GLOBAL ADVANCES IN ECOLOGY AND MANAGEMENT OF GOLDEN APPLE SNAILS

Ravindra C. Joshi
Leocadio S. Sebastian
Editors

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Trunklines: 63(44) 456-0394, -0426, -0649, -0651, -0652
Email: prri@philrice.org.ph
Home page: www.philrice.org.ph

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What Are Apple Snails? Confused Taxonomy and Some Preliminary Resolution

Robert H. Cowie,[1] Kenneth A. Hayes,[1] and Silvana C. Thiengo[2]

Abstract

Apple snails belong to the family Ampullariidae. They occur throughout the humid tropics and subtropics. A number of South American species have been introduced to Southeast Asia and elsewhere and have become serious pests of wetland crops, primarily rice, as well as invading important natural wetlands. The identities of the invasive species have not been clarified, and numerous names, including misspellings and junior synonyms, have been used in the literature. These problems result primarily from the confused state of the taxonomy of the species in their native South America. To address these problems, we are undertaking taxonomic and phylogenetic research, involving morphological and molecular analyses, that will help us to delimit *Pomacea* species, elucidate the relationships among them, and determine the geographic origins and identities of species that have been introduced to Southeast Asia and elsewhere. We have obtained DNA sequence data from 19 New World species of *Pomacea*. Our preliminary molecular results suggest that at least two species, *P. canaliculata* and a species we tentatively identify as *P. insularum*, have been introduced to Southeast Asia, in addition to *P. diffusa* introduced to Sri Lanka and *P. scalaris* to Taiwan. Our Southeast Asian specimens cluster closely in the phylogenetic tree with species from Argentina and Brazil. Further work will include additional species and will allow all the introduced species to be identified, thereby laying the foundation for more rigorous research on the ecology and behavior of the pests that is necessary for the development of improved pest management.

Key words: Ampullariidae, *Pomacea*, identification, nomenclature, taxonomy, mitochondrial DNA, morphology, phylogeny

[1]Center for Conservation Research and Training, University of Hawaii, 3050 Maile Way, Honolulu, Hawaii 96822, US; E-mail: cowie@hawaii.edu, khayes@hawaii.edu

[2]Departamento de Malacologia, Instituto Oswaldo Cruz/Fiocruz, Av. Brazil 4365, 21045-900 Rio de Janeiro, RJ, Brazil; E-mail: sthiengo@ioc.fiocruz.br

What Are Apple Snails?

Apple snails are freshwater snails in the family Ampullariidae. They are distributed predominantly in humid tropical and subtropical habitats in Africa, South and Central America, and Asia. They include the largest of all freshwater snails (Fig. 1) and are often a major constituent of the native freshwater mollusk faunas of these regions. Among the seven to ten genera usually recognized, the two largest are *Pila*, with about 30 species (Berthold 1991), and *Pomacea*, with perhaps about 50 real species, although 117 nominally valid species were recognized by Cowie and Thiengo (2003). Snails in these two genera, particularly, are often known as "apple snails" because many species exhibit large, round, often greenish shells. The term "apple-shell" was first used by Perry (1810-1811) in his introduction of the name *Pomacea* for his new species *Pomacea maculata* because of "its general resemblance to…an apple" (*pomum* in Latin).

Classification, Diversity, and Natural Range

Ampullariidae, of which the name Pilidae is a junior synonym and should no longer be used (Cowie 1997b, ICZN 1999), are operculate snails. They are most closely related to the Viviparidae or Cyclophoridae within the Caenogastropoda (Ponder and Warén 1988, Bieler 1992, Ponder and Lindberg 1997, Simone 2004).

Various authors have traditionally subdivided the family into seven to ten genera. Pain (1972) briefly reviewed the history of taxonomic work on the family. More recently, Berthold (1991, pp. 245-250) recognized ten genera (and three subgenera) with approximately 120 species. His detailed anatomical account treated representative species from each of these generic groupings. He divided the family into two subfamilies: the Afropominae (containing just a single Recent African species in the genus *Afropomus*); and the Ampullariinae, which he subdivided into the tribes Sauleini (one genus, *Saulea*, containing two African species, one Recent, one fossil) and Ampullariini (the remainder). He further subdivided the Ampullariini into the groups Heterostropha and Antlipneumata. These divisions and names were criticized

Fig. 1. A shell of *Pomacea maculata* in the Muséum National d'Histoire Naturelle, Paris. Shell height ~17 cm.

by Bieler (1993), who reanalyzed Berthold's data and showed that, although the various groupings of genera remained similar, the relationships among these groups were inconsistent. One of the ten genera recognized by Berthold (1991), *Pseudoceratodes* (African, fossil only), was included in the family only tentatively. Of the remaining nine genera, six contain only one to seven species each: *Afropomus* and *Saulea* are African; *Asolene*, *Felipponea*, *Pomella,* and *Marisa* are South American. The three genera *Lanistes*, *Pila,* and *Pomacea* comprise the great majority of species in the family. *Lanistes* is African (including Madagascar). Species of *Lanistes* are distinguished by their hyperstrophic and hence superficially sinistral shells; that is, their shells appear to coil to the left, while those of all other ampullariids are dextral, coiling to the right (c.f., Fig. 1). *Pila*, of which *Ampullaria* and *Ampullarius* are junior synonyms and should not be used (Cowie 1997b, ICZN 1999), is African and Asian. *Pomacea* is South and Central American. Given the overall poor level of understanding of taxonomy in the family, it is unwise at this stage to adopt any suprageneric nomenclature within it. Furthermore, within South America, where there are five genera, assigning species to particular genera is difficult and probably will be achieved satisfactorily only once a comprehensive taxonomic revision of the group has been accomplished that includes analyses of both DNA sequences and morphological data.

Berthold (1991) hypothesized a Gondwanan origin for the family, specifically an origin in that part of Gondwana that was to become Africa. The group is assumed to have spread and diversified onto the South American and Indian plates, but failed to reach the Australian plate prior to its split from Gondwana. As the plates moved to their present positions, the group probably spread and diversified within the humid tropics and subtropics (in particular from the Indian plate into Southeast Asia) to their physiological/ecological limits, defined approximately by the 10 °C minimum annual temperature isotherm and the 600 mm annual precipitation isohyet. The limit of their distribution in Southeast Asia (genus *Pila*) corresponds approximately to the boundary between the Asian and Australasian plates, despite New Guinea and parts of Australia apparently being suitable climatically (Baker 1998); ampullariids simply have not yet reached Australasia naturally.

