



Faunal survey and identification key for the trematodes (Platyhelminthes: Digenea) infecting *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae) as first intermediate host

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Abstract

A diverse guild of digenean trematodes infects the New Zealand mud snail, *Potamopyrgus antipodarum*, as first intermediate host. This manuscript offers an initial systematic treatment of these trematodes and relies on published and new information. I list 20 trematode species, for which I provide taxonomic affinities, life-cycle information, and an identification key. A species account section presents photographs, diagnostic information, additional descriptive notes, and information on relevant research concerning the listed species. The major aim of this manuscript is to facilitate research on this trematode guild by providing information and identification tools, and by highlighting gaps in our knowledge.

Key words: Parasites, parasitic castrators, New Zealand, streams, biodiversity

Introduction

How many trematode species infect, as first intermediate host, the New Zealand mud snail, *Potamopyrgus antipodarum* (Gray)? To what families do these parasitic castrators belong? What types of hosts might they infect at other parts of their life cycles? What other information is known about these species? How can one go about identifying them? This manuscript aims to address these questions, and serve as a tool to permit at least a provisional answer to the last.

Potamopyrgus antipodarum serves as first intermediate host for a speciose guild of trematode parasitic castrators (Jokela & Lively 1995; McArthur & Featherston 1976; Winterbourn 1974). The snail and these parasites have been the subject of numerous biological, ecological, and evolutionary studies (references below). This includes classic empirical work concerning host-parasite coevolution and local adaptation of parasites for their hosts (e.g., Lively 1987). This freshwater snail is also of interest because it is introduced in several areas throughout the world (Ponder 1988), including southeastern Australia, Japan, North America, and Europe. Introduced populations lack or are rarely parasitized by trematode castrators (Gerard & Le Lannic 2003; Zbikowski & Zbikowska 2009), outside of Australia (e.g., see Schreiber *et al.* 1998).

There have been no systematic treatments of this trematode guild. Winterbourn (1974) provided an initial, extensive depiction of the trematodes that he encountered during his thorough investigations of the systematics and biology of *P. antipodarum* throughout New Zealand. He listed 14 species. MacFarlane (1939;1945;1951) had previously described the life cycles of three of Winterbourn's 14. Winterbourn provided descriptive information for the 11 unreported species. He classified the trematodes into basic, non-taxonomic, morphological cercaria-type categories. Bisset (1978) described two species, but did not relate them to Winterbourn's list. Other surveys have generally followed Winterbourn's listing (e.g., Jokela & Lively 1995), or otherwise categorized the trematodes into non-taxonomic, cercarial morphological categories (e.g., McArthur & Featherston 1976). Hence, most of most of the constituent species in the guild of trematodes infecting *P. antipodarum* have not been adequately described, or placed within taxa to the extent possible.

This manuscript treats the trematodes known to infect *P. antipodarum* as first intermediate host. It relies

particularly heavily on trematodes that I briefly examined and collected during an ecological study of the snail and its trematode parasites from 79 populations from streams and rivers throughout both main islands of New Zealand (Hechinger *et al.*, in prep.). The purpose of that study was not a detailed systematic investigation of the trematodes. However, I believe that I made headway in this regard, and that it is worthwhile to share this information. I include 20 species, including three listed by Winterbourn that I did not encounter. Two congeneric species that I list remain indistinguishable from each other. Rather than classify trematodes into non-taxonomic, morphological, cercaria-type categories, I attempt to recognize their taxonomic affinities based upon general knowledge of trematode larval stages. This permits depiction of probable second intermediate host use and final host use for those species whose life cycles have not been determined. I also include a dichotomous key to facilitate identification of the trematodes. For several reasons, this treatment should be considered provisional. First, in addition to the known species that are currently indistinguishable, additional “cryptic species” likely exist. I highlight several such cases. Further, this manuscript does not solve the problem of the lack of adequate descriptions for most of the trematode species in this guild. However, I offer photographs, diagnostic information, some additional descriptive information, and information on relevant research pertaining to the listed species. This manuscript highlights the need for future, careful morphological, life cycle, and genetic work to improve our understanding of these trematodes. I hope that a major function of this manuscript is to facilitate such research, and to immediately assist ecological and evolutionary research involving this host-parasite system.

Material and methods

Snails originated from streams and rivers throughout both islands of New Zealand in summer (Jan–Feb) 2009. Hechinger *et al.* (in prep.) report the details of the sampling. Briefly, snails were haphazardly collected from each of 79 study sites and up to 100 were dissected to detect infection as first intermediate hosts. This entails cracking the shell of snails, immersing the snail in a drop of fresh water, removing shell pieces, and using fine forceps to inspect and tease apart snail tissues to observe and acquire parasite stages. Parthenitae (daughter sporocysts, rediae) and cercariae were examined alive using the dissecting scope and mounts at the compound scope. Vouchers were fixed using hot 10% formalin (adding 4 times the volume of 10% formalin to the water containing the specimens) and/or 95% EtOH. When vouchers come from 95% EtOH, they were removed from samples that were fixed for ongoing molecular genetic work. I examined some of the fixed specimens after mounting in glycerin, sometimes followed by acetocarmine staining. I deposited vouchers at the US National Parasite Collection. Unless otherwise specified, photos are of vouchered specimens and are of live, fresh material.

I usually avoid unnecessary reliance on jargon, particularly that which has no intrinsic meaning or is misleading (e.g., “monostomatous,” which refers to lacking a ventral sucker and has nothing to do with mouths, of which all trematodes have but one).

All measurements are in microns.

Results and discussion

Table 1 provides a taxonomic listing of the 20 species that I believe we can currently recognize or logically infer as infecting *P. antipodarum* as first intermediate host. Species are listed and numbered in a general phylogenetic order (Olson *et al.* 2003), except for Winterbourn’s two “gymnocephalous” cercariae, which I did not encounter and whose taxonomic status is more speculative than the others’. One species (sp. 12, *Coitocaecum zealandicum*) has not been reported from *P. antipodarum*, but it very likely infects this snail (see species account); I list it to foster future recognition of it.

Fig. 1 provides a composite drawing of the parthenitae and cercariae for the members of the trematode ensemble. The drawing emphasizes readily observable, key features.

Table 2 provides documented and inferred life cycle information for the species.

The key primarily uses characteristics of the cercariae, and should be used in conjunction with parthenital and cercarial characteristics indicated in the figures and species accounts. I also remind readers that they should strive to not force encountered species to match one of those depicted in the key (that is, avoid “pigeon-holing” additional species into one of those depicted here).

TABLE 1. Taxonomic list of trematode species using *Potamopyrgus antipodarum* as first intermediate host and correspondence to species in Winterbourn's (1974) treatment.

Trematode	Code ^a	Winterbourn (1974)	Superfamily	Family
1. <i>Apatemon</i> sp. I	Apa1	F1	Diplostomoidea	Strigeidae
2. Aporocotylid sp. I (small aporocotylid) ^b	Apo1	F2	Schistosomatoidea	Aporocotylidae
3. Aporocotylid sp. II (large aporocotylid) ^b	Apo2	-	Schistosomatoidea	Aporocotylidae
4. Pronocephaloid sp. I (eyeless pronocephaloid)	Pro1	M1	Pronocephaloidea	Notocotylidae? Pronocephalidae?
5. <i>Notocotylus gippensis</i> ^c	Nogi	M2, M3	Pronocephaloidea	Notocotylidae
6. <i>Notocotylus tadornae</i> ^c	Nota	M2, M3	Pronocephaloidea	Notocotylidae
7. Pronocephaloid sp. IV (finned pronocephaloid)	Pro4	M4	Pronocephaloidea	Notocotylidae? Pronocephalidae?
8. <i>Stegodexamine anguillae</i>	Stan	<i>S. anguillae</i>	Lepocreadioidea	Lepocreadiidae
9. Lepocreadiid sp. II (12 penetration gland lepocreadiid)	Lep2	-	Lepocreadioidea	Lepocreadiidae
10. <i>Telogaster opisthorchis</i>	Teog	<i>T. opisthorchis</i>	Opisthorchioidea	Cryptogonimidae
11. <i>Coitocaecum parvum</i> ^c	Copa	<i>C. anaspidis</i>	Allocreadioidea	Opocoelidae
12. <i>Coitocaecum zealandicum</i> ^{c, d}	Coze	-	Allocreadioidea	Opocoelidae
13. <i>Microphallus</i> sp. "lively!"	Mili	Metacercaria A	Microphalloidea	Microphallidae
14. <i>Microphallus</i> sp. "poulimi"	Mipo	-	Microphalloidea	Microphallidae
15. Acaudate xiphidocercaria sp. I	Axi1	C1	Microphalloidea?	Microphallidae?
16. Virgulate sp. I (small virgulate cercaria)	Vir1	-	Microphalloidea	Lecithodendriid-like families
17. Virgulate sp. II (large virgulate cercaria)	Vir2	X1	Microphalloidea	Lecithodendriid-like families
18. Plagiorchioid sp. I	Pla1	-	Plagiorchioidea	Plagiorchiidae?
19. Gymnocephalous sp. I (haploporid?)	Gym1	G1	Gorgoderoidea?	Haploporidae?
20. Gymnocephalous sp. II (psilostomid?)	Gym2	G2	Echinostomatoidea?	Psilostomidae?

^a Species codes are usually the first three letters and the number following "sp." for those species with no species binomial, and the first two letters of the genus and specific epithet for those with binomials.

^b Aporocotylidae is now recognized as the senior synonym of Sanguinicolidae (Bullard *et al.* 2009).

^c The two *Notocotylus* spp. and the two *Coitocaecum* spp. are not yet distinguishable. The Fig. 1 codes for them are the first four letters of the genus.

^d *C. zealandicum* has not been reported from *P. antipodarum*, but I list it because it is almost certain that it infects that host snail (see text).

TABLE 2. Life-cycle information for the trematodes using *Potamopyrgus antipodarum* as first intermediate host (see text for further information and references).

Trematode	Second intermediate host	Final host	Information source
1. <i>Apatemon</i> sp. I	fishes	birds	Dr. B. Presswell (pers. comm)
2. Aporocotylid sp. I (small aporocotylid)	na	fishes	taxonomic affiliation
3. Aporocotylid sp. II (large aporocotylid)	na	fishes (eels?)	taxonomic affiliation / literature
4. Pronocephaloid sp. I (eyeless pronocephaloid)	<i>P. antipodarum</i> +? ^a	birds	literature / observed
5. <i>Notocotylus gippyensis</i>	<i>P. antipodarum</i> and vegetation +? ^a	birds	literature / observed
6. <i>Notocotylus tadornae</i>	<i>P. antipodarum</i> and vegetation +? ^a	birds	literature / observed
7. Pronocephaloid sp. IV (finned pronocephaloid)	<i>P. antipodarum</i> +? ^a	birds	literature / observed
8. <i>Stegodexamine anguillae</i>	fishes	eels	literature
9. Lepocreadiid sp. II (12 pen. gland lepocreadiid)	invertebrates? fishes?	fishes	taxonomic affiliation
10. <i>Telogaster opisthorchis</i>	fishes	eels	literature
11. <i>Coitocaeacum parvum</i>	small crustaceans	fishes	literature
12. <i>Coitocaeacum zealandicum</i>	small crustaceans?	fishes	taxonomic affiliation / literature
13. <i>Microphallus</i> sp. "livelyi"	<i>P. antipodarum</i>	birds	literature
14. <i>Microphallus</i> sp. "poulini"	small crustaceans	birds	literature / taxonomic affiliation
15. Acaudate xiphidocercaria sp. I	invertebrate or fishes	?	taxonomic affiliation
16. Virgulate sp. I (small virgulate cercaria)	arthropods	ecto- or endothermic tetrapod	taxonomic affiliation
17. Virgulate sp. II (large virgulate cercaria)	arthropods	ecto- or endothermic tetrapod	taxonomic affiliation
18. Plagiorchioid sp. I	invertebrate or ectothermic vertebrate	ecto- or endothermic vertebrate	taxonomic affiliation
19. Gymnocephalous sp. I (haploporid?)	vegetation? ^a	fishes?	taxonomic affiliation
20. Gymnocephalous sp. II (psilostomid?)	mollusks?	birds and/or mammals?	taxonomic affiliation

^a Metacercariae encyst on outside surface of the "host."

