A Contribution to our Knowledge of the Mermithidae (Nematoda)

W. R. NICKLE[1]

Abstract: The genera of the insect parasitic nematode family Mermithidae are reviewed, and 16 of them are redescribed and illustrated. Information is given on methods of rearing adult mermithid specimens and on host specificity. The four types of mermithid life cycles are described in detail. One figure shows the variety of insects parasitized by mermithids and the location and size of the nematode within the insect. Several mermithid eggs are illustrated, and their usefulness in identification is discussed.

Taxonomically, the primary emphasis is on the adult stages of the mermithids with larval and egg characteristics supplementary. An emended family diagnosis is given. *Mermis subnigrescens* is considered a synonym of *M. nigrescens*, and *M. tahitiensis* is synonymized with *M. mirabilis. Hydromermis contorta* is accepted, leaving the genus *Paramermis* in an uncertain position. Study of the Steiner collections of *Limnomermis bathybia* indicates that *Limnomermis* is accepted as a valid genus. The adults of *Agamermis decaudata* are described and illustrated for the first time. The genus *Gastromermis* is limited to the long single-spiculed forms, as it is now apparent that five or more genera have ventrally shifted mouth orifices. *Amphimermis tinyi* n. sp. is described from damselflies from Louisiana. The genus *Lanceimermis* is accepted, and three species in this genus are illustrated. The taxon *Reesimermis nielseni* has been accepted for this important parasite of more than 20 mosquito species. This nematode previously has been referred to as *Romanomermis* sp. *Romanomermis iyengari* is transferred to the genus *Reesimermis. Diximermis peterseni* n. gen., n. sp., from anopheline mosquitoes, is described and illustrated. The adults of *Agamomermis culicis* which parasitize *Aedes sollicitans*, are described for the first time, and the species placed in a new genus, *Perutilimermis*. The new genus *Neomesomermis* is proposed for *Mesomermis flumenalis* Welch, 1962. Several problems on mermithid morphology and taxonomy are discussed. Type material is established for some of the taxa. *Key words:* insect parasites, review, taxonomy, life cycles, host ranges.

The Mermithidae is a family of nematodes parasitic in many kinds of insects, spiders, leeches, crustaceans, nematodes, and other invertebrates throughout the world. Insects are by far the most common hosts of mermithids which attack at least 15 different orders of insects. Parasitism by a mermithid is usually fatal to the host. Mermithid larvae are usually found in the body cavities of all stages of susceptible insect species. The nematode parasite undergoes several molts within the insect body cavity, taking nourishment from the insect's blood, and increases in length from about 0.5 mm to 10.0 mm or more. It is not unusual to find mermithids 20-50 cm in length inside insects. Epizootics of insects, caused by mermithid parasitism, occur; and population levels of blackflies, mosquitoes, chironomids, grasshoppers, walkingsticks, ants, certain lepidopterans, and other insects are held down by these self-perpetuating biological control agents. Workers interested in the pathologies and epizootics of insects caused by mermithids are referred to my chapter (36) in the new *Textbook of Insect Pathology* (Marcel Dekker, Inc.), G. E. Cantwell [ed.].

There are over 50 nominal genera in the family Mermithidae. Many are poorly and inadequately described, as they are based on a larva, or on a single male or female found in a lake or in the soil with no host information. Quite often these early descriptions have led to a considerable amount of guesswork and subsequent instability.

The main purpose of this paper is to describe or redescribe 16 of the more important and better known genera of the Mermithidae. The descriptions and redescriptions are based mainly on specimens in the USDA Nematode Collection, Beltsville, Maryland, or specimens collected by the author or loaned by other scientists. Some of the other 34 described genera are also valid, but were unavailable for this study. I have used the paper by Hagmeier (23) as the base for my work. He brought together the mermithid taxonomy in a form useful to us, and his taxonomic handling of this group has made his paper a classic work in mermithid taxonomy. The taxonomy of the other family in the Mermithoidea, the Tetradonematidae, is not considered here as this group has recently been reviewed (35).

The first reference to what was probably a mermithid was in 1747 by Gould (22). He found these worms in *Lasius flavus* (F.) and

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[1] Plant Science Research Division, Agricultural Research Service, U.S. Department of Agriculture, Beltsville, Md. 20705. The writer thanks Drs. J. J. Petersen and H. C. Chapman of the Entomology Research Division, Lake Charles, La., for sending me their mermithid material. The use of the USDA Nematode Collection and the technical assistance of Mrs. Patricia A. Pilitt are appreciated.

called attention to their lethal effect on ants. A quote here of the paragraph from this rare book is as follows: "Amongst other incidents that tend to lessen and destroy ant-flies, it is observable that abundance of them are demolished by a white and long kind of worm, which is often met within their bodies. You may frequently take three from the insides of the large, but seldom more than one from the small ant-fly. These worms lie in a spiral form, and some may be extended half an inch." In 1782, Goeze (21) apparently found some nematodes which were probably *Mermis nigrescens* Dujardin, 1842: "In June of 1781 after a hard rain storm, they were widely distributed in the garden in the newly dug flowerbeds and wound or coiled by the hundreds like thin filaments around the boarder of boxwoods."

Bremser (4), in his *New Atlas of Intestinal Worms*, records Leblond's discussion of the findings of Audouin concerning the mermithid-like worm found in considerable quantity in larval cockchafers (May, June beetles) in France. Dujardin (18) very adequately described the first species, *Mermis nigrescens*, distinguishing it from *Gordius*. This distinction was significant because it solved one of the taxonomic problems of that period. He found material in flowerbeds after a rain in France. Dujardin (19) described two aquatic nematodes, and though he said that they resembled *Mermis* he placed them in the genus *Filaria*. Bugnion (5) found this same nematode, apparently with two spicules, in the chironomid, *Tanypus nebulosus* Meigen, according to von Linstow (31). Von Linstow (31) described the genus *Paramermis* as having only one spicule, whereas the members of the genus *Mermis* have two spicules. He placed (30) two species, *Mermis crassa* von Linstow, 1889, and *Mermis aquatilis* Dujardin, 1845, in his new genus and later designated *P. crassa* as type species. *P. crassa* was parasitic in *Chironomus plumosus* (L.) and other insects. In 1902, Corti (16) set up the genus *Hydromermis*, for *H. rivicola*, also from a nematode specimen taken from a chironomid. Later workers have decided that this nematode is synonymous with von Linstow's *M. contorta*, and have recognized the pointed-tailed adults of *H. rivicola* as the basis for the taxon *H. contorta*. Stiles (55) set up the genus *Agamomermis* for larval mermithids. The genera *Pseudomermis* de Man, 1903, in Zykov (60) and *Neomermis* von Linstow, 1904 (32) have not received much support.

Daday (17) described four genera of aquatic mermithids: *Limnomermis, Bathymermis, Mesomermis,* and *Eumermis. Limnomermis bathybia* Daday, 1911, is the blunt-tailed mermithid from chironomids that has wide distribution in Europe. *Bathymermis fuhrmanni* Daday, 1911, is very short and cigar-shaped. *Mesomermis zschokkei* Daday, 1911, was described from a male taken from a lake with no host data, and should be set aside, as this is not sufficient information to differentiate this genus. *Eumermis* Daday, 1911, has not received much support.

The best early work on mermithid taxonomy was done by Hagmeier in 1912. The quality of his drawings was excellent. Most workers, including the writer, recognize this paper as a classic reference and the basis for their work.

The three genera described by Cobb (11), *Bolbinium* Cobb, 1920, *Colpruella* Cobb, 1920, and *Nanomermis* Cobb, 1924, were not sufficiently described (12).

A classic life history study was done by Christie (10) on the mermithid, *Agamermis decaudata* Cobb, Steiner, and Christie, 1923. Adults of this nematode (13) were never described and are described herein.

Steiner (50) described two larvae as *Hexamermis acuminata*, and set up the genus *Hexamermis* on this basis. Later workers decided that *H. acuminata* was the same as *Mermis albicans* von Siebold, 1848, but gave Steiner credit for the genus *Hexamermis*.

The genus *Allomermis* was described by Steiner in 1924 (49) from specimens taken from soil in Jamaica. Morphologically, this genus is quite distinct from other genera, but no host information is available.

Micoletzky (33) grouped all mermithids with ventrally shifted mouth openings into his new subgenus *Gastromermis*. It appears now that this ventral shifting is common in many diverse mermithids, and cannot be used in this restrictive sense. *Gastromermis* is limited here to the long single-spiculed forms such as *G. haempeli.*

Tetramermis Steiner, 1925 (52), *Eomermis* Steiner, 1925 (51), and *Octomermis* Steiner, 1929 (53), are insufficiently described. Müller's drawings and descriptions (34) of *Eurymermis* and *Megalomermis* from *Chrysops* Meigen and *Melolontha* Fab. in Germany leave some doubts

as to their identity, and they need to be redescribed.

Though Hagmeier (23) had described *Mermis elegans* as having two long twisted spicules, it was not until 1932 that Kuburaki and Imamura (27) based the genus *Amphimermis* on this character. Filipjev (20), not knowing of the Japanese work, set up *Complexomermis* for the mermithids with long twisted spicules, but his genus must become a synonym of *Amphimermis*.

Filipjev (20) used Hagmeier's *Mermis tenuis* as type species of his new genus *Amphidomermis*. Also, Polozhentsev and Artyukhovsky, 1958 (43), used *Mermis tenuis* of Hagmeier as type species of their new genus *Filipjevimermis*. Later, Artyukhovsky (1) found the duplication and synonymized these two genera.

Gordiomermis Heinze, 1934 (24) is insufficiently described and *Heydonius* Taylor, 1935 is a catch-all for fossil mermithids. Polozhentsev (40), the Soviet worker who has studied mermithids longer than anyone else, described *Psammomermis* in 1941 from a May beetle, *Melolontha hippocastani* (F.). This genus is well described. Polozhentsev (41) also described *Skrjabinomermis* from a June beetle, *Melolontha melolontha* (L.), and later Polozhentsev and Artyukhovsky (44) synonymized the French genus (48) *Tunicamermis* Schuurmans Stekhoven, Mawson, et Couturier, 1955 with it.

Coman (14, 15) described four genera of aquatic mermithids from Romania: *Isomermis, Phreatomermis, Romanomermis,* and *Quadrimermis*. Kirjanova *et al.* (28) proposed the genus *Pologenzevimermis* based on specimens taken from sandy soil in the USSR.

Johnson (26) described *Octomyomermis itascensis* from *Chironomus plumosus* L. in the USA. It has large amphids, two spicules, and a barrel-shaped vagina.

Artyukhovsky (1, 2) described six new genera of mermithids from the USSR: *Spiculimermis, Melolonthinimermis, Amphibiomermis, Lanceimermis, Oesophagomermis,* and *Comanimermis*. These were proposed on the basis of new combinations of described species.

Rubtsov (46) proposed *Capitomermis crassiderma* from the chironomids *Tanytarsus* and *Thienemanniella* from the USSR. Later, in 1969 (47), he proposed the genus *Strelkovimermis* for Strelkov's 1964 species, *Filipjevimermis singularis*, and synonymized *Romanomermis* under *Eurymermis*. Recently, Zahidov and Poinar (59) described another new mermithid genus from *Chironomus plumosus* in the USSR and named it *Kurshymermis*. Hominick and Welch (25) described two new nematodes from chironomids in Canada and discussed the systematics of the genera *Gastromermis* and *Hydromermis*.

In the diagnostic statements presented below, the most important differential characteristics of each genus are in *italics*.

TAXONOMY OF SOME REPRESENTATIVE GENERA OF THE MERMITHIDAE

Family:

Mermithidae (Weinland, 1858) Braun, 1883
Syn. Mermidacea Weinland, 1858

Diagnosis (emended): Mermithoidea. Long slender worms often attaining a length of 1-50 cm. Cuticle smooth, but may contain crisscross fibers. Head with four submedian and two lateral papillae. Amphids present, pouches may be very large in some aquatic forms. Mouth and esophagus probably nonfunctional in adults. Esophagus without four large cells (Tetradonematidae). Stoma of preparasitic and postparasitic larvae with a piercing tooth. Intestine in adult replaced by a pseudo-intestine or trophosome, serving as a storage organ; anus absent. Gonads paired in both sexes. Vulva equatorial in position and leading to a muscular S-shaped or barrel-shaped vagina. Uteri filled with eggs in sexually mature specimens. *Eggs* with or without byssi, variable in size depending on genus. Spicules paired or single. Male tail papillae numerous, arranged in three or more rows, rows often bifurcating around opening for spicule. Larval stages parasitic in terrestrial and aquatic invertebrates. Adults not found in insect body cavity, free living, do not feed.

Type Genus: *Mermis* Dujardin, 1842

Mermis Dujardin, 1842 (Figs. 3, 4)

Diagnosis: Mermithidae. Usually long nematodes, 5-20 cm in length. Mouth opening terminal. Amphids small. Parasitic in terrestrial insects. Tail tips of both sexes bluntly rounded. *Male:* With *two short spicules*. Tail papillae in three single rows, center row bifurcates around cloacal opening. *Female:* Vagina S-shaped; vulval flap absent; vulval cone not well developed. *Preparasitic Larva:* Does not

amputate tail. *Postparasitic Larva:* Lacking tail appendage. *Eggs:* Many small eggs present in uterus; *with elaborate byssi.*

Type Species:

Mermis nigrescens Dujardin, 1842

Syn. *Mermis subnigrescens* Cobb, 1926

Other Species:

Mermis mirablis von Linstow, 1903

Syn. *Mermis tahitiensis* Baylis, 1944

Geographical Distribution: Worldwide

Host Insect: Grasshoppers

Discussion: There are over 75 species described in the genus *Mermis*, most of which do not belong in that genus. Unfortunately, their disposition is beyond the generic nature of this paper and will be taken up in a later work. The eggs of *Mermis* species have byssi (filamentous attachments) (Fig. 3) which aid in attachment to leaves. *Mermis* is the only mermithid genus that is known to have the biological characteristic whereby the mermithid deposits eggs on leaves of plants and the eggs are ingested by insects during feeding. It has not been proven whether *Allomermis* also has this characteristic. In the great majority of the mermithids, the preparasitic larva hatches from the egg and actively seeks and penetrates the insect host.

Hydromermis Corti, 1902 (Figs. 1-C, 3, 5)

Diagnosis: Mermithidae. Usually short nematodes, 10-25 mm in length. Mouth opening terminal or slightly ventral. Amphids large. Parasitic in aquatic insects. *Tail tips of both adult sexes pointed. Male: Spicule single, large.* Tail papillae in 3 single rows, center row bifurcates around spicule opening. *Female: Vagina S-shaped;* vulval flap present; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* With digitate appendage. *Eggs:* Many small eggs present in uterus; without byssi.

Type Species:

Hydromermis contorta (von Linstow, 1889) Hagmeier, 1912

Syn. *Mermis contorta* von Linstow, 1889 (in part)

Mermis crassa (von Linstow, 1889) Stiles, 1892

Hydromermis rivicola Corti, 1902

Hydromermis implicata Corti, 1906

Paramermis contorta (von Linstow, 1889) Kohn, 1905

Other Species: There are probably other valid species.

Geographical Distribution: Worldwide

Host Insects: Chironomids

Discussion: *Hydromermis contorta* is limited here to the sharply pointed-tail adults from chironomids figured by Stiles, 1892 (54) and Hagmeier, 1912 (23). Much has been written about the nomenclature of these mermithids and a consensus seems rightfully to support the Kohn, 1905, emended description (29) of von Linstow's *contorta*. In a plea for stability, the writer urges the acceptance of the above synonymy even though the genus *Paramermis* is cast aside in an uncertain position.

