


LICE (AMBLYCERA AND ISCHNOCERA) AS VECTORS OF EULIMANDA SPP. (NEMATODA: FILARIOIDEA) IN CHARADRIIFORM BIRDS AND THE NECESSITY OF SHORT REPRODUCTIVE PERIODS IN ADULT WORMS

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Abstract: Lice transmit species of Eulimandina. Larvae of Eulimandina wongae are described from Charadriomoides longirostris and Charadrius alexandri (Amblycera) and Cardicus chalybeus (Ischnocera) collected on a marbled godwit (Limosa fedoa). Larvae of Eulimandina baenae are described from the same ischnotepus phaeopus (Amblycera) and Lymnocryptus nuchalis (Ischnocera) from a whimbrel (Nannematodes phaeopus). Adults of species of Eulimandina in charadriiform birds and Peletoctes fulicaenaeus in crows produce microfilariae for a short period only and then die and are resorbed (species of Eulimandina), a phenomenon called ephemeralism; or become reproductive synestersis. Microfilariae inhabit the skin and presumably survive for a prolonged period. The short period of production of microfilariae may be related to the fact that transmission is by permanent ectoparasites (lice) constantly exposed to microfilariae in the skin and the dangers of lice acquiring lethal numbers of microfilariae. Ephemeralism may also evolve in species in which adult ocussing where, when they die, the skin is harmless resorbed (e.g., species of Eulimandina in the neck). Reproductive synesteresis may evolve in species that occupy sites where, if they were to die, they might provoke a life-threatening inflammation (e.g., P. fulicaenaeus near joints in the leg).

Eulimandina species are parasites mainly of charadriiform birds (Bartlett et al., 1989). Adult worms occur in the neck and are unusual among filariaids in that they are ephemeral (Bartlett et al., 1989; Bartlett and Anderson, 1990; Bartlett, 1992). Amblyceral lice (Mallophaga) were suggested previously (Bartlett et al., 1989; Bartlett and Anderson, 1990) as vectors. The present study provides conclusive evidence that amblyceral and ischnoceral lice serve as vectors; it describes larval larvae in lice from a marbled godwit (Limosa fedoa) infected with Eulimandina wongae and a whimbrel (Nannematodes phaeopus) infected with Eulimandina baenae.

Bartlett and Anderson (1990) hypothesized that ephemeralism of adult worms of Eulimandina species, which results in a short period of production of microfilariae, is related to vectors. The present paper, having clearly established that lice are the vectors, clarifies this hypothesis and broadens it to include another loose-transmitted larid of birds, namely Peletoctes fulicaenaeus in crows (Gruiformes). Peletoctes fulicaenaeus also has a short period of production of microfilariae that...
Table 1. Numbers of adult female and male lice of different species on a marbled godwit (Limosa fedoa) infected with Eulimadana wongae and a whimbrel (Numenius phaeopus) infected with Eulimadana bainae, and numbers of first- through third-stage filaroid larva found in these lice.

| Filaroid Larva | Number of larvae infected examined | Number of larvae infected examined | Details of infection in each infected louse
<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Actinotriches bainae</td>
<td>0.8</td>
<td>0.7</td>
<td>MFL: 1 L1; 1 L1;</td>
</tr>
<tr>
<td>Actinotriches lamari</td>
<td>1.0</td>
<td>0.7</td>
<td>1 L1;</td>
</tr>
<tr>
<td>Cardiceps clarv</td>
<td>4.3</td>
<td>0.7</td>
<td>1 L1; 1 L1;</td>
</tr>
<tr>
<td>Loxocephalum clarv</td>
<td>0.7</td>
<td>0.7</td>
<td>1 L1;</td>
</tr>
<tr>
<td>Retrundicceps pseudolamari</td>
<td>0.7</td>
<td>0.7</td>
<td>1 L1;</td>
</tr>
<tr>
<td>Wurmberti</td>
<td>0.3</td>
<td>0.3</td>
<td>1 L1;</td>
</tr>
</tbody>
</table>

* Larval filaroids from each infected female louse followed by those from each infected male louse; data from individual lice separated by semicolons; MFL, microfilariae; L, provascular or vascular first-stage larva; MFL, molting first-stage larva; L1, second-stage larva; L2, third-stage larva.

References used were Clay (1959) for Actinotriches, Clay (1962) for Actinotriches, and Tammerschik (1969) for Cardiceps, Cardiceps pseudolamari, and I. bainae. Larvae of E. wongae were found in some individuals of the first 3 species (Table 1).

The whimbrel harbored 45 adult lice including Amblycerus (Actinotriches bainae) and I. bainae (Cardiceps clarv, Loxocephalum clarv, Retrundicceps pseudolamari, and Wurmberti). Larvae of E. wongae were found in some individuals of the first 2 species (Table 1).

