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# SINGAPORE MOLLUSCA: 7. THE FAMILY AMPULLARIIDAE (GASTROPODA: CAENOGASTROPODA: AMPULLARIOIDEA)

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ABSTRACT. — The freshwater snails of the family Ampullariidae in Singapore are reviewed. This family is represented in Singapore by Pila ampullacea, Pila scutata, and the introduced Pomacea canaliculata and Pomacea maculata. Pila scutata and Pomacea canaliculata were once the only known Ampullariidae species in Singapore. Here, we discuss in further detail the other two ampullariids that have only been recently confirmed to be part of the malacofauna of Singapore—Pila ampullacea and Pomacea maculata. Two other species of non-native Ampullariidae, Pomacea diffusa and Marisa cornuarietis are sold in the local aquarium trade, but have not been recorded in the wild to date.

**KEY WORDS.** — Mollusca, Ampullariidae, *Pila*, *Pomacea*, apple snails, invasive species, alien species, taxonomy, synonymy, records, Singapore

## INTRODUCTION

The Ampullariidae Gray, 1824, commonly known as apple snails, is a large family of freshwater snails, found across the tropics and subtropics of Africa, Asia, and the Americas. The family consists of nine extant genera and more than 150 recognised species (Hayes et al., 2009). It includes the largest freshwater snails, with several species attaining sizes of more than 100 mm in shell height (Perera & Walls, 1996; Cowie, 2002). Ampullariids commonly occur in many freshwater bodies throughout Singapore. They appear to prefer ponds and similar lentic habitats, but are also found in canals and streams (Fig. 1).



Fig. 1. Live ampullariids in situ: A, *Pila scutata* (ca. 30 mm in shell height) at Tampines Eco Green; B, *Pomacea maculata* at Kranji Marsh (ca. 60 mm in shell height). See Figs. 3 & 5 for locations. (Photographs by: T. H. Ng [A] and Kelvin K. P. Lim [B]).

Two genera are found in Singapore—*Pila* Röding, 1798, which is native to the Southeast Asia, and *Pomacea* Perry, 1810, originating from the Americas. Hitherto, four ampullariid species have been recorded from Singapore, namely *Pila ampullacea* (Linnaeus, 1758), *Pila scutata* (Mousson, 1848), *Pomacea canaliculata* (Lamarck, 1822), and *Pomacea maculate* Perry, 1810 (see Hayes et al., 2008; S. K. Tan & Woo, 2010: 27; Hayes et al., 2012; S. K. Tan et al., 2012: 126, 127; M. E. Y. Low et al., 2013). These are reviewed here, with descriptions and notes on their taxonomy, nomenclature, and local distribution. Details of records in the literature, and other notes of interest are also included.

#### MATERIAL AND METHODS

Relevant literature on the taxonomy of the Ampullariidae was reviewed. Records of ampullariid species were compiled from the published literature. Primary synonyms and records mentioning Singapore are listed. Abbreviations used for collections are: ZRC = Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore; NTH = collection of the first author; and TSK = collection of the second author. Measurements are given in the form of shell height (SH)  $\times$  shell width (SW). Shell height is defined as the distance from the apex to the lowest part of the basal side of the peristome, and shell width is the distance between the edges of the widest part of the body whorl perpendicular to the coiling axis. All measurements are in millimetres (mm).

#### **SYSTEMATICS**

## **SUPERFAMILY AMPULLARIOIDEA GRAY, 1824**

**Remarks.** — First established at family-level rank (see below).

## **FAMILY AMPULLARIIDAE GRAY, 1824**

Ampullariadae Gray, 1824: 276 (type genus *Ampullaria* Lamarck, 1799). Pilidae Preston, 1915: 96 (type genus *Pila* Röding, 1798).

**Remarks.** — The family-group name Ampullariidae was originally spelt as Ampullariadae (see Bouchet & Rocroi, 2005: 25). The family-group name Ampullariidae Gray, 1824, has been placed on the *Official List of Family-Group Names in Zoology* in Opinion 1913 (ICZN, 1999a: 74). See Cowie (1997: 85, 86) for a discussion on the nomenclature of the family-group name Pilidae Preston, 1915.

## Genus Pila Röding, 1798

*Pila* Röding, 1798: 145 (type species *Helix ampullaceal* Linnaeus, 1758, by subsequent designation by Dall, 1904: 53; gender feminine).

Ampullaria Lamarck, 1799: 76 (type species Helix ampullaceal Linnaeus, 1758, by monotypy).

Ampullarius Montfort, 1810: 242, 243 (unjustified emendation, and junior objective synonym, of Ampullaria Lamarck, 1799).

**Remarks.** — For a discussion on the nomenclature of these genus-group names, see Cowie (1997: 83, 84) and ICZN (1999a: 74).

## Pila ampullacea (Linnaeus, 1758)

(Fig. 2, 3)

Helix ampullacea Linnaeus, 1758: 771, no. 592 (type locality: "Asia").

Ampullaria fasciata Roissy, 1805: 374 (type locality: none stated/traced).

Pomacea orbata Perry, 1811: pl. 38, fig. 5, one unnumbered page of caption text (type locality: none stated/traced).

Ampullaria celebensis Quoy & Gaimard, 1834: 167-169 (type locality: "Manado").

Ampullaria sumatrensis Philippi, 1851: 59, pl. 19, fig. 1–2 (type localities: "der fluss Danu-luar in Sumatra; Java?").

Ampullaria turbinis Lea, 1856: 110 (type locality: "Siam").

Ampullaria dalyi Blanford, 1903: 281, pl. 8, no. 1 (type locality: "Siam").



Fig. 2.  $Pila\ ampullacea$  from the Venus Drive area, Singapore (SH  $58.5 \times$  SW 50.9 mm) (ZRC MOL.5450). See Fig. 3 for location. Scale bar = 10 mm. (Photographs by: S. K. Tan).

## Singapore records:

Ampullaria ampullacea – Wheeler, 1885: 37 (first record). Pila ampullacea – S. K. Tan & Woo, 2010: 27. — M. E. Y. Low et al., 2013: 55.

*Material examined.* — Singapore. Venus Drive, near Island Country Club (ZRC.MOL.5450), 1977–1978.

*Distribution in Singapore.* — See Fig. 3.

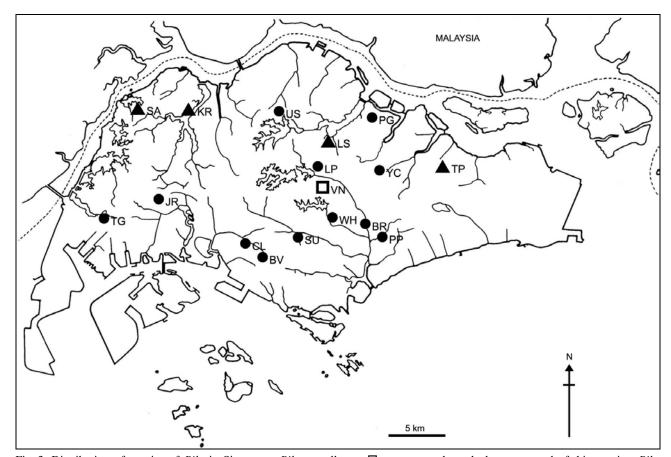


Fig. 3. Distribution of species of *Pila* in Singapore. *Pila ampullacea*: □, represents the only known record of this species. *Pila scutata*: ♠, represents historical distribution; ♠ represents extant populations. Abbreviations used: BR, Braddell Road; BV, Buona Vista ponds; CL, Clementi Road ponds; JR, Jurong Road ponds; KR, Kranji Reservoir; LP, Lower Peirce Reservoir; LS, Lower Seletar Reservoir; PP, Potong Pasir ponds; PG, Punggol; SA, Sarimbun Reservoir; SU, Former University of Singapore; TG, Tengeh Reservoir; TP, Tampines Eco Green & Sungei Tampines; US, Upper Seletar Reservoir; VN, Venus Drive; WH, Sungei Whampoa; YC, Yio Chu Kang Road.

*Habitat.* — Fresh water sites of the lowlands, lakes, ponds, marshes, rice fields, irrigation works, often in great numbers (W. S. S. van Benthem Jutting, 1956).

