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# The temperate Australasian genus *Papawera* Oskars and Malaquias, 2019 (Gastropoda: Cephalaspidea: Haminoeidae), with a redescription of *P. zelandiae* and *P. maugeansis*

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**ABSTRACT**

The genus *Papawera* includes two species of haminoeid snails found only in temperate waters of New Zealand and southeastern Australia. In this work, we redescribe the *Papawera* species based on characters of their external morphology, shells, and anatomical features such as radulae, jaws, gizzard plates, and male reproductive systems, using for the first time, scanning electron microscopy. A multi-locus phylogenetic hypothesis and the species delimitation method Automatic Barcode Gap Discovery based on DNA sequences of the cytochrome *c* oxidase subunit I gene were used to corroborate species status. The type species of the genus, *P. zelandiae*, is restricted to New Zealand and *P. maugeansis* is only known from South Australia, Victoria, and Tasmania. These species are easily distinguished externally by the shape of the shell, colouration of the living animal, and morphology of the cephalic shield. Anatomically they have differences in the number of marginal teeth, distribution of rods in the gizzard plates, and anatomy of the fundus in the male reproductive system.

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Anatomy; biodiversity; bubble shells; DNA barcoding; Heterobranchia; Mollusca

## Introduction

The genus *Papawera* Oskars and Malaquias, 2019 was erected to accommodate two haminoid species of temperate affinity distributed across southern Australia and northern New Zealand (Oskars and Malaquias 2019), namely *Papawera maugeansis* (Burn, 1966a; originally *Haminoea maugeansis*) and *P. zelandiae* (Gray 1843; originally *Bulla zelandiae*). The species *P. maugeansis* is restricted to southeastern Australia, where it occurs intertidally in tide pools on rocky platforms and subtidally on muddy seagrass beds (Burn 1966a, 1969; Hales 2010; Burn and Wilson 2011). *Papawera zelandiae* is endemic to New Zealand, where it is relatively common on intertidal and subtidal sheltered sandy-mud flats and on rocky shores with algae turfs (Rudman 1971a, 1971b; Powell 1979; Morley and Hayward 2015).

Despite the early description of *P. zelandiae* by Gray (1843) and its junior synonym *Haminea obesa* (Sowerby, 1868), the anatomy and ecology of this species was only

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studied much later. Rudman (1971a, 1971b) first described several anatomical features and its diet. Willan (1979), Hayward (1979) and Morley and Hayward (2015) also provided data on diet as well as ecological aspects such as habitat and distribution.

Burn (1966a) described the species *Haminoea maugeansis* from Victoria, South Australia, and Tasmania, based on the shell, external morphology, and several anatomical features of the digestive system (jaws, radula and gizzard plates) but only included a drawing of the shell and one row of the radula (Burn 1966a, p. 330, Figures 1, 2). Before the description of *H. maugeansis*, the name *Haminoea tenera* (Adams, 1850) was

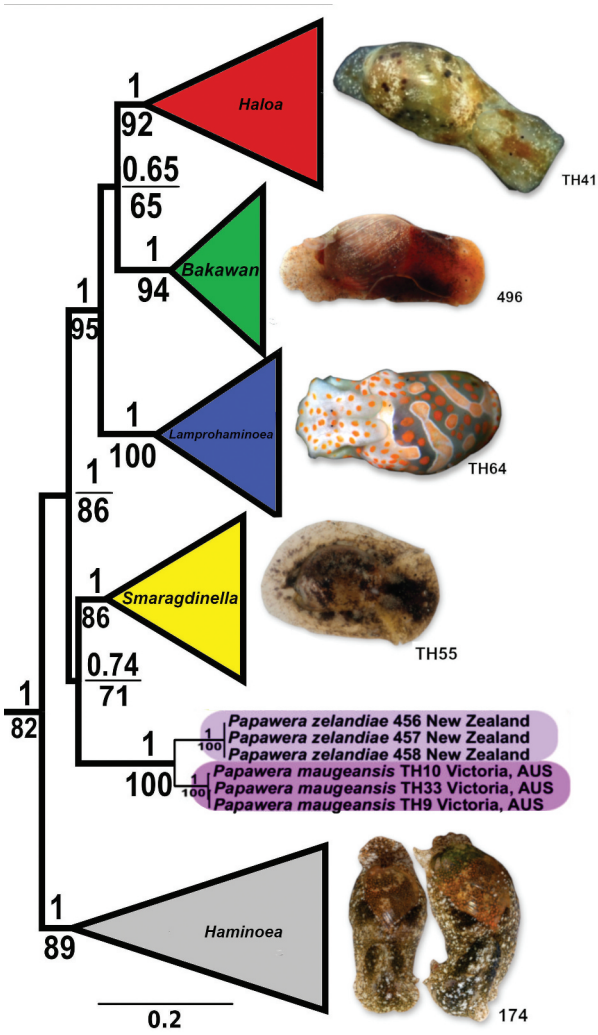


**Figure 1.** Bayesian phylogeny depicting relationships and species diversity of the genus *Papawera*. Hypothesis based on the combined analysis of the mitochondrial COI, 16S rRNA and 12S rRNA and nuclear 28S rRNA and Histone H3 genes. The tree is a composite based on Figures 1 and 2 from Oskars & Malaquias (2019). Values above branches are BI posterior probabilities and below branches are bootstrap values derived by ML (Oskars & Malaquias, 2019). Images of *Lamprohaminoea cymbalum*, Mozambique (TH64), courtesy of Y. Tibiriçá; *Bakawan rotundata*, Singapore (496), courtesy of K. Jensen; *Smaragdinella* cf. *sieboldi*, Mozambique (TH55), courtesy of Y. Tibiriçá; *Haminoea alfredensis*, South Africa, NHMUK 20070315 (174), courtesy of G. Branch and C. Griffiths.

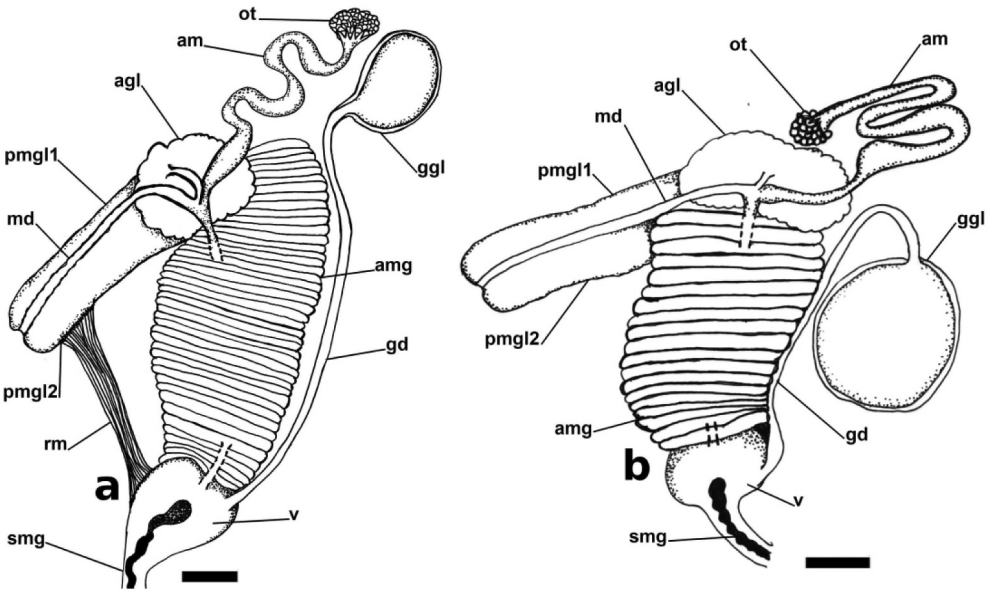


**Figure 2.** Female reproductive system. (a) *Papawera zelandiae*, Hokianga, Northland, New Zealand, (AM 79176, H = 11 mm). (b) *Papawera maugeansis*, Curlewis Reef, Clifton Springs, Victoria, Australia (ZMBN 125459 ex NVM F194630, H = 5.7 mm). Abbreviations: agl, albumen gland. am, ampulla. amg, anterior mucous gland. gd, gameloytic duct. ggl, gametolytic gland. md, medial duct. ot, ovotestis. pmgl1, posterior mucous gland lobe 1, pmgl2, posterior mucous gland lobe 2. rm, retractor muscle. smg, external seminal groove. v, vestibule. Scale bars: a, b = 0.5 mm.

often employed to refer to haminoeid snails from the southern states of Australia, mostly because the influential Australian naturalist George French Angas (1871) used this name for shells from New South Wales. Consequently, the binomen was largely adopted by many authors to refer to *Haminoea*-like shells in these Australian regions (e.g. Pritchard and Gatliff 1903; MacPherson and Gabriel 1962; Burn 1966a, 1966b; Jansen 1995).

