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INSIGHTS FROM AN INTEGRATED VIEW OF THE BIOLOGY OF APPLE SNAILS

(CAENOGASTROPODA: AMPULLARIIDAE)

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ABSTRACT

Apple snails (Ampullariidae) are among the largest and most ecologically important fresh-
water snails. The introduction of multiple species has reinvigorated the field and spurred a burgeoning body of research since the early 1990s, particularly regarding two species intro-
duced to Asian wetlands and elsewhere, where they have become serious agricultural pests. This review places these recent advances in the context of previous work, across diverse fields ranging from phylogenetics and biogeography through ecology and developmental biology, and the more applied areas of environmental health and human disease. The review does not deal with the role of ampullariids as pests, nor their control and management, as this has been substantially reviewed elsewhere. Despite this large and diverse body of research, significant gaps in knowledge of these important snails remain, particularly in a comparative framework. The great majority of the work to date concerns a single species, Pomacea canaliculata, which we see as having the potential to become a model organism in a wide range of fields. How-ever, additional comparative data are essential for understanding this diverse and potentially informative group. With the rapid advances in genomic technologies, many questions, seem-ingly intractable two decades ago, can be addressed, and ampullariids will provide valuable
insights to our understanding across diverse fields in integrative biology.
Key words: behavior, benthic macroinvertebrates, development, dormancy, ecology, evolu-
tion, freshwater, Gastropoda, immune system, invasive species, parasitology, reproduction, symbiosis.

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INTRODUCTION

Apple snails (Ampullariidae) are freshwater and amphibious snails predominantly distrib-uted throughout the humid tropics and subtrop-ics of Africa, the Americas and Asia (Berthold, 1991), where they often constitute a major por-tion of the native freshwater molluscan fauna (Fig. 1). They are commonly referred to as apple snails because oftheir large, round shells and include the largest of all freshwater snails. The family belongs to the Caenogastropoda, a large and diverse clade containing roughly 60% of living Gastropoda (Ponder et al., 2008). Increasing interest in apple snail research has been driven in part by the introduction of several species as aquarium pets or food to many locations around the world, where they frequently have become major agricultural and

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FIG. 1. Known (shaded grey) and probable (hashed) native distributions of Asolene (A), Fe-lipponea (В), Marisa (С), Pomacea (D), Lanistes and Pila in Africa (E), and Pila in Asia (Е). Afropomus and Lanistes are restricted to western Africa in Sierra Leone and Liberia, and the genus Forbesopomus is known only from a single location in the Philippines. Known distribu-
tions of New World taxa determined from literature and historical and recent collection data. Probable distributions estimated based on habitat suitability. Distributions for Lanistes and
Pila based primarily on historical and recent collections.

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environmental pests (Cowie, 2002; Joshi & Sebastian, 2006; Cowie & Hayes, 2012). This interest has been further fueled by questions surrounding the origin of several novel ana-
tomical and behavioral characteristics, some associated with the transition from aquatic to terrestrial habitats (Hayes et al., 2009a). Addressing these questions in an integrative framework may provide insights fundamental to understanding the evolutionary biology of snails and freshwater taxa more generally (Hayes et al., 2009a), and has the potential to elevate apple snails to a valuable model system. Cowie (2002) reviewed what was then known of apple snail biology, focusing on their ecology and behavior, impacts as pests and approaches to managing them. At the time of that review, the true identity ofthe pest species was not well understood, but this has since been clarified (Rawlings et al., 2007; Hayes et al., 2008, 2012; Tran et al., 2008). Since then, there has been a burgeoning of studies, primarily by South American, Asian and North American authors, focused mainly on the pest species Pomacea canaliculata (Lamarck, 1822) and Pomacea maculata Perry, 1810. The present review provides an update and extension of Cowie (2002) and focuses on studies on fundamental biology and applied topics in human health and ecotoxicology undertaken in the interven-ing years, as well as on topics not covered in that review, but excluding pest management, which has been covered extensively by Joshi & Sebastian (2006).
Much of the review focuses inevitably on species of Pomacea, most notably Pomacea canaliculata. However, various species of Pila are also frequently mentioned. To avoid con-fusion, we only abbreviate Pomacea to “Р.”

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always spelling out Pila in full.

CLASSIFICATION, DIVERSITY AND TAXONOMY

Classification

Ampullariids are basal members of the Caenogastropoda. The family Ampullariidae Gray, 1824 (junior synonym: Pilidae — Cowie, 1997; ICZN, 1999), is in the superfamily Ampul-larioidea within the informal group Architaenio-glossa, which also includes the Cyclophoroidea and Viviparoidea (Bouchet & Rocroi, 2005). The Architaenioglossa has been resolved as paraphyletic in higher-order analyses using

both molecular and morphological data (e.g., Harasewych et al., 1998; Colgan et al., 2003, 2007; Ponder et al., 2008). The Campaniloidea also may be closely related. Although marine ancestry of the architaenioglossan taxa is as-sumed by most, relationships among the four superfamilies and the resolution of the base of the Caenogastropoda remain unresolved (Pon-der & Lindberg, 1997; McArthur & Harasewych, 2003; Strong, 2003; Simone, 2004; Colgan et al., 2003, 2007; Jorgensen et al., 2008; Ponder et al., 2008; Hayes et al., 2009b).

Diversity and Taxonomy

There are ten genera with approximately 120 species currently considered valid within the Ampullariidae. One of these genera, Pseudo-ceratodes (African, fossil only), is included in the family only tentatively (Berthold, 1991). The great majority of the remaining species are referred to just three genera (Table 1): Pila (Ampullaria and Ampullarius are junior syn-onyms — Cowie, 1997; ICZN, 1999), Lanistes and Pomacea. The remaining six genera each contain only one or a few species (Table 1). Ampullariid taxonomy has relied almost ex-clusively on shell morphology. However, it has been extremely confused because of the gross morphological similarity within major groups accompanied by considerable intra-specific variation. Consequently, species boundaries have been very difficult to assess based solely on conchology. Berthold (1991) published very detailed descriptions not only of the shells but also of the soft anatomy of a selection of 36 species spanning the family. This work re-mains the most detailed analysis of ampullariid morphology to date, although the anatomy of Pomacea canaliculata and P. maculata has recently been redescribed in detail by Hayes et al. (2012), with significant modification to the interpretations of Berthold (1991). Additional anatomical information has been provided for Ротасеа diffusa Blume, 1957, Р figulina (Spix in Wagner, 1827), P. glauca (Linnaeus, 1758), P. lineata (Spix in Wagner, 1827), P. scalaris (d’Orbigny, 1835) and Р sordida (Swainson, 1823) by Thiengo et al. (2011). Hayes et al. (2012) also synonymized the genus Pomella (which contained three valid species; Cowie & Thiengo, 2003) with Pomacea. In addition, these authors treated a number of species as synonyms of P. canaliculata, and others, including Р insularum (d’Orbigny, 1835), as synonyms of P maculata. In the latter case, be-

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TABLE 1. Numbers of nomenclaturally available species-group names and numbers of taxa of Ampul-lariidae (excluding fossil taxa).

Currently valid Estimated actual
Genus Distribution species!

Afropomus Africa 1
Asolene South America 8

Felipponea South America 3
Forbesopomus Asia 1
Lanistes Africa 43
Marisa South America 2
Pıla Africa and Asia 29

Pomacea South, Central and 96
North America
Saulea Africa 1

Total 186

Subspecies,
species diversity2 varieties, etc. Synonyms!

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a J 3
4 5 ы

20 16 34
$ - 6
30 16 84
50 22 M2

1 = %

117 97 250

1For the New World, from Cowie & Thiengo (2003), and taking into account changes subsequent to that publication, as tabu-lated by Cowie (in preparation); and for the Old World, Cowie (in preparation). Homonyms considered by Cowie & Thiengo (2003) and Cowie (in preparation) to represent taxonomically valid species and infraspecific taxa are counted as such. 2From Berthold (1991), Hayes & Cowie (unpublished).

cause Hayes et al. (2012) designated the same
specimen as the neotype of Р maculata and
as the lectotype of P insularum, these become
objective synonyms and the name insularum
d’Orbigny, 1835, is no longer valid.

PHYLOGENETICS AND BIOGEOGRAPHY

Phylogenetics

Morphological
The first morphological phylogenetic analyses of ampullariids were those of Berthold (1991), who included conchological and anatomical characters, as well as characters of the eggs and reproductive behavior (i.e., deposition of egg masses above or below the water surface). The analyses were criticized by Bieler (1993) owing to Berthold’s use of Hennigian argumen-tation without formal presentation of a character state matrix; when Bieler (1993) re-analyzed the data, a tree that differed in certain fundamental aspects resulted, most notably in the relative positions of Saulea and Afropomus and in the monophyly/paraphyly of Pomacea (Hayes et al., 2009b). Amore recent and extensive character set (Simone, 2004) included only ten species, all from the New World, and produced a unique ar-

rangement with Felipponea and Asolene nested within a paraphyletic Pomacea, and Marisa as sister to this assemblage.

Molecular
J@rgensen et al. (2008) published the first major molecular phylogeny of Ampullariidae, with a focus on African species and only three New World and four Asian species. Their five-locus analysis of 21 species recovered Old and New World taxa as non-monophyletic groups. Using a similar suite of markers (COI, 16$, НЗ, 18S and elongation factor 1 alpha instead of 28S), Hayes et al. (2009b) analyzed 40 spe-cies representing nine ampullariid genera and potential outgroups that included five viviparids, the only extant campanilid, and a cyclophorid. Their results contradicted those of Jorgensen et al. (2008) and showed that the Old and New World ampullariids are indeed recipro-cally monophyletic. However, although four Old World genera (Afropomus, Saulea, Pila, Lanistes) were recovered as monophyletic, only Asolene was monophyletic among the five New World genera represented by more than a single species, with Marisa paraphyletic and Pomella (now a junior synonym of Pomacea: Hayes et al., 2012), nested within the polyphyl-etic Pomacea (Fig. 2).

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Consistent with Jgrgensen et al. (2008),
Lanistes and Pila were robustly supported
as reciprocally monophyletic sister clades, a relationship not supported by the morphologi-
cal analyses (Berthold, 1991; Bieler, 1993). A monophyletic Pila consisted of two strongly-supported sister clades, one Asian and one African. Saulea was not supported as the sister taxon to New World ampullariids (Jargensen

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Marisa

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canaliculata
clade

FIG. 2. Phylogenetic tree showing generic rela-tionships within Ampullariidae and among major clades within the New World genus Pomacea. Redrawn from Hayes et al. (2009b) and Hayes (2009).

et al., 2008), but was recovered as the basal member of the Old World ampullariids, con-sistent with the reanalysis of Berthold’s (1991) data by Bieler (1993). The genus Forbesopo-mus has not been included in any phylogenetic analysis. Hayes et al. (2009b) demonstrated the importance of outgroup choice for inferring relationships among ampullariid genera, and for understanding evolutionary patterns within the group broadly. The remaining uncertainty regarding family-level relationships among basal caenogastropods is an area ripe for research incorporating additional anatomical and genomic data.
In early 2003, 20 years after the initial release of NCBI’s (National Center for Biotechnology Information) GenBank sequence database, there were only nine ampullariid sequences, including three mitochondrial and six nuclear ribosomal, from individuals representing four Pomacea spp. and Marisa cornuarietis (Lin-naeus, 1758). As of May 2014, a little more than a decade later, ampullariid sequence data on GenBank included 1,050 entries representing all extant genera except Forbesopomus. The majority ofthese (69%) are mitochondrial gene fragments (e.g., COI, 16S) commonly used in phylogenetic and phylogeographic analyses (e.g., Rawlings et al., 2007; Jorgensen et al., 2008; Hayes et al., 2008, 2009b; Bian et al., 2013) representing 54 species.
The advent of next-generation sequencing techniques has made feasible the genera-tion of large amounts of genomic data, such as transcriptomes from whole organisms or from different organs and cost effective. Sun et al. (2012a) have made a significant step forward by conducting a de novo assembly of the transcriptome of Р canaliculata. They reported the identification of 128,436 unigenes with an average length of 419 bp and listed a number of genomic resources that may be useful for ecological and physiological studies including 2,439 unigenes with transposable elements, 3,196 microsatellites and 15,412 single-nucleotide polymorphisms. However, much ofthese data are not available on public databases and remain uncharacterized with-out an annotated expressed sequence tag database and comparative data from other closely related taxa. More recently, Sun et al. (2013) have made further advances through identification of 1,040 proteins from Pomacea canaliculata, among which more than 50 were differentially expressed under active and a estivating conditions. These efforts, combined with those of a number of ongoing genomic

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research projects, will soon yield vast amounts of data that will provide broad insights into the evolution and ecology of ampullariids.

Biogeography

Ampullariids probably originated from Gond-wanan lineages that inhabited what is now Africa (Hayes et al., 2009b). Although fossil records are scarce (e.g., Prashad, 1925a; Pils-bry & Bequaert, 1927; Fischer, 1963; Boss & Parodiz, 1977; Martin & De Francesco, 2006), the Gondwanan origin is supported in part by the distribution of the two most basal genera inthe family, Saulea and Afropomus, in current day Sierra Leone and Liberia on the African west coast, and the presence in Africa of two remaining Old World genera Lanistes and Pila. New World taxa (Felipponea, Asolene, Marisa and Pomacea) evolved in South and Central America after the South American continent split from Africa in the early Cretaceous (Hayes et al., 2009b).
The estimated timing of the split between the African and Asian clades of Pila occurred after the separation of Madagascar and India from Africa (Hayes et al., 2009b), which does not support the Out-of-India dispersal hypothesis (McKenna, 1973) that has been suggested to account for many Asian biotic elements with Gondwannan origins. Thus, if Pila originated in Africa (Berthold, 1991), instead of rafting on the Indian land mass, it may have reached Asia via North Africa and the Middle East. Alternatively, Pila originated in Asia from an unknown ances-tor, subsequently dispersing into Africa. The find-ing ofa 160 Mya ampullariid operculum in China (Wang, 1984) is more consistent with this latter hypothesis. This pattern of sister clades in Africa and Asia is seen in other groups (e.g., Bossuyt & Milinkovitch, 2001; Rutschmann et al., 2004; Sparks, 2004), but additional sampling of Asian and African lineages and the incorporation of biogeographic, anatomical and molecular data are necessary to evaluate the various hypoth-eses above (Hayes et al., 2009b).

SHELL MORPHOLOGY

Until recently, gross shell morphology of am-pullariids has been the main feature on which their taxonomy has been based and is therefore well characterized (Fig. 3). Here we focus on recent advances in understanding and quanti-fying various aspects of shell morphology and

variation, previously reviewed by Estebenet et al. (2006) for South American species.

Shell Size and Thickness

Apple snails range greatly in size and include the largest freshwater snails, with the shell of P maculata capable of reaching 17 cm in maximum dimension (Cowie et al., 2006). In contrast, adults of P curumim Simone, 2004, rarely grow larger than the size of Р urceus (Muller, 1774) hatchlings (10.5 mm on average; Burky, 1974; Simone, 2004). Shells range from very thick and porcelain-like (e.g., Asolene spp., Felipponea spp.) to much thinner (e.g., certain populations of Pomacea), and in P. pa-pyracea (Spix in Wagner, 1827) they are almost devoid of calcium carbonate, with a very high relative content of organic matter and a thick periostracum (Berthold, 1989; Brown, 1994; Perera & Walls, 1996; Hayes, 2009). Shell thickness is highly variable within some species of Pomacea, increasing with calcium content and pH ofthe water (Glass & Darby, 2009) and decreasing with growth rate (Estebenet & Mar-tin, 2003; Estebenet et al., 2006). Release of lactic acid generated by anaerobic metabolism during aestivation corrodes calcium carbonate and reduces the shell weight of Pila globosa (Swainson, 1822) by 5.25% after five months (Haniffa, 1978). The shells of males tend to be thicker than those of females in P canali-culata, probably because of the investment of calcium in the egg shells and perivitelline fluid (Cazzaniga, 1990; Estebenet & Martin, 2003; Tamburi & Martin, 2012) or perhaps because of their lower growth rates (Estebenet et al., 2006; Tamburi & Martin, 2012).

Shell Shape and Ontogeny

Most apple snails are globose in shape and dextrally coiled, with the notable exception of species of Marisa, which are planispiral, and species of Lanistes, which are dextral but hyperstrophic and thus outwardly appear sinistral (Fig. 3). Although the globose bauplan places a general constraint on shell shape, some species express many variations on this theme, resulting in significant confusion for their shell-based taxonomy. In P. canalicu-lata, the inter-population variation has both a genetic and an environmental basis (Estebenet & Martin, 2003). Sexual dimorphism is also well known in P. canaliculata. The shell of female P. canaliculata is relatively more globose and

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with a broader body whorl than that of males (Tamburi & Martin, 2012); this dimorphism is
not affected by growth rate, while the relative aperture width increases with growth rate in
both sexes. Hanning (1979) showed sexual dimorphism in some populations of P. palu-dosa (Say, 1829). The shell of P. canaliculata has been studied recently using geometric morphometrics (Tabugo et al., 2010; Torres et al., 2011; Moneva et al., 2012; Tamburi & Martin, 2013) to disentangle the relationship between size and shape. Both sexes exhibit static allometry (i.e., adults at the same stage of maturity but of different sizes have different shapes); spire height decreases with size in both sexes, whereas aperture and body whorl size increase with size in males and females, respectively (Tamburi & Martin, 2013). Changes in shape through ontogeny have only been studied by Estebenet (1993) in P canaliculata and Youens & Burks (2008) in P. maculata. In the former, many dimensions of the shell show slightly allometric growth relative to shell length and hence shell shape

changes gradually during ontogeny. However, there is a clear change in growth pattern in the operculum and aperture of males (Estebenet et al., 2006).

