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Two new *Gordionus* species (Nematomorpha: Gordiida) from the southern Rocky Mountains (USA)

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Abstract

The phylum Nematomorpha contains approximately 350 species in 19 extant genera. The genus *Gordionus* contains 56 species, four of which occur in the contiguous United States of America. Here we describe two new *Gordionus* species from the southern Rocky Mountains. Worms were collected at three sites in the Santa Fe National Forest in northern New Mexico in the southernmost tip of the Rocky Mountains. Sites consisted of first order streams above 3120m in aspen/pine woodland. *Gordionus lokaaus* **n. sp.** has flat, polygonal or roundish, areoles covering all parts of the body. The male cloacal opening is surrounded by broad bristles with stout apexes forming a unique tube-like opening. Adhesive warts are small and postcloacal spines are thin and triangular-shaped. *Gordionus bilaus* **n. sp.** also has flat polygonal or round shaped areoles, but has indistinct interareolar furrows making neighboring areoles appear fused. The male cloacal opening is surrounded by stout, finger-like bristles in 2–3 rows. Adhesive warts are larger and postcloacal spines are broad and mound-shaped. These species double the number known from the state of New Mexico and are the first gordiids described from the southern part of the Rocky Mountains.

Key words: *Gordionus lokaaus*, *Gordionus bilaus*, hairworm, cloaca, postcloacal spines, biodiversity, DNA sequencing, morphology, taxonomy

Introduction

The phylum Nematomorpha is the sister phylum to the Nematoda (Dunn *et al.* 2008). Nematomorphs are arthropod parasites and are found in freshwater and marine habitats. The freshwater nematomorphs or gordiids (Nematomorpha: Gordiida), are parasites largely of orthopterans, coleopterans, and mantids (Hanelt *et al.* 2005) and contain about 350 species within 18 genera (Schmidt-Rhaesa 2001a; Zanca & Schmidt-Rhaesa 2008).

The genus *Gordionus* was recognized by Müller, in 1927, to separate several unique species from the genus *Parachordodes* based on the presence of adhesive warts (Müller 1927). Adhesive warts are limited to males, and are elevated cuticular structures on both sides of the ventral midline about 0.5mm anterior to the cloacal opening, and often contain canoe-shaped elevations. However, adhesive warts as a character has become problematic in gordiid systematics since few *Gordionus* species descriptions mention adhesive warts, likely due to the lack of study of the body area containing these structures (Schmidt-Rhaesa *et al.* 2003). Instead, taxonomists have subsequently used the number of areole types to separate *Gordionus*, having one areolar type, from *Parachordodes*, having two areolar types. Areoles are elevated epicuticle surface ornamentations. Use of this single cuticle character to separate these genera has introduced much taxonomic uncertainty and the monophyly of both genera is in doubt (Schmidt-Rhaesa 2001a), and has resulted in the description of some *Gordionus* species without adhesive warts and some *Parachordodes* species with adhesive warts.

Currently, *Gordionus* species are characterized by a bifurcating male posterior end, which is longer than wide,

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where bristles or tubercles surround the body laterally and anterior to the cloaca, in a crescent-shape. The cuticle has only 1 areole type, which is moderately protruding and round or polygonal. Interareolar furrows, the space between areoles, can be shallow and subtle to deep and well defined. Interareolar structures are present or absent, and can contain a variable number and distribution of tubercles and bristles. The male cloacal opening can have long or short spines; in some species spines are absent. Precloacal bristle fields or rows of bristles and postcloacal spines are present in all species.

The genus *Gordionus* contains 56 species, which have been described worldwide (Schmidt-Rhaesa 1997; 2001a). Gordiids have been collected and reported from throughout the Nearctic (Schmidt-Rhaesa *et al.* 2003), and four *Gordionus* species have been described from the contiguous United States. However, little is known about gordiids from high altitude alpine ecosystems within the Rocky Mountains. Here we describe the first gordiids, two new species of *Gordionus*, from New Mexico's southern Rocky Mountains.

