Ecological Questions 35 (2024) 4: 53–58 http://dx.doi.org/10.12775/EQ.2024.047

Nematomorpha – poorly known parasites of invertebrates

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Received: 7 March 2024 / Accepted 21 July 2024

Abstract. Nematomorpha, also known as 'horsehair worms', is a poorly known group of animals that parasitize as larvae both, invertebrates and, less frequently vertebrates. There are approximately 360 species within this phylum, and previously, they were incorrectly classified as representatives of nematodes due to morphological similarity. Nematomorpha are cosmopolitan, found in fresh and salt water, and on land, usually in humid habitats. Their life cycles are simple or complex and usually associated with the phenomenon of 'parasitic manipulation' of the host. This term refers to parasites that can take control of their host's body and behaviour. These efforts mainly lead to the host's death in the name of parasites' survival. The level of knowledge about Nematomorpha is insufficient, as is the role of these behaviour-altering parasites in the ecosystem. This is mainly due to their relatively low species representativeness and a secretive lifestyle in which, alongside free-living adults, there are parasitic larvae. The aim of this article is a review of the literature on 'horsehair worms' and an attempt to determine further directions of research on this systematic group.

Keywords: Nematomorpha, parasitic manipulation, behaviour-altering parasites, host, praying mantids, life cycle.

1. Introduction

Nematomorpha is a poorly recognized phylum of invertebrates widespread in freshwater, rare in salt-water reservoirs, and humid land habitats, mainly in temperate and tropical zones (Poinar, 2017; Anaya et al., 2021). They are called 'Gordian worms' or 'horsehair worms'. The first name is because free-living individuals loop together during copulation, creating the so-called "Gordian knot". In turn, the 'horsehair worm' is related to the old belief that the hair falling out of the horse's tail turns into the mentioned worm. The lifespan of Nematomorpha depends on the species and can last from a month, e.g. *Paragordius varius* Leidy, 1851 to over eight months (Hanelt and Janovy, 2004). Larvae are associated with aquatic invertebrates. Juveniles of 'horsehair worms' are primarily associated with various groups of invertebrates, including Coleoptera, Mantodea or Orthoptera (Schmidt-Rhaesa, 2012), and sometimes they also occur in vertebrates (Poinar, 2017). In Europe, Nematomorpha has been recorded mainly in carabid beetles (Poinar et al., 2004), in grasshoppers (Baker and Capinera, 1997), and in tropical and subtropical regions in praying mantises (Schmidt-Rhaesa and Yadav, 2004).

The body diameter of Nematomorpha is up to 2 millimetres, but they are very long and usually range from 10 to 20 centimeters (Schmidt-Rhaesa 2001). The longest specimen, a representative of the species *Gordius fulgur* Baird, 1861, exceeded 2 meters in length. Adult females are typically longer and thicker than males (Bolek et al., 2015). In terms of the body structure of adult forms, the anterior part is round like Gordius or a slight tapering like Chordodes (Schmidt-Rhaesa, 2012), while the posterior part can be round (both sexes), has two (males) or three-lobed caudal processes (female) (Poinar, 2010). The body colour, which depends not only on the species, but also on the development stage, is from shades of yellow to black shades, sometimes with darker patches present in some Chordodes. White spots are present in Gordius. The cuticle in adult representatives differs from that in juvenile forms, as it is visibly thicker in the cross-section. The circulatory system, as well as the respiratory and excretory systems, are absent in adult Nematomorpha. In contrast, the digestive system is strongly reduced, including the disappearance of the mouth in some individuals (Błaszak and Skoracki, 2009). . Individuals with a mouth have it in the front, the conical part of the body, which is always lighter in colour. Individuals of the genus Gordioida just behind the lighter front of the body, have a darker ring (Schmidt-Rhaesa, 2012). The larvae that parasitize on the host feed similarly to nematodes, which means that they absorb nutrients throughout the surface of their body. The reproductive system of Gordioida joins the posterior end of the intestine to form the cloaca, present in front of the caudal processes. Nematomorpha are characterized by gonochorism, i.e. the presence of two sexes – male and female. The number of gonads depends on the cluster and they have a cylindricalsac-like structure. Fertilization in Nematomorpha is internal, although *Paragordius obmai* Hanelt, 2012 reproduces parthenogenetically (Hanelt et al., 2012).

