Non-native apple snails: systematics, distribution, invasion history and reasons for introduction

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Abstract

The freshwater snail family Ampullariidae includes nine extant genera. Species of *Pomacea* in particular, but also species of *Pila* and *Marisa*, have become invasive where they have been introduced. Introduction of *Pomacea* spp. to Asia around 1980, initially to Taiwan, followed by their rapid range expansion and development as serious agricultural pests, especially of wetland rice, led to a dramatic increase in research not only in the means to control them but also in the basic systematics necessary to identify them. Ampullariid systematics has always been confused but the advent of molecular approaches, combined with modern morphological study, including extensive study of type material, determined that the two key invasive species in Asia, as well as in the USA and elsewhere, are *Pomacea canaliculata* and *Pomacea maculata*. Additional introduced species, both in Asia and elsewhere, include *Pomacea scalaris* (Taiwan), *Pomacea diffusa* (Sri Lanka, Australia, USA) and *Marisa cornuarietis* (Caribbean islands, Spain, USA). *Pila scutata* may have been transported widely in Asia but its native or introduced status in many Asian countries is not clear; however, it has been introduced to and is established in Hawaii. The main reasons for introduction of these species have included introduction as a human food resource, as a domestic aquarium snail, for biocontrol of other snails that act as vectors of the parasites causing schistosomiasis, and for control of aquatic weeds.

Additional keywords: Ampullariidae, Gastropoda, identification, introduced, *Pomacea*

Introduction

Ampullariidae are freshwater snails predominantly distributed in humid tropical and sub-tropical habitats in Africa, South and Central America and Asia. They include the largest of all freshwater snails (up to 17 cm in maximum dimension) and are a major component of the native freshwater mollusc faunas of many regions (Hayes *et al*., 2015). Among the nine genera usually recognised (Hayes *et al*., 2015), species of the two genera *Pomacea* and *Pila* in particular are frequently known as 'apple snails' because many of them bear large, round, sometimes greenish shells.

This contribution summarises recent advances in understanding of the systematics of invasive ampullariids in particular, since the treatment of Cowie *et al*. (2006) (see also Hayes *et al*., 2015). It also summarises the history of the introduction of apple snails, most notably *Pomacea canaliculata* and *Pomacea maculata*, and current knowledge of their invasive ranges. Much has been written about apple snails as pests, and their management. This large body of work was reviewed by Cowie (2002) and treated extensively by the contributions in the book edited by Joshi & Sebastian (2006), with a more recent review focussing specifically on impacts on wetlands (Horgan *et al*., 2014a). We now know that at least some of these publications may not have correctly identified the species involved, as it has only been possible to identify them definitively since the advent of molecular approaches (Cowie *et al*., 2006; Rawlings *et al*., 2007; Hayes *et al*., 2008). However, we do not attempt to re-review these and more recent studies, as they generally have not added to our broad understanding of apple snails as pests and have not offered any novel breakthroughs in terms of their management. The basic biology of apple snails (ecology, physiology, behaviour, etc.) was reviewed by Cowie (2002) and recently and extensively by Hayes *et al*. (2015), who concentrated primarily on the extensive body of research that has been undertaken since around the start of the 21st century throughout both the native and the invaded ranges of apple snails; these aspects are also not reviewed here.

Systematics

Classification

Ampullariids are basal members of the Caenogastropoda. The family Ampullariidae is in the superfamily Ampullarioidea. The family name Pilidae is a junior synonym of

Ampullariidae (Cowie, 1997; ICZN, 1999) and should not be used. The Cyclophoroidea and Viviparoidea are closely related within the group Architaenioglossa (Bouchet & Rocroi, 2005). The Campaniloidea may also be closely related. Although marine ancestry of the Architaenioglossa is assumed by most, relationships among the four superfamilies and the resolution of the base of the Caenogastropoda remain unresolved (Hayes *et al*., 2015).

Diversity, taxonomy, nomenclature

There are nine genera of extant ampullariids with almost 200 species currently considered valid (Table 1), although it is likely that with additional research this number may be reduced to around 120 (Cowie, 2015; Hayes *et al*., 2015). The great majority of the species are referred to just three genera: *Pila* (*Ampullaria* and *Ampullarius* are junior synonyms and should not be used – Cowie, 1997; ICZN 1999), *Lanistes* and *Pomacea*. The remaining six genera each contain only one or a few species.

Species of *Pomacea* especially, introduced to southern and eastern Asia and islands of the Pacific, have become major agricultural pests, notably in rice and taro but also other crops (Cowie, 2002; Joshi & Sebastian, 2006). *Pomacea* species have also been introduced to the continental USA (Rawlings *et al*., 2007), Europe (Andree & López, 2013), Israel (Roll *et al*., 2009), Australia (Hayes *et al*., 2008), to some Pacific islands, notably the Hawaiian Islands (Tran *et al*., 2008), and to non-native locations within South and Central America (Hayes *et al*., 2008).

The name 'golden apple snail' has been used widely in Asia for introduced *Pomacea* (Lai *et al*., 2005; Joshi & Sebastian, 2006), implying a single species, although it had been identified or misidentified as numerous different species, often incorrectly spelled or in combination with an incorrect genus name, also often misspelled (see Cowie *et al*., 2006). It had also been suggested, in some cases based on misidentifications, that more than one species was present in Asia (e.g. Keawjam & Upatham, 1990; Mochida, 1991; Yipp *et al*., 1991). And the name 'golden apple snail' has even been considered as referring to 'an ill-defined group including several species such as *Pomacea insularis* [sic], *P. canaliculata*, *P. vigas* [sic], *Ampullaria gigas*, and *Pila leopoldvillensis* (Simpson *et al*., 1994; Roger, 1996).

