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Description of a new genus of scale insect with a discussion of relationships among families related to the Kermesidae (Homoptera: Coccoidea)

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Abstract. A new kermesid genus, *Eriokermes*, is described for three species previously placed in the Eriococcidae: *Eriokermes gillettei* (Tinsley) comb.n.; *E.juniperi* (Goux) comb.n.; and *E.juniperinus* (De Lotto) comb.n. Keys to Nearctic kermesid genera, *Eriokermes* species, and immatures and adults of *E.gillettei* are provided. Four female and five male instars of *E.gillettei* are described. *Eriokermes* is placed in Kermesidae based on a cladistic estimate of its phylogenetic position.

Introduction

The Kermesidae or gall-like scales have been hypothesized as being closely related to the Eriococcoidae or felt scales (D. R. Miller, 1991). First and second instars of both families are morphologically very similar; however, adult females are quite different. Most adult female eriococcids produce a white, felt-like ovisac that encloses a pyriform body, and have two well-developed anal lobes that have several enlarged dorsal setae. Conversely, adult female kermesids are rotund, usually do not produce an ovisac, and lack well-developed anal lobes with enlarged setae.

Eriokermes gillettei (Tinsley, 1899), *Eriokermes juniperi* (Goux, 1936) and *Eriokermes juniperinus* (De Lotto, 1954) were previously considered eriococcids. The adult females not only produce felt-like ovisacs but also have enlarged dorsal setae and well-developed anal lobes. However, Miller (1983) believed the similarities of *E.gillettei* to other eriococcids were superficial and other characters suggested placement in the Kermesidae. To test this hypothesis, a phylogenetic analysis is presented here. Characters traditionally used for the adult female have not satisfactorily resolved placement of *Eriokermes*. All instars are therefore described and analysed in detail.

A new kermesid genus, *Eriokermes*, is erected for three species. Descriptions and illustrations of the adult male and adult female, fourth (pupal) and third (prepupal) instar males, second instar male and female, and the first instars of *E.gillettei* are presented and keys are provided to the immature and adult stages. Keys to Nearctic kermesid genera and the species of *Eriokermes* are also given.

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Methods

Morphological terminology follows Bullington & Kosztarab (1985) for adult females, Koteja & Zak-Ogaza (1972) for the adult male, and Baer & Kosztarab (1985) for first and second instars. Measurements and numbers are from ten specimens, when available, and are given as a mean with ranges in parentheses.

Cladistic analyses of the characters were performed using Hennig 86 (Farris, 1988). Characters were selected from adult males, adult females, and first instars.

Depositories of specimens are: California Department of Food and Agriculture, Sacramento (CDA); National Museum of Natural History, Washington, D.C. (USNM); Natural History Museum, London (NHM); University of California at Davis (UCD); Virginia Polytechnic Institute and State University, Blacksburg (VPI).

Key to genera of Nearctic Kermesidae

(modified from Bullington & Kosztarab, 1985)

1 Prominent protruding anal lobes lacking; antennae short, indistinctly segmented; associated with Fagaceae 2

– Prominent protruding anal lobes present (Fig. 1f); antennae distinctly 5- to 8-segmented (Fig. 1g); associated with Cupressaceae .... *Eriokermes*, gen.n.

2(1) Tubular ducts of 1 type; anal lobes membranous, indistinct, with numerous setae 3

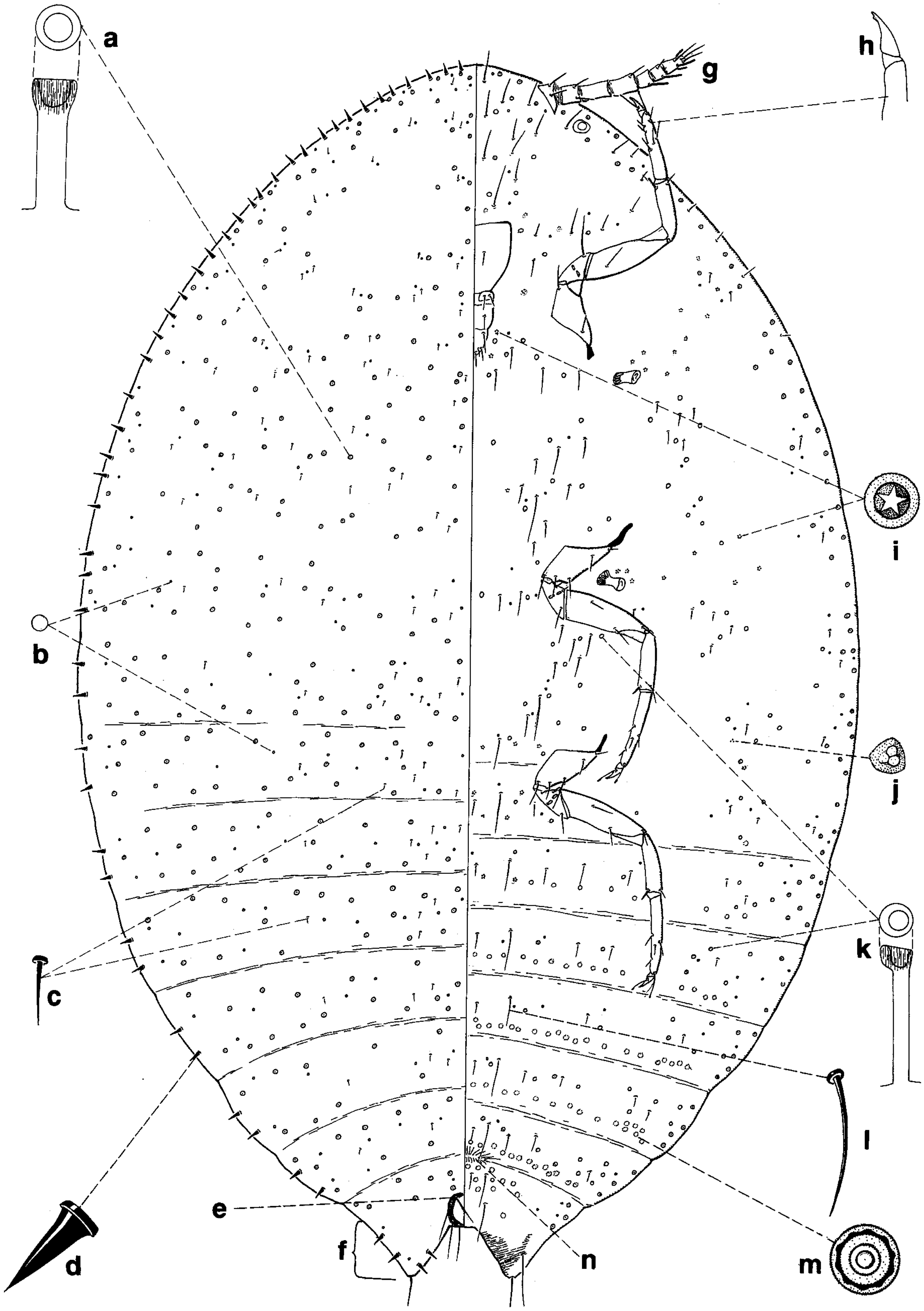

Fig. 1. Adult female of *E.gillettei*. 8 mi. W. Datil, New Mexico, 1.vii.18, ex *Juniperus pachyphlaea*. a, large-size macrotubular duct; b, simple disc pore; c, dorsal body seta; d, enlarged seta; e, anal ring; f, anal lobe; g, antenna; h, tarsal claw; i, 5-locular pore; j, 3-locular pore; k, small-size macrotubular duct; l, lanceolate body seta; m, 10-locular pore; n, vulva.

– Tubular ducts of 2 types; anal lobes sclerotized with a single seta . . . . *Nanokermes* Bullington & Kosztarab

3(2) Dorsum with heavily sclerotized, spinescent 8-shaped pores 4

– Dorsum without heavily sclerotized, spinescent 8-shaped pores . . . . *Kermes* Boitard

4(3) Dorsal margin with wide band of tubular ducts and disc pores; mid-dorsal longitudinal row of setae absent . . . . *Allokermes* Bullington & Kosztarab

– Dorsal margin without band of tubular ducts and disc pores; mid-dorsal longitudinal row of setae present . . . . *Olliffiella* Cockerell

Eriokermes D. Miller & G. Miller, gen.n.

