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CONTENTS

Four New Monogenea (Axinidae and Heteraxinidae) from Eastern Pacific Ocean Fishes

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ABSTRACT: Five species of Monogenea are reported from fishes of the eastern Pacific Ocean along the coast of California, U.S.A., and Baja California, Mexico. *Nudaciraxine cabosanlucensis* sp. n. (Axinidae: Axinoidinae) from gills of *Ablennes* sp. (Belonidae) from south of Cabo San Lucas, Baja California Sur, Mexico, differs from *N. gracilis* in clamp width, outer marginal hook size and shape, testes number and arrangement, and vaginal pore location. *Zeuxapta taylori* sp. n. (Heteraxinidae: Heteraxininae) from gills of *Thunnus albacares* (Scombridae) from southwest of San Diego, California, U.S.A., differs from *Z. kahala* in mouth structure, cirrus shape, esophageal diverticula, and host family. *Allencotyla pricei* (Heteraxinidae: Heteraxininae) is reported from new hosts, *Embiotica jacksoni* (Embiotocidae) and *Phanerodon atripes* (Embiotocidae), and the geographic distribution is extended southward from the waters off Redondo Beach, California, to La Jolla, California, and northward to Morrow Bay, California. *Leuresthicola robersoni* sp. n. (Heteraxinidae: Monaxininae) from gills of *Atherinops affinis* (Atherinidae) from off La Jolla, California, differs from *L. olsoni* in clamp number, size and structure, testes number, genital atrium spine size, and host genus. *Cynoscionicola powersi* (Heteraxinidae: Cynoscionicolinae) from gills of *Seriphus politus* (Sciaenidae), *Menticirrhus undulatus* (Sciaenidae), and *Umbrina roncador* (Sciaenidae) from off La Jolla, California, differs from *C. srivastavai* in haptor shape, anterolateral atrial pouch trirooted spines, and host species.

KEY WORDS: Monogenea, Axinidae, Heteraxinidae, *Nudaciraxine cabosanlucensis* sp. n., *Zeuxapta taylori* sp. n., *Allencotyla pricei*, *Leuresthicola robersoni* sp. n., *Cynoscionicola powersi* sp. n., eastern Pacific Ocean, California, U.S.A., Baja California, Mexico, fishes, *Ablennes* sp., *Thunnus albacares*, *Embiotica jacksoni*, *Phanerodon atripes*, *Atherinops affinis*, *Seriphus politus*, *Menticirrhus undulatus*, *Umbrina roncador*, zoogeography.

This paper is the fourth in a series (Payne, 1986, 1987a, b) on Monogenea from fishes from the eastern Pacific Ocean off California, U.S.A., and Baja California, Mexico, and deals with the description and zoogeography of several species belonging to the families Axinidae Monticelli, 1903 and Heteraxinidae Unnithan, 1957. Unnithan (1957) raised Axininae Monticelli, 1903 to family status and emended the diagnosis. The family was reviewed by Price (1962a) and Yamaguti (1963). Price (1962b) elevated Heteraxininae Unnithan, 1957 to family status, believing the asymmetrical haptor and posteriorly directed ends of the ovary to be of familial taxonomic importance. This view was supported by Kritsky et al. (1978) in their brief review of Heteraxinidae.

Materials and Methods

The fish collection methods and the techniques for the preparation and study of the monogeneans were those described by Payne (1986, 1987a, b). Figures were drawn with the aid of a drawing tube. Measurements are in micrometers unless otherwise indicated;

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ranges are followed by means in parentheses. Larval hook terminology follows Llewellyn (1970). Representative specimens have been deposited in the United States National Museum (USNM) Helminthological Collection, Beltsville, Maryland, and the Harold W. Manter Laboratory (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln; the balance of the specimens are in the author's collection.

Results

Axinidae Monticelli, 1903

Axinoidinae Price, 1962

Nudaciraxine cabosanlucensis sp. n.
(Figs. 1-6)

DESCRIPTION (based on 2 specimens): With characters of the genus. Total length 1.762–1.919 (1.840) mm, maximum width 329–439 (384) at level ovary, both specimens markedly contracted. Buccal suckers 35–42 (39) wide, aseptate with row of minute denticles around aperture. Haptor asymmetrical; 705 long with single row of 48–54 (52) clamps. Clamps 31–33 (32) long by 48–57 (54) wide with thin muscular base; sclerites slender; lateral sclerites of dorsal jaw jointed; median sclerite spring with prominent bifid terminations. One pair hamuli, 1 pair marginal

Figures 1–6. *Nudaciraxine cabosanlucensis* sp. n., holotype, all ventral view. 1. Whole mount. 2. Marginal hooks and hamuli. 3. Vaginal spine. 4. Female reproductive system. 5. Genital atrium. 6. Entire clamp. Abbreviations: C, cirrus; CP, cirrus pouch; GA, genital atrium; GIC, genitointestinal canal; OOT, ootype; OV, ovary; OVD, oviduct; PC, prostatic cells; UT, uterus; VR, vitelline reservoir. Scales in micrometers.

hooks present, 19–20 clamp spaces from posterior; hamuli 30 long, handle 17–20 (18), blade 10–15 (13); marginals I between hamuli, slender, 43 long, handle 33, blade 10.

Mouth subterminal, 62–73 (68) wide. Pharynx 33–44 (39) long by 20–23 (22) wide. Esophagus bifurcating immediately posterior to pharynx. Ceca diverticulate laterally, occasionally medially.

Testes 32, irregular, 20–62 (36) long by 37–92

(70) wide, intercecal. Vas deferens sinuous, median. Cirrus unarmed within muscular cirrus pouch; cirrus pouch 64–70 (67) long by 22–31 (27) wide; prostatic cells lining posterior portion of cirrus pouch. Genital atrium 48–52 (50) wide, 93–99 (96) posterior to pharynx, unarmed.

Ovary U-shaped, 253–396 (324) long, near midbody. Seminal receptacle not observed. Genitointestinal canal sinistral. Ootype somewhat dextral, lying anterior to proximal end of ovary; uterus somewhat thickened, medial, extending anteriorly. Vitelline follicles coextensive with ceca, posterior to level vagina; vitelline reservoir sinuous near ootype. Vaginal pore median, 136–183 (160) posterior to genital atrium, armed with horn-shaped spine 29–33 (31) long by 11 wide. Eggs not observed.

Host: *Ablennes* sp. (needlefish), Belonidae, 45.0 cm S.L.

Habitat: Gill lamellae.

Locality: South of Cabo San Lucas, Baja California Sur, Mexico (22°34′N, 109°06′W).

Depth: Surface (caught by dipnet at night).

Prevalence and intensity: 2 specimens on the 1 fish examined.

Specimens deposited: Holotype: USNM Helm. Coll. No. 80948. Paratype: USNM Helm. Coll. No. 80949.

Etymology: The specific name recognizes the type locality.

Remarks: *Nudaciraxine cabosanlucensis* most closely resembles *N. gracilis* (Linton, 1940) Price, 1962 in shape of body, buccal suckers, and haptor; by having an unarmed cirrus and genital atrium; and in distribution of vitellaria. It differs from *N. gracilis* by having narrower clamps (48–57 versus 75–100 wide), smaller lateral marginal hooks (30 versus 32–38 long), lateral marginal hook shape, more testes (32 versus 20–22), testes not tandemly arranged, a cirrus bulb or pouch provided with prostatic cells, and a median vaginal pore.

Previous to this study, *Nudaciraxine* was monotypic. Because *N. cabosanlucensis* agrees with the original generic diagnosis (Price, 1962a) in all details except the location of the vaginal pore, the original generic diagnosis should be emended as follows: Vaginal pore dorsal, median to submedian, armed with hornlike spine.

Nudaciraxine gracilis has been reported from the Atlantic needlefish, *Strongylura marina* (Walbaum), from Woods Hole, Massachusetts, and the New York Aquarium (Linton, 1940), Alligator Harbor, Florida (Hargis, 1956), and

Veracruz, Mexico (Bravo-Hollis, 1984). This is the first report of *Nudaciraxine* from the Pacific Ocean.

Heteraxinidae Unnithan, 1957

Heteraxininae Unnithan, 1957

Zeuxapta taylori sp. n.
(Figs. 7–13)

Description (based on 6 specimens, 5 measured): With characters of the genus. Body elongate, slender. Total length 7.497–14.469 (10.986) mm, maximum width 470–983 (810) immediately anterior to haptor. Buccal suckers 82–117 (106) long by 101–195 (143) wide, aseptate. Haptor 3.015–3.97 (3.493) mm long, asymmetrical, with 60–89 (80) clamps total; long row of 30–46 (41) clamps; short row of 30–44 (39) clamps. Clamps of *Microcotyle* type, 44–117 (75) long by 59–215 (125) wide, largest clamp long row 121–215 (164) wide, largest clamp short row 129–169 (145) wide; median sclerite spring with prominent bifid terminations, slender trident-shaped accessory piece at dorsal termination of median sclerite. Smallest specimen with 2 pairs larval hooks: 1 pair large hamuli 48–53 (51) long by 36–44 (40) wide, 1 pair slender marginals I 48–51 (50) long.

Mouth subterminal, wide, with convoluted ventral margin. Pharynx subspherical, 55–63 (59) long by 51–59 (55) wide, weakly muscular, between buccal suckers. Esophagus diverticulate; ceca simple from bifurcation to anterior margin of vitellaria, with lateral and median diverticula throughout remainder of body proper, extending into haptor; not confluent posteriorly.

Testes subspherical, 62–133 (92) wide, approximately 105–120 in number. Vas deferens running anteriorly along median axis, convoluted distally; ejaculatory duct convoluted in muscular ejaculatory bulb; cirrus a small stout papilla. Genital atrium 157–294 (239) long by 137–254 (200) wide, surrounded by circular muscles; genital pore 86–137 wide, midventral, 839–1,137 (988) from anterior end.

Ovary slender, 2.753–3.876 (3.552) mm long by 147–210 (167) wide, intercecal, in third quarter of body length; proximal end dextral, extending anteriorly short distance, crossing median line to sinistral side, descending to near level of proximal end, turning and ascending to anteriormost extent, recrossing median line, and descending on dextral side almost to point of origin; oviduct short; genitointestinal canal dex-
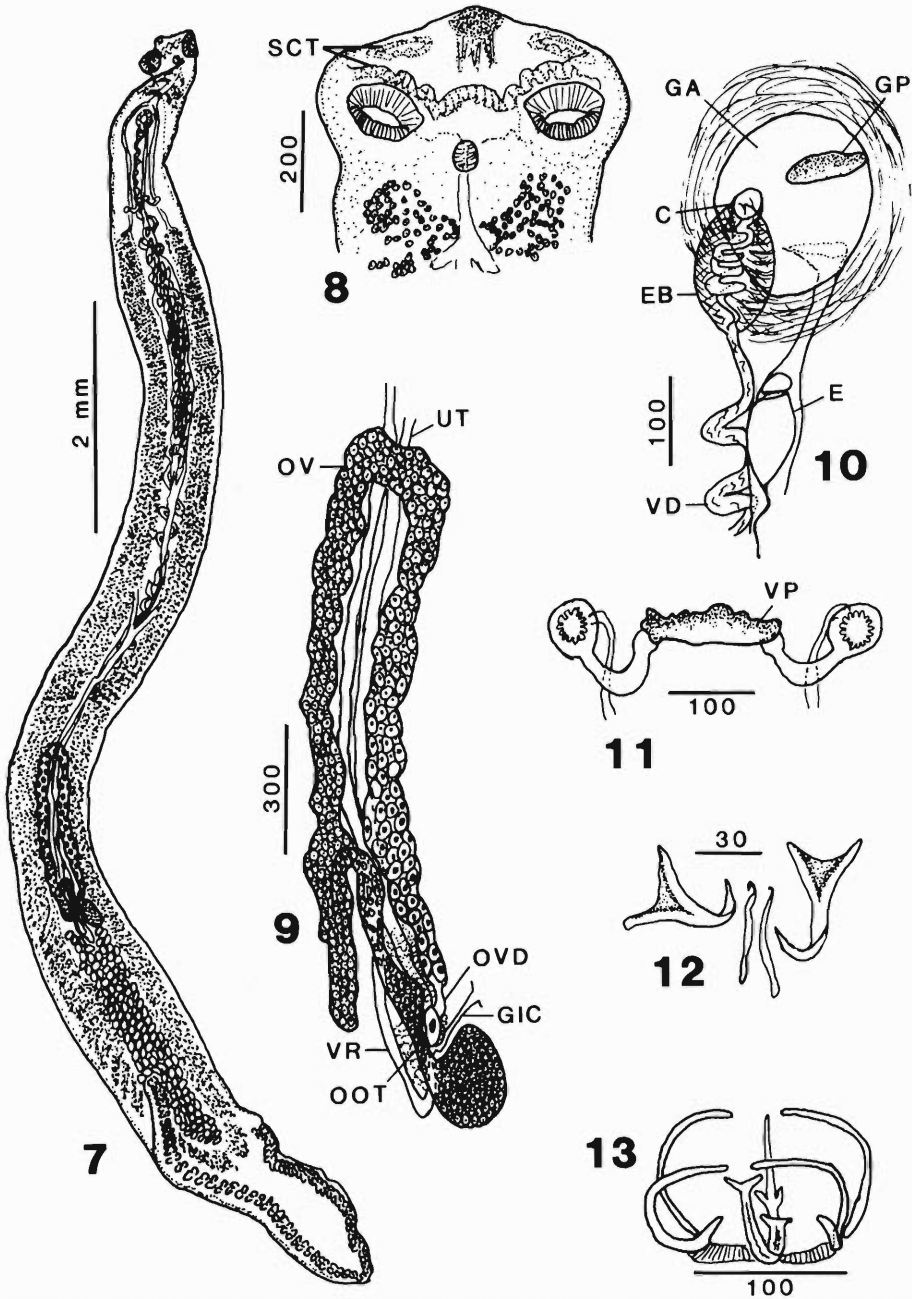
Figures 7–13. *Zeuxapta taylori* sp. n., all holotype and dorsal view unless otherwise stated. 7. Whole mount. 8. Anterior end, paratype. 9. Female reproductive system. 10. Genital atrium. 11. Vagina, paratype. 12. Marginal hooks and hamuli, paratype. 13. Entire clamp. Abbreviations: E, egg; EB, ejaculatory bulb; GP, genital atrium pore; SCT, sticky convoluted tegument; VD, vas deferens; VP, vaginal pore; other abbreviations as in Figures 1–6. Scales in micrometers.

tral. Ootype with Mehlis's cells in region between proximal and distal ends of ovary. Vitelline reservoir Y-shaped, slender, median; vitelline follicles small, coextensive with cecal diverticula, extending short distance into haptor. Uterus median, extending anteriorly, opening into genital atrium, distended with eggs in gravid specimens. Vagina dorsomedian, 1.405–1.954 (1.665) mm

from anterior end; pore transversely oval, opening laterally into paired spherical chambers lined with villi. Eggs elliptical, 117–129 (124) long by 55–62 (59) wide, with long fine filament at abopercular pole.

HOST: *Thunnus albacares* (Bonnaterre) (yellowfin tuna), Scombridae.

HABITAT: Gill lamellae.

LOCALITY: Pacific Ocean, southwest of San Diego, California (32°30′N, 117°30′W).

DEPTH: Less than 50 m.

PREVALENCE AND INTENSITY: On 1 of 6 fish examined (16.7%), 6 per host.

SPECIMENS DEPOSITED: Holotype: USNM Helm. Coll. No. 80950. Paratypes: USNM Helm. Coll. No. 80951, HWML No. 31158.

ETYMOLOGY: The specific name honors Mr. Arthur Taylor, owner-operator of the *M/V Searcher*.

REMARKS: *Zeuxapta taylori* most closely resembles *Z. kahala* (Yamaguti, 1968) Ogawa and Egusa, 1980 (=*Z. kahara* of Ogawa and Egusa, 1980) in size and shape of body, buccal suckers, clamps, ovary, eggs, and vagina; number of clamps; and distance of genital atrium from anterior end. It differs from *Z. kahala* in shape of cirrus and lack of cirrus bulb and by having a mouth with a conspicuous convoluted surface along the ventral margin, prebifurcal diverticula, a haptor with a sinistral long side, larger maximum clamp width (215 versus 180), and a host from a different family. Rohde (1981) studied the ultrastructure of the buccal organs of *Z. seriolae* (Meserve, 1938) Price, 1962 and described the convoluted surface as "sticky" tegument. Rohde (1978) synonymized *Z. japonica* Yamaguti, 1963 with *Z. seriolae* and discussed the distribution of the genus. The transfer of *Aspinatrium kahala* Yamaguti, 1968 to *Zeuxapta* by Ogawa and Egusa (1980) extended the distribution of the genus into the central tropical Pacific. The present study extends the distribution of the genus to the somewhat cooler waters of the California Current off the coast of southern California and northern Baja California, Mexico.

Allencotyla pricei
Kritsky, Noble, and Moser, 1978

DESCRIPTION (based on 14 specimens, 6 measured): With characters of the genus. Total length 4.25–7.817 (6.098) mm; maximum width 1.331–2.202 (1.646) mm at level of ovary. Buccal suckers 62–93 (82) wide, aseptate. Haptor 1.705–3.049 (2.595) mm long by 0.961–2.495 (1.973)

mm wide, asymmetrical. Clamps 44–57 (52) total; long side clamps 29–42 (36) in number, 81–136 (106) long by 78–155 (122) wide; short side clamps 15–17 (16) in number, 74–127 (99) long by 93–143 (122) wide.

Pharynx spherical; esophagus laterally diverticulate. Ceca with lateral and medial diverticula, not confluent posteriorly.

Testes subspherical to irregular, 74–127 (99) in number, intercecal. Genital atrium 87–99 (93) wide, armed with 7 or 8 bent spines and numerous straight spines.

Ovary question mark-shaped. Vagina 217–260 (239) wide, armed with numerous elongate spines 54–80 (70) long, and 2 large lateral spines 83–99 (93) long. Genitointestinal canal dextral.

HOSTS: *Embiotoca jacksoni* Agassiz (black perch), Embiotocidae, 15.7–18.0 cm S.L. (new host record); *Phanerodon atripes* (Jordan and Gilbert) (sharpnose seaperch), Embiotocidae, 18.1–20.4 cm S.L. (new host record); *Rhacochilus vacca* (Girard) (pile perch), Embiotocidae, 25.3–26.2 cm S.L.

HABITAT: Gill lamellae.

LOCALITIES: *E. jacksoni* from La Jolla, California (32°52′N, 117°15′W), and UCSB Beach, Goleta, California (34°27′N, 119°50′W); *P. atripes* from Morrow Bay, California (35°20′N, 120°51′W); *R. vacca* from Leadbetter Beach, Santa Barbara, California (34°25′N, 119°42′W).

DEPTH: Less than 10 m.

PREVALENCE AND INTENSITY: On 4 of 23 *E. jacksoni* examined (17.4%), 1–4 per host; on 1 of 2 *P. atripes* examined (50%), 1 per host; on 2 of 2 *R. vacca* examined (100%), 2 or 3 per host.

SPECIMENS DEPOSITED: USNM Helm. Coll. Nos. 80952, 80953; HWML Nos. 31150, 31152.

REMARKS: Kritsky et al. (1978) described *Allencotyla pricei* from the gills of *Damalichthys vacca* (now in *Rhacochilus*) from Redondo Beach, California. The 16 specimens studied in the present collection agree with the type series in general morphology. All measurement ranges overlapped, but those in the present study had lower averages: total length 6.098 versus 7.660 mm, buccal suckers 82 versus 93 wide, haptor length 2.595 versus 2.910 mm, haptor width 1.973 versus 2.230, dextral clamps 106 long by 122 wide versus 118 by 138, sinistral clamps 99 long by 122 wide versus 111 by 128, genital atrium width 93 versus 110, and vagina width 239 versus 296.

The geographic range of *A. pricei* is extended along the coast of southern California from Los Angeles County southward to San Diego County

and northward to Monterey County. The following species of embiotocids collected from the California coast were not found to be infected with *Allencotyla pricei*: 5 *Embiotica lateralis* Agassiz collected from near Pt. Arguello and San Francisco Bay, 3 *Phanerodon furcatus* Girard, and 5 *Rhacochilus toxotes* Agassiz collected from La Jolla, California.

Monaxininae Unnithan, 1957
Leuresthicola robersoni sp. n.
(Figs. 14-19)

DESCRIPTION (based on 3 specimens): With characters of the genus. Body broadly fusiform, anterior one-fourth narrow. Total length 2.817–3.931 (3.535) mm, maximum width 1.527–2.036 (1.718) mm at level ovary. Buccal suckers 42–46 (44) long by 48–55 (51) wide, paired, aseptate, subspherical. Haptor asymmetrical, 1.018–1.440 (1.192) mm long with single row of 25–31 (27) clamps. Clamps 44–59 (56) long by 62–70 (66) wide; median sclerite spring with prominent bifid terminations; slender accessory piece at dorsal termination median sclerite; dorsal jaw with 6 or 7 delicate tegumental bars.

Mouth subterminal. Pharynx subspherical 48–55 (51) long by 44–46 (45) wide. Esophagus with lateral diverticula; ceca with lateral and medial diverticula, confluent in haptor.

Testes 46–117 (73) long by 53–148 (100) wide, 20–25 (22) in number, intercecal. Vas deferens median, extending anteriorly. Prostatic vesicle absent. Cirrus unarmed. Genital atrium cup-shaped, 57–62 (59) long by 55–88 (76) wide, armed with 36 spines; 3 lateral spines on each side 23–27 (25) long, bottle- or club-shaped; remaining spines 9–15 (12) long, with terminal hook.

Ovary 1.440–1.632 (1.528) mm long, question mark-shaped, ends directed posteriorly. Seminal receptacle ovoid, 84–87 (86) long by 56–67 (63) wide, dextral between proximal and distal ends of ovary, genitointestinal canal dextral. Ootype median, between proximal portion of ovary and anteriormost testes, Mehlis's gland cells sinistral, extending anteriorly. Vitelline follicles coextensive with intestinal ceca, extending in 2 narrow bands to level of genital corona; vitelline reservoir Y-shaped. Uterus median. Eggs 203–289 (240) long by 91–133 (107) wide, filamented both poles; long filament on opercular pole; shorter filament with distal knob.

HOST: *Atherinops affinis* (Ayres) (topsmelt), Atherinidae, 14.2–19.5 cm S.L.

HABITAT: Gill lamellae.

LOCALITY: Scripps Institution of Oceanography, La Jolla, California (32°52'N, 117°15'W).

DEPTH: Less than 10 m.

PREVALENCE AND INTENSITY: On 2 of 8 fish examined (25%), 1 or 2 per host.

SPECIMENS DEPOSITED: Holotype: USNM Helm. Coll. No. 80954. Paratypes: USNM Helm. Coll. No. 80955, HWML No. 31157.

ETYMOLOGY: The specific name honors Mr. Wiley G. Roberson for his friendship and contribution to marine biology education in Los Angeles County.

REMARKS: *Leuresthicola robersoni* most closely resembles *L. olsoni* Price, 1962 (type and only other species in the genus) in shape of body, ovary, genital atrium, atrial spines, and testes, in location of seminal receptacle, and in distribution of vitellaria. It differs from *L. olsoni* by having fewer clamps (25–31 versus 37–41), smaller clamps (62–70 versus 90–100 wide), a median sclerite bearing accessory piece, fewer testes (20–25 versus 34–37), smaller atrial spines (9–15 versus "about 20" for smaller spines and 23–27 versus "about 30" for larger bottle-shaped spines), and a different host genus.

The genus *Leuresthicola* has been reported only from the waters of the eastern Pacific Ocean off San Diego and La Jolla, California (Price, 1962b; Bravo-Hollis, 1978).

Cynoscionicolinae Bravo-Hollis, 1981
Cynoscionicola powersi sp. n.
(Figs. 20-27)

DESCRIPTION (based on 27 specimens, 10 measured): With characters of the genus. Body elongate, 3.214–4.875 (4.438) mm long by 282–647 (490) wide immediately anterior to haptor. Buccal suckers ovoid, 35–53 (46) long by 42–86 (61) wide, septate. Haptor gradually narrows posteriorly, somewhat asymmetrical with 2 rows of clamps; long side dextral, 1.566–2.932 (2.302) mm long with 60–89 (74) clamps; short side sinistral, 1.308–2.371 (1.701) mm long with 45–66 (56) clamps. Clamps of *Microcotyle* type; sclerites thin; lateral sclerites of dorsal jaw covered with thin layer of muscles distally; median spring sclerite with straight delicate accessory piece. Dextral clamps: anteriormost clamp 20–41 (34) long by 29–68 (47) wide; largest clamp
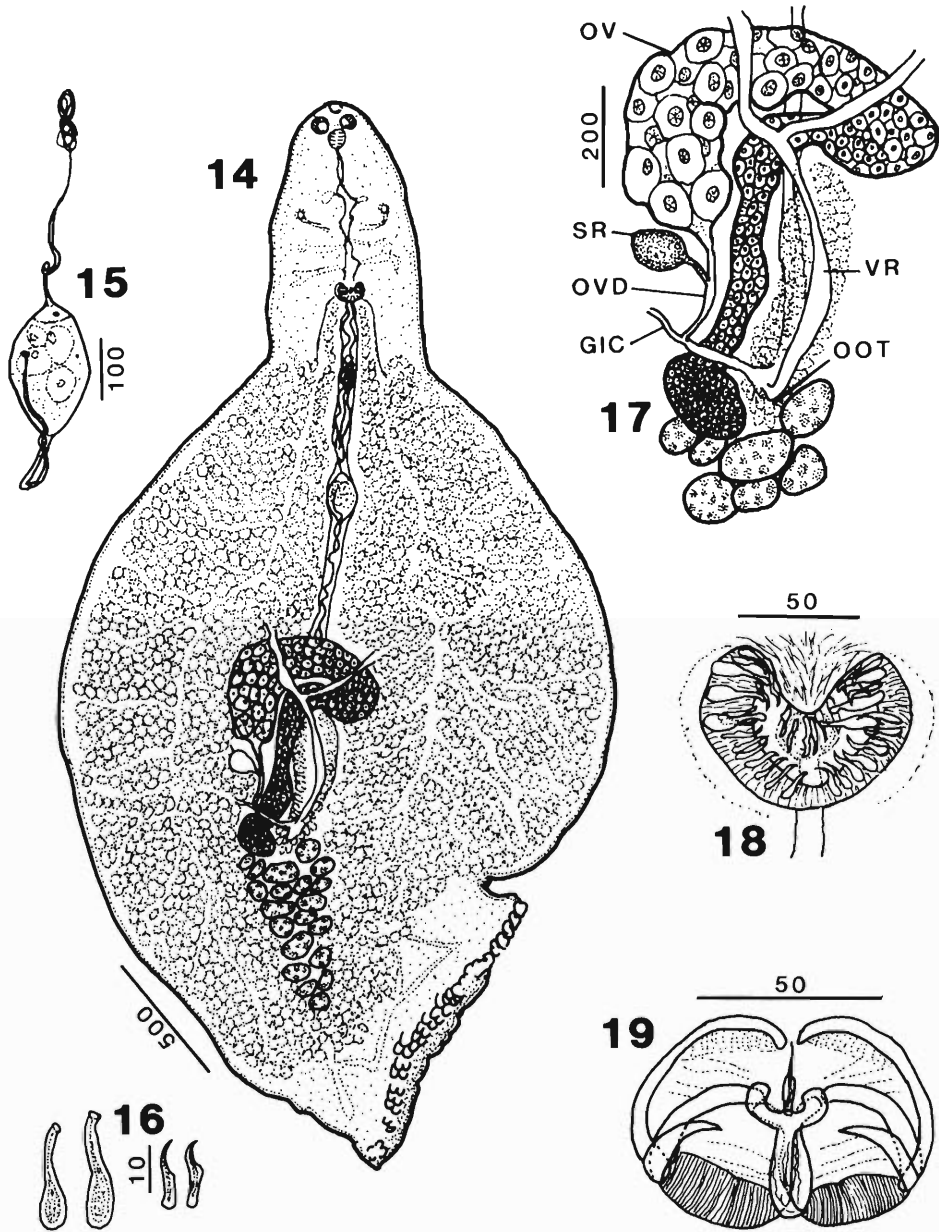
Figures 14–19. *Leuresthicola robersoni* sp. n., all holotyope and ventral view. 14. Whole mount. 15. Egg. 16. Genital atrium spines. 17. Female reproductive system. 18. Genital atrium. 19. Entire clamp. Abbreviations: SR, seminal receptacle; other abbreviations as in Figures 1–13. Scales in micrometers.

33–48 (39) long by 59–81 (74) wide; terminal clamp 29–37 (31) long by 46–51 (48) wide. Sinistral clamps: anteriormost clamp 20–55 (32) long by 33–70 (45) wide; largest clamp 33–51 (42) long by 55–86 (73) wide; terminal clamp

26–31 (29) long by 40–50 (45) wide. Larval marginal hooks not observed.

Mouth subterminal. Pharynx 62–84 (76) long by 48–68 (58) wide, anterior one-third constricted. Esophagus 198–253 (222) long, simple, bi-
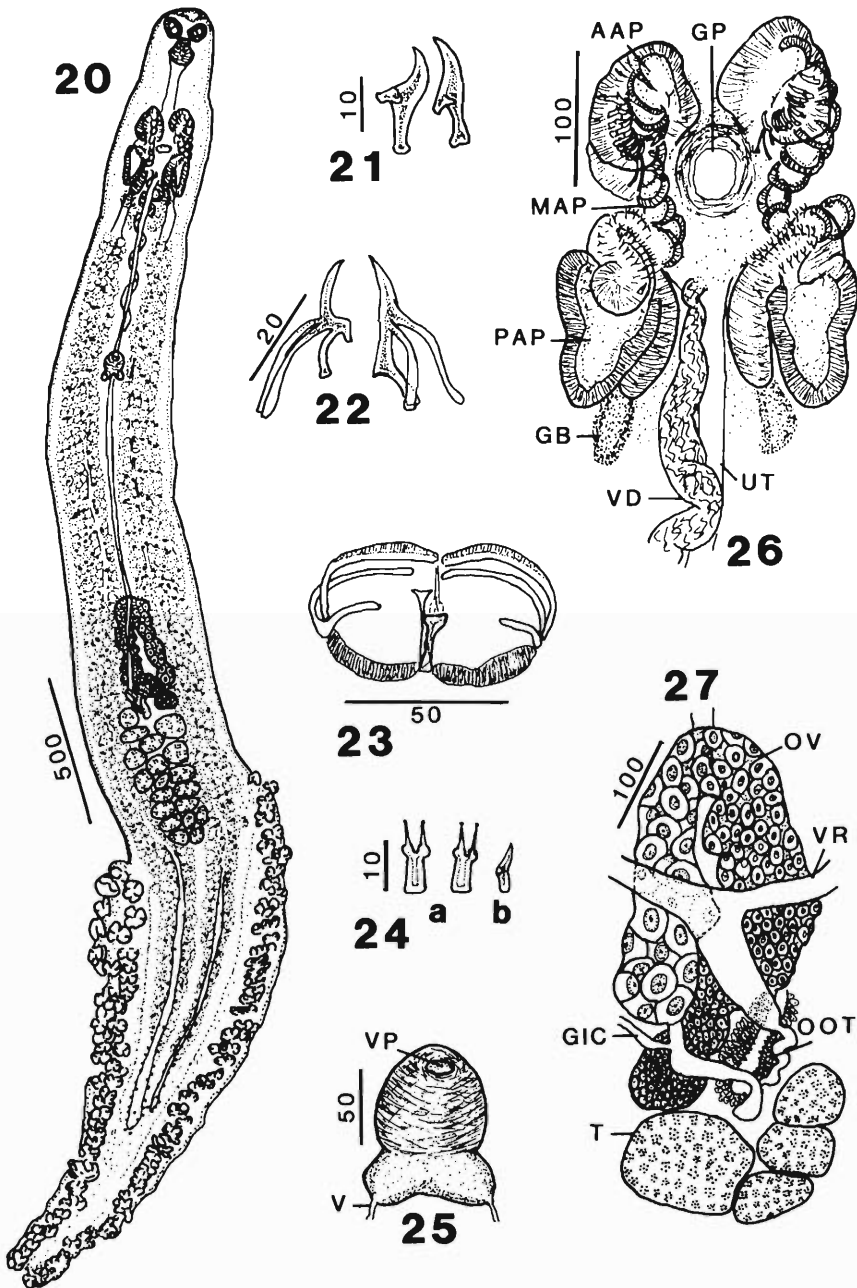
Figures 20–27. *Cynoscionicola powersi* sp. n., all holotype and dorsal view unless otherwise stated. 20. Whole mount. 21. Anterolateral atrial pouch spines. 22. Anterolateral atrial pouch trirooted spines, paratypes. 23. Entire clamp. 24a. Posterolateral atrial pouch bifid spine, paratype. 24b. Posterolateral atrial pouch simple spine, paratype. 25. Vagina. 26. Genital atrium complex. 27. Female reproductive system, ventral view. Abbreviations: AAP, anterolateral atrium pouch; GB, glandular base; MAP, middle atrium pouches; PAP, posterolateral atrium pouch; T, testis; V, vagina; other abbreviations as in Figures 1–13. Scales in micrometers.

furcating at level of genital atrium. Ceca with small lateral and medial diverticula, extending as simple ceca deep into haptor, unequal in length, not confluent.

