

Mallophagan vectors and the avian filarioids: new subspecies of *Pelecitus fulicaeatrae* (Nematoda: Filarioidea) in sympatric North American hosts, with development, epizootiology, and pathogenesis of the parasite in *Fulica americana* (Aves)

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Subspecies of *Pelecitus fulicaeatrae* (Diesing, 1861) Lopez-Néyra, 1956 are proposed for the first time. The parasite in the original type host, i.e., the Common Coot (*Fulica atra* L.) in Great Britain, becomes the nominotypical subspecies, namely *Pelecitus fulicaeatrae fulicaeatrae* (Diesing, 1861) n.subsp.; it requires further taxonomic study. Subspecies in two sympatric North American hosts are described, and transmission by lice (Mallophaga: Amblycera) is suggested to have played a role in their evolution. *Pelecitus fulicaeatrae americanae* n.subsp. in the American Coot (*Fulica americana* Gmelin) has narrower lateral alae at midbody in the male, tighter helical twisting and more rotations in the body of the adult female, and a vulva that tends to be closer to the end of the oesophagus than that of *Pelecitus fulicaeatrae grisegenae* n.subsp. in the Red-necked Grebe (*Podiceps grisegena* (Boddaert)). Development of *P. f. americanae* was followed in experimentally infected American Coots. At 20 days postinfection, worms had migrated to the definitive site in the ankles and developed to the adult stage; these worms were sexually immature and also differed in other morphologic ways from mature specimens. Worms at 210 and 265 d resembled those from wild-caught coots, and females contained microfilariae. *Pelecitus f. americanae* is reported for the first time in Wisconsin, North Dakota, and California and probably is widespread in coots in North America. Both nesting and wintering coots contained three age-classes of adult female worms (too young to produce microfilariae, producing microfilariae, senescent), suggesting that transmission is not restricted to any particular period during the year. In general, no evidence of infection was apparent upon external examination of intact wild-caught infected coots, whereas ankles of intact wild-caught infected grebes were frequently swollen. Upon internal examination of coots, a visible response to worms was also generally not observed. In a few coots, however, worms were within soft, thin-walled capsules and histologic examination revealed chronic proliferative tenosynovitis.

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La division en sous-espèces de *Pelecitus fulicaeatrae* (Diesing, 1861) Lopez-Néyra, 1956 est proposée ici pour la première fois. Le parasite de l'hôte type original, i.e., la Foulque macroule (*Fulica atrae* L.) de Grande-Bretagne, devient la sous-espèce nominale type, sous le nom de *Pelecitus fulicaeatrae fulicaeatrae* (Diesing, 1861) n.subsp., taxon qui devra être réexaminé. Deux autres sous-espèces, décrites ici, ont été trouvées chez des hôtes nord-américains sympatrides; la transmission de ces parasites par des ricins (Mallophaga : Amblycera) semble avoir joué un rôle dans leur évolution. Chez *Pelecitus fulicaeatrae americanae* n.subsp., trouvé chez la Foulque d'Amérique (*Fulica americana* Gmelin), les ailes latérales à mi-corps du mâle sont plus étroites, l'enroulement hélicoïdal du corps de la femelle est plus serré et le nombre de rotations de son corps est plus élevé, enfin, la vulve est plus près de l'extrémité de l'oesophage que chez *Pelecitus fulicaeatrae grisegenae* n.subsp., parasite du Grèbe jougris (*Podiceps grisegena* (Boddaert)). Le développement de *P. f. americanae* a été suivi chez des Foulques d'Amérique infectées artificiellement. Vingt jours après la transmission du parasite, les vers avaient atteint leur site terminal dans les chevilles de l'oiseau où ils se transformaient en adultes; ces vers étaient encore immatures sexuellement et différaient aussi des adultes par d'autres caractéristiques morphologiques. Aux jours 210 et 265 après l'infection, les vers avaient le même aspect que ceux recueillis chez des foulques capturées en nature et les femelles contenaient des microfilaries. *Pelecitus f. americanae* est mentionné pour la première fois au Wisconsin, dans le Dakota du Nord et en Californie et ce parasite est probablement très répandu en Amérique du Nord chez les foulques. Des femelles adultes de trois classes d'âge (trop jeunes pour produire des microfilaries, en pleine production de microfilaries, sénescences) ont été recueillies chez des foulques aussi bien durant l'hiver que pendant la période de nidation, ce qui indique que la transmission n'est pas restreinte à une période particulière de l'année. En général, les foulques porteuses capturées en nature ne portaient pas de symptômes d'infection, alors que plusieurs grèbes infectés capturés en nature avaient les chevilles enflées. L'examen interne de foulques infectées a révélé que les oiseaux ne semblaient pas réagir de façon visible à la présence des parasites. Chez quelques foulques cependant, les vers étaient entourés d'une capsule molle à paroi mince et un examen histologique a révélé que les oiseaux montraient des signes de ténosynovite prolifère chronique.

[Traduit par la revue]

Introduction

Pelecitus fulicaeatrae (Diesing, 1861) Lopez-Néyra, 1956 is a commonly reported filarioid nematode parasite in birds in the families Rallidae (Gruiformes) and Podicipedidae (Podicipedi-

formes) in the Holarctic. There are also reports in various other birds in the Palaearctic, although Bartlett and Greiner (1986) considered many to be of questionable validity. In the present study we had the opportunity to examine numerous mature specimens from two sympatric North American hosts, namely the American Coot (*Fulica americana* Gmelin) (Rallidae) and the Red-necked Grebe (*Podiceps grisegena* (Boddaert)) (Podicipedidae). Minor morphologic differences found necessitate

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that the two groups be designated as subspecies, herein described as *P. f. americanae* n. subsp. from the American Coot and *P. f. griseogenae* n. subsp. from the Red-necked Grebe. The parasite in coots is transmitted by amblyceran chewing lice (Mallophaga) (see Bartlett and Anderson 1987), and we suggest that such vectors have contributed to the parasites' isolation and led to subspeciation.

In both coots and grebes, adult worms occur among tissues near the ankle and microfilariae inhabit the skin (Bartlett and Anderson 1987). Development of *P. f. americanae* to the infective stage in the louse *Pseudomenopon pilosum* (Scopoli) was described by Bartlett and Anderson (1987). The present study describes development of this subspecies from the sexually immature stage to the reproducing adult stage in experimentally infected American Coots, thus providing the first such information on *Pelecitus* spp. in birds. The present study also provides information on transmission and microfilarial production of *P. f. americanae* and describes the histologic response to adult worms in wild-caught coots.

Methods and materials

Legs from American Coots collected in various localities in the United States were frozen and sent to the University of Guelph by personnel of the National Wildlife Health Center of the United States Fish and Wildlife Service in Madison, Wisconsin. Legs were thawed and examined for adult filarioids; adults found were fixed in hot glycerin-alcohol and studied in glycerin. En face and transverse sections were cut freehand, using a mounted razor blade. Microfilariae were sought in the immediate vicinity of adult worms by adding a drop of saline to the area, extracting the saline with a pipette, and examining it on a slide with a compound microscope. Studies were also made of worms from adult American Coots and Red-necked Grebes examined by Bartlett and Anderson (1987, 1989) and T. M. Stock and C. M. Bartlett (unpublished data, in Bartlett and Anderson 1987).

Live third-stage larvae of *Pelecitus f. americanae* were obtained from lice (*Pseudomenopon pilosum*) on live, wild-caught adult American Coots (Bartlett and Anderson 1987). Fifteen larvae were inoculated subcutaneously into the thighs of four juvenile coots and 18 larvae into a fifth. Juvenile coots had been hatched in captivity and housed separately from wild-caught coots (Bartlett and Anderson 1987). Experimentally infected coots were killed (with an overdose of sodium pentobarbital) at 20, 30,² 55, 210, and 265 d postinfection and tissues near the ankle (intertarsalis or tibiotarso-tarsometatarsalis articulation) were examined for worms. Those found were fixed in hot glycerin-alcohol and studied in glycerin. Microfilariae were sought in the immediate vicinity of adult worms (as explained above) and, if they were present, snips of skin from the feathered portion of the midcrus and the scale-feather junction of the leg were also examined for microfilariae (Bartlett and Anderson 1987). In addition, snips of feathered crus skin were examined for microfilariae at 200 d post infection in the coot killed at 210 d, and at 205 and 255 d post-infection in the coot killed at 265 d.