Type species. *Eriococcus gillettei* Tinsley.

Diagnosis. Adult female elongate oval with anal lobes protruding, simple disc pores present, microtubular ducts absent; adult male with 5 pairs of simple eyes, postocciput present; first instar with dorsal abdominal setae in 4 longitudinal rows.

Notes. The protruding anal lobes and shape of the adult female easily distinguish *Eriokermes* from all other kermesids. This is the only kermesid genus associated with Cupressaceae.

Etymology. *Eriokermes* literally means 'wool-Kermes'. This name reflects the ability of the adult female to produce a wooly ovisac and its superficial resemblance to eriococcids. The name of the genus is masculine in gender.

Species placed in Eriokermes

Eriokermes gillettei (Tinsley), **comb.n.**
Eriococcus gillettei Tinsley, 1899: 46. Lectotype ♀ (present designation), U.S.A., Colorado, Salida (USNM).
Nidularia gillettei (Tinsley); Lindinger, 1933: 116.
Eriokermes juniperi (Goux), **comb.n.**
Eriococcus juniperi Goux, 1936: 353. Holotype ♀, France, Marseille (depository unknown).
Nidularia juniperi (Goux); Lindinger, 1943: 223.
Eriokermes juniperinus (De Lotto), **comb.n.**
Eriococcus juniperinus De Lotto, 1954: 217. Holotype ♀, Eritrea, Saganeiti (NHM).

Key to adult females of *Eriokermes*

1 Anal lobes with 3 dorsal enlarged setae 2

– Anal lobes with 4 dorsal enlarged setae (Fig. 1f) . . . . *E.gillettei* (Tinsley)

2 Antennae 5- or 6-segmented; 5-locular pores abundant, distributed in spiracular, abdominal, and lateral areas of venter (see De Lotto, 1954) . . . . *E.juniperinus* (De Lotto)

– Antennae 7-segmented; 5-locular pores sparse, distributed in the ventral posterior abdominal segments (see Goux, 1936) . . . . *E.juniperi* (Goux)

Key to adult and immature stages of *Eriokermes gillettei* (Tinsley)

1 Meso- and metathorax without wings or wing pads 2

– Meso- and metathorax with wings or wing pads 5

2(1) Macrotubular ducts (Figs 1a, 1k) present on abdomen 3

– Macrotubular ducts absent from abdomen 4

3(2) Vulva present (Fig. 1n); anal ring with 4 pairs of setae (Fig. 1e); ventral body setae (Fig. 1l) on abdominal segment I 49 μm long or greater (Fig. 1) . . . . adult female

– Vulva absent; anal ring with 3 pairs of setae; ventral body setae on abdominal segment I 32 μm long or shorter (Fig. 7) . . . . second-instar male

4(2) Macrotubular ducts present between antennae; ventral body setae on abdominal segment I 12 μm or longer (Fig. 2) . . . . second-instar female

– Macrotubular ducts absent; ventral body setae on abdominal segment I 10 μm or shorter (Fig. 3) . . . . first instar (sexes indistinguishable)

5(1) Wings well developed; mesothorax with well-developed sclerites; genital capsule heavily sclerotized, with aedeagus (Fig. 4) . . . . fifth-instar male (adult)

– Wing buds present only; thoracic region with little sclerotization; genital capsule lightly sclerotized and without aedeagus 6

6(5) Hamulohalterae present; front wing buds greater than 370 μm long; ocular region conspicuous (Fig. 5) . . . . fourth-instar male (pupa)

– Hamulohalterae absent; front wing buds less than 260 μm long; ocular region difficult to discern (Fig. 6) . . . . third-instar male (prepupa)

Eriokermes gillettei (Tinsley), comb.n.

Synonymy: *Eriococcus gillettei* Tinsley, 1899: 46–47.
Nidularia gillettei (Tinsley); Lindinger, 1933: 116.

Type material. Lectotype, adult ♀, U.S.A.: From the syntypes we have chosen and marked as lectotype an adult female labelled 'Types *Eriococcus gillettei* Tins. on Conifer, Salida, Colo. Oct. 8, 1898 coll. C. P. Gillette' (USNM). There are 7 paralectotypes on the slide; the specimen located vertically in the middle of the coverslip and horizontally farthest to the right, nearest the label, is the lectotype. A label has been placed on the slide giving the exact location of the lectotype. *Paralectotypes*, 14 adult ♀♀, U.S.A.: In addition to the 7 paralectotypes associated on the slide with the lectotype, there are 7 paralectotypes on another slide. Both slides exhibit the same collection data.

Other specimens examined. We have examined 113 adult females, 15 second-instar females, 37 first instars, 11 adult males, 8 fourth-instar males, 2 third-instar males, and 46 second-instar males.

Distribution. U.S.A.: Arizona, California, Colorado, District of Columbia, Florida, Idaho, Maryland, Nevada, New Mexico, Oregon, and Virginia.

Host plants. All specimens were collected on species

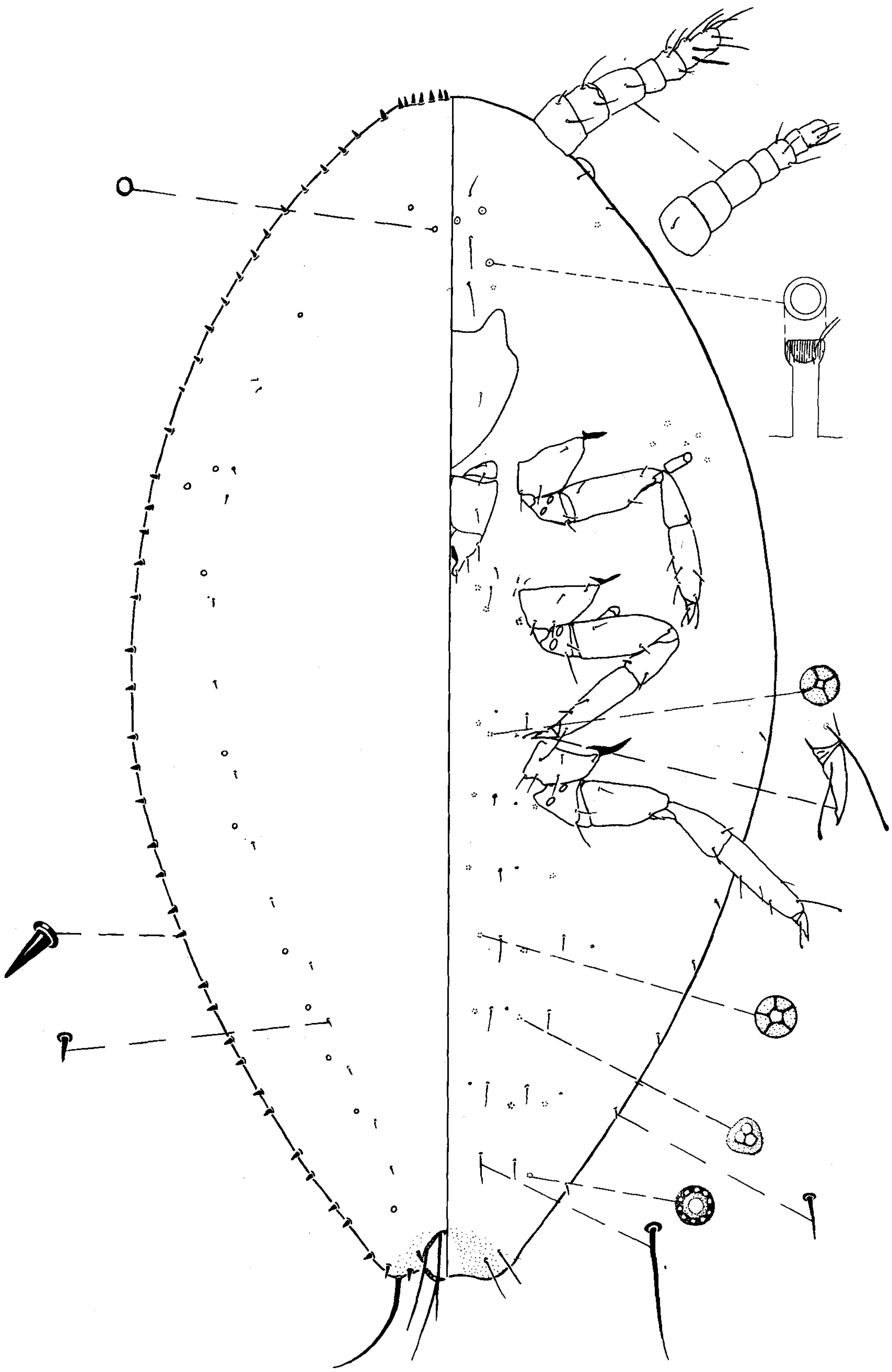

Fig. 2. Second-instar female of *E.gillettei*. Wheaton Region Park, Maryland, 24.vi.71, ex *Juniperus virginiana*.

