Discovery of snakeworm gnats in Alaska: a new species of Sciara Meigen (Diptera: Sciaridae) based on morphological, molecular, and citizen science data

Authors: Pereira, Thalles P. Lavinscky, Heller, Kai, Sutou, Mitsuaki, and Sikes, Derek S.

Source: Integrative Systematics: Stuttgart Contributions to Natural History, 6(2) : 91-111

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/2023.673937

Integrative Systematics 6 (2): 91–111; published online 30.XII.2023; DOI: 10.18476/2023.673937

RESEARCH ARTICLE

Discovery of snakeworm gnats in Alaska: a new species of *Sciara* Meigen (Diptera: Sciaridae) based on morphological, molecular, and citizen science data

Thalles P. Lavinscky Pereira[1], Kai Heller[2], Mitsuaki Sutou[3] & Derek S. Sikes[4]

Abstract

A new species of *Sciara* Meigen, 1803, *Sciara serpens* Pereira, Heller & Sutou, **sp. n.**, is described based on morphological, molecular, and citizen science data. The new species forms larval masses moving in columns, referred to as "snakeworms" or "armyworms" in the literature, and is closely related to *Sciara mirabilis* (Bechstein, 1794). *Sciara minor* Strobl, 1898, **restit. et stat. n.** is revalidated based on morphological and molecular data. *Sciara mirabilis* is used for a European species previously referred to under its junior synonym *Sciara militaris* Nowicki, 1868. An estimate of the mitochondrial phylogeny of representative *Sciara* species, a summary of snakeworm sightings in North America, and a brief review of hypotheses for why such larval mass-movement behavior occurs are provided.

Keywords: armyworms, black fungus gnats, *COI* sequence, DNA Barcoding, iNaturalist, taxonomy.

Zusammenfassung

Sciara serpens Pereira, Heller & Sutou, **sp. n.**, eine neue Art der Gattung *Sciara* Meigen, 1803, wird anhand morphologischer und molekularer Merkmalen sowie anhand von „Citizen Science"-Daten beschrieben. Die neue Art formiert sich in larvalen Massenansammlungen zu Kolonnen, in der Literatur als „Schlangenwürmer" oder „Heerwürmer" bekannt, und ist nahe verwandt zu *S. mirabilis* (Bechstein, 1794). *Sciara minor* Strobl, 1898, **restit. et stat. n.** wird auf Basis morphologischer und molekularer Daten erneut als Art eingestuft. *Sciara mirabilis* (Bechstein, 1794) wird für eine europäische Art verwendet, die zuvor unter dem synonymen Namen *Sciara militaris* Nowicki, 1868 geführt wurde. Des Weiteren wird ein molekularer Stammbaum ausgewählter Sciara-Arten aufgrund mitochondrialer Merkmale präsentiert. Ebenso wird eine Übersicht der Heerwurm-Sichtungen in Nordamerika sowie ein kurzer Überblick über die Hypothesen gegeben, die zur Bildung solcher Larvenzüge führen könnten.

Introduction

Members of the family Sciaridae are commonly known as dark-winged, dusty-winged, or black fungus gnats. In North America there are 27 genera (Mohrig et al. 2013; Vilkamaa & Menzel 2019; Vilkamaa et al. 2023) and around 250 species (Mohrig et al. 2013, 2019; Heller et al. 2015; Mohrig & Kauschke 2016a, 2016b, 2017, 2019; Eiseman et al. 2018; Vilkamaa & Menzel 2019; Menzel & Vilkamaa 2021; Vilkamaa et al. 2023).

Sciara Meigen, 1803 is a large genus of the family Sciaridae with hundreds of species described. Most of these are in need of revision, because in the 18th and 19th centuries nearly all Sciaridae were described in the genus *Sciara* (Vilkamaa & Menzel 2019). *Sciara* in its current sense (see extensive list of characters in Menzel & Mohrig 2000) has 17 species in the Palaearctic (Menzel & Mohrig 2000) and six in the Nearctic regions (+ seven *nomina dubia* and + eight *incertae sedis*) (Mohrig et al. 2013). The monophyly of the genus was strongly supported in a multigene phylogenetic analysis by Shin et al. (2013).

Most sciarid larvae are terrestrial decomposers (Shin et al. 2013). There are reports of sciarid larvae moving in masses while keeping body contact with each other, thus forming conspicuous long columns–over one meter in length (Becker 1914; Craik et al. 2005). This behavior is relatively rare in Diptera. In the literature, several larval mass movements have been recorded worldwide for nine species of black fungus gnats. In Europe, commonly known as armyworms, the species: *Cratyna perplexa* (Winnertz, 1867), *Ctenosciara hyalipennis* (Meigen, 1804), *Bradysia bicolor* (Meigen, 1818), *Sciara analis* Schiner, 1864, *Sciara hemerobioides* (Scopoli, 1763) [= *Sciara thomae* (Linnaeus, 1767)], and *Sciara mirabilis* (Bechstein, 1794) [= *Sciara militaris* Nowicki, 1868] (Nowicki 1868; Menzel & Mohrig 2000; Craik et al. 2005; Menzel et al. 2020); Indonesia, the species *Chaetosciara lygropis* (Edwards, 1928) (de Meijere 1935); Philippines, *Sciara* sp. (Brues

1951); in Japan, *Sciara kitakamiensis* Sutou, 2004 (Sutou et al. 2011); and Venezuela, *Odontosciara beebei* (Shaw & Shaw, 1950) (Shaw & Shaw 1950; Amorim 1992).

The first report in a scientific journal in the Nearctic described these larval masses as looking like a "thin grey snake", based on sightings made between 1864 and 1867 in Pennsylvania, USA (Cope 1867). Although such larvae have also been called "armyworms", this term is commonly used in North America and elsewhere for various species of noctuid moth larvae that are economically damaging to crop plants (Sparks 1979; Richards & Davies 2013). For this reason, we prefer the use of the common name "snakeworm gnats" for North American species of Sciaridae that engage in such larval mass movements and "snakeworms" for the larval mass movement. Richards & Davies (2013: 994) stated that "The migratory columns are elongate in form, and have been termed "snake worms" in the United States, on account of their snake-like movements and appearance, which are said to resemble a thin grey reptile."

In North America there were two previously-known snakeworm gnat species, *Sciara fraterna* Say, 1824 (*nomen dubium*), as reported from Poolesville, Maryland by Pratt (1899), and *Sciara congregata* Johannsen, 1914 (species *incertae sedis*), as reported from Arkansas by Becker (1914). Unfortunately, the taxonomic validity of *S. fraterna* is uncertain (Steffan 1966; Mohrig et al. 2013). *Sciara congregata* was redescribed and figured by Pettey (1918) and later listed as a species *incertae sedis* by Mohrig et al. (2013). The type specimens of these species are damaged or lost (Mohrig et al. 2013).

In July 2007, Margaret Billington, a citizen of Ester, Alaska and a docent at the University of Alaska Museum, presented to one of us (DS) specimens of fly larvae and accompanying photos showing their mass movement behavior, which she had documented near her home in Ester. Later that month, a similar report was made via the University of Alaska Cooperative Extension. Due to the short-lived and unpredictable nature of this phenomenon, DS visited the site (Pika Road, Fairbanks) immediately and was able to photograph and collect larvae which he reared to adulthood in captivity. Given the conspicuous nature of these larval mass movements, it was unusual that no Alaska residents had reported sightings before 2007. In subsequent years, more reports came in from distant locations in Alaska (e.g., Dillingham, Katmai National Park, Kenai Fjords National Park, Denali National Park), including a report from Wasilla, Alaska that had been made in the year 2000 but was not reported until a newspaper article was published on the phenomenon in 2022. A preliminary morphological study by MS and KH of the reared adult males, the only life stage that can be morphologically identified to species in *Sciara*, concluded they were likely *Sciara mirabilis* [= *S. militaris*]. However, preliminary genetic results obtained by Sikes et al. (2017) and MS suggested they were likely distinct.

In this paper, we describe a new species of snakeworm gnat from Alaska in the genus *Sciara* Meigen based on morphological, molecular, and citizen science data, revalidate a species, summarize taxonomic information about snakeworm gnats in North America, redefine the European "armyworm" species and provide a brief review of hypotheses attempting to explain such larval mass movements.

Material and methods

Specimens and data

Specimen occurrence data were compiled from the literature, University of Alaska Museum (UAM) records, and citizen science data. UAM specimen and observation data are publicly available via the Arctos database (https://arctos.database.museum/search.cfm?guid_prefix=UAM%3AEnto%2CUAMObs%3AEnto&scientific_name=Sciara%20serpens&scientific_name_match_type=match&family=Sciaridae), which shares data with aggregators like GBIF.org. Records were georeferenced following the MaNIS georeferencing guidelines (Chapman & Wieczorek 2006). Specimens were photographed using a Leica DFC425 camera mounted on a Leica MZ16 stereomicroscope in combination with the Leica Application Suite software v.3.8.0. Editing of drawings and final plates was done in Inkscape 0.91. The map (Fig. 6) was made with SimpleMappr (Shorthouse 2010). The terminology used follows Hippa et al. (2010). For the genus *Sciara*, we do not use the term "megasetae" for the apical spines on the gonostylus as they are usually not constant in number and are more likely homologous with the awl-like setae in the genera *Trichosiopsis*, *Leptospina*, and *Hirtipennia*. Campbell (1991) was used to key the beetles collected in 2007, by DS, in association with the snakeworms.

iNaturalist data. We analyzed 6,192 observations, filtered as: made between Jun 13, 2012 and July 12, 2022, from North America, with photos, attribute life stage = larva, identified as Sciaridae. Because this filtered set included non- snakeworm observations, we flagged snakeworm observations manually with an Observation Field named "larval mass movement [yes]". Using the same filters, an iNaturalist Collection Project was created, named "Snakeworm gnats of North America", to gather these observations (n = 85). Currently, projects cannot be filtered on custom-made Observation Fields. For this reason, we created a URL to add this custom filter (https://www.inaturalist.org/observations?place_id=any&project_id=snakeworm-gnats-of-north-america&subview=table&verifiable=any&field:larval%20mass%20movement=yes), which selected only the "larval mass movement [yes]" observations of the project to create a map of just the snakeworm observations (n = 58).

Abbreviations

The sciarid material discussed is deposited in the following collections:

NMBA	Naturhistorisches Museum der Benediktiner-Abtei, Admont, Austria;
NSMT	National Museum of Nature and Science, Tsukuba, Japan;
PKHH	Private Collection of Kai Heller, Heikendorf, Germany;

SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany;
SNSB	Bavarian Natural History Collections, Munich, Germany;
UAM	University of Alaska Museum, Fairbanks, Alaska, USA.

The following abbreviations and indices/ratios are used in the text: **bM** = basal part of media; **C** = costal vein; **c** = distance between apex of R_5 and end of C veins; **CuA_1** = first (anterior) branch of cubital vein; **CuA_2** = second (posterior) branch of cubital vein; **c/w** = length ratio between c and w; **LW-index** = length/width index; **M_1** = first branch of media; **M_2** = second branch of media; **R** = radius, or radial vein; **R_1** = anterior branch of radius; **R_5** = third branch of radius; **r-m** = radius/media sector as basal part of R_5; **stCuA** = stem of cubital veins CuA_1 and CuA_2; **stM** = stem of medial veins M_1 and M_2; **w** = distance between apex of R_5 and apex of M_1.

DNA sequencing

Tissue from four specimens (UAM:Ento:26033, UAM:Ento:457585, UAM:Ento:457586, UAM:Ento:457589) was sent to the Canadian Centre for DNA Barcoding (CCDB), University of Guelph, Canada. The CCDB followed standardized high-throughput protocols for DNA extraction, amplification, and bidirectional sequencing (Ivanova et al. 2006; deWaard et al. 2008). DNA barcode [cytochrome oxidase subunit I (*COI*) gene] data were archived in the Barcode of Life Data System (BOLD) (Ratnasingham & Hebert 2007). Four specimens (UAM:Ento:26793, UAM:Ento:26784, UAM:Ento:27668a, UAM:Ento:27668b) had their DNA extracted and sequenced by MS using the same methodology as Sutou et al. (2011) and later archived in BOLD (DNA barcode process IDs UAMIC4422-21, UAMIC4421-21, UAMIC4420-21, and UAMIC4419-21).