Shell Banding

Many species exhibit a pattern of dark spiral bands that varies considerably both within and among species. Some species consistently lack bands, for example Pomacea scalaris (d’Orbigny, 1835), P. papyracea, P. curumin and Pila virescens (Deshayes, in Bory de Saint Vincent, 1824) [Pila polita (Deshayes, 1830) is an objective junior synonym of Pila virescens; Cowie & Heros, 2012] (Keawjam, 1986; Simo-ne, 2004). Unbanded individuals also often ap-pear in normally banded species, for example M. cornuarietis, P. canaliculata, Pila pesmei
(Morlet, 1889) and Pila gracilis (Lea, 1856)
(Keawjam, 1986; Dillon, 2002; Estebenet et
al., 2006). At least т P. canaliculata, the bands
are not in the periostracum, but are the result of
pigments produced by specialized cells in the

FIG. 3. Type species of extant Ampullariidae genera (except Forbesopomus) showing the diversity of shell morphology in the family. A: Saulea vitrea; В: Pila ampullacea; С: Afropomus balanoidea; D: Lanistes carinatus; Е: Marisa cornuarietis; Е: Asolene platae; С: Felipponea neritiniformis; H: Pomacea maculata. Scale bar = 1 cm; Photos: Hayes; except B: J.-P. Pointier and D: Muséum National d'Histoire Naturelle, Paris.

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mantle margin and deposited in the outer layer of the shell (Estebenet et al., 2006). Banding seems to be controlled by simple Mendelian inheritance, with the unbanded condition reces-sive (Dillon, 2002; Yusa, 2004a). However, the environment may also influence the expression of banding, with bands often appearing, disap-pearing or changing in intensity coincident with strong growth lines (Estebenet et al., 2006). Saulea vitrea (Born, 1778) exhibits a quite different banding pattern, with highly variable coaxial zigzag brown and yellow bands, or may lack bands entirely (Brown, 1994).

Operculum

A calcified operculum is present only in the genus Pila, with all other ampullariids possess-ing a proteinaceous, horny operculum. The adult operculum of Pomacea maculata is thicker and more rigid than that of P canaliculata or Asolene spp. (Bachmann, 1960; Hayes et al., 2012). In contrast to P maculata, the flexible edge of the operculum in P canaliculata enables it to seal the shell hermetically, but is not as effective for this purpose in larger P. maculata with much thicker operculae (Bachman, 1960; Yoshida et al., 2014). However, even in cases in which it does form a substantial seal, some water is still lost during aestivation (Little, 1968; Giraud-Billoud et al., 2011). In PR canaliculata, the operculum of hatchlings and juveniles of both sexes is concave (Estebenet et al., 2006; Gamarra-Luques et al., 2013). The female operculum remains concave throughout life, but becomes convex toward the posterior margin in males as the animal grows (Estebenet et al., 2006). This change in shape of the male oper-culum starts when shell length reaches 15-20 mm (Gamarra-Luques et al., 2013).

REPRODUCTIVE MORPHOLOGY

Rather than describing the complete internal anatomy of ampullariids in detail, which has been covered elsewhere (e.g., Hylton Scott, 1958; Andrews, 1964; Berthold, 1991; Catalan et al., 2002; Hayes et al., 2012; Gamarra-Luques et al., 2013), this section summarizes key recent advances in the understanding of the structure and function of the reproductive system. This system deserves special atten-tion, as reproductive biology has significance for understanding biogeographical patterns, invasion biology and possibly the evolution of

the amphibious habit seen in most ampullariids. The majority of studies have focused on Р canaliculata, and unless otherwise indicated, descriptions refer to this species.

Male Reproductive System

Testis and Sperm
The male gonad is a sponge-like mass of interconnected tubules that are delimited by a continuous layer of Sertoli cells (= tubular ‚зотайс cells) (Gamarra-Luques et al., 2006) that are flattened rather than columnar, as in other caenogastropods (Buckland-Nicks & Chia, 1986). The large ovoid nuclei of Sertoli cells contain one or more conspicuous nucleoli (Gamarra-Luques et al., 2006) and deep invagi-nations (Winik et al., 2009), and are polyploid, with 4 to 64 times the haploid nuclear DNA content (Cueto et al., 2006). The Sertoli cell cytoplasm contains abundant smooth endo-plasmic reticulum and multilamellar bodies (Winik et al., 1994) made up of circularly ar-ranged membranes. No interstitial epithelioid cells similar to the androgen-secreting inter-stitial cells of vertebrates have been observed (Gamarra-Luques et al., 2006).
The spermatogenic epithelium is arranged in nests of germinal cells at the same devel-opmental stage. However, development is markedly asynchronous among contiguous nests (Gamarra-Luques et al., 2006), assur-ing continuous sperm production during the breeding season. This may be correlated with the repeated copulations (two to three per week) observed in reproductively active snails (Albrecht et al., 1996) and may contribute to the rapid growth of invasive populations.
As in many caenogastropods, the testis of P. canaliculata produces fertile sperm (“eu-pyrene sperm” or “eusperm”), as well as in-fertile “apyrene” and “oligopyrene” parasperm that lose all or part of their chromatin during spermiogenesis, respectively. Among ampul-lariids, parasperm have also been reported in P. maculata (Sachwatkin, 1920) and Asolene pulchella (Anton, 1838) (Tiecher et al., 2014). Eupyrene sperm in P. canaliculata result from a typical spermatogenic process and are of the basic monoflagellate “introsperm” type (Rouse 8 Jamieson, 1987; Catalán et al., 1997). While eusperm are only able to produce erratic lateral movements in testicular squashes, the highly motile fusiform parasperm, lacking chromatin and resembling those of other gastropods, are propelled by three to five flagellae (Buckland-

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Nicks, 1998; Hodgson, 1999; Winik et al.,
2001). They are produced at an apparently
lower rate than eusperm (Winik et al., 2001).
Pomacea canaliculata also produces monofla-
gellate oligopyrene parasperm that are unique
among known gastropod sperm. They are simi-lar to the externally fertilizing “ectaquasperm” (Rouse & Jamieson, 1987) found in the Radiata and many Bilateria and may be produced by a truncation of euspermiogenesis, during which an ephemeral acrosome is formed at the an-terior cell pole, by loss of contact with Sertoli cell projections (Buckland-Nicks & Scheltema, 1995; Winik et al., 2009).
The functional role of parasperm, particu-
larly in the context of sperm competition and paternity assurance, is a matter of speculation (Buckland-Nicks, 1998; Till-Bottraud et al., 2005). In P canaliculata, mating with a second male displaces sperm deposited by a previous one (Yusa, 2004a), and both eusperm and parasperm from the second male are likely to participate in displacing rival sperm.

Male Tract and Sperm Transfer
Sperm produced in the testis are transported to the tip of the penis along a path that com-prises two distinct segments: (1) gonoduct
derivatives, that is, vas deferens, seminal
vesicle, prostate and genital papilla; and (2) mantle edge derivatives, that is, the copulatory apparatus, which is uniquely derived in the family, and varies among and sometimes within genera and hence is of considerable taxonomic utility (Berthold, 1991; Hayes et al., 2012). As there is no direct connection between the genital papilla at the anterior end of the prostate, and the copulatory apparatus, sperm are deposited in a “sperm pit” (Andrews, 1964; Berthold, 1989) at the base of the copulatory apparatus, and from there are drawn, pre-sumably through muscular contraction, into the spermiduct that extends the length of the penial complex. The copulatory apparatus is composed of a penial sheath and a penis (ora penial complex) in all studied species (Berthold, 1989). The penial sheath is short and non-glandular in Afropomus, Saulea and Lanistes (Berthold, 1989; Hayes, 2009), larger but “deli-cate” in Pila (Prashad, 1925b; Andrews, 1964) and stout and muscular in Marisa and Pomacea (Hylton Scott, 1958; Andrews, 1964; Berthold, 1989; Schulte-Oehlmanmn et al., 1994; Hayes et al., 2012; Giraud-Billoud et al., 2013a).
When present, there is considerable diversity among species in the number, structure and

placement of penial sheath glands. An “outer gland” embedded at the sheath’s base in Pila, Marisa and Pomacea extrudes quantities of a mucous secretion through an anterior duct during copulation, a “nuptial gift” eaten by the female, at least т Р canaliculata (Burela & Mar-tin, 2007, 2014). There may also be one or more superficial glands lined with irregularly textured epithelia on the right margin of the penial sheath groove, which differ among genera and species (Hayes, 2009). They have been given different names by different authors reflecting conflicting interpretations about the number and homology of these glands (Table 2).
In their studies of the copulatory apparatus of P. canaliculata, Giraud-Billoud et al. (2013a) observed branched microvilli at the surface of the distal gland, which at the nanoscale level increase adhesion of this gland when inserted into the female’s mantle cavity during copula-tion. A secretion composed of coarse protein granules may also play a role in enhancing adhesion, as suggested by Andrews (1964). The penial complex comprises a muscular penial bulb (absent in Old World taxa) and a long penis that contains an open (Old World) or aclosed (New World) spermiduct (Berthold, 1991). When at rest, the slender penis is enclosed in the penial pouch, which has an opening through which the penis passes to lie within the groove of the penial sheath (Hayes et al., 2012; Giraud-Billoud et al., 2013a). In Pomacea species the muscular penial bulb may also play a role in pumping fluid within the hemolymphatic spaces ofthe penis to deploy it from its resting coiled position (Giraud-Billoud et al., 2013a). However, the lack of the penial bulb in Old World taxa leaves the question of sperm transfer and penis deployment incom-pletely answered with regard to ampullariid functional morphology.

Female Reproductive System

Ovary
The ovary forms a layer of arborescent tu-bules beneath the mantle epithelium (Thiengo, 1987, 1989; Thiengo et al., 1993). The tubules are lined by the germinal epithelium, composed of Sertoli cells and oogenic cells (i.e., oogonia and previtellogenic and vitellogenic oocytes; Martin, 1986). Even though vitellogenic oocytes exhibit ultrastructural indications of active protein synthesis and endocytosis of tubular fluid (Winik & Castro-Vazquez, 2015), they never attain the massive accumulation of

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TABLE 2. Presence or absence of penial sheath glands in some ampullariid species, and proposed equivalence of names by various authors. The works of Sachawatkin (1920), Hägler (1925), Prashad (1925c), Hylton Scott (1958) and Andrews (1964) are not included, because they referred to these ” kk glands collectively as “sheath glands”

,

“superficial glands” or “marginal glands.

Gland || Ill IV

Pila globosa (Swainson, 1822) outer! absent! absent! distal!
Marisa cornuarietis (Linnaeus, 1758) outer! absentt.4 proximal! distal!
gland 34 gland 24 gland 14
Pomacea canaliculata (Lamarck, 1822) outer1,2 absent1,2,7 proximal!, 2 distal1.2
ventral basals medial3 apical’
Pomacea maculata Perry, 1810 ventral basals basal3 absent apical3

Pomacea figulina (Spix in Wagner, 1827)a basal outer® absents inner medians apicals

Pomacea sordida (Swainson, 1823) basal outer® absent6 inner median® apical6

Pomacea urceus (Müller, 1774) outer" absent! proximal! distal!

1Berthold (1989), 2Giraud-Billoud et al. (2013a), 3Hayes et al. (2012), 4Schulte-Oehlmann et al. (1994), 5Thiengo (1987), 6Thiengo (1989), "Thiengo et al. (1993), amisidentified as Pomacea lineata by Thiengo (1987).

vitelline material observed in other caenogas-
tropods (e.g., Cledón et al., 2005; Averbuj et
al., 2010). This difference may be explained by
the observation of periodic oocyte formation
and gonadal evacuation in those studies but
that occur continuously during the breeding season in P canaliculata (Albrecht et al., 1996). Another correlate о the meager provisioning of oocytes is that developing embryos must rely mostly on perivitelline fluid for nutrition (Heras et al., 1998) (see Egg Proteins: Structure and Role in Defense).

Female Tract

The visceral oviduct (“renal” oviduct of many
authors, at least in part) derives from the
visceral section of primordial gonoduct and is homologous with the vas deferens in males (Gamarra Luques et al., 2013). It is also a slen-der tube, lined by a ciliated epithelium, that runs along the columellar axis to join the seminal receptacle, which is a complex structure at least in Marisa (Schulte-Oehlmann et al., 1994) and
Pomacea (Andrews, 1964; Catalan et al., 2002:
Hayes et al., 2012). The seminal receptacle is the site for sperm storage and fertilization (Hylton Scott, 1958; Andrews, 1964), and the sperm stored in the seminal receptacle may remain fertile for up to 140 days after copulation (Estebenet & Cazzaniga, 1993; Albrecht et al., 1996; Estebenet & Martin, 2002).
The more distal sections of the female tract of Р canaliculata (the albumen and capsule

glands) are derivatives of the female pallial
gonoduct (Gamarra-Luques et al., 2013)
and are referred to collectively as the “pallial oviduct” (Catalan et al., 2002, 2006; Simone, 2004; Hayes et al., 2012) or primarily in the older literature as the “uterus” or “uterine gland” (Blainville, 1822; Sachwatkin, 1920; Hagler, 1923; Hylton Scott, 1958; Catalan de Canelada & Moreno, 1984; Giraud-Billoud et al., 2013a). The pallial oviduct of Pomacea, with its cham-bered seminal receptacle, branching albumen gland and coiled capsule gland, all embedded ina spongy mass of parenchymal tissue, is one of the most complex among the caenogastro-pods. Accordingly, understanding its structure and function is a field of active research and many aspects remain unresolved.
The seminal receptacle and the albumen and capsule gland ducts are connected in series in at least Pila (Keawjam, 1987), Marisa (Schulte-Oehlmann et al., 1994) and Pomacea (Berthold, 1991; Hayes et al., 2012), as in most caenogastropods (e.g., Hyman, 1967; Fretter
& Graham, 1994). Nonetheless, descriptions
by several authors (Catalan de Canelada &
Moreno, 1984; Catalan et al., 2002) have sug-
gested that the albumen and capsule glands
are not connected in series in Pomacea,
requiring that the fertilized oocytes receive a perivitelline quota at the junction ofthe albumen and capsule ducts in P canaliculata (Andrews, 1964; Catalan et al., 2002, 2006). However, Hayes et al. (2012) have hypothesized that, like

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other caenogastropods, the fertilized oocytes
enter the albumen gland (“albumen gland di-verticula” or “albumen duct” of other authors)
and traverse its entire periphery via a ciliated
tract while being coated with albumen. As in
other caenogastropods (Ponder & Lindberg, 1997; Strong, 2003; Ponder et al., 2008), the bursa copulatrix has been considered as a place to receive sperm during copulation before transferring them into the seminal receptacle (Andrews, 1964; Hayes et al., 2012), although others (Giraud-Billoud et al., 2013a) have hypothesized that the bursa is an organ for sperm resorption and phagocytosis, that is, analogous to the “ingesting glands” of higher caenogastropods (Ponder & Lindberg, 1997). The structural relationships among these complex ducts still require further research, as do functional aspects, for example whether and how sperm are resorbed and how the egg envelopes are provided.

DEVELOPMENT

The field of ampullariid development has re-cently experienced a revival but can be traced back to Semper’s (1862) monograph on Pila virescens (as Ampullaria polita). Subsequent work during the 20th century treated a few species but has never been comprehensively reviewed. Future integrated studies of morphol-ogy, gene expression and proteomics may shed light on the mechanisms by which aspects of ampullariid development are controlled.

Initial Stages of Development

The eggs of ampullariids are fertilized inter-nally and develop externally in calcareous or non-calcareous eggs, deposited in clutches or in gelatinous masses respectively, on submerged vegetation, rocks or other firm substrates (Hayes et al., 2009a, 2012; Burks et al., 2010; Tiecher et al., 2014). The eggs of some species contain pigmented proteins col-lectively referred to as perivitellins, the colors of which range from white to vivid pink, orange and green, which play diverse functions in the developing embryo (see Egg Laying under Reproductive Behavior and Egg Proteins, for details; Heras et al., 2007; Dreon et al., 2008, 2013; Hayes et al., 2009a).
Eggs exhibit distinct animal and vegetal poles before the first cleavage in Pila globosa, Pomacea canaliculata and Marisa cornuarietis

(see Ranjah, 1942; Hylton Scott, 1934; Demian & Yousif, 1973a, respectively). Gastrulation is the result of invagination (emboly) in Pila globosa and P. canaliculata, but is epibolic in M. cornuarietis according to Ranjah (1942), Hylton Scott (1958) and Demian & Yousif (1973a), respectively; both of these patterns of gastrulation occur in other caenogastropods (e.g., Hyman, 1967).
Like other gastropods lacking a planktonic larval phase, the prototroch in Pila globosa, P. canaliculata and M. cornuarietis does not develop into a full velum (Brooks & McGlone, 1908; Hylton Scott, 1934; Ranjah, 1942; Demi-an & Yousif, 1973a, 1975; Koch et al., 2009). The rudiment of the mantle cavity forms at an early stage in Pila globosa according to Ranjah (1942) and in P canaliculata (see Brooks & McGlone, 1908; Fernando, 1931; Hylton Scott, 1934; Koch et al., 2009) as an ectodermal depression close to the anus and immediately
beneath the pericardial rudiments. It seems
to occur later in M. cornuarietis according to
Demian & Yousif (1973a). In all cases, the
growing shell gland engulfs the primitive mantle cavity and turns to the left and front during ano-pedal flexure and torsion.
A protein-expression approach has been applied for the first time to the development of a gastropod in a study of P canaliculata eggs at stages when most of the organs are formed (Sun et al., 2010). Of the 125 most abundant proteins, 65 were identified and associated with 11 types of cellular functions or pathways. Of these 65, 63% were related to either metabo-lism (11%), energy (11%), protein fate (29%) or to proteins with binding functions or cofactor requirements (12%).