One juvenile coot which had been hatched in captivity was placed in a pen containing wild-caught adult coots harbouring *P. pilosum* and *P. f. americanae*. The coot was killed 120 d later and worms in the ankles were fixed and studied. Studies were also made of worms mentioned by Bartlett and Anderson (1987) from three juvenile coots subjected to the same experimental regime.

Ankles of adult coots shot near Oak Lake, Manitoba, in early June, 1987, were preserved in 10% buffered formalin, decalcified in formic acid, embedded in paraffin, and sectioned following routine histologic procedures. Sections were stained with haematoxylin and eosin.

Ankles from coots A-12 and A-13 of Bartlett and Anderson (1987) were similarly preserved and sectioned.

Specimens of worms have been deposited in the parasite collection of the Canadian National Museum of Natural Sciences in Ottawa, Canada, as catalogue numbers NMCP1989-0074 to NMCP1989-0090.

Results

Pelecitus fulicaeatrae griseogenae n. subsp.

(Figs. 1–6, 17–20; Tables 1, 2)

GENERAL: Filarioidea, Onchocercidae, Dirofilarinae, *Pelecitus* Railliet and Henry, 1910 (sensu Bartlett and Greiner 1986). Body regularly and dextrally twisted. Body width uniform over most of length but tapering gradually towards bluntly rounded anterior and posterior extremities (Figs. 1, 2, 18, and as in Fig. 29 for *P. f. americanae*). Alae present, commencing behind nerve ring and extending to tip of tail; from point of origin, alae rapidly becoming markedly asymmetric in shape (Figs. 3, 19), with left larger than right; asymmetry continuing along most of body length; alae in caudal region becoming nearly symmetric (Fig. 4). (Note: The symmetry of alae in the caudal region of males can only be accurately determined in transverse section because, when mounts of whole worms are examined, the helical twisting of the body causes the left ala to appear much wider than the right.) Cuticle thick, with well-defined transverse striations. Amphids not protuberant. Cephalic papillae slightly protuberant from level of hypodermis but recessed from external surface of cuticle, recession causing dimpling in cuticle immediately around papillae (Figs. 1, 18). Pre-oesophageal ring present, inconspicuous. Oesophagus not externally divided, posterior end slightly swollen (Figs. 1, 18). Oesophageal-intestinal junction clearly demarcated. Two postdeirids present in posterior region of body, one in left ala and one in right, protruding from hypodermis into cuticle of dorsal region of each ala but not beyond external cuticular surface (not illustrated, see Fig. 13 (*P. f. americanae*)), one generally more anterior than other.

MALE: $N = 10$, all specimens from infections in which females containing microfilariae were also present; measurements given in Table 1, with those of holotype listed below. Body generally in form of helix, occasionally spiral, with 2–3 rotations present (exclusive of tail); tail in half to full coil. Alae at midbody broad (Table 1) and similar or nearly similar in width (despite asymmetry of shape), with left 0–10 μm wider than right. Body width from nerve ring to oesophageal-intestinal junction increasing slightly (Fig. 1). Four groups of caudal papillae present (Fig. 2), as follows: I, large pedunculate pre-anal papillae extending into alae, generally 3 on both sides but occasionally either side with 1, 2, or 4; II, smaller semipedunculate post-anal papillae extending into alae, generally 2 on both sides but occasionally either side with 1; III, small sessile papillae on slight mound near tail extremity, 2 or 3 on both sides, frequently closely grouped; IV, small sessile peri-anal papillae, 1 laterally elongate immediately anterior to anus and generally 4, occasionally 5, round papillae immediately posterior to anus. Delicate hyaline inclusions frequently present within alae near caudal papillae of groups I and II (Fig. 2). Spicules delicate, subequal to unequal, dissimilar, with distal end of right spicule rounded (Fig. 5) and distal portion of left spicule in form of filament (Fig. 6). (Note: In most specimens, the morphology of the distal half of both spicules was difficult to ascertain.) Postdeirids delicate and semipedun-

²This coot was mentioned by Bartlett and Anderson (1987).

TABLE 1. Major dimensions (in micrometres unless otherwise stated) of adult male *Pelecticus fulicaeatrae americanae* n.subsp. from experimentally infected American Coots (*Fulica americana*) at specific times postinfection and from wild-caught American Coots, and of adult male *P. fulicaeatrae griseogenae* n.subsp. from wild-caught Red Necked Grebes (*Podiceps griseogenae*)

	<i>Pelecticus f. americanae</i> from experimentally infected coots					<i>Pelecticus f. americanae</i> from wild coots (N = 10)	<i>Pelecticus f. griseogenae</i> from grebes (N = 10)
	20 d (N = 4) ^a	30 d (N = 2)	55 d (N = 3)	210 d (N = 7)	265 d (N = 2)		
Total length (mm)	2.5, 3.0, 3.2, 3.3	6.1, 6.4	4.2, 7.5, 8.3	8.2, 8.5, 9.1, 9.5, 9.7, 10.5, 10.6	8.8, 10.5	8.9±1.6 (7.2-11.8)	9.2±0.7 (8.2-10.2)
Maximum width	75, 80, 75, 90	205, 220	110, 260, 270	340, 280, 340, 340, 325, 330, 330	300, 320	300±53.7 (220-410)	319±22.0 (270-340)
Width left ala at midbody	10, 10, 10, 10	30, 30	20, 40, 50	50, 45, 55, 60, 55, 60, 50	55, 55	52±6.5 (40-62)	83±7.1 (70-95)
Width right ala at midbody	10, 10, 10, 10	20, 25	15, 35, 40	40, 35, 40, 45, 40, 45, 40	41, 45	39±4.8 (30-45)	77±8.6 (65-90)
Striations midbody over 100 µm	80, 85, 75, 75	46, 38	58, 28, 25	19, 27, 21, 25, 26, 22, 26	25, 25	24±3.4 (21-32)	18±2.3 (14-21)
Nerve ring from anterior	75, 75, 70, 70	95, 100	110, 100, 125	140, 135, 135, 165, 135, 135, 145	115, 110	115±13.0 (110-145)	116±9.4 (100-130)
Width at nerve ring	60, 75, 60, 62	95, 100	70, 85, 105	135, 120, 120, 115, 120, 125, 125	110, 115	110±15.7 (85-135)	106±7.5 (90-115)
Oesophagus length	300, 300, 300, 295	400, 340	405, 370, 430	520, 415, 500, 520, 510, 470, 500	440, 440	474±51.5 (410-560)	403±41.2 (350-480)
Width of oesophagus	25, 25, 20, 25	30, 35	30, 40, 35	40, 45, 40, 40, 40, 45, 42	40, 45	43±5.4 (35-55)	49±3.9 (45-55)
Width at oesophageal intestinal junction	70, 65, 60, 70	135, 140	95, 130, 155	160, 170, 175, 155, 175, 175, 180	155, 165	156±20.6 (130-195)	160±3.7 (155-165)
Posteirid from posterior ^b (mm)	0.2, 0.2, 0.2, 0.2	0.3, 0.6	0.3, 0.5, 0.4	0.6, 0.5, 0.4, 0.5, 0.6, 0.4, 0.7	0.5, 0.5	0.4±0.15 (0.2-0.6)	0.5±0.15 (0.2-0.7)
Length right spicule	55, 55, 55, 40	65, 65	60, 60, 45	50, 55, 65, 65, 60, 55, 60	55, 65	60±7.3 (50-68)	57±5.9 (48-67)
Length left spicule	60, 70, 60, 55	65, 85	70, 75, 60	70, 65, 80, 75, 75, 70, 70	70, 80	74±3.6 (68-80)	71±5.8 (61-78)
Anus from posterior	30, 35, 30, 40	30, 40	35, 40, 55	40, 35, 40, 45, 45, 40, 45	45, 30	41±2.3 (37-44)	45±3.0 (42-50)
Width at anus	35, 35, 35, 35	40, 45	45, 55, 55	60, 50, 70, 55, 60, 65, 55	50, 45	46±5.7 (34-52)	50±3.3 (45-57)

NOTE: Measurements are given for each specimen from experimentally infected coots; mean ± standard deviation, with range in parentheses, for specimens from wild-caught coots and grebes.

^aSexually immature worms.

^bTwo posteirids present; measurement is of the one farthest from posterior extremity.

culate, located within coiled region of tail. Phasmids delicate and pedunculate, located near tip of tail, one on either side but asymmetric in position (Fig. 2).