Diagnosis. — The following diagnosis is based on W. S. S. van Benthem Jutting (1956), and Brandt (1974). Shell subglobose, often somewhat reversely conic; surface smooth, usually with fine axial lines; to about 100 mm in shell height; spire low, conical to almost flat, suture distinct, but not deeply impressed; body whorl large, rounded or indistinctly angular at the shoulder, especially in juveniles; peristome not continuous except in large shells, which is joined by a thin parietal callus; columellar and basal margin of aperture slightly reflexed; umbilicus open, small and partly hidden by apertural margin. Shell colour yellowish-green with tinge of orange, occasionally plain, but mostly with numerous brown spiral lines of varying thickness, which are visible inside the aperture, occasionally with axial brown lines marking previous stages of growth rest, interior margin of aperture usually yellow or light orange; periostracum olive green, with soft lustre in fresh shells.

**Remarks.** — S. K. Tan & Woo (2010: 27) listed *Pila ampullacea* as a previously unpublished record based on the specimen figured here (Fig. 1). However, the first known record of this species was actually by Wheeler (1885: 37) who listed "Ampullaria (typical) ampullacea, Linn. Singapore... The type of its genus, a large olive-coloured shell marked with revolving, narrow, green bands." This brief description of a largish shell marked with revolving, narrow, green bands agrees well with the current taxonomic concept of *Pila ampullacea* (e.g., Brandt, 1974: 50, pl. 4, figs. 58. 59; also see Fig. 1).

This species has not been recorded since the late 1970s. The last known living population comprised of about a few dozen individuals in aquatic plant ponds at Venus Drive (H. E. Ng, pers. comm.). Based on the record by Wheeler (1885: 37), and the former observation of a living population and a single voucher specimen from this population (Fig. 1), we consider *Pila ampullacea* to be an unambiguous part of the malacofauna of Singapore. However, it remains unclear if it is indigenous to Singapore (see **Discussion**).

Although Cowie & Heros (2012) considered *Ampullaria celebensis* Quoy & Gaimard, 1834, to be a valid species, we here regard it as a synonym of *Pila ampullacea* as the conchological characteristics of the lectotype (MNHN 23077; see Cowie & Héros, 2012: 803; Fig. 2B) are within the intraspecific variation of the latter. Nevertheless, we acknowledge that the taxonomy of many ampullariid species groups remains confused and a taxonomic revision, preferably complemented by genetic analyses, is needed to properly resolve the matter.

## Pila scutata (Mousson, 1848)

(Figs. 3, 4, 8A, 8A', 8C, 8C')

Ampullaria conica W. Wood, 1828: 22, 29, pl. 7, fig. 22 (type locality: none stated/traced) [junior homonym of Ampullaria conica Lamarck, 1804, and Ampullaria conica Swainson, 1823, see M. E. Y. Low et al., 2013: 55].

Ampullaria scutata Mousson, 1848: 268, pl. 8, fig. 2 (type localities: "Java").

Ampullaria orientalis Philippi, 1849: 192 (type localities: "Insula Java, Philippinae, China").

Ampullaria borneensis Philippi, 1852: 31, pl. 8, fig. 3 (type locality: "Borneo").

Ampullaria javanica Reeve, 1856: pl. 20, fig. 96, unnumbered caption to fig. (type locality: "Java").

Ampullaria stoliczkana Nevill, 1877: 11 (type locality: Penang).

Ampullaria perakensis de Morgan, 1885: 418 (type locality: Perak).

Ampullaria wellesleyensis de Morgan, 1885: 419 (type locality: "environs de Boukit Tamboun").

Pachylabra javanica var. fruhstorferi Kobelt, 1913: 90, pl. 38, fig. 6, 7 (type locality: "Java").

## Singapore records:

Ampullaria conica var. borneensis – Nevill, 1884: 5 (first record).

*Pila conica* – Ghosh, 1929: 393 (along Kim Keat Road). — Chou et al., 1994: 73. — Perera & Walls, 1996: 82.

Pila scutata — Johnson, 1973: 116, 120. — Khoo et al., 1977: 10 (Seletar Reservoir). — P. K. L. Ng, 1991: 129. —
Wee, 1992: 71 (Lower Peirce Reservoir). — P. K. L. Ng et al., 1993: 22–23. — Chan, 1996: 185–186. — Goh et al., 2002: 103–104. — Taylor, 2003: 123 (Singapore: ditch from Seletar Reservoir, 100 m west of Upper Thompson Road). — Clements et al., 2006: 144. — S. K. Tan & Woo, 2010: 27. — S. K. Tan & Yeo, 2010: 99. —
S. K. Tan et al., 2012: 126–127. — M. E. Y. Low et al., 2013: 55–60, fig. 1C, D. — S. K. Tan et al., 2013: 135–141.

Material examined. — Singapore. Buona Vista pond: (ZRC1989.398–1989.399) 20 Nov.1957, (ZRC1989.389–1989.397) 11 Nov.1958; Jurong Road, 11th mile (ZRC1989.452–1989.453), 20 Jul.1960; Jurong Road, pond: (ZRC1989.433–1989.437, ZRC1989.446–1989.451) 23 May 1962, (ZRC1989.438–1989.445) 28 May 1962; Jurong Road, 17¾th mile (ZRC1989.425–1989.432) 28 May 1962; Braddell Road, Sungei Kallang (ZRC1989.403) 16 May 1962; MacRitchie Reservoir, Sungei Whampoa (ZRC1989.404–1989.407) 16 May 1962; Clementi Road: ditches (ZRC1989.417–1989.419) 21 May 1962; pond (ZRC1989.420–1989.422) 21 May 1962, (ZRC1989.423–1989.432) no date; Kian Teck Road (ZRC1989.1949) 23 Jun.1962; Potong Pasir (ZRC1989.379–1989.385) 27 Jun.1962,

(ZRC1989.1947) 2 Jul.1962; Yio Chu Kang Road, 8th mile (ZRC1989.408–414) 25 Aug.1962; University of Malaya: Botany Department tank (ZRC1989.386–1989.388), 25 May 1962, pond (ZRC1989.466) 15 May 1962; North Buona Vista Road (ZRC1989.467–1989.481) 21 May 1962; Seletar Reservoir: (ZRC1989.400–1989.402) 4 Feb.1981, (ZRC1990.17176–1990.17177) 6 Dec.1990; Kranji Reservoir: (ZRC1991.20053–1991.20066) 31 Aug.1988, (ZRC1990.843–1990.851) 2 Sep.1988, (ZRC.MOL.6) 7 Jul.2002, (ZRC.MOL.3094) 2009; Institute of Education (ZRC1990.16215–1990.16223), 10 Sep.1988 Lower Peirce Reservoir (ZRC1990.15654–1990.15671) 21 Jul.1990, (ZRC1990.674) 29 Nov.1990; Tengeh Reservoir (ZRC1990.17452–1990.17456), 26 Dec.1990; Pasir Ris Drive 1, canal (ZRC.MOL.5), 13 May 2002; Punggol: (TSK 1803) Aug.1997, (TSK) 14 Sep.2003; Tampines Eco Green Park: (ZRC.MOL.3132), 2 Jul.2011, (NTH) 21 Oct.2013; Lower Seletar Close, canal under Lentor Ave (ZRC.MOL.3135) Oct.2010.

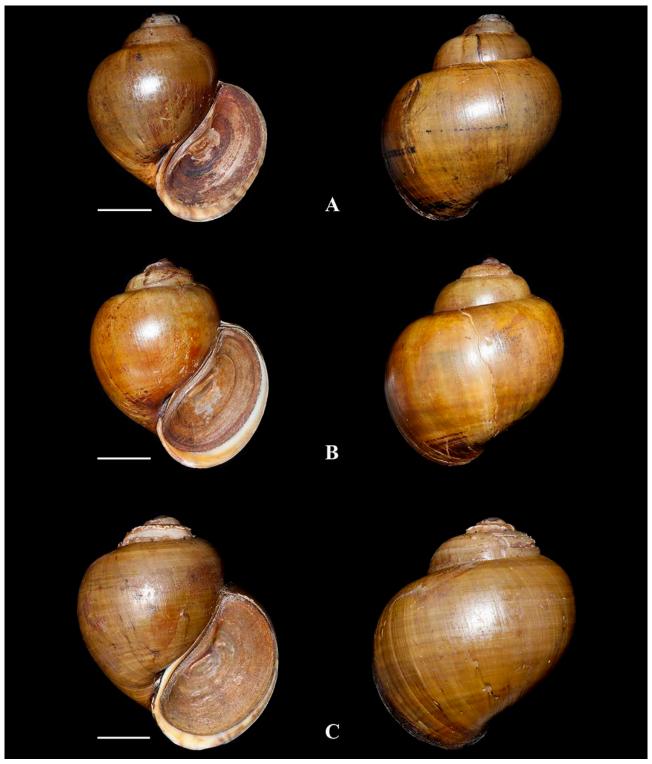


Fig. 4. *Pila scutata* from Singapore. A–C, Punggol Port Road (A, SH 39.9  $\times$  SW 33.4 mm; B, SH 40.0  $\times$  SW 33.1 mm; C, SH 44.1  $\times$  SW 37.4 mm). (TSK). See Fig. 3 for location. Scales bars = 10 mm. (Photographs by: S. K. Tan).

