



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

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ABSTRACT

The cephalaspidean gastropod genus *Haminoea* has been considered a worldwide radiation with species living in intertidal and shallow areas with algae, seagrass sandy-mud, mangroves, and coral reefs. Recently this monophyletic status was questioned and it was suggested that *Haminoea* proper only included Atlantic plus eastern Pacific species, whereas the Indo-West Pacific species were a separate radiation belonging to the genus *Haloa*. In this work we used an extended dataset of *Haminoea sensu lato* including to our best knowledge representatives of all Indo-West Pacific species, plus a large representation of Atlantic and eastern Pacific species. Bayesian and maximum likelihood molecular phylogenetic analyses using three mitochondrial (COI, 12S rRNA, 16S rRNA) and two nuclear genes (28S rRNA and Histone-3) were employed to study relationships and diversification including also the closely related genus *Smaragdinella*. Our results support a monophyletic Atlantic + eastern Pacific *Haminoea* clade and a monophyletic Indo-West Pacific radiation with five genera all defined by unique morphological characters and ecological requirements, namely *Haloa* proper with tropical and sub-tropical species spread across the Indo-West Pacific, *Lamprohaminoea* including only colourful species of tropical and sub-tropical affinity, *Bakawan* gen. nov. with species associated with mangrove habitats across the tropical eastern Indian Ocean and western Pacific, *Papawera* gen. nov. restricted to temperate waters of Australasia, and *Smaragdinella* the only cephalaspidean genus inhabiting intertidal hard substrates across sub-tropical and tropical regions of the Indo-West Pacific. This result suggests the role of the closure of the Tethys seaway structuring the phylogeny of worldwide “*Haminoea*” snails and of ecology driving the phylogenetic structure of the Indo-West Pacific radiation.

1. Introduction

The family Haminoeidae (115 species; [MolluscaBase, 2018a](#)) is the most diverse radiation of the gastropod Order Cephalaspidea (779 species; [MolluscaBase, 2018b](#)), with species present worldwide mainly inhabiting soft bottoms and algae or seagrass mats in shallow waters of temperate and tropical latitudes. Recently [Oskars et al. \(2019\)](#) found *Haminoea Turton and Kingston (1830)*, the type genus of the family, to be polyphyletic. *Haminoea sensu lato* was formed by three distinct clades, namely a clade containing all Indo-West Pacific (IWP) species, sister to the intertidal rock-dweller haminoeid genus *Smaragdinella* A. Adams (1848), and these two clades sister to a radiation including all Atlantic (Atl) and eastern Pacific (EP) species of *Haminoea* plus one single species from South Africa living in temperate waters of the Indian Ocean. In order to reflect the phylogeny, the authors have reinstated the

genus *Haloa* Pilsbry (1921) for the IWP species and maintained the Atl + EP species in the genus *Haminoea sensu stricto* (type species *Haminoea hydatis* Linnaeus (1758) from the Mediterranean Sea) ([Oskars et al., 2019](#)).

The subdivision of *Haminoea* was earlier suggested by Pilsbry (1921) based on the shape of the columella of the shell. The author introduced the subgenera *Haminaea* proper (type species *Bulla hydatis*), *Haloa* (type species *Haminea crocata* Pease, 1860 from Hawaii), and *Liloa* (type species *Haminea curta tomaculum* Pilsbry, 1917 from Hawaii). According to Pilsbry (1921) both *Haminoea* and *Haloa* had a concave columella but differed by the fact that in *Haminoea* the columella is tightly fused to the last whorl of the shell, whereas in *Haloa* it is separated from the shell whorl by a furrow. *Liloa* was distinguished by having only slightly concave columella and a narrower shell with spiral striae throughout the shell.

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The genus *Liloea* has been regarded as a valid genus by most authors (Higo et al., 1999, 2001; Too et al., 2014; Gosliner et al., 2015) and its monophyly was suggested by Too et al. (2014) based on the shared presence of unique traits of the gizzard plates and male reproductive system, and was confirmed by Oskars et al. (2019) using molecular phylogenetics.

On the other hand, the genus *Haloa* has largely been regarded as a synonym of *Haminoea* (Rudman, 1971a; Burn and Thompson, 1998) and only few authors have referred to it as valid after its original introduction (Habe, 1952; Higo et al., 1999, 2001; Hori, 2001).

Several genera were throughout the first half of the 20th century introduced for IWP “*Haminoea*”. Iredale (1929) erected the genus *Penthominea* for the Australian species *Bulla wallisii* Gray, 1824 and Kuroda and Habe (1952) erected the genera *Lamprohaminoea* for *Bulla cymbalum* Quoy & Gaimard, 1832, *Parahaminoea* for *Haminaea binotata* Pilsbry, 1895a, and *Vitreohaminoea* for *Bulla vitrea* A. Adams, 1850. However, Kuroda and Habe (1952) did not include any generic descriptions or reference to other works, which rendered their generic names invalid according to ICZN (1999) art.13 (see Oskars et al., 2019).

Habe (1952) raised *Haloa* to genus level based on the presence of a secondary cusp on the inner edge of the lateral teeth and synonymized *Penthominea* and *Parahaminoea* with *Haloa* without including any justification. However, because Habe (1952) did not find any additional cusp in *H. vitrea* he maintained *Vitreohaminoea* for the latter species, yet as a subgenus of *Haloa*. Habe (1952) additionally introduced the subgenus *Sericohaminoea* for the new species *Haloa (Sericohaminoea) yamagutii* Habe, 1952 based on the presence of conspicuous spiral striae and a thicker columellar callus. Rudman (1971a) after studying specimens of *H. crocata* from Hawaii (type species and type locality of *Haloa*) could not find a secondary cusp in the inner lateral teeth and consequently saw no reason to separate *Haloa* or the genera introduced by Habe (1952) and Kuroda and Habe (1952) from *Haminoea*.

Haloa (sensu Oskars et al., 2019) is the most diverse genus of the family Haminoeidae with an estimated 22 species (MolluscaBase, 2018c) nearly all inhabiting tropical shallow waters of the IWP with few lineages extending into temperate latitudes, such as *Haloa japonica* (Pilsbry, 1895a) and *H. maugeansis* (Burn, 1966). The genus includes dull-coloured species associated with sandy-mud flats, algae, and seagrass meadows (e.g. *Haloa japonica*, *H. natalensis* (Krauss, 1848); Rudman, 1971a; Gosliner, 1987; Gibson and Chia, 1989; Miranda and Renzo-Perissinotto, 2012; Tibiriçá and Malaquias, 2017), colourful species some with flamboyant patterns typically inhabiting coral reefs (e.g. *Haloa cymbalum* (Quoy & Gaimard, 1832), *H. ovalis* (Pease, 1868), *H. cyanomarginata* (Heller and Thompson, 1983); Rudman, 1999a, 1999b, 1999c; Cruz-Rivera and Paul, 2006; Gosliner et al., 2008, 2015; Tibiriçá and Malaquias, 2017; Pittman and Fiene, 2018), and mangrove dweller species (e.g. *H. fusca* (Adams, 1850); Riek 2013, 2014; Gosliner et al., 2015; Cobb, 2018).

Species of *Haloa (sensu Oskars et al., 2019)* have demonstrated potential for invading and establish viable populations in regions outside their native ranges. For example, Hanson et al. (2013a) found that *Haloa japonica* from the western Pacific has replaced the native *Haminoea vesicula* (Gould, 1855) in Boundary Bay, Canada. The same has been reported by Macali et al. (2013) for the Mediterranean Sea in the Laguna di Sabaudia, Italy where the native *Haminoea* species were outcompeted and replaced by the invasive *H. japonica*. The Red Sea endemic colourful species *Haloa cyanomarginata* is regarded a Lessepsian immigrant and has now spread all over the Mediterranean Sea (Koehler, 2003; Yokes, 2003; Rudman, 2003a; Zenetos et al., 2004, 2008, 2010; Mifsud, 2007; Crocetta and Vazzana, 2009; Fernández-Vilert et al., 2018). Its impact in local faunas is not yet clear, but according to Mollo et al. (2008) the presence of brominated secondary metabolites in *H. cyanomarginata* is an effective feeding deterrent for native predators. Additionally, the invasive *H. japonica* has been identified in California to be a potential human hazard as vector of *Schistosoma* parasites that can cause cercarial dermatitis or swimmer's itch in

humans (Brant et al., 2010; Hanson et al., 2013b).

Several molecular phylogenetic studies had previously included representatives of *Haminoea sensu lato* and *Smaragdinella* (e.g. Wägele et al., 2003; Malaquias et al., 2009; Oskars et al., 2015). However, none of these studies produced a clear pattern of relationships between the Atl + EP and IWP species and the genus *Smaragdinella*, most likely because of the reduced diversity of taxa included. Consequently, the monophyly of the genus *Haminoea* was never questioned. It is only with the work by Oskars et al. (2019) that the phylogeny of the Haminoeidae is comprehensively studied and became clear that *Haminoea* as traditionally defined is not a natural group but instead encompasses three independent monophyletic lineages (*Haloa*, *Haminoea*, *Smaragdinella*) all supported by several morphological synapomorphies (Oskars et al., 2019).

An interesting finding suggested by the latter authors was the possible occurrence of three clades in *Haloa* each of them with unique morphological and ecological features, which the authors have informally named *Haloa* clade 1 with dull-coloured species, *Haloa* clade 2 only with colourful species, and *Haloa* clade 3 containing mangrove-associated lineages.

In the present contribution, we further explore the systematics and taxonomic composition of the IWP *Haloa* based on an expanded taxon set with specimens from all previously recognized subclades and biogeographic regions. An integrative approach combining molecular phylogenetics (based on a combination of mitochondrial and nuclear genes) together with detailed conchological and morpho-anatomical characters is used to define clades, establish relationships, and infer putative synapomorphies.

2. Methods

2.1. Sampling

Novel material used in the present study was collected by the authors or obtained from the collections of the Department of Natural History, University Museum of Bergen, Norway (ZMBN), and loans from the Museum National d'Histoire Naturelle, Paris (MNHN), The Natural History Museum, London (NHMUK), The California Academy of Science (CAS), The Australian Museum, Sydney (AMS), Museum Victoria, Australia (MV), The Auckland Museum, New Zealand (AM), The Natural History Museum of Florida (UF), the Bavarian Collections of Zoology (ZSM), and the Museum of Zoology, University of Michigan, USA (UMMZ).

Outgroup taxa consisting of species from six haminoeid genera, namely *Atys*, *Aliculastrum*, *Bullacta*, *Diniatys*, *Liloea*, *Phanerophthalmus*, were included in the analyses together with representatives of mini haminoeids (Carlson et al., 1998; Oskars et al., 2019). The tree was rooted with the cephalaspidean species *Bulla cf. peasiana* Pilsbry, 1895a. In total, this study includes 237 specimens (137 IWP *Haloa*, 31 Atlantic/EP *Haminoea*, 8 *Smaragdinella*, 60 other Haminoeidae and 1 Bullidae) a total of 858 sequences were gathered for analyses from 222 specimens of 84 species (Table 1).

2.2. DNA extraction, amplification, and sequencing

DNA was extracted from tissue obtained from the foot or parapodial lobes using the Qiagen DNeasy® Blood and Tissue Kit (catalogue no. 69504) following the protocol recommended by the manufacturer. DNA from alcohol fixed samples more than 100 years old of “*Haloa fusca* (A. Adams, 1850) from the collections of the MNHN, Paris (spcs TH42, TH83, TH84; see Table 1) collected by C. Semper in 1875 in the Philippines, was extracted with the E.Z.N.A.® Mollusc DNA Kit (Omega Bio-tek, D3373-01). The manufacturer's protocol was followed with minor modifications. The tissue was lysed by incubating overnight at 37 °C and was then homogenized in a Qiagen TissueLyzer at 15 Hz for 25 s. The lysate was then incubated at 60 °C for 1 h, before continuing

Table 1
List of specimens used for phylogenetic analyses, with sampling localities, voucher numbers, and GenBank accession numbers (numbers marked with asterisk * are novel sequences generated for this study). Taxa highlighted in bold are the type species of genera.

