Pelecitus fulicaeatrae (Nematoda: Filarioidea) of coots (Gruiformes) and grebes (Podicipediformes): skin-inhabiting microfilariae and development in Mallophaga

CHERYL M. BARTLETT AND R. C. ANDERSON

Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ont., Canada N1G 2W1

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Pelecitus fulicaeatrae (Diesing, 1861) was found among tendons near the ankle (tibiotarso-tarsometatarsalis articulation) in 11 of 15 adult coots (*Fulica americana*) from Brooks, Alberta, Canada, in 6 of 9 adult coots from Delta, Manitoba, Canada, and in 2 of 4 adult red-necked grebes (*Podiceps grisegena*) from Brooks. Microfilariae of *P. fulicaeatrae* were found in skin of the feathered portions of the legs of infected birds, generally in the dermis around feather follicles; this is the first report of skin-inhabiting microfilariae among avian filarioids. Development of *P. fulicaeatrae* to the third stage in the chewing louse *Pseudomenopon pilosum* (Scopoli) (Mallophaga: Amblycera) is described. Microfilariae and developing first-stage larvae were found in nymphal and adult lice but third-stage larvae were found only in adults; prevalence of third-stage larvae was significantly higher in females than in males. Adult *P. fulicaeatrae* were recovered from an experimentally inoculated, laboratory-reared coot and from laboratory-reared coots that had been housed with infected and infested wild-caught coots. *Pelecitus fulicaeatrae* is the first filarioid in the Dirofilariinae known to be transmitted by lice and the third found in birds. *Pseudomenopon pilosum* was found on 40 (85%) of 47 coots of undetermined ages from Alberta and *Pseudomenopon dolium* (Rudow) was found on all of 5 juvenile red-necked grebes also from Alberta. Possibly, *P. pilosum* occasionally transfers to grebes and (or) *P. dolium* also transmits *P. fulicaeatrae*.

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Pelecitus fulicaeatrae (Diesing, 1861) a été retrouvé parmi les tendons viosins de la cheville (articulation du tibiotarse et du tarsométatarse) chez 11 de 15 foulques adultes (*Fulica americana*) récoltées à Brooks en Alberta, Canada, chez 6 de 9 foulques provenant de Delta Marsh au Manitoba, Canada, chez 2 de 4 Grèbes jougris (*Podiceps grisegena*) de Brooks. Les microfilaires se retrouvent dans la peau sous les plumes des pattes des oiseaux, généralement dans le derme autour des follicules des plumes. C'est la première fois qu'est signalée l'existence de microfilaires dans la peau d'oiseaux. Le développement de *P. fulicaeatrae* jusqu'au troisième stade a pu être décrit chez le ricin *Pseudomenopon pilosum* (Scopoli) (Mallophaga : Amblycera). Les microfilaires et les larves de premier stade en croissance se retrouvent chez les larves et les adultes du ricin, mais les larves de troisième stade n'habitent que les ricins adultes où leur fréquence est plus grande chez les femelles que chez les mâles. Des adultes de *P. fulicaeatrae* ont été récoltés chez une foulque élevée et infectée en laboratoire ainsi que chez des foulques de laboratoire gardées en présence de foulques porteuses d'infestations et d'infections naturelles. *Pelecitus fulicaeatrae* est le premier filaroïde de la sous-famille des Dirofilariinae capable d'être transmis par les ricins, et le troisième à être signalé chez des oiseaux. Parmi 47 foulques d'âges indéterminés capturées en Alberta, 40 (85%) portaient des *Pseudomonepon pilosum* et des *Pseudomenopon dolium* (Rudow) ont été trouvés chez les 5 grèbes juveniles capturées. Il se peut que *P. pilosum* puisse vivre à l'occasion sur les grèbes ou alors que *P. dolium* puisse transmettre *P. fulicaeatrae*; ou peut-être les deux phénomènes coexistent-ils.

[Traduit par la revue]

Introduction

Pelecitus is the only genus in the filarioid subfamily Dirofilariinae that contains parasites of birds and 16 valid species from 17 of the 27 extant avian orders have been recognized, making *Pelecitus* the most widely distributed of the 16 avian filarioid genera (Bartlett and Greiner 1986; Bartlett and Anderson 1987*a*, 1987*b*). *Pelecitus* also contains two species from mammals and all species occur among muscles and tendons near joints in the host's legs or feet (Bartlett and Greiner 1986). Two species are known from birds in North America, i.e., *P. tubercauda* Vanderburgh, Anderson, and Stock, 1984 from yellowthroats (Passeriformes: Parulidae) in Ontario and *P. fulicaeatrae* (Diesing, 1861) from coots (Gruiformes: Rallidae) and grebes (Podicipediformes: Podicipedidae) in Alberta. *Pelecitus fulicaeatrae* has also been reported in the Old World from coots, other rallids, grebes, and birds in five other orders although some of these latter reports require confirmation (Bartlett and Greiner 1986).

Pelecitus fulicaeatrae is reported herein to develop in amblyceran lice on American coots (*Fulica americana*) and is the first species in Dirofilariinae and the fourth in Filarioidea found to be transmitted by Mallophaga. The present study also provides the first detailed description of the microfilariae of *P. fulicaeatrae* and reports their presence in the host's skin. Skin-inhabiting microfilariae have not previously been reported for any of the more than 140 known species (Bartlett and Anderson 1987*a*) of avian filarioids.

Materials and methods

Material was examined from the following wild birds: three groups (A–C) of adult American coots (*Fulica americana* Gmelin), one group (D) of coots of undetermined ages, one group of adult red-necked grebes (*Podiceps grisegena* (Boddaert)), one group of juvenile red-necked grebes, a single little grebe (*Podiceps ruficollis* (Pallas)), and a single moorhen (*Gallinula chloropus* L.). Material was also examined from juvenile coots (group E) reared in captivity.

Fourteen coots (group A, A-1 to A-14) and 4 adult red-necked grebes were livetrapped (Blums et al. 1983) near Brooks, Alberta, Canada, between 25 May and 12 June 1986 and held in captivity at the Brooks Wildlife Centre. Coots were maintained in outdoor pens and were fed commercial duck ration. Grebes were maintained in outdoor pools and were fed fish. Within 1 d of capture, blood was collected from the brachial vein in haematocrit capillary tubes (two to five per bird) and examined for the presence of microfilariae (Woo 1971). Later, some birds were transferred to the University of Guelph, Guelph, Ontario, where coots were housed together in an outdoor flight pen and grebes, in an indoor tank.

Small (2–3 mm^2) pieces of skin were excised, at various times after

capture, from the midregion of the medial side of the feathered portion of the left and right crus of all live coots except A-1. These pieces were torn into smaller pieces in three or four drops of saline on a microscope slide and examined with a dissecting microscope (×40) for microfilariae. A few birds died in captivity and others were killed with an overdose of sodium pentobarbital. Two to three drops of heart and lung blood were placed on a microscope slide, covered with a cover glass, and examined with a compound microscope (×100) for microfilariae. Skin from the crus and other regions (see Table 2) of the body of four dead coots (A-3, A-8, A-10, A-11) and one dead red-necked grebe was also examined as described above, except that a compound (×100) rather than a dissecting microscope was used.