Burn (1966a) maintained the species in the genus *Haminoea* Turton and Kingston 1830 but discussed possible different generic assignments. For example, he considered *Haloa* Pilsbry, 1921 because features of the shell matched Pilsbry's (1921) original description. These included the thick, reflected columellar lip separated by a furrow. Burn (1966a) also considered *Lamprohaminoea* Habe, 1952 (as described by Habe 1952; Kuroda and Habe 1952) because of the colouration of the animal – orange blotches combined with a smooth and polished shell.

Later Burn (1969, p. 68, fig. 1) illustrated a complete animal and the Hancock's organ and stated that the 'ribbed' Hancock's organ with its dorsal branches prevented the species from being included in *Lamprohaminoea*, which Er. Marcus and Burch (1965) showed to have a ridge-like Hancock's organ. Interestingly, Oskars and Malaquias (2019) found this organ to have relevant differences at the genus level. Notably, the presence of a Hancock's organ with a central ridge and prominent dorsal and ventral branches was considered by the authors an apomorphy of the genus *Papawera* (Oskars and Malaquias, 2019).

The anatomy of *P. zelandiae* and *P. maugeansis* is relatively well known thanks to the works by Rudman (1971a, 1971b) and Burn (1966a, 1969, 1974). However, modern techniques of

electron microscopy were never employed to look at certain details of the radula and gizzard plates and, the male reproductive system of *P. maugeansis* has never been studied. In this work, we use the molecular phylogenetic framework by Oskars and Malaquias (2019) to discuss the systematics of the genus and we redescribe its two species based on fine anatomical work, scanning electron microscopy, and DNA barcoding.

## Materials and methods

### *Taxa sampling and morpho-anatomical work*

Specimens were obtained by loan from the collections of The Australian Museum, Sydney, Australia (AMS), Museum Victoria, Melbourne, Victoria, Australia (NMV), The Auckland War Memorial Museum Tāmaki Paenga Hira, Aukland, New Zealand (AM) and The Natural History Museum, London, United Kingdom (NHMUK).

The body of the animal was gently separated from the shell with the aid of forceps. The female reproductive systems, male reproductive systems, gizzards, and buccal bulbs were dissected out of the animals under a stereo-microscope. Shells were measured (total height, H) and imaged with a DSLR camera equipped with macrolens. The reproductive systems were drawn using a stereo-microscope fitted with a drawing tube. The gizzard and buccal bulb were dissolved in a solution containing 180 µl buffer ATL and 20 µl of proteinase K, incubated at 56°C for 4–6 hours to separate and dissolve tissue surrounding the gizzard plates, jaws, and radulae (protocol modified from Holznagel (1998) and Vogler (2013)) [buffer and enzymes were obtained from the Qiagen DNeasy® Blood and Tissue Kit, catalogue no. 69504]. Gizzard plates and jaws were critical-point dried to maintain natural shape and, together with radulae, were mounted on metallic stubs using carbon sticky tabs and coated with gold-palladium for scanning electron microscopy. All samples were scanned and imaged with a Zeiss Supra 55VP scanning electron microscope.

### *Phylogenetic analyses and molecular species delimitation*

In this work, the phylogenetic hypothesis generated by Oskars and Malaquias (2019) for the genus *Papawera* based on the combination of three mitochondrial genes (cytochrome *c* oxidase subunit I [COI] + 16S rRNA + 12S rRNA) and two nuclear genes (28S rRNA + Histone H3) was used as our framework for species recognition and relationships (Figure 1; see Oskars and Malaquias 2019 for methodological details). The DNA sequences of the COI gene used to estimate genetic distances and test species delimitation hypotheses were those included in Oskars and Malaquias (2019) (see Table 1).

COI uncorrected *p*-distances were calculated in MEGA 7 (Kumar et al. 2016) (Table 2). The species delimitation method Automatic Barcode Gap Discovery (ABGD; Puillandre et al. 2012) was employed to test species hypotheses by using default settings and three different models (Jukes-Cantor [JC69], Kimura TS/TV = 2.0 [K80], Simple Distance).

All figures were made in Inkscape 0.92 (Inkscape Team 2015) and Gimp 2.10 (Mattis et al. 1995; Natterer 2018).

**Table 1.** List of specimens used in the ABGD analyses including voucher and GenBank accession numbers.

| Species | DNA extract code | Locality | Voucher No. | COI |
|---|---|---|---|---|
| *Papawera maugeansis* (Burn 1966a) | TH9 | Shoreham Beach, Victoria, Australia | NMV F 209129 | MK473519 |
| *Papawera maugeansis* (Burn 1966a) | TH10 | Curlewis Reef, near Clifton Springs, Victoria, Australia | ZMBN 125458 (ex NVM F 112,423) | MK473517 |
| *Papawera maugeansis* (Burn 1966a) | TH33 | Inverloch, Town Area, Victoria Australia | ZMBN 125459 (ex NVM F 194630) | MK473518 |
| *Papawera zelandiae* (Gray 1843) | 456 | Waitemata harbour, north end of Eastern Beach, New Zealand | MA 119920 | MK473515 |
| *Papawera zelandiae* (Gray 1843) | 458 | Waitemata harbour, north end of Eastern Beach, New Zealand | MA 119920 | MK473516 |

**Table 2.** COI inter- and intra-specific uncorrected *p*-distances (%) calculated in MEGA 7.

| Specimens | 456 | 458 | TH10 | TH33 | | Intra-specific *p*-dist |
|---|---|---|---|---|---|---|
| ***Papawera zelandiae* 456** | - | | | | | |
| ***Papawera zelandiae* 458** | 0.3 | - | | | ***P. zelandiae*** | 0.3 |
| ***Papawera maugeansis* TH10** | 13.8 | 13.8 | - | | | |
| ***Papawera maugeansis* TH33** | 13.5 | 13.5 | 0.9 | - | | |
| ***Papawera maugeansis* TH9** | 13.6 | 13.6 | 1.1 | 0.2 | ***P. maugeansis*** | 0.2–1.1 |

## Results

The phylogeny of *Papawera* (Oskars and Malaquias, 2019) suggests the presence of two species in this genus, which is corroborated by ABDG analysis using all three-distance methods (Figure S1). The minimum COI uncorrected *p*-distance between both species was 13.5% (Table 2).

### *Taxonomy*

Class **Gastropoda** Cuvier 1795
Sub-class **Heterobranchia** Burmeister 1837
Order **Cephalaspidea** P. Fischer 1883
Family **Haminoeidae** Pilsbry 1895
Genus ***Papawera*** Oskars and Malaquias 2019

*Bulla* (in part) – Gray 1843, p. 243.
*Haminea* (in part) – Pilsbry 1895, p. 365. Kobelt 1896, p. 118. E. A. Smith 1873, p. 5. Pritchard and Gatliff 1903: 217. Thompson 1976, p. 34, 45.
*Haminoea* (in part) – MacPherson and Gabriel 1962, p. 243. Burn 1966a, p. 330, 1966b, p. 266, 1969, p. 68. Rudman 1971a, p. 545, 1971b, p. 649. Burn 1974, p. 48. Powell 1979, p. 275. Willan 1979, p. 269. Jansen 1995, p. 86. Rudman 1999. Furneaux 2003. Rudman 2003. Burn 2006, p. 8. Rudman 2006. Eichler 2007. Rudman 2007. Hales 2010, p. 249. Burn and Wilson 2011. Burn 2015, p. 65. Morley and Hayward 2015, p. 57. Grove 2018.

### *Type species*

*Bulla zelandiae* Gray, 1843. Holotype untraceable; iconotype illustrated in Smith (1873, p. 5, Table 1, fig. 10).

### *Type locality*

New Zealand (Gray 1843).

### *Diagnosis*

Animal light grey, yellowish-grey or brown to nearly black; orange blotches and opaque white dots may be present. Cephalic shield, broad, shallowly or deeply bilobed; periocular area pigmented or unpigmented; always minute. Hancock organ ridge-like, with prominent dorsal and ventral branches. Shell oval to rounded; smooth with faint growth lines; whitish in colour; periostracum transparent to yellowish; aperture wide, tapering posteriorly, columella thick, separated from last whorl by short furrow; furrow covered by callus posteriorly. Radula formula 27–5.1.1.1.5–27; rachidian tricuspid, elongate, central cusp longer, lateral cusps reduced; outer lateral teeth hook shaped, smooth, decreasing in size outwardly; cusp of inner lateral slightly bulbous, tip pointed. Jaws semi-circular, rods slightly serrated on outer edge. Gizzard plates with 8–20 transverse ridges, top of ridges covered in minute rods, smooth in between ridges. Three gizzard bristled spines, resembling feather-like dusters inserted in raised triangular fleshy base. Reproductive system with oblong annulated prostate; short seminal duct, with semi-enclosed hollow duct; fundus semi-enclosed with glandular epithelium; thick, non-muscular atrium. Female reproductive system with elongate, lamellate anterior mucous gland; thick, blunted and indented bilobed posterior mucous gland, lobes separated by median duct; albumen gland globular with irregular surface, partially surrounding posterior mucous gland and ampulla; gametolytic gland, rounded (Gray 1843; Sowerby 1868; Pilsbry 1895; Burn 1966a, 1969, 1974. Rudman 1971a; Rudman 1971b, 1999, 2003, 2006, 2007; Furneaux 2003; Eichler 2007; Burn and Wilson 2011; Grove 2018).

