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ABSTRACT

Three instars of the female and five instars of the male *Puto kosztarabi* are described and illustrated. This represents the first described species from eastern North America. A checklist of the known species of *Puto*, keys to the adult male *Puto*, North American female *Puto*, and instars to *P. kosztarabi* are included. A cladistic analysis utilizing 23 taxa and 38 characters supports the monophyly of the *Puto* group.

NARRATIVE

The genus *Puto* Signoret includes 57 species and is known from the Holarctic and Neotropics. In the United States, 22 species have been described to date, all of which occur in the western states. The "*Puto* group" (McKenzie, 1967) is closely related to the pseudococcids, but there has been some disagreement in deciding whether it should be treated taxonomically as a pseudococcid (Williams & de Willink, 1992) or as a separate family (Beardsley, 1969). There also has been some speculation about the relationship of *Puto* to other annectant genera such as *Pityococcus* McKenzie, *Steingelia* Nassonov, and *Phenacoleachia* Cockerell (Miller, 1983). These taxa each have males with more than

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three pairs of eyes and distinct tail-forming pore clusters, and two of the three have abdominal spiracles.

The objectives of this paper are: 1) to describe the first species of *Puto* known from the eastern United States and place it in a key to species; 2) to present a preliminary key to the adult males of available *Puto* species; 3) to provide a world checklist of *Puto* species; and 4) to report on the relationships of *Puto* with selected margarodid, pseudococcid, and phenacoleachid genera.

MATERIALS AND METHODS

Morphological terminology follows McKenzie (1967) for the adult female, Afifi (1968) for the adult male, and Miller (1991) for first and second instars. Measurements and numbers are from 10 specimens, when available, and are given as a mean with ranges in parentheses. Specimens of the genus *Puto* exhibit an array of sclerotized areas that contain concentrations of conical setae and trilocular pores. In most mealybugs, these areas would be called cerarii, but most authors have treated only those areas that are located near the body margin as true cerarii, and have termed similar areas within the confines of the body perimeter as setal areas with basal sclerotization. We will continue this usage, but also note that many specimens of *Puto kosztarabi* have cerarian-like structures scattered over most of the dorsum. Some specimens of *P. kosztarabi* were reared in the greenhouse on *Spartina alterniflora* Loisel. because this grass was readily available and its natural host of *Danthonia spicata* (L.) Beauvois ex R. & S. was not easily accessible. *Spartina alterniflora* should not be considered a natural host of this species.

Cladistic analyses were performed using Hennig86 (Farris, 1988). The data matrix consisted of 23 taxa and 38 characters. Outgroup comparison was used to determine polarities of characters. The Margarodidae were considered the most primitive Coccoidea by Beardsley (1968), and *Matsucoccus bisetosus* Morrison was chosen as a root outgroup species. The implicit enumeration (ie) command was applied to determine the most parsimonious trees. A strict consensus tree was generated by using the "Nelson" command.

Characters were selected from adult males, adult females, and first instars. Thirty-eight characters were used in the analysis. Characters 4, 9, 13, and 21 (treated as non-additive) and 1, 11, 12, 14, 19, 27, 28, 29,

and 32 (treated as additive) have three or more states; all others are binary. Plesiomorphic characters were coded as 0. Apomorphic characters were either coded as 1 to 3 (if additive) or a and b (if non-additive).

Character states were determined through examination of specimens deposited in the National Museum of Natural History Collection and through previously published descriptions. These species were selected since either slide-mounted material or published descriptions were available for adult males, adult females, and first instars of each species.

All available adult males of *Puto* were examined in the collections of the California Department of Food and Agriculture (Sacramento), The Natural History Museum (London, U.K.), National Museum of Natural History (Beltsville, Maryland), and University of California, Davis. Depositories of specimens are: National Museum of Natural History, Washington, D.C. (USNM); The Natural History Museum, London, U.K. (NHM); University of California, Davis ((UCD); and Virginia Polytechnic Institute and State University, Blacksburg (VPI).

SYSTEMATIC TREATMENT

Checklist of Known Species of *Puto*

References to the listed species correspond to citations in this paper or the following bibliographies of the Coccoidea: Morrison & Renk (1957), Morrison & Morrison (1965), Russell et al. (1974), and Kosztarab & Kosztarab (1988). Known distribution for each species follows each citation.

1. *Puto acirculus* McKenzie, 1967: California
2. *Puto albicans* McKenzie, 1967: California
3. *Puto ambiguus* (Fullaway, 1910a): California
4. *Puto antennatus* (Signoret, 1875b): Europe
5. *Puto antioquensis* (Murillo, 1931): Colombia
6. *Puto arctostaphyli* Ferris, 1950b: California
7. *Puto asteri* (Takahashi, 1932): Japan
8. *Puto atriplicis* McKenzie, 1961: Western U.S.
9. *Puto barberi* Cockerell, 1895q: Caribbean and Venezuela
10. *Puto borealis* Borchsenius, 1948b: Palearctic
11. *Puto bryanthi* Ferris, 1950b: California
12. *Puto caballeroi* (Gomez-Menor, 1948): Spain

13. *Puto calcitectus* (Cockerell, 1901j): New Mexico
14. *Puto californicus* McKenzie, 1967: California
15. *Puto caucasicus* Hadzibejli, 1956: Republic of Georgia
16. *Puto clematidis* Matesova, 1957: Kazakhstan
17. *Puto cupressi* (Coleman, 1901): Western U.S. and Canada
18. *Puto decorosus* McKenzie, 1967: California
19. *Puto echinatus* McKenzie, 1961: California
20. *Puto erigeroneus* (Kanda, 1959a): Japan
21. *Puto euphorbiaefolius* Bodenheimer, 1943: Iraq
22. *Puto ferrisi* (Kiritshenko, 1936a): Russia
23. *Puto graminis* Danzig, 1972b: Sakhalin Island
24. *Puto kosztarabi* n. sp.
25. *Puto janetscheki* Balachowsky, 1953m: France, Czech Republic, and Slovakia
26. *Puto jarvdensis* Tang, 1992: China (possibly not a *Puto*)
27. *Puto kiritshenkoi* (Borchsenius, 1949): Russia
28. *Puto kondarensis* (Borchsenius, 1948c): Tadzhikistan
29. *Puto konoi* Takahashi, 1941c: Sakhalin Island
30. *Puto lamottei* Matile-Ferrero, 1985: Venezuela
31. *Puto lasiorum* (Cockerell, 1901j): Western U.S.
32. *Puto laticribellum* McKenzie, 1961: California
33. *Puto marsicanus* Marotta & Tranfaglia, 1993: Italy
34. *Puto megriensis* (Borchsenius, 1948b): Armenia
35. *Puto mexicanus* Cockerell, 1893o: Texas and Mexico
36. *Puto mimicus* McKenzie, 1967: California (possibly not a *Puto*)
37. *Puto nulliporus* McKenzie, 1960: California (possibly not a *Puto*)
38. *Puto orientalis* Danzig, 1978c: Sakhalin Island
39. *Puto ornatus* (Green, 1922): India and China (possibly not a *Puto*)
40. *Puto orthezioides* (Cockerell, 1903a): Mexico
41. *Puto pacificus* McKenzie, 1967: California
42. *Puto palinuri* Marotta & Tranfaglia, 1993: Italy
43. *Puto paramoensis* Matile-Ferrero, 1985: Venezuela
44. *Puto pilosella* (Sulc, 1898): Europe
45. *Puto pini* Danzig, 1972b: Far East
46. *Puto porterii* (Bodenheimer, 1943): Israel

47. *Puto pricei* McKenzie, 1960: California
48. *Puto profusus* McKenzie, 1960: California
49. *Puto sandini* Washburn, 1965: Utah
50. *Puto simmondsiae* McKenzie, 1961: California and Mexico
51. *Puto subericola* (Vayssiere, 1927): Morocco
52. *Puto superbus* (Leonardi, 1907b): Europe
53. *Puto tauricus* (Borchsenius, 1948b): Crimea, China, Greece, Italy
54. *Puto tubulifer* Danzig, 1978c: Far East
55. *Puto ulter* Ferris, 1950b: Central and South America
56. *Puto usingeri* McKenzie, 1962: Peru
57. *Puto vaccinii* Danzig, 1978c: Far East
58. *Puto yuccae* (Coquillett, 1890): U.S. and Mexico

Treatment of Adult Male

The following preliminary key to known males of the world *Puto* is the first to be presented for this genus. Few male specimens were available for many of the species; consequently, the limits of intraspecific variation for most species are poorly known, and many of the characters used in the key may be subject to future revision. The species of *Puto* examined for the following key are listed below followed by locality, collection date, number of specimens studied, and depository. The following specimens were examined: *Puto albicans*: Bass Lake, California, VI-20-78, 1 male (CDA); *P. ambiguus*: Alameda, California, V-?-06, 1 male (USNM); *P. antennatus*: Berchtesgaden, Germany, VII-30-51, 2 males (USNM); *P. antioquensis*: Fredonia, Colombia, XII-7-29, 2 males (USNM); *P. arctostaphyli*: New Indria, California, VI-?-1884, 3 males (USNM); Grass Valley, California, VI-20-72, 3 males (CDA); *P. atriplicis*: Murphy, Idaho, VI-5-63, 1 male (USNM); Chalfont, California, VIII-7-73, 1 male (USNM); Bishop, California, X-4-73, 2 males (CDA); Mountain Home, Idaho, IX-10-75, 2 males (USNM); *P. calcitectus*: Beulah, New Mexico, VII-27-00, 1 male (USNM); *P. cupressi*: Eugene, Oregon, 1976, 3 males (USNM); *P. decorosus*: Camp Angelus, California, 1 male (USNM); *P. echinatus*: Carpenteria, California, IV-1-82, 1 male (CDA); *P. kosztarabi*: see description of adult male; *P. mexicanus*: Mexico, VIII-9-39, 1 male (USNM); Kenedy, Texas, X-24-40, 1 male (USNM); Mexico, V-22-41, 1 male (USNM); Durango, Mexico, III-13-72, 2 male (USNM);

Mexico, I-27-74, 1 male (USNM); Mexico, XII-8-80, 1 male (USNM); Mexico, IV-25-87, 1 male (USNM); *P. sandini*: Thousand Mountain Lake, Utah, VIII-4-53, 1 male (USNM); Loa, Utah, VIII-24-55, 2 males (USNM); *P. simmondsiae*: Black Hill, California, IV-22-78, 1 male (USNM); *P. superbus*: Furth, N. Bavaria, VI-2-50, 1 male (USNM); Athens, Greece, IV-15-68, 1 male (CDA); *P. ulter*: Guatemala, V-8-46, 1 male (USNM); Mexico, III-21-52, (1 male) (USNM).

