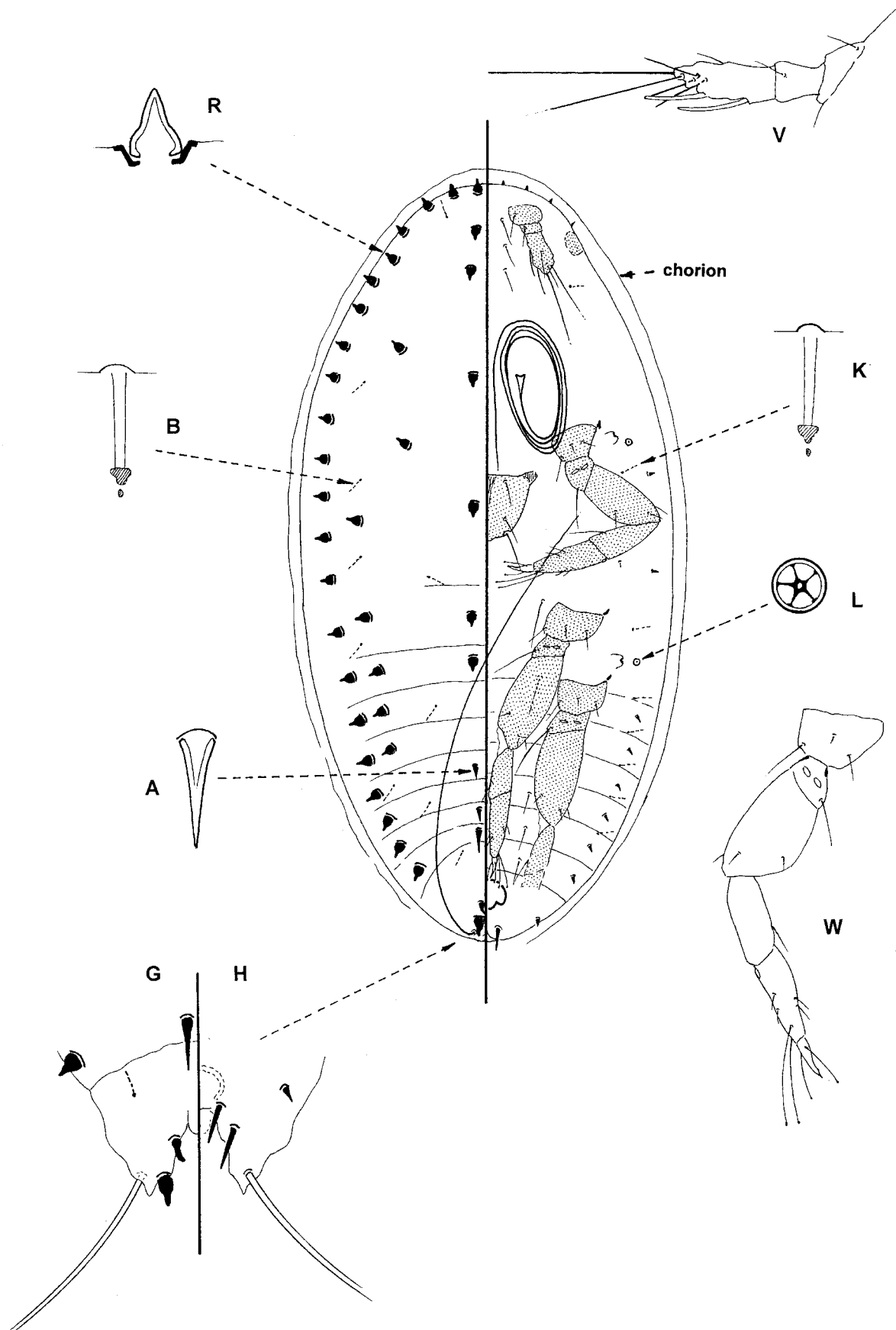


FIGURE 4. *Aculeococcus morrisoni* Lepage. First-instar nymph inside egg-case; where A = dorsal spinose seta; B = dorsal microtubular duct; G = dorsal view of anal lobes; H = ventral view of anal lobes; K = ventral microtubular duct; L = ventral loculate pore; R = marginal seta; V = antenna, and W = metathoracic leg.

Antennae possibly 3 segmented, total length 43–45 μm long; setal distribution possibly as follows: scape 3; pedicel 1 + a campaniform sensillum; segment III 3 fleshy setae + about 3–5 setose setae; apical seta about 50 μm long; other lateral long seta 40 μm long. Clypeolabral shield not yet clearly developed but labium distinct, 1 segmented; about 25–27 μm long, with 3 pairs of setae near apex (longest 20–25 μm long) and another pair more basally. Spiracles very small, width of peritreme about 2.5 μm wide; spiracular apodeme apparently absent. Legs hard to discern but perhaps lengths (metathoracic leg (μm)): coxa 21; trochanter + femur 50; tibia + tarsus 45–52; claw 13–14; tibia generally subequal to or slightly longer than tarsus; setae: coxae 3, trochanter perhaps only 1, femur 3, tibia 1, tarsus 4; long trochanter seta 8–12 μm long; tarsal campaniform sensillum present; claw quite elongate, with a distinct denticle; both tarsal digitules on all 3 pairs of legs finely capitate and equal in size; claw digitules similar and probably longer than claw.

Comment. The first-instar nymph of *A. morrisoni* is separable from the other known first-instar nymphs from the Neotropics in having the following combination of characters: (i) antennae 3 segmented; (ii) dorsal spinose setae mainly spinnerette shaped; (iii) each anal lobe apparently without a spinose seta on outer margin; (iv) microtubular ducts present on both dorsal and ventral surface; (v) loculate pores restricted to just laterad to each spiracle; (vi) no cruciform pores; and (vii) claw digitules similar. It is somewhat similar to the first-instar nymph of *Pseudotectococcus anonae* in having 3-segmented antennae and anal lobes but the latter has: (i) rather parallel-sided spinose dorsal setae; (ii) cruciform pores; (iii) no microtubular ducts on the venter; (iv) a spinose seta on the outer margin of each anal lobe; and (v) dissimilar claw digitules.

***Apiococcus* Hempel**

Apiococcus Hempel 1900: 401. Type species *Apiococcus gregarius* Hempel 1900: 402–403.

Generic diagnosis. Adult female (Fig. 5). Globular; derm entirely membranous. *Dorsum*. Derm with areolations. Setae of 2 types: large, roundly conical setae in segmental rows, and narrower setae on posterior abdominal segments. Macrotubular ducts absent. Microtubular ducts appearing bilocular, frequent throughout. Loculate pores each with mainly 5 loculi, present in bands across posterior abdominal segments and in a large group on head. Anal lobes barely developed, each with a group of setae; also with an elongate invagination or pouch with internal loculate pores possibly associated with each anal lobe; median plate absent. Anal ring apparently represented by a membranous opening. *Margin*. Not defined. *Venter*. More lateral setae as on dorsum but other setae rather hairlike. Macrotubular ducts absent. Microtubular ducts as on dorsum, throughout but sparse in places. Loculate pores similar to those on dorsum, in bands across abdomen and less frequent elsewhere. Cruciform pores absent. Antennae 1 segmented. Frontal lobes and antennal tubercles absent. Labium with unknown number of segments. Legs entirely absent. Vulva not detected.

Known only from Myrtaceae.

Comment. *Apiococcus* currently contains 4 species (*A. asperatus* Hempel, *A. globosus* Hempel, *A. gregarius*, and *A. singularis* Hempel) all currently known only from Brazil. We have examined specimens of all but *A. globosus*. *Apiococcus* differs from all other eriococcid genera in having 2 elongate invaginations near the anal area which contain many loculate pores. It also is rotund, has distinctively cupolate-shaped setae, lacks legs, has 1-segmented antennae, and forms a test on the host.

***Apiococcus gregarius* Hempel.**

Apiococcus gregarius Hempel, 1900: 402.

Material examined: Syntypes: *Apiococcus gregarius* Hempel: **BRAZIL**, Ypiranga, on Myrtaceae, no date, A. Hempel (USNM): 1/2 adff (in good to fair condition) + 1/9 first-instar nymphs (in fair to good condition). We have not selected a Lectotype as we believe the primary type should be chosen from material deposited in a Brazilian collection.

Also "*Tectococcus ovatus* Hempel" (now *Apiococcus ovatus* (Hempel)): BRAZIL, Ypiranga, on Myrtaceae, 1900, no collector (USNM): 1/3 admm (in fair condition).

Adult Female (Fig. 5)

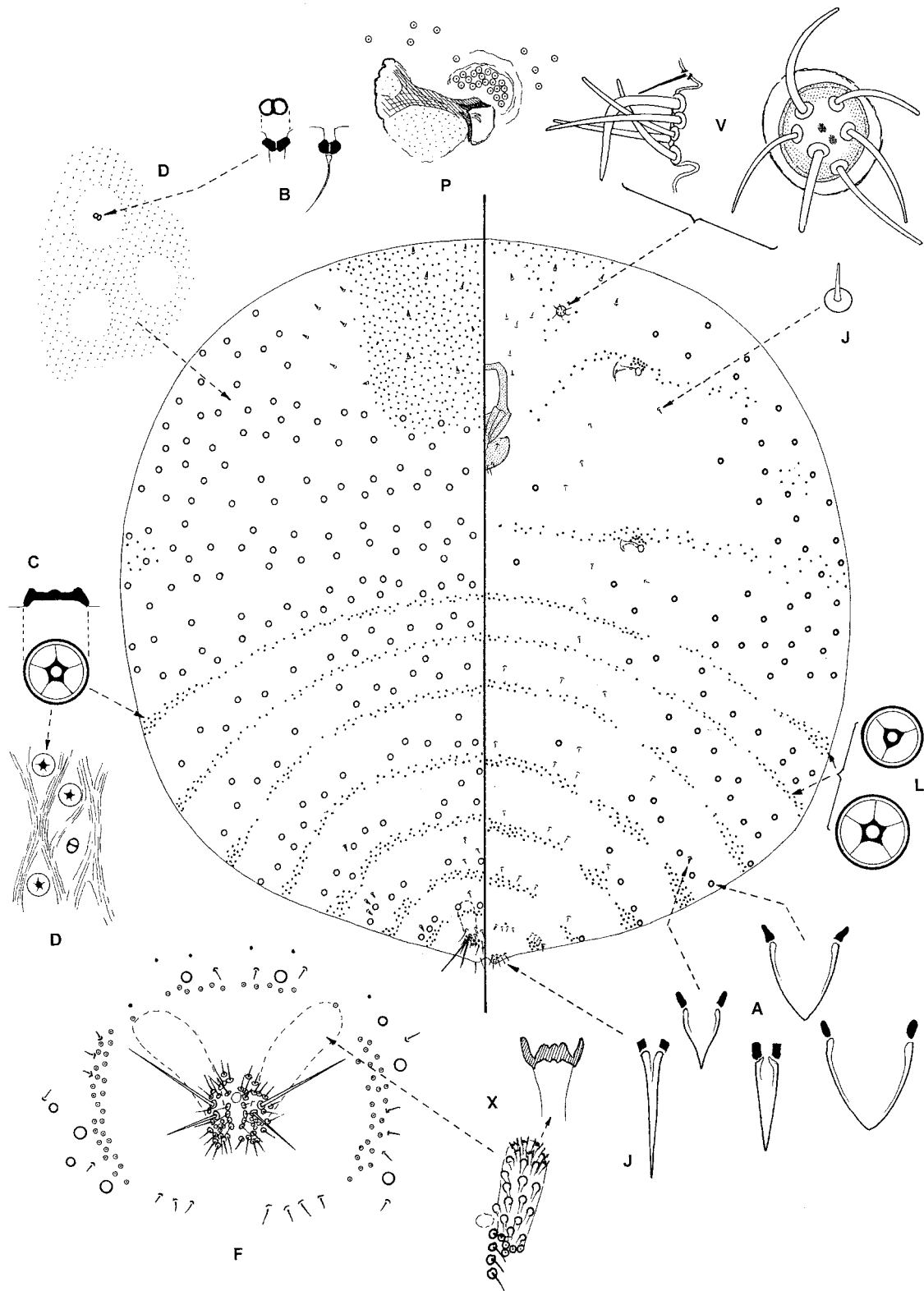


FIGURE 5. *Apiococcus gregarius* Hempel. Adult female, where A = variously-shaped dorsal setae; B = dorsal microtubular duct; C = dorsal loculate pore; D = area of derm showing position of microtubular ducts and loculate pores; F = view of anal area, showing position of inner pouches; J = ventral setae; L = ventral loculate pore; P = spiracle; V = antenna, and X = anal pouch with sunken loculate pores.

Unmounted material. Forms a hard, spherical test that is brown in color with a slightly roughened surface (Hempel, 1900).

Mounted material. Body apparently globular, derm entirely membranous, with areolations. Length 0.75–1.33 mm, width 0.7–1.35 mm.

Dorsum. Derm membranous but with a faint reticulate pattern of striations on abdomen and forming larger areolations on thorax. Dorsal setae of 2 or 3 types: (i) large and roundly conical setae, each 4–5 μm long and about 5 μm wide; basal socket narrow, subequal to width of setal base; abundant in segmental rows over almost entire surface, but rather narrower and much more pointed dorsally on head and laterally on most posterior abdominal segments, where each about 3–4 μm long; and (ii) stout setae but narrower than type (i), few on posterior abdominal segments, intermingled amongst type (i). Macrotubular ducts absent. Microtubular ducts about 2/3rds size of loculate pores and appearing bilocular, probably with a thin inner ductule; each about 3 μm long; abundant throughout although with few on abdominal segment VIII and sparse on head. Loculate pores, each 2–2.5 μm wide, with 3–5 (mainly 5) loculi: in bands about 3–5 pores wide across 7 preanal segments and in a large oval group anteriorly on head; apparently absent on thorax and rest of head. Anal lobes barely developed, each a small terminal convexity, unsclerotised, each with a group of 19–27 setose setae (each 13–22 μm long), plus 1 long apical flagellate seta, about 30–60 μm long and 1 intermediate seta, about 35 μm long. Median lobe absent. Anal ring and anal ring setae absent, anus possibly represented by a 6–7 μm wide membranous opening antero-dorsally between groups of anal lobe setae. No clearly defined anterior or posterior suranal setae present. A small group of loculate pores present on inner margin of each anal lobe, which appear to be associated with two elongated invaginations or pouches, each about 35–40 μm long, with walls covered in about 25–40 loculate pores, here thought to have a membranous outer ductule.

Margin. Undefined. However, loculate pore bands (similar to those on dorsum) forming more or less complete rings around abdominal segments, but with two breaks ventro-laterally, possibly defining pleural regions, suggesting that perhaps 2/3rds of body represents dorsum. Spinose setae (type (i) on dorsum) also extending into pleural regions, along with a few type (ii) setae. Microtubular ducts also extending abundantly into pleural regions. Eyespots not detected.

Venter. Derm membranous. Setae of 2 types; (i) setose setae, sparse and all rather short, each 3–5 μm long; without long setae associated with meso- and metacoxae; with a total of about 6 setae in a row across each abdominal segment; with about 6–10 short setae between antennae; other setae rather randomly placed; (ii) conical setae similar to those on the dorsum, mainly restricted to marginal areas but with a few more medially, particularly on thorax. Macrotubular ducts absent. Ventral microtubular ducts similar to those on dorsum and present throughout, except in anal area on segment VIII and sparse medially on thorax. Loculate pores of similar structure to those on dorsum, in bands across all abdominal segments (7 segments), but with only 0–3 on segment VIII; also present in a band associated with posterior spiracle, extending across ventral and pleural areas of mesothorax, band possibly not quite complete medially but extending laterally onto dorsum; a similar but shorter band present associated with anterior spiracle; with a small group of loculate pores present pleurally between these 2 spiracular bands; each spiracle with a small concavity along anterior margin, each cavity with 15–24 pores; with a few pores around each antenna and also along anterior margin of head associated with dorsal group.

Each antenna represented by a single round to oval, flattened segment, about 13–17 μm across, lying in a shallow depression, with 5–8 mainly fleshy setae; sometimes with a setose seta on margin. Clypeolabral shield about 160–170 μm long; labium with probably 4 pairs of setae; number of labial segments unknown. Spiracles: width of peritremes 15–17 μm . Legs entirely absent, not even represented by clumps of setae. Vulva not detected.

Comment. For a comparison of the adult female of *Apiococcus* with other eriococcid genera see the “Comment” section after the generic diagnosis of *Apiococcus*.

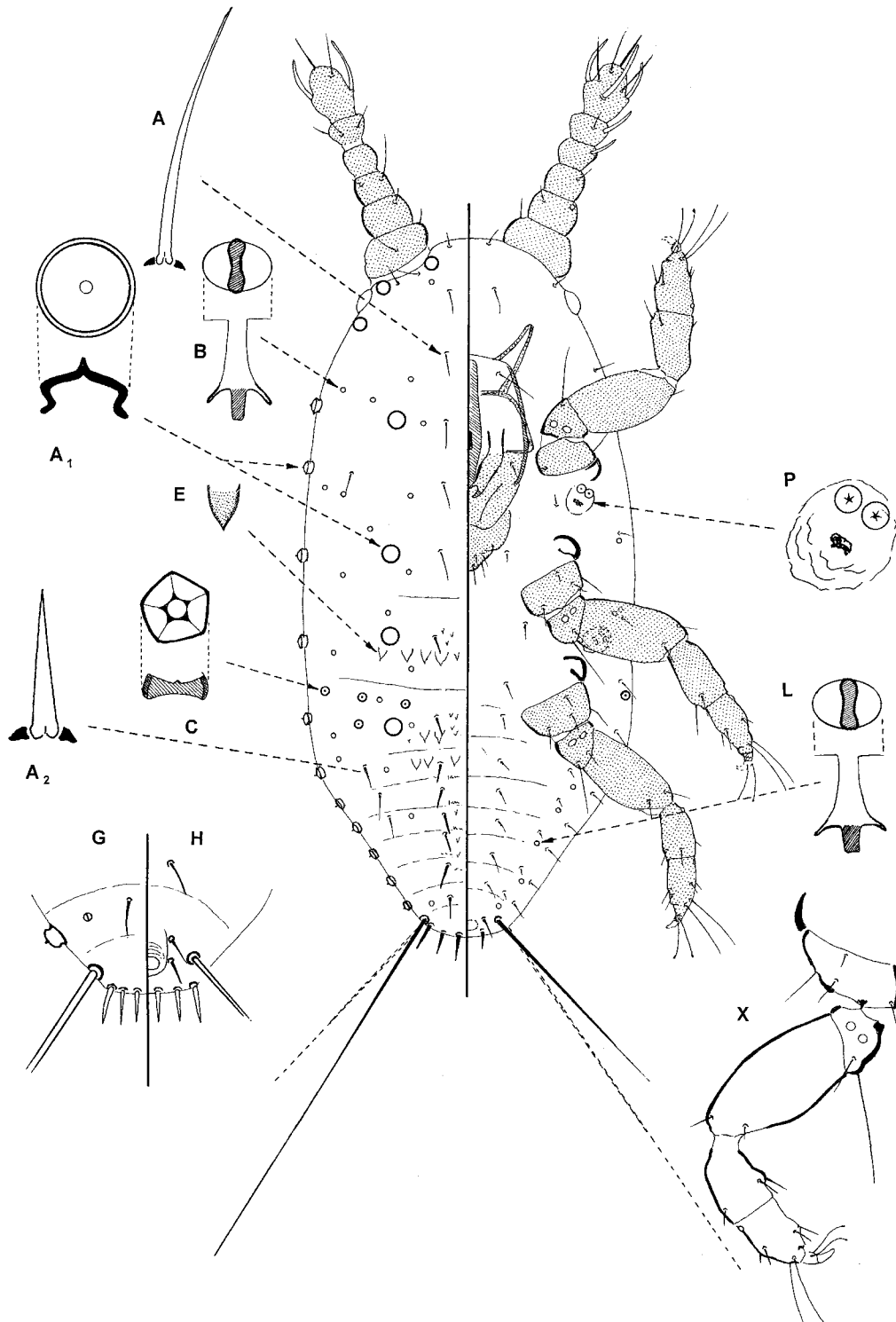


FIGURE 6. *Apiococcus gregarius* Hempel. First-instar nymph, where A = dorsal setose seta; A₁ = marginal and dorsal broad spinose setae; A₂ = dorsal spinose seta; B = dorsal microtubular duct; C = dorsal loculate pore; E = enlarged dermal spinules; G = dorsal view of anal area; H = ventral view of anal area; L = ventral microtubular duct; P = spiracle with loculate pores, and X = metathoracic leg.

First-Instar Nymph (probably female) (Fig. 6)

Unmounted material. Body orange yellow.

Mounted material. Body oval, possibly slightly more pointed posteriorly. Length about 235 µm, width 115–120 µm.

Dorsum. Derm membranous, with enlarged dermal spinules medially, these particularly obvious on metathorax and abdominal segments I and II; smaller ones present elsewhere. Dorsal setae of 2 types: (i) spinose, broad, cupolate-shaped setae, each about 10 μm wide and 5 μm tall, with a narrow basal socket: in 2 submedial lines, with a pair on 1st abdominal segment plus pairs on meta- and mesothorax, and posteriorly on head (+ a pair occasionally present on prothorax and abdominal segment II, these appearing to be more conical); and (ii) setose setae, each 6–12 μm long, as follows: in a pair of mid-dorsal lines, with 1 pair of setae per segment on abdomen and metathorax, each fairly stout and not flagellate; pairs of more flagellate setae, each 10–12 μm long, on meso- and prothorax and with 3 pairs on head; also with pairs of submarginal setae on abdominal segments II–IV, on prothorax and 3 pairs submarginally on head. Macrotubular ducts absent. Microtubular ducts rather large, with an oval, strongly sclerotised, apparently bilocular, pore at the end of a short outer ductule; each duct about 3 μm long; no inner ductule noted; apparently rather randomly distributed, but with a pair on abdominal segments VII, IV and II, perhaps 4 pairs on abdominal segment I, and perhaps 3 pairs on each thoracic segment and 5 pairs on head. Loculate pores, each with 5 loculi and about 2x width of microtubular ducts: with 4 on either side of abdominal segment I. Anal lobes absent or rounded, membranous; without microtubular ducts; each with a long apical flagellate seta about 130–150 μm long; each with 3 pairs of spinose setae between long apical setae on margin, each about 15–17 μm long. Anus appearing ventral, slightly oval, membranous, without an anal ring or anal ring setae; width about 6 μm ; with 2 rather spinose setae on either side dorsally (each about 6.5–10 μm long) plus a pair of much longer seta ventrally, each 75–85 μm long.

Margin. Marginal setae spinose, about 5 μm wide, similar in shape to those on dorsum but smaller; with 4 between eyespots, 3 on each side between eyes and point opposite anterior spiracles, 2 on each side laterally between anterior spiracles and abdomen and with 1 on each side of abdominal segments I–VII. Eyespots large and oval, greatest width 10 μm , situated on margin near base of antennae.

Venter. Derm membranous. With 3 pairs of long flagellate setae between antennae (each 18–22 μm long) (1 pair near anterior margin); with rather shorter setae mesad to meso- and metacoxae (11–15 μm long) and even shorter mesad to procoxae (about 7 μm); also with a pair of setae medially on abdominal segments II–VII, each about 8 μm long. Submarginal setae hairlike, with a seta on each side of abdominal segments I–VII, 2 laterally between spiracles and 3 on head (2 posterior to each eyespot and 1 pair between antennae); also with a submedial line of very short setae (length 2–3 μm) on abdomen, 1 seta on each side of segments I–VII. Microtubular ducts apparently similar to those on dorsum, with a pair submedially on each abdominal segment and 1 or 2 submarginally on each thoracic segment. Loculate pores with mainly 5 loculi: with 2 immediately laterad of each peritreme, possibly in a small cavity; also with a single pore close to margin on abdominal segment I.

Antennae 6 segmented, total length 73–75 μm long; setal distribution: scape 2; pedicel 2 + a sensillum; segment III 3; IV 1 short fleshy seta; V 1 fleshy setae + 4 setose setae and VI 3 fleshy setae + about 5 setose setae; apical seta about 35 μm long. Clypeolabral shield particularly large, about 69–75 μm long; labium perhaps 2 segmented, about 33–38 μm wide, with 4 pairs of setae. Spiracles very small, width of peritreme about 3 μm wide; spiracles surrounded by an oval area, possibly a shallow cavity. Legs well developed; lengths (metathoracic leg (μm)): coxa 30; trochanter + femur 46; tibia + tarsus 45; claw unknown; tibia generally subequal to or slightly shorter than tarsus; setae: coxae 4, trochanter 2, femur 2, tibia 4, tarsus 4; long trochanter seta 30 μm long; tarsal campaniform sensillum present; claw shape and structure uncertain; both tarsal digitules on all three pairs of legs capitate and equal in size; claw digitules similar and probably longer than claw.

Comment. First-instar nymphs were also available of *A. singularis* Hempel. These showed significant differences between what are assumed to be male and female crawlers. For a comparison of first-instar nymphs of *Apiococcus* with first-instar nymphs of other eriococcid genera see the “Comment” section after the treatment of *A. singularis* (first-instar male).

Apiococcus singularis Hempel

Apiococcus singularis Hempel, 1900: 403.

First-Instar Nymph (considered to be female) (Fig. 7)

Material examined: "Types": BRAZIL, São Paulo, Ypiranga, on Myrtaceous shrub, 1900, coll. unknown (USNM): 1/5 first-instar nymphs: 2ff (one in good condition, other very poor) + 3mm (2 in fair condition, 1 poor).

Unmounted material. Body elliptical and clear yellow (Hempel, 1900).

Mounted material. Body oval. Length about 310–350 µm, width 155–180 µm.

Dorsum. Derm membranous, with enlarged dermal spinules medially, these particularly obvious on meso- and metathorax and abdominal segments I–III; smaller ones present medially elsewhere. Dorsal setae of 2 types: (i) spinose and broad, with a rather rounded surface posteriorly, becoming more convex anteriorly; each about 6.5–7 µm wide, with a narrow basal socket and each raised slightly on a small membranous prominence: in 2 submedial lines, with a pair on abdominal segment I plus pairs on each thoracic segment and posteriorly on head; and (ii) setose setae, each 8–13 µm long, as follows: in a pair of mid-dorsal lines, 1 pair per segment on abdomen and thorax, and with 4 pairs on head; also with pairs of submarginal setae on abdominal segments II–IV; possibly absent elsewhere. Macrotubular ducts absent. Microtubular ducts rather large, with an oval, strongly sclerotised, apparently bilocular, pore at the end of a short outer ductule; each duct about 6–7 µm long, with a short inner ductule; distribution uncertain but perhaps rather random, with a pair on abdominal segments I–IV, 1 or 2 on most thoracic segments and a few on head. Loculate pores each 3–4 µm wide and with 5 loculi, in 2 transverse rows across abdominal segment I, with (on each side) 11 or 12 along anterior margin and 7 or 8 along posterior margin. Anal lobes absent or rounded, membranous; without microtubular ducts; each with a long apical flagellate seta of unknown length; marginally with 2 or 3 pairs of spinose setae between long apical setae, each about 8 µm long. Anus on posterior apex, slightly oval, membranous, without an anal ring or anal ring setae; width 8 µm; with 2 rather spinose setae on either side (each about 6.5–12 µm long) plus a much longer seta, length unknown as all broken.

Margin. Marginal setae spinose, similar in shape to those on dorsum but perhaps slightly smaller, each 6–7 µm wide and on a distinct membranous prominence; anterior setae becoming more convex and cone-like; with 4 between eyespots, 4 on each side between eyes and point opposite anterior spiracles, 2 on each side laterally between anterior spiracles and abdomen and with 1 on each side of abdominal segments I–VII. Eyespots large and oval, greatest width 11–13 µm, situated on margin near base of antennae.

Venter. Derm membranous. With 2 or 3 pairs of long flagellate setae between antennae (each about 18–20 µm long); with rather shorter setae mesad to meso- and metacoxae (11–17 µm long) and even shorter mesad to procoxae; also with a pair of setae medially on abdominal segments II–VII, each about 6–10 µm long. Submarginal setae hairlike, with a seta on each side of abdominal segments I–VII, 2 laterally between spiracles and with 3 on head; also with a submedial line of very short setae (length 2–3 µm) on abdomen (as on *A. gregarius*), with 1 seta on each side of segments I–VII. Microtubular ducts apparently similar to those on dorsum: distribution uncertain but with some submedially on abdomen, in each thoracic segment and near eyespot. Loculate pores with mainly 5 loculi: with 2 or 3 immediately laterad of each peritreme, possibly in small cavity; also with 3 or 4 pores on abdominal segment I between margin and each posterior spiracle.

Antennae 6 segmented, total length 83–88 µm long; setal distribution: scape 2; pedicel 1 + a campaniform sensillum; segment III 3; IV 1; V 1 fleshy setae + 3 setose setae and VI 3 fleshy setae + about 4 setose setae; apical seta about 35 µm long. Clypeolabral shield particularly large, about 80 µm long; labium perhaps 2 segmented; with 4 pairs of setae. Spiracles very small, width of peritreme about 3 µm wide; spiracles surrounded by an oval area, perhaps a shallow cavity. Legs well developed; lengths: metathoracic leg (µm): coxa 31–33; trochanter + femur 59–63; tibia + tarsus 65–68; claw 15–18; tibia generally subequal to or slightly shorter than tarsus; setae: coxae 4 or 5, trochanter 2, femur 2, tibia 4, tarsus 3; long trochanter seta 45 µm long; tarsal campaniform sensillum present; claw with a distinct denticle; tarsal digitules on all legs capitate and equal in size; claw digitules both fine and longer than claw.

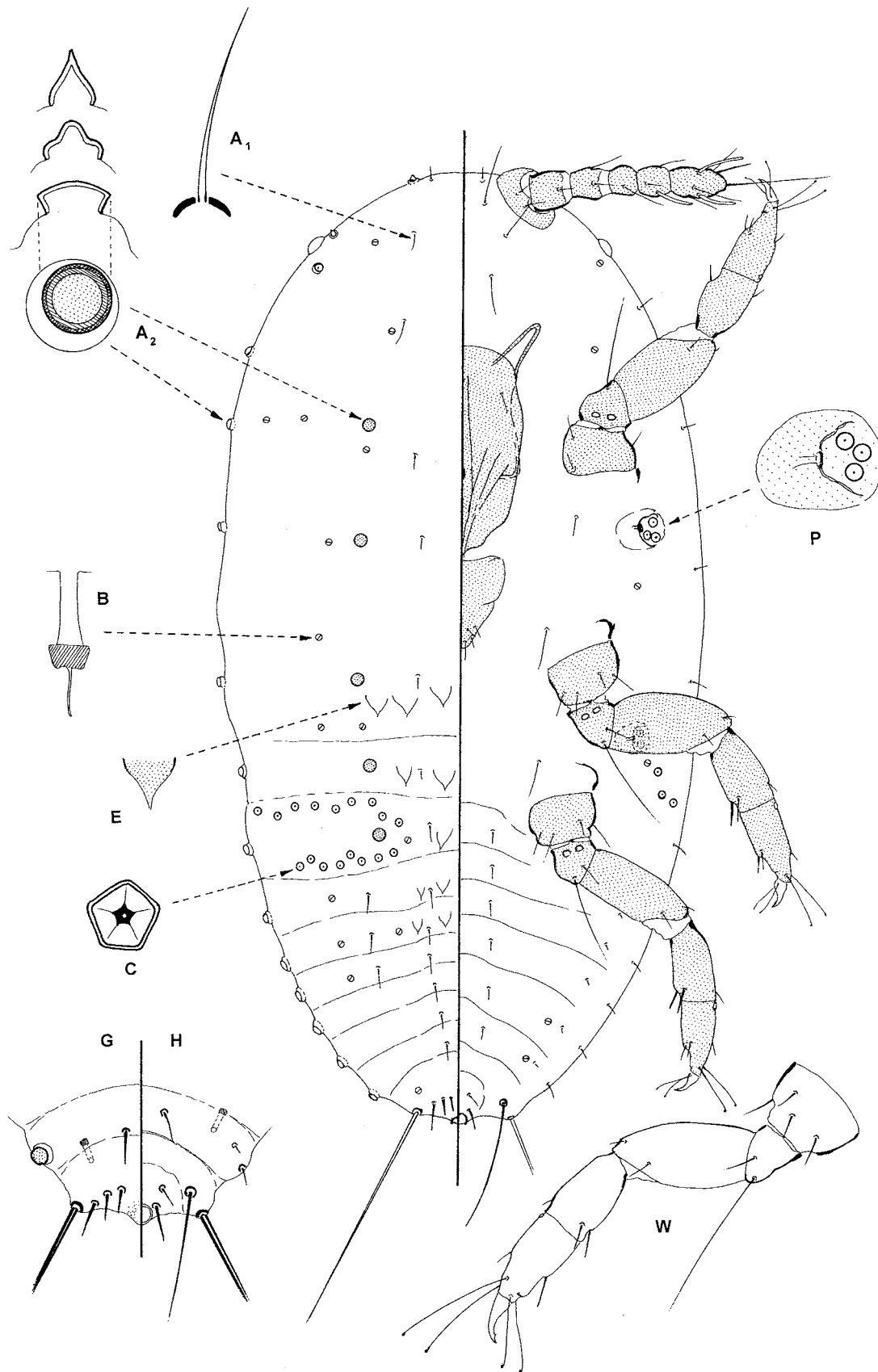


FIGURE 7. *Apiococcus singularis* Hempel. First-instar nymph, probably female, where A₁ = dorsal setose seta; A₂ = marginal and dorsal broad spinose setae; B = dorsal microtubular duct; C = dorsal loculate pore; E = enlarged dermal spinules; G = dorsal view of anal area; H = ventral view of anal area; P = spiracle with loculate pores; W = metathoracic leg.

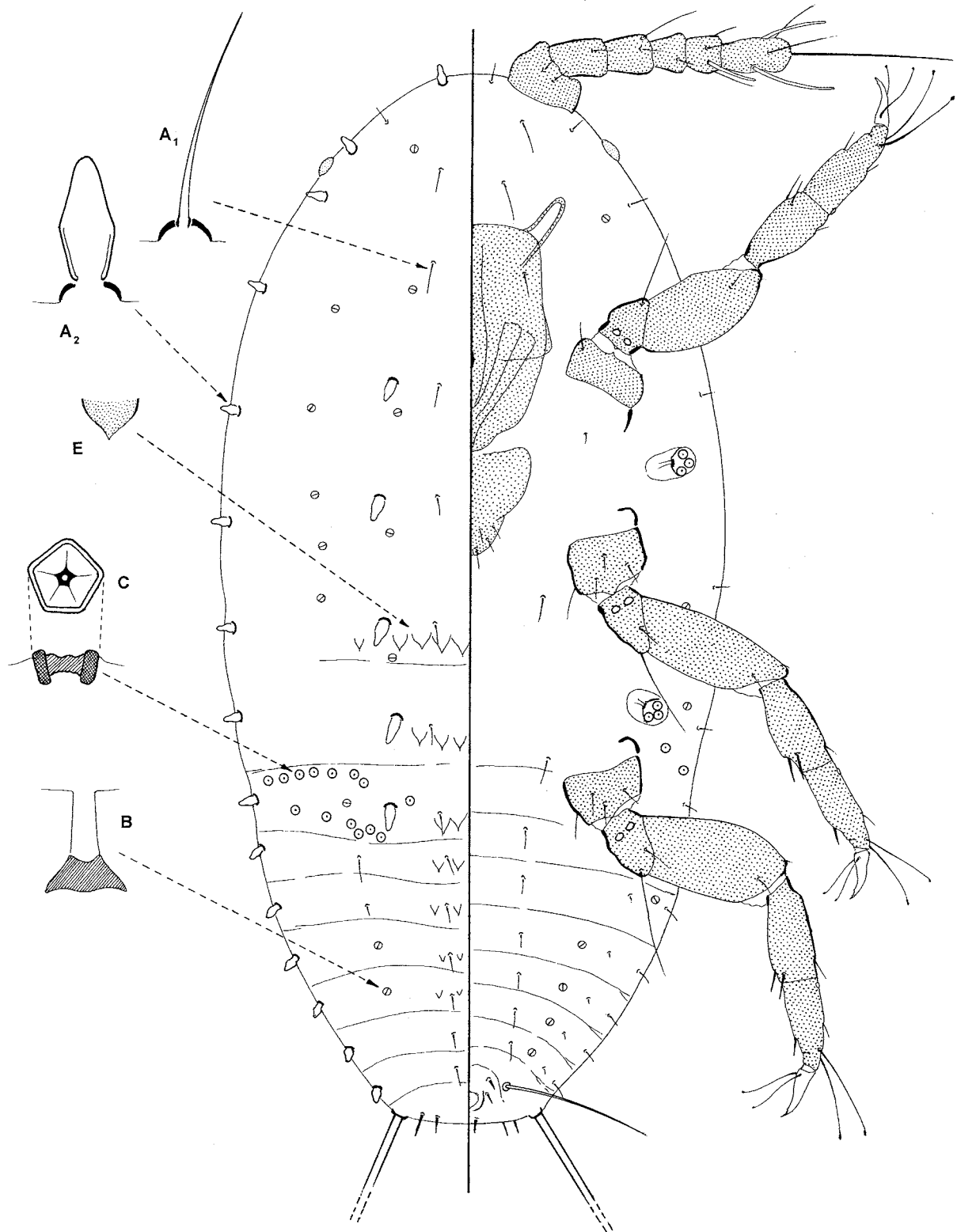


FIGURE 8. *Apiococcus singularis* Hempel. First-instar nymph, probably male, where A_1 = dorsal setose seta; A_2 = marginal and dorsal broad spinose setae; B = dorsal microtubular duct; C = dorsal loculate pore; E = enlarged dermal spinule.

Comment. Presumed to be female as the marginal and dorsal spinose setae are approximately the same shape as those on the adult female. For a comparison of first-instar nymphs of *Apiococcus* with other eriococcid genera see the “Comment” section after the treatment of *A. singularis* (male).

First-Instar Nymph (considered to be male) (Fig. 8)

Unmounted material. Body elliptical and clear yellow (Hempel, 1900).

Mounted material. Body oval. Length about 250–315 μm , width 125–155 μm .

Dorsum. Basically identical to presumed female nymph described above except that type (i) spinose setae, elongate and stoutly spinose, each 10–12 μm long, each broadest medially, with a blunt apex; each with a narrow basal socket and not clearly raised on a small membranous prominence; distribution as on female crawler; and type (ii) setae as on female crawler but with only 2 pairs of submarginal setae on abdomen, on segments II and III, latter possibly shorter than former. Microtubular ducts probably distributed similarly but unclear. Loculate pores similar in structure and distribution, but with perhaps 8 on each side along anterior margin of abdominal segments I and 6–8 along posterior margin. Anal lobes similar; each long apical flagellate seta about 175 μm long. Other setae associated with anal lobes and anus distributed similarly but perhaps slightly shorter; longer seta on each side of anus about 58–62 μm long.

Margin. Marginal setae spinose, similar in shape to those on dorsum but smaller, each 7.5–9 μm long, without a distinct membranous prominence; anterior setae similar to posterior setae; distribution as on female crawler. Eyespots similar.

Venter. Similar to female crawler. Setal distribution similar to that on female crawler. Microtubular ducts as in female crawler: distribution uncertain. Loculate pores: with 2 or 3 immediately laterad of each peritreme; also with 2 or 3 pores between margin on abdominal segments I and each posterior spiracle.

Antennae similar to female crawler, total length perhaps marginally shorter, 75–83 μm long; setal distribution similar; apical seta about 55 μm long. Clypeolabral shield and labium similar. Spiracles very small. Legs well developed but possibly marginally shorter; lengths (metathoracic leg (μm)): coxa 30; trochanter + femur 60; tibia + tarsus 65; claw 13–17; other leg details similar.

Comment. The differences between the shape of the marginal and dorsal spinose setae on the presumed male and female first-instar nymphs are very clear and immediately separates these 2 lots of crawlers.

The first-instar nymphs of *Apiococcus* are easily separable from those of other genera known from the Neotropics in having a band of loculate pores dorsally across abdominal segment I. In addition, they have the following characters: (i) 6-segmented antennae; (ii) microtubular ducts present on both dorsum and venter; (iii) no cruciform pores; (iv) enlarged dermal spinules medially on the dorsum of meso- and metathorax and abdominal segments; (v) several loculate pores associated with each spiracle; (vi) anal plates not differentiated; and (vii) dorsal setae of clearly 2 types, a strongly spinose type and a setose type.

***Capulinia* Signoret**

Capulinia Signoret, 1875: 27–28. Type species *Capulinia sallei* Signoret 1875: 28–29.

Generic diagnosis. Adult female (Fig. 9). On leaves of host, secreting an extraordinarily long ovisac. Body apparently globular; derm entirely membranous, all segmentation apparently absent. **Dorsum.** Setae finely spinose, sparse. Macrotubular ducts absent. Microtubular ducts highly varied, of possibly 3 or 4 types: a long thin duct immediately around anus, a larger and broader duct forming a complete band around abdomen on about abdominal segment IV; a duct somewhat similar to first type but very sparse throughout dorsum and another somewhat like second type but pore apparently 8-shaped, sparse. Loculate pores absent. Anal lobes possibly totally absent. Anal ring probably with a partially sclerotised ring. **Margin.** Undefined. **Venter.** Setae setose. Macrotubular ducts absent. Microtubular ducts similar to first 3 types on dorsum, sparse. Loculate pores mainly with 4–6 loculi, restricted to near each spiracle. Antennae 1 or 2 segmented. Frontal lobes and antennal tubercles absent. Number of labial segments unknown. Legs very much reduced; those anteriorly merely membranous lobes, metathoracic legs showing slight signs of segmentation but segmentation obscure and setae absent. Hind legs positioned very far posteriorly, therefore abdomen probably small; translucent pores absent. Vulva not detected.

Known only from Myrtaceae.

Comment: *Capulinia* contains 4 species, 1 (*C. orbiculata* Hoy) from New Zealand, the type species (*C. sallei*) from Cuba and Mexico, and 2 species (*C. crateriformis* Hempel and *C. jaboticabae* Ihering) from Brazil. *Capulinia* differs from all other South American eriococcid genera in having the hind legs modified into membranous lobes that are located near the posterior apex of the abdomen. *Opisthoscelis* also has enlarged hind legs located near the posterior apex of the abdomen but these 2 genera differ as follows: *Capulinia* has (*Opisthoscelis* character states in parentheses): (i) numerous microtubular ducts forming a circle around the anal opening (without microtubular ducts); (ii) loculate pores restricted to spiracular area (scattered around anal area); and (iii) hind legs smaller than length of labium (hind legs much longer than labium). There are significant differences between *C. sallei*, the type species of *Capulinia*, and the other species currently placed in this genus.

***Capulinia sallei* Signoret.**

Capulinia sallei Signoret 1875: 28–29.

Material examined: CUBA, Santiago de los Vegas, on *Eugenia tuberculata* (Myrtaceae) 14.i.1908, W.T. Horne (USNM): 1/1adf, (in good condition). Also: as previous 2/23 1st instars (mainly in good condition). MEXICO, Arroyo San Isidro, no host, June 1897, Townsend (USNM): 1/8adff (rather poor specimens) (see discussion after description). Also: no collection data but perhaps as previous (USNM): 1/3admm (1 in fair condition, other 2 poor; wings folded over body or absent; few legs complete; only 1 penial sheath complete). [Type material has not been seen. This species also has been recorded from *Eugenia axillaris* (Myrtaceae) and *Muntingia calabura* (Elaeocarpaceae) (Hoy, 1963)]

Adult Female (Fig. 9)

Unmounted material. Occurs on the leaves of its host. Forms an extraordinarily long ovisac which can exceed 15 mm, is not attached to the host, is tubular, and looks like a piece of cotton thread.

Mounted material. Body apparently globular, derm entirely membranous. Length and width about 1.4 mm. All segmentation apparently absent.

Dorsum. Derm membranous, without striations or a reticulate pattern of areolations. Dorsal setae finely spinose, each mostly about 3–5 μm long but those anterior to anus up to 12 μm long; basal socket broad; sparsely distributed in no apparent pattern. Macrotubular ducts absent. Microtubular ducts of perhaps 3 or 4 types: (i) a long thin microduct, abundant on perhaps posterior 5 abdominal segments of both dorsum and venter, each about 10–12 μm long and 0.8–1.2 μm wide, with a small sclerotised distal apex, apparently without an inner ductule; (ii) a rather larger and broader microduct, abundant in a complete band around abdomen on about abdominal segment IV, each 8–11 μm long and 2.0–2.5 μm wide, with a strongly sclerotised distal end, apparently without an inner ductule; (iii) a microduct rather similar to (i) but slightly wider and longer (length about 12 μm , width about 1.5 μm), with an inner ductule, present throughout entire dorsum and venter but much sparser than types (i) and (ii); and (iv) a larger microduct rather similar to type (ii), length 6–7 μm , width 3.0–3.5 μm , apparently narrowly oval in cross section, inner sclerotised end appearing 8-shaped, with an inner ductule; rather scarce and probably restricted to dorsal surface. Loculate pores absent. Anal lobes barely developed or absent, unsclerotised, without a discernable pattern of anal lobe setae homologous to those on other eriococcids but with a few setae in general area, each about 8–12 μm long. Median lobe absent. Anal ring possibly represented by a partially sclerotised ring, about 18 μm wide; anal ring setae absent; derm around anus with numerous micro-folds.

