

The symbiotic role of *Wolbachia* in Onchocercidae and its impact on filariasis

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Abstract

Symbiotic associations between eukaryotes and microorganisms are frequently observed in nature, and range along the continuum between parasitism and mutualism. The genus *Wolbachia* contains well-known intracellular bacteria of arthropods that induce several reproductive phenotypes that benefit the transmission of the bacteria. Interestingly, *Wolbachia* bacteria have been found in the Onchocercidae, a family of filarial nematodes, including species that cause human filarial diseases, e.g. lymphatic filariasis and onchocerciasis. The endosymbiont is thought to be mutualistic in the Onchocercidae, and to provide essential metabolites to the filariae. Currently, *Wolbachia* bacteria are targets of antibiotic therapy with tetracyclines, which have profound effects on the development, viability and fertility of filarial parasites. This overview article presents the Onchocercidae and *Wolbachia*, and then discusses the origin and the nature of the symbiosis. It highlights the contribution of *Wolbachia* to the survival of the filariae and to the development of pathology. Finally, the infection control implications for filariases are debated. Potential directions for future research are also discussed.

Keywords: Antibiotherapy, filariasis, onchocercidae, symbiosis, *Wolbachia*

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Introduction

Among the Nematoda, the order Spirurida encompasses the family Onchocercidae, commonly known as filariae. They infect a broad range of terrestrial vertebrates, and many of them are responsible for medical and veterinary issues in mammals (Table 1) [1–27]. They are all transmitted by haematophagous arthropod vectors that are either pool-feeders (telmophagous) (e.g. black flies for onchocerciasis transmission, or tabanid flies for loiasis) or vessel-feeders (solenophagous) (e.g. mosquitoes for lymphatic filariasis transmission, or ticks for canid filariasis) (Table 1). Filarial nematode species can host *Wolbachia* bacterial endosymbionts. Research on the symbiosis of *Wolbachia* and Onchocercidae has highlighted the contributions of bacteria to the reproduction of filariae, the inflammatory disease pathogenesis, and the immunomodulation of the vertebrate host, and has led to the consideration of antibiotic therapy as a novel method of treatment.

Biology of Filariae and their Endosymbiont *Wolbachia*

The microfilariae (stage 1 or L1) are taken up by the vector during a blood meal. In this intermediate host, they moult and develop until they become stage 3 (infective) larvae (L3). Throughout this development, the larvae migrate from the ingested blood to other tissues, depending on the vector species [28]. During another blood meal of the vector, the infective larvae are passed to the dermis of the vertebrate's skin. Once there, the L3 larvae moult into stage 4 larvae within 2 days for the genera *Onchocerca* and *Dirofilaria*, and within approximately 10 days for the other genera [28]. Most of the species migrate through the host's body from the skin to their definitive niche, mainly the lymphatic system, the coelomic cavities, the cardiopulmonary system, and connective tissues (Table 1). The fourth and final moult results in adult male or female worms.

