

**TWO NEW GENERA AND SPECIES OF MEALYBUGS  
(HEMIPTERA: COCCOIDEA: PSEUDOCOCCIDAE) THAT PRODUCE  
PLANT GALLS**

DOUGLAS J. WILLIAMS AND DOUGLASS R. MILLER

(DJW) Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.; (DRM) Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, Bldg. 046, BARC-West, Beltsville, MD 20705-2350, U.S.A. (e-mail: dmiller@sel.barc.usda.gov).

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**Abstract.**—In the mealybug family Pseudococcidae, only 23 species in 14 genera are known to be gall formers. The purpose of this paper is to describe two new South American genera and species that cause galls; namely *Miconicoccus ruebsaameni* and *Quadrigallicoccus lauracearum*. These mealybugs are legless and apparently are related to *Antonina* Signoret. They are the first gall-forming mealybugs known from the continental land mass of the New World. A review of gall-forming mealybugs from other parts of the world is also presented.

**Key Words:** gall-forming mealybugs, galls, Coccoidea, Pseudococcidae, new genera, new species, *Miconicoccus ruebsaameni*, *Quadrigallicoccus lauracearum*, South America, review

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Gall producing scale insects have long been a subject of general interest (Beardsley 1984), particularly in Australia where a significant proportion of the Coccoidea biota produces galls (Gullan 1984). Scale insects in 10 families are gall formers, including the Margarodidae (2 species in 2 genera), Pseudococcidae (23 species in 14 genera), Eriococcidae (more than 100 species in at least 21 genera), Kermesidae (4 species in 3 genera), Coccidae (1 species in 1 genus), Asterolecaniidae, Cerococcidae, and Lecanodiaspididae (most species in these families form at least a pit or depression on their host, some form galls that enclose the body of the female), Beesoniidae (all species of this family form galls some of which are colonial), and Diaspididae (16 species in 12 genera).

There is a surprising paucity of true gall formers within the Pseudococcidae; in fact,

outside of Hawaii only 5 other species of mealybugs are known to form definite galls, i.e., *Cataenococcus gallicolus* (Mamet), *Eurycoccus sternlichti* Williams, *Grewia-coccus gregalis* Brain, *Lantanacoccus sauroides* Williams and Granara de Willink, and *Pseudoripersia turgipes* (Maskell). In Hawaii, 11 species in 5 genera are known to produce galls (Beardsley 1984) (actually Beardsley did not mention *Pseudococcus antricolens* Ferris and *Gallulococcus tenoriori* Beardsley but included 2 species in his figures that do not produce galls).

Since information on gall-forming mealybugs has not been reviewed since Beardsley (1984), we felt that it would be useful to provide a summary as part of the introduction. While writing this section and examining illustrations of each species, we were struck by the fact that many of the true gall-forming species have one or more mor-



phological modifications that are shared by other unrelated gall-forming mealybugs and apparently relate to the gall-forming habit. These apparent, gall-mediated, morphological characteristics include: a series of large conical setae on at least the posterior apex of the abdomen, often these are modified anal-lobe cerarii; a pear-shaped body with the posterior apex narrowest; hind legs that are enlarged or modified in some manner; the posterior apex of the body that is sclerotized and may be modified. Species that fall in this category are as follows: *Gallulococcus tenorioi* has the body pear shaped; it forms shallow pocket galls on the leaves of its *Metrosideros* (Myrtaceae) host (Beardsley 1971). *Grewiacoccus gregalis* has enlarged hind coxae and the posterior apex of the abdomen is covered with enlarged conical setae; it forms a blunt leaf gall on the undersides of its *Grewia* (Tiliaceae) host in South Africa (Brain 1918). *Lantanacoccus sauroides* has numerous dorsal enlarged setae; it forms deep, hardened gall-like depressions on the leaves of *Lantana* (Verbenaceae) in Haiti and Jamaica (Williams and Granara de Willink 1992). *Nesopedronia acanthocauda* (Beardsley) has the anal-lobe cerarii so enlarged that they form a continuous row of setae across the apex of the abdomen and has only the hind two pair of cerarii present; the gall is formed from a rolled fern pinnule on its *Dicranopteris* (Gleicheniaceae) host (Beardsley 1957). *Nesopedronia crypta* (Beardsley) has the anal-lobe cerarii so enlarged that they form a continuous row of setae across the apex of the abdomen; the gall is formed from a rolled fern pinnule on its *Dicranopteris* (Gleicheniaceae) host (Beardsley 1957). *Nesopedronia dura* (Beardsley) has the posterior apex of the abdomen sclerotized and developed into a small pygidial-like flap; it forms a hard, gall-like roll at the apex of each affected pinnule on its *Dicranopteris* (Gleicheniaceae) host (Beardsley 1957). *Pseudoripersia turgipes* has dorsal conical setae, large robust legs, and a large anal-lobe cerarius with many setae; it

produces galls on *Casuarina* (Casuarinaceae) by causing branchlets to become distorted and curl around the body of the insect; it occurs in Australia (Williams 1985). *Phyllococcus oahuensis* (Ehrhorn) has a heavily sclerotized and flattened posterior portion of the abdomen that is specialized for sealing the entrance to the gall; it forms erect galls on the leaves of *Urera* (Urticaceae) (Ferris 1948).

We were surprised to find that several true gall-forming species seem to have no unusual morphological modifications. Within this category of mealybug gall former we found species that have gall-forming congeners with morphological modifications. Species without obvious modifications include: *Cataenococcus gallicolus* which forms galls on the twigs of an unidentified creeper in Madagascar (Mamet 1954). *Eurycoccus sternlichti* Williams forms galls on the twigs of *Quercus ithuburensis* (Fagaceae) that are up to 8 cm long and 3 mm thick in Israel (Williams 1958). *Nesopedronia cibotii* (Beardsley) does not always cause host deformation; when galling occurs it is limited to the edges of the pinnules which are curled on its *Cibotium* (Dicksoniaceae) host (Beardsley 1957). *Nesopedronia hawaiiensis* (Ferris) forms a rosette-like gall of fern pinnules (Beardsley 1959) on its *Dicranopteris* (Gleicheniaceae) host. *Pseudococcus antricolens* produces finger-like galls on the upper surface of the leaves of *Santalum freycinetianum* (Santalaceae) in Hawaii (Ferris 1948). *Pseudococcus gallicola* Ehrhorn produces pocket galls on the upper surface of *Santalum* (Santalaceae) leaves (Ferris 1948). *Pseudotrionymus multiductus* Beardsley forms a gall by rolling the entire leaf near the midrib of its *Syzygium* (Myrtaceae) host (Beardsley 1959). *Pseudotrionymus refertus* (Ferris) forms a gall by rolling the leaf margins of its *Eugenia* (Myrtaceae) host (Beardsley 1959).

*Ohiaoccus cryptus* Beardsley was reported as forming galls (Beardsley 1984) but as far as we can determine it does not cause any host deformation. According to



the original description of Beardsley (1971) “All the specimens were found at the bases of leaf petioles where these were tightly appressed to the twigs and where the insects [were] imbeded in thick tomentum which is characteristic of the *typica* variety of ohia.”

There are several species of mealybugs that cause host deformation but are not obligate gall formers and are not specialized morphologically for gall habitation. They include: *Hypogeococcus festerianus* (Lizer y Trelles) on *Cereus* (Cactaceae) and *Echinopsis* (Cactaceae) in Argentina (Williams and Granara de Willink 1992); *H. pungens* Granara de Willink mainly on *Cereus* and *Eriocerus* (Cactaceae) in Argentina and Brazil (Williams and Granara de Willink 1992); *Maconellicoccus hirsutus* (Green) on many hosts in many parts of the world (Williams 1996); *Nipaecoccus viridis* (Newstead) on several hosts in Jordan (Sharaf and Meyerdirk 1987); *Phenacoccus herreni* Cox and Williams on *Manihot esculenta* (Euphorbiaceae) in South America (Cox and Williams 1981); *Phenacoccus manihoti* Matile-Ferrero on *Manihot esculenta* and several other hosts in South America (Cox and Williams 1981); *Phenacoccus parvus* Morrison on many hosts throughout the world (Williams, personal observations).

