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Nematode-induced demasculinization of Nearctic Dolichopodidae (Diptera) with five new synonyms

JUSTIN B. RUNYON
Rocky Mountain Research Station, USDA Forest Service, 1648 S. 7th Avenue, Bozeman, Montana 59717, USA
justin.runyon@usda.gov; https://orcid.org/0000-0002-0271-0511

Abstract

Demasculinization, the reduction of male sexual characters due to parasitic nematode infection, is described in Nearctic Dolichopodidae. Five species are confirmed to be demasculinized (3 species of *Dolichopus* Latreille and 1 species each of *Rhaphium* Meigen and *Tachytrechus* Haliday) by nematodes in two families (apparent Mermithidae and Parasitylenchidae). The following nematode-infected males were inadvertently described as new species and are here proposed as synonyms: *Dolichopus hurleyi* Runyon, 2008 = *D. dorycerus* Loew, 1864, **syn. nov.**; *Dolichopus frosti* Runyon, 2008 = *D. sincerus* Melander, 1900, **syn. nov.**; *Tachytrechus boharti* Harmston, 1968 = *T. sanus* Osten Sacken, 1877, **syn. nov.**; *Tachytrechus duplicatus* Harmston, 1972 = *T. sanus* Osten Sacken, 1877, **syn. nov.**; *Tachytrechus mchughi* Harmston, 1972 = *T. sanus* Osten Sacken, 1877, **syn. nov.** A conspectus is presented of the scope of taxonomic problems caused by nematodes in Nearctic *Dolichopus* and *Tachytrechus*, which suggests that ten additional names in *Dolichopus* could be based on infected specimens. Guidelines are provided for recognizing nematode infection to avoid erroneous species descriptions.

Key words: Nematoda, Mermithidae, parasitism, Parasitylenchidae, *Dolichopus*, *Rhaphium*, *Tachytrechus*

Introduction

Nematodes are among the most abundant animals on Earth and many species are internal parasites of insects (Poinar 1975). Nematodes sometimes alter the external morphology of the insects they parasitize. For example, nematode-induced changes to external host morphology have been described in Ephemeroptera (Vance 1996), Hymenoptera (Csősz 2012; Poinar 2012; Laciny *et al.* 2017), and Diptera (Molloy 1981; Wülker 1985; Kahanpää 2008; Muñoz-Muñoz *et al.* 2016). In ants (Formicidae), parasitized individuals often bear morphological features that are intermediate between castes (Poinar 2012). In Ephemeroptera and Diptera, parasitism by nematodes can feminize male hosts (by reducing male primary and secondary sexual characters) but has little or no effect on external morphology of females (Wülker 1964; Vance 1996; Muñoz-Muñoz *et al.* 2016). The mechanisms by which nematodes demasculinize their hosts are unknown, but hosts are likely infected as larvae or pupae, and hormonal manipulation and/or nutrient depletion have been hypothesized (Bailey & Gordon 1973).

Aberrant morphology due to nematode infection can cause taxonomic confusion. For example, parasitized ants with intercast phenotypes have inadvertently been described as new species (Radchenko & Elmes 2003; Csősz 2012; Borowiec & Salata 2015; Laciny *et al.* 2017) and more such erroneous ant 'species' likely exist (Czechowski *et al.* 2007; Csősz 2012). In European Dolichopodidae (Diptera), infection by apparent mermithid nematodes can demasculinize male *Dolichopus* and infected specimens have been mistakenly described as new species on at least eight occasions (Kahanpää 2008; Germann *et al.* 2010). These examples aside, reports of taxonomic problems resulting from nematode infection appear to be uncommon. However, there is little doubt that more unjustified nematode-infected insect 'species' await discovery.

In 2008, I described three new species of Nearctic *Dolichopus* Latreille from Pennsylvania, USA (Runyon 2008). When this paper was in press, I was surprised to see Kahanpää (2008) reporting nematode-induced demasculinization of *Dolichopus* in Finland, as telltale signs of nematode infection were evident in two of the new Nearctic *Dolichopus* species. Dissection revealed that specimens of both 'species' were infected by mermithid-like nematodes. Since

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then, I have scrutinized thousands of specimens of Dolichopodidae for signs of nematode infection and found just three additional parasitized species (one species each of *Dolichopus*, *Rhaphium* Meigen, and *Tachytrechus* Haliday). The purposes of this paper are to (1) document and described nematode-induced demasculinization in Nearctic Dolichopodidae, (2) synonymize five species mistakenly described using nematode-infected specimens, (3) provide a conspectus of the scope of the taxonomic problem caused by nematodes in Nearctic *Dolichopus* and *Tachytrechus* with a list of potentially demasculinized species, and (4) offer guidelines for recognizing nematode infection to avoid erroneous species descriptions.

Materials and methods

Terminology used for adult structures follows McAlpine (1981) and Cumming & Wood (2009). Material from this work is housed in or borrowed from the following institutions: Bohart Museum of Entomology, University of California, Davis, USA (UCDC); California Academy of Sciences, San Francisco, USA (CAS); Montana Entomology Collection, Montana State University, Bozeman, USA (MTEC); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ); Frost Entomological Museum, Pennsylvania State University, University Park, USA (PSUC); United States National Museum of Natural History, Washington D.C., USA (USNM). The term demasculinization is used following Kahanpää (2008). Male secondary sexual characters (MSSCs) are non-genitalic characters found only on the male body.

Male specimens infected with nematodes were recognized using the characters in Table 1 which mirror those reported by Kahanpää (2008). Since 2008, I have watched for signs of nematode infection in the dolichopodid specimens I have collected and/or identified (ca. 20,000 males representing most genera, mostly from the Nearctic Region but also Central America and the West Indies). I also examined male specimens in the MTEC of *Dolichopus* (ca. 7,000 males representing about 175 species) and *Tachytrechus* (ca. 700 males representing 23 species). The abdomen of at least one male specimen of each species with signs of nematode infection was dissected to confirm presence of nematode(s). For most specimens, the abdomen was cut off near the base using iris scissors then the abdomen was soaked in water (with *ca.* 10% ethanol) overnight to soften before further dissection. The unique holotype of *D. hurleyi* was dissected by soaking the entire pinned specimen in water (as above) and then partially cutting open the abdomen to reveal the nematode(s). The abdomen and nematode(s) were then placed in glycerin, transferred to plastic micro-tubes, and placed on a pin with the remainder of the corresponding specimen. Nematodes were classified as mermithid-like if they were relatively large in size, with only 1 or 2 nematodes occurring in each host, and the outer cuticle with cross-fibers. Although these nematodes appear to belong to Mermithidae, only juveniles were found (likewise, only juvenile Mermithidae occur in the host), making confident identification difficult. The Parasitylenchidae from this study were identified and described by Poinar & Runyon (2021). Parasitylenchidae can be distinguished from mermithid-like nematodes by their smaller size, occurrence in large numbers, and the presence of eggs, developing juveniles and adults within hosts.

