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Seasonal Dynamics and Community Structure of Helminths of Spotted Sunfish, *Lepomis miniatus* (Osteichthyes: Centrarchidae) from an Oligohaline Estuary in Southeastern Louisiana, U.S.A.

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ABSTRACT: The seasonal dynamics of the helminth community of the spotted sunfish *Lepomis miniatus* Warren, 1992, from an oligohaline estuary were investigated over a 1-yr period. From 26 May 1991 to 25 May 1992, 7 helminth species (3 Trematoda, 2 Nematoda, 2 Acanthocephala) were recovered from the gastrointestinal tracts of 200 specimens of *L. miniatus*. The parasite community of this host was dominated by the trematodes *Barbulostomum cupuloris* and *Genarchella* sp. Both helminths were recruited and matured in this host throughout the year, but their times of peak abundance differed. *Barbulostomum cupuloris* was most abundant in February–May, whereas *Genarchella* sp. abundance peaked in November–February. *Camallanus oxycephalus* and *Leptorhynchoides thecatus* showed a similar pattern of seasonal abundance, which was highest in May–August for both species. The remaining 3 helminths, *Crepidostomum cornutum*, *Neoechinorhyncus cylindratus*, and *Spinitectus carolini*, were too rare to detect annual patterns of abundance. Infra- and component community diversity and richness did not vary seasonally, but infracommunity predictability was greatest in February–May.

KEY WORDS: parasite, helminth, seasonal dynamics, Centrarchidae, *Lepomis miniatus*, estuary, infracommunity, component community, community, Louisiana, USA.

Seasonal fluctuations in prevalence and abundance are common in many helminths of freshwater fishes (Eure, 1976; Chubb, 1979), but the mechanisms influencing seasonality are sometimes difficult to identify. Chubb (1979) concluded that, in general, seasonal patterns of occurrence of helminths are often species-specific and dependent upon: 1) how the helminth invades its host, 2) helminth growth and maturation, 3) accumulation of eggs, and 4) loss of gravid worms. Abiotic factors such as temperature may also affect the seasonal cycles of many helminths (Chappell, 1969; Anderson, 1974, 1976; Eure, 1976; Granath and Esch, 1983a–c).

Seasonal patterns of abundance of the helminths of centrarchid fishes in freshwater environments have been previously examined (McDaniel and Bailey, 1974; Cloutman, 1975; Eure, 1976), but studies addressing temporal variability of helminths in nongame centrarchids are lacking. More importantly, the helminth fauna of centrarchid fishes inhabiting estuarine environments has received little attention. Fiorillo and Font (1996) characterized the helminth communities of 4 species of *Lepomis* from a low-salinity estuary and showed that the compound community of centrarchid fishes in brackish water habitats differed from that of centrarchids in freshwater environments.

In this study, we examined the seasonal pattern of abundance of all helminths that utilize *Lepomis miniatus* Warren, 1992, as a definitive host in an oligohaline estuary. In addition, we used community measures to investigate seasonal fluctuations in the infracommunity and component community structure of *L. miniatus*.

Materials and Methods

From 26 May 1991 to 25 May 1992, 200 specimens of *L. miniatus* were collected from a 1.1-km section of a canal along Interstate Highway 55 located between the south bank of Pass Manchac and Ruddock, Louisiana, in St. John the Baptist Parish. This man-made canal is part of the oligohaline Lake Pontchartrain-Lake Maurepas estuary located in southeastern Louisiana. The salinity of this large estuary ranges from 0 ppt at the western shore of Lake Maurepas to 15 ppt at the eastern shore of Lake Pontchartrain, but at our study site, salinity never exceeded 3 ppt. Temporal variation in water temperature was determined using a Datasonde 3® water quality data logger (Hydrolab Corporation, Austin, Texas) located near our study site at the Turtle Cove Research Station on Pass Manchac, Louisiana.

Our 1-yr collection period was divided into 4 periods of equal duration. Forty-five specimens were collected during the May–August period (May 26–August 26), 53 during August–November (August 27–November 26), and 51 each during the November–February

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(November 27–February 26) and February–May (February 27–May 25) periods. There was a minimum interval of 1 mo between collections made in different time periods. All hosts were captured by angling or with hoop nets and crab traps baited with cat food and checked at 1–2-day intervals. The sex and standard length of each fish were recorded, and the stomach, pyloric ceca, and intestinal tract were examined for adult helminths. Trematodes were fixed in Berland's solution (9 parts acetic acid, 1 part 37% formaldehyde) and stored in AFA (alcohol-formalin-acetic acid). Nematodes were fixed in Berland's solution and placed in glycerine alcohol. After acanthocephalans were refrigerated in distilled water overnight to extrude the proboscis, several small holes were made in the body wall with fine dissecting pins prior to fixation in AFA. Trematodes and acanthocephalans were stained with Semichon's carmine, dehydrated in a graded alcohol series, cleared in xylene, and mounted in Permount®. Nematodes were cleared and mounted in glycerine jelly.

The influence of host body size (standard length, mm) on helminth abundance and community attributes was examined with Pearson's correlations. The prevalence and abundance (Bush et al., 1997) of all helminths were calculated overall and for each time period. Helminth abundance data were square root transformed prior to statistical analyses. Seasonal patterns of helminth prevalence and abundance were analyzed with chi-square tests and ANOVA or ANCOVA, respectively.

Because *Barbulostomum cupuloris* and *Genarchella* sp. were the most abundant helminths in the component community of this host, a contingency table analysis was used to examine for concurrent patterns of infection. Based on gonadal development, these 2 trematodes were assigned to 1 of 3 developmental stages. Specimens of *B. cupuloris* were scored as immature, mature, or gravid, and specimens of *Genarchella* sp. were categorized as nongravid, gravid, or heavily gravid. Immature specimens of *B. cupuloris* were defined as individuals having incomplete gonadal development and lacking vitellaria. Mature worms were characterized by complete gonadal development, but egg production had not yet begun. Individuals with eggs and highly packed vitellaria were classified as gravid. Specimens of *Genarchella* sp. that possessed incompletely developed gonads and lacked eggs were classified as nongravid. Gravid worms were characterized by completely formed testes and ovary, but the lobes of the vitellaria of these specimens were not clearly distinct. The uteri of these gravid specimens contained eggs, but they were only slightly convoluted and well confined within the intercecal space. Heavily gravid worms were characterized by vitellaria possessing distinct lobes. The uteri of heavily gravid specimens were distended with eggs, highly convoluted, and typically extended laterally beyond the ceca. The seasonal patterns of abundance of these developmental stages were examined with ANOVA or ANCOVA. Voucher specimens of all species and developmental stages have been deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland, under USNPC accession numbers 84483–84485, 84489, 84490, 88573 and 88574.

Overall and within each time period, Brillouins's diversity index, which is appropriate for fully censused communities (Pielou, 1977), was used to estimate infracommunity and component community diversity. Seasonal mean infracommunity diversity was compared using ANOVA. As a measure of infracommunity predictability, Renkonen's coefficient of similarity was used to determine overall and within-season infracommunity similarity. Seasonal mean infracommunity similarity was compared using ANOVA, and in addition, Renkonen's coefficient of similarity was used to compare the component community of this host among time periods.

Results

Seven helminth species (3 Trematoda, 2 Nematoda, 2 Acanthocephala), *Barbulostomum cupuloris, Genarchella* sp., *Crepidostomum cornutum, Camallanus oxycephalus, Spinitectus carolini, Leptorhynchoides thecatus,* and *Neoechinorhyncus cylindratus,* were recovered from the alimentary tracts of 200 *L. miniatus* (standard length in mm: $\bar{x} \pm$ SE, range; 96.9 ± 0.91, 68–126) collected from the Lake Pontchartrain-Lake Maurepas estuary. Host body size differed significantly among seasons (ANOVA, $P < 0.05$). The largest hosts were collected in the May–August time period (104 ± 1.51, 84.5–126). Host body size decreased through August–November (101 ± 1.3, 83.1–121) and November–February (99.1 ± 1.42, 78.1–118) and was lowest in February–May (84.0 ± 1.6, 68.0–109). Water temperature in this oligohaline estuary was highest in July and gradually decreased to its lowest value in January (Fig. 1).

With the exception of *C. cornutum,* whose abundance was greater in female hosts ($\bar{x} \pm$ SE, range; 0.12 ± 0.04, 0–3) (male hosts, 0.02 ± 0.02, 0–2) (*t*-test, $P < 0.05$), there were no sex-related differences in helminth abundance. In addition, only *C. cornutum* ($\chi^2 = 5.137$, $P < 0.05$) and *L. thecatus* ($\chi^2 = 10.442$, $P < 0.05$) showed host sex-related differences in prevalence, and as a result, both sexes were pooled for subsequent statistical analyses.

Only the abundance of *B. cupuloris* displayed a statistically significant relationship with host body size (overall, $r = -0.254$, $P < 0.01$). In addition, no statistically significant correlations between host size and helminth species abundance were found within each collecting period ($P > 0.05$).

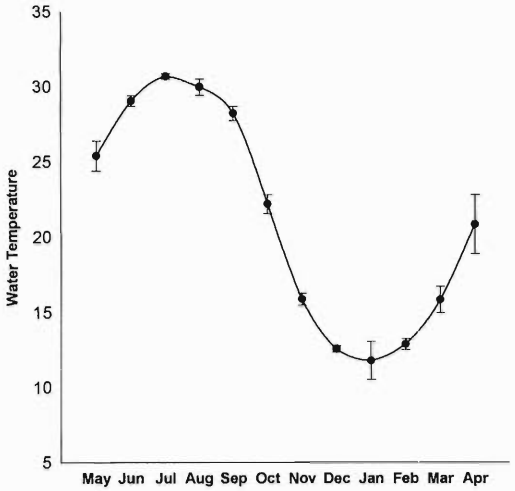

Figure 1. Mean monthly water temperature (°C) in Lake Pontchartrain-Lake Maurepas estuary (1992–1995). Vertical bars represent ±1 standard error of the mean.

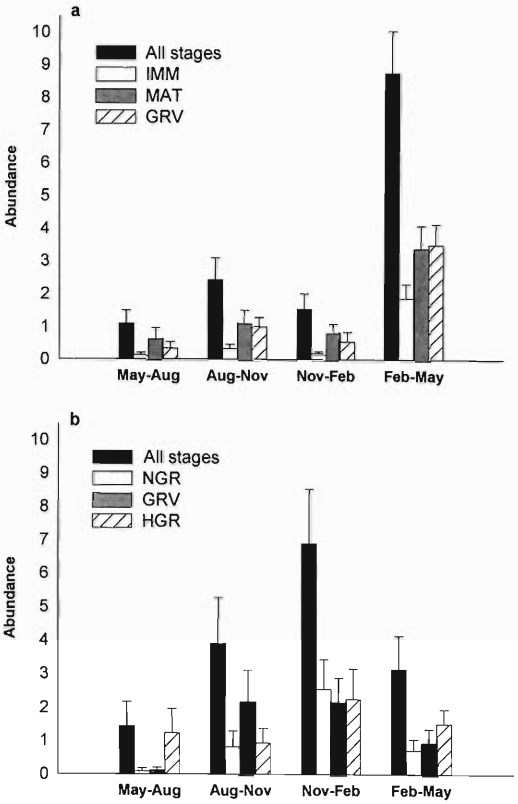

Figure 2. Seasonal abundances of (a) *Barbulostomum cupuloris* (all stages) and each developmental stage (IMM, immature; MAT, mature; GRV, gravid); (b) *Genarchella* sp. (all stages) and each developmental stage (NGR, nongravid; GRV, gravid; HGR, heavily gravid). Vertical bars represent ±1 standard error of the mean.

Helminth seasonal dynamics

Prevalence of *B. cupuloris* differed significantly among time periods ($\chi^2 = 28.98$, $P < 0.05$). Thirty-six percent of hosts examined in May–August harbored at least 1 specimen. Prevalence increased to 40% in August–November and 41% in November–February before reaching 82% in February–May. Irrespective of developmental stage, *B. cupuloris* was most abundant in February–May (8.8 ± 1.28, 0–37), displaying an 82% increase in abundance from the previous November–February time period (1.6 ± 0.47, 0–20) and a considerable decrease in the subsequent May–August period (1.1 ± 0.4, 0–15) (2-way ANCOVA, $P < 0.05$) (Fig. 2a). Abundance also differed with respect to developmental stage (2-way ANCOVA, $P < 0.05$), but no interaction effect was found (2-way ANCOVA, $P > 0.05$). Mature specimens were most abundant (1.5 ± 0.24, 0–21), followed by gravid specimens (1.4 ± 0.22, 0–18) and immature worms (0.6 ± 0.13, 0–14). In addition, each developmental stage of *B. cupuloris* showed a statistically significant seasonal cycle of abundance (ANCOVA, $P < 0.05$ for each stage). The abundance of each stage was lowest in May–August, remained low in the following August–November and November–February periods, and reached maximum abundance in February–May (Fig. 2a).

Thirteen percent of hosts in May–August were infected with *Genarchella* sp. Prevalence increased through August–November (34%) to reach a peak in November–February (49%) before decreasing in February–May (39%) ($\chi^2 = 13.69$, $P < 0.05$). *Genarchella* sp. was most abundant in November–February (6.9 ± 1.62, 0–41), a 44% increase from the previous August–November time period (3.9 ± 1.39, 0–43) and showed its lowest abundance in May–August (1.4 ± 0.74, 0–23) (2-way ANOVA, $P < 0.05$) (Fig. 2b). Overall, there was no difference in abundance among developmental stages and no interaction effect (2-way ANOVA, $P > 0.05$). Both nongravid and gravid worms showed statistically significant seasonal cycles of abundance (ANOVA, $P < 0.05$ for each stage). Nongravid and gravid worms were most abundant in November–February (2.5 ± 0.89, 0–27) and Au-

gust–November (2.2 ± 0.94, 0–41), respectively, and least abundant in May–August (nongravid: 0.09 ± 0.09, 0–4; gravid: 0.1 ± 0.08, 0–3) (Fig. 2b).

Camallanus oxycephalus was most prevalent and abundant in May–August (36%) (0.7 ± 0.26, 0–11). Prevalence and abundance declined throughout the year and were lowest in February–May (10%) (0.1 ± 0.05, 0–2), ($\chi^2 = 12.888$, $P < 0.05$) (ANOVA, $P < 0.01$), respectively (Table 1, Fig. 3). Prevalence of *L. thecatus* did not change seasonally ($\chi^2 = 5.278$, $P > 0.05$) (Table 1), but its abundance did vary among time periods and peaked in May–August (0.6 ± 0.19, 0–5) (ANOVA, $P < 0.05$) (Fig. 3). *Crepidostomum cornutum, S. carolini,* and *N. cylindratus* were uncommon (prevalence of each, < 7%), and too few individuals (abundance of each, < 0.1) were recovered to determine seasonal patterns of prevalence and abundance (Table 1).

Parasite abundance (overall: 8.2 ± 0.8, 0–56) differed significantly among time periods (ANCOVA, $P < 0.05$). Abundance was lowest in May–August (4.0 ± 0.87, 0–26), increased during August–November (7.3 ± 1.66, 0–53) and November–February (8.5 ± 1.54, 0–45), and reached its highest value during February–May (12.8 ± 1.81, 0–56).

Infracommunity analysis

Overall, host body size was correlated with infracommunity diversity ($r = 0.18$, $P < 0.05$), but this relationship was not significant within time periods. The most diverse infracommunity was found in November–February (1.294 ± 0.197, 0.0–4.14), whereas in February–May, infracommunity diversity was lowest (0.689 ± 0.136, 0.0–3.35). The remaining 2 time periods, May–August and August–November, showed intermediate levels of infracommunity diversity (0.889 ± 0.151, 0.0–3.40 and 0.959 ± 0.185, 0.0–4.01, respectively). However, infracommunity diversity did not differ significantly among time periods (ANCOVA, $P > 0.05$). Overall infracommunity diversity was 0.963 ± 0.087 (0.0–4.14).

Both overall and within time periods, host body size did not influence infracommunity species richness. Helminth richness was lowest in May–August (1.244 ± 0.143, 0–4) and increased in August–November (1.302 ± 0.139, 0–3) and November–February (1.353 ± 0.096, 0–3). Infracommunity richness was greatest in February–May (1.549 ± 0.113, 0–3). However, infracommunity species richness did not differ significantly among time periods (ANOVA, $P > 0.05$). Overall infracommunity species richness was 1.365 ± 0.062 (0–4). Infracommunity predictability differed significantly among time periods (ANOVA, $P < 0.001$). Infracommunity similarity was greatest in February–May (0.56 ± 0.01, 0–1) and lowest in May–August (0.22 ± 0.01, 0–1). In August–November and November–February, infracommunity similarity values were intermediate (0.31 ± 0.01, 0–1 and 0.34 ± 0.01, 0–1, respectively). Overall infracommunity similarity was low (0.31 ± 0.003, 0–1).

Component community analysis

The trematodes *B. cupuloris* and *Genarchella* sp. were the most prevalent and abundant helminths and dominated the component community of *Lepomis miniatus* (Table 1). *Barbulostomum cupuloris* was most prevalent (50%), and although *Genarchella* sp. was recovered from fewer hosts (35%), its overall abundance (3.9 ± 0.64, 0–43) did not differ significantly from that of *B. cupuloris* (3.5 ± 0.46, 0–37) (*t*-test, $P > 0.05$). Although together these 2 trematodes accounted for 1,485 of the total 1,662 worms recovered during this study (89%), no significant association was found between them with respect to concurrent patterns of infection ($\chi^2 = 0.032$, $P > 0.05$). The nematode *C. oxycephalus* was recovered from 24% of hosts examined, but its abundance was low (0.4 ± 0.08, 0–11). The remaining 4 helminth species showed low prevalence and abundance and, together with *C. oxycephalus,* represented only 11% of the total helminth specimens recovered (Table 1).

Component community diversity was low (0.47). It was greatest in February–May (1.16), progressively declined through May–August (0.63) and August–November (0.45), and was lowest in November–February (0.34). Component community species richness changed slightly over the year. Six helminth species were recovered during May–August, August–November, and November–February, whereas 7 helminth species were found in February–May (Table 1). The trematode *C. cornutum* and the acanthocephalan *N. cylindratus* were the only helminths not found in all 4 time periods (Table 1). Component community comparisons among time periods were made using Renkonen's co-

Table 1. Overall and seasonal prevalence, abundance, and range of helminths of *Lepomis miniatus*.

Helminth	May–Aug., n = 45	Aug.–Nov., n = 53	Nov.–Feb., n = 51	Feb.–May, n = 51	Overall, n = 200
Barbulostomum cupuloris (Ramsey, 1965)	36, 1.1 ± 0.4, 0–15	40, 2.4 ± 0.67, 0–23	41, 1.6 ± 0.47, 0–20	82, 8.8 ± 1.28, 0–37	50, 3.5 ± 0.46, 0–37
Genarchella sp.	13, 1.4 ± 0.74, 0–23	34, 3.9 ± 1.39, 0–43	49, 6.9 ± 1.62, 0–41	39, 3.1 ± 1.00, 0–36	35, 3.9 ± 0.64, 0–43
Crepidostomum cornutum (Stafford, 1904)	0, 0	11, 0.1 ± 0.05, 0–2	2, 0.06 ± 0.06, 0–3	8, 0.1 ± 0.06, 0–2	6, 0.08 ± 0.07, 0–3
Camallanus oxycephalus (Ward and Magath, 1916)	36, 0.7 ± 0.26, 0–11	34, 0.6 ± 0.14, 0–5	18, 0.4 ± 0.13, 0–3	10, 0.1 ± 0.05, 0–2	24, 0.4 ± 0.08, 0–11
Spinitectus carolini (Holl, 1928)	2, 0.02 ± 0.02, 0–2	2, 0.04 ± 0.04, 0–2	2, 0.04 ± 0.04, 0–2	1, 0.04 ± 0.04, 0–2	2, 0.04 ± 0.02, 0–2
Leptorhynchoides thecatus (Kostylew, 1924)	24, 0.6 ± 0.19, 0–5	9, 0.09 ± 0.04, 0–1	20, 0.3 ± 0.11, 0–3	12, 0.1 ± 0.05, 0–1	16, 0.3 ± 0.05, 0–5
Neoechinorhyncus cylindratus (Van Cleave, 1919)	13, 0.3 ± 0.13, 0–5	0, 0	0, 0	2, 0.06 ± 0.06, 0–3	3.5, 0.08 ± 0.03, 0–5

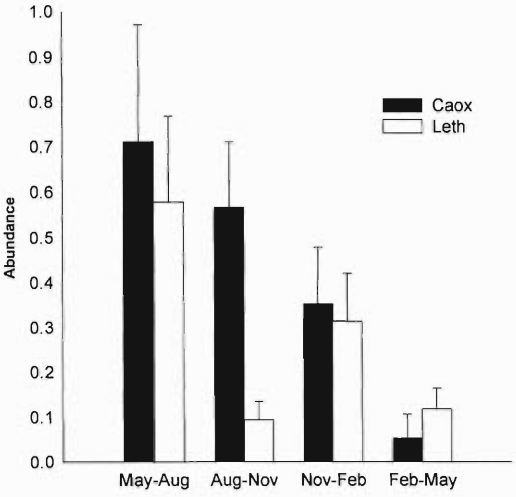

Figure 3. Seasonal abundance of *Camallanus oxycephalus* (Caox) and *Leptorhynchoides thecatus* (Leth). Vertical bars represent ±1 standard error of the mean.

efficient of similarity. Mean seasonal component community similarity was 0.53 ± 0.058, 0.41–0.77. The helminth community of *L. miniatus* in August–November and November–February showed the greatest similarity (0.77), whereas the May–August and November–February communities were least similar (0.45). The remaining comparisons are shown in Table 2.

Discussion

The species composition, richness, and diversity of the helminth community of *L. miniatus* were similar throughout the year. Species-specific and overall abundance of these helminths, infracommunity similarity, and host body size did vary somewhat with season. The trematodes *B. cupuloris,* described from *L. miniatus* (as *Lepomis punctatus* (Valenciennes, 1831)) collected within our study site (Ramsey, 1965), and *Genarchella* sp. were the most prevalent and abundant helminths recovered in this study. These parasites have been reported only in estuarine centrarchid fishes (Fiorillo and Font, 1996), in which they showed distinct seasonal cycles of prevalence and abundance.

Barbulostomum cupuloris was the only helminth to show, possibly as a result of an ontogenetic shift in diet, a significant relationship with host body size. However, the influence of host size was removed statistically from the subsequent seasonal abundance analysis. As a result, the nature of the observed seasonal patterns of this and all other helminth species is biological and not a result of changes in host demographics.

Table 2. Renkonen's coefficients of component community similarity of helminths of *Lepomis miniatus* between paired time periods.

	Aug.–Nov.	Nov.–Feb.	Feb.–May
May–Aug.	0.46	0.41	0.46
Aug.–Nov.		0.77	0.62
Nov.–Feb.			0.45

Seasonal dynamics of helminth infections

Conditions were optimal for the recruitment and maturation of *B. cupuloris* in February–May, when prevalence was greatest, and each developmental stage of this worm displayed maximum abundance. Following that period, the abundance of each developmental stage and the overall prevalence declined to their lowest values (Fig. 2a). Overall, most *B. cupuloris* specimens recovered were mature or gravid. These data suggest that *B. cupuloris* matures quickly after recruitment. Immature, mature, and gravid specimens were recovered in all 4 collecting periods, indicating that recruitment and egg production occurred throughout the year, irrespective of water temperature. Because of south Louisiana's near-subtropical climate, seasonal changes in water temperature are not extreme (Fig. 1). Although water temperature does not affect egg production in *B. cupuloris,* temperature can influence timing and rate of cercarial production and dispersal (Chappell, 1969; review in Chubb, 1979) and the seasonal abundance of first or second intermediate hosts (Fernandez and Esch, 1991a, b). It is likely that both factors interact to affect the seasonal abundance of *B. cupuloris* in its definitive host.

Similarly, water temperature did not affect recruitment and maturation of *Genarchella* sp. in *L. miniatus.* As with *B. cupuloris,* all 3 developmental stages of *Genarchella* sp. were found throughout the year, but this helminth showed a more gradual increase in recruitment, which peaked in November–February (Fig. 2b). At that time of year, many gravid worms were also recovered. The seasonal cycles of *Genarchella* sp. and *B. cupuloris* were asynchronous. Unlike *B. cupuloris,* which showed maximum prevalence

and abundance in February–May, *Genarchella* sp. was more common and numerous in November–February (Fig. 2a, b). However, as in *B. cupuloris,* the seasonal cycle of *Genarchella* sp. in *L. miniatus* may be linked to the seasonal dynamics of cercarial production and dispersal and to the abundance of the intermediate host.

The life cycles of *B. cupuloris* and *Genarchella* sp. are not known but are probably dependent on brackish water food webs for successful transmission (Ramsey, 1965; Fiorillo and Font, 1996). The lack of a concurrent pattern of infection, as well as the apparent asynchrony in the seasonal cycles of these trematodes, suggest that they do not share the same intermediate hosts.

A qualitative analysis of the gut contents of *L. miniatus* in May–August showed that this centrarchid preyed primarily on amphipods (Fiorillo and Font, 1996). Similarly, Levine (1980) reported that amphipods made up 75% of all prey items of *L. miniatus* in the Lake Pontchartrain-Lake Maurepas estuary. However, Fiorillo and Font (1996) showed that in May–August, both helminths were much more prevalent and abundant in redear sunfish *Lepomis microlophus* (Günther, 1859), a host well known for its specialized diet of bivalves and other mollusks (Wilburn, 1969; Lauder, 1983). In this estuary, Levine (1980) reported that the diet of *L. microlophus* consisted primarily of molluscs, but some amphipods were also taken. A qualitative gut analysis in May–August showed that *L. microlophus* preyed on amphipods, isopods, and bivalves (Fiorillo and Font, 1996). These data suggest that amphipods and bivalves may represent potential second intermediate hosts for these 2 trematodes.

The nematode *C. oxycephalus* was most prevalent and abundant in May–August. Prevalence and abundance declined through the subsequent time periods and were lowest in February–May. It is likely that the seasonal dynamics of *C. oxycephalus* in this estuary are dependent on the seasonal abundance of its copepod intermediate host as shown by Stromberg and Crites (1975) in Lake Erie. Unfortunately, we have no data on the seasonal dynamics of copepod populations in the Lake Ponchartrain-Lake Maurepas estuary to support this assumption, but, generally, zooplankton populations in temperate climates increase in the summer months (Pennak, 1989). Although in our study *C. oxycephalus* abundance was low, we did recover gravid specimens, suggesting that *L. miniatus* is a suitable host for this nematode.

As in *C. oxycephalus,* abundance of *L. thecatus* was low, but this acanthocephalan did show a seasonal cycle of abundance that peaked in May–August. Fiorillo and Font (1996) showed that, in this estuary, *L. thecatus* was much more prevalent and abundant in redear sunfish, *L. microlophus,* and *C. oxycephalus* occurred more frequently in bluegill, *L. macrochirus* Rafinesque, 1819, suggesting that *L. miniatus* is a suitable rather then a required host for these helminths. Leong and Holmes (1981) suggested that, within its environment, the seasonal cycle of a helminth is mostly determined by its seasonal dynamics within its most common host in which the parasite can become reproductive (required host). Therefore, the seasonal cycles of *L. thecatus* and *C. oxycephalus* in *L. miniatus* may not be indicative of the seasonal pattern found in *L. microlophus* and *L. macrochirus,* respectively. Too few specimens of the remaining 3 helminth species were found to determine seasonal cycles of prevalence and abundance, but all are common parasites of centrarchids and other fishes from freshwater environments (see Hoffman, 1967) (Table 1).

Mostly because of increases in abundance of *B. cupuloris* and *Genarchella* sp. (Fig. 2a, b), the overall parasite abundance was greatest in February–May. That time of year is generally associated with an increase in the feeding activity of fishes in Louisiana as water temperature begins to rise (Fig. 1) and many centrarchid species approach the reproductive season (Carlander, 1977). Many invertebrate potential intermediate hosts also show seasonal changes in density, with abundance peaks in early spring (Heard, 1982). Seasonal dynamics of invertebrate intermediate hosts, coupled with seasonal variation in feeding rates and diet of *L. miniatus,* may play an important role in determining the seasonal cycles of abundance of these helminths.

Infracommunity structure

Kennedy (1990) characterized the helminth community of freshwater fishes as depauperate and isolationist. The infracommunity of *L. miniatus* displayed both characteristics. Infracommunities were characterized by a lack of helminth interactions, were species-poor, and included a small number of worms. Consequently,

overall mean infracommunity diversity and species richness of *L. miniatus* were low, similar to other freshwater fishes (Kennedy et al., 1986).

Most fish display indeterminate growth (Wooten, 1990), so that body size is often highly correlated with age (Ricker, 1979; Swales, 1986). In the present study, larger hosts harbored a more diverse infracommunity. This was probably because of greater exposure time, which may increase the probability of these hosts being colonized by the less common helminth species. Cloutman (1975) noted a similar relationship between age and helminth diversity in largemouth bass, *Micropterus salmoides* (Lacépède, 1802).

Seasonality did not affect infracommunity diversity and species richness. With the exception of *C. cornutum* and *N. cylindratus,* all remaining helminths were recovered in all time periods, suggesting that the larval forms of the majority of these helminths are capable of colonizing *L. miniatus* year-round. However, the proportion of infected intermediate hosts, as shown by Fernandez and Esch (1991a, b), may have changed seasonally, resulting in the discrete cycles of abundance shown by some of these helminths.

Overall, the infracommunity structure of *L. miniatus* was not highly predictable, suggesting that each infracommunity represented a random subset of the parasites found in the component community of this host. Poulin (1997) noted that low infracommunity predictability is also a characteristic of isolationist communities, because helminth interactions, which often result in more predictably structured assemblages, are lacking.

Infracommunity predictability did differ among time periods. Infracommunity structure was most and least predictable in February–May and May–August, respectively. In February–May, increases in prevalence and abundance of *B. cupuloris* were largely responsible for the greatest degree of infracommunity similarity, whereas reductions in prevalence and abundance of this trematode, along with *Genarchella* sp., may have contributed to low infracommunity predictability in the following season. The greater predictability in February–May suggests that larval helminths are more prevalent in their intermediate hosts during that time of year so that the probability of individual hosts acquiring a similar suite of parasites is greater.

Component community structure

The trematodes *B. cupuloris* and *Genarchella* sp. were the dominant species in the component community of *L. punctatus* and accounted for the majority of all worms recovered during this year-long study. These helminths are not found in freshwater centrarchids but have been reported from other *Lepomis* spp. in the Lake Pontchartrain-Lake Maurepas estuary (Fiorillo and Font, 1996). Ramsey (1965) noted that *B. cupuloris* was replaced by the closely related *Homalometron armatum* (MacCallum, 1895) in centrarchid hosts collected in freshwater ponds located near this estuary. In this estuary, *B. cupuloris* and *Genarchella* sp. are more prevalent and abundant in *L. microlophus* (Fiorillo and Font, 1996), suggesting that *L. miniatus* is a suitable but not a required host for these trematodes (Leong and Holmes, 1981). However, the specificity of *B. cupuloris* and *Genarchella* sp. for estuarine hosts reaffirms the importance of ecological associations to the component community structure of *L. miniatus.*

The remaining 5 helminths recovered from *L. miniatus* are common parasites of freshwater centrarchid fishes (see Hoffman, 1967). Although mature forms were found in *L. miniatus,* these helminths showed low prevalence and abundance (Table 1). However, all 5 species were more prevalent and abundant in other *Lepomis* spp. from this estuary (Fiorillo and Font, 1996). These patterns suggest that *L. miniatus* is a suitable host for these helminths (Leong and Holmes, 1981) but that their occurrence in *L. miniatus* may represent accidental infections.

Component community diversity was low and similar to that of other freshwater fishes (Kennedy et al., 1986). Qualitatively, component diversity varied seasonally and was greatest in February–May when *B. cupuloris* and *Genarchella* sp. occurred frequently and abundances were high. The component community of this host in August–November and November–February was most similar. In those time periods, most of the helminths recovered displayed similar measures of prevalence and abundance (Table 1), resulting in a greater degree of similarity.

Overall, the helminth species composition of *L. miniatus* was similar to that of other centrarchid hosts in this estuary (see Fiorillo and Font, 1996). All helminths found in the present study were also recovered in *L. macrochirus* and, with the exception of *C. cornutum,* in *L. megalotis.* However, compared to *L. miniatus,* species richness was much lower in *L. microlophus.* Dietary differences between and among hosts may ac-

count for this result (Bell and Burt, 1991), but unequal sampling effort may have biased this pattern (see Levine, 1980; Fiorillo and Font, 1996, for diet analyses).

Further studies are necessary to determine the life cycles of *B. cupuloris* and *Genarchella* sp. Knowledge of the intermediate hosts of these trematodes and their seasonal patterns of abundance, as well as of temporal changes in the trophic interactions of intermediate hosts and fish, is essential to our understanding of the mechanisms that determine the seasonal dynamics of these helminths and the parasite community structure of this centrarchid host. In addition, a better understanding of these life cycles and seasonal patterns of incidence and abundance would further elucidate the importance of *L. miniatus* to the circulation of these helminths in this estuarine ecosystem.

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Nematodes and Acanthocephalans of Raccoons (*Procyon lotor*), with a New Geographical Record for *Centrorhynchus conspectus* (Acanthocephala) in South Carolina, U.S.A.

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ABSTRACT: From April 1997 through April 1998, 128 raccoons (*Procyon lotor* (Linnaeus)) collected from 7 sites representing 4 physiographic areas in South Carolina were examined for gastrointestinal helminth parasites. Four species of nematodes (*Gnathostoma procyonis* (Chandler), *Physaloptera rara* Hall and Wigdor, *Arthrocephalus lotoris* (Schwartz), and *Molineus barbatus* Chandler) and 2 species of acanthocephalans (*Macracanthorhynchus ingens* (von Linstow) and *Centrorhynchus conspectus* Van Cleave and Pratt) were collected. The finding of 11 immature *C. conspectus* in 3 South Carolina raccoons represents a new geographical record for this species.

KEY WORDS: *Centrorhynchus conspectus,* raccoon, *Procyon lotor,* Nematoda, Acanthocephala, helminths, *Gnathostoma procyonis, Physaloptera rara, Arthrocephalus lotoris, Molineus barbatus, Macracanthorhynchus ingens,* South Carolina, U.S.A.

The raccoon (*Procyon lotor* (Linnaeus, 1758)) is an omnivore that ranges over most of North America and occurs in both rural and urban settings. Consequently, the range of zoonoses for raccoons is important in assessing risk to humans and domestic animals. In South Carolina, only limited studies on helminth parasites of raccoons have been reported previously (Harkema and Miller, 1964; Stansell, 1974). More recent reports of serious human illnesses from the northern and midwestern United States, such as cerebrospinal nematodiasis because of infection with the gastrointestinal nematode *Baylisascaris procyonis* (Stefanski and Zarnowski, 1951), led to the current study, which includes raccoons collected statewide from a wide variety of habitats (e.g., mountains, farms, urban areas, beaches, swamps, and barrier islands), allowing for a comparison of parasite burdens and consideration of human health risks associated with these parasites (Williams et al., 1997; Boschetti and Kasznica, 1995).

Materials and Materials

Raccoons (n = 128) were collected between April 1997 and April 1998 with foot-hold traps or wire live-traps. Traps were set at 7 sites that included 4 of the 5 physiographic areas of South Carolina. Site 1 included both urban and waterfowl management areas (WMA) in Pickens County (Foothills); Site 2 was a WMA in Union County (Piedmont); Site 3 was inland farm areas of Horry County (Lower Coastal Plains North, LCPN); Site 4 included both beach and wooded habitats in the tourist area of Myrtle Beach, Horry County (LCPN); Site 5 was a swamp located on the Savannah River in Hampton County (Lower Coastal Plains South, LCPS); and Sites 6 and 7 were both on barrier islands located in Charleston County (LCPS). John's Island (Site 6), next to and continuous with the mainland at times of low tide, is primarily forest and farmland with many freshwater ponds, whereas Seabrook Island (Site 7) is a small residential island about 1.5 km offshore, which lacks freshwater habitats. Each raccoon was subjected to multiple evaluations, which included not only our study of gastrointestinal helminth parasites, but also seroprevalence, culture and DNA studies for *Trypanosoma cruzi,* and museum study specimens. In addition, most animals were included in a trap-type capture effectiveness study conducted by the South Carolina Department of Natural Resources (SCDNR).

Raccoons were either euthanized by intramuscular injection of 0.2 ml/kg ketamine/xylazine followed by intraperitoneal injection of 1 ml/kg sodium pentobarbital, or were hunter-shot. Stomach and intestines from each animal were examined as soon as possible after death (within 1–2 hr). However, animals from 2 of the physiographic regions (Sites 3–7) were frozen at −4°C for 1–3 mo prior to examination for helminths because of the use of the animals for a trap-type study conducted by the International Association of Fish and Wildlife Agencies. Therefore, trematodes and cestodes were excluded from the overall analyses because freezing of a large number of hosts resulted in difficult collection and unreliable identification of flatworms.

All nematodes collected from the stomachs and small intestines of raccoons were preserved and stored in a 70% ethanol–5% glycerine solution. Representative specimens of each nematode were mounted in glycerine jelly. Acanthocephalans collected from the small

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intestine were placed in water until the proboscis everted, preserved in acetic acid-formalin-alcohol (AFA), and stored in 70% ethanol. Temporary wet mounts and permanent Mayer's acid carmine-stained mounts in Canada balsam were made for identification. Voucher specimens deposited at the U.S. National Parasite Collection in Beltsville, Maryland, have been assigned USNPC accession numbers 87838–87843. Fisher's exact test was used to detect significant differences ($P < 0.05$) in helminth prevalence (%) between study sites. Two-thirds of the animals caught were male, and 85% of all animals were mature. Because of the large bias toward males and adults, no statistical analyses were performed.

Results and Discussion

Of the 128 raccoons examined, 103 (80%) were infected with 1 or more of the 4 nematodes and 2 acanthocephalans listed in Table 1. *Gnathostoma procyonis* Chandler, 1942, and *Physaloptera rara* Hall and Wigdor, 1918, were recovered primarily from the stomach. *Arthrocephalus* (=*Placoconus*) *lotoris* (Schwartz, 1925) and *Molineus barbatus* Chandler, 1942, were collected from the posterior and anterior ends of the small intestine, respectively. Both *Macracanthorhynchus ingens* (von Linstow, 1879) and *Centrorhynchus conspectus* Van Cleave and Pratt, 1940, were recovered exclusively from the small intestine. Interestingly, 96.1% of raccoons examined from Sites 1–6 were infected with at least 1 helminth species, whereas only 5 of 26 (19.2%) raccoons examined from Seabrook Island (Site 7) were infected.

Gnathostoma procyonis, a stomach nematode that forms large nodules in the mucosa, was found at Sites 3 and 5 in significantly larger numbers than at other sites (Table 1). Extensive freshwater habitats were present at both sites, providing a favorable environment for the required first intermediate host, which is 1 of several species of cyclopoid copepods (Miyazaki, 1960). In contrast, no infections of *G. procyonis* were observed at 2 coastal locations (Sites 4 and 7), which lacked permanent freshwater habitats.

Physaloptera rara, a spirurid nematode recovered from both the stomach and small intestine of hosts, does not require the presence of freshwater habitats, because raccoons become infected by ingestion of various terrestrial arthropods (e.g., *Gryllus pennsylvanicus* Burmeister, 1838, Pennsylvania field cricket; *Blattella germanica* (Linnaeus, 1767), German cockroach; and *Centophiles* spp., camel crickets) (Lincoln and Anderson, 1973). Compared to all other sites, a sig-

Table 1. Summary data of nematodes and acanthocephalans from 128 raccoons, *Procyon lotor,* collected in South Carolina from April 1997 through April 1998.

Species of parasite	Site in host*	Within-area numbers of hosts infected (%)							State-wide	Intensity	
		Site 1 $n = 25$	Site 2 $n = 5$	Site 3 $n = 14$	Site 4 $n = 12$	Site 5 $n = 35$	Site 6 $n = 11$	Site 7 $n = 26$	$n = 128$	Mean ± SE	Range
Nematoda											
Gnathostoma procyonis	S	4 (15)	2 (40)	11 (79)	0 (0)	29 (83)	6 (55)	0 (0)	52 (41)	4.2 ± 0.51	1–17
Physaloptera rara	S, SI	20 (80)	0 (0)	1 (7)	1 (8)	25 (71)	2 (18)	0 (0)	49 (38)	38.7 ± 5.7	1–156
Arthrocephalus lotoris	SI, LI	15 (60)	2 (40)	3 (21)	3 (25)	7 (20)	5 (45)	1 (4)	36 (28)	19.9 ± 3.6	1–84
Molineus barbatus	SI	8 (32)	0 (0)	1 (7)	2 (17)	4 (11)	1 (9)	0 (0)	16 (13)	23.6 ± 6.9	1–94
Acanthocephala											
Macracanthorhynchus ingens	SI	12 (46)	1 (20)	9 (64)	8 (67)	28 (80)	6 (55)	4 (17)	68 (53)	9.7 ± 1.3	1–43
Centrorhynchus conspectus	SI	0 (0)	0 (0)	2 (14)	0 (0)	0 (0)	1 (9)	0 (0)	3 (2)	3.7 ± 2.7	1–9

* S, stomach; SI, small intestine; LI, large intestine.

nificantly higher prevalence of *P. rara* was observed in raccoons trapped at Site 1, with urban-captured animals dominating the number of infected animals. Because broad host specificity has been documented for physalopteroids, domesticated animals could accumulate large numbers of these worms by ingesting an infected intermediate host that commonly occurs in urban settings (Morgan, 1941).

High prevalences of both the raccoon hookworm, *A. lotoris,* and the trichostrongylid, *M. barbatus,* frequently have been reported in previous surveys (Harkema and Miller, 1964; Cole and Shoop, 1987). In the present study, however, overall prevalence of *A. lotoris* and *M. barbatus* was 28.1 and 12.5%, respectively (Table 1). Data from Seabrook Island are consistent with those of Harkema and Miller (1962), who previously reported an almost complete absence of *A. lotoris* and *M. barbatus* from Cape Island, South Carolina. These investigators suggested that the low prevalence of these 2 nematodes on coastal islands was due possibly to the detrimental effect of high tides, salinity of soil, and dry habitats on the free-living larval stages of these helminths. Additionally, seasonal variations have been documented, with lower prevalence during winter months (Smith et al., 1985), which could have contributed to the lower numbers observed in the current survey.

Although *B. procyonis* was not collected from any raccoon examined in this study, surveillance for this parasite should be continued because of its medical and veterinary significance and its reported widespread distribution in the United States (Kazacos and Boyce, 1989). Based on reports from southeastern states, Jones and McGinnes (1983) suggested that *B. procyonis* was found primarily in the more mountainous regions. The northwestern range of our study site, although classified as "Foothills," is not truly mountainous, which might account for the lack of *B. procyonis.* In contrast, however, *B. procyonis* recently was found in 70% of 33 raccoons examined in southern coastal Texas (Kerr et al., 1997). These investigators suggested that the nematode could have been acquired by ingestion of larvae in migratory wild birds, introduced from infected translocated raccoons, or the result of a northern expansion from Latin America. This recent finding of *B. procyonis* in southern Texas and limited reports from the adjacent state of Georgia (only 2 reports, each of a single infected raccoon [Babero and Shepperson, 1958; Kazacos and Boyce, 1989]) suggests the possibility of introduction of this nematode into South Carolina.

The most prevalent parasite collected was the acanthocephalan *M. ingens.* Infections occurred in raccoons from all study sites, with an overall prevalence of 53%. Although not considered a threat to public health, *M. ingens* infection in humans has been reported (Dingley and Beaver, 1985).

Six species of the acanthocephalan genus *Centrorhynchus* have been reported from North American birds of prey; however, little is known about the life cycle, geographical distribution, or prevalence of these acanthocephalan species. Read (1950) demonstrated experimentally that *Centrorhynchus spinosus* (Kaiser, 1893) was capable of developing to adults in laboratory rats, suggesting that members of this genus have the ability to complete development not only in bird definitive hosts, but also in mammalian hosts. One raccoon from John's Island (Site 6) and 2 raccoons from the Horry County inland site (Site 3) were infected with immature *C. conspectus.* Prior to the current study, immature forms of *C. conspectus* had been reported from 26 mammals representing 6 host species (3 *Didelphis virginiana* Kerr, 1792, Virginia opossum; 3 *P. lotor,* raccoon; 17 *Mustela vison* Schreber, 1775, mink; 1 *Spilogale putorius* (Linnaeus, 1758), spotted skunk; 1 *Blarina brevicauda* Gray, 1838, short-tailed shrew; and 1 *Urocyon cinereoargenteus* Schreber, 1775, gray fox) from 5 states (Virginia, Arkansas, North Carolina, Ohio, and Florida) (Nickol, 1969; see Richardson and Nickol, 1995). The largest number of worms previously reported from any individual mammalian host was 2 worms, whereas 1 raccoon in the current survey from the inland Horry County site (Site 3) was infected with 9 *C. conspectus* (see Richardson and Nickol, 1995). Several owl species, including *Bubo virginianus* (Gmelin, 1788), the great horned owl; *Otus asio* (Linnaeus, 1758), the eastern screech owl; and *Strix varia* Barton, 1799, the barred owl, have been reported as definitive hosts for *C. conspectus* (Richardson and Nickol, 1995). No intermediate host has been identified, although cystacanths of *C. conspectus* have been found in paratenic hosts (*Nerodia sipedon* (Linnaeus, 1758), the water snake, from North Carolina; *Rana clamitans* Latreille, 1801, the aquatic green frog, from Virginia; and *Des-*

mognathus fuscus (Green, 1818), the northern dusky salamander and *Plethodon glutinosus* (Green, 1818), the slimy salamander from Louisiana) (Nickol, 1969; see Richardson and Nickol, 1995). The finding of 11 immature *C. conspectus* in 3 South Carolina raccoons represents a new geographical record for this species. The collection only of immature *C. conspectus* from raccoons in this study supports earlier reports that suggested that wild mammals are aberrant hosts for this parasite (Richardson, 1993).

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Nematode Parasites of Yellow Perch, *Perca flavescens*, from the Laurentian Great Lakes

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ABSTRACT: Yellow perch, *Perca flavescens* (Mitchill), from 4 localities in the Laurentian (North American) Great Lakes were examined for nematodes: from eastern Lake Michigan in 1990; from southern Lake Michigan in 1991; from The Black Hole, Saginaw Bay, Lake Huron in 1991; and from Oak Point, Saginaw Bay, Lake Huron in 1996. *Dichelyne cotylophora* (Ward and Magath) infected perch from each location and had the highest prevalence, mean intensity, and mean abundance at Oak Point. *Eustrongylides tubifex* (Nitzsch) Jägerskiold was a common parasite of perch from Saginaw Bay, but it infrequently infected Lake Michigan perch. *Philometra cylindracea* (Ward and Magath) Van Cleave and Mueller was found in perch only from Saginaw Bay. *Contracaecum* sp. infrequently infected perch from Lake Michigan and The Black Hole. A comparative summary of the literature on nematodes infecting yellow perch from the Great Lakes is presented, listing 27 studies published since 1917. Four nematode genera utilize perch as intermediate hosts, and 5 genera utilize them as definitive hosts. Information on the life cycles and pathology caused by nematodes infecting yellow perch is presented.

KEY WORDS: Yellow perch, *Perca flavescens,* Percidae, Pisces, parasites, nematodes, Laurentian Great Lakes, Lake Michigan, Lake Huron, Saginaw Bay.

Several nematodes have been reported from yellow perch, *Perca flavescens* (Mitchill, 1814) (Percidae), in the Laurentian (North American) Great Lakes. In recent years, federal and state fisheries personnel, aquaculturists, and anglers have asked me to identify nematodes infecting yellow perch from the Great Lakes and to answer questions about them. Declines in the catch rates of perch have been reported in southern Lake Michigan; Saginaw Bay, Lake Huron; and western Lake Erie (Francis et al., 1996). The present study reports on the occurrence of *Dichelyne cotylophora* (Ward and Magath, 1917); *Eustrongylides tubifex* (Nitzsch, 1819) Jägerskiold, 1909; *Philometra cylindracea* (Ward and Magath, 1917) Van Cleave and Mueller, 1934; and *Contracaecum* sp. in yellow perch from Lake Michigan and Saginaw Bay, Lake Huron. A summary of the nematodes infecting yellow perch from the Great Lakes is presented, with accompanying information on their life cycles and pathology. The possible relationship between the decline of yellow perch populations in some areas of the Great Lakes and the occurrence of parasitic nematodes is also discussed.

Materials and Methods

A total of 364 yellow perch was collected by beach seine and trawl from southern Lake Michigan (Michigan City, Indiana) in 1991; eastern Lake Michigan (Ludington, Michigan) in 1990; Saginaw Bay, Lake Huron (The Black Hole) in 1991; and Saginaw Bay, Lake Huron (Oak Point) in 1996. Ludington is approximately 247 km north of Michigan City. Fish were sampled from the open water in Lake Michigan and also along the shore at Ludington. Saginaw Bay, a large shallow eutrophic bay divided into inner and outer areas, is the southwestern extension of Lake Huron located in east central Michigan. The inner area is shallower and warmer than the outer area, and is enriched with domestic, agricultural, and industrial inputs from the Saginaw River. The Black Hole in the Inner Saginaw Area and Oak Point in the Outer Saginaw Area are approximately 50 km apart.

Perch were put on ice in the field, frozen at the laboratory, and measured and sexed at necropsy when the abdominal cavity, viscera, muscle, gastrointestinal tract, and head were examined. *Dichelyne cotylophora, Eustrongylides tubifex,* and *Contracaecum* sp. were preserved in 70% alcohol and later cleared in glycerin for identification. *Philometra cylindracea* were broken during necropsy and pieces were placed in glycerin on a glass slide, allowed to clear, and examined with a light microscope; specimens were not kept. Prevalence is the percentage of fish infected in each sample, mean intensity is the mean number of nematodes of a species per infected fish, and mean abundance is the mean number of worms per examined fish. Voucher specimens have been deposited in the United States National Parasite Collection (USNPC), Beltsville, Maryland 20705: *Dichelyne cotylophora* (USNPC 88506) and *Eustrongylides tubifex* (USNPC 88507).

Results

Yellow perch from 2 locations in Lake Michigan and 2 locations in Saginaw Bay, Lake Huron, were examined for nematodes (Table 1).

Table 1. Number, collection time, and mean total length (mm) of *Perca flavescens* examined from Lake Michigan and Saginaw Bay, Lake Huron.

Location	Month(s), year	Mean total length ± SD (range, 95% confidence interval)
Michigan City, Indiana, southern Lake Michigan (100)*	August 1991	154 ± 67 (50–280, 141–168)
Ludington, Michigan, eastern Lake Michigan (64)*	May–September 1990	136 ± 23 (105–177, 131–142)
The Black Hole, inner Saginaw Bay, Lake Huron, Michigan (100)*	September 1991	172 ± 36 (110–278, 164–178)
Oak Point, outer Saginaw Bay, Lake Huron, Michigan (100)*	August 1996	202 ± 23 (170–287, 197–206)

* (Number of yellow perch examined.)

There was a significant difference in the lengths of perch between locations (analysis of variance, $F = 35.9$, $P < 0.0001$) with those from Oak Point being larger. Forty-eight percent (48) of yellow perch from Michigan City in 1991, 26% (17) from Ludington in 1990, 96% (96) from The Black Hole in 1991, and 98% (98) from Oak Point in 1996 were infected with 1 or more nematodes.

Gravid *Dichelyne cotylophora* infected the intestines of yellow perch from each location (Table 2). It was significantly more prevalent in perch from Michigan City than from Ludington, Michigan (chi-square, $\chi^2 = 26.6$, $P < 0.005$); intensities were not significantly different, but abundances were (Mann–Whitney test, $U = 9{,}187$, $P < 0.0001$). In Saginaw Bay, prevalence (chi-square, $\chi^2 = 128.6$, $P < 0.005$) and abundance (Mann–Whitney test, $U = 6{,}064$, $P < 0.0001$) of *D. cotylophora* were significantly higher in perch from Oak Point than from The Black Hole. *Contracaecum* sp. infrequently occurred encysted on the surface of the heart, in the liver, and associated with the mesentery of perch from Lake Michigan and The Black Hole.

Eustrongylides tubifex was most common in perch from Saginaw Bay. The intensity (Mann–Whitney test, $U = 9{,}773$, $P < 0.0001$) and abundance (Mann–Whitney test, $U = 12{,}798$, $P < 0.0001$) of *E. tubifex* were significantly higher in perch from The Black Hole than from Oak Point. Larvae occurred in capsules associated with the mesentery on the surface of the ovaries, testes, liver, spleen, and gastrointestinal tract and free in the body cavity, viscera, and muscle. Of the 303 *E. tubifex* found in perch from Oak Point in 1996, 92% of the worms or capsules with worms were seen with the unaided eye, whereas 8% were detected only with a dissecting microscope. Small and large *E. tubifex* were found in perch from both Saginaw Bay locations.