HOLOTYPE MEASUREMENTS: Body with 2 rotations. Total length 8.2 mm. Maximum width 340 μm . Width at midbody of left ala 80 μm , of right ala 70 μm . Sixteen striations present within a 100- μm interval at midbody. Distance from anterior extremity to nerve ring 115 μm . Width of body at nerve ring 110 μm . Length of oesophagus 360 μm . Maximum width of oesophagus 40 μm . Width of body at oesophageal-intestinal junction 155 μm . Postdeirids 275 μm from posterior extremity. Length of right spicule 50 μm , of left spicule 65 μm . Distance from posterior extremity to anus 43 μm . Width of body at anus 55 μm . Numbers of caudal papillae in each group: I, 3 on each side; II, 2 on each side; III, 2 or 3 on each side; IV, 1 anterior and 4 posterior.

FEMALE: $N = 20$, all specimens containing microfilariae; measurements given in Table 2, with those of allotype listed below. Body in form of helix with 3.5–5.5 relatively loose rotations present (Fig. 17, upper specimen). Left ala at midbody 10–30 μm wider than right. Body width from nerve ring to oesophageal-intestinal junction increasing considerably (Fig. 18). Vulva generally behind oesophageal-intestinal junction (Fig. 18) (anterior to junction in 1 specimen and at junction in another); cuticular lips of vulva thick, not protuberant. Proximal extremity of vagina projecting slightly into body cuticle (Fig. 18); vagina directed posteriorly from vulva, lumen in anterior portion constricted or dilated and containing few or many microfilariae. Uteri convoluted, lumen dilated and containing few or many microfilariae. Junction between uterus and oviduct well developed but generally obscured by loops of reproductive tract. Oviducts and ovaries convoluted. Terminal ends of ovaries generally in posterior half of body, rarely in anterior half. Postdeirids more anterior in location than in male, robust and mound-like, frequently difficult to find because of twisting of body but readily apparent when found, often more discernable on one side than other. Body width decreasing considerably from postdeirids to tail extremity. Two terminal sublateral caudal papillae and one terminal dorsal caudal papilla present (Fig. 20); sublateral papillae readily apparent or obscure, conical, with tips recessed; dorsal papilla inconspicuous, slender, with tip recessed. Two small sublateral swellings occasionally present posterior to or at level of anus, one on either side of body. Phasmids located immediately adjacent to terminal sublateral papillae, generally not visible.

ALLOTYPE MEASUREMENTS: Body with 4.5 rotations. Total length 27 mm. Maximum width 640 μm . Width at midbody of left ala 120 μm , of right ala 100 μm . Nine striations present within a 100- μm interval at midbody. Distance from anterior extremity to nerve ring 110 μm . Width of body at nerve ring 140 μm . Length of oesophagus 450 μm . Maximum width of oesophagus 50 μm . Width of body at oesophageal-intestinal junction 220 μm . Distance from anterior extremity to vulva 530 μm . Width of body at vulva 250 μm . Length of vagina 1.1 mm. Postdeirids not located. Distance from posterior extremity to anus 60 μm . Width of body at anus 100 μm .

MICROFILARIA: As described from Red-necked Grebe by Bartlett and Anderson (1987).

TYPE HOST: Red-necked Grebe, *Podiceps grisegena* (Boddaert) (Podicipediformes: Podicipedidae).

LOCALITIES: Type locality: Bistcho Lake, Alberta, Canada

(59°45'N, 118°50'W). Additional localities: other sites in Alberta (Gallimore 1964; Bartlett and Anderson 1987).

SPECIMENS: Types, from a wild-caught individual: holotype, No. 0074; allotype, No. 0075; paratypes, No. 0076. Others, from wild-caught individuals: Nos. 0077–0079. (All specimens have been deposited in the Canadian National Museum of Natural Sciences under NMCP1989 catalogue numbers.)

ETYMOLOGY: *grisegenae*, from the name of the host.

Pelecitus fulicaeatrae americanae n. subsp.

(Figs. 7, 10–17, 21, 25, 29, 31, 35; Tables 1, 2)

GENERAL: Filarioidea, Onchocercidae, Dirofilarinae, *Pelecitus* Railliet and Henry, 1910 (sensu Bartlett and Greiner 1986). Similar to *P. f. grisegenae*.

MALE: $N = 19$, all specimens from infections in which females containing microfilariae were also present; measurements given in Table 1 under "210 d," "265 d," and "wild coots," with those of holotype listed below. Similar to *P. f. grisegenae*, with the following exceptions: body with 3–3.5 rotations present (exclusive of tail); alae at midbody narrow (Table 1) and noticeably dissimilar in width, with left 10–20 μm wider than right.

HOLOTYPE MEASUREMENTS: Body with 3 rotations. Total length 11.1 mm. Maximum width 340 μm . Width at midbody of left ala 55 μm , of right ala 40 μm . Twenty-one striations present within a 100- μm interval at midbody. Distance from anterior extremity to nerve ring 125 μm . Width of body at nerve ring 130 μm . Length of oesophagus 525 μm . Maximum width of oesophagus 50 μm . Width of body at oesophageal-intestinal junction 185 μm . Postdeirids 600 μm from posterior extremity. Length of right spicule 62 μm , of left spicule 72 μm . Distance from posterior extremity to anus 43 μm . Width of body at anus 50 μm . Numbers of caudal papillae in each group: I, 3 on each side; II, 2 on each side; III, 2 or 3 on each side; IV, 1 anterior and 4 posterior.

FEMALE: $N = 22$, all specimens containing microfilariae; measurements given in Table 2 under "210 d," "265 d," and "wild coots," with those of allotype listed below. Similar to *P. f. grisegenae*, with the following exceptions: body with 4.5–6.5 relatively tight rotations present (Fig. 17, lower specimen); left ala at midbody 10–40 μm wider than right; vulva near oesophageal-intestinal junction (Fig. 21) (anterior to junction in 12 specimens, at junction in 4, posterior in 6).

ALLOTYPE MEASUREMENTS: Body with 5.5 rotations. Total length 35 mm. Maximum width 710 μm . Width at midbody of left ala 110 μm , of right ala 75 μm . Nine striations present within a 100- μm interval at midbody. Distance from anterior extremity to nerve ring 190 μm . Width of body at nerve ring 185 μm . Length of oesophagus 670 μm . Maximum width of oesophagus 65 μm . Width of body at oesophageal-intestinal junction 325 μm . Distance from anterior extremity to vulva 600 μm . Width of body at vulva 310 μm . Length of vagina 2.2 mm. Postdeirids not located. Distance from posterior extremity to anus 80 μm . Width of body at anus 130 μm .

MICROFILARIA: As described from American Coots by Bartlett and Anderson (1987).

TYPE HOST: American Coot, *Fulica americana* Gmelin (Gruiformes: Rallidae).

LOCALITIES: Type locality: Brooks, Alberta, Canada (50°35'N, 111°53'W). Additional localities: Canada: Manitoba and other sites in Alberta; United States: Wisconsin,

TABLE 2. Major dimensions (in micrometres unless otherwise stated) of adult female *Pelecitus fulicaeatrae americanae* n. subsp. from experimentally infected American Coots (*Fulica americana*) at specific times postinfection and from wild-caught American Coots, and of adult female *P. fulicaeatrae griseigenae* n. subsp. from wild-caught Red Necked Grebes (*Podiceps griseigena*)

