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Guide to the trematodes (Platyhelminthes) that infect the California horn snail (*Cerithideopsis californica*: Potamididae: Gastropoda) as first intermediate host

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Abstract

The California horn snail, *Cerithideopsis californica*, lives in estuarine habitats from California (USA) in North America to Piura (Peru) in South America. Throughout this range, the snail serves as first intermediate host for a diverse guild of digenean trematodes. These parasites are used in teaching laboratories, and have been subject to a large amount of taxonomic, biological, evolutionary, and ecological research. Despite the abundance of research on these trematodes, we lack a satisfactory guide to these parasites. This manuscript treats the 19 trematode species that we are currently able to distinguish morphologically. I provide taxonomic affinities, information on second intermediate host use, an identification key focused on cercaria traits, information and a key for regressed infections lacking cercariae, information on early infections, and species accounts. The species accounts present photographs, additional diagnostic information, taxonomic notes, information concerning cryptic species, and connections to relevant literature. The primary aim of this manuscript is to facilitate research on this trematode guild by serving as an identification tool, and by providing background information, including highlighting gaps in our knowledge.

Key words: *Cerithidea californica*, parasites, parasitic castrators, Trematoda, Digenea, biodiversity, estuary, Baja California, indicators

Introduction

What trematode species infect, as first intermediate host, the California horn snail, *Cerithideopsis californica* (Haldeman) (= *Cerithidea californica*, see Reid and Claremont [2014])? How can one go about identifying these parasitic castrators? What types of second intermediate hosts do cercariae of these species infect? Are there taxonomic or life-cycle issues remaining to be resolved? This manuscript addresses these questions, and aims to serve as a species identification tool for the parthenita and cercaria life-stages of these parasites.

The California horn snail lives in estuarine habitats from California (USA) in North America to Piura (Peru) in South America (Keen 1971; Miura *et al*. 2010). Throughout this range, the snail serves as first intermediate host for a diverse guild of digenean trematodes (Torchin *et al*. 2015).

These parasites are used in teaching laboratories (pers. obs.), and have been subject to a large amount of taxonomic, biological, evolutionary, and ecological research (references below). This research has revealed that this trematode guild is taxonomically diverse, and ecologically and evolutionarily important. These parasites influence host individuals and populations (e.g., Hechinger 2010; Lafferty 1993a;b; Sousa 1983; Yoshino 1975), and can play a substantial role in food-web robustness (Lafferty & Kuris 2009) and ecosystem energetics (Kuris *et al.* 2008). These trematodes have also been used as model systems to probe basic questions of community ecology (Hechinger *et al*. 2008; Mordecai *et al*. 2016; Torchin *et al*. 2015), dispersal ecology (Fingerut *et al*. 2003b), evolutionary ecology (Hechinger 2010; Lafferty 1993b), and ecological parasitology (Buck *et al*. 2017; Hechinger & Lafferty 2005; Lafferty *et al*. 1994). Further, the discovery that trematodes can have complex social organization involving a soldier caste was initially documented using a member of this trematode guild (Hechinger *et al*. 2011b); subsequent work has documented soldiers in several of the other guild members (Garcia-Vedrenne *et al*. 2017; Garcia-Vedrenne *et al*. 2016). Finally, these trematodes have also been explored as an ecological indicator tool for assessing estuarine condition and function (e.g., Hechinger *et al*. 2007; Huspeni & Lafferty 2004; Whitney *et al*. 2007).

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Despite the abundance of research on this trematode guild, we currently lack a recently published identification guide to these parasites. Most recent research has relied on an unpublished key created by the author. Other research and teaching has usually relied on Martin's (1972) identification key, which Martin published after having worked on these trematodes for over two decades, but which has some problems.

An updated identification guide would be helpful for several reasons. First, perhaps because he did not encounter them, Martin (1972) did not include two distinct species that we currently recognize as being widespread. Second, several couplets in Martin's key can be troublesome. For instance, some couplets rely on cercaria traits that are difficult to discern, traits that are inconsistently observed, or require knowledge of what the cercariae infect as second intermediate hosts. Third, when dissecting snails, it is often very helpful to use parthenita traits to assist or confirm identifications. However, parthenita details are not consistently included in Martin's key. Fourth, it is possible to construct a dichotomous key to these trematodes that separates species in a greater alignment with taxonomy, particularly to the family level. Finally, a large amount of research has been undertaken on these species, and this literature has not been consolidated anywhere.

Hence, this manuscript provides a guide to the trematodes that infect California horn snails as first intermediate host. I seek to at least partially solve the above problems by providing species accounts and a newly structured identification key that focuses on readily and consistently observable characters, permits identification using only cercaria traits, but is supplemented by information on parthenitae to facilitate identification when dissecting snails. I also provide information on early and seasonally regressed infections (which often produce no cercariae), including a separate key to help identify the latter. The species accounts also include information on relevant research and other issues concerning each listed species, focusing on first intermediate host stages. This guide should be considered provisional, as five of the species still lack thorough descriptions, and because there are issues concerning cryptic species (see accounts). The major goal of this guide is to facilitate a wide range of research and education involving this host-parasite system, in part by serving as an immediately useable identification tool and, in part, by indicating specific areas where morphological, life cycle, and genetic work can improve our understanding of these trematodes.

Methods

I constructed the guide for users having at least a basic background in trematode biology (e.g., at the level found in a basic zoology or parasitology class or text book). The guide focuses on the trematodes' cercariae and daughter parthenitae (rediae or sporocysts). When "parthenita", "sporocyst", or "redia" is used by itself, it refers to daughter parthenitae; when I refer to the "mother sporocyst" it will be spelled out. Following the rationale of Hechinger *et al*. (2011b), I refer to the group of conspecific parthenitae comprising an infection as a colony.

I created two new dichotomous keys. The first key focuses on cercaria characteristics, but also includes some information on parthenitae. I focused on traits I have found to be consistently and readily observable in both shed cercariae and cercariae obtained from dissected snails. If dissecting, then the parthenitae should always be examined (in addition to cercariae) to confirm specific identity, a lack of contamination, and to detect multi-species infections. Identification with the key should be confirmed by examining the species accounts, particularly the diagnoses, which have more traits than has the key. Although not fully taxonomically based, this key does recover trematode species grouped by at least family and genus.

A section on seasonal regression summarizes our knowledge about such infections, which are difficult to identify given the frequent lack of cercariae. I also created an identification key for seasonally regressed infections that is based solely on parthenita traits.

I also summarize our impartial knowledge concerning the state of early infections for these species to facilitate identification of such infections.

Each species account includes a brief diagnosis, information on general cercaria swimming behavior (the consistency of which are not as well-validated as the morphological traits), a comparison to the most similar species in the California horn snail guild, a remarks section, and photographs.

TABLE 1. Taxonomic and biological information for the trematode species that infect *Cerithideopsis californica* (Gastropoda: Potamididae) as first intermediate host.[a]

Superfamily	Family	Species	Species code	Parthenita type	Host-tissue use[c]	Primary second intermediate hosts used
Diplostomoidea	Cyathocotylidae	*Mesostephanus appendiculatus*	Meap	sporocysts	m	fishes
		Small cyathocotylid[d]	Smcy	sporocysts	g+dg+bvm	fishes
Schistosomatoidea	Schistosomatidae	*Austrobilharzia* sp.[d]	Ausp	sporocysts	g+dg+bvm	-
Pronocephaloidea	Notocotylidae	*Catatropis johnstoni*	Cajo	rediae	m	molluscs[e]
Echinostomatoidea	Himasthlidae	*Acanthoparyphium spinulosum*[b]	Acsp	rediae	g	molluscs
		Himasthla rhigedana	Hirh	rediae	g	decapods[e], molluscs[e]
		Himasthla sp. B[d]	Hisb	rediae	g+bvm	gastropods
	Philophthalmidae	*Cloacitrema michiganensis*	Clmi	rediae	g+bvm	decapods[e], molluscs[e]
		Parorchis sp.[b, d]	Pasp	rediae	g+bvm	decapods[e], molluscs[e]
Opisthorchioidea	Heterophyidae	*Acanthotrema hancocki*	Acha	rediae	g	fishes
		Euhaplorchis californiensis	Euca	rediae	g	CA killifish
		Phocitremoides ovale	Phov	rediae	g	fishes
		Pygidiopsoides spindalis	Pysp	rediae	g	fishes
Microphalloidea	Renicolidae	*Renicola buchanani*	Rebu	sporocysts	m	fishes
		Renicola cerithidicola	Rece	sporocysts	m	fishes
		Renicola sp. "martini"	Rema	sporocysts	g+dg	molluscs
		Renicola sp. "polychaetophila"	Repo	sporocysts	g+dg	polychaetes
	Microphallidae	*Probolocoryphe uca*	Pruc	sporocysts	g+dg+bvm	crabs
		Small microphallid[d]	Smmi	sporocysts	g	amphipods

[a] The table includes species as we currently morphologically recognize them. Cryptic species undoubtedly occur (see species accounts).

[b] For these two species, there is available preliminary morphological evidence that may permit distinguishing cryptic species (see species accounts).

[c] g = gonad, dg = digestive gland, bvm = basal visceral mass, m = mantle; Information mostly from (Hechinger *et al*. 2009; Sousa 1993; Yoshino 1975).

[d] Species is not yet carefully described.

[e] "Ectometacercariae", which encyst on the outside of the host (e.g., on the shell or exoskeleton).

The diagnoses in the species accounts are not thorough descriptions, but include a suite of characters to facilitate identification and distinguish a particular species from others in this trematode guild, given current understanding. Further, the diagnoses include traits that are observable during dissections of live and unstained material, and, to the extent possible, focus on traits that are easily observable. These traits include overall colony, single parthenita, and cercaria morphological characteristics. Parthenita colony information in the species accounts is based on the seasonally "ripe" condition (spring through fall). Further, parthenita diagnostic information focuses on reproductive parthenitae, not immatures or soldiers. Point estimates for cercaria size provide rough expectations for sizes that can vary given degree of contraction/extension, degree of coverslip pressure, and intraspecifically. A crude size-range is provided for parthenitae, which vary more conspicuously in size within infections than do cercariae. I also focus on cercaria traits that are observable whether the cercariae were dissected or shed from a host.

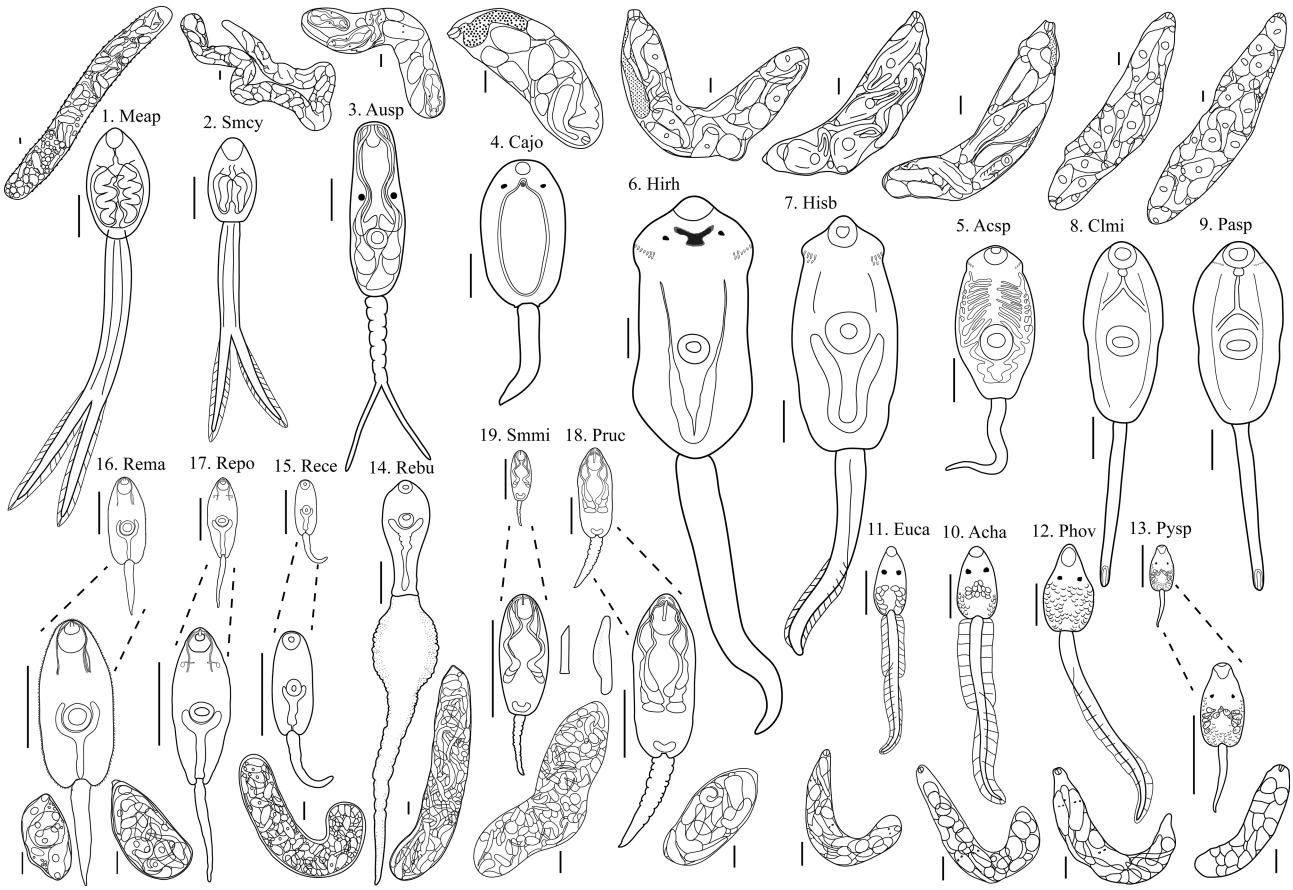
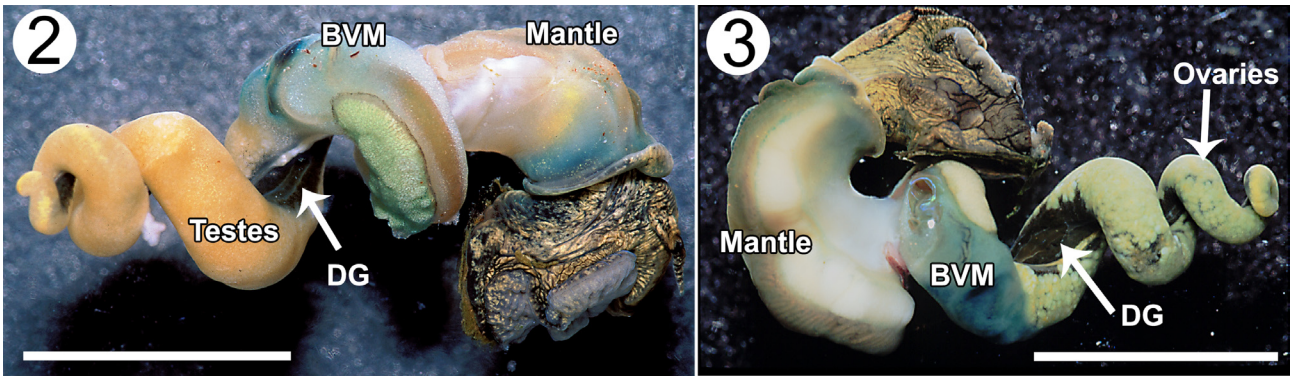


FIGURE 1. General characteristics of the parthenitae and cercariae of the trematodes infecting *Cerithideopsis californica* as first intermediate host. Species numbers and codes follow Table 1 and species accounts. Cercariae are all to scale, with additional magnified views of six small species (indicated by dashed lines). Note the oral stylets (presented in right lateral view) for Pruc and Smmi. Parthenitae are not to scale. Scale bars consistently indicate 100 μm.



FIGURES 2–3. Uninfected and freshly deshelled California horn snails, *Cerithideopsis californica*. **2**, Male. Note the ripe, orange testes. **3**, Female. Note the ripe, green ovaries. BVM = basal visceral mass. DG = digestive gland. Scale bars = 1 cm.

The remarks section first includes taxonomic notes, connections between the listed species and those detailed in the earliest surveys of the California horn snail trematodes (Hunter 1942; Martin 1955; Maxon & Pequegnat 1949), and information concerning the occurrence of cryptic species. Following the taxonomic remarks, I include information from relevant literature or unpublished observations, focusing on the first intermediate host infections or cercariae.

My colleagues and I took all the photographs; I give photo credit when I did not take the photograph. I enhanced all photos using Adobe Photoshop, with guidance from the "Zootaxa Digital Imaging Guide, Ver. 1.2" (D. Geiger, http://www.mapress.com/zootaxa/imaging/ index.html).

Although this guide focuses on parthenitae and cercariae, I do provide information on the general types of second intermediate hosts used by each species (the most up to date list of known second intermediate host species can be obtained from published food webs of three Baja California/California estuaries [Hechinger *et al*. 2011a]).

Results and discussion

Table 1 provides a taxonomic listing of the 19 species that we currently recognize based on morphology. Species are numbered in general phylogenetic order (following Bray *et al.* (2008); Gibson *et al*. (2002); Jones *et al*. (2005); Tkach *et al*. [2016]). I assign four-letter codes to each species, usually based on the first two letters of the genus and the specific epithet. These codes are used in Fig. 1 and in the text. [Note that these codes are different than the codes my colleagues and I have used in previous work (starting with Kuris (1990), which were usually based on the first three or four letters of the genus, and have now become unsatisfactory with newly recognized species and name changes.] The table also includes information on the species' type of parthenita, host tissue-site use, and the types of second intermediate hosts used, which is largely based on my familiarity with the system (see Hechinger *et al.* (2011) for specific hosts used).

Fig. 1 provides a schematic drawing of parthenitae and cercariae for the species in the trematode guild. The drawing emphasizes readily observable, key traits.

The species accounts are preceded by the dichotomous key that focuses on cercariae, the section and key for seasonally regressed infections, the summary of early infections, and Figs. 2 and 3 (which show the appearance of deshelled, uninfected male and female snails with labelling of important body regions).

Although most of our experience with these trematodes has been in California and Baja California, the key applies much more broadly. My colleagues and I have used the key on samples originating from numerous populations along the Pacific coast from Central California south to Panama (e.g., see Torchin *et al*. 2015). Further, we have also applied the key to trematodes from the Atlantic horn snail, *Cerithideopsis pliculosa* (= *Cerithidea pliculosa*), which is a sister species of *C. californica* (Miura *et al*. 2010), with the realization that at least some of those trematode species are not the same, but are closely related, similar species (e.g., see Torchin *et al*. 2015). Analyses of DNA sequence data has been undertaken (e.g., Miura, Torchin, & Hechinger, unpublished data), which will clarify many issues concerning species identities.

Dichotomous key to the trematodes infecting *Cerithideopsis californica* as first intermediate host (focused on cercariae)

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

1 Cercaria with forked tail . . . . . (diplostomatans: Smcy, Meap, Aust) 2

- Cercaria with unforked tail (e.g., simple, finned, or bulbous) 4

2 Cercaria with eyespots and well-developed ventral sucker; sporocysts occur throughout the snail visceral mass, whitish, elongate . . . . . [3] *Austrobilharzia* sp.