Species	DNA extract code	Locality	Voucher No.	COI	16S rRNA	12S rRNA	28S rRNA	Histone-H3
<i>Bakawan fusca</i> (Adams, 1850)	TH42	The Philippines	MINHN Vayssière no.24 1921 (reddish periostracum)	MK473530*	-	-	-	-
<i>Bakawan fusca</i> (Adams, 1850)	TH83	The Philippines	MINHN Vayssière no.24 1921 (reddish periostracum)	-	-	-	-	MK473563*
<i>Bakawan fusca</i> (Adams, 1850)	TH84	The Philippines	MINHN Vayssière no.24 1921 (reddish periostracum)	-	-	-	-	MK473564*
<i>Bakawan rotundata</i> (Adams, 1850)	170	Khor Kalba, Gulf of Oman, United Arab Emirates	NHMUK 20070022	MH933109	MH933153	MK474404*	MH933342	MH933412
<i>Bakawan rotundata</i> (Adams, 1850)	401	Surat Thani, Thailand	ZMBN 125460	MH933110	MH933192	MK474401*	MH933388	MH933464
<i>Bakawan rotundata</i> (Adams, 1850)	496	Lim Chu Kang, Johor Strait, Singapore	ZMBN 89276	MK473520*	MK474215*	MK474405*	MK474275*	MK473610*
<i>Bakawan rotundata</i> (Adams, 1850)	497	Sungei Buloh Wetland Reserve, Lim Chu Kang, Johor Strait, Singapore	ZMBN 89277	MK473521*	MK474216*	MK474406*	MK474276*	MK473611*
<i>Bakawan rotundata</i> (Adams, 1850)	TH11	Sarawak, Borneo, Malaysia	ZMBN 125443	MK473522*	MK474217*	MK474403*	MK474273*	MK473612*
<i>Bakawan rotundata</i> (Adams, 1850)	TH35	Sarawak, Borneo, Malaysia	ZMBN 125443	MK473523*	MK474218*	MK474402*	MK474274*	MK473613*
<i>Bakawan rotundata</i> (Adams, 1850)	TH81	Hub River Delta, Pakistan	ZMBN125424	MH638588	-	-	-	-
<i>Bakawan rotundata</i> (Adams, 1850)	TH82	Hub River Delta, Pakistan	ZMBN125424	MH638587	-	-	-	-
<i>Bakawan</i> sp. 1	C37	Panglao, the Philippines	MINHN 42265 (Whitish periostracum)	KF615821	MH933205	MK474407*	KF615788	MH933477
<i>Bakawan</i> sp. 2	TH23	Junction of Susan and Mary rivers, Kangaroo Island, Queensland, Australia	AMS c.458281	MK473524*	MK474220*	MK474408*	-	MK473614*
<i>Bakawan</i> sp. 2	TH73	Junction of Susan and Mary rivers, Kangaroo Island, Queensland, Australia	AMS c.458281	MK473525*	MK474219*	MK474409*	MK474251*	MK473615*
<i>Haloa apiei</i> Bharate et al. (2018)	TH29	Miticoy Is. Lakshadweep	BNHS opistho 1361	MH638590	MK474182*	MK474385*	MK474296*	MK473604*
<i>Haloa apiei</i> Bharate et al. (2018)	TH30	Miticoy Is. Lakshadweep	BNHS opistho 1361	MH638591	MK474235*	MK474386*	MK474297*	MK473605*
<i>Haloa apiei</i> Bharate et al. (2018)	MB3	Burmanallah, Andaman	BNHS opistho 1344	MH638603	-	-	-	-
<i>Haloa apiei</i> Bharate et al. (2018)	MB4	Burmanallah, Andaman	BNHS opistho 1344	MH638604	-	-	-	-
<i>Haloa crocata</i> (Pease, 1860)	321	Hekili point, Maui, Hawaii	ZMBN 81705	MK473471*	MK474223*	MK474391*	MK474280*	MK473593*
<i>Haloa crocata</i> (Pease, 1860)	322	Hekili point, Maui, Hawaii	ZMBN 81705	MK473469*	MK474224*	MK474392*	MK474281*	MK473594*
<i>Haloa crocata</i> (Pease, 1860)	487	Kahului Harbor, Maui, Hawaii	ZMBN 88215	-	-	-	MK474277*	MK473595*
<i>Haloa crocata</i> (Pease, 1860)	TH65	Beach House, Kauai, Hawaii	ZMBN 97228	MK473470*	MK474222*	MK474393*	MK474278*	MK473537*
<i>Haloa crocata</i> (Pease, 1860)	TH66	Speckselsville, Maui, Hawaii	ZMBN 92892	MK473472*	MK474175*	MK474394*	MK474279*	MK473538*
<i>Haloa crocata</i> (Pilsbry, 1895a, 1895b)	149	Barcarès, Salsès-Leucaté Lake, Mediterranean France	NHMUK 20070065	KF615823	MH933146	MK474410*	KF615787	MH933407
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	164	Barcarès, Salsès-Leucaté Lake, Mediterranean France	NHMUK 20070028	KF615822	MK474245*	MK474411*	KF615785	MK473549*
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	251	Bahia de Ogrove, Galicia, Spain	ZMBN 81700	MK473510*	MK474246*	MK474414*	MK474265*	MK473532*
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	252	Bahia de Ogrove, Galicia, Spain	ZMBN 81700	MK473511*	MK474247*	MK474412*	MK474266*	MK473550*
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	C52	Barcarès, Salsès-Leucaté Lake, France, Mediterranean	NHMUK 20070029	KF615824	MH933147	MK474413*	KF615786	MH933480
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	TH67	Heshikitya, Okinawa	ZMBN 91233	MK473509*	MK474248*	-	MK474264*	MK473533*
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	GH1	Wando, South Korea	GenBank	JN830668	-	-	-	-
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	GH2	Sagami Bay, Japan	GenBank	JN830670	-	-	-	-
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	GH3	Hakodate, Japan	GenBank	JN830656	-	-	-	-
<i>Haloa japonica</i> (Pilsbry, 1895a, 1895b)	GH8	San Juan Islands, Washington, USA	GenBank	JN830725	-	-	-	-
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	207	Cocos, Guan	UF 376783	MK473466*	MK474227*	MK474396*	MK474259*	MK473597*
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	TH7	Heshikitya, Okinawa	ZMBN 112928	MK473467*	MK474232*	MK474400*	MK474290*	MK473600*
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	TH41	Heshikitya, Okinawa	ZMBN 112928	MK473464*	MK474230*	MK474336*	MK474291*	MK473546*
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	TH17	Baie De Maputo: Inhaca, Xixuane, Mozambique	MINHN IM-2013-52910	MK473465*	MK474228*	MK474397*	MK474286*	MK473601*
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	TH40	Baie De Maputo: Inhaca, Xixuane, Mozambique	MINHN IM-2013-52911	MK473461*	MK474229*	MK474335*	MK474287*	MK473547*
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	TH38	Parry Is., Eiwotek Atoll, Marshall Islands	UMMZ 230625	-	-	-	-	MK473598*
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	TH46	North Urelapa Island, Vanuatu	MINHN IM-2013-52945	MK473463*	MK474231*	MK474398*	MK474288*	MK473596*
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	TH48	North Urelapa Island, Vanuatu	MINHN IM-2013-52935	MK473460*	MK474225*	MK474399*	MK474289*	MK473599*
<i>Haloa musetta</i> (Er. Marcus and Burch, 1965)	TH75	Mauritius	CASIZ 188581	MK473462*	MK474226*	MK474395*	MK474285*	MK473536*
<i>Haloa natalensis</i> (Krauss, 1848)	68	United Arab Emirates	NHMUK 20060104	KF615826	-	-	KF615783	-
<i>Haloa natalensis</i> (Krauss, 1848)	153	Catalina Bay, St. Lucia, South Africa	NHMUK 20070186	KF615825	MH933148	MK474416*	KF615784	MH933408

(continued on next page)

Table 1 (continued)

Species	DNA extract code	Locality	Voucher No.	COI	16S rRNA	12S rRNA	28S rRNA	Histone-H3
<i>Haloa natalensis</i> (Krauss, 1848)	177	Kaempang, Thailand	NHMUK 20070033	–	–	–	MK474260*	MK473541*
<i>Haloa natalensis</i> (Krauss, 1848)	181	Sheung Pak, Hong Kong	NHMUK 20070604	–	–	MK474415*	MK474261*	MK473544*
<i>Haloa natalensis</i> (Krauss, 1848)	TH18	Baie de Maputo, Inhaca, Saco da Inhaca, Mozambique	MNHN IM-2013-52914	MK473512*	MK474233*	MK474417*	–	MK473543*
<i>Haloa natalensis</i> (Krauss, 1848)	MB9	Mandavi, Gujarat India	BNHS opistho 1326	MH638608	–	–	–	–
<i>Haloa natalensis</i> (Krauss, 1848)	MB19	Mandavi, Gujarat India	BNHS opistho 1336	MH638596	–	–	–	–
<i>Haloa natalensis</i> (Krauss, 1848)	MB34	Sundarban, West Bengal, India	BNHS opistho 547	MH638602	–	–	–	–
<i>Haloa cf. nigropunctatus</i> (Pease, 1868)	478	Makemo, Takaveke, Thaiti, French Polynesia	ZMBN 88222	MK473473*	MK474236*	–	MK474293*	–
<i>Haloa cf. pennipis</i> (Philippi, 1847)	91	Shelly beach, Townsville, Queensland, Australia	NHMUK 20060107	MK473529*	–	–	–	MK473606*
<i>Haloa cf. pennipis</i> (Philippi, 1847)	178	Budou-gai, Suna-machi, Maisaka-cho, Hamamatsu, Japan	NHMUK 20070446	MH933106	MH933156	MK474379*	MH933343	MH933415
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH1	Red Sea, Djibouti	MNHN Col: Jousseauime 1893, Det: Pruvot-Fol.	MK473475*	–	MK474381*	–	–
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH2	Red Sea, Djibouti	MNHN Col: Jousseauime, 1894, Det: <i>Vaysière 1906</i>	MH638609	MK474242*	MK474383*	–	MK473607*
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH44	West of Lavanono, South Madagascar	MNHN IM-2013-52895	MH638610	MK474244*	MK474382*	MK474283*	MK473609*
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH54	Nuarro Mangrove, Momba, Namputa, Mozambique	ZMBN 121234	MK473477*	MK474241*	MK474380*	MK474282*	MK473608*
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH56	Doxa Rock Pool, Zavora, Mozambique	ZMBN 125449	MK473480*	–	MK474375*	–	–
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH57	Doxa Rock Pool, Zavora, Mozambique	ZMBN 125453	MK473478*	–	MK474376*	–	–
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH60	Juan's surprise, Zavora, Mozambique	ZMBN 125455	MK473476*	MK474243*	MK474374*	MK474284*	MK473535*
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH61	Doxa Rock Pool, Zavora, Mozambique	ZMBN 125455	MK473479*	–	MK474377*	–	–
<i>Haloa cf. pennipis</i> (Philippi, 1847)	TH70	Lavanono, South Madagascar	MNHN IM-2013-52897	–	–	MK474378*	–	–
<i>Haloa cf. pennipis</i> (Philippi, 1847)	MB5	Undi, Maharashtra, India	MH638605	MH638605	–	–	–	–
<i>Haloa cf. pennipis</i> (Philippi, 1847)	MB11	Mirya, India	MH638593	MH638593	–	–	–	–
<i>Haloa cf. pennipis</i> (Philippi, 1847)	MB17	Punaged, Maharashtra, India	MH638594	MH638594	–	–	–	–
<i>Haloa sp. 1</i>	C26	Panglao, the Philippines	MNHN 42261	KF615810	MH933201	MK474370*	KF615809	MH933473
<i>Haloa sp. 2</i>	TH22	Ambatobe, Soamanitse Mozambique	MNHN IM-2013-52896	MK473527*	MK474234*	MK474372*	MK474252*	MK473592*
<i>Haloa sp. 3</i>	TH58	Doxa Rock Pool, Zavora, Mozambique	ZMBN 125445	MK473468*	–	MK474373*	MK474294*	–
<i>Haloa sp. 3</i>	TH6	King's Beach, Queensland, Australia	ZMBN 112928	MK473474*	MK474237*	MK474390*	MK474295*	MK473603*
<i>Haloa sp. 3</i>	93	East side of Dili Bay, East Timor	NHMUK 20060109	KF615835	–	MK474371*	KF615808	MK473602*
<i>Haloa sp. 3</i>	327	Queensland, Australia	ZMBN 81709	MH933107	MH933179	MK474389*	MH933374	MH933449
<i>Haloa sp. 3</i>	328	Queensland, Australia	ZMBN 81709	MH933108	MH933180	MK474387*	MH933375	MH933450
<i>Haloa sp. 3</i>	C3	South East, Sulawesi, Indonesia	NHMUK 20050660	DQ974673	MH933202	MK474388*	DQ927230	MH933474
<i>Haloa sp. 4</i>	180	Fiti, Solomon Islands	NHMUK 20070590	MH933105	MH933157	MK474384*	MH933344	MH933416
<i>Haminioea alfredensis</i> (Bartsch, 1915)	174	Kartega river estuary, Kenton, South Africa	NHMUK 20070314	KF615816	MH933154	MK474355*	KF615774	MH933413
<i>Haminioea alfredensis</i> (Bartsch, 1915)	182	Kenton on Sea, Kartega river estuary, South Africa	NHMUK 20070315	KF615815	MK474187*	MK474353*	KF615775	MK492113*
<i>Haminioea alfredensis</i> (Bartsch, 1915)	183	Kenton on Sea, Kartega river estuary, South Africa	NHMUK 20070315	KF615814	MH933155	MK474354*	KF615773	MH933417
<i>Haminioea alfredensis</i> (Bartsch, 1915)	459	Kynsna lagoon, South Africa	ZMBN 86406	MK473513*	MK474188*	MK474343*	MK474257*	MK473560*
<i>Haminioea antillarum</i> (d'Orbigny, 1841)	460	Kynsna lagoon, South Africa	ZMBN 86406	MK473514*	MK474184*	–	MK474256*	MK473561*
<i>Haminioea antillarum</i> (d'Orbigny, 1841)	158	Bocana, Sisal, Yucatan, Mexico	NHMUK 20070094	KF615811	MK474186*	MK474356*	KF615779	MK473562*
<i>Haminioea antillarum</i> (d'Orbigny, 1841)	160	Bocana, Sisal, Yucatan, Mexico	NHMUK 20070093	KF615820	MH933150	MK474357*	KF615781	MH933410
<i>Haminioea antillarum</i> (d'Orbigny, 1841)	176	Jupiter inlet, Palm Beach, Florida	NHMUK 20070316	KF615817	MH933151	MK474358*	KF615778	MH933414
<i>Haminioea fusari</i> (Álvarez, et al., 1993a)	167	Lago di Miseno, Naples, Italy	NHMUK 20070177	KF615840	MH933152	MK474368*	KF615801	MH933411
<i>Haminioea hydatis</i> (Linnaeus, 1758)	166	Port Barcarès, Salces-Leucaeté Lake, Mediterranean France	NHMUK 20060326	KF615841	KJ022796	MK474367*	KF615802	KJ022925
<i>Haminioea hydatis</i> (Linnaeus, 1758)	C53	Mediterranean France	NHMUK 20060326	DQ974674	MH933208	MK474369*	DQ927231	MH933481
<i>Haminioea navicula</i> (da Costa, 1778)	129	Canal de Mira, Aveiro, Portugal	NHMUK 20070018	KF615838	MK474221*	MK474364*	KF615804	MK473548*
<i>Haminioea navicula</i> (da Costa, 1778)	131	Triângulo da Barra, Aveiro, Portugal	NHMUK 20070020	KF615839	MH933144	MK474365*	KF615805	MH933405
<i>Haminioea navicula</i> (da Costa, 1778)	147	Eight Acre Pond, Hampshire, UK	NHMUK 20070021	KF615836	MH933145	MK474366*	KF615806	MH933406
<i>Haminioea orbignyana</i> (Férussac, 1822)	MM1	Faro, Portugal	NHMUK 20030296	KF615813	KJ022794	MK474360*	KF615776	MK473540*
<i>Haminioea orbignyana</i> (Férussac, 1822)	148	Faro, Portugal	NHMUK 20030296	KF615812	MK474185*	MK474359*	KF615777	MK473539*
<i>Haminioea orbignyana</i> (Férussac, 1822)	275	Rabat, Morocco	ZMBN 81791	MH933103	MH933174	MK474352*	MH933369	MH933444
<i>Haminioea orteci</i> Talavera, Murrillo & Templado, 1987	48	Barronco Hondo, Tenerife, Canary Islands	NHMUK 20030836	KF615846	MK474239*	–	KF615792	MK473555*

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Table 1 (continued)