The genus *Pomacea*, which is the main focus of this article as it contains most of the pest species, occurs naturally throughout most of South and Central America and the Caribbean, with a single species, *P. paludosa*, extending into the southeast of the United States (US). The genus is divided into two subgenera, *Pomacea sensu stricto* and *Effusa* (Cowie and Thiengo 2003). However, the relationships among these two subgenera and the genera *Marisa* and *Asolene* are not well resolved (Bieler 1993, Simone 2004), and, at least in terms of shell morphology, the four taxa intergrade (Cowie, personal observations). In a few locations, species of *Pila* have also become pests following their introduction, notably in Hawaii (Cowie 1995, 1997a; Levin et al. 2006).

Apple Snails as Invasive Species

There are a few instances of ampullariids causing damage to crops, predominantly wetland rice, in their native ranges (e.g., van Dinther and Stubbs 1963). More significantly, certain species have been introduced outside their native ranges and have become serious agricultural pests. Most notably, they have become major rice pests in many Southeast Asian countries (e.g., Mochida 1991, Naylor 1996, Cowie 2002, Lai et al. 2005, other contributions in this volume), but they have also become pests of rice and other crops elsewhere, e.g., in the Dominican Republic (D.G. Robinson, personal communication) and Hawaii (Cowie 1995, 1997a; Levin et al. 2006). At least five species have also been introduced to the continental US, including *Marisa cornuarietis*, *Pomacea diffusa* (generally identified as *P. bridgesii*), and three species that have been provisionally identified as

P. canaliculata, *P. insularum*, and *P. haustrum* (Clench 1966; Winner 1996; Thompson 1997; Cerutti 1998; Cowie 2001; T.A. Rawlings, K.A. Hayes, R.H. Cowie, and T.M. Collins, in preparation); some of these species have invaded natural wetlands, including the Everglades of Florida, as well as rice-growing regions of Texas and a number of other localities (Howells et al. 2006).

Nomenclatural and Taxonomic Confusion

Common Names

Many English common names have been used widely for various species of ampullariids, including "apple snail," "mystery snail," "miracle snail," and "golden snail." The major invasive species in Southeast Asia are generally known as "golden apple snails" or "GAS"—"golden" either because of the color of their shells, which is sometimes a bright orange-yellow, or because they were seen as an opportunity for major financial success when they were first introduced. They have also been called "cherry snails" (Wood et al. 2005). The major invasive species in the continental US are known as "channeled apple snails," an anglicization of "*canaliculata,*" the specific epithet of the single species they were first thought to be. "Spike-topped apple snail" has been used in the US for *P. diffusa* (which has generally been identified as *P. bridgesii*), as has "giant ramshorn snail" for *Marisa cornuarietis*. Some of these names have been used for more than one species of ampullariid; for instance, "golden snail" and "mystery snail" have been used primarily for orange/yellow varieties of both *P. canaliculata* and *P. diffusa* (as *P. bridgesii*), notably in the aquarium trade, in some cases without realizing that they are different species, or without being able to distinguish them, or simply misidentifying them (e.g., misidentifications in Perera and Walls 1996).

The term "golden apple snail" has been used widely in Asia to refer to the pest species, without necessarily realizing, or perhaps disregarding the fact, that this included at least two actual introduced species; it is often now used collectively for this group of species (Lai et al. 2005). Similarly, although "channeled apple snail" has been used for the species introduced to the continental US, we are now beginning to realize that there are at least two species subsumed under this umbrella. In Hawaii, "apple snail" is used collectively to refer to invasive species of both *Pomacea* and *Pila*. In addition, "mystery snail" has also been used for various species in a different family, the Viviparidae. Furthermore, even the acronym "GAS" can be confusing, as it is also used, especially in the agriculture and pest management arena, for *Achatina fulica*, the giant African snail, an unrelated terrestrial invasive pest.

Scientific Names

The confusion in use of common names reflects in part the underlying and notoriously confused taxonomy of ampullariids (e.g., Alderson 1925; Pain 1964; Keawjam 1986; Cazzaniga 1987, 2002). Correct identification of many ampullariid species is extremely difficult—certainly the case regarding the pest species in Southeast Asia (e.g., Schnorbach 1995, Wada 1997), which have been identified as a number of different species (Table 1). In many cases, names have also been misspelled, for instance, *insularis*, *insularus,* and *insularius* instead of *insularum*, which is the genitive plural of "*insula*," Latin for "island." Junior synonyms have been used, for instance, *Ampullarius* and *Ampullaria*, both of which are junior synonyms of *Pila*; *Pomacea cuprina*, which is a junior synonym of *P. glauca*; and *Ampullaria levior*, a junior synonym of *P. lineata*. These junior synonyms have also sometimes been misspelled, for instance, *Ampularius* and *Ampullarium* instead of *Ampullarius*. Snails have been identified as hybrids of named species without any

Table 1. A selection of the scientific names and variant spellings used for the pest species of Ampullariidae in Southeast Asia, with examples of literature in which they appear. In some cases authors recognized more than one species.

Name	Literature Examples
Ampullaria levior	Yipp et al. 1991
Hybrid [of] *Ampullaria canaliculata* and *Ampullaria cuprina*	Anderson 1993
Ampullarium canaliculatus	Uchikawa et al. 1986, Chao et al. 1987, Yen et al. 1990, Tsai et al. 2001
Ampullarium insularum	Uchikawa et al. 1986
Ampullarium sp.	Uchikawa et al. 1986
Ampularius sp. a hybrid of undetermined origin	Lacanilao 1990
Ampullarius canaliculatus	see Yipp et al. 1991
Pila sp.	see Guerrero 1991
Pomacea canaliculata	Keawjam and Upatham 1990, Hendarsih et al. 1994, Wood et al. 2005, many others
Three strains of *Pomacea canaliculata*	von Brand et al. 1990, Fujio et al. 1991
Pomacea cf. *canaliculata*	Ng et al. 1993
Pomacea cuprina	Mochida 1991, Nugaliyadde et al. 2001
Pomacea gigas	see Guerrero 1991, Mochida 1991, Nugaliyadde et al. 2001
Pomacea insularis	see Acosta and Pullin 1991
Pomacea insularum	see Mochida 1991
Pomacea insularus	Keawjam and Upatham 1990
Pomacea lineata	Cheng 1989, Laup 1991
Pomacea sp.	Keawjam and Upatham 1990, Acosta and Pullin 1991, many others

actual evidence of hybridization. And identifications have been made without reference to type specimens or other reliably identified specimens.