Legs from four coots were fixed in 10% buffered formalin and samples of skin and associated muscles from the medial crus were then excised, dehydrated, embedded, and sectioned (8 μm) following standard histologic techniques. Sections were stained with Harris's haematoxylin and Putt's eosin.

Fifteen coots (group B) were shot near Brooks, Alberta, between 18 May and 7 June 1986, and 9 coots (group C) were shot at Delta Marsh, Manitoba, Canada, between 26 May and 2 June 1986. Two to three drops of heart and lung blood from each bird were placed on a microscope slide and examined for microfilariae. In addition, heart blood from group B coots was collected in haematocrit capillary tubes (two or three per bird) and examined for microfilariae.

Dead birds were examined for adult *P. fulicaeatrae*, and, with one exception, worms recovered were fixed in hot 5% glycerin – 70% alcohol and cleared by evaporation to glycerin. One gravid female from coot A-7 was fixed in 10% formalin.

Microfilariae of *P. fulicaeatrae* were studied using material from four coots (A-1, A-3, A-7, A-8) and one red-necked grebe. Coot A-1 was killed 1 d after capture in June 1986, A-3 died in November 1986, A-7 died in February 1987, and A-8 was killed in February 1987. The grebe was killed 6 d after capture in June 1986. Live microfilariae were obtained from fluid around gravid female worms, placed in saline or in equal volumes of saline and 2% formalin on a microscope slide previously stained with brilliant cresyl blue (Schillhorn van Veen and Blotkamp 1972), then covered with a vaseline-ringed cover glass. Live microfilariae were also obtained from the skin of coot A-8 and studied in equal volumes of saline and 2% formalin. Dead microfilariae were obtained from preserved, gravid female worms by excising a short segment of the vagina and teasing free the microfilariae.

Microfilariae from the vagina of gravid females from the little grebe and the moorhen were also studied. The little grebe was collected at Roath Lake, Cardiff, England, before 1945 by C. Matheson and the moorhen was found dead at Worth Matravers, Dorset, England, in 1983 by C. Stoate. Worms from these birds were borrowed from the British Museum (Natural History) (Nos. 1945.10.23.1-6 and 1985.1-10, respectively). They had been fixed by unknown means; we transferred them to glycerin–alcohol.

Biting lice removed from 47 coots (group D) collected in Alberta in 1963 and 1964 by M. H. Colbo and J. C. Holmes were borrowed through the courtesy of Professor Holmes, University of Alberta. Carcasses of five juvenile red-necked grebes collected in Alberta in 1979 and 1981 were given to the authors by T. M. Stock and J. C. Holmes and were examined for lice.

Lice (*Pseudomenopon pilosum* (Scopoli)) were removed from dead group A coots that harboured gravid female *P. fulicaeatrae*. Lice were also removed from live group A coots in which microfilariae of *P. fulicaeatrae* had been found; lice congregated around the eyes of manually restrained birds and could then be removed with fine forceps.

Lice were dissected in saline by gently pulling the body apart. Developing first- and second-stage larvae and some third-stage larvae of *P. fulicaeatrae* from lice were fixed in 2% formalin, transferred to hot glycerin–alcohol, and cleared by evaporation to glycerin. Other third-stage larvae were fixed directly in hot glycerin–alcohol, then cleared.

Coot eggs were collected from nests near Brooks, Alberta, in May 1986 and were hatched in incubators. Hatchlings were fed a mixture of wet commerical duck ration and dog food until they were approximately 1 month old, after which they were fed dry duck ration. These birds were the laboratory-reared group E coots. They were housed separately from louse-infested group A coots, except as noted below.

Fifteen live third-stage larvae from lice were inoculated subcutaneously into the legs of one 8-month-old group E coot. This coot (housed separately from louse-infested coots) was killed 30 d later and examined for *P. fulicaeatrae*. Seven additional group E coots, ranging in age from 1.5 to 3 months, were placed in the pen containing group A coots; these birds were kept together for 1–7 months. All Group E coots were later killed and examined for *P. fulicaeatrae*.

Use of "prevalence," "intensity," and "abundance" follows Margolis et al. (1982). Adjusted χ^2 (Alder and Roessler 1972) was used to test for difference in prevalence of third-stage larvae between female and male lice.

Adult *P. fulicaeatrae* have been deposited in the parasite collection of the United States National Museum in Beltsville, Maryland (USNM Nos. 79931–79933 from coots and 79934 from red-necked grebes) and also in the parasite collection of the British Museum (Natural History) in London, England (BM Nos. 1987.1534–1543 from coots and 1987.1544–1568 from red-necked grebes). Third-stage *P. fulicaeatrae* from lice were deposited in the USNM (No. 79935).

Lice were identified according to Price (1974). Adult *Pseudomenopon pilosum* (Scopoli) from adult group A coots were deposited in the USNM (No. 79937) and the BM (No. 1987.230) as were adult *Pseudomenopon dolium* (Rudow) from juvenile red-necked grebes (USNM No. 79938, BM No. 1987.230).

Results

Examination of wild birds for nematodes and lice

Adult P. fulicaeatrae

Eleven livetrapped coots (group A), some of which were held in captivity for up to 9 months, were examined for adult worms and all were infected (intensity: range = 1–10, mean = 5). Eight birds contained both male and female worms in one or both legs; when males were present females were gravid. Uteri of most females were distended with microfilariae while other females contained few microfilariae but considerable amounts of reproductive detritis. Three livetrapped coots (A-12, A-13, A-14) remain alive.

Mature adult worms were found in 11 (73.3%) of the coots shot in Alberta (group B) (intensity: range = 1–6, mean = 3.5) and 6 (66.7%) of the coots shot in Manitoba (group C) (intensity not determined).

Adult red-necked grebes were killed within 1 month of capture and two were infected. One, killed 6 d after capture, had three gravid females and four males. The other grebe, killed 26 d after capture, had nine small, immature females and males.

All worms were among tendons at the ankle joint (intertarsalis or tibiotarso-tarsometatarsalis articulation).

