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A Synopsis of the Obligate and Facultative Insect Parasitic Nematodes

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There are great challenges ahead in the field of insect nematology, as members of most insect orders are known to have nematode parasites. A few aspects of nematode parasitism of insects have been given. The host external and internal effects, host behavior, and incidents of host mortality resulting from nematode parasitization is discussed. Microscopical examination is usually necessary for classifying nematodes. A modification of a method for the fixing and mounting of insect parasitic nematodes is provided. A key to the obligate and the facultative nematode parasites of insects is presented. The families Mermithidae, Tetradonematidae, Diplogasteridae, Rhabditidae, Steinernematidae, Panagrolaimidae, Allantonematidae, Syrphonemetidae, Neotylenchidae, Sphaerulariidae, Entaphelenchidae, Aphelenchoididae, Thelastomatidae, and Carabonematidae have been included. Reference has been made to original literature for descriptions and diagrams of nematodes of each family as an aid to identification.

INTRODUCTION

Many believe that three nematode families, Steinernematidae, Allantonematidae, and Mermithidae, have the greatest potential for insect parasitism. The Steinernematidae have been considered to be the most adaptable because of their high reproductive potential, ability to parasitize many insect species, and ease of culture (Poinar, 1972). The Allantonematidae and the Mermithidae have potential for future insect control as they are obligate insect parasites (Nickle, 1967; Poinar, 1971b). On the other hand, Poinar (1972) has shown that the facultative parasities also have the capability of damaging or killing their hosts. Poinar (1972) defined facultative parasitic nematodes as those capable of parasitizing healthy insects yet retaining an ability to reproduce and develop in a free-living situation.

Wachek (1955) and Ruhm (1956) have presented excellent treatises on the biology, ecology, and systematics of the insect-parasitic Tylenchida of Europe. The use of nematodes to control insects have been reviewed by Welch (1958, 1962a), Poinar (1971b), Nickle (1972b), Benham and Poinar (1973), Gordon et al. (1973), and Peterson (1973).

Welch (1965), and more recently Nickle (1973), have stated that there are very few specialists in the field of insect nematology. It is because of this and the recent interest in insect nematology, i.e., Symposium on Parasitic Nematodes as a Means of Biological Control of Insects held at Lehigh University during June of 1972, that I feel a key to the obligate and facultative insect parasitic nematode families would aid invertebrate pathologists and entomologists in general. Aids in preparing specimens for identification are also presented. Reference has been made to the original literature for descriptions and diagrams of nematodes for each family in the key.

The effect of a nematode on its host may be a result of whether or not the nematode is well adapted to the host and whether the host is a normal host. Stoffolano (1970) is

of the opinion that many reports of parasitization are only incidental. More thorough investigations on the ecology, behavior, and physiology of nematodes may be necessary to determine normal hosts (Stoffolano, 1973). Along this line, Poinar (1965) felt that a sphaerulariid may be poorly adapted to its host as it sacrificed most of its own numbers by killing most of the host population. The effect of parasitism depends upon the characteristics of both the host and the parasitic nematode. The nemotodes have to endure and adapt to their host's life cycles. Host evolution and synchrony are part of the nematode's adaptations. Recently, efforts have been made to better understand host-parasite relationships (Davey and Hominick, 1973; Moore, 1973; Nappi, 1973; Webster, 1973). It is beyond the scope of this paper to review all the nematode-insect relationships that have been reported. Instead, I wish to discuss only a few selected instances of nematode parasitism.

Insect Host Effects from Nematode Parasitism

External Effects

Dissections are usually necessary to reveal the presence of parasitic nematodes (Welch, 1965). However, there are several other ways in which the effects of nematode parasitism can be observed. In some cases, the wings of ants and grasshoppers are shortened (Sugiyama, 1956), the elytra of weevils may be malformed (Poinar and Gyrisco, 1962), and primary and secondary sexual characteristics may be altered by the formation of intercastes and intersexes in the social insects Rempel et al., 1962). Besides the obvious exit from their hosts, mermithids may also cause a discoloration or transparency to the host cuticle sometimes enabling them to be seen (Welch, 1960; Poinar and Gyrisco, 1962). Insects parasitized by members of the Tetradonematidae display swollen abdomens (Ferris and Ferris, 1966). The head capsule of immature flies parasitized by tetradonematids is often small, indicating that the maggots fail to make normal molts. Ants that are parasitized by mermithids take on distinct morphological shapes from the norm which makes their classification difficult (Wheeler, 1928). Wulker (1964) has also reported morphological changes in chironomids due to nematode parasitism.