In this paper we describe two genera and two species from Central and South America that are the first gall-producing mealybugs to be described from continental land masses in the New World. These genera can be distinguished from others in the area by the following key modified from couplets 2 and 3 of the key to genera in Williams and Granara de Willink (1992):

- 2. Minute ducts present ventrally in distinct oval to round areas posterior of hind spiracles . . . . . *Chaetococcus* Maskell
- Minute ducts absent ventrally posterior of hind spiracles; sometimes with minute pores in this area . . . . . 3a
- 3a. Antennae each with 2 or 3 segments . . . . . 3b
- Antennae each represented by unsegmented sclerotized area . . . . . 3c
- 3b. Anal ring either on surface at posterior end of

- abdomen or at base of anal tube, always with setae at least as long as diameter of ring . . . . . *Antonina* Signoret
- Anal ring on surface, situated about twice its diameter from posterior end of body, with setae shorter than diameter of ring . . . . . *Paludicoccus* Ferris
- 3c. Posterior end of body pointed. Anal ring at end of anal tube, with 6 setae. Multiple circuli present. Cluster of minute pores absent from each side of vulva. . . . . *Miconicoccus* Williams and Miller, n. gen.
- Posterior end of body rounded. Anal ring on body surface, not at end of anal tube, without setae. Circuli absent. Cluster of minute pores present on each side of vulva. . . . . *Quadrigallicoccus* Williams and Miller, n. gen.

METHODS

Terminology in the descriptions follows that of Williams and Watson (1988) and Gimpel and Miller (1996). Sclerotized slits are present laterad of the hind legs of the first instar and laterad of the middle legs of the second-instar male of *Quadrigallicoccus lauracearum*. We have not observed these structures before and are uncertain of their function. Measurements and numbers are from 10 specimens when available, and are given as an average followed by the range in parentheses. Depositories of specimens are: The Natural History Museum, London (BMNH); National Museum of Natural History, Beltsville, MD (USNM); R. M. Bohart Museum, Davis, CA (UCD); Muséum National d’Histoire Naturelle, Paris (MNHN). The coauthors are equally responsible for the research and production of this paper.

RESULTS

*Miconicoccus* Williams and Miller, new genus

Type species.—*Miconicoccus ruebsaameni* Williams and Miller.

Diagnosis.—*Adult female*: Body rotund; posterior apex sclerotized; segmental line between segments VII and VIII heavily sclerotized, with associated apophysis. Cerarii represented by paired spine-like setae at apex of opening of anal tube. Trilocular



pores uncommon; multilocular pores present. Oral-collar tubular ducts of *Antonina* type with partial external tube surrounding internal vestibule; oral collars abundant. Multiple circuli present. Anal ring with numerous pores, invaginated in long tube that has second ring near opening of invagination; anal-ring setae apically capitate. Legs absent. Spiracles without pores in atrium. Antennae represented by unsegmented, sclerotized area containing several setae.

*First instar:* With 2 sizes of trilocular pores. Without ostioles. Anal-ring setae enlarged, with blunt apices. Enlarged setae on dorsum of segment VII. Cerarii present on posterior 2 abdominal segments. With 2 or 3 circuli. Apex of abdomen sclerotized.

*Etymology.*—The name of this genus is formed from the generic name of the plant host *Miconia* (Melastomataceae) and the Latin *coccum* meaning seed or scale insect. *Miconicoccus* is a masculine noun.

*Notes.*—This genus is remarkably similar to *Antonina* Signoret and undoubtedly is closely related, but differs by having multiple circuli on the ventral abdomen, antennae represented by an unsegmented sclerotized area, and paired, conspicuous spine-like setae on either side of the opening to the anal tube. *Antonina* lacks circuli or has only 1, has antennae that are 2- or 3-segmented, and lacks paired setae at apex of opening of anal tube. The first instars of these genera are virtually identical except that *Miconicoccus* has 2 or more circuli and lacks ostioles. *Antonina* rarely has circuli, but when present there is only 1, and always has at least the posterior pair of ostioles (Yang and Kosztarab 1967).

***Miconicoccus ruebsaameni* Williams and Miller, new species**

*Type material.*—The holotype adult female is mounted singly on a slide with the following information: Left label "Peru, Tarapoto/ on *Miconia ibaguensis*/ galls/ E. H. Rübsaamen/ X. 1902 No 95/gall no 548/ see Marcellia 1907 6:164/ 165; right label "*Miconicoccus/ ruebsaameni/ Williams &*

Miller/Holotype/C.I.E./B.M.196" (USNM). In addition there are 3 other adult female paratypes, 2 immature paratypes, and 4 first instar paratypes in USNM; there is 1 adult female paratype and 1 immature paratype in BMNH. All material is apparently from the same location although one USNM slide indicates "On *Miconia*/ Dr. Edw. Rübsaamen, coll./ rec'd 1907" while the second says "(larvae)/ on *Miconia* sp./ from Edw. Rübsaamen/ July 1, 08."

*Notes.*—This species was first mentioned by Rübsaamen (1907) for whom the species is named; he described the gall and compared the appearance of the anal wax with that of *Xylococcus filiferus* Löw. His description indicated that the gall is a knotty swelling on the branch and frequently is formed at a branch node.

*Description.*—*Adult female* (Fig. 1): Slide-mounted holotype 1.2 mm long, 1.0 mm wide; paratypes 1.3(0.8–1.6) mm long, 1.2(1.0–1.5) mm wide. Body nearly round, posterior apex sclerotized. Segments V and VI fused laterally.

Dorsum with trilocular pores present in small numbers in medial and mediolateral areas from head to segment V (on some paratypes triloculars were not located). Discoidal pores uncommon, in small numbers on submarginal areas of segments VI and VII, smaller than diameter of trilocular pore. Oral-collar tubular ducts of 3 variable sizes becoming smaller anteriorly, abundant over surface except absent from segment VIII. Setae on segment VIII abundant, posterior setae enlarged and spine-like; 1 or 2 setae on segment VII also enlarged; setae on remainder of dorsum very small and inconspicuous, becoming thinner anteriorly. Segments VII and VIII, and posterior part of VI sclerotized. Segmental line between segments VII and VIII heavily sclerotized with conspicuous internal apophysis; segmental line between segments VI and VII also heavily sclerotized, with smaller apophysis.

Anal ring represented by heavy band of more than 200 pores; present at end of in-