Philometra cylindracea, some of which were larvigerous, occurred free in the body cavity of perch only from Saginaw Bay, and was most common at Oak Point. Remains of crenulated and hardened masses of nematodes, probably dead *P. cylindracea* from past infections, were found in the body cavities and viscera of yellow perch from The Black Hole and Oak Point. All perch from Saginaw Bay in 1991 and 69% of them in 1996 that were infected with *P. cylindracea* were concurrently infected with *E. tubifex.* Ninety-six percent of Oak Point perch harbored at least 1 *E. tubifex* or *P. cylindracea* or remains of dead *P. cylindracea.*

There were no significant differences in the prevalence (chi-square analysis, $P > 0.05$) and intensity or abundance (Mann–Whitney test, $P > 0.05$) of *D. cotylophora, E. tubifex, P. cylindracea,* and *Contracaecum* sp. between female and male perch at any location. There were no significant correlations between the intensities of each nematode species and host length.

Discussion

At least 27 studies mentioning the nematode parasites of yellow perch from the Great Lakes have been published since 1917. The number of studies (in parentheses) performed in each Great Lake and associated connecting waters are: Lake Michigan (5), Lake Superior (1), St. Marys River (1), Lake Huron (7), Lake St. Clair (1), Lake Erie (12), and Lake Ontario (3) (Table 3). Many of these investigations did not report the number, length, and age of perch. Rosinski et al. (1997) reported that the nematode fauna of yellow perch in Saginaw Bay, Lake Huron, and Lake Huron proper are similar.

Table 2. Prevalence (P), mean intensity (MI), maximum number (max.), and mean abundance (MA) of nematodes infecting *Perca flavescens* from Lake Michigan and Saginaw Bay, Lake Huron.

Nematode	LM, MC* (100)†			LM, L* (64)†			SB, BH* (100)†			SB, OP* (100)†		
	P	MI ± SD (max.)	MA ± SD	P	MI ± SD (max.)	MA ± SD	P	MI ± SD (max.)	MA ± SD	P	MI ± SD (max.)	MA ± SD
Contracaecum sp.	3	1	0.03 ± 0.2	8	2.00 ± 1.2 (4)	0.15 ± 0.6	4	1	0.04 ± 0.2	—	—	—
Dichelyne cotylophora	47	4.60 ± 4.4 (19)	2.15 ± 3.8	19	4.20 ± 4.7 (18)	0.78 ± 2.6	4	1.30 ± 0.5 (2)	0.05 ± 0.3	84‡	5.50 ± 4.6 (23)‡	4.26 ± 4.6‡
Eustrongylides tubifex	3	1	0.03 ± 17	—	—	—	95	9.10 ± 7.5 (27)	8.60 ± 7.5	74	4.10 ± 3.4 (13)	3.05 ± 3.4
Philometra cylindracea	—	—	—	—	—	—	10	1	0.11 ± 0.3	16	1.60 ± 1.4 (6)	0.26 ± 0.8

* LM, MC = Lake Michigan, Michigan City; LM, L = Lake Michigan, Ludington; SB, BH = Saginaw Bay, The Black Hole; SB, OP = Saginaw Bay, Oak Point.
† (Number of yellow perch examined.)
‡ Values calculated from 87 fish.

A total of 15 nematode taxa has been reported from yellow perch in the Great Lakes (Table 3). Of these, *Agamonema* sp., *Contracaecum* sp., *E. tubifex, Eustrongylides* sp., *Hysterothylacium brachyurum* (Ward and Magath, 1917) Van Cleave and Mueller, 1934, *Raphidascaris acus* (Bloch, 1779) Railliet and Henry, 1915, and *Raphidascaris* sp. are represented by larval or immature stages. Of the 10 nematodes identified to species, 6 mature in the intestine of perch. Prevalence data from the literature indicate that *D. cotylophora* is the most common nematode infecting perch from Lake Michigan, *R. acus* is most common in Lake Superior perch, and *D. cotylophora* and *E. tubifex* are most common in perch from Lakes Huron and Erie. The nematodes of perch from Lake Ontario have prevalences of 8% or less. The report of Bangham and Hunter (1939) of *Agamonema* sp. from perch in Lake Erie refers to an unidentified larval form, an immature nematode (J. Crites, pers. comm.), and will not be considered further.

In the present study, *Contracaecum* sp. is reported for the first time from perch in Lakes Michigan and Huron; all other nematodes found have been reported infecting perch from these lakes. Four nematode taxa were found in perch in the present study compared to the 15 nematode taxa reported in the literature. There are several possible reasons for this, including 1) I only examined perch from 2 Lake Michigan locations and Saginaw Bay, 2) more parasitological studies have been done on perch in Lakes Erie and Huron, and 3) it is difficult to determine if fish were collected from different habitats. It is pointless to discuss whether some nematodes of yellow perch have disappeared in the Great Lakes, because so few studies have been done in the past to which I can compare this study.

Dichelyne cotylophora infects yellow perch from all the Great Lakes and is commonly found in the anterior intestine. Visible lesions were not observed at the sites of adult attachment. I have found worms up to 8 mm in length. Based on experimental evidence, Baker (1984b) suggested that prey fish (cyprinid minnows) are intermediate hosts for *D. cotylophora.* This parasite is not host-specific to perch, since it has been reported from several fish species in Lake Michigan, St. Marys River, Lake Huron, Lake St. Clair, Lake Erie, and Lake Ontario (Ward and Magath, 1917; Pearse, 1924; Bangham, 1933, 1955; Bangham and Hunter, 1939; Muzzall,

Table 3. Reported nematodes of *Perca flavescens* from the Laurentian Great Lakes.

Species	Lake*	Prevalence†	Locality	Reference
Agamonema sp.‡	E	2 (2/128)	OH	Bangham and Hunter, 1939
Contracaecum sp.‡	M	3 (3/100)	IN	Michigan City, this study
		8 (5/640)	MI	Ludington, this study
	H	4 (4/100)	MI	The Black Hole, this study
Camallanus oxycephalus	H	—§	MI	Rosinski et al., 1997
	E	2 (1/45)	OH, ONT	Bangham and Hunter, 1939
		5 (5/93)	OH	Bangham, 1972
		—§	OH	Stromberg and Crites, 1972
		6 (45/735)	OH	Cooper et al., 1977
		7 (27/408)	ONT	Dechtiar and Nepszy, 1988
Dichelyne cotylophora	M	—§	WI	Pearse, 1924
		9 (1/11)	WI, IL	Amin, 1977
		47 (47/100)	IN	Michigan City, this study
		19 (12/64)	MI	Ludington, this study
	S	42 (10/24)	ONT	Dechtiar and Lawrie, 1988
	SMR	33 (24/73)	MI	Muzzall, 1984
	H	—§	ONT	Smedley, 1934
		55 (110/201)	ONT	Bangham, 1955
		2 (3/134)	ONT	Dechtiar et al., 1988
		—§	MI	Rosinski et al., 1997
		4 (4/100)	MI	The Black Hole, this study
		68 (68/100)	MI	Oak Point, this study
	LSC	—§	—	Ward and Magath, 1917
	E	—§	ONT	Smedley, 1934
		65 (45/69)	OH, ONT, NY, PA	Bangham and Hunter, 1939
		10 (76/735)	OH	Cooper et al., 1977
		—§	ONT	Baker, 1984a
		50 (6/12)‖	ONT	Baker, 1984b
		6 (25/408)	ONT	Dechtiar and Nepszy, 1988
	O	—§	ONT	Tedla and Fernando, 1969
		—§	ONT	Tedla and Fernando, 1970
		5 (7/150)	ONT	Dechtiar and Christie, 1988
Eustrongylides tubifex‡	M	2 (4/374)	MI	Allison, 1966
		3 (3/100)	IN	Michigan City, this study
	H	35 (293/831)	MI	Allison, 1966
		2 (3/134)	ONT	Dechtiar et al., 1988
		80 (193/240)	MI	Rosinski et al., 1997
		95 (95/100)	MI	The Black Hole, this study
		74 (74/100)	MI	Oak Point, this study
	E	38 (19/50)	OH	Measures, 1988b
	E	41 (304/735)	OH	Cooper et al., 1977
		—§	OH	Cooper et al., 1978
		—§	OH	Crites, 1982
		50 (204/408)	ONT	Dechtiar and Nepszy, 1988
	O	8 (5/150)	ONT	Dechtiar and Christie, 1988
Eustrongylides sp.‡	E	8 (8/98)	OH	Bangham, 1972
Hysterothylacium brachyurum†	S	33 (8/24)	ONT	Dechtiar and Lawrie, 1988
	E	4 (16/408)	ONT	Dechtiar and Nepszy, 1988
	O	8 (5/150)	ONT	Dechtiar and Christie, 1988
Philometra cylindracea	H	1 (2/201)	ONT	Bangham, 1955
		4 (5/134)	ONT	Dechtiar et al., 1988
		—§	MI	Salz, 1989
		24 (57/240)	MI	Rosinski et al., 1997
		10 (10/100)	MI	The Black Hole, this study
		16 (16/100)	MI	Oak Point, this study

Table 3. Continued.

Species	Lake*	Prevalence†	Locality	Reference
	E	1 (1/128)	OH, ONT	Bangham and Hunter, 1939
		8 (62/735)	OH	Cooper et al., 1977
		—§	OH	Crites, 1982
		10 (40/408)	ONT	Dechtiar and Nepszy, 1988
	O	5 (8/150)	ONT	Dechtiar and Christie, 1988
Raphidascaris acus‡	S	63 (15/24)	ONT	Dechtiar and Lawrie, 1988
	H	2 (3/134)	ONT	Dechtiar et al., 1988
Raphidascaris sp.‡		—§	MI	Rosinski et al., 1997
Rhabdochona canadensis Moravec and Arai, 1971	E	8 (32/408)	ONT	Dechtiar and Nepszy, 1988
Rhabdochona ovifilamenta Weller, 1938	M	1 (1/136)	MI	Weller, 1938
	S	8 (2/24)	ONT	Dechtiar and Lawrie, 1988
Spinitectus carolini Holl, 1928	E	9 (6/69)	OH	Jilek and Crites, 1981
	S	8 (2/24)	ONT	Dechtiar and Lawrie, 1988
Spinitectus gracilis Ward and Magath, 1917	O	1 (2/150)	ONT	Dechtiar and Christie, 1988
Spinitectus sp.	E	5 (5/98)	OH	Bangham, 1972

* E, Lake Erie; M, Lake Michigan; H, Lake Huron; S, Lake Superior; SMR, St. Marys River; LSC, Lake St. Clair; O, Lake Ontario.

† Percent infected (number of fish infected/number of fish examined).

‡ Larval stage.

§ Parasite present but prevalence not given.

‖ Prevalence calculated from winter 1984 sample.

1984; Dechtiar and Christie, 1988). Cooper et al. (1977) demonstrated that the prevalence of *D. cotylophora* in perch in the western basin of Lake Erie decreased from 1927–1929, to 1957, to 1974.

Rhabdochona spp. and *Spinitectus* spp. infrequently occur in yellow perch from Lakes Michigan, Superior, and Erie, and Lakes Superior, Erie, and Ontario, respectively. Both genera are found in the intestine of several fish species and do little or no damage to their hosts. They utilize mayfly larvae and other arthropods as intermediate hosts.

Species not found as adults in the intestine of yellow perch are: *H. brachyurum, R. acus, Raphidascaris* sp., *Contracaecum* sp., *P. cylindracea, E. tubifex,* and *Eustrongylides* sp. Larval *H. brachyurum* have been reported in perch from 3 of the Great Lakes. Dechtiar and Lawrie (1988) found *H. brachyurum* and *R. acus* larvae in the liver of perch from Lake Superior and suggested that moderate to heavy liver damage occurred with fibrosis. Similarly, encysted *H. brachyurum* caused liver damage to perch in Lake Ontario (Dechtiar and Christie, 1988). Piscivorous fishes serve as definitive hosts for *H. brachyurum* and *Raphidascaris* spp. *Contracaecum* spp. mature in piscivorous birds and mammals.

The redworm nematode complex of yellow perch in the Great Lakes is composed of *Camallanus oxycephalus, P. cylindracea,* and *E. tubifex.* The term "redworm" was coined by anglers asking the question, "What are these red worms in my fish?" (J. Crites, pers. comm.). *Camallanus oxycephalus* has been reported from yellow perch in 2 of the Great Lakes. Stromberg and Crites (1974) found that during July and August in Lake Erie, female *C. oxycephalus* protrude from the anus of white bass, *Morone chrysops,* and rupture, releasing infective larvae that are ingested by copepods. The life cycle is completed when infected copepods or small paratenic forage fish hosts are eaten by larger fish. Cooper et al. (1977) found that the prevalence of *C. oxycephalus* in yellow perch in western Lake Erie increased from 1927–1929, to 1957, to 1974.

In the present study, *P. cylindracea* only occurred in yellow perch from Saginaw Bay. Copepods are intermediate hosts for *P. cylindracea* (see Molnar and Fernando, 1975; Crites, 1982). It is not known if *P. cylindracea* utilizes a trans-

port host in its life cycle. *Philometra cylindracea* has been found in perch from 3 of the Great Lakes, occurring unencysted in the body cavity. This nematode matures in, and is host-specific to, yellow perch, since it has been reported from no other fish species. Mature females are about the same length as males (4 mm) or longer. Larvigerous females, which are delicate and have a thin transparent cuticle, may exceed 100 mm in length and are easily broken during host necropsy.

Eustrongylides tubifex had significantly higher prevalences, mean intensities, and mean abundances in yellow perch from Saginaw Bay than in those from Lake Michigan. Karmanova (1968) and Measures (1988a, b) reported that tubificid oligochaetes serve as intermediate hosts for *E. tubifex*. Although Brinkhurst (1967) and Schneider et al. (1969) found large numbers of tubificids in Saginaw Bay, Haas and Schaeffer (1992) did not find tubificids in perch stomachs in Saginaw Bay, and Rosinski et al. (1997) found them to be infrequent. The lack of tubificids in stomachs is surprising, since perch from Saginaw Bay and other areas of Lake Huron are heavily infected. Tubificids have been found in the stomachs of yellow perch from Lake Erie (J. Crites, pers. comm.), another lake where *E. tubifex* commonly occurs. The difference in infection values of *E. tubifex* between Saginaw Bay and Lake Michigan may be explained by the large number of tubificids in the bay and by the small numbers of them in Lake Michigan. Piscivorous birds (e.g., mergansers, *Mergus merganser* Linnaeus, 1758; see Measures, 1988c) serve as definitive hosts for *E. tubifex,* and differences in their numbers between these locations may also play a role in this difference.

Eustrongylides tubifex has been reported from yellow perch in 4 of the Great Lakes. It is infrequent in Lake Michigan, and the small number of perch examined from Lake Superior may not reflect its absence. Allison (1966) reported perch from the Detroit River infected with *E. tubifex*. Dechtiar and Christie (1988) found *E. tubifex* in several fish species from Lake Ontario and suggested that it caused damage to perch. This nematode is very common in yellow perch from Lake Erie. Interestingly, Bangham and Hunter (1939) did not report *E. tubifex* in an extensive survey of parasites of Lake Erie fishes, including 128 yellow perch. Bangham (1972) was the first to report the occurrence of *E. tubifex* in yellow perch collected in 1957 from Lake Erie.

Eustrongylides tubifex is pink to red in color and thicker than *P. cylindracea*. Larval *E. tubifex* in fish intermediate hosts can reach 10 cm in length. Cooper et al. (1978) and Crites (1982) demonstrated experimentally that *E. tubifex* can be transferred when a small infected fish is eaten by a larger one. Crites (1982) reported that *E. tubifex* can live in capsules of host origin for at least 1.5 yr and demonstrated that the walls of the capsule have several different tissues and are furnished with capillaries. The larvae are nourished during their development and growth in these capsules. Measures (1988b) reported on the pathology of *E. tubifex* in fishes, including the yellow perch. It appears that *E. tubifex* infections in perch do not give rise to immunity, since larvae of different lengths were found in the same perch in the present study.

Crites (1982) showed that *E. tubifex* and *P. cylindracea* were associated with weight loss in yellow perch. It is not known if this weight loss affected fecundity. In addition, *P. cylindracea* sometimes infected the ovaries of perch, but whether this impairs reproductive capacity was not determined. Allison (1966) and Salz (1989) suggested these *E. tubifex* and *P. cylindracea* play a role in reduced perch growth and high mortality.

Excluding the Salmoniformes, percids are probably the most important group of fishes in the Great Lakes. Based on a review of the literature and the present study, it appears that nematodes do not greatly harm yellow perch, except for *E. tubifex* and *P. cylindracea,* which commonly infect perch in Saginaw Bay, other areas of Lake Huron, and Lake Erie (Allison, 1966; Crites, 1982; Salz, 1989; Rosinski et al., 1997). These are Great Lakes areas where the catch rates of perch have declined (Francis et al., 1996), but the direct effects of *E. tubifex* and *P. cylindracea* on reducing the numbers of perch in these areas are not known.

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NOTICE

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A Taxonomic Reconsideration of the Genus *Plagiorhynchus* s. lat. (Acanthocephala: Plagiorhynchidae), with Descriptions of South African *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* from Shore Birds and *P.* (*P.*) *malayensis*, and a Key to the Species of the Subgenus *Prosthorhynchus*

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ABSTRACT: A population of *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Goeze) Schmidt and Kuntz is described from 4 species of shore birds in South Africa. Specimens of 3 supposed synonyms of *P.* (*P.*) *cylindraceus*, namely *P.* (*P.*) *formosus* Van Cleave, *P.* (*P.*) *taiwanensis* Schmidt and Kuntz, and *P.* (*P.*) *transversus* (Rudolphi) Travassos, were studied and this synonymy was verified. The taxonomic status of *Plagiorhynchus* s. str. and of *Prosthorhynchus* was reconsidered, and both were retained as subgenera. Females of *Plagiorhynchus* (*Prosthorhynchus*) *malayensis* (Tubangui) Schmidt and Kuntz (*nec malayense*) are described for the first time; males are redescribed. A key to species of the subgenus *Prosthorhynchus* is provided.

KEY WORDS: Acanthocephala, *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus*, description, South Africa, shore birds, Aves, subgenera *Plagiorhynchus* s. str. and *Prosthorhynchus*, *Plagiorhynchus* (*Prosthorhynchus*) *malayensis*, taxonomic key.

A collection of acanthocephalans was made by one of us (A.G.C.) from 7 species of shore birds in South Africa in 1981. All 7 species yielded a new centrorhynchid acanthocephalan, *Neolacunisoma geraldschmidti* Amin and Canaris, 1997. Additionally, 5 of these 7 host species harbored 2 species of plagiorhynchid acanthocephalans.

One unidentified species of *Plagiorhynchus* infected 1 host species, and the other 4 host species were infected with *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966. The study of the latter species, a number of its synonyms, and various plagiorhynchid species prompted reconsideration of the generic–subgeneric status of *Plagiorhynchus* and *Prosthorhynchus* and the construction of a key to species of the latter subgenus. Among the acanthocephalans borrowed for this study were a few specimens of *Plagiorhynchus* (*Prosthorhynchus*) *malayensis* (Tubangui, 1935) Schmidt and Kuntz, 1966 (*nec malayense*), that were sufficiently informative to describe females for the first time and redescribe males. This paper reports on these findings.

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Materials and Methods

Twenty-eight individuals (12 males and 16 females) of *P.* (*P.*) *cylindraceus* were recovered from 4 species of shore birds (Charadriiformes) collected by one of us (A.G.C.) from the Berg River, Cape Province, South Africa, between 24 May and 31 July 1981. The host species were the curlew sandpiper (*Calidris ferruginea* (Pontoppidan, 1763), 1 individual infected with 25 acanthocephalans); Kittlitz' plover (*Charadrius pecuarius* (Temminck, 1823), 1 of 4 individuals infected with 1 acanthocephalan); triple-banded plover (*Charadrius tricollaris* (Vieillot, 1818), 1 of 5 individuals infected with 1 acanthocephalan); and blacksmith plover (*Holopterus armatus* (Burchell, 1822), 1 of 7 individuals infected with 1 acanthocephalan). In addition, 26 unidentifiable plagiorhynchid acanthocephalans were collected by A.G.C. from 2 white-fronted sand plovers (*Charadrius marginatus* Vieillot, 1818) and 10 uninformative plagiorhynchid acanthocephalans from the stilt (*Himantopus himantopus* (Linnaeus, 1758)), *H. armatus*, *Charadrius pallidus* Strickland, 1852, and *C. pecuarius*. These unidentified specimens are in the collection of M. Kinsella, Missoula, Montana.

Specimens were processed by the late Gerald D. Schmidt. We do not know the processing method used. Measurements, made using an ocular micrometer and conversion table, are in micrometers unless otherwise stated. Width measurements refer to maximum width. Most specimens were deposited in the United States National Parasite Collection (USNPC), Beltsville, Maryland, and a few were retained in the collection of the first author (O.M.A.). A few study specimens were

loaned from USNPC, but most were from the Harold W. Manter Laboratory Collection (HWMLC), University of Nebraska State Museum, Lincoln, Nebraska. We report the results of examination of the specimens collected from the South African shore birds.

Results and Discussion

Plagiorhynchus (*Plagiorhynchus*) sp.

The 26 specimens of *Plagiorhynchus* (*Plagiorhynchus*) sp. collected from *C. marginatus* were slender, with the proboscis wider near its middle, long lemnisci and uterus, a near-terminal female gonopore, elliptical eggs with polar prolongation of the fertilization membrane, and cement glands of unequal length and altogether about as long as the 2 testes. The specimens were not sufficiently informative to make a specific designation.

Plagiorhynchus (*Prosthorhynchus*) *cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966

Except for 1 female in the ovarian ball stage, all 13 other female and 11 male *P.* (*P.*) *cylindraceus* collected from the single curlew sandpiper examined were sexually mature adults with ripe eggs and sperm, respectively. Of the other 3 host species examined, 1 individual of each was infected with 1 immature female. The curlew sandpiper appears to be the natural host of *P.* (*P.*) *cylindraceus* in South Africa.

Our South African specimens were diagnosed as *P.* (*P.*) *cylindraceus* based on their close similarities with that species and taxa now synonymized with it, as listed in Amin (1985) and compared herein (Table 1). Measurements of the 1 available female *Plagiorynchus* (*Prosthorhynchus*) *transversus* (Rudolphi, 1819) Travassos, 1926, the other supposed synonym (USNPC #65269) agreed with those listed in the table. Some of the specimens examined, and particularly European *P.* (*P.*) *cylindraceus,* however, appeared less robust and more slender, and females as long as 40 mm were reported (Golvan, 1956, Fig. 1). Another difference was related to the roots of the middle proboscis hooks, which were longer than the blades in European *P.* (*P.*) *cylindraceus* (see Golvan, 1956, pl. 1A). This was also observed in some but not all *P.* (*P.*) *cylindraceus* from Long Island, New York, and New Hampshire, U.S.A. (HWMLC 33444–33452), but not in specimens from Israel (HWMLC 34871). Golvan's specimens reached lengths of 15 mm in males and 40 mm in females and had as many as 24 longitudinal rows of proboscis hooks. In all other respects, the synonymy of *P.* (*P.*) *cylindraceus, P.* (*P.*) *transversus, Plagiorhynchus* (*Prosthorhynchus*) *formosus* Van Cleave, 1918, and *Plagiorhynchus* (*Prosthorhynchus*) *taiwanensis* Schmidt and Kuntz, 1966, was upheld.

Description of South African *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus*

GENERAL: Specimens robust and bluntly pointed, females not much longer but more plump than males. Subdermal nuclei discoidal, in shallow ameboid branched interconnected vesicles, appearing rod-shaped in profile, with vertical orientation at almost regular intervals from anterior end of trunk to short distance from posterior end. Secondary lacunar vessels transverse throughout trunk. Proboscis hooks in straight longitudinal rows, without dorsoventral or any other differentiation. Blades generally similar in length, but becoming slightly shorter abruptly anteriorly and more gradually posteriorly (Table 1). Hook roots simple, posteriorly directed, and usually about as long as or slightly shorter than blades. Posterior 2 hooks of each row spiniform, second to last hook with short root which may be further reduced to large knob; last hook rootless and invariably with small knob instead. Lemnisci long and slender, much longer than proboscis receptacle, nucleated, subequal, sometimes branched or multiple, may extend past posterior end of posterior testis. Testes ovoid, contiguous, usually in anterior half of trunk. Four cement glands in 2 sets of 2 each, originating at various levels beginning anteriorly near posterior end of posterior testis. Four separate cement gland ducts originating anteriorly at level of anterior end of Saefttigen's pouch and joining pouch at its posterior end. Gonopore near-terminal in adult males but distinctly subterminal in adult females, vagina usually curved anteriad in a 90 degree angle. Ripe eggs mostly elliptical with concentric shell and no polar prolongation of fertilization membrane. Fertilization membrane of a few eggs in gravid females (5–15%) may exhibit unipolar or, less frequently, bipolar prolongation.

SPECIMENS DEPOSITED: USNPC 88031 (10 males and 10 females on 10 slides from *Calidris ferruginea* in the Berg River, Cape Province, South Africa).

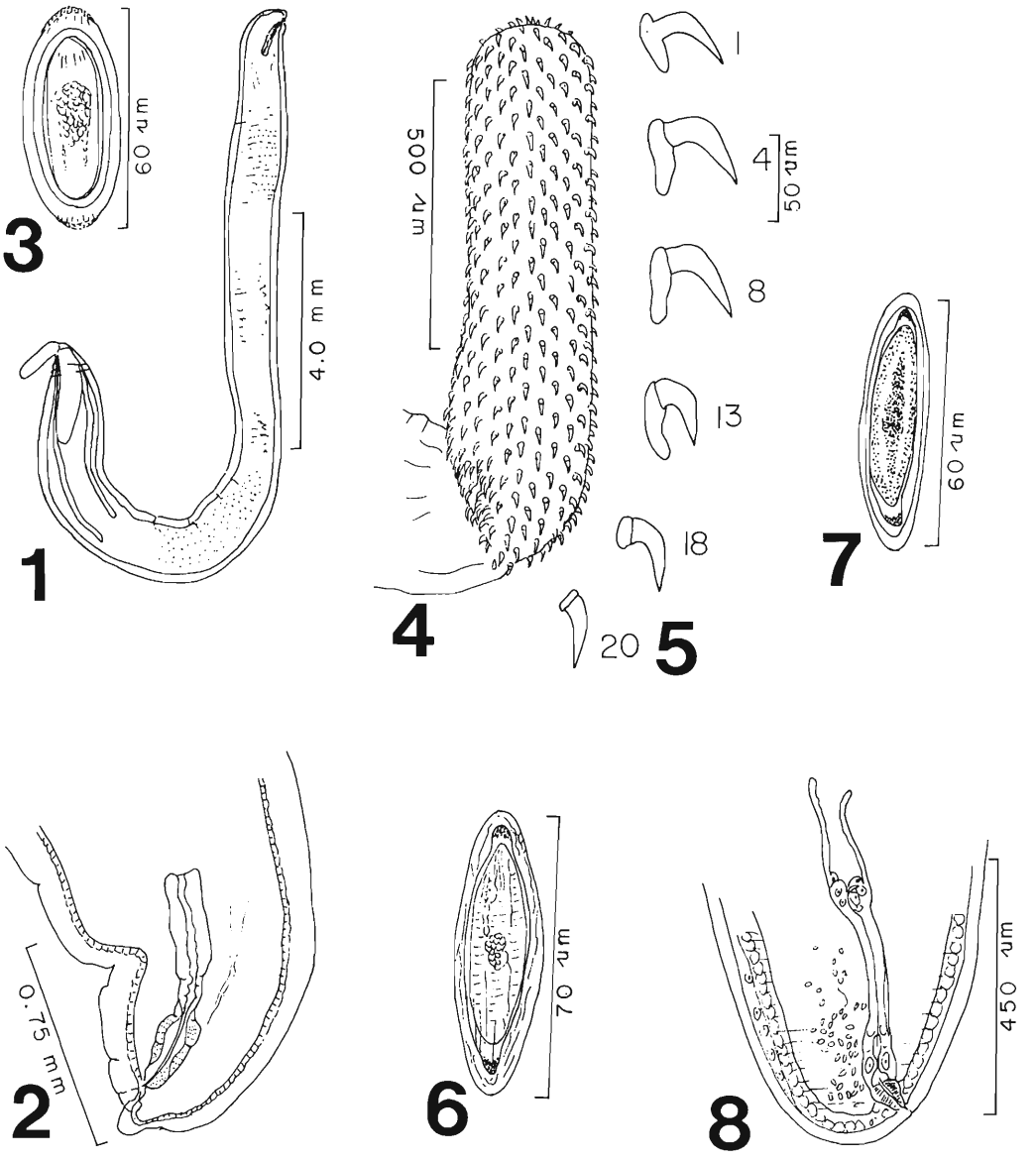
Table 1. Comparison between the South African *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* and synonyms as reported by others or measured (this paper) in selected diagnostic characteristics.

	P. cylindraceus			*P. formosus*		*P. taiwanensis*	
	South Africa, this paper (n = 23)	Golvan, 1956 (n = ?)	This paper (n = 20)	Van Cleave, 1918, 1942; Schmidt and Olsen, 1964 (n = ?)	This paper (n = 20)	Schmidt and Kuntz, 1966 (n = 60)	This paper (n = 8)
Trunk (mm)							
Males	7.79–0.15 × 1.67–1.88	10–15 ×	4.545–10.45 × 0.61–1.82	8–13 × 1.5–2.5	5.61–12.42 × 1.24–2.45	10.0–14.0 × 1.75–2.75	8.03–11.21 × 1.57–2.30
Females	8.97–11.06 × 2.06–2.55	20–40 ×	5.15–12.12 × 0.45–2.818	9–15 × 2–3	8.03–13.32 × 1.33–2.88	13.0–16.0 × 2.5–3.0	9.09–15.0 × 1.88–3.18
Proboscis (mm)							
Males	1.15–1.21 × 0.21–0.24	—	0.88–1.03 × 0.24–0.33	0.80–1.10 × 0.25–0.33	0.94–1.12 × 0.24–0.30	—	0.88–1.06 × 0.24–0.26
Females	1.24–1.39 × 0.24–0.27	—	0.97–1.15 × 0.27–0.33	0.80–1.10 × 0.25–0.33	1.00–1.21 × 0.21–0.36	—	1.00–1.33 × 0.29–0.35
Proboscis hooks							
Rows (no.)	14–17	14–20, up to 24	16–17	15–18	13–17	14–16	16–17
Hooks/row	15–18	10–18	13–15	11–15	13–15	11–15	13–16
Proboscis hooks (mean length from anterior)							
	M (11)*	F (12)*	M F	M (8)	F (12)	V.C. S.&O.	M (10) F (10)	M (?)† F (?)†	M (3) F (5)
	59	56	NG‡ NG	53	55	71 60	56 59	62 67	59 69
	62	66	NG NG	66	67	77 79	56 64	65 73	62 76
	64	69	NG NG	67	66	83 79	62 72	65 76	67 72
	68	69	NG NG	66	72	83 79	70 77	67 85	67 74
	68	69	NG NG	70	73	83 79	72 78	67 85	67 77
	71	73	NG NG	70	79	83 79	73 79	70 85	69 78
	70	75	NG NG	69	79	83 79	77 81	70 85	69 76
	71	76	NG NG	74	78	83 79	77 81	73 85	69 76
	69	76	NG NG	71	82	83 79	75 77	73 85	62 78
	72	73	NG NG	67	80	77 79	73 78	67 85	60 82
	71	73	NG NG	71	75	77 79	75 74	59 85	56 77
	69	73	NG NG	71	72	77 79	69 73	59 88	57 78
	68	69	NG NG	66	64	65 79	66 68	56 91	57 73
	62	66	NG NG	66	63	— 60	63 64	56 88	56 70
	59	62	NG NG	56	61	— 60	60 57	— 73	52 64
	56	60	NG NG	—	—	— —	— —	— —	— —
	53	60	NG NG	—	—	— —	— —	— —	— —
Eggs	64–78 × 25–28	80 × 30	42–70 × 12–34	40–75+ × 18–30+	56–73 × 25–31	65–75 × 24–27	53–73 × 22–28

* Numbers in parentheses indicate the numbers of specimens used for determination.

† ?, Number of specimens examined not given.

‡ NG, not given.



Figures 1–8. Species of *Plagiorhynchus* (*Prosthorhynchus*) and *P.* (*Plagiorhynchus*). 1–5. *Plagiorhynchus* (*Prosthorhynchus*) *malayensis*, female. 1. Lateral view of whole specimen. 2. Posterior end and reproductive system. 3. Egg from the body cavity. 4. Proboscis. 5. Proboscis hook numbers 1, 4, 8, 13, 18, 20 of 1 row. 6. *Plagiorhynchus* (*Prosthorhynchus*) *bullocki,* egg from the body cavity of a gravid female. 7, 8. *Plagiorhynchus* (*Plagiorhynchus*) *paulus*. 7. Egg from the body cavity of a gravid female. 8. Posterior end and reproductive system of a female, showing the subterminal position of the gonopore.

SPECIMENS EXAMINED: *P.* (*P.*) *cylindraceus* adults: HWMLC 33443–33449, 33451, 35658, 36785 (Nebraska, New Hampshire, New York, U.S.A.); 34871, 34882 (Israel). *P.* (*P.*) *formosus* adults: USNPC 4598 (syntypes), 60023; HWMLC 30539, 30978, 30983, 30987, 31037, 33877, 33938–33941, 34480, 34652, 35005 (Colorado, Oregon, and Kansas, U.S.A.), many slides of larvae from various intermediate hosts. HWMLC 30975, 30978, 30983, 30987, 31037, 31037, 31061 labeled "*Plagiorhynchus formosus* ex. *Sturnus vulgaris,* intestine; Kansas"

were clearly misidentified and placed in the wrong genus as judged by their thin body form and small size, proboscis size and armature, and eggs; some had spiny trunks. *P.* (*P.*) *taiwanensis* adults: USNPC 60718 (paratypes). HWMLC 34124–34126 (paratypes). *P.* (*P.*) *transversus* adult: USNPC 65269.

The examined specimens provided additional data that are not included in Table 1: 1 *P.* (*P.*) *transversus* female (USNPC 65269) had hook roots that were considerably longer than the blades and eggs with concentric membranes, with no more than 5% having polar prolongation of the fertilization membrane. The position of the gonopore was obscured. The *P.* (*P.*) *formosus* specimens had proboscides with only up to 15 hooks per row. The roots of the middle proboscis hooks were longer than the blades in some specimens. Gravid females had up to 10% of their ripe eggs showing some polar prolongation of the fertilization membrane. The female gonopore was invariably and definitively subterminal. The *P.* (*P.*) *taiwanensis* specimens were robust and almost identical to *P.* (*P.*) *formosus*. Distinct differences in lemniscal length, which were used to justify the designation of *P.* (*P.*) *taiwanensis* as a separate species (Schmidt and Kuntz, 1966), were not observed in this study, in agreement with later observations by Schmidt (1981). The proboscis had only up to 15 hooks per row. The roots of the middle proboscis hooks were invariably slightly shorter than the blades. Up to 15% of the ripe eggs had some polar prolongation of the fertilization membrane. The female gonopore was definitively subterminal.

Plagiorhynchus (*Prosthorhynchus*) *malayensis* (Tubangui, 1935) Schmidt and Kuntz, 1966 (Figs. 1–5)

GENERAL: Tubangui (1935) originally described this species from 1 male specimen obtained from the gruiform bird, the banded landrail *Gallirallus* (=*Hypotaenidia*) *philippensis* Linnaeus, 1766, in Luzon, Philippines, as *Oligoterorhynchus malayensis*. It was later transferred to the genus *Prosthorhynchus* by Yamaguti (1963) because of its cylindrical proboscis. Schmidt and Kuntz (1966) redescribed the males based on 2 new specimens (USNPC 60730) collected from 2 other species of gruiform birds from Taiwan (the white-breasted water hen, *Amaurornis phoenicurus chinensis* (Boddaert, 1783) and the banded crake, *Rallina eurozonoides formosana* Seebohm, 1894) and on the original description. The female remained unknown. Eleven specimens (6 males and 5 females on 8 slides) of the same species, all from the G. D. Schmidt collection, became available for this study (10 specimens from HWMLC, 1 from USNPC). Seven of the 8 slides were dated 1965; the remaining slide (1 male specimen) was dated 1972. One of the 2 males described by Schmidt and Kuntz (1966) (USNPC 60730) was also dated 1965. The 5 female specimens in this collection were adequate for description. The 6 male specimens in the same collection also provided additional new information.

FEMALE: Trunk elongate, slender, cylindrical (Fig. 1), 11.5–18.2 ($\bar{x}$ = 15.1) mm long by 1.12–1.37 (1.23) mm wide. Proboscis cylindrical, rounded anteriorly 1.06–1.30 (1.18) mm long by 0.26–0.30 (0.28) mm wide (Fig. 4), with 19 hook rows, each with 20–21 hooks. All hooks similar in shape, except basal hooks spiniform. Hooks increasing in size posteriorly to hooks 4–8, then gradually decreasing to hooks 20, 21, reaching size of anterior hooks. Lengths of 1 row of hooks of 1 female (Figs. 1, 4, 5) from anterior 48, 53, 56, 56, 62, 62, 62, 64, 62, 62, 62, 59, 56, 56, 56, 56, 56, 53, 53, 50, 50. Roots of posterior 4 hooks in each row greatly and more progressively reduced posteriorly, well developed in all other hooks, and with anterior manubria in anterior 4–6 hooks; manubria most developed anteriorly (Fig. 5). Neck of same female 303 long by 333 wide. Proboscis receptacle 1.97–2.03 (2.00) mm long by 0.27–0.48 (0.37) mm wide. Lemnisci narrow and much longer than proboscis receptacle, 4.30–5.45 (4.74) mm long by 0.12 mm wide. Reproductive system short, robust with well-developed vagina, very short uterus, and comparatively large uterine bell, 757 long (5% of trunk length). Gonopore decidedly subterminal (Fig. 2). Eggs elongate ovoid, 53–84 (64) long by 22–31 (28) wide; external shell sculptured with elevated ridges and grooves particularly at poles, all shells concentric (Fig. 3) with less than 5% of ripe eggs showing mild to moderate polar prolongation of fertilization membrane.

FEMALE (Fig. 1): HWMLC 36329.

OTHER FEMALES: HWMLC 33878, 36327, 36328.

HOST: *Amaurornis phoenicurus* (Boddaert, 1783).

SITE OF INFECTION: Intestine.

LOCALITY: Borneo, Indonesia; Taiwan.

MALE: Trunk slender, cylindrical, 10.0–13.0 (11.5) mm long by 0.82–1.42 (1.09) mm wide. Proboscis cylindrical with rounded anterior end, 1.00–1.21 (1.11) mm long by 0.20–0.24 (0.23) mm wide. Proboscis with 16–21 longitudinal rows of 20–22 hooks each. Differences between anterior, middle, and posterior hook sizes and shape and size of roots comparable to females. Lengths of hooks from anterior 42 (42), 48–56 (52), 53–56 (54), 53–59 (56), 50–59 (54), 50–62 (57), 50–56 (54), 48–59 (54), 48–64 (57), 48–56 (53), 45–56 (52), 45–59 (53), 48–56 (53), 48–56 (53), 48–56 (53), 45–56 (51), 45–56 (50), 45–56 (51), 45–53 (49), 45–50 (47), 42–48 (45). Neck 151–242 (181) long by 212–333 (273) wide. Proboscis receptacle 1.88–2.12 (1.98) mm long by 0.30–0.42 (0.34) mm wide. Lemnisci narrow and markedly longer than proboscis receptacle, 2.36–3.33 (2.82) mm long. Testes ovoid, contiguous, at middle of trunk. Anterior testis 0.94–1.15 (1.05) mm long by 0.45–0.70 (0.52) mm wide. Posterior testis 0.91–1.88 (1.14) mm long by 0.45–0.73 (0.55) mm wide. Four tubular cement glands, 2.12–4.24 (3.14) mm long by 0.09–0.30 (0.18) mm wide; cement glands begin at posterior end of posterior testis and join into 2 cement ducts posteriorly at level of anterior end of Saefftigen's pouch, which they join at its posterior end. Saefftigen's pouch 1.21–1.36 (1.29) mm long by 0.45–0.48 (0.47) mm wide. Bursa 0.94–1.36 (1.15) mm long by 0.97–1.21 (1.09) mm wide.

SPECIMENS EXAMINED: USNPC 60730; HWMLC 33878, 36327, 36328, 36329.

Other species of the 2 *Plagiorhynchus* subgenera were studied to help with the construction of the following key. This study produced the following unexpected information, which demonstrated the wide variability within the genus *Plagiorhynchus* and provided a context against which its taxonomic complexity could be evaluated.

Plagiorhynchus (*Prosthorhynchus*) *bullocki* Schmidt and Kuntz, 1966

The specimens (5 males and 4 females from the Formosan hill partridge, *Arborophilia crudigularis* (Swinhoe, 1864) from Taiwan) were in general agreement with the original description, except that proboscis hooks numbered 17–18 in each of 14–16 longitudinal rows (instead of 16–17, 16) and most ripe eggs (at least 80%) showed mild to strong polar prolongation of the fertilization membrane (Fig. 6). Schmidt and Kuntz (1966) did not refer to a polar prolongation of the fertilization membrane, and their figure 11 shows none. The gonopore of both sexes is decidedly subterminal. The above 2 traits are in conflict with the traditional criteria for the subgenus *Prosthorhynchus* (females with subterminal gonopore and eggs with concentric shells) or the subgenus *Plagiorhynchus* (females with terminal gonopore and eggs with polar prolongation of fertilization membrane). See Remarks following.

SPECIMENS EXAMINED: HWMLC 34074, 34133.

Plagiorhynchus (*Prosthorhynchus*) *gracilis* (Petrochenko, 1958) Schmidt and Kuntz, 1966

One male from the intestine of the masked lapwing, *Vanellus miles* (Boddaert, 1783), in Tasmania was slender and somewhat robust anteriorly, with lemnisci about as long as the proboscis receptacle. The proboscis had 21 rows of more than 15 hooks each and 6 tubular cement glands. All of Petrochenko's (1958) male specimens were "wrinkled," and the resulting "corrugation" affected the "subsequent distribution of internal organs." His males had 20 proboscis hook rows, each with 16 hooks and only 3 tubular cement glands (Petrochenko, 1958, p. 182).

SPECIMEN EXAMINED: HWMLC 39385.

Plagiorhynchus (*Prosthorhynchus*) *golvani* Schmidt and Kuntz, 1966

Observations on 1 male from the intestine of a collared bush-robin, *Tarsiger* (=*Erithacus*) *johnstoniae* (Ogilvie-Grant, 1906) (Turdidae), in Taiwan were in agreement with the original description.

SPECIMEN EXAMINED: HWMLC 34299.

Plagiorhynchus (*Plagiorhynchus*) *charadrii* (Yamaguti, 1939) Van Cleave, 1951

The specimens (9 males and 12 females on 10 slides), dated 1965 to 1978 and collected from shore birds in Taiwan, Hawaii, and Tasmania, generally agreed with the descriptions of Yamaguti (1939) and Schmidt and Kuntz (1966). The proboscides had 17–18 rows of 14–15 hooks each. The gonopore was terminal in both sexes, but eggs varied considerably in size and

degree of polar prolongation of the middle membrane, if any. For example, females collected from the Kentish plover, *Charadrius alexandrinus* Deignan, 1941, and the golden plover *Pluvialis dominica* Gmelin, 1789, in Taiwan and Hawaii had eggs up to 85 × 28 and 132 × 50, respectively. These eggs mostly had a polar prolongation of the middle membrane as described by Yamaguti (1939) and Schmidt and Kuntz (1966), whose specimens' eggs measured 105–120 × 30–45. Some females from the red-capped plover, *Charadrius (Alexandrinus) ruficapillus* Temminck, 1822, in Tasmania had larger eggs, up to 168 × 67, that mostly had no visible prolongation of the fertilization membrane. In most other females examined, however, about 80% of the eggs normally had no polar prolongation. This extreme variation in the polar swelling of the fertilization membrane poses taxonomic problems and is clearly not related to egg size or maturity. It may be associated with host species or with unknown geographical factors.

SPECIMENS EXAMINED: HWMLC 34128, 34747, 39347, 39374.

Plagiorhynchus (*Plagiorhynchus*) *paulus* Van Cleave and Williams, 1951

Measurements of 2 males and 2 females from the varied thrush, *Zoothera* (=*Ixoreus*) *naevius* (Gmelin, 1784), in the State of Washington, U.S.A., did not agree with the original description. For example, testes were longer (anterior 0.848 × 0.364 mm, posterior 0.666 × 0.364 mm), proboscis receptacle 1.060 × 0.212 mm in 1 male and 1.394 × 0.273 mm in 1 female, cement glands 0.697 × 0.106 mm to 1.515 × 0.121 mm and eggs 50–76 (66) × 14–28 (19) (n = 8). A few (5–10%) of the eggs showed no polar prolongation of the fertilization membrane, but most did (Fig. 7). The female gonopore was, however, not terminal as would be expected in a species placed in *Plagiorhynchus*. The female gonopore was actually subterminal (Fig. 8). No reference to the position of the female gonopore was made in the original description (Van Cleave and Williams, 1951) or in subsequent accounts by other authors (e.g., Petrochenko, 1958). Based on this character alone, this species would be assigned to *Prosthorhynchus*. However, the polar prolongation of the egg fertilization membrane, among other factors discussed below, further complicates the issue. No reassignment is made at this time.

SPECIMEN EXAMINED: HWMLC 34333.

Inclusion of species in the key

Amin (1985) listed 19 species in the subgenus *Prosthorhynchus,* and Golvan (1994) listed 27, while Hoklova (1986) listed 11 species from land vertebrates. Part of this discrepancy is because of synonyms not acknowledged by Golvan (1994) or Hoklova (1986) and hence not included in the key. The following species are not recognized as valid: *P.* (*P.*) *formosus, P.* (*P.*) *taiwanensis,* and *P.* (*P.*) *transversus* (synonyms of *P.* (*P.*) *cylindraceus*, see this paper; Schmidt, 1981; Amin, 1985). Other synonyms of *P.* (*P.*) *cylindraceus* noted by Golvan (1994) are *P.* (*P.*) *rosai* (Porta, 1910) Meyer, 1932, and *P.* (*P.*) *upupae* Lopez-Neyra, 1946. *Rhadinorhynchus asturi* Gupta and Lata, 1967, was erroneously named *Prosthorhynchus asturi* by Golvan (1994); this species, with a spinose trunk, is clearly a rhadinorhynchid. Golvan (1956) proposed other synonymies that he later retracted (Golvan, 1994). *Plagiorhynchus* (*Prosthorhynchus*) *pupa* (von Linstow, 1905) Meyer, 1931, is a synonym of *Polymorphus pupa* (von Linstow, 1905) Kostylev, 1922 (see Amin, 1992). Golvan (1994) removed *Prosthorhynchus* (*Prosthorhynchus*) *limnobaeni* Tubangui, 1933, to the subgenus *Plagiorhynchus* despite the fact that this species is known from only 2 males. This reassignment to *Plagiorhynchus* is unjustified, and the species is retained in the subgenus *Prosthorhynchus*. It is not, however, included in the key because of controversy regarding the only usable diagnostic trait, the proboscis armature. Tubangui (1933) indicated that proboscis hooks are "in forty-three alternating anteroposterior rows of eight hooks each," but his Plate 5, Figure 1 shows a proboscis with about 18–20 longitudinal rows, each with 30 hooks. Golvan (1956) accepted the 43 × 8 formula and Petrochenko (1958, after Meyer, 1932–1933) indicated 16 longitudinal rows of 17 hooks each. Yamaguti (1963) quoted both figures, 43 × 8 and 16 × 17. Both Petrochenko (1958) and Yamaguti (1963) retained the species in *Prosthorhynchus* as originally described. Golvan (1956, 1994) synonymized *P.* (*Prosthorhynchus*) *rectus* Sphern, 1942 *nec* Linton, 1892, with "*Prosthorhynchus schmidti* nom. nov." This entity, originally described as *Echinorhynchus rectus*

Linton, 1892, was declared incertae sedis by Schmidt and Kuntz (1966) and is not recognized here. Golvan (1956, 1994) removed *P. (Prosthorhynchus) reticulatus* (Westrumb, 1821) Schmidt and Kuntz, 1966, to the subgenus *Plagiorhynchus* without any justification. The reassignment is not accepted, and the species is included in the key. *Plagiorhynchus (Prosthorhynchus) rostratum* (de Marval, 1902) Meyer, 1932, was considered incertae sedis by Amin (1985) and is not included in the key. Golvan (1994) also listed "*Prosthorhynchus luehei* Travassos, 1916" (=*Echinorhynchus spirula* Rudolphi, 1819; *E. spirula* Linstow, 1878, 1897; *Gigantorhynchus spirula* Porta, 1908, 1909; *Prosthenorchis luhei* Travassos, 1916; *Prosthorhynchus spiralis* (Rudolphi, 1809) Schmidt and Kuntz, 1966). The species is considered incertae sedis (Schmidt and Kuntz, 1966) and is not included in the key because its inadequate description does not allow its placement in either of the 2 subgenera of *Plagiorhynchus.* Another species, *Plagiorhynchus kuntzi* Gupta and Fatma, 1988, is not included in the key because it is not assignable to either subgenus. The position of the female gonopore was described as "terminal or subterminal"; the description was based on only 1 female and 1 male (Gupta and Fatma, 1988). Petrochenko (1958) and Yamaguti (1963) listed 22 and 21 species of *Prosthorhynchus,* respectively, but the taxonomic status and assignment of many of these species also has been changed since.

Based on the above account, 21 species are considered valid and are included in the following key. Petrochenko's (1958) key is outdated and did not include newer taxa and recent concepts as outlined in our present work. The shorter key by Hoklova (1986) addressed only species from the former U.S.S.R., some of which are synonyms.

Key to Species of the Subgenus *Prosthorhynchus*

1. Proboscis with 30 rows of hooks; eggs small (40 × 20); trunk pigmented ..... *P. (P.) pigmentatus* (Marval, 1902) Meyer, 1932
   Proboscis with 8–21 rows of hooks; eggs larger; trunk not pigmented 2
2. All proboscis hooks of almost uniform size (50–54 long), with rectangular well-developed roots ..... *P. (P.) limnobaeni* (Tubangui, 1933) Golvan, 1956
   Posterior 1–8 hooks smaller, spine-like, with underdeveloped, rudimentary, or no roots .. 3
3. Proboscis with 7–8 spine-like hooks posteriorly 4
   Proboscis with 1–7 spine-like hooks posteriorly 5
4. Spine-like hooks rootless ..... *P. (P.) varispinus,* Wang 1966
   Spine-like hooks with laterally split roots and manubrium ..... *P. (P.) golvani* Schmidt and Kuntz, 1966
5. Proboscis with 5–7 rootless spine-like hooks ..... *P. (P.) bullocki* Schmidt and Kuntz, 1966
   Proboscis with 1–4 spine-like hooks 6
6. Proboscis with 3–4 spine-like hooks having greatly reduced but definite roots ..... *P. (P.) malayensis* (Tubangui, 1935) Schmidt and Kuntz, 1966
   Proboscis with 1–3 spine-like hooks having underdeveloped, rudimentary, or no roots .. 7
7. Adults very long (males 45 mm, females 60 mm) ..... *P. (P.) scolopacidis* (Kostylev, 1915) Schmidt and Kuntz, 1966
   Adults shorter (males up to 30 mm, females up to 40 mm long) 8
8. Eggs large, 125–130 × 45–50 ..... *P. (P.) pittarum* (Tubangui, 1935) Schmidt and Kuntz, 1966
   Eggs smaller than 125–130 × 45–50 9
9. Proboscis with 8 rows of hooks, posterior hooks with very short roots; most eggs with polar prolongation of fertilization membrane ..... *P. (P.) russelli* (Tadros, 1970) Golvan, 1994
   Proboscis with 14 or more rows of hooks, posterior hooks with greatly reduced, rudimentary, or no roots; most eggs with concentric shells 10
10. Vaginal sphincter strongly developed on 1 side ..... *P. (P.) asymmetricus* Belopolskaja, 1983
    Vaginal sphincter symmetrical 11
11. Lemnisci considerably shorter than proboscis receptacle; proboscis with 18 rows, each with 20 hooks ..... *P. (P.) angerense* (Travassos, 1926) Schmidt and Kuntz, 1966
    Lemnisci slightly or considerably longer than proboscis receptacle; proboscis with 14–20 rows, each with 10–22 hooks 12
12. Ventral surface of female gonopore with elevated papilla ..... *P. (P.) genitopapillosus* Lundstrom, 1942
    No papilla at female gonopore 13
13. Proboscis small, 640–770 × 190–230, with 18 rows of hooks ..... *P. (P.) ogati* (Fukui and Morisita, 1936) Schmidt and Kuntz, 1966
    Proboscis larger, with 14–20 rows of hooks 14
14. Proboscis less than 1.0 mm long 15
    Proboscis 1.0 mm long, or longer 16
15. Proboscis 800–900 × 200 with 16–18 rows of 15–18 hooks each, hooks very small, middle and posterior hooks 23 and 4 long; females 17 mm long; eggs 70 × 10 ..... *P. (P.) rheae* (Marval, 1902) Schmidt and Kuntz, 1966
    Proboscis 957 × 65 with 16–18 rows of 20–22 hooks each, middle and posterior hooks

39 and 13 long; females 4.6 mm long; eggs 44–46 × 26–28 ..... *P. (P.) rossicus* (Kostylev, 1915) Schmidt and Kuntz, 1966

16. Proboscis consistently longer than 1.0 mm ... 17
Proboscis length averaging about 1.0 mm 20
17. Proboscis with 18–20 rows of hooks 18
Proboscis with 14–16 rows of hooks 19
18. Proboscis 1.25–1.44 × 0.33 mm with 18–20 rows of 15 hooks each, middle hooks 58–59 long, posterior 3 hooks rootless ..... *P. (P.) gallinagi* (Schachtachtinskaia, 1953) Schmidt and Kuntz, 1966

Proboscis 1.18 × 0.260–0.033 mm with 20 rows of 16 hooks each, middle hooks 71–77 long, posterior 3 hooks with underdeveloped but definite roots ..... *P. (P.) gracilis* (Petrochenko, 1958) Schmidt and Kuntz, 1966

19. Proboscis 1.0–1.3 mm long with 16–17 hooks per row, 1–3 basal hooks with broadened base but no definite root; females 12–15 mm long; eggs 80 × 40 ..... *P. (P.) reticulatus* (Westrumb, 1821) Golvan, 1956

Proboscis 1.1 × 0.3 mm with 14–15 hooks per row, posterior hooks spiniform and rootless; females 7.0–8.5 mm long; eggs 70 × 35 .... *P. (P.) nicobarensis* (Soota and Kansal, 1970) Zafar and Farooqi, 1981

20. Proboscis 0.96–1.1 × 0.19–0.22 mm with 20 rows of 19–20 hooks each, most posterior hooks rootless; proboscis receptacle 1.8 mm long; males 7 × 1.1 mm, females 8 × 1.1 mm ..... *P. (P.) longirostris* (Travassos, 1927) Amin, 1985

Proboscis 0.8–1.3 × 0.2–0.36 mm with 14–20 (usually 14–18) rows of 10–18 (usually 13–18) hooks each, posterior 1–3 spiniform hooks with greatly reduced or no roots; proboscis receptacle 2.0–2.5 mm long; males 4.5–30 × 0.6–2.4 mm, females 5–40 × 0.4–3.2 mm ..... *P. (P.) cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966

Remarks

Plagiorhynchinae was established by Meyer (1931) as a subfamily of Polymorphidae, within which he included the genera *Plagiorhynchus* Lühe, 1911, and *Prosthorhynchus* Kostylew 1915, as well as *Sphaerechinorhynchus* Johnston and Deland, 1929, and *Porrorchis* Fukui, 1929. Golvan (1956, 1960) erected 2 new subfamilies, Porrorchinae and Sphaerechinorhynchinae, to accommodate forms with short spheroid proboscides. This left only 2 genera, *Plagiorhynchus* and *Prosthorhynchus,* in the Plagiorhynchinae. Petrochenko (1956) established the family Prosthorhynchidae to contain *Prosthorhynchus,* among other genera, that infect terrestrial vertebrates as adults and terrestrial insects as larvae and that have eggs with concentric shells and no polar prolongations. Yamaguti (1963) placed Plagiorhynchidae Golvan, 1960 emend. in Echinorhynchidea Southwell and Macfie, 1925, in which adult and larval worms infected aquatic vertebrates and crustaceans, respectively, and eggs had a polar prolongation of the middle membrane. Schmidt and Kuntz (1966) synonymized *Prosthorhynchus* with *Plagiorhynchus* and reduced the 2 genera to subgenera of the genus *Plagiorhynchus* s. lat. Schmidt and Kuntz (1966) observed that the only 2 consistent morphological differences between the 2 taxa, the position of the female genital pore and the presence or absence of polar swelling in the egg fertilization membrane, were "not invariable." Amin (1982, 1985) accepted Schmidt and Kuntz's (1966) classification, and additional documentation was produced by this study. Hoklova (1986) and Golvan (1994), however, preferred to retain the original independent status of the 2 genera in Polymorphidae.

