

Review articles

Multiple strategies of digenean trematodes to complete their life cycles

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ABSTRACT. This review aims to summarize our most recent knowledge of the unique mechanisms employed by digeneans to complete their complex life cycles. It is based on validated data from scientific literature and integrates both authors' personal experiences. Several dynamic strategies utilized by digeneans are discussed in relation to their presence in three environments: aquatic, semi-aquatic and terrestrial. The following topics are discussed: transmission from host to host, which involves transmission of free-living stage of miracidium and cercaria: in active transmission – specific responses to environmental signals showing the presence of potential hosts (several papers of Haas et al.); in passive transmission – trophic transmission and mimicry by way of resemblance to natural food of potential host; and finally, transmission of the parasitic larvae (metacercaria and mesocercaria) – trophic transmission, manipulation of host behavior, and incorporating the intermediate host into food web of definitive host. This review also highlights several types of behavioral manipulations, including compensatory processes (Poulin, Lefèvre et al., Thomas et al.), and other mechanisms of manipulation (de Jong-Bring et al.). State-dependent alternative cycles demonstrating the difference between the terms „life cycle” and „life history” (Poulin, Thomas et al.) and the concept of „shared phenotype” (Lefèvre et al.) are also discussed.

Key words: Digenea, life cycles, life cycle and life history, manipulation of host behavior, mimicry, shared phenotype, transfer from host to host, trophic transmission

Introduction

Digenean trematodes are the most abundant group of parasitic plathyhelminthes. Their hosts belong to all vertebrate groups and also represent most of the terrestrial, freshwater, and marine invertebrates. Their life cycle is complex with few parthenogenetic generations and a single hermaphroditic generation. Parthenogenetic generations are associated with molluscan hosts, or rarely annelids (traditionally called the first intermediate host) while the development of hermaphroditic generation is related to some invertebrates (the second intermediate host of larvae) and all vertebrate groups (the second intermediate host for some larvae and the definitive host for adult stages of digeneans). Digenean life cycle takes place exclusively in: **a)** an aquatic environment with all hosts being obligatory aquatic animals or living in close association with water; **b)** a semi-aquatic

environment, in which parthenogenetic generations and metacercariae parasitize aquatic organisms and the definitive host represents a terrestrial species; or **c)** a terrestrial environment, and then the entire life cycle utilizes terrestrial animals. Digeneans evolved multiple strategies in each of these habitats allowing them to fully complete their complex life cycles.

1. Host invasion strategies displayed by free-living dispersive stages of digeneans

It is very characteristic for most of the life cycles of digeneans to have two free-living dispersive stages: **a)** miracidium – the larva of mother sporocyst, which is the first stage of parthenogenetic generation; and **b)** cercaria – the first larva of hermaphroditic generation. The transmission to proper host can be achieved by both larval stages in two ways, i.e., active and passive.

Miracidium

Miracidium always leaves the maternal parasitic organism and the definitive host while within the egg, i.e., confined by the egg shell. In active invasion the first intermediate host, the miracidium hatches from the egg in external environment. After hatching, there is a little time, i.e., literally hours, for finding a new host. Miracidium swims erratically from the beginning until intercepting a chemical signal originating from potential hosts, i.e., molluscan or more rarely, an annelid host, by the signal-receiving organ located on the body surface. Miracidium swims along the gradient of this chemical compound toward the direction of the potential hosts, adheres to the host's surface, and initiates host penetration through the surface [1]. During penetration, the miracidium sheds ciliated plates from its surface which are being replaced by the instantly forming tegument. The information on mechanisms responsible for interception of the chemical signals by miracidia that direct them toward a potential host is scant. Haas et al. [1] determined that *Schistosoma japonicum* miracidia react to the aminoglycans of 30 kDa molecular weight (i.e., serine and N-acetylglucose), and their observations also indicate that miracidia were able to differentiate among signals originating from various molluscan host species: miracidia approached snails belonging to two species; however, adhered only to the specimens representing one species (i.e., *Biomphalaria glabata*) which sustained the appropriate host for this specific parasite species.

In the passive invasion the miracidium does not leave the egg shell in external environment. The egg is ingested by a mollusk and reaches its digestive system together with plant debris and the detritus to which the egg adheres (i.e., trophic transmission). The miracidium hatches in the intestine and penetrates the circulatory system of a molluscan host.