Taxon sampling

DNA sequences for target and representative *Sciara* and two outgroup species within the subfamily Sciarinae [*Leptosciarella rejecta* (Winnertz, 1867) and *Leptosciarella trochanterata* (Zetterstedt, 1851)] were downloaded from BOLD (Appendix 1). Outgroup choice was based on the analysis of Shin et al. (2013), which found that these species were in a sister clade to *Sciara*. BOLD has over 2,000 sequences of *Sciara* so we assembled a dataset of representatives using one pair per species when possible, or a single sequence per species when multiple sequences were not available, with the goal of including all species of *Sciara* identified to the species level in BOLD at the time. Representative *Sciara* sequences were chosen that had 658 base pairs and no missing data, stop codons, or contamination issues. Target sequences included all *Sciara mirabilis* [= *S. militaris*] (n = 5), *Sciara hemerobioides* (n = 4), *Sciara analis* (n = 3), and *Sciara minor* (n = 5) sequences, and all Alaskan sequences of our presumed new species (n = 8), regardless of sequence length (two sequences were 180 bp and six ranged from 603 to 657 bp). Voucher specimens for these sequences are in the BioFokus collection, Oslo, Norway; the Centre for Biodiversity Genomics, University of Guelph, Canada; the National Museum of Nature and Science, Tsukuba, Japan; the Research Collection of Jukka Salmela, University of Turku, Finland; the Zoologische Staatssammlung München, Munich, Germany; the Tromsø University Museum, Norway; the University of Alaska Museum, Fairbanks, USA; and the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Data analyses

Sequences were aligned using EMBL-EBI's implementation (Madeira et al. 2019) of MUSCLE (Edgar 2004). The alignment is archived as Supplementary File 1. A best fitting model was estimated using the ModelFinder tool (Kalyaanamoorthy et al. 2017) within IQ-TREE, which chose the 56th most-complex model of 88 evaluated (TIM+F+I+G4) based on the BIC. Maximum Likelihood analysis using the best fitting model was conducted with W-IQ-TREE (Trifinopoulos et al. 2016) using default options which completed model testing, tree inference, and clade support in under one minute. Clade support was assessed via 1,000 replicates for the SH-aLRT test of Guindon et al. (2010) and 1000 replicates of the ultrafast bootstrap (UFB) of Hoang et al. (2017). We consider nodes with support values of both SH-aLRT ≥ 80 and UFB ≥ 95 well supported (Nguyen et al. 2015), nodes with either SH-aLRT < 80 or UFB < 95 were considered weakly supported, and nodes with both SH-aLRT < 80 and UFB < 95 were considered unsupported.

Phylogenetic results

Our goal with this analysis was to estimate the relationship between our new species and other *Sciara*, and also estimate the relationships of *S. analis* and *S. minor* to each other and to other *Sciara*. The IQ-TREE estimate of the mtDNA gene tree (Fig. 1) using DNA barcode sequences indicates that the new species from Alaska likely shares a more recent mitochondrial ancestor with the European *S. mirabilis* [= *S. militaris*] than any other *Sciara* species in our analysis, although this branch was not supported (SH-aLRT = 76.3, UFB = 87.0). The support for reciprocal species monophyly of our new species and *S. mirabilis* was strong (SH-aLRT > 94.8, UFB > 97.0). There was also strong support for *S. analis* and *S. minor* sharing a unique recent common mitochondrial ancestor (SH-aLRT = 99.4, UFB = 100), with strong support for reciprocal species monophyly of each (SH-aLRT > 92.0, UFB > 95.0).

In BOLD, the sequences of *S. mirabilis* are in BIN BOLD:AAH3977, which has five members all identified as the same species, an average genetic distance of 0.04% (p-distance), a maximum distance of 0.16%, and a distance to its nearest neighbor (BIN BOLD:AEM0716) of 7.88%. Five sequences of our new species are the only members of its BIN (BOLD:ACG1481), which has an average and maximum genetic distance of 0.0% (p-distance) and a distance to its nearest neighbor (BIN BOLD:AEM0716) of 5.42%. Thus, BIN BOLD:AEM0716 is closer to *S. mirabilis* and our new species than these species are to each other. This BIN has a single non-public sequence from China identified only to the family Sciaridae, which did not meet the criteria to be included in our analysis. We predict it will prove to be another undescribed species of snakeworm gnat.

Taxonomy

Family Sciaridae Billberg, 1820
Genus *Sciara* Meigen, 1803

Sciara mirabilis Bechstein, 1794
(Fig. 1)

Tipula mirabilis J. M. Bechstein, 1794: 1095. References: J. M. Bechstein (1794: 1095); Lumnitzer (1826: 78); L. Bechstein (1850: 318); L. Bechstein (1851: 2, 26); Berthold (1856: 48); Nowicki (1868: 9); Beling (1883: 255); Menzel & Mohrig (2000: 17, 745); Schedl (2002: 295); Krivosheina et al. (2019: 737).

Sciara militaris Nowicki, 1868. References: Nowicki (1868: 4, 25, 46, plate 1, figs. 1–8); Beling (1883: 255); Menzel & Mohrig (2000: 17, 524; in part); Craik et al. (2005: 22, figs. 1–8); Krivosheina et al. (2019: 737); not sensu Menzel (1992: 234, figs. 1, 2; misidentification and incorrect synonymy, = *Sciara frauenfeldi* var. *minor* Strobl, 1898).

Semisciara agminis Kjellander, 1943. References: Kjellander (1943a: 56, figs. 1–17, 1943b: 105, figs. 1–15).

Sciara mirabilis: Reissenberger in Fuss (1851: 174); Dahl (1906: 575); Knauer (1909: 217); Ramann (1911: 485).

Lycoria (*Lycoria*) *militaris*: Lengersdorf (1928–1930: 27, pl. 1, fig. 27).

Lycoria (*Sciara*) *militaris*: Schedl (2002: 295).

Lycoria militaris: Schedl (2002: 291).

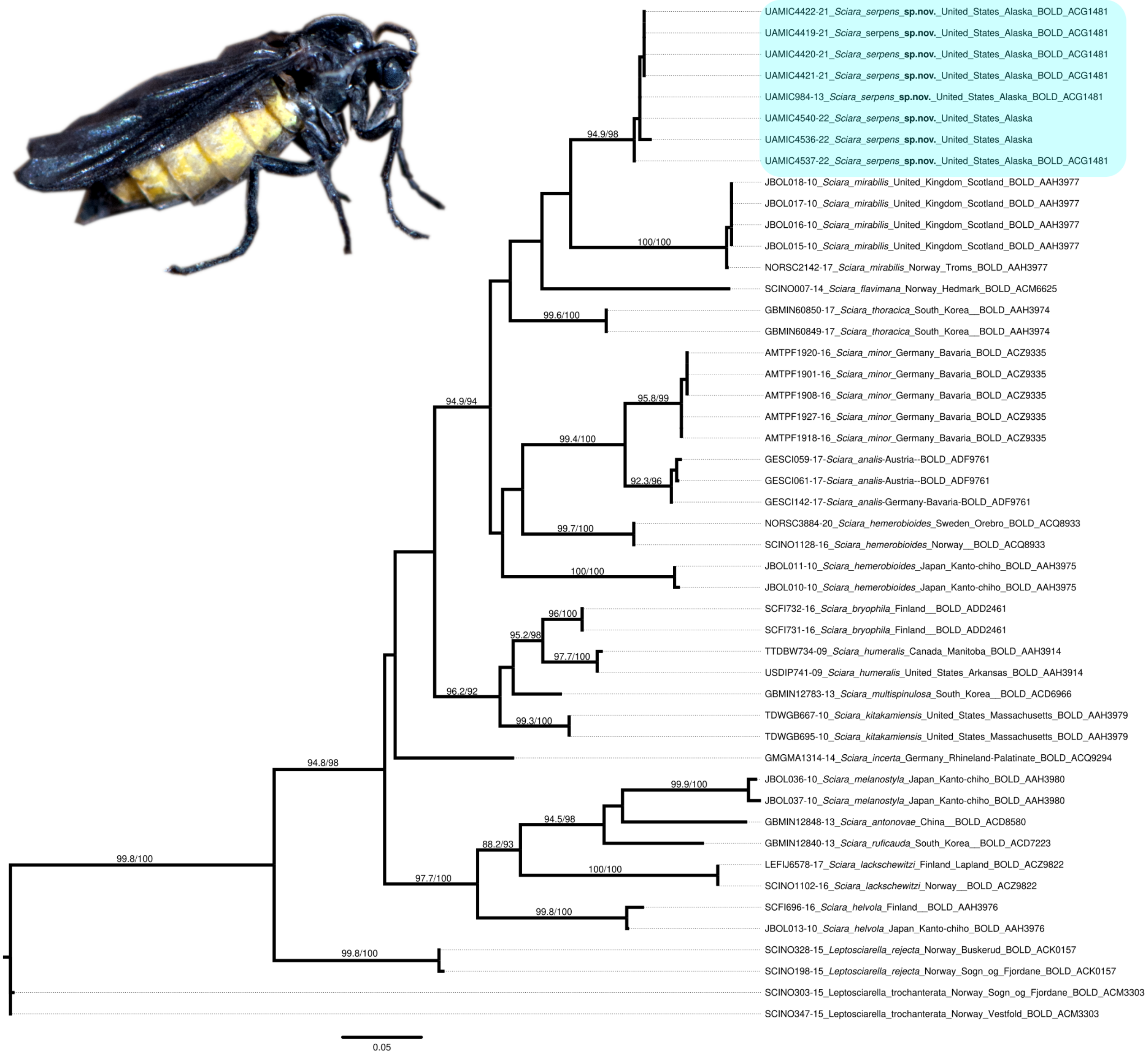

Fig. 1. IQ-TREE estimate of the mtDNA gene tree. Tip labels include the BOLD process ID, taxon, country, province or state, and the BOLD BIN, if known. Alaskan *Sciara serpens* Pereira, Heller & Sutou, **sp. n.** sequences highlighted in blue.

Type locality

"auf dem Thüringerwalde" [= Germany, state of Thuringia, Thuringian Forest].

Type material

Syntypes, larvae, "im Julius, ... in den Waldungen" [= in July, in forests], depository unknown (syntypes probably lost).

Taxonomic remarks

The name *Tipula mirabilis* was published for the armyworm of central Europe by J. M. Bechstein (1794). However, none of the tipulids known to science exhibit larval mass-movement behavior, and none are as small as the "size of a flea", as reported by Bechstein (1794). The naturalist Johann M. Bechstein appears to have copied much of his description from Kühn (1782), who had named the armyworm as "Wunderthier" (animal of miracle), which is not a Latin binomen. Therefore, J. M. Bechstein (1794) chose the name "*Tipula mirabilis*" for this species and gave the first valid description of it by indicating its size and mentioning the larval mass movement behavior in July in the Thuringian Forest of Germany. All further citations mainly just copied the same content (Lumnitzer 1826; L. Bechstein 1850, 1851; Berthold 1856; Beling 1883).

J. M. Bechstein possibly did not see any specimens himself. The type material, studied by Kühn (1782) (undesignated), probably does not exist anymore, but based on the description and locality it matches the European species *Sciara militaris* Nowicki, 1868. Dahl (1906: 575–576) used the name and the combination *Sciara mirabilis* (Bechstein) and established *S. militaris* as its junior synonym (Knauer 1909; Ramann 1911). However, Menzel & Mohrig (2000) questionably placed J. M. Bechstein's *T. mirabilis* in the family Tipulidae, without further analysis. In light of this, we are using the older name, *Sciara mirabilis* Bechstein, 1794, to follow article 23.1. "Statement of the Principle of Priority" of the International Code of Zoological Nomenclature.

***Sciara minor* Strobl, 1898, restit. et stat. n.**

(Figs. 1, 2)

Type locality

Austria, Styria, Scheiblstein.

Type material

Lectotype ♂, leg. Strobl, 06.ix.1897 (NMBA); designated by Menzel (1992: 235).

Paralectotype ♂, same collection data as for lectotype (NMBA). The lectotype was studied and well illustrated by Menzel (1992) and we examined both the lectotype and the paralectotype.

Other material

5 ♂♂, GERMANY: Bavaria: Allgäu, Oberstdorf, Koblat, 47.4215, 10.3546, elev. 2033 m, 05.ix.2014, snow valley, Malaise trap, Doczkal, D., Schmidt, S. & Voith, J. col., [SNSB - BC-ZSM-DIP-27706-A01; BC-ZSM-DIP-27706-A08; BC-ZSM-DIP-27706-B06; BC-ZSM-DIP-27706-B08; BC-ZSM-DIP-27706-C03].

Literature

Strobl (1898: 278, as *Sciara frauenfeldi* var. *minor*); Lengersdorf (1928–1930: 37, as *Lycoria* (*Neosciara*) *frauenfeldi* var. *minor*); Menzel (1992: 234, figs. 1–2, as synonym of *Sciara militaris*; misidentification and incorrect synonymy; redescription based on type material of *S. frauenfeldi* var. *minor*).

Diagnosis

Sciara minor is characterized by the posterior pronotum bearing numerous fine setae, a character state which is currently unique in Sciaridae. Otherwise, the species is similar to other members of the *hemerobioides* group like *Sciara hemerobioides*, *S. analis*, and *S. mirabilis*, the former two having a larger body size (more than 4 mm), and the latter a smaller body size (less than 3 mm). The gonostylus resembles mostly that of *Sciara mirabilis* in having a narrow apical lobe (Fig. 2b). This lobe has a few scattered awl-like setae dorsally and ventrally, which are lacking in *S. mirabilis*. The tegmen is also much longer and of a different shape in *S. minor.*

Description (♂)

Head. Eye bridge with 4–5 rows of facets. Antenna unicolored. LW-index of 4th flagellomere 1.7–2.0 (Fig. 2c); neck 0.25–0.37 × segment width; transition of basal part to neck bottle-neck like. Neck unicolor. Antennal setae shorter than segment width; fine; sparse; salient. Palpus darkened; 3 palpomeres. First palpomere elongate; with 5–7 setae; with only sparse sensilla. Second palpomere elongate. Third palpomere as long as first. Thorax. Color brown. Notum unicolor. Thoracic setae weak; brown. Posterior pronotum setose. Postpronotal setae 10–20; fine. Mesothoracic sclerites bare. Legs. Yellow-brown. Hind coxa of same color as femora. Setae on front coxa darkened. Front tibial organ as patch of setae; pale; front tibial organ not bordered. Tibial setae on hind legs weak and inconspicuous. Tibial spurs of equal length. Claws untoothed. Wing. Posterior veins with macrotrichia; haltere darkened. Abdomen. Abdominal setae weak; dense and brown. Hypopygium concolorous with abdomen; LW-index 0.55–0.70. Base of gonocoxites with weak setae; gonocoxites fused; inner membrane of hypopygium bare (Fig. 2a); ventral margin of gonocoxite with short setae. Gonostylus elongate; LW-index 1.5–1.9; inner margin convex; apex bulbous. Apical tooth absent. Awl-like setae long. Tegmen 1.3–1.5 × longer than broad; trapezoid, or laterally emarginate; central process absent. Length of ejaculatory apodeme 5–10% of hypopygium length; base of ejaculatory apodeme present. Field with inconspicuous aedeagal teeth. Measurements. Wing length 3 mm. Body size 3–4 mm. Hind tibia 1.2–1.3 mm.