### *Remarks*

The female reproductive system of *P. zelandiae* was found to be consistent with the description by Rudman (1971a, p. 552, fig. 7a). The system differs from that of taxa within the genera *Bakawan, Haloa*, and *Lamprohaminoea* by having a straight and shorter posterior mucous gland and a rounded albumen gland with an irregular surface. The female reproductive system of *P. maugeansis* was also consistent with *P. zelandiae*, only differing in the shape of the gametolytic gland, which is nearly twice the size in *P. maugeansis* (Figure 2a,b). A retractor muscle connecting the posterior mucus gland with the vagina was not observed in the studied specimens of *P. maugeansis.*

## ***Papawera zelandiae* (Gray 1843)**

Figures 2 (a), 3 (a–c), 4, 5

*Bulla zelandiae* Gray, 1843, p. 243.

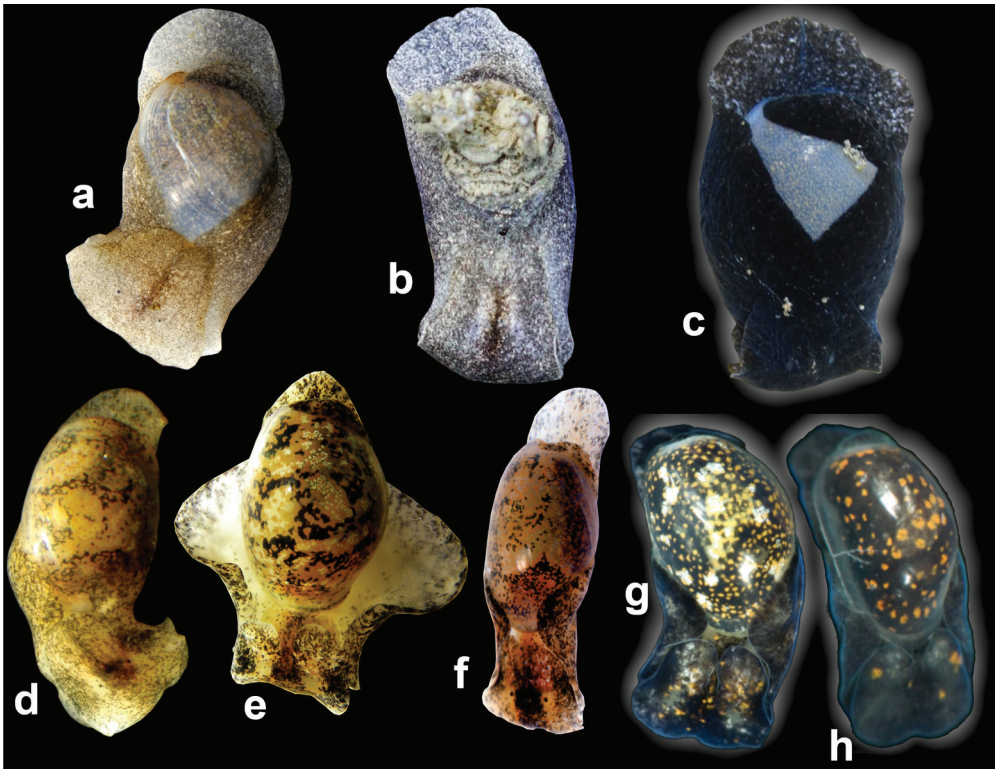


**Figure 3.** Live animals of *Papawera zelandiae* (Gray, 1843) (a–c), *Papawera maugeansis* (Burn, 1966a) (d–h). (a) Blockhouse Bay, Auckland, New Zealand (D. Crisp, CC BY-NC, iNaturalist.org). (b) Ambury Farm, Mangere Bridge, Auckland, New Zealand, courtesy of J. Geux. (c) Mahurangi West, North Island, New Zealand (D. Wilson, CC BY-NC, iNaturalist.org). (d) Hamers Haven, courtesy of J. Hales. (e) Inverloch, Victoria, Australia, courtesy of J. Hales. (f) Australia, Victoria, Westernport, Shoreham, (AMS c.105854, H = 11 mm), courtesy of G. Millen. (g) Victoria, Australia, courtesy of L. Altoff. (h) Cape Paterson, Inverloch, Victoria, Australia, courtesy of L. Altoff.

*Haminea zelandiae* – E. A. Smith 1873, p. 5. Kobelt 1896, p. 118. Suter 1913, p. 538.
*Haminea zelandica* (misspelled) – Pilsbry 1895, p. 373 (as synonym of *Haminea pemphix*).
*Haminea pemphix* (misspelled) – Pilsbry 1895, p. 373.
*Haminoea zelandiae* – Rudman 1971a, p. 545–559., 1971b, p. 647–675. Hayward 1979, p. 175. Powell 1979, p. 275. Willan 1979, p. 269. Rudman 1999. Furneaux 2003. Rudman 2003. Morley and Hayward 2015, p. 57.
*Haminea obesa* Sowerby II in Reeve 1868: no page numbers, pl. 2, fig.13.
*Papawera zelandiae* – Oskars and Malaquias 2019, p. 6.

### *Diagnosis*

Animal light grey or brown to completely black. Shell rounded, bulbous; smooth with faint growth lines; whitish-translucent in colour; periostracum transparent to yellowish; aperture wide, tapering posteriorly, columella thick, separated from last whorl by short furrow, furrow covered by callus posteriorly. Cephalic shield, broad, shallowly bilobed; large parapodial and pallial lobes covering nearly whole shell; periocular area pigmented