The introduced species are certainly of New World origin, with the exception of an Asian species (*Pila conica*) in Hawaii (Cowie 1995, 1997a; Levin et al. 2006) and an African species (*Pila leopoldvillensis*) in Taiwan (Wu and Lee 2005). All names of New World Ampullariidae have been cataloged by Cowie and Thiengo (2003), which is the most recent authoritative nomenclatural work on them. This catalog, in conjunction with any subsequent taxonomic revisions that may appear, should be used to ascertain correct spellings, synonymies, and availability of names. It also lists type localities and location of type material, if known. It has been suggested that more than one species has been introduced to Asia (we confirm this below), for instance in Thailand (Keawjam and Upatham 1990) and the Philippines (Mochida 1991), and it is likely that one of these species, perhaps the most widespread, is indeed *Pomacea canaliculata*. In addition, *P. scalaris* has been introduced to Taiwan (Wu and Lee 2005) and *P. diffusa* to Sri Lanka (Mordan et al. 2003, Cowie and Hayes 2005 [identified therein as *P. bridgesii*]).

Synonyms

The following specific epithets were reported by Cowie and Thiengo (2003) as having been considered by various authors as synonyms either of *P. canaliculata* or of other species synonymized with *P. canaliculata*: *australis*, *chaquensis*, *dorbignyana*, *haustrum*, *immersa,* and *vermiformis*. Some of these synonyms have also been considered synonyms of other *Pomacea* species by some previous authors. Future research may show that some of them are in fact valid species. Also, other species have been considered synonyms of *P. canaliculata* by some previous authors but were not listed as such by Cowie and Thiengo (2003).

It is possible that one of the other species that is part of the complex that constitutes the "golden apple snail" is *P. maculata*, although this is a very preliminary suggestion that depends on further research. Synonyms of *P. maculata* or of other species synonymized with it, as reported by Cowie and Thiengo (2003), are *australis*, *crosseana*, *fasciata*, *georgii*, *gigas*, *insularum*, *vermiformis,* and *vickeryi*.

Some names appear in the lists of synonyms of both *P. canaliculata* and *P. maculata*, reflecting the opinions of different authors and the current state of taxonomic confusion in the group. It is also very possible that other species should be considered synonyms, but there is at this time no definite evidence for this.

Taxonomy and Identification

Ampullariid species-level taxonomy has relied heavily on shell morphology, yet snail shells, and especially those of many ampullariid species, exhibit much intraspecific variation. The taxonomy and systematics of most species have not been adequately researched since their original descriptions. Overall, however, ampullariid shell morphology is highly conserved, and this, in combination with the high intraspecific variation, makes their taxonomic study extremely difficult. The pest species in Southeast Asia nevertheless appear to belong to a group of more or less morphologically similar species from South America. However, within this group, the species and their relationships are very poorly understood. We tentatively refer to this group as the "*canaliculata* group." From time to time, some of the species within the *canaliculata* group have been formally synonymized, informally linked together, distinguished as separate species, and so on. This confusion was discussed but not resolved by Alderson (1925), the most recent author to revise *Pomacea* and *Pila* widely (referring to the two genera together as "*Ampullaria*"). He implicitly recognized most of the species in the *canaliculata* group as a more or less closely knit group. Within this group he further recognized a number of rather vaguely defined associations of species, for instance explicitly linking *P. amazonica*, *P. immersa,* and *P. haustrum*, although without formally synonymizing them (the latter two have both been synonymized with *P. canaliculata* by some authors—see Cowie and Thiengo 2003), and informally referring to another subset of the group as "the *lineata* group." However, he did retain most species as valid. It is quite possible that, just as for the large number of Central American species synonymized under *P. flagellata* by Pain (1964), many other "species" of Ampullariidae, including those in the *canaliculata* group, do not deserve distinct specific status (Pain 1960; Cazzaniga 1987, 2002). A modern revision, involving not only shell morphology but also internal anatomy and molecular characters, might reduce the *canaliculata* group to many fewer species. Until such work is complete, however, the status of these numerous nominal species will remain obscure.

The predominant pest may indeed be *P. canaliculata*. However, this is a widespread and morphologically highly variable species in South America (Cazzaniga 1987, Estebenet and Martín 2003). How distinct it really is from the various nominal South American species also reported from Southeast Asia is not clear. The distinction between *P. canaliculata* and *P. insularum* has been especially unclear, despite attempts to clarify it (Hylton Scott 1958, Keawjam and Upatham 1990). *P. insularum* has been considered a synonym of *P. gigas* by some authors, and *P. gigas* and *P. maculata* have also been synonymized by others (Cowie and Thiengo 2003). However, our ongoing research suggests that *P. maculata* and *P. insularum* are distinct species, so we retain them as such here, pending resolution of this issue. In many populations, the maximum shell height of *P. canaliculata* is around 3 cm, but in other populations, females can reach heights of 7-8 cm (Wada 1997), and some individuals may even be over 9 cm (Estebenet and Cazzaniga 1992). Sexual dimorphism in size (e.g., Estebenet and Martín 2003) and shape (e.g., Cazzaniga 1990), combined with this overall morphological variability and the existence of considerable intraspecific variation in shell color and banding pattern, no doubt confound attempts at accurate identification. Identification based only on shell size is unreliable. Nevertheless, preliminary results (see below) suggest that at least some of the snails found in Southeast Asia may be a different species, perhaps *P. insularum*; this has also been suggested by Keawjam and Upatham (1990) and Mochida (1991).

Problems Caused by Confused Nomenclature and Taxonomy

These problems of nomenclature and identification cast doubt on the correctness of the names applied both in the pest-related literature and in much of the ecological, physiological, behavioral, and other literature on species in this group. Comparability among studies is therefore unreliable. The problems are compounded when no precise natural provenance information is available, as is the case with studies dealing with introduced populations in Southeast Asia and elsewhere.

Because the taxonomy of the *canaliculata* group of species is so confused, it is difficult to assess natural species distributions. For instance, *P. canaliculata* itself has been considered to be extremely widely distributed, from the Plata River system in Argentina to Guyana and from the easternmost tip of Brazil to Bolivia (Hylton Scott 1958, Cazzaniga 2002). However, study of museum material (Cowie, personal observations) suggests that it does not extend north of Brazil, and that perhaps *P. dolioides* (possibly a synonym of *P. lineata*) replaces it in Suriname, French Guiana, Guyana, and Venezuela. Ongoing research suggests that *P. canaliculata* may in fact be restricted to more southerly regions (Hayes, Cowie, and Thiengo, unpublished).

In addition to the confusion about the real identities of the pest species, the use of common names, especially "golden apple snail" and "channeled apple snail," to refer collectively to more than one real species leads to misunderstanding of the pest problem by regulating agencies, farmers, control practitioners, and the public, who essentially ignore the fact that these are different species that may exhibit different ecology, behavior, and threat to agriculture and the environment, and that may respond differently to control measures.