The microfilaria of E. wongae differed morphologically from the provascular (a first-stage larva) of E. bainae, and the 2 are described separately below. The sausage (a first-stage larva, the molting first-stage larva, and all but the posterior extremity of the third-stage larva of the 2 species were similar. They are described together below.

**Microfilaria of E. wongae**

The microfilaria (n = 1) (Fig. 1) was 8.0 μm wide, 145.0 μm long, and lacked a sheath. Many small nuclei filled the body but the R and G cells were not distinguishable. The esophageal thread was visible. The tail was long and pointed.

**Presurgical larva of E. bainae**

The presurgical stage (n = 1) (Fig. 12) was 10.0 μm wide, 115.0 μm long, and lacked a sheath. Many small nuclei filled the body but the R and G cells were not distinguishable. The esophageal thread and excretory pore and vesicle were visible. The anal pore was 22.0 μm from the posterior extremity of the body. The tail was short and pointed.

**Sausage larva of E. wongae and E. bainae**

The sausage stage of E. wongae (n = 1) (Fig. 2, Table II) and of E. bainae (n = 1) (Fig. 13, Table II) contained large cells that formed the subectosomal body wall. The excretory pore in E. wongae was 43.0 μm from the anterior extremity of the body and in E. bainae it was 62.0 μm. The nerve ring, excretory pore and vesicle, esophageal primordium, and intestinal primordium were visible. A small plug protruded from the anal pore. The genital primordium was not observed.

**Molting first-stage larva of E. wongae and E. bainae**

The molting first stage of E. wongae (n = 1) (Figs. 3, 4; Table II) and of E. bainae (n = 1) (Figs. 14, 15; Table II) had detached cuticle at the anterior and posterior extremities of the body. The esophagus was divided into a narrow anterior portion and a broader posterior portion. The esophageal-intestinal junction was distinct. The intestinal lumen was visible but not contiguous with the rectal lumen. An anal plug was present. The genital primordium was not observed.

**Results**

The godwit harbored 119 adult lice including Amblycerus (Actinotriches bainae) and I. bainae (Cardiceps clarv, Loxocephalum clarv, Retrundicceps pseudolamari, and Wurmberti). Larvae of E. wongae were found in some individuals of the first 3 species (Table 1).

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TABLE II. Major dimensions (μm) of sausage first-stage, molting first-stage (M1), and infective third-stage (L3) larvae of Eutimdana wongae from lice on a marbled godwit (Limosa fedoa) and Eutimdana bainae from lice on a whimbrel (Numenius phaeopus).

<table>
<thead>
<tr>
<th></th>
<th>E. wongae</th>
<th>E. bainae</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>M1</td>
<td>L1</td>
</tr>
<tr>
<td>Number measured</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Length</td>
<td>180</td>
<td>300</td>
</tr>
<tr>
<td>Maximal width</td>
<td>22</td>
<td>36</td>
</tr>
<tr>
<td>Neck ring from anterior end</td>
<td>35</td>
<td>47</td>
</tr>
<tr>
<td>Length of muscular esophagus</td>
<td>20*</td>
<td>55</td>
</tr>
<tr>
<td>Length of glandular esophagus</td>
<td>30*</td>
<td>70</td>
</tr>
<tr>
<td>Total length of esophagus</td>
<td>60</td>
<td>145</td>
</tr>
<tr>
<td>Lumen from posterior end</td>
<td>48</td>
<td>155</td>
</tr>
</tbody>
</table>

* Presumed length of lumen of first-stage larva followed by tip of cuticle on tail of second-stage larva.

Infective third-stage larva of E. wongae and E. bainae

The infective third-stage of E. wongae (n = 2) (Figs. 5–11; Table II) and E. bainae (n = 1) (Figs. 16–21; Table II) had a cephalic extremity with a round oral opening, 4 pairs of papillae, and amphids. The cuticle was marked by delicate transverse striations. The buccal cavity consisted of an anterior non sclerotized portion 2 μm long and a posterior sclerotized portion 4 μm long. The excretory pore was not visible. The anterior portion of the esophagus was narrow; the posterior portion was broad and granular. The intestinal lumen was contiguous with the rectal lumen. The anus was patent. The genital primordium were 133 and 162 μm from the anterior extremity in 2 females of E. wongae but were not observed in E. bainae. The posterior extremity of the body of E. wongae has 2 subventral, sublateral tonguelike structures, 1 terminal pointed structure, and 2 subdorsal, sublateral tonguelike structures. The posterior extremity of the body of E. bainae has 2 subventral, sublateral tonguelike structures and 1 terminal pointed structure. Tiny phasmids were visible near the subventral, sublateral structures in both species.