Methods

Field collections. Worms were collected from three sites. Two sites (sites 1 and 2) consisted of unnamed first order streams crossing Aspen Vista road near the Santa Fe ski area, within the Santa Fe National Forest in the southern Rocky Mountains, New Mexico. Both streams flow into the North Fork of Tesuque Creek. The third site (site 3) consisted of an unnamed first order stream, flowing just to the northwest of the Santa Fe ski area, and which merges with the Rio en Medio. Collections were made from 2005–2011 during summer and early fall (June to September). Worms were placed in plastic containers with stream water and brought to the laboratory at the University of New Mexico (UNM), Albuquerque, New Mexico, USA.

Biological material and microscopy. In the laboratory, worms were rinsed with and placed in tap water. Some worms were retained for breeding experiments and maintained in water. For the remaining worms, the length and width of unfixed worms was measured taking the precaution not to stretch worms. The anterior, posterior, and midsections were removed with a razor blade and put into 10% formalin or 70% ethanol for subsequent scanning electron microscopy (SEM) work. The rest of the body was preserved in 100% ethanol and stored at -70C, for molecular work. For SEM, worm pieces were dehydrated in an increasing ethanol series, dried with CO_2 in a critical point dryer, and coated with gold in a sputter coater. Observations were made and digital images were taken using a LEO SEM 1524 (Carl Zeiss, Jena, Germany) at 10kV.

Molecular methods. DNA was analyzed from 88 individuals as well as from 2 undescribed *Gordionus* species from Washington State (Begay, unpublished) as outgroups. For each sample a 0.5 cm section was cut from the worm pieces previously placed in 100% EtOH, dried at room temperature for 1–3 hours, and used for DNA extraction using the E.Z.N.A.® Mollusc DNA Kit (Omega Bio-Tek, Norcross, Georgia) following the manufacturer's instructions and stored at -70C. A ~450 base pair barcoding region of *cox*1 was amplified using GoTaq® Flexi DNA Polymerase (Promega Corp., Madison, Wisconsin) and degenerate primers specifically designed for the genus *Gordionus*. The primers used were: cox1-Gordionus-R1: TGT TGA AAT ARA ATA GGG TCC C, and cox1-Gordionus-F1: GCK GTA ATA CCY ATT TTG GT using standard polymerase chain reaction (PCR) protocol. The PCR reaction products were analyzed by agarose gel electrophoresis, using 1.0% agarose gels, stained with 0.5% GelRed Nucleic Acid Gel Stain (Biotium, Hayward, California), and visualized on a UV transilluminator. Amplicons were purified by ethanol precipitation and sequenced using the BigDye version 3.1 kit (Applied Biosystems, Foster City, California) on an ABI 3130x sequence analyzer (Applied Biosystems). Both strands of the amplified DNA fragments were sequenced, edited in Sequencer version 5.0 (Gene Codes, Ann Arbor, Michigan), manually corrected for ambiguous base calls and finally trimmed to equal lengths. Identical sequences were removed.

Sequences were aligned using ClustalW2 (Larkin *et al.* 2007). Evolutionary history was inferred by using the maximum likelihood method based on the Kimura 2-parameter model (Kimura 1980) in MEGA5 (Tamura *et al.* 2011). All positions containing gaps and missing data were eliminated from analysis leaving a total of 376 positions in the final dataset. Internal support was assessed using 1,000 bootstrap replicates.

Results

Taxonomy

***Gordionus lokaaus* n. sp.**
(Figs. 1, 2)

Holotype. Deposited at the Museum of Southwestern Biology-Parasitology Division (MSB: PARA): 101. Male collected from a tributary of the North Fork Tesuque Creek (35.7699, -105.7954).