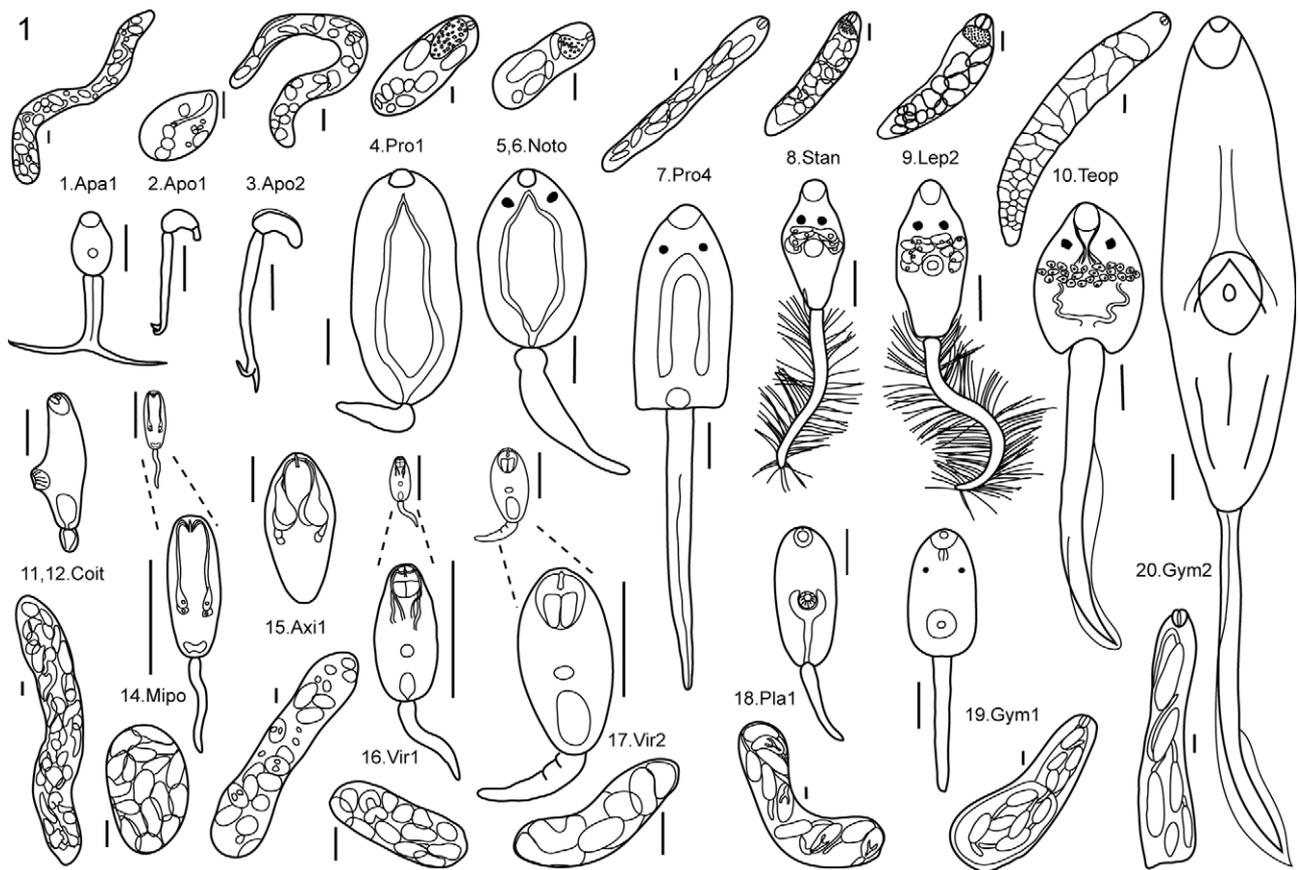


FIGURE 1. General characteristics of the parthenitae and cercariae of the trematodes infecting *Potamopyrgus antipodarum* as first intermediate host. *Microphallus* sp. “livelyi” (sp. 13), whose embryos develop directly to metacercariae, is not figured. Species numbers and codes follow Table 1 and species accounts. Cercariae are all to scale, with additional magnified views of three small cercariae (indicated by dashed lines). Parthenitae are not to scale. Scale bars consistently indicate 100 μ m.

The species accounts follow Table 1’s numbering and order, and the key references the species numbers to facilitate looking up species. The species accounts include standard faunal survey information (stages, host, site in host, voucher localities, prevalence, specimens deposited, diagnosis, descriptive notes, and remarks). Diagnoses present the suite of parthenital and cercarial characters that, in combination, permits distinguishing the species from the others listed. I sometimes include further descriptive notes. These may help future recognition of cryptic species or comparisons to related taxa in other geographic areas. I provide approximate sizes and size-ranges, emphasizing those pertaining to live specimens, rather than relying on precise measurements taken on a limited amount of fixed material. For those stages that are previously described, readers can consult the referenced literature for such information. I reiterate the need for thorough, high-quality morphological investigations to be made on additional and better material for most of these species. Such work should include examination of shed (versus dissected) cercariae, to ensure adequate study of mature cercaria. I also note that future work elucidating the life cycles and taxonomy of these trematodes can benefit from the New Zealand host-parasite checklists compiled by Hine *et al.* (2000) for fish parasites and McKenna (2010) for bird parasites.

Key to trematodes infecting *Potamopyrgus antipodarum* as first intermediate host

[Species number in brackets preceding name matches numbering in Fig. 1 and Table 1, and the ordering in the species accounts section.]

1. Lacking daughter parthenitae (sporocysts or rediae), free embryos appear to develop directly to over 100 spherical metacercariae that fill much of visceral mass. [13] *Microphallus* sp. “livelyi”

-	With parthenitae	2
2.	Cercariae lacking tail, with oral stylet	[15] <i>Acaudate xiphidiocercaria</i> sp. I
-	Cercariae with tail (small cup-like, simple, forked, finned or bristled); with or without stylet	3
3	Tail small and cup-like (not more than 2x long as wide); stylet with two anterior points	[11, 12] <i>Coitocaecum</i> spp.
-	Tail elongate (e.g., >3x long as wide); if stylet present, lacking two anterior points	4
4	Tail forked	5
-	Tail not-forked	7
5	Tail stem and furcae each about same length as body	[1] <i>Apatemon</i> sp. I
-	Tail stem at least 2x body length; caudal furcae short (much less than 1/2 stem length)	(aporoctylids) 6
6	Cercaria smaller than 6b (body < 100 long, tail stem < 200 long); sporocysts round to slightly oblong	[2] Aporoctylid sp. I
-	Cercaria larger than 6a (body > 130 long, tail stem > 200 long); sporocysts elongate	[3] Aporoctylid sp. II
7	Cercaria with oral stylet (may be minute & non-descript—see Plagiorchioid sp. I)	8
-	Cercaria lacking oral stylet	11
8	With virgula organ (sack-like organ in posterior oral sucker)	9
-	Lacking virgula organ	10
9	Cercaria smaller than 9b (body < 100 long), virgula organ wider than long, faintly bipartite or not bipartite	[16] Virgulate sp. I
-	Cercaria larger than 9a (body > 130 long); virgule organ longer than wide, clearly bipartite	[17] Virgulate sp. II
10	With prominent ventral sucker, Y-shaped bladder, small bullet-shaped stylet (less than 1/5 oral sucker length), and obscuring cystogenous glands throughout most of body	[18] Plagiorchioid sp. I
-	Lacking ventral sucker, with elongate stylet (> 1/2 oral sucker length); body translucent with prominent penetration glands just posterior to equator	[14] <i>Microphallus</i> sp. "poulini"
11	With pigmented eyespots	12
-	Lacking pigmented eyespots	17
12	With ventral sucker	13
-	Lacking ventral sucker	15
13	Tail simple, not ornate	[19] Gymnocephalous sp. I
-	Tail with lateral bristles	(lepocreadiids) 14
14	With 4 pairs of penetration glands	[8] <i>Stegodexamine anguillae</i>
-	With 6 pairs of penetration glands	[9] Lepocreadiid sp. II
15	Lacking dorso-ventral tail fin; sometimes with medial eye	[5, 6] <i>Notocotylus</i> spp.
-	With dorso-ventral tail fin	16
16	With penetration glands (gland bodies just pre-equator and gland ducts empty at anterior oral sucker); lacking longitudinal pigment bands	[10] <i>Telogaster opisthorchis</i>
-	Lacking penetration glands; with two longitudinal pigment bands	[7] Pronocephaloid sp. IV
17	Lacking ventral sucker; tail simple; body filled with opaque cystogenous glands (white with reflected light); prominent lateral arms of excretory system connect anteriorly; smaller than 17b (body length ~500)	[4] Pronocephaloid sp. I
-	With ventral sucker; tail with dorso-ventral fin; larger than 17a (body length ~1000)	[20] Gymnocephalous sp. II

Species accounts

(Numbering and coding beneath species names matches use in Fig. 1 and Table 1)

Apatemon sp. I

(1. Apa1; Figs. 1, 2–3)

Stages: sporocysts (daughter) and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts primarily in mantle, but also in digestive gland and basal visceral mass

Voucher localities: Mohaka River, North Island, New Zealand (-39.0805° lat, 177.1403° long); Mataura River, South Island (-46.3894° lat, 168.7968° long)

Prevalence: 2% ($n = 100$) at Mohaka River; 1% ($n = 100$) at Mataura River

Specimens deposited: USNPC #s: 105672-105674.

Diagnosis: Sporocysts active, opaque, elongate (at least 10:1 length:width). Length ~2000. Developing cercariae appear to number over 100.

Cercaria non-oculate, longifurcate (tail fork length > 1/2 tail stem), pharyngeate, with anterior organ (modified oral sucker), and ventral sucker (a "Strigea cercaria"). Body length ~130. Tail stem and fork length about equal to each other and to body length.

Descriptive notes: Cercaria tail stem with transverse tegmental annulations, central excretory vessel surrounded by about 6–7 pairs of large "caudal bodies" (over 1/4 tail width) [caudal bodies contain glycogen stores

(Ginetsinskaya 1968)]. Anterior organ length 1/4 to 1/3 body length. Ventral sucker just post-equatorial, smaller (~1/3 the area) than the anterior organ (the modified oral sucker). Excretory bladder, small, V-shaped.

Remarks: I believe that this trematode corresponds to Winterbourn's "F1", despite his reporting the cercarial tail stem to be relatively much shorter (half the body length instead of approximately equal length) and the sporocysts to have a length:width ratio of only about 4:1, versus 10:1. Winterbourn appears to have had very little material to examine and the specimen he measured may not represent the typical condition.

I had recognized this trematode as likely belonging to the Strigeidae or the Diplostomidae (both within the superfamily Diplostomoidea). Dr. Bronwen Presswell (University of Otago) recently informed me that it is, indeed, one or more species of the strigeid genus, *Apatemon* (personal communication). She has a manuscript in preparation documenting this, and that it uses small fishes as second intermediate hosts and ducks as final hosts.



FIGURES 2–3. *Apatemon* sp. I. 2, Sporocyst with developing cercariae. Scale bar = 100. Numerical scale division = 25. 3, Cercaria. Scale bar = 100. Numerical scale division = 5.