A review of the descriptions of Nearctic species of *Dolichopus* (317 spp.) and *Tachytrechus* (38 spp.) was conducted looking for signs of nematode infection (Table 1). Original descriptions of all species were reviewed, and also the re-descriptions of *Dolichopus* species in Van Duzee (1921). These two genera were chosen because they contain species known to be demasculinized by nematodes and characteristics of infection that are likely to appear in descriptions. Species described on the basis of nematode-infected males usually have the following characteristics in common: unusually small genitalia, a wide face, and usually known from only one specimen. To try to identify the putative infected species, I checked to see if other species were collected at the same site and/or date (if demasculinization caused by parasitism is rare, then uninfected specimens are likely to be co-collected) and assessed if these species might represent a demasculinized form of a co-collected species.

Results

Confirmed demasculinized species

Specimen(s) of the following Nearctic species were confirmed to be demasculinized by nematodes. No Neotropical specimens examined had signs of nematode infection.

TABLE 1. Characteristics of nematode-induced demasculinization in male Dolichopodidae. Specimens with signs of demasculinization should be dissected to verify nematode infection[1].

Character	Description
Genitalia small and poorly rotated	Genitalia uncharacteristically small and usually not fully folded beneath abdomen (Figs 2, 17, 19, 31); often twisted and sticking out or held to one side. Color of cerci often darker than in normal males (e.g., Figs 17, 19).
Face wide	Infected males have a face width intermediate between normal males and females; face color intermediate or more similar to female (Figs 7–15, 24–29).
MSSCs weakly developed or absent	Nematode infection reduces development of MSSCs, including antennal modifications (Figs 4, 21, 34–39), pterostigmata and costal enlargements, and ornaments (Figs 6, 23) and cilia on legs. The degree of demasculinization can vary (e.g., Figs 34–39) perhaps due to number and size of nematodes infecting the host.
Often only one specimen known	Many confirmed and suspected demasculinized species are known from only one specimen. However, numerous demasculinized specimens are sometimes collected and some species appear to be more prone to infection than others.
Often collected with unparasitized specimens	If parasitism is uncommon, uninfected specimens are likely to be collected with demasculinized specimens. Most confirmed demasculinized specimens presented here were co-collected with normal male specimens. In some cases, the host species might only be confidently known once infected males are collected with uninfected counterparts.

[1] To date, the nematodes known from Dolichopodidae reside within the abdomen. Demasculinized males of *Dolichopus* have been reported without nematodes but with a circular scar in the pleural membrane (presumably an exit wound) (Kahanpää 2008).

Dolichopus dorycerus Loew, 1864a

(Figs 1–9)

Dolichopus dorycerus Loew, 1864a: 93.
Dolichopus hurleyi Runyon, 2008: 368, **syn. nov.**

Nematode. Apparent Mermithidae.

Demasculinized male examined. Holotype ♂ of *Dolichopus hurleyi*: USA, Pennsylvania, Centre County, Black Moshannon State Park, Moss-Hanne Trail, Shirks Run, 580 m, 18 June 2007, N 40°53.396′ W78°02.584′, JB Runyon, from vegetation in wooded swamp (USNM) [abdomen partly cut open to reveal mermithid-like nematode within].

Remarks. The demasculinized male has smaller than normal genitalia (cf. Figs 1, 2) that are held off-center beneath abdomen, a less-well developed lamella on arista (cf. Figs 3, 4), wider silvery face (cf. Figs 7, 8), and lacking costal enlargement at apex of R_1. MSSCs of the legs that are lacking include the longer black setae on posterior surface of front femur and the slightly raised, minutely pilose area on posterior surface of the hind tibia (a characteristic of this species group). Notably, the size of lobes of the modified front tarsi are reduced with tarsomere 5 wholly black (mostly white in normal males) (cf. Figs 5, 6). Numerous normal males of *D. dorycerus* were collected at this site with the single demasculinized specimen.