We now know that more than one species has indeed been introduced to Asia. Cowie *et al*. (2006) provided preliminary molecular and morphological data identifying the 'golden apple snail' as two species, *Pomacea canaliculata* and *P. maculata*

Table 1. Numbers of nomenclaturally available species-group names and numbers of taxa of Ampullariidae (excluding fossil taxa). From Hayes *et al*. (2015)

Genus	Distribution	Currently valid species[a]	Estimated actual species diversity[b]	Subspecies, varieties, etc.[a]	Synonyms[a]
Afropomus	Africa	1	1	1	-
Asolene	South America	8	8	2	14
Felipponea	South America	3	3	-	-
Forbesopomus	Asia	1	1	-	-
Lanistes	Africa	43	20	16	34
Marisa	South America	2	3	-	6
Pila	Africa and Asia	3	30	17	83
Pomacea	South, Central and North America	97	50	22	109
Saulea	Africa	1	1	-	-
Total		187	117	58	246

[a] For the New World, from Cowie & Thiengo (2003), and taking into account changes subsequent to that publication, as tabulated by (Cowie, 2015); and for the Old World, Cowie (2015); homonyms considered by Cowie & Thiengo (2003) and Cowie (2015) to represent taxonomically valid species and infraspecific taxa are counted as such. [b] From Berthold (1991), Hayes & Cowie (unpublished).

(as *P. insularum*, which is now a junior synonym of *P. maculata*, according to Hayes *et al*., 2012). They also noted *P. diffusa* in Sri Lanka and *P. scalaris* in Taiwan. Hayes *et al*. (2008) confirmed these identifications, with *P. canaliculata* widespread in Southeast Asia, *P. maculata* somewhat less widespread, and *P. diffusa* and *P. scalaris* only in Sri Lanka and Taiwan, respectively. Subsequently, an additional 'group', perhaps a distinct but as yet unidentified species, has been detected in phylogenetic analyses focussed on *P. canaliculata* and *P. maculata* in China (Lv *et al*., 2013; Q. Yang, pers. comm., 2016). Furthermore, hybrids between *P. canaliculata* and *P. maculata* have been detected in both the invaded and native ranges (Hayes *et al*., 2012; Matsukura *et al*., 2013; Q. Yang, pers. comm., 2016). As the common name 'golden apple snail' encompasses at least two species, to avoid future confusion regarding which species is being referred to, it is preferable to avoid using the term.

Hayes *et al.* (2008) clarified the identities of the invasives in Southeast Asia, and subsequently (Hayes *et al.*, 2012) redescribed *P. canaliculata* and *P. maculata*, distinguishing them in an integrative taxonomic framework that included anatomical, biogeographic and phylogenetic systematics data (Table 2; Figs. 1, 2). These two species are not sister taxa, and in fact are not especially closely related to each other (Hayes *et al*., 2009a). Hayes *et al*. (2012) synonymised a number of species with *P. canaliculata*, and designated a neotype for this species, as the original type material is considered lost. A single specimen was designated as the neotype of both *P. maculata* and *P. gigas* (a name also previously used for the species in Southeast Asia) and as the lectotype of *P. insularum* (selected from among syntypes in the Natural History Museum, UK), thereby rendering all three nominal species objective synonyms. *Pomacea maculata* is thus the correct, valid scientific name for the invasive species formerly known as *P. insularum*.

The comparatively recent resolution of this taxonomic confusion means that many publications prior to 2012 failed to distinguish *P. maculata* and *P. canaliculata* in Southeast Asia. For example, the snails from Cambodia, illustrated by Cowie (2002) as *P. canaliculata*, are in fact *P. maculata*, and some of the information given by Cowie (2002) for *P. canaliculata* is undoubtedly confounded with information for *P. maculata*.

In addition to these species of *Pomacea* in Asia, the African species *Pila leopoldvillensis*, considered a synonym of *Pila wernei* by Cowie (2015), has been reported in the Philippines (Barcelo & Barcelo, 1991) and Taiwan (Wu & Lee, 2005). Barcelo & Barcelo (1991) used *P. leopoldvillensis* as the name for the 'golden snail', noting that it originated in the Amazon River basin and laid pink eggs, even though