In both cases, i.e., passive and active invasion, if a mollusk represents an appropriate host species, the further development of the parasite takes place, and the miracidium develops into a mother sporocyst. After the mother sporocyst is developed, multiplication of the parasite through parthenogenetic reproduction sustains subsequent generations of the sporocysts or rediae, which locate themselves in the hepatopancreas of a mollusk. The final stage of parthenogenetic reproduction is development of cercariae.

Both types of host invasion displayed by miracidia have some advantages and disadvantages. The definitive disadvantage of active host invasion is the short life-span of the miracidium outside the host. However, this is compensated by much higher chances of finding an appropriate host species because of miracidium's ability of intercepting a specific (and potentially host-specific) chemical signal emitted by the mollusk to the aquatic environment. The disadvantage of the passive invasion is a high risk of penetrate an inappropriate mollusk, which could be the cause of high mortality of miracidia. However, advantage of this type of invasion is a considerably longer survival time of miracidia within egg shell in aquatic environments (i.e., weeks, and even months vs. hours for the active invasion) which considerably increases the chances of reaching the appropriate host by miracidium, and assures further development and reproduction of the parasite.

Both, passive and active invasion take place in aquatic habitats; however, only passive invasion occurs on land.

Cercaria

Achieving a subsequent host by cercariae which simultaneously initiates the second phase of the life cycle (i.e., development of hermaphroditic generation) can also occur in a passive or active way; however, evolution-evolved strategies are more differentiated for cercariae than in the case of the miracidium.

The active host finding behavior displayed by cercariae is made possible by well developed sensory apparatus that occurs on the cercarial body and in some cercarial groups also on their tail. The penetration through host body surfaces is supported and enhanced by the penetration glands of cercariae. As determined by Rohde et al. [2] the sensory apparatus of parasitic platyhelminthes is much more sophisticated than that of free living platyhelminthes. Literature data on the host invasion strategies of cercariae is more abundant than that on the invasion by miracidia. Haas [3] and Haas et al. [1], based on their observations and data from the literature, described the standard model behavior of cercariae in aquatic habitats. This behavior consists of two phases: **a)** dispersion, when cercariae are leaving the first intermediate host; and **b)** directional host finding, when cercariae are reaching the active space of their host. During the

dispersion phase, the cercariae predominantly utilize signals originating from the ambient aquatic habitat, i.e., gravity, water current, light, temperature and concentration of ions. During the host finding phase, the cercariae react to signals coming from the host such as the host's shadow or water currents caused by the host, and they direct their movement along the chemical gradient of various host-originating compounds. Unlike miracidium, cercariae react to substances occurring in the environment at low molecular weight, mainly peptides. Such particles cause excitement, and movement of cercariae toward the moving objects. The first contact does not have a specific character; however, in some cases, quite possibly because of the numerous sensors on the cercarial body, the appropriate host is recognized and penetrated.

The passive way of host invasion by cercariae requires special adaptations, which assure that they are being included into the food web of their subsequent hosts (i.e., trophic transmission). One such well known strategy is the mimicry, i.e., taking the shape of food items consumed by the potential hosts – such as insect larvae, aquatic crustacean, etc. Most frequently this is related to the development of structures that increase the body size of cercariae. This is particularly relevant to the tail, which is distinct not only because of the size but also because of its various shapes (Niewiadomska et al. [4]).

Similarly as in the case of miracidium, the active invasion of the hosts by cercariae is possible only within the aquatic environment; however, the passive invasion occurs in both, water and land.

2. Strategies for ultimate completion of the life cycles

The invasion of hosts by cercariae and the subsequent parasite development within the host demonstrate a high variability in terms of utilized strategies; however, some patterns are repeatable in various habitats and environments. Very frequently between cercaria and the adult trematode stages, the intermediate stages occur; this is related to the subsequent developmental forms of the parasite (i.e., metacercaria and in rare cases, the mesocercaria), as well as to the subsequent hosts (i.e., intermediate and paratenic) in the life cycle.

