



Three new species of *Puto* giant mealybugs (Hemiptera: Coccoomorpha: Putoidae) from Mexico and Guatemala, with keys to New World adult females and World adult males

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Abstract

Three new species of *Puto* Signoret, 1876 are described and illustrated from material intercepted at US plant quarantine inspection, including the adult females, all available immature stages, and for two species, the adult male. *Puto philo* Powell & Miller, **sp. n.** and *Puto brom* Powell & Miller, **sp. n.** are described from Mexico, and *Puto spath* Powell & Miller, **sp. n.** is described from Guatemala. Three keys are included to: the instars of *Puto*, the New World species of *Puto* based on adult females, and a world key to the adult males of *Puto*.

Key words: Sternorrhyncha, Coccoidea, scale insects, taxonomy, quarantine, regulatory

Introduction

The genus *Puto* Signoret, 1876 currently includes 46 extant species: 24 Nearctic, 6 Neotropical, two Oriental, 14 Palearctic, and two Eocene fossil species from Baltic amber (García Morales *et al.* 2016). Species of *Puto* occur on a wide array of hosts including representatives of 71 plant families and are most abundant on Asteraceae (11 species), Pinaceae (9), Ericaceae (8), Poaceae (7), Amaranthaceae (6), and Fabaceae (6) (García Morales *et al.* 2016). Most species of giant mealybug are known from one or two host-plant families (33) but 10 are more polyphagous, occurring on three to 26 families; *Puto barberi* (Cockerell, 1895) and *P. superbus* (Leonardi, 1907) have been collected on the greatest range of host families (García Morales *et al.* 2016).

Puto was placed in the Pseudococcidae for nearly 100 years (McKenzie 1967; Williams *et al.* 2011), but recent evidence supports its placement in a separate family, the Putoidae (Downie & Gullan 2004; Hardy *et al.* 2008; Veá & Grimaldi 2016; Williams *et al.* 2011; Choi and Lee 2022). There has been contention surrounding the status of the Putoidae as a family distinct from the Pseudococcidae given a lack of apomorphic character states; *Ceroputo* is treated by some authors as a subgenus of *Puto* in the Pseudococcidae (Gavrilov-Zimin & Danzig 2012; Danzig & Gavrilov-Zimin 2014). However, there are many derived character states that support a separate Putoidae lineage including molecular data and morphological features of the first-instar nymphs, adult males, adult females, and their endosymbionts (Downie & Gullan 2004; Hodgson & Foldi 2006; Hardy *et al.* 2008; Williams *et al.* 2011; Hodgson & Hardy 2013; Hodgson 2014; Veá & Grimaldi 2016; Choi & Lee 2022). Given the current evidence, we continue to recognize Putoidae as a valid family.

Here we describe three new species of giant mealybug taken in quarantine at borders of the United States. Between 1952 and 1956, several shipments of *Philodendron* Schott and *Monstera* Adans. were intercepted in Texas from Mexico with giant mealybugs infesting the leaves. In 1974, two adult females of a giant mealybug on a bromeliad from Mexico were taken in quarantine and in the following year, a single collection was made of a male on the same host. Similarly, in 1976, shipments of *Spathiphyllum* Schott (peace lilies) infested with giant mealybugs were repeatedly intercepted in Texas from Guatemala. On these plants were three undescribed species of *Puto*, each recognized at the

time as new. To our knowledge, none of these species have ever become established in the United States, probably owing to the increased domestic cultivation of these ornamentals and increased regulatory efforts at ports of entry.

The objective of this paper is to describe these species based on the adult females and available adult males and immature instars, to provide keys to the instars of *Puto*, to all species of the New World based on adult females, and to the world species of adult males of *Puto* where they are described or available in collections.

Materials and methods

Measurements and counts are taken from five specimens for each instar, when available. Morphological terminology used for females and immatures follows McKenzie (1967), Miller (1991), and Williams *et al.* (2011). The morphological terminology used for adult males follows Afifi (1968) and Hodgson & Foldi (2006); terminology for the wing venation follows Wu & Xu (2022). Past authors have used different terminology inconsistently to describe the dorsal oral-rim type tubular ducts in *Puto*. McKenzie (1967) and Miller & Miller (1993) used “oral-rim type tubular ducts”; Danzig & Gavrillov-Zimin (2014) used “large tubular ducts”; Williams & Granara de Willink (1992) used “enlarged tubular ducts”; and Williams *et al.* (2011) used “wide ducts”. Herein, we use the term oral-rim type tubular ducts to describe the ducts in the cerarii and over the dorsum following McKenzie (1967). We define the antefrontal cerarii as the submarginal area(s), sometimes sclerotized, beset with conical setae, and often associated trilocular pores, mediolateral or posterior to the frontal cerarius: that is, any extra cerarii mesad to the frontal cerarius (see Fig. 1). The frontal cerarius is defined as the cerarius mediolateral to the preocular cerarius, following Williams (2004).

For the key to adult males, the key in Miller & Miller (1993) was modified and all new available material was examined from the United States National Museum (USNM) in Beltsville, Maryland.

Illustration procedures, specimen depositories, plant names, and abbreviations of adult male structures follow Miller & Stocks (2022). Measurements were made using a Zeiss Axio Imager.M2 using ZEN 3.7 Pro software, and illustrations were made with a Leica DMRB compound light microscope with 10x, 20x, 40x, and 100x objectives. Male wing photographs were acquired and stitched with a Zeiss Axio Imager.M2 using ZEN 3.7 Pro software with a 20x objective, stacked with Helicon Focus 8.2.2, and edited in Adobe PhotoShop 25.3.1.

Under “Material examined”, holotype collection data is listed using ‘/’ to indicate the positions of the line breaks on the labels.

Specimen depositories

FSCA—Florida State Collection of Arthropods, Gainesville, Florida, U.S.A.

NHM—Natural History Museum, London, U.K.

UCD—University of California, Davis, California, U.S.A.

USNM—United States National Museum, Beltsville, Maryland, U.S.A.

Key to the instars of all described *Puto* species

1(0)	Without wings or wing pads	2
-	With wings or wing pads	6
2(1)	Anal-lobe cerarius containing more than 2 conical setae	3
-	Anal-lobe cerarius containing 2 conical setae	First-instar nymph
3(2)	Antenna 7-segmented, rarely 8-segmented; translucent pores absent	4
-	Antenna 8- or 9-segmented; hind tibia usually with translucent pores	5
4(3)	Dorsal surface outside of cerarii with oral-collar tubular ducts	Second-instar male
-	Dorsal surface outside of cerarii without oral-collar tubular ducts	Second-instar female
5(3)	Vulva present; antenna 9- (rarely 8) segmented; trochanter with 3 or 4 campaniform sensilla on each surface	Adult female
-	Vulva absent; antenna 8-segmented; trochanter with 2 campaniform sensilla on each surface	Third-instar female
6(1)	Wings well developed; genital capsule with sclerotized aedeagus	Adult male
-	Wings in form of pads; genital capsule without sclerotized aedeagus	7
7(6)	Lateral margins of abdominal segments without sclerotized projections; dorsal oral-collar tubular ducts present	Third-instar male (pre-pupa)

- Lateral margins of abdominal segments with some sclerotized projections; dorsal oral-collar tubular ducts absent Fourth-instar male (pupa)

Key to adult females of *Puto* from the New World (revised from McKenzie 1967)

Note: *Puto orthezooides* (Cockerell, 1903) is known only from a third-instar female and is not included in the key.

1(0)	Circulus complete, without constriction or division, or circulus absent	2
-	Circulus partially or completely divided into two parts	27
2(1)	Circulus absent	3
-	Circulus present	4
3(2)	Ostioles without conical setae on lips; anal-lobe cerarius usually with fewer than 30 cerarian setae	<i>Puto kosztarabi</i> Miller & Miller, 1993 (in part)
-	Ostioles with conical setae on lips; anal-lobe cerarius usually with more than 30 cerarian setae	<i>Puto acirculus</i> McKenzie, 1960
4(2)	Cerarii without oral-rim type tubular ducts in sclerotized area	5
-	Cerarii with oral-rim type tubular ducts in sclerotized area (beware of dorsal oral-rim type tubular ducts adjacent to, but not in, sclerotized area)	16
5(4)	Circulus oval or circular, approximately as wide as long, less than three times as wide as long, often with smooth margin	6
-	Circulus laterally expanded, often three times as wide as long, usually with crenulate margin	7
6(5)	Medial or mediolateral areas with oral-rim type tubular ducts	<i>Puto pacificus</i> McKenzie, 1967 (in part)
-	Medial or mediolateral areas without oral-rim type tubular ducts	<i>Puto bryanthi</i> Ferris, 1950
7(5)	Twenty-five or more conical setae in each anal-lobe cerarius	8
-	Less than 25 conical setae in each anal-lobe cerarius	9
8(7)	Abdomen without ventral submarginal multilocular pores	40
-	Abdomen with ventral submarginal multilocular pores	<i>Puto barberi</i> (Cockerell, 1895) (in part)
9(7)	More than five multilocular pores in area between meso- and metacoxa	10
-	Fewer than five multilocular pores in area between meso- and metacoxa	13
10(9)	Abdominal segment VI with multilocular pores near anterior margin	11
-	Abdominal segment VI without multilocular pores near anterior margin	<i>Puto atriplicis</i> McKenzie, 1961
11(10)	Ostioles with setae on lips	12
-	Ostioles without setae on lips	<i>Puto kosztarabi</i> Miller & Miller, 1993 (in part)
12(11)	Anal ring with six setae, setae with acute apices; abdominal segment VII without multilocular pores near anterior margin	<i>Puto calcitectus</i> (Cockerell, 1901)
-	Anal ring with more than six setae, setae with conspicuously capitate apices; abdominal segment VII with multilocular pores near anterior margin	<i>Puto decorosus</i> McKenzie, 1967 (in part)
13(9)	Ventral multilocular pores on most abdominal segments	14
-	Ventral multilocular pores restricted to abdominal segments VII and VIII	<i>Puto profusus</i> McKenzie, 1967
14(13)	Anal-lobe cerarii each with fewer than 16 conical setae; apices of anal-ring setae acute	15
-	Anal-lobe cerarii each with 16 or more conical setae; apices of anal-ring setae sometimes slightly enlarged	<i>Puto californicus</i> McKenzie, 1967 (in part)
15(14)	Multilocular pores scattered on thorax and head; length of antennae longer than 1.1 mm	<i>Puto pricei</i> McKenzie, 1960
-	Multilocular pores on thorax restricted to around spiracles; length of antennae shorter than 1.1mm	<i>Puto sandini</i> Washburn, 1965
16(4)	Medial or mediolateral areas of dorsum with oral rim-type tubular ducts	17
-	Medial or mediolateral areas of dorsum without oral-rim type tubular ducts	22
17(16)	Venter of thorax with multilocular pores abundant, with more than five in area between meso- and metacoxa	18
-	Venter of thorax with multilocular pores sparse or absent, with five or less in area between meso- and metacoxa	37
18(17)	Cerarii on head without associated oral-rim type tubular ducts	19
-	Cerarii on head with associated oral-rim type tubular ducts	20
19(18)	With multilocular pores scattered around each spiracle; without ventral multilocular pores on margins of anterior abdominal segments	<i>Puto cupressi</i> (Coleman, 1908)
-	With conspicuous cluster of multilocular pores around each spiracle; with numerous multilocular pores on margins of anterior abdominal segments	<i>Puto laticribellum</i> McKenzie, 1961 (in part)
20(18)	Without clusters of oral-rim type tubular ducts surrounding cerarii	21
-	With clusters of oral-rim type tubular ducts surrounding cerarii	<i>Puto salinasi</i> Foldi & Kozár, 2006
21(20)	With fewer than 25 oral-rim type tubular ducts on dorsum excluding those in cerarii	<i>Puto echinatus</i> McKenzie, 1961 (in part) (San Miguel (in part), Santa Cruz, and San Nicholas Islands, winged male)
-	With more than 25 oral-rim type tubular ducts on dorsum excluding those in cerarii	<i>Puto echinatus</i> McKenzie 1961 (in part) (inland mainland, winged male)
22(16)	Cerarii on head each with oral-rim type tubular ducts in sclerotization	23

-	Cerarii on head each without oral-rim type tubular ducts in sclerotization	38
23(22)	Multilocular pores present in submarginal areas of abdominal segments III–VI	24
-	Multilocular pores absent from submarginal areas of abdominal segments III–VI	26
24(23)	Anal-lobe cerarii each smaller than hind coxae	25
-	Anal-lobe cerarii each larger or equal in size to hind coxae	<i>Puto arctostaphyli</i> Ferris, 1950
25(24)	Anal-lobe cerarii each with fewer than eight oral-rim type tubular ducts; tubular ducts in anal-lobe cerarii each about same diameter as setal socket of largest conical seta	39
-	Anal-lobe cerarii each with eight or more oral-rim type tubular ducts; tubular ducts in anal-lobe cerarii each twice as large as diameter of setal socket of largest conical seta	<i>Puto brom</i> Powell & Miller, sp. n.
26(23)	Anal-lobe cerarii each normally with more than five oral-rim type tubular ducts	<i>Puto mexicanus</i> (Cockerell, 1893)
-	Anal-lobe cerarii each normally with fewer than five oral-rim type tubular ducts	<i>Puto yuccae</i> (Coquillett, 1890)
27(1)	Oral-rim type tubular ducts present within confines of sclerotization of cerarii	28
-	Oral-rim type tubular ducts absent from within confines of sclerotization of cerarii	30
28(27)	Circulus with constriction but not divided into two pieces	29
-	Circulus divided into two pieces	<i>Puto antioquiensis</i> (Murillo, 1931)
29(28)	Claw and tarsal digitules acute; claw digitules not reaching tip of claw	<i>Puto usingeri</i> McKenzie, 1962
-	Claw and tarsal digitules clubbed; claw digitules extending beyond tip of claw	<i>Puto ulter</i> Ferris, 1950 (in part)
30(27)	Circulus divided into two or more pieces	31
-	Circulus with constriction but not divided into two pieces	36
31(30)	Claw denticle present	32
-	Claw denticle absent	35
32(31)	Circulus on abdominal segment III only; ventral multilocular pores scattered over entire surface	33
-	Circuli on abdominal segments III and IV; ventral multilocular pores restricted to abdomen and near spiracles	<i>Puto lamottei</i> Matile-Ferrero, 1985
33(32)	Ostioles each poorly developed or absent, lips with few or no conical setae	34
-	Ostioles each well developed, lips with numerous conical setae	<i>Puto spath</i> Powell & Miller, sp. n.
34(33)	Tarsal and claw digitules apically enlarged	<i>Puto bicirculatus</i> Gavrilov-Zimin, 2023
-	Tarsal and claw digitules apically acute	<i>Puto kosztarabi</i> Miller & Miller, 1993 (in part)
35(31)	Area between meso- and metacoxa with multilocular pores rare or absent	<i>Puto philo</i> Powell & Miller, sp. n.
-	Area between meso- and metacoxa with multilocular pores abundant	<i>Puto paramoensis</i> Matile-Ferrero, 1985
36(30)	Tarsal digitules simple; body margin on anterior abdominal segments with multilocular pores; usually with 17 pairs of cerarii, frontal cerarius usually comprising fusion of frontal and antefrontal cerarii	<i>Puto barberi</i> (Cockerell, 1895) (in part)
-	Tarsal digitules clubbed; body margin on anterior abdominal segments and thorax with multilocular pores absent; usually with 18 pairs of cerarii, frontal cerarii and antefrontal cerarii separate	<i>Puto ulter</i> Ferris, 1950 (in part)
37(17)	Ventral abdominal segment VII with posterior row of multilocular pores only	<i>Puto simmondsiae</i> McKenzie, 1961
-	Ventral abdominal segment VII with anterior and posterior rows of multilocular pores	<i>Puto echinatus</i> McKenzie, 1961 (in part) (coastal, with associated wingless male; inland mainland, with associated winged male; San Miguel (in part) and Santa Barbara Islands, with associated winged male)
38(22)	Submarginal areas of abdomen with multilocular pores abundant; anal-ring setae apically acute; occurring in mountainous areas on conifers	<i>Puto laticribellum</i> McKenzie, 1961 (in part)
-	Submarginal areas of abdomen with multilocular pores absent or sparse; anal-ring setae apically enlarged; occurring in salt marshes on <i>Sarcocornia</i>	<i>Puto ambiguus</i> (Fullaway, 1910) (in part)
39(25)	Submarginal area of thorax and head with multilocular pores sparse or absent; dorsomedial setae on posterior abdominal segment VII with basal sclerotization	<i>Puto lasiorum</i> (Cockerell, 1901)
-	Submarginal area of thorax and head with multilocular pores abundant; dorsomedial setae on abdominal segment VII without basal sclerotization	<i>Puto albicans</i> McKenzie, 1967
40(8)	Anal ring with three pairs of setae	41
-	Anal ring with more than three pairs of setae	<i>Puto decorosus</i> McKenzie, 1967 (in part)
41(40)	Area between meso- and metacoxa with 5 or more multilocular pores	<i>Puto ambiguus</i> (Fullaway, 1910) (in part)
-	Area between meso- and metacoxa with less than 5 multilocular pores	<i>Puto californicus</i> McKenzie, 1967 (in part)

Key to species of *Puto* based on adult males (modified from Miller & Miller 1993)

Notes: We were not able to find characters to distinguish the adult males of *Puto yuccae* from the winged *Puto echinatus* from the California Channel Islands or the inland areas of the western US and Mexico. *Puto echinatus* from coastal California, as described, is associated only with a wingless male but populations on the California Channel Islands and in inland areas of the western USA and Mexico have only been found with associated winged males; see “Discussion” for more information on the taxonomic issues surrounding *Puto echinatus*.