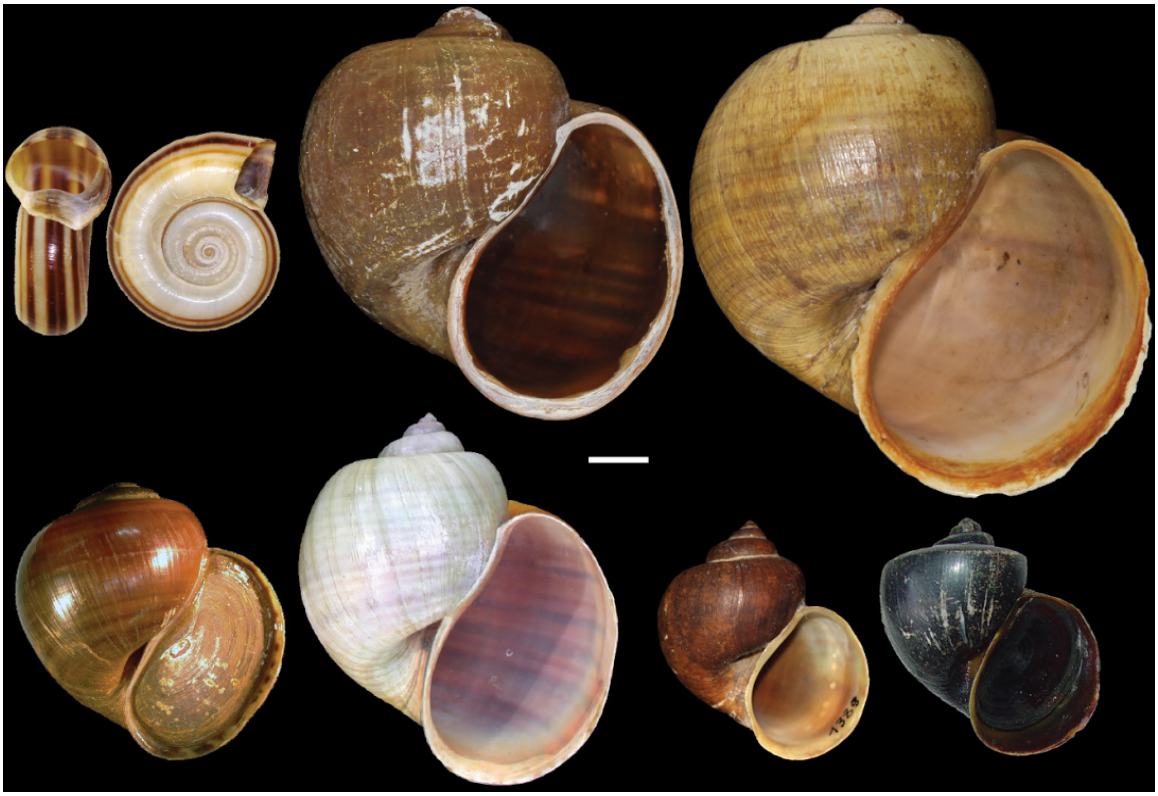

Fig. 1. Shells of introduced ampullariids. Top row, left to right: *Marisa cornuarietis*, *Pomacea canaliculata*, *P. maculata*; bottom row, left to right: *Pila scutata*, *Pomacea* sp. (incorrectly identified as *P. haustrum* by Rawlings *et al*., 2007), *P. diffusa*, *P. scalaris*. Scale bar: 1 cm. Shell morphology and colour is for many species a poor character on which to base identification, as there is considerable intra-specific variation.

Pila species are African and Asian and are not known to lay pink eggs, with most species reported to lay opaque white or cream colored eggs. The name '*leopoldvillensis*' refers to the capital (now Kinshasa) of the Democratic Republic of the Congo, the type locality of this species (Cowie, 2015). No doubt this was a misidentification of *Pomacea canaliculata*, as it was probably the only *Pomacea* species present in the Philippines at that time (Hayes *et al*., 2008; Matsukura *et al*., 2013). On the other hand, the illustration of Wu & Lee (2005), labelled as *Pila leopoldvillensis*, indeed appears to be of a species of *Pila*. There are no native Taiwanese ampullariids (Pace, 1973) and it seems much more likely that it is an Asian species, possibly the widely distributed *Pila scutata*. Roll *et al*. (2009) reported *Pomacea bridgesii* (almost certainly misidentified *P. diffusa*), *P. canaliculata*, *P. maculata* (as '*insularum*') and *P. paludosa* associated with human dominated habitats in Israel, but the identifications need verification.

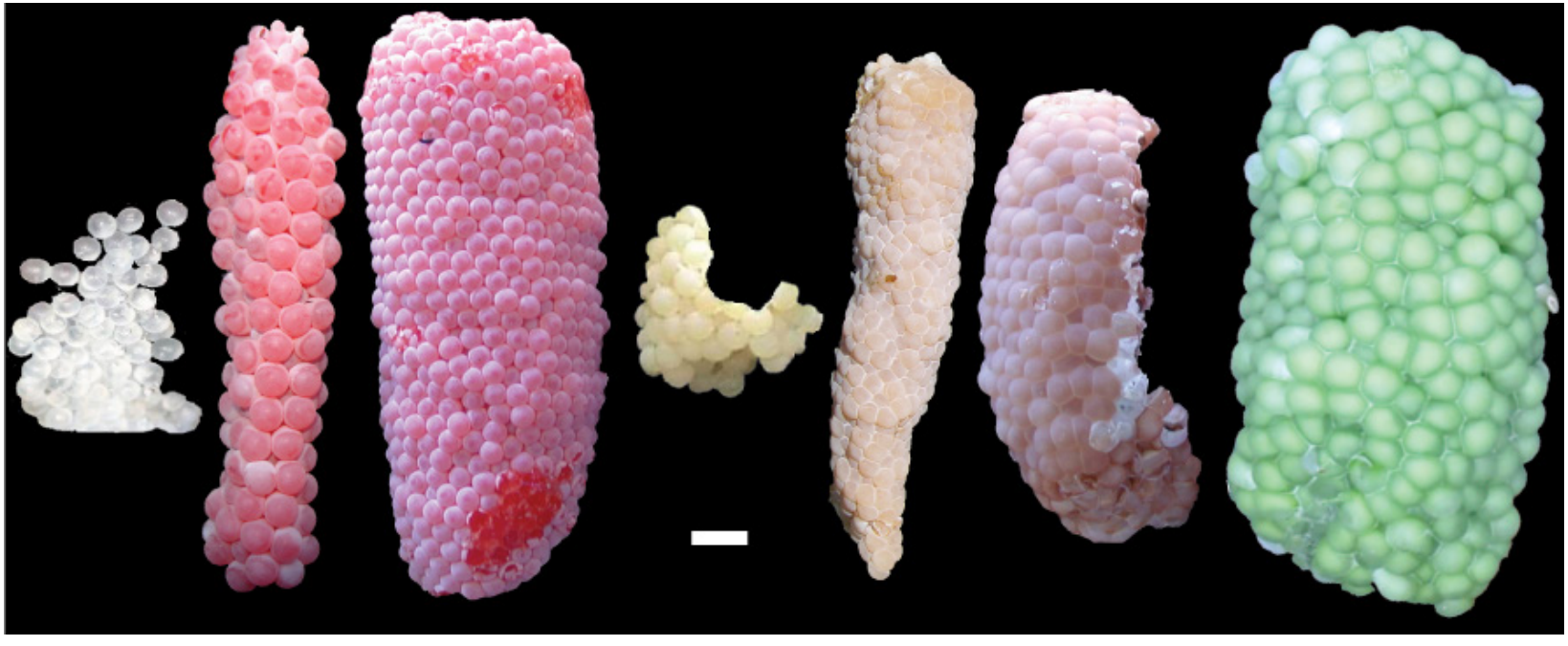

Fig. 2. Egg masses of introduced ampullariids. From left: *Marisa cornuarietis*, *Pomacea canaliculata*, *Pomacea maculata*, *Pila scutata*, *Pomacea. diffusa*, *Pomacea scalaris*, *Pomacea* sp. (incorrectly identified as *Pomacea haustrum* by Rawlings *et al.*, 2007). Scale bar: 5 mm. Eggs of *M. cornuarietis* are laid under water; those of *Pila scutata* are laid on the substrate surface just above the water line; and those of the *Pomacea* species are laid above water on emergent vegetation, rocks, walls, pilings, etc. Egg morphology and colour are often useful for distinguishing species.