Dolichopus partitus Melander & Brues, 1900

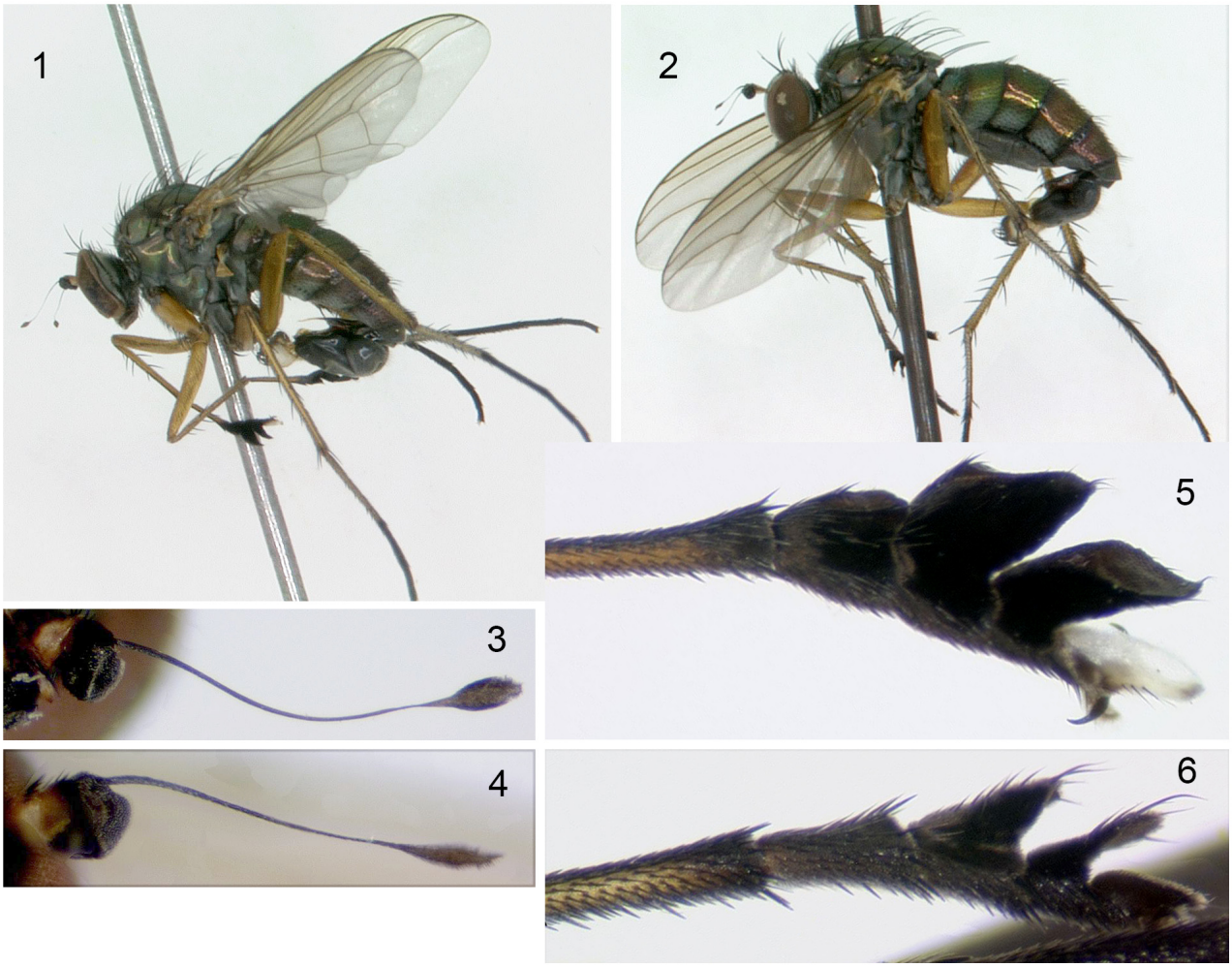
(Figs 10–12, 16, 17)

Dolichopus partitus Melander & Brues, 1900: 135.

Nematode. Apparent Mermithidae.

Demasculinized male examined. 1 ♂, USA, Montana, Granite County, Copper Creek, wetland, N46.06099° W113.55637°, 22 July 2020, JB Runyon (MTEC).

Remarks. The demasculinized specimen has small, very poorly rotated genitalia with darker cerci (cf. Figs 16, 17), a wider face (cf. Figs 10, 11), pterostigma absent, and with the long ventral ciliation of hind femora greatly reduced. The infected specimen was collected with a normal male of *D. partitus* in a sedge-dominated boggy wetland with scattered willows.



FIGURES 1–6. Comparison of normal male of *Dolichopus dorycerus* Loew versus male infected by mermithid-like nematodes. **1.** Habitus, normal male. **2.** Habitus, infected male. Note smaller genitalia and smaller size of modified front tarsomeres. **3.** Antenna, normal male. **4.** Antenna, infected male. **5.** Front tarsomeres, normal male. **6.** Front tarsomeres, infected male. Note smaller size and lack of white on apical tarsomere.

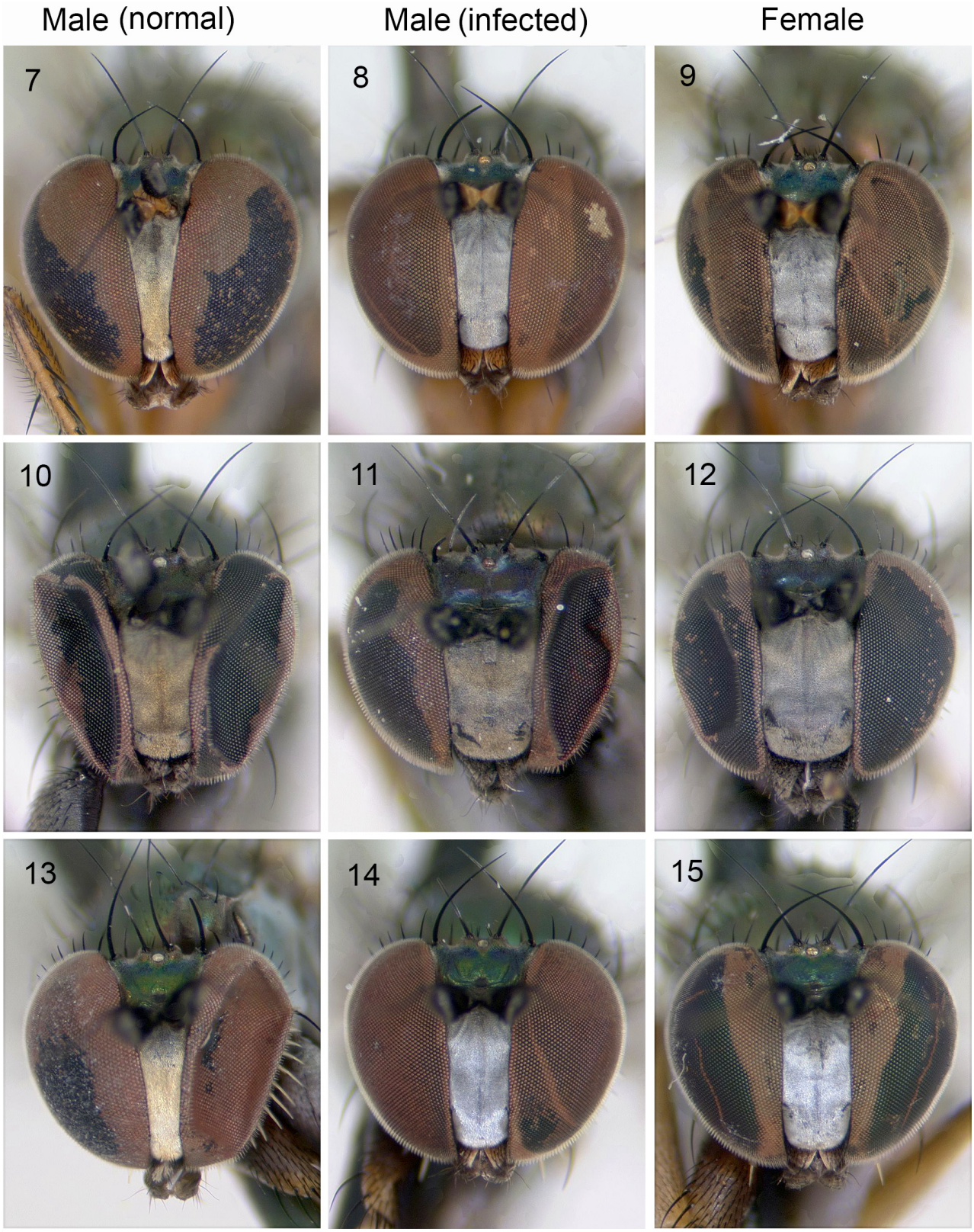
Dolichopus sincerus Melander, 1900

(Figs 13–15, 18, 19)

