

HOST-PARASITE RELATIONSHIP BETWEEN FISH NEMATODES (GENUS: THWAITIA) AND THEIR HOSTS

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Studies on the incidence and developmental cycle of *Thwaitia* (Philometra) species in Hungary (MOLNÁR, 1966) have disclosed certain correlations providing information on the wide variety of host-parasite relationships within one and the same genus.

It was found that in some hosts the sexual maturation of *Thwaitia* females was preconditioned by factors in the absence of which their development came to a halt even if the intensity of infestation was high.

The *Thwaitia* species are particularly suited for the study of host-parasite relationship for the following reasons: (1) their development takes place through a one-year cycle in well-defineable season-dependent stages; (2) normally developed and retarded parasites can be regularly encountered in most hosts and even the dead worms are retained; (3) after the relatively short period of fertilization, the development of worms takes a long time; the length of females is 3—3.5 mm at fertilization and 3—12 cm at the discharge of larvae; (4) in the developmental cycle two phases, one beneath the air bladder serosa and another outside it, can be clearly differentiated.

Our examinations were performed in the course of faunistic studies on fishes found to be infested with *Thwaitia* species; accordingly, the material examined originated from different habitats in Hungary.

Up to now the occurrence of four *Thwaitia* species has been noted: *Thwaitia ovata* (Zeder, 1803), *Th. rischta* (Skrjabin, 1917), *Th. abdominalis* (Nybelin, 1928) and *Th. kodani* (Molnár, 1969). Out of them *Th. ovata*, *Th. rischta* and *Th. kodani* occur primarily in the host population of large stagnant waters and rivers, whereas *Thwaitia abdominalis* occurs in brook fishes. The fish species harbouring *Thwaitia* and the number of hosts examined are shown in Table I.

In some cases complete parasitological sectioning was carried out, but mostly only the air bladder and other specific localizations were examined. The usually hardly visible but vigorously moving parasites were recovered under stereomicroscope from beneath the bladder serosa and were placed in saline.

Table I
Species and hosts of *Thwaitia*

<i>Thwaitia scata</i>		<i>Thwaitia rickia</i>		<i>Thwaitia abdominalis</i>	
Hosts	Number of fishes examined	Hosts	Number of fishes examined	Hosts	Number of fishes examined
<i>Abramis brama</i> *	1500	<i>Abramis brama</i> *	1500	<i>Phoxinus phoxinus</i>	210
<i>Abramis ballerus</i>	40	<i>Abramis ballerus</i>	40	<i>Gobio gobio</i>	40
<i>Rutilus rutilus</i> *	600	<i>Alburnus alburnus</i>	600	<i>Leuciscus</i>	36
		<i>Blicca bjoerkna</i>	60	<i>Leuciscus leuciscus</i>	6
		<i>Scardinius erythrophthalmus</i>	90		

* Exclusively in fishes from the Lake Balaton

It should be noted that a much greater number of hosts was examined than shown in Table I, but percentual evaluation was limited to those which were studied exclusively with the aim to obtain information on the occurrence and developmental cycle of *Thwaitia*. For example, fishes younger than two summers, so far not known to harbour *Thwaitia*, were not included in the evaluation.

Previous studies (MOLNÁR, 1966b, 1967, 1969) have shown that the developmental cycles of the four *Thwaitia* species in question are essentially the same. The main features of the cycle are briefly outlined as follows.

1. The developmental cycle of the *Thwaitia* parasites studied lasts one year. The females reach full maturity in the host by the end of May or early in June; at this stage the body cavities of the worms are filled with larvae. The discharge of larvae to the outside world can take place in two ways: (a) the females either migrate to the external cloacal region where they release the larvae by bursting in the hypotonic medium, or (b) they disintegrate while in the abdominal cavity and the larvae migrate into the water through the cloaca.

2. The further development of *Thwaitia* larvae takes place in cyclopes where they undergo two moults.

3. Fishes become infected during June or early July.

4. The parasites ingested by the fishes with the cyclopes migrate from the intestine to the air bladder and settle beneath its serous membrane. Also copulation takes place in that location.