Table 2. Summary of features used to distinguish *Pomacea maculata* and *P. canaliculata* by Hayes *et al*. (2012).

Feature	*Pomacea maculata*	*Pomacea canaliculata*
Adult Shell		
Maximum adult shell height	> 165 mm	~ 60 mm
Body whorl shoulder	Angulate	Rounded
Inner pallial lip	Pigmented yellow-orange-red	Unpigmented
Alimentary System		
Radula	Rachidian base concave	Rachidian base convex
Buccal ganglion	Six nerves	Five nerves
Mid-oesophagus	Tall, highly branched longitudinal folds	Low, simple longitudinal folds
Gastric caecae	Large	Small
Rectal gland	Large	Small
Reno-Pericardial System		
Kidney anterior chamber	Narrow set of anterior leaflets	Broad set of anterior leaflets
Ampulla	Pericardial artery lacking	Pericardial artery present
Reproductive System		
Dorsal penis sheath glands	Smooth apical gland tissue lacking; medial gland absent; basal gland present	Smooth apical gland tissue present, medial gland present
Bursa copulatrix	Large	Small
Eggs		
Average clutch size	~1500 eggs	~260 eggs
Average egg diameter	< 2.00 mm	> 3.00 mm
Mean hatchling width, height	1.19 mm, 1.25 mm	2.60 mm, 2.75 mm
Mean hatchling first whorl width	0.81 mm	2.41 mm

Three species have been introduced to the Hawaiian Islands: *Pomacea canaliculata*, *Pomacea diffusa* and *Pila scutata*. Cowie (1995a) also recorded *Pomacea paludosa* but this was a misidentification, and the species identified by Cowie (1995a) as *P. bridgesii* is correctly identified as *P. diffusa* (Cowie *et al*., 2007). *Pomacea diffusa* was originally described as a smaller subspecies of *P. bridgesii* (see Cowie & Thiengo, 2003), but these two species are genetically distinct and their type specimens are sufficiently different that they are now considered separate species (Cowie *et al*., 2006; Rawlings *et al*., 2007; Hayes *et al*., 2008, 2009a). Indeed, all global records of *P. bridgesii* as an introduced species are probably correctly referred to *P. diffusa*. *Pila conica* is a junior synonym of *Pila scutata* (Low *et al*., 2013). Thus, *Pila scutata* is the correct name for the species identified as *P. conica* by Cowie (1995a).

In the continental USA, introduced *Pomacea* were initially identified primarily as *Pomacea canaliculata* and given the common name 'channeled apple snail' (American spelling of 'channelled' as the name was coined in the USA), an anglicisation of the specific epithet (Howells *et al*., 2006). However, Rawlings *et al*. (2007) distinguished three species within what had been identified previously as 'channeled apple snails' (i.e. *P. canaliculata*), namely: 1) *P. canaliculata*, 2) *P. maculata* (as *P. insularum*, and which had therefore been given the common name 'island apple snail' as '*insularum*' is Latin for 'of islands') and 3) *Pomacea* sp. (misidentified as *P. haustrum*) (Hayes *et al*., 2012). Rawlings *et al*. (2007) also confirmed the presence of *Pomacea diffusa* and *Marisa cornuarietis* in addition to *Pomacea paludosa*, the only apple snail species native to North America.

In Europe, apple snails have been introduced to two locations, both in Spain. *Pomacea maculata* (as '*insularum*') seems well established in the Ebro Delta (López *et al*., 2010; MMAMRM, 2011; EFSA Panel on Plant Health, 2012; Horgan *et al*., 2014a; Andree & López, 2013). In addition, Andree & López (2013) reported DNA sequences, from empty shells collected in the field, that were consistent with *P. canaliculata*, so it appears that both species have been introduced. Arias & Torralba-Burrial (2014) recorded *Marisa cornuarietis* from a single locality in northern Spain.

Distributions

The native and non-native ranges of ampullariid species are summarised in Table 3. The following sections provide additional information and analysis of the more significant introductions.

Native ranges of introduced ampullariid species

The taxonomic confusion surrounding *Pomacea canaliculata* has obscured its true natural range until recently. Many species that molecular studies have shown to be distinct (Hayes *et al*., 2008, 2009a), have been confused with *P. canaliculata* in the past, to the extent that some authors suggested that many of these nominal species might be synonyms of *P. canaliculata* and therefore that its range extended throughout much of South America (see Hylton Scott, 1958; Cazzaniga, 2002, 2006; Cowie, 2002; Wu & Xie, 2006). The natural range of *P. canaliculata* is now known to be much more restricted (Hayes *et al*., 2012), consisting of the Lower Paraná, Uruguay and La Plata basins, although based on habitat similarity and watershed connections it is possible that it may also occur in the lower reaches of the Upper Paraná and parts of southern Brasil. It is not present in the Amazon basin. Its southern limit in Argentina seems to be limited by temperature and this may limit its spread to higher latitudes in its invaded range (Seuffert *et al*., 2010, 2012).

Pomacea maculata has a much wider native range in South America extending from the lower Paraná River basin in the Rio de la Plata region of Argentina and Uruguay, through Paraguay and northwards in Brasil through the Pantanal to north of Manaus in Amazonia, overlapping with the range of *P. canaliculata* in the south, and perhaps extending west into Bolivia, Ecuador and Peru (Hayes *et al*., 2008, 2009a, b, 2012; Thiengo *et al*., 2011).