Testes 9–22 (17) in number; rounded to ovoid, largest 33–139 (82) long by 68–222 (112) wide. Vas deferens extending sinuously along median line. Cirrus absent. Genital atrium complex, ventral to cecal bifurcation. Anterolateral pouches 81–110 (94) long by 57–77 (69) wide, muscular, somewhat reniform; aperture armed with 8–14 (10) curved, rooted spines 15–22 (19) long; 1 or 2 large, trirooted spines 26–38 (30) long of variable shape and sometimes fused; 1 or 2 small stout spines 7–9 (8) long. Posterolateral pouches 117–139 (125) long by 70–106 (87) wide, somewhat cordate; thickened muscular aperture armed with 17–24 (22) bifid spines; 1 or 2 simple spines 9–13 (10) long; median muscular part extending posteriorly, terminating in glandular base. On each side anterolateral and posterolateral pouches connected by series of 11–17 (14) small spherical unarmed pouches. Genital pore 308–409 (367) from anterior end.

Ovary 717–838 (760) long by 59–117 (89) wide, pretesticular, U-shaped; proximal end dextral, crossing diagonally to sinistral, extending anteriorly some distance, recrossing median line, descending to just anterior to proximal end. Ootype somewhat sinistral, 88–137 (112) long by 18–27 (21) wide; surrounded by numerous Mehlis's cells. Vitellaria follicular, coextensive with cecal diverticula. Vitelline reservoir Y-shaped, 215–220 (218) long by 35–47 (42) wide. Vaginal pore dorsomedial, 0.912–1.162 (1.016) mm from anterior end; vaginal chamber muscular, 88–97 (91) long by 57–88 (77) wide, with 2 posterolateral chambers; vaginae paired, thin, difficult to follow. Eggs 110–130 (117) long by 44–73 (60) wide, with single long filament at abopercular pole.

HOSTS: *Seriphus politus* Ayres (queenfish), Sciaenidae, 13.5–16.4 cm S.L. (type host); *Menticirrhus undulatus* (Girard) (California corbina), Sciaenidae; 35.2–46.3 cm S.L.; *Umbrina roncador* Jordan and Gilbert (yellowfin croaker), Sciaenidae, 14.2–27.2 cm S.L.

HABITAT: Gill lamellae.

LOCALITY: Scripps Institution of Oceanography, La Jolla, California (32°52′N, 117°15′W).

DEPTH: Less than 10 m.

PREVALENCE AND INTENSITY: On 7 of 16 *S. politus* examined (43.8%), 1–7 per host; on 2 of 8 *M. undulatus* examined (25%), 1–5 per host; on 1 of 2 *U. roncador* examined (50%), 1 per host.

SPECIMENS DEPOSITED: Holotype: USNM Helm. Coll. No. 80956. Paratypes: USNM Helm. Coll. Nos. 80957–80959, HWML Nos. 31153–31156.

ETYMOLOGY: The specific name honors Dr. Donald R. Powers, Biology Department, George Fox College, Newberg, Oregon, for his friendship and contributions to the biology program of Biola University.

REMARKS: *Cynoscionicola powersi* most closely resembles *C. srivastavai* Bravo-Hollis and Caballero-Rodriguez, 1970 in general morphology of genital atrium, ovary, clamps, and bifid atrial spines, in number of testes, and in size of clamps. It differs from *C. srivastavai* by having wider buccal suckers (42–86 versus 34–36), a haptor that narrows gradually rather than having anterior wide and posterior constricted to form an appendagelike portion, ceca not confluent, large trirooted spines in anterolateral atrial pouches, more numerous middle atrial pouches (11–17 versus 4–8), 1 or 2 simple spines in posterolateral atrial pouch, and hosts of different species.

Price (1962b) established Heteraxinidae for species in the family Microcotylidae Taschenberg, 1879 having asymmetrical haptors and ovaries with both ends directed posteriorly. Kritsky et al. (1978) discussed and accepted the validity of Heteraxinidae. Price (1962b) placed *Microcotyle heteracantha* Manter, 1938 and *M. pseudheteracantha* Hargis, 1957 in *Cynoscionicola* (Heteraxinidae, Gonoplasiinae) and diagnosed the genus as having a genital atrium with 2 multiloculate armed anterior pockets and 2 posterior lateral muscular pouches armed with bident or trident spines. Lambert and Euzet (1979) described *C. similis* and *C. jamaicensis* and, in their review of the genus, placed *Cynoscionicola* in Microcotylidae, Microcotylinae on the basis of clamp anatomy alone. Bravo-Hollis (1982) added new hosts and localities for *C. sciaeniae* Tantalean, 1974 and *C. srivastavai*; retaining the genus in Heteraxinidae, she established the subfamily Cynoscionicolinae. Mamaev (1986) supressed Cynoscionicolinae in his revision of Microcotylidae and placed *Cynoscionicola* in Anchoromicrocotylinae Bravo-Hollis, 1981 with *Anchoromicrocotyle guaymensis* Bravo-Hollis, 1981 by emending the subfamily diagnosis to include the complex genital atrium

and "subsymmetrical haptor." However, *Anchoromicrocotyle* has a symmetrical haptor, large larval protohaptoral anchors, and an unarmed genital atrium completely different from *Cynoscionicola* (see Bravo-Hollis, 1981). An asymmetrical haptor and an ovary with both ends directed posteriorly are characters that justify Heteraxinidae. Because *Cynoscionicola* lacks a symmetrical haptor with large larval anchors and has an armed complex genital atrium, it is returned to Cynoscionicolinae (Heteraxinidae).

The geographic distribution of *Cynoscionicola* extends from Massachusetts to Florida, to the Gulf of Mexico, and to Guyana in the western Atlantic Ocean and from Peru to Mexico and the Gulf of California to southern California in the eastern Pacific Ocean.

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MEETING SCHEDULE
HELMINTHOLOGICAL SOCIETY OF WASHINGTON
1990–1991

(Wed) 10 Oct 1990	"Student Competition," Uniformed Services University of the Health Sciences, Bethesda, MD
(Wed) 14 Nov 1990	"Recent Advances in Protozoan Diseases in Domestic Animals," Parasitology Unit, U.S. Department of Agriculture, Beltsville, MD
(Wed) 5 Dec 1990	"To Be Announced," Plant Protection Institute, U.S. Department of Agriculture, Beltsville, MD
(Wed) 9 Jan 1991	"To Be Announced," Laboratory of Parasitic Diseases, National Institutes of Health, Bethesda, MD
(Wed) 13 Feb 1991	"New Developments in Malaria Research," Department of Immunoparasitology, U.S. Naval Medical Research Institute, Bethesda, MD
(Wed) 13 Mar 1991	"Chemotherapy of Parasitic Diseases," Division of Experimental Therapeutics, Walter Reed Army Institute of Research, Washington, DC
(Wed) 10 Apr 1991	"To Be Announced," School of Hygiene and Public Health, The Johns Hopkins University; and Medical College, University of Maryland, Baltimore, MD
(Sat) 4 May 1991	"To Be Announced," Department of Pathobiology, Veterinary School, University of Pennsylvania, New Bolton, PA; Royal Society of Tropical Medicine and Hygiene; and New Jersey Society for Parasitology

Establishment, Survival, and Fecundity in *Echinostoma caproni* (Trematoda) Infections in Hamsters and Jirds

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ABSTRACT: The population regulation (establishment, survival, and fecundity) was studied in *Echinostoma caproni* infections in hamsters and jirds. The *E. caproni*/hamster model had a high level of compatibility, using the criterion of initial worm establishment. The *E. caproni*/hamster model, using infections within the range of 6–50 metacercariae per hamster, was also characterized by metacercarial infectivity that was infection–dose independent, a limited capacity to expel primary infections and to mount a regulatory response to superimposed challenge worm establishment, and a reproductive potential that was negatively infection–dose dependent, using the criterion of number of eggs in the uterus of the worm. In contrast, the *E. caproni*/jird model exhibited a low level of compatibility, with a generally low and variable primary worm establishment, a limited capacity to expel primary infections, and a marked capacity to mount an effective regulatory response to both superimposed and secondary challenge infections.

KEY WORDS: Trematoda, *Echinostoma caproni*, hamster, jird, population regulation, establishment, survival, fecundity, primary infection, challenge infection, host-specific components, reproductive success.

Reproductive rate is a central issue in describing the population dynamics of parasites. Any realistic approach to analyzing this rate for helminth species with a broad spectrum of definitive hosts must take into account the host-specific component of reproductive success (Whitfield et al., 1986). The reproductive capability in the helminth–definitive host relationship is governed in part by the natural and acquired regulatory responses of the host to the parasite infection. These responses are commonly host specific and may influence essential parameters like initial worm establishment, survival, and fecundity.

The mouse possesses the capacity to mount a marked acquired regulatory response to primary and challenge *Echinostoma caproni* Richard, 1964 infection (Christensen et al., 1988; Odaibo et al., 1988, 1989). In contrast, findings by Franco et al. (1986) and Mabus et al. (1988) indicate that the ability of the hamster (*Mesocricetus auratus*) to mount an effective regulatory response to *Echinostoma* infection is quite limited. Preliminary observations in our laboratory have shown that the jird (*Meriones unguiculatus*) has low susceptibility to infection with *E. caproni*. Taken together, these findings indicate that the *E. caproni*/rodent (mouse, hamster, jird) system might be useful as a model for elucidating definitive host-specific components of the reproductive capacity of intestinal helminths.

Our study supplements available information on the regulatory response to *E. caproni* infection in NMRI mice (Odaibo et al., 1988, 1989) and provides quantitative information concerning the regulatory response in hamsters and jirds to *E. caproni* infection. The species terminology used is that introduced by Kanev (1985) (see also Christensen et al., 1988).

Materials and Methods

Four-mo-old outbred female hamsters (State Serum Institute, Copenhagen, Denmark) weighing 80–100 g and 4–6-mo-old jirds weighing 60–80 g were used in this study. Metacercariae of *E. caproni* (Egyptian strain) were obtained from *Biomphalaria glabrata* as described by Christensen et al. (1980). Rodents were infected with metacercariae via a stomach tube. Recovery of worms was conducted according to the procedure described by Christensen et al. (1986). To determine worm localization in hamster experiments, the small intestine was divided into 5 equal sections, starting from the pylorus. The number of eggs in the uterus of 10 worms from each group at each observation point was determined by dissection. The time pattern of worm expulsion was determined by recovery of worms or by weekly examination of feces for eggs, using the direct smear technique.

The statistical tests used for analyzing worm survival and challenge worm establishment were the Wilcoxon rank sum test and the Kruskall–Wallis analysis of variance of ranks. Student's *t*-test and an analysis of variance were used to analyze difference in means of uterine egg counts. This study was divided into two series of experiments.

Series 1 comprised experiments on the pattern of expulsion of primary nonchallenged infections. Groups of hamsters were inoculated with 6, 25, or 50 metacercariae per hamster, and a group of jirds was inoculated with 25 metacercariae per animal. At regular intervals following hamster infections, number of worms, uterine egg counts, and worm localization were recorded. In jird experiments, only worm numbers were recorded. Three to 6 animals were used at each recording. Series 2 comprised a study on resistance to

challenge infection in hamsters and jirds. Hamsters harboring 3-, 5-, and 12-wk-old primary infections with 6, 20, or 25 metacercariae per hamster and previously noninfected hamsters were given a challenge infection. Necropsy took place day 8 postchallenge. Jirds harboring 3-wk-old infections with 25 metacercariae per animal, jirds having expelled primary 8-wk-old infections with 6 metacercariae 2–3 wk earlier, and previously noninfected jirds were also given a challenge infection. Necropsy took place day 10 postchallenge. Within each experiment, the challenge control group was necropsied the same day as the challenged group(s). In animals given a challenge infection, worms from the primary and challenge infections were distinguished based on worm size. The percentage resistance was calculated using the following formula:

$$100 - \left(\frac{\text{mean number of worms of the challenge infection}}{\text{mean number of worms of the control group}} \times 100 \right).$$

Results

Initial worm establishment in hamsters, expressed as mean percentage worm recovery for up to week 2 postinfection, was infection–dose independent ($P > 0.05$) in infections with 6 and 25 metacercariae per hamster (63.2 and 71.2%, respectively). The variance/mean ratio of 1.3 and 2.0, respectively, in infections with 6 and 25 metacercariae per hamster revealed an only limited heterogeneity in response to primary *E. caproni* infection in the hamster. The mean percentage worm recovery of 64% at week 4 following infection with 50 metacercariae per hamster was comparable ($P > 0.05$) with the initial worm establishment in infections with 6 and 25 metacercariae per hamster. Thus, primary *E. caproni* percentage worm establishment in hamsters is infection–dose independent in the infection range of 6–50 metacercariae per hamster (Fig. 1).

The mean percentage worm recovery in infections with 6 and 25 metacercariae per hamster remained stable ($P > 0.05$) throughout the 11–13 wk observation period (Fig. 1). In infections with 50 metacercariae per hamster, worm recovery remained at the stable mean level of 30–35 worms per hamster for up to week 9. The apparent reduction in worm recovery week 11 was not statistically significant (Fig. 1). Thus, the ability of the hamster to expel primary infections with *E. caproni* for up to 13 weeks postinfection was very limited.

Number of eggs in the uterus of worms was negatively infection–dose dependent (Fig. 1). From week 4 postinfection and onwards, uterine
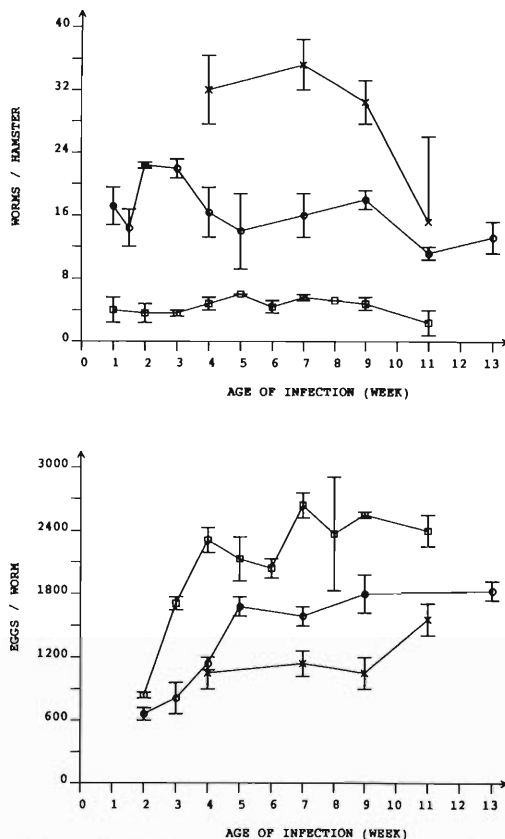
Figure 1. *Echinostoma caproni* worm recovery ($\bar{x} \pm$ SE) and number of eggs in uterus ($\bar{x} \pm$ SE) at increasing age (weeks) in infections with 6 (□), 25 (○), and 50 (×) metacercariae in hamsters.

egg counts per worm from infections with 6 metacercariae per hamster exceeded those from infections with 25 and 50 metacercariae per hamster, and uterine egg counts in infections with 25 metacercariae per hamster generally exceeded those from infections with 50 metacercariae per hamster from week 5 following infection and onwards (Fig. 1). At most observations, the differences remained statistically significant. Thus, using the criterion of uterine egg counts, the reproductive capacity per worm was negatively infection–dose dependent.

In infections with 6 metacercariae per hamster, worms were recovered only from sections 4 and 5, i.e., in the last ⅖ of the small intestine. In infections with 25 metacercariae per hamster, worms were occasionally found in section 3, especially from week 4 postinfection and onwards. In infections with 50 metacercariae per hamster, however, worms were constantly recovered from

Table 1. Resistance to secondary and superimposed *Echinostoma caproni* infections in jirds and hamsters.

Experiment no.	Experimental host	No. of animals	Age of primary infection at challenge (wk)	No. of metacercariae administered (primary/challenge)	*E. caproni* recovery ($\bar{x} \pm$ SD, range) Primary	*E. caproni* recovery ($\bar{x} \pm$ SD, range) Challenge	% resistance when significant ($P < 0.05$)
1	jird	5	3	25/10	8.8 ± 5.5 (3–15)	0.6 ± 1.3 (0–3)	87.2
		6	—	—/10	—	4.7 ± 2.3 (0–6)	
2	jird	5	8	6/25	expelled 2–3 wk prior to challenge	0	100
		8	—	—/25	—	5.8 ± 6.0 (0–17)	
3	hamster	4	5	20/10	10.0 ± 1.8 (8–12)	5.0 ± 1.4 (3–6)	
		3	3	20/10	12.0 ± 5.6 (6–15)	5.3 ± 3.2 (3–9)	
		3	—	—/10	—	6.0 ± 1.7 (4–7)	
4	hamster	6	12	6/25	3.8 ± 1.5 (1–5)	18.2 ± 5.1 (13–25)	
		7	12	25/25	11.4 ± 2.2 (8–14)	11.9 ± 5.1 (5–21)	41.4
		8	—	—/25	—	20.3 ± 6.2 (9–25)	

all sections except section 1. Increasing worm burdens thus result in involvement of the more anterior parts of the small intestine.

The jird exhibited a variable and overall low susceptibility to primary *E. caproni* infection. Thus, the worm establishment ($\bar{x} \pm$ SD) week 1 following infection with 25 metacercariae was 5.8 ± 6.0 (23.2%; range, 0–17 worms/jird; variance/mean ratio = 6.2). Worm establishment at week 2 and week 8 was 7.6 ± 7.1 and 5.3 ± 5.7, respectively. Although the variance/mean ratio remained high throughout the 8-wk period of observation, the mean percentage worm recovery remained stable ($P > 0.05$). Thus, if allowed to become established, worms from infections with 25 metacercariae per jird persisted for a period of at least 8 wk. However, low level infections in jirds with 6 metacercariae per jird may be expelled 5–6 wk following infection (Table 1; Experiment 2, Series 2).

Results from studies on resistance to challenge *E. caproni* infection are presented in Table 1. There was marked resistance (87.2%) to superimposed infection at challenge of jirds harboring 3-wk-old infections with 3–15 worms per animal ($\bar{x} = 8.8$). Complete (100%) resistance to secondary infection was observed at challenge 2–3 wk following expulsion of a primary infection with 6 metacercariae given 8 wk earlier (Table 1). In the hamster, the challenge worm and challenge control worm recovery remained comparable at challenge weeks 3 and 5 following establishment of primary infections with 8–12 or 6–15 worms/hamster ($\bar{x} = 10$ and 12, respectively) and also at challenge week 12 for hamsters

harboring primary infections with 1–5 worms ($\bar{x} = 3.8$) (Table 1). At challenge week 12 for hamsters harboring primary infections of 8–14 worms per hamster ($\bar{x} = 11.4$), there was a significant ($P < 0.05$) reduction in challenge worm recovery of 41.4%.

Discussion

Increased attention has recently been paid to the *Echinostoma*/hamster model in studies on the intestinal trematode/definitive host relationship. Fried et al. (1988) reported on the reproductive behavior in single- and 5-worm infections of *E. trivolvis*. Aspects of the infectivity, growth, and development of *E. trivolvis* were described by Franco et al. (1986, 1988), and Huffman et al. (1988) reported on some aspects of the heterologous interactions arising in concurrent infections with *E. trivolvis* and *E. caproni* in the hamster. Clinical and pathological effects and humoral and cellular responses in infections with *E. trivolvis* in the hamster were reported by Huffman et al. (1986) and Mabus et al. (1988), respectively. The present study extends earlier findings by providing information on the regulatory response of the hamster and the jird to primary and challenge *E. caproni* infections. Available information concerning the regulatory response of the mouse to *Echinostoma* infections has recently been reviewed by Christensen et al. (1988).

The results from the present study show a high level of compatibility in the *E. caproni*/hamster model, using the criterion of initial worm establishment. The *E. caproni*/hamster model is also

characterized by a primary worm establishment percentage that is infection–dose independent, a limited capability to expel primary infections and to mount a regulatory response to superimposed challenge infections, and a reproductive potential that is negatively infection–dose dependent, as judged using the criterion of uterine egg counts. Overall, the general findings from the present study on the *E. caproni*/hamster model agree with those from previous studies on the *E. trivolvis*/hamster model (Franco et al., 1986, 1988; Huffman et al., 1988; Mabus et al., 1988). In contrast to the *E. caproni*/hamster model, the *E. caproni*/jird model exhibited a low level of compatibility with a variable and overall low primary worm establishment, but with a marked capacity to mount an effective regulatory response to both superimposed and secondary challenge infections. A comparison of the regulatory response of the hamster and jird to *E. caproni* infection with that of mice (data from Christensen et al., 1988; Odaibo et al., 1988, 1989) reveals some interesting differences. Thus, the mouse and hamster may, in contrast to the jird, be categorized as highly susceptible to primary *E. caproni* establishment, and species-specific differences in expulsion capacity and in challenge worm establishment also exist. The differential response of the mouse, jird, and hamster to infection with *E. caproni* makes the *E. caproni*/rodent system highly suitable as a model for elucidating quantitative aspects of definitive host-specific components of the reproductive success of intestinal trematodes.

Acknowledgments

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Clistobothrium carcharodoni gen. et sp. n. (Cestoda: Tetraphyllidea) from the Spiral Valve of the Great White Shark (*Carcharodon carcharias*)

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ABSTRACT: *Clistobothrium carcharodoni* gen. et sp. n. from the spiral valve of the great white shark *Carcharodon carcharias* is described. *Clistobothrium* gen. n. differs from its most similar genus *Carpobothrium* in lacking 2 opposing flaps with minute marginal loculi covering each bothridium and possessing 4 large bothridia on extendable bothridial stalks and a single retractable lappet over each sucker.

KEY WORDS: Cestoda, *Clistobothrium carcharodoni* sp. n., Phyllobothriidae, *Clistobothrium* gen. n., great white shark, *Carcharodon carcharias*, southern California.

On 30 August 1982, a large (4.9 m, 1.417 kg) female great white shark, *Carcharodon carcharias* (Linnaeus, 1758), was caught in a gill net set at 6 m, 5 km off Pt. Dume, Los Angeles County, California. The shark was brought to the Pioneer Fish Co., San Pedro, California, where the stomach and spiral valve were removed for study. The stomach contained 1 entire partially digested northern elephant seal. The spiral valve contained a tetraphyllidean cestode that is new to science and is described in this paper.

Materials and Methods

The living worms were fixed in hot (60°C) alcohol–formalin–acetic acid for 24 hr and stored in 70% ethanol. Whole mounts were stained in Semichon's acetocarmine and celestine blue B, dehydrated in a graded ethanol series, cleared in methyl salicylate, and mounted in permount. Specimens for SEM were critical point dried using CO_2 as the transition fluid in a Polaron critical point dryer and mounted on specimen stubs using conductive graphite paint (TV tube coat). Specimens were coated for 10 min at 10 mA with gold–palladium in a Technics Hummer V sputter coater and examined with a Cambridge Steroscan 150 at 8–20 kV. All measurements are in micrometers unless otherwise indicated and are given as the mean with ranges in parentheses. Illustrations were made with the aid of a drawing tube.

Clistobothrium carcharodoni gen. et sp. n.
(Figs. 1–6)

Clistobothrium carcharodoni gen. et sp. n. Phyllobothriidae Braun, 1900. The following description is based on 10 specimens.

SPECIFIC DIAGNOSIS: Medium-sized, acraspedote, anapolytic worms measuring 33 mm (24–40) in length. Strobila composed of 79 (73–85) segments. Neck short, 436 (374–494) in length, with anterior segments wider 797 (681–915) than

long 369 (348–390). Mature segments (65–69) longer than wide, to 982 (563–1,504) long by 737 (640–873) wide. In gravid worms, terminal proglottids approximately 2.5 times longer than wide, 1,851 (1,426–2,765) long by 790 (679–912) wide. Scolex 819 (736–1,260) long by 667 (605–901) wide, with 4 suckers ringed by a folded lappet or hood on retractable stalks separated by a cruciform-shaped apex. Sucker diameter 438 (417–461) long by 371 (333–398) wide. Testes spherical to oblong, 107 (91–123) in number; antiporal, 59 (43–69) with approximately equal numbers occurring pre- 20 (15–24) and postporally 26 (24–30), measuring 53 (32–67) long by 33 (24–59) wide. Vas deferens forming small mass of coils in mature proglottid. Cirrus sac large, extending to midsegment, 421 (364–489) long by 182 (161–208) wide. Cirrus armed with minute spines distally. Genital pores lateral, irregularly alternating, slightly anterior to middle of segment. Ovary posterior, bilobed in cross-section with each lobe shaped as an extended wing when viewed either dorsally or ventrally. Vitellaria large, follicular, in lateral bands. Vitellaria extend behind the ovary in gravid but not in mature segments. Eggs round to oblong, mammilated, 286 long by 260 wide.

HOST: Great white shark, *Carcharodon carcharias*.

LOCATION: Spiral valve.

LOCALITY: Off Pt. Dume, Los Angeles County, California, 33°55′N, 118°48′W.

HOLOTYPE: USNM Helm. Coll. No. 80985.

PARATYPES: USNM Helm. Coll. No. 80985, Univ. Neb. State Mus. HWML No. 31397.

ETYMOLOGY: Clisto (Gr.) = closed; bothrios (Gr.) = pit.
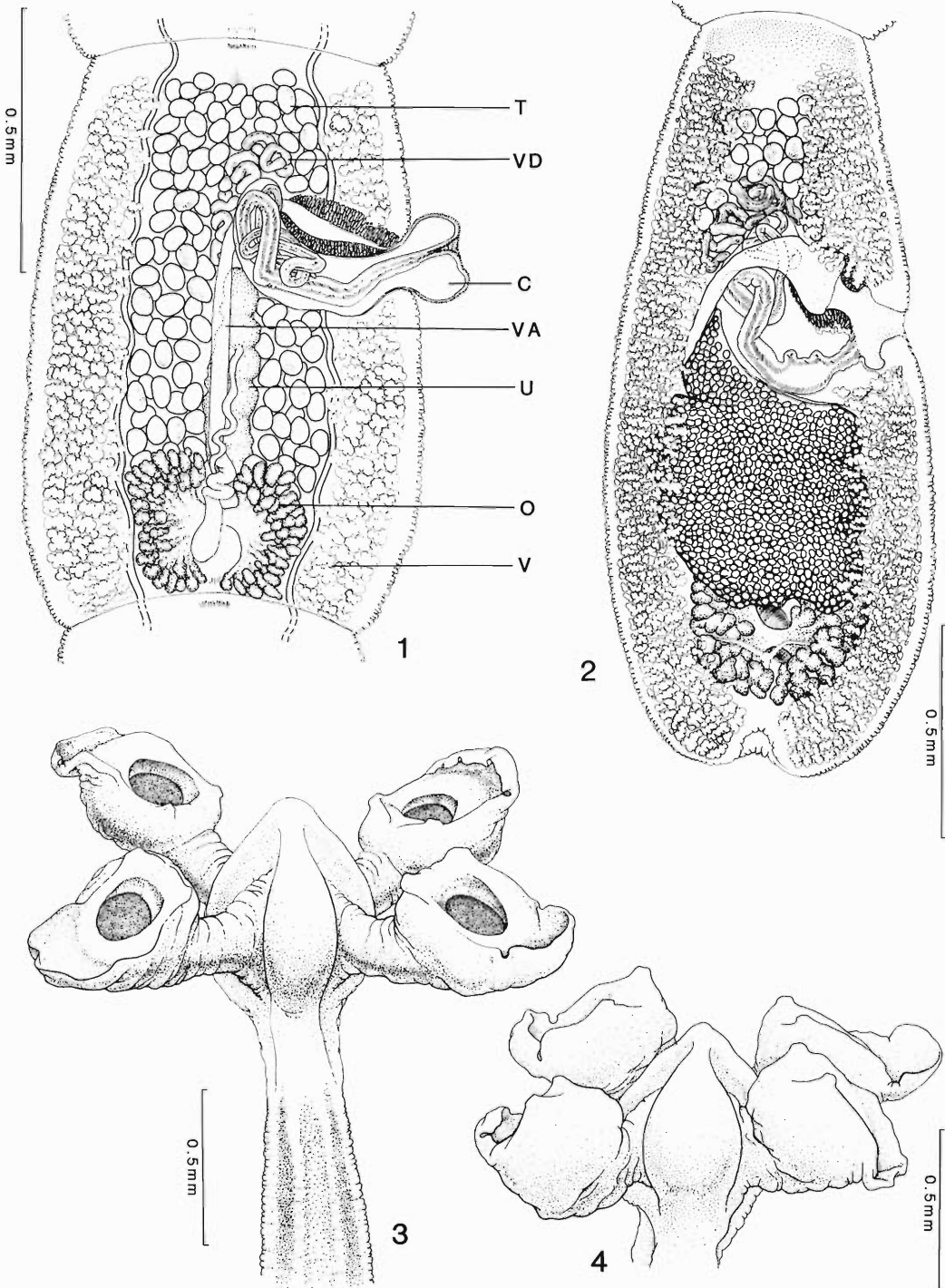
Figures 1–4. *Clistobothrium carcharodoni* gen. et sp. n. 1. Mature segment. 2. Terminal segment with gravid uterus. 3. Scolex with bothridial stalks extended. 4. Scolex contracted. Abbreviations: C, cirrus; O, *ovary*; T, testis; U, uterus; V, vitellarium; VA, vagina; VD, vas deferens.
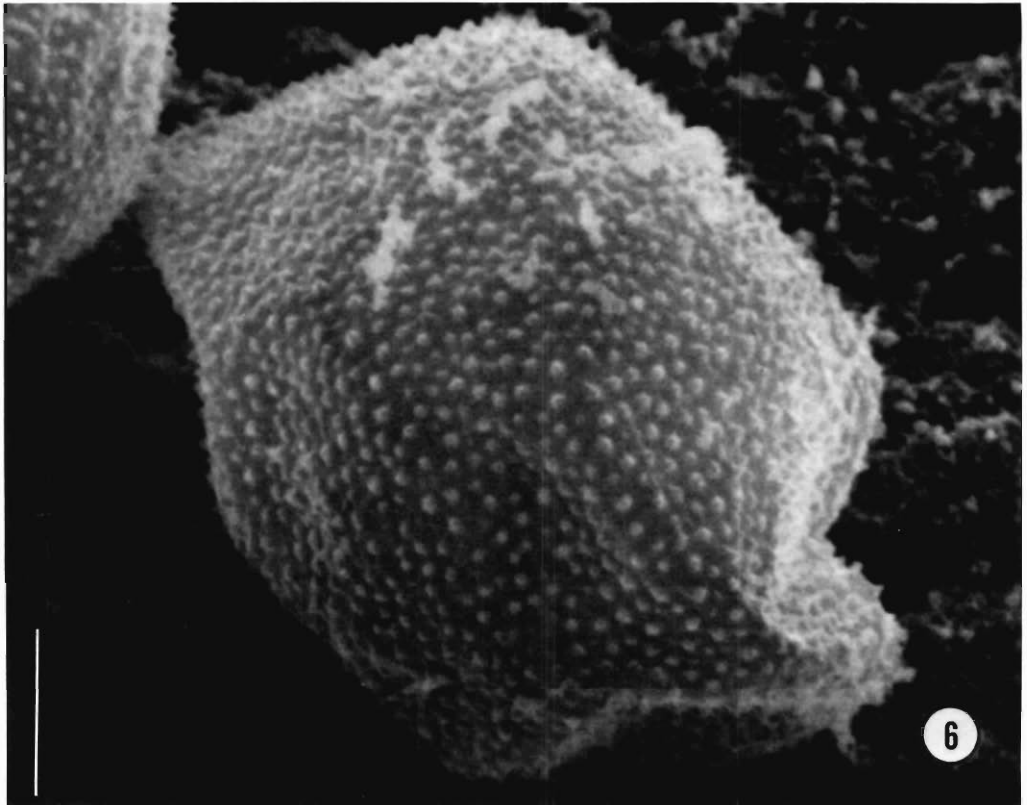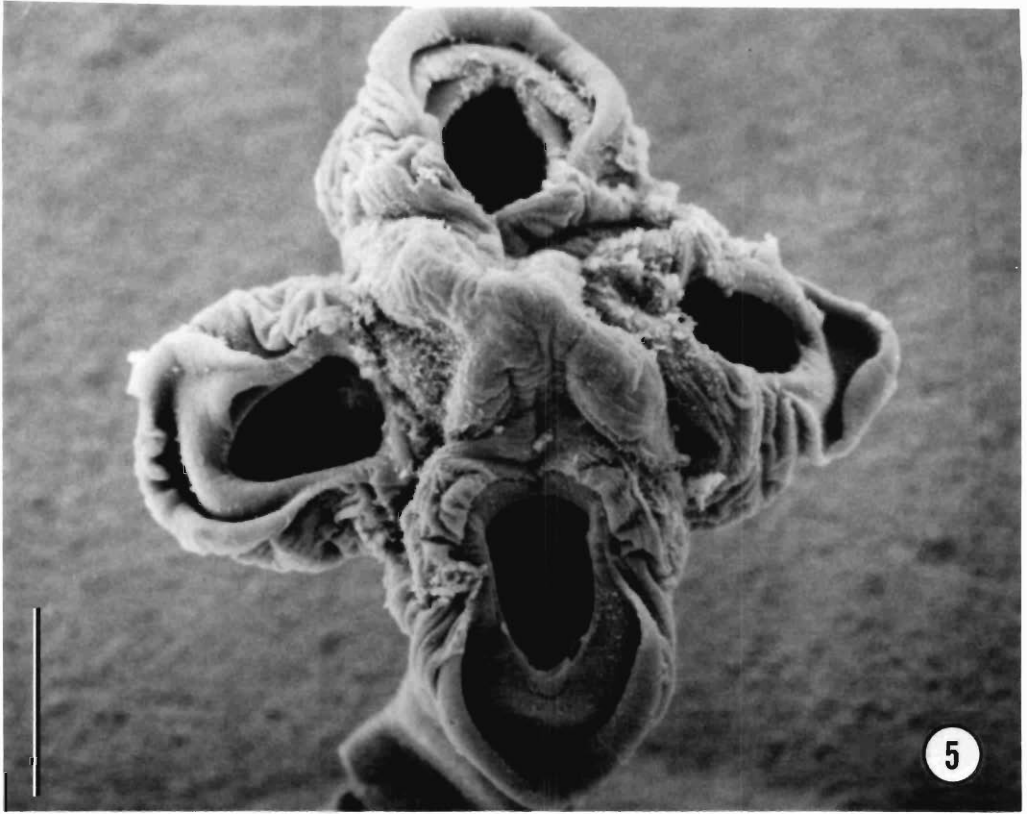
Figures 5, 6. 5. En face view of scolex showing cruciform-shaped apex, contracted suckers with external folded lappets. Scale bar = 400 μm. 6. Egg showing mammilated surface. Scale bar = 10 μm.

