The Golden Apple Snail: *Pomacea* species including *Pomacea canaliculata* (Lamarck, 1822) (Gastropoda: Ampullariidae)

DIAGNOSTIC STANDARD

Prepared by

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1. PREFATORY COMMENTS

The term 'apple snail' refers to species of the freshwater snail family Ampullariidae primarily in the genera *Pila*, which is native to Asia and Africa, and *Pomacea*, which is native to the New World. They are so called because the shells of many species in these two genera are often large and round and sometimes greenish in colour.

The term 'golden apple snail' is applied primarily in south-east Asia to species of *Pomacea* that have been introduced from South America; 'golden' either because of the colour 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. 'Golden apple snail' does not refer to a single species. The most widely introduced species of *Pomacea* in south-east Asia appears to be *Pomacea canaliculata* (Lamarck, 1822) but at least one other species has also been introduced and is generally confused with *P. canaliculata*. At this time, even mollusc experts are not able to distinguish the species readily or to provide reliable scientific names for them.

This confusion results from the inadequate state of the systematics of the species in their native South America, caused by the great intra-specific morphological variation that exists throughout the wide distributions of the species. DNA sequencing is beginning to resolve the problem but is at a very early stage.

Hence, it is not possible to provide a definitive diagnostic standard for the 'golden apple snail'. Much of the information that follows refers to *Pomacea canaliculata* (to the extent that studies reported in the literature have identified the species correctly). Additional information, referring to other species of Ampullariidae, is provided if appropriate. An outline of their biology, pest status and management has been provided by Cowie (2002), with some more recent information on nomenclature provided by Cowie and Hayes (2005), and an assessment of their current (2004) pest status in Asia by Lai et al. (2005).

2. DIAGNOSTIC IMAGES OF GOLDEN APPLE SNAILS

Pomacea canaliculata (Lamarck, 1822). Two views of the lectotype – Muséum d'Histoire Naturelle de Genève. Shell height 61 mm (Mermod, 1952). [Photos: Y. Finet].

The photographs above are two views of the lectotype of *Pomacea canaliculata*, that is, the actual shell from which Lamarck is thought to have originally described the species. The following images, however, illustrate some of the wide range of shell shape and colour that are exhibited by ***P. canaliculata***. Note that the degree of indentation ("chanellisation") of the suture (the junction between successive whorls) can be considerably less than in the lectotype. Colouration is highly variable.

Pomacea sp., probably *P. canaliculata*, from a single population in its native range in Argentina. Scale: 1 cm. [Photo: R.H. Cowie].

Some of the range of shell colour and banding variation, and to some extent shell shape variation, exhibited within a single introduced population of *Pomacea* (probably *P. canaliculata*) from Singapore. Scale: 1 cm. [Photo: R. H. Cowie].

A sample of snails from a single population of *Pomacea* (probably *P. canaliculata*) from the Philippines, characteristically covered in part by fine dried mud from the paddy fields from which they were collected. Scale: 1 cm. [Photo: R.H. Cowie].

Pomacea canaliculata in Hawaii. Left – a relatively large adult. Scale: 1 cm. [Photo: R.H. Cowie]. Centre – crawling in a taro patch. [Photo: K.A. Hayes and R.H. Cowie]. Right – in an aquarium. [Photo: R.A. Englund, Hawaii Biological Survey, used with permission].

Left – *Pomacea* sp. from Cambodia. Scale: 1 cm. [Photo: R.H. Cowie]. Right – *Pomacea* sp. from Texas. Note the extremely eroded shell, which is natural. Scale: 1 cm. [Photo: R.H. Cowie]. Note that both these snails are much larger than the largest *P. canaliculata* in Hawaii (above); they belong to a different species.

3. ORGANISMS THAT OCCUR IN AUSTRALIA WITH WHICH GOLDEN APPLE SNAILS MIGHT BE CONFUSED

3.1. Native freshwater snails

Pomacea species are so distinctive in relation to native Australian freshwater snail species that no native species are likely to be confused with *Pomacea canaliculata*, with other species of *Pomacea* or indeed with other species of Ampullariidae (e.g. *Pila* spp.). Most native Australian freshwater snails are small, with the exception of six species of Viviparidae and nine Thiaridae (Ponder, 1997). None of these reach a size of more than ~40 mm shell height. *Pomacea canaliculata* in south-east Asia generally reaches an adult size of ~40 mm shell height, some Argentinian *P. canaliculata* may grow as large as ~70 mm, and 'golden apple snails' in some parts of south-east Asia (probably not *P. canaliculata*) reach ~90 mm. Other *Pomacea* spp. that may be part of the 'golden apple snail' group reach larger sizes; for instance *P. maculata* has been recorded as exceeding 155 mm (Pain, 1960).

Viviparids are viviparous (giving birth directly to small snails), the overall shape of the upper shell whorls is rather conical and the aperture is rather round. In contrast, *Pomacea* spp. are oviparous (laying eggs), the shell is generally globular not conical and the aperture is more elongate.

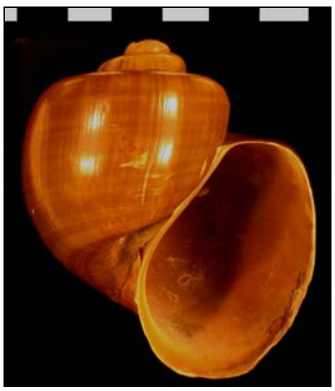
Australian thiarids have tall thin shells with many whorls, sometimes with the upper whorls broken off.

An example of an Australian viviparid, *Notopala waterhousei* (Adams & Angus, 1864) (Viviparidae). Scale: 1 cm. [Photo: Cochlea (http://www.ne.jp/asahi/dexter/sinister/index.html), used with permission].

Examples of Australian thiarids. Left, *Melanoides denisoniensis* (Brot, 1877); centre, *Thiara balonnensis* (Conrad, 1850); right, *Syrmylasma venustula* (Brot, 1877). [Photos: Martin Kohl, used with permission].

3.2. Non-native freshwater snails

One species of *Pomacea*, *P. bridgesii* (Reeve, 1856), has been introduced to Australia, almost certainly via the domestic pet and aquarium trade. It has been reported in the wild in both Queensland and Western Australia, in small locally confined populations, but it is not clear whether it is truly established. This species has also been introduced widely around the world (e.g. Florida, Hawaii, Sri Lanka). However, because of taxonomic uncertainty it is not clear whether these introduced populations are the nominotypical *P. bridgesii*, which may reach an adult shell height of ~70 mm, or the subspecies *P. bridgesii diffusa* Blume, 1957, which is generally smaller and may in fact be a distinct full species. Introduced *P. bridgesii*, both in Australia and elsewhere, generally only reach a maximum size of 50-60 mm, which may indicate that they are *P. b. diffusa*.



Pomacea bridgesii (Reeve, 1856). Lectotype – the Natural History Museum, London. Scale: 1 cm. [Photo: R.H. Cowie].

Pomacea bridgesii diffusa Blume, 1957. Two views of the holotype – Zoologische Staatssammlung München. Scale: 1 cm. [Photos: R.H. Cowie].

P. bridgesii sensu lato (i.e. both the nominotypical subspecies and *P. b. diffusa*) can be distinguished from the various species that constitute the 'golden apple snail' by the more square-shouldered whorls of *P. bridgesii* and the fact that the suture (the junction between successive whorls) is not deeply channelled, the character that gives *P. canaliculata* its scientific name (see diagrams in section 7.2). However, distinguishing these species on the basis of these shell characteristics is not easy and requires considerable experience, especially given the variability in shell shape within these species. Nevertheless, the illustrations provided here should assist in making the distinction.

Note that shell colour, the pattern of darker bands running spirally around the shell and the colour of the animal inside should not in any sense be considered diagnostic of species of *Pomacea*, and cannot be used to distinguish *P. b. bridgesii* or *P. b. diffusa* from *Pomacea canaliculata* or other 'golden apple snails' (see section 7.1.2, below).

3.3. Land snails

There are a number of large, native Australian land snail species. Many ampullariids, including *Pomacea* species, are able to survive out of water for considerable lengths of time. This means that one cannot assume that because a snail is out of water it is not an apple snail. However, none of these large native Australian land snails possesses an operculum, as do all Ampullariidae including species of *Pomacea* (see section 7.5).

4. ORGANISMS THAT DO NOT OCCUR IN AUSTRALIA BUT WHICH MIGHT BE INTERCEPTED BY QUARANTINE OFFICIALS AND WHICH COULD BE CONFUSED WITH GOLDEN APPLE SNAILS

A number of species of large snails in the families Ampullariidae and Viviparidae that are regularly transported around the world and have become established in a number of non-native locations might be confused with 'golden apple snails'. These include various species of *Pomacea* and *Pila* (Ampullariidae) and of *Viviparus*, *Cipangopaludina* and *Bellamya* (Viviparidae). The genus *Marisa* (Ampullaridae) is readily distinguished from 'golden apple snails' and other Ampullariiidae by its planispiral shell.

The following short key will distinguish these major groups.

1. a) Viviparous (gives birth directly to small snails); overall shape of upper shell whorls rather conical……………………………………………………………………..Viviparidae
   b) Oviparous (lays eggs); shell generally globular, not conical (Ampullariidae, excluding *Marisa*)
   …………………………………………………………….…………………2
2. a) Operculum calcified, hard and brittle, often appearing pearly on the inner surface…..*Pila*
   b) Operculum not calcified, horny and pliable………………………………...…*Pomacea*

The following illustrations are of some of these species of Viviparidae and Ampullariidae that have been introduced widely around the world.

