

The systematics and phylogeny of
Haminoeidae (Mollusca,
Cephalaspidea), with special focus on
the taxonomy and phylogeny of the
genus *Haloa sensu lato*

Trond Roger Oskars

Thesis for the Degree of Philosophiae Doctor (PhD)
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Scientific environment

This PhD project was financed through a four-year PhD candidate position at the University Museum of Bergen, the University of Bergen. The work for this thesis was carried out at the Department of Natural History, Section of Taxonomy and Evolution, at the University Museum of Bergen within the research group Phylogenetic Systematics and Evolution. Additional funding for laboratory and travel expenses was funded by grants graciously awarded by the Meltzer Research Fund and the Malacological Society of London.

Taxonomy (the science of classification) is often undervalued as a glorified form of filing— with each species in its folder, like a stamp in its prescribed place in an album; but taxonomy is a fundamental and dynamic science, dedicated to exploring the causes of relationships and similarities among organisms. Classifications are theories about the basis of natural order, not dull catalogues compiled only to avoid chaos.

Stephen Jay Gould (1989: 98) *Wonderful Life*

Acknowledgements

As long as I can remember, I have always loved nature and the relationships between creatures. From my brother Frode filming a four year old me hosting my own ‘nature documentary’ on living fossils to standing in pet shops studying the feet of particularly confused parrots revelling in their dinosaur-like feet. It was not until the second year of my bachelor, during general zoology, I fell for the mystery of molluscs. How could something so simple, still be simultaneously so complex? However, I was completely sold after attending an incredibly enthusiastic and motivational Manuel Malaquias’ course on Systematic Zoology, which also gave me a love for the world of invertebrates. When the time was ripe for looking for advisors and potential topics for my master thesis, my first and only choice was Manuel, and I would take any project that allowed me to study molluscs through classical dissections and DNA. Thanks to Manuel I have now studied Cephalaspidea gastropods for close to eight years, from my last year of the bachelors reading selected papers, through my master thesis and now my PhD. Manuel has always been a great support, both showing me great faith and challenging my ideas and hypotheses, constantly driving me up and forward. Manuel has always been accessible and ready to help, either behind a door ajar or by e-mail with tropical snakes slithering around the floor of his hut. I am also deeply thankful for my secondary advisor Endre Willassen whose knowledge on phylogenetics and taxonomy is only matched by his many amazing anecdotes from a long life dedicated to science. His advice and discussions have saved me a lot of frustration when battling phylogenetic software and I have always learned something new when I knocked on his door. This thesis would not exist without Manuel and Endre’s dedication as advisors, teachers and co-authors. The thesis would also not have been possible without the co-authors of my papers namely Deepak Apte, Sadar Aslam, Monisha Bharate, Appukuttannair Biju Kumar, Constantino Mifsud, Paula M. Mikkelsen, Sumantha Narayana, Raveendhiran Ravinesh, David Rees, Ghazala Siddiqui and Chin Chin Too.

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Abstract

The family Haminoeidae consist of herbivorous snails found worldwide in tropical to temperate shallow waters on reefs, seagrass beds, rocky shores and mangroves. The family is the most diverse within the Order Cephalaspidea, but it has been plagued by systematic and taxonomic confusion due to many species and genera being vaguely defined only on shell or inconsistently on a few anatomical features. In this thesis I aim to resolve the taxonomy and systematics of the family and genera based on an integrative approach using a combination of molecular phylogenetic analyses using the mitochondrial genes cytochrome *c* oxidase subunit I, 12S rRNA, 16S rRNA, and the nuclear genes 18S rRNA, 28S rRNA, and Histone 3 coupled with morpho-anatomical data, the latter resulting from a revision of anatomical characters based in literature and dedicated anatomical dissections. Several of the traditional Haminoeidae genera were synonymized (*Austrocylichna*, *Limulatys*, *Micraenigma*, *Nipponatys*, *Tepidatys*) resurrected (*Haloa*, *Haminella*, *Lamprohaminoea*, *Roxaniella*, *Weinkauffia*) or showed to not belong in the family (*Cylichnium*, *Hamineobulla*, *Micratys*, *Mimiatys*, *Mnestia*, *Osorattis*, *Roxania*, *Spissitydeus*). The results showed that the family is composed of 17 genera including the new genus here described *Vellicolla* and the informal clade “Mini-haminoeids”. Further, the type genus *Haminoea* was shown to be non-monophyletic, with three main radiations, namely *Haminoea* (Atlantic + eastern Pacific), *Haloa sensu lato* (Indo-West Pacific), and *Smaragdinella*. A comprehensive study of *Haloa s. l.* based on an expanded taxon sampling including representatives from putatively all species demonstrated that this clade consist of four clades warranting generic status with unique ecological, biogeographic, and morphological features, namely *Haloa sensu stricto* (13 species with dull colours distributed across the Indo-West Pacific), *Lamprohaminoea* (5 species with bright colours distributed across the Indo-West Pacific), and the two new genera here described *Bakawan* (4 species restricted to mangrove habitats) and *Papawera* (2 species restricted to temperate waters of Australasia). Systematic revisions were conducted for the four genera and 7 new species were found and described (*Haloa* [2], *Lamprohaminoea* [3], *Bakawan* [2]).

List of Publications

- I. Oskars, T. R., Mifsud, C. and Malaquias, M. A. E. (2017). Redescription of the Cephalaspidea gastropod *Atys jeffreysi* (Weinkauff, 1866) (Haminoeidae), with a discussion on the phylogenetic affinities of the Mediterranean species of the genus. *Journal of Natural History*, 51(27–28): 1593–1608.
- II. Bharate, M., Oskars, T. R., Apte, D. and Malaquias, M. A. E. (2018). *Diniatys callosa* (Preston, 1908), new combination name for *Haminoea callosa* from the Andaman Islands (India) *Journal of Conchology*, 43(2): 213–215.
- III. Oskars T. R., Too C. C., Rees D., Mikkelsen P. M., Willassen E., and Malaquias M. A. E. (2018). A molecular phylogeny of the gastropod family Haminoeidae *sensu lato* (Heterobranchia: Cephalaspidea)—a generic revision. *Invertebrate Systematics*, accepted.
- IV. Bharate, M., Oskars, T. R., Narayana, G., Ravinesh, R., Kumar A. B., and Malaquias, M. A. E. (2018). Description of a new species of *Haminoea* (Gastropoda, Cephalaspidea) from India, with an account on the diversity of the genus in the region. *Journal of Natural History*, 52(37–38): 2437–2456
- V. Aslam, S., Oskars, T. R., Siddiqui, G. and Malaquias, M. A. E. Beyond shells: First detailed morphological description of the mangrove-associated gastropod *Haminoea fusca* (A. Adams, 1850) (Cephalaspidea: Haminoeidae), with a COI phylogenetic analysis. *Zoosystema*, accepted.
- VI. Oskars, T. R., and Malaquias, M.A.E. A molecular phylogeny of the Indo-West Pacific gastropods *Haloa sensu lato* (Cephalaspidea: Haminoeidae): Tethyan vicariance, higher generic diversity, and ecological specialization. *Molecular Phylogenetics and Evolution*, accepted with revisions.
- VII. Oskars, T. R., and Malaquias, M.A.E. Systematic revision of the Indo-West Pacific colourful snails of the genus *Lamprohaminoea* Lin, 1997 (Cephalaspidea: Haminoeidae). Intended journal: *Invertebrate Systematics*, manuscript.
- VIII. Oskars, T. R., and Malaquias, M.A.E. Systematic revision of the Indo-West Pacific mangrove-associated snails of the genus *Bakawan* Oskars and Malaquias, submitted (Cephalaspidea: Haminoeidae). Intended journal: *Journal of Molluscan Studies*, manuscript.
- IX. Oskars, T. R., and Malaquias, M.A.E. The temperate Australasian genus *Papawera* Oskars and Malaquias, submitted (Cephalaspidea: Haminoeidae): redescription of *P. zelandiae* and *P. maugeansis*. Intended journal: *Journal of Natural History*, manuscript.

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- X. Oskars, T. R., and Malaquias, M.A.E. Systematic revision of the Indo-West Pacific bubble-snails of the genus *Haloa* Pilsbry, 1921 (Cephalaspidea: Haminoeidae). Intended journal: *Zoological Journal of the Linnean Society*, manuscript.

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1. Introduction

1.1 Introducing the family Haminoeidae

The family Haminoeidae Pilsbry, 1895a belongs to the gastropod order Cephalaspidea Fischer, 1883, which is a highly diverse group belonging to the marine Heterobranchia Burmeister, 1837 (*e.g.* in part the traditional Opisthobranchia). Haminoeidae is a highly successful group of herbivores that feed predominantly on diatoms and filamentous algae (Usuki 1966a, b; Rudman 1971a, b, 1972a; Burn and Thompson 1998; Malaquias 2010; Malaquias and Cervera 2006; Too *et al.* 2014; Austin *et al.* 2018; Papers I–X). They are usually found in shallow tropical to temperate waters where they inhabit subtidal habitats like sand flats, mud flats, seagrass beds, algal mats or coral reefs, but also intertidal environments such as rock pools and mangroves (Er. Marcus and Burch 1965; Burn 1974, 1978; Rudman 1971a, 1972a; Burn and Thompson 1998; Carlson and Hoff 2003; Malaquias and Cervera 2006; Gosliner and Behrens 2006; Gosliner *et al.* 2008, 2015; Too *et al.* 2014; Austin *et al.* 2018; Papers I–X).

Many genera and species of Haminoeidae were first described on their usually thin, delicate shells, and many species are still only known by this character (Paper III). The shells can be similar between genera and species, but can also be variable within species (Fig. 1; Paper III). The most common shape is the bubble-like oval or rounded shells such as those found in the genera *Atys* Montfort, 1810, *Haminoea* Turton & Kingston, 1830 and *Haloa* Pilsbry, 1921. Whereas genera like *Bullacta* Bergh, 1901, *Phanerophthalmus* A. Adams, 1850 and *Smaragdinella* A. Adams, 1848 have more flattened shells. The colour of the shells is generally whitish transparent, white, pale brown or rarely yellowish green as in *Smaragdinella*. The shells usually have a smooth surface, but can be sculptured with spiral striae and in some cases axial growth lines. The shells also have an outer layer or periostracum, which is transparent, faint yellow to dark brownish-red in colour. Although all these features may vary within and between genera, a common feature of the shells is the reduced innermost whorls (Er. Marcus 1957, 1958; Burn 1978; Mikkelsen 1996; Burn and Thompson 1998; Too *et al.* 2014, Paper III).

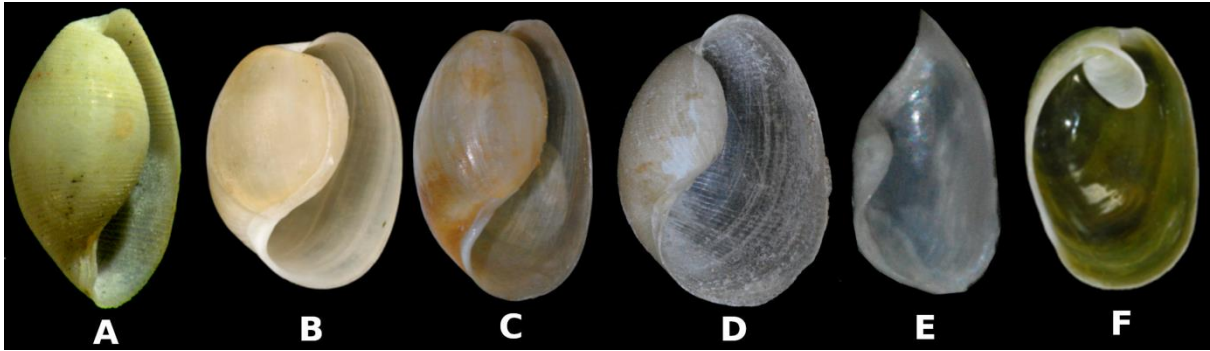


Figure 1. Shells of Haminoeidae. A. *Alys ooformis* (Habe, 1952), Wakayama Pref., Honshu, Japan. (NSMT 38605, H = 12.6 mm). B. *Haminoea navicula* (Da Costa, 1778), Vigo, Spain (NHMUK 1851.7.1.9, H = 27 mm). C. *Haloa crocata* (Pease, 1860), Hawaii (NHMUK 1961194, *Haminea glabra*, H = 18 mm). D. *Bullacta caurina* (Benson in Cantor, 1842) Shanghi, China Sea (NHMUK 196946 H = 17 mm). E. *Phanerophthalmus minikoiensis* (Smith, 1903), Minicoy, Lakshadweep, India (NHMUK 1903.9.14.10, holotype, H = 4 mm). F. *Smaragdinella calyculata* (Broderip & Sowerby, 1829), Okinoshima Island, Kochi Prefecture, Japan (NSMT 51281, H = 12 mm).

Externally the animals can be quite similar in morphology and colour patterns between species and genera (Fig. 2), but genera like *Bullacta*, *Phanerophthalmus* and *Smaragdinella* are more distinctively shaped (see Paper III). Most species are translucent to whitish or dull-coloured in hues of green to brown and usually mottled with dots and blotches. However, notable exceptions are brightly coloured such as species of the genera *Lamprohaminoea* Lin, 1997 and *Vellicolla* Oskars *et al.* (Paper III) (Fig. 2).

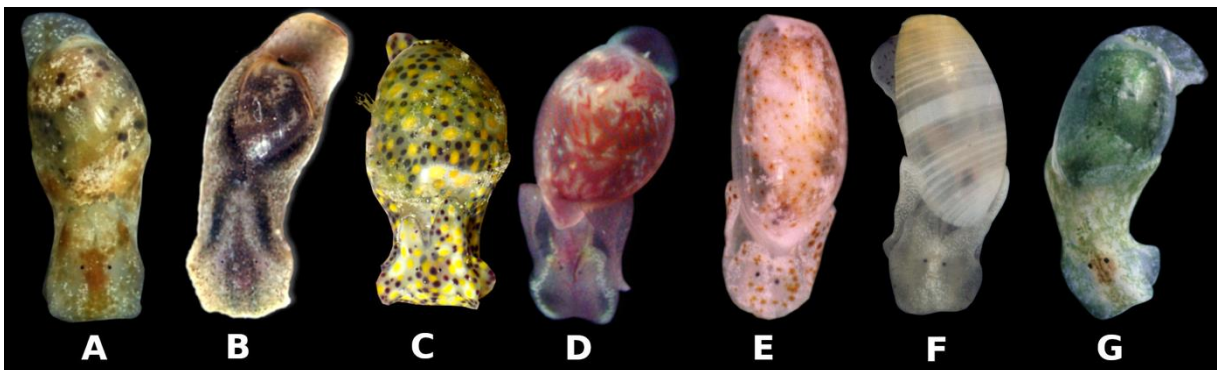


Figure 2. Typical Haminoeidae. A. *Haloa musetta* (Er. Marcus & Burch, 1965), Okinawa, Japan (ZMBN 112938). B. *Haminoea orbignyana* (Feürussac, 1822) Rio Mira, Portugal of courtesy of M. A. E. Malaquias. C. *Lamprohaminoea* sp. 3, Panglao, the Philippines (MNHN 42252) courtesy of M. A. E. Malaquias. D. *Vellicolla amphorella* (A. Adams, 1862) Panglao, the Philippines (MNHN, Paris B14_OT652 BC_1104) courtesy of MNHN, Paris. E. *Roxaniella jeffreysi* (Weinkauff, 1866), Fomm ir-Rih Bay, Malta, courtesy of C. Mifsud. F. *Weinkauffia macandrewii* (E. A. Smith, 1872) Gnejna Bay, Malta, courtesy of C. Mifsud. G. *Diniatys dentifer* (A. Adams, 1850) Guam (UF 374130), courtesy of C. Carlson.