- Cercaria lacks eyes and lacks a well-developed ventral sucker . . . . . .(cyathocotylids) 3

3 Cercaria gut branches at 1/4–1/3 body length, caeca with 3–4 pronounced, sinuous undulations; cercaria body >150 µm, usually over 200 µm (larger than 3b, Smcy); sporocysts localized in snail mantle, very elongate, very active, with transverse mobile annulations . . . . . [1] *Mesostephanus appendiculatus*

- Cercaria gut branches just anterior to mid-body, caeca with weak undulations; cercaria body < 150 µm long (smaller than 3a,

Meap); sporocysts occur throughout snail visceral mass, inactive, extremely elongate . . . . . [2] Small cyathocotylid

4 Cercaria lacks ventral sucker . . . . . (microphallids, heterophyids, Cajo) 5

- Cercaria with ventral sucker . . . . . (renicolids, philophthalmids, himasthlids) 11

5 Cercaria lacks eyespots and has oral stylet. . . . . (microphallids) 6

- Cercaria with eyespots and lacks oral stylet. . . . . (heterophyids, Cajo) 7

6 Cercaria body ~175 µm long (larger than 6b, Smmi); oral stylet 25–30 µm long (longer than 6b), with dorsal flange . . . . . [18] *Probolocoryphe uca*

– Cercaria body ~120 µm long (shorter than 6a, Pruc); oral stylet 12–14 µm long (shorter than 6a), lacks dorsal flange…[19] Small microphallid

7 Cercaria body >300 µm long (larger than 7b, heterophyids), opaque tan/orange to white; main excretory ducts usually very evident and filled with concretions, connected anteriorly; tail lacking fins; often encysts as highly convex metacercaria on hard substrates in dish; rediae localized to mantle . . . . . [4] *Catatropis johnstoni*

- Cercaria body <250 µm long (smaller than 7a, Cajo), generally translucent colorless to white; main excretory ducts remain separate anteriorly; tail with or without fins; rediae localized to gonadal space . . . . . (heterophyids) 8

8 Cercaria tail lacks fins, body usually ~100 µm long (smaller than 8b), tail length ~equal to body length . . . . . [13] *Pygidiopsoides spindalis*

- Cercaria tail with fins (dorsal-ventral only, or also with lateral fins), body usually >150 µm long (larger than 8a. Pysp), tail length at least 2x body length. . . . . (Phov, Acha, Euca) 9

9 Cercaria tail with only a dorso-ventral fin (originating at least 1/5 down the tail length); cystogenous glands prominent in posterior ¾ of cercaria body (whitish in reflected light) . . . . . [12] *Phocitremoides ovale*

- Cercaria tail with lateral fins (originating at tail base) and a dorso-ventral fin (originating distally); cyst glands not very prominent (therefore posterior ¾ of cercaria body does not appear whitish in reflected light as does 9a, Phov). . . . . (Acha, Euca) 10

10 Cercaria penetration glands form compact cluster anterior to genital primordium (which is clear in unstained specimens) and excretory bladder . . . . . [10] *Acanthotrema hancocki*

- Cercaria penetration glands distributed from anterior of genital primordium, laterally around excretory bladder, to posterior of cercaria body . . . . . [11] *Euhaplorchis californiensis*

11 Cercaria with Y-shaped excretory bladder with arms embracing ventral sucker . . . . . (renicolids) 12

- Cercaria lacking Y-shaped excretory bladder. . . . . (philophthalmids, himasthlids) 15

12 Cercaria with stylet in oral sucker anterior; sporocysts localized to visceral mass . . . . . (Rema, Repo) 13

- Cercaria lacking stylet; sporocysts localized to mantle region . . . . . (Rebu, Rece) 14

13 Cercaria body with tegumental spines (readily apparent at 100x, often at 40x, at compound microscope), penetration gland ducts all open next to oral stylet. . . . . [16] *Renicola* sp. "martini"

- Cercaria body lacking tegumental spines, penetration gland ducts open in a 2[(1+3+1)+1] pattern. . . . . [17] *Renicola* sp. "polychaetophila"

14 Cercaria with a bulbous tail; cercaria body ≥ 190 µm (larger than 14b, Rece); sometimes swimming cercariae aggregate together to form a cluster. . . . . [14] *Renicola buchanani*

- Cercaria with a simple tail; cercaria body ≤ 140 µm (smaller than 14a, Rebu); swimming cercariae never form a cluster . . . . . [15] *Renicola cerithidicola*

15 Cercaria tail with distinct parenchymous cells and invaginated tip . . . . . (philophthalmids) 16

- Cercaria tail with simple tip (not invaginated). . . . . (echinostomatids) 17

16 Cercaria esophagus long, > 3x pharynx length, extending more than ½ to ventral sucker before branches into ceca; with tegumental body spines (most easily observed in unflattened specimens); like 16b Clmi, can encyst as hemi-ovoid metacercaria on hard substrates (including dish and pipettes) . . . . . .[9] *Parorchis* sp.

- Cercaria esophagus exceedingly short to non-existent, ≤ pharynx length, branches into ceca almost immediately after pharynx; no tegumental body spines; like 16a Pasp, can encyst as hemi-ovoid metacercaria on hard substrates (including dish and pipettes) . . . . . [8] *Cloacitrema michiganensis*

17 Cercaria with two eyespots and ocular medial pigmented region; often encysts as flattened hemispherical metacercaria on hard substrates (including dish and pipettes) . . . . . [6] *Himasthla rhigedana*

- Cercaria lacking eyes . . . . . .Acsp, Hisb 18

18 Cercaria tail with dorso-ventral fin; lacking pronounced pinnately branched excretory system, but usually with dilated concretion-filled arms of excretory bladder . . . . . [7] *Himasthla* sp. B

- Cercaria lacking tail fin; pronounced pinnately branched excretory system, lacking dilated concretion-filled arms of excretory bladder . . . . . [5] *Acanthoparyphium spinulosum*

Seasonal regression

At least in the northern part of their range (California and Baja California), most colonies undergo a winter regression, likely associated with diminished resources and lower temperatures (Hechinger *et al*. 2009; unpublished observations). Cercaria production decreases and sometimes ceases (Fingerut *et al*. 2003b; Lafferty *et al*. unpublished data), making identification more difficult. The parthenitae typically become empty, flaccid, and thinner. The entire colony shrinks in size (Hechinger *et al*. 2009), but is still dispersed throughout the typical colony locus (Table 1).

This distribution usually clearly distinguishes seasonally regressed infections from early infections, which are characterized by parthenitae being concentrated in only part of the final colony locus.

Although more difficult, it still is often possible to identify many regressed infections to one taxonomic level or another. There are often a few cercariae developed enough to permit making a species-level identification. However, even when lacking developed cercariae, one can always place the infection into a restricted subset of the species, if not still identify the species. This is possible by examining basic characteristics of the parthenitae and their distribution in the snail body. The below dichotomous key helps identify seasonally regressed infections. It takes identifications to the level that I consider currently possible for most workers. It could be enhanced by careful work examining parthenita morphology (including soldiers) during the regressed season (with proper consideration of intraspecific variation and cryptic species issues).

Dichotomous key to the trematodes infecting *Cerithideopsis californica* as first intermediate host (seasonally regressed infections, using parthenita characteristics)

1	Colony locus in the mantle	(Cajo, Meap, Rebu, Rece) 2
-	Colony locus in the visceral mass	4
2	Parthenitae are rediae	[4] Cajo
-	Parthenitae are sporocysts	(Meap, Rebu, Rece) 3
3	Sporocysts active, with transverse muscle bands, very elongate	[1] Meap
-	Sporocysts inactive, lacking transverse bands, usual thick-walled	[14] Rebu or [15] Rece
4	Parthenitae are sporocysts	(Smcy, Rema, Repo, Pruc, Smmi) 5
-	Parthenitae are rediae	(heterophyids or echinostomoids) 7
5	Sporocysts extremely elongate, threaded throughout digestive gland tissue, translucent whitish	[2] Smcy
-	Sporocysts are relatively much shorter	(Rema, Repo, Pruc, Smmi) 6
6	Sporocysts relatively thick-walled	[16] Rema or [17] Repo
-	Sporocysts relatively thin-walled	[18] Pruc or [19] Smmi
7	Rediae lacking collars and appendages, elongate (up to 10:1 length:width), and relatively small (≤1000 μm)	heterophyid (Acha, Euca, Phov, Pygi)
-	Rediae with collars and appendages, ovoid to mildly elongate (up to 6:1 length:width), often relatively large (>1000 μm; if smaller, then still relatively wider than the heterophyids)	echinostomatoids 8
8	Rediae with orange-pigmented body wall	[5] Acsp or [7] Hisb
-	Rediae lacking orange-pigmented body wall	echinostomatoid (Acsp, Hirh, Hisb, Clmi, Pasp)

Early infections

By observing thousands of natural infections in various stages of development, we have obtained information concerning the state of early infections (usually before cercaria production) of most of these species. Such information can be useful concerning identification for a few reasons. First, one can usually identify an early infection, if not to species, to at least a restricted subset of possible species. Second, the early stages of infection, occurring outside of the main colony locus, can often be helpful in detecting second or third species in multi–species infections. Therefore, I briefly summarize our impartial knowledge concerning early infections.

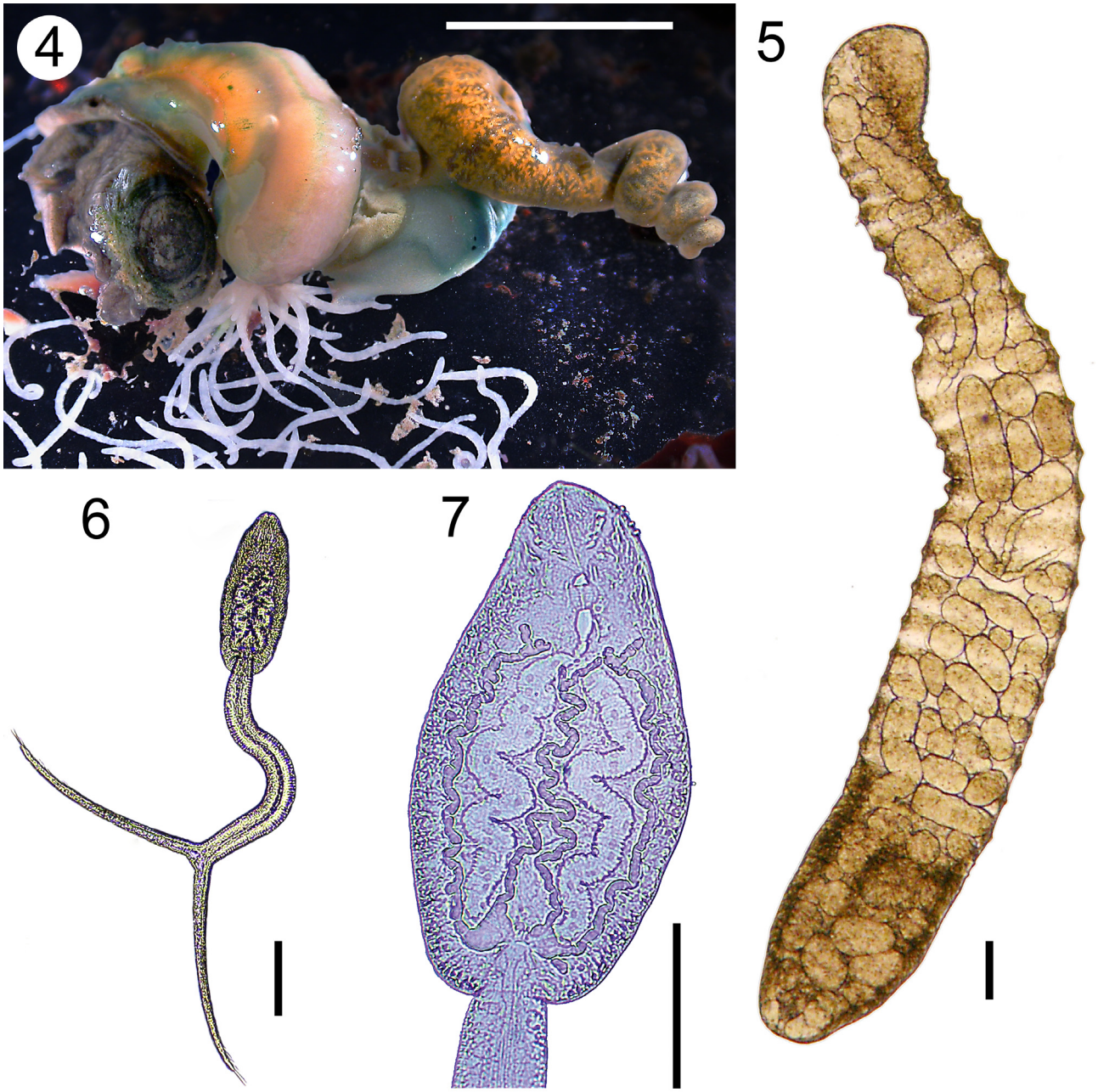
The heterophyids, renicolids, and microphallids typically initiate infections in the basal visceral mass next to the stomach or intestine, as generally expected for species that infect the snail with ingested eggs (Galaktionov & Dobrovolskij 2003). For the four heterophyids (Acha, Euca, Phov, and Pysp), the mother sporocyst is often detectable, forming a large (~2–3 mm), globoid, sometimes branching mass filled with small daughter rediae (first pointed out to me by Todd Huspeni). This mother sporocyst often persists, diminishing in size and reproductive activity, until *after* the colony has filled up the area of its primary locus.

Concerning the renicolids and microphallids, although we have not detected a clear mother sporocyst, daughter sporocysts also initially appear in the basal visceral mass. One can usually distinguish the renicolids from the microphallids by sporocyst wall thickness: thick in renicolids and thin in microphallids (see photos in species accounts). At this stage, the renicolids that use the mantle as the colony locus (Rebu and Rece) can sometimes be distinguished from renicolids using the distal visceral mass (Rema and Repo) by their more elongate sporocysts (in addition to the colony appearing to be moving toward the mantle instead of the gonad-digestive gland region).

Pre-cercaria daughter sporocysts of the schistosomatid and cyathocotylids can often be distinguished, even if

they are still constrained to the basal visceral mass. Those of Meap already are very elongate, active, and with transverse bands. Similarly, Smcy is inactive and very to extremely elongate, while Aust sporocysts are also inactive, but less elongate, with their characteristic "sausage-shape" and opaque whiteness.

Pre-cercaria daughter rediae of the himasthlids and philophthalmids are also often first detected in the basal visceral mass, sometimes associated with the snail pericardium. Their characteristic appendages, collars, and large size easily distinguish them from the much smaller daughter rediae of heterophyids. If the rediae have orange-colored body walls, they are likely Acsp or Hisb. Hisb also appears to sometimes have a mother redia located in the snail's heart lumen (pers. observations; first recognized by Todd Huspeni). If the rediae are not orange colored, but translucent white or colorless, they are likely Hirh, Clmi, or Pasp (but note that both Acsp and Hisb sometimes seem to also be translucent white or colorless).



FIGURES 4–7. *Mesostephanus appendiculatus* (Meap). **4**, Overview of a colony in a freshly deshelled, infected horn snail in sea water, showing the way the active sporocysts "spill out" of their infection site in the mantle upon host dissection. Note the host snail's non-functional, orange ovaries. Scale bar = 1 cm. **5**, Sporocyst, live, with developing cercariae, under slight coverslip pressure. Scale bar = 100 µm. **6**, Cercaria, live. Scale bar = 100 µm. **7**, Cercaria body, live, under coverslip pressure to better reveal key traits. Scale bar = 100 µm.

Species accounts

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

Mesostephanus appendiculatus (Ciurea)

(1. Meap; Figs. 1, 4–7)

Diagnosis: *Parthenitae*. Colony comprised of very active sporocysts, densely concentrated in snail mantle (in enlarged perirectal sinus). Sporocysts translucent white; usually over 1200 μm long, very elongate (length:width up to ~15:1), of relatively consistent width but with tapering anterior and bluntly rounded posterior; body wall with muscular, transverse, crest-shaped annulations, developing cercariae visible through translucent sporocyst wall.

Cercaria. Body translucent colorless; non-oculate; with oral sucker modified as "anterior organ" and no ventral sucker; with typical cyathocotylid excretory system, wherein main collecting ducts have lateral and medial branches all connecting anteriorly, the anterior blind ducts diverge (point antero-laterally); gut branches at 1/4–1/3 body length, caeca each with 3–4 pronounced, sinuous undulations; body ~220 μm long, ~1/2 the length of tail stem; tail forked, with dorso-ventral fins on furcae.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim intermittently with short bursts followed by longer periods of resting and slow sinking; frequently swim in response to vibration.

Similar species: Meap cercariae are readily distinguished from Smcy [2] by their larger size, more anterior position of gut branching, pronounced caeca undulations, and (usually) diverging anterior blind excretory ducts. If the host snail has been dissected, the sporocyst distribution, activity, and annulations provide the easiest way to distinguish Meap from Smcy.

Remarks: Martin (1961) documented the life cycle. He described the sporocysts and cercariae from naturally infected *C. californica* (although he reported the sporocysts as residing in the visceral mass, which is not consistent with our repeated observations (n > 1000) that they use the perirectal sinus in the mantle). Martin also experimentally infected second intermediate host fishes with metacercariae, using those to infect chicks to get adults. He described the adult and identified it as *Mesostephanus appendiculatus*. Because *M. appendiculatus* was originally identified from Romania, it seems likely that it represents a globally distributed species complex.

This species likely corresponds to "*Cercaria cerithidia* 22" of Hunter (1942), the "Furcocercous Cercaria" of Maxon and Pequegnat (1949), and the "large strigeid" of Martin (1955).

Small cyathocotylid

(2. Smcy; Figs. 1, 8–11)

Diagnosis: *Parthenitae*. Colony comprised of inactive sporocysts, sparsely distributed throughout snail gonad, digestive gland, and basal visceral mass regions. Sporocysts translucent white to colorless; up to over 3000 μm long, extremely elongate (length:width > 20:1), of relatively consistent width but with tapered anterior and bluntly rounded posterior; difficult to separate intact from snail tissues.

Cercaria. Body translucent colorless; non-oculate; with oral sucker modified as "anterior organ" and no ventral sucker; with typical cyathocotylid excretory system, wherein main collecting ducts have lateral and medial branches all connecting anteriorly, the anterior blind ducts converge (point antero-medially); gut branches just anterior of mid-body, caeca with only slight undulations; body ~110 μm long, ~1/2 the length of tail stem; tail forked, with dorso-ventral fins on furcae.

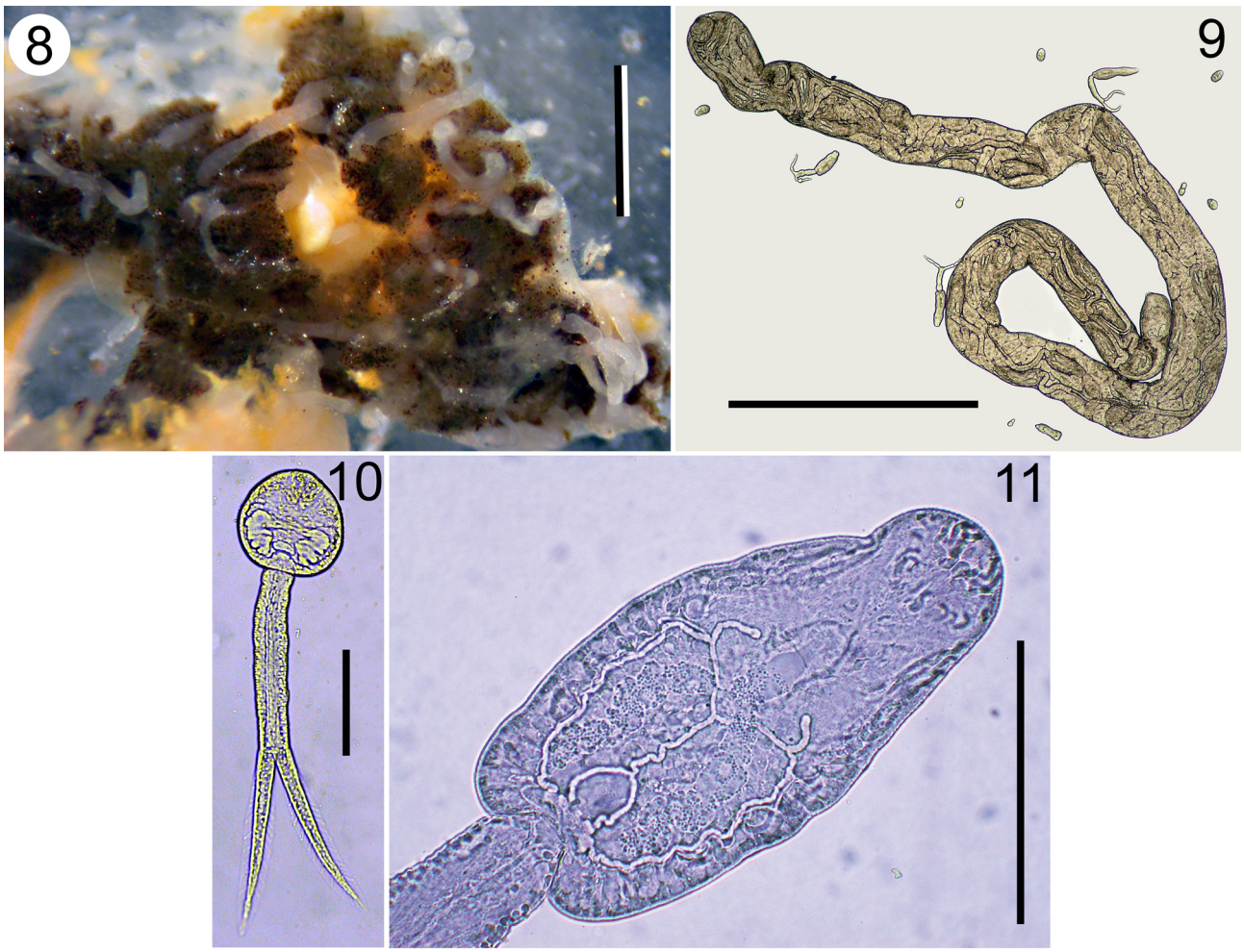
Cercaria behavior: Fresh, emerged cercariae remain in water column, swim intermittently with short bursts followed by longer periods of resting and slow sinking; frequently swim in response to vibration.

Similar species: Smcy cercariae are readily distinguished from Meap [1] by their smaller size, more posterior position of gut branching, lack of pronounced caeca undulations, and converging anterior blind excretory ducts. If the host snail has been dissected, the sporocyst distribution, inactivity, and lack of annulations provide the easiest way to distinguish Smcy from Meap.

Remarks: The sporocysts and cercariae have not been formally described or connected with any described adult trematode.

This species corresponds to the "Strigeid cercaria" in Martin (1972) and the "small strigeid" of Martin (1955). Mature, ripe colonies comprise ~17% the soft-tissue weight of an infected snail (summer-time estimate derived from [Hechinger *et al*. 2009]).