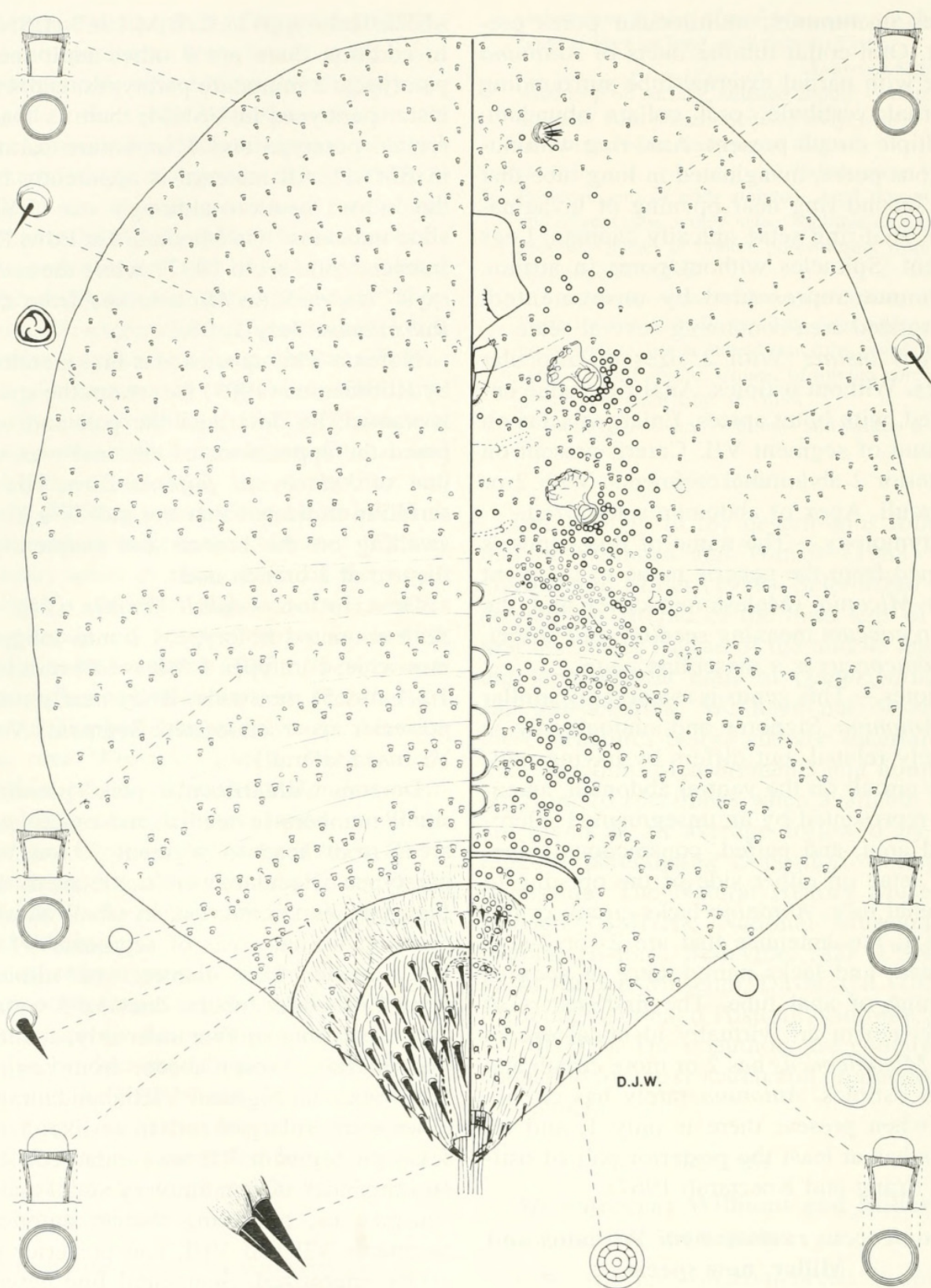


Fig. 1. *Miconicoccus ruebsaameni*. Adult female.



vaginated anal tube about 200  $\mu$  long; ring with 6 setae that protrude from end of tube, each seta with small distal club; anal tube with heavy band on venter anterior of exit to exterior.

Venter with multilocular pores of 2 sizes, smaller size on thorax and head and on segment VIII, larger size in medial and mediolateral areas from posterior thorax to segment VII, multilocular pores concentrated around spiracles, but not in atrium. Discoidal pores of 2 sizes, smaller size in small numbers in mediolateral areas of segments II to VI, with clear center, larger size in medial and mediolateral areas of metathorax to segment IV (some paratypes with pores absent on segment IV) with heavy rim and granular center. Trilocular pores absent. Oral-collar tubular ducts of same 3 sizes as on dorsum, abundant over surface except absent from segment VIII. Excluding anal-lobe seta, longest setae on segment VIII; anal-lobe seta anterior of anal opening, setae on rest of surface unusually small except on segment VIII where posterior and lateral setae are slightly enlarged. Segment VIII heavily sclerotized.

With 5 oval circuli, present on segments II to VI; middle circulus largest (1 paratype with middle circulus divided medially to form 2 lateral circuli). Labium 3-segmented, 84  $\mu$  long; paratypes 91(86–99)  $\mu$  long. Antennae represented by unsegmented sclerotized knob containing 7 or 8 setae. Legs absent; usually with small dermal pockets in position of legs.

Notes: The above description is based on 5 specimens.

*Immature female* (probably third instar)(Fig. 2): Slide-mounted paratypes 0.9(0.7–1.1) mm long, 0.7(0.5–0.9) mm wide. Body nearly round, posterior apex sclerotized.

Dorsum with anal-lobe cerarii composed of 1 pair of conical setae. Trilocular and discoidal pores absent. Oral-collar tubular ducts of 3 variable sizes, becoming smaller anteriorly, abundant over surface except absent from segment VIII. Setae on segment

VIII abundant, posterior setae enlarged and spine like; setae on remainder of dorsum very small and inconspicuous. Segments VII and VIII, and posterior part of VI sclerotized. Segmental line between segments VII and VIII heavily sclerotized with conspicuous lateral apophysis; segmental line between segments VI and VII also heavily sclerotized, without apophyses.

Anal ring represented by heavy band of more than 200 pores; present at end of invaginated anal tube 105(99–111)  $\mu$  long; ring with 6 setae that protrude from end of tube; anal tube without heavy band anterior of exit to exterior.

Venter with multilocular pores of 2 sizes, smaller size near spiracles and on segment VIII, larger size in medial and mediolateral areas from just anterior of mouthparts posterior to segment VII; concentrated around spiracles, but not in atrium. Discoidal pores absent. Trilocular pores absent. Oral-collar tubular ducts of same sizes as on dorsum, abundant over surface except absent from segment VIII. Excluding anal-lobe seta, longest setae on segment VIII; anal-lobe seta near edge of anal tube opening; setae on rest of surface unusually small. Segment VIII heavily sclerotized.

With 4 or 5 oval circuli, present on segments II or III to VI; middle circulus largest. Labium about 56  $\mu$  long. Antennae represented by unsegmented sclerotized knob containing 7 or 8 setae. Legs absent; with small dermal pockets in position of legs.

Notes: The above description is based on 3 specimens.

*First instar* (gender not determined) (Fig. 3): Slide-mounted paratypes 0.5(0.4–0.5) mm long, 0.3(0.2–0.3) mm wide. Body elongate oval.

Dorsum with conspicuous cerarii on segments VII and VIII; those on segment VII each with 2 conical setae, 1 large trilocular pore, 1 small trilocular pore, and 1 discoidal pore; those on segment VIII each with 2 conical setae, 1 small-sized trilocular pore, and 1 discoidal pore; 2 thin setae and 1 or 2 associated trilocular pores on margin of



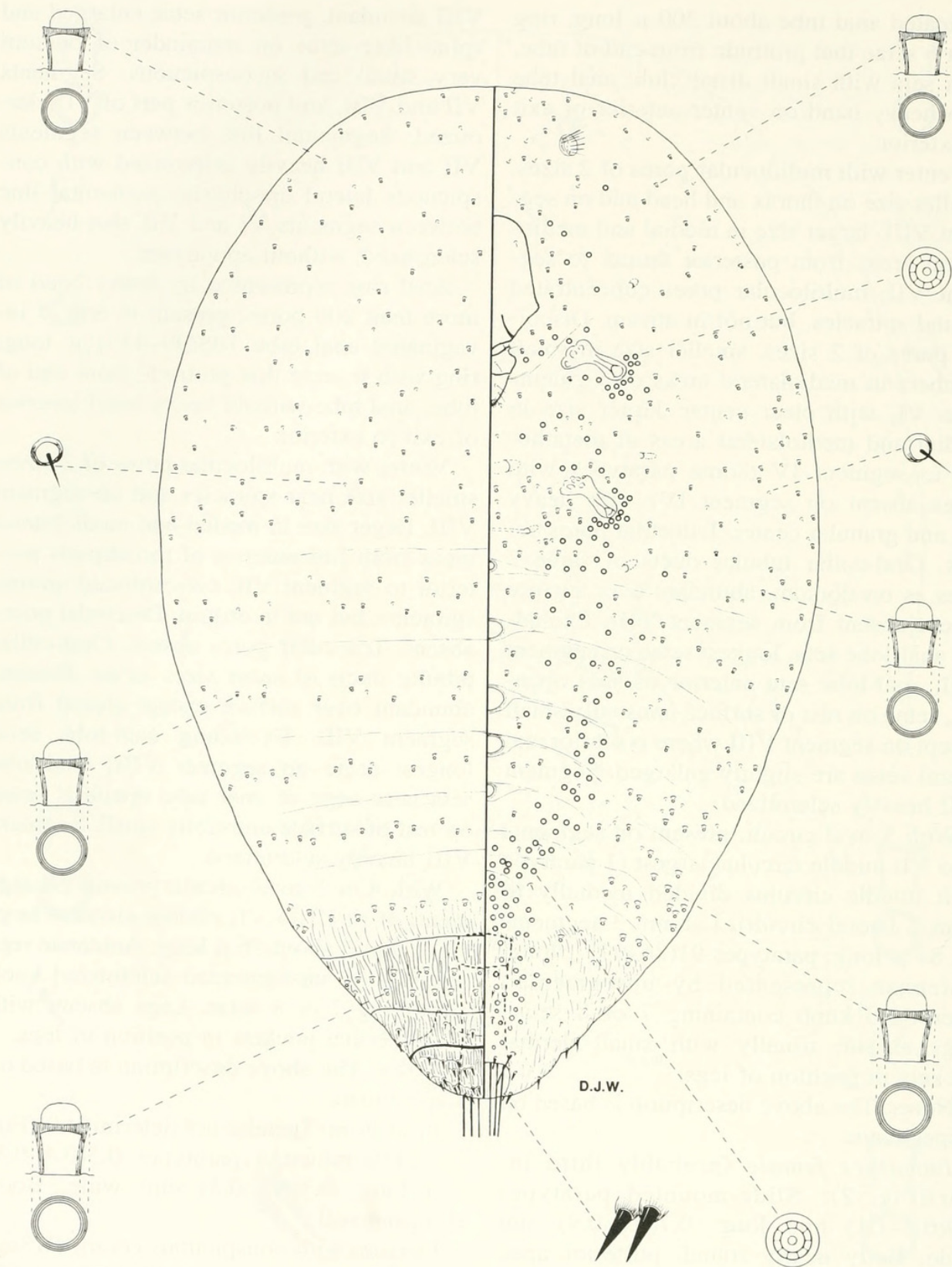


Fig. 2. *Miconicoccus ruebsaameni*. Third-instar female.