Margin. Undefined; apparently without differentiated marginal setae. Eyespots not detected.

Venter. Derm membranous. Setae very sparse, short, each 3–5 μm long, although up to 10 μm near anus (but rather finer than those on dorsum); without long setae medioventrally between antennae and mesad to coxae; setae on abdominal segments possibly in segmental lines, with perhaps 4 or 5 in each line, otherwise apparently randomly distributed. Macrotubular ducts absent. Ventral microtubular ducts of perhaps 3 types, similar in structure and distribution to types (i)–(iii) on dorsum. Loculate pores, with mainly 5 loculi, restricted to 4–6 near each spiracle, immediately laterad and anterior to each spiracular peritreme.

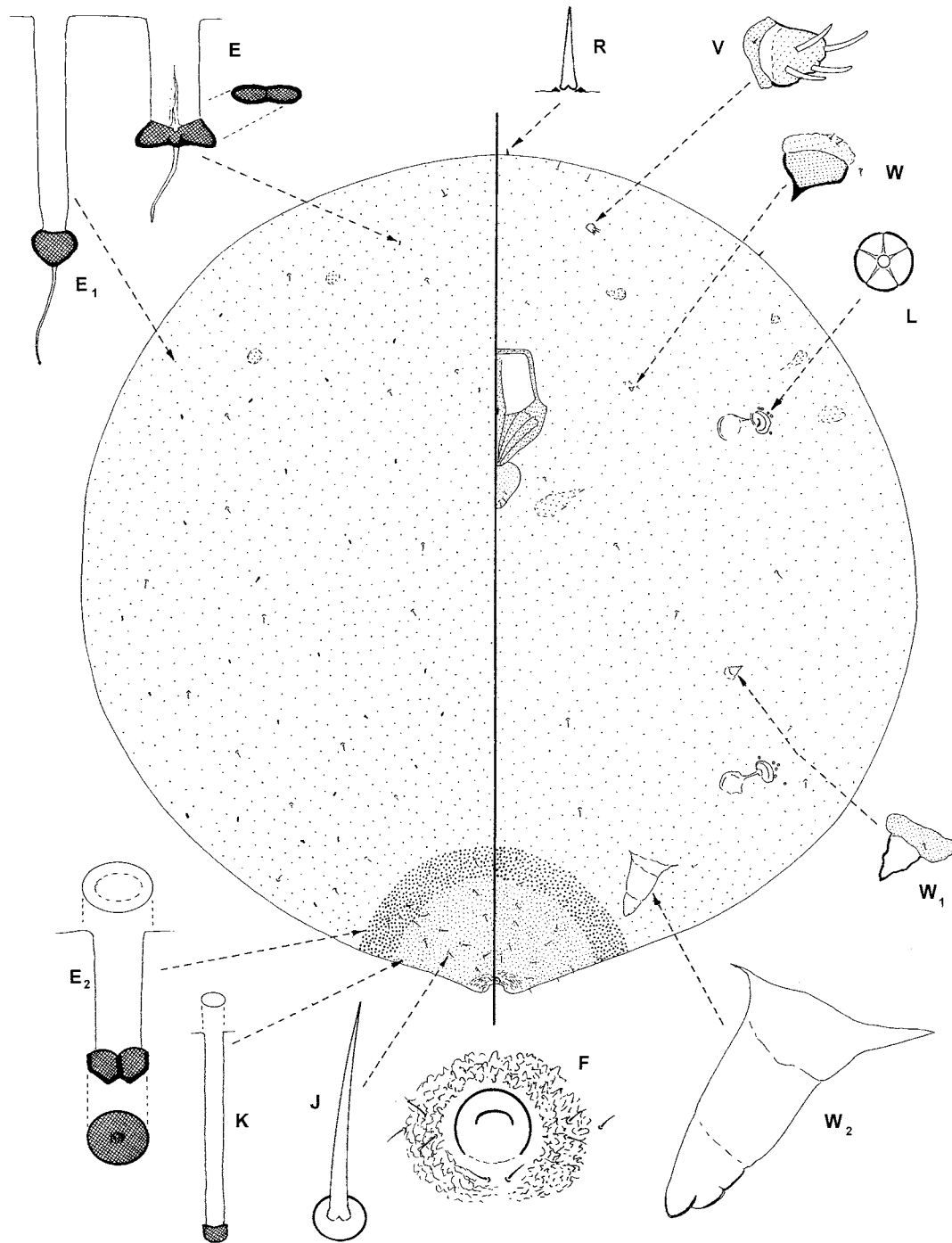


FIGURE 9. *Capulinia sallei* Signoret. Adult female, where E, E₁, E₂ = enlarged microtubular ducts; F = view of anal area; J = dorsal setae on abdomen; K = smaller microtubular ducts on abdomen; L = ventral loculate pore; R = marginal seta; V = antenna, and W, W₁, W₂ = legs.

Antennae represented by a pair of very short structures, each 1 (or perhaps 2) segmented, each about 23–25 μm long, with perhaps 4 fleshy setae on apical segment and 1 very small seta on basal segment. Clypeolabral shield about 100 μm long; labium, probably 1 segmented and with 4 pairs of setae. Spiracles: width of peritremes 30–33 μm ; length of muscle plate (apodeme) 48–50 μm . Legs very much reduced: prothoracic legs each represented by a membranous basal segment (with a few minute setae) and a sclerotised claw-like structure; total length about 15–18 μm ; mesothoracic legs slightly larger, with an unsclerotised basal area and a sclerotised distal part, perhaps representing fused tibia, tarsus + claw, total length about 18 μm ; and

metathoracic legs much larger but segmentation very poorly defined; mainly membranous and without setae; with median segment (femur?) about 55–60 μm wide, basal "coxal" part much wider, and distal part, perhaps composed of fused tibia, tarsus plus claw; total length 100–140 μm ; position of metathoracic legs far back, and therefore abdomen very short. Vulva not detected.

Comment. Of the material studied, the rather poor specimens labelled *C. sallei* from Mexico appeared to be very similar to the series studied above as far as could be seen except that the pro- and mesothoracic legs were slightly larger and the metathoracic legs more clearly defined, perhaps with a distinct claw and even with claw digitules. The body is also rather larger, up to perhaps 2.6 mm in length and width. For a comparison of the adult female of *Capulinia* with other eriococcid genera, see the "Comment" section after the generic diagnosis of *Capulinia*.

First-Instar Nymph (gender not determined) (Fig. 10)

Unmounted material. Not seen.

Mounted material. Body oval, slightly more pointed posteriorly. Length about 490–625 μm , width 285–375 μm .

Dorsum. Derm membranous, without obvious dermal spinules. Dorsal setae spinose, tending to be rather swollen in basal quarter, each 15–19 μm long, with a narrow basal socket, in 2 medial lines, with pairs on abdominal segments I–V, 2 pairs on pro-, meso- and metathorax plus 2 pairs on head; also with submarginal setae on meso- and metathorax and on head, plus a submedial pair posteriorly on head. Macrotubular ducts absent. Microtubular ducts with an 8-shaped, strongly sclerotised, dermal pore, with an outer ductule about 5 μm long, probably with an inner dividing membrane, and a heavily sclerotised distal apex; no inner ductule noted; distributed as follows: with a submarginal pair on abdominal segments VIII, V, III and I and on meta- and mesothoracic segments, plus another submarginally on head; also with pairs medially on abdominal segment IV, and on meta- and mesothorax and 3 pairs on head; plus a submedial and a sublateral pair on prothorax. Loculate pores absent. Anal lobes absent or rounded, membranous; each with a very long apical flagellate seta about 175–190 μm long; marginally with 3 pairs of spinose setae between long apical setae, each about 12–19 μm long. Anus slightly oval, about 5 μm wide, without an anal ring or anal ring setae, but with two pairs of minute setae on each side ventrally, each about 2 μm long plus a much longer seta, 35–45 μm long (anterior suranal seta?). Anus surrounded by a sclerotised crescent, outer width of crescent 8 μm , width of opening about 3 μm .

Margin. Marginal setae spinose, similar in shape to those on dorsum and about same size, each 15–17 μm long; with 6 between eyespots, 4 on each side between eyes and point opposite anterior spiracles, 4 on each side laterally between anterior spiracles and abdomen and with 1 on each side of abdominal segments I–VII. Eyespots fairly small, each 8 μm wide, situated on margin near base of antennae.

Venter. Derm membranous. With 3 pairs of long setae between antennae plus pairs mesad to each meso- and metacoxa (these setae long, each about 17 μm); no setae present medially on abdominal segments I–VII. Submarginal setae strongly spinose, each 11–13 μm long, somewhat similar to marginal setae but basal swelling less pronounced; with a pair on each side of abdominal segments I–VII, 4 on each side of thorax and 2 on each side of head. Microtubular ducts apparently similar to those on dorsum, with pairs submarginally on abdominal segments II, III, VI and VIII, between meso- and metathorax, and with 1 pair between antennae and 2 pairs posteriorly on head; also with a duct between each pro- and mesocoxae. Loculate pores with mainly 5 loculi: with 2 or 3 immediately laterad of each peritreme, in a small cavity.

Antennae 6 segmented, each 75–80 μm long; segment IV particularly short and ring-like; setal distribution: scape 3; pedicel 0 or 1; segments III and IV 0; V 1 setose seta + 1 fleshy seta; VI 3 fleshy setae, 3 short setose setae plus 3 long setae, length of longest about 50 μm . Clypeolabral shield about 66–77 μm long; labium perhaps 1 segmented; about 33–42 μm wide, with possibly 2 pairs of short setae + 1 pair rather long setae on apex. Spiracles small, peritremes 11–12 μm wide, each with a lateral membranous cavity, and with 2 or 3 loculate pores. Legs well developed; lengths (metathoracic leg (μm)): coxa 21–25; trochanter + femur 50–53; tibia 25–30; tarsus 25; claw 15; tibia generally subequal to or slightly shorter than tarsus; setae: coxae 3, trochanter 2, femur 2, tibia 2, tarsus 3; long trochanter seta 18–20 μm long; tarsal campaniform sensillum present; claw without a denticle; both tarsal digitules on all legs capitate and equal in size; claw digitules alike with small capitate apices.

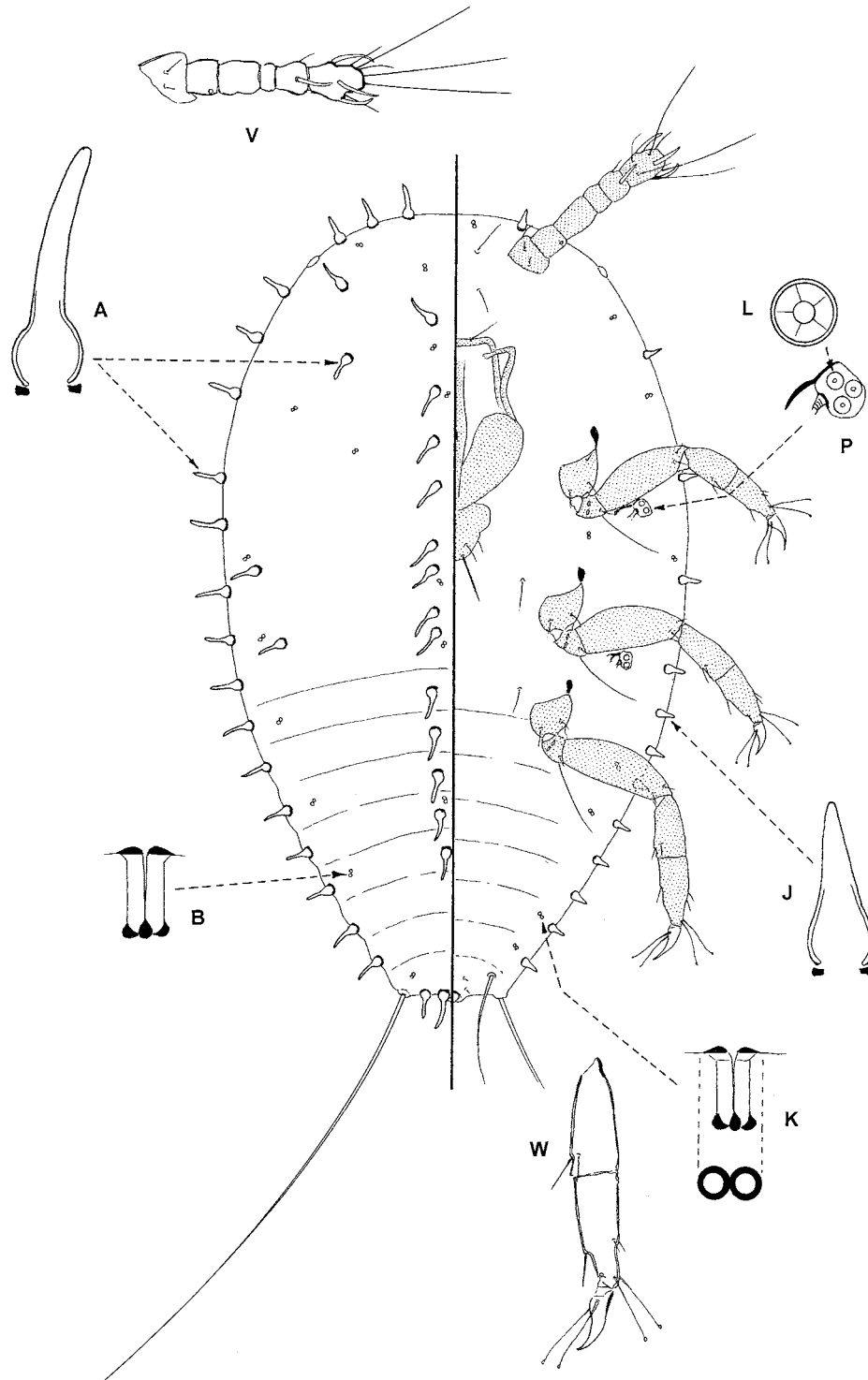


FIGURE 10. *Capulinia sallei* Signoret. First-instar nymph, where A = dorsal spinose seta; B = dorsal microtubular duct; J = ventral submarginal seta; K = ventral microtubular duct; L = ventral loculate pore, P = anterior spiracle, V = antenna, and W = distal end of metathoracic leg.

Comment. The first-instar nymphs of *C. sallei* are characterised by the following combination of characters: (i) 6-segmented antennae; (ii) dorsal setae all of 1 type, spinose with a swollen base; (iii) anal lobes poorly differentiated and not sclerotised; (iv) microtubular ducts present on both dorsum and venter; (iv) absence of cruciform pores; (v) loculate pores restricted to cavity laterad to each spiracle; and (vi) claw

digitules similar. The first-instar nymph of *Chilechiton lynnae* also has dorsal spinose setae with swollen bases but is otherwise rather different (see first-instar nymph diagnosis under that genus).

Adult Male (Fig. 11)

Mounted material. Total body length about 1.2 mm; antennae short, about half total body length; body with relatively few setae; fleshy setae (fs) long (each about 26–35 μm long) and thin, similar to long, fine hair-like setae and not easily distinguishable, therefore mainly just referred to as setae below, except on antennae.

Head. Approximately oval to slightly 6-sided in dorsal view; width across genae about 182 μm ; length about 178 μm . Median crest (mc) represented by 2 almost parallel arms extending anteriorly from postoccipital ridge (por), almost touching median margin of dorsal eyes; not reticulated; postoccipital ridge (por) distinct, extending laterally and slightly posteriorly; with about 14 or 15 pairs of dorsal head setae (dhs); head without pores of any sort. Mid-cranial ridge: dorsal ridge (dmcr) present as a short extension dorsally from lateral arms of mid-cranial ridge; ventral ridge (vmcr) with a pair of distinct lateral arms (lmcr) and a ventral extension almost to ocular sclerite posteriorly; with 6–9 ventral mid-cranial ridge setae (vmcrs) on either side anterior to occipital sclerite. Dorsal ocular setae absent. Genae (g) not reticulated but with 15 or 16 genal setae (gs) on each side laterad to postoccipital ridge. Eyes: with 2 pairs of round, simple eyes; dorsal eyes (dse) subequal in size to ventral eyes (vse), each 38–42 μm wide. Ocelli (o) absent. Ocular sclerite (ocs) barely sclerotised; reticulation only visible immediately around each simple eye, although perhaps with a small area laterad to each dorsal eye. Preocular ridge (procr) extremely short or absent, possibly represented only by an antennal articulatory sclerite. Postocular ridge (pocr) strongly developed, extending dorsally to about level with or just past posterior margin of each dorsal eye. Ventral head setae (vhs): rather abundant, with about 18 long setae between ventral simple eyes, and a further 20–30 on each side anterior and laterad to each ventral simple eye. Preoral ridge (pror) absent. Cranial apophysis (ca) apparently absent. Mouth present as a small membranous opening.

Antennae. Ten segmented and filiform, segment III longest and then each segment becoming smaller towards apex; length about 635 μm long (ratio of total body length to antennal length 1:0.53). Scape (scp): 50–56 μm long and 45–50 μm wide, with about 9–12 setae, mainly on ventral surface. Pedicel (pdc): length 48–66 μm , width 37–42 μm ; without concentric ridging distally; with 18–27 setae, some probably fs, plus 1 campaniform sensillum. Flagellar segments 20–27 μm wide; fs about 40–50 μm long; lengths of segments (μm): III 90–112; IV 81–92; V 95–100; VI 85–90; VII 70–75; VIII 47–63; IX 50–58 and X 46–53; approximate number of setae per segment: III–IX 14–24 fs, no hs; X 10–15; segment IX with 1 bristle (ab), segment X also with 2 bristles and 4–7 capitate setae (caps); sensilla basiconica not detected.

Thorax. Prothorax: pronotal ridge (pnr) present and fused medially on dorsum; lateral pronotal sclerites (prn) distinct, each with faint ridging; without lateral pronotal setae. Medial pronotal and post-tergital setae apparently absent, but perhaps with 1 propleural seta (pl₁s) on each side. Post-tergites (pt) lightly sclerotised. Sternum (stn₁) not sclerotised and without radial striations; transverse ridge well developed and sclerotised, but possibly without apophyses laterally; median ridge faintly indicated or absent; with 1–8 pairs of prosternal setae (stn₁s). Proepisternum + cervical sclerite (pepcv) showing nothing distinctive. Anteprosternal setae: perhaps 0 or 1 present; antemesopiracular setae absent.

Mesothorax: prescutum (prsc) oval, 91–112 μm long; 120–130 μm wide; sclerotised but not reticulated; with 4–7 prescutal setae (prscs) on each side; prescutal ridges (pscr) well developed; prescutal suture (pscs) only lightly sclerotised; prealare (pra) and triangular plate (tp) well developed. Scutum (sct): median area sclerotised, without reticulations; distance between prescutum and scutellum about 25–57 μm , with 10 or 11 setae (scts) on each side posterior to prescutum; without other setae laterally; prealar ridge weak. Scutellum (scl) 140–150 μm wide and 37–46 μm long; with an inverted U-shaped scutellar ridge; probably not tubular and lacking a foramen; scutellar setae (scls): 3–5 pairs; posterior notal wing process (pnp) quite long, more or less transverse and heavily sclerotised. Basisternum (stn₂) 248–265 μm wide and 103–112 μm long; median ridge either entirely absent or indicated by a faint sclerotisation; bounded anteriorly by a moderately strong marginal ridge (mr) and posteriorly by strong precoxal ridges (pcr₂); with 20–30 pairs fs basisternal setae (stn₂s), mainly distributed posterolaterally and anteriorly; lateropleurite (lpl) with suggestions of striations, but without a marginal ridge extension; furca (f) well developed, narrow-waisted, arms divergent and extending to

anterior marginal ridge. Mesopostnotum (pn₂) well developed; postnotal apophysis (pna) well developed. Area bounded anteriorly by scutellum and laterally and posteriorly by mesopostnotum not sclerotised. Mesepisternum (eps₂) not reticulated; subepisternal ridge (ser) strongly sclerotised. Postalare (pa) well developed; without postalare setae. Mesothoracic spiracle (sp₂) of moderate size: width of peritreme 25 µm. Postmesospiracular setae (pms): with 10–17 on each side, extending across full width of segment between spiracles. Tegula (teg) present; with about 3 tegular setae (tegs).

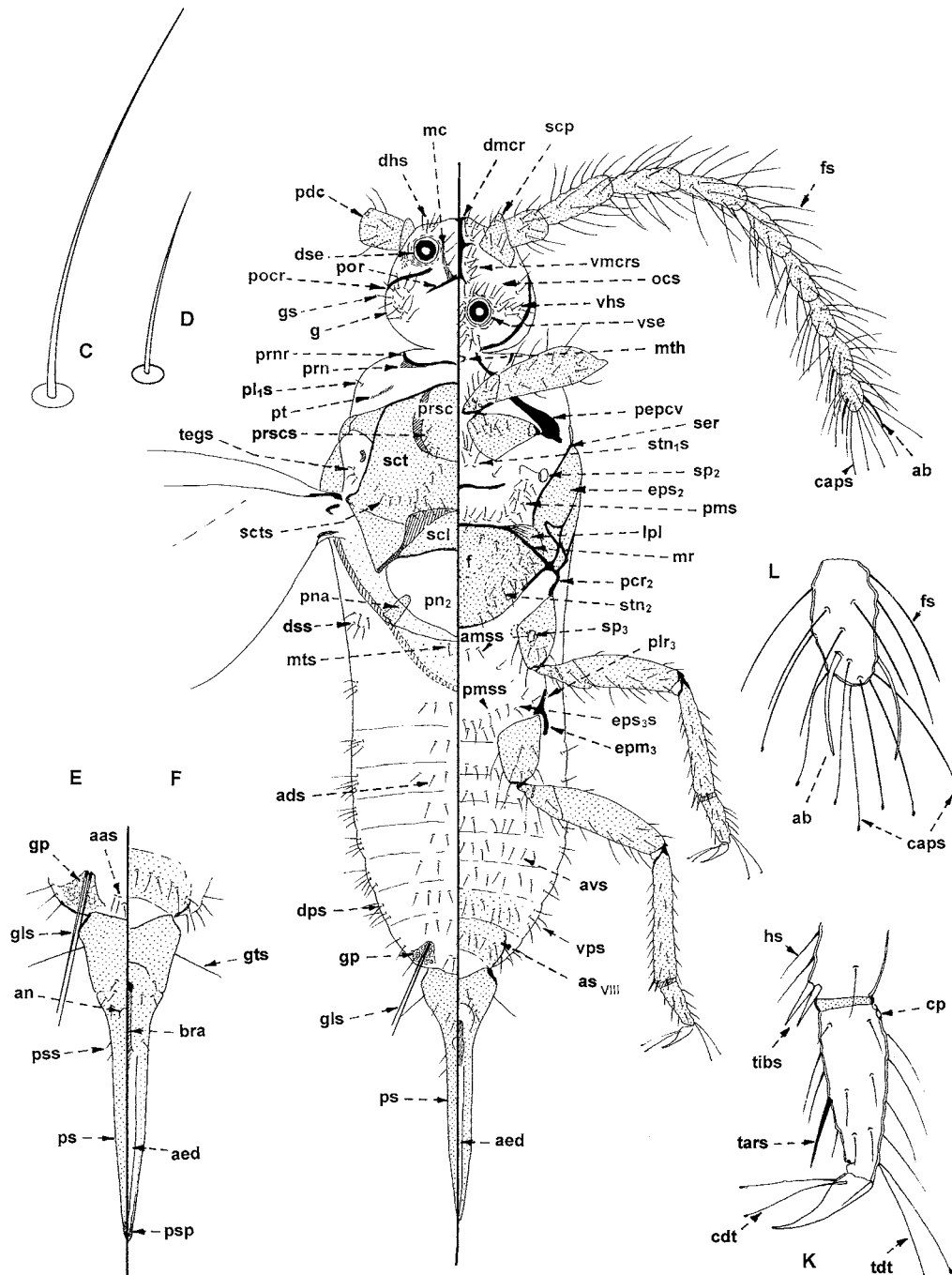


FIGURE 11. *Capulinia sallei* Signoret. Adult male, where C = fleshy seta, D = hair-like seta, E = dorsal view of penial sheath; F = ventral view of penial sheath; L = apical antennal segment, and K = distal end of metathoracic leg. For other abbreviations, see under 'Figure captions' on p.5.

Metathorax: with 1 pair of hs metatergal setae (mts) medially. Dorsospiracular setae (dss): 10–14 on each side. Dorsal part of metapleural ridge absent; ventral part of metapleural ridge (plr₃) short; episternum (eps₃) unsclerotised, with 3–6 postmetaspiracular setae (eps_{3s}) on each side; precoxal ridge (pcr₃) arising close to metacoxae. Metepimeron (epm₃) sclerotised but without setae. Antemetaspiracular setae absent. Metathoracic spiracle (sp₃) of moderate size: width of peritreme 22–25 µm. Metasternum (stn₃) membranous and without metasternal apophyses; with a total of 6–8 anterior metasternal setae (amss) and 9–15 posterior metasternal setae (pmss).

Wings: hyaline, probably about 760 µm long but width unknown (ratio of total body length to wing length 1:0.63); alar lobe and alar setae absent. Hamulohalteres absent.

Legs: metathoracic legs marginally longest. Coxae (cx): I 85–95; II 85–100; III 85–100 µm long; with 11 setae on each coxa III; long apical seta on each coxa not differentiated, but seta in this position about 30 µm long. Trochanter (tr) + femur (fm): I 178–195; II 157–180; III 178–205 µm long; trochanter III with 11–15 setae; campaniform sensilla oval and in a diagonal line; long trochanter seta not differentiated but setae in this position about 33 µm long; femur III with about 14 setae. Tibia (tib): I 153–166; II 153; III 170 µm; tibia III with a total of 38–40 setae, mainly hs, a few becoming spur-like on distal third of leg; without fleshy setae on dorsal surface; with 2 or 3 apical spurs (tibs), length 20–22 µm. Tarsi (tar): I 70–78; II 66; III 75 µm long (ratio of length of tibia III to that of tarsus III 1:0.44); tarsi 2 segmented, proximal segment ring-like; tarsus III with about 13 setae, mainly spur-like; tarsal spurs (tabs) differentiated, but not most distal seta, length 27 µm; tarsal campaniform sensillum (cp) present; tarsal digitules (tdt) subequal to or longer than length of claw, with small apical knobs. Claws (c) quite long and thin, much longer than width of tarsi, almost straight, without a denticle; length: III: 28–30 µm; claw digitules (cdt) distinctly longer than claw, with minute apical knobs.

Abdomen. Segments I–VII: tergum (at) and sternum (as) both membranous, except on segment VII, where sternum lightly sclerotised; without obvious oval membranous areas in inter-segmental membranes. Pleurites unsclerotised. Caudal extension (ce) of segment VII absent. Dorsal setae (ads): segments I–VII with 3–7 setae on each side. Pleural setae: dorsopleural + ventropleural setae (dps + vps on each side): segments I–VII 5–9 on each side. Ventral setae (avs) (on each side): II–VII 4–9.

Segment VIII: tergum (at) unsclerotised; sternite (as) distinctly sclerotised, with more strongly sclerotised areas laterally; tergite with 5 ante-anal setae (aas); sternite with about 16 ventral abdominal setae (avs); caudal extension (ce) absent; with about 6 pleural setae, subequal in length. Glandular pouches (gp) present, with a fairly broad opening, each with many loculate pores, all within pouch; glandular pouch setae (gls) each about 115–125 µm long.

Genital segment: penial sheath (ps) rather swollen anteriorly (probably representing segment IX), then rapidly narrowing and becoming more or less parallel over middle 1/2, before gradually narrowing to a fairly sharp apex; total length 320 µm, width anteriorly 97 µm (ratio of total body length to length of penial sheath 1:0.26); anal opening medially on dorsal surface; with 1 longish seta (gts) laterally on each side of swollen section, each about 20–33 µm long; plus 3–6 shorter setae (pss) dorsally anterior to anal opening and 3 or 4 on each side just anterior to base of basal rod, each 10–15 µm long. Aedeagus (aed) tapering slightly, and extending almost to tip of penial sheath; length 150 µm. Basal rod (bra) quite long, 33–35 µm long, possibly with a sclerotised internal genital aperture (iga) at anterior end. Penial sheath also with a few small sensilla (psp) near apex.

Comment. The adult male of *C. sallei* can be separated from the other known males from the Neotropics in having the following combination of characters: (i) a long penial sheath (at least 3x as long as basal width); (ii) 10-segmented antennae, with fleshy setae clearly longer than width of each segment; (iii) fleshy setae on body hard to distinguish from hair-like setae; and (iv) claws long and thin, without a denticle.

Carpochloroides Cockerell

Carpochloroides Cockerell, 1899: 12. Type species *Carpochloroides viridis* Cockerell, 1899: 12–13.

Generic diagnosis. Adult female (Fig. 12). Body globular. Derm membranous, without visible segmentation but with large faint reticulations. *Dorsum*. Setae finely spinose, very sparse. Macrotubular ducts absent. Microtubular ducts small, mainly present in centre of each reticulation. Loculate pores each with mainly 3–5 loculi, with 1 per reticulation, present over a broad area anterior to anal ring. Anal lobes absent. Median plate absent. Anus with a sclerotised ring without setae or pores. *Margin*. Undefined. *Venter*. Setae similar to those on dorsum, sparse. Macrotubular ducts absent. Microtubular ducts longer and narrower than those on dorsum, frequent throughout. Loculate pores similar to those on dorsum; exact distribution uncertain but associated with each spiracle and elsewhere on at least thorax. Cruciform pores absent. Antennae apparently 1 segmented. Frontal lobes and antennal tubercles both absent. Mouthparts with a pair of large apodemes arising from tentorial box, at least on old adults. Labium probably 2 segmented. Spiracles large. Pro- and mesothoracic legs absent; metathoracic legs represented by a pair of short membranous protuberances; translucent pores absent. Position of vulva unclear.

Known only from Myrtaceae.

Comment. *Carpochloroides* currently contains 2 species, *C. mexicanus* Ferris from Mexico and the type species from Brazil. We have only examined the type species. *Carpochloroides* is similar to some other genera of South American eriococcids such as *Capulinia* and *Apiococcus* but differs in having the following combination of characters: (i) enlarged apodemes attached to the tentorial box (also present on *Aculeococcus* and *Tectococcus* – but see “Comment” under the adult female below); (ii) a reticulate pattern on the derm, each reticulation with a pore or duct in its center, and (iii) reduction of the antennae to either a indistinct tubercle or completely absent. According to Gullan *et al.* (2005), only *C. mexicanus* induces galls; in this case, on the petioles.

Carpochloroides viridis Cockerell

Carpochloroides viridis Cockerell, 1899: 12–13.

Material examined: No data but labelled *Carpochloroides viridis* Cockerell, Cornell University No. 981 (USNM): 2/2adff (1 in fair condition, other poor) + 1/6 first-instar nymphs, many in egg membranes (mostly in poor condition; because of the size of the dorsal setae, many other structures hard to discern with certainty). Slides that were acquired with the Cockerell Collection are labelled as this species, “Co-type, on *Eugenia*, Brazil, Cockerell Coll.” (USNM): 1/1 adf (in poor condition) and 1/12 first-instar nymphs (in fair condition) + 1/9 first-instar nymphs (good condition). On *Eugenia*, Ypiranga, Brazil, Hempel (USNM): 1/1 adf (fair condition, but rather distorted) + 8 first-instar nymphs (in poor condition), + 1/1 adm (in fair to good condition but wings distorted and only 1 antenna complete) + 1/7 first-instar nymphs (fair condition). True type material not seen, but slides from the Cockerell Collection could be from the type series. Type collection data: Brazil, Sao Paulo, Campinas, on *Eugenia* sp. (Myrtaceae), -ix.1898, F. Noack.

Adult female (Fig. 12)

Unmounted material. “Adult females, as seen alive, clear green, in form and colour very much like the young fruits of *Eugenia*.” (Cockerell, 1899).

Mounted material. Body apparently globular, derm entirely membranous. Length 4–6 mm, width 4–6 mm. No body segmentation visible and without any indications of a margin; apparently without pro- and mesothoracic legs; metathoracic legs and antennae reduced to small prominences.

Dorsum. Derm membranous but with a faint pattern of quite large reticulations probably throughout most of dorsum and on areas laterad to spiracles. Dorsal setae all finely spinose, each 25–35 μm long, with broad basal sockets; very sparse, perhaps most abundant posteriorly on abdomen. Macrotubular ducts absent. Microtubular ducts rather small, each outer ductule 5–7 μm long (rather shorter than those found ventrally),

apparently without an inner filament; relatively sparse, with 1 in most dorsal reticulations but perhaps absent posteriorly in areas with loculate pores. Loculate pores with 3–5 (mainly 5) loculi, each 5 μm wide, with 1 per reticulation over a broad area anterior to anal ring. Anal lobes entirely absent; with a group of about 3 setae on each side of anus, but without any clearly defined anterior or posterior suranal setae. Median lobe absent. Anal opening in centre of a sclerotised ring, without setae or pores; outer diameter of sclerotised ring about 25 μm wide; actual opening oval, about 18 μm wide and 5 μm long.

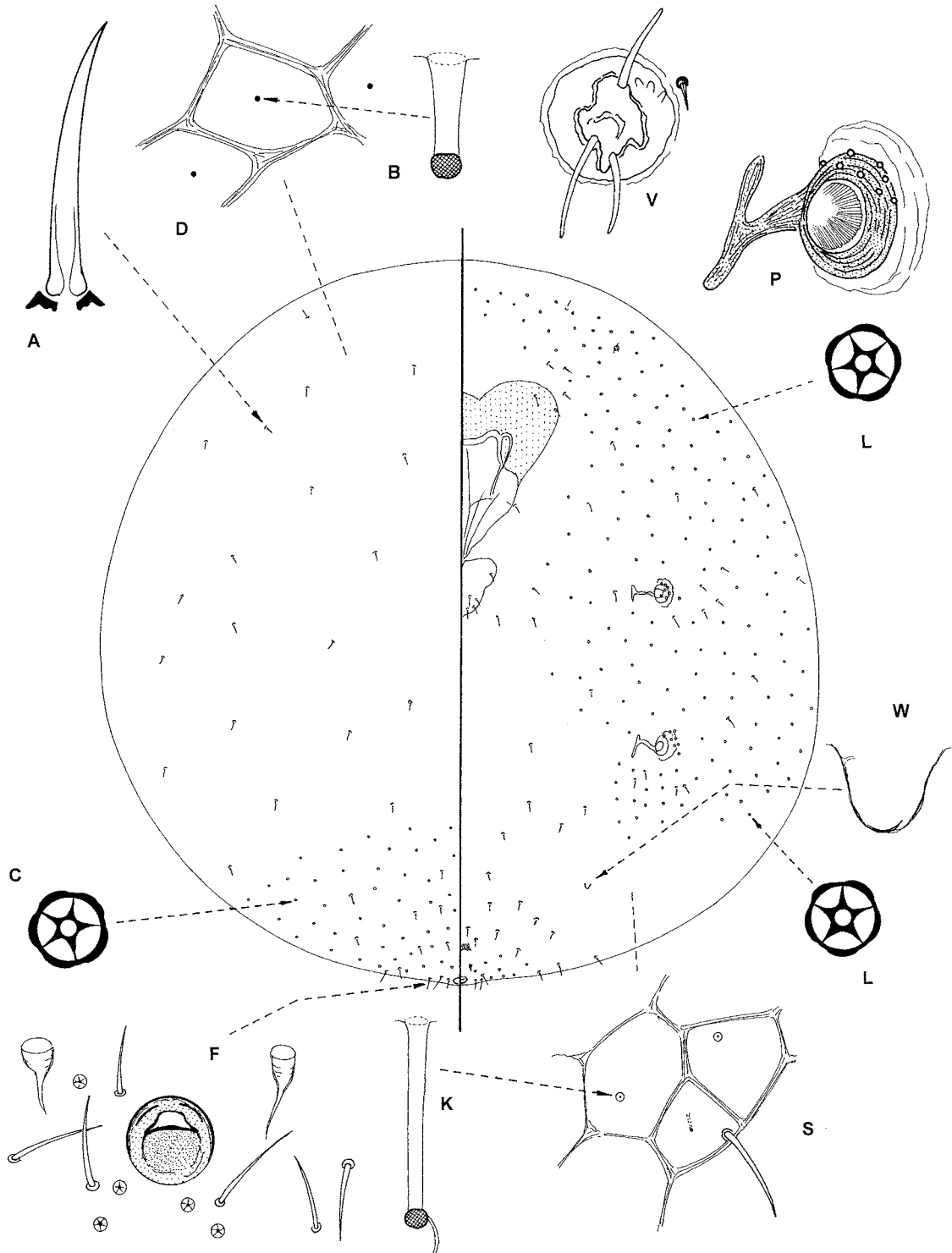


FIGURE 12. *Carpochloroides viridis* Cockerell. Adult female, where A = dorsal spinose seta; B = dorsal microtubular duct; C = dorsal loculate pore; D = derm showing reticulate pattern with microtubular ducts; F = view of anal area, K = ventral microtubular duct; L = ventral loculate pore; P = anterior spiracle; S = view of ventral derm showing reticulations, etc; V = antenna, and W = mesothoracic leg.

Margin. Undefined, without any setae differentiated from dorsal or ventral setae. However, approximate lateral margin of venter possibly indicated by absence of loculate pores. Eyespots not detected.

Venter. Derm membranous. Setae sparse and similar to those on dorsum; those posteriorly on abdomen possibly in transverse segmental rows but this not clear. Macrotubular ducts absent. Ventral microtubular ducts longer and narrower than those on dorsum; frequent throughout but perhaps less abundant medially posterior to labium. Loculate pores similar in structure to those on dorsum; exact distribution uncertain but apparently in a broad submarginal band which extends mesad to spiracles but absent medially on thoracic and most abdominal segments but with a few pores present just anterior to anus; also with a small group of 7–9 on fleshy margins of spiracular cavity.

Antennae roundish (about 28 μm wide), mildly sclerotised, apparently 1 segmented, with perhaps 3 fleshy setae but structure hard to determine; with a short stout spinose seta laterad to base. Clypeolabral shield large, about 275 μm long, but mouthparts with (barely present on female labelled from Ypiranga on oldest specimens) 2 large internal, sclerotised plate-like apodemes extending anteriorly from anterior margin of the tentorial box, each about 175 μm long and total width about 500 μm ; labium probably 2 segmented, with perhaps 5 pairs of setae. Spiracles large, with a wide, strong ventral valve, each in a fairly deep cavity: width of peritremes 90–92 μm . Pro- and mesothoracic legs absent; metathoracic legs represented by a pair of short membranous protuberances, each about 15 μm wide and 8 μm long (not detected on female labelled from Ypiranga); with little sign of any segmentation and no setae or translucent pores; located about mid-way between posterior spiracles and anus. Vulva present a short distance anterior to anus. Also with a pair of small, cone-shaped tubular structures located just anterolaterally to anus, each broadest on derm surface (where duct about 6–8 μm wide), each about 10–12 μm long ending distally in a filamentous inner ductule (not detected on female labelled from Ypiranga).

Comment. The function of the small cone-shaped tubular structures anterolateral to the anus is unknown but similar structures have been noted previously on the adult females of *Pseudotectococcus anonae* Hempel and *P. rollinae* Hodgson & Gonçalves (Hodgson *et al.*, 2004), which also are gall-inducing eriococcids from South America.

The apodemes associated with the mouthparts probably become more sclerotised with age, as they are barely visible on the youngest specimen. This almost certainly also applies to other species in which these apodemes have been noted, i.e. *Aculeococcus morrisoni* and *Tectococcus ovatus*.

For a comparison of the adult female of *Carpochloroides* with other eriococcid genera, see the “Comment” section after the generic diagnosis of *Carpochloroides*.

First-instar nymph (gender not determined) (Fig. 13)

Unmounted material. Not seen.

Mounted material. Body oval, slightly more pointed posteriorly. Length about 320–410 μm , width 140–160 μm (but venter perhaps slightly wider).

Dorsum. Derm membranous, without obvious dermal spinules. Dorsal setae strongly spinose; many very long, broadest basally and gradually narrowing to a sharp point, highly variable in length but those medially much longer (longest each 75–100 μm and shortest 15–50 μm), with a narrow basal socket, distributed as follows: mainly in 4 medial lines, with 2 pairs (outer much shorter than inner pair) on abdominal segments I and on pro-, meso- and metathorax and posteriorly on head + 1 pair medially on head; also with submarginal setae as follows: 1 on each side of abdominal segment I, 1 pair on each side of meso- and metathorax but none on prothorax (outer seta of each pair much longer than inner seta); also 1 submarginally on each side near posterior margin of head and 2 submarginally on anterior margin. Other types of setae absent. Discoidal pores (probably modified microtubular ducts) appearing as dark spots, probably representing a sclerotised dermal ring: with single ducts submarginally on abdominal segments III–VI, and submedially on pro-, meso- and metathoracic segments, plus another submedially on head. Loculate pores and macrotubular ducts absent. Anal lobes absent or rounded, membranous; each with a very long, flagellate apical seta about 300+ μm long; marginally with 2 pairs of spinose setae between long apical setae, outer pair 20–30 μm long, inner pair about 8–13 μm long.

Margin. Marginal setae strongly spinose, similar in shape to those on dorsum, rather variable in length, each 25–70 μm long; with 4 between eyespots, 4 or 5 on each side between eyes and point opposite anterior spiracles, 4 or 5 on each side laterally between anterior spiracles and abdomen and with 1 on each side of abdominal segments I–VII. Eyespots rather pronounced, each 13–15 μm wide, situated on margin near base of antennae.

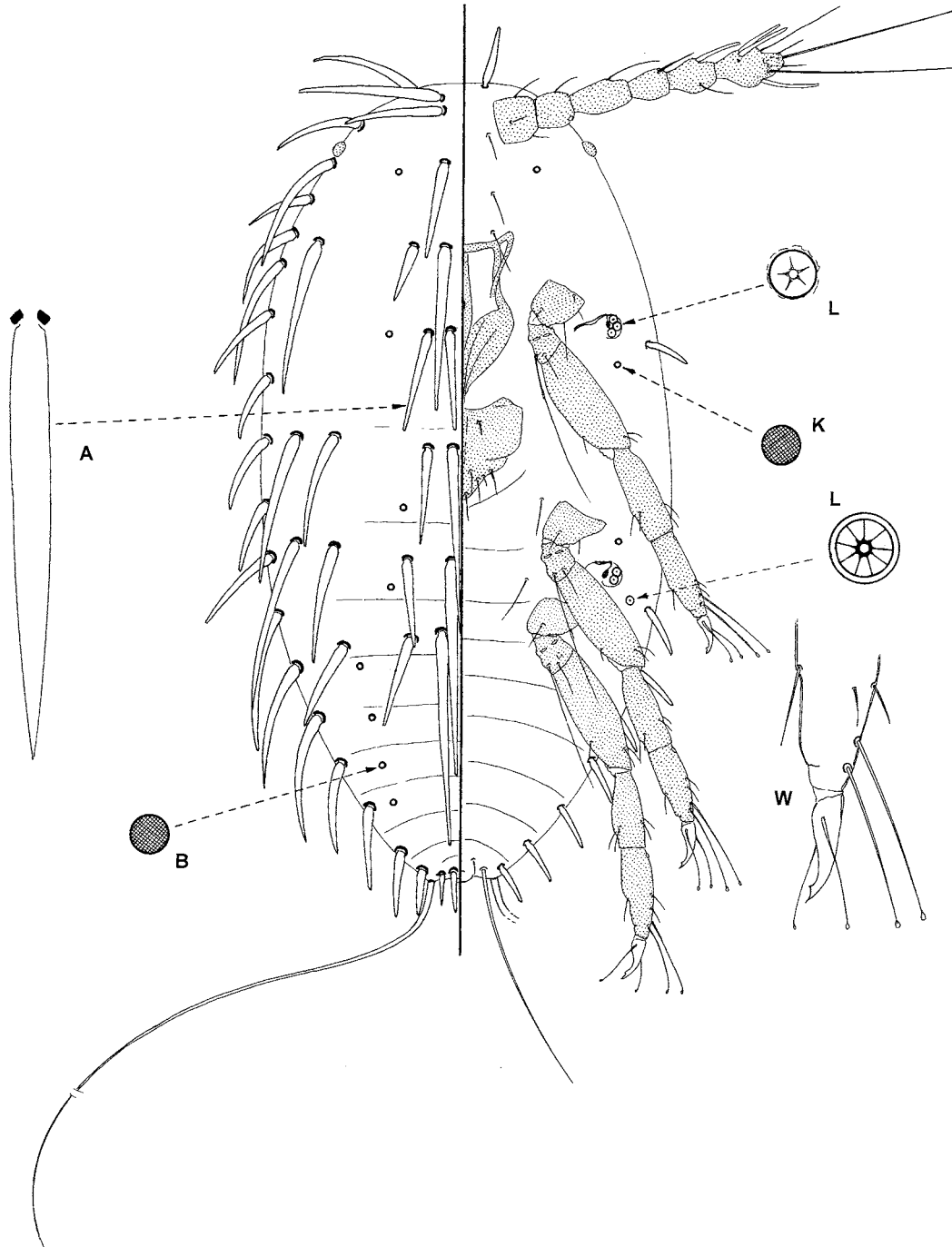


FIGURE 13. *Carpochloroides viridis* Cockerell. First-instar nymph, where A = dorsal spinose seta; B = dorsal discoidal pores; K = ventral discoidal pores; L = ventral loculate pores, and W = distal end of metathoracic leg.