1(0)	With fully developed wings	2
-	Without wings or brachypterous	21

2(1)	Aedeagus acute or bifurcate apically.	3
-	Aedeagus blunt apically	14
3(2)	Denticle on claw present	4
-	Denticle on claw absent. <i>Puto philo</i> Powell & Miller, sp. n.	5
4(3)	Tarsal digitules simple, not enlarged.	5
-	Tarsal digitules enlarged <i>Puto ulter</i> Ferris, 1950	6
5(4)	Antennal segment II with several elongate setae with basal satellite setae	6
-	Antennal segment II without elongate setae with basal satellite setae <i>Puto atriplicis</i> McKenzie, 1961	7
6(5)	Multilocular pores absent or with eight or fewer total in medial and mediolateral areas of ventral abdominal segments III–VII	7
-	Multilocular pores present and with more than eight total in medial and mediolateral areas of ventral abdominal segments III–VII	16
7(6)	Longest seta on antennal segment IX less than 400 µm long	8
-	Longest seta on antennal segment IX greater than 400 µm long. <i>Puto antioquiensis</i> (Murillo, 1931)	9
8(7)	Aedeagus apex without teeth; aedeagus with teeth proximally from apex	9
-	Aedeagus apex with teeth; aedeagus without teeth proximally from apex.	10
9(8)	Each side of unsclerotized area anterior to ocular sclerite and preocular ridge with 10 or more multilocular pores	10
-	Each side of unsclerotized area anterior to ocular sclerite and preocular ridge with 6 or fewer multilocular pores	11
10(8)	Head with fewer than 20 multilocular pores.	11
-	Head with more than 20 multilocular pores. <i>Puto decorosus</i> McKenzie, 1967 (part)	12
11(10)	Tegulae each with fewer than 15 setae	12
-	Tegulae each with more than 15 setae.	13
12(11)	Longest seta on antennal segment IX less than 270 µm long	13
-	Longest seta on antennal segment IX more than 270 µm long. <i>Puto yuccae</i> (Coquillett, 1890); <i>Puto echinatus</i> McKenzie, 1961 (in part) (California Channel Islands)	14
13(11)	Glandular pouches each with less than 200 pores. <i>Puto simmondsiae</i> McKenzie, 1961	14
-	Glandular pouches each with more than 200 pores. <i>Puto brom</i> Powell & Miller, sp. n.	15
14(2)	Antennal segment III less than 350 µm long; six or seven (normally six) eyes on each side of head plus one ocellus	15
-	Antennal segment III more than 350 µm long; seven eyes on each side of head plus one ocellus	16
15(14)	Head (anterior to preocular ridge) with fewer than 5 multilocular pores <i>Puto cupressi</i> (Coleman, 1908)	16
-	Head (anterior to preocular ridge) with more than 5 multilocular pores. <i>Puto sandini</i> Washburn, 1965	17
16(6)	Glandular pouches each with fewer than 350 pores; diameter of each cluster less than 300 µm.	17
-	Glandular pouches each with more than 350 pores; diameter of each cluster more than 300 µm	18
17(16)	Multilocular pores in glandular pouches each with 4 or 5 loculi	18
-	Multilocular pores in glandular pouches each with 6 loculi, rarely 5. <i>Puto huangshanensis</i> Wu, 2001	19
(18)(17)	Antennal segment III less than 400 µm long	19
-	Antennal segment III greater than 400 µm long. <i>Puto arctostaphyli</i> Ferris, 1950	20
19(18)	Tegulae each with less than 12 setae, less than 6 ventral multilocular pores on head (anterior to preocular ridge).	20
-	Tegulae each with more than 12 setae, more than 6 ventral multilocular pores on head (anterior to preocular ridge).	21
20(19)	Body densely setose, medial and mediolateral area of abdominal segment III with more than 40 ventral setae	21
-	Body not conspicuously setose, medial and mediolateral area of abdominal segment III with fewer than 40 ventral setae	22
21(1)	6 or 7 eyes on each side of head; aedeagus apically acute or bifurcate	22
-	4 eyes on each side of head; aedeagus blunt apically. <i>Puto superbus</i> (Leonardi, 1907)	23
22(21)	Antennae each 10-segmented <i>Puto echinatus</i> McKenzie, 1961 (coastal California)	23
-	Antennae each 9-segmented <i>Puto ambiguus</i> (Fullaway, 1910)	24

Puto philo Powell & Miller, **sp. n.**

Suggested common name: philodendron giant mealybug

Material examined

Holotype adult ♀, second specimen from left of four specimens when examining slide with naked eye. Left label: “*Puto* / 521475 / On *Monstera* / Mexico: at Laredo / Sept. 18, 1952 / Leary, Cary Fouts / Laredo 53226.” Right label gives map of holotype position and states “*Puto philo* / Powell & Miller / n.sp.” Holotype slide (USNM) also contains 1 ad. ♀, 1 third-instar ♀, 1 second-instar ♂ (repeated below).

Paratypes: MEXICO: taken in quarantine at Brownsville, Texas, XI-7-1955, on *Philodendron* sp., collector?, 56955 (2 ad. ♀♀ together on 1 slide) NHM; taken in quarantine at Brownsville, Texas, VII-2-1956, on *Philodendron* sp., Heinrich and Allen, 561098 (1 third-instar ♀ on 1 slide) USNM; taken in quarantine at Brownsville, Texas, VIII-14-1956, on *Philodendron* cuttings, collector?, 561108 (1 second-instar ♂ on 1 slide) USNM; taken in quarantine at Brownsville, Texas, IX-19-1956, on *Philodendron* seedlings, collector?, 561197 (3 third-instar ♀♀, 5 second-instar ♂♂, 1 first-instar nymph together on 1 slide) USNM; taken in quarantine at Laredo, Texas, V-13-1952, on *Philodendron* sp., Cary and Fouts, 52809 (1 second-instar ♂, 2 first-instar nymphs together on 1 slide) USNM; taken in quarantine at Laredo, Texas, VI-26-1952, on *Philodendron* sp., Cary and Fouts, 521001 (1 ad. ♀, 2 second-instar ♀♀, 2 second-instar ♂♂, 2 first-instar nymphs together on 1 slide) FSCA; taken in quarantine at Laredo, Texas, VII-29-1952, on *Philodendron* sp., Lewis and Fouts, 521147 (2 second-instar ♀♀, 2 second-instar ♂♂, 3 first-instar nymphs together on 1 slide) USNM; taken in quarantine at Laredo, Texas, VIII-15-1952, on *Philodendron* sp., Cary and Fouts, 521153 (1 ad. ♀ on 1 slide) UCD; taken in quarantine at Laredo, Texas, VIII-26-1952, on *Philodendron* sp., Cary, Weedmark and Fouts, 521447 (1 ad. ♀, 3 second-instar ♂♂ together on 1 slide) USNM; taken in quarantine at Laredo, Texas, VIII-30-1952, on *Philodendron* sp., Ragsdale and Fouts, 521446 (1 second-instar ♀, 3 second-instar ♂♂, together on 1 slide) USNM; taken in quarantine at Laredo, Texas, IX-12-1952, on *Monstera* sp., Cary and Heinrich, 521445 (2 ad. ♂♂, 5 second-instar ♂♂, 1 second-instar ♀ on 2 slides) USNM; taken in quarantine at Laredo, Texas, X-7-1952, on *Philodendron* sp., Watt, Fouts, Babb, and Ostrem, 521579 (1 ad. ♀, 1 third-instar ♀, 2 second-instar ♂♂ together on 1 slide) FSCA; taken in quarantine at Laredo, Texas, XI-6-1952, on *Philodendron* sp., Leary, Lewis and Fouts, 521648 (5 second-instar ♂♂, 1 first-instar nymph together on 1 slide) USNM; taken in quarantine at Laredo, Texas, IX-18-1952, on *Monstera*, Leary, Cary and Fouts, 521475 (1 ad. ♀ holotype, 1 third-instar ♀ and 1 second-instar ♂ on one slide, second slide containing 1 ad. ♀ paratype and 1 second-instar ♂) both USNM; taken in quarantine at Laredo, Texas, I-12-1953, on “*Monstera canes*”, Danos and Fouts, 530415 (1 ad. ♂ on 1 slide) FSCA; taken in quarantine at Laredo, Texas, I-12-1953, on *Monstera canes*, Danos and Fouts, 530416 (2 second-instar ♂♂, together on 1 slide) USNM; taken in quarantine at Laredo, Texas, III-3-1953, on *Philodendron* sp., Cary and Fouts, 530612 (2 ad. ♀♀ together on 1 slide) USNM. Vera Cruz, XII-16-1952, on *Philodendron* sp., Lewis and Averill, 530437 (1 ad. ♀ on 1 slide) USMN.

Etymology: The species epithet “*philo*” is a noun in apposition based on an abbreviation of the scientific name of the host plant genus, *Philodendron*.

Adult female

(Fig. 1)

Description: Slide-mounted holotype 2.49 mm long, 1.56 mm wide; paratypes 2.55–4.83 mm long, 1.78–3.34 mm wide; body elongate oval.

Dorsum with 16 pairs of cerarii; anal-lobe cerarii each containing 11 lanceolate setae (paratypes 10–12) and 23 trilocular pores (paratypes 19–25); frontal cerarii each containing 15 lanceolate setae (paratypes 9–13) and 15 trilocular pores (paratypes 9–12); antefrontal cerarii not distinct, each containing 5–9 loosely clustered setae, without basal sclerotization; cerarii without associated discoidal pores or oral-rim type tubular ducts; and marginal cerarii with basal sclerotization. Anterior and posterior ostioles present. Multilocular disc-pores absent; trilocular pores of 1 size, numerous, scattered over body and present on lips of ostioles; discoidal pores scattered over body. Oral-rim type tubular ducts and oral-collar tubular ducts absent. Dorsal setae lanceolate, without basal sclerotization, forming rows across abdominal segments II–VII, clustered on lips of ostioles and scattered on head and thorax, with many on margin between cerarii especially on head and thorax, absent from medial area of abdominal segment VIII; longest seta on abdomen 21 µm (paratypes 21–25 µm) long, longest seta in abdominal cerarii 31 µm (paratypes 27–33 µm) long.

Anal ring dorsal, bearing 6 anal-ring setae with acute apices; posterior anal-ring setae each about 201 µm long (paratypes 207–217 µm); 1.3 times (paratype 1.5–1.6 times) as long as greatest diameter of anal ring.

Venter with multilocular disc-pores in posterior areas of abdominal segments IV–VIII, in anterior areas of segments V–VIII, sparse on segment IV, those on abdomen present medially and submedially, sparse or absent on margin; also present on medial areas of head near mouthparts; multilocular disc-pores on abdomen predominantly each 9-locular, with some 10-locular, those on head 7-locular. Trilocular pores of 1 size, numerous, scattered over body; discoidal pores scattered over body. Oral-collar tubular ducts of 2 sizes; shorter oral-collar

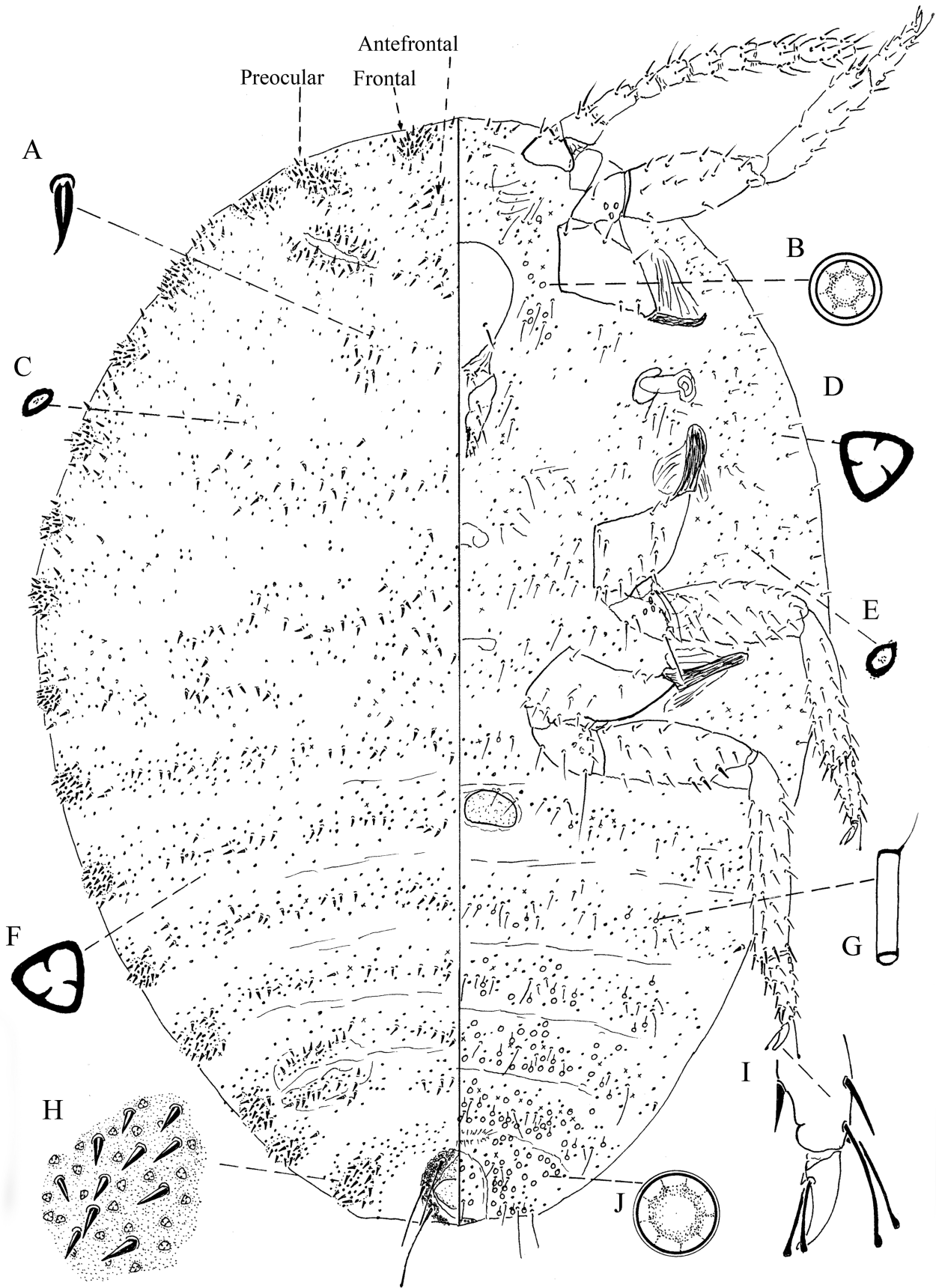


FIGURE 1. *Puto philo* Powell & Miller, *sp. n.*, adult female holotype, Mexico at Laredo, September 18, 1952, Leary, Cary, and Fouts, on *Monstera*, #521475. A=dorsal seta; B=7-locular pore; C, E=discoidal pores; D, F=trilocular pores; G=oral-collar tubular duct; H=anal-lobe cerarius; I=claw; J=9-locular pore.

tubular ducts on abdomen, in transverse rows across segments II–VIII, numerous on submarginal areas of segments VI–VIII, rare on head and thorax; longer oral-collar tubular ducts absent from head and thorax of holotype female (paratype females with 0–6 in medial area of head anterior to mouthparts). Long hair-like setae arranged in rows across abdomen, longest seta on medial area of abdomen 62 μm (paratypes 69–76 μm) long, longest seta on medial area of segment V 62 μm (paratypes 60–73 μm) long; head setae broken on holotype (longest seta on head of paratypes 137–163 μm long). Circulus divided into 2 oval parts on segment III, sometimes asymmetrical in size, diameter of each part 117–127 μm (paratypes 66–142 μm). Labium 254 μm long (paratypes 226–257 μm). Antennae each 9-segmented, total length about 802 μm (paratypes 691–794 μm); apical segment about 133 μm long (paratypes 113–133 μm), segment III about 101 μm long (paratypes 88–104 μm); with intersegmental sensilla present between segments III and IV, IV and V, and VI and VII; and with a pair of coeloconic sensilla on segments IV, V and IX. One paratype female with aberrant antennae, having one side with 5 segments and the other side with pseudoarticulations, incompletely forming nine segments. Hind tibiae each with small translucent pores. Femora each about 386 μm long (paratypes 333–392 μm), tibiae each about 464 μm long (paratypes 438–484 μm), tibia/tarsus 2.8 (paratypes 2.7–2.9). Hind trochanters each with 3 or 4 campaniform sensilla on each surface. Tarsal digitules capitate, claw digitules capitate and longer than claw; claw denticle absent; basal spurs present.

Diagnosis: Adult females of *P. philo* differ from other *Puto* species by having the following combination of characters: a single, divided circulus; claw denticle absent; and dorsal oral-rim type tubular ducts, including those associated with cerarii, absent.

Puto philo is similar to *P. lamottei* Matile-Ferrero, 1985 in having no oral-rim type tubular ducts in the cerarii, no dorsal oral-rim type tubular ducts in the medial areas, and a divided circulus. *Puto philo* lacks a claw denticle, whereas *P. lamottei* has one.

The new species is also similar to *P. spath* (described below) in that both have a divided circulus, but no dorsal oral-rim type tubular ducts in medial areas, and no oral-rim type tubular ducts in the cerarii. However, *P. philo* differs from *P. spath* as follows (character states of *P. spath* are presented in parentheses): (i) claw denticle absent (claw denticle present); (ii) no multilocular disc-pores in the medial area of the thorax (with multilocular disc-pores in the medial area of the thorax); and (iii) with typical multilocular disc-pores of one size (multilocular disc-pores of two sizes, with large multilocular disc-pores each with a trilocular center).

Puto philo also resembles *P. paramoensis* Matile-Ferrero, 1985 in having no denticle, no dorsal oral-rim type tubular ducts, and no dorsal multilocular disc-pores. However, it differs from *P. paramoensis* as follows (character states of *P. paramoensis* are presented in parentheses): (i) ventral multilocular disc-pores on the thorax absent (with many ventral multilocular disc-pores in the medial and marginal areas of the thorax); (ii) multilocular disc-pores predominantly each with 9 loculi but with some 10-locular disc-pores near the vulva (two distinct sizes of multilocular disc-pores, 10- and 6-locular, with the larger size near the vulva); and (iii) claw digitules capitate (claw digitules simple).

Third-instar female

(Fig. 2)

Description: Slide-mounted, 1.57–2.08 mm long, 0.96–1.26 mm wide; body elongate oval.

Dorsum with 16 pairs of cerarii; anal-lobe cerarii each containing 7–9 lanceolate setae and 16–19 trilocular pores; frontal cerarii each containing 6–11 lanceolate setae and 5–8 trilocular pores; antefrontal cerarii not distinct, without sclerotization, each containing loose cluster of 7–11 setae; cerarii without associated discoidal pores or oral-rim type tubular ducts; and marginal cerarii each with basal sclerotization. Anterior and posterior ostioles present. Multilocular disc-pores absent; trilocular pores of 1 size, numerous, scattered over body, with more on dorsum than on venter, also present on lips of ostioles; discoidal pores scattered over body. Oral-rim type tubular ducts and oral-collar tubular ducts absent. Dorsal setae lanceolate, forming rows across abdominal segments II–VII, also clustered on lips of ostioles and scattered on head and thorax, with many on margin between cerarii, but absent from medial area of abdominal segment VIII; longest seta on abdomen 17–23 μm long, longest seta in abdominal cerarii 26–28 μm long.

Anal ring dorsal, bearing 6 anal-ring setae with apices acute; posterior anal-ring setae each 135–157 μm long, 1.3–1.5 times as long as greatest diameter of anal ring.