Dolichopus sincerus Melander, 1900: 3.
Dolichopus subdirectus Van Duzee, 1921: 118.
Dolichopus frosti Runyon, 2008: 370, **syn. nov.**

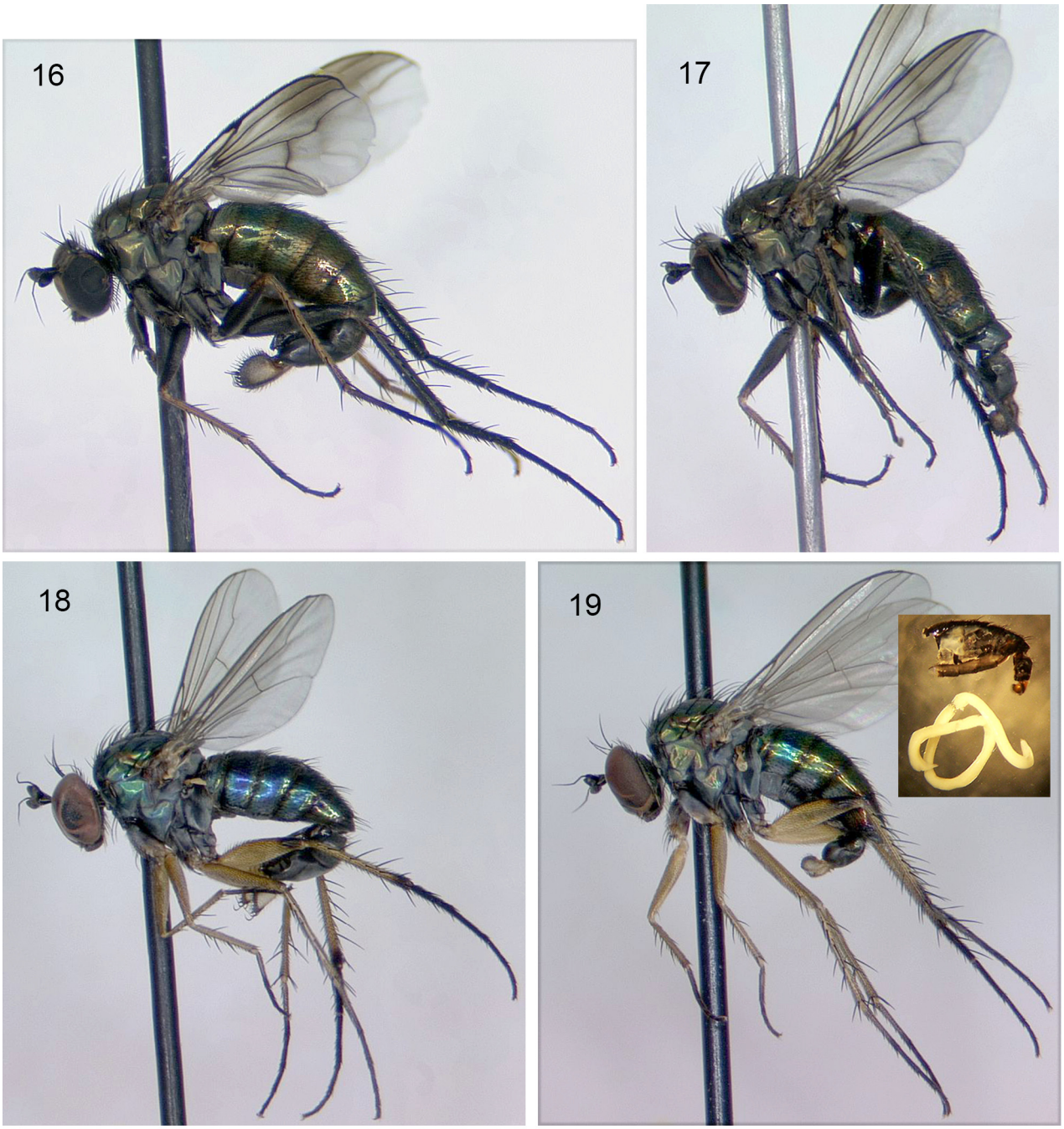
Nematode. Apparent Mermithidae.

Demasculinized males examined. 4 ♂ (including holotype of *Dolichopus frosti*), USA, Pennsylvania, Centre County, Black Moshannon State Park, Moss-Hanne Trail, Shirks Run, 580 m, 23 July 2006, N 40°53.396' W78°02.584', muddy trail through sphagnum bog, JB Runyon; 4 ♂, same as previous, 26 July 2007 (MTEC, PSUC, USNM).



FIGURES 7–15. Effects of mermithid-like nematode infection on faces of male *Dolichopus* species. Normal males (left column), infected males (middle column), and females (right column). **7–9.** *Dolichopus dorycerus* Loew. **10–12.** *Dolichopus partitus* Melander & Brues. **13–15.** *Dolichopus sincerus* Melander.

Remarks. Infected specimens of *D. sincerus* differ from normal specimens in having unusually small and incompletely rotated genitalia (cf. Figs 18, 19), a wider face with silver pruinosity (cf. Figs 13, 14), costa without or with at most indistinct enlargement at apex of R_1, abdominal sternite 2 with longer ventral hairs (similar to female), and in lacking a broad, lustrous, posterodorsal spur at apex of the hind tibia. Twenty-three normal males of *D. sincerus* were collected at the site with eight demasculinized male specimens.



FIGURES 16–19. Comparison of normal male of *Dolichopus* versus those infected by mermithid-like nematodes. **16.** Habitus of normal *Dolichopus partitus* Melander & Brues. **17.** Habitus of infected *D. partitus*. **18.** Habitus of normal *Dolichopus sincerus* Melander. **19.** Habitus of infected *D. sincerus*. Inset shows mermithid-like nematode removed from abdomen of *D. sincerus*.