Venter. Derm membranous. With 3 pairs of long setae between antennae plus pairs mesad of meso- and metacoxae, each about 30–35 μm long; no setae present medially on abdominal segments I–VII. Submarginal setae strongly spinose, similar to marginal setae but smaller, each 13–30 μm long; with a pair on each side of

abdominal segments I–VII, 1 on each side of thorax and 1 pair anteriorly on head. Discoidal pores apparently similar in structure to those on dorsum, with single pore anterior to each posterior spiracle, posterior to each anterior spiracle and posterior to each scape. Loculate pores probably with mainly 5–7 loculi: with 2 or 3 immediately laterad of each peritreme, in a small cavity, plus 1 postero-laterally to each posterior peritreme near margin. Anus slightly oval, membranous, width perhaps 13–16 μm ; without an anal ring or anal ring setae; with 1 small seta on each side, each about 10–12 μm long, plus a much longer seta, 80–100 μm long.

Antennae 6 segmented, 124–128 μm long; setal distribution: scape 3; pedicel 1 + campaniform sensillum; segments III and IV 1 hair-like seta; V 2 setose seta + 1 fleshy seta; VI 3 fleshy setae, 5 short setose setae plus 2 long setae, length of longest about 80–90 μm . Clypeolabral shield about 70–105 μm long; labium 2 segmented; about 50 μm wide, with possibly 5 pairs of short setae on apical segment and 1 pair on proximal segment. Spiracles small, peritremes possibly 5 μm wide, each with a lateral membranous cavity with loculate pores, cavity about 14–17 μm wide. Legs well developed; lengths (metathoracic leg (μm)): coxa 35–45; trochanter + femur 65–80; tibia 38–50; tarsus 33–45; claw 17–23; setae: coxae 2 or 3, trochanter 2, femur 3, tibia 4, tarsus 3; long trochanter seta 65–70 μm long; tarsal campaniform sensillum present; claw with a distinct denticle; both tarsal digitules on all legs capitate and equal in size; claw digitules alike with small capitate apices.

Comment. The first-instar nymphs of *C. viridis* are immediately recognisable by the extremely long spinose setae on the head, thorax and anterior abdominal segments, almost all of which are longer than the width of a segment. In addition, they have: (i) 6-segmented antennae; (ii) discoidal pores (probably modified microtubular ducts) on both dorsum and venter; (iii) anal lobes not differentiated and unsclerotised; (iv) loculate pores restricted to a cavity laterad to each spiracle (apart from 1 pore just posterior to each posterior spiracle); (v) no cruciform pores, (vi) no median anal plate; and (vii) dorsal setae of just 1 type. The first-instar nymph of *Exallococcus laureliae* Miller & González also has rather large dorsal spinose setae but these are much shorter than on *C. viridis*, and it also differs in having: (i) the anal lobes differentiated and sclerotised; (ii) loculate pores in a fairly wide longitudinal band ventrally; (iii) cruciform pores; and (iv) a median anal plate.

Adult male (Fig. 14)

Unmounted material. Not seen.

Mounted material. Total body length 1.3 mm; width across triangular plates 360 μm . Antennae quite long, about 2/3rds total body length; capitate setae only present on apical segment. Body rather setose, almost all fleshy setae (fs); fleshy setae (fs) long and rather similar to hair-like setae (hs). Pores absent. Wings perhaps slight shorter than total body length; without alar setae or alar sensory pores. Hamulohalteres absent.

Head: approximately rather square oval, broadest across genae; length about 230 μm , width across genae about 220 μm . Dorsally, median crest (mc) not demarcated and not reticulated but with a short, indistinct mid-cranial ridge (dmcr), not reaching postoccipital ridge posteriorly; postoccipital ridge (por) indistinct, with arms extending only laterally; with (on each side) about 10 fs dorsal head setae (dhs); pores absent. Ventral mid-cranial ridge (vmcr) quite short and narrow, extending from lateral arms (lmcr) posteriorly almost to ocular sclerite (ocs); without any reticulation laterally. Genae (g) not reticulated; each with 12–14 fs genal setae (gs). Eyes: with 2 pairs of round, simple eyes; dorsal eyes (dse) placed rather anteriorly, above each scape, each about 35–37 μm wide; ventral simple eyes (vse) placed quite far posteriorly, each about 40–43 μm wide. Ocelli (o) large, situated laterally, each about 16 μm widest, just touching postocular ridge and with an extension up dorsal margin. Ocular sclerite (ocs) only partially sclerotised, particularly around and between simple eyes; lightly reticulated around each vse. Preocular ridge (procr): short both dorsally and ventrally, latter possibly extending to anterior to each vse. Postocular ridge (pocr) strongly developed, extending posteroventrally from near dmcr postero-laterally past each ocellus to neck region. Interocular ridge probably absent. Dorsal ocular setae absent. Ventral mid-cranial ridge setae (vmcrs) 1–3 fs on each side; ventral head setae (vhs): with 6–9 fs + 2–9 hs on each side just anterior to and laterad of each vse, plus about 7 hs medially posterior to vse. Preoral ridge (pror) absent. Cranial apophysis (ca) not detected.

Antennae: 10 segmented and filiform; about 875 μm long (ratio of total body length to antennal length 1:0.67). Fleshy setae several times longer than width of flagellar segments, each about 65–75 μm long. Scape

(scp) 50 μm long and 66 μm wide, with 3 fs + 2 hs. Pedicel (pdc) 60 μm long, 54 μm wide; with a few faint concentric ridges, mainly on distal half; with 6 hs + 16 fs; no campaniform pore detected. Segments III–X each about 16–25 μm wide; lengths of segments (μm): III 128; IV 95; V 112; VI 125; VII 103; VIII 75; IX 75 and X 70; approximate number of setae per segment: III–IX 16–20 fs + 0–3 hs; VIII & IX both with 1 antennal bristle, and segment X with 13 fs, 3 hs, 3 or 4 large + 2 smaller antennal bristles + 3 capitate setae (caps); sensilla basiconica not detected.

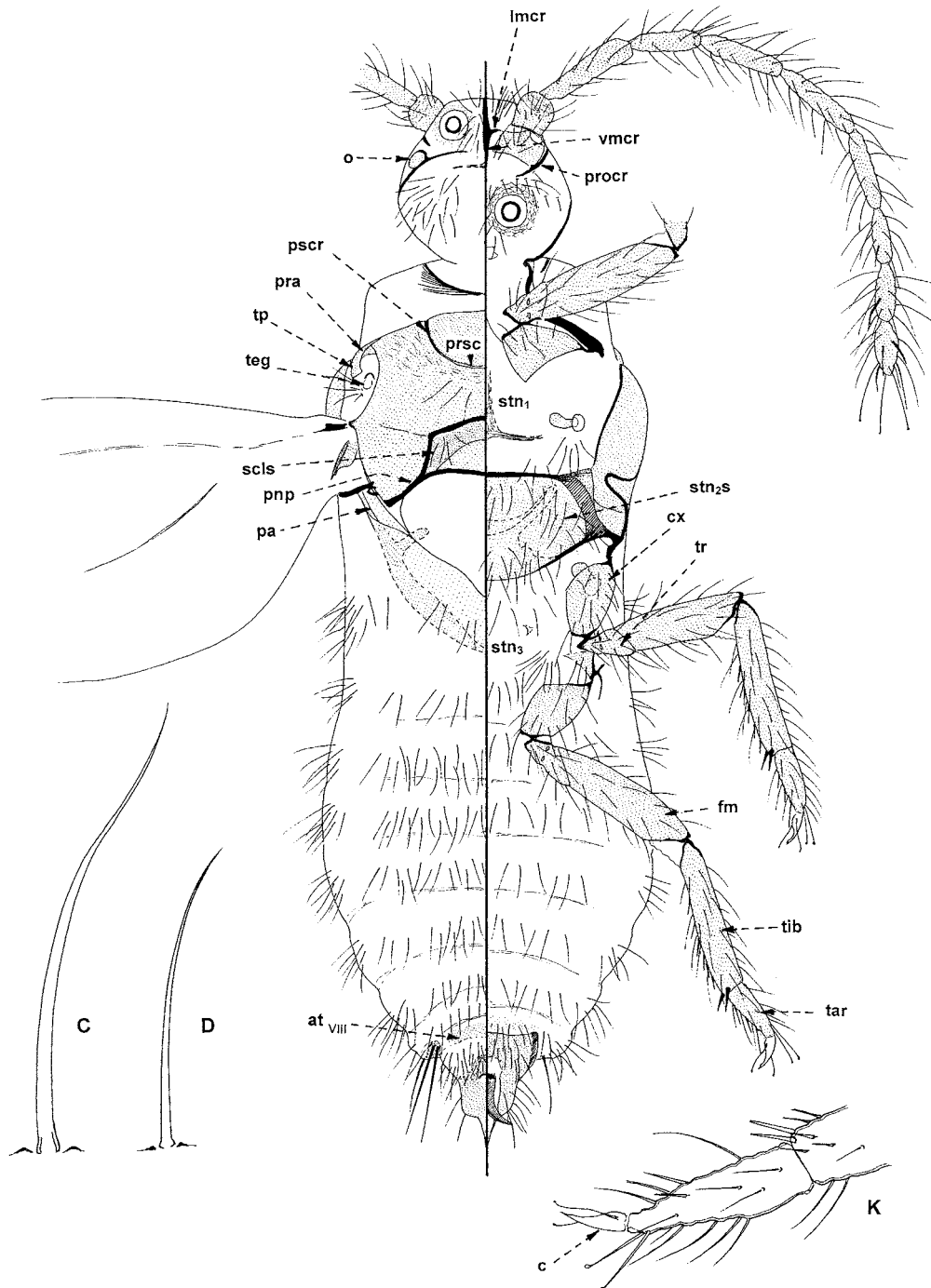


FIGURE 14. *Carpochloroides viridis* Cockerell. Adult male, where C = fleshy seta; D = hair-like seta, and K = distal end of metathotactic leg. For other abbreviations, see under ‘Figure captions’ on p.5.

Thorax. Prothorax: pronotal ridge (prnr) well-developed but not fused dorsally; pronotal sclerite (prn) represented by a large triangular area dorsolaterally; without lateral pronotal setae (lpns). Medial pronotal setae absent; post-tergite not detected, without post-tergital setae or pores. Sternum (stn₁) lightly sclerotised,

with a distinct median and transverse ridge; without prosternal setae (stn_1s) or pores. Anteprosternal setae ($astn_1s$) absent.

Mesothorax: prescutum ($prsc$) oval, 70 μm long, 130 μm wide; sclerotised but not reticulated, without prescutal setae; prescutal ridge ($pscr$) well developed anteriorly but quickly narrowing; prescutal suture ($pscs$) present. Scutum (sct): median area without unsclerotised areas; distance of prescutum from scutellum about 70 μm ; scutal setae ($scts$) few, perhaps 4 hs on each side; lateral margins with faint ridging laterad to prescutum; prealare (pra) and triangular plate (tp) well developed. Scutellum (scl) 170 μm wide and 75 μm long; with a distinct scutellar ridge but no foramen; scutellar setae ($scls$): 3 or 4 fs on each side; postnotal wing process (pnp) relatively narrow but broadening laterally. Basisternum (stn_2) 255 μm wide and 135 μm long; without a median ridge; bounded anteriorly by a strong marginal ridge (mr), very broad antero-laterally, and with strong precoxal ridges (pcr_2); with about 50 fs basisternal setae (stn_2s); lateropleurite (lpl) broad, with a distinct extension from marginal ridge along anterior margins; furca (f) well developed, narrow-waisted, arms very divergent and extending almost to marginal ridge anteriorly. Mesopostnotum (pn_2) well developed; postnotal apophysis (pna) well developed. Area bounded anteriorly by scutellum and laterally and posteriorly by mesopostnotum not sclerotised. Mesepisternum (eps_2) not reticulated; subepisternal ridge (ser) long and well developed. Postalare (pa) without postalare setae (pas). Mesothoracic spiracle (sp_2): width of peritreme 30 μm , without associated loculate pores. Postmesospiracular setae (pms) 4–7 fs + 1–3 hs on each side. Tegula (teg) present, with about 3 fs + 2–4 hs tegular setae ($tegs$).

Metathorax: with perhaps 4 fs metatergal setae (mts) on each side and 2 fs laterally on each side; metapostnotal sclerite (pn_3) not detected. Dorsospiracular setae (dss) about 11 fs on each side. Dorsal part of metapleural ridge (plr_3) absent; ventral part of metapleural ridge well developed; metepisternum (eps_3) sclerotised, each with 3 fs postmetaspiracular setae (eps_3s) plus 6 fs in a group slightly more medially; precoxal ridge (pcr_3) absent; metasternal apophysis (st_3a) present. Metepimeron (epm_3) sclerotised, but without setae. Antemetaspiracular setae absent. Metathoracic spiracle (sp_3): width of peritreme 32 μm , without loculate pores. Metasternum (stn_3) membranous, with about 12 fs anterior metasternal setae ($amss$) and 7 fs + 2 hs posterior metasternal setae ($pmss$).

Wings: both misshapen; hyaline, maybe 1075 μm long; width unknown; alar lobe (al) probably absent; alar setae absent; circular sensoria absent. Hamulohalteres absent.

Legs: mesothoracic leg shortest. Fleshy setae (fs) present on all segments, each as long as on body; setose but with many setae broken and therefore fs and hs not distinguishable. Coxae (cx): I 120; II 108; III 116 μm long; long setae on each coxa not differentiated. Trochanter (tr) + femur (fm): I 245; II 225; III 245 μm long; each trochanter with 2 campaniform sensoria on each side in a line; long trochanter seta not differentiated. Tibia (tib): I 205; II 205; III 205 μm ; some setae spur-like on distal half; with 2 apical spurs ($tibs$) on all legs; length of longest 20–25 μm . Tarsi (tar) 1 segmented, length: I 80; II 85; III 85 μm long (ratio of length of tibia III to length of tarsus III 1:0.41); tarsal spurs differentiated, each about 25 μm long; tarsal campaniform pore present; tarsal digitules (tdt) capitate, slightly shorter than claw. Claws (c) subequal to or slightly longer than width of tarsus; length III: 30 μm ; with a small denticle; claw digitules (cdt) with small capitate apices and slightly longer than claw.

Abdomen: segments I–VII: tergites and sternites unsclerotised and without obvious oval membranous areas in inter-segmental membranes. Caudal extension (ce) of segment VII absent. Without loculate pores. Dorsal setae (ads) almost all fs , each about 50 μm long, in bands of about 16–20 across segments; pleural setae: dorsopleural setae (dps) all fs in groups of about 10–15 on each side; ventropleural setae (vps) all or mainly fs , in a small group of about 4 setae, but these often joined to dps ; ventral setae (avs) sparser than ads , mainly fs , each slightly shorter, about 40 μm long.

Segment VIII: both tergite (at) and sternite (as) sclerotised in transverse bands; tergite with about 30 fs ads , extending full width of segment; sternite with about 20 fs avs across segment; caudal extension (ce) rounded, each with about 14 or 15 fs + 1 hs pleural setae, 1 rather longer (about 60 μm long) and stouter than other setae. Glandular pouches (gp) present, moderately deep, each with loculate pores restricted to within pouch; each with 2 non-capitate setae (gls) about 120 μm long.

Genital segment [note: segmentation in description below speculative!]: apparently divided into 2 sections: (i) a broad anterior part (probably representing segment IX) and a short, triangular posterior section; anterior part about 140 µm wide at base and about 60 µm long; dorsally perhaps not heavily sclerotised with about 30 fs extending across segment and with an oval area medio-posteriorly with about 9 long hs ante-anal setae (aas) and with anal opening present along posterior margin; ventrally, anterior part (segment IX) probably heavily sclerotised, particularly near lateral margins, with about 8 fs on each side and about 9 hs on either side of central indentation. Penial sheath (ps) proper (posterior part) pointed but slightly constricted near mid-length; 70 µm wide at base and 90 µm long; with 7–9 long setae (pss) on each side, apparently restricted to ventral and lateral margins. Basal rod (bra) very short, about 10 µm long. Aedeagus C-shaped, scythe-like, total length perhaps 65 µm. Tip of penial sheath with a few minute pores (psp).

Comment. The adult male of *C. viridis* can be separated from the other known male eriococcids from the Neotropics in having the following combination of characters: (i) 10 segmented antennae, with fleshy setae clearly longer than width of antennal segments; (ii) very short penial sheath, length subequal to basal width; (iii) hair-like and fleshy setae all long, rather similar and hard to separate; (iv) tarsi all 1 segmented; and (v) dorsal abdominal setae more abundant than ventral abdominal setae (other way round on all other species). In having only 1-segmented tarsi, the male of *C. viridis* is unusual for Eriococcidae. The only other adult male eriococcid known to the authors with well-developed legs which appears to have a 1 segmented tarsus are *Opisthoscelis verrucula* Froggatt and *Cylindricoccus spiniferus* Maskell, both from Australia but these two species are gall-inducing and have a very long thin abdomen. However, *O. verrucula* also shares with *C. viridis*: (i) long fleshy setae all over its body; (ii) lacks a hamulohaltere; and (iii) has capitate setae on the antennae restricted to the apical segment. The adult male of *C. spiniferus* has very few setae but also lacks hamulohalteres and has capitate setae restricted to the apical antennal segment (Gullan, 1978).

***Chilechiton* Hodgson & Miller**

Chilechiton Hodgson & Miller, 2002: 195–198.

Type species: *Chilechiton lynnae* Hodgson & Miller, 2002: 198–200.

Generic diagnoses. Adult female (Fig. 15). *Dorsum*. Body nearly round; derm membranous. Setae of enlarged type only; setose setae lacking. Macrotubular ducts absent. Microtubular ducts with long outer ductule. Loculate pores absent. Anal lobes represented by 2 heavily sclerotised, plate-like anal lobes, together quadrate; withdrawn onto dorsal surface; each lobe with microtubular ducts, 4 enlarged setae on margins and C-shaped or irregular indentations on dorsal surface. Median plate present. *Margin*. Marginal enlarged setae similar to setae on dorsum but generally smaller; margin of anal cleft without marginal setae. Anal ring located between anal lobes, with 2 incomplete rows of pores and 8 basally enlarged setae. Anal cleft present. *Venter*. Derm membranous. Setae all hairlike; suranal setae unmodified. Macro- and microtubular ducts absent. Loculate pores each usually with 5 loculi; present in medial and mediolateral areas of abdomen. Cruciform pores absent. Preantennal tubercles present; frontal lobes absent. Antennae each 6 segmented. Labium 3 segmented; basal segment very small, represented by a small sclerotised plate partially or completely fused with second segment, bearing 1 or 2 pairs of setae. Legs well developed, large translucent pores present on metacoxae and femur; tibia shorter than tarsus; claw digitules with 1 conspicuously swollen, other about same size as a tarsal digitule. Opening of vulva situated between segments VI and VII.

Known only from Nothofagaceae.

Comment. The adult females of *Chilechiton* have several unusual or unique features, namely: (i) vulva between abdominal segments VI and VII (only shared by *Icelococcus* and perhaps *Neotectococcus*); (ii) spinose setae in a dense line around margin, each rather clearly differentiated from dorsal spinose setae; and (iii) C-shaped markings on the dorsal surface of each anal lobe.

First-instar nymph (gender not determined) (Fig.16)

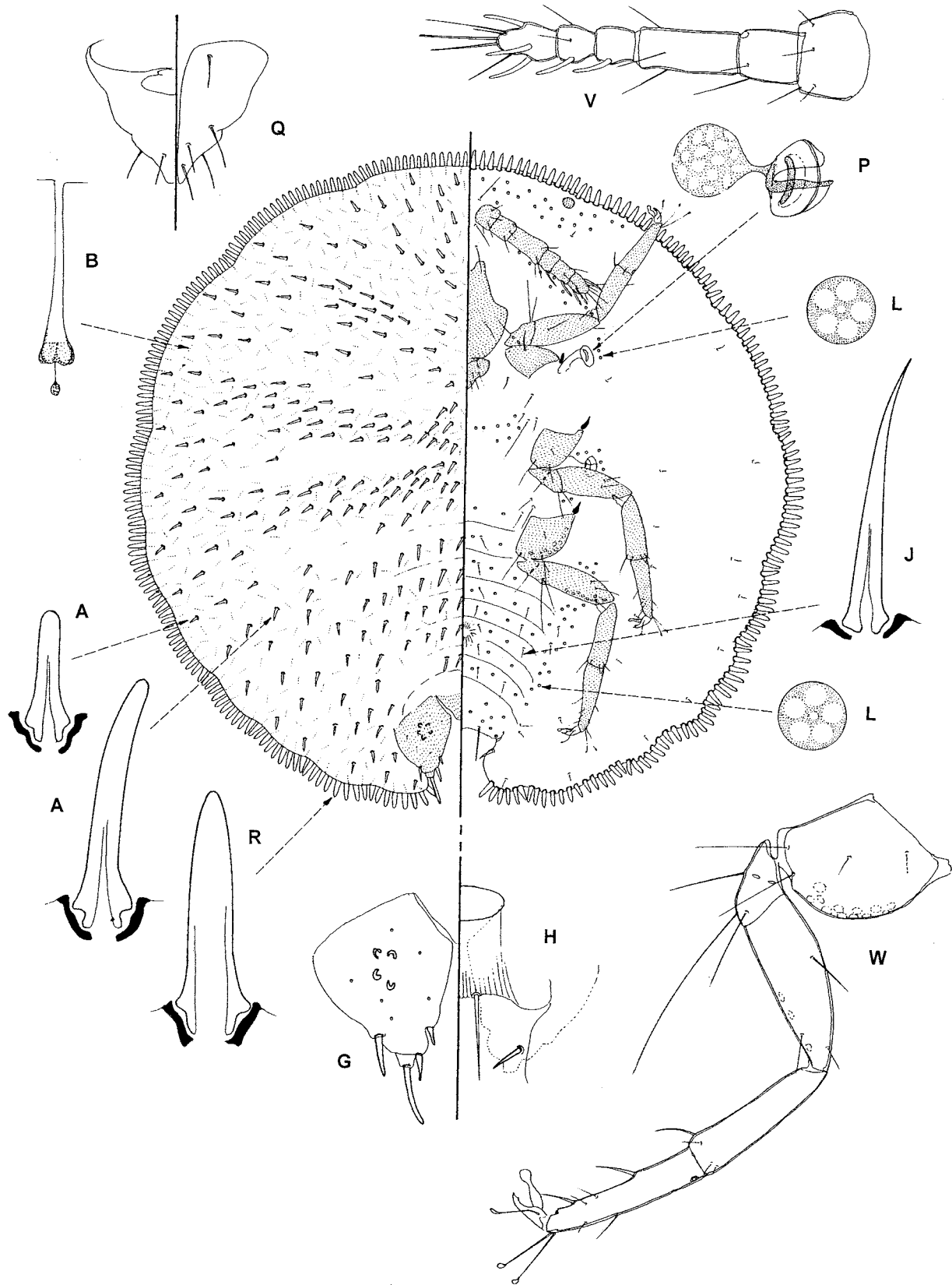


FIGURE 15. *Chilechiton lynnae* Hodgson & Miller. Adult female, where A = dorsal spinose setae; B = dorsal microtubular duct; G = dorsal view of anal plate; H = ventral view of anal plate; J = ventral loculate pores; L = ventral loculate pores; P = anterior spiracle; Q = labium; R = marginal spinose seta; V = antenna and W = metathoracic leg (modified after Hodgson & Miller, 2002).

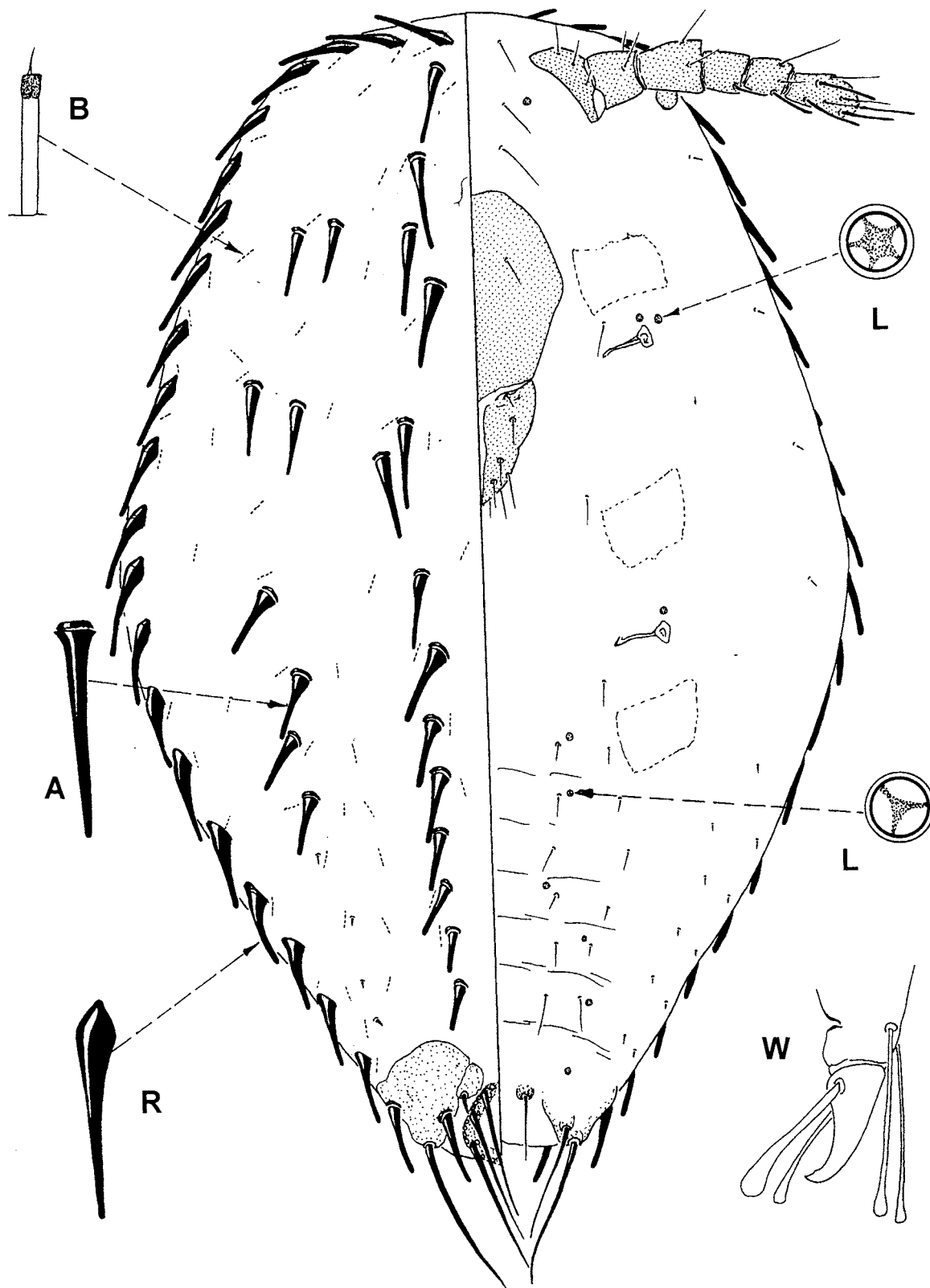


FIGURE 16. *Chilechiton lynnae* Hodgson & Miller. First-instar nymph, where A = dorsal spinose seta; B = dorsal microtubular duct; R = marginal spinose seta; L = loculate pores, and W = claw (modified after Hodgson & Miller, 2002).

Diagnosis (from embryos). *Mounted material*. Body oval. *Dorsum*. Enlarged setae (excluding marginal setae) straight or slightly curved, of 2 sizes, arranged in 2 pairs of longitudinal lines, one pair submedial and one pair mediolateral; smaller setae present at posterior end of mediolateral line; large setae conspicuous, slightly longer than marginal setae. Macrotubular ducts absent. Microtubular ducts scattered. Loculate pores absent. Anal lobes platelike, each with a longitudinal fold; each also with two spinose setae on inner margin, one on outer margin + a longer apical; each lobe with 1 or 2 microtubular ducts and several C-shaped or irregular indentations. Medial plate absent. *Margin*. Marginal setae each slightly smaller than dorsal setae, curved, with enlarged setal base, apex slightly rounded, pointing posteriorly. Anal ring without anal tube but with pores and 6 anal-ring setae. *Venter*. Loculate pores few, restricted to mediolateral areas of abdomen, each with 3–5 loculi, plus 1 or 2 pores near each spiracle and each antennal base. Macrotubular and microtubular ducts absent. Cruciform pores absent. Suranal setae: both anterior and posterior pairs hairlike. Ventral setae arranged segmentally. Antennae 6 segmented. Labium 3 segmented, basal segment with 1 or 2 setae. Legs well developed, probably without pores; each with tibia shorter than tarsus; tarsal digitules slightly capitate; claw with denticle; claw digitules different, one with enlarged apex other narrow.

Comment. *Chilechiton* currently contains 1 species, known only from Chile. For a description of the adult female and first-instar nymph of *C. lynnae*, see Hodgson & Miller, 2002: 195.

***Chilecoccus* Miller & González**

Chilecoccus Miller & González, 1975: 132.

Type species: *Chilecoccus browni* Miller & González 1975: 132–134.

Generic diagnosis. Adult female (Fig. 17). On undersides of leaves. Body approximately round, widest across metathorax, more pointed posteriorly. *Dorsum*. Derm membranous, segmentation indefinite. Setae small, spinose, rather randomly abundant over surface. Macro- and microtubular ducts abundant. Loculate pores absent. Anal lobes usually ventral, flattened, heavily sclerotised, not protruding, each with 3 or 4 setae and 1 or 2 loculate pores. Anus usually lying ventrally, with an unusually broad sclerotised area surrounding opening containing setae and pores. *Margin*. Marginal setae of same size as adjacent spinose setae. *Venter*. Derm membranous. Setae on abdomen spinose except those in medial areas of head and thorax hairlike; spinose setae fairly abundant especially submarginally, where slightly smaller than those on dorsum. Macro- and microtubular ducts in submarginal and marginal areas, about same size as those on dorsum. Loculate pores usually with 5 loculi, arranged in distinct pattern, forming longitudinal line in submedial area of abdomen, several present medially on thorax, rare or absent from head. Cruciform pores absent. Antenna 6 segmented. Presence of frontal lobes uncertain, possibly absent; antennal tubercles absent. Labium probably 1 segmented. Legs each well-developed; metacoxa swollen, with numerous large pores on each surface, without microspinules; claw digitules equal in size and longer than claw. Vulva between segments VII and VIII.

Known only from Nothofagaceae.

Comment: *Chilecoccus* currently contains 2 species (the type species, *C. browni*, and *C. spinosus* Miller & González), both known only from Chile, neither of which are thought to induce galls. For a description of the adult female of *C. browni*, see Miller & González, 1975, p. 132.

Adult female *Chilecoccus* are characterised by: (i) flattened form of anal lobes; (ii) abundant small spinose setae on dorsum and submarginally on venter; (iii) presence of macrotubular ducts on both dorsum and venter; (iv) unusually large anal ring with 2 or 3 rows of pores; and (v) 3 segmented labium.

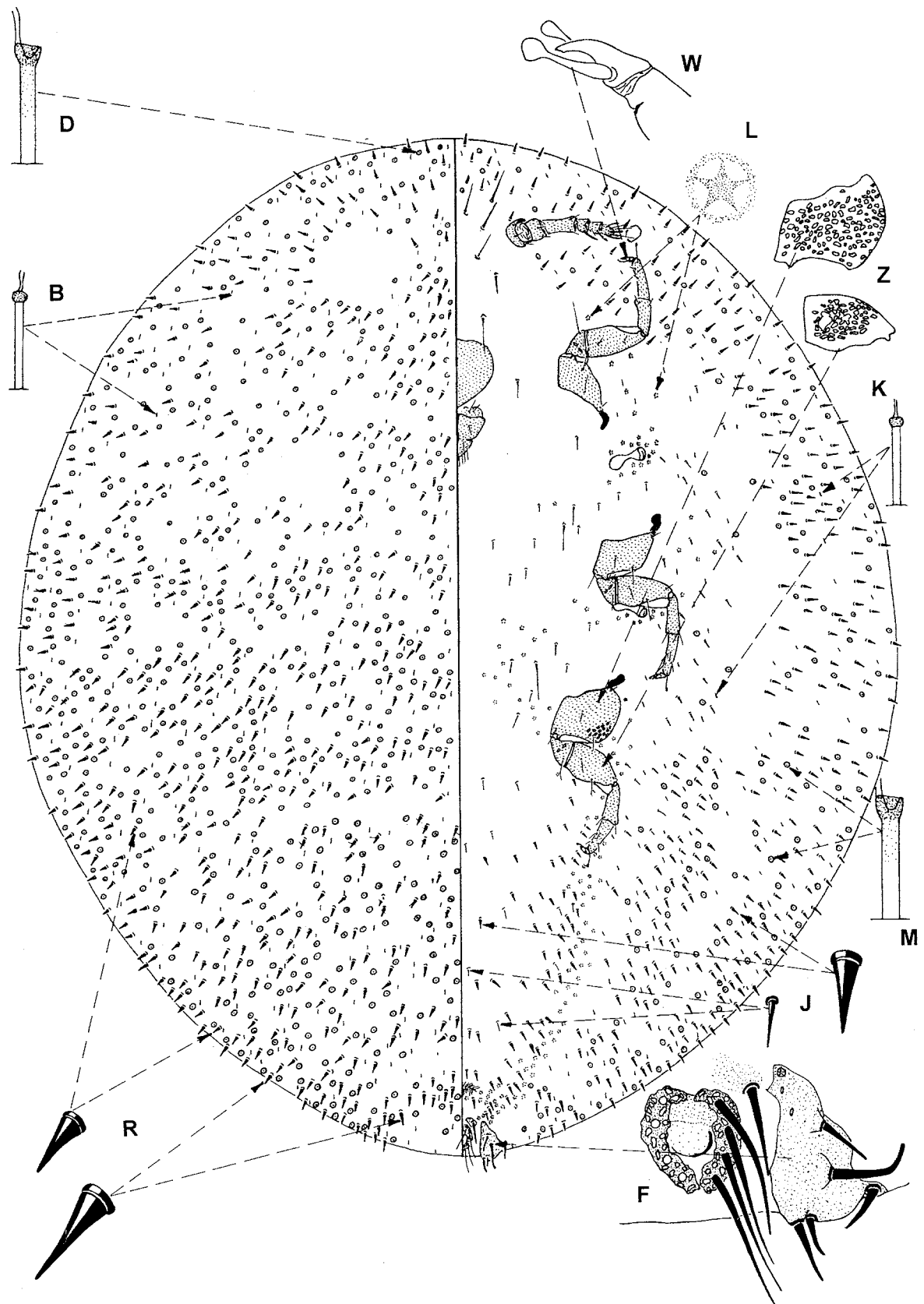


FIGURE 17. *Chilecoccus browni* Miller & González. Adult female, where B = dorsal microtubular duct; D = dorsal macrotubular duct; F = view of anal ring and anal lobe area with suranal seta; J = ventral setae; K = ventral microtubular duct; L = ventral loculate pore; M = ventral macrotubular duct; R = marginal spinose seta; W = claw of prothoracic leg, and Z = coxa and femur of metathoracic leg (modified after Miller & González, 1975).

Coxicoccus Kozár

Coxicoccus Kozár (in Kozár & Konczné Benedicty 2008: 118–119)

Type species: *Coxicoccus foldi* Kozár & Konczné Benedicty 2008: 119–121.

Generic diagnosis. Adult female (Fig. 18). *Dorsum*. With spine-like setae of more or less 1 size. Macrotubular ducts narrow, long, inner ductule ending in flower-like terminal gland; present throughout. Microtubular ducts long with bifurcate orifice, few but often associated with base of dorsal spinose setae. Anal lobes well developed, dorsal surface with 3 strong, curved spinose setae. Anal ring sclerotised, not well developed, with 8 setae, each twice as long as width of anal ring; anal ring pores few. Median plate absent. *Margin*. Not differentiated. *Venter*. Setae capitate on posterior abdominal segment; suranal setae also capitate and longer than length of anal lobes; ventral surface of each anal lobe with 1 short apical seta + a capitate subapical seta. Macrotubular ducts sparse throughout. Microtubular ducts submarginal. Cruciform pores absent. Loculate pores present medially, mainly on abdomen. Antennae 7 segmented. Frontal lobes and antennal tubercles absent. Labium 1 (?) segmented; basal segment with 1 pair setae. Legs long, tibia shorter than tarsus; all coxae with spinulae; metacoxae with small translucent pores. Vulva present between abdominal segments VII and VIII. (Modified after Kozár & Konczné Benedicty, 2008).

Host plant unknown.

Comment. Kozár & Konczné Benedicty (2008) state that this genus is close to *Eriococcus* and *Acanthococcus*. It resembles *Eriococcus* in having: (i) only 1 seta on basal segment of labium; (ii) long microtubular ducts with a bifurcate orifice; and (iii) in lacking cruciform pores. It differs in: (i) absence of enlarged tubular ducts; (ii) absence of frontal lobes; and (iii) presence of translucent pores on metacoxa, femur and tibia. It resembles *Acanthococcus* in having: (i) enlarged spine-like setae on dorsum; and (ii) micro- and macrotubular ducts; it differs in the absence of: (i) cruciform pores; (ii) frontal lobes; and (iii) a median plate, and presence of (iv) only 1 pair of setae on basal segment of labium. In addition, it differs from both genera in having clavate setae posteriorly on the venter. Note that the vulva lies between VII and VIII, not as illustrated in Kozár & Konczné Benedicty (2008).

Coxicoccus is a monotypic genus known only from Chile. For a description of the adult female of the type species, see Kozár & Konczné Benedicty (2008).

Eriobalachowskya Kozár

Eriobalachowskya Kozár (in Kozár & Konczné Benedicty, 2008: 121–123).

Type species: *Eriococcus valenzuelae* Balachowsky 1959: 363–365.

Generic diagnosis. Adult female (Fig. 19). Occuring on the leaves of *Inga* sp. in a coffee plantation. Body of adult female broadly oval, red, and covered with a pure white ovisac. *Dorsum*. Dorsal setae all spine-like, of rather variable size, each conical, with acute or slightly rounded apices. Macrotubular ducts absent. Microtubular ducts with a characteristically-shaped orifice, a long outer ductule and a filamentous inner ductule, common throughout. Anal lobes well developed, inner margins sclerotised and serrate; dorsal surface with 3 strong spinose setae; ventral surface with 4 setose setae. Anal ring sclerotised and well developed, with 8 anal ring setae, each twice as long as width of anal ring; anal ring pores few. Median plate rather large, of characteristic shape and sclerotised. *Margin*. Not demarcated. *Venter*. Setae of 2 types: (i) setose setae, each quite long, mainly present medially and submedially, and (ii) short spinose conical setae, much smaller than those on dorsum, present in large segmental clusters submarginally, and also submedially on thorax. Macro- and microtubular ducts absent. Cruciform pores numerous along margins. Quinquelocular pores frequent throughout. Antennae 8 segmented. Frontal lobes absent but antennal tubercles present. Labium 2 segmented, basal segment with 2 pairs of setae. Stylet loop long. Legs long, tibia shorter than tarsus; coxae of all legs with spinulae; posterior coxae with numerous translucent pores. Claw with denticle. (Modified after Kozár & Konczné Benedicty, 2008).

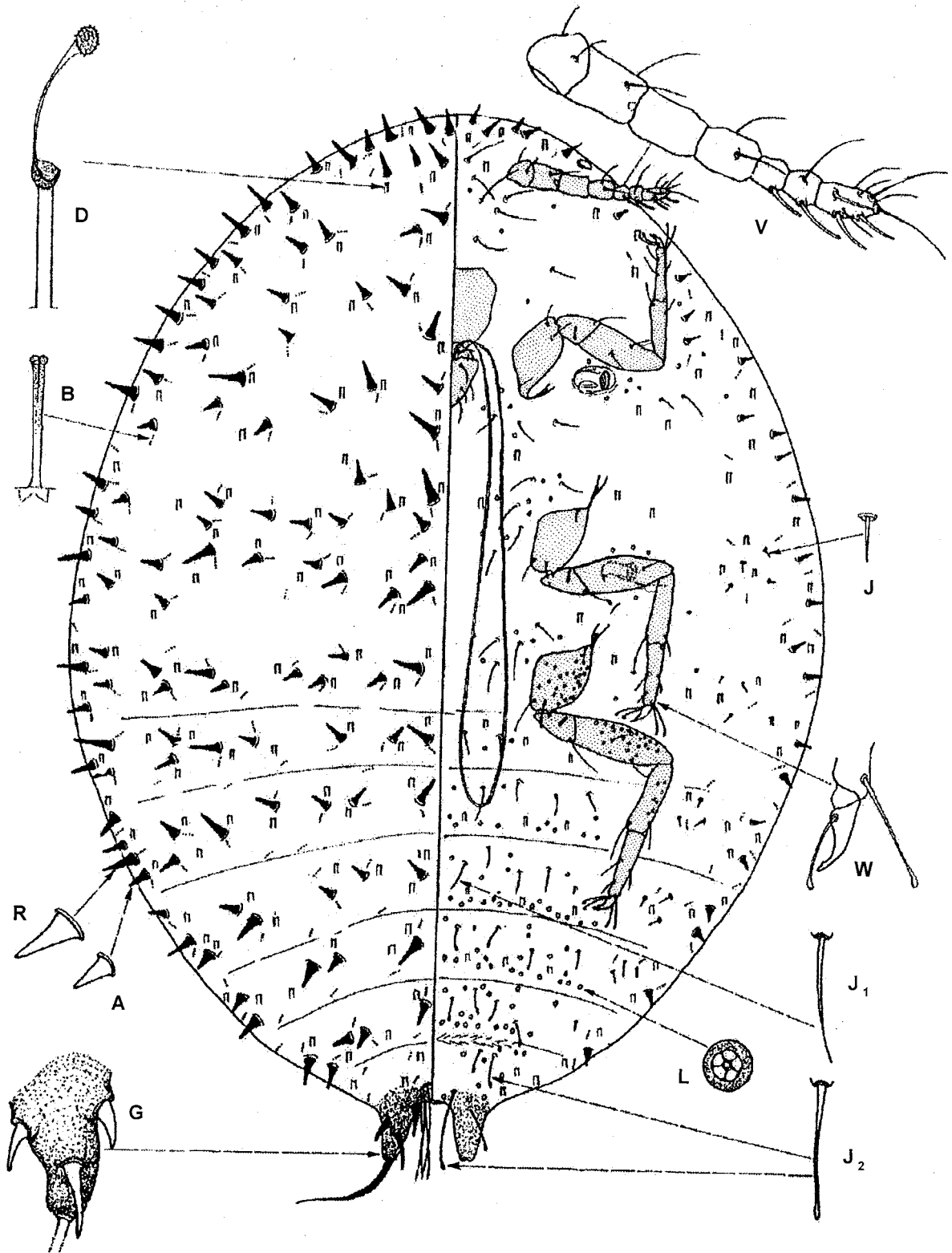


FIGURE 18. *Coxicoccus foldi* Kozár & Konczné Benedicty. Adult female, where A = dorsal spinose seta; B = dorsal microtubular duct; D = dorsal macrotubular duct; G = dorsal view of anal plate; J, J₁, J₂ = ventral setae; L = ventral loculate pore; R = marginal spinose seta; V = antenna, and W = claw of mesothoracic leg (modified after Kozár & Konczné Benedicty, 2008).