Species	DNA extract code	Locality	Voucher No.	COI	16S rRNA	12S rRNA	28S rRNA	Histone-H3
<i>Haminioea orteci</i> Talavera, Murrillo & Templado, 1987	197	Boca das Caldeirinhas, Faial, Azores	NHMUK 2007/0458	KF615844	MH933160	MK474363*	KF615791	MH933422
<i>Haminioea orteci</i> Talavera, Murrillo & Templado, 1987	198	Boca das Caldeirinhas, Faial, Azores	NHMUK 2007/0458	KF615845	MK474238*	MK474361*	KF615790	MK492112*
<i>Haminioea orteci</i> Talavera, Murrillo & Templado, 1987	253	Lago Lucrino, Naples, Italy	ZMBN 81701	KX383914	MH933172	–	MH933367	MH933442
<i>Haminioea vesicula</i> (Gould, 1855)	202	Bodega Harbor, Sonoma Co., California	CASIZ 97502	KF615843	MH933161	MK474362*	KF615789	MH933423
<i>Haminioea vesicula</i> (Gould, 1855)	481	Long Beach, California	ZMBN 88214	–	–	–	MK474262*	MK473557*
<i>Haminioea virescens</i> (Sowerby II, 1833)	489	Long Beach, California	ZMBN 88213	–	–	–	MK474255*	MK473559*
<i>Haminioea virescens</i> (Sowerby II, 1833)	GH4	Venice, California	GenBank	AF156142	AF156126	AF156110	–	–
<i>Haminioea</i> sp. 1	471	Piura, Cultivos Puerto Rico, Sechurra Bay, Peru	ZSM Mol-20090704	–	MK474240*	–	–	MK473556*
<i>Haminioea</i> sp. 2	475	Piura, Mancora, Peru	ZSM Mol-20100737	–	MK474183*	–	–	MK473558*
<i>Haminioea</i> sp. 3	152	Florida, USA	NHMUK 2007/0180	KF615829	MK474212*	MK474348*	KF615797	MK473551*
<i>Haminioea</i> sp. 3	190	Pine Channel, Florida	NHMUK 2007/060	KF615832	MK474214*	MK474350*	KF615795	MK473553*
<i>Haminioea</i> sp. 3	188	Banana River, Florida	NHMUK 2007/0448	KF615828	MK474213*	MK474349*	KF615798	MK473552*
<i>Haminioea</i> sp. 4	161	Bocana, Sisal, Yucatan, Mexico	NHMUK 2007/0090	KF615833	MK474211*	MK474347*	KF615793	MK473554*
<i>Lamprohaminioea cyanomarginata</i> (Heller & Thompson, 1983)	262	Lazaro, Regio, Calabria, Italy	ZMBN 81762	MH933111	MH933173	MK474433*	MH933368	MH933443
<i>Lamprohaminioea cyanomarginata</i> (Heller & Thompson, 1983)	263	Lazaro, Regio, Calabria, Italy	ZMBN 81762	MK473485*	MK474192*	MK474422*	MK474304*	MK473571*
<i>Lamprohaminioea cyanomarginata</i> (Heller & Thompson, 1983)	276	Ihl Rabat, Malta	ZMBN 81803	MH933112	MH933175	MK474423*	MH933370	MH933445
<i>Lamprohaminioea cyanomarginata</i> (Heller & Thompson, 1983)	TH62	Split, Croatia	ZMBN 125456	MK473487*	–	MK474434*	–	–
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	16	Pasar Wajo, Buton Is., South East Sulawesi, Indonesia	NHMUK 2003/0302	KF615842	MH933149	MK474443*	KF615807	MH933409
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	323	Magilao, Guam, Mariana Islands	ZMBN 81711	KF992182	KJ022812	MK474446*	KJ023037	KJ022908
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	324	Magilao, Guam, Mariana Islands	ZMBN 81711	MK473501*	MK474200*	MK474447*	MK474311*	MK492114*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	325	Magilao, Guam, Mariana Islands	ZMBN 81711	MK473495*	MK474201*	MK474442*	MK474312*	MK473587*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	C28	Panglao, the Philippines	MNHN 42249	DQ974675	MK474202*	MK474444*	DQ927232	MK473581*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	TH21	Palkkulo Peninsula, Vanuatu	MNHN IM-2013-52940	MK473502*	MK474203*	MK474448*	MK474313*	MK473582*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	TH26	Lakshadweep, India	ZMBN 125446	MK473504*	–	MK474449*	MK474310*	MK473583*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	TH27	Lakshadweep, India	ZMBN 125457	MK473499*	MK474204*	MK474450*	MK474314*	MK473584*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	TH28	Lakshadweep, India	ZMBN 125452	MK473500*	MK474205*	MK474445*	MK474315*	MK473585*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	TH50	Segond Channel, vicinity of Marime College, Vanuatu	MNHN IM-2013-52939	MK473497*	MK474206*	MK474453*	MK474317*	MK473586*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	TH59	Tidal reef, Paintdane, Mozambique	ZMBN 125454	MK473503*	MK474199*	MK474451*	MK474316*	MK473534*
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	TH63	Paintdane, Mozambique	ZMBN 125451	MK473496*	–	MK474454*	–	–
<i>Lamprohaminioea cymbalum</i> (Quoy & Gaimard, 1832)	TH64	Paintdane, Mozambique	ZMBN 125448	MK473505*	–	MK474452*	–	–
<i>Lamprohaminioea cf. ovalis</i> (Pease, 1868)	187	Airport Beach, Maui, Hawaii	NHMUK 2007/0031	MK473489*	MK474173*	MK474427*	MK474250*	MK473570*
<i>Lamprohaminioea cf. ovalis</i> (Pease, 1868)	333	Maui, Hawaii	ZMBN 81689	KF992184	KJ022814	MK474425*	KJ023035	KJ022906
<i>Lamprohaminioea cf. ovalis</i> (Pease, 1868)	490	Manza Beach, Okinawa	ZMBN 88230	MK473491*	MK474193*	MK474426*	MK474298*	–
<i>Lamprohaminioea cf. ovalis</i> (Pease, 1868)	491	Manza Beach, Okinawa	ZMBN 88230	MK473488*	MK474194*	MK474428*	MK474303*	MK473568*

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Table 1 (continued)

Species	DNA extract code	Locality	Voucher No.	COI	16S rRNA	12S rRNA	28S rRNA	Histone-H3
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	C34	Panglao the Philippines	MNHN 42252	DQ974677	MH933204	MK474436*	DQ927234	MH933476
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH15	South Moorea, Tahiti, French Polynesia	AMS c.46947	MK473490*	MK474195*	MK474429*	MK474299*	MK473575*
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH16	Morena, Maatea, Tahiti, French Polynesia	AMS c.46947	MK473528*	—	MK474430*	MK474300*	MK473576*
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH19	Plage de Lavonono, Madagascar	MNHN IM-2009-16288	MK473506*	MK474207*	MK474437*	—	MK473577*
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH32	Panglao, the Philippines	MNHN IM, 512 MP588	MK473492*	MK474196*	MK474431*	—	MK473578*
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH43	Ranavalona, Madagascar	MNHN IM-2013-52894	MK473526*	MK474208*	MK474438*	MK474308*	MK473578*
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH49	Ranavalona, Madagascar	MNHN IM-2013-52902	MK473507*	MK474209*	MK474439*	MK474309*	MK473579*
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH51	Malo, Vanuatu	MNHN IM-2013-52931	MK473493*	MK474197*	MK474432*	MK474301*	MK473573*
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH53	Plage de Lavonono, Madagascar	MNHN IM-2009-16293	—	MK474210*	—	—	—
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH71	Lavanono, Madagascar	MNHN IM-2013-52898	—	MK474441*	—	—	—
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH74	Red Sea, Saudi Arabia	CASIZ 192351	MK473486*	MK474198*	MK474424*	MK474302*	MK473569*
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	TH76	Line Islands, Palmyra Atoll, West Lagoon	CASIZ 174196	MK473494*	—	MK474435*	—	—
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	MB25	Andaman islands	BNHS opistho 1340	MH638599	—	—	—	—
<i>Lamprohaminoea cf. ovalis</i> (Pease, 1868)	MB26	Andaman islands	BNHS opistho 1340	MH638600	—	—	—	—
<i>Lamprohaminoea sp. 1</i>	TH8	Rock Walk, Vamizi Island, Quirimbas, Mozambique.	ZMBN 105076	MK473483*	MK474191*	MK474421*	MK474305*	MK473574*
<i>Lamprohaminoea sp. 2</i>	211	Guam, Mariana Is.	UF 374145	MK473481*	—	—	—	—
<i>Lamprohaminoea sp. 2</i>	C36	Panglao, the Philippines	MNHN 42264	MK473457*	MK474189*	MK474418*	MK474307*	MK473566*
<i>Lamprohaminoea sp. 2</i>	TH52	Guam, Mariana Is.	UF 374127	MK473482*	MK474190*	MK474420*	—	MK473567
<i>Papawera maugeansis</i> (Burn, 1966)	GH9	Great Barrier Reef, Australia	GenBank	—	AF249258	—	—	—
<i>Papawera maugeansis</i> (Burn, 1966)	TH9	Shoreham Beach, Victoria, Australia	NMV F 209129	MK473519*	MK474181*	MK474458*	MK474271*	MK473591*
<i>Papawera maugeansis</i> (Burn, 1966)	TH10	Curlwey Reef, near Clifton Springs, Victoria, Australia	ZMBN 125458 (ex NVM F 112423)	MK473517*	MK474180*	MK474457*	MK474272*	MK473589*
<i>Papawera maugeansis</i> (Burn, 1966)	TH33	Inverloch, Town Area, Victoria Australia	ZMBN 125459 (ex NVM F 194630)	MK473518*	MK474179*	—	MK474270*	MK473590*
<i>Papawera zelandiae</i> (Gray, 1843)	456	Waitemata harbour, north end of Eastern Beach, New Zealand	MA 119920	MK473515*	MK474176*	MK474455*	MK474267*	—
<i>Papawera zelandiae</i> (Gray, 1843)	457	Waitemata harbour, north end of Eastern Beach, New Zealand	MA 119920	—	MK474177*	MK474456*	MK474268*	MK473531*
<i>Papawera zelandiae</i> (Gray, 1843)	458	Waitemata harbour, north end of Eastern Beach, New Zealand	MA 119920	MK473516*	MK474178*	—	MK474269*	MK473588*
<i>Smaragdinella calyculata</i> (Broderip & G. B. Sowerby 1, 1829)	336	Maui, Hawaii	ZMBN 81648	KF992185	KJ022815	—	KJ023034	KJ022905
<i>Smaragdinella cf. sieboldi</i> (Adams, 1864)	TH55	Mozambique	ZMBN 125447	MK473459*	MK474249*	MK474345*	MK474253*	MK473616*
<i>Smaragdinella sp. 1</i>	GH6	Moorea, Tahiti, French Polynesia	GenBank	KT149314	—	—	—	—
<i>Smaragdinella sp. 2</i>	GH5	Red Sea	GenBank	AF249806	AF249257	—	—	—
<i>Smaragdinella sp. 3</i>	C42	Panglao, the Philippines	MNHN 42257	DQ974682	KJ022786	—	DQ927242	KJ022936
<i>Smaragdinella sp. 4</i>	GH7	New Caledonia	GenBank (MT genome)	DQ991938	DQ991938	DQ991938	—	—
<i>Smaragdinella sp. 5</i>	184	Pulau Jung, Singapore Strait, Singapore	NHMUK 20070586	KF992166	MH933158	MK474346*	KJ023052	KJ022923
<i>Smaragdinella sp. 5</i>	185	Pulau Jung, Singapore Strait, Singapore	NHMUK 20070586	MH933104	MH933159	MK474344*	MH933345	MH933418
Outgroups								
<i>Alicatstrum cylindricum</i> (Helbling, 1779)	C6	Panglao, the Philippines	MNHN 42237	DQ974671	—	—	DQ927228	MH933482
<i>Alicatstrum cylindricum</i> (Helbling, 1779)	237	Palau	UF 301616	MH933140	MH933170	MK474327*	MH933362	MH933437
<i>Alicatstrum debilis</i> (Pease, 1860)	C5	Sulawesi, Indonesia	NHMUK 20050665	DQ974669	MH933207	—	DQ927227	MH933479
<i>Alicatstrum debilis</i> (Pease, 1860)	238	Bile Bay, Guam, Mariana Islands	UF 374152	KF992177	KJ022808	MK474328*	KJ023041	KJ022896
<i>Alicatstrum parallelum</i> (Gould, 1846)	219	Bile Bay, Guam, Mariana Islands	UF 374138	KF992171	KJ022802	—	KJ023047	KJ022902
<i>Alicatstrum parallelum</i> (Gould, 1846)	340	Guam, Mariana Islands	ZMBN 81670	KF992188	KJ022818	—	KJ023031	KJ022901
<i>Alys kuhnsi</i> Pilsbry, 1917	350	Maui, Hawaii	ZMBN 81660	KF992194	KJ022824	—	KJ023025	KJ022902
<i>Alys nauticum</i> (Linnaeus, 1758)	236	Palau	UF 301586	KF992176	KJ022807	—	KJ023042	KJ022913
<i>Alys cf. semistriatus</i> Pease, 1860	222	Tupungan Channel, Guam, Marianas Islands	UF 374125	KF992174	KJ022805	—	KJ023044	KJ022915
<i>Alys cf. semistriatus</i> Pease, 1860	433	Valpoopo, Tahiti, French Polynesia	ZMBN 125436	MH933115	MH933193*	—	MH933389	—
<i>Bulla cf. peccanina</i> Pilsbry (1895a, 1895b)	347	Maui, Hawaii	ZMBN 81656	KF992192	KJ022822	—	KJ023027	KJ022897
<i>Bullacta caurina</i> Benson 1842	395	Kauai, Hawaii	ZMBN 88208	MK473458*	MK474174*	MK474324*	MK474254*	MK473542*
<i>Bullacta caurina</i> Benson 1842	213	Kinko River, Chongkio City, Korea	NHMUK 20070444	GQ332576	MK472800	MK474342*	HM100714	KJ022920
<i>Bullacta costulosa</i> (Pease, 1868)	GB44	Whenzou, China	LSGB 25302	HQ833986	HQ833986	HQ833922	—	HQ834193
<i>Diniatys costulosa</i> (Pease, 1868)	344	Maui, Hawaii	ZMBN 81692	KF992191	KJ022821	—	KJ023028	KJ022898

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Table 1 (continued)