Perhaps the third most widely introduced *Pomacea* species is *P. diffusa*. In much of the literature, this species had been identified incorrectly as *Pomacea bridgesii* (see above). *Pomacea diffusa* is widely distributed through much of the Amazon basin, whereas *P. bridgesii* is restricted to Bolivia and the western Amazon basin (Pain, 1960; Rawlings *et al*., 2007; Hayes *et al*., 2008; Hayes, Cowie & Thiengo, unpublished).

Pomacea scalaris ranges from Buenos Aires in Argentina northwards through the Pantanal to Cuiabá in Mato Grosso state (Hayes *et al*., 2008) and perhaps more widely.

Table 3. Native and non-native ranges of introduced ampullariids in the wild (records in captivity and records in artificial thermal outflows not listed). Some, especially earlier, references listed for *Pomacea canaliculata* may in fact be based on *P. maculata*.

Species	Native range	Non-native range	First record or known date of introduction	Representative references for non-native range
Marisa cornuarietis	Colombia Venezuela	Costa Rica	?	Nguma *et al*., 1982
		Cuba	1950	Hunt, 1958
		Dominican Republic	1986	Vargas *et al*., 1991; Perera & Walls, 1996
		Egypt[a]	1972	Demian & Kamel, 1973; Brown, 1994
		French Guyana[b]	2005	Mansur, pers. comm., in Massemin *et al*., 2009
		Grenada	2009	Barker, 2016
		Guadeloupe	1973	Pointier & David, 2004
		Guyana	?	Nguma *et al*., 1982; Massemin *et al*., 2009
		Martinique	1987	Pointier, 2001
		Panama	?	Nguma *et al*., 1982
		Puerto Rico	1952	Harry & Cumbie, 1956; Hunt, 1958; Peebles *et al*., 1972; Jobin *et al*., 1977; Nguma *et al*., 1982; Perera & Walls, 1996
		St. Kitts	1950s	Ferguson et al., 1960
		Spain	2012	Arias & Torralba-Burrial, 2014
		Sudan[a]	1981	Haridi *et al*., 1985; Brown, 1994
		Surinam	?	Nguma *et al*., 1982
		Tanzania[a]	1977	Nguma *et al*., 1982; Brown, 1994
		USA (continental)	1957	Hunt, 1958; Neck, 1984, Cowie, 2002; Howells *et al*., 2006; Rawlings *et al*., 2007
Pila scutata	Southeast Asia[c]	Guam	1984	Smith, 1992; Cowie, 2002
		Hawaii	1966	Cowie, 1995; Tran *et al*., 2008
		Palau[d]	1984-1985	Eldredge, 1994, Cowie, 2002
		Taiwan[e]	1975	Wu & Lee, 2005

Pomacea canaliculata	Argentina Uruguay Paraguay southern Brasil	Bangladesh[f]	2006	Ranamukhaarachchi & Wikramasinghe, 2006; Wu & Xie, 2006
		Cambodia[g]	2006	Ranamukhaarachchi & Wikramasinghe, 2006
		Chile	2008	Letelier & Soto-Acuña, 2008
		China	1981-1985	Hayes *et al*., 2008; Kwong *et al*., 2008
		Dominican Republic	1991	Rosario & Moquete, 2006
		Ecuador	2005	Horgan *et al*., 2014b
		Egypt[f]	2006	Wu & Xie, 2006
		Guam	1989	Smith, 1992; Hayes *et al*., 2008
		Hawaii	1989	Cowie, 1995; Hayes *et al*., 2008; Tran *et al*., 2008
		India[f]	2006	Ranamukhaarachchi & Wikramasinghe, 2006; Wu & Xie, 2006
		Indonesia	1981-1984	Mochida, 1991; Hayes *et al*., 2008
		Japan	1981	Mochida, 1991; Hayes *et al*., 2008
		Laos	1991-1994	Douangboupha & Khamphoukeo, 2006; Halwart & Bartley, 2006; Hayes *et al*., 2008
		Malaysia	1987-1992	Mochida, 1991; Halwart, 1994; Naylor, 1996; Yahaya *et al*., 2006; Hayes *et al*., 2008
		Mexico	2009	Campos *et al*., 2013
		Myanmar (Burma)	2008	Wu & Xie, 2006; Hayes *et al*., 2008
		Papua New Guinea	1991	Laup, 1991; Hayes *et al*., 2008
		Philippines	1980	Mochida, 1991; Hayes *et al*., 2008
		Singapore	1991	Ng, 1991; Ng *et al*., 2014
		South Africa[h]	before 1991	Berthold, 1991
		South Korea	1981-1986	Mochida, 1991; Hayes *et al*., 2008
		Spain	2001	Andree & López, 2013
		Taiwan	1979-1981	Mochida, 1991; Cheng & Kao, 2006; Yang *et al*., 2006; Halwart & Bartley, 2006; Hayes *et al*., 2008; Wu *et al*., 2010
		Thailand	1982-1990	Mochida, 1991; Halwart & Bartley, 2006; Hayes *et al*., 2008

