



***Barbenigma* Powell & Miller, a bizarre new genus and two new species of scale insects (Hemiptera: Coccoomorpha: Ortheziidae) from the United States**

ERIN C. POWELL^{1*}, DOUGLASS R. MILLER^{1,2,3} & OLIVER KELLER⁴

¹Florida State Collection of Arthropods, Division of Plant Industry, 1911 SW 34th St., Gainesville, FL 32608, U.S.A.

²Retired Research Entomologist, Systematic Entomology Laboratory, Agricultural Research Service, USDA, Rm. 328, Bldg. 003, Beltsville, MD 20705, U.S.A.

³✉ rtchok@gmail.com; <https://orcid.org/0000-0003-4909-8654>

⁴Michigan Pathogen Biorepository, Department of Ecology and Evolutionary Biology, University of Michigan, 3600 Varsity Drive, Ann Arbor, MI 48108, U.S.A.

✉ okeller@umich.edu; ✉ okeller1977@gmail.com; <https://orcid.org/0000-0001-5067-3316>

*Corresponding author: ✉ Erin.Powell@fdacs.gov; ✉ erin.powell94@gmail.com; <https://orcid.org/0000-0002-2483-1883>

Abstract

A strange new genus and two species of scale insect from the United States, *Barbenigma* Powell & Miller, **gen. nov.** and *Barbenigma biza* Powell & Miller, **sp. nov.** and *B. boscus* Powell & Miller, **sp. nov.** (Hemiptera: Coccoomorpha: Ortheziidae) are described and illustrated, including the adult female and immature stages available. *Barbenigma boscus* was recently collected in Nebraska on the roots of grasses; *B. biza* is described from a series of undetermined specimens from Florida found in the Florida State Collection of Arthropods. These species, which have three-segmented antennae, no wax plates, conspicuous clusters of quadrilocular ducts on the abdomen, thoracic and abdominal spiracles set in a ring of pores, legs reduced in size, sparse ornate fimbriate dorsal setae, and very few capitate spines, stretch our current concept of the family Ortheziidae. The anal ring morphology, a fused trochanter and femur, presence of abdominal spiracles, large differentiated setae on the apex and subapex of the terminal segment of the antenna, a reduced number of ventral abdominal segments, and the presence of modified quadrilocular pores (most likely homologous to the ovisac band), support placement in Ortheziidae. We provide an updated phylogenetic analysis of Ortheziidae based on morphological characters with the new species included. The analysis demonstrates that the four species previously placed in the family Carayonemidae and the two new species of *Barbenigma* form a monophyletic group that should be placed within the Ortheziidae as the subfamily Carayoneminae Richard **new synonymy and change of rank**. The tribes Carayonemini Richard and Barbenigmini Powell & Miller **tribe nov.** are proposed as subunits within the subfamily. A revised key to the world species of Carayoneminae is provided.

Key words: Sternorrhyncha, Coccoidea, Archaeococcoidea, subterranean, roots, grasses

Introduction

The scale insect family Ortheziidae (Hemiptera: Coccoomorpha) currently comprises 216 species in 24 genera; several of these are extinct and are known only from specimens in amber (García Morales *et al.* 2016). Notable comprehensive contributions on Ortheziidae include Morrison (1925, 1952), Kozár (2004), and more recently, a morphological phylogeny by Veá & Grimaldi (2012) and work on the adult male morphology by Veá (2014).

A new genus described herein, *Barbenigma* Powell & Miller, **gen. nov.**, stretches our current concept of Ortheziidae. Characters that support its placement in Ortheziidae include: ventral thoracic spiracles; three pairs of abdominal spiracles; a fused trochanter and femur; a large, well-developed anal ring; pores present on ring surrounding anal opening; modified quadrilocular pores; and differentiated apical setae on the antennae. The new genus shares many character states with the four species previously placed in the small family Carayonemidae as follows: having the trochanter and femur fused; trochanter with two campaniform sensilla on each surface; three-segmented antennae; apical and subapical antennal setae differentiated; dorsal setae with fimbriate apices, and

presence of abdominal spiracles; but it lacks the dorsal thoracic spiracles and bilocular pores that have been used to set this family apart from the Ortheziidae. Sharing character states of both families, *Barbenigma* Powell & Miller **gen. nov.** supports a close relationship between the Ortheziidae and Carayonemidae, as posited by other authors including Foldi (1997), Kozár & Konczné Benedicty (2000), Kozár & Foldi (2002), Gullan & Cook (2007), and Gavrillov-Zimin (2018). Our phylogenetic analysis using morphological characters supports that the four species previously placed in the family Carayonemidae and the two new species of *Barbenigma* form a monophyletic group that we place within the Ortheziidae as the subfamily Carayoneminae Richard **new synonymy and change of rank.**

The distribution of this new genus containing two species is peculiar, with specimens from Nebraska and Florida and no collections from anywhere in between. We were first prompted to study it when DRM collected three specimens on the roots of grass on a disturbed roadside in rural Nebraska in July 2023. We subsequently examined the undetermined material in the Florida State Collection of Arthropods (FSCA) and found multiple additional collections from Florida labeled as “Margarodidae”. Specimens are found in the soil associated mainly with grass roots and previous Florida collections probably came from nematode assays, primarily from turf. We also examined undetermined Ortheziidae and Margarodidae material in the United States National Museum (USNM) collection and the Bohart Museum (UC Davis) but did not find similar specimens.

Materials and methods

Descriptions and figures

The terminology used follows Veá & Grimaldi (2012) and Kozár (2004) with the exception of the simple pores. Kozár (2004) illustrates a wide array of structures under the heading of simple pores. Some of them possess a central area that can protrude by as much as the diameter of the pore, whereas others have a central area that protrudes slightly or not at all. We have described these structures as dome-shaped or acorn-shaped setae when they occur on the head or the anal-lobe area and have an obvious central projection. Other pores that have little or no central projection and are located elsewhere, are considered to be simple pores. We note that the dome- or acorn-shaped seta on the anal area of the immatures transforms into a fimbriate seta in the adult. The structures that we have called tubular ducts also are considered to be simple pores by Kozár (2004), but with a central tube and an attached filament they seem to be more similar to the tubular ducts found in other scale insects. We call them tubular ducts herein. The illustration procedures used follow Miller & Stocks (2022). Measurements were made using a Zeiss Axio Imager.M2 using ZEN 3.7 Pro software. Photographs were taken and stitched with the same software, then stacked with Helicon Focus 8. Illustrations were made with a Leica DMRB compound light microscope with 10×, 20×, 40×, and 100× objectives.

Phylogenetics

We coded 77 morphological characters, following Veá & Grimaldi (2012), for *B. biza* **sp. nov.** and *B. boscus* **sp. nov.**, as well as specimens from what previously was known as the Carayonemidae, a small family consisting of four species that share character states with *Barbenigma* species. We included all four carayonemid species in our analysis: *Baloghicoccus costaricaensis* Kozár & Konczné Benedicty, 2000; *Carayonema orousseti* Richard, 1986; *Foldicoccus monikae* Kozár & Konczné Benedicty, 2000; and *Mahunkacoccus mexicanensis* Kozár & Konczné Benedicty, 2000. The two *Barbenigma* species and *F. monikae* were coded according to our own observations of slide-mounted specimens with a Zeiss Axio Imager.M2; and *B. costaricaensis*, *C. orousseti*, and *M. mexicanensis* were coded using the literature (Richard 1986; Kozár & Konczné Benedicty 2000). Morphological data were added to the matrix provided by Veá & Grimaldi (2012), available in Morphobank (project P610; <http://dx.doi.org/10.7934/P610>) (O’Leary & Kaufman 2012). We added eight new characters in addition to the 69 characters in the Veá & Grimaldi (2012) matrix, these specific to Carayoneminae and the two new *Barbenigma* species, totaling 77 morphological characters for adult females. Outgroups followed Veá & Grimaldi (2012) and positions of outgroup taxa do not reflect higher-level relationships amongst Coccoomorpha.

Additional characters

70. Bilocular pores: In the four species now placed in Carayoneminae, bilocular pores are present. These are typically absent in Ortheziidae and they are absent in the two new *Barbenigma* species. States: 0 = absent; 1 = present.

71. Fimbriate setae: In Carayoneminae, and the new species of *Barbenigma*, ornate fimbriate setae are present on the dorsum and/or venter. These are absent in Ortheziidae. States: 0 = absent; 1 = present.

72. Position of the thoracic spiracles: While some ortheziids have abdominal spiracles placed on the dorsum, the thoracic spiracles are always ventral. The two new species of *Barbenigma* both have ventral abdominal spiracles. Carayoneminae have dorsal thoracic spiracles. States: 0 = dorsal; 1 = ventral.

73. Quadrilocular pores on the ventral surface: The matrix by Veá & Grimaldi (2012) considered quadrilocular pores on the dorsal surface, which is characteristic of Ortheziidae. The new species of *Barbenigma*, however, only have modified quadrilocular pores on the venter, not the dorsum. Many ortheziid species also have ventral quadrilocular pores. Carayoneminae do not have quadrilocular pores on either surface. States: 0 = absent; 1 = present.

74. Quadrilocular duct clusters: Ortheziid species such as *Newsteadia* with modified quadrilocular pore ducts have them present singly, never in clusters each set within a sclerotized ring. The latter character state is unique to both the new species of *Barbenigma* and is absent in Carayoneminae. States: 0 = absent; 1 = present.

75. Spines: Ortheziidae are typically characterized by having spines, typically abundant. Carayoneminae have uniquely modified setae but do not have spines, whereas the new *Barbenigma* species do possess spines. States: 0 = absent; 1 = present.

76. Anal ring invaginated, set in pocket: Carayoneminae and the two new *Barbenigma* species have the anal ring invaginated, set in a pocket marginally. States: 0 = no; 1 = yes.

77. Legs long or short: Ortheziidae typically have long legs, whereas the legs of Carayoneminae, the ortheziid *Acropygorthezia williamsi* LaPolla & Miller in LaPolla *et al.*, 2008, and the new *Barbenigma* species are shorter. We define legs as long when the hind leg reaches abdominal segment V and legs as short when the hind leg does not reach abdominal segment V. States: 0 = long; 1 = short.

Modified characters

We added character states for two characters in the Veá & Grimaldi (2012) matrix to encompass the Carayoneminae and the two new *Barbenigma* species. Character states were added for (14) and (31).

14. Type of unspecialized setae on antenna: Carayoneminae have branched fimbriate setae on the antennae so this character state was added. 0 = hair-like; 1 = spine-like; 2 = branched.

31. Setae on tibia and tarsus: We added two states for this character. The new species of *Barbenigma* have the setae on the tibia and tarsus spiniform ventrally and setiform dorsally, whereas carayonemines have branched setae on both leg surfaces. States: 0 = all setiform; 1 = all spiniform; 2 = spiniform ventrally and setiform dorsally; 3 = spiniform dorsally and setiform ventrally; 4 = some branched.

Phylogenetic analysis

Analyses were performed using TNT (maximum parsimony) (Goloboff *et al.* 2008) and IQTree (maximum likelihood) (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016). The run performed using TNT was conducted using the following commands after holding 10,000 trees in memory: mult = tbr replic 10,000 hold 100. Bootstrap values were calculated for the resulting strict consensus tree: resample boot replic 10000. The IQTree analysis used the built-in ModelFinder (Kalyaanamoorthy *et al.* 2017), and ML + rapid bootstrap settings with 1,000 replicates (Hoang *et al.* 2017). ModelFinder selected MK+FQ+ASC+G4 as the best-fit model. The resulting trees were viewed and edited in FigTree v.1.4.4 (Rambaut 2012), and final edits were done in Adobe Illustrator® 2024 (Version 28.5, Adobe®, San Jose, CA).

Specimen depositories

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

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

Taxonomy

Subfamily Carayoneminae Richard, 1986

Diagnosis: Adult female with a combination of the following characters: trochanters each with two campaniform sensilla on each surface; trochanter and femur fused; tibia and tarsus separate; dorsal setae ornate fimbriate; labium about as wide as long, rotund; antennae each three-segmented, each with enlarged apical and subapical setae; without eyes.

Tribe Carayonemini Richard, 1986

Type genus: *Carayonema* Richard, 1986

Diagnosis: Adult female with a combination of the following characters: with dorsal thoracic spiracles protruding, each without pores in atrium; with bilocular pores and clavate setae; without spines; without quadrilocular ducts; without tubular ducts.

Tribe Barbenigmini Powell & Miller, tribe nov.

Type genus: *Barbenigma* Powell & Miller **gen. nov.** by current designation.

Diagnosis: Adult female with a combination of the following characters: with ventral thoracic spiracles protruding, each with pores in atrium; with spines; compound duct clusters of quadrilocular ducts; with tubular ducts; with conical setae with central raised area, these dome- or acorn-shaped.

Genus *Barbenigma* Powell & Miller, gen. nov.

Type species: *Barbenigma biza* Powell & Miller **sp. nov.** by current designation.

Diagnosis: Adult female with a combination of the following characters: antennae each three-segmented, apical and subapical setae differentiated. Legs reduced in size, tibia and tarsus not fused, trochanter with two campaniform sensilla on each surface, trochanter and femur fused. Ovisac band modified. Wax plates, multilocular pores, and eyes absent. With three pairs of abdominal spiracles, atria of both thoracic and abdominal spiracles each with ring of raised pores. Abdomen with eight quadrilocular duct and spine clusters. Setae on dorsum and margin robust and fimbriate, spines on dorsum and margin each with swollen rounded apices, setae and spines reduced in number.