Cardiac, Respiratory and Renal Organogenesis

The pericardium (and thus the heart) devel-ops in the mesoderm dorsal to the gut as either a single or a double rudiment (Fernando, 1931; Ranjah, 1942; Demian & Yousif, 1973b). The ctenidium develops in the mantle cavity, but Demian & Yousif (1973c) traced it back to an ectodermal thickening on the right, posterior side of the embryo in M. cornuarietis. The lung develops later during intracapsular develop-ment as an outgrowth of the mantle cavity’s roof (between the ctenidium and the osphradium) in Pila globosa, P. canaliculata and M. cornuarietis (Brooks & McGlone, 1908; Hylton Scott, 1934, 1958; Ranjah, 1942; Demian € Yousif, 1973c, d; Koch et al., 2009). The lung of Asolene pul-

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chella develops in the same location but only after hatching (Tiecher et al., 2014).
In Pila globosa, P. canaliculata and M. cor-nuarietis, the rudiment of the post-torsional left kidney develops as an outgrowth of the primi-tive pericardium and connects with the rudiment of the ureter, which itself is an ectodermal out-growth of the primitive mantle cavity (Fernando, 1931; Ranjah, 1942; Demian & Yousif, 1973d). The embryonic kidney and ureter become the posterior and anterior kidney chambers of the adult, respectively. The latter opens to the rear of the mantle cavity and communicates with the posterior kidney through a small opening; the posterior kidney is connected to the pericar-dium via the reno-pericardial duct.
The gonadal sector of the gonoduct in Pila globosa originates from a thickening of the pericardial cavity (Ranjah, 1942). The embry-onic, post-torsional right kidney, which would give rise to the visceral (or renal) sector of the gonoduct, has also been reported in Pila globosa (Ranjah, 1942) and Р maculata [as Ampullaria (Pila) gigas Spix in Wagner, 1827] (Fernando, 1931), but has not been found in P. canaliculata (see Hylton Scott, 1934; Koch et al., 2009) and M. cornuarietis (see Demian & Yousif, 1973b, d).

Digestive Tract

The cells lining the archenteron, or primitive gut, are large and yellowish in Pila globosa and M. cornuarietis according to Ranjah (1942) and Demian & Yousif (1973d), respectively. In P canaliculata, they are colorless until the stomodaeum connects with the archenteron and the perivitelline fluid starts to be ingested (Koch et al., 2009), at which point they become reddish-pink and increase in size (that is,

“giant
cells’; Koch et al., 2009). Pomacea canalicu-lata embryos rely heavily on the pink-reddish perivitelline fluid for their nutrition (Heras et al., 1998), rather than the limited amount of yolk invested in the oocytes (Winik & Castro-Vazquez, 2015).
As development proceeds, the foregut, mid-gut and hindgut become clearly differentiated (Hylton Scott, 1934; Ranjah, 1942; Demian & Yousif, 1973c; Koch et al., 2009). In Pila globosa, P. canaliculata and M. cornuarietis, the foregut gives rise to the pharyngeal bulb with the radula and to the esophagus with the salivary glands and crop. The midgut gives rise to the three-chambered stomach (vestibule, gizzard, style sac) and the midgut gland. The

hindgut gives rise to the intestine. The midgut gland develops as two lobes (anterior and posterior), but even though the anterior lobe is initially larger it disappears with development and only the posterior lobe persists into adult-hood (Ranjah, 1942; Demian & Yousif, 1973a; Koch et al., 2009). The detailed origin and putative functions of the cells lining the midgut lobes and forming the midgut alveoli have been described in varying degrees of detail in M. cornuarietis by Lutfy & Demian (1967) and Demian & Yousif (1973a) and in P. canaliculata by Koch et al. (2006, 2009), appearing similar in the two species.

Post-Hatching Reproductive Development

At hatching, the primordial gonoduct of P. canaliculata is formed by interconnected cell cords contained within the posterior wall of the mantle cavity. It takes about ten days (by which time the juveniles have reached 5 mm in shell height) for these cords to develop into a sexually undifferentiated primordial gonoduct. At about the same time, the primordium of the copulatory apparatus appears near the inner right mantle edge and will develop either into the full copulatory apparatus of adult males or the rudimentary apparatus of adult females (Gamarra-Luques et al., 2013). The occur-rence of this copulatory rudiment has also been reported in adult females of other Pomacea species (Thiengo, 1987, 1989; Thiengo et al., 1993) and of M. cornuarietis (see Schulte-Oehlmann et al., 1995), but is not attributed to masculinizing pollutants often associated with this phenomenon in other gastropods. Al-though sometimes apparently lacking (Liu et al., 2006), this rudimentary copulatory apparatus in females can continue to grow after sexual maturity, even in the absence of masculinizing pollutants (Gamarra-Luques et al., 2013; see Environmental Health and Pollution).
In P canaliculata, the gonad is sexually dif-ferentiated in 10 mm juveniles, but the pallial section of the gonoduct remains undifferenti-ated and the copulatory rudiment is similar in both sexes. In 15 mm juveniles (30 days old), the pallial gonoduct has differentiated in both sexes, and includes all the components that will be present in the adults. Copulation takes place once snails reach 20 mm (40 days old), but no eggs are laid, which may be related to the in-ability of males to fertilize females (oviposition may be directly related to fertilization as most deposited eggs are fertile in P. canaliculata)

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or to the inability of females to provide egg envelopes. The snails appear reproductively
mature at 25 mm as their copulations result in
the deposition of fertile eggs, and their anatomi-
cal and histological features are those of adults (Gamarra-Luques et al., 2013).

LIFE HISTORY

Life Cycle and Reproductive Seasonality

Published estimates of longevity in apple snails range from one to four years in Pomacea Spp., three years or more in Marisa cornuarietis and Pila spp., and up to ten years in Lanistes nyassianus Dohrn, 1865 (reviewed by Cowie, 2002);
At the southernmost extreme of its native range, in Argentina, P canaliculata may remain inactive for several months due to low winter temperatures (Seuffert et al., 2010) and usually has three to four annual reproductive periods (Estebenet & Cazzaniga, 1993; Estebenet & Martin, 2002; Martin & Burela, personal observations). À one- to two-year life span, similar to that observed in laboratory popula-tions reared at 25°C (Estebenet & Cazzaniga, 1993; Estebenet & Martin, 2002; Martin & Estebenet, 2002), may be expected in warmer, subtropical and tropical areas where winter temperatures are not low enough for the snails to become inactive. In their introduced range of more temperate southern Japan, high winter mortality means that the proportion of snails that survive two summers is low (Yoshida et al., 2009). However, a water temperature of 18°C seems to be adequate to trigger repro-ductive activity in overwintering Р canaliculata (Albrecht et al., 1999), and reproductive activity still proceeds if temperature is lowered from 25°C to 18°C (Albrecht et al., 2005). In Hong Kong, with minimum water temperatures of 16°C, the recruitment period extends up to ten months (Kwong et al., 2010). Photoperiod is not important for initiating and continuing reproduc-tion, because the shortest winter day length (10 h) for the southernmost populations sufficed, given adequate temperatures (Albrecht et al., 1999, 2005). At the other extreme, P canali-culata reared since hatching under constant illumination, matured, copulated and laid eggs normally (Estebenet & Martin, 2002; Martin & Estebenet, 2002).
Also in temperate Argentina, adult P scalaris and Asolene platae (Maton, 1811) were present

throughout the year (although inactive during winter), and egg-laying and recruitment were observed from late spring to late summer (March) (Martin, 1984, 1993).
Whereas reproduction in temperate regions is more thermally regulated, in tropical regions it is much more related to water availability. Adults of the Indian Pila globosa remain dormant, buried in dry mud, for up to eight months dur-ing the dry season but begin to copulate and lay eggs as soon as the bottom sediments are covered by water at the start of the rainy
season (Bahl, 1928; Raut, 1984). They attain
maximum size at four years, but the life span is thought to be longer (Haniffa, 1980). Pomacea
urceus, in tropical Venezuela, lives for 2.5-3.5
years and breeds during two to three seasons (Burky, 1974); most females attain maturity in their first year (Lum-Kong & Kenny, 1989). Adults begin to copulate just before the onset of the dry season, a decrease in water level being necessary for mating and egg-laying to begin (Ramnarine, 2003).
Pomacea paludosa in Florida has a short life span (1-1.5 years) and throughout much of its range, the majority of egg-laying occurs during spring/summer, followed by a post-reproductive die-off (Darby et al., 2003, 2008). In this case, both water temperature and depth are critical to oviposition and hatchling growth. Snails become inactive when temperatures drop be-low 13°C (Stevens et al., 2002), and relatively cool temperatures may delay oviposition in the spring (Hanning, 1979). The spring oviposition peak is associated with the dry season, which often culminates in a dry down (i.e., the water table falls below ground level) during which the snails become inactive (Darby et al., 2002, 2008), but, following summer rains, they re-initiate reproduction (O’Hare, 2010).
Thus, reproduction in ampullariids may occur if water is available and if temperatures are high, as during summer in temperate regions or throughout the year in many tropical and sub-tropical regions. In seasonally wet/dry tropical and subtropical regions, the reproductive cycle
seems to be timed to allow hatchlings to reach
a large enough size to survive the dry season, while in temperate regions, reproduction only
occurs above a threshold temperature.

Life History Variation

Inter-population variation in many life history traits of P canaliculata has both a genetic and an ecophenotypic basis. Although snails show dif-

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ferences in size at hatching, maturity and maxi-mum size, often in response to different densities (Tanaka et al., 1999; Yoshida et al., 2009, 2013), such differences disappeared in snails reared under homogeneous laboratory conditions, indi-cating a strong environmental influence; slightly higher mortality, growth and oviposition rates in laboratory snails from unstable and unproductive habitats were attributable to genetic differences among source populations (Martin & Estebenet, 2002). The high environmental tolerance of Р canaliculata and its successful establishment in new environments may be associated with this high level of ecophenotypic plasticity (Estebenet & Martin, 2002).
The environmental factors involved are not fully understood. Population density and per capita food availability are probably important (Tanaka et al., 1999; Yoshida et al., 2009, 2013). For P. canaliculata, the relationship of food availability with size, age at maturity and reproductive performance differ between males and females (Estebenet & Martin, 2002; Estoy et al., 2002a, b; Tamburi & Martin, 2009a, 2011). When food availability is lower than opti-mum, the reproductive strategy of females is to delay maturation and the onset of reproduction (Estoy et al., 2002b; Tamburi & Martin, 2009a). With reductions in food availability, the mean number of eggs laid during the first reproduc-tive month decreased, although without a sig-nificant decrease in the number of clutches or egg size (Estoy et al., 2002b; Tamburi & Martin, 2011). The size of P canaliculata eggs does not differ relative to food availability (Albrecht et al., 2005; Tamburi & Martin, 2011) or among populations (Estebenet & Cazzaniga, 1993). The survival rates of Р canaliculata offspring under starvation actually increase if the moth-ers are faced with chronic food restrictions (Tamburi & Martin, 2011).
On the other hand, P canaliculata males mature at the same age irrespective of food availability. Growth rates, and hence matura-tion sizes, are strongly negatively affected by reduced food availability (Tamburi & Martin, 2009a), but there is no apparent negative effect on reproductive success (Estoy et al., 2002a; Burela & Martin, 2011; Tamburi & Martin, 2011).
In laboratory studies of P canaliculata, mor-tality rate was not affected by food availability, up to a point. Most snails completed their life cycle with food available 30-100% of the time (Estoy et al., 2002a) and with 20-100% of the ad libitum daily consumption (Tamburi & Martin,

2009a). In addition, male growth rate was not reduced with the onset of copulatory activity, while that of females decreased at the start of reproduction (Tamburi & Martin, 2009a, 2011). This decrease was also observed in isolated cohorts of P. canaliculata females that were not allowed to reproduce (Estebenet & Caz-zaniga, 1998) and is probably caused by the decrease in ingestion rates and food conver-sion efficiencies as snails grow (Tamburi & Martin, 2009b).
Food quality may also be important because P. canaliculata prefers to consume plant spe-cies on which it achieves higher growth rates, and despite its broad food preferences avoids certain plants (Estebenet, 1995; Estebenet & Martin, 2002; Lach et al., 2000; Morrison & Hay, 2011a). Therefore, even among highly productive habitats, life history variation in P. canaliculata could result from differences in availability of preferred food. Interspecific dif-ferences in the nutritional value and chemical and physical defenses of plants are correlated with changes in growth, oviposition and mortal-ity rates (Qiu & Kwong, 2009).
Life history traits, such as number of eggs, age at maturity in females, size at maturity in males and offspring endurance, are highly plastic and influenced by food availability in the environment. This adjustment to different food availabilities allows other traits (that is, egg lay-ing rate, maturation size in females and matu-ration age in males) to remain unchanged or conserved, probably because these are subject to the strongest selection pressures (Whitman & Agrawal, 2009). Pomacea canaliculata exhib-its the same sexually dimorphic reproductive patterns and the same combination of cana-lized and plastic traits between native (Tamburi & Martin, 2009a, 2011) and introduced (Estoy et al., 2002a, b) populations, indicating that this strategy in the non-native range is neither the product of founder effects nor of anthropogenic selective pressures, but an adaptive strategy evolved in its native environment.

REPRODUCTIVE BEHAVIOR

Mating

Mating behaviour has been studied in several ampullariids, mostly in the laboratory but in a few cases in the field (Bahl, 1928; Nono & Mane, 1931; Demian & Ibrahim, 1971; Han-ning, 1979; Guimaraes, 1981a, b; Berthold,

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1989, 1991; Faraco et al., 2002; Heiler et al.,
2007; Tiecher et al., 2014), although thoroughly
only in Pomacea canaliculata (Andrews, 1964; Albrecht et al., 1996; Burela & Martin, 2007,
2009, 2011, 2014). All descriptions of copula-
tion agree on a basic pattern. Copulation and sperm transfer occur under water, during which the male’s foot adheres to the right side of the body whorl of the female while gripping the rim of her shell with the penis sheath. The penis is guided by the penial sheath to the vaginal opening, and from there it passes along the central channel of the capsule gland towards the proximity of the seminal receptacle (Giraud-Billoud et al., 2013a).
There is great inter- and intra-specific varia-tion in length of copulation in apple snails, ranging from an average of 38 min to as long as 20 h (Burela & Martin, 2011). The lengthy copulations may be attributed to the complexity ofthe male and female reproductive anatomy, to the high fecundity of the females, to the existence of mate guarding behavior, or some combination of these (Burela 8 Martin, 2011). In P. canaliculata, copulation may occur during the day or night, with females able to continue to move about freely. Both males and females mate frequently with different partners (Albrecht et al., 1996; Burela & Martin, 2011; Liu et al., 2012), and mating can be distinguished into four distinct phases: precourtship, court-ship, copulation and post copulation (Burela 8 Martín, 2009). The precourtship phase, contact with tentacles, palps, feet or snouts, lasts a few seconds. The courtship phase frequently begins with the male circling the female shell but often ends prior to the copulation phase, with the female swinging her shell to dislodge the male. The insertion of the penis sheath into the mantle during the initiation of the copulation phase frequently elicits swinging and withdraw-al-wrestling behavior in the female, interrupting the copulation in many cases (Nono & Mane, 1931; Hanning, 1979). This rejection indicates a possible underlying mate choice mechanism in females (Burela 8 Martín, 2009). Copulation may last 13 h on average, and can extend up to almost 20 h, with most of this time seemingly devoted to the transfer of eusperm (Burela 8 Martín, 2011). During copulation the male of-ten secretes a nuptial gift from the outer basal sheath gland. Females feed on this gift, which is probably a mechanism for enticing females to remain in copula (Burela 8 Martín, 2011, 2014). Postcopulation has only been observed in a few cases, and may last as long as 1 h,

during which the male remains mounted on the female’s shell with its sheath retracted into the mantle, a behavior explained as possible mate guarding (Burela & Martín, 2011).