Morphological Diagnosis of *Pomacea* Species

Although the shell may be extremely variable, as in the *P. canaliculata* group, it is definitively the first step in morphological diagnosis. In some species it is sufficiently characteristic that identification is possible just by examination of the shell. For example, the whorls of *P. scalaris*, *P. bridgesii,* and *P. diffusa* have a distinctive stair-like appearance, with the steps more sharply prominent in *P. scalaris*; the shell of *P. papyracea* is fragile and horny, with an almost black periostracum; and the shell of *P. urceus* is thick, solid, and black, with distinctive transverse ridges. Nevertheless, rather few *Pomacea* species can be identified definitively on the basis of the shell alone, and other morphological characters must be investigated to assist in correct identification. Also, the juveniles of many species are indistinguishable.

As in many other mollusk groups, the jaw and radula exhibit little variation at the level of species, having little taxonomic value below the family level. It is necessary, then, to investigate the anatomy of the internal organs.

Few species of *Pomacea* have been adequately described anatomically. Sachwatkin (1920) described the morphology of the excretory and reproductive system of *P. gigas* (synonym of *P. maculata*). Souza-Lopes (1955; 1956a, b) described the shell and reproductive system of some Brazilian species: *P. canaliculata*, *P. haustrum*, *P. lineata,* and *P. sordida*. Hylton Scott (1958) described the anatomy of the Argentinian species: *P. scalaris*, *P. canaliculata,* and *P. insularum*, which was treated as a synonym of *P. maculata* by Cowie and Thiengo (2003). Andrews (1964; 1965a, b) described the microanatomy of *P. canaliculata.* More recent work has described both the shell and soft-part morphology of *P. lineata* (Thiengo 1987) and *P. sordida* (Thiengo 1989) and has compared them with the morphology of *P. canaliculata* (Thiengo et al. 1993). Tillier (1980) described the male reproductive system of *P. dolioides*, *P. glauca*, *P. sordida,* and *P. urceus* from French Guyana.

As is usual in mollusks, morphological diagnoses of ampullariid species are based chiefly on the reproductive system, principally of males. Among the characters most commonly used are the shape and size of the prostate, penis, penis pouch, and penis sheath; and the presence or absence and position of glands on the inner and outer surface of the penis sheath. The ratios of dimensions among some of these structures are also important. Other useful characters involve the excretory, respiratory, and digestive systems, for example the shape and size of the kidney, osphradium, gill, and intestine, and the ratios among them.

Based on the shell and the limited knowledge of the anatomy of South American species of *Pomacea*, we can distinguish the group of *P. canaliculata* (*P. canaliculata, P. lineata*, *P. insularum,* and *P. maculata*; the latter two may be synonyms – Cowie and Thiengo 2003) and the group of *P. scalaris* (*P. scalaris*, *P. bridgesii*, *P. diffusa*).

To evaluate the use and significance of shell and soft-part anatomy in delineating species, these morphological characters need to be placed in a character/state matrix and analyzed in a phylogenetic framework. However, until such work is complete, we can provide only a preliminary summary of the qualitative morphological features that appear to be diagnostic of these two groups of species. We also provide preliminary details of the species that have been reported in Asia that belong to these two groups.

Group of *Pomacea canaliculata*

Species in this group have globose shells, often with marked dark spiral bands, a whip-like penis, and a penis sheath that is rather broad at the base. The calcareous-shelled eggs are bright pink-reddish and round (Fig. 2).

Pomacea canaliculata. The shell (Fig. 3) is globose, moderately heavy, with greenish or horn-colored periostracum and often with dark spiral bands. Adult shells have 5-6 whorls, increasing rather rapidly and separated by a deeply channeled suture. The apex is subelevated, although this character is extremely variable. The aperture is large and rounded to subelongated; the lip or peristome is sometimes reddish. The umbilicus is large and deep. The operculum is corneous, entirely closing the aperture. Adult shells usually achieve medium size, up to about 50 mm in height, but this varies widely among populations, and some individuals may be larger than this.

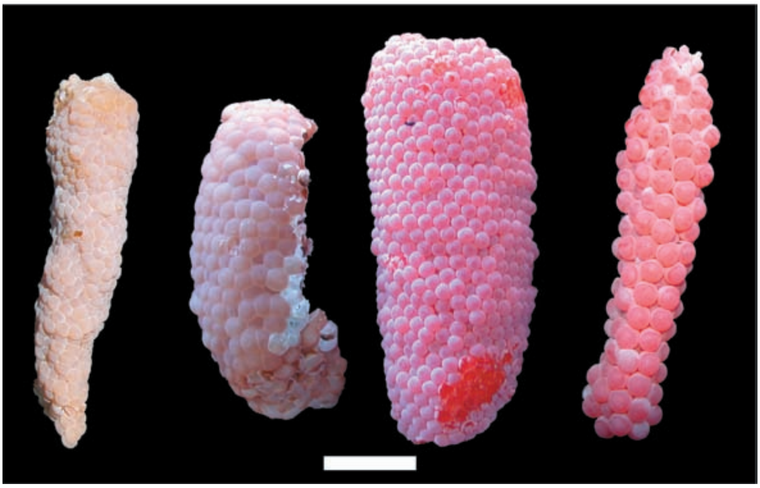

Fig. 2. Egg masses of *Pomacea* species. From left: *P. diffusa*, *P. scalaris*, *P. insularum* (tentatively identified), *P. canaliculata*. All photographs taken in Brazil, except *P. canaliculata* taken in Hawaii. All to the same scale. Bar = 1 cm. Egg mass size is not diagnostic of the species, but may be related to female size.

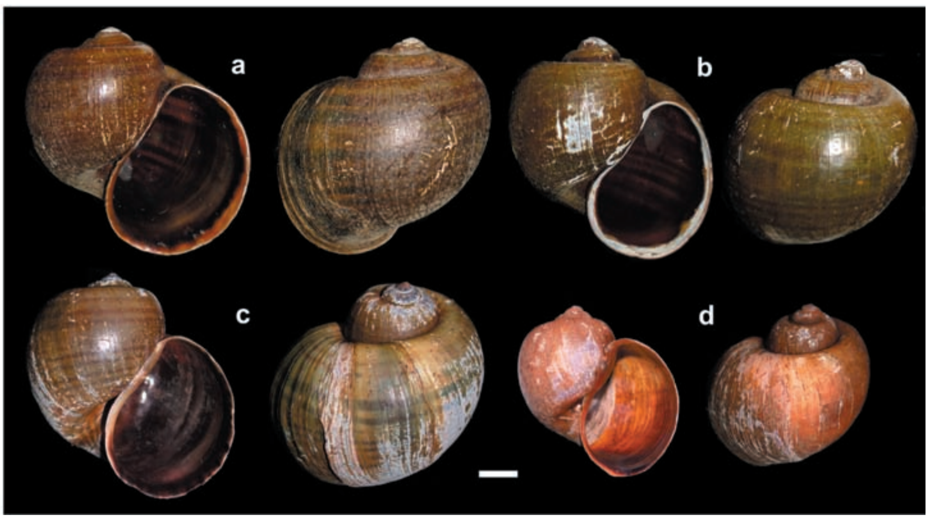

Fig. 3. *Pomacea canaliculata.* a, b: two specimens from Argentina; c: specimen from Hawaii; d: specimen from the Philippines. Bar = 1 cm.