Limnomermis Daday, 1911 (Figs. 1-G, 3, 6)

Diagnosis: Mermithidae. Usually short nematodes, 10-20 mm in length. Mouth opening terminal or slightly ventral. *Amphids very large.* Parasitic in aquatic insects. *Tail tips* of both adult sexes blunt. *Male: Spicule single.* Tail papillae in 3 single rows. *Female:* Vagina S-shaped; vulval flap present; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* Tail with short, digitate appendage. *Eggs:* Many small eggs present in uterus; without byssi.

Type Species:

Limnomermis bathybia Daday, 1911

Syn. *Limnomermis limnobia* Daday, 1911

Other Species: Probably others

Geographical Distribution: Europe, Canada

Host Insects: Chironomids

Discussion: *L. bathybia* is widespread over Europe and North America as a parasite in chironomids (Fig. 1-G). There are three collections of this nematode in Steiner's material collected in 1918, 1925, and 1926 from various European lakes. Recently, I have received several collections of this nematode from British Columbia, Canada. It is easily distinguished by its enormous amphids, blunt tails in both adult sexes, single spicule and chironomid host.

Bathymermis Daday, 1911 (Figs. 3, 7)

Diagnosis: Mermithidae. Usually *very short, 5-15 mm in length.* Mouth opening terminal or slightly ventral. Amphids medium sized. Parasitic in aquatic insects. Tail tips of both adult sexes bluntly rounded. *Male:* With two long, slender, curved spicules. Tail papillae in 3 single rows. *Female: Vagina barrel-shaped;* vulval flap absent; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* Unknown. *Eggs:* Many medium-sized eggs present in uterus; without byssi.

Type Species:
Bathymermis fuhrmanni Daday, 1911
Other Species: Probably others
Geographical Distribution: Europe
Host Insects: Unknown. Found in Neuenburgersee.
Type Material: Neotype Female.–L = 10.0 mm; W = 0.28 mm; V = 50%. Egg diameter = 65 μ.

Other Females (5).–L = 8.5-12.0 mm; W = 0.25-0.35 mm; V = 44.2-55.4%; Egg diameter = 60-70 μ.

Males (5).– L = 4.6-6.8 mm; W = 0.15-0.20 mm; Spicule L = 0.32 mm (0.28-0.34 mm).

Steiner collected this material from the type locality between 1914-1916. It agrees well with the description, and this genus appears to be distinct.

Neotype Female.–Slide SM-T-1-t deposited in the Steiner Mermithid Collection of the USDA Nematode Collection, Beltsville, Maryland. Other females and males deposited in the California Nematode Survey Collection, Davis, California, and Canada National Nematode Collection, Ottawa, Canada.
Discussion: Though no host information is available for this mermithid, it is easy to differentiate because of its small size, barrel-shaped vagina, and two long spicules.

Agamermis Cobb, Steiner and Christie, 1923 (Figs. 3, 8)

Diagnosis: Mermithidae. Usually long nematodes, 30-465 mm in length. Mouth opening terminal. Amphids small. Parasitic in terrestrial insects. Tail tips of both adult sexes bluntly rounded. *Male:* With two short spicules; tail papillae in 4-6 rows (as in *Hexamermis*). *Female:* Vagina S-shaped; vulval flap absent; *vulval cone well developed, cuticularized. Preparasitic Larva: Amputates tail;* i.e., *75% of body at the node just before penetrating insect. Postparasitic Larva: With crater-like appendage from decaudated tail. Eggs:* Few large eggs present in uterus; without byssi.
Type Species:
Agamermis decaudata Cobb, Steiner, Christie, 1923
Other Species: Probably others
Geographical Distribution: USA
Host Insects: Grasshoppers
Type Material: Lectotype Male–Slide T-139t; L = 80 mm; W = 0.210 mm; Spicule L = 170 μ.

Paralectotypes (9). Three paralectotypes; Male–Slide T-1150 p; female–Slide T-1144 p-T-1149 p (6 slides); and larva–Slide T-1151 p deposited in the USDA Nematode Collection, Beltsville, Maryland. Three paralectotypes; one male, one female, and one preparasitic larva, deposited in the University of California Survey Collection, Davis, California and also the same deposited in the Canada National Nematode Collection, Ottawa, Canada.

Other Males (5).–L = 70 (10-120 mm); W = 200 μ (150-250 μ); Spicule L = 175 μ (150-180 μ).

Other Females (5).–L = 280 mm (50-465 mm); W = 0.50 mm; V = 58% (50-60%); Egg diameter = 170 μ (150-180 μ).
Discussion: The adults of *A. decaudata* have not been illustrated before and are described here (Fig. 8). They are similar to *Hexamermis* which was described 1 year after *Agamermis*. However, the decaudation of the preparasitic larval tail, host range, and our lack of knowledge would mitigate against the synonymy of *Hexamermis* under *Agamermis*.

Hexamermis Steiner, 1924 (Figs. 3, 9)

Diagnosis: Mermithidae. Usually long nematodes (except *H. brevis*), 30-200 mm in length. Mouth opening terminal. Amphids small. Parasitic in terrestrial insects. Tail tips of both adult sexes bluntly rounded. *Male:* With *two short spicules.* Tail papillae in 4-6 rows in a typical pattern. *Female:* Vagina S-shaped; vulval flap absent; *vulval cone well developed, cuticularized. Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* Tail with short, finger-like appendage. *Eggs:* Few, medium to large eggs present in uterus; without byssi.

Type Species:
Hexamermis albicans (Siebold, 1848) Polozhentsev & Artyukhovsky, 1959
Syn. *Mermis albicans* Siebold, 1848
Mermis acuminata Leidy, 1875
Hexamermis meridionalis Steiner, 1924
Other Species:
H. brevis (Hagmeier, 1912) Polozhentsev & Artyukhovsky, 1959.
Geographical Distribution: Worldwide
Host Insects: Numerous terrestrial insects. Moths, flies, beetles.
Discussion: *H. albicans* has a wide host range of terrestrial insects and a worldwide distribution. This nematode has been described as new several times since its original description.

These descriptions will be dealt with in a later work.

Allomermis Steiner, 1924 (Figs. 3, 10)

Diagnosis: Mermithidae. Usually short nematodes, 10-15 mm in length. *Mouth opening with very strong ventral shifting.* Amphids not large. Probably parasitic in terrestrial insects. Tail tips of both adult sexes bluntly rounded. *Male:* With two short spicules. *Numerous tail papillae in typical 3 double rows. Female:* Vagina S-shaped; vulval flap absent; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* Unknown. *Eggs:* Many small eggs in uterus; *with typical hair-like processes.*

Type Species:

Allomermis trichotopson Steiner, 1924

Other Species: None

Geographical Distribution: Jamaica

Host Insects: Unknown. Found in soil.

Type Material: Two original paratype females and one original paratype male were found in Steiner's mermithid collection. They have been remounted, designated as Slides SM-T-2-p, SM-T-4-p, and placed in the Steiner Mermithid Collection of the USDA Nematode Collection, Beltsville, Maryland.

Discussion: The significant aspect of this tropical nematode genus is that the eggs have typical hair-like processes reminiscent of *Mermis nigrescens* and *Mermis mirabilis*. The ant parasite *Mermis myrmecophila* was placed in the genus *Allomermis*; but the eggs as drawn by Baylis (3) do not have these hair-like processes. Life cycle studies of these mermithids are needed.

Gastromermis Micoletzky, 1925 (Figs. 1-H, 3, 11)

Diagnosis: Mermithidae. Usually short nematodes, 10-20 mm in length. *Mouth opening with ventral shift.* Amphids very large. Parasitic in aquatic insects. Tail tips of both adult sexes bluntly rounded. *Male: With one long slender spicule.* Tail papillae in 3 single rows, center row bifurcates around spicule opening. *Female:* Vagina long, S-shaped; vulval flap absent; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* With short to medium length digitate appendage. *Eggs:* Many small eggs present in uterus; without byssi.

Type Species:

Gastromermis haempeli Micoletzky, 1923

Other Species:

G. viridis Welch, 1962 and others

Geographical Distribution: Worldwide

Host Insects: Black flies

Discussion: It now appears that many different kinds of mermithids have ventrally-shifted mouths, and so I am limiting this genus to those with a single, long spicule as shown in the type species and also shown for *G. viridis*.

Amphimermis Kaburaki & Imamura, 1932
Syn. *Complexomermis* Filipjev, 1934 (Figs. 3, 12)

Diagnosis: Mermithidae. Usually medium to long nematodes, 40-200 mm in length. Mouth opening with slight *ventral shifting.* Amphids large. Parasitic in both aquatic and terrestrial insects. Tail tips of both adult sexes bluntly rounded. *Male:* With *two long twisted spicules.* Tail papillae in 3 single rows, center row bifurcates around spicule opening. *Female:* Vagina S-shaped; *vulval flap present;* vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* With short digitate tail appendage. *Eggs:* Many medium-sized eggs present in uterus; without byssi.

Type Species:

Amphimermis zuimushi Kaburaki & Imamura, 1932

Other Species:

Amphimermis elegans (Hagmeier, 1912) Welch, 1963

Syn. *Mermis elegans* Hagmeier, 1912

Complexomermis elegans (Hagmeier, 1912) Filipjev, 1934

Amphimermis bogongae Welch, 1963

Amphimermis ghilarovi (Polozhentsev & Artyukhovsky, 1958) Welch, 1963

Syn. *Complexomermis ghilarovi* Polozhentsev & Artyukhovsky, 1958

Amphibiomermis ghilarovi (Polozhentsev & Artyukhovsky, 1958) Artyukhovsky, 1969

Geographical Distribution: Worldwide

Host Insects: Grasshoppers, *Stenobothrus* Fischer and *Decticus* Fab.; Rice borer, *Chilo simplex* Butler; the gypsy moth, *Porthetria dispar* (L.); the winter moth, *Operophtera brumata* (L.); Bogong moth, *Agrotis infusa* (Boisd.); Damselflies, *Ischnura* Fab. and *Anomalagrion* Fab.

Discussion: This genus appears to have the potential of having a large number of species. I

have seen one species with twisted spicules over eight mm long from a terrestrial habitat. The new species described here is from an aquatic environment and has spicules under one mm long.

Amphimermis tinyi n. sp. (Figs. 3, 12)

Type Material: Hototype Male.–L = 12.0 mm; W = 0.120 mm; Spicule L = 710 μ.

Allotype Female.–L = 30.0 mm; W = 0.225 mm; V = 48%; Egg diameter = 65 μ.

Paratypes: Males (5).–L = 14.0 mm (11.0-17.0 mm); W = 0.150 mm (0.120-0.210 mm); Spicule L = 750 μ (700-860 μ).

Paratypes: Females (5).–L = 30.0 mm (25.0-35.5 mm); W = 0.207 mm (0.194-0.224 mm); V = 48% (45-50%); Egg diameter = 65 μ (60-72 μ).

The Hototype Slide T-140t, Allotype Slide T-141t, and two Paratypes Slides, T-1152p and T-1153p, are deposited in the USDA Nematode Collection, Beltsville, Maryland. Two paratypes, one of each sex, are deposited in the University of California Nematode Survey Collection, Davis, California, and also two paratypes, one of each sex, are deposited in the Canada National Nematode Collection, Ottawa, Canada.

Discussion: This species is typical of the genus, but has the shortest spicules among the described species and is from damselflies (*Ischnura posita* and *Anomalagrion hastatum*) in Louisiana. This species is named after O. R. "Tiny" Willis.

Psammomermis Polozhentsev, 1941 (Fig. 13)

Diagnosis: Mermithidae. Usually very long nematodes, 70-350 mm in length. Mouth opening terminal. Amphids small. Parasitic in terrestrial insects. Tail tips of both adult sexes bluntly rounded. *Male: With two long slender spicules.* Tail papillae in 3 single rows. *Female:* Vagina barrel-shaped; vulval flap absent; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* Unknown. *Eggs:* Moderate number of large eggs in the uterus; without byssi.

Type Species:

Psammomermis korsakowi Polozhentsev, 1941

Other Species: None

Geographical Distribution: USSR

Host Insect: June beetle, *Melolontha hippocastani* (F.)

Discussion: This large nematode was found killing up to 60% of the cockchafers in the USSR. The barrel-shaped vagina, two long spicules, and lack of a vulval cone separate it easily from the other genera.

Lanceimermis Artyukhovsky, 1969 (Figs. 3, 14)

Diagnosis: Mermithidae. Usually small nematodes, 10-25 mm in length. Mouth opening terminal. *Amphids large.* Parasitic in aquatic insects, tail tips of both adult sexes bluntly rounded. *Male: With one long spicule, with characteristic J-shape;* tail papillae in 3 single rows. *Female:* Vagina S-shaped; *vulval flap present;* vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* With medium length, digitate tail appendage. *Eggs:* Many small eggs present in uterus; without byssi.

Type Species:

Lanceimermis prolata (Coman, 1961) Artyukhovsky, 1969

Other Species:

L. austriaca (Micoletzky, 1913) Artyukhovsky, 1969

L. zschokkei (Schmassman, 1914) Artyukhovsky, 1969

L. trachelata (Steiner, 1929) Artyukhovsky, 1969

Geographical Distribution: Europe, USSR

Host Insects: Unknown. Found in lakes.

Discussion: Specimens of *L. austriaca, L. zschokkei,* and *L. trachelata* collected by Steiner were remounted and illustrated. The study of these specimens supports Artyukhovsky in his assignment of these species to the same generic group. The vulval flap and the one, long characteristically shaped spicule are diagnostic.

Reesimermis Tsai & Grundmann, 1969 (Figs. 1-B, 3, 15)

Diagnosis: Mermithidae. Usually small nematodes, 5-25 mm in length. Mouth opening terminal. Amphids large. Parasitic in aquatic insects. Tail tips of both adult sexes bluntly rounded. *Male:* With *two long separate spicules;* tail papillae in 3 single rows, center row bifurcating around spicule opening. *Female: Vagina barrel-shaped;* vulval flap absent; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* With very long pointed appendage. *Eggs:* Many medium-sized eggs present in uterus; without byssi.

Type Species:

Reesimermis nielseni Tsai & Grundmann, 1969

Other Species:

R. iyengari (Welch, 1964) n. comb.

Geographical Distribution: USA–Wyoming, Florida and Louisiana

Host Insects: Many species of mosquitoes

Type Material: Ten males and ten females of the original paratype material (56) were given to the author for more permanent deposition. These specimens were separated into three groups and were deposited in the USDA Nematode Collection, Beltsville, Maryland, the University of California Nematode Survey Collection, Davis, California, and the Canada National Nematode Collection, Ottawa, Canada.

Discussion: One can easily trace the lumen of the esophagus from the front end of this nematode species almost to the tip of the tail. Several papers have used the name *Romanomermis* sp. for this nematode; however, this was an earlier identification of mine and it has now changed. The nematode was found in a coiled form in the thorax of culicine mosquitoes (Fig. 1-B) and the abdomen of anopheline mosquito hosts.

Octomyomermis Johnson, 1963 (Fig. 16)

Diagnosis: Mermithidae. Usually medium-sized nematodes, 18-60 mm in length. Mouth opening terminal. *Amphids medium-sized.* Parasitic in aquatic insects, *tail tips of both adult sexes bluntly rounded with nipple-like tip. Male:* With two short spicules; tail papillae in 3 single rows, center row bifurcating around spicule opening. *Female: Vagina barrel-shaped;* vulval flap absent; *vulva protrudes;* vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* Unknown. *Eggs:* Many medium-sized eggs present in the uterus; without byssi.

Type Species:

Octomyomermis itascensis Johnson, 1963

Other Species: None

Geographical Distribution: Minnesota, USA

Host Insect: *Chironomus plumosus* (L.)

Discussion: These nematodes are fairly large for an aquatic insect parasite. They parasitize about 20% of the population of *Chironomus plumosus* (L.) in certain Minnesota lakes. They are often found in adult chironomids, and the nematode was observed (26) to emerge quickly when the insect touched water.

