Description and Bionomics of *Mesomermis camdenensis* n. sp. (Mermithidae), a Parasite of Black Flies (Simuliidae)[1]

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Abstract: Mesomermis camdenensis n. sp. is described from larvae of *Simulium tuberosum* (Lundstroem) collected in Camden Valley Creek, Washington County, New York. This species possesses a barrel-shaped vagina, vulval flap, two short separate spicules, terminal mouth, six longitudinal chords, six cephalic papillae, large sexually dimorphic amphids, an esophagus of uniform width which extends for less than one-third of the body length, and a cone-shaped tail directed ventrally without appendage. Juveniles also are described and illustrated.

A detailed morphological comparison with the mermithid *M. flumenalis* Welch is presented. The most pronounced morphological differences between these species are in the shape of the vulva, juvenile tail, and infective stage. Cross-mating trials support the integrity of the new species.

The life cycle of *M. camdenensis* is closely synchronized with that of its primary host, *S. tuberosum* larvae. Infected *S. tuberosum* larvae were first collected in May. Emergence of postparasites from late instars took place from mid-June through mid-October. Sampling data indicate a lower susceptibility to infection among *S. venustum* Say larvae. *Key Words:* taxonomy, bionomics, *Mesomermis* spp., *Simulium tuberosum*.

In his taxonomic review of the Mermithidae, Nickle (8) considered *Mesomermis* as a *genus inquirendum* and designated the black fly parasite *M. flumenalis* Welch, 1962 as type species of the new genus, *Neomesomermis*. The generic description of *Neomesomermis* was later emended (5). This author, however, still recognizes the validity of *Mesomermis*. Although Daday's (4) original description of *Mesomermis* in 1911 is scant, Welch (16) gave a thorough redescription of the genus in 1962. Many of the early original descriptions of mermithid genera (e.g., *Paramermis, Hydromermis, Limnomermis*) are similarly weak. Substituting another name for one that has already been redefined and in use is considered inappropriate.

This paper describes a new species of *Mesomermis* from an eastern New York population of black flies and provides additional information on the bionomics of this species. Comparison with the closely related North American species *M. flumenalis* is also given.

METHODS AND MATERIALS

Taxonomy: Simulium tuberosum (Lundstroem) larvae infected with *M. camdenensis* were collected from Camden Valley Creek, Shushan, New York, during July and August, 1975. Some black fly larvae were immediately dissected and the parasitic juvenile morphology studied, while others were held in aerated aquaria at 12(±1/2)C for emergence and collection of nematodes. Postparasites were pipetted from the aquaria, transferred in groups of 10 to plastic dishes (V = 8 cm^3) containing sand overlaid by streamwater, and incubated at 12(±1)C. Adults, eggs, and preparasites were obtained with this method.

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Mermithids were heat-killed in distilled water, fixed in an aqueous solution of 3% formalin and 2% glycerin, and then processed to glycerin by modification of the technique of Saunders and Norris (15) (i.e., because of their size, nematodes were left in each solution for at least twice the recommended period). Histological sections for longitudinal chord determination were made by fixing in Bouin's fluid, passing them through an alcohol series to paraffin, sectioning at 10 μm, and staining with Mallory's triple stain. *En face* mounts were prepared after Buhrer (1). Taxonomic observations were made under the light microscope. Nematodes were prepared for scanning electron microscopy by critical-point drying with liquefied CO_2 and coating with gold palladium.

Cross-mating trials between a Rensselaerville, N.Y., population of *M. flumenalis* and the Camden Valley Creek population of *M. camdenensis* were conducted in 1975. The nematodes used in these trials had emerged in mid-April and early July 1975, respectively, and their virginity was guaranteed by their sexual isolation during subsequent laboratory rearing. Plastic rearing dishes (described above) served as the mating chambers, each containing three males of one species and a female of the other. Fourteen such dishes were used to cross the two species. Five control dishes were also maintained for each species. Dishes were incubated at 12(±1)C and examined for copulation and egg production at least every three weeks for 6 months.