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Clistobothrium gen. n.

GENERIC DIAGNOSIS: Phyllobothriidae. Scolex with 4 large bowl-shaped suckers, each sucker on extendable stalk with a folding lappet that projects over sucker opening when extended. Large cruciform-shaped apex of scolex dividing sucker margins. Myzorhynchus absent. Neck short. Mature proglottids more than twice as long as broad. Cirrus armed. Testes numerous, fill intervitelline field anterior to ovary. Vagina anterior to cirrus pouch. Ovary bilobed, posterior. Vitellaria in lateral bands. Uterus reaching only to posterior margin of cirrus pouch. Parasites of *Carcharodon carcharias.*

TYPE SPECIES: *Clistobothrium carcharodoni.*

Discussion

Clistobothrium carcharodoni does not closely resemble any of the existing members of the Phyllobothriidae. It differs from the genus *Phyllobothrium* in scolex morphology and the lack of a tetralobed ovary in cross-section. The only other genus in the family Phyllobothriidae with 4 muscular pedunculate bothridia with flaps is *Carpobothrium chiloscyllii* Shipley and Hornell, 1906. *Carpobothrium chiloscyllii* was described from the waters off Sri Lanka from the slender bambooshark, *Chiloscyllium indicum* (Gmelin, 1789) from which the parasite gets its name. This worm has also been recovered by Southwell (1925) from the giant guitarfish and a dasyatid ray, both from the Ceylon Pearl Banks.

Clistobothrium carcharodoni differs from *C. chiloscyllii* in lacking 2 opposing flaps with minute marginal loculi covering each bothridium. *Clistobothrium carcharodoni* also differs from *C. chiloscyllii* in lacking conspicuous muscle pads on each flap and by possessing 4 large bothridia on extendable pedunculate stalks and a single retractable lappet over each sucker. The 2 species are similar in that neither has a myzorhynchus or accessory suckers. The internal anatomy of the mature segment is similar but *C. carcharodoni* is a much larger worm (30 mm as opposed to 10 mm for *C. chiloscyllii*) with approximately 3 times as many segments (73–85 for *C. carcharodoni,* 18–25 for *C. chiloscyllii*). No gravid segments were observed for *C. chiloscyllii,* so eggs cannot be compared.

Three species from 2 genera (*Dinobothrium* and *Phyllobothrium*) of the family Phyllobothriidae have been reported previously from the great white shark (Love and Moser, 1983). *Dinobothrium septaria* Beneden, 1889 was reported from Woods Hole, Massachusetts. The genus *Phyllobothrium* is represented by *P. lactuca* Beneden, 1850 and *P. tumidum* Linton, 1922. The latter species has been previously reported from the great white shark in California waters by Riser (1955).

The larval form of this parasite could very well be 1 of the 11 *Phyllobothrium delphini* Bosc, 1802 morphotypes found in marine mammals by Testa and Dailey (1977). These tetraphyllidean metacestodes are found primarily in the blubber of cetaceans but have also been reported from a number of pinnipeds (Dailey and Brownell, 1972). The hypothetical life cycles of *P. delphini* have been discussed by Southwell and Walker (1936) and Skrjabin (1972).

Linton (1922) published evidence that indicated to him that the *P. loliginis* (considered synonymous with *P. delphini*) found in cephalopods was the larval form of *P. tumidum,* described by him from the mackerel and great white sharks. In the present study, the shark was found with an entire young northern elephant seal in its stomach. Large numbers of phyllobothriid metacestodes have been reported from the blubber of the southern elephant seal, *Mirounga leonina* (Linnaeus, 1758), by Lauckner (1985). However, to date, none have been reported from the northern elephant seal, *Mirounga angustirostris* (Gill, 1866).

Acknowledgments

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Report on the Brayton H. Ransom Memorial Trust Fund

The Brayton H. Ransom Memorial Trust Fund was established in 1936 to "encourage and promote the study and advance of the Science of Parasitology and related sciences." Income from the Trust currently provides token support of the *Journal of the Helminthological Society of Washington* and limited support for publication of meritorious manuscripts by authors lacking institutional or other backing. Contributions may be directed to the Secretary-Treasurer.

Financial Report for 1989

Balance on hand, 1 January 1989	$11,609.58
Receipts: Net interest received in 1989	936.34
	$12,545.92

Disbursements:

Grant to the Helminthological Society of Washington for 1989	($	50.00)
Membership in the American Association for Zoological Nomenclature for 1989	($	50.00)
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Cestoda from Lake Fishes in Wisconsin: The Ecology and Pathology of *Proteocephalus ambloplitis* Plerocercoids in Their Fish Intermediate Hosts

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ABSTRACT: Seventeen species of fish in 5 families were infected with parenteric plerocercoids of *Proteocephalus ambloplitis* in 2 southeastern Wisconsin eutrophic lakes. The records from *Carpiodes cyprinus* and *Moxostoma erythrurum* are new. Prevalence and intensity were considerably higher in the land-locked Silver Lake compared to the river-connected Tichigan Lake. Plerocercoids were present in various hosts during all seasons but were most prevalent and numerous during the spring; subsequent decreases of plerocercoids in bass were attributed to parenteric recruitment into bass gut. Recruitment via the nonparenteric route is believed to have a significant role in the *P. ambloplitis* suprapopulation cycling in Wisconsin, particularly when fish other than bass, e.g., *Amia calva,* are involved as definitive hosts. Accordingly, recruitment does not have to occur only once a year, and the critical May temperatures of 7–12°C would not be required under all circumstances. Parenteric plerocercoids were localized mostly in the intestinal mesenteries during the spring but shifted to the gonads, liver, and spleen in summer and autumn. Some pathological observations are noted including the unilateral hypertrophy of infected ovaries in centrarchid fishes.

KEY WORDS: *Proteocephalus ambloplitis,* plerocercoids, Wisconsin fishes, ecology.

The bass tapeworm, *Proteocephalus ambloplitis* (Leidy, 1887), has been reported throughout the United States and southern Canada by many authors. Cooper (1915) and Bangham (1927) provided some early observations on its life history, which was more completely worked out by Hunter (1927, 1928) and Hunter and Hunter (1929). It was not until the work of Fischer and Freeman (1969, 1973) in Ontario that the actual life history of *P. ambloplitis* in bass became available. Findings by these latter authors corrected some of the earlier misconceptions and clarified for the first time the actual contribution of parenteric plerocercoids to the development of enteric *P. ambloplitis* in bass. Freeman (1973) classified 4 types of *P. ambloplitis* plerocercoids: (1) plerocercoid I in the copepod, (2) initial plerocercoid II in the body cavity of *Micropterus* or other fish genera, (3) middle plerocercoid II only in the body cavity of bass, and (4) terminal plerocercoid II only in the gut of bass either by entry from parenteral sites in the same fish (termed parenteric recruitment) or cannibalism. Anatomical aspects of these plerocercoid types are currently being examined and evaluated by our laboratory. Other reports that, at least partially, dealt with the role of plerocercoids include those of Esch et al. (1975) in Michigan and Eure (1976) in South Carolina. None of the above reports, however, examined the seasonal ecology of parenteric plerocercoids in their fish intermediate hosts, the subject matter of this report. New aspects of plerocercoid pathology are also included.

Materials and Methods

The fishes examined were from Silver Lake (Kenosha County), a 188-ha eutrophic land-locked lake, and from Tichigan Lake (Racine County), a 458-ha lake in an advanced state of eutrophication on the Fox River (a tributary of the Mississippi River). Seasonal collections were made from both lakes during the spring (April), summer (June, July, and early August), and autumn (late October and November) between 1977 and 1979 and from Silver Lake during the summer of 1976. One thousand eight hundred twelve fishes representing 32 species from 10 families (Amiidae, 1 species; Catostomidae, 7; Centrarchidae, 9; Cyprinidae, 2; Esocidae, 2; Ictaluridae, 4; Lepisosteidae, 1; Percidae, 2; Salmonidae, 2; Serranidae, 2) were captured by electroshocking from both lakes. An additional 1,543 fishes representing 29 species from 11 families (Amiidae, 1; Catostomidae, 3; Centrarchidae, 6; Cyprinidae, 5; Cyprinodontidae, 2; Esocidae, 2; Gasterosteidae, 1; Ictaluridae, 4; Percidae, 3; Serranidae, 1; Umbridae, 1) were captured primarily using seines or minnow traps in a channel draining the swampy western area of Tichigan Lake during 1978 and 1979.

Fish were systematically dissected shortly after capture. Plerocercoids were individually dissected out of visceral organs, i.e., liver, spleen, gonads. Fish infected with uncounted (few to >1,000) young encysted plerocercoids in their intestinal walls are included in the prevalence but not the mean values (Table 1). Specimens were processed as in Amin (1986a) and mounted whole for microscopical examination. Paraffin-embedded histopathologic sections were cut 10 μm thick and stained in hematoxylin and eosin.

Results and Discussion

Plerocercoids of *P. ambloplitis* were found in 17 species of fishes from 5 families. Centrarchidae included the largest number of species (7) with the heaviest infection (Table 1). The infections recorded from *Carpiodes cyprinus* and *Moxostoma erythrurum* (Catostomidae) are new host records. Fish species negative for parenteric plerocercoid infections in both lakes as well as in Tichigan Lake canal were *Amia calva* (55 fishes) (Amiidae); *Carpiodes carpio* (3), *Catostomus commersoni* (75), *Moxostoma anisurum* (4), *M. carinatum* (3) (Catostomidae); *Chaenobryttus gulosus* (1), *Pomoxis annularis* (19) (Centrarchidae); *Cyprinus carpio* (82), *Notropis cornutus* (107), *N. umbratilis* (33), *Pimephalus* sp. (765) (Cyprinidae); *Fundulus notatus* (19), *F. notti* (6) (Cyprinodontidae); *Esox americanus* (5), *E. lucius* (44) (Esocidae); *Culaea inconstans* (182) (Gasterosteidae); *Noturus gyrinus* (2) (Ictaluridae); *Etheostoma nigrum* (123) (Percidae); *Oncorhynchus mykiss* (1), *Salmo trutta* (1) (Salmonidae); *Roccus chrysops* (23), *R. mississippiensis* (1) (Serranidae); and *Umbra limi* (86) (Umbridae).

Lake distribution

Prevalence and intensity of infection were considerably higher in the land-locked Silver Lake than in the larger river-connected Tichigan Lake in all seasons. This pattern corresponds with that of enteric *P. ambloplitis* infecting both species of bass and *Amia calva* during the same seasons (Amin and Cowen, 1990). The populations of some fish parasites, e.g., caryophyllaeid cestodes, neoechinorhynchid acanthocephalans (Amin, 1986a, b) appear to become larger and better established in closed lake systems, e.g., Silver Lake, than in open lakes having continuous exchange with a river system, e.g., Tichigan Lake. Whether this pattern is related to the distribution and abundance or diapause patterns of the crustacean intermediate hosts or factors relating to the fish intermediate hosts is not known. Differences in lake turnover rates may be important.

Seasonal distribution

Parenteric plerocercoids were present during all seasons investigated but were clearly most prevalent and numerous during the spring and decreased during the summer and further during the autumn. The presence of parenteric plerocercoids in their fish hosts throughout the year was also reported in Ontario (Fischer and Freeman, 1969), Michigan (Esch et al., 1975), South Carolina (Eure, 1976), Oklahoma (McDaniel and Bailey, 1974), and Arkansas (Cloutman, 1975). Maximum seasonal means in South Carolina were observed during April and May (Eure, 1976). More than 50% of the Wisconsin parenteric plerocercoids from Silver Lake (287/510) during the spring were from *M. salmoides* (Table 1). The loss of parenteric middle plerocercoid II individuals to enteric penetration in bass is likely responsible for the subsequent decreases in observed parenteral infection. Such parenteral entry was documented mostly during May in bass from Ontario (Fischer and Freeman, 1969) and Michigan (Esch et al., 1975), when critical temperatures of 7–12°C were reached. The postspring decline in parenteric plerocercoid numbers may have also been influenced by seasonal changes in fish host size, assuming that larger fish will ingest greater volumes of the same food items eaten by smaller fish. Of the 3 most important host species in Silver Lake, in terms of level of infection and sample size (Table 1), largemouth bass showed a decline in size (total length in cm) from a mean of 36.4 (range, 21–48) in the spring to 29.2 (17–46) and 23.7 (12–42) in summer and autumn, respectively. Bluegill size was stable at 15.7 (8–21), 14.3 (11–17), and 15.6 (10–21), respectively; and walleye summer decline in size disappeared by the autumn with 37.1 (28–53), 27.7 (16–33), and 38.9 (25–54), respectively. Size composition of plerocercoids was not a good indicator of infection periodicity; it was more closely associated with the body cavity organs they infected. The recovery of well-developed plerocercoids that were smaller than less-developed ones was not uncommon.

Recruitment (parenteric entry of middle plerocercoid II into bass gut) may also occur parenterally once a year in Wisconsin during the spring (Table 2; Amin and Cowen, 1990) once the critical temperature of 7–12°C is reached, as has been suggested both by Fischer and Freeman (1969) in Ontario and by Esch et al. (1975) in Michigan (up from 4°C), and by Eure (1976) in South Carolina (down from 26°C). Less-developed plerocercoids not so recruited would remain in extraintestinal sites of bass, as well as other fish species, as a future source of adults. For further discussion, see Seasonal site selection and Kennedy (1983). Bailey's (1984) observation of increased intensity of *P. ambloplitis* plerocercoids with increasing age of *Lepomis macrochi-*

Table 1. Seasonal distribution of parenteric plerocercoids of *Proteocephalus ambloplitis* from fishes in Silver and Tichigan lakes proper, 1976–1979.*

Fish species	Silver Lake			Tichigan Lake		
	Spring (Apr)	Summer (late Jun–early Aug)	Autumn (late Oct; Nov)	Spring (Apr)	Summer (late Jun–early Aug)	Autumn (late Oct; Nov)
Catostomidae						
Carpiodes cyprinus	−†	—	—	—	1/13 (7), 0, 0 (1)	0/6
Erimyzon sucetta	2/27 (7), 3, 0.1 (0)	0/25	2/42 (5), 7, 0.2 (0)	—	—	—
Moxostoma erythrurum	—	—	—	—	0/4	2/4 (50), 0, 0 (2)
Centrarchidae						
Ambloplites rupestris	3/4 (75), 3, 0.8 (3)	4/8 (50), 40, 5.0 (1)	4/13 (31), 1, 0.1 (4)	2/2 (100), 0, 0 (2)	—	—
Lepomis cyanellus	0/5	5/13 (38), 0, 0 (5)	—	2/7 (29), 0, 0 (2)	0/5	1/6 (17), 0, 0 (1)
Lepomis gibbosus	5/6 (83), 18, 3.0 (0)	0/9	1/1 (100), 0, 0 (1)	0/15	0/32	0/13
Lepomis macrochirus	34/62 (55), 66, 1.1 (0)	29/98 (30), 36, 0.4 (0)	50/141 (35), 50, 0.3 (0)	0/51	0/74	1/87 (1), 1, 0.01 (0)
Micropterus dolomieui	2/2 (100), 3, 1.5 (0)	1/2 (50), 25, 12.5 (0)	—	1/6 (17), 0, 0 (1)	0/10	0/2
Micropterus salmoides	18/28 (64), 287, 10.3 (0)	19/38 (50), 378, 9.9 (0)	2/6 (33), 5, 0.8 (0)	1/2 (50), 0, 0 (1)	5/19 (26), 24, 1.3 (0)	5/23 (22), 7, 0.3 (0)
Pomoxis nigromaculatus	5/25 (20), 70, 2.8 (0)	2/4 (50), 8, 2.0 (0)	2/18 (11), 2, 0.1 (0)	0/70	0/33	2/59 (3), 0, 0 (2)
Ictaluridae‡						
Ictalurus melas	0/1	0/1	1/1 (100), 1, 1.0 (0)	0/6	—	0/2
Ictalurus natalis	1/2 (50), 6, 3.0 (0)	1/2 (50), 6, 3.0 (0)	—	0/7	0/1	—
Ictalurus punctatus	—	—	—	1/17 (6), 3, 0.2 (0)	1/12 (8), 0, 0 (1)	0/6
Lepisosteidae						
Lepisosteus osseus	3/3 (100), 15, 5.0 (0)	5/11 (45), 14, 1.3 (0)	—	—	0/9	—
Percidae						
Perca flavescens	0/4	2/37 (5), 4, 0.1 (0)	2/26 (8), 3, 0.1 (0)	0/57	0/3	0/17
Stizostedion vitreum	9/21 (43), 39, 1.9 (0)	3/10 (30), 4, 0.4 (0)	5/23 (22), 5, 0.2 (0)	0/4	0/20	0/28
Total	82/188 (44), 510, 2.7 (3)	71/258 (27), 516, 2.0 (6)	69/271 (25), 74, 0.3 (5)	7/244 (3), 3, 0.01 (6)	7/235 (3), 24, 0.1 (2)	11/253 (4), 8, 0.03 (5)

* Number of fish infected/number examined (% prevalence), number of plerocercoids recovered, mean plerocercoids per examined fish (number of fish infected with encysted plerocercoids in intestinal wall, calculated in prevalence but not in mean intensity because of the undetermined number of cysts).

† No fish examined.

‡ The gut wall of one *Ictalurus nebulosus* from Tichigan Lake (misc. coll.) was studded with many encysted plerocercoids (Figs. 3, 4).

Table 2. Parenteric distribution of *Proteocephalus ambloplitis* plerocercoids in fishes from Silver and Tichigan lakes (combined) during spring, summer, and autumn, 1976-1979.

	Total number of worms (*N*) and proportion (%) recovered from											
	Spring (Apr)				Summer (late Jun–early Aug)				Autumn (late Oct, Nov)			
Fish species	*N*	% in M*	% in Go†	% in L/S‡	*N*	% in M	% in Go	% in L/S	*N*	% in M	% in Go	% in L/S
Catostomidae												
Erimyzon sucetta	3	—	100	—	0	—	—	—	7	—	100	—
Centrarchidae												
Ambloplites rupestris	3	—	100	—	40	88	—	12	1	100	—	—
Lepomis gibbosus	18	67	—	33	0	—	—	—	0	—	—	—
Lepomis macrochirus	66	35	18	47	36	3	11	86	51	31	—	69
Micropterus dolomieui	3	100	—	—	25	80	—	20	0	—	—	—
Micropterus salmoides	287	57	39	4	402	6	72	22	12	—	58	42
Pomoxis nigromaculatus	70	98	2	—	8	100	—	—	2	100	—	—
Ictaluridae												
Ictalurus melas	0	—	—	—	0	—	—	—	1	—	—	100
Ictalurus natalis	6	100	—	—	6	—	—	100	0	—	—	—
Ictalurus punctatus	3	100	—	—	0	—	—	—	0	—	—	—
Lepisosteidae												
Lepisosteus osseus	15	—	—	100	14	—	—	100	0	—	—	—
Percidae												
Perca flavescens	0	—	—	—	4	—	—	100	3	—	—	100
Stizostedion vitreum	39	31	2	67	4	100	—	—	5	100	—	—
Total	513	57	25	18	536	16	55	29	82	30	18	52

* Primarily from the mesenteries but occasionally including non-site-specific forms in the body cavity.

† From the gonads, almost exclusively the ovaries.

‡ Mostly from the liver but occasionally the spleen.

rus was interpreted as reflecting plerocercoid longevity. This pattern of infection is interpreted as a means of dispersal in time augmenting the common method of dispersal in space (via host movement) characteristic of most cestodes. Such brevipatent one-time seasonal breeders as *P. ambloplitis* in bass with a short adult life span and long plerocercoid life are semelparous. Of course, Bailey's (1984) observations may also express an increased probability of exposure due to greater food intake by larger fish. The extended residence of some cestodes, e.g., certain pseudophyllideans, in the crustacean intermediate host may also provide an alternate explanation of *P. ambloplitis* dispersal in time.

Although Fischer and Freeman (1969), Esch et al. (1975), and Eure (1976) discussed recruitment only in the context of parenteric entry of plerocercoids into the bass gut, the potential importance of cannibalism was not recognized. Only Fischer and Freeman (1973) pointed to the potential ecological importance of transport fish hosts as a link between copepods and bass. Findings from Wisconsin suggest a considerably greater significance of this pathway in the cycling of *P. ambloplitis* in its fish hosts. For example, parenteric plerocercoids infected a wide diversity of fish hosts (Table 1) throughout the year but with seasonality, not limited to bass, that was similar to that of enteric stages (above; Amin and Cowen, 1990) and although temperatures of 7–12°C may be critical for parenteric recruitment into the intestines of some bass during the spring, no critical temperatures for recruitment via cannibalism are indicated from the Wisconsin data. Actually the term "cannibalism" is misleading because it implies that only *Micropterus* can become the definitive host of enteric *P. ambloplitis* by feeding on other *Micropterus* infected with parenteric middle plerocercoid II. In several lakes in Wisconsin, *A. calva* harbors even larger populations of adult *P. ambloplitis* than bass (Amin and Cowen, 1990) which can be acquired by feeding on plerocercoid-infected bass. *Amia calva* was not infected with *P. ambloplitis* plerocercoids in Wisconsin. The role of other fish species as an intermediate link between copepods and bass (or bowfin) cannot be overemphasized.
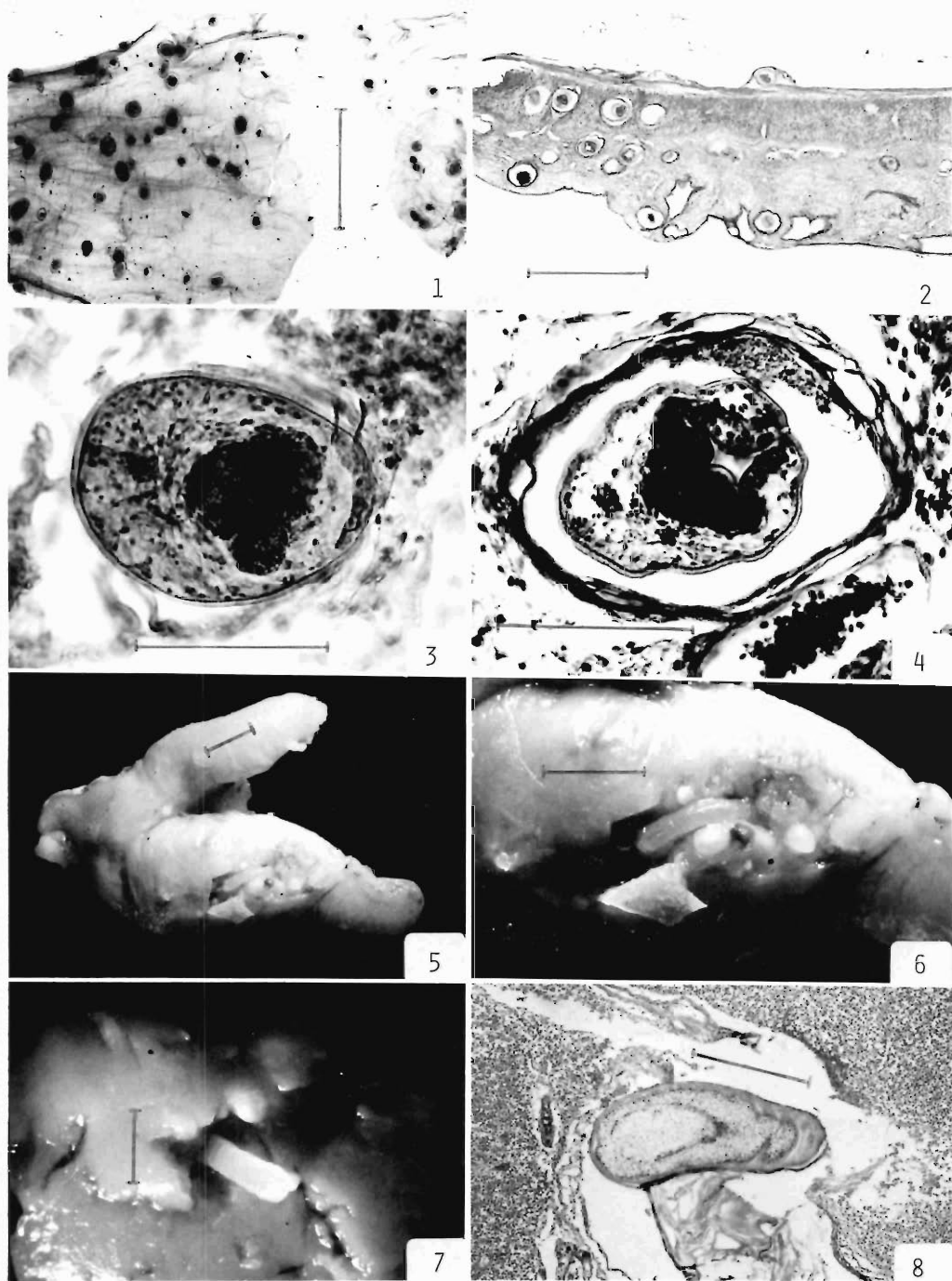
Figures 1–8. Histopathology of *Proteocephalus ambloplitis* plerocercoids in various organs of some Wisconsin fish intermediate hosts. 1. A section of *Lepomis gibbosus* intestinal wall studded with encysted larvae. 2. A longitudinal section of *Ambloplites rupestris* gut wall showing migrating cysts. 3. A differentiating encysted plerocercoid in the gut wall of *Ictalurus nebulosus*; note the vacuolated host tissue. 4. A later stage of encysted plerocercoid in the gut wall of *I. nebulosus*. 5. Unilateral enlargement in infected *L. macrochirus* ovary. 6. Enlargement of infected ovary in Figure 5; the dark eggs are dead. 7. Intrahepatic invasion by grown plerocercoid(s). 8. A histopathologic section from same liver in Figure 7 showing part of the plerocercoid and host tissue vacuolation and leukocytosis. Figures 5–7: dark field. Scale bars in Figures 1, 2, 8 = 1.0 mm; 3, 4 = 100 μm; 5–7 = 5.0 mm.

Probably, recruitment into the adult *P. amblo-plitis* suprapopulation as a whole does not have to occur once a year and is not limited to bass in the spring but may extend to other definitive hosts, e.g., *A. calva*, where the parenteric pathway is not applicable. The role of other definitive hosts, e.g., *Roccus chrysops* and *R. mississippiensis* (Arnold et al., 1968; McReynolds and Webster, 1980) remains unknown. In the *A. calva* case, "critical" May temperatures of 7–12°C would not be required unless this temperature is necessary for transformation of middle to terminal plerocercoid II regardless of the mode of entry into the definitive host gut. The findings of Amin and Cowen (1990) that recruitment into *A. calva* extends through the summer and autumn months do not support that possibility. Copepod dynamics, e.g., timing and duration of diapause, may be important in establishing variability in recruitment cycles.

Seasonal site selection

Information on the seasonal distribution of parenteric plerocercoids in various body cavity sites is available from 13 species of fish (Table 2). Plerocercoids were mostly localized in intestinal mesenteric tissue (57%) during the spring but shifted to the gonads (55%) during the summer and the liver and spleen (52%) during the autumn. This was particularly true in *M. salmoides* that had the largest sample. In bass, the shift was primarily to gonadal sites and probably represents parenteric (intestinal mesentery) loss of middle plerocercoid II individuals to the gut. Whether gonadal, splenic, and hepatic forms become available to recruitment into the intestine at a later date or become lost except for possible transfer to a predator fish is not known. In *Lepomis macrochirus*, a considerable and increasing presence in the liver was noted. The decrease in intestinal mesentery sites between spring and summer (Table 2) is attributed to the migration of plerocercoid I across the bluegill intestinal wall prior to transformation to initial plerocercoid II in extraintestinal sites. The above data (Tables 1, 2) provide qualified field support for the Fischer and Freeman (1969) initial explanation of the migration and recruitment of the plerocercoid stage(s) of *P. ambloplitis*.

Pathology

The mass migration of encysted plerocercoid I individuals was observed in a few centrarchid fishes, particularly *Ambloplites rupestris* during all seasons (Table 1). Whole intestines were seen studded with hundreds of such cysts (Figs. 1, 2). Some of these cysts were clearly double walled, with the outer wall appearing to be of host origin (Figs. 3, 4)—a new observation. This cyst stage directly follows the ingestion of infected copepods by these fish intermediate hosts. The mode of plerocercoid penetration through the intestinal wall of these fish while enclosed within a cyst wall is not known. Many of the larger plerocercoids infecting other body cavity sites were also encysted. The relationships between the developmental stage, size, and envelope of these plerocercoids and their migration and infectivity still need to be resolved.

In gonadal tissue of centrarchids, plerocercoid penetration of ovarian expansive stroma, as described by Esch and Huffines (1973), was commonly observed. Penetration of plerocercoids into advanced vitellogenic oocytes, as described by McCormick and Stokes (1982), was rarely observed. The unilateral hypertrophy of infected ovaries in the presence of many plerocercoids was also observed (Figs. 5, 6), with the resulting death of many eggs. Blockage of circulation appeared to have been involved based on the appearance of some blood vessels. Hepatic damage was observed in bluegill by plerocercoids at different developmental stages (Figs. 7, 8). Vacuolation and hepatic necrosis (Fig. 8) were observed on a number of occasions.

