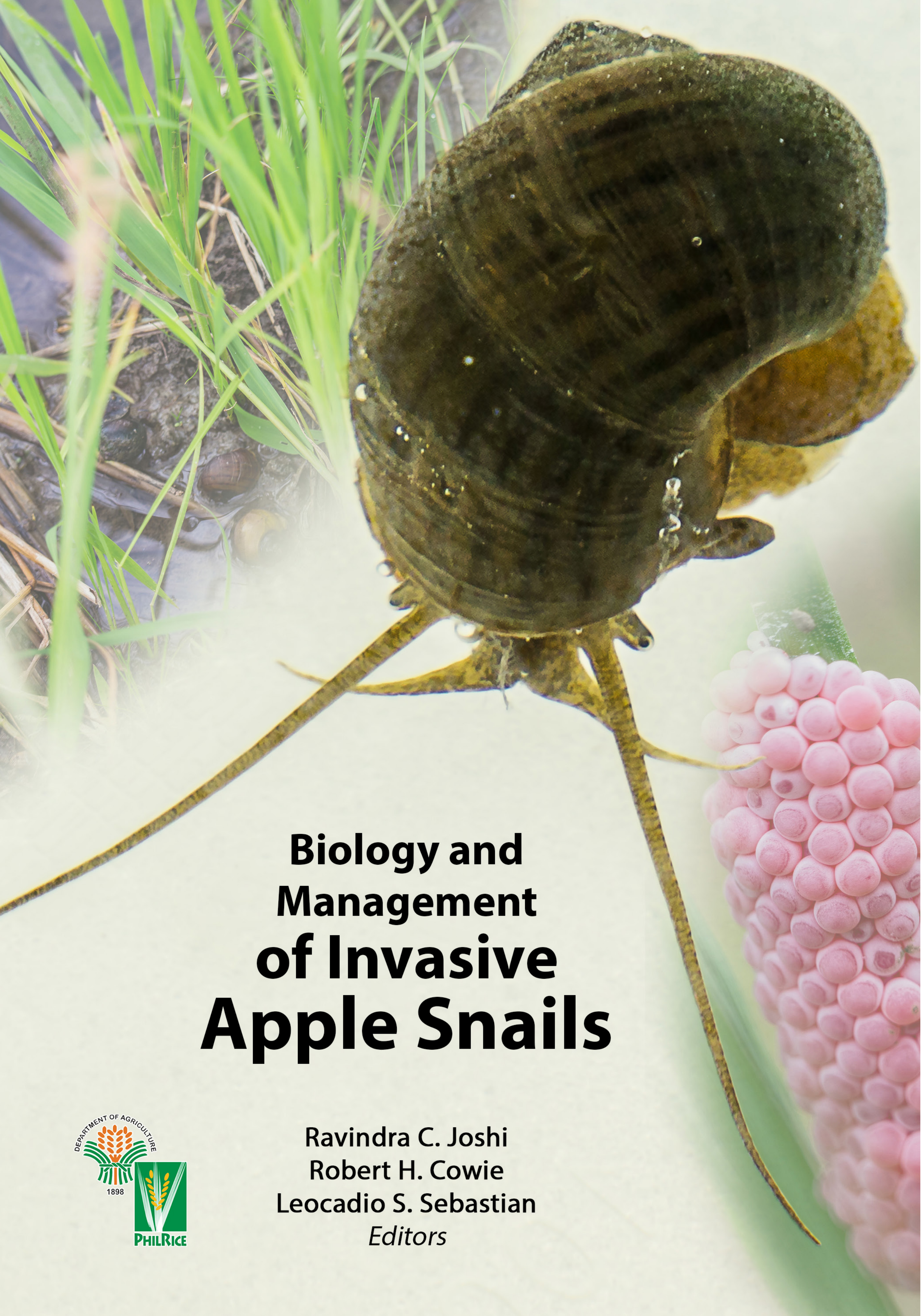

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Ravindra C. Joshi
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Symbionts and diseases associated with invasive apple snails

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Abstract

This contribution summarizes knowledge of organisms associated with apple snails, mainly *Pomacea* spp., either in a facultative or obligate manner, paying special attention to diseases transmitted via these snails to humans. A wide spectrum of epibionts on the shell and operculum of snails are discussed. Among them algae, ciliates, rotifers, nematodes, flatworms, oligochaetes, dipterans, bryozoans and leeches are facultative, benefitting from the provision of substrate, transport, access to food and protection. Among obligate symbionts, five turbellarian species of the genus *Temnocephala* are known from the branchial cavity, with *T. iheringi* the most common and abundant. The leech *Helobdella ampullariae* also spends its entire life cycle inside the branchial cavity; two copepod species and one mite are found in different sites inside the snails. Details of the nature of the relationships of these specific obligate symbionts are poorly known. Also, extensive studies of an intracellular endosymbiosis are summarized. Apple snails are the first or second hosts of several digenean species, including some bird parasites. A number of human diseases are transmitted by apple snails, angiostrongyliasis being the most important because of the potential seriousness of the disease.

Additional keywords: Ampullariidae, *Angiostrongylus*, commensals, diseases, epibionts, parasites, *Pomacea*, symbiosis

Introduction

The term “apple snail” refers to a number of species of freshwater snails belonging to the family Ampullariidae (Caenogastropoda) inhabiting tropical and subtropical regions (Hayes *et al*., 2015). Some species have invaded parts of the world to which they are not native, altering ecosystems and becoming problematic for a range of human activities.

Because of their morphology (e.g. shape and size of the shell, possession of a mantle cavity), behaviour and peculiar amphibious life habit, apple snails are a suitable habitat for species that associate and interact among themselves and with the snails, whether negatively or positively and including facultative or obligate associations (Fig. 1). Several studies have been carried out in their native ranges on the interactions of these snails with associated species. However, studies dealing with the detailed nature and significance of these relationships are few.

This contribution summarizes current knowledge of organisms associated with apple snails, mainly *Pomacea* spp., either in a facultative or obligate manner. Special attention is paid to diseases transmitted via these snails to humans.

