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LICE (AMBLYCERA AND ISCHNOCERA) AS VECTORS OF *EULIMDANA* 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 *Eulimdana*. Larvae of *Eulimdana wongae* are described from *Austroropen limosa* and *Actornithophilus limosae* (Amblycera) and *Cardiceps clayae* (Ischnocera) collected on a marbled godwit (*Limosa fedoa*). Larvae of *Eulimdana bairae* are described from *Austroropen phaeopus* (Amblycera) and *Limacops numenius phaeopi* (Ischnocera) from a whimbrel (*Numenius phaeopus*). Adults of species of *Eulimdana* in charadriiform birds and *Pelecius fulicaeatae* in coots produce microfilariae for a short period only and then die and are resorbed (species of *Eulimdana*), a phenomenon called ephemerality, or become reproductively senescent but remain alive (*P. fulicaeatae*). 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. Ephemerality may have evolved in species in which adults occupy sites where, when they die, they are harmlessly resorbed (e.g., species of *Eulimdana* in the neck). Reproductive senescence may have evolved in species that occupy sites where, if they were to die, they might provoke a life threatening inflammation (e.g., *P. fulicaeatae* near joints in the legs).

Eulimdana species are parasites mainly of charadriiform birds (Bartlett et al., 1989). Adult worms occur in the neck and are unusual among filarioids in that they are ephemeral (Bartlett et al., 1989; Bartlett and Anderson, 1990; Bartlett, 1992). Amblyceran lice (Mallophaga) were suggested previously (Bartlett et al., 1989; Bartlett and Anderson, 1990) as vectors. The present study provides conclusive evidence that amblyceran and ischnoceran lice serve as vectors; it describes filarioid larvae in lice from a marbled godwit (*Limosa fedoa*) infected with *Eulimdana wongae* and a whimbrel (*Numenius phaeopus*) infected with *Eulimdana bairae*.

Bartlett and Anderson (1990) hypothesized that ephemerality of adult worms of *Eulimdana* 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 louse-transmitted filarioid of birds, namely *Pelecius fulicaeatae* in coots (Gruiformes). *Pelecius fulicaeatae* also has a short period of production of microfilariae that,

however, results from reproductive senescence of adult worms (Bartlett and Anderson, 1989) rather than ephemerality of adults.

MATERIALS AND METHODS

The godwit and whimbrel were examined initially by Bartlett (1992), the godwit furnishing the type specimens of *E. wongae* and the whimbrel those of *E. bairae*. The godwit had been shot, immediately placed in a plastic bag, frozen, and later thawed. It was examined for lice by washing the carcass in 3 changes of soapy water and passing all water through a sieve (Endecott's test sieve no. 100 with a 150- μ m aperture). Lice remaining on the sieve or carcass were transferred to a dish containing 7.5% physiologic saline. It is not known how soon after collection the whimbrel was placed in a plastic bag. It was frozen and later thawed and examined for lice by manually searching the feathers and skin. Lice were transferred to saline.

Nymphs were preserved in 70% alcohol. Adult lice were teased in 2-3 drops of saline on a glass slide and the tissues and saline were examined for filarioid larvae. Remnants of the louse's body then were removed and preserved in a vial of 70% alcohol. If filarioid larvae were found, 2-3 drops of 2% buffered formalin were added to the saline, and the preparation was covered with a vaseline-ringed coverslip. Larvae were studied with the aid of a compound microscope equipped with differential interference lighting. Drawings were made with the aid of a drawing attachment.

Lice from other godwits and whimbrels examined by Bartlett (1992) were identified to species. The major

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TABLE 1. Numbers of adult female and male lice of different species on a marbled godwit (*Limosa fedoa*) infected with *Eulimdana wongae* and a whimbrel (*Nanenus phaeopus*) infected with *Eulimdana bairae*, and numbers of first- through third-stage filarioid larvae found in these lice.

	Number of ♀ lice infected examined	Number of ♂ lice infected examined	Details of infection in each infected louse*
Marbled godwit			
<i>Austromenopon limosae</i>	2/8	0/1	MF: 1 L ₁
<i>Actornithophilus limosae</i>	1/10	0/5	1 L ₁
<i>Cardiiceps clayae</i>	4/33	3/33	MF: 1 L ₁ ; 1 S; 1 mL; 1 S; 1 S; 1 S
<i>Limaceps clayae</i>	0/7	0/7	
<i>Rotundiceps condati</i>	0/7	0/3	
<i>Saemundssonina</i> sp.	0/3	0/0	
Whimbrel			
<i>Austromenopon phaeopodis</i>	2/6	3/4	4 S; 2 S; 1 mL; 2 S; 1 S
<i>Limaceps nanus phaeopi</i>	2/17	0/14	1 L ₁ ; 1 L ₁
<i>Saemundssonina scolopacisphaeopodis</i>	0/3	0/1	

* Larval filariae from each infected female louse followed by those from each infected male louse; data from individual lice separated by semicolons. MF, microfilariae; S, presavage or sausage first-stage larva; mL, molting first-stage larva; L₁, second-stage larva; L₂, third-stage larva.

references used were Clay (1962) for *Actornithophilus*, Clay (1959) for *Austromenopon*, Timmermann (1954a) for *Cardiiceps*, Timmermann (1954b) for *Limaceps*, Edwards (1952) for *Rotundiceps*, and Timmermann (1969) for *Saemundssonina*.