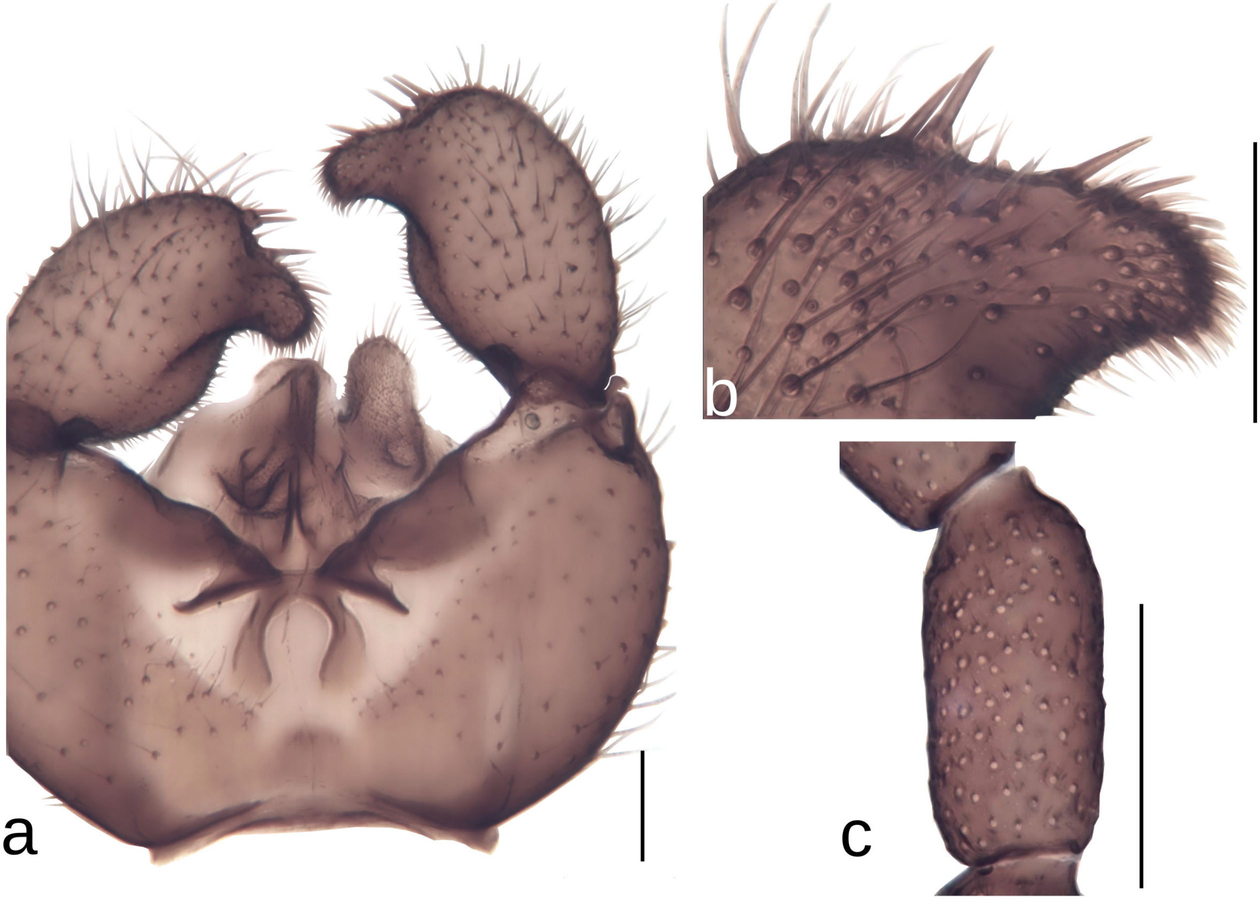

Fig. 2. *Sciara minor* Strobl, 1898, male. **a**. Hypopygium, ventral view. **b**. Apex of gonostylus, ventral view. **c**. 4th flagellomere, lateral view. Scale bars: 0.1 mm.

Ecology

At present, *Sciara minor* is not known to produce larval mass movements and seems to be an active flier in contrast to *Sciara mirabilis*. Both currently known collecting events took place in the Alps, so it appears to be a strictly Alpine species.

Distribution

Austria, Germany.

DNA barcoding

The *COI* sequence is assigned to BIN BOLD:ACZ9335. Average distance 0.3%, maximum distance 0.72%, n = 5, distance to nearest neighbor 4.85% (p-dist).

Taxonomic remarks

Sciara minor was originally treated as a variety of *Sciara frauenfeldi* Winnertz. *Sciara frauenfeldi* is in fact a synonym of *Schwenckfeldina carbonaria* (Meigen, 1830), as stated by Menzel & Mohrig (2000). Later, Menzel (1992: 234) synonymized *Sciara minor* with *Sciara militaris* (herein, *S. mirabilis*) based on the similarly-shaped gonostylus and short antennae. However, the first illustration of the male genitalia of the "armyworm" species *Sciara militaris* by Craik et al. (2005) revealed some notable differences, and also the DNA barcode differs to a degree indicative of a separate species, as seen also in our phylogenetic analysis (Fig. 1). The DNA barcode of *S. minor* is most similar to that of *Sciara analis* (Fig. 1). The gonostylus of the barcoded material matches and completely agrees with that of the lectotype and the paralectotype.

***Sciara serpens* Pereira, Heller & Sutou, sp. n.**

(Figs. 1, 3–6)

Diagnosis (♂)

Gonostylus (Fig. 3a) oval-shaped with weakly developed apical spines, with densely setose apical lobe, and small, densely setose medial lobe with 6–7 strong awl-like setae on the base of the underside of the bristled lobe. Tegmen with a dorsal finger-like process. Aedeagal teeth numerous and short.

Etymology

The epithet is the Latin name for snake, in reference to the snake-like appearance (Fig. 4a) of the larval mass movements. It is a noun in apposition. Aiming to engage citizens and educate them on the continuing importance of taxonomy, we offered a choice of three species' names to students in the University of Alaska Fairbanks Summer Sessions' "Adult Bug Camp" and "Kids Bug Camp" courses, that DS runs annually. The name that received the most votes was *Sciara serpens*.

Type material

Holotype, ♂. UNITED STATES OF AMERICA: Alaska: Pika Road, 64.90833, -147.80061, 288–308 m, 13–21.vii.2007, Derek S. Sikes col., reared from larvae collected 13.vii.2007, pupation 17–19.vii.2007, emerged 20–21.vii.2007, slide, [UAM:Ento:26024/UAM100009137].

Paratypes, 35 adults (2 ♂♂, 33 ♀♀). 1 ♀, UNITED STATES OF AMERICA: Alaska: Pika Road, 64.90833, -147.80061, 288–308 m, 13–21.vii.2007, Derek S. Sikes col., reared from larvae, slide [UAM:Ento:26041/UAM100009175]; 1 ♂, same collection data as for holotype, slide (PKHH) [UAMObs:Ento:26027/UAM100009120]; 1 ♀, same collection data as for holotype, slide (PKHH) [UAMObs:Ento:26042/UAM100009174]; 1 ♂, same collection data as for holotype, slide NSMT [UAM:Ento:26040/UAM100009204]; 4♀♀, same collection data as for holotype, slide NSMT [UAM:Ento:26031/UAM100009115; UAM:Ento:26032/UAM100009139; UAM:Ento:26034/UAM100009173; UAM:Ento:26035/UAM100009132]; 9 ♀♀, same collection data as for holotype, pinned [UAM:Ento:26026/UAM100009123 (SDEI); UAM:Ento:26030/UAM100009125 (SDEI); UAM:Ento:26028/UAM100009138 [damaged specimen]; UAM:Ento:26025/UAM100009140 [damaged specimen]; UAM:Ento:26029/UAM100009180 [damaged specimen]; UAM:Ento:26036/UAM100009199 (NSMT); UAM:Ento:26037/UAM100009186 (NSMT); UAM:Ento:26038/UAM100009178 (NSMT); UAM:Ento:26039/UAM100009176 (NSMT)]; 1 ♀, same collection data as for holotype, pinned [UAM:Ento:26033/UAM100009172, GenBank: KU876147, BOLD Process ID: UAMIC984-13]; 6 ♀♀, UNITED STATES OF AMERICA: Alaska: Pika Road, 64.90833, -147.80061, 288–308m, 23.vii.2007, Derek S. Sikes col., reared from larvae collected 13.vii.2007, in ethanol [UAM:Ento:26781 / barcode:106844 (NSMT); UAM:Ento:26783 / barcode:106833 (NSMT); UAM:Ento:26784 / barcode:106838 / BOLD Process ID: UAMIC4420-21; UAM:Ento:26788 / barcode: 106847; UAM:Ento:26790 (NSMT) / barcode: 106835; UAM:Ento:26793 (NSMT) / barcode: 106826 / BOLD Process ID: UAMIC4419-21]; 11 ♀♀, UNITED STATES OF AMERICA: Alaska: Pika Road, 64.90833, -147.80061, 288–308 m, 23.vii.2007, Derek S. Sikes col., reared from larvae collected 13.vii.2007, in ethanol - liquid nitrogen-cooled cryovats [UAM:Ento:26789 / barcode:106827; UAM:Ento:26782 / barcode:106848; UAM:Ento:26791 / barcode:106837; UAM:Ento:26792 / barcode:106845; UAM:Ento:26794 / barcode:106842; UAM:Ento:26785 / barcode:106843; UAM:Ento:26786 / barcode:106832; UAM:Ento:26787 / barcode:106830; UAM:Ento:26779 / barcode:106846; UAM:Ento:26780 / barcode:106841; UAM:Ento:26778 / barcode:106817].

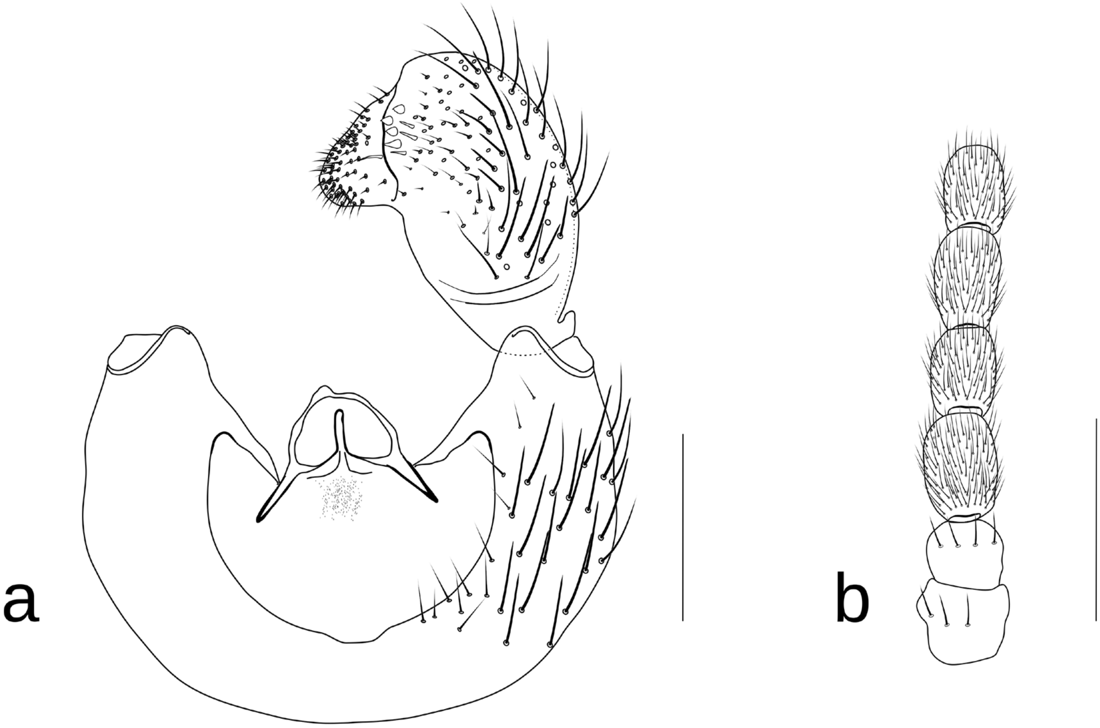

Fig. 3. *Sciara serpens* Pereira, Heller & Sutou, **sp. n.**, male. **a**. Hypopygium, ventral view. **b**. Scape, pedicel, and flagellomeres 1–4, lateral views. Scale bars: 0.2 mm.