Aquatic life cycles

The life cycle that involves three hosts is

considered to be the most typical one for digeneans; cercaria, which leaves a mollusk and subsequently penetrates the second intermediate host, and in this host (which simultaneously is one of the links in the food web of the definitive host) develops into the metacercarial stage. Metacercariae never leave the intermediate host and are only transmitted to the next host (i.e., definitive host) *via* a passive mean, i.e., being ingested with food (trophic transmission). The advantages of this strategy includes the following: **a)** incorporation of a moveable intermediate host assures high dispersal rates for the parasites; and **b)** metacercariae do not expend energy on host seeking movement, thus, this energy can be directed toward their development within the intermediate host, which, as a matter of fact, accelerates the development of the parasite in the definitive hosts.

Some species of digeneans utilize the strategy of shortening their life cycle *via* elimination of some hosts, and also *via* elimination of some developmental stages. The hosts that harbor metacercariae have most frequently been eliminated from the life cycle. This generates the life cycles with two hosts instead of three hosts. More rarely, the life cycle has been shortened to a single host. In such a life cycle, the cercariae do not leave mollusk, but they reach their sexual maturity in the same host by the mean of progenetic development throughout the stage of metacercaria up to the adult trematode that produces the eggs. Such development is observed in *Paralepoderma progenetica*, *Asymphylodora progenetica*, and *Metorchis progeneticus* life cycles.

In many life cycles completed in aquatic environment, cercariae utilize the strategy of mimicry, which facilitates achieving the next host. In life cycles that have three hosts, this relates for example to the cercariae from the genus *Echinochasmus* and *Rhipidocotyle* transmitted to the intermediate hosts; in life cycles with two hosts, this relates to cercariae from the genus *Azygia*, *Phyllodistomum*, and *Halipegus* transmitted to the definitive hosts. The similarity of the cercariae to the food items consumed by the definitive host is frequently supported by the advancements of the cercarial body which, as a consequence, reaches the stage which is functionally equivalent to the metacercaria even before leaving the molluscan host.

Alternative strategies related to the developmental forms of parasites and the food regime of

their potential host represent very interesting phenomena. For example, cercariae of *Phyllodistomum elongatum* can leave the mollusk-host, or alternatively not leave this host and reach the developmental stage of the metacercaria inside the sporocysts or after they leave the sporocysts but still inside the same mollusk specimen. In the first case, free-living cercariae are ingested by the fry due to the similarity of cercariae to the plankton (i.e., mimicry), and the adult parasite develops directly from the cercaria stage inside the growing fry, or eventually fish. In the second case, the metacercaria stage is developed in an older fish that feeds on mollusks. In both cases, the life cycle consists of two hosts without the second intermediate host; however, in the first case, one developmental stage of the parasite (i.e., metacercaria) has been eliminated. The metacercarial stage is still present in the second case; however, the role of the second intermediate host is then played by the first intermediate host (i.e., mollusk).

Semi-aquatic life cycles

The characteristic feature of these digenean's life cycles is their allogeny, i.e., transition of the parasites through various ambient habitats and environments. The parthenogenetic phase, up to the development of cercaria, and the beginning of the hermaphroditic phase (i.e., metacercaria) takes place in aquatic organisms, and the sexual development in terrestrial vertebrates. Completion of such parasitic life cycles requires certain sophistication in its strategies.

In the three-host life cycles all developmental stages of the parasite occur; however, the aquatic insects are the predominant hosts in which the larvae of parasites develop, and then the adult insects (i.e., imago) retain them and move the parasites in their bodies out of water onto land. Such life cycles are characteristic for parasites of various vertebrate groups that live on land and feed on insects (i.e., amphibians, birds, and mammals – bats, in particular). An example can be provided by the trematode *Lecithodendrium granulorum* which metacercariae develop in the mosquito larvae, and the adult flukes reach maturity in the *Eptesicus serotinus* bats which feed on adult mosquitoes. The transfer of the parasites from water onto land can be also achieved by amphibians and reptiles. An advantage of the strategy with a three-host life cycle that utilizes insects as the intermediate hosts is the

increased possibility of territorial invasions and extension by parasites, in particular for life cycles in which the definitive hosts are sustained by birds and/or bats.

The phenomenon of shortening parasite's life cycles by elimination of one of the hosts is quite common among digeneans. Typical examples of such phenomenon could be provided by flukes from the family Fasciolidae (i.e., *Fasciola hepatica* and *Parafasciolopsis fasciolaemorpha*) in which all developmental stages occur; however, the host(s) of metacercariae has been eliminated. The cercariae, after expulsion from a mollusk, settle in the water on the surfaces of plants, water meniscus, shells and other objects, develop the cyst and metamorphose within the cyst into the metacercariae (i.e., adolescariae), and the definitive host living on land is getting infected by grazing on wetlands, indented pastures, or by visiting water holes.