Bionomics: From 1973 through 1976 (primarily May through September of each year) over 4,000 larvae and 600 pupae (primarily *S. tuberosum* and *S. venustum* Say) were collected from Camden Valley Creek and examined for parasites. From these sampling data emerged a general understanding of host-parasite life cycle synchrony and the incidence of infection. The rearing of *M. camdenensis* nematodes for taxonomic purposes (as described above) also provided an opportunity to obtain data on the biology of the free-living stages of this mermithid. Fifteen rearing dishes containing five males and five females each were checked every four days, and oviposition and preparasite hatching recorded.

RESULTS AND DISCUSSION

I. Taxonomy

Mermithidae Braun, 1883

Mesomermis camdenensis n. sp.

Holotype female: L = 9.4 mm; W at vulva = 0.156 mm; amphidial pouch W × L = 8.8 × 11.0 μm; amphidial pore W × L = 8.8 × 6.6 μm; distance from anterior end to nerve ring = 0.207 mm; V = 51%; vulval flap L = 40 μm; vagina L = 66 μm.

Paratype females (n = 10): L = 10.6 (8.1–14.2) mm; amphidial pouch W × L = 9.9 × 10.8 (8.8–11.0 × 9.2–11.2) μm; amphidial pore W × L = 8.2 × 6.2 (7.7–8.6 × 4.4–6.8) μm; distance from anterior end to nerve ring = 0.200 (0.180–0.222) mm; W at vulva = 0.162 (0.131–0.194) mm; V = 52 (48–56)%; vulval flap L = 43 (33–55) μm; vagina L = 73.7 (66.0–81.4) μm.

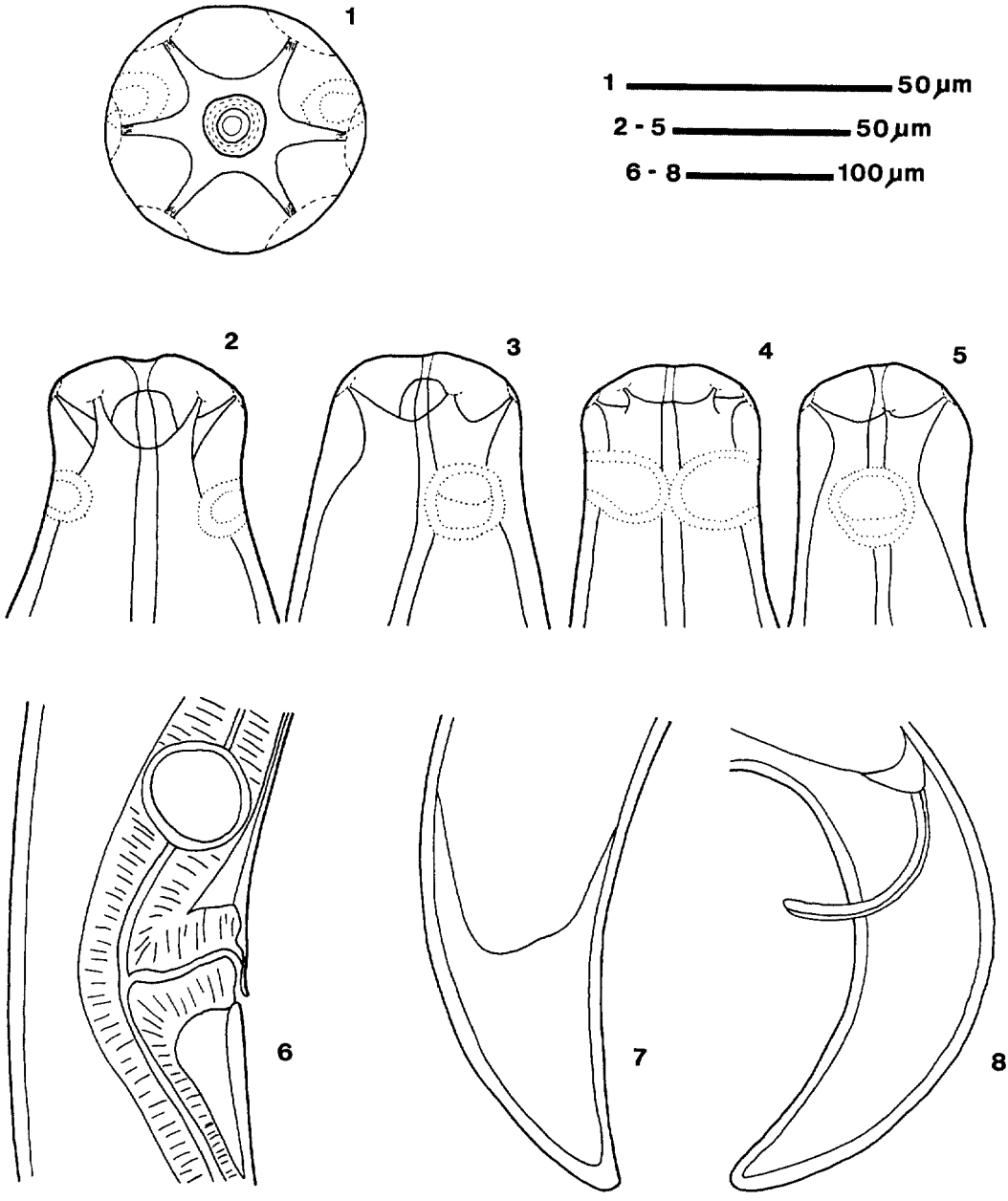
Allotype male: L = 8.5 mm; W at midbody = 0.084 mm; amphidial pouch W × L = 19.8 × 17.6 μm; amphidial pore W × L = 19.8 × 13.2 μm; distance from anterior end to nerve ring = 0.194 mm; tail length = 0.216 mm; spicule L × W (lateral view) = 169.0 × 6.6 μm.