Aporocotyloid sp. I (small aporocotyloid)

(2. Apo1; Figs. 1, 4–5)

Stages: sporocysts (daughter) and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts in gonad, digestive gland, basal visceral mass, and mantle.

Voucher localities: Grey River, South Island (-42.4528° lat, 171.2995° long); Waimakariri River, South Island (-43.4148° lat, 172.6517° long)

Prevalence: 1% ($n = 100$) at Grey River; 1% ($n = 100$) at Waimakariri River

Specimens deposited: USNPC #s: 105675, 105676

Diagnosis: Sporocysts translucent, irregularly round to ovoid to slightly oblong. Length ~300–400, small relative to cercariae (often about as long as an entire cercaria). Developing cercariae number less than 10, with more developed cercariae folded in the relatively small space.

Cercaria non-oculate, brevifurcate (tail fork length less than $\frac{1}{3}$ tail stem) apharyngeate, with protrusible anterior organ (modified oral sucker), no ventral sucker, with dorsal body fin (typical aporocotyloid-type cercaria). Body length < 100. Tail stem length < 200, about twice body length. Body and furcal fins not readily detectable and not observed in fixed samples.

Remarks: This species is most readily distinguished from *Aporocotyloid* sp. II by its smaller size and generally spheroidal (versus very elongate) sporocysts.

Aporocotyloid 1 corresponds to Winterbourn's F2, which also has standard aporocotyloid cercaria morphology.

Cercariae of aporocotyloids directly infect final host fishes.

Aporocotyloid 1 is potentially one or both of the aporocotyloids reported from introduced *P. antipodarum* popu-

lations in France (Gerard & Le Lannic 2003) and Poland (Zbikowski & Zbikowska 2009), which have similarly sized and shaped sporocysts and cercariae. If so, adult stages of the parasite may have been imported to Europe with live New Zealand eels (Hine 1978; Morley 2008), which may serve as the final host in New Zealand. See remarks for *Aporocotylid* sp. II for further comments relevant to *Aporocotylid* sp. I.



FIGURES 4–5. *Aporocotylid* sp. I. **4,** Sporocysts, live, with developing cercariae (Grey River voucher). Scale bar = 100. Numerical scale division = 10. **5,** Cercaria, live (Waimakariri River voucher). Scale bar = 100.

***Aporocotylid* sp. II (large aporocotylid)**

(3. Apo2; Figs. 1, 6–7)

Stages: sporocysts (daughter) and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts in (at least) gonad, digestive gland and basal visceral mass

Voucher locality: Grey River at Waipuna, South Island (-42.3544° lat, 171.7874° long)

Prevalence: 1% ($n = 100$)

Specimens deposited: USNPC #: 105677

Diagnosis: Sporocysts translucent, elongate (~10:1 length:width). Length ~1000. Developing cercariae number up to over 30.

Cercaria non-oculate, brevifurcate (tail fork length less than $\frac{1}{2}$ tail stem) apharyngeate, with protrusible anterior organ (modified oral sucker), no ventral sucker, with dorsal body fin and dorso-ventral furcal fins (typical aporocotylid-type cercaria). Body length >130, about $\frac{1}{2}$ tail stem length. Tail stem length >200. Furcal and, particularly, body fins readily apparent in live and fixed specimens.

Remarks: This species is most readily distinguished from *Aporocotylid* 1 by its larger size and elongate sporocysts.

Aporocotylid sp. II does not correspond to any of Winterbourn's species.

Aporocotylid sp. II may represent the larval stages of *Paracardicoloides yamagutii* Martin, 1974, adults of which Hine (1978) reported to be widespread in New Zealand eels. The sporocysts and cercariae are similar to those of *Pa. yamagutii*, which Nolan and Cribb (2004) recently described from the Australian hydrobiid, *Posticobia brazieri* Smith, in Brisbane, Australia (north of the distribution of invasive *Potamopyrgus antipodarum* in Australia). Brisbane is the area from which Martin (1974) originally described *Pa. yamagutii* from adults infecting Australian long-finned eels. Hence, if *Aporocotylid* sp. II does correspond to *Pa. yamagutii* reported from New Zealand eels, then *Pa. yamagutii* is widespread and characterized by geographic variation in intermediate and final host use. Alternatively, the *Pa. yamagutii* reported in New Zealand truly represents a different species than the one described from Australia.



FIGURES 6–7. Aporocotylid 2 (large aporocotylid). **6,** Sporocyst, live, with developing cercariae. Scale bar = 100. Numerical scale division = 10. **7,** Cercaria, live. Scale bar = 100. Numerical scale division = 10.

Pronocephaloid sp. I (eyeless pronocephaloid)

(4. Pro1; Figs. 1, 8–9)

Stages: rediae and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Rediae in gonad, digestive gland, basal visceral mass, and mantle regions

Voucher locality: Manawatu River, North Island (-40.373° lat, 175.6419° long)

Prevalence: 1% ($n = 100$)

Specimens deposited: USNPC #: 105678

Diagnosis: Redia translucent, ovoid to slightly oblong, ~500–1000 long, with gut ending slightly anterior or posterior to equatorial region and at least sometimes filled with what may be snail digestive gland tissue. Pharynx small (<50), round. Cercaria embryos around 10, with posterior to anterior developmental gradient (germ balls to one or two immature cercariae close to birth).

Cercaria non-oculate, with simple tail, with small circular oral sucker, no ventral sucker, no penetration glands, no stylet (a "monostome-like" cercaria). Body length ~400–500. Tail $\frac{1}{3}$ – $\frac{1}{2}$ body length.

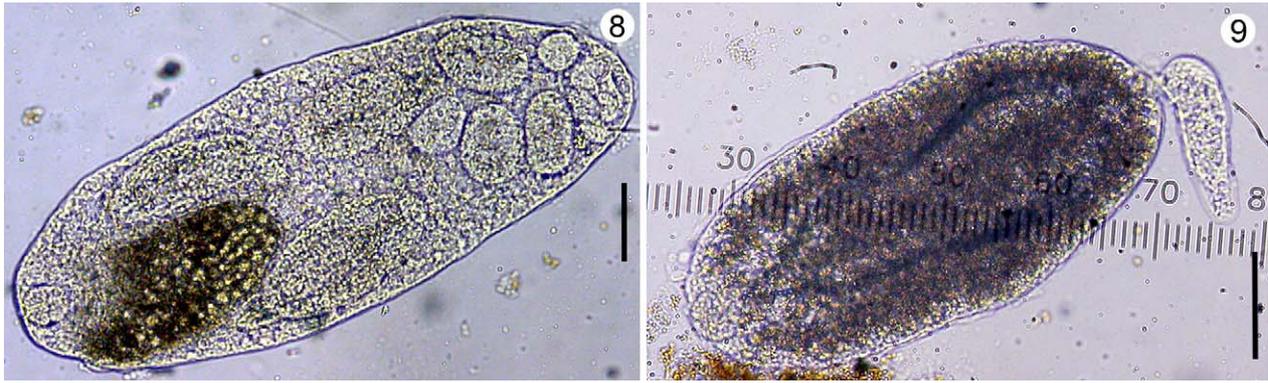
Metacercariae typically occur on operculum and shell of first intermediate host individuals. Diameter ~150.

Descriptive notes: Cercariae do much development outside of rediae, grow to be almost as large as redia. Undeveloped cercariae translucent. Mature cercaria body filled with reflective material except at oral sucker, provides whitish appearance under reflected light and appears dark with transmitted light. Main excretory ducts filled with refractile vesicles, readily apparent, gradually approach mid-line as go anterior to join to each other forming acute angle just posterior to oral sucker. Two gut caeca extend to just before posterior body margin.

Remarks: Pronocephaloid 1 corresponds to Winterbourn's "M1".

Two species may be subsumed within Pronocephaloid sp. I based upon differences in redia gut length. The gut ends pre-equatorially in the Manawatu voucher, but post-equatorially in at least one specimen I carefully examined from the Taieri River, South Island. Future work should determine whether this difference consistently occurs and lines up with intra- or interspecific variation.

Cercariae of pronocephaloidean species frequently encyst as "ectometacercariae" on the first intermediate host individual's operculum and shell, arthropod exoskeletons, or on aquatic vegetation (Schell 1985; Yamaguti 1975). Described pronocephaloidean ("monostome") cercariae that lack eyespots and leave their first intermediate hosts are not common or non-existent (e.g., I believe none are listed in Yamaguti (1975)). Hence, it would be very interesting to determine the life cycle and/or taxonomic position of this trematode. As a group, pronocephaloideans infect a wide range of ecto- and endothermic vertebrates as final hosts (Barton & Blair 2005).



FIGURES 8–9. Pronocephaloid sp. I. **8,** Redia, live. Scale bar = 100. **9,** Cercaria, live. Scale bar = 100. Numerical scale division = 10.

Notocotylus spp. (*N. gippyensis* (Beverley-Burton, 1958), and *N. tadornae* Bisset, 1977)

(5, 6. Noto; Figs. 1, 10–11)

[These two species are currently indistinguishable in first intermediate hosts]

Stages: rediae and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Rediae in gonad, digestive gland, basal visceral mass, and mantle

Voucher locality: Hurunui River, South Island (-42.8983° lat, 173.0966° long)

Prevalence: 1% ($n = 100$)

Specimens deposited: USNPC #: 105679

Diagnosis: Redia translucent, ovoid to oblong (~3:1 to 4:1 length:width), with gut ending before equatorial region and usually containing what may be snail digestive gland tissue. Length ~300–900. Cercaria embryos number less than ~8 with only 1 or 2 more developed cercariae close to birth in redia anterior.

Cercariae oculate with simple tail, with no ventral sucker and no penetration glands (a "monostome" in the "Imbricata Group" (Rothschild 1938)). Body ~250–400 long. Tail translucent, equal to or longer than body. Cercariae do much growth and development outside of redia, and occur in two large, developmental stages. Large, undeveloped cercariae immobile, filled with white reflective material except at oral sucker (much like *Pronocephaloid* sp. I), with much diffuse black pigment around two lateral eyespots that can give rise to a transverse eye band. Developed cercariae become slightly smaller, opaquely tan colored, with two distinct eyespots and often a medial third that may barely be evident (variation evident between cercariae of the same infection).

Descriptive notes: Cercaria oral sucker small, circular. Main excretory ducts become filled with refractory vesicles, proceed anteriorly following the body margin (about ¼ into body) until just posterior to the eyes where they course antero-medially and then anteriorly between the lateral eyespots to join each other just anterior to the lateral eyespots and the medial eyespot (if developed), posterior to oral sucker.

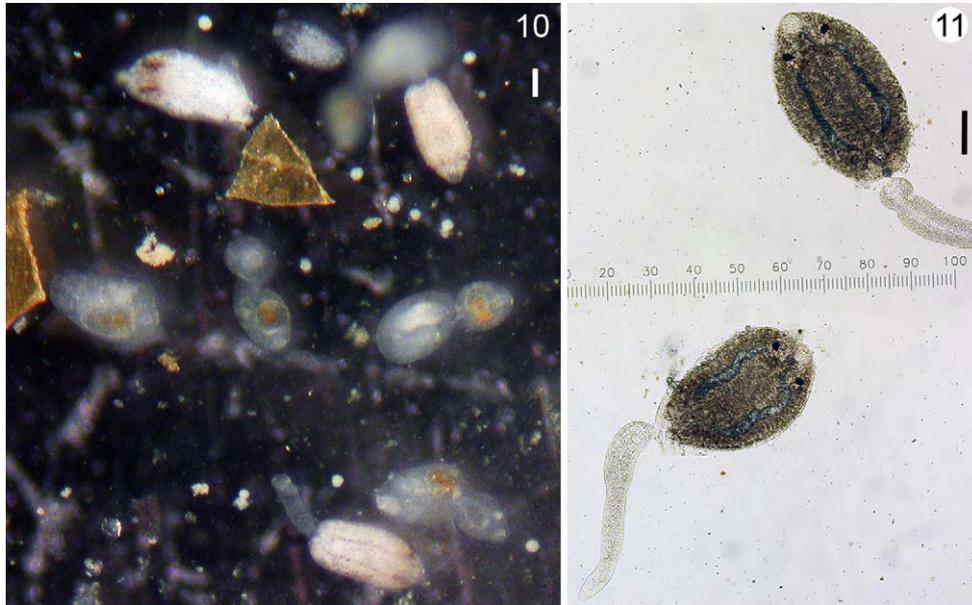
Remarks: My observations of 10 infections suggest that Winterbourn's M2 and M3 correspond to cercariae at different ontogenetic stages. I believe that his M2 represent the younger, immobile cercariae and that his M3 represents the developed cercariae.