Internal Effects

There are many accounts of nematodes causing some degree of reduction in the host's reproductive capacity. Members of the Allantonematidae (Ruhm, 1956), the Neotylenchidae (Bedding, 1968), and the Tetradonematidae (Van Waerebeke and Remillet, 1973) may cause complete sterility. In some cases there may be a complete prevention of egg production (Schvester, 1957). Treece and Miller (1968) and Stoffolano (1970) reported castration of face flies due to allantonematid parasitization. Poinar (1970) found a rhabditid in the bursa copulatrix of female scarabaeids. It is unknown whether the nematode was responsible for a reduction in the number of viable sperm cells passing through the bursa copulatrix to the spermatheca. Another rhabditid was found in the pharyngeal glands of the argentine ant, and gland function was evidently lost(Markin and McCoy, 1968). Infected bark beetles may have reduced fat bodies (Massey, 1960b). Members of the Thelastomatidae develop and reproduce within the alimentary canal of insects; lesions of the alimentary canal wall have been detected (Poinar, 1973). Members of the Rhabditidae may damage the walls of the proventriculus of bark beetles (Nickle, 1963).

Host Behavior

Bumblebees infected with a sphaerulariid did not build nests during the spring but continued to swarm through the summer until death (Poinar and Van der Laan, 1972). Sciarid flies heavily parasitized with sphaerulariids were observed to stop feeding and throw their heads into the air making biting motions at their anal region (Poinar, 1965). Stoffolano (1970) has ob-

served a failure of allantonematid parasitized face flies to frequent breeding places. Ashraf and Berryman (1970) found that bark beetle flight might be impaired. Also, infected adults displayed an aberrant attack behavior. The reduction in the length of bark beetle ovipositional gallery formation may be directly proportional to the per cent of parasitization (Massey, 1962, 1966).

Host Mortality

Host mortality is the result of infection by members of the Mermithidae and Steinernematidae. The infective mermithid juvenile usually enters the host by direct cuticular penetration. After a period of growth (completely occupying host interior), the juvenile leaves its host, killing it, to enter the environment and mature. According to Ferris and Ferris (1966), hosts heavily parasitized with tetradonematids leave several thousand eggs in the host cadaver.

Third-stage steinernematid juveniles are ingested by their hosts. These nematodes immediately penetrate through the alimentary canal into the hemocoel and become adults. Death of the insect host results in approximately 48 hr from a bacterium which has been introduced into the host hemocoel by the nematode (Dutky, 1959; Poinar, 1966; Poinar and Himsworth, 1967; Poinar and Thomas, 1967). After 2 weeks, the third-stage juveniles from second generation adults exit from the host cadaver.

Allantonematids may cause massive cellular necrosis in the internal organs and disruption of the digestive processes, such as entering and obstructing the rectum resulting in death of the host (Filipjev and Stekhoven, 1959). Death resulted to a cerambycid beetle (Merrill and Ford, 1916) and to lepidopterous larvae (Weiser, 1966) following intestinal penetration by diplogasterids. Many diplogasterids and other rhabditids may enter the host cadaver to feed on bacteria and other microorganisms; these should not be confused with being the cause of death.

Preparation of Nematodes

When searching for nematode parasites, host insects should be dissected in saline or Ringer's solution to prevent rupturing of the nematode brought about by a change in the osmotic concentration. Nematodes are killed, fixed, and preserved in the following manner.

Specimens are gently heated in a drop of water on a microslide until they stop moving. Continuous observation under a dissecting microscope will determine when death occurs. The nematodes should be fixed in a 3% solution of formalin or, even better if available, TAF (2 ml of triethylamine, 91 ml of water, and 7 ml of 40% formalin). Nematodes should never be placed directly into a fixative, because they will invariably become distorted.

There are a number of methods to process the fixed specimens to glycerin (see Southey, 1970), but the following gives good success in most instances. The nematodes are placed in a beaker of 20 parts ethanol, 79 parts water, and 1 part glycerin. Place this beaker into a second beaker containing 95% alcohol and transfer to an oven at 35–40°C for 12 hr. Next, transfer the nematodes into another beaker containing 7 parts glycerin and 93 parts of 95% alcohol. Cover partially with a lid (to allow for evaporation of the alcohol) and allow to set at room temperature (approximately 20°C) for 7 days.