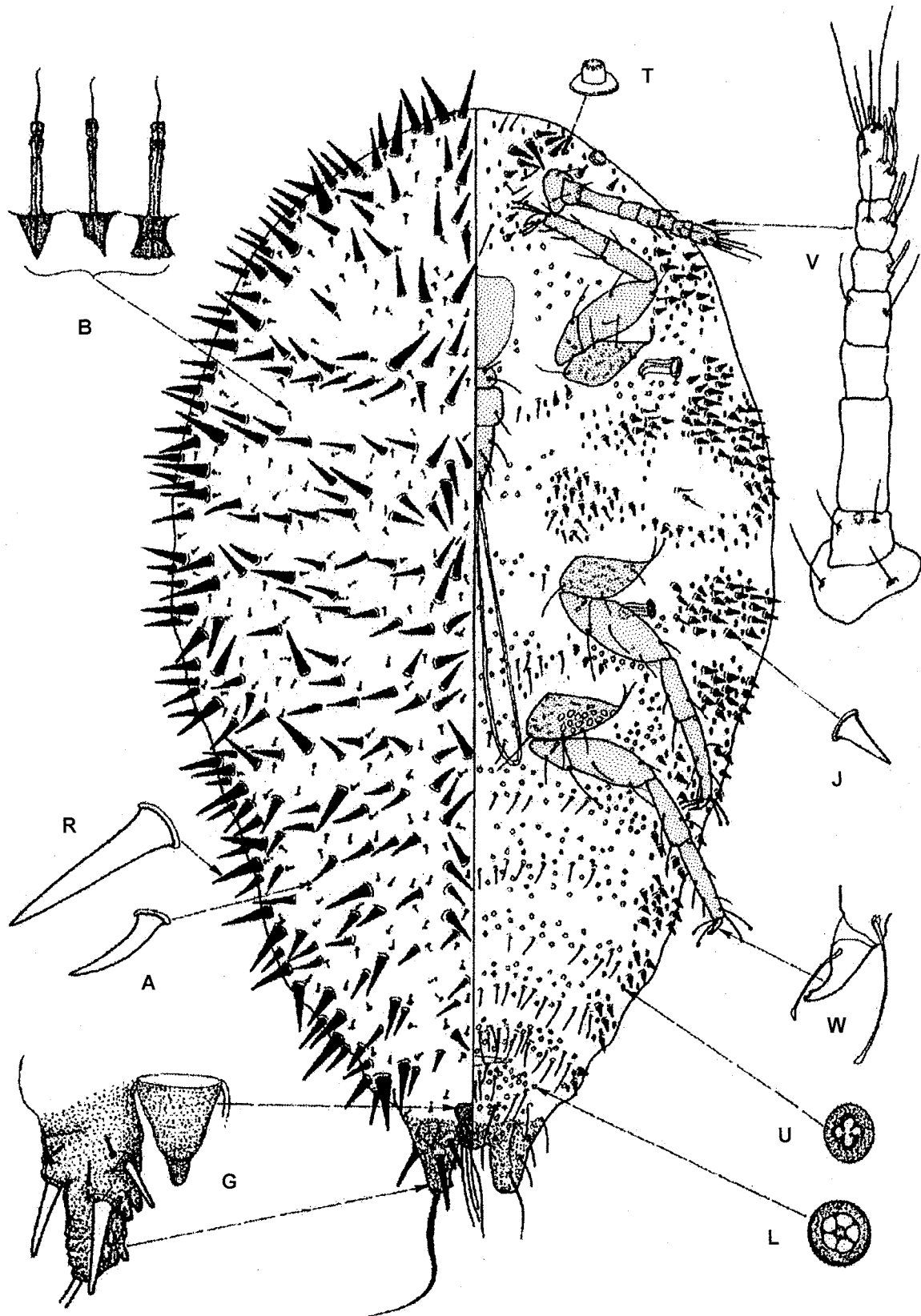


FIGURE 19. *Eriobalachowskyia valenzualae* (Balachowsky). Adult female, where A = dorsal spinose seta; B = dorsal microtubular ducts; G = dorsal view of anal plates; J = ventral submarginal spinose seta; L = ventral loculate pore; R = marginal spinose seta; T = preantennal tubercle; U = cruciform pore; V = antenna, and W = claw of metathoracic leg (modified after Kozár & Konczné Benedicty, 2008).

Known from Fabaceae.

Comment. *Eriobalachowskyia* is a monotypic genus known from Colombia and Ecuador. According to Kozár & Konczné Benedicty (2008), *Eriobalachowskyia* differs from all other eriococcid genera in: (i) having 8-segmented antennae; (ii) microtubular ducts with a particularly large and unusually-shaped dermal orifice; and (iii) a median plate swollen basally and with a pointed apex. It is somewhat similar to *Acanthococcus*, *Eriococcus* and *Gossyparia* in having enlarged, spine-like setae on the dorsum but differs in; (i) absence of macro-tubular ducts; and (ii) presence of frontal tubercles.

For a description of the adult female of *E. valenzuelae* (Balachowsky), see Kozár & Konczné Benedicty (2008) and Balachowsky (1959).

***Eriococcus* Targioni Tozzetti**

Eriococcus Targioni Tozzetti 1868: 726.

Type species: *Coccus buxi* Boyer de Fonscolombe 1834: 218.

Based on evidence provided by Cook and Gullan (2004), all South American species (with the exception of *Eriococcus dombeyae* González; see below) previously assigned to *Eriococcus* are either here transferred to *Acanthococcus* or have been placed previously in *Acanthococcus* or other genera by Miller and Gimpel (2000) or Kozár & Konczné Benedicty (2008). Because there may be confusion about the current placement of South American species of eriococcids, we have included a checklist of the genera and species in South America (see Appendix 1) and have listed all of the species previously placed in *Eriococcus* with their current generic designation. We suspect that many of these placements will change in the near future. We do not believe that the genus *Eriococcus* occurs in South America, even though *E. dombeyae* currently is placed in this genus. Thus, we are not including a description of the genus nor is it included in the generic key to adult females. González (2008a) gives a detailed description of *E. dombeyae* and a key for the separation of the adult females of species then included in *Eriococcus* from Argentina.

***Exallococcus* Miller & González**

Exallococcus Miller & González 1975: 148.

Type species: *Exallococcus laureliae* Miller & González 1975: 150–152.

Generic diagnosis. Adult female (Fig. 20). Found on leaves of host plant. Body oval, widest medially. **Dorsum.** Derm membranous, segmentation indefinite. Dorsal setae primarily spinose, straight or slightly curved, subequal in size; with a few hair-like setae in medial and mediolateral areas. Macro-tubular ducts with sclerotised dermal orifice. Microtubular ducts abundant. Loculate pores absent. Simple pores abundant over surface. Anal lobes heavily sclerotised, with small teeth near apex. Median plate weakly sclerotised. Anus apparently invaginated between anal lobes, difficult to discern, apparently with a small sclerotised ring, few pores, and 4 pairs of setae. **Margin.** Marginal setae same size as dorsal spinose setae. **Venter.** Derm membranous. Setae on abdomen weakly spinose, those in medial areas of head and thorax more hairlike. Macro- and microtubular ducts absent. Loculate pores usually with 5 loculi, arranged in distinct pattern, forming longitudinal line in submedial area of head, thorax, and abdomen. Cruciform pores present on lateral areas of head, thorax and anterior abdominal segments. Antenna 6 segmented. Frontal lobes present but antennal tubercles absent. Labium probably 3 segmented. Legs each well developed; each hind coxa swollen, with numerous large pores on each surface, without microspinules; hind femur swollen, with numerous large pores on dorsal surface; tibiae each with 3 setae; tarsi each with 4 setae; claws short and broad, each with digitules equal in size and longer than claw; each claw with a denticle near apex. Vulva present between segments VII and VIII.

Known only from Antherospermataceae.

Comment. *Exallococcus* is a monotypic genus known only from Chile. Adult females of *Exallococcus* species can be separated from other South American eriococcid adult females by the presence of: (i) an

invaginated anal ring; (ii) antennal segments rather long and narrow; (iii) anal lobes heavily sclerotised with a longitudinal fold; (iv) macrotubular ducts on dorsum only; (v) labium 1 segmented; and (vi) dorsum with many simple pores.

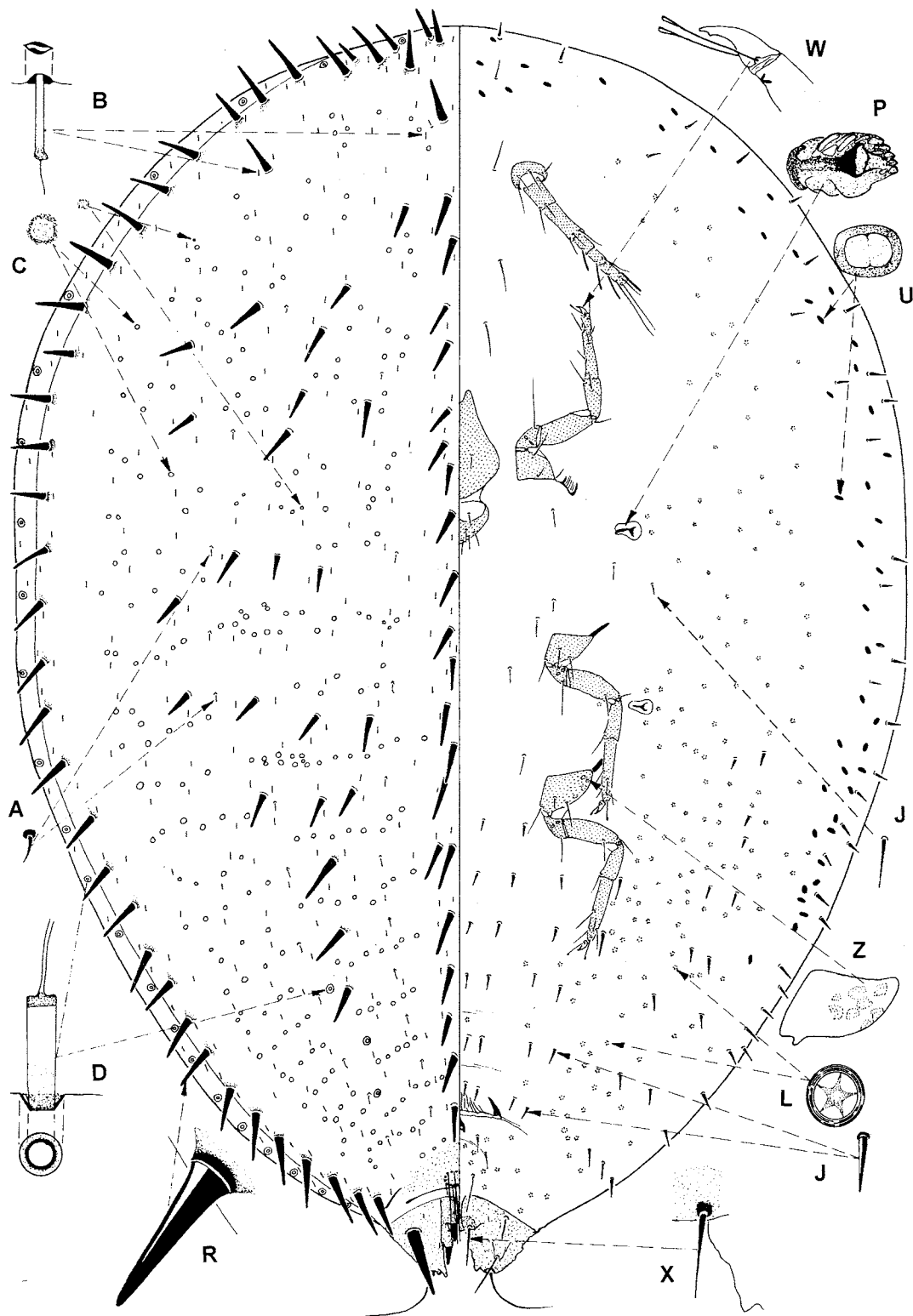


FIGURE 20. *Exallococcus laureliae* Miller & González. Adult female. Where A = dorsal seta; B = dorsal microtubular duct; C = dorsal simple pores; D = dorsal macrotubular duct; J = ventral setae; L = ventral loculate pore; P = anterior spiracle; R = marginal spinose seta; U = cruciform pore; W = claw of prothoracic leg; X = suranal seta, and Z = coxa of metathoracic leg (modified after Miller & González, 1975).

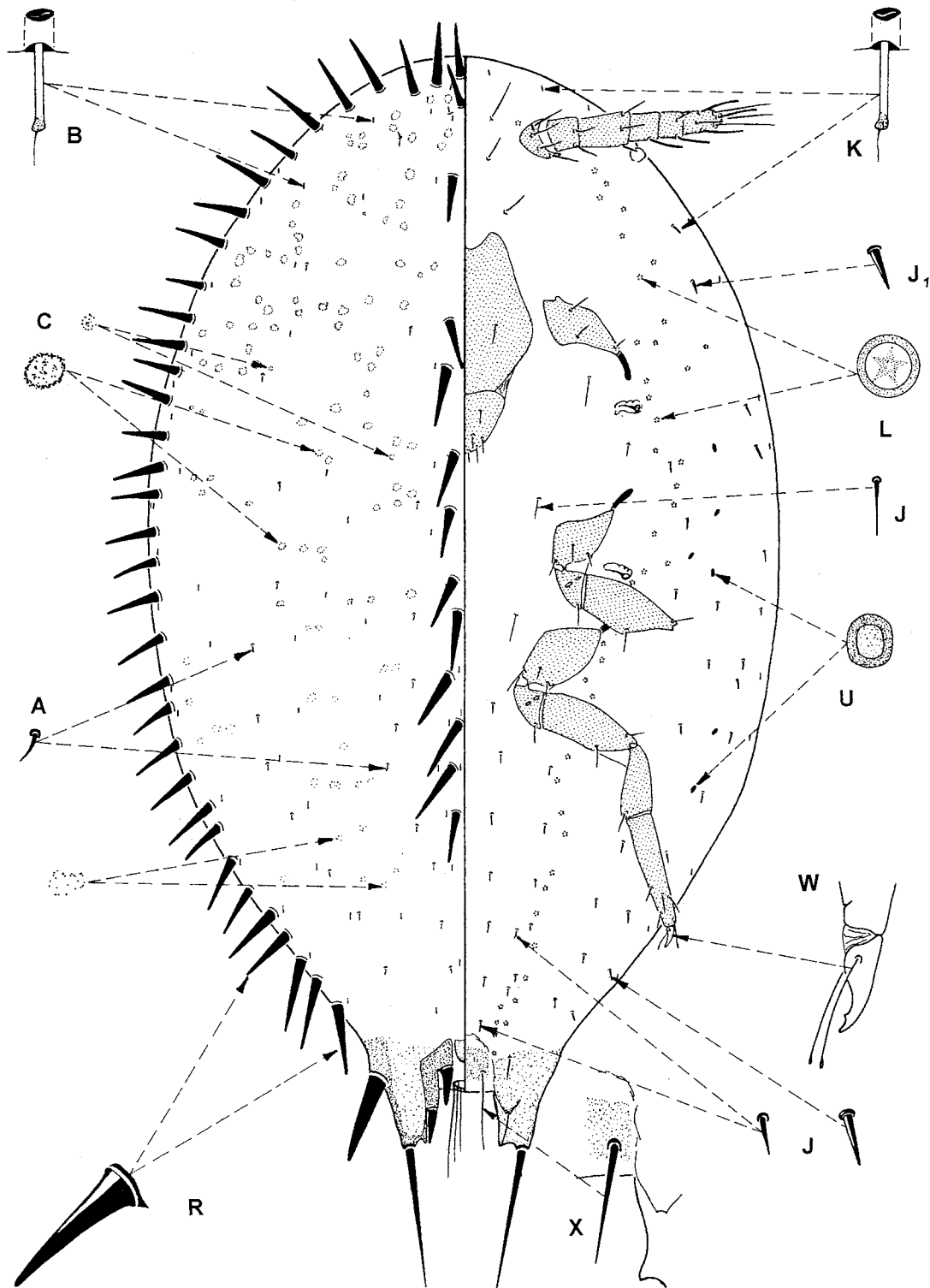


FIGURE 21. *Exallococcus laureliae* Miller & González. First-instar nymph, where A = dorsal seta, B = dorsal microtubular duct; C = dorsal simple pores; J = ventral setae; J₁ = spinose submarginal ventral seta; K = ventral microtubular ducts; L = ventral loculate pore; R = marginal spinose seta; U = cruciform pore; W = claw of metathoracic leg; X = suranal seta (modified after Miller & González).

First-instar nymph (sex not determined) (Fig. 21)

Diagnosis. *Mounted material.* Body oval, more pointed at posterior end. *Dorsum.* Dorsal setae of 2 sizes: enlarged setae spinose, in 2 lines medially and forming a marginal line, and small setae very small, hairlike, mainly in a submedian line and a submarginal line. Macrotubular ducts absent. Microtubular ducts small,

scattered. Simple pores present, scattered. Anal lobes sclerotised, each with a longitudinal fold and 2 thick spinose setae on inner margin and another on outer margin, plus longer apical seta. Median plate present. *Margin*. Delineated by band of enlarged dorsal setae. *Venter*. Setae of 2 types: those near margin slightly spinose, those more medially hairlike. Macrotubular ducts absent. Microtubular ducts restricted to near margin. Loculate pores, each with 5 loculi, present in a longitudinal band mediolaterally. Cruciform pores few, submarginal on anterior abdominal segments and thorax. Antennae 6 segmented. Labium 1 segmented. Legs without pores; tarsus much longer than tibia; tarsal digitules capitate; claw with a denticle; claw digitules similar both with small capitate apices.

Comment. The first-instar nymph of *Exallococcus* is somewhat similar to that of *Chilechiton lynnae* in having a longitudinal fold in each anal lobe but is otherwise easily separated by the shape and distribution of the dorsal setae, the distribution of the ventral loculate pores, the presence of cruciform pores and in having both claw digitules similar.

For a description of the adult female and first-instar nymph of *E. laureliae*, see Miller & González, 1975: 150.

***Hempelicoccus* Kozár**

Hempelicoccus Kozár (in Kozár & Konczné Benedicty, 2008: 123–125).

Type species: *Eriococcus paranaensis* Foldi & Kozár 2007: 59.

Generic diagnosis. Adult female (Fig. 22). *Dorsum*. Setae spine-like, present throughout but variable in size. Macrotubular ducts long and narrow, inner ductule with flower-like glandular end. Microtubular ducts long, with oval or bifurcate orifice, either few or forming groups. Loculate pores absent. Anal lobes well developed and sclerotised. Median plate not developed. Anal ring well developed, sclerotised, with 4 pairs of setae, each twice as long as width of anal ring; anal ring pores few. *Margin*. Often clearly demarcated by a line of enlarged spinose setae. *Venter*. Setae mainly hairlike and quite long but with a few spinose setae, similar to those on dorsum, present around margin. Macrotubular ducts present, of various sizes. Microtubular ducts absent. Loculate pores generally with 5 loculi but pores with more loculi common; frequent throughout. Cruciform pores present submarginally. Antennae 7 segmented. Frontal lobes present, antennal tubercles absent. Labium 3 segmented with 2 pairs of setae. Legs long, tibia and tarsus subequal in length; coxae of meso- and metathoracic legs with spinulae; metacoxae and femur with many large, irregularly-shaped translucent pores. Vulva present between segments VII and VIII. (Modified after Kozár & Konczné Benedicty, 2008).

Currently known from Asteraceae, Fabaceae and Nothofagaceae.

Comment. According to Kozár & Konczné Benedicty (2008), *Hempelicoccus* resembles *Eriococcus* in having: (i) spine-like setae on the dorsum; (ii) long microtubular ducts with a bifurcate orifice; and (iii) frontal lobes; but it differs in lacking: (i) enlarged tubular ducts; and in having: (ii) 2 pairs of setae on the basal labial segment; (iii) cruciform pores; and (iv) groups of microtubular ducts on the dorsum. It is also similar to *Acanthococcus* in having: (i) 2 pairs of setae on the basal labial segment; (ii) cruciform pores; and (iii) frontal lobes. However it differs from *Acanthococcus* in having groups of microtubular ducts on the dorsum and in lacking a median plate. It is also close to *Coxicoccus* in having: (i) enlarged spine-like setae on dorsum; and (ii) long microtubular ducts with a bifurcate orifice, but differs in having: (i) frontal lobes; (ii) 2 pairs of setae on the basal labial segment; and (iii) absence of clavate setae ventrally on posterior abdominal segments.

Kozár & Konczné Benedicty (2008) included 4 species in this genus, *H. brasiliensis* (Cockerell), *H. leguminicola* (Morrison), *H. mendozae* (Morrison), and *H. paranaensis* (Foldi & Kozár). In addition, *E. santiaguensis* and *E. tucumanensis*, described in *Eriococcus* by González & Granara de Willink (2009) and *E. pumiliae*, described in *Eriococcus* by P. González (2008a), are here transferred to *Hempelicoccus* as *H. santiaguensis* (González & Granara de Willink) **n. comb.**, *H. tucumanensis* (González & Granara de Willink) **n. comb.** and *H. pumiliae* (González) **n. comb.**, because they possess the dorsosubmedial clusters of microtubular ducts typical of this genus. It should be noted that González & Granara de Willink (2009) dispute

the validity of *Hempelicoccus* because of variation found in all of the diagnostic characters listed by Kozár & Konczné Benedicty (2008) except for the presence of clusters of dorsal microducts. Hopefully a detailed phylogenetic analysis using morphological and molecular characters of taxa currently placed in the Eriococcidae will clarify the position of many of the currently controversial groupings. As presently understood, *Hempelicoccus* is restricted to South America. For a description of the adult female of the type species, see Foldi & Kozár 2007: 59.

First-instar nymph (based on *E. tucumanensis* (González & Granara de Willink); gender not determined) (Fig. 23)

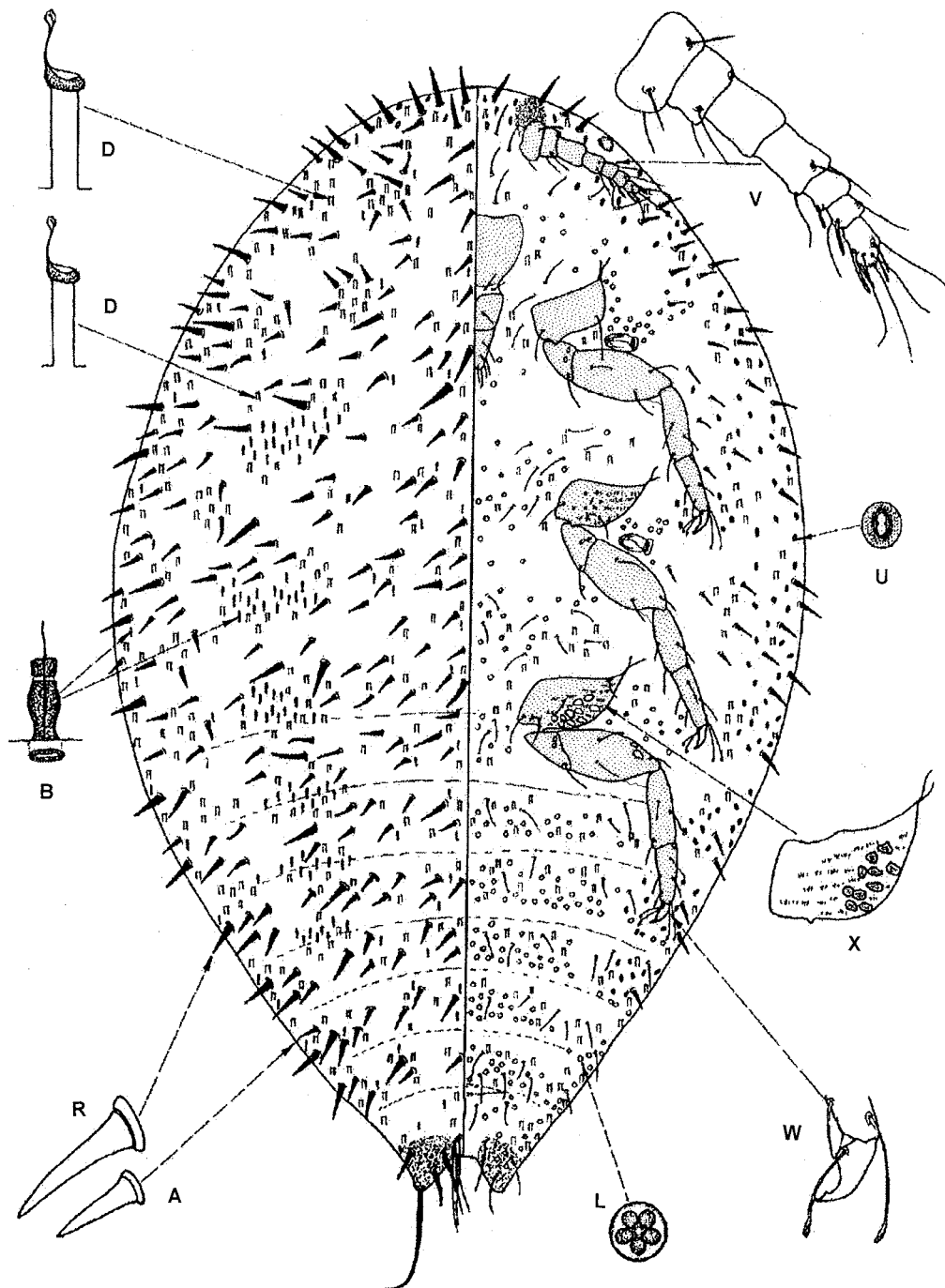


FIGURE 22. *Hempelicoccus paranaensis* (Foldi & Kozár). Adult female, where A = dorsal spinose seta; B = dorsal microtubular duct; D = dorsal macrotubular ducts; L = ventral loculate pore; U = cruciform pore, V = antenna; W = claw of metathoracic leg, and X = coxa of metathoracic leg (modified after Kozár & Konczné Benedicty, 2008).

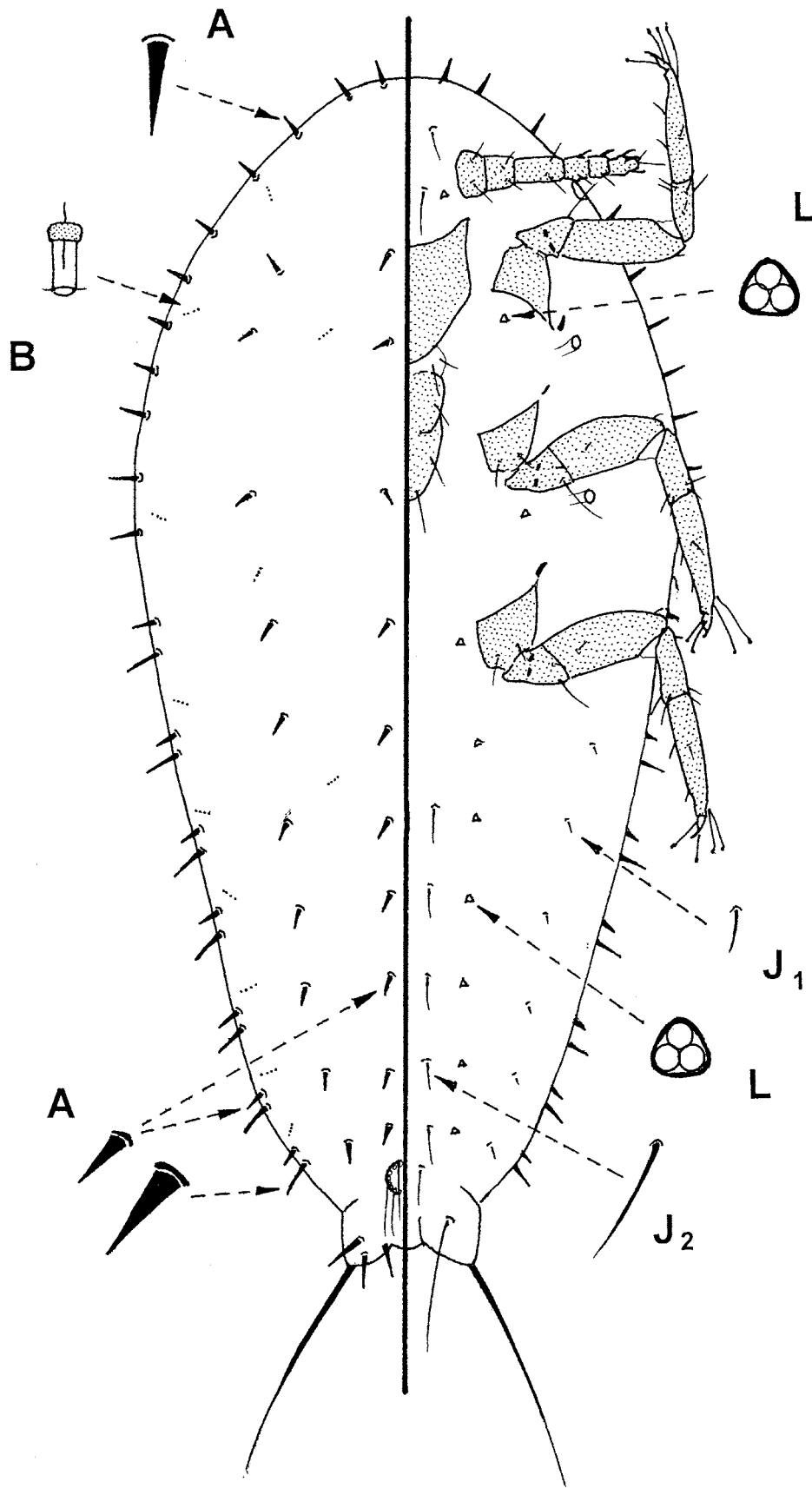


FIGURE 23. *Hempelicoccus paranaensis* (Foldi & Kozár). First-instar nymph, where A = dorsal spinose setae; B = dorsal microtubular duct; J₁ = small ventral seta; J₂ = large ventral setae, and L = ventral triloculate pore (redrawn and modified after González & Granara de Willink, 2009).

Diagnosis. *Mounted material.* Body oval. *Dorsum.* Enlarged setae (excluding marginal setae) straight or slightly curved, of 2 sizes, arranged in 2 pairs of longitudinal lines, one pair submedial and one pair mediolateral; smaller setae present in submedial and mediolateral lines. Macrotubular ducts absent. Microtubular ducts loosely associated with lines of setae. Loculate pores absent. Anal lobes protruding, not platelike, each with two or three enlarged setae + a longer apical seta; lobes without microtubular ducts. Medial plate absent. *Margin.* Marginal setae each larger than dorsal setae, straight or slightly curved, apex pointed or slightly rounded, (*H. tucumanensis* has two submarginal lines of marginal setae). Anal ring without anal tube but with pores and 6 anal-ring setae. *Venter.* Loculate pores few, restricted to submedial areas of head, thorax and abdomen, usually with 3 loculi, sometimes with 5 locular pore near spiracles. Macrotubular and microtubular ducts absent. Cruciform pores absent. Suranal setae: both anterior and posterior pairs hairlike. Ventral setae arranged segmentally. Antennae 6 segmented. Labium 3 segmented, basal segment with 2 setae. Legs well developed, without pores; each with tibia shorter than tarsus; tarsal digitules slightly capitate; claw apparently without a denticle; claw digitules equal. (Modified after González & Granara de Willink, 2009).

Comment. The first-instar nymphs of *Hempelicoccus* are very similar to those of *Acanthococcus* but differ by lacking cruciform pores which are present in first-instar *Acanthococcus*.

***Icelococcus* Miller & González**

Icelococcus Miller & González 1975: 152.

Type species: *Icelococcus charlini* Miller & González, 1975: 152–154.

Generic diagnosis. Adult female (Fig. 24). According to Miller and González (1975), *I. nothofagi* adult females occur in the twig axils of *Nothofagus*. The adult females are dark grey and do not form an ovisac. *Dorsum.* Dorsal setae of 2 sizes: (i) larger spinose setae along margin and medially; and (ii) smaller setae elsewhere. Macrotubular ducts absent. Microtubular ducts with a long ductule and unsclerotised orifice. Loculate pores absent. Anal lobes heavily sclerotised and rugose, with many medial teeth and 3 dorsal enlarged spinose setae. Median plate present. Anal ring apical, not invaginated, with 4 pairs of anal ring setae and numerous pores. *Margin.* Demarcated by a line of enlarged spinose setae. *Venter.* Ventral setae of 2 sizes: (i) spinose setae, similar to those on dorsum, present marginally and medially on head; and (ii) setose setae, sparse elsewhere. Macrotubular ducts present in a mediolateral band on *I. charlini*, absent on other two species. Microtubular ducts restricted to anterior portion of head. Loculate pores frequent throughout. Cruciform pores sparse submarginally, most frequent on abdomen. Labium 3 segmented; with 2 pairs of setae on basal segment. Antennae 6 segmented. Frontal lobes and antennal tubercles absent. Legs relatively small; metacoxae and metafemur each with a few irregularly-shaped translucent pores; tarsal digitules similar; claw digitules similar; claw with a small denticle. Vulva present between segments VI and VII.

Known only from Anacardiaceae and Nothofagaceae.

Comment. *Icelococcus* contains 3 species, the type species (*I. charlini*), *I. lithrae* Hodgson & Miller and *I. nothofagi* Miller and González and is known only from Chile.

Adult female *Icelococcus* are characterised by: (i) anal lobes with teeth on inner margin; (ii) few or no macrotubular ducts; (iii) labium distinctly 3 segmented; (iv) cruciform pores present on venter; and (v) median plate present. For further details see Miller & González (1975).

First-instar nymph (of *I. lithrae* Hodgson & Miller, sex not determined) (Fig. 25)

Diagnosis. *Mounted material.* Body oval, more pointed at posterior end. *Dorsum.* Dorsal setae of 1 type but rather variable in size, more or less in 2 submedial lines, 2 mediolateral lines and around margin. Macrotubular ducts absent. Microtubular ducts small, with a bifurcate dermal orifice, scattered. Anal lobes sclerotised, each with a rather serrate inner margin. Median plate present. *Margin.* Delineated by band of spinose dorsal setae. *Venter.* Setae of 2 types: those near margin slightly spinose, those more medially hairlike. Macrotubular ducts absent. Microtubular ducts absent. Loculate pores, each with 3 loculi, present in a very sparse longitudinal line mediolaterally. Cruciform pores few, submarginal on thorax. Antennae 6 segmented.

Labium clearly 3 segmented, basal segment with 2 pairs of setae. Legs without pores; tarsus much longer than tibia; tarsal digitules capitate; claw with a denticle; claw digitules similar both with small capitate apices.

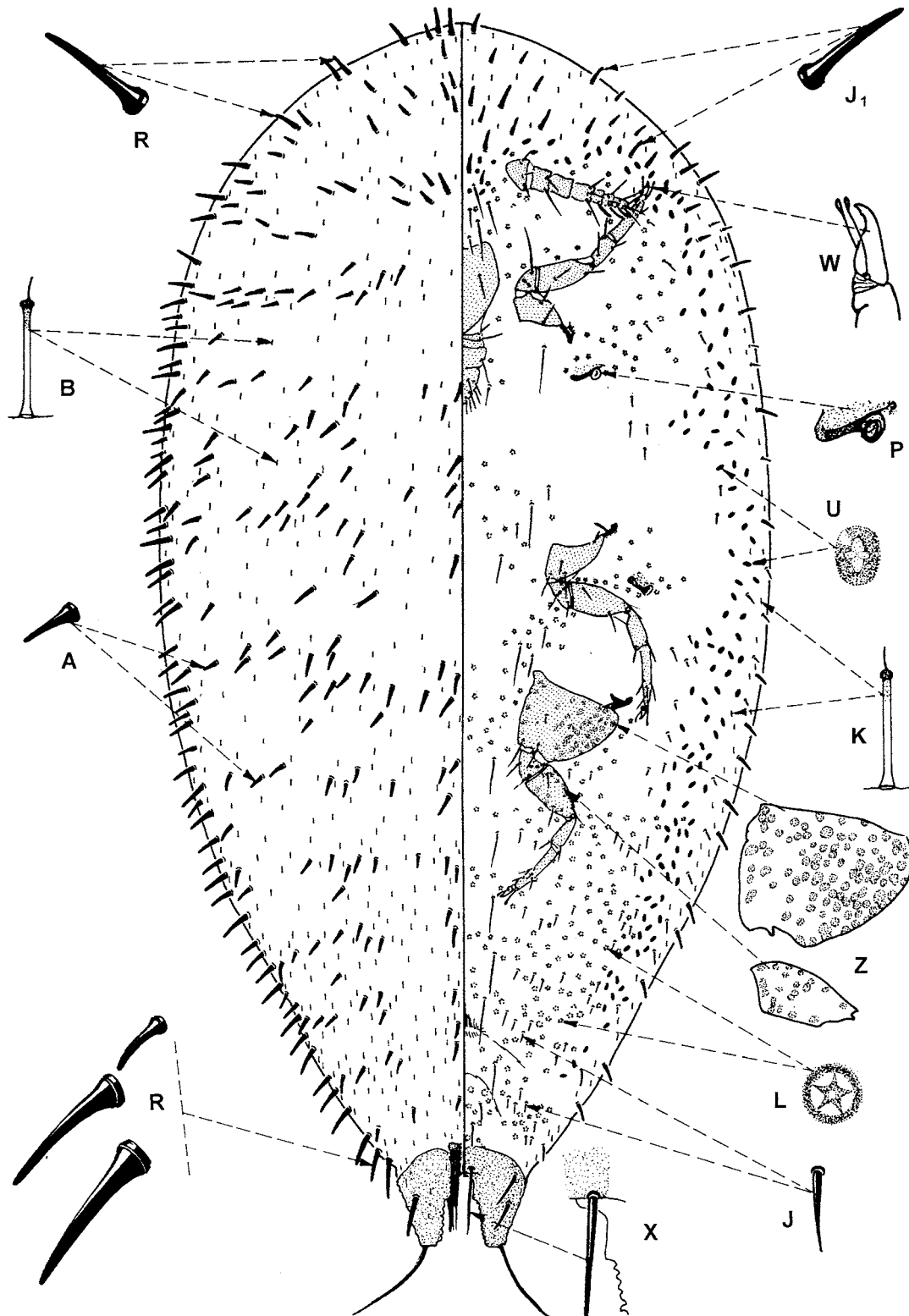


FIGURE 24. *Icelococcus nothofagi* Miller & González. Adult female, where A = dorsal spinose seta; B = dorsal microtubular duct; J = ventral seta; J₁ = ventral submarginal spinose setae; K = ventral microtubular duct; L = ventral loculate pore; P = anterior spiracle; R = marginal spinose seta; U = cruciform pore; W = claw of prothoracic leg; X = suranal seta, and Z = coxa and femur of metathoracic leg (modified after Miller & González, 1975).

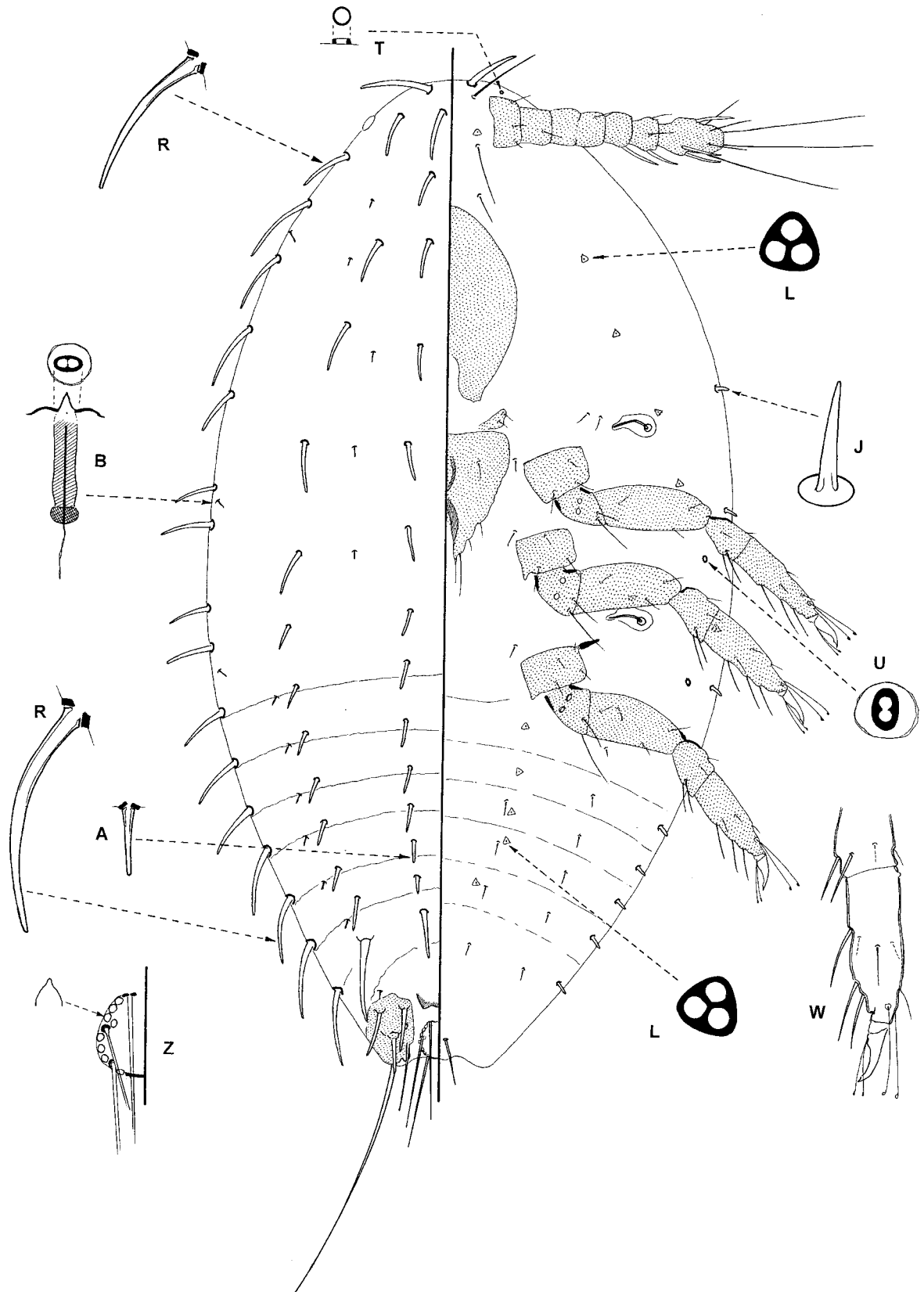


FIGURE 25. *Icelococcus lithreae* Miller and González. First-instar nymph, where A = dorsal seta; B = dorsal microtubular duct; J = spinose submarginal seta; L = ventral trilocular pores; R = marginal setae; T = antennal tubercle; U = cruciform pore; W = distal end of metathoracic leg, and Z = left side of anal ring.

Comment. The only other South American first-instar nymphs with sclerotised anal lobes and 6 segmented antennae are *Chilechiton* and *Exallococcus*. These latter 2 genera also share with *Icelococcus* the mediolateral line of loculate pores on the venter but are otherwise rather different, both of the latter having much more strongly spinose dorsal setae and only a 2-segmented labium. For other differences, see key.

Intecticoccus Kondo

Intecticoccus Kondo (in Kondo, Hardy, Cook and Gullan, 2006): 24–26.

Type species: *Intecticoccus viridis* Kondo (in Kondo, Hardy, Cook and Gullan, 2006): 26–29.

Generic diagnosis. Adult female (Fig. 26). In life, covered by thin layer of glassy wax, not producing an ovisac; eggs laid in concavity beneath female. Adult female with sclerotised anal lobes variable in shaped, protruding posteriorly. *Dorsum*. Setae short, slightly spinose, of 1 size. Macrotubular ducts absent. Microtubular ducts with longitudinal division. Loculate pores absent. *Margin*. Not demarcated. *Venter*. Setae relatively small, slightly spinose or hairlike, most abundant medially, uncommon elsewhere; suranal seta present on sclerotised extension of anal lobes. Macrotubular ducts absent. Microducts present between antennae and in row near anterior spiracles. Loculate pores primarily quinquelocular. Cruciform pores absent. Antennae 6 segmented. Frontal lobes and antennal tubercles absent. Labium 3 segmented; basal segment with 2 pairs of setae. Metathoracic legs with translucent pores on coxa. Claw digitules similar; claw without denticle. Vulva present between VII and VIII.

Known only from Nothofagaceae.

Comment: *Intecticoccus* is a monotypic genus known only from Chile and Argentina. For a description of the adult female of *I. viridis*, see Kondo *et al.*, 2006. Kondo *et al.* state that *I. viridis* can be distinguished from other species of eriococcids in having the following combination of characters: (i) in life, with bare dorsum, not covered in a felted sac; (ii) very small dorsal and marginal setae, each 3–7 µm long; (iii) claws without a denticle; and (iv) absence of cruciform pores. It shows some similarities to *Icelococcus charlini* Miller & González and to *Chilechiton lynnae* Hodgson & Miller. For differences, see Kondo *et al.*, 2006.

Macracanthopyga Lizer y Trelles

Macracanthopyga Lizer y Trelles, 1955: 37.

Type species: *Macracanthopyga verganiana* Lizer y Trelles, 1955: 37–38.