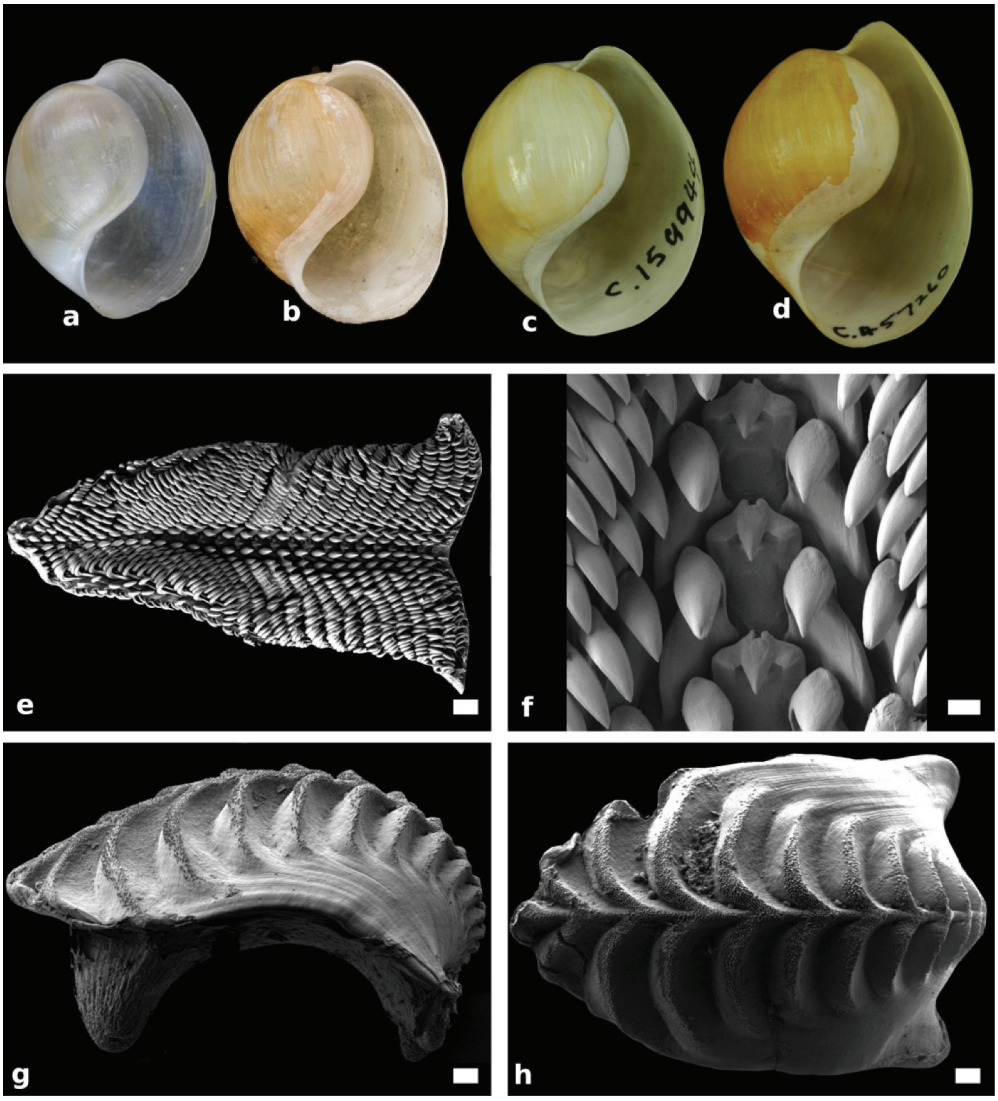


**Figure 4.** *Papawera zelandiae* (Gray, 1843). (a) apertural view of shell (AM 79,176, H = 11 mm; New Zealand). (b) apertural view of shell (NHMUK 20170322, *Haminea obesa*, holotype; H = 17 mm; New Zealand). (c) apertural view of shell (AMS C.159944, H = 22 mm; New Zealand). (d) apertural view of shell, (AMS c.457260, H = 27 mm; New Zealand). (e) SEM, whole radula (AM 119920, H = 11 mm; New Zealand). (f) SEM, detail of rachidian and first laterals in central part of radula (AM 119920, H = 11 mm; New Zealand). (g) Right lateral view of whole gizzard plate (AM 119920, H = 11 mm; New Zealand). (h) SEM, dorsal surface of whole gizzard plate (AM 119920, H = 11 mm; New Zealand). Scale bars: e, g, h = 100 µm. f = 0.15 µm.

or small, unpigmented. Hancock's organ thick ridge, with prominent dorsal and ventral branches. Radula formula 16–25 x 27–22.1.1.1.22–27; rachidian tricuspid, central cusp triangular, narrow, pointed; lateral cusps, reduced, barely raised form base. Gizzard plates with 8–16 transverse ridges; minute rods present along upper inner part of posterior side of ridges and rachis only; rachis present. Male reproductive system with oblong, tapering,

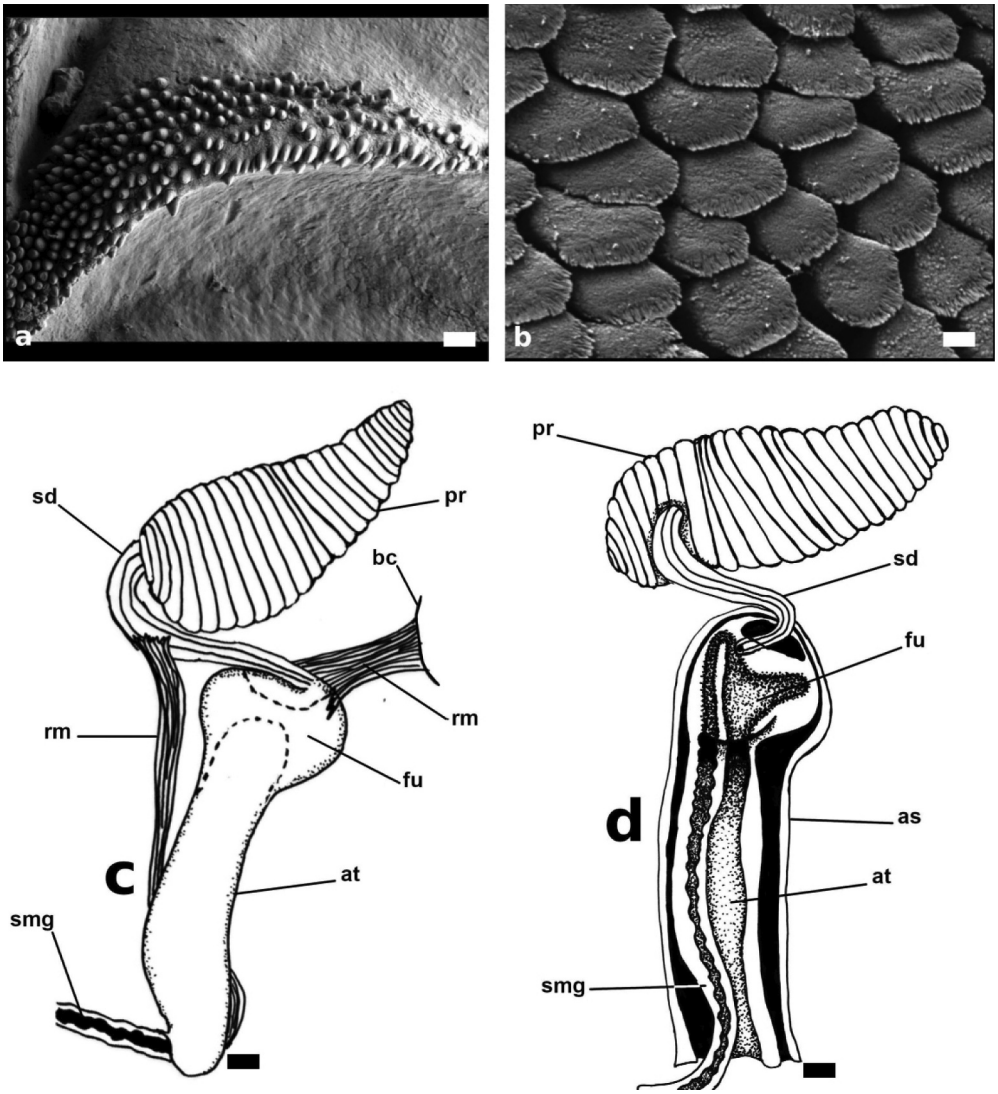


**Figure 5.** *Papawera zelandiae* (Gray, 1843). (a) SEM, detail of ridges of gizzard plate (AM 119920, H = 11 mm; New Zealand). (b) SEM, Detail of jaws (AM 119920, H = 11 mm; New Zealand). (c) detail of external male reproductive system (AM 119920, H = 11 mm; New Zealand). (d) detail of interior of ventrally opened atrium and fundus (AM 119920, H = 11 mm; New Zealand). Abbreviations: as, atrium sheet. at, atrium. bc, body cavity. fu, fundus. pr, prostate. sd, seminal duct. smg, seminal groove. rm, retractor muscles. Scale bars: a = 20 µm. F = 4 µm. c, d = 0.25 mm.

annulated prostate, fundus semi-enclosed with glandular epithelium. Distribution restricted to New Zealand (Gray 1843; Sowerby 1868; Pilsbry 1895b; Rudman 1971a; 1971b, 1999, 2003; Rudman 2006; Furneaux 2003).

### *Type locality*

New Zealand (Gray 1843). Holotype untraceable; iconotype illustrated in Smith (1873, p. 5, Table 1, fig. 10).

### *Material examined*

New Zealand, 1 shell, *Haminea obesa* Sowerby 1868, holotype, NHMUK 20170322; H = 17 mm. New Zealand, Auckland, Waitemata Harbour, 3 specimens (1 dissected, 3 sequenced), AM 119920, H = 11 mm. New Zealand, Waitemata Harbour, Herne Bay, AMS c.159944, H = 22 mm. New Zealand, Auckland, Manu Kau Harbour, 7 shells, NHMUK unnumbered, Col. Cornwallis in 1946, Stratton Collection Acc. No. 1894, H = 19 mm. New Zealand, Northland, Hokianga, 3 specimens (2 dissected), AM 79176, H = 11–14 mm. New Zealand, South Island, Awarua, 1 shell, AMS c.457260, H = 27 mm.

### *External morphology (Figure 3(a–c))*

Animal light grey or brown to nearly black. Cephalic shield, squarish, broad; shallowly bilobed, posterior part extending over shell. Eyes visible, periocular areas small, may be pigmented or unpigmented. Hancock's organ elongate, horizontal ridge with prominent dorsal and ventral branches. Parapodial lobes large, covering shell anteriorly and laterally. Rounded pallial lobe extends beyond apex.

### *Shell (Figure 4(a–d))*

Shell rounded, bulbous; smooth with faint growth lines. Whitish in colour; periostracum transparent to yellowish. Aperture wide, tapering posteriorly, columella thick, separated from last whorl by short furrow, furrow covered by callus posteriorly. Outer lip rounded; shoulder rounded.