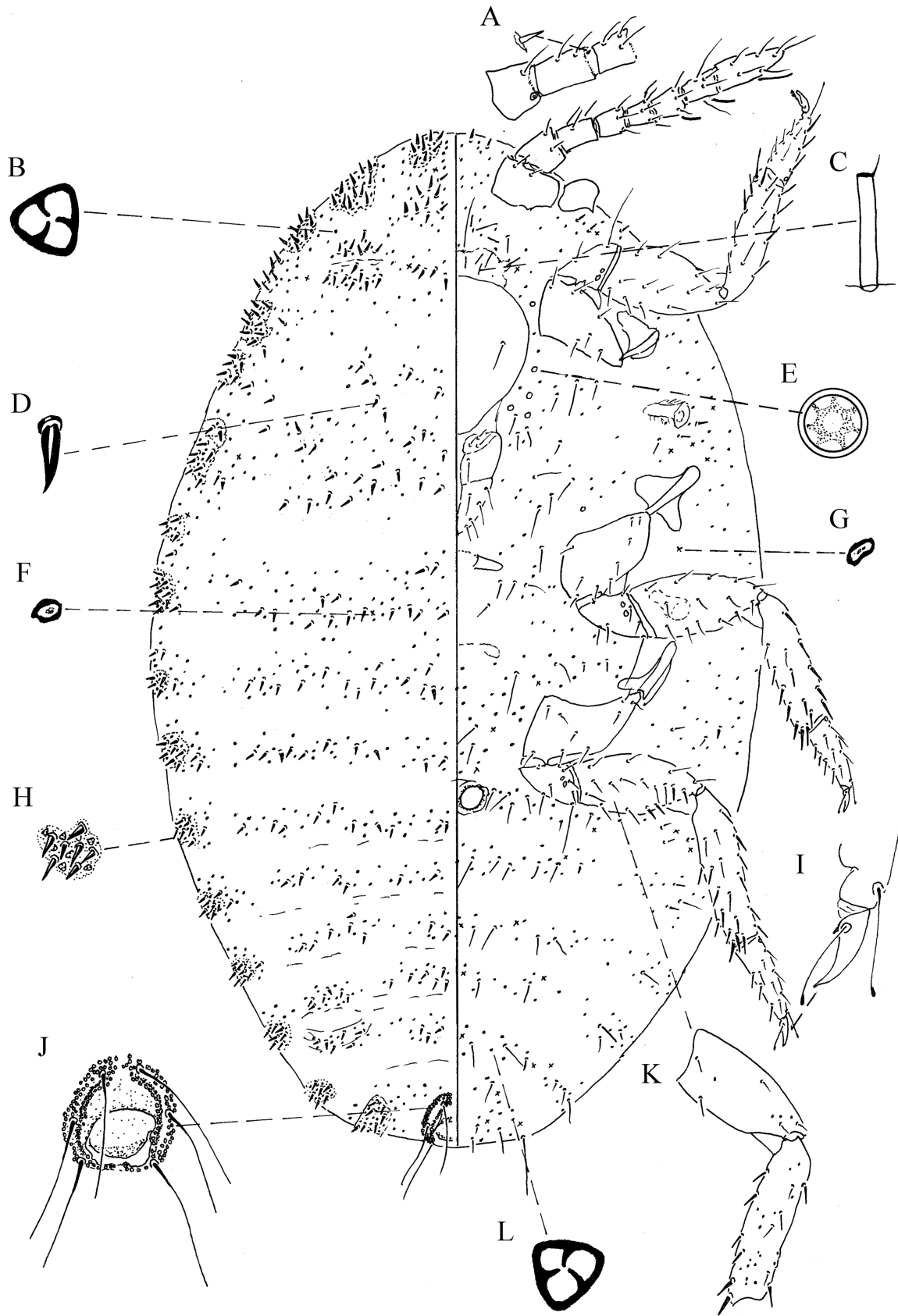


FIGURE 2. *Puto philo* Powell & Miller, *sp. n.*, third-instar female paratype, Mexico at Laredo, September 18, 1952, Leary, Cary, and Fouts, on *Monstera*, #521475. **A**= antennal intersegmental sensilla; **B**, **L**=trilocular pores; **C**=long oral-collar tubular duct; **D**=dorsal seta; **E**=7-locular pore; **F**, **G**=discoidal pores; **H**=cerarius; **I**=claw; **J**=anal ring; **K**=translucent pores on hind femur and tibia.

Venter with multilocular disc-pores present in medial area of thorax near mouthparts, predominantly each 7-locular. Trilocular pores of 1 size, scattered over body; discoidal pores scattered over body. Long oral-collar tubular ducts forming cluster (12–20) on head anterior to mouthparts, absent from thorax and abdomen. Long hair-like setae forming rows across abdomen, longest ventral seta on medial area of abdomen 47–57 µm long, longest seta on medial area of segment V 43–53 µm long, longest seta on head 95–114 long. Circulus divided into 2 oval parts on segment III, sometimes asymmetrical in size, each part 34–62 µm in diameter. Labium 191–206 µm long. Antennae each 8-segmented, total length 579–654 µm; apical segment 114–132 µm long, segment III 80–97 µm long; antennal intersegmental sensilla present between segments V and VI; coeloconic sensilla present on segments IV and VIII. Hind tibia and distal femur with few translucent pores. Femora each 264–285 µm long; tibiae each 316–337 µm long, tibia/tarsus 1.9–2.1. Hind trochanters each with 2 campaniform sensilla on each surface. Tarsal digitules capitate, claw digitules capitate and longer than claw; claw denticle absent but basal spurs present.

Diagnosis: A comparison of the third-instar females of *P. philo* and *P. spath* is presented in the “Diagnosis” section of the latter species.

Second-instar female

(Fig. 3)

Description: Slide-mounted, 1.41–1.74 mm long, 0.79–1.12 mm wide; body elongate oval.

Dorsum with 16 or 17 pairs of cerarii; anal-lobe cerarii each containing 5–7 lanceolate setae and 11–13 trilocular pores; frontal cerarii each with basal sclerotization, containing 5–7 lanceolate setae and 4–6 trilocular pores; antefrontal cerarii not distinct, without sclerotization, each containing 4–6 loosely clustered setae; cerarii each without associated discoidal pores or oral-rim type tubular ducts; and marginal cerarii each with weak basal sclerotization. Ostioles weakly developed. Multilocular disc-pores absent; trilocular pores of 1 size, larger than those on venter, numerous, scattered over body, with more on dorsum than on venter, also present on lips of ostioles; discoidal pores scattered over body. Oral-rim type tubular ducts and oral-collar tubular ducts absent. Dorsal setae lanceolate, few, scattered across body, present on lips of ostioles; longest seta on abdomen 17–19 µm long, longest seta in abdominal cerarii 25–28 µm long.

Anal ring dorsal or bent around body apex, bearing 6 anal-ring setae with apices acute; posterior anal-ring setae each 121–137 µm long, 1.3–1.8 times as long as greatest diameter of anal ring.

Venter with multilocular disc-pores in medial area of pro- and mesothorax, predominantly each 7-locular. Trilocular pores of 1 size, smaller than those on dorsum, scattered over body; discoidal pores scattered over body. Long oral-collar tubular ducts of 1 size forming cluster (6–11) anterior to mouthparts. Long hair-like setae sparse, forming rows across abdomen, longest on head, longest seta on medial area of abdomen 38–56 µm long, longest seta on medial area of segment V 33–49 µm long, longest seta on head 99–111 µm long. Circulus divided into 2 oval parts on segment III, each part 24–38 µm in diameter. Labium 154–167 µm long. Antennae each 7-segmented, total length 506–554 µm, apical segment 115–125 µm long, segment III 96–116 µm long; antennal intersegmental sensilla present between segments IV and V; coeloconic sensilla present on segments III and VII. Hind legs without translucent pores. Femora each 216–233 µm long; tibiae each 233–286 µm long, tibia/tarsus 1.6–1.9. Hind trochanters each with 2 campaniform sensilla on each surface. Tarsal digitules capitate, claw digitules capitate, longer than claw; claw denticle absent; basal spurs present.

Diagnosis: A comparison of the second-instar females of *P. philo* and *P. spath* is presented in the “Diagnosis” section of the latter species.

Second-instar male

(Fig. 4)

Description: Slide-mounted, 1.54–2.56 mm long, 0.88–1.60 mm wide; body elongate oval.

Dorsum with 16 or 17 pairs of cerarii; anal-lobe cerarii each containing 4–8 lanceolate setae and 10–16 trilocular pores; frontal cerarii each with basal sclerotization, containing 5–7 lanceolate setae and 4–11 trilocular pores; antefrontal cerarii not distinct, without sclerotization, each containing 4–7 loosely clustered setae; cerarii without associated discoidal pores or oral-rim type tubular ducts; and marginal cerarii each with weak basal sclerotization.

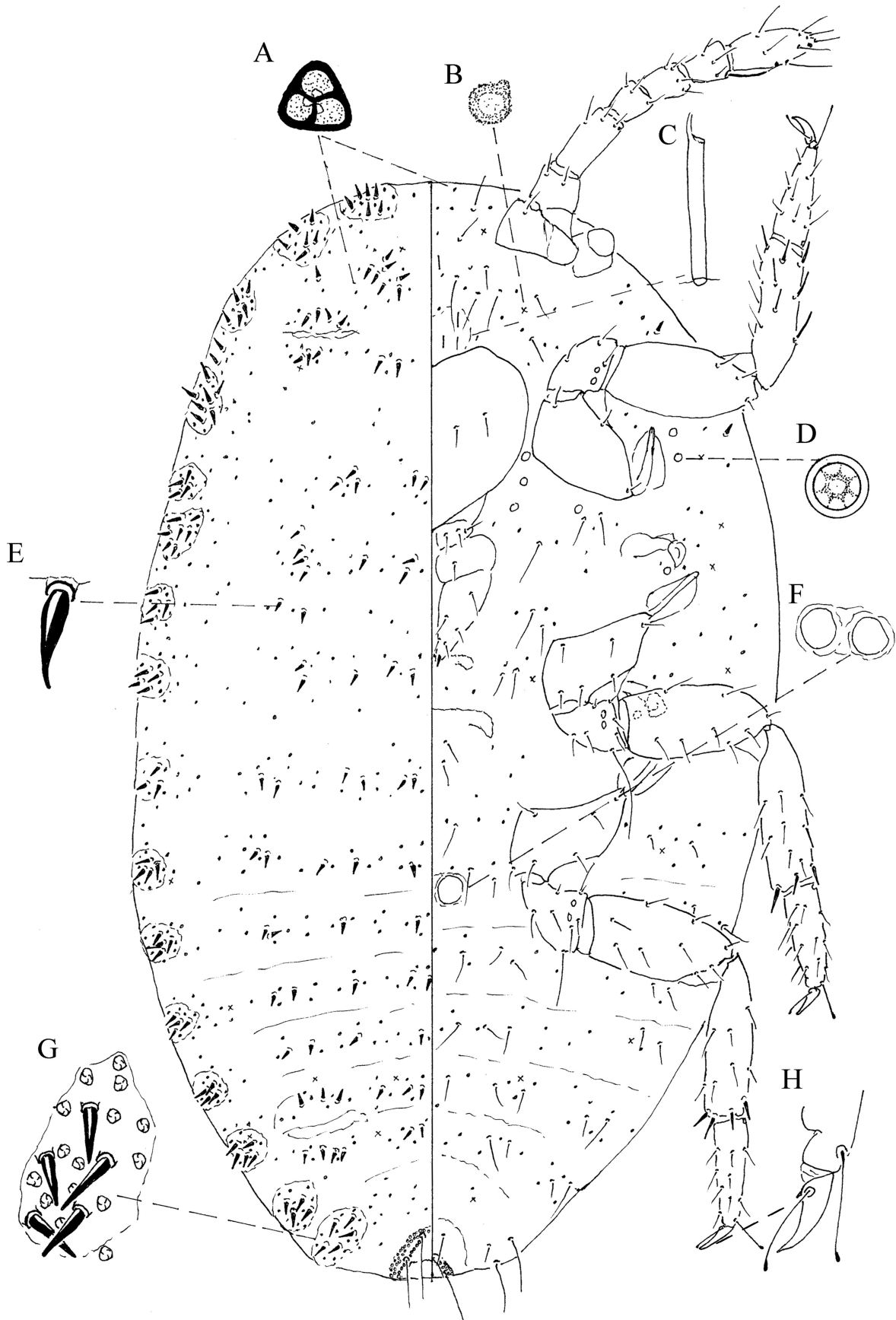


FIGURE 3. *Puto philo* Powell & Miller, **sp. n.**, second-instar female paratype, Mexico at Laredo, September 12, 1952, Cary and Heinrich, on *Monstera*, #521445. **A**=trilocular pore; **B**=discoidal pore; **C**=long oral-collar tubular duct; **D**=7-locular pore; **E**=dorsal seta; **F**=divided circulus; **G**=anal-lobe cerarius; **H**=claw.

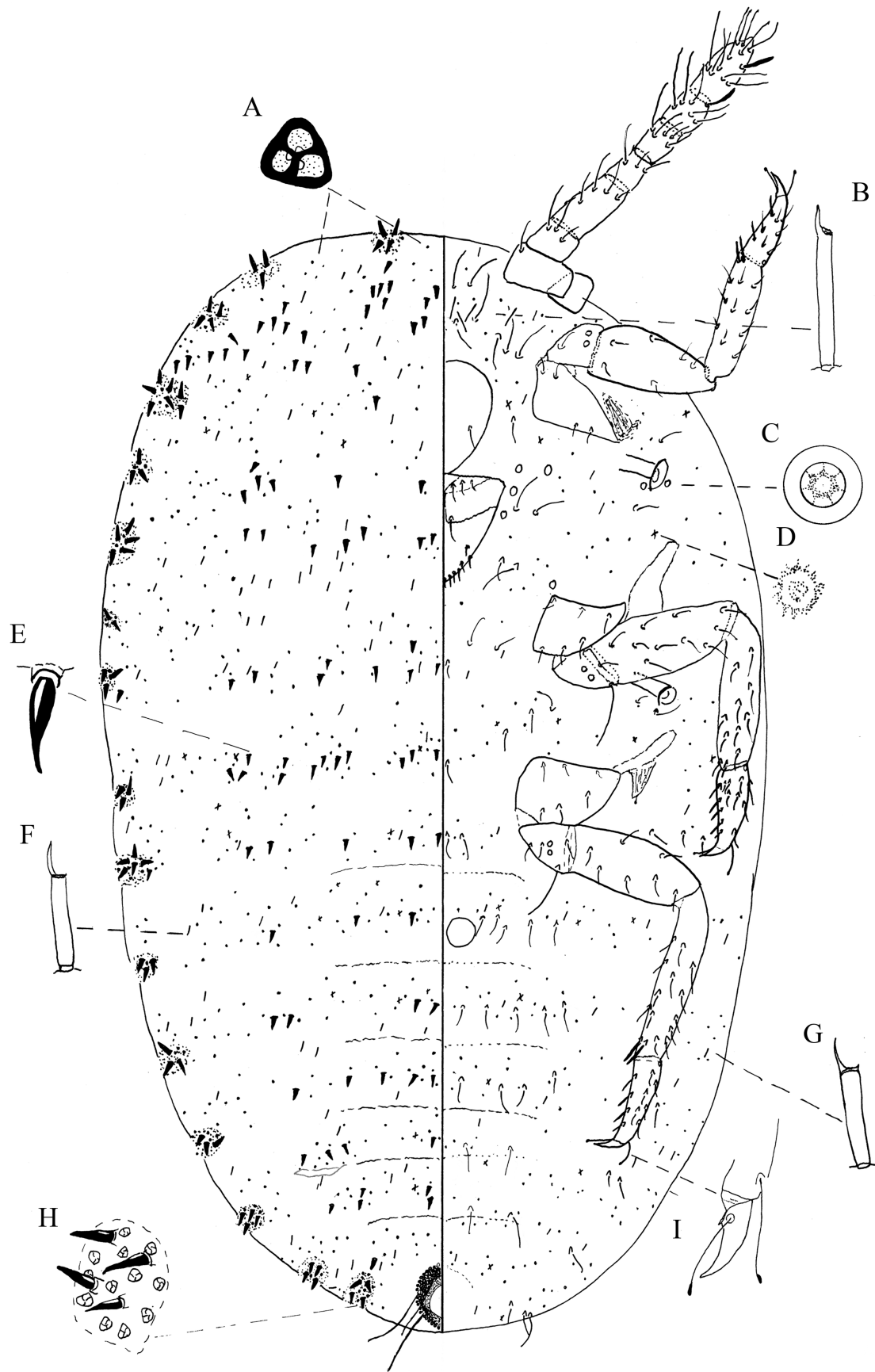


FIGURE 4. *Puto philo* Powell & Miller, *sp. n.*, second-instar male paratype, Mexico at Laredo, August 26, 1952, Cary, Weedmark, and Fouts, on *Philodendron*, #521447. **A**=trilocular pore; **B**=long oral-collar tubular duct; **C**=7-locular pore; **D**=discoidal pore; **E**=dorsal seta; **F**, **G**=oral-collar tubular ducts; **H**=anal-lobe cerarius; **I**=claw.

Anterior ostioles absent, posterior ostioles weakly developed. Multilocular disc-pores absent; trilocular pores of 1 size, larger than those on venter, numerous, scattered over body, with more on dorsum than on venter, few present on anterior lip of ostioles; discoidal pores scattered over body. Oral-collar tubular ducts of 1 size, scattered over body. Oral-rim type tubular ducts absent. Dorsal setae lanceolate, few, scattered across body; few present on anterior lip of ostiole; longest seta on abdomen 17–20 µm long, longest seta in abdominal cerarii 24–26 µm.

Anal ring dorsal, bearing 6 anal-ring setae with apices acute; posterior anal-ring setae each 144–163 µm long, 1.5–1.8 times as long as greatest diameter of the anal ring.

Venter with multilocular disc-pores in medial area of pro- and mesothorax, predominantly each 7-locular. Trilocular pores of 1 size, smaller than those on dorsum, scattered over body; discoidal pores scattered over body. Oral-collar tubular ducts of 2 sizes, shorter ones scattered over entire body, long oral-collar tubular ducts forming cluster (5–10) anterior to mouthparts. Long hair-like setae sparse, forming rows across abdomen, longest on head, longest seta on medial area of abdomen 46–69 µm long, longest seta on medial area of segment V 43–52 µm long, longest seta on head 103–147 µm long. Circulus divided into 2 oval parts on segment III, in some specimens each part fully separated, in other specimens pieces touching, each part 32–55 µm in diameter. Labium 169–180 µm long. Antennae each 7-segmented, total length 532–584 µm, apical segment 111–116 µm long, segment III 117–129 µm long; antennal intersegmental sensilla present between segments IV and V; coeloconic sensilla present on segments III and VII. Hind legs without translucent pores. Femora each 236–273 µm long; tibiae each 278–327 µm long, tibia/tarsus 1.7–2.2. Hind trochanters each with 2 campaniform sensilla on each surface, one specimen with 3 on one side. Tarsal digitules capitate, claw digitules capitate, longer than claw; claw denticle absent; basal spurs present.

Diagnosis: A comparison of the second-instar males of *P. philo* and *P. spath* is presented in the “Diagnosis” section of the latter species.

First-instar nymph (sexes undetermined)

(Fig. 5)

Description: Slide-mounted, 0.80–1.16 mm long, 0.43–0.70 mm wide; body elongate oval.

Dorsum with 18 or 19 pairs of cerarii, anal-lobe cerarii each containing 2 lanceolate setae and 4–6 trilocular pores; frontal cerarii each containing 2–3 lanceolate setae and 2–4 trilocular pores; antefrontal cerarii containing 1 or 2 setae, with basal sclerotization, situated laterad of frontal cerarius; sometimes with another pair of setae posteriorly without basal sclerotization; cerarii each without associated discoidal pores or oral-rim type tubular ducts; and marginal cerarii with basal sclerotization. Anterior ostioles absent, posterior ostioles weakly developed. Multilocular disc-pores absent; trilocular pores of 1 size, numerous, unevenly scattered across body, those on dorsum larger and more numerous than on venter, absent from lips of ostioles; discoidal pores absent. Oral-rim type tubular ducts and oral-collar tubular ducts absent. Dorsal setae lanceolate, few, forming 2 pairs of longitudinal lines on thorax and abdomen, absent from lips of ostioles; longest seta on abdomen 14–20 µm long, longest seta in abdominal cerarii 24–26 µm long.

