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ECOLOGY OF MAYFLY INFECTIONS

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Abstract. In comparison with the mayflies themselves, their infections are unsatisfactorily known. Infections often escape the attention since they mostly occur in inapparent form in nymphs retarded in their development. Mayfly pathogens show some adaptation to reach the proper host. These are discussed in fungi *Coelomycidium* and *Polycaryum* and Microsporidia. Microsporidia infecting mayflies are reviewed and specificity of pathogens from different aquatic habitats is mentioned.

Nymphs, pathogens, Fungi, Microsporidia

Compared with the wide distribution of mayflies in different regions and climates of the world, the known diseases of this group of hosts are present only in a very limited number of spots: only there, where investigatcrs tried to find them. This is a very unsatisfactory situation. It urges all collectors of mayflies to try to fill the gaps and find in each region local pathogens, adapted to the ecology of each species. In most cases it is not very difficult to find infected animals. If collected nymphs are brought under the dissecting microscope in a dish with black bottom, infected ones are clearly visible. They are opaque, milky white, with white masses of the parasites in different parts of the fat body, sometime deforming the body with tumor-like hypertrophic lobes. In other cases where the whole interior of the body of a host is turbid, pink or yellow. In cases where the midgut is infected, the host does not differ in staining from healthy animals. In dissected animals we usually find resistent stages of the pathogen in watermounts of different tissues.

The frequency of infected animals is changing from locality to locality, from season to season and population to population. Most frequent are inapparent infections in 5 - 10 % of animals in a closed population. Usually healthy nymphs develop faster and the infected ones postpone the hatching for up to 10 days . So can the percentage of infected animals grow to 50% and more. More frequent are infections during the winter and early spring, when the slow development of ephemerids gives enough time for the infection and development of the disease. In summer and in the tropics the relatively short period of development makes the infection less common or are present other pathogens than in conditions of the cold period.

Pathogens of aquatic animals usually have some adaptation which enables to spores or other infectious stages to reach the proper host. In diseases of mosquitoes, midges or blackflies this are different flotators, surface structures, mucose sheats or appendages, or there are motile stages which were able to find and invade the host. The last are typical for fungus infections. Coelomycidium ephemerae and C. caulleryi are typical for stagnant waters and invasions of Baetis and Cloeon. Vegetative thali appear in the body cavity of nymphs as minute spherical masses. The content of thali is a multinucleate mass which finally breaks into several hundred pear shaped zoospores with one flagellum. During their cleavage and maturation they are motile inside the membrane of the sphere, now representing the sporangium. Finally the sporangia break and release active zoospores. At that time the host insect dies and zoospores spread to find another host. For their orientation they have a specific organelle, rumfosome, which directs light from outside do a giant mitochondrium. A second fungus attacking Ephemeroptera is Polycaryum ecdyonuris and P. legeri. The fungus appears in current waters and is known from Ecdyonurus and Rhithrogena. Here oval, thickwalled sporangia leave the body of the host after its death. They fall to the bottom and later they open with a round lid protruding on a tube from the centre of the sporangium. Released germs fill one niche of the habitat and here they are collected by susceptible hosts.

More than 20 microsporidia infect ephemerids. Again,some of them are typical for stagnant waters, but others are found only in torrents. Most species have smooth spores, single or in groups (pansporoblasts). They sediment soon and are part of the sapropel which is the food of nymphs. Some have specific adaptations for distribution. Mitoplistophora angularis produces pansporoblasts in form of flat cushions with three ends, protruding in membranous filaments. They infect a rather quiet habitat of Ephemera danica. A very similar pathogen, but only with 8 spores in a pansporoblast infects Simothraulus in Vietnam. The angular protrusion change the pattern of distribution of both, one in stagnant, the other in current water. Trichoduboscqia epeori has spherical pansporoblasts with 16 spores which have on their persistent membrane long needles, 4 on each pansporoblast. When the host dies and the content of the white cyst with these stages is released, the needles, first coiled around the spherules, are extended and connected together in forming a cloud-like mass. This mass is easier fixed on the surface of stonee or plants in currents and is easier introduced into food of its torrenticolous hosts, Rhithrogena and Epeorus.