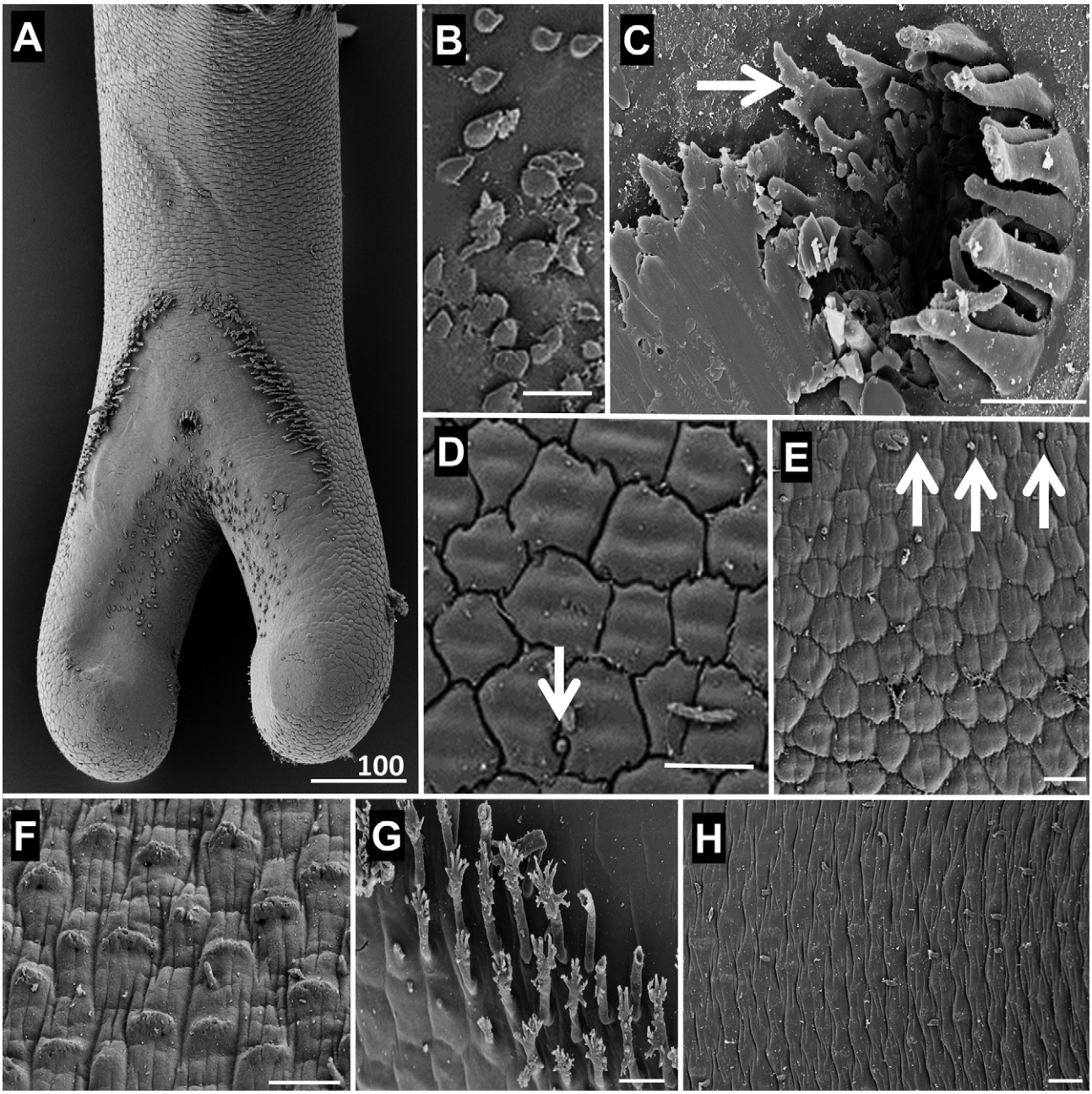

FIGURE 1. *Gordionus lokaaus* **n. sp.** (A) Male posterior end showing thin row of precloacal bristles and postcloacal spines. (B) Postcloacal spines. Note thin, triangular shape. (C) Cloacal spines surrounding cloacal opening are broad and stout, forming a tube-like structure. Note that several of the spines appear to be branching (arrow). (D and E) Cuticle with one type of flat, irregularly-sized areoles, with tubercles between areoles (arrows). Note that some areoles have (D) serrated edges, and others (E) smooth edges. (F) Adhesive warts showing canoe-shaped bulges. (G) Precloacal bristles are branched apically. (H) In some areas the areoles disappear and are replaced with grooves, which run perpendicular to the body axis. Scale bars = 10 µm, except where indicated.