The word symbiosis is used here as a comprehensive concept, setting aside the role played by the two species and the benefits and/or costs derived from their relationships. Symbionts can be specific, associated with one or a few host species, or generalist, associated with a wide range of species (Buckland-Nicks *et al*., 2013). Facultative symbionts (epibionts) temporarily or opportunistically associated with the host species can be easily distinguished from obligate symbionts (parasites, commensals, mutualists) that depend on their host species to live. One instance involves endocytobiosis, i.e. intracellular endosymbiosis (Vega *et al*., 2006).

Facultative symbionts (epibionts)

Epibionts are organisms associated facultatively with the surface of living substrates, in this case the shell and operculum of the snails (Fig. 1). Epibionts such as algae, ciliates and other sessile organisms settle on apple snail shells. This epibiont community could have various effects on the host, including camouflage, increased resistance to water and modification of predator attraction. Epibiosis may be advantageous for epibionts because of host behaviour (e.g. transport of epibionts to more favourable areas, facilitation of access to food, provision of permanent substrate). Other aspects of behaviour can be

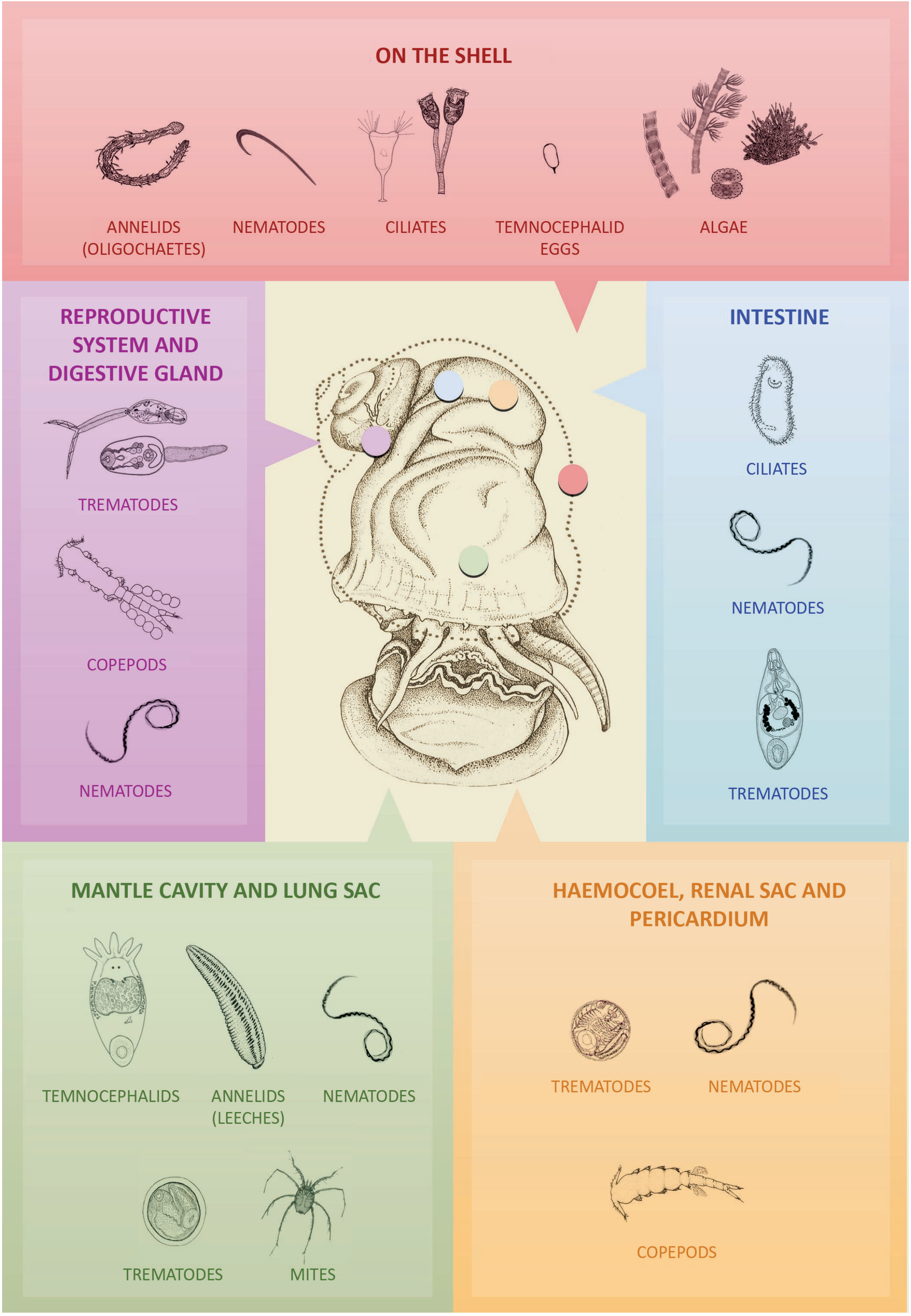

Fig. 1. The main taxonomic groups associated with various parts of the body and shell of apple snails.