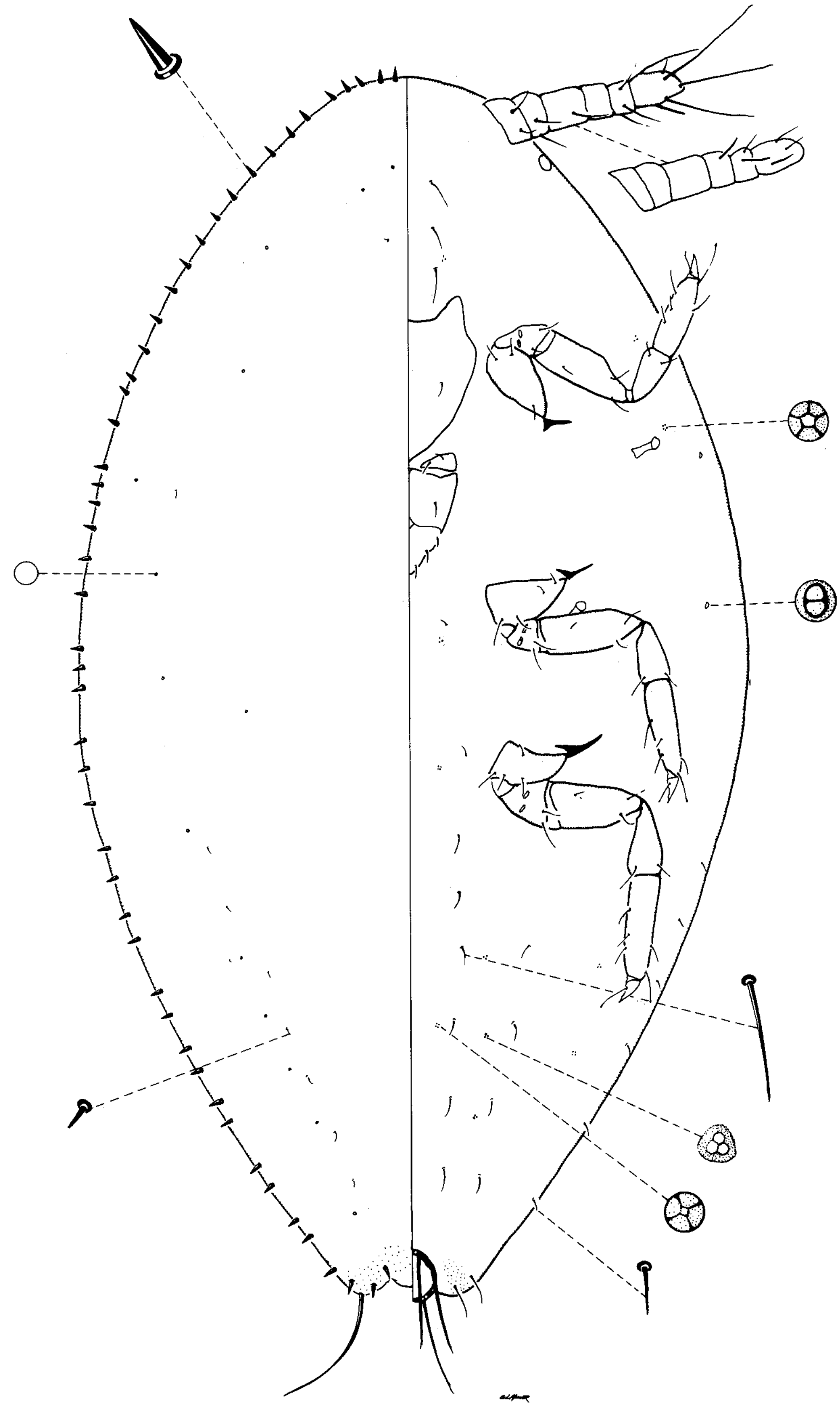

Fig. 3. First-instar of *E.gillettei*. Wheaton, Maryland, 3.v.70, ex *Juniperus virginiana*.

of *Juniperus* (Cupressaceae) including: *J.californica*, *J.occidentalis*, *J.pachyphlaea*, *J.virginiana*.

Adult female (Fig. 1)

Field features. Adult female dorsally yellow with brown mottling, ventrally brown with flavous legs and black eyes; older individuals have long crystalline rods on anal lobes. Ovisac heavily felted with 72 (34–101) eggs; eggs yellow after deposition, purpurescent prior to eclosion. First instars brown or purple after emergence, turning yellow after feeding.

In Maryland, *E.gillettei* overwinters in the adult female or egg stage. Eggs hatch within the ovisac by late April and crawlers begin to settle in early May. Adult males are present in late June and adult females are present by mid July. There is one generation per year.

Recognition characters. Adult female, mounted, 1.76 (1.31–2.38) mm long, 1.01 (0.70–1.58) mm wide. Anal lobes (Fig. 1f) apically acute, lightly sclerotized; each lobe dorsally with 4 enlarged setae (all approximately same size), with 2 (1–4) simple disc pores; each lobe ventrally with 2 slender body setae and no sessile pores.

Dorsum with enlarged setae (Fig. 1d) of 1 size, distributed along body margin, with 2 present on margin or each abdominal segment. Largest seta 18 (12–25) μm long, smallest seta 14 (12–22) μm. These setae straight with 'needle-sharp' apices; setal rings thickened. Remaining dorsal setae (Fig. 1c) short, thin, appearing much like small body setae; setal rings large. Dorsal setae in 6 longitudinal lines (paired medial, sublateral, lateral). Macrotubular ducts (Fig. 1a) large, present on posterior and anterior margins of abdominal segments VII–I, scattered randomly on thorax and head. Simple disc pores (Fig. 1b) scattered in small numbers over surface.

Anal ring (Fig. 1e) normally dorsal, with 2 complete rows of pores, and 4 pairs of setae.

Venter with lanceolate body setae elongate (Fig. 1l) (largest seta on abdominal segment VII 43 (35–57) μm long, on segment I 66 (49–94) μm long), medial setae slender, apices acute. Enlarged setae absent. Macrotubular ducts of two kinds: larger size same as on dorsum, present along lateral margins; smaller size (Fig. 1k) relatively abundant, distributed throughout medial and sublateral areas of entire surface. Simple disc pores scattered in small numbers over surface. Multilocular pores of three kinds: 10-loculars (Fig. 1m) present on abdominal segments II–VIII, absent from thorax and head; 5-loculars (Fig. 1i) present on anterior 2 or 3 abdominal segments, thorax, and head; 3-loculars (Fig. 1j) occasionally present. Multilocular pores absent from anterior margins of abdominal segments.

Legs normally long and slender; leg pores absent; femora each with 5 setae; tibiae each with 4 setae; inner, apical tibial setae robust; tarsi usually longer than tibiae (hind tibia/tarsus ratio 0.74 (0.62–1.03); claws (Fig. 1h) with denticle near tip. Antennae (Fig. 1g) 7- or 8-segmented, third segment longest, sometimes showing signs of division. Terminal segment with 3 sensory setae; penultimate segment with 1 equal in size to single sensory seta of antepenultimate segment.