TABLE I. Prominent filarial species of human and veterinary interest

Species	Vectors Genus (family)	Vertebrate hosts	Main tissue localization of adult worms	Main pathologies	Localization of microfilariae	Wolbachia supergroup	References
<i>Onchocercinae</i>							
<i>Acanthocheilonema draconuloides</i> (Cobbold, 1870)	Hippoboscidae	Canids	Coelomic cavity and subcutaneous tissue	Blood	Usually asymptomatic	NA	[1.2]
<i>Acanthocheilonema reconditum</i> (Grassi, 1889)	Heterodoktus (Boopidae)	Canids	Subcutaneous tissue	Blood	Usually asymptomatic	Absent	[1.3]
<i>Acanthocheilonema viteae*</i> (Krepkogorskaya, 1933)	Pulex (Pulicidae)	Rodents	Subcutaneous tissue	Blood	Usually asymptomatic	D	[1.4.5]
<i>Brugia malayi</i> (Brug, 1927)	Heterodoktus (Boopidae)	Humans, ^a	LS, LN, testes	Blood	Adenopathy	D	[1.6.7]
<i>Brugia pahangi</i> (Buckley & Edeson, 1956)	Mansonia (Aigaiae)	Dogs, felids ^{b, c}	LS, LN, testes	Blood	Lymphoedema	D	[1.6.7]
<i>Brugia timori</i> (Parsons et al., 1977)	Anopheles (Culicidae)	Humans	LS, LN, testes	Blood	Lymphoedema	D	[1.7.8]
<i>Cercopithilanus grassii</i> (Noë, 1907)	Aedes (Culicidae)	Dogs	Subcutaneous tissue	Skin	Usually asymptomatic	NA	[1.9.10]
<i>Litomosoides sigmodontis*</i> (Chandler, 1931)	Rhipecephalus (Ixodidae)	Rodents	Coelomic cavity	Blood	Usually asymptomatic	D	[1.1.1]
<i>Mansoniella (Mansoniella) ozzardi</i> (Manson, 1897)	Omniomyiasidae (Macrotonysidae)	Humans	Coelomic cavity	Blood	Usually asymptomatic	F	[1.1.1]
<i>Mansoniella (Esslingeria) perstans</i> (Manson, 1891)	Culicoides (Ceratopogonidae)	Humans and monkeys	Coelomic cavity	Blood	Usually asymptomatic	F	[1.1.3]
<i>Mansoniella (Esslingeria) streptocerca</i> (Macfie & Corson, 1922)	Callicoides (Ceratopogonidae)	Humans and monkeys	Intradermal	Skin	Dermatitis	NA	[1.1.4]
<i>Onchoocerca cervicalis</i> (Railliet & Henry, 1910)	Culicoides (Ceratopogonidae)	Equids	Nuchal ligament	Skin	Dermatitis	D	[1.1.5]
<i>Onchoocerca gutturosa</i> (Neumann, 1910)	Simulium (Simuliidae)	Bovids	Nuchal ligament	Skin	Ocular trauma	Dermatitis	[1.1.6]
<i>Onchoocerca lupi</i> (Rodonaja, 1967)	Calicoides (Ceratopogonidae)	Canids	Intradermal	Skin	Ocular trauma	Nodules	[1.1.7]
<i>Onchoocerca ochengi</i> (Bwangano, 1969)	Unknown	Bovids	Subcutaneous tissue	Skin	Dermatitis	C	[1.1.1, 18, 19]
<i>Onchoocerca volvulus</i> (Leuckart, 1893)	Simulium (Simuliidae)	Humans	LS, LN, testes	Skin	Ocular trauma	C	[1.20]
<i>Wuchereria bancrofti</i> (Cobbold, 1877)	Gulex (Culicidae)	Humans		Blood	Lymphoedema	D	[1.7.21]
<i>Dirofilariae</i>							
<i>Dirofilaria immitis</i> (Leidy, 1856)	Aedes (Culicidae)	Canids, felids ^d	Right ventricle	Blood	Heart worm disease	C	[1.22.23]
<i>Dirofilaria repens</i> (Railliet et Henry, 1911)	Aedes (Culicidae)	Canids, felids ^e	Pulmonary artery	Blood	Subcutaneous tissue nodules	C	[1.24]
<i>Loa loa</i> (Cobbold, 1864)	Culex (Culicidae)	Humans	Vena cava	Blood	Calabar swelling	Absent	[1.25]
<i>Setaria equina</i> (Abildgaard, 1789)	Chrysops (Tabanidae)		Subcutaneous tissue	Blood	Ocular trauma		
<i>Setaria equina</i> (Abildgaard, 1789)	Aedes (Culicidae)	Horses	Connective tissue	Blood	Usually asymptomatic	Absent	[1.26.27]

Lymph nodes (L), lymphatic system; NA: data not available. Extra hosts are indicated by ^{a,b,c}; monkeys, cats, dogs, viverrids, mandrills, viremurs; ^b: cebids, erinaceids, pangolins; ^c: transmissible to humans; d: ferrets.

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