The phylum of Nematomorpha is divided into two classes depending on the type of water in which they can be observed – Gordioida and Nectonematida (Nikolaeva et al., 2023). The first of the classes – Gordioida, is a freshwater group whose individuals usually reach a smaller size than the representatives of Nectonematida (even over 2 meters in body length). Gordioid has been divided into 19 extant genera and 2 extinct, which include approximately 360 species of Nematomorpha (Schmidt-Rhaesa, 2013). These individuals can be observed in various types of freshwater bodies, such as swimming pools, puddles, lake shores, toilets, unfiltered water straight from the tap and even water bowls for pets. Juvenile gordioids live in the host's body, while adults occur in the water bodies mentioned above. Gordioid parasitizes mainly on Orthoptera, cockroaches (Blattodea), caddisflies (Trichoptera) and beetles (Coleoptera) (Błaszak and Skoracki, 2009). The second of the mentioned classes, Nectonematida, includes salt-water representatives living in the pelagic seas. This is a much less well-known group compared to Gordioida. In the presented cluster, there is only one genus – *Nectonema* Verril, 1879 which includes five species of Nematomorpha (Bleidorn et. al., 2002). Males, unlike females, are physically active. Their most characteristic morphological feature is the presence of swimming setae along the vertal and dorsal longitudinal midline. Nectonematida parasitizes mainly on sea crabs from the genera *Palaemon*, *Pandalus* and *Munida* (Błaszak and Skoracki, 2009).

A long time ago, for many years, scientists misclassified Nematomorpha as nematodes due to morphological similarity and because of some features of internal structure. Researchers classified them into one group called Nematoida (Błaszak and Skoracki, 2009). It was also considered that Nematomorpha and Nematoda constitute a group of individuals having the same ancestor called Ecdysozoa, i.e. moults (Hanelt et al., 2005). Nematomorpha larvae undergo one moult, unlike Nematoda larvae, which undergo as many as four moults. Mature male individuals do not have spicules used to open the female vulva, unlike nematodes. Earlier the main reason for the misclassification of Nematomorpha was their great similarity to members of the phylum Nematoda, especially the family Mermithoidea, which also uses arthropods as its hosts and has a very similar life cycle to Nematoda.

The aim of this article is to review the literature on Nematomorpha, indicating further research perspectives on this poorly understood group of parasites.

2. The biology and ecology of Nematomorpha

The life cycle of Nematomorpha is usually one- or two-hosts, with only definitive, or intermediate and definitive hosts, respectively. The intermediate host is merely a vector between the aquatic and terrestrial environments (Fig. 1).

In a simple cycle, free-living, mature Nematomorpha females lay about a million eggs into the water within a few days. After emerging, parasitic larvae can enter the host's body in two ways – passively, i.e. with water swallowed by the host, or actively – using a combination of hooks and stylets which , allows penetration through the tissues of the future host. The parasite then settles in the host's abdomen in the body cavity and feeds mainly on its fat body and, after transformation, also on its gonads (Bolek and Hanelt, 2024). In the host's body, the juvenile reaches a size of between 100 μm and several centimetres. When Nematomorpha reaches sexual maturity, it somehow makes the host enter the water despite the host is not an animal that is connected with this environment (Schmidt-Rhaesa, 2001). The host is used for the survival of the Nematomorpha species so that it can escape and then look for a partner to mate with.