Cipangopaludina chinensis (Gray, 1834). Specimens from introduced populations in Hawaii, illustrating the range of shell colour this species may adopt. Scale: 1 cm. [Photo: R.H. Cowie].

Cipangopaludina chinensis is the most widely introduced viviparid. *C. japonica*, which has in the past been synonymized with *C. chinensis*, may be a distinct species. Both species have been placed in the genus *Bellamya* by some authors (e.g. Smith, 2000).

Marisa cornuarietis (Linnaeus, 1758). Views of a specimen from Florida, where the species has been introduced. Top left – apertural view; top right – oblique view; bottom left – apical (top) view; bottom right – umbilical (bottom) view. Scale: 1 cm. [Photos: R.H. Cowie].

Although belonging to the same family (Ampullariidae) the distinctive shape of the shell allows ***M. cornuarietis*** to be readily distinguished from 'golden apple snails'. ***M. cornuarietis*** has been widely introduced around the world both by the domestic aquarium trade and for use as a biological control agent against aquatic weeds. It is inappropriate for the latter purpose because of its potentially serious impacts on non-target, native plants and their associated faunas (Cowie, 2001).

Pomacea haustrum (Reeve, 1856), possible syntype – the Natural History Museum, London. Scale: 1 cm. [Photo: R.H. Cowie].

Pomacea haustrum has been Introduced from South America to Florida. At this time this species is not distinguishable from large 'golden apple snails' by any known character other than by the fact that it lays greenish eggs, rather than the bright pink eggs laid by 'golden apple snails'. It has been synonymized with *Pomacea canaliculata* by some authors, probably incorrectly.

Pomacea paludosa (Say, 1829). Two views of the lectotype – Academy of Natural Sciences of Philadelphia. [Photos: P. Callomon, Academy of Natural Sciences of Philadelphia, used with permission].

Pomacea paludosa was Introduced from Florida, where it is native, to Hawaii, although it seems not to have become established in Hawaii. It can be distinguished relatively easily from ‘golden apple snails’ by its much less indented sutures (the junction between successive whorls), these being distinctly channelled in ‘golden apple snails’ (see diagrams in section 7.2).

Two views of a specimen of *Pila conica* (Gray, 1828) from an introduced population in Hawaii. Scale: 1 cm. [Photos: K. A. Hayes & R. H. Cowie].

Pila conica (Gray, 1828) from an introduced population in Hawaii. Left: Shell with operculum in place. Scale: 1 cm. Right: magnified views of the operculum; internal (left) and external (right) surfaces.

Note that the operculum closing the shell aperture of *Pila conica* is calcified and brittle, not horny (corneous) as in *Pomacea* spp. Not also the rather eroded shell of the lower specimen of *Pila conica*, a frequent occurrence in both *Pila* and *Pomacea* species.

5. IMAGES OF DAMAGE CAUSED BY GOLDEN APPLE SNAILS

Top left: Missing plants in direct seeded rice in the Philippines.
Top right: Missing hills in transplanted rice in the Philippines.
Middle left: High density of 'golden apple snails' feeding on rice seedlings in the Philippines.
Middle right: The distinctive egg masses of *Pomacea canaliculata*, laid on the stems of taro plants in Hawaii; each egg mass may contain 200 or more eggs.
Bottom left: A relatively undamaged taro patch in Hawaii.
Bottom right: High density of *P. canaliculata* feeding on the few remaining taro plants in a badly infested taro patch in Hawaii.
[Philippines rice photos: R.C. Joshi, used with permission. Hawaii taro photos: K.A. Hayes and R.H. Cowie].

6. SAMPLING

6.1. Number of specimens to be collected

About ten specimens should be collected. There are subtle differences between males and females in shell shape, and there is considerable within population variation in shell shape. This number should be sufficient to obtain a representative sample of this variation.

6.2. Preferred stages to be collected

These snails do not go through 'stages' as such. They hatch as miniature (1-2 mm) versions of the adults, growing by adding new shell material to the edge of the shell aperture, thereby adding more shell whorls. Ampullariid species are very difficult to distinguish at the best of times, and especially if only small individuals are available. Therefore, the largest specimens available should be collected.

6.3. How to collect

Hand collect the snails into plastic bottles or jars with sufficient water so that the snails can be fully immersed but with sufficient air above the water to permit the water to remain oxygenated and for the snails to breathe air when they wish to.

6.4. Collection of eggs

'Golden apple snails' lay their eggs in conspicuous egg masses containing up to 200+ eggs above the water surface on emergent vegetation, rocks, logs, etc. The eggs of different species differ in colour to some extent. If the eggs are laid on stems of plants, cut the stem above and below the egg mass and place the section of stem with the egg mass in a dry plastic bottle or jar. Otherwise, carefully prise the egg mass of the surface with a knife blade and place it in a bottle or jar.

6.5. How to preserve golden apple snails

'Golden apple snails' should be preserved in 70 % ethanol and stored indefinitely. However, the snails should not be simply put into a jar of ethanol. If simply immersed in ethanol they will withdraw into the shell, closing the operculum (the trap-door like structure that seals the animal inside the shell when it withdraws – see section 7.2, below) and sealing themselves within the shell. The ethanol will then not be able to penetrate into the animal, which will simply rot inside the shell. Therefore, in order that the ethanol can penetrate the animal and preserve it, either the shell must be cracked (but not smashed into small pieces), by hitting it with a hard implement or in some other way making a hole in it, or the operculum must be prevented from closing, by inserting something (e.g. matchsticks, toothpicks) between the shell and the almost closed operculum. After 24 hours in the ethanol, the ethanol should be replaced. The snails can then be kept indefinitely.

If shells only – no animals – are being kept, then there are no special procedures for storage, unless they are intended for long-term museum storage, in which case they should be stored in acid-free conditions in order to prevent deterioration of the shells as a result of the reaction between the calcium carbonate of the shells and acid vapours in the storage atmosphere (for instance as given off by wood or non acid-free cardboard and paper).

6.6. How to transport golden apple snails

Most of the ethanol from the storage bottle or jar should be poured off and replaced with cotton wool soaked in ethanol. The jar should then be sealed to avoid leakage and packed with cushioning material in a strong box. Empty shells can be packed in cotton wool in a bottle, jar or small box, which is then packed with cushioning material in a strong box.

7. INFORMATION ON GOLDEN APPLE SNAIL

7.1. Names

7.1.1. Scientific names

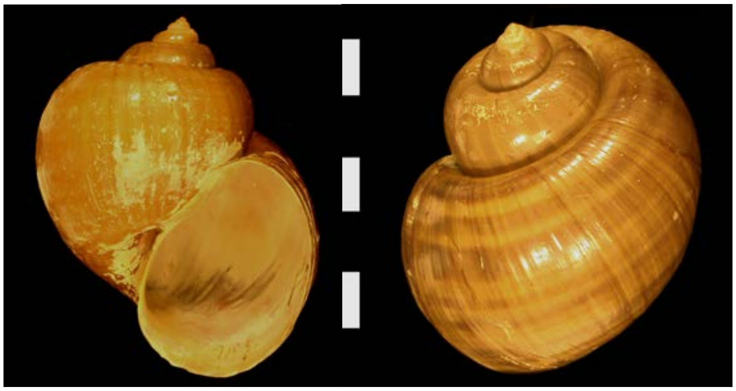
There has been much confusion regarding the correct scientific name(s) for the 'golden apple snail' introduced to Asia and elsewhere. Table 1 is a selection of names that have been used in the pest-related literature for the 'golden apple snail'. Recent molecular genetic analysis (Cowie & Hayes, 2005) has demonstrated that there are at least two species of *Pomacea* that have been referred to as 'golden apple snails'. One of these is most likely *Pomacea canaliculata* (Lamarck, 1822) but the identity of the other is not yet certain. It is possible that this other species is ***P. maculata*** Perry, 1810, of which ***P. gigas*** (Spix, 1827) and ***P. insularum*** (d'Orbigny, 1835), both names that have been used for the pests (Table 1), may be junior synonyms (see Cowie & Thiengo, 2003). However, verification of the identity of this second species requires further research. There are a number of synonyms of both *P. canaliculata* and *P. maculata*, some of which have been used in the pest-related literature. These synonyms are listed below. It seems unlikely that *P. lineata* (Spix, 1827) is one of the pest species. And although there is as yet no evidence for hybridisation among the pest populations, this remains a possibility, which will increase the difficulty of providing a definitive species identification.

Table 1. Scientific names that have been used for the pest species of Ampullariidae in south-east Asia, with comments on their validity.