Notes: *Barbenigma* species are similar to the four species previously placed in the Carayoneminae in having: trochanters each with two campaniform sensilla on each surface, trochanter and femur fused, tibia and tarsus separate; dorsal setae ornate fimbriate; labium small and rotund; antennae each three-segmented, each with enlarged apical and subapical setae; and eyes absent. *Barbenigma* species have (shared contrasting character states in species of *Baloghicoccus* Kozár, *Carayonema* Richard, *Foldicoccus* Kozár, and *Mahunkacoccus* Kozár are given in parentheses): compound duct clusters of quadrilocular pores (quadrilocular duct clusters absent); without bilocular pores (with bilocular pores); with spines (without spines); ventral thoracic spiracles, each with pores in atrium (dorsal thoracic spiracles, each without pores in atrium); with tubular ducts (without tubular ducts); and with dome-shaped or acorn-shaped setae (with flagellate setae).

The species of *Barbenigma* do not fit in any of the currently known subfamilies of Ortheziidae.

Barbenigma species are similar to the Australian ortheziid ant inquiline *A. williamsi* in having: eyes absent; a reduced or absent ovisac band; no wax plates; a reduced number of antennal segments; and two campaniform sensilla on each surface of the trochanter. However, *Barbenigma* species have (*A. williamsi* character states in parentheses): three-segmented antennae (two-segmented); atria of thoracic and abdominal spiracles each with ring of pores (spiracular atria without pores); ventral clusters of quadrilocular pores and spines on abdomen (ventral

quadrilocular pores present singly); few dorsal spines scattered over body (densely covered in spines); ventral spines absent except marginally and in pore clusters (entire venter densely covered in spines); and anal ring well developed with pores, situated at apex of abdomen (anal ring without pores, situated at center of body).

The ortheziid subfamily Newsteadinae, which includes only the genus *Newsteadia* Green 1902 (62 species), is defined by (*Barbenigma* species character states presented in parentheses): first antennal segment conspicuously larger than other antennal segments (antennal segments about equal); dorsal wax lobes present (dorsal wax lobes absent); tubular ducts on dorsum between wax spines (tubular ducts present on dorsum but wax spines sparse); and venter without a band of spines inside ovisac band (ovisac band heavily modified). *Barbenigma* species resemble *Newsteadia* in having: tubular ducts with four loculi, these probably modified quadrilocular pores; tarsus longer than tibia; and tubular ducts on dorsum. Some species of *Newsteadia* also have three-segmented antennae. However, the new genus differs in having (*Newsteadia* characters given in parentheses): thick differentiated apical seta on apical antennal segment (hair-like apical seta on apical antennal segment); apical segment of antenna about equal to other segments (apical segment conspicuously larger than other segments); and tibia and tarsus separate (tibia and tarsus fused or only partly separated by fine suture).

Barbenigma species and members of the subfamily Ortheziinae are similar in having tibia and tarsus separate but differ in having (*Barbenigma* species character states in parentheses): distinctive short, stout apical setae on terminal antennal segment (apical setae long, exceeding length of apical segment); and presence of two enlarged spines on tibia (enlarged spines on tibia absent). *Barbenigma* species bear some similarity to certain species of the ortheziine tribe Arctortheziini, which includes only the genus *Arctorthezia* Cockerell, 1902, in having a series of circular clusters of pores on margin and spiracles with associated pores. However, *Barbenigma* species have eight ventral duct clusters, containing modified quadrilocular pores and spines, on margin and median area of abdomen, whereas *Arctorthezia* species with pore plates (e.g., *Arctorthezia pseudoccidentalis* Morrison, 1925 and *A. vardziae* Hadzibejli, 1963) have between 16–18 dorsal pore plates, each consisting of simple pores without loculi around body margin, sometimes extending up to thorax and head. *Arctorthezia* is a more typical ortheziid with (*Barbenigma* species character states are presented in parentheses): 7–8 antennal segments (antennae three-segmented); large eyes (eyes absent); body densely covered in spines (spines sparse); and with an ovisac band (ovisac band absent). The tribe Ortheziini is defined by having (*Barbenigma* species character states are in parentheses): tibia and tarsus bearing hair-like setae dorsally and spine-like setae ventrally (bearing spine-like setae dorsally and hair-like setae ventrally); and thoracic spiracles without pores (with a ring of pores).

Barbenigma species are similar to members of the ortheziid tribe Mixortheziini in having a reduced number of antennal segments and short anal-ring setae. However, the Mixortheziini have an ovisac band, typical elongate legs, and the eye present. Some *Mixorthezia* Morrison, 1925 species have large bare areas on the dorsum similar to *Barbenigma* species but this feature is seemingly not restricted to any one subfamily (e.g., *Orthezia nuda* Ferris 1919 in Ortheziinae).

Barbenigma species and the ortheziid tribe Nipponortheziini are similar in having reduced antennal segments (usually three) but differ in having (*Barbenigma* species character states in parentheses): long antennal segments (short antennal segments); eyes present (eyes absent); large, elongate labium (short, rotund labium); and wax plates present (wax plates absent).

Barbenigma species are seemingly unrelated to the subfamily Ortheziolinae, which is defined by (*Barbenigma* species character states are presented in parentheses): a well-developed pseudobasal segment at the base of the antennae (no pseudobasal segment); three setae inserted in one basal socket on the labium (all setal sockets with only one seta); sclerotized plate anterior to anal ring (sclerotized plate absent), and claw digitule setiform (claw digitule spiniform). The Ortheziolinae also are defined by having ‘thumb-like pores’ on each side of the anal ring but it is unclear whether the dome- and acorn-shaped setae concentrated in a cluster on the head of *Barbenigma* could be homologous.

Etymology: The genus name *Barbenigma* is from the abbreviated name “*Barb*” (from Barbara) and the suffix “*enigma*”. The name serves as a dedication to Barbara Denno. She has contributed immensely to the coccidology community through her tireless dedication to ScaleNet and has supported DRM in his extensive collecting trips, including the trip on which the holotype of *B. boscus* was collected. Moreover, the given name Barbara is derived from the Greek “*barbaros*”, meaning “stranger” or “foreign”. This comparison is fitting for a scale insect for which the family placement has been puzzling. The ending “*enigma*” is Greek for a riddle, or something or someone that is a puzzle or a mystery. The name is a neuter noun.

Barbenigma biza Powell & Miller, sp. nov.

Material examined

Holotype: adult ♀, mounted singly. FLORIDA: Alachua Co., Gainesville, 23 III 1999, on *Rumex hastatulus* (Polygonaceae), coll. R. Esser, E99-879, FSCA_00073114 (FSCA).

Paratypes: FLORIDA: Alachua Co., Gainesville, Paynes Prairie Preserve, 23 III 1999, on *Rumex hastatulus*, coll. R. Esser and C. Zamora, E99-879 (1 ad. ♀ and 1 first-instar? nymph (FSCA_00073115) on 2 slides) (FSCA); Brevard, Co., Merritt Island, 4 VII 1988, on *Stenotaphrum secundatum* (Poaceae), coll. S. Walker (5 ad. ♀♀ (FSCA_00073116–FSCA_00073120), 1 second-instar? nymph (FSCA_00073121) on 6 slides) (FSCA, USNM); Palm Beach Co., West Palm Beach, 15 XI 1965, on *Stenotaphrum secundatum*, coll. R.S. Mullin, N. Bezona, 124942 (2 ad. ♀ (FSCA_00073122–FSCA_00073123 on 2 slides) (FSCA).

Other material examined: FLORIDA: Broward Co., Lighthouse Point, 17 VI 1974, on *Stenotaphrum secundatum*, coll. F. Donaldson (1 second-instar? nymph (FSCA_00073124) and 1 third-instar? nymph (FSCA_00073125) on 2 slides) (FSCA); Orange Co., Maitland, 5 XI 1969, in soil (lawn), coll. H.M. VanPelt, DPI# 125664 (3 second-instar? nymphs (FSCA_00073126–FSCA_00073128) on 3 slides) (FSCA); Marion Co., Belleview, 15 IX 1966, in soil, coll. H. Myers (1 second-instar? nymph (FSCA_00073129) on 1 slide) (FSCA); Miami-Dade Co., Miami, 14 X 1971, on *Cocos nucifera* (Arecaceae), coll. R. Brown, B-7925 (1 second-instar? nymph (FSCA_00073130) on 1 slide) (FSCA).

Etymology: The epithet “*biza*” is an abbreviation of the English word “bizarre” and is to be treated as a noun in apposition.

Adult female (Figs 1–4)

Description: Slide-mounted holotype 1.25 mm long, 1.1 mm wide; paratypes (n=8) 0.64–1.26 mm long, 0.23–0.95 mm wide; body rotundly oval in mature female (Figs 1–2), narrow elongate in young females (Fig. 3).

Dorsum with robust fimbriate setae (Figs 1c, 3m), each with up to five tines, sparse, two present marginally on each side of each abdominal segment, one present submedially on each abdominal segment, roughly in single longitudinal line on thorax and head, holotype with one instance of two setae arising from single socket on head, longest seta on submedial area of abdomen 19 µm long (paratypes 18–23 µm), longest seta on margin 22 µm long (paratypes 16–30 µm), longest seta on head 22 µm long (paratypes 19–24 µm). Dorsal spines each without setal base (Figs 1o, 3n), with swollen, rounded apex, sparse, one to three on each side of each abdominal segment, longest spine on submedial area of abdomen 17 µm long (paratypes 14–19 µm), longest spine on thorax and head 14 µm long (paratypes 14–23 µm). Tubular ducts scattered over body (Figs 1q, 3o). Multilocular pores absent. Short conical setae similar to simple pores, either dome-shaped or acorn-shaped, with conical projection, definite setal base (Figs 1b, 3a), one to several clustered near base of each antenna, 4 µm in height, 4 µm wide (paratypes 3–5 µm by 3–4 µm). Simple pores each with slightly raised, rounded center, scattered over body (Figs 1e, 3f). One paratype specimen with structure near each antenna with unequal sides, without base, longest side 7 µm. Anal lobes each bearing enlarged fimbriate seta 48 µm long (paratypes 27–33 µm), enlarged capitate seta broken on holotype (paratypes 48–53 µm), spine with swollen apex, 27 µm long (paratypes 17–21 µm), on each side of anal ring (Fig. 1n). Microtrichia absent. Derm smooth.

Anal ring (Fig. 3l) wrapping around margin, invaginated in pocket, forming setal basket, with ring of conical pores, bearing six robust anal-ring setae with truncate apices, about equal in size, each about 39 µm long (paratypes 29–33 µm), 0.7 times (paratype 0.7–1.0 times) as long as greatest diameter of anal ring.

Venter with two pairs of thoracic spiracles (Figs 1d, 3d), spiracular openings projecting above derm, three pairs of abdominal spiracles (Fig. 1f), spiracular openings flush with derm. Atria of thoracic and abdominal spiracles each with ring of pores, without loculi, in single row. Anterior thoracic spiracles with 10 (paratypes 6–9) pores in ring around opening, 12 µm in diameter (paratypes 10–12 µm). Abdominal spiracles with 7–11 (paratypes 7–11) pores in ring around opening, anterior abdominal spiracular opening 13 µm in diameter (paratypes 12–15 µm). Body setae (Fig. 1k) with blunt apices, not capitate, those on abdomen longer than those on thorax and head, longest seta on thorax or head 14 µm long (paratypes 10–14 µm), longest seta on abdomen 36 µm long (paratypes 31–39 µm). Robust fimbriate setae and spines with swollen apices marginal. Eye absent. Labium two-segmented, small, about as wide as long, round, bent upward on holotype (paratypes 34–44 µm long by 31–42 µm wide), only one seta arising from basal sockets. Vulva wide, 230 µm wide (paratypes 72–201 µm), with smooth margins, one heavily sclerotized lateral bar on each side of vulva. Margins of abdominal segments with heavily sclerotized areas (probably muscle attachment points) (not illustrated in Figs 1, 3, see Fig. 2), the posterior two sclerotizations each typically with two