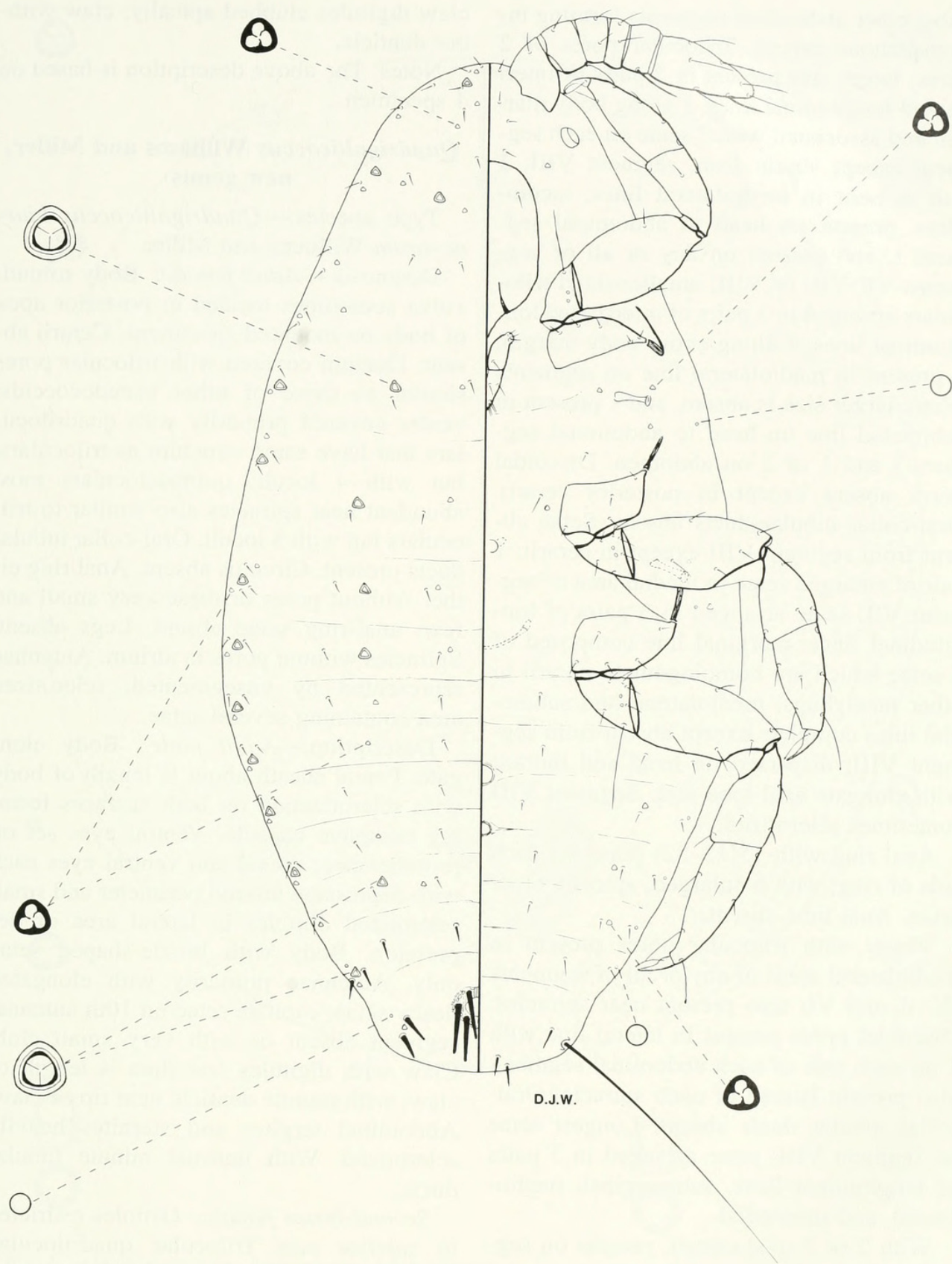


Fig. 3. *Miconicoccus ruebsaameni*. First instar.



most other abdominal segments forming inconspicuous cerarii. Trilocular pores of 2 sizes; larger size present in 2 pairs of interrupted longitudinal lines, 1 along body margin and associated with 2 setae on each segment except absent from segment VIII, 1 pair present in mediolateral lines, incomplete, present on head to abdominal segment I, and present on any or all of segments VI, VII, or VIII; smaller-sized triloculars arranged in 3 pairs of interrupted longitudinal lines, 1 along entire body margin, 1 present in mediolateral line on segments where larger size is absent, and 1 present in submedial line on head to abdominal segment I and 1 or 2 on abdomen. Discoidal pores absent except in posterior cerarii. Oral-collar tubular ducts absent. Setae absent from segment VIII except in cerarii; 1 pair of enlarged setae in medial area of segment VII; setae arranged in 3 pairs of longitudinal lines; marginal line composed of 2 setae which are homologous to cerarii in other mealybugs; mediolateral and submedial lines complete except absent from segment VIII; dispersed on head and thorax; with elongate anal-lobe seta. Segment VIII sometimes sclerotized.

Anal ring with 15(13–32) pores on each side of ring; with 6 enlarged, apically blunt setae. Anal tube absent.

Venter with trilocular pores present in mediolateral areas of any or all of segments IV, V, and VI; also present near spiracles. Discoidal pores present in lateral line with 1 on each side of each abdominal segment, also present laterad of each spiracle. Oral-collar tubular ducts absent. Longest setae on segment VIII; setae arranged in 3 pairs of longitudinal lines, submarginal, mediolateral, and submedial.

With 2 or 3 oval circuli, present on segments IV and V, sometimes present on segment III. Labium 62(57–67)  $\mu$  long. Antennae 6-segmented, 128(124–136)  $\mu$  long. Legs well developed, hind femur 49  $\mu$  long; hind tibia 35  $\mu$  long; hind tarsus 42  $\mu$  long; tibia/tarsus 0.8; femur/tibia 1.4; tarsal and

claw digitules clubbed apically; claw without denticle.

Notes: The above description is based on 4 specimens.

***Quadrigallicoccus* Williams and Miller,  
new genus**

Type species.—*Quadrigallicoccus lauracearum* Williams and Miller.

Diagnosis.—*Adult female*: Body rotund; vulva sometimes located at posterior apex of body on mounted specimens. Cerarii absent. Dorsum covered with trilocular pores similar to those of other pseudococcids; venter covered primarily with quadriloculars that have same structure as triloculars, but with 4 loculi; quinqueloculars most abundant near spiracles also similar to triloculars but with 5 loculi. Oral-collar tubular ducts present. Circulus absent. Anal ring either without pores or these very small and few; anal-ring setae absent. Legs absent. Spiracles without pores in atrium. Antennae represented by unsegmented, sclerotized area containing several setae.

Description.—*Adult male*: Body elongate. Penial sheath about  $\frac{1}{4}$  length of body with sclerotization on both surfaces forming complete capsule. Ventral eyes set on protuberance; dorsal and ventral eyes each with depression around perimeter and small sclerotized dimples in lateral area of depression. Body with bristle-shaped setae only. Antennae primarily with elongated fleshy setae; capitate setae on 10th antennal segment absent or with very small club. Claw with digitules less than  $\frac{1}{4}$  length of claw; with minute denticle near tip of claw. Abdominal tergites and sternites heavily sclerotized. With unusual minute tubular ducts.