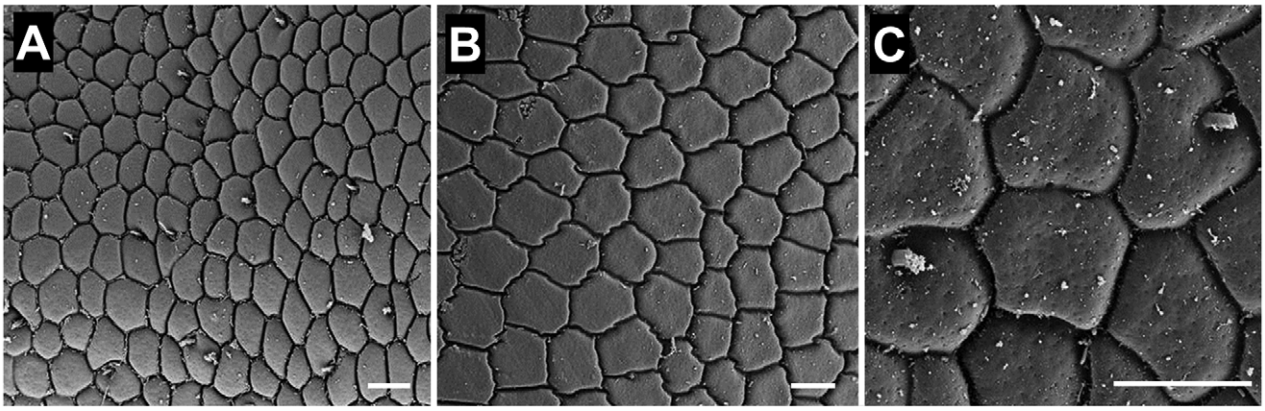

FIGURE 2. *Gordionus lokaaus* **n. sp.** cuticle of female. (A) Cuticle in anterior end. Note the roundish appearance of areoles. (B) Cuticle in posterior end. Note the polygonal shape of areoles with serrated edges. (C) Megaeroles with tubercles situated in hollows. Scale bars = 10 µm.

Paratypes. Allotype. MSB: PARA 102. Female collected from a tributary of the North Fork Tesuque Creek (35.7699, -105.7954). **Other paratypes.** MSB: PARA: 103–110.

Etymology. The species epithet is derived from the Navajo word for bamboo, lókaa'tsoh, which describes the hollow tube-shape formed by the spines surrounding the male's cloaca (Fig. 1C).

Distribution. Rocky Mountains, Santa Fe National Forest, New Mexico. Found at two sites (sites 1 and 2) consisting of unnamed first order streams crossing Aspen Vista road, off of NM State route 475 (Hyde Park road) near the Santa Fe ski area: Site 1 (35.7699, -105.7954) at an elevation between 3,200–3,290m, and site 2 (35.7788, -105.7953) at an elevation of 3,127m.

Type locality. Site 1 (35.7699, -105.7954) at an elevation between 3,200–3,290m.

Bionomics. The worms were collected in the free-living, post-parasitic, adult stage, and the paratenic and definitive hosts remain unknown. Most individuals of this species were collected from August to September (n = 51), and a few were collected in late June (n = 3).

Material examined. Of 54 worms (27 males; 27 females) collected, DNA was amplified for all individuals. For each of these worms, partial *cox*1 was amplified and sequenced. The anterior, posterior, and midsection of seven individuals were used for SEM studies.

Description of male. Adult males were 73–220 ($\bar{x}$ = 141.2)mm long and white in color. Areoles of one type, mostly flat; ranging in shape from polygonal to round (Figs. 1D and E). In some areas areoles have serrated edges (Fig. 1D), while in others the margins appear much smoother (Fig. 1E). Interareolar furrows are distinct.