### *Jaws (Figure 5(b))*

Semi-circular; shape of rods rounded with serrated edge.

### *Radula (Figure 4(e, f))*

Radular formula 28 × 25.1.1.1.25 (AM112090, H = 6 mm), 16 x 27–22.1.1.1.22–27 (Rudman 1971a, 1971b). Rachidian tricuspid; central cusp triangular, narrow, pointed; lateral cusps reduced, barely raised form base.

### *Gizzard plates (Figures 4(g, h) and 5(a))*

Rachis present, 8–16 transverse ridges; minute rods present along upper inner part of posterior side of ridges and rachis only.

### *Male reproductive system (Figure 5(c, d))*

Male reproductive system with oblong, tapering, annulated prostate, fundus semi-enclosed with glandular epithelium. Two retractor muscles; one connecting upper part of fundus to body cavity, the other attached to seminal duct and lower part of atrium.

### *Distribution*

The species is most frequently recorded around New Zealand's North Island and the northern parts of the South Island (Rudman 1971a; Rudman 1971b, 1999, 2003, 2006; Powell 1979; Furneaux 2003; Morley and Hayward 2015). However, the species also can be found on the southern coast of the South Island (based on one shell housed at the AMS c.457260), but to our knowledge, it has not been observed alive so far south.

### *Remarks*

This species occurs intertidally in sheltered areas in sandy-mud bottoms, seagrass and coralline algae turfs on rocky platforms, and has been reported to feed on green algae such as *Ulva, Enteromorpha* (= *Ulva*), *Cladophora* and *Rhizoclonium* and to scrape diatoms from seagrass leaves and sediment (Rudman 1971b, 2003; Hayward 1979; Willan 1979). During this study, we found the gut of one specimen filled with filamentous algae.

## ***Papawera maugeansis* (Burn, 1966)**

Figures 2 (b), 3 (d – h), 6, 7, 8

*Haminoea maugeansis* Burn 1966a, p. 330, 1969, p. 68, 1974, p. 8, 2006, p. 8 Eichler 2007. Rudman 2007. Hales 2010. p/ 249. Burn and Wilson 2011. Burn 2015, p. 65. Grove 2018.
*Papawera maugeansis* – Oskars and Malaquias 2019, p. 6.
*Haminea tenera* (Adams 1850) – Pritchard and Gatliff 1903, p. 217.
*Haminoea tenera* (Adams 1850) (in part) – Jansen 1995, p. 86.
*Haminoea tenera* (Adams 1850) – MacPherson and Gabriel 1962, p. 243. Burn 1966b, p. 266.

### *Diagnosis*

Animal light yellowish-grey or light brown to densely black; orange blotches of variable size present on mantle; opaque white dots may be present on cephalic shield and parapodial lobes. Cephalic shield, broad, deeply bilobed; periocular area unpigmented. Hancock organ ridge-like, with prominent dorsal and ventral branches. Shell oval; smooth with faint growth lines; whitish-translucent in colour; periostracum transparent; aperture wide, tapering posteriorly, columella narrow, separated from last whorl by short furrow; furrow covered by broad, flat, callus posteriorly. Radula formula 24–30 x 7–5.1.1.1.5–7; rachidian tricuspid; central cusp triangular, narrow, pointed; lateral cusps reduced, barely visible. Gizzard plates with 14–20 transverse ridges; single row of rods present along top of ridges; pseudo-rachis present. Male reproductive system with oblong, oval, annulated prostate; fundus open, pocket-like. Distribution restricted to southeastern Australia.

### *Type locality*

Port MacDonnell, South Australia, Australia (Burn 1966a).

### *Material examined*

Australia, South Australia, Port MacDonnell, Holotype, NMV F26134, H = 7 mm (image seen, https://ozcam.ala.org.au/occurrences/e789bb90-d64b-4e07-ad0b-89aed83c5a5b).

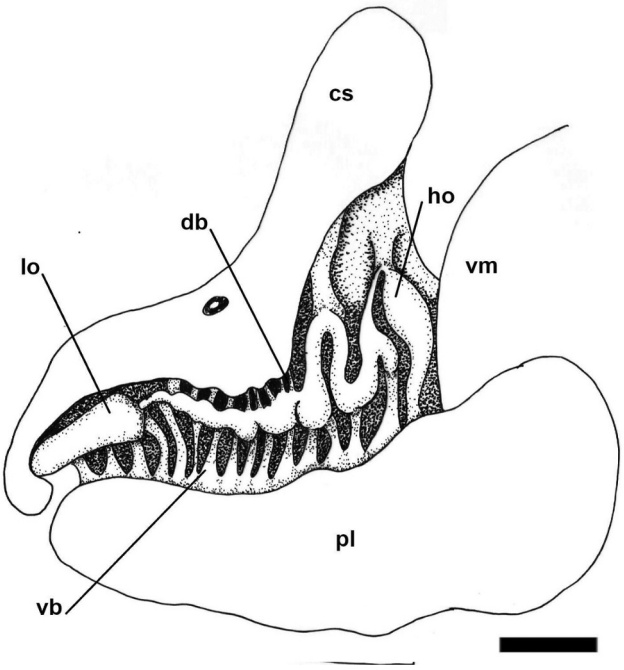


**Figure 6.** *Papawera maugeansis* (Burn, 1966a). Detail of left lateral Hancock's organ, dorsal branches partially covered by cephalic shield (ZMBN 125458, H = 8 mm). Abbreviations: cs, cephalic shield. db, dorsal branch. ho, Hancock's organ. lo, labial organ. pl, parapodial lobe. vb, ventral branch. vm, visceral mass. Scale bar = 0.3 mm.

Australia, Victoria, Shoreham, Westernport, 10 specimens (2 dissected), AMS c.105854, H = 3–8 mm. Australia, Victoria, Shoreham, Shoreham Beach, 1 specimen (sequenced), NMV F209129, H = 5 mm. Australia, Victoria, Inverloch, Town Area, 1 specimen (sequenced, dissected), ZMBN 125459 ex NVM F194630, H = 5.7 mm. Australia, Victoria, Clifton Springs, Curlewis Reef, 1 specimen (sequenced, dissected), (ZMBN125458 ex NVM F112423, H = 8 mm). Australia, Victoria, 1 shell, *Haminea tenera*, NHMUK unnumbered, MacAndrew Collection Acc. No. 1563, H = 7.5 mm.

### *External morphology (Figures 3(d–h), 6)*

Animal light grey or brown to completely black; orange blotches of variable size present on mantle; opaque white dots may be present on cephalic shield and parapodial lobes. Cephalic shield squarish, broad; deeply bilobed, posterior part extending over shell. Periocular area unpigmented. Hancock's organ elongate, horizontal ridge with long dorsal and ventral branches, dorsal branches may be partially hidden by cephalic shield. Parapodial lobes small, partially covering anterior part of shell, do not meet dorsally. Rounded pallial lobe extends beyond apex.