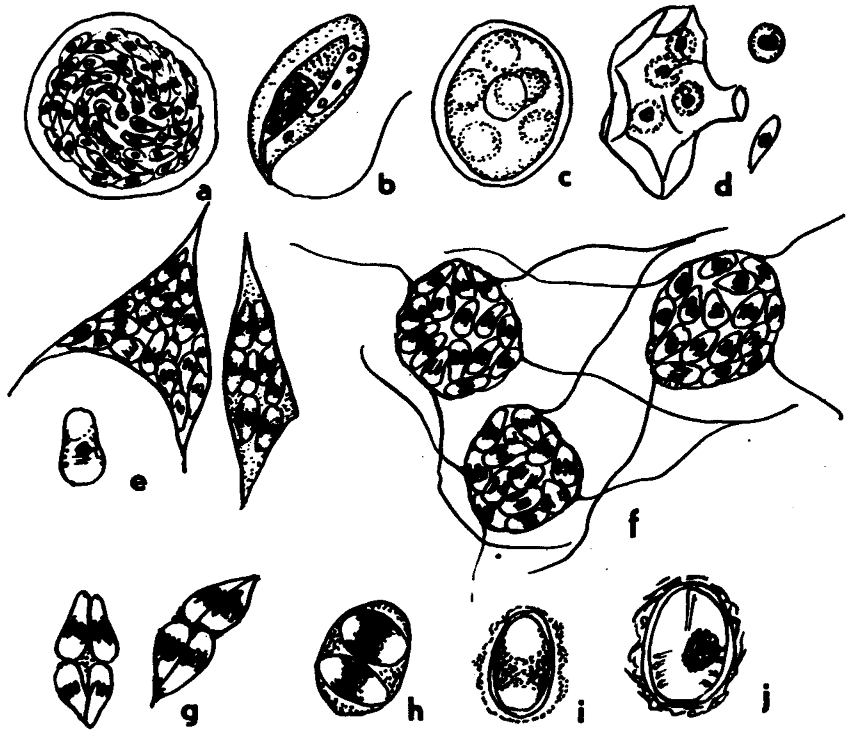

Fig. 1. a - Coelomycidium ephemerae, sporangium with circling zoospores. b - zoospore under high magnification. c, d - sporangia of Polycarium ecdyonuris. e - Mitoplistophora angularis, triangular pansporoblasts. f - Trichoduboscqia epeori, pansporoblasts connected by filiform appendages in a network. g - Gurleya legeri, tetrasporous pansporoblasts. h - Telomyxa glugeiformis - twin of spores in a rigid mass of the pansporoblast. i - single spore of Tuzetia with a subtle mashwork of membranous structures on surface. j - spore of Tuzetia baeticida with filamentous cover on surface.

Another extremous case, unique in ephemerids in Europe is Telomyxa glugeiformis. Twins of spores are enbedded in a transparent hart substance forming oval bodies. For long time these twins were described as single, bienergid spores. The organism is rare and its real structure could be recognized recently when it was collected again. It represents a type of parasite which is prepared to reach the bottom in the shortest way.

A final example of a complexity of adaptations of microsporidia for the aquatic habitat is Tuzetia baeticida, a microsporidian of the midgut epithel of Baetis. Its spores produce during maturation on the surface a spongious mass of tubules protruding from the exospore and increasing the flotation of the spore. Infecting the gut, this pathogen is released with the gut content. All gut infecting species are released with regenerating cells and in many instances do not destroy the host

Table 1. Review of microsporidia infecting ephemerid nymphs

Pathogen	Host	tissue	spore size	shape
Species with uninucleate spores				
G. Pleistophora : in sporogony multinucleate plasmodia, spores in irregular groups of spores closed in membrane or sticking together.				
P. vayssierei	B. rhodani	FB	3-4 x 1-2	pyrif.
P. centroptilii	C. luteolum	FB	4.5 x 2-3	oval
P. bohemica	P. bifidum	FB	6-7 x 2-3	oval
G. Mitoplistophora : pansporoblasts of fusiform or triangular shape. Each angle prolonged in a sinuous filament, 8,16,32 or more spores.				
M. angularis	E. danica	FB	4 x 2	pyrif.
G. Trichoduboscqia : pansporoblasts with 16 or 8 spores in membrane. On its outer surface 4 long needleshaped pro trusions, appendages.				
T. epeori	E. torrentium R. semicolorata	FB	5-5.5 x 2.5-3	pyrif.
G. Stempellia : pansporoblasts with 4, 8 and 16 spores of different size. 16 spores minor, 4 spores major /orig. mass identical/.				
S. mutabilis	E. vulgata	FB	2x1,4x2,6x2.5	oval
G. Thelohania : pansporoblasts mainly with 8 spores, some aberant with 16 or 4. All spores the same size.				
T. wurmi	B. muticus	Gut	5-6 x 2	oval
T. baetica	B. pygmaeus	FB	4-4.5 x 2.5	oval
T. rhithrogenae	R. hybrida	FB	5-5.5 x 2.5-3	oval
T. mutabilis	A. ludens	FB	3.8-5.5 x 2.5-3	oval
G. Gurleya : Spores in pansporoblasts grouped in packs of 4.				
G. legeri	E. ignita	FB	4-5 x 2.5	oval
*G. linearis	E. danica	FB	4-5 x 2	oval

G. Telomyxa : pansporoblast containing two spores filled with a hard mass so that it resembles one single spore. Groups of 8, 16 etc.

T. glugeiformis	E. vulgata	FB	6.5 x 4 /4x2.5/	oval

Species with binucleate spores

Nosema : spores single, in EM sections without surface cover sheet.

N. schneideri	E. vulgata	Gut	4 x 2	oval
N. baetis	Baetis, Cloeon Ecdyonurus	FB	3-4 x 1.5-2.5	oval
N. ephemerae	Ephemera sp.	Gut	3.5-4 x 2-2.5	oval
N. leptophlebiae	L. vespertina	Gut	2-3 x 2	oval
N. tatrica	E. ignita	FB	3.3-3.5 x 1.7-2	oval

G. Octosporea : spores short tubular, binucleate, in groups.

*O. intestinalis	R. semicolorata	Gut	6	oval

G. Tuzetia : spores closed in a membrane, single.

*T. entericola	R. semicolorata	Gut	6-7	oval
*T. lipotropha	R. semicolorata	FB	6	oval
*T. baeticida	B. vernus	Gut	5	oval
*O. hypertrophians	B. vernus	FB	5-6	tub.

* - indicated names are nomida nuda

Infections of the fat body fill the cells of the fat body and are free only after the host died and the tissues were autolysed. All infections are released with faeces of fish predators. There is no known infection of the ovary which may enable the transmission inside the eggs. In some cases of late infections, spores of parasites were retained during formation of adults and during their flight and oviposition they reach the upper streams. In large areas they are transported on feathers of migratory birds and in the gut of fish.

In pathogens distributed in species in stagnant waters there is no strong host specificity, rather a specificity for one habitat. In torrenticolous species the conditions are rather specific and this makes the decision on host specificity difficult. As mentioned in the introduction, we do not have data on zoogeographic distribution of the different species and this aspect will need a concentrated effort of all students of mayflies in the world.

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