At least two *Notocotylus* species infect *P. antipodarum* but it is not currently clear how to distinguish them. Bisset (1978) described the life cycles of *N. gippyensis* and *N. tadornae*, both of which used *P. antipodarum* as first intermediate host. However, his descriptions of the rediae and cercariae do not permit distinguishing the two species. Although Bisset described them as "virtually indistinguishable," his measurements suggest that the rediae and cercariae of *N. gippyensis* might be slightly larger than *N. tadornae*. Careful morphological work can probably uncover good, discriminatory traits. Such work can also determine whether the above-described ontogenetic development characterizes both species.

Bisset (1978) reported that he detected metacercariae of both species on undersurface of aquatic vegetation in the wild. However, as Winterbourn (1974) noted, and I have observed, the metacercariae also form on the opercu-

lum and shell of the infected first intermediate host snail. Hence, “second intermediate host” use is not completely resolved for these species. However, the species appear to use at least ducks (anatids) as final hosts (Beverley-Burton 1958; Bisset 1978; Osnas & Lively 2011).

N. gippyensis was described originally from adult stages from ducks in England by Beverley-Burton (1958). But the parasite is likely a New Zealand native that was introduced to the England with imported ducks or with *P. antipodarum* (Bisset 1978; Morley 2008).



FIGURES 10–11. *Notocotylus* spp. **10**, Rediae and cercariae (live) at various ontogenetic stages showing appearance under dissecting scope. Note the large, immobile, undeveloped cercaria and the slightly smaller, but further developed, tan-colored cercaria, both of which can be as large as the rediae (Hurunui River voucher). Scale bar = 100. **11**, Cercariae, developed, live (Clutha River, South Island, no voucher). Scale bar = 100. Numerical scale division = 10.

Pronocephaloid sp. IV (finned pronocephaloid)

(7. Pro4; Figs. 1, 12–13)

[Winterbourn’s M4, which I did not encounter]

Stages: rediae and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Rediae at least in the gonad and digestive gland.

Voucher locality: na

Prevalence: na

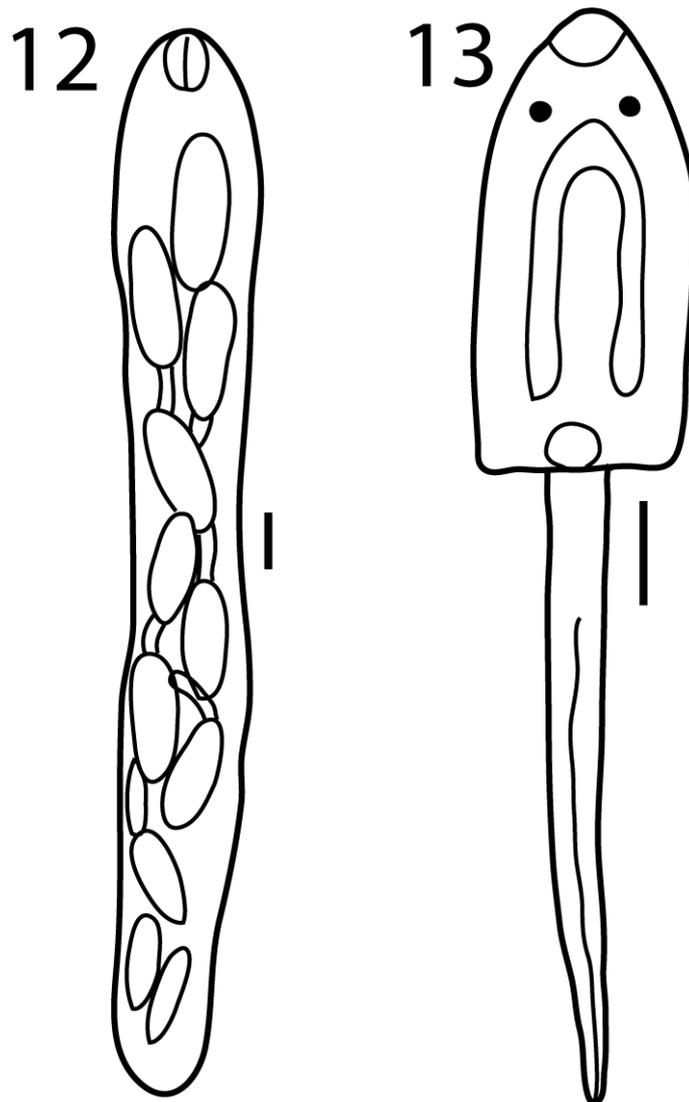
Specimens deposited: na

Diagnosis: [Derived from Winterbourn 1974] Redia translucent, elongate (~10:1 length:width). Length up to ~2000. Cercaria embryos number ~11 in various developmental stages.

Cercaria oculate with dorso-ventral tail fin, with small circular oral sucker, no ventral sucker, no penetration glands (a “monostome-like” cercaria). Body ~290–430 long, opaque (presumably white under reflected light). Tail translucent, equal to or twice body length.

Descriptive notes: [Derived from Winterbourn 1974] Cercaria body with postero-lateral adhesive papillae. Tail fin extends over $\frac{3}{4}$ of dorsal surface and entire ventral surface. Metacercariae reported as identical to *Notocotylus* spp. (above) and encyst on *P. antipodarum* shells.

Remarks: I have not encountered this species. Winterbourn’s description suggests that it is a pronocephaloid, although I am aware of no other such cercariae with a dorso-ventral tail fin. It would be very interesting to determine the life cycle and/or taxonomic position of this trematode. As a group, pronocephaloideans infect a wide range of ecto- and endothermic vertebrates (Barton & Blair 2005) as final hosts.



FIGURES 12–13. Pronocephaloid sp. IV. **12,** Redia. **13,** Cercaria. Drawings modified from Winterbourn (1974). All scale bars = 100.

***Stegodexamine anguillae* MacFarlane, 1951**

(8. Stan; Figs. 1, 14–16)

Stages: rediae and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Rediae in gonad, digestive gland, and basal visceral mass

Voucher locality: Opuha River, South Island (-44.0804° lat, 170.9788° long)

Prevalence: 2% ($n = 100$) (assuming neither was Lepocreadiid II, see remarks for that species)

Vouchers deposited: USNPC #: 105680

Diagnosis: Redia translucent, slightly elongate (~5:1 length:width), body widest anteriorly (near posterior gut margin) and barely narrows until posterior. Length ~1000. Cercaria embryos number up to ~30 with posterior to anterior developmental gradient.

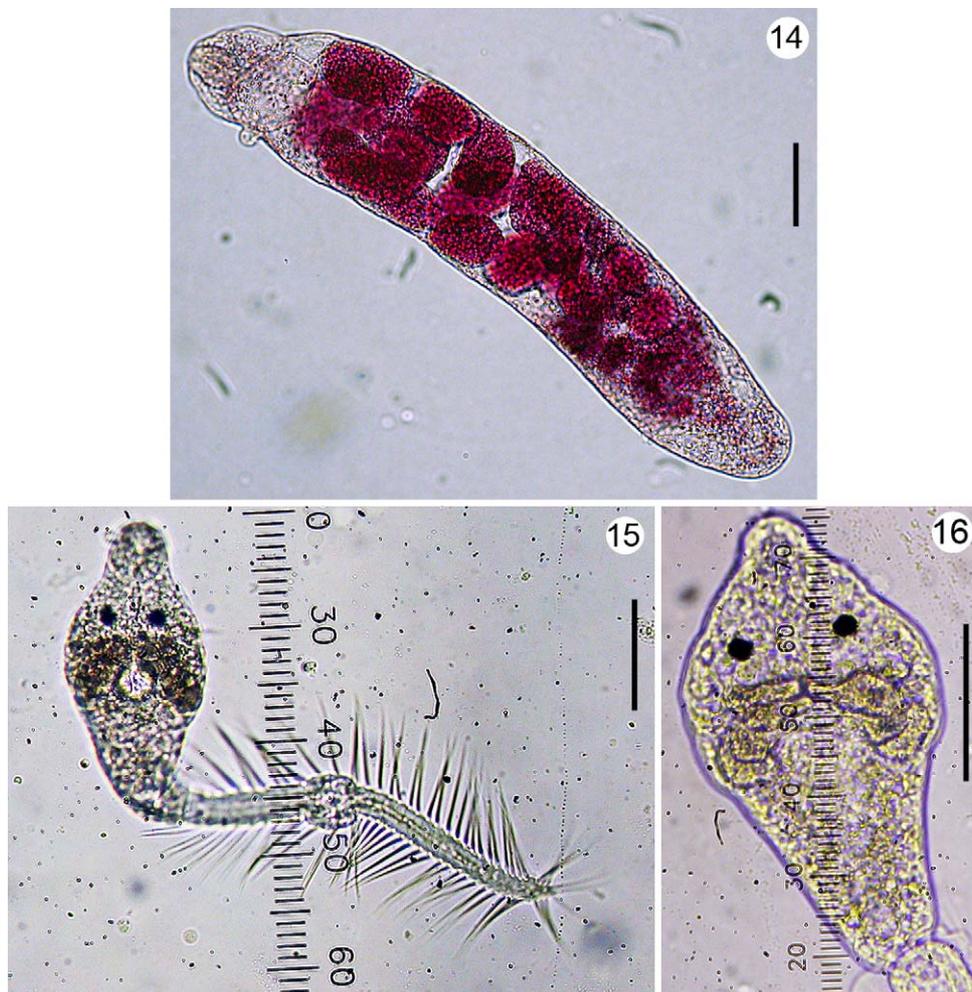
Cercaria oculate, bristle-tailed, pharyngeate, with oral and ventral sucker, and 4 pairs of penetration glands. Body length up to ~275. Tail length at least ~1.1–1.5 body length.

Remarks: *Stegodexamine anguillae* and the other lepecreadiid (Lepocreadiid sp. II) can be distinguished from

all the other trematodes parasitizing *P. antipodarum* by having bristle-tailed cercariae. Early infections, where embryonic cercariae have not yet developed tail bristles, can be distinguished from *Telogaster opisthorchis* (sp. 10, which have similar looking rediae) by at least two criteria. First, *S. anguillae* cercariae develop ventral suckers early in ontogeny and these are evident as a ventral protrusion (*T. opisthorchis* lacks a ventral sucker). Second, rediae are relatively wider than *T. opisthorchis* and have fewer embryonic cercariae with a less pronounced posterior-anterior developmental gradient. Currently, *S. anguillae* can be positively distinguished from Lepocreadiid sp. II by having 4 versus 6 pairs of penetration glands. See Lepocreadiid sp. II for further comments.