Diximermis n. gen. (Figs. 1-E, 3, 17)

Diagnosis: Mermithidae. Usually small nematodes, 5-15 mm in length. *Mouth opening ventrally shifted.* Amphids large. Parasitic in aquatic insects. Tail tips of both adult sexes bluntly rounded. *Male: With two short spicules;* tail papillae in 3 single rows, center row bifurcating around spicule opening. *Female:* Vagina S-shaped; vulval flap present; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* With short digitate tail appendage. *Eggs:* Many small eggs present in uterus; without byssi.

Type species:

Diximermis peterseni n. sp.

Type Material: Hototype Male.–L = 5.0 mm; W = 0.190 mm; Spicule L = 186 μ.

Allotype Female.–L = 11.50 mm; W = 0.148 mm; V = 55%; Egg diameter = 55 μ.

Paratypes.–Two Males–L = 8.0 mm (5.0-14.5 mm); W = 0.280 mm (0.236-0.346 mm); Spicule L = 190 μ (182-213 μ).

Paratypes.–Two Females–L = 12.0 mm (10.0-14.0 mm); W = 0.170 mm (0.140-0.209 mm); V = 55% (50-60%); Egg diameter = 55 μ (52-58 μ).

The Holotype Slide T-183t, Allotype Slide T-184t, and two Paratypes Slides T-1154p and T-1155p are deposited in the USDA Nematode Collection, Beltsville, Maryland. Two paratypes, one of each sex, are deposited in the University of California Nematode Survey Collection, Davis, California, and also two paratypes, one of each sex are deposited in the Canada National Nematode Collection, Ottawa, Canada.

Discussion: This nematode has appeared in the literature as *Gastromermis* sp., but I now limit *Gastromermis* to the single long-spiculed forms. *D. peterseni* (Fig. 1-E) has been found to kill 85% of the mosquito larvae in some pools (6). The genus can be differentiated by the ventrally shifted oral opening, two short spicules, and only larval anopheline mosquitoes as hosts. This species is named after J. J. Petersen.

Type locality: Louisiana and Florida, USA

Type Host: *Anopheles crucians* Wiedemann

Other Hosts: *A. punctipennis* (Say), *A. quadrimaculatus* Say

Perutilimermis n. gen. (Figs. 1-D, 3, 18)

Diagnosis: Mermithidae. Usually small nematodes, 8-25 mm in length. Mouth opening terminal. *Amphids small.* Parasitic in aquatic

insects. Tail tips of both adult sexes bluntly rounded. *Male: With a single short spicule;* tail papillae small, in 3 single rows, center row bifurcating around spicule opening. *Female:* Vagina long, S-shaped; vulval flap absent; vulval cone not well developed; *vulva protrudes. Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* With short digitate tail appendage. *Eggs:* Many small eggs present in uterus; without byssi.

Type Species:

Perutilimermis culicis (Stiles, 1903) n. comb.

Syn. *Agamomermis culicis* Stiles, 1903

Type Material: Males (5).–L = 8.0 mm (8.0-9.0 mm); W = 0.180 mm (0.160-0.220 mm); Spicule L = 90 μ (85-108 μ).

Females (5).–L = 13.0 mm (12.0-15.0 mm); W = 0.255 mm (0.150-0.300 mm); V = 55% (52-62%); Egg diameter = 45 μ (43-46 μ).

Adult specimens of this species are described for the first time and, though no types could be set up for this material, specimens of each sex are deposited in the USDA Nematode Collection, Beltsville, Maryland, the University of California Nematode Survey Collection, Davis, California, and the Canada National Nematode Collection, Ottawa, Canada.

Geographical Distribution: Atlantic and Gulf Coasts, USA

Host Insect: *Aedes sollicitans* (Walker), the saltmarsh mosquito

Other Species: None

Discussion: This nematode is found in the adult mosquito (Fig. 1-D) and seems to be host specific. It develops only slightly in the larval and pupal stages of the insect. This nematode kills up to 65% of the saltmarsh mosquitoes along the Atlantic and Gulf coasts (38). I have identified it from New Jersey, Florida, and Louisiana. The single short spicule, the protruding vulva, and the development in the adult mosquito separate the genus from other mermithid genera.

Neomesomermis n. gen. (Fig. 19)

Diagnosis: Mermithidae. Usually short nematodes, 10-20 mm in length. Mouth opening terminal. *Amphids large.* Parasitic in aquatic insects. Tail tips of both adult sexes bluntly rounded. *Male: With two medium-sized spicules.* Tail papillae in 3 single rows, center row bifurcates around spicule opening. *Female: Vagina barrel-shaped;* vulval flap absent; vulval cone not well developed. *Preparasitic Larva:* Does not amputate tail. *Postparasitic Larva:* With swollen, bluntly-rounded tail appendage. *Eggs:* Not found.

Type Species:

Neomesomermis flumenalis (Welch, 1962) n. comb.

Other Species: Probably others.

Geographical Distribution: Ontario, Newfoundland, Canada; Wisconsin, USA

Host Insects: Blackflies: *Simulium venustum* Say, *Simulium latipes* (Meigen), *Prosimulium mixtum* Syme & Davies.

Discussion: *Mesomermis zschokkei* was set up as type of the genus *Mesomermis* (7). The description was based on a single male specimen which was poorly illustrated and collected from a lake with no host data. No female was described. The original drawings and description could fit several existing genera. Therefore, it seems best to use the well-described species *M. flumenalis* as the type species of this new genus, *Neomesomermis*, and to consider *Mesomermis* as a *genus inquirendae*. The aquatic host, large amphids, two spicules, barrel-shaped vagina and blunt tail tips in both adult sexes separate this genus from other genera.

DISCUSSION OF MORPHOLOGY AND TAXONOMY

Filipjev in 1934, wrote that the taxonomy of the mermithids was not yet set up on a firm basis. Even today there are still many obstacles in the path of easy identification of mermithids. A few of these obstacles will be presented. Analysis of the several hundred described mermithid species in 50 different genera shows that few descriptions have the basic requirements of taxonomic studies, such as descriptions of the male, female, egg, larva, and the host species. This has led to much guesswork and, along with the unavailability of specimens for comparison, has discouraged research in this otherwise interesting and beneficial group of nematodes. Many species and indeed some genera have been described from larval forms. If a nematologist described a new genus or species of plant-parasitic nematode based on a description of a larva, the review committees and journal editors would certainly reject the paper. Also, a description of just one sex of the nematode should not be sufficient for publication unless the species is parthenogenetic.

One of the characters used in the taxonomy

of mermithids at the genus and species level is the number of chords. Nowhere else in the whole nematode phylum do we use the number of chords in larval and adult nematodes as taxonomic characters. I urge the rapid abandonment of this character, as it seems to add little to the clarification of mermithids. Adult mermithids have excellent taxonomic characters, and are as easy to identify as any other large group of nematodes. Descriptions of eggs (Fig. 3) and preparasitic and postparasitic larvae serve to supplement the adult characters.

There are some aberrant forms and also some intersexes in the Mermithidae. I have seen some male specimens of *Amphimermis* with two very short, peg-like spicules instead of the usual long twisted spicules. Dr. S. A. Sher, University of California, Riverside, sent me a male mermithid from California with one spicule 4400 μ long and the other spicule 175 μ long. It is not known for certain whether this was an aberrant form or a new genus. The relative length of a nonaberrant adult mermithid can be useful taxonomically. Most aquatic genera are usually less than 25 mm, and terrestrial genera are usually from 50 to 500 mm. However, Christie (9) mentions that female specimens of *Agamermis decaudata* vary from 50 to 465 mm in length; and males, from 10 to 120 mm. Thus, descriptions of parasitic species based on relative length alone will cause problems for future workers.

The mouth opening in *Allomermis*, *Gastromermis*, and *Diximermis* is ventrally displaced, and it is partially so in *Hydromermis*, *Limnomermis*, *Bathymermis*, and *Amphimermis*. Although these genera may be related in terms of the ventral displacement of the mouth opening, grouping them under the same genus would seem illogical because of the wide variation observed in the form of the spicules, vaginas, egg shapes, and other characters. In this work, *Gastromermis* is limited to those species with one long spicule as in the type species.

Amphids on specimens of the aquatic mermithid genera are usually large, especially on the male. In *Limnomermis* and *Gastromermis*, the amphid pouches are so large that they almost reach the lumen of the esophageal canal. The amphids are small on mermithid parasites of terrestrial insects.

The use of the presence or absence of crisscross fibers in the cuticle of mermithids as a generic character is inaccurate (8). However, *Mermis nigrescens* has very distinct cuticular cross fibers (Fig. 4-A), and the position, form, and degree of development are of taxonomic value at both the generic and specific level.

Larval characters are not very useful, though the few preparasitic larvae that have been described show a variation in length. *Agamermis decaudata* is the only nematode with a node (Fig. 8-B). The node is the predetermined point on the body of the infective preparasitic larva, at which 75% of the nematode is broken off just prior to its penetration of the grasshopper. The postparasitic larvae have certain useful characters, such as the length and shape of the tail appendage and the length of the stomatal tooth. However, the adult forms are needed for identification.

Eggs are very useful in the identification of the Mermithidae (Fig. 3). Presence or absence of byssi, relative size, and the relative numbers of eggs produced, appear to be stable characters.

The vagina is either barrel-shaped or S-shaped. *Bathymermis*, *Psammomermis*, *Reesimermis*, *Octomyomermis*, and *Neomesomermis* have barrel-shaped vaginas. A vulval flap is present in *Hydromermis*, *Lanceimermis*, *Limnomermis*, *Amphimermis*, and *Diximermis*. A well-developed cuticular vulval cone is present in the closely related genera *Hexamermis* and *Agamermis*.

The number, shape, and size of the spicules and the number of rows and total number of pre- and post-anal papillae are important characteristics of male mermithids.

LIFE CYCLES OF THE MERMITHIDAE

Unlike the tetradonematids, in which adult nematodes develop in the host insects, mermithids are not normally found as adults inside the body cavities of insects. They almost always emerge from the insect as the last larval stage, called the postparasitic larva. This natural emergence is necessary for adult development because the mermithid molts to the last larval stage just before coming out of the insect. This molt predisposes the worm physiologically for the outside life.

The postparasitic mermithid larva is equipped with a lance-like tooth which is used to perforate the insect cuticle from the inside. Sometimes this emergence occurs quickly and is triggered by circumstances, such as a chironomid touching water in a mock

oviposition. The hole in the insect's body caused by the exist of this large mermithid is usually the cause of death of the insect due to loss of body fluids. After the mermithid leaves the insect, it does not feed and is dependent upon the food stored in the trophosome. There are four known types of life cycles among mermithids.

1. *Mermis nigrescens* from grasshoppers. The female, after mating in the soil, crawls to the top of leafy plants early in the morning after a heavy rain or heavy dew and deposits hundreds of eggs on the leaves. After the eggs are laid, the female nematode goes back into the soil. The eggs (Fig. 3), which have filamentous appendages on the shell, called byssi, dry out and adhere well to the leaves, awaiting consumption by grasshoppers. After the eggs are ingested by the grasshopper, they hatch quickly in the insect gut, and the preparasitic nematode larvae pierce into the body cavity of the grasshopper. The nematode grows within the body cavity of the grasshopper, molts, and eventually uses its lance-like tooth to make a large hole from the inside and, after exerting pressures in the weakened area, emerges from the insect body cavity. This last-stage larva then goes into the soil and molts to the adult stage. After mating, the male dies and the impregnated female deposits her eggs on the leaves of plants. It would appear that *Mermis mirabilis* and perhaps *Allomermis trichotopson*, both tropical parasites, have this same type of life cycle.

2. *Reesimermis nielseni* from mosquitoes. The eggs of this mermithid are laid at the bottom of a mosquito pool; and, after hatching, the preparasitic larva (Fig. 15-H) penetrates an early instar mosquito larva. This small nematode often migrates to the thorax (Fig. 15-J), grows quickly, obtaining nourishment from the insect haemolymph, and emerges from the last instar mosquito larva, which is killed before pupation. The nematode exits from the mosquito larva, and within 2-3 weeks molts, mates, and lays up to 3000 eggs at the bottom of the pool. This mermithid has a wide host range of over 20 species of mosquitoes (37). This parasite can be reared on mosquitoes in the laboratory at a nominal cost, and has been used in field control of mosquitoes all over the world.

3. *Perutilimermis culicis* from the saltmarsh mosquito, *Aedes sollicitans* Walker).

The eggs of this mermithid are laid by the thousands at the bottom of a mosquito pool, and the small preparasitic larva hatches and penetrates an early instar mosquito larva. The mermithid remains in the head or thorax, but does not grow. When the mosquito pupates, the mermithid migrates to the abdomen but does not begin to enlarge until the mosquito reaches the adult stage (Fig. 18-L) and after it has had a blood meal. The nematode then grows quickly and sterilizes the female mosquito. The emergence of the nematode as a postparasitic larva kills the mosquito. The nematode then enters the pond, molts, mates, and lays thousands of eggs. This mermithid is host-specific.

4. *Amphimermis bogongae* and *Hexamermis cavicola* from the Bogong moth, *Agrotis infusa* (Boisduval).

The eggs of these mermithids are laid in the soil and mosses of caves. The preparasitic larvae hatch and crawl up the sides of the cave and penetrate adult bogong moths. These adult moths remain quiescent on the roofs of the caves for several months and, later, parasitized individuals fall to the floor of the cave and die. Though this environment is somewhat unique, parasitism occurs only on adult moths (57). Young stages of the insect are not present in the cave.

DISCUSSION OF HOST SPECIFICITY

Host information (Figs. 1, 2) is important for mermithid identifications, as is true also for plant- and animal-parasitic nematodes. If a person found a mermithid in a grasshopper, he would not need to concern himself with the numerous nematode taxa dealing with mosquito or chironomid mermithids. The excellent works of Christie (10), Polozhentsev (42), Polozhentsev and Artyukhovsky (45), Wülker (58), and Petersen *et al.* (37, 38) have given us much useful information on host specificity, and have made the work of the mermithid taxonomist considerably easier. Generally, it appears that mermithids that parasitize insect larvae have a wider host range than those that live in adult insects. We are finding that some mermithids, e.g., *Perutilimermis culicis*, are host species-specific; some mermithids, e.g., *Diximermis peterseni*, can parasitize several species in one genus; and some mermithids, e.g., *Mermis nigrescens* and *Agamermis decaudata*, parasitize only grasshoppers, with a few exceptions. In contrast to these examples of host specificity, some

mermithids such as *Reesimermis nielseni* can parasitize 23 species of mosquitoes in the field and a total of 55 species in several different genera in the laboratory (37). Some mermithids, including *Hexamermis albicans*, can attack insects in several different orders.

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FIGURE LEGENDS

FIG. 1. Mosquitoes and other aquatic insects parasitized by mermithids. **A.** *Aedes stimulans* parasitized by a mermithid (courtesy of D. L. Haynes). **B.** *Culex pipiens quinquefasciatus* larvae parasitized by *Reesimermis nielseni* (courtesy of J. J. Petersen). **C.** Adult chironomid parasitized by *Hydromermis contorta* (courtesy of R. P. Esser and J. B. MacGowan). **D.** Adult *Aedes sollicitans* parasitized by *Perutilimermis culicis* (courtesy of J. J. Petersen). **E.** *Anopheles crucians* larva with *Diximermis peterseni* emerging (courtesy of J. J. Petersen). **F.** *Aedes vexans* with mermithid parasite (courtesy of J. A. Shemanchuk). **G.** Chironomid larva (*Pseotrocladius* sp.) parasitized by *Limnomermis bathybia* (courtesy of V. J. E. McCauley). **H.** Blackfly larvae (*Simulium vittatum*) with mermithid parasite (courtesy of G. R. De Foliart).

FIG. 2. Some insects parasitized by mermithids.

FIG. 3. Morphological variation in mermithid eggs.