1.2 Morphology and anatomy of Haminoeidae

As mentioned above, many species are mostly known from their shells or external morphology, which can show both high similarity and variation. Despite this fact, shells and morphology have subtle differences that can be useful to distinguish genera and species especially in light of molecular phylogenetic frameworks as revealed by recent revisionary work (e.g. Too *et al.* 2014; Austin *et al.* 2018; Papers I–X).

The general appearance of most haminoeids consists of a large, external, posterior shell and the anterior head region, which includes the dorsal cephalic shield, the ventral foot with its lateral projections, the parapodial lobes. The cephalic shield usually has a pair of visible eyes and posterior lobes (cephalic lobes). Ventrally the pallial lobe, an extension of the mantle that functions as a secondary foot, exits the opening of the shell (aperture) and projects behind the shell (Fig. 3).

However, some genera have a more distinct morphology, which is likely an adaptation to their lifestyles. *Bullacta* has a flattened philinid body shape, and lives intertidally on mud flats of estuaries (Malaquias 2010; Ge *et al.* 2013; Shi *et al.* 2018). *Phanerophthalmus* is narrowly elongate and has a reduced shell (Austin *et al.* 2018) and crawls on the surface of the substrate like most haminoeids. However, species of the genus have been observed to also show limited swimming capacities by flapping their large parapodial lobes (Quoy and Gaimard 1833; A. Adams 1850; H. Adams and A. Adams 1854; pers. obs.). *Smaragdinella* is flattened and quite rounded in shape with large pallial and parapodial lobes. The shape is likely due to the limpet like lifestyle of the genus, with species living on rocky substrates in the upper intertidal (A. Adams 1848, 1850; Risbec 1951; Er. Marcus and Burch 1965; Miller 1969; Rudman 1972, 2004) or inside empty shells of barnacles (Chaban and Chernyshev 2016).

The external Hancock's organ is a mostly ridge-like chemical sensory organ (Göbblers and Klusmann-Kolb 2006) which is found laterally on the head between the cephalic shield and the parapodial lobes (Fig. 4). This organ can be quite distinctly shaped in some genera (Papers III, VI).

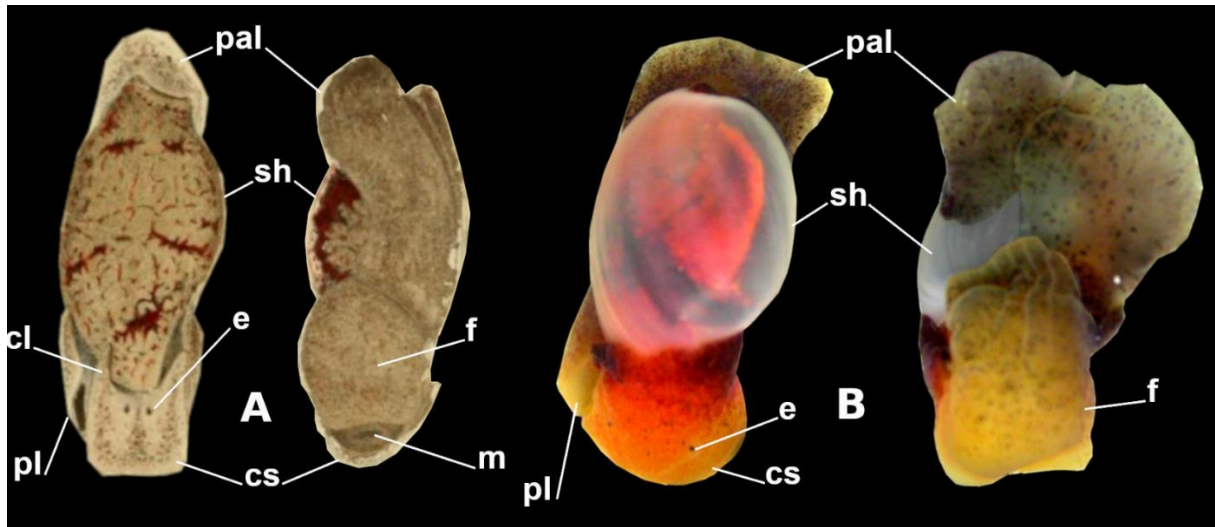


Figure 3. External morphology of Haminoeidae. A. *Weinkauffia turgidula* (Forbes, 1844), dorsal view (left image), ventral view (right image) Mediterranean, modified from Vayssière (1893). B. *Bakawan* sp. 1, Panglao, the Philippines courtesy of M. A. E. Malaquias. Abbreviations: cl, cephalic lobes. cs, cephalic shield. e, eyes. f, foot. m, mouth. pal, pallial lobe. pl, parapodial lobes. sh, shell.

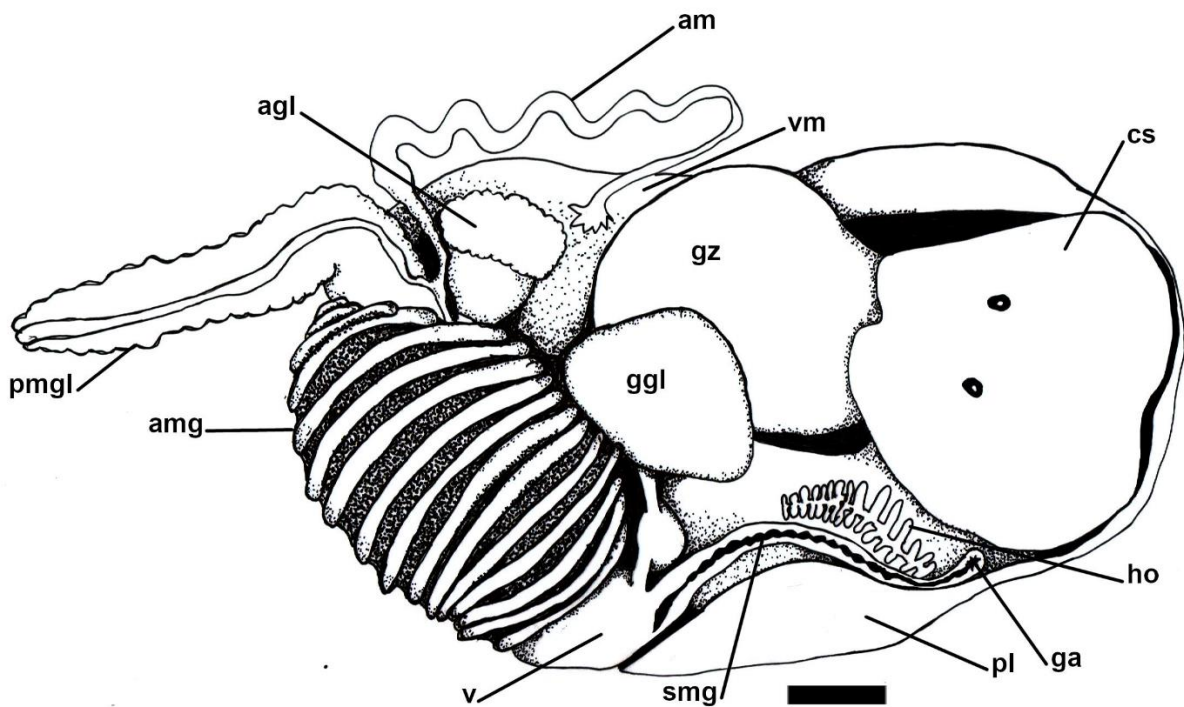


Figure 4. *Haminoea alfredensis* (Bartsch, 1915) (ZMBN 86406, H = 16 mm; South Africa) with shell and mantle removed showing Hancock's organ and female reproductive system. Abbreviations: agl, albumen gland. am, ampulla. amg, anterior mucous gland. cs, cephalic shield. ga, genital atrium. ggl, gametolytic gland. gz, gizzard. ho, Hancock's organ. pl, parapodial lobes. pmgl, posterior mucous gland. smg, external seminal groove. v, vestibule. vm, visceral mass.

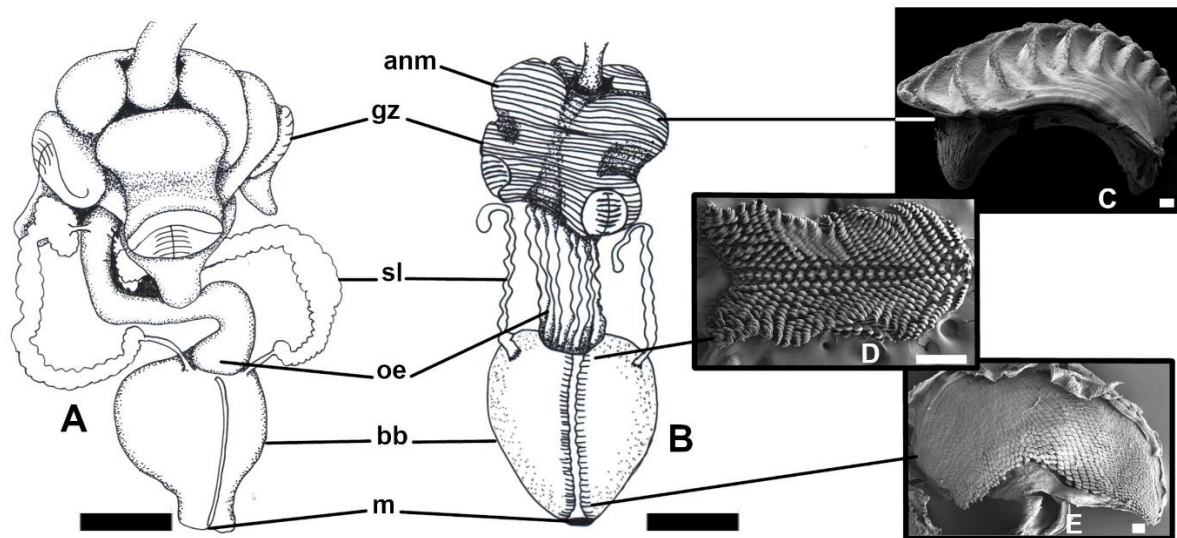


Figure 5. Anterior digestive system. A. *Haminoea alfredensis* (ZMBN 86406, H = 16 mm; South Africa). B. *Smaragdinella* cf. *sieboldi* (ZMBN 125447, H = 7 mm; Mozambique), Mozambique (AM 119920, H = 11 mm; New Zealand). C. SEM, right lateral view of gizzard plate of *Papawera zelandiae* (AM 119920, H = 11 mm; New Zealand). D. SEM, radula of *Haloa japonica* (ZMBN 91233, animal length 5.5 mm; Japan). E. SEM, jaw of *Haloa crocata* (ZMBN 88215, H = 12 mm; Hawaii). Abbreviations: bb, buccal bulb. anm, annulated muscles. gz, gizzard. m, mouth. oe, oesophagus. sl, salivary glands.

Despite some external morphological useful taxonomic characters, the internal anatomy is in most cases much more useful for recognising and defining genera and species. The details of the digestive tract and the hermaphroditic reproductive organs have been shown to be of great systematic significance in Cephalaspidea gastropods (e.g. Eilertsen and Malaquias 2013; Too *et al.* 2014; Malaquias *et al.* 2016; Austin *et al.* 2018). The anterior digestive system is formed by the mouth, followed by the muscular buccal bulb, salivary glands, and a muscular gizzard (Fig. 5). The buccal bulb holds the semi-circular jaws that are composed of numerous, small chitinous elements that aid the radula in grasping and holding food (Rudman 1971b). The buccal bulb holds the radula, which can be highly variable in shape within and between genera and species. The radula is generally composed by several rows, ranging between 16–65 (Too *et al.* 2014; Austin *et al.* 2018; Papers IV–X), generally the number increases with the size of the animal. Each row consists of a central rachidian tooth flanked on each side by the inner lateral tooth and 1–58 outer lateral teeth (Paper III). The radula transports the food to the oesophagus, which leads to the gizzard. The gizzard is covered in annulated musculature and holds three chitinous gizzard plates that are used to crush the food prior to digestion (Rudman 1971b; Thompson 1976). Some genera, such as *Haminoea*, *Haloa*, *Lamprohaminoea*, *Bakawan* Oskars & Malaquias, VI and *Papawera*

Oskars & Malaquias, VI may have bristles or spines anterior to the gizzard plates (Vayssière 1885; Thompson 1976; 1988; Schaefer 1992; Álvarez *et al.* 1993a; Malaquias and Cervera 2006; Papers VI–X). These likely restrict the amount of food entering the gizzard at one time (Rudman 1971b; Thompson 1976).

The hermaphroditic reproductive system consists of the posterior female glands and the anterior male reproductive system. The female system lies within the mantle cavity over the visceral mass (most vital organs such as digestive organs) (Fig. 4). From the vestibule (the opening, also called vagina) of the female reproductive system, a seminal groove runs externally on the right side of the body until the genital aperture just beyond the Hancock's organ. The genital aperture opens to the male reproductive system, which generally consists of a penial sheath enveloping a muscular penis, a seminal duct, and a prostate (Fig. 6).

In several genera such as *Haminoea* and *Roxaniella* (Papers I, III, VI) the penial sheath covers a muscular penis that connects directly to the seminal duct (Fig. 6). Some genera lack a penis, but possess a hollow atrium enveloped by a sheath. In genera with an atrium, the seminal duct empties into a constriction or modified region of the upper atrium called the fundus (*sensu* Er. Marcus and Burch, 1965). The fundus can be empty (*e.g.* *Papawera*, Paper IX), modified with thickened walls and/or soft warts/ridges (*e.g.* *Haloa*, *Smaragdinella*, *Bakawan*; Papers VI, VIII, X) or can be filled with chitinous spines (*e.g.* *Haminella*, *Lamprohaminoea*, Papers III, VII).

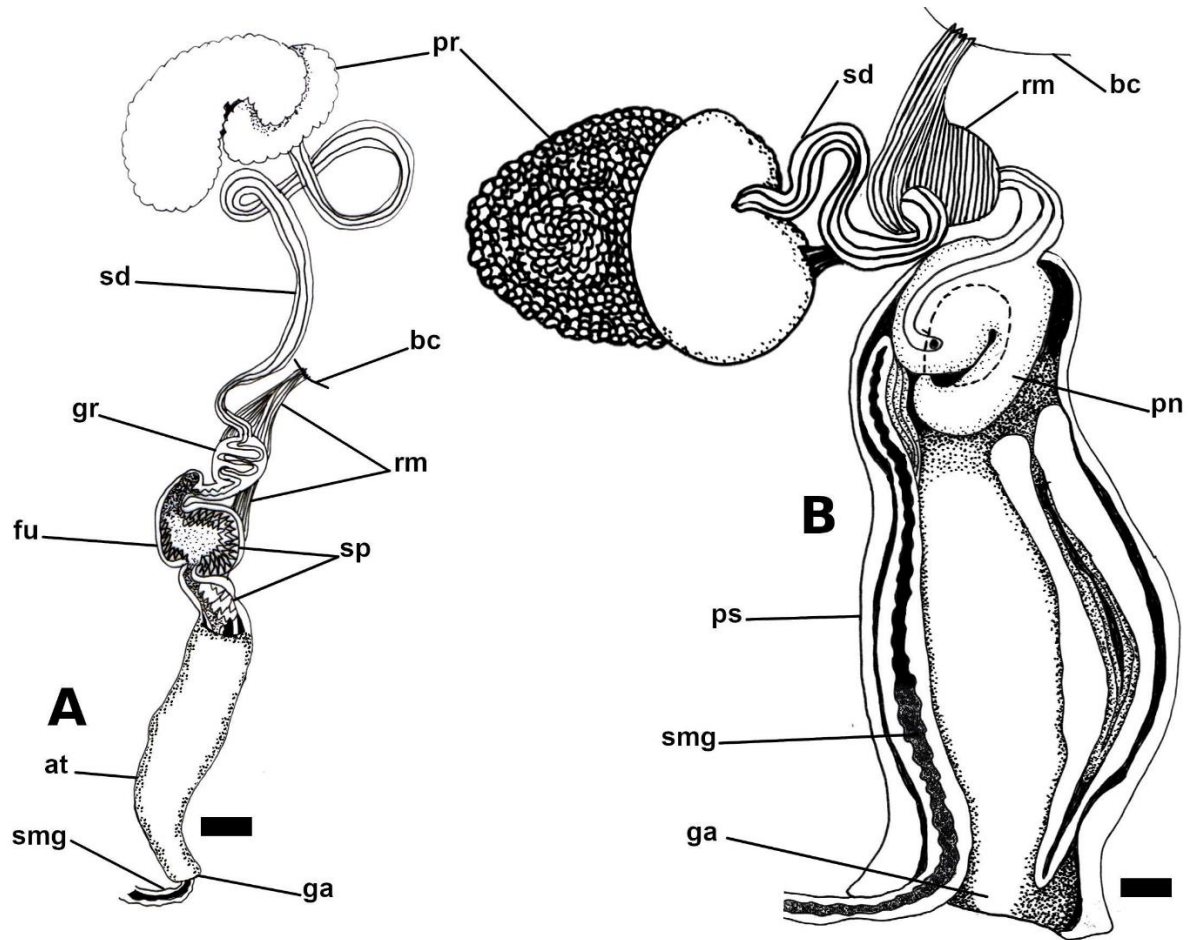


Figure 6. Male reproductive systems of Haminoeidae. A. *Lamprohaminoea* sp. 3 (MNHN IM-2013-52894, H = 5 mm; Madagascar). B. *Haminoea alfredensis* (ZMBN 86406, H = 16 mm; South Africa. Scale bars: A, B = 0.5 mm. Abbreviations: as, atrium sheath. ag, accessory gland. as, atrium sheath. asp, anterior spines. at, atrium. bc, body cavity. fu, fundus. gr. glandular region. msp, median spines. pn, penis. pr, prostate. psp, posterior spines. sd, seminal duct. smg, seminal groove. rm, retractor muscles.