Smcy infection causes (stolen) snail bodies to grow over 2x faster than uninfected snails (Hechinger 2010).



FIGURES 8–11. Small cyathocotylid (Smcy). **8**, Sporocysts, live, in the teased apart digestive gland and residual gonadal tissues of a freshly dissected horn snail, indicating the relative diffuse packing of this species' extremely elongate sporocysts. Scale bar = 2 mm. **9**, Sporocyst, live, with developing cercariae, under slight coverslip pressure. Scale bar = 1 mm. **10**, Cercaria, live, under slight coverslip pressure. Scale bar = 100 µm. **11**, Cercaria body, live, under heavy coverslip pressure to better reveal key traits. Scale bar = 100 µm.

Austrobilharzia sp.

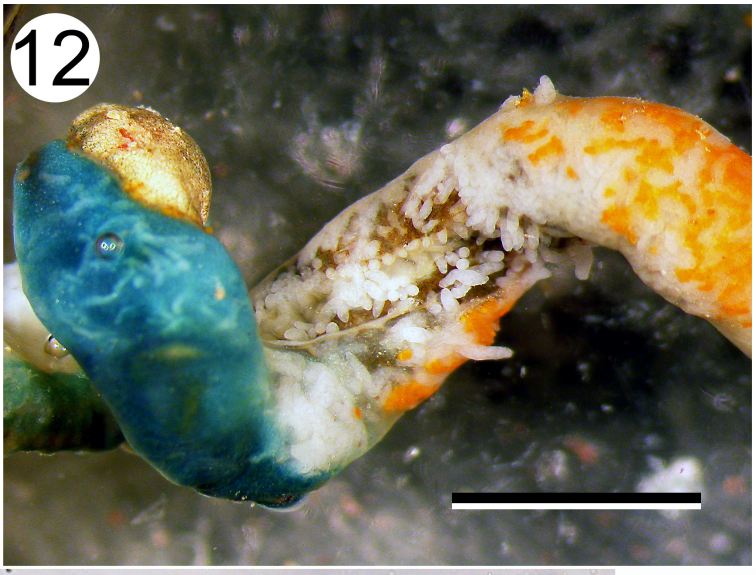
(3. Aust; Figs. 1, 12–14)

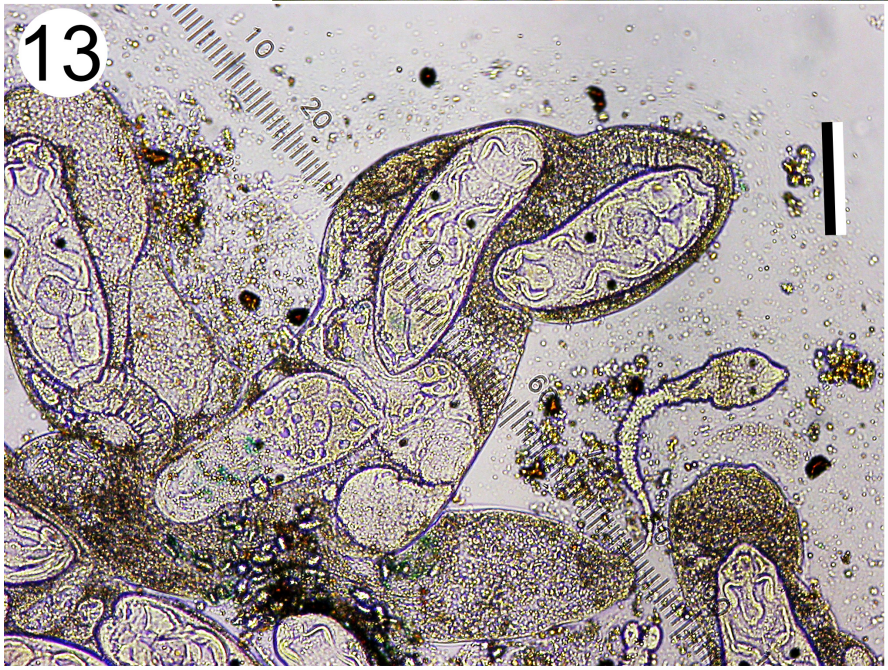
Diagnosis: *Parthenitae.* Colony comprised of inactive sporocysts, often loosely distributed in snail gonad, digestive gland, and basal visceral mass regions (often in mixed-species infections). Sporocysts nearly opaque white; up to over 1000 µm long, elongate (length:width ~5:1), sausage-shaped.

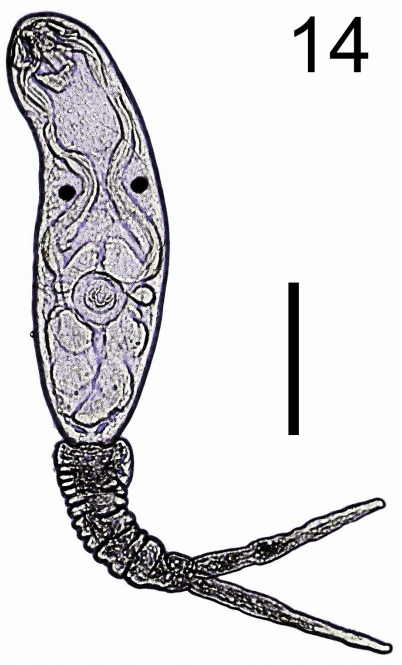
Cercaria. Body translucent colorless; oculate; with oral sucker (modified as "anterior organ") and ventral sucker; body ~194 µm long, ~equal in length to tail; tail forked, with no fins.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim in relatively long bursts by undulating tail (forming a distinctive, elongate, figure 8).

Similar species: The cyathocotylids (Meap [1] and Smcy [2]) are the only other fork-tailed cercariae. Aust is most readily distinguished from them by having pigmented eyespots. Aust's inactive sporocysts are readily distinguished from those of Smcy by their much shorter body lengths.







FIGURES 12–14. *Austrobilharzia* sp. (Aust). **12**, Close-up of an infection (white sporocysts) that has presumably invaded an already established *Acanthoparyphium spinulosum* (Acsp) colony (orange rediae) in a freshly deshelled, horn snail in sea water. The Aust sporocysts have infiltrated the snail gonadal, digestive gland, and green basal visceral mass regions. Scale bar = 0.5 cm. Base photo credit: Todd Huspeni. **13**, Sporocyst, live, with developing cercariae, squashed with heavy coverslip pressure. Note the much smaller heterophyid cercaria that was in this mixed-infection. Ocular micrometer unit = 10 µm. Scale bar = 100 µm. **14**, Cercaria, live, under slight coverslip pressure. Scale bar = 100 µm.

Remarks: The sporocysts and cercariae have not been formally described. We have initiated work to determine how this species is related to other *Austrobilharzia* species (Brant & Hechinger, unpublished).

This species corresponds to the "schistosome cercaria" of Martin (1955).

This species is frequently observed in mixed-species infections, where it appears to be invading and killing the other species (this is why we have moved it to the top of the interspecific dominancy hierarchy that characterizes the species in this guild [Hechinger 2010; Huspeni 2000]). These observations are consistent with what Walker (1979) documented for *A. terrigalensis* (Johnston) in *Velacumantus australis* (Quoy & Gaimard). Research is warranted to understand how Aust interacts with heterospecifics.

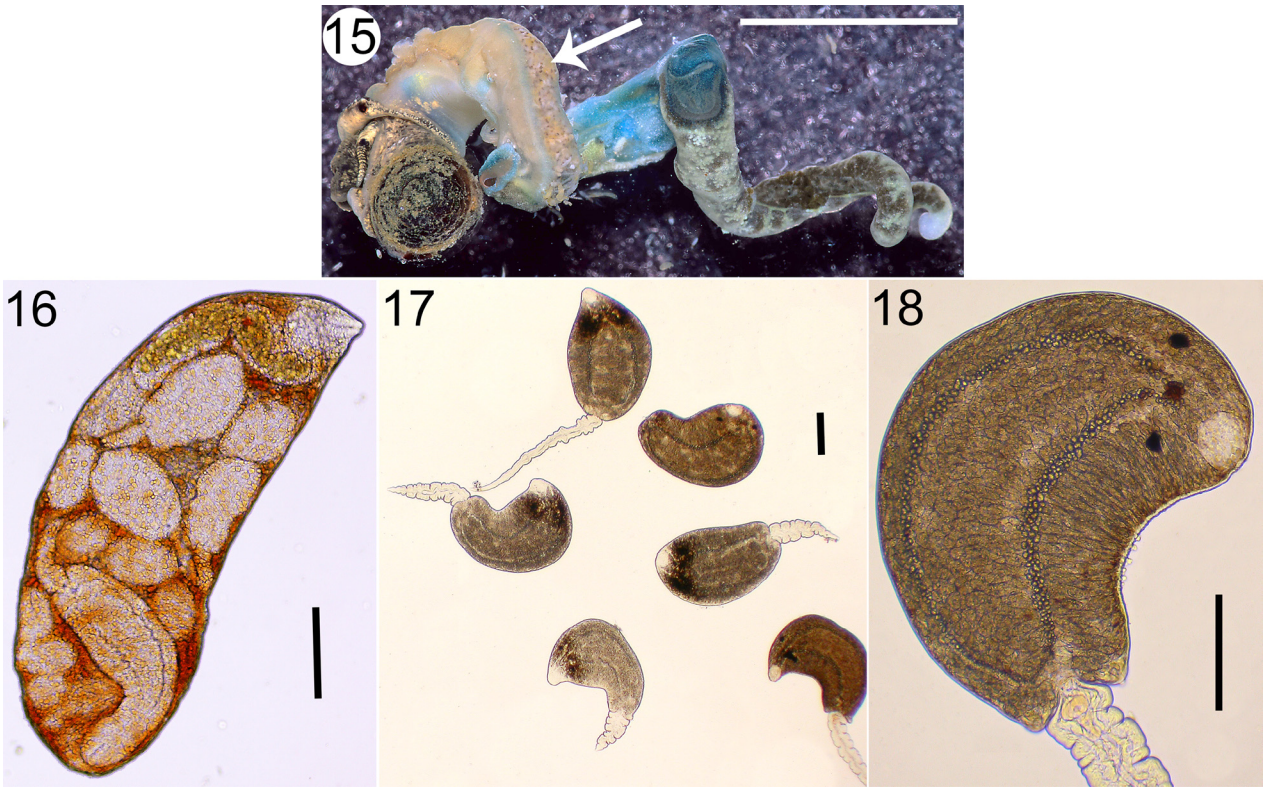
Nadakal (1960a) presents information on the cercaria eye-spot pigments of this species.

Like all schistosomatids, Aust lacks a second intermediate host and directly infects its final host (birds).

***Catatropis johnstoni* Martin**
(4. Cajo; Figs. 1, 15–18)

Diagnosis: *Parthenitae.* Colony comprised of barely active rediae, densely concentrated in snail mantle (in enlarged perirectal sinus). Rediae translucent orange, yellow, or colorless; ~500–900 µm long, pyriform, ovoid to elongate (length:width up to ~8:1), often narrows anteriorly.

Cercaria. Body opaque tan when developed, opaque white with anterior diffuse black transverse band (eye pigment) when younger; oculate, often with a weak median pigment spot; with oral sucker and no ventral sucker; with one pair postero-lateral "adhesive glands", but these not consistently obvious; with main excretory ducts connecting near eyes to form a ring ("cyclocoel"); body ~350 µm long, ~equal in length to tail; tail simple.



FIGURES 15–18. *Catatropis johnstoni* (Cajo). **15**, Overview of a colony in a freshly deshelled, infected female horn snail in sea water. The arrow indicates the colony, which is localized in the mantle. Scale bar = 1 cm. **16**, Redia, live, with developing cercariae, under coverslip pressure. Scale bar = 100 µm. **17**, Cercariae, live, showing ontogenetic variation of cercariae present after they have left rediae. Scale bar = 100 µm. **18**, Close-up of cercaria body, live, under slight coverslip pressure to better reveal key traits. Scale bar = 100 µm.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim intermittently with periods of resting; readily encyst on snail shell and operculum, dissection dish, or inside pipettes during transfer.

Similar species: Cajo could possibly be confused with the himasthlid Hirh [6], but it is readily distinguished by lacking a ventral sucker, lacking a spined collar, having a cyclocoel excretory system, and having the redia colony locus in the mantle.

Remarks: Martin (1956) documented the life cycle. He described the sporocysts, cercariae, metacercariae, and adults obtained by experimentally infecting young domestic chickens.

Mature, ripe colonies comprise ~22% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Cajo does not have a physical caste of soldier rediae (Garcia *et al*., submitted).

Cercariae do a substantial amount of development after they leave the rediae, but before they leave the snail (Martin 1956).

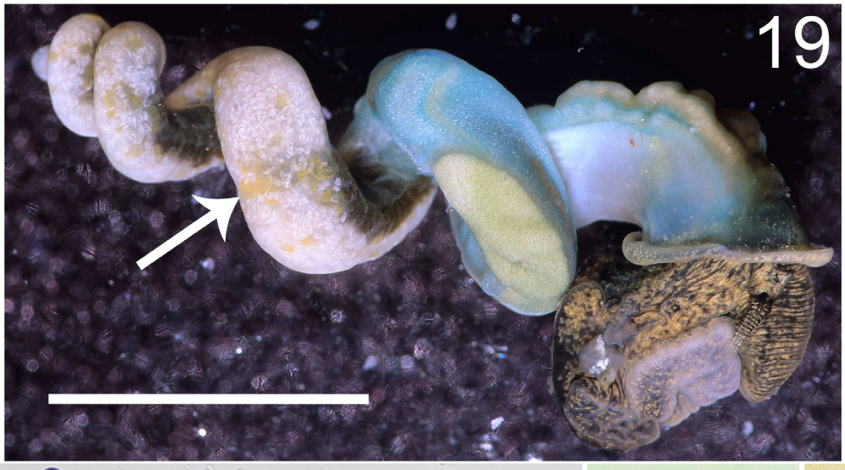
Cajo appears to make infected snails much more likely to die under stressful conditions, as we have qualitatively noted for years, and as indicated by a re-analysis of Sousa and Gleason's (1989) data (Hechinger *et al*. 2009).

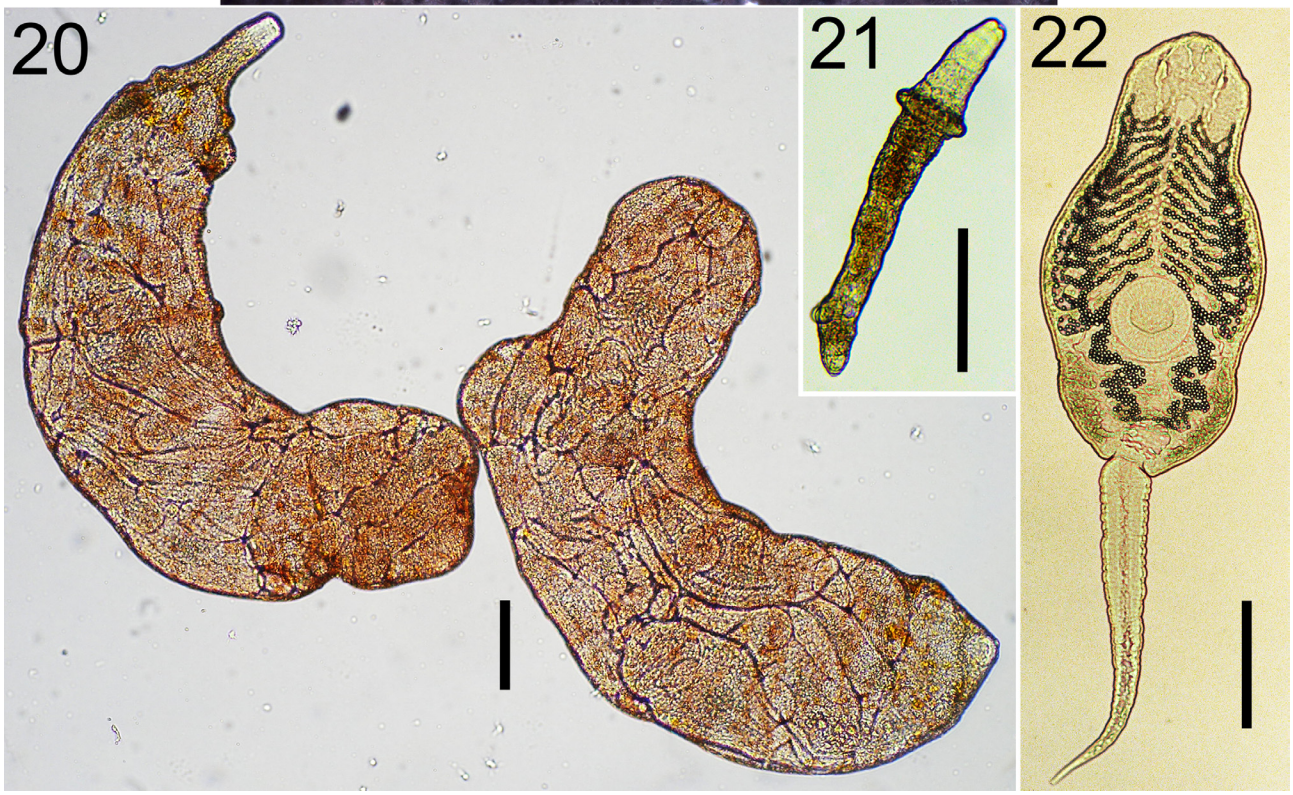
***Acanthoparyphium spinulosum* Johnston**
(5. Acsp; Figs. 1, 19–22)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad region. Rediae translucent orange, yellow, or colorless; redial gut often yellow; ~400–900 µm long, ovoid to oblong (length:width typically < 3.5:1), with collar and posterior appendages that are often not pronounced.

Cercaria. Body translucent colorless, often with opaque and refringent white granules in distinctive, pinnately branched excretory system; non-oculate; with oral and ventral sucker; with two lateral pinnately branched excretory ducts; body ~320 µm long, ~equal in length to tail; tail simple.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously, lashing tail back and forth.





FIGURES 19–22. *Acanthoparyphium spinulosum* (Acsp). **19**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. The arrow indicates the colony, which is localized in the gonadal region. Note the prominent white areas, which are masses of cercariae that have left the orange rediae. Scale bar = 1 cm. Base photo credit: Todd Huspeni. **20**, Reproductive rediae, live, with developing cercariae, under coverslip pressure. Scale bar = 100 µm. **21**, Soldier redia, live. Scale bar = 100 µm. Base photo credit: Ana Garcia-Vedrenne. **22**, Cercariae, live, under coverslip pressure. Scale bar = 100 µm. Base photo credit: Todd Huspeni.

Similar species: The Acsp cercaria is readily separated from the other himasthlids by its pronounced pinnately-branched excretory system. It is readily distinguished from Hisb [7] by lacking a tail fin; Acsp is also often smaller than Hisb, but there is overlap, so this is not a consistently reliable distinguishing trait. Acsp's collar spine count of 23 is also diagnostic, but seeing this requires mounting at the compound scope.

Remarks: Martin and Adams (1961) document the life cycle. They described miracidia, rediae, cercariae, and metacercariae from experimentally infected horn snails, and adults from experimentally infected young domestic chickens. They identified the adults as *Acanthoparyphium spinulosum*, which was originally described from adults naturally occurring in Australian birds, indicating *A. spinulosum* likely represents a broadly distributed species complex.

There are almost certainly at least two cryptic species subsumed within *A. spinulosum* of California horn snails, but we have not yet determined clear morphological traits to distinguish them. Martin (1972) included two *Acanthoparyphium* species in his key: *A. spinulosum* and "*Acanthoparyphium* sp.", which he reported as having smaller cercaria than *A. spinulosum* and as forming metacercariae within polychaetes and snail feces. Similarly, we have regularly noted natural and experimental infections of *Acanthoparyphium* metacercariae in both bivalves, horn snails, and polychaetes (but never in feces) (Hechinger *et al*. 2007; Nguyen *et al*. 2015; Hechinger, unpublished data). This disparate host use may reflect one or more cryptic species, each of which would have more restricted host use. Additionally, DNA sequence data indicates the existence of cryptic *Acanthoparyphium* spp. in California horn snails (Nguyen *et al*. 2015; Miura, Torchin, & Hechinger, unpublished data). However, the sequence data has not been connected to specimens suitable for morphological examination, and results of experimental infections have been ambiguous (Nguyen *et al*. 2015; Hechinger, unpublished data). Hence, research is called for to resolve the existence of, morphological differences of, and host use by cryptic species of *A. spinulosum*.

This species almost certainly corresponds to the "small echinostome" of Martin (1955).

Mature, ripe colonies comprise ~20% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Acsp infection causes (stolen) snail bodies to grow over 1.5x faster than uninfected snails (Hechinger 2010).

This species has a caste of soldier rediae (Garcia-Vedrenne *et al*. 2016).

Nadakal (1960b) presents information on the pigments of the rediae and cercariae of this species (as his "small echinostome").

As part of one of the first studies documenting the syncytial nature of trematode integuments, Bils and Martin (1966) examined the fine structure and development of the tegument for the rediae and cercariae (and metacercariae and adults) of this species.