Egg Laying

The majority of species, those in Pomacea and Pila, deposit calcareous eggs out of water. Most Pomacea species lay them well above the water line on stems of emergent plants, trunks of riparian trees, rocks and other hard structures, such as bridge supports, and Pila deposit them on vegetation at the water line or directly on the soil surface at the margin of the water (Hurdle, 1973; Hanning, 1979; Turner, 1996; Cowie, 2002; Hayes et al., 2009a; Burks et al., 2010; Kyle et al., 2013). Some Pila spe-cies dig a depression in the mud near the shore
in which to deposit their eggs (Bahl, 1928;
Cowie, 2002). Pomacea paludosa in Florida exhibits preferences for certain plant species on which to lay its eggs, perhaps related in part to the ability of larger stems to support a mature female (Turner, 1996).
Oviposition usually occurs during the night or early morning, probably to reduce the risk of predation by terrestrial animals and the heat and desiccation stress on females and eggs, which take time to harden (Schnorbach, 1995;
Albrecht et al., 1996; Estebenet & Martín,
2002). Oviposition may last up to several hours and occurs with the right side of the foot forming a longitudinal groove that conducts the eggs from the vagina to the substrate at intervals that depend on species (Bahl, 1928; Bachman, 1960; Andrews, 1964; Hanning, 1979; Albrecht etal., 1996; Estebenet & Martin, 2003). Among species, the average number of eggs per egg mass is inversely related to egg size (Turner & McCabe, 1990; Cowie, 2002; Martín & Este-benet, 2002; Barnes et al., 2008; Burks et al., 2010; Kyle et al., 2013).
Aerial egg laying may have evolved to avoid the predation or cannibalism that submerged egg masses suffer (Turner, 1998; Cowie, 2002; Horn et al., 2008; Saveanu & Martín, 2014), but it incurs diverse costs. There may also be a cost of producing the calcium coating of the eggs, resulting in a trade off between production of progeny and maternal defense, inasmuch as shells of female P. canaliculata tend to be thinner than those of males (see Shell Morphology).
A notable exception among Pomacea spe-cies to this normal egg laying strategy is the

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behavior of P urceus, which adopts a strategy apparently unique among ampullariids. These snails bury themselves in the drying mud at the beginning of the dry season to aestivate, prior to which females lay their eggs within their shells, between the aperture and the operculum (Burky et al., 1972; Burky, 1974; Lum-Kong & Kenny, 1989). Development takes place during the dry season and the females release some of their own body water at intervals to cool themselves and their progeny (Burky et al., 1972), which are very sensitive to desiccation (Ramnarine, 2003). The hatchlings emerge as the wet season begins.
All other species of apple snails for which information is available, that is, in the genera Afropomus, Asolene, Felipponea, Lanistes, Marisa and Saulea, deposit non-calcareous eggs in a gelatinous matrix under water (Hayes et al., 2009a; Thiengo et al., 2011). The process

is Similar to that described for Р canaliculata. Deposition of gelatinous packages of three to four eggs usually occurs during the night or early morning on submerged plant stems or leaves in a process that can last 1-3 h (М. cornuarietis — Demian & Ibrahim, 1971;
Schulte-Oehlmann et al., 1994; Asolene pul-
chella — Tiecher et al., 2014).

SEX RATIO, SEX DETERMINATION AND KARYOLOGY

The sex ratio in wild (introduced) populations of Pomacea canaliculata in Japan is 0.5 overall
but highly variable among egg masses (Yusa
& Suzuki, 2003; Yusa, 2004b). Chromosomes
have been studied in species of Lanistes, Pila,
Pomacea and Marisa and there appear to be
no dimorphic sex chromosomes (Table 3),

TABLE 3. Ampullariid chromosomes. Unless otherwise indicated, numbers refer to the haploid complement.

Haploid
Species number Chromosome groups! Reference

m sm st t

Lanistes bolteniana (Deshayes 8 14 : - - - Lutfy & Demian, 1965
Milne Edwards, 1838)2
Lanistes bolteniana (Deshayes & 13 8 0 2 3 Yaseen etal., 1991
Milne Edwards, 1838)2
Pila ovata (Olivier, 1804) 14 - - - - Lutfy & Demian, 1965
Pila virens (Lamarck, 1822) 14 - - - - Choudhury & Pandit, 1997
Pila globosa (Swainson, 1822) 14 9 5 0 O Choudhury & Pandit, 1997
Pomacea canaliculata 14 20” 6 28 0* von Brand et al., 1990
(Lamarck, 1822)3 19* er 2#7 9
Pomacea canaliculata 14 11 3 0 О Mercado-Laczkó € Lopretto,
(Lamarck, 1822)4 1998
Ротасеа sp.> 14 9 4 1 O Kawano et al., 1990
Pomacea flagellata (Say, 1829) 13 9 4 0 O Diupotex-Chong et al., 2007
Pomacea patula catemacensis 13 9 A 0 O Diupotex-Chong et al., 2004
(Baker, 1922)
Marisa cornuarietis 14 - - - - Lutfy & Demian, 1965
(Linnaeus, 1758)

Dashes indicate no information reported.
1Abbreviations: m, metacentric; sm, submetacentric; st, subtelocentric; t, telocentric.
2Incorrectly referred to as “Бойепг.
3Animals introduced in Japan. One star indicates the diploid complement in females, two stars that in males. 4Animals from the native range (Buenos Aires).
5Animals from Sao Paulo, Brasil.

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with the possible exception of P. canaliculata (perhaps misidentified P maculata) (von Brandt
et al., 1990). Instead, sex in Р canaliculata
is determined by a small number of nuclear
genes, inherited from both parents (Yusa,
2006a, 2007a, b).
The haploid complement seems to ben = 14, with п = 13 only reported for Р flagellata (Say, 1829) and Р раша catemacensis (Baker, 1922), two taxa from Mexico, and the African Lanistes bolteniana (Deshayes & Milne Edwards, 1838), though there are conflicting reports for this spe-cies (Table 3). Metacentric chromosomes are predominant in all species (8-11 chromosomes/pairs), followed by submetacentric ones (3-5 chromosomes/pairs, with the exception of the L. bolteniana of Yaseen et al., 1991). Subtelo-centric or telocentric chromosomes are absent in most species (Table 3).
With the single exception of P. patula
catemacensis, in which rather long chromo-
somes have been observed (Diupotex-Chong et al., 2004, 2007), ampullariid chromosomes are much contracted in metaphase, so that
measurement error may explain some of the
differences summarized above.

HABITATS AND DETERMINANTS
OF DISTRIBUTION

There is no information concerning the
ecological determinants of the distributions of the Neotropical genera Marisa, Asolene and Felipponea, nor a quantitative description of their preferred habitats. Similarly, data on Old World taxa are almost lacking.

Habitats

Most reports of ampullariid habitats are quali-tative descriptions, with only a few quantitative studies (Ichinose et al., 2000; Ito, 2002; Kar-unaratne et al., 2006; Seuffert 8 Martín, 2010, 2013a). Apple snails inhabit a wide variety of habitats, but are generally found in shallow, slow-moving or stagnant waters, including waterbodies that dry seasonally (e.g., Brown, 1994; Turner, 1994, Ichinose et al., 2000; Darby et al., 2002; Karatayev et al., 2009; Burlakova et al., 2010; Kwong et al., 2010). Nearly all Old World taxa have been reported from ditches, creeks, small rivers and streams, lakes, pools, reservoirs, swamps, monsoon canals and ar-eas generally associated with shallow, slowly flowing waters, macrophytes, muddy bottoms

and shade (McCullough, 1964; Ndifon & Ukoli, 1989; Brown, 1994; Omudu & lyough, 2005; Clements et al., 2006).
A few Old World ampullariids seem adapted to live in flowing waters (Prashad, 1925b; Starmúhiner, 1979; Keawjam, 1986; Brown, 1994), and some species of Lanistes can occur to depths of 27-82 m (Louda & McKaye, 1982; Brown, 1994). Similarly, species of Felipponea and some species of Pomacea inhabit faster flowing waters, including those in the highlands of the northern Andes and rivers associated with rocky substrates (Dall, 1904; Faraco et al., 2002; Scarabino, 2004; Corrao et al., 2006; Hayes, 2009).
Pomacea canaliculata is most often con-sidered a lentic species (Hylton Scott, 1958; Castellanos & Fernández, 1976) although in its native range it is found in both lotic and lentic
environments (Martín et al., 2001; Martínez &
Rojas, 2004; Martín & De Francesco, 2006; Martello et al., 2006). In both habitat types, it is generally found near the margins, associated with macrophytes, slow currents and shallow depths (Lanzer & Schafer, 1985; Ichinose et al., 2000; Kwong et al., 2010; Maltchik et al., 2010; Seuffert & Martin, 2010, 2013a). Although Р
canaliculata is not commonly found in fast
flowing environments, it is able to resist current velocities that are among the highest recorded
in streams in the Argentinian Pampas (1.61
m.s-1; Seuffert & Martin, 2012, 2013a).
Pomacea species are more abundant in the
shallow marginal areas rich in vegetation in diverse habitat types (Guimaraes, 1981b; Kara-tayev et al., 2009; Burks et al., 2010; Burlakova et al., 2010; Pomacea Project, 2013). They require emergent surfaces including plants for laying eggs above the waterline and, in some cases, for climbing to the water’s surface for respiration (Turner, 1996), and prefer marshes with low to moderate density of emergent plant stems over lily-pad dominated habitats (Karunaratne et al., 2006). In some cases, species of Pomacea exhibit preferences for specific vegetation types (Bryan, 1990; Kyle et al., 2011). For example, in the Everglades of Florida, the greatest concentrations of egg clutches occur along the ecotone created by sawgrass and wet prairie or slough habitat (Darby et al., 1999). For all these species, the association with microhabitats close to the margins or with emergent vegetation is prob-ably due not only to availability of adequate substrates for oviposition but also to a combi-nation of factors including predator avoidance,

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food availability and the need for frequent lung ventilation (Seuffert & Martin, 2010).

Determinants of Distribution

In general, ampullariids are typically regarded as freshwater snails that do not live in brackish
waters (Lanzer & Schafer, 1985; Cowie, 2002:
Hamli et al., 2013). Factors determining the distribution of P. canaliculata across different waterbodies have been investigated both in its native range (Southern Pampas; Martin et al., 2001; Seuffert & Martin, 2013a) and in a non-native region (Hong Kong; Kwong et al., 2008). These two regions have contrasting climates and topographies, semi-arid to arid plains and subtropical humid hilly terrains, respectively. These studies indicate that P. canaliculata distributions are determined by a combination of physicochemical (salinity, alkalinity) and geo-graphic (mountains) barriers in conjunction with stochastic patterns of extinction-colonization
events related to local variability of climatic
and hydrological conditions (Martin et al., 2001; Martin & De Francesco, 2006; Seuffert & Martin, 2013a). However, in the non-native range this species can be found in sub-optimal habitats, indicating that it can at least survive in these habitats for a period of time (Kwong et al., 2008).
Low calcium availability and low pH (< 6.5) limit the growth of Р paludosa in Florida and lead to thinner, more eroded and more fragile
shells (Glass & Darby, 2009), probably re-
stricting its distribution (Hurdle, 1973; Glass & Darby, 2009). In the southeastern USA, the models of Byers et al. (2013) show that a pH of < 5.5 probably precludes invasion by P. maculata. Nevertheless, in Cuba, P. paludosa
seems to be more tolerant than pulmonates of
the acidic waters in most reservoirs as it is the only snail present, although in none of them is the pH less than 6.0 (Perera & Yong, 1984). In Nigeria, the abundance of Lanistes libycus (Morelet, 1849) shows no significant correlation with any physicochemical variable (Owojori et al., 2006).
Temperature limits the range of many ampul-lariids as it is a key determinant of their activity thresholds (Stevens et al., 2002; Heiler et al., 2008; Seuffert et al., 2010), growth (Estebenet & Cazzaniga, 1992; Seuffert & Martin, 2013b), reproduction (Estebenet & Martin, 2002; Albrecht et al., 1999, 2005), development (Seuffert et al., 2012) and survival (Matsukura & Wada, 2007; Wada & Matsukura, 2007; Mat-

sukura et al., 2009a; Seuffert & Martin, 2013b). Temperature has therefore been used, among other climatic factors, to predict the potential spread of both P canaliculata (Baker, 1998; Zhou et al., 2003; Kwong et al., 2008; Lv et al., 2009a, 2011; EFSA, 2013) and Р maculata (Byers et al., 2013) in their non-native ranges. Ecological niche modeling, combining such climatic models with developmental rates at different temperatures, could be used to predict the isotherms limiting the expansion of ampul-lariids to higher latitudes, both in their native and non-native ranges (e.g., Lv et al., 2011). At the southernmost limit of its native range P. canaliculata is occasionally exposed to temperatures near 0°C (Seuffert et al., 2010). However, it cannot tolerate freezing (Matsukura et al., 2009a), suggesting that the isotherm limiting its southern expansion may be close to its actual southernmost extent (37-38°S; Martin et al., 2001; Seuffert et al., 2010). The northern limit of P canaliculata, in its non-native range, is 36°N in Japan (Ito, 2002) and around 31°N in China (Lv et al., 2011). For P maculata in Europe it is between 40 and 41°N, in the Ebro Delta in Spain (López et al., 2010; Anonymous, 2011); this may also be the limit for P. canaliculata as it may also be present in the Ebro Delta.

AMPHIBIOUSNESS

Ampullariids are unique among freshwater snails in possessing both a fully functional lung for aerial respiration and a gill for aquatic breathing (Andrews, 1965; Berthold, 1989, 1991). The possession of a lung allows many apple snail species to dwell in habitats with poorly oxygenated waters or that frequently dry out (Darby et al., 2002, 2003, 2008; Yusa et al., 2006b; Seuffert & Martin, 2009). The long siphon of some species allows ventila-tion of the lung without the snail completely surfacing (Prashad, 1925c; McClary, 1964; Andrews, 1965; Berthold, 1991). Juvenile P. canaliculata begin aerial respiration within three hours of hatching, and lung ventilation frequency increases with shell size (Seuffert & Martin, 2009). In contrast, Burky & Burky (1977) showed that lung ventilation frequency decreases with body size in P. urceus, perhaps related to metabolic depression in the adults during aestivation. The number of pumping movements per lung ventilation increases with snail size in both species (McClary, 1964;

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Burky & Burky, 1977; Seuffert & Martin, 2009), probably because of an increase in the volume
of the respiratory dead space in the lung and
siphon (Seuffert & Martin, 2009).
While they are primarily aquatic, ampullariids
display varying degrees of amphibiousness that range from greater (Asolene, Felipponea, Marisa, Lanistes, and presumably Afropomus and Saulea) to lesser (Pomacea, Pila) reli-ance on water for the completion of their life cycle (Hayes et al., 2009a). The shift from aquatic to amphibious habits, including aerial oviposition, was probably a key innovation that may have facilitated, at least in part, the diversification and spread of Pilaand Pomacea (Hayes et al., 2009a)T.he cleidoic eggs of most Pomacea species are adapted to exposure to extreme conditions and have developed a physiological dependence on aerial incubation such that they will not develop completely if submerged (Turner, 1993; Pizani et al., 2005; Horn et al., 2008). The deposition of cleidoic eggs above water by Pomacea and Pila and the observation that most Pila virescens die if covered totally by water indicate that they are truly amphibious (Andrews, 1965; Keawjam, 1986; Berthold, 1989, 1991; Cowie, 2002; Hayes, 2009; Hayes et al., 2009a; Seuffert & Martin, 2010). However, the eggs of some Pila
spp. (deposited in pits dug in the ground or at
the bases of plants) and P. urceus (incubated within the mother’s shell) depend on deposition in humid microenvironments, and the embryos are highly susceptible to desiccation (Bahl, 1928; Ramnarine, 2003). In contrast, the other genera, with their gelatinous eggs deposited under water, are linked to aquatic habitats from hatching to maturity (Hayes et al., 2009a).
In Pomacea species, males and females do not differ in lung ventilation frequency nor in oxygen consumption rates (Freiburg & Hazel-wood, 1977; Santos & Mendes, 1981; Seuffert & Martin, 2009). However, when access to the water surface for aerial respiration was restricted, females of P. canaliculata died or became comatose more frequently than males, which may be a consequence of decreased efficiency of water flow over the gill in females due to the bulging of the albumen gland into the mantle cavity (Seuffert & Martin, 2010).
A reduced lung and a more aquatic mode of
life with no air breathing has been suggested for species of Lanistes that occur at deeper depths (Berthold, 1990). However, Bandel (1998) reported that these snails always had air in the lung, even when found 500 m from the

shoreline and 6 m deep, apparently a result of their ability to capture air bubbles released by aquatic vegetation in the mantle cavity.

DORMANCY

The fluctuating and highly variable habitats of many ampullariids have influenced the evo-lution of many aspects of their behavior and physiology, including those underlying aestiva-tion, hibernation and seasonal reproduction. These processes may be entrained by largely predictable changes (e.g., annual changes in photoperiod and mean temperature) but also to less predictable changes (e.g., occasional temperature fluctuations, droughts, rains or floods).
Many ampullariids become dormant in re-sponse to drought and/or cold temperatures (d’Orbigny, 1847; Lal & Saxena, 1952; Meenak-shi, 1956, 1964; Oya et al., 1987; Yusa et al., 2006b; Seuffert et al., 2010). Although aestiva-tion is most commonly thought of as a response to high temperatures, it is here defined as when dormancy is induced by lack of water caused by natural or anthropogenic lowering of the water below ground level (e.g., Lal & Saxena, 1952; Little, 1968; Watanabe et al., 2000). De-fined as such, aestivation may occur in either winter or summer (e.g., d’Orbigny, 1847; Wada & Matsukura, 2007). Hibernation in ampul-lariids is here defined as dormancy when the ambient temperature becomes low. However, the snails do not enter a deep lethargic state that persists during the entire cold season but show a rather quick response to instantaneous temperature changes, being able to reactivate as soon as conditions are favorable (Seuffert et al., 2010).
Burrowing and closing the shell with the oper-culum are common apple snail behaviors as-sociated with dormancy. Closing the operculum during dormancy may minimize exposure to the environment, conserve body water (during aestivation) and protect the snail from predators (Meenakshi, 1956, 1957; Coles, 1968; Stevens et al., 2002; Seuffert et al., 2010). Burrowing may occur at the onset of either aestivation or hibernation and may vary diurnally during summer, with maxima around noon and minima around midnight (Oya et al., 1987; Wada & Yoshida, 2000). High water temperatures (35-40°C) increased adult male burrowing behavior, but had no effect on females and juveniles. Lower temperatures (< 10°C) led to

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increased proportions of snails buried (Wada & Yoshida, 2000; Stevens et al., 2002).