On ventral side, areoles in some areas are much less defined and the surface appears grooved perpendicular to the longitudinal axis (Fig. 1H). Tubercles are present but not abundant between areoles (megareolar pattern, Fig. 1D, E); more abundant in anterior end. Precloacal bristles are long, conical and arranged into thin rows (Fig. 1A); bristles branch apically (Fig. 1G). Cloacal opening is surrounded by broad spines of irregular shape (Fig. 1C), which together appear to form a tube; some spines appear to be branched slightly (Fig. 1C). Postcloacal spines start immediately posterior to the cloacal opening and extend onto the inner side of the tail lobes (Figs. 1A, B). Postcloacal spines appear thin and triangular; some with serrated edges (Fig. 1B). Canoe-shaped adhesive warts are present anterior to the precloacal rows of bristles (Fig. 1F), and are relatively narrow (8–10µm).

Description of female. Adult females were white and 52–200 ($\bar{x}$ = 142.8) mm long. Areoles of one type mostly flat; range in shape from polygonal to round (Figs. 2A and B). In some areas areoles have serrated edges (Fig. 2B), while in others the margins appear smooth (Fig. 2A). Round areoles predominate in the anterior end. Megareolar pattern present (Figs. 2A and B) moderately throughout, but more abundant in anterior end. Most tubercles situated in hollows formed on the edges of areoles (Fig. 2C).

***Gordionus bilaus* n. sp.**
(Figs. 3, 4)

Holotype. MSB: PARA: 111. Male collected from a tributary of the North Fork of Tesuque Creek (35.7699, -105.7954).

Paratypes. Allotype. MSB: PARA: 112. Female collected from a tributary of the North Fork Tesuque Creek (35.7699, -105.7954). **Other paratypes.** MSB: PARA 113–120

Etymology. The species epithet is derived from the Navajo word for fingers, 'bila', which describes the shape of spines surrounding the cloaca (Fig. 3C).