Notes. The adult female of this species is very similar to the description of the French species, *E.juniperi*. However, no specimens of *E.juniperi* could be obtained for examination. Based on the previously published description, both species have multilocular pores, simple disc pores, and tarsi longer than tibiae. *Eriokermes juniperi* differs from *E.gillettei* in having 5-locular pores restricted to the venter of the abdomen and only 3 enlarged setae on each anal lobe; *E.gillettei* has many 5-locular pores on the thorax and head and 4 enlarged setae on each anal lobe.

Eriokermes juniperinus, an African species, is also similar to *E.gillettei*. The holotype and 4 paratypes in the NHM and a paratype deposited in the USNM collection were examined. Both species also have multilocular pores, simple disc pores, and tarsi longer than tibiae. *Eriokermes juniperinus* differs from *E.gillettei* in having 5- or 6-segmented antennae, 5-locular pores on lateral margin of the abdomen, and 3 dorsal enlarged setae on each anal lobe; *E.gillettei* has 7- or 8-segmented antennae, no 5-locular pores on lateral margin of abdomen, and 4 dorsal enlarged setae on each anal lobe.

Second-instar female (Fig. 2)

Recognition characters. Second-instar female differs from adult female as follows: mounted, 1.12 (1.01–1.20) mm long, 0.64 (0.53–0.71) mm wide.

Dorsum with largest enlarged seta 14 (12–15) μm long, smallest enlarged seta 9 (7–10) μm. Macrotubular ducts absent. Simple disc pores fewer.

Anal ring with 3 pairs of setae.

Venter with largest lanceolate body setae on abdominal segment VII 20 (17–24) μm long, on segment I 13 (12–15) μm long. Macrotubular ducts present between antennae. Multilocular pores fewer, predominately 5-locular with comparatively fewer 3-locular and 10-locular present, occasionally 4-locular pores present. Simple disc pores fewer.

Hind tibia/tarsus ratio 0.46 (0.42–0.50). Antennae 6-segmented.

First instar (Fig. 3)

Recognition characters. Sexes of first instar indistinguishable. First instar differs from second-instar female as follows: mounted, 0.59 (0.51–0.78) mm long, 0.29 (0.22–0.40) mm wide.

Dorsum with largest enlarged seta 10 (7–12) μm long, smallest enlarged seta 5 (5–7) μm. Dorsal abdominal setae in 4 longitudinal rows (paired sublateral and lateral). Simple disc pores fewer.

Venter with largest lanceolate body setae on abdominal segment VII 19 (15–24) μm long, on segment I 7 (5–10) μm long. Macrotubular ducts absent. Bilocular pores present near spiracles. Multilocular pores fewer, predominately

3-locular but some 4-locular pores present on median abdominal segments; single 5-locular near anterior spiracle; 10-locular pores absent. Simple disc pores absent.

Hind tibia/tarsus ratio 0.49 (0.44–0.54).

Adult male (Fig. 4)

Recognition characters. Mounted, 1.23 (1.12–1.38) mm long, 0.39 (0.32–0.44) mm wide at mesothorax.

Head capsule. Head rounded in dorsal and ventral views with heaviest sclerotization around ocular region; 215 (190–229) μm long, 222 (180–259) μm wide. Dorsum with median crest weakly sclerotized and occasionally with weak striations, bounded posteriorly by transverse postoccipital ridge and sclerotized plate of vestige of postocciput. Dorsal setae on and around median crest. Midcranial ridge dorsally absent; anteroventrally Y-shaped, extending posteriorly to preocular ridge, interrupted at ocular sclerite, occasionally extending to base of cranial apophysis. Genae dorsally weakly sclerotized, finely punctate. Ventral head setae anterior to preocular ridge. Preocular ridge long, ventrally uninterrupted. Ocular sclerites strongly sclerotized, finely punctate, occasionally weakly reticulate. Five pairs of eyes and a pair of ocelli present; corneal diameter of dorsal eyes 31 (27–32) μm; dorsolateral eyes 18 (17–22) μm; mediolateral eyes 18 (15–22) μm; ventrolateral eyes 29 (27–32) μm; ventral eyes 32 (27–35); ocelli smaller, 14 (12–15) μm. Postocular ridge not forked below ocellus. Preoral ridge well developed throughout, connected to postocular ridge by triangular plates. Mouth opening situated on mouth tubercle. Cranial apophysis rectangular; tentorial bridge stout, anterior and posterior tentorial arms and tentorial pits present.

Antennae filiform, setose, 10-segmented, 816 (741–884) μm long.

Thorax. Prothorax. Pronotal ridge medially interrupted by weak sclerotization. Lateral pronotal sclerites large, posttergites small. Proepisternum + cervical sclerite well developed. Prosternum triangular, sclerotized with basal transverse ridge, without setae.

Mesothorax. Prescutum sclerotized with 3–5 setae, laterally bounded by prescutal ridges which extend posteriorly to scutellum along membranous area of scutum, posteriorly delineated by prescutal suture. Scutum sclerotized, membranous medially. Prealare sclerotized, anterolateral to scutum; tegular bulge weakly sclerotized and reticulated with several setae. Scutellum oval, heavily sclerotized with semicircular median oval foramen and a pair of setae. Anterior margin of mesopostnotum exposed, sclerotized; postnotal apophysis and postalare well developed. Basisternum hexagonal, without median ridge, bounded by strong marginal and precoxal ridges. Furca large, furcal pit present. Mesothoracic spiracle cephalad to lateropleurite. Lateropleurite partially sclerotized, bounded anteriorly by extension of marginal ridge. Episternum sclerotized, bounded by subepisternal ridge. Mesopleural ridge strong, ventrally forming process for articulation with coxa and dorsally connecting with pleural wing process. Pleural wing process connected with episternum by basalare; subalare small. Wing articulation similar to other Coccoidea. Wings hyaline, 1063 (988–1084) μm long, 455 (395–494) μm wide, covered with microtrichia; radius, media, and costal complex veins present. Alar lobe present.

Metathorax. Metanotum represented by internal sclerite and 2 suspensorial sclerites. Metapostnotum consisting of a single transverse sclerite. Metasternum triangular with 2 anterior apophyses. Pleural ridge well developed, interrupted near middle, anteriorly expanded to form pleural wing process. Metepisternum and metepimeron subtriangular, weakly sclerotized. Precoxal ridge posteriorly vestigial, anteriorly longer. Metathoracic spiracle cephalad to pleural ridge. Hamulohalterae hyaline each with sclerotized anterior margin, 99 (84–111) μm long, with single apical hooked seta.

Legs. Setose, tarsi 2-segmented, prothoracic legs 707 (615–758) μm long; mesothoracic legs 692 (610–736) μm long; metathoracic legs 712 (642–746) μm long.

Abdomen. Primarily membranous. Weakly sclerotized tergites, sternites, and pleurites present on all segments. Dorsally 2–6, ventrally 0–3, and laterally 1–4 setae on segments I–VIII. Glandular pouch on segment VIII with 2 long setae and 28 (21–36) 3-, 4- and 5-locular pores. Penial sheath 111 (104–111) μm long, 89 (79–106) μm wide; basal part cylindrical with several setae; style short, abruptly tapered.

Fourth-instar male (pupa) (Fig. 5)

Recognition characters. Mounted, 1.24 (1.06–1.31) mm long, 0.42 (0.35–0.46) mm wide.

Dorsum membranous with sclerites on segments VIII–X, setae becoming shorter toward head; abdominal segments with 2–4 dorsal setae. Segments I–VIII with 2–3 dorsolateral setae, largest seta on segment VIII 87 (84–91) μm long. Genital area conical, lightly sclerotized. Front wing buds 426 (371–494) μm long. Hamulohalterae present. Ocular region conspicuous.

Venter membranous with sclerites on segments VIII–X, abdominal setae slightly longer than corresponding dorsal setae; abdominal segments with 0–6 setae. Mouth and ocular region weakly discernible.

Hind tibia 148 (133–153) μm long, hind tarsus 93 (79–104) μm long; hind tibia/tarsus ratio 1.6 (1.5–1.7). Antenna 545 (474–583) μm long.