		Trinidad	2014	Mohammed, 2015
		USA (continental)	1997	Cerutti, 1998; Rawlings *et al*., 2007
		Vietnam	~1988	Cuong, 2006; Halwart & Bartley, 2006; Hayes *et al*., 2008
Pomacea diffusa[i]	Amazonia	Australia	2004	Hayes *et al*., 2008; Ponder *et al*., 2016
		Brasil (Pará)	2008	Hayes *et al*., 2008
		Brasil (Pernambuco)	2006	Hayes, unpublished
		Brasil (Rio de Janeiro)	2008	Hayes *et al*., 2008
		Colombia	2008	Hayes, unpublished
		French Guiana	~1930	Tillier, 1980 (as *Ampullaria sordida*); Massemin *et al*., 2009
		Hawaii	1962	Cowie, 1995
		New Zealand[j]	2010	Collier *et al*., 2011
		Panama	2008	Hayes *et al*., 2008
		Sri Lanka	early 1980s	Epa, 2006; Hayes *et al*., 2008; Wijesekara, 2010
		USA (continental)	1950s-1960s	Howells *et al*., 2006; Rawlings *et al*., 2007
		Venezuela	2009	Hayes, unpublished
Pomacea sp.[k]	Amazonia	USA	2007	Rawlings *et al*., 2007
Pomacea maculata	Argentina to Amazonia	Cambodia	before 1995	Cowie, 1995b; Hayes *et al*., 2008
		China	2006-2007	Lv *et al*., 2013
		Israel	2008	Roll *et al*., 2009
		Japan	2008/2013	Matsukura *et al*., 2008, 2013
		Malaysia	2008	Hayes *et al*., 2008
		Pakistan[l]	2009	Baloch, 2017
		Philippines	2013	Matsukura *et al*., 2013
		Singapore	2008	Hayes *et al*., 2008; Ng *et al*., 2014
		South Korea	2008	Hayes *et al*., 2008; Matsukura *et al*., 2013
		Spain	2009	López *et al*., 2010; MMAMRM, 2011; European Food Safety Authority; 2012; Andree & López, 2013; Horgan *et al*., 2014a

		Thailand	1990	Hayes *et al*., 2008
		USA (continental)	1989	Martin *et al*., 2012; Byers *et al*., 2013
		Vietnam	2008	Hayes *et al*., 2008
Pomacea scalaris	Argentina Southern Brasil	Taiwan	1989	Hayes *et al*., 2008; Wu *et al*., 2010, 2011

[a] not known whether widely established; [b] presence remains to be confirmed; [c] native and non-native range difficult to disentangle (see text); [d] thought to have been eradicated; [e] tentative identification based on the record of *Pila leopoldvillensis* by Wu & Lee (2005); [f] unconfirmed; [g] unconfirmed; may refer to *P. maculata*, which is present in Cambodia; [h] identified as *Pomacea lineata* but probably *P. canaliculata*; possibly not established; [i] the record in Puerto Rico of Horgan *et al*. (2014a) appears to be in error; [j] a single specimen, may not be established; [k] identified incorrectly as *P. haustrum* by Rawlings *et al*. (2007); [l] originally identified as *P. canaliculata* (see Horgan *et al*., 2014a).

The true native range of *Pila scutata* is difficult to determine (Tan *et al*., 2013). In Singapore, it has declined drastically (Tan *et al*., 2013; Ng *et al*., 2014), but it used to be widespread and seemed to be strongly associated with anthropogenically disturbed habitats. It has been considered native in Singapore, with the first record in 1847 (not definitive) or 1885 (Low *et al*., 2013), but has also been recorded from Indonesia, Peninsular Malaysia, Myanmar, Borneo, Vietnam, Cambodia, Laos and the Philippines, and with doubt from Thailand and China (Low *et al*., 2013; Tan *et al*., 2013) and Taiwan (as *Pila leopoldvillensis*, see above). However, whether it occurred naturally in these countries or whether it became widespread as a widely introduced popular food item, is not clear (Tan *et al*., 2013).

The native range of *Marisa cornuarietis* may only encompass Venezuela and Colombia (Nguma *et al*., 1982). However, it occurs widely in other parts of northern South America (Table 2) but it is not clear whether its presence in at least some of these areas is natural or the result of introductions. It is often confused with two congenerics, *M. planogyra*, which occurs throughout the Pantanal of central west Brasil, and *M. rotula*, which occurs north of the eastern Andean cordillera in Colombia and Panama.

Non-native ranges

The most widespread species in Asia is *Pomacea canaliculata* (Table 3). *Pomacea maculata* is also widespread in Asia, but not to the extent of *P. canaliculata* (Hayes *et al*., 2008; Lv *et al*., 2013). In the USA, *P. maculata* is present in the southeast, contrasting with the initial distribution of *P. canaliculata* in the west, although *P. canaliculata* is also now present in Florida (Rawlings *et al*., 2007). An unidentified species of *Pomacea*,

incorrectly identified by Rawlings *et al*. (2007) as *P. haustrum*, is also present in Florida (Hayes *et al*., 2012). Within South America, *P. canaliculata* has been reported beyond its native range, in Chile and Ecuador (Letelier & Soto-Acuña, 2008; Horgan *et al*., 2014b. Both *P. maculata* and *P. canaliculata* are present in Spain (Andree & López, 2013).

In Hawaii, *Pomacea canaliculata* is widely distributed and locally abundant on five of the main islands (Lach & Cowie, 1999; Cowie *et al*., 2007). *Pomacea diffusa*, also reported from Hawaii, was not widespread or abundant and has not been seen since 1998 (Cowie *et al*., 2007, unpublished) and may no longer be present. The Asian *Pila scutata* has been recorded from the islands of Maui, Molokai and Oahu (Cowie, 1995a), although it was not recorded on Maui and Molokai by Cowie *et al*. (2007) and Tran *et al*. (2008). It has since been confirmed as still present on Oahu (Cowie, Hayes, C. Tran & K. Matsukura, unpublished). In the Pacific, it was also introduced to Guam (Smith, 1992) and Palau, where it was eradicated (Eldredge, 1994), and is probably the species identified as the African *Pila leopoldvillensis* in Taiwan (see above). It is widespread in Asia but its native range in Asia is not known definitively and it is possible that part of this wide Asian distribution results from introductions (see above). *Pomacea scalaris* has been introduced to Taiwan, its only known non-native location.

Pomacea diffusa is also established in Sri Lanka (Nugaliyadde *et al*., 2001; Wijesekara, 2010), and in non-native regions of South and Central America (Hayes *et al*., 2008) and the southeastern USA (Rawlings *et al*., 2007). Introduced populations of *P. diffusa* exhibit very little genetic variation, with a single COI haplotype shared by individuals from Australia, Sri Lanka, New Zealand, Panama and parts of Brasil where the species has been introduced, and by specimens from pet stores in Hawaii, Florida and Iran (Hayes *et al*., 2008; Thiengo *et. al*., 2011) as well as Singapore, Hong Kong and Washington DC (Hayes, unpublished).