FIG. 4. *Mermis nigrescens.* **A.** Lateral view of female head, showing subcuticular pattern. **B.** Postparasitic juvenile tail. **C.** Preparasitic larva. **D.** Vagina, lateral view. **E.** Egg with byssi. **F.** Male tail, lateral view. **G.** Female tail, lateral view. **H.** Grasshopper host.

FIG. 5. *Hydromermis contorta.* **A.** Head of female. **B.** Female tail. **C.** Postparasitic juvenile tail. **D.** Female vagina. **E.** Egg. **F.** Male tail. **G.** Chironomid intersex host (intersex having female type antennae with male genitalia).

FIG. 6. *Limnomermis bathybia.* **A.** Head of adult male, showing large amphids. **B.** Head of adult female. **C.** Female vagina. **D.** Egg. **E.** Postparasitic juvenile head, showing tooth, used in emerging from host. **F.** Male tail, ventral, showing papillae pattern. **G.** Spicule. **H.** Postparasitic juvenile tail. **I.** Male tail. **J.** Female tail. **K.** Chironomid host.

FIG. 7. *Bathymermis fuhrmanni.* **A.** Head of male. **B.** Male tail. **C.** Vagina. **D.** Egg. **E.** Ventral view of male tail showing papillae pattern. **F.** Female tail.

FIG. 8. *Agamermis decaudata.* **A.** Female head. **B.** Preparasitic juvenile showing node. **C.** Young male tail, ventral view, showing papillae pattern and peg-like tail tip from cast off tail. **D.** Egg. **E.** Female vagina. **F.** Male tail. **G.** Female tail. **H.** Grasshopper host.

FIG. 9. *Hexamermis albicans* and *H. brevis.* **A.** *H. albicans,* female head. **B.** *H. brevis,* egg. **C.** *H. albicans,* vagina. **D.** *H. albicans,* male postparasitic juvenile tail. **E.** *H. albicans,* egg. **F.** *H. brevis,* papillae pattern. **G.** *H. albicans,* female tail. **H.** *H. albicans,* male tail. **I.** *H. albicans,* papillae pattern. **J.** Gypsy Moth caterpillar host.

FIG. 10. *Allomermis trichotopson.* **A.** Female head, showing ventral opening. **B.** Male tail. **C.** Female tail. **D.** Egg. **E.** Papillae pattern of male tail. **F.** Vagina (E and F after Steiner).

FIG. 11. *Gastromermis viridis.* **A.** Female head. **B.** Female tail. **C.** Female vagina. **D.** Male head. **E.** Postparasitic juvenile tail. **F.** Papillae pattern of male tail. **G.** Egg. **H.** Male tail, lateral view. **I.** Adult *Simulium vittatum* host. **J.** Larval blackfly host.

FIG. 12. *Amphimermis tinyi* n. sp. **A.** Male head. **B.** Postparasitic juvenile tail. **C.** Male tail, showing papillae pattern. **D.** Female vagina. **E.** Male tail, showing twisted spicules. **F.** Female tail. **G.** Egg. **H.** Damselfly naiad host.

FIG. 13. *Psammomermis korsakowi.* **A.** Female head. **B.** Vagina of young female. **C.** Vagina of older female. **D.** Male tail. **E.** Female tail. **F.** June beetle grub host (drawings after Polozhentsev, 1941).

FIG. 14. *Lanceimermis austriaca, L. zschokkei,* and *L. trachelata.* **A.** *L. austriaca,* female head. **B.** *L. zschokkei,* male head, showing large amphid. **C.** *L. austriaca,* female vagina. **D.** *L. austriaca,* egg. **E.** *L. trachelata,*

female tail. **F.** *L. austriaca*, female tail. **G.** *L. trachelata*, female vagina. **H.** *L. austriaca*, male tail. **I.** *L. austriaca*, spicule. **J.** *L. zschokkei*, spicule. **K.** *L. zschokkei*, male tail.

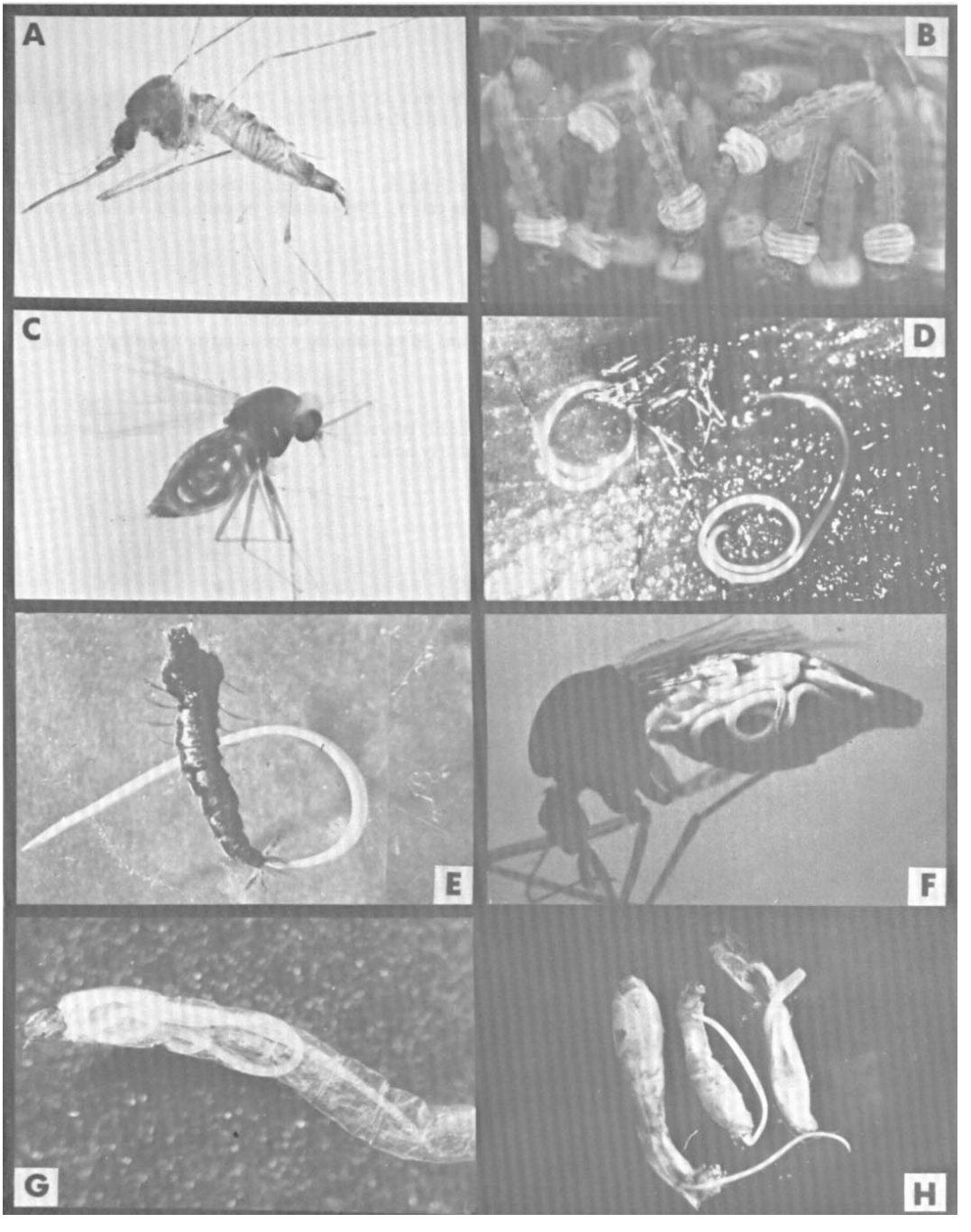
FIG. 15. *Reesimermis nielseni.* **A.** Female head. **B.** Postparasitic juvenile tail. **C.** Male papillae pattern. **D.** Female vagina. **E.** Egg. **F.** Male tail. **G.** Female tail. **H.** Preparasitic larva. **I.** Postparasitic juvenile stoma showing tooth. **J.** Mosquito larva host.

FIG. 16. *Octomyomermis itascensis.* **A.** Female head. **B.** Male head, lateral view. **C.** Female vagina. **D.** Male head, dorsal-ventral view. **E.** Spicule. **F.** Female tail. **G.** Male tail. **H.** *Chironomus* host.

FIG. 17. *Diximermis peterseni* n. gen., n. sp. **A.** Female head. **B.** Postparasitic juvenile stoma, showing tooth. **C.** Female vagina. **D.** Preparasitic larva. **E.** Egg. **F.** Female tail. **G.** Postparasitic juvenile tail. **H.** Male, papillae pattern. **I.** Anopheline mosquito larva host. **J.** Male tail.

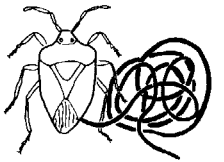
FIG. 18. *Perutilimermis culicis* n. gen. **A.** Female head. **B.** Preparasitic larval head. **C.** Postparasitic larval stoma, showing tooth. **D.** Female vagina. **E.** Preparasitic juvenile. **F.** Egg. **G.** Spicule, ventral. **H.** Postparasitic juvenile tail. **I.** Female tail. **J.** Male tail. **K.** *Aedes sollicitans* larva, showing a penetrating preparasitic larva. **L.** *Aedes sollicitans* adult host.

FIG. 19. *Neomesomermis flumenalis* n. comb. **A.** Male head, lateral view. **B.** Female head, dorsal-ventral view. **C.** Female vagina. **D.** Male tail. **E.** Female tail. **F.** Larval blackfly host.