There are few studies on how copulation occurs in Haminoeidae, but in *Lamprohaminoea*, the atrium everts to reveal the chitinous spines that line the fundus. However, this structure does not seem to be used for penetration, but probably to hold to the mating partner (Fig. 7).

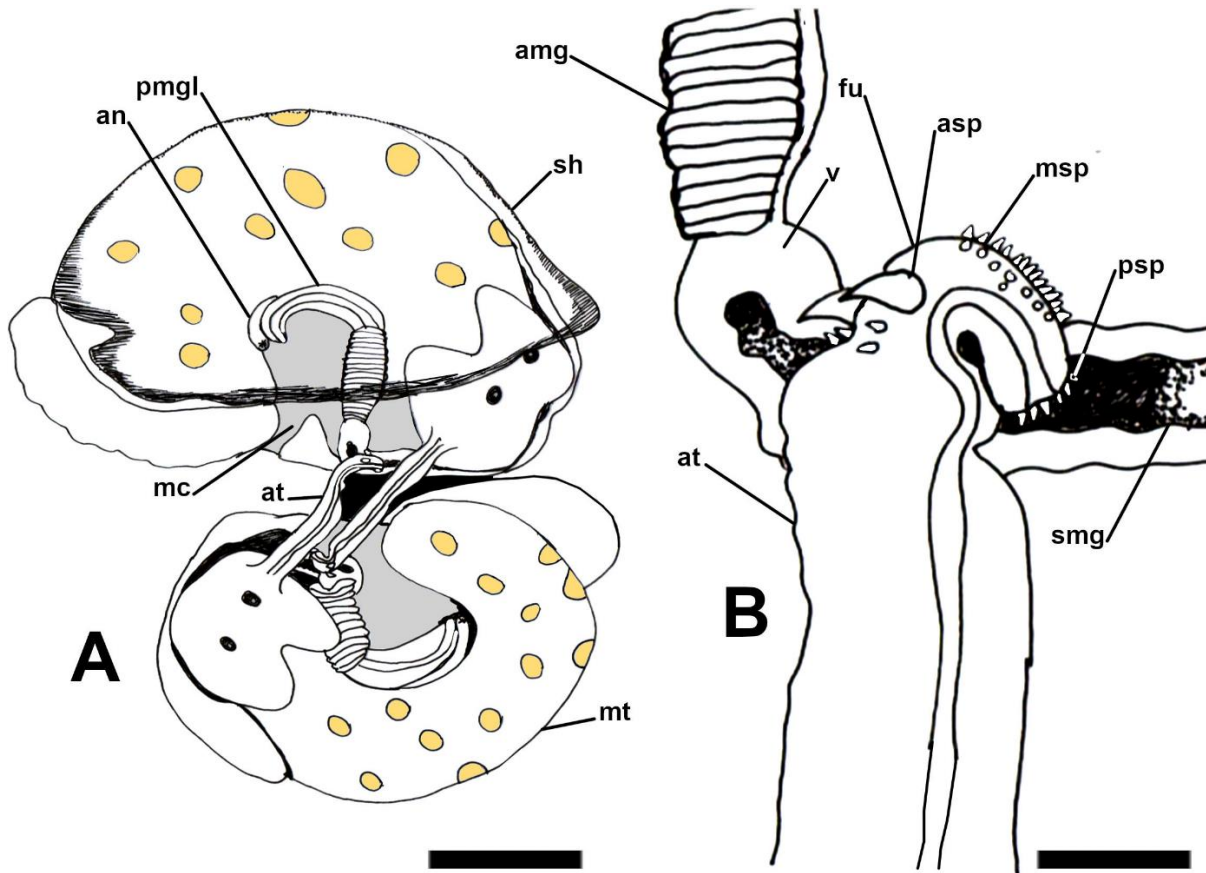


Figure 7. *Lamprohaminoea ovalis* (IM-2013-52931, H=2 mm, H = 3 mm; Vanuatu). A. specimens mating. B. close up of fundus connecting to external seminal groove. Scale bars: A = 1 mm; B = 0.2 mm. Abbreviations: amg, anterior mucous gland. an, anus. As, atrium sheath. asp, anterior spines. at, atrium. bc, body cavity. Fu, fundus. mc, mantle cavity. Msp, median spines. mt, mantle. pmgl, posterior mucous gland. psp, posterior spines.sh, shell. v, vestibule.

1.3 Haminoeidae: species diversity, biology, and human impact

Within the Cephalaspidea, Haminoeidae is the most diverse family with about 115 species considered valid (MolluscaBase, 2018a). However, the diversity is likely much higher as new species are frequently discovered (Too *et al.* 2014; Austin *et al.* 2018; Paper IV) and several are yet to be formally named (*e. g.* Papers III, VII–X). Historically the family consisted of 46 genera that have been moved back and forth between Haminoeidae and other families, but presently fewer are considered valid and part of the Haminoeidae (*e.g.* Oskars *et al.* 2015; Papers III, VI). The family Haminoeidae is thus quite important as they constitute a considerable part of Cephalaspidea diversity, but it also entails relevant ecological, economic, and human health aspects.

Species of Haminoeidae are important prey for predatory cephalaspids of the family Aglajidae (Rudman 1972b; Burn 1974; Zamora-Silva and Malaquias 2016), *Conus* gastropods (Kohn 1959), sea stars (Loh and Todd 2011) and coral reef fishes (Leray *et al.* 2013). Some species like *Haminoea orbignyana* (Férussac, 1822) can be highly productive and constitute large parts of faunal communities (Malaquias and Sprung 2005; Zabbey and Malaquias 2013), and the egg masses of this species are a food source for other gastropods such as the nudibranch *Calliopaea bellula* d'Orbigny, 1837 (Coelho *et al.* 2006).

Human consumption of Haminoeidae is not particularly common. However, species of “*Haminoea*”-like gastropods (*e.g.* *Haloa*, *Smaragdinella*, *Bakawan*) are called “Siput Bawang” or Onion Snails in Singapore and eaten with soy sauce or bean paste (Ng and Sivasothi 2001; Wild Singapore 2016). Additionally, the North West Pacific endemic *Bullacta caurina* (Benson in Cantor, 1842) [commonly referred in the literature as *B. exarata* (Philippi, 1849)], is eaten and used in Chinese traditional medicine (Ye and Lu 2001; Liu *et al.* 2013; Liao *et al.* 2017). The species is also commercially important, and is harvested and farmed in aquaculture (Ying *et al.* 2004; Li *et al.* 2014). *Bullacta* may also be useful in other respect, as compounds with potential antioxidant, antibacterial, and antitumor abilities have been isolated from the species (Liu *et al.* 2013; Ma *et al.* 2013; Liao *et al.* 2017).

This biomedical aspect is also interesting as several marine Heterobranchia have defensive secondary metabolites that may be useful as medical compounds (Cimino and Gavagnin 2007). Haminoeidae is no exception as defensive chemicals such as polypropionates, dubbed Haminols, have been isolated from species of *Haminoea* (Cimino *et al.* 1991; Marin *et al.* 1999; Cutignano *et al.* 2007; Nuzzo *et al.* 2015) and the cytotoxic polypropionate Nalodionol has been isolated from *Smaragdinella calyculata* (Broderip & Sowerby, 1829) (Szabo *et al.* 1996). Polypropionates have gained a lot of interest because of their properties as potential anticancer, antibiotic, antiparasitic and immunorepressing compounds (Davies-Coleman and Garson 1998; Peltari *et al.* 2002; Chênevert *et al.* 2003; Kigoshi and Kita 2015). Additionally, alkylphenols and alkylcatechols have been isolated from *Haloa japonica* (Pilsbry, 1895b) (as *Haminoea callidegenita*; Spinella *et al.* 1998; Marin *et al.* 1999; Izzo *et al.* 2000), which are interesting molecules for biomedicine as they seem to have cytotoxic antibiotic and DNA strand cutting abilities (Izzo *et al.* 2000).

As highlighted in theme 1.2, some species and even genera of Haminoeidae can be difficult to tell apart, and this does not only lead to taxonomic complications, as it also causes

conservation challenges. A good example is the highly invasive species *Haloa japonica*, which was not widely recognised until quite recently. The first detailed study of the species was by Gibson and Chia (1989) who described it as the new species *Haminoea callidegenita* Gibson & Chia, 1989 occurring in Washington State, USA. Later the species was also found in the Mediterranean and the Atlantic coast of North West Spain (Álvarez *et al.* 1993b as *H. callidegenita*). Álvarez *et al.* (1993b) suggested that the species could have been introduced in the 1930's with import of oysters from Washington, USA to be used in European aquaculture. It was not until Gosliner and Behrens (2006) found specimens occurring in California and compared their internal anatomy with specimens from Japan, that *H. callidegenita* was confirmed to be a synonym of *H. japonica*. This Indo-West Pacific (IWP) origin was later confirmed by molecular analyses as the species was shown to be a close relative of *Haminoea natalensis* (Krauss, 1848; = *Haloa wallisii* Gray, 1824) and other IWP species (Hanson *et al.* 2013a, b; Paper VI). *Haloa japonica* seems to be spreading north in Europe, as it was recently recorded in the Netherlands (Faase 2018).

The difficulty to identify correctly *H. japonica* was largely due to lack of knowledge about the diversity and taxonomy of species in the genus (Gosliner and Behrens 2006; Hanson *et al.* 2013a). One of the obvious consequences of lack taxonomic knowledge is that the introduction of species in alien regions can go unnoticed for long periods, with potentially negative implications. For example, *Haloa japonica* has replaced populations of the native *Haminoea vesicula* (Gould, 1855) in Boundary Bay, Canada (Hanson *et al.* 2013b) and of several native *Haminoea* species in the Laguna di Sabaudia, Italy (Macali *et al.* 2013). Additionally, it was demonstrated that *H. japonica* in California could be a potential medical and economical problem as it is an intermediate host for *Schistosoma* parasites causing cercarial dermatitis or swimmer's itch in humans (Brant *et al.* 2010; Hanson *et al.* 2013b). This is of economical concern as it may affect the recreational businesses connected to the use of local beaches (Hanson *et al.* 2013b). Interestingly, the species has not been found to host similar parasites in its native range (Hanson *et al.* 2013b) and this association between parasite and host could be a novel interaction between previously unconnected species.

Another example is *Lamprohaminoea cyanomarginata* Heller and Thompson, 1983 that is widely known as a Red Sea species, which has invaded the Mediterranean Sea through the Suez Canal (Lessepsian immigrant). The species is now spread across the eastern, south and central Mediterranean Sea (Köhler 2003; Yokes 2003; Rudman, 2003; Zenetos *et al.* 2004,

2008, 2010; Mifsud 2007; Crocetta and Vazzana 2009; Rizgalla *et al.* 2018; Paper VII) and recently was reported for the first time in the western part of this basin (Spain: Fernández-Vilert *et al.* 2018).

Fernández-Vilert *et al.* (2018) noted that the range of the species was not restricted to the Red Sea, as Köhler (2018) reported it from Oman. In addition to this, our results further showed that this species is a junior synonym of *Lamprohaminoea ovalis* (Pease, 1868) which is widely distributed from Hawaii and French Polynesia in the East, to Okinawa in the North and Australia in the South (Papers VI, VII). Species of *Lamprohaminoea* were believed to feed exclusively on cyanobacteria (Cruz-Riviera and Paul 2006), but likely also feed on diatoms (Paper VII). Cruz-Riviera and Paul (2006) found that *L. ovalis* was less selective on which genera of cyanobacteria it fed on, than other members of the genus. This broader diet and the extensive range suggest that the species can thrive in a wide range of habitats, and may be part of the success of the species outside its natural range.–The species of *Lamprohaminoea* are brightly coloured, which is likely to signal distastefulness as the species have predator deterring secondary metabolites. This may also have aided in *L. ovalis* invasion of the Mediterranean (Mollo *et al.* 2008). An unnamed brominated tetrahydropyranol has been isolated from Mediterranean specimens of *L. ovalis* (as *L. cyanomarginata*; Mollo *et al.* 2008) and from Indian specimens of the *L. ovalis* species-complex (Fontana *et al.* 2001; VII), whereas the structurally similar brominated tetrahydropyranol, kumepaloxane, has been isolated from *L. cymbalum* from Fiji (Poiner 1989). Nevertheless, it is unknown whether the metabolites of *Lamprohaminoea* are produced by the gastropods themselves or originate from their food (Poiner *et al.* 1989; Mollo *et al.* 2008).

1.4 Aims of the Thesis

The first major aim of this thesis is to resolve the systematics and taxonomy of the family Haminoeidae. The goal was to define the family, by establishing its generic diversity and affiliation within the Cephalaspidea. This was attempted by producing a phylogenetic hypothesis of the relationship of Haminoeidae to other cephalaspids and relationships of the genera within the family (Paper III). In addition to this we described the diagnostic characters of each genus based on available literature and revisionary studies (*e.g.* Too *et al.*, 2014; Austin *et al.*, 2018; Papers I, III, VI).

The second aim is to sort out the systematics and taxonomic composition of the Indo-West Pacific *Haloa sensu lato*. The goal was to define the phylogenetic relationships of the three well-supported clades recovered within *Haloa* (Paper III) and the closely related genera *Smaragdinella* and *Haminoea*. This was attempted by expanding the taxon set of paper III with specimens from all previously suggested subclades (*e.g.* Papers IV, V) and biogeographic regions. Additionally, an integrative approach combining molecular phylogenetics, conchological and morpho-anatomical characters was used to define and describe the recovered clades, establish putative relationships, and determine potential synapomorphies (Paper VI).

The third aim was to describe and characterise the species of *Haloa sensu lato* and revise their systematics through the study of conchological and morpho-anatomical characters anchored in a molecular phylogenetic framework (Papers VII, VIII, IX, X).