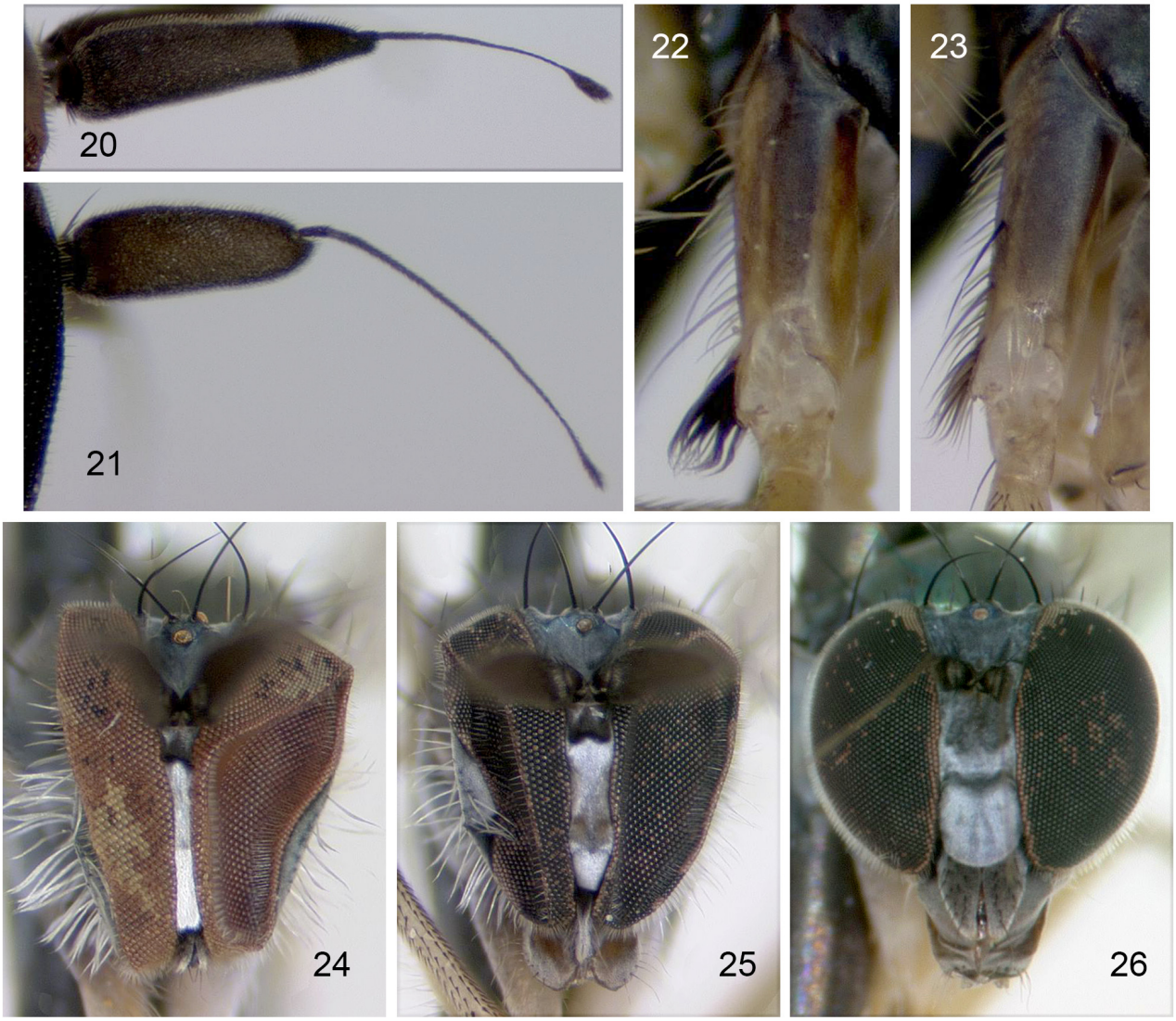
***Rhaphium signiferum* (Osten Sacken), 1878**
(Figs 20–26)

Rhaphium signiferum (Osten Sacken), 1878: 242.

Nematode. Apparent Mermithidae.

Demasculinized male examined. 1 ♂, USA, Pennsylvania, Centre Co., Black Moshannon State Park, Moss-Hanne Trail, Shirks Run, 580 m, 20 June 2007, JB Runyon (MTEC).

Remarks. The demasculinized specimen was initially thought to represent an undescribed species. Recognition that two species of *Dolichopus* from this site were infected by mermithid-like nematodes (*D. dorycerus* and *D. sincerus*) spurred re-examination that indicated this specimen to be a demasculinized form of *R. signiferum*, a common species at the site. The genitalia of the infected specimen is smaller and not fully centered beneath the abdomen. Most MSSCs are weakly developed in the infected specimen, including: postpedicel shorter with longer arista and smaller apical lamella (cf. Figs 20, 21), face broader (cf. Figs 24, 25), postocular setae scarcely flattened, mid coxa with poorly developed cluster of fused apical setae (cf. Figs 22, 23), weak development of longer white setae on front and mid femora, and smaller apical swelling of the front basitarsus.



FIGURES 20–26. Comparison of normal male of *Rhaphium signiferum* (Osten Sacken) versus male infected by mermithid-like nematodes, and female. **20.** Antenna, normal male. **21.** Antenna, infected male. **22.** Mid coxa (lateral view), normal male. **23.** Mid coxa (lateral view), infected male. Note reduced development of apical setae. **24.** Head of normal male. **25.** Head of infected male. **26.** Head of female.

Tachytrechus sanus Osten Sacken, 1877
(Figs 27–39)

Tachytrechus sanus Osten Sacken, 1877: 316.
Tetrechus spinitarsus Van Duzee, 1924: 43.
Tachytrechus boharti Harmston, 1968: 15, **syn. nov.**
Tachytrechus duplicatus Harmston, 1972: 157, **syn. nov.**
Tachytrechus mchughi Harmston, 1972: 156, **syn. nov.**

Nematode. *Parasitylenchus myiophagus* Poinar & Runyon (Parasitylenchidae).