Koprivnikar *et al*. (2010) performed laboratory experiments to examine the effects of salinity, temperature, and pH on survivorship and activity of Acsp cercariae from Bolinas Lagoon (central California).

Himasthla rhigedana **Dietz**

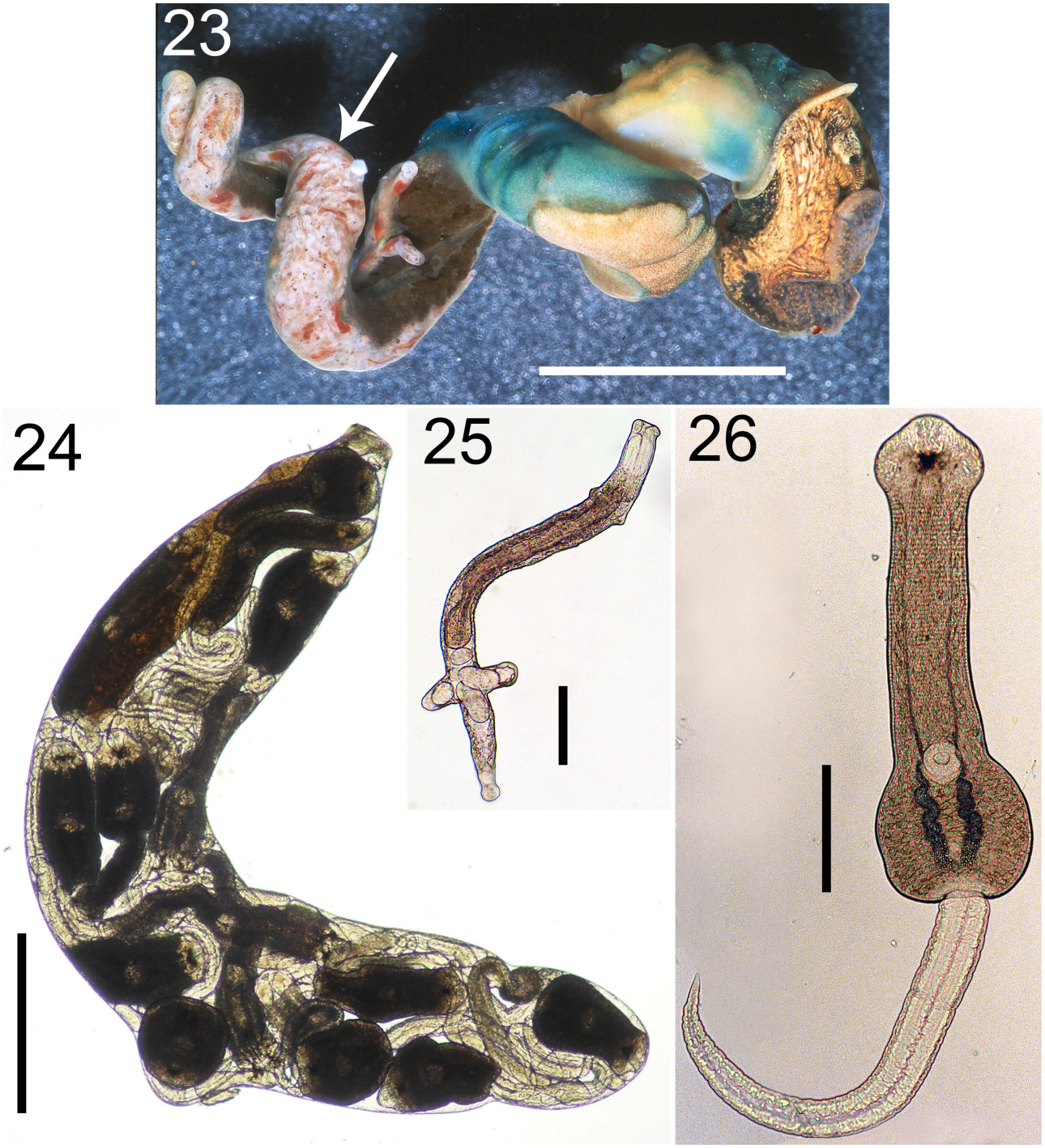
(6. Hirh; Figs. 1, 23–26)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad region. Rediae translucent white to colorless, often with prominent pigmented gut; when filled with cercariae, rediae appear opaque white with scattered black pigment (actually, the cercariae's anterior pigment); ~1300–1700 μm long, oblong to elongate (length:width up to ~6:1), with posterior appendages that are often not pronounced.

Cercaria. Body opaque white with black pigment between and around eyespots; oculate; with oral and ventral sucker; with main excretory ducts forming a tall "v" in which the anteriorly extending branches greatly narrow anterior to ventral sucker; body ~600 μm long, ~equal in length to tail; tail simple.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously, lashing tail back and forth, forming a figure 8, and will often encyst on dissection dish or in pipette during transfer.

Similar species: Hirh is readily separated from all the other echinostomatoids by having pigmented eyespots. It is easily separated from the notocotylid Cajo [4] by having a ventral sucker, a spined collar, and the redia colony being localized in the visceral mass.



FIGURES 23–26. *Himasthla rhigedana* (Hirh). **23**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. The arrow indicates the colony, which is localized in the gonadal region. Scale bar = 1 cm. Base photo credit: Todd Huspeni. **24**, Reproductive redia, live, with developing cercariae, under coverslip pressure. Scale bar = 500 µm. **25**, Soldier redia, live. Scale bar = 100 µm. Base photo credit: Ana Garcia-Vedrenne. **26**, Cercariae, live, under coverslip pressure. Scale bar = 200 µm. Base photo credit: Todd Huspeni.

Remarks: Adams and Martin (1963) demonstrated the life cycle. They described miracidia, rediae, cercariae, metacercariae from experimentally infected horn snails, and adults from experimentally infected young domestic chickens. Adams and Martin (1963) identified the adults as *Himasthla rhigedana*, which was originally described from naturally occurring adults from birds in Tunisia. This suggests that *H. rhigedana* represents a globally distributed cryptic species complex.

Deblock (1966) felt that the collar spine pattern of this species, as illustrated in Adams and Martin (1963), differed from the pattern characterizing *H. rhigedana* (based on Dietz's original description and on Deblock's observations). Deblock therefore proposed a new name for this species, *H. californiensis*. This nomenclatural act is not widely known, and the species in *C. californica* has typically been referred to as *H. rhigedana*. Further, I do not adopt Deblock's proposed name, as the supposed difference is based on an illustration in Adams and Martin (1963), and that illustration does not adequately depict the spine pattern as we have observed it or as it is figured in Maxon and Pequegnat (1949). The discrepancy with Maxon and Pequegnat (1949) is particularly important, as Adams and Martin (1963) wrote that they and Maxon and Pequegnat (1949) dealt with the same species. Careful morphological and molecular work would resolve this issue, including whether cryptic species explain some of the discrepancies.

This species corresponds to "*Himasthla* sp." of Hunter (1942), "Echinostome I of Maxon and Pequegnat (1949), and the "large pigmented echinostome" of Martin (1955).

Mature, ripe colonies comprise ~23% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Hirh infection causes (stolen) snail bodies to grow ~2x faster than uninfected snails (Hechinger 2010).

This species has a caste of soldier rediae (noted in Hechinger *et al*. (2011b) and carefully documented in Garcia-Vedrenne *et al*. [2016]).

Nadakal (1960a;b) presents information on the pigments of the rediae and cercariae of this species.

As part of one of the first studies documenting the syncytial nature of trematode integuments, Bils and Martin (1966) examined the fine structure and development of the tegument for the rediae and cercariae of this species. Dimitrov *et al*. (2001) characterize the distribution of cercaria tegumental papillae for this species.

Oates and Fingerut (2011) used histology to carefully document what is readily observed in fresh dissections: that Hirh cercaria, like most or all of the trematodes in the guild, make their way to, and accumulate in, the host snail's perirectal sinus before exiting the host. The authors used videography to document that the cercariae exit snail tissues from an area near the snail's anus.

Fingerut *et al*. (2003a) and Zimmer *et al*. (2009) examined several behavioral and environmental aspects of cercaria emergence and dispersal ecology for this species.

***Himasthla* sp. B**

(7. Hisb; Figs. 1, 27–29)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad with dispersion into basal visceral mass regions. Rediae translucent orange to colorless; ~750–2000 μm long, oblong to elongate (length:width up to ~5:1), with posterior appendages that are often not pronounced.

Cercaria. Body opaque white; non-oculate; with oral and ventral sucker; with main excretory ducts forming a broad "v"; with basal portions of main excretory ducts being particularly inflated and filled with large, distinct granules; collar with 25 collar spines in a single row, and 4 in a second row (2 pairs of "corner spines"); body ~550 μm long, ~equal in length to tail; tail dorso-ventrally finned.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously, body ventrally flexed (~forming an overall spheroidal shape), lashing tail back and forth.

Similar species: Hisb is most readily distinguished from all the echinostomatoids by having a tail fin.

Remarks: The rediae and cercariae of this species have not been thoroughly described. However, Hechinger *et al*. (2011b) present several aspects of redia morphology.

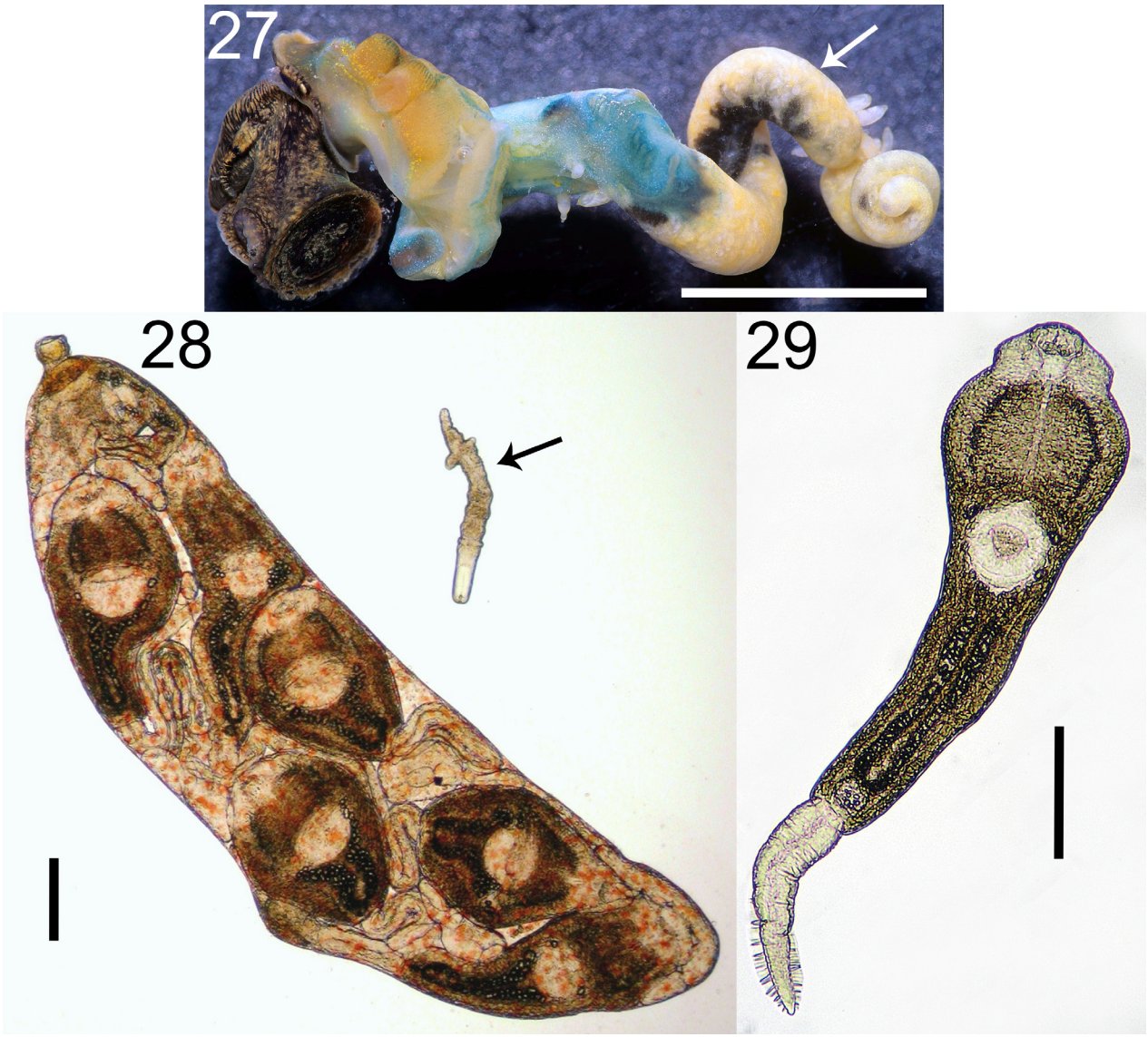
This species corresponds to the 'fin-tailed echinostome" of Martin (1955) and the "*Echinoparyphium* sp." of Martin (1972), but it has been considered to be a species of *Himasthla* since Huspeni's unpublished thesis (2000). Based on observations of natural infections at various stages of development, it appears that the initial mother sporocyst frequently invades the snail heart lumen (first pointed out to me by TC Huspeni; pers. observations).
Mature, ripe colonies comprise ~24% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Hisb infection causes (stolen) snail bodies to grow ~2x faster than uninfected snails (Hechinger 2010).

Hisb has a caste of soldier rediae (Hechinger *et al*. 2011b). In fact, it is first trematode species for which it was documented that trematodes can have a reproductive division of labor and a soldier caste.

Nadakal (1960b) presents information on the pigments of the rediae and cercariae of this species (as his "fin-tailed echinostome").

As part of one of the first studies documenting the syncytial nature of trematode integuments, Bils and Martin (1966) examined the fine structure and development of the tegument for the rediae and cercariae of this species (as *Molinella* sp.).



FIGURES 27–29. *Himasthla* sp. B (Hisb). **27**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. The arrow indicates the colony, which is localized in the gonadal region and part of the basal visceral mass. Scale bar = 1 cm. Base photo credit: Todd Huspeni. **28**, Reproductive redia, live, with developing cercariae, under coverslip pressure, with an adjacent soldier redia indicated by the black arrow. Scale bar = 100 µm. **29**, Cercariae, live, under coverslip pressure. Scale bar = 100 µm.

Cloacitrema michiganensis McIntosh

(8. Clmi; Figs. 1, 30–33)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad region with dispersion into basal visceral mass. Rediae translucent white to colorless, often with prominent pigmented gut; when filled with cercariae, rediae appear opaque white; ~1000–2000 µm long, oblong to elongate (length:width up to ~6:1), often tapers in width gradually toward anterior and posterior ends, with posterior appendages that are often not pronounced.

Cercaria. Body opaque white, usually translucent colorless through ventral sucker; non-oculate; with oral and ventral sucker; with very short esophagus that bifurcates far anterior of ventral sucker (just posterior to pharynx); body ~425 µm long, ~equal in length to tail; tail with distal gland (tip appears invaginated).

Cercaria behavior: Fresh, emerged cercariae remain in water column, lengthen body and swim by rapidly ventrally folding body with tail extended (often forming a graceful, undulating S), and will often encyst on dissection dish or in pipette during transfer.

Similar species: Clmi is most readily distinguished from the only other philophthalmid (Pasp [9]) by having almost no esophagus anterior to the gut branching; Clmi also lacks tegumental spines, but these are sometimes difficult to see on Pasp, so be wary of using this as a sole distinguishing trait. Like Pasp, Clmi is easily separated from the himasthlids by having a distal tail gland.

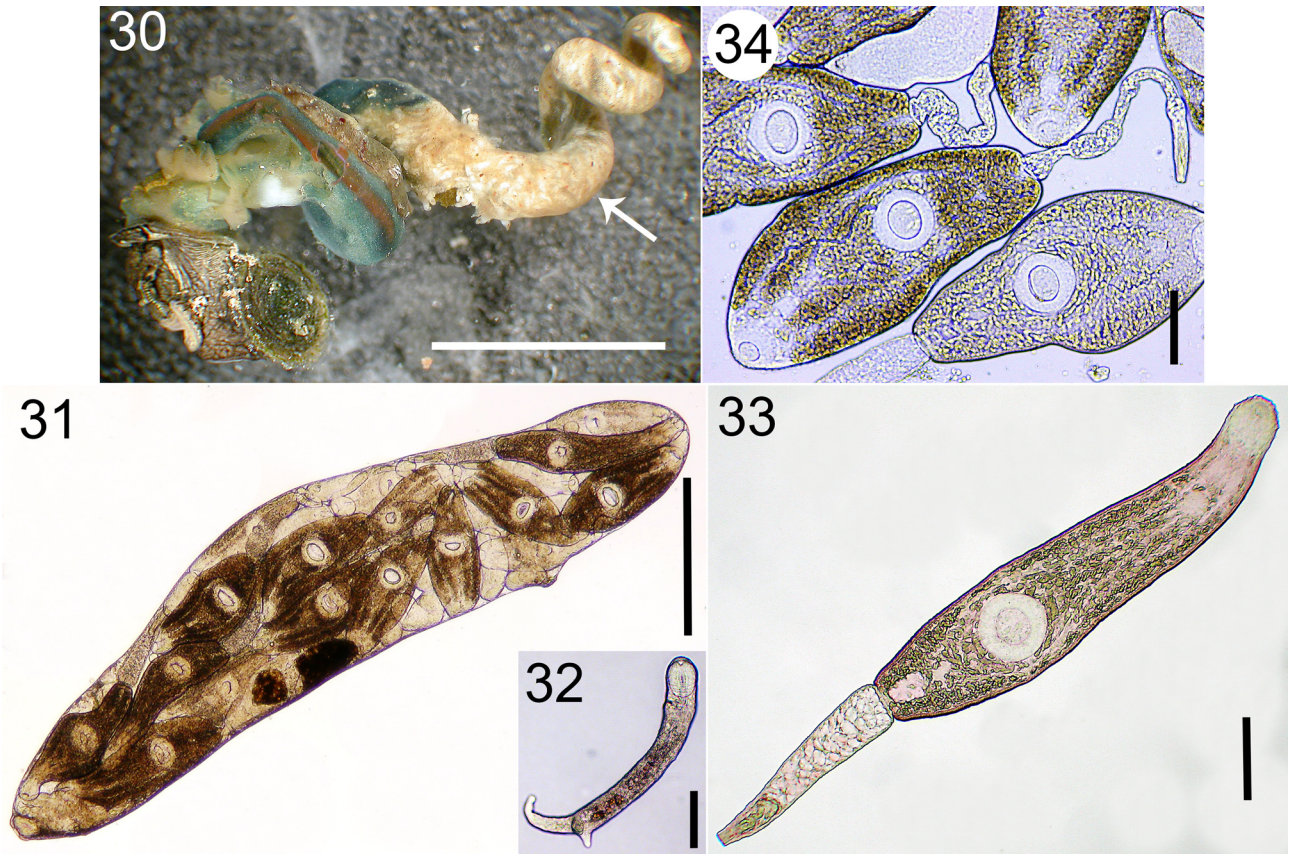
Remarks: LeFlore *et al*. (1985) document the life cycle (see also Robinson (1952) and Martin [1972]), describing the miracidia, rediae, cercariae, metacercariae, and experimentally obtained adults, which they identified as *Cloacitrema michiganensis*, which was originally described from eastern North American shorebirds.

Mature, ripe colonies comprise ~24% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Infection causes (stolen) snail bodies to grow ~2x faster than uninfected snails (Hechinger 2010).

This species has a caste of soldier rediae (noted in Hechinger *et al*. (2011b) and carefully documented in Garcia-Vedrenne *et al*. [2016]).

Nadakal (1960b) presents information on the pigments of the rediae and cercariae of this species.