In the life cycles with two hosts involved, besides the elimination of the host that usually harbors metacercariae, the elimination of some parasite generations during the parthenogenesis process is sometimes observed. In particular, a very interesting example can be provided by the life cycles of Cyclocoelidae. The miracidium not only does not metamorphose into the mother sporocysts, but while in the egg it develops into the redia with small embryonic masses of cercariae; thus, the mother sporocyst and some generations of subsequent rediae are eliminated. After hatching within the host, the miracidium releases the redia into the host's body, and then this redia, using their locomotory structures, reach the appropriate locus inside the snail, i.e., the hepatopancreas or other snail organ or tissue. The cercariae do not leave the snail but either metamorphose into the metacercaria inside the redia or they leave the redia and develop cysts in the snail tissue neighboring to their original site. The life cycle is completed when the mollusk is eaten by the definitive host (i.e., reptiles, birds, or mammals). In this life cycles, the reproduction of parthenogenetic generations is almost completely eliminated as only a single event of such reproduction takes place, i.e., origination of cercariae from a single redia. The decreased reproduction of the parthenogenetic generations can, to a certain extent, compensate for the lack of the free-living phase of cercariae (which always increases the possibility of ecological elimination before the reproduction). Production of a high number of eggs by the adult fluke – the uterus fills

out almost completely in its body from the oral sucker to the end, also compensates for the lack of the free-living cercariae.

It is frequently observed in the semi-aquatic life cycles that the developmental cycle is usually extended by incorporation of additional intermediate hosts in which the mesocercaria is being developed. Mesocercaria is an additional transitional parasitic stage between cercariae and metacercariae presented in the food web of the definitive hosts (i.e., in the life cycles of the species from the genus *Alaria*, *Strigea* and *Microphallus*). Usually the presence of mesocercariae in the life cycle is associated with the introduction of paratenic hosts, which additionally increases the number of hosts in the life cycle. In the paratenic host, the parasite avoids digestion and does not reach the next developmental stage; it merely penetrates the intestinal wall and settles in the host's tissue. Further development can only occur in the appropriate host. There are a lot of paratenic hosts observed in the life cycle of *Alaria alata* [5]. The advantages of this strategy are undisputable: **a)** extension of the mesocercariae life span that simultaneously assures the survival of the parasite in the ecosystem(s); **b)** possibility of expanding the range of the intermediate hosts; and **c)** creation of new connections and links between parasites and their potential hosts. A disadvantage includes an increased chance of transferring into a host which is completely unsuitable for the completion of the life cycle of the parasite.

In some marine life cycles, for example in the cycle of *Parvatrema homeotecnum*, additional multiplication of generations of germinatory sacks (that have very specific morphology) occurs. The morphology of these germinatory sacks differs from the morphology of the sporocysts and the redia. The cercariae developing inside these sacs are losing their tails and develop into metacercariae while inside these sacks. Birds eating infected mollusks are getting infected with the parasite.

It is worth to mention about the strategy for the differentiation of the developmental rate for the specific developmental stages in the life cycle of some digeneans. The life cycle of *Posthodiplostomum cuticola* can be completed in a bit over three months (i.e., development of miracidium takes approximately 15 days, development of cercariae in snails takes approximately 26 days, development of metacercariae takes approximately 26 days, and the adult trematode develops from 2 to 3 days).

However, the same life cycle can also last for over 5 years (i.e., development of the miracidium takes approximately 189 days, development of cercariae in snails can take an entire year, metacercariae remain viable for three years, and then the adult develops within 15 days). The shortest life cycles can be completed within a single summer season, and the long cycles assure the survival of this parasite species in case of adverse environmental conditions, such as the lack of definitive hosts, i.e., stopping over migratory animals that serve as definitive hosts [6].