Remnants of dissected lice were compared to identified, whole specimens and thus also identified to species.

RESULTS

The godwit harbored 119 adult lice including *Amblycera* (*Austromenopon limosae* and *Actornithophilus limosae*) and *Ischnocera* (*Cardiiceps clayae*, *Limaceps clayae*, *Rotundiceps condati*, and *Saemundssonina* sp.). Larvae of *E. wongae* were found in some individuals of the first 3 species (Table I).

The whimbrel harbored 45 adult lice including *Amblycera* (*Austromenopon phaeopodis*) and *Ischnocera* (*Limaceps nanus phaeopi* and *Saemundssonina scolopacisphaeopodis*). Larvae of *E. bairae* were found in some individuals of the first 2 species (Table I).

The microfilaria (a first-stage larva) of *E. wongae* differed morphologically from the presavage (a first-stage larva) of *E. bairae*, 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 µm wide, 145 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.

Presavage larva of *E. bairae*

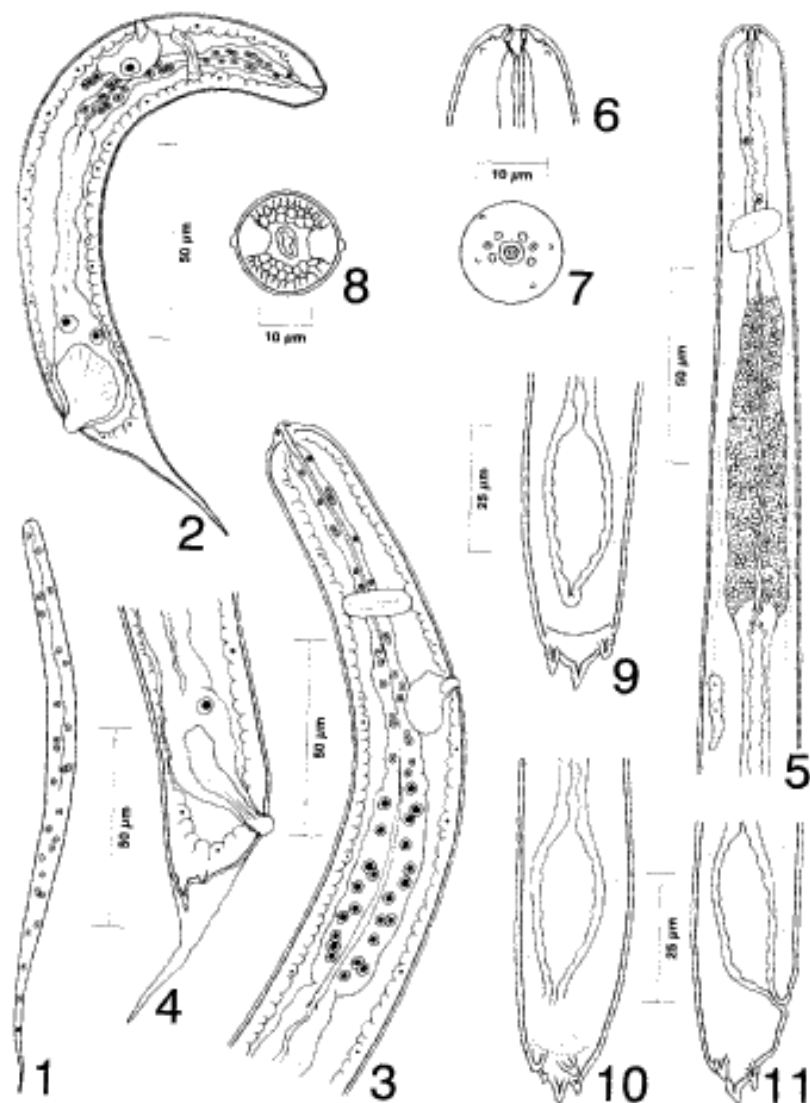
The presavage stage (n = 1) (Fig. 12) was 10 µm wide, 114 µm long, and lacked a sheath. Many small nuclei filled the body but the R and G cells were not distinguishable. The esophageal thread and excretory pore and vesicle were visible. The anal pore was 22 µm from the posterior extremity of the body. The tail was short and pointed.