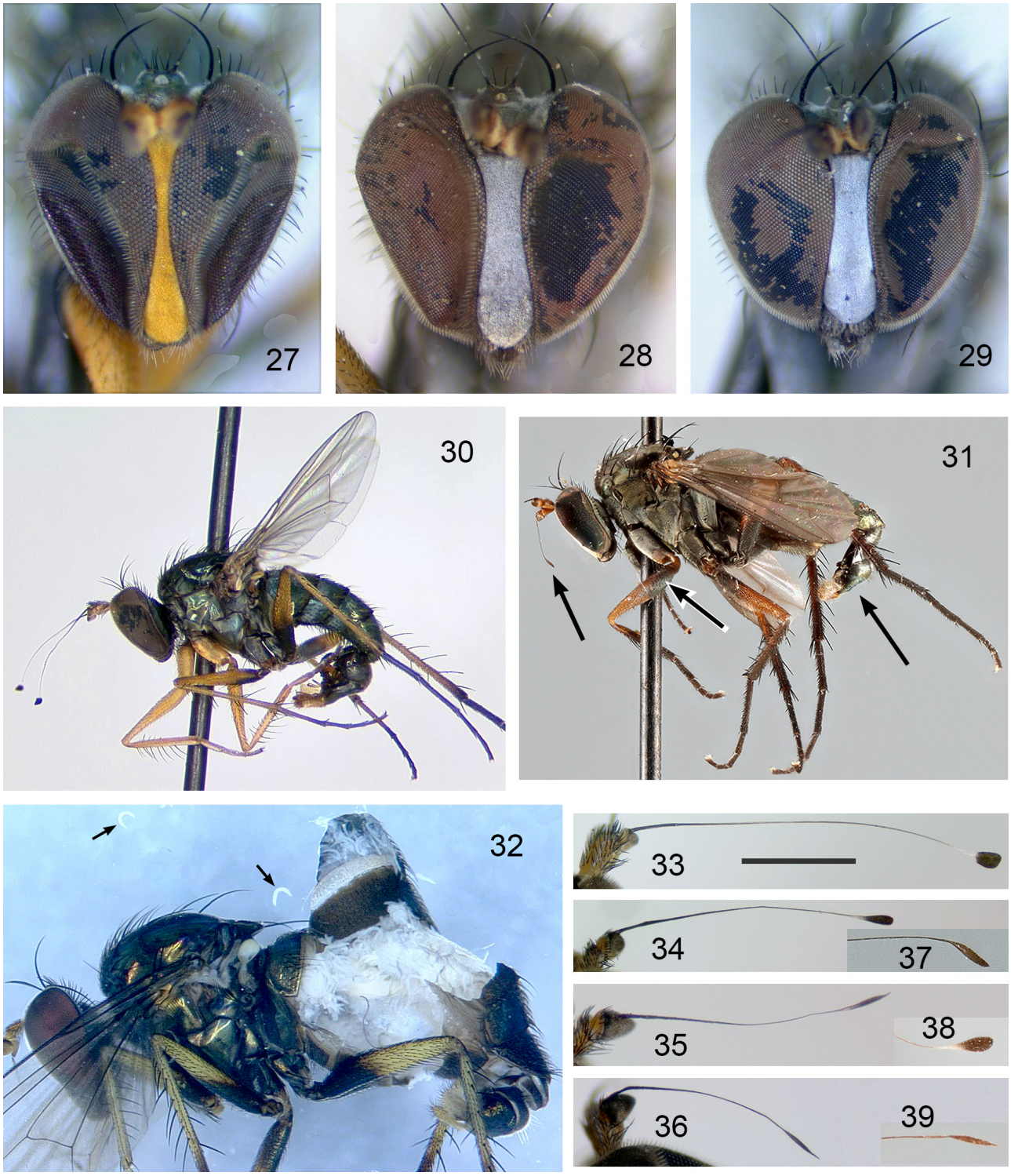
Demasculinized males examined. Holotype ♂ of *Tachytrechus boharti*, USA, California, Sierra County, Yuba Pass, 7 July 1964, RM Bohart (UCDC) [photos]; holotype ♂ of *Tachytrechus duplicatus*, USA, Oregon, Baker [City], 25 July 1965, FC Harmston (CAS) [photos]; holotype ♂ of *Tachytrechus mchughi*, USA, Oregon, Latourele [Latourell] Falls, 2 August 1962, RA McHugh (CAS) [photos]; 1 ♂, USA, California, Trinity County, Scott Mountains, Stoddard Mine, 7200 ft, 25 July 1981, DM Gordon (MTEC); 2 ♂, USA, Montana, Ravalli County, 0.8 km NW Skalkaho Pass, roadside seep, 18 August 2002, 7270 ft, R Hurley & J Runyon (MTEC); 4 ♂, USA, Montana, Gallatin County, Bridger Mountains, Johnson Canyon, large hillside spring, 30 July 2010, N45°57.73′ W111°01.61′, JB Runyon (MTEC).

Remarks. Demasculinized males of *T. sanus* are characterized by having: (1) a wider face that is light yellow to wholly silver (cf. Figs 27, 28), (2) arista shorter with reduced lamella, but arista length and size of lamella is variable (Figs 33–39), (3) legs darker: fore coxa mostly dark, all femora with approximately basal half dark brown, mid and hind tibiae brown on apical third or more (cf. Figs 30, 31), (4) the posterior row of setae on front tibia reduced in size (noticeably thickened and flattened in normal males) and usually in number (4–8 in infected versus 8–10 in normal males), (5) front tarsus lacking silvery pile, and (6) hypopygium unusually small and incompletely rotated (cf. Figs 30, 31). The darker legs are an interesting example of infected males converging with the female form. Females of *T. sanus* have wholly dark front coxae and mostly dark femora and tibiae, but these are mostly yellow in normal males. The characters above vary considerably across the infected specimens (especially the arista, extent of brown on legs, size and number of setae on front tibia, and size of the genitalia), perhaps related to the extent of nematode infection.

Harmston described *T. boharti* from one male collected at Yuba Pass, California noting that it is distinguished by the spear-shaped arista (Fig. 37). *Tachytrechus duplicatus* was described from one male collected at Baker, Oregon and *T. mchughi* from two males collected at Latourell Falls, Oregon. A close resemblance of both species to *T. boharti* was noted. Although the presence of nematode(s) within the holotypes of *T. boharti*, *T. duplicatus*, and *T. mchughi* have not been confirmed, synonymy with *T. sanus* is proposed based on: (1) demasculinized specimens of *T. sanus* match the descriptions of *T. boharti*, *T. duplicatus*, and *T. mchughi* (Harmston 1968, 1972), and (2) the holotypes each show signs of nematode-caused demasculinization that fall within the spectrum of variation caused by nematode-induced demasculinization of *T. sanus* (see above). Normal males of *T. sanus* were collected with demasculinized specimens at most sites, including four normal specimens with the *T. boharti* holotype (UCDC).