Terrestrial life cycles

All terrestrial life cycles are related to terrestrial snails and require other strategies for completion than aquatic or semi-aquatic life cycles. The most important feature is that the miracidia never leave the egg and invade the first intermediate host by trophic transmission. Cercariae, when they leave a snail, are surrounded in the mucus, and have limited possibilities of movement and as a rule, infect the subsequent host *via* a passive way, i.e., being ingested by another creature. Despite, or maybe because of these limitations, a variety of strategies for completing life cycles have been developed on land. For example, trematodes from the family Dicrocoeliidae have three or even four hosts in their life cycles, including the paratenic host. Panin [7] differentiated among known life cycles (as the development of many parasite species is still unknown) three types (i.e., standards or models) related to taxons, subfamilies or genera. **Type Dicrocoelium** – hosts: snails → arthropods (mainly insects) → birds and terrestrial mammals; long-tailed xiphidiocercariae are secreted in, so called, slime balls which support their survival in the environment. *Dicrocoelium dendriticum*, among other species, develop according to this standard. **Type Eurytrema** – hosts: snails → arthropods → terrestrial mammals; xiphidioecercariae that have rudimental tail are secreted to the inside of the maternal sporocyst. **Type Platynosomum** – is similar to type Eurytrema; however, includes an amphibian or a reptile as the paratenic host; xiphidiocercariae have also rudimental tail and are frequently surrounded by the cyst inside the mother sporocysts. Their definitive hosts include birds and mammals.

In the life cycles with three hosts which are utilized by the family Brachylamidae, the second

intermediate hosts are snails, very frequently representing the same species as the hosts in which parasite parthenogenetic generations are developed. Cercariae with rudimental tail (i.e., cercariaeum) leave the mollusk and by using their suckers they can crawl for small distances seeking a host which is then entered *via* the respiratory opening [8,9]. It is quite possible that the cercariae utilize some signals emitted by the snails to the environment; however, so far nothing certain is known about the character of these potential signals. It is also uncertain, whether or not the cercariae can penetrate the same snail from which they have been deported. As a matter of fact, in field research, not a single snail specimen had been found harboring both sporocysts and metacercariae; this may indicate that the presence of sporocysts prevents the secondary invasion and development of cercariae [8–10].

In a very interesting two-host life cycle in which the development of metacercariae takes place in the first host is the development of digeneans representing the genus *Leucochloridium*. The parthenogenetic phase is limited to the well morphologically developed and functionally differentiated mother sporocyst. The central part of the mother sporocyst, located in the hepatopancreas of the snail, may be called „germinative part” as there the parasite perpetuates the process of reproduction, i.e., development of cercariae. Numerous small and bigger sack exvaginations serve as the areas where cercariae aggregate and undergo development. Some bigger sacks that are connected by a thin canal with the central parasite body and penetrate the snail antennae serve as a „storage area” for the new generations that have matured to the stage of metacercariae which are then being confined by a cyst. Simultaneously, the sophisticated mimicry – the colors and pulsate movement of these sacks in snails antennae, resembling insect caterpillars – lures the definitive hosts (i.e., birds) to feed on them. Various strategies can be observed in this life cycle: **a)** elimination of the second intermediate host; **b)** elimination of some stages of the parthenogenetic development (which is compensated by the extended time for cercaria reproduction); **c)** mimicry that facilitates the contact with the definitive hosts, and **d)** manipulation of the hosts by the parasite which as a consequence changes the host behavior (presented in the next paragraph).

3. Strategies employed in the manipulation of the host behavior by parasites in order to facilitate their own transmission

As seen from the examples presented above, in many cases it is the metacercaria which represents a vital and important connection between the intermediate and the definitive hosts. However, this larva is not, and should not be, perceived as a kind of „hitchhiker” merely being delivered to the definitive host by the food web. In fact, the metacercaria helps in various ways to initiate environmental contacts with subsequent potential hosts causing simultaneous changes in the behavior of that host, which in return facilitate its own transmission. In a general sense, the metacercariae can cause the infected host to: **a)** move unwisely close to the predator; **b)** be captured and consequently consumed by the predatory species; or **c)** be easier spotted by a predator in the environment and hunted down.

The best example of the manipulation of the behavior of the host by parasites comes from the life cycle of *Dicrocoelium dendriticum*, in which the metacercaria located in the ventral pharyngeal cord junction of an ant causes such a strong compression of the ant jaws on a grass blade that the ant is immobilized. As such, the ant is more often ingested by cattle grazing on the pastures and reaches the intestine of cattle together with the consumed grass.