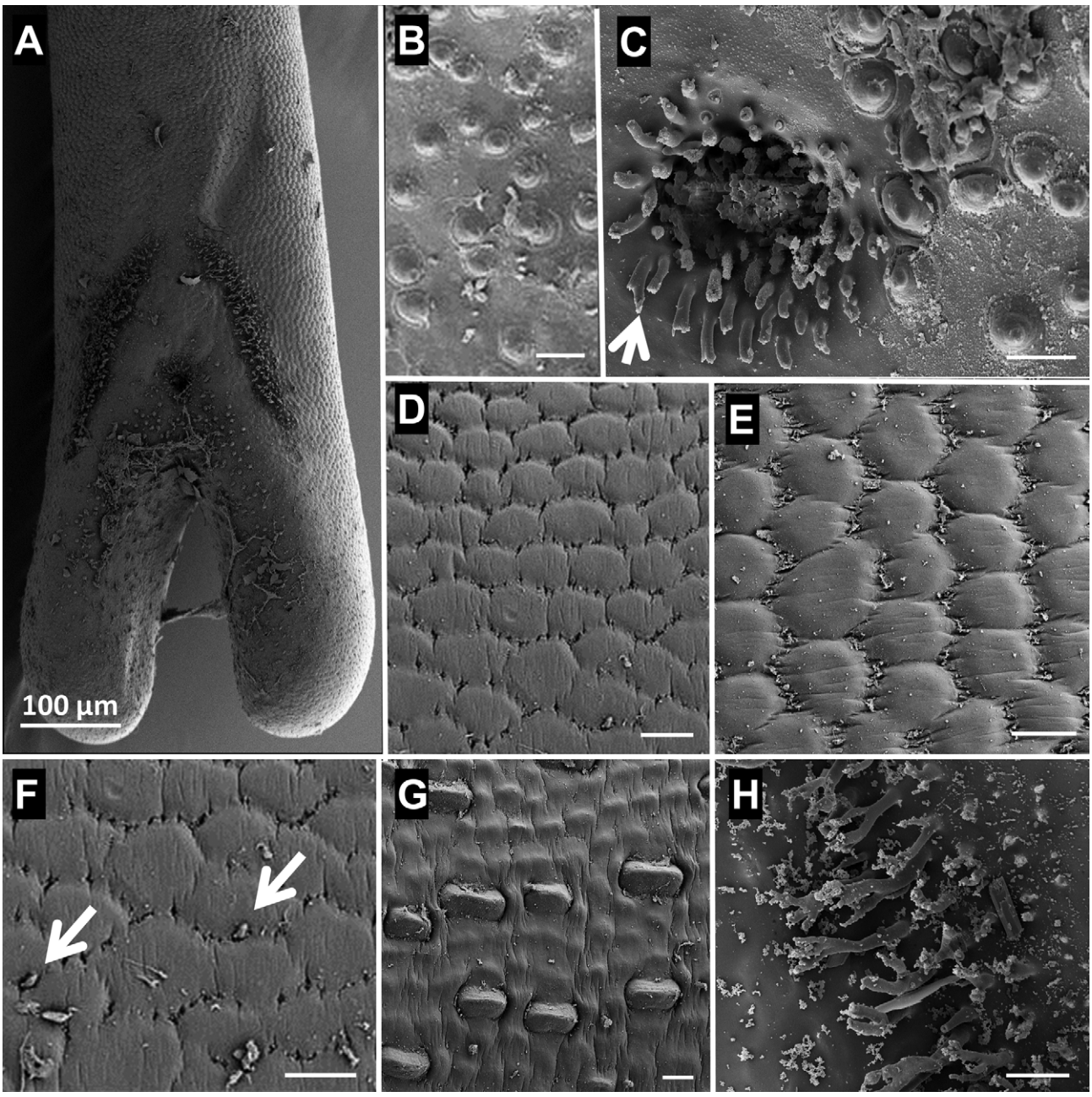

FIGURE 3. *Gordionus bilaus* **n. sp.** (A) Male posterior end showing thin row of precloacal bristles and postcloacal spines. (B) Postcloacal spines. Note mound-like appearance. (C) Rows of broad bristles with stout apexes surrounding the cloaca. Note that some bristles are branched (arrow). Cuticle showing flat (D) polygonal or (E) roundish areoles. Note the indistinct interareolar furrows, making areoles appear fused. (F). Cuticular tubercles in between areoles. (G) Adhesive warts are present anterior to the cloacal opening on the ventral sided. (H) Precloacal bristles are branched apically. Scale bars = 10 µm except where indicated.