Names	Validity
Pila sp.	Misidentification – incorrect genus
Pomacea canaliculata	Probably correct for some populations
Pomacea cf. *canaliculata*	Some populations probably *P. canaliculata*
Pomacea cuprina	Misidentification – incorrect species
Pomacea gigas	Not rigorously determined
Pomacea insularum	Not rigorously determined
Pomacea insularis	Misspelling of *P. insularum*
Pomacea insularus	Misspelling of *P. insularum*
Pomacea lineata	Not rigorously determined
Pomacea sp.	Correct but no species determination
Ampularius sp. a hybrid of undetermined origin	No evidence of hybridization Misspelling of a junior synonym of *Pila*
Hybrid of *Ampullaria canaliculata* and *A. cuprina*	No evidence of hybridization *Ampullaria* is a junior synonym of *Pila*

7.1.2. Synonyms

The synonyms of *Pomacea canaliculata* listed below are taken from the most recent authoritative nomenclatural work on New World Ampullariidae (Cowie and Thiengo, 2003). Some of these synonyms have also been considered synonyms of other *Pomacea* species by some previous authors. Most were originally described in the genus *Ampullaria* and many of these have never formally been placed in *Pomacea*, so are listed here as *Ampullaria*. Further research may show that some of them are in fact valid species. Also, other species have been considered synonyms of *Pomacea canaliculata* by some previous authors but are not listed as such by Cowie and Thiengo (2003).
Ampullaria australis Orbigny, 1835
Pomacea canaliculata chaquensis Hylton Scott, 1948
Ampullaria dorbignyana Philippi, 1852
Ampullaria immersa Reeve, 1856
Ampullaria vermiformis Reeve, 1856



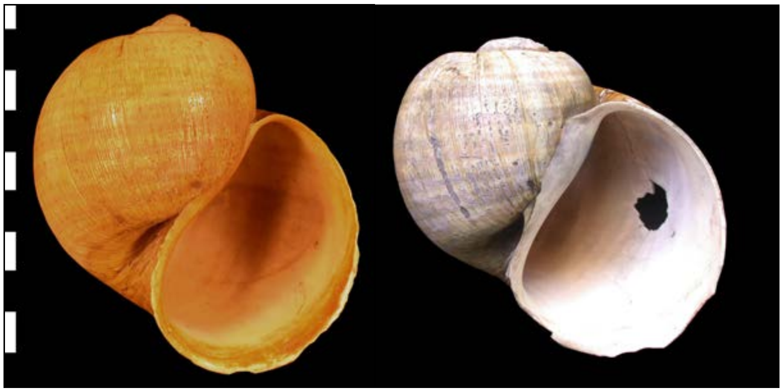
Ampullaria australis Orbigny, 1835. Two views of a syntype – the Natural History Museum, London. Scale: 1 cm. [Photos: R.H. Cowie].

Ampullaria immersa Reeve, 1856. Syntype – the Natural History Museum, London. Scale: 1 cm. [Photo: R.H. Cowie].

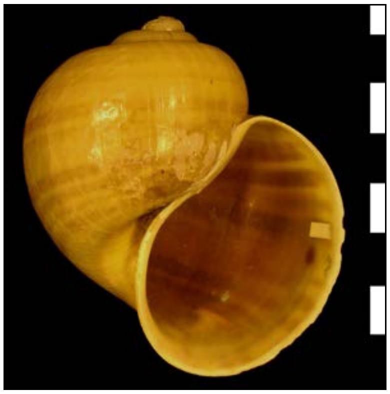
Ampullaria vermiformis Reeve, 1856. Syntype – the Natural History Museum, London. Scale: 1 cm. [Photo: R.H. Cowie].

It is possible that the other species that is/are part of the complex that constitutes the 'golden apple snail' should be referred to ***Pomacea maculata***, although this is a very preliminary suggestion that depends on further research. Its synonyms, as listed by Cowie & Thiengo (2003) are as follows. Some names appear in this list and in the list of synonyms of ***P. canaliculata***, reflecting the opinions of different authors and the current state of taxonomic confusion in the group.
Ampullaria australis d'Orbigny, 1835
Ampullaria crosseana Hidalgo, 1871
Ampullaria fasciata Reeve, 1856
Ampullaria georgii Williams, 1889
Pomacea gigas (Spix, 1827)
Pomacea insularum (d'Orbigny, 1835)
Ampullaria vermiformis Reeve, 1856
Pomacea vickeryi Pain, 1949

The following illustrations show some of these synonymous species.



Pomacea insularum (d'Orbigny, 1835). Two syntypes: left – the Natural History Museum, London; right – the Muséum National d'Histoire Naturelle, Paris. Scale bar: 1 cm. [Photos: R.H. Cowie]. Note the intraspecific differences in shall shape between these two syntypes.



Ampullaria fasciata Reeve, 1856. Lectotype – the Natural History Museum, London. Scale: 1 cm. [Photo: R.H. Cowie].

Pomacea vickeryi Pain, 1949. Holotype – the Natural History Museum, London. Scale: 1 cm. [Photo: R.H. Cowie].

7.1.3. Common names

Numerous common names, in English as well as local languages, have been used for these species in both the pest related field and the domestic aquarium trade. The following list is not comprehensive.

Golden apple snail, or GAS – the commonly used name in south-east Asia

Golden snail

Apple snail – a general term for all ampullariids, but sometimes used more restrictively for the pest species

Mystery snail – primarily in the domestic aquarium trade, and also often used for *Pomacea bridgesii*, with which *P. canaliculata* is often confused

Miracle snail

Channelled apple snail, or CAS – the name used in the USA by various government agencies, derived from the Latin name '*canaliculata*', which means 'channelled'.

Kuhol – used in the Philippines

Bisocol – used in the Filipino community in Hawaii

7.2. Distinctive features

Pomacea species are large snails. They range in adult size from ~15 mm to about 155 mm (*Pomacea maculata*). Those species that fall under the umbrella of the 'golden apple snail' range in adult size from about 30 mm (a small *P. canaliculata*) to about 90 mm (undetermined *Pomacea* species observed in south-east Asia) but may reach larger sizes.

In shape, 'golden apple snails' are generally globose, as seen in the illustrations in sections 2, 3.1, 4 and 7.1.2. The shell aperture – the opening from which the animal extends when crawling – is to the right of the shell when looking at the aperture with the spire of the shell uppermost, that is the shell is 'dextral' as opposed to 'sinistral' if the shell coiled in the opposite direction.

All ampullariids, including *Pomacea* spp., possess an operculum. The operculum is a hard structure (of a horny texture like fingernail in 'golden apple snails', but brittle and calcified in the related genus *Pila*) that is carried on the dorsal surface of the rear of the crawling snail's foot. When the snail retracts into its shell, withdrawing its foot last, the operculum seals the aperture of the shell, with the animal inside, like a trap-door. The operculum is shown in the illustrations below.

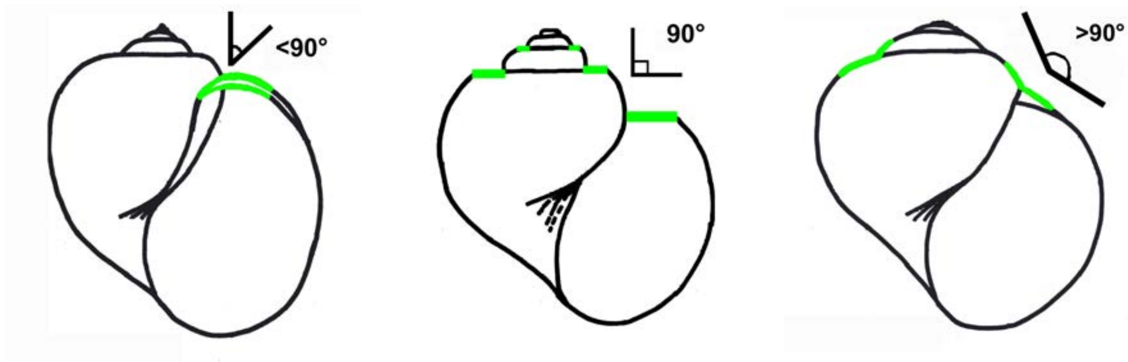
A 'golden apple snail' from Cambodia showing the operculum attached to the animal, which is withdrawn within the shell. Scale: 1 cm. [Photo: R.H. Cowie].

A 'golden apple snail' from the Philippines with the operculum removed from the body. Scale: 1 cm. [Photo: R.H. Cowie].

Note the large difference in size and shape between the two snails illustrated above, both of which are adult. The one from the Philippines is probably *Pomacea canaliculata*; the one from Cambodia is probably a different species of *Pomacea*.

Shell colour, the pattern of darker bands running spirally around the shell and the colour of the animal inside should not in any sense be considered diagnostic of species of *Pomacea*. Although some species in the wild appear to be relatively uniform in these characteristics, there is variation in these characters in many natural populations of many *Pomacea* spp. In addition, most of the species that are in circulation around the world have at some time or other been selectively bred in the aquarium trade such that there are snails with shells of a range of colours including dark brownish black, tan, bright orange, yellow, and almost white, and with or without darker spiral bands. The animal inside can range from almost black to almost white, with a range of browns, oranges, yellows and creams in between.

Distinguishing among the various species of *Pomacea* is extremely difficult. The following diagrams illustrate the differences in the channellisation of the suture (the junction between successive shell whorls) among the three species of *Pomacea* most likely to be encountered in the aquarium trade: *Pomacea canaliculata*, *P. bridgesii*, and *P. paludosa*. These differences are subtle, and given the extensive variation in shell characteristics within species, distinguishing these species requires considerable experience (see also section 3.2).



Pomacea canaliculata *Pomacea bridgesii* *Pomacea paludosa*
[Diagrams modified from http://www.applesnail.net/ (S. Ghesquiere); see also Howells (2003)].

7.3. Distribution

The natural distribution of *Pomacea canaliculata* and the other snail species listed above as synonyms (section 7.1.2), includes the following countries (from Cowie and Thiengo, 2003):
Argentina
Bolivia
Brasil
Paraguay
Uruguay
However, some authors (e.g., Cazzaniga, 2002) consider *P. canaliculata* to be a very variable species that may be more widespread than this within South America, dependent upon synonymizing it with other species recorded from other countries. In addition, other as yet undetermined species of *Pomacea* are also represented under the 'golden apple snail' umbrella and these may be present in other countries of South America.