2. Materials and Methods

2.1 Studied Material

The majority of my studied material was made available as loans from collections of the following institutions: Australian Museum, Sydney (AMS), California Academy of Sciences, San Francisco, CA, USA (CAS); Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (FLMNH), Muséum national d'Histoire naturelle, Paris, France (MNHN), The Museum of Comparative Zoology, Harvard (MCZ, USA), Museum Victoria, Melbourne, Australia (MV), The Natural History Museum, London, United Kingdom (NHMUK, formerly BMNHUK, British Museum of Natural History), Royal Belgian Institute of Natural Science, Brussels, Belgium (RBINS), Royal British Columbia Museum, Canada (RBCM), National Museum of Natural History (Naturalis), Leiden, the Netherlands (RMNH), Santa Barbara Museum of Natural History, CA, USA (SBMNH), the Museum of Zoology, University of Michigan, USA (UMMZ), Museum für Naturkunde, Humboldt University, Berlin, Germany (ZMB) and the Zoological Museum, Natural History Museum of Denmark (ZMUC). The study also benefited from the generous donations of material of colleagues worldwide, and fieldwork conducted by Manuel Malaquias that resulted in the material available to me housed at the Invertebrate collections of the University Museum of Bergen (Department of Natural History), Norway (ZMBN). Study of shells and especially type material was made possible by research visits to the National Museum of Nature and Science, Collection Centre at Tsukuba, Japan (NSMT) and to The

Natural History Museum, London, United Kingdom (NHMUK). Relevant type material was also made available by public online collections, such as The Academy of Natural Sciences of Drexel University (ANSP) and Online Zoological Collections of Australian Museums (OZCAM).

I was also fortunate to have carried out fieldwork in Okinawa, Japan and Taiwan to collect new samples. In those cases, the living animals were relaxed in 7.5% magnesium chloride solution (mass of hydrated crystals in relation to the volume of fresh water), or frozen for 1–5 hours in sea water, and then fixed and preserved in 96% ethanol.

2.2 Phylogenetic methods

The phylogenetic study of Haminoeidae was the culmination of projects previously started by P. M. Mikkelsen, M. A. E. Malaquias and C. C. Too. Thus, a large amount of sequences was available for my phylogenetic analyses. In addition to this, the DNA extractions of these projects were available to me to amplify missing DNA markers. Some molecular data was available for haminoeids in the NCBI GenBank, most of it generated by M. A. E. Malaquias and colleagues. Nonetheless, the sequences available in GenBank were largely sufficient to perform BLAST searches to check for contaminations.

However, for *Haminoea sensu lato* the number of species with sequences on Genbank was restricted to only a few represented mostly by the cytochrome *c* oxidase subunit I (COI) gene and some sequences of the 28S rRNA gene. Therefore, considerable time was spent in the laboratory extracting and amplifying DNA from additional specimens from different localities to build up a large comparative sequence library.

For the family level phylogeny of Haminoeidae (Paper III) and for the genus and species level phylogeny of *Haloa sensu lato* (Paper VI) the molecular analyses built on the primer selection and gene selection that had proven useful for cephalaspids including haminoeids in previous studies (e.g. Malaquias *et al.* 2009; Hanson *et al.* 2013a; Oskars *et al.* 2015; Austin *et al.* 2018). The standard gene markers used in the phylogenetic analyses were the mitochondrial gene markers COI and 16S rRNA, which have relatively fast mutation rates and usually return good resolution at species and genus level. The nuclear gene markers 28S rRNA and Histone H3 have slower mutation rates and usually have good resolution on generic, family and higher taxonomic levels (e.g. Malaquias *et al.* 2009; Oskars *et al.* 2015). For the phylogeny of Haminoeidae (Paper III) the nuclear 18S rRNA gene was also included

as it showed good resolution on higher taxonomic levels before (Malaquias *et al.* 2009). For the phylogeny of *Haloa sensu lato* (Paper IV) the less frequently employed mitochondrial gene 12S rRNA (12S) was included as it previously showed to yield promising results in separating molluscan species (Järnegren *et al.* 2007; Puillandre *et al.* 2009).

For papers I, IV, V, which were mainly focused on species identification and delimitations, the standard barcode gene COI was chosen for the phylogenetic analyses, and the species hypotheses were tested with the species delimitation method Automatic Barcode Gap Discovery (ABGD). The principle of this method focuses on the barcode gap, which assumes that the genetic distance of specimens within a species is lower than the genetic distance between species. The ABGD method detects a “gap” in the genetic distance of analysed sequences where there is little or no overlap between intraspecific and the interspecific genetic distance. Following this, sequences are clustered into hypothetical species, based on a set upper threshold on the intraspecific distance. The method then partitions the sequences into groups/species based on the next gap between intra- and interspecific distance and repeats this method until the data cannot be further partitioned (Puillandre *et al.* 2012). For papers VII, VIII, IX and X the COI sequences used in paper VI were analysed with the ABDG method to compare with species distinguished by anatomical characters.

The phylogenetic analyses of Haminoeidae and *Haloa sensu lato* followed the methods that had proven most useful for previous studies on cephalaspids. The individual gene datasets were concatenated (fused) to a single dataset and analysed by Bayesian analysis (Malaquias *et al.* 2009; Hanson *et al.* 2013a; Eilertsen and Malaquias 2013; Oskars *et al.* 2015; Moles *et al.* 2017; Austin *et al.* 2018). Additional tree-building methods were used to test for congruency of results. For both phylogenetic analyses using several gene markers (Papers III, VI) the datasets were additionally run under maximum likelihood models (ML) and in paper III we also used maximum parsimony (MP). Because Bayesian analysis can overestimate support values for nodes (Simmons *et al.* 2004), we also tested robustness of the clades with bootstrap analyses in ML and MP.

2.3 Morpho-anatomical methods

When the phylogenetic framework was in place, specimens from distinct geographical origins representing each lineage were selected to characterise the morphological and

anatomical features of species. The laboratory work performed for all the papers followed the same methods and workflow.

2.3.1 Dissections

The animals were gently separated from the shell with the aid of forceps, but when the animals were deeply retracted, the shells were broken to facilitate extraction. The female reproductive system, male reproductive system, gizzard, and buccal bulb were dissected out by opening the cephalic shield dorsally. Shells from museum collections and dissected specimens were imaged with a DSLR camera equipped with macro-lens. The dissected organs and Hancock's organs were drawn using a stereo microscope fitted with a drawing tube. Drawings were later traced and shaded on lime paper with pigment markers.

2.3.2 Scanning electron microscopy (SEM)

The gizzard and buccal bulb were dissolved and the gizzard plates, gizzard bristles, jaws, and radulae were cleaned by digesting the surrounding tissue with enzymes following a protocol modified from the studies of Holznagel (1998) and Vogler (2013). The structures were incubated at 56°C for approximately 4–6 hours, in a solution of the protein degrading enzyme proteinase K suspended in ATL buffer (see Papers I–X). For formalin fixed material for which the aforementioned method did not work, maceration took place in a 10–30% solution of lye (NaOH).

Prior to SEM, gizzard plates, gizzard bristles and jaws were critical-point dried (CPD) to avoid distortion resulting from dehydration. This distortion is caused by the effects of surface tension acting on the tissue as the liquid medium (*e.g.* water, ethanol (EtOH)) crosses the phase boundary from liquid phase to gaseous phase. CPD works by gradually replacing EtOH with liquid carbon dioxide (CO₂), and then increasing the temperature and pressure until the critical point of temperature and pressure is reached. At the critical point (CO₂: 31°C; 74 bar/73 atm) the physical differences between liquid and gaseous phases are close to identical and the phase boundary between the phases dissipates. In other words, the liquid can pass directly to gaseous phase, eliminating the effects of surface tension (Anderson 1951, 1966; Bozzola & Russell, 1999).

All anatomical parts were mounted on metallic stubs using carbon sticky tabs. The radulae were mounted directly by orienting this structure inside a drop of water and flattening with a

fragment of glass cover slip until they dried. The stubs were then coated with gold-palladium prior to imaging.

2.3.3 Graphic images

All images and plates in the thesis and the papers were made in Inkscape 0.92 (Inkscape Team, 2015) and Gimp 2.10 (Mattis *et al.*, 1995; Natterer *et al.*, 2018).

3. Redefining the family Haminoeidae

3.1.1 The systematics and phylogeny of

Haminoeidae (I–III)

Many species and genera of Haminoeidae are known only from their shells or a few anatomical characters. Additionally, there is substantial taxonomic uncertainty due to vague original descriptions of many of the taxa. The systematics of the family is also complicated by the inconsistent use of shells and anatomy to build classification systems. This inconsistency of character choice has been the rule for classification of most cephalaspideans (Mikkelsen 1993).

Historically, 46 genera have been assigned to Haminoeidae (Iredale 1929, 1936; Habe 1952; Kuroda and Habe 1952; Burn 1974, 1978; Burn and Thompson 1998; Higo *et al.* 1999; Too *et al.* 2014; Paper VI). However, only 13 to 17 names have been used in recent literature (Too *et al.* 2014), and only 15 are recognised as valid in MolluscaBase (2018a). The first species described belonging to the Haminoeidae are *Atys naucum* (Linnaeus, 1758) and *Haminoea hydatis* (Linnaeus, 1758), and as most cephalaspids they were originally assigned to the genus *Bulla* Linnaeus, 1758. Only later, *B. naucum* was ascribed by Montfort (1810; as *A. cymbulus*) to the genus *Atys*, which was the first true haminoeid genus.

The species *B. hydatis* was selected by Turton and Kingston (1830) as the type species of *Haminoea*, which later became the type genus of Haminoeidae. At the time, Turton and Kingston (1830) assigned their new genus to the recently described family Bullidae Gray, 1827, which held most of the cephalaspids. In the following years several more bubble-shelled genera were described such as *Alicula* Ehrenberg, 1831 (= *Aliculastrum* Pilsbry, 1896), *Roxania* Leach 1847 (now part of Alacuppidae Oskars, Bouchet & Malaquias, 2015, Paper III), *Dinia* H. Adams & A. Adams, 1854 (= *Diniatys* Iredale, 1936), *Weinkauffia*

Weinkauff, 1873 and *Roxaniella* Monterosato, 1884. Of these, Fischer (1883) only considered *Dinia* and *Alicula*, and regarded them subgenera of *Atys*. Fischer (1883) retained *Haminoea* in Bullidae, but reassigned *Atys* and *Smaragdinella* A. Adams, 1848 to Scaphandridae G. O. Sars, 1878 and *Phanerophthalmus* A. Adams, 1850 to Philinidae Gray, 1850.

Later, Pilsbry (1895a) regarded all the aforementioned bubble-shelled genera as subgenera of *Atys*, but retained the system of Fischer (1883). On the other hand, he included *Haminoea* as the single genus of the subfamily Haminoeinae Pilsbry (1895a) which he placed in Akeridae Mazarelli, 1890. The latter family is now part of the sea-hare order Anaspidea Fischer, 1883. Bergh (1900, 1901, 1905) regrouped most of the haminoeids back under Bullidae based on characters like shells, radulae and reproductive systems. On the other hand, he described the family Ophthalmidae Bergh, 1905 to accommodate the flat-shelled *Smaragdinella*, *Phanerophthalmus*, and *Cryptophthalmus* Ehrenberg, 1828.

Thiele (1925) using similar characters, was the first to establish the traditional concept of haminoeids, by uniting them in the family Atyidae¹ Thiele, 1925. He further split the family into two subfamilies. The first was Atyinae for *Atys*, *Bullacta*, *Haminella* Thiele, 1925, *Haminoea*, and *Liloea* Pilsbry, 1921. Whereas, the second was Smaragdinellinae Thiele, 1925, for *Smaragdinella*, *Cryptophthalmus*, and *Phanerophthalmus*. Later, Thiele (1926) also separated out *Bullacta* and placed it in its own subfamily Bullactinae Thiele, 1926.

By the early 21st century, most of the haminoeid genera were split within three widely accepted families Haminoeidae, Smaragdinellidae (for *Smaragdinella* and *Phanerophthalmus*) and Bullactidae (for *Bullacta*) (Burn and Thompson 1998; Bouchet and Rocroi 2005; Bouchet *et al.* 2017). Nevertheless, the first molecular phylogenetic studies focused on cephalaspids suggested a different systematic arrangement. For example, *Smaragdinella* and *Phanerophthalmus* did not form a distinct family as they consistently clustered with other Haminoeidae genera (Malaquias *et al.* 2009; Oskars *et al.* 2015). The genus *Bullacta* was found to be sister to the remaining Haminoeidae, but its internal anatomy suggested its inclusion in the family (Malaquias 2010; Oskars *et al.* 2015). Additionally genera traditionally considered part of the Haminoeidae, such as *Mnestia* H. Adams & A.

¹ Due to homonymy with Atyidae De Haan, 1849 (Crustacea) the emended correct family name is Atydidae. See Opinion 1553. Bulletin of Zoological Nomenclature 46(3), September 1989.

Adams, 1854 (often called *Ventomnestia* Iredale, 1936), were showed to belong elsewhere deserving in some cases their own family assignment (e.g. family Mnestiidae Oskars, Bouchet & Malaquias, 2015; Malaquias *et al.* 2009; Oskars *et al.* 2015; Paper III).

However, the affiliation of most of the 46 genera associated with the family has not been tested in a phylogenetic framework. This coupled with the lack of modern systematic revisions of most lineages means that the validity and affiliation of many of the haminoeid genera remained until now uncertain (Oskars *et al.* 2015). In addition to this, the knowledge on the anatomy of several species and genera is restricted, as most studies have focused on few characters (e.g. Habe 1952) or few selected species and genera (e.g. Er. Marcus and Burch 1965; Burn 1966; 1969, 1974; Ev. Marcus and Er. Marcus 1970; Rudman 1971a, b, 1972a; Gibson and Chia 1989; Gosliner 1994; Carlson and Hoff 2000a, b; Gosliner and Behrens 2006; Malaquias and Cervera 2006).

Burn (1978) was the first to give a comparative overview of the anatomy of *Atys*-like genera, but focused on species occurring in Australia. Burn (1978) studied characters such as external morphology, shells, radulae and male reproductive systems of the genera *Austrocylichna* Burn, 1974, *Nipponatys* Habe, 1952, *Cylichnatys* Habe, 1952, and *Diniatys*, which led him to regard the genera as distinct. Later Too *et al.* (2014) conducted a detailed anatomy-based study that aimed to define the synapomorphies for genera commonly confused with *Atys*, which led them to redefine the genera *Aliculastrum*, *Diniatys* and *Liloa*. These studies made, at least in some cases, possible to reevaluate taxonomic affiliations based only on characters of the shell. This was shown in paper II, as the species *Haminoea callosa* Preston, 1908, was found to possess a projection on the columella. Too *et al.* (2014) found this feature to be unique for *Diniatys*, which led us to reassign the species to genus *Diniatys*.

On the other hand, Too *et al.* (2014) could not find any synapomorphies for the genus *Atys* suggesting that the genus could be an artificial group. In paper I we investigated the Mediterranean and Macaronesian species *Atys jeffreysi* (Weinkauff, 1866) which is the type species of the subgenus *Roxaniella* (e.g. Pilsbry, 1895a). We compared this species to the ampho-Atlantic *Atys macandrewii* E. A. Smith, 1872 that is the only other confirmed *Atys* species to occur in the Mediterranean. The study also included a phylogeny based on the gene cytochrome *c* oxidase sub-unit I (COI), including all available sequences of *Atys*, and the closely related *Aliculastrum* and *Liloa*. The results pointed towards the possible paraphyly of *Atys* supporting the conclusion of Too *et al.* (2014; paper I) and this was

corroborated by our much broader analysis of the Haminoeidae based on a multilocus approach and extensive taxon sampling (Paper III).