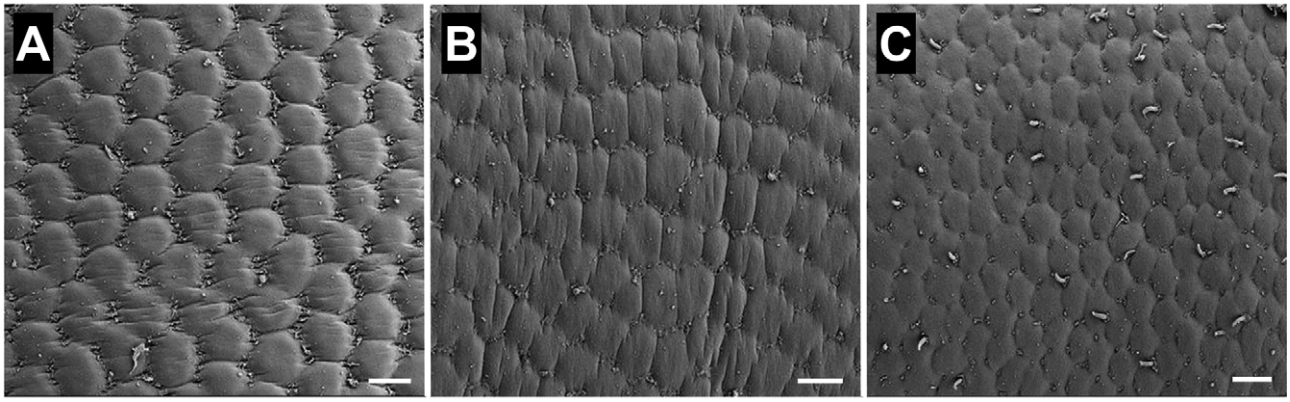

FIGURE 4. *Gordionus bilaus* **n. sp.** cuticle of female. (A and B) Cuticle contains both polygonal and more roundish areoles. Note the indistinct interareolar furrows giving neighboring areoles a fused appearance end. (C) Cuticle near the anterior end showing numerous tubercles. Scale bars = 10 µm.

Distribution. Rocky Mountains, Santa Fe National Forest, New Mexico. Found at two sites. The first site (site 1), is also where *G. lokaaus* **n. sp.** was found, (35.7699, -105.7954), at an elevation between 3,200–3,290m. The second site (site 3) consisted of an unnamed first order stream (35.7970, -105.8028), flowing just to the northwest of the Santa Fe Ski Area. This smaller stream merges with the Rio en Medio and the exact collection site was situated in a large grassy meadow surrounded by aspen/pine woodlands at an elevation of 3,230m.

Type locality. Site 1 (35.7699, -105.7954).

Bionomics. The worms were collected in the free-living, post-parasitic, adult stage, and the paratenic and definitive hosts remain unknown. Adults of this species were collected from late June through early August.

Material examined. Thirty four worms (26 males, 8 females) were extracted, amplified, and sequenced. The anterior, posterior, and midsection of eight individuals were used for SEM.

Description of male. Adult males brown in color, with the exception of one individual which was white, and measured 55–126 ($\bar{x}$ = 87.0) mm long. Areoles of one type, mostly flat; ranging in shape from polygonal (Fig. 3D) to round (Fig. 3E and F). Interareolar furrows are not as distinct as *G. lokaaus* **n. sp.**, and in many areas areoles appear fused with neighboring areoles (Fig. 3D, E, and F). Tubercles between areoles present in moderate quantity (Fig. 3F). Rows of small precloacal bristles present in posterior end, which are branched (Fig. 3H). Cloacal opening surrounded by broad bristles (Fig. 3C) with a stout apex; some bristles appear to be branching. Bristles around cloaca arranged into 2–3 rows (Fig. 3C). Postcloacal spines begin immediately posterior to the cloacal bristles and extend to the inner-side of the tail lobes (Fig. 3A). The shape of the postcloacal spines is mound-like and tall with a diameter of 4–8µm (Fig. 3B). Adhesive warts are present anterior to cloacal opening (Fig. 3G), canoe-shaped, and relatively wide (12–22µm).

Description of female. Adult females white in color, with one exception which was brown, and measured 59–200 ($\bar{x}$ = 73.1) mm long. Cuticle resembles that of the male (Fig. 4A and B). Tubercles are slightly longer and more abundant in the anterior end (Fig. 4C).

Diagnoses and taxonomic comments. Several morphological characters clearly separate these two new species. The spines/bristles surrounding the cloaca are dense and form a tube-like structure in *G. lokaaus* **n. sp.** (Fig. 1C) but are finger-like and much narrower in *G. bilaus* **n. sp.** (Fig. 3C). The areoles are clearly defined by interareolar furrows in *G. lokaaus* **n. sp.** (Fig. 2A–C) but appear almost fused by the absence of interareolar furrows in *G. bilaaus* **n. sp.** (Figs. 4A–C). Adhesive warts are thin, triangular and 2-dimensional in *G. lokaaus* **n. sp.** (Fig. 1B) but tall, stout, mound-like, and 3-dimesional in *G. bilaus* **n. sp.** (Fig. 3B). Finally, the adhesive warts of *G. bilaaus* **n. sp.** appear much broader (Fig. 3G) than those of *G. lokaaus* **n. sp.** (Fig. 1F).