When the nematodes are now in pure glycerin, transfer 6 or 7 specimens to a drop of glycerin on a microscope slide. Position them as if they were spokes of a wheel separating every other nematode with a fine wire or a piece of crushed glass equal to the diameter of the specimens. These will act as a support so that the coverslip will not crush the nematodes. The rim of the coverslip is then sealed to the slide with ZUT, Epoxy enamel, or fingernail polish.

Key to Insect Parasitic Nematode Families

When attempting to classify nematodes, one should become familiar with

the terminology used to describe the buccal region (stoma), esophagus, male and female reproductive systems, and the male and female tail ends. A glossary of nematological terms has been prepared by Caveness (1964). For a good view of a generalized nematode, refer to Jenkins and Taylor (1967); important diagnostic characters are shown and labeled.

My purpose is to present a key to the obligate and facultative insect parasites, therefore, I have not included the Spiruroidea and Filarioidea. Members of these latter groups are parasitic in vertebrates and use insects as intermediate hosts. The spirurids commonly occur in insects such as scarabaeids, tenebrionids, and blattarians that feed on animal droppings. Spirurids are encapsulated within the wall of the host insect alimentary canal. Some spirurids have been found in the hemocoel. Microfilariae may be found in the blood-sucking insects such as culicids, tabanids, simuliids, and siphonapterans, which serve as intermediate hosts. Recently, Beckett (1971) has found that mosquito flight muscles may be damaged when third-stage juveniles leave the muscles and enter the hemocoel.

The Cylindrocorpidae, Chambersiellidae, Cephalobidae, Tylenchidae, Paurodontidae, and Aphelenchidae have not been included because members of these families have only been found in close association with insects such as in the larval and egg galleries and feces of bark beetles (Sharga, 1932; Filipjev and Stekhoven, 1959; Massey, 1960a, 1963, 1967; Massey and Hinks, 1970). Future investigations may show these to be insect parasites. Also, the Nematomorpha have not been included. These "hairworms" or "horse hairworms," as they are commonly called, are not nematodes, yet are often confused with merimithids. They differ by being entirely brown and having an outer cuticle which is thick and leathery.

The key is based almost entirely on nematode structure, and only in a few instances are references made to ecological situations. Refer to Table 1 for a listing of the families in the key. References to the original descriptions are given to obtain representative diagrams for each family.

1A. Nematodes filiform in shape, elongated, and threadlike, generally over 1 cm in length; usually only juveniles are present in the host . . . DORYLAIMIDA, Mermithoidea 2

B. Nematodes variable in shape, rarely filiform; usually under 1 cm long; various stages including adults may occur in the host 3

2A. Juvenile nematodes in insect host only (with the exception that some adult nematodes have been found in chironomid hosts); adult nematodes are free-living and are white, yellow, rose, green, or sometimes partly brown; musculature, amphids, and cephalic papillae in adults well developed; esophagus (stichosome) bearing 8 or 16 large cells (stichocytes) . Mermithidae

B. Insect host containing newly formed adult nematodes; mating may occur and eggs may be deposited, but do not hatch in living host; musculature, amphids, and cephalic papillae in adult nematodes inconspicuous; esophagus bearing 4 large cells (tetrad) . . . . . Tetradonematidae

3A. Stoma a hollow tube lined with 5 triads of rhabdions; terminal esophageal bulb with valves (except for the Diplogasteroidea); teeth, when present, on metarhabdions; excretory system with 2 lateral canals; body cuticle usually smooth . . . . . RHABDITIDA 4

B. Stoma containing a hollow spear; terminal esophageal bulb without valves; excretory system with a single lateral canal; body cuticle annulated except in parasitic female TYLENCHIDA 10

4A. Dauer-stage nematodes covered with an oily film (lipophilic); anterior part of esophagus with a muscular valvated median bulb; terminal esophageal (basal) bulb glandular and without valves; metarhabdion of stoma modified into a tooth . . . . . .Diplogasteroidea, Diplogasteridae