Species	DNA extract code	Locality	Voucher No.	COI	16S rRNA	12S rRNA	28S rRNA	Histone-H3
<i>Diniatys dentifer</i> (Adams, 1850)	221	Cocos, Guam, Mariana, Islands	UF 376781	MH933126	MH933163	–	MH933352	MH933426
<i>Diniatys dentifer</i> (Adams, 1850)	242	Tulamben, Bali, Indonesia	UF 381717	MH933127	MH933171	–	MH933363	MH933438
<i>Diniatys dubia</i> (Schepman, 1913)	220	Bile Bay, Guam, Mariana Islands	UF 374148	KF992173	KJ022804	–	KJ023045	KJ022916
<i>Diniatys dubia</i> (Schepman, 1913)	227	Outhouse Beach, Apra Harbor, Guam, Mariana Islands	UF 299907	MH933125*	MH933165*	–	MH933355*	MH933429*
<i>Diniatys monodonta</i> (A. Adams, 1850)	229	Cocos, Guam, Mariana Islands	UF 376788	KF992178	KJ022809	–	KJ023040	KJ022912
<i>Diniatys</i> sp. 1	326	Guam, Mariana Islands	ZMBN 81661	MH933123*	MH933178*	MK474329*	MH933373*	MH933448*
<i>Diniatys</i> sp. 2	338	Guam, Mariana Islands	ZMBN 81663	KF992187	KJ022817	–	KJ023032	KJ022903
<i>Diniatys</i> sp. 3	394	Maui, Hawaii	ZMBN 87963	MH933128	MH933191	MK474330*	MH933387	MH933463
<i>Diniatys</i> sp. 4	212	Bile Bay, Guam, Mariana Islands	UF 374128	MH933122	MH933128	–	MH933351	MH933425
<i>Haminella solitaria</i> (Say, 1822)	299	Connecticut, USA	ZMBN 81699	MH933113	MH933176	MK474340*	MH933371	MH933446
<i>Haminella solitaria</i> (Say, 1822)	301	Connecticut, USA	ZMBN 81699	MH933114	MH933177	MK474341*	MH933372	MH933447
<i>Liloa mongii</i> (Audouin, 1826)	C40	Panglao, Philippines	MHNH 42255	DQ974672	MH933206	MK474323*	DQ927229	MH933478
<i>Liloa porcellana</i> (Gould, 1859)	248	Tepungan Channel, Guam, Marianas Islands	UF374131	KF992180	–	–	KJ023039	KJ022910
<i>Liloa porcellana</i> (Gould, 1859)	345	Maui, Hawaii	ZMBN 81659	MH933132	MH933185	MK474263*	–	MH933456
<i>Liloa porcellana</i> (Gould, 1859)	451	Maui, Hawaii	ZMBN 89712	KF992202	KJ022836	MK474331*	KJ023018	KJ022887
<i>Liloa porcellana</i> (Gould, 1859)	452	Maui, Hawaii	ZMBN 89712	MH933131	MH933196	–	MH933392	MH933468
Long Tail Haminoeid sp. 1	358	Maui, Hawaii	ZMBN 81794	–	–	–	MH933386	MH933462
Long Tail Haminoeid sp. 2	194	Maalea Bay, Maui, Hawaii	NHMUK 20070587	–	–	–	MH933348	MH933420
Long Tail Haminoeid sp. 2	195	Maalea Bay, Maui, Hawaii	NHMUK 20070587	–	–	–	MH933349	MH933421
Mini Haminoeid sp. 1	192	Whaler's Village, Maui, Hawaii	NHMUK 20070588	MH933121	–	MK474318*	MH933346	–
Mini Haminoeid sp. 1	193	Whaler's Village, Maui, Hawaii	NHMUK 20070588	MH933120	–	MK474321*	MH933347	MH933419
Mini Haminoeid sp. 2	230	Bile Bay, Guam, Mariana Islands	UF 381707	MH933119	–	MK474320*	MH933432	MH933455*
Mini Haminoeid sp. 3	TH20	Palikulo Bay, Vanuatu	MHNH IM-2013-52942	MK473508*	MK474172	MK474322*	MK474258*	MK473545*
Mini haminoeid sp. 4	332	Micronesia	ZMBN 81667	MH933118*	–	–	MH933378*	MH933453*
<i>Phanerophthalmus cylindricus</i> (Pease, 1861)	341	Maui, Hawaii	ZMBN 81693	KF992189	KJ022819	MK474337*	KJ023030	KJ022900
<i>Phanerophthalmus luteus</i> (Quoy and Gaimard, 1832–1835)	C4	SE Sulawesi, Indonesia	NHMUK 20050661	KF992160	KJ022784	MK474326*	DQ927241	KJ022938
<i>Phanerophthalmus smaragdinus</i> (Rüppell and Leuckart, 1830)	218	Mangrove Bay, Egypt, Red Sea	NHMUK 20070584	KF992170	MH933162	–	KJ023048	KJ022918
<i>Roxaniella jeffreysi</i> (Weinkauff, 1866)	TZ11	Gnejna Bay, Malta	ZMBN 81800	KX523206	MH933211	–	–	MH933487
<i>Roxaniella pittmani</i> (Too, Carlson, Hoff & Malaquias, 2014)	342	Maui, Hawaii	ZMBN 81673	KF735657	MH933184	MK474319*	MH933380	MH933455
<i>Roxaniella multiseriata</i> (Schepman, 1913)	226	Bile Bay, Guam, Mariana Islands	UF 374136	KX523204	MH933164	–	MH933354	MH933428
<i>Roxaniella multiseriata</i> (Schepman, 1913)	351	Guam, Mariana Islands	ZMBN 81664	MH933138	MH933187	–	MH933382	MH933458
<i>Roxaniella</i> sp. 1	228	Bile Bay, Guam, Mariana Islands	UF 374149	MH933136	–	MK474325*	MH933356	MH933430
<i>Roxaniella</i> sp. 1	235	Bile Bay, Guam, Mariana Islands	UF 374150	MH933135	MH933169	–	MH933361	MH933436
<i>Roxaniella</i> sp. 2	225	Family Beach, Guam, Mariana Islands	UF 295897	MH933134	–	–	MH933353	MH933427
<i>Roxaniella</i> sp. 2	254	Guam, Mariana Islands	ZMBN 81662	MH933133	MH933189	–	MH933384*	MH933460*
<i>Vellicolla amphorella</i> (A. Adams, 1862)	C25	Panglao, the Philippines	MHNH IM, B1_4_OT1652 BC_1104	MH933116	MH933200	–	–	MH933472
<i>Vellicolla muscaria</i> (Gould, 1859)	355	Maui, Hawaii	ZMBN 81795	MH933117	MH933190	MK474332*	MH933385	MH933461
<i>Vellicolla tortuosa</i> (A. Adams, 1850)	TZ3	Tangoa Island, Vanuatu	MHNH IM-2013-52826	MH933213	MH933213	–	–	MH933489
<i>Vellicolla</i> sp. 1	330	Maui, Hawaii	ZMBN 81655	–	–	–	–	MH933451
<i>Vellicolla</i> sp. 1	331	Maui, Hawaii	ZMBN 81654	MH933181	MH933181	MK474338*	MH933376	MH933451
<i>Weinkauffia macandrewii</i> (E. A. Smith, 1872)	349	Gnejna Bay, Malta	ZMBN 81801	MH933182	MH933182	MK474339*	MH933377	MH933452
<i>Weinkauffia macandrewii</i> (E. A. Smith, 1872)	TZ9	Gnejna Bay, Malta	ZMBN 81801	MH933186	–	–	MH933381	MH933457
<i>Weinkauffia macandrewii</i> (E. A. Smith, 1872)	TZ10	Gnejna Bay, Malta	ZMBN 81801	MH933210	MH933210	–	MH933404	MH933493
<i>Weinkauffia ukulele</i> (Too et al., 2014)	453	Maui, Hawaii	ZMBN 87910	MH933101	MH933197	–	MH933399	MH933486
<i>Weinkauffia ukulele</i> (Too et al., 2014)	454	Maui, Hawaii	ZMBN 89707	KF735658	MH933198	MK474333*	MH933393	MH933469
<i>Weinkauffia ukulele</i> (Too et al., 2014)	455	Maui, Hawaii	ZMBN 87911	MH933102	MH933199	–	MH933395	MH933470

the protocol. Finally, the solution was eluted two times with 75 μ L elution buffer (total 150 μ L DNA extract).

Partial sequences of the mitochondrial genes cytochrome *c* oxidase subunit I (COI; primers: LCO1490 (F) GGTCAACAAATCATAAAGATAT TGG, HCO2198 (R) TAAACTTCAGGGTGACCAAAAATCA (Folmer et al., 1994), 16S rRNA (16S; primers: 16S ar-L (F) CGCCTGTTTATCAAAAA CAT, 16S br-H (R) CCGTCTGAACTCAGATCACGT (Palumbi et al., 1991) and 12S rRNA (12S; primers: 12Sa-L (F) AAA CTG GGA TTA GAT ACC CCA CTA T, 12Sa-H (R) GAG GGT GAC GGG CGG TGT GT (Palumbi, 1996), as well as the nuclear genes Histone H3 (H3: H3AD5'3' (F) ATGGCTCGTACCAAGCAGACVGC, H3BD5'3' (R) ATAT-CCTTRGGCATRATRGTGAC (Colgan et al., 1998), and 28S rRNA (28S; LSU5-F TAGGTGACCCGCTGAAYYTAAAGCA (Littlewood et al., 2000); 900-F CCGTCTTGAACACGGACCAAG (Olson et al., 2003); LSU1600-R (Williams et al., 2003); ECD2S-R CTTGGTCCGTGTTTCAAGACGG (modified from Littlewood et al., 2000) were amplified and sequenced.

Polymerase chain reactions (PCR) for the COI and 28S genes followed the protocols described by Malaquias et al. (2009), whereas for the 16S and H3 genes followed the protocols described by Oskars et al. (2015). PCR reactions for the 12S gene were performed in 50 μ L volume, including 19.5 μ L Sigma water, 5 μ L CoraLoad buffer, 5 μ L dNTP, 10 μ L Q-solution, 5 μ L MgCl, 2 μ L of each of the primers, 0.5 μ L Taq, and 1 μ L DNA. PCR cycling for 12S rRNA consisted of 40 cycles with initial denaturation at 95 °C for 3 min, denaturation at 94 °C for 45 s, annealing phase with an optimal annealing temperature of 49.4 °C for 45 s, ramp to 72 °C for 1 °C/sec. and extension at 72 °C for 2 min, followed by a final extension at 72 °C for 10 min. For samples that did not amplify with Qiagen Taq, additional 25 μ L reactions were set with TaKaRa Ex Taq Polymerase HS (250 U) (Cat. number: RR006A), following the protocol described by Oskars et al. (2015). The cycling was the same as above, but a hot start step of 94 °C for 5 min was included at the beginning of the cycle. For samples extracted with E.Z.N.A. Mollusc DNA Kit the same protocols were followed, but 2–2.5 μ L DNA were used instead.

The quality and quantity of PCR products were assessed by gel-electrophoresis following standard methods (see Eilertsen and Malaquias, 2013). For PCR products that yielded weak bands or double bands the products were reamplified by Gel Stabbing (Rees, D. pers. com.) where a sample of gel with the desired product was extracted with a cut pipette tip, and re-run under the original PCR protocol.

Successful PCR products were purified according to the EXO-SAP method described in Eilertsen and Malaquias (2013). Sequence reactions were run on an ABI 3730XL DNA Analyser (Applied Biosystems).

2.3. Morpho-anatomical methods

Animals were carefully separated from the shells with the aid of forceps. The male reproductive system, buccal bulb, and gizzard were dissected out of the animals. Shells were imaged with a DSLR camera equipped with macro lenses. The reproductive systems were drawn using a stereo microscope fitted with a drawing tube. The anterior digestive system was dissected and the gizzard plates and gizzard bristles were extracted. The gizzard plates, radulae, and jaws were cleaned using a solution containing 180 μ L buffer ATL and 20 μ L of proteinase K (obtained from the Qiagen DNeasy® Blood and Tissue Kit catalogue no. 69504) incubated at 56 °C for approximately 4–6 h (protocol modified from Holznagel (1998) and Vogler (2013)). For formalin fixed specimens, gizzard plates, radulae, and jaws were immersed in a 10–30% solution of sodium hydroxide (NaOH) until free of tissue. The gizzard plates, gizzard bristles and jaws were critical-point dried after cleaning to maintain their natural shape, and mounted together with the radulae on metallic stubs using carbon sticky tabs and coated with gold–palladium. The samples were scanned and imaged with a Zeiss Supra 55VP scanning electron microscope.

2.4. Phylogenetic analyses

Sequencher (v. 4.10.1, Gene Codes Corp.) and Geneious (v. 8.1.8 Biomatters Ltd., Kearse et al., 2012) were used to inspect, edit, and assemble the chromatograms of the forward and reverse DNA strands. All sequences were blasted in GenBank to check for contamination. Single gene sequences were aligned with Muscle (Edgar 2004a, 2004b) implemented in Geneious. Alignments were trimmed to a position where at least 50% of the sequences had nucleotides and missing positions at the ends were coded as missing data (?). All sequences were deposited in GenBank (Table 1).

Blocks of ambiguous data in the single gene alignments were identified and excluded using Gblocks with stringent and relaxed settings (Talavera and Castresana, 2007; Kück et al., 2010) (Table S1). The results obtained with the relaxed settings for the 16S and 12S genes showed no difference from the un-masked datasets, thus the latter were used for analyses. Saturation was tested for the first, second, and third codon positions of the protein coding genes COI and H3 using MEGA7 (Kumar et al. 2016) by plotting general time-reversible (GTR) pairwise distances against total substitutions (transitions + transversions). The JModeltest software (Darriba et al., 2012) was used to find the best-fit model of evolution for each single gene dataset under the Akaike information criterion (Akaike, 1974) (Table S2).

Eleven individual gene analyses were initially preformed: COI (Fig. S1; 639 bp), COI with 3rd codon excluded (Fig. S2; 426 bp), 12S Gblocks-no masking (Fig. S3; 393 bp), 12S Gblocks-stringent (Fig. S4; 349 bp), 16S Gblocks-no masking (Fig. S5; 438 bp), 16S Gblocks-stringent (Fig. S6; 395 bp), 28S Gblocks-no masking (Fig. S7; 1151 bp), 28S Gblocks-relaxed (Fig. S8; 1044 bp), 28S Gblocks-stringent (Fig. S9; 1000 bp), H3 (Fig. S10; 330 bp), and H3 with 3rd codon excluded (Fig. S11; 220 bp).

Concatenations were based on sequences yielded from the same specimen with the single exception of the samples of “*Haloa*” *fusca* from the Philippines collected by C. Semper in 1875 because only spc. TH42 yielded a COI sequence and spcs TH83 and TH84 were the only ones to yield H3 sequences. Yet, sequenced specimens came from the same lot (i.e. collected together at the same spot, same time and their morpho-anatomical study confirmed conspecificity).

Bayesian inference analyses (BI) using MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) were run on the initial single gene datasets (Figs S1–S11) and all-genes concatenated dataset (Fig. S12; 2844 bp). The analyses used three parallel runs of 4 million generations for the single gene analyses and 8 million generations for the concatenated dataset, with sampling every 100 generations. The concatenated dataset was partitioned by gene and each partition was run under the best-fit model of evolution (Table S2). Convergence of runs was inspected in Tracer v1.7 (Rambaut et al., 2018) with a burn-in set to 25% by comparing the likelihood of trees drawn by the independent runs. Posterior probabilities (PP) higher than 0.95 were considered statistically significant (Huelsenbeck et al., 2001; Alfaro et al., 2003). A Maximum Likelihood analysis (ML) of the concatenated dataset (Fig. S13; 2844 bp) was run with the RAxML (v.7.2.8; Stamatakis, 2006) plug-in implemented in Geneious (v. 8.1.8, Biomatters Ltd.; Kearse et al., 2012). The analysis was partitioned by gene and run under the “rapid bootstrapping and search for best scoring ML tree” algorithm, using a random starting tree and the model GTR + G + I with 1000 bootstrap (BS) replicates. Bootstrap values higher than 75% were considered significantly supported (Felsenstein, 1985), whereas BS values above 70% were considered as nearly supported (Hillis and Bull, 1993). Consensus phylograms were generated in MrBayes and Geneious, and annotated and converted to graphics in FigTree v1.3.1 (Rambaut and Drummond, 2009). All figures were made in Inkscape 0.48.4 (Inkscape Team, 2013) and Gimp 2.10 (Mattis et al., 1995; Natterer et al., 2018).

3. Results

3.1. Sequence analysis

Both COI and H3 genes showed saturation in third codon positions. However, as the third codon positions may contain phylogenetic information (Williams and Ozawa, 2006; Malaquias et al., 2009; Oskars et al., 2015), gene analyses with and without third codons were performed. In both cases, the tree topologies were better resolved and had higher node support when third codon positions were included (Figs. S1, S2, S10, S11). For the 12S, 16S, and 28S genes, unmasked and Gblocks relaxed datasets yielded trees better resolved with higher node support than those obtained with Gblocks stringent datasets (Figs. S3, S4, S5, S6, S7, S8, S9). Therefore, the all-genes concatenated dataset was based on the COI with third codon (639 bp; 197 sequences), 12S-unmasked (393 bp; 144 sequences), 16S-unmasked (438 bp; 165 sequences), H3 with third codon (330 bp; 181 sequences), and 28S-relaxed (1044 bp; 171 sequences) and includes a total of 2844 base pairs.