Paper III is the most comprehensive study of the family to date, and it revealed several novelties regarding the systematics of Haminoeidae. For example species of the genus *Cylichnium* Dall, 1908 which has been placed both within Haminoeidae (Thiele 1925, 1931; Nordsieck 1972) and Scaphandridae (Dall 1908; Bouchet 1975; Valdés 2008; Valdés and McLean 2015), branched off alone and most likely belong to a distinct family. *Hamineobulla* Habe 1950 has been included in Bullidae (Habe 1950; MolluscaBase 2018b) or Haminoeidae (Kitao and Habe 1982; Higo *et al.* 1999, 2001). However, Rudman (2000) suggested that *Hamineobulla* might be related to Scaphandridae, as they had similar radulae, a relationship that was strongly supported by our analyses (Paper III). The genera *Mimatys* Habe, 1950 and *Roxania* have both been included in Haminoeidae (Habe 1950; Bouchet 1975; Gantes and Coronet 1981) or Scaphandridae/Cylichnidae (Thompson 1976, 1988; Higo *et al.* 1999; Valdés 2008), but both belonged to the family Alacuppidae.

Another novelty was that the two most well known genera of the family, *Atys* (70 species; MolluscaBase 2018c) and *Haminoea* (61 species; MolluscaBase 2018d) were confirmed as non-monophyletic. On the other hand, the genera *Aliculastrum*, *Diniatys* and *Liloa* as defined by Too *et al.* (2014) were found to be valid. Lineages traditionally ascribed to *Atys* split in four clades, namely *Roxaniella*, *Weinkauffia*, *Vellicolla*, and *Atys* proper. *Roxaniella* was found to be closer to *Aliculastrum* and *Liloa*, whereas *Weinkauffia* branched off as the second most basal genus within Haminoeidae (Paper III). *Atys* was redefined to include only three known species, namely the type species *A. naucum*, *A. kuhnsi* Pilsbry, 1917, and *A. semistriatus* Pease, 1860. Several genera were synonymized such as *Limulatys* Iredale, 1936 (= *Weinkauffia*) *Nipponatys* (= *Aliculastrum*), *Micraenigma* Berry, 1953 (= *Diniatys*) and *Austrocylichna* (= *Roxaniella*) and one new genus was described, namely *Vellicolla* to accommodate several of the brightly coloured haminoeids (Paper III). A group to which no name is available was rendered and is here referred informally as Mini Haminoeids (Paper III).

As mentioned above, *Haminoea* did not form a monophyletic group, but the extent of the paraphyly of *Haminoea* was not in any way anticipated (Paper VI). The Atlantic species *Haminoea solitaria* (Say, 1822), an established member of the genus, was found to belong to the resurrected genus *Haminella* (Paper III). Yet, the remaining *Haminoea sensu lato*

formed a well-supported clade, but with the genus *Smaragdinella* nested inside as sister to all IWP species. Thus, we retrieved an Atlantic + East Pacific clade of *Haminoea*, sister to an IWP clade, containing *Smaragdinella*.

However, the limpet like, rocky intertidal genus *Smaragdinella* is anatomically distinct (see Risbec 1951; Er. Marcus and Burch 1965; Rudman 1972a; Chaban and Chernyshev 2016) from the IWP *Haminoea* (see Er. Marcus and Burch 1965; Rudman 1971a, b; Gosliner and Behrens 2006) and the IWP *Haminoea* have features that are not present in the Atlantic + East Pacific ones, such as the presence of a fundus lacking a muscular penis in the male reproductive system (Fig. 5) (Papers III, VI). Therefore, and thus we re-erected the genus *Haloa* to accommodate the IWP species.

However, Paper III did not include all known species of the IWP genus *Haloa sensu lato*. When the taxon set was expanded to include these (Paper VI), the analyses found four distinct clades of these snails. The *Haloa* proper with dull coloured species from the entire IWP (Paper X), the new genus *Papawera* Oskars & Malaquias, VI with Australasian temperate species (Paper IX), *Lamprohaminoea* Lin, 1997 only with the colourful species (Paper VII), and the new genus *Bakawan* Oskars & Malaquias, VI only with mangrove-associated species (Paper VIII).

The results of paper III severely reduced the number of the 46 genera historically connected to Haminoeidae to only 14 valid genera. Additionally, of the 13 to 17 commonly recognised genera mentioned by Too *et al.* (2014), three were regarded as synonyms and we suggested the exclusion of several valid genera from Haminoeidae. Unfortunately, we could not test some of these molecularly, but their shell and anatomical features clearly suggest a distant affiliation (*e.g.* *Osorattis* Iredale, 1929, *Spissitydeus* Iredale, 1936 and *Micratys* Habe, 1952; Paper III). Based on the results of papers III and VI we retrieved a total of 17 genera, of these, *Vellicolla*, *Bakawan* and *Papawera* were new to science and the Mini Haminoeids formed an additional eighteenth group that is likely one or possibly two undescribed genera.

However, there are still several unanswered questions, as some genera synonymized based on anatomical characters were not available for molecular analyses. *Cylichnatys* is one of these genera with a unique external morphology and internal anatomy that sets it apart from all other genera of haminoeids (Burn 1978; Chaban and Chernyshev 2014). Due to this, we considered the genus valid, but it remains uncertain where it fits within the family.

Even though the systematics of Haminoeidae is now much better known (Papers III, VI), it is not so straight forward to define the family based on morphological synapomorphies. The traditionally recognised synapomorphies of the family are the three chitinous gizzard plates and the reduction of the interior whorls of the shells due to reabsorption (Er. Marcus 1957, 1958; Burn 1978; Mikkelsen 1996; Burn and Thompson 1998; Too *et al.* 2014, Papers III, VI). Nevertheless, these features have also been found in the genus *Mnestia* (Carlson and Hoff 2000b), which now belongs on its own family (Oskars *et al.* 2015). However, a novel character that is a potential synapomorphy was found in the female reproductive system, namely a lamellate anterior mucous gland, which so far is only documented in genera of the Haminoeidae (see Bergh 1901; Er. Marcus 1958; Ev. Marcus 1970; Rudman 1971a, b, 1972a; Gosliner 1994; Papers VII–X; Figs 4, 6). However, it is not yet confirmed whether this feature occurs in all genera of the Haminoeidae.

3.1.2 The systematics and taxonomy of genus *Haloa* *sensu lato* (IV–X)

The result of papers III, IV and V suggested that the systematics of *Haloa* needed to be further investigated. This led to paper VI where we studied the phylogenetic and taxonomic composition of *Haloa* based on an expanded taxon set with all available specimens from all putative species across their geographical distributions. The results supported the hypothesis that *Haloa* in reality consists of four distinct clades of generic level, *Haloa* Pilsbry, 1921, *Lamprohaminoea* Lin, 1997 and the new genera *Bakawan* Oskars & Malaquias, VI and *Papawera* Oskars & Malaquias, VI with unique morphological synapomorphies and ecologies (paper VI).

The name *Lamprohaminoea* was re-erected for the clade of brightly coloured species all distributed across sub-tropical and tropical waters of the IWP, possessing distasteful secondary metabolites that act as predator deterrents (Poiner *et al.* 1989; Fontana *et al.* 2001; Mollo *et al.* 2008). The genus is distinguished by having a seminal duct, which consist of a circular lumen within an outer duct, and a fundus filled with chitinous spines (Paper VI). Five species were recognised (Paper VII), including the species *L. cymbalum* (Quoy & Gaimard, 1832) and *L. ovalis* (Pease, 1868) and an additional three undescribed species. The previously well-established species “*Haminoea*” *cyanomarginata* Heller & Thompson, 1983

was showed to be conspecific with *L. ovalis*, which is highly polychromatic. This polychromy may cause *L. ovalis* to look quite similar to the other species, but the species can be separated by the internal fundus, where the spines form distinctive patterns (Paper VII).

The new genus *Bakawan* Oskars & Malaquias, (Paper VI) includes species that are restricted to mangrove habitats in the Indian Ocean and western Pacific (Cobb 2018; Yonow and Jensen 2018; Papers V, VIII). *Bakawan* has a unique seminal duct with a cross-section showing 6–8 grooves radiating from the central lumen and a thick-walled fundus with modified lateral walls (Paper VI). Four species were recognised in the genus including two undescribed (Papers VI, VIII). The shells and jaw elements show subtle yet distinctive differences between species, but the best character to discriminate is the shape of the right lateral wall of the fundus, which has unique modifications in all species.

The genus *Papawera* Oskars & Malaquias, (Paper VI) was erected for the temperate Australasian species *Papawera zelandiae* (Gray, 1843), endemic to New Zealand, and *P. maugeansis* (Burn, 1966), endemic to temperate southern Australia. The genus has a unique annulated prostate and a seminal duct with a cross-section depicting a semi-enclosed duct within an outer layer (Paper VI). In paper IX we redescribed these two species, which have different external morphologies, but share similar radulae, jaws and architecture of the male reproductive system, however with distinct prostates and fundi.

Haloa includes only dull-coloured species distributed across the IWP (Papers III, VI, X) and is distinguished by a cross-section of the seminal duct with four grooves radiating from the lumen forming a cross and a fundus filled with soft flaps, warts, or ridges (Paper VI).

Thirteen species were recognised including three undescribed species. The external morphology and colour patterns are similar between species making distinction difficult. However, the species can be separated by the internal fundus, which is modified with thickened walls or thin walls lined with distinctive patterns (Paper X).

4. Summary of main results

- The historical taxonomic diversity of Haminoeidae, was largely based on shells and a few anatomical characters, with 46 genera historically being ascribed to the family and only 13–17 genera commonly accepted in recent literature. However, a combination of molecular phylogenetics with a revision of the anatomical features of

the genera redefined the number of genera to 17 and one undescribed group that likely is a distinct genus (papers III, VI).

- The valid genera *Cylichnium*, *Haminoebulla*, *Micratys*, *Mimatys*, *Mnestia*, *Osorattis*, *Spissitydeus* and *Roxania*, which have historically been connected to Haminoeidae was shown to not belong to the family (Paper III).
- Although several characters such as the external morphology, shells, radulae and gizzard plates were previously difficult to use on their own, after our molecular phylogenetic framework and systematic revision of the genera, it is now possible to use these morpho-anatomical features for generic identification (Papers II, III).
- At species level, the external morphology, shells, radulae and gizzard plates are difficult to use alone for identification but often when combined are possible to use in species recognition (Papers III, VI). However, the male reproductive system can in most cases confidently recognise genera and species.
- The genus *Atys* was confirmed polyphyletic, and redefined to include only three IWP species. The genera *Roxaniella*, *Vellicolla*, *Weinkauffia*, previously considered subgenera or junior synonyms of *Atys*, were shown to be valid genera (Paper III).
- The genus *Haminoea sensu lato* was shown to be paraphyletic with three main radiations: *Haminoea sensu stricto* (Atlantic + EP), *Smaragdinella* (IWP), and *Haloa sensu lato* (IWP) (Paper III).
- The IWP *Haloa sensu lato* consist of four molecularly and anatomically distinct genera, including *Haloa*, *Lamprohaminoea* and two the new genera here described, namely *Bakawan* and *Papawera*.
- *Lamprohaminoea* have distinctly colourful species, with distasteful metabolites that deter predation. Although reported to only feed on cyanobacteria (Cruz-Riviera and Paul 2006) it was found that they also feed on diatoms. The well-known invasive species *L. cyanomarginata* is a junior synonym of *L. ovalis* (Paper VII).
- Specimens of what is often named “*Haminoea fusca*” (Paper V) belong to the new genus here described *Bakawan*, and includes four externally cryptic species but with distinct anatomies. Most records of “*Haminoea fusca*” refer in fact to other species of the genus and the most wide spread species is *Bakawan rotundata*, whereas the “true” *B. fusca* is only confirmed from the Philippines (Paper VIII).
- *Papawera* is a genus that consist of only two species, *P. maugeansis* and *P. zelandiae*, restricted to temperate Australasia (Papers VI, IX).

- *Haloa sensu stricto* is restricted to the IWP and is ecologically diverse and rich in species, but external similarity between lineages makes species recognition difficult. The species *Haloa japonica* is highly invasive in the Mediterranean Sea, North East Atlantic and North East Pacific (Paper X).

5. General conclusions and future perspectives

The traditionally preferred characters for classifying haminoeids have been the shells and the radulae. However, these morphological characters may be very similar in different groups and difficult to use in taxonomic work. A lesson from our comparative studies is that the hard parts of the internal anatomy, radulae, jaws and gizzard plates are quite useful in delimiting genera, but have limited value in species identifications except when used in combination with other characters. On the other hand, the characteristics of the soft internal anatomy, especially the details of the hermaphroditic reproductive system, hold great value on all taxonomic levels, but the male part is especially useful at species level. The systematics of Haminoeidae and their evolutionary relationships have been clarified thanks to comprehensive molecular analyses combined in an integrative approach with anatomical studies (Paper III). As the most complete revision of Haminoeidae to date, we have emended the systematics of the family, but also exposed holes that need to be filled by future studies.

Two of the considered defining features of the family are the presence of three chitinous gizzard plates and the reduction of the interior whorls of the shells (Er. Marcus 1957, 1958; Burn 1978; Mikkelsen 1996; Burn and Thompson 1998; Too *et al.* 2014, Paper III). Similar features have been reported in the family Mnestiidae (genus *Mnestia*) by Carlson and Hoff (2000b). *Mnestia* has not been studied in depth and future studies should clarify the anatomy of this elusive genus to determine if these features apparently shared with the Haminoeidae are in fact the same and thus likely the result of convergent evolution. However, the presence of lamellate mucous glands in the female part of the reproductive system seems to be unique to the Haminoeidae.

Remaining problems rest with some of the more obscure genera that were not available for molecular phylogenetic analyses. For instance, the genus *Cylichnatys* was found to be anatomically distinct (*e.g.* Burn 1978; Chaban and Chernyshev 2014) and is considered a valid genus, but its phylogenetic position within the family is unknown (Paper III). Yet, features of the reproductive system suggest a possible connection to *Liloa* and *Aliculastrum*

(Paper III), but this should be investigated further with DNA and other data. The type species of *Weinkauffia* (*W. turgidula*) from the Mediterranean was described in detail by Vayssière (1893), but was also unavailable for sequencing. Future studies should aim to redescribe and sequence the species to compare with IWP species ascribed to this genus. *Limulatys* was regarded a junior synonym of *Weinkauffia* (III), but the type species of *Limulatys*, (*Weinkauffia reliquus*) has an unknown anatomy and should be studied and sequenced to confirm the taxonomic status of the genus. The genus *Nipponatys* was regarded a junior synonym of *Aliculastrum* and *Austrocylichna* was synonymised with *Roxaniella* (Paper III), but this was drawn from shell and anatomical characters only, because no specimens were available for sequencing. These genera need to be investigated in the future to confirm their taxonomic status and affiliation.

Although some well-known genera have been redefined, there are still major gaps in the knowledge of their systematics and taxonomy. The genus *Haminoea sensu stricto* includes around 18 species occurring in the Atlantic, EP and temperate South Africa. However, most species of *Haminoea* have not been comprehensively revised across its entire range and most of the information available on the species is from the original descriptions or regional studies (e.g. Malaquias and Cervera 2006). *Smaragdinella* includes the well-known species *S. calyculata* and *S. sieboldi* A. Adams, 1864 that were described based on shells. Luckily, these shells are quite distinctive as *S. calyculata* only has a small cup-shaped remnant of the interior whorls (Habe 1952; Burn and Thompson 1998, Paper III), whereas *S. sieboldi* has an apparent coil of the last whorl (Chaban and Chernyshev 2016, Paper IV). However, our results (Papers III, VI) show that the genus contains two distinct clades that conform to either shell type, but both clades seem to hold several species (Paper VI, fig 1A). A comprehensive revision of the genera *Haminoea* and *Smaragdinella* is needed to fully understand their diversity and systematics.