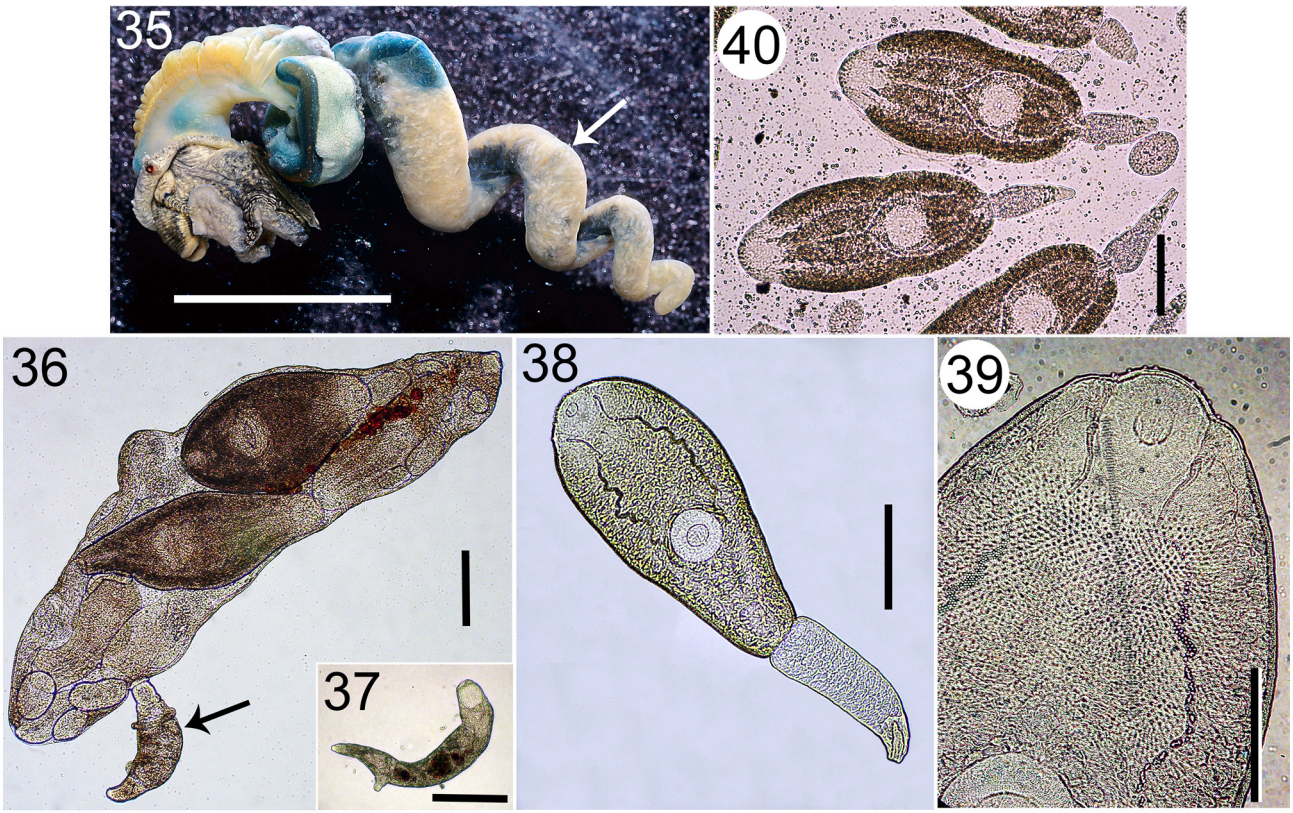
FIGURES 30–34. *Cloacitrema michiganensis* (Clmi). **30**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. The arrow indicates the colony, which is localized in the gonadal region and part of the basal visceral mass. Scale bar = 1 cm. Base photo credit: Andrew Turner. **31**, Reproductive rediae, live, with developing cercariae, under coverslip pressure. Scale bar = 500 µm. **32**, Soldier redia, live, under coverslip pressure. Scale bar = 100 µm. **33**, Cercariae, live, under coverslip pressure. Scale bar = 100 µm. Base photo credit: Andrew Turner. **34**, Developing cercariae, live, under heavy coverslip pressure to make visible the anterior branching of the gut (~ non-existent esophagus). Scale bar = 100 µm.

***Parorchis* sp.**

(9. Pasp; Figs. 1, 35–40)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad region with dispersion into basal visceral mass. Rediae translucent white to colorless, often with prominent pigmented gut; when

filled with cercariae, rediae appear opaque white; ~1000–2000 µm long, oblong to elongate (length:width up to ~6:1), often tapers in width gradually toward anterior and posterior ends, with posterior appendages that are often not pronounced.



FIGURES 35–40. *Parorchis* sp. (Pasp). **35**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. The arrow indicates the colony, which is localized in the gonadal region. Scale bar = 1 cm. Base photo credit: Todd Huspeni. **36**, Reproductive redia, live, with developing cercariae, under coverslip pressure. The arrow indicates an attacking soldier redia of *Himasthla* sp. B from an *in vitro* experiment (Hechinger *et al.*, 2010). Scale bar = 200 µm. **37**, Soldier redia, live. Scale bar = 200 µm. Base photo credit: Andrew Turner. **38**, Cercaria, live, under coverslip pressure. Scale bar = 200 µm. **39**, Close up of cercaria anterior with particularly obvious tegumental body spines. Scale bar = 100 µm. **40**, Developing cercariae, live, under heavy coverslip pressure to make the long esophagi visible. Scale bar = 200 µm.

Cercaria. Body opaque white; non-oculate; with oral and ventral sucker; with indistinct row of collar spines; with body spines covering much of tegument; with long esophagus that bifurcates just anterior to ventral sucker; body ~425 µm long, ~equal in length to tail; tail with distal gland (tip appears invaginated).

Cercaria behavior: Fresh, emerged cercariae remain in water column, lengthen body and swim by rapidly ventrally folding body with tail extended (often in a somewhat jerky fashion), and will often encyst on dissection dish or in pipette during transfer.

Similar species: Pasp is most readily distinguished from the only other philophthalmid (Clmi [8]) by having the long esophagus anterior to gut branching. Pasp also has tegumental spines, but these are not always readily observable. Like Clmi, Pasp is easily separated from the himasthlids by having a distal tail gland.

Remarks: This species corresponds to "*Cercaria cerithidia* 2" of Hunter (1942). Martin (1972) included this species in his key, asserting it was *Parorchis acanthus*, which had been reported from European and East Coast North American birds, with first intermediate host infections in neogastropod snails in eastern North America (e.g., Lebour 1914, Stunkard and Cable 1932). The use of taxonomically disparate first intermediate hosts suggests that *P. acanthus* represents a wide-spread species complex. So too, does careful consideration of adult morphologies (Dronen & Blend 2008), which suggests that there actually may be no *P. acanthus* in North America. We have two cryptic species in California horn snails, as indicated by analysis of mitochondrial CO1 sequences [Huspeni 2000, unpublished thesis]). The cercariae of one cryptic species appears to be larger than the other (Huspeni 2000), but we have not yet confirmed how to distinguish them in practice. It may be that one species has more prominent body

spines and an esophagus that branches just anterior to the ventral sucker, while the other has less prominent spines with a shorter esophagus, branching ~midway from pharynx to ventral sucker (unpublished observations). Given all the above, it seems best to abandon referring to this species as *P. acanthus*, versus *Parorchis* sp.

Mature, ripe colonies comprise ~26% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

This species has a caste of soldier rediae (noted in Hechinger *et al*. (2011b) and carefully documented in Garcia-Vedrenne *et al*. [2016]).

Nadakal (1960b) presents information on the pigments of the rediae and cercariae of this species.

As part of one of the first studies documenting the syncytial nature of trematode integuments, Bils and Martin (1966) examined the fine structure and development of the tegument for the rediae and cercariae of this species. Fingerut *et al*. (2003a) presents information on the relationship between cercaria emergence and temperature for this species.

Acanthotrema hancocki (Martin)

(10. Acha; Figs. 1, 41–44)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad region. Rediae translucent white, grey, weak yellow, or colorless; ~500–1000 µm long, elongate (length:width ~4:1 to 10:1), sausage-shaped.

Cercaria. Body mostly translucent colorless; oculate; with oral sucker and no ventral sucker; with seven pairs of penetration glands, the bodies of which lie in a relatively compact cluster, anterior to the genital primordium and excretory bladder; body ~175 µm long, much shorter than tail (< 1/2 length); tail with dorso-ventral fins (originating in middle third of tail length, extending around tail tip) and lateral fins (originating basally, next to cercaria body, and inserting in middle third of tail length).

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim intermittently in short bursts, with periods of resting and slow sinking.

Similar species: Acha is most reliably and readily distinguished from Euca [11] by the position of the penetration gland bodies, which are readily observable with flattened cercariae at 100x on a compound scope (and even sometimes at the dissection scope). Although Acha does have wider lateral tail fins than Euca on average, there appears to be overlap; so, tail fin width is not a consistently reliable distinguishing trait. Martin (1972) used the flame cell grouping to distinguish Acha from Euca (groups of 3 versus 2, respectively), but the flame cells are difficult to see, requiring leaving specimens on a slide for a while and 1000x magnification.

Remarks: Martin (1950b) documented the life cycle and described this species (as *Parastictodora hancocki*). He described the mother sporocyst, rediae and cercariae from natural infections, and metacercariae and adults from experimentally infected second intermediate and final hosts. I suspect that cercariae of *Acanthotrema hancocki* were accidentally pooled with *Euhaplorchis californiensis* to comprise Maxon and Pequegnat's (1949) Pleurolophocercous I and pooled with *Phocitremoides ovale* cercariae to comprise their Pleurolophocercous II.

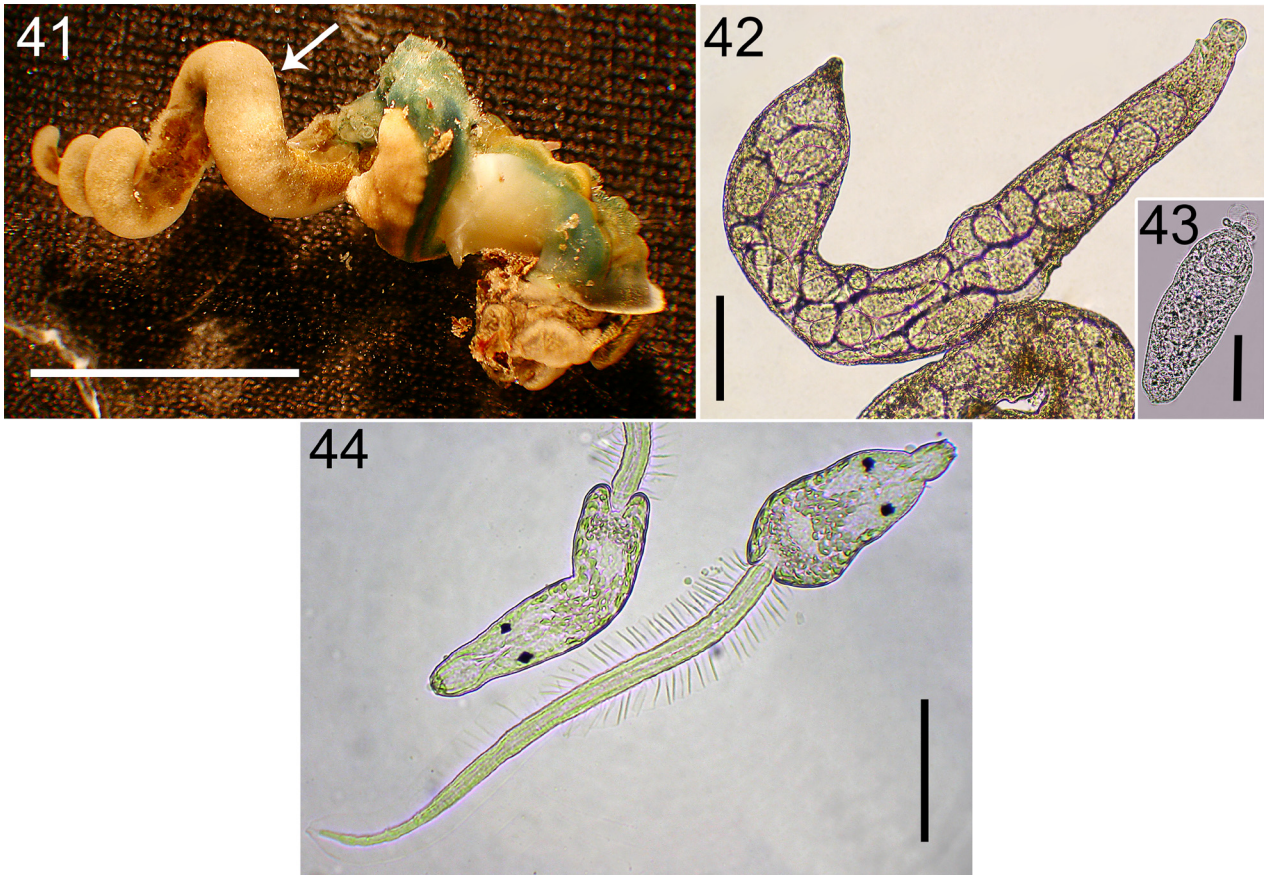
This species has also been referred to as *Stictodora hancocki* in ecological and evolutionary papers, but, since Lafuente *et al*. (2000), the appropriate genus has been *Acanthotrema*.

Mature, ripe colonies comprise ~18% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Acha infection causes (stolen) snail bodies to grow over 1.5x faster than uninfected snails (Hechinger 2010).

This species has a caste of soldier rediae (Garcia-Vedrenne *et al*. 2017).

Using Acha (reported as Euca, see Euca remarks) from Bolinas Lagoon (central California), Koprivnikar *et al*. (2010) performed laboratory experiments examining the effects of salinity, temperature, and pH on cercaria survivorship and activity.



FIGURES 41–44. *Acanthotrema hancocki* (Acha). **41**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. The arrow indicates the colony, which is localized in the gonadal region. Scale bar = 1 cm. **42**, Reproductive rediae, live, with developing cercariae, under coverslip pressure. Scale bar = 100 µm. **43**, Soldier redia, live, under coverslip pressure. Scale bar = 50 µm. Base photo credit: Andrew Turner. **44**, Cercariae, live, under coverslip pressure. Scale bar = 100 µm.

Euhaplorchis californiensis Martin

(11. Euca; Figs. 1, 45–48)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad region. Rediae translucent white, grey, weak yellow, or colorless; ~200–600 µm long, elongate (length:width ~4:1 to 8:1), sausage-shaped.

Cercaria. Body mostly translucent colorless; oculate; with oral sucker and no ventral sucker; with seven pairs of penetration glands, the bodies of which are interspersed from anterio-medial of genital primordium to posterior body wall lateral to excretory bladder; body ~150 µm long, much shorter than tail (< 1/2 length); tail with dorso-ventral fins (originating in middle third of tail length, extending around tail tip) and lateral fins (originating basally, next to cercaria body, and inserting in middle third of tail length).

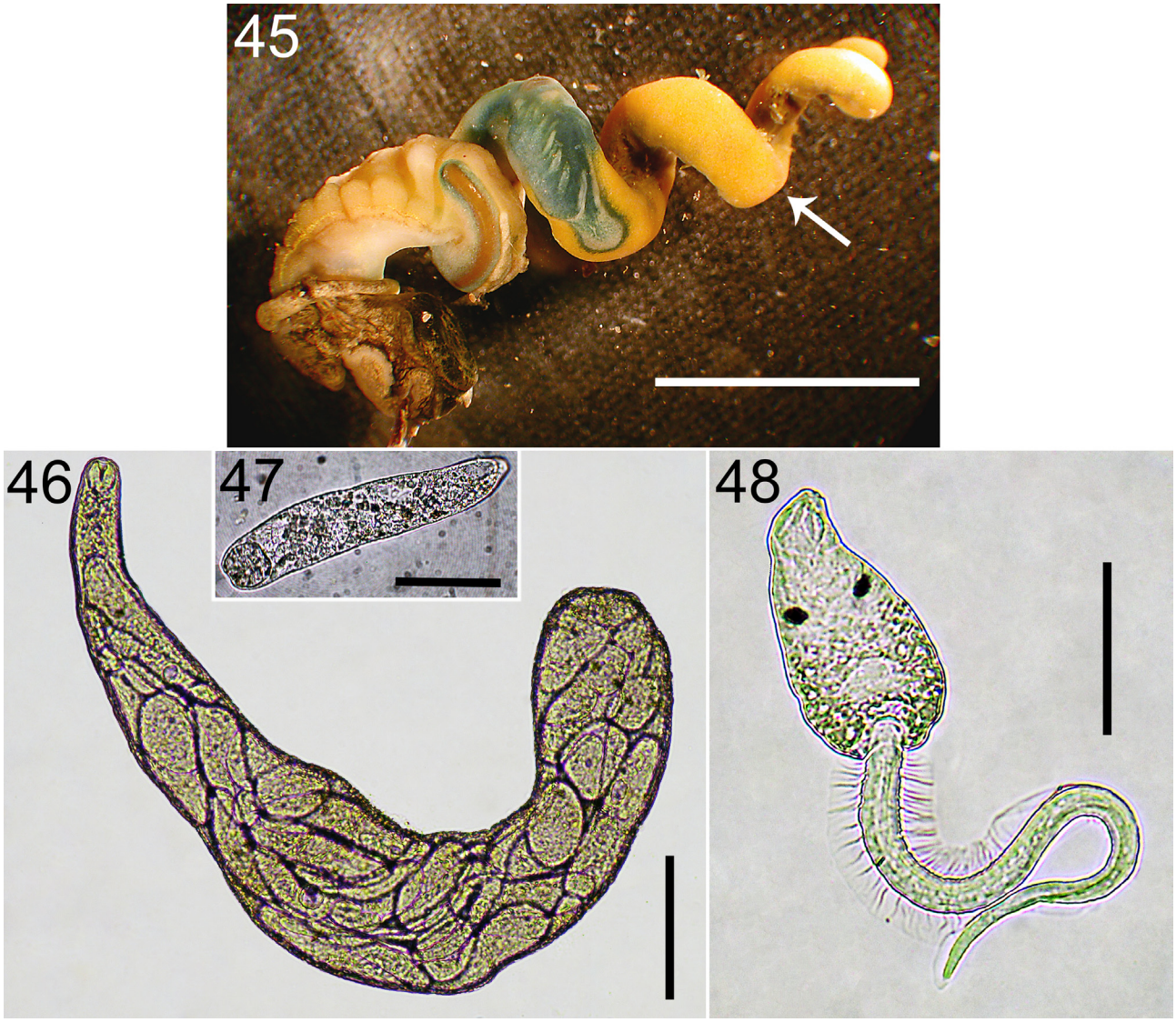
Cercaria behavior: Fresh, emerged cercariae remain in water column, swim intermittently in short bursts, with periods of resting and slow sinking.

Similar species: Euca is most reliably and readily distinguished from Acha [10] by the position of the penetration gland bodies, which are readily observable with flattened cercariae at 100x on a compound scope (and even sometimes at the dissection scope). Although Euca does have narrower lateral tail fins than Acha on average, there appears to be overlap; so, tail fin width is not a consistently reliable diagnostic trait. Martin (1972) used the flame-cell grouping to distinguish Acha from Euca, but the flame cells are difficult to see, requiring leaving specimens on a slide for a while and 1000x magnification.

Remarks: Martin (1950a) documented the life cycle and described the species; he described the rediae and cercariae from natural infections, and metacercariae and adults from experimentally infected second intermediate

and final hosts. I suspect that cercariae of *Euhaplorchis californiensis* were accidentally pooled with *Acanthotrema hancocki* to comprise Maxon & Pequegnat's (1949) Pleurolophocercous I.

Readers should note that I believe that reports of Euca in California horn snails at Bolinas Lagoon (central California) in some ecological research (Koprivnikar *et al*. 2010; Sousa 1993) are a result of misidentification, and that the research actually dealt with *A. hancocki* (Acha), which otherwise went unrecognized in those studies. I base this idea mostly on dissections of thousands of snails from Bolinas Lagoon and nearby areas (since early this century) that indicate an almost complete absence of Euca in central California north of Morro Bay, but relatively common Acha (Hechinger *et al*., unpublished data). We also might expect Euca to be missing from Bolinas because its only known second intermediate host, the California Killifish (*Fundulus parvipinnis* Girard) does not occur that far north. Careful work should examine whether a cryptic species of Acha explains the likely misidentification.



FIGURES 45–48. *Euhaplorchis californiensis* (Euca). **45**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. Arrow indicates the colony, which is localized in the gonadal region. Scale bar = 1 cm. **46**, Reproductive rediae, live, with developing cercariae, under coverslip pressure. Scale bar = 100 µm. **47**, Soldier redia, live, under coverslip pressure. Scale bar = 50 µm. Base photo credit: Andrew Turner. **48**, Cercariae, live, under coverslip pressure. Scale bar = 100 µm.

Mature, ripe colonies comprise ~19% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Unlike many other trematodes in the guild, infection by Euca appears to cause (stolen) snail bodies to grow at the same rate as uninfected (male) snails (Hechinger 2010).

Euca has a caste of soldier rediae (Garcia-Vedrenne *et al*. 2017).

Nadakal (1960a;b) presents information on the pigments of the rediae and cercariae of this species.

As part of one of the first studies documenting the syncytial nature of trematode integuments, Bils and Martin (1966) examined the fine structure and development of the tegument of the rediae and cercariae of this species.

Oates and Fingerut (2011) used histology to carefully document what is readily observed in fresh dissections: that Euca cercaria, like most or all of the trematodes in the guild, make their way to, and accumulate in, the host snail's perirectal sinus before exiting the host. The authors used videography to document that the cercariae exit snail tissues from an area near the snail's anus.

Fingerut *et al*. (2003a) presents information on the relationship between cercaria emergence and temperature for this species.

Cercariae of this species are positively phototactic and negatively geotactic (Weinersmith *et al*. 2018).

This species is famous for modifying the behavior of its second intermediate host fish. Infected fishes exhibit 8x more conspicuous behaviors in the laboratory and are 10–30x more likely to be eaten by final host birds (Lafferty & Morris 1996).

Phocitremoides ovale **Martin**

(12. Phov; Figs. 1, 49–52)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad region. Rediae translucent white, grey, weak yellow, to colorless; ~500–1000 µm long, elongate (length:width ~4:1 to 10:1), sausage-shaped.