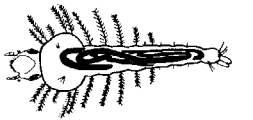
1

Aphid

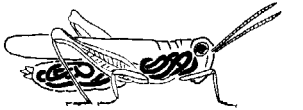


Stink Bug

Black Fly

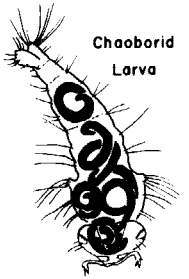


Anopheline Mosquito
Larva



Grasshopper

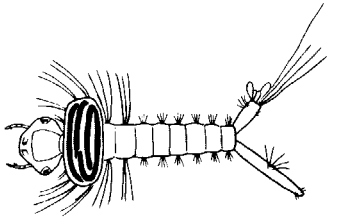
Plant Bug



Chaoborid
Larva

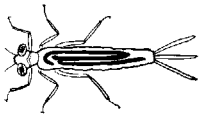
Termite

Ant

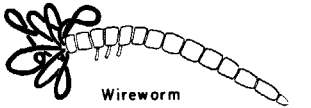


Culicine Mosquito
Larva

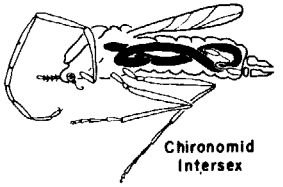
Sciarid
Larva



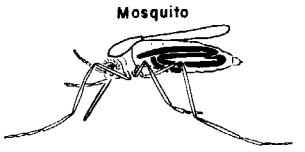
Damselfly
Nymph



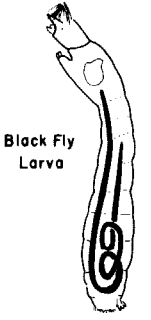
Wireworm



Chironomid
Intersex

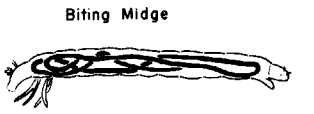


Mosquito

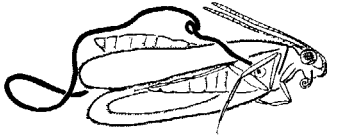


Black Fly
Larva

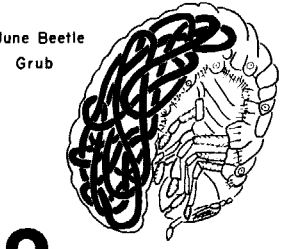
Potato
Beetle



Biting Midge

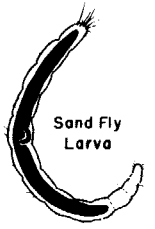


Apple Ermine Moth



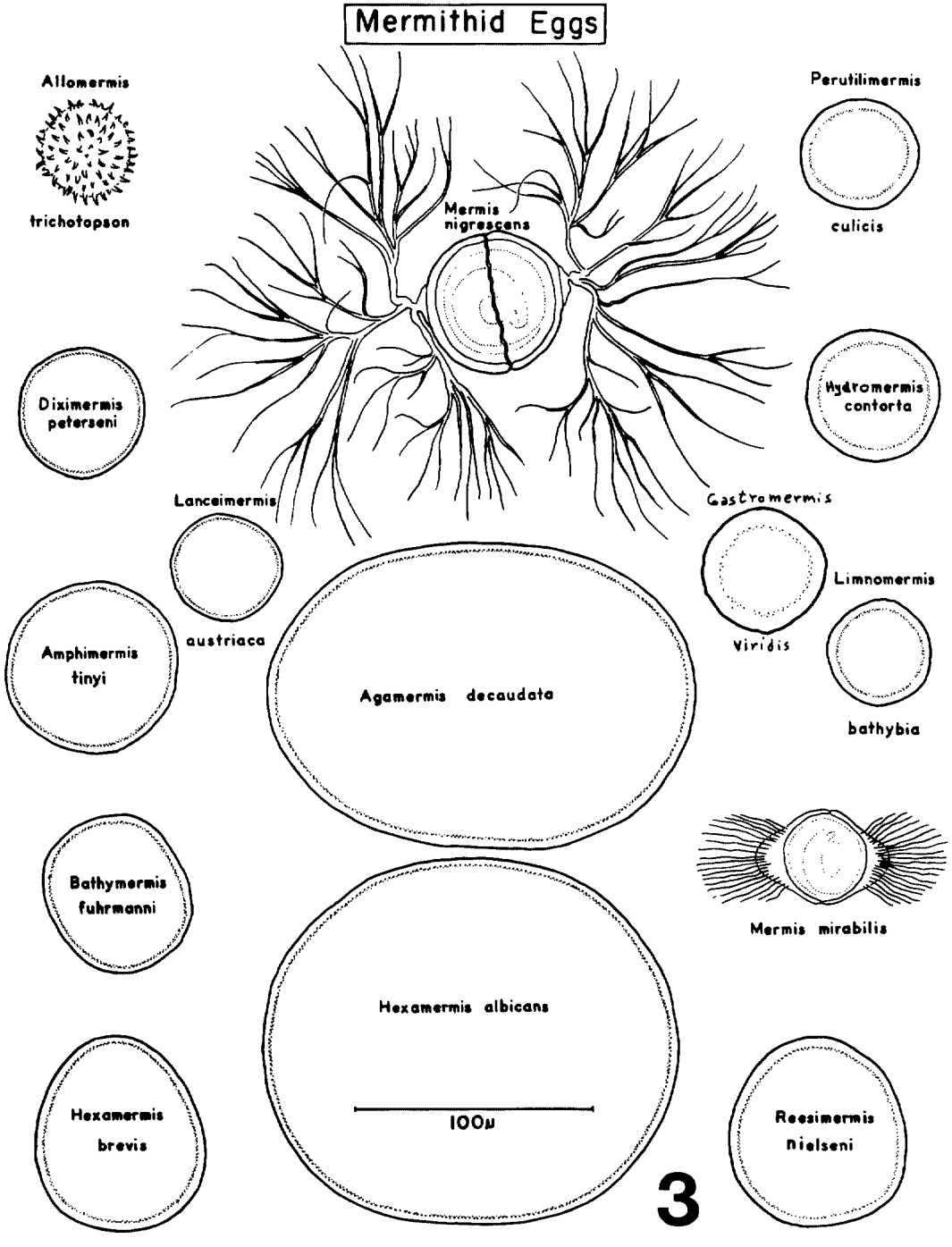
June Beetle
Grub

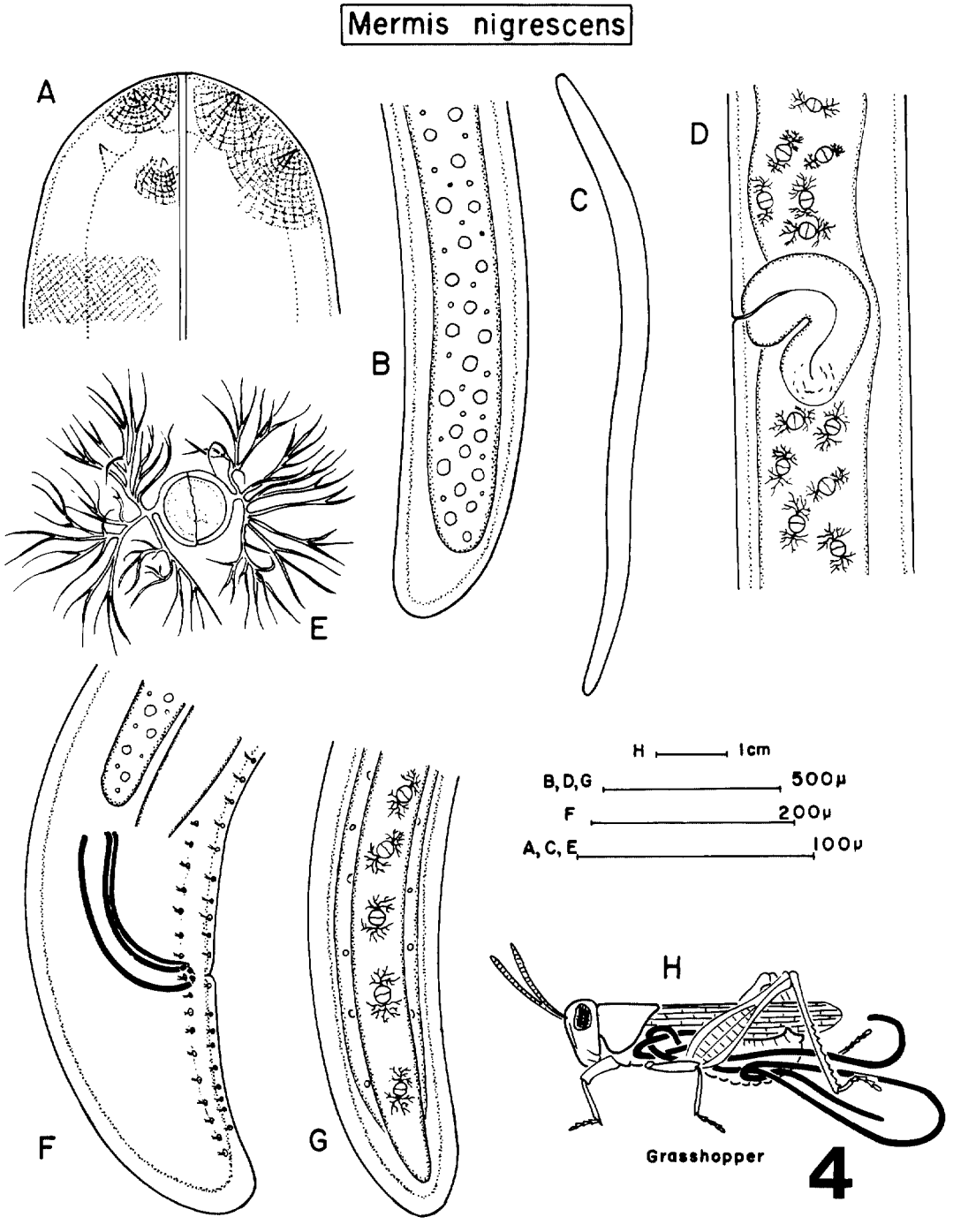
Gypsy Moth
Caterpillar

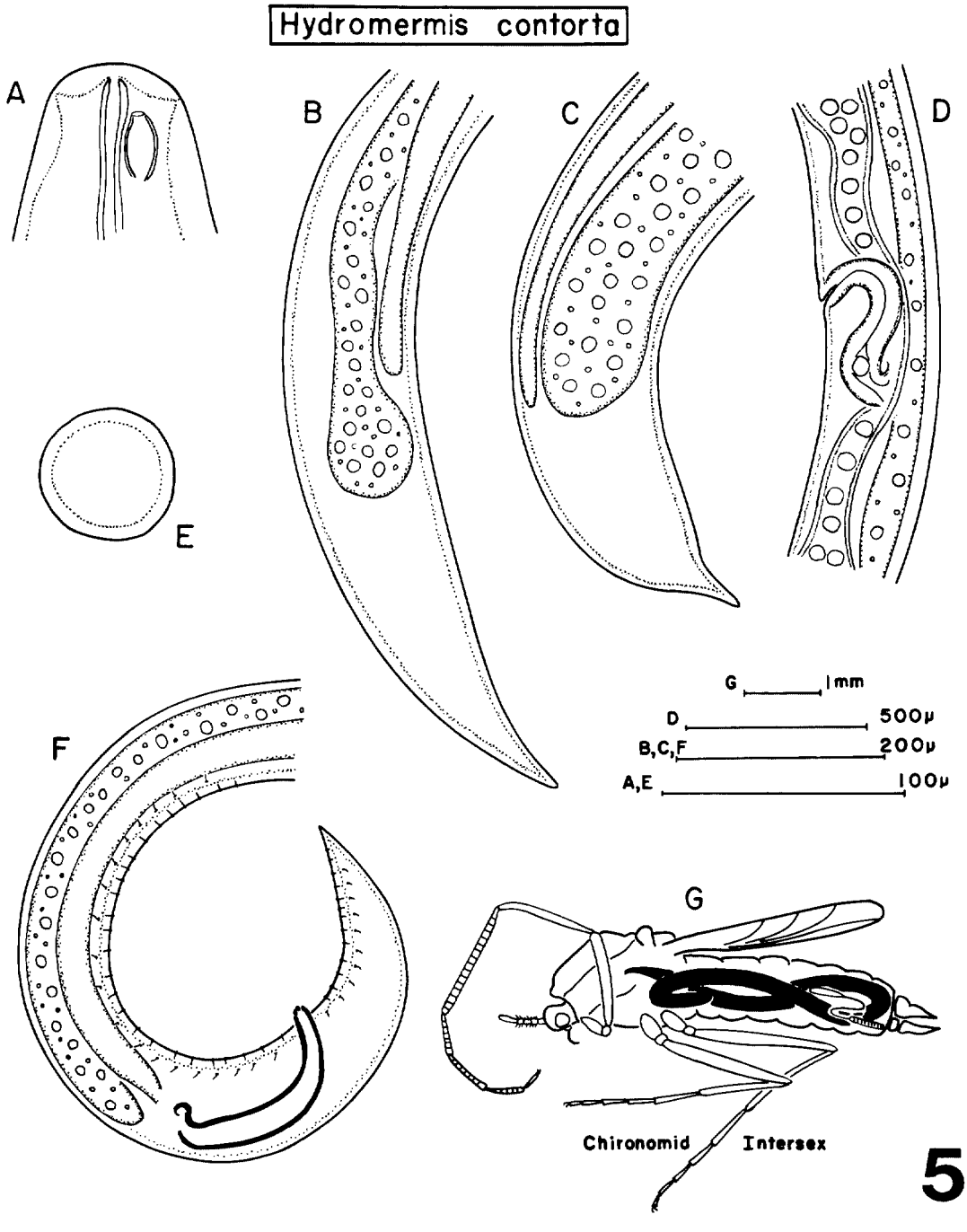


Sand Fly
Larva

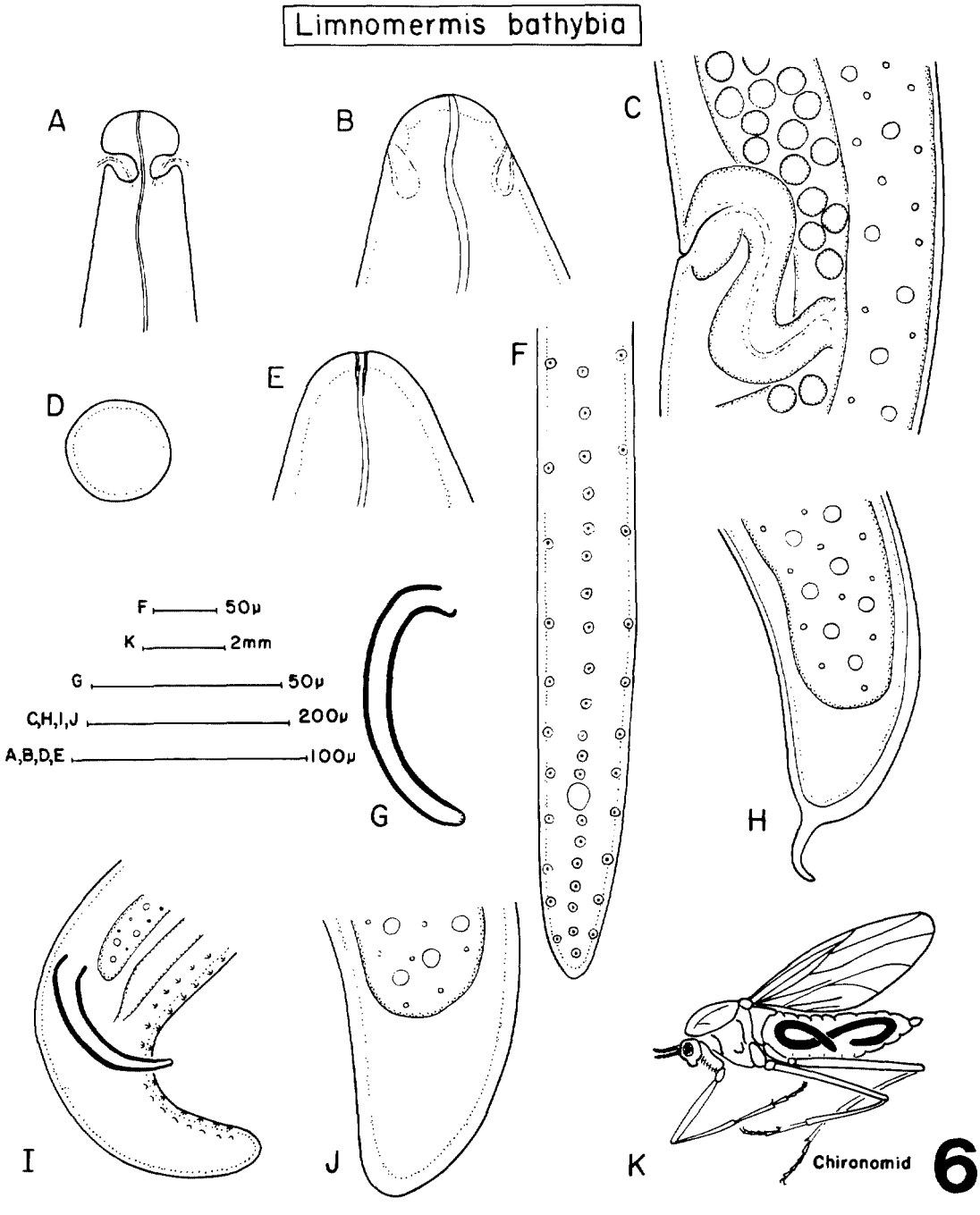
2


Mermithid Eggs
Allomermis
trichotopson
Perutilimermis
culicis
Mermis
nigrescens
Diximermis
peterseni
Hydromermis
contorta
Lanceimermis
austriaca
Gastromermis
viridis
Limnomermis
bathybia
Amphimermis
tinyi
Agamermis decaudata
Bathymermis
fuhrmanni
Mermis mirabilis
Hexamermis albicans
100µ
Hexamermis
brevis
Reesimermis
nielseni
3

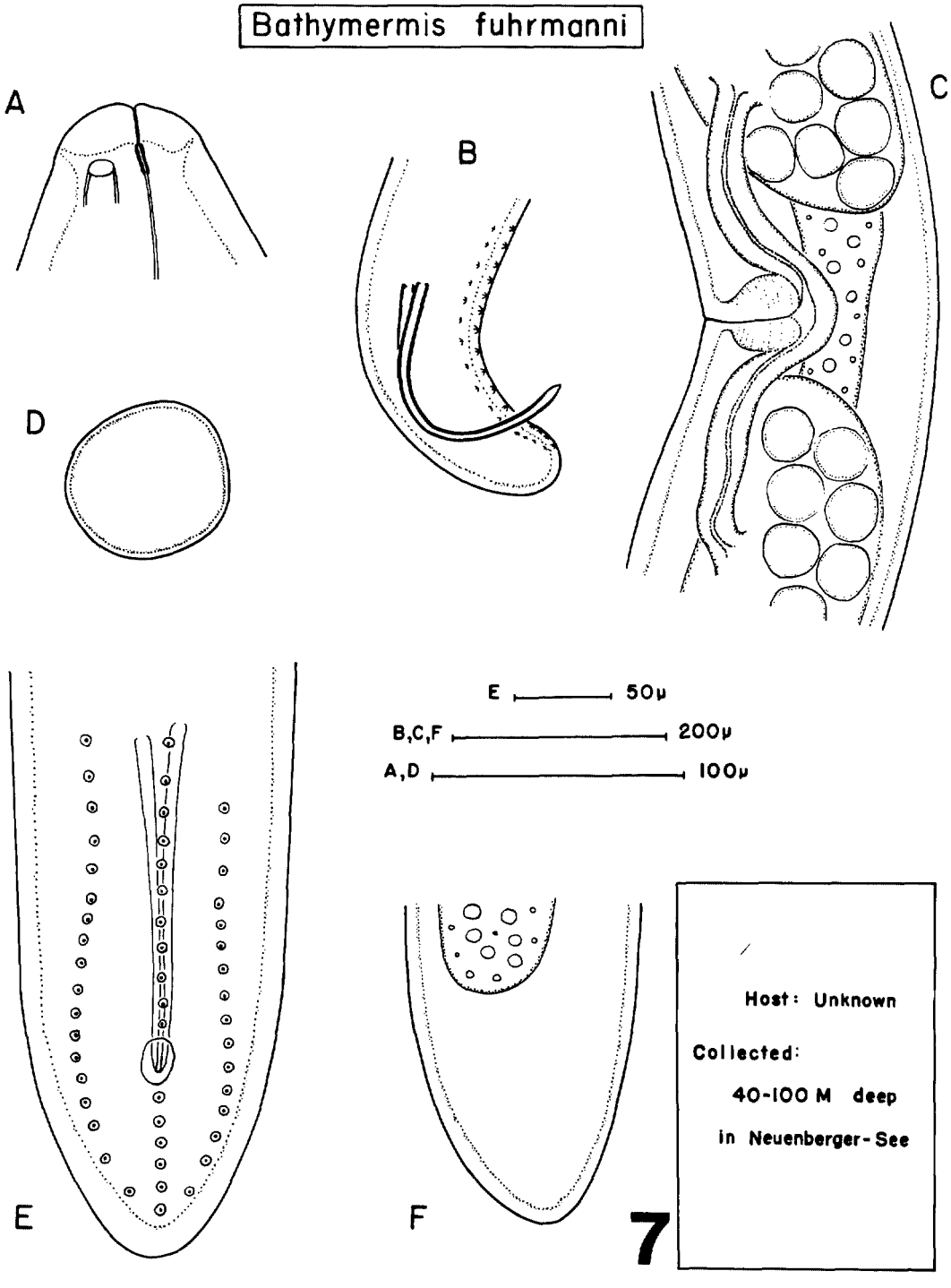

Mermis nigrescens
A
B
C
D
E
F
G
H
H 1cm
B, D, G 500μ
F 200μ
A, C, E 100μ
Grasshopper
4