Key to Known Adult Males of *Puto*

1 Male wingless or brachypterous 2
Male fully winged 3

2(1) 4 eyes and 1 ocellus on each side of head; wings absent; aedeagus blunt apically . . . . . .***superbus*** (Leonardi)
6 or 7 eyes and 1 ocellus on each side of head; wings represented by small lobes; aedeagus apically acute or bifurcate . . . . . .***ambiguus*** (Fullaway) and ***echinatus*** McKenzie

3(1) Aedeagus blunt apically; ventral surface of ocular sclerites with sclerotization restricted to area near eye 4
Aedeagus acute or bifurcate apically; ventral surface of ocular sclerites with sclerotization continuous from preocular ridge to postocular ridge 5

4(3) 7 eyes and 1 ocellus on each side of head; dorsal surface of penial sheath without sclerotization around base of setae; antennal segment 3 more than 350 μm long . . . . . .***cupressi*** (Coleman)
6 eyes and 1 ocellus on each side of head; dorsal surface of penial sheath with sclerotization around base of setae; antennal segment 3 less than 350 μm long . . . . . .***antennata*** (Signoret) and ***sandini*** Washburn

5(3) Aedeagus with 2 sclerotized teeth on ventral surface proximal of apex; without teeth on apex of aedeagus (Figs. 2g & 2h) 6
Aedeagus without sclerotized teeth on ventral surface proximal of apex; with several teeth on apex of aedeagus 7

6(5) Each tail-forming pore cluster with less than 250 pores excluding tubular pores (Fig. 2d) . . . . . .*kosztarabi*, n. sp.
Each tail-forming pore cluster with more than 250 pores excluding tubular pores . . . . . .*calcitectus* (Cockerell)

7(5) Each tail-forming pore cluster with 200 or more pores excluding tubular pores 8
Each tail-forming pore cluster with less than 200 pores excluding tubular pores 9

8(7) Each tail-forming pore cluster with more than 400 pores excluding tubular pores; longest seta on antennal segment 9 greater than 450 µm . . . . . *antioquensis* (Murillo)
Each tail-forming pore cluster with less than 400 pores excluding tubular pores; longest seta on antennal segment 9 less than 450 µm . . . . . *albicans* McKenzie, *arctostaphyli* Ferris, *mexicanus* (Cockerell) (in part), *ulter* Ferris, *yuccae* (Coquillett)

9(7) Genal setae with associated multilocular pores; body setae fleshy, with slightly rounded apices; third antennal segment predominantly with setae less than half length of segment . . . . . *atriplicis* McKenzie
Genal setae without associated multilocular pores; body setae filamentous, with acute apices; third antennal segment predominantly with setae longer than half length of segment (excluding setae associated with base of long setae) . . 10

10(9) Sclerotized portion of each side of penial sheath with more than 75 setae; more than 25 setae on tegula . . . . . *decorosus* McKenzie
Sclerotized portion of each side of penial sheath with less than 60 setae; with less than 20 setae on tegula . . . . . *mexicanus* (Cockerell) (in part)

Key to Adult Females of *Puto* in North America
(modification of McKenzie [1967])

1 Ventral multilocular disk pores present on last 2 abdomi-

nal segments 3
Ventral multilocular disk pores absent on last 2 abdominal segments 2

2(1) Oral-rim type tubular ducts present, sparingly distributed on dorsum; usually not more than 18 enlarged conical setae in anal cerarius . . . . . *nulliporus* McKenzie
Tubular duct of any kind absent on dorsum; often as many as 28–30 enlarged conical setae in anal lobe cerarius . . . . . *mimicus* McKenzie

3(1) Dorsal setae with basal sclerotization, coalesced into cerarii-like structures . . . . . A
Dorsal setae without basal sclerotization or with sclerotization restricted to area around setal socket, not coalesced into cerarii-like structures . . . . (continue at couplet 4 in McKenzie's 1967 key)

A(3) Cerarii without oral collar tubular ducts (Fig. 1d) . . . . . B
Cerarii with oral collar tubular ducts . . . . . *lasiorum* (Cockerell)

B(A) Head without large-sized tubular ducts near body margin adjacent to anterior cerarii C
Head with large-sized tubular ducts near body margin adjacent to anterior 1 or 2 cerarii (Fig. 1e) . . . . *kosztarabi*, n. sp.

C(B) Circulus present. . . . . *calcitectus* (Cockerell)
Circulus absent . . . . . *acirculus* McKenzie

TREATMENT OF SPECIES

Key to Instars (Except Third-instar Female) of *Puto kosztarabi*

1 Without wings or wing pads 2
With wings or wing pads 4

2(1) Vulva present; antenna 9-segmented; frontal cerarius with 18 or more conical setae (Fig. 1) . . fourth-instar female (adult)
Vulva absent; antenna 7-segmented; frontal cerarius with

8 or fewer conical setae 3

3(2) Oral-collar tubular ducts abundant, scattered over dorsal surface, along ventral lateral margin, and anterior of mouthparts (Fig. 6) . . . . . second-instar male
Oral-collar tubular ducts few, restricted to area anterior of cerarii on dorsal and ventral surfaces, and anterior of mouthparts (Fig. 5) . . . . . second-instar female

4(1) Wings well developed; legs and antennal setae with associated short basal setae; genital capsule with sclerotized aedeagus (Fig. 2) . . . . . fifth-instar male (adult)
Wings in form of pads; legs and antennal setae without associated short basal setae; genital capsule without sclertized aedeagus 5

5(4) Wing pads greater than 700 μm long; lateral sclerite of abdominal segment VII with fimbriate projection (Fig. 3) . . . . . fourth-instar male
Wing pads less than 125 μm long; lateral sclerite of abdominal segment VII without fimbriate projection (Fig. 4) . . . . . third-instar male

Puto kosztarabi, new species
(Figures 1-8)

Suggested Common Name: Buffalo Mountain Mealybug

Diagnosis: Adult female with numerous dorsal conical setae on sclerotized bases, large-sized tubular ducts restricted to anterior head region, and circulus present or absent.

Type Data: ***Holotype***, adult female, U.S.A. We have chosen and marked as holotype an adult female labeled "***Puto kosztarabi/*** D. Miller & G. Miller/ VIRGINIA/ Floyd Co./ Buffalo Mtn./ 4 August 1992/ M. Kosztarab coll./ ex: ***Danthonia spicata***" (USNM). There is also a paratype on the slide; the specimen located horizontally near the edge of the coverslip is the holotype. A label has been placed on the slide giving the exact location of the holotype. ***Paratypes***, 22 adult females, 9 adult males, 4 pupal males, 2 prepupal males, 3 second-instar females, 3

second-instar males, 19 first instars, U.S.A.: In addition to the paratype associated on the slide with the holotype, there are 61 paratypes on 37 slides (NHM, UCD, USNM, VPI). Complete collection information is presented in the corresponding "Specimens examined" section for the adult and immature stages.

Etymology: The species is named in honor of Michael Kosztarab, who has diligently added to the systematic knowledge of scale insects through his personal research and the research of his students. This species was collected by Michael in his quest to better understand the diversity of insect life in Virginia.

Habitat: *Puto kosztarabi* is associated with the grass *Danthonia spicata* on Buffalo Mountain (elev. 3,972 ft.), Floyd County, Virginia. Both mealybug and grass are found near the summit's higher elevations in unique prairie-like glades that contain magnesium-rich soils. The Buffalo Mountain site is the only known site of this mealybug. Nine other similar ecological habitats in Virginia and North Carolina were examined in 1992 and 1993, but *P. kosztarabi* was not collected in any of these other sites (Michael Kosztarab, pers. comm.).

Adult female (fourth instar)

Figure 1

Slide-mounted characters: Holotype oval, length 2.4 mm, width 1.0 mm; paratypes 3.6 (2.5-4.6) mm, 1.9 (1.4-2.6) mm.

Dorsum: With 21 pairs of cerarii, paratypes 20 (19-21); anal-lobe cerarius (Fig. 1d) with 29 conical setae, paratypes 29 (26-33) and 46 trilocular pores, paratypes 54 (39-61), without associated discoidal pores or tubular ducts; frontal cerarius with 19 conical setae, paratypes 22 (18-28) and 13 trilocular pores, paratypes 12 (9-19), without associated discoidal pores or tubular ducts; all cerarii with basal sclerotization. Multilocular disc pores absent; trilocular pores (Fig. 1c) scattered; discoidal pores (Fig. 1b) of 1 size, most abundant along body margin and on thorax and head. Oral-collar tubular ducts of large size (Fig. 1e) located near anterior cerarii on dorsal and ventral surface, with 3 ducts on each side of head, paratypes with 3 (1-7), oral collars absent elsewhere. Body setae conical (Fig. 1a), usually with basal sclerotization and associated trilocular pores, often coalesced with other dorsal setae, longest seta on abdomen 26 μm long, paratypes 33 (29-36) μm, about same size as cerariian setae; with 53 setae on segment V, excluding those in cerarii, paratypes with 53 (45-59).