Other material (pupae and larvae)

12 pupae, same collection data as for holotype, in ethanol, [UAM:Ento:27666/UAM100034127]; 6 pupae, same collection data as for holotype, in ethanol [UAM:Ento:27669/UAM100008073] (NSMT); 147 larvae, UNITED STATES OF AMERICA: Alaska: Fairbanks: Ester, 64.85983, -148.03184, 380–410 m, 09.vii.2007, Margaret Billington col., in ethanol, [UAM:Ento:24913/UAM100034126]. 19 larvae, UNITED STATES OF AMERICA: Alaska: Fairbanks: Ester, 64.85983, -148.03184, 380–410 m, 09.vii.2007, Margaret Billington col., in ethanol, [UAM:Ento:27668/UAM100008000 / BOLD Process ID: UAMIC4422-21, UAMIC4421-21 (NSMT)]; 48 larvae, UNITED STATES OF AMERICA: Alaska: Nikiski, Bishop Drive, ridge between lakes, 60.686, -151.222, 30–34 m, 05.viii.2021, Rosy Thompson col., in ethanol, [UAM:Ento:450160/UAM100097150]; 102 larvae, UNITED STATES OF AMERICA: Alaska: Nikiski, Bishop Drive, ridge between lakes, 60.686, -151.222, 30–34 m, 05.viii.2021, Rosy Thompson col., in ethanol, [UAM:Ento:450154/UAM100097149]; 1 larva, UNITED STATES OF AMERICA: Alaska: Nikiski, Bishop Drive, ridge between lakes, 60.686, -151.222, 30–34 m, 05.viii.2021, Rosy Thompson col., [UAM:Ento:457589/UAM100102567/ BOLD Process ID: UAMIC4540-22][destroyed during the process of DNA extraction]; 1 larva, UNITED STATES OF AMERICA: Alaska: Fairbanks: 1195 Powellite Dr, 64.914, -147.513, 27.vi.2021, Ted Johnson col. [UAM:Ento:457586/UAM100102570 / BOLD Process ID: UAMIC4537-22] [destroyed during the process of DNA extraction]; 1 larva, UNITED STATES OF AMERICA: Alaska: Fairbanks: 1195 Powellite Dr, 64.914, -147.513, 27.vi.2021, Ted Johnson col. [UAM:Ento:457585/UAM100102571 / BOLD Process ID: UAMIC4536-22] [destroyed during the process of DNA extraction]; 1 larva, UNITED STATES OF AMERICA: Alaska: Fairbanks: 1195 Powellite Dr, 64.914, -147.513, 27.vi.2021, Ted Johnson col., in ethanol [UAM:Ento:447339/UAM100095525].

Snakeworm observations (larvae)

UNITED STATES OF AMERICA: Alaska: North Pole, 64.75111, -147.34944, 12.vii.2007, Jan Thacker obs., [UAMObs:Ento:245725]; Fairbanks, 1263 Upland Dr, 64.90241, -147.7680, 20.vi–22.ix.2009, Joseph Rueter obs., [UAMObs:Ento:232721]; Dillingham, 59d 3min N/158d 30 min W, 16.vii.2010 [UAMObs:Ento:245722]; Kenai Fjords National Park, Exit Glacier, 60.18790, -149.63122, 30.vii.2011, Deborah Kurtz obs. [UAMObs:Ento:244488]; Katmai National Park, Brooks Camp, 58.55648, -155.7782, 18.vii.2014, Michael Fitz (National Park Service) obs., [UAMObs:Ento:232720]; Fairbanks, Eagle Ridge and Gull Roads, 64.911373, -147.667603, 17.vii.2017, Sarah Keller obs., [UAM:Ento:360119]; Fairbanks, 17.5 Miles Chena Hot Springs Road, 64.87112, -147.06269, 5.vi.2020, Julie Stricker obs., [UAMObs:Ento:244491]; Fairbanks, Driveway on Shadow Lane, 64.89229, -147.84889, 8.vii.2020, Loretta Winton obs., [UAMObs:Ento:244483]; Fairbanks, 3.9 mile Gilmore Trail, 64.947312, -147.530107, 23–25.vii.2020, Lynn Cornberg obs., [UAMObs:Ento:244487]; Camp Denali, near staff cabins 63.51921, -150.89793, 8.vii.2022, Jenn Hamm [UAMObs:Ento:245723].

Description

Male. Head: dark brown, antenna brown and unicolor, maxillary palpus dark brown. Eye bridge 2–4 facets wide. Face with 8–10 setae, clypeus with 3 setae. Maxillary palpus with 3 segments, segment 3 longest; palpomere segment 1 with 8 setae. Antenna (Fig. 3b) with body of 4th flagellomere 1.3 times as long as wide, without distinct apical margin, neck much shorter than broad, sensilla pale and fine, longest sensilla shorter than width of flagellomere. Thorax: dark brown to black, pleura of same color. Setae dark. Anterior pronotum with 3 setae. Posterior pronotum with 8 setae. Prothoracic episternum with 4–6 setae. Scutum with short and long dorsocentrals and long laterals with some shorter ones. Scutellum with many long setae. Wings: fumose black. Length = 2.2–2.4 mm (n = 2). Width = 0.85–1.0 mm (n = 2). Anal lobe present. Veins distinct. R1/R = 1.4 (n = 1). c/w = 0.55 (n = 1). r-m/bM = 0.8 (n = 1). Wing veins M_1, M_2, CuA_1, and CuA_2 setose; stCuA, stM, r-m and bM non-setose. Legs: dark brown, coxae darker. Coxal setae dark. Fore tibial organ with pale and fine vestiture forming a subtriangular patch. Fore tibial spur as long as distal tibial width. Hind tibia without spinose setae. Claws without teeth. Abdomen: dark brown to black. Setae dark, robust, and rather long. Hypopygium (Fig. 3a) brown, concolorous with abdomen. Gonocoxae robust and short, slightly longer than gonostyli, mesial margin with sparse setosity. Gonostylus (Fig. 3a) oval. L/W-index 1.3–1.4, with weakly-developed apical spines, with densely setose apical lobe and small, densely setose medial lobe with 6–7 strong awl-like setae on the base of the underside of the bristled lobe. Tegmen with a dorsal finger-like process, aedeagal teeth numerous and short; aedeagal apodeme sclerotised and very short.

Female. Similar to male except for the yellow abdominal pleura (Fig. 5b) and larger body size. Body of 4th flagellomere 1.2–1.4 times as long as wide. Wing length 2.9–3.6 mm (n = 9). Like other *Sciara* species, *Sciara serpens* **sp. n.** has yellow abdominal pleurites when alive (Nowicki 1868: 61; Craik et al. 2005: 25).

Taxonomic remarks

Mohrig et al. (2013) reported six species of the genus *Sciara* in North America, but with no reliable records from Alaska. The new species represents the third species of *Sciara* reported for Alaska. However, of the two species previously reported from Alaska, *Sciara borealis* Rübsaamen, 1898 (Coquillett 1900; Stone & Laffoon 1965) was listed by Mohrig et al. (2013) as a 'questionable record; material not seen', and *Sciara abbreviata* Walker was transferred by them to the genus *Lycoriella*, as *L. abbreviata* (Walker, 1848). Thus, our new species is the first well-documented *Sciara* species for Alaska.

Sciara serpens **sp. n.** belongs to the *Sciara hemerobioides* group in the sense of Menzel & Mohrig (2000). Species of this group have very strong and relatively short gonocoxites with, at most, short setae on the inner side, club-shaped, oval to spherical gonostyli, and a uniformly dark body (Craik et al. 2005).

Sciara serpens **sp. n.** is similar to *S. mirabilis*, as described by Nowicki (1868: figs. 1–8, as *S. militaris*) from

Kopaliny near Bochnia (Poland) and redescribed by CRAIK et al. (2005: 21, figs. 1–7). *Sciara serpens* **sp. n.** is similar to *S. mirabilis* in the shape of the gonostyli but differs in having weakly developed apical spines on the gonostyli and a shorter tegmen. Furthermore, besides the differences in the male genitalia, the length of the flagellomeres distinguishes the new species within the *Sciara hemerobioides* group (CRAIK et al. 2005): *Sciara serpens* **sp. n.** is similar to *S. mirabilis* in having the 4th male flagellomere 1.3 times as long as wide, whereas in *S. analis* it is 2.0–2.3 times as long as wide and in *S. hemerobioides* 2.7–3.2 times as long as wide. In addition to the figures of CRAIK et al. (2005), see fig. 2 in MENZEL (1992: 235) drawn as "*S. militaris*" [= *S. minor* in our present study].

Sciara congregata is one of two named North American snakeworm gnat species (BECKER 1914). However, we believe it is unlikely that *S. congregata* is conspecific with *S. serpens* **sp. n.**, for the following reasons: 1) based on examination of the damaged holotype and the original description, MOHRIG et al. (2013) suggested that *S. congregata* might instead belong to the genus *Trichosia* Winnertz, subgenus *Mouffetina* Frey [now genus *Mouffetina* (SHIN et al. 2019)]; 2) Arkansas, only record for *S. congregata*, shares no species of Sciaridae with Alaska that we know of (MOHRIG et al. 2013) and 3) has a very different climate. The only other named snakeworm gnat species in North America, *S. fraterna*, documented from Minnesota (SAY 1824) and Maryland (PRATT 1899), also occurs in a different bioclimatic region than Alaska, suggesting that it is probably not conspecific with our new species. The type specimens of *S. fraterna* are lost and those of *S. congregata* are partly damaged/lost (MOHRIG et al. 2013), so to study the conspecificity of these three species will require someone to rear snakeworm gnat larvae in Arkansas, Minnesota, and Maryland to obtain adult males and/or DNA-barcoded specimens from these areas to test our hypothesis.

Although we have numerous reports of snakeworms in Alaska (Fig. 6, white dots), we have only been able to confirm the species identity of some of these. We have DNA barcodes and adult males from the type locality in Fairbanks, and a partial DNA barcode (180 bp) from the Kenai Peninsula (UAM:Ento:457589). The other Alaskan records are likely conspecific with *Sciara serpens* **sp. n.**, but this is an assumption. The Kenai Peninsula DNA sequence, which is geographically remote from the type locality, groups within the new species clade (Fig. 1), which supports our assumption that the other equally remote records in Alaska are likely conspecific with *Sciara serpens* **sp. n.** The short Kenai sequence is one of two 180 bp sequences from recently collected specimens. We submitted seven other recently-collected specimens for DNA barcoding that failed to sequence entirely and two additional specimens produced short sequences that were flagged as contaminated. It is unknown why sequencing did not work, while for other specimens of different taxa on the same plate it did.

It is interesting that, in our analysis, this new species appears more closely related to the European species *Sciara mirabilis* than the two North American *Sciara* species (Fig 1). This pattern of distribution, with Old World and Alaskan species being closely related, or conspecific, has been documented in other taxa such as grasshoppers (HABERSKI et al. 2021) and staphylinid beetles (SIKES et al. 2016; BRUNKE et al. 2020) and is likely to have resulted from dispersal across the Bering Land Bridge, which connected Alaska to Eurasia during much of the Pleistocene (BRUNKE et al. 2020).

COI sequence of paratype
(UAM:Ento:26784/barcode:106838/UAMIC4420-21)

ACTTTATATTTTATTTTTGGAACATGAGCTA-
GAATAGTGGGTACTTCCCTTAGTATATTGATTCGT-
GCAGAATTAGGTTATCCAAACTCTTTAATTGGG-
GATGATCAAATTTATAATGTTATTGTAACAGCTCAT-
GCTTTTATTATAATTTTTTTTATAGTAATACCAAT-
TATAATTGGAGGGTTTGGAAATTGATTAGTCCCCT-
TAATATTAAGAGCCCCAGATATAGCATTTCCCCGATT-
GAATAATATAAGTTTTTGACTTCTTCCACCCTCTT-
TAACTTTATTATTATCAAGTAGATTAGTAGAAAAA-
GGAACAGGAACAGGTTGAACAGTTTACCCTCCAT-
TATCTTCAACTATTTCCCATTCCGGGGCATCTG-
TAGACTTATCAATTTTTTTCCCTTCATTTAGCAGG-
TATTTCATCTATTTTAGGAGCAGTAAATTTTATTTCC-
ACAATTATTAATATACGAACCCCAGGAATATTATTTGA-
TAAAATACCATTATTTGTCTGATCTGTATTTATTACG-
GCTATTTTATTATTACTCTCCCTTCCAGTATTAGCAG-
GAGCTATTACTATATTATTAACAGATCGAAACCTAAAT-
ACATCATTTTTTGACCCAGCTGGGGGAGGGGACC-
CAATTTTATATCAACACTTATTT [657 bp]

Discussion

North American snakeworm records

North American records of snakeworms were presented or summarized in the following publications dating from 1867 through 1969: COPE (1867: 222–225, reporting sightings made in 1864–1867), West Chester in Pennsylvania, presumed *Sciara* sp.; GLOVER (1874: 115–116), Leesburg in Virginia, *Sciara* sp.; RILEY & HOWARD (1891: 214–215), Missouri, *Sciara* sp.; WEBSTER (1894: 109), West Lafayette in Indiana, "rope of maggots"; JONES (1893: 361), Oberlin in Ohio, *Musca domestica* [misidentification, the author described larvae with a sclerotized head which *Musca* does not have]; PRATT (1899: 263–264), Maryland, *Sciara fraterna*, "snake-like mass"; FELT (1901: 992–994), Franklin in New York, *Sciara* sp.; BECKER (1914: 94–95), Fayetteville in Arkansas, *Sciara congregata*; NOTMAN (1921: 57), Adirondack Mountains in New York, *Sciara* sp.; COLE & SCHLINGER (1969: 128), Berkeley in California, *Sciara* sp.