The mitochondrial genes COI, 12S, and 16S showed good performance in consistently clustering genera and species, but the latter two genes failed in some cases to separate what seem to be recently diverged sister species (those with lower COI uncorrected *p*-distances between 6 and 8%). The nuclear 28S and H3 genes showed in general good resolution at genus level and were able to consistently cluster representatives of most species. However due to the lower phylogenetic signal of conserved nuclear genes, the analysis failed to tell apart some lineages (28S: *Bakawan* gen. nov.; *Haloa aptei*/H. cf. *nigropunctatus* and *Haloa* sp. 1 / *Haloa* sp. 2; H3: *Lamprohaminoea cymbalum*/L. cf. *ovalis*; *Haloa* sp. 1 / *Haloa* sp. 3). Tree resolution improved with concatenation and both BI and ML analyses resulted largely in the same topology (Figs. 1, 2, S12, S13).

3.2. Paraphyly of *Haminoea sensu lato*

The monophyly of the traditional genus *Haminoea s. l.* was not supported as the genus *Smaragdinella* forms a clade nesting within (PP = 1, BS = 82; Figs. 1 and 2). *Smaragdinella* clustered together with all other IWP *Haminoea* (= *Haloa sensu* Oskars et al. 2019; PP = 1, BS = 86; Figs. 1, 2), whereas *Haminoea s. s.* (*sensu* Oskars et al. 2019), including the type species *Haminoea hydatis* plus one temperate Indian Ocean species restricted to South Africa (*H. alfredensis* (Bartch, 1915)), formed a separate clade (PP = 1, BS = 89; Figs. 1 and 2). The IWP clade with *Haloa* and *Smaragdinella* and the Atl + EP clade were sister to each other (PP = 1, BS = 86; Figs. 1 and 2).

3.3. Indo-West Pacific radiation: *Haloa sensu lato* + *Smaragdinella*

The clade with *Haloa sensu lato* and *Smaragdinella* (PP = 1, BS = 86; Figs. 1 and 2) contains five sub-clades all supported and defined by unique morphological characters (see Taxonomic section), but their sister relationships were not in all cases fully resolved. For example, the clade referring to the new genus here described *Papawera* gen. nov. (PP = 1, BS = 100; Figs. 1 and 2), appears in the trees as sister to *Smaragdinella* (PP = 1, BS = 86; Figs. 1 and 2) but with no support in BI and marginally supported by ML analysis (PP = 0.74, BS = 71; Figs. 1 and 2). The clade ascribed to the genus *Lamprohaminoea* (PP = 1, BS = 100; Figs. 1 and 2) was rendered sister (PP = 1, BS = 95) to *Haloa sensu stricto* plus the new genus *Bakawan* gen. nov. (PP = 1, BS = 94; Figs. 1 and 2), but the relationship between the latter two was not resolved (PP = 0.65, BS = 65; Figs. 1 and 2).

3.4. *Haloa sensu stricto* Pilsbry (1921)

The genus *Haloa* represented by 11 putative species including the type species *Haloa crocata* was highly supported (PP = 1, BS = 92; Figs. 1 and 2).

3.5. *Lamprohaminoea* Lin (1997) ex Habe and Kuroda (1952)

This genus is here resurrected and is represented by five putative species (PP = 1, BS = 100; Figs. 1 and 2), including the type species *Lamprohaminoea cymbalum* (see Taxonomic section and Discussion).

3.6. *Bakawan* gen. nov.

The new genus *Bakawan* gen. nov. (PP = 1, BS = 94; Figs. 1 and 2) with type species *Bakawan rotundata* (A. Adams, 1850) (see Taxonomic section and Discussion), includes four putative species, namely *B. fusca*, *B. rotundata* plus two unidentified lineages (*Bakawan* sp.1 [C37] and *Bakawan* sp. 2 [TH23, TH73]).

3.7. *Papawera* gen. nov.

This new genus here described (see Discussion and Taxonomic section) is represented by two species, namely *P. zelandiae* (type species here designated) and *P. maueansis* (PP = 1, BS = 100; Figs. 1 and 2) (see Taxonomic section and Discussion).

3.8. *Smaragdinella* A. Adams, 1848

Smaragdinella was highly supported (PP = 1, BS = 86; Figs. 1 and 2) and the phylogeny suggested two sub-clades, but this split could be an artefact of missing data since one of the species is mostly represented by specimens with only nuclear genes mined from GeneBank (GH5, GH6, GH7; Fig. 1, Table 1).

3.9. Taxonomic section

Order Cephalaspidea P. Fischer, 1883

Superfamily Haminoeioidea Pilsbry, 1895b

Family Haminoeidae Pilsbry, 1895b

Genus *Haloa* Pilsbry, 1921 (Figs. 1, 2A, B, 3A, 4A1–A6).

Diagnosis: Animal mottled in green or brownish colour, may have opaque white, black and orange dots on body. Cephalic shield deeply bilobed; cephalic lobes elongated, often overlapping; eyes inserted in large circular unpigmented periorcular areas (Fig. 1). Hancock organ ridge-like, short dorsal branches may be present (Fig. 4A2). Shell oval to rounded, faint to conspicuous spiral striae present; whitish-translucent to brownish in colour; periostracum pale yellow or pale brown, aperture narrow, wider anteriorly, tapering apically, columellar callus thick, separated from last whorl by narrow furrow (Fig. 4A1). Jaws semi-circular with diamond-shaped rods (Fig. 4A6). Radula formula 21–5.1.1.1.5–21; rachidian tricuspid, cusps triangular with pointed tips, central cusp larger, lateral cusps reduced; lateral teeth hook shaped, smooth; inner lateral may have secondary smaller cusp (Fig. 4A5). Gizzard plates with 12–17 transverse ridges covered with rods; grooves between ridges often smooth. Three gizzard bristled spines, resembling feather dusters inserted in raised triangular fleshy base. Male reproductive system with rounded to oblong prostate with single lobe; twisted seminal duct; lumen of seminal duct cross-shaped; atrium elongated, atrium sheath thick non-muscular; fundus thin walled, formed by constriction of upper hollow atrium, fundus walls with soft flaps, warts or ridges (Fig. 2A, B; 4A3, A4).

Relevant references: Pease (1860, 1868), Bergh (1901), Pilsbry (1921), Habe (1952), Er. Marcus and Burch (1965), Rudman (1971a), Kay (1979), Gibson and Chia (1989), Álvarez et al. (1993b), Gosliner (1994), Gosliner and Behrens (2006), Bharate et al. (2018), Oskars et al. (2019), Pittman and Fiene (2018).

Type species: *Haminea crocata* Pease, 1860. **Type locality:** Hawaii (“Sandwich Islands”).

Material examined: *Haminea crocata* Pease, 1860, lectotype, NHMUK 1961199-200, Sandwich Islands, H = 12 mm (see Kay, 1965:

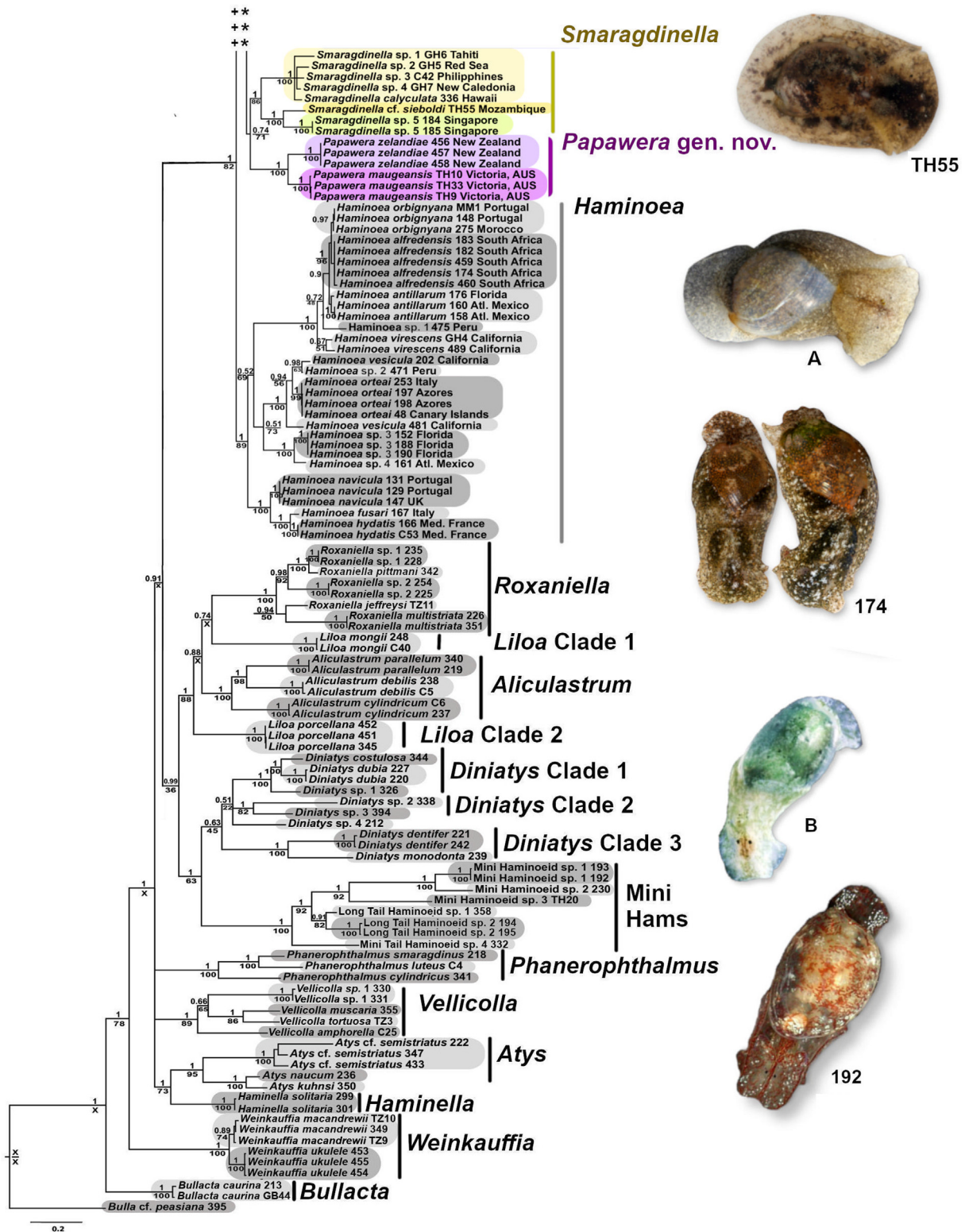


Fig. 1. Bayesian phylogeny of the *Haminoea sensu lato* based on the combined analysis of the mitochondrial COI, 16S rRNA and 12S rRNA and nuclear 28S rRNA and Histone H3 genes. The tree was rooted with the cephalaspid *Bulla cf. peasiانا*. Figures above branches are BI posterior probabilities and below branches bootstrap values derived by ML. Images by the authors, but A. *Papawera zelandiae*, Auckland, New Zealand, photo: D. Crisp (INaturalist, CC-BY-NC 4.0); B. *Diniatys dentifer*, Guam, UF 374130, photo: courtesy of C. Carlson; 192. Mini Haminoeid sp., Hawaii, photo: courtesy of C. Pittman; TH64. *Lamprohaminoea cymbalum*, Mozambique, photo: courtesy of Y. Tibirićá; TH55. *Smaragdinella cf. sieboldi*, Mozambique, photo: courtesy of S. Bruck and Y. Tibirićá; 496. *Bakawan rotundata*, Singapore, photo: courtesy of K. Jensen; 153. *Haloa natalensis*, South Africa, photo: courtesy of N. Miranda; 321, *Haloa crocata* Hawaii, 333, photo: courtesy of C. Pittman; *Lamprohaminoea cf. ovalis*, Hawaii, photo: courtesy of C. Pittman; 174. *Haminoea alfredensis*, South Africa, NHMUK 20070315, photo: courtesy of G. Branch and C. Griffiths.

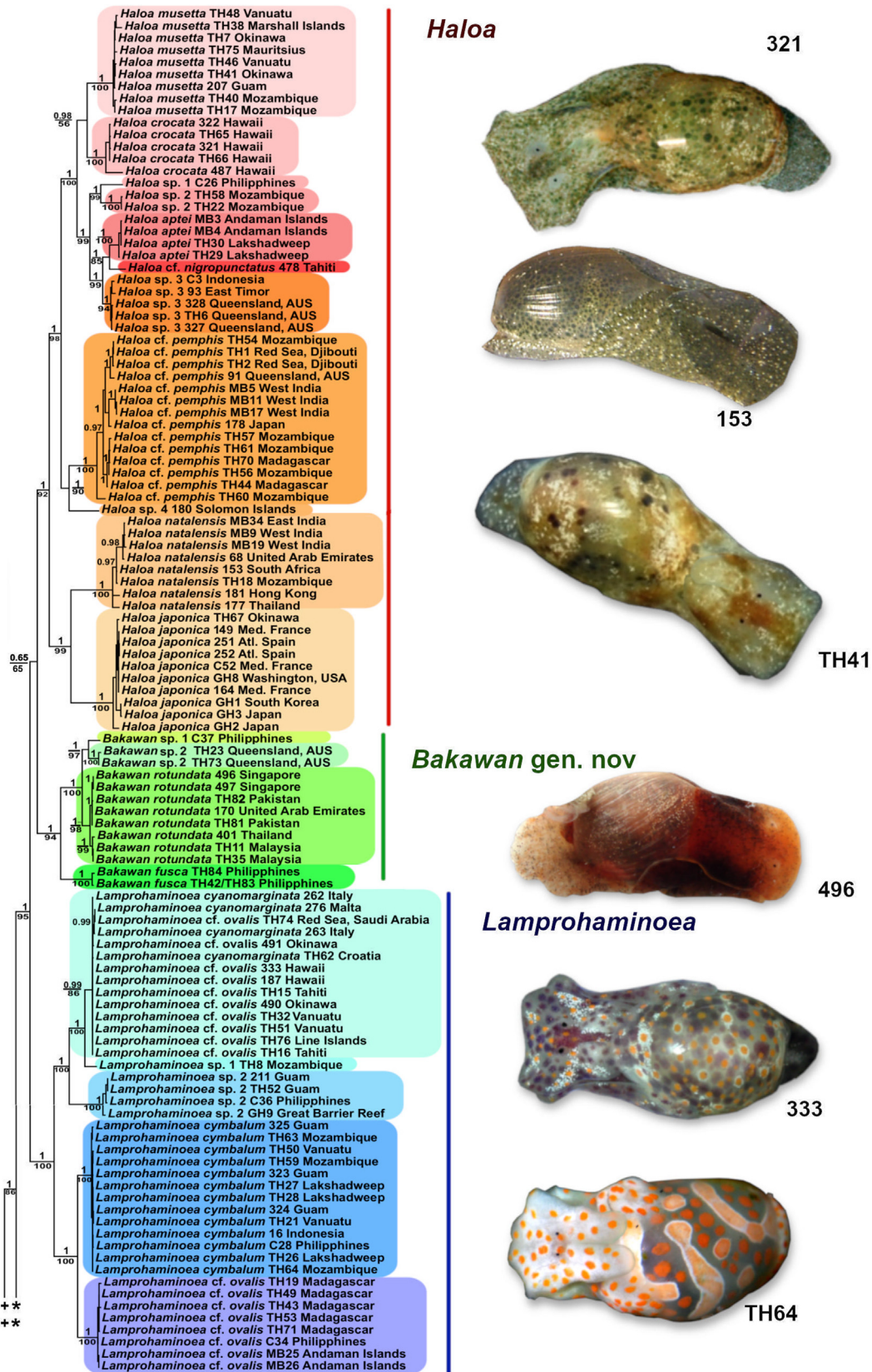


Fig. 1. (continued)

7, pl. 1, Figs. 9, 10). *H. crocata*, paralectotype (see Johnson, 1994), MCZ 88127, Hawaii H = 11 mm (image seen: <https://mczbase.mcz.harvard.edu/guid/MCZ:Mala:88127>). *H. crocata*, paralectotype, MCZ 398239, Hawaii, H = 8 mm (image seen: <https://mczbase.mcz.harvard.edu/>

<https://mczbase.mcz.harvard.edu/guid/MCZ:Mala:298239>). *H. crocata*, paralectotype, MCZ 297883, Hawaii H = 10 mm (image seen: <https://mczbase.mcz.harvard.edu/guid/MCZ:Mala:297883>). *Haloa crocata* (Pease, 1860), AMS c.159942, Near Koloa, Kawai, Hawaii, H = 6 mm (see Rudman, 1971a: 554, Fig. 10A).