In the present work, an examination of many specimens and a review of relevant literature provided additional documentation and justification of Schmidt and Kuntz's (1966) decision to reduce *Plagiorhynchus* s. str. and *Prosthorhynchus* to subgenera of the genus *Plagiorhynchus* s. lat. All characteristics examined were found to vary considerably within each taxon, and to overlap between the 2 taxa. Characters found with some degree of variation and with very little but evident overlap include hosts, egg membranes, and female gonopore. Species of the subgenus *Plagiorhynchus* s. str. normally infect shore and aquatic arthropods (crustaceans and insects) as larvae, have a terminal gonopore in the female, and have eggs with polar prolongation of the fertilization membrane. Species of subgenus *Prosthorhynchus* normally infect terrestrial birds and occasionally mammals as adults and terrestrial arthropods as larvae, have a subterminal gonopore in the female, and have eggs with concentric shells showing no prolongation of any membrane. Despite Golvan's (1994) assertions and Hoklova's (1986) reservations, we have found exceptions to each of these 3 more stable characteristics, constituting an overlap between the concept of *Plagiorhynchus* s. str. and that of *Prosthorhynchus.* Our *P. (Prosthorhynchus) cylindraceus* specimens from South Africa were collected from 5 species of shore birds, suggesting an aquatic life cycle in the definitive and intermediate hosts. The same specimens and many others reported as syno-

nyms of the same species included females having up to 15% of their eggs with polar prolongation of the fertilization membrane. Most eggs (at least 80%) of the *P.* (*Prosthorhynchus*) *bullocki* female specimens examined also had polar prolongation of the fertilization membrane. Females of *P.* (*Prosthorhynchus*) *bullocki* have a definite subterminal gonopore; thus, this taxon remains in limbo between the 2 subgenera. Similarly, females of *P.* (*Plagiorhynchus*) *paulus* with eggs mostly having prolongation of the fertilization membrane have a subterminal gonopore. Because the eggs vary in size, shape, and the presence and degree of polar prolongation and because host ecological parameters are not consistent within each subgenus, the position of the female gonopore becomes the only remaining reliable trait distinguishing the 2 subgenera. Examples of the limitations to sole use of this characteristic include that of *P.* (*P.*) *paulus* and the fact that males cannot be keyed out. Variability within and between the 2 subgenera in all 3 characteristics (host, female gonopore, eggs) should be considered in toto while considering the limitations inherent in each.

Despite the above documented variations and limitations, no new subgeneric diagnoses are given or believed necessary; those provided by Schmidt and Kuntz (1966) are considered adequate.

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Sciadocephalus megalodiscus Diesing, 1850 (Cestoda: Corallobothriinae), a Parasite of *Cichla monoculus* Spix, 1831 (Cichlidae), in the Paraná River, State of Paraná, Brazil

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ABSTRACT: *Sciadocephalus megalodiscus* Diesing, gen. et sp. inquirenda, is redescribed from the tucunaré, *Cichla monoculus* Spix, collected in the Paraná River, Brazil. The position of the reproductive system of the parasite is clarified, thus revalidating the genus and species. *Sciadocephalus megalodiscus* is recorded from the Paraná River for the first time.

KEY WORDS: Cestoda, Proteocephalidae, *Sciadocephalus megalodiscus, Cichla monoculus,* Cichlidae, Teleostei, Paraná River, Brazil.

The basis of the taxonomy of the South American cestodes of the Order Proteocephalidea Mola, 1928, parasitizing freshwater fishes was established by W. N. F. Woodland, who, in a series of studies published in the 1930's, described numerous proteocephalid parasites of fishes of the Amazon basin. Some older species were described by Diesing (1850, 1855). Interest in these helminths has increased recently, and new cestodes are frequently being added to the South American species list (Rego et al., 1999). Some of the older species were placed as species inquirenda, as is the case with *Sciadocephalus megalodiscus* Diesing, 1850, which Diesing (1850) described from the tucunaré, *Cichla monoculus* Spix, 1831, collected in the state of Mato Grosso, Brazil. This parasite was later found by Woodland (1933) in Amazonia from the same fish species. Because there were doubts as to the subfamily to which this species belonged, because the position of the reproductive organs (a fundamental character in classification of the taxon) was unclear, Wardle and McLeod (1952) and Rego (1994) preferred to treat it as genus and species inquirenda.

Sciadocephalus megalodiscus had not previously been found in the Paraná River. It is important to note that *C. monoculus* is not native to the Paraná River, where it was introduced some years ago. Recently, one of us (P.M.M.) had the opportunity to collect several specimens of this parasite, and with the present description, the genus and species are revalidated.

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Materials and Methods

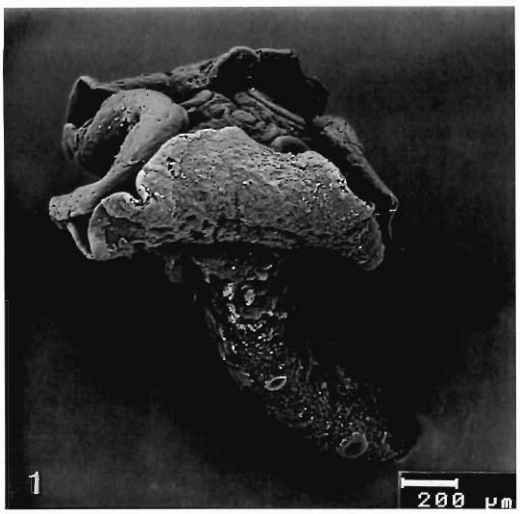
A total of 136 *C. monoculus* were caught in the Paraná River from July 1996 through October 1997. After removal from the intestine, the cestodes were fixed in 4% hot formalin. Cestodes were stained with alcoholic carmine or Delafield's hematoxylin, dehydrated in an alcohol series, cleared in Eugenol® or in beech creosote, and mounted in Canada balsam. Cestodes for histological sections were embedded in paraffin, cut in 8 μm cross-sections, and stained with hematoxylin and eosin. Illustrations were made with the aid of a drawing tube. Measurements are in millimeters (mm). Photomicrographs were made with a scanning electron microscope (SEM). The terms "prevalence" and "mean intensity of infection" are used according to Bush et al. (1997). Representative specimens were deposited in the Helminthological Collection of the Fundação Instituto Oswaldo Cruz (FIOCRUZ), Rio de Janeiro, state of Rio de Janeiro, Brazil, under accession numbers 33951, 33952, and 33953a–c.

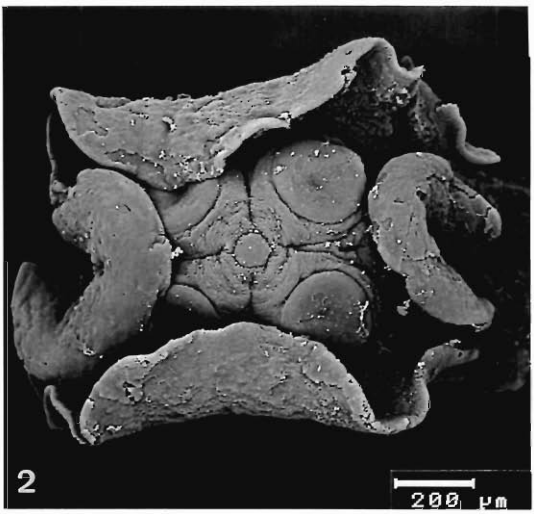
Results

Proteocephalidae La Rue, 1911
Corallobothriinae Freze, 1965
Sciadocephalus megalodiscus Diesing, 1850 (Figs. 1–7)

Description

GENERAL (based on 11 specimens): Strobila 6.1–9.3 (7.9) long × 1.1–1.7 (1.3) wide. Strobila comprised of 17–22 proglottids, including 6–8 (7) immature proglottids, 4–6 (5) mature proglottids, 8–12 (10) gravid proglottids. All proglottids several times wider than long. Scolex





Figures 1, 2. SEM photomicrographs of *Sciadocephalus megalodiscus* Diesing, 1850. 1. Small specimen (entire). 2. Scolex and metascolex. Apical view.

wider than strobila, with umbrella-shaped metascolex with borders turned upwards. Scolex enveloped by these borders, comprised of 4 muscular suckers and 1 apical sucker (Figs. 1–3). Scolex and metascolex 1.4–2.2 (1.9) long × 2.8–2.9 (2.8) wide; suckers 0.385–0.515 (0.454) in diameter and apical sucker 0.115 in diameter. Neck inconspicuous. Immature proglottids wider than long, 0.1 × 1.8 to 0.2 × 1.4 (0.2 × 1.6). Gravid proglottids wider than long, 0.3 × 1.8 to 0.9 × 1.4 (0.6 × 1.7). Last few proglottids more or less rectangular. Genital opening in anterior ⅓ of proglottid, alternating irregularly. Vagina opening anterior or posterior to cirrus pouch. Vaginal sphincter inconspicuous. Cirrus pouch long and narrow, 0.3 × 0.1 to 0.4 × 0.1 (0.4 × 0.1). Cirrus pouch about 0.2 times width of proglottid. Testes about 26, medullar, 0.07 in diameter, arranged in 2 distinct fields, separated by ovary. Ovary medullar, compact, indistinctly bilobate, central, 0.415–0.465 (0.442) in width. Vitellaria medullar, diffuse, not forming follicles, occupying lateral body region. Uterus medullar, rapidly resolving into capsules containing varying numbers of eggs. In last segments, some capsules not containing eggs and modified in form (Figs. 4, 7). Some capsules passing from medulla to cortex, opening through tegument. Eggs not containing developed embryos. Hexacanth hooks not observed. Musculature with numerous isolated longitudinal fibers, distributed throughout entire proglottid. Demarcation between medulla and cortex indicated by delicate transverse fibers situated next to longitudinal fibers (Fig. 6). Tegument of strobila with 2–4 longitudinal sulci (Fig. 5).

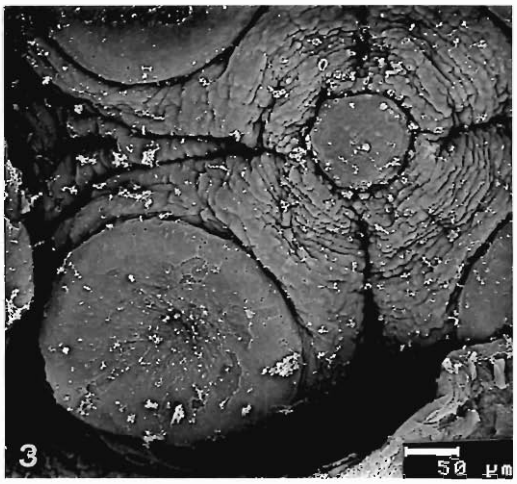


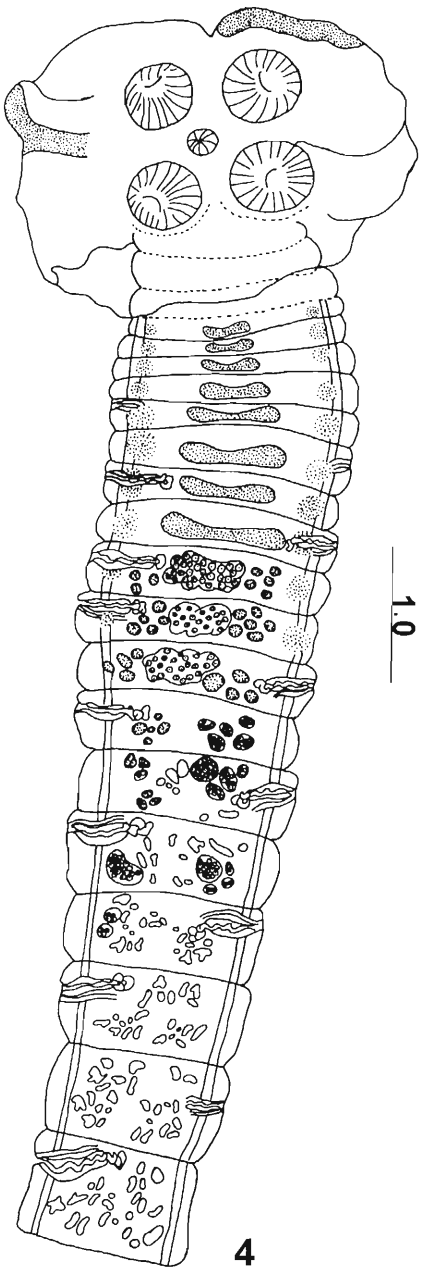
Figure 3. SEM photomicrograph of the scolex, detail of a sucker and apical sucker of *Sciadocephalus megalodiscus* Diesing, 1850.

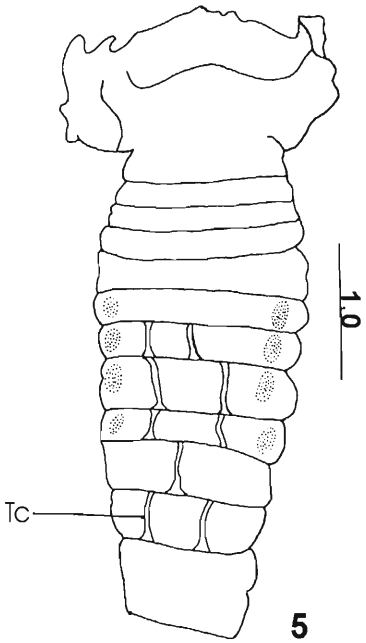
Taxonomic summary

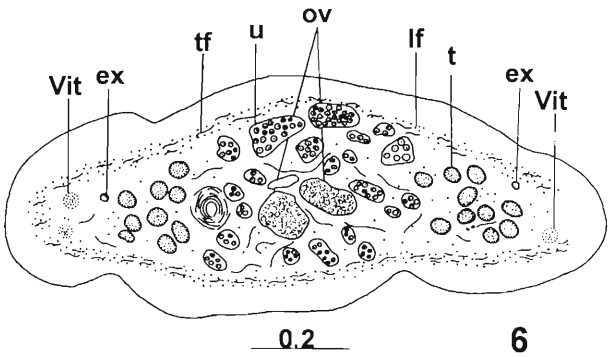
HOST: *Cichla monoculus* Spix, 1831 (Cichlidae), "tucunaré."

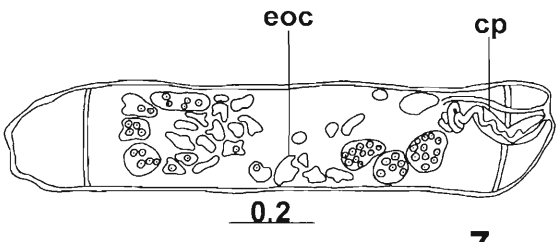
LOCALITY: Paraná River, region of Porto Rico, State of Paraná, Brazil.

SITE OF INFECTION: Intestine.









Figures 4–7. ***Sciadocephalus megalodiscus*** **Diesing, 1850. Scales in millimeters (mm). 4. Entire specimen; note that most proglottids are gravid. 5. Small specimen; note small sulci present on tegument (tc). 6. Cross-section of gravid proglottid, showing vitellaria (Vit), excretory canal (ex), testes (t), transverse fibers (tf), uterus (u), ovary (ov), longitudinal fibers (lf). 7. Gravid proglottid; note some ovigerous capsules with eggs and others without eggs and modified; empty ovigerous capsule (eoc), cirrus pouch (cp).**

PREVALENCE: 13.2%.
MEAN INTENSITY OF INFECTION: 8.6.

Discussion

This is the third report of *S. megalodiscus*. The species was initially described by Diesing (1850) from *C. monoculus* in the state of Mato Grosso, Brazil. Woodland (1933) redescribed it from the same fish species in Brazilian Amazonia. The latter author's description of the arrangement of the reproductive system was incomplete in that he did not note whether this system is medullar or cortical. Woodland (1933, p. 193) stated that "It is important to note that a definite band of longitudinal muscle fibres is entirely absent, though individual fibres may be scattered in the parenchyma. There is no question as to organs being medullary or cortical in position." The classification system for proteocephalids (sensu Freze, 1965) defined 2 families, Proteocephalidae and Monticelliidae, according to whether the gonads are located in the medullar or cortical parenchyma. For this reason, some authors (Wardle and McLeod, 1952; Rego, 1994) considered the genus and species as inquirenda.

Sciadocephalus megalodiscus have no groups of longitudinal fibers separating the cortex from the medulla (Woodland, 1933). However, as described in the present work (Fig. 6), the isolated fibers, together with the transverse fibers, sufficiently delimit the medulla from the cortex. We can therefore determine that the gonads and the vitelline glands are entirely medullar. Vitellaria do not form true follicles as in the majority of the proteocephalids, but appear as diffuse bodies, arranged laterally in the proglottids.

The metascolex is the most interesting characteristic of this species. Its umbrella form is different from typical "collar-type" metascolices found in genera of proteocephalids such as *Amphoteromorphus* Woodland, 1935; *Goezeella* Fuhrmann, 1916; and *Spatulifer* Woodland, 1934. Rego (1999) defined the metascolex as "any development of folds and wrinkles in the posterior part of the scolex or on the surface of the scolex proper, encircling the suckers or not." There are several types of metascolex, as many as the number of described species with metascolices. The scolex of *Sciadocephalus* has some resemblances to that of *Corallotaenia* Freze, 1965. Brooks and Deardorff (1980) reported an unidentified *Corallotaenia* sp. from the flatnose catfish, *Ageneiosus caucanus* Steindachner, 1880, in Colombia. Unfortunately, the authors did not provide a formal description of the worms. *Sciadocephalus* differs from *Corallotaenia* by the umbrella-shaped metascolex, the disposition of the ovary, the nonfolliculate vitellaria, and the uterus resolving into ovigerous capsules. It is important to emphasize that the other South American genera that possess a metascolex have the reproductive systems arranged variously, but partly or entirely located in the cortical parenchyma. *Sciadocephalus megalodiscus* is an exception; the gonads and vitellaria are entirely medullar.

Brooks and Rasmussen (1984) stated the importance of the metascolex to eliminate cases of parallel evolution in a cladogram. However, subsequent authors did not attribute much importance to these structures, probably because of difficulties in characterizing the metascolex types. Rego et al. (1999) produced a phylogenetic analysis of the subfamilies of Proteocephalidea, but in regard to the character metascolex, they stated: "only two states (presence versus absence) were considered until such time as the various forms of metascolices are clearly defined and distinguished." The preliminary results of a phylogenetic analysis of South American genera (Rego et al., unpubl.) indicate a closer phylogenetic relationship between *Sciadocephalus* and *Megathylacus* Woodland, 1935. It therefore becomes necessary to present a new generic diagnosis in order to revalidate the genus.

Sciadocephalus Diesing, 1850

GENERIC DIAGNOSIS: Strobila small. Scolex wider than strobilus. Metascolex umbrella-shaped, sometimes with edges turned upwards. Suckers muscular, round, and turned upwards. Apical sucker conspicuous. Genital openings alternating in regular fashion. Ovary compact, central. Testes in 2 fields, separated by ovary. Vitellaria diffuse, not forming follicles. Cirrus pouch elongate. Vaginal opening posterior or anterior to cirrus pouch. Uterus rapidly resolving into ovigerous capsules, with varying numbers of eggs. Eggs not embryonated. Longitudinal canals in tegument of strobilus. Gonads and vitellaria entirely medullar. Musculature consisting of numerous isolated, irregularly arranged longitudinal fibers, present in medullar parenchyma, but concentrated in cortex/medulla separa-

tion. Cortex/medulla separation best characterized by presence of transverse fibers.

Acknowledgments

We are grateful to Dr. Alain de Chambrier, Geneva, Switzerland, for preparing the SEM micrographs, and to Dr. Ricardo Massato Takemoto, State University of Maringá, for assistance in preparing drawings and sectioning proglottid material. The editors, Drs. Janet W. Reid and Willis A. Reid, Jr., assisted in translating the text into English.

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Obituary Notice

FRANCIS G. TROMBA
1920–1999

Elected to Membership in 1951;

Recording Secretary, 1957;

Vice President, 1962 President, 1963;

Editor, 1967–1970; Life Member, 1983;

Anniversary Award, 1991

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Revisions of *Protoancylodiscoides* and *Bagrobdella*, with Redescriptions of *P. chrysichthes* and *B. auchenoglanii* (Monogenoidea: Dactylogyridae) from the Gills of Two Bagrid Catfishes (Siluriformes) in Togo, Africa

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ABSTRACT: The generic diagnoses of *Protoancylodiscoides* Paperna and *Bagrobdella* Paperna, are emended based on the study and redescription of the respective type species: *P. chrysichthes* Paperna from the gills of the bagrid catfishes *Chrysichthys nigrodigitatus* (Lacépède) and *B. auchenoglanii* Paperna from the gills of *Auchenoglanis occidentalis* (Cuvier and Valenciennes) collected from Togo, Africa. *Protoancylodiscoides* is characterized by species possessing hook shanks comprised of 2 subunits (proximal subunit variably expanded) in hook pairs 1, 6, and 7; a dorsal striated pouch (onchium) through which the extrinsic dorsal muscles extend; a sinistral vaginal pore; a V-shaped ventral bar and straight dorsal bar; tandem (or slightly overlapping) gonads (germarium pretesticular); and 2 seminal vesicles. *Bagrobdella* includes species with tandem gonads (germarium pretesticular); a sinistral vaginal aperture; hook pairs 1–4, 6, and 7 with shank comprised of 2 subunits (basal subunit variably expanded); and straight bars. The ventral bar in species of *Bagrobdella* possesses a long anteromedial projection associated with a lightly sclerotized skirt; the dorsal bar is adorned with a shield-like projection originating from the posterior margin of the bar.

KEY WORDS: Monogenoidea, Dactylogyridae, *Protoancylodiscoides, Bagrobdella, Protoancylodiscoides chrysichthes, Bagrobdella auchenoglanii, Chrysichthys nigrodigitatus, Auchenoglanis occidentalis,* catfish, Siluriformes, Bagridae, Pisces, Togo, Africa.

This paper is a continuation of our series on dactylogyrid genera from Africa. Earlier papers dealt with *Characidotrema* Paperna and Thurston, 1968, *Quadriacanthus* Paperna, 1961, and *Schilbetrema* Paperna and Thurston, 1968 (see Kritsky et al., 1987; Kritsky and Kulo, 1988; 1992a, respectively). In addition, 2 new genera of African Dactylogyridae have been proposed: *Quadriacanthoides* Kritsky and Kulo, 1988 (a junior subjective synonym of *Paraquadriacanthus* Ergens, 1988; see Kritsky, 1990), and *Schilbetrematoides* Kritsky and Kulo, 1992 (see Kritsky and Kulo, 1992b). In the present paper, *Protoancylodiscoides* Paperna, 1969, and *Bagrobdella* Paperna, 1969, are revised, and *Protoancylodiscoides chrysichthes* Paperna, 1969, and *Bagrobdella auchenoglanii* Paperna, 1969, the type species of their respective genera, are redescribed from the gills of siluriform fishes in Togo, Africa.

Materials and Methods

Fish hosts *Chrysichthys nigrodigitatus* (Lacépède, 1803) and *Auchenoglanis occidentalis* (Cuvier and Valenciennes, 1840) were collected from localities in Togo during 1995–1996. Methods of collection, preservation, mounting, and illustration of helminths were those described by Kritsky et al. (1987). Measurements, all in micrometers, were made with a filar micrometer according to procedures of Mizelle and Klucka (1953), except that length of the male copulatory organ (MCO) of *P. chrysichthes* is an approximation of total length obtained by using a calibrated Minerva curvimeter on camera lucida drawings. Average measurements are followed by ranges and the number (*n*) of specimens measured in parentheses. Flattened specimens mounted in Gray and Wess' medium were used to obtain measurements of the hooks, anchors, and the copulatory complex. All other measurements were obtained from unflattened specimens stained with Gomori's trichrome or Mayer's carmine and mounted in synthetic resin. Voucher specimens of *P. chrysichthes* and *B. auchenoglanii* collected from Togo were deposited in the U.S. National Parasite Collection (USNPC), the helminth collections of the H. W. Manter Laboratory (HWML) of the University of Nebraska State Museum, and the Musée Royal de l'Afrique Centrale (MRAC) as indicated in the respective redescriptions. For comparative purposes, the following type specimens were examined: holotype and 3 paratypes (all on 1 slide) of *Protoancylodiscoides mansourensis* El-Naggar, 1987 (British Museum of Natural History [BMNH], London, 1985.1.8.1-2); 9 paratypes (all on 1 slide) of *Protoancylodiscoides malapteruri* Bilong, Birgi, and Le Brun, 1997 (BMNH 1996.4.7.6-7); 17

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paratypes (on 2 slides) of *P. malapteruri* (Muséum National d'Histoire Naturelle [MNHN 113 HF], Paris); holotype of *P. chrysichthes* Paperna, 1969 (MRAC 35.566); holotype of *B. auchenoglanii* Paperna, 1969 (MRAC 35.581); holotype of *Bagrobdella fraudulenta* Euzet and Le Brun, 1990 (MRAC 35.915).

Results

Class Monogenoidea Bychowsky, 1937
Order Dactylogyridea Bychowsky, 1937
Dactylogyridae Bychowsky, 1933
Protoancylodiscoides Paperna, 1969

EMENDED DIAGNOSIS: Body elongate, fusiform, comprised of cephalic region, trunk, peduncle, haptor. Tegument thin, smooth. Two terminal, 2 bilateral cephalic lobes; head organs present; cephalic glands unicellular, lateral or posterolateral to pharynx. Two pairs of eyes; granules subspherical. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus present; 2 intestinal ceca, confluent posterior to gonads, lacking diverticula. Genital pore midventral near level of intestinal bifurcation. Gonads intercecal, tandem or slightly overlapping; germarium pretesticular. Vas deferens looping left cecum, ascending to level of genital pore where it empties into saccate seminal vesicle; short duct arises from seminal vesicle dilating into large granule-filled vesicle that empties into base of male copulatory organ (MCO). Copulatory complex comprising nonarticulated tubular MCO, accessory piece; accessory piece serving as guide for MCO; 2 dorsal glandular masses lying immediately posterior to genital atrium; prostatic reservoir present. Seminal receptacle pregermarial; vaginal aperture sinistral. Vitellaria coextensive with intestine, frequently extending into peduncle. Haptor with dorsal, ventral anchor/bar complexes, 7 pairs of hooks with ancyrocephaline distribution (Mizelle, 1936; see Mizelle and Price, 1963); hook pairs 1, 6, 7 with shanks comprised of 2 subunits, proximal subunit expanded; pairs 2–5 with shanks of 1 subunit. Dorsal striated tissue pouch (onchium) present. Ventral bar V-shaped; dorsal bar straight. Parasites of gills of African siluriform fishes.

TYPE SPECIES: *Protoancylodiscoides chrysichthes* Paperna, 1969, from *Chrysichthys nigrodigitatus* (Bagridae).

OTHER SPECIES: *Protoancylodiscoides malapteruri* Bilong, Birgi, and Le Brun, 1997, from *Malapterurus electricus* Gmelin, 1789 (Malapteruridae); *P. mansourensis* El-Naggar, 1987, from *Chrysichthys auratus* Geoffroy, 1809 (Bagridae).

REMARKS: Paperna (1969) proposed *Protoancylodiscoides* for *P. chrysichthes* from the gills of *Chrysichthys nigrodigitatus* collected from 3 locations in Volta Lake, Ghana. He characterized the genus and differentiated it from *Ancylodiscoides* Yamaguti, 1937, by species having a "non-sclerotized bar" associated with the tip of the superficial root of each dorsal anchor, hooks of 2 different morphological types, and male reproductive organs shifted to the extreme posterior end of the body. Paperna (1969) clearly erred when describing the "non-sclerotized bars," as these structures represent the well-developed dorsal extrinsic muscles that insert on the tip of the superficial root of each dorsal anchor and extend to the midline of the haptor where their direction abruptly curves toward their origins in the peduncle or trunk (El-Naggar, 1987; Bilong et al., 1997). At the midline of the haptor, these muscles extend through a superficial dorsal pouch-like structure (onchium) before proceeding anteriorly toward their origins (Fig. 4). Contraction of the muscles apparently results in lateral displacement of the anchor points, thereby embedding its tip in host tissue during attachment.

Apparently Paperna (1969) considered "hooks of two types" to refer to the hook shank being composed of either 1 or 2 subunits, with the proximal subunit (when present) dilated to varying degrees. However, the presence of multiple hook types within species of Dactylogyridae is common and should probably not be used to differentiate genera without determination of the type present in homologous hook pairs. Hook types similar to those shown in Figures 5, 6, 9, and 10 for hook pairs 1, 6, and 7 in *Protoancylodiscoides chrysichthes* are also found in some African and Asian species infesting siluriform fishes: *Quadriacanthus* Paperna, 1961 (pairs 1, 6, and 7; see Kritsky and Kulo, 1988); *Bychowskyella* Achmerow, 1952 (pairs 1, 6, and 7; see Lim, 1991); and *Bagrobdella* Paperna, 1969 (pairs 1–4, 6, and 7). Also, in species of *Chauhanellus* Bychowsky and Nagibina, 1969 (all marine), and some (but not all) freshwater species of *Demidospermus* Suriano, 1983 (neotropical), all of which infest siluriform fishes, similar hooks have been reported (pairs 1–4, 6, and 7 in *Chauhanellus*; and pairs 1, 2, and 7 in *Demidospermus* (see Lim, 1994; Kritsky and

Gutiérrez, 1998, respectively). Based on hook types, therefore, species of *Protoancylodiscoides* show affinity to those of *Quadriacanthus* and *Bychowskyella* and perhaps those of *Bagrobdella* and *Chauhanellus*.

Although *Protoancylodiscoides chrysichthes* and *P. mansourensis* have elongate MCOs that extend from the level of the ovary to that of the esophageal bifurcation, the positions of this and other male reproductive organs are not outstanding. The only "shifting" of organs posteriorly in these 2 species are those of the distal seminal vesicle and prostatic reservoir to near the body midlength; both shifts are apparently accommodations to the posterior position of the base of the elongate MCO. In *P. malapteruri,* with a comparatively shorter MCO, these organs lie in the usual position of the anterior trunk (Bilong et al., 1997). Although Paperna (1969) showed the testis far posterior to the germarium in his whole-mount drawing of *P. chrysichthes,* the specimen on which the drawing was based was clearly distorted and flattened, which may have produced the pattern illustrated. In the present specimens, including the types of *P. mansourensis* and *P. malapteruri,* the gonads are tandem or slightly overlapping.

Based on its emended diagnosis, *Protoancylodiscoides* is now characterized by the combined presence of 1) hook shanks comprised of 2 subunits (proximal subunit expanded to varying amounts) in hook pairs 1, 6, and 7; 2) a striated pouch (onchium) on the dorsal surface of the haptor and through which the dorsal extrinsic muscles extend; 3) a sinistral vaginal pore; 4) a V-shaped ventral bar and a straight dorsal bar; 5) tandem (or slightly overlapping) gonads; and 6) a proximal saccate seminal vesicle followed by a fusiform distal vesicle.

Protoancylodiscoides chrysichthes Paperna, 1969 (Figs. 1–14)

HOST AND LOCALITY: Gills of *Chrysichthys nigrodigitatus,* Bagridae; Anié River, Kpéhoun, Togo.

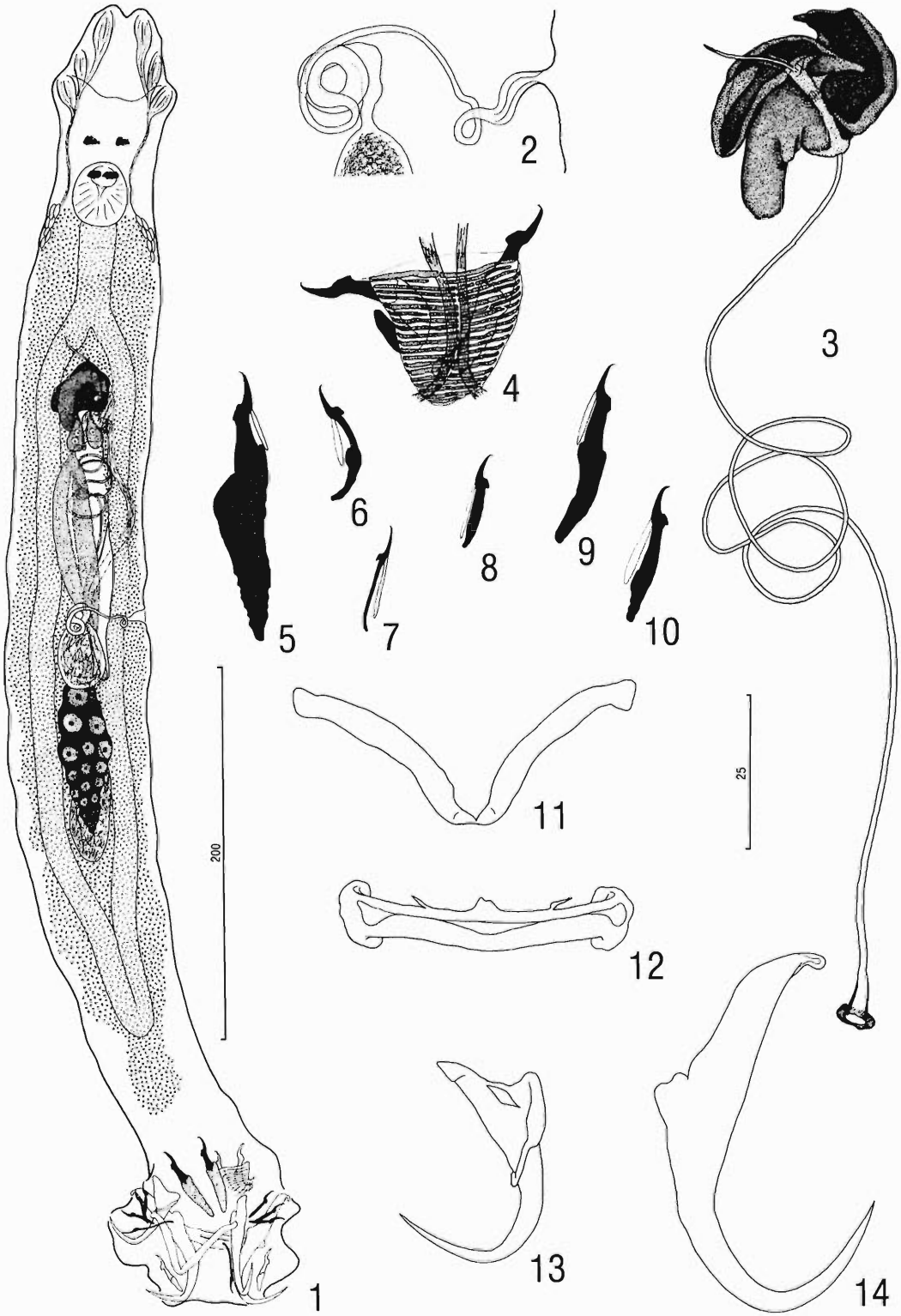
PREVIOUS RECORDS: *Chrysichthys nigrodigitatus* from 3 localities on Volta Lake, Ghana (Paperna, 1969, 1979); *C. auratus* from Lake Tiga, Kano, northern Nigeria (Ndifon and Jimeta, 1990).

SPECIMENS STUDIED: Forty-nine voucher specimens, USNPC 88263, 88264, 88265, 88266, 88267, HWML 39924, MRAC 37.422 (all from Togo).

REDESCRIPTION: Body 637 (410–884; n = 29) long; greatest width 90 (73–115; n = 33) near midlength. Cephalic region ventrally concave, lobes moderately developed, 3 bilateral pairs of head organs. Members of posterior pair of eyes slightly larger, closer together than those of anterior pair; subspherical granules moderately large; accessory granules absent or few in cephalic region. Pharynx ovate, greatest diameter 30 (23–43; n = 35); esophagus elongate. Peduncle elongate; haptor subhexagonal, 99 (79–140; n = 29) long, 94 (74–127; n = 23) wide. Ventral anchor 33 (29–38; n = 5) long; with differentiated roots connected by delicate or perforated web; thickened ridge originating from posterior margin of deep root, extending across base of shaft; shaft curved, point elongate; base 20 (17–22; n = 3) wide. Dorsal anchor 64 (55–69; n = 10) long, with elongate superficial root with curled tip, short truncate deep root, curved shaft, elongate point; base 31 (27–36; n = 6) wide. Ventral bar 68 (55–80; n = 12) long, 45 (35–69; n = 15) between ends, V-shaped, with slightly enlarged terminations; dorsal bar 41 (34–46; n = 20) long, straight, with short blunt anteromedial projection, pair of bilateral sliver-like projections frequently present on anterior margin, ends enlarged. Hook pairs 1, 6, 7 with shank of 2 subunits, proximal subunit lightly sclerotized, variably expanded, point delicate; hook pairs 2, 3, 4 with shank comprised of 1 subunit, slightly expanded; hook pair 5 delicate, with depressed thumb. Hook pair 1: 42 (38–45; n = 3); hook pairs 2, 3, 4: 16 (14–17; n = 12); hook pair 5: 18 (17–19; n = 4); hook pair 6: 23 (20–26; n = 6); hook pair 7: 30 (22–35; n = 4) long;

→

Figures 1–14. ***Protoancylodiscoides chrysichthes*** **Paperna, 1969. All figures are drawn to the 25 μm scale, except Figure 1 (200 μm scale). 1. Whole mount (ventral, composite). 2. Vagina and distal seminal receptacle. 3. Copulatory complex (ventral). 4. Dorsal pouch, dorsal extrinsic muscle and hook pair 7. 5. Hook pair 1. 6. Hook pair 1 (variant). 7. Hook pair 5. 8. Hook pair 4. 9. Hook pair 7. 10. Hook pair 6. 11. Ventral bar. 12. Dorsal bar. 13. Ventral anchor. 14. Dorsal anchor.**



hook pair 1 (variant): 22 (n = 1) long. Filamentous hooklet (FH) loop extending to proximal end of distal subunit of shank. MCO an elongate tube winding from base at level of germarium to genital atrium near level of intestinal bifurcation, base of MCO with sclerotized margin; MCO 255 (162–365: n = 5) long. Accessory piece variable, comprising 2 or 3 articulated subunits, elongate nipple (preputium) guiding distal portion of MCO shaft. Testis 50 (32–71; n = 8) long, 24 (21–32; n = 8) wide, elongate ovate; saccate proximal seminal vesicle subconical, lying sinistral to genital atrium, separated from distal vesicle by short duct with sphincter-like muscle; distal vesicle fusiform; prostatic reservoir fusiform, lying ventral to left cecum at midlength of body. Germarium fusiform, with irregular margins, 85 (61–113; n = 15) long, 31 (21–40; n = 15) wide; oviduct, ootype not observed; vaginal aperture at body midlength; vagina comprising distal thick-walled funnel, proximal coiled tube poorly sclerotized with 2–3 rings (ring direction counterclockwise proximally, reversing to a clockwise direction distally), emptying into subovate seminal receptacle overlying anterior extremity of germarium; diameter of vaginal ring 16 (13–20; n = 26); vitellaria dense throughout trunk, extending into peduncle, absent in regions of other reproductive organs.

REMARKS: *Protoancylodiscoides chrysichthes* is very similar to *P. mansourensis,* and differentiation of the 2 species is based on relatively few morphometric characters. Comparison with the holotype and 3 paratypes of the latter species has revealed the following differences: 1) in *P. chrysichthes,* the coiled vagina has 2–3 rings (4–5 rings in *P. mansourensis*); 2) the diameter of the rings of the vagina is greater in *P. mansourensis* (24 to 27 μm) than in *P. chrysichthes* (13 to 20 μm).

In addition, El-Naggar (1987) differentiated the 2 species utilizing morphometric features, the presence/absence of a "preputium" associated with the tip of the MCO, and a haptoral funnel-like structure through which the dorsal extrinsic muscles extend. However, our measurements of the type specimens of *P. mansourensis* showed that body length (497–650 μm) does not differ from that of our specimens of *P. chrysichthes* (410–884 μm). Indeed, our measurements of body length of the flattened holotype and paratypes of *P. mansourensis* did not fall within the range (710–1,000 μm) reported by El-Naggar (1987), indicating that some of his conversions were in error. Although measurements of body length presented by Paperna (1969) for *P. chrysichthes* had only 1 significant digit, resulting in difficulty in determining the rounding effects, his range (400–500 μm) falls within those reported herein for the types of *P. mansourensis* and for our specimens from Togo.

With the exception of the total length of the dorsal anchor, differences in all other measurements of *P. chrysichthes* and *P. mansourensis* reported herein may be explained by potential rounding effects. In specimens of *P. chrysichthes* from Togo, the length of the dorsal anchor ranged from 55 to 69 μm, whereas our values for the type specimens of *P. mansourensis* were 78 to 83 μm. Paperna (1969) reported 100 to 110 μm for this parameter, but this range does not necessarily exclude our measurements because of possible rounding effects. Therefore, dorsal anchor length is problematic in differentiating *P. mansourensis* from *P. chrysichthes.*

Although Paperna (1969) described a "preputium" associated with the distal end of the MCO, we were unable to find this structure in our specimens. However, it is likely that Paperna's "preputium" refers to a small, elongate, often longitudinally striated portion of the accessory piece through which the tip of the MCO projects. A similar component of the accessory piece is also visible in the holotype and paratypes of *P. mansourensis.* Finally, presence of a dorsal "funnel-like structure" (of El-Naggar, 1987) or "onchium" (of Bilong et al., 1997) through which the dorsal extrinsic muscles of the haptor extend is probably a generic character, because it also occurs in our specimens of *P. chrysichthes.*

It is clear that *P. chrysichthes* and *P. mansourensis* are poorly differentiated, and they may be synonyms. However, we do not feel that available information on the 2 forms (species) justifies proposal of synonymy at this time. Additional collections from throughout the range of the host would be necessary to determine intraspecific variation within the species. If the 2 species are distinct, the record of *P. chrysichthes* from *C. auratus* in Nigeria (Ndifon and Jimeta, 1990) must be confirmed.

Protoancylodiscoides malapteruri is easily differentiated from the 2 species discussed above by the presence of a elongate proximal rod in the accessory piece (absent in *P. chrys-*

ichthes and *P. mansourensis*). In *P. malapteruri,* the MCO is shorter and less convoluted than that of *P. chrysichthes* or *P. mansourensis.*

Bagrobdella Paperna, 1969

EMENDED DIAGNOSIS: Body robust, fusiform, comprised of broad cephalic region, trunk, peduncle, haptor. Tegument thin, smooth. Two terminal, 2 bilateral cephalic lobes; head organs present; cephalic glands unicellular, posterolateral to pharynx. Two pairs of eyes; granules subspherical. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short; 2 intestinal ceca, confluent posterior to gonads, lacking diverticula. Genital pore dextroventral about ½ distance between germarium and intestinal bifurcation. Gonads intercecal, tandem; germarium pretesticular. Vas deferens looping left cecum; seminal vesicle a simple dilation of vas deferens. Copulatory complex a coiled tube with clockwise rings (see Kritsky et al., 1985), directed posteriorly from MCO base, lacking accessory piece; prostatic vesicle present. Seminal receptacle pregermarial; vaginal aperture sinistral. Vitellaria coextensive with intestine. Haptor with dorsal, ventral anchor/bar complexes, 7 pairs of hooks with ancyrocephaline distribution (Mizelle, 1936; see Mizelle and Price, 1963); pairs 1–4, 6, 7 with shanks comprised of 2 subunits, proximal subunit expanded; pair 5 with shank of 1 subunit. Ventral bar straight, with long anterior projection associated with lightly sclerotized skirt; dorsal bar straight, with posterior shield-like projection. Parasites of gills of siluriform fishes.

TYPE SPECIES: *Bagrobdella auchenoglanii* Paperna, 1969, from *Auchenoglanis occidentalis* (Bagridae).

OTHER SPECIES: *Bagrobdella fraudulenta* Euzet and Le Brun, 1990 (syn. *B. auchenoglanii* of Paperna, 1971), *B. anthopenis* Euzet and Le Brun, 1990, both from *Auchenoglanis occidentalis.*

REMARKS: Euzet and Le Brun (1990) emended the diagnosis of *Bagrobdella* and corrected some initial observations on internal anatomy and haptoral sclerites offered by Paperna (1969). Our emendation adds to their diagnosis the morphologic differences between respective hook pairs and details of the coil of the MCO.

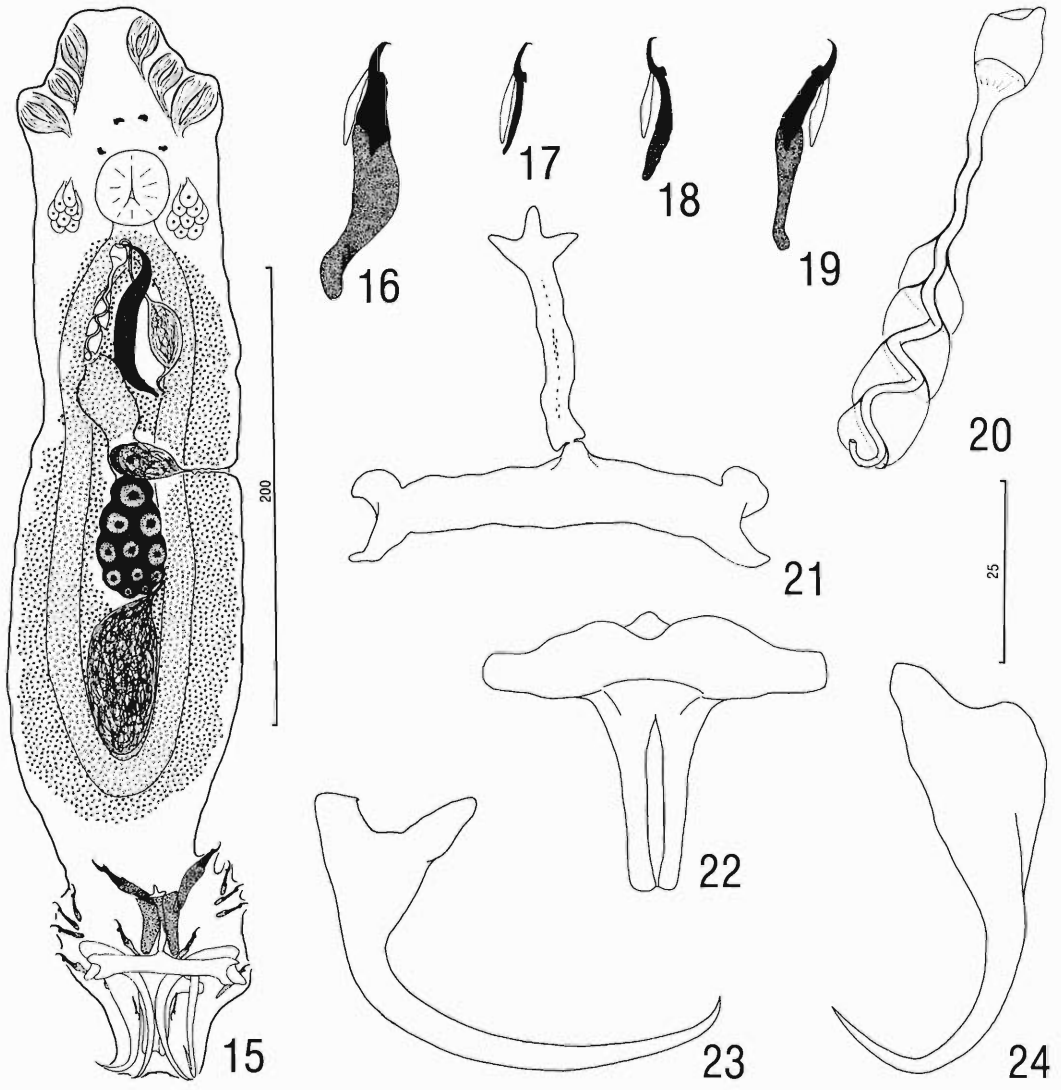
Bagrobdella auchenoglanii Paperna, 1969 (Figs. 15–24)

HOST AND LOCALITY: Gills of *Auchenoglanis occidentalis,* Bagridae; Barrage du "Chantier Rouge," Kara River, Kara, Togo.

PREVIOUS RECORDS: *Auchenoglanis occidentalis,* Volta Lake, Ghana (Paperna, 1969, 1979); Niger River at Bamako, Mali (Euzet and Le Brun, 1990).

SPECIMENS STUDIED: Forty-four vouchers, USNPC 88258, 88259, 88260, 88261, 88262, HWML 39925, MRAC 37.423 (all from Togo).

REDESCRIPTION: Body 457 (361–686; n = 25) long; greatest width 103 (78–130; n = 25) in posterior trunk. Cephalic region broad; cephalic lobes well developed. Eyes subequal; members of posterior pair farther apart than members of anterior pair; granules small; accessory granules absent, infrequently few in cephalic region. Pharynx subspherical to ovate, 28 (24–33; n = 24) in greatest diameter. Peduncle broad; haptor subhexagonal, 91 (78–113; n = 25) long, 93 (79–104; n = 27) wide. Ventral anchor 42 (37–45; n = 11) long, with short roots, evenly curved elongate shaft abruptly flexed immediately distal to anchor base; tip of point recurved; base 22 (19–24; n = 10) wide. Dorsal anchor 56 (50–58; n = 11) long, with poorly differentiated roots, curved shaft, long point; base 22 (18–25; n = 7) wide. Ventral bar 46 (42–53; n = 17) long, with bifurcated ends surrounding superficial surface of anchor base; anteromedial projection 27 (24–31; n = 19) long, distally trifid; skirt delicate. Dorsal bar 59 (53–65; n = 24) long, yoke shaped, with subtrapezoidal posterior shield; shield 35 (31–40; n = 25) long. Hook pair 1: 35 (30–37; n = 11), pairs 2, 3, 4: 21 (20–23; n = 14), pairs 6, 7: 29 (26–36; n = 10) long, each with truncate thumb, delicate shaft, point, proximal subunit of shaft variable in length between hook pairs; hook pair 5: 16–17 (n = 3) long, with delicate point, shaft, shank with 1 subunit; FH loop about length of distal subunit of shank. MCO 63 (52–74; n = 11) long, a coil of about 6 rings, proximal 3 rings poorly defined, distal 3 rings with delicate cup-like processes; base expanded, lightly sclerotized. Testis 40 (28–53; n = 10) long, 28 (20–35; n = 7) wide, ovate; seminal vesicle ovate; prostatic reservoir elongate fusiform. Germarium pyriform, 44 (35–56; n = 22) long, 29 (20–42; n = 22) wide; oviduct broad; ootype not



Figures 15–24. ***Bagrobdella auchenoglanii*** **Paperna, 1969. All figures are drawn to the 25 μm scale, except Figure 15 (200 μm scale). 15. Whole mount (ventral, composite). 16. Hook pair 1. 17. Hook pair 5. 18. Hook pairs 2, 3, 4, 7. 19. Hook pair 6. 20. Copulatory complex (ventral). 21. Ventral bar. 22. Dorsal bar. 23. Ventral anchor. 24. Dorsal anchor.**

observed; uterus delicate; vagina a simple nonsclerotized straight tube; seminal receptacle submedian, pregermarial. Vitellaria dense throughout trunk, except absent in regions of other reproductive organs.