Distribution in Singapore. — See Fig. 3.

*Habitat.* — Shallow depth among vegetation in freshwater marshes, lakes, ponds, and other lentic water bodies, also in ditches or runoffs with moderate flow; appears to favour natural banks that are shady and sheltered (T. van Benthem Jutting, 1937; S. K. Tan et al., 2012; pers. obs.).

**Diagnosis.** — The following diagnosis is based on specimens from Singapore, and additional information in W. S. S. van Benthem Jutting (1956). Shell sub-globose, surface smooth, usually with fine axial growth lines; to about 50 mm in shell height; spire elevated, profile step-like with rounded whorls; suture impressed; body whorl rounded; peristome not continuous except in mature shells, which is joined by a thin parietal callus; columellar and basal margin of aperture slightly expanded; umbilicus usually obsolete and hidden by parietal margin. Shell colour yellowish green or brownish green, plain or with several irregular brown spiral lines or bands, which are visible inside the aperture; periostracum olive green, with soft lustre in fresh shells, often covered with brownish "rust" stains.

**Remarks.** — Despite the large number of forms of *Pila ampullacea* and *Pila scutata* known, separating the two is usually easy. Mature *Pila scutata* shells are only about half the size of those of *Pila ampullacea* (50 mm versus 100 mm). The umbilicus is usually obsolete in *Pila scutata* compared to the small open umbilicus of *Pila ampullacea*, and the shell of *Pila ampullacea*, with a lower spire and usually reversely conical shape, also appears more globose than that of the former.

In recent years, living populations of *Pila scutata* have been observed only at Sarimbun Reservoir, Kranji marshes, and Tampines Eco Green. This species used to be very common in Singapore (S. K. Tan et al., 2013). Although many of the historical localities in Singapore where *Pila scutata* was found no longer exist, owing to rapid development over the past half century, suitable habitats still certainly exist. It is also known to be a hardy species that can thrive in disturbed or weed-free and polluted habitats (Ponniah, 1962; Johnson, 1973), but populations have declined drastically in the past decade, apparently coinciding with the introduction of the confamilial *Pomacea* species (S. K. Tan et al., 2013).

*Pila conica* (W. Wood, 1828) has sometimes been used for *Pila scutata*, but the former is a rejected junior homonym and the latter is the valid name for this species (see M. E.Y. Low et al., 2013: 55, 56). However the taxonomy of this species group remains rather confused. Our list of synonyms tends towards lumping and largely concurs with the lists of Alderson (1925), W. S. S. van Benthem Jutting (1956), and Brandt (1974). It should also be noted that Cowie & Héros (2012) regard a couple of the synonyms listed here, namely *Ampullaria perakensis* de Morgan, 1885, and *Ampullaria wellesleyensis* de Morgan, 1885, as valid taxa.

## Genus Pomacea Perry, 1810

*Pomacea* Perry, 1810 (in 1810–1811): pl. 12, two unnumbered pages of caption text (type species *Pomacea maculata* Perry, 1810, by monotypy; gender feminine).

**Remarks.** — Pomacea Perry, 1810 (in 1810–1811) has been placed on the Official List of Generic Names in Zoology in Opinion 1913 (ICZN, 1999a: 74).

## Pomacea maculata Perry, 1810 (Figs. 5, 6)

*Pomacea maculata* Perry, 1810 (in 1810–1811): pl. 12, two unnumbered pages of caption text (type locality: Paraná, Argentina [see discussion below and Hayes et al., 2012]).

### Singapore records:

Pomacea insularum - Hayes et al., 2008: 702, 706 (first record). — M. E. Y. Low et al., 2013: 55.

Material examined. — Singapore. Sungei Tengah Road (ZRC 1990.17328–17331) 24 Feb.1989; Jurong Lake (ZRC 1991.19726–19729), Apr.1991; Kranji Reservoir: (ZRC 1990.17012–17029) 5 Oct.1989, (ZRC 1991.3111) 5 Oct.1989, (ZRC.MOL.7) 7 Jul.2002; Seletar East Farmway 1, ornamental fish farm (TSK 1809), Dec.1997; Lower Peirce Reservoir (ZRC.MOL.10), 8 Aug.2002; Singapore Botanic Gardens (ZRC.MOL.5691), 2002; Lentor Road, tributary of Sungei Seletar (NTH), 20 Nov.2010; Lower Seletar Reservoir (ZRC.MOL.5692), 4 Mar.2009.

Distribution in Singapore. — See Fig. 5.

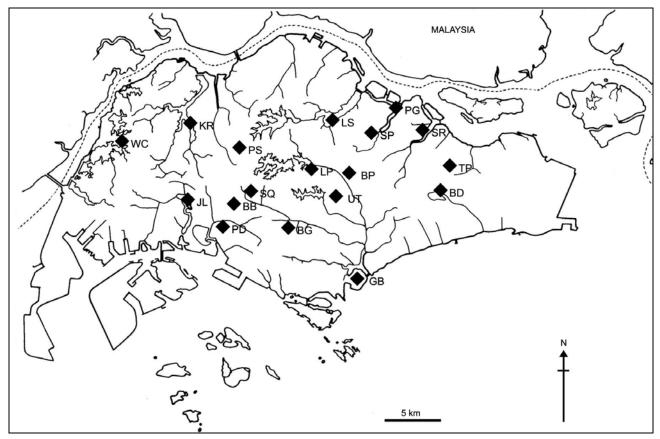


Fig. 5. Distribution of species of *Pomacea* in Singapore represented by a ♠. Abbreviations used: BB, Bukit Batok Nature Park; BD, Bedok Reservoir; BG, Singapore Botanic Gardens; GB, formerly Marina City Park, now Gardens by the Bay; JL, Jurong Lake and tributaries (Sungei Jurong, Sungei Lanchar); KR, Kranji Reservoir and tributaries (Kranji marshes, Sungei Tengah); LP, Lower Peirce Reservoir; LS, Lower Seletar Reservoir and tributaries (Sungei Seletar, Sungei Seletar Simpang Kanan); PG, Punggol Reservoir and tributaries (Seletar Wet Gap); BP, Bishan-Ang Mo Kio park; PD, Sungei Pandan; PS, Pang Sua pond; SP, Sengkang Riverside Park; SQ, Singapore Quarry; SR, Serangoon Reservoir; TP, Tampines Eco Green Park; UT, Upper Thomson Road; WC, Western Catchment Reservoirs. The map does not show the respective localities for the two *Pomacea* species because the information is as yet unavailable, and each locality may have either or both species. Populations are mainly established in modified, urban freshwater habitats; *Pomacea* are now found in more than half of the reservoirs in Singapore and their associated tributaries and canals, and at various artificial ponds in parks.

**Habitat.** — Commonly found grazing at the littoral zone of reservoirs and along in shallow water along edges of canals, leaving the water to mate and lay eggs. Clusters of their bright pink eggs can often be found on the surfaces of rocks or concrete banks, and also on reeds. This apple snail does not appear to have any particular preference for type of substrate; it thrives at sites regardless of bank type—granite rock walls or more natural vegetated shorelines, as well as steep concrete banks (e.g., canals and storm-water drains), or substrate type—soft muddy, sandy, and concrete bottoms.

Diagnosis. — The following diagnosis is based on specimens from Singapore, and information in Hayes et al. (2012). Shell rather globose, surface generally smooth, with fine axial growth lines, occasionally malleated; to more than 150 mm in shell width; spire height variable, usually low, apical whorls rounded; suture deep, channel-like; body whorl well rounded; peristome incomplete in juvenile shells, but parietal callus may be thickened and the peristome continuous in senile shells, parietal callus; columellar side of lip reflexed, basal margin slightly expanded; umbilicus open, slightly obscured by aperture margin. Shell colour yellowish brown, plain or with reddish to green or dark brown spiral lines or bands of varying thickness, which are visible inside the aperture, interior margin of aperture usually pigmented with yellow to reddish orange; periostracum thick, yellow to olive green or dark chestnut, with soft lustre in fresh shells.

**Remarks.** — The type locality of *Pomacea maculata* given by Perry (1810 in 1810–1811: pl. 12, unnumbered page of caption text) was "the South Sea". The type locality is now Paraná, Argentina, as determined by the origin of the neotype designated by Hayes et al. (2012) (Article 76.3, ICZN, 1999b: 87).