Location of microfilariae of P. fulicaeatrae

Microfilariae were found in skin from the feathered portion of the crus of the one red-necked grebe and seven of the livetrapped coots (group A) that contained gravid females (note: skin from coot A-1 was not examined). These seven coots were all examined antemortem, but microfilariae were detected in only three; in live birds microfilarial numbers ranged from 1 to 14 (Table 1). Microfilariae were, however, detected postmortem in skin of the four other coots (Table 1). In addition, microfilariae were found in skin of the three coots (A-12, A-13, A-14) that remain alive (Table 1); numbers in these birds ranged from 1 to 3 (Table 1). Microfilariae were only found in the skin of those legs that contained gravid females and few microfilariae were found in skin from regions of the body other than the legs (Table 2). Microfilariae of *P. fulicaeatrae* were never observed

TABLE 1. Results of examining live and dead coots (*Fulica americana*) and a red-necked grebe (*Podiceps grisegena*) for microfilariae and adults of *Pelecitus fulicaeatrae*

	No. of microfilariae in skin sample[a] from live bird						Presence (+)[b] or absence (−) of microfilariae in skin sample from dead bird	
	Left leg		Right leg, 17 Oct. 1986	Date bird died (d) or was killed (k)	No. of gravid females			
	28 June 1986	27 Aug. 1986			Left leg	Right leg	Left leg	Right leg
Coots								
A-2	0	1	NE[c]	11 Sept. 1986 (d)	1	3	NE	NE
A-3	0	0	0	1 Nov. 1986 (d)	0	1	NE	+
A-6	14	NE	1	23 Jan. 1987 (d)	3	4	NE	NE
A-7	0	10	0	15 Feb. 1987 (d)	3	0	NE	NE
A-8	0	0	0	17 Feb. 1987 (k)	2	1	+	+
A-10	0	0	0	23 Feb. 1987 (k)	0	1	−	+
A-11	0	0	0	25 Feb. 1987 (k)	0	4	−	+
A-12	0	0	3	Still alive				
A-13	1	NE	1	Still alive				
A-14	0	0	1	Still alive				
Grebe	NE	NE	NE	9 June 1986 (k)	2	1	8[a]	NE

[a]A 2- to 3-mm^2 piece of skin was excised from the medial side of the midregion of the feathered portion of the crus, torn into tiny pieces in three or four drops of saline on a microscope slide, and examined for microfilariae.
[b]See details in Table 2.
[c]Not examined.

TABLE 2. Numbers of microfilariae and gravid females of *Pelecitus fulicaeatrae* observed in four dead coots (*Fulica americana*) and one dead red-necked grebe (*Podiceps grisegena*)

	Coot A-3			Coot A-8			Coot A-10			Coot A-11			Grebe		
	L	R	Other	L	R	Other	L	R	Other	L	R	Other	L	R	Other
Gravid females (in leg)	0	1		2	1		0	1		0	4		2	1	
Microfilariae[a]															
Crus															
Feather–scale junction	—	—		46	156		0	56		0	19		30	—	
Feathered portion															
Midmedial	—	10		0	0		0	13		0	0		8	—	
Midlateral	—	—		0	0		0	18		0	4		—	—	
Thigh															
Midmedial	—	4		0	0		0	0		0	0		0	1	
Midlateral	—	—		0	0		0	0		0	0		—	—	
Eyelid	—	—		—	—		0	0		0	1		—	—	
Top of head			—			0			3			0			—
Other			0[b]			0[c]			0[c]			0[c]			+[d]

NOTE: L, left; R, right; —, not examined.
[a]A 2- to 3-mm^2 piece of skin was excised, torn into tiny pieces in three or four drops of saline on a miscroscope slide, and examined for microfilariae.
[b]Right cheek.
[c]Areas examined included 1 cm anterior to vent, midabdomen, midbreast, tail, midback, both armpits, midulnar region of both wings, left and right midneck, left and right cheeks, chin.
[d]Positive areas included 1 cm anterior to vent and midbreast, each with one microfilaria. Negative areas included upper breast, left and right midneck, left and right cheek.

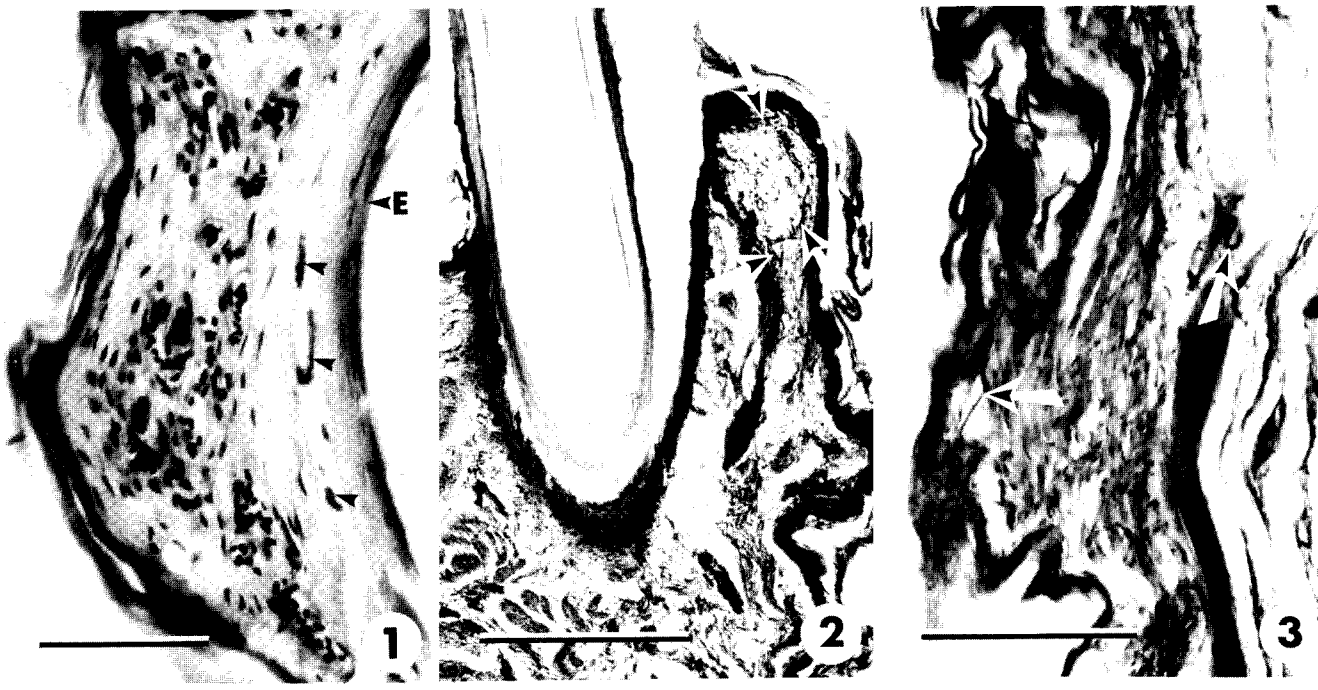
in peripheral blood of live birds or in heart and lung blood of dead birds. Microfilariae were abundant in the fluid around gravid female worms.

With histological techniques, microfilariae were commonly found in the dermis around feather follicles (Fig. 1), particularly that of the follicular collar (Fig. 2). Microfilariae were also occasionally noted in the dermis in areas not immediately adjacent to feather follicles (Fig. 3). Microfilariae were among connective tissue fibres and apparently not in capillaries or lymphatics.