	<i>Pelecitus f. americanae</i> from experimentally infected coots				<i>Pelecitus f. americanae</i> from wild coots (N = 20) ^c	<i>Pelecitus f. griseigenae</i> from grebes (N = 20) ^c
	20 d (N = 4) ^a	30 d (N = 6) ^a	55 d (N = 4) ^b	210 d (N = 1) ^c	265 d (N = 2)	
Total length (mm)	3.4, 3.7, 3.8, 4.1	5.9, 7.8, 7.9, 8.1, 8.6, 10.9	9.6, 10.5, 11.7, 13.5	23	21 ^b , 21 ^c	25 ± 2.5 (20-29)
Maximum width	85, 85, 85, 85	160, 215, 220, 180, 235, 255	270, 280, 240, 350	465	490, 540	580 ± 78.2 (520-660)
Width left ala at midbody	10, 10, 8, 10	30, 35, 40, 35, 30, 45	40, 40, 35, 45	85	80, 85	112 ± 11.8 (90-130)
Width right ala at midbody	9, 9, 8, 9	20, 25, 30, 25, 20, 35	35, 35, 30, 40	65	60, 60	90 ± 13.4 (60-110)
Striations midbody over 100 μm	110, 90, 90, 85	45, 32, 33, 39, 30, 26	32, 31, 32, 18	14	14, 14	10 ± 1 (9-12)
Nerve ring from anterior	60, 70, 75, 75	85, 110, 100, 90, 95, 105	100, 140, 125, 105	130	135, 115	123 ± 10.4 (100-140)
Width at nerve ring	65, 62, 58, 62	100, 105, 100, 110, 100, 110	105, 110, 110, 120	150	140, 155	137 ± 9.5 (125-150)
Oesophagus length	365, 350, 350, 355	400, 445, 480, 390, 410, 400	480, 440, 485, 470	590	560, 540	425 ± 52.9 (320-500)
Width of oesophagus	25, 25, 25, 25	30, 40, 40, 35, 30, 50	40, 40, 40, 45	60	55, 55	53 ± 8.6 (40-80)
Width at oesophageal intestinal junction	70, 75, 75, 80	135, 165, 165, 145, 160, 165	160, 160, 170, 200	270	245, 275	231 ± 14.4 (210-255)
Vulva from anterior	185, 150, 220, 210	280, 305, 345, 260, 300, 285	350, 345, 435, 470	500	545, 510	535 ± 74.0 (405-650)
Width at vulva	70, 80, 75, 80	120, 145, 145, 130, 150, 150	140, 150, 165, 200	270	245, 265	263 ± 19.2 (230-285)
Vagina length	145, 210, 220, 200	340, 645, 840, 750, 340, 735	815, 560, 1050, 1775	1500	1000, 1500	1400 ± 500 (1200-2100)
Postdeirids from posterior (mm)	0.5, 0.5, 0.5, 0.5	— ^d , —, 1.1, 1.1, —, 1.4	—, —, 2.5, 2.1	2.0	2.6, 2.8	(1.6-3.6) ^e
Anus from posterior	30, 45, 40, 35	50, 45, 40, 50, 60, 65	45, 80, 40, 75	45	70, 85	72 ± 15.6 (50-100)
Width at anus	40, 45, 40, 40	85, 80, 80, 90, 90, 100	85, 105, 90, 120	130	130, 140	114 ± 15.8 (110-150)

NOTE: Measurements are given for each specimen from experimentally infected coots; mean ± standard deviation, with range in parentheses, for specimens from wild-caught coots and grebes.

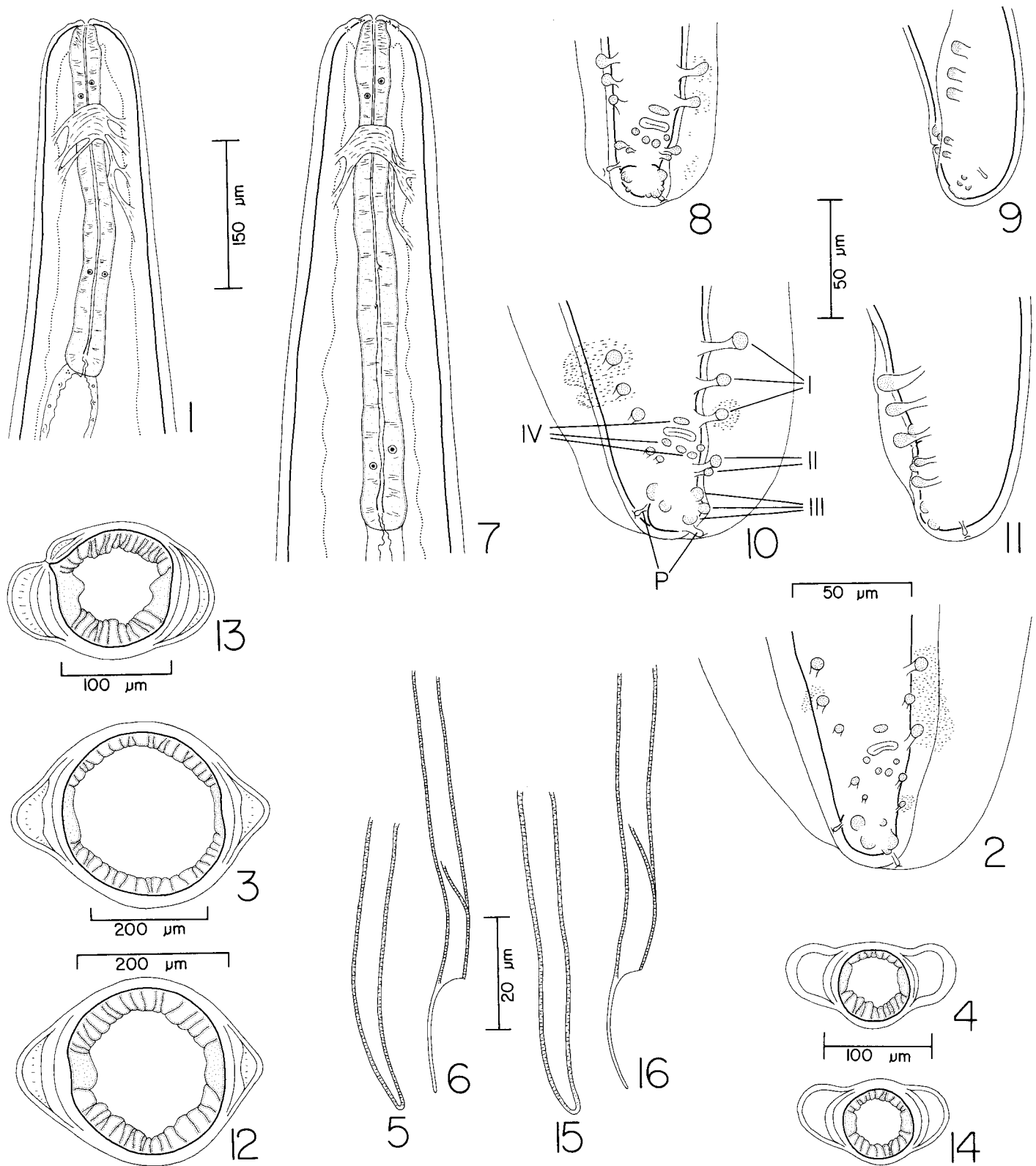
^aSexually immature worms.

^bSexually mature worm(s) without microfilariae.

^cFemale containing microfilariae.

^dNot located.

^eRange only.



FIGS. 1–16. Male *Pelecitus fulicaeatrae*. Figs. 1–6. *Pelecitus f. grisegenae* n. subsp. from wild-caught *Podiceps grisegenae*. Fig. 1. Anterior end, lateral view. Fig. 2. Posterior extremity, ventral view. Fig. 3. Transverse section at midbody. Fig. 4. Transverse section slightly anterior to anus. Figs. 5 and 6. Right and left spicules, respectively. Figs. 7–16 of *P. f. americanae* n. subsp. from wild-caught (unless specified as at a particular time in an experimental infection) *Fulica americana*. Fig. 7. Anterior end, lateral view. Figs. 8 and 9. Posterior extremity at 20 d postinfection, ventral and lateral views, respectively. Figs. 10 and 11. Posterior extremity at 265 d postinfection, ventral and lateral views, respectively. Figs. 12–14. Transverse section at midbody, left postdeirid, and slightly anterior to anus, respectively. Figs. 15 and 16. Right and left spicules, respectively. I–IV, caudal papillae groups I–IV; P, phasmids.

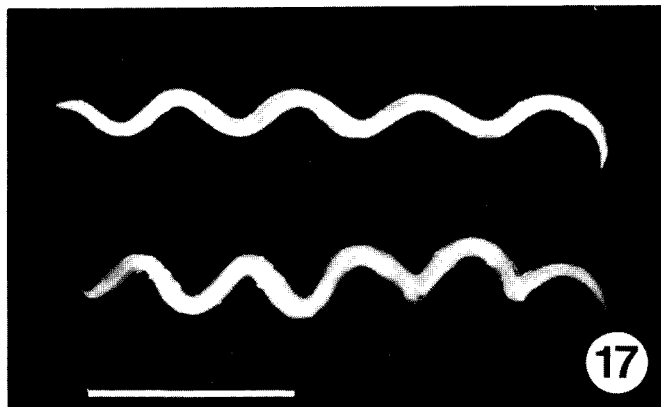


FIG. 17. Photomicrograph of female *Pelecitus fulicaeatrae* *grisegena* n.subsp. (top) from wild-caught *Podiceps grisegena* and female *P. f. americanae* n.subsp. (bottom) from wild-caught *Fulica americana*. Scale bar = 1 cm.