MacFarlane (1951) described *S. anguillae* and its life cycle. Cercariae encyst and form metacercariae in fishes (particularly small eleotrids). The parasite infects eels (*Anguilla* spp.) as final hosts. Moravec and Justine (2007) reported adults in New Caledonian eels. Because *P. antipodarum* is not introduced to New Caledonia, *S. anguillae* there infect a different first intermediate host or represent a different species.

MacFarlane (1952) contributed a forward-thinking ecological consideration of how host behavioral ontogeny interacts with parasite encounter rates to dictate patterns of infections in second intermediate hosts and final hosts for both *S. anguillae* and *Telogaster opisthorchis*. MacFarlane (1951) noted that metacercariae progenetically mature, particularly those infecting host gonads. For further investigations of this probable adaptive life cycle truncation, see, for instance, Herrmann and Poulin (2011); Holton (1984a); Poulin and Lefebvre (2006).



FIGURES 14–16. *Stegodexamine anguillae*. **14**, Redia, EtOH-fixed and acetocarmine-stained. Scale bar = 100. **15**, Cercaria, live. Scale bar = 100. Numerical scale division = 10. **16**, Close-up of live cercaria body to better indicate the four pairs of penetration glands. Scale bar = 100. Numerical scale division = 5.

Lepocreadiid sp. II (12 penetration gland lepopocreadiid)

(9. Lep2; Figs. 1, 17–18)

Stages: rediae and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Rediae in gonad, digestive gland, and basal visceral mass

Voucher localities: Hutt River, North Island (-41.1962° lat, 174.9216° long); Opihi River at Rockwood, South Island (-44.1682° lat, 170.9422° long)

Prevalence: 1% ($n = 100$) at Hutt River; 8% ($n = 100$) at Opihi River (assuming none were *Stegodexamine anguillae*, see remarks).

Specimens deposited: USNPC #: 105681, 105682

Diagnosis: Redia translucent, slightly elongate (~5:1 length:width), body widest anteriorly (near posterior gut margin) and continually narrows to posterior. Length up to ~900. Cercaria embryos number up to ~30 with posterior to anterior developmental gradient.

Cercaria oculate, bristle-tailed, pharyngeate, with oral and ventral sucker, and 6 pairs of penetration glands. Body length up to ~275. Tail length ~1.1–1.5 body length.

Remarks: This species has not been previously recognized. I had erroneously pooled it with *Stegodexamine anguillae* (sp. 8) during field work, and only recognized its existence afterwards (from photos and fixed samples). See remarks for *S. anguillae* concerning how to distinguish *S. anguillae* and Lepocreadiid sp. II from other trematodes infecting *P. antipodarum*. Currently, this species is most readily distinguished from *S. anguillae* by the penetration gland count (having 6 versus 4 pairs). Note that for accurate counts, one should observe the single large nucleus in each penetration gland cell body. Interestingly, when MacFarlane (1951) described *S. anguillae*, he noted that a few atypical cercariae had 6 pairs of penetration glands. Because penetration gland counts are normally a good, discriminatory taxonomic character, I provisionally recognize Lepocreadiid sp. II as a different species rather than atypical *S. anguillae*. Other possible differences may exist, including redia shape (gradually tapering or not), and the size of the redia pharynx relative to the body (potentially larger and more square-like in Lepocreadiid sp. II). My observations of the tail bristles indicate that both species have 37–39 total and that there is no terminal medial bristle, versus a terminal pair, but this should be confirmed.

As a group, lepopocreadiids infect a wide range of invertebrate and fish second intermediate hosts, and fishes as final hosts.



FIGURES 17–18. Lepocreadiid sp. II. **17,** Redia, live. Scale bar = 100. Numerical scale division = 10. **18,** Cercaria, live. Scale bar = 100. Numerical scale division = 10. Both photos are of the Opihi River voucher.

***Telogaster opisthorchis* MacFarlane, 1945**

(10. Teop; Figs. 1, 19–20)

Stages: rediae and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Rediae in gonad, digestive gland, basal visceral mass, and mantle.

Voucher locality: Waimakariri River, South Island (-43.4148° lat, 172.6517° long)

Prevalence: 5% ($n = 100$)

Specimens deposited: USNPC #: 105683

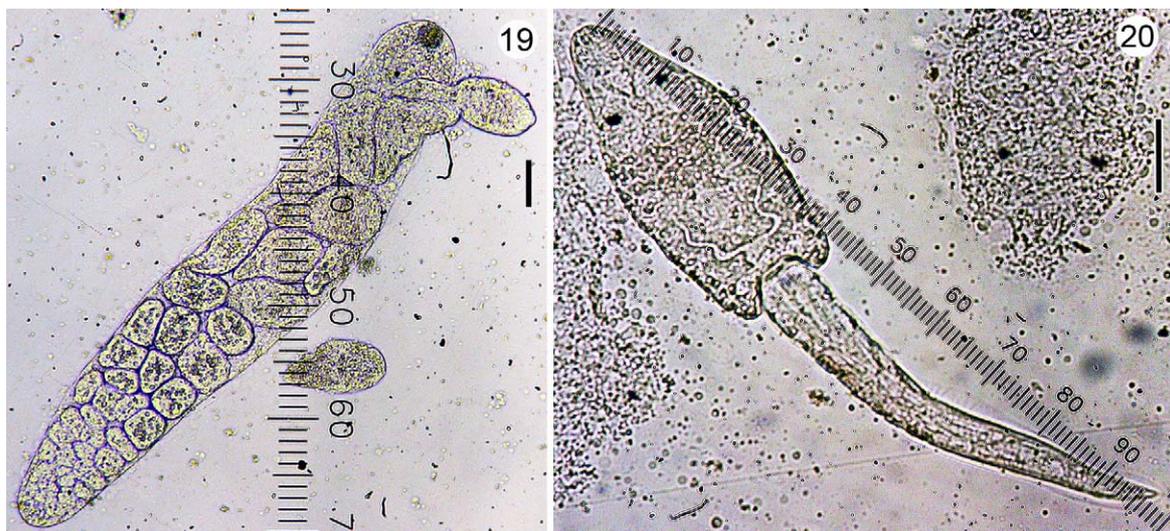
Diagnosis: Redia translucent, elongate (~5:1 to 9:1 length:width), gradually tapering anterior to posterior. Length up to ~2000. Cercaria embryos number up to over 50, typically tightly packed and exhibit very pronounced posterior to anterior developmental gradient. Pharynx appears to be relatively small compared to *S. anguillae* or *Lepocreadiid* sp. II, < 1/3 width of anterior redia body width.

Cercaria oculate, with dorso-ventral tail fin, no ventral sucker, with penetration glands. Main excretory collecting ducts frequently pronounced, sinusoidal, empty into small squarish bladder. Body length ~220–400. Tail length greater than 1.3 times body length. Tail fin originates dorsally ~1/5 into tail from base, continues around posterior tip to insert ~1/3 into tail from tip.

Descriptive notes: Redia pharynx < 1/3 width of anterior redia. Cercaria tail fin originates dorsally ~1/5 into tail, continues around posterior tip, inserts ~1/3 into tail from tip.

Remarks: MacFarlane (1945) described *T. opisthorchis* and its life cycle. Cercariae encyst as metacercariae in fishes (particularly in muscles of small eleotrids) and infect eels (*Anguilla* spp.) as final hosts. Cribb (1986) reported adults from eels in SE Australia, where *P. antipodarum* is introduced, and describes aspects of adult morphology.

MacFarlane (1952) contributed a forward-thinking ecological consideration of how host behavioral ontogeny interacts with parasite encounter rates to dictate patterns of infections in second intermediate hosts and final hosts for both *T. opisthorchis* and *Stegodexamine anguillae* (sp. 8). Kelly *et al.* (2010b) showed that infection of a threatened galaxiid fish second intermediate host results in deformities in juvenile fish, potentially with strong effects on recruitment to fish populations. Further, the widely used herbicide, glyphosate, can influence cercarial output by infected snails under laboratory conditions, and infection by metacercaria appears more likely to kill fish that are also exposed to the herbicide (Kelly *et al.* 2010a).



FIGURES 19–20. *Telogaster opisthorchis*. **19**, Redia, live, with embryonic cercaria being pressed out of birth pore. Scale bar = 100. Numerical scale division = 25. **20**, Cercaria, live. Scale bar = 100. Numerical scale division = 10.

***Coitocaecum* spp. (*C. parvum* Crowcroft, 1945; and *C. zealandicum* Hine, 1977)**

(11, 12. Coit; Figs. 1, 21–23)

[It is almost certain that both of these congeners infect *P. antipodarum*, but are currently indistinguishable.]

Stages: sporocysts (daughter) and cercariae

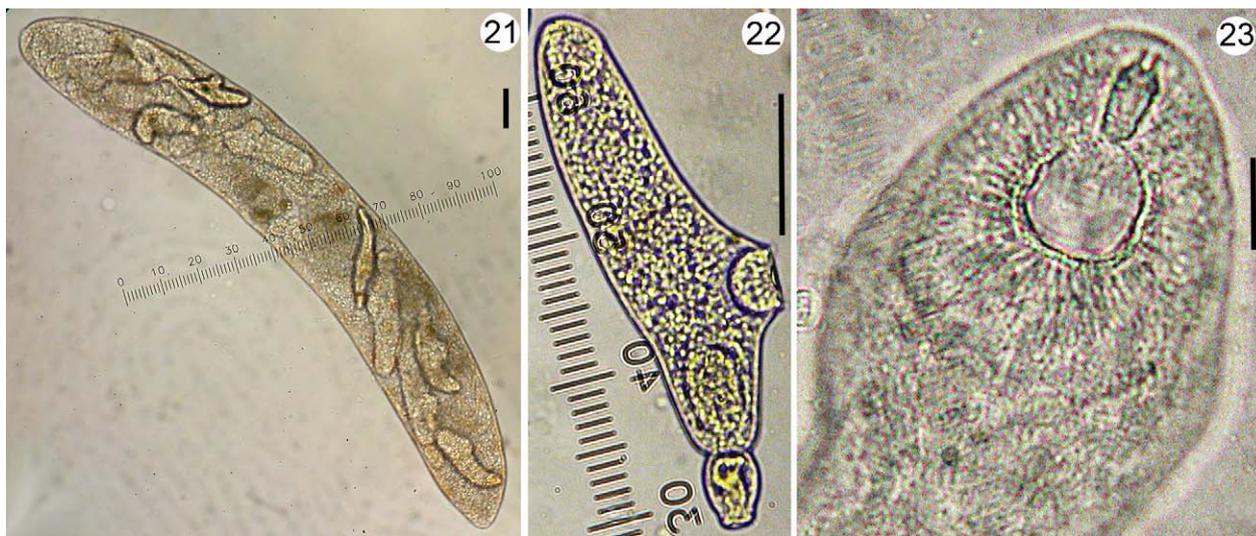
Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts in gonad, digestive gland, basal visceral mass, and mantle

Voucher localities: Ngaruroro River, North Island (-39.3803° lat, 176.3326° long); Taieri River, South Island (-45.2572° lat, 170.2716° long); Maitara River, South Island (-46.3894° lat, 168.7968° long)

Prevalence: 6% at Ngaruroro River ($n = 100$); 8% at Taieri River ($n = 100$); 3% ($n = 100$) at Maitara River

Specimens deposited: USNPC #s: 105684-105686



FIGURES 21–23. *Coitocaecum* spp. **21**, Sporocyst, live (Taieri River Voucher). Scale bar = 100. Numerical scale division = 10. **22**, Cercaria, live (photo of a Maitara River specimen different than voucher). Scale bar = 100. Numerical scale division = 10. **23**, Close up of cercaria oral sucker showing two-pointed oral stylet, live (Ngaruroro River voucher). Scale bar = 15.