In the complex development cycle, Nematomorpha are often found among aquatic organisms, but they can only develop into adults in the appropriate definitive host. It was discovered that one of the vectors between the terrestrial and aquatic environment for infecting mantises with 'horsehair worms' are larvae from the orders: Trichoptera, Diptera and Ephemeroptera. For instance, the larval form of *Chordodes japonensis* Inoue, 1952 enters the vector's body, encysts and undergoes metamorphosis, then the final host, e.g. a praying mantis, eats the intermediate host and becomes infected with the Nematomorpha. An important issue is that larvae actively break through the intestine and encyst in the tissue nearby. The larvae become more active when they come into contact with the intestinal fluids of Myriapoda or insects (Dorier, 1930). Over time, the larvae next juvenile transform into adults and increase their body size. In carabid beetles, adult forms are located in the abdomen, occupying the place of all organs except the intestine. In praying mantids, the parasite can be observed in their enlarged abdomen. Nematomorpha, while living in the host's body, lead to physiological impairment of the host's functioning (Studier et al.,1991). Once a Nematomorpha reaches sexual maturity, as in a simple life cycle, it creates a strong need for the host to be near water. Once the host enters the water, the Nematomorpha escape into the aquatic environment through the flexible covering on the abdomen between the host's posterior segments (Schmidt-Rhaesa, 2001). The released individual looks for another individual of its species to ensure the species' survival, and the cycle ends. In both simple and complex life cycles, the host often survive, but sometimes it ends in death for the host by drowning. If the host survives the parasite leaving its body, it is usually unable to reproduce because Nematomorpha damages or completely consumes its gonads causing 'parasitic castration' (Schmidt-Rhaesa, 2012).

3. 'Horsehair worms' in invertebrates – case studies

3.1. Annelids

Studies on the presence of "horsehair worms" in annelids were conducted by Anaya et al. (2021). The authors observed that a lot of nematomorphs and earthworms started to appear simultaneously on the pavement during the rainy season. It was shown that in each of 21 analyzed locations (USA, Oklahoma, Stillwater) at least one earthworm had Nematomorpha cysts, presumably belonging to *Gordius terrestris* Linnaeus, 1758. It was also confirmed by experimental studies, indicating the intensity of the invasion from 2 to 37 cysts. The authors also confirmed the seasonality of the presence of Nematomorpha in the environment (Anaya et al., 2021). The vast majority of the "horsehair worms" were collected between December and January, while no Nematomorpha were recorded between April and September. During the observations, it was also noticed that although in December and January, there were more 'horsehair worms' after rain than in other months,