'Golden apple snails' (*P. canaliculata* and one or more other undetermined species of *Pomacea*) have been introduced to the following countries:
Cambodia, China (including Hong Kong), Dominican Republic, Indonesia, Japan, Laos, Malaysia, Myanmar, Papua New Guinea, Philippines, Singapore, South Korea, Taiwan, Thailand, United States (California, Florida, Hawaii, Texas, Arizona), Vietnam

A number of other identified species of *Pomacea* have also been introduced and are present in the wild, as follows. They may in fact be more widespread than this list indicates.
Pomacea bridgesii (Reeve, 1856) – Sri Lanka, Australia, United States (Florida, Hawaii)
Pomacea haustrum (Reeve, 1856) – United States (Florida)
Pomacea paludosa (Say, 1829) – United States (Hawaii; it is native to Florida)
Pomacea scalaris (d'Orbigny, 1835) – Taiwan

7.4. Plants known to be attacked

Many ampullariids, and 'golden apple snails' in particular, are voracious generalist feeders on aquatic macrophytes. As such, these snails will feed on many aquatic crops. Table 2 lists crops that have been documented as being attacked in particular countries. Undoubtedly the impacts are not constrained to the plants/countries listed but affect these and other crops wherever they occur in the introduced range of 'golden apple snails'. Despite this wide range of attacked crops, there is some evidence of preferences in their diets. In Hawaii, experiments on *Pomacea canaliculata* showed that it fed preferentially on certain plants among the suite of mostly non-native, non-crop plants provided to it; notably it did not feed on the invasive aquatic weed water hyacinth (*Eichhornia crassipes*) (Lach *et al*. 2001). However, no comparable preference experiments have been undertaken on the various crops listed in Table 2, nor on any aquatic plants native to Australia; all should be considered threatened.

Table 2. Crops that are attacked by ampullariids. This is not a comprehensive list, but simply a brief compilation from some of the more accessible literature, illustrating the susceptibility of a wide range of plants. Derived from the review of Cowie (2002) and the contributions to a symposium on 'golden apple snails' held in Taiwan in 2004 (Lai et al., 2005).

Plant	Regions
Aibika (*Abelmoschus manihot*)	Papua New Guinea
Arrowhead (*Sagittaria* sp.)	China
Azolla (*Azolla* spp.)	Japan, Philippines
Chinese mat rush (*Cyperus monophyllus*)	Japan
Chinese milk vetch (*Astragalus sinicus*)	China
Japanese parsley/dropwort (*Oenanthe javanica*)	Japan
Lotus (*Nelumbo nucifera*)	Hong Kong, Japan, Taiwan, Thailand
Mat rush (*Juncus decipiens*)	Japan
Phak krached (*Neptunia oleracea*)	Thailand
Rice	Cambodia, China, Dominican Republic, Indonesia, Japan, Laos, Malaysia, Papua New Guinea, Philippines, South Korea, Taiwan, Thailand, Vietnam
Taro (*Colocasia esculenta*)	Hawaii, Japan, Papua New Guinea, Taiwan
Water bamboo (*Zizania latilolia*)	Taiwan
Water chestnut/singhara nut/krajap (*Trapa bicornis*)	Japan, Taiwan, Thailand
Water chestnut (*Eleocharis tuberosa*)	Thailand
Water cress (*Rorippa* spp., formerly *Nasturtium* spp.)	Hawaii, Hong Kong
Water hyacinth (*Eihhornia crassipes*)	Hong Kong
Water lily (*Nymphaea* spp.)	Thailand
Water spinach/swamp cabbage (*Ipomea aquatica*)	Hawaii, Hong Kong, Japan, Taiwan, Thailand
Wild rice (*Zizania latifolia*)	Japan
Yard long bean (*Vigna unguiculata var. sesquipedalis*)	Papua New Guinea

7.5. Part of plants affected

Macrophyte-feeding species of *Pomacea*, which includes the species subsumed in the category 'golden apple snail', are generalist not only in terms of the plant species they will attack (Table 2) but also inasmuch as they will feed on most parts of these plants.

Documented knowledge of preferences for particular parts of plants is very limited. In Hawaii, *P. canaliculata* will feed on all parts of taro plants, including corms, stems and leaves, if the leaves bend over and reach the water surface. However, in South-east Asia, rice plants tend to be resistant once they are beyond a certain age, 20-40 days depending on variety.

Egg masses, which are bright pink, are laid above the water surface, on any relatively rigid emergent surface, including rocks, walls and logs, as well as on plants, including affected crop plants.

Left: *Pomacea* sp. egg masses on rice plants [Photo: M. Halwart]. Right: *Pomacea canaliculata* egg masses on young taro. [Photo: R.H. Cowie].

7.6. Biology

The name 'golden apple snail' refers to more than one species (Cowie and Hayes, 2005). One of these species is *Pomacea canaliculata* (Lamarck, 1822) and this is probably the most widespread invasive species of *Pomacea* in south-east Asia and elsewhere. However, the correct scientific name for the other species (one or more) that is also included as 'golden apple snail' is not known, although one species may be *Pomacea maculata* Perry, 1810.

Unfortunately, detailed knowledge of the biology of ampullariids is sparse and scattered. However, *Pomacea* is the best known genus, and various species have been the subject of basic studies of systematics, anatomy, physiology, genetics, distribution, behaviour, and so on. Nevertheless, there have been few studies directly focusing in detail on aspects of the biology of the pest species that might be most relevant to the development of control or management measures. In the sections that follow, I have summarized what is known in these areas regarding species of *Pomacea*. I have not addressed areas of less relevance, such as embryology, anatomy and histology, karyology, genetics, biochemistry and physiology, all of which have been addressed by various authors; introductory citations to these areas are given by Cowie (2002).

7.6.1. Habitat

Ampullariids are freshwater snails. Some may be able to tolerate low levels of salinity (Prashad, 1925; Hunt, 1961; Fujio *et al.*, 1991a; Santos *et al.*, 1987), but they generally do not live in brackish water habitats. Most species are amphibious, able to spend significant lengths of time out of water breathing air. Many species, including species of *Pomacea*, inhabit slow-moving or stagnant water in lowland swamps, marshes, ditches, lakes and rivers (e.g., Pain, 1950a, 1960; Andrews, 1965; Robins, 1971; Louda and McKaye, 1982; Keawjam, 1986). Some species could be considered pre-adapted for living in rice paddies, taro patches, and other similar artificial habitats in which aquatic crops are grown. There may be differences in habitat among closely-related species. For instance in Argentina, Hylton Scott (1958) reported that *Pomacea canaliculata* (Lamarck) inhabited relatively still water, while the almost indistinguishable *P. insularum* (d'Orbigny) was found in rivers. Species of *Limnopomus* Dall, a sub-group of *Pomacea* treated as a distinct genus or subgenus by some authors but as a synonym by Cowie & Thiengo (2003), also inhabits swiftly-flowing mountain streams (e.g., Pain, 1950a, b, 1960).

7.6.2. Reproduction, growth and demographics

7.6.2.1. Breeding system

Ampullariids are dioecious (separate sexes), internally fertilizing and oviparous. There is evidence that females are larger than males in some species (Prashad, 1925; Robins, 1971; Keawjam, 1987; Marwoto, 1988; Lum-Kong and Kenny, 1989; Cazzaniga, 1990a; Perera and Walls, 1996; Wada, 1997; Estebenet and Cazzaniga, 1998). The dimorphism appears to be slight in *Pomacea canaliculata* (Cazzaniga, 1990a) but dramatic in other species of 'golden apple snails' (e.g. Cowie, 2002, Fig. 5.1, in which the species illustrated was incorrectly identified as *P. canaliculata*).

7.6.2.2. Mating, oviposition, eggs and fecundity

Breeding in many species is seasonal and related to latitude, temperature and rainfall (Andrews, 1964). In equatorial regions, many species aestivate during the dry seasons as their habitat dries up (see below), breeding in the rainy season; in subtropical regions, they may only breed during summer, once temperatures reach a certain level (Hylton Scott, 1958; Andrews, 1964). Local variation in reproductive regime may be related to local climatic variation, especially availability of water (Bourne and Berlin, 1982).

Species of *Pomacea* generally lay their eggs above water on the exposed parts of vegetation, rocks, etc., perhaps to avoid aquatic predators or in response to low oxygen tension in their often near-stagnant aquatic habitats (Snyder and Snyder, 1971).

In *Pomacea canaliculata*, and other species (e.g., *P. dolioides* (Reeve): van Dinther, 1956; *P. haustrum* (Reeve): Guimarães, 1981a, b; *P. paludosa*: Perry, 1974), oviposition (above water) takes place predominantly at night, or in the early morning or evening (Andrews, 1964; Chang, 1985; Halwart, 1994; Schnorbach, 1995; Albrecht *et al*., 1996), about 24 h after copulation (up to two weeks after mating, according to Chang, 1985). Andrews (1964) and Albrecht *et al*. (1996) described copulation in *P. canaliculata* in detail; it occurs at any time of day or night (Naylor, 1996; personal observations), although there may be some diurnal rhythm, and it takes 10-18 h. Copulation takes place about three times per week (Albrecht *et al*., 1996). On each oviposition occasion, a single clutch is laid, of highly variable egg number (see Appendix). The interval between successive ovipositions has been reported as 12-14 days (Chang, 1985) and about five days (Albrecht *et al*., 1996) for *P. canaliculata* and 8-16 days for an unidentified '*Ampularius* sp.', presumably *P. canaliculata* (Lacanilao, 1990). Hatching generally takes place about 2 weeks after oviposition, but this period varies greatly (Appendix). Newly hatched snails immediately fall or crawl into the water. One snail can produce an average of 4375 (maximum observed 8680) eggs per year (Mochida, 1988a, 1991), which, if clutch size is about 200 (Appendix), translates into about 22 clutches (see also Anon., 1989, which gave an even higher figure of up to 1200 eggs per month). Development is highly dependent on temperature (e.g., Robins, 1971; Demian and Yousif, 1973; Aldridge, 1983; Mochida, 1988a, b; Estebenet and Cazzaniga, 1992; Schnorbach, 1995), and therefore locality, which probably largely accounts for the variability in the data for *P. canaliculata* in the Appendix.