The genus *Atys* previously held around 70 species from all oceans, but our results restricted the number to IWP species as many others have been reassigned to other genera. However, there are still several elusive species that are only known from the shell and therefore have an uncertain affiliation (MolluscaBase 2018c). Of the three confirmed species, the internal anatomy has only been described for *A. naucum* (Bergh 1901; Carlson and Hoff 1999), whereas *A. kuhnsi* is only known from external morphology (Pittman and Fiene 2018) and DNA (Oskars *et al.* 2015). However, preliminary molecular and anatomical data of

specimens conforming to shells of *A. naucum*, suggest it to be a complex of species (Oskars pers. obs.). Our results from paper **III**, further suggested a similar case for the IWP species *A. semistriatus*, which may in fact be a complex of several lineages. Two species names available that resemble *A. semistriatus* are *A. oiformis* (Habe, 1952) from Japan and *A. xarifae* Er. Marcus & Ev. Marcus, 1960, from the Maldives. Likewise, a broader study of the genus *Atys* is needed to determine the true diversity of species.

Haminella is the sister genus of *Atys*, but its type species *H. maltzani* Thiele, 1925 from Dakar, Senegal is only known from the original description. The only specimens available for study belonged to the species *Haminella solitaria* from the West Atlantic coast of USA. It remains to be clarified whether in fact there is one amphi-Atlantic species or two species. New collecting efforts in West Africa are necessary.

Our phylogenetic analyses revealed seemingly undescribed species in the genera *Aliculastrum*, *Diniatys*, *Haminoea* and *Roxaniella* that could be formally described in future studies (Papers **III**, **IV**).

The new informal group “Mini-haminoeids” (Paper **III**) warrants a name and the formal description of its species diversity. Several species are known in this group, but none are described. At last, the new genus here described *Vellicolla* was defined based on shells, external morphology, and molecular data, but the anatomy remains unknown. *Vellicolla* was rendered sister to the “Mini-haminoeids” and hopefully in light of novel specimens its anatomy can also be studied.

6. References

- Adams, A. (1848). ‘Notes from a journal of research into the natural history of the countries visited during the voyage of HMS Samarang: under the command of Captain Sir Edward Belcher’. (Reeve, Benham, and Reeve: London, UK).
- Adams, A. (1850). ‘Monograph of the family Bullidae. In Thesaurus Conchyliorum, or Monographs of Genera of Shells, vol. II’. (Ed. G. B. Sowerby) pp. 553–608 (Sowerby: London, UK).
- Adams, A. (1862). On Some New Species of Cylichnidae, Bullidae and Philinidae from the Seas of China and Japan. *The Annals and Magazine of Natural History* **39**, 150–161.

-
- Adams, A. (1864). XXXI.— On some new genera and species of Mollusca from the seas of China and Japan. *The Annals and Magazine of Natural History* **13**, 307–310.
- Adams, H., and Adams, A. (1854). ‘The Genera of Recent Mollusca, arranged according to their organization. Vol. 2’. (John Van Voorst: London, UK).
- Álvarez, L. A., García, F. J., and Villani, G. (1993a). A new Mediterranean species of *Haminaea* Leach, 1820 (Gastropoda: Opisthobranchia: Cephalaspidea). *Journal of Molluscan Studies* **59**, 339–345.
- Álvarez, L. A., Martínez, E., Cigarría, J., Rolán, E., and Villani, G. (1993b). *Haminaea callidegenita* Gibson and Chia, 1989 (Opisthobranchia: Cephalaspidea), a Pacific species introduced in European coasts. *Iberus* **11(2)**, 59–65.
- Anderson, T. F. (1951). Techniques for the preservation of three-dimensional structure in preparing specimens for the electron microscope. *Transactions of the New York Academy of Sciences* **13(4, II)**, 130–134.
- Anderson, T. F. (1966). ‘Electron microscopy of microorganisms, in Physical Techniques in Biological Research, 2nd ed., Vol. 3’ (Eds. Oster, G. and Pollister, A.) pp. 319–387 (Academic Press, New York, USA).
- Austin, J., Gosliner, T., and Malaquias, M. A. E. (2018). Systematic revision, diversity patterns, and trophic ecology of the tropical Indo-West Pacific sea slug genus *Phanerophthalmus* A. Adams, 1850 (Cephalaspidea, Haminoeidae). *Invertebrate Systematics*, **32**, 1336–1387.
- Bartsch, P. (1915). Report on the Turton Collection of South African marine mollusks, with additional notes on other South African shells contained in the United States National Museum. *Bulletin of the United States National Museum* **91**, XII + 1–305.
- Benson, W. H. (1842) in Cantor, T. (1842). LIII. General Features of Chusan, with remarks on the Flora and Fauna of that Island. *Journal of Natural History* **9(60)**, 481–493.
- Bergh, R. (1900). Reisen im Archipel der Philippinen von Sr. C. Semper, Wissenschaftliche Resultate. 7. Band. In: ‘Malacologische Untersuchungen. 4. Abtheilung. 2. Abschnitt,

-
- Tectibranchia, Lophocercidae, Ascoglossa, 1. Lieferung' pp. 159–208, pls. 13–16 (pl. XIII–XVI). (C. W. Kreidel: Wiesbaden, Germany).
- Bergh, R. (1901). Reisen im Archipel der Philippinen von Sr. C. Semper, Wissenschaftliche Resultate. 7. Band. In: 'Malacologische Untersuchungen. 4. Abtheilung. 3. Abschnitt, Bullacea. 1. Lieferung' pp. 209–312, pls 17–24 (pls XVII–XXIV). (C. W. Kreidel: Wiesbaden, Germany).
- Bergh, R. (1905). 'Die Opisthobranchiata der Siboga–Expedition. Monographie 50'. (E. J. Brill: Leiden, the Netherlands).
- Berry, S. S. (1953). Notices of new west American marine Mollusca. *Transactions of the San Diego Society of Natural History* **1116**, 405–428.
- Bouchet, P. (1975). Opisthobranches de profondeur de l'Océan Atlantique:- Cephalaspidea. *Cahiers de biologie marine* **16**, 317–365.
- Bouchet, P., and Rocroi, J. P. (2005). Classification and nomenclator of gastropod families. *Malacologia* **47**, 1–397.
- Bouchet, P., Rocroi, J. P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M., and Strong, E. E. (2017). Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* **61(1–2)**, 1–526.
- Bozzola, J. J., and Russell, L. D. (1999). 'Electron microscopy: principles and techniques for biologists'. (Jones & Bartlett Learning, Burlington, USA).
- Brant, S. V., Cohen, A. N., James, D., Hui, L., Hom, A., and Loker, E. S. (2010). Cercarial dermatitis transmitted by exotic marine snail. *Emerging Infectious Diseases* **16(9)**, 1357–1365.
- Broderip, W. J., and Sowerby, G. B. (1829). Observations on new or interesting Mollusca contained, for the most part, in the Museum of the Zoological Society. *Zoological Journal* **4**, 359–379.
- Burmeister, H. 1837. 'Handbuch der Naturgeschichte, vol. 2, Zoologie'. (Enslin: Berlin, Germany).

-
- Burn, R. (1966). Port Phillip Bay Survey 1957–1963. Opisthobranchia. *Memoirs of Museum Victoria* **27**, 265–288.
- Burn, R. (1969). A memorial report on the Tom Crawford collection of Victorian Opisthobranchia. *Journal of the Malacological Society of Australia* **12**, 64–72.
- Burn, R. (1974). Notes on some benthonic opisthobranchs from Port Phillip Bay, Victoria. *Journal of the Malacological Society of Australia* **31**, 43–57.
- Burn, R. (1978). A review of Australian species of *Austrocylichna*, *Nipponatys*, *Cylichnatys* and *Diniatys* (Mollusca: Gastropoda: Haminoeidae). *Journal of the Malacological Society of Australia* **41–2**, 93–112.
- Burn, R., and Thompson, T. E. (1998). Order Cephalaspidea. In: 'Fauna of Australia, Mollusca: The Southern Synthesis. Part B, VIII, vol. 5. (Eds Beesley, P. L., Ross, G.J.B., and Wells, A.A.) pp. 943–959 (CSIRO publishing: Melbourne, Australia).
- Carlson, C., and Hoff, P. J. (1999). 'Atys naucum gizzard plates'. Sea Slug Forum, Dec. 23. Available at <http://www.seaslugforum.net/find/1704>
- Carlson, C., and Hoff, P. J. (2000a). Notes on *Atys multistriatus* Schepman, 1913 (Opisthobranchia: Cephalaspidea: Haminoeidae). *Micronesica* **33 (1/2)**, 169–178.
- Carlson, C., and Hoff, P. J. (2000b) '*Ventomnestia villica* (Gould, 1859)'. Sea Slug Forum, Feb. 3. Australian Museum, Sydney. [Accessed 20 Dec 2018] <http://www.seaslugforum.net/factsheet/ventvill>
- Carlson, C., and Hoff, P. J. (2003). The opisthobranchs of the Mariana Islands. *Micronesica* **35(36)**, 271–293.
- Cimino, G., Passeggio, A., Sodano, G., Spinella, A., and Villani, G. (1991). Alarm pheromones from the Mediterranean opisthobranchs *Haminoea navicula*. *Experientia* **47(1)**, 61–63.
- Cimino, G., and Gavagnin, M. (2007). 'Molluscs: from chemo-ecological study to biotechnological application (Vol. 43)'. (Springer Science & Business Media, Berlin, Germany).

- Cobb, G. (2018). 'Haminoea fusca (A. Adams, 1850)' Sea Slugs of the Sunshine Coast [Accessed 5 Nov 2018] <http://www.nudibranch.com.au/pages/5016b.html>
- Coelho, R., Malaquias, M., and Calado, G. (2006). *Calliopaea bellula* feeding upon egg-masses of *Haminoea orbignyana*: oophagy among opisthobranch molluscs. *Journal of the Marine Biological Association of the United Kingdom*, **86**(2), 423–424.
- Cruz-Rivera, E., and Paul, V.J. (2006). Feeding by coral reef mesograzers: algae or cyanobacteria? *Coral Reefs* **25**, 617–627.
- Da Costa, E. M. (1778). 'The British conchology'. (Elmsley and Robson Booksellers: London, UK).
- Chaban, E. M., and Chernyshev, A. V. (2014). Opisthobranch cephalaspidean mollusks (Gastropoda: Opisthobranchia) of Vostok Bay, Sea of Japan. Part 1. *Bulletin of the Russian Far East Malacological Society* **18**, 41–62.
- Chaban, E. M., and Chernyshev, A. V. (2016). First finding of the opisthobranch mollusk *Smaragdinella sieboldi* A. Adams, 1864 (Opisthobranchia: Haminoeidae) in the South China Sea with description of the anatomy of the species. *БИОЛОГИЯ МОРЯ/Biologiya morya* **42**(4), 311–316.
- Chênevert, R., Courchesne, G., and Caron, D. (2003). Chemoenzymatic enantioselective synthesis of the polypropionate acid moiety of dolabriferol. *Tetrahedron: Asymmetry* **14**(17), 2567–2571.
- Cutignano, A., Blihoghe, D., Fontana, A., Villani, G., d'Ippolito, G., and Cimino, G. (2007). Fusaripyrones, novel polypropionates from the Mediterranean mollusc *Haminoea fusari*. *Tetrahedron* **63**(52), 12935–12939.
- Dall, W. H. (1908). Descriptions of new species of mollusks from the Pacific coast of the United States, with notes on other mollusks from the same region. *Proceedings of the United States Museum* **34**, 245–357.
- Davies-Coleman, M. T., and Garson, M. J. (1998). Marine polypropionates. *Natural product reports* **15**(5), 477–493.

-
- Ehrenberg, C. G. (1828–1831). ‘Symbolae Physicae, seu icons et descriptions animalum evertebratum seposis insectis quae ex itinere per Africanum Borealum et Asiam Occidentalem–novae ant illusratae redierunt. Decas 1 Mollusca’. Vol. 1, 1828. plates, Vol. 2, 1831, text. (Mittler, Officina Academica: Berlin, Germany).
- Eilertsen, M. H., and Malaquias, M. A. E. (2013). Systematic revision of the genus *Scaphander* (Gastropoda, Cephalaspidea) in the Atlantic Ocean, with a molecular phylogenetic hypothesis. *Zoological Journal of the Linnean Society* **167**(3), 389–429.
- Fernández-Vilert, R., Giménez, J., Mas, G., Figueroa, I., and Moles, J. (2018). First records of the Red Sea alien mollusc *Haminoea cyanomarginata* (Gastropoda: Heterobranchia: Cephalaspidea) in the Western Mediterranean. *Journal of Natural History* **52**(27–28), 1817–1823.
- Férussac, D. D. (1822). ‘Dictionnaire classique d’histoire naturelle, Vol. 2’. (Rey et Gravier, Libraires-Éditeurs: Paris, France).
- Faase, M. (2018). *Haminoea japonica* Pilsbry, 1895 (Gastropoda: Cephalaspidea) new to the Netherlands. *Spirula* **416**, 16–19.
- Fischer, P. (1883). ‘Manuel de Conchyliologie et de Paléontologie Conchyliologique Tome 31’. (Crosse: Paris, France).
- Fontana, A., Ciavatta, M.L., DeSouza, L., Mollo, E., Naik, C.G., Parameswaran, P.S., Wahidullah, S., and Cimino, G. (2001). Selected chemo-ecological studies of marine opisthobranchs from Indian coasts. *Journal of the Indian Institute of Science* **81**, 403–415.
- Forbes, E. (1844). Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution, considered as bearing on geology. *Reports of the British Association for the Advancement of Science for 1843*, 130–193.
- Gantes, H., and Coronet, M. (1981). Précisions nouvelles sur l’anatomie de *Roxania utriculus* (Brocchi, 1814) (Mollusques, Gastropode, Opisthobranchie). *Bulletin de la Société Zoologique de France* **106**, 183–186.

- Ge, B. M., Bao, Y. X., Cheng, H. Y., Zhang, D. Z., and Tang, B. P. (2013). Temporal and spatial distribution pattern of *Bullacta exarata* in a tidal flat at south shore of Hangzhou Bay, China. *Iranian Journal of Fisheries Sciences* **12(1)**, 96–104.
- Gibson, G. D. and Chia, F. S. (1989). Description of a new species of *Haminoea*, *Haminoea callidegenita* (Mollusca: Opisthobranchia), with a comparison with two other *Haminoea* species found in the northeast Pacific. *Canadian journal of zoology* **67(4)**, 914–922.
- Gomont, M. (1892–1893). Monographie des Oscillariées (Nostocacées Homocystées). Deuxième partie. - Lyngbyées. *Annales des Sciences Naturelles, Botanique, Série 7* **16**, 91–264.
- Gosliner, T. M. (1994). Gastropoda: Opisthobranchia. *Microscopic anatomy of invertebrates* **5**, 253–355.
- Gosliner, T. M., and Behrens, D. W. (2006). Anatomy of an invasion: systematics and distribution of the introduced opisthobranch snail, *Haminoea japonica* Pilsbry, 1895 (Gastropoda: Opisthobranchia: Haminoeidae). *Proceedings of the California Academy of Sciences* **57(37)**, 1003–1010.
- Gosliner, T. M., Behrens, D. W., and Valdés, Á. (2008). ‘Indo–Pacific nudibranchs and sea slugs: a field guide to the world's most diverse fauna’ (Sea Challengers Natural History Books and California Academy of Sciences: California, USA).
- Gosliner, T. M., Valdés, Á., and Behrens, D. W. (2015). ‘Nudibranch & Sea Slug Identification: Indo–Pacific’. (New World Publications: Jacksonville, USA).
- Gould, A.A. (1855). ‘Catalogue of shells collected by W.P. Blake, with descriptions of the new species. In: Preliminary geological report of a reconnaissance and survey in California in connection with explorations for a predictable railway route from the Mississippi River to the Pacific Ocean in 1853 by Lt. R.S. Williamson’ (Ed. Blake, W.P.) Appendix, part 2, pp. 22–28 (House of Representatives, Doc. 129, 33rd Congress, 1st session: Washington D.C., USA).
- Gould, S. J. (1989). ‘Wonderful life: the Burgess Shale and the nature of history’. (Vintage Books, London, UK).