As noted above, the native range of *Marisa cornuarietis* may only encompass Venezuela and Colombia, with its presence in other parts of northern South America (Table 3) due to human activities, although it is yet possible that it occurs in these areas naturally. It is widely introduced elsewhere, especially in the Caribbean, as well as in the USA, especially in the southeast (Rawlings *et al*., 2007), and Spain (Arias & Torralba-Burrial, 2014). It is present in Hungary but only in an urban section of a stream close to the outflow from a thermal spa (Frisóczki *et al*., 2016).

Records of other introduced ampullariid species are the results of misidentifications (Table 4).

Table 4. A selection of misidentifications, and the corresponding correct names, of introduced *Pomacea* species. This list does not include the numerous early misidentifications of *Pomacea maculata* as *P. canaliculata* (see text).

Region	Misidentification	Correct name	Author(s)
Asia (Hong Kong)	*Ampullaria levior*	*Pomacea canaliculata*	Yipp *et al*., 1992
Asia (Indonesia)	*Pomacea paludosa*	*Pomacea canaliculata*	Hendarsih-Suharto *et al*., 2006
Asia (Philippines)	*Pomacea cuprina*	Probably *Pomacea canaliculata*	Mochida, 1991
Asia (Sri Lanka)	*Pomacea bridgesii*	*Pomacea diffusa*	Nugaliyadde *et al*., 2001
Asia (Taiwan)	*Pila leopoldvillensis*	Probably *Pila scutata*	Barcelo & Barcelo, 1991; Wu & Lee, 2005
Asia (Taiwan)	*Pomacea lineata*	*Pomacea canaliculata*	Cheng, 1989
Asia (Vietnam)	*Pomacea bridgesii*	*Pomacea canaliculata* or *Pomacea maculata*	Cuong, 2006
Hawaii	*Pomacea paludosa*	*Pila conica*	Cowie, 1995
Hawaii	*Pomacea bridgesii*	*Pomacea diffusa*	Cowie, 1995
USA (Texas)	*Pomacea canaliculata*	*Pomacea maculata*	Neck, 1986; Neck & Schulz, 1992
USA (Florida)	*Pomacea haustrum*	*Pomacea* sp.	Rawlings *et al*., 2007

Introduction history and reasons

Introductions for food

Some ampullariids are used as human food in their native ranges, mostly in Asia but also in South America and Africa. However, deliberate introduction as a novel human food resource is probably the most important cause of their spread and establishment, although the aquarium trade is of major importance in some regions (see below).

In the Pacific, *Pila scutata* was introduced without authorisation, either accidentally or deliberately as a food item to both Hawaii (first recorded 1966; Cowie, 1995a) and Guam (first recorded 1984; Smith, 1992), probably from the Philippines (Tran *et al*.,

2008). It was also introduced to Palau in 1984 or 1985, probably for the same purpose, but was eradicated by 1987 (Eldredge, 1994). But it is the South American *Pomacea* species that have attracted most attention, notably in southern and eastern Asia, where they have become major agricultural pests.

At some time between 1979 and 1981, what became widely assumed to be a single species of *Pomacea* was introduced to Asia, initially from Argentina to Taiwan (Mochida, 1991), although it may have been introduced earlier in the 1970s to the Philippines, China and Vietnam (Wu & Xie, 2006). Undoubtedly this was *Pomacea canaliculata*, the only widespread species in Taiwan. *Pomacea scalaris*, also present in Taiwan, may have been introduced accidentally, perhaps with the original introduction(s) of *P. canaliculata* as their native ranges overlap (Wu & Lee, 2005; Wu *et al*., 2011). The initial introduction of *P. canaliculata* to Taiwan was illegal, its purpose being to develop the species for both local consumption and export to the gourmet restaurant trade. The subsequent spread of these snails in Asia and the Pacific, distributed primarily for the same purposes, has been summarised by Cowie (2002), Halwart & Bradley (2006), Wu & Xie (2006) and others (generally not distinguishing *P. canaliculata* and *P. maculata*). Halwart and Bradley (2006) listed the origins of many of the Asian introductions as 'Amazon basin', which is incorrect except possibly for *Pomacea diffusa*. In 1981 snails were taken from Taiwan to Japan, Korea (Lee & Oh, 2006), China and Indonesia. By 1982 they had been introduced to the Philippines and introductions to the Philippines continued from various sources as snail-farming was promoted by governmental and non-governmental organisations. By 1983 about 500 snail businesses had opened in Japan; they were present in Okinawa by at least 1984. *Pomacea maculata* may have been first introduced around this time, from Argentina and southern Brasil (Hayes *et al*., 2008). Later, the snails were taken to parts of Malaysia (Sarawak and Peninsular Malaysia, 1987), Vietnam (1988 or 1989), Thailand (1989 or 1990) and Laos (1992). They were present in Hong Kong and Singapore by 1991 and Cambodia by at least 1994. In the Pacific they were in Hawaii by 1989 or perhaps earlier (Cowie *et al*., 2007), Guam by 1989 (perhaps introduced from Taiwan or more likely the Philippines; Tran *et al*., 2008), and Papua New Guinea in 1990 (Orapa, 2006), probably introduced from the Philippines.

Prior to the clarification by Hayes *et al*. (2008), most of these reports assumed that a single species was involved, usually identified as *Pomacea canaliculata*. Hayes *et al*. (2008) concluded, based on mitochondrial DNA (mtDNA) diversity, that the Asian populations of both *P. canaliculata* and *P. maculata* resulted from multiple introductions. Tran *et al*. (2008) showed that only a single haplotype was present in Hawaiian *P.*

canaliculata, suggesting a single introduction or multiple introductions from a single location, probably the Philippines.