Paratype males (n = 10): L = 8.2 (7.3–9.5) mm; W at midbody = 0.086 (0.081–0.108) mm; amphidial pouch W × L = 18.9 × 18.9 (15.4–20.9 × 16.5–22.0) μm; amphidial pore W × L = 18.5 × 12.7 (15.4–19.8 × 11.0–15.4) μm; distance from anterior end to nerve ring = 0.186 (0.154–0.205) mm; tail length = 0.228 (0.209–0.246) mm; spicule L × W (lateral view) = 167.0 × 8.0 (154.1–189.0 × 6.6–8.8) μm.

Description:

Adults: Cross fibers lacking; mouth terminal in cone-shaped depression, not displaced; trophosome white; six longitudinal chords; six cephalic papillae; amphids large and sexually dimorphic, without a commissure; esophagus of uniform width and extending for less than one-third of the body length; cone-shaped terminus directed ventrally; no caudal appendage.

Adult females (Figs. 1, 2, 3, 6, 7, 9): Amphidial pouch rounded to oblong (rarely globular) with globular pore; vagina short, barrel-shaped, lying at 30 to 45 degrees to the transverse body axis; vulval flap directed posteriad; vulval lips do not protrude; lateral chords about one-third body

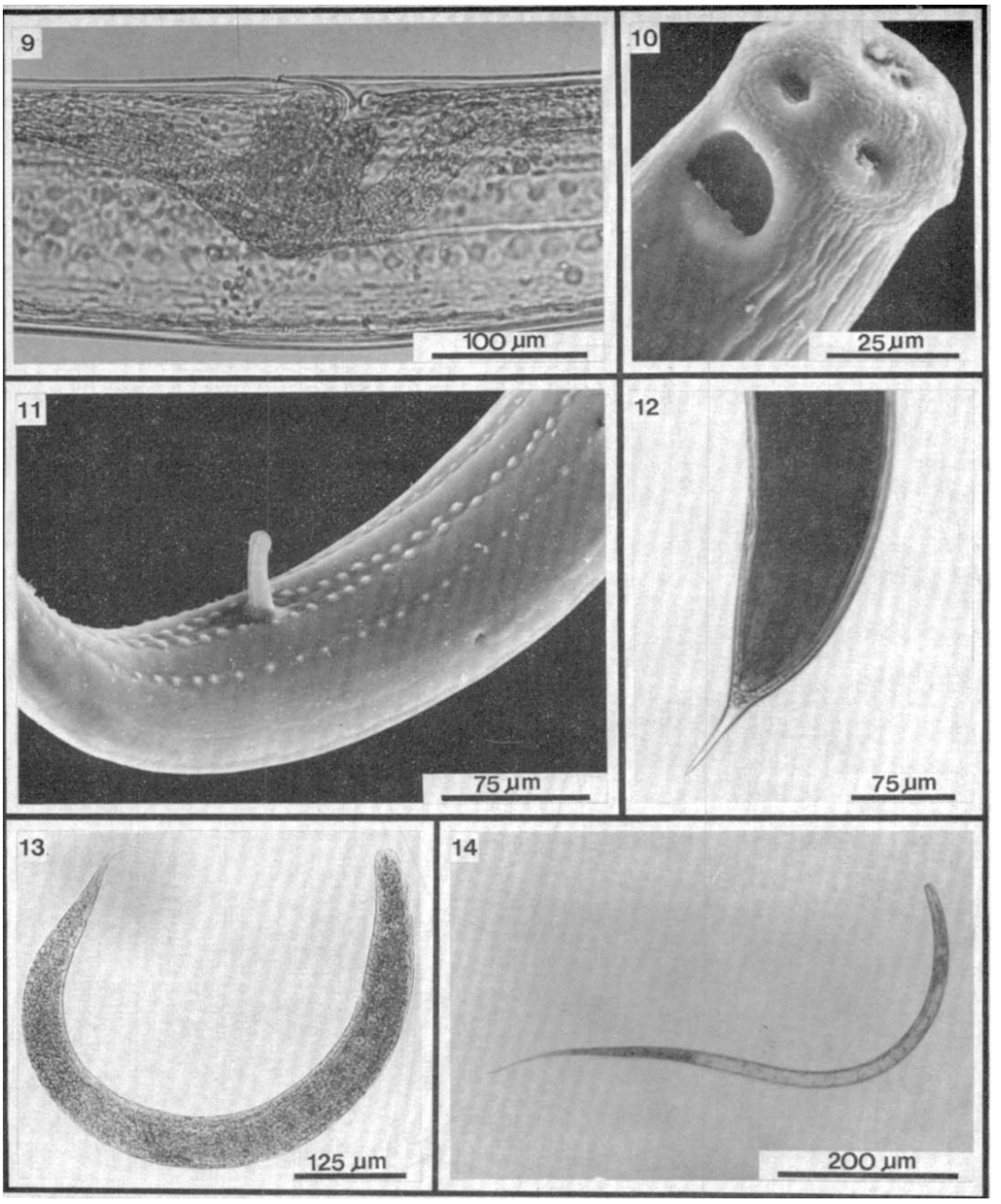


FIGS. 1–8. *Mesomermis camdenensis* n. sp. adults. 1) *En face* view of female. 2) Female head, dorsoventral view. 3) Female head, lateral view. 4) Male head, dorsoventral view. 5) Male head, lateral view. 6) Vagina with egg in oviduct, lateral view. 7) Female tail, lateral view. 8) Male tail, lateral view.

width at midbody and composed of three cell rows throughout most of the body length.

Adult males (Figs. 4, 5, 8, 10, 11): Amphidial pouches globular to oblong with elliptical pores; two short separate spicules, shafts parallel sided, tips smoothly rounded, curved in slight reflex; tail papillae in three single well-defined rows, center row bifurcating around cloaca; tail tip more pointed than in female; lateral chords about one-third body width at midbody and composed of two irregular cell rows with traces of a third interposed between them throughout most of the body length.

Postparasites (Fig. 12): Body size and shape similar to adult but with medium length digitate tail appendage (L[n = 10]



FIGS. 9–14. *Mesomermis camdenensis* n. sp. 9) Adult female vagina, lateral view. 10) Adult male head, lateral view. 11) Adult male tail with extended spicules, lateral view. 12) Postparasitic female tail, lateral view. 13) Early parasitic stage. 14) Preparasitic stage.