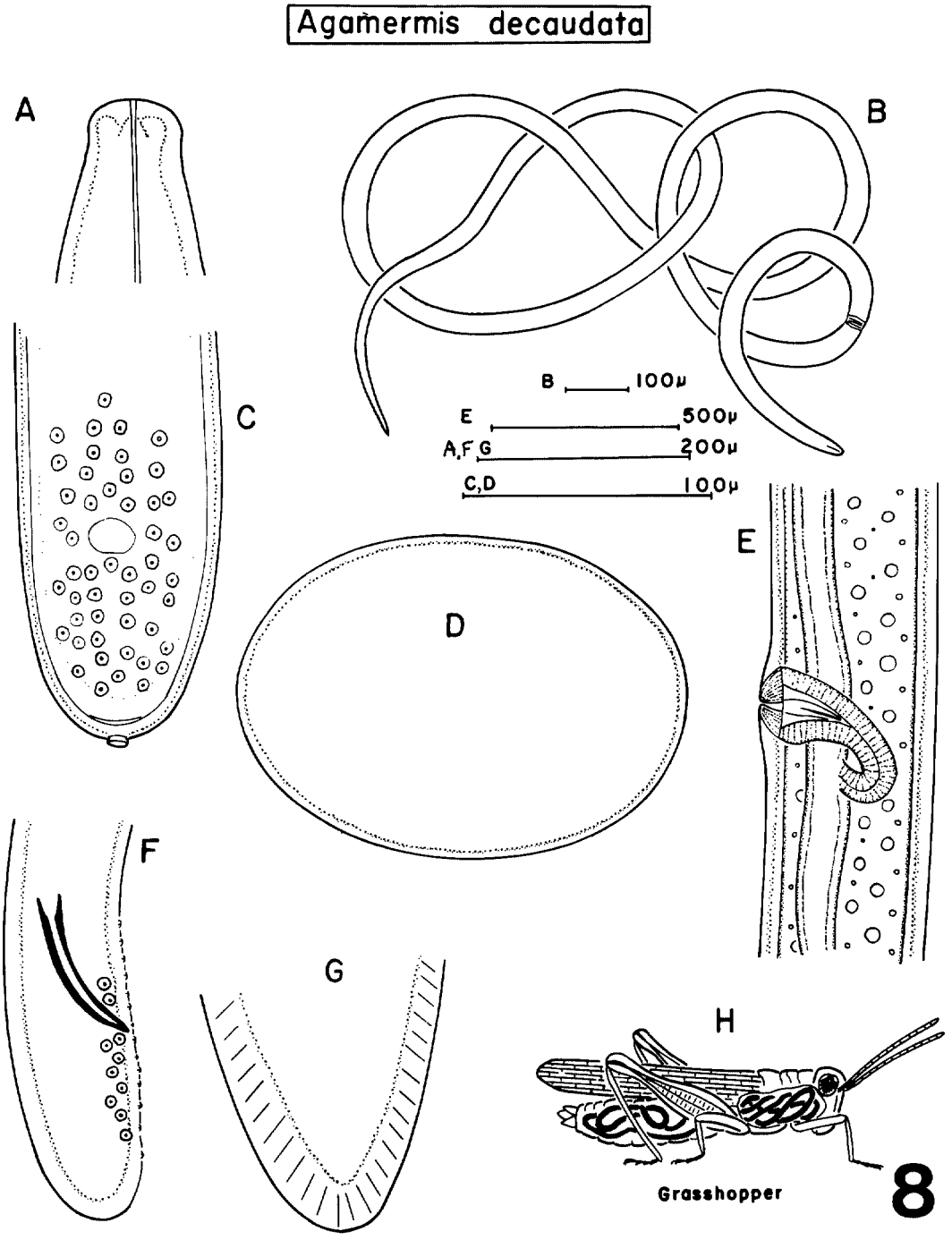

Hydromermis contorta
A
B
C
D
E
F
G
G 1mm
D 500µ
B,C,F 200µ
A,E 100µ
Chironomid Intersex

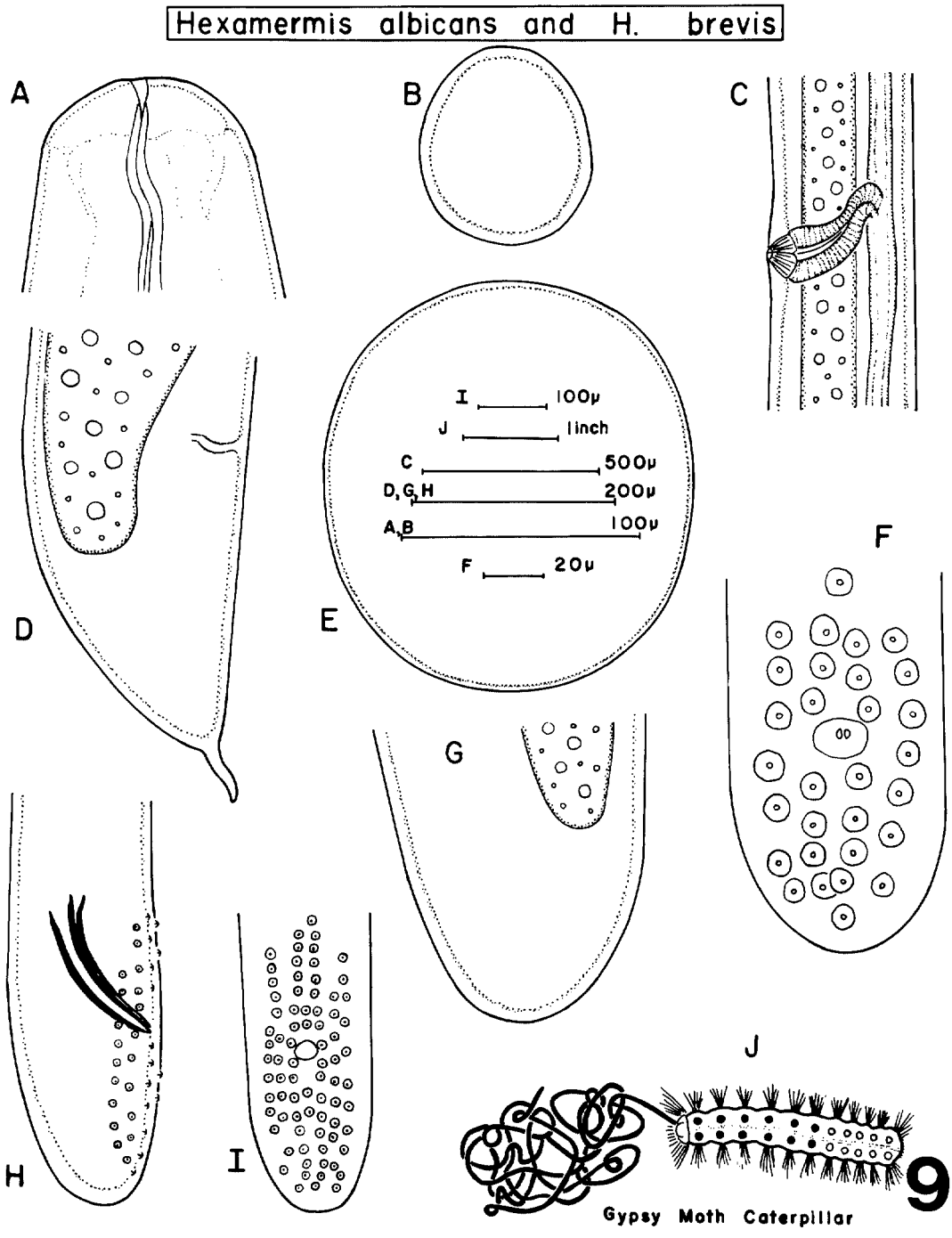
5

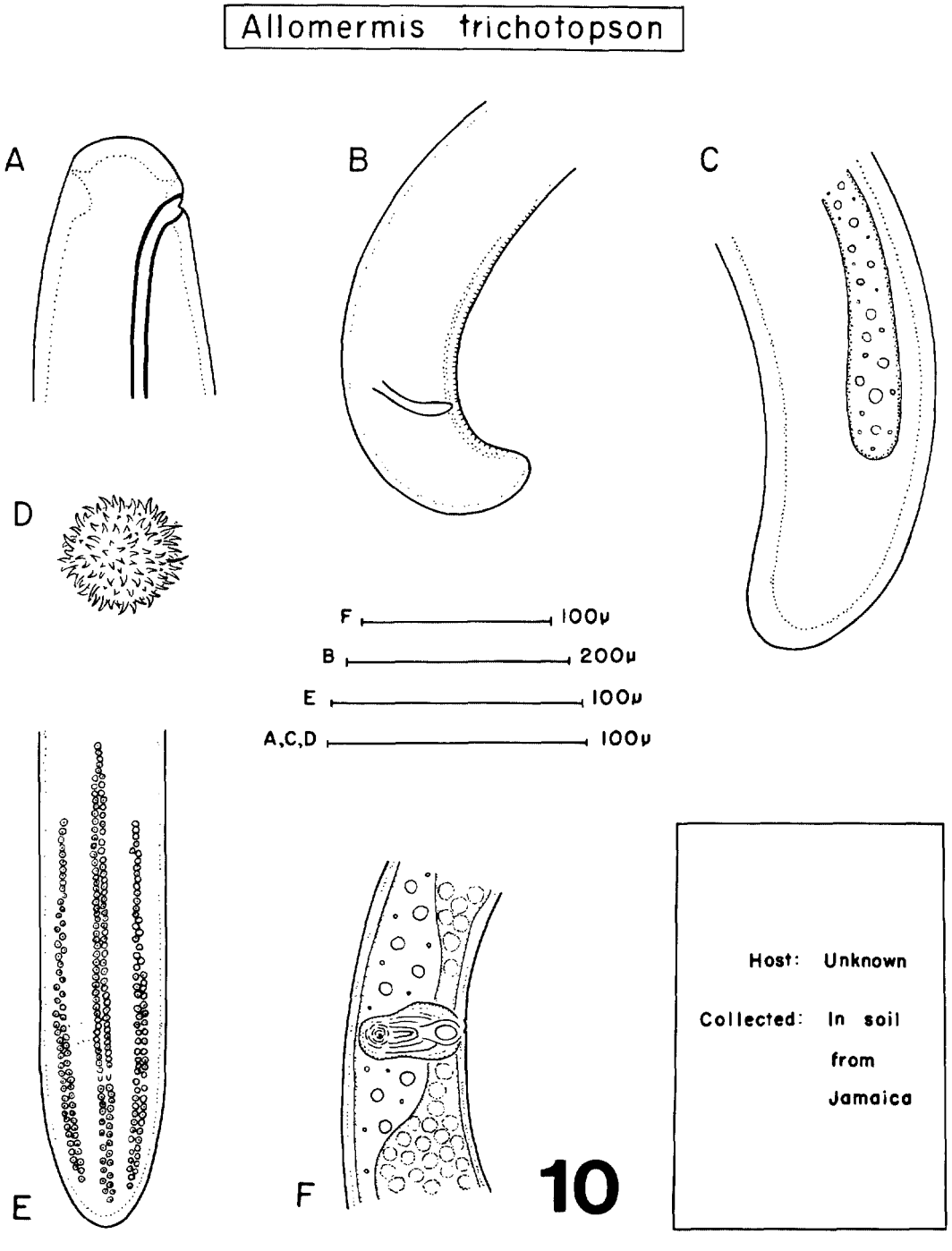

Limnomermis bathybia
A
B
C
D
E
F
F 50μ
K 2mm
G 50μ
C,H,I,J 200μ
A,B,D,E 100μ
G
H
I
J
K
Chironomid

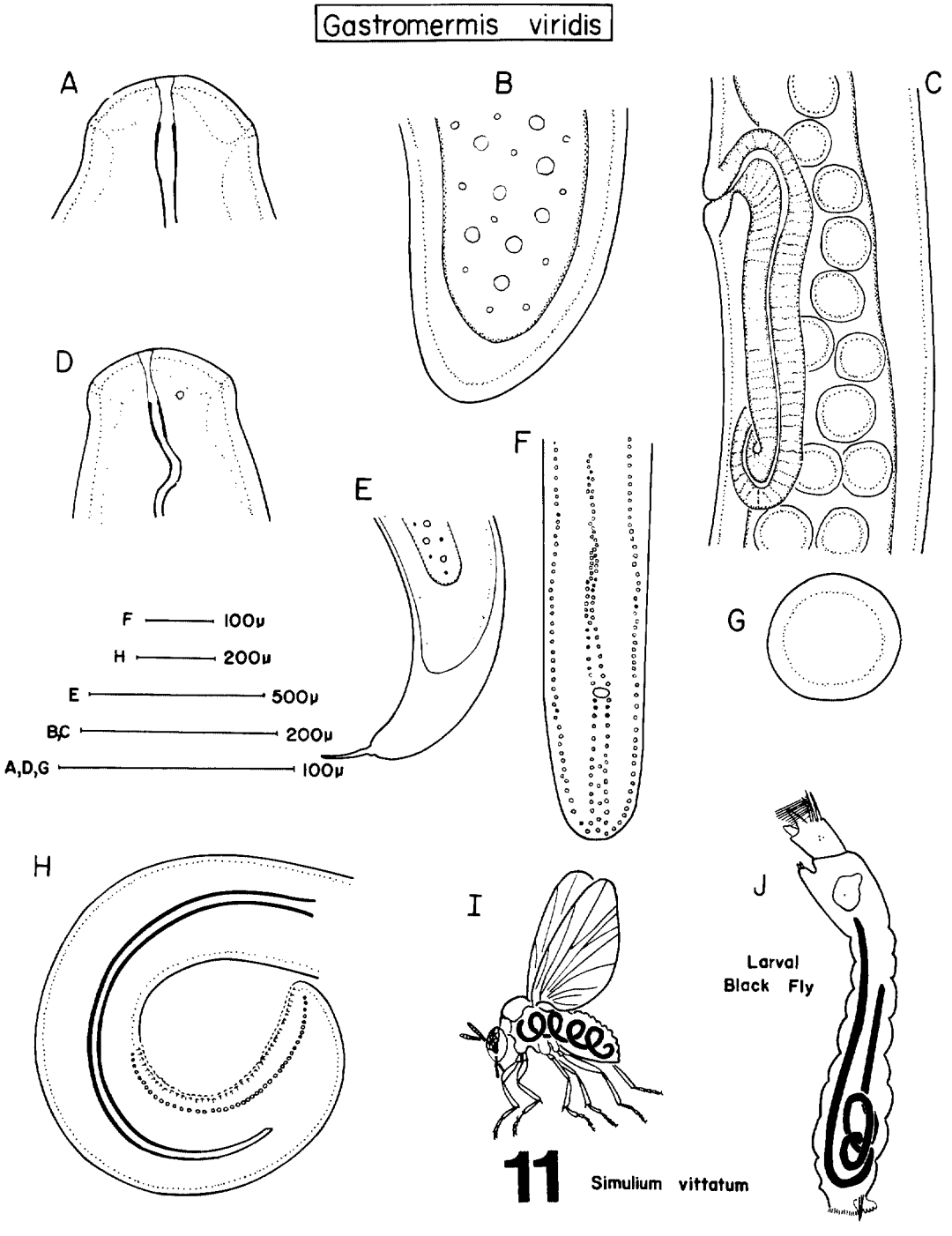
6


Bathymermis fuhrmanni
A
B
C
D
E
F
E 50µ
B,C,F 200µ
A,D 100µ
Host: Unknown
Collected:
40-100 M deep
in Neuenberger-See
7