REMARKS: Measurements of specimens of *Bagrobdella auchenoglanii* from Togo compare favorably with those reported by Euzet and Le Brun (1990) for their material from Mali. Paperna's (1969) measurements are generally greater than those reported herein. Reported differences between respective studies are not considered sufficient to separate the collections into separate species and likely represent intraspecific variability between geographic localities.

Because Paperna's (1971) redescription of *Bagrobdella auchenoglanii* from *Auchenoglanis occidentalis* in Lake Albert, Uganda, was based on specimens of *B. fraudulenta* (see Euzet and Le Brun, 1990), the Ugandan records reported

by Paperna (1971, 1979) are for the latter species. *Bagrobdella auchenoglanii* is not known from Uganda.

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Redescription of *Pseudacanthostomum panamense* Caballero, Bravo-Hollis, and Grocott, 1953 (Digenea: Acanthostomidae), a Parasite of Siluriform Fishes of the Family Ariidae, with Notes on Its Biology

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ABSTRACT: The acanthostomid trematode *Pseudacanthostomum panamense* Caballero, Bravo-Hollis, and Grocott is redescribed on the basis of examination of its holotype and new material from *Galeichthys* (=*Ariopsis*) *seemani* (Günther) (type host) from Colombia (new geographical record), and *Ariopsis assimilis* (Günther) and *Arius guatemalensis* (Günther) (new host records) (all Siluriformes: Ariidae) from the Atlantic and Pacific coasts of Mexico (new geographical record). It was found that *P. panamense* possesses intestinal ceca that are connected with the excretory bladder near the posterior extremity and opening outside by an uroproct. The actual number of circumoral spines of the holotype is 27; the number of spines is stable, with most specimens possessing 27 spines and a very few 26 or 28. *Pseudacanthostomum floridensis* Nahhas and Short, described from *Galeichthys* (=*Arius*) *felis* (Linnaeus) from Florida, U.S.A., is considered a synonym of *P. panamense*. Metacercariae of *P. panamense* from the eleotrid fishes *Dormitator latifrons* (Richardson) and *Gobiomorus maculatus* (Günther) from the Pacific coast of Mexico (Jalisco state) are described for the first time.

KEY WORDS: *Pseudacanthostomum panamense*, Digenea, metacercariae, Acanthostomidae, taxonomy, catfish, Siluriformes, Ariidae, Pisces, Mexico, Colombia.

During parasitological examination of fish from Colombia and Mexico, acanthostomid trematodes were found, both as adults in catfish of the family Ariidae and as metacercariae in eleotrid fish. They were identified as *Pseudacanthostomum panamense* Caballero, Bravo-Hollis, and Grocott, 1953, a species described from *Galeichthys* (=*Ariopsis*) *seemani* (Günther, 1864) from Panama (Caballero et al., 1953). Examination of the holotype of *P. panamense* showed that its original description had not provided data on some taxonomically important features such as the morphology of the intestinal ceca; in addition, no information about intraspecific variability of this taxon was provided. Therefore, *P. panamense* is redescribed here on the basis of new material from different hosts and geographical regions. Metacercariae of this trematode are described for the first time, and the taxonomic status of *Pseudacanthostomum floridensis* Nahhas and Short, 1965, the only congeneric species, is discussed.

Materials and Methods

Trematodes studied were found in *Ariopsis seemani* (7 specimens examined) from Colombia (locality not known; May 1996); *Ariopsis assimilis* (Günther, 1864), from Laguna Bacalar near the village of Bacalar, Quintana Roo, Mexico, January 1995 (1 specimen), and from Chetumal Bay, Quintana Roo, Mexico, October 1996 (96 specimens); and *Arius guatemalensis* (Günther, 1864) (3 specimens) from Marismas de Chalacatepec, Jalisco, Mexico, May 1995. Metacercariae were found in the eleotrid fish *Dormitator latifrons* (Richardson, 1844) from Boca del Río San Nicolás, Jalisco, Mexico, September and November 1994 (21 fish examined), from Marismas de Chalacatepec, Jalisco, Mexico, March 1995 (24 specimens), and from the Cuitzmala River at the village of Emiliano Zapata,

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Jalisco, Mexico, September 1995 (7 specimens); and in *Gobiomorus maculatus* (Günther, 1859) from the Cuitzmala River at Emiliano Zapata, Jalisco, Mexico, January, March, and September 1995 (89 specimens).

Holotypes of *P. panamense* from *Ariopsis seemani* from Panama (National Helminthological Collection of the Institute of Biology, National Autonomous University of Mexico, Mexico City, Mexico-CNHE 947) and *P. floridensis* from *Galeichthys* (=*Arius*) *felis* (Linnaeus, 1766) from Florida (U.S. National Parasite Collection, Beltsville, Maryland, U.S.A.-USNPC 60087) were compared with the present material.

Measurements (length and width) of 59 undeformed, uncollapsed eggs of *P. panamense* (from *Ariopsis seemani,* Panama and Colombia and *A. assimilis,* Bacalar and Chetumal, Mexico) and *P. floridensis* (from *Arius felis,* Florida, U.S.A.) were compared by ANOVA (Tukey's HSD for unequal *N*; Spojotvoll/Stoline test).

The specimens studied are deposited in the helminthological collections of the Institute of Parasitology, České Budějovice, Czech Republic (IPCAS D-384); Institute of Biology, National Autonomous University of Mexico, Mexico City, Mexico (CNHE 3239); Laboratory of Parasitology, CINVESTAV-IPN Merida, Mexico (CHCM 181); and the U.S. National Parasite Collection, Beltsville, Maryland, U.S.A. (USNPC 87809, 87810). The nomenclature of the fish hosts (catfish) follows that presented by Eschmeyer (1998). Measurements are in micrometers unless otherwise noted.

Results

Comparison of acanthostomid trematodes occurring in *Ariopsis seemani* from Colombia and *A. assimilis* and *A. guatemalensis* from Mexico with the holotype of *Pseudacanthostomum panamense* from *A. seemani* from Panama revealed their conspecificity (Figs. 1, 2; Table 1). All specimens, including the holotype of *P. panamense* (Fig. 1), possess long intestinal ceca connected near the posterior extremity with the excretory bladder, thus forming an uroproct (Figs. 1D, 2D, F). Vitelline follicles are distributed between the ventral sucker and the anterior testis (Figs. 1B, 2A, C, F, G), ventrally forming 2 separate fields and, in the same specimens, are dorsally confluent at the ovarian level (Figs. 1F–H, 2C). The uterine loops are sinuous, filling the space between the ventral sucker and the posterior extremity (Figs. 1C, 2A, C, G). A thin-walled, coiled seminal vesicle is situated posterodextrally to the ventral sucker (Figs. 1B, 2C, F), and a genital pore is located just anterior to the ventral sucker (Fig. 1B). With the exception of 3 specimens, all trematodes (N = 40), including the holotype (Fig. 1A), had 27 circumoral spines (Table 2).

The present study also demonstrated that the trematodes studied are identical in all but 1 morphological and biometrical character to *P. floridensis,* a species described from *Arius felis* from Florida, U.S.A (Nahhas and Short, 1965; see Table 1). No significant difference between these 2 taxa was found in the size (length and width) of eggs (Fig. 3). The only difference between *P. panamense* and *P. floridensis* is the more anterior position of the vitelline follicles in the latter species. However, the distribution of the vitelline follicles is rather variable (Fig. 1E–H), and its suitability as a discriminative character between *P. panamense* and *P. floridensis* is doubtful. Consequently, *P. floridensis* is considered a junior synonym of *P. panamense.*

Because the original description of *P. panamense* was incorrect in some features (the number of circumoral spines, the presence of an uroproct, and the spination of the posterior part of the body), its redescription based on extensive material from 4 fish hosts is provided herein. In addition, metacercariae from the eleotrid fishes *Dormitator latifrons* and *Gobiomorus maculatus* from Mexico, considered to be conspecific with *P. panamense,* are described.

Pseudacanthostomum panamense Caballero, Bravo-Hollis, and Grocott, 1953 (Figs. 1, 2)

SYNONYMS: *Pseudacanthostomum floridensis* Nahhas and Short, 1965 (new synonymy).

Pseudacanthostomum sp. of Pineda-López et al. (1985) (new synonymy).

Pelaezia sp. of Scholz and Vargas-Vázquez (1998) (new synonymy).

DESCRIPTION: Adult (measurements in Table 1): Body elongate, densely covered with fine tegumental spines, including post-testicular region. Oral sucker terminal, cup-shaped, with large buccal cavity; ventral sucker small, pre-equatorial. Oral sucker surrounded by 1 row of 27 large, straight circumoral spines (Figs. 1A, 2B, J, K); exceptionally 26 or 28 spines present (Table 2). Prepharynx present and short (Fig. 1A) or absent (Fig. 2A); pharynx strongly muscular; esophagus very short. Intestinal bifurcation pre-equatorial; intestinal ceca long, connected with excretory bladder and opening outside by uroproct (Figs. 1D, 2D). Testes tandem, close to posterior extremity. Vas deferens forming numerous loops, widened near ventral sucker to form coiled seminal vesicle; cirrus-sac lacking, ejaculatory duct slightly curved, opening into hermaphroditic

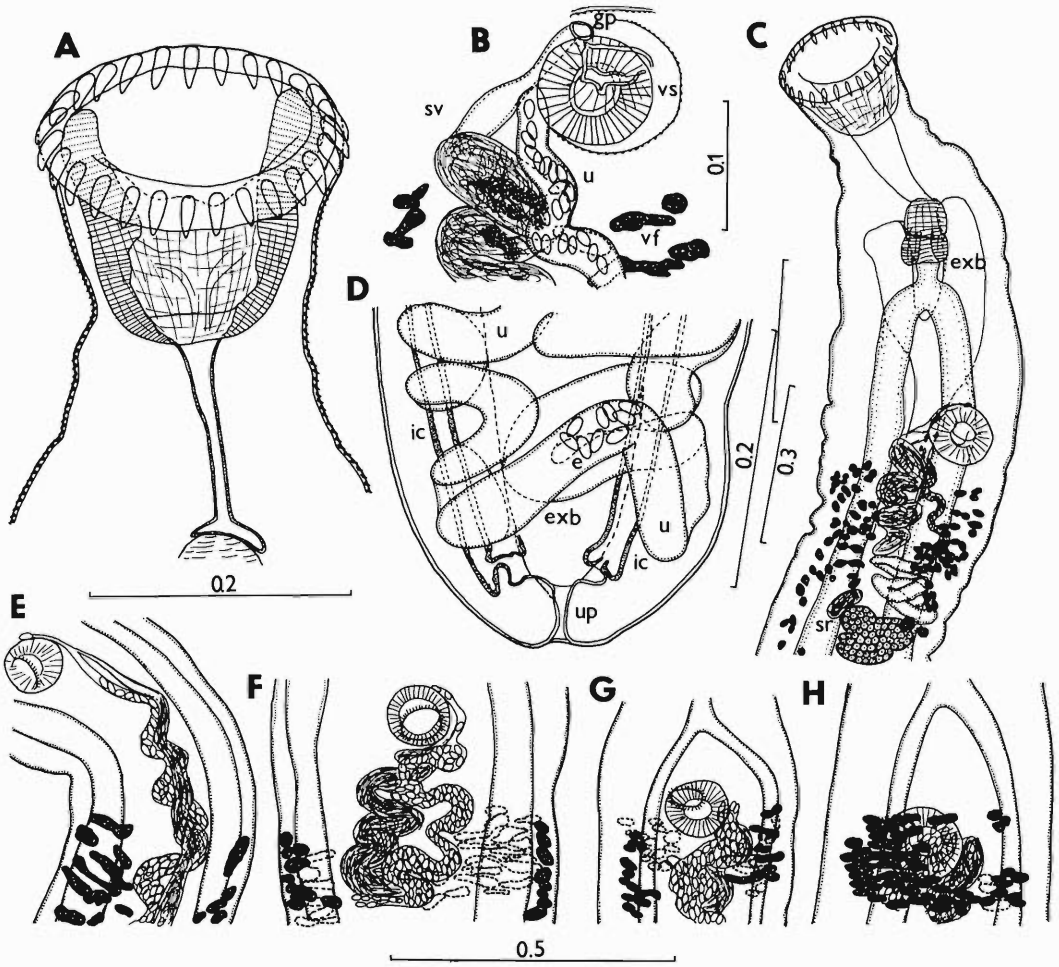

Figure 1. *Pseudacanthostomum panamense*. **A–D, holotype from *Galeichthys* (=*Arius*) *seemani*, Panama (IBUNAM 947), ventral view. A: oral sucker; B: ventral sucker and terminal genitalia; C: anterior part of body; note extent of vitelline follicles; D: posterior extremity; note connection of intestinal ceca with excretory bladder and presence of uroproct; E–H, acetabular region; note variation in anterior extent of vitelline follicles (E, F: specimens from *Ariopsis assimilis*, Mexico; G, H: specimens from *A. seemani*, Columbia; E: dorsal view, ventral follicles omitted; F, G: ventral view, dorsal follicles dashed; H: ventral view but dorsal follicles drawn in full and ventral follicles dashed). Scale bars in millimeters. Abbreviations: e, eggs; exb, excretory bladder; gp, genital pore; ic, intestinal ceca; sr, seminal receptacle; sv, seminal vesicle; u, uterus; up, uroproct; vf, vitelline follicles; vs, ventral sucker.**

duct; genital pore close to anterior margin of ventral sucker (Fig. 1B). Ovary transversely elongate, slightly lobate (Fig. 1C) or with almost indistinct lobes (Fig. 2A), pretesticular. Seminal receptacle oval, preovarial or anterolateral to ovary (Fig. 1C). Vitelline follicles numerous, dorsally filling space between ventral sucker and ovary, ventrally forming 2 lateral bands starting at acetabular level or posterior to ventral sucker and reaching posteriorly to anterior margin of anterior testis (Figs. 1E–G, 2G); exceptionally, vitelline follicles preacetabular. Uterus sinuous, with numerous loops, reaching to body extremity posteriorly and completely filling body posterior to ovary (Fig. 2A, G, F). Metraterm thin-walled, opening into hermaphroditic duct. Eggs operculate, rather variable in size (Figs. 3, 4). Excretory bladder Y-shaped, long, with anterior branches anterolateral to intestinal ceca, reaching to pharynx (Figs. 1C, 2A, C, F).

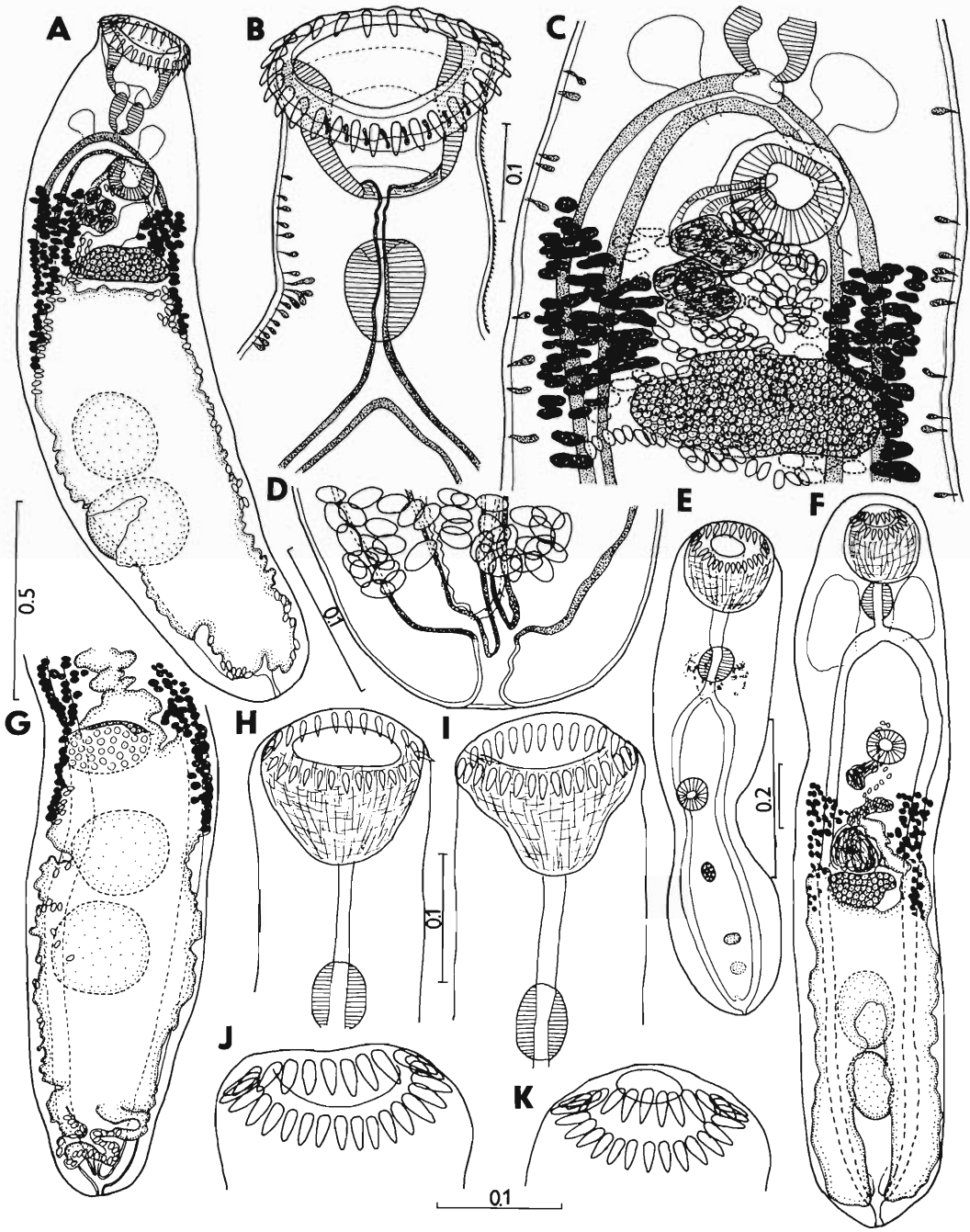

Figure 2. *Pseudacanthostomum panamense.* Adults from *Ariopsis seemani,* Colombia (A–D, G); metacercariae from *Dormitator latifrons*, Mexico (E, H, I); adults from *A. assimilis*, Mexico (F, J, K). A, E, F: total view. B, H–K: oral sucker with circumoral spines. B: tegumental spines on only the right side and subtegumental gland cells on the left side are illustrated. C: detail of acetabular region with terminal genitalia; note connection of dorsal vitelline follicles (dashed) at level of ovary. D: posterior extremity with connection of intestinal ceca, opening to the outside, with the excretory bladder (uroproct). G: posterior part of body; note vitelline follicles reaching posteriorly to level of anterior testis. Scale bars in millimeters.

Table 1. Measurements of *Pseudacanthostomum panamense* from different hosts* (in micrometers).

Species	*P. panamense*				*P. floridensis*	
Host	*A. seemani*		*A. assimilis*	*A. seemani*	*A. felis*	
Locality	Panama		Mexico	Colombia	U.S.A.	
Author	Caballero et al., 1953	Present data†	Present data	Present data	Nahhas and Short, 1965	Present data†
N	3	1	8	4	2	1
Body length	2,440–2,540	2,784	2,150–3,650	1,850–2,580	2,630–3,000	3,050
Body width	332–481	360	230–370	408–512	489–750	730
Oral sucker						
Length	76–133	211	123–195	186–208	180–294	266
Width	171–228	214	130–238	227–259	309–330	314
Spines (no.)	26	27	26–27	27	28	28
Spine length	30–38	31–37	28–45	37–54	42–60	26–59
Spine width	11	12–13	8–13	9–12	18–24	15–19
Prepharynx	95–133	154	30–138	45–56	—	15
Pharynx						
Length	122–171	125	78–105	99–122	129–206	218
Width	95–106	99	63–98	85–102	—	144
Esophagus	11–19	14	13–42	22–23	v. short	—
Ventral sucker						
Length	87–114	83	70–103	82–108	118–155	154
Width	106–114	86	68–103	83–118	155–170	170
Sucker ratio	0.33–0.50	0.40	0.41–0.68	0.38–0.51	0.54	0.56
Anterior testis						
Length	175–232	173	180–300	214–250	283–309	278
Width	114–194	118	78–180	179–256	180–283	173
Posterior testis						
Length	194–285	202	180–380	208–272	—	317
Width	125–228	128	115–220	205–266	—	176
Ovary						
Length	103–129	112	90–170	99–122	232–260	224
Width	133–236	141	55–190	230–272	298–309	317
Eggs						
Length	19–21	21.5–25	20–27.5	23–28	20–25	23–26
Width	11	12.5–13.5	10–14	12–14.5	11–14	12–13.5
Uroproct	absent	present	present	present	present	present

* Specimens from *A. assimilis* from Bacalar, Mexico, are not included because they were flattened during fixation.
† Measurements of the holotypes (CNHE 947 and USNPC 60087).

Table 2. Number of circumoral spines of *Pseudacanthostomum panamense*.

Host and country	Number of spines			Number of specimens
	26	27	28	
Ariopsis seemani (Panama)	—	1	—	1
Ariopsis seemani (Colombia)	—	4	—	4
Arius felis (U.S.A.)	—	—	1	1
Ariopsis assimilis (Mexico)	1	14	2	17
Arius guatemalensis (Mexico)	—	17	—	17
*Dormitator latifrons** (Mexico)	—	4	—	4
Total	1	40	3	44

* Metacercariae.

HOSTS: *Ariopsis seemani* (type host), *A. assimilis, Arius guatemalensis,* and *A. felis* (all Siluriformes: Ariidae) (Table 3).

SITE: Intestine.

GEOGRAPHIC DISTRIBUTION: Panama Viejo, Pacific coast, Panama (type locality); Colombia; Mexico (states of Tabasco and Quintana Roo, Atlantic coast; state of Jalisco, Pacific coast), U.S.A. (state of Florida) (Caballero et al., 1953; Nahhas and Short, 1965; Yamaguti, 1971; Pineda-López et al., 1985; Scholz and Vargas-Vázquez, 1998).

METACERCARIA: (based on 4 specimens from *Dormitator latifrons*; Fig. 2E, H, I): Body of excysted metacercariae elongate, 630–845 long by 147–182 wide. Oral sucker terminal, cup-

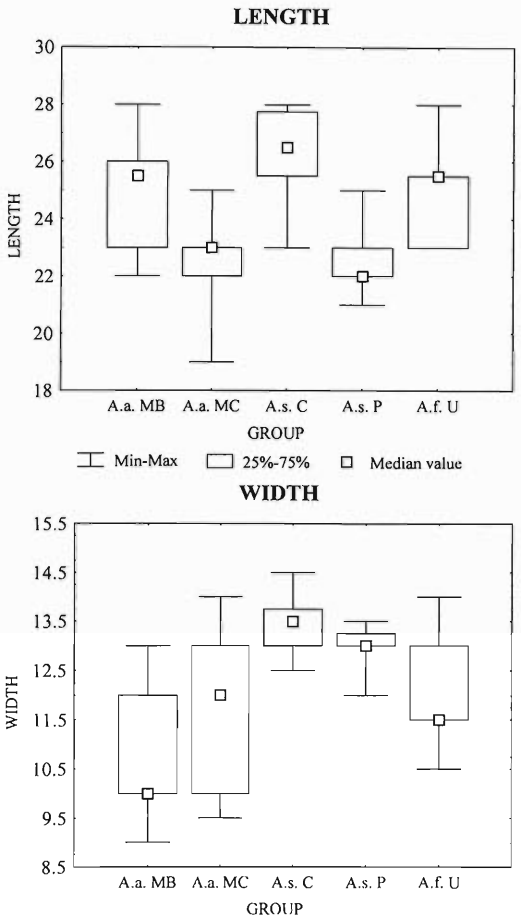

Figure 3. Length (above) and width (below) of eggs of *Pseudacanthostomum panamense* from different hosts and geographical regions. Measurements in micrometers. Groups: A.a. MB, *Ariopsis assimilis*, Bacalar, Mexico; A.a. MC, *A. assimilis*, Chetumal Bay, Mexico; A.s. C, *A. seemani*, Colombia; A.s. P, *A. seemani*, Panama (holotype: CNHE 947); A.f. U, *Arius felis*, Florida, U.S.A. (holotype of *P. floridensis*: USNPC 60087).

shaped, 111–124 long by 115–147 wide. Ventral sucker small, equatorial, 35–44 long by 35–41 wide. Sucker ratio 1:0.31–0.34. Oral sucker armed with 1 circle of 27 spines; spines on dorsal side 21–28 long by 4–7 wide; on ventral side 15–21 long by 4–5 wide. Prepharynx 49–90 long; pharynx oval, 52–59 long by 36–52 wide; esophagus short. Intestinal ceca long, connected with excretory bladder near posterior extremity and opening outside by uroproct. Primordium of ovary postacetabular; testis primordia tandem, near posterior extremity.

HOSTS: *Dormitator latifrons* and *Gobiomorus maculatus* (both Perciformes: Eleotridae) (Table 3).

SITE: Liver, more rarely musculature of gills, mesentery, intestinal wall, occasionally muscles, heart, gonads, fins, scales.

GEOGRAPHICAL DISTRIBUTION: Mexico (state of Jalisco, Pacific coast).

Discussion

Acanthostomid trematodes from 3 different definitive hosts, the ariid catfish *Ariopsis seemani, A. assimilis,* and *Arius guatemalensis,* and 2 geographical regions (Colombia and Mexico) were found to be conspecific with *Pseudacanthostomum panamense.* Examination of the holotype of *P. panamense* has shown that the original description (Caballero et al., 1953) was incorrect in reporting the following characters: 1) 26 circumoral spines (there are in fact 27 spines in the holotype; Fig. 1A); 2) the absence of tegumental spines in the post-testicular region, which is actually spined; and 3) the absence of an uroproct (i.e., a connection of the intestinal ceca with the excretory bladder), which is actually present (Fig. 1D). Consequently, the species diagnosis of *P. panamense,* the type species of the genus *Pseudacanthostomum* Caballero, Bravo-Hollis, and Grocott, 1953, is emended accordingly.

In 1965, Nahhas and Short described another species, *P. floridensis,* to accommodate 2 specimens from *Galeichthys* (=*Arius*) *felis* from Florida, U.S.A. The authors differentiated this species from *P. panamense* by the number of circumoral spines (28 compared with 26), the greater extent of the vitellaria, and the presence of an uroproct.

The presence of an uroproct in *P. panamense* was not reported by Caballero et al. (1953), who stated that there is no connection between the intestinal ceca and excretory bladder ("Los ciegos intestinales . . . no se abren en la vesícula excretora" [p. 121] and "Los ciegos intestinales no desembocan a la vesícula excretora" [p. 122]). However, this study has demonstrated that an uroproct is in fact present in *P. panamense* (Fig. 1D). Consequently, *P. panamense* and *P. floridensis* do not differ in this character (Table 1).

Although the number of circumoral spines is fairly stable in acanthostomid trematodes and can be species-specific (Brooks, 1980), some

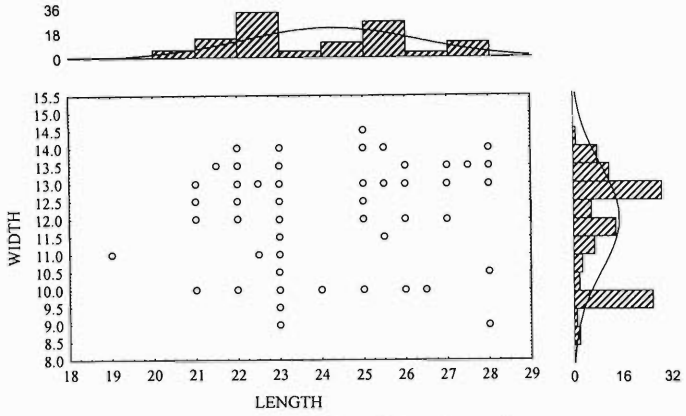

Figure 4. Range of size of eggs (length and width) of *Pseudacanthostomum panamense*. Measurements of all eggs measured (N = 59) grouped together. Values in micrometers.

variability apparently exists (Brooks and Overstreet, 1977; Ostrowski de Núñez, 1984; Scholz et al., 1995a, b). This is also the case in the present material (Table 2). Although a majority of specimens (93%) had 27 spines, including the holotype of *P. panamense* (see Results and Fig. 1A), a few specimens had a different number of spines. One trematode from *A. assimilis* from Bacalar (Mexico) possessed 26 spines, and 2 specimens from the same host (*A. assimilis*) from Chetumal (Mexico) had 28 spines (i.e., the identical number reported for *P. floridensis*) (Table 2).

The extent of distribution of vitelline follicles in the holotype of *P. floridensis* is actually more anterior than in *P. panamense* specimens. However, there is great variability in this feature. Trematodes from *Ariopsis seemani* have follicles reaching to the acetabular level (Fig. 1G) or even to the anterior margin of the ventral sucker (Fig. 1H), whereas those from *A. assimilis* have vitelline follicles mostly restricted to the postacetabular region (Fig. 1E, F) with vitelline follicles reaching to the posterior border of the ventral sucker in only a few specimens. It also seems that contraction of the body influences the position of follicles; in contracted specimens vitelline follicles usually reach to the acetabular level (Fig. 1G, H), whereas in protracted worms, the follicles start rather far posterior to the ven-

Table 3. Survey of hosts, localities, dates of collection, and parameters of infection with *Pseudacanthostomum panamense*.

Host	Country and locality	Date	No. of fish infected/ examined	Mean intensity	Minimum–maximum
Adults					
Ariopsis seemani	Colombia	5/96	4/7	1.5	1–2
Ariopsis assimilis	Bacalar, Quintana Roo, Mexico	1/95	1/1	12	—
	Chetumal Bay, Quintana Roo, Mexico	10/96	39/96	7.5	1–30
Arius guatemalensis	Marismas Chalacatepec, Jalisco, Mexico	3/95	3/3	24	9–52
Metacercariae					
Dormitator latifrons	Marismas Chalacatepec, Jalisco, Mexico	3/95	1/24	39	39
	Río San Nicolás, Jalisco, Mexico	11/94	1/5	52	52
		9/95	2/16	1	1
	Río Cuitzmala, Jalisco, Mexico	9/95	5/7	(not counted)	
Gobiomorus maculatus	Río Cuitzmala, Jalisco, Mexico	1/95	0/25	—	—
		3/95	2/37	3	1–5
		9/95	22/31	(not counted)	

tral sucker (Fig. 1E). It is evident that this character is not sufficiently stable and its taxonomic importance is questionable. Because *P. floridensis* was described on the basis of only 2 specimens, the anterior position of vitellaria should be confirmed in much more extensive material.

Statistical analysis of egg measurements has revealed a great intraspecific variability in egg length and width (Fig. 4). Nevertheless, this analysis has not demonstrated any significant differences in the length and width of eggs of *P. panamense* and *P. floridensis* (Fig. 3). Eggs of *P. panamense* specimens from Colombia were larger than those of conspecific worms from Mexico, thus being more similar to eggs of *P. floridensis* (Fig. 3). Because of the identity of *P. floridensis* with *P. panamense* in almost all morphological and biometrical characters (the distribution of vitelline follicles is considered a doubtful and unsuitable taxonomic criterion for differentiation of these taxa), the former species is synonymized with *P. panamense.*

On the basis of the proposed synonymy, the genus *Pseudacanthostomum* becomes monotypic, currently containing only 1 species, *P. panamense.* In the presence of an uroproct, *P. panamense* resembles members of the genus *Pelaezia* Lamothe-Argumedo and Ponciano-Rodríguez, 1986, of the subfamily Acanthostominae Nicoll, 1914 (see Lamothe-Argumedo and Ponciano-Rodríguez, 1986). However, *Pelaezia* differs, as all other genera of the Acanthostominae, in that the uterus is never situated posterior to the testes (mostly completely preovarial), whereas its loops reach to the posterior extremity in *Pseudacanthostomum,* the type genus of the subfamily Pseudacanthostominae Yamaguti, 1958. In addition, both species of *Pelaezia, P. unami* (Peláez and Cruz-Lozano, 1953), the type species, and *P. loossi* (Pérez-Vigueras, 1957), have different numbers of circumoral spines (30 and 23, respectively; Peláez and Cruz-Lozano, 1953; Pérez-Vigueras, 1957; Brooks, 1980; Salgado-Maldonado and Aguirre-Macedo, 1991).

The subfamily Pseudacanthostominae Poche, 1926 contains only 2 genera, *Pseudacanthostomum* and *Pseudallacanthochasmus* Velasquez, 1961, members of which parasitize marine fish in the Americas and Southeast Asia, respectively (Yamaguti, 1971). This subfamily differs from the Acanthostominae in possessing a long prepharynx (Yamaguti, 1971, p. 212). However, as demonstrated in this study, the prepharynx is usually short or even absent (Fig. 2A, F) in many *P. panamense* specimens. Moreover, the length of the prepharynx is highly variable, depending mainly on the state of contraction of the worms. Therefore, this feature should not be used as a differential criterion for the diagnosis of this subfamily. In other features, the subfamiliar diagnosis presented by Yamaguti (1971)—i.e., the uterus extending to the posterior extremity (different from other acanthostomid subfamilies except for Anisocladiinae Yamaguti, 1958)—the ceca being equal and reaching to the posterior extremity, the ventral sucker being well apart from the anterior extremity, and the vitelline follicles being both anterior and posterior to the ovary (differing from Anisocladiinae) well characterize the subfamily Pseudacanthostominae.

Metacercariae found in eleotrid fishes from the Pacific coast of Mexico are considered to be conspecific with *P. panamense* because of their morphology (Fig. 2E, H, I), in particular the presence of 27 circumoral spines (Fig. 2H, I) and the morphology of the intestinal ceca, which are connected with the excretory bladder near the posterior extremity, thus forming an uroproct (Fig. 2E). This is the first record of *P. panamense* from the second intermediate host. It can be assumed that the life cycle of this taxon resembles that of other acanthostomid trematodes (Yamaguti, 1975). The first intermediate host is a mollusk (snail), in which the cercariae develop; the second intermediate hosts are fish in which the metacercariae are encysted. The definitive host, an ariid catfish, becomes infected by ingesting fish with metacercariae. *Dormitator latifrons* and *Gobiomorus maculatus* are fish living in brackish water, i.e., in the same habitat in which ariid catfish occur; the latter become infected after consuming prey fish harboring metacercariae.

Pseudacanthostomum panamense seems to be a common parasite of catfishes of the family Ariidae. Existing records of *P. panamense* from the southern U.S.A. (Florida), Mexico (both Atlantic and Pacific coasts), Panama (Pacific coast), and Colombia indicate that it is a species with a wide distribution in the Neotropical zoogeographical region on both the Pacific and Atlantic coasts.

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Ultrastructure of the Female Reproductive System of the Lesion Nematode, *Pratylenchus penetrans* (Nemata: Pratylenchidae)

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ABSTRACT: Transmission electron microscopy of the reproductive system of adult females of *Pratylenchus penetrans* (Cobb) Filipjev and Schuurmans Stekhoven revealed details of oocyte development and the transformation of oocytes into eggs. Oogonial cell divisions were not observed; however, oogonial development into oocytes was distinctive in that most of the nuclei of ovarian cells were in the pachytene stage (i.e., prophase I of meiosis). In the midsection of the ovary, the oocytes increase in number, enlarge, and accumulate in a single row. Next, the oocytes enter a muscular oviduct and begin to accumulate lipid bodies and protein granules. The plasma membrane of the oviduct becomes plicated and forms cisternae; centralized membrane junctions establish openings for oocytes to enter the spermatheca. Spermatozoa traverse the lumen of the uterus and accumulate in the spermatheca. Each oocyte then passes through the spermatheca proximally and then traverses between columnar cells. The posteriad regions of the columnar cells attach to other uterine cells to form the central lumen of the uterus that extends beyond the vaginal opening and into the postvulvar uterine branch of the reproductive system. The fertilized egg is deposited to the exterior after passing between cuticle-lined vaginal and vulval walls supported by anteriad and posteriad muscle bands, which have ventrosublateral insertions on the body wall.

KEY WORDS: transmission electron microscopy, lesion nematode, female reproductive system, *Pratylenchus penetrans*, Nemata, Pratylenchidae.

The lesion nematodes, *Pratylenchus* spp., are among the most destructive plant pathogenic nematodes world-wide (Mai et al., 1977; Dropkin, 1989; Zunke, 1990a). Dropkin (1989) reviewed the disease symptoms and pathogenesis of *Pratylenchus* species, which occur as single parasites or in combination with other pathogens. The ectoparasitic and endoparasitic feeding behavior of *Pratylenchus penetrans* (Cobb, 1917) Filipjev and Schuurmans Stekhoven, 1941, has been studied using video-enhanced contrast light microscopy (Zunke and Institut für den Wissenschaftlichen Film, 1988; Zunke, 1990b) and transmission electron microscopy (TEM) (Townshend et al., 1989). Light microscopic studies also have described embryogenesis and postembryogenesis, including the molting process and the development of the reproductive system, in several species of *Pratylenchus* (Roman and Hirschmann, 1969a, b). In a related study of *Ditylenchus triformis,* Hirschmann (1962) illustrated the development of male and female reproductive systems during postembryogenesis, beginning with the genital primordium. Recently, we used TEM to describe the general anatomy of *P. penetrans* (Endo et al., 1997) and the development of the testis, including the production and morphology of spermatozoa (Endo et al., 1998). These observations complement extensive studies on spermatogenesis and sperm ultrastructure of various species of cyst nematodes (Shepherd et al., 1973; Cares and Baldwin, 1994a, b, 1995). To extend these studies, TEM was used to describe the ultrastructure of the female reproductive system of *P. penetrans,* with emphasis on oocyte development in the ovary and the morphology of the oviduct, spermatheca, columnar cells, and central uterus. The studies of development of the eggs include evaluation of egg shell depositions in the uterus and the vaginal and vulval muscle morphology as they relate to egg laying.

Materials and Methods

Infective and parasitic stages of *P. penetrans* were obtained from root cultures of corn (*Zea mays* Linnaeus 'Ichief') grown in Gamborg's B-5 medium without cytokinins or auxins (Gamborg et al., 1976). Adults and juveniles were collected from infected root segments that were incubated in water. The samples were prepared for electron microscopy as previously described (Endo and Wergin, 1973; Wergin and Endo, 1976). Briefly, nematodes, which were embedded in 2% water agar or in infected roots, were chemically

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fixed in buffered 3% glutaraldehyde (0.05 M phosphate buffer, pH 6.8) at 22°C for 1.5 hr, washed for 1 hr in 6 changes of buffer, postfixed in buffered 2% osmium tetroxide for 2 hr, dehydrated in an acetone series, and infiltrated with a low-viscosity embedding medium (Spurr, 1969). Silver-gray sections were cut on an ultramicrotome with a diamond knife and mounted on uncoated 75 × 300 mesh copper grids. The sections were stained with uranyl acetate and lead citrate and viewed in a Philips 400T® electron microscope operating at 60 kV with a 30-μm objective aperture.

Results

The female reproductive system of *P. penetrans* has amphidelphic development during early stages of postembryogenesis. However, later in the adult development, the posterior region of the ovary becomes reduced to a postvulvar uterine branch (Fig. 1). This change results in a telogonic gonad having a prodelphic orientation and a short postvulvar uterine branch that consists of epithelial cells. The cells in the anterior terminus of the ovary have spheroid nuclei, numerous polyribosomes, and high concentrations of rough endoplasmic reticulum (RER), mitochondria, Golgi, and electron-dense granules (Fig. 2 on Foldout 1). These germinal cells are completely ensheathed by spindle-shaped epithelial cells (Figs. 2, 3, 5, 6 on Foldout 2) that lie adjacent to and between the ovarian cells. In longitudinal view, the anterior gonad occupies about half the diameter of the body cavity (Figs. 1, 6, 7). Nuclear divisions of oogonia were not observed in the specimens studied. However, as the ovarian cells increase in number and size, the germ cells contribute to a double row of overlapping oogonia (Figs. 3–5). Posteriorly, oocytes occur in a single row in the ovary and attain a slightly larger size than the germinal cells in the anterior region (Figs. 6–8 on Foldout 3). The cellular organelles of the oocytes found in the midregion and proximal sites of the ovary are similar to those present in the oogonia (Figs. 2–5). The well-defined nuclei of oocytes in the midregion of the ovary contain fragments of synaptonemal complexes, indicating that the oocytes are at the pachytene stage of prophase I (Figs. 4, 5). The synaptonemal complex is a tripartite structure consisting of a central scalariform element and a pair of lateral elements. This complex is surrounded by condensed chromatin (Fig. 5). The nucleoli are prominent, large, and electron-dense (Figs. 3, 5–7). Nuclei occupy a major part of the enlarged volume of oocytes in the proximal region of the ovary (Fig. 7). In actively reproducing females, oocytes near the anterior entrance of the oviduct or within the oviduct channel have an accumulation of electron-translucent lipid droplets (Fig. 10).

Oviduct

The oviduct (Fig. 11 on Foldout 4) consists of a series of irregularly shaped cells having plicated plasma membranes. Although adjacent cells are generally separated by many intercellular spaces, membrane junctions interconnect the cells and allow for the extensive opening of the oviduct that is required during passage of the enlarged oocytes. Muscle filaments are associated with most of the cells along the length of the oviduct (Fig. 9). Oviduct cells contain mitochondria and nuclei with irregularly shaped nuclear membranes lined with electron-dense chromatin. The cells occupy the ventral region of the body cavity and lie adjacent to the intestinal epithelium (Fig. 11). In the distal portion of the oviduct, the cells are more tightly packed and have centrally located membrane junctions (Fig. 12). In this region, the cells are not associated with muscle filaments. These closely arranged cells appear to function as a valve for the entry of oocytes into the spermatheca. Sperm were not observed on this side of the spermatheca.

Spermatheca

The terminal cells of the oviduct are attached closely to spindle-shaped cells of the spheroid spermatheca (Fig. 11). Membranes of the cells of the spermatheca are joined together with prominent lateral membrane junctions. Spermatozoa in the center of spermatheca have prominent masses of chromatin that are surrounded by clusters of mitochondria and widely dispersed fibrillar bundles (Fig. 11). These structures are similar to the major sperm protein bodies that have been identified and described in other nematode species (Shepherd et al., 1973). The spermatozoa seem to be suspended in a moderately electron-dense fluid similar in appearance to the contents of the vas deferens of males. The posteriad boundary of the spermatheca joins a series of columnar cells of the uterus (Figs. 11, 13).

Columnar cells of the uterus

Columnar cells leading posteriad from the spermatheca have plicated limiting membranes (Fig. 15 on Foldout 5) similar to those of cells in the oviduct (Fig. 8) but differing by the ab-

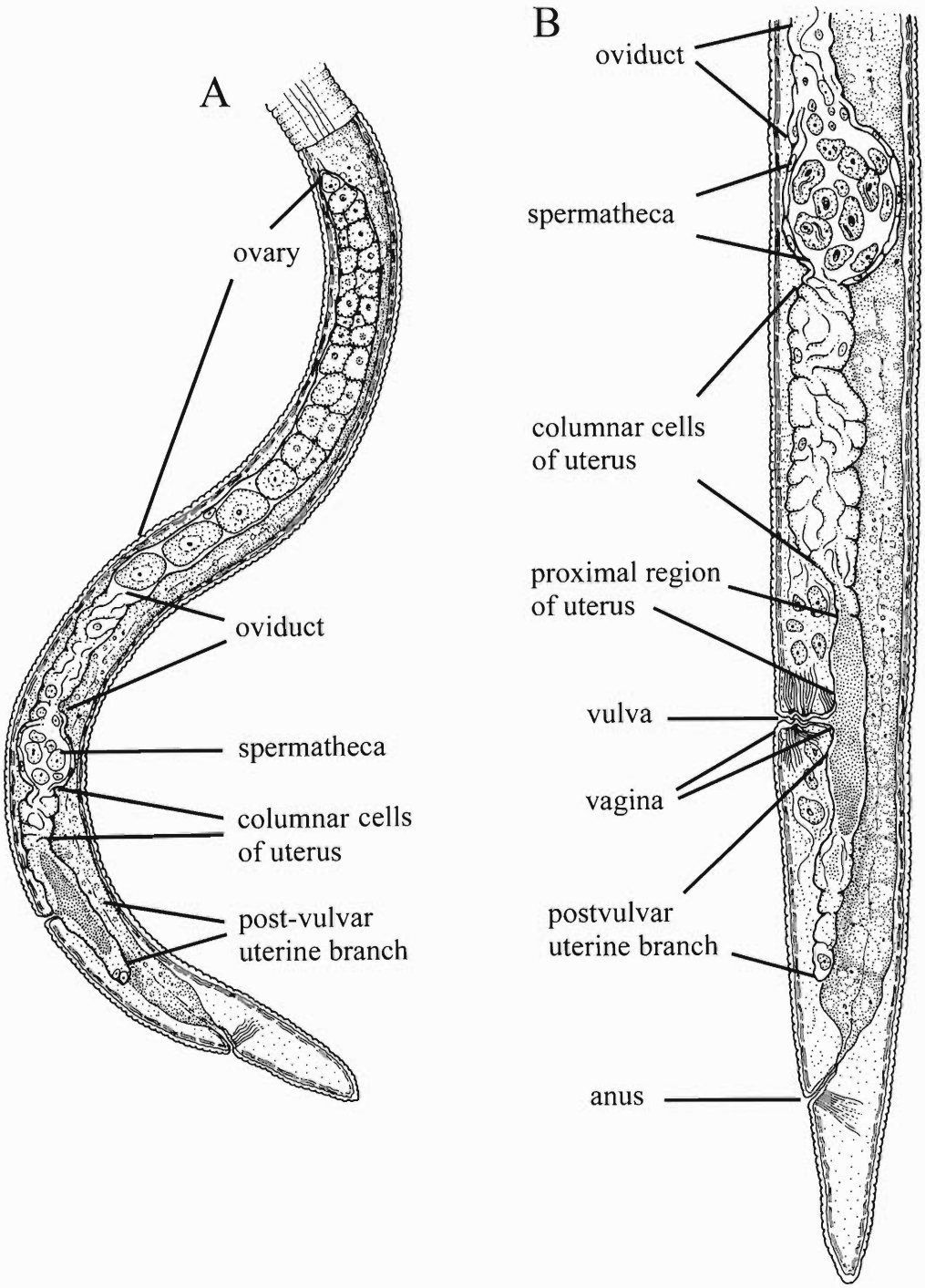

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Figure 1. Line drawings of the female reproductive system of *Pratylenchus penetrans*, illustrating the features of pseudomonodelphic reproductive development. (A) Anterior region of the gonad containing oogonial cells and oocytes in growth phase. (B) Posterior region of the reproductive system showing a postvulvar uterine branch. Posteriad to the oocytes are the oviduct, spermatheca, columnar cells of the uterus, and the vaginal-vulval regions.

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Figure 2. Distal region of the ovary of *P. penetrans* showing 3 enlarged distal cells. Germinal cells (GC) are precursors to oocyte development. Cells of the gonad epithelium lie adjacent to linearly arranged germ cells (i.e., oogonia and oocytes). GEN, gonad epithelium nucleus; M, mitochondria. (Note: In this and in later longitudinal figures that are illustrated with fold-outs (Figs. 2, 6, 8, 11, 15, 20), the proximal or left axis is toward the head of the nematode, whereas the distal or right axis is toward the tail. In the longitudinal sections that are illustrated in the single plates, the head to tail orientation is top to bottom.)

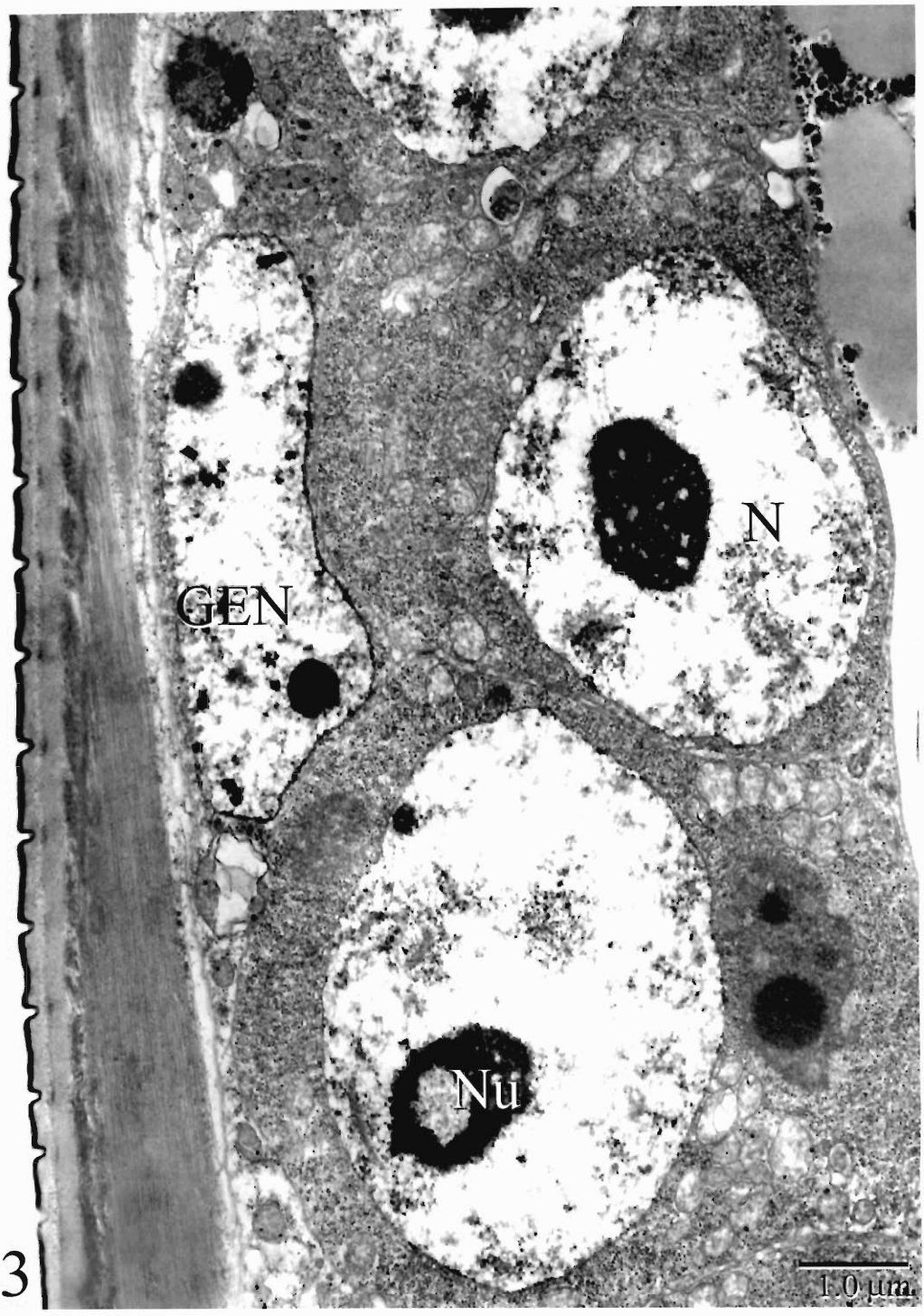

Figure 3. Longitudinal section through oocytes of *P. penetrans* in the region of their growth phase. Nucleoplasm with fragments of chromatin and electron-dense nucleolus (Nu). GEN, gonad epithelium nucleus; N, oocyte nucleus.