Description of microfilariae of P. fulicaeatrae

Microfilariae from coots (Figs. 4–8) and the red-necked grebe were similar and the following description is based on microfilariae from fluid around a gravid female in a naturally infected coot (A-3). Microfilariae were placed in saline and stained with brilliant cresyl blue.

Cuticle transversely striated. Anterior extremity bluntly rounded, with minute, slightly protuberant, terminal, tooth-like cuticular structure. Body widest at midbody, tapering slightly towards anterior extremity, tapering markedly towards posterior extremity (Fig. 6). Posterior extremity sharply pointed. Delicate constriction (Fig. 8) visible in tail 7–10 μm from extremity in most specimens. Body filled with numerous small nuclei. Excretory pore and vesicle visible. Inner body absent. G1 cell and R2–R4 cells visible in some specimens. Anal pore



FIGS. 1–3. Microfilariae of *Pelecitus fulicaeatrae* in skin from the feathered portion of the crus of coots (*Fulica americana*). Fig. 1. Transverse section of feather follicle showing microfilariae (arrowheads) in dermis; E, epidermis of feather follicle. Scale bar = 50 μm. Fig. 2. Longitudinal section of feather follicle showing microfilariae (arrows) in dermis of follicular collar. Scale bar = 200 μm. Fig. 3. Microfilariae (arrows) in dermis in areas not immediately adjacent to feather follicles. Scale bar = 200 μm.

and vesicle present. Loose sheath present, maximum width greater than that of microfilarial body.

The following measurements (in micrometres, range followed by mean in parentheses) of microfilariae are based on specimens from four coots and one red-necked grebe (N = 20 for each sample). The site from which microfilariae were obtained and the study technique used varied from bird to bird but are indicated for each set of measurements. Female worms had been fixed in hot glycerin–alcohol unless otherwise indicated.

Coot A-1—(*i*) From fluid around gravid females, microfilariae in formalin–saline, not stained, length 92–116 (107), maximum width 6–8, sheath width 8–10; (*ii*) from vagina of a female, microfilariae in glycerin, not stained, length 65–75 (71), maximum width 4–7, sheath width 7–9. (Note: Microfilariae from the vagina appeared degenerate (Fig. 5) and the vagina also contained reproductive detritis, i.e., granular material and degenerate ova.)

Coot A-3—(*i*) From fluid around a gravid female, microfilariae in saline, stained with brilliant cresyl blue, length 108–122 (115), maximum width 6–7, sheath width 8–10; (*ii*) from fluid around a gravid female, microfilariae in formalin–saline, stained with brilliant cresyl blue, length 110–122 (116), maximum width 7, sheath width 8–10; (*iii*) from vagina of a female, microfilariae in glycerin, not stained, length 78–88 (84), maximum width 4–6, sheath width 6–8. (Note: The vagina contained only microfilariae and all were normal in appearance (Fig. 4)).

Coot A-7—From vagina of a female fixed in 10% formalin, microfilariae in formalin, not stained, length 82–110 (97), maximum width 6–7, sheath width 9–10. (Note: In addition to these microfilariae, which were normal in appearance, the vagina contained reproductive detritus.)

Coot A-8—From skin of the crus, microfilariae in formalin-saline, not stained, length 91–114 (107), maximum width 6–7, sheath width 8–11.

Red-necked grebe—(*i*) From fluid around gravid females, microfilariae in formalin–saline, not stained, length 94–115 (105), width of body and sheath not determined; (*ii*) from vagina of a female, microfilariae in glycerin, not stained, length 60–70 (65), maximum width 6–7, sheath width 7–11. (Note: Microfilariae in the vagina appeared degenerate, as in coot A-1, and the vagina also contained reproductive detritus.)

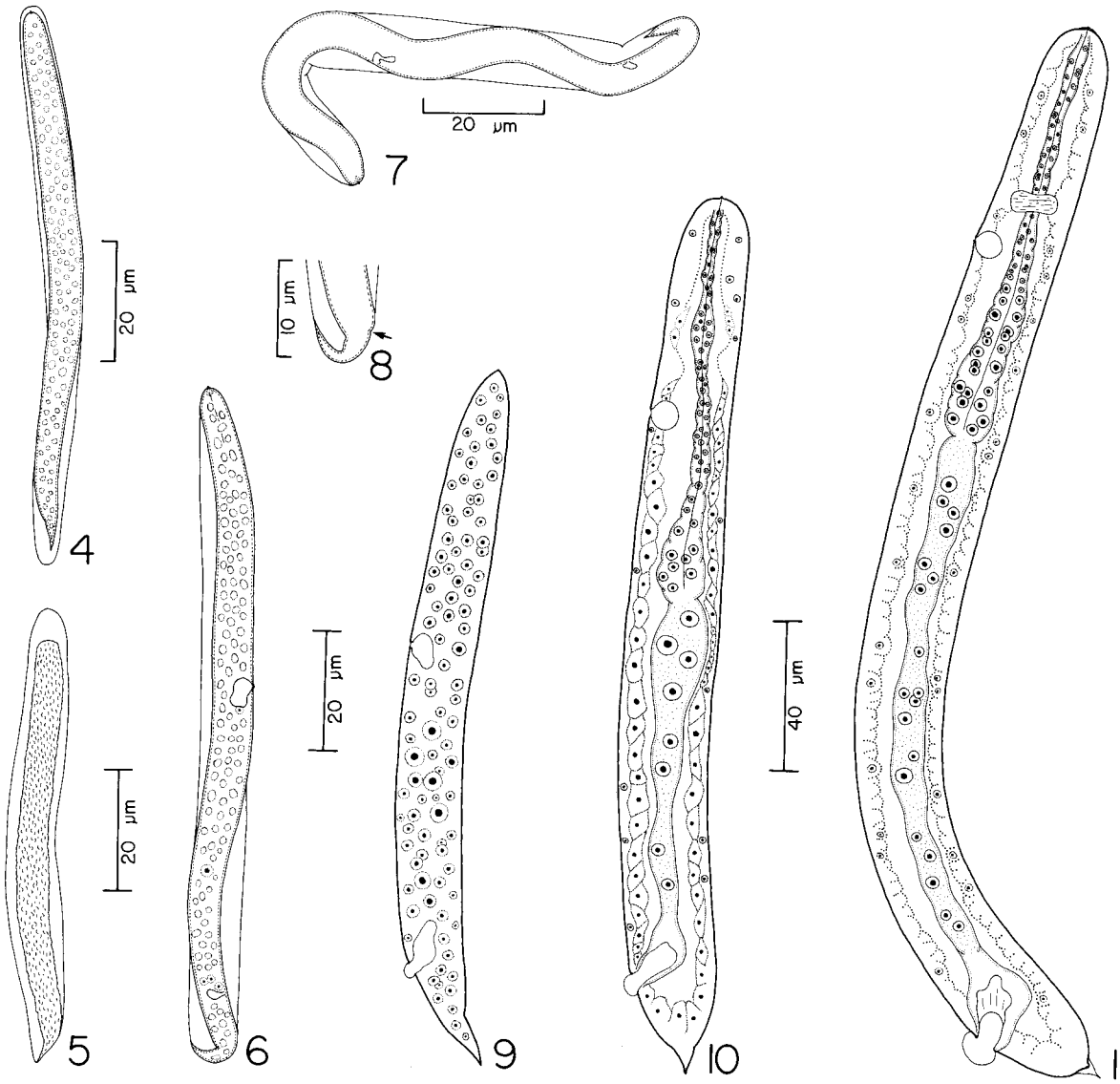
Microfilariae from the vagina of a female from the moorhen were similar to those from the vagina of coots A-3 and A-7 except that a sheath was not observed. They were 83–91 (86) μm long and 4–5 μm in maximum width (N = 20). Microfilariae (N = 5) from the vagina of a female from the little grebe were also morphologically similar to those from coots except that a sheath was not observed. They were 62–73 (68) μm long and 6–7 μm in maximum width. In addition to these latter microfilariae that appeared normal, the vagina contained some degenerate microfilariae (as in coot A-1 and the red-necked grebe) and reproductive detritus.