Diagnosis: Sporocysts sometimes active, translucent, elongate (~5:1 to 9:1 length:width), bluntly tapered at each both ends. Length up to ~2000. Cercaria number from ~10 to over 45, in various developmental stages lacking pronounced antero-posterior developmental gradient.

Cercaria non-oculate, with short glandular sucker-like tail, oral and ventral suckers, a two-pointed oral stylet ("a cotylocercous xiphidiocercaria"). Body length up to ~300. Tail length ~1/6 body length, not more than two times tail width. Stylet ~15 long.

Remarks: At least two species likely infect *P. antipodarum*: *Coitocaecum parvum* and *C. zealandicum*. MacFarlane (1939) described the life cycle of *C. parvum* and documented that it uses *P. antipodarum* as first intermediate host in New Zealand. However, he misidentified it as *C. anaspidis* Hickman 1934, and this name has been widely promulgated in the literature (see Holton 1983; Holton 1984b). Adults of both *C. parvum* and *C. zealandicum* have been found in freshwater fishes on both North and South Islands (Hine 1978; Hine *et al.* 2000; Holton 1983; Holton 1984b). It appears almost certain that *C. zealandicum* also infects *P. antipodarum* as first intermediate host as there is no obvious alternative first intermediate host for *C. zealandicum* to use. I list it here to foster its recognition in future surveys.

Coitocaecum parvum infects small crustaceans (e.g., mysidaceans, amphipods, copepods) as second intermediate hosts, where it can become progenetic (mature and produce eggs) while encysted (Holton 1984a; Lefebvre & Poulin 2005; MacFarlane 1939). *Coitocaecum zealandicum* likely also used crustaceans as second intermediate hosts. However, this cannot be certain as opacoelids can infect a wide range of other invertebrates or even fishes (Cribb 2005). As typical final hosts, *C. parvum* uses a range of fishes (Crowcroft 1945; Holton 1983; Holton 1984b; MacFarlane 1939). *Coitocaecum zealandicum* has been reported from eels, torrent fish (Cheimarrichthyidae), and *Gobiomorphus* spp. (Eleotridae) (Hine *et al.* 2000).

Coitocaecum parvum infection is associated with smaller and narrower snails compared to uninfected snails (Lagrué *et al.* 2007a). This appears to be adaptive for the parasite by permitting an increased mass of reproductive tissues (sporocysts) for a given shell size (Lagrué *et al.* 2007a). Lagrué *et al.* (2007b) developed markers for nine microsatellite (=short tandem repeat) loci, and Lagrué *et al.* (2007a) used this tool to show that multi-clone infections can occur in *C. parvum* first intermediate host infections.

A substantial amount of research has examined aspects of the biology, ecology, and evolution of *C. parvum* at other life stages, beyond the above citations. Interested readers can consult the literature for this work, most of which has been undertaken by Dr. Robert Poulin's Evolutionary and Ecological Research Group at Otago University in Dunedin, South Island.

Coitocaecum parvum was originally described from Tasmanian adult stages (Crowcroft 1945). If the Tasmanian and New Zealand *C. parvum* are actually the same species, it is possible that the parasite was introduced to Tasmania with *P. antipodarum*, which has been invasive in Tasmania since at least the 1800s (Ponder 1988). Determining the first intermediate host used by *C. parvum* in Tasmania would clarify this matter.

Citing ICZN Cord Art. 33.3.1, Yoshida and Urabe (2005) argued that the original spelling of this genus (*Coitocoecum* Nicoll 1915) should be adopted. This may be due to a misunderstanding of what is meant by "prevailing use." It is clear that prevailing use is of *Coitocaecum*, including attribution to Nicoll 1915, justifying maintaining the "incorrect" spelling as is done here.

***Microphallus* sp. "livelyi"**

(13. Mili; Fig. 24)

Stages: embryonic and encysted metacercariae

Host: *Potamopyrgus antipodarum*

Site in host: embryonic and encysted metacercariae in gonad, digestive gland, and basal visceral mass

Voucher locality: Monowai Stream, South Island (-45.8067° lat, 167.5308° long)

Prevalence: 7% ($n = 100$)

Specimens deposited: USNPC #: 105687

Diagnosis: Parthenitae not-present. Cercariae not present. Initial infection with hundreds of germ balls and embryonic metacercariae that appear to develop directly to encysted metacercariae that fill most of distal visceral mass (gonad and digestive gland region) and much of basal visceral mass. Developed encysted metacercaria spherical to ovoid, ~100–120 diameter, with developing vitelline follicles apparent as two dark brown blotches.

Remarks: This species corresponds to Winterbourn's Metacercaria A. I never detected daughter sporocysts for these infections, including in very early-stage infections. As mentioned by other workers (e.g., Krist & Lively 1998), developing infections progress from only having unencysted germinal balls and embryos, to having an increasing proportion of well-developed, fully-encysted metacercariae. All stages appear to develop freely in snail tissues or hemocoelomic spaces. Future histological work could confirm whether this species truly lacks daughter sporocysts. My colleagues and I are currently maintaining this species in the laboratory, and I am working to resolve its specific identity.

Microphallus sp. "livelyi" possesses an evolutionarily modified lifecycle, using the first intermediate host as second intermediate host. Hence, it is a "trophically transmitted parasitic castrator," sensu Lafferty and Kuris (2002). Adults use birds, particularly ducks, as final hosts (Osnas & Lively 2011). Domestic mice serve as suitable laboratory hosts (Lively & McKenzie 1991).

Other microphallids that have similar lifecycles wherein the first intermediate host individual also serves as second intermediate host. For such species, metacercaria embryos have variously been termed "blastocercariae" (e.g., Deblock 1974) or "cryptocercariae" (Galaktionov & Dobrovolskij 2003). However, those embryos appear to always form within sporocysts. If *Microphallus* sp. "livelyi" (or its ancestor) has indeed lost daughter sporocysts, it represents a variation on the theme characterizing these abbreviated live cycles.

Explaining my working name, this is the "*Microphallus* sp." extensively worked on by Curt Lively and colleagues (e.g., Mark Dybdahl, Jukka Jokela, Ed Levri, Kayla King). This research, using this trematode-snail host interaction, includes classic empirical evidence for parasitism underlying the evolutionary maintenance of sexual reproduction, local adaptation of parasite host specificity, and coevolutionary cycling of hosts and parasites

(e.g., Dybdahl & Lively 1998; Jokela & Lively 1995; Lively 1987; Lively 1989). Additionally, this trematode appears to adaptively modify the behavior of infected snails to increase trophic transmission to final host birds (e.g., see Levri 1999; Levri & Lively 1996). Infection also decreases growth in juvenile snails (Krist & Lively 1998) and is also related to shell shape and defense morphology (Levri *et al.* 2005). Please consult the literature for additional work on this system.

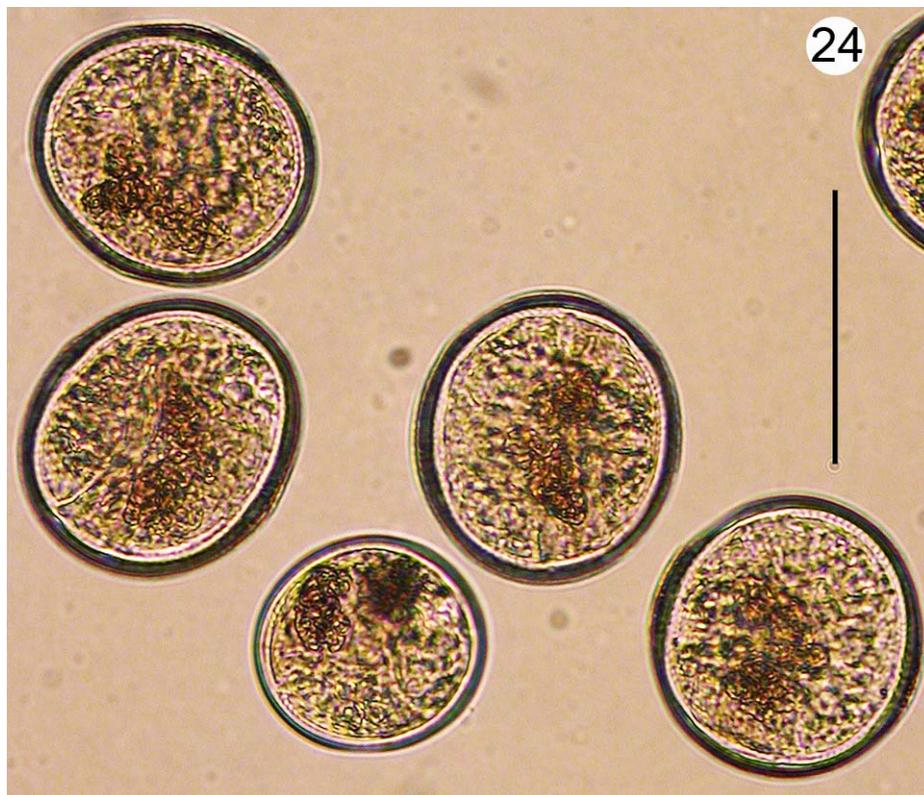


FIGURE 24. *Microphallus* sp. "livelyi". Group of encysted metacercariae (scale bar = 100). Photo of samples collected by C. Lively in January 2012 from Lake Alexandrina, New Zealand.

***Microphallus* sp. "poulini"**

(14. Mipo; Figs. 1, 25–27)

Stages: sporocysts (daughter) and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts in gonad, digestive gland, basal visceral mass, and mantle

Voucher localities: Waimakariri River, South Island (-43.4148° lat, 172.6517° long); Opihi River, South Island (-44.1682° lat, 170.9422° long); Sutton Stream, South Island (-45.5971° lat, 170.0949° long)

Prevalence: 2% ($n = 100$) at Waimakariri; 2% ($n = 100$) at Opihi; 0.06% ($n = 160$) at Sutton

Specimens deposited: USNPC #: 105688-105690

Diagnosis: Sporocyst translucent, globose to oblong (2:1 length:width). Length ~400–500. Developing cercariae number up to over 20.

Cercaria non-oculate with simple tail, no ventral sucker, prominent penetration glands, and oral stylet. Body length ~90–130. Tail length 1/2 to 1 times body length. Penetration glands post-equatorially in the third fourth of body. Stylet length ~12. Penetration glands can extrude contents into the gland ducts that become inflated anteriorly, resulting in gland bodies being less apparent. Penetration glands in many cercariae often opaque brown, in smaller, compact cluster just post-equator. In some infections, unusual cercariae occur alongside the normal cercariae: they are immobile, larger (length up to 180), elliptical, with the smaller, rounded, opaque, brown penetration glands, and appear to lack tail. I do not know whether this represents ontogenetic variation, dead cercariae, or something else.

Remarks: The “normal” cercariae from some infections are consistently under 100 microns long, while those from others appear to typically be around 130. This may represent intraspecific variation or the existence of multiple microphallid species.

This species appears to have not been included in Winterbourn (1974). However, explaining my working name, it is the “*Microphallus* sp.” that has been the subject of several investigations out of Dr. Robert Poulin’s research group at Otago University, Dunedin, South Island. This work has focused on metacercariae, particularly their impacts on second intermediate hosts, which are copepods and amphipods (e.g., Coats *et al.* 2010; Hansen & Poulin 2005; Rauque *et al.* 2011). Please consult the literature for additional research.



FIGURES 25–27. *Microphallus* sp. “poulini” **25**, Sporocyst, live (Sutton Stream voucher). Scale bar = 100. Numerical scale division = 10. **26**, Cercariae, showing the two observed forms, live (Waimakariri River voucher). Scale bar = 100. Numerical scale division = 10. **27**, Cercaria showing inflated penetration-gland ducts, live (Opihi River voucher). Scale bar = 100. Numerical scale division = 2.5.