5. In the appropriate host the fertilized females migrate in July, or August to specific locations (abdominal cavity, fins, gill cover), where they slowly but steadily reach larval maturation by the next summer.

occurring in Hungary

Thwaitia koelani		Species not harboring Thwaitia as assessed by examination of 50 specimens	
Hosts	Number of fishes examined		
<i>Aspius aspius</i>	41	<i>Cyprinus carpio</i> <i>Carassius carassius</i> <i>Barbus barbus</i> <i>Tinca tinca</i> <i>Gobio albipinnatus</i> <i>Vimba vimba</i> <i>Abramis sapa</i>	<i>Rhodeus sericeus amarus</i> <i>Chondrostoma nasus</i> <i>Barbus meridionalis Petényi</i> <i>Leuciscus idus</i> <i>Alburnoides bipunctatus</i> <i>Pelecus cultratus</i>

6. The males and, in inappropriate hosts, also the females are retained under the bladder serosa throughout the year. Occasionally numerous living, but retarded worms, 2 to 3.5 mm in length are encountered in that location. (*Thwaitia rischta* is an exception as also the males migrate from the bladder subserosa.)

I. Host-parasite relationship in fishes infested by *Thwaitia ovata*

Thwaitia ovata parasites have been found in three fish species: *Rutilus rutilus*, *Abramis brama*, *Abramis ballerus*.

1. Fully developed, or developing abdominally localized females were encountered in

(a) 100% of *Abramis brama* and *Rutilus rutilus* fishes with ligulosis;*

* Some authors reporting simultaneous occurrence of *Ligula* and *Thwaitia* (*Philometra*) infestation in lakes have noted that in spite of the massive infestation with *Th. ovata*, part of the fishes were infected with *Ligula* alone.

MARKOV and KOSAREVA (1962) and DONTSOV (1968) found simultaneous occurrence of *Ligula* and *Thwaitia* in the majority of *Abramis brama* fishes, but the minority of them had ligulosis but no *Thwaitia* infection.

This phenomenon might be explained by the following reasons: 1. The authors, if not familiar with the seasonal cycle of *Thwaitiae*, may have examined the fishes in a period (June) when the mature worms had been eliminated and reinfection had not yet taken place. 2. The authors might have disregarded that part of the developmental cycle of *Thwaitiae* takes place beneath the bladder serosa and that particular period (July, August) may not be suited for statistical evaluation. 3. Further to this, no developing *Thwaitia* females are encountered in fishes with ligulosis if *Ligula* infection took place after the invasion of *Thwaitia* larvae. In the course of our faunistic studies we have ourselves encountered some young *Ligula*-infected *Abramis brama* and *Rutilus rutilus* hosts in which *Thwaitia* infection was in the latent (subserous) phase even in autumn and in spring. But aimed examinations for *Thwaitiae* of fishes with manifest ligulosis invariably revealed a 100% incidence of mature *Thwaitiae* females, indicating that in those cases ligulosis had preceded the invasion of *Thwaitia* larvae.

With regard to the above considerations we examined the host-parasite relationship exclusively in fishes collected during the fall and spring season.

(b) 2.5% of *Rutilus rutilus* hosts not infected with *Ligulae*.

2. Males localized under the bladder serosa and retarded females were encountered in

(a) 100% and 67% of *Ligula*-free *Abramis brama* and *Rutilus rutilus* fishes, respectively, from the Lake Balaton;

(b) approximately 50% of *Abramis brama*, *Abramis ballerus* and *Rutilus rutilus* fishes from rivers.