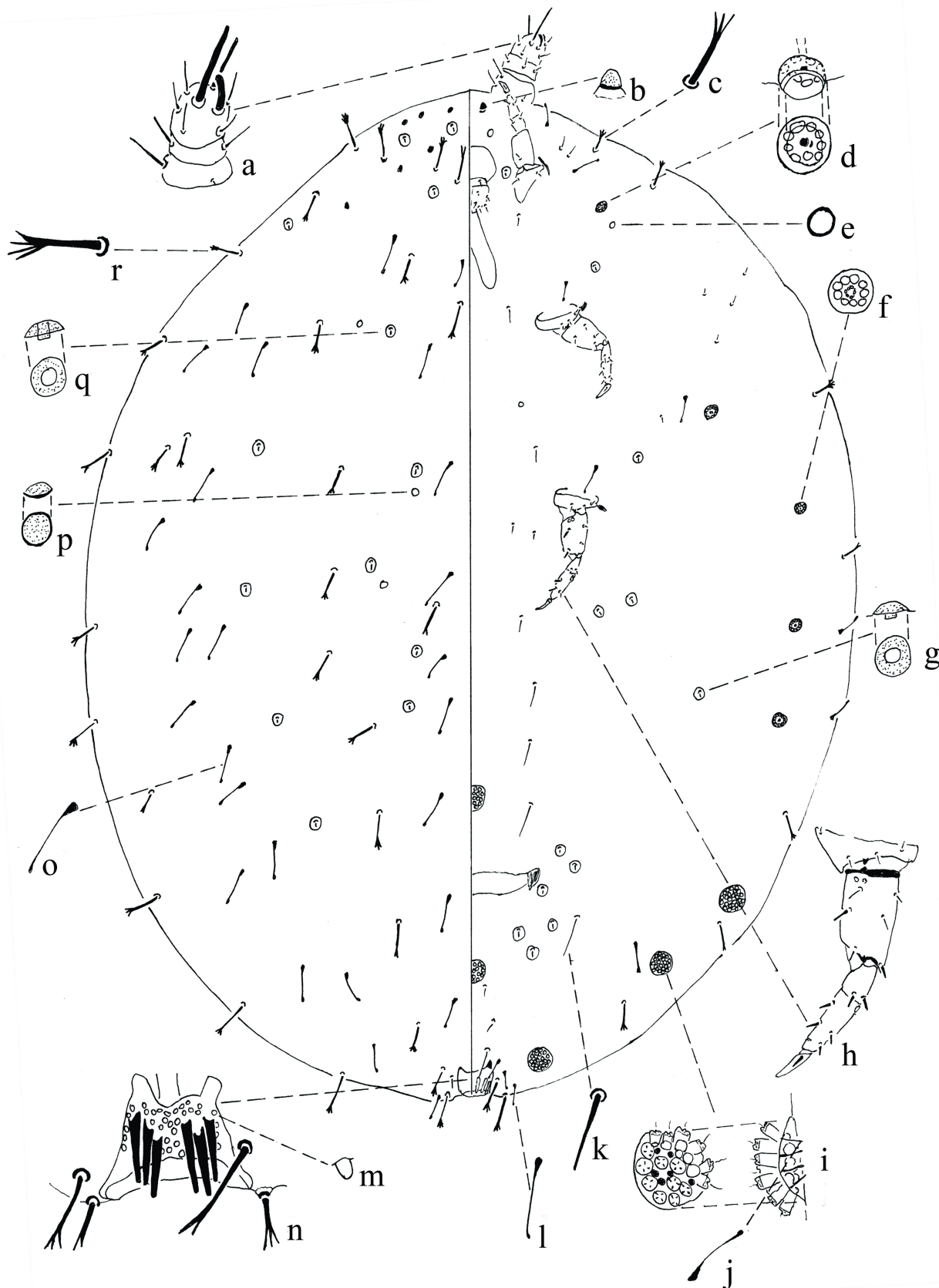


FIGURE 1. *Barbenigma biza* Powell & Miller, **sp. nov.**, adult female. The illustration utilized both the holotype female and a paratype female with the following data: holotype, Florida: Alachua Co.: Gainesville, 23 III 1999, R. Esser, C. Zamora, *Rumex hastatulus*, E99-879, FSCA_00073114; paratype, Florida: Brevard Co.: Merritt Island, 4 VII 1988, S. Walker, *Stenotaphrum secundatum*, FSCA_00073118. **a**=antenna; **b**=dome-shaped seta; **c**=fimbriate seta; **d**=anterior thoracic spiracle; **e**=simple pore; **f**=first abdominal spiracle; **g**=tubular duct; **h**=metathoracic leg; **i**=quadriocular duct cluster; **j**=spine; **k**=hair-like seta; **l**=spine; **m**=pore in anal ring; **n**=anal ring; **o**=spine; **p**=simple pore; **q**=tubular duct; **r**=fimbriate seta.

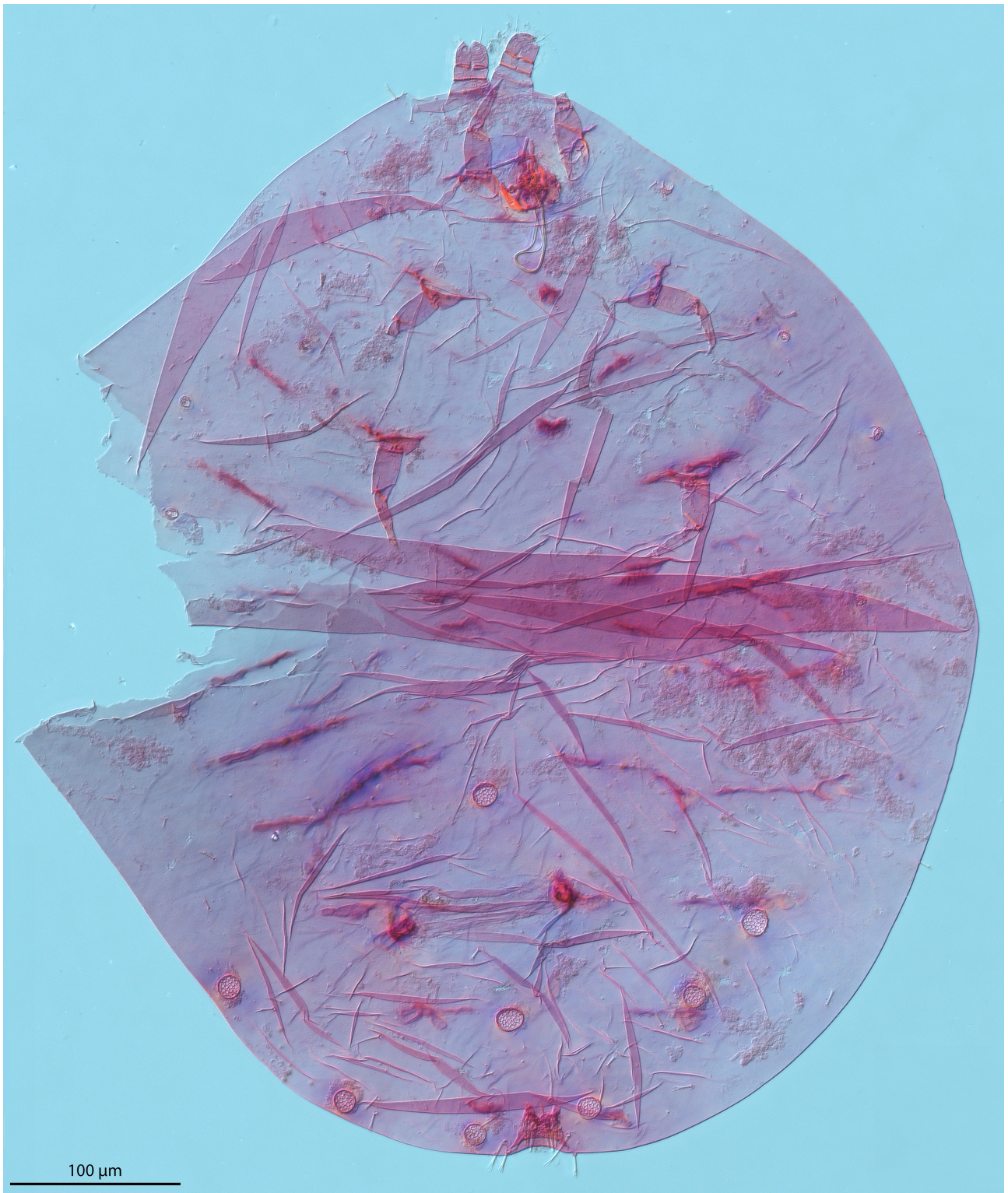


FIGURE 2. *Barbenigma biza* Powell & Miller, **sp. nov.**, adult female holotype. Florida: Alachua Co.: Gainesville, 23 III 1999, R. Esser, C. Zamora, *Rumex hastatulus*, E99-879, FSCA_00073114.

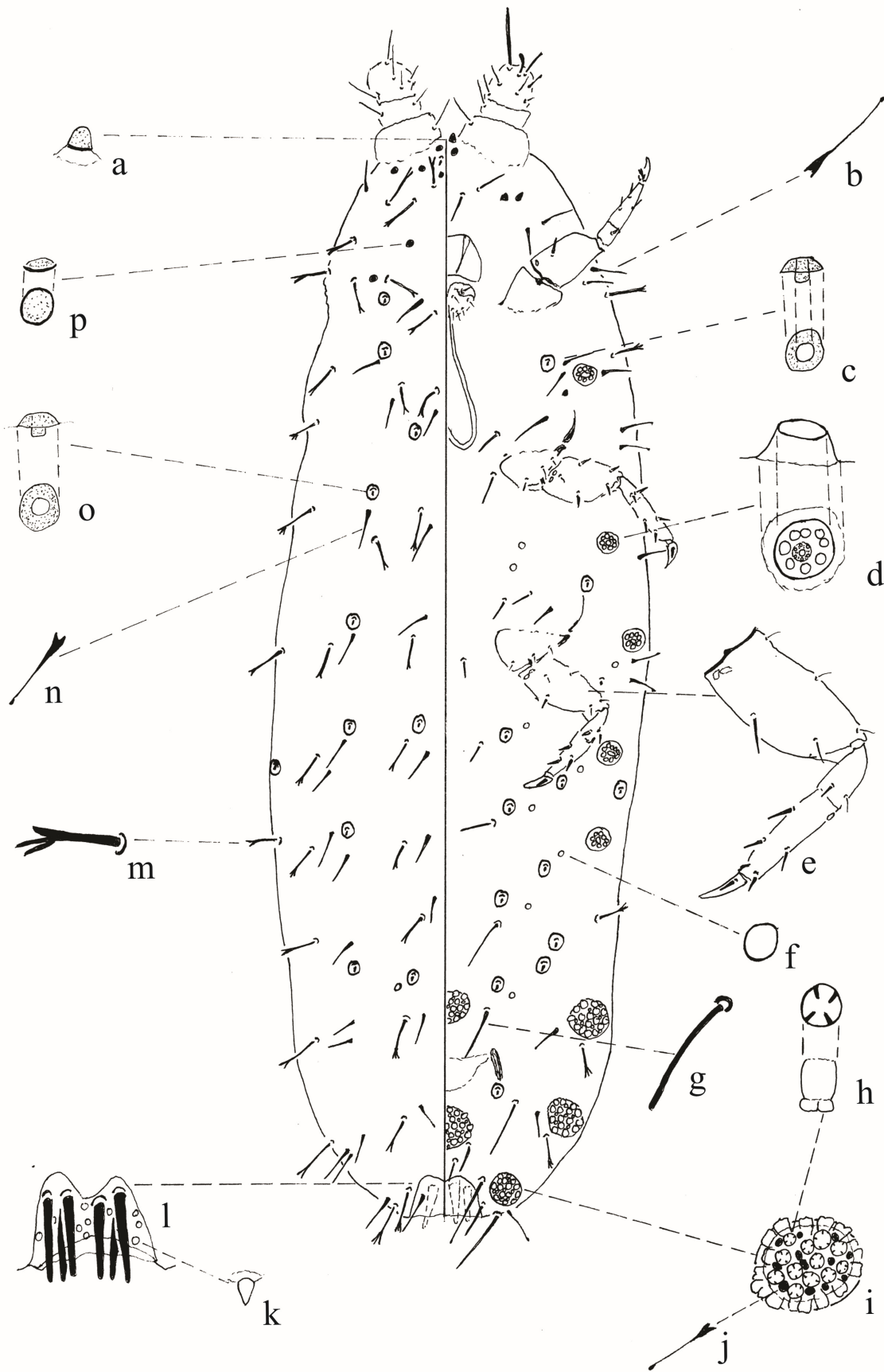


FIGURE 3. *Barbenigma biza* Powell & Miller, **sp. nov.**, adult female paratype. Florida: Brevard Co.: Merritt Island, 4 VII 1988, S. Walker, *Stenotaphrum secundatum*, FSCA_00073119. **a**=dome-shaped seta; **b**=spine; **c**=tubular duct; **d**=posterior thoracic spiracle; **e**=metathoracic leg; **f**=simple pore; **g**=ventral seta with blunt, not capitate, apex; **h**=quadrilocular duct; **i**=quadrilocular duct cluster; **j**=spine; **k**=pore in anal ring; **l**=anal ring; **m**=fimbriate seta; **n**=spine; **o**=tubular duct; **p**=dome-shaped seta.