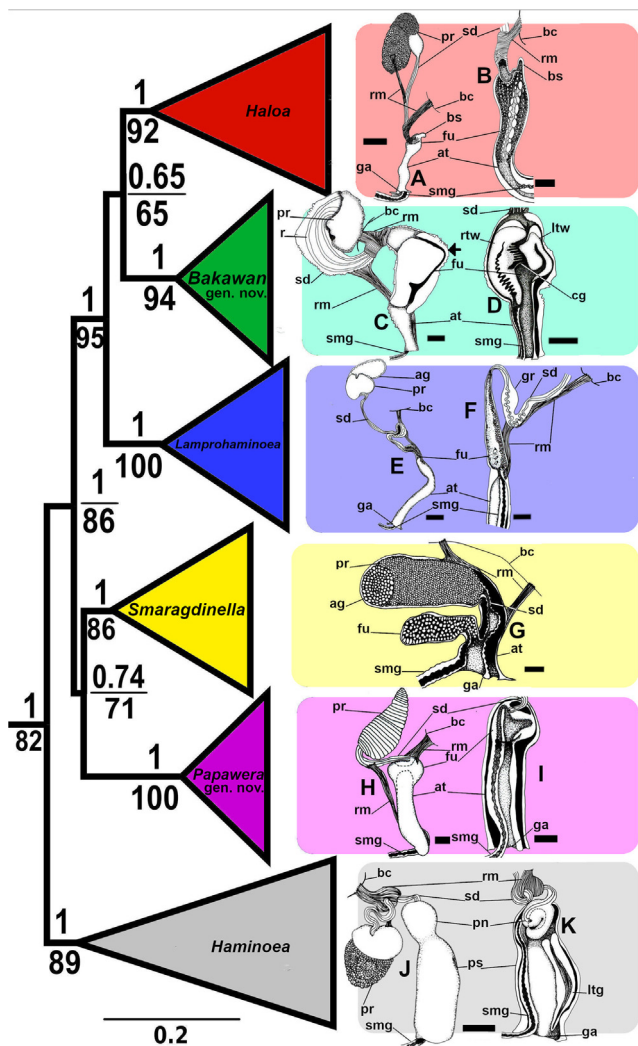


Fig. 2. Same tree as in Fig. 1 with generic nodes collapsed and outgroups removed for clarity, depicting archetype configurations of the male reproductive systems of genera. Figures above branches are BI posterior probabilities and below branches bootstrap values derived by ML. A, C, E, G, H, J refer to the whole male reproductive system. B, D, F, I refer to detail of fundus region. K, detail of penial region. Scale bars: A, J, K = 1 mm; B, C, D = 0.25 mm; E, G, H, I = 0.5 mm; F = 0.2 mm. Abbreviations: ag, accessory gland. at, atrium. bc, body cavity. bs, blind sac. cg, central groove. fu, fundus. ga, genital aperture. Itg, lateral thickened groove. Itw, left lateral fundus wall. pr, prostate. pn, penis. ps, penial sheath. rm, retractor muscle. rtw, right lateral fundus wall. sd, seminal duct. smg, seminal groove.

H. crocata, ZMBN 81705, Hawaii, H = 9–14 mm (Fig. 1, Fig. 3A). *H. crocata*, ZMBN 88215, Hawaii, H = 8 mm (Figs. 2B, 4A2). *Haloa* cf. *pemphis* (Philippi, 1847), MNHN, unnumbered (Col. Jousseume in 1893, Det: Pruvot-Fol), Djibouti, Red Sea, H = 17 mm. *H. cf. pemphis*, MNHN unnumbered (Col. Jousseume in 1894, Det: Vayssière in 1906), Djibouti, Red Sea, H = 18 mm (see Vayssière, 1906: 23, pl. 3, Figs. 38–44). *Haloa japonica* (Pilsbry, 1895a), ZMBN 81700, Galicia, Spain, H = 8–13 mm (Fig. 4A6). *H. japonica*, ZMBN 91233, Okinawa, Japan, animal length 5.5 mm (Fig. 4A5). *Haloa natalensis* (Kraus, 1848), NHMUK 20070186, Catalina Bay, St. Lucia, South Africa (Fig. 1). *Haminoea musetta* Er. Marcus & Burch, 1965, paratype, UMMZ 230625, Einwetok Atoll, Marshall Islands, H = 8.5 mm. *Haloa musetta* (Er. Marcus and Burch, 1965), ZMBN 112938 Uruma, Okinawa, Japan, H = 2–4 mm (Fig. 1).

Distribution: Widespread in the IWP. From the Red Sea (Vayssière, 1906; Yonow, 2008) and Indian Ocean (Gosliner, 1987; Tibiriçá and Malaquias, 2017) to the West Pacific in Japan (Higo et al., 1999, 2001; Hori, 2001; Hanson et al., 2013b), southwards to New South Wales and northern Western Australia (Beechey, 2018; Nimbs and Smith, 2016), and Central Pacific including Hawaii (Rudman, 1971a) and Tahiti, French Polynesia (Pease, 1868; Tröndlé and Boutet, 2009; Salvat and Tröndlé, 2017).

Habitat: Tidal flats, sea grass beds, muddy-sand bottoms and algae (Er. Marcus and Burch, 1965; Gibson and Chia, 1989; Álvarez et al., 1993b; Gosliner et al., 2008, 2015; Bharate et al., 2018).

Genus *Lamprohaminoea* Lin, 1997 ex Kuroda & Habe, 1952 (Figs. 1, 2E, F, 4B1–B5)

Diagnosis: Animal background colour white or whitish-green, with yellow, orange and/or purple blotches, black dots sometimes present (Fig. 1). Cephalic shield deeply bilobed, cephalic lobes elongate, often overlapping; eyes narrowly spaced, periocular area sometimes with colourful blotches. Hancock organ long, ridge-like (Fig. 4B2). Shell oval, smooth, whitish translucent; periostracum transparent; aperture narrow tapering apically, columella broad, separated from last whorl by narrow furrow, callus folding back over furrow (Fig. 4B1). Jaws semi-circular, rods with denticulate edges (Fig. 4B5). Radula formula 13–5.1.1.1.5–13; rachidian tricuspid, broad, cusps sharp, central longer; lateral teeth hook shaped, often smooth, inner lateral sometimes serrated along inner edge or both edges (Fig. 4B4). Gizzard plates with 17 fine transverse ridges; smooth or covered in many minute rods; area between ridges smooth. Three gizzard bristled spines, resembling feather dusters inserted in raised triangular fleshy base. Reproductive system with rounded to oblong prostate; nodulous accessory glands; long twisted seminal duct, parts of duct folded within thickened glandular region; lumen of seminal duct circular. Atrium elongated with thick muscular sheet. Fundus small, thin walled, transparent, containing chitinous spines. Short retractor muscle connects lower seminal glandular mass and fundus (Figs. 2E, F; 4B3).

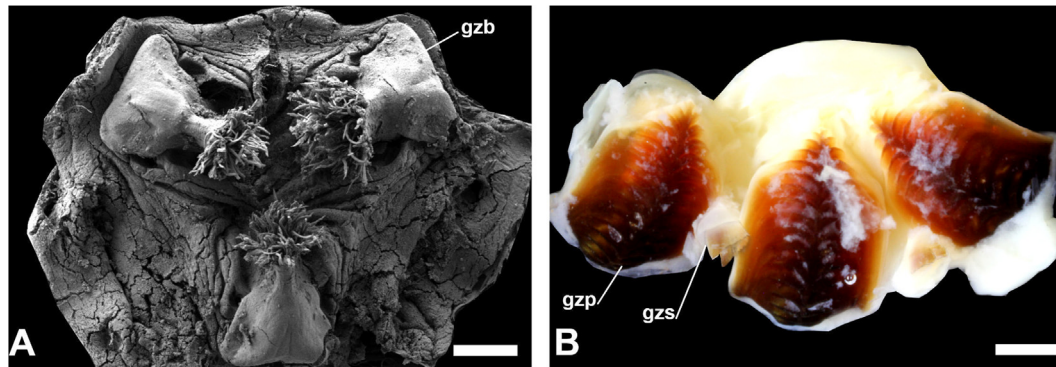


Fig. 3. A. SEM of the anterior part of the interior of the gizzard depicting the bristled spines resembling feather-like dusters of *Haloa crocata* (ZMBN 81705, Hawaii, H = 14 mm). B. macrophotography of gizzard plates and spines in the interior of the gizzard of *Haminoea alfredensis* (ZMBN 86406, Knysna lagoon, South Africa, H = 16 mm). Abbreviations: gzb, gizzard bristle. gzs, gizzard spine. gzp, gizzard plate. Scale bars: A = 200 µm; B = 0.5 mm.

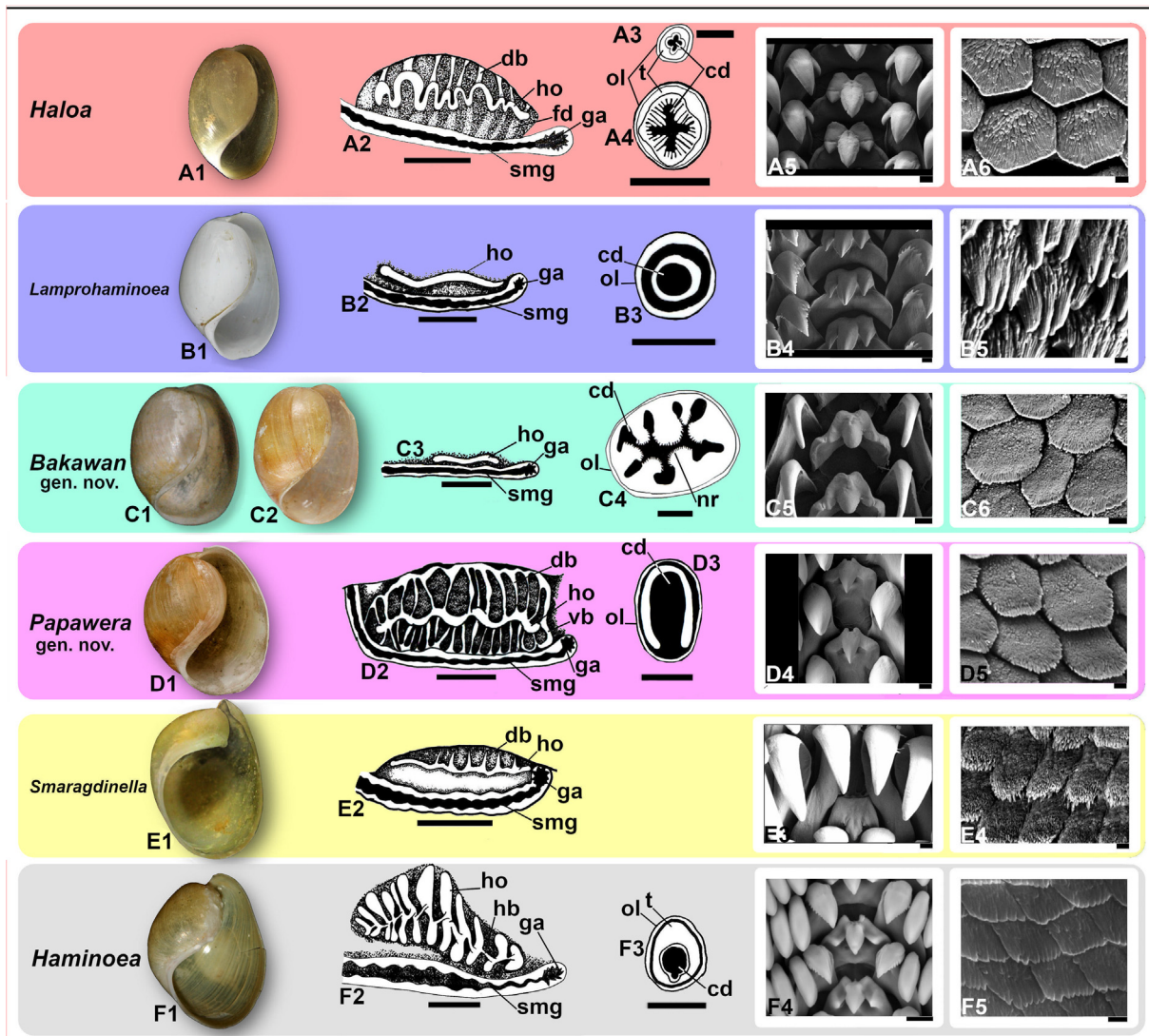


Fig. 4. Graphical representation of the archetypical morphology of diagnostic characters shells, hancock organs, cross-sections of seminal ducts, radulae and jaws microsculpture of the genera A, *Haloa*, B, *Lamprohaminoea*, C, *Bakawan*, D, *Papawera*, E, *Smaragdinella*, and F, *Haminoea*. For descriptions, see theme 5. *Taxonomic section* and Table 2. Scale bars: A2, D2, E2, F2 = 0.5 mm; B2, C3 = 0.25 mm; A3, F3 = 300 μ m; B3 = 130 μ m; C4 = 250 μ m; D3 = 160 μ m; F4 = 25 μ m; A5, C5, D5 = 10 μ m; B4, E3 = 5 μ m; A6, D5, F5 = 2 μ m; B5, E4 = 1 μ m; C6 = 3 μ m. Abbreviations: Abbreviations: cd, central duct of lumen. db, dorsal branch. fd, folds. ga, genital aperture. hb, horizontal branch. ho, hancock organ. nr, nodulous ridge. ol, outer layer. smg, external seminal groove. t, tissue. vb, ventral branch.