Anal ring dorsal, bearing 6 anal-ring setae with apices acute, posterior anal-ring setae each 112–122 µm long, 1.7–1.9 times as long as greatest diameter of the anal ring.

Venter with multilocular disc-pores present near mouthparts, near spiracles, and on thorax, predominantly each with 7-loculi. Trilocular pores of 1 size, scattered over body. Discoidal pores marginal, associated with marginal hair-like setae on abdomen, and in cluster on margin of head. Cluster of 2–4 long oral-collar tubular ducts present anterior to mouthparts. Long hair-like setae longest on head, forming rows across abdomen, longest seta on medial area of abdomen 31–46 µm long, longest seta on medial area of segment V 29–36 µm long, longest seta on head 99–125 µm long. Single undivided circulus present on abdominal segment III, 27–33 µm in diameter. Labium 128–134 µm long. Antennae each 7-segmented, total length 421–468 µm, apical segment 108–116 µm long, segment III 57–79 µm long; antennal intersegmental sensilla present between segments IV and V; coeloconic sensilla present on segment VII. Hind legs without translucent pores. Femora each 166–237 µm long; tibiae each 176–212 µm long, tibia/tarsus 1.3–1.5. Hind trochanters each with 2 campaniform sensilla on each surface. Tarsal digitules capitate, claw digitules capitate, each longer than claw; claw without denticle; basal spurs present.

Diagnosis: A comparison of the first-instar nymphs of *P. philo* and *P. spath* is presented in the “Diagnosis” section of the latter species.

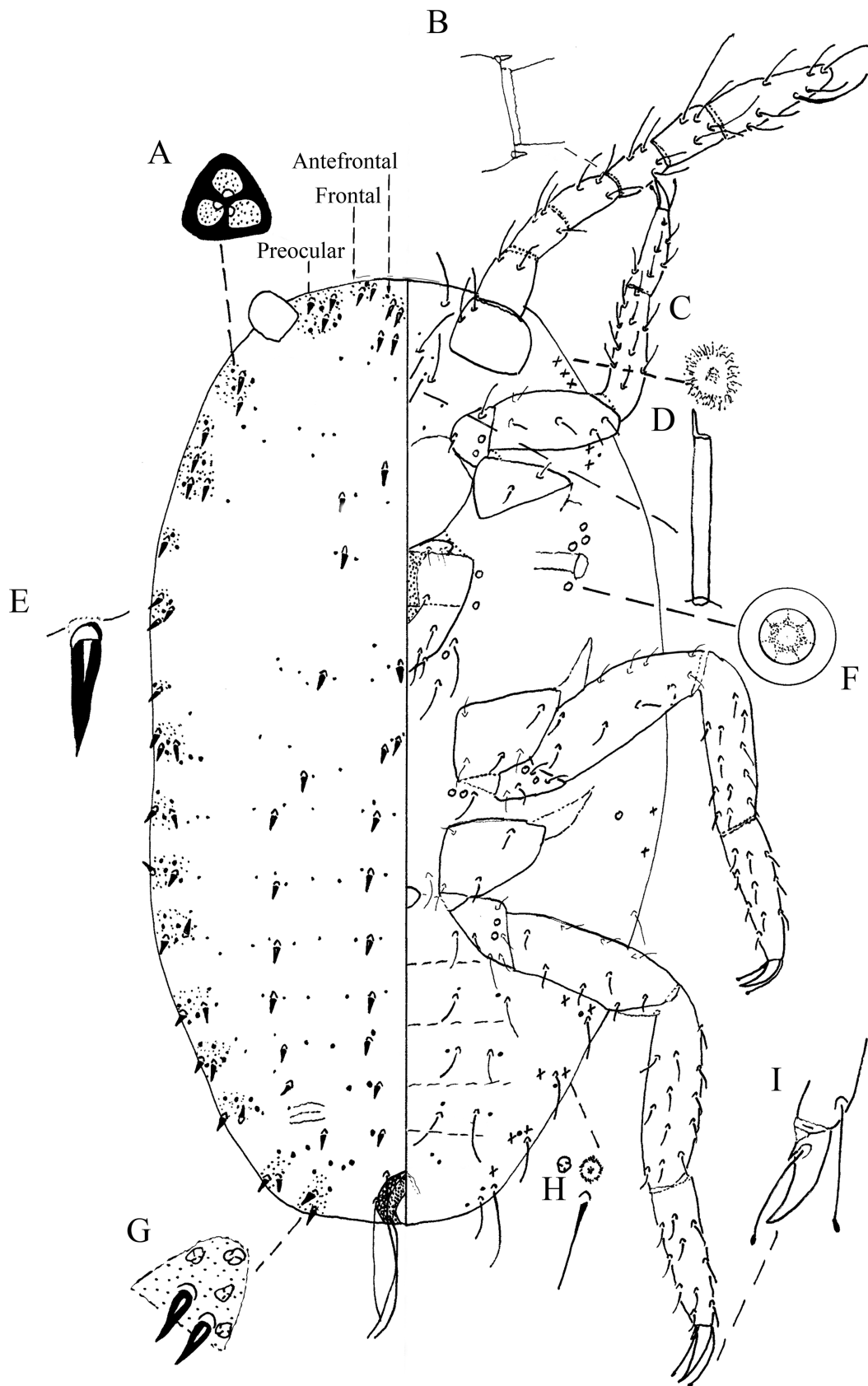


FIGURE 5. *Puto philo* Powell & Miller, *sp. n.*, first instar (sex undetermined) paratype, Mexico at Laredo, June 26, 1952, Cary and Fouts, on *Philodendron*, #521001. **A**=trilocular pore; **B**= antennal intersegmental sensilla; **C**=discoidal pore; **D**=long oral-collar tubular duct; **E**=dorsal seta; **F**=7-locular pore; **G**=anal-lobe cerarius; **H**=ventral seta with associated trilocular and discoidal pores; **I**=claw. Note that the illustration utilized two specimens on the same slide.

Adult male (macropterous)

(Figs 6, 14a)

Description: Slide-mounted, 2.85–3.21 mm long, 0.77–0.80 mm wide; body elongate, with segment VIII produced laterally.

Dorsum with 1 pair of glandular pouches (gp); each glandular pouch with 2 central setae, each apically acute, setae all approximately same size, 247–302 µm long. Multilocular disc-pores present in glandular pouches, each pouch containing about 263–290 tightly clustered pores, predominantly each with 5 loculi; discoidal pores predominantly situated on margin of pouch; setae forming row across anterior margin of pouch; and with tubular ducts (gpt) forming cluster at base of glandular pouch setae (gls). Multilocular disc-pores forming cluster on prothorax, present in segmental rows from metathorax to abdominal segment VII, predominantly each with 4 or 5 loculi. Discoidal pores present near multilocular disc-pores. Hair-like setae slender, apically acute, approximately same length as those on venter, forming segmental rows, with marginal clusters on each side of each segment; setae present on pro-, meso- and metathorax. Head with setae anterior to postoccipital ridge (por), on ocular sclerite (ocs), and along dorsal arm of midcranial ridge (dmcr). Microtrichia present on all abdominal segments (not illustrated). Posterior ostioles (pos) present, weakly developed, without associated setae or pores. Abdominal tergites (at) with two areas of sclerotization on posterior margin of each of segments II–VII; segment VIII with heavily sclerotized yoke-shaped medial tergal plate (mtp) on anterior margin; metapostnotal sclerite present (pn₃); metapostnotal ridge absent. Scutellum (scl) well developed, with 42–48 setae; scutellar ridge (sclr) well developed. Scutum (sct) sclerotized throughout, except for medial triangular clear area (mta) anterior to scutellum. Prescutum, prescutal suture, and prescutal setae absent. Pronotal ridges (prnr) well developed; pronotal sclerites (prn) present. Hamulohalteres present, each with 3 setae (sometimes only 2) (hams). Wings each 2.62–3.04 mm long, covered in microtrichia, each with alar lobe (al), alar sclerites (alsc) and veins (wv), without setae or sensoria; subcosta (sc) arising from alar sclerites; radius (r) joining subcosta; possible media (m) represented by sclerotized area arising ¼ distance from alar sclerite, cubitus anterior (cua) present, not joined with other veins; cubitus posterior (cup) arising from alar sclerites, with additional band of sclerotization anterior to cubitus anterior; irregular patches of sclerotization present on distal half of each wing. Tegula (teg) each with 12–14 setae. Postoccipital ridge (por) well developed, fused with postocular ridge (pocr). Dorsal arm of midcranial ridge (dmcr) narrow, touching postoccipital ridge posteriorly; with anterior swelling, connected to lateral (lmcr) arms anteriorly; surrounded by median crest (mc) with irregular sclerotization and 13–20 setae on each side, also with membranous area between ocular sclerite and sclerotization surrounding dorsal arm of midcranial ridge; ocular sclerite with setae in 2 clusters, one anterolateral with 8–9 setae and one posteromedial with 7–8 setae on each side. With 3 dorsal simple eyes (de) on each side, those nearest dorsal arm of midcranial ridge (dmcr) largest, each 40–42 µm in diameter, those on lateral edge smallest, each 34–35 µm in diameter. Lateral ocellus (lo) about same size as lateral simple eye, each 42–44 µm in diameter. Anus (an) small, situated on membranous dorsal surface of penial sheath. Penial sheath (ps) 498–525 µm long; elongate, about 237 µm wide; width/length 0.45, apically with several small papillae (pap); anterior portion with 15–17 long setae (each about 48–69 µm long), posterior portion with about 10–13 small setae (each 7–9 µm long). Aedeagus (ae) U-shaped, attached on membranous surface, about 0.95–1.08 mm long, apex bifurcate with 3 small denticles.

Venter with multilocular disc-pores (mp), predominantly each with 4 loculi, present near anterior (asp) and posterior spiracles (psp), in marginal longitudinal line clusters on each segment, also present medially between mesothoracic legs, in cluster laterad to proepisternum + cervical sclerite (pepcv), in cluster (of about 15) on unsclerotized area anterior to ocular sclerite and preocular ridge (pocr) together with associated setae and discoidal pores (disc). Hair-like setae, apically acute, approximately same length as those on dorsum (79–94 µm on abdominal segment VIII), present in lateral clusters and segmental rows on abdomen, less abundant anteriorly with a few setae mediolaterally on mesothorax, and medially on metathorax and prothorax. Head setae abundant in cluster (about 21–31 on each side) on medial area of ocular sclerite (osc) under ventral simple eyes (vse), present (9–12 on each side) near midline of head between antennal base and ventral eye (vse), anterior to preocular ridge. Microtrichia present on abdominal segments IV–VIII. Abdominal sternites with sclerotization weakly developed on medial and mediolateral areas of segments II–VII, segment VIII with heavier sclerotization mediolaterally. Metapleural ridge (plr₃) well developed, with 2 precoxal ridge extensions, the anterior extension longer, reaching to metasternal apophysis. Mesosternum (stn₂) well developed, with large furca (f); lateropleurites (lpl) on mesothorax triangular, with membranous area between each lateropleurite and mesepisternum (eps₂). Mesopleural ridge (plr₂) with precoxal ridge of mesothorax (pcr₂) and additional posterior ridge extension anterior to mesocoxal articulation.

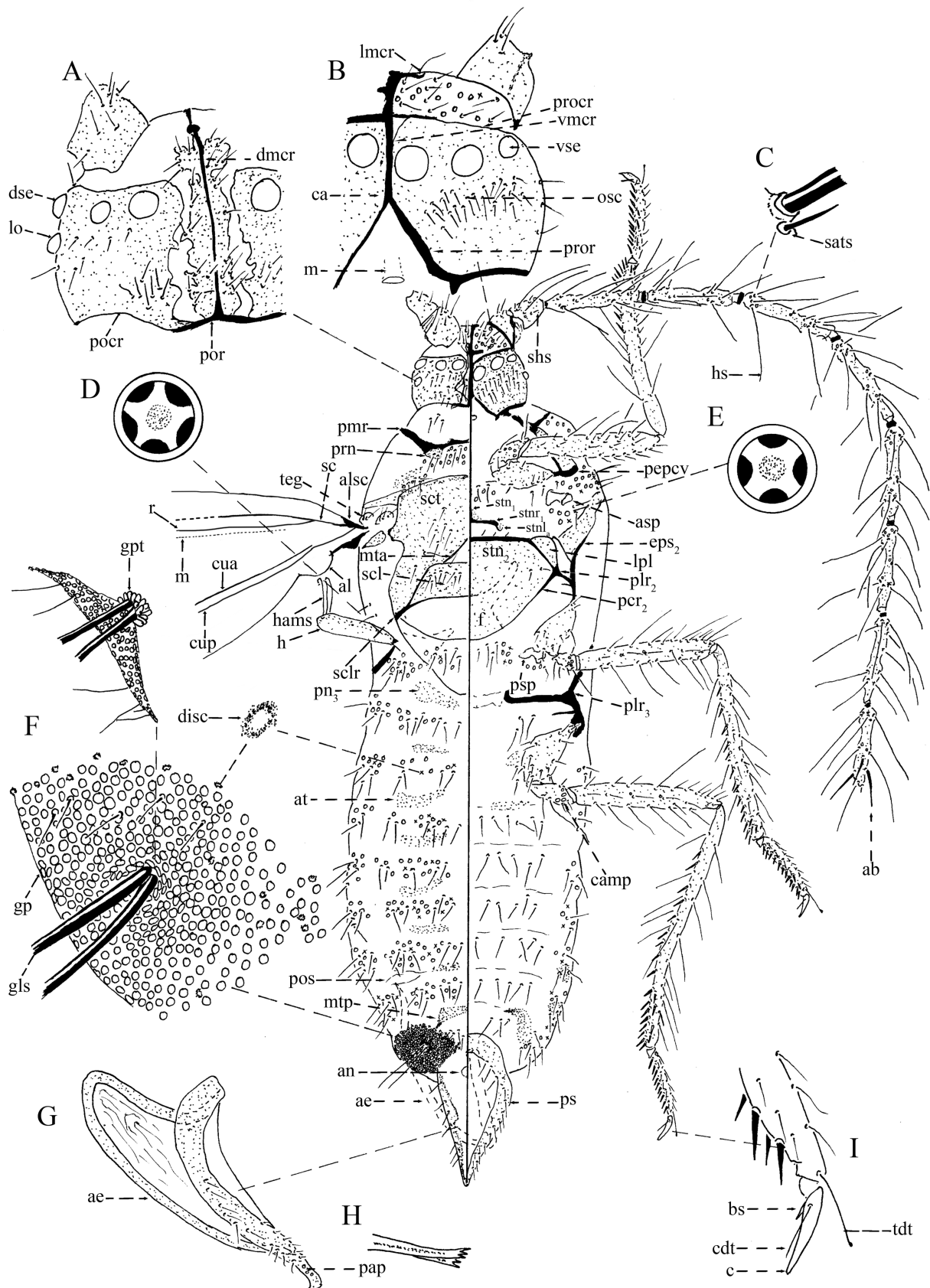


FIGURE 6. *Puto philo* Powell & Miller, **sp. n.**, adult male paratypes, Mexico at Laredo, September 12, 1952, Cary and Heinrich, on *Monstera*, #521445. **A**=dorsum of head; **B**=venter of head; **C**=satellite seta next to long hair-like setae; **D**=quinelocular pore; **E**=quadriocular pore; **F**=glandular pouch and tubular ducts; **G**=lateral view of penial sheath; **H**=apex of aedeagus; **I**=claw. Note that the illustration utilized two specimens in fair condition with the thorax twisted on both specimens.

Prosternum (stn_1) with sclerotized prosternal ridge ($stnr_1$) that ends with prosternal apophysis ($stn1a$), surrounded by poorly developed triangular sclerite. Proepisternum and cervical sclerite well developed. Preoral ridge ($pror$) well developed, fused with postocular ridge ($pocr$). Ventral midcranial ridge ($vmcr$) well developed anteriorly, extending to lateral arms ($lmcr$) between antennae, fused with preocular ridge and preoral ridge. Ocular sclerite (ocs) sclerotized throughout, area anterior to preocular ridge unsclerotized. Mouth (m) present, unsclerotized, without tubercle. Cranial apophysis (ca) sclerotized, conical, arising at base of ventral midcranial ridge. With 3 ventral simple eyes (vse) on each side, those nearest dorsal arm of midcranial ridge ($dmcr$) largest (each 46–48 μm in diameter), those on lateral edge smallest (each 26–30 μm in diameter); with a total of 6 pairs of simple eyes and a pair of ocelli wrapping around head. Metathoracic legs longest, with coxa (cx) 227–268 μm long, trochanter (tr) 143–175 μm long, femur (fm) 527–573 μm long, tibia (ti) 830–899 μm long, tarsus (ta) 269–285 μm long, and claw 65–71 μm long; tibia/tarsus 3.00–3.15. Hind trochanters typically each with 4 campaniform sensilla ($camp$) on each surface, the left metathoracic trochanter of one specimen with 3. Each claw (cl) without denticle; with pair of basal spurs (bs); digitules on tarsus (tdt) capitate, shorter than claw; digitules on claw (cdt) acute, shorter than claw. Spine-like setae present on tarsus and tibia; also with long hair-like setae on tibia, femur, trochanter, and coxa; many hair-like setae on trochanter, femur, and tibia with satellite setae ($sats$); short hair-like setae present on all leg segments. Legs without translucent pores.

Antennae 10-segmented, each 2.58–2.85 mm long, with segments III–VII longest, approximately equal in length, third segment about 1.2–1.5 times longer than apical segment, last segment apically rounded or pointed. Antenna with elongate hair-like setae (hs) on segments II–X, many with a very small satellite seta ($sats$); with short setae (shs) on first 3 segments, and antennal bristles (ab) on apical 3 segments; a pair of antennal intersegmental sensilla present between segments III and IV, IV and V, and VII and VIII (not illustrated); coeloconic sensilla present on segments II and X (not illustrated).

Remarks: The description is based on four specimens collected in association with females and immatures. The illustration utilized two specimens which are in fair condition but with the thorax twisted on both specimens. The genitalia were mounted laterally on three of the four males examined for the description. Male wing venation is interpreted with a maximalist approach, though we recognize that the veins observed may not be true veins and further study is required. For instance, in *Matsucoccus pini* (Green, 1925), only one true vein (the radius) was detected when cross-sections were examined, whereas previously this species was described as having three veins (Franielczyk-Pietryra *et al.* 2023). What we have labeled as veins may be thickenings, lines, or folds rather than real veins, particularly what we interpret as the media (Figs 6, 13, and 14). To our knowledge, the wing venation of Putoidae has not been studied in detail.

Diagnosis: The male of *P. philo* is the only known *Puto* male with both a bifurcate aedeagus and the claw denticle absent. It is similar to the male of *P. yuccae* (Coquillett, 1890) in having the apex of the aedeagus bifurcate, but differs from it as follows (*P. yuccae* characters are presented in parentheses): (i) claw without denticle (denticle present); (ii) tarsal digitules clubbed (acute); (iii) 6 pairs of simple eyes (7 or 8 pairs); (iv) with 3, sometimes 2, hamulohaltere setae (with 4); and (v) abdominal segments each with multiple rows of multilocular disc-pores (each with one row).