Lice

Pseudomenopon pilosum (Scopoli) was found on 40 (85%) of the coots collected in Alberta in 1963 and 1964 (group D) and was the only species of *Pseudomenopon* present. This was also the only species of *Pseudomenopon* found on coots that we livetrapped in Alberta (group A). *Pseudomenopon dolium* (Rudow) was present on all juvenile red-necked grebes and was the only species of *Pseudomenopon* present.

Examination of lice for worms

Third-stage larvae of *P. fulicaeatrae* were only found in adult *P. pilosum* and prevalence was always higher in females than in males. Overall, third-stage larvae were found in 9.5% of 568



FIGS. 4–11. Microfilariae and other first-stage larvae of *Pelecitus fulicaeatrae*. Fig. 4. Normal microfilaria from vagina of preserved female. Fig. 5. Degenerate microfilaria from vagina of preserved female. Fig. 6. Microfilaria from fluid around adult worms, stained with brilliant cresyl blue. Fig. 7. Microfilaria from fluid around adult worms, unstained, in 2% formalin. Fig. 8. Posterior extremity of microfilaria showing delicate constriction (arrow). Fig. 9. Pre-sausage-stage larva. Fig. 10. Sausage-stage larva. Fig. 11. Fully developed first-stage larva.

females and 3.5% of 768 males from four naturally infected coots (group A). Prevalence of larvae in lice varied among coots, however, and declined in the only coot (A-14) examined on numerous occasions (Table 3). Difference in prevalence of third-stage larvae between female and male lice was tested using data from two coots (A-6 and A-14, Table 3) and prevalence was significantly higher ($p < 0.01$) in females than in males ($\chi^2 = 12.9$ for A-6 and 9.9 for A-14). Overall intensity of third-stage larvae in female lice was 1–5 (mean = 1.4) and in males 1–3 (mean = 1.2). Overall abundance of third-stage larvae in females was 0.14, in males 0.04.

Some adult lice contained microfilariae and first- and second-stage larvae as well as third-stage larvae of *P. fulicaeatrae*. Adult lice (119 females and 70 males) from one coot (A-6) were examined for all stages (including microfilariae); 31.9% of the females and 15.7% of the males were infected, and 65.8% of infected females and 63.6% of infected males contained third-stage larvae.

Only microfilariae and developing first-stage larvae were found in nymphal lice and infected individuals were found among each of the three nymphal stages. Of 100 nymphs from the above-mentioned coot (A-6), 20% were infected; one to eight microfilariae and one to three developing first-stage larvae were found in infected nymphs.

Microfilariae were found within the crop and free in the abdominal haemocoele of lice. All other larvae were found only in the abdomen and most were found free in saline during the dissection of the louse. However, some first- and second-stage larvae were found in the fat body, which was normal in appearance, and a few third-stage larvae were in delicate, clear sacs which apparently were remnants of the infected fat body.

Descriptions of larvae of P. fulicaeatrae

The descriptions below are based on specimens from adult lice. Measurements for each of the substages of the first-stage larva and for the second-stage larva are based on one specimen

TABLE 3. Results of examining lice (*Pseudomenopon pilosum*) for third-stage larvae of *Pelecitus fulicaeatrae*

	No. of lice examined	No. of lice infected	Prevalence (%)	Intensity		Abundance
				Range	Mean	
Coot A-3[a]						
Adult ♀ lice	128	3	2.3	1	1	0.02
Adult ♂ lice	85	0		—	—	—
Coot A-6[b]						
Adult ♀ lice	171	34	19.9	1–5	1.3	0.26
Adult ♂ lice	286	21	7.3	1–3	1.2	0.09
Nymphal lice	100	0		—	—	—
Coot A-8[c]						
Adult ♀ lice	32	0		—	—	—
Adult ♂ lice	37	0		—	—	—
Coot A-14[d]						
Adult ♀ lice						
20 Oct. 1986[e]	24	4	16.7			
21 Oct. 1986	71	8	11.3			
22 Oct. 1986	106	5	4.7			
31 Oct. 1986	19	0				
17 Nov. 1986	17	0				
Total	237	17	7.2	1–5	1.6	0.11
Adult ♂ lice						
20 Oct. 1986	16	1	6.2			
21 Oct. 1986	137	0				
22 Oct. 1986	130	3	2.3			
31 Oct. 1986	42	0				
17 Nov. 1986	35	2	5.7			
Total	360	6	1.7	1–2	1.2	0.02

NOTE: Lice were obtained from three dead coots (*Fulica americana*) which harboured gravid female *P. fulicaeatrae* and from one live coot which had microfilariae of *P. fulicaeatrae*.
[a]Died 1 Nov. 1986, one gravid female present.
[b]Died 23 Jan. 1987, four gravid females present.
[c]Killed 17 Feb. 1987, three gravid females present.
[d]Still alive.
[e]Dates when lice were removed and examined.