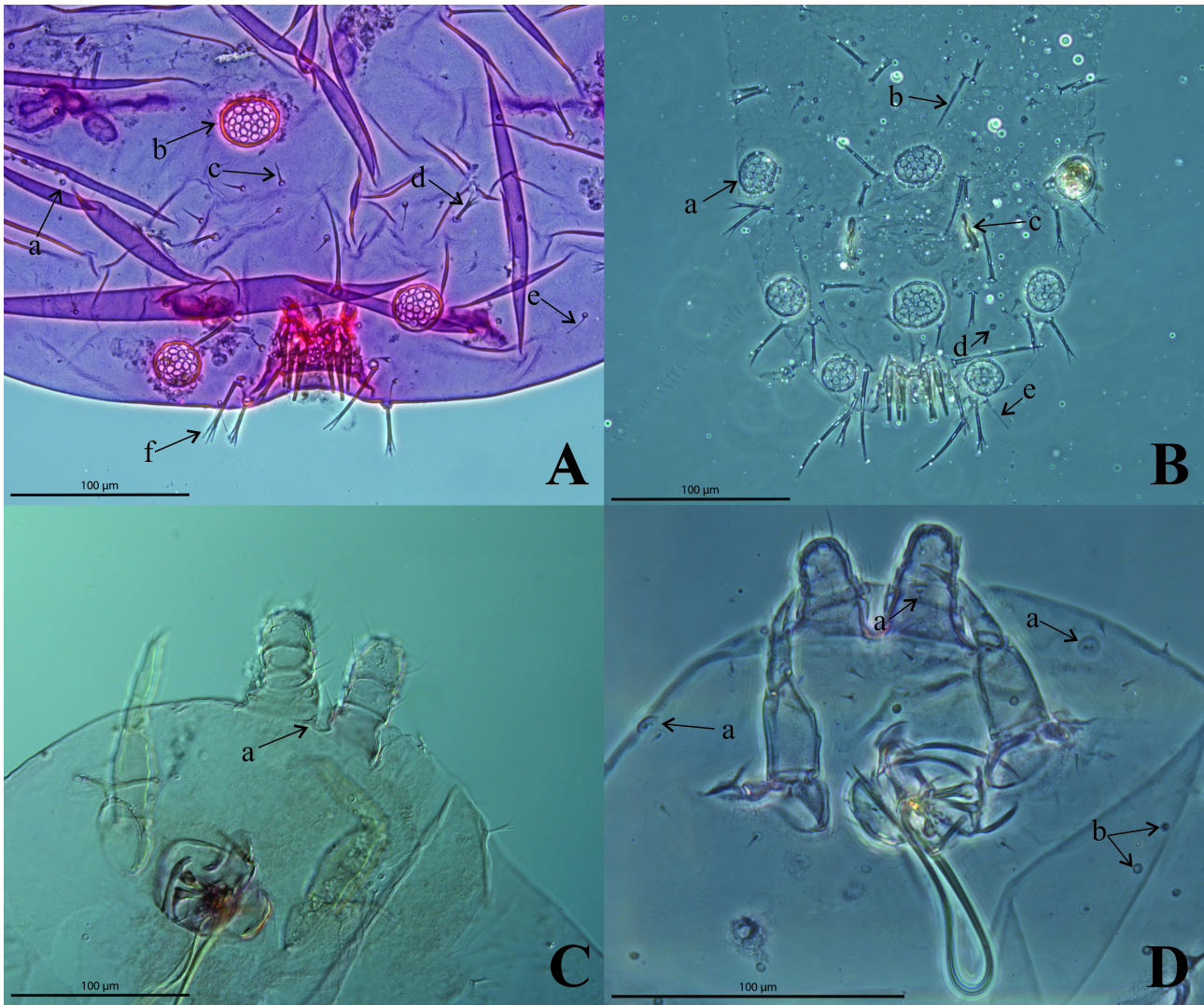


FIGURE 4. (A) *Barbenigma biza* Powell & Miller, **sp. nov.**, holotype adult female, Florida: Alachua Co.: Gainesville, 23 III 1999, R. Esser, C. Zamora, *Rumex hastatulus*, E99-879, FSCA_00073114. **a**= tubular duct; **b**=quadrilocular duct cluster; **c**=ventral hair-like seta; **d**=fimbriate seta; **e**=spine; **f**=fimbriate seta. (B) *Barbenigma biza* Powell & Miller, **sp. nov.**, adult female paratype. Florida: Brevard Co.: Merritt Island, 4 VII 1988, S. Walker, *Stenotaphrum secundatum*, FSCA_00073119. **a**=quadrilocular duct cluster; **b**=ventral hair-like seta; **c**=sclerotized right edge of vulva; **d**=tubular duct; **e**=spine. (C) *Barbenigma biza* Powell & Miller, **sp. nov.**, adult female paratype. Florida: Palm Beach Co.: West Palm Beach, 15 XI 1965, R.S. Mullin, N. Bezona, *Stenotaphrum secundatum*, 124942, FSCA_00073122. **a**=acorn-shaped seta between antennae. (D) *Barbenigma biza* Powell & Miller, **sp. nov.**, second-instar. Orange Co., Maitland, 5 XI 1969, in soil (lawn), coll. H.M. VanPelt, DPI# 125664, FSCA_00073126. **a**=tubular ducts set in raised circular area; **b**=tubular ducts.

associated tubular ducts on each side. Compound duct clusters (Figs 1i, 3i, 4Ab and Ba) present marginally, clusters of tubular ducts with quadrilocular centers, spines arising from between quadrilocular tubular ducts, clusters set in sclerotized ring, three pairs on submargins of abdomen, one on each side of each of segments VI–VIII, two medially (one posterior to vulva, one anterior to vulva), eight duct clusters total on abdomen, median clusters 32–34 µm in diameter (paratypes 19–39 µm), 26 ducts per median cluster (paratypes 14–27), marginal clusters 27–28 µm in diameter (paratypes 22–32 µm), 15–21 ducts per marginal cluster (paratypes 10–18). Multilocular pores absent. Dome- and acorn-shaped setae, with raised rounded blunt apex, singly or in cluster on head, about same size as those on dorsum. Simple pores few, scattered on thorax and abdomen, about same size as those on dorsum. Microtrichia absent. Derm smooth. Anal lobes indistinct, each side of lobe area bearing group of two enlarged capitate setae, 52 µm long (paratypes 52–53 µm), one small fimbriate seta (both broken on holotype) (paratypes 10–12 µm), one spine with swollen apex, 21 µm long (paratypes 20–21 µm). Antennae (Fig. 1a) each three-segmented, segments

short, segments I and III subequal in length, total length about 78 μm (paratypes 53–66 μm), segment I about 30 μm long (paratypes 18–37 μm), segment II about 17 μm long (paratypes 15–18 μm), apical segment about 31 μm long (paratypes 24–35 μm). Apical segments each with one long fleshy apical seta, straight with rounded blunt tip (broken on holotype) (paratypes 34–38 μm), one short fleshy subapical seta, curved with rounded blunt tip, 17 μm long (paratypes 15–20 μm), third fleshy seta at apex, microseta adjacent to apical setae, one capitate spine on apex, unspecialized setae long and straight. Pseudobasal antennal segment absent. Legs (Figs 1h, 3e) reduced in size, all about equal, trochanter and femur fused, two campaniform sensilla on each surface of trochanter, tibia and tarsus not fused, tarsus one-segmented, coxa 54 μm long (paratypes 45–51 μm), trochanter + femur 60 μm long (paratypes 54–63 μm), tibia 25 μm long (paratypes 19–22 μm), tarsus 43 μm long (paratypes 34–38 μm), tibia/tarsus 0.6 (paratypes 0.5–0.6), claw 19 μm long (paratypes 14–23 μm). Leg setae sparse, straight, spiniform dorsally and setiform ventrally, enlarged spines between tibia and tarsus absent. Sensory pore between tibia and tarsus present, sensory seta between tibia and tarsus absent. Tarsal digitules absent. Claw digitules each spine-like with acute apex, shorter than claw, claw denticle absent.

Notes: *Barbenigma biza* differs from *B. boscus* (described below) (*B. boscus* character states in parentheses) in having: more spines on the dorsal abdomen, spines typically occurring in pairs on submargin of each side of each abdominal segment (spines occurring singly); body setae with blunt, but not capitate, apices (body setae with capitate apices); spines on the dorsum short, 14–23 μm long (spines on the dorsum long, 22–31 μm long); and dorsal fimbriate setae short, 16–30 μm long (dorsal fimbriate setae long, 26–39 μm long).

We illustrated two forms of adult female. The change in body shape between young adult females (Fig. 3) and older females with eggs (Fig. 1) is remarkable, with the young adult females thin and elongate, half the length and only a quarter of the width of mature females. These young adult females are so different in body shape that they were labeled as “male”, perhaps because previous curators thought they were second-instar nymphs or pre-pupae. However, they have both a distinct vulva, with lateral sclerotized bars, and quadrilocular duct clusters that we posit are homologous with an ovisac band (Figs 3, 4B). We found no morphological differences between either form beyond the difference in body shape.

The simple pores on the thorax and abdomen may not be homologous to the ones on the head, and we call these simple pores rather than setae. The ones on the head have a lot of depth, easily visible when the structures are viewed from the side. However, those on the thorax and abdomen (both ventral and dorsal) did not have such obvious depth.

Third-instar? nymph

(Fig. 5)

Description: Slide-mounted specimen 0.76 mm long, 0.28 mm wide, body elongate oval (n=1).

Dorsum with robust fimbriate setae (Fig. 5j, n), often with up to five tines, sparse, in segmental rows on abdomen, thorax, and head, arranged in two pairs of longitudinal lines (submedial and lateral) on abdomen, longest seta on submedial area of abdomen 20 μm long, longest seta on margin 23 μm long, longest seta on head 17 μm long. Dorsal spines without setal base (Fig. 5m), with enlarged base, swollen, rounded apices, in segmental rows on abdomen, thorax, and head, arranged in two pairs of longitudinal lines near fimbriate setae, longest spine on submedial area of abdomen 24 μm long, longest spine on thorax and head 24 μm long. Small tubular ducts (Fig. 5l) most abundant on abdomen, rare on thorax, present submedially and mediolaterally on abdomen. Multilocular pores absent. Discoidal pores absent. Pair of dome- or acorn-shaped setae (Fig. 5a), 4 μm in height, 4 μm width. Anal lobes indistinct, each side of lobe area bearing two enlarged fimbriate setae, 27 μm long, and spine 27 μm long on each side of anal ring. Microtrichia (Fig. 5k) uncommon, in small patches on thorax and abdomen. Entire derm alveolar with polygonal and elongate cell-like reticulations (Fig. 5c, f, k).

Anal ring (Fig. 5i) wrapping around margin, invaginated in pocket, forming setal basket, with conical projections mostly obscured, with tubular structure on each side of ring, bearing six short spine-like anal-ring setae with rounded apices, about equal in size, each about 10 μm long, 0.3 times as long as greatest diameter of anal ring.

Venter with two pairs of thoracic spiracles (Fig. 5c), spiracular openings each slightly projecting above derm, each atrium with ring of 4–6 pores, without loculi, in single row around spiracle, spiracular opening 10 μm in diameter. Abdomen with three pairs of spiracles (Fig. 5e) on anterior segments, each volcano shaped, difficult to distinguish from cell-like reticulations, with unobvious tracheae. Robust fimbriate setae, in segmental rows on abdomen,

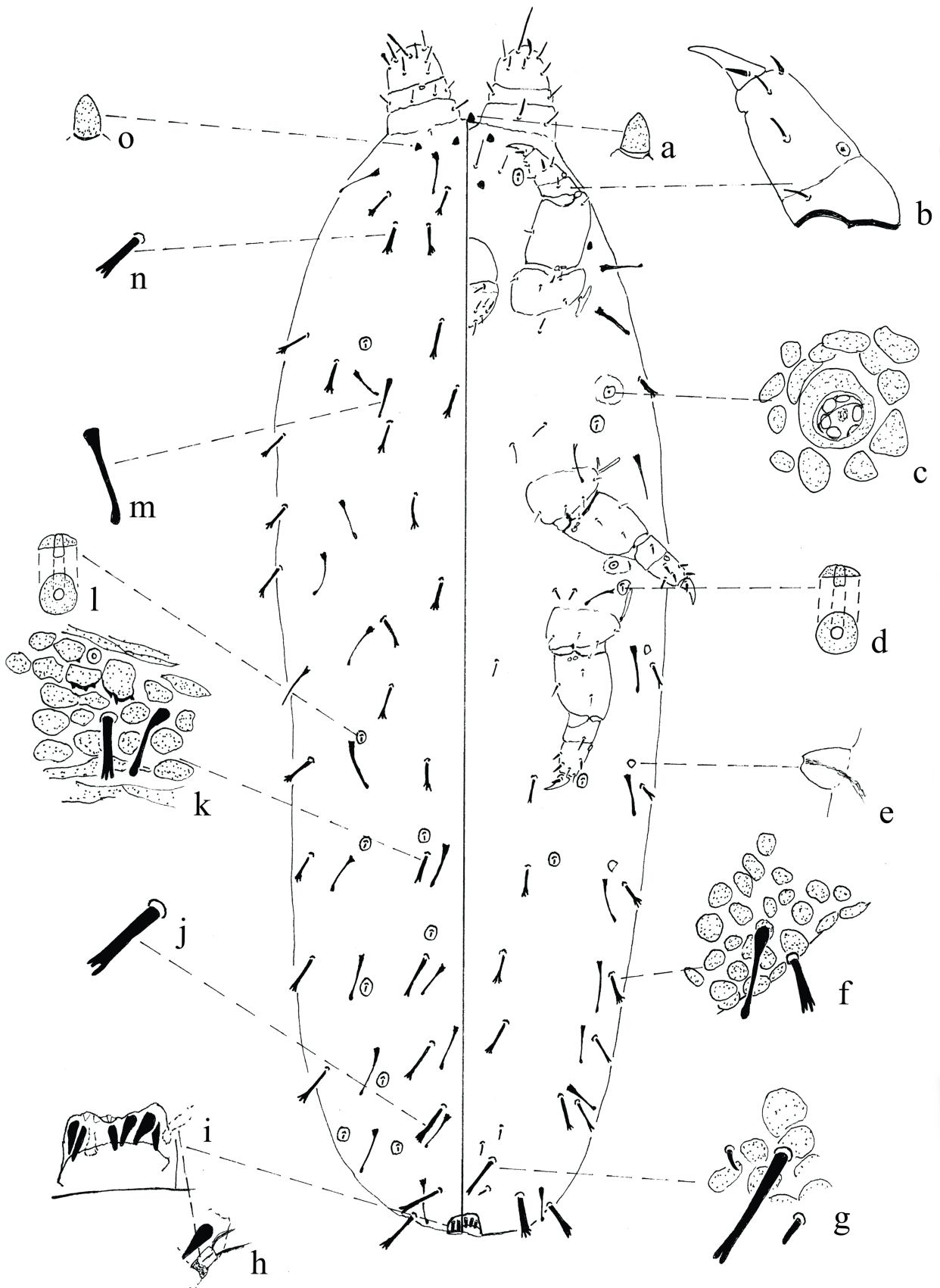


FIGURE 5. *Barbenigma biza* Powell & Miller, **sp. nov.**, third instar?, Florida: Broward: Lighthouse Point, 17 VI 1974, F. Donaldson, *Stenotaphrum secundatum*, FSCA_00073125. **a**=acorn-shaped seta; **b**=prothoracic leg; **c**=alveolar derm surrounding the anterior thoracic spiracle; **d**=tubular duct; **e**=second abdominal spiracle; **f**=alveolar derm with spine and fimbriate seta; **g**=alveolar derm with fimbriate and hair-like setae; **h**=edge of anal ring; **i**=anal ring; **j**=fimbriate seta; **k**=alveolar derm with setae and patches of microtrichia; **l**=tubular duct; **m**=spine; **n**=fimbriate seta; **o**=acorn-shaped seta.