*Second-instar female*: Ostioles restricted to anterior pair. Trilocular, quadrilocular, and quinquelocular pores with swirled pattern. Antenna 6-segmented. Oral collar tubular ducts present. Anal ring on dorsal surface removed from apex. Sclerotized slit present laterad of mid pair of legs.

*Second-instar male*: Trilocular, quadril-



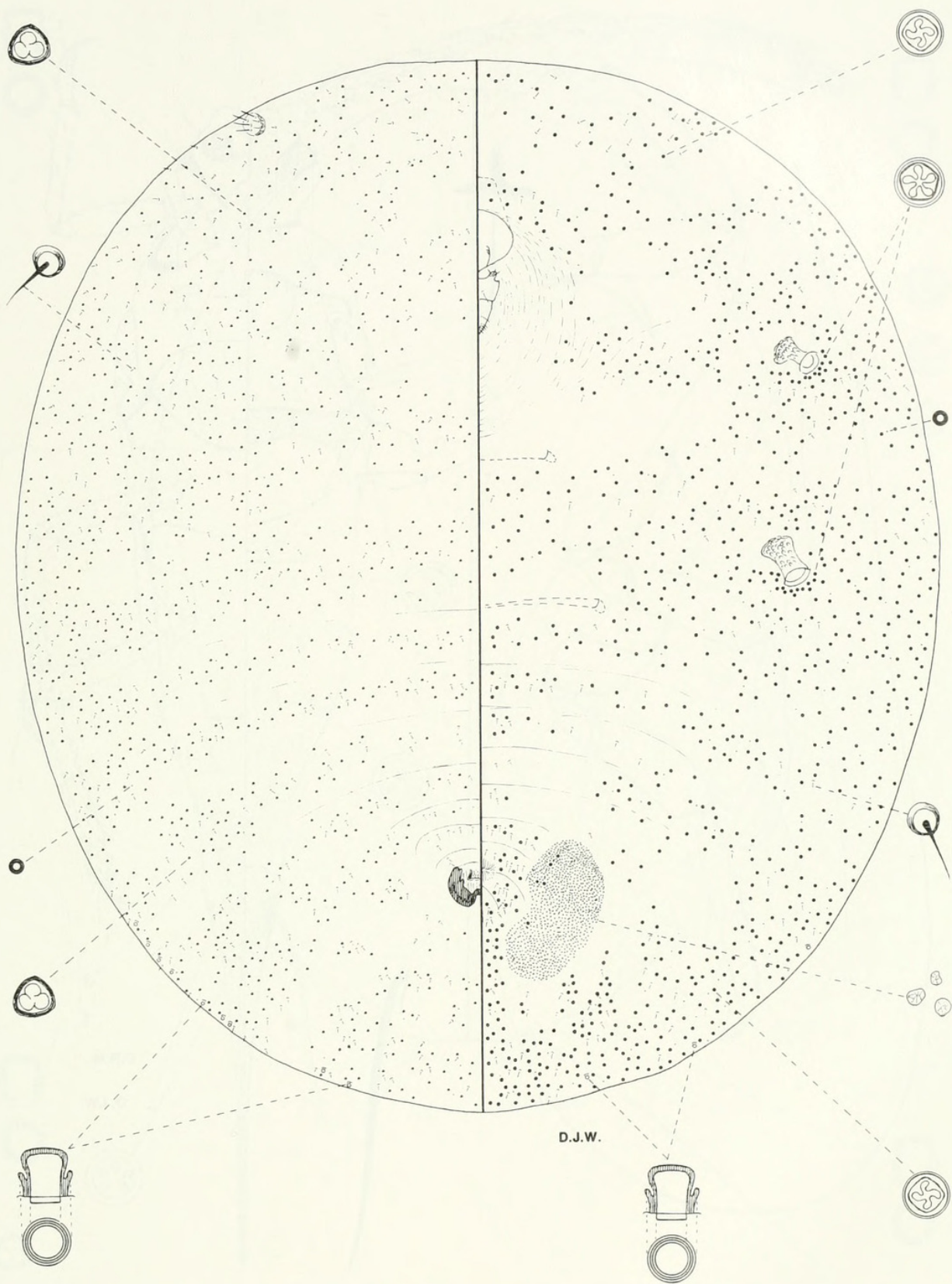


Fig. 4. *Quadrigallicoccus lauracearum*. Adult female.



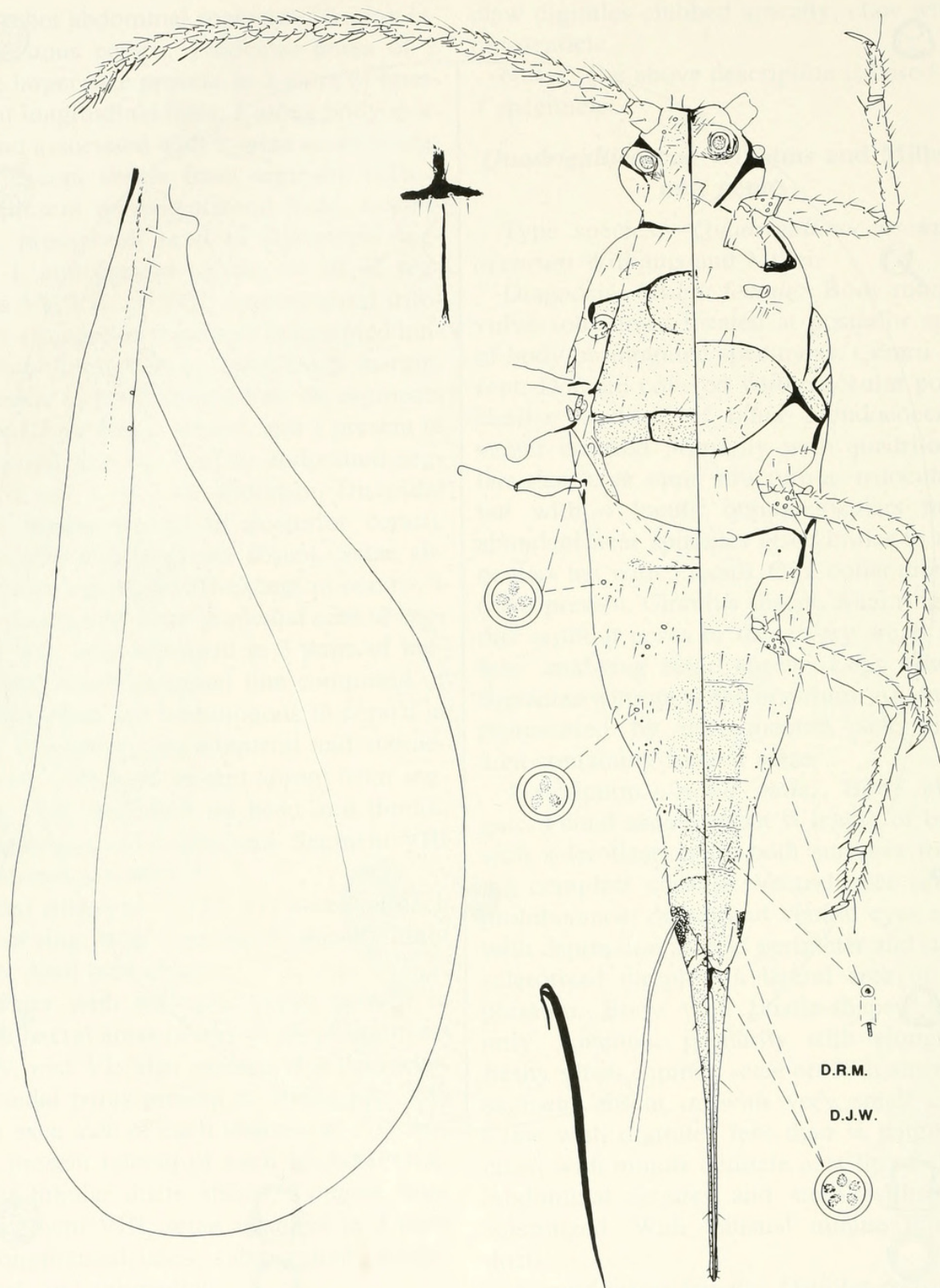


Fig. 5. *Quadrigallicoccus lauracearum*. Adult male.

ocular, and quinquelocular pores with swirled pattern. Antenna 7-segmented. Oral collar tubular ducts absent; minute tubular ducts present. Anal ring on dorsal surface

near apex of abdomen. Sclerotized slit present laterad of hind pair of legs.