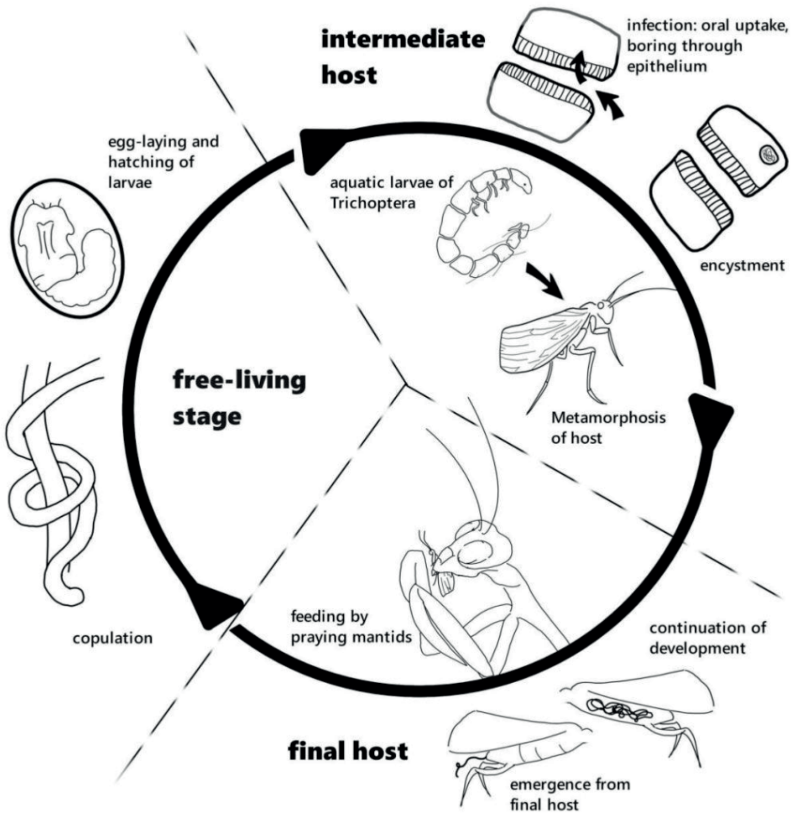

Figure 1. The complex life cycle of Nematomorpha based on Trichoptera and mantids example (Schmidt- Rhaesa and Ehrmann, 2001)

the rainfall was the lowest at that time. The sex ratio of Nematomorpha depended on the month and year, but the number of females was always lower than the number of males.

3.2. Arthropods

A new species of marine Nematomorpha, *Nectonema zealandica* Poinar & Brockerhoff, 2001 was discovered in southern New Zealand in crab species *Hemigrapsus edwardsi* Hilgendorf, 1882 (Poinar and Brackerhoff, 2001). This is the first reported case of *Nectonema* in the south of Pacific Ocean, which is also the southern most point of occurrence of this parasite. In 1998-2000, 636 crabs of this species collected in Canterbury were examined (447 females, 189 males), and the prevalence of *N. zealandica* was 12,7%. However, it was observed that invertebrate hosts defended themselves against parasites. Individuals of *N. zealandica* located in the body of the crabs were surrounded by the host's blood cells, resulting in a shell separating the parasites from healthy tissues. The areolas had different colours, from yellow and brown to darker, and they also differed in size (Poinar and Brockerhoff, 2001).

3.3. Molluscs

Hanelt (2009) found that *Physa gyrina* Say, 1821 snails were simultaneously infected with trematodes and Nematomorpha. After parasitological diagnosis, which first involved cercariae releasing from the snail and then dissecting the mollusc, trematode larvae from the Notocotylidae family, and 'horsehair worms' were found. The researcher also found *Paragordius varius* Leidy, 1851 inside rediae of Notocotylidae in these snails. The phenomenon of parasites infecting other parasites is called hyperparasitism, and it is still poorly understood in nature (see e.g., Kanarek et al., 2023).

4. Conclusions and perspectives of research on Nematomorpha

The level of knowledge about Nematomorpha is insufficient compared to other groups of invertebrates, such as annelids, molluscs and arthropods, especially those of economic importance. The reason for the poor knowledge of this group of parasites may be the difficulty in finding Nematomorpha, resulting, among other things, from the small body size of these animals. Because of the diameter of these parasites, they are very hard to look for them and very short body length they may go unnoticed. Also for most of their lives, they are inside hosts' bodies who very often show no symptoms of infection.

Undoubtedly, an interesting, although poorly understood, issue in research on Nematomorpha is the phenomenon of "parasitic manipulation". It assumes that the parasite can influence the behaviour and/or appearance of its host (Combes, 1999). According to some hypotheses, Nematomorpha causes a strong need in the host to be near a reservoir of water. It is supported by observations of the suicidal behaviour of praying mantids from France (Schmidt-Rhaesa and Ehrmann, 2001). This hypothesis suggests that only adults, with a permanent cuticular pattern on their body, leave the host. A moment after jumping into the water, Nematomorpha began to emerge from the mantid's abdomens. While comparing infected and uninfected crickets in laboratory conditions, it was observed that the former jumped into the water more often than those without the parasite (Thomas et. al., 2002). It is difficult to say what mechanism causes the cricket to lose its inhibitions towards entering water. Regardless of which hypothesis is correct, to be able to leave the host's body, the parasite must receive information about the presence of water outside the host's body. However, it is not entirely known whether the parasite leaves the host when it reaches sexual maturity or whether it only reaches it in water. It also happens that Nematomorpha leaves the host's body without the use of water (Schmidt-Rhaesa and Ehrmann, 2001), which may question the hypothesis of 'parasitic manipulation'. After killing the mantis, its abdomen was tapped with a wooden stick, which resulted in Nematomorpha emerging from its abdomen after a while (Schmidt-Rhaesa and Ehrmann, 2001).