Acaudate xiphidiocercaria I (*Microphallidae*?)

(15. Axi1; Figs. 1, 28–29)

Stages: sporocysts (daughter) and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts in gonad, digestive gland, basal visceral mass, and mantle

Voucher localities: Waiiau River, Coromandel Peninsula, North Island (-36.8° lat, 175.52° long)

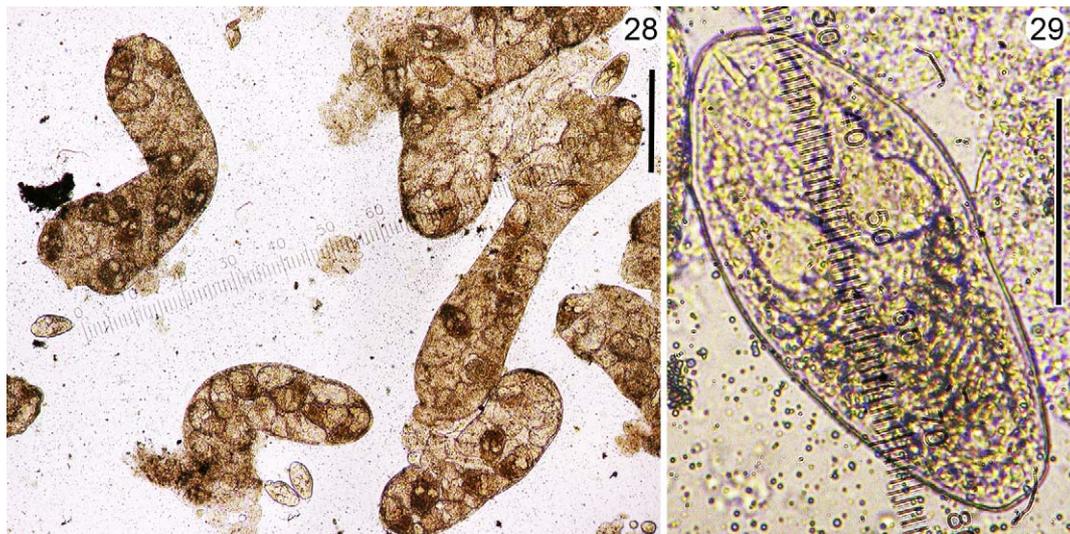
Prevalence: 1% ($n = 100$)

Specimens deposited: USNPC #: 105691

Diagnosis: Sporocyst thin-walled, oblong to slightly elongate (up to ~5:1 length:width). Length ~1500; width ~380. Developing cercariae number up to over 20, with about 1/3 fairly well-developed.

Cercaria non-oculate, with no tail, with oral sucker, no ventral sucker, simple stylet, elliptic to ovate to oblong, with obvious penetration glands equatorially and in second fourth of body. Penetration gland ducts often greatly inflated anteriorly. Body ~250. Stylet length ~11.

Remarks: I only encountered three, freshly dead infections of this trematode, each from the Coromandel Peninsula. Further work on this species can confirm or refute the speculations I posit here. The lack of a detectable ventral sucker, the penetration gland morphology, and the possession of daughter sporocysts suggest that this trematode is a tailless microphallid. Tailless microphallid cercariae typically do not leave their first intermediate host; they form metacercariae (with or without a cyst) within the first intermediate host and consequently use their first intermediate host as second intermediate host (see Deblock 1980; Galaktionov & Dobrovolskij 2003). Acaudate xiphidiocercaria I is similar to Winterbourn's C1, which may represent further developed worms, as indicated by the weakly developed ventral sucker that he described. However, the well-developed penetration glands and stylet suggest that the cercariae of Acaudate xiphidiocercaria I leave the first intermediate host. If so, and if this trematode is a microphallid, it likely infects an arthropod as second intermediate host and birds as final hosts. However, Winterbourn's C1 and Acaudate xiphidiocercaria I may be different, and workers should be alert to the possibility of at least two tailless cercariae in *P. antipodarum*, one with a ventral sucker and one without. In fact, a zoogonid trematode (which are typically tailless and have a ventral sucker), *Deretrema philippae* Hine, 1977, has been reported from New Zealand fish (Hine 1977; Hine *et al.* 2000). It may use *P. antipodarum* as first intermediate host.



FIGURES 28–29. Acaudate xiphidiocercaria I. **28,** Sporocysts, live. Scale bar = 500. Numerical scale division = 25. **29,** Cercaria, live. Scale bar = 100. Numerical scale division = 5.

Virgulate sp. I (small virgulate cercaria)

(16. Vir1; Figs. 1, 30–32)

Stages: sporocysts (daughter) and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts in gonad, digestive gland, basal visceral mass, and mantle

Voucher localities: Grey River at Waipuna, South Island (-42.3544° lat, 171.7874° long); Taieri River, South Island (-45.2572° lat, 170.2716° long)

Prevalence: 1% ($n = 100$) at Grey River; 1% ($n = 100$) at Taieri River

Specimens deposited: USNPC #s: 105692, 105693

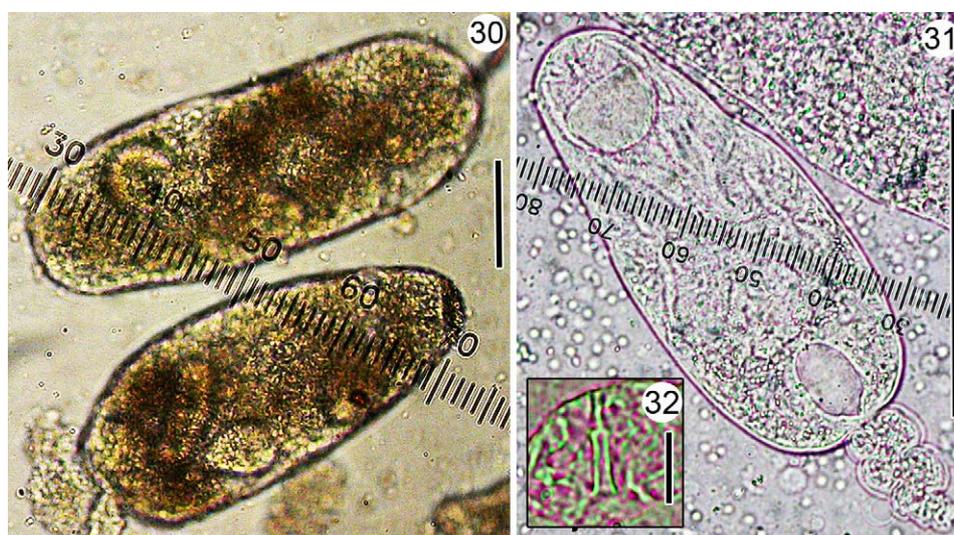
Diagnosis: Sporocyst ovoid to oblong (~3.5:1 length:width). Length ~200–450. Width ~150. Developing cercariae number up to ~8, fairly well-developed.

Cercaria non-oculate, with simple tail, oral sucker, weakly developed ventral sucker smaller than oral sucker, an ornamented oral stylet, a pouch-like organ in posterior half of oral sucker (the "virgula organ"). Body elliptic to ovate, length < ~90 (to 140 when flattened). Tail length ½ to 1 times body length. Bladder sac-like, oval. Virgula organ often wider than long, medial membrane absent to weakly developed. Stylet overall thin (~6:1 length:width), with shoulder at tip/shaft juncture; shaft broadens slightly toward base; length ~15; tip ~1/3 total stylet length.

Remarks: I encountered this small virgulate cercaria much more frequently than *Virgulate* sp. II, which appears to correspond to Winterbourn's X1 in terms of size. The small size of *Virgulate* sp. I readily distinguishes it from *Virgulate* sp. II, as do the longer than wide virgula organ, and the relatively stout oral stylet.

Virgula organs are filled with glandular material that can serve several functions for the free-swimming cercaria and during the infection process of second intermediate hosts (Kruidenier 1951).

Virgulate cercariae belong to a (potentially paraphyletic) group of five digenean families within the Microphalloidea (Lotz & Font 2008). They infect arthropods as second intermediate hosts and various mammals (often bats), birds, amphibians, reptiles as final hosts (Lotz & Font 2008; Schell 1985; Yamaguti 1975).



FIGURES 30–32. *Virgulate* sp. I. **30**, Sporocysts, live (Taieri River voucher). Scale bar = 100. Numerical scale division = 10. **31**, Cercaria, live (Taieri River voucher). Scale bar = 100. Numerical scale division = 2.5. **32**, Close up of cercaria oral stylet showing oral stylet, live (Grey River voucher). Scale bar = 10.

Virgulate sp. II (large virgulate cercaria)

(17. Vir2; Figs. 1, 33–35)

Stages: sporocysts (daughter) and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts in gonad, digestive gland, basal visceral mass, and mantle regions

Voucher locality: Waimakariri River, South Island (-43.4148° lat, 172.6517° long)

Prevalence: 1% ($n = 100$)

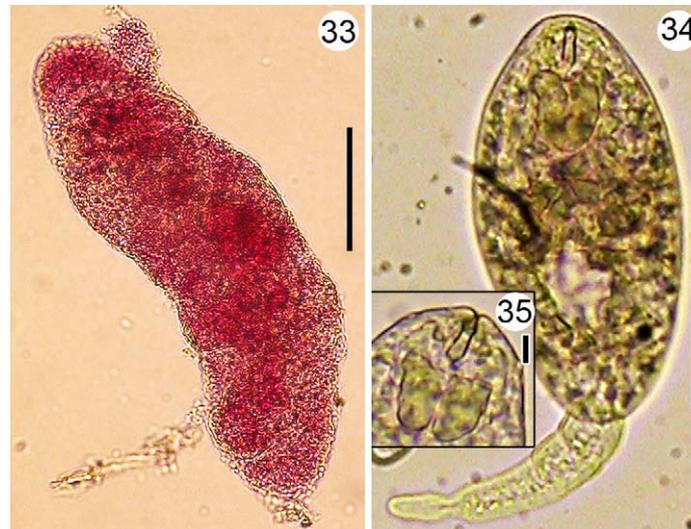
Specimens deposited: USNPC #: 105694

Diagnosis: Sporocyst ovoid to slightly elongate (~3.5:1 length:width ratio). Length ~450. Width ~185. Developing cercariae number up to ~8, fairly well-developed.

Cercaria non-oculate, with simple tail, oral sucker, weakly developed ventral sucker ~1/3 oral sucker size, a shouldered oral stylet, and a pouch-like organ in posterior half of oral sucker (the "virgula organ"). Body elliptic to irregularly ovate, length ~140–200. Tail length 1/2 to 1 times body length. Bladder sac-like, oval. Virgula organ often longer than wide, with distinct medial dividing membrane. Stylet overall relatively stout (~4:1 L:W) with shoulder at tip/shaft juncture; shaft broadens at base; length ~20, tip ~1/4 total stylet length.

Remarks: Virgulate sp. II may correspond to Winterbourn's X1, based particularly on cercaria size (his reported length is 150 microns). Winterbourn reported that the excretory bladder was V-shaped with a long stem, versus sac-like. This may indicate the existence of further cryptic species of virgulate cercariae, as bladder shape can reflect species differences for virgulate cercariae (Hall 1960).

See remarks for Virgulate sp. I concerning virgula organ form and function, taxonomic position, and life-cycle information for virgulate cercariae.



FIGURES 33–35. Virgulate sp. II. **33,** Sporocyst, formalin-fixed and acetocarmine stained. Scale bar = 100. **34,** Cercaria, live. Scale bar = 100. **35,** Anterior end of a different cercaria that better indicates stylet shape, live. Scale bar = 10. All are of Waimakariri voucher.