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Obituary Notice

RICHARD L. BEAUDOIN

8 June 1931–22 May 1990
Elected Member December 1965
Executive Committee Member-at-Large
1973–1974
Awards Committee 1977, 1982

Cestoda from Lake Fishes in Wisconsin: The Ecology of *Proteocephalus ambloplitis* and *Haplobothrium globuliforme* in Bass and Bowfin

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ABSTRACT: Findings on *Proteocephalus ambloplitis* (Leidy) from bass in 2 southeastern Wisconsin eutrophic lakes show the importance of critical temperatures and host size in the parenteric recruitment of this tapeworm during the spring. The effect of latitudinal differences in the seasonal development of *P. ambloplitis* in southeastern Wisconsin compared with collections from elsewhere in North America are also noted. Enteric worms survived for up to 8 mo but lived and reproduced for longer periods in bowfin (*Amia calva*) in which recruitment was only dependent on the ingestion of plerocercoid-infected fish intermediate hosts. In southeastern Wisconsin, bowfin appeared to be the important host in which the majority of the *P. ambloplitis* population circulates. The tapeworm's initial establishment, maturation, and reproduction occurred in anteriormost digestive tract locations in both bass and bowfin. Establishment of *Haplobothrium globuliforme* Cooper, 1914 occurs anteriorly in bowfin, but adult and gravid worms are found only in the large intestine during peak breeding in the summer. Adults live up to 1 yr in the gut of bowfin. The mud minnow (*Umbra limi*) is a new intermediate host for *H. globuliforme* plerocercoids. The 2 tapeworm species had considerably denser populations in the closed system of Silver Lake than in the larger river-connected Tichigan Lake. The seasonal development of both *P. ambloplitis* and *H. globuliforme* in bowfin is reported here for the first time. Notes on concurrent infections with acanthocephalans, other *Proteocephalus* species, and hyperparasitism are also included.

KEY WORDS: Cestoda, *Proteocephalus ambloplitis*, *Proteocephalus* spp., *Haplobothrium globuliforme*, seasonal ecology, recruitment, infectious cycle, site selection, bass, bowfin, Wisconsin, concurrent infections, hyperparasitism.

The role of 16 fish species in the ecology of *Proteocephalus ambloplitis* (Leidy) plerocercoids in 2 southeastern Wisconsin eutrophic lakes was reported by Amin (1990). In the same 2 lakes, adults of this cestode species infect largemouth bass, *Micropterus salmoides* (Lacépède), and smallmouth bass, *M. dolomieui* Lacépède, as well as bowfin, *Amia calva* Linnaeus, which is also infected with *Haplobothrium globuliforme* Cooper, 1914. The ecological relationships among these organisms in southeastern Wisconsin are herein reported against a background that lacks any such information on *H. globuliforme* but involves various interpretations of some basic developmental and ecological phenomena unique to *P. ambloplitis* known only from bass.

Cooper (1914, 1917) described *H. globuliforme* and the fragmentation of its primary scolex. The study of the life history of this ancient and intriguing cestode was initiated by Essex (1929) and Thomas (1930) but was completed by Meinkoth (1947), based on material from Michigan. The most recent work on *H. globuliforme* is descriptive in nature, particularly at the ultrastructural level, e.g., MacKinnon and Burt (1985a, b, c). This tapeworm infects only *A. calva,* an ancient fish itself, throughout the United

States and southern Canada. *Proteocephalus ambloplitis* has a similar distribution range. Cooper (1915, 1918) and Bangham (1927) provided early descriptions of the life history of the bass tapeworm, which was more completely investigated by Hunter (1928) and Hunter and Hunter (1929). Freeman (1973) and Fischer and Freeman (1969, 1973), however, provided the first complete account of its life history and the actual role of plerocercoids in bass from Ontario. Subsequently, the Ontario reference line was used to compare findings on the same cestode species from Michigan and South Carolina bass by Esch et al. (1975) and Eure (1976), respectively. Related findings from Wisconsin bass are described and compared, and those from bowfin are reported for the first time. The ecology of *H. globuliforme* in its only host, bowfin, is also reported here for the first time.

Materials and Methods

The fishes examined were from Silver Lake (Kenosha County), a 188-ha eutrophic land-locked lake, and from Tichigan Lake (Racine County), a 458-ha lake in an advanced state of eutrophication on the Fox River (a tributary of the Mississippi River). Seasonal collections were made from both lakes during the spring (April), summer (June, July, and early August), and

Table 1. Prevalence and intensity of *Proteocephalus ambloplitis* and *Haplobothrium globuliforme* in fishes of Silver and Tichigan lakes proper, 1976-1979.

Cestode species	Fish species	Season	Silver Lake Fish N	Inf. (%)	Cestodes N	$\bar{x}$/fish	Max.	Tichigan Lake Fish N	Inf. (%)	Cestodes N	$\bar{x}$/fish	Max.
Proteocephalus	*Amia calva*	Spring	7	7 (100)	845	120.7	372	13	12 (92)	619	47.6	195
ambloplitis		Summer	8	6 (75)	757	94.6	451	5	5 (100)	218	43.6	112
		Autumn	3	3 (100)	88	29.3	40	5	4 (80)	225	45.0	112
		Total	18	16 (89)	1,690	93.8	451	23	21 (91)	1,062	46.17	195
	Micropterus	Spring	28	26 (93)	543	19.4	86	2	0	0	—	0
	salmoides	Summer	38	13 (34)	67	1.8	37	19	1 (5)	2	0.1	2
		Autumn	6	1 (17)	7	1.2	7	23	5 (22)	8	0.4	2
		Total	72	40 (56)	617	8.57	86	44	6 (14)	10	0.27	2
	Micropterus	Spring	2	2 (100)	9	4.5	6	6	0	0	—	0
	dolomieui	Summer	2	0	0	—	0	10	0	0	—	0
		Autumn	0	0	0	—	0	2	0	0	—	0
		Total	4	2 (50)	9	2.25	6	18	0	0	0	0
Haplobothrium	*Amia calva*	Spring	7	2 (29)	149	21.2	127	13	2 (15)	42	3.2	41
globuliforme		Summer	8	6 (75)	305	38.1	94	5	4 (80)	62	12.4	41
		Autumn	3	1 (33)	117	39.0	117	5	2 (40)	4	0.8	3
		Total	18	9 (50)	571	31.7	127	23	8 (35)	108	4.70	41

Table 2. The relationship between the size and sex of *Micropterus salmoides* and *M. dolomieui* from Silver and Tichigan lakes and infection with *Proteocephalus ambloplitis*, 1976-1979.

Fish species	Lake	Fish total length (cm)	No. of male fish		*Proteocephalus ambloplitis*				No. of female fish	
						$\bar{x}$ per				
			Exam.	Inf. (%)	N	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)
Micropterus	Silver	11–20	2	2 (100)	10	5.0	5.0	7	5	0 (0)
salmoides		21–30	16	7 (41)	15	0.9	2.1	4	10	6 (60)
		31–40	11	4 (36)	41	3.7	10.2	18	17	10 (59)
		41–50	0	0	0	–	–	0	11	11 (100)
Totals			29	13 (45)	66	2.3	5.1	18	43	27 (63)
	Tichigan	11–20	6	0 (0)	0	–	–	0	5	0 (0)
		21–30	6	1 (17)	1	0.2	1.0	1	12	2 (17)
		31–40	4	0 (0)	0	–	–	0	8	1 (12)
		41–50	0	0	0	–	–	0	3	2 (67)
Totals			16	1 (6)	1	0.01	1.0	1	28	5 (18)
Micropterus	Tichigan	18–20	3	1 (33)	4	1.3	4.0	4	0	0
dolomieui		28	1	1 (100)	5	5.0	5.0	5	0	0
Totals			4	2 (50)	9	2.25	4.50	5	0	0

autumn (late October and November) between 1977 and 1979 and from Silver Lake during the summer of 1976. One thousand eight hundred twelve fishes representing 32 species and 10 families (Amiidae, 1 species; Catostomidae, 7; Centrarchidae, 9; Cyprinidae, 2; Esocidae, 2; Ictaluridae, 4; Lepisosteidae, 1; Percidae, 2; Salmonidae, 2; Serranidae, 2) were captured by electroshocking from both lakes. An additional 1,543 fishes representing 29 species and 11 families (Amiidae, 1; Catostomidae, 3; Centrarchidae, 6; Cyprinidae, 5; Cyprinodontidae, 2; Esocidae, 2; Gasterosteidae, 1; Ictaluridae, 4; Percidae, 3; Serranidae, 1; Umbridae, 1) were seined or minnow trapped in a channel draining the swampy western area of Tichigan Lake during 1978, 1979, and 1981.

Fish were systematically dissected shortly after capture. Specimens of parasites were processed as in Amin (1986a). The plerocercoid terminology of Freeman (1973) and Fischer and Freeman (1973) is used here. Representative specimens were deposited in the U.S. National Museum Helminthological Collection (USNM Helm. Coll.) and in the University of Nebraska State Museum's Harold W. Manter Laboratory Collection (HWML Coll.).

Results and Discussion

Host distribution

Prevalence and mean intensity of infections with *P. ambloplitis* were considerably greater in *A. calva* (89%, 93.9) than in either *M. salmoides* (56%, 8.6) or *M. dolomieui* (50%, 2.2) from Silver Lake. This pattern was consistent and more extreme than in Tichigan Lake, where infections were considerably lighter (Table 1). It is clear that the bowfin plays a major role in the flow of the *P. ambloplitis* suprapopulation in its fish definitive hosts in southeastern Wisconsin; see

Amin (1987) for a discussion of host role changes. Parenteric recruitment of middle plerocercoid II into the bass gut, particularly in smallmouth bass, as originally described by Fischer and Freeman (1969) is not relevant to infections in bowfin. The cycle of *P. ambloplitis* in southeastern Wisconsin was clearly influenced by bowfin predation on plerocercoid-infected fish intermediate hosts, e.g., bowfin are not intermediate hosts of *P. ambloplitis* (see Amin, 1990). Accordingly, the "critical" spring temperatures of 7–12°C necessary for parenteric recruitment in bass (up from 4°C in Ontario and Michigan [Fischer and Freeman, 1969; Esch et al., 1975] and down from 26°C in South Carolina [Eure, 1976]) is not relevant to bowfin. This may explain why infection parameters of bowfin in the large river-connected Tichigan Lake were similar in all seasons (Table 1). Parameters in bowfin from the smaller landlocked Silver Lake, which shows greater fluctuations in seasonal temperature, were probably indicative of the higher intensity of fish feeding during spring and summer compared with autumn (Table 1).

Lake distribution

Both tapeworms (Table 1) had larger populations in Silver Lake than in Tichigan Lake, as noted earlier for *P. ambloplitis* plerocercoids (Amin, 1990), caryophyllaeid cestodes (Amin, 1986a), and some acanthocephalan species (Amin, 1986b). The closed system in the landlocked Silver Lake clearly enhanced the popu-

Table 2.   Continued.

| | *Proteocephalus ambloplitis* | | | | | | *Proteocephalus ambloplitis* | | |
| | x̄ per | | | Total no. of fish | | | x̄ per | | |
N	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)	N	Exam. fish	Inf. fish	Max.
0	—	—	0	7	2 (29)	10	1.4	5.0	7
89	8.9	14.8	81	26	13 (50)	104	4.0	8.0	81
303	17.8	30.3	86	28	14 (50)	344	12.3	24.6	86
159	14.5	14.5	32	11	11 (100)	159	14.4	14.4	32
551	12.8	20.4	86	72	40 (56)	617	8.6	15.4	86
0	—	—	0	11	0 (0)	0	—	—	0
3	0.3	1.5	2	18	3 (17)	4	0.2	1.3	2
2	0.3	2.0	2	12	1 (8)	2	0.2	2.0	2
6	2.0	3.0	5	3	2 (67)	6	2.0	3.0	5
11	0.4	2.2	5	44	6 (14)	12	0.3	2.0	5
0	—	—	0	3	1 (33)	4	1.3	4.0	4
0	—	—	0	1	1 (100)	5	5.0	5.0	5
0	—	—	0	4	2 (50)	9	2.3	4.5	5

lation density of these helminths. Other variables related to the different state of eutrophication in the 2 lakes may include species composition, distribution and density of the intermediate hosts, and the feeding strategy of the definitive hosts involved. The lower visibility in Tichigan Lake could negatively affect feeding on infected prey by bass (a sight feeder) and contribute to the large difference in prevalence in the 2 lakes (Table 1). Feeding of the bottom-dwelling bowfin (probably an olfactory and tactile feeder) would not be strongly affected by decreased visibility.

Host size and sex

Two of 7 *M. salmoides* below 20.0 cm in total length (less than 2 yr old; see Pasch [1974]) from Silver Lake were lightly infected with enteric *P. ambloplitis*; none of 11 similar fishes from Tichigan Lake were infected. Heavier and more frequent infections were largely confined to mature larger bass (Table 2). The shift from a microcrustacean and insect diet to a fish diet in larger largemouth bass started in 5-cm long bass (Pasch, 1974, among others). It is not certain whether these data support the hormone factor hypothesis of Fischer and Freeman (1969) and Esch et al. (1975), who suggested that sex hormones of mature bass >15.0 and >20.0 cm in length, respectively, may affect the parenteric migration of middle plerocercoid II in the bass gut. The possible contribution of cannibalism to the abundance of enteric *P. ambloplitis* in bass in not known. In both lakes, female largemouth bass

were considerably more heavily and more frequently infected than males (Table 2). Whether female sex hormones have greater effect than male hormones in promoting parenteric recruitment is not known. Fischer and Freeman (1969) indicated that proper rise in temperature and bass size (maturity), but "apparently" not bass sex, were important for penetration. The feeding behavior of male vs. female bass is not known.

In *A. calva,* the smallest fish examined were infected with *P. ambloplitis* (Table 3). Although virtually all bowfin were infected, larger fish from both lakes had heavier worm burdens, which would correspond with the larger volume of food (infected bass) eaten by these fish. Unlike the pattern in bass (Table 2), there appeared to be no marked difference in infection parameters by sex of *A. calva* (Table 3).

The pattern of *H. globuliforme* infection in *A. calva* (Table 4) was similar to that of *P. ambloplitis* from the same host (Table 3) except that the increase in *H. globuliforme* burden by fish size was smaller, whereas the difference between female and male host infection parameters was greater. The life history of *H. globuliforme* is similar to that of *P. ambloplitis* in *A. calva* but without the complication of the different types of plerocercoids. Bowfin appear to become infected by ingesting a second fish intermediate host, e.g., *Lepomis* or *Ictalurus* infected (with extraintestinal plerocercoids) from feeding on plerocercoid-infected copepods. The considerably greater intensity and higher prevalence of

Table 3. The relationship between the size and sex of *Amia calva* from Silver and Tichigan lakes and the intensity of infection with *Proteocephalus ambloplitis*, 1976-1979.

Lake	Fish total length (cm)	No. of male fish		N	*x̄* per		Max.	No. of female fish	
		Exam.	Inf. (%)		Exam. fish	Inf. fish		Exam.	Inf. (%)
Silver	20–29	0	0	0	—	—	0	55	55 (100)
	30–39	0	0	0	—	—	0	1	1 (100)
	40–49	2	2 (100)	241	120.5	120.5	159	1	1 (100)
	50–59	5	3 (60)	100	20.0	33.3	44	4	4 (100)
	60–69	0	0	0	—	—	0	0	0
Totals		7	5 (71)	341	48.7	68.2	159	11	11 (100)
Tichigan	20–29	1	1 (100)	63	63.0	63.0	63	0	0
	30–39	0	0	0	—	—	0	0	0
	40–49	2	2 (100)	4	2.0	2.0	3	3	2 (67)
	50–59	11	10 (91)	450	40.9	45.0	112	4	3 (75)
	60–69	0	0	0	—	—	0	2	2 (100)
Totals		14	13 (93)	517	36.9	39.8	112	9	7 (78)

* Nine of these hosts were also infected with *Haplobothrium globuliforme*.

† Eight of these hosts were also infected with *Haplobothrium globuliforme*.

infection in female than in male bowfin suggests a larger volume of food intake in females vs. males of the same size. This argument may also hold for bass.

Seasonal distribution

The distribution of *P. ambloplitis* in *M. salmoides* from Silver Lake shows peak prevalence and mean intensity in the spring (93%, 19.4), decreasing in the summer and autumn to 34%, 1.8, and 17%, 1.2, respectively; the number of worms from the same host in Tichigan Lake was much smaller (Table 1). Most of the spring tapeworms were recently recruited immatures (7% plerocercoids and 78% juveniles) (Table 5) that must have reached enteric sites during April and May, and possibly earlier. Some recently recruited plerocercoids in bass and bowfin were considerably smaller (occasionally little more than a scolex) than many of those infecting body cavity organs (particularly ovaries) of fish intermediate hosts (Amin, 1990). The summer worms included a considerably higher proportion of mature adults (58%) and gravid adults (8%), which

Table 4. The relationship between the size and sex of *Amia calva* from Silver and Tichigan lakes and the intensity of infection with *Haplobothrium globuliforme*, 1976-1979.

Lake	Fish total length (cm)	No. of male fish		N	*x̄* per		Max.	No. of female fish	
		Exam.	Inf. (%)		Exam. fish	Inf. fish		Exam.	Inf. (%)
Silver	20–29	0	0	0	—	—	0	5	3 (60)
	30–39	0	0	0	—	—	0	1	1 (100)
	40–49	2	0	0	—	—	0	1	1 (100)
	50–59	5	0	0	—	—	0	4	4 (100)
	60–69	0	0	0	—	—	0	0	0
Totals		7	0	0	—	—	0	11	9 (82)
Tichigan	20–29	1	1 (100)	1	1.0	1.0	1	0	0
	30–39	0	0	0	—	—	0	0	0
	40–49	2	0	0	—	—	0	3	2 (67)
	50–59	11	1 (9)	3	0.3	3.0	3	4	2 (50)
	60–69	0	0	0	—	—	0	2	2 (100)
Totals		14	2 (14)	4	0.3	2.0	3	9	6 (67)

* All these hosts were also infected with *Proteocephalus ambloplitis*.

Table 3. Continued.

| | Proteocephalus ambloplitis | | | | | | Proteocephalus ambloplitis | | | |
| | $\bar{x}$ per | | | Total no. of fish | | | $\bar{x}$ per | | | |
N	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)	N	Exam. fish	Inf. fish	Max.
127	25.4	25.4	54	5	5 (100)	127	25.4	25.4	54
372	372.0	372.0	372	1	1 (100)	372	372.0	372.0	372
451	451.0	451.0	451	3	3 (100)	692	230.7	230.7	451
399	99.8	99.8	132	9	7 (78)	499	55.4	71.3	132
0	—	—	0	0	0	0	—	—	0
1,349	122.6	122.6	451	18*	16 (89)	1,690	93.9	105.6	451
0	—	—	0	1	1 (100)	63	63.0	63.0	63
0	—	—	0	0	0	0	—	—	0
114	38.0	57.0	112	5	4 (80)	118	23.6	29.5	112
50	12.5	16.7	27	15	14 (93)	651	43.4	46.5	151
230	115.0	115.0	195	2	2 (100)	230	115.0	115.0	195
394	43.8	56.3	195	23†	21‡(91)	1,062	46.2‡	50.6‡	195

‡ One 57-cm-long fish was not sexed. It contained 151 worms. This fish and its parasites were included in the totals but not under either male or female columns.

disappeared from the dwindling autumn population in October and November. The above findings suggest a major recruitment (possibly mostly parenteric) beginning in late March and extending at least through June (25% of summer material were juveniles, Table 5). Maturation proceeded sufficiently fast to produce breeding gravid adults in the summer. By autumn most worms had already disappeared, leaving only 7 adults in 1 out of 6 bass examined. Mature adults of the autumn were considerably smaller than the more robust ones of the summer. Clearly there is no reason to suspect winter *P. ambloplitis* in the gut of *M. salmoides*. The few data from *M. dolomieui* (Tables 1, 5) fit the pattern described in *M. salmoides.* Findings from bass thus suggest an enteric *P. ambloplitis* life span of no more than 8 mo in southeastern Wisconsin, which may be a few weeks longer than that of the same tapeworm species in *M. dolomieui* reported in more northern locations, e.g., Fischer and Freeman (1969) and Esch et al. (1975) from Ontario and Michigan, respectively. Temperature gradient was probably involved in this latitudinal

Table 4. Continued.

| | Haplobothrium globuliforme | | | | | | Haplobothrium globuliforme | | | |
| | $\bar{x}$ per | | | Total no. of fish | | | $\bar{x}$ per | | | |
N	Exam. fish	Inf. fish	Max.	Exam.	Inf. (%)	N	Exam. fish	Inf. fish	Max.
123	24.6	41.0	51	5	3 (60)	123	24.6	41.0	51
22	22.0	22.0	22	1	1 (100)	22	22.0	22.0	22
94	94.0	94.0	94	3	1 (33)	94	31.3	94.0	94
332	83.0	83.0	127	9	4 (44)	332	37.0	83.0	127
0	—	—	0	0	0	0	—	—	0
571	51.9	63.4	127	18	9* (50)	571	31.7	63.4	12
0	—	—	0	1	1 (100)	1	1.0	1.0	1
0	—	—	0	0	0	0	—	—	0
9	3.0	4.5	8	5	2 (40)	9	1.8	4.5	8
43	10.8	21.5	41	15	3 (20)	46	3.1	15.3	41
52	26.0	26.0	41	2	2 (100)	52	26.0	26.0	41
104	11.6	17.3	41	23	8* (35)	108	4.7 ·	13.5	41

variation. In all other respects, our results from Wisconsin are in agreement with those of the above authors and are thus supportive of the critical temperature of parenteric recruitment in bass. The longer life span of parenteric *P. ambloplitis* plerocercoids in bass or other species of fish intermediate hosts (Amin, 1990) classes *P. ambloplitis* among the semelparous brevipatent one-time seasonal breeders with short adult life span (in bass); see Kennedy (1983). The increase in intensity of *P. ambloplitis* plerocercoids in older *Lepomis macrochirus* body cavity locations was interpreted by Bailey (1984) as reflecting plerocercoid longevity. Bailey's (1984) observation may also express an increased probability of exposure due to greater food intake by large fish. The seasonal maturation in this type of life history is clearly timed to coincide with the optimal period for transmission when plankton are most abundant. Seasonality may thus be more effectively determined at the level of the intermediate host, its seasonal and spatial availability, and dormancy.

The seasonal pattern of tapeworm infection in bowfin adds a new dimension to the developmental aspects of *P. ambloplitis* population ecology that is of major importance because *A. calva* appears to be the major definitive host in southeastern Wisconsin (Table 1). The parenteric recruitment and its associated critical spring temperatures as well as the potential hormonal factor excluding recruitment in immature bass are not parts of the bowfin biological system (see Host distribution, Host size and sex, above). The most important remaining variable is the feeding behavior. The prevalence of *P. ambloplitis* in *A. calva* from both lakes as well as the mean intensity of infection in Tichigan Lake showed no seasonal differences. The mean intensity in Silver Lake was, however, lower in the autumn, probably reflecting less feeding activity (Table 1). The smaller land-locked Silver Lake probably shows more extremes of seasonal temperatures. In that lake, the proportion of mature worms in bowfin in the spring (37%) was considerably higher than in largemouth bass (15%), was stable through the summer (38%), and peaked in the autumn (83%) (Table 5). Freshly recruited plerocercoids and juveniles as well as gravid worms were also represented in the autumn. These conditions were even more pronounced in Tichigan Lake where 84% of the spring worms were mature (3 specimens were gravid) and 16% of the autumn specimens were gravid. It is clear from the above findings, and in the absence of the constraints operating on bass, that the recruitment season in bowfin must begin well before April, with egg laying extending well past November. This significantly increases the length of the breeding season of *P. ambloplitis* in *A. calva* and thus increases its reproductive potential. It is interesting to come across 2 such different reproductive strategies of the same tapeworm infecting 2 genera of fish definitive hosts in the same body of water.

Infection parameters of *H. globuliforme* in *A. calva* were more or less seasonally stable in Silver Lake but were less consistent in Tichigan Lake (Table 1). Like *P. ambloplitis* in bowfin, the life cycle of *H. globuliforme* involves a copepod and fish intermediate hosts whose distribution and seasonal availability may differ in both lakes. Recently recruited *H. globuliforme* juveniles were represented in all collections from both lakes, but in Silver Lake, a high proportion (41%) was present during the spring, suggesting more active recruitment then. Primary scolices were found only on about one-half of the juvenile worms; the rest of the juveniles and all other stages had only secondary scolices (Table 6). Worms with primary scolices were clearly the youngest and represented the earliest recruitments. MacKinnon and Burt (1985c) also observed a higher proportion of *H. globuliforme* collected from *A. calva* in Lake Ontario in late June than in late August. In Silver Lake, maturation and breeding increased during the warmer months from 36% mature and 19% gravid in the spring to 33% and 37% in the summer; no gravid worms were recovered during the autumn but recruitment continued (Table 6). Worms matured more rapidly in Tichigan Lake, but both mature and gravid worms disappeared by October. The above observations and the lighter autumn infections, particularly in Tichigan Lake, suggest the absence of *H. globuliforme* from bowfin during the winter.

Twenty-four *H. globuliforme* plerocercoids were recovered from the body cavity of 19 of 66 (29%) mud minnows, *Umbra limi* (Kirtland), examined from Tichigan Lake canal during the summer. Most of these were excysted from double-walled cysts. The outer cyst wall appeared to be of host origin—a new observation. The plerocercoids resembled the pyriform ones reported by Meinkoth (1947, Fig. 1) from the liver of

Table 5. Seasonal development of *Proteocephalus ambloplitis* in fishes from Silver and Tichigan lakes, 1976-1979.

Lake	Fish species	Spring (Apr)					Summer (Jun–early Aug)					Autumn (late Oct, Nov)				
		N	Plerocercoids* (%)	Juveniles† (%)	Mature (%)	Gravid (%)	N	Plerocercoids (%)	Juveniles (%)	Mature (%)	Gravid (%)	N	Plerocercoids (%)	Juveniles (%)	Mature (%)	Gravid (%)
Silver	*Amia calva*	845	461 (54)	73 (9)	311 (37)	0	757	248 (33)	190 (25)	291 (38)	28 (4)	88	2 (2)	9 (10)	73 (83)	4 (5)
	Micropterus salmoides	543	40 (7)	424 (78)	79 (15)	0	67	17 (25)	6 (9)	39 (58)	5 (8)	7	0	0	7 (100)	0
	Micropterus dolomieui	9	6 (67)	0	3 (33)	0	0	0	0	0	0	0	0	0	0	0
Total		1,397	507 (36)	497 (36)	393 (28)	0	824	265 (32)	196 (24)	330 (40)	33 (4)	95	2 (2)	9 (10)	80 (84)	4 (4)
Tichigan	*Amia calva*	619	25 (4)	70 (11)	521 (84)	3 (1)	218	3 (1)	19 (9)	144 (66)	52 (24)	225	21 (9)	26 (12)	140 (62)	38 (17)
	Micropterus salmoides	0	0	0	0	0	2	0	0	0	2 (100)	8	0	1 (13)	7 (87)	0
Total		619	25 (4)	70 (11)	521 (84)	3 (1)	220	3 (1)	19 (9)	144 (65)	54 (25)	233	21 (9)	27 (12)	147 (63)	38 (16)

* Terminal plerocercoids.

† Segmented but still small and sexually immature.

Table 6. Seasonal development of *Haplobothrium globuliforme* in *Amia calva* of Silver and Tichigan lakes, 1976-1979.

Lake	Spring (Apr)						Summer (Jun–early Aug)						Autumn (late Oct, Nov)					
	N	Juv. 1* (%)	Juv. 2† (%)	Young‡ (%)	Mature (%)	Gravid (%)	N	Juv. 1 (%)	Juv. 2 (%)	Young (%)	Mature (%)	Gravid (%)	N	Juv. 1 (%)	Juv. 2 (%)	Young (%)	Mature (%)	Gravid (%)
Silver	149	29 (19)	32 (22)	6 (4)	54 (36)	28 (19)	305	39 (13)	8 (3)	44 (14)	102 (33)	112 (37)	117	17 (15)	11 (9)	32 (27)	57 (49)	0
Tichigan	42	2 (5)	0	9 (21)	20 (48)	11 (26)	62	4 (7)	0	2 (3)	18 (29)	38 (61)	4	4 (100)	0	0	0	0

* Juveniles with primary scolex.

† Juveniles with secondary scolex.

‡ Larger worms but still without sexually mature segments.

Table 7. Seasonal site selection of *Haplobothrium globuliforme* in *Amia calva* and *Proteocephalus ambloplitis* in *Amia calva, Micropterus salmoides,* and *Micropterus dolomieui* from Silver and Tichigan lakes, 1976-1979.

Cestode	Host species	Lake	Spring (Apr) (%)*							
			N	A†	Ce	B1	B2	C1	C2	C3
Haplobothrium	*Amia calva*	Silver	149	—	—	1.3	—	23.5	33.6	41.6
globuliforme		Tichigan	42	—	—	—	—	83.3	14.3	2.4
Proteocephalus	*Amia calva*	Silver	845	49.1	—	41.9	1.3	6.9	0.2	0.6
ambloplitis		Tichigan	619	26.0	—	38.9	—	33.6	0.5	1.0
	Micropterus	Silver	543	38.3	38.7	11.4	6.6	1.9	3.1	—
	salmoides	Tichigan	—	—	—	—	—	—	—	—
	Micropterus	Silver	9	33.3	11.1	55.6	—	—	—	—
	dolomieui	Tichigan	—	—	—	—	—	—	—	—

* % of worms in intestinal regions.

† A: stomach; Ce: cecum; B1, B2: small intestine; C1–C3: large intestine. (*Amia calva* has no cecum and *Micropterus* has no C3.)

guppies, *Poecilia reticulata* Peters. The Wisconsin specimens, however, were more elongate with a distinct long cylindrical neck and a bladder that was either abruptly spheroidal (in 1 specimen) or gradually enlarged distally. *Umbra limi* is a new intermediate host for *H. globuliforme*.

Seasonal site selection

Data from Table 7 show anteriormost localization of *H. globuliforme* during the summer. During the summer, stomach (A) and small intestine (B1, B2) were occupied by 9.2, 32.1, and 36.7% of worms, respectively (Table 7). Quick posterior migration would clearly reduce competition with *P. ambloplitis,* which usually occupy anterior locations. Regions A and B in *A. calva* were practically free of *H. globuliforme* infections during autumn and spring.

Site selection of *P. ambloplitis* in *A. calva* did not show any particular seasonal predeliction. The anteriormost gut regions (A, B1) appear to be the optimum sites for maturation and breeding, as they are for initial establishment of *P. ambloplitis* in *A. calva* during all seasons.

In bass, different forces appear to be involved in the seasonal site selection of *P. ambloplitis.* Here the major parenteric recruitment occurred largely during the spring, but most of the worms from Silver Lake (the larger sample) were in the stomach (38.3%) and the cecum (38.7%) (Table 7). The ceca of bass appear to be optimum for *P. ambloplitis* maturation and breeding. The stomach distribution appears to have been an artifact of regurgitation upon capture. Worms found in other intestinal locations (also from *M. dolomieui*) were mostly enteric plerocercoids

(terminal-II) that must have just penetrated the gut wall.

Concurrent infections

Both species of *Micropterus* were also commonly infected with *Neoechinorhynchus cylindratus* (Van Cleave, 1913) Van Cleave, 1919 and *Leptorhynchoides thecatus* (Linton, 1891) Kostylev, 1924 (Acanthocephala) and less commonly with *Camallanus oxycephalus* Ward and Magath, 1916 (Nematoda) in both lakes. Rare infections with *Neoechinorhynchus prolixoides* Bullock, 1963 in both bass species were also noted from Silver Lake, and 1 largemouth bass from Tichigan Lake was infected with 1 *Pomphorhynchus bulbocolli* Linkins *in* Van Cleave, 1919 (Acanthocephala). The anterior position of both *P. ambloplitis* and *L. thecatus* did not show significant seasonal changes, whereas *N. cylindratus* underwent marked posterior migration between autumn and summer (see Amin [1986b] for details).

Amia calva was also occasionally infected with the trematodes *Azygia longa* (Leidy, 1851) in both lakes, *A. angusticauda* (Stafford, 1904) Manter, 1926 in Tichigan Lake, and *Macroderoides spiniferus* Pearse, 1924 in Silver Lake. *Azygia* spp. primarily occupied the stomach, and *M. spiniferus* were confined to the posterior 75% of the gut (Amin, 1982).

Hyperparasitism

One adult *P. ambloplitis* in the cecum of a 36-cm-long male largemouth bass from Silver Lake examined during the spring was penetrated by a male *L. thecatus.* Similarly, a *P. ambloplitis* ple-

Table 7. Continued.