Generic diagnosis. Adult female (Fig. 27). Forms a hard wax cover that is firmly attached to the branch of the host plant. Body rounded anteriorly, bluntly pointed posteriorly; abdomen rather short, posterior 6 abdominal segments all covered dorsally with long spinose setae. *Dorsum*. Derm mostly membranous, segmentation only clear in abdominal region. Setae of 3 types: (i) short, fine setose setae, very sparse; (ii) cupolate-shaped spinose setae; distribution rather variable; and (iii) stout, strong, elongate spinose setae, each with a very strongly sclerotised basal socket, present on posterior 6 or 7 abdominal segments. Macrotubular ducts absent. Microtubular ducts most abundant across anterior abdominal segments and meso- and metathorax. Loculate pores absent. Anal lobes strongly sclerotised, with spinose setae. Median plate apparently absent. Anal ring perhaps with 3 pairs of setae. *Margin*. Not demarcated anterior to abdomen, where lateral spinose setae present. *Venter*. Derm nodulose laterally on abdominal segments V–VII, otherwise membranous. Setae of 3 types present: (i) setose setae, sparse; (ii) cupolate-shaped setae, similar to those on the dorsum, present laterally on abdominal segment I and metathorax; and (iii) a pair of long, finely spinose setae anterior to anal ring. Macro- and microtubular ducts absent. Loculate pores with mainly 5 loculi: present in broad groups laterad to each spiracle and in loose groups on either side of abdominal segments II–IV. Cruciform pores absent. Anal lobes strongly sclerotised ventrally. Suranal setae spinose. Antennae 1 segmented. Frontal lobes and antennal tubercles absent. Clypeolabral shield proportionately quite large; labium apparently 1 segmented. Spiracles each with a very large roundly-oval, sclerotised muscle plate. Legs

entirely absent. With a large, oval concavity along margin between metathorax and abdominal segment II, approximately in position of metacoxa. Vulva not detected.

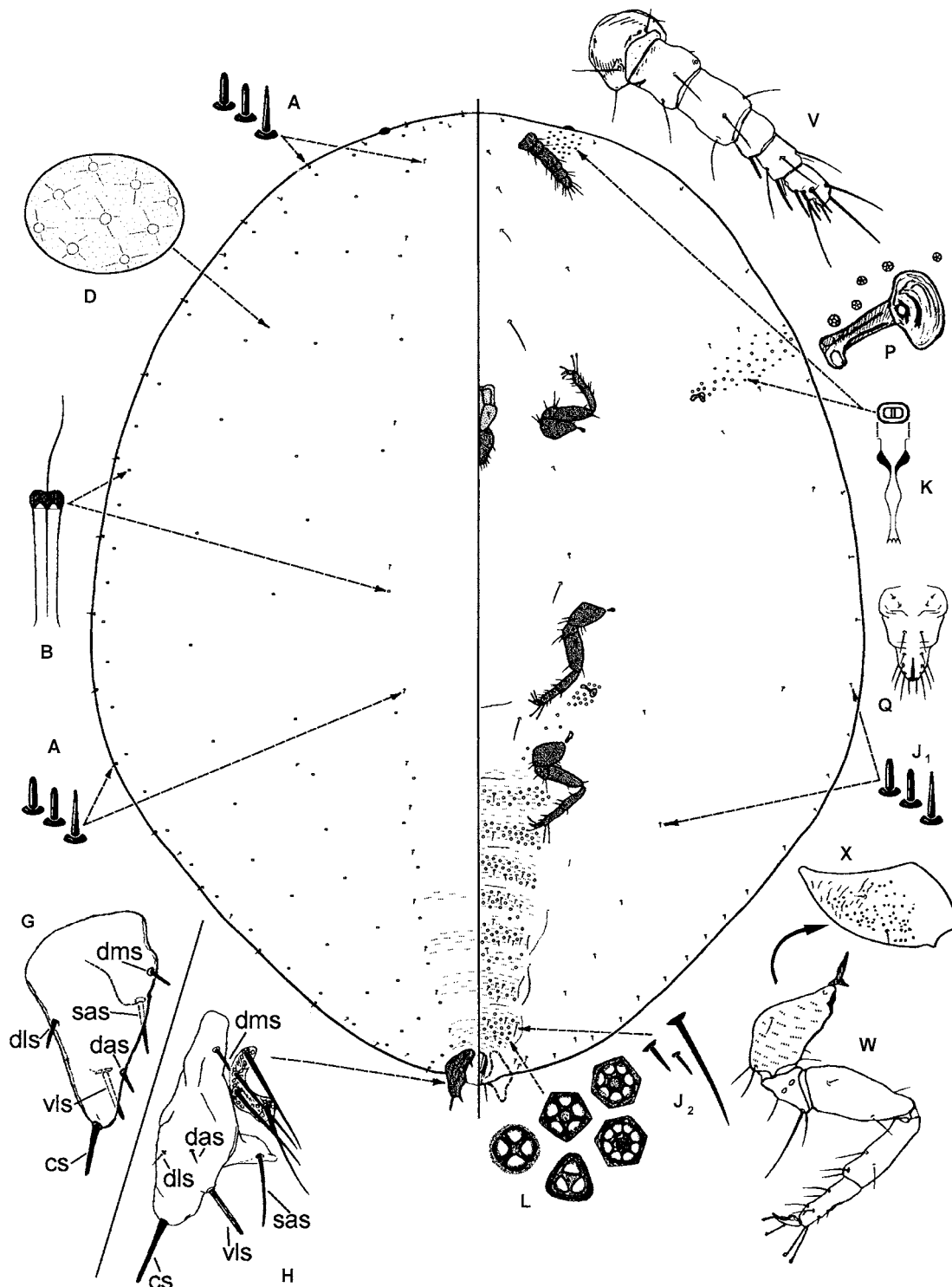


FIGURE 26. *Intecticoccus viridis* Kondo. Adult female, where A = dorsal setae; B = dorsal microtubular duct; D = dorsal derm, showing areolations; G = dorsal view of anal lobe; H = side view of anal plate plus anal ring; J₁, J₂ = ventral setae; K = ventral microducts; P = anterior spiracle; Q = labium; V = antenna; W = metathoracic leg, and X = coxa of metathoracic leg. And where dls = dorsolateral lobe seta; dms = dorsomedial lobe seta; das = dorsoapical lobe seta; cs = caudal seta; vls = ventral lobe seta, and sas = suranal seta (modified after Kondo *et al.*, 2006).

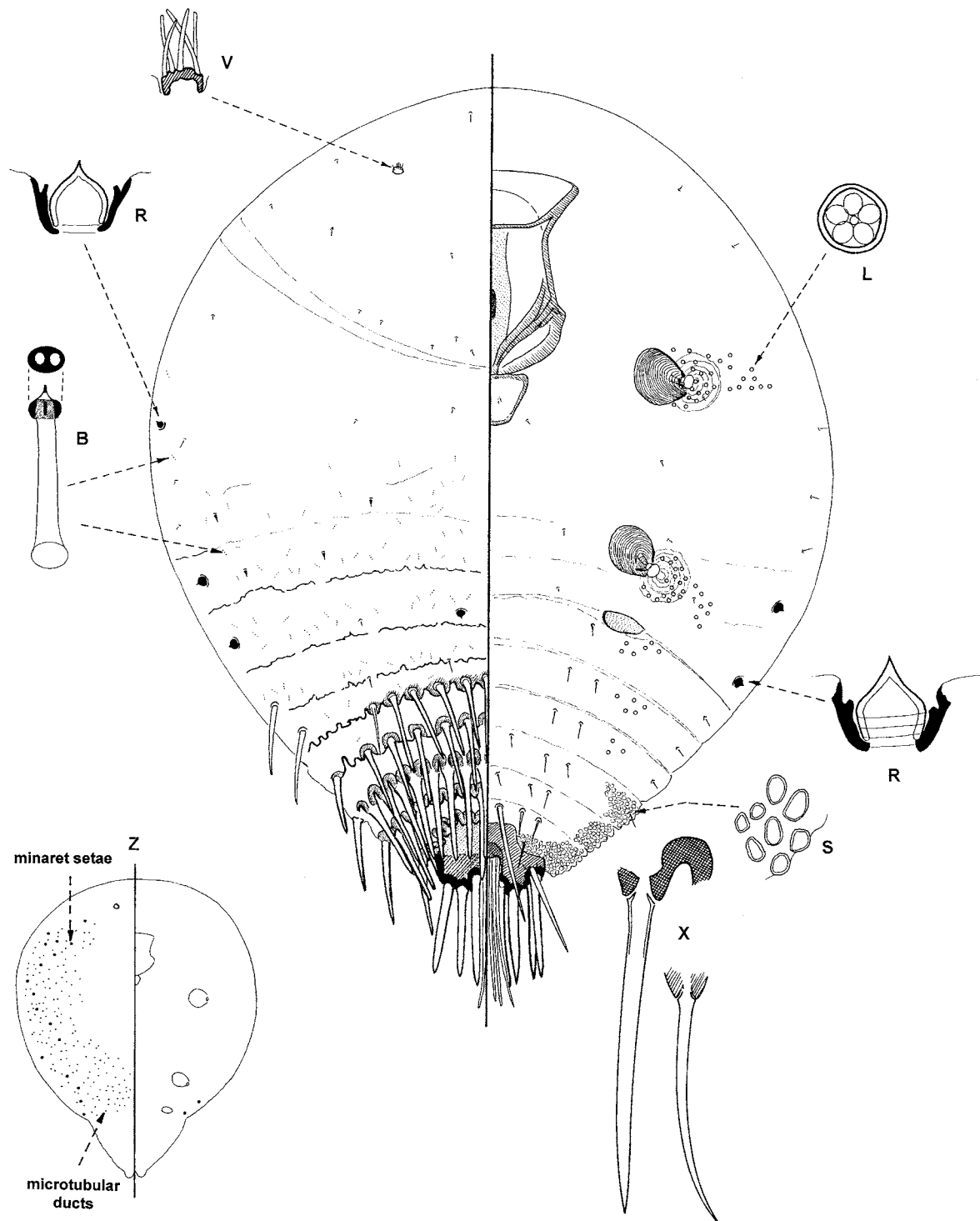


FIGURE 27. *Macracanthopyga verganiana* Lizer y Trelles. Adult female; where B = dorsal microduct; L = ventral loculate pore; R = marginal spinose seta; S = nodulose derm on abdominal margin; V = antenna; X = setae on anal plates, and Z = view of specimen with more frequent cupulate-shaped (minaret) setae and dorsal microtubular ducts.

Known only from Myrtaceae.

Comment: *Macracanthopyga* is a monotypic genus, known only from Argentina. It has been thought to induce enclosed galls (Ferris, 1957; Beardlsey, 1984) but Gullan *et al.* (2005) indicate that the original text states that it is covered by a hard wax test on the branch of its host plant.

The adult females of *Macracanthopyga* are easily separated from all other South American adult female eriococcids by the presence of the very long spinose setae on the dorsum of the abdomen. They also have: (i) no legs; (ii) reduced antennae; (iii) well-developed anal lobes, each with very long spinose setae; (iv) sunken, spinnarette-shaped spinose setae; and (v) microtubular ducts restricted to the dorsum.

***Macracanthopyga verganiana* Lizer y Trelles**

Macracanthopyga verganiana Lizer y Trelles, 1955: 37–38

Material examined: No collection data but slide labelled *Macracanthococcus virgansi* Liz. (presumably a manuscript name), sent by Lizer y Trelles, GF7 (BME): 1/11adf in fair condition (believed to be syntype material). Also: **ARGENTINA**, Province of Corrientes, no date, ex *Campomanesia* sp. (Myrtaceae), no coll. (BME): 2/25adff — slide in poor condition and specimens hard to see but major characters discernable (believed to be syntype material). “These specimens are probably syntypic – Lizer y Trelles (1955) states that he sought an opinion from Dr. Ferris and so it is likely that the specimens now in the BME were those sent by Lizer y Trelles. I did check Ferris’ library for any correspondence from Lizer y Trelles, but found nothing” (personal correspondence P. J. Gullan, November 17, 2009).

Adult female (Fig. 27)

Unmounted material. On the branches of a species of *Campomanesia* (Myrtaceae) (Lizer y Trelles, 1955).

Mounted material. Length 0.43–0.80 mm, width 0.38–0.83 mm. Rounded anteriorly, bluntly pointed posteriorly; abdomen rather short, posterior 6 abdominal segments all covered dorsally with long spinose setae. With sclerotised anal lobes.

Dorsum. Derm mostly membranous, segmentation only clear in abdominal region, but some specimens with a distinct membranous line anteriorly possibly delineating posterior margin of head. Dorsal setae of 3 types: (i) fine setose setae, all short, mostly about 3–4 μm long but those on head marginally longer (up to 8 μm long); very sparse, perhaps most abundant on head; (ii) cupolate-shaped spinose setae, each about 5–12 μm tall and wide; distribution rather variable but generally with single setae laterally on abdominal segment I and on meso- and metathorax, but occasionally rather more frequent (see discussion below); also often with 1 medially on abdominal segment I; and (iii) stout, strong, elongate spinose setae, each with a very strongly sclerotised basal socket, present on posterior 6 or 7 abdominal segments, those more laterally 25–35 μm long, those medially largest, up to 65 μm long, as follows: segment II with 0 or 1 laterally; III about 8–17 large spines medially and a pair laterally; IV about 11–20 large spines medially plus a marginal pair; V about 17–21 very large spines medially and a pair laterally; VI possibly with 3 on each side and 1 medially; VII possibly with only a single spine on each side, and VIII (anal lobe) with 3 particularly stout spines (each 45–70 μm long) along dorsal posterior margin, plus other stout spines on each inner and outer margin more ventrally. Macrotubular ducts absent. Microtubular ducts about 8–10 μm long: most abundant across abdominal segments I & II, and meso- and metathorax, but also with a few in abdominal segments II and IV and also perhaps laterally in prothorax (but can be more abundant when cupolate-shaped setae more abundant — see discussion). Other pores absent. Anal lobes strongly sclerotised, each about 20 μm long, 25 μm wide; anal cleft about 25–30 μm deep; lobes with spinose setae, as described above. Median plate apparently absent. Anal ring thought to have 3 pairs of setae, each about 80–90 μm long.

Margin. Margin not demarcated apart from on abdomen, where lateral spinose setae mark margin; other marginal setae absent. Eyespots apparently absent.

Venter. Derm laterally on abdominal segments V–VII nodulose, otherwise derm membranous. Setae of 3 types: (i) setose setae, sparse, particularly on head and thorax; larger setae restricted to 1–3 pairs on each abdominal segment, range 8–27 μm , longest posteriorly; (ii) cupolate-shaped setae similar to those on dorsum, generally present laterally on abdominal segment I and metathorax, and (iii) a pair of long, finely spinose setae anterior to anal ring on abdominal segment VII, each 80–90 μm long. Macrotubular and microtubular ducts absent. Loculate pores with mainly 5 loculi: present in broad groups laterad to each

spiracle, with 20–40 in each anterior group and 20–30 in each posterior group; loculate pores also present in loose groups on either side of abdominal segments II–IV: II with 2–6, III 1–4 and IV 1–3. Cruciform pores absent. Anal lobes strongly sclerotised ventrally, with a pair of posterior suranal spinose setae, each about 55–70 µm long.

Antennae 1 segmented, each with about 5 fleshy setae; width of segment about 8 µm. Clypeolabral shield proportionately quite large, about 105–125 µm long; labium apparently 1 segmented; number of setae unknown. Spiracles each with a very large, roundly-oval, sclerotised muscle plate, each about 28–35 µm wide; actual peritreme very narrow, about 3–10 µm wide; each with a membranous cavity laterad to peritreme, each about the same size as muscle plate. Legs entirely absent. With a large, oval concavity along margin between metathorax and abdominal segment II, approximately in position of metacoxa; each cavity about 30–35 µm wide and 15–25 µm long. Vulva not detected.

Comment. This species was illustrated by Ferris (1957), probably from the slides cited above. The present description agrees reasonably closely but his description of the clypeolabral shield was much smaller and he did not note the microtubular ducts. His figure also showed more cupolate-shaped setae, including a group dorsad to the clypeolabral shield. Two of the specimens seen during this study had significantly more of these cupolate-shaped setae than on the other specimens but their distribution was difficult to determine. However, it was considered that the extra spines were restricted to 1 side only and none were present medially above the mouthparts. On these latter specimens, the microtubular ducts were also much more abundant on the side with the spines, extending anteriorly into the head (as shown in the small figure in Fig. 27).

***Madarococcus* Hoy**

Madarococcus Hoy 1962: 15, 21, 151–163, 200.

Type species: *Rhizococcus pulchellus* Maskell 1890: 143–144.

Generic diagnosis. Adult female. Body variable in shape; anal lobes variable but all with 3 dorsal setae, an apical seta and a ventral seta. *Dorsum.* Dorsal derm usually nodulose; setae variable, ranging from minute and digitate to enlarged and spinose. Macrotubular ducts present or absent; when present variable in structure. Microtubular ducts small, generally with 1–5 at base of enlarged dorsal setae. Loculate pores generally absent. Cruciform pores absent. *Margin.* With or without marginal setal fringe. *Venter.* Setae flagellate or spinose. Suranal setae spatulate on most species. Macrotubular ducts present or absent. Microtubular ducts present along margin or absent. Loculate pores, each with 3 or 5 loculi, present on abdomen. Anal ring well developed, with pores and 3 or 4 pairs of setae. Antennae 6 or 7 segmented. Frontal lobes perhaps absent but antennal tubercles sometimes present. Labium either 3 segmented or composed of 2 fused segments. Metathoracic coxae, femur and tibia often with translucent pores. Vulva present between abdominal segments VII and VIII. (Modified after Hardy *et al.*, 2008).

Apparently restricted to Nothofagaceae.

Comment. The genus *Madarococcus* has recently been revised by Hardy *et al.* (2008) based on nucleotide sequence data and morphology. As part of this review, they transferred 4 South American species previously included in *Eriococcus* to *Madarococcus*, namely *E. chilensis* Miller and González (from Chile), *E. eurythrix* Miller and González (from Argentina and Chile), *E. navarinoensis* Hoy (from Argentina and Chile) and *E. rhadinothrix* Miller and González (from Chile). All of these species are known only from *Nothofagus* (Nothofagaceae). We suspect that 1 of the species recently described by González (González, 2008a) from Argentina on *Nothofagus* (*Eriococcus dombeyi*) will eventually also be transferred to *Madarococcus*. Hardy *et al.* also included species in this genus from New Zealand and Australia.

Recent molecular data have demonstrated that previous concepts of genera such as *Acanthococcus*, *Eriococcus*, *Gossyparia*, *Greenisca*, *Rhizococcus*, etc. need careful re-analysis, because species that are similar morphologically differ considerably using molecular characters (Cook & Gullan, 2004; Kondo *et al.*, 2006; Hardy *et al.*, 2008). The lack of diagnostic morphological characters for characterizing *Madarococcus* (Hardy *et al.*, 2008) adds further confusion to the status of these genera. Until more definitive analyses are

undertaken, we will adhere to the current classification except where more detailed analyses have been undertaken, as is the case in the paper by Hardy *et al.* (2008).

We note, however, that 3 of the 4 South American *Madarococcus* species mentioned above, i.e., *M. chilensis*, *M. navarinoensis*, and *M. rhadinothrix* could just as easily be placed in a taxon separate from *Madarococcus* based on the morphological phylogeny of Hardy *et al.* (2008), with only *M. eurythrix* placed outside of the lineage, separated by *M. occultus* Hardy & Gullan. The molecular phylogeny could also be interpreted so that the South American species of “*Madarococcus*” would be placed in a separate taxon, but in this case *M. eurythrix* and *M. navarinoensis* would be included. Apparently, no specimens of *M. chilensis*, *M. rhadinothrix*, or *M. occultus* were available for DNA analysis. Hardy *et al.* (2008) point out that the morphological, DNA, and combined morphological and DNA trees are variable in the placement and support of the South American *Madarococcus* species. Their classification strategy was to minimize disruption to the generally accepted system and still be consistent with their phylogenetic results, but this has left a lack of diagnostic morphological characters for characterizing *Madarococcus*. It appears that more research is needed to clearly understand the species composition of *Madarococcus*, particularly in South America.

***Melzeria* Green**

Melzeria Green 1930: 215–216.

Type species: *Melzeria horni* Green 1930: 215–216.

Generic diagnosis. Adult female (Fig. 28). Adult female broadly oval; without protruding anal lobes. *Dorsum.* Dorsal setae all hairlike; without enlarged spinose setae. Macrotubular ducts of 3 sizes, all with a sclerotised dermal rim; larger ducts each with 1–3 setae on dermal rim; other ducts of medium and small size, without associated setae. Microtubular ducts small, very similar to smallest macrotubular ducts, each with 8-shaped dermal orifice, frequent throughout. Cruciform pores absent. Loculate pores each with 5 loculi, apparently restricted to submargin on thorax. Anal lobes only represented by a long seta. *Margin.* Undefined. *Venter.* Setae hairlike, infrequent. Macrotubular ducts, similar to medium and small types on dorsum; larger ducts mainly in a broad submarginal band, smaller ducts restricted to posterior abdomen. Microtubular ducts, similar to those on dorsum, mainly present submarginally. Small sclerotised areas, which may be ducts, present. Loculate pores, each mainly with 5 loculi, present submarginally and medially on abdomen. Cruciform pores absent. Anal ring simple but widening posteriorly, without pores but with 2 pairs of setae. Antennae 7 segmented. Presence of frontal lobes and antennal tubercles uncertain but probably absent. Labium 2 segmented; setal arrangement unclear. Metathoracic coxae, femur and tibia often with translucent pores. Vulva present between abdominal segments VII and VIII.

Host plant unknown.

Comment: *Melzeria* is a monotypic genus known only from Brazil. The familial placement of this genus was uncertain until the type species was restudied by Miller & Williams (1998). They concluded that *Melzeria* is clearly an eriococcid because of the presence of: (i) enlarged setae on first-instar nymphs; (ii) tibiae with reduced number of setae; (iii) translucent pores on hind legs of adult female; and (iv) microtubular ducts. It is separable from all other adult female South American eriococcids in having the following combination of characters: (i) absence of spinose setae; (ii) some macrotubular ducts with setae associated with orifice; (iii) macrotubular ducts present on both dorsum and venter; (iv) absence of anal lobes; and (v) 7 segmented antennae (Miller & Williams (1998) illustrate this species with 7 segmented antennae but state six in text). We have re-examined the specimens and all specimens have 7 segmented antennae. The relationship of *Melzeria* within the Eriococcidae, however, remains unclear.

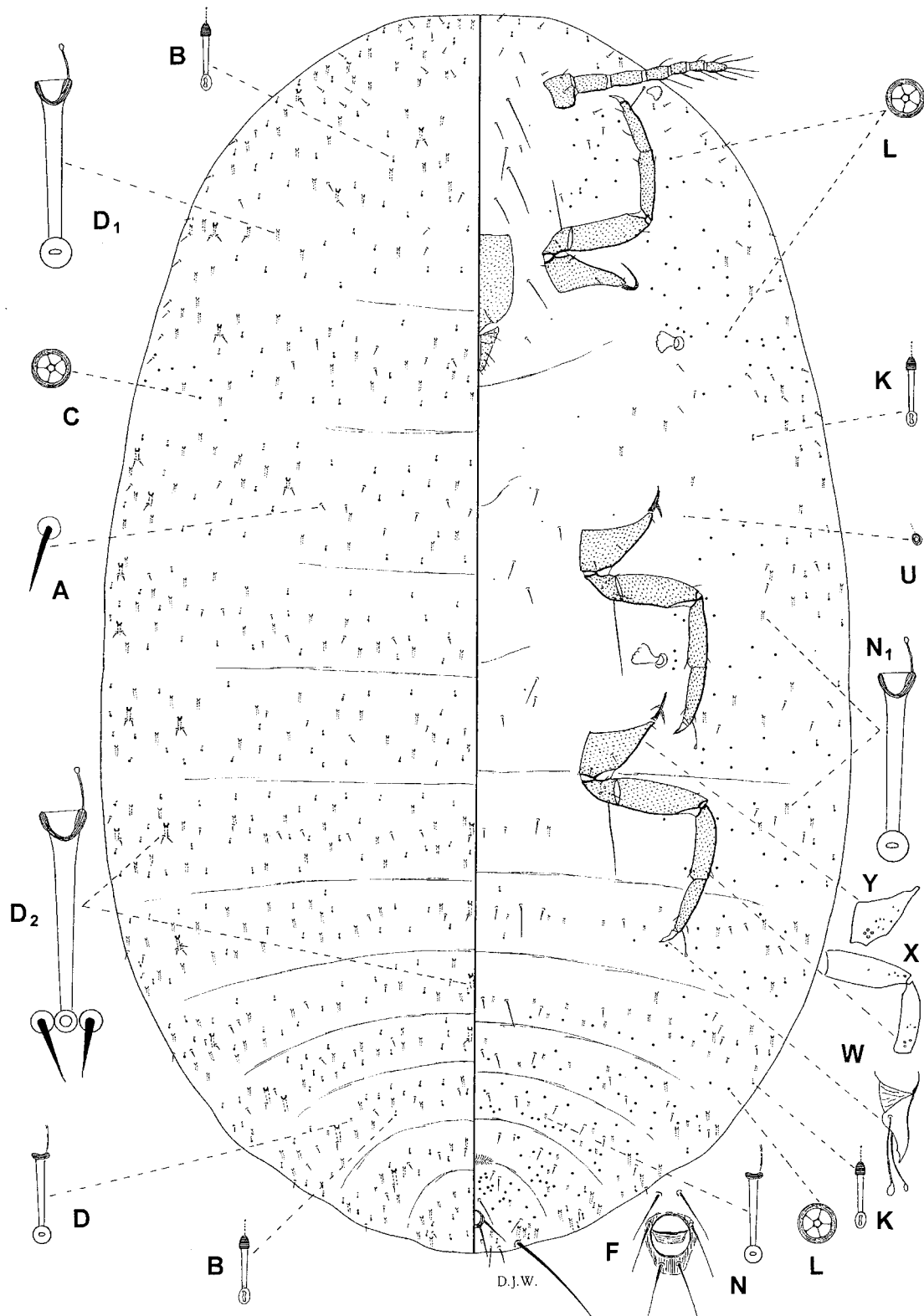


FIGURE 28. *Melzeria horni* Green. Adult female, where A = dorsal seta; B = dorsal microtubular ducts; C = dorsal loculate pore; D, D₁, D₂ = dorsal macrotubular ducts; F = view of anal area; K = ventral microtubular duct; L = ventral loculate pore; N, N₁ = ventral macrotubular ducts; U = cruciform pore; W = claw of metathoracic leg; X = femur and tibia of metathoracic leg, and Y = coxa of metathoracic leg (modified after Miller & Williams, 1998).

Melzeria horni Green

Melzeria horni Green 1930: 215–216.

First-instar nymph (gender not determined) (Fig. 29)

Material examined: BRAZIL: São Paulo, Sanat Amaro, on foliage of unknown plant, no date, Julius Melzer (BMNH, USNM): 2/6 first-instar nymphs in mostly fair to good condition. Probably part of type series.

Unmounted material. Not seen.

Mounted material. Body oval, about equally rounded at both ends. Length about 220–255 μm , width 100–125 μm .

Dorsum. Derm membranous, without obvious dermal spinules. Dorsal setae hairlike, each 2–5 μm long; approximately in 2 medial lines, with pairs on all abdominal segments, 1 pair on pro-, meso- and metathorax, plus 2 pairs on head; also with submarginal setae on meso- and metathorax and on head, plus a possible submedial pair on 1st-abdominal segment. Microtubular ducts with a particularly long outer ductule, each about 16–18 μm long, possibly with a small membranous dermal rim; also with a strongly sclerotised distal end, which appears to have a narrow duct running through it; distributed as follows: with a duct opening located just dorsad to each marginal spinose seta on thorax and abdomen, plus 2 further pairs along margin of head (where marginal spines absent); also with pairs submedially on head, mesothorax and 1st-abdominal segment. Loculate pores and macrotubular ducts absent. Anal lobes absent or rounded, membranous; each with a very long apical flagellate seta about 112–116 μm long. Marginally with 2 pairs of short setae between long apical setae, each about 3 μm long. Anus small, 2 μm wide, without an anal ring or anal ring setae but with 2 minute setae on each side ventrally, each about 1 or 2 μm long. Anus surrounded by a slightly quadrate membranous plate, about 7 μm wide.

Margin. Marginal setae cupolate-shaped, 14 μm long, each with a broad base (3 μm wide) and a short sharp point; each in a dermal pocket of about same depth as length of seta; with 1 pair on each abdominal and thoracic segment but none present on head. Eyespots fairly small, each 6–7 μm wide, situated on margin near base of antennae.

Venter. Derm membranous. Loculate pores with mainly 5 loculi: with 1 immediately laterad to each peritreme plus another near margin on each side of metathoracic segment. Microtubular and macrotubular ducts absent. With 3 pairs of long setae between antennae (anterior pair longest (about 10 μm long) and possibly submarginal); setae mesad of meso- and metacoxae apparently absent; with a pair of small setae (each 2–3 μm long) medially on abdominal segments II–VI; submarginal setae as follows: 1 minute seta on abdominal segments I–VII, 1 or 2 near each thoracic marginal spine and 1 on either side of simple eye; also with 1 on each side of abdominal segment II–VII in an inner submarginal line.

Antennae 6 segmented, about 50–59 μm long; segment IV shortest; setal distribution: scape 1; pedicel probably 0; segments III 0 or 1 setose setae; IV & V 1 setose seta + 1 fleshy seta; VI 3 fleshy setae, 2 short setose setae plus 3 long setae; length of longest about 30 μm . Clypeolabral shield about 60–68 μm long, apparently extended somewhat anteriorly; labium probably 2 segmented, about 28 μm wide, 22 μm long, with possibly 3 pairs of short setae distally near apex. Spiracles very small, peritremes possibly 4 μm wide, probably without lateral membranous cavity. Legs well developed; lengths: (metathoracic leg (μm)): coxa 20–21; trochanter + femur 28–34; tibia 18–20; tarsus 11–13; claw 9; setae: coxae 0?, trochanter 1 longish seta, femur 1, tibia 1 (?), tarsus 2; long trochanter seta 13 μm long; tarsal campaniform sensillum present; claw with a small denticle; both tarsal digitules on all legs capitate and equal in size; claw digitules alike with small capitate apices.

Comment. The first-instar nymphs of *M. horni* are easily separable from those of other eriococcid first-instar nymphs known from the Neotropics in having only setose dorsal setae (all other South American eriococcid first-instar nymphs have some spinose dorsal setae). In addition, the first-instar nymph of *M. horni* has: (i) 6 segmented antennae; (ii) exceptionally long microtubular ducts restricted to the dorsum and margin; (iii) cupolate-shaped marginal spinose setae; (iv) no cruciform pores; (v) single loculate pores laterad to each spiracle; and (vi) anal lobes unsclerotised and not differentiated.

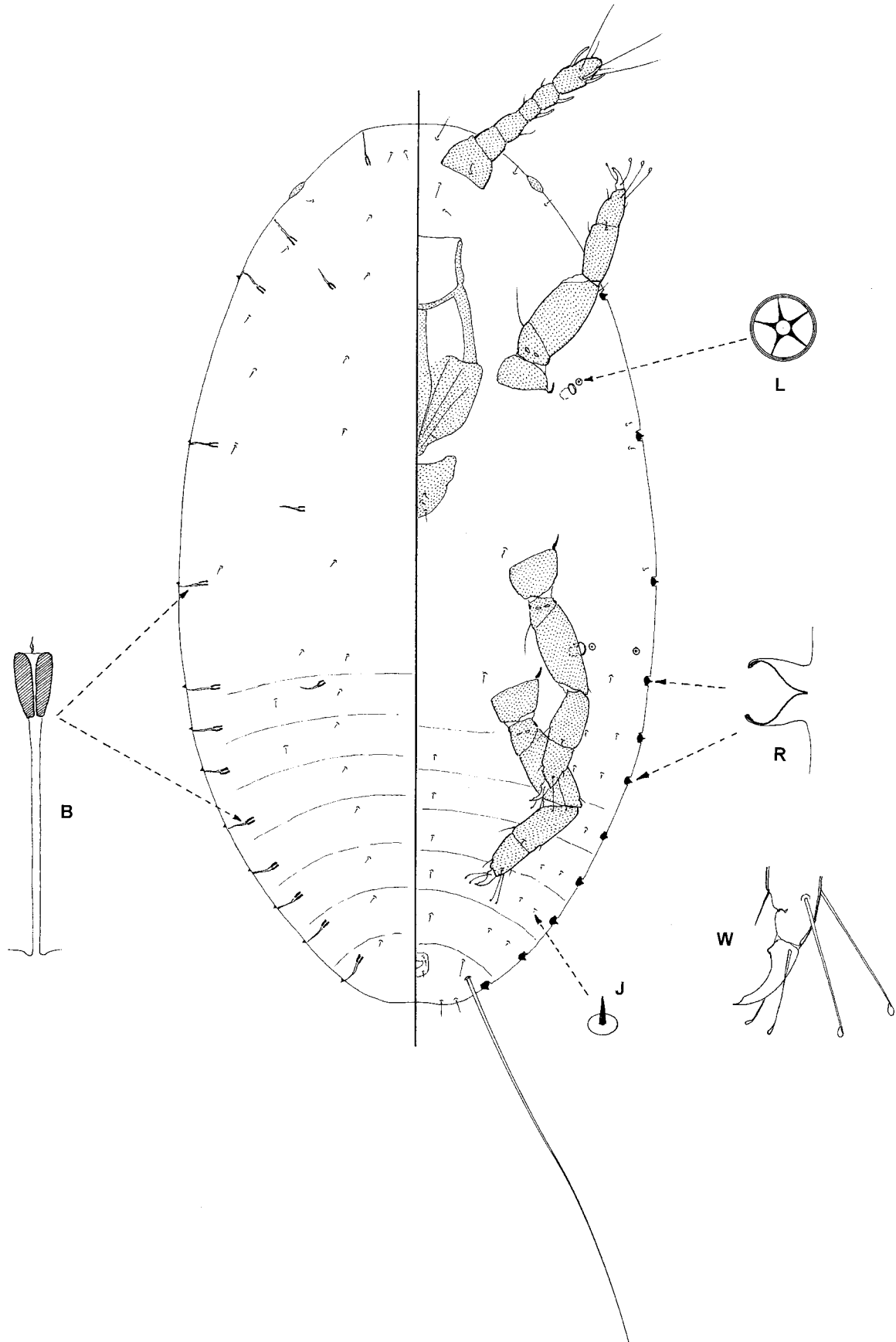


FIGURE 29. *Melzeria horni* Green. First-instar nymph, where B = dorsal microtubular duct; J = ventral seta; L = ventral loculate pore; R = marginal spinose seta, and W = claw of metathoracic leg.

Neotectococcus Hempel

Neotectococcus Hempel, 1937: 5, 19.

Type species: *Neotectococcus lenticularis* Hempel 1937: 5, 19.

Generic diagnosis. Adult female. In life, inducing a lense-like gall on leaves similar to pit scale galls. Adult female with anal lobes absent. *Dorsum.* Derm membranous, covered with small papillae. Setae of 2 types: spinose setae in medial and mediolateral areas of thorax; longer hair-like setae scattered over surface, even among spinose setae on thorax. Macro- and microtubular ducts apparently absent. Loculate pores present. *Margin.* Without demarcation. *Venter.* Setae hairlike, present throughout. Macro- and microtubular ducts apparently absent. Loculate pores present. Cruciform pores apparently absent. Antennae 5–7 segmented. Presence of frontal lobes and antennal tubercles unknown. Segmentation of labium not determined. Legs unusually large, metathoracic legs apparently without translucent pores. Claw digitules thin, difficult to see; claw straight, with denticle. Vulva apparently present between VI and VII (Modified after Hempel, 1937).

Host plant unknown.

Comment. *Neotectococcus* is a monotypic genus known only from Brazil. Based on Hempel's description, the adult female of *Neotectococcus* is characterised by: (i) sclerotised circular area on dorsum of head and thorax with numerous spinose setae; (ii) absence of macro- and microtubular ducts; (iii) absence of anal lobes; (iv) anal ring without pores or setae; (v) loculate pores on venter abundant on abdomen; and (vi) vulva present between abdominal segments VI and VII.

Neotectococcus lenticularis Hempel

Neotectococcus lenticularis Hempel 1937: 5, 19.

Adult female. No material of this species was seen during this study but the original collection details were: BRAZIL, São Paulo, Itatinga, on native shrub, 18.x.1935, collector ? (Instituto Biologico de São Paulo). The following description taken from Hempel (1937).

Unmounted material. Inducing a lens-like gall on leaves when viewed laterally. Gall is similar to pit of pit scales. Upper leaf surface with a concave pit, circular and about 3 mm in diameter. Gall on lower leaf surface, swollen and convex, with a small orifice in center. Gall lighter in colour than leaf.

Mounted material. Length 1.1 mm, width 0.9 mm. Body pear-shaped or cordiform, widest across meso- or metathorax, more pointed posteriorly.

Dorsum. Derm membranous, possibly sclerotised in medial and mediolateral area of thorax, covered with numerous small papillae, segmentation distinct. Dorsal setae of 2 kinds: (i) spinose setae concentrated in medial and mediolateral areas of thorax, straight or slightly curved, with acute apices, becoming smaller laterally, and (ii) setose setae, longer than spinose setae, present in transverse rows on abdomen and abundant elsewhere. Macro- and microtubular ducts apparently absent. Loculate pores present on posterior abdominal segments, and also possibly on thorax near spinose setae. Anal lobes absent. Anal ring without pores and setae.

Margin. Marginal setae hairlike, slightly longer than adjacent dorsal setae, with possibly 3 or 4 on each lateral margin of each abdominal segment. Eyes large and conspicuous, present on venter near body margin.

Venter. Derm membranous. Setae hairlike, longer than on dorsum; spinose setae absent. Macro- and microtubular ducts absent. Cruciform pores absent. Loculate pores present in lateral areas of meso- and metathorax, abundant on abdominal segments. With 10–20 pairs of interantennal setae; with a longer seta mesad to each coxa (about 80 µm long); without elongate setae medially on each abdominal segment.

Antenna 5–7 segmented, each about 190 µm long, located submedially on head; apparently without setae. Clypeolabral shield present; number of labial segments unknown. Spiracles: each peritreme surrounded by a broad sclerotised plate. Legs each well developed but apparently without setae; metathoracic legs: lengths

(μm): coxa 195 wide; trochanter + femur 255; tibia 170, tarsus 42, claw 17; tarsal and claw digitules thin and difficult to see; each claw straight, with a denticle near apex. Vulva present between segments VI and VII.

Comment. Unfortunately, we were unable to obtain specimens of this species and base our description on Hempel (1937). For a comparison of the adult female of this genus with other South American eriococcids see the “Comment” section of the “Generic diagnosis” of *Neotectococcus*.

***Opisthoscelis* Schrader**

Opisthoscelis Schrader 1863: 7

Type species: *Opisthoscelis subrotunda* Schrader 1863: 7 – by subsequent designation by Fernald 1903: 46.

The only species in this genus currently known from South America is *O. prosopidis* Kieffer & Jorgensen (Kieffer & Jorgensen, 1910). *Opisthoscelis* currently contains 15 species, all of which are restricted to Australia apart from *O. prosopidis*, which is known only from the original description from Argentina (Aragon, Alto Pencoso, on *Prosopis adesmiodes*). As pointed out by Lizer y Trelles (1939), the species was only placed in this genus tentatively by Kieffer & Jorgensen and, on the basis of the original description and on the distribution of the other species in the genus, Lizer y Trelles did not believe that this species belonged to *Opisthoscelis*. This was also the view of Hoy (1963). Miller & Gimpel (2000) state that the type status and type designation are unknown, and no depository is known. The original description does have an illustration of the gall and it may be possible in the future to clarify the identity of this species by finding similar galls on *Prosopis* species in the type locality. Until such time, it is felt best to assume that this species is unidentifiable and that it is unlikely to belong to *Opisthoscelis* Schrader.

***Orafortis* Hardy**

Orafortis Hardy: in Kondo, Hardy, Cook and Gullan, 2006: 29–30.

Type species: *Orafortis luma* Hardy, in Kondo, Hardy, Cook and Gullan, 2006: 30–33.

Generic diagnosis. Adult female (Fig. 30). In life, covered by spiky test, cryptic on hairy stems or stem axils. Adult female with sclerotised anal lobes, protruding posteriorly; suranal seta slightly enlarged. *Dorsum*. Derm nodulose, sclerotised posteriorly. Setae spinose, of 1 size except posteriorly where smallest. Macrotubular ducts of 2 sizes: smaller size with sclerotised rim; larger size without rim. Microtubular ducts with longitudinal division, often associated with base of spinose setae. Loculate pores absent. *Margin*. Undefined. *Venter*. Setae hairlike medially, spinose laterally, smaller than dorsal setae except on head where about same size. Macrotubular ducts of small size only, most abundant posteriorly. Microtubular ducts absent. Loculate pores primarily quinquelocular. Cruciform pores absent. Antennae 6 segmented. Frontal lobes and antennal tubercles absent. Labium 3 segmented; basal segment with 1 pair of setae. Metathoracic legs with translucent pores on coxa. Claw digitules similar; claw with denticle. Vulva present between VII and VIII.

Known only from Myrtaceae.

Comments. *Orafortis* is a monotypic genus known only from Chile. For a detailed description of the adult female, see Kondo *et al.* (2006), who considered that *O. luma* was superficially like *Eriococcus* Targioni Tozzetti (all species currently in the genus *Eriococcus* from South America are here considered to belong to other genera (See Appendix 1)) but can be distinguished from all those known from Chile in having: (i) distinct sclerotic rims around dermal orifices of macrotubular ducts; (ii) sclerotic nodules on dorsal surface of posterior abdominal segments; (iii) microtubular ducts opening at bases of enlarged dorsal spinose setae; and (iv) 2 sizes of dorsal macrotubular ducts. Kondo *et al.* discuss the differences between *O. luma* and other *Eriococcus* (*Acanthococcus*) species from Myrtaceae from Chile. Kondo *et al.* (2006) also make some comments on the structure of the first-instar nymph of *O. luma* but do not describe it in detail.

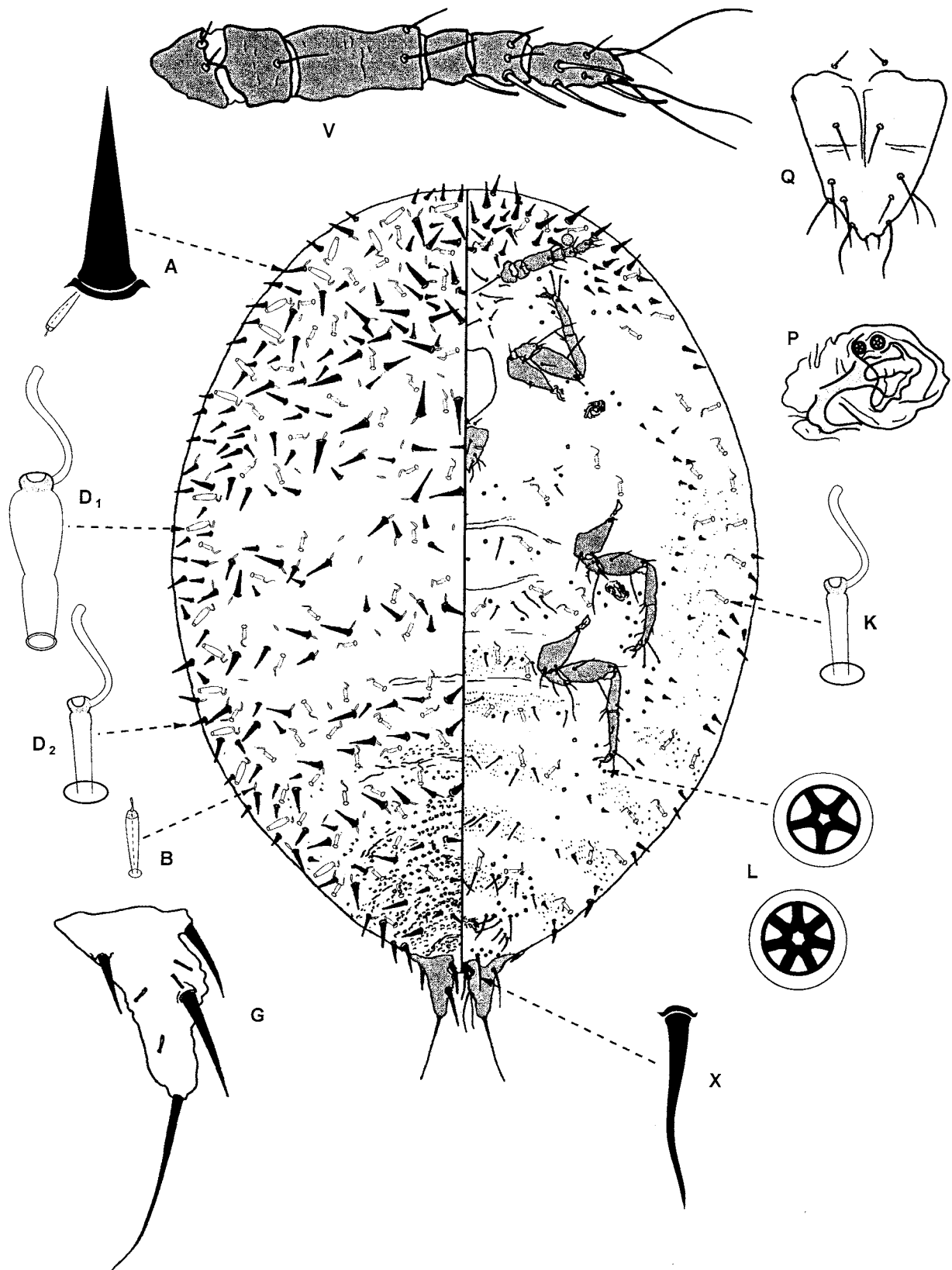


FIGURE 30. *Orafortis luma* Hardy. Adult female, where A = dorsal spinose seta with associated microtubular duct; B = microtubular duct; D₁, D₂ = dorsal macrotubular ducts; G = dorsal view of anal lobe; K = ventral macrotubular duct; L = ventral loculate pore; Q = labium; P = spiracle with loculate pores; V = antenna, and X = suranal seta (modified after Kondo *et al.*, 2006).