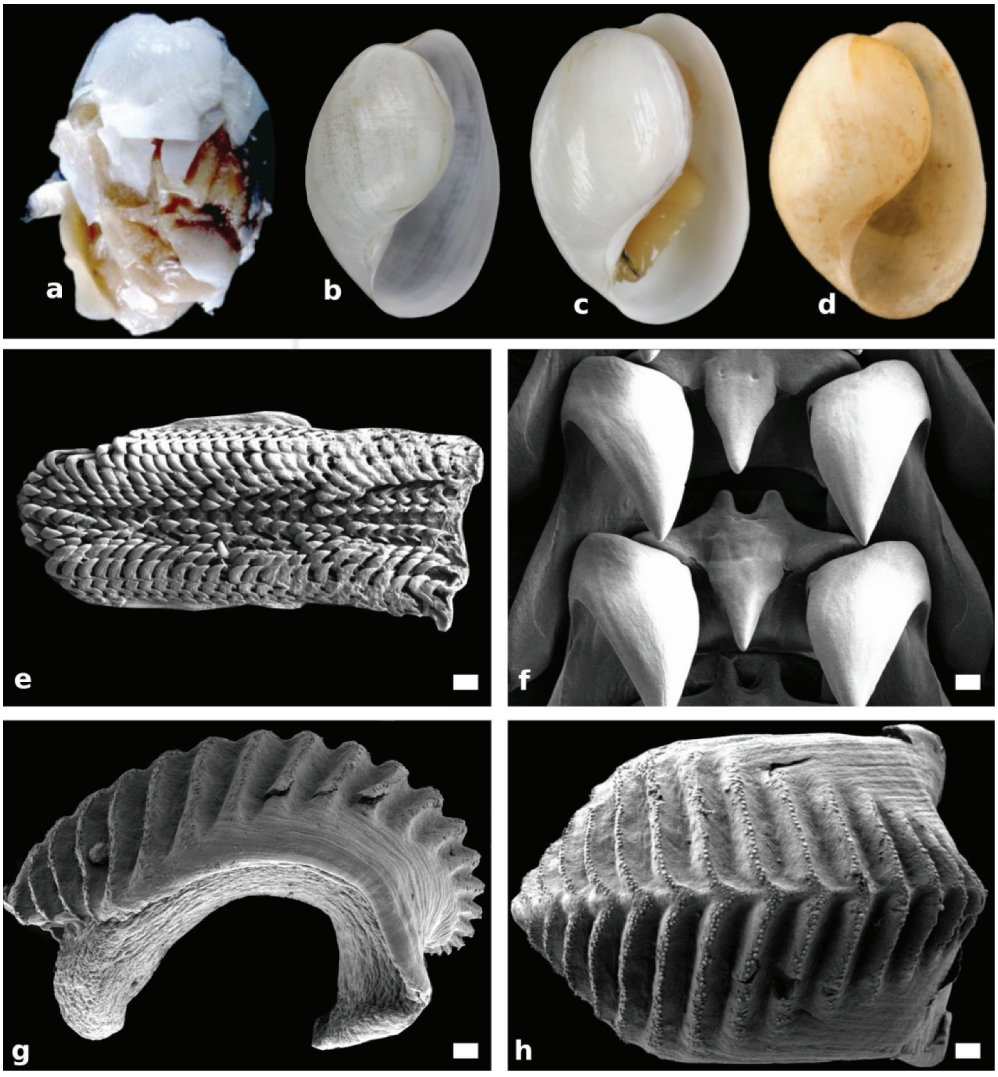


**Figure 7.** *Papawera maugeansis* (Burn, 1966a). (a) adpertural view of holotype (NMV F26134, H = 7 mm; Australia). (b) apertural view of shell (ZMBN 125458, H = 8 mm; Australia). (c) apertural view of shell (AMS c.105854, H = 5 mm; Australia). (d) apertural view of shell, (NHMUK MacAndrew col. 1563, H = 7.5 mm; Australia). (e) SEM, whole radula (AMS c.105854, H = 5 mm; Australia). (f) SEM, detail of rachidian and inner laterals in central part of radula (ZMBN 125458, H = 8 mm; Australia). (g) Right lateral view of whole gizzard plate (ZMBN 125458, H = 8 mm; Australia). (h) SEM, dorsal surface of whole gizzard plate (ZMBN 125458, H = 8 mm; Australia). Scale bars: e = 100 µm. f = 50 µm. g, h = 30 µm.

### *Shell (Figure 7(a–d))*

Shell oval; smooth with faint growth lines. Whitish-transparent in colour; periostracum transparent. Aperture wide, tapering posteriorly, columella narrow, separated from last whorl by short furrow; furrow covered by broad, flat, callus posteriorly. Outer lip gently curved; shoulder rounded.

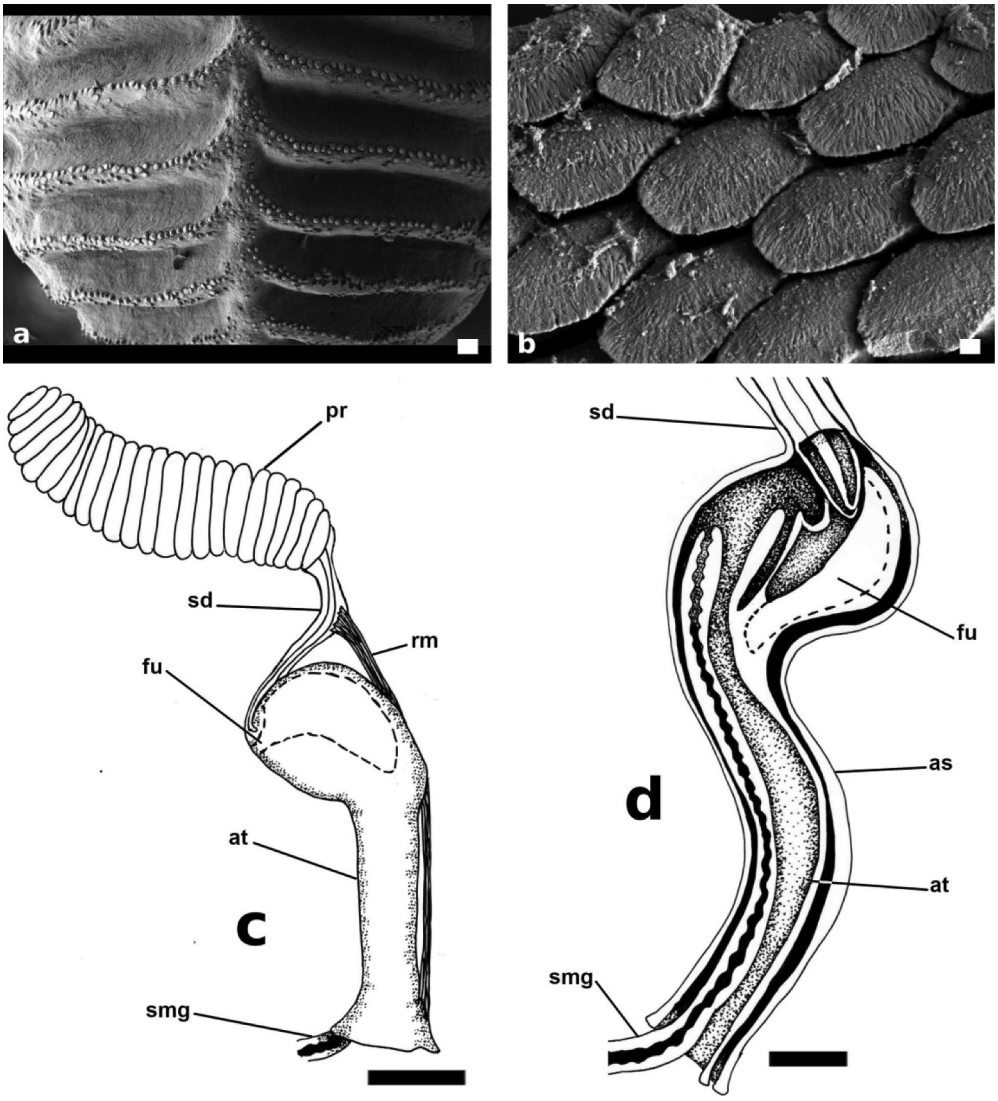


**Figure 8.** *Papawera maugeansis* (Burn, 1966a). (a) SEM, detail of ridges of gizzard plate (ZMBN 125458, H = 8 mm). (b) SEM, Detail of jaws (AMS c.105854, H = 5 mm). (c) detail of external male reproductive system (AMS c.105854, H = 5 mm). (d) detail of interior of ventrally opened atrium and fundus (ZMBN 125458, H = 8 mm). Abbreviations: as, atrium sheet. at, atrium. fu, fundus. pr, prostate. sd, seminal duct. smg, seminal groove. rm, retractor muscles. Scale bars: a = 20 µm. b = 2 µm. c = 0.5 mm, d = 0.25 mm.

### *Jaws (Figure 8(b))*

Semi-circular; shape of rods rounded with serrated edge, serration seems slightly worn.

### *Radula (Figure 7(e, f))*

Radular formula 25 × 6.1.1.1.6 (AMS c.105854, H = 8 mm), 30 × 7.1.1.1.7 (ZMBN 125458, H = 8 mm), 24 × 5.1.1.1.5 (as 6.1.6, NMV F26134, H = 7 mm; Burn 1966a).

Rachidian tricuspid; central cusp triangular, narrow, pointed; lateral cusps reduced, barely visible.

*Gizzard plates (Figures 7(g, h) and 8(a))*

Fourteen to 20 transverse ridges. Pseudo-rachis present. Ridges with a single row of minute rods along top edge.

*Male reproductive system (Figure 8(c, d))*

Male reproductive system with oblong, oval, annulated prostate, fundus open, pocket-like. Retractor muscle connects seminal duct to lower part of atrium.

### *Distribution*

This species is endemic to the Maugean cool-temperate province (Burn 1966a) and has been recorded from Victoria, South Australia and Tasmania (Burn 1966a, 2006).