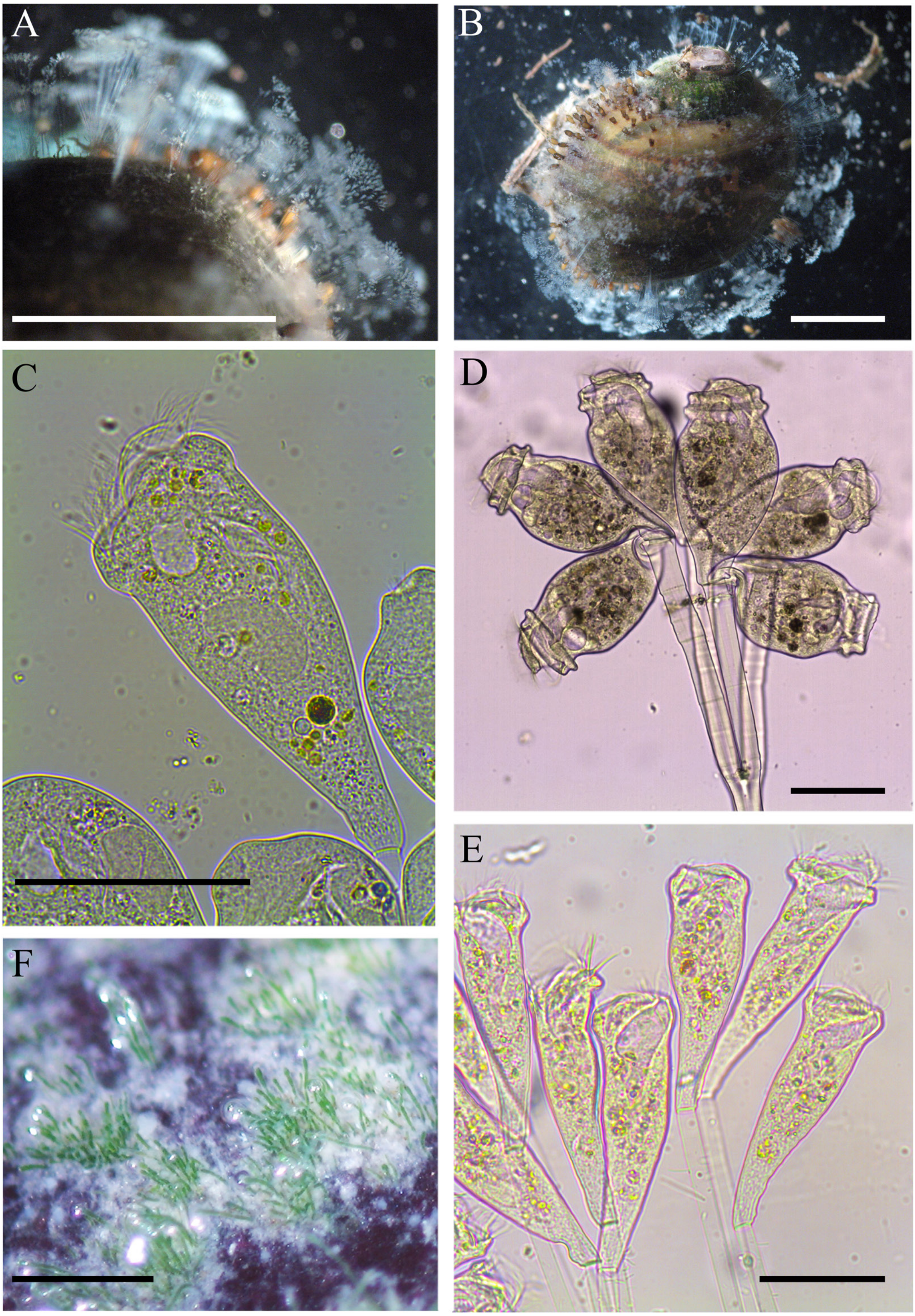

Fig. 2. Epibionts of *Pomacea canaliculata.* A, B: general view of the shell of P. *canaliculata* with ciliates and eggs of *Temnocephala iheringi*. C-E: ciliates, Peritrichida (*Epistylis* sp.). F: Chlorophyceae, Chaetophorales. Scale bars: A, B: 1 cm; C-F: 100 µm.

disadvantageous for epibionts (e.g. burial during unfavourable periods or air exposure due to amphibious habits) (Dias *et al*., 2008).

Observations in different environments in the Río de la Plata River Basin (South America) revealed that in some *Pomacea canaliculata* populations, epibionts cover the shell surface thickly and uniformly while in others the epibiont community is sparse (Fig. 2). When the population density of *P. canaliculata* is high and/or the environment is poor in food, the snails are frequently found grazing on each other's shells.

One of the earliest contributions to knowledge of the diversity of epibionts living on three native species of *Pomacea* commonly inhabiting the Río de la Plata River Basin was by Di Persia & Radici de Cura (1973), who mentioned the presence of a large suite of taxa (Table 1) including many different groups (algae, ciliates, rotifers, nematodes, flatworms, oligochaetes, dipterans, bryozoans, etc.), some of them very common and abundant, others sporadic. In Brasil, Dias *et al*. (2006, 2008, 2010) studied the ciliates adhering to the shell surface of two species of *Pomacea* and Gorni & Alves (2006) studied the oligochaetes inhabiting the umbilicus of *Pomacea bridgesii* (probably correctly identified as *P. diffusa*; R.H. Cowie, pers. comm.). Four species of leeches in the family Glossiphoniidae have been recorded in the umbilicus of *P. canaliculata* and occasionally in the mantle cavity (Damborenea & Gullo, 1996), and in the mantle cavity, foot and on the shell of *P. diffusa* (De-Carli *et al*., 2014). These species benefit from shelter and food provided by the snail during their reproductive period, but they ordinarily live free in the environment and thus form a facultative association with the apple snail.

Table 1 summarizes the main epibiont taxa mentioned as being associated with various species of *Pomacea*.

Commensal symbionts

Temnocephalids (Platyhelminthes: Temnocephalidae) are commensal symbionts frequently associated with apple snails*,* with which they form an obligate association. Five species of temnocephalids have been described in association with different species of ampullariids, i.e. *Temnocephala colombiensis*, *T. iheringi*, *T. haswelli*, *T. rochensis* and *T. lamothei* (Damborenea & Cannon, 2001; Damborenea & Brusa, 2008; Garcés *et al.*, 2013). Among these, *Temnocephala iheringi* has the widest distribution (Table 2). These temnocephalid species have a close and permanent relation with their ampullariid hosts, but no information is available regarding its functional significance. They are found in the mantle cavity and lung sac (Fig. 3), near the gill and by the opening of the lung sac, all year round. They do not live on the shell, but deposit their egg capsules on it, especially in the umbilicus and where the channelled suture meets the aperture. Temnocephalids feed on algae or small animals entering the mantle cavity in the breathing currents generated by the host snail.

There are a number of studies on populations of *Temnocephala iheringi*, especially in the Río de la Plata River Basin and southern Buenos Aires Province (Damborenea, 1996, 1998; Martín *et al*., 2005). During a study of the symbiotic species assemblages associated with *Pomacea canaliculata* in streams connected with the Río de la Plata, Damborenea *et al*. (2006) found a high prevalence of temnocephalids (80-100 % of the snails) in most sampling stations, with average abundance varying among localities, and with the maximum number of temnocephalids within a snail being 167. The distribution

Table 1. Epibionts found on *Pomacea* species.