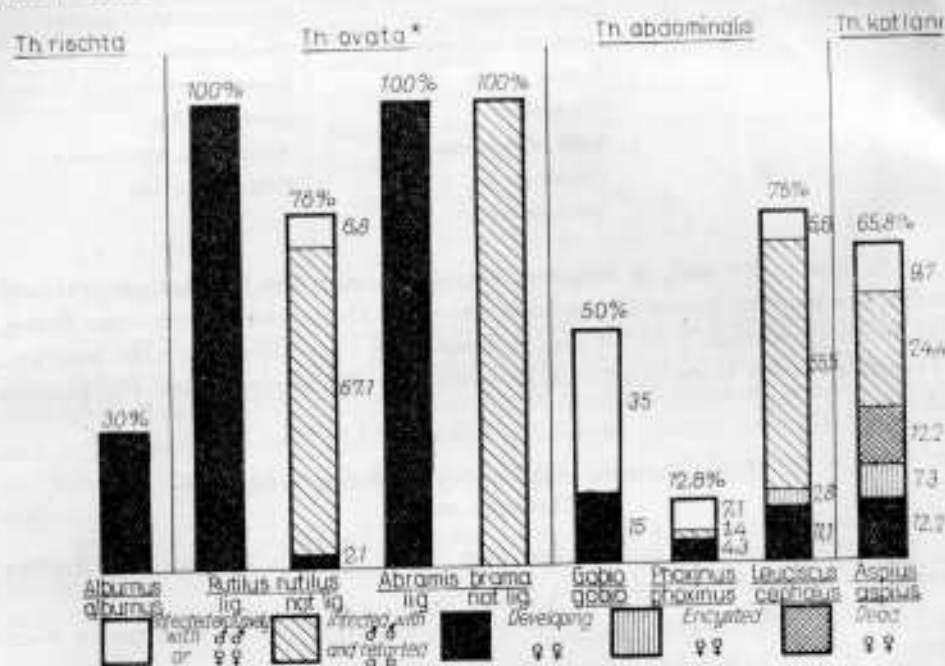


Fig. 1. Type and extent of infestation with *Thwaitia* of different fish species

II. Host—parasite relationship in fishes infested by *Thwaitia abdominalis*

Thwaitia abdominalis was found in four fish species: *Gobio gobio*, *Phoxinus phoxinus*, *Leuciscus cephalus*, *Leuciscus leuciscus*.

1. Fully developed or developing, abdominally localized females were found in

(a) *Gobio gobio* fishes which contained at least one male and one female parasite as well as in the majority of *Phoxinus phoxinus* fishes infested by *Thwaitia abdominalis*;

(b) approximately 15% of *Leuciscus cephalus* and *Leuciscus leuciscus* fishes infested by *Thwaitia abdominalis*.

2. Males parasitizing the bladder serosa or retarded females were found in (a) hosts harbouring exclusively males or females;

(b) the majority of *Leuciscus cephalus* and *Leuciscus leuciscus* hosts infested by *Thwaitia abdominalis*.

3. Further to this, in the abdominal cavity of a *Leuciscus cephalus* specimen 2 developing female parasites were found encapsulated in thick connective tissue; their lengths were only one half compared to the rest of parasites which at the same time measured 40–50 mm.

III. Host—parasite relationship in fishes infested by *Thwaitia kotlani*

1. Fully developed or normally developing abdominally localized females were found in 12% of *Aspius aspius* fishes.

2. Abdominally localized, developing, but slightly retarded females encapsulated in connective tissue were encountered in 7.3% of the examined *Aspius aspius* specimens.

3. Abdominally localized females which died after having reached a length of 10–25 mm (in April) and had dry cuticles overgrown by connective tissue were found in 12.7% of *Aspius aspius* fishes.

4. Males and females localized under the bladder serosa were found in 24.4% of *Aspius aspius*.

5. Living males or females localized under the bladder serosa were found in 9.7% of *Aspius aspius*.

IV. *Thwaitia rischta*

Though it has a wide host range, it is unsuitable for the study of host—parasite relationship as after fertilization both the males and females leave the bladder serosa and, accordingly, the factors limiting their development can hardly be identified.

Discussion

An analysis of the host—parasite relationship between the various *Thwaitia* parasites and their hosts has shown that undisturbed development of a given parasite takes place in only some host specimens, implying that *Thwaitia* parasites have more and less favourable hosts and even in the case of *Thwaitiae* having a single known host, the adaptation of the parasite may vary widely (Fig. 1).

From this angle, exclusively the adaptation of *Th. abdominalis* can be regarded perfect; of the range of hosts *Gobio gobio* and *Phoxinus phoxinus*

appear to provide optimum conditions for practically undisturbed development if both males and females are present.*

In contrast, for *Th. abdominalis* *Leuciscus cephalus*, for *Th. ovata*, *Ligula*-free *Rutilus rutilus* and for *Th. kotlani*, *Aspius aspius* represent the host species in which full development takes place only in the minority of the specimens, even if the intensity of infestation is high. Only few of the settled parasites start to develop and reach full maturity. The often limited development of *Thwaitia* in the above fish species suggests that the latter are less favourable hosts. The scanty data available on *Leuciscus leuciscus* permit no definitive conclusion.