Cercaria. Body posterior 2/3 opaque white; oculate; with oral sucker and no ventral sucker; body ~200 µm long, much shorter than tail (< 1/2 length); tail dorso-ventrally finned.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim intermittently in short bursts, with periods of resting and slow sinking.

Similar species: Phov is readily distinguished from the other two heterophyids with tail fins by only having a dorso-ventral fin (lacking the proximal lateral fins). Additionally, the penetration gland distribution imparts a distinctive coloration pattern to the body, with the anterior 1/3 being translucent and the posterior 2/3 being more homogeneously white (with reflected light) or dark (with transmitted light).

Remarks: Martin (1950c) described Phov and documented its life cycle; he described the rediae and cercariae from natural infections, and metacercariae and adults from experimentally infected second intermediate and final hosts. I suspect that cercariae of this species were accidentally pooled with Acha to comprise Maxon & Pequegnat's (1949) Pleurolophocercous II.

Mature, ripe colonies comprise ~16% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Garcia-Vedrenne *et al*. (2017) presents several lines of evidence indicating that this species has a caste of soldier rediae. However, the in vitro attack trials had limited success.

Pygidiopsoides spindalis **Martin**

(13. Pysp; Figs. 1, 53–56)

Diagnosis: *Parthenitae.* Colony comprised of active rediae, densely concentrated in snail gonad region. Rediae almost opaque white to translucent white or grey; ~300–400 µm long, oblong to elongate (length:width ~3:1 to 8:1), sausage-shaped.

Cercaria. Body mostly translucent colorless; oculate; with oral sucker and no ventral sucker; body ~100 µm long, ~equal in length to tail; tail simple.

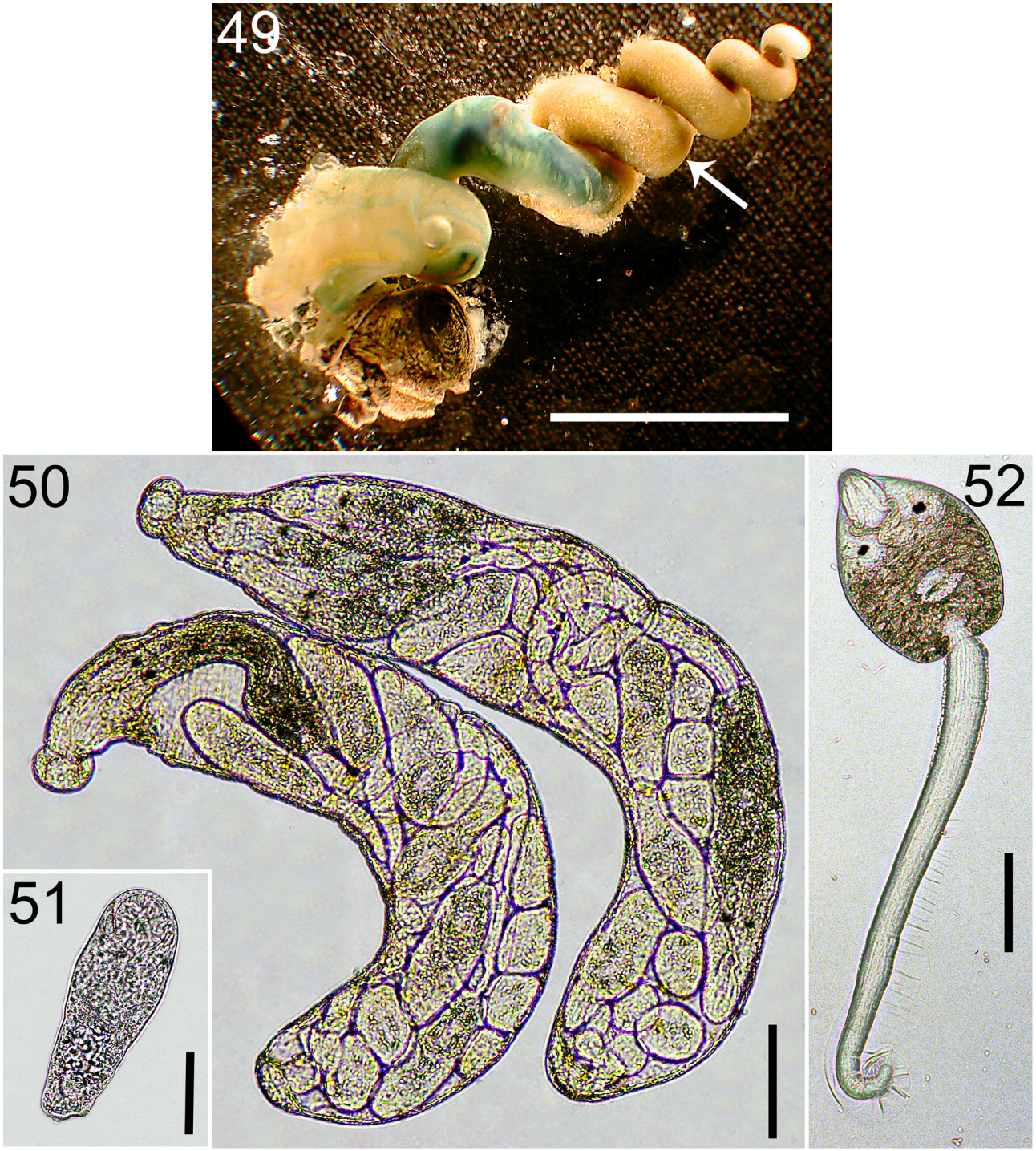
Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously.

Similar species: Pysp is readily separable from the other heterophyids by the lack of a cercaria tail fin, in addition to its relatively short tail, blunt anterior, and small size.

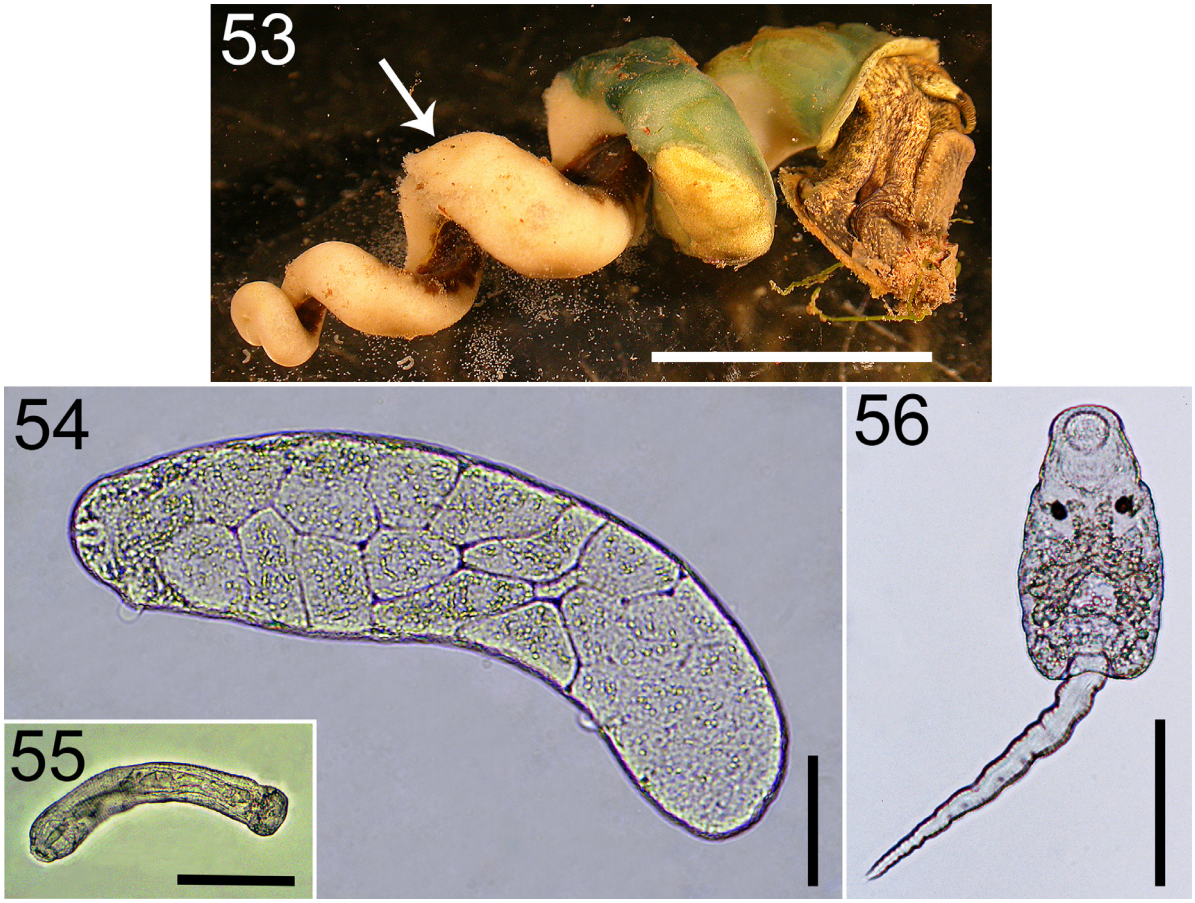
Remarks: Martin (1951) described this species from adults obtained by feeding metacercariae from naturally

infected *Fundulus parvipinnis* to chicks and cats. He later documented the life cycle, and described rediae and cercariae from naturally infected California horn snails and metacercariae from experimentally infected second intermediate hosts (Martin 1964). This species likely corresponds to the "small opisthorchioidea" in Martin (1955).

Garcia-Vedrenne *et al*. (2017) presents several lines of evidence indicating that this species has a caste of soldier rediae (however, the in vitro attack trials had limited success).



FIGURES 49–52. *Phocitremoides ovale* (Phov). **49**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. Arrow indicates the colony, which is localized in the gonadal region. Scale bar = 1 cm. Base photo credit: Andrew Turner. **50**, Reproductive rediae, live, with developing cercariae, under coverslip pressure. Scale bar = 100 µm. **51**, Soldier redia, live, under coverslip pressure. Scale bar = 50 µm. Base photo credit: Ana Garcia-Vedrenne. **52**, Cercariae, live, under coverslip pressure. Scale bar = 100 µm. Photo credit: Todd Huspeni.



FIGURES 53–56. *Pygidiopsoides spindalis* (Pysp). **53**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. Arrow indicates the colony, which is localized in the gonadal region. Scale bar = 1 cm. **54**, Reproductive redia, live, with developing cercariae, under heavy coverslip pressure. Scale bar = 100 µm. **55**, Soldier redia, live, under slight coverslip pressure. Scale bar = 50 µm. Base photo credit: Ana Garcia-Vedrenne. **56**, Cercariae, live, under coverslip pressure. Scale bar = 100 µm. Base photo credit: Todd Huspeni.

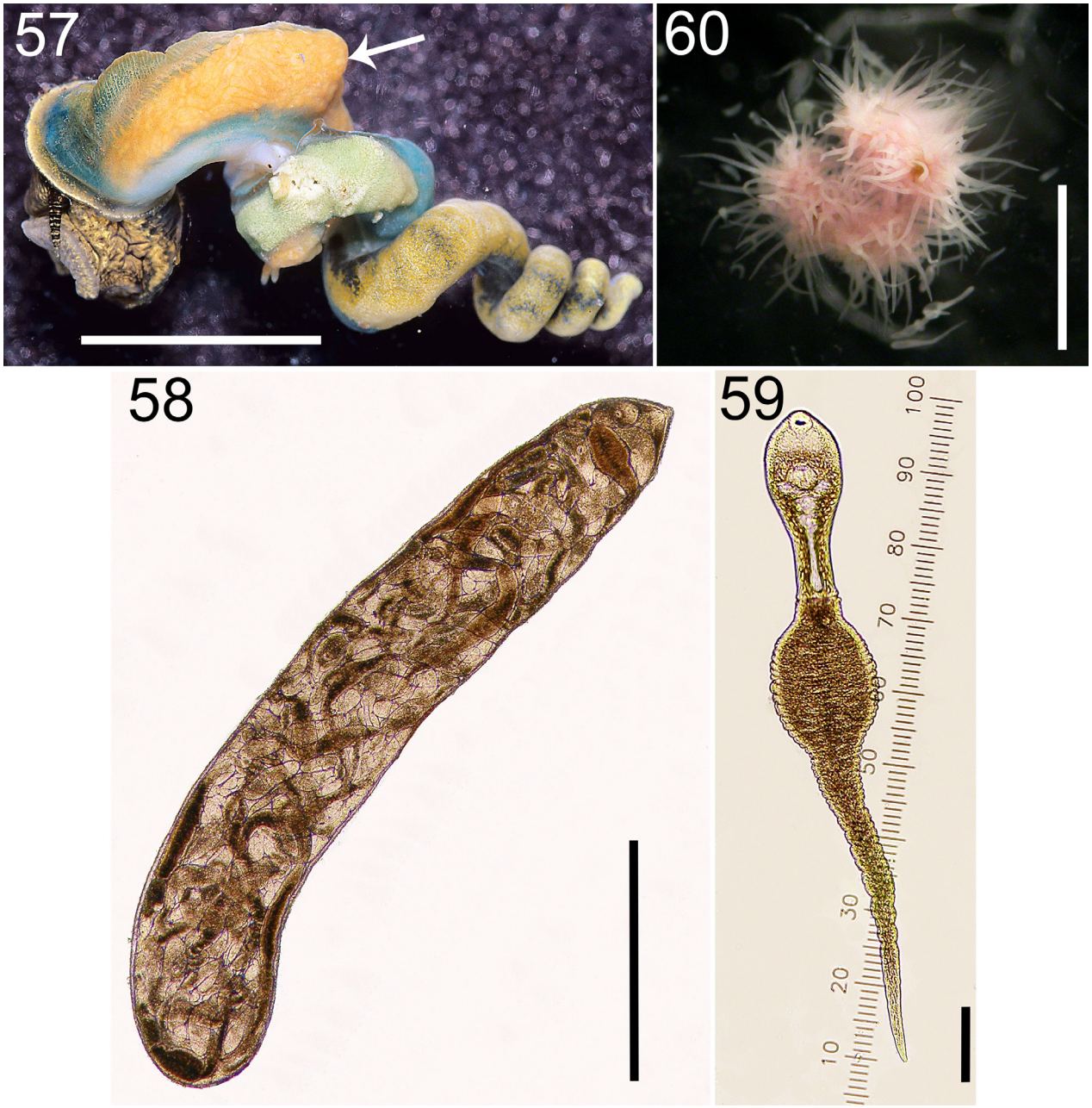
Renicola buchanani (Martin and Gregory)

(14. Rebu; Figs. 1, 57–60)

Diagnosis: *Parthenitae.* Colony comprised of inactive sporocysts, densely concentrated in snail mantle (in enlarged perirectal sinus). Sporocysts translucent orange, yellow, sometimes white; 1000–2000 µm long, elongate (length: width up to ~6:1), ~sausage-shaped.

Cercaria. Body opaque white; non-oculate; with oral and ventral sucker; with a large Y-shaped excretory bladder, the arms of which wrap around sides of ventral sucker; body ~228 µm long, much shorter than tail (< 1/2 length); tail narrow at base, but then with large, sometimes bulbous, proximal portion that narrows distally to a simple tip.

Cercaria behavior: Upon emergence, cercariae either (1) swim solitarily, lashing the distal potion of tail while pressing body adjacent to the greatly inflated, egg-shaped, proximal portion of tail, or (2) form aggregations, where they attach to each other using adhesive proximal-most portions of tail (Martin & Gregory 1951). Cercariae that aggregate together are best referred to as known as "zygocercariae" (see review by Beuret & Pearson 1994). Our unpublished observations clarify that cercariae from the same infection may exhibit these different behaviors (often in different shedding events) (D.C. Metz, unpublished data).



FIGURES 57–60. *Renicola buchanani* (Rebu). **57**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. Arrow indicates the colony, which is localized in the mantle. Scale bar = 1 cm. **58**, Sporocyst, live, with developing cercariae, under coverslip pressure. Scale bar = 1 mm. **59**, Cercaria, live, under coverslip pressure. Scale bar = 100 µm. Ocular micrometer hatch mark = 10 µm. **60**, Cercariae, live, aggregated clump formed under water at bottom of dissection dish after release from host. Scale bar = 1000 µm.

Similar species: The "magnacercous" Rebu is not confusable with any of the other trematodes in this guild.

Remarks: Martin and Gregory (1951) described the sporocysts and cercariae (as *Cercaria buchanani*). Based on morphological similarities, Martin (1971) decided that renicolid metacercariae he encountered in estuarine fish livers were the same species, and he assigned the species to *Renicola*. Hechinger and Miura (2014) provided COI and ITS1 DNA sequence data for this species.

Early Rebu infections can be detected. The sporocysts appear to typically initially form in the basal visceral mass, as generally expected for species that infects the snail with ingested eggs (Galaktionov & Dobrovolskij 2003) (unpublished observations).

Mature, ripe colonies comprise ~17% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Nadakal (1960b) presents information on the pigments of the sporocysts and cercariae of this species.

As part of one of the first studies documenting the syncytial nature of trematode integuments, Bils and Martin (1966) examined the fine structure and development of the tegument for the sporocysts and cercariae of this species.

Fingerut *et al*. (2003a) presents information on the relationship between cercaria emergence and temperature for this species.

***Renicola cerithidicola* Martin**

(15. Rece; Figs. 1, 61–64)

Diagnosis: *Parthenitae.* Colony comprised of inactive sporocysts, densely concentrated in snail mantle (in enlarged perirectal sinus). Sporocysts translucent yellow, orange, sometimes white; ~500–1500 µm long, ovoid to elongate (length:width up to ~6:1), ~sausage-shaped.

Cercaria. Body mostly opaque white; non-oculate; with oral and ventral sucker; with a large Y-shaped excretory bladder, the arms of which wrap around sides of ventral sucker; body ~117 µm long, ~equal in length to tail; tail simple.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously, lashing tail back and forth.

Similar species: Rece is readily distinguished from the two other small renicolid cercariae (Rema [16] and Repo [17]) by its lack of an oral stylet and by the colony locus being in the mantle.

Remarks: Martin (1971) described this species based on the sporocysts, cercariae, and experimentally obtained metacercariae (he was able to get only immature adult specimens in young California gulls). Hechinger and Miura (2014) provided COI and ITS1 DNA sequence data for this species.

Specimens of this species may have been included, along with specimens of *Renicola* sp. "polychaetophila", in the material Hunter (1942) used to describe her "*Cercaria cerithidia* 19" (Hechinger & Miura 2014). This species corresponds to the "Y-bladder cercaria" of Martin (1955).

Early Rece infections can be detected. The sporocysts appear to typically initially form in the basal visceral mass, as generally expected for species that infects the snail with ingested eggs (Galaktionov & Dobrovolskij 2003) (unpublished observations).

Mature, ripe colonies comprise ~17% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Rece infection causes (stolen) snail bodies to grow ~2x faster than uninfected snails (Hechinger 2010).

***Renicola* sp. "martini" (sensu Hechinger and Miura [2014])**

(16. Rema; Figs. 1, 65–70)

Diagnosis: *Parthenitae.* Colony comprised of inactive sporocysts, densely concentrated to irregularly clustered in snail gonad region, with dispersion into digestive gland. Sporocysts translucent orange to white; ~100–800 µm long, spheroidal to slightly elongate (length:width up to ~4:1).

Cercaria. Body mostly opaque white; non-oculate; with oral sucker bearing a stylet (a xiphidiocercaria) and with ventral sucker; with tegumental spines over much of surface; with all penetration gland ducts opening at stylet; with a large Y-shaped excretory bladder, the arms of which wrap around sides of ventral sucker; body ~200 µm long, ~equal in length to tail; tail simple.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously, lashing tail back and forth.