in two pairs of longitudinal lines on abdomen (submedial and lateral), present marginally on thorax and head, longest seta on abdomen 34 μm long, longest seta on thorax 16 μm long, shorter slightly enlarged setae in cluster on segment VIII, 8 μm long, slightly longer enlarged setae near base of each antenna. Spines with enlarged base, swollen, rounded apices, submarginal on abdomen, thorax, and head, longest spine on head 25 μm long (Fig. 5f). Eye absent. Labium two-segmented, small, about as wide as long, round, only one seta arising from all basal sockets. Vulva absent. Multilocular pores absent. Modified quadrilocular ducts absent. Dome- or acorn-shaped setae with raised rounded blunt apex scattered on head, same size as those on dorsum. Small tubular ducts uncommon, arranged in longitudinal line mediolaterally on each side of head, thorax, and anterior abdominal segments. Anal lobes indistinct, each anal lobe area bearing two enlarged fimbriate setae, 28 μm long, one spine (apex obscured by wax) on each side. Entire derm alveolar with polygonal cell-like reticulations. Antennae each three-segmented, segments short, total length 59 μm long, segment I 19 μm long, segment II 16 μm long, apical segment 27 μm long. Apical segment with long fleshy apical seta, straight with rounded blunt tip, 35 μm long, short fleshy subapical seta, curved with rounded blunt tip, 18 μm long, third fleshy seta at apex, 28 μm long, two microsetae adjacent to apical setae, each clubbed apically, unspecialized setae spine-like. Segment I with small, hair-like seta near base. Pseudobasal antennal segment absent. Legs (Fig. 5b) reduced in size, all about equal, trochanter and femur fused, with two campaniform sensilla on each surface, tibia and tarsus not fused, tarsus one-segmented, coxa 54 μm long, trochanter + femur 48 μm long, tibia 18 μm long, tarsus 29 μm long, tibia/tarsus 0.6, claw 18 μm long. Leg setae sparse, straight, spiniform dorsally and ventrally, enlarged spines between tibia and tarsus absent. Sensory pore between tibia and tarsus present, sensory setae between tibia and tarsus absent. Tarsal digitules absent. Claw digitules each spine-like with acute apex, shorter than claw, claw denticle absent.

Notes: This specimen was collected with a second-instar nymph (described below) but no adult females. We include it in material examined but not as a paratype for this reason.

Second-instar? nymph

(Figs. 4D, 6)

Description: Slide-mounted specimen 0.42–0.53 mm long, 0.22–0.35 mm wide, body rotund oval (n=7).

Dorsum with hair-like setae (Fig. 6k), sparse, in three pairs of longitudinal lines (submedial, mediolateral, submarginal), in segmental rows on abdomen, scattered on thorax and head, longest seta on submedial area of abdomen 6–10 μm long, longest seta on thorax or head 5–9 μm long. Spines absent. Multilocular pores absent. Tubular duct in center of circular area present on head (Fig. 6b). Dome-shaped setae, on submedial apex of head, set on raised area, 4–5 μm in height, 4 μm wide, sparse (Fig. 5l). Simple pores (Fig. 6e, j) scattered on thorax and abdomen, sparse. Anal lobes indistinct, each with single apical seta. Microtrichia absent. Entire derm coriaceous.

Anal ring (Fig. 6g, h) usually ventral, sometimes wrapping around margin, invaginated in pocket, forming setal basket, with 6 or 8 pores anterior to anal opening, bearing six short spine-like anal-ring setae each with acute to slightly rounded apex, about equal in size, each about 10 μm long, most specimens with setae coming straight up on slide, difficult to measure, about 0.7 times as long as greatest diameter of anal ring, 15–23 μm in diameter, derm with heavier sclerotization around anal ring.

Venter with two pairs of thoracic spiracles (Fig. 6c), spiracular openings projecting above derm, atrium with ring of 4–5 pores, without loculi, in single row, spiracular opening 7–9 μm in diameter. Abdominal spiracles unobvious or absent. Hair-like setae sparse, in two pairs of longitudinal lines (marginal and submedial), longest seta on submedial area of abdomen 4–9 μm long, longest seta on thorax or head 6–9 μm long. Eyes absent. Labium two-segmented, small, about as wide as long, round, 25–31 μm long, 30–34 μm wide, only one seta arising from basal sockets. Vulva absent. Multilocular pores absent. Modified quadrilocular ducts absent. Tubular ducts, each in center of circular area, present on each side of head, sometimes also present between antennal bases, smaller ducts present near base of each leg. Dome- or acorn-shaped setae; 4–5 μm in height, 4 μm wide, sparse. Simple pores sparsely scattered on head, anterior to each coxa, and laterally on anterior abdominal segments, same size as those on dorsum. Cluster of 6 short hair-like setae anterior to anal ring, 3–4 μm long, two elongate hair-like setae on each side of anal ring, 23–27 μm long. Anal lobes indistinct, each lobe area with two hair-like setae, 9–11 μm long, single dome- or acorn-shaped seta set on raised base on margin (Fig. 6g, h). Antennae coriaceous, each three-segmented, segments short, total length 27–49 μm long, segment I 8–16 μm long, segment II 9–12 μm long, apical segment 17–22 μm long. Apical segment with long fleshy apical seta, straight with rounded blunt tip, 31 μm long, short fleshy subapical seta, curved with a rounded blunt tip, 9–15 μm long, unspecialized setae hair-like. Pseudobasal antennal segment absent.

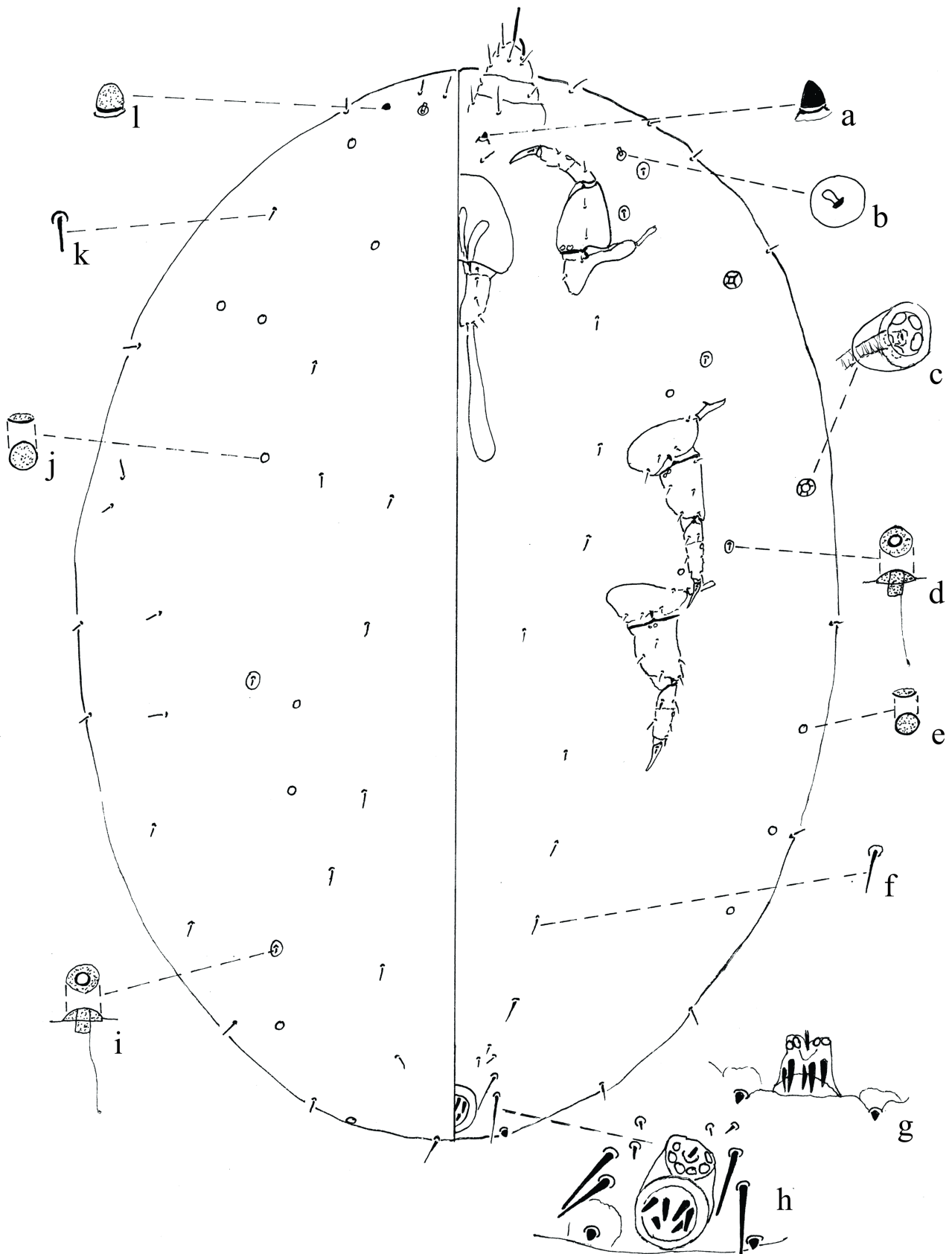


FIGURE 6. *Barbenigma biza* Powell & Miller, **sp. nov.**, second instar?, Florida: Orange Co.: Maitland, 5 XI 1969, H.M. VanPelt, in soil (lawn), FSCA_00073127. The anal ring enlargement utilized a second specimen with the following data: Florida: Marion Co.: Belleview, 15 IX 1966, H. Myers, in soil, DPI #125664, FSCA_00073129. **a**=acorn-shaped seta; **b**=tubular duct set in circular area; **c**=posterior thoracic spiracle; **d**=tubular duct; **e**=simple pore; **f**=hair-like seta; **g**=anal ring viewed from venter; **h**=looking straight down at anal ring; **i**=tubular duct; **j**=simple pore; **k**=hair-like seta; **l**=dome-shaped seta.

Legs coriaceous, reduced in size, all about equal, trochanter and femur fused, with two campaniform sensilla on each surface, tibia and tarsus not fused, tarsus one-segmented, area anterior to each coxa with more sclerotization, coxa 32–39 μm long, trochanter + femur 28–35 μm long, tibia 6–14 μm long, tarsus 9–18 μm long, tibia/tarsus 0.7–0.9, claw 11–15 μm long. Leg setae sparse, straight, spiniform dorsally and setiform ventrally, enlarged spines between tibia and tarsus absent. Sensory pore between tibia and tarsus present, sensory setae between tibia and tarsus absent. Tarsal digitules absent. Claw digitules each spine-like with acute apex, shorter than claw, claw denticle absent.

Notes: Only one of the six nymphs examined was collected in association with an adult female to verify the identification. However, we could find no differences between the specimens and utilized all of them in the description.

First-instar? nymph

(Fig. 7)

Description: Slide-mounted specimen 0.34 mm long, 0.14 mm wide, body rotund oval (n=1).

Dorsum with hair-like setae (Fig. 7h) sparse, arranged in rows, with two pairs of longitudinal lines (submedial and submarginal) on abdomen, thorax, and head, about 9 μm long. Spines and fimbriate setae absent. Small tubular ducts (Fig. 7j) uncommon, restricted to abdomen. Tubular ducts (Fig. 7b) in center of circular area on each side of head, present on alveolar nodules. Multilocular pores absent. Simple pores scattered on abdomen, each with slightly raised center (Fig. 7e, g). Pair of acorn- or dome-shaped seta (Fig. 7a, k) on submedial apex of head, 4 μm in height, 4 μm in width. Simple pores sparsely scattered on thorax and abdomen. Anal lobes indistinct, each lobe area bearing two hair-like setae, 25 μm long, one acorn-shaped seta on posterior margin (Fig. 7f). Microtrichia absent. Entire derm alveolar with polygonal and elongate cell-like reticulations (Fig. 7b, c, f, i).

Anal ring (Fig. 7f) ventral, near abdominal apex, invaginated in pocket, forming setal basket, with 6 pore-like structures at anterior apex of ring, bearing six short, spine-like, anal-ring setae each with slightly rounded apex, about equal in size, 8 μm long, 0.4 times as long as greatest diameter of anal ring.

Venter with two pairs of thoracic spiracles (Fig. 7c), spiracular openings slightly projecting above derm, atrium with ring of 4–5 pores, these without loculi, in single row, spiracular opening 8 μm in diameter. Abdominal spiracles unobvious or absent. Hair-like setae in two pairs of longitudinal lines (submedial and lateral) on each side of body, present on each abdominal segment, 8 μm long. Spines and fimbriate setae absent. Eye absent. Labium not clearly visible. Vulva absent. Multilocular pores absent. Modified quadrilocular ducts absent. Simple pores present near each pair of legs, with associated small tubular duct, also present in submarginal line on each side of some anterior abdominal segments, these about the same size as those on dorsum. Small tubular ducts uncommon, arranged in longitudinal line mediolaterally on each side of head, thorax, and anterior abdominal segments. Anal lobes indistinct, each lobe area bearing enlarged hair-like seta on margin, about 6 μm long, two hair-like ventral setae level with anal ring, each about 25 μm long. Acorn-shaped seta submedially, between antennal bases, 3 μm in height, 3 μm width. Entire derm alveolar with polygonal cell-like reticulations. Cluster of 4 short hair-like setae anterior to anal ring, 3–4 μm long, two elongate hair-like setae on each side of anal ring, 23–27 μm long, acorn-shaped seta on each side of anal ring at posterior apex. Antennae each three-segmented, segments short, total length 39 μm . Apical segment with long fleshy apical seta, straight with rounded blunt tip, 29 μm long, short fleshy subapical seta, curved with rounded blunt tip, 14 μm long, third fleshy seta at apex, 19 μm long, unspecialized setae long and hair-like. Pseudobasal antennal segment absent. Legs reduced in size, all about equal. Trochanter and femur fused, with two campaniform sensilla on each surface. Tibia and tarsus not fused, tarsus one-segmented. Coxa 37 μm long, trochanter + femur 31 μm long, tibia 10 μm long, tarsus 16 μm long, tibia/tarsus 0.6, claw 12 μm long. Leg setae sparse, straight, spiniform dorsally and ventrally, enlarged spines between tibia and tarsus absent. Sensory pore between tibia and tarsus present, sensory setae between tibia and tarsus absent. Tarsal digitules absent. Claw digitules each spine-like with acute apex, shorter than claw, claw denticle absent.