Oregmopyga Hoy

Oregmopyga Hoy, 1963: 179 (replacement name for *Onceropyga* Ferris, 1955: 208).

Type species: *Eriococcus neglectus* Cockerell, 1895: 8.

Generic diagnosis. Adult female (Fig. 31). Oval, often becoming rotund when gravid. Body covered in feltlike sac. *Dorsum*. Setae often of 2 types: (i) spinose, short and broadly conical, with a broad basal socket, and (ii) smaller setose setae. Macrotubular ducts present or absent, when present, without a sclerotised dermal rim. Microtubular ducts present, without protruding orifice; inner ductule divided into sclerotised and unsclerotised halves. Loculate pores present, each with 5–7 loculi. Anal lobes present, unsclerotised. *Margin*. Undefined. *Venter*. Body setae slender. Macrotubular ducts present, similar to those on dorsum. Microtubular ducts present or absent. Loculate pores present. Cruciform pores present or absent. Anal ring ventral, complete, with or without pores and setae. Antennae 6 or 7 segmented. Frontal lobes present on *O. neglecta* but absent on *O. peruviana* Granara de Willink & Diaz; antennal tubercles absent on *O. neglecta* but present on *O. peruviana*. Labium 3 segmented; basal segment with 2 pairs of setae. Legs relatively small; hind coxae with or without translucent pores; tarsal and claw digitules with expanded, equal-sized apices; claws with small subapical denticle. Vulva present between segments VII and VIII.

On various plant families including Poaceae.

Comment. The genus *Oregmopyga* is mainly restricted to North America. However, a single species, *O. peruviana* Granara de Willink & Diaz, has been described from Peru on *Vitis* sp. (Vitaceae) by Granara de Willink & Diaz (2007). Their paper includes a key to the adult females of all 10 species of *Oregmopyga*. *Oregmopyga* is very similar to *Ovaticoccus* Kloet (diagnosed below) but differs in having anal lobes and usually having pores in the anal ring.

First-instar nymph. Generic diagnosis (based on *O. peruviana* Granara de Willink & Diaz) (Fig. 32).

Mounted material. Body oval. *Dorsum*. Enlarged setae (including marginal setae) of 1 size, arranged in 3 pairs of longitudinal lines on abdomen, and in 2 pairs on thorax and head. Macrotubular ducts absent. Microtubular ducts few, scattered. Loculate pores absent. Anal lobes small, unsclerotised. Medial plate absent. *Margin*. Marginal setae as described above. Anal ring without anal tube but with pores and 6 anal-ring setae. *Venter*. Loculate pores, each with 5 loculi, in a submarginal line on abdomen, plus single pores associated with each spiracle, near clypeolabral shield and on head. Macrotubular and microtubular ducts absent. Cruciform pores present near margin. Suranal setae hairlike. Ventral setae arranged segmentally. Antennae 6 segmented. Labium probably 3 segmented, number of setae on basal segment unknown. Legs well developed; each with tibia shorter than tarsus; tarsal and claw digitules similar and capitate; claw with denticle. (Modified after Granara de Willink & Diaz, 2007).

Comment. Of the genera known from the Neotropics for which the first-instar nymphs are known, only *Exallococcus*, *Icelococcus* and *Pseudotectococcus* share with *Oregmopyga* the presence of cruciform pores. The first-instar nymph of *O. peruviana* differs from all of them in having non-sclerotised anal lobes. It also differs from those of *Exallococcus* in having (character-states for *Exallococcus* in brackets): (i) only spinose setae on dorsum (hair-like setae present as well as spinose setae); (ii) no median plate (present); and (iii) ventral loculate pores present in a submarginal band on abdomen (submedially on abdomen). It differs from those of *Icelococcus* in having (character-states on *Icelococcus* in brackets): (i) short, stout dorsal spinose setae (long and narrow); (ii) only 1 type of dorsal seta (hair-like setae present in addition to spinose setae); (iii) all ventral loculate pores mainly quinquelocular (trilocular); and (iv) ventral loculate pores on abdomen submarginal (submedial). It differs from the first-instar nymphs of *Pseudotectococcus* in having (character-states on *Pseudotectococcus* in brackets): (i) antennae 6 segmented (3 segmented); (ii) dorsal setae more abundant on abdomen than on thorax (more abundant on thorax than on abdomen); (iii) ventral setae in three pairs of longitudinal lines on abdomen (only submarginally); and (iv) loculate pores present submarginally on abdomen (absent on abdomen).

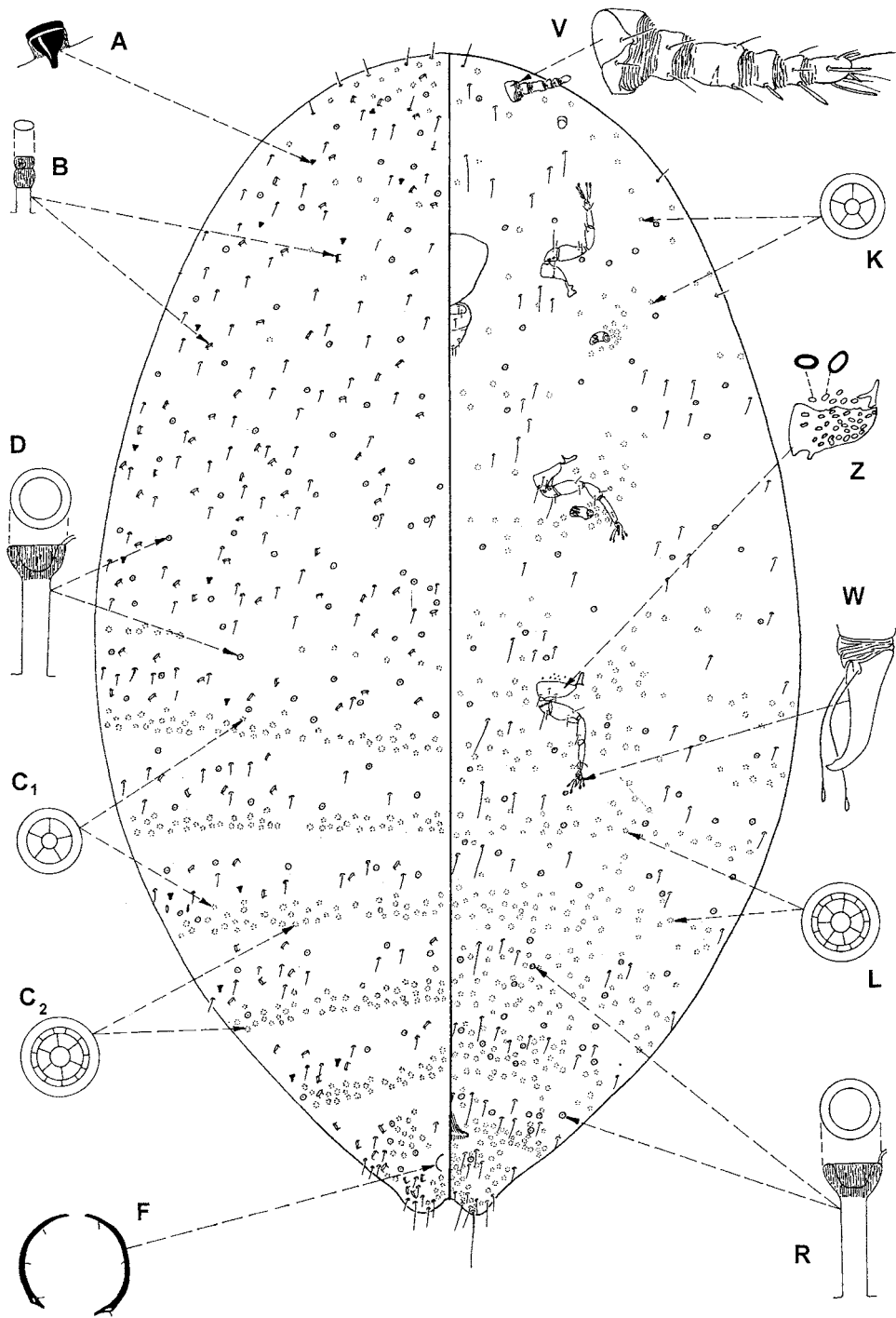


FIGURE 31. *Oregmopyga neglecta* (Cockerell). Adult female, where A = dorsal seta; B = dorsal microduct, C₁ & C₂ = dorsal loculate pores; D = dorsal macroduct; F = anal ring; K & L = ventral loculate pores; R = ventral microduct; V = antenna; W = claw and Z = metathoracic coxa with coxal pores (modified after Miller and McKenzie, 1967).

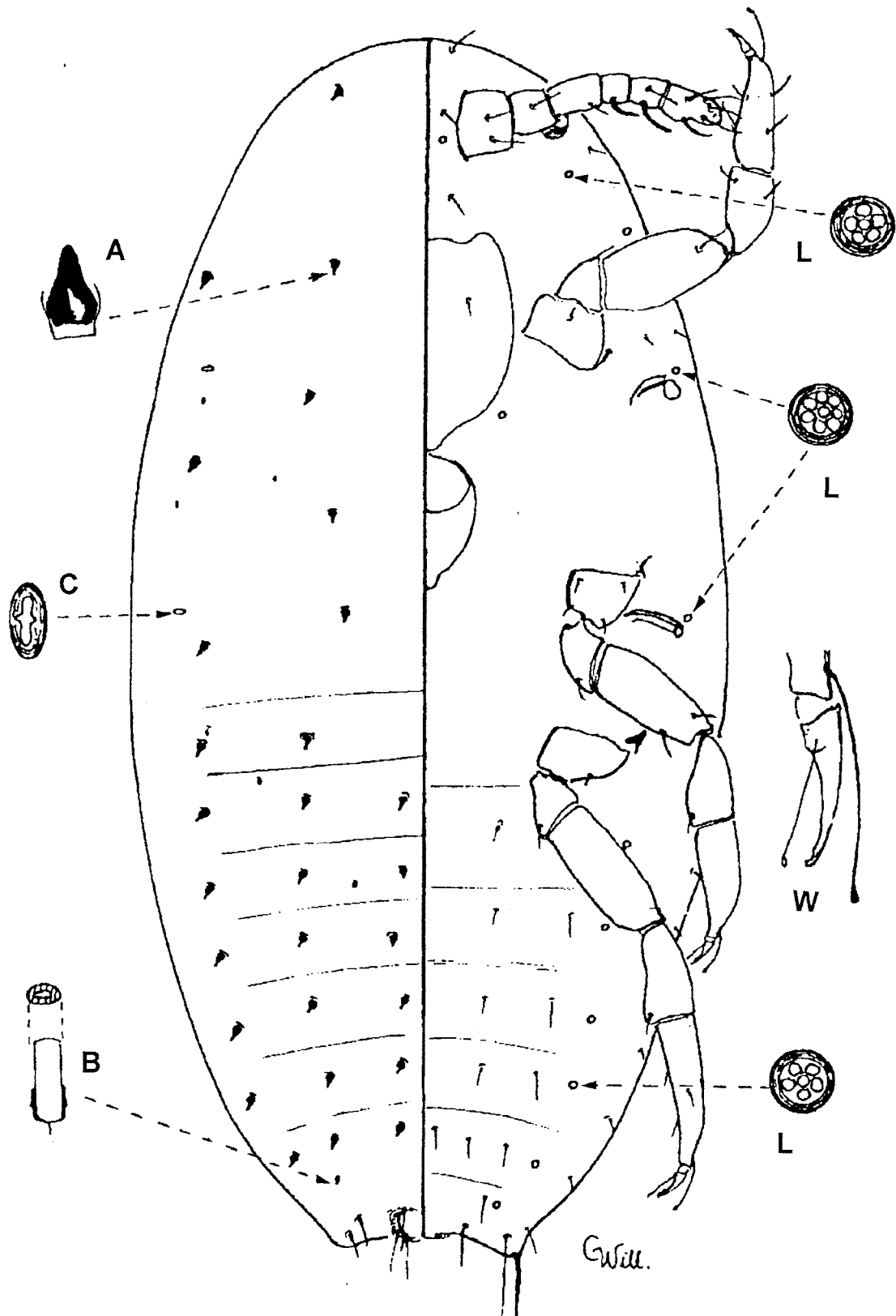


FIGURE 32. *Oregmopyga peruviana* Granara de Willink & Diaz. First-instar nymph, where A = dorsal spinose seta; B = dorsal microtubular duct; C = ventral cruciform pore; L = ventral loculate pore; W = distal end of leg (modified after Granara de Willink & Diaz, 2007)

Ovaticoccus Kloet

Ovaticoccus Kloet 1944: 86.

Type species: *Coccus agavium* Douglas, 1888: 150.

Generic diagnosis. Adult female (Fig. 33). Oval, often becoming rotund when gravid. Body covered in white bloom. Secretes a loose, poorly defined ovisac. *Dorsum*. Setae generally of 2 types: (i) spinose, short and broadly conical, with a broad basal socket, arranged in 3 pairs of longitudinal lines; and (ii) smaller setose setae. Macrotubular ducts without a sclerotised dermal rim. Microtubular ducts present, without protruding orifice; inner ductule divided into sclerotised and unsclerotised halves. Loculate pores present, each with 5–7 loculi. Anal lobes absent. *Margin*. Undefined. *Venter*. Body setae slender. Macrotubular ducts present, similar to those on dorsum. Microtubular ducts present or absent. Quinquelocular pores present. Cruciform pores present. Anal ring ventral, incomplete, without pores, composed of 2 sclerotised crescents. Antennae 6 or 7 segmented. Frontal lobes present but antennal tubercles absent. Labium 3 segmented; basal segment with 2 pairs of setae. Legs relatively small: hind coxae with or without translucent pores; tarsal and claw digitules with expanded, equal-sized apices; claws with small subapical denticle. Vulva present between segments VII and VIII. (Modified after Boratynski, 1958, and Miller & Miller, 1993).

Known from a diversity of hosts.

Comments. *Ovaticoccus* currently contains 11 species, mostly from the United States of America. Only *O. lahillei* (Leonardi) has been recorded from South America, in Argentina. Recently, González (2009) redescribed the adult female of *O. lahillei* based on cotype material, described the first-instar nymph and transferred it to *Eriococcus*. We agree with this decision but, because we consider all South American *Eriococcus* are better placed in *Acanthococcus* as discussed under *Acanthococcus* above, we here transfer this species to *Acanthococcus*, i.e., *A. lahillei* **n. comb.** However, based on the present distribution of *Ovaticoccus*, there seems little reason to doubt that this genus will be found in South America in the future.

Poliloculus González

Poliloculus González, 2008b: 12–13.

Type species: *Poliloculus stipae* González, 2008b: 13–15.

Generic diagnosis. Adult female (Fig. 34). Habit not described. Body approximately round. *Dorsum*. Membranous throughout; segmentation rather obscure. Setae few, all narrow, blunt, with parallel sides; infrequent. Macrotubular ducts small; present submarginally on abdomen. Microtubular ducts minute, extremely sparse. Loculate pores absent. Anal lobes triangular, short and lightly sclerotised; median lobe present. *Margin*. Indicated by a line of setae similar to those on dorsum. *Venter*. Membranous. Setae fairly long; sparse. Macrotubular ducts similar to those on dorsum; sparse across abdominal segments. Ventral microtubular ducts similar to those on dorsum; very sparse submarginally. Loculate pores, each with mainly 5–9 loculi; present across all abdominal segments and in a dense group associated with each spiracular atrium. Cruciform pores present on head and prothorax. Anus with a single ring of pores and 5 pairs of anal ring setae. Antenna small, 6 segmented. Frontal lobes and antennal tubercles apparently absent. Clypeolabral shield normal; labium 3 segmented, with 2 pairs of setae on basal segment. Legs quite well developed but small; metacoxae with translucent pores; claws without a denticle. Vulva present between abdominal segments VII and VIII.

Known only from Poaceae.

Comments. *Poliloculus* is a monotypic genus known only from the original collection in Argentina. According to González (2008b), this genus is similar to *Spiroporococcus* Miller (known only from the Nearctic) because both genera have a concentration of loculate pores near the opening of the spiracles and both occur on grasses. *Spiroporococcus* differs in having 3 pairs of poorly developed anal ring setae (5 pairs of conspicuous setae on *Poliloculus*), loculate pores with primarily 5 loculi (5–9 in *Poliloculus*), claw with a denticle (absent in *Poliloculus*), and 7-segmented antennae (6 in *Poliloculus*). Other important characters of

Poliloculus are: (i) dorsal setae very sparse; (ii) anal lobes small; (iii) median plate present; and (iv) macrotubular and microtubular ducts present on both surfaces.

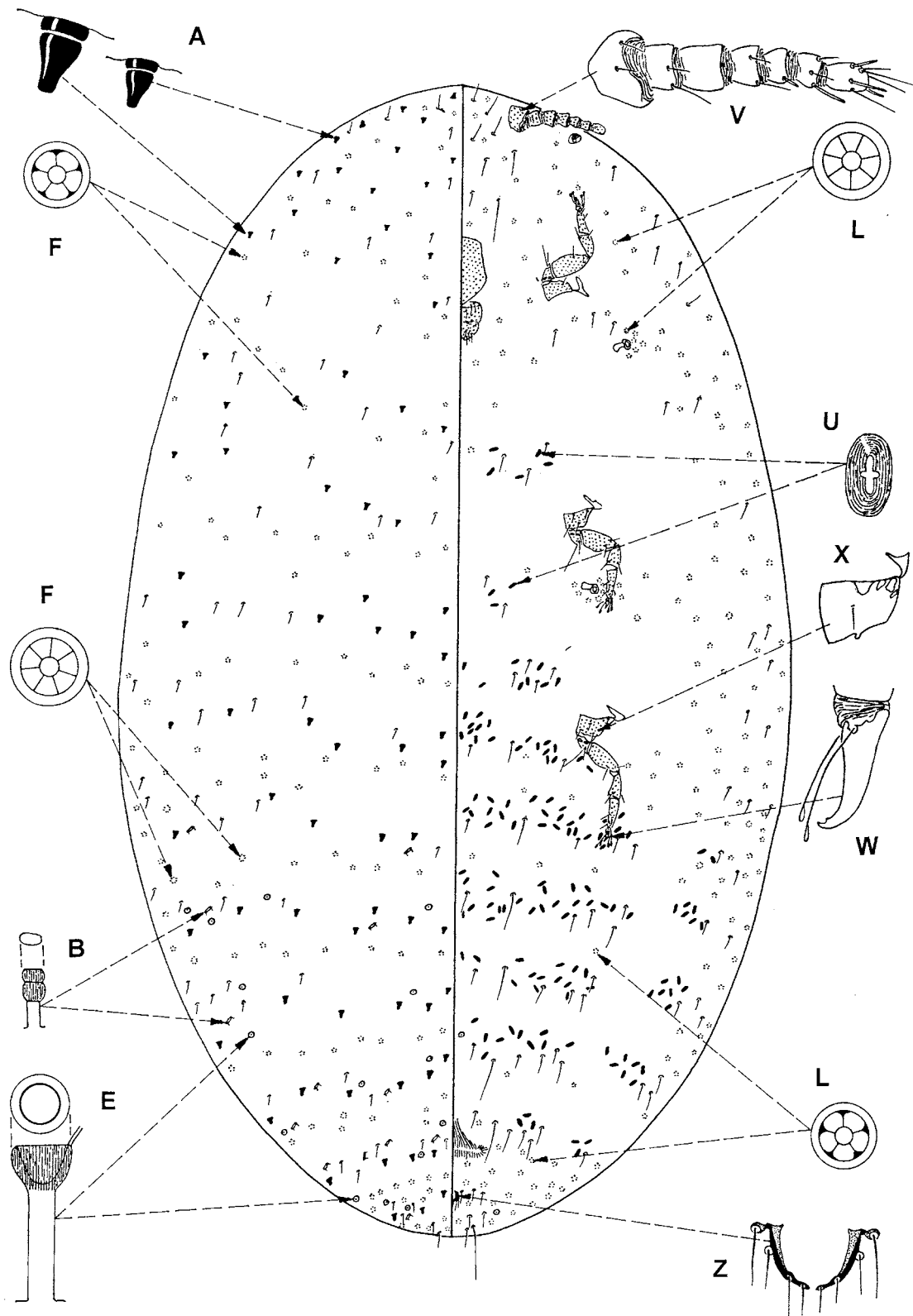


FIGURE 33. *Ovatococcus agavium* (Douglas). Adult female, where A = dorsal spinose setae; B = dorsal microtubular duct; E = dorsal macrotubular duct; F = dorsal loculate pores; L = ventral loculate pores; U = cruciform pore; W = claw; X = coxa, and Z = anal area (modified after Miller & McKenzie, 1967).

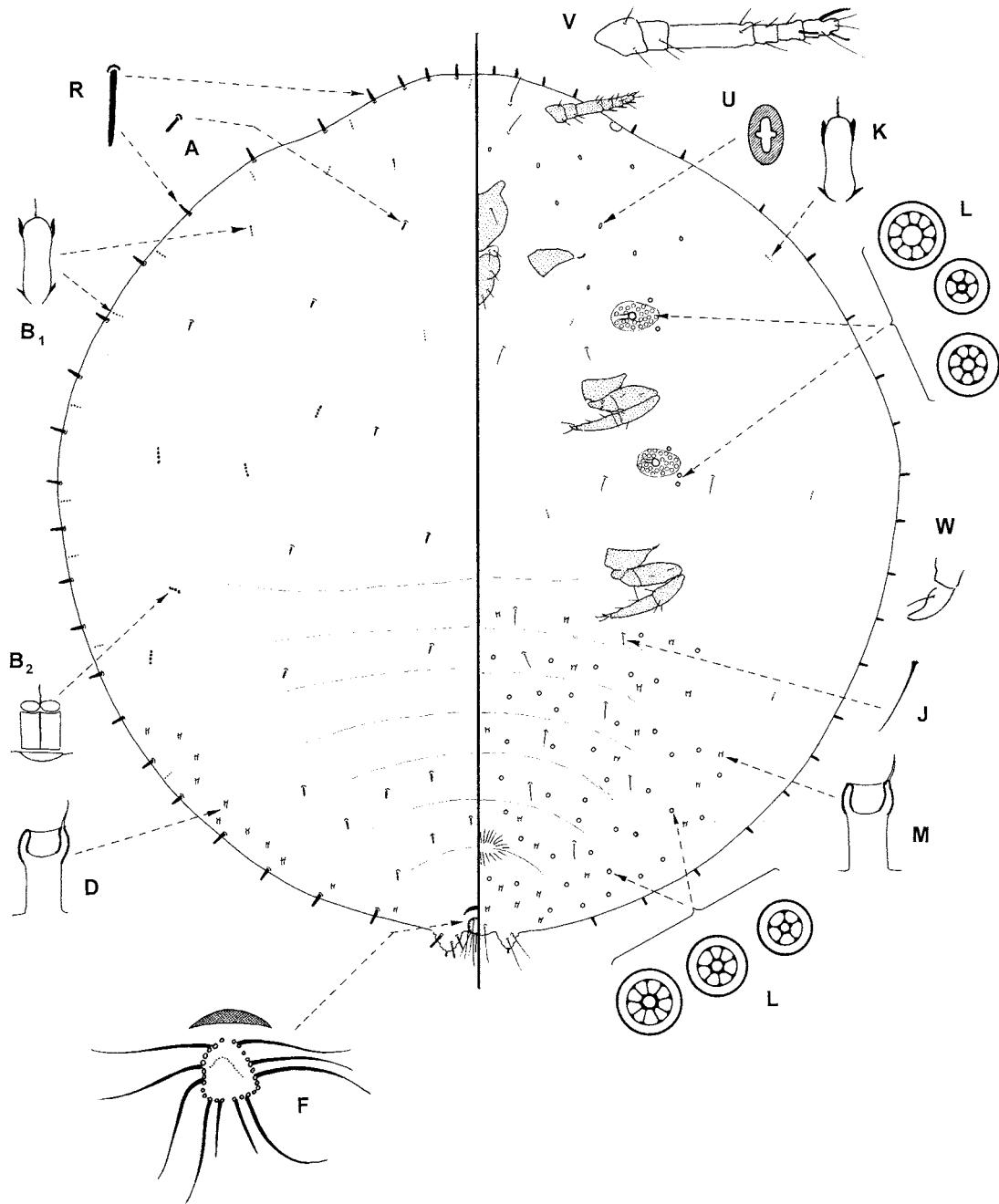


FIGURE 34. *Poliloculus stipae* González. Adult female, where A = dorsal seta; B₁, B₂ = dorsal microtubular ducts; D = dorsal macrotubular duct; F = view of anal area; J = ventral seta; K = ventral microtubular duct; L = ventral loculate pores; M = ventral macrotubular duct; U = cruciform pore; V = antenna, and W = claw of metathoracic leg (redrawn and modified after González, 2008).

Pseudocapulinia Hempel

Pseudocapulinia Hempel 1932: 319.

Type species: *Pseudocapulinia lanosa* Hempel 1932: 319–320.

Generic diagnosis. Adult female (Fig. 35). In life, covered in soft white wax. Body approximately egg shaped, widest across thorax, more pointed posteriorly. *Dorsum*. Membranous throughout; segmentation rather obscure. Setae few, all rather short and thin. Macrotubular ducts small; most abundant near margins. Microtubular ducts minute, frequent throughout except posterior abdominal segments. Loculate pores absent.

Anal lobe membranous and short. *Margin*. Undefined but probably marked by a line of slightly larger and more spinose setae. *Venter*. Membranous. Setae short and very sparse as on dorsum. Macrotubular ducts similar to those on dorsum. Ventral microtubular ducts similar to those on dorsum; sparse throughout. Loculate pores each with mainly 5 loculi; present in groups in a cavity laterad to each spiracular peritreme and sparsely in submarginal areas of each thoracic segment. Cruciform pores absent. Anus variable, sometimes without an anal ring but with a sclerotised bar along anterior margin; other times with complete ring around opening; with 3 pairs of short setae along posterior margin. Antenna reduced, 5 or 6 segmented. Frontal lobes and antennal tubercles absent. Clypeolabral shield proportionately quite large; labium probably 2 segmented, with 1 pair of setae on basal segment. Legs entirely absent. Vulva present in a distinct fold between abdominal segments VII and VIII.

Host plant unknown.

Comment. *Pseudocapulinia* is a monotypic genus known only from Brazil. The adult female differs from other South American genera by having the following combination of characters: (i) legs absent; (ii) loculate pores restricted to thoracic areas near spiracles but absent from abdomen; (iii) anal ring highly reduced, without pores; (iv) without conspicuously enlarged setae; (v) macro- and microtubular ducts present on both dorsum and venter; and (vi) antennae reduced, 5 or 6 segmented.

Pseudocapulinia lanosa Hempel

Pseudocapulinia lanosa Hempel 1932: 319–320.

Material examined: BRAZIL: São Paulo, Itarari, on forest tree, Aug. 20th 1928, A. Hempel (USNM): 3/3adff (in good condition) + 1/6 first-instar nymphs (in good condition) + 1/1 second-instar nymph (in good condition). After his retirement, Adolfo Hempel sent “cotype” specimens of 34 Brazilian scale species to Harold Morrison on March 4, 1940. Part of this series included the specimens mentioned above. We have not selected a lectotype from the series because we believe the primary type should be deposited in a Brazilian collection.

Adult female (Fig. 35)

Unmounted material. Body of adult female covered in soft white wax which indicates position of insects in crevices in bark of trunk of host.

Mounted material. Length 1.19 mm, width 0.93 mm. Body approximately egg shaped, widest across thorax, more pointed posteriorly.

Dorsum. Membranous throughout; segmentation rather obscure, most obvious on abdomen; derm surface of posterior abdominal segments thrown into shallow ridges. Dorsal setae few, all rather short, varying in length from about 2.5 μm long medially to about 8 μm long nearer margins. Macrotubular ducts small, each long and narrow (about 15–18 μm long, and 1.5–2.0 μm wide); most abundant near margins but also with a few more medially, especially on more posterior abdominal segments. Microtubular ducts minute, each about 1.0–1.5 μm long; frequent throughout except absent on posterior abdominal segments. Loculate pores absent (a single pore noted on abdominal segment III). Eyespots apparently absent. Anal lobe membranous and short, about 30 μm long, 33 μm wide at base; with a long apical seta (probably at least 150 μm long but broken); apparently with only 1 other seta, about 12 μm long, on ventral surface. With a single pair of spinose setae along ventral outer margin posterior to anus, each about 10 μm long.

Margin. Undefined but probably marked by a line of slightly larger and more spinose setae, each about 8–10 μm long.

Venter. Membranous. Ventral setae very sparse and short, as on dorsum; with perhaps 3 pairs of short setae between antennae, 3 pairs of short setae approximately in position of procoxae and single setae in position of meso- and metacoxae. Macrotubular ducts similar in structure to those on dorsum and rather similarly distributed but perhaps with a slight concentration medially on prothorax. Ventral microtubular ducts

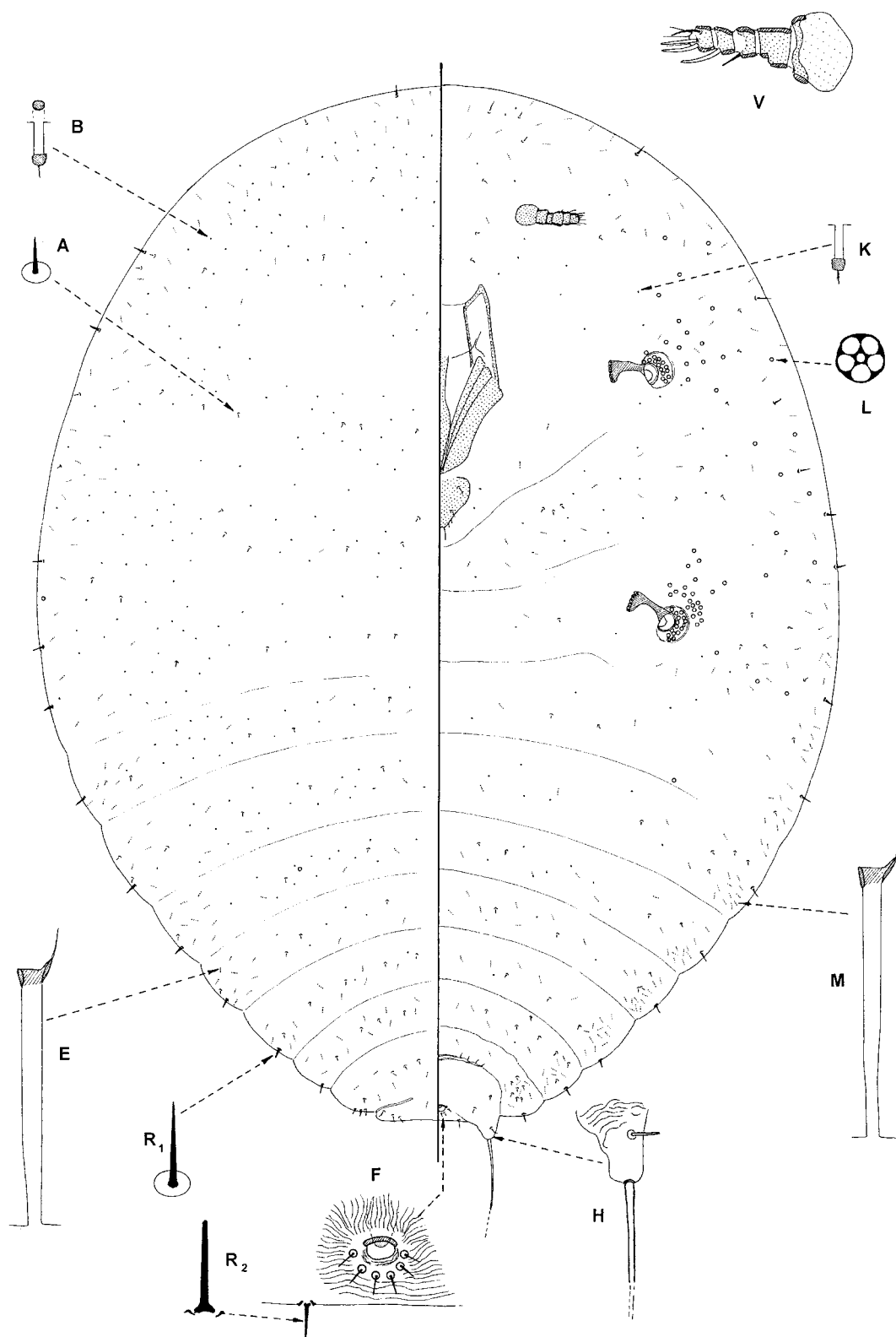


FIGURE 35. *Pseudocapulinia lanosa* Hempel. Adult female, where A = dorsal seta; B = dorsal microtubular duct; E = dorsal macrotubular duct; F = view of anal area; H = ventral view of anal lobe; K = ventral microtubular duct; L = ventral loculate pore; M = ventral macrotubular duct; R₁, R₂ = marginal setae, and V = antenna.

similar to those on dorsum; sparse throughout. Loculate pores each about 3.0–3.5 μm wide, with mainly 5 loculi; present in groups of about 14–20 in a cavity laterad to each spiracular peritreme; also sparse in submarginal areas of each thoracic segment. Cruciform pores absent. Anus ventral, some specimens without

an anal ring but with a sclerotised bar anteriorly, other specimens with complete ring around opening; also with a lightly sclerotised tongue-like structure internally; width of anal opening 11 μm . Anus with 3 pairs of short setae posteriorly, each 6–7 μm long, without anal ring pores.

Antenna reduced, 5 or 6 segmented although basal 2 segments sometimes appear fused; each antenna about 68–74 μm long; apparently without setae on segments I–III, segment IV with 1 strong seta; V with 1 fleshy seta and VI probably with 3 fleshy setae and about 3 other setae, none long. Clypeolabral shield proportionately quite large, about 215 μm long; labium probably 2 segmented, with 1 pair of setae on proximal segment and 4 pairs on distal segment, longest about 13 μm . Spiracles: width of peritremes about 25 μm . Legs entirely absent. Vulva present in a distinct fold between abdominal segments VII and VIII, with 4 pairs of setae along anterior margins.

Comment. For a comparison of the adult female of this genus with other South American eriococcids see the “Comment” section of the “Generic diagnosis” of *Pseudocapulinia*.

First-instar nymph (sex not determined) (Fig. 36)

Unmounted material. Not recorded.

Mounted material. Body oval. Length 305–400 μm , width 140–200 μm .

Dorsum. Derm membranous, with dermal spinules most obvious on posterior abdominal segments. Dorsal setae strongly spinose, tending to swell towards base, with a narrow basal socket; in 3 pairs of longitudinal lines, although those on head and prothorax more randomly placed; setae in median and submedian lines each 2.5–3.5 μm long, those in submarginal lines 3.5–5 μm long; those on abdominal segment VII distinctly larger, each 5–8 μm tall. Microtubular ducts minute, less than 1 μm long; with a pair on each thoracic segment, and on abdominal segments V and VI. Macrotubular ducts and loculate pores absent. Anal lobes absent.

Margin. Marginal setae strongly spinose, similar in shape to those on dorsum but distinctly larger, particularly on posterior abdominal segments, where each 9–10 μm long; those on head 3–4.5 μm long; with 2 anteriorly on head, 4 on each side between eyes and point opposite anterior spiracles, 3 on each side laterally between anterior spiracles and abdomen and with 1 on each side of abdominal segments I–VII. Posterior margin of abdomen with 2 pairs of spinose setae appearing to be on dorsal surface, medial pair each 5–6 μm long, lateral pair 8–12 μm long, plus an apparently ventral pair posterior to anus, each 5–6 μm long. Also with 2 pairs of long setose setae posteriorly, 1 pair very long, each 100–125 μm long, other shorter, each 40–45 μm long. Eyespots fairly small, each 9–12 μm wide, situated on margin posterior to base of antennae.

Venter. Derm membranous, with dermal spinules particularly obvious on posterior abdominal segments but smaller than those on dorsum. Loculate pores with mainly 5 loculi: with 2 or 3 within each cavity associated with each spiracular opening; also with 1 pore near margin just posterior to each posterior spiracle. Microtubular ducts minute, apparently similar to those on dorsum, with pairs submarginally on abdominal segments VI and VII, submarginally just posterior to each anterior spiracle and also laterad to clypeolabral shield. With 3 pairs of long setae between antennae (longest 23–28 μm long); a minute seta present posterior to each procoxa; longer setae laterad to each meso- and metacoxa; plus pairs medially on abdominal segments II–VII (each 8–12 μm long) plus pairs of submedial setae on abdominal segments IV–VII. Submarginal setae hairlike and minute, with a pair on each abdominal segment; apparently absent more anteriorly. Anus almost round, apparently placed ventrally, with a distinct sclerotised anal ring without setae or pores; anus about 5–6 μm wide, with, on each side, a small spinose seta 5–6 μm long, plus a setose seta 6–8 μm long.

Antennae 6 segmented, 63–76 μm long; segments II–V rather ring-like, about as wide as long; setal distribution: scape 4; pedicel 2 + campaniform sensillum; segment III 3; IV 1 setose seta (hs) + 1 small fleshy seta (fs); V 4 or 5 hs + 1 large fs; VI 2 fs, about 7 shortish hs plus 2 long setae, length of longest about 35–40 μm . Clypeolabral shield about 70–85 μm long; labium probably 2 segmented, division indicated by inconspicuous fold with perhaps 4 or 5 pairs of short setae + 1 pair of rather long setae on apex, each 11–13 μm long, without setae on basal segment. Spiracles small, each cavity about 10–12 μm wide, sclerotised opening about 6.5–7.5 μm wide. Legs well developed; lengths (metathoracic leg (μm)): coxa 18–20 wide; trochanter + femur 35–42; tibia 18–22; tarsus 13–16; claw 9–10; tibia clearly longer than tarsus; setae: coxae 4, trochanter 2, femur 2, tibia 4, tarsus 2 or 3; long trochanter seta 26–30 μm long; tarsal campaniform

sensillum present; tarsal digitules on all 3 pairs of legs capitate and equal in size; claw digitules alike with minute capitate apices. Claw narrowing abruptly at proximal end and then margins almost parallel; with a distinct denticle.

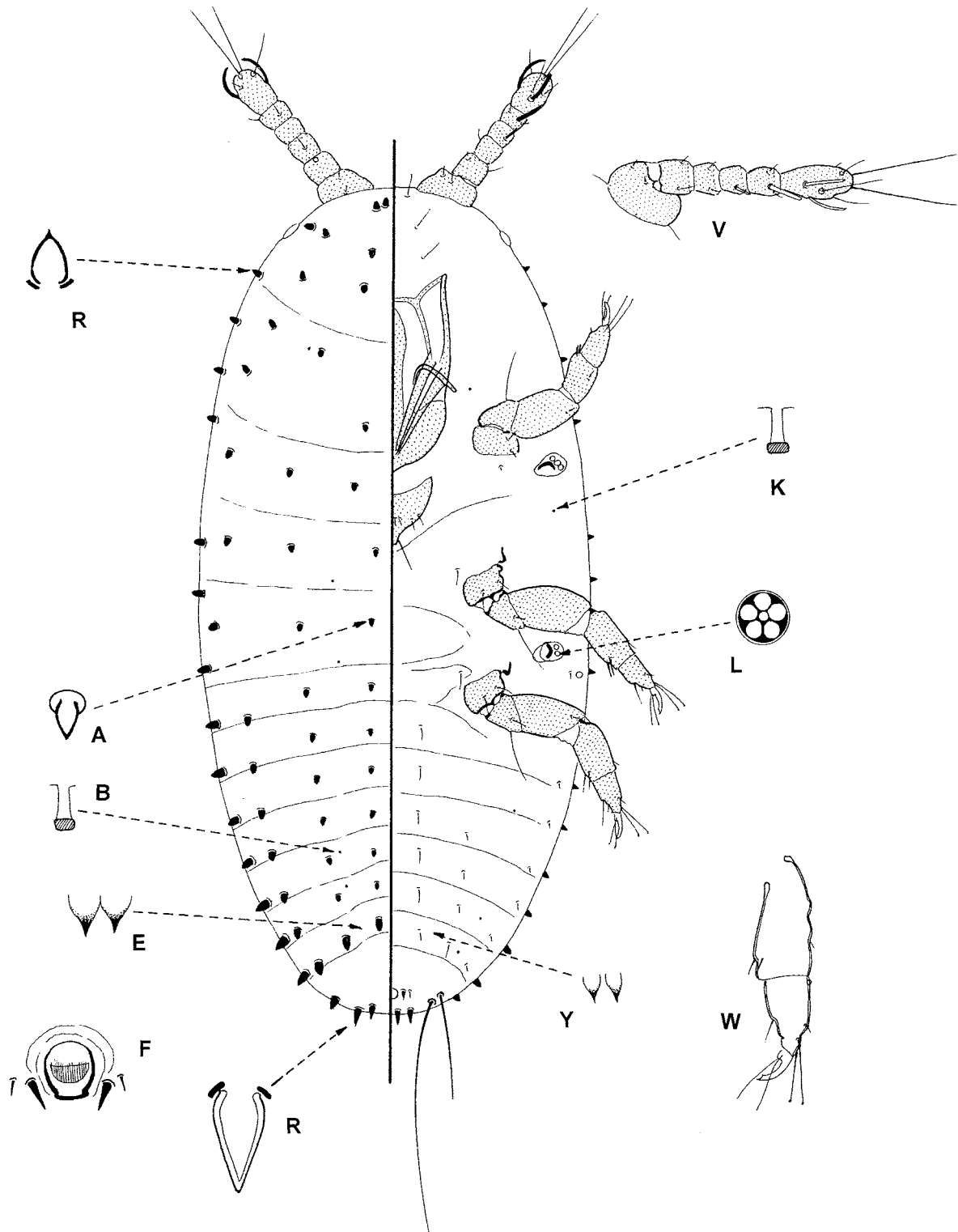


FIGURE 36. *Pseudocapulinia lanosa* Hempel. First-instar nymph, where A = dorsal spinose seta; B = dorsal microtubular duct; E = dorsal dermal spinules; F = view of anal area; K = ventral microtubular duct; L = ventral loculate pore; R = marginal spinose seta; V = antenna; W = distal end of metathoracic leg, and Y = ventral dermal spinules.

Comment. The first-instar nymphs of *P. lanosa* are rather typical eriococcid crawlers, having: (i) 6 segmented antennae; (ii) anal lobes unsclerotised and not differentiated; (iii) dorsal setae of 1 type only,

broadly spinose; (iv) microtubular ducts present on both dorsum and venter; (v) cruciform pores absent; and (vi) loculate pores more or less restricted to cavity laterad to each spiracle (plus 1 near margin near each posterior spiracle). They differ from those of other species in having the following combination of characters: (i) antennae 6 segmented; (ii) loculate pores absent from dorsum; (iii) spinose setae not cupolate; (iv) submedial row of loculate pores absent; (v) hind tibia with 3 or 4 setae; (vi) dorsal spinose setae shorter than segmental width; and (vii) discoidal pores absent from dorsum.

***Pseudotectococcus* Hempel**

Pseudotectococcus Hempel, 1934: 139.

Type species: *Pseudotectococcus anonae* Hempel 1934: 139-140.

Generic diagnosis. Adult female (Fig. 37). Galls of both sexes on upper leaf surface, those of females slightly rounder and blunter than those of males; gall openings all ventral. Adult females rather globose, with rounded head, broad across thorax and tapering posteriorly, but abdomen cone-shaped. *Dorsum*. Derm membranous. Setae spinose and conical; in fairly distinct bands across each abdominal segment but less clear across each thoracic segment and with a group anteriorly on head. Macrotubular ducts rather large, with a stout outer ductule; each with a conspicuous rim around dermal orifice. Microtubular ducts with a lightly sclerotised rim on derm and an undivided main duct. Anal lobes strongly protruding, narrow, apically acute, distinctly sclerotised. Median plate generally distinct and sclerotised. Anal ring located beneath median lobe, without an anal tube but with 3 pairs of setae. *Margin*. Poorly defined but demarcated by an uneven band of spinose setae, similar to those on dorsum but generally shorter and thinner. *Venter*. Setae mainly rather flagellate. Macrotubular ducts clearly different from those on dorsum, each outer ductule generally shorter but with a slightly longer, narrow inner ductule; generally restricted to abdominal segments. Ventral microtubular ducts perhaps slightly shorter and stouter than dorsal microtubular ducts, each with a more distinctly sclerotised dermal pore. Loculate pores mainly 5-locular: present in broad bands across abdominal segments II–VI. Cruciform pores absent. Antennae probably 3–5 segmented but segmentation rather obscure. Frontal lobes and antennal tubercles absent. Clypeolabral shield normal; labium probably 2 segmented. Legs moderately well developed, sometimes distorted; hind coxae swollen, with or without translucent pores; tarsal digitules slightly longer than claw digitules; claw long and slender, with 1 digitule significantly broader than other and both longer than claw; each claw generally with a small denticle near apex. Vulva placed between segments VII and VIII.