Third-instar male (prepupa) (Fig. 6)

Recognition characters. Third-instar male differing from fourth-instar male as follows: mounted, 1.21 (1.17–1.25) mm long, 0.55 (0.46–0.57) mm wide.

Dorsum with fewer setae; setae on head region parallel to anterior margin, abdominal segments with 0–3 dorsal setae. Segments I–VIII with 2–5 dorsolateral setae, largest dorsolateral seta on segment VIII 45 μm long.

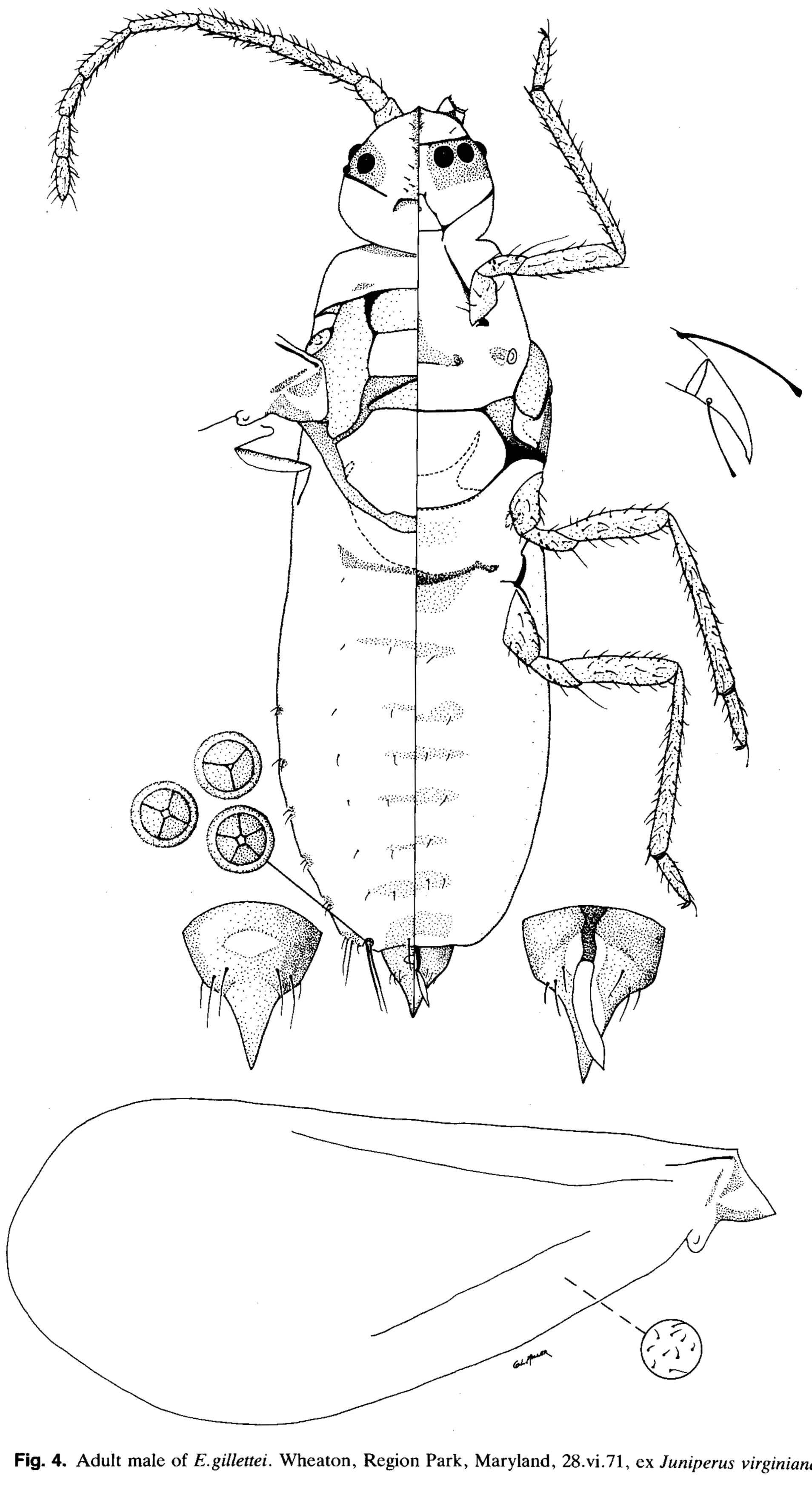

Fig. 4. Adult male of *E.gillettei*. Wheaton, Region Park, Maryland, 28.vi.71, ex *Juniperus virginiana*.

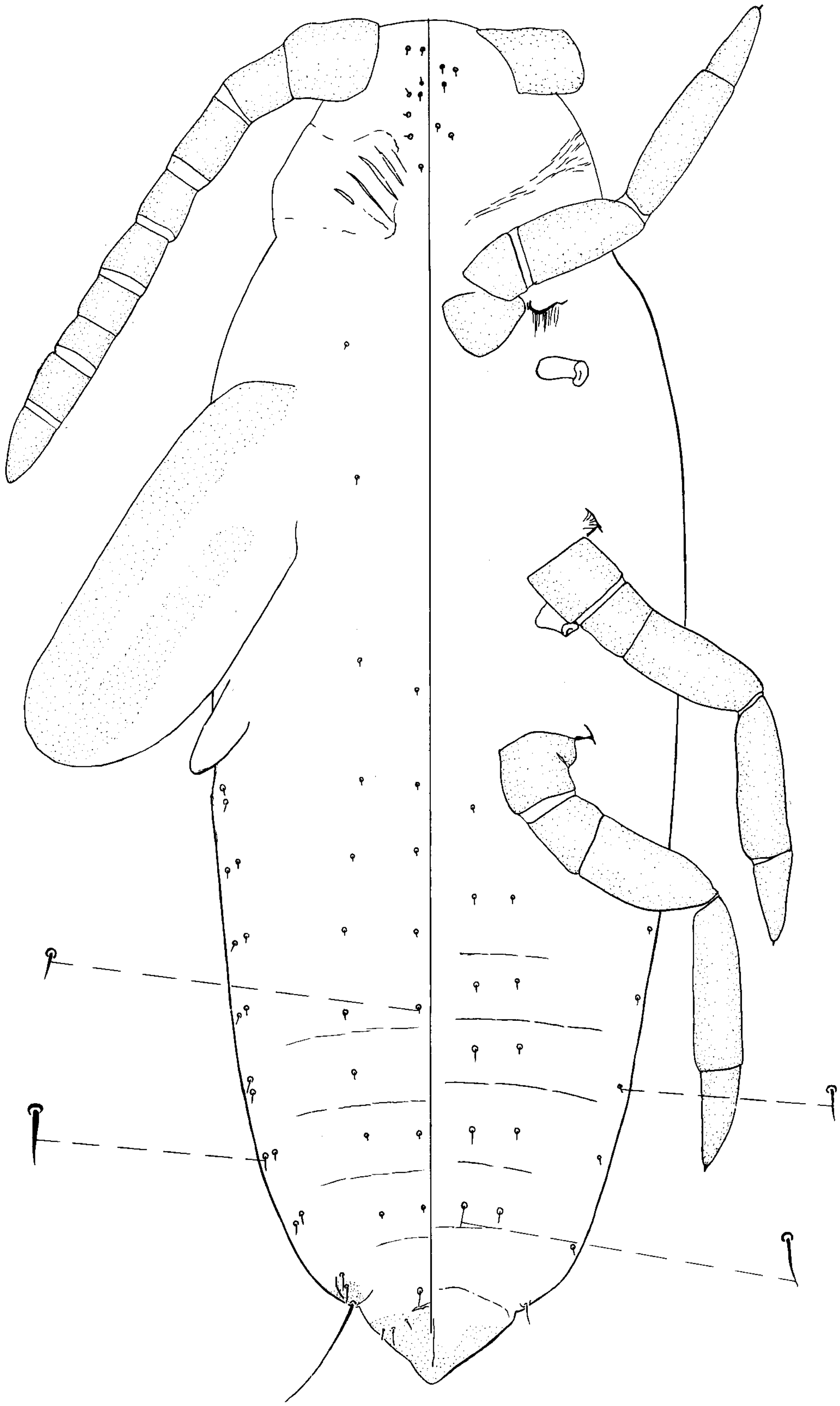

Fig. 5. Fourth-instar male of *E.gillettei*. Wheaton, Region Park, Maryland, 21.vi.71, ex *Juniperus virginiana*.