A very different strategy is adopted by *Pomacea urceus* (Burky, 1973, 1974; Lum-Kong and Kenny, 1989). This species mates towards the end of the rainy season. Females then bury into the muddy substrate and aestivate as their marshy habitat dries out. Snails living in permanent rivers also aestivate, burying into the river banks above the water level. Eggs are laid at the start of the aestivation period and are maintained within the shell, between the operculum and the aperture. Development takes place during the dry season, within the female's shell (even if she dies). The young snails hatch but remain and aestivate within the female's shell until the start of the rainy season. Burky *et al*. (1972) argued that this strategy protects the newly hatched juveniles from high (possibly lethal) temperatures and water loss during the dry season. *P. urceus* is the only ampullariid known to adopt this strategy.

The eggs of most species of *Pomacea* are brightly coloured, perhaps as a warning of unpalatability since the eggs appear to be distasteful, at least to vertebrates although perhaps not to invertebrates (Snyder and Snyder, 1971; Kushlan, 1978). They are various shades of pink, orange and red in *Pomacea australis* (d'Orbigny), *P. bridgesii* (Reeve), *P. canaliculata*, *P. dolioides* (Reeve), *P. hanleyi* (Reeve), *P. insularum*, *P. lineata*, *P. megastoma* (Sowerby), *P. paludosa* and *P. sordida* (Swainson) (van Dinther, 1956, 1973; Snyder and Snyder, 1971; Thiengo, 1987, 1989; Winner, 1989, 1996; Keawjam and Upatham, 1990; Thiengo *et al*., 1993; Perera and Walls, 1996). The eggs are green in *Pomacea glauca* (Linnaeus), *P. pyrum* (Philippi), *P. decussata* (Moricand) and *P. nais* Pain (Pain, 1950b; van Dinther, 1956, 1973; Snyder and Snyder, 1971; Perera and Walls, 1996). Snyder and Snyder (1971) hesitated to consider green eggs to have evolved for camouflage because they generally remained distinctly visible, at least to humans. The eggs of *P. falconensis* Pain and Arias, *P. flagellata* (Say), *P. gossei* (Reeve), *P. fasciata* (Roissy) and *P. cuprina* (Reeve) are white (Andrews, 1933; Snyder and Snyder, 1971; Perera and Walls, 1996). Eggs of *P. urceus* are reported as either white (Burky, 1973; 1974), orange (Lum-Kong and Kenny, 1989), or to vary from orange to pale green (Perera and Walls, 1996); those of *P. haustrum* have been reported as both green (Winner, 1989, 1996) and red/pink (Snyder and Snyder, 1971; Guimarães, 1981a); in both cases this may represent taxonomic confusion. Comfort's (1947) report that the eggs of *P. glauca* are red is based on a misidentification of a species (perhaps *P. canaliculata*) from Argentina. Egg colour may change somewhat as the egg surface dries following oviposition and subsequently as the dark-coloured embryo develops inside (Snyder and Snyder, 1971).

7.6.2.3. Growth and longevity

Little is known of these aspects of the biology of ampullariids (Appendix; and see Estebenet and Cazzaniga, 1992). A number of studies have investigated growth in the laboratory (Appendix) but it is difficult to relate these studies to growth in the wild, which is probably dependent on season, food availability, temperature, etc. One laboratory study, on *Pomacea canaliculata* in its native Argentina (Estebenet and Cazzaniga, 1992), did however demonstrate the crucial role of temperature in growth and reproduction. At a constant 25°C, snails matured in 7 months and then bred continuously for a single 'season' of about 4 months, then died. In contrast, under seasonally fluctuating temperatures (7-28°C), the snails took 2 yr to reach maturity; they then bred for two distinct annual breeding seasons, for a life-span of about 4 yr. In the wild in Argentina, *P. canaliculata* breeds only during the summer (Hylton Scott, 1958), and the life-cycle under the fluctuating laboratory temperature regime may indeed reflect the life-cycle in the wild. Under semi-artificial conditions in Japan (an outdoor pond but with food provided), *Pomacea canaliculata* grew to maturity in less than two months (Chang, 1985). In Hawaii, *P. canaliculata* takes about 10 months to reach full size (Lach et al., 2001). In tropical regions of south-east Asia, release from the seasonality of its natural range may be at least one reason why *P. canaliculata* is so prolific; rapid growth and breeding, and hence rapid succession of generations, are permitted year round (Naylor, 1996), leading to rapid population expansion and high population densities. A short life might then be predicted, but longevity in the wild under such conditions has not been reported. A similar situation may obtain in northern Australia, should *P. canaliculata* be introduced.

A multitude of other biotic and abiotic factors may influence growth. For instance, growth rate of *Pomacea dolioides* in its native South America is determined by food availability, as well as by the quantity of water and the duration and intensity of the dry season (van Dinther, 1956, 1962; Donnay and Beissinger, 1993). Population density (Cazzaniga and Estebenet, 1988) and both inter- and intra-specific competition may also have an effect on growth rate.

Maximum size varies greatly among populations (e.g., Keawjam, 1986; Estebenet and Cazzaniga, 1992; Donnay and Beissinger, 1993) and may be related to a number of environmental factors, including habitat size (Johnson, 1958), microclimatic variation and differing water regimes (Donnay and Beissinger, 1993), and population density. Maximum size of *Pomacea canaliculata* in Hawaii is about 30 mm, but in Asia it has been reported as reaching at least 65 mm (Schnorbach, 1995) or even 90 mm (Heidenreich *et al*., 1997); however, these reports quite possibly refer to species other than *P. canaliculata*, since the largest specimens in recent DNA sequencing studies of ‘golden apple snails’ (Cowie & Hayes, 2005) were not *P. canaliculata*.

7.6.2.4. Population dynamics and densities

Few studies have addressed ampullariid population dynamics directly. It is clear, however, that seasonal changes in water availability are important. In Florida, recruitment of *Pomacea paludosa* was dramatically enhanced during years when the water table remained high, allowing the snails to remain active instead of having to aestivate; larger snails were also thought to be more able to withstand dry periods (Kushlan, 1975). *P. urceus* will only enter aestivation once a shell length of 85 mm has been reached (Burky *et al*., 1972). In Venezuela, habitats with more permanent standing water (rice fields, as opposed to natural wetlands) allowed *Pomacea dolioides* to grow larger and achieve higher population densities, essentially because the period spent in aestivation (no growth) was shorter; densities ranged from three per 100 m^2 in natural wetlands to 33 per 100 m^2 in rice fields (Donnay and Beissinger, 1993). In Hawaii, densities of *P. canaliculata* in taro patches have been recorded over 130 m^{-2} (12.9 ft^{-2}: Tamaru, 1996; Tamaru and Hun, 1996). Densities of *P. canaliculata* in rice paddies in the Philippines generally are 1-5 m^{-2} but densities up to 150 m^{-2} have been reported (Halwart, 1994; Schnorbach, 1995). Anderson (1993), perhaps mistakenly, reported ‘1,000 mature snails per square metre’ in the Philippines. In rice in Japan, studies have reported 3-7 m^{-2} (Okuma *et al*., 1994) and 12-19 m^{-2} (Litsinger and Estano, 1993). Clearly, in irrigated systems with water present longer than would naturally be the case, snails can reach maturity in a shorter period. Fluctuations in population density in *Pomacea haustrum* in Brasil (maximum 215 m^{-2}) were reported by Freitas *et al.* (1987), although the underlying reasons for the fluctuations were unclear. Again, numerous other biotic and abiotic factors may be involved, e.g., vegetation type (Bryan, 1990), food availability, temperature, water hardness (Perera and Yong, 1990). Over the reproductive season in Florida, *Pomacea paludosa* populations were estimated to produce 1.2-1.5 million snails per ha (= 120-150 m^{-2}) (Hanning, 1978).

Clearly, following hatching, densities in the immediate vicinity of the clutch will be high. However, few of the above reports are sufficiently detailed to assess the impact of survivorship on density, although clearly some species, especially when introduced, are able to achieve remarkably high adult population densities.

7.6.3. Natural enemies

7.6.3.1. Predators

Perhaps the best known predator of New World ampullariids is the kite *Rostrhamus sociabilis* d’Orbigny (in Florida, known as the Everglades Kite and considered endangered in the USA), which has a long, slender hooked bill adapted for extracting snails, its almost exclusive prey (Pain, 1950b; van Dinther, 1956; Snyder and Snyder, 1971; Kushlan, 1975; Beissinger *et al*., 1994). In Florida, the kite’s natural prey is *Pomacea paludosa*; in South America it preys on a number of other species of *Pomacea*, as well as *Marisa cornuarietis*. Another important New World avian predator is the limpkin (*Aramus guarauna* d’Orbigny), a large wading bird similar to an ibis. Limpkins are found virtually throughout the New World distribution of ampullariids, which constitute a major part of their diet (Peterson, 1980). Caiman lizards (*Dracaena guianensis* Daudin) feed almost exclusively on ampullariids. Other predators include slender-billed kites, boat-tailed grackles, white ibises, crocodilians, various fish, turtles, crayfish and aquatic insects (Robins, 1971; Snyder and Snyder, 1971; Kushlan, 1975; Donnay and Beissinger, 1993). However, insufficient work has been done to evaluate whether any of these predators impact snail population dynamics significantly (Donnay and Beissinger, 1993), although personal observations in Brasil suggest that the impacts are great.