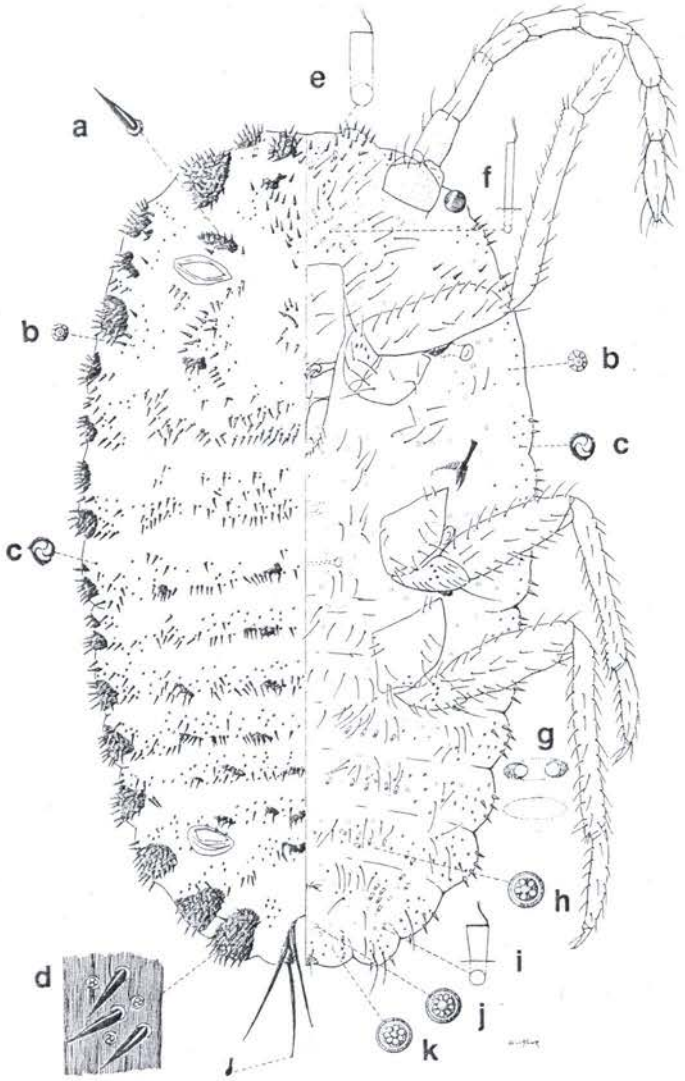


Fig. 1. Adult female of *P. kosztarabi*. Buffalo Mtn., Floyd Co., Virginia, VIII-4-1993, on *Danthonia spicata*. a. conical body seta; b. discoidal pore; c. trilocular pore; d. cerarian setae; e. frontal oral-collar tubular duct; f. large-sized oral-collar tubular duct; g. circulus variation; h. 5-locular pore; i. small-sized oral-collar tubular duct; j. 9-locular pore; k. 7-locular pore.

Longest anal-ring seta 247 μm long, paratypes 243 (233-317) μm, apices capitate; 1.7 times as long as greatest diameter of ring, paratypes 1.5 (1.1-1.8) times.

Venter: With multilocular pores in posterior areas of segments III-VIII, paratypes III or IV-VIII, in anterior areas on segments I-VIII, with pores abundant on thorax and head; loculi variable, some specimens with predominantly 5 (Fig. 1h) and 7 (Fig. 1k) locular pores, others with predominantly 9 (Fig. 1j) and 10 locular pores. Trilocular pores of 2 sizes, smaller size in irregular rows across medial and mediolateral areas of each abdominal segment, larger size present near body margin; triloculars absent on medial and mediolateral areas of thorax and head. Discoidal pores scattered over surface. Oral-collar tubular ducts smaller than on dorsum, of 2 sizes, smaller size (Fig. 1i) arranged in transverse rows on abdominal segments III-VIII, paratypes II or III-VIII, larger size (Fig. 1f) restricted to raised area on head anterior of mouthparts, with 48 ducts on holotype, paratypes 56 (43-63). Ventral setae arranged in rows on abdomen, with 28 setae on segment V, paratypes 33 (28-38), longest seta on segment V 99 μm long, paratypes 103 (96-113) μm; longest anal-lobe seta 96 μm long, paratypes 120 (90-146) μm; longest seta on trochanter of hind leg 151 μm long, paratypes 196 (163-227) μm.

Circulus absent or reduced (Fig. 1g), of 20 paratypes examined, 7 lack circulus, 8 possess 2 oval areas representing circulus remnants, and 5 have well-developed circulus; when present located on posterior margin of segment III. Labium 189 μm long, paratypes 215 (192-236) μm. Posterior spiracle greatest length 108 μm, paratypes 136 (96-160) μm. Antennae 9-segmented, antenna 984 μm long, paratypes 1190 (1080-1296) μm, apical segment 143 μm long, paratypes 174 (160-183) μm, segment II 105 μm long, paratypes 118 (108-128) μm, segment III 134 μm long, paratypes 159 (140-180) μm; length of segment IX divided by length of segment II 1.4, paratypes 1.5 (1.3-1.6), length of segment IX divided by length of segment III 1.1, paratypes 1.1 (1.0-1.2). Legs with 8 translucent pores on hind femur, paratypes 5 (2-8), with 39 translucent pores on hind tibia, paratypes 36 (23-35). Femur 447 μm long, paratypes 540 (504-588) μm; tibia 612 μm long, paratypes 733 (696-758) μm; tarsus 252 μm long, paratypes 286 (252-300) μm. Tibia/tarsus 2.4, paratypes 2.5 (2.4-2.8). Hind tarsus with 23 setae, paratypes 23 (19-26). Hind trochanter with 4 sensory pores on each surface.

Unusual variation. One specimen has many more than 6 anal-ring setae.

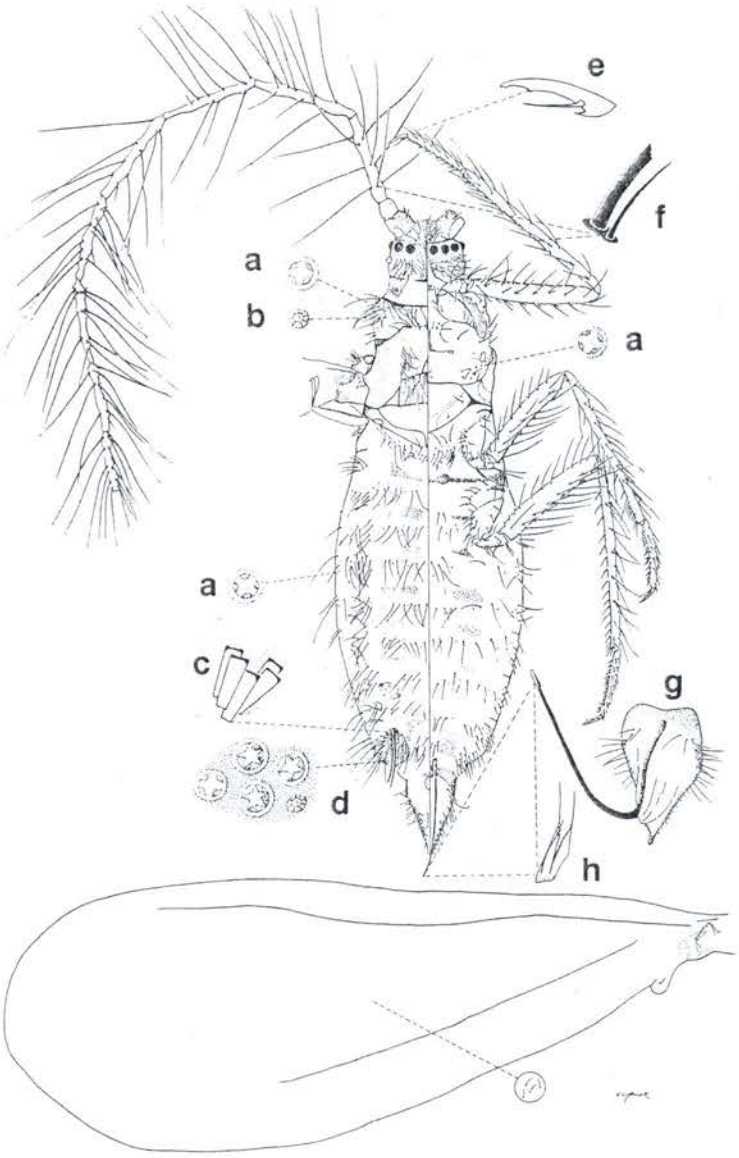


Fig. 2. Adult male of *P. kosztarabi*. Buffalo Mtn., Floyd Co., Virginia, VIII-4-1993, on *Danthonia spicata*. a. 4-locular pore; b. discoidal pore; c. tubular pore; d. multilocular pores; e. tarsal claw; f. seta and associated basal seta; g. genital capsule; h. tip of aedeagus.

Specimens examined. VIRGINIA, Floyd Co.: S. slope Buffalo Mountain, VIII-1-76, on *Danthonia spicata*, R. L. Hoffman (8 paratypes on 4 sl.) USNM; Buffalo Mountain, VIII-4-92, on *Danthonia spicata*, M. Kosztarab (1 holotype, 14 paratypes on 11 sl.) NHM, UCD, USNM, VPI.

Adult male (fifth instar)

Figure 2

Slide-mounted characters: Body length 3.1 (2.8-3.5) mm; greatest width at thorax 0.8 (0.7-0.9) mm.

Dorsum: With 1 pair of tail-forming pore clusters on segment VIII, each with 2 central setae with slightly swollen apices, longest seta 215 (186-247) μm long, with 143 (116-176) multilocular pores (Fig. 2d), 40 (32-62) tubular pores (Fig. 2c) surrounding central setal bases, 15 (7-22) discoidal pores, and 28 (22-32) associated setae. Posterior ostioles present. Multilocular pores normally with 4 loculi, rarely 3 or 5, arranged in rows near setal bases on all abdominal segments (abdominal segment V with 28 [23-38] pores), abundant in membranous area anterior of metapostnotum and posterior of pronotal ridge, absent on head. Discoidal pores (Fig. 2b) most abundant near body margin, occasionally in medial and mediolateral areas near bases of setae. Body setae slightly shorter than those on venter (longest seta on segment V 106 [87-128] μm), in lateral cluster and in transverse row on each abdominal segment, present on metathorax, scutellum, posterior portion of prescutum, with 1 or 2 on each side of scutum, on tegula with 7 (4-9) on each side, in row posterior of pronotal ridge, on pronotal sclerite, in genal cluster with 8 (5-10) in each cluster, on ocular sclerites abundant on dorsomedial sclerite with 28 (24-33) setae on each side of mid-cranial ridge excluding setae on occipital sclerite. Abdominal tergites with 2 areas of sclerotization on anterior margin of segments VI-II, abdominal tergite VIII with 2 roughly triangular plates that normally are not connected. Metapostnotal ridge usually represented by single sclerotized area. Scutellum with distinct scutellar suture and scutellar ridge. Prescutum with prescutal ridge absent or represented by weak suture connected to scutellum thus dividing scutum in 2 pieces. Triangular clear area present anterior of scutellum. Pronotal ridge present, with conspicuous pronotal sclerites. Postoccipital and postocular nearly contiguous, weakly divided by swelling in lateral apex of postoccipital ridge; dorsal arm of midcranial ridge touching postoccipital ridge posteriorly, with broad lateral arms of midcranial ridge at apex of head. Preocular ridge beginning near lateral margin of sclero-