B. Dauer-stage nematodes not lipophilic; anterior part of esophagus cylindrical (rarely with a slight swelling), if a slight median bulb is present, it lacks valves; terminal esophageal (basal) bulb with values; stoma an open tube with rhabdions separate or fused . . Oxyuroidea, Rhabditoidea 5

5A. Female (sometimes male) nematode tail drawn out to form a long spike; nematodes found in alimentary canal . . . . . Oxyuroidea, Thelastomatidea

B. Nematode tail not drawn out to form a long spike; with the exception of the Syrphonematidae, nematodes usually are not found in alimentary canal . . . . . Rhabditoidea 6

6A. Esophagus straight, lacking a median and basal bulb 7

B. Esophagus variable, with a median and/or basal bulb 8

7A. Nematodes occurring in the alimentary canal lumen of syrphid flies . . . . . Syrphonematidae

B. Nematodes occurring in the body cavity of carabid beetles . . . . . Carabonematidae

8A. Adult female nematode with a single ovary reflexed 2 to 3 times past vulva; stoma V-shaped, anterior portion a wide chamber . . . . . Panagrolaimidae

B. Adult female nematode with an ovary or ovaries only slightly reflexed past vulva; stoma with parallel sides 9

9A. Stoma long, easily seen; reproducing female nematodes not elongate and swollen (usually less than 0.5 cm in length) . . . . . Rhabditidae

B. Stoma very short, difficult to see; reproducing female nematodes often elongated and swollen and may reach 1 cm or more (especially first generation females found in dead insect host) . . . . . Steinernematidae

10A. Nematodes with an esophageal median bulb . . . . . Aphelenchoidea 11

B. Nematodes without an esophageal median bulb . . . . . Sphaerularioidea, Neotylenchoidea 12

11A. Juvenile nematodes in body cavity . . . . . Aphelenchoididae

B. Adult nematodes in body cavity . . . . . Entaphelenchidae

12A. Adult parasitic nematodes with only 2 esophageal glands, lacking a functional dorsal esophageal gland opening (there may be a remnant) . . . . . Sphaerularioidae, Sphaerulariidae

B. Adult parasitic nematodes with 3 esophageal glands . . . . Neotylenchoidea 13

13A. With 2 types of free-living female nematodes, one capable of parasitizing insects and one capable of establishing a feeding cycle on fungi . . . . . Neotylenchidae

B. With 1 type of free-living female nematode which is only capable of infecting insects, no plant feeding generation has been established . . . . . Allantonematidae

TABLE 1

THE FACULTATIVE AND OBLIGATE NEMATODE FAMILIES PARASITIC IN INSECTS WITH REFERENCES TO SELECTED REPRESENTATIVE ORIGINAL DESCRIPTIONS

Category	Reference
RHABDITIDA	
Rhabditoidea	
Rhabditidae	Massey (1956)
	Poinar (1970)
	Massey (1971)
	Poinar (1971a)
Steinernematidae	Steiner (1929)
	Poinar (1967)
Syrphonematidae	Laumond and Lyon (1971)
Carabonematidae	Stammer and Wachek (1952)
Panagrolaimidae	Lazarevskaya (1960)
Diplogasteroidea	
Diplogasteridae	Fedorko and Stanuszek (1967)
Oxyuroidea	
Thelastomatidae	Poinar (1973)
DORYLAIMIDA	
Mermithoidea	
Mermithidae	Welch (1960)
	Welch (1962b)
	Poinar (1968)
	Poinar and Welch (1968)
	Nickle (1972a)
Tetradonematidae	Cobb (1919)
	Ferris and Ferris (1966)
	Nickle (1969)
	Van Waerebeke and Remillet (1973)
TYLENCHIDA	
Neotylenchoidea	
Neotylenchidae	Hocking (1967)
	Bedding (1968)
Allantonematidae	Cobb (1921)
	Oldham (1930)
	Oldham (1933)
	Welch (1959)
	Massey (1960b)
	Poinar (1973)
	Poinar and Nelson (1973)
Spaerularioidea	
Sphaerulariidae	Bovien (1932)
	Khan (1957)
	Poinar (1965)
	Poinar and Van der Laan (1972)
Aphelenchoidea	
Aphelenchoididae	Massey (1956)
	Ruhm (1956)
	Massey (1960b)
	Poinar (1969)
Entaphelenchidae	Wachek (1955)
	Nickle (1970)

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