Some species (*Pomacea paludosa* and to a lesser degree *P. glauca* and *P. dolioides*), exhibit an alarm response on detecting chemical stimuli in the water from predators (turtles), the juices of damaged conspecifics (Snyder and Snyder, 1971), and in response to mechanical disturbance of vegetation they are sitting on (Perry, 1974). The snails drop to the substrate (if they are not already on it) and bury themselves into it.

7.6.3.2. Parasites and pathogens

Little has been published in this area. Various ampullariid species, including *Pomacea canaliculata*, are vectors of *Angiostrongylus cantonensis* (Chen), the rat lungworm (Wallace and Rosen, 1969; Keawjam, 1986; Chao *et al.*, 1987; Mochida, 1991; Naylor, 1996). They may also harbour schistosomes (Hanning and Leedom, 1978; Leedom and Short, 1981) and flukes (Keawjam, 1986). Three species of temnocephalid flatworms are reported living symbiotically in the mantle cavity of species of *Pomacea* and *Asolene* in South America (León, 1989). Whether any of these parasites cause harm to the snail host is unknown. One study (Chobchuenchon & Bhumiratana, 2003) has shown that a number of soil microorganisms exhibit pathogenicity to *Pomacea canaliculata*. Other than this there appears to be no knowledge of natural microbial pathogens in apple snails, although other snails, especially land snails, are known to be associated with microorganisms, especially protozoa, both as parasites and as symbionts or commensals (Godan, 1983). Again, whether any of these parasites or pathogens play (or could play) a role in population regulation is unknown.

<u>7.6.4. Food and feeding</u>

The feeding habits of ampullariids are microphagous, zoophagous, and macrophytophagous, none being mutually exclusive (Estebenet, 1995). Ciliary feeding on particulate matter on the water surface has been described for some species (McClary, 1964). Some species will feed on insects, crustaceans, frogs, small fish, etc., mostly as carrion but not always so (McLane, 1939; Estebenet, 1995; R.H. Cowie, personal observations). Some species (e.g., *Marisa cornuarietis*, *Pomacea canaliculata*, *P. bridgesii*) will attack other snails and their eggs (Demian and Lutfy, 1966; Robins, 1971; Aldridge, 1983; Cedeño-León and Thomas, 1983; Cazzaniga, 1990b; Aditya and Raut, 2002). However, the predominant feeding habit of ampullariids is macrophytophagous, which from an agricultural and environmental pest standpoint is also the most significant. *P. canaliculata* shows preferences among different food plants; its rate of growth correlates with its feeding on the preferred plant; and it is able to detect its food plants from some distance using chemical cues in the water (Estebenet, 1995; Lach et al., 2001), as can *Pomacea paludosa* (McClary, 1964). However, despite exhibiting such preferences, *P. canaliculata* appears relatively generalist and indiscriminate (e.g., Schnorbach, 1995), and, as suggested for *Marisa cornuarietis* by Robins (1971), it may be 'more pertinent to determine what the animal does not eat than what it will eat'. In fact, anecdotal comments (Neck, 1986) suggest that the *Pomacea* species reported from Texas (which was originally reported as *P. canaliculata*, but which in fact is the same species as one of the other 'golden apple snail' species in south-east Asia) is particularly voracious compared to other ampullariids.

These voracious and generalist feeding habits are clearly of great relevance to quarantine implementation. As many *Pomacea* species are difficult to distinguish, and because the feeding habits of many species are poorly known but probably also voracious and generalist, quarantine should err on the side of caution and restrict all species of *Pomacea*, and probably all species of Ampullariidae. The suggestion that *P. bridgesii* is preferentially an algal feeder (Howells, 2002, 2003) has led to its being exempted from such restrictions in certain U.S. regulations, but there is also evidence that it feeds on macrophytic plant material (Raut and Aditya, 1999) and the exemption may be unjustified.

7.6.5. Respiration

Many ampullariids are amphibious, both in physiology and behaviour. The mantle cavity contains both a ctenidium (‘gill’) and a portion modified as a pulmonary sack or ‘lung’ (Andrews, 1965). Ventilation of the lung in *Pomacea* species is by extending the siphon (a structure like a snorkel) to the water surface periodically, more frequently under conditions of low oxygen tension. Ventilation of the lung, as well as being used for respiration, is also used to adjust buoyancy levels, such that snails can float at the water surface under periods of low oxygen tension. Lung ventilation is obligatory, but the snails can nevertheless survive extended periods without ventilation: up to 6 h in *Pomacea lineata* (van Dinther, 1956). There are differences among species in the relative significance of aerial and aquatic respiration (Andrews, 1965). Work on respiration rate and its relation to temperature and oxygen tension has been reviewed by Aldridge (1983) and Santos *et al*. (1987). The ability to use the ctenidia and the ‘lung’ for respiration allows many ampullariids to survive significant periods out of water and to disperse significant distances over land. This is clearly of adaptive value for species that live in marshy or other habitats that dry out periodically, but it also means that when introduced to new habitats, such as rice paddies or taro patches, the snails may be difficult to contain within circumscribed areas as it is possible that they could cross the raised burms between paddies. It also means that they can be transported readily for periods of days with no access to water, during which time they withdraw into the shell and close the operculum.

7.6.6. Aestivation

Many ampullariids aestivate during dry periods (Lum-Kong and Kenny, 1989). When the snails’ habitat dries out, they bury themselves into the mud. Some species (e.g., *Pomacea urceus*) bury only superficially, with part of the shell remaining above the surface of the hardened mud (Burky *et al*., 1972); others bury up to 1 m deep (e.g., *Pila ampullacea* (Linnaeus), *P. pesmei* (Morelet); see Keawjam, 1986). They can survive in this state in some cases for extended periods (in laboratory experiments) far longer than are likely to be necessary in the wild: e.g., 8 months for *Pomacea glauca* (van Dinther, 1956), 13 months for *P. lineata* (Little, 1968), 17 months for *P. urceus* (Burky *et al*., 1972), at least a year for *Pila ampullacea* and *P. pesmei* (Keawjam, 1986) and 25 months for *Pila globosa* (Chandrasekharam *et al*., 1982). *Pomacea canaliculata* is only reported to survive buried in the earth up to 3 months (Schnorbach, 1995). They can withstand significant loss of soft tissue weight during aestivation; in *Pomacea lineata* up to 50 % (Little, 1968) and in *P. urceus* up to 62 % (Burky *et al*., 1972). *Pila virens* (Lamarck) and *Pila globosa* lose considerably less weight (5 %) but can nevertheless aestivate for at least 6 months; the shell and operculum appear to be effective barriers to water loss, especially as the operculum is sealed in the shell opening with dried mucus (Meenakshi, 1964). Metabolism during aestivation is anaerobic in *Pila virens* and *P. globosa* (Meenakshi, 1964; Aldridge, 1983), but aerobic in *Pila ovata* (Olivier) and *Pomacea urceus* (Burky *et al*., 1972). *Pila virens* and *P. globosa* (and other species of *Pila*) aestivate buried very deep in the ground; their anaerobic aestivation metabolism may be an adaptation to this, in contrast to the aerobic respiration of the shallow burying *Pomacea urceus*.

7.6.7. Physiology

7.6.7.1. Lethal temperatures

During aestivation, *Pomacea urceus* regulates its body temperature below 41 °C, in part through evaporative cooling, and has an upper lethal temperature between 40 and 45 °C (Burky *et al*., 1972). Adult *P. urceus* are more tolerant of high temperature than are juveniles (Burky *et al*., 1972), perhaps because adults can afford to lose more water through evaporative cooling. In both *Pomacea paludosa* and *Marisa cornuarietis*, 40 °C is lethal when snails are exposed for 1-4 h. (Freiburg and Hazelwood, 1977), although Thomas (1975) reported that they could withstand temperatures up to 45 °C. Robins (1971) gave 39 °C as the ‘upper limit of short-term heat tolerance’ for *M. cornuarietis*, with juveniles more tolerant than adults at 37 °C, and both adults and juveniles feeding normally between 33.5 and 35.5 °C; eggs did not develop normally at 35-37 °C. Mochida (1991) reported for *P. canaliculata* that mortality is high at water temperatures above 32 °C (35 °C in Mochida, 1988b, and Eversole, 1992). *Pila virens* and *Pila globosa* cannot survive 2 days at 40 °C (Meenakshi, 1964). *Pomacea lineata* survived 1 h exposure at 40 °C (Santos *et al*., 1987).

Regarding low temperature tolerance, Robins (1971; see also Neck, 1984) reported that *M. cornuarietis* could survive over 24 h at 11 °C (although egg development ceased at this temperature) but succumbed in 5 h when exposed to 8 °C, although Thomas (1975) reported that it could withstand 6 °C. *Pomacea paludosa* can survive exposure at 5 °C (Freiburg and Hazelwood, 1977). Mochida (1991) reported for *P. canaliculata* that the snails can survive 15-20 days at 0 °C, 2 days at -3 °C but only 6 h at -6 °C (see also Neck and Schultz, 1992; Wada, 1997). *Pomacea lineata* survived 1 h exposure at 5 °C (Santos *et al*., 1987). *Pila virens* and *Pila globosa* cannot survive 4 days at 20 °C and die within 1 day at 10 °C (Meenakshi, 1964).

Differences among species in both their upper and lower lethal limits may reflect adaptation to their natural climatic environment. There appears to be less variability in the upper limit, which in general appears to be around 40 °C for many aquatic organisms. Comparability among the studies mentioned above is poor, largely because experimental procedures, especially exposure time, differed. Nevertheless, *Pomacea canaliculata*, of more temperate habitats (Argentina), seems to have a lower limit than other more tropical species such as *Pomacea urceus*, *Marisa cornuarietis* and the two *Pila* species. Lower limits seem more variable, with *P. canaliculata* able to tolerate freezing temperatures, in marked contrast to the *Pila* species, which are unable to survive at 20 °C for extended lengths of time. These differences probably have significant consequences for the potential establishment, reproduction, growth and population dynamics of apple snails when they are introduced to new regions with climates differing from those in their natural ranges.