Based on the material seen, *Pomacea maculata* appears to be more widespread than *Pomacea canaliculata* in Singapore. Although the two species may be distinguished using morphological characteristics, shell characteristics are often ambiguous and they are best differentiated using molecular genetic methods (see Matsukura et al., 2008; Hayes et al., 2012). Identification of the material listed here was however, based solely on conchological characteristics, and there is thus far only one Singapore record of *Pomacea maculata* confirmed using molecular genetic methods (Fig. 6A;

as *Pomacea insularum* [in Hayes et al., 2008]). However, the specimens were obtained from the local aquarium trade (R. C. Joshi, pers. comm.). Preliminary observation of day-old juveniles of *Pomacea maculata* appear to be different from those figured in Hayes et al. (2012). Thus, there remains a likelihood that the populations of *Pomacea maculata* in Singapore may be hybridising with *Pomacea canaliculata* (see Matsukura et al., 2013), or is a different species altogether. See also Discussion.

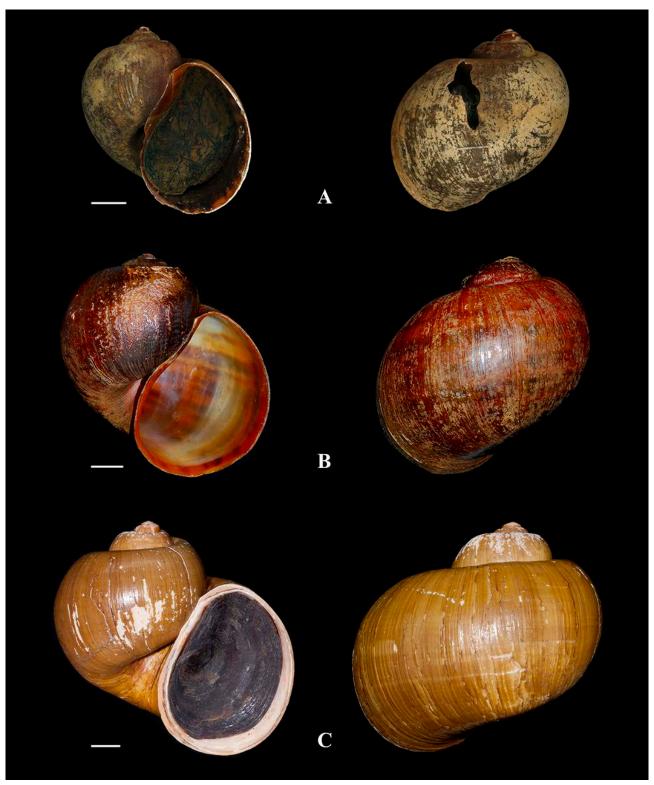


Fig. 6. *Pomacea maculata* from Singapore: A, local aquarium shop (SH 54.3 × SW 49.5 mm); B, Lower Seletar Reservoir (SH 71.3 × SW 67.5 mm) (ZRC.MOL.5692); C, Singapore Botanic Gardens (SH 84.2 × SW 83.5 mm) (ZRC.MOL.5691); See Fig. 3 for locations. Scale bars = 10 mm. (Photographs by: Kenneth Hayes [A] and Siong Kiat Tan [B, C]).

## Pomacea canaliculata (Lamarck, 1822)

(Figs. 5, 7, 8B, 8B', 8D, 8D')

Ampullaria canaliculata Lamarck, 1822: 178 (type locality: Palermo, Buenos Aires, Argentina [see Hayes et al., 2012]) [not Ampullaria canaliculata Lamarck, 1804 = Amauropsina canaliculata (Lamarck, 1804)].

Ampullaria australis d'Orbigny, 1835: 32 (type locality: "lacubus Pampas meridionalibus Buenos-Ayres [= Buenos Aires, Argentina]").

Ampullaria gualtieri d'Orbigny, 1835: 52 [unavailable name; see discussion below].

Ampullaria dorbignyana Philippi, 1852: 65, pl. 21, fig 4 (type locality: none stated/traced).

Pomacea canaliculata chaquensis Hylton Scott, 1948: 242 (type locality: "Madrejón de Ingeniero Juárez, Chaco salteño. Formosa").

## Singapore records:

Pomacea sp. — P. K. L. Ng, 1991: 130 (first record).

Pomacea lineata — Maassen, 2001: 47. — M. E. Y. Low et al., 2013: 55.

*Pomacea canaliculata* — P. K. L. Ng et al., 1993: 20, 22–23. — Chan, 1996: 185–186. — Goh et al., 2002: 103. — Clements et al., 2006: 144. — S. K. Tan & Yeo, 2010: 94, 96, 98. — S. K. Tan et al., 2012: 129. — M. E. Y. Low et al., 2013: 55.

*Material examined.* — **Singapore**. Marina City Park (ZRC 1995.676), 28 May 1995; ; Western Catchment reservoirs (NTH), May 2009; Singapore Quarry (NTH), 12 Jun.2013; Tampines Eco Green (NTH), 21 Oct.2013.

Distribution in Singapore. — See Fig. 5.

*Habitat.* — As for *Pomacea maculata*.

**Diagnosis.** — The following diagnosis is based on specimens from Singapore, and information in Hayes et al. (2012). Shell sub-globose, surface generally smooth with fine axial growth lines; to about 60 mm in shell height; spire usually low, but distinctly elevated, apical whorls rounded; suture sunken, channel-like; body whorl rounded; peristome continuous, joined by a thin parietal callus; columellar side of lip reflexed, basal margin slightly expanded; umbilicus open, slightly obscured by aperture margin. Shell yellowish green to brown, plain or with numerous reddish to dark brown spiral lines or bands of varying thickness, which are visible inside the aperture, interior margin of aperture usually unpigmented; periostracum yellow brown to olive green or dark chestnut, with soft lustre in fresh shells.

Remarks. — Two species of Pomacea in Singapore are now known, but both have been treated as Pomacea canaliculata in nearly all literature to date. It would be impossible, to verify the species involved in each mention, and these historical records are therefore treated tentatively as of *Pomacea canaliculata* in the broad sense for convenience. Recent preliminary efforts to identify the snails using molecular genetics have identified an individual from an established population (Singapore Quarry) as Pomacea canaliculata (unpublished data). Pomacea canaliculata and Pomacea maculata have shells that are remarkably similar morphologically. Compared to Pomacea canaliculata, Pomacea maculata attains a much larger adult size (to more than 150 mm), has a more angulate shoulder of the body whorl, a larger and generally ovoid aperture, and pigmented inner side of the pallial lip (Hayes et al., 2012). The conchological characteristics are however quite variable and rather subjective. Identification of other material listed here was based solely on conchological characteristics and should be regarded as provisional (see Discussion). The name Ampullaria canaliculata had been used twice by Lamarck (1804: 32; 1822a: 178) for two different taxa. Ampullaria canaliculata Lamarck, 1804, is now Amauropsina canaliculata, a fossil species closely related to the naticids (see Cowie et al., 2001: 15). The ICZN has ruled in Opinion 1997 (ICZN, 2002: 137) that the junior homonym, Ampullaria canaliculata Lamarck, 1822, is an available name despite it being a junior homonym, and can thus be used for the taxon known as Pomacea canaliculata (Lamarck, 1822). The name Ampullaria gualtieri was listed in the synonymy of Ampullaria canaliculata by d'Orbigny (1835: 32), and is thus not an available name (see Cowie & Thiengo, 2003: 65; Hayes et al., 2012: 737). Although d'Orbigny (1835: 32) listed "Ampullaria gualtieri, Sowerby", no Sowerby is known to have used the name (see Cowie & Thiengo, 2003: 65; Petit, 2009: 120).

*Pomacea lineata* Spix in Wagner, 1827, is another species that is remarkably similar to *Pomacea canaliculata* in terms of conchological characteristics Although *Pomacea lineata* has been recorded as one of the alien apple snails of the region (e.g., Cheng, 1989; Maassen, 2001), its presence has thus far not been confirmed. We therefore regard the record of it from Singapore by Maassen (2001) to be a misidentification of *Pomacea canaliculata* sensu lato.