= 64[53–73] µm) with pointed tip; trophosome white.

Parasitic juveniles (Fig. 13): Size and shape dependent on stage of development; the digitate caudal appendage possessed in mid-to-late stages similar to that of postparasite; early parasitic juveniles closely resemble preparasites.

Preparasites (Fig. 14): L (n = 5) = 683 (625–775) µm; W at midbody (n = 5) = 15.8 (15.4–16.5) µm; head with well-developed stylet; cauda tapers to fine tip.

Eggs (Fig. 6): *In situ* variable in shape; when first laid, spherical, with diameter (n = 10) = 72 (70–73) µm; unornamented, but covered with thin gelatinous substance.

Type locality: Camden Valley Creek, Washington County, New York, USA; 45°06'N and 73°18'W.

Type host: Simulium tuberosum (Lundstroem) larvae.

Other host: Simulium venustum Say larvae.

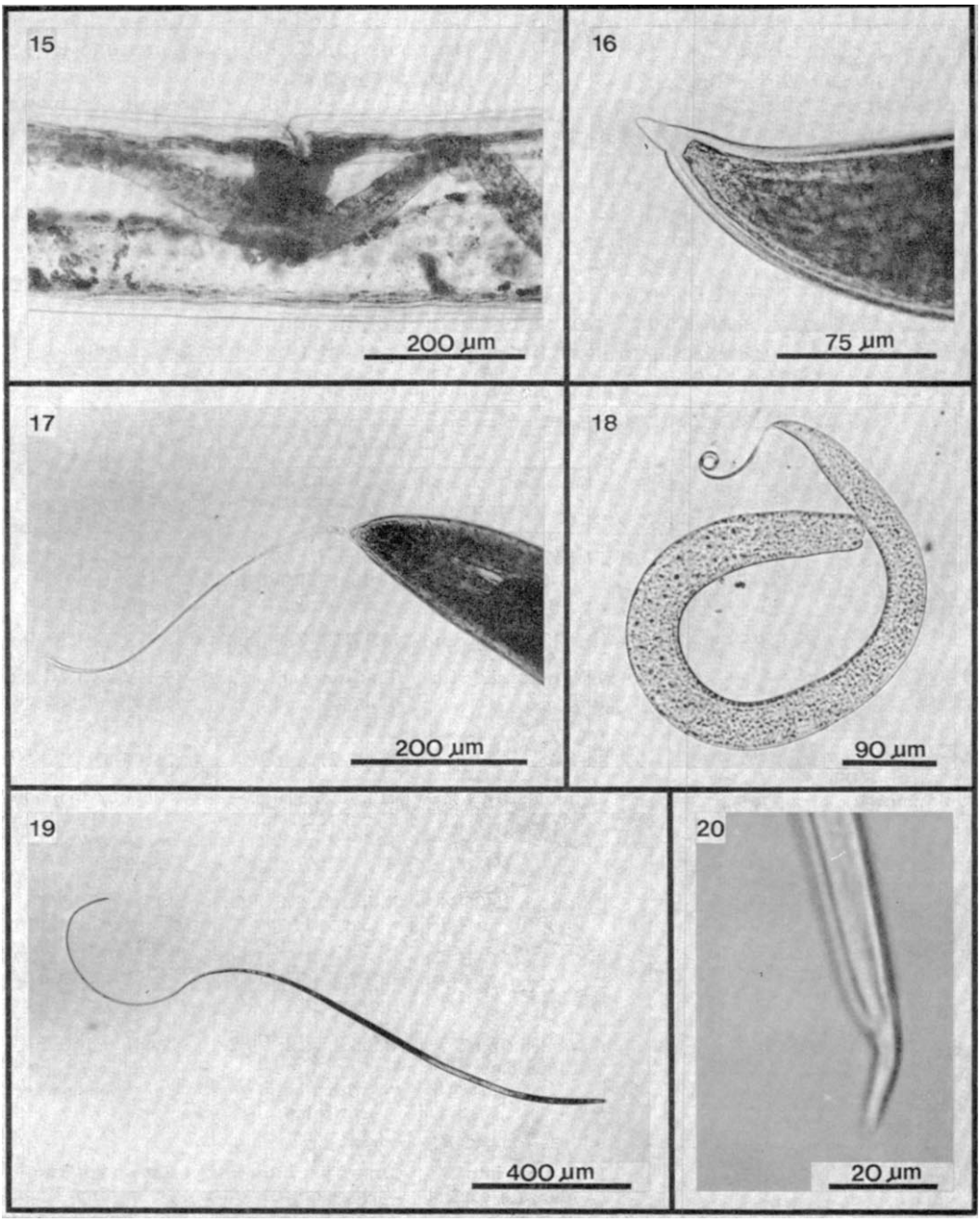
Deposition of type material: The holotype (Catalog No. 35036) and the allotype (Catalog No. 35037) plus two paratypes of each sex (Catalog Nos. 35038–35041) are deposited in the New York State Museum Collection, Albany, New York. Two paratypes of each sex are also deposited at the following institutions: Canadian National Nematode Collection, Ottawa, Ontario; University of California Nematode Collection, Davis, California; USDA Nematode Collection, Beltsville, Maryland; Zoological Institute, Academy of Sciences, Leningrad, USSR.