Epibiont taxon	Host	Country	References	Location
Chlorophyta				
Stigeoclonium sp.	*P. canaliculata*	Argentina	Di Persia & Radici de Cura, 1973	shell
Oedogonium sp.	*P. maculata*			
	P. scalaris			
Chrysophyta				
Gonphonema sp.	*P. canaliculata*	Argentina	Di Persia & Radici de Cura, 1973	shell
	P. maculata			
	P. scalaris			
Cyanophyta				
Oscilatoriales	*P. canaliculata*	Argentina	Di Persia & Radici de Cura, 1973	shell
	P. maculata			
	P. scalaris			
Ciliophora - Peritrichia				
Carchesium polypinum	*P. figulina*	Brasil	Dias *et al*., 2008, 2010	shell
Carchesium sp.	*P. lineata*	Brasil	Dias *et al*., 2006	
Epistylis plicatilis	*P. figulina*	Brasil	Dias *et al*., 2008	
	P. canaliculata	Brasil	Utz, 2007	
Epistylis sp.	*P. canaliculata*	Argentina	this work	
	P. lineata	Brasil	Dias *et al*., 2006	
	P. figulina	Brasil	Dias *et al*., 2008	
Opercularia sp.	*P. figulina*	Brasil	Dias *et al*., 2008	
	P. lineata	Brasil	Dias *et al*., 2006	
Vaginicola sp.	*P. lineata*	Brasil	Dias *et al*., 2006	
Vorticella microstoma	*P. figulina*	Brasil	Dias *et al*., 2008	
Vorticella campanula	*P. figulina*	Brasil	Dias *et al*., 2008	
Vorticella sp.	*P. lineata*	Brasil	Dias *et al*., 2006	

Ciliophora - Suctoria				
Acineta sp.	*P. lineata*	Brasil	Dias *et al*., 2006	shell
Tokophrya fasciculata	*P. figulina*	Brasil	Dias *et al*., 2008	
Tokophrya sp.	*P. lineata*	Brasil	Dias *et al*., 2006	
Annelida - Oligochaeta				
Aelosoma sp. *Chaetogaster* sp.	*P. canaliculata* *P. maculata* *P. scalaris*	Argentina	Di Persia & Radici de Cura, 1973	shell
Naididae (several species)	*P. bridgesii* (probably *P. diffusa*)	Brasil	Gorni & Alves, 2006	umbilicus of the shell
Annelida - Hirudinea - Glossiphoniidae				
Gloiobdella michaelseni *Helobdella adiastola* *H. simplex* *H. triserialis lineata* *H. triserialis nigricans*	*P. canaliculata*	Argentina	Damborenea & Gullo, 1996	shell, especially in the umbilicus; sometimes inside the mantle cavity
H. triserialis	*P. canaliculata* *P. diffusa*	Brasil	De Carli *et al*., 2014	shell, mantle cavity, foot
Bryozoa				
Hyalinella vahiriae	*P. canaliculata*	Argentina	Cazzaniga, 1988	shell
Mollusca - Bivalvia				
Limnoperna fortunei	*P. canaliculata*	Brasil	Darrigran & Damborenea, 2005	shell (Fig. 5)
Nematoda				
Actinolaimus sp.	*P. canaliculata* *P. maculata* *P. scalaris*	Argentina	Di Persia & Radici de Cura, 1973	among algae growing on the shell

Fig. 5. *Pomacea canaliculata* with *Limnoperna fortunei* attached to the umbilicus. Scale bar: 2 cm. (Photos: Gustavo Darrigran)

Table 2. Symbiont species (commensals and parasites) associated with *Pomacea canaliculata* and other ampullariid species.

Symbiont taxon	Host	Country	References	Location	Type of relationship
Ciliophora - Heterotrichea					
Plagiotoma kempi	*Pila globosa*	India	Bathia, 1936	rectum	parasites or commensals?
Parasicuophora ampullarium	*Pomacea canaliculata*	Uruguay	Gascón, 1975	digestive tract	
Parasicuophora corderoi	*Pomacea canaliculata*	Uruguay	Gascón, 1975	digestive tract	
Platyhelminthes – "Turbelaria" -Temnocephalidae					
Temnocephala colombiensis	*Pomacea* sp.	Colombia	Garcés *et al.*, 2013		
Temnocephala haswelli	*P. canaliculata*	Uruguay	Ponce de León, 1989	youngs and adults in the mantle cavity; egg capsules deposited on the shell	commensals
		Brasil	Seixas *et al*., 2010a		
Temnocephala iheringi	*P. canaliculata*	Argentina	Di Persia & Radici de Cura, 1973; Damborenea, 1992, 1996; Martin *et al*., 2005		
		Brasil	Seixas *et al*., 2010b		
		Uruguay	Dioni, 1967; Ponce de León, 1979		
	Pomacea lineata	Brasil	Pereira & Cocuolo, 1941		
	Asolene platae	Argentina	Hyman, 1955		
	Pomella megastoma	Argentina	Damborenea *et al*., 1997		
Temnocephala lamothei	*Pomella megastoma*	Argentina	Damborenea & Brusa, 2008		
Temnocephala rochensis	*Pomacea canaliculata*	Uruguay	Ponce de León, 1979		
		Brasil	Seixas *et al*., 2010c		
Platyhelminthes - Digenea - cercariae					
Xiphidiocercariae					
Cercaria unidentified (1 species)	*Pomacea canaliculata*	Argentina	Ostrowski de Nuñez, 1979		parasites
Xiphidiocercariae unidentified	*Pomacea canaliculata*	Argentina	Damborenea *et al*., 2006	digestive gland	
Cercariae unidentified (2 species)	*Pomacea crassa*	Venezuela	Uribe, 1925	liver	
Cercariae unidentified (5 species)	*Pomacea glauca*	Venezuela	Nasir, 1965; Nasir & Díaz, 1968a, 1973; Nasir *et al*., 1969		
Cercaria unidentified (1 species)	*Pomacea urceus*	Venezuela	Nasir, 1971		
Cercariae unidentified (5 species)	*Marisa cornuarietis*	Venezuela	Nasir, 1965, 1971; Nasir & Díaz, 1968a		
Stomylotrema gratiosus	*Pomacea maculata*	Brasil	Pinto *et al*., 2015		
Metacercariae					
Echinostoma parcespinosum	*Pomacea canaliculata*	Argentina	Martoreli, 1987; Damborenea *et al*., 2006	mantle cavity	parasites
	Pomacea lineata	Brasil	Machado & Sampaio, 1980		
Dietziella egregia	*Pomacea canaliculata*	Argentina	Digiani & Ostrowski de Nuñez, unpublished; Damborenea *et al*., 2006	renal cavity	
Edietziana malacophilum	*Pomacea paludosa*	Cuba	Pérez Vigueras, 1944		
Echinochasmus zubedakhaname	*Pomacea glauca*	Venezuela	Nasir & Díaz, 1968b		
Stephanoprora heteroglandula	*Pomacea glauca*	Venezuela	Nasir *et al*., 1969		
Echinostoma ilocanum	*Pila luzonica*	Philippines, Cambodia	Sohn *et al*., 2011		
Echinostomatidae unidentified	*Pomacea canaliculata*	Thailand	Keawjam *et al*., 1993	foot	
Cercaria unidentified (1 species)	*Pomacea glauca*	Venezuela	Nasir *et al*., 1969		