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

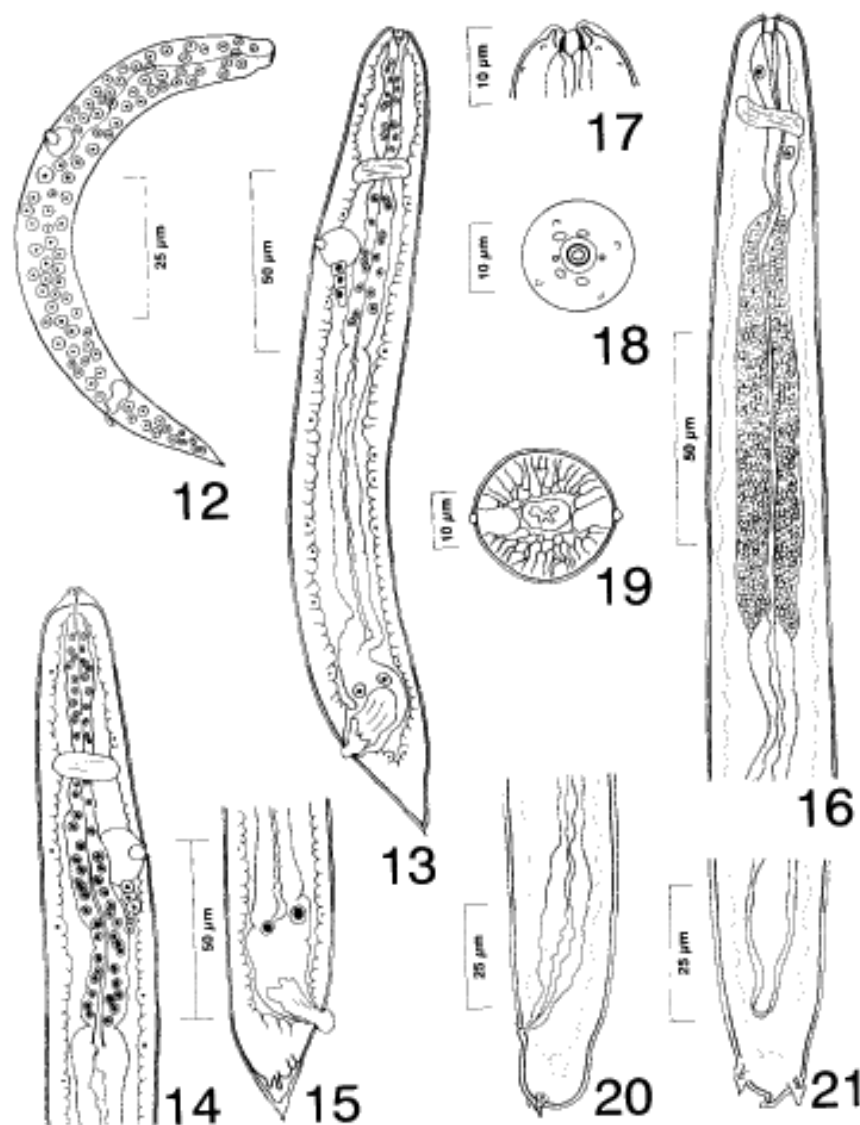
The sausage stage of *E. wongae* (n = 1) (Fig. 2; Table II) and of *E. bairae* (n = 1) (Fig. 13; Table II) contained large cells that formed the subcuticular body wall. The excretory pore in *E. wongae* was 45 µm from the anterior extremity of the body and in *E. bairae* it was 62 µm. The nerve ring, 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. bairae*

The molting first stage of *E. wongae* (n = 1) (Figs. 3, 4; Table II) and of *E. bairae* (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.



FIGURES 1-11. Developmental stages of *Eulimdana wongae* from the abdominal hemocoel of lice found on a marbled godwit (*Limosa fedoa*). 1, Microfilaria. 2, Sausage-stage larva. 3, Anterior end, molting first-stage larva. 4, Posterior end, molting first-stage larva. 5-11, Infective third-stage larva. 5, Anterior end; lateral view. 6, 7, Anterior extremity; lateral and en face views, respectively. 8, Transverse section, midbody. 9-11, Posterior extremity; ventral, dorsal, and lateral views, respectively.



FIGURES 12-21. Developmental stages of *Eulimdana bairae* from the abdominal hemocoel of lice found on a whimbrel (*Numenius phaeopus*). 12, Presausage-stage larva. 13, Sausage-stage larva. 14, Anterior end, molting first-stage larva. 15, Posterior extremity, molting first-stage larva. 16-21, Infective third-stage larva. 16, Anterior end, lateral view. 17, 18, Anterior extremity; lateral and en face views, respectively. 19, Transverse section, midbody. 20, 21, Posterior extremity, early third-stage larva; lateral and ventral views, respectively.