7.6.7.2. Salinity tolerance

Marisa cornuarietis can withstand up to about 30 % salt water (Hunt, 1961; Robins, 1971; Santos *et al*., 1987). *Pila globosa* can ‘live in salt water of low salinity’ (Prashad, 1925). Fujio *et al.* (1991a) indicated differences in salinity tolerance among three ‘strains’ of *Pomacea canaliculata*. Preliminary observations in Hawaii (reported by Cowie, 2002) suggest that *P. canaliculata* is sufficiently tolerant of sea water to survive long enough to be carried by currents from one stream mouth to another, thereby expanding its distribution. However, although exhibiting some tolerance of salinity, ampullariids generally live only in fresh water, and brackish water may limit the spread of newly introduced species.

7.6.8. Dispersal

Adult *Pomacea lineata* travel several meters an hour (van Dinther, 1956). *Lanistes nyassanus* moves an average 2.8 m per day (Louda and McKaye, 1982). *Pila globosa* makes long excursions on land both for going from one source of water to another and for the purpose of laying eggs (Prashad, 1925). Short-term dispersal activity, however, does not necessarily translate into long-term, long-distance dispersal. There is little documentation of the spread of ampullariids from a focus of introduction. In a canal in Florida, an introduced population of *Marisa cornuarietis* expanded by at least 1.5 km downstream in 6-8 months (Hunt, 1958), and by 1970 was distributed in virtually the entire freshwater canal system in the Miami area, dispersal being predominantly by floating downstream on vegetation (Robins, 1971). Floating downstream (unattached to vegetation) has been seen in Hawaii and no doubt facilitates rapid dispersal, but crawling upstream is also possible. However, the rapid dispersal of *Pomacea* species to most parts of the Philippines (and within other countries in South-East Asia) following their initial introduction has been predominantly human mediated.

8. ECONOMIC IMPORTANCE

8.1. Rate of spread

8.1.1. Rice

The history of the introduction of non-native apple snails into South-East Asia (above) and the damage they cause to rice farming have been reviewed by Halwart (1994) and Naylor (1996), among others. One or more species of *Pomacea* (usually identified as *Pomacea canaliculata*) have become pests of paddy rice in all the Asian countries to which they have been introduced (section 7.3, above), but probably most seriously in the Philippines. The following few paragraphs outline the rapid spread of the snails throughout the rice-growing regions of some of the countries infested; details of the snails' spread in other countries are not readily available.

8.1.1.1. Taiwan

In Taiwan, where *Pomacea* was first introduced between 1979 and 1981, 17,000 ha of rice and other crops had been infested by 1982, increasing rapidly to 171,425 ha by 1986 (Mochida, 1991).

8.1.1.2. Philippines

In the Philippines the spread of *Pomacea* has been even more rapid, from 9500 ha of rice in 1986 to over 400,000 ha in late 1988, 500,000 ha by 1989, and occurring in most provinces (Adalla and Morallo-Rejesus, 1989; Mochida, 1991; Olivares *et al*., 1992; Anderson, 1993; Litsinger and Estano, 1993), 800,000 ha by 1995 (Palis *et al*., 1996), and 1.2-1.6 million ha by 2004 (Cuaterno, 2005). They are the most important pest of rice in the Philippines (Mochida, 1988a, 1991; Cheng, 1989; Acosta and Pullin, 1991; Halwart, 1994; Naylor, 1996; Vitousek *et al*., 1996; Cuaterno, 2005).

8.1.1.3. Japan

Introduced in 1981, *Pomacea* had spread to 35 out of 47 prefectures by 1989 (Mochida, 1991). By 1995 it occurred in over 50,000 ha of paddy fields (Wada, 1997), and by 2001 in almost 70,000 ha (Ichinose, 2005a).

8.1.1.4. Thailand

First reported in 1988, by 2004 the snails were present in all 76 provinces, with damage to rice reported in 43 provinces (Chanyapate, 2005).

8.1.1.5. Vietnam

Pomacea was also introduced to Vietnam in 1988; by 1997 the total area sustaining damage to rice was 110,000 ha; by 2001 it was 199,000 ha; and in 2003, 23,000 ha were damaged seriously, while 250,000 ha suffered medium or light damage (Nguyen, 2005).

8.1.1.6. Malaysia

In Peninsular Malaysia, the snails were first reported in 1991 and by 2004 had infested 6,000 ha of rice-growing areas (Arshad and Bindin, 2005). In Sabah (East Malaysia), they were first reported in 1992 and had spread to an area of more than 5,000 ha by 2004 (Teo, 2005).

8.1.1.7. Dominican Republic

Problems caused by *Pomacea canaliculata* are not totally confined to South-East Asia. In 1990/91 infestation of rice-growing areas in the Dominican Republic by a species tentatively identified as ***P.***

canaliculata was reported, and by 1997, 40% of this country's rice-growing areas were infested, with losses up to 75 % in some areas (reported by Cowie, 2002).

8.1.2. Other crops

Other crops reported as being attacked by ampullariids are listed in Section 7.2, Table 2, but levels of damage have not been documented to the same extent as for rice.

As an example, in about 1989 *Pomacea canaliculata* was introduced to the Hawaiian Islands. Within 3 yr it been taken deliberately to most of the main islands in the archipelago and had escaped and/or been deliberately released into taro patches, which are similar ecologically to rice paddies. It rapidly became the most important taro pest in Hawaii, in some cases driving farmers out of business (Cowie, 1995, 1996, 1997). By 1998, when a thorough survey of the Hawaiian island of Oahu was undertaken, it was in 20 % of the 98 suitable bodies of water investigated, both taro paddies and natural water bodies (Lach & Cowie, 1999). It continues to spread (R.H. Cowie, unpublished).

8.2. Yield loss and economic cost of ampullariid damage

Annual global agricultural economic losses from 'golden apple snails' have been stated as ranging from US$55 to 248 billion per year (Joshi, 2005).

Yield loss can be massive but variable. In rice in the Philippines (Naylor, 1996), where probably the most serious damage occurs, losses vary from 5 % to 100 % depending on locality and the level of infestation. Yield loss is related to the density and size of the snails. In experimental studies, one snail per m^2 can reduce rice crop stand by 20 %, but eight snails can reduce it by over 90 % (see also Olivares ***et al.***, 1992; Schnorbach, 1995); a single snail eats 7-24 rice seedlings per day (Litsinger and Estano, 1993). Densities in infested rice paddies in the Philippines are generally 1-5 m^{-2} but densities up to 150 m^{-2} have been reported (Halwart, 1994). In Japan, 3-19 m^{-2} have been reported in rice (Litsinger and Estano, 1993; Okuma ***et al.***, 1994; Ichinose, 2005b).

However, little detailed quantitative yield loss or economic information is available. In Taiwan, loss of rice was estimated as US$2.7 million in 1982, increasing rapidly to US$30.9 million in 1986 (Mochida, 1991). Huge areas were treated with pesticides (103,350 ha in 1986) at additional enormous cost, estimated at US$1 million per year between 1982 and 1990 (Cheng and Kao, 2005). In Japan, control in just 176 ha cost US$64,385 (Mochida, 1991). In the Philippines, between 1987 and 1990, farmers spent US$10 million on pesticides (Anderson, 1993); and by 2004 the cost of pest management in the Philippines was estimated as US$7.4 million per year (Joshi, 2005).

The most detailed published economic analysis so far is that of Naylor (1996), reported also by Vitousek ***et al.*** (1996), for the Philippines. This analysis included not only the cost of loss of rice, but also the costs of replanting, application of pesticides and hand-picking snails. Total costs in 1990 resulting from *Pomacea* infestation were estimated as US$28-45 million. This was 25-40 % of what the Philippines spent on rice imports in 1990. Naylor (1996) also compared the costs of control measures (pasturing ducks in the paddies, hand-picking the snails, and applying insecticides) in the Philippines with costs in Vietnam. She showed that the relative implementation of each of these techniques differed because of different costs in the two countries, but also because infestation in Vietnam had not reached the extreme levels that it had in the Philippines, and hand-picking combined with duck pasturing was relatively more feasible and effective in keeping snail numbers low. As snail populations increase and spread in Vietnam this may change. No doubt, tailoring the suite of management practices to local needs will differ both among and within the other countries impacted; research will be necessary and costs will vary.

9. CONSEQUENCES IF INTRODUCED TO AUSTRALIA

Introduction of one or more of the species that are known as ‘golden apple snails’ into Australia has potentially huge consequences both for agriculture and for the natural environment. Climatic modelling has shown that they have the potential to invade large parts of Australia (Baker, 1998).

‘Golden apple snails’ are now the most important pest of wetland (paddy) rice in south-east Asia. If introduced to wetland rice in Australia they will be equally destructive. Any other crops grown in paddy systems (e.g. water cress) are equally at risk. There are no adequate and safe control measures available that are not extremely labour-intensive.

If introduced to natural environments (e.g. Kakadu National Park) they could cause immense environmental disturbance by altering the composition of the aquatic vegetation, including the destruction of native Australian plants.

10. PREPAREDNESS FOR SPECIALIST EMERGENCY DIAGNOSIS

10.1. Diagnostic expertise required

Definitive diagnosis of 'golden apple snails' is not possible at this time, inasmuch as the term 'golden apple snail' refers to more than one species that have not yet been definitively identified. Nevertheless, *Pomacea canaliculata* and a number of other species that probably are part of the 'golden apple snail' complex are readily distinguished as members of the family Ampullariidae, and can be readily distinguished from other genera in the family. Ability to distinguish Ampullariidae from snails in other snail families should be demonstrated, as should ability to distinguish members of the genus *Pomacea* from other members of the family.