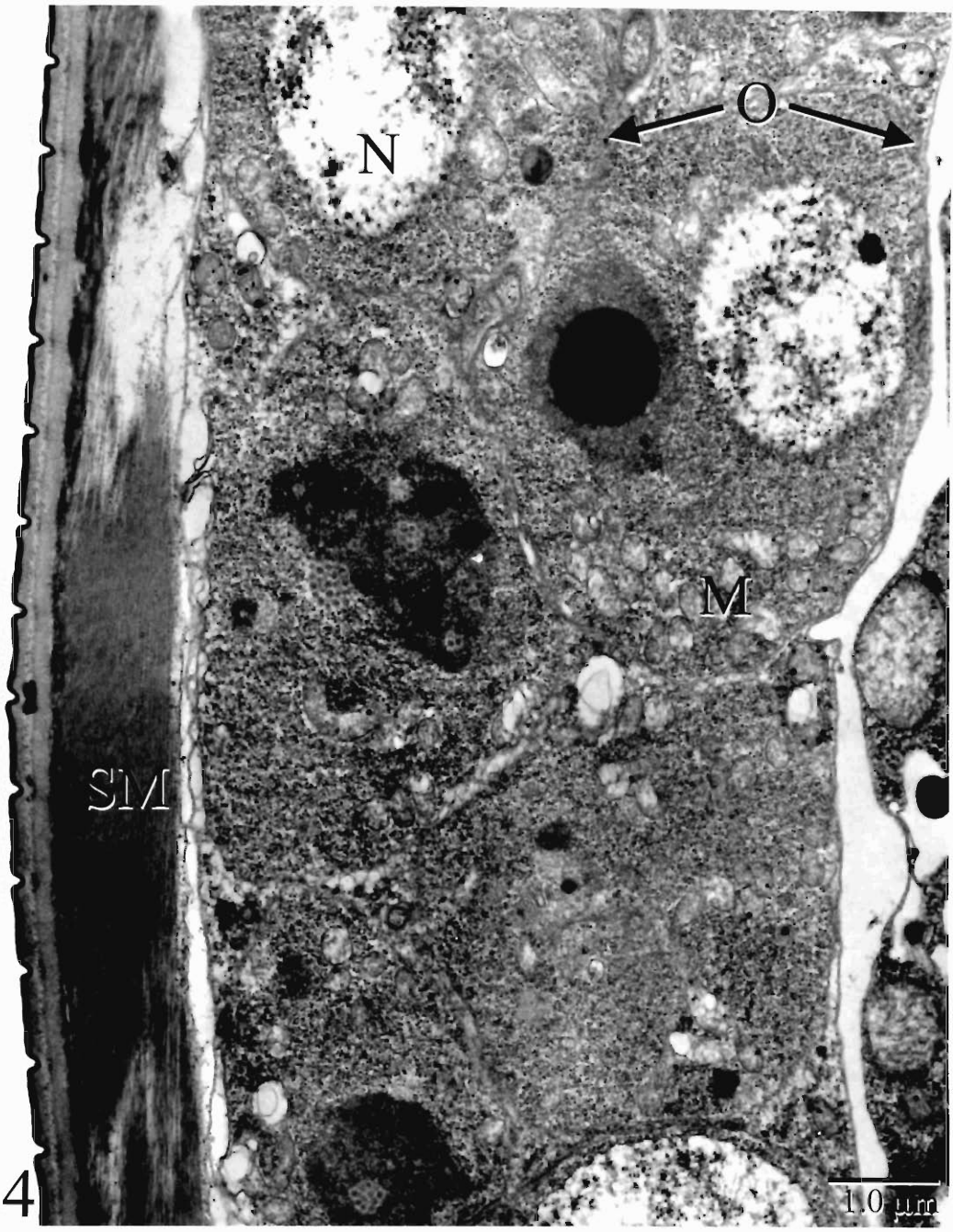

Figure 4. Longitudinal, submedian section of ovary of *P. penetrans* showing oocytes (O) during initial stages of meiosis. M, mitochondria; N, nucleus; SM, somatic muscles.

sence of muscle filaments within their cell boundaries. Membrane junctions between cells near the spermatheca define the region in which a lumen may form during oocyte passage (Fig. 13). However, a preformed lumen is not apparent. In this region, the spermatozoa may be displaced from the spermatheca as the oocyte moves through the central part of the uterus.

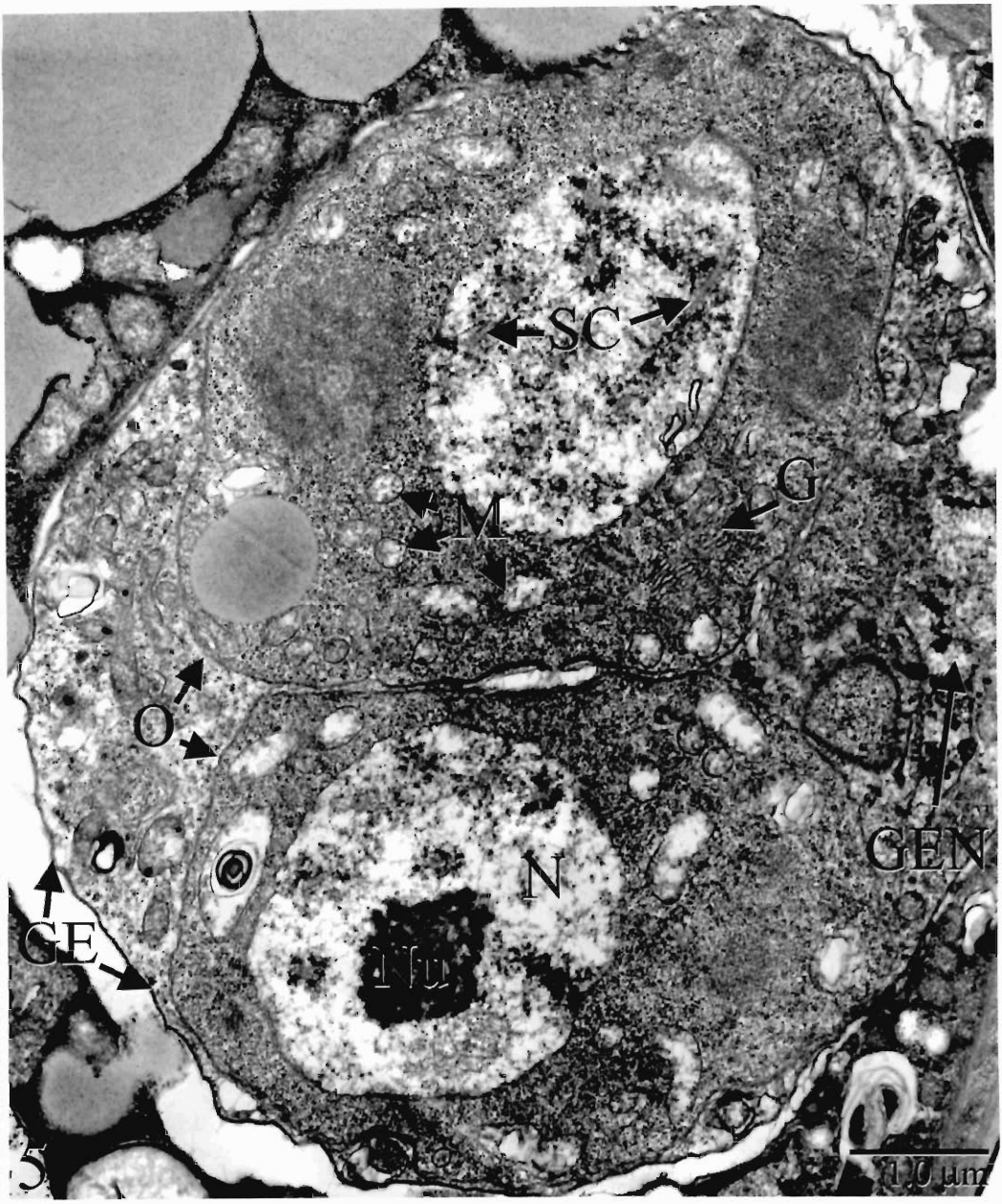

Figure 5. Transverse section of midregion of an ovary of *P. penetrans*, showing oocytes at pachytene stage of meiosis. Oocytes (O) are surrounded by gonad epithelial cells (GE), whose cytoplasm extends between the germinal cells. GEN, gonad epithelium nucleus; G, Golgi apparatus; M, mitochondria; Nu, nucleolus; N, nucleus; SC, synaptonemal complex.

When this occurs, the invagination of the plasma membrane of the columnar cell results in a spermatozoan that appears to have a double membrane (Fig. 13). Fertilization was not evident in the oocytes observed. Columnar cells of the uterus have dense clusters of mitochondria and numerous polyribosomes throughout the cytoplasm (Figs. 13, 15). The distal columnar cells of the uterus contain relatively large clusters of electron-dense material (Fig. 15). The lumen,

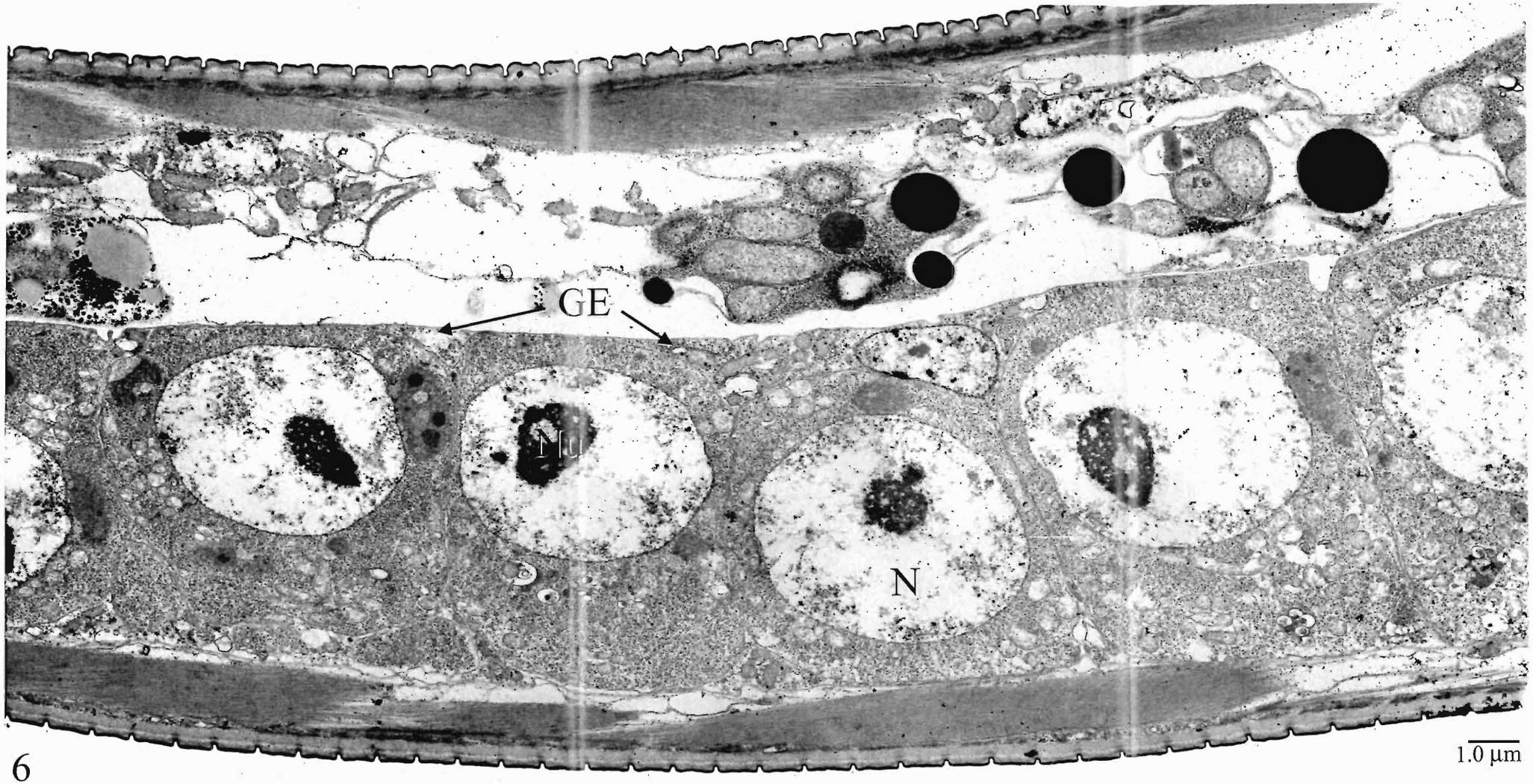

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Figure 6. Longitudinal section of the proximal region of the ovary of *P. penetrans*, illustrating growth stage of oocytes. GE, gonad epithelium; Nu, nucleolus; N, nucleus.

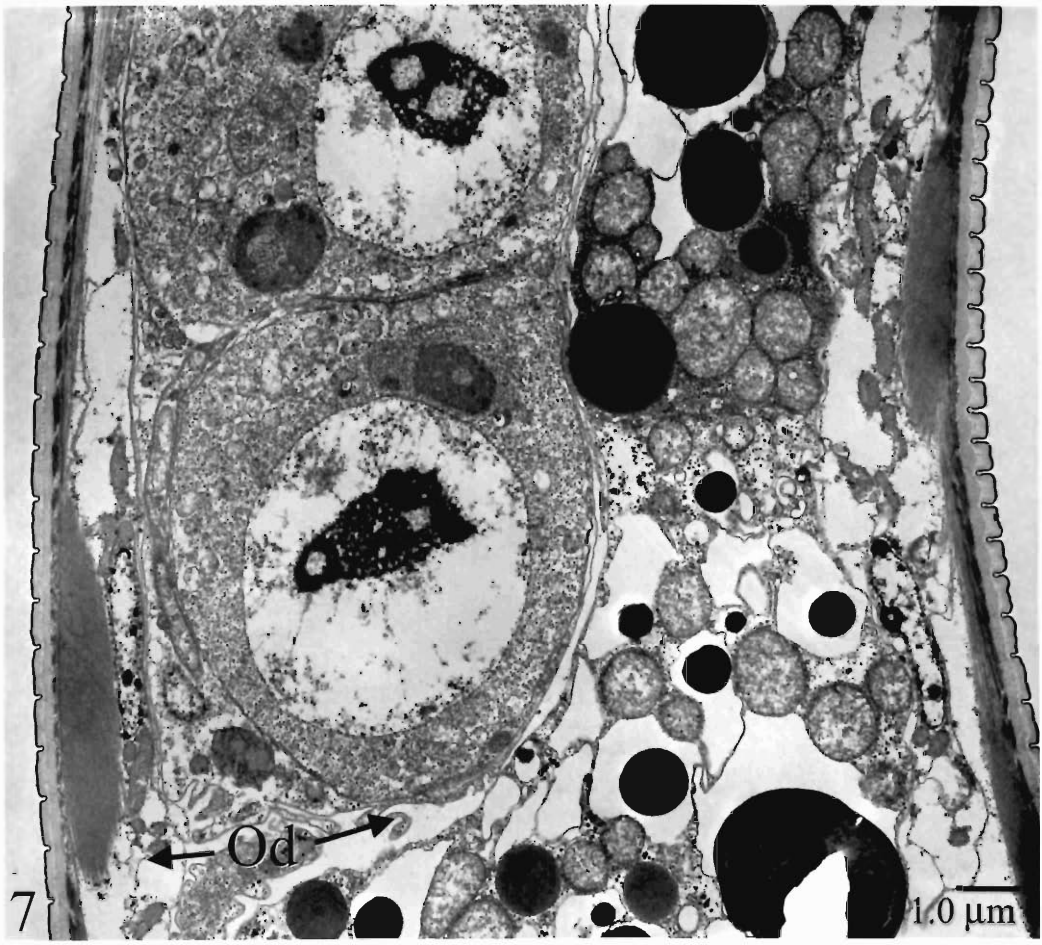

Figure 7. Longitudinal section of oocytes in proximal region of ovary of *P. penetrans*. An oocyte lies adjacent to the plicated cell membrane of the oviduct (Od).

which forms as the egg passes into the columella, merges with the central, fluid-filled channel of the uterus (Fig. 15). The main channel of the uterus continues posteriad as a flattened or collapsed region that extends across the ventral sector of the body, terminating in a postvulvar uterine branch (Figs. 17–19). The uterus opens ventrally through the cuticle-lined vagina and vulva (Fig. 16).

Egg passage

The traversing of an oocyte or egg through the spermatheca or between columnar cells compresses epithelial cells (Figs. 14, 20 on Foldout 6). In the absence of an egg within the uterus, the abundance of mitochondria and ribosomes and the occurrence of scattered secretory globules suggest that the columnar cells are metabolically active (Fig. 15). In the presence of an egg in the uterine channel, secretory granules occur intracellularly in compressed regions of uterine cells and extracellularly in the space between the surface of the egg and the limiting membrane of the columnar cells (Fig. 20). The accumulated secretory granules appear to contribute to the electron-dense deposits that form the egg shell. These deposits (Figs. 20, 21 on Foldout 6) accumulate on the vitelline layer, which is derived from the oolemma and has a unit membrane-like structure. Just below the vitelline layer is a chitinous layer followed by a lipid layer. The egg shell appears to be separated from the egg cytoplasm by a unit membrane. Tangential sections through the egg revealed

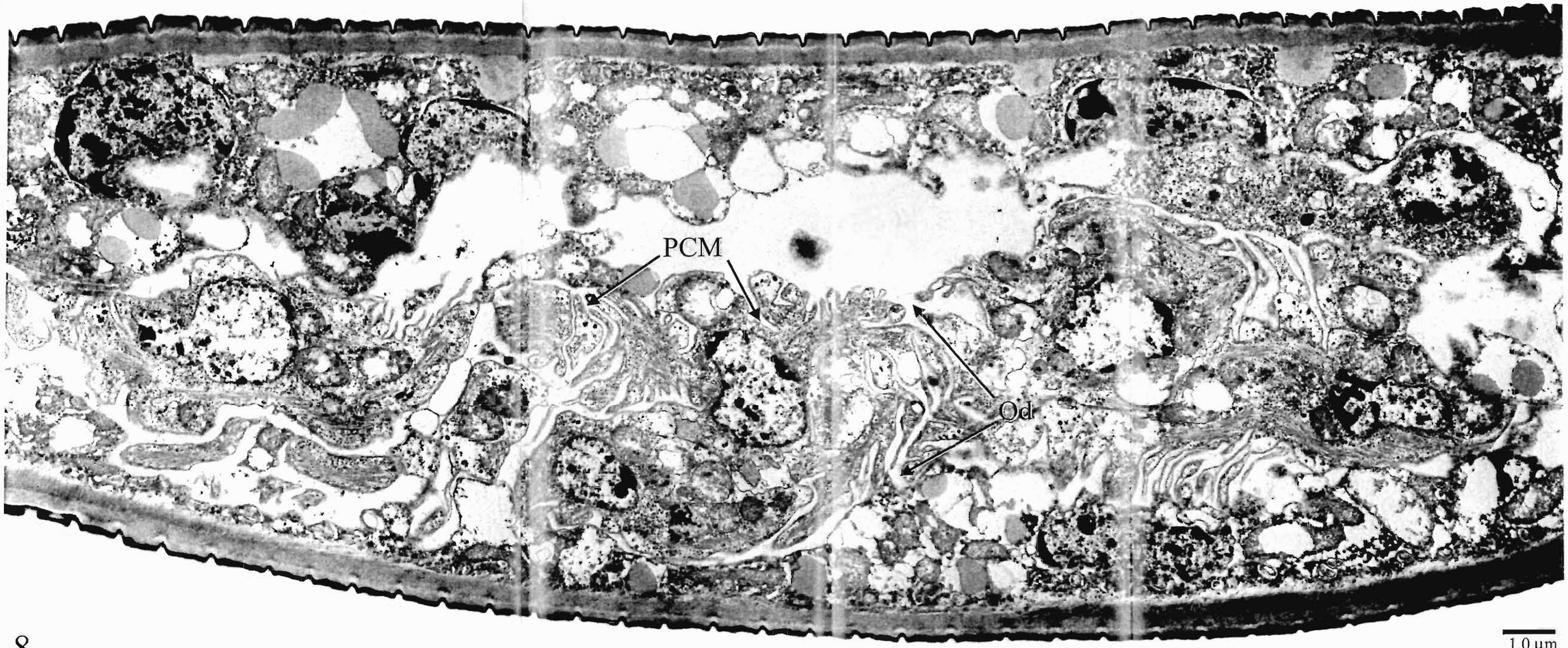

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Figure 8. Longitudinal section of oviduct of *P. penetrans*. Plicated cell membranes (PCM) form cisternae-like invaginations among the enlarged irregularly shaped cells along the oviduct (Od), which lacks a preformed lumen.

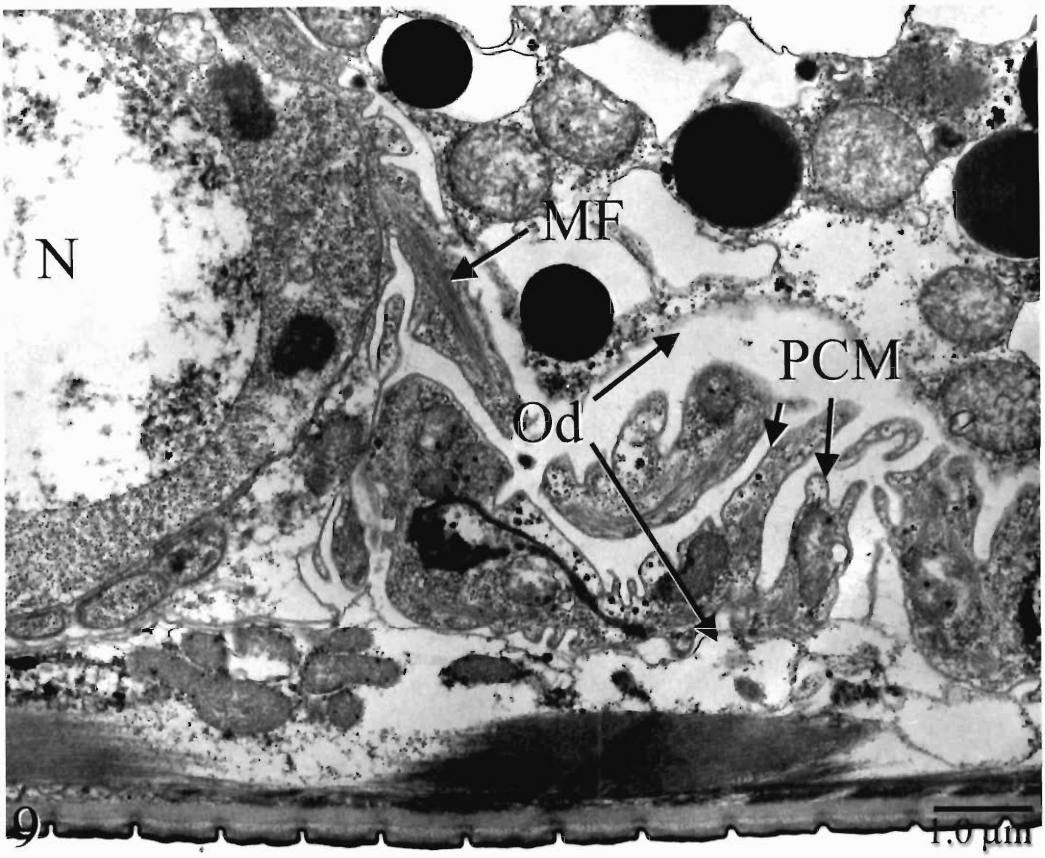

Figure 9. Longitudinal section of *P. penetrans* showing the junction between an oocyte and the oviduct (Od) supported by plicated cell wall membranes (PCM). Some cells with plicated membranes are associated with muscle filaments (MF). N, nucleus.

electron-transparent lipid bodies, numerous electron-dense protein granules (Fig. 20), and the sperm or egg nucleus, which contains prominent chromatin (Figs. 20, 22 on Foldout 6).

The vaginal-vulvar region

The wall of the vagina is continuous with the body cuticle (Fig. 16). Hemidesmosomes attach pairs of broad muscle bands to anteriad and posteriad portions of the vulva cuticle. These 4 fiber bands extending anteriad are believed to correspond to the anterior dilatores vulvae, whereas the posteriad muscle fibers are the posterior dilatores vulvae (Fig. 16). The muscle bands project ventrolaterally and connect with somatic muscles along the body cuticle (Fig. 17). Adjacent and internal to the vulva wall muscles is a broad band of sphincter muscles or the constrictor vaginae. Adjacent and dorsal to the constrictor muscles are the anterior and posterior dilatores vaginae (Fig. 16). The cuticle of the vaginal wall is continuous with the ventral lining of the uterine channel.

Anal region

The body wall cuticle forms the lining of the anus and invaginates into the body cavity to form the lining of the rectum, which extends dorsoanteriad and subterminally into the tail region (Fig. 23). Proximally, the cuticular rectal channel is flat and broad (Fig. 25); distally it becomes elongate and oblong (Fig. 24). The noncuticularized region of the lumen is supported by rectal cells. The lumen may also be occluded by membrane evaginations of rectal cells joined laterally by membrane junctions. The H-shaped conformation of cells surrounding the rectum (Figs. 24, 25) coincides with the position

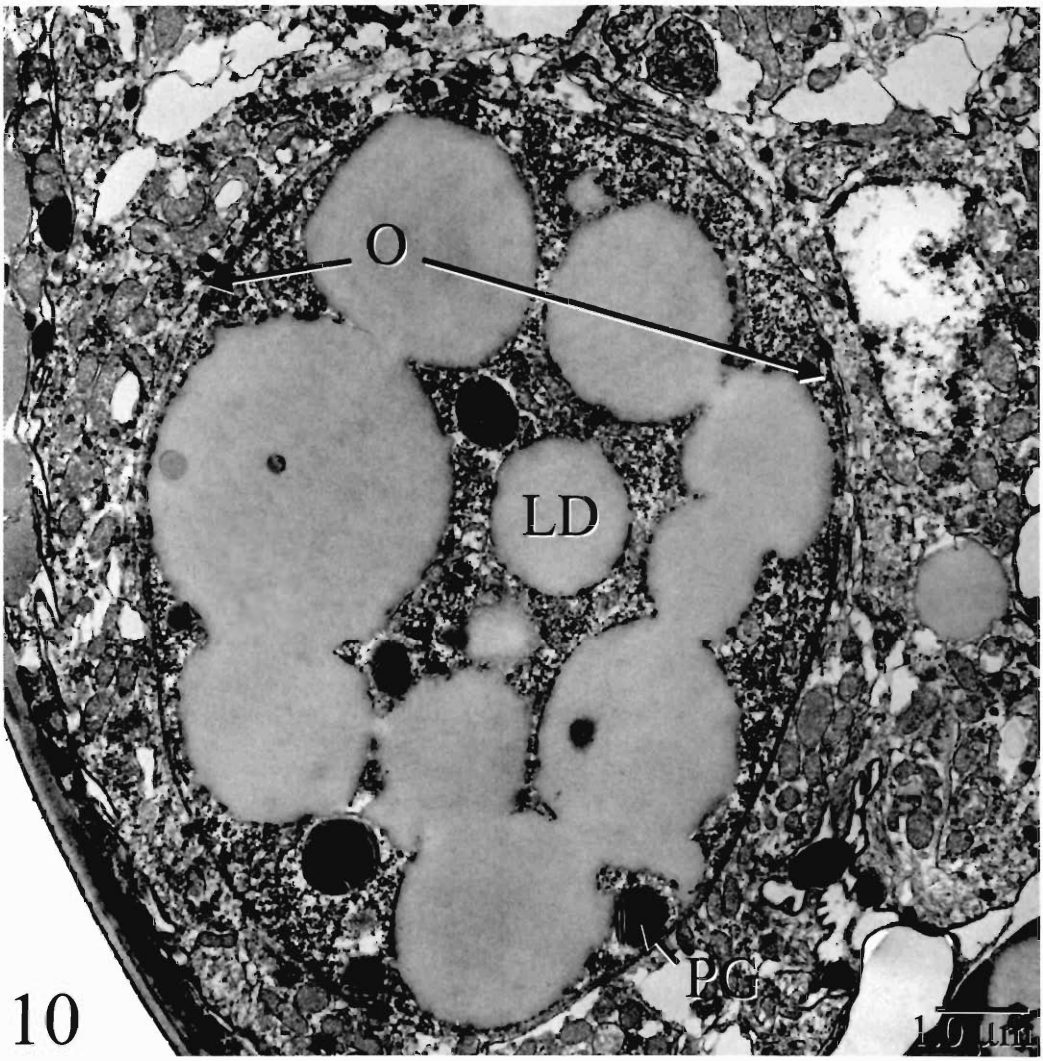

Figure 10. Transverse section of an oocyte (O) within the oviduct of *P. penetrans*. The oocyte is filled with large merging lipid droplets (LD) and a few protein granules (PG) that lie within the cytoplasmic matrix.

of the depressor ani muscles that connect the dorsal rectal cuticle to the dorsal lateral body cuticle via hemidesmosomes.

Discussion

In a study of postembryogenesis, Roman and Hirschmann (1969a) determined that several species of *Pratylenchus,* including *P. vulnus, P. coffeae, P. penetrans, P. brachyurus, P. zeae, P. neglectus,* and *P. crenatus,* have an amphidelphic pattern of gonad development. However, the monosexual species *P. scribneri* follows a monodelphic pattern. In the amphidelphic species, 2 gonads develop until the fourth molt, then the posterior gonad deteriorates. The remaining gonad is prodelphic, similar to that of *P. penetrans.* The distal end of the telogonic gonad is occupied by an ovary with a short germinal zone and an elongated growth zone. The germinal zone contains oogonial cells that undergo rapid mitotic divisions. In the growth zone, the oocytes enlarge. The ovary is followed by a narrowly folded oviduct that is connected to the spermatheca by a 12-celled constriction (Roman and

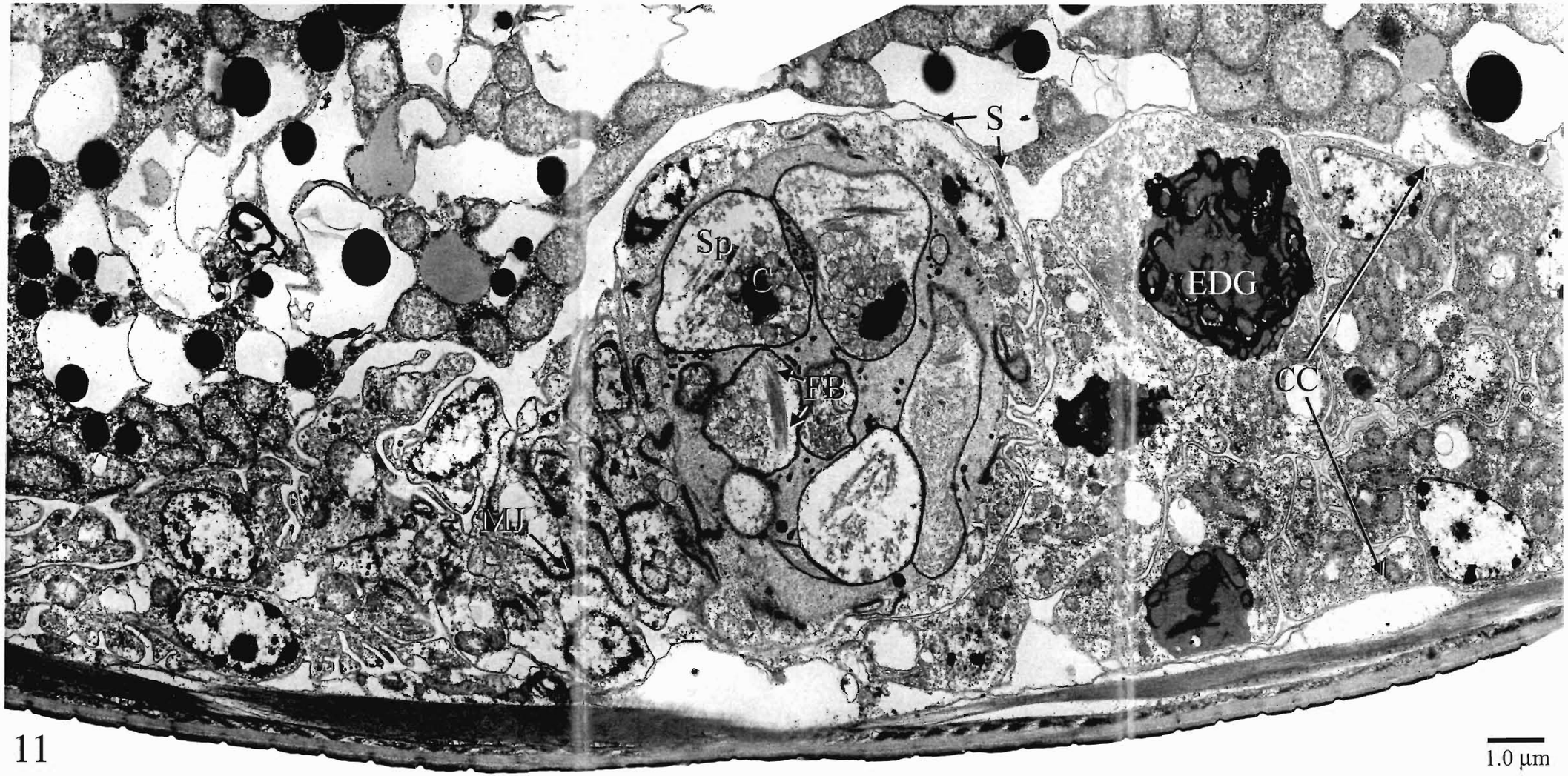

Figure 11. Longitudinal section of spermatheca of *P. penetrans*. The anterior boundary of the spermatheca (S) is surrounded by epithelial cells that are joined by membrane junctions (MJ). Spermatozoa (Sp) within the spermatheca contain electron-dense chromatin (C), mitochondria, and fibrillar bundles (FB). The posteriad boundary of the spermatheca merges with enlarged columnar cells (CC) of the uterus. Columnar cells near the spermatheca contain enlarged electron-dense globules (EDG), numerous mitochondria, and ribosomes.

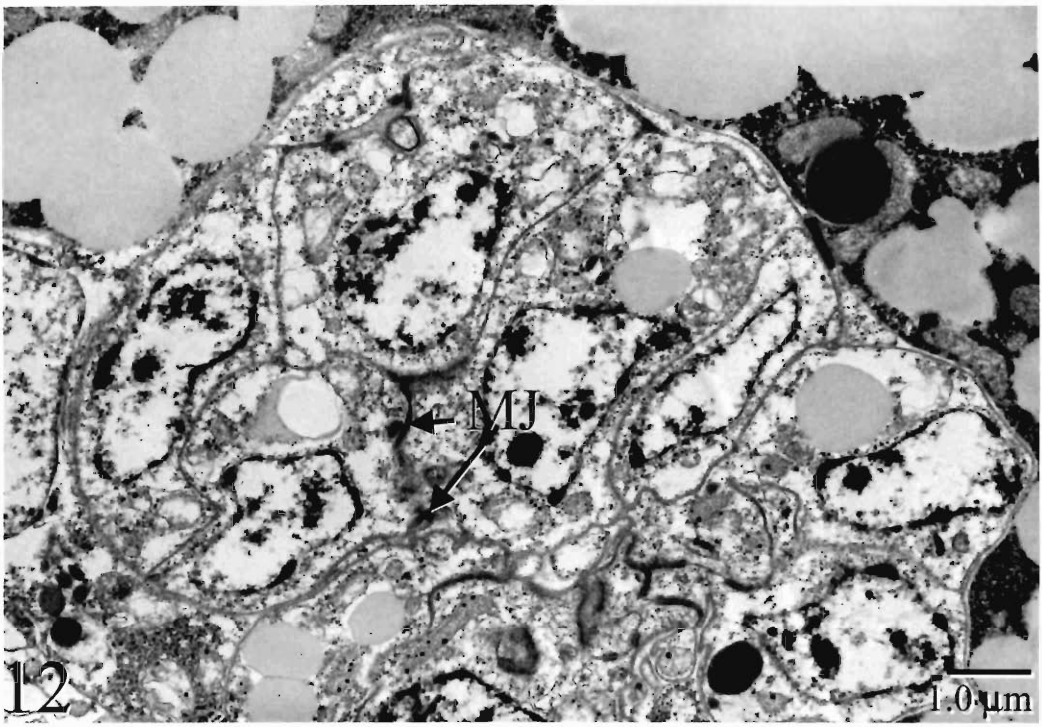

Figure 12. Transverse section through cells at the proximal region of the oviduct and anterior region of the spermatheca of *P. penetrans*. Membrane junctions (MJ) join adjacent cells so that a lumen is formed for the oocyte passage into the spermatheca.

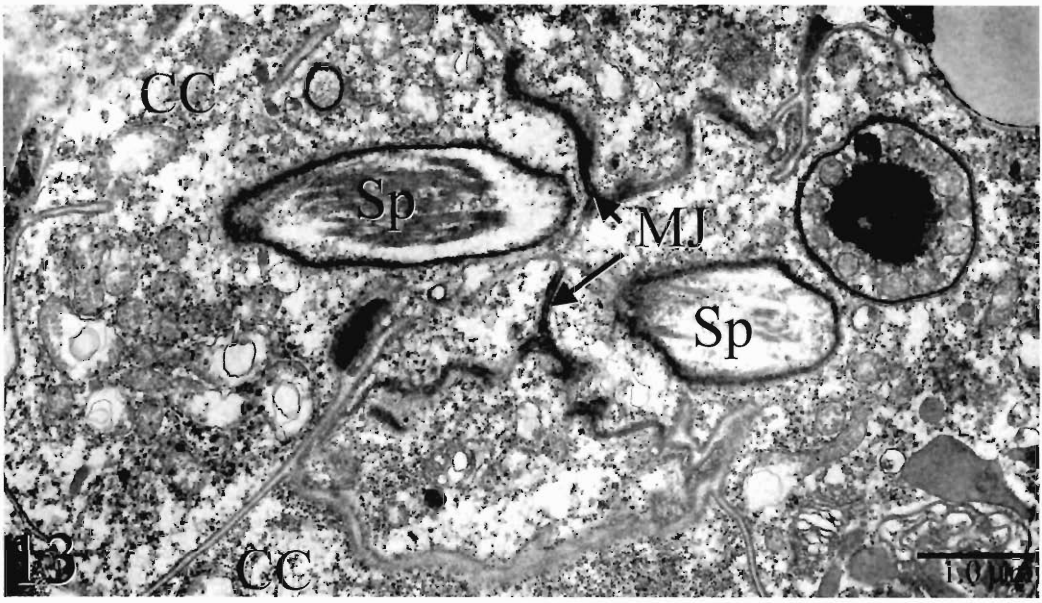

Figure 13. Transverse section near the posteriad region of the spermatheca of *P. penetrans*. Spermatozoa (Sp) appear to be outside the spermatheca and in the invaginated boundaries of the columnar cells (CC). Membrane junctions (MJ) result in adjoined cells that will form the lumen for egg passage.

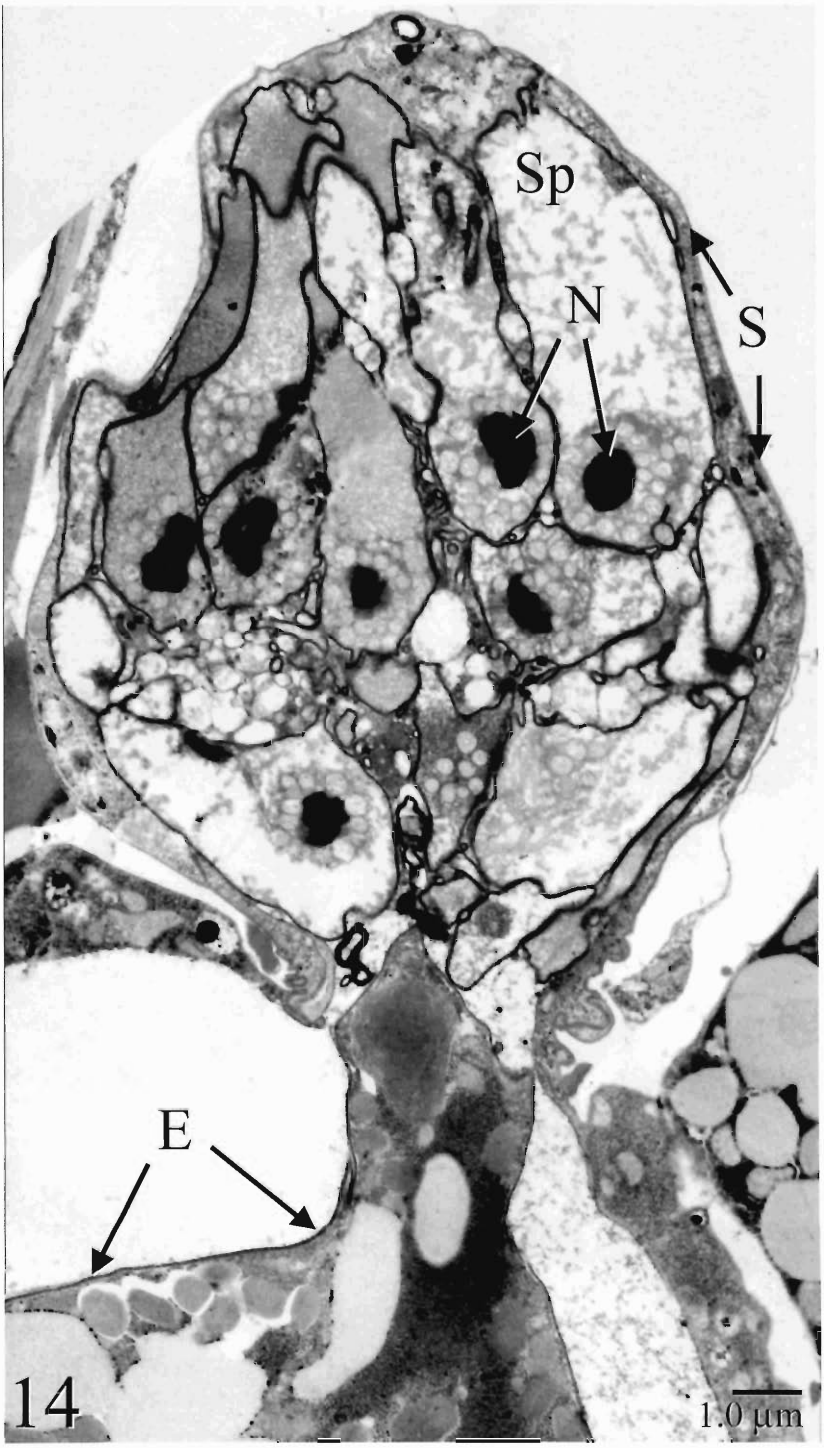

Figure 14. Longitudinal section of an egg emerging from a spermatheca in a female *P. penetrans*. Spermatozoa (Sp) remaining in spermatheca (S) after oocyte passage appear to be oriented toward the emerged egg (E). Their electron-dense nuclei (N) and mitochondria adhere to the internal surface of the leading membrane of the spermatozoa. The membrane trailing the major body of the egg is intact and clearly separated from the spermatheca and its contents.

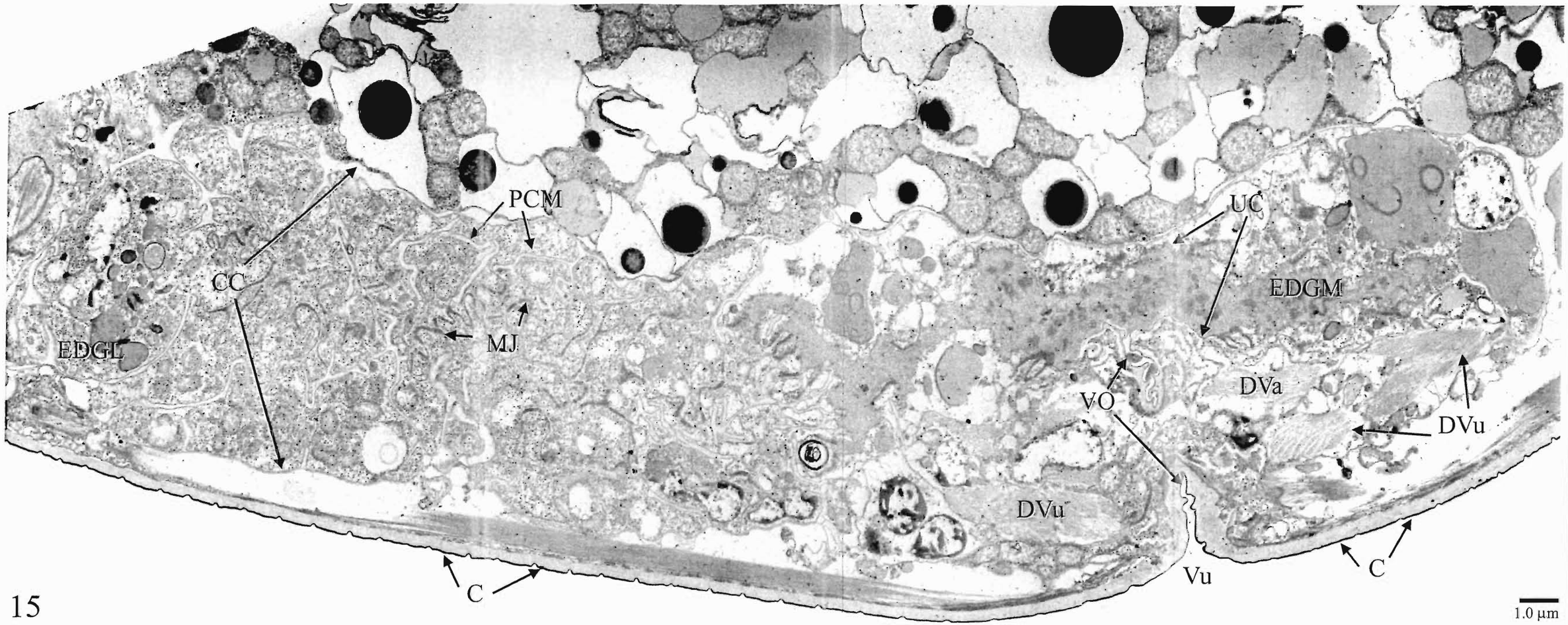

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Figure 15. Submedian longitudinal section of columnar cells (CC) that delineate the lumen in the distal region of the uterus. The uterine channel (UC) posteriad from the columnar cells is filled with electron-dense granular material (EDGM) that extends from beyond the vagina into the postvulvar uterine region of the reproductive system. This submedian section illustrates the continuity of the lining of the vaginal lumen (VO) with the body wall cuticle (C), but not with the lumen of the uterus. Tangential sections show muscle fibers that belong to the dilatores vaginae (DVa) and dilatores vulvae (DVu), which play a major role in egg deposition. EDGL, electron-dense globules; MJ, membrane junctions; PCM, plicated cell membranes; Vu, vulva.

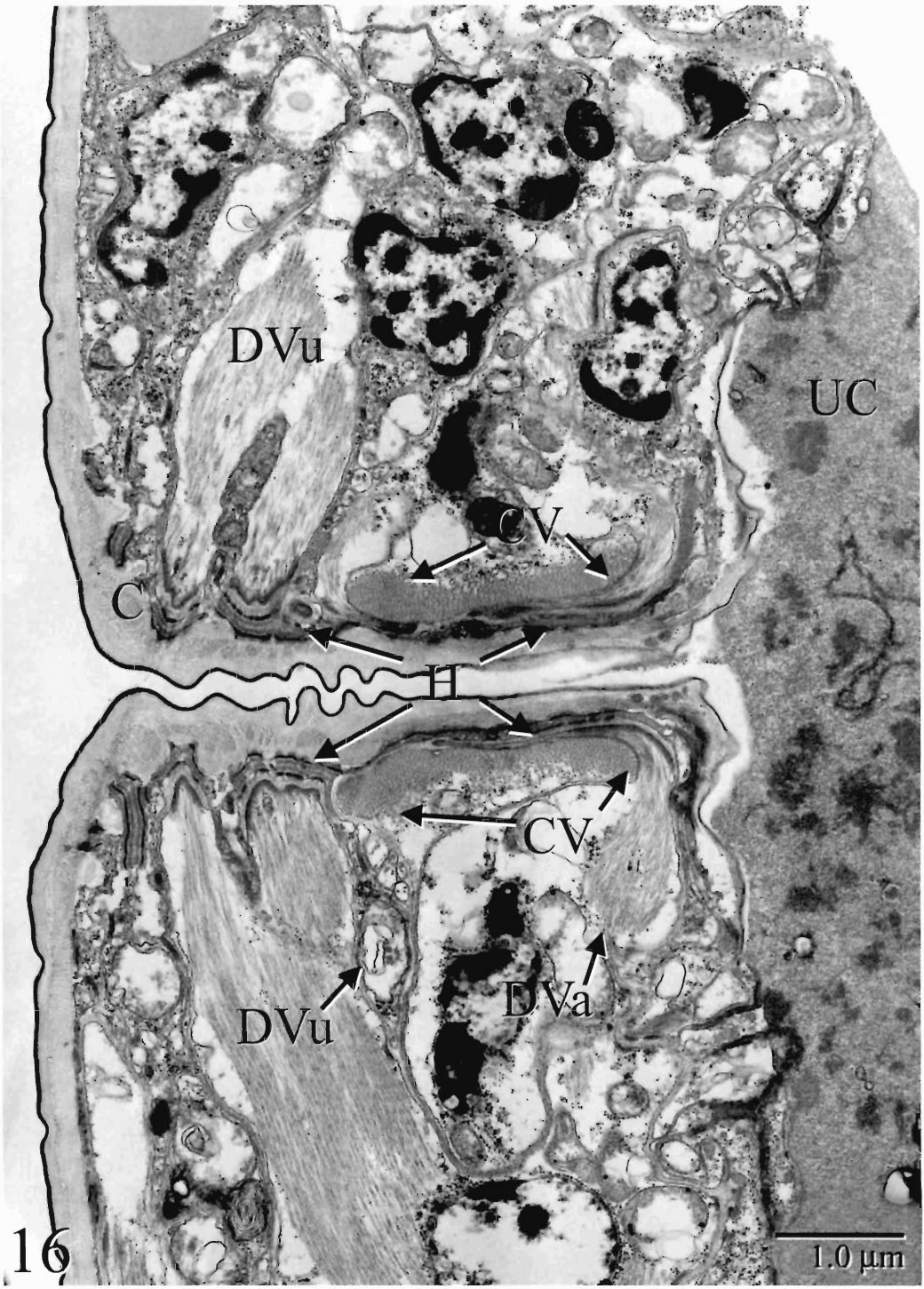


Figure 16. Longitudinal section of the uterus and vagina of *P. penetrans*. The cuticular lining of the vagina is continuous with the body wall cuticle (C) and extends internally to join the uterine channel (UC). Hemidesmosomes (H) attach the dilatores vaginae (DVa) and dilatores vulvae (DVu) muscles to the cuticle lining the vulva and vagina. Constrictores vaginae (CV) or sphincters surround and attach to the cuticle that forms the inner region of the vagina.

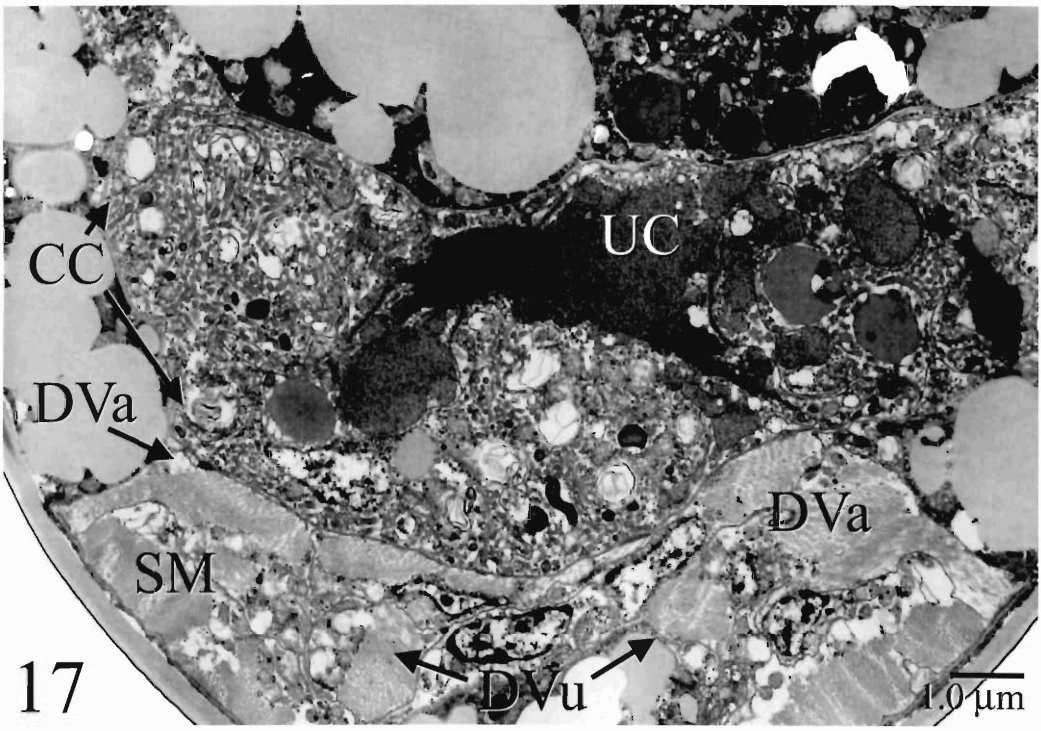


Figure 17. Transverse section through columnar cells (CC) of the uterus surrounding the proximal end of the uterine channel (UC) of *P. penetrans*. Muscle elements adjacent to the columnar cells are extensions of dilatores vaginae (DVa) or dilatores vulvae (DVu) muscles. Other extensions of these muscles (DVa and DVu) contact the laterosubventral somatic muscles. SM, somatic muscles.

Hirschmann, 1969b). The spermatheca, which is composed of about 10 epithelial cells, is followed by the uterus that consists of 2 portions. The distal portion is composed of 12 large gland cells arranged in 4 rows of 4 cells each (tricolumella) that could have a role in egg shell deposition. The proximal portion is a short tube lined with a flat epithelium. This portion enters the vagina, which is lined with cuticle and supported by muscles and opens through the vulva. Specialized muscles dilate the vulva during oviposition (Hirschmann, 1971).