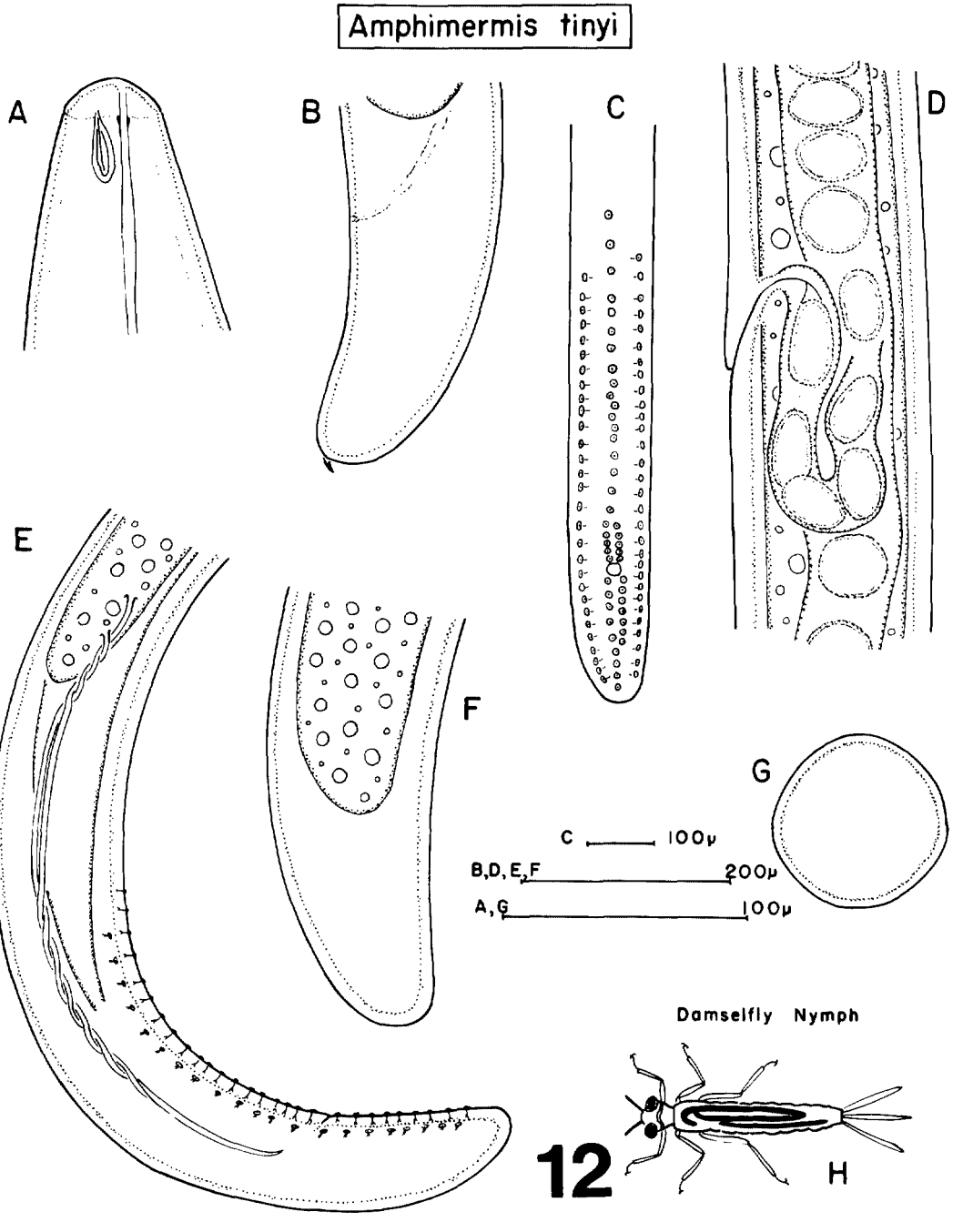

Agamermis decaudata
A
B
C
D
E
F
G
H
B 100μ
E 500μ
A,F,G 200μ
C,D 100μ
Grasshopper
8


Hexamermis albicans and H. brevis
A
B
C
D
E
I 100μ
J 1inch
C 500μ
D, G, H 200μ
A, B 100μ
F 20μ
F
G
H
I
J
Gypsy Moth Caterpillar
9

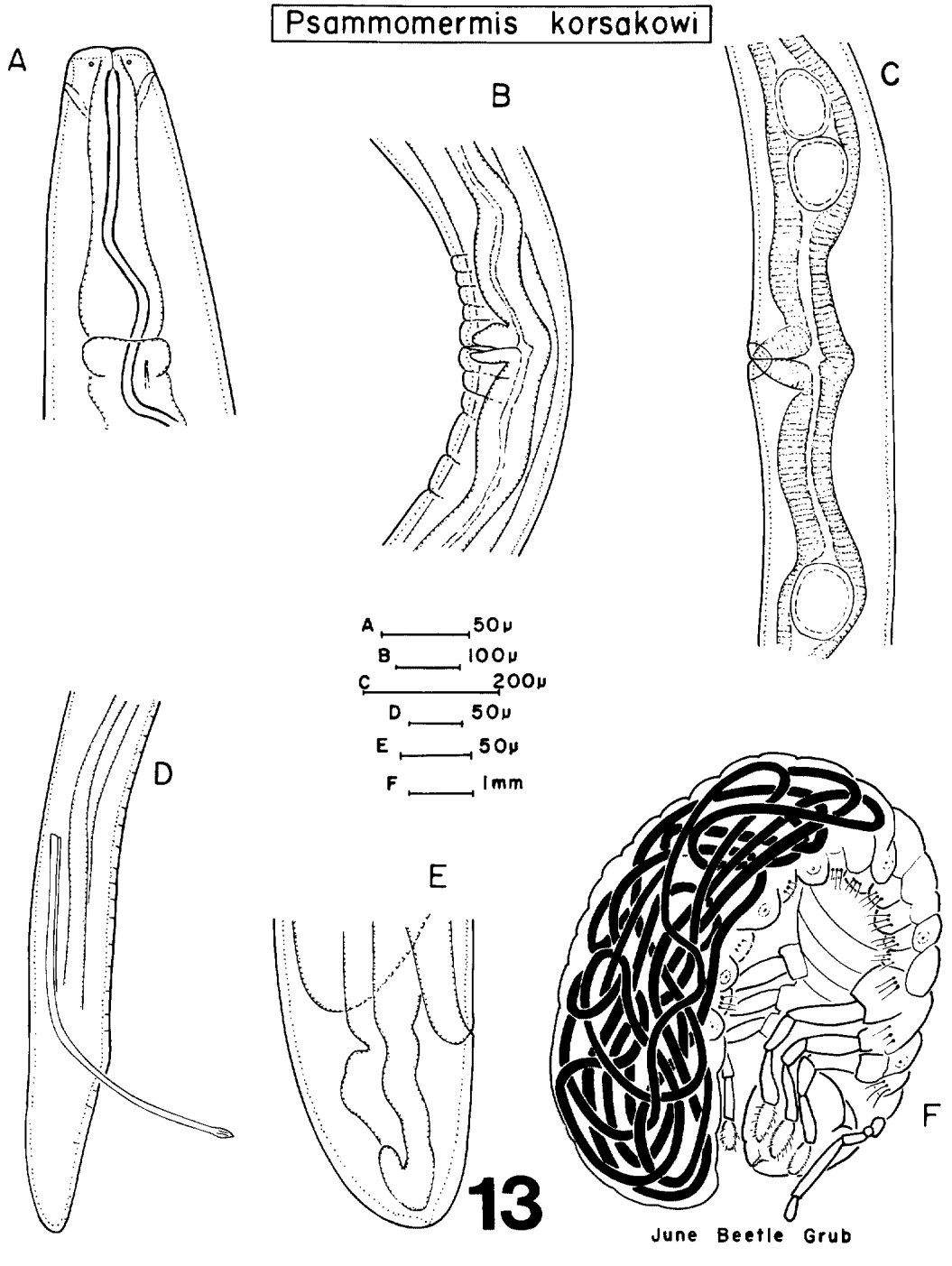

Allomermis trichotopson
A
B
C
D
F 100μ
B 200μ
E 100μ
A,C,D 100μ
E
F
10
Host: Unknown
Collected: In soil from Jamaica