-
- Gray J. E. (1824). A list and description of some species of shells not taken notice of by Lamarck. *Annals of Philosophy* **9**, 134–140; 407–415.
- Gray, J. E. (1827). ‘Plate Mollusca, pl. Mollusca III, pl. Mollusca IV, in: E. Smedley, H. J., Rose and H. J. Rose (Eds). *Encyclopaedia Metropolitana*, volume 7, Plates to Zoology’ (B. Fellows. London, UK).
- Gray, J. E. (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. (1843). ‘Travels in New Zealand with contributions to the Geography, Botany and Natural History of that country. Vol II. Fauna of New Zealand’. pp. 228–263. (J. Murray, London, UK).
- Gray, J. E. (1850). Explanation of Plates and List of Genera. In Gray ME. (Ed) ‘Figures of Molluscous Animals, Selected from Various Authors. Vol. 4’. (Longman, Brown, Green and Longmans, London, UK)
- Göbbeler, K., and Klussmann-Kolb, A. (2006). Paddle cilia on the cephalic sensory organs (CSOs) of Opisthobranchia (Mollusca: Gastropoda) – genuine structures or artefacts. *Bonner Zoologische Beiträge* **55**, 223–229.
- Habe, T. (1950). Hydatinidae, Bullidae, and Akeridae in Japan. *Illustrated Catalogue of Japanese Shells* **3**, 17–24.
- Habe, T. (1952). Atyidae in Japan. *Illustrated Catalogue of Japanese Shells* **20**, 137–152.
- Hanson, D., Cooke, S., Hirano, Y., Malaquias, M. A., Crocetta, F., and Valdés, Á. (2013a). Slipping through the cracks: The taxonomic impediment conceals the origin and dispersal of *Haminoea japonica*, an invasive species with impacts to human health. *PloS One* **810**, e77457.
- Hanson, D., Hirano, Y., and Valdés, Á. (2013b). Population genetics of *Haminoea (Haloa) japonica* Pilsbry, 1895, a widespread non-indigenous sea slug (Mollusca: Opisthobranchia) in North America and Europe. *Biological Invasions* **15(2)**, 395–406.

- Heller, J., and Thompson, T. E. (1983). Opisthobranch molluscs of the Sudanese Red Sea. *Zoological Journal of the Linnean Society* **78(4)**, 317–348.
- Higo, S., Callomon, P., and Goto, Y. (1999). ‘Catalogue and Bibliography of the Marine Shell-Bearing Mollusca of Japan. Gastropoda, Bivalvia, Polyplacophora, Scaphopoda’. (Elle Scientific Publications: Oskaka).
- Higo, S., Callomon, P., and Goto, Y. (2001). Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan: Type Figures. (Elle Scientific Publications: Oskaka).
- International Code of Zoological Nomenclature [ICZN], (1989). Opinion 1553 Atyidae de Haan, 1849 (Crustacea, Decapoda) and Atyidae Thiele, 1925 (Mollusca, Gastropoda): homonymy removed. *The Bulletin of zoological nomenclature* **46(3)**, 201–202.
- Inkscape Team, (2015). Inkscape 0.91, [Accessed 5 Oct 2018]. Software: www.inkscape.org.
- Iredale, T. (1929). Strange molluscs in Sydney Harbour. *The Australian Zoologist* **5**, 337–352.
- Iredale, T. (1936). Australian molluscan notes. No. 2. *Records of Australian Museum* **19**, 267–340.
- Izzo, I., De Caro, S., De Riccardis, F., and Spinella, A. (2000). Synthesis of alkylphenols and alkylcatechols from the marine mollusc *Haminoea callidegenita*. *Tetrahedron Letters* **41(20)**, 3975–3978.
- Järnegren, J., Schander, C., Sneli, J. A., Rønningen, V., and Young, C. M. (2007). Four genes, morphology and ecology: distinguishing a new species of *Acesta* (Mollusca; Bivalvia) from the Gulf of Mexico. *Marine Biology* **152(1)**, 43–55.
- Kigoshi, H., and Kita, M. (2015). Antitumor effects of sea hare-derived compounds in cancer. In (Ed. Kim S-K,) ‘Handbook of anticancer drugs from marine origin’ (Springer: Cham, Switzerland) pp. 701–739.
- Kitao, K., and T. Habe, T. (1982). Systematic positions of *Haminoebulla kawamurai* Habe, 1950 and *Pseudophilina hayashii* Habe, 1976 (Opisthobranchia). *Venus* **411**, 61–63.

-
- Kohn, A. J. (1959). The ecology of *Conus* in Hawaii. *Ecological monographs* **29**(1), 47–90.
- Krauss, F. (1848). ‘Die Südafrikanischen Mollusken. Ein Beitrag zur Kenntniss der Mollusken des Kap- und Natallandes und zur Geographischen Verbreitung derselben mit Beschreibung und Abbildung der neuen Arten’ (Ebner and Seubert: Stuttgart, Germany).
- Kuroda, T., and Habe, T. (1952). ‘Check list and bibliography of the Recent Marine Mollusca of Japan’. (Leo. W. Stach: Tokyo)
- Köhler, E., (2003). ‘Cephalaspidean? from Turkey’. Sea Slug Forum, Jan 6. Australian Museum, Sydney. [Accessed 5 Nov 2018] <http://www.seaslugforum.net/find/8770>
- Köhler, E. (2018). ‘*Haminoea cyanomarginata* Heller & Thompson, 1983’ Medslugs [Accessed 5 Nov 2018] http://www.medslugs.de/E/Ind-NW/Haminoea_cyanomarginata/Selection.htm
- Leach, W. E. (1847). The classification of the British Mollusca. *Annals and Magazine of Natural History* **20**, 267–273.
- Leray, M., Yang, J. Y., Meyer, C. P., Mills, S. C., Agudelo, N., Ranwez, V., Boehm, J. T., and Machida, R. J. (2013). A new versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity: application for characterizing coral reef fish gut contents. *Frontiers in zoology* **10**(1), 34.
- Li, X., Leng, Y., Dong, Z., Liu, Y., Wen, R., Liu, X., and He, P. (2014). Isolation of fourteen novel polymorphic microsatellite markers for alien or invasive species: monitoring and management of the mud snail *Bullacta exarata* Philippi, 1849. *Conservation Genetics Resources* **6**(2), 259–261.
- Liao, N., Sun, L., Chen, J., Zhong, J., Zhang, Y., and Zhang, R. (2017). A novel polysaccharide conjugate from *Bullacta exarata* induces G1-phase arrest and apoptosis in human hepatocellular carcinoma HepG2 cells. *Molecules* **22**(3), 384.
- Lin, G. Y. (1997). ‘Fauna Sinica. Mollusca, Gastropoda, Subclass Opisthobranchia, Order Cephalaspidea’ (Beijing Science Press, Beijing).

- Linnaeus, C. (1758). 'Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis'. Editio decima (Ed. 10), reformata. (Laurentius Salvius: Stockholm).
- Liu, D., Liao, N., Ye, X., Hu, Y., Wu, D., Guo, X., Zhong J., Wu J., and Chen, S. (2013). Isolation and structural characterization of a novel antioxidant mannoglucan from a marine bubble snail, *Bullacta exarata* (Philippi). *Marine drugs* **11(11)**, 4464–4477.
- Loh, K. S., and Todd, P. A. (2011). Diet and Feeding in the Sea Star *Astropecten indicus* (Döderlein, 1888). *Raffles Bulletin of Zoology* **59(2)**, 251–258.
- Ma, J., Huang, F., Lin, H., and Wang, X. (2013). Isolation and purification of a peptide from *Bullacta exarata* and its impact on apoptosis of prostate cancer cells. *Marine drugs* **11(1)**, 266–273.
- Macali, A., Conde, A., Smriglio, C., Mariottini, P., and Crocetta, F. (2013). The evolution of the molluscan biota of Sabaudia Lake: a matter of human history. *Scientia Marina* **77(4)**, 649–662.
- Malaquias, M. A. E. (2010). Systematics, phylogeny, and natural history of *Bullacta exarata* (Philippi, 1849): an endemic cephalaspidean gastropod from the China Sea. *Journal of Natural History* **44(33–34)**, 2015–2029.
- Malaquias, M. A. E., and Sprung, M. J. (2005). Population biology of the cephalaspidean mollusc *Haminoea orbygniana* in a temperate coastal lagoon (Ria Formosa, Portugal). *Estuarine, Coastal and Shelf Science* **63(1–2)**, 177–185.
- Malaquias, M. A. E., and Cervera, J. L. (2006). The genus *Haminoea* (Gastropoda: Cephalaspidea) in Portugal, with a review of the European species. *Journal of Molluscan Studies* **72(1)**, 89–103.
- Malaquias, M. A. E., Mackenzie-Dodds, J., Bouchet, P., Gosliner, T., and Reid, D.G. (2009). A molecular phylogeny of the Cephalaspidea *sensu lato* (Gastropoda: Euthyneura): Architectibranchia redefined and Runcinacea reinstated. *Zoologica Scripta* **38 (1)**, 23–41.

-
- Malaquias, M. A. E., Ohnheiser, L. T., Oskars, T. R., and Willassen, E. (2016). Diversity and systematics of philinid snails (Gastropoda: Cephalaspidea) in West Africa with remarks on the biogeography of the region. *Zoological Journal of the Linnean Society* **180(1)**, 1–35.
- Marcus, Er. (1957). On Opisthobranchia from Brazil (2). *Zoological Journal of the Linnean Society* **43(292)**, 390–486.
- Marcus, Er. (1958). Notes on Opisthobranchia. *Boletim do Instituto Oceanográfico* **7**, 1–2, 31–78.
- Marcus, Er., and Marcus Ev. (1960) Opisthobranchia aus dem Roten Meer und von den Malediven. *Akademie der Wissenschaften und der Literature, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse* **12**, 873–934.
- Marcus, Er., and Burch, J. B. (1965). Marine euthyneuran Gastropoda from Eniwetok Atoll, western Pacific. *Malacologia* **3(2)**, 235–262.
- Marcus, Ev., and Marcus, Er. (1970). Some gastropods from Madagascar and West Mexico. *Malacologia* **10(1)**, 181–223.
- Marin, A., Álvarez, L. A., Cimino, G., and Spinella, A. (1999). Chemical defence in cephalaspidean gastropods: origin, anatomical location and ecological roles. *Journal of Molluscan Studies* **65(1)**, 121–131.
- Mattis, P., Kimball, S., and Singh, M. (1995). GIMP: GNU image manipulation program. [Accessed 8 Aug 2018] www.gimp.org.
- Mazzarelli, G. (1890). Ricerche sulla morfologia e fisiologia della glandola del Bohadsch nelle Aplysiidae (Glandula opalina del Vayssière) e diagnosi di una nuova specie di Aplysia. *Atti della Accademia delle Scienze Fisiche e Matematiche di Napoli* **2**, 1–14.
- Moles, J., Wägele, H., Schrödl, M., and Avila, C. (2017). A new Antarctic heterobranch clade is sister to all other Cephalaspidea (Mollusca: Gastropoda). *Zoologica Scripta* **46(2)**, 127–137.
- Mollo, E., Gavagnin, M., Carbone, M., Castelluccio, F., Pozzone, F., Vassilios Roussis, V., Templado, J., Ghiselin, M. T., and Guido Cimino, G. (2008). Factors promoting

-
- marine invasions: a chemoecological approach. *Proceedings of the National Academy of Sciences* **105(12)**, 4582–4586.
- MolluscaBase, (2018a). ‘Haminoeidae Pilsbry, 1895’ MolluscaBase [Accessed 5 Nov 2018]
<http://www.molluscabase.org/aphia.php?p=taxdetails&id=23052>
- MolluscaBase, (2018b). ‘*Hamineobulla* Habe, 1950’. MolluscaBase [Accessed 5 Nov 2018]
<http://www.molluscabase.org/aphia.php?p=taxdetails&id=599468>
- MolluscaBase, (2018c). ‘*Atys* Montfort, 1810’. MolluscaBase [Accessed 5 Nov 2018]
<http://www.molluscabase.org/aphia.php?p=taxdetails&id=138052>
- MolluscaBase, (2018d). ‘*Haminoea* Turton & Kingston [in Carrington], 1830.’
MolluscaBase [Accessed 5 Nov 2018]
<http://www.molluscabase.org/aphia.php?p=taxdetails&id=138054>
- Monterosato, T. A. (1884). ‘Nomenclatura generica e specifica di alcune conchiglie mediterranee’. (Virzi: Palermo, Italy).
- Montfort, D. (1810). ‘Conchyliologie systématique, et classification méthodique des coquilles. Coquilles Univalves, non cloisonnées. Vol. 2’. (F. Schoell: Paris, France).
- Mikkelsen, P.M. (1993). Monophyly versus the Cephalaspidea (Gastropoda, Opisthobranchia) with an analysis of traditional cephalaspid characters. *Bollettino malacologico* **29**, 115–138.
- Miller, M. C. (1969). The habits and habitats of the opisthobranch molluscs of the British Solomon Islands, 541–548. In (Ed. E. J. H. Corner) ‘A discussion of the results of the Royal Society Expedition to the British Solomon Islands Protectorate, 1965’. *Philosophical Transactions of the Royal Society London, series B, Biological Science* **255(800)**, 285–631.
- Natterer, M., and Neumann, S., Nordholts, M. *et al.* (2018). GIMP 2.10.0. [Accessed 8 Aug 2018]. <https://www.openhub.net/p/gimp/contributors/summary>
- Ng, P. K. L., and Sivasothi, N. (2001). Guide to the Mangroves of Singapore, Molluscs. [Accessed 2018 Jun 02] <http://mangrove.nus.edu.sg/guidebooks/text/2088.htm>.
Excerpt from Ng, P. K. L., and Sivasothi, N ‘A Guide to Mangroves of Singapore.

Volume 2: Animal Diversity'. (Eds Lim, K. K. P., Murphy, D. H., Morgany, T., Sivasothi, N., Ng, P. K. L., Soong, B. C., Hugh, T. W., Tan, K., Tan, S., and Tan, T. K) (Raffles Museum of Biodiversity Research, the National University of Singapore & the Singapore Science Centre, Singapore).

- Nordsieck, F. (1972). 'Die europaischen Meeresschnecken (Opisthobranchia mit Pyramidellidae; Rissoacea) vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer'. (Gustav Fischer Verlag: Stuttgart, Germany)
- Nuzzo, G., Cutignano, A., Moles, J., Avila, C., and Fontana, A. (2016). Exiguapyrone and exiguaone, new polypropionates from the Mediterranean cephalaspidean mollusc *Haminoea exigua*. *Tetrahedron Letters* **57(1)**, 71–74.
- d'Orbigny, A. D. (1837). Mémoire sur des espèces et sur des genres nouveaux de l'ordre des nudibranches observés sur les côtes de France. *Magasin de Zoologie* 7, classe **5**, 1–16.
- Oskars, T. R., Bouchet, P., and Malaquias, M. A. E. (2015). A new phylogeny of the Cephalaspidea (Gastropoda: Heterobranchia) based on expanded taxon sampling and gene markers. *Molecular Phylogenetics and Evolution* **89**, 130–150.
- Pease, W. H. (1860). Descriptions of new species of Mollusca from the Sandwich Islands. *Proceedings of the Zoological Society of London* **28**, 18–36, 141–148.
- Pease, W. H. (1868). Descriptions of marine Gasteropoda, inhabiting Polynesia. *American Journal of Conchology* **4**, 71–80, 91–102.
- Peltari, E., Matikainen, J., and Elo, H. (2002). Antimicrobial activity of the marine alkaloids haminol and puloupone and related compounds. *Zeitschrift für Naturforschung C* **57(5–6)**, 548–552.
- Philippi, A. (1847). Testaceorum novorum centuria. *Zeitschrift für Malakozoologie* **4**, 113–127.
- Philippi, R. A. (1849). Centuria altera testaceorum novorum. *Zeitschrift für Malakozoologie* **9**, 129–144.