Furcocercariae					
Cercaria unidentified (1 species)	*Pomacea canaliculata*	Argentina	Ostrowski de Nuñez, 1978		parasites
Furcocercariae unidentified	*Pomacea canaliculata*	Argentina	Damborenea *et al*., 2006	digestive gland	
Cercaria unidentified (1 species)	*Pomacea glauca*	Venezuela	Nasir *et al*., 1969		
Gymnocephala					
Guaicaipuria pseudoconcilia	*Pomacea glauca*	Venezuela	Nasir *et al*., 1969		parasites
Guaicaipuria parapseudoconcilia	*Pomacea glauca*	Venezuela	Nasir & Silva, 1972		
Cercariae unidentified (5 species)	*Pomacea glauca*	Venezuela	Nasir, 1971; Nasir & Acuña, unpublished; Nasir & Díaz, 1968a, 1973		
Amphistoma					
Amphistoma unidentified	*Pomacea canaliculata*	Thailand	Keawjam *et al*., 1993	foot	parasites
Distomes					
Distomes unidentified	*Pomacea canaliculata*	Thailand	Keawjam *et al*., 1993	heart, kidney and foot muscle	parasites
Macrocerca					
Cercariae unidentified (2 species)	*Pomacea glauca*	Venezuela	Nasir *et al*., 1969	intestine	parasites
Platyhelminthes - Digenea - Paramphistomatidae - adults					
Catadiscus pomaceae	*Pomacea canaliculata*	Argentina	Hamann, 1992	adults in intestine	parasites
Annelida - Hirudinea - Glossiphoniidae					
Helobdella ampullariae	*Pomacea canaliculata*	Argentina	Di Persia & Radici de Cura, 1973; Ringuelet, 1985; Damborenea & Gullo, 1996	young and adults in mantle cavity	commensals or parasites?
	Pomacea maculata	Argentina	Ringuelet, 1949, 1985		
	Pomella megastoma	Argentina	Ringuelet, 1945, 1985		
Maxillipeda - Cyclopoida - Ozmanidae					
Ozmana huarpium	*Pomacea canaliculata*	Argentina	Gammarra *et al*., 2004	in penis sheath, ctenidium and mantle cavity	commensals
Ozmana haemophila	*Pomacea maculata*	Brasil	Ho & Thatcher, 1989	haemocel	
Acari - Hydrachnidia - Unionicolidae					
Unionicola (*Ampullariatax*) *ampullariae*	*Pomacea canaliculata*	Argentina	Di Persia & Radici de Cura, 1973	larvae, nymphs and adults in mantle cavity	commensals
	Pomacea maculata	Argentina	Di Persia & Radici de Cura, 1973		
		Brasil	Rosso de Ferradás & Fernández, 2005		
Nematoda - Secernentea - Metastrongylidae					
Angiostrongylus cantonensis	*Pomacea canaliculata*	China	Lv *et al*., 2009	youngs in "lung"	parasites
	Pomacea paludosa	Cuba	Aguiar *et al*., 1981		
		Hawaii	Briceño Lobo, 1986		
			Wallace & Rosen, 1969a	experimental infestation	
	Pila ampulacea	Thailand	Panyagupta, 1965; Woodruff & Upatham, 1993		
	Pila gracilis	Thailand	Harinasuta *et al*., 1965; Woodruff & Upatham, 1993		
	Pila scutata	Malaysia	Lim *et al*., 1965		
	Pila virescens	Thailand	Harinasuta *et al*., 1965		
Angiostrongylus costaricensis	*Pomacea flagellata*	Costa Rica	Briceño-Lobo, 1986	young in viscerae, foot and mantle; experimental infestation	parasites

Nematoda - Secernentea - Gnathostomatidae					
Gnathostoma spinigerum	*Pomacea canaliculata*	Thailand	Komalamisra, 2009	young (L3) in viscerae and mantle; experimental infestation	parasites
	Pila ampullacea	Thailand	Komalamisra, 2009	foot and viscerae	
Nematoda					
Unidentified	*Pomacea canaliculata*	Argentina	Damborenea *et al*., 2006	larvae in mantle cavity	parasites?

of temnocephalids in the host snail did not differ between host sexes. There is an increase in abundance whenever temperature rises and the snails become more active. The life cycle of the host and the commensal temnocephalids are synchronized in order to enhance reproduction and colonization of new hosts.

Martín *et al*. (2005) studied the factors affecting the distribution and abundance of *T. iheringi* among populations of *P. canaliculata* in southern Buenos Aires Province (Argentina), which is the southern boundary of the snail's native range. They found that only 23 % of the apple snail populations inhabiting streams harboured temnocephalids, but higher frequencies (71 %) were observed in lentic localities. The commensals were found in localities with bicarbonate concentrations below 6.6 meq l^{-1} and could tolerate low water temperatures (4-5 ºC in winter).

