New insights into the origin of the orthonectids' parasitic plasmodium (Bilateria: Orthonectida)

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Background

Orthonectids are invertebrate parasites of marine Metazoa. They are highly derived annelids who underwent secondary reduction and acquired a unique for bilaterians adaptation to parasitism – so-called parasitic plasmodium (Fig.1). Multinucleated shapeless plasmodium penetrates the host body and can cause collateral damage. Sexual generation emerges from the plasmodium and leaves the host for copulation.

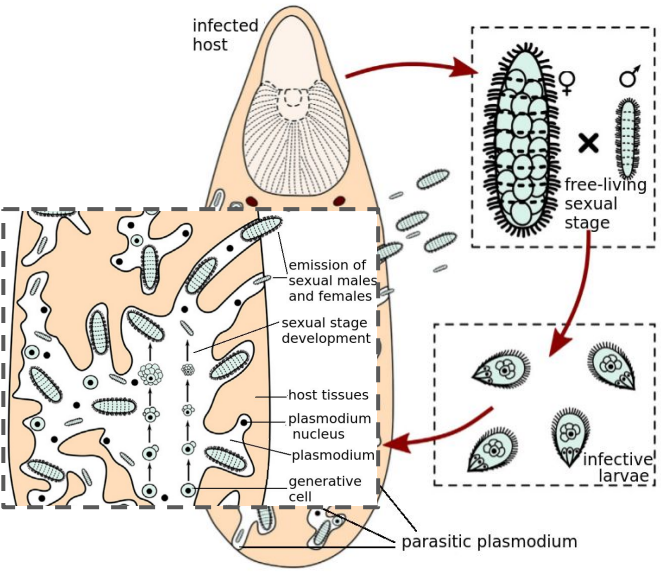

Fig.1. Detailed scheme of the parasitic plasmodium and the orthonectids' life cycle. From *Slyusarev et al., 2020*, with alterations.

The origin of the orthonectids' plasmodium remains controversial – it is either an enlarged cytoplasmic portion of a parasitised host cell or an independent organism, the parasitic generation of the orthonectids' life cycle.

Results: fine structure of the plasmodium

We examined the plasmodium of *Intoshia linei* with TEM and CLSM. It is a multinucleated parasitic body separated from host tissues by two plasma membranes (Fig.3, Fig.2B). Its cytoplasm contains organelles and nuclei typical for other orthonectids' stages (Fig.2A, Fig.3).

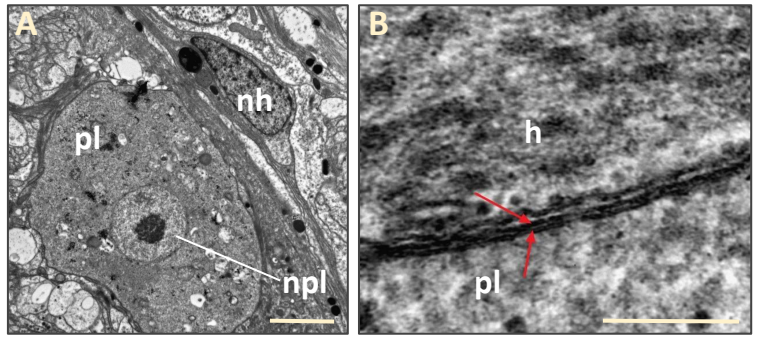

Fig.2. Ultrathin sections of the *I. linei* plasmodium. A. Nucleus in the plasmodium cytoplasm; *scale bar* 2 µm. B. Two plasma membranes of the plasmodium; *scale bar* 200 nm. *pl*, plasmodium; *npl*, plasmodial nucleus; *h*, host; *nh*, host nucleus. Arrows point to the membranes of the plasmodium.

Fig.3. CLSM of *I.linei* plasmodium, scale bar 5 µm. TRITC-phalloidin (*red*), DAPI (*blue*) staining; α-tubulin (*magenta*), serotonin-positive (*green*) immunoreactivity. *npl*, plasmodial nuclei; *e*, *I. linei* embryos; *ad*, *I.linei* adults; *nh*, host nuclei.

Results: plasmodial proteins

By analysing stage-specific RNA-seq of *I. linei* and *I. variabili*, we detected hundreds of orthonectids' putative proteins expressed only at the parasitic stage. They are involved in the defence against the host, host nutrients uptake, growth inside the host and host-parasite communication (Tab.1). Some of them are known effectors of other endoparasites.

Obtained results indicate orthonectids' plasmodium is an independent organism of a parasitic origin.

Tab.1. Plasmodium-specific protein families and superfamilies and their potential role

Function	Protein family/superfamily
Defence against host immunity	pepsin-like protease, serpin and elafin-like protease inhibitors, C-type lectins, apyrase, saposins, other secreted proteins
Host cells engulfment, nutrients uptake	saposins, C-type lectins, vesicle-associated proteins (RAVE, SNARE), GPCRs, EGF-Rs, Ras proteins, enolase, NAD(P)+ transhydrogenase, other enzymes
Growth inside the host	GPCRs, EGF-Rs, other receptors, aspartic protease, serpin and elafin-like protease inhibitors
Host-parasite communication	GPCRs, EGF-Rs, ABC and MFS transporters, other transmembrane transporters and receptors

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