Relevant references: Pease (1860, 1868), Bergh (1901), Pilsbry (1921), Ostergaard (1950), Habe (1952), Er. Marcus and Burch (1965), Rudman (1971a, 1999a, 1999b), Kay (1979), Heller and Thompson (1983), Lin (1997), Carlson and Hoff (1999), Pittman and Fiene (2018).

Type species: *Bulla cymbalum* Quoy and Gaimard, 1832. **Type locality:** Guam.

Material examined: *Lamprohaminoea cymbalum* (Quoy & Gaimard, 1832), AMS c.103327; Fungalei Islet, Wallis Is, Wallis and Futuna, H = 16 mm (Fig. 4B1, B3). *L. cymbalum*, MNHN IM-2013-52940; Palikulo Peninsula, Vanuatu, H = 8.8 mm (Fig. 2E). *L. cymbalum*, AMS c.132490; Great Detached Reef, Queensland, Australia, H = 8 mm (Fig. 2F). *L. cymbalum*, ZMBN 125454, Paindane, Mozambique, H = 5 mm, animal length 14 mm (Fig. 4B2). *L. cymbalum*, ZMBN 125448, Paindane, Mozambique, H = 5 mm, animal length 12 mm (Fig. 1). *Haminea simillima* Pease, 1868, lectotype selected by Johnson (1994), MCZ 297875, Tahiti, French Polynesia, H = 10 mm (image seen: <https://mcbase.mcz.harvard.edu/guid/MCZ:Mala:297875>); paralectotypes, MCZ 303194, Tahiti, French Polynesia, 12 shells, H = 10 mm (image seen: <https://mcbase.mcz.harvard.edu/guid/MCZ:Mala:303194>). *Haminoea linda* Marcus and Burch, 1965,

paratype, UMMZ 230627, Marshall Islands, H = 7 mm. *Haminea ovalis* Pease, 1868, lectotype selected by Johnson (1994), MCZ 297877, Tahiti, French Polynesia, H = 10 mm (image seen: <https://mcbase.mcz.harvard.edu/guid/MCZ:Mala:297877>); paralectotypes, MCZ 303195, Tahiti, French Polynesia, 3 shells, H = 10 mm (image seen: <https://mcbase.mcz.harvard.edu/guid/MCZ:Mala:303195>). *L. cf. ovalis*, MNHN IM-2013-52939, Vanuatu, Segond Channel, H = 16 mm (Fig. 4B5). *L. cf. ovalis*, AMS c.469475.001, Moorena, Tahiti, French Polynesia, H = 3 mm (Fig. 4C4). *L. cf. ovalis*, ZMBN 81689, Maui, Hawaii, H = 3 mm (Fig. 1).

Distribution: Widespread in the tropical and sub-tropical latitudes of the IWP. From the Red Sea (Heller and Thompson, 1983; Yonow, 2008) and western Indian Ocean (Tibirić and Malaquias, 2017); western Pacific from the Amami Islands, Japan (Higo et al., 1999; Hori, 2001, 2017), southward to West Australia and New South Wales, Australia (Nimbs and Smith, 2016, 2018). In the central Pacific including Hawaii (Rudman, 1971a; Pittman and Fiene, 2018) and Tahiti, French Polynesia (Pease, 1868; Tröndlé and Boutet, 2009; Salvat and Tröndlé, 2017).

Habitat: Shallow waters on coral reefs, coral rubble, rocks covered

in algae and algae beds (Cruz-Rivera and Paul, 2006; Gosliner et al., 2008, 2015; Tibiriçá and Malaquias, 2017; Pittman and Fiene, 2018).

Remarks: Lin (1997) is here regarded as the authority of *Lamprohaminoea* because she was the first to include a diagnosis for the genus and type species (see Oskars et al., 2019).

Genus *Bakawan* gen. nov. (Figs. 1, 2C, D, 4C1–C6)

Diagnosis: Animal greenish to brownish-orange, black blotches maybe present on body. Cephalic shield squarish, shallowly indented posteriorly. Eyes widely spaced, inserted in small circular unpigmented periocular areas (Fig. 1). Hancock organ, short, ridge-like (Fig. 4C2). Shell rounded, whitish-translucent to brownish in colour; surface covered in deep, conspicuous spiral striae, tightly spaced; periostracum transparent, light orange to reddish-brown; aperture wide, narrower apically, columellar callus narrow, raised, separated from last whorl by a furrow (Fig. 4C1). Jaws semi-circular rounded rods slightly serrated on outer edge (Fig. 4C6). Radula formula 16–10.1.1.1.10–16; rachidian tricuspid, central cusp larger with rounded tip; lateral cusps vestigial; lateral teeth, narrow, hook shaped, smooth, decrease in size outwardly (Fig. 4C5). Gizzard plates with flat surface, whole surface covered by tiny rods. Three gizzard bristled spines, resembling feather dusters inserted in raised triangular fleshy base. Reproductive system covered in small warts; prostate small, rounded, nodulous, almost continuous with short, thick seminal duct; lumen of seminal duct start-shaped with 6–8 grooves; seminal duct empties into fundus apically; fundus thick walled, externally looking as a rounded bulge (Fig. 2C, arrow), internally with distinct left and right lateral walls separated by narrow central groove; both walls crossed by deep grooves. Atrium thin walled. External seminal groove enters genital aperture, runs along atrium upwards, merging with left lateral wall of fundus (Figs. 2C, D; 4C4).

Relevant references: A. Adams (1850), Bergh (1901), Struck (1998), Ng and Sivasothi (2001), Lozouet and Plaziat (2008), Hung (2013), Riek (2013, 2014), Mujiono (2016), Cobb (2018), Yonow and Jensen (2018).

Type species: *Bulla rotundata* A. Adams (1850). **Type locality:** Singapore, Johor Strait, Lim Chu Kang.

Etymology: The genus is named after the Tagalog Philippine name for mangroves, as three of the species are found in the Philippines.

Material examined: *Bulla (Haminea) rotundata* A. Adams, 1850, syntypes, NHMUK 196970; locality unknown, Cumming collection, 2 shells, H = 9.5 mm (Fig. 4C1), H = 8 mm (broken). *Bakawan rotundata* (A. Adams, 1850), ZMBN 125443, Sarawak, Borneo, Indonesia, H = 6 mm (Fig. 4C2). *B. rotundata*, ZMBN 89276, Lim Chu Kang, Johor Strait, Singapore, H = 8 mm (Fig. 1). *B. rotundata*, AMS c.150784, Darwin, Northern Territory, Australia, H = 16 mm (Figs. 2C, 4B4, E5). *B. rotundata*, AMS c.458566, Magnetic Island, Queensland, Australia, H = 8 mm (Fig. 2D). *B. rotundata*, ZMBN 125424, Hab River Delta, Sindh, Pakistan, H = 3–7 mm (Fig. 4C5). *Bulla (Haminea) fusca* A. Adams, 1850, syntypes, NHMUK 196945, Cagayan, Mindanao Island, the Philippines, Cumming collection, 4 shells, H = 10 mm, 18 mm, 2 shells broken. *Bakawan fusca* (A. Adams, 1850) (reddish periostracum), MNHN Vayssière no.244 1921, the Philippines, H = 13 mm. *Bakawan* sp. 1 (transparent periostracum), MNHN 42265, Panglao, the Philippines, H = 8 mm. *Bakawan* sp. 2, AMS c.458281, Kangaroo Island, Susan River, Queensland, Australia, H = 3–5 mm.

Distribution: Found in the eastern Indian Ocean and western Pacific (Gosliner et al., 2008, 2015; Riek, 2013, 2014; Mujiono, 2016; Cobb, 2018; Yonow and Jensen, 2018; this study).

Habitat: Restricted to mangrove habitats (Riek, 2013, 2014; Mujiono, 2016; Cobb, 2018; Yonow and Jensen, 2018; this study).

***Bakawan rotundata* (A. Adams, 1850) comb. nov.**

Diagnosis: Animal can vary from light-green to brownish-orange, black blotches present on body. Shell rounded, whitish-translucent; periostracum light orange; aperture wide, narrower apically, columella deeply concave, anterior aperture extends deeply into last whorl of shell. Radula formula 16–10.1.1.1.10–16; rachidian tricuspid, central cusp larger with rounded tip; lateral cusps vestigial. Jaw plates semi-

circular, rods rounded slightly serrated on outer edge. Reproductive system covered in small warts; prostate small, rounded, nodulous, almost continuous with short, thick seminal duct; thin walled atrium; with thick walled fundus, inner lobe of right lateral wall short and thick.

Type material: Lectotype here designated *Bulla (Haminea) rotundata* A. Adams, 1850, NHMUK 196970; locality unknown, Cumming collection, H = 9.5 mm (Fig. 4C1).

Type locality: Singapore, Johor Strait, Lim Chu Kang (by subsequent designation; fixed here according to ICZN (1999) art. 76A.1.4; based on specimen ZMBN 89276).

Distribution: From the United Arab Emirates eastwards to Singapore and China, the Philippines, southwards along Queensland, Australia.

Genus *Papawera* gen. nov. (Figs. 1, 2H, I, 4D1–D5)

Diagnosis: Animal light grey or brown to completely black; orange blotches and opaque white dots may be present. Cephalic shield, broad, shallowly or deeply bilobed; periocular area pigmented or unpigmented (Fig. 1). Hancock organ ridge-like, with long dorsal and ventral branches (Fig. 4D2). Shell oval to rounded; smooth with faint growth lines; whitish in colour; periostracum transparent to yellowish; aperture wide, tapering posteriorly, columella thick, separated from last whorl by short furrow; furrow covered by callus posteriorly (Fig. 4D1). Radula formula 27–5.1.1.1.5–27; rachidian tricuspid, elongate, central cusp longer, lateral cusps vestigial; outer lateral teeth hook shaped, smooth, decreasing in size outwardly; cusp of inner lateral slightly bulbous, tip pointed (Fig. 4D4). Jaws semi-circular, rods slightly serrated on outer edge (Fig. 4D5). Gizzard plates with 8–14 transverse ridges, top of ridges covered in minute rods, smooth between ridges. Three gizzard bristled spines, resembling feather dusters inserted in raised triangular fleshy base. Reproductive system with oblong annulated prostate; short seminal duct, with semi-enclosed hollow duct; fundus semi-enclosed with glandular epithelium; thick, non-muscular atrium (Figs. 2H, I; 4D3).

Relevant references: Gray (1843), Sowerby III (1868), Pilsbry (1895b), Burn (1966, 1969, 1974). Rudman (1971a, 1971b), Rudman (1999c), Furneaux (2003). Rudman (2003b, 2006, 2007), Eichler (2007), Burn and Wilson (2011), Grove (2017).

Type species: *Bulla zelandiae* Gray, 1843. **Type locality:** New Zealand.

Etymology: The genus name is erected after Robert Burn renowned Australian malacologist. The name is composed by two parts: “papa” meaning to set fire in the Bunganditj or Boandik language of the indigenous people of Port MacDonnell, southern Australia (see Blake, 2003), and “wera” which means burn in the Maori language of the indigenous people of New Zealand.

Material examined: *Haminea obesa* Sowerby III, 1868, holotype, NHMUK unnumbered, New Zealand, H = 17 mm (Fig. 4D1; Sowerby, 1868, pl. 2, Fig. 13). *Papawera zelandiae* (Gray, 1843), AM 119920; Waitemata harbour, Auckland, New Zealand, H = 11 mm (Figs. 2H, I, 4E4, E5). *P. zelandiae*, AM 79176; Hokianga, Northland, New Zealand, H = 14 mm (Fig. 4D2, D3). *Haminoea maueansis* Burn, 1966, holotype, NVM F 26134; Shoreham, Victoria, Australia, H = 7 mm (Image seen, <https://collections.museumvictoria.com.au/specimens/643579>). *Papawera maueansis* (Burn, 1966), ZMBN 125458 ex NVM F112423; Curlew Reef, near Clifton Springs, Victoria, Australia, H = 8 mm. *P. maueansis*, ZMBN 125459 ex NVM F194630, Inverloch, Town Area, Victoria, Australia, H = 5.7 mm. *P. maueansis*, AMS c.105854, Shoreham, Victoria, Australia, H = 4 mm.

Distribution: Restricted to temperate parts of Australasia, New Zealand and southern Australia (Burn 1966, 1969, 1974; Rudman, 1971a, 1971b, 1999c; Furneaux, 2003; Rudman, 2003b, 2006, 2007; Eichler, 2007; Burn and Wilson, 2011; Grove, 2017).

Habitat: Intertidally to sub-tidally on sandy-mud flats, muddy seagrass beds, exposed rocky shores, rock platforms, tide pools and rock pools (Burn, 1966, 1969; Rudman, 1971a, 1971b; Burn and Wilson,

2011).

***Papawera zelandiae* (Gray, 1843) comb. nov.**

Diagnosis: Animal light grey or brown to nearly black. Cephalic shield, broad, shallowly bilobed. Shell rounded and bulbous; smooth with faint growth lines; whitish in colour; periostracum transparent to yellowish. Radula formula 27–22.1.1.1.22–27. Gizzard plates with 8–9 transverse ridges, top of ridges covered in minute rods, smooth between ridges. Reproductive system with oblong tapering, annulated prostate.

Type material: holotype untraceable; iconotype illustrated in Smith (1873: 5, tab. 1, Fig. 10). **Type locality:** New Zealand (Gray, 1843).

Distribution: North Island and northern part of South Island of New Zealand (Rudman, 1971a, 1971b, Rudman, 2003b, 2006; Furneaux, 2003; this study).

4. Discussion

4.1. Tethyan vicariance, relictualism, and ecological specialization

Oskars et al. (2019) showed the paraphyly of the genus *Haminoea* with all Atl + EP species (plus a temperate Indian Ocean species from South Africa) clustering together in a sister position to a clade containing the IWP and Australasia species of “*Haminoea*” (= *Haloa sensu lato*; Oskars et al., 2019) plus the genus *Smaragdinella*. The current study confirms this pattern and showed the occurrence of four distinct clades with unique morphological traits and ecologies among *Haloa sensu lato*.

Our phylogeny suggests vicariance on an ancestral lineage or lineages caused by the closure of the Tethys Sea after the collision of the African and Eurasian continental plates during the middle Miocene around 18–19 Mya (Vrielynck et al., 1997; Rögl, 1998; Okay et al., 2010; Hamon et al., 2013), followed by radiations on both sides and presumably extinctions (Harzhauser et al., 2007, 2009, 2002). The final closure of the Tethys seaway around 14 Mya (Harzhauser et al., 2007; Hamon et al., 2013; Uribe et al., 2017) is known to have shaped the deep phylogenetic structure of many marine groups of organisms by isolating regions that overtime developed their own biological identity (e.g. gastropods, Meyer, 2003; Williams and Reid, 2004; Frey and Vermeij, 2008; Malaquias and Reid, 2009; Uribe et al., 2017; fish, Teske et al., 2004; Alfaro et al., 2007; Floeter et al., 2008; sea urchins, Lessios et al., 2001; amphipods, Liu et al., 2018).