Summer (Jun–early Aug) (%)								Autumn (late Oct, Nov) (%)							
N	A	Ce	B1	B2	C1	C2	C3	N	A	Ce	B1	B2	C1	C2	C3
305	9.2	—	32.1	36.7	15.8	2.6	3.6	117	—	—	—	—	95.7	1.7	2.6
62	3.2	—	24.2	—	72.6	—	—	4	—	—	—	—	75.0	25.0	—
757	83.5	—	11.5	1.1	1.4	0.3	2.2	88	80.7	—	19.3	—	—	—	—
218	59.2	—	39.4	—	—	0.5	0.9	225	46.2	—	31.1	—	9.4	13.3	—
67	43.3	23.9	3.0	10.4	3.0	16.4	—	7	—	—	28.6	42.9	—	28.5	—
2	100.0	—	—	—	—	—	—	10	10.0	20.0	40.0	20.0	10.0	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

rocercoid in the liver of a 46-cm-long female largemouth bass from Tichigan Lake examined during the autumn was penetrated by a female *L. thecatus. Leptorhynchoides thecatus* occasionally passes into extraintestinal sites of centrarchids (Amin, unpubl.). Both incidents appear to be chance occurrences. Two other similar associations were previously reported by Miller (1946) of *Echinorhynchus salvelini* Schrank, 1788 (=*Pomphorhynchus laevis*) (Zoega *in* Müller, 1776) Van Cleave, 1924 attached to *Eubothrium salvelini* (Schrank, 1790) and by Muzzall and Rabalais (1975) of *Acanthocephalus jacksoni* Bullock, 1962 (=*A. dirus* (Van Cleave, 1931) Van Cleave and Townsend, 1936) attached to *Proteocephalus* sp. The first case was attributed to overcrowding and the second to chance occurrence.

Other helminths

A few individuals of at least 3 species of *Proteocephalus* Weinland, 1858 were found in the ceca and intestines of largemouth bass from both lakes. One species (1 mature individual 130 mm long) in a Silver Lake bass had 4 suckers, each with pointed apex, and a sizable vestigial fifth sucker in a broad anterior depression. Another species (6 immature worms 20–40 mm long) from Silver Lake had 4 large highly muscular suckers deeply set in an expanded bulbous scolex well set off from a long neck, with faint segmentation. A third species (7 immatures 1–3 mm long and 6 mature adults 9–23 mm long) from both lakes had a gradually expanded scolex with 4 ovoidly expanded suckers and a dome-shaped fifth, almost equally expanded and not much smaller.

The juveniles and adults of this third species may actually belong to 2 different species. The above material was not sufficiently informative to assign satisfactory specific identifications. All specimens clearly only accidentally infected bass.

Conclusions

All work reported so far on the life history and development of *P. ambloplitis* since Cooper's (1918) earliest account has reported bass, *Micropterus* spp., as the definitive host. The more recent additions to Hunter's (1928) and Hunter and Hunter's (1929) scheme and the understanding of parenteric migration of plerocercoids by Fischer and Freeman (1969, 1973), Esch et al. (1975), and Eure (1976) were also based on studies of *M. dolomieui*. Records of bowfin as a host of adult *P. ambloplitis* were noted by Hoffman (1967). This study shows that bowfin, and not bass, is the major host of *P. ambloplitis* in southeastern Wisconsin This host specificity occurs in the presence of large populations of bass in the same waters. This is clearly a matter of more than "host role change" as explained by Amin (1987) and must involve a certain element of host preference. The role of other definitive hosts, e.g., *Morone chrysops* and *M. mississippiensis* (Arnold et al., 1968; McReynolds and Webster, 1980) in the biology of *P. ambloplitis* is not known.

Bowfin become infected by ingesting plerocercoid (middle-II)-infected fish intermediate hosts. Enteric *P. ambloplitis* has a longer life span and a longer breeding season in bowfin than in bass, even though it also seems to disappear during the winter. In bass, *P. ambloplitis* is present for

no more than 8 mo, with parenteric recruitment occurring mostly during the spring and possibly influenced by host size (sexual maturity), as has been reported in Ontario and Michigan by Fischer and Freeman (1969) and Esch et al. (1975), respectively. In these 2 locations, the life span of enteric *P. ambloplitis* appeared to be somewhat shorter than in Wisconsin bass (this study). Enteric infections in the winter (absent between September and November) were reported in South Carolina (Eure, 1976). The following factors thus appear to influence the seasonal development of *P. ambloplitis*: (1) temperature, (2) latitudinal differences, (3) host size (hormonal factors), and (4) host species. The first 3 factors were explored earlier (Fischer and Freeman, 1969; Esch et al., 1975; Eure, 1976) in bass and are, at least partially, supported by this study.

Initial establishment and maturation of *P. ambloplitis* appear to occur in the anteriormost locations of both bass and bowfin digestive tracts. These traits were not significantly seasonally variable. Although initial establishment of *H. globuliforme* appeared also to have occurred in the anteriormost gut locations of the bowfin, further development and breeding occurred exclusively in the large intestine. Metabolic requirements of maturation and reproduction as well as decreasing competition with *P. ambloplitis*, which consistently occupied anterior gut regions of this host, probably influenced the location of *H. globuliforme*. Recruitment of *H. globuliforme* in *A. calva*, like that of *P. ambloplitis*, depended on the ingestion of plerocercoid-infected fish intermediate hosts, involving at least *U. limi* in Tichigan Lake during the summer, with active reproduction occurring during the spring and peaking in the summer. Adult *H. globuliforme* appear to live in *A. calva* from recruitment of initial juveniles in spring and summer to gravid adults in the same summer. The seasonal ecology of *H. globuliforme* in its fish definitive host, *A. calva*, is reported here for the first time.

Both tapeworm species had larger population sizes in the smaller land-locked Silver Lake than in the larger river-connected Tichigan Lake. The difference in tapeworm distribution and prevalence between lakes may also have been related to differences in eutrophication levels affecting intermediate host population parameters and visibility as well as definitive host feeding strategies. The enhancement of population density of other helminth species in closed systems like Silver Lake has also been demonstrated (Amin,

1986a, b). Seasonal differences in temperature (more extreme in Silver Lake than in Tichigan Lake) appeared to have affected the feeding behavior and subsequently the recruitment of tapeworms, e.g., *P. ambloplitis*, by *A. calva*.

Of the relatively common helminth associates in bass, only *L. thecatus* shared anterior gut locations with *P. ambloplitis*; neither helminth showed significant seasonal changes in site selection. This clearly provided the opportunity for an accidental (opportunistic?) attachment of 1 *L. thecatus* to an individual *P. ambloplitis*.

Deposited Specimens

Haplobothrium globuliforme from *A. calva* from Tichigan Lake (USNM Helm. Coll. Nos. 80515–80518) and from Silver Lake (HWML Coll. Nos. 24913–24922). *Proteocephalus ambloplitis* from *A. calva* from Tichigan Lake (USNM Helm. Coll. Nos. 80519–80522) and from Silver Lake (HWML Coll. Nos. 24923–24933), and from *M. salmoides* from Tichigan Lake (USNM Helm. Coll. Nos. 80523–80525) and from Silver Lake (HWML Coll. Nos. 24934–24946).

Acknowledgments

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Cestoda from Lake Fishes in Wisconsin: Occurrence of *Proteocephalus* in *Esox* and Other Fish Species

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ABSTRACT: At least 4 species of *Proteocephalus* are reported from Silver and Tichigan lakes in southeastern Wisconsin: *P. pinguis* LaRue, 1911 and *P. percae* (Müller, 1780) from northern pike, *Esox lucius,* and *P. perplexus* LaRue, 1911 and *P. singularis* LaRue, 1911 from longnose gar, *Lepisosteus osseus. Proteocephalus singularis* was also recovered from a bluegill, *Lepomis macrochirus* (a new host record). One thousand eight hundred twelve fishes from 32 species from both lakes and 1,543 fishes from 27 species from connected waters were examined. Many larval forms of *Proteocephalus,* including *P. ambloplitis* (Leidy, 1887), are also reported from 10 species of fish. *Proteocephalus percae* appears to represent a new geographic record in North America. The most common species was *P. pinguis.* This tapeworm was considerably larger than previous descriptions indicate and was equally abundant in both lakes surveyed. It was more common in males than females and in older than younger *Esox.* Recruitment occurred in late summer and autumn, development in winter, and sexual maturity and reproduction in the spring. The infectious cycle in the definitive host was from August–September to April–May and in the intermediate host was during the summer. No seasonal migration was observed. For the most part, worms established, developed, matured, and reproduced in the anterior part of the small intestine. The helminth fauna of *E. lucius* in southeastern Wisconsin is considered poor compared to that of the same host in more northern latitudes. The only other helminth parasites recovered were *Leptorhynchoides thecatus* (rare), *Camallanus oxycephalus* (rare), and *Neoechinorhynchus cylindratus* (more common). This is the first report of the seasonal ecology of *P. pinguis* in North America.

KEY WORDS: Cestoda, Wisconsin fish, *Proteocephalus* spp., ecology, host distribution, seasonal distribution, host sex, host size, site selection.

This is the fourth in a series of reports on the ecology and seasonal relationships of cestode parasites of fish from 2 eutrophic lakes (1 river-fed and 1 land-locked) in southeastern Wisconsin. The first report on Caryophyllaeidae (Amin, 1986a) included the description of a new species, *Isoglaridacris multivitellaria.* The second (Amin, 1990) dealt with *Proteocephalus ambloplitis* (Leidy, 1887) Benedict, 1900 in its fish intermediate hosts. The third (Amin and Cowen, 1990) elucidated the role of bowfin, *Amia calva,* largemouth bass, *Micropterus salmoides,* and smallmouth bass, *M. dolomieui,* in the cycling of *P. ambloplitis* suprapopulations in Wisconsin and the seasonal ecology of *Haplobothrium globuliforme* Cooper, 1914 in bowfin. This paper also included records of at least 3 other species of *Proteocephalus* accidentally infecting bass. The present work addresses all other species of *Proteocephalus* obtained from these 2 lake systems, with particular emphasis on the ecology of the most common species, *P. pinguis.*

Previous studies of fish parasites in various Wisconsin waters usually included parasite–host lists, which were occasionally annotated. Those studies that contained host records similar to those found in the present investigation include Pearse (1924), Bangham (1944), and Fischthal (1947, 1952). Additional data from pike were reported from elsewhere by Hunter (1929), Van Cleave and Mueller (1934), Watson and Dick (1980), and Muzzall (1984). Most recently, Shostak and Dick (1989) studied the position of *P. pinguis* within the intestine of naturally infected *E. lucius* relative to host stomach contents. The ecological information included herein is reported for *P. pinguis* in North America for the first time.

Materials and Methods

The fishes examined were from Silver Lake (Kenosha County), a 188-ha eutrophic land-locked lake, and from Tichigan Lake (Racine County), a 458-ha lake in an advanced state of eutrophication on the Fox River (a tributary of the Mississippi River). Seasonal collections were made from both lakes during the spring (April), summer (June, July, and early August), and autumn (late October and November) between 1977 and 1979 and from Silver Lake during the summer of 1976.

One thousand eight hundred twelve fishes representing 32 species and 10 families (Amiidae, 1 species; Catostomidae, 7; Centrarchidae, 9; Cyprinidae, 2; Esocidae, 2; Ictaluridae, 4; Lepisosteidae, 1; Percidae, 2; Salmonidae, 2; Serranidae, 2) were captured by electroshocking from lakes. An additional 1,543 fishes representing 27 species and 11 families (Amiidae, 1; Cato-

Table 1. Comparison between the major anatomical features of *Proteocephalus pinguis* from Wisconsin and those from the original description by LaRue (1914).

Character	Wisconsin material* $\bar{x}$ (range)	Original description
Strobila		
Length (mm)	206.93 (114–440)	Up to 90
Max. width (mm)	2.00 (1.20–2.60)	1.24
Scolex		
Length (mm)	2.28 (1.60–2.40)	0.20–0.25†
Max. width (mm)	0.91 (0.72–1.20)	0.35; up to 0.45
Sucker diameter (μm)	160 (133–210)	95–105
5th sucker diameter (μm)	103 (70–140)	50–75
Testis		
Dimensions (μm)	92×78 (42–140×42–112)	50×40–50
Number	60 (49–82)	54–70
Cirrus sac		
Length (μm)	261 (154–420)	130–140
Max. width (μm)	102 (70–140)	50–60
Egg dimensions (μm)	22×19 (19–26×16–26)	18×16

* $N = 15$; all mature adults, some gravid, obtained during the spring.
† Probably a misprint for 2.0–2.5 mm.

stomidae, 3; Centrarchidae, 6; Cyprinidae, 5; Cyprinodontidae, 2; Esocidae, 2; Gasterosteidae, 1; Ictaluridae, 4; Percidae, 3; Serranidae, 1; Umbridae, 1) were collected in a channel draining the swampy western area of Tichigan Lake, using seines or minnow traps.

Fish were systematically dissected shortly after capture. Parasites were systematically recovered from predesignated gut regions comprising the stomach (region A), small intestine (region B), and the first and second halves of the large intestine (regions C1 and C2). Cestodes were processed and mounted as in Amin (1986a) and placed in 3 categories: juveniles (strobila with only immature proglottids), adults (posterior proglottids sexually mature), and gravid (at least some proglottids with eggs). Mean values refer to the number of worms recovered/number of fish examined. Representative specimens were deposited in the U.S. National Museum Helminthological Collection (USNM Helm. Coll.) and in the University of Nebraska State Museum's Harold W. Manter Laboratory Collection (HWML Coll.). Slides of additional material are in the author's collection.

Results

Proteocephalus pinguis LaRue, 1911

Major anatomical structures of *P. pinguis* were measured and compared with those in the original description of LaRue (1914) (Table 1). All specimens studied were recovered from *E. lucius* in both Silver and Tichigan lakes proper during autumn, spring, or summer.

The prevalence and intensity of infection of *P.*

pinguis in *E. lucius* were almost identical from the land-locked Silver Lake (75%, 10.8) and the river-fed Tichigan Lake (73%, 10.5) (Table 2). In addition, 1 55-cm-long northern pike obtained in February 1978 from Silver Lake yielded 9 worms (1 gravid and 8 mature), 2 other *E. lucius* obtained on 30 May 1979 in Tichigan Lake canal yielded 87 worms (17 gravid, 53 adults, and 17 juveniles), and 1 of 3 pickerel, *Esox americanus,* examined from Silver Lake yielded 1 juvenile *P. pinguis* in October 1978.

The prevalence and intensity of *P. pinguis* infections in *E. lucius* males and females of various sizes (total length) are shown in Table 3. Infections were more prevalent and heavier in males (87%, 12.8) than in females (58%, 8.1) and in larger than in smaller fish.

Both prevalence and intensity of *P. pinguis* in *E. lucius* from both lakes were lowest in the summer (43%, 1.9), increased in the autumn (68%, 8.5), and peaked in the spring (100%, 19.2) (Table 2). Gravid worms and juveniles were recovered during all seasons, but the largest proportion of juveniles (74%) and smallest proportion of gravid worms (3%) were observed in the autumn (Table 4). Most worms (96%) matured by April, and one-half of these were gravid. The few worms recovered in the summer were mostly juveniles (77%).

The largest concentration of worms in pike was

Table 2. Prevalence and intensity of *Proteocephalus pinguis* infections in *Esox lucius* from Silver and Tichigan lakes proper, 1977 and 1978.

Lake	Autumn (late Oct, Nov)	Spring (Apr)	Summer (Jun–early Aug)	Total
Silver				
Fish: inf./exam. (%)	10/15 (67)	5/5 (100)	0/0	15/20 (75)
Cestodes: no. ($\bar{x}$/fish) max.	128 (8.5) 37*	88 (17.6) 32	0*	216 (10.8) 37
Tichigan				
Fish: inf./exam. (%)	5/7 (71)	8/8 (100)	3/7 (43)	16/22 (73)
Cestodes: no. ($\bar{x}$/fish) max.	58 (8.3) 15	161 (20.1) 49	13 (1.9) 9	232 (10.5) 49
Total				
Fish: inf./exam. (%)	15/22 (68)	13/13 (100)	3/7 (43)	31/42 (74)
Cestodes: no. ($\bar{x}$/fish) max.	186 (8.5) 37	249 (19.2) 49	13 (1.9) 9	448 (10.7) 49

* One of 2 *Esox americanus* collected during the autumn was infected with 1 juvenile *P. pinguis,* and another *E. americanus* examined during the summer was not infected.

in the region of the small intestine directly behind the stomach during all seasons (Table 5). In the autumn, spring, and summer, 32%, 5%, and 8% of the worms, respectively, were distributed elsewhere.

Proteocephalus percae (Müller, 1780)

This was the only other species of *Proteocephalus* recovered from *E. lucius* in this study. Ten specimens were obtained: 7 worms (3 gravid and 4 mature) from 2 *E. lucius* in Silver Lake in November 1978, 2 (1 gravid and 1 juvenile) from 1 *E. lucius* in Tichigan Lake in July 1978, and 1 gravid worm from *E. americanus* in Tichigan Lake canal in June 1978.

Proteocephalus perplexus LaRue, 1911

Only 1 gravid worm of this species was recovered from the stomach of a 59-cm male longnose gar, *Lepisosteus osseus,* in Silver Lake on 25 June 1978. Fourteen and 9 gar were examined from Silver and Tichigan lakes, respectively.

Proteocephalus singularis LaRue, 1911

Four gravid worms were recovered from the stomach (1 extended considerably into gut region B directly behind the stomach) of a 89-cm female longnose gar in Silver Lake on 21 June 1978. An additional gravid worm was recovered from the intestine of a bluegill, *Lepomis macrochirus,* in Silver Lake on 1 May 1982; this is a new host record. Three hundred one and 212 bluegill were examined from Silver and Tichigan lakes, respectively.

Proteocephalus spp.

Plerocercoids of at least 2 other species of *Proteocephalus* were recovered from the intestine or body cavity of 10 fish species from 7 families from Tichigan Lake canal and Silver Lake (Table 6). As with *P. ambloplitis* (Amin, 1990), most of these were recovered from other hosts, with the definite exception of those from starhead topminnow, *Fundulus notti,* and blackstripe topminnow, *F. notatus* (see footnotes of Table 6).

Table 3. Prevalence and intensity of *Proteocephalus pinguis* infections based on sex and size of *Esox lucius* from Silver and Tichigan lakes.

Fish total length (cm)	Male fish	Female fish	Total
10–24	2/3 (67) 4.7*	0/2	2/5 (40) 2.8
25–39	2/3 (67) 2.0	1/1 (100) 1.0	3/4 (75) 1.8
40–54	12/13 (92) 15.7	2/4 (50) 9.7	14/17 (82) 14.3
55–69	2/2 (100) 15.5	6/9 (67) 11.9	8/11 (73) 12.5
≥70	2/2 (100) 19.5	2/3 (67) 2.3	4/5 (80) 9.2
Total	20/23 (87) 12.8	11/19 (58) 8.1	31/42 (74) 10.7

* No. of fish infected/no. of fish examined (% prevalence) $\bar{x}$ intensity.

Table 4. Seasonal development of *Proteocephalus pinguis* in *Esox lucius* from Silver and Tichigan lakes (combined), 1977 and 1978.

Cestode developmental stages	Total no. of worms	No. and prevalence (%) of worms		
		Autumn (late Oct, Nov)	Spring* (Apr)	Summer (Jun–early Aug)
All stages	448	186	249	13
Juvenile (%)†	158	138 (74)	10 (4)	10 (77)
Mature (%)	163	43 (23)	119 (48)	1 (8)
Gravid (%)	127	5 (3)	120 (48)	2 (15)

* One *E. lucius* from Tichigan Lake canal collected on 30 May 1979 yielded 87 worms (17 juveniles, 53 mature, and 17 gravid adults).

† The percent prevalence compares data in vertical columns.

Discussion

The classical features of spatulate scolex, sucker interrelationships, and reproductive details characteristic of *P. pinguis* were clearly evident in the Wisconsin specimens, which were, however, considerably larger than those in the original description. The strobilae of some of the Wisconsin specimens were about 5 times as long as the maximum of 90 mm reported by LaRue (1914) and Hunter (1929). Meyer's (1958) specimens from Iowa did not "exceed the limits prescribed for this species except in the dimension of the cirrus pouch." Size differences in the structures compared in Table 1 suggest that ratios among measurements of certain structures, e.g., suckers or suckers and scolex, may be more important than raw measurements for species diagnosis. Differences in the dimensions of such critical diagnostic characteristics as suckers, testes, cirrus sac, and eggs are particularly noteworthy.

The recovery of *P. pinguis* solely from *Esox,* although 32 species of fish (N = 1,812) were examined from Silver and Tichigan lakes and 27

species (N = 1,543) from Tichigan Lake canal, agrees with the previously published literature indicating the high host specificity of this widely distributed cestode.

In *Esox,* infections with *P. pinguis* may be quite heavy because 2 links in the food chain, crustaceans and fish as intermediate hosts (first noted by Hunter, 1929), serve to infect younger and older pike, respectively. Van Cleave and Mueller (1934), Watson and Dick (1980), and Muzzall (1984) reported prevalences of 100%, 96.2%, and 92%, respectively, with an average intensity of 70 worms per fish reported by Watson and Dick (1980) and up to 100 worms per fish reported by Van Cleave and Mueller (1934). These values do not vary much from those obtained in the present study (Table 2).

The main variation, however, appears to result from latitudinal differences in the complexity of the helminth fauna of *E. lucius.* The parasite fauna of *E. lucius* is considerably richer in diversity in more northern waters. For example, Fischthal (1953) and Watson and Dick (1980) found 21 and 18 helminth species in *E. lucius* from northern Wisconsin and Manitoba, respectively. Of the 5 species in the family, the holarctic *E. lucius* has the greatest tolerance to cold environments and is the only species to extend into the arctic (Lee et al., 1980). Southern Wisconsin is near the southern edge of the natural range of *E. lucius.* Fish closer to the center of their range appear to harbor richer parasitic faunas than those of marginal distribution. In addition to *P. pinguis* (and *P. percae*), only the acanthocephalans *Leptorhynchoides thecatus* (Linton, 1891) Kostylev, 1924 (3 juveniles from 2/20 fish in Silver Lake [Amin, 1988]) and *Neoechinorhynchus cylindratus* (Van Cleave, 1913) Van Cleave, 1919 (590 worms from 9/20 fish in Silver Lake [Amin, 1986b]) and the nematode *Camallanus oxycephalus* Ward and Magath, 1916 (4 worms from

Table 5. Seasonal site selection of *Proteocephalus pinguis* in *Esox lucius* from Silver and Tichigan lakes proper (combined), 1977 and 1978.

Season	No. of worms	% worms in intestinal regions (juvenile, adult, gravid)*			
		A	B	C1	C2
Autumn	186	9 (100, 0, 0)	68 (67, 33, 0)	11 (86, 14, 0)	12 (100, 0, 0)
Spring	249	0	95 (4, 49, 47)	4 (0, 25, 75)	1 (0, 50, 50)
Summer	13	0	92 (75, 8, 17)	0	8 (100, 0, 0)

* Juvenile = worms with only immature segments, adult = worms with sexually mature segments, gravid = adult worms with segments containing eggs. A, stomach; B, small intestine; C1 and C2, first and second halves of large intestine.

Table 6.   Plerocercoids of *Proteocephalus* recovered from various Tichigan Lake canal (TLC) and Silver Lake (SL) fishes, 1977-1979.

Fish species	Location	No. of fish infected/no. examined (no. of worms)			Site of infection	Remarks
		Autumn (late Oct, Nov)	Spring (Apr)	Summer (Jun–early Aug)		
Centrarchidae						
*Lepomis macrochirus**	TLC	0/0	0/57	3/64 (4)	Gut lumen	Minute larvae
	SL	0/141	3/62 (4)	3/98 (3)	Gut lumen	Large (up to 35 mm) larvae
*Pomoxis nigromaculatus**	SL	0/18	3/25 (6)	0/4	Gut lumen	Minute and small larvae
Cyprinodontidae						
Fundulus notatus†	TLC	0/0	1/1 (10)	6/18 (22)	Gut lumen	Long (up to 20 mm), slender
Fundulus notti†	TLC	0/0	0/0	4/6 (70)	Gut lumen	Larvae–juveniles (some segmented)
Gasterosteidae						
Culaea inconstans	TLC	0/2	0/45	4/135 (4)	Gut lumen	Minute larvae, in 3 hosts
					Gut wall	Cysts, in 1 host
Ictaluridae						
Ictalurus melas	SL	0/0	0/0	1/1 (1)	Gut lumen	20-mm larva
Lepisosteidae						
*Lepisosteus osseus**	SL	0/0	0/3	1/11 (12)	Gut lumen	ca. 10-mm larvae
Percidae						
Etheostoma nigrum	TLC	0/1	2/108 (many)	0/14	Gut wall	Minute cysts
*Perca flavescens**	TLC	0/0	0/0	1/2 (3)	Gut lumen	Minute larvae
Umbridae						
Umbra limi	TLC	1/10 (4)	2/66 (70)	0/10	Body cavity	Mostly minute cysts

* Parenteric plerocercoids of *Proteocephalus ambloplitis* have been reported from these fish intermediate hosts in Tichigan and Silver lakes proper (Amin, 1990).
† Worms from these fish are definitely not *Proteocephalus ambloplitis*.

3/22 fish in Tichigan Lake [Amin, 1984]) were reported in southeastern Wisconsin.

The almost identical infection parameters of *P. pinguis* in *E. lucius* from the land-locked Silver Lake and the larger, more eutrophic, and river-fed Tichigan Lake (Table 2) suggest that these environmental factors do not significantly affect infection of northern pike with this cestode. In all other helminth species examined, some were either more dominant in Silver Lake, e.g., *P. ambloplitis* (Amin, 1990; Amin and Cowen, 1990), caryophyllaeid cestodes (Amin, 1986a), and *Neoechinorhynchus* spp. (Amin, 1986b), or in Tichigan Lake, e.g., *Pomphorhynchus bulbocolli* Linkins *in* Van Cleave, 1919 (Amin, 1987).

The relatively higher values of prevalence and mean intensity of *P. pinguis* infections in larger fish (Table 3) probably reflect the greater volume of food, including infected fish as intermediate hosts, consumed by these pike (Lawler, 1965; Kipling and Frost, 1970). Cannibalism, as suggested by Hunt and Carbine (1951) in Michigan and Lawler (1965) in Canada, may also contribute an additional source of infection of larger pike. However, the abundance of *P. pinguis* in Manitoba was found to be independent of *E. lucius* age or sex (Watson and Dick, 1980); no data were supplied. This was attributed to "constant intake of *P. pinguis* during the transition of diet from copepods to small fish. . . ." The sizes of Watson and Dick's (1980) fish were not indicated, and the relevance of their interpretation to the data presented here remains questionable because most of the Wisconsin pike reported have already passed that "transitional" stage.

Data in Tables 2 and 4 indicate that recruitment of *P. pinguis* begins in the summer, when pike are scarcely infected. Major recruitment, however, occurs in the autumn, when worm numbers show significant build-up. Maturation, reproductive activity, and abundance reach a peak in the spring (April) before worms are subsequently lost. The few juvenile and gravid worms obtained during the summer (Table 4) are new recruits and late evacuees, respectively. The generation cycle of *P. pinguis* thus appears to take <1 yr in *E. lucius,* with the immature stages developing in the crustacean intermediate hosts mostly during the summer. *Esox* acquire *P. pinguis* infections by feeding on infected crustacean or fish intermediate hosts. Watson and Dick (1980) also reported highest abundance of *P. pin-*

guis in *E. lucius* during "late winter" (the Manitoba winter extends January–April). They provided no numerical data but mentioned the "loss of gravid worms during spring" (May–June). Hunter (1929) also recovered an adult *P. pinguis* from a pike on 15 August in New York and indicated that "the parasite may reach maturity in one year."

Related species of *Proteocephalus* showing a similar seasonal abundance pattern include *P. pearsei* LaRue, 1914 from yellow perch (*Perca flavescens*) in Ontario (Cannon, 1973), *P. exiguus* LaRue, 1911 from lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*) in Manitoba (Watson and Dick, 1979) and from grayling (*Thymallus arcticus*; in which the tapeworm does not mature) in Lake Baikal, U.S.S.R. (Rusinek, 1987a, b), and *P. filicollis* Rudolphi, 1802 from *C. artedii* in Manitoba (Watson and Dick, 1979). Only Watson and Dick (1979) referred to the May loss of gravid adults and their replacement by immatures in June. Similar seasonal patterns were better documented for *P. filicollis* from threespine stickleback (*Gasterosteus aculeatus*) in England (Hopkins, 1959), *P. torulosus* (Batsch, 1786) from dace (*Leuciscus leuciscus*) in England (Kennedy and Hine, 1969), and *P. percae* from *E. lucius* in Czechoslovakia (Moravec, 1979).

The gut region directly behind the stomach of *E. lucius* appears to be the site in which *P. pinguis* undergoes establishment, development, maturation, and sexual reproduction. Most mature and gravid worms as well as juvenile worms were localized in this gut region during the spring and autumn, respectively. The autumn juveniles found in the stomach or large intestine (Table 5) may have been either incoming or evacuating after unsuccessful establishment. *Proteocephalus pinguis* thus does not appear to undertake seasonal migration in the intestinal tract of *E. lucius.* Shostak and Dick (1989) observed that *P. pinguis* did not migrate in the intestine of *E. lucius* from Manitoba in response to feeding activity of the host.

Proteocephalus percae is normally reported from *Perca* and *Esox,* among other fishes, in Europe (LaRue, 1914; Yamaguti, 1959). I am not aware of any record of *P. percae* in North America. The anatomical similarities to LaRue's (1914) description of the species were compelling even though some measurements did not quite match.

Proteocephalus perplexus appears to be a com-

mon cestode of *Amia calva* and *Lepisosteus*; *P. singularis* is common in *Lepisosteus* in Wisconsin and elsewhere in North America (Pearse, 1924; Bangham, 1944; Fischthal, 1947, 1952; Hoffman, 1967). The record of *P. singularis* from *Lepomis macrochirus* is new but not considered accidental because the worm was gravid. Like *P. pinguis*, measurements of *P. singularis* were considerably larger than those included in LaRue's (1914) description.

Pomoxis nigromaculatus, Lepomis macrochirus, Ictalurus melas, Perca flavescens, and *Lepisosteus osseus,* from which plerocercoids resembling those of *P. ambloplitis* were recovered (Table 6), are intermediate hosts of *P. ambloplitis* in the same waters (Amin, 1990). *Umbra limi* also had plerocercoids of *Haplobothrium globuliforme* Cooper, 1914, which, like *P. ambloplitis,* utilizes *A. calva* as a definitive host (Amin and Cowen, 1990). The plerocercoids from *Etheostoma nigrum* and *Culaea inconstans* were similar to those from *U. limi;* all 3 host species are common forage fish for *A. calva* (Amin, unpubl.). This suggests that the plerocercoids from *U. limi, E. nigrum,* and *C. inconstans* may be *P. ambloplitis.* Plerocercoids from *Fundulus notti* and *F. notatus* were clearly different.

Deposited Specimens

Proteocephalus pinguis from *E. lucius:* Silver L., HWML Coll. Nos. 31136–31140; Tichigan L., USNM Helm. Coll. Nos. 80847–80850. *Proteocephalus* sp. from *U. limi* (Tichigan L.): HWML Coll. No. 31141 and USNM Helm. Coll. No. 80851; from *F. notti* (Tichigan L.): HWML Coll. Nos. 31142, 31147; from *F. notatus* (Tichigan L.): USNM Helm. Coll. No. 80852; from *C. inconstans* (Tichigan L.): HWML Coll. No. 31144 and USNM Helm. Coll. No. 80853; from *L. macrochirus:* Silver L., HWML Coll. Nos. 31144, 31148; Tichigan L., USNM Helm. Coll. No. 80854. *Proteocephalus percae* from *E. lucius* (Silver L.): HWML Coll. No. 31145 and USNM Helm. Coll. No. 80855. *Proteocephalus singularis* from *L. osseus* (Silver L.): HWML Coll. Nos. 31146, 31149 and USNM Helm. Coll. No. 80856. Slides of other material are in the author's collection.

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An Aberrant Acephalic Metacestode and Other Parasites of *Masticophis flagellum* (Reptilia: Serpentes) from Texas

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ABSTRACT: Two of 12 (17%) western coachwhip snakes, *Masticophis flagellum testaceus,* from Texas were found to be infected with parasites. Several aberrant metacestodes occurred free in the pericardial cavity of 1 snake. Each lacked a scolex and possessed a disorganized body musculature and a highly vacuolated parenchyma. These aberrant metacestodes were structurally similar to metacestodes reported as *Sparganum proliferum* (Stiles, 1908) from various mammalian hosts, but asexual proliferation could not be confirmed in the present case. This snake also harbored numerous tetrathyridia of *Mesocestoides* sp. Vaillant, 1863, which were encapsulated in the intestinal wall. The tetrathyridia showed no sign of deformity or asexual activity. Other parasites infecting this snake included *Eimeria zamenis* Phisalix, 1921, *Ochetosoma georgianum* (Byrd and Denton, 1938), and *Physaloptera* sp. Rudolphi, 1819. The only other parasitized snake harbored *Sarcocystis* sp. Lankester, 1882. New host and locality records are reported herein.

KEY WORDS: Cestoda, coachwhip snake, *Eimeria zamenis, Masticophis flagellum, Mesocestoides,* metacestode, *Ochetosoma georgianum, Physaloptera,* Reptilia, *Sarcocystis, Sparganum proliferum,* tetrathyridium.