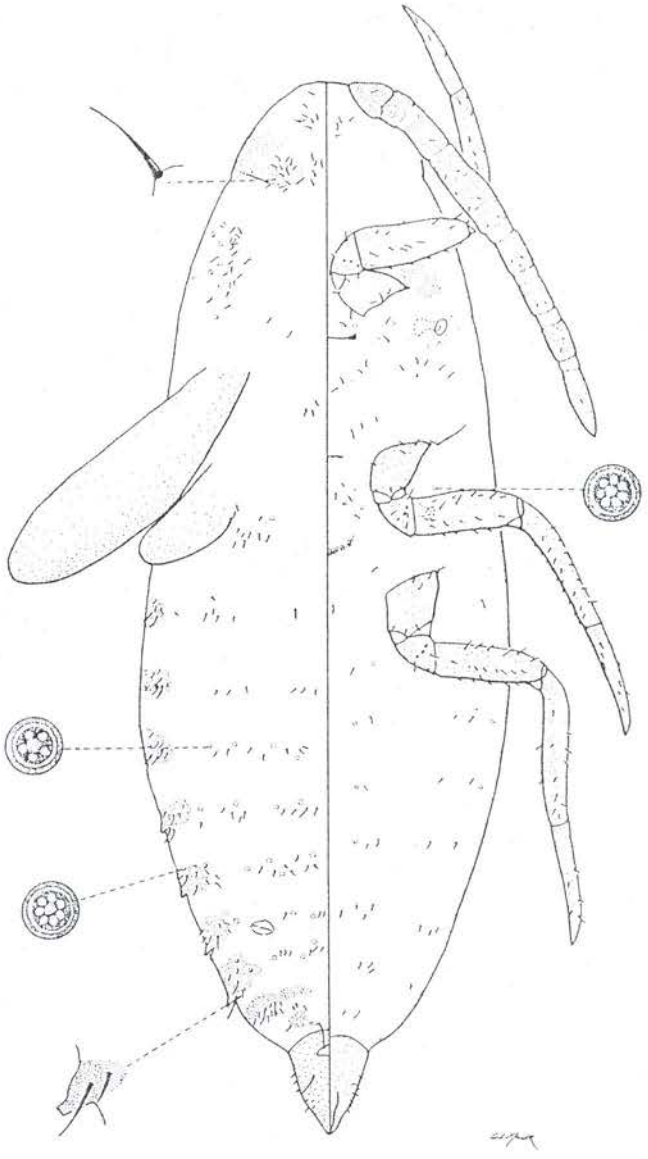


Fig. 3. Fourth-instar male of *P. kosztarabi*. Buffalo Mtn., Floyd Co., Virginia, VIII-4-1993, on *Danthonia spicata*.

tized area of dorsomedial sclerite, continuing laterally as anterior boundary of ocular sclerite. Dorsomedial sclerite nearly contiguous with sclerotization of ocular sclerite; sclerotization of ocular sclerite present within boundaries of preocular and postocular ridges except on posteromedial portion. Normally with 2 or 3 dorsal eyes, largest 49 (44-57) μm in diameter; ocellus 43 (29-49) μm in diameter. Head with 7 (6 or 7) pairs of eyes and 1 pair of lateral ocelli. Hamulohalterae each 267 (240-288) μm long, with 3 (3 or 4) apical setae. Mesothoracic wings each 2.9 (2.5-3.3) mm long, wing length/body length 0.9 (0.9-1.0), without setae or circular sensoria.

Penial sheath (Fig. 2g) membranous, except for narrow sclerotized band forming triangular framework around sheath perimeter; frame continuous, without sutural lines. Sclerotized area bearing numerous setae on lateral aspect, on ventral surface anteriorly with 51 (45-55) setae on each side of sheath, setae increasing in length anteriorly, with longest seta 96 (84-108) μm long, 4 (2-5) setae on dorsal aspect of sheath posterior of anal opening; penial sheath 523 (480-576) μm long. Aedeagus U-shaped, with basal portion attached to membrane, apical portion (Fig. 2h) exercible, apex simple laterally bearing 2 conspicuous denticles, apex with divided sclerotization dorsally connected by membrane; total length 986 (924-104-4) μm.

Venter: Multilocular pores predominantly with 4 loculi (Fig. 2a), present in lateral areas of each abdominal segment, with small numbers of pores in medial and mediolateral areas of abdominal segments VIII-II (e.g., segment V with 12 [7-16] pores), also abundant around anterior spiracle, near prosternum, and on head near midcranial ridge anterior of preocular ridge. Discoidal pores most abundant laterally, also present near multilocular pores on head. Body setae in lateral clusters and in transverse row on each abdominal segment, on membranous areas of thorax, on mesosternum and ocular sclerite, and near ventral arm of midcranial ridge anterior of preocular ridge. Metapleural ridge present from articulation of coxa to hamulohaltera, with dorsally projecting ridge believed by Beardsley (1962) to represent posterior margin of metepimeron; with 2 precoxal ridge extensions, 1 extending to conspicuous metasternal apophysis. Metasternum evident as single sclerite. Mesosternum with distinct marginal ridge, and conspicuous mesosternal apophyses. Prosternum represented by heavily sclerotized prosternal ridge that ends at conspicuous prosternal apophyses, central anteriorly projecting ridge surrounded by weakly sclerotized triangular sclerites. Propleura about

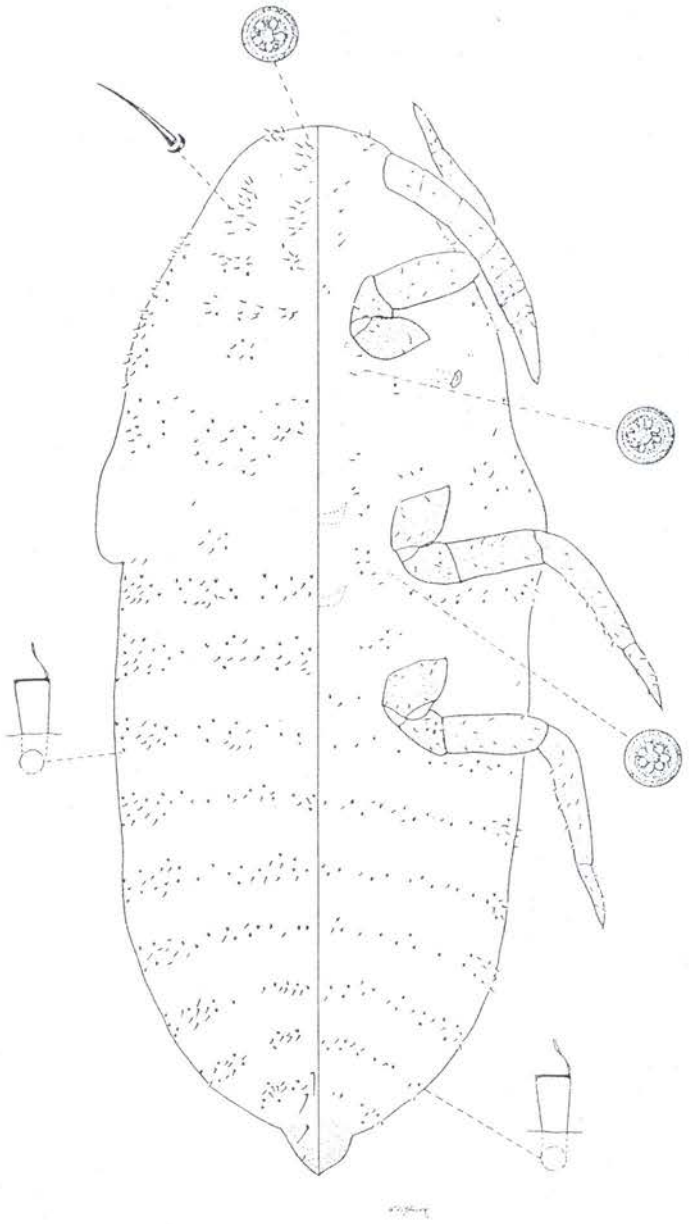


Fig. 4. Third-instar male of *P. kosztarabi*. Beltsville, Prince Georges Co., Maryland, 17-VIII-1979, on *Spartina alterniflora* in greenhouse.

1/2 to 3/4 size of procoxa. Preoral ridge connected to postocular ridge to form boundary of ocular sclerite. Preocular ridge touching ventral arm of midcranial ridge. Ocular sclerite sclerotized in all areas except near preoral ridge and near posterior connection of postocular ridge. Ventral arm of midcranial ridge connected posteriorly to preoral ridge and anteriorly to dorsal and lateral arms of midcranial ridge. Head set on unusually long neck; ventral surface with 4 or 5 pairs of eyes.

Setae on trochanter, femur, and tibia with 1 (1-3) smaller setae closely associated with setal base (Fig. 2f). Trochanter with 4 (2-5) sensoria on each surface, tibia of hind leg 898 (780-984) μm long; tarsus 328 (288-366) μm long; tibia/tarsus 2.7 (2.5-2.8); claw 87 (80-102) μm long, with pair of basal denticles, large denticle about 3/4 of distance from claw base to tip, and small denticle near tip; claw digitules apically acute, extending to large denticle on plantar surface; tarsal digitules apically acute not reaching tip of claw (Fig. 2e). Antennae 10-segmented, 3.4 (2.9-3.6) mm long; apical segment 266 (228-300) μm long; segment III 436 (384-480) μm long; apical segment/ segment III 0.6 (0.6-0.7); most abundant type of seta unusually long and with associated smaller setae near setal base, this type present on all but segment 1; antennal bristles on apical 3 segments; hair-like setae on all segments, with 2 small setae on intersegmental membrane at apex of segments 3 and 4, base of most segments with more heavily sclerotized ring giving appearance of separate small segment.

Specimens examined. VIRGINIA, Floyd Co.: Buffalo Mountain, VIII-4-92, on *Danthonia spicata*, M. Kosztarab (9 paratypes on 9 sl.) NHM, UCD, USNM, VPI.