Puto spath Powell & Miller, sp. n.

Suggested common name: peace lily giant mealybug

Material examined

Holotype adult female is on left side on a slide containing 2 adult females and is circled on slide cover. Left label “Puto / Guatemala / ex *Spathiphyllum* sp. / IX-16-1976 plant / New Orleans 9134. / W. Stafford, B. Davis / Balsam”. Right label gives map of holotype position and states “Puto spath / Powell & Miller / n.sp.”, USNM.

Paratypes: GUATEMALA: taken in quarantine at New Orleans, Louisiana, IX-9-1976, on *Spathiphyllum* sp., C. Garcia, W. Harris and B. Davis (1 ad. ♀, 1 second-instar ♀ together on 1 slide) USNM; taken in quarantine at New Orleans, Louisiana, IX-16-1976, on *Spathiphyllum* sp., W. Stafford and B. Davis (2 ad. ♀♀, 2 third-instar ♀♀, 3 second-instar ♂♂, 1 first-instar nymph mounted on 3 slides) USNM; taken in quarantine at New Orleans, Louisiana, IX-24-1976, on *Spathiphyllum* sp., leaf, B. Davis (1 ad. ♀, 2 third-instar ♀♀, 2 second-instar ♂♂ together on 1 slide) USNM, (1 ad. ♀, 1 third-instar ♀, 2 second-instar ♂♂ together on 1 slide) FSCA; taken in quarantine at New Orleans, Louisiana, X-7-1976, on *Spathiphyllum* sp. stems, R. Sharp (2 third-instar ♀♀, 1 second-instar ♂, 2 first-instar nymphs together on 1 slide) USNM; taken in quarantine at Miami, Florida, X-20-

1976, on *Spathiphyllum* sp., stem, F. Matthews (2 third-instar ♀♀, 2 second-instar ♂♂ together on 1 slide) USNM, (1 ad. ♀ on 1 slide) UCD.

Etymology: The species epithet “*spath*” is a noun in apposition based on an abbreviation of the scientific name of the host plant, *Spathiphyllum*.

Adult female

(Fig. 7)

Description: Slide-mounted holotype 2.34 mm long, 1.27 mm wide; paratypes 2.66–3.98 mm long, 1.58–2.80 mm wide; body elongate oval.

Dorsum with 16 pairs of cerarii; anal-lobe cerarii each containing 14–16 lanceolate setae (paratypes 10–17) and 20–22 trilocular pores (paratypes 17–24); frontal cerarii each containing 17–20 lanceolate setae (paratypes 16–18) and 12–14 trilocular pores (paratypes 13–16); antefrontal cerarii not distinct, each with 11–22 loosely clustered setae and without sclerotization; each cerarius without associated discoidal pores or oral-rim type tubular ducts; and all marginal cerarii with basal sclerotization. Anterior and posterior ostioles present. Multilocular disc-pores absent; trilocular pores of 1 size, numerous, concentrated in rows across abdominal segments, scattered across thorax and head, more numerous on dorsum than venter, present on lips of ostioles; discoidal pores scattered over body. Oral-rim type tubular ducts and oral-collar tubular ducts absent. Dorsal setae lanceolate, forming rows across segments II–VII, clustered on lips of ostioles; scattered on head and thorax, on margin between cerarii on head and thorax, but absent from submedial and medial area of segment VIII. Longest seta on abdomen 29 µm (paratypes 25–32 µm) long, longest seta in abdominal cerarii about 35 µm (paratypes 33–36 µm) long.

Anal ring dorsal, bearing 6 anal-ring setae with apices acute (one paratype female with 7 setae); posterior anal-ring setae each about 239 µm long (paratypes 231–273 µm long); 1.5 times (paratype 1.5–2.0 times) as long as greatest diameter of anal ring.

Venter with multilocular disc-pores abundant on segments II–VIII, especially abundant on VII–VIII, also on thorax and head; multilocular disc-pores of 2 sizes, larger multilocular disc-pores each with 10 outer loculi and trilocular center restricted to posterior segments VII–VIII; smaller disc-pores 7-locular and 9-locular, with simple centers, scattered over entire body. Trilocular pores of 1 size, numerous, scattered over body; discoidal pores scattered over body. Oral-collar tubular ducts of 2 sizes; shorter oral-collar tubular ducts arranged in transverse rows on abdominal segments IV–V, and in submarginal and marginal areas of abdominal segments VI–VIII; longer oral-collar tubular ducts present in cluster of 19 (paratypes 14–25) anterior to mouthparts. Long hair-like setae arranged in segmental rows across abdomen, longest seta 96 µm (paratypes 82–106 µm) long, longest seta on abdominal segment V 73 µm (paratypes 72–97 µm) long, longest seta on head 93 µm (paratypes 83–95 µm) long. Circulus divided into 2 oval parts on abdominal segment III, each part 71–72 µm (paratypes 71–104 µm) in diameter; one paratype female with 1 additional circulus on segment IV, only present on right side, 89 µm in diameter. Labium 226 µm (paratypes 240–249 µm) long. Antennae each 9-segmented, each about 735 µm (paratypes 777–848 µm) long; apical segment 131 µm (paratypes 137–146 µm) long, segment III 108 µm (paratypes 116–123 µm) long; antennal intersegmental sensilla present between segments III and IV, IV and V, and VI and VII; coeloconic sensilla present on segments II, V, and IX. Hind tibiae each with small translucent pores. Femora each 363 µm (paratypes 387–419 µm) long, tibiae each 459 µm (paratypes 486–504 µm) long, tibia/tarsus 2.9 (paratypes 2.7–3.0). Hind trochanters each with 3 campaniform sensilla on each surface. Tarsal digitules capitate, claw digitules capitate, longer than claw; claw denticle present but basal spurs present.

Diagnosis: *Puto spath* differs from all other described species of *Puto* by having the following combination of character states: a single divided circulus; claw with a denticle; dorsal oral-rim type tubular ducts absent; oral-rim type tubular ducts associated with cerarii absent; two sizes of ventral multilocular disc-pores abundant; and larger multilocular disc-pores each with 9 outer loculi and a trilocular center present on the posterior abdominal segments.

Puto spath is most similar to *P. bicirculatus* Gavrillov-Zimin, 2023 by having: (i) a divided circulus; (ii) dorsal oral-rim type tubular ducts absent; (iii) claw denticle present; (iv) oral-rim type tubular ducts in the cerarii absent; (v) ventral multilocular disc-pores widely distributed over the body; and (vi) tarsal and claw digitules enlarged/capitate. It differs from *P. bicirculatus* by having (*P. bicirculatus* character states are presented in parentheses): (i) rows of multilocular disc-pores 6 or 7 pores wide on the abdomen (1–2 pores wide); and (ii) well-developed ostioles with setae and trilocular pores on lips (ostioles poorly developed and invisible in paratype specimens).

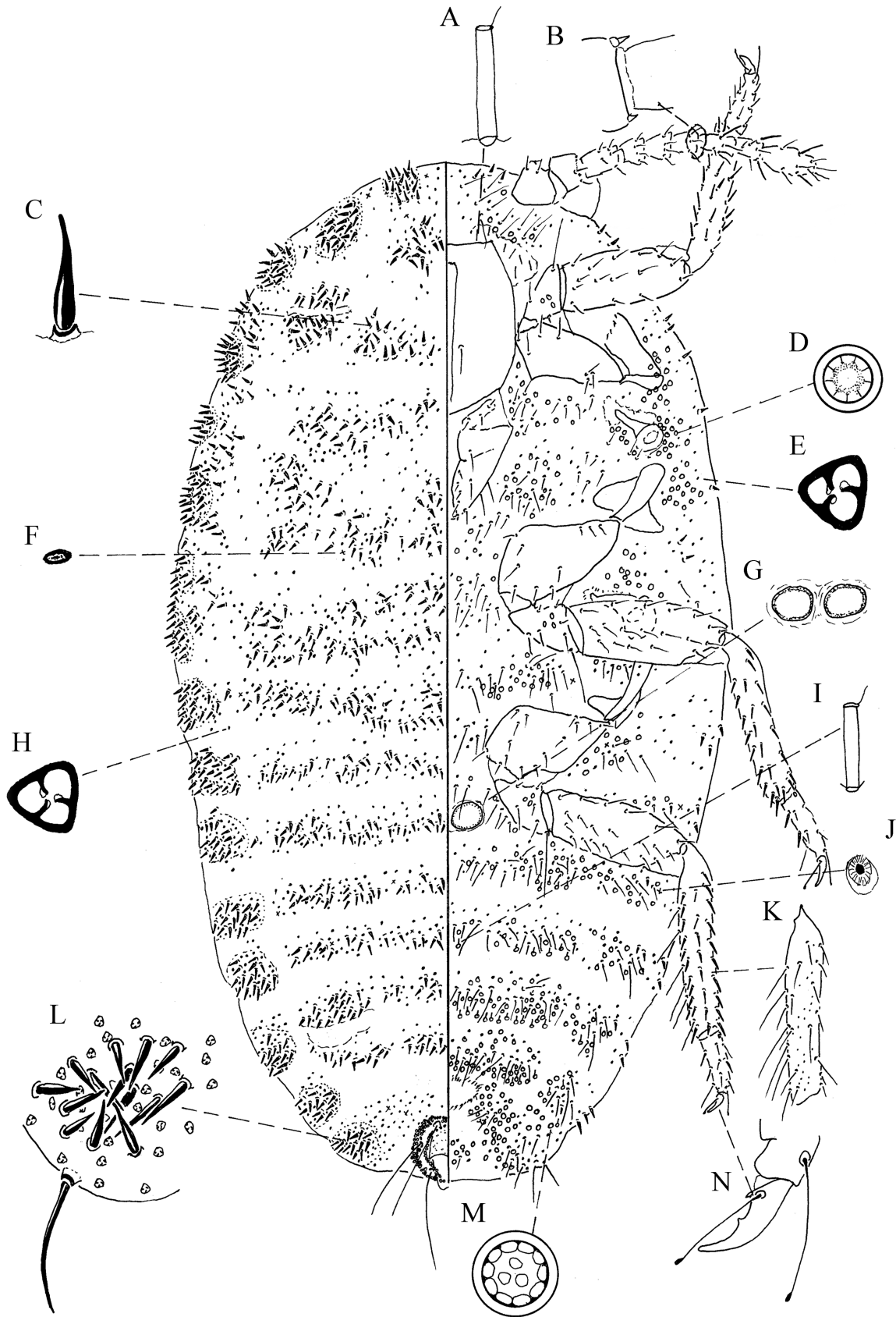


FIGURE 7. *Puto spath* Powell & Miller, *sp. n.*, adult female holotype, Guatemala at New Orleans, September 16, 1976, Stafford and Davis, on *Spathiphyllum*, #9134. **A**=long oral-collar tubular duct; **B**=antennal intersegmental sensilla; **C**=dorsal seta; **D**=9-locular pore; **E**, **H**=trilocular pores; **F**, **J**=discoidal pores; **G**=divided circulus; **I**=oral-collar tubular duct; **K**=translucent pores on hind tibia; **L**=anal-lobe cerarius; **M**=large 10-locular pore with trilocular center; **N**=claw.

Puto spath is similar to *P. lamottei* by having: (i) a claw denticle; (ii) oral-rim type tubular ducts in the cerarii absent; and (iii) a divided circulus. It differs from *P. lamottei* by having (*P. lamottei* character states are presented in parentheses): (i) usually only a single divided circulus (a divided circulus on abdominal segment III and a single undivided circulus on abdominal segment IV); and (ii) many multilocular disc-pores in the medial areas of the head and thorax (no multilocular disc-pores in the medial area of the head and thorax, multilocular disc-pores restricted to around the spiracles and vulva).

Third-instar female

(Fig. 8)

Description: Slide-mounted, 2.02–2.28 mm long, 1.06–1.14 mm wide; body elongate oval.

Dorsum with 16 pairs of cerarii; anal-lobe cerarii each with 6–8 lanceolate setae and 12–16 trilocular pores; frontal cerarii each with 7–14 lanceolate setae and 8–12 trilocular pores; antefrontal cerarii not distinct, each with 4–9 loosely clustered setae, without sclerotization; cerarii without associated discoidal pores or oral-rim type tubular ducts; and marginal cerarii with basal sclerotization. Anterior and posterior ostioles present. Multilocular disc-pores absent, trilocular pores of 1 size, numerous, scattered across body; present on lips of ostioles; discoidal pores rare, scattered over body. Oral-rim type tubular ducts and oral-collar tubular ducts absent. Dorsal setae lanceolate, forming rows across abdominal segments II–VII, scattered on head and thorax, with many on margin between cerarii especially on head, but absent from medial area of abdominal segment VIII. Longest seta on abdomen 20–27 µm long, longest seta in abdominal cerarii 27–31 µm long.

Anal ring bent around posterior apex, bearing 6 anal-ring setae with apices acute; posterior anal-ring setae each 175–220 µm long, 1.4–1.9 times as long as greatest diameter of anal ring.

Venter with multilocular disc-pores present on segments II–V, absent from posterior segments, scattered on thorax and head, predominantly 7- and 9-locular. Trilocular pores of 1 size, scattered over body; discoidal pores scattered over body, more abundant on venter than on dorsum. Long oral-collar tubular ducts forming cluster (13–20) on head anterior to mouthparts, absent from rest of thorax and abdomen. Long, hair-like setae forming rows across abdomen, longest ventral setae 71–80 µm long, longest seta on abdominal segment V 57–72 µm long, longest seta on head 73–102 µm long. Circulus divided into 2 oval parts on segment III, each part 39–51 µm in diameter. Labium 197–215 µm long. Antennae each 8-segmented, 664–706 µm long in total; apical segment 123–136 µm long, segment III 99–111 µm long; antennal intersegmental sensilla present between segments V and VI; coeloconic sensilla present on segments IV and VIII. Hind tibia and distal femur with a few translucent pores. Femora each 305–324 µm long; tibiae each 342–398 µm long, tibia/tarsus 2.0–2.2. Hind trochanters each with 2 campaniform sensilla on each surface. Tarsal digitules capitate, longer than claw, claw digitules capitate, longer than claw; claw denticle and basal spurs present.

Diagnosis: The third-instar female of *P. spath* is similar to that of *P. philo* by having: (i) a circulus that is divided into two parts; (ii) ventral multilocular disc-pores present; (iii) tarsal and claw digitules capitate; (iv) dorsal ostioles present; (v) numerous long oral-collar tubular ducts in cluster anterior to mouthparts; and (vi) translucent pores on hind tibiae and sometimes on hind femora. *Puto spath* differs from *P. philo* as follows (distinguishing character states of *P. philo* are given in parentheses): (i) claw denticle present (absent); and (ii) multilocular disc-pores abundant on head, thorax, and anterior abdominal segments (multilocular disc-pores few, present on pro- and mesothorax).

When compared with third-instar females collected 15 miles S. of Nampa, Idaho, March 25, 1955 on shadscale (USNM), determined as *P. atriplicis* McKenzie, 1961, the third-instar females of *P. spath* are similar by having: (i) claw denticle present; (ii) with multilocular disc-pores on venter of head, thorax, and anterior abdominal segments; and (iii) ostioles present. *Puto spath* differs from *P. philo* as follows (distinguishing character states of *P. atriplicis* are given in parentheses): (i) circulus divided (circulus undivided); and (ii) tarsal and claw digitules capitate (digitules apically acute).

Second-instar female

(Fig. 9)

Description: Slide-mounted, 1.59–1.77 mm long, 0.87–1.05 mm wide; body elongate oval.

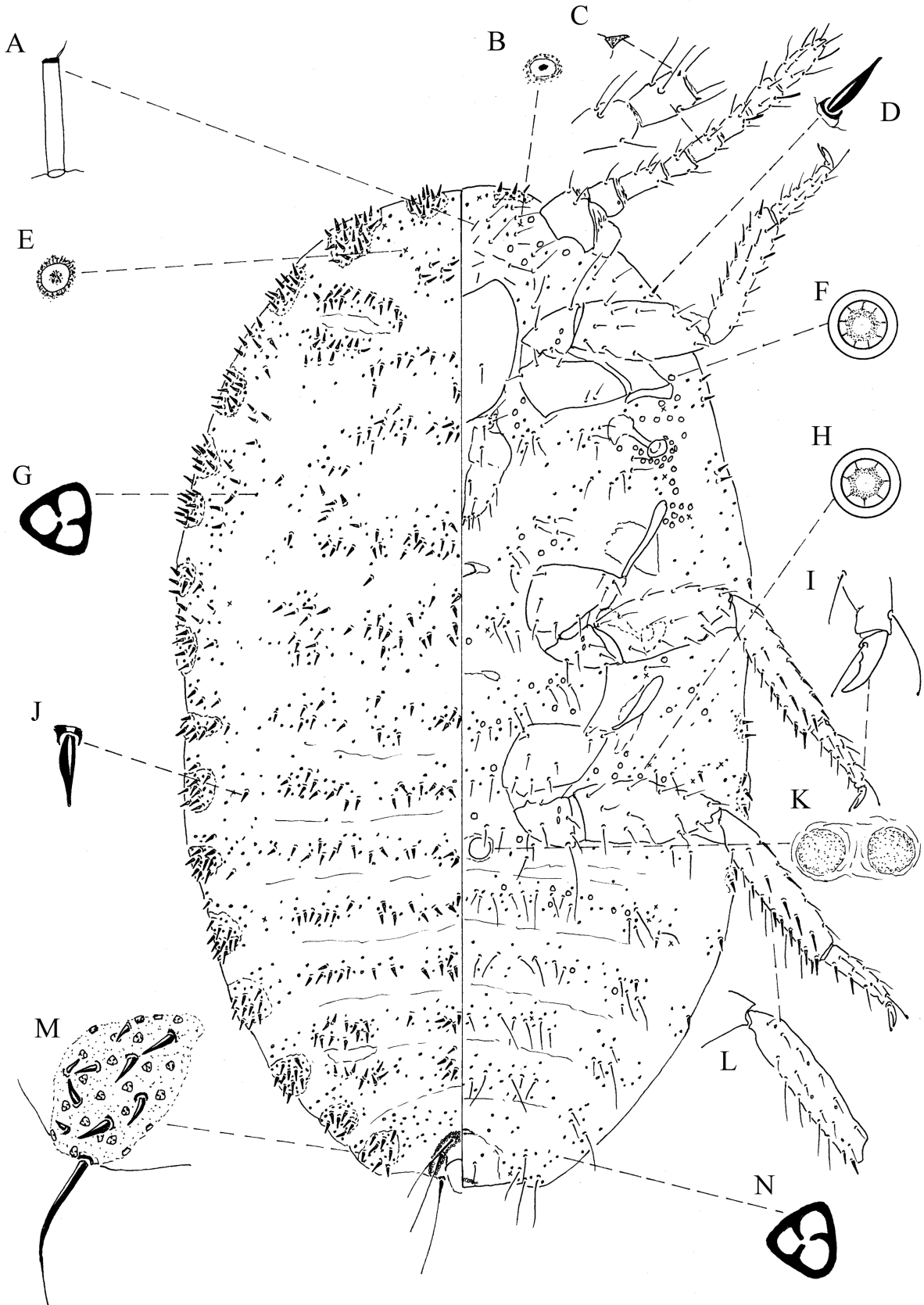


FIGURE 8. *Puto spath* Powell & Miller, *sp. n.*, third-instar female paratype, Guatemala at New Orleans, September 24, 1976, Davis *et al.*, on *Spathiphyllum*, #9154. **A**=long oral-collar tubular duct; **B**, **E**=discoidal pores; **C**=antennal intersegmental sensilla; **D**=marginal seta; **F**=9-locular pore; **G**, **N**=trilocular pores; **H**=7-locular pore; **I**=claw; **J**=dorsal seta; **K**=divided circulus; **L**=translucent pores on hind tibia; **M**=anal-lobe cerarius.