Diagnosis (Table 1): Adults of *M. camdenensis* closely resemble those of *M. flumenalis*. *M. camdenensis* females differ from *M. flumenalis* by the possession of a distinctive vulval flap, shorter vagina and body length, and rounded to oblong amphidial pouch (Figs. 6, 9, 15). The males of

TABLE 1. Comparison of characters useful in separating *Mesomermis* spp.[a]

Life stage	Character	*M. flumenalis*[b]		*M. camdenensis*
		Welch 1962	Ebsary and Bennett 1974	
Adult females	Amphidial pouch (W × L)	Globular, 20–23 × 13–17	Globular, 12.5 (12–16) × 10.0 (7–15)	Rounded to oblong, 9.9 (8.8–11.0) × 10.8 (9.2–11.2)
	Body length	18.0 (10.2–18.0) mm	13.0 (11.1–17.8) mm	10.6 (8.1–14.2) mm
	Vulva	Transverse slit with lips	Transverse slit with lips	Distinct vulval flap with length of 43 (33–55)
	Vaginal length	80–100	85 (77–97)	74 (66–81)
Adult males	Amphidial pouch (W × L)	Ellipsoid, 26–28 × 17–19	Ellipsoid, 30.0 (27–32) × 20 (17–27)	Globular to oblong, 18.9 (15.4–20.9) × 18.9 (16.5–22.0)
	Amphidial pore (W × L)	Elliptical, 21–26 × 6–8	Elliptical, 27.5 (25–32) × 12.5 (7–17)	Elliptical, 18.5 (15.4–19.8) × 12.7 (11.0–15.4)
	Spicule (W × L)	— × 230.0	10.3 (10–12) × 222 (200–242)	8.0 (6.6–8.8) × 167.0 (154.1–189.0)
Postparasites	Caudal appendage	A swollen tip of cone shape	Cone-shaped; sometimes tipped with a long cuticular filament	Medium length (52–95) digitate appendage
Parasitic juveniles	Cauda	Drawn out into elongate, conical terminus	Drawn out into long caudal appendage	Drawn out into medium length digitate appendage
Preparasites	Body length	—	1.07 (1.04–1.28) mm	0.68 (0.63–0.78) mm
	Cauda	—	Long whiplike with characteristic tip	Short with a simple pointed tip
Eggs	Size	—	89.5 (85.0–93.8) × 78.0 (75.0–81.3)	72 (70–73)

[a]Measurements in micrometers unless indicated otherwise.
[b]*M. flumenalis* from New York State do not differ significantly from those cited in this Table.



FIGS. 15–20. *Mesomermis flumenalis*. 15) Adult female vagina, lateral view. 16) Postparasitic female tail, lateral view. 17) Late parasitic stage tail, lateral view. 18) Early parasitic stage. 19) Preparasitic stage. 20) Curved apical tail tip of preparasitic stage.