TABLE 4. Major dimensions (in μm, range followed by mean in parentheses) of fully developed first-, second-, and third-stage larvae of *Pelecitus fulicaeatrae* from *Pseudomenopon pilosum*

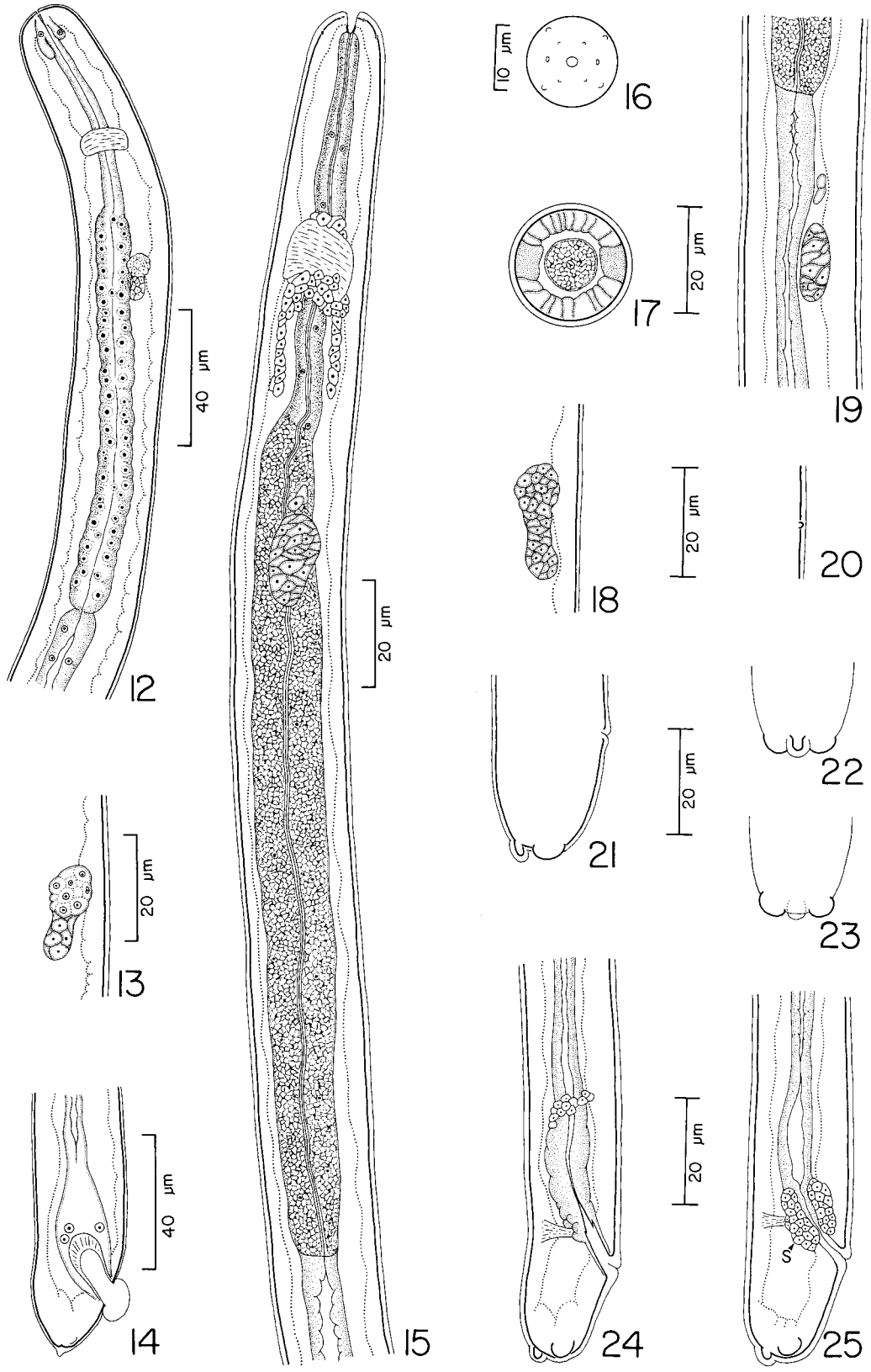
	First-stage (2% formalin)	Second-stage (2% formalin, ♀)	Third stage			
			2% formalin		Glycerin–alcohol	
			♂♂	♀♀	♂♂	♀♀
N	1	1	5	5	5	5
Length	300	515	640–790(715)	690–865(785)	580–685(635)	610–745(680)
Maximum width	25	27	22–25 (24)	23–25 (24)	22–28 (24)	21–24 (22)
Nerve ring[a]	50	40	45–60 (50)	45–55 (52)	40–45 (43)	45–50 (47)
Muscular oesophagus[b]	—	60	70–100(90)	75–105(90)	60–80 (70)	70–85 (80)
Glandular oesophagus[b]	—	115	120–230(190)	120–210(180)	165–200(175)	115–180(155)
Total oesophagus[b]	115	175	190–320(280)	215–300(270)	240–260(245)	190–265(235)
Genital primordium[a]	—	80	210–330(295)	80–100(90)	250–275(265)	80–95 (85)
Anus[c]	20	19	17–25 (22)	18–24 (22)	17–18 (18)	18–20 (19)

[a]Distance from anterior extremity.
[b]Length.
[c]Distance from posterior extremity.

fixed in 2% formalin; other descriptive observations are based on additional, but damaged, formalin-fixed specimens. Measurements and other descriptive observations of third-stage larvae are based on 10 (5 male and 5 female) specimens fixed in formalin and 10 (5 male and 5 female) specimens fixed in glycerin–alcohol.

First stage (Table 4, Figs. 9–11)

Pre-sausage-stage larva (Fig. 9) wider (10 μm) than microfilaria, length (115 μm) similar to that of microfilaria. Sheath absent. Excretory pore and vesicle visible. Small plug protruding from anal pore. Numerous small nuclei filling body. R and G cells not distinguishable. Posterior extremity sharply pointed.



FIGS. 12–25. Second-stage (Figs. 12–14) and third-stage (Figs. 15–25) larvae of *Pelecitus fulicaeatrae* (note: all figures are based on specimens fixed in glycerin–alcohol except Figs. 12–14 and 21–23 which are based on specimens fixed in 2% formalin). Fig. 12. Anterior end, female, lateral view. Fig. 13. Genital primordium in female, lateral view. Fig. 14. Posterior extremity, female, lateral view. Fig. 15. Anterior end, female, ventral view. Fig. 16. Anterior extremity, *en face* view. Fig. 17. Transverse section of body near end of glandular oesophagus. Fig. 18. Genital primordium in female, lateral view. Fig. 19. Genital primordium in male, lateral view. Fig. 20. Postdeirid, lateral view. Figs. 21–23. Posterior extremity, lateral, dorsal, and ventral views, respectively. Fig. 24. Posterior extremity of female, lateral view. Fig. 25. Posterior extremity of male, lateral view. Note spicular pouch primordia (S).

Sausage-stage larva (Fig. 10) wider (25 μm) and considerably longer (235 μm) than pre-sausage-stage larva. Large cells forming subcuticular body wall. Oesophageal and intestinal primordia distinct, apparently syncytial. Posterior extremity sharply pointed.

Fully developed first-stage larva (Fig. 11) slightly longer (Table 4) than sausage-stage larva. Cells of subcuticular wall beginning to coalesce. Nerve ring visible. Oesophagus occupying 38% of body length. Anal plug large. Cuticle at posterior extremity sharply pointed and detached from hypodermis; hypodermis rounded, with small, conical, terminal protuberance.