Snakeworm behavior
(Fig. 4)

There are various hypotheses to explain the mass movement behavior of snakeworm gnats, but none have been adequately tested. We review and supplement these ideas here; first those that address the question of why the larvae might leave one area for another and then those that address the more perplexing question of why the larvae do so as a group, maintaining body contact in such remarkable and long columns. A complete explanation must address why the larvae do not disperse individually in many directions, like calliphorid larvae leaving a consumed carcass. The rarity of snakeworm sightings suggests that these larval mass movements are not an annual part of their life cycle (Nowicki 1868) but occur only when relatively rare conditions arise. It is also important to explain why the larvae crawl on top of one another in multiple layers (thus, most make body contact laterally, ventrally, and dorsally). The larvae in the rear crawl over the top of their companions and make faster forward progress than those on the bottom, who eventually are exposed and commence moving on top of those who have already progressed and gained contact with the substrate (Becker 1914) in a conveyor-belt fashion (Nowicki 1868) (Supplementary File 3).

Regarding the question of why the mass movement is initiated, Menzel & Mohrig (2000), in reviewing the literature addressing this phenomenon, cited Kjellander (1943a, 1943b), who argued against a depletion of food being an explanation because such mass-moving larvae are well-fed final instars and show little interest in feeding; this was corroborated by Craik et al. (2005; as *S. militaris*) regarding larvae of *S. mirabilis* they examined in Scotland. However, food depletion could still be an explanation if they are moving to an area with more food for their offspring [but are decaying leaves and fungi, their apparent food source (Becker 1914) ever depleted by fungus gnat larvae?]. In contrast, Becker (1914) reported that captive larvae of *Sciara congregata* found in Arkansas, USA "fed actively for several days" on "oak leaf mold", and that pupae were seen three days later. Menzel & Mohrig (2000) reviewed some of the literature explaining these larval mass movements and suggested that the behavior could instead be a response to stress resulting from overpopulation. However, it is unclear why this stress response would be advantageous for mostly (Nowicki 1868) final-instar larvae ready to pupate (Riley & Howard 1891). If overpopulation was the cause, would they not be better served by dispersing individually in different directions? Would they not be equally overpopulated in their new environment once they arrived? It is unknown what percentage of a population departs en masse, so this is an area requiring more research. Based on an analysis of ancestral larval habitats, Shin et al. (2013) proposed that the mass movement behavior could have evolved as a method of habitat selection in response to environmental changes during the larval stage, such as flooding, as suggested by Webster (1894), or changes in humidity levels, as suggested by Notman (1921). Brues (1951) mentioned that the larval mass movement he observed in the Philippines appeared to be moving from wetter to drier ground. We suggest that the initiation of the movements may serve for dispersal, because the known adults of species that show these behaviors are not very flight active (Craik et al. 2005), thus the larval movement may compensate for the lack of adult dispersal.

Although these various ideas, including overpopulation, dispersal, and environmental changes, address the initiation of movement, none address the second and more perplexing question of why the larvae disperse in the same direction in close bodily contact. These movements seem to happen just prior to pupation, so perhaps the larvae stay together to more easily find mates after eclosing as adults—since they may be less capable of finding mates via flight. But do they stay together because they are poor fliers due to some other cause? Or are they poor fliers because they stay together, making flight for mate-finding unnecessary? In either case, maybe the congregation of many larvae is advantageous because the founding population in a new habitat is larger than it would be if the larvae dispersed in random directions.

Wynne-Edwards (1967: 114–118; as *S. militaris*) used this phenomenon as one example among many of a possible epideictic display, in which members of a group of animals advertise their presence in such a way as to supposedly allow others of the group to assess the density of the population. Although the advantage of doing this for individual larvae was not explained by Wynne-Edwards (1967). Craik et al. (2005) attempted to elaborate on this idea while also pointing out that it has not gained support in the literature as an explanation for these larval mass movements. Craik et al. (2005) also suggested that the body-contact behavior could help in the digestion of food if the friction produced by the mass movement increases their body temperatures. This novel idea predicts that such mass movements would be related to external temperatures.

We suggest that moving in body-contact in long columns may serve two functions simultaneously: 1) as suggested by Felt (1901), the larvae may behave in this manner when moving across drier, more exposed habitats to reduce water loss by minimizing surface area exposed to air and drier ground; 2) these columns look somewhat like a snake or relatively large animal/object, and could thus deter predators such as birds from investigating them as a source of prey. Nowicki (1868), who observed this phenomenon many times, reported never seeing any birds preying on the larval masses. Our, and

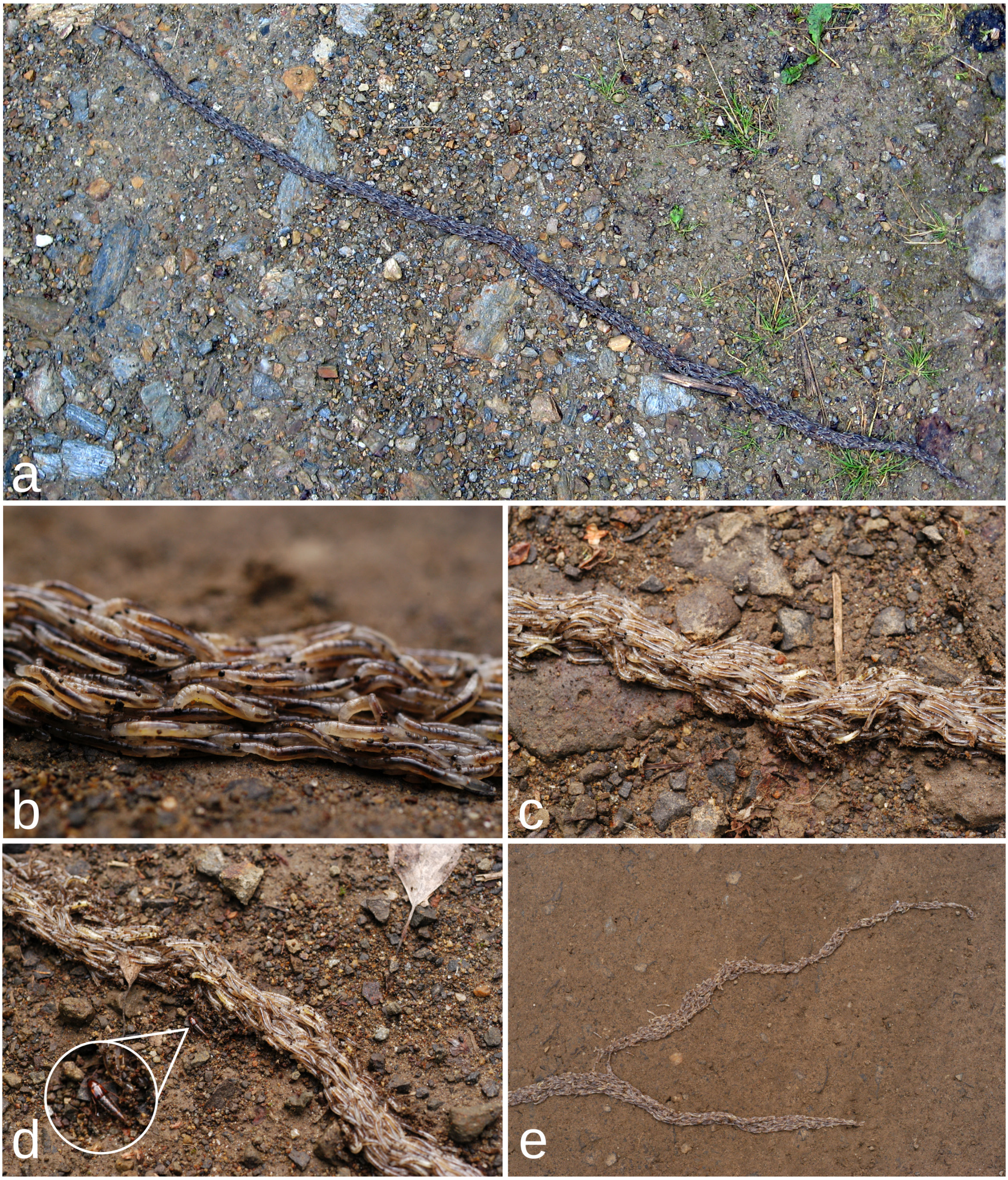

Fig. 4. *Sciara serpens* Pereira, Heller & Sutou, **sp. n. a–e**. Larval mass movement behavior. White circle (d) showing *Mycetoporus americanus* Erichson (UAM:Ento:24892) (Coleoptera: Staphylinidae) running alongside the *Sciara serpens* **sp. n.** snakeworm. (Photos: Margaret Billington [a]; Derek Sikes [b–e])

Fig. 5. *Sciara serpens* Pereira, Heller & Sutou, **sp. n.**, preimaginal stages and adults. **a**. Male front, female back. **b**. Female. **c**. Egg mass laid by reared specimens. **d**. Pupae.

other, reviews of the literature found no reports of bird predation on snakeworm gnats or, more surprisingly, any prior suggestion the behavior could play an anti-predator role. However, one of the most recent snakeworm reports, by Jenna Hamm at Camp Denali, Alaska (https://arctos.database.museum/guid/UAMObs:Ento:245723), included observations of what she thinks were white-crowned sparrows [*Zonotrichia leucophrys* (Forster, 1772)] and/or dark-eyed juncos [*Junco hyemalis* (Linnaeus, 1758)] preying on the few straggling larvae left behind after the column had crossed a footpath and had begun to disperse into the leaf litter (Hamm 2022). Although this hypothesis of snake mimicry is appealing and testable, given that some birds prey on snakes (Guthrie 1932), it may not be the primary driver of the phenomenon.

In support of the water loss idea of Felt (1901) is the fact that, at least in Alaska, these columns of moving larvae have been only seen on roads and trails that are more exposed to sun and dry air than the damp leaf-litter covered and shaded ground inside adjacent forests. Of course, such dry areas are where they would be most obvious to humans, which could explain the lack of off-trail observations, so additional study on this question is needed. Nevertheless, our limited observation data in Alaska indicate that the column breaks up and that the larvae disperse once they enter the forest after crossing a trail or road (Hamm 2022). Billington & Dauenhauer (2007) reported seeing these columns over many days in different locations. One shared feature of their observations and other time-stamped Alaskan observations was that the larvae were seen only on cool mornings and not in the warmer afternoons, aside from some desiccated, dead, or dying larvae. Felt (1901), reporting on an observation of snakeworms in New York, USA, stated “They kept in the shade of trees and when exposed to the sun, succumbed in two to three hours.” This suggests that avoiding desiccation while crossing drier terrain could be an important factor in understanding the mass-movement behavior. Felt (1901) stated as much: “These tender, moist larvae are very susceptible to sun and dryness, and their peculiar method of progression reduces these perils very largely." This preference for moist habitats and activity limited to cooler time periods of the day was also noted by NOWICKI (1868). We consider FELT's (1901) ideas on these issues to be among the best thought-out in the literature. He suggested that the preference for the larvae to maintain contact with moist surfaces and move in a direction of least resistance is all that would be needed for the formation of these columns. Once the larvae hit a surface they find too dry, they slow down or stop and the larvae behind crawl over their companions until they hit the dry surface, leading to their companions in the rear extending the column further by climbing over each other in layers until they all eventually reach an acceptable habitat. Although this explains their behavior while crossing drier substrates, it does not explain why they are already in close proximity while in moist leaf litter before reaching the drier substrate. Perhaps the ecotone between humid forest and dry ground triggers the grouping behavior? We hypothesize that when individually dispersing larvae encounter dry ground they turn left or right to move parallel to the ecotone. This would lead to about half of them finding each other, thus enabling a mass movement across the dry ground, with the other half individually dispersing parallel to the ecotone in opposite directions. Clearly, various lines of investigation remain to be explored.