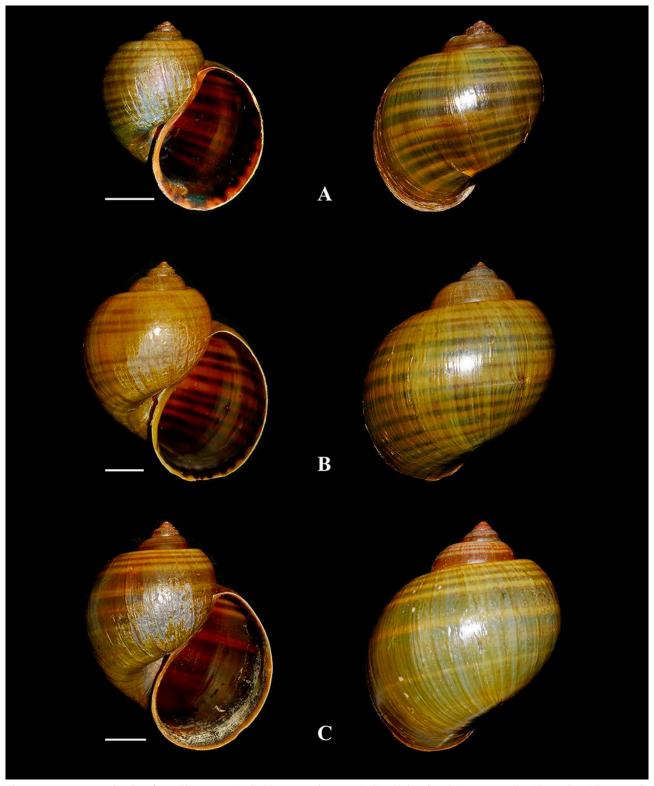


Fig. 7. *Pomacea canaliculata* from Singapore. A–C, Singapore Quarry (A, SH  $40.2 \times$  SW 35.5 mm; B, SH  $52.7 \times$  SW 44.7 mm; C, SH  $56.5 \times$  SW 46.8 mm) (NTH). See Fig. 3 for location. Scale bars = 10 mm. (Photographs by: S. K. Tan).

## DISCUSSION

Two genera are found in Singapore—*Pila*, which is native to the Southeast Asian region, and *Pomacea*, originating from the Americas. They can easily be differentiated by their operculum, which is corneous, thin, and flexible in *Pomacea*, and calcareous and stiff in *Pila*. The New World *Pomacea* was introduced, mainly as a food resource and aquarium pets, into Asia where they have attained pest status; first into Taiwan in 1979, then subsequently into numerous countries in the region during the decade and half that followed (Halwart, 1994; Naylor, 1996; Joshi, 2007). In Singapore, the alien *Pomacea* has been established in Singapore for at least two decades (S. K. Tan et al., 2013).

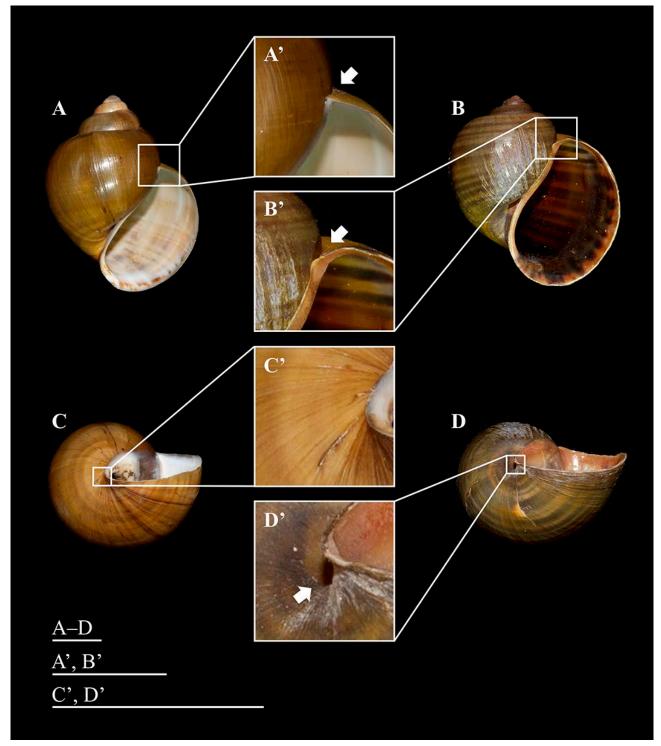


Fig. 8. A comparison of the diagnostic characteristics of the genera *Pila* and *Pomacea* from Singapore, exemplified by similarly sized shells of *Pila scutata* (A, A', C, C', SH 40.8 × SW 31.6 mm; Punggol Port Road) and *Pomacea canaliculata* (B, B', D, D', SH 40.2 × SW 35.5 mm; Singapore Quarry). Species of *Pila* lack a channeled suture (A', arrow) and an open umbilicus (C'), while species of *Pomacea* possess both a channeled suture (B', arrow) and an open umbilicus (D', arrow). Scale bars = 10 mm. (Photographs by: S. K. Tan).

The earliest record of an Ampullariidae in Singapore was of an unidentified *Ampullaria* species by Traill (1847). However, the identification of the species is impossible owing to the lack of further details and the unavailability of physical specimens. The first verifiable published instance of an ampullariid species from Singapore is *Pila scutata* by Nevill (1884; as *Ampullaria conica* var. *borneensis*). *Pila scutata* appears to have been very common and widespread in the region, and was widely eaten (W. S. S. van Benthem Jutting, 1956; Berry, 1974; Lim et al., 1978). It has also been introduced to some Pacific islands for food (Cowie & Hayes, 2012; as *Pila conica*). While its actual distribution in the Malay Peninsula has never been mapped in detail, *Pila scutata* is probably the commonest ampullariid (T. van Benthem Jutting, 1931; Berry, 1974), and has always been considered native to Singapore (e.g., P. K. L. Ng, 1991; S. K. Tan et al., 2012, 2013). Conversely, it is likely that the population of living *Pila ampullacea* observed in the

vicinity of Lower Peirce Reservoir in the 1970s represented an introduced (or escaped) population as they occurred only in ponds of aquatic plant farmers (H. E. Ng, pers comm.). The species is also known to be common only in the northern states of Peninsular Malaysia (Annandale, 1921; Berry, 1974), although it is also found in adjacent Sumatra and Java (T. van Benthem Jutting, 1931; W. S. S. van Benthem Jutting, 1956). However, with the rapid development of the area and destruction of the ponds where *Pila ampullacea* was last found in Singapore, the question of whether it represents a native component of Singapore's malacofauna is unlikely to be resolved.

The non-native ampullariids, *Pomacea canaliculata* and *Pomacea maculata* have both been introduced extensively worldwide, mostly as food, and also via the aquarium trade (including accidental introduction with ornamental aquatic plants) (Cowie & Hayes, 2012). The presence of both species in Singapore have been confirmed by our preliminary investigations (unpub. data). However, we cannot, as yet, map the specific distribution and occurrence of the two with confidence because of their remarkably similar shell characteristics, as well as the likelihood of sympatric occurrence. Confirmation with molecular methods is thus preferred to properly establish the specific identity and species composition in localities around Singapore where these snails occur. Molecular sequencing of local populations of *Pomacea* has yet to be carried out extensively. Hybridisation of the two species in their invaded range has also been suggested by Matsukura et al. (2013), which would render identification based on shell morphology impossible. The hybridising of two supposedly distinct species has also thrown a spanner into the works attempting to clarify the already confused taxonomy of ampullariids as the home ranges of the two are supposed overlap considerably (see Hayes et al., 2012). There also remains a possibility that more taxa belonging to this species-group than the currently recognised two have been introduced into Asia. Further studies are needed to answer these questions.

The aquarium trade is believed to be the main pathway for the introduction of *Pomacea* species to Singapore (Yeo & Chia, 2010), and both of the already established *Pomacea* species are still available in the local aquarium trade to date (pers. obs.; R. C. Joshi, pers. comm.). *Pomacea* has also been cultivated in Singapore, apparently for human consumption, by the Agri-Food and Veterinary Authority (AVA) from at least the mid-1990s (C. C. A. Tan & Ho, 2001). The snails are, however, not commonly eaten in Singapore today, although the cultured golden varieties are occasionally available at local seafood restaurants (Fig. 9). Two other species of non-native Ampullariidae, *Pomacea diffusa* Blume, 1957, and *Marisa cornuarietis* (Linnaeus, 1758), are also imported for sale in the local aquarium trade (see Fig. 10). Although neither has been recorded in the wild to date, both species have been introduced beyond their native ranges (Cowie, 1993, as *Pomacea bridgesii* [see Hayes et al., 2008]; Rawlings et al., 2007; Hayes et al., 2008), and may potentially be introduced into Singapore in the future.



Fig. 9. Pomacea sp. (possibly Pomacea maculata) being sold at a local restaurant. (Photograph by: S. K. Tan).