Aestivation

Ampullariids can tolerate prolonged drying of their shallow freshwater habitats (Lal & Saxena, 1952; Meenakshi, 1956, 1964; Little, 1968; Wada & Yoshida, 2000; Yusa et al., 2006b), and dormancy seems to be a contingent event precipitated by the dry down of their habitats. Although some species switch to anaerobic respiration at some stage during dry-down events, the capacity for aerial gas exchange is particularly significant during such events, when the snails burrow in the mud (Meenak-shi, 1956, 1964; Burky et al., 1972; Thomas & Agard, 1992). The behavior displayed dur-ing experimental induction of aestivation and arousal from it are similar in P lineata and P canaliculata, but the process of entering aes-tivation takes 2-4 times longer in P lineata (Little, 1968; Giraud-Billoud et al., 2011). Only in P urceus is this dry dormancy thought to be an obligatory part of the life cycle, as drying conditions are a cue for the onset of reproduc-tion (Ramnarine, 2003; see Life History). Mortality during aestivation in Pomacea species may be affected by duration, water conditions and body size (Little, 1968; Burky et al., 1972; Fan et al., 2000; Darby et al., 2003; Giraud-Billoud et al., 2011). Species differences seem particularly evident in mor-tality as a function of aestivation duration, but detailed comparisons are difficult, because most reports are of extreme survival times rather than changes in mortality rate over time (Cowie, 2002; Giraud-Billoud et al., 2011). Percent body mass loss during aestivation may be critical for survival. In P canaliculata, a ~50% loss of body mass was accompanied by a relatively low mortality rate and appeared mostly related to water loss (Giraud-Billoud et al., 2011). Mortality rates were similar in both laboratory and semi-field conditions (Yusa et al., 2006b; Giraud-Billoud et al., 2011). A similar figure for body mass loss was reported for P. lineata by Little (1968), but Meenakshi (1964) reported only a 5% loss in Pila globosa. Water loss may be limited by rising solute concentrations and hence the osmolality of body fluids. Urea and both uric and lactic ac-ids are accumulated during water deprivation in several ampullariids (see Giraud-Billoud et al., 2011, for references) and may help to retain water, as in other gastropods (Withers

et al., 1996). However, the actual increase in osmolality during aestivation in P. lineata was lower than expected on the basis of water loss alone (Little, 1968). In fact, deposition of uric acid in urate tissues may reduce osmolality by removing this purine from circulation (Giraud-Billoud et al., 2011).
Reduction in metabolic rate is also important for long-term survival during aestivation and/or hibernation because the greater the reduction in metabolic rate, the longer a fixed nutritional reserve can sustain basal metabolism (Sto-rey, 2002). Reduction of oxygen consumption (Burky et al., 1972) and eventual shifting to anaerobic metabolism (in some species) may thus occur during aestivation. Both Pila globosa and P. urceus accumulate lactic acid during aestivation, according to Meenakshi (1956) and Burky et al. (1972), respectively, indicating such a shift.
A physiologically significant challenge that limits survival after dormancy is tissue reoxy-genation during arousal (Hermes-Lima et al., 1998), which is more sudden after aestivation (and hence, more challenging) than after hibernation. The damaging effects of tissue reoxygenation may be worse than those of the preceding hypoxia (Hermes-Lima et al., 1998). Pulmonates have evolved a variety of enzymatic mechanisms that allow them to endure oxyradical production during tissue reoxygenation (Hermes-Lima et al., 1998; Hermes-Lima & Zenteno-Savin, 2002; Ramos-Vasconcelos et al., 2005), and recently enzy-matic and non-enzymatic antioxidant defense mechanisms have been characterized during the activity-aestivation cyle in Р canaliculata (Giraud-Billoud et al., 2011, 2013b). Nothing else is known of the process of reoxygenation following dormancy in ampullariids, and this is an area where additional ecophysiological research may provide crucial insights.
In P. canaliculata there is an array of tissues containing intracellular urate crystalloids, which exhibit a sequential process of formation and lysis, suggesting active turnover of uric acid (Giraud-Billoud et al., 2008). Urate tissues begin to differentiate several days before hatch-ing (Koch et al., 2009). Although such tissues have not been reported in other ampullariids, uric acid accumulates during aestivation in both Pila globosa and Pila virens (Lamarck, 1822) (Meenakshi, 1964; Reddy et al., 1974; Chaturvedi & Agarwal, 1981). Uric acid concen-tration increases in soft tissues of P. canalicu-lata during aestivation, and drops after arousal.

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Also the concentration of allantoin, a urate oxidation product, increases in kidney and foot
tissue after arousal, indicating that uric acid is
used as a significant antioxidant defense in the activity-aestivation cycle (Giraud-Billoud et al.,
2011, 2013b). Reduced glutathione also seems to participate as an antioxidant in the activity-aestivation cycle. Furthermore, changes in the expression of molecular chaperones (Hsc 70, Hsp 70s, Hsp 90) indicate they may participate in protecting the proteome during aestivation and arousal (Giraud-Billoud etal., 2013b). Sun et al. (2013) quantified and compared 701 proteins isolated from P. canaliculata dur-ing the activity-aestivation cycle, revealing 53 proteins that were differentially regulated dur-ing the cycle. Proteins known to be critical for translation, duplication and energy production were all down-regulated during aestivation, probably because the snails need to conserve resources during aestivation and therefore become hypometabolic. Likewise, hydrocar-bon digesting enzymes were down-regulated. Proteins related to lipid metabolism were up-regulated, which is consistent with the use of lipids as an energy source during fasting. In the context of enzymatic and non-enzymatic protection against oxidative damage, catalase and a small heat shock protein (SHsp) were up-regulated during aestivation (Sun et al., 2013). Also, two proteins participating in uric acid synthesis were up-regulated, which is in agreement with the central role of this purine as an antioxidant during the activity-aestivation cycle (Giraud-Billoud et al., 2011, 2013b). The accumulation of uric acid in both active and aestivating ampullariids may also serve other functions (Athawale & Reddy, 2002; Vega et al., 2007; Giraud-Billoud et al., 2011). Ampullariids may be confronted with drastic environmental changes during which the avail-ability and demand for combined nitrogen may change, and a nitrogen store in the form of uric acid may be adaptive. The reuse of nitrogen contained in uric acid requires its oxidation to allantoin, and then conversion to smaller molecules that can enter the pathways for amino acid and nucleic acid synthesis (Nelson & Cox, 2004). Uric acid oxidation may occur non-enzymatically (acting as an oxyradical scavenger) or may be catalyzed by urate oxi-dase. Urate oxidase activity has been found in the midgut gland, foot, lung and gut of P canaliculata (Giraud-Billoud et al., 2011) and in several symbiotic gut bacteria (Koch et al., 2014). However, the incorporation of uric acid

nitrogen into protein and nucleic acids has not been demonstrated directly in ampullariids.

Hibernation and Cold Hardiness

Hibernation in ampullariids has not received as much attention as aestivation, perhaps be-cause most ampullariid species live in tropical or subtropical regions. However, Р. canaliculata occurs widely intemperate zones of Argentina, as far south as 38°S (Albrecht, 1998; Martin et al., 2001), and invasive populations in Japan also reach similar latitudes (approx. 36°N), withstanding cold temperatures and freezing conditions (Oya et al., 1987; Ito, 2002). During the coldest months in temperate climates, the snails hibernate lying on the bottom or burying in the mud (Seuffert et al., 2010), but the physiological changes during the activity-hibernation cycle have not been studied. Instead, recent work on P. canaliculata has been focused on the related subject of cold hardiness. In invaded areas of temperate Japan, snails increase their cold tolerance before the onset of winter (Wada & Matsukura, 2007; Matsukura et al., 2008). The gradually decreasing temperature in autumn is the main environmental cue to enhance cold tolerance (Matsukura & Wada, 2007). Dry conditions enhance cold tolerance, but photoperiod has no clear effect. After winter, cold tolerance of overwintered snails decreases (Matsukura et al., 2009b).
Cold-tolerant snails in winter accumulate glyc-erol and possibly glucose in their bodies while glycogen concentration decreases (Matsukura et al., 2008). Among other low-molecular-weight compounds, glutamine and carnosine con-centrations increased while phenylalanine decreased. These compunds may be acting as cryoprotectants, as they do in insects (Lee, 1991; Storey & Storey, 1997), preventing protein denaturation and membrane damage (Michaud et al., 2008; Sjursen & Somme, 2000). However, glycerol concentration in the snails was much lower than in many insects, and no differences in supercooling points were observed in snails with or without cold tolerance (Lee, 1991; Mat-sukura et al., 2008, 2009a).
Death of P. canaliculata may occur at tem-peratures as high as 10°C, well above the temperature (ca. -7°C) at which the snails freeze (Wada & Matsukura, 2007; Matsukura & Wada, 2007; Matsukura et al., 2009b). The mechanism of lethal injury by chilling in the ab-sence of freezing is not well understood, and so

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the actual function of glycerol in Р canaliculata is unknown.
Cold tolerance appears to have evolved in ampullariids well before they became invasive species (Seuffert et al., 2010), as populations ofP. canaliculata established in the Philippines have never experienced cold temperatures in the three decades since their introduction, yet individuals are able to enhance their cold tolerance (Wada & Matsukura, 2011). Similar responses are noted with snails from northern Argentina (Yoshida et al., 2014). Pomacea canaliculata may not have successfully colo-nized these temperate areas without some abil-ity to adapt to cold conditions (Ito, 2002; Yoshida et al., 2009), and juveniles of Р canaliculata are more tolerant to both cold and desicca-tion than those of P maculata (Yoshida et al., 2014). (Unfortunately, the specimens identified by Yoshida et al. (2014) as P maculata are almost certainly a much more narrowly distrib-uted species, which would lead to considerably different interpretations of their data; Hayes, unpublished.). Linkage of cold tolerance with desiccation tolerance is found in both temperate and tropical snails: cold-tolerant snails survive longer after desiccation exposure than cold-intolerant snails (Wada & Matsukura, 2011). There are often similarities in the mechanisms underlying adaptation to cold and desiccation, notably accumulation of metabolites including polyols and sugars, and adjustments of water content and habitat choice (Ring & Danks, 1994; Michaud et al., 2008). Because the most impor-tant abiotic stress on snails in the tropics seems to be drought, this linkage may contribute to retention of the ability to adapt to cold.

FOOD, FEEDING AND DIGESTION

Feeding has been a major focus of recent ampullariid research. In contrast to the majority of freshwater caenogastropods, which tend to be phytophagous, omnivorous or deposit feed-ers (Dillon, 2000; Strong et al., 2008), many ampullariids are generalists and capable of feeding on a variety of items such as biofilms, periphyton, floating, submerged and emergent macrophytes, living animals and animal carrion (Cowie, 2002).

Phytophagy and Preferences

Macrophytes, periphyton and plant detritus are the main food items for ampullariids (Fell-

erhoff, 2002; Shuford et al., 2005; Kwong et al., 2010). Some species can detect macrophytes from a distance (Estebenet, 1995). While they generally are not known as major pests in their native ranges (Cazzaniga, 2006), P maculata and P canaliculata cause major damage to wet-land agriculture, notably to rice, taro and semi-aquatic vegetables, in their invaded ranges (Joshi & Sebastian, 2006). Pomacea species also have direct grazing effects on macrophytes in non-agricultural wetlands (Carlsson & La-coursiere, 2005; Burlakova et al., 2009; Wong et al., 2009; Fang et al., 2010) and indirect ef-fects on wetland water quality and ecosystem processes (Carlsson et al., 2004а).
Given the substantial impact of grazing by Pomacea species on macrophyte diversity and ecosystem processes, several labora-tory studies have examined their feeding on macrophytes: P. canaliculata in Argentina (Estebenet, 1995), Hawaii (Lach et al., 2000) and Hong Kong (Qiu & Kwong, 2009; Fang et al., 2010; Wong et al., 2010), and Р macu-lata in the U.S.A. in Georgia (Morrison & Hay, 2011a), Texas (Boland et al., 2008; Burlakova et al., 2009; Burks et al., 2011) and Florida (Baker et al., 2010). These studies show that although these species will feed on a diversity of plant species, they do exhibit preferences among them. Snails feeding on their preferred macrophyte species exhibit higher growth rates than snails that have access only to unpalatable food; these snails feed very little, have a low survivorship and grow little.
Other species seem to prefer periphyton, metaphyton (floating mats of detached benthic algae) or floating algae (Rich, 1990; Browder et al., 1994; Sharfstein & Steinman, 2001; Shuford et al., 2005; Morrison & Hay, 2011a). Some species are capable of feeding by pedal surface collecting (McClary, 1964; Cazzaniga & Estebenet, 1984; Saveanu & Martin, 2013), in which particles on the water surface are collected by ciliary action of the foot sole and periodically ingested. Periphyton is a major food source of Р paludosa but vascular plant material may also be important (Rich, 1990) and this species feeds readily on Chara sp. (muskgrass) and Najas marina (spiny naiad) in the field (Hurdle, 1973).
Food preference in herbivores is affected by several characteristics of the plants (Lodge, 1991). Physical defenses include external and internal structures that deter grazing (e.g., spines, hairs, tough leaves, cellulose, lignin). Studies of physical defenses against grazing

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by ampullariids have used toughness (Qiu &
Kwong, 2009) and dry matter content (DMC),
with snail feeding rate in both P. canaliculata
and P. maculata negatively correlated with
DMC (Burlakova et al., 2009; Wong et al.,
2010).
Plant secondary metabolites (e.g., phenolics, alkaloids, terpenes, wax) that are toxic or that interfere with digestion affect food preference in generalist herbivores (Lodge, 1991; Burks et al., 2006). The leaves of Myriophyllum spp. contain high levels of phenolic compounds (Burks & Lodge, 2002). Incorporating an extract of Myriophyllum spp. into reconstituted but otherwise palatable food reduces the feeding rate of Р canaliculata and P. maculata, and, when fed on Myriophyllum aquaticum alone, P. canaliculata do not grow or reproduce (Boland et al., 2008; Qiu & Kwong, 2009; Wong et al., 2010). Non-phenolic secondary plant metabo-lites may also be involved in defense against ampullariids. For instance, Alternanthera philoxeroides containing low phenolic content and a medium level of DMC was not palatable to P. canaliculata, and an A. philoxeroides extract greatly reduced its feeding rate (Wong et al., 2010). Pomacea canaliculata will use both fresh and decaying macrophyte leaves as long as they contain adequate levels of nutrients and low levels of phenolics (Qiu et al., 2011). Ampullariid grazing can also induce the production of unidentified defense chemicals (Morrison & Hay, 2011b).
Preferences also reflect the nutritional value of the plants, with snails preferring to feed on plants with higher nitrogen, phosphorous and chlorophyll content than those that are more easily digested but with lower amounts of nutritionally important compounds (Grantham et al., 1993; Sharfstein & Steinman, 2001; Wong et al., 2010). Similarly, growth rate and egg production were positively correlated with phosphorus and nitrogen content, respectively (Qiu & Kwong, 2009).

Intraspecific Variation in Feeding and Assimi-lation

Specific ingestion rates (weight:weight) decrease inversely with snail size (Haniffa & Pandian, 1974; Haniffa, 1980; Boland et al., 2008; Burlakova et al., 2009; Tamburi & Martin, 2009a). This has been related to an allometric decrease in the gut cross-sectional area rela-tive to the biomass that must be nourished as body size increases (Tamburi & Martin, 2009b)

and is probably coupled to an ontogenetic de-
crease in metabolic rate. Similarly, gender dif-
ferences in ecophysiological performance can be substantial in some species. For instance, the specific ingestion rate in P. canaliculata is 50% higher in females than males of the same size (Tamburi & Martin, 2009a), perhaps related to the smaller mid-gut gland of males (61-72% the size of that of females) (Koch et al., 2006), which may restrict the amount of food that can be processed per unit time. Growth rates in male P. canaliculata are lower than in females, probably also as a consequence of their smaller mid-gut glands, which in turn results in lower food assimilation (Tamburi & Martin, 2009b). These findings, in combination with a tendency to mature later (Tamburi & Martin, 2009b), may explain the common pattern of females growing to be larger than males (Estebenet & Martin, 2002, 2003; Estebenet et al., 2006). This size difference was also seen in M. cornuarietis by Demian € Ibrahim (1972), P. urceus by Burky (1974) and Lum-Kong & Kenny (1989), P. paludosa by Hanning (1979) and Pila spp. by Keawjam (1987), although the possibility ofdif-ferent ingestion rates or growth efficiencies has not been investigated in these species.
In Р canaliculata some studies have shown that young snails are microphagous, chang-ing to macrophytophagy when reaching 15 mm shell height (Halwart, 1994; Schnorbach, 1995). However, Carlsson & Brönmark (2006)
found no ontogenetic changes in diet in this
species, although they did indicate that small snails had higher specific grazing rates, inter-preted as higher competitive abilities. Also, hatchlings will survive and grow when fed only fresh vascular plants in the laboratory (e.g., Es-tebenet & Cazzaniga, 1992, 1998; Estebenet, 1995; Tamburi & Martin, 2009b; Qiu & Kwong, 2009). Furthermore, the relative preference for different macrophytic plants does not change with age (Estebenet, 1995), although large and small snails may feed on different parts of the
same plant (Carlsson & Brönmark, 2006). In
Pila globosa, the relative weight of the radula is inversely related to body weight, which was suggested as the cause of declining feeding rates as the snails grow (Haniffa & Pandian, 1974).