Notes: The illustration and description are based on a single specimen that was mounted laterally and not completely cleared, making it difficult to determine the exact location of some structures. This specimen was collected in association with the holotype adult female.

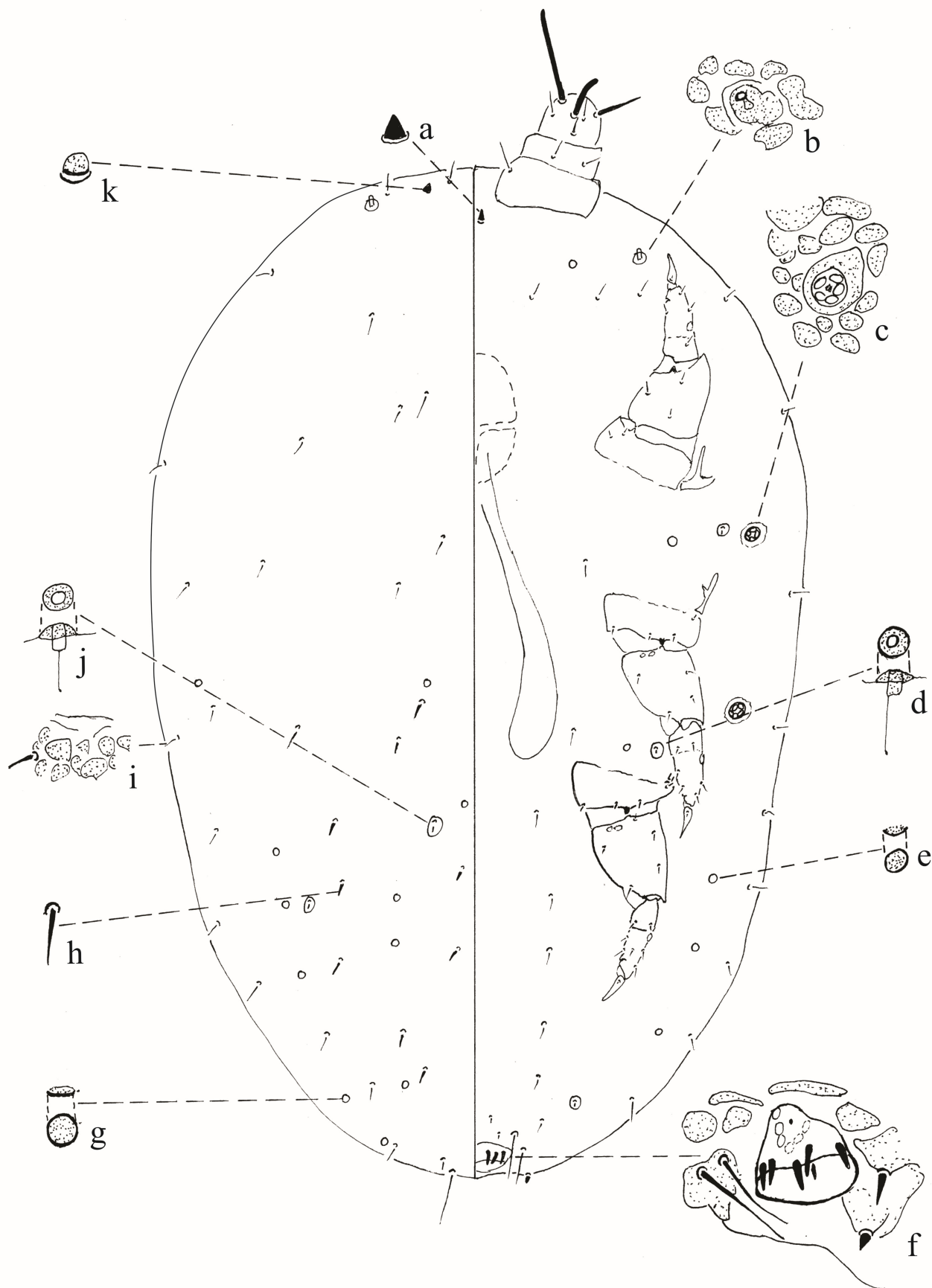


FIGURE 7. *Barbenigma biza* Powell & Miller, **sp. nov.**, first instar?, Florida: Alachua Co.: Gainesville, 23 III 1999, R. Esser, C. Zamora, *Rumex hastatulus*, E99-879, FSCA_00073115. **a**=acorn-shaped setae; **b**=tubular duct on alveolar derm nodule; **c**=alveolar derm with anterior thoracic spiracle; **d**=tubular duct; **e**=simple pore; **f**=anal ring (specimen rolled), showing part of venter and part of dorsum; **g**=simple pore; **h**=hair-like seta; **i**=alveolar derm with marginal hair-like seta; **j**=tubular duct; **k**=dome-shaped seta.

Barbenigma boscus Powell & Miller, sp. nov.

Material examined

Holotype: adult ♀, mounted singly. NEBRASKA: Furnas Co., Arapahoe, junction of Highway 6 and 46 (40.308056, -99.863611), 8 July 2023, on roots of *Bromus inermis* (Poaceae) on roadside, coll. D.R. Miller and B.D. Denno, 2023-07304, FSCA_00073131 (FSCA).

Paratypes: 2 adult ♀♀ with same data as holotype mounted singly on 2 slides (FSCA_00073132–FSCA_00073133) (FSCA, USNM).

Etymology: The species epithet is a noun in apposition derived from the Medieval Latin word “*boscus*” meaning “bush”, referring to the duct clusters on this species.

Adult female (Figs 8 and 9)

Description: Slide-mounted holotype 1.18 mm long, 0.90 mm wide, with several large eggs retained inside body; paratypes (n=2) 1.04–1.29 mm long, 0.74 mm wide; body rotund oval.

Dorsum with robust fimbriate setae (Fig. 8r), with up to five times, sparse, one present marginally on each abdominal segment, one present medially on each abdominal segment, roughly in single longitudinal submedial line on thorax and head, longest seta on medial area of abdomen 26 µm long (paratypes 30–36 µm), longest seta on margin 31 µm long (paratypes 36–39 µm), longest seta on head 25 µm long (paratypes 25–27 µm). Dorsal spines (Fig. 8q) each without setal base, with swollen, rounded apex, sparse, one to three on each side of each abdominal segment, longest spine on medial area of abdomen 31 µm long (paratypes 27–31 µm), longest spine on thorax and head 22 µm long (paratypes 28–29 µm). Tubular ducts (Fig. 8h, n, p) scattered over body. Multilocular pores absent. Short conical setae dome- or acorn-shaped (Fig. 8b) one to several clustered near base of each antenna, 4 µm in height, 4 µm wide (paratypes 4–5 µm by 4 µm). Simple pores (Fig. 8c, s) each with slightly raised rounded center, scattered over body. Some specimens with unknown structure (Fig. 8t) near each antenna with unequal sides, without base, longest side 6–7 µm. Anal lobes (Fig. 8o) indistinct, each lobe area bearing enlarged fimbriate seta, 45 µm long (paratype 39 µm), enlarged capitate seta 56 µm long (paratype 59 µm), spine with swollen apex 25 µm long (paratype 34 µm), on each side of anal ring. Microtrichia absent. Derm smooth.

Anal ring (Fig. 8o) wrapping around margin, invaginated in pocket, forming setal basket, with ring of pores, bearing six robust anal-ring setae each with truncate apices, one paratype specimen with seven anal-ring setae, about equal in size, 40 µm long (paratype 41 µm), 0.9 times (paratype 0.8 times) as long as greatest diameter of anal ring.

Venter with two pairs of thoracic spiracles (Fig. 8f), spiracular openings projecting above derm by about 7 µm, three pairs of abdominal spiracles, spiracular openings flush with derm; thoracic and abdominal spiracle atria each with ring of pores, these without loculi, typically in single row around spiracle, one thoracic spiracle on holotype with one pore in double row, 7–11 (paratypes 9–10) pores in ring around anterior thoracic spiracle, opening 16 µm in diameter (paratypes 17–18 µm), 8–11 (paratypes 10–11) pores in ring around each abdominal spiracle, first abdominal spiracular opening 14 µm in diameter (paratypes 15–17 µm). Body setae (Fig. 8j) with capitate apices, those on abdomen longer than those on thorax and head, longest seta on thorax or head 18 µm (paratypes 18 µm), longest seta on abdomen 36 µm (paratypes 33–40 µm). Robust fimbriate setae and spines with swollen apices, marginal. Dome- and acorn-shaped setae, each with raised rounded blunt apex, in cluster on head, about same size as those on dorsum. Eye absent. Labium two-segmented, small, about as wide as long, round, 34 µm long, 36 µm wide (paratype 35 µm by 40 µm), only one seta arising from all basal sockets. Vulva wide, 215 µm wide (paratypes 192–194 µm), with smooth margins, with heavily sclerotized lateral bars on either side of vulva. Margins of abdominal segments with heavily sclerotized areas (probably muscle attachment points) (not illustrated in Fig. 8 but see Fig. 9B), the posterior two sclerotizations each typically with two associated tubular ducts on each side (Fig. 9B). Compound duct clusters (Fig. 8l) present marginally, clusters of tubular ducts (Fig. 8k) with quadrilocular centers, spines (Fig. 8m) arising from between quadrilocular ducts, clusters set in sclerotized ring, three pairs on abdomen, one on each side of each of segments VI–VIII, two medially (one posterior to vulva, one anterior to vulva), eight duct clusters total on abdomen, 16–22 ducts per median cluster (paratypes 15–25), 14–16 ducts per marginal cluster (paratypes 15), median clusters 27–32 µm in diameter (paratypes 22–33 µm), marginal clusters 25–30 µm in diameter (paratypes 25–29 µm). Multilocular pores absent. Simple pores few, scattered on thorax and abdomen, about same size as those on dorsum. Microtrichia absent. Derm smooth. Anal lobes indistinct, each lobe area bearing cluster of two enlarged capitate setae, 53–57 µm long (paratype 56 µm), one small seta (fimbriate on one side but not on other on holotype, fimbriate on paratype specimens), 15 µm long (paratype 14 µm), and one spine with swollen apex, 26 µm long (paratype 33 µm). Antennae (Fig. 8a) each three-segmented, segments short,