Fourth-instar male (pupa)

Figure 3

Slide-mounted characters: Body length, 2.58 (2.37-2.87) mm, width 0.71 (0.68-0.74) mm. Body elongate.

Dorsum: Predominantly membranous with abdominal sclerites and antennal, ocular, and wing bud sclerotization. Multilocular disk pores with 5-9 loculi located on lateral, submedial, and medial areas of thorax and abdomen; absent from head. Longest body setae 42 (35-54) μm on segment IX and genital capsule. Postocular ridge represented by weak sclerotized band, ocular sclerites present. Front wing buds 754 (719-815) μm long, with partial sclerotization; hamulohalterae present. Posterior ostioles present. Lateral abdominal sclerites on segments on I-VIII, seg-

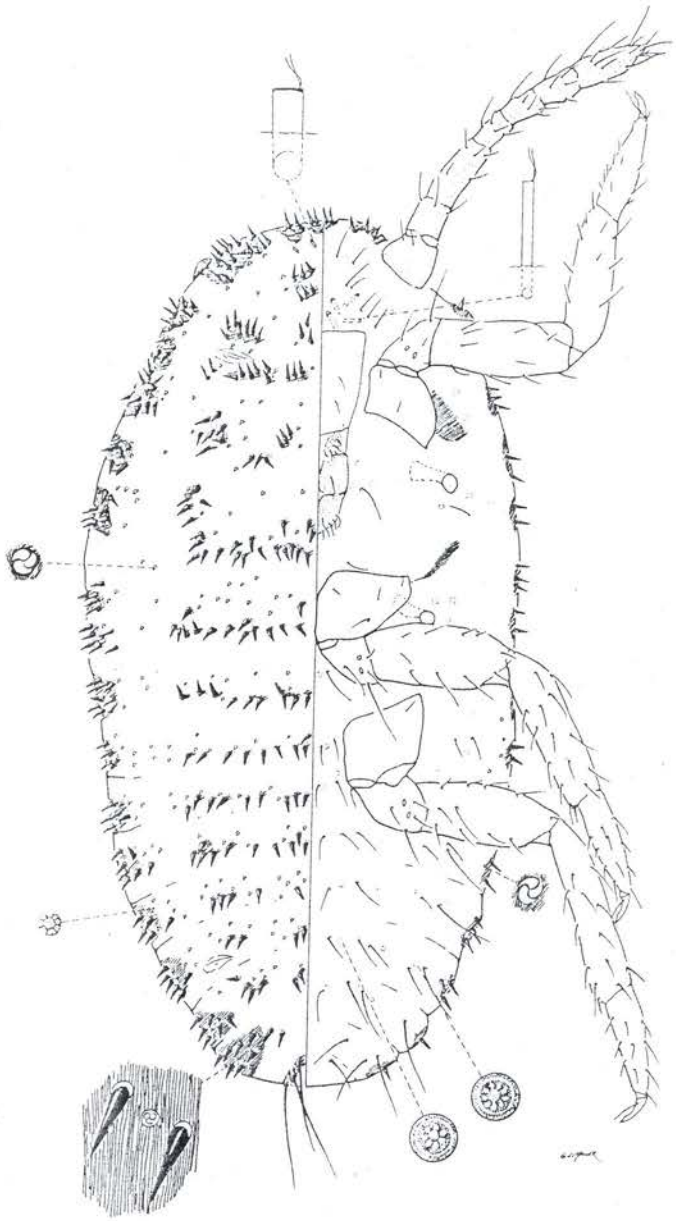


Fig. 5. Second-instar female of *P. kosztarabi*. Beltsville, Prince Georges Co., Maryland, 26-VI-1979, on *Spartina alterniflora* in greenhouse.

ment VIII extending medially. Sclerotization present on medial areas of segment IX. Sclerites of segments VI-VII and occasionally IV-V with fimbriate projections. Genital capsule conical, sclerotized throughout except near dorsal anal opening. Genital slit represented by small invagination. Genital capsule 246 (237-259) µm long, 232 (209-259) µm; width/length ratio of capsule 0.94 (0.86-1.06).

Venter: Membranous with fewer body setae and multilocular pores. Mouth and ventral cavity weakly discernible. Ocular region and postocular ridge inconspicuous. Antenna 1.25 (1.11-1.48) mm long. Prosternal ridge, mesosternal apophysis (furca), and metasternal apophysis evident. Legs sclerotized; hind tibia 407 (375-64) µm long, hind tarsus 293 (277-319) µm; hind tibia/tarsus ratio 1.4 (1.3-1.5). Abdominal sternites absent.

Specimens examined. VIRGINIA, Floyd Co.: Buffalo Mountain, VIII-4-92, on *Danthonia spicata*, M. Kosztarab (4 paratypes on 2 sl.) USNM.

Third-instar female
(not observed)

Third-instar male (prepupa)
Figure 4

Slide-mounted characters: Same as pupa except as follows: Body length, 2.37 (2.26-2.48) mm, width 0.96 (0.94-0.99) mm.

Dorsum: Predominantly membranous with antennal and wing bud sclerotization. Multilocular disk pores with 5 loculi located on medial area head. Longest body setae 48 (47-49) µm on segment IX and genital capsule. Front wing buds 110 (100-120) µm long, with partial sclerotization; hamulohalterae inconspicuous. Oral-collar tubular ducts short, sclerotized, scattered over surface. Lateral abdominal sclerites absent. Genital capsule 148 (143-153) µm long, 220 (217-222) µm wide; width/length ratio of capsule 1.49 (1.43-1.55).

Venter: Antenna 643 (593-692) µm long. Multilocular disk pores with 7-9 loculi. Hind tibia 371 (n=1) µm long, hind tarsus 128 (n=1) µm; hind tibia/tarsus ratio 2.9.

Specimens examined. MARYLAND, Prince Georges Co.: Beltsville, VIII-17-1979, on *Spartina* in greenhouse, W. Sweeney (1 paratype) USNM; VIRGINIA, Floyd Co.: S. slope Buffalo Mountain, VIII-1-1976, on *Danthonia spicata*, R. L. Hoffman (1 paratype) USNM.

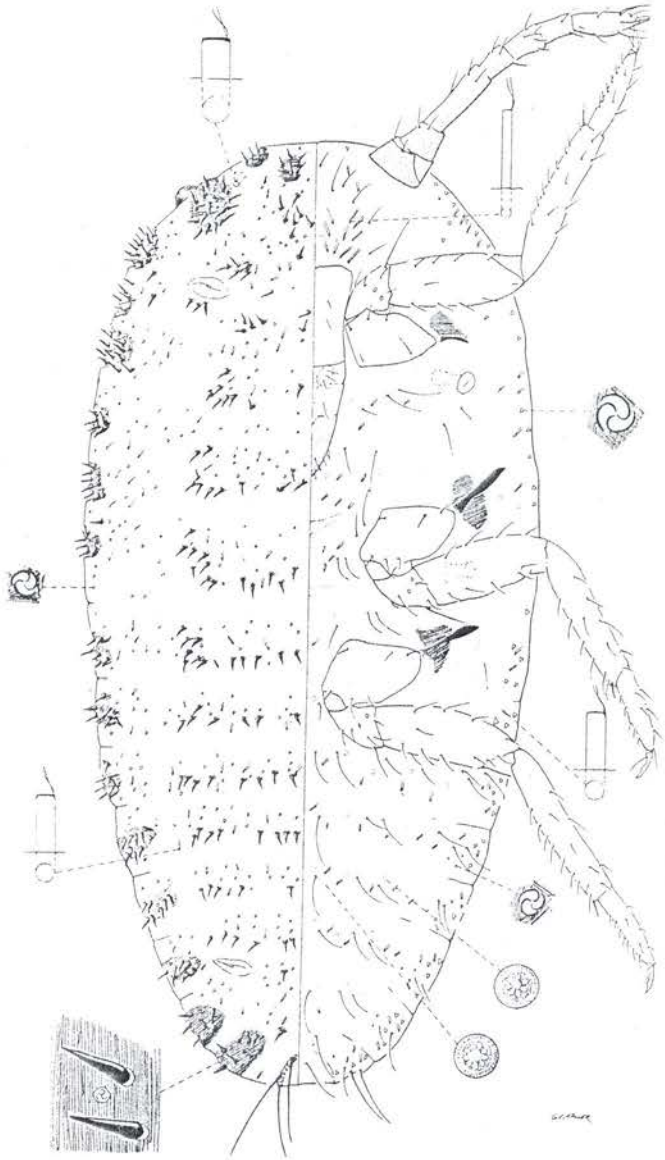


Fig. 6. Second-instar male of *P. kosztarabi*. Beltsville, Prince Georges Co., Maryland, 17-VIII-1979, on *Spartina alterniflora*.

Second-instar female

Figure 5

Slide-mounted characters: Same as adult female except as follows: Body length 1.4 (1.3-1.5) mm; width 0.7 (0.6-0.8) mm.

Dorsum: With 18 (18 or 19) pairs of cerarii; anal-lobe cerarius with 8 (7-9) setae and 16 (15-17) trilocular pores; frontal cerarius with 7 (6 or 7) conical setae and 3 (2 or 3) trilocular pores. Trilocular and discoidal pores less abundant than on adult female, of same distribution. Oral-collar tubular ducts of large size located near anterior cerarii on dorsal and ventral surface, with 2 (2-3) ducts on each side of head. Longest body seta on abdomen 32 (31 or 32) μm long; with 15 (13-17) setae on segment V, excluding those in cerarii.

Anal-ring seta 159 (157-163) μm long; 1.4 (1.3-1.4) times as long as greatest diameter of ring.

Venter with multilocular pores in anterior bands on all abdominal segments, sometimes with short posterior band near margin of anterior 3 or 4 segments, with pores abundant on thorax and head. Trilocular pores of 2 sizes, restricted to sublateral areas of body. Discoidal pores less abundant than on adult female, scattered over surface. Oral-collar tubular ducts absent from abdomen an thorax, restricted to raised area on head anterior of mouthparts, with 18 (12-23) ducts. Ventral setae arranged in rows on abdomen, with 9 (9 or 10) setae on segment V, longest seta on segment V 65 (61-70) μm long; longest anal-lobe seta 94 (81-96) μm long; longest seta on trochanter of hind leg 103(102-105) μm long.