In addition to the aforementioned epibiont hirudinean species, there is an additional species, *Helobdella ampullariae* (Fig. 3), that inhabits the mantle cavity of ampullariid snails, establishing an obligatory association (Ringuelet, 1945, 1949; Di Persia & Radici de Cura, 1973). A seventeen-month study of a population of apple snails from Bagliardi Beach, Buenos Aires, Argentina (Damborenea & Gullo, 1996) showed that *H. ampullariae* is associated with the host all year round and completes its life-cycle entirely in this association. Juveniles, adults, adults with cocoons and brooding adults are found inside the mantle cavity of the snails. The reproductive period of the leech is long (December to June), beyond the season in which their hosts are buried. Ringuelet (1945) considered this species as a parasite feeding on the snail, but in fact there is no knowledge of the feeding habits of the leeches.

Two species of copepods are known as symbionts of ampullariids, i.e. *Ozmana haemophila* in the haemocoel of *Pomacea maculata* in the Amazon basin, Brasil (Ho & Thatcher, 1989), and *Ozmana huarpium* in the haemocoel, mantle cavity, ctenidium and penis-sheath groove of *P. canaliculata* in Palermo Park, Buenos Aires city, Argentina, where prevalence of the symbiont is 100 % in both sexes (Gamarra-Luques *et al*., 2004).

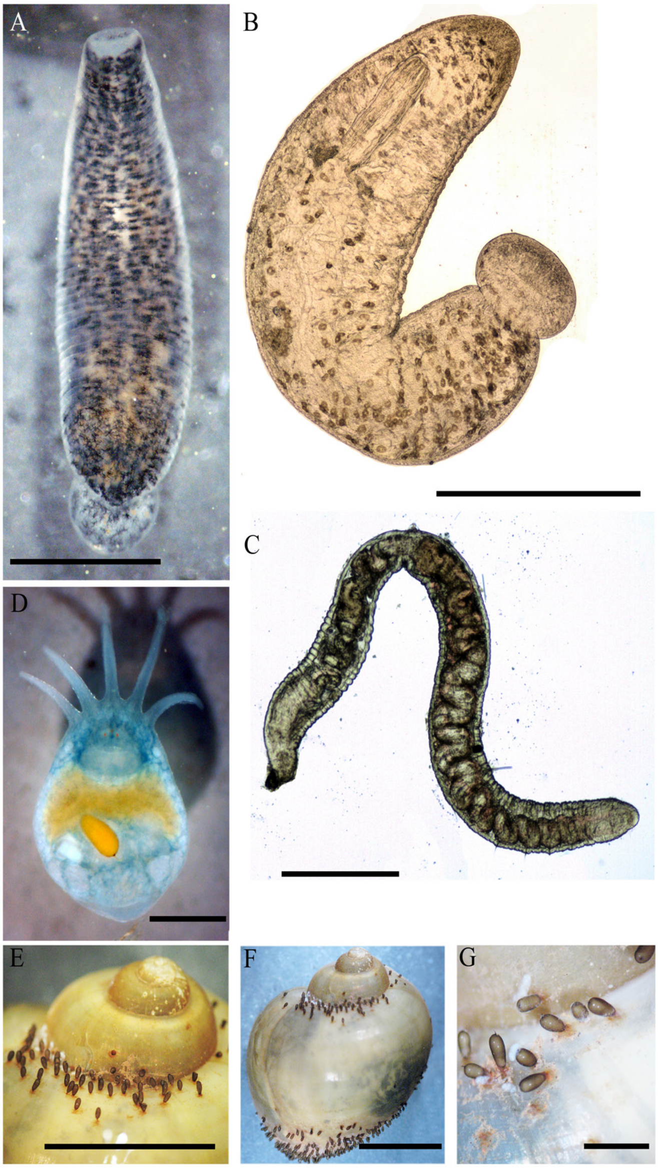

Fig. 3. Commensals of the mantle cavity of *Pomacea canaliculata*. A: general view of *Helobdella ampullariae*. B: detail of *H. ampullariae* under optical microscope. C: Oligochaeta. D: *Temnocephala iheringi*. E-G: eggs of *T. iheringi*. Scale bars, A, B: 2 mm; C, G: 1 mm; D: 500 µm; E: 6 mm, F: 10 mm.

Gamarra-Luques *et al*. (2004) made numerous biological observations on *O. huarpium*, including showing in experiments that it is transmitted to parasite-free hosts during copulation.

A species of unionicolid mite, *Unionicola* (*Ampullariatax*) *ampullariae*, also lives in the mantle cavity of *Pomacea canaliculata* and *P. maculata* (Di Persia & Radici de Cura, 1973; Rosso de Ferradás & Fernández, 2005), *P. maculata* now being the senior synonym of *P. insularum*, which was the name used by these authors (see Hayes *et al*., 2012). Di Persia & Radici de Cura (1973) recorded larvae, nymphs and adults in the mantle cavity and under the mantle of the snails.

Epithelium cells of the midgut gland of some species of ampullariids carry two kinds of pigmented endosymbiont prokaryote corpuscles belonging to the same organism (Castro-Vazquez *et al*., 2002; Koch *et al*., 2006). Corpuscles are also found in faeces and sediment, indicating a life-cycle alternating endosymbiotic and free phases. These endosymbionts have been extensively studied in *P. canaliculata,* although they have also been found in other species, including *P. maculata*, *P. scalaris*, *Asolene pulchella* and *Marisa cornuarientis* (no faeces were found in the latter) (Vega *et al*., 2006). Bacterial

DNA attributed to 16S rRNA demonstrated a close relationship of the corpuscles with representatives of the orders Chroococcales or Pleurocapsales (Cyanobacteria) (Vega *et al*., 2005, 2006). Koch *et al*. (2003) demonstrated that transmission was vertical from mother to offspring.

Godoy *et al*. (2013) identified proteases in the digestive system of *P. canaliculata*. Protease 30kDa was found in the mid-gut and in the endosymbiotic corpuscles, where activity was detected. Endosymbionts are liberated into the stomach vestibule via the ducts of the mid-gut gland. This suggests protease secretion is a possible function, in addition to detoxification, as suggested by the accumulation of various metals in the corpuscles, which are later liberated in the faeces (Vega *et al*., 2012).