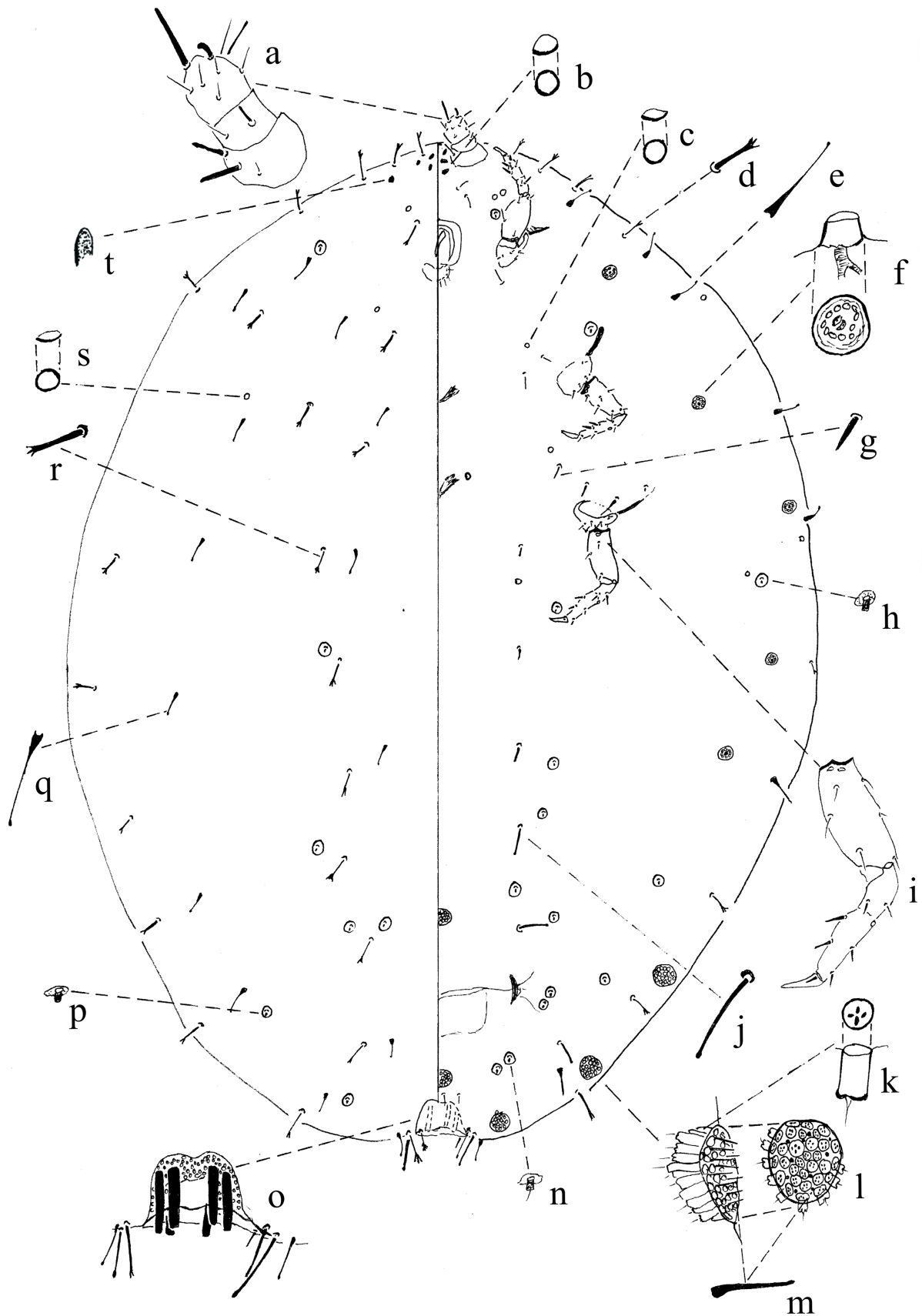


FIGURE 8. *Barbenigma boscus* Powell & Miller, **sp. nov.**, adult female holotype. Nebraska: Furnas Co., Arapahoe, 8 VII 2023, D.R. Miller, B.D. Denno, *Bromus inermis*, E-2023-07304, FSCA_00073131. **a**=antenna; **b**=dome-shaped setae; **c**=simple pore; **d**=fimbriate seta; **e**=spine; **f**=posterior thoracic spiracle; **g**=ventral seta; **h**=tubular duct; **i**=metathoracic leg; **j**=ventral setae with capitate apex; **k**=quadrilocular duct; **l**=quadrilocular duct cluster; **m**=spine, **n**=tubular duct, **o**=anal ring, **p**=tubular duct; **q**=spine; **r**=fimbriate setae; **s**=simple pore; **t**=unequal-sided structure.

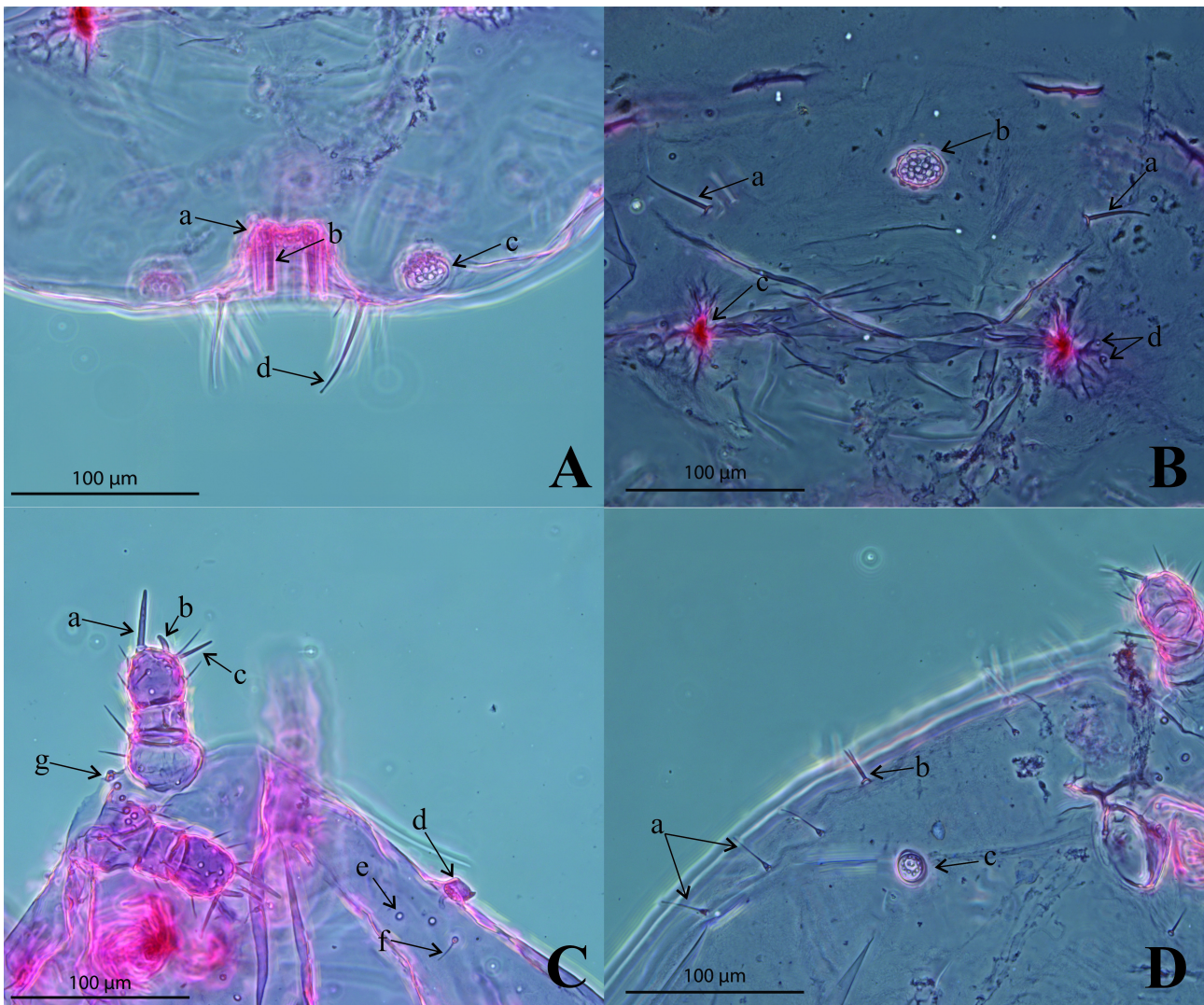


FIGURE 9. *Barbenigma boscus* Powell & Miller, **sp. nov.**, adult female holotype. Nebraska: Furnas Co., Arapahoe, 8 VII 2023, D.R. Miller, B.D. Denno, *Bromus inermis*, E-2023-07304, FSCA_00073131. (A) a=anal ring; b=truncate anal ring seta; c=quadrilocular duct cluster, d=capitate seta. (B) a=capitate setae, b=quadrilocular duct cluster; c=sclerotized left edge of vulva; d=tubular ducts. (C) *Barbenigma boscus* Powell & Miller, **sp. nov.**, adult female paratype. Nebraska: Furnas Co., Arapahoe, 8 VII 2023, D.R. Miller, B.D. Denno, *Bromus inermis*, E-2023-07304, FSCA_00073132. a=apical seta on antenna; b=subapical seta on antenna; c=subapical seta on antenna; d=anterior thoracic spiracle pictured on side; e=tubular ducts; f=spine; g=acorn-shaped and dome-shaped setae in cluster between antennae. (D) Adult female holotype. a=ventral spines; b=marginal fimbriate seta; c=anterior thoracic spiracle.

segments I and III subequal, holotype antennae coming straight up on slide, paratypes total length 83–88 µm, segment I 34–37 µm long, segment II 24–28 µm long, apical segment 34 µm long. Apical segment with one long fleshy apical seta, straight with a rounded blunt tip, 30 µm long (paratypes 34 µm), one short fleshy subapical seta, curved with a rounded blunt tip, 18 µm long (paratypes 17 µm), a third fleshy seta at apex, microseta adjacent to apical setae, one capitate spine on apex, unspecialized setae long and straight. Pseudobasal antennal segment absent. Legs (Fig. 8i) reduced in size, all about equal. Trochanter and femur fused, with two campaniform sensilla on each surface. Tibia and tarsus not fused, tarsus one-segmented. Coxa 52 µm long (paratypes 47–49 µm), trochanter + femur 68 µm long (paratypes 67–68 µm), tibia 26 µm (paratypes 26 µm), tarsus 47 µm long (paratypes 46–47 µm), tibia/tarsus 0.6 (paratypes 0.6), claw 22 µm long (paratypes 19–21 µm). Leg setae sparse, straight, spiniform dorsally and setiform ventrally, enlarged spines between tibia and tarsus absent. Sensory pore between tibia and tarsus present, sensory seta between tibia and tarsus absent. Tarsal digitules absent. Claw digitules each spine-like with acute apex, shorter than claw, claw denticle absent.

Notes: See the ‘Notes’ section of *B. biza* for a comparison of the two species.

As in *B. biza*, the simple pores on the thorax and abdomen may not be homologous to the ones on the head, and we call these simple pores rather than setae. The ones on the head have a lot of depth, easily visible when seen in lateral view; however, those on the thorax and abdomen (both ventral and dorsal) did not have such obvious depth.

The antennae of the adult females of both new species are very difficult to measure accurately because the segments are short and round, rarely lying flat (see Figs 4C, D; 9C). When mounted flat, they are crushed and distorted. One of the paratype specimens is mounted in such a way that it was impossible to measure the setae and spines in and around the anal ring.

Key to species of Carayoneminae, based on slide-mounted adult females (revised from Kozár & Konczně Benedicty 2000)

- 1(0) Quadriocular tubular duct clusters present; bilocular pores absent; thoracic spiracles ventral (Barbenigmini) 2
- Quadriocular tubular duct clusters absent; bilocular pores present; thoracic spiracles dorsal (Carayonemini) 3
- 2(1) Ventral setae with acute apices; dorsal spines typically occurring in pairs on submargin of each side of each abdominal segment *Barbenigma biza* Powell & Miller, **sp. nov.**
- Ventral setae with capitate apices; dorsal spines typically occurring singly on submargin of each side of each abdominal segment *Barbenigma boscus* Powell & Miller, **sp. nov.**
- 3(1) Second segment of antenna heavily sclerotized *Carayonema ousseti* Richard, 1986
- Second segment of antenna not sclerotized 4
- 4(3) Tibia and tarsus fused *Mahunkacoccus mexicanensis* Kozár & Konczně Benedicty, 2000
- Tibia and tarsus not fused 5
- 5(4) Umbelliform setae present *Foldicoccus monikae* Kozár & Konczně Benedicty, 2000
- Umbelliform setae absent *Baloghicoccus costaricaensis* Kozár & Konczně Benedicty, 2000

Phylogenetic results

To test the placement of the new genus *Barbenigma*, we scored both species for 77 morphological characters and included them in an expanded dataset from Veá & Grimaldi (2012). The resulting maximum likelihood consensus tree and parsimony strict consensus tree (Figs 10 and 11) recovered *Barbenigma* **gen. nov.** as sister to the clade consisting of the four included Carayonemidae species. The clade was nested within Ortheziidae, rendering the family polyphyletic. We therefore decided to sink Carayonemidae to a subfamily level, Carayoneminae Richard **new synonymy and change of rank**, within the Ortheziidae.

Discussion

There is considerable uncertainty surrounding the family placement, designation of nymphal instars, body shape, extent of alveolation, species designation, geographic range, and ant association of this collection of just plain weird scale insects. In light of this, we have called it enigmatic and hope that additional specimens will be available, not only for morphological analysis and studies of natural history, but also for molecular analysis.

Barbenigma species possess a suite of character states that occur in species of both ortheziids and carayonemids, e.g., antennae with a conspicuous differentiated seta on apical segment, abdominal spiracles, a reduced number of ventral abdominal segments, no tarsal digitules, and some leg segments fused. Character states shared by *Barbenigma* species with carayonemids include: fimbriate setae; three-segmented antennae; labium small and rounded; a reduced number of abdominal spiracles; protruding thoracic spiracles; two campaniform sensilla on each surface of each trochanter; and an invaginated anal ring. Notably, a nymph of the new species *B. biza* mounted laterally bears a striking resemblance to the profile illustration of an adult female *Carayonema ousseti* Richard (1986), with a bumpy, alveolate derm both dorsally and ventrally; however, the adults of *B. biza* have a smooth derm. *Barbenigma*, which shares character states with both families, supports a close relationship between the Ortheziidae and Carayonemidae, as posited by other authors including Foldi (1997), Kozár & Konczně Benedicty (2000), Kozár & Foldi (2002), Gullan & Cook (2007), and Gavrillov-Zimin (2018). Yet a lack of molecular data for any carayonemine has and continues to limit our ability to draw conclusions about relationships amongst the archaeococcoids. Our phylogenetic

analysis using morphology demonstrates that the four species previously placed in the family Carayonemidae and the two new species of *Barbenigma* form a monophyletic group that should be placed within the Ortheziidae as the subfamily Carayoneminae (Figs 10 and 11). Kozár in Kozár & Konczné Benedicty (2000) erected three subfamilies and three tribes for the four monotypic genera of Carayonemidae. However, Gavrilov-Zimin (2018) argued that there was no justification for these actions and we agree. We recognize two tribes of Carayoneminae: Carayonemini Richard with four accepted genera (*Baloghicoccus*, *Carayonema*, *Foldicoccus*, and *Mahunkacoccus*) and a new monotypic tribe, Barbenigmini Powell & Miller, containing *Barbenigma*.