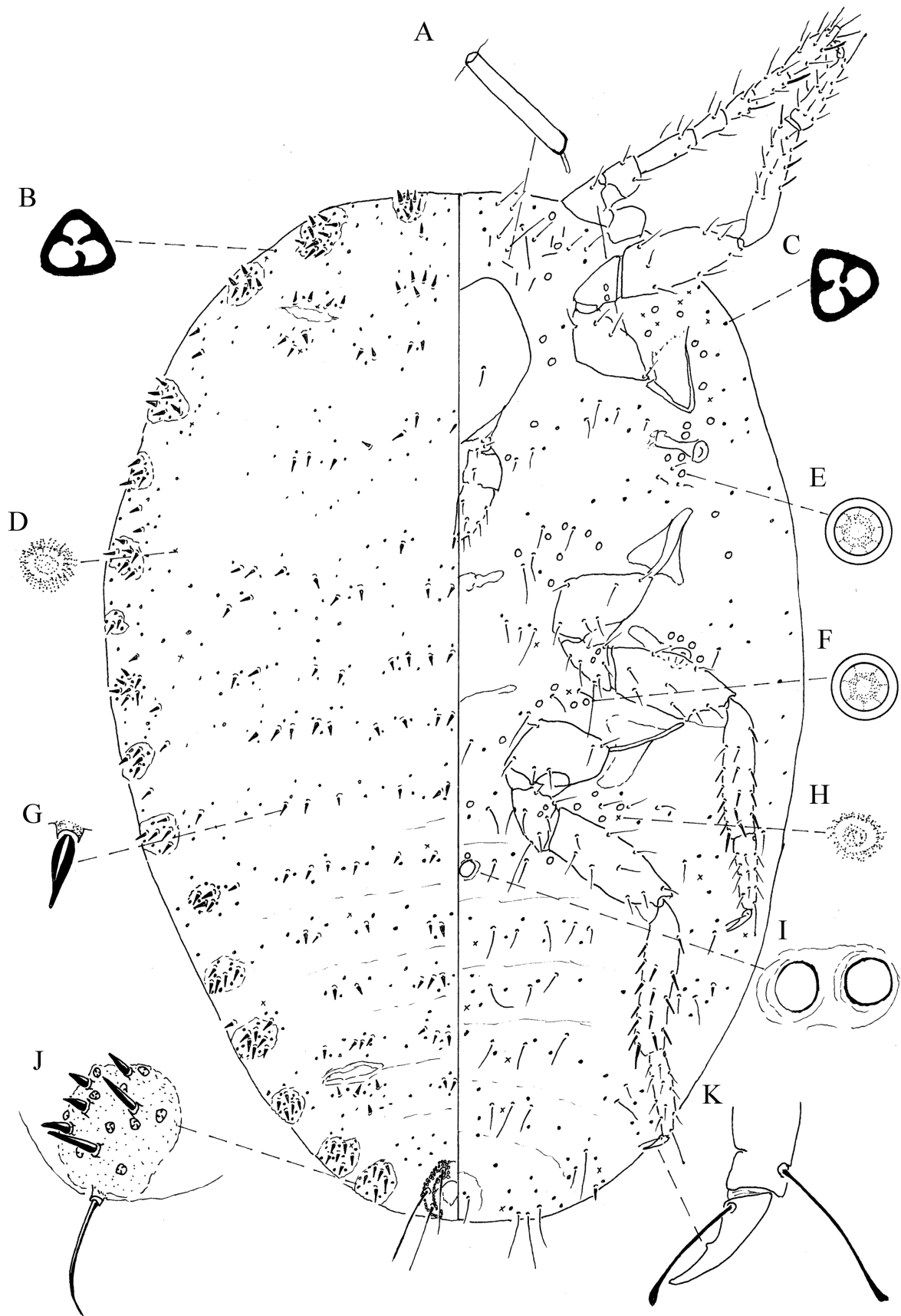


FIGURE 9. *Puto spath* Powell & Miller, *sp. n.*, second-instar female paratype, Guatemala at Miami, October 20, 1976, Matthews, on *Spathiphyllum*, #14810. **A**=long oral-collar tubular duct; **B**, **C**=trilobular pores; **D**, **H**=discoidal pores; **E**=9-locular pore; **F**=7-locular pore; **G**=dorsal seta; **I**=divided circulus; **J**=anal-lobe cerarius; **K**=claw.

Dorsum with 16 pairs of cerarii, anal-lobe cerarii each with 5–6 lanceolate setae and 7–12 trilocular pores, frontal cerarii each with 6–9 lanceolate setae and 8–9 trilocular pores; antefrontal cerarii not distinct, each with 3–7 loosely clustered setae, without sclerotization; cerarii without associated discoidal pores or oral-rim type tubular ducts; and marginal cerarii with weak basal sclerotization. Anterior and posterior ostioles present. Multilocular disc-pores absent; trilocular pores of 1 size, larger than those on venter, numerous, scattered over body, more numerous on dorsum than on venter, present near, or on, lips of ostioles; discoidal pores few, scattered over body. Oral-rim type tubular ducts and oral-collar tubular ducts absent. Dorsal setae lanceolate, scattered across body and present near, or on, lips of ostioles; longest seta on abdomen 21–25 µm long, longest seta in abdominal cerarii 28–29 µm long.

Anal ring dorsal or bent around posterior apex, bearing 6 anal-ring setae with apices acute; posterior anal-ring setae each 132–152 µm long, 1.4–1.6 times as long as greatest diameter of anal ring.

Venter with multilocular disc-pores in medial area from head to segment III, predominantly each 7-locular. Trilocular pores of 1 size, smaller than those on dorsum, scattered over body; discoidal pores scattered over body. Long oral-collar tubular ducts of 1 size forming cluster (10–13) on head anterior to mouthparts. Long, hair-like setae sparse, forming rows across abdomen, longest on head, longest seta on abdomen 54–70 µm long, longest seta on segment V 45–51 µm long, longest seta on head 68–72 µm long. Circulus divided into 2 oval parts on segment III, each part 19–25 µm in diameter. Labium 168–178 µm long. Antennae each 7-segmented, total 548–600 µm long, apical segment 112–123 µm long, segment III 116–133 µm long; antennal intersegmental sensilla present between segments IV and V; coeloconic sensilla present on segments III and VII. Hind legs without translucent pores. Femora each 238–265 µm long; tibiae each 274–312 µm long, tibia/tarsus 1.7–1.9. Hind trochanters each with 2 campaniform sensilla on each surface. Tarsal digitules capitate, claw digitules capitate, longer than claw; claw denticle and basal spurs present.

Diagnosis: The second-instar female of *P. spath* is similar to that of *P. philo* by having: (i) a circulus that is divided into two parts; (ii) ventral multilocular disc-pores present; (iii) tarsal and claw digitules capitate; (iv) dorsal ostioles present; and (v) numerous long oral-collar tubular ducts in cluster anterior to mouthparts. It differs from *P. philo* by having (character states of *P. philo* are given in parentheses): (i) the claw denticle present (absent); and (ii) multilocular disc-pores abundant of head, thorax, and anterior abdominal segments (with few multilocular disc-pores, present on the pro- and mesothorax).

When compared with second-instar females collected 18 miles S.W. of Mt. Home, Idaho, April 6, 1958 on shadscale (USNM), determined as *P. atriplicis*, the second-instar females of *P. spath* are similar by having: (i) claw denticle present; (ii) ostioles present; and (iii) oral-collar tubular ducts absent from both body surfaces. It differs from *P. atriplicis* as follows (distinguishing character states of *P. atriplicis* are given in parentheses): (i) circulus divided (circulus undivided); (ii) tarsal and claw digitules capitate (digitules apically acute); and (iii) with multilocular disc-pores on venter of head, thorax, and anterior abdominal segments (multilocular disc-pores on pro- and mesothorax).

Second-instar male

(Fig. 10)

Description: Slide-mounted, 1.74–2.75 mm long, 1.03–1.46 mm wide; body elongate oval.

Dorsum with 16 pairs of cerarii, anal-lobe cerarii each with 4–7 lanceolate setae and 10–13 trilocular pores; frontal cerarii each with 6–9 lanceolate setae and 7–10 trilocular pores; antefrontal cerarii not distinct, each with 4–10 loosely clustered setae, without sclerotization; marginal cerarii each with basal sclerotization; and cerarii without associated discoidal pores or oral-rim type tubular ducts. Anterior and posterior ostioles weakly developed. Multilocular disc-pores absent; trilocular pores of 1 size, larger than those on venter, numerous, scattered across body, more numerous on dorsum than on venter, present on lips of ostioles; discoidal pores few, scattered across body. Oral-collar tubular ducts of 1 size, scattered over body. Oral-rim type tubular ducts absent. Dorsal setae lanceolate, few, scattered across body, longest seta on abdomen 20–23 µm long, longest seta in abdominal cerarii 28–30 µm long.

Anal ring dorsal, bearing 6 anal-ring setae with apices acute; posterior anal-ring setae each 125–164 µm long, 1.3–1.7 times as long as greatest diameter of anal ring.

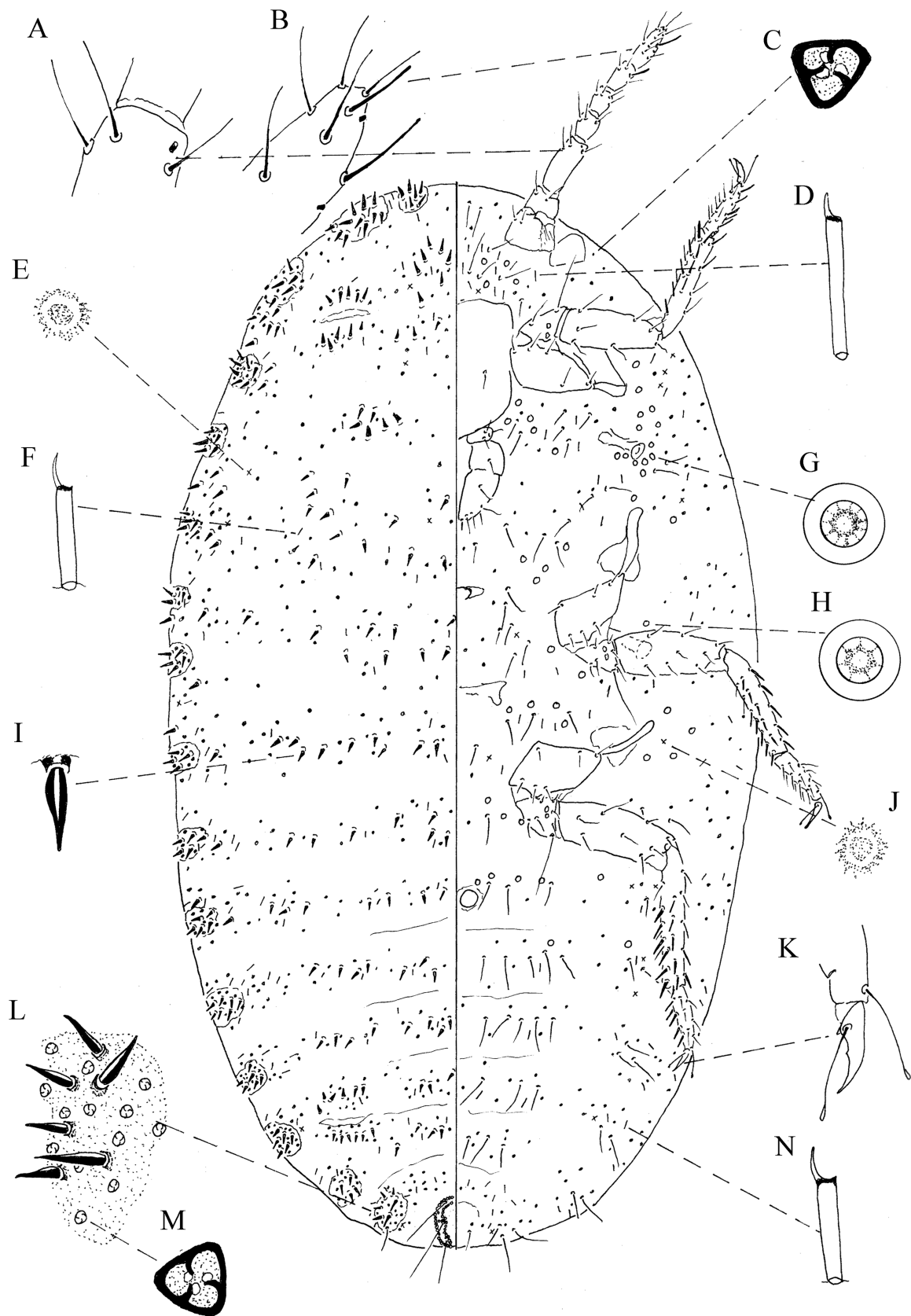


FIGURE 10. *Puto spath* Powell & Miller, *sp. n.*, second-instar male paratype, Guatemala at New Orleans, September 24, 1976, Davis *et al.*, on *Spathiphyllum*, #9154. **A**=coeloconic sensilla on third segment of antenna; **B**=coeloconic sensilla on apical segment of antenna; **C**, **M**=trilocular pores; **D**=long oral-collar tubular duct; **E**, **J**=discoidal pores; **F**, **N**=oral-collar tubular duct; **G**=11-locular pore; **H**=7-locular pore; **I**=dorsal seta; **K**=claw; **L**=anal-lobe cerarius.

Venter with multilocular disc-pores scattered over thorax and head, and on segments II–IV, predominantly 7-locular but with some 11-locular. Trilocular pores of 1 size, smaller and fewer than those on dorsum, scattered across body; discoidal pores scattered across body. Oral-collar tubular ducts of 2 sizes, shorter ones scattered over entire body, longer oral-collar tubular ducts forming cluster (9–10) anterior to mouthparts. Long, hair-like setae sparse, forming rows across abdomen, longest on head, longest seta on abdomen 61–74 μm long, longest seta on segment V 44–67 μm long, longest seta on head 78–101 μm long. Circulus divided into 2 oval parts on segment III, each part 29–42 μm in diameter. Labium 185–194 μm long. One specimen with horizontal eight-shaped circulus (not fully divided) 86 μm long. Antennae each 7-segmented, total 600–656 μm long, apical segment 112–132 μm long, segment III 129–143 μm long; antennal intersegmental sensilla present between segments IV and V; coeloconic sensilla present on segments III and VII. Hind legs without translucent pores. Femora each 278–295 μm long; tibiae each 346–358 μm long, tibia/tarsus 2.1–2.3. Hind trochanters each with 2 campaniform sensilla on each surface. Tarsal digitules capitate, claw digitules capitate, longer than claw; claw denticle and basal spurs present.

Diagnosis: The second-instar male of *P. spath* is similar to that of *P. philo* by having: (i) oral-collar tubular ducts scattered over both body surfaces; (ii) a circulus that is divided into two parts; (iii) ventral multilocular disc-pores present; and (iv) tarsal and claw digitules capitate. It differs from *P. philo* as follows (distinguishing character states of *P. philo* are given in parentheses): (i) claw denticle present (absent); and (ii) multilocular disc-pores abundant on head, thorax, and anterior abdominal segments (few multilocular disc-pores few, restricted to pro- and mesothorax).

When compared with second-instar males collected 18 miles S.W. of Mt. Home, Idaho, April 6, 1958 on shadscale (USNM), determined as *P. atriplicis*, the second-instar males of *P. spath* are similar by having: (i) claw denticle present; (ii) multilocular disc-pores on venter of head, thorax, and anterior abdominal segments; (iii) ostioles present; and (iv) oral-collar tubular ducts present over both body surfaces. It differs from *P. atriplicis* as follows (distinguishing character states of *P. atriplicis* are given in parentheses): (i) circulus divided (circulus undivided); and (ii) tarsal and claw digitules capitate (digitules apically acute).

First-instar nymph (sexes undetermined)

(Fig. 11)

Description: Slide-mounted, 0.90–1.41 mm long, 0.58–0.89 mm wide; body elongate oval.

Dorsum with 17 pairs of cerarii, some split, anal-lobe cerarii each with 2 lanceolate setae and 6–8 trilocular pores; cerarii without associated oral-rim type tubular ducts; frontal cerarii each with 3–5 setae and 4–6 trilocular pores; antefrontal cerarii not distinct, each with 3–5 loosely clustered setae, without sclerotization; marginal cerarii with basal sclerotization but level of sclerotization variable among specimens. Ostioles undetectable. Multilocular disc-pores absent; trilocular pores of 1 size, numerous, scattered across body, more numerous on dorsum than on venter; discoidal pores large, about same size as trilocular pores, present in basal sclerotization of some posterior cerarii. Oral-rim type tubular ducts and oral-collar tubular ducts absent. Dorsal setae lanceolate, few, in three pairs of longitudinal lines, longest seta on abdomen 18–20 μm long, longest seta in abdominal cerarii 26–28 μm long.

Anal ring bent around abdominal apex, bearing 6 anal-ring setae with apices acute, posterior anal-ring setae each 108–128 μm long, 1.5–1.6 times as long as greatest diameter of anal ring.

Venter with multilocular disc-pores present on thorax and head, predominantly each 9-locular. Trilocular pores of 1 size, scattered across body; discoidal pores marginal, large, about same size as trilocular pores, in clusters associated with marginal hair-like setae on abdomen, and in marginal clusters on head. Cluster (5–7) of long oral-collar tubular ducts present anterior to mouthparts. Long hair-like setae, longest on head, forming rows across abdomen, longest seta on abdomen 43–48 μm long, longest seta on segment V 39–44 μm long, longest seta on head 96–102 μm long. Single undivided circulus present on segment III, 26–32 μm in diameter. Labium 132–140 μm long. Antennae each 7-segmented, total 459–538 μm long, apical segment 109–156 μm long, segment III 91–98 μm long; antennal intersegmental sensilla present between segments IV and V; coeloconic sensilla present on segment VII. Hind legs without translucent pores. Femora each 199–208 μm long; tibiae each 237–256 μm long, tibia/tarsus 1.5. Hind trochanters each with 2 campaniform sensilla on each surface. Tarsal digitules capitate, claw digitules capitate, each longer than claw; claw denticle and basal spurs present.