Suspected demasculinized species

The following potentially demasculinized species were gleaned from descriptions in the literature. Aside from photos of *D. bolsteri* Van Duzee, no specimens were examined. If a candidate infected species could be ascertained, the potential host is provided but should be viewed as tentative. These species are not synonymized here, pending additional evidence and/or confirmation of nematode infection. Nearly all of these species are known from only the male holotype and dissection of these unique specimens is probably unwarranted. Non-destructive techniques, like X-ray microtomography, have been used to verify mermithid nematodes within holotypes of ants (Csősz 2012), and might prove valuable for confirming nematode infection in these dolichopodid species. However, for several species listed below, even if nematode infection is confirmed the unparasitized species is unknown. In such cases, the host species might only be confidently known once demasculinized males are collected with normally developed counterparts. In fact, these species might only be described from demasculinized specimen(s), and in such cases the name is valid.



FIGURES 27–39. Effects of parasitism by parasitylenchid nematodes on males of *Tachytrechus sanus* Osten Sacken. **27.** Head of normal male. **28.** Head of infected male. **29.** Head of female. **30.** Habitus, normal male. **31.** Habitus, infected male (holotype of *T. boharti* Harmston). Note shorter arista (left arrow), darker front coxae and femora (middle arrow), and smaller genitalia (right arrow). **32.** Male with abdomen opened to reveal nematodes of *Parasitylenchus myiophagus* Poinar & Runyon. Note numerous nematodes in abdominal cavity. Arrows indicate two nematodes removed from abdomen. **33.** Male antenna, normally developed. **34–39.** Antennae of infected males, showing variation caused by nematodes. **34, 35.** Antennae of two infected males collected together in Ravalli County, Montana, USA. **36.** Antenna of infected male from Gallatin County, Montana, USA. **37.** Apex of arista, holotype of *T. boharti*. **38.** Apex of arista, holotype of *T. duplicatus* Harmston. **39.** Apex of arista, holotype of *T. mchughi* Harmston.

Dolichopus abbreviatus Van Duzee, 1921: 144

Potential infected species: unknown.

Dolichopus abbreviatus was described from two male specimens, one from Labrador, Canada and one from Maine, USA. The face is wide and the hypopygium is "remarkably short" with small cerci. Van Duzee remarked that *D. abbreviatus* is similar to *D. cuniculus* Van Duzee and *D. ramifer* Loew (Van Duzee 1921: 145). *Dolichopus cuniculus* is also potentially demasculinized (see below) and might prove synonymous with *D. abbreviatus*. *Dolichopus ramifer* is not likely to be the host species since both sexes have a stump vein (lacking in *D. abbreviatus*) and shiny bluish frons (green in *D. abbreviatus*), characters that are not expected to be altered by nematode infection.

Dolichopus beatus Van Duzee, 1921: 63

Potential infected species: *Dolichopus bisetosus* Van Duzee, 1921: 77.

Dolichopus beatus was described from one male collected at Craig Mountain, Idaho, USA. The male is described as having a wide face and a very small hypopygium that is "about the size of the fifth abdominal segment". Eight males of the putative host species, *D. bisetosus*, were also collected at Craig Mountain, Idaho. Both species belong to Group B of the North American species of *Dolichopus* (Van Duzee 1921) and differ in width of the face, size of the postabdomen, and extent of yellow on the middle femur (in *D. beatus* the femur is darker and more like the female which has black femora).

Dolichopus bolsteri Van Duzee, 1921: 249

Potential infected species: unknown.

Dolichopus bolsteri was described from one male collected at Little River, Newfoundland, Canada. The male is described having a wide face and rather short postabdomen with small cerci. Photos of the holotype male (MCZ, https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:7615) show clear signs of demasculinization: the hypopygium is characteristically small and poorly rotated (and in one photo can be seen projecting out to one side of abdomen).

Dolichopus brevicauda Van Duzee, 1921: 108

Potential infected species: *Dolichopus xanthocnemus* Loew, 1864b: 31.

Dolichopus brevicauda was described from one male from Mount Washington, New Hampshire, USA. The face is wide and hypopygium is small and not much larger than the cerci. *Dolichopus xanthocnemus*, also collected at Mount Washington, is possibly the infected species. *Dolichopus brevicauda* differs from *D. xanthocnemus* by the small genitalia with darker cerci, lack of yellow cilia on hind femur, and lacking a knot-like enlargement on the costa.

Dolichopus comptus Van Duzee, 1921: 160

Potential infected species: *Dolichopus hastatus* Loew, 1864b: 59.

Dolichopus comptus was described from one male collected near Lake Tahoe, California, USA. Van Duzee noted that this species is very similar to *D. hastatus* but differs in having a much shorter hypopygium with very much smaller cerci, a less enlarged lamella on the arista, and a less sinuous posterior margin of the wing. Illustrations of the arista (Van Duzee *et al.* 1921, figs 109a, b) suggest that the *D. comptus* arista could be a demasculinized form of the arista of *D. hastatus*.

Dolichopus cuniculus Van Duzee, 1921: 145 (= *Dolichopus remotus* Walker, 1849: 666)

Potential infected species: possibly *Dolichopus remotus*.

Dolichopus cuniculus was described from one male collected on Grand Island, New York, USA. This male has a short, rather slender hypopygium and Van Duzee commented "The name was suggested by the small hypopygium which reminded me of a rabbit's tail" (Van Duzee 1921: 146). The illustration of the apex of the abdomen and postabdomen (Van Duzee *et al.* 1921, fig. 98) shows a small and improperly rotated hypopygium that is characteristic of nematode infection.

Parent (1934) synonymized *D. cuniculus* with *D. remotus* but gave no justification. It is possible that types of both species are demasculinized. Van Duzee noted the similarity of *D. cuniculus* to *D. abbreviatus* (see above) and the widespread species *D. ramifer* (Van Duzee 1921: 145). *Dolichopus ramifer* is unlikely to be the host species since both sexes have a stump vein (lacking in *D. cuniculus*) and shiny bluish frons (green in *D. cuniculus*), characters not predicted to be affected by nematode infection. *Dolichopus abbreviatus*, on the other hand, could be synonymous with *D. cuniculus*.