DISCUSSION

Development of filarialis to the infective third stage in lice indicates lice are suitable vectors. Larvae in lice from the godwit were undoubtedly E. wongae, the only filarialis present in the godwit. Similarly, only E. bainae was present in the whimbrel. Furthermore, microfilariae in the hemocoe of lice from the godwit were identical to microfilariae of E. wongae from the bird’s skin (Bartlett, 1992) except they lacked the sheath that would have been shed in the midgut of the vector. Prenasal-stage larvae in lice from the whimbrel had the short tail characteristic of microfilariae of E. bainae (see Bartlett, 1992). Plectorus fulicarectus of coots, the sole louse-transmitted avian filarialis previously studied in detail, attains the infective stage only in adult lice (Bartlett and Anderson, 1987). Thus, only adults were examined herein. In ambylocerans adults, prevalence (of all larval stages) of E. wongae is 12% of 24 and of E. bainae, 50% of 10. Bartlett and Anderson (1987) reported P. fulicarectus in 26% of 119 ambyloceran adults (from coot A-6). The prevalence of E. bainae should be viewed cautiously because ambylocerans often leave a carcass as it cools and because it is not known when the whimbrel was placed in a bag and whether any lice left it.

In addition to the above avian filarialis, Eutimdana cypselli of swifts (Apodiformes) and Sarconema eurycerca of geese and swans (Anseriformes) are transmitted by lice (Dutton, 1905; Nelson, 1962; Seagar et al., 1976; Cohen et al., 1991). The present study is the first to show that ischnocerans, in addition to ambylocerans, are vectors. Kettle’s (1977) report of an unidentified larval nematode in an ischnoceran (Rallicola sp.) from an Australian rail (Gruiformes) is of unknown significance.

Bartlett et al. (1989: 628) mentioned “filarial larvae in lice on a bird harbouring skin-inhabiting microfilariae of an undescribed species of Eutimdana.” That statement can now be clarified. The bird was a marbled godwit, the filarialis was E. wongae, and the louse was Actornithophilus limosus. Two third-stage larvae were found in 1 female louse and microfilariae in a second. Actornithophilus limosus also contained a third-
stage larva in the present study; third-stage larvae in the 2 studies were identical.

Transmission by a vector that is a permanent ectoparasite is unusual among filarioides as is the life history strategy found in species of *Eulindana* and *P. fulicataeaeae* in which production of microfilariae by adult females is curtailed. The 2 unusual features may be related, as the following paper attempts to explain. Firstly, and obviously, filarioids transmitted by permanent ectoparasites must not jeopardize the survival of their vectors or the latter could be extinguished on individual hosts. Filarioids would jeopardize survival of a vector if microfilariae accumulated and became superabundant in the vertebrate host and, at the same time, the number of microfilariae ingested by the vector was correlated positively with the number of microfilariae present and large numbers of ingested microfilariae were harmful to the vector. Large numbers of ingested microfilariae may, for example, decrease the life expectancy of some dipteran vectors (Lavou- pierre, 1958). Secondly, the microfilariae of *E. montae* and *E. batuanae* inhabit skin and possibly live as long as the host (numerous microfilariae are commonplace in adult birds that lack adult worms in natural hosts). Similarly, microfilariae of *P. fulicataeaeae* inhabit skin and are possibly also long lived. If microfilariae were both long lived and produced over a prolonged period, they would likely eventually saturate the skin (Bartlett and Anderson, 1990). Therefore, selection may have favored individual worms that curtailed production of microfilariae before the skin became saturated. Among species of *Eulindana*, production is curtailed by ephemerality of post- reproductive adult worms. In *P. fulicataeaeae*, on the other hand, production is curtailed by early reproductive senescence of adult worms although the latter remain alive (Bartlett and Anderson, 1989).

The existence of 2 means (ephemerality and reproductive senescence) to a similar life history strategy (curtailment of production of microfilariae) may be related to the fate of dead versus living adult worms in different sites. Adults of species of *Eulindana* inhabit the neck region, reproduce, die, and quickly are harmlessly resorbed (Bartlett et al., 1989; Bartlett, 1992). Adult *P. fulicataeaeae* live near joints in the legs, reproduce and undergo senescence, but do not die and, as living worms, do not provoke severe inflammation (Bartlett and Anderson, 1987). If they were to die, they might provoke chronic inflammation as do other dead nematodes near joints (e.g., *P. sculptipes* in snowshoe hares [Bartlett, 1984] and *Dicrocoelium* in humans [Shastry, 1946; Reddy et al., 1968]). Te- nosynovitis or arthritis in the legs might be life threatening to hosts such as coots that run across water to become airborne. Bartlett et al. (1989) suggested that ephemerality and resorption of adults in species of *Eulindana* might also be selected if it served to remove the immunogenic stimuli of adults and if this benefited microfilariae that are required to live for long periods but likely share some antigens with their parents. Anderson (1992) noted the similarity in the life histories of species of *Eulindana* and *Trichinella*. In both, adults are ephemeral and eliminated by the host, and progeny flood the tissues and are long lived.

ACKNOWLEDGMENTS

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