Diagnosis: The first-instar nymph of *P. spath* is most similar to that of *P. philo* by having: (i) a circulus; (ii) three pairs of longitudinal lines of lanceolate setae on the dorsum of the abdomen; (iii) multilocular disc-pores on

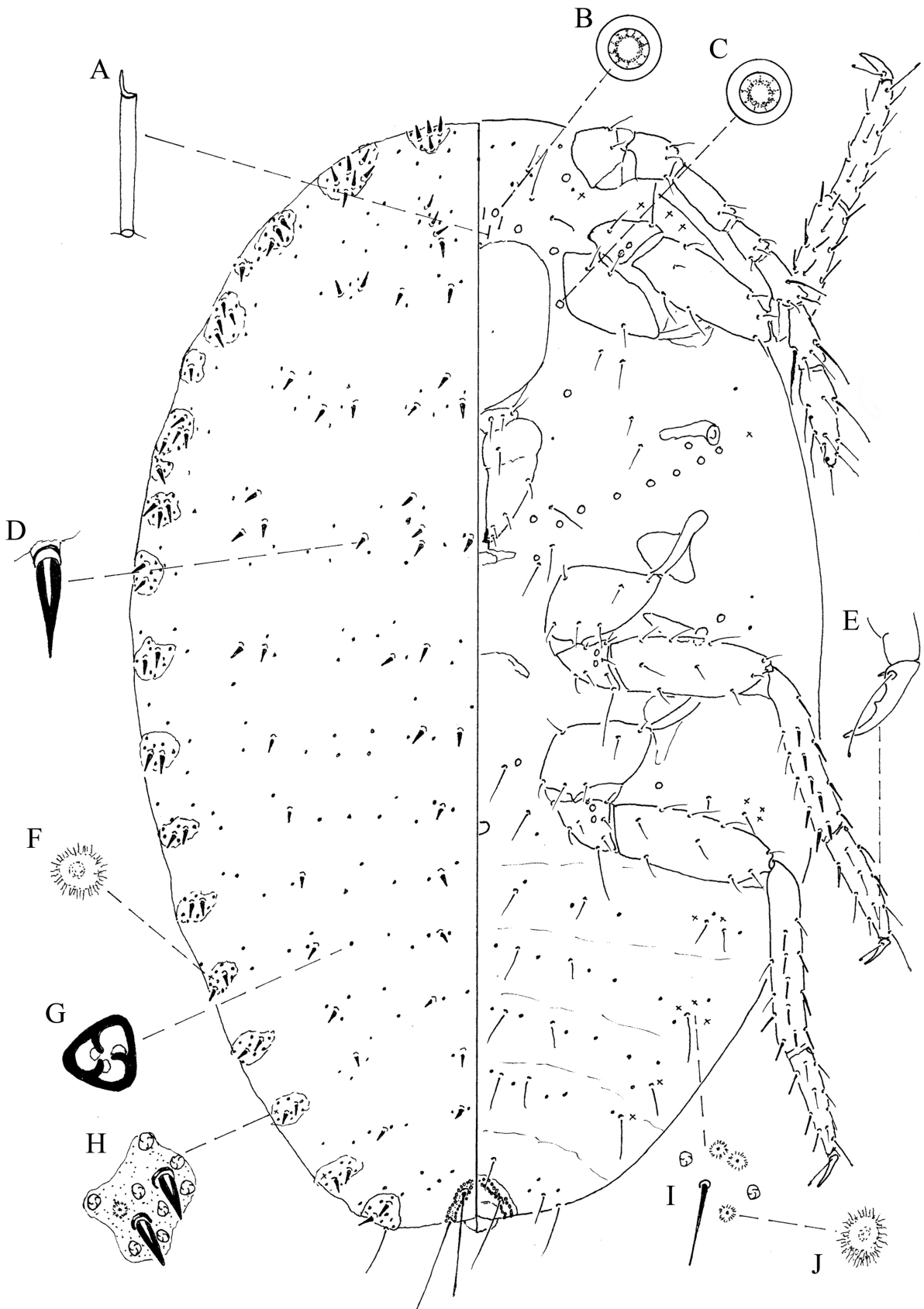


FIGURE 11. *Puto spath* Powell & Miller, *sp. n.*, first instar (sex undetermined) paratype, Guatemala at New Orleans, September 16, 1976, Stafford and Davis, on *Spathiphyllum*, #9134. **A**=long oral-collar tubular duct; **B**=11-locular pore; **C**=9-locular pore; **D**=dorsal seta; **E**=claw; **F**, **J**=discoidal pores; **G**=trilocular pore; **H**=cerarius; **I**=ventral seta with associated trilocular and discoidal pores.

the thorax; (iv) multilocular disc-pores absent from the abdomen; ventral discoidal pores in marginal clusters on abdomen and head; and (iv) a cluster of oral-collar tubular ducts anterior to the mouthparts. It differs from *P. philo* as follows (character states of *P. philo* are presented in parentheses): (i) multilocular disc-pores on the head (absent from the head); (ii) claw with a denticle (without a claw denticle); and (iii) discoidal pores in the posterior abdominal cerarii (without discoidal pores in the posterior cerarii).

When compared with first-instar nymphs collected in Wrightwood, California, on *Eriodictyon* sp., February 9, 1997 (USNM), determined as *P. yuccae*, the first-instar nymphs of *P. spath* are similar by having: (i) ventral multilocular disc-pores; (ii) three pairs of longitudinal lines of lanceolate setae on the dorsal abdomen; and (iii) discoidal pores in marginal areas of the venter. It differs from *P. yuccae* as follows (character states of *P. yuccae* are presented in parentheses): (i) a small circulus (circulus absent); (ii) no multilocular disc-pores on the abdomen (multilocular disc-pores present on the abdomen); and (iii) ostioles absent (present).

When compared with first-instar nymphs collected from Weeks, Nevada, on *Atriplex* sp., July 5, 1968 (USNM), determined as *P. atriplicis*, the first-instar nymphs of *P. spath* are similar in having: (i) ventral multilocular disc-pores; (ii) no multilocular disc-pores on the abdomen; (iii) three pairs of longitudinal lines of lanceolate setae on the abdomen; and (iv) a circulus. It differs from *P. atriplicis* as follows (character states of *P. atriplicis* are presented in parentheses): (i) capitate tarsal and claw digitules (digitules apically acute); and (ii) usually with more than one submarginal discoidal pore on each side of each abdominal segment (usually with one on each side of each abdominal segment).

***Puto brom* Powell & Miller, sp. n.**

Suggested common name: bromeliad giant mealybug

Material examined

Holotype adult female mounted singly on slide. Left label “Puto / Mexico / ex Bromeliad leaf / IX-23-74 / Nogales 2962 / J. Kaiser, R. Duke / Balsam.” Right label “Puto brom / Powell & Miller / n.sp.”, USNM.

Paratype: Same data as holotype (1 adult ♀ on 1 slide) USNM.

Other material examined: MEXICO: Veracruz, taken in quarantine at Brownsville, Texas, September 17, 1975, coll. Burgess, Chace, Arsego, ex. bromeliad leaf. (1 ad. ♂ on 1 slide) USNM.

Etymology: The species epithet “*brom*” is a noun in apposition based on an abbreviation of the scientific name of the host plant, an unknown species of Bromeliaceae.

Adult female

(Fig. 12)

Description: Slide-mounted holotype 8.65 mm long, 5.4 mm wide; paratype 8.7 mm long, 5.15 mm wide; body elongate oval.

Dorsum with 18 or 19 pairs of cerarii; anal-lobe cerarii each with 15–17 lanceolate setae (paratype 16–19), 14 or 15 trilocular pores (paratype 12–13), 10–12 large-sized oral-rim type tubular ducts (paratype 11–12), each duct 18–19 µm in diameter, and 1 or 2 smaller-sized oral-rim type tubular ducts also in sclerotized area, each about 11 µm in diameter (paratype 8 µm); additional areas of large-sized oral-rim type tubular ducts, cerarian setae with basal sclerotization, and trilocular pores, present marginally outside of sclerotized cerarii; frontal cerarii each with 9–11 lanceolate setae (paratype 10 or 11), 4 or 5 trilocular pores (paratype 2–3), and 4 oral-rim type tubular ducts (paratype 4); each cerarius without associated discoidal pores; marginal cerarii with basal sclerotization. Anterior and posterior ostioles present. Multilocular disc-pores absent; trilocular pores of 1 size, numerous, concentrated in medial and submedial clusters with dorsal setae on abdominal segments, scattered over thorax and head, abundant on lips of ostioles; discoidal pores scattered over body. Small oral-rim type tubular ducts only present marginally, interspersed with large oral-rim type tubular ducts. Dorsal setae lanceolate, forming concentrated medial and submedial clusters on abdominal segments II–VII and scattered elsewhere, clustered on lips of ostioles, scattered on head and thorax, and present on margin between cerarii on head and thorax. Longest seta on abdomen about 26 µm (paratype 22 µm) long, thinner than cerarian setae, longest seta in abdominal cerarii 32 µm (paratype 34 µm) long.

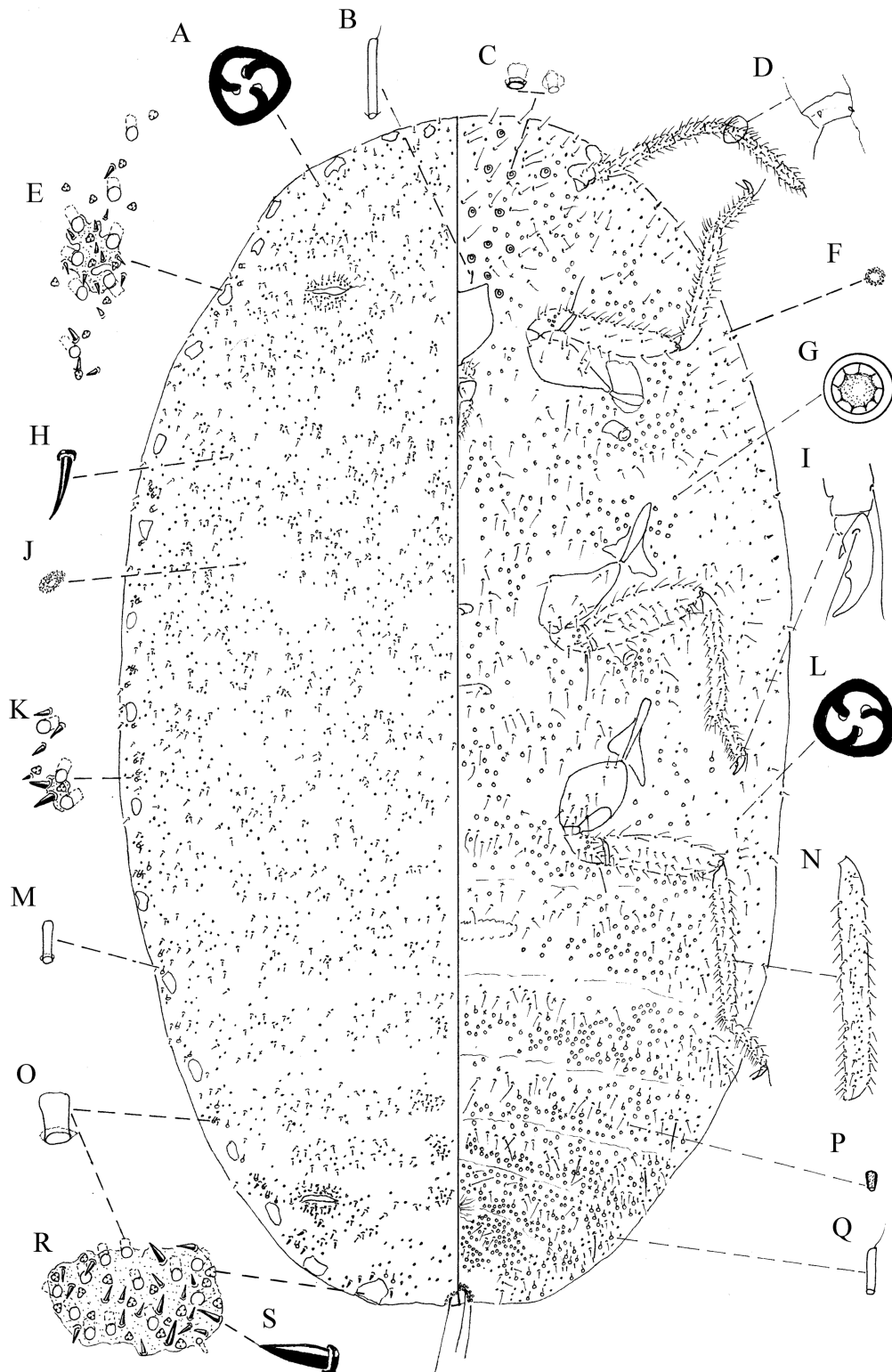


FIGURE 12. *Puto brom* Powell & Miller, *sp. n.*, adult female holotype, Mexico at Nogales, September 23, 1974, Kaiser and Duke, on bromeliad leaf, #3962. **A, L**=trilocular pores; **B**=long oral-collar tubular ducts; **C, P, Q**=three types of oral-collar tubular ducts; **D**=antennal intersegmental sensilla; **E**=cerarius with broken areas of large oral-rim type tubular ducts, cerarian setae, and basal sclerotization; **F, J**=discoidal pores; **G**=9-locular pore; **H**=dorsal seta; **I**=claw; **K**=areas of oral-rim type tubular ducts, cerarian setae with basal sclerotization, and trilocular pores between cerarii; **M**=small oral-rim type tubular duct; **N**=translucent pores on tibia; **O**=marginal large oral-rim type tubular ducts; **R**=anal-lobe cerarius; **S**=cerarian seta. Note that cerarii are illustrated as open irregular ovals on margin because the specimen was too large to incorporate fine detail, see enlargement **R**.

Anal ring bent around abdomen apex, bearing 6 anal-ring setae with apices acute; posterior anal-ring setae each 428 µm (paratype 408 µm) long; 2 times (paratype 1.83 times) as long as greatest diameter of anal ring.

Venter with multilocular disc-pores abundant on abdominal segments II–VIII, especially abundant on posterior margin of V and on VI–VIII, also on thorax and head; multilocular disc-pores on abdomen predominantly 9-locular, with some 10-locular. Trilocular pores of 1 size, numerous, scattered over body; discoidal pores scattered over body. Oral-collar tubular ducts of 4 sizes; with 2 sizes of shorter oral-collar tubular ducts abundant on segments IV–VIII, and scattered on thorax and head; 1 or 2 long oral-collar tubular ducts present anterior to mouthparts; and fourth type of oral-collar tubular duct scattered, numbering 10 (paratype 12) anterior to mouthparts, poorly sclerotized, wide and short, unlike typical elongate oral-collar tubular ducts in cluster anterior to mouthparts found in other species of *Puto*. Long hair-like setae forming rows across abdomen, longest ventral seta 226 µm (paratype 201 µm) long, longest seta on segment V 169 µm (paratype 151 µm) long, longest seta on head 226 µm (paratype 200 µm) long. Circulus elongate oval, 890 µm long by 127 µm wide (paratype 818 µm long by 147 µm wide). Labium 440 µm (paratype 448 µm) long. Antennae each 9-segmented, total length 1.99 mm (paratype with both antennae broken); apical segment 238 µm long, segment III 323 µm (paratype 340 µm) long; antennal intersegmental sensilla present between segments III and IV, IV and V, and VI and VII; coeloconic sensilla present on segment IX. Hind tibiae each with small translucent pores. Femora each 1.03 mm (paratype 1.07 mm) long, tibiae each 1.21 mm (paratype 1.31 mm) long, tibia/tarsus 3.16 (paratype 3.00). Hind trochanters each with 4 campaniform sensilla on each surface. Tarsal digitules acute, claw digitules acute, as long as claw; claw denticle and basal spurs present.

Remarks: Coeloconic sensilla were difficult to observe on these specimens due to the stain. We only observed them on segment IX on this species but anticipate that they could be present on other segments, given what we have seen in other species of *Puto*.

Diagnosis: *Puto brom* is most similar to *P. lasiorum* (Cockerell, 1901) by having: (i) oral-rim type tubular ducts in the cerarii but not in the medial areas of the dorsum, and (ii) clusters of lanceolate setae dorsomedially on the posterior abdominal segments. It differs from *P. lasiorum* as follows (characters of *P. lasiorum* are presented in parentheses): (i) small cerarii, with the anal-lobe cerarius about half the size of the hind coxa (anal-lobe cerarius about equal in size to the hind coxa); (ii) dorsomedial clusters of lanceolate setae without conspicuous sclerotization (with conspicuous sclerotization); and (iii) two sizes of oral-rim type tubular ducts outside of abdominal cerarii on dorsum (with one size of oral-rim type tubular duct outside of the abdominal cerarii on dorsum).

Adult male (macropterous)

(Figs 13, 14b)

Description: Slide-mounted; body elongate, with abdominal segment VIII produced laterally.