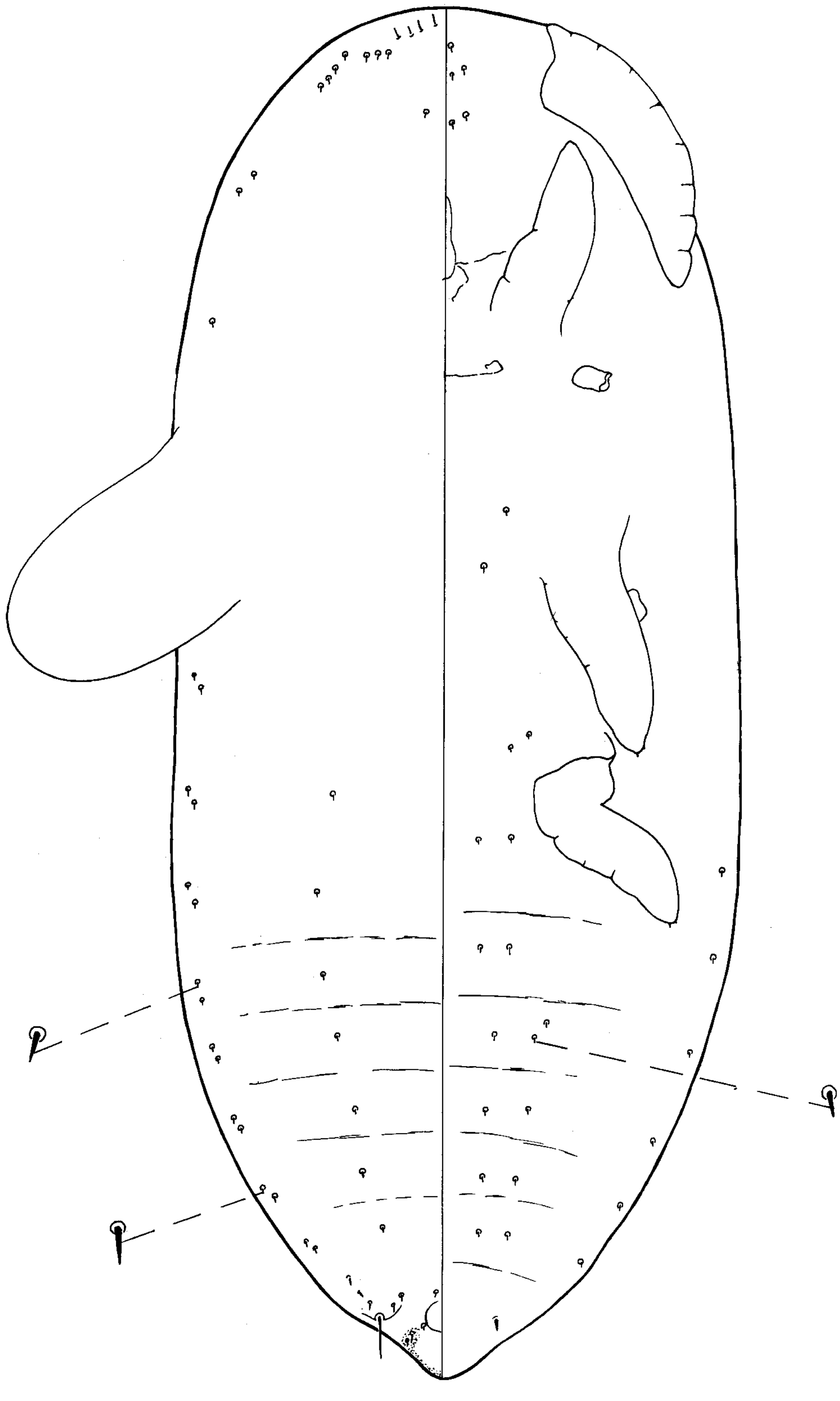

Fig. 6. Third-instar male of *E.gillettei*. Wheaton, Region Park, Maryland, 21.vi.71, ex *Juniperus virginiana*.

Genital area less pronounced, with less sclerotization. Front wing buds 235 (210–259) μm long. Hamulohalterae absent. Ocular region difficult to discern.

Venter with fewer setae; abdominal segments with 0–5 setae. Mouth weakly discernible.

Hind tibia 49 μm long, hind tarsus 42 μm long; hind tibia/tarsus ratio 1.2. Antenna 294 (291–296) μm long.

Second-instar male (Fig. 7)

Recognition characters. Second-instar male differs from adult female as follows: mounted, 1.10 (0.84–1.21) mm long, 0.56 (0.41–0.70) mm wide.

Dorsum with largest enlarged seta 13 (12–17) μm long, smallest enlarged seta 9 (7–10) μm. Simple disc pores fewer.

Anal ring with 3 pairs of setae.

Venter with largest lanceolate body setae on abdominal segment VII 28 (22–32) μm long, on segment I 28 (25–32) μm long. Smaller size macrotubular ducts fewer. Multilocular pores fewer, predominately 5-locular with few 3-locular pores; 10-locular pores absent. Simple disc pores fewer.

Hind tibia/tarsus ratio 0.54 (0.51–0.60).

Phylogenetic analysis

Methods. Cladistic analyses of the characters were performed on 20 taxa and 26 characters using Hennig 86 (Farris, 1988). The 'mhennig' with branch swapping (bb) options were applied. Outgroup comparison was used to determine polarities of characters. The Margarodidae are considered the most primitive of the Coccoidea (Beardsley, 1968) and a representative species was selected for the outgroup.

Characters. Character distributions for the 20 taxa are summarized in Table 1. Unknown characters were coded as missing data. Twenty-six characters were used in the analysis. Characters 10 and 17 (treated as non-additive) and 15 (treated as additive) have three states, all others are binary. Plesiomorphic characters were coded as 0. Apomorphic characters were coded as 1 or 2 (if additive) or a or b (if non-additive).

Character states were determined through examination of specimens deposited in the Museum of Natural History Collection and through previously published descriptions. Publications consulted for the included taxa are: *Acanthococcus araucariae* (Maskell) (Afifi, 1968; Miller & Miller, 1992); *Acanthococcus droserae* Miller *et al.* (1992); *Brevennia rehi* (Lindinger) (Miller, 1975); *Coccus hesperidum* L. (Giliomee, 1967; Gill *et al.*, 1977); *Eulecanium caryae* (Fitch) (Williams & Kosztarab, 1972; G. L. Miller, 1991); *Gossyparia spuria* (Modeer) (Afifi, 1968; Miller & Miller, 1993); *Heterococcus raui* Miller (1975); *Kermes bytinskii* Sternlicht (1969); *Kermes quercus* (L.) (Borchsenius, 1960; Koteja & Zak-Ogaza, 1972); *Matsucoccus thunbergianae* Miller & Park (1987); *Nanokermes pubescens* (Bogue) (Baer & Kosztarab, 1985; Bullington & Kosztarab, 1985); *Neolecanium cornuparvum* (Thro) (Ray & Williams, 1983); *Ovaticoccus agavium* (Douglas) (Afifi, 1968; Miller & Miller, 1993); *Phenacoccus dearnessi* King (Miller & Appleby, 1971); *Planococcus citri* (Risso) (Giliomee, 1967; McKenzie, 1967); *Pseudococcus affinis* Maskell (McKenzie, 1967; Afifi, 1968); *Pulvinaria acericola* (Walsh & Riley) (Giliomee, 1967; Williams & Kosztarab, 1972) *Sphaerolecanium prunastri* (Fonscolombe) (Giliomee, 1967; Kosztarab & Kozar, 1988); and *Stibococcus cerinus* Miller & Gonzalez (1975). These species were selected since either slide mounted material of published descriptions were available for adult males, adult females, and first instars of each species.