Feeding on Other Animals

Some ampullariids will prey on the eggs, juve-niles and adults of various other snail species (Demian & Lutfy, 1965a, b, 1966; Cedeño-Leôn

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& Thomas, 1983; Cazzaniga, 1990; Aditya & Raut, 2002; Anto et al., 2005; Wong et al., 2009). For this reason, they have been pro-posed as biocontrol agents against other snail species that are intermediate hosts of human parasites (e.g., Pointier et al., 1988, 1991) as well as against invasive plants, although such approaches can have serious non-target im-pacts and have been criticized (Cowie, 2001). In Asia, the invasion of Р canaliculata may have caused a delay in reproduction and a longer recruitment period in Radix plicatulus (Benson, 1842), perhaps in response to high juvenile mortality from apple snail predation (Lam, 1994). Pomacea canaliculata has also been suggested as causing the decline of Pila species, but whether this occurred through pre-dation or competition remains unclear (Acosta & Pullin, 1991; Halwart, 1994). Apple snails will even consume conspecific eggs (Horn et al., 2008; Tiecher et al., 2014; Saveanu & Martin, 2014), hatchlings and juveniles (Yusa et al., 2006a).
Ampullariids may prey on other small ani-mals, such as freshwater oligochaetes (Aditya & Raut, 2001) and bryozoans (Wood et al., 2005, 2006), as well as eggs of fish (Phillips et al., 2010) and amphibians (Karraker & Dud-geon, 2014). They will also feed on many kinds of carrion, for example, dead frogs (Cowie & Hayes, personal observation) and fish (Qiu, personal observation).
It is not known whether some species are capable of detecting their animal prey at dis-tance. However, their large size and a crawling speed that is faster than their prey allow them to search a large area and thus enhance their prey encounter rate; the predation rate varies with the species and life stage of the predator and the size, shape, and shell crushing resistance of the prey (Kwong et al., 2009). Consumption rates vary widely among and within species (Cedeño-León & Thomas, 1983; Cazzaniga, 1990; Aditya 8 Raut, 2002; Anto et al., 2005; Kwong et al., 2009).

Digestion

Polysaccharides, including cellulose and hemicellulose (the major components of plant cell walls) and starch (a cytoplasmic compo-nent), are universally present in the diet of ampullariids. The ability of P. canaliculata to digest cellulose (Vega et al., 2006) has recently been confirmed by cloning and expression of two endogenous cellulases (Imjongjirak et al., 2008). Another cellulase produced by an

endosymbiotic Bacillus has been reported in a species that is probably also P. canaliculata (Zhang et al., 2007). Hemicellulose can be hydrolized by endo-1,4-B-D-xylanase, which has been purified from soft tissue extracts of P. canaliculata (Yamaura et al., 1997), and starch can be hydrolyzed by an amylase found in the midgut gland (Sun et al., 2013). Carbohydrate residues can be released from macromolecules by several enzymes (a-and
B-mannosidase, B-N-acetylglucosaminidase,
B-galactosidase and a-fucosidase; Hirata et al., 1996, 1998a-c).
Several proteases have been reported in P canaliculata, including one produced by the salivary glands and two in the intestine; one associated with С and К morphotypes of an en-dosymbiont released from midgut gland cells, is ubiquitous in the digestive tract (Godoy et al., 2013) (see Symbiotic Associations).

PREDATORS AND PREDATOR
AVOIDANCE

Predators

The best-known natural enemies of apple snails throughout much of their natural range in North, South and Central America include limpkins (Aramus guarauna) and snail kites (Rostrhamus sociabilis), for which apple snails are the almost exclusive food source (Snyder & Snyder, 1969; Snyder & Kale, 1983; Tanaka et al., 2006; Mapelli & Kittlein, 2011; Bergmann et al., 2013). Predation presents a strong selec-tive pressure on shell color and shell size of Central American Pomacea flagellata (Reed & Janzen, 1999), and is likely to have similar effects on other apple snail species, includ-ing Р paludosa (Darby et al., 2007; Cattau et al., 2010). In Florida, although the snail kite's natural prey is Р paludosa, since the introduc-tion of P maculata (Rawlings et al., 2007), this non-native species has become a common prey, despite the kites’ difficulty in handling the largest individuals (Darby et al., 2007; Cattau et al., 2010; Pomacea Project, 2013).
In their native range, apple snails are also eaten by caimans (Alligatoridae) (Halwart, 1994; Laporta-Ferreira & Salomäo, 2004) cai-man lizards (Dracaena spp., Teiidae) (Perera & Walls, 1996) and a wide range of avian and aquatic predators that target all size classes. These include more generalist avian predators such as boat-tailed grackles (Quiscalus major) and white ibis (Eudocimus albus), aquatic

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predators such as redear sunfish (Lepomis microlophus), turtles (Тпопух ferox, Trachemys
scripta elegans, Sternotherus spp., Kinoster-
non spp.) and alligators (Alligator mississip-
piensis) (reviewed in Pomacea Project, 2013;
Burks, unpubl. dat.).
Yusa (2006b) provided a relatively compre-hensive but non-exhaustive list of known preda-tors of invasive apple snails in Asia, including 46 species in 16 orders. This list, together with additional predators noted by other authors in-dicates apple snails are on the menu for a wide array of insects, crustaceans, fish, reptiles, leeches, birds and mammals (Yusa et al., 2000; Yusa, 2001; Ichinose et al., 2002; Carlsson et al., 2004b; Wong et al., 2009; Sawangproh & Poonswad, 2010).
The relatively small size of many Pomacea hatchlings (e.g., Р canaliculata shell height < 3 mm; Hayes et al., 2012) and their relatively thin shells allow them to be readily consumed. An additional suite of predators target juvenile apple snails in their native range including crayfish (Procambarus sp.) and aquatic insects (water bugs, Belostoma sp.; dragonfly naiads, Coryphaeschna ingens; and diving beetles, Dytiscus marginalis) (Snyder & Snyder, 1971). However, in general, apple snails become decreasingly vulnerable to predation with size, and after reaching 20 mm, relatively few preda-tors in the non-native range in Asia can prey on them. The effectiveness of carp, tilapia, ducks and turtles has been evaluated in the field in the context of biological control (Yusa, 2006b; Yoshie & Yusa, 2008, and references therein). Each of them acts fairly well as a biocontrol agent, although their use may have negative impacts on other aquatic animals and plants (Yoshie & Yusa, 2008; Wong et al., 2009). Direct comparisons of predation pressures on native snails and introduced Pomacea have been few, but two species of rats both prefer P. canaliculata over native Semisulcospira libertina (Gould, 1859) or Radix quadrasi (Мб|- lendorff, 1898), respectively (Yusa et al., 2000; Joshi et al., 2006). In the laboratory, common carp readily consume P. canaliculata while rejecting the thicker-shelled Sinotaia quadrata (Benson, 1842) (Kwong et al., 2009). In Japan, while apple snails rapidly multiply in rice fields and other shallow wetlands with few predators (Yusa, 2006b), predators seem to effectively control their populations in canals, creeks and rivers (Yusa, 2006b; Yusa et al., 2006a) in an apparent example of biotic resistance to an invasive species (Yamanishi et al., 2012).

Predator Avoidance

In addition to the fact that the largest Poma-cea individuals are not readily preyed upon, these species exhibit two major predator avoid-ance strategies: chemical defenses during the egg/hatchling stages (see Egg Proteins: Structure and Role in Defense) and predator avoidance behaviors.
The presumably aposematic color of Pomacea eggs is due to pigmented proteins that adver-tise the presence of neurotoxins, antinutrivitve proteins and digestive inhibitors at least in P. canaliculata (Heras et al., 2008; Dreon et al., 2010, 2013). Eggs of various Pomacea species have been reported as being ingested by a few species, including ants, Hemiptera and Or-thoptera, but only the fire ant Solenopsis gemi-nata is known to consume them significantly (Yusa, 2001, 2006a). Other observations of birds (Guimaraes, 1981b), fish, a frog and a millipede (Snyder & Snyder, 1971), a land snail (Ng & Tan, 2011) and turtles (Burks, unpublished) all require additional study to ascertain whether they represented anything more than acciden-tal ingestion or ingestion only under captive experimental conditions. Whether other apple snail eggs deposited above water but lacking pigmentation (i.e., Pila spp.) or laid under water possess such protections is not known. Ampullariids avoid predators by crawling out of the water, situating themselves near the water surface, burying themselves in the mud, and falling from substrates on which they were crawling (Snyder & Snyder, 1971; Ichinose, 2002; Ichinose et al., 2003; Carlsson et al., 20045; Aizaki & Уиза, 2009, 2010). In P canaliculata, these behavioral repertoires are size-dependent: hatchlings tend to crawl out of the water; juveniles mainly bury themselves or use near-surface habitats; larger snails are less responsive (Ichinose, 2002). These behaviors are in part innate, but can be learned in some instances when exposed to novel predators (Aizaki & Yusa, 2010) and may be predator specific (Ueshima & Yusa, 2014). These di-verse strategies have surely played a role in their success in the native range and probably also enhance invasiveness.

EGG PROTEINS: STRUCTURE AND
ROLE IN DEFENSE

The main components ofthe egg vitellus (lip-ids, proteins, carbohydrates) are incorporated

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during vitellogenesis into primary oocytes to serve mainly as energetic and structural sourc-esforthe developing embryo. Most gastropods, however, contain a limited amount of vitellus, and instead, egg reserves are accumulated sur-rounding the fertilized oocyte as a perivitelline fluid (De Jong-Brink et al., 1983).
The successful strategy of laying eggs above water results in a variety of selective challenges as the eggs are exposed to stressful environ-mental conditions that may affect embryonic development and survival of offspring (Prze-slawski, 2004). Ampullariids have evolved to handle these challenges through the production of several egg proteins found in the perivitell-ine fluid, referred to as perivitellins. Although the eggs of many snail species face intense predation pressure, those of Р canaliculata have very few predators (Yusa, 2001) (see Predators and Predator Avoidance) because of a suite of chemical defenses provided by the perivitellins. These defenses are advertised by the conspicuous color of the eggs (Heras et al., 2007).
At the biochemical level, the eggs of at least some Pomacea species possess a unique group of perivitellins, which are multifunctional complexes functioning in storage, predator defense and protection from the environment (e.g., Dreon et al., 2008, 2013). In spite of the central role of perivitellins in reproduction and development, there is little information on their structural features in invertebrates. Studies in molluscs are limited essentially to the perivitell-ins of Pomacea, mostly in P. canaliculata but also P. scalaris and Р maculata (Ituarte et al., 2012; Pasquevich et al., 2014).

Perivitellin Structure and Synthesis

Two major perivitellins, now known as PcOvo and PcPV2, have been characterized from the perivitelline fluid of P. canaliculata (Chees-man, 1958; Garin et al., 1996; Dreon et al., 2004a, 2010, 2013; Ituarte et al., 2010; Sun et al., 2012b). Both perivitellins are multimeric proteins with remarkabe thermal stability up to 100°C and 60°C, respectively, and over a wide range of pH (Dreon et al., 2008; Frassa et al., 2010). They are highly resistant to the com-bined action of pepsin and trypsin proteases, and PcOvo has proteinase inhibitor activity (Norden, 1972; Dreon et al., 2010).
The perivitelline fluid of P. scalaris contains two major perivitellins, of which only the pig-mented one, PsSC, which is structurally similar

to PcOvo, has been characterized (Ituarte et
al., 2008, 2012). The perivitelline fluid of P
maculata is also similar, with two major perivi-tellins, PmPV1 and PmPV2 (Pasquevich et al., 2014). PcOvo, PSSC and PmPV1 act as carriers of antioxidant carotenoid cofactors, notably astaxanthin, which are extremely labile in solution but are not degraded when bound to the perivitellins (Ituarte et al., 2008; Pasquevich et al., 2014). PcOvo and PsSC also carry phosphate groups attached to serine residues that may serve as a phosphorous reserve for the embryo, as do other egg proteins (Ituarte et al., 2010).
Synthesis of PCOvo and PcPV2 occurs in the albumen gland with no circulating perivitellin precursors in the hemolymph (Dreon et al., 2002, 2003). Analysis of the albumen gland transcriptome indicated that other compo-nents of the perivitelline fluid, as well as these perivitellins, are also exclusively synthesized in the albumen gland (Sun et al., 2012b). In the parenchymal mass of this gland, albumen secretory cells and labyrinth cells are involved in the synthesis of perivitelline fluid, but only the albumen secretory cells are involved in PcOvo and PcPV2 synthesis, with both proteins packed into the same secretory granules, to-gether with galactogen (Catalan et al., 2006).

Perivitellin Functions

Analysis of the perivitellin sequences of Р canaliculata, based on the Kyoto Encyclopedia
of Genes and Genomes (KEGG), classified
the 59 sequenced proteins into “unknown” (34),

“environmental information processing”
(10),

“metabolism” (7),

“organismal systems”
(2),

“cellular processes” (3), and “others” (3). Among the “environmental information pro-cessing” cluster, nine proteins are related to innate immunity (Sun et al., 2012b). These results indicate that maternal investment in P. canaliculata eggs is complex.
In P canaliculata PcOvo and PcPV2 are storage proteins that provide energetic and
structural precursors for the embryos, since
they are consumed during development (Heras et al., 1998). The different glycosylation pat-terns of these two perivitellins probably allow the differential uptake and protein targeting observed during embryogenesis (Heras et al., 1998). In addition, PcOvo carries and stabilizes astaxanthin within the perivitelline fluid and when embryos take up PcOvo (Heras et al., 1998), this potent antioxidant carotenoid can be

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incorporated into their cytoplasmic membranes
for protection, while providing the pink-reddish
color of the eggs (Dreon et al., 2004b). PcOvo
also helps eggs cope with the harsh above-
water conditions. First, the saccharide moiety
of PcOvo, together with the high levels of galactogen in the perivitellline fluid (Heras et al., 1998), prevents egg desiccation. Second, the pigmented perivitellins may also protect the embryos against solar radiation, acting as filters (Dreon et al., 2004b).
PcPV2 is a potent neurotoxin (Heras et al.,
2008). Each of the four dimeric units of PcPV2
consists of a carbohydrate-binding protein
(probably the targeting module) attached to a pore-forming subunit (probabltyhe toxic moi-ety). Due to their high pH stability and protease resistance, the dimers are able to reach the in-testine while still biologically active and to bind to enterocytes, eventually reaching the circula-tory system. PcPV2 is the first proteinaceous egg neurotoxin reported, and bears structural resemblance to botulinic and ricin heterodi-meric toxins, the so called “AB toxins” previ-ously only known in bacteria and plants (Dreon et al., 2013). However, as PcPV2 is rather slow-acting (at least in mice) it seems unlikely that it could by itself account for the extremely low levels of predation. Some sort of synergy occurs with PcOvo, which rapidly decreases rat growth when administered orally, probably involving both the inhibition of trypsin activity (antidigestive role) and resistance of the protein to digestion by gut enzymes (antinutritive role), thereby limiting the predator’s capacity to digest egg nutrients (Dreon et al., 2010).
PcOvo and PcPV2 are also present in the
midgut gland of new P canaliculata hatchlings. In the laboratory, goldfish (Carassina gibelio) will not eat new hatchlings after they sample them (Yusa, personal observations). Similar observations have been made on eggs of P. paludosa (Snyder & Snyder, 1971; Romer, 1972). Also, the albumen gland cytosol of Р canaliculata is lethal to mice after intraperito-neal administration (Cadierno, Dreon & Heras, unpublished). The toxicity seems to be due to the presence of an active PcPV2 neurotoxin as the mice showed similar signs to those exhibited by mice that had been administered purified PcPV2 (Cadierno, Dreon & Heras, unpublished). It is possible that toxic perivi-tellins together with still unknown compounds present in the albumen gland of adult Pomacea females may explain why some predators avoid eating the gland while consuming the

rest of the body, as for example rats and crows in the non-native range and the snail kite and limpkins in the native range (Yusa et al., 2000; Heras, personal observations; Yusa, personal observations).
In P. scalaris, apart from its assumed nutritive role, PSSC acts as a carotenoid carrier, giving pigmentation to the eggs and supplying the embryos with antioxidant molecules, as does PcOvo (ltuarte et al., 2008). However, unlike PcOvo, this perivitellin is a carbohydrate bind-ing protein, which agglutinates erythrocytes, showing a high specificity for galactosamine and glucosamine containing glycans (Ituarte et al., 2012). Carbohydrate binding proteins may have an immune function, agglutinating bacteria or other pathogens. However, given that PcSC is resistant to pH changes and gas-trointestinal digestion, it may also have an an-tipredator function; there are multiple examples of a similar function in plants, in which lectins from seeds protect the embryos (Peumans &
Van Damme, 1995). Although P. scalaris eggs
do not possess an active PcPV2-like toxin, and the perivitelline fluid seems non-toxic to mice (Ituarte, personal observations), predation on these eggs has not been reported.