A large amount of information is available on the natural history and ecology of the coachwhip snake, *Masticophis flagellum* (Shaw, 1802). Wilson (1973b), in a species account, summarized data on the biology of the various taxa of this snake; however, little is known regarding its parasites.

The first report of parasites from coachwhips appears to be that of Leidy (1856), who described *Physaloptera abjecta* in *Psammophis flagelliformis* Holbrook, 1842 (=*M. flagellum*) from an unknown locality in the southern United States. Later, Nicoll (1911) reported *Neochetosoma* (=*Ochetosoma* Braun, 1901) *formosus* in *Zamensis flagelliformis* (=*M. flagellum*). Harwood (1932) described a nematode, *Kalicephalus agkistrodontis flagellus,* from a single *Coluber* (=*Masticophis*) *flagellum* in Texas, and Reiber et al. (1940) reported *Physaloptera variegata* (=*P. abjecta* Leidy, 1856) (see Morgan, 1943) from a coachwhip from Georgia. Schad (1962), in a revision of *Kalicephalus,* reported *Kalicephalus* (*Kalicephalus*) *costatus parvus* Ortlepp, 1923 and *K.* (*Inermiformis*) *inermis coronellae* (Ortlepp, 1923) Lichtenfels, 1980 from *M. flagellum.* Hubbard (1938) reported over 1,000 unidentified cestode plerocercoids from a single specimen of *Coluber* (=*Masticophis*) *flagellum flavigularis* (Hallowell) from Oklahoma. Loomis (1956) recovered 3 species of ectoparasitic chigger mites from coachwhips from Kansas. Roudabush

(1937) reported a coccidian, *Eimeria zamenis* Phisalix, 1921, from a single *M. f. flagellum* from Iowa. To our knowledge, the only other report of parasites of *M. flagellum* was by Hilman and Strandmann (1960), who reported an intraerythrocytic hematozoan, *Hepatozoon serpentium,* from 4 *M. flagellum* in Texas.

During a survey of parasites of various reptile species in Texas, we found 1 *M. flagellum* that harbored a remarkable infection of aberrant acephalic metacestodes. These worms were similar to some occasionally reported from mammals, but they have not been reported previously from nonmammalian hosts. This report provides data on the morphology and histology of these metacestodes and documents the occurrence of other parasites in 2 of the 12 *M. flagellum* examined.

Materials and Methods

Between May 1986 and May 1988, 12 (6 male, 6 female) juvenile and adult western coachwhips, *Masticophis flagellum testaceus* (Say, 1823), were collected from Hood ($N = 3$), Johnson ($N = 5$), Somervell ($N = 3$), and Palo Pinto ($N = 1$) counties in north-central Texas. Snakes were taken either alive or as fresh road kills, measured (snout–vent length [SVL]: $\bar{x} \pm SD = 838.3 \pm 298.6$, range = 430–1,300 mm), and examined for parasites. Road-killed snakes were placed on ice and examined within 8 hr of collection; live snakes were killed within 24 hr with an overdose of sodium pentobarbital. A midventral incision was made, and the gastrointestinal tract, heart, liver, spleen, lungs, and

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oral cavity were examined for helminths. Fecal and intestinal contents were removed and placed in individual vials of 2.5% (w/v) aqueous potassium dichromate solution and examined for coccidian oocysts following methods of Upton and McAllister (1990). Trematodes were placed in distilled water to allow for ejection of eggs and then transferred onto glass slides and, with gentle coverslip pressure, fixed in alcohol–formalin–acetic acid (AFA). They were stained with Semichon's acetocarmine and mounted whole in Permount. Nematodes were killed in hot AFA, transferred to glycerine, and examined as temporary mounts.

Metacestodes from the pericardial cavity of 1 host were removed and fixed in 10% neutral-buffered formalin (NBF) and prepared as whole mounts by staining in acetocarmine, dehydrating in ethanol, clearing in methyl salicylate, and mounting in damar. Others were embedded in JB-4 methacrylate plastic, sectioned at 2 μm, stained with Harris' hematoxylin and eosin (H&E), and mounted in damar. The small intestine of the same snake appeared to be infected by encapsulated helminths and was fixed in NBF, embedded in Paraplast, sectioned at 10 μm, stained in H&E, and mounted in damar.

Voucher specimens of parasites were deposited in the U.S. National Parasite Collection, Beltsville, Maryland, with the following accession numbers: *Ochetosoma georgianum* (80820), *Physaloptera* sp. (80821), aberrant metacestode (80835), *Mesocestoides* sp. tetrathyridium (80836). Host voucher specimens were deposited in the Arkansas State University Museum of Zoology (ASUMZ).

Results

Of the 12 snakes examined, only 2 (17%) harbored parasites. One of the infected snakes (ASUMZ 7659), a female (SVL = 730 mm) collected in Somervell County on 18 April 1987, was infected with sporocysts of an unknown species of *Sarcocystis* Lankester, 1882 (see Upton and McAllister, 1990).

The other infected snake (ASUMZ 8419), a male (SVL = 1,300 mm) collected from Palo Pinto County on 18 July 1987, harbored several parasite species. This snake was moribund and malodorous when collected, but still alive. Sporulated coccidian oocysts recovered from the feces and gall bladder were identified as *Eimeria zamenis* Phisalix, 1921 (see Upton and McAllister, 1990). Two spirurid nematodes, *Physaloptera* sp. Rudolphi, 1819, were found in the stomach. Because only male worms were present, species identification was not possible.

Eight ochetosomatid flukes matching the description of *Ochetosoma georgianum* (syn. *Neorenifer georgianus*) (Byrd and Denton, 1938) were found in the oral cavity and upper esophagus of ASUMZ 8419. Measurements were as follows (mean length × width followed by the range in parentheses in μm unless otherwise stated): body 3.3 mm × 1.1 mm (2.9–3.6 mm × 1.0–1.2 mm); oral sucker 322 × 348 (274–340 × 329–388); acetabulum 426 × 455 (404–450 × 433–488); pharynx 163 × 170 (141–199 × 125–198); ovary 174 × 184 (131–197 × 140–254); testes 279 × 265 (187–370 × 168–387); eggs 42 × 28 (36–50 × 20–33).

Histologic sections of the small intestine of ASUMZ 8419 revealed nodules that were situated in the intestinal wall on each side of the muscularis layer. Each contained a tetrathyridium of *Mesocestoides* sp. (Fig. 1). These metacestodes were morphologically typical for the genus, possessing a solid hind body, highly organized musculature, well-developed unarmed tetraacetabulate scolex, and deep invagination canal. None showed any sign of asexual activity.

Several metacestodes occurred in the pericardium and pericardial cavity of ASUMZ 8419. These worms lacked scolices and primary lacunae (Figs. 2–4). They had various body forms, always with a poorly organized musculature and a highly vacuolated parenchyma. Some contained unidentified parenchymal inclusions that stained intensely with acetocarmine (Fig. 3). Some of the worms were asymmetrically branched, but no attempt was made to determine whether they were reproducing asexually. Histologic sections revealed that the parenchymal vacuoles were lined by a homogeneous eosinophilic layer. The vacuoles appeared to be extensive anomalous diverticula of the excretory system, with the eosinophilic lining conforming to the structure of the syncytial excretory epithelium (Figs. 5, 6). No gross pathology of the heart was noted in association with the worms' presence. These metacestodes did not occur in any other part of the host's body.

Discussion

The present study establishes a host record for *Sarcocystis* sp. Most of the parasites reported here have been reported previously from *M. flagellum,* although some of those reports are questionable. The ubiquitous *E. zamenis* has been reported previously from other North American colubrid snakes, including *M. f. flagellum* from Iowa (Roudabush, 1937; Upton and McAllister, 1990). Nematodes of the genus *Physaloptera* are common helminths of various colubrid snakes in North America (Baker, 1987) and were reported from *M. flagellum* by Leidy (1856).
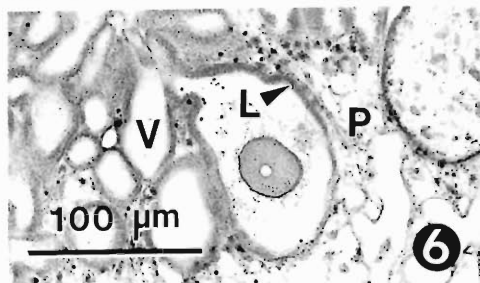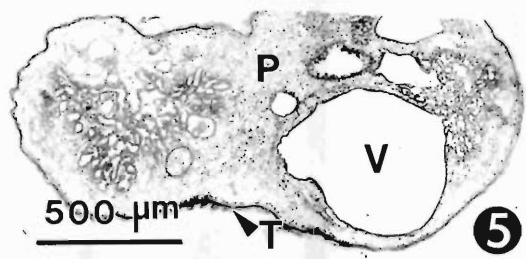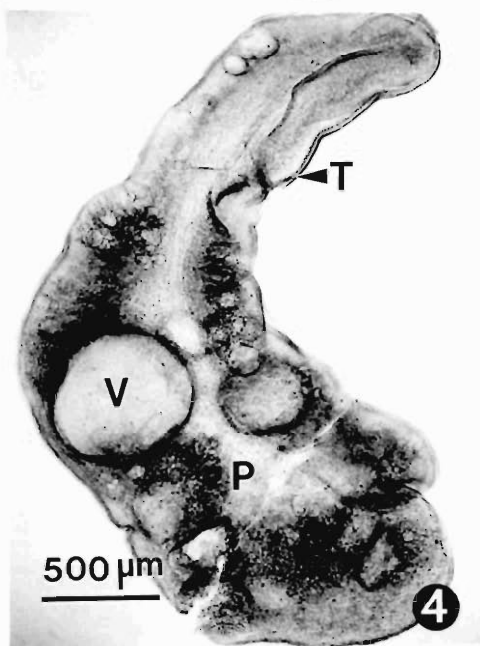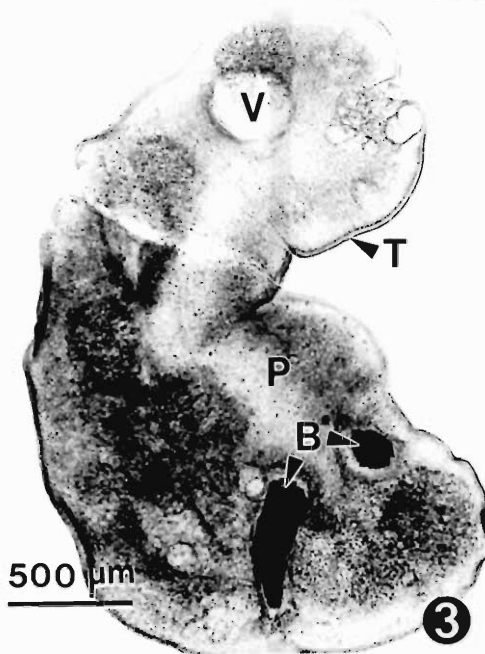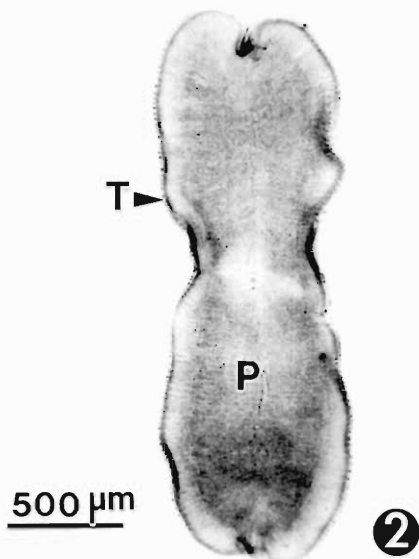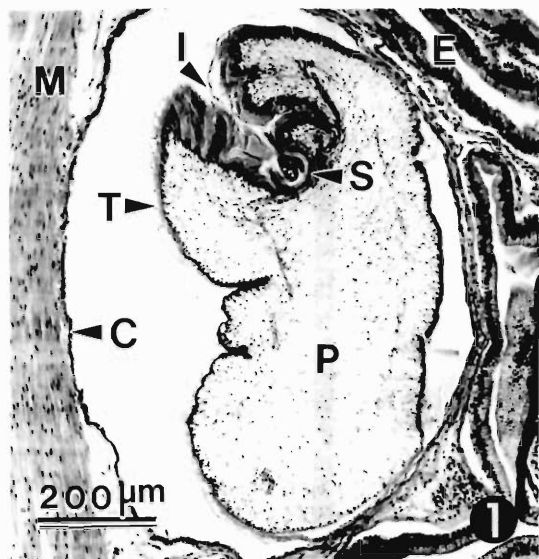
Figures 1–6. Metacestodes from *Masticophis flagellum*. 1. Longitudinal section of *Mesocestoides* sp. tetra-thyridium encapsulated between the mucosa and muscularis of the small intestine. Note prominent scolex, deep

Ochetosoma georgianum has been reported previously from the northern black racer, *Coluber constrictor constrictor,* in Georgia (Byrd and Denton, 1938) and Tennessee (Parker, 1941) and from the speckled kingsnake, *Lampropeltis getulus holbrooki,* and the Florida kingsnake, *L. g. floridana,* in Tennessee and Florida, respectively (Parker, 1941). *Ochetosoma formosus* was reported previously from *Leptodira annulata* and *M. flagellum* in South America (Nicoll, 1911). However, it is likely that the latter host was misidentified because *M. flagellum* ranges no farther south than northern Veracruz and Queretaro, Mexico (Dixon et al., 1972). Only *Masticophis mentovarius* is known to range as far south as northwestern Colombia and northern Venezuela (Wilson, 1973a). Thus, the present report probably represents a new host record from the genus *Ochetosoma.*

This is the first definite report of *Mesocestoides* sp. from *M. flagellum.* The unidentified plerocercoids reported by Hubbard (1938) were tetraacetabulate when large but lacked suckers when small. In 2 reviews, Hughes et al. (1941a, b) suggested that the plerocercoids reported by Hubbard (1938) might be *Mesocestoides* tetrathyridia, although they expressed some reservations. Hubbard's (1938) written report and drawings do not provide enough information to identify the worms, but they were undoubtedly a cyclophyllidean or proteocephalidean.

As far as we can determine, this is the first report of an aberrant acephalic metacestode from a naturally infected nonmammalian host. The worms reported here were structurally similar to many such metacestodes that have been reported from mammals throughout the world (see review by Beaver and Rolon, 1981). Because the scolex is lacking, it is impossible to obtain adults from such worms for definitive identification. However, certain morphological hallmarks allow some narrowing of possibilities. For example, the presence of a primary lacuna would suggest that a metacestode is either a taeniid cysticercus (Voge

and Berntzen, 1963), an anomalous hymenolepidid cysticercoid (Lucas et al., 1980), or some other cyclophyllidean (McAllister et al., 1989).

The aberrant worms reported in the present study lacked a primary lacuna, but their otherwise solid bodies possessed large vacuoles, apparently resulting from deformation of the excretory canals. Similar abnormalities were reported in metacestodes tentatively identified as *Sparganum proliferum* by Mueller (1938) and in unidentified metacestodes by Beaver and Rolon (1981). Other reports have tentatively identified aberrant acephalic metacestodes from European (Neumann, 1896; Sendrail and Cuillé, 1906; Ssolonitzin, 1933) and North American (Orthoefer et al., 1974; Barsanti et al., 1979; Greve et al., 1979) dogs as *Mesocestoides* tetrathyridia. However, the true identity has not been confirmed in any of the reported cases. The only verified report of aberrant tetrathyridia from a naturally infected host was that of Specht and Voge (1965), who collected asexually proliferative (and thus aberrant) forms from a single lizard population; however, these forms differed from the other aberrant metacestodes reported above in having well-developed scolices and lacking extensive vacuolation.

Solid-bodied metacestodes, such as pseudophyllideans, proteocephalideans, and *Mesocestoides* spp., are difficult to distinguish without the scolex. The organization of the body musculature allows differentiation of pseudophyllidean plerocercoids from *Mesocestoides* tetrathyridia in normal specimens (Andersen, 1983), but such distinctions break down in aberrant specimens such as those reported here. Thus, the identity of the present aberrant worms is unknown. It is possible that they are plerocercoids of a pseudophyllidean or proteocephalidean or tetrathyridia of *Mesocestoides.* The co-occurrence of the aberrant metacestodes and normal tetrathyridia in the same host does not argue for or against any of these possibilities. The snake was obviously exposed to infection by numerous par-

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← invagination canal, and solid hindbody parenchyma. 2–6. Unidentified aberrant metacestodes from the pericardial cavity. Note well-developed tegument and absence of scolex in all specimens. 2. Whole mount showing typical plerocercoidlike body form with solid hind body. 3. Whole mount showing vacuolated parenchyma and unidentified acidophilic bodies. 4. Whole mount showing highly vacuolated parenchyma. 5. Transverse section showing clusters of large and small vacuoles in the parenchyma. 6. Transverse section showing a high magnification of the thin uniform eosinophilic lining of the parenchymal vacuolations, resembling excretory duct epithelium. B, unidentified acidophilic bodies; C, host capsule; E, intestinal epithelium of host; I, invagination canal; L, eosinophilic lining of parenchymal vacuole; M, smooth muscle of host intestine; P, parenchyma; S, sucker of tetraacetabulate scolex; T, tegument; V, parenchymal vacuole.

asite species, and the 2 types of metacestodes could have been acquired at different times.

Acknowledgments

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Editor's Acknowledgment

Parasitism of Cottontail Rabbits (*Sylvilagus floridanus*) by *Obeliscoides cuniculi* in Response to Habitat Modification in the Cross Timbers of Oklahoma

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ABSTRACT: The influence of habitat modification on populations of *Obeliscoides cuniculi* in cottontail rabbits (*Sylvilagus floridanus*) was examined from 1987 to 1988 in the Cross Timbers ecosystem of Oklahoma. Five experimental brush control treatments, using combinations of the herbicides tebuthiuron and triclopyr with or without prescribed burning, were replicated 4 times on 20 32.4-ha pastures. Two hundred five rabbits (25 juvenile and 180 adult) were collected with an overall prevalence of infection of 97%. Prevalence in adult hosts apparently was not influenced by brush treatment, season, or year. Distribution of populations of *O. cuniculi* within cottontail rabbits was influenced significantly by season, with a higher degree of overdispersion in winter. The influence of brush treatment on the degree of overdispersion was not clear, but seasonal variation was low on untreated control pastures. Abundance of infections of *O. cuniculi* was significantly affected by brush treatment, season, and year of collection. Mean abundances were lower on annually burned pastures treated with triclopyr than on all other experimental pastures. Abundance of *O. cuniculi* in cottontail rabbits was higher in summer (58.8 ± 7.0) than winter (23.0 ± 4.4). Variations in the intensity of the prescribed burns and in season were probably important factors that influenced parasitism of cottontail rabbits by *O. cuniculi*.

KEY WORDS: cottontail rabbit, *Sylvilagus floridanus*, brush management, *Obeliscoides cuniculi*, Trichostrongylidae, herbicides, prescribed burning, tebuthiuron, triclopyr.

Parasitism in wildlife populations is strongly influenced by the type of habitat in which the host resides (Custer and Pence, 1981; Pence et al., 1983; Corn et al., 1985). Geographic variation in communities of helminths in wildlife appears to be associated in part with changes in selected habitat attributes. For example, Mollhagen (1978) suggested that the composition of the helminth community in cotton rat (*Sigmodon hispidus*) populations in Texas was influenced by moisture characteristics of the habitat. Similarly, Kinsella (1974) reported significant differences in prevalence and abundance of nematodes and cestodes among populations of cotton rats in freshwater marshes, saltwater marshes, and relatively xeric upland habitats from north-central to south-central Florida. Jacobson et al. (1978) noted significant differences in abundances of nematodes and cestodes in populations of eastern cottontail rabbits (*Sylvilagus floridanus*) between southeast and southwest Virginia; however, these 2 areas differed markedly in altitude, topography, length of growing season, soil pH, and land management practices, which made interpretation difficult.

Although previous studies demonstrate a strong relationship between parasite communities of a host and habitat attributes when compared across geographic regions, they provide little insight into host–parasite relationships following habitat alterations in a local area. Natural and human-induced successional changes are a common component of wildlife habitats. Intensive land-use and range/wildlife improvement practices are capable of drastic alterations of both the structure and composition of wildlife habitat, especially in the vegetative component. Management techniques such as prescribed burning and herbicide applications are routinely used to reverse succession across large areas of habitat, with lasting effects. Changes in physical and biological attributes of habitat undoubtedly occur following intensive treatments such as these and potentially can alter host–parasite community ecology.

Our understanding of effects of local habitat modification on host–parasite relationships is limited. Issac (1963) discovered that diseases of black-tailed deer (*Odocoileus hemionus columbianus*) caused by liver flukes and lungworms were curtailed by the Tillamook burn in Oregon in 1933. Bendell (1974) found that although internal and external parasitism of blue grouse

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(*Dendragapus obscurus*) initially decreased following an intense wildfire, parasite species richness and frequency of infection increased 12 yr later. Forrester et al. (1987) suggested that agricultural practices, including prescribed burning and herbicide treatment, affected the helminth parasitism of round-tailed muskrats (*Neofiber alleni*).

Obeliscoides cuniculi (Graybill, 1923) is a common trichostrongylid stomach worm of cottontail rabbits that is widely distributed in North America (Ward, 1934; Morgan and Waller, 1940; Moore and Moore, 1947; Franklin et al., 1966; Stringer et al., 1969; Andrews et al., 1980; Strohlein and Christensen, 1983). Several studies on *O. cuniculi* have reported on life history (Alicata, 1932), effects on nutritional physiology of rabbits (Pace and Fransden, 1982), seasonal variation (Gibbs et al., 1977), and arrested development (Michel et al., 1975). However, only one study has reported the distribution, abundance, and ecological relationships of this trichostrongylid nematode within the Cross Timbers ecosystem of central Oklahoma (Ward, 1934) where range improvement practices are commonly used. Our objective was to determine if brush management strategies using combinations of fire and herbicides influence the distribution, abundance, or prevalence of *O. cuniculi* infections in populations of cottontail rabbits in the Cross Timbers ecosystem of Oklahoma.

Materials and Methods

Study area

Our study was conducted on the Cross Timbers Experimental Range (CTER), which is located approximately 11 km west of Stillwater, Oklahoma. The CTER is a 648-ha research area originally composed of blackjack oak (*Quercus marilandica*)–post oak (*Q. stellata*) and eastern redcedar (*Juniperus virginiana*) upland forest intermixed with tall grass prairie (Ewing et al., 1984). The CTER includes 20 32.4-ha (0.42- × 0.83-km) fenced experimental pastures, representing 4 replications of 4 brush management treatments, using combinations of herbicide and annual prescribed burning, and an untreated control. This provides a 2 × 2 factorial design consisting of 4 replications of 5 treatments (Fig. 1). The experimental treatments included (1) tebuthiuron (N-[1,1-dimethyl-ethyl]-1,3,4-thiadiazol-2-yl]-N,N′-dimethylurea), a soil-applied herbicide (Elanco Products Co., Division of Eli Lilly and Co., Indianapolis, Indiana 46285) applied aerially at 2.0 kg/ha in March 1983; (2) tebuthiuron applied (as with treatment #1) with annual prescribed burning beginning in April 1985; (3) triclopyr ([(3,5,6-trichloro-2-pyridinyl)oxy]acetic acid), a foliage-applied herbicide (Dow Chemical Co., Midland, Michigan 48674) ap-
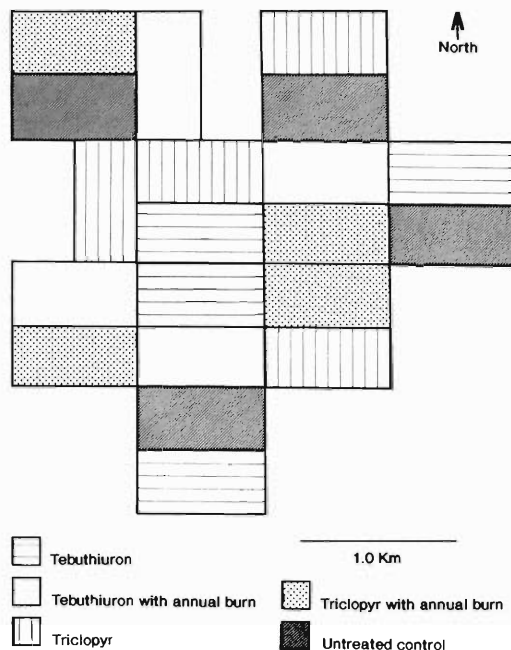
Figure 1. Map of the Cross Timbers Experimental Range, Payne County, Oklahoma, consisting of 20 experimental pastures representing 4 replications of 4 brush treatments and an untreated control.

plied aerially at 2.2 kg/ha in June 1983; (4) triclopyr applied (as with treatment #3) with annual prescribed burning beginning in April 1985; and (5) untreated control. None of the treated areas were burned in 1988. All experimental pastures were moderately grazed by cattle during the spring and summer.

Herbicide-treated pastures produced more grasses and forbs compared to untreated control pastures (Engle et al., 1987). Both herbicides killed a high proportion of the dominant overstory oak species, but woody understory species such as buckbrush (*Symphoricarpos orbiculatus*), elm (*Ulmus americana*), and chittamwood (*Bumelia lanuginosa*) were not reduced as much by triclopyr as by tebuthiuron (Stritzke et al., 1987). Competition by understory woody species reduced the production of herbaceous plants after the triclopyr treatment.

Data collection

Two hundred five cottontail rabbits (*Sylvilagus floridanus* (Allen)) were collected during winter (January) and summer (July) of 1987 and 1988. An attempt was made to collect 5 specimens from each of 2 replications for each treatment. Carcasses were necropsied within 24 hr of collection or frozen until necropsy could be performed. Stomach worms that were recovered from the gastric mucosa and food contents were counted and stored in 70% ethanol. Specimens of *O. cuniculi* were cleared with lactophenol and identified by microscopic examination. Representative specimens of *O. cuniculi* recovered from this study were deposited in the U.S.

National Parasite Collection, Beltsville, Maryland (accession no. 80494).

Data analysis

Abundance and prevalence were used as defined by Margolis et al. (1982). Host age was determined using a combination of reproductive status and body weight. Cottontail rabbits ≥800 g body weight and reproductively active individuals between 650 and 799 g were considered adults. Only abundance data for adult cottontail rabbits ($N = 180$) were used in data analyses for the main effects of treatment, season, year, and sex.

Overdispersion as defined by Bliss and Fisher (1953) has been used to describe frequency distributions of helminths in which a small number of host individuals harbor many helminth individuals and many hosts harbor few or no individuals of a particular species of helminth (Corn et al., 1985; Waid et al., 1985). Overdispersion was indicated when helminth frequency distributions had a variance significantly larger ($P \leq 0.05$) than the mean abundance, using a chi-square distribution. The degree of overdispersion was measured by the negative binomial parameter k (Bliss and Fisher, 1953), which is an inverse measure of the degree of overdispersion. Differences in overdispersion (k) among brush treatments and seasons were then evaluated by analysis of variance using Anscombe's transform, $\log_{10}(x + \frac{1}{2}k)$, of abundance data (Bliss and Owen, 1958). Overdispersed *O. cuniculi* abundances for the adult cottontail rabbits were independently rank transformed prior to data analysis as a method to analyze nonnormally distributed data (Conover and Iman, 1981; Waid et al., 1985).

Main and interactive effects of treatment, season, and year on rank-transformed abundances were examined with a factorial analysis of variance. Biological significance was set at $P \leq 0.100$. Specific contrasts (1 df) were utilized to compare variation among treatment components (burned vs. unburned, untreated control vs. brush treatments, tebuthiuron vs. triclopyr). Protected multiple comparisons (LSD) were used when significant ($P \leq 0.05$) differences were detected by analysis of variance. The Statistical Analysis System (SAS) was used for all data analyses (SAS, 1985). Copies of the raw and rank-transformed data are available upon request from R.L.L.

Results and Discussion

Prevalence

Ninety-five male (86 adult) and 110 female (94 adult) cottontail rabbits were collected from the CTER with an overall prevalence of 97% for *O. cuniculi* (Table 1). Juvenile cottontail rabbits ($N = 25$) were not included in data analyses because of significant differences in *O. cuniculi* mean abundances ($P \leq 0.001$) when compared with adults. Prevalence of *O. cuniculi* infections in our study was higher than other studies in Oklahoma where Ward (1934) and Smith (1940) reported prevalences of 47% and 0% in samples of 52 and 31 cottontail rabbits, respectively. Franklin et al. (1966) found a prevalence of 16% in a sample of 138 cottontail rabbits from Kansas, and Measures and Anderson (1983) reported a prevalence of 15% in southern Ontario. *Obeliscoides cuniculi* infections in our study were similar to those in surveys in the southeastern United States where prevalences approached 100% (Moore and Moore, 1947; Jacobson et al., 1978; Andrews et al., 1980). No differences in prevalence were found among cottontail rabbits from the brush treatments or controls.

Distribution and overdispersion

Variances were significantly larger than the mean number of *O. cuniculi* individuals/adult cottontail rabbit for all treatments in each season (Table 2), which was indicative of an overdispersed parasite distribution (Bliss and Fisher, 1953). Low k values (≤ 1.0) indicated a high degree of parasitic aggregation (Bliss and Fisher, 1953; Corn et al., 1985) within our host population, but there was no significant difference ($P \geq 0.100$) in k values due to brush treatment. Cottontail rabbits from herbicide-treated pastures showed a greater amount of variation in k values between seasons than those from untreated control pastures. Common k statistics from 1988 indicated differences ($P < 0.055$) in *O. cuniculi* overdispersion between control and brush-treated pastures. Degree of overdispersion was significantly greater ($P < 0.001$) in winter than summer for both years. The k value of 25 juvenile cottontail rabbits that were collected primarily in summer was 2.90.

Distribution of *O. cuniculi* infections in cottontail rabbit populations in the Cross Timbers area supports previous studies that indicate seasonal changes foster overdispersion (Pence and Windberg, 1984; Corn et al., 1985). However, other factors such as habitat heterogeneity (Anderson, 1982) could also be important in overdispersion in *O. cuniculi* as indicated by differences in the seasonal variation of k values between treated and untreated pastures. Natural successional changes, vegetative composition, patchiness of treatments, and microclimates occurring on herbicide-treated pastures could have contributed to these observed differences as compared with untreated controls. Intrinsic host-related variables such as habitat use by cottontails also may be factors that contribute to overdispersion of *O. cuniculi* on our study area.

Table 1. Prevalence (number infected/number examined) of *Obeliscoides cuniculi* in cottontail rabbits collected from 5 experimental brush-control treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma.

Brush treatment	1987		1988	
	Winter	Summer	Winter	Summer
Tebuthiuron	10/10	10/10	13/13	10/10
Tebuthiuron with annual burning	10/11	10/10	9/10	10/10
Triclopyr	10/10	10/10	10/10	10/10
Triclopyr with annual burning	9/10	10/10	10/10	10/10
Control	9/10	11/11	9/10	10/10
Total	48/51	51/51	51/53	50/50

Abundance and intensity

Infection intensities ranged from 1 to 435 worms/host; only 5 uninfected rabbits were observed in the winters of 1987 and 1988. Mean *O. cuniculi* abundances (Table 3) were significantly different between seasons ($P < 0.001$), treatments ($P < 0.057$), and years ($P < 0.053$), and a significant ($P < 0.013$) brush treatment × year interaction occurred. Mean rank abundances were considerably higher in summer than in winter for both years sampled. Mean abundances for *O. cuniculi* across all treatments were 58.8 ± 7.0 and 23.0 ± 4.4 worms/host (wph) for summer and winter, respectively. Mean abundance was higher in 1987 (42.8 ± 5.8 wph) than 1988 (34.0 ± 5.8 wph).

Mean rank abundances of *O. cuniculi* in cottontail rabbits collected in 1988 from annually burned treatments (48.0 ± 3.7 wph) were lower

($P < 0.040$) than those from unburned experimental treatments (41.1 ± 4.2 wph). Multiple comparisons among treatments showed triclopyr treatments subjected to annual prescribed burning had a mean rank abundance for *O. cuniculi* that was lower ($P < 0.050$) than the other 4 treatments. Abundances of *O. cuniculi* were not different ($P > 0.230$) between triclopyr- and tebuthiuron-treated pastures in 1987 or 1988. There were no significant ($P > 0.150$) differences in abundances between control and treated pastures for 1987.

Seasonal differences between winter and summer *O. cuniculi* abundances in cottontail rabbits are well documented across the United States. Andrews et al. (1980) found that *O. cuniculi* abundances in cottontail rabbits collected in spring were 2–4 times greater than those in winter. Jacobson et al. (1978) reported similar results for cottontail rabbits from Virginia and speculated that variable climate and host hormonal changes influenced *O. cuniculi* abundance. In our study, seasonal variation was more profound during 1988 than 1987, as demonstrated by a larger summer/winter ratio of mean rank abundance. This was probably due to a harsh winter in 1988, during which record snowfalls and ice storms were recorded. The winter of 1987 was mild and wet and probably provided optimal conditions for parasite transmission (Alicata, 1932), resulting in less variation in intensities of helminths between seasons.