Citizen science

Alaska's citizens have made a big contribution to this study. Most of the records are from observations and material collected by them (see Material examined and Other material under the new species description). In 2007, snakeworm observations were published in local Alaskan periodicals, with an impressive richness of detail (THACKER 2007; BILLINGTON & DAUENHAUER 2007). In the same year, DS created a webpage with some information about this phenomenon, resulting in him receiving additional reports, photos, and videos. In 2021 we posted on the Facebook group "Bugs and Plants of Alaska", which has over 9,000 members, a "Wanted poster" asking for information on snakeworm observations, and subsequently received additional data and material from new Alaskan localities, demonstrating how social media can be a resource to connect researchers and citizen naturalists. We combined these data with observations on iNaturalist

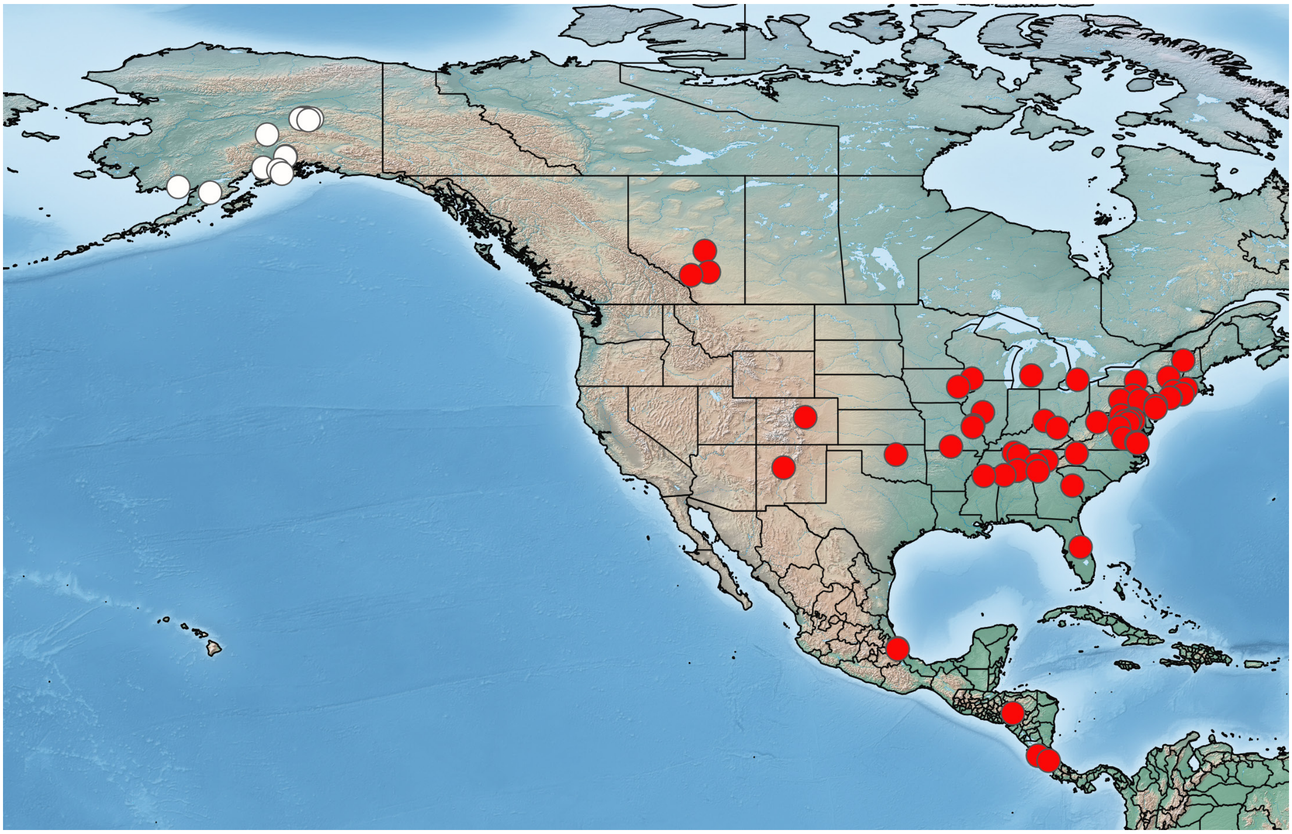

Fig. 6. Snakeworm sightings in North and Central America. White dots: localities of *Sciara serpens* **sp. n.**; red dots: localities of other snakeworms without genus/species identification.

(Supplementary File 2) to produce a map of snakeworm sightings in North and Central America (Fig. 6). Although these non-Alaskan records are clearly of larval mass movements of species in the family Sciaridae, to identify the genus/species it would be necessary to collect material to rear adult males and/or identify them using DNA barcoding.

Closing remarks

Several investigatory lines for future work remain before this unusual larval mass movement phenomenon is well understood. "*Sciara hemerobioides*" from Japan is genetically distinct from European *S. hemerobioides* and is probably a different, and likely new, species (Fig. 1). There are two BINs in Europe with an uncorrected genetic distance of 3.85% from each other, which may represent different species and need more careful study. Thus, there may be three species included under the name *S. hemerobioides*. In addition, the taxonomic and nomenclatural status of *Sciara thomae*, which may be conspecific with European *Sciara hemerobioides* (Mohrig et al. 2013), needs to be reassessed.

Some observers of snakeworms in Alaska reported seeing beetles running alongside the columns of larvae. DS saw these and collected some, which he identified as the staphylinid *Mycetoporus americanus* Erichson (UAM:Ento:24892) (Fig. 4d). At least four other observations of rove beetles running alongside *Sciara* larval columns in Alaska have been reported [Cathy Turner, pers. comm.; Michael Fitz, pers. comm.; Jenn Hamm, pers. comm.; Sandy Dauenhauer (Billington & Dauenhauer 2007)]. Staphylinid larvae were reported feeding on snakeworms in Pennsylvania by Cope (1867). DS had placed together in a petri dish one beetle and six *Sciara serpens* **sp. n.** larvae and observed that the beetle mostly ignored the larvae but eventually killed two. Perhaps the larvae smelled like fungus attractive to the beetle? This is just one of many aspects that beg further investigation.

Acknowledgements

The authors thank citizens who reported observations and/or collected specimens for study: Margaret Billington, Diane Clausen, Lynn Cornberg, Michael Fitz, Jenn Hamm, Ted Johnson, Sarah Keller, Deborah Kurtz, Jerry Moses, Joseph Rueter, Tim Sands, Julie Stricker, George Strother, Jan Thacker, Rosy Thompson, Cathy Turner, and Loretta Winton. We also thank the University of Alaska Fairbanks Cooperative Extension and Morgan Krakow of the Anchorage Daily News, who helped connect citizens to DS. Funding for some of the DNA barcodes used herein was provided by the United States Fish and Wildlife Service's Alaska Region NWRS Inventory and Monitoring Initiative. We thank the students in the University of Alaska Fairbanks Summer Sessions' "Adult Bug Camp" and "Kids Bug Camp" courses, who helped us decide on the specific epithet of our new species. We also thank all those who collected, curated, identified, and made publicly available DNA barcodes for Sciaridae on BOLD, including Björn Rulik (ZFMK), who shared non-public sequences of *S. analis* with us. TPLP thanks the Centennial Postdoctoral Initiative (University of Alaska Fairbanks) for Post-Doctoral Fellowship support. The authors thank Adam Broadley and Frank Menzel and Daniel Whitmore for their valuable comments and suggestions.

References

Amorim, D. S. (1992): A catalogue of the family Sciaridae (Diptera) of the Americas South of the United States. – Revista Brasileira de Entomologia **36** (1): 55–77.

Bechstein, J. M. (1794): Kurzgefaßte gemeinnützige Naturgeschichte des In- und Auslandes für Schulen und häuslichen Unterricht. Ersten Bandes zweite Abtheilung. Fische, Insecten und Würmer, i–viii + 613–1352 pp.; Leipzig (Siegfried Leberecht Crusius).

Bechstein, L. (1850): Der Heerwurm und die Wildschützen. Thüringerwaldgeschichte. – In: Dräxler-Manfred, E. (ed.): Rheinisches Taschenbuch auf das Jahr 1850, pp. 275–397; Frankfurt am Main (J. D. Sauerländers Verlag).

Bechstein, L. (1851): Der Heerwurm, sein Erscheinen, seine Naturgeschichte und seine Poesie, vi + 82 pp.; Nürnberg (Verlag der Friedrich Korn'schen Buchhandlung). https://doi.org/10.5962/bhl.title.144071

Becker, G. G. (1914): Migrating larvae of *Sciara congregata* Johannsen. – Psyche **21** (3): 94–95. https://doi.org/10.1155/1914/59650

Beling, T. (1883): Der Heerwurm, die Heerwumsmücke und die Thomas-Trauermücke. – Zeitschrift für Naturwissenschaften **5**: 253–271.

Berthold, A. A. (1856): Der Heerwurm gebildet von Larven der Thomas-Trauermücke, *Sciara Thomae* [sic]. – Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen. Physikalische Classe **6** [1853–1855]: 39–88 + 1 pl.

Billington, M. & Dauenhauer, S. (2007): What we saw last summer or, a minor discourse on the espial of strange beings in the environs of the settlement of Ester. – The Ester Republic **9** (11): 14–16.

Brues, C. T. (1951): A migrating army of sciarid larvae in the Philippines. – Psyche **58** (2): 73–76. https://doi.org/10.1155/1951/36389

Brunke, A. J., Salnitska, M., Hansen, A .K., Zmudzinska, A., Smetana, A., Buffam, J. & Solodovnikov, A. (2020): Are subcortical rove beetles truly Holarctic? An integrative taxonomic revision of north tem_perate *Quedionuchus* (Coleoptera: Staphylinidae: Staphylininae). – Organisms Diversity & Evolution **20** (1): 77–116. https://doi.org/10.1007/s13127-019-00422-2

Campbell, J. M. (1991): A revision of the genera *Mycetoporus* Mannerheim and *Ischnosoma* Stephens (Coleoptera: Staphylinidae: Tachyporinae) of North and Central America. – The Memoirs of the Entomological Society of Canada **123** (S156): 3–169. https://doi.org/10.4039/entm123156fv

Chapman, A. D. & Wieczorek, J. (eds.) (2006): Guide to best practices for georeferencing, vi + 80 pp.; Copenhagen (Global Biodiversity Information Facility). http://www.gbif.org/resource/80536

Cole, F. R. & Schlinger, E. I. (1969): The flies of western North America. Volume 340, xiv + 693 pp.; Berkeley (University of California Press).

Cope, E. D. (1867): On the habits of a Tipulideous larva. – Proceedings of the Academy of Natural Sciences of Philadelphia **19**: 222–226.

Coquillett, D. W. (1900): Papers from the Harriman Alaska Expedition. IX. Entomological results (3): Diptera. – Proceedings of the Washington Academy of Sciences **2**: 389–464.

Craik, J. C. A., Wormell, P., Smith, J. E. & Menzel, F. (2005): Long columns of "army worms" in west Scotland – the first record of *Sciara militaris* Nowicki (Diptera, Sciaridae) in the British Isles? – Dipterists Digest. Second Series **12** (1): 21–27.

Dahl, F. (1906): Briefkasten. – Naturwissenschaftliche Wochenschrift, Neue Folge **5** (36): 575–576.

deWaard, J. R., Ivanova, N. V., Hajibabaei, M. & Hebert, P. D. (2008): Assembling DNA barcodes. – In: Cristofre Martin, C. (ed.): Environmental genomics, pp. 275–294; Totowa (Humana Press).
https://doi.org/10.1007/978-1-59745-548-0_15

Edgar, R. C. (2004): MUSCLE: multiple sequence alignment with high accuracy and high throughput. – Nucleic Acids Research **32** (5): 1792–1797.
https://doi.org/10.1093/nar/gkh340

Eiseman, C. S., Heller, K. & Rulik, B. (2018): A new dark-winged fungus gnat (Diptera: Sciaridae) mining leaves of *Clintonia borealis* (Aiton) Raf. (Liliaceae). – Proceedings of the Entomological Society of Washington **120** (3): 500–507.
https://doi.org/10.4289/0013-8797.120.3.500

Felt, E. P. (1901): Snakeworm (*Sciara* species). – In: Felt, E. P. (ed.): 16th Report of the state entomologist on injurious and other insects of the state of New York, 1900. – Bulletin of the New York State Museum **36** (7): 992–994.

Fuss, C. (1851): Vereinsnachrichten. – Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt **2** (11): 172–175.

Glover, T. (1874): Report of the entomologist and curator of the museum. – In: Report of the Commissioner of Agriculture for the year 1872, pp. 112–138; Washington, D.C. (Government Printing Office).

Guindon, S., Dufayard, J. F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010): New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. – Systematic Biology **59**: 307–321.
https://doi.org/10.1093/sysbio/syq010

Guthrie, J. E. (1932): Snakes versus birds; birds versus snakes. – The Wilson Bulletin **44** (2): 88–113.

Haberski, A., Woller, D. A. & Sikes, D. S. (2021): Orthoptera of Alaska: a photographic key, new records, and synonymy of *Melanoplus gordonae*. – Canadian Journal of Arthropod Identification **44**: 1–51.
https://doi.org/10.3752/cjai.2021.44

Hamm, J. (2022): Am I hallucinating?! – Ptarmigan Tracks: The Newsletter of Camp Denali and Parkside Guest House **47**: 2.
https://campdenali.com/online-newsletter/262069?show=262071

Heller, K., Hippa, H. & Vilkamaa, P. (2015): Taxonomy of *Bradysia* Winnertz (Diptera, Sciaridae) in the Northern Holarctic, with the description of four new species. – European Journal of Taxonomy **122**: 1–15.
https://doi.org/10.5852/ejt.2015.122

Hippa, H., Vilkamaa, P. & Heller, K. (2010): Review of the Holarctic *Corynoptera* Winnertz, 1867, s. str. (Diptera, Sciaridae). – Zootaxa **2695** (1): 1–197.
https://doi.org/10.11646/zootaxa.2695.1.1

Hoang, D. T., Chernomor, O., Haeseler, A. von, Minh B. Q. & Vinh, L. S. (2017): UFBoot2: improving the ultrafast bootstrap approximation. – Molecular Biology and Evolution **35** (2): 518–522.
https://doi.org/10.1093/molbev/msx281

Ivanova, N. V., DeWaard, J. R. & Hebert, P. D. (2006): An inexpensive, automation-friendly protocol for recovering high-quality DNA. – Molecular Ecology Notes **6** (4): 767–1656.
https://doi.org/10.1111/j.1471-8286.2006.01428.x

Jones, L. (1893): A rope of maggots. – Science. New Series **22** (569): 361.
https://doi.org/10.1126/science.ns-22.569.361.a

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K., Haeseler, A. von & Jermiin, L. S. (2017): ModelFinder: fast model selection for accurate phylogenetic estimates. – Nature Methods **14** (6): 587–589.
https://doi.org/10.1038/nmeth.4285

Kjellander, E. (1943a): Einige Beobachtungen über den Heerwurm in Schweden mit Beschreibung der ihn bildenden Miicke *Semisciara agminis* n. gen. n. sp. – Opuscula Entomologica **8** (1–2): 44–58.