North Dakota, and California (Colbo 1965; Bartlett and Anderson 1987, 1988; present study).

SPECIMENS: Types, from a wild-caught individual: holotype, No. 0080; allotype, No. 0081; paratypes, No. 0082. Others, from wild-caught individuals: Nos. 0083-0087. Others, from experimentally infected individuals at 210 and 265 d post-infection: No. 0088. (All specimens have been deposited in the Canadian National Museum of Natural Sciences under NMCP1989 catalogue numbers.)

ETYMOLOGY: *americanae*, from the name of the host.

Taxonomic diagnosis

The two subspecies of *P. fulicaeatrae* described above are distinguished on the basis of (i) the lateral alae at midbody in males (they are narrower in *P. f. americanae* (left, 40–62 μ m; right, 30–45 μ m) than in *P. f. grisegena* (left, 70–95 μ m; right, 65–90 μ m), and in *P. f. americanae* the left is 10–20 μ m wider than the right, but in *P. f. grisegena* it is only 0–10 μ m wider); (ii) the conformation of the adult female body (helical twisting is tighter and more rotations are present in *P. f. americanae* than in *P. f. grisegena*); and (iii) the oesophagus (it tends to be longer, and thus the vulva tends to be closer to the oesophageal–intestinal junction, in *P. f. americanae* than in *P. f. grisegena*).

Pelecitus f. americanae in experimentally infected coots

Fifth-stage (i.e., adult) *P. f. americanae* were found near the ankles of all experimentally infected coots (Table 3), and 20–53% of the numbers of worms inoculated were recovered. At 20 d postinfection, males and females were sexually immature. At 30 and 55 d, females contained unembryonated ova, and at 210 and 265 d, females contained microfilariae if they occurred in the same ankle as males (Table 3). Microfilariae were present in the fluid surrounding adult worms at 210 and 265 d but were not found in skin from the feathered portion of the lower crus. However, a few (six) microfilariae were found in skin from the scale–feather junction of the left leg of the coot killed at 265 d.

At 210 and 265 d, males and females were morphologically similar to those from wild-caught coots, and worms from these experimental infections composed part of the material for the taxonomic description of *P. f. americanae* provided earlier. However, at 20, 30, and 55 d, some morphologic features differed from those in specimens on which the taxonomic descrip-

TABLE 3. Numbers and locations of male and female *Pelecitus fulicaeatrae americanae* in American Coots (*Fulica americana*) hatched in captivity and subsequently either experimentally inoculated with *P. f. americanae* (group 1) or housed with naturally infected wild-caught coots (group 2)

Duration ^a (d)	Right ankle		Left ankle	
	Males	Females	Males	Females
Group 1^b				
Coot 1	2	2	2	2
Coot 2	1	4	1	2
Coot 3	3	3	—	1
Coot 4	7	1	—	—
Coot 5	—	1	2	1
Group 2^c				
Coot 1	2	3	2	1
Coot 2	2	3	1	1
Coot 3	—	1	—	—
Coot 4	—	2	—	1

^aTime postinoculation for group A coots; time postplacement of group B coots.

^bEach coot was inoculated with 15 third-stage larvae of *P. f. americanae*, except coot 5 which was inoculated with 18.

^cEach coot was placed in a pen containing wild-caught adult coots which harboured natural infections of *P. fulicaeatrae* and natural infestations with the louse vector *Pseudomenonpon pilosum*.

tion is based. These differences are outlined in Table 4 and illustrated in Figs. 8, 9, 22–24, 26–28, 30, and 32–34; measurements are provided in Tables 1 and 2. (Note: Specimens at 20, 30, and 55 d postinfection have been deposited in the Canadian National Museum of Natural Sciences, No. NMCP1989–0089.)

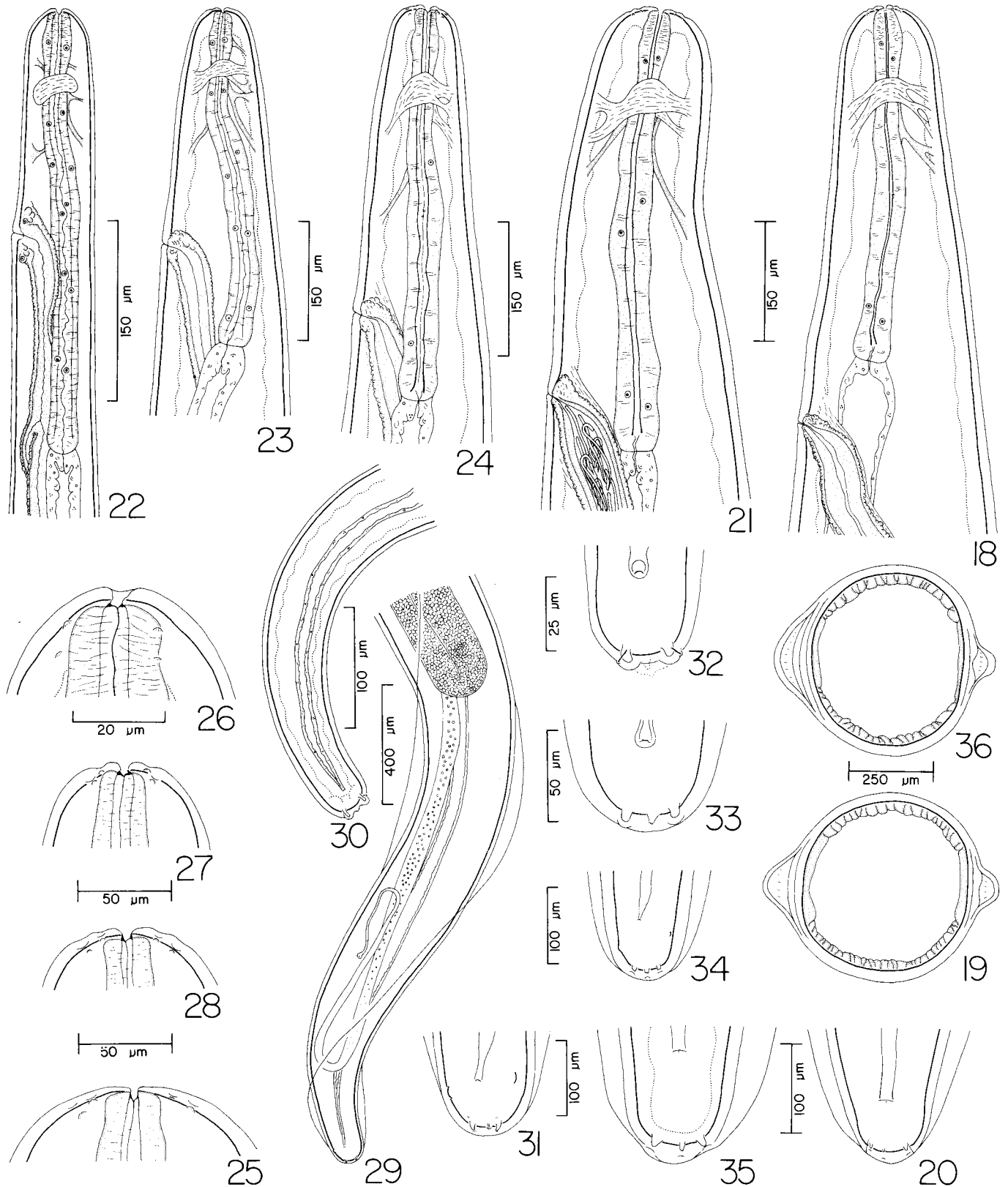
Pelecitus f. americanae in juvenile coots housed with adult coots

The juvenile coot housed for 120 d with wild-caught adults became infected with *P. f. americanae*, as did three juvenile coots mentioned by Bartlett and Anderson (1987) (Table 3). Microfilariae of *P. f. americanae* were not present in any females, nor in fluid around adults. Numbers of rotations in the bodies of females from coots housed for 60, 120, 150, and 210 d were 4.5, 4, 4.5, and 5, respectively. (Note: These specimens have been deposited in the Canadian National Museum of Natural Sciences, No. NMCP1989-0090.)