Apparently restricted to Annonaceae.

Comment. *Pseudotectococcus* currently contains 2 species, the type species (*P. anonae* Hempel) and *P. rollinae* Hodgson & Gonçalves, both known only from Brazil. For full descriptions of the adult females of both species, and all other stages of *P. rollinae*, see Hodgson *et al.* (2004).

Adult female *Pseudotectococcus* can be separated from those of other South American eriococcids by the following combination of characters: (i) elongate, sharply pointed abdomen; (ii) ventral abdominal segments with many loculate pores; (iii) antennae reduced, 3–5 segmented; (iv) anal lobes well developed and elongate; and (v) macrotubular ducts on dorsum and venter different in structure.

***Pseudotectococcus anonae* Hempel**

Pseudocapulinia lanosa Hempel 1934: 139–140.

First-instar nymph (sex not determined) (Fig. 38)

Diagnosis. *Unmounted material.* Elongate oval. *Mounted material.* Body oval. *Dorsum.* Dorsal setae conical, sometimes slightly curved, of 1 rather variable size, arranged in a pair of submedial lines and in a pair of mediolateral lines. Macrotubular ducts absent. Microtubular ducts rather large, with a small, sclerotised, cone-like pore; sparse, in a mediolateral line and also marginally. Loculate pores absent. Anal lobes sclerotised, elongate, each with a rounded apex; without microtubular ducts. Median plate present. *Margin.*

Marginal setae spinose, similar in size and shape to those on dorsum. Anal ring located between anal lobes, with 6 setae. *Venter*. Setae of 2 sizes, short setae submarginally and longer setae medially; suranal setae rather

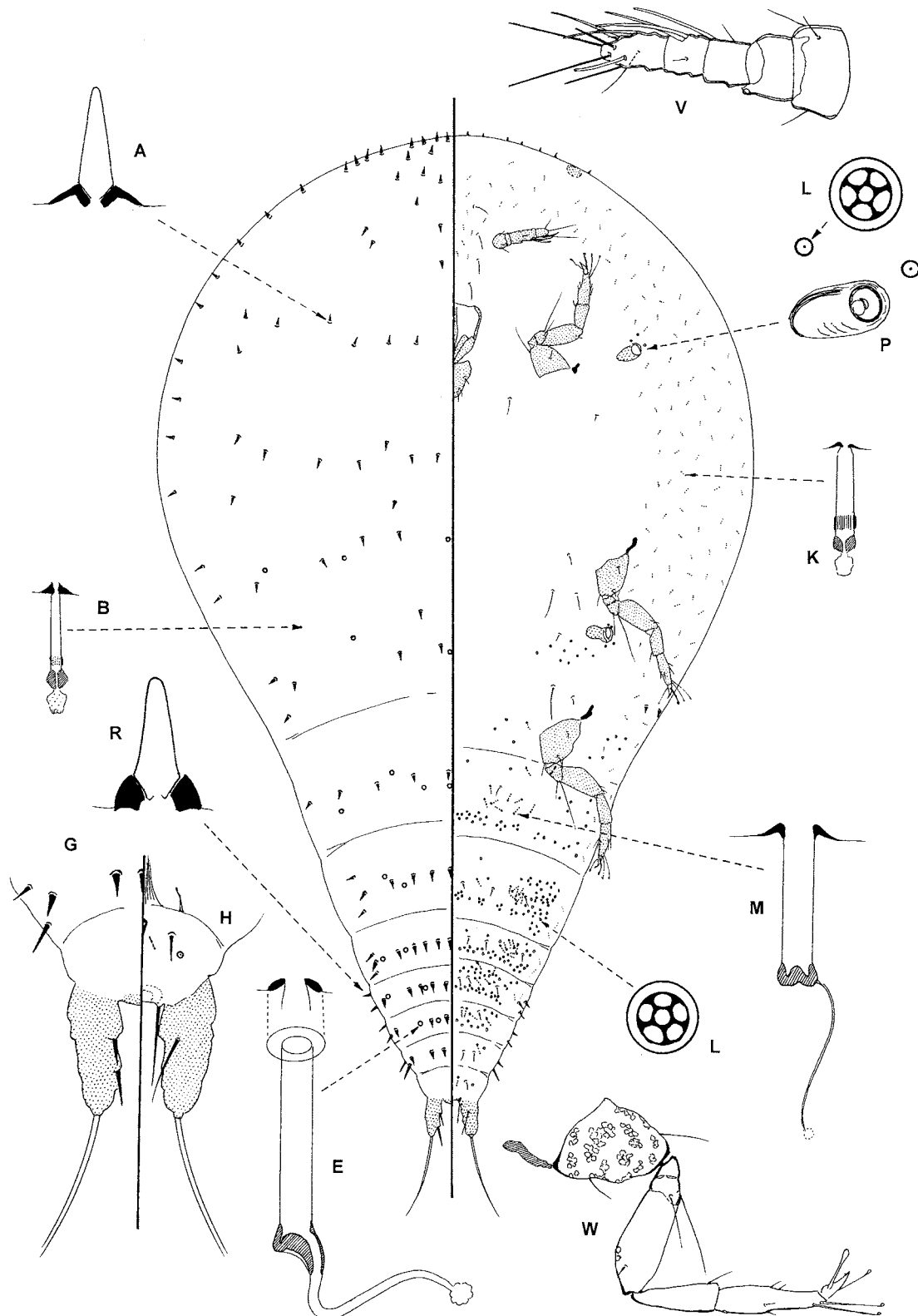


FIGURE 37. *Pseudotectococcus anonae* Hempel. Adult female, where A = dorsal spinose seta; B = dorsal microtubular duct; E = dorsal macrotubular duct; G = dorsal view of anal lobes; H = ventral view of anal lobes; K = ventral microtubular duct; L = ventral loculate pore; P = anterior spiracle; R = marginal spinose seta; V = antenna, and W = metathoracic leg (modified after Hodgson *et al.*, 2004).

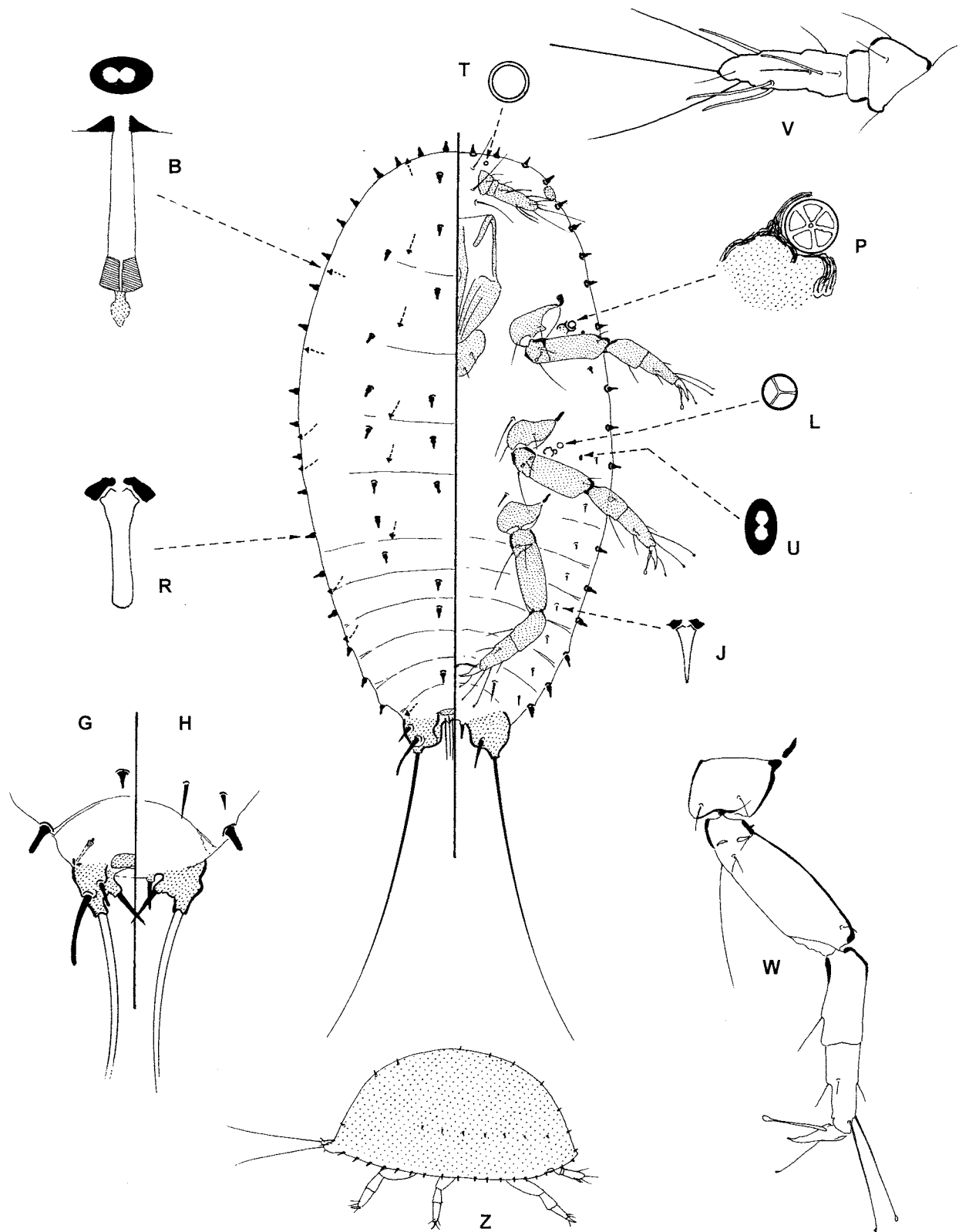


FIGURE 38. *Pseudotectococcus anonae* Hempel. First-instar nymph, where B = dorsal microtubular duct; G = dorsal view of anal lobe; H = ventral view of anal lobe; J = ventral submarginal seta; L = ventral loculate pore; P = anterior spiracle; R = marginal spinose seta; T = preantennal tubercle; U = cruciform pore; V = antenna, W = metathoracic leg, and Z = side view of nymph (modified after Hodgson *et al.*, 2004).

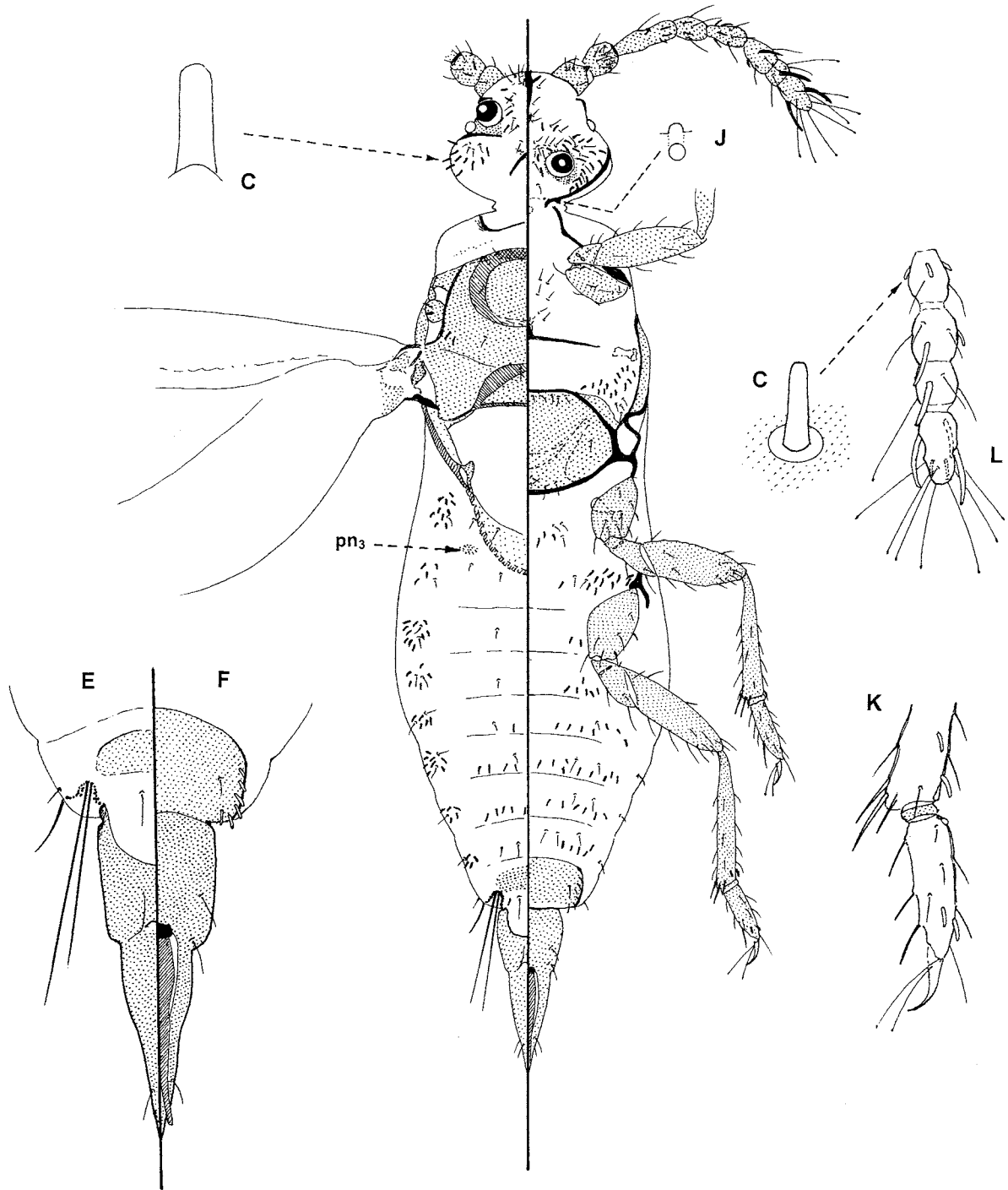


FIGURE 39. *Pseudotectococcus anonae* Hempel. Adult male, where C = fleshy setae; E = dorsal view of penial sheath; F = ventral view of penial sheath; L = apical four antennal segments, and K = distal end of metathoracic leg (modified after Hodgson *et al.*, 2004). For other abbreviations, see under 'Figure captions' on p.5.

spinose, each on a small protuberance. Macrotubular and microtubular ducts absent. Cruciform pores: 1 present near margin on thorax. Loculate pores each with 3 or 5 loculi, 1 near each peritreme. Antennae 3 segmented. Labium probably 2 segmented. Legs well developed, without pores; tibia slightly shorter than tarsus; tarsal digitules capitate, about equal in size; claw probably with a denticle; claw digitules dissimilar, with 1 conspicuously swollen, other about same size as tarsal digitules.

Comment. The first-instar nymphs of *P. anonae* are quickly separated from other known eriococcid first-instar nymphs in having 3-segmented antennae, sclerotised anal lobes and cruciform pores. Other important

characters are: (i) microtubular ducts present only on dorsum; (ii) loculate pores present singly just laterad to each spiracle; and (iii) claw digitules dissimilar, 1 broader than other. It is perhaps most similar to *Aculeococcus*, but the latter genus lacks cruciform pores and has cupulate-shaped dorsal setae. For other differences, see in the key.

Adult male (Fig. 39)

Diagnosis. *Mounted material.* Less than 1 mm long. Loculate and other pores absent. Most setae fleshy, each short and stout, clearly different from hair-like setae. *Head.* With 2 pairs of subequal simple eyes. Most setae fleshy, frequent both on occipital ridge and genae. Dermal reticulations absent. Postoccipital ridge an inverted U shape. Antennae short, 8 segmented; hair-like setae quite long; fleshy setae short and fat, clearly shorter than width of segments; capitate setae present on apical 2 segments. *Thorax.* Prothorax with prosternal setae but no antespircular setae and no setae dorsally. Meso- and metathorax showing nothing distinctive. *Forewings* without an alar lobe, alar setae and alar sensoria. Hamulohalteres absent. *Legs.* Well developed; campaniform pores on each trochanter oval and in a line; trochanter setae all short; tarsi 2 segmented; tarsal digitules not capitate; claw without a denticle; claw digitules probably minutely capitate; fleshy setae short and stout, as elsewhere. *Abdomen.* Dorsal abdominal setae few, fewer than ventral abdominal setae; pleural setae in distinct groups; tergites and sternites only present on segment VIII; glandular pouches present, pouch pores present only with pouch; glandular pouch setae well developed. Penial sheath typical of Eriococcidae, divided into 2 parts, anterior part about half length of penial sheath, parallel-sided, with anus at posterior end; posterior part narrower, narrowing to a sharp apex; setae few.

Comment. The most distinct characters of the adult male of *P. anonae* are: (i) rather thick fleshy setae on antennae, body and legs, very obviously different from hair-like setae; (ii) rather long penial sheath, more than 2x the basal width and with the anterior half only slightly shorter than the posterior half; and (iii) 8 segmented antennae.

Stibococcus Miller & González

Stibococcus Miller & González, 1975: 154–156.

Type species: *Stibococcus cerinus* Miller & González, 1975: 156–159.

Generic diagnosis: Adult female (Fig. 40). In life, forming a characteristic ovisac beneath and behind the body of the adult female on the underside of the leaves of the host. Adult female with small membranous anal lobes, normally not protruding. *Dorsum.* Setae spinose, of basically 2 sizes: (i) larger setae in a marginal band and a medial line; and (ii) smaller setae elsewhere. Macrotubular ducts with characteristic sclerotised dermal rim, those on dorsum unusually large. Microducts with a narrow sclerotised rim. Loculate pores absent. *Margin.* Poorly defined. *Venter.* Setae mainly small and hairlike but those near margin similar to smaller spinose setae on dorsum. Macrotubular ducts of 2 types, both smaller than dorsal type; more or less restricted to posterior half of body; smaller type in large clusters on abdomen. Quinquelocular pores present in submarginal band from head to apex of abdomen, present medially on most abdominal segments. Cruciform pores absent. Antennae 6 segmented. Frontal lobes absent but antennal tubercles present. Labium 1 segmented. Metathoracic legs with translucent pores on coxa, femur and sometimes tibia. Claw digitules similar; claw with a small denticle. Vulva present between segments VII and VIII.

Known only from Myrtaceae.

Comment. *Stibococcus* is a monotypic genus known only from Chile. For description of the adult female, adult male and pupa of *S. cerinus*, see Miller & González (1975: 154). Miller & González (1975) indicate that the adult females of this genus differ from all other eriococcid genera by having the following combination of characters: (i) macrotubular ducts with a sclerotized orifice; (ii) clusters of macrotubular ducts present across most abdominal segments; (iii) small anal lobes; (iv) 1 segmented labium; and (v) characteristic ovisac.

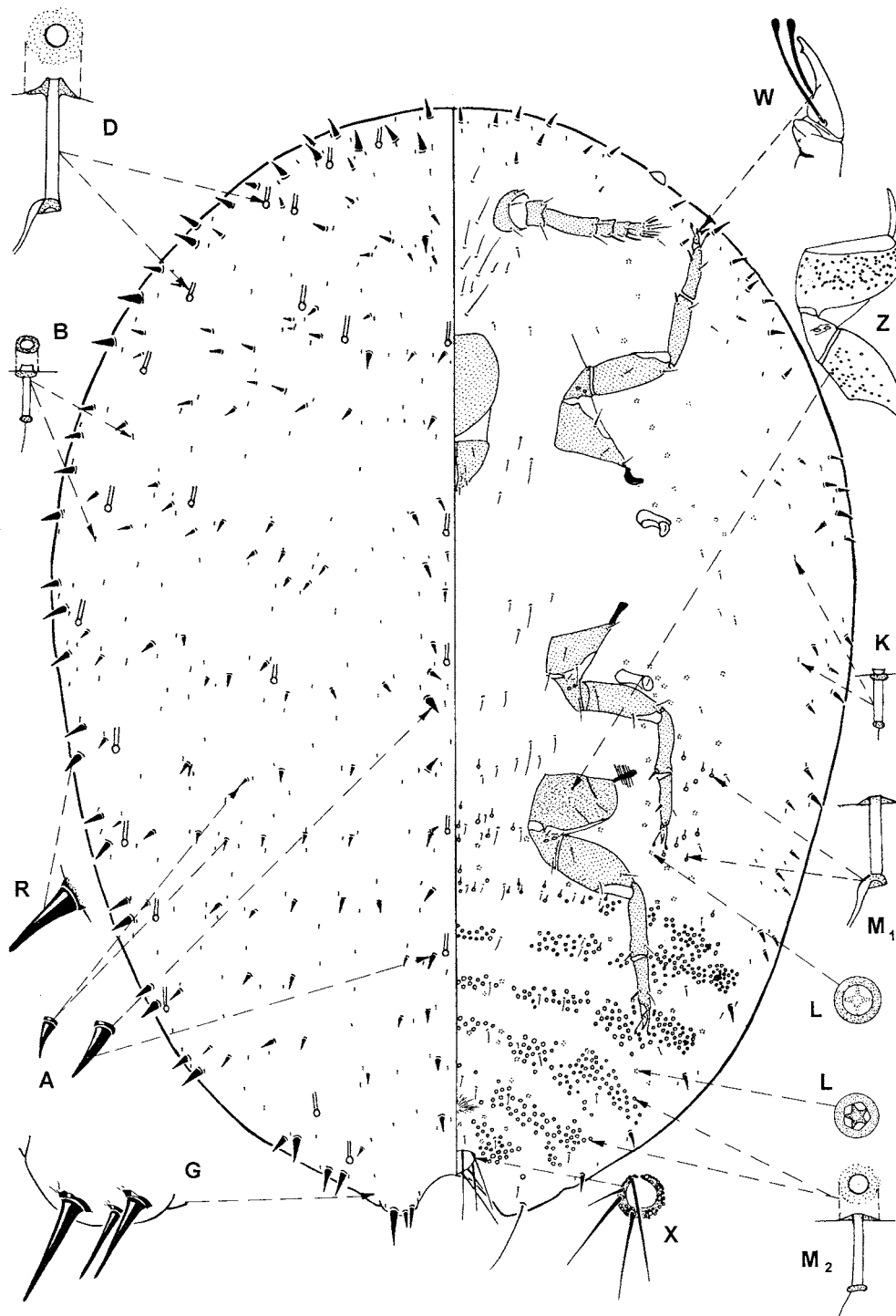


FIGURE 40. *Stibococcus cerinus* Miller & González. Adult female, where A = dorsal spinose setae; B = dorsal microtubular duct; D = dorsal macrotubular duct; G = dorsal view of anal lobe; K = ventral microtubular duct; L = ventral loculate pores; M₁, M₂ = ventral macrotubular ducts; R = marginal spinose seta; W = claw or prothoracic leg; X = anal ring, and Z = proximal end of metathoracic leg (modified after Miller & González, 1975).

Adult male (Fig. 41)

Diagnosis. *Mounted material.* Size about 1 mm long. Loculate pores absent on body; X-type pores present dorsally on head. Body setae hairlike. *Head.* With 2 pairs of subequal simple eyes. Setae quite abundant on ocular sclerite and genae. Dermal reticulations absent. Postoccipital ridge with both anterior and posterior arms. Antennae long, 10 segmented; setae generally longer than width of segment; capitate setae present on apical segment only. *Thorax.* Prothorax with prosternal setae but no antespinal setae and no

setae dorsally. Meso- and metathorax showing nothing distinctive. *Forewings* probably without an alar lobe, alar setae and alar sensoria. Hamulohalteres absent. *Legs*. Well developed; campaniform pores on each trochanter oval and in a line; trochanter setae all short; tarsi two segmented; tarsal digitules capitate; claw without a denticle; claw digitules capitate; fleshy setae not well differentiated. *Abdomen*. Dorsal abdominal setae few, fewer than ventral abdominal setae; pleural setae in distinct groups; tergites and sternites only present on segment VIII; glandular pouches present, pouch pores tending to spread out of pouch; glandular pouch setae short, slightly capitate. Penial sheath typical of Eriococcidae, divided into two parts, anterior part about half length of penial sheath, parallel-sided, with anus at posterior end; posterior part narrower, narrowing to a sharp apex; setae quite abundant.

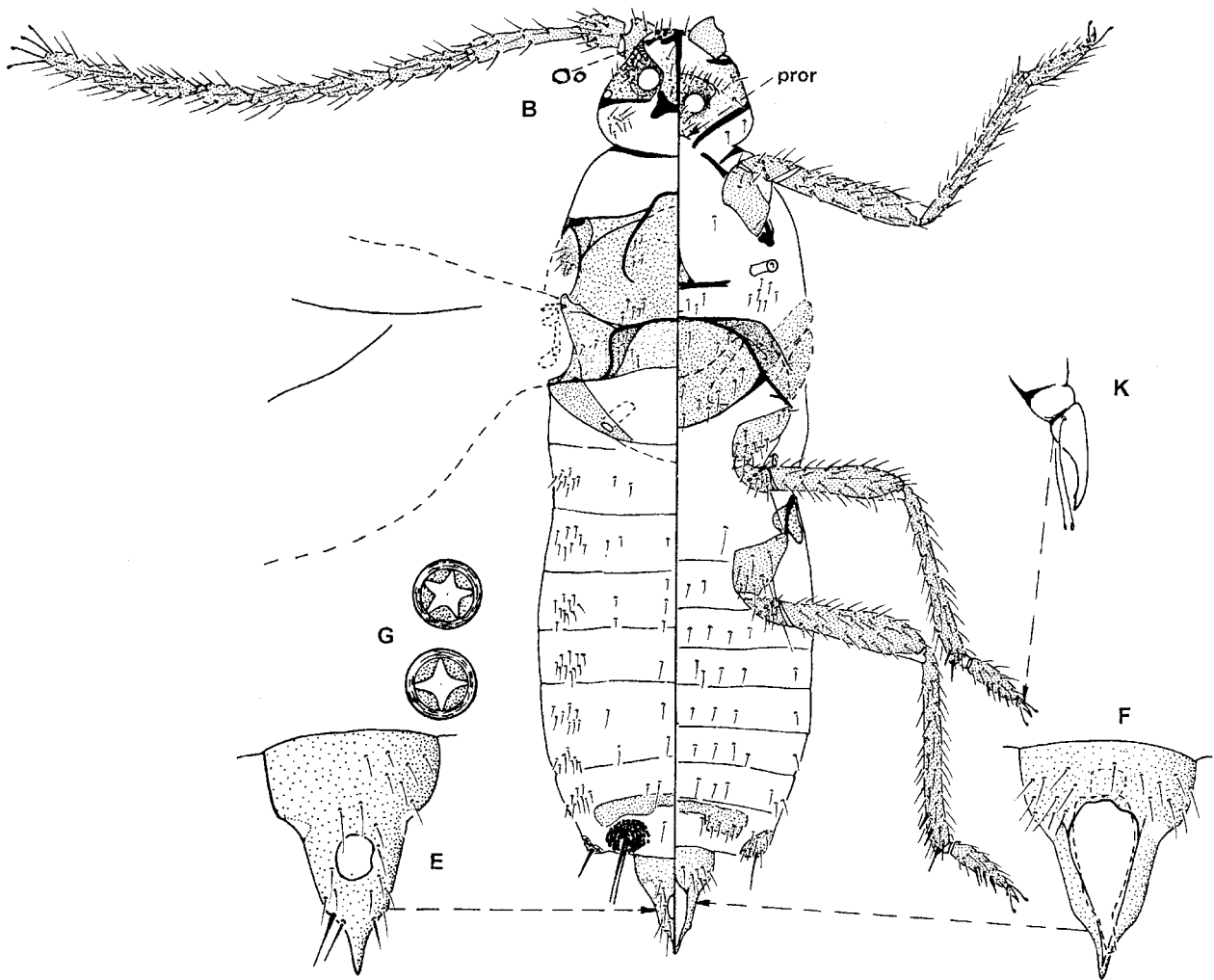


FIGURE 41. *Stibococcus cerinus* Miller & González. Adult male, where B = pores on dorsal epicranium; E = dorsal view of penial sheath; F = ventral view of penial sheath; G = loculate pores, and K = claw of mesothoracic leg (modified after Miller & González, 1975). For other abbreviations, see under 'Figure captions' on p5

Comment. The most distinctive characters of the adult male of *S. cerinus* are: (i) penial sheath short, only about 1.5x longer than basal width; (ii) 10 segmented antennae, with setae slightly longer than width of segment; (iii) presence of pores on head; (iv) abdominal tergite VIII sclerotised.

***Tectococcus* Hempel**

Tectococcus Hempel 1900: 379, 406.

Type species: *Tectococcus ovatus* Hempel 1900: 406–407.

Generic diagnosis. Adult female (Fig. 42). Induces circular galls on both sides of leaf. Adult female ovate, swollen, dusted with white powder. Body outline approximately egg-shaped, broadest across thorax, with rounded head and pointed abdomen. *Dorsum*. Derm membranous. Setae spinose, with blunt apices; frequent; rather variable in size. Microtubular ducts small; extremely scarce, apparently most abundant medially on metathorax. Macrotubular ducts much larger, with a narrow outer ductule; absent on abdominal segment VIII but frequent to abundant on segments I–VII, particularly medially, becoming less frequent anteriorly. Loculate pores each with mainly 5 loculi; frequent in segmental bands throughout. Anal lobes absent. Anus unclear, apparently ventral, but with a V-shaped sclerotised structure; without setae or pores; with a pair of long, flagellate setae on each side of anus; anal area without microtubular ducts but loculate pores abundant. *Margin*. Poorly defined. *Venter*. Setae clearly hairlike and flagellate. Macrotubular ducts different in structure to those on dorsum; apparently restricted to abdomen. Microtubular ducts similar to those on dorsum; very sparse. Cruciform pores absent. Loculate pores each with mainly 5 loculi, in broad, dense bands across abdominal segments III–VIII; much sparser elsewhere. Antennae probably 6 segmented but segmentation obscure. Frontal lobes absent but antennal tubercles present. Mouthparts with a pair of large sclerotised, wing-like apodemes arising anteriorly from tentorial box, plus 2 even larger unstained (presumably less sclerotised) "wings" anterolaterally; labium probably 2 segmented; basal segment with 1 pair of setae. Legs moderately well developed; each hind coxa slightly swollen, with a few translucent pores and transverse rows of microspinules; femur slightly swollen and misshapen, perhaps with a few pore-like areas dorsally; tibia each with 3 setae and a few pale pore-like areas; tarsi each with 3 setae; claws each with 1 digitule slightly broader than other and both longer than claw; each claw with a strong denticle near apex. Vulva present between segments VII and VIII.

Known from Myrtaceae and Thymeliaceae.

Comment: *Tectococcus* is a monotypic genus known only from Brazil. Adult female and adult male recently redescribed by Vitorino *et al.* (2000), along with some details of its biology.

Adult female *Tectococcus* can be separated from those of other South American eriococcids by the following combination of characters: (i) abdomen rather pointed, without anal lobes; (ii) macrotubular ducts on dorsum and venter of different structure; (iii) macrotubular ducts and loculate pores abundant on both dorsal and ventral surfaces of abdomen; (iv) loculate pores present throughout; and (v) anus without pores or setae.

***Tectococcus ovatus* Hempel**

Tectococcus ovatus Hempel 1900: 406–407.

Material examined: BRAZIL: São Paulo, on shrub, Feb. 1929, A. Hempel (USNM): 2/2adff (in excellent condition). **COTYPES: BRAZIL,** São Paulo, on Myrtaceae, 1900, A. Hempel (USNM): 1/11 first-instar nymphs (described from 3 specimens in fair to good condition but most specimens mounted laterally; some characters checked on other 8; most claws poor) + 1/1 adf and 1 2nd-instar male; **BRAZIL:** locality ?, on *Psidium cattleiana*, 23.ix.1993, M. D. Vitorino (USNM): 9/19 adff (fair condition) + 1 2nd instar male (good condition) + 5 2nd-instar females. **HAWAII:** Oahu (in quarantine facility), on *Psidium cattleiana*, 2.x.2002, A. Berry (USNM): 2/3admm (in fair to poor condition, much muscle still present in thorax and head, and wings very crumpled).

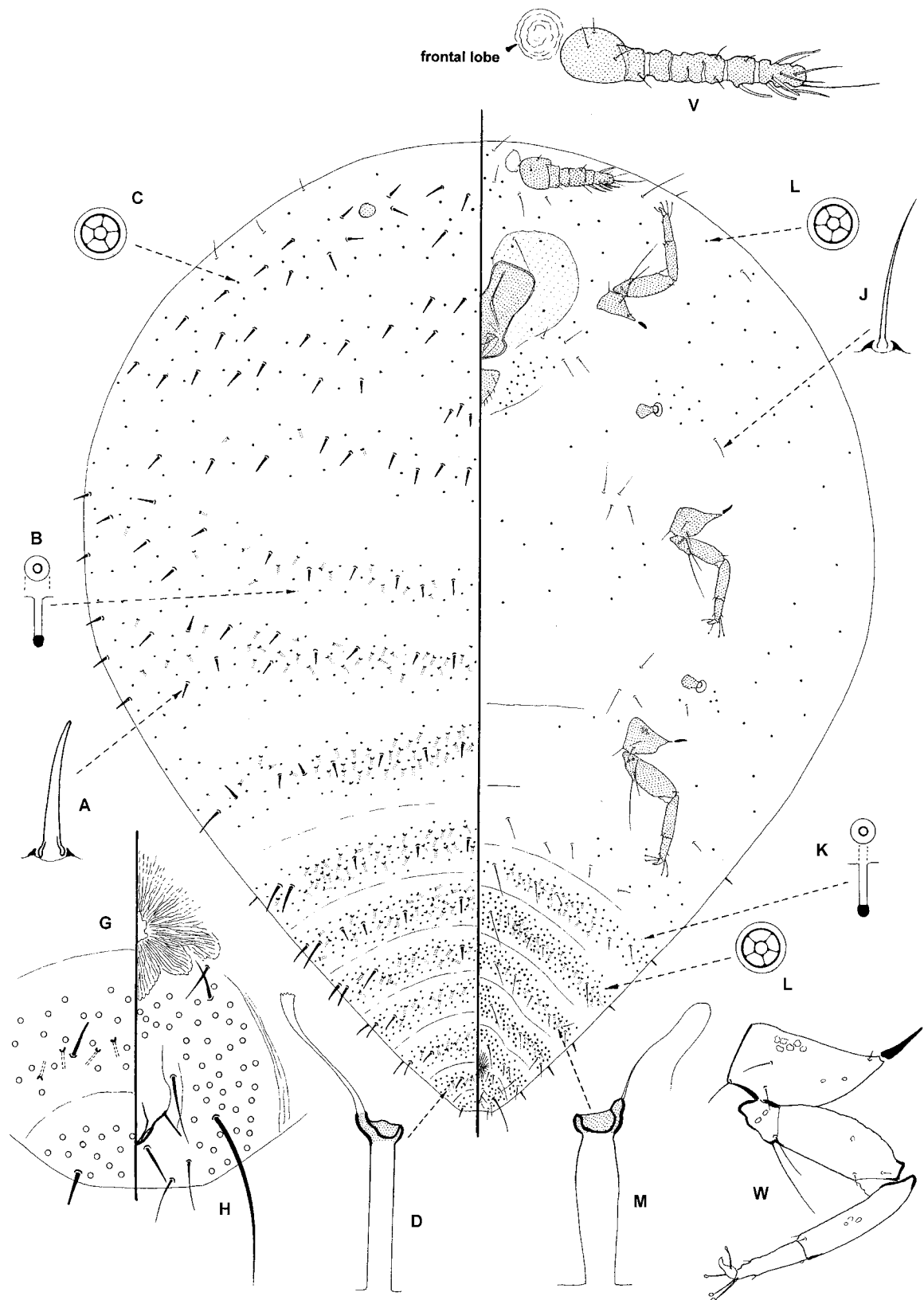


FIGURE 42. *Tectococcus ovatus* Hempel. Adult female, where A = dorsal spinose seta; B = dorsal microtubular duct; C = dorsal loculate pore; D = dorsal macrotubular duct; G = dorsal view of anal area; H = ventral view of anal area; J = ventral seta; K = ventral microtubular duct; L = ventral loculate pore; M = ventral macrotubular duct; V = antenna with frontal lobe, and W = metathoracic leg.

Adult female (Fig. 42)

Unmounted material. Induces circular galls, convex on both sides, largest 8 mm diameter. Galls formed

on both sides of leaf and open on underside, where surface somewhat raised, with white wax. Inside of gall smooth, dusted with white wax. Adult female ovate, inflated, brown, dusted with white powder.

Mounted material. Body outline approximately egg-shaped, broadest across thorax, with rounded head and pointed abdomen; thorax rather long and therefore legs rather far apart. Length 2.3 mm, width 1.98 mm.

Dorsum. Derm membranous. Dorsal setae spinose, with blunt apices; frequent; rather variable in size, each about 16–20 μm long medially but up to about 35 μm on margin of head and posterior abdomen; distributed in sparse bands across thorax and abdomen but more randomly on head; becoming infrequent posteriorly on abdomen. Microtubular ducts small, perhaps 4 μm long and 0.5 μm wide; extremely scarce, apparently most abundant medially on metathorax; possibly with a convex dermal pore. Macrotubular ducts much larger, with a narrow outer ductule (each about 1.5 μm wide and 16 μm long) and a shorter inner ductule (8–10 μm long) broadening slightly towards apex where truncated; dermal pore not apparently sclerotised: distribution: absent on abdominal segment VIII but frequent to abundant on segments I–VII, particularly medially, becoming less frequent on thoracic segments, with very few on prothorax; absent on head. Loculate pores each about 4–5 μm wide, with mainly 5 loculi; frequent in segmental bands throughout (more random on head), but most abundant on abdominal segments. Anal lobes absent; segments VII and VIII each with a single pair of spinose setae. Anus unclear, apparently ventral, but with a V-shaped sclerotised structure; without setae or pores, although with a pair of setae along lateral margin, each about 25 μm long. Also with a pair of long, flagellate setae (each about 125 μm long) on each side of anus; plus three pairs of setae posterior to anus, each 15–22 μm long, and another, longer pair anteriorly (each 25–28 μm long); anal area without microtubular ducts but loculate pores abundant (see under venter).

Margin. Margin poorly defined but probably demarcated by change from spinose dorsal setae to flagellate ventral setae; marginal setae probably absent.

Venter. Setae clearly hairlike and flagellate, longest between antennae and mesad to each coxa, largest 66–80 μm long; sparse, with 4 pairs between antennae and 3–5 mesad to each coxa; also with smaller setae in sparse bands across each abdominal segment. Macrotubular ducts different in structure to those on dorsum, with each outer ductule about twice as broad (about 3.5 μm wide and about 15 μm long); inner ductule filamentous and probably rather long, without a glandular end; apparently restricted to abdominal segments III–VI (i.e., absent from VII and VIII). Microtubular ducts apparently structurally similar to those on dorsum; very sparse, perhaps only present submarginally on some abdominal segments. Cruciform pores absent. Loculate pores each with mainly 5 loculi: present in broad, dense bands across abdominal segments III–VIII; much sparser elsewhere although more or less present throughout, with small concentrations laterad to labium and to each spiracle.

Antennae probably 6 segmented but segmentation of segment IV rather obscure; length about 90 μm ; with possibly 3 setae on scape, 1 + a campaniform sensillum on pedicel, segment III with 0 setae; IV with 2 setose setae; V with 1 fleshy seta + 1 setose seta, and VI with 3 fleshy setae, 3 long and 2 short other setae, longest about 50 μm . Frontal lobes conspicuous. Eyespot rather large, possibly protuberant, each about 17 μm across; located laterad to each antenna. Mouthparts with a pair of large sclerotised, wing-like apodemes arising anteriorly from tentorial box, plus 2 even larger unstained (presumably less sclerotised) "wings" anterolaterally; clypeolabral shield 240 μm long; sclerotised wing-like apodemes 275 μm wide, and unstained "wings" 425 μm wide; labium probably 2 segmented, with 5 pairs of setae. Spiracles: width of peritremes: 15–17 μm . Legs each moderately well developed; metathoracic legs: lengths (μm): 145 wide; trochanter + femur 165; tibia 100, tarsus 57, claw 16; each hind coxa slightly swollen, with a few translucent pores and transverse rows of microspinules; each trochanter with 2 long setae, longest about 80 μm long; femur slightly swollen and misshapen, with 3 setae plus a few pore-like areas dorsally; tibia each with 3 setae and a few pale pore-like areas; tarsi each with 3 setae; tarsal campaniform sensillum present; tarsal digitules subequal in length to claw digitules but longer than claw, capitate; claws short and broad, each with 1 digitule slightly broader than other; each claw with a strong denticle near apex. Vulva placed between segments VII and VIII.

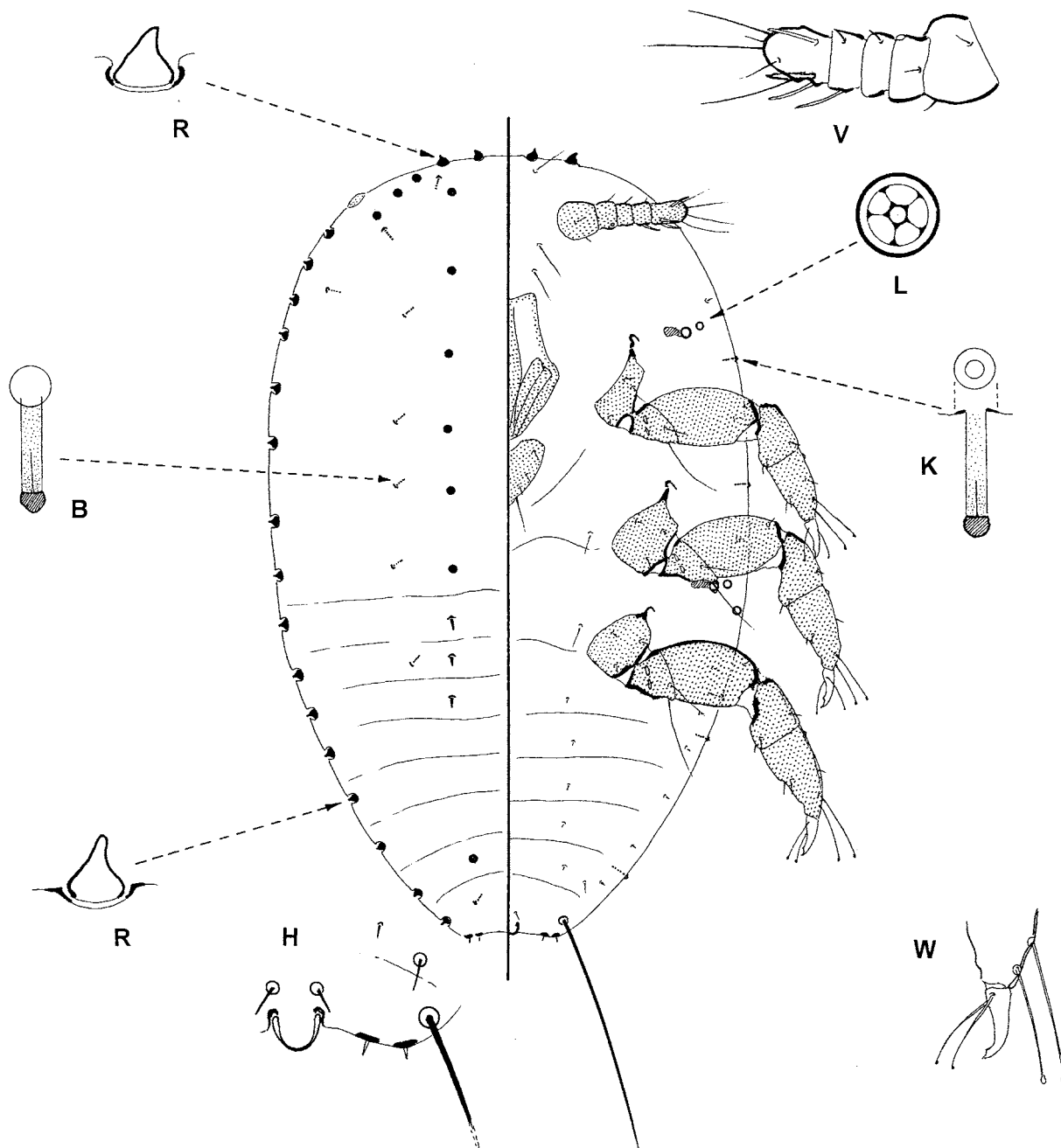


FIGURE 43. *Tectococcus ovatus* Hempel. First-instar nymph, where B = dorsal microtubular duct; H = ventral view of anal area; K = ventral microtubular duct; L = ventral loculate pore; R = spinose marginal and dorsal setae, V = antenna, and W = claw of metathoracic leg.

Comment. For a comparison of the adult female of this species with other South American eriococcid genera see the “Comment” section after the “Generic diagnosis” of *Tectococcus*.

First-instar nymph (gender not determined) (Fig. 43)

Unmounted material. Not seen.

Mounted material. Length about 250–265 μm , width 160 μm . Body oval, slightly more pointed posteriorly.