Evolutionary and Ecological Implications of Egg Defenses

Pomacea canaliculata is the first animal known to deter predation with a combination of antinutritive, antidigestive and neurotoxic compounds, a widespread defensive strategy in plants. Among predator avoidance tactics, conspicuous coloration advertises antipreda-
tor defense across many taxa. However, P.
canaliculata eggs are unusual in that PcOvo not only provides the warning signal but also par-ticipates in the biochemical defense. Another unusual aspect is that the defensive molecules are at the same time storage proteins that are later consumed by embryos and hatchlings (Heras et al., 1998), making synthesis particu-larly cost-effective. Also, as the toxins are pro-teins, females do not need to ingest toxic prey to endow the eggs with chemical defenses,
a common practice in other organisms. The
multiple functions of these egg proteins are summarized in Figure 4.
Considering that aerial eggs with conspicuous coloration are frequent across the Ampullarii-dae, biochemical defenses similar to those of P. canaliculata are probably more widespread in the genus, providing a potentially important

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PcOvo

fraction

Pepva rn

Reduce egg digestibility

PcPV3

Neurotoxic

(Antinutritional)

Proteinase inhibitor

(Antidigestive +
protect toxic components)

Warning coloration
(Aposematic)

FIG. 4. The multiple roles of egg proteins in Pomacea canaliculata.

model for the study of the evolution of apos-
ematism and defense using perivitellins (Heras
et al., 2007; Dreon et al., 2010).

SYMBIOTIC ASSOCIATIONS

Ampullariids have established an amazing
variety of symbiotic associations, but like much of the other information for apple snails, knowl-edge ofthese symbioses comes primarily from studies of P. canaliculata.

Epibiotic Organisms

The periostracum of relatively large and slowly moving snails like apple snails provides a potential surface for the attachment of many aquatic organisms. Di Persia & Radici de Cura (1973) described diverse assemblages of epibionts including filamentous cyanobacteria, chlorophytes and chrysophytes, and sessile ciliates, with a diverse assemblage of motile organisms living within this algal mat, including euglenophytes, ciliates, rotifers, annelids and dipteran larvae. Additional epibionts recorded on apple snails include the colonial sessile peritrich Epistylis plicatilis (Vega et al., 2006; Utz, 2007), the ectoproct Hyalinella vaihiriae (see Cazzaniga, 1988) and naidid oligochaetes in the umbilicus (Gorni & Alves, 2006).

Endosymbiotic Animals

Numerous animal taxa have been reported in the mantle cavity, hemocoel or connective tissue as symbionts of various ampullariids

(Table 4). Leeches are the most frequently reported annelids in the mantle cavity. All life stages of Helobdella ampullariae (juveniles, adults and adults with both cocoons and broods) were found inside P. canaliculata but never free in the habitat (Damborenea & Gullo, 1996). The abundance of H. ampullariae on P canaliculata increases with host size, with up to 65 in the largest snails. Transmission of the symbiont seems to occur during copulation (Damborenea & Gullo, 1996). Adult brooders and juveniles of H. ampullariae were also found in autumn and winter, while the four other Hirudinea species were only found dur-ing the spring and summer (Damborenea & Gullo, 1996).
Although the two cyclopoid copepods (Table 4) are found in the hemocoel, Ozmana huarpium is more common in the mantle cavity (63-65% of mature forms), where it occurs mainly in the ctenidium (in both sexes) and in the penial sheath groove in males. Female O. huarpium are more frequent than males in the mantle cav-ity, and mature females bearing egg sacs seem to be the infecting stage, and to be transmitted by copulation (Gamarra-Luques et al., 2004). Cyclopoid copepods are primarily marine spe-cies, but two of the ten recognized families are associated exclusively with freshwater hosts: the Lernaeidae with freshwater fish and the Oz-manidae with ampullariids (Ho, 1994; Boxshall & Strong, 2006).
Trematodes and nematodes occur in the mantle cavity, hemocoel and connective tissue of various organs or the gut lumen of ampullari-ids (Table 4; see Human Health Concerns). In addition, Keawjam et al. (1993) reported meta-

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TABLE 4. Animal endosymbionts of Ampullariidae.

Symbiont

Turbellaria
Temnocephala iheringi2

T. haswelli
T. rochensis
T. lamothei
Hirudinea
Helobdella ampullariae!

H. triserialis
H. simplex
H. adiastola
Gloiobdella michaelseni
Acari

Host ampullariid species

Pomacea canaliculata (Lamarck, 1822) Pomacea haustrum (Reeve, 1856) Pomacea lineata (Spix in Wagner, 1827) Pomacea megastoma (Sowerby, 1825) Asolene platae (Maton, 1811)
Pomacea canaliculata (Lamarck, 1822) Pomacea canaliculata (Lamarck, 1822) Pomacea megastoma (Sowerby, 1825)

Pomacea canaliculata (Lamarck, 1822) Pomacea megastoma (Sowerby, 1825)
Pomacea maculata Perry, 1810
Pomacea canaliculata (Lamarck, 1822)
Pomacea canaliculata (Lamarck, 1822)
Pomacea canaliculata (Lamarck, 1822)
Pomacea canaliculata (Lamarck, 1822)

Unionicola (Ampullariatax) Pomacea canaliculata (Lamarck, 1822) ampullariae!
Copepoda
Ozmana haemophila3
O. huarpium1,3
Trematoda

Cercaria pomaceae

Schistosomatidae

Echinostoma spp.

Echinostoma
parcespinosum
Dietziella egregia

Catadiscus pomaceae

Rotifera
Bdelloidea
Nematoda

Angiostrongylus
cantonensis

Pomacea maculata Perry, 1810

Pomacea maculata Perry, 1810 Pomacea canaliculata (Lamarck, 1822)

Pomacea paludosa (Say, 1829)

Pomacea canaliculata (Lamarck, 1822) Pomacea figulina (Spix in Wagner, 1827) Pomacea lineata (Spix in Wagner, 1827) Pomacea maculata Perry, 1810
Pila scutata (Mousson, 1848)
Pila spp.
Pomacea canaliculata (Lamarck, 1822) Pomacea canaliculata (Lamarck, 1822)

Pomacea canaliculata (Lamarck, 1822)

Pomacea canaliculata (Lamarck, 1822)

Pomacea canaliculata (Lamarck, 1822)

Pomacea canaliculata (Lamarck, 1822)

References

Damborenea, 1996: Dambore-
nea & Cannon, 2001; Martin
et al., 2005

Seixas et al., 2010a
Seixas et al., 2010b
Damborenea & Brusa, 2008

Ringuelet, 1945, 1985; Dambo-renea & Gullo, 1996

Damborenea & Gullo, 1996
Damborenea & Gullo, 1996
Damborenea & Gullo, 1996
Damborenea & Gullo, 1996

Di Persia & Radici de Cura,
1973

Ho & Thatcher, 1989
Gamarra-Luques et al., 2004

Hanning & Leedom, 1978;
Leedom & Short, 1981
Ostrowski de Nuñez, 1979; Di-giani & Ostrowski de Nuñez,
2000; Damborenea et al.,
2006; Thiengo, unpublished
Graczyk & Fried, 1998;
Weerachai et al., 2011

Martorelli, 1987

Digiani & Ostrowski de Núñez,
2000
Hamann, 1992

Vega et al., 2006

Lv et al., 2008, 2009a, b, 2011

(continues)

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(continued)

Symbiont Host ampullariid species References

Pomacea lineata (Spix in Wagner, 1827) Thiengo et al., 2010
Pomacea maculata Perry, 1810
Pomacea paludosa (Say, 1829)
Lanistes carinatus (Olivier, 1804)
Pila ampullacea (Linnaeus, 1758)
Pila virescens (Deshayes, in Bory de
Saint Vincent, 1824)5
Pila pesmel (Morlet, 1889)
Pila gracilis (Lea, 1856)
Pila scutata (Mousson, 1848)

1Detected in mantle cavity.
2Detected in lung.
3Detected in hemocoel.

Teem et al., 2013
Wallace & Rosen, 1969
Ibrahim, 2007
Punyagupta, 1965
Tesana et al., 2009

Tesana et al., 2009
Tesana et al., 2009
Tesana et al., 2009

4Perhaps incorrectly identified, as P. paludosa is not otherwise known from Hawaii (Cowie et al., 2007). SReported as Pila polita, which is an objective junior synonym of P. virescens (Cowie & Héros, 2012).

cercariae ofthree trematodes (an amphistome,
a distome and an echinostome) in introduced
P. canaliculata in Thailand.

Endosymbiotic Protists and Bacteria

Among protists, two species of large ciliates
have been found in the gut of P canaliculata (Gascön, 1975). Numerous coccoid or rod-like heterotrophic bacteria occur in the gut of ampullariids but almost no attempt has been made to identify them or to explore their func-tions, such as cellulose digestion (Vega et al., 2005). Several endoglucanases have been isolated from Pomacea *insularus” (probably P canaliculata or perhaps P. maculata) (Yamaura & Matsumoto, 1993; Yamaura et al., 1997; Li et al., 2005), which were probably of bacterial origin. Specifically, a cellulase is secreted by a Bacillus strain (Zhang et al., 2007) (see Diges-tion), and bacteria in the genera Pseudomonas, Enterobacter, Citrobacter and Lactoccocus degrade uric acid (Koch et al., 2014).

Intracellular Pigmented Corpuscles in the Midgut Gland

At least some ampullariids bear two types of intracellular pigmented corpuscles (named C and K corpuscles) in the midgut gland that are eliminated in the feces and for which a symbiotic nature has been proposed. These include the Neotropical Pomacea canaliculata, P maculata, P. scalaris, Marisa cornuarietis,

Asolene pulchella and A. spixii (d’Orbigny, 1838) (Castro-Vazquez et al., 2002; Vega et al., 2006; Takebayashi, 2013) and the Asian Pila virens (Meenakshi, 1955; Devi et al., 1981) and Pila scutata (Mousson, 1848) (as conica Wood, 1828, a junior synonym of scutata; Ng et al., 2014) introduced in Hawaii (Takebayashi, 2019);
Among all the symbiotic associations sum-marized here, this is the only one that appears to be obligate for the host, as the symbionts are present in all individuals of all studied popula-tions (Vega et al., 2006). Both morphotypes together account for 8-11% ofthe midgut gland mass (Vega et al., 2005). Because they have a plasma membrane and thick, electron dense wall, but lack a nucleus (Koch et al., 2006), they have been considered as prokaryotes. Even though axenic cultures of these corpuscles have not been obtained (Koch, 2008), mor-photype C may persist for at least 3 years in aquarium sediments that had contained fecal droppings of P canaliculata, while morphotype K tends to disappear with time (Koch et al., 2006).
Morphotypes C and K occur respectively in columnar and pyramidal cells of the midgut gland tubular alveoli (Koch et al., 2006). These cells originate in the midgut gland before hatching, before pigmented corpuscles can be recognized, and have been described in both Marisa cornuarietis by Demian & Yousif (1973b) and Р canaliculata by Koch et al. (2009) (see Development: Digestive Tract). Pyramidal cells

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have large nuclei and conspicuous nucleoli,
and are polyploid, with a nuclear DNA content
ranging from 4 to 16 С (Cueto et al., 2006).
This large DNA endowment is correlated with
great development of the rough endoplasmic reticulum (Koch et al., 2006, 2009), which may contribute to the secretion of the multiple lamel-lae of K corpuscles (Koch et al., 2006).
Both С and К corpuscles contain chlorophyll-like pigments identified as steryl pheophorbides (Vega et al., 2012b). However, because the shell filters out most photosynthetically active radiation (Dellagnola, 2010) and the pheophor-bides are not suitable for light harvesting, their significance is not clear. They may be inter-preted as evolutionary remnants in a formerly photosynthetic organism that has been strongly modified by endosymbiosis in darkness.

IMMUNE DEFENSES

Molluscs, as all invertebrates so far investi-gated, possess defense mechanisms analo-gous to those of the innate immune system of vertebrates that are based mainly on cellular responses and on circulating and fixed lectins (Ottaviani, 2006, 2011). They serve a variety of functions, such as recognition and phago-cytosis of invaders (Bayne, 1983), capsule formation around parasites (e.g., Yousif et al., 1980; Lv et al., 2009b), hemostasis, wound healing, shell formation and repair (Franchini & Ottaviani, 2000) and storage/transport of nutrients (e.g., Travers et al., 2008). Hemocytes have also been involved in stress response through the release of vertebrate-like endocrine molecules (Ottaviani et al., 1991). Development of in vitro culture systems for ampullariid hemocytes may be critical for understanding many aspects of their biology. However, a culture system has only been reported for Р canaliculata (see Cueto et al., 2013); it uses a medium mimicking the physi-cochemical and chemical characteristics of the snail’s internal milieu (Cueto et al., 2011).

Ampullariid Hemocytes

Substantial information has been gathered regarding hemocyte structure and function in the ampullariids Pila globosa (see Mahilini & Rajendran, 2008) and P canaliculata (Shozawa & Suto, 1990; Cueto et al., 2007, 2013, sub-mitted; Ray et al., 2012; Accorsi et al., 2013). Recent authors (Mahilini & Rajendran, 2008;

Ray et al., 2012; Accorsi et al., 2013) have used various names for the different kinds of hemocytes, but in an attempt to standardize the nomenclature, Cueto et al. (submitted) adopted the classical terminology of Cheng (1975), recognizing three types: agranulocytes, hyalinocytes and granulocytes.
Agranulocytes constitute 28% of circulating cells in Р canaliculata according to Cueto et al. (2013) and are likely to include circulating blasts (Ray et al., 2012; Accorsi et al., 2013), though this hypothesis needs testing. Hyalino-cytes are larger cells with membrane-bound granules of moderate electron density and may be lysosomes (Cueto et al., submitted). Approximately one quarter of circulating hyal-inocytes show phagocytic activity and may par-ticipate in circulation and storage of glycogen (Cueto et al., 2013). Granulocytes are about the size of hyalinocytes but show no evidence of phagocytosis. They contain conspicuous eo-sinophilic granules that are membrane-bound, large and rod-shaped and show a high electron density. These granules merge and form even larger ones when granulocytes are exposed to microbes and may degranulate in a kind of “compound exocytosis” (Pickett & Edwardson, 2006). Degranulation of granulocytes has been linked to the release of lysozyme and other bactericidal hydrolases in other molluscs (e.g., Ottaviani, 1991).

Hemocyte-Producing Organs and/or Immune Barriers

Many authors have reported that gastropod hemocytes are generated in the circulation (Sminia, 1981; Monteil& Matricon-Gondran, 1991; van der Knaap et al., 1993; Souza & Andrade, 2006). However,

“amoebocyte-
producing organs” have also been reported in the pericardial wall of some heterobranchs (Lie et al., 1975; Rondelaud & Barthe, 1982; Jeong et al., 1983; Ruellan & Rondelaud, 1992) and in the roof of the lung of M. cornuarietis (see Yousif et al., 1980). No such organs have been found in P. canaliculata, although spheroidal hemocyte aggregates, similar to those formed in vitro (Cueto et al., 2013), were found in the lung following injection of yeast cells into the visceral hump (Rodriguez et al., 2012), sug-gesting a role of the hemocytes in fighting in-fection. Also, large hemocyte islets occupy the hemocoelic spaces in the kidney of P. canalicu-lata (Cueto, 2011; Giraud-Billoud et al., 2013b; Cueto et al., submitted), and it is possible that

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TABLE 5. Mean metal concentrations (mg/kg dry weight) in the soft tissues of apple snails reported in previous studies. (Dashes indicate no data available.)

Species and tissue Cu Cd Pb

Pila ovata (viscera) 2.0-5.8 - -

Pila ovum’! 24.6 1-0 4.8

Lanistes libycus 48.2 0.8 5.42

Pomacea canaliculata 32-90 0.4-2.5 5-32

(head-foot)
Pomacea canaliculata 60-170 5-29 160-620 3000-6400 Guangdong, China
(viscera)
Pomacea paludosa 23.9-732 - >

Pomacea paludosa 44-145 - -
(foot)
Pomacea paludosa 15-229 - -
(viscera)

23.6-45.0 Southern Nigeria

70-240 Guangdong, China

zn Location Reference

Ezemonye et al.,
2006

- Southwestern Nigeria Adewunmi et al.,
1996

- Southwestern Nigeria Adewunmi et al.,
1996

Deng et al.
2008

Deng et al.,
2008

Frakes et al.,
2008

Hoang et al.,
2008

Hoang et al.,
2008

- Florida, USA

- Florida, USA

- Florida, USA

1Misnamed; could be either Lanistes ovum Troschel, 1845 or Pila ovata.

they function as a hemocyte-producing organ.
Also, hemocyte spheroids are formed in these
islets after the injection of yeast cells in the foot (Rodriguez et al., 2012), demonstrating the reactivity of the islets to an immune challenge.
The presumptive hemopoietic role of the lung roof and the kidney in ampullariids needs to be further explored, but their role as immune barriers against intruders seems clear.

ENVIRONMENTAL HEALTH AND POLLUTION

This review has focused thus far on the basic biology of ampullariids. However, there are important applied issues, notably their role as major agricultural pests, environmental pests, vectors of human disease and in ecotoxicol-ogy. Their role as crop pests, primarily of rice in Asia but also of taro and other crops in Asia and elsewhere, has been thoroughly reviewed elsewhere (Cowie, 2002; Joshi & Sebastian, 2006), and the limited understanding of their importance as environmental pests has been covered in the present review. However, their role in ecotoxicological research has been extensive in the last two decades but has not been reviewed. Also, important work regarding

their role as human parasitic disease vectors has appeared since the review of Hollingsworth & Cowie (2006). Therefore these topics are reviewed briefly.