In addition to mechanical stimulation, there are also speculations that 'parasitic manipulation' may have a chemical basis (Combes, 1999). However, there is no detailed information about the proteins produced by Nematomorpha to motivate the host to migrate to water. It is also not entirely known how the mentioned molecules are constructed and what determines their presence – the achievement of sexual maturity by the parasite or perhaps other factors. Testing for these substances would be possible when examining a host group, for example, a species of grasshopper infected with Nematomorpha. The composition of the hosts' hemolymph should be examined at certain time intervals to obtain reliable results. If unknown proteins or other substances were found in the hemolymph, their origin and possible impact on the host would need to be determined. One example of the influence of substances from a parasite on the host may be the relationship between a parasitic wasp *Hymenoepimecis argyraphaga* Gauld, 2000, and a spider *Plesiometa argyra* Walckenaer, 1842 (Eberhard, 2001). The wasps immobilize the spider with their stinger so that they can attach the egg containing the larva to its body. The larva feeds on the host's hemolymph flowing from small holes on its abdomen that it has made itself. When the parasite matures and is close to transforming into the imago form, toxins are injected into the spider's body. Thanks to substances from the larva, the host begins to weave a stronger web so that the parasite can get off the spider and then eat it. The larva then creates a cocoon, from which the adult hatches after less than two weeks. There is also a trematode species, *Dicrocoelium dendriticum* Rudolphi, 1819, which also takes control over the behaviour of its hosts (Combes, 1999). Cercariae develop in a land snail, are excreted together with the mucus, and then eaten by ants – the second intermediate host. Only one metacercariae inside the ant's body reaches the brain and transforms into the so-called 'neural metacercariae'. This causes changes in the ant's behaviour. When the weather is cooler, the ant does not return to the anthill but waits at the top of the grass blades to be accidentally eaten by one of the ruminants. When the intermediate host is eaten by a ruminant, the parasite infects the final host and the parasite completes its development cycle (Deryło, 2011).

Another unexplored issue is how the Nematomorpha 'know' that the host is in a body of water. We do not have information about the presence of receptors that would enable them to identify the environment in which the host is currently located. There is also no evidence as to whether water entering the host's body affects Nematomorpha. However, some studies describe Nematomorpha emerging from the bodies of dead hosts after mechanical stimulation of the host's abdomen (Schmidt-Rhaesa and Ehrmann, 2001). This may suggest a hypothesis that Nematomorpha needs information from the environment in the form of mechanical stimulation. Therefore, they presumably have mechanoreceptors in their bodies. Tapping the abdomen of a dead host with a stick or a host vigorously swinging its legs while drowning may be a suitable stimulant for emergence from the host's body.

Nematomorpha has been detected in humans in various regions of the world. They have been recorded in the orbital tumour, excreted gastric contents, urinary tract, faeces and even in the external auditory canal (Schmidt-Rhaesa, 2003). A total of 67 cases of human infection with Nematomorpha have been identified worldwide, including 20 different species of these parasites (Ali-Khan and Ali-Khan, 1977). People often unknowingly expose themselves to Nematomorpha and possibly have pseudoparasite or it is wrong called „infection" Most often, it is associated with eating dirty, not thoroughly washed vegetables or fruits, as well as by eating crickets or beetles, (which are quite popular in Asia.) Mainly humans by eating final hosts with adult parasite inside incorrectly identify that as parasitic infection. Infection would not be possible due to the developmental stage of the Nematomorpha, in this case it involves eating the adult form of parasite. There is only a few cases of Nematomorpha in humans or other vertebrates were recorded, there is no information about medical or veterinary importance as a parasite of these groups.

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