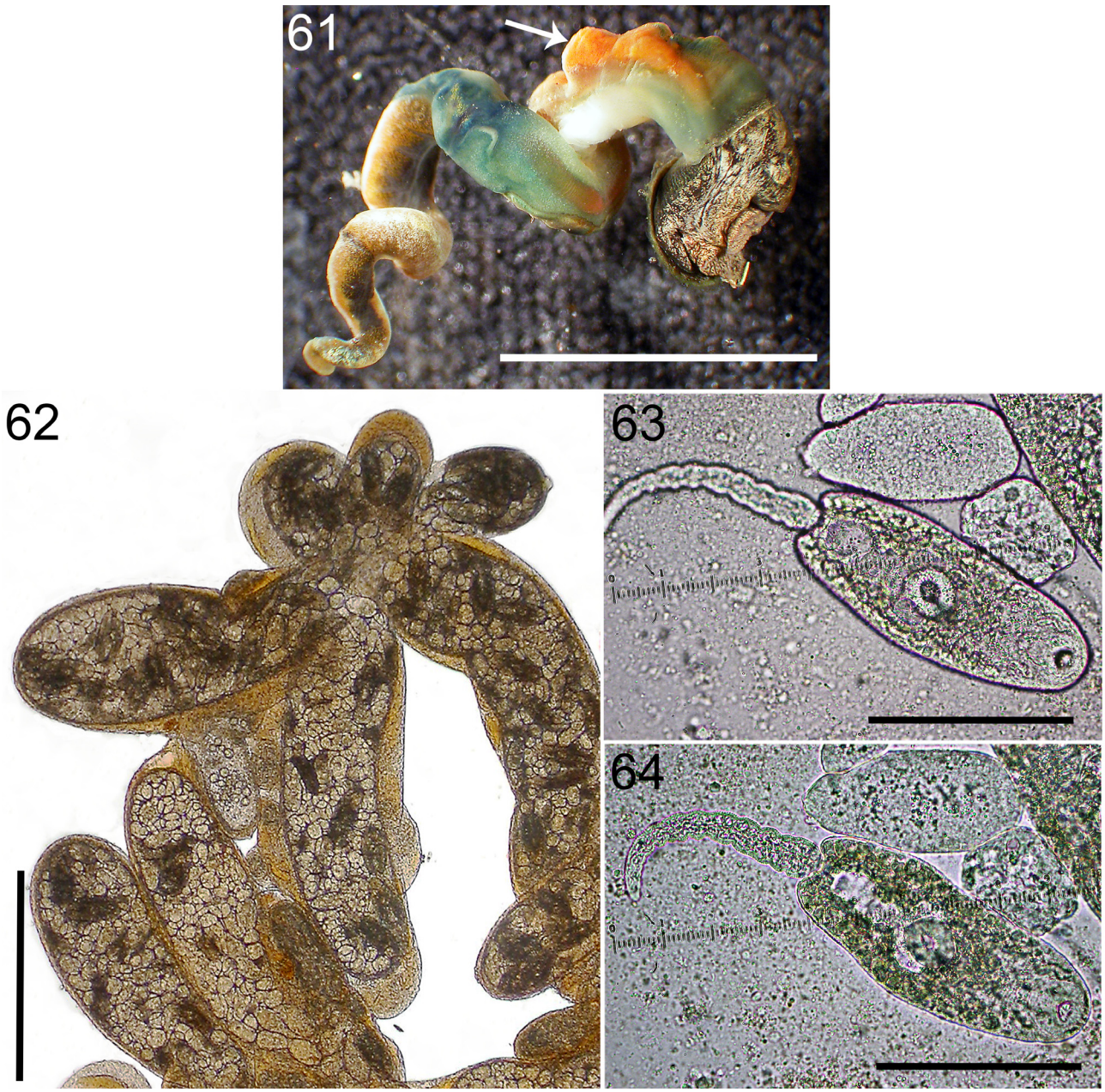
Similar species: Rema is most readily distinguished from Repo [17] by the cercariae having tegumental spines and by the penetration gland duct arrangement.

Remarks: Hechinger and Miura (2014) described the sporocysts and cercariae, and provided COI and ITS1 DNA sequence data.

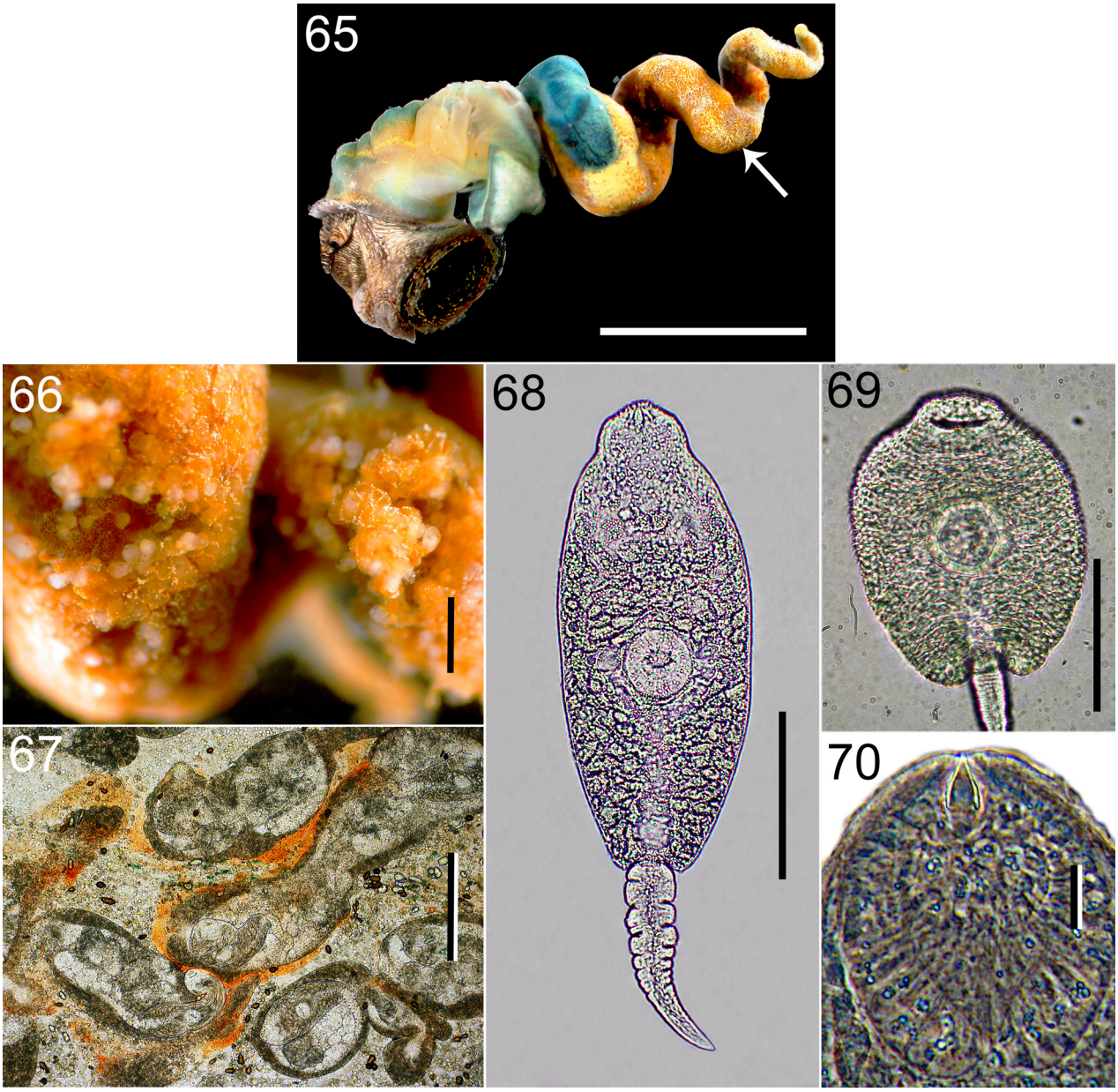
This species was not included in Martin (1972), but likely corresponds to "*Cercaria cerithidia* 23" of Hunter (1942). This species, along with *Renicola* sp. "polychaetophila", was previously referred to as "large xiphidiocercaria" in some ecological and evolutionary research (e.g., Hechinger *et al*. 2007; Kuris 1990).

Mature, ripe colonies comprise ~20% the soft-tissue weight of an infected snail (summer-time estimate derived from information on "Lgxi" in [Hechinger *et al*. 2009]).

Nadakal (1960b) presents information on the pigments of the sporocysts and cercariae of this species (seemingly pooled with *Renicola* sp. "polychaetophila") as his "Y-bladder cercaria".



FIGURES 61–64. *Renicola cerithidicola* (Rece). **61**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. Arrow indicates the colony, which is localized in the mantle. Scale bar = 1 cm. Base photo credit: Andrew Turner. **62**, Sporocysts, live, with developing cercariae, under heavy coverslip pressure. Note the paletot surrounding each sporocyst's tegument. Scale bar = 500 µm. **63**, Cercaria, live, under coverslip pressure. Scale bar = 100 µm. Ocular micrometer hatch mark = 2.5. **64**, Same cercaria as 63, but with a different focal plane, highlighting the Y-shaped excretory bladder. Scale bar = 100 µm. Ocular micrometer hatch mark = 2.5.

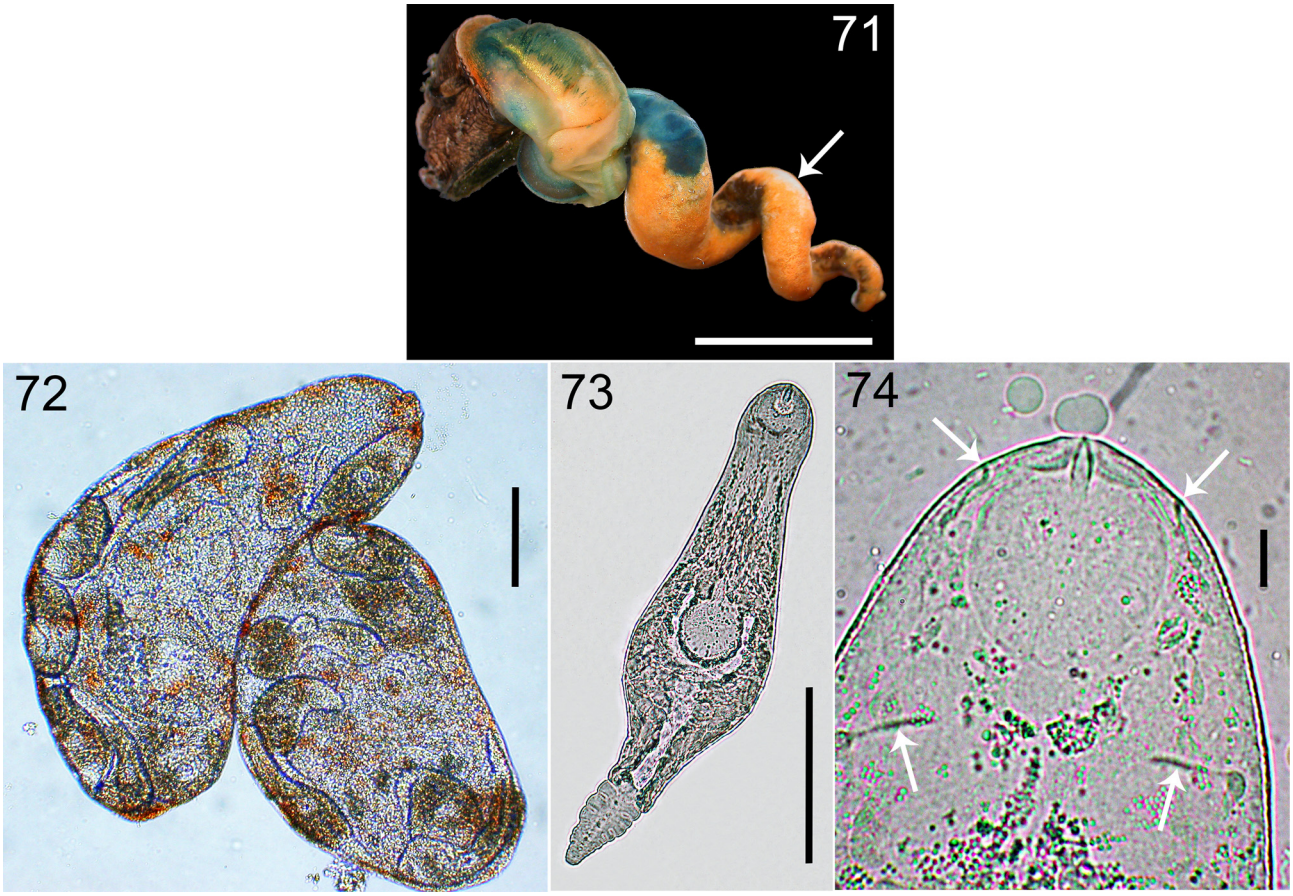


FIGURES 65–70. *Renicola* sp. "martini" (Rema). **65**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. Arrow indicates the colony, which is localized in the gonadal region with infiltration of the digestive gland. Scale bar = 1 cm. Photo from Hechinger and Miura (2014). **66**, Close-up of part of a slightly teased apart colony from a freshly dissected horn snail. Individual sporocysts are discernable. Scale bar = 1 mm. **67**, Sporocysts, live, with developing cercariae, under heavy coverslip pressure. Note the paletot surrounding the sporocyst tegument. Scale bar = 200 µm. **68**, Cercaria, live, under coverslip pressure. Scale bar = 100 µm. **69**, Cercaria, live, with no coverslip pressure, with tegumental spines visible. Scale bar = 100 µm. **70**, Close-up of cercaria oral sucker, stylet visible, under heavy coverslip pressure, using phase contrast. Scale bar = 10 µm.

Renicola sp. "polychaetophila" (sensu Hechinger and Miura [2014])

(17. Repo; Figs. 1, 71–74)

Diagnosis: *Parthenitae.* Colony comprised of inactive sporocysts, densely concentrated to irregularly clustered in snail gonad region, with dispersion into digestive gland. Sporocysts translucent orange to white; ~100–800 µm long, spheroidal to slightly elongate (length:width up to ~4:1).



FIGURES 71–74. *Renicola* sp. "polychaetophila" (Repo). **71**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. Arrow indicates the colony, which is localized in the gonadal region with infiltration of the digestive gland. Scale bar = 1 cm. Photo from Hechinger & Miura (2014). **72**, Sporocysts, live, with developing cercariae, under coverslip pressure. Scale bar = 100 µm. **73**, Cercaria, live, under coverslip pressure. Scale bar = 100 µm. **74**, Close-up of cercaria anterior end, heavy coverslip pressure, oral stylet visible, as are dorsal penetration duct openings and posterior-ventral "cross ducts" (white arrows). Scale bar = 10 µm.

Cercaria. Body mostly opaque white; non-oculate; with oral and ventral sucker; with no tegumental spines; with penetration gland duct opening arrangement of 2[(1+3+1)+1], with 3 pairs opening adjacent to oral stylet, 1 diverging to open more dorsally, 1 ventrally, with 1 separated pair forming characteristic ventral "cross ducts" posterior to oral sucker; with a large Y-shaped excretory bladder, the arms of which wrap around sides of ventral sucker; body ~180 µm long, ~equal in length to tail; tail simple.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously, lashing tail back and forth.

Similar species: Repo is most readily distinguished from Rema [16] by the cercaria penetration gland duct arrangement (particularly the posterior-most "cross ducts") and lack of tegumental spines.

Remarks: Hechinger and Miura (2014) described the sporocysts and cercariae, and provided COI and ITS1 DNA sequence data.

This species was not included in Martin (1972), but specimens of it may have been included, along with specimens of *Renicola cerithidicola* in the material Hunter (1942) used to describe her "*Cercaria cerithidia* 19" (Hechinger & Miura 2014). This species, along with *Renicola* sp. "martini" was previously referred to as "large xiphidiocercaria" in some ecological and evolutionary research (e.g., Hechinger *et al*. 2007; Kuris 1990).

Mature, ripe colonies comprise ~20% the soft-tissue weight of an infected snail (summer-time estimate derived from information on "lgxi" in [Hechinger *et al*. 2009]).

Nadakal (1960b) presents information on the pigments of the sporocysts and cercariae of this species (likely pooled with *Renicola* sp. "martini"), as his "Y-bladder cercaria".

***Probolocoryphe uca* Sarkisian**
(18. Pruc; Figs. 1, 75–78)

Diagnosis: *Parthenitae.* Colony comprised of inactive sporocysts, densely concentrated in snail gonad region, with dispersion into digestive gland and basal visceral mass. Sporocysts translucent golden to orangish; ~250–600 µm long, spheroidal to oblong (length:width up to ~2:1).

Cercaria. Body translucent colorless; non-oculate; with oral sucker and no ventral sucker; with oral stylet, ~25 µm long, with distinctive dorsal flange; with a small bi-lobed excretory bladder at posterior-most edge of cercaria body; body ~175 µm long, ~equal in length to tail; tail simple.

Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously, lashing tail back and forth.

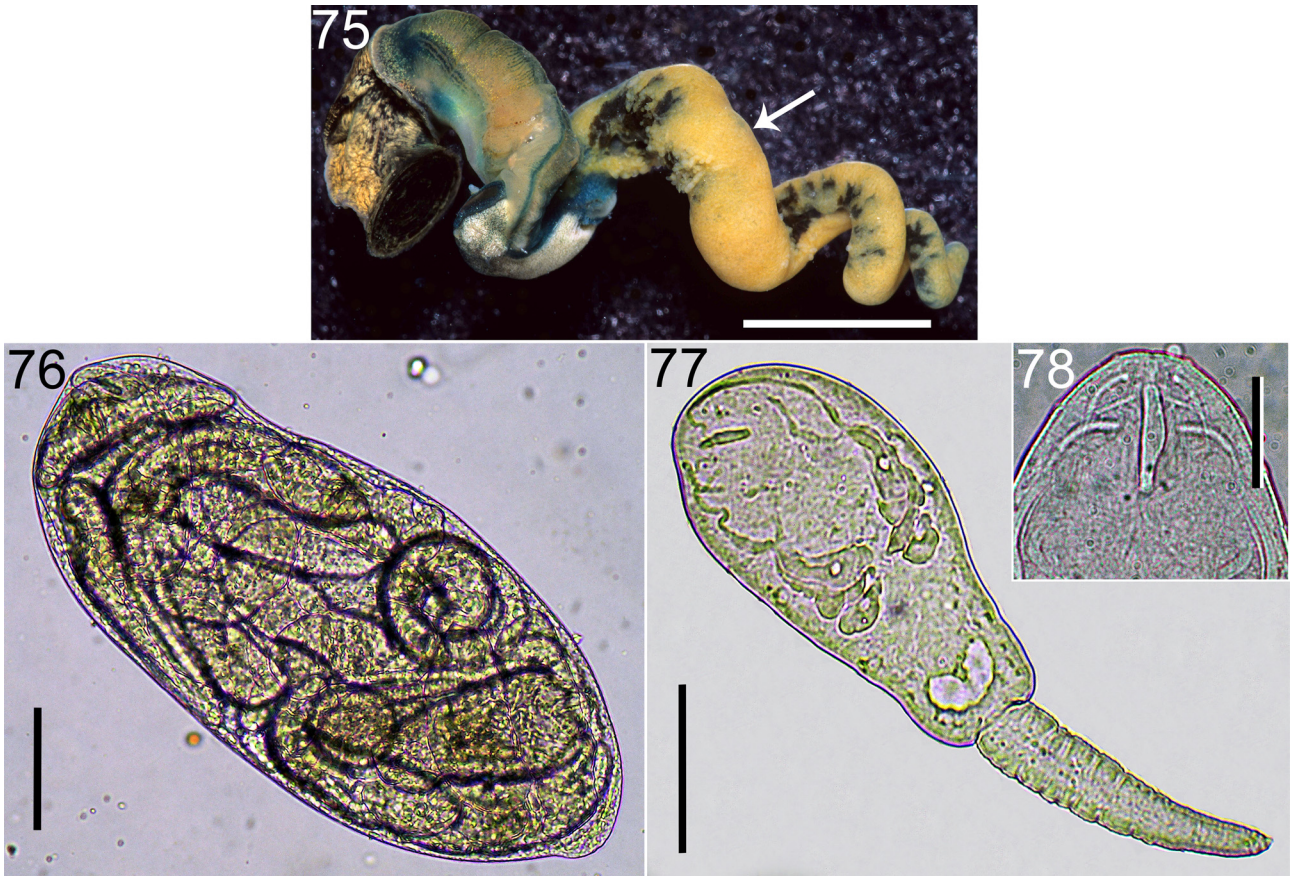
Similar species: Pruc is most readily distinguished from Smmi [19] by the difference in stylet morphology and larger body size.

Remarks: The sporocysts and cercariae have not been formally described, but Garcia-Vedrenne *et al*. (submitted) provide measurements of sporocyst size for three colonies. Sarkisian (1957) described the metacercariae from fiddler crabs (*Uca crenulata*) infected with microphallid cercariae shed from *C. californica*.

This species likely corresponds to the "Xiphidiocercaria" of Maxon and Pequegnat (1949), the "large xiphidiocercaria" of Martin (1955), and to "Microphallid 1" of Martin (1972).

Mature, ripe colonies comprise ~41% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).

Nadakal (1960b) presents information on the pigments of the sporocysts and cercariae of this species.



FIGURES 75–78. *Probolocoryphe uca* (Pruc). **75**, Overview of a colony in a freshly deshelled, infected horn snail in sea water. Arrow indicates the colony, which is localized in the gonadal region, with invasion of the digestive gland and basal visceral mass. Scale bar = 1 cm. Base photo credit: Todd Huspeni. **76**, Sporocyst, live, with developing cercariae, under coverslip pressure. Scale bar = 100 µm. **77**, Cercaria, live, under heavy coverslip pressure. Scale bar = 100 µm. **78**, Close-up of cercaria anterior end, under heavy coverslip pressure, oral stylet pressed on its side to reveal the dorsal flange. Scale bar = 25.

Small microphallid
(19. Smmi; Figs. 1, 79–81)

Diagnosis: *Parthenitae.* Colony comprised of inactive sporocysts, densely concentrated in snail gonad region. Sporocysts translucent orangish to white; ~300–750 µm long, oblong to elongate (length:width up to ~4:1).

Cercaria. Body translucent colorless; non-oculate; with oral sucker and no ventral sucker; with oral stylet (a "xiphidiocercaria"), ~12 µm long, lacking dorsal flange; with a small bi-lobed excretory bladder at posterior-most edge of cercaria body; body ~120 µm long, ~equal to subequal in length to tail; tail simple.