Plagiorchioid sp. I

(18. Pla1; Figs. 1, 36–38)

Stages: sporocysts (daughter) and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Sporocysts in digestive gland, basal visceral mass, and mantle regions

Voucher locality: Tukituki River, North Island (-39.7151° lat, 176.927° long); Manawatu River, North Island (-40.373° lat, 175.6419° long)

Prevalence: 1% ($n = 100$) at Tukituki River; 1% ($n = 100$) at Manawatu River

Specimens deposited: USNPC #s: 105695, 105696

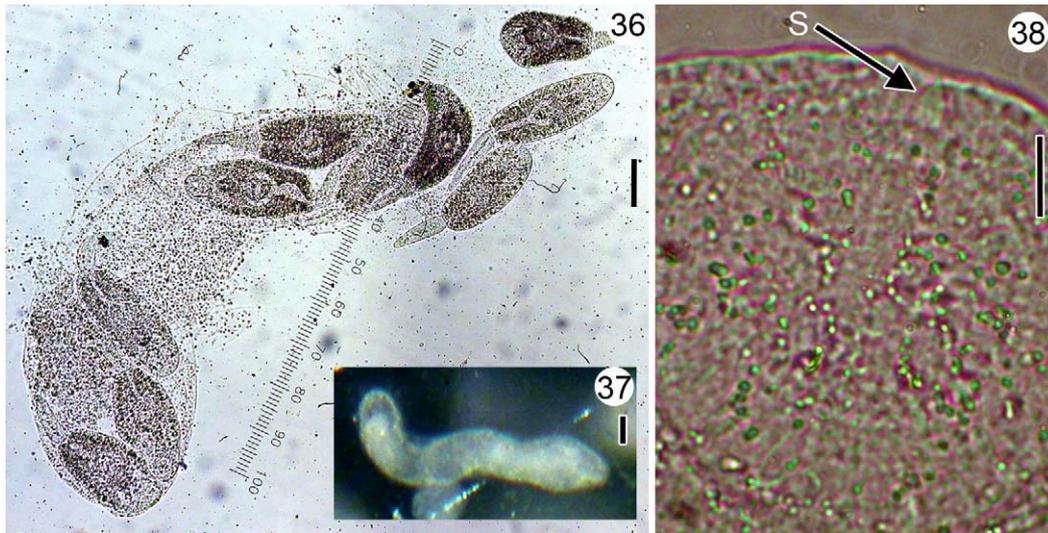
Diagnosis: Sporocyst thick-walled, elongate (~7:1 length:width), can be irregular in width (with constrictions), difficult to separate from snail tissues. Length up to over 1000. Developing cercariae number up to over 10 at various developmental stages with no obvious ontogenetic gradient.

Cercaria non-oculate, with oral and ventral suckers, Y-shaped excretory bladder, simple tail and oral stylet (an “Armatae” cercaria). Body length ~250. Tail usually $\frac{1}{2}$ – $\frac{3}{4}$ cercaria body length. Oral stylet minute (6.4 long), bullet-shaped, in roof of oral sucker. Ventral sucker equatorial, approximately equal size as oral sucker. Excretory bladder arms embrace ventral sucker and extend to anterior margin of ventral sucker.

Remarks: This species has not previously been reported infecting *P. antipodarum*.

The Plagiorchioidea contains numerous families with species that collectively parasitize a wide range of aquatic invertebrates, amphibians, and fishes as second intermediate hosts, and ecto and endothermic vertebrates as FHs.

Given the general marine trematode taxonomic affinities of the trematodes parasitizing *P. antipodarum*, Plagiorchioid 1 may actually be a renicolid, which are common in marine systems (Martin 1971; Wright 1956). The Rencolidae is currently classified in the Microphalloidea, not the Plagiorchioidea (Gibson 2008).



FIGURES 36–38. Plagiorchioid sp. I. **36**, Sporocyst, squashed with developing cercariae, live (Tukituki River voucher). Scale bar = 100. Numerical scale division = 10. **37**, Sporocyst, live (Manawatu River voucher). Photo taken with reflected light at stereomicroscope, Scale bar = 100. **38**, Anterior portion of flattened cercaria, showing the small oral stylet (s) in anterior of oral sucker, live (Manawatu River voucher). Scale bar = 10.

Gymnocephalous sp. I (Haploporidae?)

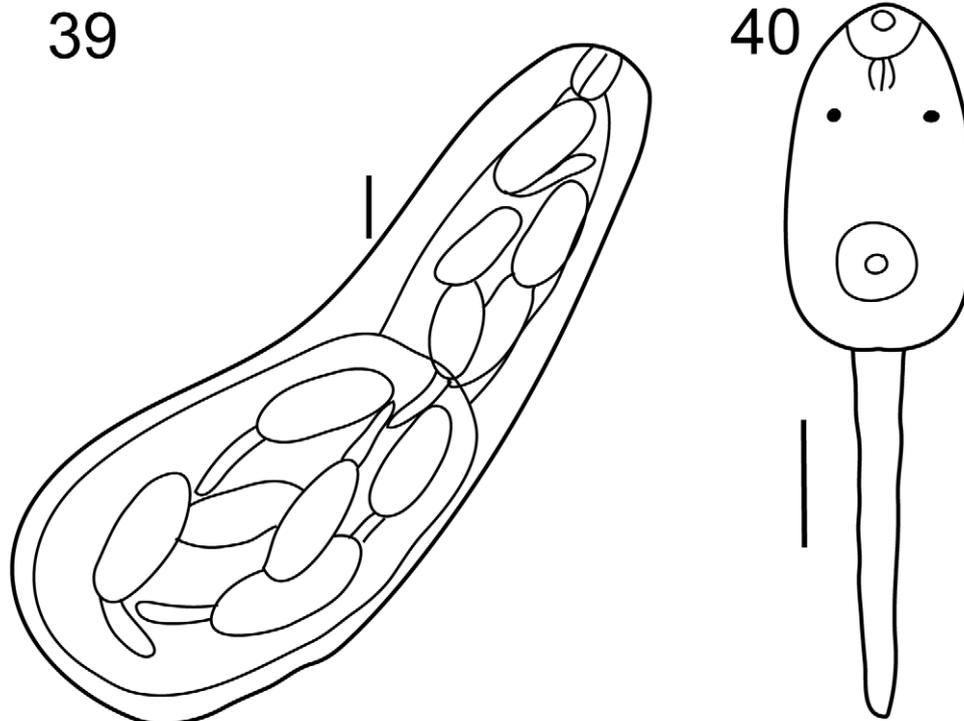
(19. Gym1; Figs. 1, 39–40)

[Winterbourn’s G1, which I did not encounter]

Stages: rediae and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Rediae at least in the gonad and digestive gland.



FIGURES 39–40. Gymnocephalous sp. I. **39**, Redia. **40**, Cercaria. Drawings modified from (Winterbourn 1974). All scale bars 100.

Locality: na

Dates collected: na

Prevalence: na

Specimens deposited: na

Diagnosis: [derived from Winterbourn 1974] Redia elongate ovoid (~3:1 length:width), broadens posteriorly. Length up to 1440. Pharynx small, inconspicuous. Developing cercariae number up to 11.

Cercaria oculate, pharyngeate with simple tail, oral and ventral suckers, no stylet, no collar spines. Body length ~250. Tail length ~3/4 to 1 times body length.

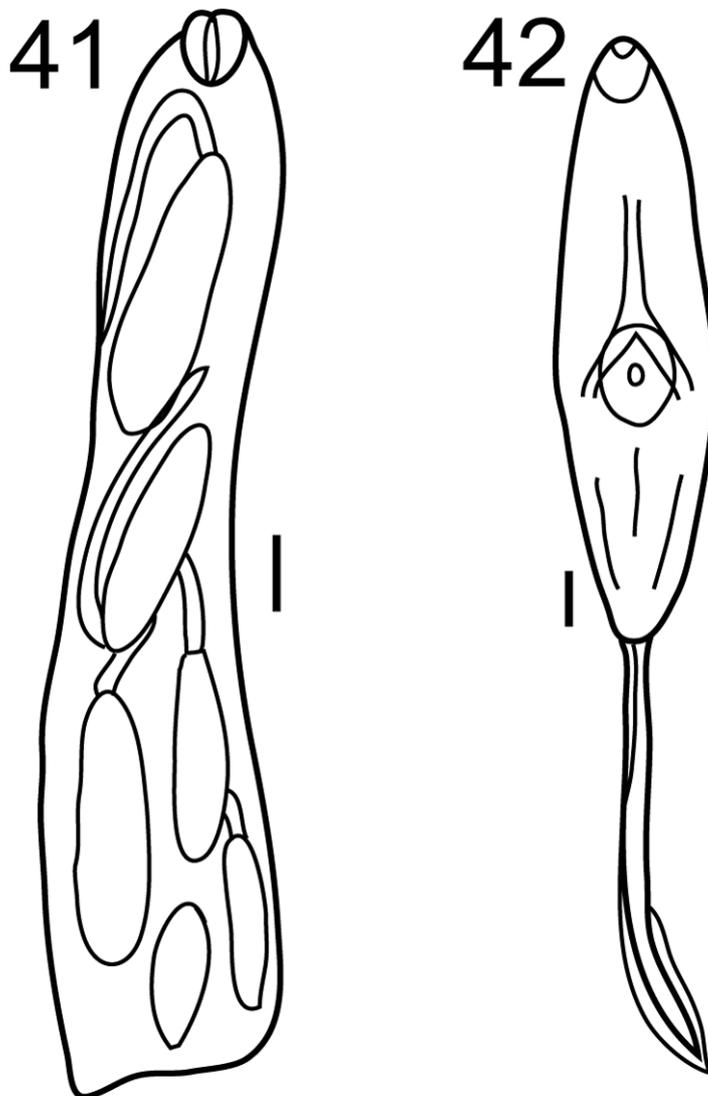
Remarks: I did not encounter this trematode. Taxonomic affinities are difficult to ascertain, so I maintain the “gymnocephalous” appellation. It potentially belongs to the Haploporidae, the cercariae of which often encyst on vegetation (Overstreet & Curran 2005; Schell 1970; Yamaguti 1975). Adults typically parasitize herbivorous fishes (Overstreet & Curran 2005).

For comparison, see Fares and Maillard (1974) and Martin (1973) for descriptions of haploporid cercariae and rediae that infect hydrobiid snails.

Gymnocephalous sp. II (Psilostomidae?)

(20. Gym2; Figs. 1, 41–42)

[Winterbourn’s G2, which I did not encounter]



FIGURES 41–42. *Gymnocephalous* sp. II. **41**, Redia. **42**, Cercaria. Drawings modified from (Winterbourn 1974). All scale bars 100.

Stages: rediae and cercariae

Host: *Potamopyrgus antipodarum*

Site in host: Rediae at least in the gonad and digestive gland

Locality: na

Prevalence: na

Specimens deposited: na

Diagnosis: [derived from Winterbourn 1974] Redia elongate (~6:1 length:width). Length up to 1500. Pharynx prominent. Developing cercariae up to 6.

Cercaria non-oculate with dorso-ventral tail fin, oral and ventral suckers, no stylet, no collar spines. Body length up to just over 1000. Tail length ~3/4 to 1.3 times body length.

Remarks: I did not encounter this trematode. Gymnocephalous sp. II may belong to the Psilostomidae. See particularly *Psilochasmus* species, such as *Psilochasmus aglyptorchis* Loos-Frank, 1968, which infects hydrobiid snails in Europe and whose metacercariae infect snails (Deblock 1980; Loos-Frank 1968). I have occasionally encountered possible psilostomid metacercariae in *Potamopyrgus antipodarum*, which may represent this species. Adult psilostomids infect birds or mammals (Kostadinova 2005), and a couple have been reported from New Zealand ducks (McKenna 2010).

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