Second stage (Table 4, Figs. 12–14)

Oesophagus occupying 34% of body length and divided; anterior portion narrow, posterior portion broad and with numerous large nuclei (Fig. 12). Oesophageal–intestinal junction distinct. Genital primordium consisting of undetermined number of cells, sexes distinguishable. Female genital primordium attached to ventral hypodermis in anterior region of glandular oesophagus (Fig. 13). Male genital primordium free within pseudocoelom near anterior region of intestine. Intestinal lumen present. Rectum and anal plug large. Posterior extremity rounded, with small, round, terminal protuberance, and two inconspicuous, ventral–lateral swellings (Fig.14).

Third stage (Table 4, Figs. 15–25)

Cephalic extremity with round oral opening, four pairs of papillae, and amphids (Fig. 16). Cuticle with delicate transverse striations. Buccal cavity consisting of anterior nonsclerotized portion, 4–6 μm long, and posterior, strongly sclerotized portion, 3-4 μm long. Excretory pore visible only in specimens fixed in formalin, 75–95 μm from anterior extremity. Oesophagus occupying 25-41% of body length and clearly divided (Fig. 15); anterior muscular portion narrow (5–7 μm), posterior glandular portion broad (8–17 μm) and distinctly granular. Oesophageal–intestinal junction distinct. Intestinal lumen contiguous with rectal lumen. Anus patent, with slightly raised cuticular lips; lips more prominent in specimens fixed in hot glycerin–alcohol than in those fixed in formalin. Two small, slightly salient postdeirids (Fig. 20) present 75–110 μm from posterior extremity of body, one 10–15 μm anterior to other. Genital primordia located as in second-stage larva, size slightly larger. Spicular pouch primordia consisting of two clusters of small cells beside rectum (Fig. 25) (note: these primordia were most readily observed in specimens fixed in glycerin–alcohol). Posterior extremity with terminal, papilla-like protuberance and two large ventral–lateral swellings (Figs. 21–23).

Examination of laboratory-reared coots

Eight immature adult *P. fulicaeatrae* were found among tendons in the ankles of the laboratory-reared coot (group E) inoculated with 15 third-stage larvae and killed 30 d postinoculation.

Pseudomenopon pilosum was found on all seven laboratory-reared coots (group E) which had been housed with the naturally infested and infected wild-caught coots (group A) and adult *Pelecitus fulicaeatrae* were found in three of the laboratory-reared coots. These three coots were housed with wild coots for 2, 5, and 7 months and were infected with eight, one, and three worms, respectively.

Discussion

Pelecitus fulicaeatrae developed to the third larval stage in the amblyceran biting louse *Pseudomenopon pilosum* and third-stage larvae were infective to a laboratory-reared American coot. In addition, laboratory-reared coots housed together with infected and infested wild-caught coots acquired *P. fulicaeatrae*. *Pelecitus fulicaeatrae* is thus the third avian filarioid species found to be transmitted by Mallophaga. Dipterans are intermediate hosts of the three other species of *Pelecitus* in which development has been studied, i.e., *P. ceylonensis* Dissanaike, 1967 of birds, *P. scapiceps* (Leidy, 1886) of lagomorphs, and *P. roemeri* (Linstow, 1905) of macropodids (see Dissanaike 1967; Spratt 1972; Bartlett 1984).

Other mallophagan-transmitted filarioids are *Eulimdana cypseli* (Annett, Dutton, and Elliott, 1901) of African swiftlets, *Sarconema eurycerca* Wehr, 1939 of holarctic geese and swans, and *Acanthocheilonema reconditum* (Grassi, 1889) (=*Dipetalonema reconditum*) of dogs. These filarioids, like *P. fulicaeatrae*, develop in species of Amblycera (see Dutton 1905; Pennington and Phelps 1969; Seegar et al. 1976). *Acanthocheilonema reconditum* reportedly also develops in species of Anoplura and Siphonaptera (see Pennington and Phelps 1969).

Blood ingestion is well known among amblyceran lice (Ash 1960; Marshall 1981) and we commonly observed blood as well as feathers in the crop of nymphal and adult *P. pilosum*. Amblycerans do not, in general, have piercing mouth parts but blood might be "procured by scratching or nibbling at the soft skin at the base of the feathers" (Ash 1960). Lice probably ingest the skin-inhabiting microfilariae of *P. fulicaeatrae* in a similar manner, particularly since microfilariae occur in the dermis around feather follicles. Mallophagan vectors are not always associated with skin-inhabiting microfilariae, however. Microfilariae of *E. cypseli* occur in "lymph" and "serous fluid" from "swollen claws" and in peripheral blood from legs and claws (Annett et al. 1901; Dutton 1905). Microfilariae of *S. eurycerca* occur in the blood (Seegar et al. 1976; Seegar 1979) as do those of *A. reconditum* (see Pennington and Phelps 1969).

Pseudomenopon pilosum was present on most coots from Alberta. This louse was originally described from the Old World common coot (*Fulica atra* L.), which occurs throughout Europe, Asia, Africa, and Australia. Price (1974) accepts as valid reports of *P. pilosum* from five other species of *Fulica* (including the American coot, *F. americana*), several other genera in Rallidae (including moorhens), one other family (Heliornithidae) in Gruiformes, and Jacanidae in Charadriiformes. Reports of *P. pilosum* from birds in other orders are controversial and Lakshminarayana (1977) briefly discusses reports from Podicipediformes, Anseriformes, and Falconiformes. *Pseudomenopon pilosum* evidently has a wide geographic distribution: Price (1974) examined specimens from all continents except Antarctica.

Mallophagans have generally been considered strongly host specific but some species are now known to occur on a wide range of host species and this has led to speculation that "the louse fauna may be a reflection of the host's lifestyle, implying that a degree of ecological or habitat specificity is involved as well" (Wheeler and Threlfall 1986). Coots and grebes are not phylogenetically closely related but do have similar habitat and nesting requirements (Godfrey 1986). For example, during the present study coots and red-necked grebes were often found nesting within 2–5 m of each other in cattail (*Typha latifolia*) marshes. Evidently, *P. pilosum* is not rigidly host specific and grebes might occasionally acquire this louse from coots. It might not be surprising, therefore, that they share a louse-transmitted filarioid. The apparent lack of host specificity of *P. fulicaeatrae* is seen in many other avian filarioid species

(Bartlett and Anderson 1980; Bartlett and Greiner 1986), although only flying insects with opportunistic feeding behaviours, such as certain species of mosquitoes or biting midges, have previously been suggested or found to be vectors.

Pelecitus fulicaeatrae has also been reported from horned grebes (*Podiceps auritus* (L.)) and eared grebes (*Podiceps nigricollis* C. L. Brehm) in Alberta (Vanderburgh et al. 1984). These grebes also often nest near coots and study of the louse species responsible for transmitting *P. fulicaeatrae* in grebe populations is required. *Pseudomenopon dolium*, the species we found on juvenile red-necked grebes, is the only species of *Pseudomenopon* recognized by Price (1974) from grebes in both the New World and the Old World. Possibly, *P. dolium* is also a vector of *P. fulicaeatrae*.