Location of the parasite is frequently a cause of change in the host behavior. Such phenomenon can be observed in the case of metacercariae representing many species from the genus *Diplostomum* which locate themselves in the eye lenses of a fish. Metacercariae debilitate the vision of a fish and even cause the fish blindness. Blind fish lose orientation in the environment and become an easy prey for the consumer (i.e., subsequent hosts of the parasite) feeding on fish.

Manipulation leading to the facilitation of the contact between the intermediate and definitive hosts occurs in the life cycle of *Leucochloridium*; infected snails show positive phototaxis and crawl to the upper surface of a leaf, where their pulsating and colorful sacks with metacercariae inside located in the snail’s antennae are well visible for hungry and foraging birds.

Another very interesting example for the parasite strategy to complete their life cycles is provided by *Paratimonia gobii*. Cercariae of these species develop in the bivalves from the genus *Abra*, and

the definitive hosts are fish (i.e., racer gobies) which feed on bivalves. The life cycle is completed because of the autotomy, i.e., fragmentation of bivalve's siphon. The metacercariae are located in the siphon and their presence accelerates the process of autotomy. The siphon floats in the water for some time resembling the movements of the benthic organisms what stimulate fish to feed. They ingest the fragments of the siphon and become infected with the metacercariae (cited after [11]).

There are many examples of manipulation of the host behavior by a parasite; however, the mechanisms of these processes are neither well known nor investigated. In the case of phototaxis in some cases related to the acanthocephalans it was possible to experimentally document the most probable physiological basis of the behavioral change. The character of phototaxis was dependent on the serotonin level – uninfected crustacean amphipods (*Gammarus* spp.) that received appropriate dose of serotonin behaved exactly as crustacean infected with the acanthocephalan larvae [12]. It has been found that the infected crustaceans had altered the ultrastructure of their neurons which may implicate as a cause for the behavioral change the amount of serotonin released by neurons to the synapses [13]. According to Lefèvre et al. [14] it is quite possible that the parasites localized in the hemocoel stimulates the nervous system of a crustacean to produce serotonin, and this increased serotonin level causes the positive phototaxis reaction. The research carried out by de Jong-Bring et al. [15–18, and other publications] who were investigating the effect of the parasites (i.e., Schistosomidae) on the host's (i.e., snails) physiology, determined among others things that the mechanisms of manipulations are generated by releasing secretory/excretory products into two systems that regulate the host organism, i.e., immunological system and endocrinological systems.

It has been observed for some time that in the literature pertaining to the evolution of life cycles of parasites, the subject that surfaces very frequently is related to the creation in the organism of the host the compensatory processes understood as a compromise to decrease physiological costs of the host for sustaining a parasitic intrusion [19–21 and other publications]. The mechanisms of defense developed by the host could be an object of natural selection and, as such be preserved in evolution, if these defensive processes simultaneously facilitate

transmission of parasite from host to host, and in other ways are also evolutionary „convenient” to the parasite. Lefèvre et al. [22] presented the example of *Podocotyle stentometra*, which metacercariae parasitize the coral polyps and slow down the growth of the coral colony. The coral „defenses” itself by inflation and turning into a pink color the metacercaria-infected polyps. Bigger and colorful polyps are more often eaten by fish than the regular ones that release the coral colony from parasites and allow the healthy part of the colony to quickly regenerate. This process is also beneficial for the parasites as fish, which usually predominantly consume the infected polyps, sustain the definitive hosts of this parasite. Another example can be provided by the gigantism of the hosts which is caused by the parasites. Bigger snails are more beneficial for parthenogenetic stages of the digeneans which can have more living space within the host's tissue(s). This is also beneficial for the snails as bigger individuals usually display more abundant fecundity [14]. Lefèvre et al. [22] have formulated the concept of the „shared phenotype” as complementary to the extended phenotype concept by Dawkins [23]. It is worth to note that the similar concept of superorganism having a single supergenome was presented earlier by Combes [11].

Lefèvre et al. [14] in their comprehensive review on the evolution of manipulation strategies in the parasite–host interactions presented their concepts for three types of manipulations.

1. Manipulation *sensu stricto* – according to the definition of extended phenotype by Dawkins, the genes of the parasite are responsible for the alteration of the host behavior (i.e., parasite genes are expressed in the host phenotype). According to this concept, the evolution selects the genes of the parasite according to their effect on the host behavior. An example: manipulation of the intermediate host (i.e., infected ant) behavior in the life cycle of *Dicrocoelium dendriticum*.