*First instar:* Without cerarii. With ostioles. Anal-ring setae absent; anal-ring pores



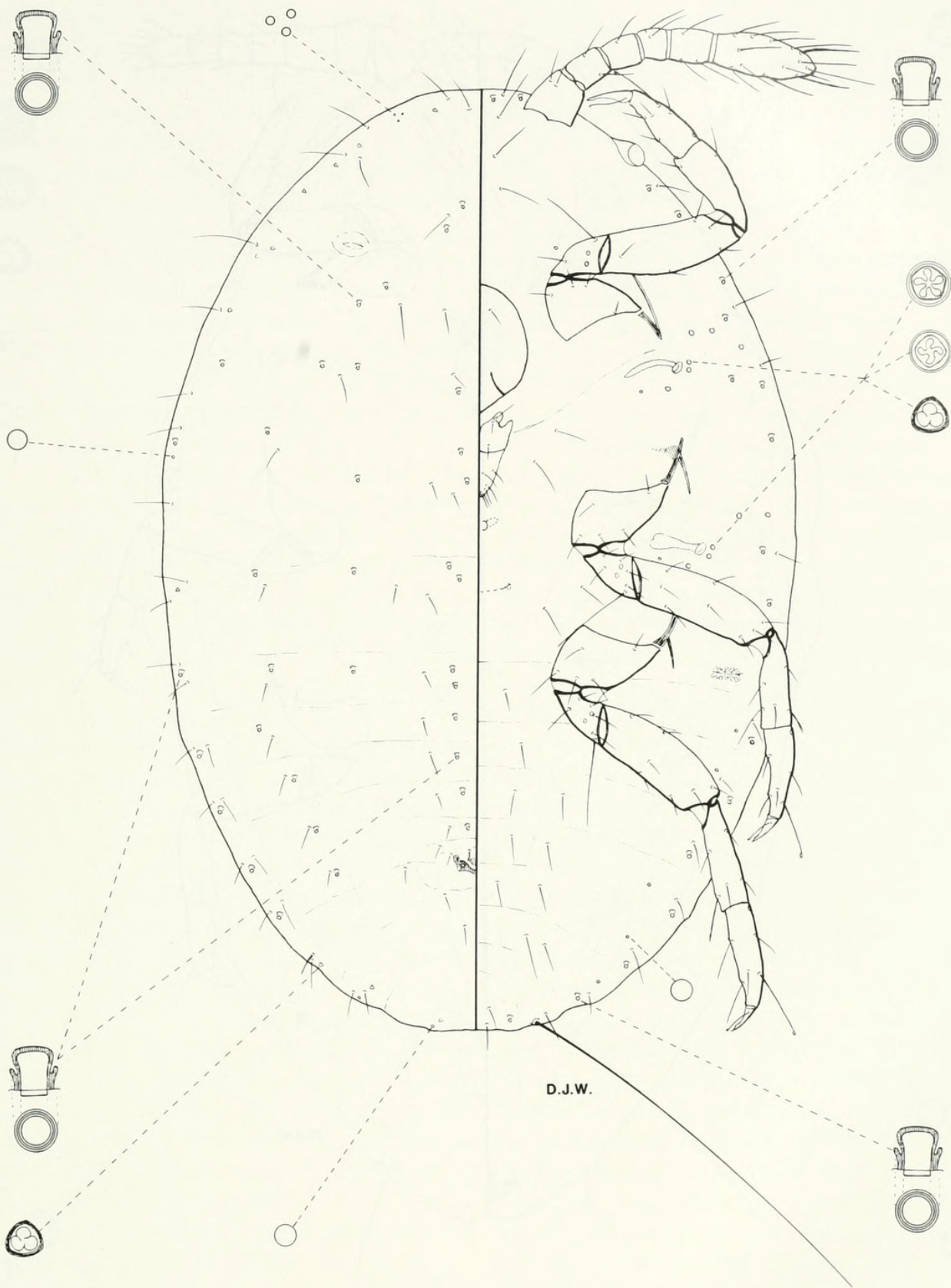


Fig. 6. *Quadrigallicoccus lauracearum*. Second-instar female.



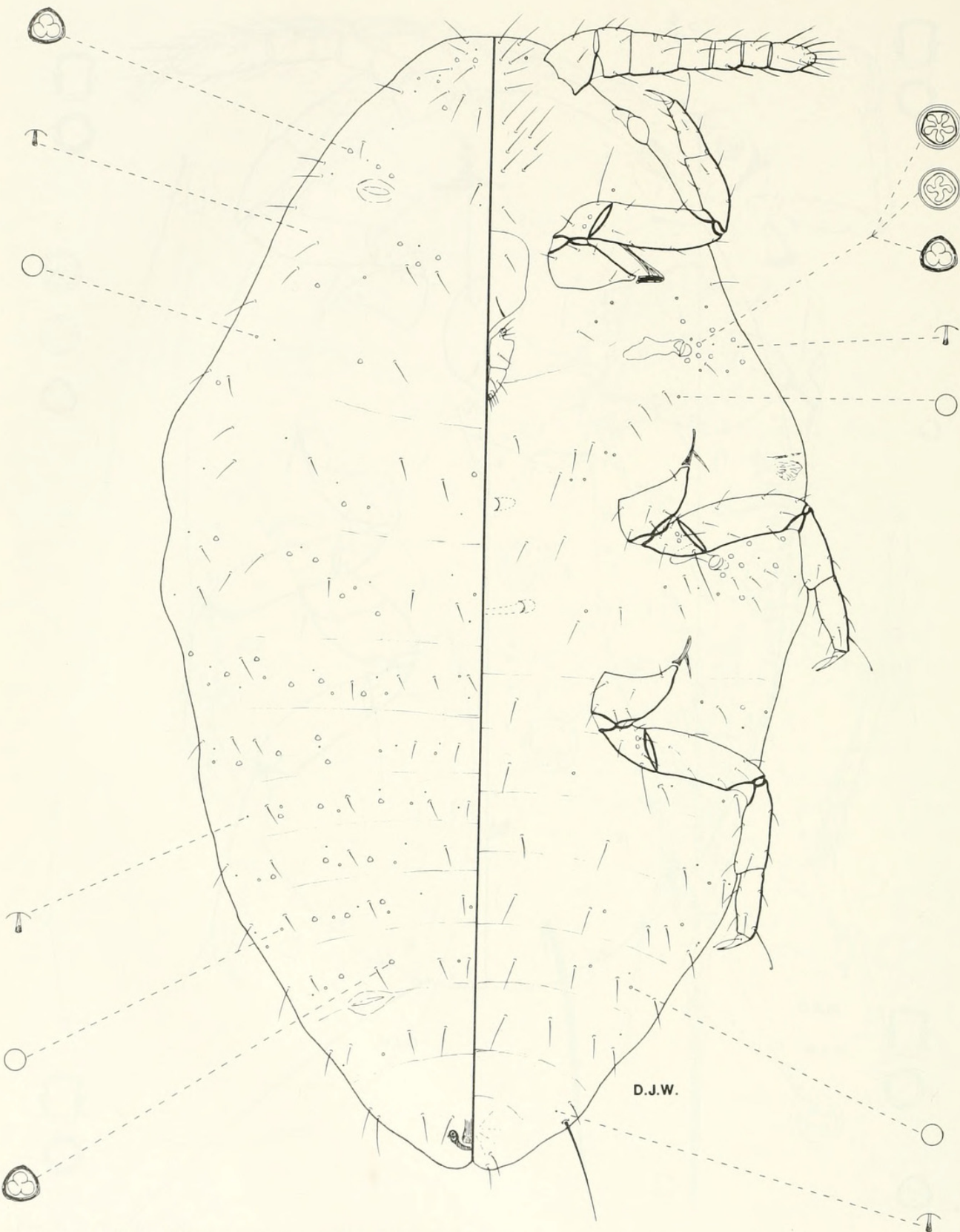


Fig. 7. *Quadrigallicoccus lauracearum*. Second-instar male.