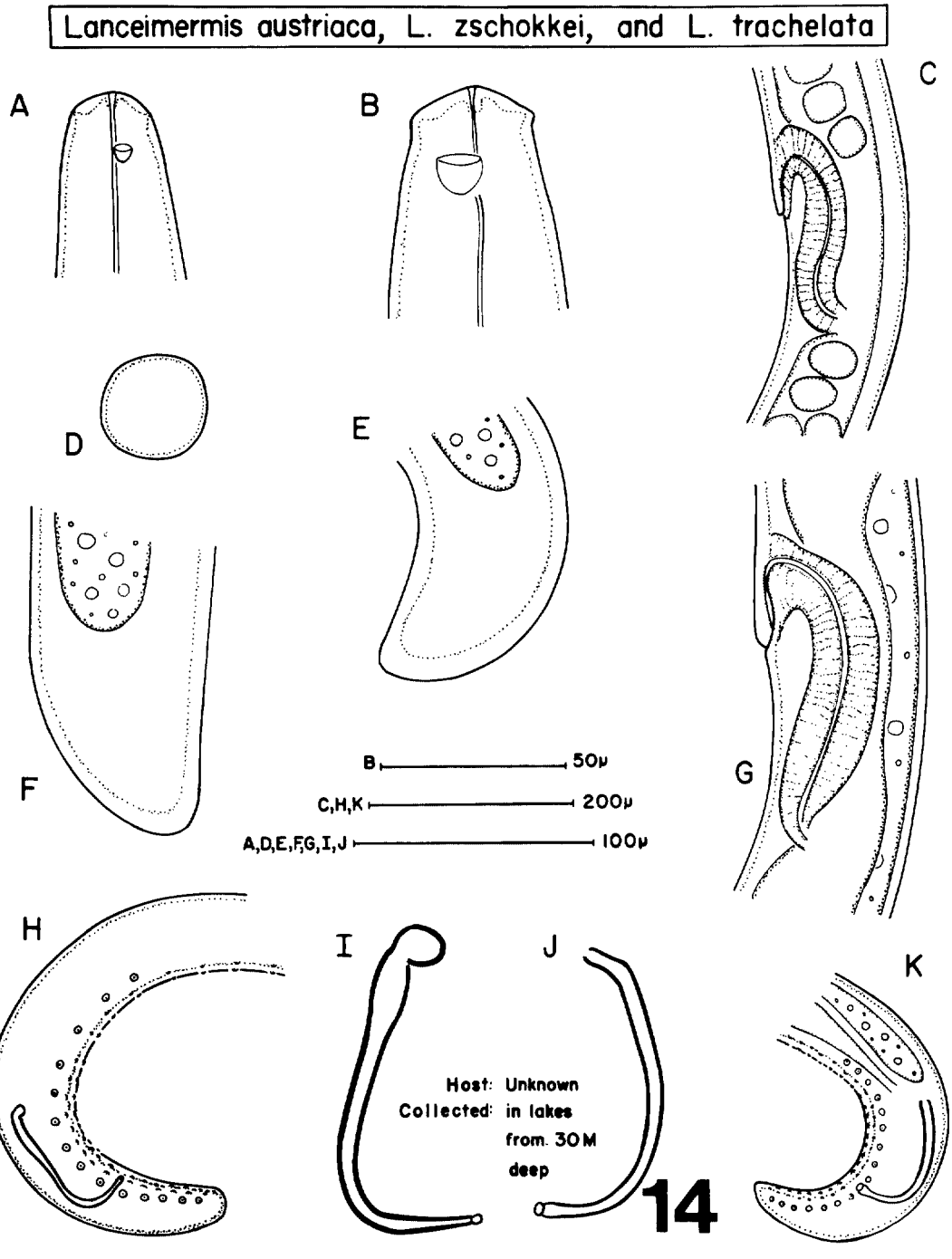
11 Simulium vittatum

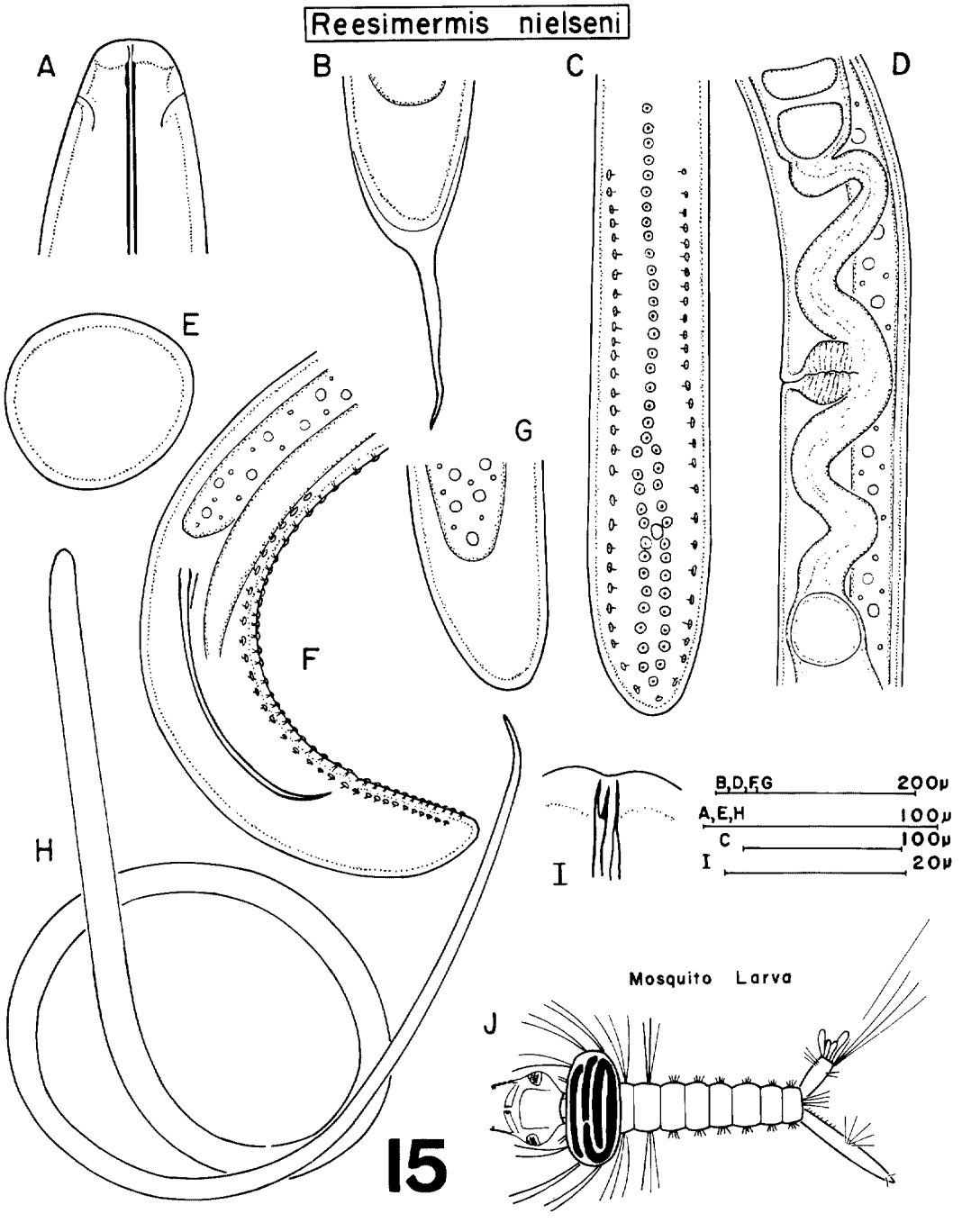

Amphimermis tinyi
A
B
C
D
E
F
G
C 100μ
B,D,E,F 200μ
A,G 100μ
Damselfly Nymph
H

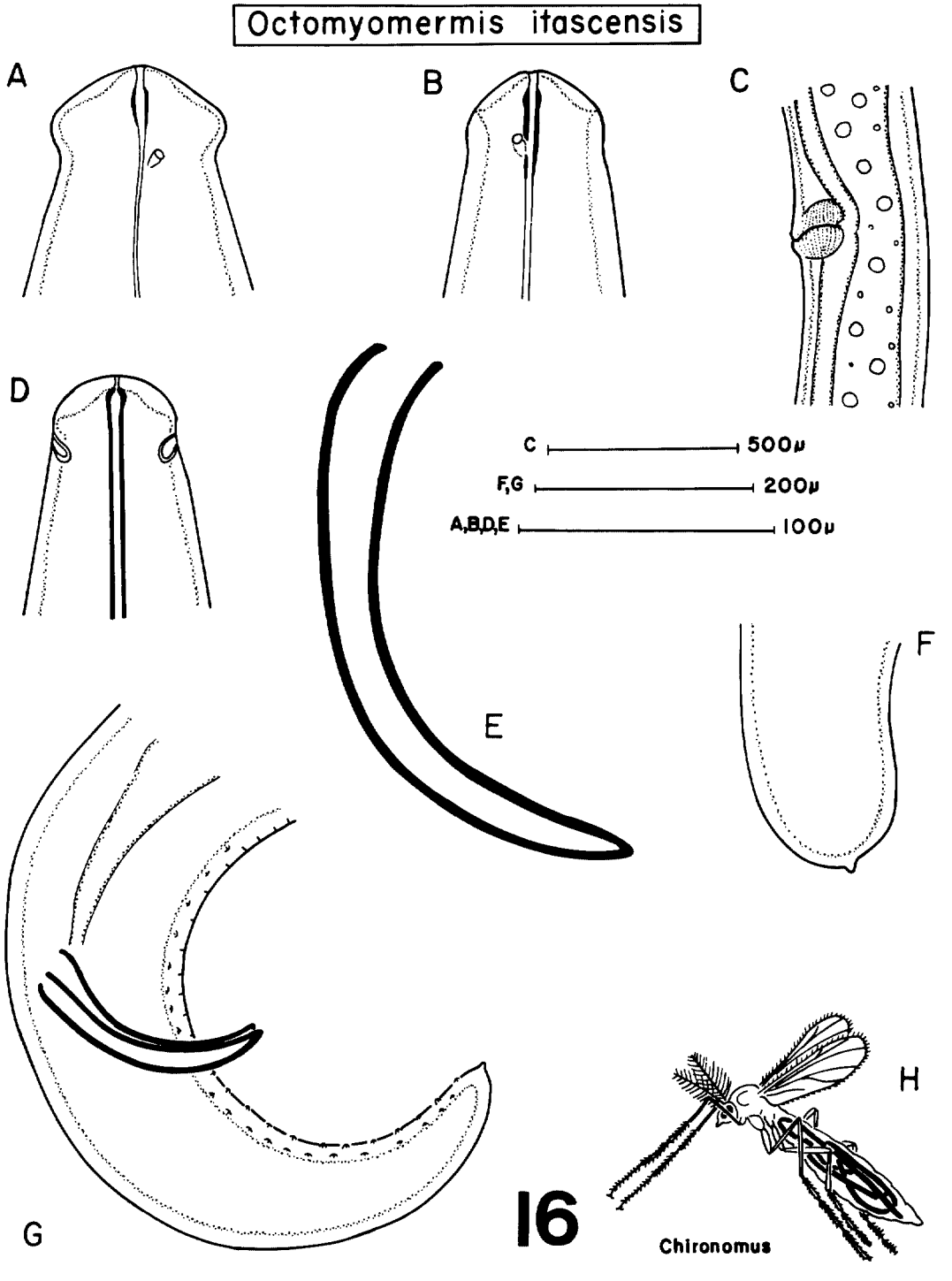
12

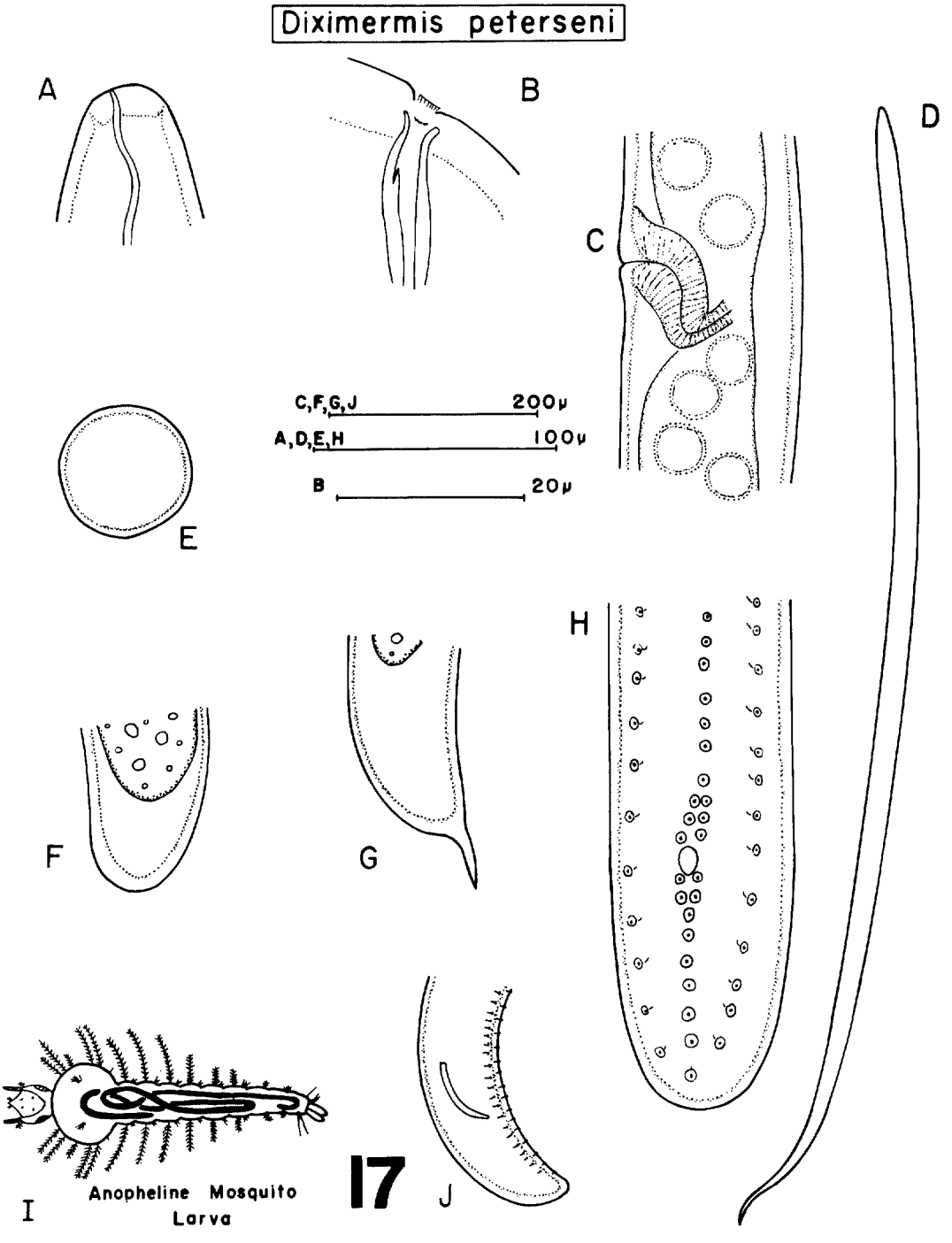

Psammomermis korsakowi
A
B
C
A 50μ
B 100μ
C 200μ
D 50μ
E 50μ
F 1mm
D
E
F
June Beetle Grub

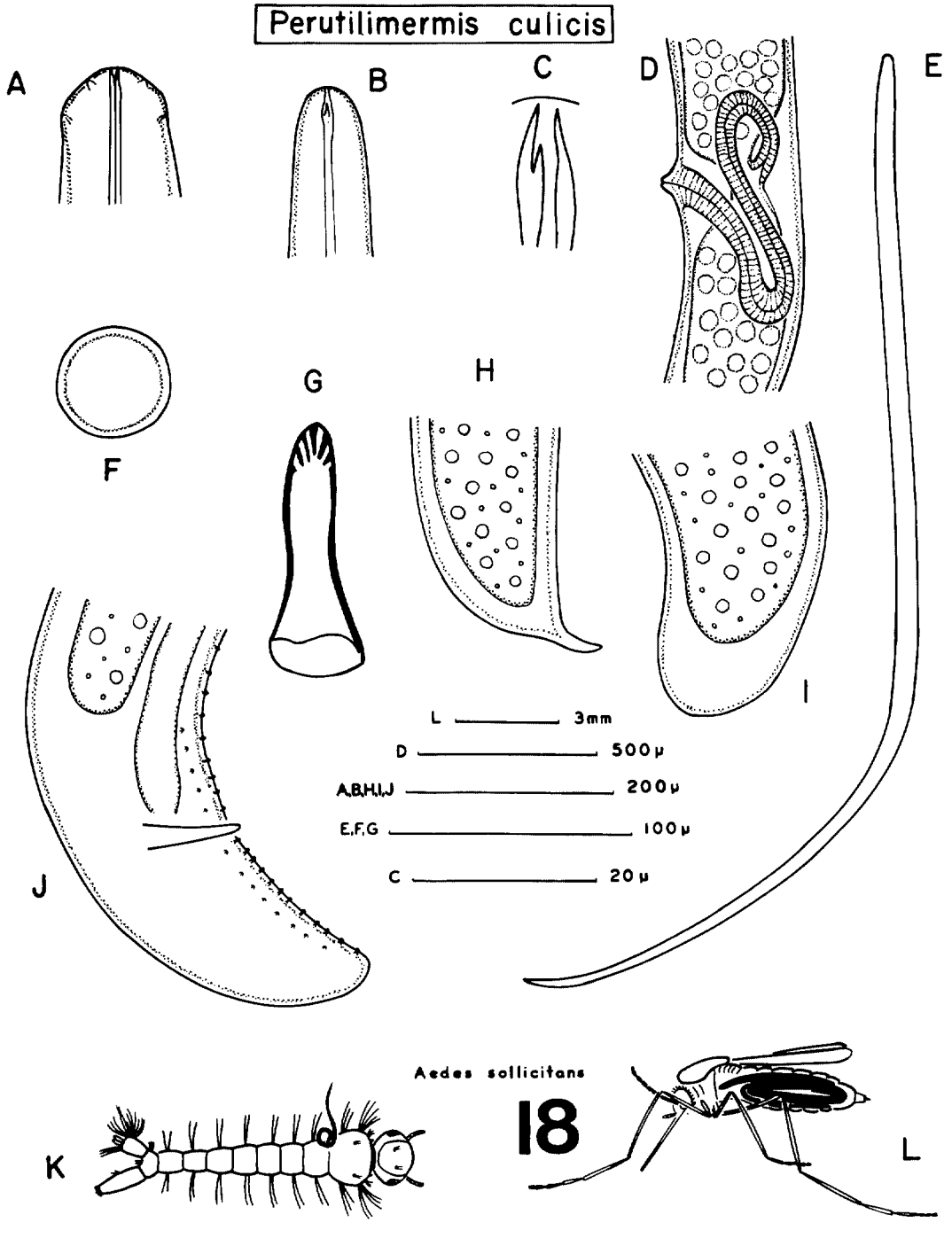
13

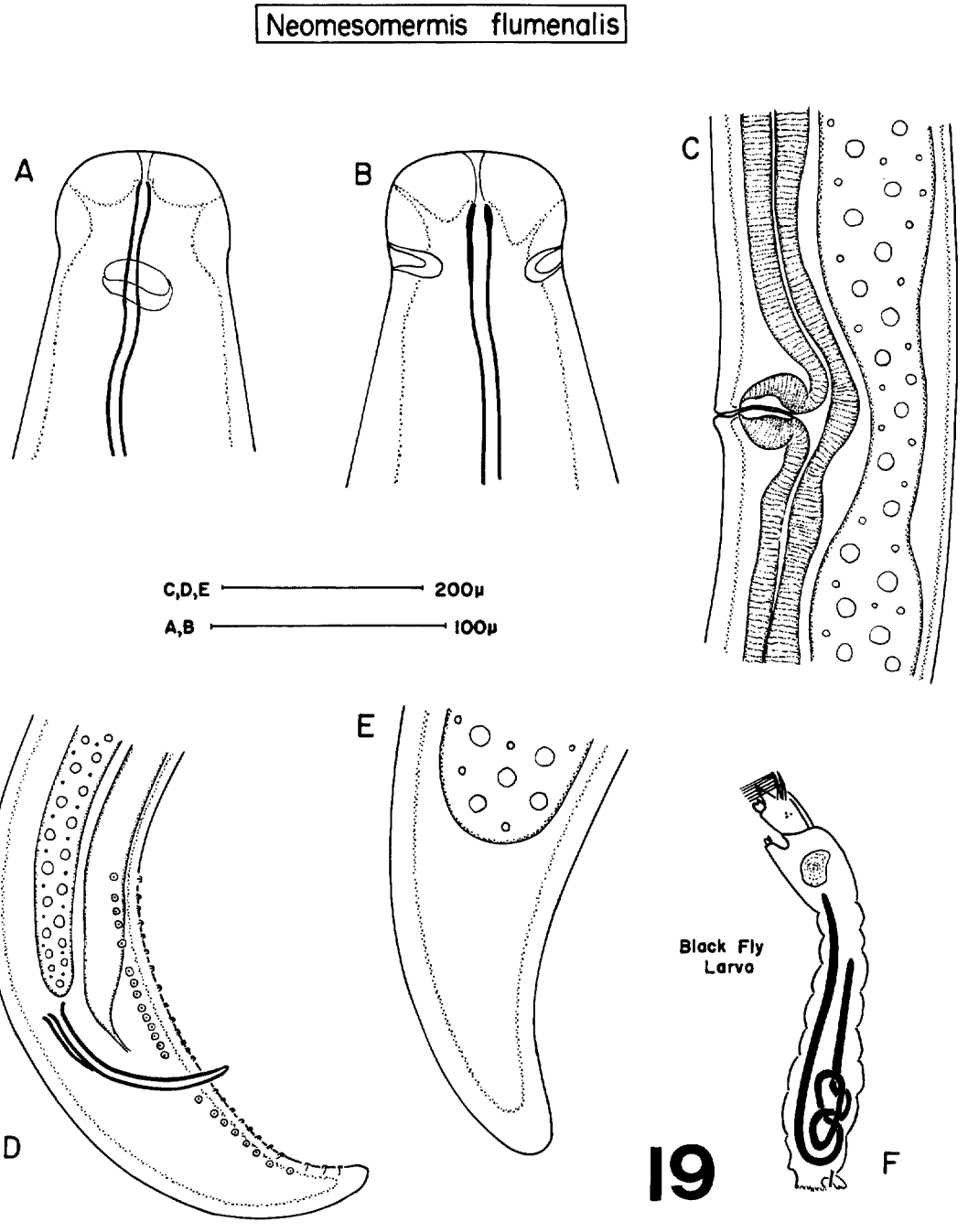

Lanceimermis austriaca, L. zschokkei, and L. trachelata
A
B
C
D
E
F
G
H
I
J
K
B 50μ
C,H,K 200μ
A,D,E,F,G,I,J 100μ
Host: Unknown
Collected: in lakes from 30 M deep
14


Reesimermis nielseni
A
B
C
D
E
F
G
H
I
B,D,F,G 200μ
A,E,H 100μ
C 100μ
I 20μ
Mosquito Larva
J
15


Octomyomermis itascensis
A
B
C
D
E
F
G
H
C 500μ
F,G 200μ
A,B,D,E 100μ
16
Chironomus


Diximermis peterseni
A
B
C
D
C,F,G,J 200μ
A,D,E,H 100μ
B 20μ
E
F
G
H
I
Anopheline Mosquito Larva
17
J


Perutilimermis culicis
A
B
C
D
E
F
G
H
I
J
K
L
L 3mm
D 500μ
A,B,H,I,J 200μ
E,F,G 100μ
C 20μ
Aedes sollicitans
18


Neomesomermis flumenalis
A
B
C
C,D,E 200μ
A,B 100μ
D
E
Black Fly Larva
F

19