Kjellander, E. (1943b): Einige Versuche mit Heerwurmern in Schweden nebst Beschreibung der Larve von *Semisciara agminis* Kjellander. – Kungliga Fysiografiska Sällskapets i Lund Förhandlingar 1**3** (11): 105–123.

Knauer, F. K. (1909): Tierwanderungen und ihre Ursachen, xi + 288 pp.; Cologne (J. P. Bachem).

Krivosheina, M. G., Krivosheina, N. P., Krivosheina, G. G. & Ozerov, A. L. (2019): Outbreaks of soil-dwelling Diptera (Insecta): has the phenomenon a natural or an anthropogenic origin. – Entomological Review **99**: 733–743.
https://doi.org/10.1134/S0013873819060034

Kühn, D. (1782): Anecdoten zur Insekten-Geschichte. Zwölftes Stück. Beschluß der Geschichte des Heerwurms. – Der Naturforscher **17**: 226–231.

Lengersdorf, F. (1928–1930): 7. Lycoriidae (Sciaridae). – In: Lindner, E. (1926–1930) (ed.): Die Fliegen der palaearktischen Region, Band 2.1 (Lieferung 24 + 43), 71 pp. + 4 pls.; Stuttgart (E. Schweizerbart'sche Verlagsbuchhandlung).

Lumnitzer, J. G. (1826): Lehrbuch für den ersten, systematischen Unterricht in der Naturgeschichte, xiii + 240 pp., 12 pls.; Vienna (Kunsthandlung des H.F. Müller).
https://doi.org/10.5962/bhl.title.97301

Madeira, F., Park, Y. M., Lee, J., Buso, N., Gur, T., Madhusoodanan, N., Basutkar, P., Tivey, A. R. N., Potter, S. C., Finn, R. D. & Lopez, R. (2019): The EMBL-EBI search and sequence analysis tools APIs in 2019. – Nucleic Acids Research **47** (W1): W636–W641.
https://doi.org/10.1093/nar/gkz268

Meijere, J. C. H. de (1935): Armyworms of the Netherland East-Indies (Dipt.). – Tijdschrift voor Entomologie **78** (1–2): 184–185.

Menzel, F. (1992): Beiträge zur Taxonomie und Faunistik der paläarktischen Trauermücken (Diptera, Sciaridae). Teil I. - Die Stroblschen Sciaridentypen des Naturhistorischen Museums des Benediktinerstifts Admont. – Beiträge zur Entomologie **42** (2): 233–258.
https://doi.org/10.21248/contrib.entomol.42.2.233-258

Menzel, F., Gammelmo, Ø., Olsen, K. M. & Köhler, A. (2020): The black fungus gnats (Diptera, Sciaridae) of Norway – Part I: species records published until December 2019, with an updated checklist. – ZooKeys **957**: 17–104.
http://dx.doi.org/10.3897/zookeys.957.46528

Menzel, F. & Mohrig, W. (2000): Revision der paläarktischen Trauermücken (Diptera: Sciaridae). – Studia Dipterologica. Supplement **6** (1999): 1–761.

Menzel, F. & Vilkamaa, P. (2021): New species and records of *Lycoriella* Frey (Diptera, Sciaridae) from the Holarctic region. Zootaxa **5072** (6): 501–530. https://doi.org/10.11646/zootaxa.5072.6.1

Mohrig, W., Heller, K., Hippa, H., Vilkamaa, P. & Menzel, F. (2013): Revision of the black fungus gnats (Diptera: Sciaridae) of North America. – Studia Dipterologica **19** (1–2) (2012): 141–286.

Mohrig, W. & Kauschke, E. (2016a): New black fungus gnats (Diptera, Sciaridae) of North America. Part I. Genus *Scatopsciara* Edwards, 1927. – Zootaxa **4150** (4): 401–435. http://doi.org/10.11646/zootaxa.4150.4.3

Mohrig, W. & Kauschke, E. (2016b): New Black Fungus Gnats (Diptera, Sciaridae) of North America. Part II. Genus *Bradysiopsis* Tuomikoski, 1960. – Zootaxa **4154(3)**: 293–302. https://doi.org/10.11646/zootaxa.4154.3.4

Mohrig, W. & Kauschke, E. (2017): New Black Fungus Gnats (Diptera, Sciaridae) of North America. Part III. Genera *Camptochaeta* Hippa & Vilkamaa, *Claustropyga* Hippa, Vilkamaa & Mohrig and *Dichopygina* Vilkamaa, Hippa & Komarova. – Zootaxa **4258** (4): 301–326. https://doi.org/10.11646/zootaxa.4258.4.1

Mohrig, W. & Kauschke, E. (2019): New black fungus gnats (Diptera, Sciaridae) of North America. Part V. Genera *Pseudolycoriella* Menzel & Mohrig and *Phytosciara* Frey. – Zootaxa **4543** (2): 261–283. https://doi.org/10.11646/zootaxa.4543.2.5

Mohrig, W., Kauschke, E. & Broadley, A. (2019): Revision of black fungus gnat species (Diptera, Sciaridae) described from the Hawaiian Islands by D.E. Hardy and W.A. Steffan, and a contribution to the knowledge of the sciarid fauna of the Galápagos Islands. – Zootaxa **4590** (4): 401–439. https://doi.org/10.11646/zootaxa.4590.4.1

Nguyen, L.-T., Schmidt, H. A., Haeseler, A. von & Minh, B. Q. (2015): IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. – Molecular Biology and Evolution **32** (1): 268–274. https://doi.org/10.1093/molbev/msu300

Notman, H. (1921): A compound larva. – Bulletin of the Brooklyn Entomological Society **16** (2): 57.

Nowicki, M. (1868): Der Kopaliner Heerwurm und die aus ihm hervorgehende *Sciara militaris* n. sp. – Verhandlungen des Naturforschenden in Brünnenden **6** (1867): 3–69 + 1 pl.

Pettey, F. W. (1918): A revision of the genus *Sciara* of the family Mycetophilidae (Diptera). – Annals of the Entomological Society of America **11** (4): 319–343. https://doi.org/10.1093/aesa/11.4.319

Pratt, F. C. (1899): A note on a bred *Sciara* larva. – Proceedings of the Entomological Society of Washington **4** (3): 263–264.

Ramann, E. (1911): Bodenkunde, 624 pp.; Berlin & Heidelberg (Springer). https://doi.org/10.1007/978-3-642-92142-1?nosfx=y

Ratnasingham, S. & Hebert, P. D. (2007): BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). – Molecular Ecology Notes **7** (3): 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Richards, O. W. & Davies, R. G. (2013): Imms' general textbook of entomology. Volume 2. Classification and biology, 934 pp.; Berlin (Springer Science & Business Media).

Riley, C. V. & Howard, L. O. (1891): Extracts from correspondence. Gregarious "Snake-worms". – Insect Life **4**: 214–215.

Say, T. (1824): Appendix. Part I – Natural History. § 1. Zoology. – In: Keating, W. H. (ed.): Narrative of an expedition to the source of St. Peter's River, Lake Winnepeek, Lake of the Woods &c. &c. performed in the year 1823, by order of the hon. J.C. Calhoun, secretary of war, under the command of Stephen H. Long, Major U.S.T.E. Volume 2, pp. 253–378; Philadelphia (H. C. Carey & I. Lea).

Schedl, W. (2002): J. W. von Goethe und die Entomologie. – Berichte des Naturwissenschaftlichen-Medizinischen Verein Innsbruck **89**: 291–302.

Shaw, F. R. & Shaw, M. M. (1950): *Sciara* (*Neosciara*) *beebei*, a new species of Sciaridae having migratory larvae. – Bulletin of the Brooklyn Entomological Society. New Series **45** (1): 14–16.

Shin, S., Jung, S., Menzel, F., Heller, K., Lee, H. & Lee, S. (2013): Molecular phylogeny of black fungus gnats (Diptera: Sciaroidea: Sciaridae) and the evolution of larval habitats. – Molecular Phylogenetics and Evolution **66** (3): 833–846. https://doi.org/10.1016/j.ympev.2012.11.008

Shin, S., Lee, H. & Lee, S. (2019): Proposal of a new subfamily of Sciaridae (Diptera: Sciaridae), with description of one new species from South Korea. – Zootaxa **4543** (1): 127–136. https://doi.org/10.11646/zootaxa.4543.1.8

Shorthouse, D. P. (2010): SimpleMappr, an online tool to produce publication-quality point maps. Available from: http://www.simplemappr.net (accessed 14 July 2022).

Sikes, D. S., Bowser, M., Morton, J. M., Bickford, C., Meierotto, S. & Hildebrandt, K. (2017): Building a DNA barcode library of Alaska's non-marine arthropods. **–** Genome **60**: 248–259. https://doi.org/10.1139/gen-2015-0203

Sikes, D. S, Trumbo, S. T. & Peck, S. B. (2016): Cryptic diversity in the New World burying beetle fauna: *Nicrophorus hebes* Kirby, 1837; new status as a resurrected name (Coleoptera: Silphidae: Nicrophorinae). – Arthropod Systematics & Phylogeny **74** (3): 299–309.

Sparks, A. N. (1979): A review of the biology of the fall armyworm. – Florida Entomologist **62** (2): 82–87. https://doi.org/10.2307/3494083

Steffan, W. A. (1966): A generic revision of the family Sciaridae (Diptera) of America north of Mexico. – University of California Publications in Entomology **44**: 1–77.

Stone, A. & Laffoon, J. L. (1965): Family Sciaridae (Lycoriidae). – In: Stone, A., Sabrosky, C. W., Wirth, W. W., Foote, R. H. & Coulson, J. R. (eds.): A catalog of the Diptera of America north of Mexico. Agriculture Handbook, no. 276, pp. 229–236; Washington, D.C. (United States Department of Agriculture).

Strobl, G. (1898): Die Dipteren von Steiermark. IV. Theil. Nachträge zum III. Theil. – Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark **34** (1897): 277–297.

Sutou, M., Kato, T. & Ito, M. (2011): Recent discoveries of armyworms in Japan and their species identification using DNA barcoding. – Molecular Ecology Resources **11** (6): 992–1001. https://doi.org/10.1111/j.1755-0998.2011.03040.x

Thacker, J. (2007): Long ropes of thousands of migrating worms mystify scientists. – Fairbanks Daily News-Miner (July 14th).

Trifinopoulos, J., Nguyen, L.-T., Haeseler, A. von & Minh, B. Q. (2016): W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. – Nucleic Acids Research **44** (W1): W232–W235. https://doi.org/10.1093/nar/gkw256

Vilkamaa, P., Burdíková, N. & Ševčík, J. (2023): The genus *Spinopygina* gen. nov. (Diptera, Sciaridae) from western North America: preliminary molecular phylogeny and description of seven new species – Insects **14** (2): 173. https://doi.org/10.3390/insects14020173

Vilkamaa, P. & Menzel, F. (2019): Re-classification of *Lycoriella* Frey sensu lato (Diptera, Sciaridae), with description of *Trichocoelina* gen. n. and twenty new species. – Zootaxa **4665** (1): 1–67. https://doi.org/10.11646/zootaxa.4665.1.1

Webster, F. M. (1894): Rope of maggots. – Science. New Series **23** (577): 109. https://doi.org/10.1126/science.ns-23.577.109.d

Wynne-Edwards, V. C. (1967): Animal dispersion in relation to social behavior, 653 pp.; Edinburgh (Oliver & Boyd).

Authors' addresses:

[1]Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA;
e-mail (corresponding author): thallesplp@gmail.com; https://orcid.org/0000-0003-2075-3643

[2]Stückenberg 58, 24226 Heikendorf, Germany; e-mail: kaiheller@gmx.de; https://orcid.org/0000-0003-4813-5302

[3]Department of General Systems Studies, Graduate School of Arts and Sciences, The University of Tokyo, 3-8-1 Komaba, Meguro-ku, 153-8902 Tokyo, Japan; e-mail: mi.sutou@r8.dion.ne.jp

[4]University of Alaska Museum and Department of Biology and Wildlife, University of Alaska Fairbanks, 1962 Yukon Drive, Fairbanks, AK 99775-6960, USA; e-mail: dssikes@alaska.edu; https://orcid.org/0000-0002-4336-2365

ZooBank registration: https://zoobank.org/References/C3B615DE-E1C6-423E-8328-094910D1F9B9

Manuscript received: 03.IX.2022; accepted: 15.VII.2023.