The testis (Fig. 4) is a cream-colored mass occupying the first three whorls of the spire. Short and numerous efferent ducts fuse into two main branches that converge into the spermiduct, which is narrow and runs to the base of the spire. Near the pericardium it turns to the right, opening into the seminal vesicle, a whitish, rounded structure. The cream-colored prostate is cylindrical, with a slit-like lumen and a pointed tip ending below the penis pouch. The penis pouch is rounded in shape and thin walled, so the coiled penis can be seen through it. The proximal end of the pouch is pink and thick, whereas its distal tip forms a U-shaped channel through which the penis extends during copulation. There is a flange of tissue between the

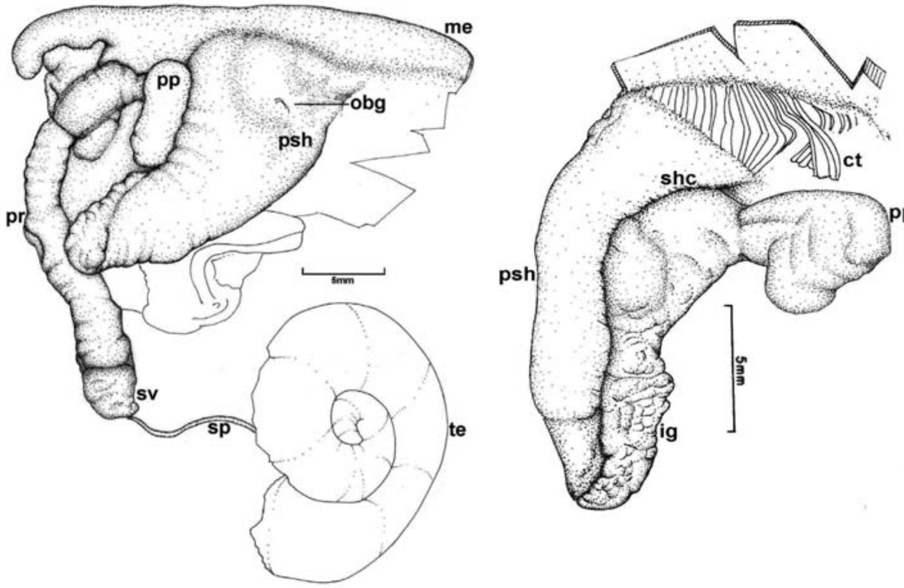

Fig. 4. *Pomacea canaliculata.* Left: male reproductive system; right: detail of the penis sheath. Abbreviations: ct - ctenidium, ig - inner gland, me - mantle edge, obg - outer basal gland, pp - penis pouch, pr - prostate, psh - penis sheath, shc - sheath channel, sp - spermiduct, sv - seminal vesicle, te - testis. Bars = 5 mm.

prostate and the penis pouch. The whip-like penis is approximately 30 mm in length in a snail with a shell 35 mm high, its duct being cylindrical and closed. The straight and well developed penis sheath rises to the left of the anus and tapers distally. It has two margins, which juxtapose, forming a median longitudinal channel in its inner surface. The right margin overlaps the left one until the beginning of the distal third of the sheath, where the penis emerges during mating. There is a large central gland embedded in its outer basal tissue with a slit-like opening, and an elongated wrinkled gland occupying the distal two-thirds of the inner surface.

The arborescent ovary (Fig. 5) lies in the same location as the testis, and its whitish branched tubules are easily distinguished from the green digestive gland. Its main branches fuse to form a thin oviduct that runs to the base of the spire and, near the pericardium, turns to the right and merges into the albumen gland before opening into the seminal receptacle. The latter is thick-walled, tapers distally, and is almost completely enclosed by the albumen gland. The large pink-reddish albumen gland entirely encloses the spiral capsule gland that begins at the receptacle and extends until it emerges from the proximal end of the albumen gland. The pallial oviduct runs along the rectum until reaching the female genital aperture beside the anus. A vestigial male copulatory apparatus (penis and its sheath) is present at the mantle edge, between the anus and the gill. The female reproductive system of *P. canaliculata* is similar to that of other congeneric species such as *P. lineata* (Thiengo 1987, Thiengo et al. 1993).

The spherical, pink-reddish, calcareous-shelled eggs (Fig. 2) are laid in clusters above the water level; the time from oviposition to hatching depends on temperature (Cowie 2002) but at a temperature of 25 °C is about 15 days.

Pomacea insularum. The shell (Fig. 6) is almost indistinguishable from that of *P. canaliculata* (Fig. 3), although it may in general be slightly larger (shell height may reach 70 mm or more) and heavier. The internal morphology of *P. insularum* (Fig. 7) is also very similar to that of *P. canaliculata* (Figs. 4–5).

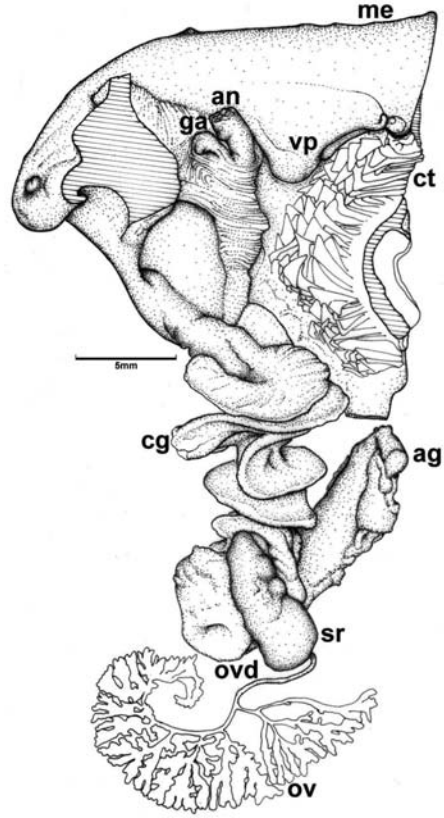

Fig. 5. *Pomacea canaliculata.* Female reproductive tract. Abbreviations: ag - albumen gland, an - anus, cg - capsule gland, ct - ctenidium, ga - genital aperture, me - mantle edge, ov - ovary, ovd - oviduct, sr - seminal receptacle, vp - vestigial penis. Bar = 5 mm.