The species identified in Taiwan as the African *Pila leopoldvillensis* is in fact probably Asian *Pila scutata* (see above). It was imported into Taiwan in 1975 for culture for food prior to the introduction of the South American *Pomacea canaliculata* (Wu & Lee, 2005), but seems to have disappeared, perhaps outcompeted by *P. canaliculata* (*P. maculata* has not been reported from Taiwan).

Pomacea canaliculata was recorded in California in 1998, perhaps introduced from Hawaii for food (Rawlings *et al*., 2007). By 2007 it was in Arizona and Florida, perhaps introduced from California.

In Asia particularly, the snails' economic potential was over-estimated and while many, mostly small aquaculture operations arose, relatively few persisted (Acosta & Pullin, 1991). In Taiwan, the local market failed because consumers disliked the snails' taste and texture (Yang *et al*., 2006). Stringent health regulations in developed nations largely precluded its importation (Naylor, 1996). Snails escaped or were deliberately released, becoming widespread and abundant, and major crop pests, in many countries. They nonetheless continue to be considered a delicacy in some regions, notably in southern China, where they are eaten raw and where they have become important transmitters of *Angiostrongylus cantonensis*, the rat lungworm, with major human health consequences (Lv *et al*., 2011).

The aquarium trade

Ampullariids are popular domestic aquarium snails (Perera & Walls, 1996; Wilstermann-Hildebrand, 2009: Ng *et al*., 2016). Various species have therefore been introduced around the world, perhaps also accidentally with aquarium plants. *Pomacea diffusa*, usually referred to as *P. bridgesii* until their distinction was clarified by Hayes *et al*. (2008), is perhaps the most widely available ampullariid in the aquarium pet trade (Perera & Walls, 1996), although a number of other species are also available (Horgan *et al*., 2014a; Ng *et al*., 2016). In the USA, *Pomacea diffusa* was probably introduced to Florida in the early 1960s and is now also established in Alabama (Rawlings *et al*., 2007). It is produced commercially on a large scale in Florida (Perera & Walls, 1996). The market has expanded since the discovery and development of bright yellow, orange and other colour variants of *P. diffusa* and to some degree other *Pomacea* species (Perera & Walls, 1996). *Pomacea diffusa* has been intercepted by customs officials in Singapore.

It is established in Australia and Sri Lanka (Epa, 2006; Hayes *et al*., 2008; Ponder *et al*., 2016) and was reported in the wild in Hawaii (Cowie, 1995a), although it may no longer be present (see above). *Pomacea canaliculata* (including brightly coloured forms) in California and Arizona was probably introduced for food (Rawlings *et al*., 2007) but the aquarium trade may also have been involved. *Pomacea maculata* has been detected in the trade in Belgium (Hayes *et al*., 2008) and Singapore (Ng et al., 2016) and its presence in Spain probably originated in the trade. Its presence in the southeastern USA may have been a result of pet trade introductions. *Pomacea diffusa* has also been sold for food in Belgium, as 'sea snails' (Thiengo, personal observation).

Keawjam & Upatham (1990) considered the *Pomacea* in Thailand to have been imported by the aquarium trade, but it is also probable that they were introduced for food, as elsewhere in Southeast Asia. *Pomacea canaliculata* is available in the aquarium trade in Singapore (Ng *et al*., 2016) and in Hawaii, locally collected *Pomacea canaliculata* are available in aquarium stores, and purchase followed by release for culture as food items may have been one reason for its spread in Hawaii (Cowie, 2002), although the original source of the aquarium snails was probably local, following their initial introduction for food. *Asolene spixii* has been seen in pet stores in Hawaii but has not yet been found in the wild. *Pomacea lineata* (probably misidentified *P. canaliculata*) has been introduced to South Africa.

Marisa cornuarietis has been introduced to several countries (e.g. the USA) (Perera & Walls, 1996) and Spain (Arias & Torralba-Burrial, 2014) and is well known in the aquarium trade (e.g., Ng *et al*., 2016).

Biological control

In the Caribbean *Pomacea glauca* and more widely *Marisa cornuarietis* have been introduced in attempts to control the snail vectors of *Schistosoma* spp., the cause of human schistosomiasis, through competition and predation (Peebles *et al*., 1972; Pointier *et al*., 1991; Perera & Walls, 1996; Pointier & David, 2004), and *M. cornuarietis* has been tested in field experiments in Egypt and Tanzania for the same purpose (Nguma *et al*., 1982), although it seems not to have become established in the wild in Africa.

Many ampullariids feed voraciously on aquatic plants, this being one reason for their success in controlling other snail species by reducing the available food. They have therefore been used or suggested for aquatic weed control in both natural wetlands and irrigated rice, e.g. *Marisa cornuarietis* in Florida and Puerto Rico (Simberloff & Stiling,

1996), *Pomacea canaliculata* in Asia (Joshi & Sebastian, 2006; Wada, 1997), although there are concerns in Asia that this might lead to farmers introducing snails to areas they have not yet reached (Wada, 2006).

Conclusions

Since the review of Cowie (2002) and book edited by Joshi & Sebastian (2006) there have been considerable advances in understanding the identities of invasive and other introduced apple snail species. Most of these advances have been the result of molecular analysis, both in the native and non-native ranges. Extensive bibliographic and museum research has brought rigour to the formerly highly confused nomenclature. And detailed morphological study, in conjunction with molecular analysis, has provided the basis not only for distinguishing the key invasive species, but also for modern systematic revision, at least of the New World taxa.

As for many species introduced deliberately, the benefits initially perceived are often outweighed by the negative impacts. The primary reason for introducing apple snails has been for human food, but they also continue to be spread through the aquarium trade. They are still used for food in many places, although not to the extent originally envisaged. But the damage to agriculture and the less well understood but potentially serious damage to non-agricultural systems, outweigh arguments for their further introduction for food. Once introduced and established, control measures become necessary. As for most introductions of the species outside their native ranges, the introduction of apple snails, even for ostensibly legitimate reasons of human health and well-being, is fraught with dangers and should be prevented.

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