Dorsum. Derm membranous, without obvious dermal spinules. Dorsal setae spinose, in a pair of submedian lines; those on head, thorax and abdominal segment VII similar to those around margin, each tending to be rather swollen basally and about 2.5 μm long, with a narrow basal socket; those on abdominal

segments I–III smaller, each about 1.5 µm long. Microtubular ducts with a sclerotised dermal pore, with outer ductule about 6 µm long, probably with an inner dividing membrane, and a heavily sclerotised distal apex; no inner ductule noted; distributed as follows: with 3 pairs submarginally on head, plus submedial pairs on head and each thoracic segment, plus another pair on abdominal segment VIII. Loculate pores and macro tubular ducts absent. Anal lobes absent or rounded, membranous; each with a very long, flagellate apical seta about 80–85 µm long. Posterior margin with 2 pairs of short setae on either side of anus, each about 1 µm long. Anus represented by a sclerotised, inverted U, about 5 µm wide, without setae or pores, but with a pair of small setae ventrally.

Margin. Marginal setae strongly spinose, similar in shape to those on dorsum and about same size, each 5 µm tall and 4 µm wide at base; with 8 between eyespots, 1 dorsad to each eyespot, 3 on each side between eyes and point opposite anterior spiracles, 4 on each side laterally between anterior spiracles and abdomen and with 1 on each side of abdominal segments I–VIII. Eyespots fairly small, each 7–8 µm wide, situated on margin posterior to base of antennae.

Venter. Derm membranous, without dermal spinules. With single loculate pores laterad to each spiracle plus a further pore on margin laterad to each posterior spiracle. Microtubular ducts apparently similar to those on dorsum, with pairs marginally on abdominal segments II, III and VI, and 2 pairs between spiracles. With 3 pairs of long setae between antennae (longest 13–17 µm long) plus pairs mesad to meso- and metacoxae (these shorter, about 10 µm long) but none mesad of procoxae; pairs of minute setae present medially on abdominal segments II–VI. Submarginal setae minute and hairlike, each about 1 µm long, with 6 on abdomen, 2 between spiracles and 1 between anterior spiracles and eyespot.

Antennae 5 segmented, 44–50 µm long; segments II–IV much wider than long; setal distribution: scape 2; pedicel 1; segment III 1; IV 1 setose seta + 1 fleshy seta, and V 2 fleshy setae, 3 long setose setae + 3 shorter setose setae, length of longest seta about 36 µm. Clypeolabral shield about 45–46 µm long; labium perhaps 2 segmented; about 33 µm wide, with possibly 4 pairs of short setae + 1 pair rather longer setae on apex. Spiracles very small, peritremes possibly 4–5 µm wide, without a lateral membranous cavity. Legs well developed; lengths (metathoracic leg (µm)): coxa (width) 20–22; trochanter + femur 40–43; tibia 18–21; tarsus 25–27, clearly much longer than tibia; claw 12–13; setae: coxae 3, trochanter 2, femur 2, tibia 3, tarsus 4; long trochanter seta 25–28 µm long; tarsal campaniform sensillum present; claw with a distinct denticle; both tarsal digitules on all 3 pairs of legs capitate and equal in size; claw digitules alike with small capitate apices.

Comment. The first-instar nymphs of *T. ovatus* have 5-segmented antennae. In addition, they have: (i) dorsal spinose setae rather cupolate-shaped, present in a submedial line and marginally; (ii) microtubular ducts restricted to the dorsum and margin; (iii) anal lobes unsclerotised and not differentiated; (iv) cruciform pores absent; and (v) loculate pores only present laterad to each spiracle. *Aculeococcus* and *Pseudotectococcus* also have shorter antennae (3 segmented), but both probably also have differentiated anal lobes.

Adult male (Fig. 44)

Unmounted material. Unknown.

Mounted material. With an elongate abdomen; total length perhaps 1.42–1.48 mm long; antennae short, less than half total body length; body with very few setae, all hairlike (hs); fleshy setae (fs) absent on body; length of fs on antennae and legs slightly less than width of antennae; glandular pouches and glandular pouch setae absent.

Head. Approximately round in dorsal view; width across genae about 160–180 µm; length about 135–145 µm. Median crest (mc) and postoccipital ridge (por) present but not heavily sclerotised; epicranium with few hs dorsal head setae (dhs) and ventral head setae (vhs) but with many pores, possibly of 2 types: a larger pore, about 2–3 µm wide, possibly loculate, common on dorsal surface, and perhaps a smaller pore about 1.5 µm wide with a dark central spot, sometimes noted ventrally between scapes. Mid-cranial ridge apparently absent both dorsally and ventrally; ventral epicranium with a few hs ventral head setae (vhs) laterad to ventral simple eye (vse) but perhaps otherwise absent. Dorsal ocular setae absent. Genae (g) not reticulated but each with 1–3 hs genal seta (gs). Eyes: with 2 pairs of round, simple eyes; dorsal eyes (dse) subequal in size to ventral eyes

(vse), each 28–32 μm wide. Ocelli (o) not very distinct, each 13 μm wide; not nearly touching postocular ridge (pocr) posteriorly. Ocular sclerite (ocs) with faint reticulations around both eyes and ocelli and some small nodulations laterally. Preocular ridge (procr) extremely short, represented only by an antennal articulatory sclerite (1 specimen had a short but distinct ridge on 1 side dorsally). Postocular ridge (pocr) strongly developed ventrally, extending dorsally to just posterior to dorsal simple eye (dse). Preoral ridge (pror) distinct. Cranial apophysis (ca) not detected.

Antennae. Eight-segmented and filiform; length 550–605 μm (ratio of total body length to antennal length 1:0.4). Scape (scp): 30–33 μm long, 40–45 μm wide, with 4–7 hs, mostly on ventral surface. Pedicel (pdc): length 45–50 μm , width 34–36 μm ; with many concentric ridges over all segment; with 5–11 hs + 1 campaniform sensillum. Flagellar segments all more or less parallel-sided, with shallow transverse ridges; each about 20–25 μm wide; lengths of segments (μm): III 106–115; IV 64–75; V 100–105; VI 85–97; VII 80–105; VIII 73–75; fs each about 18–25 μm long; approximate number of setae and sensilla per segment: III 1 or 2 fs, 0–2 hs + 1 sensilla basiconica; IV 5–10 fs, 0 or 1 hs + 0 or 1 capitate seta (caps); V 19–25 fs + 0 or 1 caps; VI 25–27 fs, 0 or 1 caps + 0 or 1 antennal bristle (abs), VII 17–26 fs, 3 or 4 caps + 1 abs; VIII 1–3 fs, 3–5 caps, 3 long, well developed + 2 smaller abs + 1 sensilla basiconica.

Thorax. Prothorax: pronotal ridge (prnr) well developed and meeting medially on dorsum; lateral pronotal sclerites (prn) indistinct, each with faint ridging; lateral pronotal setae absent. Medial pronotal and post-tergital setae apparently absent. Post-tergites absent. Sternum (stn_1) not sclerotised and without striations; transverse ridge well developed and sclerotised; prosternal apophyses absent; median ridge absent; prosternal setae (stn_1s) absent. Proepisternum + cervical sclerite (pepcv) showing nothing distinctive. Anteprosternal setae and antemesospiracular setae absent.

Mesothorax: prescutum (prsc) more or less quadrate, about 90 μm long, 95 μm wide; sclerotised, without nodulations; prescutal ridges (pscr) well developed; prescutal suture (pscs) represented by a faint line; prealare (pra) and triangular plate (tp) well developed. Scutum (sct): median area sclerotised, about 50 μm long between prescutum and scutellum; with 1–3 pairs of hs (scts); without nodulations anterolaterally; prealar ridge weak. Scutellum (scl) 100–110 μm wide, 45–49 μm long; with an inverted U-shaped scutellar ridge; probably not tubular and lacking a foramen; scutellar setae (scls): 1 pair hs near anterior margin; posterior notal wing process (pnp) short. Basisternum (stn_2) 165–185 μm wide, 90–100 μm long; median ridge absent; bounded anteriorly by a moderately strong marginal ridge (mr) and posteriorly by strong precoxal ridges (pcr_2); with about 10 hs basisternal setae (stn_2s) on each side; lateropleurite (lpl) indistinct but broad; extension from marginal ridge along anterior border either short or absent; furca (f) well developed, narrow-waisted, arms divergent and extending almost to anterior marginal ridge. Mesopostnotum (pn_2) well developed; postnotal apophysis (pna) well developed. Area bounded anteriorly by scutellum and laterally and posteriorly by mesopostnotum not sclerotised. Mesepisternum (eps_2) not reticulated; subepisternal ridge (ser) well developed. Postalare (pa) well developed but not reticulated anteriorly; with 1 or 2 postalare setae (pas). Mesothoracic spiracle (sp_2): width of peritreme about 28 μm . Postmesospiracular setae (pms): probably 1–3 hs posterior to each spiracle + 0–4 medially. Tegula (teg) present, with 4–10 hs tegular setae (tegs) on each side.

Metathorax: metapostnotum not sclerotised; with 2 or 3 pairs of hs metatergal setae (mts). Dorsospiracular setae (dss): probably 1 or 2 hs on each side. Dorsal part of metapleural ridge absent; ventral part of metapleural ridge (plr_3) unusually short; precoxal ridge (pcr_3) absent; episternum (eps_3) unsclerotised, without postmetaspiracular setae. Metepimeron (epm_3) short, without setae. Antemetaspiracular setae absent. Metathoracic spiracle (sp_3): width of peritreme about 26 μm . Metasternum (stn_3) membranous, metasternal apophyses not detected; with possibly 2 hs anterior metasternal setae (amss) and 2 pairs of hs posterior metasternal setae (pmss).

Wings: hyaline; alar setae (als) generally present; alar lobe and alar pores absent. Hamulohalteres absent.

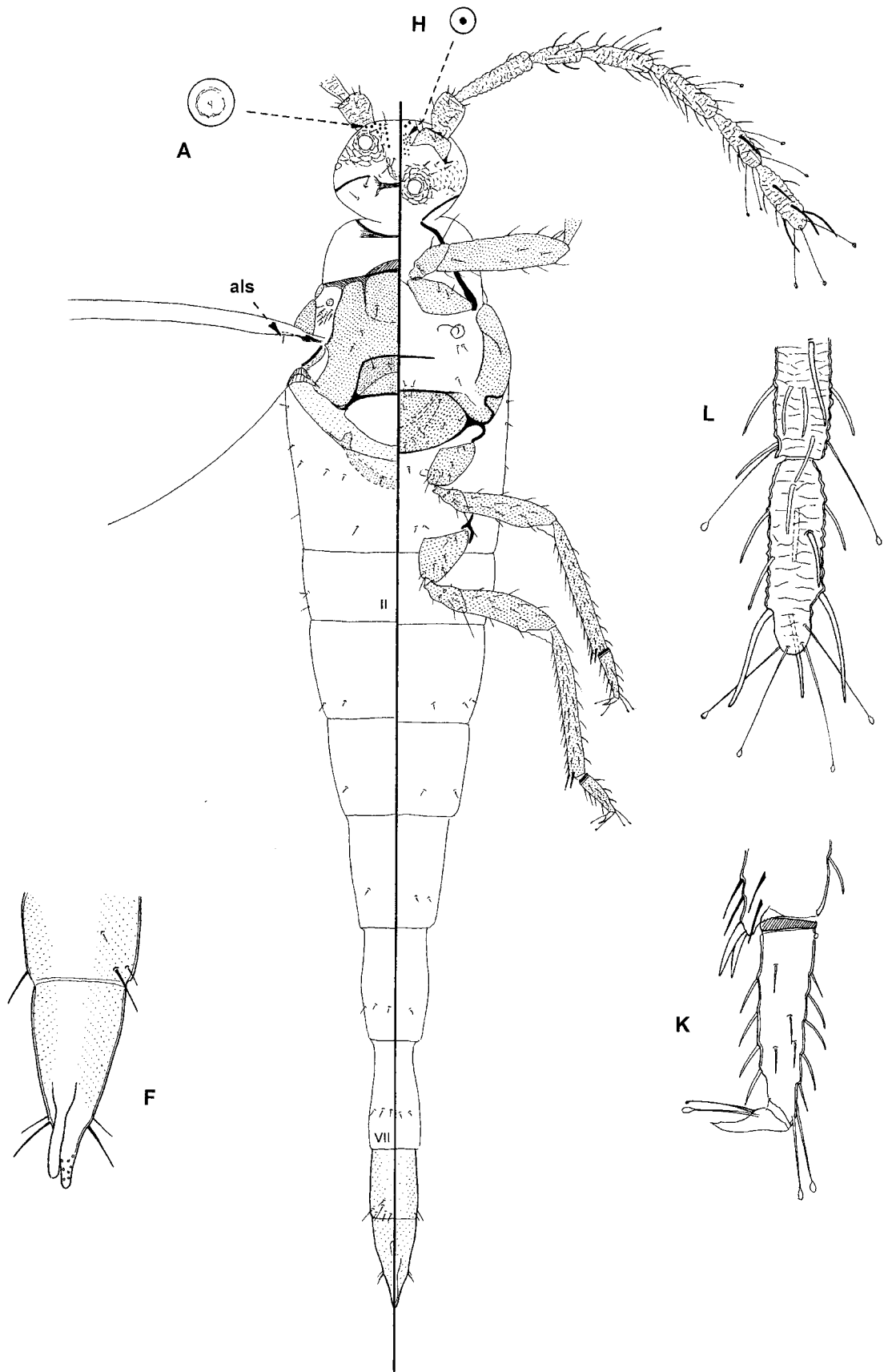


FIGURE 44. *Tectococcus ovatus* Hempel. Adult male, where A = pores on dorsal epicranium; F = ventral view of posterior end of abdomen; K = distal end of metathoracic leg, and L = apical antennal segments. For other abbreviations see 'Figure captions' on p. 5.

Legs: legs subequal in length. Coxae (cx): I 83–95; II 75–80; III 75–82 μm long; each coxa III with 6 or 7 hs; long apical seta not differentiated. Trochanter (tr) + femur (fm): I 174–200; II 155–175; III 165–185 μm long; trochanter III with 8 hs; campaniform sensilla oval and in a diagonal line; each long trochanter seta short, about 50 μm ; femur III with 11–15 hs. Tibia (tib): I 170–200; II 170–190; III 165–207 μm ; tibia III with a total of about 30–35 setae, mainly spur-like on distal third of leg but with 1 or 2 fs on dorsal margin distally; with 2 apical spurs (tibs), each about 13 μm long. Tarsi (tar): I 68–75; II 62–74; III 62–70 μm long (ratio of length of tibia III to that of tarsus III 1:0.36); tarsi 2 segmented; tarsus III with about 13 setae, mainly spur-like, but with 1 or 2 fs on dorsal margin; tarsal spurs about 13 μm long; tarsal campaniform sensillum (cp) present; tarsal digitules (tdt) perhaps slightly subequal in length to claw, with rather small apical knobs. Claws (c) longer than width of tarsi, with a distinct denticle; length III: 20–22 μm ; claw digitules (cdt) distinctly longer than claw, one narrower than other, both with small apical knobs.

Abdomen. Long, tapering to penial sheath; unsclerotised apart from segment VIII, which appears to be lightly sclerotised. Caudal extensions (ce) of segments VII & VIII absent. Setae all short hs, each 5–7 μm long, in a band across each segment, frequency (totals) approximately as follows: I 6; II–V 9–11; VI 6–10; VII 9–12; VIII 11–12, but with 2 or 3 longer, up to 17 μm long. Glandular pouches (gp) absent.

Genital segment: penial sheath (ps) triangular, narrowing to a sharp apex posteriorly; length about 105–110 μm , width anteriorly about 50 μm (ratio of total body length to length of penial sheath 1:0.07); anal opening (an) apparently in a groove medially on dorsal surface; with 2 pairs of longer hs (gts) just laterad to aedeagus, each 12–17 μm long; shorter setae absent. Aedeagus (aed) short and narrowing towards apex; length 45–50 μm , about 11 μm wide basally. Basal rod (bra) apparently absent. Penial sheath with a few small sensilla (psp) near apex.

Comment. The adult male of *T. ovatus* can be separated from other adult male eriococcids from the Neotropics by the following combination of characters: (i) abdomen much elongated, narrowing to a narrow penial sheath; (ii) body setae very few, all hair-like setae; (iii) antennae with 8-segments; (iv) capitate setae present on most antennal segments; and (v) pores present on head dorsally (and maybe ventrally). The adult male of *T. ovatus* shows some similarity to the eriococcid genera *Apiomorpha* and *Opisthoscelis* (see under Discussion below).

This species has been tested as a biological control agent of the strawberry guava *Psidium cattleianum* in Hawaii and a petition has been written to begin introductions (Johnson, 2005). This process has been heavily criticized by several groups in Hawaii and it is not clear if the introductions will take place. The males mentioned above were reared in Hawaii in quarantine.

Key to the Genera of the Eriococcidae of South America (Adult Females)

- | | | |
|------|---|------------------------|
| 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 (Fig. 27) or cupulate-shaped and robust scattered over thorax and abdomen (Fig. 5) | 4 |
| 3(2) | Antennae segmented; quinquelocular pores restricted to ventral thorax mostly near spiracles, absent from dorsum | <i>Pseudocapulinia</i> |
| - | Antennae each represented by an unsegmented knob; quinquelocular pores present on both body surfaces | <i>Carpochloroides</i> |
| 4(2) | Enlarged setae of 2 types present, cupulate-shaped setae on anterior abdomen, thorax, and head, and elongate setae on posterior abdominal segments | <i>Macracanthopyga</i> |
| - | Enlarged setae cupulate-shaped only present, scattered over dorsum | <i>Apiococcus</i> |
| 5(1) | Antennae with 6 or more segments | 10 |
| - | Antennae with 5 or fewer segments | 6 |
| 6(5) | Without ring of tubular ducts surrounding apex of abdomen | 7 |
| - | With ring of tubular ducts surrounding apex of abdomen | <i>Capulinia</i> |

7(6)	Legs large, well developed	8
-	Legs small, abortive	<i>Aculeococcus</i>
8(7)	Enlarged setae not grouped in circular area on thorax and head	9
-	Enlarged setae grouped in circular area on thorax and head	<i>Neotectococcus</i> (in part)
9(8)	Anal lobes protruding, heavily sclerotized.....	<i>Pseudotectococcus</i>
-	Anal lobes absent or very small, unsclerotized	<i>Tectococcus</i> (in part)
10(5)	Anal lobes absent or, if present (sclerotised or not), not protruding noticeably past posterior apex of abdomen ..	22
-	Anal lobes present, clearly protruding from posterior apex of abdomen.....	11
11(10)	Macrotubular ducts present on dorsum	15
-	Macrotubular ducts absent from dorsum.....	12
12(11)	Antennae 6 segmented; without a cluster of spinose setae ventrally between meso- and prothoracic legs.....	13
-	Antennae 8 segmented; with a cluster of spinose setae ventrally between meso- and prothoracic legs.....	<i>Eriobalachowskya</i>
13(12)	Loculate pores absent from spiracular atria; anal ring with 8 setae and with a double row of pores	14
-	Loculate pores present in spiracular atria; anal ring with 10 setae and with a single row of pores.....	<i>Poliloculus</i>
14(13)	Dorsal setae large, conspicuously spiniform; translucent pores on hind coxa represented by large openings	<i>Icelococcus</i>
-	Dorsal setae small, slightly spiniform; translucent pores on hind coxa represented by small dots ...	<i>Intecticoccus</i>
15(11)	At least some macrotubular ducts on dorsum with a conspicuous rim surrounding dermal orifice	20
-	Macrotubular ducts on dorsum without a conspicuous rim surrounding dermal orifice	16
16(15)	Without groups of microducts on dorsum of thorax and anterior abdominal segments	17
-	With conspicuous groups of microducts on dorsum of thorax and anterior abdominal segments... <i>Hempelicoccus</i>	
17(16)	Setae in medial areas of ventral abdomen with acute apices; translucent pores present on some, but not all, of the following hind leg segments: coxa, femur and tibia.....	18
-	Some setae in medial areas of ventral abdomen slightly capitate; translucent pores present on all of the following hind leg segments: coxa, femur and tibia	<i>Coxicoccus</i>
18(17)	Anal lobes conspicuous and sclerotized.....	19
-	Anal lobes small and unsclerotized	<i>Oregmopyga</i> (in part)
19(18)	Anal lobes plate-like, not protruding strongly	<i>Chilecoccus</i> (in part)
-	Anal lobes not plate-like, protruding strongly	<i>Acanthococcus</i> and <i>Madarococcus</i>
20(15)	Venter with tubular ducts; dorsum without simple pores; cruciform pores absent	21
-	Venter without tubular ducts; dorsum with numerous simple pores; cruciform pores present on venter near body margin	<i>Exallococcus</i>
21(20)	Venter with large clusters of tubular ducts; posterior abdomen without sclerotised nodules; anal lobes unsclerotised	<i>Stibococcus</i> (in part)
-	Venter with tubular ducts scattered; posterior abdomen with sclerotised nodules; anal lobes heavily sclerotised ..	<i>Orafortis</i>
22(10)	Anal lobes without conspicuous sclerotisation	24
-	Anal lobes conspicuously sclerotised.....	23
23(22)	Enlarged setae forming conspicuous band around body margin.....	<i>Chilechiton</i>
-	Enlarged setae not forming conspicuous band around body margin	<i>Chilecoccus</i> (in part)
24(22)	Enlarged setae absent or, if present, not grouped in circular area on dorsum of thorax and head	25
-	Enlarged setae grouped in circular area on dorsum of thorax and head.....	<i>Neotectococcus</i> (in part)
25(24)	Venter without large clusters of tubular ducts on abdomen	26
-	Venter with large clusters of tubular ducts on abdomen	<i>Stibococcus</i> (in part)
26(25)	Largest dorsal macroducts without associated setae	27
-	Largest dorsal macroducts with 1–3 associated setae	<i>Melzeria</i>
27(26)	Some dorsal setae cupulate; without wing-like apodemes arising from mouthparts	<i>Oregmopyga</i> (in part)
-	Dorsal setae not cupulate; with large wing-like apodemes attached to mouthparts.....	<i>Tectococcus</i> (in part)

Note: the above key does not include *Eriococcus* (see under *Acanthococcus* above), nor *Opisthoscelis* or *Ovaticoccus*. See above text under the latter 2 genera for the reasons for their exclusion.

**Key to the Genera of the Eriococcidae of South America
(First-instar Nymphs)**

1	Antennae with 6 or more segments.....	4
-	Antennae with fewer than 6 segments.....	2
2(1)	Thorax with 3 pairs of longitudinal lines of spinose setae dorsally (including marginal setae); anal lobes conspicuous; antennae with 3 or fewer segments.....	3
-	Thorax with 2 pairs of longitudinal lines of spinose setae dorsally (including marginal setae); anal lobes absent or slightly rounded; antennae with 4 or more segments.....	<i>Tectococcus</i>
3(2)	Hind femur with 1 seta; anal lobes sclerotized.....	<i>Pseudotectococcus</i>
-	Hind femur with 3 setae; anal lobes apparently unsclerotized.....	<i>Aculeococcus</i>
4(1)	Loculate pores absent from dorsum; much enlarged spinules absent from dorsum.....	5
-	Loculate pores present on dorsum of abdominal segment I; dorsum with much enlarged spinules medially on posterior thoracic and anterior abdominal segments.....	<i>Apiococcus</i>
5(4)	Body margin without conspicuous microducts (if microducts present, marginal microducts same size as other dorsal microducts); spinose setae not cupolate-shaped, not in dermal pocket.....	6
-	Body margin with conspicuous microducts (marginal microducts conspicuously larger than other dorsal microducts); marginal spinose setae cupolate-shaped and in small dermal pocket.....	<i>Melzeria</i>
6(5)	Submedial row of ventral loculate pores absent (if loculate pores present, in a submarginal row).....	7
-	Submedial row of ventral loculate pores present.....	10
7(6)	Cruciform pores present submarginally on thorax; loculate pores present in a submarginal band on abdomen.....	<i>Oregmopyga*</i>
-	Cruciform pores absent; loculate pores restricted to near spiracles, absent from abdominal segments.....	8
8(7)	Spinose setae without conspicuously bulbous base; hind tibia with 3 or 4 setae.....	9
-	Spinose setae with base conspicuously bulbous; hind tibia with 2 setae.....	<i>Capulinia</i>
9(8)	Spinose setae longer than length of abdominal segment; discoidal pores present on dorsum (probably modified microtubular ducts).....	<i>Carpochloroides</i>
-	Spinose setae shorter than length of abdominal segment; discoidal pores absent on dorsum.....	<i>Pseudocapulinia</i>
10(6)	Cruciform pores present.....	12
-	Cruciform pores absent.....	11
11(10)	Anal lobes platelike, not protruding from body margin, heavily sclerotized.....	<i>Chilechiton</i>
-	Anal lobes plate not platelike, not protruding from body margin, weakly sclerotized.....	<i>Hempelicoccus*</i>
12(10)	Labium 3 segmented; dorsum without simple pores.....	13
-	Labium 1 segmented; dorsum with many simple pores.....	<i>Exallococcus</i>
13(12)	Anal lobes weakly sclerotized, not platelike; ventral abdomen with 4 pairs of longitudinal lines of setae.....	<i>Acanthococcus</i>
-	Anal lobes heavily sclerotized, platelike; ventral abdomen with 3 pairs of longitudinal lines of setae.....	<i>Icelococcus</i>

* As shown by the first-instar nymph of *Oregmopyga peruviana* and *Hempelicoccus santiaugensis* and *H. tucumanensis*.

**Key to the Genera of the Eriococcidae of South America
(Adult Males)**

1	Antennae with 8 or fewer segments.....	5
-	Antennae with 10 segments.....	2
2(1)	Penial sheath less than half length of abdomen.....	3
-	Penial sheath more than half length of abdomen.....	<i>Capulinia</i>
3(2)	Antennae with long, narrow fleshy setae, similar to hair-like setae.....	4
-	Antennae with thicker fleshy setae, obviously different from hair-like setae.....	<i>Acanthococcus</i>
4(3)	Glandular pouch shallow, with pores spreading out of pouch onto dorsum; glandular pouch setae short, only extending to about half length of penial sheath; dorsal abdominal setae not as abundant as ventral abdominal setae.....	<i>Stibococcus</i>
-	Glandular pouch deep, with pores restricted to within pouch; glandular pouch setae long, extending to about level with tip of penial sheath; dorsal abdominal setae more abundant than ventral abdominal setae ...	<i>Carpochloroides</i>
5(1)	Abdomen not attenuated; with glandular pouches.....	<i>Pseudotectococcus</i>
-	Abdomen attenuated; without glandular pouches.....	<i>Tectococcus</i>

Discussion

At the present time, 25 genera and 66 species of Eriococcidae (see Appendix 1) are known from South America. As very large areas of this region have yet to be surveyed, it seems highly likely that this is only a small proportion of the total that will finally be discovered there.

Possible relationships as suggested by adult female morphology. Although the habit of many of the species in these genera is not reported in the literature, they appear to be divisible into 2 groups: those in which the adult females have well-developed legs, and those in which the adult females have very reduced legs and clearly live (or have lived) in a very restrictive environment. The former group is also divisible into 2 groups: those that, despite the presence of well-developed legs and antennae, are known to induce enclosed galls (see Cook & Gullan, 2004), and those that are thought to live “exposed” on the plant. The morphology of this latter group tends to be somewhat similar to *Acanthococcus*. They mostly have (in addition to well-developed legs) enlarged spinose dorsal setae (at least around the margin), well-developed antennae, well-developed anal lobes and (frequently) macrotubular ducts. Several of them also have a median plate anterior to the anal ring dorsally and cruciform pores ventrally. This group includes *Acanthococcus*, *Chilechiton*, *Chilecoccus*, *Coxicoccus*, *Eriobalachowskyia*, *Exallococcus*, *Hempelicoccus*, *Icelococcus*, *Intecticoccus*, *Melzeria*, *Orafortis*, *Oregmopyga*, *Poliloculus*, and *Stibococcus*. However, even within this group there is an intriguing dichotomy, with *Chilechiton* and *Icelococcus* [and maybe *Neotectococcus*] having the vulva between abdominal segments VI and VII, whereas the rest of the genera appear to have the vulva between segments VII and VIII. The reason for this difference is unknown.

The second group, which includes *Pseudotectococcus* and *Tectococcus*, induce conical galls on the leaves. The adult females of these two genera have the macrotubular ducts concentrated on the abdomen whereas, when present, these ducts are widespread on the females of other genera. In addition, the adult females of *Pseudotectococcus* and *Tectococcus* tend to have rather more pointed abdomens. Both of these features are, perhaps, adaptations for plugging the gall orifice, with the macrotubular ducts secreting the wax for the plug. *Neotectococcus* may also belong to this group but not enough is known about it.

The other group, which lacks well-developed legs and antennae, includes the genera: *Aculeococcus*, *Apiococcus*, *Capulinia*, *Carpochloroides* and *Macracanthopyga*. Of these, only *Aculeococcus* is thought to induce enclosed galls. The gall-inducing habit within the Eriococcidae was reviewed by Cook & Gullan (2004). They concluded that it had arisen multiple times, even within the relatively few species that they included (44 in Eriococcidae *sensu lato*). Although no such analysis has been undertaken in this review, one might have supposed that there would be some parallels in the structures developed to guard or plug the gall opening. However, the structure of adult female *Aculeococcus* is quite different from that of *Pseudotectococcus* and *Tectococcus*, each genus appearing to use a very different strategy. *Aculeococcus* has evolved sclerotised plates on the abdomen; whilst *Pseudotectococcus* and *Tectococcus* have many pores and ducts on the abdomen and these probably secrete a wax plug. Thus, even within the few taxa discussed in this paper, there does seem to be strong support for the view that the gall-inducing habit in South American eriococcids has arisen several times.

The remainder of this last group (i.e., *Apiococcus*, *Capulinia*, *Carpochloroides* and *Macracanthopyga*) appear to be well adapted for life within a gall even though they are not thought to induce them. Cook & Gullan (2004), whilst discussing similar apparent morphological adaptations for life within a gall for the Australian non-gall inducing species, *Callococcus acaciae* (Maskell), suggested that this was “consistent with the non-gall inducing lineage (of *C. acaciae*) having undergone morphological reductions during a period of gall-habitation and then a subsequent return to a non-galling habit”. Perhaps this reversion is frequent and has also happened to some species in the above South American genera. Indeed, although the type species of *Capulinia* (*C. sallei*) and of *Carpochloroides* (*C. viridis*) are not reported to induce galls, *Capulinia crateriformis* Hempel and *Carpochloroides mexicanus* Ferris do induce galls. However, there is some doubt as to whether *Capulinia crateriformis* and *Carpochloroides mexicanus* are congeneric with the type species of the genus.

Another interesting feature of some gall-inducing genera is that, whilst the pro- and mesothoracic legs are either extremely reduced or even absent, the metathoracic legs can be well developed or even greatly enlarged. In the Neotropics, this applies to *Capulinia* and *Macracanthopyga* but is even more extreme in the Australian genus *Opisthoscelis*. The reasons for this morphology are unknown.

As pointed out by Cook & Gullan (2004), 80% of Australian eriococcids are found on myrtaceous plants, even though the Myrtaceae only comprise about 10% of the Australian flora. In Australia, the main myrtaceous host, especially of galling eriococcids, appears to be *Eucalyptus* (Gullan *et al.* 2005). In South America, where the hosts are known, there is a similar strong preference for Myrtaceae, particularly by the enclosed gall-inducing genera.

Possible relationships as suggested by first-instar nymphal morphology. The morphology of the first-instar nymphs of the species discussed above suggests that they might fall into 4 groups: Group I. *Melzeria* only, particularly characterised by: (i) lack of spinose dorsal setae (although these are present around the margin), and (ii) microtubular ducts with a uniquely long outer ductule (both features not shared by other genera). Group II. *Acanthococcus*, *Chilechiton*, *Exallococcus*, *Hempelicoccus* and *Icelococcus*, all of which have loculate pores in a more or less distinct line mediolaterally on the venter. They also have (i) differentiated and sclerotised anal lobes (sometimes unsclerotised in *Acanthococcus*) and (ii) an anal ring with 3 pairs of setae. *Pseudotectococcus* might also belong to this groups as it also has well-developed anal lobes and a well-developed anal ring with 3 pairs of setae, but it lacks the mediolateral bands of loculate pores; it also shares with *Chilechiton* dissimilar claw digitules. Group III. *Apiococcus*, which has: (i) loculate pores on the dorsum of abdominal segment I, and (ii) enlarged spinules medially on the dorsum (both characters not shared by the other genera discussed here). In addition, sexual dimorphism was also noted in the first-instar nymphs of *Apiococcus*. Sexual dimorphism has been noted before in the Eriococcidae (e.g. in all species of *Apiomorpha*, including a few species in which the males induce galls on the galls of conspecific females (Cook *et al.*, 2000); *Callococcus* sp. (Cook *et al.*, 2000), *Cystococcus* spp. (Gullan & Cockburn, 1986) (all from Australia), and in *Calycicoccus merwei* Brain from South Africa (Gullan *et al.*, 2006). And group IV, the remaining genera: *Aculeococcus*, *Carpochloroides*, *Capulinia*, *Pseudocapulinia* and *Tectococcus*. Although otherwise rather variable, this group is characterised by: (i) lack of differentiated anal lobes (although these may be present on *Aculeococcus*); (ii) a simple anal ring, without pores or setae; (iii) loculate pores restricted to near spiracles; (iv) absence of cruciform pores; and (v) microtubular ducts present on both the dorsum and venter.

Adult males. Of the 5 species discussed in this paper for which males are available, only 2 are known to belong to gall inducing genera: *Pseudotectococcus rollinae* and *Tectococcus ovatus*. One might have expected similar adaptations in these 2 species for reaching the female within the gall but only *T. ovatus* appears to be so modified, with a very long abdomen, narrowing posteriorly, and without glandular pouches or glandular pouch setae. This type of structure has been seen in several other (Australian) gall-inducing eriococcids (e.g. *Cylindrococcus spiniferus* Maskell (Gullan, 1978), *Apiomorpha spinifer* Froggatt and *Opisthoscelis verrucula* Froggatt (Hodgson, unpublished)). The galls induced by *T. ovatus* are on leaves and are well developed, with only a small orifice on the lower surface through which copulation would presumably occur and through which the crawlers must escape. The male of *Calycicoccus merwei* is morphologically rather similar to that of *P. rollinae* (Gullan *et al.*, 2006) and the galls of females of *C. merwei* and *P. rollinae* are also somewhat similar. Perhaps the genital apertures of the female are close to the gall opening in these 2 species, allowing reasonably easy access for the male, whereas in *T. ovatus* (and the other species mentioned above), the distance to the female apertures is much greater, requiring the much extended abdomen? As indicated by Gullan (1978), this is likely to be the case for *C. spinifera* as the female is within tightly imbricate bracts on the *Allocasuarina* host plant.

One interesting feature of all of the adult males known from the Neotropics is that they all lack hamulohalteres and associated structures (alar lobes, suspensorial sclerites, dorsal part of metapleural ridge), and also alar setae. These 2 lots of characters are present (as far as is known) on the males of the acanthococcid and beesoniid-stictococcid-*Eriococcus* clades of Cook and Gullan (2004) (e.g. *Eriochiton* spp. and *Eriococcus aceris* (Signoret) in the former, and *Eriococcus buxi* (Boyer de Fonscolombe) (plus several

other *Eriococcus* spp. from the Palaearctic and Nearctic) in the latter) but are thought to be generally absent from the Gondwanan clade, suggesting that all of the species (for which males are known) from the Neotropics might belong to the Gondwanan clade.

Among the few males that are discussed above, 2 have a reduced number of antennal segments (*Pseudotectococcus* and *Tectococcus*); 2 genera have small pores on the head (*Stibococcus* and *Tectococcus*); 2 have noticeably thickened fleshy setae (*Pseudotectococcus* and *Tectococcus*), and *Carpochloroides* has 1-segmented tarsi. The significance of these character-states in terms of relationships is uncertain.

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Appendix 1. Current placement of species previously in *Eriococcus*

Eriococcus amomidis Gómez-Menor Ortega = *Acanthococcus*
Eriococcus araucariae Maskell = *Acanthococcus*
Eriococcus brasiliensis Cockerell = *Hempelicoccus*
Eriococcus campinensis Hempel = *Acanthococcus*
Eriococcus chilensis Miller & González = *Madarococcus*
Eriococcus clapsae González = *Acanthococcus*
Eriococcus christopherus Foldi & Kozár = *Acanthococcus*
Eriococcus coccineus Cockerell = *Acanthococcus*
Eriococcus coffeae Hempel = *Acanthococcus*
Eriococcus costaricensis Cockerell & Robinson = *Acanthococcus*
Eriococcus cuneifoliae González = *Acanthococcus*
Eriococcus curassavicus Reyne = *Acanthococcus*
Eriococcus divaricatae González = *Acanthococcus*
Eriococcus diversispinus Leonardi = *Acanthococcus*
Eriococcus dombeyae González probably = *Madarococcus*
Eriococcus dubius Cockerell = *Acanthococcus*
Eriococcus eurythrix Miller & González = *Madarococcus*
Eriococcus jorgenseni Morrison = *Acanthococcus*
Eriococcus lanatus Hempel = *Acanthococcus*
Eriococcus lahillei (Leonardi) = *Acanthococcus*
Eriococcus leguminicola Morrison = *Hempelicoccus*
Eriococcus longisetosus Foldi & Kozár = *Acanthococcus*
Eriococcus maximus Foldi & Kozár = *Acanthococcus*
Eriococcus mendozae Morrison = *Hempelicoccus*
Eriococcus navarinoensis Hoy = *Madarococcus*
Eriococcus papillosus Morrison = *Acanthococcus*
Eriococcus paranaensis Foldi & Kozár = *Hempelicoccus*
Eriococcus perplexus Hempel = *Acanthococcus*
Eriococcus piptandeniae Hempel = *Acanthococcus*
Eriococcus pituilensis González = *Acanthococcus*
Eriococcus pumiliae González = *Hempelicoccus*
Eriococcus rhadinothrix Miller & González = *Madarococcus*
Eriococcus santiaguensis González & Granara de Willink = *Hempelicoccus*
Eriococcus tholothrix Miller & González = *Acanthococcus*
Eriococcus tucumanensis González & Granara de Willink = *Hempelicoccus*
Eriococcus tucurinae Laing = *Acanthococcus*
Eriococcus valenzuelae Balachowsky = *Eriobalachowskyia*
Eriococcus venezuelaensis Foldi & Kozár = *Acanthococcus*

In the following list, the host plant genus (or genera) and/or family are specified after the eriococcid name:

1 *Acanthococcus*

1. *amomidis* (Gómez-Menor Ortega), *Amomis* (Myrtaceae)
2. *araucariae* Maskell, primarily *Araucaria* (Araucariaceae)
3. *campinensis* (Hempel), *Mimosa* (Fabaceae)
4. *christopherus* (Foldi & Kozár), *Eugenia* (Myrtaceae)
5. *clapsae* (González), *Larrea* (Zygophyllaceae)
6. *coccineus* (Cockerell), primarily Cactaceae
7. *coffeae* (Hempel), *Coffea* (Rubiaceae)
8. *costaricensis* (Cockerell & Robinson), *Vaccinium* (Ericaceae)
9. *cuneifoliae* (González), *Larrea* (Zygophyllaceae)
10. *curassavicus* (Reyne), *Malvastrum* (Malvaceae)
11. *divaricatae* (González), *Larrea* (Zygophyllaceae)
12. *diversispinus* (Leonardi), *Zuccagnia* (Fabaceae)
13. *dubius* (Cockerell), many hosts
14. *jorgenseni* (Morrison), *Psidium* (Myrtaceae) & *Myrcia* (Myricaceae)

15. *lahillei* (Leonardi), *Larrea* (Zygophyllaceae)
16. *lanatus* (Hempel), *Eugenia* (Myrtaceae)
17. *longisetosus* (Foldi & Kozár), *Annona* (Annonaceae)
18. *maximus* (Foldi & Kozár), *Psidium* (Myrtaceae)
19. *microspinus* Kozár & Konczné Benedicty, host unknown
20. *papillosus* (Morrison), *Heliotropium* (Boraginaceae)
21. *perplexus* (Hempel), 3 genera of Myrtaceae
22. *piptandeniae* (Hempel), *Piptandenia* (Fabaceae)
23. *pituilensis* (González), *Larrea* (Zygophyllaceae)
24. *pseudolongisetosus* Konczné Benedicty & Kozár, host unknown
25. *tholothrix* (Miller & González), *Nothofagus* (Nothofagaceae) & *Eucryphia* (Eucryphiaceae)
26. *tucurinae* Laing, *Ulex* (Fabaceae)
27. *venezuelaensis* (Foldi & Kozár), *Eugenia* (Myrtaceae)
28. *ventrispinus* Kozár & Konczné Benedicty, *Weinmania* (Cunoniaceae)
29. *willinkae* Kozár & Konczné Benedicty, unknown host

2 *Aculeococcus*

30. *morrisoni* Lepage, host unknown, induces galls

3 *Apiococcus*

31. *asperatus* Hempel, *Eugenia* (Myrtaceae)
32. *globosus* Hempel, (Myrtaceae)
33. *gregarius* Hempel, (Myrtaceae)
34. *singularis* Hempel, (Myrtaceae)

4 *Capulinia*

35. *crateraformis* Hempel, *Eugenia* (Myrtaceae) induces galls
36. *jaboticabae* Ihering, *Eugenia* (Myrtaceae)
37. *sallei* Signoret, *Eugenia* (Myrtaceae) plus 1 other family

5 *Carpochloroides*

38. *mexicanus* Ferris, *Eugenia* (Myrtaceae) induces galls
39. *viridis* Cockerell, *Eugenia* (Myrtaceae)

6 *Chilechiton*

40. *lynae* Hodgson & Miller, *Nothofagus* (Nothofagaceae)

7 *Chilecoccus*

41. *browni* Miller & González, *Nothofagus* (Nothofagaceae)
42. *spinus* Miller & González, *Nothofagus* (Nothofagaceae) plus 1 other genus

8 *Coxicoccus*

43. *foldi* Kozár & Konczné Benedicty, host unknown

9 *Eriobalachowskya*

44. *valenazuelae* Balachowsky, *Inga* (Fabaceae)

10 *Exallococcus*

45. *laureliae* Miller & González, *Laurelia* (Atherospermataceae)

11 *Hempelicoccus*

46. *brasiliensis* (Cockerell), *Baccharis* (Asteraceae)
47. *mendozae* (Morrison), *Prosopis* (Fabaceae)
48. *leguminicola* (Morrison), 3 genera (Fabaceae)
49. *paranaensis* (Foldi & Kozár), *Baccharis* (Asteraceae)
50. *pumiliae* (González), *Nothofagus* (Nothofagaceae)
51. *santiaguensis* (González & Granara de Willink), 2 genera (Fabaceae)
52. *tucumanensis* (González & Granara de Willink), *Acacia* (Fabaceae)

- 12 *Icelococcus*
53. *charlini* Miller & González, *Nothofagus* (Nothofagaceae)
54. *lithraeae* Hodgson & Miller, *Lithraea* (Anacardiaceae)
55. *nothofagi* Miller & González, *Nothofagus* (Nothofagaceae)
- 13 *Intectococcus*
56. *viridis* Kondo, *Nothofagus* (Nothofagaceae)
- 14 *Macracanthopyga*
57. *verganiana* Lizer y Trelles, *Campomanesia* (Myrtaceae) induces galls
- 15 *Madarococcus*
58. *chilensis* (Miller & González), *Nothofagus* (Nothofagaceae)
59. *dombeyae* González — possibly belongs in *Madarococcus*, *Nothofagus* (Nothofagaceae)
60. *eurythrix* (Miller & González), *Nothofagus* (Nothofagaceae)
61. *navarinoensis* (Hoy), *Nothofagus* (Nothofagaceae)
62. *rhadinothrix* (Miller & González), *Nothofagus* (Nothofagaceae)
- 16 *Melzeria*
63. *horni* Green, host unknown
- 17 *Neotectococcus*
64. *lenticularis* Hempel, host unknown, induces galls
- 18 *Orafortis*
65. *luma* Hardy, *Amomyrtus* (Myrtaceae)
- 19 *Oregmopyga*
66. *peruviana* Granara de Willink & Diaz, *Vitis* (Vitaceae)
- 20 *Poliloculus*
67. *stipae* González, *Stipa* (Poaceae)
- 21 *Pseudocapulinia*
68. *lanosa* Hempel, host unknown
- 22 *Pseudotectococcus*
69. *anoniae* Hempel, *Annona* (Annonaceae) induces galls
70. *rollinae* Hodgson & Goncalves, *Rollinia* (Annonaceae) induces galls
- 23 *Stibococcus*
71. *cerinus* Miller & González, *Myrceugenia* (Myrtaceae)
- 24 *Tectococcus*
72. *ovatus* Hempel, *Psidium* (Myrtaceae) & *Daphnopsis* (Thymelaeaceae) induces galls
- 25 Genus undetermined, not considered part of *Opisthoscelis*
73. *prosopidis* Kieffer & Jorgensen, *Prosopis* (Fabaceae) induces galls