Group of ***Pomacea scalaris***

The main characteristics of this group are the stair-like appearance of the shell whorls, and the elongated and tapered penis sheath with its distal end turned to the right. Also, the calcareous-shelled eggs are dull pale yellowish or orangish, or very pale brown, not bright pink as in the group of *P. canaliculata*. They are formed into polygonal shapes with their edges abutting each other in *P. diffusa* and *P. scalaris*. They are also laid above the water level (Fig. 2).

Pomacea scalaris. The shell (Fig. 8) is rather oblong, heavy, with dark brown or black-colored periostracum. The apex is elevated and sharply pointed. Adult shells have 4-5 sharply shouldered whorls, increasing rather rapidly. The aperture is oblong, violaceous internally, and yellowish toward the border; the lip or peristome is sharp. The umbilicus is narrow and deep. Adult shells are medium in size, reaching a height of up to about 50 mm.

Pomacea diffusa. The shell (Fig. 8) is rather oblong, moderately heavy, usually with horn-colored periostracum and often with dark brown spiral bands. However, color is highly variable, especially because numerous brightly colored varieties have been developed in the aquarium

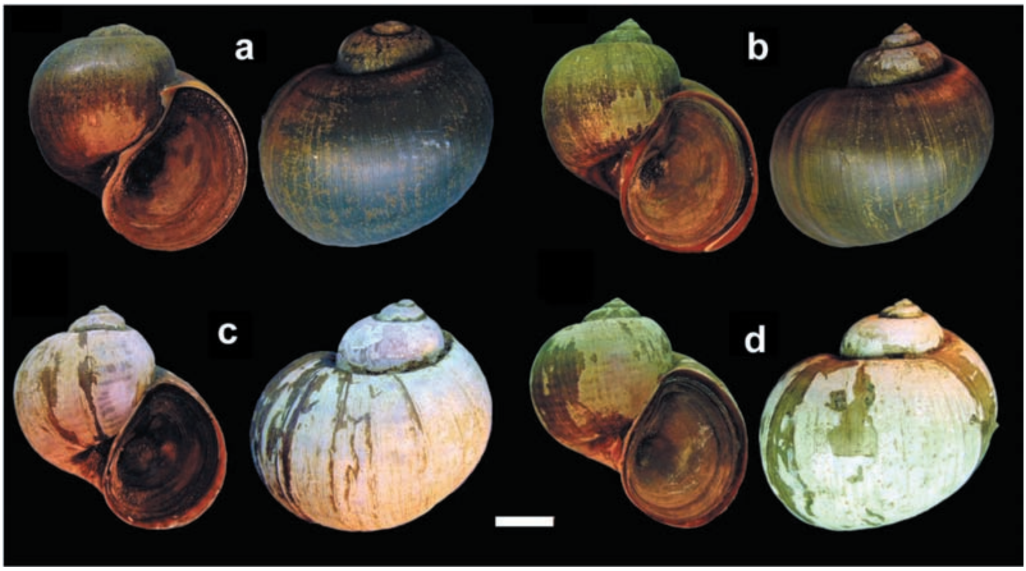

Fig. 6. ***Pomacea insularum.*** **a, b: two specimens from Brazil; c, d: two specimens from Texas. Bar = 1 cm.**

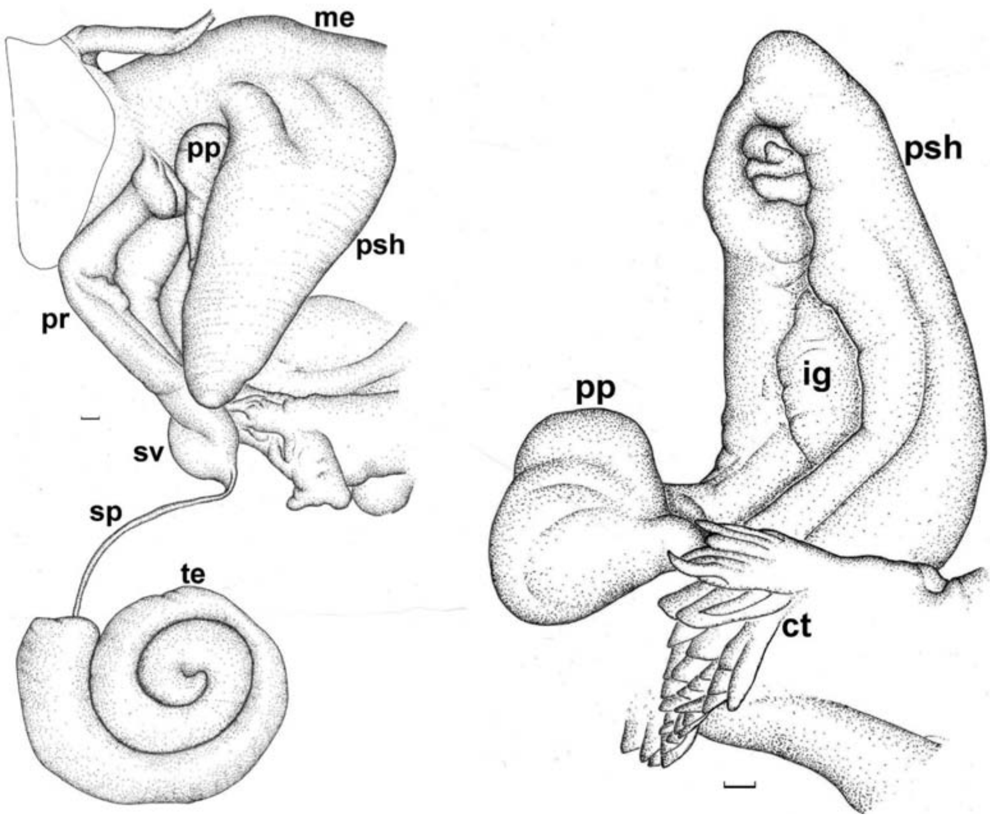

Fig. 7. ***Pomacea insularum.*** **Left: male reproductive system; right: detail of the penis sheath. Abbreviations: ct - ctenidium, ig - inner gland, me - mantle edge, pp - penis pouch, pr - prostate, psh - penis sheath, sp - spermiduct, sv - seminal vesicle, te - testis. Bar = 1 mm.**