Prevalence of *P. fulicaeatrae* is generally higher and intensity lower in coots than grebes. Colbo (1965) found *P. fulicaeatrae* in 41% of 94 adult coots in Alberta (range of intensity = 1–11, mean intensity = 2.8) and we found it in 73% of 15 coots shot in Alberta (range of intensity = 1–6, mean = 3.5) and 67% of 9 coots shot in Manitoba (intensity not determined). T. M. Stock and C. M. Bartlett (unpublished data) found *P. fulicaeatrae* in 27% of 30 adult red-necked grebes (range of intensity = 1–175, mean = 50), Gallimore (1964) found it in 40% of 30 (range of intensity = 1–234, mean = 44), and we found it in 50% of 4 (range of intensity = 7–9) in Alberta. Gallimore (1964) also reported *P. fulicaeatrae* in 11% of 98 eared grebes (range of intensity = 1–27, mean = 6) and 8% of 39 horned grebes (range of intensity = 3–34, mean = 15) in Alberta. High prevalence and low intensity in coots suggest development of a protective immunity and perhaps coots are the normal host of *P. fulicaeatrae*.

In the Old World *P. fulicaeatrae* has been reported from moorhens, crakes (Gruiformes), ospreys, buzzards, harriers (Falconiformes), terns, gulls (Charadriiformes), bitterns, egrets, herons (Ciconiiformes), and rollers (Coraciiformes) (see Bartlett and Greiner 1986), as well as from coots and grebes. Since *P. fulicaeatrae* is now known to be transmitted by lice, many of these reports require confirmation. Reports of *P. pilosum* on various hosts should be kept in mind, as well as the possibility that other lice might also transmit the parasite. Bartlett and Greiner (1986) questioned reports of *P. fulicaeatrae* in Falconiformes and Ciconiiformes since other species of *Pelecitus* have been described from birds in these orders.

Microfilariae of *P. fulicaeatrae* varied in length, according to the site from which they were obtained and the medium in which they were fixed or studied, and we do not regard the smaller size of microfilariae from the least grebe to be taxonically significant. Apparently normal microfilariae from New and Old World birds were morphologically similar except that those from coots and red-necked grebes in North America were ensheathed whereas a sheath was not observed around those from the moorhen and little grebe in Europe. A sheath is often difficult or impossible to observe in specimens extracted from the vagina of females preserved for long periods, however. A sheath is present in all other species of *Pelecitus* in which the microfilaria has been described, and adult *P. fulicaeatrae* from New and Old World birds are similar (Bartlett and Greiner 1986). We have provided descriptions of microfilariae from New World birds based on material from different sources and studied in different ways. A new study of *P. fulicaeatrae* microfilariae using fresh material from European birds is now required and if a sheath is truly absent then the taxonomic status of the species in North America must be reevaluated. The type host of *P. fulicaeatrae* is the Old World common coot, *Fulica atra*, and the type locality is presumably Britain (Bartlett and Greiner 1986). Unfortunately, earlier descriptions of the microfilariae of *P. fulicaeatrae* are ambiguous and illustrations were not included. Yamaguti (1935), working with material from little grebes in Japan, stated that the "fully developed embryos [of *Spirofilaria podicipitis* (= *P. fulicaeatrae*)], up to 0.1 mm long, are without sheath." Yamaguti did not indicate where these specimens were obtained although his use of "embryo" suggests uteri. Baylis (1944) stated only that microfilariae from uteri "appear to be enclosed in delicate membranes" but it is not clear if this is based on material from a Madagascaran crake or a British little grebe, or both. The specimens that we examined from the little grebe were probably the same as those examined by Baylis. Pike (1969) stated that female *P. fulicaeatrae* from a moorhen in England "contain sheathed larvae measuring 0.108 to 0.120 mm long."

Bartlett (1987) stated that no single adult character distinguished species in *Pelecitus* from those in the reptilian filarioid genus *Foleyella* and pointed out that the morphology of the microfilarial sheath may be more useful, i.e., "in *Foleyella* the sheath generally is oval or spindle, thus lying loose along the entire length of the microfilarial body.... In *Pelecitus* the sheath is always elongate and the same width as the anterior two-thirds of the microfilarial body." However, the microfilarial sheath in *P. fulicaeatrae*, illustrated herein for the first time, resembles that of *Foleyella* spp., not that of *Pelecitus* spp. Bartlett (1987) also stated "In both genera the body of the microfilariae has bluntly rounded extremities." In *P. fulicaeatrae*, the posterior extremity is sharply pointed. Adult *P. fulicaeatrae* have a corkscrew-shaped body as do many other species of *Pelecitus*, whereas all adults of *Foleyella* species are straight or gently curved. A combination of adult and microfilarial characters will, therefore, distinguish the two genera.

Third-stage larvae of *P. fulicaeatrae* were only found in adult *P. pilosum* although microfilariae and developing larvae were found in nymphs, suggesting that development to the third stage is physiologically tied to the adult louse stage, or that the developmental period is longer than the combined duration of the three nymphal stages. The life cycle of *P. pilosum* has not been studied and, in general, longevity data for amblyceran lice are scarce. Marshall (1981) cites 3 days for each of the three nymphal stages of *Menacanthus stramieus* and 13 days for the adult female and he cites 9, 9, and 12 days for the nymphs of *Ricinus elongatus* and 100 days for the adult female.

The significantly higher prevalence of third-stage larvae of *P. fulicaeatrae* in female *P. pilosum* than in males may reflect a tendency of the larger bodied and ovipositing females to consume more food, and consequently acquire more microfilariae. We are not aware of any such studies, however, nor of any showing that female lice feed in different locations from males. Microfilariae of *P. fulicaeatrae* occur predominantly in skin of the feathered portion of the lower legs and it is presumably mainly there that lice ingest microfilariae.

Prevalence of infection in lice varied considerably among infected coots and was higher when microfilariae and first through third larval stages were included rather than just the third stage. Prevalences reported herein are lower than those reported for other louse-transmitted avian filarioids. Dutton (1905) found larvae of *E. cypseli* in 54% of 11 carefully examined lice ("unidentified species of Leiothinae") and Seegar et al. (1976) found larvae of *S. eurycerca* in 60% of 45 *Trinoton anserinum* taken directly from infected whistling swans.

Transmission by means of a louse vector requires that the infected louse transfer to a new host individual. We do not know whether infected lice exhibit altered behaviour that facilitates transfer but we did observe a decline in the prevalence of infected lice from 16.7 to 0 in females and from 6.2 to 0 in males on coot A-14 during four sampling periods in a 12-day interval, suggesting that infected lice were among the first removed by the human investigator.

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