Accumulation of Pollutants

Several reports, notably from Nigeria, China and Florida, of heavy metal concentrations have shown that apple snails have the potential to accumulate high concentrations of these elements in their tissues, especially the viscera (Table 5). Thus they have the potential to af-fect animals at higher trophic levels, including humans. The high tissue concentrations of lead and zinc reported in P. canaliculata from a lead/zinc mine in southern China were probably due to accumulation and detoxification through binding to proteins or ligands, as in Lymnaea stagnalis (Linnaeus, 1758) (Desouky, 2006), rather than contamination by sediment. In some cases, there is a positive correlation between tissue burden and environmental concentra-tion of toxicants, such that these ampullariids may serve as bioindicators of environmental pollution.
Vega et al. (2012b) determined the bio-
concentration factors (BCFs) for a range of
elements in tissues, eggs and midgut gland

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endosymbionts of Р canaliculata. The high-
est BCF was exhibited by barium (Ba) in all studied tissues, including the pallial oviduct,
as well as the eggs, which showed the lowest
BCFs for the other elements, suggesting the existence of a barrier protecting the eggs from most metal pollutants. Other tissues exhibited a range of BCFs for other elements. The BCFs for barium were extremely high in the intracel-lular endosymbionts (C and K morphotypes) and other more toxic pollutants (e.g., uranium, mercury, arsenic, bromine) were also heavily concentrated. The endosymbionts are released in the snail’s feces so may serve a detoxifica-tion function.
The accumulation of metal pollutants by ampullariids and their endosymbionts indicates the potential harm of using these snails as soil fertilizers or animal food (Halwart, 1994; Vega et al., 2012a). Also, ampullariids are considered a delicacy in some parts of the world (Diupotex-Chong et al., 2004; Eamsobhana et al., 2010; Lv et al., 2011), and industrial development in such areas may transform these traditional foods into hazardous ones. In Florida, Р palu-dosa have high tissue concentrations of copper, accumulated primarily via the diet, related to high levels in the sediment due to the use of copper-based fungicides in citrus plantations, which is thus a serious concern for the Ever-glades snail kite (Rogevich et al., 2008).

Toxicity of Pollutants to Apple Snails

Apple snail toxicity assays for metals and organic pesticides appear very sensitive (Sawasdee & Köhler, 2009), and apple snails may therefore have potential as toxicity test
organisms. However, their responses to dif-
ferent pollutants are complex and not broadly
understood. For example, the toxicity of copper,
to which Pomacea spp. are especially sensitive (Cazzaniga, 1981; Sun, 2013), may depend on a number of factors, including animal age and such water quality parameters as pH and dissolved oxygen concentration (Rogevich et al., 2008; Sun, 2013). In adult P canaliculata, there are also complex feeding and growth rate relationships to exposure time and cop-per concentration (Peña & Pocsidio, 2007). Few studies have investigated the detailed
responses to toxins. However, in sublethal
toxicity tests on M. cornuarietis embryos, in which copper and nickel were more toxic than other metals, there were significant delays in formation of tentacles and eyes; and various concentrations of zinc, palladium, nickel and

lithium also reduced heart rate or resulted in a delay in hatching (Sawasdee & Köhler, 2009, 2010). Toxicity assays have also been conducted using organic pesticides, including Diclobenil, Diuron and Simizina (Cazzaniga, 1981) and Paraquat (Melo et al., 2000). The effects of Atrazine and Imidacloprid on hatch-ing rate of embryos have been investigated, with the former much more toxic (Sawasdee & Köhler, 2009). However, it is even more difficult to draw broad conclusions about the effects of such pesticides, not only because only very few studies have been undertaken on the immense diversity of pesticides in use but also because of lack of methodological standardization and a focus on either lethal or specific sublethal effects in different studies.

Mechanisms of Toxicity

The above studies have evaluated both lethal and non-lethal toxicity, mostly driven by the need for control of pest apple snails and envi-ronmental monitoring, but little is known about the mechanisms actually causing the toxicity. For example, several hypotheses have been proposed to explain the endocrine disrupting effects of organotins on female snails, although none appears exclusive (Oehlmann et al., 2007). The masculinizing compound tributyltin (TBT) induces lipid and fatty acid accumulation in female M. cornuarietis according to Janer et al. (2007), just as organotin compounds induce adipogenesis in vertebrates through interaction with retinoid X receptor (RXR) and peroxisome proliferator-activated y receptor (Grün et al., 2006). In the neogastropod Thais clavigera (Kuster, 1860), TBT also binds to RXR with high affinity (Nishikawa et al., 2004). In addition, TBT has spermicidal action, targeting the seminal receptacle (Giraud-Billoud et al., 2013c).
As well as effects on survival of juveniles and adults, endocrine disrupting effects have been reported in females exposed to several environmental contaminants, including TBT and TPT (triphenyltin), at different ages from hatching to adulthood (Schulte-Oehlmann et al., 1995, 2000; Tillmann et al., 2001). However, during development, different physiological control mechanisms may be acting at different times, each potentially generating different re-sponses to pollutants. Because masculinizing substances act on the copulatory rudiment that is normally present in juvenile and adult female apple snails (e.g., Schulte-Oehlmann et al., 2000) and because this rudiment con-tinues to grow even after females reach sexual

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maturity (Gamarra-Luques et al., 2013), stud-ies of female masculinization (“imposex”) in ampullariids should consider age at exposure (Giraud-Billoud et al., 2013c).
The endocrine disrupting effects of bisphenol
A are less clear than those of masculinizing
pollutants. Bisphenol A has estrogenic effects on many aquatic invertebrates (Kang et al., 2007). In M. cornuarietis females, exposure at low concentrations resulted in formation of additional female organs, enlarged acces-sory sex glands, malformations of the pallial oviduct, enhanced egg and clutch production, and increased female mortality (Oehlmann et al., 2000, 2006). However, these studies were criticized for flaws in experimental design, analysis and interpretation (Staples et al., 2002; Dietrich et al., 2006). Subsequent studies exposing M. cornuarietis at higher concentra-tions detected no effect on eggs/female/month, percentage of eggs hatching successfully and time to hatching (Forbes et al., 2007a, b) and
showed that a major part of the variability in
such traits was simply individual differences (Forbes et al., 2008).
Sun (2013) examined the responses of the
proteome of juvenile P. canaliculata after ex-posure to copper and cadmium. Eleven differ-entially expressed proteins were identified that function in many vital cellular functions, such as antioxidation, energy metabolism, detoxifica-tion, signaling transduction and cytoskeleton disruption. Although some of these functions are non-specific stress responses (i.e., anti-oxidation and energy metabolism), others may
serve as biomarkers of exposure as they may
be related to metal toxicity pathways.

HUMAN HEALTH CONCERNS

At least three human diseases are caused by transmission of parasites from ampullariids: angiostrongyliasis or rat lungworm disease
caused by the nematode Angiostrongylus
cantonensis, cercarial dermatitis or swim-mer’s itch caused by schistosome cercariae, and echinostomiasis caused by species in the trematode genus Echinostoma. The following brief review updates that of Hollingsworth & Cowie (2006).

Angiostrongyliasis

Infection by A. cantonensis, the rat lung-
worm, is the most common cause of eosino-
philic meningitis worldwide (Graeff-Teixeira

et al., 2009; Cowie, 2013a). It is an acute
disease, with mild infections spontaneously resolving in a few weeks, but heavier infec-tions sometimes entailing serious sequelae, although rarely death (Dorta-Contreras et al., 2009; Graeff-Teixeira et al., 2009; Cowie,
2013a; Murphy & Johnson, 2013). Widely
and probably naturally occurring in much of Southeast Asia, this zoonosis is by far the most serious disease transmitted by ampullariids. It has been considered an emerging disease, as its geographical range has been expanding rapidly in recent years (Lv et al., 2011; Cowie, 2013a; Morassutti et al., 2014), and it has now been reported from over 30 countries (Wang et al., 2008; Cowie, 2013b; Kim et al., 2014). As development of the larvae depends on the temperature of their intermediate snail hosts, for example, P. canaliculata (Lv et al., 2006), global climate change may lead to further range expansion (Lv et al., 2011). However, with the exception of the many cases in parts of Asia, most reports are not associated with ampullariids.
The life cycle of A. cantonensis (Graeff-Teixeira et al., 2009; Cowie, 2013b) involves rats as definitive hosts and numerous species
of terrestrial and freshwater gastropods as
intermediate hosts (Kim et al., 2014), including a number of ampullariid species (Table 6). Hu-mans become infected mainly through inges-tion of raw or undercooked snails (as well as crabs or other paratenic hosts) (Cowie, 2013c). Deliberate ingestion is the primary route of infection in parts of Asia. In southern China, where non-native P canaliculata is widespread, the number of cases of angiostrongyliasis has been increasing, with most cases directly relat-ed to the deliberate consumption of introduced P. canaliculata, which is currently considered the main cause of the spread of the disease in China (Lv et al., 2008, 2009a, b, 2011; Yang et al., 2013). Pomacea canaliculata is also a major source of infection in Taiwan (Tsai et al., 2013). Similarly, in Thailand, native Pila spp. are widely eaten and the main source of infection (Eam-sobhana et al., 2010). Inadvertent ingestion of infected snails associated with vegetables, green salads, fresh vegetable juice and other produce is also an important avenue of infec-tion (Lv, 2009a; Cowie, 2013c), but ingestion of larvae on produce contaminated with snail slime, drinking of contaminated water, or via breaks in the skin have not been demonstrated and ampullariids have not been implicated in these infection pathways (Hollingsworth & Cowie, 2006; Cowie, 2013c).

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TABLE 6. Known ampullariid hosts of Angiostrongylus cantonensis. Data from Kim et al. (2014). (‘Experimental infection only.)

Species

Lanistes carinatus (Olivier, 1804)
Marisa cornuarietis (Linnaeus, 1758)*
Pila ampullacea (Linnaeus, 1758)
Pila angelica (Annandale, 1920)*
Pila gracilis (Lea, 1856)
Pila pesmei (Morlet, 1889)
Pila scutata (Mousson, 1848)
Pila turbinis (Lea, 1856)
Pila virescens (Deshayes, in Bory de Saint Vincent, 1824) [as polita Deshayes, 1830]
Pomacea canaliculata (Lamarck, 1822)
Pomacea lineata (Spix in Wagner, 1827)
Pomacea maculata Perry, 1810
Pomacea paludosa (Say, 1829)

According to published reports, abdominal angiostrongyliasis caused by the closely re-lated Angiostrongylus costaricensis, primarily in South and Central America (Rodriguez et al., 2008), is not associated with ampullariids.

Cercarial Dermatitis

Various trematode parasites of birds and mammals use freshwater snails as inter-mediate hosts (Brown, 1994; Muller, 2002). Transmission is achieved by swimming larvae, that is, the miracidia and cercariae that are infective to the intermediate and definitive hosts, respectively (Muller, 2002). Species of the genus Schistosoma are by far the most important trematodes from a medical viewpoint as they cause schistosomiasis that affects millions of people in tropical regions (Muller, 2002). Various species of other genera of Schistosomatidae may cause cercarial der-matitis or swimmer’s itch in humans, in which the cercariae penetrate the skin but do not develop further (Muller, 2002; Burke & Tester, 2002). Among ampullariids, only Р paludosa has been definitively demonstrated as a vec-tor, and only of cercarial dermatitis, in Florida (Hanning & Leedom, 1978). In Brazil, although there is no record of cercarial dermatitis associ-ated with species of Pomacea, schistosomatid cercariae have been detected in P lineata and

Location

Egypt

Thailand

Thailand
Thailand

Indonesia, Malaysia, Thailand
Thailand

China, Thailand

China, Hawaii, Okinawa (Japan), Taiwan
Brazil

China, Louisiana (USA)
Cuba, Hawaii (possible misidentification)

P. maculata by Mattos et al. (2013) and in P figulina by Thiengo (unpublished).

Echinostomiasis

Human echinostomiasis is a food-borne, zoonotic parasitosis attributed to various spe-cies of digenean trematodes, many of which are transmitted by freshwater snails. This zoonosis, endemic in Southeast and eastern Asia, causes intestinal problems involving severe diarrhea and abdominal pain, eosinophilia, edema and hepatomegaly (Eveland & Haseeb, 2003; Grac-zyk & Fried, 1998). The life cycle of Echinos-toma spp. involves birds and small mammals as definitive hosts, and snails, clams, and fishes as first and second intermediate hosts. Humans become infected through the ingestion of raw or undercooked intermediate hosts infected with the metacercariae of the parasite.
Eating raw or undercooked Pila luzonica (Reeve, 1856) (probably a synonym of Pila scutata) has been considered the main route of transmission in the Philippines (Graczyk & Fried, 1998), though it is also possible that because of the difficulty non-experts have in distinguishing ampullariid species, P. canali-culata, which is now widely distributed in the Philippines (Hayes et al., 2008), is involved. In Thailand, Pila spp. and Р canaliculata (and perhaps P. maculata, with which Р canaliculata

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has frequently been confused; Hayes et al., 2008, 2012) have been identified as intermedi-ate hosts of Echinostoma spp. (Weerachai et al., 2011). The high incidence of the disease in northern Thailand (Graczyk & Fried, 1998) and other parts of Asia is probably also a re-sult of consuming raw apple snails, as for an-giostrongyliasis (Eamsobhana et al., 2010).

CONCLUSION AND FUTURE RESEARCH OPPORTUNITIES

The large amount of information that has been gathered makes the Ampullariidae one of the more intensively studied families of Gastropoda. However, nearly all studies have focused on a single species, P. canaliculata, and have done so in a non-comparative con-text, limiting their general applicability for understanding the biology of the family as a whole. These two issues suggest the need for (1) comparative data for other species to provide insight into the evolution, ecology and biology of Ampullariidae broadly, and (2) infor-mation on particular areas of the biology of P canaliculata, particularly (but not exclusively) genomics, which would support the develop-ment of this species, and perhaps other apple snails, as “emerging model organisms’ in physi-ology, development and ecology (in the sense of Behringer et al., 2008). The significance of the family as a model for studies in evolutionary and invasion biology in particular has already been discussed by Hayes et al. (2009a). Ad-ditional priorities for future ampullariid research, in no particular order, are:
- Integrative eco-physiological and compara-tive genomic studies aimed at understanding the evolution of the family as a whole and the novel behavioral, biochemical, anatomi-cal and physiological traits that may have driven diversification and transitions among habitats.
- Comparative behavioral studies to reveal patterns across genera and within the fam-ily that may have played a role in ecological adaptation and speciation.
- Proteomic and biochemical studies of perivi-tellins and associated egg proteins to explore their origins, functions and ecological and evolutionary roles in diversification.
- Functional anatomical studies of male and female reproductive systems, particularly as they relate to evolution and ecology of amphibious traits and behavior.

- Phylogenetics, systematics and biogeography
of Old World Ampullariidae.
- Integrative studies exploring the role of be-
havior, sexual selection and trophic ecology in the invasive and evolutionary success of the family.
- Studies integrating population genomics and captive rearing to better understand the role of hybridization in the native and non-native ranges of ampullariids.
- Comparative evolutionary-developmental
studies. |
- Ampullariid medical malacology, particularly
at the interface of disease ecology and inva-sion biology.
- Ecosystem services provided by ampullariids,
particulary in the context of conservation.
In all studies on ampullariid evolution and ecology, there is a need for a deeper and broader comparative investigation into the de-gree of dependence on aquatic and terrestrial resources for all species and the processes that have driven adaptations (Hayes et al., 2009a). For example, the shift to aerial oviposition in some groups was probably a key event in am-pullariid evolution (Hayes et al., 2009a). Apple snail eggs provide an exceptional model to study the evolution of biochemical and physi-ological adaptations, which may have profound implications for addressing questions of ecol-ogy and evolution (Dreon et al., 2013). Among predator avoidance tactics, the egg defenses of P. canaliculata open new perspec-tives on the study of aposematism (Dreon et al., 2010). Further studies on perivitellins of other ampullariids, particularly of below-water egg laying species, will reveal if this peculiar group of proteins is an acquisition exclusive to the aerial egg laying ampullariids.
There is therefore a clear need for more comparative work on the factors that shaped the evolution of amphibious traits. This will al-low a better understanding of the successful reproductive strategy of Pomacea species and the selective pressures that have driven these acquisitions. Ampullariids and their close rela-tives offer a unique and potentially powerful system for addressing the physiological and behavioral ramifications of the transition from aquatic to terrestrial modes of life.
Additional specific areas of need and op-portunity include the basic documenting of species diversity, especially in Africa and Asia, considerable progress having already been made in this regard in South America (Hayes et al., 2009b), and the resulting understand-

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ing of evolutionary patterns has provided the necessary framework for interpreting many of
the studies discussed herein. There remains

much more that could be learned regarding detailed aspects of life-history and its variation,
even of the most well understood species (Р. canaliculata and to a lesser extent P maculata), which in a comparative framework could en-lighten fundamental ideas about the evolution of life histories. Much basic ecology remains to be discovered, includinhgow such abiotic factors as water level, temperature and quality influence apple snail behavior. Population dy-namics, including the impacts of predation, has barely been addressed. Finally, there remain fascinating questions arising from the invasion of apple snails into new regions, which can be considered a natural experiment in evolution and ecology (Hayes et al., 2009a).

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