Four *Gordionus* species have been described from the contiguous United States: *G. lineatus* (Leidy, 1851) from the eastern United States, *G. longiareolatus* (Montgomery, 1898) from California, *G. platycephalus* (Montgomery, 1898) from southern Montana (and also from Guatamala), and *G. violaceus* (Baird, 1853) from throughout the United States (and also found in Europe). In addition, *Gordionus longistriatus* Schmidt-Rhaesa, 2004 has been described from Hawaii (Schmidt-Rhaesa 2004) and *Gordionus alascensis* (Montgomery, 1907) has been described from Alaska.

The new forms described here are distinguished from all other *Gordionus* species by their unique combinations of cuticle and circumcloacal spine structures. The cuticle of *G. lokaaus* **n. sp.** resembles that of *G. lineatus*. However, in *G. lineatus* the circumcloacal spines are thin and long (Schmidt-Rhaesa *et al.* 2003; Smith 1991). The broad and tube-like circumcloacal spines of *G. lokaaus* **n. sp.** are unique within this genus and thus, distinguish this new species from *G. lineatus*. The cuticle of *G. bilaus* **n. sp.** resembles most closely that of *G. violaceus*, which has recently been shown to vary considerably throughout its European range (Schmidt-Rhaesa 2001b). However, the circumcloacal spines of *G. violaceus* are thin and long (Schmidt-Rhaesa 2001b) and resemble those of *G. lineatus* from the eastern United States (Schmidt-Rhaesa *et al.* 2003). The broad circumcloacal spines set *G. bilaus* **n. sp.** apart from all other previously described *Gordionus* species.

Laboratory rearing: Of almost 10 worm pairs of both species maintained in the laboratory for breeding purposes, mating was not observed and worm pairs never produced eggs. In addition, exhaustive searches in the field failed to find egg strings. Thus, measurements of eggs, larvae, and cysts could not be included in this manuscript.

Molecular analyses: Of the 88 worms sequenced, 30 unique nucleotide sequences were recovered. The phylogenetic tree based on the *cox*1 barcoding region shows that the 2 new species produce 2 well-supported, monophyletic groups (Fig. 5). Sequences have been deposited in GenBank (JX244228–JX244257).

FIGURE 5. Molecular phylogenetic analysis by maximum likelihood method of *Gordionus bilaus* **n. sp.** and *Gordionus lokaaus* **n. sp.** collected from the Santa Fe National Forest. Two unidentified *Gordionus* species from Washington State (WA) were used as outgroups. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Only bootstrap values with a value of 85% or higher are shown.

Discussion

These two new species double the number of gordiids known from the state of New Mexico. Previously, only *Paragordius varius* from an unknown locality (Montgomery 1907) and *Gordius robustus* from the Sandia (Hanelt & Janovy 1999) and Manzano Mountains (Hanelt & Janovy 2003), located in the northern central part of the state, have been described from New Mexico. Both of these previously-described species are wide-spread through North America and *P. varius* has also been described from South America. The new species included in this description represent reports of species unique to the state of New Mexico, and may represent endemics.

These new species are among only a few gordiids to be recorded from an altitude above 3,000 meters. Additional sampling within the Rocky Mountains will elucidate whether this pattern is due to lack of study, or whether these closely related *Gordionus* species are unique in their adaptation to extreme alpine habitats.

Finally, it is interesting to note that although the new *Gordionus* species are sympatrically distributed, they appear to be mostly temporally isolated. *Gordionus bilaus* **n. sp.** was collected during the early weeks of summer (June), while *G. lokaaus* **n. sp.** was collected during mid and late summer (July through August) with only three exceptions. Although we are uncertain about the mechanism of isolation, it is possible that the time for development of worms within their definitive host or difference in host use by each species could be controlling factors. Future studies focused on the identity of the paratenic and definitive hosts should elucidate the mechanisms used by these two species to temporally isolate themselves in an alpine habitat and could shed light on the evolutionary mechanism which led to sympatric speciation.

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