### *Remarks*

The species *P. maugeansis* has been historically misidentified as several other haminoid species. Pritchard and Gatliff (1903) identified specimens from around Victoria as *Haminea tenera*, and Jansen (1995) reported the occurrence of *Haminoea tenera* from mid-New South Wales to South Australia and Tasmania. However, as previously mentioned herein, *H. tenera* is a distinct species although its taxonomic status remains elusive, but is under investigation by Oskars and Malaquias (work in progress). Janssen (1995) gave only a general description of the shells and noted that they were 'translucent white brown', but did not mention any feature of the sculpture. Thus, her records from New South Wales could be any tropical species of *Haloa* (see Nimbs and Smith 2016). On the other hand, records from South Australia and Tasmania are likely of *P. maugeansis*, which is the only species known to occur in Victoria, South Australia and Tasmania (Burn 1966a, 1966b, 2006; Burn and Wilson 2011; Grove 2018).

*Papawera maugeansis* occurs in intertidal and shallow subtidal seagrass beds in sheltered areas and in rocky platforms (Rudman 2007). The species feeds on algae and diatom films that it scrapes from the substrate (Burn 1966a, 1966b, 1974; Rudman 2007). Burn (1974) reported that *P. maugeansis* is preyed on by the headshield sea slug, *Philinopsis taronga* (Allan, 1933).

## Discussion

*Papawera* is a genus recently introduced by Oskars and Malaquias (2019) for two species with a temperate Australasian distribution, *P. maugeansis* and *P. zelandiae*. Both inhabit intertidal and shallow sheltered waters where they can be locally common (Powell 1979; Burn 2006; Morley and Hayward 2015; Oskars and Malaquias 2019). The sister relationship of the genus is still not resolved, but the phylogenetic hypothesis by Oskars and Malaquias (2019; Figure 1) suggested a possible sister relationship with the tropical IWP genus *Smaragdinella*. Yet, this was only marginally supported by maximum likelihood

analysis (bootstrap support = 71), and did not receive support in Bayesian analysis (posterior probability = 0.74).

Several previous works have included details about the morphology and ecology of *P. maugeansis* and *P. zelandiae* (Burn, 1966a, 1969, 1974; Rudman, 1971a, 1971b, 2003; Burn and Wilson, 2011), but the current contribution is the first to study these snails using SEM methods in order to provide ultrastructural data on the radula, jaws and gizzard plates. It is also the first to describe the male reproductive system of *P. maugeansis* and the female reproductive system of both species. The two species are externally quite distinct, with *P. zelandiae* bearing a large rounded shell, a cephalic shield with a minute posterior indentation, and large parapodial lobes, whereas, *P. maugeansis* is small with an elongate shell and a deeply bilobed cephalic shield with short parapodial lobes. Chromatically, *P. maugeansis* has orange blotches on the mantle, which are absent in *P. zelandiae* (Figure 3; see Table 3 for a synopsis).

Despite the sharp external differences, these species share several unique morphoanatomical traits supporting their close relationship. These include the morphology of the Hancock's organ with its prominent upper and lower vertical branches, the rachidian tooth with an elongated and narrow central cusp combined with inconspicuous lateral cusps, the male reproductive system with an annulated prostate, and the female part of the reproductive system with a blunt posterior mucous gland and a globular albumen gland with an irregular surface (see Taxonomy for details).

The shells of these snails are smooth with few growth lines, although some authors have reported the presence of faint spiral striae in *P. zelandiae* (Suter, 1913) and *P. maugeansis* (as *H. tenera*; MacPherson and Gabriel 1962), but we could not observe this feature, which was also not mentioned by Burn (1966a, 1966b) or Rudman (1971b).

**Table 3.** Synopsis of the most useful morphological characters for diagnosis of species in the genus *Papawera*.

| Characters/Species | *Papawera zelandiae* (Gray 1843) | *Papawera maugeansis* (Burn 1966a) |
|---|---|---|
| **1. External morphology** | | |
| *Animal colouration* | Light grey or brown to completely black | Animal light yellowish-grey or light brown to densely black; orange blotches and white dots maybe present |
| *Cephalic shield* | Shallowly bilobed | Deeply bilobed |
| *Parapodial and pallial lobes* | Large, meet dorsally | Small, do not meet dorsally |
| **2. Shell** | | |
| *Shape* | Rounded, bulbous | Oval-elongate |
| *Shell colour* | Whitish; periostracum transparent to yellowish | Whitish transparent; periostracum transparent |
| **3. Radula** | | |
| *Formula* | 27–22.1.1.1.22–27 | 7–5.1.1.1.5–7 |
| **4. Gizzard plates** | | |
| *Ridges* | Rachis present; 8–16 ridges | Pseudo-rachis present; 14–20 ridges |
| *Sculpture* | Rods along rachis and inner part of posterior side of ridges | Single row of rods along top of ridges |
| **5. Male reproductive system** | | |
| *Prostate* | Oblong, tapering, annulated | Oblong, oval, annulated |
| *Penial sheath/Atrium* | Fundus semi-enclosed with glandular epithelium | Fundus open, pocket-like |
| **6. Key References** | Rudman 1971a, 1971b | Burn 1966a, 1969, 1974 |

According to Clemens-Seely and Phillips (2011), *P. zelandiae* is poecilogonous laying egg masses from wherein both free swimming lecithotrophic veligers and fully developed juveniles hatch, a developmental mode among haminoeids only known in *Haloa japonica* (Gibson and Chia, 1991).

The shallow water molluscan fauna of Australasia is well known and the fact that only two species were detected to be part of the genus *Papawera* is most likely not a matter of undersampling but reflects, instead, a low diversity genus. Understanding the evolutionary history of the genus is hampered by ambiguity about its sister relationship, yet, the temperate distribution of these two species points to adaptation to colder waters, whereas all closer relatives (e.g., *Bakawan, Haloa, Lamprohaminoea, Smaragdinella*) have evolved and diversified largely in tropical waters. New Zealand split away from Australia around 80–60 million years ago (Mya) and full separation took over 20 Mya, with the Tasman Sea reaching its present width of 2000 km around 55 Mya (Knox 1980). Due to the age of this separation together with the fact that fossils of these snails are only known in Australia from the Pleistocene (*ca* 2.58 Mya to 11,700 years ago; Kendrik, 1960; Semeniuk 1995), the allopatric distribution of *P. maugeansis* and *P. zelandiae* is more parsimoniously explained by recent dispersal across the Tasmanian passage followed by speciation on both sides, rather than the outcome of vicariance associated with the separation of New Zealand from Australia.

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## References

Adams A. 1850. Monograph of the family Bullidae. In: Sowerby GB, editor. Thesaurus conchyliorum, or monographs of genera of shells. Vol. II. London (UK): Sowerby; p. 553–608, pl. 119–125.

Allan JK. 1933. Opisthobranchs from Australia. Rec Aust Mus. 18(9):443–450. doi:10.3853/j.0067-1975.18.1933.747.

Angas GF. 1871. A list of additional species of marine Mollusca to be included in the fauna of Port Jackson and the adjacent coasts of New South Wales. Proc Zool Soc London. 1871:87–101.

Burmeister H. 1837. Handbuch der Naturgeschichte. Vol. 2. Berlin (DEU): Enslin; p. 369–858. Zoologie.

Burn R. 1966a. Notes on some opisthobranchs mainly from South Australia. Rec Sou Aust Mus. 15 (2):329–352.

Burn R. 1966b. Opisthobranchia. Port Phillip Survey 1957-1963. Mem Nation Mus Victoria. 27:265–288. doi:10.24199/j.mmv.1966.27.15.

Burn R. 1969. A memorial report on the Tom Crawford collection of Victorian Opisthobranchia. J Malacol Soc Aust. 1(12):64–72. doi:10.1080/00852988.1969.10673833.

Burn R. 1974. Notes on some benthonic opisthobranchs from Port Philip Bay, Victoria. J Malacol Soc Aust. 3(1):43–57. doi:10.1080/00852988.1974.10673877.

Burn R. 2006. A checklist and bibliography of the Opisthobranchia (Mollusca: Gastropoda) of Victoria and the Bass Strait area, south-eastern Australia. Mus Victoria Sci Rep. 10(142):7–13.

Burn R. 2015. Nudibranchs and related molluscs. Melbourne (AUS): Museum Victoria; p. 256.

Burn R, Wilson R 2011. Bubble Shell, *Haminoea maugeansis*, in Taxonomic Toolkit for marine life of Port Phillip Bay, Museum Victoria. [accessed 2020 Feb 22. http://136.154.202.208:8098/species/4183

Clemens-Seely K, Phillips NE. 2011. Effects of temperature on hatching time and hatchling proportions in a poecilogonous population of *Haminoea zelandiae*. Biol Bull. 221(2):189–196. doi:10.1086/BBLv221n2p189.

Cuvier G. 1795. Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième [30 May 1795]. Mag Encyclo J Sci Let Arts. 2:433–449.