Circulus absent. Labium 143 (131-151) μm long. Posterior spiracle greatest length 77 (70-81) μm. Antennae 7-segmented, length of right antenna 580 (564-588) μm, apical segment 132 (122-140) μm, segment II 72 (70-73) μm, segment III 119 (113-122) μm; length of segment VII divided by length of segment II 1.9 (1.8-2.0), length of segment VII divided by length of segment III 1.1 (1.0-1.2). Legs without translucent pores. Length of femur 256 (250-262) μm; tibia 314 (303-332) μm; tarsus 186 (183-192) μm. Tibia/tarsus 1.6 (1.6 or 1.7). Hind tarsus with 17 (16 or 17) setae.

Specimens examined. MARYLAND, Prince Georges Co.: Beltsville, VI-26-79 and VII-5-79, on *Spartina alterniflora* in greenhouse, W. Sweeney (3 paratypes on 3 sl.) USNM. The infestation originated from Buffalo Mountain, Virginia.

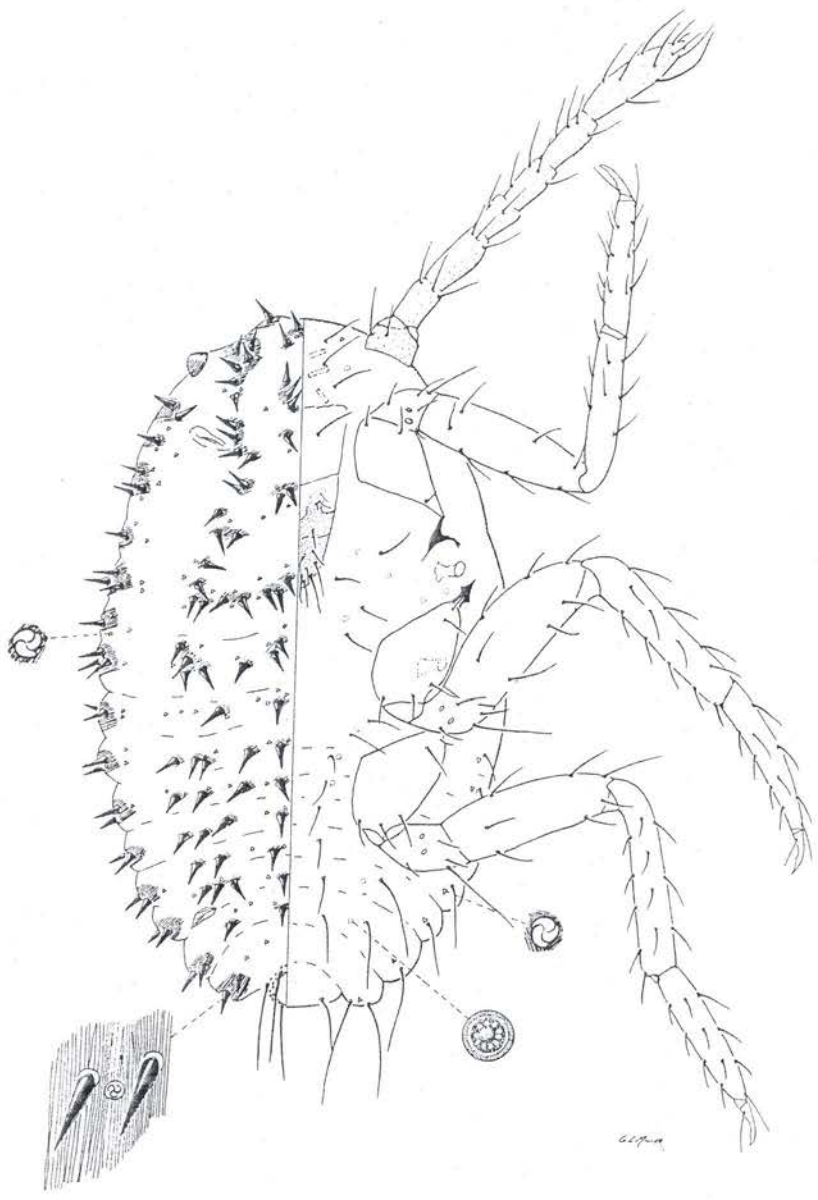


Fig. 7. First-instar of *P. kosztarabi*. Buffalo Mtn., Floyd Co., Virginia, VIII-4-1993, on *Danthonia spicata*.

Second-instar male
Figure 6

Slide-mounted characters: Same as adult female except as follows: Body length 2.4 (2.1-2.6) mm; width 1.2 (1.1-1.4) mm.

Dorsum: With 18 (18 or 19) pairs of cerarii; anal-lobe cerarius with 9 (7-10) setae and 19 (16-22) trilocular pores; frontal cerarius with 7 (6-8) conical setae and 4 (3-5) trilocular pores. Trilocular and discoidal pores less abundant than on adult female, of same distribution. Oral-collar tubular ducts of 2 sizes, small size scattered over surface, large size located near anterior cerarii on dorsal and ventral surfaces, with 2 (1-3) ducts on each side of head, 1 specimen with a single large duct between cerarius 1 and 2. Longest body seta on abdomen 33 (31-35) μm long; with 15 (13-18) setae on segment V, excluding those in cerarii.

Anal-ring seta 177 (172-183) μm long; 1.4 (1.3-1.5) times as long as greatest diameter of ring.

Venter with multilocular pores in anterior bands on all abdominal segments, sometimes with short posterior band on most anterior abdominal segments, with pores abundant on thorax and head. Trilocular pores of 2 sizes, restricted to sublateral areas of body. Discoidal pores less abundant than on adult female, scattered over surface. Oral-collar tubular ducts in rows across segments, also present on raised area on head anterior of mouthparts, with 17 (15-20) ducts. Ventral setae arranged in rows on abdomen, with 11 setae on segment V, longest seta on segment V 74 (70-81) μm long; longest anal-lobe seta 94 (81-102) μm long; longest seta on trochanter of hind leg 125 (119-131) μm long.

Circulus absent. Labium 150 (137-166) μm long. Posterior spiracle greatest length 92 (79-102) μm. Antennae 7-segmented, length of right antenna 696 (648-720) μm, apical segment 133 (128-143) μm, segment II 79 (73-84) μm, segment III 149 (137-163) μm; length of segment VII divided by length of segment II 1.7 (1.6-1.8), length of segment VII divided by length of segment III 0.9. Legs without translucent pores. Length of femur 295 (279-317) μm; tibia 383 (364-419) μm; tarsus 190 (186-198) μm. Tibia/tarsus 2.0 (2.0 or 2.1). Hind tarsus with 16 (16 or 17) setae.

Specimens examined. MARYLAND, Prince Georges Co.: Beltsville, VII-24-79 and VIII-17-79, on *Spartina alterniflora* in greenhouse, W. Sweeney (3 paratypes on 3 sl.) USNM. The infestation originated from Buffalo Mountain, Virginia.

First instar (sexes undetermined)
Figure 7

Slide-mounted characters: Same as adult female except as follows: Body length 1.2 (0.9-1.4) mm, width 0.7 (0.5-0.9) mm.

Dorsum: With 18 pairs of cerarii; anal-lobe cerarius with 2 conical setae; cerarii 2 through 8 each with 2 conical setae; cerarius 9 with 3; 10 with 1; 11 with 3; 12 with 1; 13 with 3; 14 with 1; 15 with 2; 16 with 6 (6 or 7); 17 with 1; 18 with 2. Trilocular pores associated with cerarii as follows: cerarius 1 with 3 pores; cerarius 2 with 3 pores; 3 with 3 (2 or 3); 4 and 5 with 2; 6 and 7 with 2 (2 or 3); 8 with 2; 9 with 2 (2 or 3); 10 with 2 (1 or 2); 11 with 3 (2 or 3); 12 with 2 (1 or 2); 13 with 3 (2 or 3); 14 with 1 (0 or 1); 15 with 3; 16 with 4 (3-6); 17 with 1 (1 or 2); and 18 with 1 (1 or 2). Trilocular pores arranged in 11 (9-13) longitudinal lines on abdomen. Body setae conical, with basal sclerotization, often with associated trilocular pores and coalesced with other dorsal setae, longest seta on abdomen 35 (32-38) μm long; with 7 (6-8) setae on segment V, excluding those in cerarii.

Anal-ring seta 47 (41-50) μm long; 1.6 (1.5-1.7) times as long as greatest diameter of ring.

Venter: With multilocular pores arranged in 2 longitudinal lines on mediolateral area of abdomen, slightly more numerous on thorax and head, mostly with 9 or 10 loculi. Trilocular pores of 2 sizes, smaller size in irregular rows across medial and mediolateral areas of each abdominal segment, larger size present near body margin, absent elsewhere. Discoidal pores associated with sublateral setae on anterior abdominal segments, thorax, and head, forming 2 longitudinal lines of pores. Oral-collar tubular ducts restricted to raised area on head anterior of mouthparts, with 3 or 4 (4) such ducts. Ventral setae arranged in rows on abdomen, with 6 setae on segment V, longest seta on segment V 59 (49-70) μm long; longest anal-lobe seta 99 (89-119) μm long; longest seta on trochanter of hind leg 81 (70-87) μm long.

Circulus absent. Labium 118 (111-128) μm long. Posterior spiracle greatest length 63 (55-70) μm long. Antennae 7-segmented, length of right antenna 454 (422-509) μm, apical segment 120 (116-128) μm, segment II 59 (58-61) μm, segment III 74 (67-84) μm; length of segment VII divided by length of segment II 2.1 (2.0-2.1), length of segment VII divided by length of segment 1.6 (1.5-1.8). Length of femur 179 (175-189) μm; tibia 212 (192-233) μm; tarsus 156 (148-163) μm. Tibia/tarsus 1.3 (1.3-1.4). Hind tarsus with 16 (15-16) setae.

Specimens examined. MARYLAND, Prince Georges Co.: Beltsville, VI-6-79 and VII-5-79, on *Spartina alterniflora* in greenhouse, W. Sweeney (3 paratypes on 3 sl.) USNM. The infestation originated from Buffalo Mountain, Virginia. VIRGINIA, Floyd Co.: Buffalo Mountain, VIII-4-92, on *Danthonia spicata*, M. Kosztarab (16 paratypes on 4 sl.) USNM.