Table 1. Character matrix for family taxa and outgroups used to generate cladogram shown in Fig. 8. Matrix symbpols: 0, plesiomorphic state; 1, 2 (if additive), or a, b (if non-additive), apomorphic states; –, state unknown.

Character number	1 123456789012345	2 678901	23456
Margarodidae			
M.thunbergianae	000000000000000	000000	00000
Pseudococcidae			
P.dearnessi	010001000a10012	1a0001	11011
H.raui	010001000a10012	1a0001	11011
B.rehi	010001000a10012	1a0001	11011
P.citri	010001000a10012	1a0001	11011
P.affinis	010001000a10012	1a0001	11011
Kermesidae			
E.gillettei	101110101b10011	0b0001	00001
K.quercus	101110101b10011	0b0001	00001
K.bytinskii	101110 01b10011	0b0001	00001
N.pubescens	101110101b10011	0b0001	00001
Eriococcidae			
O.agavium	001011100a10012	1b1011	10000
G.spuria	001011000a10012	0b1011	10000
A.araucariae	001011000a10012	1b1011	10000
A.droserae	001111000a10012	1b1011	10000
S.cerinus	001011000a10012	1b1001	10000
Coccidae			
N.cornuparvum	100111010a11102	0b0101	00101
E.caryae	100110010a11101	0b0101	00101
S.prunastri	100110010a11102	0b0101	00101
C.hesperidum	100111010a11102	0b0101	00101
P.acericola	100111010a11102	0b0101	00101
	ad. ♂	ad. ♀	first

Adult male

1. Prescutal ridge, extending into scutum: (0) no; (1) yes.
2. Ungual digitules, apices: (0) knobbed; (1) acute.
3. Scutellar ridge: (0) absent; (1) present.
4. Scutum, central clear area: (0) absent; (1) present.
5. Tergite 9 + 10: (0) free; (1) fused with genital capsule.

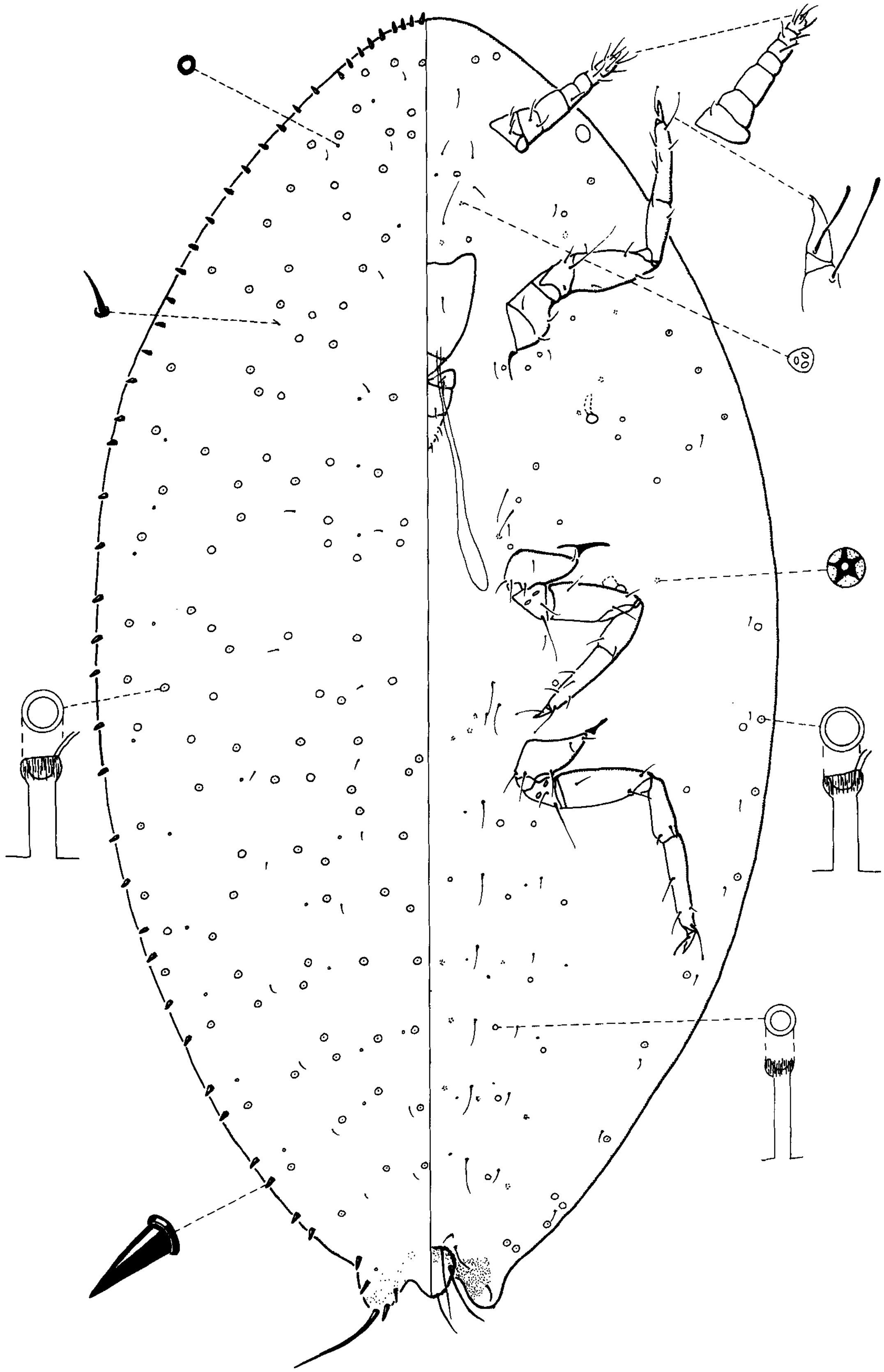

Fig. 7. Second-instar male of *E.gillettei*. Wheaton, Region Park, Maryland, 21.vi.71, on *Juniperus virginiana*.

6. Genal setae: (0) absent; (1) present.
7. Mouth tubercle: (0) absent; (1) present.
8. Postoccipital ridge: (0) present; (1) absent.
9. Postocciput: (0) absent; (1) present.
10. Preocular ridge: (0) absent; (a) interrupted ventrally; (b) continuous ventrally.
11. Tarsal digitule, apices: (0) acute; (1) knobbed.
12. Metasternal apophysis: (0) present; (1) absent.
13. Basisternal median ridge: (0) absent; (1) present.
14. Tarsi: (0) 1-segmented; (1) 2-segmented.
15. Eyes: (0) multifaceted; (a) 5 pairs of simple eyes; (b) 2 pairs of simple eyes.

Adult female

16. Translucent pores on metathoracic legs: (0) absent; (1) present.
17. Tubular ducts: (0) absent; (1) invaginated; (2) not invaginated.
18. Microtubular ducts: (0) absent; (1) present.
19. Paired triangular anal plates: (0) absent; (1) present.
20. Cruciform pores: (0) absent; (1) present.
21. Abdominal spiracles: (0) present; (1) absent.

First instar

22. Paired median rows of longitudinal abdominal setae: (0) absent; (1) present.
23. Proximal marginal femoral seta: (0) absent; (1) present.
24. Spiracular setae: (0) undifferentiated from marginal setae; (1) differentiated from marginal setae.
25. Ostioles: (0) absent; (1) present.
26. Simple disc pores: (0) absent; (1) present.

Results

Analysis of the Coccoidea data results in two equally parsimonious cladograms (length = 38, ci = 0.75, ri = 0.92). The preferred cladogram is shown in Fig. 8. The alternative cladogram placed *K.bytinskii* as the sister group to *E.gillettei*, *K.quercus* and *N.pubescens*. This cladogram was rejected because it resolved *K.bytinskii* based on unknown data.

Discussion of the family level clades is presented below. Bracketed numbers in the description of the clades represent characters.

Stem 1 (Fig. 8) represents the primitive condition for characters in the matrix.