Pelecitus f. americanae in wild-caught coots

Infections in wild-caught coots were of three types: type A, in which both male and female worms were present and females contained microfilariae; type B, in which both males and females were present but females did not contain microfilariae; and type C, in which only females or only males were present. The information given below pertains to individual coots, each of which has been assigned a number; information about worms in each ankle is given in parentheses, the right ankle followed by the left, as follows: number of female worms [number of body rotations of each female], number of male worms, type of infection. An asterisk (*) indicates that microfilariae were present in the fluid surrounding adult worms. Absence of an asterisk indicates that microfilariae were not present or, as indicated for particular groups of coots, fluid was not examined. Information about infections in coots mentioned in earlier publications was not previously reported.

Infections found in 11 (73.3%) of the 15 adult group B coots collected by Bartlett and Anderson (1987) near Brooks, Alberta,



FIGS. 18–36. Female *Pelecitus fulicaeatrae*. Figs. 18–20. *Pelecitus f. griseganae* n. subsp. from wild-caught *Podiceps grisegana*. Fig. 18. Anterior end, lateral view. Fig. 19. Transverse section at midbody. Fig. 20. Posterior extremity, ventral view. Figs. 21–36 of *P. f. americanae* n. subsp. from wild-caught (unless specified as at a particular time in an experimental infection) *Fulica americana*. Figs. 21–24. Anterior end at 265, 20, 30, and 55 d, respectively, lateral view. Figs. 25–28. Anterior extremity at 265, 20, 30, and 55 d, respectively, lateral view. Figs. 29 and 30. Posterior end at 265 and 20 d, respectively, ventral view. Figs. 31–34. Posterior extremity at 265, 20, 30, and 55 d, respectively, ventral view. Fig. 35. Posterior extremity, ventral view. Fig. 36. Transverse section at midbody.

TABLE 4. Morphologic features in different age groups of male and female *Pelecitus fulicaeaeatrae americanae* n. subsp. from experimentally infected American Coots (*Fulica americana*)

	At 20 d	At 30 d	At 55 d
General features			
Form of body	Loose spiral decreasing towards tail	*	*
Pre-oesophageal ring	Readily apparent	Readily apparent	Readily apparent
Body width from nerve ring to oesophageal—intestinal junction	Increasing negligibly	Increasing slightly	Increasing slightly
Male features			
No. of rotations in body (exclusive of tail)	1	2	2-3
No. of rotations in tail	0.5	0.5	0.5-0.8
Female features			
Position of vulva	Near midoesophagus	Near posterior third of oesophagus	Between posterior third of oesophagus and oesophageal—intestinal junction
Vagina	Constricted along entire length	Constricted along entire length or slightly dilated in posterior portion	Constricted or slightly dilated in anterior portion, markedly dilated in posterior portion
Uteri	Not convoluted, constricted in anterior portion, lumen absent in posterior portion	Slightly convoluted, lumen dilated along entire length	Markedly convoluted, lumen dilated along entire length
Remainder of reproductive tract	Not fully differentiated	Fully differentiated, junction between uterus and oviduct not easily distinguished	*
Postdeirids	Delicate and stalk-like	*	*
Body width from postdeirid to posterior extremity	Decreasing negligibly	*	*
Sublateral swellings near anus	Absent	Absent	*
Terminal sublateral caudal papillae	Readily apparent, pedunculate, with markedly protuberant tips	Readily apparent, pedunculate, with slightly protuberant tips	Readily apparent, pedunculate, with slightly recessed tips
Terminal dorsal caudal papilla	Readily apparent, conical, with markedly protuberant tip	Readily apparent, conical with slightly recessed tip	Inconspicuous, squarish, with slightly recessed tip

*Morphology as in taxonomic description.

in late May and early June, 1986, were as follows (fluid was not examined for microfilariae) (note: these birds were nesting):

1. (0) + (1[4.5],4,A)
2. (0) + (1[5.5],1,B)
3. (0) + (1[6.5],2,B)
4. (1[4],1,B) + (2[4.5;5],1,B)
5. (1[5.5],1,B) + (0)
6. (2[4.5;4.5],0,C) + (0,3,C)
7. (0) + (1[6]2,A)
8. (0) + (4[5;5.5;5.5;6],2,B)
9. (0) + (1[6.5]4,A)
10. (0,1,C) + (0)
11. (0,1,C) + (1[4.5],0,C)

Infections found in seven (87.5%) of the eight adult coots collected by Bartlett and Anderson (1989) near Brooks, Alberta, in early June, 1987, were as follows (numbering below follows that in Bartlett and Anderson 1989) (note: these birds were nesting):

1. (1[5],0,C) + (0)
2. (1[5.5],2,A)* + (0)
3. (0,1,C) + (0,3,C)
5. (1[4.5],2,A)* + (0)
6. (1[6],2,A) + (0,1,C)
7. (4[4.5;4.5;5.5],1,A)* + (1[5.5],0,C)
8. (1[5]1,A) + (2[5;5.5],0,C)

Infections found in 5 (100%) of the five adult coots collected by Bartlett and Anderson (1989) near Oak Lake, Manitoba, in early June, 1987, were as follows (note: these birds were nesting):

1. (2[5.5;5.5]6,A)* + (2[2;2],0,C)
2. (0) + (1[4],1,B)
3. (0) + (1[5],0,C)
4. (0,1,C) + (1[5],1,A)*
5. (1[4.5],0,C) + (1[6.5],0,C)

Three of the four (75.0%) coots collected in September 1986 at the J. Clark Salyer National Wildlife Refuge (NWR) in North Dakota, and two of the five (40.0%) collected in October 1986 at Horicon NWR in Wisconsin, were infected with *P. f. americanae* (note: these birds had either nested in the area or were migrants). Intensity of infection, presence or absence of microfilariae, and ages of the coots were not determined.

Five of the 7 (71.4%) and 14 of the 30 (46.7%) coots (of undetermined ages) collected during March and April 1986 and January–April 1987, respectively, at Kesterson Reservoir NWR in California were infected with *P. f. americanae* (note: these birds were wintering). Infections in the birds in 1986 were as follows:

1. (0) + (0,1,C)
2. (1[5],4,B)* + (0)
3. (2[5.5;5.5]1,B)* + (0)
4. (1[5.5]2,A) + (1[6],1,A)
5. (1[5.5],1,B) + (0)

Infections in the coots in 1987 were as follows:

1. (1[5.5],4,B) + (0)
2. (2[5;5.5],0,C) + (3[4.5;4.5;4.5],2,B)
3. (0) + (1[5.5],0,C)
4. (3[4.5;5.5]2,B) + (0)
5. (2[4.5;4.5],0,C) + (0)
6. (1[5],0,C) + (2[5;6],0,C)
7. (0) + (1[5.5],1,B)
8. (2[4.5;4.5],1,B) + (0)

9. (1[5.5],1,A)* + (4[4.5;4.5;6;6.5],0,C)
10. (2[4;4.5],4,B) + (0)
11. (1[5],0,C) + (2[5;5],2,B)
12. (1[5]2,A) + (0)
13. (1[4.5],0,C) + (0)
14. (1[5.5],0,C) + (0,1,C).

Gross observations of coot ankles

Worms were always found along the distal tibiotarsus near the ankle (intertarsalis joint) and generally were within, or in pockets near, the sheath of the achilles tendon adjacent to the cartilago tibialis (see definition in Baumel et al. 1979; Rosser et al. 1982) or within 1.5 cm proximal to the cartilago tibialis. The achilles tendon becomes flat as it runs through the cartilago tibialis, and worms within the tendon sheath in this area were generally on the side closest to the centre of the ankle (note: in the histologic description below, this side is referred to as the anterior margin of the achilles tendon, following the orientation of Lucas and Stettenheim (1972)). Rarely, worms were within sheaths of tendons of the digital flexor bundle. Worms were occasionally found in more than one location in an individual ankle.

Infections were not detectable upon external examination of intact coots, with the exception of one coot (A-1 of Bartlett and Anderson 1987) in which worms were within nodules approximately 1 cm in diameter. When tissues were exposed, a grossly visible response to worms was generally not apparent. However, in a few birds, worms were within soft, thin-walled capsules and in the one coot identified above, worms were within fibrous, thick-walled capsules. Clear viscous (synovial) fluid covered the surface of worms in situ, but little such fluid was present in host tissues themselves.