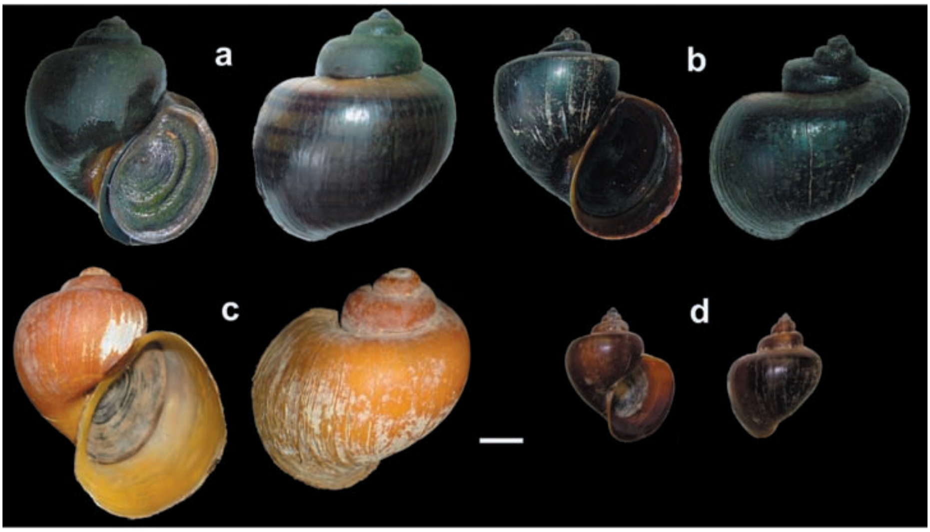

Fig. 8. *Pomacea bridgesii*, *P. scalaris*, and *P. diffusa*. a: *P. bridgesii* from Brazil; b: *P. scalaris* from Brazil; c: *P. diffusa* from Australia; d: *P. scalaris* from Taiwan. Bar = 1 cm.

trade (Perera and Walls 1996). The apex is elevated. Adult shells have 5-6 shouldered whorls, increasing rather rapidly. The aperture is oblong and whitish; the lip is effused. The umbilicus is large and deep. Adult shells are medium in size, reaching a shell height of up to about 50 mm.

The testis (Fig. 9) is cream-colored, and the mantle covering it is generally darkly pigmented. Numerous short efferent ducts fuse into two main branches that converge to a narrow spermiduct that runs to the base of the spire. Near the pericardium it runs to the right, opening into the seminal vesicle. The prostate, notable by its creamy color and cylindrical shape, follows the seminal vesicle and continues along the left side of the rectum until it reaches the anal papilla (Fig. 9). The penis is whip-like and is housed in a pouch when not in use. Microanatomical studies show that the penis has a closed cylindrical spermiduct enclosed within fibers that circle the spermiduct transversely and are covered with an outer layer of loose connective tissue. The penis sheath is well developed and rises to the left of the prostate opening. It tapers distally, bearing two margins that juxtapose, thus forming a median longitudinal channel. During copulation the penis moves along this channel and emerges to enter the pallial oviduct. The penis sheath is about 1/6 of the pallial cavity volume; slightly triangular; with a broad, thick base and with a slender distal tip turned to the right. The small outer basal gland aperture is in the left outer dorsal region of the penis sheath base. The basal gland is elliptical and situated in the right lateral region of the penis sheath.

The female reproductive system (Fig. 9) is similar to that of *P. canaliculata* described above, except for the pale-yellowish albumen gland.

It is possible that ongoing and future work to describe and analyze the internal anatomy of other species of *Pomacea* comparatively will discover means to identify these species definitively. In conjunction with molecular analyses (below) we hope to clarify the taxonomy and phylogenetic relationships within the genus *Pomacea* and thereby to ascertain the true identity and geographic origins of the pest species.

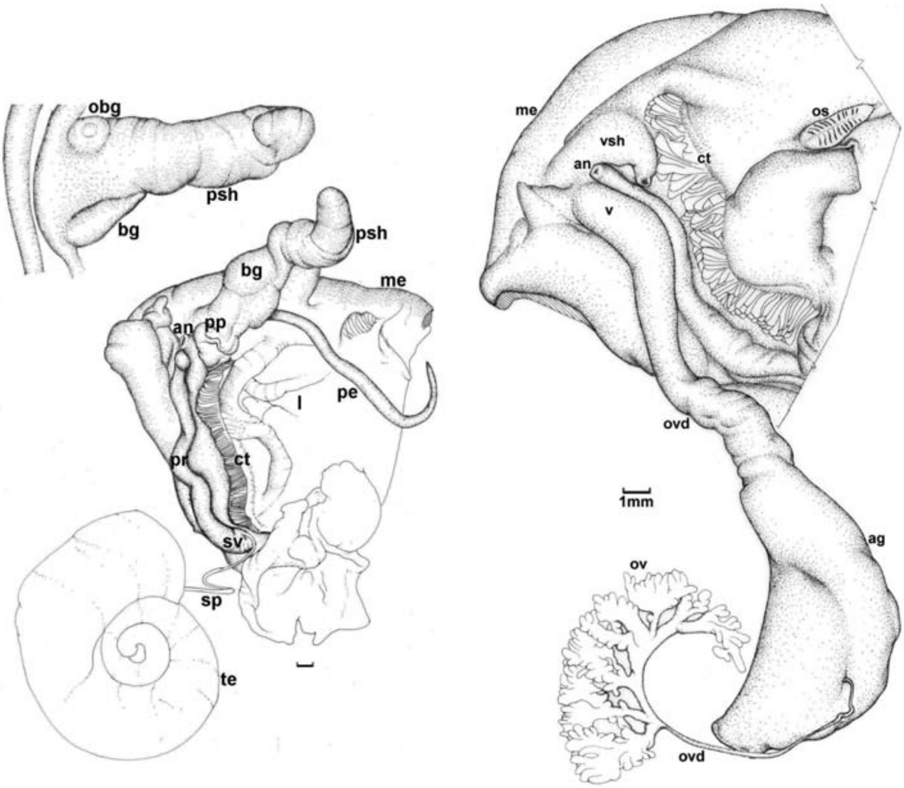

Fig. 9. *Pomacea diffusa.* Left: male reproductive tract; right: female reproductive tract. Abbreviations: ag - albumen gland, an - anus, bg - basal gland, ct - ctenidium, ig - inner gland, l - lung, me - mantle edge, obg - outer basal gland, os - osphradium, ov - ovary, ovd - oviduct, pe - penis, pp - penis pouch, pr - prostate, psh - penis sheath, sp - spermiduct, sv - seminal vesicle, te - testis, v - vagina, vsh - vestigial sheath. Bars = 1 mm.

Molecular Analyses: Some Preliminary Results

We are undertaking a study of molecular genetics (DNA sequencing) that will help us to delimit extant *Pomacea* species and elucidate the relationships among them and with closely related ampullariid outgroups (*Asolene* spp., *Marisa* spp., *Pila* spp.). This phylogenetic framework will then be used to help determine the geographic origins and identities of species that have been introduced to Southeast Asia and elsewhere (Hawaii, continental US). Here, we present some of our preliminary findings, updating those of Cowie and Hayes (2005).