M. camdenensis differ in having a smaller spicule (length and width) and not exhibiting ellipsoid amphidial pouches. Ross and Smith (9) found that the ratio of total body length to spicule length was a valuable diagnostic feature in separating *Romanomermis* spp. Such ratios, computed from data of Welch (16) and Ebsary and Bennett (5), are respectively 41 and 43. The ratio for the type specimens of *M. camdenensis* is 49 (43–60).

The caudal appendage of postparasitic and parasitic *M. camdenensis* juveniles (Figs. 12, 13) contrasts sharply with *M.*

flumenalis (Figs. 16, 17, 18). *M. camdenensis* preparasites (Fig. 14) are smaller and lack a long cauda and curved apical tail tip as in *M. flumenalis* (Figs. 19, 20). Eggs of *M. camdenensis* are also smaller.

The above-mentioned adult and juvenile characteristics distinguish *M. camdenensis* from other *Mesomermis* spp. (2, 7, 9–14).

Interspecific mating: The cross-mating trials with *M. flumenalis* supported the integrity of this new species. The proportions of females producing fertilized eggs were: *M. camdenensis* controls (3/5), *M. flumenalis* controls (5/5), and crosses (0/14). Although mating was not observed between species, some *M. camdenensis* females in dishes with *M. flumenalis* males did exhibit ovarian development somewhat resembling that of fertilized females; no eggs were laid, however.

II. Bionomics

The life cycle of *M. camdenensis* is closely synchronized with that of its primary host, *S. tuberosum*. Larvae of this simuliid species are present in Camden Valley Creek from May through October, with population densities highest in July. Hatching of *M. camdenensis* preparasites occurs from the end of May through mid-September, as evidenced by very-early-stage parasitic juveniles within *S. tuberosum* larvae during that period. Infection rates of 10% in June, 25% in July, and 10% in August are typical among *S. tuberosum* larvae throughout the stream. *S. venustum* also has a high-density population in Camden Valley Creek during June and early July, yet infection of larvae of this species by *M. camdenensis* was $< 1\%$ (6/860). Of the *Simulium* spp. pupae (primarily *S. tuberosum*) collected, $< 0.5\%$ (3/623) contained *M. camdenensis* nematodes. The rarity of pupal infection was not surprising, since infected late instars were seldom seen to have histoblast development. *Prosimulium* spp. larvae, which occur at a relatively low density from November through May, were never found to be parasitized by *M. camdenensis* (0/223).

From a comparison of infection rates, larvae of *S. tuberosum* appear to be more susceptible to *M. camdenensis* infection than do *S. venustum* larvae. Susceptibility to mermithid infection differed similarly in a field trial with *M. flumenalis*, in which rates of infection were markedly higher for *S. venustum* than for *S. vittatum* Zett. larvae (6).

The effect of mermithid parasitism on black fly metamorphosis differs between *M. camdenensis* and *M. flumenalis*. While pupae and adults (primarily *S. venustum*) infected with *M. flumenalis* were collected in Camden Valley Creek, *M. camdenensis* was almost invariably found only in larval black flies. This inhibition of pupation as a result of mermithid infection occurs similarly in other hosts (e.g., mosquitoes parasitized by *R. culicivorax* [8]). Physiological mechanisms responsible for such a disturbance in host development are reviewed by Condon and Gordon (3). They suggest that prevention of pupation in mermithid-infected black flies is probably a result of host nutrient depletion, not of active manipulation of the host's hormonal system by the parasite.

The laboratory rearing of *M. camdenensis* was successful. The first signs of oviposition were noted six weeks after emergence, with eggs beginning to hatch in about another six weeks. Preparasites could be observed within the water of the rearing containers; they were typically less active than *M. flumenalis* preparasites, only infrequently wriggling and moving through the water. Further observation after four months of rearing was prevented by high nematode mortality due to an incubator malfunction. Until that time, however, adults continued to mate and oviposit.

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