Dorsum with 1 pair of glandular pouches (gp); each glandular pouch with 2 setae, each apically acute, setae approximately same size, about 280 µm long. Multilocular disc-pores in glandular pouches, each glandular pouch with about 263 tightly clustered pores, each multilocular disc-pore with predominantly 5 loculi with some 4 loculi; discoidal pores absent, setae around margin of glandular pouches; tubular ducts (gpt) present at base of glandular pouch setae (gls). Multilocular disc-pores in cluster on prothorax, segmental row one pore wide on metathorax and abdominal segments I–VII, predominantly with 4 loculi. Hair-like setae (hs) slender, apically acute, shorter than those on venter, in segmental rows, with marginal clusters on each side of each segment; setae on pro-, meta-, and mesothorax; head setae anterior to postoccipital ridge (por), on ocular sclerite (ocs), along dorsal arm of midcranial ridge (dmcr). Microtrichia (not illustrated) on all abdominal segments. Posterior ostioles (po) present (not illustrated), poorly developed. Abdominal tergites (at) with 2 areas of sclerotization on posterior margin of each segment from abdominal segments II–V; segment VIII with heavily sclerotized yoke-shaped medial tergal plate (mtp) on anterior margin; metapostnotal sclerite present (not illustrated); metapostnotal ridge absent. Scutellum (scl) well developed, with 38 setae; scutellar ridge (sclr) well-developed. Scutum (sct) sclerotized throughout, except for medial triangular membranous area (mta) anterior to scutellum. Prescutum, prescutal suture, and prescutal setae absent. Pronotal ridges (prnr) well developed (not illustrated); pronotal sclerites (prn) present (not illustrated). Hamulohalteres each with 3 or 4 setae (not illustrated). Wings each 3.05 mm long, covered in microtrichia, each with alar lobe (al), alar sclerites (alsc), and veins (wv) including subcosta (sc) arising from alar sclerites; radius (r) joining subcosta; possible media (m) represented by sclerotized area arising 1/4 distance from alar sclerite, cubitus anterior (cua) present, not joined with other veins; cubitus posterior (cup) arising from alar sclerites, additional

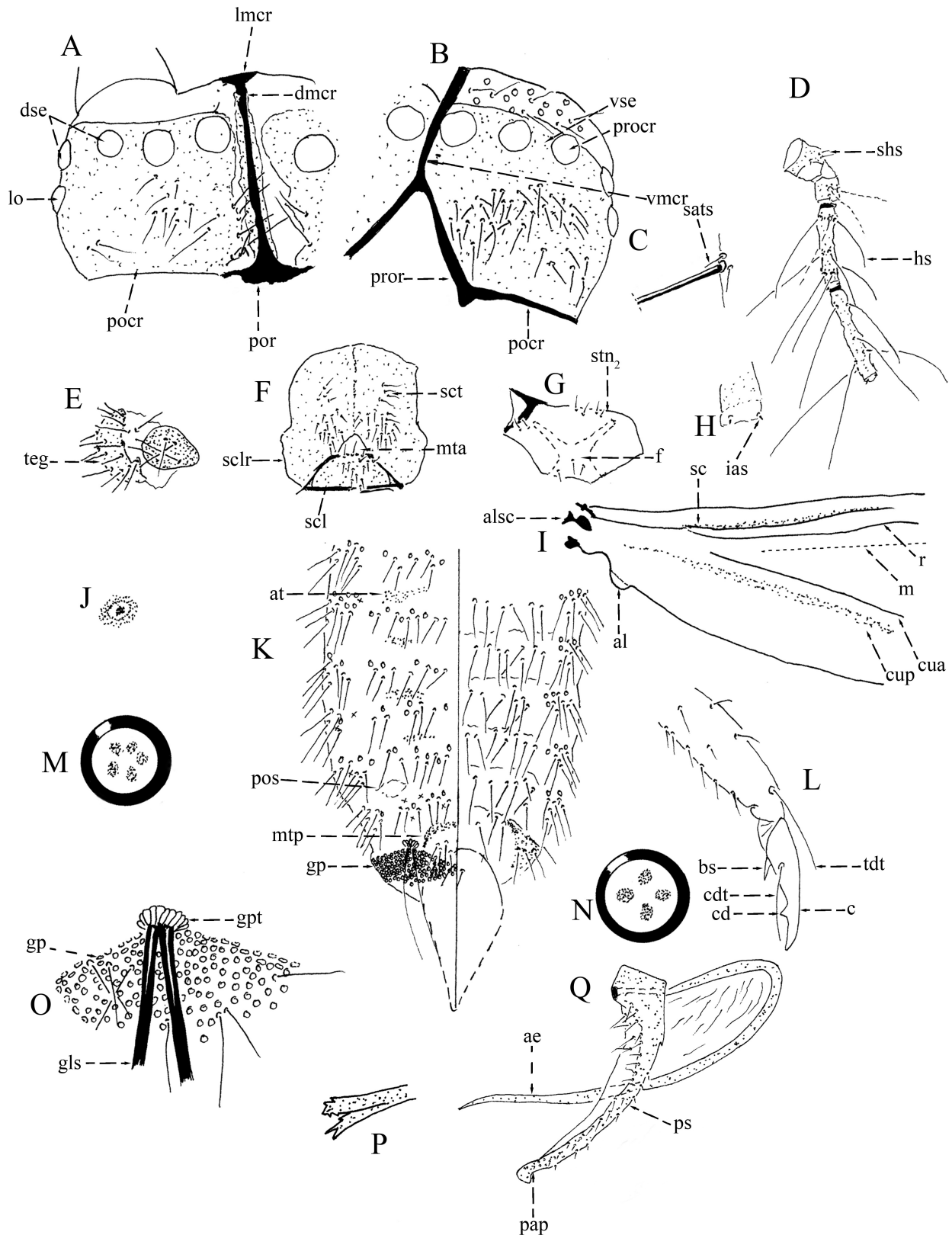


FIGURE 13. *Puto brom* (?) Powell & Miller, *sp. n.*, adult male, Veracruz, Mexico at Brownsville, July 17, 1975, Burgess, Chase, and Arsego, on bromeliad leaf, #5230. **A**=dorsum of head; **B**=venter of head; **C**=satellite setae next to long hair-like seta; **D**=first four segments of antenna; **E**=tegula; **F**=scutellum; **G**=sternum; **H**=antennal intersegmental sensilla; **I**=wing; **J**=discoidal pore; **K**=abdomen, ventral and dorsal views; **L**=claw; **M**=quinquelocular pore; **N**=quadrilocular pore; **O**=glandular pouch; **P**=apex of aedeagus; **Q**=lateral view of penial sheath. Note that the illustrations are based on a single specimen dissected into many pieces.

band of sclerotization anterior to cubitus anterior; without setae and sensoria. Tegula (teg) each with 20 setae. Postoccipital ridge (por) well developed, fused with postocular ridge (pocr). Dorsal arm of midcranial ridge (dmcr) narrow, touching postoccipital ridge posteriorly; with anterior swelling, connected to lateral (lmcr) arms anteriorly; surrounded by median crest (mc) with irregular sclerotization with about 2 setae, with membranous area between ocular sclerite and sclerotization surrounding dorsal arm of midcranial ridge; ocular sclerite with setae not in distinct clusters, with 18 setae on each side. With 3 dorsal simple eyes (dse) on each side, those nearest dorsal arm of midcranial ridge largest, each 53 μm long, on lateral edge smallest, each 38 μm long. Lateral ocellus (lo) about same size as lateral simple eye, each 43 μm in diameter.

Genitalia on side, anus not visible. Penial sheath (ps) 625 μm long; elongate, apically with several small papillae (pap); anterior portion with 17 long setae, each about 90 μm long, posterior portion with about 10 small setae, each about 12 μm long. Aedeagus (ae) u-shaped, attached on membranous surface, about 1.43 mm long, apex bifurcate, one side with three small denticles, other with five.

Venter with multilocular disc-pores present near anterior and posterior spiracles (not illustrated), in marginal clusters on abdominal segments II–VII, medially between mesothoracic legs (not illustrated), anterior to mesosternum (stn_2), in cluster laterad to proepisternum + cervical sclerite (pepcv) (not illustrated), in cluster (10) on unsclerotized area anterior to ocular sclerite and preocular ridge (pocr). with predominantly 4 loculi on abdomen, with predominantly five-loculi around spiracles, with both 4 and 5 loculi on head. Discoidal pores present around spiracles (not illustrated). With hair-like setae, apically acute, longer than those on dorsum, in lateral clusters and in segmental rows on abdomen, in clusters on metathorax, mesothorax, and prothorax; head setae abundant in cluster, about 35 on each side, on medial area of ocular sclerite (ocs) posterior to ventral simple eyes (vse), present (about 12) (specimen rolled) near midline of head between antennal base and ventral eye (ve) anterior to preocular ridge. Microtrichia on II–VIII (not illustrated). Abdominal sternites without sclerotization, abdominal segment VIII with sclerotization mediolaterally. Metapleural ridge well developed, with two precoxal ridge extensions, the anterior one longer, reaching the metasternal apophysis (not illustrated). Mesosternum (stn_2) well-developed, with large furca (f); lateropleurites on mesothorax triangular, with membranous area between lateropleurite and mesepisternum (not illustrated). Mesopleural ridge with precoxal ridge of mesothorax and additional posterior ridge extension anterior to mesocoxal articulation (not illustrated). Prosternum (stn_1) with sclerotized prosternal ridge that ends with a prosternal apophysis, surrounded by well-developed sclerotized triangular sclerite (not illustrated). Proepisternum and cervical sclerite (pepcv) well developed (not illustrated). Preoral ridge (pror) well developed, fused with postocular ridge (pocr). Ventral midcranial ridge (vmcr) well developed anteriorly, extending to lateral arms (lmcr) between antennae, fused with preocular ridge and preoral ridge. Ocular sclerite (ocs) sclerotized throughout, area anterior to preocular ridge unsclerotized. Mouth displaced, but apparently present (not illustrated). Cranial apophysis not clearly visible. With 4 ventral simple eyes (vse) on each side, those nearest dorsal arm of midcranial ridge largest, each 55 μm long, those on lateral edge smallest, each 41 μm long. Totalling seven pairs of simple eyes and one pair of ocelli wrapping around head. Metathoracic legs longest, coxa 303 μm long, trochanter 177 μm long, femur 647 μm long, tibia 1.00 mm long, tarsus 284 μm long, claw (c) 72 μm long, tibia/tarsus 3.5. Hind trochanter each with 4 campaniform sensilla (camp) on each surface. Claw with denticle (dt) and pair of basal spurs (bs); digitules on tarsus (tdt) acute, shorter than claw; digitules on claw (cdt) acute, shorter than claw. Spine-like setae on tarsus, tibia; long hair-like setae on tibia, femur, trochanter, and coxa; many hair-like setae on trochanter, femur, and tibia with satellite setae, short hair-like setae on all segments. Antenna likely 10-segmented; third antennal segment about 1.6 times longer than apical segment, last segment apically rounded or pointed. Elongate hair-like setae (hs) on segments II–X, many with a very small satellite seta (sats); short setae (shs) on first 3 segments, antennal bristles (not illustrated) on apical 3 segments; a pair of antennal intersegmental sensilla present at least between segments III and IV; coeloconic sensilla present at least on segments II and X.

Remarks: The male was not collected in association with the females, but both were taken in quarantine from Mexico on the same host, within the span of a year. Thus, we cannot be sure that the male described above is *P. brom* and the specimen is therefore not included in the type series. The description is based on a single specimen that was dissected into many pieces. Parts of the description (e.g., total body length or width of penial sheath) are missing where measurements were not able to be taken and the illustration reflects the condition of the specimen. Nineteen antennal segments were broken into ten separate pieces on the slide, making it difficult to ascertain which segments were which. Segments I–IV from the right side of the head were together and intact and the apical three segments of an unknown side were also still together. See the “Remarks” section of the *P. philo* adult male for comments about wing venation.

Diagnosis: The male of presumed *P. brom* keys out separately from any other known *Puto* male. It is most similar to *P. simmondsiae* McKenzie, 1961 but differs in that the glandular pouch of *P. brom* is larger, each with about 230 pores (160 pores in *P. simmondsiae*). Only two other species of *Puto* are known from Guatemala: *P. mexicanus* (Cockerell, 1893) and *P. ulter* Ferris, 1950. The male of *P. brom* (?) has more setae on each tegula (20) than that of *P. mexicanus* (12) or *P. ulter* (8). Only two species of *Puto* are presently known on bromeliads, *P. ulter* and *P. barberi*. In addition to having fewer setae on the tegula, *P. ulter* also has clubbed tarsal digitules while *P. brom* (?) has simple tarsal digitules. *Puto barberi* is apparently parthenogenetic, no males are known (Villegas García *et al.* 2013).

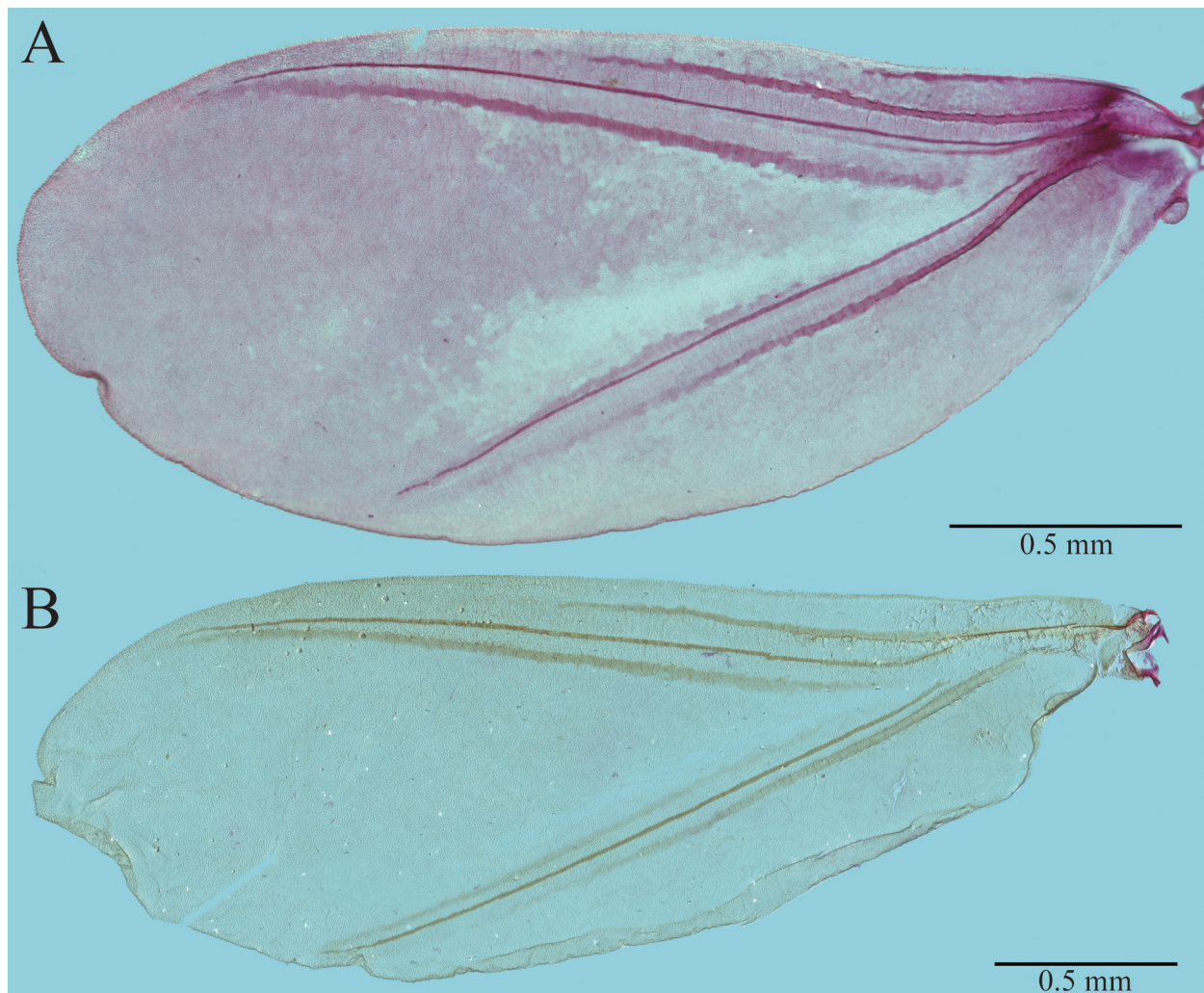


FIGURE 14. The wings of (A) *Puto philo* Powell & Miller, **sp. n.** adult male paratype, Mexico at Laredo, September 15, 1952, Leary, Cary, and Fouts, on *Monstera*, #521475, and (B) *Puto brom* (?) **n. sp.** adult male, Veracruz, Mexico at Brownsville, July 17, 1975, Burgess, Chase, and Arsego, on bromeliad leaf, #5230.

Discussion

We describe three new species of *Puto* giant mealybugs, each taken in quarantine at the US borders several decades ago. The New World *Puto* have not had a revised key since McKenzie (1967) and this key only included North and Central American species. Herein, we provide a key to all of the New World species based on adult females. A key to the World species of *Puto* for adult males was last given in Miller & Miller (1993) and we update and improve that key herein.

Our morphological analyses of these three new species continue to support the placement of *Puto* in its own family, Putoidae. The combination of character states unique to Putoidae is as follows: number of campaniform sensilla on the trochanter; the presence of antennal intersegmental sensilla; a basal spur on the claw of all life stages;

seven-segmented antennae on the first-instar; a row of unicorneal eyes plus a pair of ocelli on adult males; the lack of a prescutum on adult males; the scutum being sclerotized throughout, except for the medial triangular clear area (mta) anterior to scutellum on the adult males; group of tubular ducts at the base of the elongate setae in glandular pouches on the adult males; the cluster of ventral oral-collar tubular ducts anterior to the mouthparts in most instars, and the presence of coeloconic sensilla on antennal segments in addition to those on the apical segment in some instars.

We also noticed a few large translucent pores on the hind tibiae and distal femora in third-instar females of both *P. philo* and *P. spath*, though most conspicuous in *P. philo*. We examined third-instar females of *P. ulter* from Guatemala and found that these also possessed translucent pores on the hind tibiae. Future work on immature *Puto* should take note of this character to determine if it is a general feature across the family. In Eriococcidae, where adults have translucent pores, the translucent pores are also present in females of the final immature instar (second instar) (Granara de Willink & Díaz 2007, Miller & Stocks 2022). For at least some Pseudococcidae, translucent pores in third-instar females are absent from species where adult females have them (Wakgari & Giliomee 2004, 2005; Waterworth *et al.* 2012) though immatures are poorly known across Coccoomorpha and this character state has probably not been considered in many descriptions.

Multiple interceptions of *P. ulter* at the US border on orchids primarily originating from Guatemala were made beginning in 1937 and continuing to 1984, these now in the USNM collection. Some of these individuals have many large conspicuous dorsal oral-rim type tubular ducts in the cerarii and scattered over the dorsum, as described in *P. ulter* (Ferris 1950; Williams & Granara de Willink 1992), while others lack dorsal oral-rim type tubular ducts entirely. Individuals of both forms were often mounted on the same slides. Though the form without oral-rim type tubular ducts was first thought to be an undescribed species by Morrison (per handwritten notes on slides); we suggest that these are two forms of *P. ulter*, evidenced by the fact that it seems unlikely for both forms to be mounted together repeatedly. No morphological differences besides the presence or absence of oral-rim type tubular ducts could be found. It is surprising that there could be this much intraspecific variation in the oral-rim type tubular ducts. We have also examined type material of *P. calcitectus* collected by Cockerell in 1900 in Beulah, New Mexico and found several oral-rim type tubular ducts on the margin and submargin, yet Ferris (1950) does not mention or illustrate these based on topotype material from Beulah or material from Jacob Lake, Arizona. Moreover, we did not find any oral-rim type tubular ducts on new *P. calcitectus* material the second author collected on *Sporobolus* in Elgin, Arizona in 2023.

In revising the keys, it also became evident that there may be a range of variation in *P. echinatus*, particularly among the individuals collected on the California Channel Islands, on the mainland coast, and in the inland areas of western United States and Mexico. Adult males are wingless in the coastal mainland populations but are winged on the Channel Islands and western U.S. and Mexican populations. Morphological differences are utilized in the new adult female and adult male keys. More work on this *P. echinatus* complex will be required to ascertain if these differences represent distinct species or intraspecific variation.

Several pairs of species are quite similar and require further analysis, particularly with comparative sequence data. *Puto pricei* McKenzie 1960 and *P. sandini* Washburn 1965 are both pine-infesting species from the western United States and are remarkably similar morphologically, with only minor differences in antenna length and multilocular disc-pore distribution. *Puto cupressi* (Coleman 1908) and *P. pacificus* McKenzie 1967 differ primarily in the presence or absence of oral-rim type tubular ducts in the cerarii as opposed to close to, but not in, the cerarii. *Puto acirculus* McKenzie 1960 and *P. calcitectus* (Cockerell 1901), both western United States grass-infesting species, differ in the presence or absence of a circulus. A third grass-infesting species, *P. kosztarabi* Miller and Miller 1993, is present in the eastern United States and is also very similar. *Puto kosztarabi* and *P. acirculus*, differ primarily in the variable development of the circulus and the setae on the ostiole lips. *Puto simmondsiae* apparently only differs from *P. echinatus* in the abundance of the multilocular disc-pores on the abdomen.

To date, molecular data are available for merely four of the now 51 species of *Puto*, all of these with only two (18S and 28S for *P. barberi*, *P. superbus*, and *P. yuccae*) or three (18S, 28S, and EF-1a for *P. albicans* McKenzie, 1967) gene fragments publicly available (Gullan *et al.* 2003; Veá & Grimaldi 2016). Regrettably, because the three species described here were collected more than 50 years ago, mounted in Canada Balsam, and never collected again to our knowledge, molecular data are not available. Specimens in ethanol in collections and species that can be recollected will be critical to reveal the relationships between *Puto* species and their higher-level classification in future work.

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