In the present study, the ultrastructural observations were of adult specimens of *P. penetrans*. The morphology of the reproductive system that we observed is similar to the modified amphidelphic mode of development described in previous studies. Briefly, in *Pratylenchus crenatus* and *P. penetrans* (Dickerson, 1962) and in a diverse group of *Pratylenchus* species (Roman and Hirschmann, 1969a), the reproductive system is comprised of a functional anterior ovary and a posterior branch of the ovary reduced to a postvulvar uterine branch. The mitotic divisions occur in the blunt anterior terminus of the developing ovary (Coomans, 1962; Dickerson, 1962; Hirschmann, 1962; Yuen, 1964; Roman and Hirschmann, 1969a). Mitotic divisions were not observed in distal cells of the ovary. These events may occur rather quickly and may not have been captured at our fixation times. No distinction could be made between oogonial and oocyte cells in the anterior region of the ovary in several mature female specimens. However, lipid accumulations were observed among oocytes in the oviduct of an actively reproducing female. In addition, our observations suggest that extracellular lipid or protein granules could nourish the oocyte.

Future work should involve labeling experiments to show the movement of secretory granules from ovarian epithelial cells across the limiting membranes of the oocyte. If this movement occurs, it could explain the accumulation of lipids and proteins that are associated with oocyte enlargement. Changes also appear to occur in

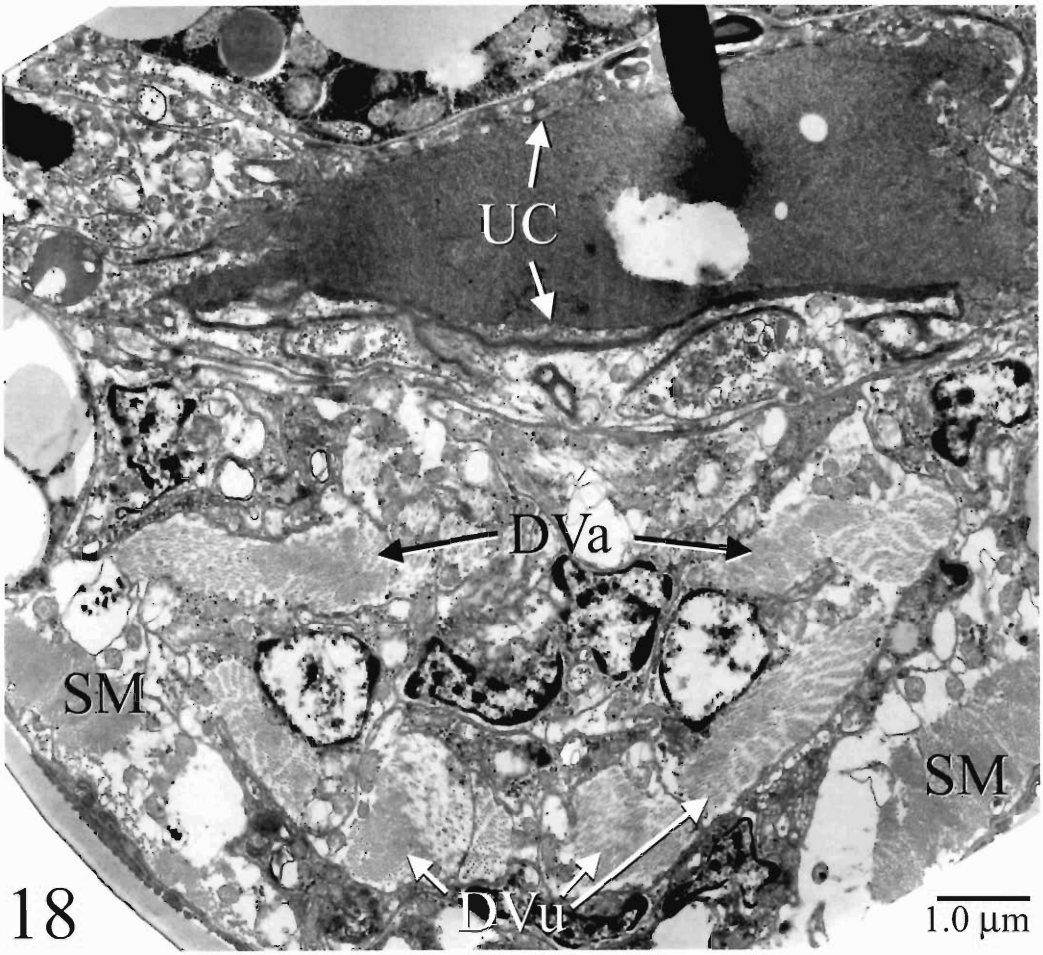


Figure 18. Transverse section of the uterine channel (UC) and muscles associated with the dilation of the vagina and vulva during egg deposition by *P. penetrans*. DVa, dilatores vaginae; DVu, dilatores vulvae; SM, somatic muscles.

the morphology and porosity of the oocyte surface as it passes through the spermatheca, becomes fertilized by sperm, and begins to receive egg shell depositions from columnar cells prior to egg deposition. The electron-dense globules observed in some cells of the distal region of the columnar cells are unusual and are dissimilar to secretory granules observed in the cells forming the oviduct and proximal regions of the uterus.

In our study, nuclear divisions were not observed in the distal region of the ovary of the mature females. This observation is consistent with the observations of Roman and Hirschmann (1969a), who found that oogonial divisions occur in the germinal zone of the ovary of fourth-stage juveniles and probably in young females, but not in mature, egg-laying females. Similarly, oogonial divisions were observed in populations of the soybean cyst nematode, *Heterodera glycines,* before and during the fourth molt. This species has a normal meiotic cycle and reproduces by cross-fertilization (Triantaphyllou and Hirschmann, 1962).

The presence of synaptonemal complexes in many of the ovary cells proximal to the anterior end indicate that many of the oocytes are in the pachytene stage of prophase I. The presence of the tripartite synaptonemal complex is consistent with observations of nuclei in the testes of *P. penetrans.* This tripartite pattern differs from that of most species of *Meloidogyne,* which have

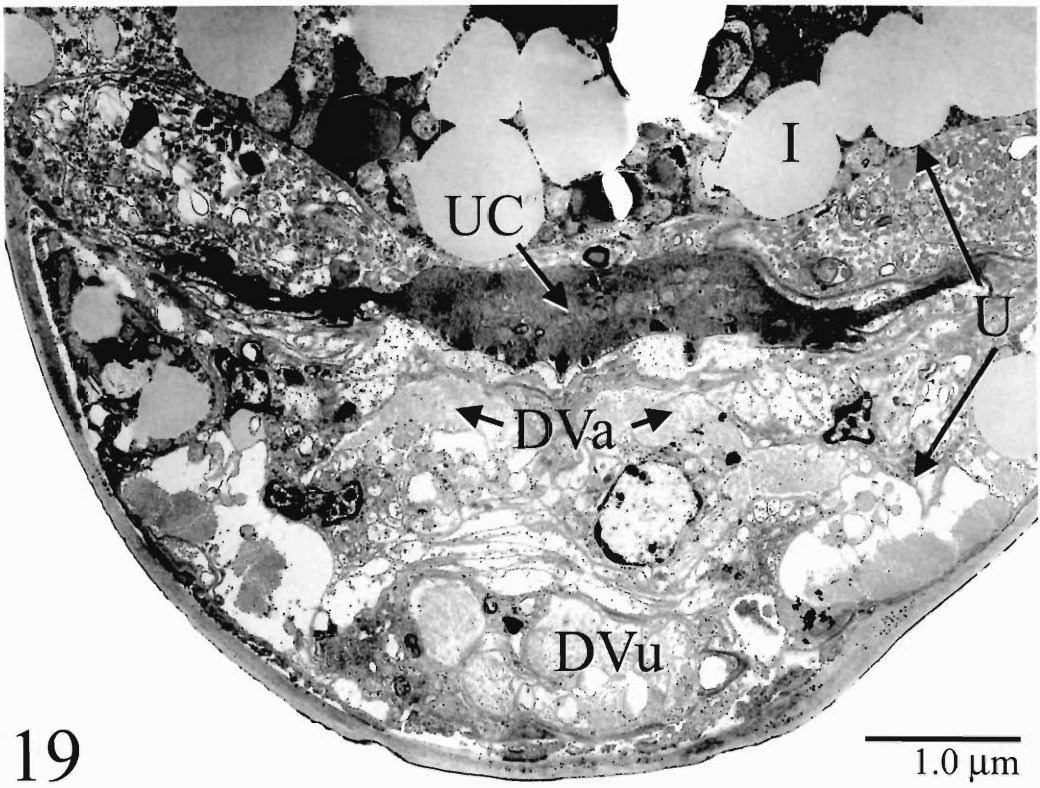
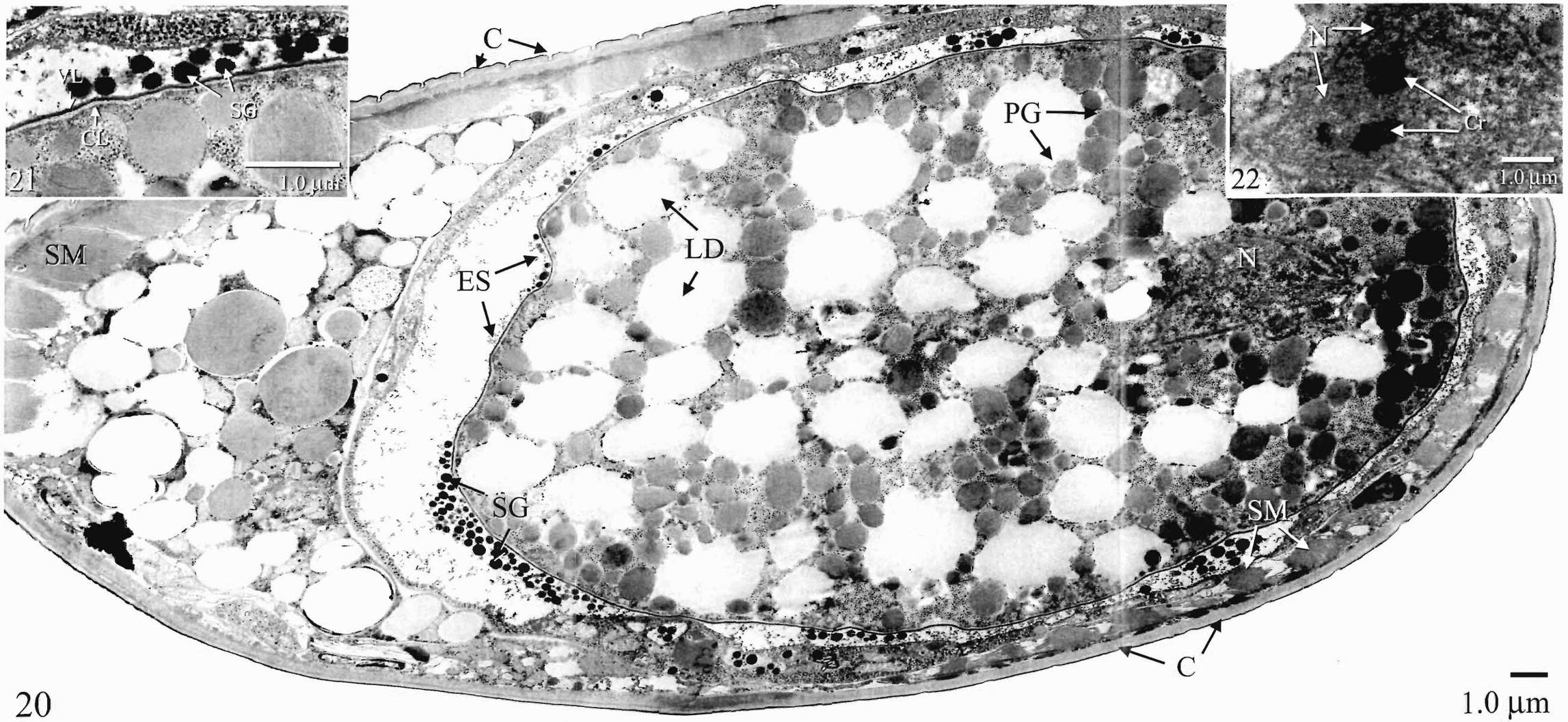


Figure 19. Transverse section through the uterine channel (UC) of *P. penetrans* showing the broad opening for egg passage. The bands of muscles adjacent to the uterine channel are the dilatores vaginae (DVa). The bands of muscles midventral and close to the body wall cuticle constitute the vulval wall muscles, dilatores vulvae (DVu). I, intestine; U, uterus.

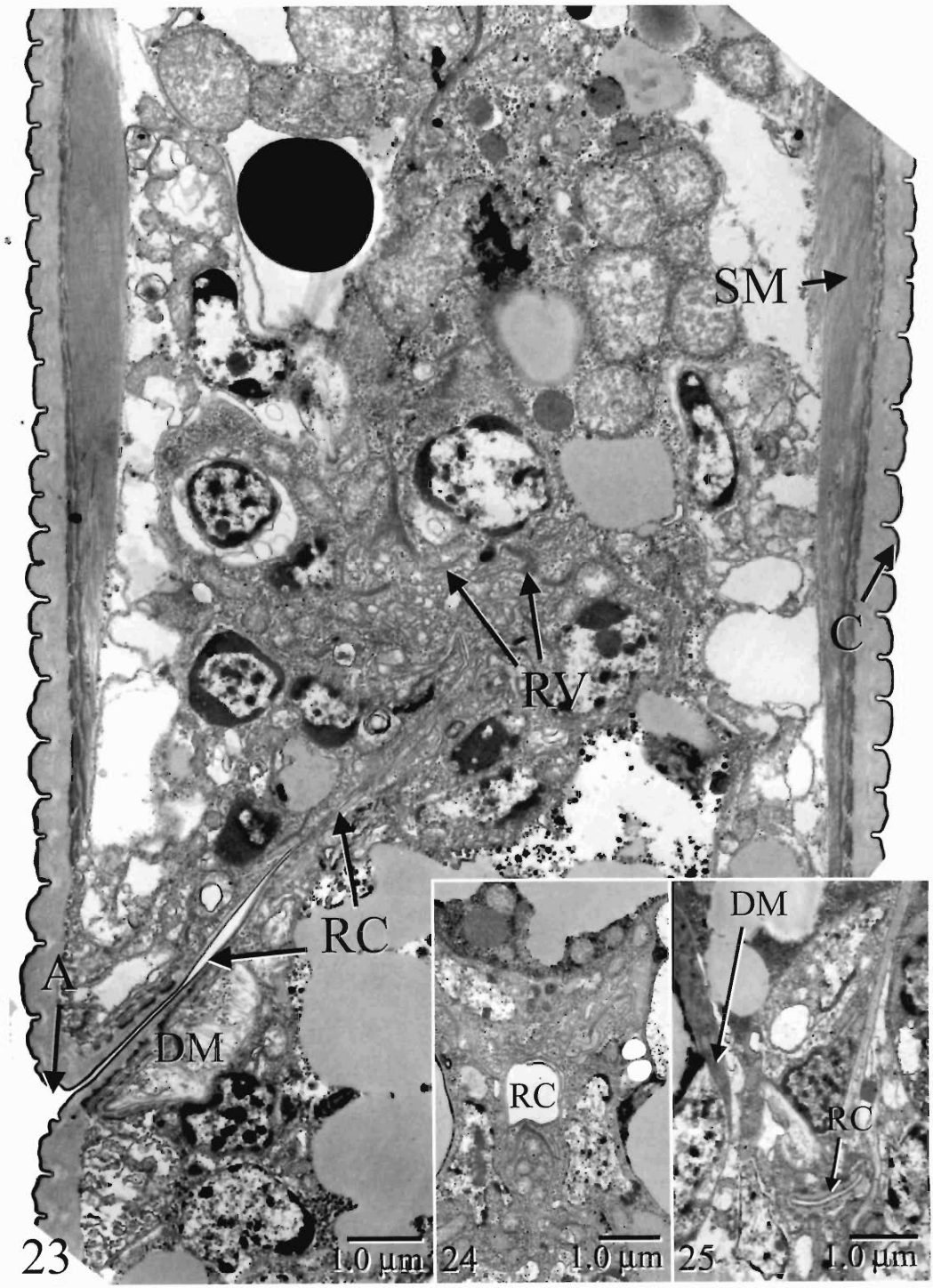
a bipartite pattern consisting of 2 lateral elements but lacking striated central elements (Westergaard and von Wettstein, 1972; Goldstein and Triantaphyllou, 1995). Whether or not the tripartite pattern of the synaptonemal complex occurs in most species of *Pratylenchus* is not yet determined. Observations of *Caenorhabditis elegans* show that developing oocytes are arranged in single file along the proximal arm of the ovary, the site of gametogenesis in a hermaphrodite. Oocytes are arrested at diakinesis in meiotic prophase I. After the oocyte is fertilized, the zygote moves through the spermatheca to the uterus, where meiosis is completed (Kimble and Ward, 1988).

In *Xiphinema theresiae,* the ovary has 2 types of cells: the ovarian epithelial cells and the germ cells (Van De Velde and Coomans, 1988). The ovarian epithelial cells form a thin layer around the germ cells and have nuclei between some of the germ cells. At some sites, processes of ovarian epithelial cells extend inward to form a central cytoplasmic mass, which has cytoplasmic contact with the germ cells. These cells develop 2 membrane-derived features, the villi and the small coated bulges, which are thought to play a role in transport. However, *X. theresiae* does not have a typical rachis, a large, clearly delineated structure, around which oogonia are arranged and make cytoplasmic contact.

Bird and Bird (1991) described a typical rachis for the telogonic and didelphic reproductive system of the female root-knot nematode, *Meloidogyne javanica.* The oogonia are radially arranged around a central anucleate rachis to which oogonia are attached by cytoplasmic bridges. In *C. elegans,* which is monodelphic, mitotic germ cells occupy the distal end of the ovary, and meiotic cells occupy the remaining portion of the gonad (Kimble and White, 1981). A typical rachis was not observed in the female reproductive system of *P. penetrans.*



Figures 20–22. Section of an egg of *Pratylenchus penetrans*. 20. Tangential section through an egg within the postvulvar uterine branch. This section is from the same specimen shown in Figure 10, which shows an oocyte in the oviduct. The oocyte cytoplasm is filled primarily with lipid bodies. In contrast, the cytoplasm of the egg contains numerous irregularly shaped electron-translucent lipid droplets (LD) and numerous electron-dense protein granules (PG) that generally occur around the lipid droplets. The nucleus (N) is located near one end of the egg. The egg shell (ES) has a well-defined electron-dense outer vitelline layer and an electron-translucent inner chitinous layer. Electron-dense secretory granules (SG) accumulate on the surface of the egg. Similar granules occur singly or in clusters within the columnar cells of the uterus or supporting cells of the uterine channel. The intercellular electron-dense granules originating in these cells appear to be secreted and deposited on the egg shell. C, cuticle; SM, somatic muscle. 21. Enlargement of a portion of the egg shell shown in Figure 20. Secretory granules (SG) near the surface of the egg shell appear to contribute to the electron-dense outer vitelline layer (VL), which is easily distinguished from the electron-translucent inner chitinous layer (CL). 22. Enlargement of nucleus (N) of egg shown in Figure 20. Chromatin (Cr) occurs within the nucleoplasm.



Figures 23–25. Section of the rectal region of *Pratylenchus penetrans*. **23.** Longitudinal section of the rectal region of an adult female. The complex of membrane junctions denotes part of the rectal valve (RV). The rectal channel (RC) extends posteriad and is supported by the cell membranes and cuticle. The depressor ani muscles (DM) are located on the dorsal surface of the rectal cuticle near the anal (A) opening. SM, somatic muscles; C, cuticle. **24.** Transverse section of the rectal channel (RC) supported by rectal cells. **25.** Transverse section of the rectal channel (RC) near the attachment of the depressor ani muscles (DM) to the cuticle lining of the channel. The depressor ani muscles have a dorsosublateral orientation.

The ovary of *P. penetrans* has cells that appear as single or double rows of germ cells enclosed by epithelial cells that are characterized by irregularly shaped nuclei. These nuclei have electron-dense chromatin that tends to accumulate along the inner surface of the nuclear membrane. Cytoplasmic contact between germ cells and epithelial cells appears to be minimal and is not similar to that described for other species (Hirschmann, 1971). The distinctive morphology of epithelial cells of *P. penetrans* ovaries was also noted in the cluster of cells anteriad to the spermatheca. These epithelial cells, in conjunction with oviduct cell wall, may affect movement of oocytes from the oviduct into the spermatheca.

The plicated membranes of cells lining the oviduct and their capacity to expand and accommodate the moving oocyte were previously illustrated for *Rotylenchus goodeyi* (Coomans, 1962) and the Hoplolaiminae (Yuen, 1964). This process may also operate in the spermatheca and columnar cells. However, a fundamental difference occurs in their cellular contents and functions. In *P. penetrans,* the presence of muscle filaments, which line the oviduct, suggests that they have an active role during oocyte passage toward the spermatheca. The cluster of cells, which have centralized membrane junctions at the anterior region of the spermatheca and are described as a 12-celled constriction in *Pratylenchus* spp. (Roman and Hirschmann, 1969b), may function as a valve, which opens or closes to regulate oocyte passage into the spermatheca. The female reproductive system of *Xiphinema meridianum* has an ovarial sac that is muscular and an outer membrane that is highly plicated. The proximal part of the oviduct is narrow and tube-like, but widens into the pars dilatata oviductus. The oviduct of *X. meridianum* lacks a preformed lumen except for the pars dilatata oviductus, where the lumen is narrow. The ultrastructure of the female gonoduct of *X. theresiae* is similar to that described for *X. meridianum* (Van De Velde et al., 1990a, b). In *P. penetrans,* the ultrastructure of the lumen of the oviduct and that of the columnar cells in the central region is similar to the plicated cell membranes described for *Xiphinema,* which also lacks a preformed oviduct lumen.

Ward and Carrel (1979) described oocyte migration in the hermaphroditic species *C. elegans.* In this species, migration is accompanied by sporadic contractions of the oviduct walls and the oocyte cytoplasm. As contractions of the oviduct wall increase, the oocyte moves through the spermathecal constriction and into the spermatheca. A similar mechanism may propel oocytes through the muscular oviduct of *P. penetrans.*

The spermatheca of *P. penetrans* is defined by the adjoining columella cells. Columella cells are joined by a junctional complex to form a continuous lumen between the spermatheca and the central uterus. The ultrastructure of the columella cells of the uterus is distinctly different from the cells forming the oviduct. In the uterus, the columella cells have more ribosomes, mitochondria, secretory granules, and membrane junctions than the cells adjoining the oviduct. In the female gonad of *Rotylenchus goodeyi,* the uterus has two regions: the quadricolumella and a thin-walled, muscular region that lies between the quadricolumella and the vagina (Coomans, 1962). This muscular region was not observed in *P. penetrans.* However, the muscle bands that were found near the vagina and vulva appear to have a major role in the movement of the oocyte or egg through the genital tract as well as in dilation of the vagina and vulva during egg deposition.

In a study of about 50 females of *R. goodeyi,* Coomans (1962) determined that the quadricolumella is a glandular region in the uterus and probably secretes the egg shell. The glandular region was particularly large and granular when a well-developed egg was found in the oviduct. As the egg passed into the uterus, the glandular cells appeared to empty and a thin layer formed around the egg shell. In *P. penetrans,* the uterus with eggs has electron-dense secretory granules in the columella cells, and cells of the uterine wall are appressed and flattened by passage of an egg. At this time, the secretory granules are found between the uterine wall and the limiting membrane of the egg.

We concur that the columella cells serve a functional role in providing secretions that contribute to formation of the egg shell, as proposed by Coomans (1962) for *R. goodeyi* and by investigators of other nematode species (Coomans, 1965; Bleve-Zacheo et al., 1976; McClure and Bird, 1976; Bird and Bird, 1991). This hypothesis is further supported by ultrastructural examinations of cross sections of egg shells of *P. penetrans* (Hilgert, 1976). Our study illustrates

sites where secretory granules appear to merge with the electron-dense outer layer of the egg shell.

Fertilization of the oocyte occurs between the oviduct and the uterus, regardless of the presence or absence of a spermatheca (Bird and Bird, 1991). In a light microscope study, Hung and Jenkins (1969) observed oogonial divisions at the apical portions of the gonads of young females of *P. penetrans* and *P. zeae.* In *P. penetrans,* only 1 sperm appears to enter each oocyte as it passes through the spermatheca. After sperm penetration, the oocyte nucleus moves centrally and undergoes maturation divisions. After the initial reduction division and the second division of meiosis, the egg pronucleus is formed, which in turn fuses with a sperm nucleus to form the zygote shortly before or after egg deposition. In *P. penetrans,* the chromosome number is 2n = 10, whereas in *P. zeae,* which reproduces by mitotic parthenogenesis, 2n = 26. In the present ultrastructural study of *P. penetrans,* the stage at which fertilization occurs could not be determined, but sperm was observed in the developing eggs inside the uterus.

In *Ascaris,* Foor (1970) showed that when male sperm and oocyte membranes establish contact, the membranes appear to fuse. In other cases, considerable interdigitation occurs between the opposing gamete surfaces. Subsequently, the sperm progresses to a position deep within the oocyte cytoplasm. In some cases, fusion appears to take place between the oolemma and the lateral margins of the sperm. After fusion of the gamete membranes, the underlying interdigitating membranes disappear and the contents of the spermatozoan are within the oocyte (Foor, 1970).

In *P. penetrans,* the ultrastructure of initial stages of gamete fusion was not examined. Hung and Jenkins (1969) used light microscopy to show that the oocyte nucleus of *P. penetrans* undergoes 2 divisions after sperm penetration. Roman and Triantaphyllou (1969) studied the maturation of oocytes and fertilization in *P. penetrans, P. vulnus,* and *P. coffeae.* In these species, oocytes in the spermatheca contain a small number of bivalent chromosomes at prometaphase I. One spermatozoan enters each oocyte, which then rapidly completes the first division. At telophase I, the chromosomes that form the first polar body nucleus are discrete and can be used to determine the haploid chromosome number. A second maturation division follows rapidly, and the sperm pronucleus is formed and then fuses with the egg pronucleus to form the zygote nucleus. Fusion of the pronuclei was observed in nondeposited eggs of *P. penetrans* and in eggs laid by *P. coffeae.* The primary oocyte of the dog heartworm, *Dirofilaria immitis,* completes meiosis only after fertilization by a male gamete in the seminal vesicle (Delves et al., 1986). After meioses I and II are completed in the oocyte and the 2 polar bodies are extruded, the haploid chromosome complement of the female unites with that of the male and re-establishes the diploid chromosome number in the zygote.

Oogenesis and the mode of reproduction were also studied in populations of the soybean cyst nematode, *H. glycines.* Triantaphyllou and Hirschmann (1962) determined that oogonial divisions occur before and during the fourth molt. Maturation of oocytes in inseminated females consists of 2 meiotic divisions and the formation of 2 polar nuclei. Nine bivalents are present at metaphase I in all populations. Sperm enters the oocytes at late prophase or early metaphase I. After the second maturation division, sperm and egg pronuclei fuse to form the zygote nucleus.

The vulval walls of *P. penetrans* are attached to 2 sets of dilatores vulvae. Four bands on each side of the vulval wall are directed anteriad and posteriad and insert ventrolaterally on the body wall. This orientation of muscles coincides with light microscopic observations of *R. goodeyi* (Coomans, 1962). The dorsally and ventrally located dilatores vaginae have been diagrammed for *P. penetrans* (Kisiel et al., 1972; Hilgert, 1976; Mai et al., 1977). Although the vulval muscles were not clearly defined in the latter studies, they did appear as prominent muscle bands in our study.

In the hermaphrodite *C. elegans* stained with phalloidin, a photomicrograph clearly showed 4 of 8 vulval muscle cells that were inserted near the vulval opening and at the lateral epidermis (Waterston, 1988; Bird and Bird, 1991). Our observations of *P. penetrans* tend to support the concept that the dilatores vulvae play a major role in egg deposition.

In conclusion, the ultrastructure of the reproductive system of *P. penetrans* increases our understanding of the anatomical, physiological, and phylogenetic relations among a vast array of nematodes, including many plant parasitic nem-

atodes. In the future, comparative studies should be conducted on reproductive anatomy and physiology of sedentary endoparasitic species such as *Meloidogyne,* the cyst nematode species, and the migratory and free-living forms, such as *C. elegans.* These observations may provide clues for modifying or disrupting nematode reproduction and could lead to new methods of control for economically destructive species.

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1999–2000 MEETING SCHEDULE OF THE HELMINTHOLOGICAL SOCIETY OF WASHINGTON

13 October 1999	Animal Parasitology Laboratories, Beltsville Agricultural Research Center, USDA, Beltsville, MD, 7:30 pm (Contact person: Eric Hoberg, 301-504-8588)
17 November 1999	Anniversary Dinner—meeting location TBA
19 January 2000	Smithsonian Institution, National Museum of Natural History, Washington, DC, 7:30 pm (Contact person: Bill Moser, 202-357-2473)
12 March 2000	Johns Hopkins Montgomery County Center (Provisional), Rockville, MD, 7:30 pm (Contact person: Tom Simpson (JHU), 410-366-8814, or Louis Miller (NIH), 301-496-2183)
10 May 2000	Joint Meeting with the New Jersey Society for Parasitology, at the New Bolton Center, University of Pennsylvania, Kennett Square, PA, 2:00 pm (Contact person: Jay Farrell, 215-898-8561)

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Skrjabinodon piankai sp. n. (Nematoda: Pharyngodonidae) and Other Helminths of Geckos (Sauria: Gekkonidae: *Nephrurus* spp.) from Australia

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ABSTRACT: *Skrjabinodon piankai* sp. n. from the large intestine of the Australian gecko *Nephrurus laevissimus* is described and illustrated. It is also reported from *Nephrurus levis* and *Nephrurus vertebralis*. *Skrjabinodon piankai* differs from 6 other Australian realm species in the number of tail filament spines and egg shape. Other helminths found include *Oochoristica piankai, Maxvachonia brygooi, Pharyngodon tiliquae, Physalopteroides filicauda, Wanaristrongylus ctenoti,* third-stage larvae of *Abbreviata* sp., third-stage larvae of *Physaloptera* sp., and *Raillietiella scincoides*. New host records are established for *O. piankai* and *R. scincoides* in *N. laevissimus*; *M. brygooi* and *P. filicauda* in *N. levis*; and *P. tiliquae* in *N. vertebralis*.

KEY WORDS: *Skrjabinodon piankai* sp. n., Pharyngodonidae, helminths, *Nephrurus laevissimus, Nephrurus levis, Nephrurus vertebralis,* Gekkonidae, Sauria, Australia.

Four species of *Skrjabinodon* Inglis, 1968 have been reported previously from reptiles of Australia. *Parathelandros oedurae* Johnston and Mawson, 1947, was originally described from specimens taken from the robust velvet gecko, *Oedura robusta* Boulenger, 1885, collected in southeast Queensland. Inglis (1968) revised *Parathelandros* Diesing, 1861, retaining the genus for parasites of Australian amphibians and erecting *Skrjabinodon* as a new genus for parasites of reptiles; 7 species, including *P. oedurae,* were placed in the new genus. *Skrjabinodon smythi* Angel and Mawson, 1968 was described from the marbled gecko, *Christinus* (=*Phyllodactylus*) *marmoratus* (Gray, 1845) collected in South Australia. *Skrjabinodon parasmythi* Mawson, 1971, from the thick-tailed gecko, *Underwoodisaurus milii* (Bory de Saint-Vincent, 1825), and *Skrjabinodon leristae* Mawson, 1971, from a skink, *Lerista* sp., were described from specimens collected on Flinders Island, South Australia. In addition, 2 species, *Skrjabinodon trimorphi* Ainsworth, 1990, from the common skink, *Leiolopisma nigriplantara* Patterson and Daugherty, 1990, and *Skrjabinodon poicilandri* Ainsworth, 1990 from the common gecko, *Hoplodactylus maculatus* Boulenger, 1885, have been described from specimens collected in New Zealand (Ainsworth, 1990).

Nephrurus Günther, 1876, is an endemic Australian gecko genus containing arid-adapted species characterized by large heads and short, fat tails that terminate in a small knob (Cogger, 1992). The spinifex knobtail gecko, *Nephrurus laevissimus* Mertens, 1958, occurs in southeastern Western Australia, northwestern South Australia, and southern parts of the Northern Territory; the smooth knobtail gecko, *Nephrurus levis* De Vis, 1886, occurs from the central coast of Western Australia to the arid parts of all states except Victoria; Storr's knobtail gecko, *Nephrurus vertebralis* Storr, 1963, occurs from the lower central interior of Western Australia to South Australia (Cogger, 1992). The ranges of these 3 nocturnal species overlap in Western Australia (Cogger, 1992). However, they are reported to favor different habitats (Pianka, 1972): *N. laevissimus* is associated with sandridges; *N. levis* occurs on sandplains vegetated with dense clumps of perennial grasses of *Triodia* Brown, 1810; and *N. vertebralis* is associated with shrubs of *Acacia* Miller, 1754.

There are 4 previous reports of nematodes from *N. laevissimus* (Jones, 1985, 1987, 1995a, b), 1 report from *N. levis* (Jones, 1995b), but, to our knowledge, no reports from *N. vertebralis*. We describe here a new species of *Skrjabinodon* that was found in the large intestines of *N. laevissimus, N. levis,* and *N. vertebralis* from Western Australia and the Northern Territory and list other helminth parasites found in these hosts.

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Table 1. Prevalence (%) and mean abundance of helminths of *Nephrurus laevissimus, N. levis,* and *N. vertebralis* from Australia.

Helminth	*Nephrurus laevissimus* (N = 36)		*Nephrurus levis* (N = 13)		*Nephrurus vertebralis* (N = 3)	
	P* (%)	$\bar{A}$ ± SD†	P (%)	$\bar{A}$ ± SD	P (%)	$\bar{A}$ ± SD
Cestoda						
Oochoristica piankai	3‡	0.14 ± 0.83	—	—	—	—
Nematoda						
Maxvachonia brygooi	—	—	15‡	1.00 ± 2.45	—	—
Pharyngodon tiliquae	—	—	—	—	33‡	4.00 ± 6.93
Physalopteroides filicauda	17	0.83 ± 2.45	31‡	16.08 ± 56.47	—	—
Skrjabinodon piankai	22‡	12.75 ± 29.77	62‡	53.69 ± 78.69	66‡	55.33 ± 94.98
Wanaristrongylus ctenoti	—	—	8	0.15 ± 0.56	—	—
Abbreviata sp. (larvae)	5	0.08 ± 0.37	31	0.85 ± 1.95	—	—
Physaloptera sp. (larvae)	3	0.03 ± 0.17	—	—	—	—
Pentastomatida						
Raillietiella scincoides	5‡	0.06 ± 0.23	—	—	—	—

* P = Prevalence (number of hosts infected with a parasite species divided by the number of hosts examined × 100).

† $\bar{A}$ ± SD = mean abundance (summation of number of individuals of a parasite species per host divided by the number of hosts examined) ± standard deviation.

‡ New host record.

Materials and Methods

Thirty-six *N. laevissimus,* 13 *N. levis,* and 3 *N. vertebralis* from the collections of the Natural History Museum of Los Angeles County (LACM) were examined: *N. laevissimus,* mean snout–vent length (SVL) = 64.6 ± 8.5 mm SD, range 51–80 mm, LACM 57145, 57146, 57156, 57159, 57160, 57162, 57163, 57165, 57170, 57173–57175, 57177, 57180–57182, 57189, 57192, 57193, 57196–57198, 57201, 57204, 57209, 57210, 57213, 57215–57217, 57219, 57220, 57225–57228, collected 34 km west of Lorna Glen homestead, Western Australia (26°14′S, 121°13′E); *N. levis,* SVL = 77.2 ± 10.2 mm SD, range 64–98 mm, LACM 57008, 57009, collected 29 km south of Neale Junction, Western Australia (28°30′S, 125°50′E), LACM 57011–57014, 38 km east of Laverton, Western Australia (28°28′S, 122°50′E), LACM 57018, 57020, 16 km southeast of Renhan's Well, Northern Territory (21°24′S, 130°53′E), LACM 57026, 57029, 11 km south of The Granite, Northern Territory (20°38′S, 130°25′E), LACM 57032, 57037, 57039, 13 km west of Neale Junction, Western Australia (28°17′S, 125°40′E); *N. vertebralis,* SVL = 81.3 ± 7.6 mm SD, range 73–88 mm, LACM 57047, 6 km east of Stony Point, Western Australia (28°05′S, 124°15′E), LACM 57049, 57051, 14 km northeast of Millrose homestead, Western Australia (26°17′S, 121°00′E). These specimens had been collected between October 1966 and January 1968 for use in an ecological study (Pianka and Pianka, 1976). Because the ecological study included stomach analysis, only small and large intestines remained with the carcasses. Each intestine was searched for helminths using a dissecting microscope. Cestodes were stained with hematoxylin and mounted in balsam for identification; other helminths were identified from the glycerol mounts. Measurements are in mm unless otherwise indicated.

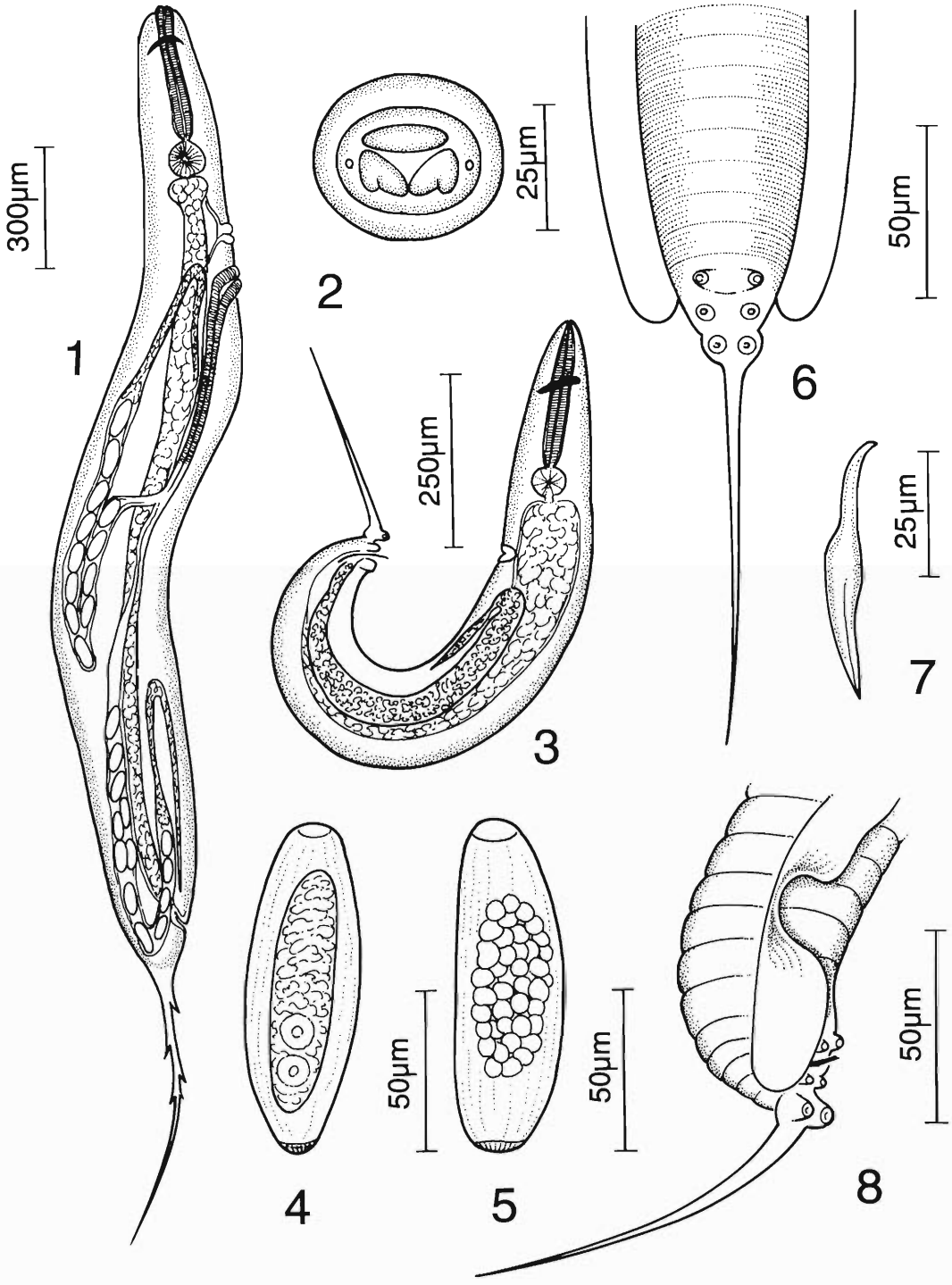
Results

Helminths representing 9 species were found: the cestode *Oochoristica piankai* Bursey, Goldberg, and Woolery, 1996; the nematodes *Maxvachonia brygooi* Mawson, 1972, *Pharyngodon tiliquae* Baylis, 1930, *Physalopteroides filicauda* Jones, 1985, *Skrjabinodon piankai* sp. n. (this paper), *Wanaristrongylus ctenoti* Jones, 1987, *Abbreviata* sp. (third-stage larvae only), *Physaloptera* sp. (third-stage larvae only); and the pentastomid *Raillietiella scincoides* Ali, Riley, and Self, 1984. Prevalence and mean abundance are given in Table 1. Selected specimens were placed in vials of alcohol and deposited in the U.S. National Parasite Collection (USNPC). These are parasites from *N. laevissimus*: *O. piankai,* USNPC 88189; *P. filicauda,* USNPC 88190; *S. piankai,* USNPC 88191; *Abbreviata* sp. (larva), USNPC 88192; *Physaloptera* sp. (larva), USNPC 88193; *R. scincoides,* USNPC 88194. *N. levis*: *M. brygooi,* USNPC 88195; *P. filicauda,* USNPC 88196; *S. piankai,* USNPC 88197; *W. ctenoti,* USNPC 88198; *Abbreviata* sp. (larva), USNPC 88199. *Nephrurus vertebralis*: *Pharyngodon tiliquae,* USNPC 88200; *S. piankai,* USNPC 88201.

Skrjabinodon piankai sp. n. (Figs. 1–8)

Description

GENERAL: Oxyurida: Pharyngodonidae Travassos, 1919, *Skrjabinodon* Inglis, 1968. Small,



Figures 1–8. ***Skrjabinodon piankai*** **sp. n. 1. Female, entire, lateral view. 2. Female, en face view. 3. Male, entire, lateral view. 4, Egg, pronuclear stage. 5. Egg, morula stage. 6. Male, posterior end, ventral view. 7. Spicule. 8. Male, posterior end, lateral view.**

cylindrical nematodes, extremities tapered in both sexes; moderate sexual dimorphism, males approximately one-third length of females. Cuticle with fine transverse striations along entire body. Mouth surrounded by 3 small lips; prominent lateral amphids just behind lips. Lateral alae present in both sexes. Tail narrowing abruptly behind anus to form filamentous appendage.

MALE (based on 10 specimens): Small, white, fusiform nematodes tapering both anteriorly and posteriorly, body usually bent to give comma-shaped appearance. Length 1.27 (1.19–1.40), body length 1.00 (0.97–1.12), tail filament 0.25 (0.22–0.29). Width at level of excretory pore 0.12 (0.10–0.14). Cuticle with striations approximately 3 μm apart. Esophagus excluding bulb 0.216 (0.204–0.242), bulb length 0.049 (0.040–0.054), bulb width 0.052 (0.046–0.057). Nerve ring 0.118 (0.103–0.125) and excretory pore 0.342 (0.306–0.383) from anterior end, respectively. Lateral alae 0.012 (0.010–0.015) wide, beginning midway between lips and nerve ring and ending just anterior to third pair of caudal papillae. Spicules 0.055 (0.051–0.057). Tail filament with 1 (0–2) small spine. Cloaca and associated papillae slightly raised from body surface but not on distinct cone. Caudal alae absent, 3 pairs of sessile papillae, 1 pair precloacal, 1 pair postcloacal, third pair occurring on base of tail filament. Single tubular testis reflexed just posterior to excretory pore.

FEMALE (based on 10 gravid specimens): Small, white nematodes tapering anteriorly and posteriorly. Length 3.21 (2.80–3.58), body length 2.55 (2.21–2.86), tail filament 0.66 (0.58–0.71). Width at level of vulva 0.22 (0.18–0.25). Lateral alae 2 μm (2–3 μm) wide, doubled, approximately 50 μm apart at midbody, beginning in a single point at level of nerve ring, ending in a single point just anterior to beginning of tail filament. Cuticle with transverse striations approximately 2 μm wide. Mouth with 3 lips, each lateral lip with 1 small papilla. Esophagus excluding bulb 0.295 (0.285–0.310), bulb length 0.073 (0.068–0.080), bulb width 0.087 (0.080–0.094). Nerve ring 0.125 (0.115–0.145), excretory pore 0.477 (0.410–0.535), and vulva 0.535 (0.485–0.610) from anterior end, respectively. Thick-walled muscular ovijector extending posteriorly 0.40 mm, then continuing as thin-walled vagina 0.18 mm in length before joining 2 uteri, 1 directed anteriorly and the other posteriorly. Ovarian and uterine coils not extending to vulva. In fully gravid females, uterus extending from slightly behind vulva to end of body. Egg barrel shaped, slightly flattened on 1 side, operculum at each end, length 105 μm (100–108 μm), width 34 μm (31–37 μm). Egg surface finely pitted, having a ground-glass appearance. Development to morula stage at deposition. Tail spines 5 (4–7).

Taxonomic summary

TYPE HOST: *Nephrurus laevissimus* Mertens, 1958.

ADDITIONAL HOSTS: *Nephrurus levis* De Vis, 1886; *N. vertebralis* Storr, 1963.

TYPE LOCALITY: 34 km west of Lorna Glen homestead, Western Australia (26°14′S, 121°13′E).

SITE OF INFECTION: Large intestine.

TYPE SPECIMENS: Holotype, male, U.S. National Parasite Collection no. 88186; allotype, female, no. 88187; paratypes (9 males, 9 females), no. 88188.

ETYMOLOGY: The specific epithet honors Eric R. Pianka, Denton A. Cooley Centennial Professor of Zoology, University of Texas at Austin, for his pioneering studies on the ecology of Australian lizards.

Remarks

Skrjabinodon piankai is the seventh species of *Skrjabinodon* to be reported from the Australian biogeographical realm; 5 from Australia and 2 from New Zealand. These species are separated on the basis of tail spines and egg shape. *Skrjabinodon oedurae* and *S. poicilandri* possess 3 caudal body spines that the other 5 species lack. Females of *S. oedurae* have 19 tail filament spines; females of *S. poicilandri* have 36–44. *Skrjabinodon leristae, S. parasmythi, S. smythi,* and *S. trimorphi* have spindle-shaped eggs; the eggs of *S. piankai* are barrel-shaped. Eggs of *S. parasmythi* and *S. smythi* have plugs at each end, those of *S. leristae* and *S. trimorphi* do not. Tail filament spines of female *S. parasmythi* are slender and pointed, those of female *S. smythi* are digitiform. Males of *S. parasmythi* have a well-developed spicule, males of *S. smythi* lack a spicule. Females of *S. leristae* have doubled lateral alae; females of *S. trimorphi* have single lateral alae.

Discussion

Other species of helminths found in this study are listed in Table 1. Previously reported hel-

minths of *N. laevissimus* include *P. filicauda, Wanaristrongylus papangawurpae* Jones, 1987, and cysts containing larvae of physalopterids; from *N. levis, W. ctenoti* and physalopterid larvae (Jones, 1985, 1987, 1995a, b).

Oochoristica piankai was first described from specimens taken from the small intestine of the thorny devil, *Moloch horridus* Gray, 1841, collected by E. R. Pianka in Western Australia (Bursey et al., 1996). *Nephrurus laevissimus* is the second host for this parasite to be reported. *Maxvachonia brygooi* was first described from the agamid genus *Amphibolurus* Wagler, 1830, by Mawson (1972); *N. levis* is a new host record for *M. brygooi* and represents the 10th lizard species to harbor this helminth. *Pharyngodon tiliquae* was first described from the skink *Tiliqua scincoides* (White, ex Shaw, 1790) by Baylis (1930); *N. vertebralis* is a new host record for *P. tiliquae* and represents the 10th lizard species to harbor this helminth. *Physalopteroides filicauda* was described from specimens taken from the stomach of a *N. laevissimus* collected by E. R. Pianka in Western Australia (Jones, 1985). It has been found in at least 38 species of Australian lizards. *Wanaristrongylus papangawurpae* and *W. ctenoti* were also described from specimens taken from the stomachs of *N. laevissimus* and *N. levis,* respectively, collected by E. R. Pianka in Western Australia (Jones, 1987). *Wanaristrongylus papangawurpae* has been found in 8 species of Australian lizards and *W. ctenoti* in 12 species (Jones, 1988, 1995a). *Raillietiella scincoides* was originally described from *T. scincoides* by Ali et al. (1984); *N. laevissimus* is the second reported host. Larvae of *Abbreviata* sp. and *Physaloptera* sp. are commonly reported in Australian reptiles (Jones, 1995a). Larvae of *Abbreviata* sp. have submedian teeth on each pseudolabium; such teeth are absent in larvae of *Physaloptera* sp.

It should be noted that the material examined by Jones (1995a, b) and our material were from the same collection of lizards by E. R. Pianka; the stomachs had been deposited in the Western Australia Museum and the carcasses in LACM. Further examination of Australian lizards will be necessary before the number of hosts for *S. piankai* can be known.

Acknowledgments

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Parapharyngodon japonicus sp. n. (Nematoda: Pharyngodonidae) from the Japanese Clawed Salamander, *Onychodactylus japonicus* (Caudata: Hynobiidae), from Japan

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ABSTRACT: *Parapharyngodon japonicus* sp. n. from the large intestine of the Japanese clawed salamander, *Onychodactylus japonicus* (Houttuyn), is described and illustrated. *Parapharyngodon japonicus* is most similar to *P. tyche* in that the anterior cloacal lip is smooth, the ovary is postbulbar, and the eggs are thin-walled and oval in outline. These 2 species differ in that the spicule of *P. japonicus* is half the length of that in *P. tyche* and the lateral alae of *P. japonicus* end abruptly about 80 μm anterior to the cloaca, whereas in *P. tyche* the lateral alae continue to the end of the body. Two species are transferred from *Parapharyngodon* to *Thelandros* and represent new combinations: *Thelandros awakoyai* (Babero and Okpala) comb. n. and *T. senisfaciecaudus* (Freitas) comb. n.

KEY WORDS: *Parapharyngodon japonicus* sp. n., Pharyngodonidae, *Onychodactylus japonicus*, Hynobiidae, Amphibia, salamander, Japan.

The validity of *Parapharyngodon* Chatterji, 1933, has been in question almost since its proposal by Chatterji (1933). Baylis (1936) considered it to be a synonym of *Thelandros* Wedl, 1862; Karve (1938), García-Calvente (1948), and Skrjabin et al. (1951) maintained this synonymy. Freitas (1957) reinstated the genus; Chabaud (1965) returned it to synonymy with *Thelandros*. Sharpilo (1976), on the basis of the presence of lateral alae, reinstated *Parapharyngodon*, but Petter and Quentin (1976) did not accept lateral alae as a differential character and again synonymized *Parapharyngodon* with *Thelandros*. Adamson (1981) reestablished *Parapharyngodon* based on the dietary habits of the host, genital cone morphology (well developed in males of *Thelandros*, reduced or absent in *Parapharyngodon*), egg morphology (operculum, if present, polar in position, larvated at deposition in *Thelandros*; subpolar operculum, deposited in early stage of cleavage in *Parapharyngodon*), and morphology of the tail of females. Castaño-Fernandez et al. (1987) supported retention of *Parapharyngodon* but restricted separation of the 2 genera to morphological characters, not dietary habits. Males of *Parapharyngodon* lack a genital cone, papillae surround the cloaca, the accessory piece is absent, and the tail is subterminal and curved dorsally, whereas males of *Thelandros* have a narrow, elongated genital cone (sometimes with an accessory piece), papillae are outside the genital cone, and the tail is terminal. Females of *Parapharyngodon* have a conical tail ending in a short spike and the eggs have a subterminal operculum and are in the early stages of cleavage when released. Females of *Thelandros* have various caudal morphologies; in some species the tail is conical, tapering evenly from the anus, whereas in others it is rounded and supports a short filiform appendage. The eggs of *Thelandros* have a terminal operculum and are larvated at deposition.

The Japanese clawed salamander, *Onychodactylus japonicus* (Houttuyn, 1782), is restricted to mountainous areas of Honshu and Shikoku Islands, Japan, where it inhabits coniferous and broad-leafed deciduous forests 20–2,000 m above sea level (Kuzmin, 1995). The ancestors of *O. japonicus* supposedly reached Japan from continental Asia by way of the Korean peninsula (Kuzmin, 1995). Previously reported helminths of *Onychodactylus japonicus* include: the monogenetic trematode, *Pseudopolystoma dendriticum* (Ozaki, 1948); the digenetic trematodes, *Cephalouterina leoi* Uchida, Uchida, and Kamei, 1986, and *Mesocoelium brevicaecum* Ochi, 1930; the cestode, *Cylindrotaenia* sp. (=*Baerietta* sp., larvae only); and the nematodes, *Amphibiocapillaria tritonispunctati* (Diesing, 1851)

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(=*Capillaria filiformis* (Linstow, 1885)), *Pseudoxyascaris japonicus* Uchida and Itagaki, 1979, *Pharyngodon* sp., and *Rhabditis* sp. (Wilkie, 1930; Pearse, 1932; Ozaki, 1948; Uchida and Itagaki, 1979; Uchida et al., 1986). To our knowledge there are no reports of *Parapharyngodon* from Japanese salamanders, although Hasegawa (1988) reported an unidentified species of *Parapharyngodon* from the scincid lizard, *Ateuchosaurus pellopleurus* Hallowell, 1860, from Okinawa, Japan. The purpose of this paper is to describe a new species of nematode, *Parapharyngodon japonicus* from a salamander *Onychodactylus japonicus* from Japan, and to provide a current list of species assigned to the genus *Parapharyngodon*.