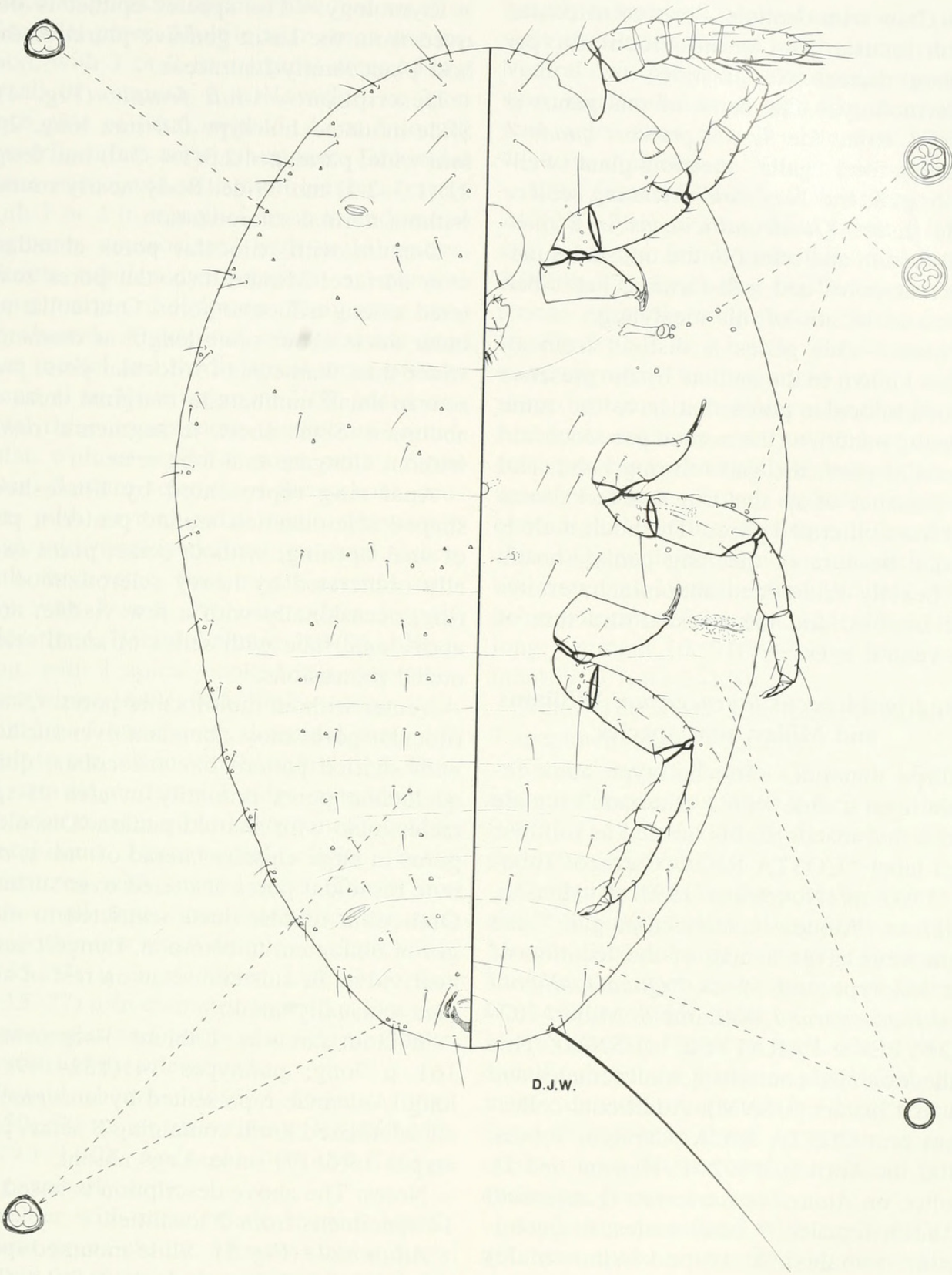


Fig. 8. *Quadrigallicoccus lauracearum*. First instar.



few. Claw with denticle. Pores of trilocular, quadrilocular, and quinquelocular type. Without dermal sclerotization.

**Etymology.**—The name of this genus is formed from the Latin prefix “*quadr-*” meaning four, “*galla*” meaning plant swelling or gall, and “*coccum*” meaning seed or scale insect. *Quadrigallicoccus* is a masculine noun and refers to the unusual quadrilocular pores and gall-forming habit that are characteristic of this mealybug.

**Notes.**—This genus is distinct from all others known to the authors by the presence of quadrilocular pores that have the same swirling pattern as the normal pseudococcid trilocular pore, the gall-forming habit, and the presence of an anal ring that lacks setae and has obliterated pores. The adult male is unique because of the long penial sheath, the heavily sclerotized abdominal sternites and tergites, and the unusual structure of the ventral eyes.

***Quadrigallicoccus lauracearum* Williams and Miller, new species**

**Type material.**—The holotype adult female is on a slide with 1 other adult female and 4 first instars and is labeled as follows: Left label “COSTA RICA/ Cartago/ Tobosi/ 1700 m/ November 1991/ P. Hanson, coll./ ex. *Aiouea*/ costaricense, gall;” the right label gives a map of the location of the holotype and states “*Quadrigallicoccus*/ *lauracearum*/ Williams & Miller/ HOLOTYPE/ & PARATYPE” (USNM). This collection also contains 7 adult females and 24 first instars (USNM). Additional collections are: COSTA RICA, Cartago, Tobosi, 1700 m, April 6, 1992/ P. Hanson and D. Hollis, on *Aiouea costaricense* (Lauraceae) (2 adult females, 7 adult males, 6 second-instar females, 1 second-instar male) (BMNH, USNM); COSTA RICA, Monte Verde Road to San Luis, March 6, 1991, J. Blackmer, on *Nectandra salicina* (Lauraceae) (5 adult females) (BMNH, MNHN, UCD, USNM).

**Notes.**—The gall is formed from the petiole of the host and is woody.

**Etymology.**—The species epithet is derived from the Latin genitive plural of the host plant family Lauraceae.

**Description.**—*Adult female* (Fig. 4): Slide-mounted holotype 2.6 mm long, 2.0 mm wide; paratypes 2.3(1.4–3.0) mm long, 2.0(1.3–2.5) mm wide. Body nearly round, without dermal sclerotization.

Dorsum with trilocular pores abundant over surface. Minute discoidal pores scattered among trilocular pores. Oral-collar tubular ducts about same length as diameter, wider than diameter of trilocular pore, present in small numbers in marginal areas of abdomen. Setae short, in segmental rows; without elongate anal-lobe setae.

Anal ring represented by horseshoe-shaped sclerotization around posterior part of anal opening; without setae; pores usually obliterated by heavy sclerotization of ring, occasionally with a few visible; area above anal tube with series of small sclerotized protrusions.

Venter without multilocular pores. Quadrilocular pores most abundant over surface, with swirled pattern like triloculars; quinquelocular pores primarily in area of spiracles, also with swirled pattern. Discoidal pores in large clusters laterad of vulva; minute discoidal pores scattered over surface. Oral-collar tubular ducts restricted to margin of abdomen, uncommon. Longest setae near vulva, in clusters; setae on rest of surface unusually small.

Without circulus. Labium 3-segmented, 161  $\mu$  long; paratypes 141(133–149)  $\mu$  long. Antennae represented by unsegmented sclerotized knob containing 8 setae, paratypes 13(6–17) setae. Legs absent.

**Notes:** The above description is based on 14 specimens from 2 localities.

*Adult male* (Fig. 5): Slide-mounted specimen 1.9(1.9–2.0) mm long, 0.5(0.4–0.5) mm wide. Body unusually elongate and narrow, with abdomen constricted and tapering distally.