A particular type of host is represented by the *Ligula*-infested *Rutilus rutilus* and *Abramis brama* fishes, as the synergistic effect of *Ligula* infection on *Thwaitias* results in a complete parasite development in both species. Considering that a *Ligula*-infested *Abramis* or *Rutilus* may harbour 50–300 females in the abdominal cavity, while a *Ligula*-free *Rutilus rutilus* only 1 or 2, if any, there is reason to suppose that the *Ligula*-infested fishes making 4.5% of the *Rutilus* and *Abramis* population play a more important role in the maintenance of the often conspicuously high *Thwaitia* incidence in the Lake Balaton than the 2.1% of *Thwaitia*-infested *Ligula*-free *Rutilus* hosts, in which complete development of *Thwaitia* may occur.

The variability of adaptation to the host is exemplified by the relation of *Th. kotlani* to *Aspius aspius*, in which some of the parasites seem to complete an undisturbed life cycle, others show retardation of development in various stages.

It appears that in the case of all species studied, the most decisive phase of the developmental cycle is the migration from the bladder subserosa, as usually in all hosts but *Gobio gobio* and *Phoxinus phoxinus*, the parasite's development comes to a halt in that phase.

A general feature of *Thwaitia* infestation is the phenomenon practically unknown with other nematodes, that the development of females takes place in two well-defined — subserous and extraserous — stages. In certain hosts a practically undisturbed development of the parasite is invariably provided, viz., the host—parasite relationship is brought to an issue in favour of the

* It should be noted that in Hungary, the incidence of *Th. abdominalis* and *Th. kotlani* is much lower than that of *Th. ovata* and the former are inferior to the latter also in respect of the extensity and intensity of infestation. Intensity is closely related to nutrition, that is, to the amount of cyclopes ingested. This may offer an explanation for the fact that the intensity of infestation is higher in fishes with ligulosis which remained plankton-feeders as compared to benthophagous ones. Accordingly, in the same habitat, the comparatively large-sized *Leuciscus* fishes which need more food, are more intensively infested as compared to the smaller *Gobio* and *Phoxinus* fishes. Thus the latter hosts are often either free of *Thwaitia* or contain a single worm or exclusively male or female worms. This, however, had no influence on the classification of the hosts as I grouped them on the basis of the proportion developing to retarded worms rather than on the basis of the percentage of absolute infestation.

latter. In contrast, in other hosts migration to, or development in, the abdominal cavity would seldom take an undisturbed course in which case the contest is decided in favour on the host. The *Thaumatocystis* are either unable to migrate from the bladder subserosa into the abdominal cavity or, though having migrated there, are stopped in their development by being encapsulated in connective tissue. The connective tissue capsule interferes with the nutrition and growth of the worm and often causes its death; in any case, it prevents larva production, stopping thereby the reproduction of the "trapped" parasites.

In the latter type of hosts the normal development of the parasite is dependent on certain factors. In a notable proportion of *Abramis* and *Rutilus* fishes, ligulosis is such a factor. It remains to be clarified whether the *Ligulae* produce this effect by improving the growth conditions of *Thaumatocystis* through the abdominal exudate due to the mechanical irritation or through reducing the general resistance of the fish host.

The available information is insufficient to decide whether the occasional normal development of *Thaumatocystis* in less favourable hosts is due to ligulosis-like factors such as other diseases, or malnutrition. Nevertheless, it seems likely that the limitation of development outlined above is not due to acquired immunity. In fact, two summer fishes did not harbour a larger number of normally developed parasites than their elder companions, though in case of an immunity a greater degree of protection of the elder fishes would be clearly apparent. Anyway, the marked influence of ligulosis on the extensity and intensity of infestation with mature *Thaumatocystis* females points to the role of predisposing factors in the normal development of the latter.

SUMMARY

Host-parasite relationship between four *Thaumatocystis* (Nematoda) species — *Th. ovata*, *Th. vischia*, *Th. abdominalis* and *Th. kotlani* — occurring in Hungary, and their fish hosts was studied.

In certain fish species these nematodes reach full maturation in only part of the infested specimens.

Retarded development may be due either to the inability of females to migrate from the bladder subserosa, or to their impairment during further development in the abdominal cavity.

In some cases of *Thaumatocystis* infection the full maturation of females needs some preconditioning factor(s). Such a factor appears to be concurrent ligulosis, which provides 100% development of *Th. ovata* females.

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