Dolichopus imperfectus Van Duzee, 1921: 240

Potential demasculinized species: unknown.

Dolichopus imperfectus was described from one male collected in Illinois, USA. Although the face is "rather narrow", the hypopygium is unlike any other in *Dolichopus* being very small with what appears to be rudiments of cerci (Van Duzee *et al.* 1921, fig. 176). Such poorly developed genitalia could be caused by nematode infection.

Dolichopus sporadicus Harmston & Knowlton, 1942: 17

Potential infected species: *Dolichopus plumipes* (Scopoli, 1763: 334).

Dolichopus sporadicus was based on one male from Utah, USA. The male face is wide and the hypopygium is small with extremely small cerci. Harmston and Knowlton noted the similarity to *D. plumipes* (common in Utah) with *D. sporadicus* differing in lacking a fringe of setae on the middle basitarsus and having small genitalia. Demasculinized specimens of *D. plumipes* are reported from Europe and have twice been mistakenly described as new species (Kahanpää 2008).

Dolichopus tarsipictis Harmston & Knowlton, 1963: 236

Potential infected species: unknown.

Dolichopus tarsipictis was described from one male collected at Baker, Oregon, USA. Nematode infection is suggested by the wide face and hypopygium that is "small for the genus". Harmston and Knowlton noted similarities to several species in the *D. latipennis* species group (= *Hygroceleuthus* Loew) and to *D. cavatus* Van Duzee.

Dolichopus umbrosus Van Duzee, 1921: 100

Potential demasculinized species: unknown.

Dolichopus umbrosus was described from one male from Wisconsin, USA. Signs of nematode infection include the male having a wide face and a very small hypopygium with dark yellow cerci. Illustration of the genitalia (Van Duzee *et al.* 1921, fig. 57a) suggests they are not fully rotated and not centered beneath the abdomen. This species is

also reported from Ontario, Canada (Pollet *et al.* 2004). Dissection of material from Ontario could determine if this species is demasculinized and might identify the host species, if collected with the unparasitized counterpart.

Discussion

Nematode-induced demasculinization of dolichopodids is now documented to occur in four extant genera: *Dolichopus*, *Gymnopternus*, *Tachytrechus*, and *Rhaphium* (Kahanpää 2008; Germann *et al.* 2010). A dolichopodid in Baltic amber (probably *Gheynia* Meunier) parasitized by tylenchid nematodes shows that nematode-dolichopodid associations are ancient (Poinar & Brown 2021). This phenomenon has been reported only from the Nearctic and Palearctic regions, but could occur in other biogeographic realms given the cosmopolitan distribution of insect parasitic nematodes (Poinar 1975). Nearly all confirmed cases of demasculinization are caused by nematodes that appear to be in the family Mermithidae, the exception being a species of Parasitylenchidae affecting *Tachytrechus sanus* in the Nearctic (Poinar & Runyon 2021). Nematodes from both families have similar effects on the morphology of male dolichopodids (Table 1).

Demasculinized Dolichopodidae are rarely collected. The rarity of demasculinized specimens could be due to parasitism itself being uncommon and/or that infected specimens are rarely collected (e.g., if parasitism increases mortality, shortens adult lifespan, or changes host behavior). Of the estimated 20,000 male dolichopodid specimens examined in this study, just eighteen showed signs of demasculinization. In Finland, 49 of 6,226 specimens of *Dolichopus* collected from boreal fens and bogs were demasculinized and infected with mermithid-like nematodes (Kahanpää 2008). Most known cases of demasculinization involve specimens of *Dolichopus*. This could be because species of *Dolichopus* are more prone to nematode infection than other genera or that these species are common, relatively large, and display recognizable signs of infection. Some *Dolichopus* species appear to be more susceptible to nematode infection than others. For example, eight species of *Dolichopus* were common at the Black Moshannon State Park site in Pennsylvania, USA, but only specimens of *D. dorycerus* (1 of 13 males) and *D. sincerus* (8 of 23 males) were demasculinized. Some Palearctic species of *Dolichopus* also appear to be more prone to infection by mermithid-like nematodes (Kahanpää 2008). Nematode infection is only reported for larger-sized dolichopodids (> ca. 5 mm). Smaller dolichopodids might escape parasitism if a minimum host size is required for development of nematodes (especially relatively large mermithids), or infection may be less noticeable in subfamilies without large, exposed male genitalia or prominent MSSCs. No nematode-infected female dolichopodids have yet been found. It is likely that females are parasitized, but lack obvious outward signs of infection, as is reported for infected females of Ceratopogonidae (Muñoz-Muñoz *et al.* 2016) and Chironomidae (Wülker 1964).

Since demasculinized dolichopodid specimens are uncommon, taxonomic problems caused by nematode infection appear to be uncommon. In Nearctic *Dolichopus*, two synonyms are proposed herein, and examination of the literature suggests that ten additional names might be based on demasculinized specimens. If all ten names prove to be described from infected specimens, this would represent slightly less than 4% of all valid Nearctic species of *Dolichopus*. In Nearctic *Tachytrechus*, three of 38 names (8%) are due to nematode demasculinization. All three of the nematode-induced names in *Tachytrechus* are the result of nematode demasculinization of *T. sanus*. This is perhaps because *T. sanus* is common in western North America, is apparently more commonly infected than other species (i.e., demasculinized males collected at multiple sites in California, Montana, and Oregon), and external morphological effects caused by infection is highly variable. A similar situation occurred in the Palearctic in which multiple names were created for infected specimens of three *Dolichopus* species (Kahanpää 2008), due to the variable effects nematodes have on hosts. Species based on demasculinized specimens can explain some of the once-only-found taxa in Dolichopodidae.

Recognizing signs of nematode infection in male Dolichopodidae is important to avoid erroneous species descriptions. Characteristics of nematode infection in male Dolichopodidae are provided in Table 1. Non-morphological clues of potential nematode infection include species for which only one specimen is known, and infected specimens are likely to be collected with their normally developed counterparts (i.e., assuming only a small percentage of adults in a population are infected and demasculinized). Habitat might also be important because all confirmed dolichopodid specimens infected with mermithid-like nematodes have been found in fens and bogs (Kahanpää 2008) and *Tachytrechus sanus* infected with *P. myiophagus* were found in boggy seeps/springs with abundant moss. Taxonomic problems can be avoided if specimens displaying signs of demasculinization are dissected to determine if they contain nematode(s) prior to description.

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