Parasitic symbionts

Three species of heterotrichid ciliates have been found in the digestive system of apple snails, i.e. *Parasicuophora ampullariarum* and *P. corderoi* both inhabiting the gut of *Pomacea canaliculata* from Uruguay (Gascón, 1975), and *Plagiotoma kempi* in the rectum of *Pila globosa* from India (Zeliff, 1933). These observations did not establish the nature of the relationship.

Several trematode larvae have been noted associated with apple snails (Fig. 4), but adults of only one species were found in them, i.e. *Catadiscus pomaceae* (Paramphistomidae) in the intestine of *Pomacea canaliculata* (Hamann, 1992). The life cycle of this species remains unknown. Probably, *P. canaliculata* may become

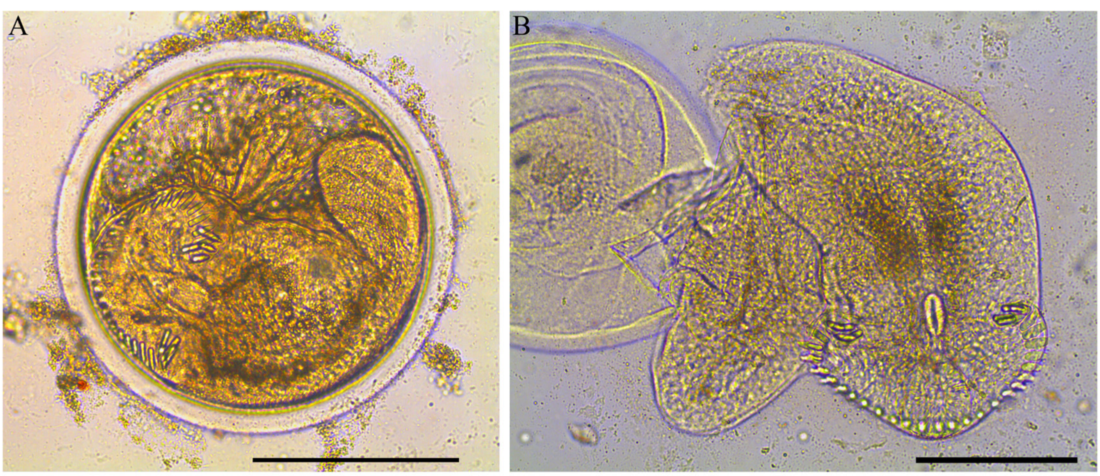

Fig. 4. Microphotographs of metacercariae found in the mantle cavity of *Pomacea canaliculata*. A: encysted metacercariae. B: metacercariae extracted from cyst. Scale bars: 200 μm.

infected by ingesting metacercariae encysted in plants and other substrata, as for other Paramphistomidae (Vega *et al*., 2006).

A large number of trematode larvae have been mentioned associated with apple snails (Table 2). Two redia generations of *Echinostoma parcespinosum* have been found in the digestive gland and gonad of *P. canaliculata* and encysted metacercariae were observed in the mantle cavity and hepatopancreas (Martorelli, 1987). The definitive hosts of this parasite are rails (in the birds' intestines). The apple snail, which is the first intermediate host, can also be the second intermediate host (among other freshwater snails). In the latter case, the life cycle of *E. parcespinosum* may be shortened without the need for another host, as cercariae have been recorded encysted within rediae (Martorelli, 1987). This peculiarity was also observed in Brasil in *Pomacea lineata* (Machado & Sampaio, 1980). Metacercariae of *Dietziella egregia* have been observed in the renal cavity of *P. canaliculata* from Argentina (M.C. Digiani & M. Ostrowski de Núñez, unpublished). Although the life cycle of this digenean is not fully known, the white-faced ibis (*Plegadis chihi*) could be the definitive host. Encysted metacercariae of *Edietziana malacophilum*, an intestinal parasite of the snail kite, *Rostrhamus sociabilis*, have been found in the hepatopancreas of *Pomacea paludosa* in Cuba (Pérez Vigueras, 1944). Other metacercariae were found in *Pomacea canaliculata* (Keawjam *et al*., 1993) in Southeast Asia (Table 2). Nasir & Díaz (1968a, b) described new species of Echinostomatidae in *Pomacea glauca*, i.e. *Echinochasmus zubedakhaname* (parasitizing a small passerine bird, *Fluvinicola pica*) and *Stephanoprora heteroglandula*. The snail also carried many cercariae of different morphological types (Table 2).

Diseases associated with apple snails

Dermatitis

Schistosome dermatitis occurs when a person becomes the accidental host of cercariae of non-human schistosome trematodes. The cercariae penetrate the skin where they soon die, causing a hypersensitive reaction of the skin (Hoeffler, 1974). Leedom & Short (1981) reported dermatitis caused by furcocercous cercariae from *Pomacea paludosa* in Florida (United States).

Echinostomiasis

This is a disease caused by infections by flukes of the family Echinostomatidae (echinostomes) via oral intake of undercooked infected snails and clams. Twenty species belonging to eight genera of this family are known to infect humans worldwide (Chai, 2009). The main clinical symptoms involve diarrhoea, abdominal pain, anaemia and eosinophilia (Mehlhorn, 2008). In cases with heavy loads of echinostomes mortality is caused by intestinal perforation or marked malnutrition and anaemia. *Echinostoma ilocanum* was discovered in the Philippines at the beginning of the twentieth century. Bonne *et al*. (1953) found it infecting humans in Malaysia, with *Pila scutata* as one of the first intermediate hosts, among other snails. Human infections with *E. ilocanum* were later reported in Indonesia, China, Thailand, India and Cambodia. The main cause of these infections was the consumption of raw or undercooked flesh of *Pila scutata* (Sohn *et al*., 2011). [Note that the name *Pila luzonica* as used by Sohn *et al*. (2011) is now considered a junior synonym of *Pila conica*, and *Pila conica* as used by Bonne *et al*. (1953) is considered a junior synonym of *Pila scutata*; see Cowie (2015)].