10.1.1. Methodology for diagnosis

Note that the bright pink egg masses of *Pomacea canaliculata* and other *Pomacea* species are often the first noticeable sign of an infestation. Sometimes it may even be difficult to find the snails, although the egg masses are a sure indication of the snails' presence.

Egg masses of *Pomacea canaliculata*.
[Photo: K.A. Hayes and R.H. Cowie]

i. Select the largest specimen available.
ii. Observe the overall size and shape of the shell – is it large and essentially globular in shape? Juveniles are smaller and may cause confusion.
iii. Does it have an operculum?
iv. Is the operculum corneous (horny), not calcified (brittle) (which would indicate *Pila* spp.)?
v. Are the sutures (the junctions between the whorls) moderately to deeply channelled?
vi. You probably have a 'golden apple snail' – *Pomacea canaliculata* or another of the *Pomacea* species that are included under the umbrella of 'golden apple snail'.

10.2. Action upon positive identification of ‘golden apple snails’

Positive identification of ‘golden apple snails’ from Australia will be immediately communicated to appropriate authorities within the Department of Agriculture Fisheries and Forestry (DAFF), including details of:

Overseas source of specimens if known (i.e. if intercepted by quarantine officials)
Details of associated plant material, if appropriate
Location of infestation(s) if already in the wild
Estimate of size of infestation if already in the wild
Reported damage, if any
Implications of the incursion
Reference to this document for images of the pest
Known distribution within Australia prior to this newly reported infestation
Estimate of potential distribution within Australia (see Baker, 1998)
Level of confidence of identitification
Date of confirmed identification
Name, position, affiliation and level of expertise of identifier

10.3. Access to expert assistance

If questions remain regarding the identity of specimens intercepted entering Australia or found in Australia that are suspected to be ‘golden apple snails’, the specimens can be sent to Dr. Robert H. Cowie, Center for Conservation Research and Training, University of Hawaii, Honolulu, Hawaii 96822, USA, for confirmation. No charge will be made for a determination of whether a particular specimen is or is not a ‘golden apple snail’. Charges, if any, for additional services will be negotiable.

11. FURTHER READING

11.1. Literature

Although many of the references cited in the text above and listed in the Literature Cited section (section 12) will be useful for obtaining additional information about 'golden apple snails', the following publications and website are of particular relevance or significance.

Baker, G.H. (1998) The golden apple snail, *Pomacea canaliculata* (Lamarck) (Mollusca: Ampullariidae), a potential invader of fresh water habitats in Australia. In: Zalucki, M.P., Drew, R.A.I. and White, G.G. (eds.) *Pest management - future challenges. Proceedings of the sixth Australasian applied entomological research conference. Brisbane, Australia. 29 September - 2nd October 1998. Volume 2.* University of Queensland Printery, Brisbane, pp. 21-26.
[This is an evaluation of the parts of Australia that are at risk from 'golden apple snails', based on climatic modelling.]

Lai, P.-Y., Chang, Y.-F. & Cowie, R.H. (eds.) 2005. *Proceedings of the APEC Symposium on the management of the golden apple snail, September 6-11, 2004, Pingtung, Taiwan*. National Pingtung University of Science and Technology, Pingtung.
[This is the proceedings of a 2004 meeting at which representatives of all the APEC countries, most of which are affected by introduced 'golden apple snails' presented reports of the impacts of the snails in their countries and the current status of measures to manage them.]

Cowie, R.H. 2002. Apple snails (Ampullariidae) as agricultural pests: their biology, impacts and management. In: *Molluscs as Crop Pests* (ed. G.M. Barker), p. 145-192. CABI Publishing, Wallingford.
[This is a fully referenced review of knowledge, as of 2002, of the basic biology of ampullariids, as it is relevant to their management, as well as a review of their world-wide introduction, the damage they cause and the measures that have been used to control them.]

Cowie, R.H. & Thiengo, S.C. 2003. The apple snails of the Americas (Mollusca: Gastropoda: Ampullariidae: *Asolene*, *Felipponea*, *Marisa*, *Pomacea*, *Pomella*): a nomenclatural and type catalog. *Malacologia* 45(1): 41-100.
[This is a catalog of all the species and genus names used for ampullariids of the New World, which is the source of the invasive species of *Pomacea*, with additional information on synonymies, type localities, location of type material, and a comprehensive bibliography of original taxonomic literature.]

Naylor, R. (1996) Invasions in agriculture: assessing the cost of the golden apple snail in Asia. *Ambio* 25, 443-448.
[This is the most thorough economic assessment of the costs of 'golden apple snail' invasion in Asia.]

11.2. Website

www.applesnail.net

12. REFERENCES

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APPENDIX

Reproduction and growth in ampullariids. Asterisks indicate laboratory studies. Some data have been reported without indicating whether they were obtained from laboratory cultures or from the wild. Some of the references listed undoubtedly simply reiterate data from others that are also listed. Some, at least, of the variability exhibited (especially by *Pomacea canaliculata*) may be due to taxonomic confusion (see text).

Species	Locality	Clutch size	Hatchability	Time to hatching	Time from hatching to maturity	Longevity	References
Pomacea canaliculata	Argentina	120-478					Cazzaniga and Estebenet, 1988
	Argentina			28 days			Scott cited by Demian and Yousif, 1973
	Argentina*			12-15 days			Thiengo *et al*., 1993
	Argentina*				7 months - 2 years	13 months - 4 years	Estebenet and Cazzaniga, 1992
	Argentina	mean 101	43%				Albrecht *et al*., 1996
	Argentina*				100-150 days		Estebenet and Cazzaniga, 1998
	Philippines	25-320		10-15 days	60 days	2-3 years	Adalla and Morallo-Rejesus, 1989
	Philippines	25-500		7-14 days	59-84 days	119 days - >3 years	Anon., 1989; Olivares *et al*., 1992
	Philippines	25-500		10-15 days	60-85 days	2-3 years	Halwart, 1994
	Philippines*	50-400	20.9-35.0%	9-12 days			Lacanilao, 1990 (as "*Ampularius* sp.")
	Philippines	50-500		10-15 days	< 1 year		Guerrero, 1991
	Philippines	25-500	80%	8-15 days			Rondon and Callo, 1991
	Philippines		80%				Bombeo-Tuburan *et al*., 1995
	Philippines	25-320	90-100%	8-21 days		3 years	Schnorbach, 1995
	Taiwan*	200-300	60%	average 12.4 days	55 days		Chang, 1985
	Japan*	average 200-700	41.9%	12 days	6 months		Fujio and von Brand, 1990; Fujio *et al*. 1991a, b
	Japan	30-700	7-90%		2 months	>2 years	Wada, 1997
	Thailand	800-1,000					Keawjam and Upatham, 1990
	Asia	321 (average)	7-90%	9-37 days	2-3 months	2-5 years	Halwart, 1994 Mochida, 1988a, b, 1991
	Asia	320	7-90%		60-90 days		Naylor, 1996
	Asia	25-500	7-90%	8-15 days	60-90 days	4 years	Heidenreich and Halwart, 1995; Heidenreich *et al*., 1997
	Hawaii	200-500		7-14 days	3-4 months	2-5 years	Glover and Campbell, 1994
	Hawaii	c. 200		3 weeks	3-4 months	3-4 years	Kobayashi *et al*., 1993
	Hawaii	350		2-3 weeks			Tamaru and Hun, 1996
	England*	100+			< 12 months		Andrews, 1964
Pomacea dolioides	Surinam	200-300 (max. 437)		13-16 days	8-12 months	c. 18 months?	van Dinther, 1956, 1962 (as "*P. lineata*")
Pomacea gigas	?			2-6 weeks			Köhler cited by Demian and Yousif, 1973
Pomacea glauca	Surinam	30-90		14-17 days	8-12 months	c. 18 months?	van Dinther, 1956, 1962
	Guadeloupe				13.5 months	c. 3 years	Pointier *et al*., 1988

continued...

APPENDIX 1 (continued)

Species	Locality	Clutch size	Hatchability	Time to hatching	Time from hatch-ing to maturity	Longevity	References
Pomacea haustrum	Brasil*			15-23 days	374-529 days		Guimarães, 1981a
	Brasil	236		9-30 days			Guimarães, 1981b
	Brasil				< 1 year		Estebenet and Cazzaniga, 1992
Pomacea lineata	Brasil*	average 100		15 days			Thiengo, 1987
Pomacea paludosa	Florida, USA	mean 26.7 (max. 141)		18-28 days			Hanning, 1978
	Florida, USA	3-50, 80		15-20 days			Perry, 1974
Pomacea urceus	Trinidad	21-93	0-84%*	22-30 days*			Lum-Kong and Kenny, 1989; Lum-Kong, 1989
	Venezuela	50-200			6-7 months	2.5-3.5 years	Burky, 1973, 1974
Marisa cornuarietis	Egypt*			8-20 days			Demian and Yousif, 1973
	Florida	max. 210		11-24 days			Robins, 1971
Pila globosa	India	200-300		c. 1 month			Andrews, 1964; Prashad, 1925
	India			10 days - 3 weeks			Ranjah cited by Demian and Yousif, 1973
Pila polita	?			<14 days			Semper cited by Demian and Yousif, 1973
Pila spp.	Thailand					at least 3 years	Keawjam, 1987
Lanistes nyassanus	Lake Malawi					5-10 years	Louda and McKaye, 1982