Using standard techniques for the analysis of mitochondrial DNA (mtDNA) sequences, we have sequenced a fragment of the mtDNA cytochrome *c* oxidase subunit I (COI) gene from samples of ampullariids collected throughout Southeast Asia, from other places where they have been introduced (Australia, Arizona, California, Florida, Hawaii, Texas), and from their native South America. These data have been analyzed using maximum likelihood and parsimony methods in PAUP* (Swofford 2003), with species of *Pila* (from Cambodia and from an introduced population in Hawaii) and *Asolene* and *Marisa* (from their native South America) as outgroups.

So far, 575 individuals have been analyzed. Both parsimony and maximum likelihood analyses of the COI sequences produced phylogenetic trees with overall nearly identical topologies. Well-supported nodes in the tree (bootstrap >50; decay analysis) result in robust clustering of 19 groups of *Pomacea*; however, the deeper nodes are as yet not well resolved, and so we are not able to determine the phylogenetic relationships among these groups. We are reasonably confident of the specific identifications of some of these groups, less confident of others; and there remain some groups that we are as yet unable to identify (Table 2).

Snails from numerous Southeast Asian locations, Hawaii, California, and Arizona cluster together with snails from Argentina, which is thought to be the origin of the one or more original introductions to Southeast Asia (Mochida 1991); we consider these snails to be *P. canaliculata* (T.A. Rawlings, K.A. Hayes, R.H. Cowie, and T.M. Collins, in preparation). Snails from introduced populations in Sri Lanka and Australia cluster with *P. diffusa* collected in Brazil. Snails intercepted by quarantine officials in Hawaii, along with introduced specimens from Cambodia, Malaysia, Thailand, Florida, and Texas cluster with specimens from Brazil; the identity of these snails, some of which are very large (~8 cm), is not entirely clear, but we tentatively refer to them as *P. insularum* (T.A. Rawlings, K.A. Hayes, R.H. Cowie, and T.M. Collins, in preparation) pending additional morphological research and study of museum material. It is clear, therefore, that at least two species, *P. canaliculata* and another species that may be *P. insularum*, have been introduced widely in Southeast Asia, in addition to the introduction of *P. diffusa* to Sri Lanka and *P. scalaris* to Taiwan. Traditionally, *P. diffusa* has been considered a subspecies of *P. bridgesii* (Cowie and Thiengo 2003), and most individuals belonging to this group that have been found in the aquarium trade and as alien species in the wild have been referred to as *P. bridgesii* (e.g., Perera and Walls 1996, Winner 1996, Warren 1997, Baker 1998, Nugaliyadde et al. 2001). However, our molecular analyses suggest that all these snails should correctly be referred to as *P. diffusa*, which we treat here as a full species. We have found what we consider to be *P. bridgesii* only at a number of locations in the Amazon Basin of Brazil, where we consider it native.

We have also sequenced material of *P. camena* from Venezuela, *P. dolioides* from Brazil and Suriname, *P. glauca* from Venezuela and Suriname, *P. guyanensis* and *P. sordida* (tentatively identified) from Brazil, *P. patula* from Mexico, *P. flagellata* from Panama, *P. haustrum* (tentatively identified) from an introduced population in Florida, and five additional species from Brazil and Suriname. We also obtained a sequence said to be of *P. paludosa*, which is native to Florida, from GenBank (accession number AF321980). We have not detected any of these species in Asia.

Conclusion

Apple snail management has thus far proven very difficult, although in some countries, a suite of control measures has given some success (e.g., Teo 2005). Pest management can be successful only against a background of clear understanding of the identity and biology of the pest species. At present, it is not entirely certain what the pest species is/are, and there is only limited understanding of the pest species' ecology and behavior. Achieving this basic taxonomic, ecological, and behavioral understanding will permit control measures to be more reliably developed and quarantine efforts to be more effective. Similar recommendations have been made by Eversole (1992), Halwart (1994), and Cowie (2002).

This article reports preliminary results from ongoing morphological and molecular studies that aim to unravel the taxonomy of the invasive species of *Pomacea* in the context of a developing understanding of the systematics of the group in its native South America. The taxonomic conclusions we have presented are preliminary, based on only limited sampling

Table 2. Species of *Pomacea* for which COI sequences have been analyzed, with the number of samples of each species and the locations from which they were collected. The question mark (?) indicates an uncertain identification. Locations considered as within the native range of each species are underlined.

Species	Number of Specimens Sequenced	Locations of Samples
Pomacea bridgesii	8	Brazil
Pomacea camena	1	Venezuela
Pomacea canaliculata	277	Argentina, Arizona, California,[1] Cambodia, People's Republic of China, Hawaii, Indonesia, Japan, Malaysia, Papua New Guinea, Philippines, Republic of Korea, Taiwan, Vietnam
Pomacea diffusa	49	Brazil, Australia, Sri Lanka
Pomacea dolioides	16	Brazil, Suriname
Pomacea figulina	2	Brazil
Pomacea flagellata	4	Panama
Pomacea glauca	10	Suriname, Venezuela
Pomacea guyanensis	12	Brazil
Pomacea haustrum	2	Florida[2]
Pomacea insularum ?	85	Brazil, Cambodia, Florida, Hawaii (quarantine interception), Malaysia, Texas, Thailand, Vietnam
Pomacea lineata	56	Brazil
Pomacea paludosa	1	Florida[3]
Pomacea patula	3	Mexico
Pomacea scalaris	40	Argentina, Brazil, Taiwan
Pomacea sordida	9	Brazil
Pomacea sp.	4	Brazil
Pomacea sp.	2	Brazil
Pomacea sp.	2	Brazil

[1] Four sequences obtained from T.M. Collins and T.A. Rawlings.
[2] One sequence obtained from T.M. Collins and T.A. Rawlings.

of the diversity, but future work will include many additional species; and analysis of both molecular and morphological data in a rigorous phylogenetic framework will provide a clearer understanding of species relationships within *Pomacea*. This taxonomic work should lay the foundation for study of the ecology and behavior of the pest species in Southeast Asia.

The necessary ecological information, as a background to implementing integrated pest management strategies, would then include data on life history, population dynamics, predators, parasites, and preferred habitat characteristics. Behavioral and physiological data on aestivation, thermal and desiccation relations, seasonality of growth and reproduction, dispersal, etc. would also be important. This information should be obtained in the native range of the pest species (South America)—some such work is already being undertaken, especially in Argentina (e.g., Albrecht et al. 1996, Martín and Estebenet 2002, Estebenet and Martín 2003)—as well as in the localities in Southeast Asia where the species has become a serious pest (e.g., Carlsson et al.

2004). In this way, changes in the snails' ecology and behavior, for instance niche expansion following relaxation of competition, that have arisen as a result of the different ecosystems in which they now function can be understood. Ultimately such studies would focus on aspects of ecology and behavior that can be manipulated as possible routes to eventual control. For all such efforts, accurate, reliable taxonomy is fundamental.

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