Dorsum with 1 pair of tail-forming pore clusters; each cluster with 2 elongate setae 356(298–397)  $\mu$  long and 44(38–52) mul-



tilocular pores; without additional setae or discoidal pores. Multilocular pores uncommon, with 1 or 2 in marginal areas of any or all of segments I to V, with 1 or 2 on each side of head, with 3, 4, or 5 loculi, quadriloculars most abundant. Discoidal pores associated with multiloculars, rarely with 1 or 2 in marginal areas of abdominal segments unassociated with multiloculars. Minute tubular ducts present in clusters along margin of abdomen. Body setae bristle shaped. Abdominal sclerotization present medial and mediolateral areas of segments II or III to segment VIII. Metapostnotal ridge conspicuous. Scutellum rectangular, without scutellar ridge, with several setae. Scutum sclerotized throughout, scutum with several small setae. Prescutum oval, with weakly defined prescutal suture, with short setae. Post tergite present, usually with 1 seta. Pronotal ridges heavily sclerotized. Hamulohalterae 109(96–120)  $\mu$  long, with 1 apical hooked seta. Mesothoracic wings 1644(1500–1767)  $\mu$  long, each with 2 or 3 basal setae, discoidal pores difficult to see, when visible with 4 or 5. Dorsal arm of midcranial ridge extending to posterior margin of dorsal eye, not touching lateral arms. Dorsomedial sclerite weakly sclerotized with several setae. Dorsal eye with small depression around lateral margin, with a few small dimples in depression, 36(35–37)  $\mu$  in diameter. Lateral ocellus 21(15–27)  $\mu$  in diameter, located at junction of preocular and postocular ridges. Ocular sclerite lightly sclerotized.

Penial sheath 544(533–564)  $\mu$  long, 56(50–62)  $\mu$  at its widest; length/width 9.8(9.1–11.0). Aedeagus 497(484–527)  $\mu$  long, apically acute.

Venter with setae bristle shaped. Multilocular pores absent. Minute tubular ducts present in clusters along margin of abdomen. Abdominal sclerotization conspicuous, present on medial and mediolateral areas of segments II or III to VIII. Prosternal ridge well developed, sternite weakly sclerotized. Preoral ridge weakly developed. Mouth tubercle with 2 setae. Ocular sclerite

weakly sclerotized. Ventral midcranial ridge well developed, broad, with lateral arms. Ventral eyes present on conspicuous protrusion, surrounded by trough like depression with sclerotized dimples laterally, 39(35–44)  $\mu$  in diameter.

Hind femur 218(207–225)  $\mu$  long; tibia 242(230–254)  $\mu$  long; hind tarsus 81(77–84)  $\mu$  long; femur/tibia 0.9; tibia/tarsus 3.0(2.8–3.2). Leg setae bristle shaped; antennae primarily with slightly fleshy setae, usually with 1 to 3 bristle shaped setae on each segment, first segment with bristle-shaped setae only; capitate setae usually absent from antennae, rarely with 1 or 2 such setae present with slightly enlarged club on apical segment. Tarsal digitules capitate; claw digitules acute, less than  $\frac{1}{4}$  length of claw; claw with inconspicuous denticle near tip. Antennae 10-segmented, 965(942–986)  $\mu$  long; segment 3 longest, 124(119–131)  $\mu$  long; segment 10, 91(79–99)  $\mu$  long; segment 3/10 1.4(1.2–1.6).

Notes: The above description is based on 7 specimens from 1 locality.

*Second-instar female* (Fig. 6): Slide-mounted specimens 0.6(0.5–0.6) mm long, 0.4(0.3–0.4) mm wide. Body oval, without dermal sclerotization.

Dorsum with trilocular pores restricted to single incomplete line along body margin. Minute discoidal pores absent or present in small numbers on body margin of thorax. Oral-collar tubular ducts of 1 size, present in 4 longitudinal lines on each side of body, usually absent on posterior abdominal segments; unusual minute tubular ducts absent. Setae shorter than those on venter, in segmental rows. Dorsal ostioles absent from abdomen, present on head.

Anal ring associated with segment VII, not near apex, represented by horseshoe-shaped sclerotization around posterior part of anal opening; without setae; pores concentrated in cluster near anterior end of each side of sclerotization of ring, usually with 2 pores on each side of ring.

Venter without multilocular pores. Other pores primarily of quadrilocular type, also



with triloculars and quinqueloculars, present near spiracles. Minute discoidal pores in single lateral line on each side of abdomen, with 1 pore associated with each spiracle, and 1 or 2 present on each side of posterior end of head. Oral-collar tubular ducts present in lateral line on each side of body. Longest setae near vulva or on segment IV or V, anal-lobe seta 280(235–309)  $\mu$  long. Sclerotized slit present laterad of hind pair of legs. Eye with anterior extension containing small swelling in addition to main swelling of eye.

Without circulus. Labium 3-segmented, 68(62–74)  $\mu$  long. Antenna 6-segmented without partially divided segments, 183(173–198)  $\mu$  long. Legs well developed, hind femur 96(94–99)  $\mu$  long; hind tibia 67(67–69)  $\mu$  long; hind tarsus 59(57–62)  $\mu$  long; hind tibia/tarsus 1.2(1.1–1.2); femur/tibia 1.4(1.4–1.5); tarsal and claw digitules clubbed apically; claw with denticle.

Notes: The above description is based on 6 specimens from 1 locality.

*Second-instar male* (Fig. 7): Slide-mounted specimen 1.2 mm long, 0.7 mm wide. Body oval, without dermal sclerotization.

Dorsum with trilocular pores scattered over surface except absent from segments VIII and sometimes VII. Minute discoidal pores scattered among trilocular pores. Oral-collar tubular ducts absent; unusual minute tubular ducts scattered among triloculars. Setae nearly as long as those on venter, in segmental rows. Dorsal ostioles on abdomen and head.

Anal ring near abdominal apex, represented by horseshoe-shaped sclerotization around posterior part of anal opening; without setae; pores concentrated in cluster near anterior end of each side of sclerotization of ring.

Venter without multilocular pores. Other pores primarily of quadrilocular type, also with triloculars and quinqueloculars, present near spiracles and on anterior abdominal segment. Minute discoidal pores scattered over surface of anterior abdomen, tho-

rax and posterior thorax except absent from medial areas. Minute tubular ducts present in lateral line on each side of body. Longest setae near vulva, anal-lobe seta about 110  $\mu$  long. Sclerotized slit present laterad of mid pair of legs. Eye with anterior extension containing small swelling in addition to main swelling of eye.

Without circulus. Labium 3-segmented, 96  $\mu$  long. Antenna 7-segmented with third segment partially divided, 279  $\mu$  long. Legs well developed, hind femur 128  $\mu$  long; hind tibia 90  $\mu$  long; hind tarsus 82  $\mu$  long; hind tibia/tarsus 1.1; femur/tibia 1.4; tarsal and claw digitules clubbed apically; claw with denticle.

Notes: The above description is based on a single specimen.

*First instar* (gender not determined) (Fig. 8): Slide-mounted paratypes 0.8(0.8–0.9) mm long, 0.5(0.4–0.5) mm wide. Body elongate oval.

Dorsum without cerarii with conical setae; homologous paired setae present along body margin. Trilocular pores arranged in 3 pairs of longitudinal lines, 1 or 2 pores along body margin and associated with 2 setae on each side of segment, 1 pair present in mediolateral lines, 1 pair in submedial area, a few others scattered on thorax and head. Discoidal pores absent. Oral-collar tubular ducts absent. Setae arranged in 3 pairs of longitudinal lines; marginal line composed of 2 setae; mediolateral and submedial lines complete; dorsal body setae unusually elongate; anal-lobe seta 244(222–259)  $\mu$  long. Ostioles present, anterior pair well developed, posterior pair weakly developed.

Anal ring horseshoe shaped, with 2(1–2) pores on each side of ring; without anal-ring setae.

Venter without trilocular pores present on abdomen; pores near spiracles with 3 to 5 swirled loculi. Discoidal pores present in lateral line with 1 on each side of each abdominal segment; also present posterior of each spiracle and or near posterior margin of head. Oral-collar tubular ducts absent.



Longest setae on posterior abdominal segments; setae arranged in 3 pairs of longitudinal lines, submarginal, mediolateral, and submedial. Slightly sclerotized slit laterad of hind pair of legs.

Without circulus. Labium 77(63–84)  $\mu$  long. Antenna 6-segmented, often with 6th segment partially divided, 214(198–229)  $\mu$  long. Legs well developed, hind femur 98(89–101)  $\mu$  long; hind tibia 71(67–74)  $\mu$  long; hind tarsus 72(69–74)  $\mu$  long; tibia/tarsus 1.0(0.9–1.0); femur/tibia 1.4(1.2–1.5); tarsal and claw digitules clubbed apically; claw with denticle.

Notes: The above description is based on 28 specimens from 1 locality.

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