- Pilsbry, H. A. (1895a). Polyplacophora. Acanthochitinidae, Cryptoplacidae and appendix. Tectibranchiata. *Manual of Conchology, structural and systematic, with illustrations of the species* **15(60)**, 181–436.
- Pilsbry, H. A. (1895b). ‘Catalogue of the Marine Shells of Japan with Descriptions of New Species and Notes on Others Collected by Frederick Stearns’. (F. Stearns: Detroit, USA).
- Pilsbry, H. A. (1896). Philinidae, Gastropteridae, Aglajidae, Aplysiidae, Oxynoeidae, Runcinidae, Umbraculidae, Pleurobranchidae. *Manual of conchology, structural and systematic, with illustrations of the species* **16(1)**, 1–262.
- Pilsbry, H. A. (1921). Marine molluscs of Hawaii – XIV, XV. *Proceedings of the Academy of Natural Sciences of Philadelphia* **72**, 360–382.
- Pittman, C., and Fiene, P. (2018). ‘*Atys kuhnsi* Pilsbry, 1917’ Sea slugs of Hawaii [Accessed 20 Dec 2018] <http://seaslugsofhawaii.com/species/Atys-kuhnsi-a.html>
- Poiner, A., Paul, V.J., and Scheuer, P.J. (1989). Kumepaloxane, a rearranged trisnor sesquiterpene from the bubble shell *Haminoea cymbalum*. *Tetrahedron* **45(3)**, 617–622.
- Preston, H. B. (1908). Descriptions of new species of land, marine and freshwater shells from the Andaman Islands. *Records of the Indian Museum* **2**, 187–210
- Puillandre, N., Strong, E. E., Bouchet, P., Boisselier, M. C., Couloux, A., and Samadi, S. (2009). Identifying gastropod spawn from DNA barcodes: possible but not yet practicable. *Molecular Ecology Resources* **9(5)**, 1311–1321.
- Puillandre, N., Lambert, A., Brouillet, S., and Achaz, G. (2012). ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* **21(8)**, 1864–1877.
- Quoy, J.R.C., and Gaimard, J.P. (1832–1835). ‘Voyage de découvertes de l’Astrolabe” exécuté par ordre du Roi, pendant les années 1826–1829, sous le commandement de M. J. Dumont d’Urville. Zoologie’ (Ed. Dumont d’Urville, M. J.). 1, 1–264; 2(1): 1–

-
- 321 [1832]; 2(2): 321–686 [1833]; 3(1): 1–366 [1834]; 3(2): 367–954 [1835]; Atlas (Mollusques): pls 1–93 [1833]. (Tastu, Paris, France).
- Risbec, J. (1951). Notes sur les Tectibranches de Nouvelle-Calédonie. *Journal de la Société des océanistes* **7(7)**, 123–158.
- Rizgalla, J., Fridman, S., Abdallah, A. B., Bron, J. E., and Shinn, A. P. (2018). First record of the non-native sea snail *Haminoea cyanomarginata* Heller & Thompson, 1983 (Gastropoda: Haminoeidae) in the Southern Mediterranean Sea. *BioInvasions Records* **4**, 411–414.
- Rudman, W. B. (1971a). On the opisthobranch genus *Haminoea* Turton & Kingston. *Pacific Science* **25**, 545–559.
- Rudman, W. B. (1971b). Structure and functioning of the gut in the Bullomorpha (Opisthobranchia) Part 1. Herbivores. *Journal of Natural History* **5(6)**, 647–675.
- Rudman, W. B. (1972a). The herbivorous opisthobranch genera *Phanerophthalmus* A. Adams and *Smaragdinella* A. Adams. *Proceedings of the Zoological Society of London* **40**, 189–210.
- Rudman, W.B. (1972b). A comparative study of the genus *Philinopsis* Pease 1860 (Aglajidae, Opisthobranchia). *Pacific Science* **26**, 381–399.
- Rudman, W. B. (2000). ‘Re: *Hamineobulla kawamurai*?’ Sea Slug Forum, Feb 9 [Accessed 5 Nov 2018] <http://www.seaslugforum.net/find/1874>
- Rudman, W.B. (2003). ‘*Haminoea cyanomarginata* Heller & Thompson, 1983’. Sea Slug Forum, Jan 3. Australian Museum, Sydney. [Accessed 5 Nov 2018] <http://www.seaslugforum.net/factsheet/hamicyan>
- Rudman, W. B. (2004 12). ‘*Smaragdinella calyculata* (Broderip and Sowerby, 1829)’. Sea Slug Forum, Jan 12. [Accessed 5 Nov 2018] <http://www.seaslugforum.net/factsheet/smarcaly>
- Sars, G.O. (1878). ‘Bidrag Til Kundskaben om Norges Arktiske Fauna. Oversigt over de i Norges arktiske region forekommende bløddyr. I, Mollusca regionis articae Norvegiae’. (Brøgger: Christiania (Oslo), Norway)

- Say, T. (1822). An account of some of the marine shells of the United States. *Journal of the Academy of Natural Science*, Philadelphia **2**, 221–248.
- Schaefer, K. (1992). *Haminaea exigua* (Gastropoda, Opisthobranchia), a new cephalaspid species from the Mediterranean Sea. *Journal of Molluscan Studies* **58(3)**, 329–336.
- Schepman, M. M. (1913). ‘Pulmonata and Opisthobranchia Tectibranchiata. Part VI of the Prosobranchia, Pulmonata and Opisthobranchia Tectibranchiata of the Siboga Expedition. Monograph 49’ (Brill: Leiden, the Netherlands)
- Shi, L., Li, J., Wu, S., and Han, J. (2018). Historical refugia and isolation by distance of the mud snail, *Bullacta exarata* (Philippi, 1849) in the northwestern Pacific Ocean. *Frontiers in genetics* **9(486)**, 1–9.
- Simmons, M. P., Pickett, K. M., and Miya, M. (2004). How meaningful are Bayesian support values? *Molecular Biology and Evolution* **21(1)**, 188–199.
- Smith, E. A. (1903). ‘The Fauna and Geography of the Maldive and Laccadive Archipelagoes: Being the account of the Work carried on and of the collections made by an Expedition during the years 1899 and 1900. Vol. 2, part 2’ (Cambridge University Press: Cambridge, UK).
- Smith, E. A. (1872). Remarks on several species of Bullidae, with descriptions of some hitherto undescribed forms and of a new species of *Planaxis*. *The Annals and Magazine of Natural History* **36**, 344–355.
- Spinella, A., Álvarez, L. A., and Cimino, G. (1998). Alkylphenols from the cephalaspidean mollusc *Haminoea callidegenita*. *Tetrahedron letters* **39(14)**, 2005–2008.
- Szabo, C. M., Nakao, Y., Yoshida, W. Y., and Scheuer, P. J. (1996). Two diverse constituents of the cephalaspidean mollusk *Smaragdinella calyculata*. *Tetrahedron* **52(29)**, 9681–9686.
- Thiele, J. (1925). ‘Gastropoden der Deutschen Tiefsee-Expedition. II Teil. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899’ (G. Fischer: Jena, Germany).

-
- Thiele, J. (1926). Mollusca. In 'Handbuch der Zoologie, Eine Naturgeschichte der Stamme des Tierreiches, vol. 5, part 2'. (Eds. Kükenthal, W., and Krumbach, T.) pp. 97–176. (De Gruyter: Berlin and Leipzig).
- Thompson, T. E. (1976). 'Biology of Opisthobranch Molluscs, Vol. I'. (Ray Society, London, UK).
- Thompson, T. E. (1988). 'Molluscs: benthic Opisthobranchs: Mollusca, Gastropoda: keys and notes for the identification of the species (Vol. 8)'. (Brill, Leiden, the Netherlands)
- Too, C. C., Carlson, C., Hoff, P. J., and Malaquias, M. A. E. (2014). Diversity and systematics of Haminoeidae gastropods (Heterobranchia: Cephalaspidea) in the tropical West Pacific Ocean: new data on the genera *Aliculastrum*, *Atys*, *Diniatys* and *Liloa*. *Zootaxa* **3794(3)**, 355–392
- Turton, W., and Kingston J.F. (1830). The natural history of the District, Cochnology. In 'The Teignmouth, Dawlish and Torquay Guide, or Lists of the different species of animals, vegetables, and minerals, and their respective localities, scientifically arranged (Ed. Carrington, N.T.)' [Pages undumbered] (Croydon: London, UK)
- Usuki, I. (1966a). The life cycle of *Haloa japonica* (Pilsbry) I. Spawning and growth. *Science Reports of Niigata University, series D (Biology)* **3**, 87–105.
- Usuki, I. (1966b). The life cycle of *Haloa japonica* (Pilsbry) II. Spawning and growth. *Science Reports of Niigata University, series D (Biology)* **3**, 107–121.
- Valdés, Á. (2008). Deep-Sea "Cephalaspidean" Heterobranchs Gastropoda from the Tropical Southwest Pacific. In Heros, V., Cowie, R. H., and Bouchet, P. (2008). Tropical Deep-Sea Benthos 25. *Mémoires du Muséum National d'Histoire Naturelle, Paris* **196**, 587–789.
- Valdés, Á., and McLean, J. H. (2015). On two abyssal species of Scaphandridae G.O. Sars, 1878 (Gastropoda: Cephalaspidea) from the eastern Pacific. *Nautilus* **129(3)**, 118–125.

- Vayssi re, M. A. (1885). Recherches zoologiques et anatomiques sur les mollusques Opisthobranches du Golfe de Marseille. Premi re partie. Tectibranches. *Annales du mus e d'histoire naturelle de Marseille* **2(3)**, 1–181.
- Vayssi re, A. (1893). Etude zoologique du *Weinkauffia diaphana*. *Journal de Conchylogie, Paris* **41**, 90–97.
- Weinkauff, H. C. (1866). Nouveau suppl ment au catalogue des coquilles marines recueillies sur les c tes de l'Alg rie. *Journal de Conchylogie, Paris* **14**, 227–248.
- Weinkauff, H. C. (1873). 'Catalog der im europ ischen Faunengebiet lebenden Meeres–Conchylien'. (R. Voigtl nder, Fischer: Cassel, Germany).
- Wild Singapore (2016). 'Haminoea' Wild Singapore [Accessed 5 Nov 2018] <http://www.wildsingapore.com/wildfacts/mollusca/slugs/cephalaspidea/hamineoa.htm>
- Ye, S. F., and Lu, J. J. (2001). Analysis on the spatial distribution of *Bullacta exarata* (Mollusca: Gastropoda: Atyidae) population in Yangtze River estuary, China. *Zoological Research* **22(2)**, 131–136.
- Ying, X. P., Yang, W. X., Jiang, N. C., and Zhang, Y. P. (2004). Ultrastructure of spermatozoa of *Bullacta exarata* (Philippi) and its significance on reproductive evolution and physio-ecological adaptation. *Journal of Zhejiang University-SCIENCE A* **5(10)**, 1211–1217.
- Yokes, B. (2003). 'Cephalaspidean from Turkey (2)'. Sea Slug Forum, Jan 6. Australian Museum, Sydney. [Accessed 5 Nov 2018] <http://www.seaslugforum.net/find/8840>
- Yonow, N., and Jensen, K. R. (2018). Results of the Rumphius Biohistorical Expedition to Ambon (1990). Part 17. The Cephalaspidea, Anaspidea, Pleurobranchia, and Sacoglossa (Mollusca: Gastropoda: Heterobranchia). *Archiv f ur Molluskenkunde* **147(1)**, 1–48.
- Zabbey, N., and Malaquias, M. A. E. (2013). Epifauna diversity and ecology on intertidal flats in the tropical Niger Delta, with remarks on the gastropod species *Haminoea*

orbignyana. *Journal of the Marine Biological Association of the United Kingdom* **93(1)**, 249–257.

Zamora-Silva, A., and Malaquias, M. A. E. (2016). Diet preferences of the Aglajidae: a family of cephalaspidean gastropod predators on tropical and temperate shores. *Journal of the Marine Biological Association of the United Kingdom* **96(5)**, 1101–1112.

Zenetos, A., Gofas, S., Russo, G., and Templado, J. (2004). ‘CIESM Atlas of exotic species in the Mediterranean. Vol. 3, Molluscs (Online update)’. (CIESM Publishers, Monaco) [Accessed 5 Nov 2018] <http://www.ciesm.org/atlas/appendix3.html>

Zenetos, A., Vassilopoulou, V., Salomidi, M., and Poursanidis, D. (2008). Additions to the marine alien fauna of Greek waters (2007 update). *Marine Biodiversity Records* **1**, 1–8, DOI: <https://doi.org/10.1017/S1755267207009281>

Zenetos, A., Gofas, S., Verlaque, M., *et al.* (2010). Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union’s Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. *Mediterranean Marine Science* **11**, 381–493.

Paper I

Redescription of the Cephalaspidea gastropod
Atys jeffreysi (Weinkauff, 1866) (Haminoeidae),
with a discussion on the phylogenetic affinities of
the Mediterranean species of the genus

Journal: Journal of Natural History

Paper II

Diniatys callosa (Preston, 1908), new combination
name for *Haminoea callosa* from The Andaman
Islands (India)

Journal: Journal of Conchology

Paper III

A molecular phylogeny of the gastropod family Haminoeidae *sensu lato* (Heterobranchia, Cephalaspidea), - a generic revision

Journal: Invertebrate Systematics

Accepted for publication

Paper IV

Description of a new species of *Haminoea*
(Gastropoda: Cephalaspidea) from India, with an
account of the diversity of the genus in the Indo-
West Pacific

Journal: Journal of Natural History

Paper V

Beyond shells: First detailed morphological description of the mangrove-associated gastropod *Haminoea* aff. *fusca* (A. Adams, 1850) (Cephalaspidea: Haminoeidae), with a COI phylogenetic analysis

Au-delà de la coquille: Une première description morphologique détaillée du gastéropode associé aux mangroves *Haminoea* aff. *fusca* (A. Adams, 1850) (Cephalaspidea: Haminoeidae), avec une analyse phylogénétique du gène COI

Journal: Zoosystema

Accepted for publication

Paper VI

A molecular phylogeny of the Indo-West Pacific gastropods *Haloa sensu lato* (Cephalaspidea: Haminoeidae): Tethyan vicariance, higher generic diversity, and ecological specialization

Journal: Molecular Phylogenetics and Evolution

Accepted with review

Paper VII

Systematic revision of the Indo-West Pacific colourful snails of the genus *Lamprohaminoea* Lin, 1997 (Cephalaspidea: Haminoeidae).

Intended journal: Invertebrate Systematics

Manuscript format

Paper VIII

Systematic revision of the Indo-West Pacific mangrove-associated snails of the genus *Bakawan* Oskars and Malaquias, submitted (Cephalaspidea: Haminoeidae).

Intended journal: Journal of Molluscan Studies

Manuscript format

Paper IX

The temperate Australasian genus *Papawera* Oskars and Malaquias, submitted (Cephalaspidea: Haminoeidae): redescription of *P. zelandiae* and *P. maugeansis*.

Intended journal: Journal of Natural History

Manuscript format

Paper X

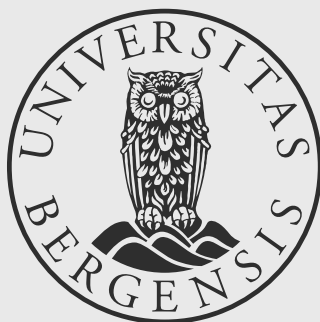
Systematic revision of the Indo-West Pacific bubble-snails of the genus *Haloa* Pilsbry, 1921 (Cephalaspidea: Haminoeidae).

Intended journal: Zoological Journal of the Linnean Society

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