Management implications

Effects of wildfire and prescribed burning on helminth parasitism have not been well docu-

Table 2. Determination of overdispersion ($\bar{x}/s^2$)* and degree of aggregation (k) of *Obeliscoides cuniculi* individuals in adult cottontail rabbits collected from 5 experimental brush-control treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma ($N = 180$).

Brush treatment	1987				1988				Total
	Winter		Summer		Winter		Summer		
	$\bar{x}/s^2$	k	$\bar{x}/s^2$	k	$\bar{x}/s^2$	k	$\bar{x}/s^2$	k	k
Tebuthiuron	0.091	0.03	0.023	1.30	0.027	0.93	0.044	2.37	0.95
Tebuthiuron with annual burning	0.011	0.54	0.047	2.74	0.153	1.34	0.055	0.45	0.40
Triclopyr	0.005	0.30	0.024	1.25	0.100	1.16	0.030	1.84	0.49
Triclopyr with annual burning	0.146	1.51	0.017	0.74	0.045	0.52	0.061	2.13	0.58
Control	0.027	1.00	0.018	1.12	0.205	1.03	0.019	1.17	0.67

* $\bar{x}$ abundance/variance, where a small number of host individuals harbor many parasite individuals and many of the hosts harbor little to no individuals of a particular parasitic species (based on the frequency distribution of individual parasites). All variances were significantly larger than respective $\bar{x}$ abundances ($P \leq 0.05$).

Table 3. Mean seasonal abundance ($\bar{x} \pm$ SE) of *Obeliscoides cuniculi* in cottontail rabbits collected from 5 experimental brush-control treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma. Sample size is in parentheses.

Brush treatment	1987				1988			
	Winter		Summer		Winter		Summer	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Tebuthiuron	10.3 ± 3.4 (10)	NC*	54.4 ± 16.1 (10)	3.0 (1)	33.5 ± 9.7 (13)	NC	51.9 ± 12.2 (10)	32.0 ± 31.0 (2)
Tebuthiuron with burn	49.2 ± 20.3 (11)	NC	55.4 ± 11.4 (10)	101.0 (1)	7.4 ± 2.2 (10)	NC	90.6 ± 45.2 (10)	67.0 (1)
Triclopyr	56.9 ± 34.9 (10)	36.0 (1)	65.4 ± 18.3 (10)	54.4 ± 49.5 (2)	10.4 ± 3.2 (10)	NC	59.3 ± 18.1 (10)	75.5 ± 23.0 (4)
Triclopyr with burn	8.8 ± 2.5 (10)	NC	43.8 ± 23.0 (10)	73.0 ± 10.0 (5)	11.0 ± 4.9 (10)	NC	33.0 ± 8.8 (10)	82.3 ± 7.4 (3)
Control	36.3 ± 11.6 (10)	NC	61.6 ± 22.1 (11)	28.5 ± 6.1 (4)	4.0 ± 1.4 (10)	NC	60.7 ± 18.8 (10)	78.0 (1)

* NC = no rabbits collected.

mented. Habitat modifications induced by wildfire can produce optimal conditions for establishment of arthropod intermediate hosts of pathogenic intestinal worms of blue grouse (Bendell, 1974). Prescribed fire for habitat management of Stone's sheep (*Ovis dalli stonei*) decreased *Protostrongylus* sp. larval counts in feces of sheep that utilized burned ranges during winter (Seip and Bunnell, 1985). Cottontail rabbits in our study area experienced similar host–parasite influences from 1987 to 1988. Prescribed burning at CTER occurred in April when infective larvae and eggs should have been abundant in the environment and conditions for transmission were ideal. Burning may have decreased the number of these infective stages available to foraging cottontail rabbits, which resulted in lower mean abundances among animals collected from burned sites. This was found to be true of rabbits collected from triclopyr-treated pastures that were burned annually. Spotty, nonuniform burns resulting from a lack of adequate fuel were probably responsible for higher survival of infective *O. cuniculi* larvae on annually burned tebuthiuron-treated pastures.

Our study provided additional evidence that habitat alterations, whether natural or human induced, can influence host–parasite population relationships in a local area. Host–parasite responses to a given habitat alteration are not always consistent; however, our study demonstrates they differ from those responses in untreated habitats. Because habitat modification practices, such as those using herbicides and fire, vary greatly in their effects on vegetation structure and how they are applied, general statements about host–parasite responses may be difficult to make. Longer-term research on entire helminth communities is needed to understand better and predict these responses.

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80th Anniversary Celebration

Society President John H. Cross (left) presenting certificate of gratitude to guest speaker Gerhard A. Schad, President of the American Society of Parasitologists.

The 80th Anniversary of the Helminthological Society of Washington was celebrated at a dinner held 23 March 1990 at the 610th meeting. Fifty-five members and guests enjoyed dinner followed by a short history of the Society summarized by Willis A. Reid. The guest speaker for the evening was Gerhard A. Schad, President of the American Society of Parasitologists, whose talk was entitled, "The Hookworm's Turn Again."

The Society thanks Merck, Sharp and Dohme Research Laboratories and Smith Kline, Beecham, for their generous support of the event.

Protospirura okinavensis sp. n. (Nematoda: Spiruridae) from Mus caroli on Okinawa Island, Japan

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ABSTRACT: *Protospirura okinavensis* sp. n. is described from *Mus caroli* on Okinawa Island, Japan. *Protospirura okinavensis* is readily distinguished from other members of the genus by the number and arrangement of caudal papillae, the size and length ratio of the spicules, and the egg dimensions.

KEY WORDS: *Protospirura okinavensis* sp. n., Nematoda, Spiruridae, taxonomy, mouse, *Mus caroli,* Rodentia, Muridae, Okinawa Island, Japan.

During a survey of the helminth fauna of the Ryukyu Archipelago, Japan, *Protospirura* sp. was recorded from the Ryukyu mouse, *Mus caroli,* on Okinawa Island (Hasegawa et al., 1986). Close examination revealed that this nematode is new to science and is described herein.

Materials and Methods

Rodents were captured with live traps in the sugar cane fields. They were killed with ether, and their viscera were examined under a dissecting microscope. Nematodes were fixed with 70% ethanol at 70°C, cleared in glycerin–alcohol solution, and mounted in 50% glycerin on slides. Figures were made with the aid of a drawing tube. Measurements given are for the holotype male and the allotype female, followed in parentheses by the ranges of paratype males and females. All measurements are in millimeters unless otherwise stated.

Description

Protospirura okinavensis sp. n.
(Figs. 1–11)

GENERAL: Nematoda, Spiruroidea, Spiruridae, Spirurinae, *Protospirura.* Medium-sized stout worm. Slightly reddish in color. Cuticle thick with transverse striations. Anterior extremity with highly developed pseudolabia raised above oral opening (Figs. 1, 2). Oral opening dorsoventrally elongated, constricted by 2 lateral elevations and 4 small submedian formations, lateral and submedian formations each with 4 teeth (Figs. 2, 3). Buccal cavity without tooth (Figs. 2, 3). Four large submedian cephalic papillae and 2 subdorsal and 2 subventral papillae in cuticular depressions, forming outer circle. Six small labial papillae present on lateral elevations and submedian formations, forming inner circle. Amphidial pores slightly inside of outer circle of cephalic papillae (Fig. 3). Pharynx thick walled, laterally compressed (Figs. 2, 3). Esophagus divided into anterior muscular and posterior glandular portions (Fig. 1). Nerve ring in posterior $\frac{1}{3}$ of muscular esophagus (Fig. 1). Excretory pore near junction of muscular and glandular portions of esophagus (Fig. 1). Deirids small, near anterior part of muscular esophagus (Fig. 1). Phasmidial pores subterminal (Figs. 4, 11).

MALE (holotype and 3 paratypes): Posterior extremity coiled (Fig. 5). Length 17.7 (16.3–24.6), maximum width in region of posterior body 0.53 (0.43–0.60). Head diameter 0.12 (0.11–0.12). Pharynx 0.07 (0.06–0.07) long. Muscular portion of esophagus 0.29 (0.28–0.33) long and 0.09 (0.09–0.10) wide; glandular portion of esophagus 3.75 (3.73–4.35) long and 0.15 (0.14–0.16) wide. Nerve ring 0.31 (0.30–0.40) and excretory pore 0.48 (0.41–0.51) from anterior extremity. Caudal alae thick. Ventral surface of posterior part ornamented with numerous striae arranged longitudinally but also irregularly or transversely in postanal portion (Figs. 4, 5). Spicules markedly dissimilar: right spicule slender, 0.62 (0.60–0.65) long; left spicule stout, alate, 0.32 (0.32–0.35) long (Fig. 7). Gubernaculum poorly chitinized, triangular in ventral view, 0.12 (0.11–0.16) long (Fig. 6). Preanal caudal papillae 5 or 6 pairs, large, and arranged asymmetrically. One large unpaired median papilla on anterior anal lip. Postanal papillae in 4 pairs: 2 pairs large, on posterior anal lip and at posterior $\frac{1}{3}$ of tail; 2 pairs small, posterior to large pair (Figs. 4, 5). Tail conical, 0.18 (0.16–0.22) long, with round tip (Figs. 4, 5).

FEMALE (allotype and 8 paratypes): Length 40.1 (27.8–44.4), width at midbody 0.84 (0.51–1.15). Head diameter 0.17 (0.16–0.19). Pharynx 0.08 (0.08–0.11) long. Muscular portion of esophagus 0.32 (0.27–0.36) long and 0.14 (0.10–0.16) wide; glandular portion of esophagus 4.57 (3.97–5.30) long and 0.23 (0.16–0.27) wide. Nerve

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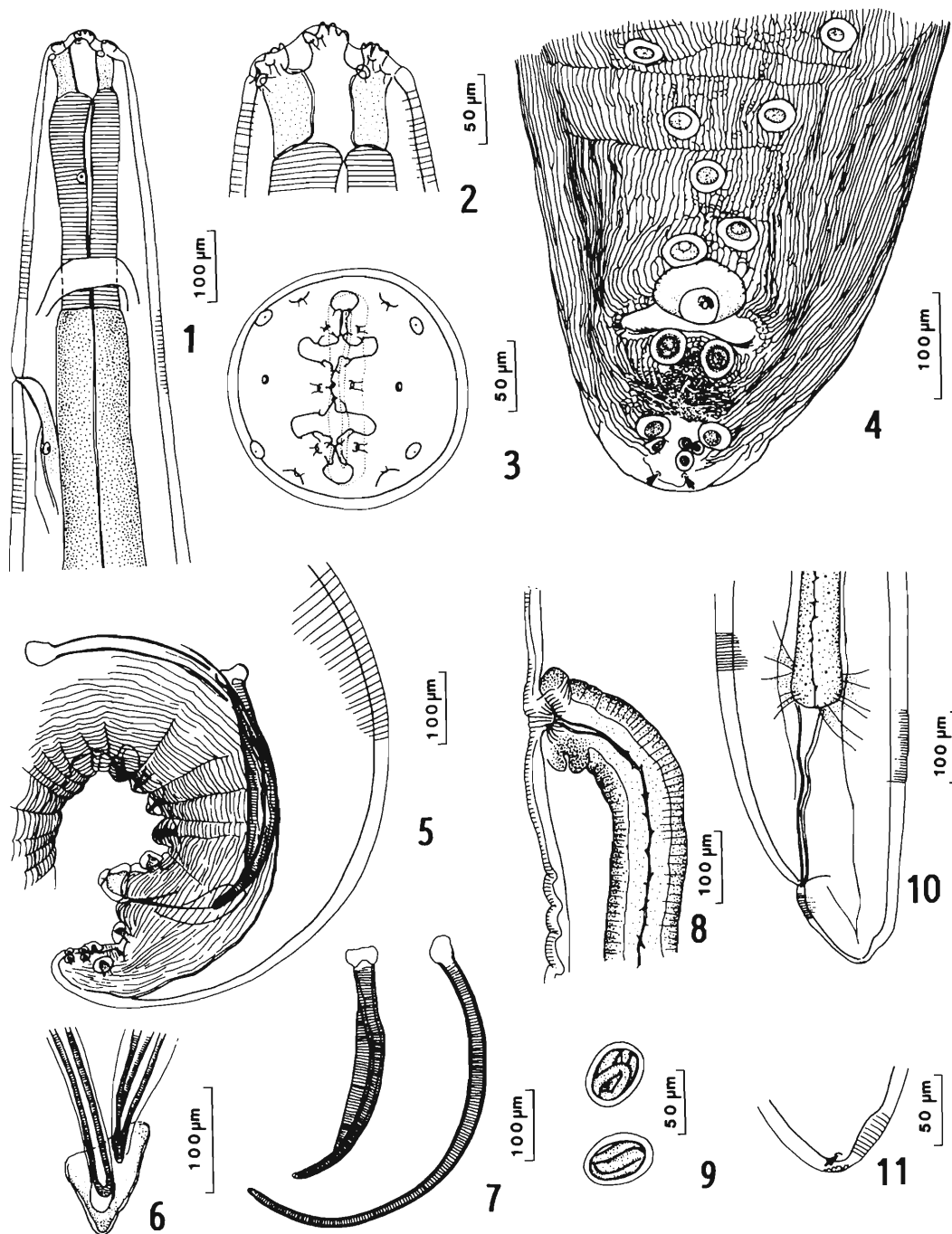
Figures 1–11. *Protospirura okinavensis* sp. n. from *Mus caroli* on Okinawa Island, Japan. 1. Anterior part of holotype male, lateral view. 2. Cephalic extremity of holotype male, lateral view. 3. Cephalic extremity of paratype female, apical view. 4. Posterior part of paratype male, ventral view. 5. Posterior part of holotype male, lateral view. 6. Gubernaculum and distal tips of spicules of paratype, ventral view. 7. Spicules of holotype, lateral view. 8. Vulva of paratype, lateral view. 9. Uterine eggs. 10. Posterior part of allotype female, lateral view. 11. Posterior extremity of allotype female, lateral view. Arrows indicate phasmidial pores.

ring 0.38 (0.33–0.42) and excretory pore 0.53 (0.44–0.54) from anterior extremity. Vulva without ornamentation, at middle of body, 19.4 (13.6–22.4) from anterior extremity (Fig. 8). Vagina directed posteriorly (Fig. 8). Tail conical, with small tuberculose area at tip, 0.29 (0.22–0.31) long (Figs. 10, 11). Eggs elliptical, thick shelled, containing developed larvae at deposition, 45–50 × 30–33 μm (Fig. 9).

HOST: *Mus caroli.*

SITE IN HOST: Stomach.

LOCALITY: Isagawa, Nago-shi, and Okuma, Kunigami-son, Okinawa Island, Japan.

DATE OF COLLECTION: 12 December 1984 (at Isagawa) and 14 August 1985 (at Okuma).

SPECIMENS DEPOSITED: Holotype and allotype in USNM Helm. Coll. No. 80944; paratypes in National Science Museum, Tokyo, NSMT As-1955.

Discussion

The genus *Protospirura* Seurat, 1914 is composed of a relatively small number of species in spite of its worldwide distribution. Quentin (1969) listed 8 species and subspecies in the genus: *P. numidica numidica* Seurat, 1914; *P. numidica criceticola* Quentin et al., 1968; *P. anopla* Kreis, 1938; *P. armeniana* Alojan, 1951; *P. chabaudi* Vuylsteke, 1964; *P. muricola* Gedoelst, 1916; *P. peromysci* Babero and Matthias, 1967; and *P. suslica* Schulz, 1916. Four species have been proposed as *Protospirura* subsequently: *P. chanchanensis* Ibáñez, 1966; *P. paucidentata* Wang et al., 1978; *P. srivastavai* Gupta and Trivedi, 1987; and *P. pseudomuris* Yokohata and Abe, 1989. However, the former 3 species are considered to belong to a different subfamily, Spirocercinae, because the pharynx is not compressed laterally (cf. Ibáñez, 1966; Chabaud, 1975; Wang et al., 1978; Gupta and Trivedi, 1987). *Protospirura pseudomuris* is a typical member of *Protospirura*. Yokohata and Abe (1989) stated that in *P. pseudomuris* the lateral elevations of the oral opening lack denticles and each of the submedian formations has only 1 denticle. However, in the cephalic ends figured by them (Figs. 9, 10) the lateral formation and the submedian formations each have at least 2 denticles.

Protospirura okinavensis is readily distinguished from other members in that all of them have more than 5 pairs of postanal papillae. Other distinguishing characteristics are as follows. *P. numidica numidica* and *P. numidica criceticola* have longer spicules (right 0.83 mm and left 0.42

mm in a male 22 mm long in *P. n. numidica*; right 1.15–1.42 mm and left 0.40–0.64 mm in males 13–22 mm long in *P. n. criceticola*) (Chitwood, 1938; Quentin et al., 1968). *Protospirura muricola* has spicules of nearly equal length (Chitwood, 1938; Quentin, 1969). *Protospirura anopla* lacks an unpaired papilla on the anterior anal lip and has 2 pairs of large papillae forming the anterior group of postanal papillae and larger eggs (39.2–61.0 × 30.4–34.8 μm; $\bar{x}$ = 52.4 × 34.8 μm) (Kreis, 1938). *Protospirura armeniana* has 3 pairs of large postanal papillae (Skrjabin and Sobolev, 1963). *Protospirura chabaudi* Vuylsteke, 1964 lacks a denticle on the lateral elevations around the oral opening and unpaired preanal papillae and has a postequatorial vulva (Vuylsteke, 1964). *Protospirura peromysci* has a longer right spicule (0.82–1.20 mm in males 11.6–18 mm long) than that of *P. okinavensis,* although the left spicule is almost the same in length (0.33–0.38 mm) (Babero and Matthias, 1967). *Protospirura suslica* has 2 pairs of large papillae arranged in a line just posterior to the anus (Skrjabin and Sobolev, 1963). *Protospirura pseudomuris* has a longer esophagus and long conical tail in both sexes; caudal alae are wider in the male, and the vulva of the female is situated in the anterior ⅓ of the body (Yokohata and Abe, 1989).

Besides *P. okinavensis,* some nematode species of the superfamily Spiruroidea have been known from mammals of the Ryukyu Archipelago: *Gongylonema neoplasticum* (Fibiger and Ditlevsen, 1914) from *Rattus norvegicus, R. rattus,* and *Apodemus speciosus* (cf. Kawashima et al., 1965; Kamiya et al., 1968; Yagi et al., 1983; Hasegawa et al., 1986); *Gongylonema* sp. and *Cylicospirura* (*Gastronodus*) *strasseni* (Singh, 1934) from *Suncus murinus* (Uchikawa et al., 1981; Hasegawa et al., 1986); *Mastophorus muris* (Gmelin, 1790) from *Apodemus speciosus* (Yagi et al., 1983); *Ascarops strongylina* (Rudolphi, 1819) and *A. dentata* (Linstow, 1904) from *Sus scrofa riukiuanus* (Shoho and Machida, 1979; Uchida et al., 1984; Hasegawa et al., 1985). *Physocephalus sexalatus* (Molin, 1860) was also found among the nematode specimens collected from *S. s. riukiuanus* on Amami-oshima Island (cf. Uchida et al., 1984, Fig. 1).

Many of the wild mammals of the Ryukyu Archipelago are considered to have come from the adjacent areas through land connections in the Pleistocene, although some were introduced rather recently. The nematodes might also have

been brought into this area by their hosts. Although many of the spiruroids listed above are cosmopolitan parasites, *C. (G.) strasseni* and *A. dentata* are known only from relatively limited areas south to the Ryukyu Archipelago (cf. Yamaguti, 1961), suggesting that their hosts had come from continental China through Taiwan. *Mus caroli,* which inhabits cultivated fields and is distributed in Southeast Asia and Taiwan as well as the Ryukyu Archipelago (Corbet and Hill, 1986), probably had its origin in Southeast Asia. *Protospirura okinavensis* or other closely related species probably parasitize *Mus caroli* in Southeast Asia and/or Taiwan.

Acknowledgments

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Research Note

Histochemical Observations on Nonspecific and Specific Phosphatases in *Cotugnia meggitti* (Cestoidea: Davaineidae)

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ABSTRACT: The location of nonspecific and specific phosphatases was determined in *Cotugnia meggitti* Yamaguti, 1935. Acid and alkaline phosphatases were localized in the tegument, subtegumental cells, longitudinal muscles, and various reproductive organs. Adenosine triphosphatase and 5-nucleotidase activity was demonstrated in the tegument and subtegumental cells. The former was also detected in the rostellar hooks, cirrus sac, vitelline gland, and ovary, whereas the latter was noted in the rostellar hooks and muscles. Glucose-6-phosphatase was noted in the tegument, female reproductive organs, and muscles. The probable role of the phosphatases is discussed.

KEY WORDS: cestode, *Cotugnia meggitti,* histochemistry, nonspecific phosphatases, specific phosphatases.

Much work has been performed on the nonspecific and specific phosphatases of cestodes (Erasmus, 1957a, b; Bogitsh, 1963; Lee and Tatchell, 1964; Ohman-James, 1968; Howells, 1969; Mayberry and Tibbitts, 1972; Varma et al., 1985). Few histochemical studies have been undertaken on the cestodes of other vertebrates (see Smyth, 1969, Table 2; Hayunga and Mackiewicz, 1988); the most recent of which, dealing with birds, is that of Roy (1979).

The distribution of phosphatases in a parasite is a reflection of where various biochemical processes are occurring, with intensity and type of reaction perhaps changing at different times during the organism's life cycle. Host intestinal physiology, pH, and location of the parasite in the gut (embedded, free in lumen, etc.) will also affect the physiological activities of the parasite. Phylogenetic differences among various hosts, and among parasite species, might also be reflected in the parasite's physiological attributes. Data concerning such speculations are at present fragmentary. A study was, therefore, initiated to determine the distribution and activity of selected phosphatases in the cestode *Cotugnia meggitti* Yamaguti, 1935 of pigeons in India and to compare the results with previous works.

Live cestodes were recovered from *Columba livia* Gmelin, washed with normal saline, and fixed for 1–2 hr in chilled 10% neutral formalin buffered with sodium phosphate. Sections were cut at 10–15 μm on a freezing microtome. A variety of techniques were then used to detect phosphatase activity. For acid phosphatase, the lead salt method was utilized, and for alkaline phosphatase, the calcium cobalt method was used (Gomori, 1952). Both methods were used to detect adenosine triphosphatase; the lead method of Wachstein and Meisel (1957) was used to demonstrate 5-nucleotidase and glucose-6-phosphatase. Media were prepared as described in Chayen et al. (1973). Controls were performed as follows: acid phosphatase, incubated as for test but 0.01 M sodium fluoride included in reaction medium; alkaline phosphatase, 3% sodium-B-glycerophosphate in medium replaced by distilled water; adenosine triphosphatase, adenosine triphosphate replaced by glycerophosphate in medium; 5-nucleotidase, adenosine 5′-monophosphate in medium replaced by sodium-B-glycerophosphate; glucose-6-phosphatase, glucose-6-phosphate in medium replaced by sodium-B-glycerophosphate (Chayen et al., 1973).

The distribution and intensity of nonspecific and specific phosphatase activity in *C. meggitti* is detailed in Table 1. In whole worms, immature proglottids showed a slightly lower degree of phosphatase activity than mature and gravid proglottids. Erasmus (1957a, b) noted that in adult *Taenia pisiformis* and *Moniezia expansa* the majority of phosphatase activity occurred in the mature middle region of the strobila but not anteriorly and posteriorly. In the present work, moderate to intense acid phosphatase activity was noted in the tegument, subtegument, longitudinal muscle bundles, ovary, vitelline glands, eggs, and rostellar hooks. This result differs from that of Roy (1979), who demonstrated similar activity in virtually all parts of proglottids of *Raillietina (Raillietina) johri*. Erasmus (1957a, b) and Arme (1966), working with *T. pisiformis, M. expansa,* and *Ligula intestinalis,* respectively, noted that acid phosphatases were confined mainly to the tegument. Moczon (1974) ob-

Table 1. Distribution of nonspecific and specific phosphatase activity in *Cotugnia meggitti* (Cestoidea) from *Columba livia* (Aves).

Structure	Acid phosphatase	Alkaline phosphatase	Adenosine triphosphatase	5-nucleo-tidase	Glucose-6-phos-phatase
Tegument	+++*	+++	+++	++	++
Subtegumental cells	+++	+++	+++	+	+
Suckers	++	++	+	−	−
Rostellum	−	−	+	−	−
Rostellar hooks	++	++	+	+	−
Parenchyma	−	−	−	−	−
Longitudinal muscle bundles	++	++	++	+	+
Testes	−	++	±	−	−
Vas deferens	+	++	−	−	−
Cirrus sac	+	++	+	−	−
Ovary	++	++	+	−	+
Vitelline gland	++	++	+	−	+
Excretory canals	−	++	−	−	−
Eggs	+++	+++	−	−	−

* +++, strongly positive; ++, moderately positive; +, weakly positive; −, negative; ±, sometimes negative, sometimes positive.

served a low acid phosphatase activity in the ovary and spermatozoa of *Hymenolepis diminuta*. During the present study, moderate acid phosphatase activity was seen in the periphery of the scolex tegument, which contrasts with the observation of Bogitsh (1963), who found no such activity in the tegument of the scolex of *Hymenolepis microstoma*. Varma et al. (1985) reported weak activity in this region of *Pseudanoplocephala crawfordi* and *M. expansa* and suggested that high acid phosphatase concentrations are characteristic of cystic forms rather than adults. Acid phosphatase presence has been used as an indicator of lysosomal activity (Duve, 1963; Novikoff, 1963) and would be expected to occur in areas where intense biosynthesis is occurring.

The distribution of alkaline phosphatase mirrors that of acid phosphatase, except for its greater presence, as demonstrated by moderate activity, in the male reproductive tract (testes, vas deferens, cirrus sac) and excretory canals. Arme and Read (1970) and Mayberry and Tibbitts (1972) suggested that alkaline phosphatase is involved in active transport and/or digestion. Roy (1979) also supported this contention and postulated that the presence of alkaline phosphatase in subtegumental cells plays an important role in the formation of the syncytial protoplasmic layer of the tegument. The nonuniform activity along the length of the worm in the present study indicates a selective absorptive function in different body regions of *C. meggitti*.

The presence of enzymatic activity in the membranes of the testes, ovary, and cirrus sac is similar to that reported for *T. pisiformis* (Erasmus, 1957a), *M. expansa* (Erasmus, 1957b), *Ligula intestinalis* (Arme, 1966), *H. diminuta* (Mayberry and Tibbitts, 1972), and *R. johri* (Roy, 1979). Alkaline phosphatase function in these organs most likely supports active transport of glycogen and other nutrients needed to maintain high energy activities (Erasmus, 1957a; Roy, 1979). The enzyme in the excretory canals may be concerned with the movement of materials to and from the protonephridial ducts, as suggested by Howells (1969) and supported by the observations of other workers (Bogitsh, 1963; Lee and Tatchell, 1964; Mayberry and Tibbitts, 1972; Roy, 1979). In contrast to these findings, Erasmus (1957b) observed only irregular alkaline phosphatase activity along the length of the ventral excretory canal in *M. expansa*, and Ohman-James (1968) found no alkaline phosphatase in the canals of *Diphyllobothrium dendriticum*.

Little work has been done on the distribution of specific phosphatases, e.g., *adenosine* triphosphatase (ATPase), 5-nucleotidase, and glucose-6-phosphatase, of cestodes. Moczon (1974) demonstrated the presence of these enzymes in the tegument of adult *Hymenolepis diminuta*, as did Roy (1979) in *R. johri*. In the present work, these enzymes were distributed along the length of the strobila, with most intense activity being detected in the tegument and subtegumental cells.

Moczon (1974) and Bogitsh (1968) suggested that ATPase functioned in the transportation of nutrients by phosphorylation, whereas Gupta and Sharma (1974) felt that its importance lay in mediating pinocytosis and active transport. The role of ATPase in the tegument is most likely concerned with supplying energy for transportation of nutrients across the various membranes. ATPase may be used as an indicator of mitochondrial activity. The presence of moderate amounts of ATPase in the energy-requiring longitudinal muscle bundles is consistent with this premise. Roy (1979) postulated that ATPase in various genital structures of *R. johri* supplies energy to these physiologically active organs. The same scenario undoubtedly exists in *C. meggitti*.

No systematic attempt has been made to localize 5-nucleotidase in cestodes to date. Moczon (1974) failed to locate this enzyme in *H. diminuta*, and Roy (1979) reported the enzyme only from eggs of *R. johri*. In *C. meggitti*, it was absent from the eggs but present in small to moderate amounts in the tegument, subtegumental cells, longitudinal muscle bundles, and rostellar hooks. In whole worms, the amount of activity increased from the immature proglottids to the mature/gravid proglottids. Suggested roles for 5-nucleotidase in animals other than cestodes include permeability and transportation processes and involvement in transmission of nerve impulses, e.g., Essner et al. (1958) and Rostgaard and Behnke (1965). The role in *C. meggitti* appears to be multifunctional as is the case for ATPase.

The distribution and activity of glucose-6-phosphatase in *C. meggitti* was similar to that of 5-nucleotidase, except for its presence in the ovary and vitelline gland and absence from the rostellar hooks. Its presence in the tegument is undoubtedly concerned with the uptake and transportation of glucose across the membrane.

It became obvious during this study that marked differences do occur in the presence/absence and distributions of various enzymes in different cestode species. Our knowledge of such anomalies is rudimentary; Arai (1980), Arme and Pappas (1983a, b), and Smyth and McManus (1989) gathered together many of the known data. A more complete understanding of the physiological and biochemical processes of cestodes will be aided by further histochemical studies. It is possible that any differences or similarities noted might be partially explained by host phylogeny and/or host physiological differences.

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Research Note

A Cestode, *Taenia mustelae,* in the Black-footed Ferret (*Mustela nigripes*) and the White-tailed Prairie Dog (*Cynomys leucurus*) in Wyoming[1]

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ABSTRACT: *Taenia mustelae* was recovered from naturally infected black-footed ferrets, *Mustela nigripes* (adult cestodes), and a white-tailed prairie dog, *Cynomys leucurus* (cysticerci), near Meeteetse, Wyoming. Cysticerci fed to a domestic ferret, *Mustela putorius,* produced adult *T. mustelae*; eggs of adult tapeworms from *M. nigripes* and *M. putorius* fed to *C. leucurus* and a white-footed mouse, *Peromyscus leucopus,* resulted in recovery of cysticerci. *Mustela nigripes* is a new host for this tapeworm.

KEY WORDS: cestode, *Taenia mustelae,* black-footed ferret, *Mustela nigripes,* white-tailed prairie dog, *Cynomys leucurus,* natural infections, experimental infections, Meeteetse, Wyoming.

The black-footed ferret, *Mustela nigripes* Audubon and Bachman, among the rarest of North American mammals, until recently was considered possibly extinct (Schreiber et al., 1989). The recovery of a carcass of this mustelid and subsequent discovery of a small colony near Meeteetse, Wyoming, in 1981 fortunately belied this pessimistic conclusion.

Necropsy of the black-footed ferret carcass resulted in the recovery of 5 apparently intact tapeworms from the small intestine. Based on internal anatomy, the tapeworms were considered probably *Taenia mustelae* Gmelin, 1790, a parasite of various species of *Martes* and *Mustela* throughout North America, Europe, and the USSR (Freeman, 1956; Verster, 1969). The ap-

Table 1. Results of experiments feeding cysts and eggs of *Taenia mustelae* to various hosts.

Host	Source	Stage fed	Stage recovered	$\bar{x}$ hook length* (range)	$\bar{x}$ hook width (range)	Age of infection (in days)	Type of infection
Cynomys leucurus	—	—	cysticerci	19.0 (16.7–21.3)	9.8 (8.5–12.2)	—	natural
Mustela putorius furo	*Cynomys leucurus*	cysticerci	adults	18.0	9.7	62	experimental
Cynomys leucurus	*Mustela putorius*	eggs	cysticerci	16.0 (15.0–17.4)	8.4 (6.5–9.1)	153	experimental
Peromyscus leucopus	*Mustela nigripes*	eggs	cysticerci	14.5	9.7	66	experimental
Cynomys leucurus	*Mustela nigripes*	eggs	cysticerci	3 cysticerci recovered and placed in formalin		155	experimental

* All measurements in micrometers (μm).

parent loss of rostellar hooks from these specimens, however, precluded definitive identification.