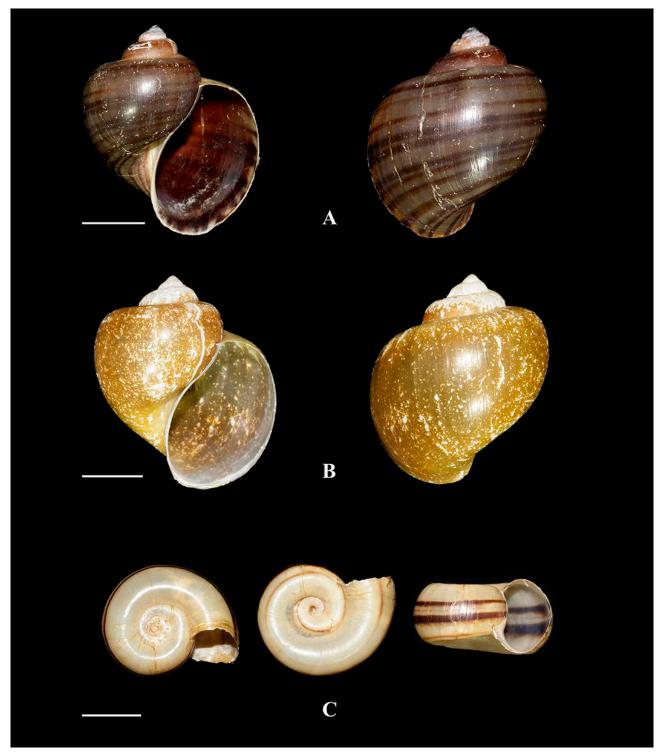


Fig. 10. Two ampullariids available from the local aquarium retail shops: A, B, *Pomacea diffusa* (A, SH  $39.9 \times SW$  28.6 mm; B, SH  $34.8 \times SW$  29.8 mm) (NTH); C, *Marisa cornuarietis* (SH  $12.6 \times SW$  23.5 mm) (NTH) (from left to right: apical, umbilical and apertural views). Scale bars = 10 mm. (Photographs by: S. K. Tan).

In Singapore, predation on *Pomacea* by *Anastomus oscitans*, a species of stork that specialises on molluscan prey, was recently reported (B. W. Low et al., 2013). Although *Pomacea* eggs contain anti-predatory chemicals (Dreon et al., 2010), some insects and terrestrial snails are apparently able to feed on the eggs (T. H. Ng & S. K. Tan, 2011). Predation pressure is however probably negligible, and *Pomacea* has successfully spread throughout Singapore over the past two decades (S. K. Tan et al., 2013). It is often among the first molluscs to colonise newly-created, freshwater habitats (pers. obs.), but their mode of dispersal is poorly understood. Accidental transport via human activities is thought to be the most likely reason.

The presence of non-native ampullariids should be regarded as a problem of utmost concern for conservation reasons since they are known to negatively impact native ecosystems, and associated flora and fauna (Anderson, 1993; Naylor, 1996; Cowie, 2002; Carlsson et al., 2004; T. S. Wood et al., 2006). The only extant *Pila* species in Singapore, *Pila* 

scutata, has apparently been dwindling since the introduction of the South American *Pomacea* species (S. K. Tan & Yeo, 2010; S. K. Tan et al., 2013). Similar observations of native ampullariids being replaced by their non-native cousins have also been made in other countries (e.g., Halwart, 1994; Thaewnon-ngiw et al., 2004; Marwoto & Isnaningsih, 2011). It is thus vital for the taxonomy, ecology, and biogeography of Southeast Asian ampullariids to be better studied before they are replaced by the introduced *Pomacea* species.

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#### LITERATURE CITED

Alderson, E. G., 1925. Studies in Ampullaria. Heffer & Sons Ltd., Cambridge. xx + 102 pp., 19 pls.

Anderson, B., 1993. The Philippine snail disaster. The Ecologist, 23: 70–72.

Annandale, N., 1921. The apple-snails of the Malay Peninsula. Journal of the Federated Malay States Museums, 10: 193-196.

Benthem Jutting, T. van, 1931. Notes on freshwater Mollusca from the Malay Archipelago. Treubia, 13: 5-14.

Benthem Jutting, T. van, 1937. Non marine Mollusca from fossil horizons in Java with special reference to the Trinil fauna. *Zoologische Mededelingen*, **20**: 83–180.

Benthem Jutting, W. S. S. van, 1956. Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. V. Critical revision of the Javanese freshwater gastropods. *Treubia*, 23: 259–477.

Berry, A. J., 1974. The anatomy of West Malaysian snails of parasitological significance. Malayan Nature Journal, 27: 131-165.

Blanford, W. T., 1903. Notes on Mr. W. M. Daly's collections of land and fresh-water Mollusca from Siam. *Proceedings of the Malacological Society of London*, **5**: 274–284.

Blume, W., 1957. Eine bis heute unbekannta Interart von Pomacea bridgesi Rve. Opuscula Zoologica, 1: 1-2.

Brandt, R. A. M., 1974. The non-marine aquatic Mollusca of Thailand. Archiv für Molluskenkunde, 105: i-iv, 1-423.

Carlsson, N. O. L., C. Brönmark & L.-A. Hansson, 2004. Invading herbivory: The golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology*, **85**: 1575–1580.

Chan, S. Y., 1996. Some freshwater gastropods of Singapore. Of Sea and Shore, 18: 184–187.

Cheng, E. Y., 1989. Control strategy for the introduced snail, *Pomacea lineata*, in rice paddy. In Henderson, I. (ed.), *Slugs and Snails in World Agriculture. British Crop Protection Council Monograph 41*. BCPC, Thornton Heath, UK. Pp. 69–73.

Chou, L. M., P. K. L. Ng & K. K. P. Lim, 1994. Animalia. In: Wee, Y. C. & P. K. L. Ng (eds.), A First Look at Biodiversity in Singapore. National Council on the Environment, Singapore. Pp 70–106.

Dall, W. H., 1904. Notes on the genus Ampullaria. Journal of Conchology, 11: 50-55.

Goh, B. P. L., N. S. Sodhi, D. Li, S. H. Ho & P. K. L. Ng, 2002. A Guide to Urban Creatures. Singapore Science Centre, Singapore. 160 pp.

Coan, E. V., A. R. Kabat & R. E. Petit, 2013. Annex 2: collation of the *Systematisches Conchylien-Cabinet* (1837–1920). In: Coan, E. V. & A. R. Kabat (eds), 2,400 Years of Malacology. Tenth Edition. American Malacological Society, USA. 89 pp.

Cowie, R. H., 1993. Identity, distribution and impacts of introduced Ampullariidae and Viviparidae in the Hawaiian Islands. *Journal of Medical and Applied Malacology*, **5**: 61–67.

Cowie, R. H., 1997. Case 2996. *Pila* Röding, 1798 and *Pomacea* Perry, 1810 (Mollusca, Gastropoda): Proposed placement on the Official List, and Ampullariidae Gray, 1824: proposed confirmation as the nomenclaturally valid synonym of Pilidae Preston, 1915. *Bulletin of Zoological Nomenclature*, **54**: 83–88.

Cowie, R. H., 2002. Apple snails as agricultural pests: Their biology impact and management. In: Barker, G. M. (ed.), *Mollusca as Crop Pests*. CAB international, Wallingford, UK. Pp. 145–192.

Cowie, R. H. & K. A. Hayes, 2012. Apple snails. In: Francis, R. A. (ed.), A Handbook of Global Freshwater Invasive Species. Earthscan, Oxon. Pp. 207–221.

Cowie, R. H. & V. Héros, 2012. Annotated catalogue of the types of Ampullariidae (Mollusca, Gastropoda) in the Muséum national d'Histoire naturelle, Paris, with lectotype designations. *Zoosystema*, **34**: 793–824.

Cowie, R. H., A. R. Kabat & N. L. Evenhuis, 2001. Case 3175. Ampullaria canaliculata Lamarck, 1822 (currently Pomacea canaliculata; Mollusca, Gastropoda): Proposed conservation of the specific name. Bulletin of Zoological Nomenclature, 58: 13–18

Cowie, R. H. & S. C. Thiengo, 2003. The apple snails of the Americas (Mollusca: Gastropoda: Ampullariidae: *Asolene*, *Felipponea*, *Marisa*, *Pomacea*, *Pomella*): A nomenclatural and type catalog. *Malacologia*, **45**: 41–100.

de Montfort, P. D., 1810. Conchyliologie systématique, et classification méthodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage

Clements, R., L. P. Koh, T. M. Lee, R. Meier & D. Li, 2006. Importance of reservoirs for the conservation of freshwater molluscs in a tropical urban landscape. *Biological Conservation*, **128**: 136–146.

- destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. Tome second. F. Schoell, Paris. [3] + 676 pp.
- Dreon, M. S., S. Ituarte & H. Heras, 2010. The role of the proteinase inhibitor ovorubin in apple snail eggs resembles plant embryo defense against predation. *PLOS One*, **5**: e15059.
- Ghosh, E., 1929. Papers on Malayan aquatic biology: Notes on some freshwater molluscs. *Journal of the Federated Malay States Museums*, **14**: 388–396.
- Goh, B. P. L., N. S. Sodhi, D. Li, S. H. Ho, & P. K. L. Ng, 2002. A Guide to Urban Creatures. Singapore Science Centre, Singapore. Pp. 103–104.
- Gray, J. E., 1824. On some new species of Ampullariadae. Philosophical Magazine and Journal, 63(312): 274-277.
- Halwart, M., 1994. The golden apple snail *Pomacea canaliculata* in Asian rice farming systems—Present impact and future threat. *International Journal of Pest Management*, **40**: 1–8.
- Hayes, K. A., R. C. Joshi, S. C. Thiengo & R. H. Cowie, 2008. Out of South America: Multiple origins of non-native apple snails in Asia. *Diversity and Distributions*, **14**: 701–712.
- Hayes, K. A., R. H. Cowie & S. C. Thiengo, 2009. A global phylogeny of apple snails: Gondwanan origin, generic relationships, and the influence of outgroup choice (Caenogastropoda: Ampullariidae). *Biological Journal of the Linnean Society*, **98**: 61–76.
- Hayes, K. A., R. H. Cowie, S. C. Thiengo & E. E. Strong, 2012. Comparing apples with apples: Clarifying the identities of two highly invasive Neotropical Ampullariidae (Caenogastropoda). *Zoological Journal of the Linnean Society*, **166**: 723–753.
- Hylton Scott, M. I., 1948. On mollusks from Northwestern Argentina. Acta Zoologica Lilloana, 6: 241-274.
- ICZN (International Commission on Zoological Nomenclature), 1999a. Opinion 1913. *Pila* Röding, 1798 and *Pomacea*, Perry, 1810 (Mollusca, Gastropoda) placed on the *Official List*, and Ampullariidae Gray, 1824: confirmed as the nomenclaturally valid synonym of Pilidae Preston, 1915. *Bulletin of Zoological Nomenclature*, **56**, 74–76.
- ICZN (International Commission on Zoological Nomenclature), Opinion 1997. *Ampullaria canaliculata* Lamarck, 1822 (currently *Pomacea canaliculata*; Mollusca, Gastropoda): specific name conserved. *Bulletin of Zoological Nomenclature*, **59**: 137–138.
- ICZN (International Commission on Zoological Nomenclature), 1999b. *International Code of Zoological Nomenclature*. Fourth Edition. The International Trust for Zoological Nomenclature, London. xxix + 306 pp.
- Johnson, D. S., 1973. Freshwater life. In: Chuang, S. H. (ed.), Animal Life and Nature in Singapore. Singapore University Press, Singapore. Pp. 103–127.
- Joshi, R. C., 2007. Problems with the management of the golden apple snail *Pomacea canaliculata*: An important exotic pest of rice in Asia. In: Vreysen, M. J. B., A. S. Robinson & J. Hendrichs (eds.), *Area-wide Control of Insect Pests*. Springer, Dordrecht, The Netherlands. Pp. 257–264.
- Khoo, H. W., S. L. Yang & C.-J. Goh, 1977. A preliminary limnological study of Seletar Reservoir. *Journal of the Singapore National Academy of Science* 6: 1–12.
- Kobelt, 1911–1915. Die Gattung *Ampullaria*. Abbildungen nach der Natur mit Beschreibungen. Neue Folge. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*, **1**(20): 1–236, pls. 22–79. [Published in parts (after Coan et al., 2013: 22): pp. 1–24, pls. 22–27 (1911); pp. 25–104, pls. 28–44 (1912); pp. 105–200, pls. 45–68 (1913); pp. 201–216, pls. 69–74 (1914); pp. 217–236, pls. 75–79 (1915)].
- Lamarck, J. B. P. A. de, 1799. Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveaux. *Mémoires de la Société d'Histoire naturelle de Paris*, 1: 63–101.
- Lamarck, J. B. P. A. de, 1804. Suite des mémoires sur les fossiles des environs de Paris. *Annales du Muséum National d'Histoire naturelle*, 5(25): 28–36.
- Lamarck, J. B. P. A. de, 1822a. Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la détermination des caractères essentiels de l'Animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la Zoologie. Tome sixième. 2<sup>me</sup>, partie. L'Auteur, Paris. 232 pp. [Published Apr.1822 (title-page)].
- Lea, I., 1856. Description of thirteen new species of exotic Peristomata. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **8**: 1–6.
- Lim, B. L., L. F. Yap, M. Krishnansamy, P. Ramachandran, & M. Sharif, 1978. Freshwater snail consumption and Angiostrongyliasis in Malaya. *Tropical and Geographical Medicine*, **30**: 241–246.
- Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio Decima, Reformata. Laurentii Salvii, Holmiae [= Stockholm], 823 pp.
- Low, B. W., K. S. Lim, F. Yap, T. K. Lee, K. C. Lim & D. L. Yong, 2013. First record of the Asian openbill, *Anastomus oscitans* (Aves: Ciconiidae) in Singapore, with notes on foraging and dispersive movements. *Nature in Singapore*, **6**: 25–29.
- Low, M. E. Y., S. K. Tan, & T. H. Ng, 2013. *Pila conica* (Wood, 1828), or *Pila scutata* (Mousson, 1848)? The correct name for the native apple snail of Singapore (Gastropoda: Ampullariidae). *Nature in Singapore*, **6**: 55–60.
- Maassen, W. 2001. A preliminary checklist of the non-marine mollusks of Malaysia. 'A hand list'. *De Kreukel*, Extra Editie, **2001**: 1–162.
- Marwoto, R. M. & N. R. Isnaningsih, 2011. Notes on the distribution of the invasive freshwater snail *Pomacea canaliculata* (Lamarck, 1822) and *P. insularum* (d'Orbigny, 1835) in Indonesia. *Biotropia*, **18**: 123–128.
- Matsukura, K., M. Okuda, K. Kubota & T. Wada, 2008. Genetic divergence of the genus *Pomacea* (Gastropoda: Ampullariidae) distributed in Japan, and a simple molecular method to distinguish *P. canaliculata* and *P. insularum. Applied Entomology and Zoology*, **43**: 535–540.
- Matsukura, K., M. Okuda, N. J. Cazzaniga & T. Wada, 2013. Genetic exchange between two freshwater apple snails, *Pomacea canaliculata* and *Pomacea maculata* invading East and Southeast Asia. *Biological Invasions*, **15**: 2039–2048.
- Morgan, J. de, 1885. Mollusques terrestres & fluviatiles du royaume de Perak et des pays voisins (presqu'Ile Malaise). *Bulletin de la Societe Zoologique de France*, **10**: 353–428.
- Mousson, A., 1848. Über die Land- und Süsswassermollusken von Java. Mittheilungen der Naturforschende Gesellschaft in Zürich, 1(3): 264–273.
- Naylor, R., 1996. Invasions in agriculture: Assessing the cost of the golden apple snail in Asia. Ambio, 25: 443–448.