Gnathostomiasis

This is an unusual human infection by larvae of the nematode *Gnathostoma spinigerum*, a parasite of felines and canids. It is acquired by eating raw or undercooked flesh of infected intermediate hosts (fish, amphibians, reptiles, birds). The larvae in the intermediate hosts enter human tissue and may migrate through many tissues causing intermittent subcutaneous swellings and (often) intestinal nodules, and an inflammatory reaction associated with production of many eosinophils. The larvae are especially destructive when they die in the brain or eye. *Pomacea canaliculata* and *Pila ampullacea* are suitable paratenic hosts for third stage larvae of *G. spinigerum* (Komalamisra *et al*., 2009).

Angiostrongyliasis

Angiostrongyliasis is caused by two species of nematodes of the genus *Angiostrongylus* (Secernentea, Metastrongyloidea). *Angiostrongylus cantonensis* causes eosinophilic meningitis and meningoencephalitis, and the disease is sometimes referred to as neuroangiostrongyliasis, while *A. costaricensis* causes abdominal angiostrongyliasis, a gastrointestinal syndrome (Mehlhorn, 2008; Murphy & Johnson, 2013).

Angiostrongylus cantonensis was discovered by Chen (1935) in the pulmonary arteries and hearts of domestic rats in China, and therefore became known as the rat lungworm. It is endemic in South Asia, the Pacific islands, Australia and the Caribbean islands. Its life cycle involves rats as definitive hosts, snails and slugs as intermediate hosts, and various other animals, including crustaceans (prawns and land crabs), land planarians, frogs and monitor lizards, as paratenic (transfer or transport) hosts (Cowie, 2013b). Humans acquire *A. cantonensis* by eating raw or undercooked intermediate or paratenic hosts that contain the infective third larval stage of the worm, or inadvertently by eating vegetables contaminated with infected snails. When infective larvae are ingested, they penetrate the intestinal wall and reach the circulatory system, and finally reach the brain where the third stage larvae develop to a sub-adult stage. These worms are not able to leave the brain and they generally die. The immune reaction causes inflammation, and the meninges and cerebral vessels are infiltrated with lymphocytes, plasma cells and eosinophils (Wang *et al*., 2008). Also, physical brain lesions, and even in the spinal cord, are caused especially by the movements of live worms (Chotmongkol & Sawanyawisuth, 2002; Cowie, 2013a). The larvae can also move to the eyes and cause ocular angiostrongyliasis, resulting in visual disturbance (Sawanyawisuth *et al*., 2006).

The first human case of angiostrongyliasis was reported in Taiwan in 1945 (Beaver & Rosen, 1964). Since then, several outbreaks of the disease have been reported in the Pacific islands and other endemic regions. In Taiwan many cases of angiostrongyliasis have been reported, mainly in children, with *Achatina fulica* and *Pomacea canaliculata* the most frequent intermediate hosts (Tseng *et al*., 2011). *Angiostrongylus cantonensis* has been reported from 13 provinces in China, where the spread of the invasive species *P. canaliculata* would facilitate expansion of the disease (Lv *et al.*, 2011). Unfortunately, *P. canaliculata* is very susceptible to *A. cantonensis* and has become an important intermediate host in these regions (Wang *et al*., 2008).

Several *Pila* spp. (*P. scutata*, *P. gracilis*, *P. virescens* and *P. ampullacea*) have been found infected with *A. cantonensis* in Malaysia and Thailand (Harinasuta *et al*., 1965). These species are used as a food resource and thus could cause human infection. *Pomacea paludosa* infected by *A. cantonensis* was found in Cuba (Aguiar *et al*., 1981). *Pomacea paludosa* was also reported to be infected in the Hawaiian Islands (Wallace & Rosen, 1969a, b) but this may have been a misidentification as this species is not known to have ever been present in the wild in the Hawaiian Islands (Cowie *et al*., 2007). However, other non-native apple snails are present in Hawaii and are used for human consumption and as aquarium pets (Cowie *et al*., 2007), and *Pomacea canaliculata* is reported to be infected (Kim *et al*., 2014). *Angiostrongylus cantonensis* has recently been found in *Pomacea maculata* introduced in the southeastern United States (Louisiana). This introduced snail is currently spreading rapidly across this region, triggering concerns about establishment of the parasite (Teem *et al*., 2013).

The first cases of human infection by *Angiostrongylus costaricensis* were diagnosed mainly in children. They are characterized by the formation of granulomas with heavy eosinophilic infiltration in the abdominal cavity (Morera & Céspedes, 1971). Rodents are the final hosts. The larvae leave the intestine in the faeces. Intermediate hosts (slugs or snails) feed on these larvae, which develop into the infectious third stage larvae. Humans are accidentally infected when in contact with the molluscs. The adult worms are localized in the mesenteric arteries of the definitive host, where inflammatory reactions are common. Many of the arterioles containing adults become thrombosed after the worms die, causing intestinal obstruction (Mehlhorn, 2008). Abdominal angiostrongyliasis has been recorded from the southern United States to northern Argentina. Up to 500 human cases are reported annually in Costa Rica. In Brasil, cases have been reported mainly in the southern states (Thiengo *et al*., 2013).

The main intermediate hosts of *A. costaricensis* are slugs. However, apple snails are potential hosts. *Pomacea flagellata* was introduced to Costa Rica for human consumption and has been successfully infected experimentally (Briceño Lobo, 1986).

Salmonellosis

Various outbreaks of food-borne illnesses such as salmonellosis have been associated with snail consumption. Salmonellosis is a disease caused by the bacterium *Salmonella*. Most people have diarrhoea, fever and stomach pains. Consumption of apple snails, known locally as *kuhol*, as a fish and meat substitute has become popular in the Philippines. The main concern about this culinary culture is undercooking the snails. *Salmonella* serotype *typhimurium* populations survive at 60 °C, while the sharpest drop in the counts of these bacteria is observed at 90 °C (Gabriel & Ubana, 2007).

Bartlett & Trust (1976) isolated different serotypes of *Salmonella* and other potential pathogens in apple snails from aquaria in North America. Their study revealed a formerly unreported zoonotic reservoir of salmonellae. There is a reason to believe that this association of salmonellae with apple snails could explain some cases of human salmonellosis, as other aquarium species have already been shown to contribute towards many cases of this infectious disease (Bartlett & Trust, 1976).

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