2. Exploitation of the host compensatory responses. Alteration of the host behavior is a result caused by the parasite that alters the host's fitness. Parasites can influence certain features of the hosts that are responsible for the host's fitness, such as fecundity and survival, and in this way parasites can stimulate compensatory responses which simultaneously increase the transmission of the parasites. In such cases, the genes of the parasite are selected according to their pathological effects which induce a host compensatory response. If

alteration of host's behavior is beneficial for both partners (i.e., decreases of physiological costs of infections for the host, and facilitation the transmission of the parasite), the natural selection is likely to favor all genes involved in such interactions. An example: reactions of polyps in the coral colony to the infection with *Podocotyle stentometra* metacercariae.

3. Mafia-like manipulation. Alteration of the host's behavior could be also considered as a forced cooperation. If the host is not cooperating, the parasite can impose on the host additional costs to the host's fitness. Parasites adopt a plastic strategy depending on the level of cooperation displayed by the host. According to this view, in the evolution process, the genes that recognize uncooperative behavior of the host and induce parasite retaliation have been favored and preserved.

The latest concept is based exclusively solely on a few observations on the behavior of Cuckoo birds which lay their eggs in the nests of the European magpie (all three publications in this paragraph are cited after Lefèvre et al. [14]). If the first egg clutch laid by a Cuckoo bird is not accepted by a magpie, then the Cuckoo bird deposits more eggs in the nest of the magpie, so there is not enough space left for the magpie eggs (Sorell et al. 1999). Alternatively, the Cuckoo birds throw all magpie eggs out of their nest (Pagel et al. 1998). Hoover and Robinson (2007) estimated that of all observed nests, the bird-parasites destroyed 56% of the nests in which their eggs were not accepted, and only 6% of the nests in which their eggs were accepted. Lefèvre et al. [14] emphasized the plasticity of the bird-parasite behavior. Mafia-like manipulation evolved not only from the evolution processes, but also from the learning experience of the individuals during their life span that depends on the actual „cooperation” between the host and parasite.

An example of cuckoo birds might not be so convincing, because not all parasitologists consider birds laying eggs in other bird nests as a „legitimate” parasite. Nevertheless it has been emphasized so many times, the amazing ability of parasites to react to specific environmental conditions, and related to this phenomenon, their plasticity reflected in their life cycles. This subject has been widely discussed in the article by Poulin [24] that describes the aspects related to the evolution of life cycle strategies of parasitic animals based on the background of characters of such processes in relation to corresponding free-living

organisms. In relation to the parasites, Poulin differentiates two terms: **a) life cycle** – which relates to the pattern that evolved from natural selection, and **b) life history** – related to individual life cycle shaping in such way that assures parasite the optimal reproduction success. The author emphasizes that in a diversified habitat the same genotype can develop a variety of phenotypes; this phenotypic plasticity is related only to a single parasitic generation and needs to be differentiated from the genetic adaptation (i.e., inheritance), which can be developed by increased number of individuals (due to the intensified fecundity) and repeatability of the phenotype. Phenotypic plasticity allows for the selection of the most optimal strategy for the life cycle, which also depends on the ambient habitat of the parasites, i.e., the inside of their hosts, and the external environment. As emphasized by Thomas et al. [25] this strategy of the parasite is „stage-dependent”, it means defined by specific environmental parameters.

Final remarks

Topics and subjects discussed in this article relate not only to the digenetic trematodes but also to other parasites from various taxonomic groups. In general, we know much more in relation to the aspect: what is the „model” of development? rather than on the aspect: why such a „model”? Very little is known about physiological basis of the mechanisms responsible for the completion of a parasitic life cycle. Also, the background of the host specificity remains still unknown. Does any alteration in the host behavior induced by a parasite represent an adaptive change? How to incorporate all the phenomena related to the parasitic life style into the theoretical framework of evolutionary and ecological scientific disciplines? These questions urged parasitologists enough that the entire issue of the journal *Behavioural Processes* has been dedicated to these problems. The discussion on these aspects has been preceded by the article of Thomas et al. [26] with a pronounced title: „**Parasitic manipulation: where are we and where should we go?**” followed by several articles that presented comments of other authors. It has been concluded that only by close collaboration of experts representing various disciplines of biological sciences the progress in resolving these exciting aspects of parasitology can be achieved and accomplished.

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