- Nevill, G., 1877. Catalogue of Mollusca in the Indian Museum, Calcutta. Part II.—Fascicule E. By Order of the Trustees [of the Indian Museum], Calcutta. iv+42.
- Nevill, G., 1884. *Hand List of Mollusca in the Indian Museum, Calcutta. Part II. Gastropoda: Prosobranchia–Neurobranchia (contd.)*. By Order of the Trustees [of the Indian Museum], Calcutta. x + 306 pp.
- Ng, P. K. L. (ed.), 1991. A Guide to Freshwater Life in Singapore. Singapore Science Centre, Singapore. 158 pp.
- Ng, P. K. L., L. M. Chou & T. J. Lam, 1993. The status and impact of introduced freshwater animals in Singapore. *Biological Conservation*, **64**: 19–24.
- Ng, T. H. & S. K. Tan, 2011. Observations of land snails feeding on eggs of Pomacea canaliculata. Nature in Singapore, 4: 79-83.
- d'Orbigny, A., 1835. Synopsis terrestrium et fluviatilium molluscorum, in suo per Americam meridionalem itinere. *Magasin de Zoologie*, **5**(61–64): 1–44.
- Perera, G. & J. G. Walls, 1996. Apple Snails in the Aquarium. T. F. H. Publications, USA. 121 pp.
- Perry, G., 1810–1811. Arcana; or the Museum of Natural History: Containing the Most Recent Discovered Objects. James Stratford, London. 84 pls. with unnumbered text. [Published in parts (dates of publication from Petit, 2003: 66): pls. 1–48 (1810); pls. 49–84 (1811)].
- Perry, G., 1811. Conchology or the Natural History of Shells: Containing a New Arrangement of the Genera and Species, Illustrated by Coloured Engravings Executed from the Natural Specimens, and Including the Latest Discoveries. W. Miller, London. 4 + [61] pp., 61 pls.
- Petit, R. E., 2003. George Perry's molluscan taxa and notes on the editions of his Conchology of 1811. Zootaxa, 377: 1–72.
- Philippi, R. A., 1849. Centuria tertia Testaceorum novorum (Contin.). Zeitschrift für Malakozoologie, 5: 186–192.
- Philippi, R. A., 1851–1852. Die Gattung *Ampullaria*. In: Abbildungen nach der Natur mit Beschreibungen. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*, **1**(20): 1–74, pls. A, 1–21. [Published in parts (dates of publication after Coan et al., 2013: 21): pp. 1–24, pls. A, 1–15 (1851); pp. 25–74, pls. 6–21 (1852)]
- Ponniah, A. J., 1962. Studies on Some Non-Marine Aquatic Gastropods of Singapore Island, with a Note on Five Species Collected from Malacca. Unpublished BSc. Honours Thesis, Department of Zoology, University of Singapore. 58 pp.
- Preston, H. B., 1915. The Fauna of British India, including Ceylon and Burma. Mollusca. (Freshwater Gastropoda & Pelecypoda). Taylor and Francis, London. xiv + 244 pp.
- Quoy, J. R. C. & J. P. Gaimard, 1834–1835. Animaux mollusques. Voyage de découvertes de l'Astrolabe execute par odre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M. J. Dumont d'Urville. Zoology. Tome troisième. J. Tatsu, Paris. 954 pp., 45 pls. [Published in two parts (dates of publication from Sherborn & Woodward, 1901: 333): pp. 1–366 (1834); pp. 367–954 (1835); plates issued in a separate Atlas].
- Rawlings, T. S., K. A. Hayes, R. H. Cowie & T. M. Collins, 2007. The identity, distribution, and impacts of non-native apple snails in the continental United States. *BMC Evolutionary Biology*, 7: 97.
- Reeve, L. A., 1856. Monograph of the genus *Ampullaria*. *Conchologia iconica: or, Illustrations of the Shells of Molluscous Animals*, **10**: [1–31], pls. 1–28.
- Roissy, F. de, 1805. Histoire naturelle genérale et particuliere des Mollusques, animaux sans vertèbres et a sang blanc. Ouvrage faisant suite aux ouvres de Leclerc de Buffon, et partie du Cours complet d'histoire naturelle rédigé par C. S. Sonnini, member de plusieurs Sociétés savants. Tome cinquième. F. Dufart, Paris. 450 pp., pls. 51–56.
- Röding, P. F., 1798. Museum Boltenianum sive catalogues cimeliorum e tribus regnis naturae. Pars secunda continens conchylia sive testacea univalvia, bivalvia et multivalvia. Johan. Christi. Trappii, Hamburgi [= Hamburg]. viii + 199 pp.
- Sherborn, C. D. & B. B. Woodward, 1901. Dates of Publication of the zoological and botanical portions of some French voyages.—
  Part. II. Ferret and Galinier's 'Voyage en Abyssinie'; Lefebvre's 'Voyage en Abyssinie'; 'Exploration scientifique de l'Algérie';
  Castelnau's 'Amerique du Sud'; Dumont d'Urville's 'Voyage de l'Astrolabe'; Laplace's 'Voyage sur la Favorite'; Jacquemont's
  'Voyage dans l'Inde'; Tréhouart's 'Commission scientifique d'Islande'; Cailliaud, 'Voyage à Méroe'; 'Expédition scientifique de
  Morée'; Fabre, 'Comission scientifique du Nord'; Du Petit-Thouars, 'Voyage de la Vénus'; and on the dates of the 'Faune
  Française.'. Annals and Magazine of Natural History, Series 7, 8(46): 333–336.
- Swainson, W., 1823. The specific characters of several undescribed shells. The Philosophical Magazine and Journal, 62: 401-403.
- Tan, C. C. A. & H. F. Ho, 2001. A parasitological survey of apple snails (*Pomacea* species) in Singapore. Singapore Journal of Primary Industries, 29: 27–29.
- Tan, S. K. & H. P. M. Woo, 2010. A Preliminary Checklist of the Molluscs of Singapore. Raffles Museum of Biodiversity Research, National University of Singapore, Singapore, 78 pp.
- Tan, S. K. & D. Yeo, 2010. The softies. In: Yeo, D. C. J., L. K. Wang & K. K. P. Lim (eds.), *Private Lives. An Exposé of Singapore's Freshwaters*. Raffles Museum of Biodiversity Research, Singapore. Pp. 94–101.
- Tan, S. K., S. Y. Chan & G. R. Clements, 2012. A Guide to Snails and Other Non-Marine Mollusca of Singapore. Singapore Science Centre, Singapore, 176 pp.
- Tan, S. K., Y.-L. Lee & T. H. Ng, 2013. The status of *Pila scutata* (Gastropoda: Ampullariidae) in Singapore. *Nature in Singapore* 6: 135–141.
- Taylor, D. W., 2003. Introduction to Physidae (Gastropoda: Hygrophila); biogeography, classification, morphology. *Revista de Biologia Tropical (International Journal of Tropical Biology and Conservation)*, **51**: 1–287.
- Thaewnon-ngiw, B., S. Klinbunga, K. Phanwichien, N. Sangduen, N. Lauhachinda & P. Menasveta, 2004. Genetic diversity and molecular markers in introduced and Thai native apple snails (*Pomacea* and *Pila*). *Journal of Biochemistry and Molecular Biology*, 37: 493–502.
- Traill, W., 1847. A few remarks on conchology and malacology: Comprising brief notices of some of the more remarkable 'Testacea' in Singapore and its neighbourhood; with an appended catalogue of Singapore shells arranged in conformity with 'Lamarck's System'. *Journal of the Indian Archipelago and Eastern Asia*, 1: 225–241. [Reprinted as Traill (1858)].
- Traill, W., 1858. A few remarks on conchology and malacology: Comprising brief notices of some of the more remarkable 'Testacea' in Singapore and its neighbourhood; with an appended catalogue of Singapore shells arranged in conformity with 'Lamarck's System'. In: Balfour, F. (ed.), The Supplement to the Cyclopaedia of India and of Eastern and Southern Asia, Commercial, Industrial and Scientific; Products of the Mineral, Vegetable and Animal Kingdoms, Useful Arts and Manufactures. C. Graves, Madras. Pp. 169–175. [Reprint of Traill (1847)]

- Wagner, J. A., 1827. Testacea fluviatilia quae in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augustissimi suscepto collegit et pingenda curavit Dr. J. B. de Spix, quondam ordinis regii coronæ Bavaricæ civilis eques, academiæ scientarum Bavaricæ socius ordinarius, musei regii zoologici, zootomici et ethnographici conservator rel. C. Wolf, Monachii [= Munich], iv + [ii] + 36 p., 29 pls.
- Wheeler, W. M., 1885. Catalogue of the Specimens of Mollusca for Sale by Henry A. Ward, Ward's Natural History Science Establishment, Rochester, N. Y. Judson J. Withall, Book and Job Printer, Rochester. [8] + 120 + [1] pp.
- Wee, Y. C., 1992. Proposed Golf Course At Lower Peirce Reservoir—An Environmental Impact Assessment. Nature Society, Singapore. 80 pp.
- Wood, T. S., P. Anurakpongsatorn, R. Chaichana, J. Mahujchariyawong & T. Satapanajaru, 2006. Heavy predation on freshwater bryozoans by the golden apple snail, *Pomacea canaliculata* Lamarck, 1822 (Ampullariidae). *The Natural History Journal of Chulalongkorn University*, 6: 31–36.
- Wood, W., 1828. Supplement to Index Testaceologicus or A Catalogue of Shells, British and Foreign. W. Wood, London. iv + [1] + 59 pp., 8 pls.
- Yeo, D. C. J. & C. S. W. Chia, 2010. Introduced species in Singapore: An overview. COSMOS, 6: 23-37.