Materials and Methods

Sixty-eight *Onychodactylus japonicus*, mean snout–vent length = 62.4 ± 4.3 mm (range 43–72 mm), were collected by hand and fixed in neutral buffered 10% formalin, preserved in 70% alcohol, examined for intestinal helminths, then deposited in the Natural History Museum of Los Angeles County (LACM). Sixty-five were from Hineomata Village (37°01′N, 139°23′E), 1,100–1,200 m elevation, Fukushima Prefecture, Honshu Island, Japan (LACM 143245–143260, collected 13 June 1995; LACM 143715–143736, 19 June 1996; LACM 144266–144292, 7 June 1997), and 3 were from Hakoné Mountain (35°12′N, 139°00′E), ca. 800 m elevation, Hakoné, Kanagawa Prefecture, Honshu Island, Japan (LACM 143714, 28 May 1980; LACM 143712, 13 May 1986; LACM 143713, 8 June 1993). The body cavity was opened by a longitudinal incision from vent to throat and the gastrointestinal tract was removed and opened longitudinally. Nematodes were removed, placed in undiluted glycerol, allowed to clear, and examined under a light microscope. Measurements are given in micrometers.

Results

Parapharyngodon japonicus sp. n. (Figs. 1–6)

Description

GENERAL: Robust nematodes with prominent annulations beginning just behind cephalic extremity and continuing to anus. Moderate sexual dimorphism. Triangular oral opening surrounded by 3 bilobed lips. One small, pedunculate amphid on each ventrolateral lip. Lateral alae present in males, absent in females. Males without caudal alae; caudal filament directed dorsally. Females with conical tail terminating in short, stiff spike.

MALE (holotype and 9 paratypes; mean and range): Length 789 (620–1,170). Width 131 (115–153). Lateral alae beginning near level of esophagus isthmus, increasing gradually in width and ending abruptly about 80 μm anterior to cloaca. Annulations about 2 μm apart. Esophagus 160 (131–177), bulb length 45 (40–51), bulb width 43 (37–48). Nerve ring 116 (86–143), excretory pore 57 (40–74) from anterior, respectively. Tail 27 (23–34), reduced to a slim appendage inserted dorsally and directed obliquely to longitudinal axis of body. Spicule 53 (45–57). Testis reflexed behind esophagus. Three pairs of caudal papillae: 1 pair ventral, precloacal; 1 pair sublateral, postcloacal; 1 pair on caudal appendage. Posterior cloacal lip thickened centrally.

FEMALE (allotype and 9 paratypes; mean and range): Length 2,493 (1,820–3,250). Without lateral alae. Width at vulva 469 (306–714). Esophagus 298 (257–336), bulb length 85 (68–100), bulb width 92 (72–114). Nerve ring 206 (125–239), excretory pore 718 (459–969), vulva 1,207 (765–1,785) from anterior, respectively. Tail 91 (57–114). Amphidelphic; uteri divergent; anterior uterus directed anteriorly, posterior uterus directed posteriorly; ovaries reflexed, remaining below level of esophageal bulb; muscular ovijector, nonsalient vulva. Egg oval, in profile slightly flattened on 1 side, 92 (77–100) by 42 (34–48), thin-shelled, with subterminal operculum. Eggs in ovijector at pronucleus stage of development.

Taxonomic summary

TYPE HOST: *Onychodactylus japonicus* (Houttuyn, 1782).

TYPE LOCALITY: Hineomata, Fukushima Prefecture, Honshu Island, Japan, 37°01′N, 139°23′E.

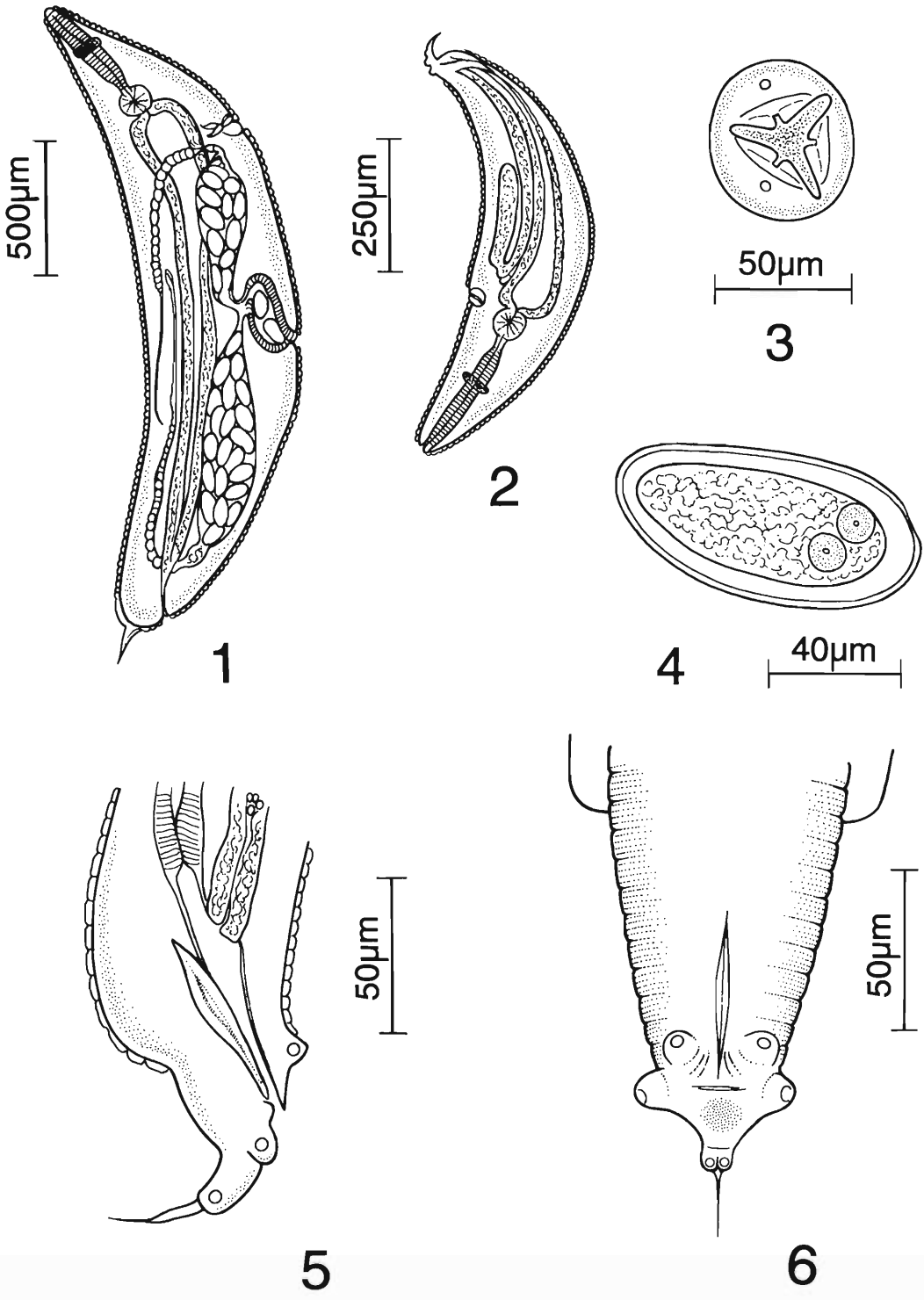
SITE OF INFECTION: Small intestine.

TYPE SPECIMENS: Holotype: male, U.S. National Parasite Collection, Beltsville, Maryland, USNPC 88238; allotype, female, USNPC 88239; paratypes (9 males, 9 females), USNPC 88240.

ETYMOLOGY: The new species is named in reference to the country of origin.

Discussion

We consider the most significant character for separation of *Parapharyngodon* and *Thelandros* to be egg morphology. Based on egg morphology, as defined by Castaño-Fernandez et al.



Figures 1–6. ***Parapharyngodon japonicus*** **sp. n. 1. Female, entire, lateral view. 2. Male, entire, lateral view. 3. Female, en face view. 4. Egg, pronuclear stage. 5. Male, posterior end, lateral view. 6. Male, posterior end, ventral view.**

Table 1. Current list and selected characters of species assigned to *Parapharyngodon*.

Biogeographical realm Species of *Parapharyngodon*	Spicule (μm)	Cloacal lip	Ovary	Egg size (μm)	Reference
Australian Realm					
P. anomalus Hobbs, 1996	63	echinate	prebulbar	83–95 × 43–50	Hobbs, 1996
P. fitzroyi Jones, 1992	80–92	echinate	prebulbar	88–96 × 48–56	Jones, 1992
P. kartana (Johnston and Mawson, 1941)	55	smooth	not given	75–90 × 35–45	Johnston and Mawson, 1941
Ethiopian Realm					
P. adramitana Adamson and Nasher, 1984	80–86	echinate	prebulbar	109–119 × 69–78	Adamson and Nasher, 1984
P. bulbosus (Linstow, 1899)	51–63	smooth	postbulbar	90–99 × 54–57	Moravec et al., 1987
P. meridionalis (Chabaud and Brygoo, 1962)	80	echinate	postbulbar	115 × 62	Chabaud and Brygoo, 1962
P. rotundatus (Malan, 1939)	96–140	smooth	prebulbar	84–108 × 52–56	Malan, 1939
P. rousseti (Tcheprakoff, 1966)	110	echinate	prebulbar	not given	Tcheprakoff, 1966
Nearctic Realm					
P californiensis (Read and Amrein, 1952)	53–76	smooth	prebulbar	90–110 × 48–52	Read and Amrein, 1952
P. iguanae (Telford, 1965)	43	echinate	prebulbar	85–98 × 43–53	Telford, 1965
Neotropical Realm					
P. alvarengai Freitas, 1957	80–100	smooth	prebulbar	78–87 × 39–52	Freitas, 1957
P. cubensis (Barus and Coy-Otero, 1969)	77	smooth	prebulbar	82–90 × 49–70	Barus and Coy-Otero, 1969
P. garciae Schmidt and Whittaker, 1975	30–45	smooth	prebulbar	80–85 × 50–56	Schmidt and Whittaker, 1975
P. largitor Alho and Oliveira-Rodrigues, 1963	54–68	smooth	prebulbar	72–82 × 32–33	Alho and Oliveira-Rodrigues, 1963
P. osteopili Adamson, 1981	53–61	echinate	prebulbar	110–129 × 47–61	Adamson, 1981
P. scleratus (Travassos, 1923)	80–109	smooth	prebulbar	77–126 × 36–54	Barus, 1973
P. verrucosus Freitas and Dobbin, 1959	55–63	smooth	prebulbar	78–82 × 35–38	Freitas and Dobbin, 1959
Oriental Realm					
P. almoriensis (Karve, 1949)	85–105	echinate	postbulbar	80–100 × 50–70	Karve, 1949
P. calotis (Johnson, 1966)	31	smooth	prebulbar	91–92 × 38–54	Johnson, 1966
P. kasauli (Chatterji, 1935)	94–114	smooth	not stated	86–102 × 55–63	Chatterji, 1935
P. maplestonei Chatterji, 1933	76–90	smooth	prebulbar	80–91 × 42–50	Chatterji, 1933
Palaearctic Realm					
P. dogieli Markov and Bogdanov, 1965	93–110	echinate	prebulbar	127–135 × 48–56	Sharpilo, 1976
P. echinatus (Rudolphi, 1819)	74–112	echinate	postbulbar	88 × 45	Seurat, 1917
P. lilfordi Castaño-Fernandez, Zapatero-Ramos, Solera-Puertas, and Gonzalez-Santiago, 1987	67–85	smooth	prebulbar	99 × 66	Castaño-Fernandez et al., 1987
P. japonicus sp. n.	45–57	smooth	postbulbar	77–100 × 34–48	this study
P. micipsae (Seurat, 1917)	88	echinate	prebulbar	91 × 50	Seurat, 1917
P. pavlovskyi Markov, Ataev, and Bogdanov, 1968	74–87	echinate	prebulbar	91–100 × 48–56	Sharpilo, 1976
P. psammodromi Roca and Lluch, 1986	absent	smooth	prebulbar	88–104 × 52–62	Roca and Lluch, 1986
P. skrjabini Vakker, 1969	139–176	smooth	prebulbar	82–93 × 46–48	Sharpilo, 1976
P. tyche Sulahian and Schacher, 1968	100–110	smooth	postbulbar	90–100 × 45–60	Sulahian and Schacher, 1968

(1987), the species harbored by *Onychodactylus japonicus* is assigned to the genus *Parapharyngodon.*

The most recent list of species of *Parapharyngodon* is that of Baker (1987), in which 33 species are listed. *Parapharyngodon aegyptiacus* Moravec, Barus, and Rysavy, 1987, has since been transferred to *Skrjabinodon* Inglis, 1968, by Moravec and Barus (1990). Six species on Baker's list have eggs with terminal opercula; thus, based on the criteria of Castaño-Fernandez et al. (1987), these species should be assigned to *Thelandros,* namely, *T. awokoyai* (Babero and Okpala, 1962) comb. n.; *T. bicaudatus* Read and Amrein, 1952; *T. maculatus* Caballero, 1968; *T. pseudothaparius* Lucker, 1951; *T. senisfaciecaudus* (Freitas, 1957) comb. n.; and *T. xantusi* Lucker, 1951. The egg morphology has not been described for 4 species from Baker's list, *P. bulbosus* (Linstow, 1899) Freitas, 1957; *P. garciae* Schmidt and Whittaker, 1975; *P. kartana* (Johnston and Mawson, 1941) Adamson, 1981; and *P. mabouia* (Rao and Hiregauder, 1962) Adamson, 1981. We were able to examine a specimen of *P. kartana* (USNPC 88241), the eggs of which had subterminal opercula. Specimens of *P. bulbosus, P. garciae,* and *P. mabouia* were not available for examination. Until egg morphology is described, we will provisionally retain *P. bulbosus* and *P. garciae*; *P. mabouia* is inadequately described and is to be considered a species inquirendae. Five additional, recently described species should be added to Baker's list, namely *P. psammodromi* Roca and Lluch, 1986; *P. lilfordi,* Castaño-Fernandez, Zapatero-Ramos, Solera-Puertas, and Gonzalez-Santiago, 1987; *P. fitzroyi* Jones, 1992; *P. anomalus* Hobbs, 1996; and *P. japonicus* sp. n. A revised list of *Parapharyngodon* is given in Table 1.

In addition to the species in Table 1, 10 species assigned to *Parapharyngodon* are considered species inquirendae: females are unknown for *P. szczerbaki* Radchenko and Sharpilo, 1975; males are unknown for *P. cincta* (Linstow, 1897) Freitas, 1957, *P. megaloon* (Linstow, 1906) Adamson, 1981, and *P. waltoni* (Read and Amrein, 1952) Adamson, 1981; inadequately described are *P. aspiculus,* Khera, 1961, *P. cameroni* (Belle, 1957) Adamson, 1981, *P. evaginatus* Fotedar, 1974, *P. fotedari* Kalyankar and Palladwar, 1977, *P. macrocerca* Fotedar, 1974, and *P. seurati* (Sandground, 1936) Freitas, 1957.

Species of *Parapharyngodon* are distinguished on the basis of the morphology of the anterior cloacal lip, the location of the ovary, and geographical distribution (Table 1). Of the 30 species in Table 1, with the exception of *P. anomalus, P. garciae,* and *P. japonicus,* all are parasites of lizards. Of the 9 species reported from the Palaearctic Realm, *Parapharyngodon japonicus* is most similar to *P. tyche* in that the anterior cloacal lip is smooth, the ovary is postbulbar, and the eggs are thin-walled and oval in outline. These 2 species differ in that the spicule of *P. japonicus* is half the length of that in *P. tyche,* and the lateral alae of *P. japonicus* end abruptly about 80 μm anterior to the cloaca, whereas in *P. tyche,* the lateral alae continue to the end of the body.

Hasegawa (1988) reported an unidentified species of *Parapharyngodon* from the lizard *Ateuchosaurus pellopleurus* Hallowell, 1860 from Okinawa, Japan. This species differs from *P. japonicus* in that its ovarian coils are prebulbar, the tail of the female is conical, and the egg has a pitted, thick wall and is somewhat triangular in outline.

Acknowledgments

We thank Tatsuo Ishihara (Hakoné Woodland Museum, Hakoné, Japan) for the samples of *Onychodactylus japonicus,* Peggy Firth for the illustrations constituting Figures 1–6, Hay Cheam and Cynthia Walser for assistance with dissections, and Serge Ferleger for Russian translation.

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Paraochoterenella javanensis gen. et sp. n. (Filarioidea: Onchocercidae) from *Rana cancrivora* (Amphibia: Anura) in West Java, Indonesia

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ABSTRACT: *Paraochoterenella javanensis* gen. et sp. n. (Filarioidea: Onchocercidae) is described from the mesentery of the frog *Rana cancrivora* Gravenhorst in West Java, Indonesia. *Paraochoterenella javanensis* presently represents the only species in this newly created genus. Three of 13 frogs contained mature male and female worms and microfilariae. *Paraochoterenella* is distinguished from the other 4 genera, *Foleyellides* Caballero, *Ochoterenella* Caballero, *Madochotera* Bain and Brunhes, and *Paramadochotera* Esslinger in the subfamily Waltonellinae Bain and Prod'hon by the presence of cuticularized parastomal structures in both sexes, a distinct cuticularized buccal capsule, the lack of both lateral and caudal alae, and the presence of scattered (nonoriented) minute bosses on the cuticle of the midbody region. The microfilariae are unsheathed and slightly narrowed at the caudal extremity, with a 10:1 length to width ratio. *Paraochoterenella* represents the second genus in the subfamily Waltonellinae present in southern Asia and the first report of a filarial species in the subfamily from an Indonesian amphibian. A revised key to the genera is presented in light of this new addition to the subfamily.

KEY WORDS: Filarioidea, Onchocercidae, Waltonellinae, *Paraochoterenella javanensis* gen. et sp. n., taxonomic key, *Rana cancrivora,* Amphibia, Anura, Ranidae, morphology, Java, Indonesia.

The majority of the species contained in the subfamily Waltonellinae Bain and Prod'hon, 1974 (Filarioidea: Onchocercidae) have been described from the Western Hemisphere, particularly neotropical areas. Esslinger (1986a, b) provided redescriptions of type material of *Ochoterenella* Caballero, 1944, and *Foleyellides* Caballero, 1935, and revisions of the 4 related genera in the subfamily. Species previously assigned to the genus *Waltonella* Schacher, 1975, were transferred into the genera *Foleyellides* and *Ochoterenella,* the name *Waltonella* was placed as a junior synonym of *Foleyellides,* and the subfamily designation Waltonellinae was retained (Esslinger, 1986a, b). Members of this filarial assemblage have only been found in the body cavities of anuran amphibians, with the exception of 1 subcutaneous parasite, *Foleyellides confusa* (Schmidt and Kuntz, 1969; see Anderson and Bain, 1976). The subfamily members are parasites of toads and frogs in the families Bufonidae, Leptodactylidae, Racophoridae, and Ranidae.

Three of 13 frogs identified as *Rana cancrivora* Gravenhorst, 1829 (Anura: Ranidae), and collected from Bekasi, West Java, Indonesia, were examined and discovered to harbor adults and microfilariae of an *Ochoterenella*-like nematode. Microfilariae found in the blood and adult male and female worms removed from the mesentery belong to a previously unknown genus and species as described herein.

Materials and Methods

Live frogs were obtained from a local food dealer residing in Jakarta. All had been captured from the same locality along drainage ditches, approximately 5 km east of the city of Jakarta proper. Live adult worms were removed from the mesentery, relaxed in 0.6% saline solution, fixed in hot 70% ethanol, and preserved in 70% ethanol/5% glycerine. All specimens were cleared and temporarily mounted and examined in lactophenol. Microfilariae were obtained from blood. Thick blood films were processed with Giemsa's stain diluted 1:15 with pH 7.2 sodium phosphate buffer for 15 min. Drawings and measurements were made with the aid of a camera lucida. All measurements are expressed as means followed by the range in parentheses and are given as length by width in micrometers (μm) unless otherwise indicated.

Results

Paraochoterenella gen. n.

DIAGNOSIS: Onchocercidae (Leiper, 1911) Chabaud and Anderson, 1959; Waltonellinae Bain and Prod'hon, 1974. Cephalic end with pair of lateral flap-like cuticularized parastomal structures. Cephalic plate with lateral axis slightly longer than dorsoventral axis; 4 pairs cephalic papillae, broad basally and tapered with nonarticulated distal portion. Distinct cuticularized

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buccal cavity. Lateral and caudal alae lacking. Esophagus divided into a short anterior muscular region and a long, wider posterior glandular portion (muscular to glandular ratio: 6.1). Vulva in posterior region of glandular portion of esophagus near esophageal–intestinal junction. Two pairs of preanal, 4 pairs of postanal papillae. Cuticular bosses minute (<2–3 μm), nonbacillary in appearance, with irregular scattered distribution from anterior cephalic to caudal region just beyond anus. Microfilaria unsheathed, slightly tapered at caudal end. Parasite of body cavity of frog (Ranidae) in tropical Southeast Asia.

TYPE AND ONLY SPECIES: *Paraochoterenella javanensis* sp. n. from *Rana cancrivora* (West Java, Indonesia).

Paraochoterenella javanensis sp. n. (Figs. 1–17)

Description

GENERAL: Adult worms small and filiform, yellow to white. Anterior end blunt. Posterior end conical and blunt. Female 2.7 times as long as male. Four pairs of submedian papillae and 2 lateral cephalic amphids (Figs. 1, 9). A pair of lateral flap-like cuticularized parastomal structures (Fig. 9). Cuticularized buccal cavity (Figs. 8, 10). Esophagus divided into anterior muscular and posterior glandular portion, the latter being longer and wider, with ratio 6.1 (Fig. 3). Vulva near esophagointestinal junction. Nerve ring at posterior half of muscular region of esophagus. Lateral and caudal alae absent. Two pairs of preanal, 4 pairs of postanal papillae; first 2 pairs well anterior to anus (Fig. 7). Larger (left) spicule long, with very slender shaft (Fig. 6). Cuticle transversely striated (Fig. 2), with minute cuticular bosses present in nonoriented, irregular distribution (Figs. 11–17).

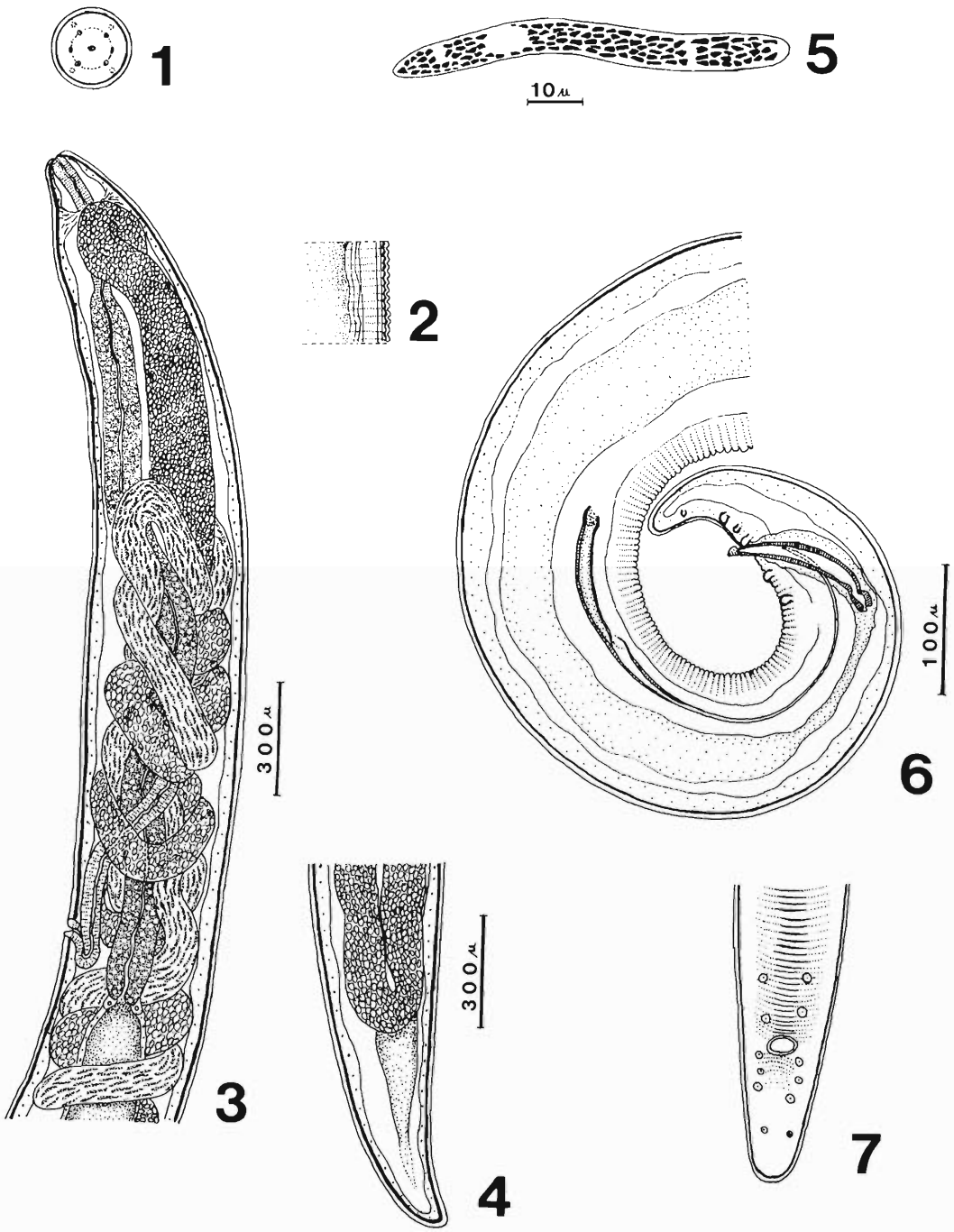
MALE (based on 3 mature specimens: 1 complete and 2 partial): Body 8.2 mm long by 52 wide at level of head; width increasing posteriorly, 104 at level of nerve ring, 156 at level of esophageal–intestinal junction, and 176 (160–200) at midlevel of body, gradually decreasing posteriorly, 71 (65–80) at level of anus and 48 (45–52) at midlevel of tail. Esophagus 1.7 mm, distinctly divided into anterior muscular portion 187 by 26 and posterior glandular region 1.51 mm by 78. Nerve ring 130 from cephalic end. Tail curved ventrally, 80 (78–85). Spicules thin, unequal in length, and dissimilar in appearance. Larger (left) spicule 389 (380–398), composed of 3 sections: a thick-walled cylindrical section 105 (99–117) having an open capitulum at proximal position, a thin-walled midsection 27 (25–39), and a long narrow rod-like distal portion 250 (234–260), ending in pointed tip (Fig. 6). Smaller (right) spicule 106 (104–110), ending in hook-like tip. Left to right spicule ratio 3.7 (3.4–3.8):1. Gubernaculum absent. Cuticle at cervical, midbody, area rugosa, and anal region (Figs. 14–17) with scattered (nonoriented) minute bosses (<2–3 μm).

FEMALE (based on 3 gravid specimens): Body 22.0 (21.8–22.5) mm by 63 (60–70) at level of head, width increasing posteriorly, 120 (110–130) at level of cervical region, 197 (190–200) at level of nerve ring, 410 (380–430) at level of vulval opening, 413 (400–440) at level of esophageal–intestinal junction, 477 (450–520) at midbody, gradually decreasing to 159 (156–166) at anal opening and 80 (70–90) at midlevel of tail. Esophagus 2.31 (2.15–2.50) mm, distinctly divided into anterior muscular region 325 (280–370) by 41 (31–47) and posterior glandular region 1.97 (1.87–2.13) mm by 120 (104–130), muscular to glandular ratio 6.1 (5.7–6.7). Nerve ring 152 (150–156) from cephalic end. Vulva, opening as transverse slit, anterior to esophageal–intestinal junction, 2.15 (2–2.26) mm from cephalic end (Fig. 3). Vagina directed anteriorly and flexing and looping posteriad before receiving bifurcated uterus at varying distance below vulva. Uteri paired, loosely entwined, joining oviduct and extending anteriorly to within 277 (140–340) from cephalic end; posterior coil extending to within 277 (140–300) from caudal end. Viviparous. Tail 230 (150–286) with blunt end (Fig. 4). Cuticular bosses as in male, minute and nonoriented (Figs. 11–13).

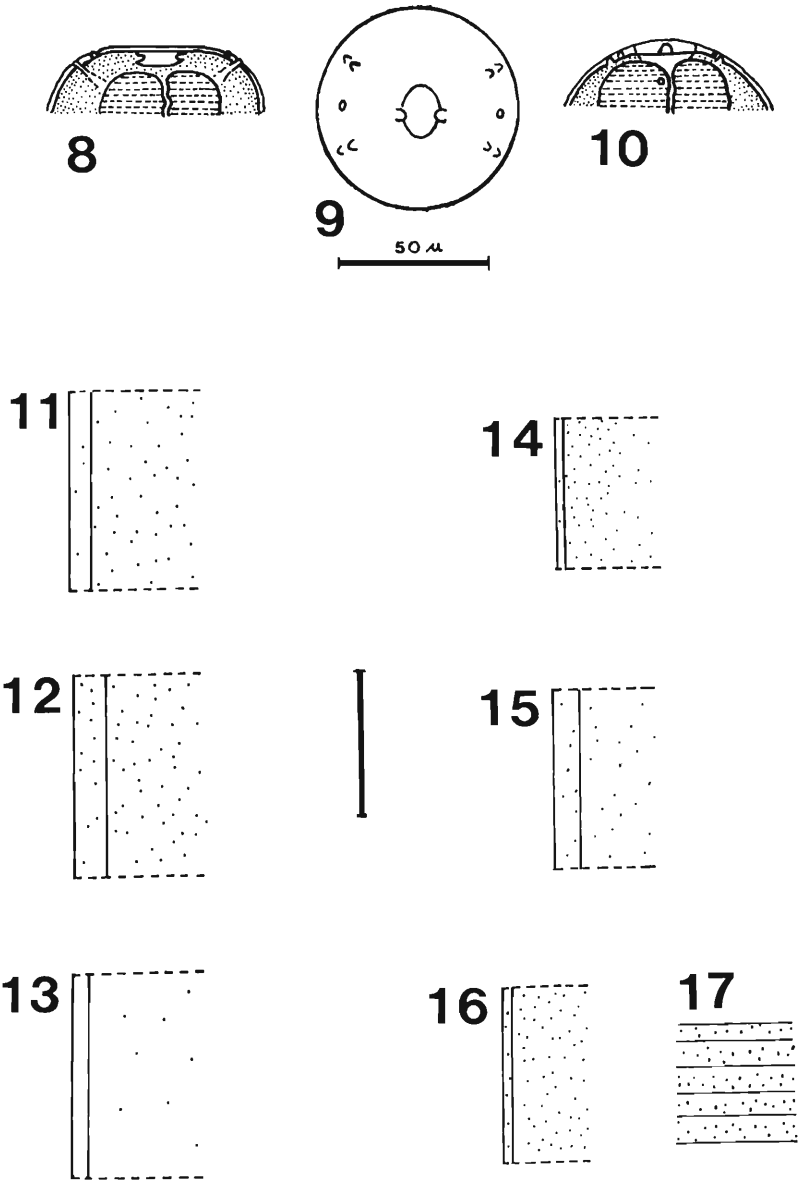
MICROFILARIA (based on 20 specimens): Body stout and elongated, unsheathed 80.8 (70–92) long. Caudal extremity slightly narrowed, not bulbous or rounded (Fig. 5). Width at level of first cephalic nucleus 6.7 (5–7), nerve ring 8.6 (8–9), excretory pore 8.5 (8–9), anal pore 7.0 (6–8), and at level of last caudal nucleus 2.3 (2–3). One single tail nucleus. Nerve ring 21.6 (19–25), excretory pore 52.3 (43–57), and anal pore 68.7 (56–78) from cephalic end. Cephalic space length to width ratio, 0.4 (0.3–0.6):1.

Taxonomic summary

TYPE HOST: The mangrove frog, *Rana cancrivora* Gravenhorst, 1829.



Figures 1–7. Adults and microfilaria of *Paraochoterenella javanensis* gen. et sp. n. 1. Generalized en face view of female showing arrangement of 4 pairs of submedian papillae and 2 lateral amphids. 2. Transversely striated cuticle of female. 3. Anterior region of female, lateral view. 4. Caudal end of female, lateral view. 5. Microfilaria from blood. 6. Caudal end of male, lateral view showing left and right spicules, cloaca, and caudal papillae. 7. Caudal end of male, ventral view showing arrangement of caudal papillae. All scale bars in μm.



Figures 8–17. ***Paraochoterenella javanensis*** **gen. et sp. n. 8. Cephalic extremity of female, dorsal view showing cuticularized buccal capsule. 9. Cephalic extremity of female, en face view showing arrangement of papillae, amphids, and parastomal structures. 10. Cephalic extremity of female, lateral view. 11, 12, 13. Minute bosses on female, lateral views of cervical region (11), midbody (12), and anal region (13). 14, 15, 16. Minute bosses on male, lateral view, cervical region (14), midbody (15), and anal region (16). 17. Detail of area rugosa of male, ventral view. Scale bars = 50 μm (Figs. 8–10) and 200 μm (Figs. 11–17).**

TYPE LOCALITY: Indonesia, West Java, Bekasi.

SITE OF INFECTION: Mesentery.

DATE OF COLLECTION: AUGUST 1990.

DEPOSITED SPECIMENS: Holotype male, USNPC 82165; allotype female, USNPC 82166; paratypes, 2 females, USNPC 82167 in 70% ethanol/5% glycerine; 1 blood slide, Giemsa-stained microfilariae (syntypes), USNPC 82168, deposited in the U.S. National Parasite Collec-

tion (USNPC), Beltsville, Maryland. Preserved frog specimens have been retained at U.S. Naval Medical Research Unit-2 in 10% formalin.

ETYMOLOGY: The specific epithet is derived from the type locality of the new species.

Remarks and Discussion

The finding of *Paraochoterenella javanensis* sp. n. from the mangrove frog, *Rana cancrivora,* in Bekasi, West Java, represents the first report of a filarial species in the subfamily Waltonellinae from an Indonesian amphibian. The subfamily members are parasites of toads and frogs in Bufonidae, Leptodactylidae, Racophoridae, and Ranidae. Of the Waltonellinae, only *Foleyellides* and *Paraochoterenella* have been definitively described from ranid frogs (Anderson and Bain, 1976). Geographically, *Ochoterenella* appears restricted to the Neotropical Region. Species of *Foleyellides* have been recorded predominantly in the Western Hemisphere, whereas species of both *Madochotera* Bain and Brunhes, 1968, and *Paramadochotera* Esslinger, 1986, have been described only from Madagascar (Bain and Brunhes, 1968, Esslinger, 1986a).

Based on described morphological measures and structures of adults and microfilariae, together with information on definitive hosts and geographic localities, the generic name *Paraochoterenella* is proposed to accommodate the new species, *P. javanensis.* The specific characters deemed important in distinguishing genera in the subfamily Waltonellinae, as revised by Esslinger (1986a, b), are the presence or absence of caudal alae and parastomal structures, the appearance and arrangement of the cuticular bosses, and the morphology of the microfilariae. *Paraochoterenella* gen. n. shares various characters with the other 4 genera, including paired cephalic papillae without articulated tips, cuticularized parastomal structures, the absence of lateral and caudal alae, a distinct buccal formation, the vulva near the base of the glandular esophagus, a thin, elongated (left) spicule shaft, and being a parasite of an anuran (Anderson and Bain, 1976). The principal characters that separate *Paraochoterenella* from other genera are the unsheathed microfilaria and the appearance and arrangement of the cuticular bosses.

Of the 4 previously recognized genera in the subfamily, *Paraochoterenella* appears most closely aligned with *Ochoterenella.* However, Esslinger (1986a, 1988) concluded that all *Ochoterenella* species are a morphologically uniform group, restricted to the Neotropical Region. With the exception of only 2 species, both recovered from leptodactylid frogs, all have been found only in the toad *Bufo marinus* Linnaeus, 1758 (Esslinger, 1988). Before Esslinger's (1986a) detailed reassessment, only 3 species of *Ochoterenella* Caballero, 1944 (Caballero, 1944; Johnston, 1967), in the subfamily (Bain and Prod'hon, 1974) had been assigned to the genus. *Ochoterenella digiticauda* Caballero, 1944, has been found in Mexico, Guatemala, and Paraguay (Lent et al., 1946; Yamaguti, 1961). *Ochoterenella papuensis* Johnston, 1967, found in the frog *Platymantis* (=*Cornufer*) *papuensis* Meyer, 1875 has been reported only from New Guinea (Johnston, 1967), whereas *Ochoterenella guibei* Bain and Prod'hon, 1974 from a racophorid frog, appears in Madagascar.

Esslinger (1988) included 14 members in *Ochoterenella,* partially the result of a previous transfer of 8 species in the genus *Waltonella* to *Ochoterenella* (Esslinger, 1986a). *Ochoterenella guibei* from Madagascar was placed in a new genus *Paramadochotera. Ochoterenella papuensis* from New Guinea, as described by Johnston (1967), was considered incertae sedis and was removed from the genus until more material could be fully described (Esslinger, 1986a). An incompletely described *Ochoterenella* species from northern Viet Nam (Moravec and Sey, 1985) is also considered incertae sedis for the present. Specific identification of the Viet Nam filariid was not possible because of the absence of males and the poor condition of the 5 female specimens. It is also noted that both Asian populations assigned to *Ochoterenella* lacked a distinct buccal cavity and the microfilariae were unsheathed, characters present in all known members of *Ochoterenella* (Esslinger, 1986a, b). However, because *O. papuensis* and the Viet Nam specimens represent the only purported members of the genus described from the Asian region, both are briefly mentioned in this discussion.

Paraochoterenella javanensis can be distinguished from *O. digiticauda* (the type species), *O. papuensis,* and *Ochoterenella* from Viet Nam (VN) by the following characters: adult male and female worms are shorter in body length (except VN sp.), the longer (left) spicule is nearly 4 times as long as the right (male not described for VN sp.), and the spicule ratio (3.7:

1) is greater (1.7:1 and 2:1, respectively). Unlike all recognized members of *Ochoterenella,* the microfilariae of *P. javanensis* are unsheathed in blood. On average, the microfilariae are shorter in length, but have a distinctly smaller length to width body ratio (10:1) compared to *O. digiticauda* and *O. papuensis* (~30:1) and *Ochoterenella* VN (~20:1). The tip of the microfilaria tail is slightly narrowed versus the rounded, usually bulbous appearance in *O. digiticauda.* The VN microfilariae were described as unsheathed.

In *Ochoterenella,* the appearance and length of individual bosses in both sexes are considered consistent within a species (Esslinger, 1986a). Depending on the site of measurement, the individual bosses of *O. digiticauda* ranged in mean size from 8.7 μm at the midbody to 4 μm at the midportion of the area rugosa (Esslinger, 1986a). The scattered appearance of minute bosses on the cuticle, in the size range of 2–3 μm, clearly set *P. javanensis* apart from *Ochoterenella* species. *Ochoterenella papuensis* female worms apparently lack surface tubercles, and tubercles were not described for the VN specimen.

The arrangement of male preanal and caudal papillae differs among the 4 descriptions. *Paraochoterenella javanensis* has 2 pairs of preanal and 4 pairs of postanal papillae, and *O. digiticauda* has 2 pairs of preanal and 3 pairs of postanal (Caballero, 1944) or 1 pair of preanal and 3 pairs of postanal papillae as reported by Lent et al. (1946) and Esslinger (1986a). *Paraochoterenella javanensis* also lacks a median ventral preanal plaque. *Ochoterenella papuensis* has 2 single preanal papillae in tandem, 2 adanal papillae, and 3 pairs of postanal papilla. *Paraochoterenella javanensis* has 4 pairs of anterior submedian papillae, 2 lateral cephalic amphids, and parastomal structures similar to those of *O. digiticauda* and the VN *Ochoterenella* sp. The position of the vulva is very near the glandular esophagointestinal junction, similar to that in *O. digiticauda.* In *O. papuensis,* the vulva was indistinct, lying slightly behind the musculoglandular esophageal junction, whereas *Ochoterenella* (VN) had it positioned at about the midpoint of the glandular esophagus. Unlike all members of *Ochoterenella, P. javanensis* has a distinct cuticularized buccal capsule, presently found elsewhere only in the genus *Paramadochotera.*

Paraochoterenella represents a second genus in the subfamily present in southern Asia. The distribution and host range of this monotypic genus is not known. To date, only *Foleyellides* (=*Waltonella*) *confusa* from the Philippines and *Foleyellides* (=*Waltonella*) *malayensis* (Petit and Yen, 1979) from peninsular Malaysia have been described. It is possible that specimens described from Viet Nam and New Guinea may be members of *Paraochoterenella,* because their microfilariae also lacked a cuticular sheath; however, a decision regarding this possibility awaits full descriptions. The limited number of species described outside the Western Hemisphere may be more reflective of the lower relative number of investigations on amphibians and their nematodes from other areas of the world (Esslinger, 1986b). Given the wide range and species diversity of anuran amphibian species present in the Asian Region, this would not seem unreasonable.

Nothing is known of the biology or transmission of *Paraochoterenella javanensis.* Larval stages have only been described from a few species of *Foleyellides* (=*Waltonella*), based primarily on experimental infections (Bain and Chabaud, 1986). Larval stage development has been observed in adipose and muscle tissue of mosquitoes. Likewise, the natural intermediate hosts of Waltonellinae are poorly known except for a few *Foleyellides.* Vectors are presumed to be blood-feeding dipterans, most likely various culicine mosquitoes (Diptera: Culicidae). In general, as more information becomes available on species morphology, biological variability, distribution, and natural host range of this group of filariids, the diagnostic significance of certain characters used to separate genera and species will become better understood. A revised simplified key to the genera is presented in light of this new addition to the subfamily.

Key to the Genera of the Subfamily Waltonellinae

1a. Cuticularized parastomal structures present 2
1b. Cuticularized parastomal structures absent ..... *Paramadochotera* (Madagascar)
2a. Lateral and caudal alae present 3
2b. Lateral and caudal alae absent 4
3a. Cuticle with transversely oriented ridges and bosses .. *Madochotera* (Madagascar)
3b. Cuticle smooth, generally lacking bosses ..... *Foleyellides* (worldwide)

4a. Cuticle of midbody with annular bands of longitudinally oriented bosses; microfilaria sheathed with tip of tail rounded, often bulbous ..... *Ochoterenella* (Neotropics)

4b. Cuticle of midbody with scattered minute bosses; microfilaria unsheathed with tip of tail slightly narrowed ..... *Paraochoterenella* (Indonesia)

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Research Note

New Records, Hosts, and SEM Observations of *Cercaria owreae* (Hutton, 1954) from the Mexican Caribbean Sea

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ABSTRACT: Digenetic trematode larvae identified as *Cercaria owreae* (Hutton) were recorded in the coela of the following chaetognath species: *Flaccisagitta enflata* (Grassi), *Serratosagitta serratodentata* (Krohn), *Ferosagitta hispida* (Conant), and *Sagitta helenae* Ritter-Zahony. The hosts and parasites were collected during 4 oceanographic cruises in February, March, May, and August 1991. The low prevalence of infection (average 0.11%) was comparable with previous records. The intensity was restricted to 1 parasite. *Ferosagitta hispida* and *Sagitta helenae* are recorded for the first time as hosts of *Cercaria owreae,* and the Mexican Caribbean Sea is reported as a new locality for the geographical distribution of this parasite.

KEY WORDS: *Cercaria owreae,* SEM, scanning electron microscopy, chaetognaths, new records, Caribbean Sea, Mexico.

Cercaria owreae (Hutton, 1954) has been reported parasitizing species of *Sagitta* in the Atlantic Ocean and the Caribbean Sea (Hutton, 1952, 1954; Suárez-Caabro, 1955; Dawes, 1958, 1959). However, parasites of holoplanktonic organisms such as chaetognaths have not been studied in the vicinity of the Mexican Caribbean Sea. The main possible reasons for this lack of information are that the larval parasites have been mistaken for food remains or the holoplanktonic organisms are seldom investigated as hosts; thus, their importance as intermediate hosts has been underestimated and frequently overlooked.

The purpose of this study is to describe larvae of the digenetic trematode *Cercaria owreae* with the aid of scanning electron microscopy (SEM), to determine the prevalence and mean intensity of parasitism in chaetognaths, and to report the chaetognaths *Ferosagitta hispida* and *Sagitta helenae* as new hosts and the Mexican Caribbean Sea as a new locality record.

Zooplankton samples were collected during scientific cruises of the Mexican Navy (Secretaría de Marina) during February, March, May, and August 1991 (cruises I to IV) in the Mexican Caribbean Sea (Fig. 1). The material was intended for studies of the composition, abundance, and species distribution of the major zooplankton groups, and it was during its analysis that trematode larval parasites were observed in the coela of some chaetognaths.

Sampling was carried out from 50 m to the surface in oblique tows with a square-mouth standard net 0.45 m per side (330 μm mesh). Zooplankton material was fixed in 4% buffered (lithium carbonate) formalin. All chaetognaths were sorted from approximately 22 samples from each cruise. Prevalence and mean intensity were calculated according to Margolis et al. (1982). Parasitized chaetognaths were stained with Harris' hematoxylin and acetic carmine, cleared with methyl salicylate, and mounted on permanent slides in synthetic resin. Some chaetognaths were dissected and parasites were extracted for SEM. Twenty-two specimens were mounted on permanent slides and examined using a compound microscope, and 2 specimens were observed and photographed using SEM techniques. Measurements (mm) of 5 parasites are given as the range and mean (in parentheses).

Specimens of the parasites are deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, under the catalogue number 3185 for parasites of *Flaccisa-*

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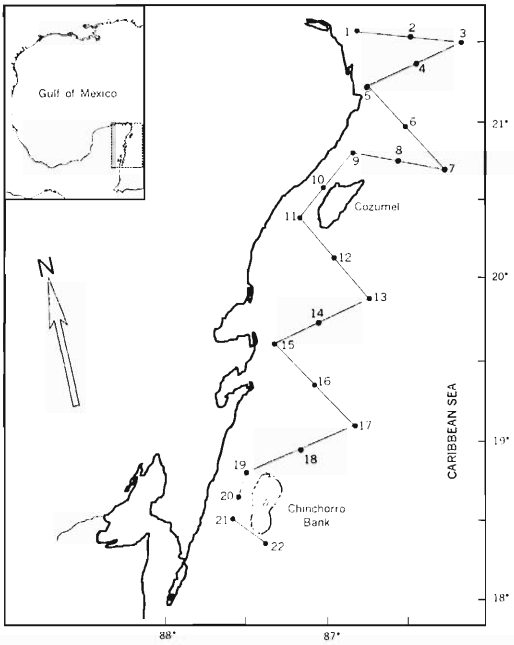


Figure 1. Study area with the locations of the stations sampled in February, March, May, and August 1991. Geographical positions of the stations were similar for the 4 cruises.

gitta enflata and number 3186 for parasites of *Serratosagitta serratodentata.* Specimens from the other 2 species were used for the SEM and are deposited in the SEM laboratory of the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico City.

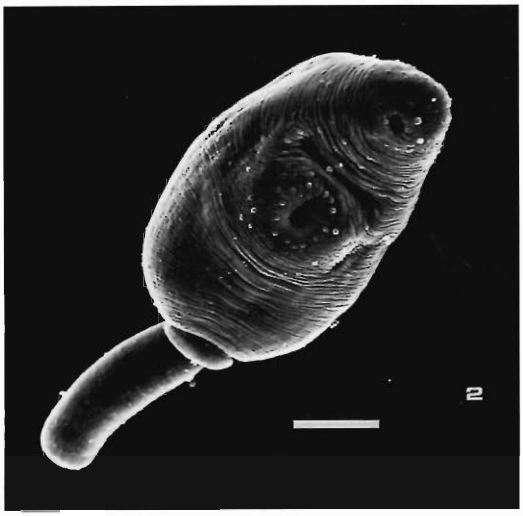
Table 1. Prevalence and intensity of *Cercaria owreae* infecting chaetognaths from the Mexican Caribbean Sea.

Chaetognath species analyzed	*Cercaria owreae**			
	N	P	%P	I
Flaccisagitta enflata	14,583	18	0.12	1
Serratosagitta serratodentata	3,638	1	0.05	1
Ferosagitta hispida	1,015	1	0.09	1
Sagitta helenae	288	2	0.69	1

* N, total number of chaetognaths analyzed; P, total number of chaetognaths parasitized; %P, percentage of chaetognaths infected; I, intensity of parasitism.

A total of 19,524 chaetognaths (prevalence 0.11%) belonging to 4 species were analyzed: *Flaccisagitta enflata* (Grassi, 1881), *Serratosagitta serratodentata* (Krohn, 1853), *Ferosagitta hispida* (Conant, 1891), and *Sagitta helenae* Ritter-Zahony, 1911, had 1 trematode larva per host (Table 1). *Ferosagitta hispida* and *S. helenae* are reported as hosts for the first time, and the Mexican Caribbean Sea is reported as a new locality.

Cercaria owreae has an oval to pyriform body 0.166–0.575 (0.333) long and 0.087–0.235 (0.154) wide and 2 posterior cylindrical appendages 0.066–0.131 (0.107) long (Fig. 2). The tegument has deep circular furrows and dermal pa-



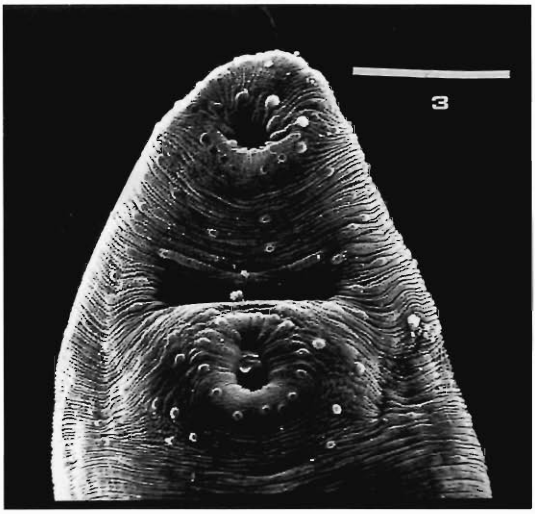


Figure 2. *Cercaria owreae*: **ventral view (SEM) of entire specimen; 1 appendage is missing. Scale 50 μm.**
Figure 3. *Cercaria owreae*: **oral and ventral suckers (SEM) showing dermal papillae. Scale 50 μm.**

pillae in the anteroventral and anterodorsal body regions extending to the acetabulum. The oral sucker, 0.041–0.079 (0.060) long and 0.041–0.1 (0.065) wide, has a subterminal mouth and is strongly muscular, with 11 papillae encircling it and another 5 distributed irregularly (Fig. 2). The acetabulum, 0.045–0.108 (0.104) length and 0.045–0.133 (0.090) width, in a preequatorial position, also has 13 papillae encircling it and 5 to 6 papillae nearby (Fig. 3). The average ratio of the diameters of the oral and ventral suckers is 1:1.7, and there is a slit-like opening anterior to the acetabulum. The muscular pharynx, which is round to oval, leads to a short esophagus and thence to a cecal bifurcation. The esophageal or cecal diverticula were not observed. The intestinal cecum is unbranched and passes into the 2 appendages. No vitelline glands or gonads were observed. The excretory vesicle is Y-shaped and does not enter the posterior appendages. Its lateral excreting tubules join together dorsally to the pharynx. The excretory pore is terminal.

Dermal papillae in the oral and ventral suckers are reported here for the first time; papillae in the anterodorsal and anteroventral body regions were reported in the family Accacoeliidae by Ödhner (1911). Subcuticular tissues from the deep fold facing the acetabulum, which are "thickenings producing small papillae," were reported by Dawes (1959), but the papillae encircling the suckers have not been reported.

Cercaria owreae has been previously reported in the Florida Current, parasitizing the chaetognaths *Flaccisagitta enflata, Flaccisagitta hexaptera* (d'Orbigny, 1836) and *Flaccisagitta lyra* (Krohn, 1853) (see Hutton, 1952, 1954) in the Caribbean Sea between Jamaica and Cuba (Dawes, 1958, 1959) and in Cuban waters in the north (Suárez-Caabro, 1955). It parasitizes *Zonosagitta pulchra* (Doncaster, 1902) northwest of Madagascar; *Serratosagitta serratodentata* var. *atlantica* and *Sagitta bipunctata* Quoy and Gaimard, 1828, in Mauritania; *F. hexaptera* in Cabo Frio and west of Mossamedes in Angola; and *F. enflata* off Gabon, Mauritania, and Liberia (Furnestin and Rebecq, 1966).