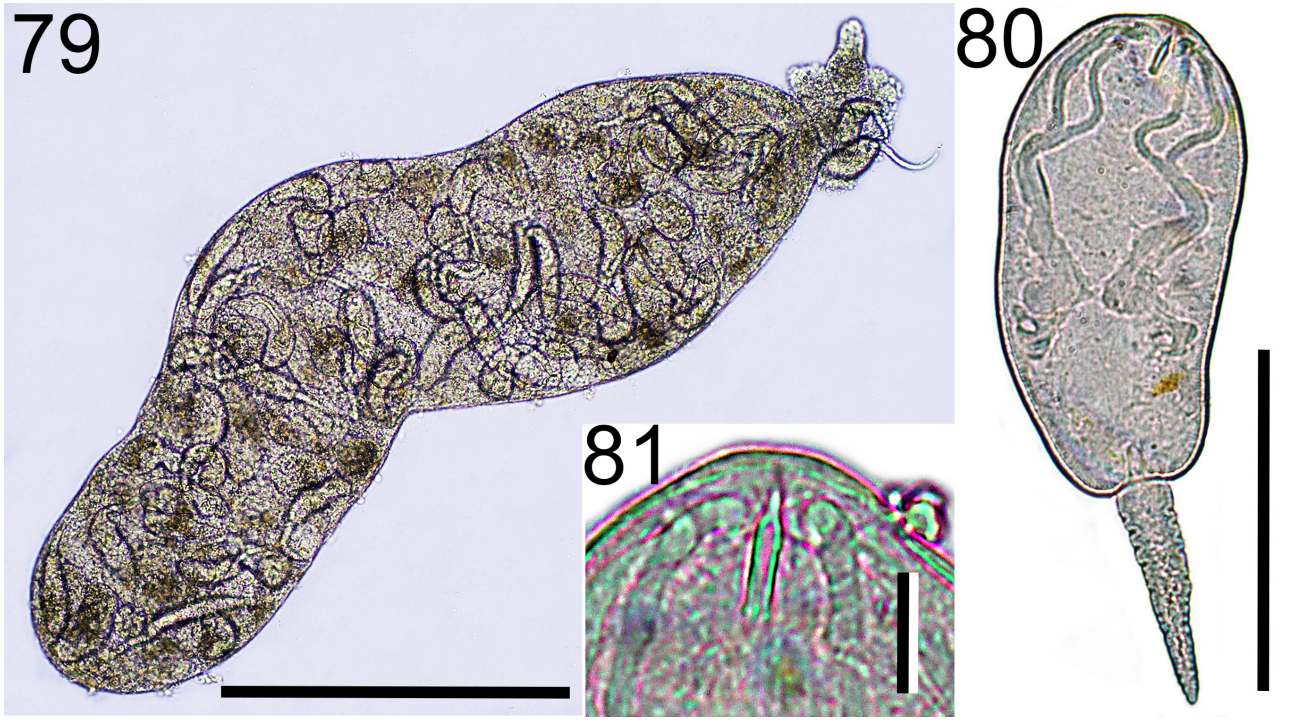
Cercaria behavior: Fresh, emerged cercariae remain in water column, swim ~continuously, lashing tail back and forth.

Similar species: Smmi is most readily distinguished from Pruc [18] by the difference in stylet morphology and smaller body size.

Remarks: The sporocysts and cercariae have not been formally described, but Garcia *et al*. (submitted) provide measurements of sporocyst size for two colonies.

This species likely corresponds to "Microphallid 2" of (Martin 1972).

Mature, ripe colonies comprise ~28% the soft-tissue weight of an infected snail (summer-time estimate derived from information in [Hechinger *et al*. 2009]).



FIGURES 79–81. Small microphallid (Smmi). **79**, Sporocyst, live, with developing cercariae, under coverslip pressure. Scale bar = 500 µm. **80**, Cercariae, live, under coverslip pressure. Scale bar = 100 µm. **81**, Close-up of cercaria anterior end, under heavy coverslip pressure, to show the oral stylet. Scale bar = 10 µm.

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References

Adams, J.E. & Martin, W.E. (1963) Life cycle of *Himasthla rhigedana* Dietz, 1909 (Trematoda: Echinostomatidae). *Transactions of the American Microscopical Society*, 82, 1–6.
https://doi.org/10.2307/3223814

Beuret, J. & Pearson, J.C. (1994) Description of a new zygocercous cercaria (Opisthorchioidea: Heterophyidae) from prosobranch gastropods collected at Heron Island (Great Barrier Reef, Australia) and a review of zygocercariae. *Systematic Parasitology*, 27, 105–125.
https://doi.org/10.1007/BF00012269

Bils, R.F. & Martin, W.E. (1966) Fine Structure and Development of the Trematode Integument. *Transactions of the American Microscopical Society*, 85, 78–88.
https://doi.org/10.2307/3224777

Bray, R.A., Gibson, D.I. & Jones, A. (2008) *Keys to the Trematoda*. CAB International and the Natural History Museum, Wallingford and New York, 824 pp.

Buck, J.C., Hechinger, R.F., Wood, A.C., Stewart, T.E., Kuris, A.M. & Lafferty, K.D. (2017) Host density increases parasite recruitment but decreases host risk in a snail-trematode system. *Ecology*, 98, 2029–2038.
https://doi.org/10.1002/ecy.1905

Deblock, S. (1966) Sur deux especes d'Echinostomes Himasthlinae (Trematodes) de Charadriiformes. Description d' *Aporchis mozambiquus* n. sp. *Memoires du Museum national dhistoire naturelle*, Serie A, Zoologie, 41, 127–134.

Dronen, N.O. & Blend, C.K. (2008) Observations on the *Parorchis acanthus* complex (Philophthalmidae : Parorchiinae) with the description of three new species of *Parorchis* Nicoll, 1907 and the replacement of the preoccupied junior homonym *Paratrema* Dronen & Badley, 1979 with *Stenomesotrema* nomen novum. *Zootaxa*, 1843 (1), 1–23.
https://doi.org/10.11646/zootaxa.1843.1.1

Fingerut, J.T., Zimmer, C.A. & Zimmer, R.K. (2003a) Larval swimming overpowers turbulent mixing and facilitates transmission of a marine parasite. *Ecology*, 84, 2502–2515.
https://doi.org/10.1890/02-4035

Fingerut, J.T., Zimmer, C.A. & Zimmer, R.K. (2003b) Patterns and processes of larval emergence in an estuarine parasite system. *Biological Bulletin*, 205, 110–120.
https://doi.org/10.2307/1543232

Galaktionov, K.V. & Dobrovolskij, A.A. (2003) *The biology and evolution of trematodes: an essay on the biology, morphology, life cycles, transmission, and evolution of digenetic trematodes*. Kluwer Academic Publishers, Dordrecht and Boston, 620 pp.

Garcia-Vedrenne, A.E., Quintana, A.C.E., DeRogatis, A.M., Dover, C.M., Lopez, M., Kuris, A.M. & Hechinger, R.F. (2017) Trematodes with a reproductive division of labour: heterophyids also have a soldier caste and early infections reveal how colonies become structured. *International Journal for Parasitology*, 47, 41–50.
https://doi.org/10.1016/j.ijpara.2016.10.003

Garcia-Vedrenne, A.E., Quintana, A.C.E., DeRogatis, A.M., Martyn, K., Kuris, A.M. & Hechinger, R.F. (2016) Social Organization in Parasitic Flatworms—Four Additional Echinostomoid Trematodes Have a Soldier Caste and One Does Not. *Journal of Parasitology*, 102, 11–20.
https://doi.org/10.1645/15-853

Gibson, D.I., Jones, A. & Bray, R.A. (2002) *Keys to the Trematoda*. CAB International and the Natural History Museum, Wallingford and New York, 521 pp.

Hechinger, R.F. (2010) Mortality affects adaptive allocation to growth and reproduction: field evidence from a guild of body snatchers. *BMC Evolutionary Biology*, 10 (136), 1–14.
https://doi.org/10.1186/1471-2148-10-136

Hechinger, R.F. & Lafferty, K.D. (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society: Biological Sciences*, 272, 1059–1066.
https://doi.org/10.1098/rspb.2005.3070

Hechinger, R.F., Lafferty, K.D., Huspeni, T.C., Brooks, A. & Kuris, A.M. (2007) Can parasites be indicators of free-living diversity? Relationships between the species richness and abundance of larval trematodes with that of local fishes and benthos. *Oecologia*, 151, 82–92.
https://doi.org/10.1007/s00442-006-0568-z

Hechinger, R.F., Lafferty, K.D. & Kuris, A.M. (2008) Diversity increases biomass production for trematode parasites in snails. *Proceedings of the Royal Society: Biological sciences*, 275, 2707–2714.
https://doi.org/10.1098/rspb.2008.0875

Hechinger, R.F., Lafferty, K.D., Mancini III, F.T., Warner, R.R. & Kuris, A.M. (2009) How large is the hand in the puppet? Ecological and evolutionary factors affecting body mass of 15 trematode parasitic castrators in their snail host. *Evolutionary Ecology*, 23, 651–667.
https://doi.org/10.1007/s10682-008-9262-4

Hechinger, R.F., Lafferty, K.D., McLaughlin, J.P., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Sandhu, P.K., Shaw, J.C., Torchin, M.E., Whitney, K.L. & Kuris, A.M. (2011a) Food webs including parasites, biomass, body sizes, and life stages, for three

California/Baja California estuaries. *Ecology*, 92, 791–791. [data paper]
https://doi.org/10.1890/10-1383.1
Hechinger, R.F. & Miura, O. (2014) Two 'new' renicolid trematodes (Trematoda: Digenea: Renicolidae) from the California horn snail, *Cerithidea californica* (Haldeman, 1840) (Gastropoda: Potamididae). *Zootaxa*, 3784 (5), 559–574.
https://doi.org/10.11646/zootaxa.3784.5.5
Hechinger, R.F., Wood, A.C. & Kuris, A.M. (2011b) Social organization in a flatworm: trematode parasites form soldier and reproductive castes. *Proceedings of the Royal Society: Biological sciences*, 278, 656–665.
https://doi.org/10.1098/rspb.2010.1753
Hunter, W.S. (1942) *Studies on cercariae of the common mud-flat snail, Cerithidea californica*. University of California, Los Angeles, 128 pp.
Huspeni, T.C. (2000) *A molecular genetic analysis of host specificity, continental geography, and recruitment dynamics of a larval trematode in a salt marsh snail*. University of California, Santa Barbara, Santa Barbara, 145 pp.
Huspeni, T.C. & Lafferty, K.D. (2004) Using larval trematodes that parasitize snails to evaluate a salt-marsh restoration project. *Ecological Applications*, 14, 795–804.
https://doi.org/10.1890/01-5346
Jones, A., Bray, R.A. & Gibson, D.I. (2005) Keys to the Trematoda. Wallingford, UK; New York, NY, USA, CAB International and the Natural History Museum, 745 pp.
Keen, A.M. (1971) *Sea shells of tropical West America marine mollusks from Baja California to Peru*. Stanford University Press, Stanford, 1064 pp.
Koprivnikar, J., Lim, D., Fu, C. & Brack, S.H.M. (2010) Effects of temperature, salinity, and pH on the survival and activity of marine cercariae. *Parasitology Research*, 106, 1167–1177.
https://doi.org/10.1007/s00436-010-1779-0
Kuris, A.M. (1990) Guild structure of larval trematodes in molluscan hosts: prevalence, dominance and significance of competition. *In:* Esch, G.W., Bush, A.O. & Aho, J.M. (Eds.) *Parasite communities: patterns and processes*. Chapman and Hall, London, pp. 69–100.
https://doi.org/10.1007/978-94-009-0837-6_4
Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A., Dobson, A.P., Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Mababa, L., Mancini, F.T., Mora, A.B., Pickering, M., Talhouk, N.L., Torchin, M.E. & Lafferty, K.D. (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature*, 454, 515–518.
https://doi.org/10.1038/nature06970
Lafferty, K.D. (1993a) Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. *Marine Ecology Progress Series*, 96, 229–237.
https://doi.org/10.3354/meps096229
Lafferty, K.D. (1993b) The marine snail, *Cerithidea californica*, matures at smaller sizes where parasitism is high. *Oikos*, 68, 3–11.
https://doi.org/10.2307/3545303
Lafferty, K.D. & Kuris, A.M. (2009) Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 364, 1659–1663.
https://doi.org/10.1098/rstb.2008.0220
Lafferty, K.D. & Morris, A.K. (1996) Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology*, 77, 1390–1397.
https://doi.org/10.2307/2265536
Lafferty, K.D., Sammond, D.T. & Kuris, A.M. (1994) Analysis of larval trematode communities. *Ecology*, 75, 2275–2285.
https://doi.org/10.2307/1940883
Lafuente, M., Roca, V. & Carbonell, E. (2000) Description of *Acanthotrema armata* n. sp. (Trematoda: Heterophyidae) from *Larus audouinii* (Aves: Laridae), with an amended diagnosis of the genus *Acanthotrema* Travassos, 1928. *Systematic Parasitology*, 45, 131–134.
https://doi.org/10.1023/A:1006293611598
LeFlore, W.B., Bass, H.S. & Martin, W.E. (1985) The life cycle of *Cloacitrema michiganensis* McIntosh, 1938 (Trematoda: Philophthalmidae). *The Journal of Parasitology*, 71, 28–32.
https://doi.org/10.2307/3281973
Martin, W.E. (1950a) *Euhaplorchis californiensis* n.g., n.sp., Heterophyidae, Trematoda, with notes on its life cycle. *Transactions of the American Microscopical Society*, 194–209.
https://doi.org/10.2307/3223410
Martin, W.E. (1950b) *Parastictodora hancocki* n. gen., n. sp. (Trematoda: Heterophyidae). with observations on its life cycle. *Journal of Parasitology*, 36, 360–370.
https://doi.org/10.2307/3273472
Martin, W.E. (1950c) *Phocitremoides ovale* n. gen., n. sp. (Trematoda: Opisthorchiidae), with observations on its life cycle. *Journal of Parasitology*, 36, 552–558.

https://doi.org/10.2307/3273288
Martin, W.E. (1951) *Pygidiopsoides spindalis* n. gen., n. sp., (Heterophyidae; Trematoda), and its second intermediate host. *Journal of Parasitology*, 37, 297–300.
https://doi.org/10.2307/3273202
Martin, W.E. (1955) Seasonal infections of the snail, *Cerithidea californica* Haldeman, with larval trematodes. *In: Essays in Natural Science in Honor of Captain Alan Hancock on the occasion of his birthday*. University of Southern California Press, Los Angeles, California, pp. 203–210.
Martin, W.E. (1956) The Life Cycle of *Catatropis johnstoni* n. sp. (Trematoda: Notocotylidae). *Transactions of the American Microscopical Society*, 75, 117–128.
https://doi.org/10.2307/3223661
Martin, W.E. (1961) Life cycle of *Mesostephanus appendiculatus* (Ciurea, 1916) Lutz, 1935 (Trematoda: Cyathocotylidae). *Pacific Science*, 15, 278–281.
Martin, W.E. (1964) Life cycle of *Pygidiopsoides spindalis* Martin, 1951 (Heterophyidae: Trematoda). *Transactions of the American Microscopical Society*, 83, 270–272.
https://doi.org/10.2307/3224579
Martin, W.E. (1971) Larval stages of renicolid trematodes. *Transactions of the American Microscopical Society*, 90, 188–194.
https://doi.org/10.2307/3225025
Martin, W.E. (1972) An annotated key to the cercariae that develop in the snail *Cerithidea californica*. *Bulletin of the Southern California Academy of Sciences*, 71, 39–43.
Martin, W.E. & Adams, J.E. (1961) Life Cycle of *Acanthoparyphium spinulosum* Johnston, 1917 (Echinostomatidae: Trematoda). *The Journal of Parasitology*, 47, 777–782.
https://doi.org/10.2307/3275470
Maxon, M.G. & Pequegnat, W.E. (1949) Cercariae from upper Newport Bay. *Journal of Entomology and Zoology*, 41, 30–55.
Miura, O., Torchin, M.E. & Bermingham, E. (2010) Molecular phylogenetics reveals differential divergence of coastal snails separated by the Isthmus of Panama. *Molecular Phylogenetics and Evolution*, 56, 40–48.
https://doi.org/10.1016/j.ympev.2010.04.012
Mordecai, E.A., Jaramillo, A.G., Ashford, J.E., Hechinger, R.F. & Lafferty, K.D. (2016) The role of competition–colonization tradeoffs and spatial heterogeneity in promoting trematode coexistence. *Ecology*, 97, 1484–1496.
https://doi.org/10.1890/15-0753.1
Nadakal, A.M. (1960a) Chemical nature of cercarial eye-spot and other tissue pigments. *Journal of Parasitology*, 46, 475–481.
https://doi.org/10.2307/3275140
Nadakal, A.M. (1960b) Types and sources of pigments in certain species of larval trematodes. *Journal of Parasitology*, 46, 777–786.
https://doi.org/10.2307/3275532
Nguyen, A.T., Kuwata, C. & Kuris, A.M. (2015) A synthetic workflow for coordinated direct observation and genetic tagging applied to a complex host-parasite interaction. *Parasitology Research*, 114, 2015–2021.
https://doi.org/10.1007/s00436-015-4437-8
Oates, J. & Fingerut, J. (2011) Internal Movement of Estuarine Digenetic Trematodes Through Their Intermediate Snail Host *Cerithidea californica*. *Journal of Parasitology*, 97, 1181–1183.
https://doi.org/10.1645/GE-2766.1
Reid, D.G. & Claremont, M. (2014) The genus *Cerithideopsis* Thiele, 1929 (Gastropoda: Potamididae) in the Indo-West Pacific region. *Zootaxa*, 3779 (1), 61–80.
https://doi.org/10.11646/zootaxa.3779.1.8
Robinson, H.W. (1952) A Preliminary Report on the Life Cycle of *Cloacitrema michiganensis* McIntosh, 1938 (Trematoda). *The Journal of Parasitology*, 38, 368–368.
https://doi.org/10.2307/3273777
Sarkisian, L.N. (1957) *Maritrema uca*, new species (Trematoda: Microphallidae), from the fiddler crab, *Uca crenulata* (Lockington). *The Wasmann Journal of Biology*, 15, 35–48.
Sousa, W.P. (1983) Host life history and the effect of parasitic castration on growth a field study of *Cerithidea californica* (Gastropoda: Prosobranchia) and its trematode parasites. *Journal of Experimental Marine Biology and Ecology*, 73, 273–296.
https://doi.org/10.1016/0022-0981(83)90051-5
Sousa, W.P. (1993) Interspecific antagonism and species coexistence in a diverse guild of larval trematode parasites. *Ecological Monographs*, 63, 103–128.
https://doi.org/10.2307/2937176
Sousa, W.P. & Gleason, M. (1989) Does parasitic infection compromise host survival under extreme environmental conditions: the case for *Cerithidea californica* (Gastropoda: Prosobranchia). *Oecologia, Berlin*, 80, 456–464.
https://doi.org/10.1007/BF00380066
Tkach, V.V., Kudlai, O. & Kostadinova, A. (2016) Molecular phylogeny and systematics of the Echinostomatoidea Looss, 1899 (Platyhelminthes: Digenea). *International Journal for Parasitology*, 46, 171–185.
https://doi.org/10.1016/j.ijpara.2015.11.001
Torchin, M.E., Miura, O. & Hechinger, R.F. (2015) Parasite species richness and intensity of interspecific interactions increase

with latitude in two wide-ranging hosts *Ecology*, 96, 3033–3042.
https://doi.org/10.1890/15-0518.1
Walker, J.C. (1979) *Austrobilharzia terrigalensis*: A schistosome dominant in interspecific interactions in the molluscan host. *International Journal for Parasitology*, 9, 137–140.
https://doi.org/10.1016/0020-7519(79)90104-8
Weinersmith, K.L., Brown, C.E., Clingen, K.B., Jacobsen, M.C., Topper, L.B. & Hechinger, R.F. (2018) *Euhaplorchis californiensis* Cercariae Exhibit Positive Phototaxis and Negative Geotaxis. *Journal of Parasitology*, 104, 329–333.
https://doi.org/10.1645/17-80
Whitney, K.L., Hechinger, R.F., Kuris, A.M. & Lafferty, K.D. (2007) Endangered species and parasites: light-footed clapper rail (*Rallus longirostris levipes*) affects parasite community structure in coastal wetlands. *Ecological Applications*, 17, 1694–1702.
https://doi.org/10.1890/06-1325.1
Yoshino, T.P. (1975) A seasonal and histologic study of larval Digenea infecting C*erithidea californica* (Gastropoda: Prosobranchia) from Goleta Slough, Santa Barbara County, California, USA. *Veliger*, 18, 156–161.
Zimmer, R.K., Fingerut, J.T. & Zimmer, C.A. (2009) Dispersal pathways, seed rains, and the dynamics of larval behavior. *Ecology*, 90, 1933–1947.
https://doi.org/10.1890/08-0786.1