Supplementary material:

Supplementary File 1: DNA sequence alignment (MUSCLE) for target and representative Sciara and two outgroup species within the subfamily Sciarinae, downloaded from BOLD.

Supplementary File 2: Snakeworm observations from iNaturalist made between June 13th, 2012 and July 12, 2022.

Supplementary File 3: *Sciara serpens* Pereira, Heller & Sutou, **sp. n.**, video showing snakeworm behavior. (Video: Sarah Keller)

Appendix 1. DNA voucher specimen data from target and representative *Sciara* and outgroup species from BOLD and GenBank.

Identification	Specimen ID	Process ID	BIN	*COI*-5P length (bp)	Locality
Leptosciarella rejecta	bf-sci-00330	SCINO328-15	BOLD:ACK0157	658[1n]	Norway, Buskerud, Ringerike, Veksalbekken, 60.1750, 10.2000, 3-Jun-2014, O. Gammelmo & K.M. Olsen
Leptosciarella rejecta	bf-sci-00199	SCINO198-15	BOLD:ACK0157	658[0n]	Norway, Sogn og Fjordane, Laerdal, Eisurda, 61.0680, 7.8200, 4-Jun-2014, K. Heller
Leptosciarella trochanterata	bf-sci-00305	SCINO303-15	BOLD:ACM3303	658[0n]	Norway, Sogn og Fjordane, Luster, S Klypenosi, 61.5000, 7.7600, 5-Jun-2014, O. Gammelmo & K.M. Olsen
Leptosciarella trochanterata	bf-sci-00349	SCINO347-15	BOLD:ACM3303	658[0n]	Norway, Vestfold, Larvik, Jordstoeyp N, 59.1940, 9.9370, 2-Jun-2014, K.M. Olsen & O. Gammelmo
Sciara analis	ZFMK-TIS-2547789	GESCI142-17	BOLD:ADF9761	658[0n]	Germany, Bavaria, Berchtesgadener Land NP, Wasseralm, 47.5000, 13.0000, 06-Oct-2010, R. Gerecke
Sciara analis	ZFMK-TIS-14859	GESCI061-17	BOLD:ADF9761	658[0n]	Austria, Gesäuse NP, Klausgraben Mündungsstrecke, 47.5800, 14.6500, 02-Aug-2012, H. Haseke
Sciara analis	ZFMK-TIS-14855	GESCI059-17	BOLD:ADF9761	658[0n]	Austria, Gesäuse NP, Klausgraben Mündungsstrecke, 47.5800, 14.6500, 12-Aug-2012, H. Haseke
Sciara antonovae	97	GBMIN12848-13	BOLD:ACD8580	658[0n]	China
Sciara bryophila	JS-COI-2016-0162	SCFI732-16	BOLD:ADD2461	658[0n]	Finland, Lapponia sompiensis, Pelkosenniemi, Sudenvaaranaapa 2, 67.1890, 27.6390, 30-Aug-2015, J. Salmela
Sciara bryophila	JS-COI-2016-0161	SCFI731-16	BOLD:ADD2461	658[0n]	Finland, Lapponia sompiensis, Pelkosenniemi, Sudenvaaranaapa 2, 67.1890, 27.6390, 30-Aug-2015, J. Salmela
Sciara flavimana	bf-sci-00007	SCINO007-14	BOLD:ACM6625	658[0n]	Norway, Hedmark, Stor-Elvdal, N Krokmyra Ved hytta, E Fafengtjorna, 61.6058, 10.8399, 21-Sep-2012, K.M. Olsen
Sciara helvola	JS-COI-2016-0126	SCFI696-16	BOLD:AAH3976	658[0n]	Finland, Ostrobottnia ultima, Ylitornio, Mellajoen SSA, 66.4020, 24.5940, 14-Jun-2015, J. Salmela
Sciara helvola	NSMT-I-Dip-6695	JBOL013-10	BOLD:AAH3976	658[0n]	Japan, Kanto-chiho, Kanagawa, Sagamihara, 35.5300, 139.3800, 2-May-2001, M. Sutou
Sciara hemerobioides	NSMT-I-Dip-6693	JBOL011-10	BOLD:AAH3975	658[0n]	Japan, Kanto-chiho, Kanagawa, Yokohama, 35.4700, 139.5800, 17-Jun-2007, M. Sutou

Identification	Specimen ID	Process ID	BIN	*COI*-5P length (bp)	Locality
Sciara hemerobioides	NSMT-I-Dip-6692	JBOL010-10	BOLD:AAH3975	658[0n]	Japan, Kanto-chiho, Kanagawa, Yokohama, 35.4700, 139.5800, 17-Jun-2007, M. Sutou
Sciara hemerobioides	bf-sci-01200	SCINO1128-16	BOLD:ACQ8933	624[0n]	Norway, More og Romsdal, Sunndal, 62.6500, 8.76100, 17-Jul-2014, K.M. Olsen
Sciara hemerobioides	TSZD-JKJ-108632	NORSC3884-20	BOLD:ACQ8933	658[1n]	Sweden, Orebro, Lindesberg, Gustav V:s berg, 59.6160, 15.4850, 14-Aug-2018, J. Hansson
Sciara humeralis	08BBDIP-1977	TTDBW734-09	BOLD:AAH3914	658[0n]	Canada, Manitoba, Riding Mountain NP, North Escarpment Trailhead, 50.6740, -99.6500, 15-Aug-2008, BIO-bus: A. Borisenko, R. Labbee, V. Levesque-Beaudin, M. Milton, J. Smith & S. Ratnasingham
Sciara humeralis	09BBDIP-0741	USDIP741-09	BOLD:AAH3914	658[0n]	United States, Arkansas, Perry Co., Toad Suck West Campground, 35.0780, -92.5470, 12-May-2009, J. Cossey, J. McCormick & J. Sones
Sciara incerta	BIOUG16218-F12	GMGMA1314-14	BOLD:ACQ9294	658[0n]	Germany, Rhineland-Palatinate, Kreis Ahrweiler, Landskrone, 50.5520, 7.1700, 25-Jul-2013, B. Rulik et al.
Sciara kitakamiensis	TDWG-0803	TDWGB667-10	BOLD:AAH3979	658[0n]	United States, Massachusetts, Barnstable Country, Woods Hole near memoriall circle cottage #24, 41.5298, -70.6547, 29-Sep-2010, BIO-bus: A. Borisenko, R. Labbee, V. Levesque-Beaudin, M. Milton, J. Smith & S. Ratnasingham
Sciara kitakamiensis	TDWG-0831	TDWGB695-10	BOLD:AAH3979	658[0n]	United States, Massachusetts, Barnstable Country, Vicinity of Falmouth, Crane WMA, Currier St. powerlines, 41.6144, -70.5403, 29-Sep-2010, M. Mello
Sciara lackschewitzi	DIPT-JS-2016-0636	LEFIJ6578-17	BOLD:ACZ9822	658[0n]	Finland, Lapland, Ostrobottnia ultima, Tervola, Pisavaara, 66.2610, 25.1050, 15-Aug-2016, J. Salmela
Sciara lackschewitzi	bf-sci-01174	SCINO1102-16	BOLD:ACZ9822	658[0n]	Norway, Sogn og Fjordane, Gloppen, Klubben N of Byrkjelo, 61.7690, 6.5020, 20-Aug-2015, O. Gammelmo.
Sciara melanostyla	NSMT-I-Dip-6718	JBOL036-10	BOLD:AAH3980	658[0n]	Japan, Kanto-chiho, Tochigi, Nikko, 36.6800, 139.730, 11-Sep-2009, M. Sutou

Identification	**Specimen ID**	**Process ID**	**BIN**	***COI*-5P length (bp)**	**Locality**
Sciara melanostyla	NSMT-I-Dip-6719	JBOL037-10	BOLD:AAH3980	658[0n]	Japan, Kanto-chiho, Tochigi, Nikko, 36.6800, 139.7300, 11-Sep-2009, M. Sutou
Sciara mirabilis	NSMT-I-Dip-6700	JBOL018-10	BOLD:AAH3977	638[0n]	United Kingdom, Scotland, Argyll, Barcaldine, 56.5000, -5.0000, 30-Jul-2004, P. Wormell
Sciara mirabilis	NSMT-I-Dip-6699	JBOL017-10	BOLD:AAH3977	630[0n]	United Kingdom, Scotland, Argyll, Barcaldine, 56.500, -5.0000, 30-Jul-2004, P. Wormell
Sciara mirabilis	NSMT-I-Dip-6698	JBOL016-10	BOLD:AAH3977	640[0n]	United Kingdom, Scotland, Argyll, Barcaldine, 56.5000, -5.0000, 30-Jul-2004, P. Wormell
Sciara mirabilis	NSMT-I-Dip-6697	JBOL015-10	BOLD:AAH3977	650[0n]	United Kingdom, Scotland, Argyll, Barcaldine, 56.5000, -5.0000, 30-Jul-2004, P. Wormell
Sciara mirabilis	TSZD-JKJ-104033	NORSC2142-17	BOLD:AAH3977	658[0n]	Norway, Troms, Storfjord, Gaelggojaervi, Pond W Myggbukta, 69.1250, 20.7490, 7-Aug-2016, J. Kjaerandsen & M.T. Dahl
Sciara minor	BC-ZSM-DIP-27706-B08	AMTPF1920-16	BOLD:ACZ9335	390[0n]	Germany, Bavaria, Allgäu, Oberstdorf, Koblat, 47.4227, 10.3573, 27-Sep-2014, D. Doczkal, S. Schmidt. J. & Voith
Sciara minor	BC-ZSM-DIP-27706-C03	AMTPF1927-16	BOLD:ACZ9335	579[1n]	Germany, Bavaria, Allgäu, Oberstdorf, Koblat, 47.4227, 10.3573, 27-Sep-2014, D. Doczkal, S. Schmidt & J. Voith
Sciara minor	BC-ZSM-DIP-27706-B06	AMTPF1918-16	BOLD:ACZ9335	588[0n]	Germany, Bavaria, Allgäu, Oberstdorf, Koblat, 47.4227, 10.3573, 27-Sep-2014, D. Doczkal, S. Schmidt & J. Voith
Sciara minor	BC-ZSM-DIP-27706-A01	AMTPF1901-16	BOLD:ACZ9335	564[4n]	Germany, Bavaria, Allgäu, Oberstdorf, Koblat, Schneetälchen, 47.4215, 10.3546, 5-Sep-2014, D. Doczkal S. Schmidt & J. Voith
Sciara minor	BC-ZSM-DIP-27706-A08	AMTPF1908-16	BOLD:ACZ9335	564[2n]	Germany, Bavaria, Allgäu, Oberstdorf, Koblat, 47.4227, 10.3573, 5-Sep-2014, D. Doczkal S. Schmidt & J. Voith
Sciara multispinulosa	653	GBMIN12783-13	BOLD:ACD6966	658[0n]	South Korea
Sciara ruficauda	306	GBMIN12840-13	BOLD:ACD7223	658[0n]	South Korea

Identification	**Specimen ID**	**Process ID**	**BIN**	***COI*-5P length (bp)**	**Locality**
Sciara serpens **sp. n.**	UAM:Ento:457589	UAMIC4540-22		180[0n]	United States, Alaska, Nikiski, Bishop Drive, 60.6860, -151.2230, 8-May-2021, R. Thompson
Sciara serpens **sp. n.**	UAM:Ento:457585	UAMIC4536-22		180[0n]	United States, Alaska, Fairbanks, 1195 Powellite Dr, 64.9140, -147.5130, 27-Jun-2021, T. Johnson
Sciara serpens **sp. n.**	UAM:Ento:457586	UAMIC4537-22	BOLD:ACG1481	603[5n]	United States, Alaska, Fairbanks, 1195 Powellite Dr, 64.9140, -147.5130, 27-Jun-2021, T. Johnson
Sciara serpens **sp. n.**	UAM:Ento:26033	UAMIC984-13	BOLD:ACG1481	658[0n]	United States, Alaska, Fairbanks, Pika Road, 64.9080, -147.8010, 20-Jul-2007, D.S. Sikes
Sciara serpens **sp. n.**	UAM:Ento:27668b	UAMIC4422-21	BOLD:ACG1481	631[0n]	United States, Alaska, Fairbanks, 64.8600, -148.0320, 9-Jul-2007, M. Billington
Sciara serpens **sp. n.**	UAM:Ento:27668a	UAMIC4421-21	BOLD:ACG1481	658[0n]	United States, Alaska, Fairbanks, 64.8600, -148.0320, 9-Jul-2007, M. Billington
Sciara serpens **sp. n.**	UAM:Ento:26784	UAMIC4420-21	BOLD:ACG1481	657[0n]	United States, Alaska, Fairbanks, Pika Road, 64.9080, -147.8010, 23-Jul-2007, D.S. Sikes
Sciara serpens **sp. n.**	UAM:Ento:26793	UAMIC4419-21	BOLD:ACG1481	649[0n]	United States, Alaska, Fairbanks, Pika Road, 64.9080, -147.8010, 23-Jul-2007, D.S. Sikes
Sciara thoracica	17826	GBMIN60850-17	BOLD:AAH3974	658[0n]	South Korea, Jeollabuk-do (JB), Gimjae
Sciara thoracica	17402	GBMIN60849-17	BOLD:AAH3974	658[0n]	South Korea, Jeollabuk-do (JB), Jinan