TABLE II. Major dimensions (μm) of sausage first-stage, molting first-stage (mL_1), and infective third-stage (L_3) larvae of *Eulimdana wongae* from lice on a marbled godwit (*Limosa fedoa*) and *Eulimdana bairae* from lice on a whimbrel (*Numenius phaeopus*).

	<i>E. wongae</i>			<i>E. bairae</i>		
	Sausage stage	mL_1	L_3	Sausage stage	mL_1	L_3
Number measured	1	1	2	1	1	1
Length	190	300	635, 690	230	375	375
Maximum width	22	30	23, 23	28	30	35
Nerve ring from anterior end	35	47	55, 55	38	45	30
Length of muscular esophagus	—	85*	77, 75	—	55	45
Length of glandular esophagus	—	60*	88, 70	—	65	100
Total length of esophagus	60	145	165, 145	90	118	145
Anus from posterior end	48	55/25†	22, 23	30	31/25†	20

* Pyloricium.

† Tip of basoanal cuticle of first-stage larva followed by tip of cuticle on tail of second-stage larva.

Infective third-stage larva of *E. wongae* and *E. bairae*

The infective third stage of *E. wongae* ($n = 2$) (Figs. 5-11; Table II) and *E. bairae* ($n = 1$) (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 nonsclerotized 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 primordia were 133 and 162 μm from the anterior extremity in 2 females of *E. wongae* but were not observed in *E. bairae*. The posterior extremity of the body of *E. wongae* had 2 subventral, sublateral tongue-like structures, 1 terminal pointed structure, and 2 subdorsal, sublateral tongue-like structures. The posterior extremity of the body of *E. bairae* had 2 subventral, sublateral tongue-like structures and 1 terminal pointed structure. Tiny phasmids were visible near the subventral, sublateral structures in both species.

DISCUSSION

Development of filarioids to the infective third stage in lice indicates lice are suitable vectors. Larvae in lice from the godwit were undoubtedly *E. wongae*, the only filarioid present in the godwit. Similarly, only *E. bairae* was present in the whimbrel. Furthermore, microfilariae in the hemocoel 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. Presausage-stage larvae in lice from the whimbrel had the short tail characteristic of microfilariae of *E. bairae* (see Bartlett, 1992).

Pelecius fulicaeatrae of coots, the sole louse-transmitted avian filarioid previously studied in detail, attains the infective stage only in adult lice (Bartlett and Anderson, 1987). Thus, only adults were examined herein. In amblyceran adults, prevalence (of all larval stages) of *E. wongae* was 12% of 24 and of *E. bairae*, 50% of 10. Bartlett and Anderson (1987) reported *P. fulicaeatrae* in 26% of 119 amblyceran adults (from coot A-6). The prevalence of *E. bairae* should be viewed cautiously because amblycerans 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 filarioids, *Eulimdana cypseli* of swifts (Apodiformes) and *Sarcocema curycera* of geese and swans (Anseriformes) are transmitted by lice (Dutton, 1905; Nelson, 1962; Seegar et al., 1976; Cohen et al., 1991). The present study is the first to show that ischnocerans, in addition to amblycerans, 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 "filaroid larvae in lice on a bird harbouring skin-inhabiting microfilariae of an undescribed species of *Eulimdana*." That statement can now be clarified. The bird was a marbled godwit, the filarioid was *E. wongae*, and the louse was *Actornithophilus limosae*. Two third-stage larvae were found in 1 female louse and microfilariae in a second. *Actornithophilus limosae* 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 filarioids as is the life history strategy found in species of *Eulimdana* and *P. fulvicastrae* in which production of microfilariae by adult females is curtailed. These 2 unusual features may be related, as the following points attempt to explain. Firstly, and obviously, filarioids transmitted by permanent ectoparasites must not jeopardize the survival of their vectors or the latter could be extirpated 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 (Lavoipierre, 1958). Secondly, the microfilariae of *E. wongae* and *E. bairiae* inhabit skin and possibly live as long as the host (numerous microfilariae are commonplace in adult birds that lack adult worms [Bartlett, 1992]). Similarly, microfilariae of *P. fulvicastrae* 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 *Eulimdana*, production is curtailed by ephemerality of post-reproductive adult worms. In *P. fulvicastrae*, 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 *Eulimdana* inhabit the neck region, reproduce, die, and quickly are harmlessly resorbed (Bartlett et al., 1989; Bartlett, 1992). Adult *P. fulvicastrae* 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 inflam-

mation as do other dead nematodes near joints (e.g., *Pelecitus scapiceps* in snowshoe hares [Bartlett, 1984] and *Dracunculus medinensis* in humans [Shastri, 1946; Reddy et al., 1968]). Tenosynovitis 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 *Eulimdana* 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 *Eulimdana* and *Trichinella*. In both, adults are ephemeral and eliminated by the host, and progeny flood the tissues and are long lived.

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