Histologic observations of coot ankles

Descriptions below of infected tissues are based on material from coots A-12 and A-13 of Bartlett and Anderson (1987). Infections were more than a year old when the birds were killed in mid-July 1987, as indicated by the presence of microfilariae in leg skin shortly after A-12 was captured in June 1986, and A-13 a few months later. Comments regarding normal or uninfected tissues are based on material from adult coots in Manitoba which did not harbour worms.

Coot A-12

Transverse sections of the posterior region of the ankle revealed the cartilago tibialis, associated tendons, skin, and worms (Fig. 38; cf. Fig. 37 which shows a slightly more distal section of normal tissues). Worms were located medially near the achilles tendon within one or two large round pockets lined in a few places by compressed layers of dense connective tissue, but generally by hypertrophic columnar and cuboidal synovial cells many layers thick (Fig. 39). The cartilago tibialis consisted of limited areas of closely adjacent vesicular chondrocytes, small amounts of eosinophilic matrix, numerous adipocytes and fibrocytes, considerable amounts of regular, dense connective tissue, scattered collagen fibers, and numerous small blood vessels. (Note: In uninfected ankles the cartilago tibialis consisted of large expanses of closely adjacent vesicular chondrocytes, small amounts of eosinophilic matrix, variable amounts of collagen fibers, and a few fibrocytes.) Lymphocytes and plasma cells were present, individually or in patches, throughout the cartilago tibialis. Sheaths containing

tendons of the digital flexor bundle were, in most places, lined by hypertrophic columnar and cuboidal synovial cells a few to many layers thick (note: in normal tissues, the synovial cells were squamous and one to three layers thick). A layer of squamous synovial cells, or a layer of hypertrophic synovial cells, or a layer of fibrocytes and loose connective tissue invaded by lymphocytes and plasma cells formed the outer margin of the digital flexor tendons. The achilles tendon was not within a well-defined sheath and was displaced laterally. The posterior and lateral margins of this tendon were formed of a layer of squamous or cuboidal synovial cells, and thin connective tissue layers separated these margins from adjacent skin. The anterior portion of the achilles tendon was fibrotic, had undergone neovascularization, and was infiltrated by numerous lymphocytes, plasma cells, and macrophages (Fig. 40); it was difficult to distinguish its margin from similar adjacent granulation tissue in the cartilago tibialis. Commonly, hypertrophic synovial cells in this region and between the medial margin of the achilles tendon and adjacent worms formed villous projections.

Coot A-13

Transverse sections of the posterior region of the right ankle revealed worms in a large round pocket lined by a thin layer of compressed, dense connective tissue. Inflammatory cells were not present in this tissue or in dermis of the medial side of the ankle. A few lymphocytes were present in loose connective tissue between the lateral edge of the pocket and nearby tendons.

Discussion

Subspecies of *Pelecitus fulicaeatrae* have not previously been proposed. The parasite in the original type host, the Common Coot (*Fulica atra* L.), becomes the nominotypical subspecies, i.e., *P. fulicaeatrae fulicaeatrae* (Diesing, 1861). Unfortunately, the type specimens of *P. f. fulicaeatrae* have been lost (Bartlett and Greiner 1986) and there is no detailed description of the parasite from the type host in the type locality, i.e., Great Britain. Bartlett and Greiner (1986) indicated that specimens from Common Coots in Germany have narrower lateral alae and a more posteriorly located vulva than *P. f. americanae*, but their redescription of "*P. fulicaeatrae*" cannot, in its entirety, be used as a taxonomic description of *P. f. fulicaeatrae* because it was based not only on specimens from coots in Germany but also on specimens from one other species in Rallidae and two in Podicipedidae. The Red-necked Grebe, designated as the type host of *P. f. griseogenae*, occurs in both the Old and New Worlds, and its range overlaps that of the Little Grebe, *Tachybaptus ruficollis* (Pallas). The latter is the type host of *Pelecitus podicipitis* (Yamaguti, 1935) which Baylis (1944) considered a synonym of *P. fulicaeatrae*. The status of *P. f. griseogenae* vis-à-vis "*P. podicipitis*," as well as worms from other grebes in the New World, requires further study.

The two subspecies of *P. fulicaeatrae* from Red-necked Grebes and American Coots in North America are distinguished on the basis of the width of the lateral alae at midbody in males, the conformation of the adult female body, and the position of the vulva with respect to the end of the oesophagus. The recognition of subspecies indicates that worms in these two sympatric hosts do not commonly interbreed. The parasite

in coots, and probably also in grebes, is transmitted by amblyceran chewing lice and the host specificity of these vectors would contribute to isolation of the parasite in different hosts. However, lice might occasionally transfer between the two hosts (Bartlett and Anderson 1987). In the laboratory, lice from coots survived briefly on grebes (Bartlett and Anderson 1989).

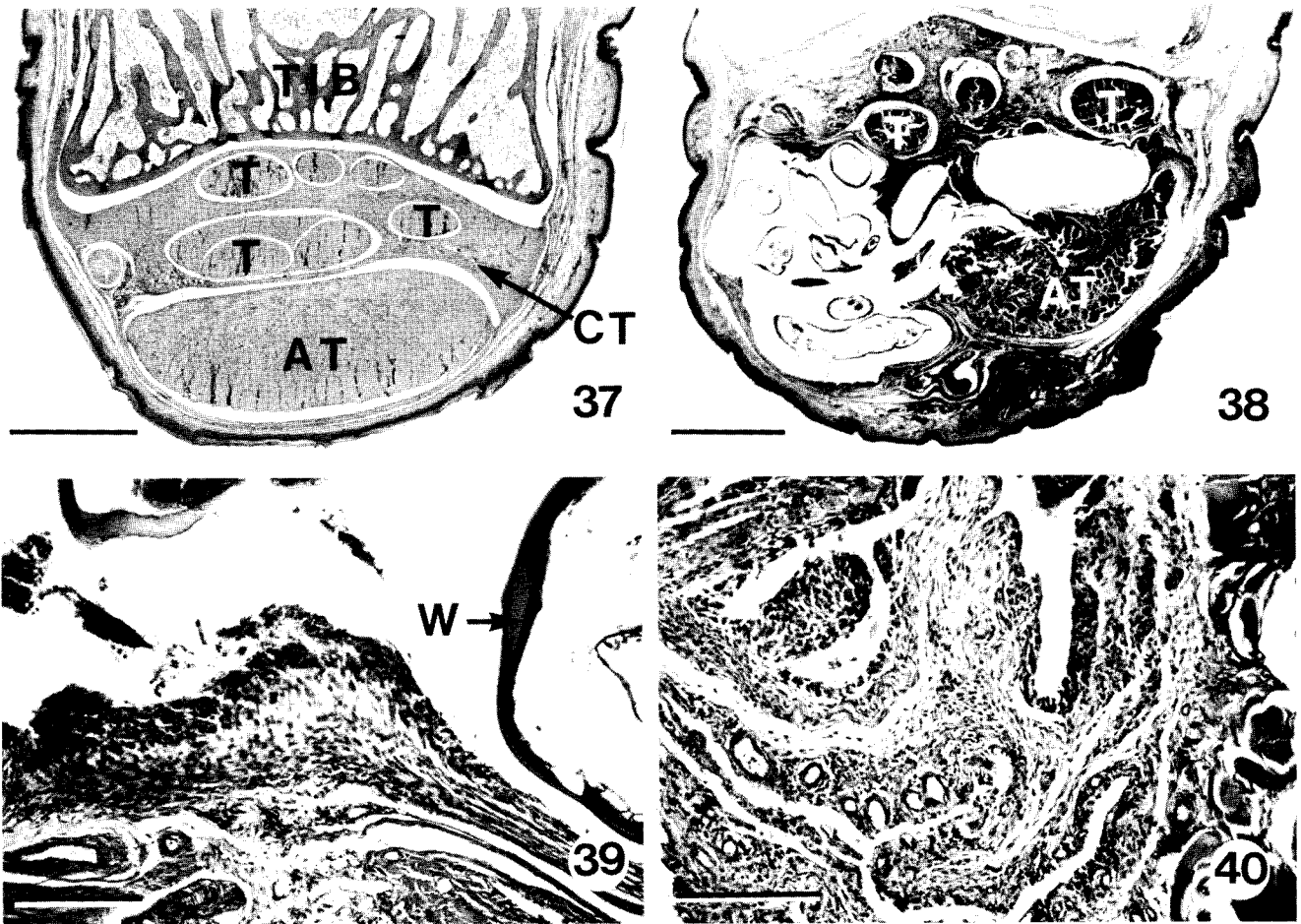
The morphology of the distal half of the spicules was particularly difficult to study. Therefore, earlier illustrations of spicules in *P. fulicaeatrae* s.l. may be misleading, and in the key to species of *Pelecitus* given by Bartlett and Greiner (1986), a filament probably is present on the left spicule of every species having the character "caudal papillae extending into alae arranged in distinct pattern of large pre-anals and smaller ad- to post-anals."