Eichler JG 2007. *Haminoea maugeansis* from Victoria. In: Sea Slug Forum, Jun 14. Sydney; Australian Museum. [accessed 2020 Feb 22]. http://www.seaslugforum.net/find/19408

Fischer P. 1883. Manuel de Conchyliologie et de Paléontologie Conchyliologique, Histoire naturelle des mollusques vivants et fossiles, Tome 31. Paris (FR): Crosse; p. 1369.

Furneaux P 2003. *Haminoea zelandiae* from Tauranga, New Zealand. In: Sea Slug Forum, Jun 6. Sydney: Australian Museum. [accessed 2020 Feb 22]. http://www.seaslugforum.net/find/10149

Gibson GD, Chia FS. 1991. Contrasting reproductive modes in two sympatric species of *Haminaea* (Opisthobranchia: Cephalaspidea). J Mollu Stud. 57(Sup 4):49–60. doi:10.1093/mollus/57.Supplement_Part_4.49.

Gray JE. 1843. Catalogue of the species of Mollusca and their shells which have hitherto been recorded as found at New Zealand, with the description of some lately discovered species. In: Dieffenbach E, editor. Travels in New Zealand with contributions to the geography, botany and natural history of that country. Vol II. Fauna of New Zealand. London (UK): John Murray; p. 228–263.

Grove SJ 2018. *Haminoea maugeansis* Burn 1966, A Guide to the Seashells and other Marine Molluscs of Tasmania web-site. [accessed 2020 Feb 22]. https://molluscsoftasmania.org.au/project/haminoea-maugeansis/

Habe T. 1952. Atyidae in Japan. Illustrated Catalogue of Japanese shells. Vol. 20. Tokyo (JP): Malacological Society of Japan.

Hales J. 2010. A list of the intertidal Opisthobranchs of Harmers Haven, South Gippsland. Vic Nat. 127:248–254.

Hayward BW. 1979. An intertidal *Zostera* pool community at Kawerua, Northland and its foraminiferal microfauna. Tane Auckland. 25:173–186.

Holznagel WE. 1998. Research note: A nondestructive method for cleaning gastropod radulae from frozen, alcohol-fixed, or dried material. Am Malacol Bull. 14:181–183.
Inkscape Team. 2015. Inkscape 0.92. [accessed 2018 Jun 01]. www.inkscape.org
Jansen P. 1995. Seashells of Central New South Wales: a survey of the shelled marine molluscs of the Sydney Metropolitan Area and adjacent coasts. Belgian Gardens (AUS): Patty Jansen (Self Published); p. 129.
Kendrick GW. 1960. The fossil Mollusca of the Peppermint Grove Limestone, Swan River district or Western Australia. West Aust Nat. 7(3):53–66.
Knox GA. 1980. Plate tectonics and the evolution of intertidal and shallow-water benthic biotic distribution patterns of the southwest Pacific. Palaeogeogr Palaeocl. 31:267–297. doi:10.1016/0031-0182(80)90022-X.
Kobelt W. 1896. Die Familie Bullidae. In: Martini FHW, Chemnitz JH, editors. Systematisches Conchylien-Cabinet 1 (9). Nürnberg (GER): Bauer Raspe; p. 190.
Kumar S, Stecher G, Tamura K. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol Biol Evol. 33(7):1870–1874. doi:10.1093/molbev/msw054.
Kuroda T, Habe T. 1952. Check list and bibliography of the Recent Marine Mollusca of Japan. Tokyo (JP): Leo W. Stach; p. 210.
MacPherson JH, Gabriel CJ. 1962. Marine molluscs of Victoria. Melbourne (AUS): Melbourne University Press; p. 475.
Marcus E, Burch JB. 1965. Marine euthyneuran Gastropoda from Eniwetok Atoll, Western Pacific. Malacologia. 3(2):235–262.
Mattis P, Kimball S, Singh M 1995. GIMP: GNU image manipulation program. [accessed 2018 Oct 01]. www.gimp.org
Morley MS, Hayward BW. 2015. Intertidal records of 'sea slugs' (nudibranchs and allied opisthobranch gastropods) from northern North Island, New Zealand. Rec Auck Mus. 50:33–75.
Natterer M. 2018. GIMP 2.10.0. [accessed 2018 Aug 01]. https://www.openhub.net/p/gimp/contributors/summary
Nimbs MJ, Smith SD. 2016. An illustrated inventory of the sea slugs of New South Wales, Australia (Gastropoda: Heterobranchia). Proc Roy Soc Victoria. 128(2):44–113. doi:10.1071/RS16011.
Oskars TR, Malaquias MAE. 2019. A molecular phylogeny of the Indo-West Pacific gastropods *Haloa sensu lato* (Cephalaspidea: Haminoeidae): tethyan vicariance, higher generic diversity, and ecological specialization. Mol Phylo Evol. 139. doi:10.1016/j.ympev.2019.106557.
Pilsbry HA. 1895. Polyplacophora. Acanthochitinidae, Cryptoplacidae and appendix. Tectibranchiata. Man Conch. 15(60):181–436.
Pilsbry HA. 1921. Marine molluscs of Hawaii, XIV, XV. Proc Acad Nat Sci Phil. 72:360–382.
Powell AWB. 1979. New Zealand Mollusca. Auckland (NZ): Collins; p. 500.
Pritchard GB, Gatliff JH. 1903. Art XIX, Catalogue of the Marine Shells of Victoria Part VI Roy Soc Victoria. 15:176–223.
Puillandre N, Lambert A, Brouillet S, Achaz G. 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Mol Ecol. 21(8):1864–1877. doi:10.1111/j.1365-294X.2011.05239.x.
Rudman WB. 1971a. On the opisthobranch Genus *Haminoea* Turton & Kingston. Pac Sci. 25:545–559.
Rudman WB. 1971b. Structure and functioning of the gut in the Bullomorpha (Opisthobranchia) Part 1. Herbivores J Nat Hist. 5(6):647–675. doi:10.1080/00222937100770491.
Rudman WB 1999. Gizzard plates of *Haminoea zelandiae*. In: Sea Slug Forum, Dec 23. Sydney: Australian Museum. [accessed 2018 Oct 15]. http://www.seaslugforum.net/factsheet/hamizela
Rudman WB 2003. *Haminoea zelandiae* (Gray, 1843). In: Sea Slug Forum, Jun 6. Sydney: Australian Museum. [accessed 2020 Feb 22]. http://www.seaslugforum.net/find/hamizela
Rudman WB 2006. Colour variability in *Haminoea zelandiae*. In: Sea Slug Forum, Oct 27. Sydney: Australian Museum. [accessed 2020 Feb 22]. http://www.seaslugforum.net/find/18126
Rudman WB 2007. *Haminoea maugeansis* Burn, 1966. In: Sea Slug Forum, Jun 13. Sydney: Australian Museum. [accessed 2020 Feb 22]. http://www.seaslugforum.net/factsheet/hamimaug
Semeniuk V. 1995. New Pleistocene and Holocene stratigraphic units in the Yalgorup Plain area, southern Swan Costal Plain. J Roy Soc West Aust. 78:67–79.

Smith EA. 1873. Mollusca. In: Richardson J, Gray JE, editors. The Zoology of HMS Erebus and Terror under the command of Captain Sir James Clark Ross, during the years 1839 to 1843 Vol. 2. London (UK): By authority of the Lords Commissioners of the Admiralty; p. 1–7.

Sowerby GB. 1868. Monograph of the genus *Haminea*. In: Reeve LA, editor. Conchologia iconica, or, illustrations of the shells of molluscous animals Vol. 16. London (UK): L. Reeve and Co; p. 1843–1878.

Suter H. 1913. Manual of the New Zealand Mollusca: with an atlas of quarto plates. Wellington: J. Mackay, Government Printer; p. 1120.

Thompson TE. 1976. Biology of Opisthobranch Molluscs. Vol. I. London (UK):Ray Society; p.205.

Turton W, Kingston JF. 1830. Part II: the natural history of the District or, lists of the different species of animals, vegetables and minerals. In: Carrington NT, editor. The Teignmouth, Guide, 2, Conchology, nº 63. London (UK): E. Croydon at the Public Library; C. and J. Rivington, Baldwin and Co. Whittaker and Co.; Gore: Dawlish; Torquay: Cole and Lascombe; Exter: Exter Booksellers.

Vogler RE. 2013. The radula of the extinct freshwater snail *Aylacostoma stigmaticum* (Caenogastropoda: Thiaridae) from Argentina and Paraguay. Malacologia. 56:329–332. doi:10.4002/040.056.0221.

Willan RC. 1979. The ecology of two New Zealand opisthobranch molluscs [Thesis (PhD–Biological Sciences)]. Auckland (NZ): University of Auckland. [accessed 2020 Feb 22]. https://researchspace.auckland.ac.nz/handle/2292/1455