The Pseudococcidae, Eriococcidae, Kermesidae and Coccidae (Fig. 8, Stem 2) collectively form a monophyletic group based on: (1) tergite 9 + 10 fused with genital capsule [5.1]; (2) a ventrally interrupted preocular ridge of the adult male [10.a]; (3) capitate tarsal digitules of the adult male [11.1]; (4) adult male tarsi 2-segmented [14.1]; (5) adult male with 5 pairs of simple eyes [15.1]; (6) tubular ducts of adult female not invaginated [17.b]; (7) adult female without abdominal spiracles [21.1]; and (8) first instar with simple disc pores [26.1].

The Pseudococcidae and Eriococcidae (Fig. 8, Stem 3) form a clade based on: (1) adult male with genal setae [6.1] (also a convergence in the clade *N.cornuparvum* + *C.hesperidum* + *P.acericola*); (2) adult male with 2 pairs of eyes [15.2] (also a covergence in the clade *S.prunastri* +

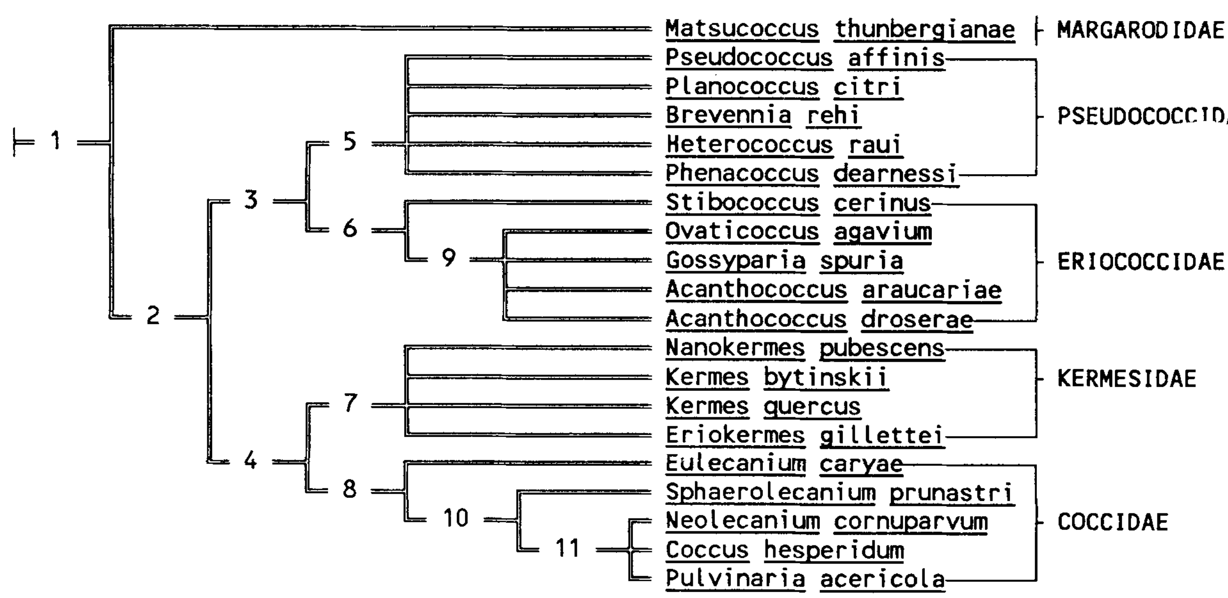

Fig. 8. Taxon cladogram determined using Hennig 86. Character changes for clades: Stem 1: 1.0, 2.0, 3.0, 4.0, 5.0, 6.0, 7.0, 8.0, 9.0, 10.0, 11.0, 12.0, 13.0, 14.0, 15.0, 16.0, 17.0, 18.0, 19.0, 20.0, 21.0, 22.0, 23.0, 24.0, 25.0, 26.0; Stem 2: 5.1, 10.a, 11.1, 14.1, 15.1, 17.b, 21.1, 26.1; Stem 3: 6.1, 15.2, 16.1, 22.1; Stem 4: 1.1, 4.1; Stem 5: 2.1, 5.0, 17.a, 23.1, 25.1; Stem 6: 3.1, 18.1, 26.0; Stem 7: 3.1, 7.1, 9.1, 10.b; Stem 8: 8.1, 12.1, 13.1, 14.0, 19.1, 24.1; Stem 9: 20.1; Stem 10: 15.2; Stem 11: 6.1.

N.cornuparvum + *C.hesperidum* + *P.acericola*); (3) adult female with translucent pores on metathoracic legs [16.1]; and (4) first instar with 2 median lines of longitudinal setae [22.1].

The monophyly of the Pseudococcidae (Fig. 8, Stem 5) is based on the following synapomorphies: (1) ungual digitules of adult male with acute tips [2.1]; (2) tergite 9 + 10 free [5.0, a reversal]; (3) adult females without invaginated tubular ducts [17.a]; (4) first instar with a proximal marginal femoral seta [23.1]; and (5) first instars with ostioles [25.1].

The monophyly of the Eriococcidae (Fig. 8, Stem 6) is justified by: (1) scutellar ridge of adult male present [3.1] (also a convergence in the Kermesidae); (2) adult female with microtubular ducts [18.1]; and (3) first instar without simple disc pores [26.0, a reversal].

The Kermesidae and Coccidae (Fig. 8, Stem 4) form a monophyletic group based on: (1) adult male with prescutal ridge extending into scutum [1.1]; and (2) scutum of adult male with central clear area [4.1] (also a convergence in *A.droserae*).

The monophyly of the Kermesidae (Fig. 8, Stem 7) is based on: (1) scutellar ridge of adult male present [3.1] (also a convergence in the Eriococcidae); (2) adult male with mouth tubercle present [7.1] (also a convergence in *O.agavium*); (3) presence of postocciput in adult male [9.1]; and (4) preocular ridge of adult male continuous ventrally [10.b].

The Coccidae (Fig. 8, Stem 8) is a monophyletic group justified by: (1) adult male without postoccipital ridge [8.1]; (2) adult male without metasternal apophysis [12]; (3) adult male with median ridge of basisternum [13.1]; (4) tarsi of adult male 1-segmented [14.0, a reversal]; (5) adult female with paired triangular anal plates [19.1]; and (6) first instar marginal setae near spiracles differentiated from other marginal setae [24.1].

Discussion

With the exception of *E.gillettei*, the preferred cladogram confirms previously accepted placements of species into family ranked clades (Margarodidae, Pseudococcidae, Eriococcidae, Kermesidae and Coccidae). The primary objective of this analysis was to determine the proper family placement of *E.gillettei*. Prior inclusion of *E.gillettei* in the Eriococcidae was based on characters of the adult female alone. The inclusion of the adult male and first instar in the present analysis suggests that the true affinities of *E.gillettei* lie with the Kermesidae, since it does not share any synapomorphies with the Eriococcidae that are not also shared by the Kermesidae. This result supports the hypothesis of Miller (1983) that *E.gillettei* is a kermesid.

Summary

Kermesids can be distinguished from eriococcids by: adult males with 5 pairs of simple eyes, presence of a postocciput, prescutal ridge extending into scutum, and scutum with central clear area; adult females with dorsal simple disc pores, without microtubular ducts, usually without protruding anal lobes, and usually with a submarginal band of tubular ducts on the tergum; and first instars with dorsal simple disc pores, with 4 dorsal rows of setae on abdominal segments excluding the posterior one, and without microtubular ducts. Conversely, eriococcids can be distinguished from kermesids by: adult males with 2 pairs of simple eyes, absence of a postocciput, presuctal ridge not extending into scutum, and scutum without central clear area; adult females without dorsal simple disc pores, with microtubular ducts, usually with protruding anal lobes, and usually with tubular ducts scattered over the venter; and first instars with microtubular ducts, with 6 dorsal rows of setae on abdominal segments excluding the posterior one, and without dorsal simple disc pores.

The present cladistic analysis provides evidence that the Eriococcidae constitute the sister group of the Pseudococcidae (Boratynski & Davies, 1971) and is contrary to the conclusions of Miller & Kosztarab (1979), Danzig (1980) and Kosztarab & Bullington (1986).

The importance of including characters from adult male and first instars in phylogenetic analyses of coccoids has been emphasized previously (Ferris, 1957; Miller & Kosztarab, 1979). The current study confirms their value for the resolution of higher level relationships within the Coccoidea.

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