Immatures are known for *B. biza* only. The designation of instars for the immatures is not fully clear. What we have designated as the first-instar and second-instar nymphs differ very little. The “first-instar” nymph is slightly smaller and narrower, the tibia length divided by tarsus length is slightly smaller, and the derm has conspicuous raised alveolations. We only have a single specimen that matches this description, so measurement comparisons give little information. In contrast, what we have called the “second-instar” nymph has a rotund body with a smoother, but coriaceous, derm. This seems unlikely to be simply a ‘stretched’ version of the extensive alveolation on the “first-instar” nymph, but we do recognize that this as a possibility. Even more puzzling, the “third-instar” nymph bears much resemblance to the adult (with many fimbriate setae, tubular ducts, dome-shaped, or acorn-shaped setae, a similar anal ring, etc.) but is again extensively alveolar on the ventral and dorsal derm. Both the tiny, narrow young adult female and the rotund mature adult female have entirely smooth derms, apparently without even microtrichia. Despite the uncertainty about the number and identity of nymphal instars, all of these immatures are associated with the adult because representatives of both the first- and second-instar nymphs were collected with an adult female, all have a similar invaginated anal ring with a “setal basket”, all have similar tubular ducts, and all bear the unique dome- or acorn-shaped setae on the head. The third-instar nymph was not collected in association with an adult female, but it was found with a second-instar nymph that is apparently identical to the series of other second-instar nymphs. Moreover, the fimbriate setae, tubular ducts, and setae present around the anal ring strongly support that it is the same species as the adult. The dome- or acorn-shaped setae on the anal lobes of all of the immature stages become fimbriate setae in the adult, further supporting our hypotheses that these dome- or acorn-shaped structures are indeed setae, rather than ducts or pores. Scanning electron microscopy (SEM) with fresh material may help to elucidate more information about these structures in the future. There are major differences in body size between young and mature adult females, with specimens only half as long and nearly five times narrower than rotund mature females. Seeing major phenological shifts in body size as adult females begin laying eggs is not particularly unusual in scale insects, but the differences in body shape are especially striking in this species. So striking, in fact, that the tiny narrow adult females (with a fully developed vulva) were mistakenly labeled by a previous curator as immature males.

Specimens were collected from disparate locations in the United States: Nebraska and Florida. Our initial hypothesis was that we were dealing with a single species, but after careful comparison of morphological character states from the two localities it seemed likely that they are two distinct species (see ‘Diagnosis’ section of *B. biza*). Florida specimens of *B. biza* have (character states of Nebraska specimens of *B. boscus* given in parentheses): more spines on the dorsal abdomen, with spines typically occurring in pairs on the submargin of each side of each abdominal segment (spines occurring singly); body setae with acute apices (body setae with capitate apices); shorter spines on the dorsum, measuring 14–23 µm long (longer spines on the dorsum, measuring 22–31 µm); and shorter dorsal fimbriate setae, measuring 16–30 µm long (longer dorsal fimbriate setae, measuring 26–39 µm). However, with only three specimens from a single locality in Nebraska and eight from three localities in Florida, it is difficult to draw robust conclusions from these measurement data, and we do find overlap in the setal and spine measurements between localities.

Specimens of *B. biza*, including both adults and immatures, have been collected from seven counties across Florida, suggesting the species is widespread in the state and could be undetected in other areas of the southeast United States, potentially being spread by the turfgrass trade. Kozár & Konczné Benedicty (2000) and Kozár & Foldi (2001) speculated that members of Carayonemidae may be adapted for aquatic living, given their dorsal elongate spiracles and fimbriate or umbelliform setae, which become coated with an amorphous substance. *Barbenigma boscus* was collected from a dry habitat that probably never floods and specific habitat information for *B. biza* is unknown. We do not expect that Barbenigmini is associated with aquatic habitat as with members of Carayonemini.

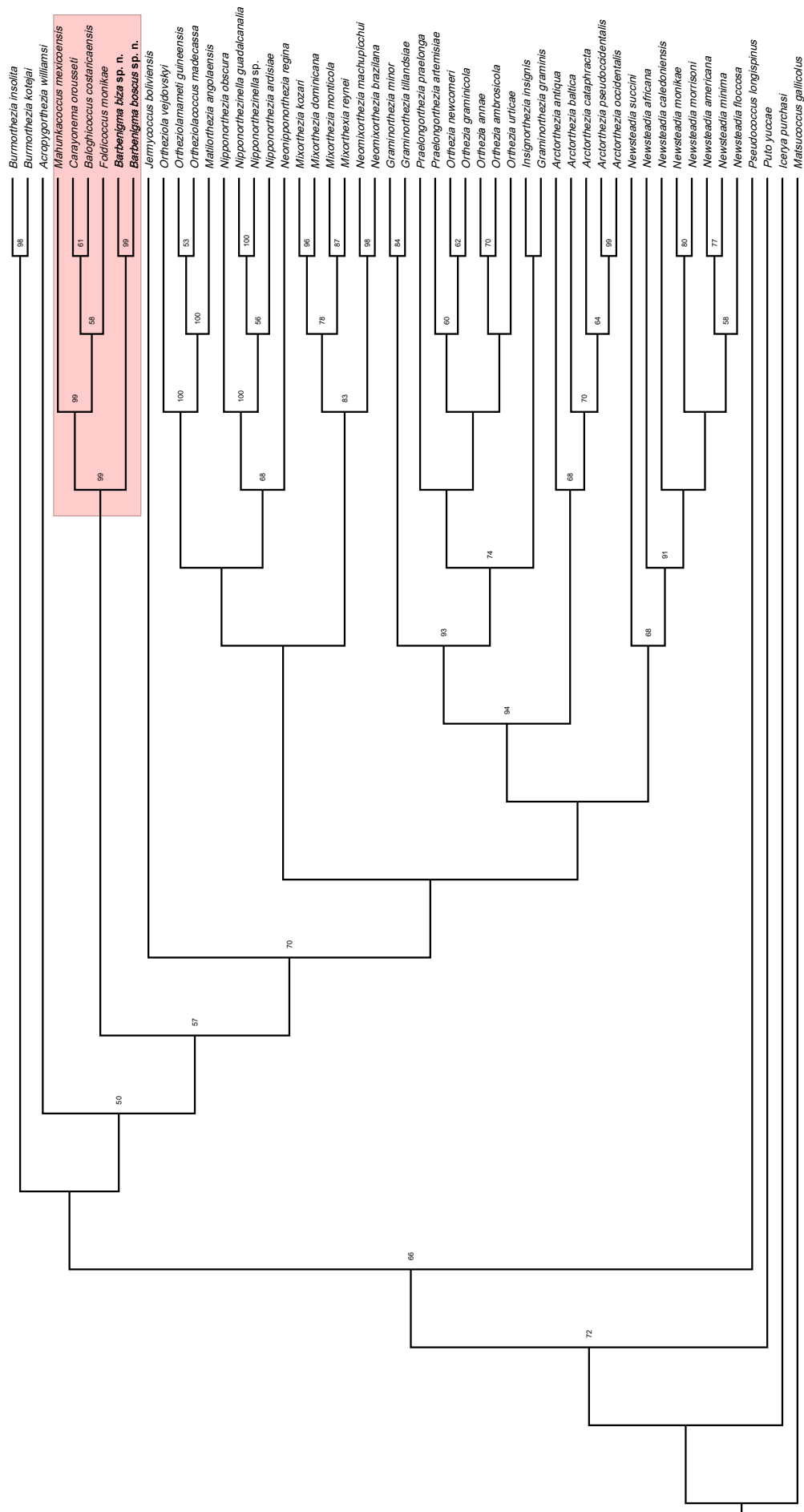


FIGURE 10. Phylogenetic consensus tree of the family Ortheziidae based on the Maximum Likelihood analysis of a morphological matrix. Node labels represent Ultrafast Bootstrap values generated in IQTree. Positions of outgroup taxa do not reflect higher-level relationships amongst Coccomorpha.

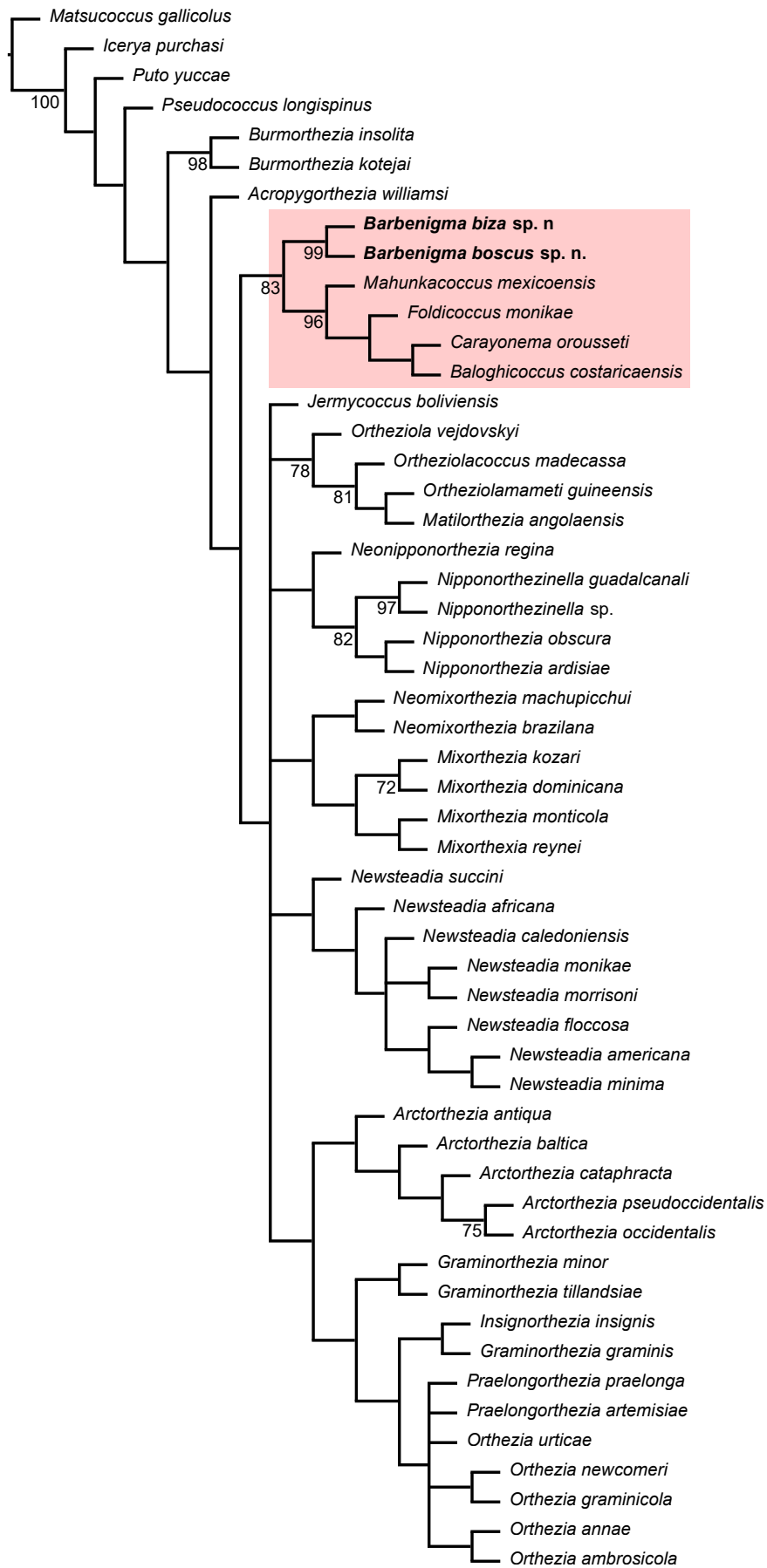


FIGURE 11. Strict consensus of the 275 most parsimonious trees obtained from TNT analysis. L = 339 steps; RI = 0.72; CI = 0.30. Positions of outgroup taxa do not reflect higher-level relationships amongst Coccoomorpha.

Ants were not observed actively tending to *Barbenigma*, however several of their characteristics resemble traits that have been tied to obligate ant-association, suggesting they may also be myrmecophilic. Given the rotund body shape of some of the adult females, morphological features such as the reduction of wax-producing structures and spines, capitate, ornate fimbriate, and dome- and acorn-shaped setae that could be considered “sensory setae” (e.g., atypical setae found in members of Xenococcidae, see Williams 1998 and Schneider & LaPolla 2011), reduced antennal segments, absence of eyes, and the subterranean habitat in which these specimens were collected, we suspect that they could be obligate associates of ants (Williams 1998; LaPolla *et al.* 2008; Schneider & LaPolla 2011; Sodano *et al.* 2023). Obligately myrmecophilous mealybugs are typically smaller than free-living mealybugs, have a rotund or pyriform body shape, have reduced antennal segmentation, and ant-associated families such as Xenococcidae and members of Rhizocercidae lack wax-producing structures (Schneider & LaPolla 2022; Sodano *et al.* 2023). Only one obligate myrmecophilic ortheziid is known: *A. williamsi* from Australia. Like *A. williamsi*, *Barbenigma* species have reduced antennal segments, no eyes, and no wax plates. While the legs of *A. williamsi* are not nearly as reduced as those on *Barbenigma*, they are proportionally small in comparison with other ortheziids (Kozár 2004; LaPolla *et al.* 2008; Sodano *et al.* 2023). Moreover, *Barbenigma* has a cluster of setae and spines around the invaginated anal ring, perhaps serving as the setal basket to suspend the honeydew for an ant to collect, as is found in xenococcids (Silvestri 1924). Gavrilov-Zimin (2018) also characterized the anal ring of the species of Carayoneminae as a ‘drop-ejecting anal apparatus’. *Acropygorthesia williamsi* has more intuitively ant-adapted structures, however, such as the centralized dorsal anal ring, and in contrast to *A. williamsi*, we would expect *Barbenigma* to make some sort of ovisac with the quadrilocular duct clusters on the ventral abdomen. More collections and observations of this species will be required to unravel more about their natural history.

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