A survey of 17 white-tailed prairie dogs, *Cynomys leucurus* Merriam, from Meeteetse in 1986 revealed cysticerci in the liver of 1 female (Seville and Williams, 1989). En face hook mounts were prepared in Hoyer's medium and measured; hook measurements (Table 1) were consistent with published reports of those of *T. mustelae* from definitive and intermediate hosts (Freeman, 1956; Verster, 1969) and the cysticerci were considered conspecific with that species. Five to 7 cysts were retained for feeding experiments (Table 1).

A program to breed black-footed ferrets in captivity was established at the Sybille Wildlife Research and Conservation Education Unit, Wheatland, Wyoming, in 1986 (Wyoming Game and Fish Department, 1987). After some time in captivity, an intact tapeworm, believed to be *T. mustelae*, was recovered from feces of a juvenile female black-footed ferret. Several gravid proglottids were removed and the remainder of the specimen placed in 10% formalin. Eggs passed in feces were also recovered from 2 other juvenile *M. nigripes*. The availability of both cysticerci and gravid proglottids prompted feeding experiments, using various intermediate and definitive hosts, for positive identification of this tapeworm species.

An adult male domestic ferret (*Mustela putorius furo* L.) was fed the cysticerci from the naturally infected prairie dog and was necropsied 62 days postinfection (PI). Eight intact tapeworms were recovered from the small intestine. One intact specimen was stained in Ehrlich's acid

hematoxylin and mounted. A hook mount in Hoyer's medium was prepared (Table 1). A few gravid proglottids were retained for further infection experiments with intermediate hosts. Eggs from the proglottids were passed via stomach-tube to 2 anesthetized (ketamine–xylazine) white-tailed prairie dogs (Table 1) and 2 white-footed mice (*Peromyscus leucopus* Rafinesque). Necropsy of these intermediate hosts revealed cysticerci in 1 prairie dog (135 days PI). Hooks, mounted in Hoyer's medium, measured 15–17 μm in length ($\bar{x} = 16$) and 6.5–9.1 μm in width ($\bar{x} = 8.4$).

Eggs from gravid proglottids of the tapeworm recovered from the black-footed ferret were used to infect 2 prairie dogs and 2 white-footed mice, using procedures identical to those above. Cysticerci were found in 1 prairie dog and 1 mouse. Necropsy of the mouse 66 days PI (Table 1) revealed cysticerci located in the liver, mesenteries, stomach wall, body wall, urinary bladder, and wall of the large bowel. Cysts containing zero to multiple scolices were recovered. Freeman (1956) reported that multiscolex cysticerci of *T. mustelae* were more common than single-scolex forms. Three cysticerci were recovered from the liver of the prairie dog necropsied 155 days PI. These cysts were preserved in formalin.

All hooks examined from all hosts possessed a prominent guard, short handle, and blade (Fig. 1). Comparative average hook measurements correspond to values obtained by Freeman in experimental feedings and natural infections of *T. mustelae* (Freeman, 1956).

These feeding experiments substantiate the contention that the specimens recovered from

and definitive hosts (black-footed ferret, domestic ferret) demonstrates a viable pattern of transmission for this tapeworm. This report of *T. mustelae* in *M. nigripes* constitutes a new host record.

Voucher specimens of *T. mustelae* adults from *M. nigripes* (#80894) and *M. putorius* (#80893) and metacestodes from *C. leucurus* (experimental—#80890, natural—#80891) and *P. leucopus* (#80892) have been deposited in the USNM Helminthological Collection.

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Figure 1.   En face mount of rostellar hooks of *Taenia mustelae* from a cysticercus from a white-tailed prairie dog experimentally infected (Table 1) with eggs from a domestic ferret previously infected with cysticerci from a white-tailed prairie dog (Table 1). Phase contrast. Bar = 20 μm.

hosts near Meeteetse, Wyoming, are *T. mustelae*. Recovery of *T. mustelae* from both the naturally and experimentally infected intermediate hosts (white-tailed prairie dog, white-footed mouse)

Research Note

Helminths of *Semotilus atromaculatus* from Sugar Creek, McLean County, Illinois

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ABSTRACT: Creek chubs were collected from Sugar Creek, Normal, Illinois, between May 1984 and June 1987. Adult helminths recovered from 1,072 chubs included *Acanthocephalus dirus* (Van Cleave, 1931), *Allocreadium lobatum* (Wallin, 1909), and *Proteocephalus buplanensis* (Mayes, 1976). Larval helminths recovered from chubs were *Posthodiplostomum minimum* (MacCallum, 1921), *Neascus* sp., *Diphyllobothrium* sp., *Archigetes* sp., and an unidentified nematode. *Posthodiplostomum minimum* exhibited the highest

Table 1. Prevalence and mean intensity of helminths found in 1,072 *Semotilus atromaculatus* from Sugar Creek.

Parasite	No. infected (prevalence)	Mean intensity ± 1 SE	No. worms recovered (range)	Location in host
Digenea				
*Allocreadium lobatum**	336 (31.3)	2.8 ± 0.2	933 (1–26)	intestine
Posthodiplostomum minimum†	585 (54.6)	—	—	peritoneal cavity
Neascus sp.†	5 (0.4)	10.2 ± 8.7	51 (1–45)	integument
Cestoda				
*Proteocephalus buplanensis**	18 (1.7)	1.3 ± 0.1	24 (1–2)	intestine
Diphyllobothrium sp.†	1 (0.1)	1.0	1	intestine
Archigetes sp.†	1 (0.1)	2.0	2	intestine
Acanthocephala				
*Acanthocephalus dirus**	336 (31.3)	2.5 ± 0.2	839 (1–30)	intestine
Nematoda				
Species unknown†	3 (0.3)	1.0	3	peritoneal cavity

* Adult parasites.
† Larval parasites.

prevalence (54.6%), whereas both larval tapeworms exhibited the lowest prevalence (0.1%). *Neascus* sp. had the highest mean intensity (10.2). *Allocreadium lobatum* and *Acanthocephalus dirus* exhibited similar prevalences and mean intensities of infection.

KEY WORDS: *Semotilus atromaculatus,* creek chubs, *Acanthocephalus dirus, Allocreadium lobatum, Archigetes* sp., *Diphyllobothrium* sp., *Neascus* sp., *Posthodiplostomum minimum, Proteocephalus buplanensis,* Sugar Creek, Illinois.

The creek chub, *Semotilus atromaculatus* (Mitchill), is a common inhabitant of freshwater streams throughout North America east of the Rocky Mountains (Eddy and Underhill, 1978) and serves as host for numerous parasites (Hughes, 1928; Evans and Mackiewicz, 1958; DeGiusti, 1962; Hinson et al., 1976; Amin, 1977; Blouin et al., 1984). Reports on the population biology of *Acanthocephalus dirus* and *Allocreadium lobatum* in creek chubs from Sugar Creek, central Illinois, have been made by Camp and Huizinga (1980) and Camp (1989). However, these authors did not report the occurrence of other parasites in the chubs. The purpose of the present study was to survey the helminth parasites of creek chubs from Sugar Creek and to compare the findings with those of other studies.

The study site was a 0.8-km section of Sugar Creek, a small (2–4 m wide) and shallow (0.2–0.6 m deep) creek that flows through Fairview Park, Normal, Illinois. Creek chubs were sampled monthly from May 1984 through June 1987. Fish were collected with a 4- × 1.5-m minnow seine (mesh size 0.5 cm²) and transported alive

to the laboratory. In the laboratory, the intestine, peritoneal cavity, and skin of each creek chub were examined for parasites. Parasites found were processed by standard methods for microscopic examination.

Terminology follows the definitions of Margolis et al. (1982). Voucher specimens of the following parasites have been deposited in the USNM Helminthological Collection: *Allocreadium lobatum* (79281), *Acanthocephalus dirus* (79283), *Proteocephalus buplanensis* (80159), and *Posthodiplostomum minimum* (80160).

One thousand seventy-two (1,072) creek chubs were examined. The mean total length of the fish was 5.1 cm (range, 2.0–14.6 cm). Three adult and 5 larval helminth species representing 4 taxonomic groups were recovered from the fish (Table 1).

Allocreadium lobatum and *Acanthocephalus dirus* were found throughout the intestines of the chubs, and prevalences and mean intensities of infection for both parasites were similar (Table 1). No attempt was made to recover all the *Posthodiplostomum minimum* larvae because of the heavy infections often found in the fish.

The larval trematodes recovered from creek chubs in the current study have been commonly found in cyprinids by other investigators. Hughes (1928) found *Posthodiplostomum minimum* in creek chubs from a stream near Urbana, Illinois, and Amin (1977) recovered *P. minimum* from creek chubs from southeastern Wisconsin. Blackspot *Neascus* spp. previously found in creek chubs

include *Crassiphiala bulboglossa* (Hinson et al., 1976) and *Neascus pyriformis* (Blouin et al., 1984). Berra and Au (1978) reported that creek chubs from an Ohio stream were infected with *Uvulifer ambloplitis*. However, this report is suspect based on results reported by Hoffman and Putz (1965), who were unable to infect creek chubs experimentally with *U. ambloplitis*. Based on the results of Hoffman and Putz (1965) and personal communication with Dr. Hoffman, the *Neascus* sp. found in the current study is most likely *N. pyriformis*.

Posthodiplostomum minimum was the most prevalent parasite found in the chubs. This is not surprising because once recruited, the metacercariae are not lost and continued recruitment of these larvae would be expected. *Allocreadium lobatum,* the only adult trematode recovered in this study, was previously found in *Semotilus atromaculatus* from southern Michigan by DeGiusti (1962). DeGiusti did not report values for prevalence or mean intensity so no comparison can be made with the current study.

Camp and Huizinga (1980) reported the occurrence of *Acanthocephalus dirus* in creek chubs from Sugar Creek. They found lower prevalence (19.1%) and mean intensity (1.8) of infection than were seen in the current investigation. The higher values seen in the current investigation may have been caused by the higher prevalence of infection in the isopod intermediate host (59.5% vs. 32.0% found by Camp and Huizinga [1980]). It is not known why the isopods examined during the current study had a higher prevalence of infection.

Creek chubs infected with *Proteocephalus buplanensis* have been found in Nebraska (Mayes, 1976) and Wisconsin (Amin, 1977). The discovery of *P. buplanensis* in central Illinois extends its known geographic range. The recovery of a larval *Diphyllobothrium* sp. is unusual in cyprinids from the U.S. (Amin, pers. comm.), and it is not clear how the fish became infected with this parasite. The finding of immature *Archigetes* sp. is also unusual because these worms usually mature within their annelid hosts. The *Archigetes* sp. recovered were too immature to identify beyond the genus (Mackiewicz, pers. comm.).

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Research Note

Endoparasites of the Red-backed Salamander, *Plethodon c. cinereus,* from Southwestern Michigan

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ABSTRACT: Three species of endoparasites were found in 171 red-backed salamanders, *Plethodon c. cinereus,* collected from southwestern lower Michigan between 27 March and 2 September 1989. The nematode, *Thelandros magnavulvaris,* had the highest prevalence (28%), and the trematode, *Brachycoelium salamandrae,* had the highest mean intensity (2.9). The ciliate, *Cepedietta michiganensis,* infected 18% of the salamanders. Michigan is a new locality record for *T. magnavulvaris.*

KEY WORDS: *Plethodon c. cinereus,* red-backed salamander, endoparasites, survey, Nematoda, Protozoa, Trematoda, Michigan.

Although the parasites of the red-backed salamander, *Plethodon c. cinereus* (Green) have been studied by several authors, most notably Rankin (1937a, b, 1945), Walton (1938), and Fischthal (1955a, b), little is known about the parasites of this terrestrial salamander from the Great Lakes area. This note presents new information on the parasites of the red-backed salamander from this region and increases the information known about the parasites of Michigan salamanders.

One hundred seventy-one red-backed salamanders were collected by hand from the Barry Game Area, Barry County, southwestern lower Michigan, between 27 March and 2 September 1989. Both color phases (red-backed and lead-backed) of this salamander species were collected in a mature forest of beech, maple, and oak trees east of Otis Lake. Salamanders were killed in MS222 (ethyl m-aminobenzoate methane sulfonic acid). The head–body length (mm), color phase, and sex were recorded before the entire salamander was necropsied within 18 hr of collection. The mean head–body length ±1 SD (range) of all red-backed salamanders examined was 40 ± 6.8 mm (20–55 mm). Parasites found were processed using conventional parasitologic techniques. Prevalence is the percentage of animals infected in a sample and mean intensity is the mean number of worms per host. Represen-

tative specimens of parasites from salamanders have been deposited in the U.S. National Parasite Collection, Beltsville, Maryland (accession nos. 80995–80997).

Ninety-one (53%) red-backed salamanders were infected with 1 or more *Thelandros magnavulvaris* (Rankin, 1937), *Brachycoelium salamandrae* (Frölich, 1789), and *Cepedietta michiganensis* Woodhead, 1928. *Thelandros magnavulvaris* had the highest prevalence, and *B. salamandrae* had the highest mean intensity (Table 1). Nine hosts (10%) were concurrently infected with *T. magnavulvaris* and *B. salamandrae,* 5 (5%) with both *T. magnavulvaris* and *C. michiganensis,* and 1 (1%) with both *B. salamandrae* and *C. michiganensis.* Although at least 20 salamanders were collected each month, infection values for each parasite species were low and/or erratic over the 7-mo period. The prevalence and mean intensity of *T. magnavulvaris* were highest in April. The prevalence and mean intensity of *B. salamandrae* were highest in September and July, respectively. The prevalence of *C. michiganensis* was highest in August. There were no significant differences in prevalence and intensity of parasitism between females and males, nor between the 2 color phases (chi-square analysis and Student's *t*-test). There were also no distinct increases in infection for each parasite species with salamander length.

Thelandros magnavulvaris (=*Batracholandros magnavulvaris* as indicated by Petter and Quentin [1976]) has been reported from a variety of salamanders by Rankin (1937a, b), Lehmann (1954), Schad (1963), Fischthal (1955a, b), Dyer and Peck (1975), Dunbar and Moore (1979), and Dyer et al. (1980). Michigan is a new locality record for *T. magnavulvaris* and extends its range northward. Dunbar and Moore (1979) reported that red-backed salamanders and other terrestrial species were not infected with *T. magna-*

Table 1. Prevalence and mean intensity of parasites found in 171 *Plethodon c. cinereus* from the Barry Game Area.

Parasite	Prevalence	Mean intensity ±1 SD (range)	Site of infection	Mean length (mm) ± 1 SD (range) of infected *P. c. cinereus*
Thelandros magnavulvaris	48 (28)*	1.9 ± 1.3 (1–7)	cloaca	43 ± 5.6 (31–55)
Brachycoelium salamandrae	26 (15)	2.9 ± 3.3 (1–16)	small intestine	41.9 ± 6.3 (33–54)
Cepedietta michiganensis	31 (18)	—	small intestine, gall bladder	42.1 ± 5.4 (29–53)

* Number infected (percent infected).

vulvaris, whereas the aquatic to semiaquatic and semiterrestrial salamanders were infected. As true in other studies on *Thelandros* spp., female *T. magnavulvaris* were much more common than males in red-backed salamanders.

Although the trematodes collected in the present study exhibited much morphological variation, they were identified as *B. salamandrae* using the information presented by Byrd (1937) and the key of Cheng (1958). In Michigan, *B. salamandrae* has been found in the salamander *Hemidactylium scutatum* by Rankin (1938) and in the frogs *Acris gryllus* and *Rana sylvatica* by Najarian (1955). Coggins and Sajdak (1982) reported *B. salamandrae* in the marbled salamander, *Ambystoma opacum,* and in red-backed salamanders from Wisconsin.

Cepedietta michiganensis (Haptophryidae) was originally described from *H. scutatum* from southeastern Michigan by Woodhead (1928). Blanchard (1923) found approximately 70% of several thousand *H. scutatum* and 1 *Ambystoma jeffersonianum* from Michigan infected with this ciliate. Since then, *C. michiganensis* has been found in other plethodontid salamanders by Hazard (1937), Rankin (1937a, b), and Powders (1967, 1970) and in *R. sylvatica* by Hazard (1937). Woodhead and Kruidenier (1936) reported that larval *H. scutatum* ingested the active protozoans in fecal matter and carried them through metamorphosis to the adult stage. Hazard (1937) suggested that red-backed salamanders became infected in the same way. In the present study, all infections of red-backed salamanders by *C. michiganensis* were very heavy, with hundreds of protozoans found. Ciliates in the gall bladder were easily observed with the dissecting microscope.

The results of the present study are similar to those of other parasitologic surveys of *P. c. cinereus* by Rankin (1945), Fischthal (1955a, b), Dunbar and Moore (1979), and Coggins and Saj-

dak (1982) in that the number of parasite species found is low and the number of red-backed salamanders concurrently infected with 2 or more parasite species is low. The most parasite species found in a population of red-backed salamanders was by Rankin (1937a) who reported 9 protozoans and 4 helminths.

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Research Note

An Apparatus for Modified Harada-Mori Cultures of Third-stage Hookworm Larvae

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ABSTRACT: An apparatus is described that allows for the filter paper culture of third-stage hookworm larvae, suitable for biochemical studies. The method used consumes less time and space than conventional Harada-Mori test tube cultures, allowing for the application of a large volume of feces over a surface area of up to 6,400 cm^2 within a box small enough for a bench-top incubator.

KEY WORDS: *Ancylostoma caninum, Necator americanus,* hookworm, nematode larva.

Although large numbers of nematode larvae can be obtained via charcoal culture, they are often contaminated with organic debris and are therefore potentially unsuitable for biochemical studies. To circumvent the problem of contamination, investigators have attempted to separate larvae from fecal sediment by either centrifugation through ficoll-sodium metrizoate (Damian, 1976) or via filter paper cultures in petri dishes (Cross and Scott, 1961; Burren, 1980; Mueller et al., 1989). In the 1950's, Harada and Mori described a method whereby hookworm larvae migrate down filter paper placed in a con-

Mori, 1955; Komiya and Yasuraoka, 1966; Faust et al., 1970). The method is also acceptable for the development of some trematode and cestode larvae (Beaver et al., 1964), but it suffers from 2 drawbacks: it is both time consuming to apply feces to multiple filter paper strips and space consuming to house multiple racks of test tubes.

These problems are alleviated by the apparatus illustrated in Figure 1. Feces are spread thinly onto the top two-thirds of Whatman number 1 filter paper. The Whatman sheets are fastened with tape onto both sides of 8 plates that slide in and out of a 20- × 20- × 10-cm box and rest on a 1-cm shoulder. Thus, a large surface area of nearly 6,400 cm² can be confined to a small box that fits into a bench-top incubator. The top of the filter paper was not routinely cut off after the first day of culture, although in some instances this may improve the yield of larvae. Approximately 300 ml of water containing 30 mg/liter mycostatin is poured in the vessel until the level is just below the fecal layer. The spigot drains water containing the active third-stage larvae. The chamber is refilled each day by pouring the same volume of water through a small funnel inserted between the plates, away from the feces. A lid with holes at the top permits air exchange.

Feces containing 800 eggs/g applied to 2 culture boxes first yielded third-stage *Ancylostoma caninum* larvae on days 4–5 and yielded a maximum number of 3,700 larvae on days 7–8 at 27°C. *Necator americanus* larvae were also recovered from infected hamster feces.

Water containing the larvae is passed through a 60-mesh sieve and then through double-layer cheesecloth to remove minor particulates, including small pieces of filter paper. Fine particulates that pass through the cheesecloth are removed by centrifuging the larvae in an eppendorf tube—the particulates form a pellet along the side of the tube and larvae sink to the bottom. Larvae are routinely washed 4–5 times with water or defined medium containing antibiotics (1,000 U/ml penicillin and 1 mg/ml streptomycin) prior to biochemical analysis.

Figure 1. Plexiglas apparatus for modified Harada-Mori cultures. a. The box is shown with its lid removed and 1 of the 8 plates lifted partially out. The spigot is plastic. b. Apparatus as viewed from the top. Plexiglas plates, 3.2 mm thick, slide in grooves cut into the sides. One of the plates is shown in place.

ical tube until they reach the pool of water at the bottom, while water flowing up through the paper via capillary action keeps the feces moist and removes soluble toxic fecal products (Harada and

Literature Cited

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Mueller, J., B. Ellenberger, A. C. Fusco, B. Salafsky, and A. A. Siddiqui. 1989. A simple method for the collection of *Necator americanus* larvae. Journal of Helminthology 63:77–78.

CALL FOR PAPERS

1990 Student Presentation Competition

The Helminthological Society of Washington is sponsoring the second Student Presentation Competition during its monthly meeting on Wednesday, 10 October 1990 at the Uniformed Services University of the Health Sciences in Bethesda, Maryland.

Eligibility: Any undergraduate or graduate student registered in a college or university degree program at the time of the presentation is eligible to compete for this award.

Conditions: Although multiple authorship is allowed, the project on which the paper is based must be substantially that of the student. The student must be the senior author and present the paper.

The presentation must be on a parasitological subject.

A student may compete with only a single presentation.

An abstract, which is limited to a single, double-spaced, typewritten page, must be provided. The abstract page also must contain the title, author(s), and institutional affiliation(s).

Presentation will be limited to 10 min. There will be approximately 5 min for questions and discussion between each presentation.

Membership in the Helminthological Society of Washington is not required.

Deadlines:

15 Aug 1990 Submission of abstract as described above together with a completed application form signed by an advisor or university official certifying the student status of the proposed presenter of the paper.

1 Sep 1990 Notification of acceptance of paper for presentation at the 10 October 1990 meeting.

10 Oct 1990 Student Presentation Competition at the 613th Meeting of the Helminthological Society of Washington.

Selection of Presentations: A maximum of 8 student presentations will be selected for the competition. The selection of an abstract will be based on the organization of the abstract, originality of the work described, and its potential contributions to parasitology.

Judging of Presentations: The presentations will be evaluated by a panel of judges on the following bases: organization, techniques, originality, contribution, interpretation of results, and knowledge of the subject.

Awards: Monetary awards in the amount of $300, $200, and $100 will be presented to the first, second, and third place papers, respectively. In addition, the Society will waive page charges if the first place manuscript is accepted for publication in the *Journal of the Helminthological Society of Washington.*

Application: Submit abstract and completed application form to:

> W. Patrick Carney, Ph.D.
> Department of Preventive Medicine
>   and Biometrics
> Uniformed Services University of
>   the Health Sciences
> 4301 Jones Bridge Rd.
> Bethesda, MD 20814-4799
> (202) 295-3701
> FAX (202) 295-3431

The application form should include the title of the paper, the name, address, and telephone number of the student competitor, the student's signature, and the signature of an advisor or university official. The student's signature verifies that the research is original work performed by a graduate or undergraduate student.

MINUTES

Six Hundred Fifth Through
Six Hundred Twelfth Meetings

605th Meeting: Uniformed Services University of the Health Sciences, Bethesda, MD, 11 October 1989, President Jeffrey W. Bier, presiding. A slate of candidates was presented for Society offices. The passing of Horace W. Stunkard was observed with a moment of silence. Bryce Redington presided over the scientific program during which the following papers were presented: Historical perspective of schistosomiasis in Zambia, by Edward Michelson; Epidemiology of cryptosporidiosis, by Beth Unger; and Seroepidemiology of toxoplasmosis in Southeast Asia, by John Cross.

606th Meeting: Animal Parasitology Institute, USDA, Beltsville, MD, 14 November 1989. The meeting was presided over by President Jeffrey W. Bier. Frank Douvres was presented with the Life Membership Award and J. Ralph Lichtenfels received the 1989 Anniversary Award. The following individuals were elected to Society offices by the membership: John H. Cross, President; Hyun S. Lillehoj, Vice-President; David J. Chitwood, Corresponding Secretary-Treasurer; and Leonard J. Francl, Recording Secretary. The scientific portion of the program was presided over by J. Ralph Lichtenfels: Current research on ruminant nematodes, by Ralph A. Bram; Systematics, identification, classification and diagnosis, by J. Ralph Lichtenfels; Structure and function of the nematode cuticle, by Ray Fetterer; Molting and development in ruminant trichostrongyles, by Ray Gamble; Factors affecting transmission of ruminant nematodes, by Louis Gasbarre; Lymphokine regulated immunity to nematode parasites, by Joseph Urban; and Role of host genetics in resistance to gastrointestinal parasites, by Chris Davies.

607th Meeting: Dinner meeting hosted by the Nematology Laboratory, USDA, Beltsville, MD, 6 December 1989, John H. Cross, presiding. Lifetime membership awards were presented to Thomas K. Sawyer and A. Morgan Golden in appreciation for their contributions to the Society and to biological science. New officers were installed. Richard Sayre presided over a roast of A. Morgan Golden in honor of his retirement.

608th Meeting: National Institutes of Health, Bethesda, MD, 10 January 1990, John H. Cross, presiding. A proposed budget for 1990 was presented by Treasurer David J. Chitwood and was accepted by the members present. Jeffrey W. Bier and Ralph P. Eckerlin were recognized for their devotion to the Society as evidenced by their recent trip to Allen Press, Lawrence, Kansas, to resolve the problem with onerous journal storage fees. The Uniformed Services University of the Health Sciences will host the Second Student Symposium in October 1990. Proceedings were turned over to Frank Neva, who presided over the scientific portion of the program: Egg production is the major stimulus of T helper-2 lymphocyte responses in murine schistosomiasis mansoni, by Jean-Marie Grzych; Molecular characterization of an onchocercal antigen useful for diagnosis, by Edgar Lobos; and Penetration of red cells by *Plasmodium falciparum,* by Stephan Dolan.

609th Meeting: Naval Medical Research Institute, Bethesda, MD, 14 February 1990, John H. Cross, presiding. David J. Chitwood presented the 1990 Treasurer's report that showed the society ending 1989 $8,353.52 in the black. Proceedings were turned over to Trevor Jones of NMRI, who conducted the scientific session: Cytotoxic T-cells recognize a peptide from the circumsporozoite protein on malaria infection hepatocytes, by Walter Weiss; Protection of mice against challenge with sporozoites of *Plasmodium yoelii* with monoclonal antibodies, by Yupin Charoenvit; and Detection of the fine specificity of a protective antibody in the *Plasmodium vivax* system, by Trevor Jones.

610th Meeting: 80th Anniversary dinner meeting hosted by the Walter Reed Army Institute of Research, Washington, DC, 23 March 1990. John H. Cross presided over the business meeting. The Executive Committee solicited reaction from

members of the society as to the advisability of spending society funds on special projects, and, if suitable, then what projects might be deserving of support. The meeting was turned over to Willis Reid, WRAIR, who presided over the scientific program. Col. Reid briefly spoke on the history of the Society and introduced the after-dinner speaker, Dr. Gerhard A. Schad, University of Pennsylvania, who spoke about his hookworm research.

611th Meeting: School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, MD, 18 April 1990, cosponsored by the Tropical Medicine Dinner Club. The meeting was called to order by Immediate Past-President Jeffrey W. Bier and turned over to Clive Shiff, who presided over the scientific portion of the meeting. Dr. Shiff introduced Drs. Elli Leontsini and Peter Winch, who jointly spoke on Community-based control of *Aedes aegypti* in Mexico and Honduras.

612th Meeting: New Bolton Center, Kennett Square, PA, 5 May 1990; joint meeting with the New Jersey Society for Parasitology and cosponsored by SmithKline Beecham Animal Health and the Laboratory of Parasitology, University of Pennsylvania. John H. Cross presided over the business meeting. It was announced that A. James Haley will receive the Anniversary Award. The meeting was turned over to Gerhard A. Schad, University of Pennsylvania, and Thomas Newby, SmithKline Beecham, who presided over the scientific program on "Parasites and proteases." Dr. Schad dedicated the meeting to Marc H. Dresden (21 July 1938–17 February 1990). Dr. Newby introduced: Dr. Peter Hotez, Yale University, who spoke on the Role of proteases and hyaluronidases in nematode larval invasion; Dr. Judy Sakanari, University of California, San Francisco, who spoke on the Role of proteases in the pathogenesis of parasitic disease; and Dr. Raymond Gamble, USDA, Beltsville Agricultural Research Center, who spoke on the Role of proteases in nematode development.

The Helminthological Society welcomed 48 new members to the Society during the meetings indicated: *605th:* Ulrich P. Kalkofen, Dharma Goud, Michael J. Patrick, Robert J. Cox, Ann M. Barse, Mario T. Philipp, Stuart K. Kim, Bruno Gottstein, and John M. Halbrendt; *606th:* John Cone; *608th:* Stephen C. Hembree and Lena Measures; *609th:* Ted Alby, Cathy A. Leadabrand, Jean-Francois Guegan, Anthony I. Okafor, Donald P. Schmitt, and Diane W. Taylor; *610th:* Joseph J. Adamo, Scott E. Baird, Lynn K. Carta, John Chittambar, Eric L. Davis, John D. Eisenbeck, Laura L. Georgi, Kerrick M. Hartman, H. Robert Horvitz, James E. Lindegren, Manuel M. Mota, John Mueller, Sarah L. Poynton, David A. Rickard, Robert D. Riggs, Paul W. Sternberg, Louis M. Wiest, Valerie M. Williamson, and Lawrence D. Young; *611th:* Myoung-Rae Cho, R. E. Harrison, Gary W. Lawrence, Terry L. Niblack, Pierre N. Sakwe, Nicola Volvas, and Wendell R. Young; *612th:* James D. Willett, Martha Sedegah, R. Pena Santiago, and Sven Bostrom.

Respectfully submitted,

LEONARD FRANCL,
Recording Secretary

AUTHOR INDEX FOR VOLUME 57

KEY WORD and SUBJECT INDEX FOR VOLUME 57

ANNIVERSARY AWARD RECIPIENTS

* Edna M. Buhrer	1960		Margaret A. Stirewalt	1975
Mildred A. Doss	1961		* Leo A. Jachowski, Jr.	1976
* Allen McIntosh	1962		* Horace W. Stunkard	1977
* Jesse R. Christie	1964		Kenneth C. Kates	1978
Gilbert F. Otto	1965		* Everett E. Wehr	1979
* George R. LaRue	1966		O. Wilford Olsen	1980
* William W. Cort	1966		Frank D. Enzie	1981
* Gerard Dikmans	1967		Lloyd E. Rozeboom	1982
* Benjamin Schwartz	1969		Leon Jacobs	1983
* Willard H. Wright	1969		Harley G. Sheffield	1984
Aurel O. Foster	1970		A. Morgan Golden	1985
Carlton M. Herman	1971		Louis S. Diamond	1986
May Belle Chitwood	1972		Everett L. Schiller	1987
* Elvio H. Sadun	1973		Milford N. Lunde	1988
E. J. Lawson Soulsby	1974		J. Ralph Lichtenfels	1989
David R. Lincicome	1975			

HONORARY MEMBERS

* George R. LaRue	1959		Justus F. Mueller	1978
Vladimir S. Ershov	1962		John F. A. Sprent	1979
* Norman R. Stoll	1976		Bernard Bezubik	1980
* Horace W. Stunkard	1977		Hugh M. Gordon	1981

CHARTER MEMBERS 1910

* W. E. Chambers	* Philip E. Garrison	* Maurice C. Hall	* Charles A. Pfender
* Nathan A. Cobb	* Joseph Goldberger	* Albert Hassall	* Brayton H. Ransom
* Howard Crawley	* Henry W. Graybill	* George F. Leonard	* Charles W. Stiles
* Winthrop D. Foster			

LIFE MEMBERS

* Maurice C. Hall	1931		David R. Lincicome	1976
* Albert Hassall	1931		Margaret A. Stirewalt	1976
* Charles W. Stiles	1931		* Willard H. Wright	1976
* Paul Bartsch	1937		* Benjamin Schwartz	1976
* Henry E. Ewing	1945		Mildred A. Doss	1977
* William W. Cort	1952		* Everett E. Wehr	1977
* Gerard Dikmans	1953		Marion M. Farr	1979
* Jesse R. Christie	1956		John T. Lucker, Jr.	1979
* Gotthold Steiner	1956		George W. Luttermoser	1979
* Emmett W. Price	1956		* John S. Andrews	1980
* Eloise B. Cram	1956		* Leo A. Jachowski, Jr.	1981
* Gerald Thorne	1961		Kenneth C. Kates	1981
* Allen McIntosh	1963		Francis G. Tromba	1983
* Edna M. Buhrer	1963		A. James Haley	1984
* Benjamin G. Chitwood	1968		Paul C. Beaver	1986
Aurel O. Foster	1972		Raymond M. Cable	1986
Gilbert F. Otto	1972		Harry Herlich	1987
* Theodor von Brand	1975		Glenn L. Hoffman	1988
May Belle Chitwood	1975		Robert E. Kuntz	1988
Carlton M. Herman	1975		Raymond V. Rebois	1988
Lloyd E. Rozeboom	1975		Frank W. Douvres	1989
* Albert L. Taylor	1975		Thomas K. Sawyer	1989

* Deceased.

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