Pelecitus f. americanae had completed its migration to the ankles by the time coots were first examined 20 d postinfection, and thus resembles *Pelecitus scapiceps* (Leidy, 1886) Bartlett and Greiner, 1986, which first appears in the ankles of cottontail rabbits (*Sylvilagus floridanus* (J. A. Allen)) at 16 d postinfection (Bartlett 1984a). *Pelecitus roemeri* (Linstow, 1905) Bartlett and Greiner, 1986 has not been found in the definitive site before 141 d in the eastern wallaroo (*Macropus robustus* Gould) and 159 d in the grey kangaroo (*Macropus giganteus* Shaw), although the former has been examined at 14 and 28 d and the latter at 15 and 71 d postinfection (Spratt 1972, 1975). At 20 d, *P. f. americanae* had already moulted to the adult stage, although worms were sexually immature. In *P. scapiceps*, this moult occurs between 12 and 14 d, but it has not been observed in *P. roemeri*. *Pelecitus scapiceps* migrates to the definitive site only after the final moult (Bartlett 1984b); this is probably also true of *P. roemeri* and *P. f. americanae* because only the fifth stage of these two species has been found in the definitive site in naturally and experimentally infected hosts (Spratt 1975; present study).

The considerable increase in body length that occurred during the adult stage of both male and female *P. f. americanae* is a feature common to many nematodes. However, morphologic changes during the adult stage (other than those associated with differentiation of the reproductive tract), such as those in *P. f. americanae*, are unusual, although they have been noted previously among filarioids. Such changes may provide clues to phylogenetic relationships of different species. Bartlett (1983, 1984b) suggested that because young adult *P. scapiceps* resemble late adult *Loaina uniformis* (Price, 1957) Eberhard and Orihel, 1984, the latter species may have evolved through paedomorphosis from the former.

In both *P. f. americanae* and *P. scapiceps*, the oesophagus of the infective third-stage larva is clearly divided into muscular and glandular portions (Bartlett 1984a; Bartlett and Anderson 1987). In *P. f. americanae* this division had disappeared by day 20 in the final host and thus an undivided oesophagus is probably characteristic of adult *P. fulicaeatrae* s.l.; Bartlett and Greiner (1986) had advised caution in the use of this character because, as in *P. scapiceps*, for example, the division may remain but become increasingly indistinct with time.

Microfilariae of *P. f. americanae* occur mainly in skin of the lower legs (crus) (Bartlett and Anderson 1987). Although female worms in the present study had begun to deposit microfilariae by 210 d postinfection, more time apparently is required before microfilariae either invade or reach detectable



FIGS. 37–40. Photomicrographs of histologic sections of the posterior ankle region of *Fulica americana* Gmelin. Fig. 37. Transverse section showing normal tissue. Scale bar = 1500 μm . Fig. 38. Transverse section showing adult *Pelecitus fulicaeatrae americanae* in a pocket near the achilles tendon. Scale bar = 1500 μm (note: Fig. 38 shows a section from a different *F. americana* than that in Fig. 37 and of a region slightly more proximal on the tibiotarsus). Fig. 39. Hypertrophic columnar and cuboidal synovial cells forming edge of pocket containing *P. f. americanae*. Scale bar = 150 μm . Fig. 40. Area of neovascularization adjacent to achilles tendon. Scale bar = 150 μm . CT, cartilago tibialis; AT, achilles tendon; T, tendons of digital flexor bundle; TIB, tibiotarsus; W, worm.

numbers in feathered portions of crus skin. The microfilariae of other species of *Pelecitus* occur in the blood, and the prepatent periods of the three species that have been studied vary between 4 and 8 months (Dissanaike 1967; Spratt 1975; Bartlett 1984b).

When adult male and female filarioids occur together in a host individual, one normally expects to find microfilariae in females. Thus, among coots infected with *P. f. americanae* we expected to find microfilariae in females when adults of both sexes occurred in the same ankle. This expectation was almost met among the nesting coots collected in Alberta and Manitoba in 1987, i.e., in 87% of expected cases, or seven of eight ankles (type A infections / type A + type B infections, see definitions in Results). However, among nesting coots collected in Alberta in 1986, it was met in only 33% (3 of 9) of expected cases, and among wintering coots collected in California it was 22% (2 of 9) in 1987 and 40% (2 of 5) in 1986. We account for the discrepancies between what was expected and what was observed in three ways: (i) a few female worms were in pockets isolated from males and had not been inseminated; (ii) some females were too young to produce microfilariae; and (iii) some females had already produced microfilariae and become senescent.

We suggest that adult females too young to produce microfilariae can be distinguished from older females on the basis of the number of body rotations present, because the number of rotations increases with age (as indicated by data from experimentally infected coots) until a maximum is reached. Adult females too young to produce microfilariae are likely represented by type B females with fewer than five body rotations; worms with five rotations from experimentally infected coots contained microfilariae.

Senescent females would be those type B females with more than five body rotations. Senescence has previously been observed among avian filarioids, i.e., in species of *Eulimdana* in Charadriiformes (see Bartlett et al. 1989). However, senescent individuals of *P. f. americanae* are commonly encountered, whereas senescent individuals of *Eulimdana* spp. are rare, apparently because they are quickly resorbed (Bartlett et al. 1989). Microfilariae of *P. f. americanae* and *Eulimdana* spp. evidently persist long after adults have become senescent. In the present study, microfilariae were found in the immediate vicinity of senescent females, as well as in their more usual location in leg skin. Microfilariae of *Eulimdana* spp. also occur in skin (Bartlett et al. 1989).

In addition to young and senescent female worms, females

producing microfilariae (type A females) were present in wintering and nesting coots. The presence of three different age groups of worms in coots indicates that infections can be acquired at different times of the year and by different age-classes of coots. Presumably, however, many coots are infected early in life when they first acquire infestations of *Pseudomenopon pilosum* from their parents (Bartlett and Anderson 1989).

The presence of a single worm or numerous worms of one sex (i.e., type C infections) was common. Bartlett et al. (1989) also commonly found such "sterile" infections in birds infected with *Eulimdana* spp. which they believe are transmitted by lice.

Evidence of the presence of *P. f. americanae* was generally not apparent upon external examination of intact coots, including those few in which worms were subsequently found to be within soft, thin-walled capsules. In contrast, infections of *P. f. griseogenae* in grebes are often readily apparent upon external examination as "swellings" in affected tissues (T. M. Stock, personal communication).

Histopathologic response varied in the two infected coots examined. Slight fibrosis and inflammation occurred in tissues near worms in one coot and chronic proliferative tenosynovitis in the other. The latter probably corresponds to the soft, thin-walled capsules occasionally seen in infected coots. Chronic, but more pronounced, proliferative tenosynovitis is common in snowshoe hares infected with *P. scapiceps* (see Bartlett 1984c) and has also been reported in a parrot (probably *Pionus m. maximiliani* (Kuhl)) infected with *Pelecitus tercostatus* (Molin, 1860) Railliet and Henry, 1910 (= *P. calamiformis* (Schneider, 1866)) (see Greve et al. 1982); in addition, marked swelling of the ankle and metatarsal region occurred in this parrot. Swelling of the feet has also been reported in other psittaciforms harbouring species of *Pelecitus* (see Paster 1983; Allen et al. 1985).

Pelecitus fulicaeatrae s.l. has previously been reported in North America only in Western Canada (Bartlett and Anderson 1987 and references therein). The present study extends the known distribution of *P. f. americanae* to Wisconsin, North Dakota, and California, but the parasite probably occurs in coots throughout North America. The known distribution of *P. f. griseogenae* is restricted to Alberta, although obviously the parasite will be present in these grebes on their wintering grounds along the Pacific coast.

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