Prevalence and mean intensity values of infection in the present study were low, comparable to those obtained by Hutton (1954) and Furnestin and Rebecq (1966), even though the host species are different. To date, 7% is the highest prevalence reported (Dawes, 1959).

The parasites reported here are the smallest reported until now (0.166–0.575). The largest (0.245–2.200) were those reported by Furnestin and Rebecq (1966). These authors reported length variability between posterior appendages and body length. They noted that the perforating trematode larvae emerging from the first intermediate host (a benthic coastal mollusk) were small parasites with similarly small appendages and that both the body of the larva and the appendages would not grow proportionately.

Cercaria owreae has been found in the tropical–subtropical zones (Furnestin and Rebecq, 1966) off the coast of Miami, Florida, in the Caribbean Sea, and in the east and northwest of Africa. However, this distribution does not match that of the chaetognath species; for example, *Flaccisagita enflata* is distributed worldwide (Alvariño, 1964, 1965). No one has recorded a holoplanktonic intermediate host; thus, it seems more plausible that the *Cercaria owreae* distribution recorded until now has been determined by the initial intermediate host, the benthic mollusk (Furnestin and Rebecq, 1966).

According to Dawes (1959), *Cercaria owreae* should be placed within the genus *Accacladocoelium* Ödhner, 1928. The length of the ceca going into the posterior appendages suggests that they could correspond to the anal openings ending in the excretory vesicle walls in the case of the adult; this feature is present in several families, but it has also been observed in 7 genera of the family Accacoeliidae. Additionally, the presence of 6 diverticula in the anterior region of the intestinal ceca on each side resembles the situation in 1 of the genera of the family. Dawes (1959) mentioned that *Accacladocoelium petasiporum* Ödhner, 1928 does not belong to this trematode larval stage because this species has a conspicuous acetabulum, which does not correspond with *Cercaria owreae.* The other 3 species, *Accacladocoelium nigroflavum* (Rudolphi, 1819), *Accacladocoelium macrocotyle* (Diesing, 1858) sensu Monticelli, 1893, and *Accacladocoelium alveolatum* Robinson, 1943, remain to be studied. It is worth mentioning that these 3 species have been reported as parasites of the sunfish *Mola mola* (Linnaeus, 1758), which could indicate that *Cercaria owreae* may parasitize this fish species.

Whatever the course of discussions in relation to the taxonomic position of this trematode, the presence of papillae circling both the oral and ventral suckers in *Cercaria owreae* is a distinc-

tive feature not reported previously in any species of *Accacladocoelium*. This feature raises the possibility of an undescribed species within the genus.

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Research Note

New Host and Locality Records for Three Species of *Glypthelmins* (Digenea: Macroderoididae) in Anurans of Mexico

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ABSTRACT: During an inventory of the helminth parasites of amphibians from several localities in Mexico, trematode parasites of the genus *Glypthelmins* from 5 species of frogs were studied. Three species of *Glypthelmins* were collected from *Rana montezumae*, *Rana dunni*, *Rana neovolcanica*, *Rana megapoda*, and *Rana vaillanti*. New host and locality records for *Glypthelmins quieta* and *Glypthelmins californiensis* in anurans from Mexico are established, and we report *Glypthelmins facioi* for the first time from *R. vaillanti* from Los Tuxtlas, Veracruz State. Diagnostic characters for each parasite species and sister-group relationships are presented.

KEY WORDS: Digenea, Macroderoididae, *Glypthelmins* spp., anurans, systematics, frogs, *Rana* spp., Mexico.

The genus *Glypthelmins* was established by Stafford (1905) to include *Distomum quietum* Stafford, 1900, parasitic in *Rana catesbeiana* Shaw, 1802, *Rana virescens* Kalm, 1878, and *Hyla pickeringii* Holb, 1890, all from Canada. At the present time there is controversy about the species comprising the genus *Glypthelmins*, primarily because the original description of the type species of *Glypthelmins* was incomplete. This, and some degree of intraspecific morphological variability among some members of the genus, have led to taxonomic uncertainty concerning the species. This confusion has resulted in investigators creating nonphylogenetic groups, and some species that should be included in *Glypthelmins* were assigned to other gen-

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Table 1. Prevalence and mean abundance of 3 species of *Glypthelmins* in 5 species of frogs from Mexico.

Host	Locality*	N†	*Glypthelmins*		
			californiensis	*quieta*	*facioi*
Rana montezumae	CLE	89	330‡/23.6§ (3.7)‖	1034/39.3 (11.6)	—
Rana dunni	LZA	73	273/46.6 (3.7)	39/15 (3.5)	—
	LPA	18	4/22.2 (1)	180/50 (20)	—
Rana megapoda	LCU	46	—	6/8.7 (0.13)	
Rana neovolcanica	MCO	34	—	231/31.7 (5.6)	—
Rana vaillanti	LAE	34	—	—	31/41.2 (0.91)

* CLE = Ciénaga de Lerma; LZA = Lago de Zacapu; LPA = Lago de Pátzcuaro; LCU = Lago de Cuitzeo; MCO = Manantiales de Cointzio; LAE = Laguna Escondida.

† *N* = sample size.

‡ Number of worms collected.

§ Prevalence of infection (expressed as %).

‖ Mean abundance of infection (mean no. of worms per host examined).

era such as *Margeana* Cort, 1919, *Microderma* Mehra, 1931, *Choledocystus* Pereira and Cucolo, 1941, *Rauschiella* Babero, 1951, *Reynoldstrema* Cheng, 1959, and *Repandum* Byrd and Maples, 1963 (Miller, 1930; Caballero, 1938; Cheng, 1959; Byrd and Maples, 1963). In Mexico, at least 4 species of the genus have been reported from frogs and toads: *Glypthelmins californiensis* (Cort, 1919) Miller, 1930, *Glypthelmins quieta* (Stafford, 1900) Stafford, 1905, *Glypthelmins intermedia* (Caballero, Bravo, and Zerecero, 1944) Yamaguti, 1958 (=*Choledocystus intermedia*), and *Glypthelmins tineri* (Babero, 1951) Brooks, 1977 (=*Rauschiella tineri*) (see Lamothe-Argumedo et al., 1997; Brooks, 1977). As part of an ongoing inventory of the helminth parasites of amphibians from different localities in Mexico, we establish herein new host and locality records for 3 species of *Glypthelmins*. During this study, we examined the species of *Glypthelmins* deposited at the Colección Nacional de Helmintos (CNHE) and produced a revised list of hosts and species in Mexico.

Between 1996 and 1997, individuals of 18 species of frogs and toads were collected from 9 localities in Mexico. Only at 5 of these localities (Ciénaga de Lerma, Estado de México [CLE], 19°17′N, 99°30′W; Lago de Pátzcuaro, Michoacán [LPA], 19°30′N, 101°36′W; Lago de Zacapu, Michoacán [LZA], 19°49′N, 101°47′W; Manantiales de Cointzio, Michoacán [MCO], 19°35′N, 101°14′W; and Laguna Escondida, Los Tuxtlas, Veracruz [LAE], 20°37′N, 98°12′W), and only in 5 of the 18 species of frogs and toads studied were several specimens of *Glypthelmins* recovered from the intestines of their hosts. Anurans were captured by hand, and in <12 hr they were killed with an overdose of sodium pentabarbitol. All organs and the body cavities of each host were examined for helminths using a stereomicroscope. Digeneans recovered from the intestine were initially placed in 7.5% saline and were subsequently fixed in Bouin's fluid for 12 hr under a coverglass. Some worms were mounted as semipermanent slides in saline and studied alive. Morphological analyses were conducted using an image analyzer (Image-Pro Plus version 1.3 for Windows). Voucher specimens have been deposited at the Colección Nacional de Helmintos, Mexico City (accession numbers 3271–3285), and at the Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska–Lincoln, Nebraska, U.S.A. (accession numbers 39954–39957).

Three species of *Glypthelmins* were found: *G. californiensis,* 607 specimens from 2 species of frogs (*Rana montezumae* Baird, 1854, CLE; *Rana dunni* Zweifel, 1957, LPA and LZA); 1,484 specimens of *G. quieta* from 4 species of frogs (*R. montezumae,* CLE; *R. dunni,* LPA and LZA; *Rana neovolcanica* Hillis and Frost, 1985, MCO; *Rana megapoda* Taylor, 1942, MCO); and 31 specimens of *Glypthelmins facioi* from *Rana vaillanti* Brocchi, 1877, in LAE. Infection data are in Table 1.

The 3 species found show morphological traits that are typical of *Glypthelmins,* including the presence of 2 symmetric or oblique intercecal testes, a median genital pore, the presence of a seminal receptacle, bipartite seminal vesicle,

and an I- or Y-shaped excretory vesicle. *Glypthelmins quieta* is characterized by having 2 groups of prominent peripharyngeal glands on each side of the pharynx extending to the cecal bifurcation, with gland ducts opening at the posterior border of the oral sucker. Vitelline follicles extend from the posterior border of the pharynx and occasionally from the midlevel of the esophagus, reaching far beyond the posterior border of the testes. In addition, *G. quieta* possesses cecal, intracecal, and extracecal uterine loops.

The original description of *G. californiensis* by Cort (1919), based on live specimens, indicated the absence of peripharyngeal glands. We have studied specimens identified as *G. californiensis* from CNHE (nos. 3280–3284) and from the personal collection of Dr. Daniel Brooks from *Rana aurora* Baird and Girard, 1852, from British Columbia, Canada. These specimens possess reduced peripharyngeal glands that surround the pharynx both ventrally and dorsally. Because the location of the holotype of this species is not known, we are unable to confirm this characteristic until a neotype is assigned and studied. However, our observations agree with those made by O'Grady (1987) who described *G. californiensis* from British Columbia, naming these glands as medial glands. *Glypthelmins californiensis* has vitelline follicles that extend anteriorly to the level of the posterior border of the pharynx and occasionally to the posterior border of the oral sucker with follicles confluent dorsally at the cecal bifurcation. The vitellaria extend to the posterior border of the testes. Uterine loops are completely intracecal. In contrast, *G. facioi* is characterized by lacking peripharyngeal glands, vitelline follicles extending anteriad from the cecal bifurcation just beyond the posterior border of the left testis, by having oblique rather than symmetric testes, cecal and intracecal uterine loops, and by having tegumentary spines that extend only along the anterior ⅔ of the body.

These 3 species of *Glypthelmins* constitute a monophyletic clade, according to the phylogenetic hypothesis proposed by Brooks (1977) and Brooks and McLennan (1993). *Glypthelmins facioi* is the sister species of the species pair *G. quieta* + *G. californiensis*. *Glypthelmins facioi* was originally described from *R. pipiens* Schreber, 1782, from Costa Rica by Brenes et al. (1959), and later redescribed by Sullivan (1976). Herein, we report *G. facioi* for the first time from Mexico, thus establishing a new host and locality record. Based on previous geographical records, this species is apparently restricted to the neotropics. *Glypthelmins quieta,* the type species of the genus, is widely distributed in North America, including the eastern U.S.A., Canada, and Central Mexico, parasitizing at least 21 species of anurans in 5 genera (*Acris* Dúmeril and Bibron, 1841, *Bufo* Laurenti, 1768, *Hyla* Laurenti, 1768, *Pseudacris* Fitzinger, 1843, and *Rana* Linnaeus, 1758). In Mexico, this species was previously recorded from *R. montezumae* from Xochimilco and Texcoco lakes, both in the vicinity of Mexico City (Lamothe-Argumedo et al., 1997). In this report we add 4 new locality records (CLE, LPA, LZA, MCO), and 3 host records, all belonging to the *R. pipiens* complex (leopard frogs) including *R. dunni, R. neovolcanica,* and *R. megapoda.*

Glypthelmins californiensis also occurs in the Nearctic Region but has a different geographic distribution than the type species; it occurs in North America, but is known only from 6 species of *Rana* and 1 species of *Hyla.* Its range extends through the western U.S.A. and Canada, converging with *G. quieta* in frogs from the central region of Mexico in localities of the Transverse Neovolcanic Axis, at the boundary between the Nearctic and Neotropical biogeographic zones. Previously, this species was reported in Mexico from *R. montezumae* and *R. pipiens* from Mexico City and Lerma (Caballero, 1942; Caballero and Sokoloff, 1934; Leόn-Règagnon, 1992) and from *R. dunni* from Lake Patzcuaro (Pulido, 1994). Herein, we establish Lake Zacapu as a new locality record for *G. californiensis.* Guillén (1992) recorded *G. californiensis* as a parasite of *Rana berlandieri* Baird, 1854, and *R. vaillanti* from Los Tuxtlas, Veracruz State. We examined specimens deposited at the CNHE (no. 1514, 5 specimens). Based on our diagnoses of the 3 species, we believe these were misidentified because in them the vitellaria extend anteriorly to the level of cecal bifurcation, and posteriorly they extend to the posterior border of the testes. The specimens do have oblique testes, and the uterine loops are intra- and extracecal. In our opinion, they are *G. facioi.*

As can be generally expected, the close phylogenetic relationship between *G. quieta* and *G. californiensis* (see Brooks, 1977; Brooks and McLennan, 1993) determines some degree of

Table 2. Species of *Glypthelmins* recorded from anurans from Mexico.

Species	Host	Locality	Reference
*Glypthelmins californiensis**	*Rana montezumae, Rana pipiens*	México, Distrito Federal Xochimilco, Distrito Federal	Caballero and Sokoloff (1934)
	R. montezumae, R. pipiens	Ciénaga de Lerma, Estado de México	Caballero (1942)
	Rana dunni	Lago de Pátzcuaro, Michoacán	Pulido (1994)
		Lago de Zacapu, Michoacán	This work
*Glypthelmins facioi**	*Rana vaillanti, Rana berlandieri*	Laguna Escondida, "Los Tuxtlas", Veracruz	This work; Guillen (1992)
Glypthelmins intermedia†‡§*	*Bufo marinus*	Rio Huixtla, Chiapas	Caballero et al. (1944)
		Tuxtepec, Oaxaca	Bravo (1948)
*Glypthelmins quieta**	*R. dunni*	Lago de Pátzcuaro and Lago de Zacapu, Michoacán	This work
	Rana megapoda	Lago de Cuitzeo, Michoacán	This work
	Rana neovolcanica	Manantiales de Cointzio, Michoacán	This work
	R. montezumae	Ciénaga de Lerma, Estado de México	This work
		San Pedro Tlaltizapan, Estado de México	León-Règagnon (1992)
		Xochimilco, Distrito Federal and Texcoco, Estado de México	Lamothe-Argumedo et al. (1997)
*Glypthelmins tineri**	"Green frog"	Mexico‖	Babero (1951)

* Intestine.
† Liver.
‡ Gall bladder.
§ Bile ducts.
‖ Locality not determined.

morphological similarity. Detailed examination of diagnostic characters allowed us to review the taxonomic status of species of *Glypthelmins* deposited at the CNHE. We examined specimens from the following lots: lot no. 1561 representing 10 specimens from *R. dunni* from Lake Patzcuaro, identified by Pulido (1994) and labeled as *G. californiensis* (1 individual is actually *G. quieta*); lot no. 1461, represented by 8 specimens from *R. montezumae* identified by León-Règagnon (1992) from Lerma, and labeled as *G. californiensis,* are *G. quieta*; lot no. 1181, 17 specimens from *R. montezumae* from Lerma, collected and identified by Caballero (1942); and lot no. 2495, represented by 8 specimens from *R. montezumae* from Lake Xochimilco, identified by Dr. Eduardo Caballero, were correctly identified as *G. californiensis*; lots no. 1562 (3 specimens) and 1563 (4 specimens), from *R. montezumae* from Lake Xochimilco and Lake Texcoco, respectively, were correctly identified as *G. quieta.*

In Table 2, we present an updated and revised list of species of *Glypthelmins* in anurans from Mexico. Adding previous records to the results, we conclude the genus *Glypthelmins* is currently represented in Mexico by 5 species (*G. quieta, G. californiensis, G. facioi, G. intermedia,* and *G. tineri*) from at least 7 species of *Rana* and 1 species of *Bufo.* The most common of these are *G. californiensis* and *G. quieta,* both found in different species of frogs in localities of the Mesa Central of Mexico. Whether or not these are all the species of *Glypthelmins* that occur in anurans from Mexico will be determined once further research on the helminth fauna of different species of amphibians in the country is finished.

The species composition of the genus *Glypthelmins,* as well as its taxonomic position and relationships to other closely related genera, are still uncertain. Yamaguti (1971) recognized 23 valid species; Brooks (1977) in his phylogenetic analysis of species of *Glypthelmins,* considered 19 species to be valid. Prudhoe and Bray (1982) proposed that some species, allocated originally to other genera, should be transferred to *Glypthelmins,* and then included 27 species in the genus. A complete revision of the genus is necessary to clarify the taxonomic composition of this group of parasites as well as to update the phylogenetic hypotheses of Brooks (1977) and Brooks and McLennan (1993). We are currently obtaining DNA sequences of 18S ribosomal

genes as an additional source of characters. Preliminary results show an agreement of sister-group relationships among the 3 species discussed here.

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Research Note

Radiographic Imaging of the Rat Tapeworm, *Hymenolepis diminuta*

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ABSTRACT: The model of *Hymenolepis diminuta* Rudolphi in laboratory rats was used to investigate potential applications of radiographic imaging in the diagnosis and/or study of tapeworm infections. Radiographic imaging successfully demonstrated the presence of *H. diminuta* in the rat intestine in the presence of a water-soluble iodinated radiographic contrast medium, Gastrografin®. Even single worms and small segments of proglottids could be detected. Optimal imaging was achieved with an exposure factor of 3.75 mAs at 54 kVp with mammography film. Visualization was improved by fasting the rat host to effect the elimination of food and fecal shadows. Elaboration of this methodology may prove useful in basic research and the incidental diagnosis of human tapeworm infection by permitting rapid diagnosis of prepatent infection, thereby providing a useful tool in efficacy testing of anthelmintics when assessing prepatent success and temporal aspects of drug activity.

KEY WORDS: radiographic imaging, tapeworm, Cestoda, *Hymenolepis diminuta,* laboratory rat, diagnosis, Gastrografin, x-ray.

Hymenolepis diminuta Rudolphi, 1819, is a cosmopolitan tapeworm of rats that occasionally infects humans. A closely related species, *Hymenolepis nana* Siebold, 1852 (syn. *Vampirolepis nana* (Siebold, 1852) Spassky, 1954), is one of the world's most common tapeworms and is especially prevalent among children, with prevalences of up to 97.3% having been reported among humans (Roberts and Janovy, 1996). Although light infections of *H. nana* are asymptomatic, heavy infections may be characterized by abdominal pain, diarrhea, headache, dizziness, anorexia, and various other nonspecific symptoms characteristic of intestinal cestodiasis (Markell et al., 1999). Sehr (1974) indicated that roentgenological recognition of *Hymenolepis* spp. in humans is relatively difficult and that radiographic findings are mostly negative or that only nonpathognomonic changes can be seen in the mucosal pattern of the intestine. Gold and Meyers (1977) reported the radiographic diagnosis of a human infection with the beef tapeworm, *Taenia saginata* Goeze, 1782, in the small intestine of a 34 year old male patient. Following a barium enema, "small bowel examination clearly outlined an intraluminal, essentially continuous linear filling defect in the distal jejunum and ileum extending into the proximal descending colon" (Gold and Meyers 1977, p. 493). In this instance, the worm extended into the proximal descending colon. It was concluded that tapeworm infection may be initially recognized on barium enema study. Unfortunately, barium enema studies would seldom be expected to be of great value in diagnosis because tapeworms are normally restricted to the small intestine. Aside from this information, little is known about radiographic imaging of tapeworm infections and, specifically, infection with *Hymenolepis* spp., although infections with other helminth species such as *Schistosoma haematobium* (Bilharz, 1852) Weinland, 1858, *Ancylostoma duodenale* (Dubini, 1843) Creplin, 1845, and *Ascaris lumbricoides* Linnaeus, 1758, are sometimes diagnosed in the course of routine radiographic examination (Reeder and Palmer, 1989). We utilized the laboratory model of *Hymenolepis diminuta* in rats to investigate potential applications of radiographic imaging in the diagnosis and/or study of *Hymenolepis* spp. The goals of this study were to determine whether infection of *H. diminuta* in rats can be diagnosed using radiography, to determine the optimal methodology for visualization of worms, and to determine what information can be obtained from radiographs of infected animals.

Laboratory infection of rats was accomplished by feeding 3 female Wistar rats 10, 10, and 30 cysticercoids, respectively, of *H. diminuta* taken from our laboratory colony of the grain beetle,

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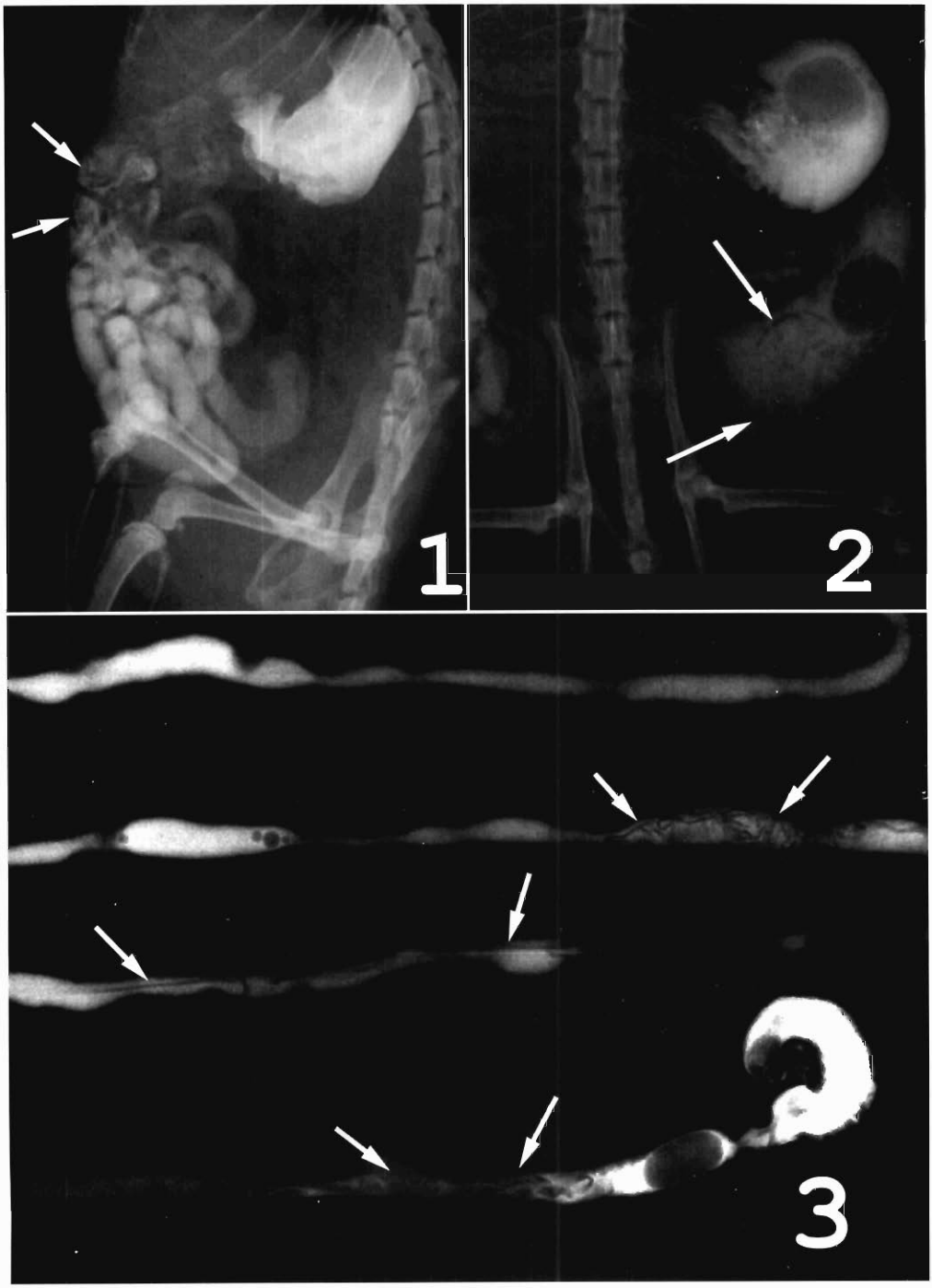
Tenebrio molitar Linnaeus, 1758. Radiographic studies were conducted at 21 days postinfection. Baseline methodologies were established using an uninfected control rat. Each rat was lightly anesthetized with the inhalation anesthesia Halothane® (Halocarbon Laboratories, River Edge, New Jersey), and a 1.5 cc bolus of a water-soluble iodinated radiographic contrast medium, diatrizoate meglumine sodium solution (Gastrografin®; Squibb Diagnostics, Princeton, New Jersey), was administered through a 6 French teflon catheter inserted into the rat's stomach. X-rays were taken at various exposure factors and with various films to determine the optimal radiographic technique. Optimal imaging was achieved with an exposure factor of 3.75 mAs at 54 kVp with Kodak Min-R® single-emulsion mammography film. The rat was placed in a posterior–anterior or dorsal–ventral position and x-rays were taken at 5-min intervals to establish the length of time required for the contrast medium to reach the ileocecal junction. By 30 min, Gastrografin had filled the entire small intestine. Food material and fecal shadows were evident in the control rat. Next, Gastrografin was administered to Rat I, which had been fed 10 cysticercoids. At 30 min, posterior–anterior and lateral x-rays were taken. Based on the lateral projections, worms were evident in the anterior portion of the small intestine (Fig. 1). Rat I was killed in a carbon dioxide chamber, and the entire gastrointestinal tract, excluding the esophagus, was removed, coiled onto a mammography cassette, and x-rayed. From the x-ray, predictions were made concerning the position and relative abundance of worms. The intestine was then longitudinally dissected and the locations of the 10 adult tapeworms were noted and compared to the predictions. It was concluded that even in the presence of food in the intestine, infection can be diagnosed and inference made regarding the location and relative abundance of worms.

Twenty-four hours after administration of Gastrografin to another infected rat, x-rays were taken to determine whether the contrast medium was taken up by or had adhered to the worms, thereby creating an outline of the worms in the alimentary canal, as may be the case with *A. lumbricoides* (Reeder and Palmer, 1989). Worms could not be visualized in x-rays of the small intestine when Gastrografin was lacking, suggesting that worms do not absorb the contrast medium. This is consistent with the observations of Gold and Meyers (1977) regarding human infection with *T. saginata* in association with a barium enema.

To determine whether fasting would improve the conditions for visualization of worms, rats were not fed for 24 hr prior to the administration of Gastrografin and radiographic examination using the methodologies outlined above. After fasting, the control rat exhibited gas bubbles, but food and fecal shadows were lacking. Radiologic examination of Rat II, which had been fed 10 cysticercoids, revealed that visualization of worms was improved by fasting because of the elimination of food and fecal shadows. The posterior–anterior projection of Rat II is shown in Figure 2. Interestingly, x-rays suggested that worms were present in the cecum. Postmortem examination confirmed this x-ray finding. The rat was killed and the intestine was removed and coiled onto a mammography cassette. Based on the x-ray (Fig. 3), predictions were made concerning the position and relative abundance of worms. The intestine was longitudinally dissected and the numbers and locations of worms were confirmed. The procedure was repeated with Rat III, which had been fed 30 cysticercoids. Even small sections of proglottids could be detected in the large intestine.

We have shown that radiographic imaging can successfully demonstrate the presence of *H. diminuta* in the rat intestine. It is possible that these findings can be extended to human infections of *H. nana.* If so, this could be useful in the incidental diagnosis of human infection in the course of routine radiographic imaging. This could be especially valuable in areas of high parasite prevalence, such as Moscow, where prevalences as high as 97.3% have been reported (Karnaukov and Laskovenko, 1984; see Roberts and Janovy, 1996). Because of the size differences of the hosts and the worms, more information concerning the radiographic imaging of *Hymenolepis* spp. in humans is warranted to better define the radiographic presentation of human infection and the utility of this methodology in diagnosis.

In addition to potential human clinical applications, this technique provides rapid diagnosis of prepatent infection without having to kill the animal. This may prove useful in studying the basic biology of *H. diminuta,* which exhibits complex emigrations and migrations within the



Figures 1–3. Radiographic imaging of *Hymenolepis diminuta*. Scale is actual size. 1. Lateral projection of Rat I showing infection of *Hymenolepis diminuta*. Arrows indicate aggregation of worms in the small intestine. 2. Posterior–anterior projection of Rat II showing infection of *Hymenolepis diminuta*. Arrows indicate worms in cecum. 3. Radiograph of intestine removed from Rat II, showing infection of *Hymenolepis diminuta*. Arrows indicate worms in a substantial portion of the small intestine.

rat intestine (Mettrick and Podesta, 1974). This may also be a useful tool in efficacy testing of anthelmintics when assessing prepatent success and temporal aspects of drug activity.

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Research Note

Helminths of Two Lizards, *Barisia imbricata* and *Gerrhonotus ophiurus* (Sauria: Anguidae), from Mexico

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ABSTRACT: The gastrointestinal tracts of 37 *Barisia imbricata* (Wiegmann) and 54 *Gerrhonotus ophiurus* Cope from Mexico were examined for helminths. The helminth fauna of *B. imbricata* consisted of 4 species of nematodes: *Cosmocercoides variabilis* (Harwood), *Oswaldocruzia pipiens* Walton, *Physaloptera retusa* Rudolphi, and *Raillietnema brachyspiculatum* Bursey, Goldberg, Salgado-Maldonado, and Méndez-de la Cruz. *Gerrhonotus ophiurus* harbored 1 trematode species, *Brachycoelium salamandrae* (Frölich), and 2 nematode species, *Cosmocercoides variabilis* and *Physaloptera retusa*. All represent new host records. With the exception of *R. brachyspiculatum*, all these helminths are generalists, which are widely distributed in other amphibian and reptile hosts.

KEY WORDS: lizards, Sauria, *Barisia imbricata*, *Gerrhonotus ophiurus*, Anguidae, Trematoda, *Brachycoelium salamandrae*, Nematoda, *Cosmocercoides variabilis*, *Oswaldocruzia pipiens*, *Physaloptera retusa*, *Raillietnema brachyspiculatum*, Mexico.

Barisia imbricata (Wiegmann, 1828) occurs in highland pine forests throughout Mexico west of the Isthmus of Tehuantepec (Good, 1988). *Gerrhonotus ophiurus* Cope, 1866, occurs in the Mexican states of Hidalgo, Puebla, San Luis Potosí, and Veracruz (Good, 1994). There are, to our knowledge, no reports of helminths from these species. We report here the helminths from populations of *B. imbricata* and *G. ophiurus*.

Thirty-seven *B. imbricata* deposited in the herpetology collection (ENEPI) of the Escuela Nacional de Estudios Profesionales Iztacala, Universidad Nacional Autónoma de México (UNAM) were examined: 23 from Estado de

[4] Corresponding author.

México, snout–vent length (SVL) = 104 mm ± 14.8 SD, range = 68–124 mm, ENEPI numbers 11, 12, 393, 616, 699, 730, 3873, 3874 (collected 1984–1985) and 4939, 5436, 5587–5591, 6333–6340 (collected 1990–1991); 14 from Hidalgo, SVL = 89 mm ± 20.5 SD, range = 61–123 mm, ENEPI numbers 4321, 4834–4836, 5841–5850 (collected 1990–1991). Fifty-four *G. ophiurus,* SVL = 112 mm ± 12 SD, range = 80–136 mm, were collected near San Antonio Ixtatetla, Municipio de Huayacocotla, Veracruz, (20°43′N, 98°22′W) during 1991, ENEPI numbers 6252–6262, 6264–6295, 6297–6303, 6305, 6306, 6308, 6309.

The abdominal cavities were opened and the gastrointestinal tracts were excised by cutting across the esophagus and rectum. The digestive tracts were each slit longitudinally and examined under a dissecting microscope. Each helminth was removed to a drop of undiluted glycerol on a glass slide for study; trematodes were regressively stained with hematoxylin and mounted in Canada balsam.

Because a statistically significant difference was found for the SVL between the Estado de México and Hidalgo populations of *B. imbricata* (Kruskal–Wallis test = 4.87, 1 df, $P < 0.05$) and because of community similarity differences (Jaccard's coefficient, 0.75; Morisita's index, 0.73), data for the 2 populations were not combined. The helminth fauna of the Estado de México population of *B. imbricata* consisted of 3 species of nematodes: *Cosmocercoides variabilis* (Harwood, 1930), *Oswaldocruzia pipiens* Walton, 1929, and *Raillietnema brachyspiculatum* Bursey, Goldberg, Salgado-Maldonado, and Méndez-de la Cruz, 1998. The helminth fauna of the Hidalgo population of *B. imbricata* consisted of 4 species of nematodes: *C. variabilis, O. pipiens, Physaloptera retusa* Rudolphi, 1819, and *R. brachyspiculatum.* Helminths of *G. ophiurus* consisted of 1 species of trematode, *Brachycoelium salamandrae* (Frölich, 1789), and 2 species of nematodes, *C. variabilis* and *P. retusa,* all representing new host and locality records. Terminology is in accordance with Bush et al. (1997). Representative specimens were placed in vials of 70% ethanol and deposited in the U.S. National Parasite Collection, Beltsville, Maryland (USNPC): *Barisia imbricata*: *Cosmocercoides variabilis,* USNPC 88291; *Oswaldocruzia pipiens,* USNPC 99292; *Physaloptera retusa,* USNPC 88293; *Raillietnema brachyspiculatum,* USNPC 88294. *Gerrhonotus ophiurus*: *Brachycoelium salamandrae,* USNPC 87245; *Cosmocercoides variabilis,* USNPC 87246; *Physaloptera retusa,* USNPC 87247. Helminths from *Barisia imbricata* were also deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología de la Universidad Nacional Autónoma de México, México, Distrito Federal, Mexico: *Cosmocercoides variabilis,* CNHE 3384; *Oswaldocruzia pipiens,* CNHE 3387; *Physaloptera retusa,* CNHE 3385; *Raillietnema brachyspiculatum,* CNHE 3386.

The number of infected lizards, number of helminths, prevalence, mean intensity ± SD, and range and mean abundance ± SD are presented in Table 1. Both lizard species harbored *C. variabilis* and *P. retusa. Brachycoelium salamandrae* was found only in *G. ophiurus; O. pipiens* and *R. brachyspiculatum* were found only in *B. imbricata.*

Brachycoelium salamandrae, the only trematode species found in this study, was found in the small intestines of 2 *G. ophiurus.* There has been controversy surrounding the assignment of species to the genus *Brachycoelium.* Rankin (1938) reduced all the American species to synonymy with *B. salamandrae,* a European species and the type species of the genus. However, Parker (1941) and Cheng (1958) did not accept the synonymy and recognized 7 and 10 species of the genus, respectively. Later Cheng and Chase (1960) and Couch (1966) described additional species, bringing to 13 the number of species assigned to the genus. Prudhoe and Bray (1982) favored a monospecific genus. Regardless of confusion in the taxonomy, the specimens collected in this study most closely resemble *B. salamandrae* as described by Cheng (1958), in that they were elongate distomes, approximately 3 mm in length, more than twice the length of any other species assigned to the genus, and the vitellaria extended beyond the ceca and did not join on the midline. The North American host list for *B. salamandrae* includes salamanders, anurans, lizards, and snakes (see Prudhoe and Bray, 1982). *Gerrhonotus ophiurus* is added to this host list.

As in the case of the identity of species of *Brachyocoelium,* some uncertainty also exists for North American species of *Cosmocercoides. Cosmocercoides variabilis,* originally described as *Oxysomatium variabilis* by Harwood (1930) from *Bufo valliceps* Wiegmann, 1833, collected

Table 1. Helminths from the anguid lizards, *Barisia imbricata* and *Gerrhonotus ophiurus*, from Mexico.

Lizard species Helminth species	Number of infected lizards	Number of helminths	Prevalence (%)	Mean intensity ± SD (range)	Mean abundance ± SD
Barisia imbricata (Estado de México, $N = 23$)					
Nematoda					
Cosmocercoides variabilis	3	4	13	1.3 ± 0.6 (1–2)	0.2 ± 0.5
Oswaldocruzia pipiens	3	6	13	2.0 ± 1.7 (1–4)	0.3 ± 0.9
Raillietnema brachyspiculatum	1	83	4	83	3.6 ± 17.3
Barisia imbricata (Hidalgo, $N = 14$)					
Nematoda					
Cosmocercoides variabilis	2	6	15	3.0 ± 2.8 (1–5)	0.4 ± 1.3
Oswaldocruzia pipiens	11	86	79	7.8 ± 6.1 (1–15)	6.1 ± 6.3
Physaloptera retusa	6	18	43	3.0 ± 3.2 (1–8)	1.2 ± 2.5
Raillietnema brachyspiculatum	1	93	7	93	6.6 ± 24.9
Gerrhonotus ophiurus (Veracruz, $N = 54$)					
Trematoda					
Brachycoelium salamandrae	2	5	4	2.5 ± 2.1 (1–4)	0.1 ± 0.6
Nematoda					
Cosmocercoides variabilis	17	21	31	1.2 ± 0.6 (1–3)	0.4 ± 0.7
Physaloptera retusa	10	65	19	6.7 ± 12.0 (1–40)	1.2 ± 5.6

at Houston, Texas, was considered a synonym of the molluscan parasite *Cosmocercoides dukae* (Holl, 1928) by Ogren (1953), who presumed that amphibians acquired *C. dukae* infections by ingesting infected mollusks. *Cosmocercoides dukae* was first described by Holl (1928) from the salamander *Notophthalmus viridescens* (Rafinesque, 1820) from North Carolina. Wilkie (1930) established the genus *Cosmocercoides,* and Travassos (1931) included both *C. dukae* and *C. variabilis* in his monograph on the Cosmocercidae. Vanderburgh and Anderson (1987) demonstrated that these 2 species of *Cosmocercoides* are distinct. The major difference in the 2 species is the number of rosette papillae of the male: *C. dukae* with 12 pairs and *C. variabilis* with 14–20. Specimens collected in our study had 16–18 papillae. The host list includes salamanders, anurans, lizards, snakes, and turtles (see Baker, 1987). *Barisia imbricata* and *G. ophiurus* are added to this list.

All North American specimens of the genus *Oswaldocruzia* have been referred to *O. pipiens* by Baker (1987). This species is widely distributed in North America and has been reported from anurans, salamanders, lizards, and tortoises (see Baker, 1987). *Barisia imbricata* is added to this host list.

Physaloptera retusa is a common parasite of North American lizards (see Baker, 1987). Both *Barisia imbricata* and *G. ophiurus* are added to this host list.

Raillietnema brachyspiculatum was recently described from the xantusiid lizard, *Lepidophyma tuxtlae* Werler and Shannon, 1957, from Veracruz, Mexico, by Bursey et al. (1998). *Barisia imbricata* is a new host record, and the states of Hidalgo and México are new locality records for this nematode.

The results reported here support previous studies on North American anguids (see Goldberg et al., 1999), which have shown that lizards of this family appear to harbor depauperate communities comprised of generalist helminths. As can be seen by the host lists above, with the exception of the recently described *R. brachyspiculatum* (for which there is insufficient information to categorize), the helminth species harbored by *B. imbricata* and *G. ophiurus* are generalists. Although host lists can easily be constructed and host distributions mapped, parasite distribution patterns are more difficult to evaluate. Reasons for varying infection rates among host populations are not understood; for example, there is a significant difference between the Estado de México and Hidalgo populations of *B. imbricata* for *O. pipiens* (chi-square = 15.8, 1 df, $P < 0.001$). Additional work will be required to understand the factors influencing

prevalence patterns of helminths in anguid lizards.

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Anniversary Award

The Helminthological Society of Washington

SHERMAN S. HENDRIX

J. Ralph Lichtenfels, right, presents the 1998 Anniversary Award to Sherman S. Hendrix

Ladies and Gentlemen, in 1989 my longtime friend, Sherm Hendrix, presented the Anniversary Award to me after I completed a term as Editor of our journal. Nine years later, it is my pleasure to switch roles and (in your behalf) honor Sherm as he completes his term as Editor.

Sherm was born June 1, 1939 in Bridgeport, Connecticut and grew up in Connecticut near Long Island Sound, where he developed an interest in biology and the marine environment. He received a B.A., with Departmental Honors, in Biology from Gettysburg College in 1961.

Shortly after graduating from Gettysburg, Sherm married his college sweetheart, Carol Seibel. Carol and Sherm have raised 2 children, Mark, an Assistant Professor of Geology at the University of Montana, and Robin, a teacher who has taken time off to raise 2 children, Anna (5) and Rachel (2). Carol is an ordained Lutheran pastor, currently serving as Assistant to the Bishop for Congregational Care.

Sherm was introduced to Parasitology at Florida State University, in courses taught by Rhodes "Buck" Holliman and Robert B. Short. Sherm received an M.S. degree from Florida State University in 1964 working under Bob Short. His thesis was titled, "Aspidogastrids from Northeastern Gulf of Mexico river drainages". While at Florida State University, he was a member of a 61-day Antarctic Scientific Cruise in 1964, on the Pacific side, out of Valparaiso.

Later that year, he returned to his alma mater, Gettysburg College, as Instructor in Biology.

While continuing his teaching career at Gettysburg, Sherm decided to pursue a Ph.D. at the University of Maryland and became a Graduate Teaching Assistant there in 1969, working under the guidance of Leo Jachowski. His doctoral dissertation, entitled, "The biology, ecology and taxonomy of *Plagioporus hypentelii,* a parasite of the hog sucker in the Monocacy River basin of Maryland and Pennsylvania", and his Ph.D. degree, were completed in 1972. He was an NIH Interamerican Fellow in Tropical Medicine at Louisiana State University in 1973 while on sabbatical from Gettysburg. By this time, Sherm had already been promoted to Assistant Professor at Gettysburg (in 1970). He became Associate Professor in 1977, and Professor in 1990, serving several terms as Chairman, Department of Biology, including a current term as Chair, begun in 1997.

Sherm has developed and managed an almost idyllic career that is a balanced blend of teaching,

research, administration and service. Now you know why he is always pleasant and looks so young! He has taught a range of courses from Introductory Biology to Electron Microscopy, including such interesting titles as Parasitology, Biostatistics, Virology, Biological Control, and Microtechniques and Histochemistry. I encourage you to visit Sherm's excellent homepage (www.gettysburg.edu/~shendrix) to learn more about his courses. He has also developed a homepage for HelmSoc (www.gettysburg.edu/~shendrix/helmsoc).

His research has centered on the morphology, systematics and zoogeography of Monogenea and Trematoda of fish and molluscans. In 1987, an NSF Grant provided an opportunity for more research support (specifically, an illustrator) which resulted in several important papers on Monogenea of fishes, including a landmark, 107-page key and monograph, "Marine Flora and Fauna of the Eastern United States. Platyhelminths: Monogenea." (NOAA Technical Report NMFS 121 of the Fisheries Bulletin). More recently he has traveled to Africa to study parasites of fish in Lake Malawi. A full-year Sabbatical in 1994–1995 provided the time to initiate the Lake Malawi research with collaborator Jay Stauffer of Penn State.

The service activities of a college Professor are many and varied, and Sherm has been recognized for outstanding service at Gettysburg College with the Alpha Phi Omega Service Award in 1979, and the Theta Chi Fraternity Chapter Service Award in 1987. Among his scientific societies, Sherm has been most active in the Pennsylvania Academy of Science and the Helminthological Society of Washington. He served as President of the Academy (1990–1992) and received its 1998 Lifetime Achievement Award.

Professor Sherman S. Hendrix has brought honor and credit to the Helminthological Society of Washington in every leadership role possible. He was Corresponding Secretary Treasurer (1979–1982), President (1984), and Editor (1993–1998). In recognition of this outstanding, dedicated service the Society bestows its highest honor, The Anniversary Award, on Professor Sherman S. Hendrix.

J. Ralph Lichtenfels
November 18, 1998

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MINUTES

Six Hundred Sixty-First Through Six Hundred and Sixty-Fifth Meeting

661st Meeting: Walter Reed Army Institute of Research, Washington, DC, 14 October, 1998. The President opened the meeting and announced a slate of nominations for society officer positions: Eric P. Hoberg for President, Ronald Neafie for Vice President, Pat Carney for Recording Secretary, Nancy Pacheco for Corresponding Secretary-Treasurer, and Willis A. Reid, Jr. and Janet W. Reid for Editors. He also discussed the rationale for changing the name of the journal and suggestions that had been made for changing the format of meetings. The meeting was then turned over to Dr. Joan Jackson who introduced the speakers: Dr. Naomi Aronson spoke on "Clinical aspects of leishmaniasis"; Dr. Ed Rowton presented his paper on "The vector in leishmaniasis", and Dr. Jackson provided an overview of her studies on "Drug research in leishmaniasis."

662nd Meeting: Sabang Indonesian Restaurant, Wheaton, MD, 18 November 1998. The Anniversary Dinner Meeting and Program were presided over by the President, Dr. Eric Hoberg. The membership in attendance approved the slate of officers for 1999. Dr. J. Ralph Lichtenfels introduced the recipient of the Anniversary Award, Dr. Sherman S. Hendrix, Gettysburg College. In his acceptance comments, Dr. Hendrix reviewed his teaching and research career at Gettysburg College and shared highlights of field expeditions in search of marine parasites.

663rd Meeting: Armed Forces Institute of Pathology, Washington, DC, January 18, 1999. The President welcomed members and visitors. He advised the membership that the Executive Committee had voted unanimously for changing the name of the *Journal of the Helminthological Society of Washington* to *Comparative Parasitology* at their September, 1998 meeting, and that an amendment to the Constitution of the Society was prepared and presented in writing to the general membership at the Anniversary Meeting in November, 1998. A motion to change the name of the journal to "Comparative Parasitology" was passed unanimously by the general membership. The membership was provided with a draft of the Society's "Mission and Vision" statements for review and comment. The meeting was then turned over to Vice President Ronald Neafie who introduced the speakers. Drs. Dennis Richardson and Richard Clopton jointly discussed "The counterpoint hypothesis: opposing forces in natural selection in parasite evolution." Dr. Mary Klassen's paper was entitled "Imitators of infectious diseases" in which she illustrated a series of artifacts that can be confused with agents of infectious diseases. Dr. Peter McEvoy gave a "case presentation" on nodular cutaneous microsporidiosis in a patient with AIDS.

664th Meeting: Uniformed Services University of the Health Sciences, Bethesda, MD, March 10, 1999. The President opened the general meeting and welcomed members and their guests. The President then discussed the rationale for developing clear Mission and Vision statements and his intent to have them in place when the name of the Journal changes in January 2000. The meeting was turned over to Dr. John Cross who introduced the speakers. Dr. Richard Andre provided an overview of "Applications of geographic information systems (GIS) for malaria control in Belize." Dr. Allen Richards reviewed research he had conducted on "Tumor necrosis factor (TNF) and associated cytokines in the host's response to malaria." Dr. Cross presented the final paper on his ongoing studies of "Cyclosporosis in Nepal."

665th Meeting: University of Pennsylvania, New Bolton Center, Kennett Square, PA, May 8, 1999. The President opened the general meeting and welcomed members and guests. The President then turned the meeting over to Dr. Jay Farrell. Dr. Farrell welcomed members and guests on behalf of the University of Pennsylvania and the New Jersey Society for Parasitology and introduced each of the speakers. Dr. Phillip LoVerde presented a paper on "Sex in schisto-

somes: a novel interplay." His presentation was followed by Dr. Phillip Cooper who discussed "The modulation of allergic inflammation by helminth infections." The final speaker was Dr. Joseph Urban who described the role of "Counter-regulatory properties of IL4/IL-13 and IFN-gamma in controlling resistance to gastrointestinal nematodes." Following the meeting a wine and cheese reception was held in the Allam House with support from Pfizer Animal Health and the Laboratory of Parasitology, University of Pennsylvania.

Respectfully submitted,
W. Patrick Carney
Recording Secretary

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AUTHOR INDEX FOR VOLUME 66

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KEYWORD AND SUBJECT INDEX FOR VOLUME 66

APPLICATION FOR MEMBERSHIP
in the
HELMINTHOLOGICAL SOCIETY OF WASHINGTON

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Name: _____

Mailing Address: _____

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Present Position and Name of Institution: _____

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Highest Degree Earned and the Year Received: _____

Are You a Student? If so, for what degree and where? _____

_____

Fields of Interest: _____

_____

_____

If you are experienced in your field, would you consent to be a reviewer for manuscripts submitted for publication in the ***Journal***? If so, what specific subject area(s) do you feel most qualified to review?

_____

_____

_____ _____

Signature of Applicant Date

_____ _____

Signature of Sponsor (a member) Date

Mail the completed application along with a check or money order (in U.S. currency) for the first year's dues (US$25 for domestic active members and US$28 for foreign active members) to the Corresponding Secretary-Treasurer, Nancy D. Pacheco, 9708 DePaul Drive, Bethesda, Maryland, U.S.A. 20817

HELMINTHOLOGICAL SOCIETY OF WASHINGTON
MISSION & VISION STATEMENTS
May 7, 1999.

THE MISSION

The **Helminthological Society of Washington,** the prototype scientific organization for parasitological research in North America was founded in 1910 by a devoted group of parasitologists in Washington, D.C. Forging a niche in national and international parasitology over the past century, the **Society** focuses on comparative research, emphasizing taxonomy, systematics, ecology, biogeography and faunal survey and inventory within a morphological and molecular foundation. Interdisciplinary and crosscutting, comparative parasitology links contemporary biodiversity studies with historical approaches to biogeography, ecology and coevolution within a cohesive framework.

Through its 5 meetings in the Washington area annually, and via the peer reviewed ***Comparative Parasitology*** (continuing the ***Journal of the Helminthological Society of Washington*** in its 67th Volume), the **Society** actively supports and builds recognition for modern parasitological research. Taxonomic diversity represented in the pages of the ***Society's journal*** treats the rich helminth faunas in terrestrial and aquatic plants, invertebrates and vertebrates, as well as parasitic protozoa and arthropods. Parasitology, among the most integrative of the biological sciences, provides data critical to elucidation of general patterns of global biodiversity.

THE VISION

The **Helminthological Society of Washington** celebrates a century of tradition and excellence in global parasitology, solving challenges and responding to opportunities for the future of society and the environment.

Members of the **Helminthological Society of Washington** contribute to understanding and protecting human health, agriculture and the biosphere through comparative research emphasizing taxonomy, systematics, ecology, biogeography and biodiversity assessment of all parasites. The **Society** projects the exceptional relevance of its programs to broader research and education in global biodiversity and conservation biology through the activities of its members and its journal, ***Comparative Parasitology.***

ANNIVERSARY AWARD RECIPIENTS

*Edna M. Buhrer	1960	*Everett E. Wehr	1979
*Mildred A. Doss	1961	*O. Wilford Olsen	1980
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*Willard H. Wright	1969	Milford N. Lunde	1988
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*Carlton M. Herman	1971	A. James Haley	1990
*May Belle Chitwood	1972	Francis G. Tromba	1991
*Elvio H. Sadun	1973	Thomas K. Sawyer	1992
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*Horace W. Stunkard	1977	Burton Y. Endo	1997
*Kenneth C. Kates	1978	Sherman S. Hendrix	1998

HONORARY MEMBERS

*George R. LaRue	1959	E. J. Lawson Soulsby	1990
*Vladimir S. Ershov	1962	Roy C. Anderson	1991
*Norman R. Stoll	1976	Louis Euzet	1992
*Horace W. Stunkard	1977	John C. Holmes	1993
*Justus F. Mueller	1978	Purnomo	1994
John F. A. Sprent	1979	Naftalé Katz	1995
Bernard Bezubik	1980	*Robert Traub	1996
Hugh M. Gordon	1981	Alan F. Bird	1997

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	*Everett E. Wehr	1977
*Albert Hassall	1931	Marion M. Farr	1979
*Charles W. Stiles	1931	John T. Lucker, Jr.	1979
*Paul Bartsch	1937	George W. Luttermoser	1979
*Henry E. Ewing	1945	*John S. Andrews	1980
*William W. Cort	1952	*Leo A. Jachowski, Jr.	1981
*Gerard Dikmans	1953	*Kenneth C. Kates	1981
*Jesse R. Christie	1956	Francis G. Tromba	1983
*Gotthold Steiner	1956	A. James Haley	1984
*Emmett W. Price	1956	*Leon Jacobs	1985
*Eloise B. Cram	1956	*Paul C. Beaver	1986
*Gerald Thorne	1961	*Raymond M. Cable	1986
*Allen McIntosh	1963	Harry Herlich	1987
*Edna M. Buhrer	1963	Glenn L. Hoffman	1988
*Benjamin G. Chitwood	1968	Robert E. Kuntz	1988
*Aurel O. Foster	1972	Raymond V. Rebois	1988
*Gilbert F. Otto	1972	Frank W. Douvres	1989
*Theodor von Brand	1975	A. Morgan Golden	1989
*May Belle Chitwood	1975	Thomas K. Sawyer	1989
*Carlton M. Herman	1975	*J. Allen Scott	1990
Lloyd E. Rozeboom	1975	Judith H. Shaw	1990
*Albert L. Taylor	1975	Milford N. Lunde	1991
David R. Lincicome	1976	Everett L. Schiller	1991
Margaret A. Stirewalt	1976	Harley G. Sheffield	1991
*Willard H. Wright	1976	Louis S. Diamond	1994
*Benjamin Schwartz	1976	Mary Hanson Pritchard	1994
*Mildred A. Doss	1977		

*Deceased.

CONTENTS

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