Phylogenetic Analysis

A phylogenetic analysis of representatives of the *Puto* group and selected outgroups was undertaken to test the validity of the hypothesis that the family is monophyletic and to infer its relationships relative to other scale insect families. The genus *Puto* has been treated as part of the Pseudococcidae (Williams & de Willink, 1992) and as a separate family, the Putoidae (Beardsley, 1969). The correct placement of these scales is confounded because some have characteristics of both the *Puto* groups and pseudococcids. For example, the putoids *P. nulliporus* and *P. mimicus* have certain pseudococcid characters such as quinquelocular pores and two trochanter sensoria, whereas the pseudococcids *Phenacoccus dearnessi* King and *Phenacoccus helianthi* (Cockerell) have the *Puto* group characters such as cerarii with more than 6 conical setae. Because of this, it seemed possible that certain species of *Puto* and *Phenacoccus* are more closely related to one another than to other members of their respective families. This would provide evidence that the *Puto* groups are not monophyletic or they should encompass certain species of pseudococcids.

Characters. Character distributions for the 23 taxa are summarized in Table 1. Unknown characters were coded as missing data.

ADULT MALE

1. Aedeagus: (0) sclerotized, non-articulated, simple apex; (1) non-sclerotized, sac-like (endophallus); (2) sclerotized, articulated, bifurcate apex; (3) sclerotized, non-articulated, simple apex.
2. Ungual digitules: (0) capitate; (1) acute.
3. Scutellar ridge: (0) absent; (1) present.
4. Scutum: (0) solid, without median clear area; (a) with median rectangular clear area; (b) with triangular clear area.

5. Penial sheath: (0) not fused dorsolaterally; (1) fused dorsolaterally.
6. Genial setae: (0) absent; (1) present.
7. Penial sheath apex: (0) simple; (1) bilobed.
8. Penial sheath: (0) simple; (1) divided.
9. Ventral preocular ridge: (0) absent; (a) incomplete; (b) complete.
10. Tarsal digitules: (0) acute; (1) capitate.
11. Eyes: (0) 1 pair, multifaceted; (1) more than 2 pairs, simple; (2) 2 pairs, simple.
12. Ostioles: (0) absent; (1) present; (2) lost (present in first instar).
13. Dorsal abdominal duct cluster of abdominal segment 8: (0) single medial; (a) lateral; (b) absent.
14. Halter setae: (0) 3-4; (1) 2; (2) 1; (3) absent.
15. Leg setae associated with small basal seta: (0) absent; (1) present.
16. Wing microtrichia: (0) absent; (1) present.
17. Abdominal spiracles: (0) present; (1) absent.
18. Ventral plate: (0) present; (1) absent.
19. Preocular & postocular ridges: (0) absent; (1) separate; (2) fused.

ADULT FEMALE

20. Translucent pores on hind legs: (0) absent; (1) present.
21. Tubular ducts: (0) absent; (a) not invaginated; (b) invaginated.
22. Microtubular ducts: (0) absent; (1) present.
23. Cruciform pores: (0) absent; (1) present.
24. Abdominal spiracles: (0) present; (1) absent.
25. Trilocular pores: (0) absent; (1) present.
26. Ostioles: (0) absent; (1) present.
27. Anal ring: (0) absent from dermal surface; (1) present on dermal surface; (2) lost (present in first instar).
28. Medial circulus: (0) absent; (1) present; (2) lost (present in first instar).
29. Tarsal digitules: (0) acute; (1) knobbed; (2) lost (present in first instar).

30. Antennal segments: (0) 9 or more; (1) 8 or less.
31. Claw denticle: (0) absent; (1) present.
32. Trochanter sensoria on each surface: (0) more than 2; (1) 2.

FIRST INSTAR

33. Median longitudinal line of abdominal setae: (0) absent; (1) present.
34. Proximal marginal femoral seta: (0) absent; (1) present.
35. Ostioles: (0) absent; (1) present.
36. Simple disk pores: (0) absent; (1) present.
37. Spiraled trilocular pores: (0) absent; (1) present.
38. Antennal segments: (0) 6-segmented; (1) 7-segmented.

RESULTS AND DISCUSSION

Two equally parsimonious trees were found (length = 86, CI = 0.61, RI = 0.86). The two trees differed only in the placement of *Pityococcus ferrisi* McKenzie. In one tree, *P. ferrisi* was placed as the sister group of Stem 6 (Fig. 8). In the second tree, this species was placed as the sister group of Stem 5 (Fig. 8). We prefer the first tree since it is defined by the presence of ostioles and medial circuli. These are both complex characters that we cannot easily envision developing independently. However, this preference is a subjective decision.

Our subsequent discussion is based on the Nelson consensus tree shown in Fig. 8. This tree contains a trichotomy immediately above Stem 3. The consensus tree is preferred over the other two parsimonious trees because of the trichotomy of Stem 4 (*Pityococcus ferrisi*) + Stem 5 + Stem 6. We feel this best reflects the current unresolved placement of *Pityococcus ferrisi*. Characters justifying the monophyly of selected higher-level clades are presented below organized by the stem numbers given in Fig. 8. Bracketed numbers refer to the characters given above.

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

Stem 2. Adult male with: preocular ridge ventrally complete [9.b]; more than 2 pairs of eyes [11.1]; dorsolateral tail-forming pore clusters on segment 8 [13.a]; 2 halter setae [14.1]; preocular and postocular ridges separate [19.1]; anal ring present on dermal surface [27.1]; adult female

Character Number	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19	20 21 22 23 24 25 26 27 28 29 30 31 32	33 34 35 36 37 38
Margarodidae			
Matsucoccus bisetosus	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0
Steingelia gorodetskia	0 0 0 b 0 0 0 1 b 0 1 0 a 1 0 1 0 0 1	0 0 0 0 0 0 0 1 0 0 1 0 0	0 0 0 0 0 0
Pityococcus ferrisi	1 1 1 0 0 0 1 0 b 0 1 1 b 2 0 1 0 0 1	0 a 0 0 0 0 0 0 1 0 1 1 0	0 0 0 0 0 1
Phenacoleachidae			
Phenacoleachia zealandica	1 0 0 0 0 1 1 0 b 0 1 0 a 2 0 1 0 0 1	0 a 0 0 0 1 1 1 0 0 0 1 0	1 1 0 0 1 1
Pseudococcidae			
Phenacoccus dearnessi	0 1 0 0 0 1 0 1 a 1 2 2 a 2 0 1 1 1 1	1 a 0 0 1 1 1 1 1 0 0 1 1	1 1 1 1 1 0
Heterococcus raui	0 1 0 0 0 1 0 1 a 1 2 2 a 2 0 1 1 1 1	1 a 0 0 1 1 1 1 2 0 0 1 1	1 1 1 1 0 0
Brevennia rehi	0 1 0 0 0 1 0 0 a 1 2 1 a 2 0 1 1 1 2	1 a 0 0 1 1 1 1 2 0 1 0 1	1 1 1 1 1 0
Planococcus citri	0 1 0 0 0 1 0 0 a 1 2 1 a 2 0 1 1 1 2	1 a 0 0 1 1 1 1 1 1 1 0 1	1 1 1 1 1 0
Pseudococcus affinis	0 1 0 0 0 1 0 0 a 1 2 1 a 2 0 1 1 1 2	1 a 0 0 1 1 1 1 1 1 1 0 1	1 1 1 1 1 0
Puto kostarabi	3 1 0 b 0 1 0 0 b 0 1 1 a 0 1 1 1 1 1	1 a 0 0 1 1 1 1 2 0 0 1 0	1 1 1 1 1 1
Puto calcitectus	3 1 0 - 0 1 0 0 b 0 1 1 a 0 1 1 1 1 1	1 a 0 0 1 1 1 1 2 0 0 1 0	- - - - - -
Puto sandini	0 1 0 b 0 1 0 0 b 0 1 1 a 0 1 1 1 1 1	1 a 0 0 1 1 1 1 1 0 0 1 0	- - - - - -
Puto mexicanus	2 1 0 b 0 1 0 0 b 0 1 1 a 0 1 1 1 1 1	1 a 0 0 1 1 1 1 1 0 0 1 0	1 1 1 1 1 1
Puto yuccae	2 1 0 b 0 1 0 0 b 0 1 1 a 0 1 1 1 1 1	1 a 0 0 1 1 1 1 1 0 0 1 0	1 1 1 1 1 1
Eriococcidae			
Ovaticoccus agavium	0 0 1 0 1 1 0 0 a 1 2 0 a 3 0 1 1 1 1	1 b 1 1 1 0 0 1 0 1 1 1 1	1 0 0 0 0 0
Gossyparia spuria	0 0 1 0 1 1 0 0 a 1 2 0 a 2 0 1 1 1 1	0 b 1 1 1 0 0 1 0 1 1 1 1	1 0 0 0 0 0
Acanthococcus araucariae	0 0 1 0 1 1 0 0 a 1 2 0 a 2 0 1 1 1 1	1 b 1 1 1 0 0 1 0 1 1 1 1	1 0 0 0 0 0
Acanthococcus droserae	0 0 1 a 1 1 0 0 a 1 2 0 a 3 0 1 1 1 1	1 b 1 1 1 0 0 1 0 1 1 0 1	1 0 0 0 0 0
Stibococcus cerinus	0 0 1 0 1 1 0 0 a 1 2 0 a 3 0 1 1 1 1	1 b 1 1 1 0 0 1 0 1 1 1 1	1 0 0 0 0 0
Kermesidae			
Eriokermes gillettei	0 0 1 a 1 0 0 0 b 1 1 0 a 2 0 1 1 1 1	0 b 0 0 1 0 0 1 0 1 1 1 1	0 0 0 1 0 0
Kermes quercus	0 0 1 a 1 0 0 0 b 1 1 0 a 2 0 1 1 1 1	0 b 0 0 1 0 0 1 0 2 1 1 2	0 0 0 1 0 0
Kermes bytinskii	0 0 1 a 1 0 0 0 b 1 1 0 a 2 0 - 1 1 1	0 b 0 0 1 0 0 1 0 2 1 1 2	0 0 0 1 0 0
Kermes pubescens	0 0 1 a 1 0 0 0 b 1 1 0 a 2 0 1 1 1 1	0 b 0 0 1 0 0 2 0 2 1 1 2	0 0 0 1 0 0
	Adult ♂	Adult ♀	1st

Table 1. Character matrix for family taxa and outgroups used to generate cladogram in Fig. 8. Matrix symbols: 0, plesiomorphic state; 1, 2, 3, or a, b, apomorphic states; -, state unknown.

with: 8 or fewer antennal segments [30.1].

Stem 3. Adult male with: scutellar ridge present [3.1]; 1 halter seta [14.2]; adult female with: tubular ducts not invaginated [21.a]; claw denticle present [31.1].

Stem 4 (*Pityococcus ferrisi*). Adult male with: non-sclerotized, sac-like aedeagus [1.1]; acute ungual digitules [2.1]; apex of penial sheath bilobed [7.1]; ostioles present [12.1]; adult female with: medial circulus [28.1] (convergent in Pseudococcidae); first instar with: 7-segmented antennae [38.1] (convergent in *P. zealandica* and *Puto* group).

Stem 5. Adult male with: penial sheath fused dorsolaterally [5.1]; tarsal digitules capitate [10.1] (convergent in the non-*Puto* group clade); abdominal spiracles absent [17.1] (convergent Pseudococcidae); ventral plate absent [18.1] (convergent in Pseudococcidae); adult female with: tubular ducts invaginated [21.2]; abdominal spiracles absent [24.1] (convergent in Pseudococcidae); tarsal digitules capitate [29.1] (convergent in the clade *Pseudococcus affinis* + *Planococcus citri*); 2 trochanter sensoria on each surface [32.1] (convergent in the non-*Puto* group clade).

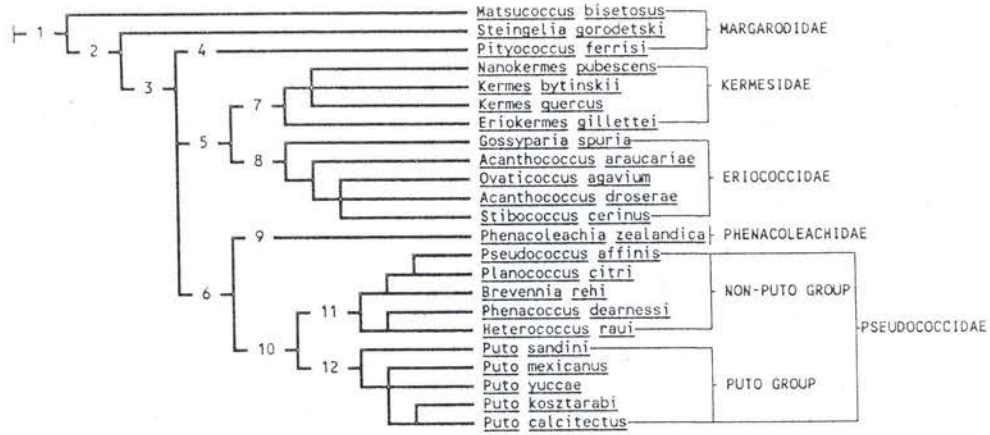
Stem 6. Adult male with: scutellar ridge absent [3.0, a reversal]; genial setae present [6.1] (convergent in Eriococcidae); adult female with: spiraled trilocular pores [25.1]; ostioles present [26.1]; 9 or more antennal [30.0, a reversal]; first instar with: median longitudinal line of abdominal setae [33.1] (convergent in Eriococcidae); proximal marginal femoral seta [34.1]; spiraled trilocular pores [37.1].

Stem 7 (Kermesidae). Adult male with: rectangular scutum [4.a] (convergent in *A. droserae*); first instar with: simple disk pores [36.1] (convergent in Pseudococcidae).

Stem 8 (Eriococcidae). Adult male with: genial setae present [6.1] (convergent in the clade *Phenacoleachia zealandica* [Maskell] + Pseudococcidae); preocular ridge incomplete [9.a] (convergent in the non-*Puto* group clade); 2 pairs of eyes [11.2] (convergent in the non-*Puto* group clade); adult female with: microtubular ducts [22.1]; cruciform pores [23.1]; first instar with: median longitudinal line of abdominal setae [33.1] (convergent in the clade *Phenacoleachia zealandica* + Pseudococcidae).

Stem 9 (*Phenacoleachia zealandica*). Adult male with: sclerotized aedeagus [1.1] (convergent in *Pityococcus ferrisi*); apex penial sheath bilobed [7.1] (convergent in *Pityococcus ferrisi*); first instar with: 7 segments [38.1] (convergent in *Pityococcus ferrisi* and the *Puto* group).

Stem 10 (Pseudococcidae). Adult male with: ungual digitules acute [2.1]



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; 27.0; 28.0; 29.0; 30.0; 31.0; 32.0; 33.0; 34.0; 35.0; 36.0; 37.0; 38.0.
Stem 2 9.b; 11.1; 13.b; 14.1; 19.1; 27.1; 30.1.
Stem 3 3.1; 14.2; 21.a; 31.1.
Stem 4 1.1; 2.1; 7.1; 12.1; 28.1; 38.1.
Stem 5 5.1; 10.1; 17.1; 18.1; 21.2; 24.1; 29.1; 32.1.
Stem 6 3.0; 6.1; 25.1; 26.1; 30.0;33.1; 34.1; 37.1.
Stem 7 4.a; 36.1.
Stem 8 6.1; 9.a; 11.2; 22.1; 23.1; 33.1;
Stem 9 1.1; 7.1; 38.1.
Stem 10 2.1; 12.1; 17.1; 18.1; 20.1; 24.1; 28.1; 35.1; 36.1.
Stem 11 9.a; 10.1; 11.2; 32.1.
Stem 12 4.b; 14.0; 15.1; 38.1.

Fig. 8. Taxon cladogram determined using Hennig86.

(convergent in *Pityococcus ferrisi*); ostioles [12.1]; abdominal spiracles absent [17.1]; ventral plate absent [18.1] (convergent in the clade Kermesidae + Eriococcidae); adult female with: translucent pores on hind legs [20.1] (convergent in *Ovaticoccus agavium* [Douglas], *Acanthococcus araucariae* [Maskell], *Acanthococcus droserae* Miller, Liu, & Howell, and *Stibococcus cerinus* Miller & Gonzalez); abdominal spiracles absent [24.1] (convergent in the clade Kermesidae + Eriococcidae); medial circulus [28.1] (convergent in *Pityococcus ferrisi*); first instar with: ostioles [35.1]; simple disk pores [36.1].

Stem 11. Adult male with: incomplete preocular ridge [9.a] (convergent in Eriococcidae); capitate tarsal digitules [10.1] (convergent in the clade Kermesidae + Eriococcidae); 2 pairs of eyes [11.2] (convergent in Eriococcidae); adult female with: 2 trochanter sensoria on each surface [32.1] (convergent in the clade Kermesidae + Eriococcidae).

Stem 12 (*Puto* group). Adult male with: triangular scutum [4.b] (convergent in *Steingelia gorodetskia*); 3-4 halter setae [14.0, a reversal]; leg setae associated with small basal seta [15.1]; first instar with: 7-segmented antennae [38.1] (convergent in *Pityococcus ferrisi* and *Phenacoleachia zealandica*).

CONCLUSIONS

The *Puto* group could be treated either as a separate family or as part of the Pseudococcidae. Our preference is for the inclusion of this group as part of the mealybugs since the only non-homoplasious character that defines the group is the presence of associated basal setae with the larger leg setae on the adult males. Although this is unique to *Puto*, *Phenacoleachia* males have similar setae on the antennae.

Our analysis confirms the problematic placement of *Steingelia* and *Pityococcus*. The presence of spiraled trilocular pores, circuli, and ostioles suggested placement of *Pityococcus* in the Pseudococcidae (Miller, 1983). However, this affinity is not borne out in the current study. In addition, *Steingelia*, which has pseudococcid-like genitalia and lateral tail-forming pore clusters in the adult male, is also placed separately from the mealybugs. Because we did not include a detailed analysis of the Margarodidae and because these groups are purported to belong to this family, we will not make any classification changes until a more detailed analysis can be completed.

The relationships of the pseudococcids, eriococcids, and kermesids is

puzzling. The present analysis includes kermesids and eriococcids as sister groups, but in a previous study (Miller & Miller, in press) the pseudococcids and eriococcids were hypothesized as sister groups. In the present paper, we included additional taxa and characters. Eight characters support the monophyli of the eriococcids and kermesids. Unfortunately, only two of these are non-homoplasious, and the majority of the homoplasy is in the form of convergences shared with the pseudococcid clade or the pseudococcid + the *Puto* group clade. We favor the results presented here since a complete penial sheath and invaginated tubular ducts are complicated structures unlikely to have developed independently, but this aspect of the phylogeny requires additional study.

This work treats the adult males of more congeneric species than in any previous Coccoidea research. In the process of our examination, we studied adult males of 17 species of *Puto* including more than 50 specimens. Because many species are represented by only one or two specimens, the results must be considered preliminary, but several conclusions merit special attention. There are two distinct groups of species within the genus: the first group (*Puto antennatus*, *P. cupressi*, *P. sandini*, and *P. superbus*) occurs on conifers and has a short, non-articulated aedeagus with a blunt apex similar to other pseudococcids; the other group (*Puto albicans*, *P. ambiguus*, *P. antioquensis*, *P. arctostaphyli*, *P. atriplicis*, *P. calcitectus*, *P. decorosus*, *P. echinatus*, *P. kosztarabi*, *P. mexicanus*, *P. simmondsiae*, *P. ulter*, and *P. yuccae*) occurs on other hosts and has a long, articulated aedeagus with a bifurcate tip. The opinion of Williams & de Willink (1992) that *Macrocerococcus* and *Puto* are synonyms is supported in this paper. However, if the conifer-infesting group were considered a separate genus, its generic name would be *Macrocerococcus*. We predict that other conifer-infesting species such as *P. laticribellum*, *P. pricei*, and *P. profusus* also will have males with a non-articulated aedeagus and a blunt apex.

The species *P. kosztarabi* and *P. calcitectus* have males with two teeth that are removed from the apex of the aedeagus. The remaining species of *Puto* occurring on non-conifer hosts have a series of teeth on the apex of the aedeagus. Based on similarities of the females of *P. kosztarabi*, *P. calcitectus*, and *P. acirculus* (presence of clusters of dorsal setae with basal sclerotization), we predict the male of *P. acirculus* will have two teeth that are slightly removed from the apex of the aedeagus.

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