The five sub-clades found within *Haloa s. l.* all have nearly distinct ecologies. *Haloa sensu stricto* includes dull-coloured species with cryptic colour patterns distributed across sub-tropical and tropical waters of the IWP. The species are seemingly generalist herbivores that feed on diatoms, dinoflagellates and green algae such as *Ulva* spp. (Usuki, 1966a, 1966b; Ito et al., 1996; Ito, 1997; Oskars and Malaquias, unpublished data).

Lamprohaminoea has a similar geographical span but only includes colourful species with flamboyant patterns associated with the presence of deterrent chemicals (Poiner et al., 1989; Fontana et al., 2001 for *L. cymbalum*; Mollo et al., 2008 for *L. cyanomarginata*), and species apparently feed on cyanobacteria (Cruz-Riviera and Paul, 2006). The development of aposematic patterns and diet specialization possibly played a role on the diversification of this clade. The genus *Bakawan* gen. nov. includes species restricted to mangrove habitats in the Indian ocean and western Pacific. The genus *Papawera* gen. nov. is restricted to temperate Australasian waters of New Zealand and southern Australia including Tasmania. On the other hand, the genus *Smaragdinella* is the only rock-dweller clade in the entire order Cephalaspeida.

This apparent ecological segregation suggests an important role of ecology, namely habitat selection and diet in shaping the phylogenetic structure of *Haloa s. l.* driving the diversification of its main lineages. The role of ecology in the formation of species, such as nutrient availability or productivity and temperature regimes, has been hypothesised to be a possible mechanism of diversification for example in cowries (Meyer, 2003), periwinkles (Williams and Reid, 2004), sponges

(Duran and Rützler, 2006), and bubble-shells (Malaquias and Reid, 2009) and we here stress its putative importance in also shaping the deep phylogenetic structure of major clades in Haminoeidae.

Another interesting aspect of the phylogeny is the occurrence of a putatively basal clade of southern Australasian species (= *Papawera* gen. nov.), which could represent a case of Tethyan relictualism. Nevertheless, caution is warranted, because some sister relationship between genera in our phylogeny, including *Papawera* gen. nov., are not fully resolved (Figs. 1 and 2). Genera that were once common in the European Eocene to Miocene and that now survive only in southern Australasia, have been interpreted as “living ‘Tethyan relicts’” (Houbrick, 1984a, 1984b; Wilson and Allen, 1987; Hall, 1998; Malaquias and Reid, 2009). However, until a calibrated phylogeny of *Haloa s. l.* and ideally better knowledge of the fossil record of these snails is available our hypothesis remains largely speculative.

4.2. Hidden diversity in *Haloa sensu lato*

Up to now, the taxonomy of the worldwide *Haminoea s. l.* snails was very much based on shells and to a lesser extent colour patterns, whereas anatomical features were only known for few species (e.g. *Haminoea hydatis*, *H. navicula*, *Haloa japonica*, *Lamprohaminoea cymbalum*, *Papawera zelandiae*). With few exceptions, the vast majority of species have similar shells that are difficult to tell apart and the colouration of the animals is complicated to use because of similar dull colour patterns. Moreover, whereas the anatomy of the Atlantic species is relatively well known (Malaquias and Cervera, 2006) few recent data is available for the IWP species (e.g. Er. Marcus and Burch, 1965; Rudman, 1971a, 1971b; Bharate et al., 2018).

Despite earlier attempts to subdivide *Haminoea s. l.* (e.g. Pilsbry, 1895a, 1985b, 1921, Iredale, 1929, Kuroda and Habe, 1952; Habe, 1952; see Introduction for a complete overview), it is only with the work by Oskars et al. (2019) that become evident the non-monophyly of *Haminoea s. l.* with *Haminoea s. s.*, *Haloa s. l.* and *Smaragdinella*. The latter authors also clearly distinguished *Haminoea s. s.* from *Haloa s. l.* by reviewing the anatomical features of the clades, where the most notable distinction was the hollow fundus of *Haloa s. l.* (Fig. 2A–I; absent in *Haminoea*) and the muscular penis of *Haminoea s. s.* (Fig. 2J, K; absent in *Haloa*). However, during the course of this study further distinctions became apparent. The gizzard in *Haloa s. l.* have three feather duster-like gizzard bristles anterior of the gizzard plates (Fig. 3A), whereas in *Haminoea s. s.* these spines are flattened (Fig. 3B) (Vayssière, 1885; Thompson, 1976, 1988; Schaefer, 1992; Álvarez et al., 1993a; Malaquias and Cervera, 2006).

Additionally, Oskars et al. (2019) pointed out to the possibility that *Haloa s. l.* could warrant further split because of the occurrence of three well supported sub-clades with unique features in the male reproductive system, parts of the digestive system, shells, and external colouration. The expanded dataset of IWP species of *Haloa s. l.* used in this work including all lineages known to us yielded a fourth sub-clade with only species of temperate affinities. Two of these clades have generic names available (*Haloa* and *Lamprohaminoea*) and two are here formally described (*Bakawan* gen. nov. and *Papawera* gen. nov.; see Results).

4.2.1. The genus *Haloa* Pilsbry (1921)

Haloa was found to be monophyletic with 11 species; however, there are 16 nominal names available in the literature, but ongoing systematic work on this group revealed that several of those names are synonyms (Oskars and Malaquias, unpublished data).

All species in the genus are restricted to tropical and sub-tropical shallow waters of the IWP, except for *H. japonica*, which has a native temperate to sub-tropical distribution (Hanson et al., 2013a, 2013b). Most species of *Haloa* are externally similar and cryptically coloured and as a result several of them have been loosely assigned to the “common” and better known species *H. natalensis* (e.g. Gosliner, 1987,

Table 2
Synopsis of the most useful morphological characters for diagnosis of genera.

Characters of genera	<i>Haloa</i> Pilsbry (1921)	<i>Lamprohamimoea</i> Lin (1997)	<i>Bakawan</i> gen. nov	<i>Papawera</i> gen. nov	<i>Smaragdina</i> A. Adams (1848) (1830)	<i>Hamimoea</i> Turton and Kingston (1830)
1. Shell Shape	Oval to rounded	Oval	Rounded	Oval to rounded	Ovoid flattened or bulloid, with cup-shaped process apically or crest embedded in first whorl	Oval to slightly pyriform
Sculpture	Faint to conspicuous spiral striae	Smooth	Conspicuous spiral striae, tightly spaced	Smooth, faint growth lines	Smooth	Smooth, with growth lines; spiral striae present in some species
Shell colour	Whitish-translucent to brownish; periostracum pale yellow to pale brown	Whitish translucent; transparent periostracum	Whitish-translucent to light brown; periostracum translucent, orange to reddish-brown	Whitish; periostracum transparent to yellowish	Brownish to greenish	Brownish translucent; periostracum transparent to pale yellow
2. External morphology						
Animal colouration	Dull coloured; orange dots maybe present	Colourful; white background with green; purple, yellow, or orange blotches	Greenish to brown-orange/reddish	Dull coloured; orange dots maybe present	Greenish to darker green; sometimes white blotches present	Dull coloured; orange dots maybe present
Cephalic shield	Deeply bilobed; eyes closely spaced	Deeply bilobed; eyes closely spaced	Squarish; shallow posterior indentation; eyes widely spaced	Both shallow and deeply bilobed. Eyes closely spaced	Squarish with minute posterior notch; eyes widely spaced	Bilobed; eyes closely spaced
Parapodial and pallial lobes	Parapodia rounded, overlapping slightly; pallial lobe rounded, extending beyond apex	Parapodia rounded, do not meet dorsally; pallial lobe rounded or pointed, extending beyond apex	Parapodia rounded, do not meet dorsally	Parapodia rounded, do not meet dorsally; pallial lobe rounded, extending beyond apex.	Parapodia large, running lengthwise the body; do not meet dorsally	Parapodia large, in some species overlapping dorsally; pallial lobe squarish/rounded, extends beyond apex
Hancock organ	Ridge-like, sometimes short dorsal branches present	Ridge-like, long, narrow	Ridge-like, short, thick	Ridge like, dorsal and ventral branches	Simple ridge, dorsal branches	Perfoliate
3. Radula Formula	21–5.1.1.1.5–21	13–5.1.1.1.5–13	16–10.1.1.1.10–16	27–6.1.1.1.6–27	26–12.1.1.1.1.2–26	58–16.1.1.1.16–58
Rachidian	Tricuspid; larger central cusp, cusps with pointed tips	Tricuspid; cusps of nearly equal length, central slightly longer	Tricuspid; larger central cusp, cusps with rounded tips	Tricuspid; elongate, larger central cusp, lateral cusps minute	Small, narrow, elongate, single cusp	Tricuspid; central cusp larger
Lateral teeth	Smooth, hook-shaped; inner lateral may have secondary cusp on inner edge	Smooth, hook-shaped; inner lateral may have denticulation on inner edge or both edges	Smooth, narrow hook-shaped	Smooth, hook shaped; inner lateral slightly more bulbous than outer laterals; outermost laterals maybe plate-like	Inner and first outer laterals hook-shaped; outermost laterals minute platelets	Inner and first outer lateral may be denticulate along outer edge; often outer laterals smooth, hook-shaped
4. Gizzard plates						
Ridges	12–17	17	Absent; flat surface	8–14	16–40; transverse or V-shaped	8–32
Sculpture	Ridges covered with rods on top; some species with rods in between ridges	Smooth or covered in many minute rods	Whole surface covered by tiny rods	Ridges covered in many or only few minute rods	Rods present on both sides of ridges	Pointed rods on ridges and rachis
Gizzard spines	Three bristled spines, located anteriorly between plates, resembling feather-dusters; spines inserted in raised triangular fleshy base	Three bristled spines, located anteriorly between plates, resembling feather-dusters; spines inserted in raised triangular fleshy base	Three bristled spines, located anteriorly between plates, resembling feather-dusters; spines inserted in raised triangular fleshy base	Three bristled spines, located anteriorly between plates, resembling feather-dusters; spines inserted in raised triangular fleshy base	Absent	Six spines; three anteriorly and three posteriorly; in between plates; spines laterally flat
5. Male reproductive system						
Prostate	Rounded to oblong	Rounded to oblong, with nodulous accessory glands	Small, rounded, nodulous, almost continuous with seminal duct	Oblong annulated prostate	Rounded, spermatic bulb apically	Bilobed
Seminal duct	Elongated; cross-section with four grooves radiating from lumen	Elongated; cross-section with simple duct within an outer duct	Short, thick; cross-section with 6–8 grooves radiating from central lumen	Short; cross-section with semi-enclosed duct within an outer layer	Short, sometimes with accessory glands	Directly connected to penis; cross-section with simple
Penial sheath/Atrium	Thick walled atrium, fundus with soft flaps, warts or ridges	Muscular atrium, fundus with chitinous spines	Thin walled atrium; thick walled fundus with modified lateral walls	Thick-walled atrium, fundus semi-enclosed with glandular epithelium	Atrium barely separated from fundus, filled with soft warts, fundus with modified, eversible pseudopenis	Contains muscular penis

(continued on next page)

Table 2 (continued)

Characters of genera	<i>Haloa</i> Pilsbry (1921)	<i>Lamprohaminoea</i> Lin (1997)	<i>Bakawan</i> gen. nov.	<i>Papawera</i> gen. nov.	<i>Smaragdinella</i> A. Adams (1848)	<i>Haminoea</i> Turton and Kingston (1830)
6. Key References	Er. Marcus and Burch (1965), Rudman (1971a), Bharate et al. (2018)	Er. Marcus and Burch (1965), Rudman (1971a), Heller and Thompson (1983)	Bergh (1901)	Burn (1966, 1969), Rudman (1971a, b)	Er. Marcus and Burch (1965), Chaban and Chernyshev (2016)	Malaquias and Cervera (2006), Oskars et al. (2019)

Gosliner et al., 2008, 2015; Tibiriçá and Malaquias, 2017; Johnson and Johnson, 2018a, 2018b; Michenet and Berberain, 2018; Pittman and Fiene, 2018). See theme 3.9. *Taxonomic section* and Table 2 for diagnostic features of *Haloa*.

4.2.2. The genus *Lamprohaminoea* Lin (1997)

We here resurrect the name *Lamprohaminoea* which was considered a synonym of *Haloa* by Oskars et al. (2019). We introduce this name for a clade with five species all characterized by flamboyant colour patterns including the common “*Haminoea*” *cyanomarginata*, “*H.*” *cymbalum*, and “*H.*” *ovalis* (e.g. Gosliner et al., 2008, 2015; Nimbs and Smith, 2016, 2018; Tibiriçá and Malaquias, 2017). (see theme 3.9. *Taxonomic section* and Table 2 for diagnostic features of *Lamprohaminoea*).

Some species in this clade are difficult to tell apart as shells have similar shapes and colour patterns can depict both interspecific similarities and intraspecific variation. An ongoing systematic review of *Lamprohaminoea* species shows that apart of the DNA the most reliable characters to separate species are features of the reproductive system (Oskars and Malaquias unpublished data).

The origin of the colourful patterns in *Lamprohaminoea* has never been thoroughly studied, but seem to be a sign of distastefulness resulting from the presence of deterring secondary metabolites. It is however, unknown whether the chemical compounds are produced *de novo* or originate from their food (Poiner et al., 1989; Mollo et al., 2008). Even though the origin of these metabolites remains unknown, it seems that the acquisition of this trait, and the bright colours signalling their presence, was determinant in the evolution and radiation of *Lamprohaminoea*.

4.2.3. The genus *Bakawan* gen. nov.

All lineages ecologically restricted to mangrove habitats have clustered together and this included species like “*Haloa*” *rotundata* and “*H.*” *fusca* plus two unidentified species that are presumably new. This clade is not only ecologically distinct, but species are also characterized by a unique morphology and colour pattern with animals possessing a uniformly pale to dark green or orange to reddish colouration in some cases with dark blotches (Riek, 2013, 2014; Mujino, 2016; Cobb, 2018; Yonow and Jensen, 2018). Therefore, we here introduce the new genus name *Bakawan* gen. nov. to reflect the phylogeny and the unique morphology and ecology of this clade. (see theme 3.9. *Taxonomic section* and Table 2 for diagnostic features of *Bakawan* gen. nov.).

All four species recognized in this clade are externally similar and only one species is often recognized in recent literature, often named as “*Haminoea*” *fusca* (e.g. Gosliner et al., 2008, 2015; Atlas of Living Australia, 2018; Cobb, 2018). Species in this clade are restricted to mangrove habitats of the eastern Indian Ocean and western Pacific. Interestingly, there are no records of *Bakawan* gen. nov. species along the extensive mangrove systems of eastern Africa or in the central Pacific islands.

4.2.4. The genus *Papawera* gen. nov.

Australasian species from temperate waters were not included in the work by Oskars et al. (2019) and their inclusion in the current study revealed the occurrence of a fourth clade within *Haloa* s. l. to which no name was available. Therefore, we here introduce the new genus *Papawera* gen. nov., which besides its molecular distinctiveness is also characterized by unique morphological features, such as its large annulated prostate and nearly monocuspid rachidian, and a geographical range restricted to temperate waters of the northern parts of New Zealand, southern Australia and Tasmania (see theme 3.9. *Taxonomic section* and Table 2 for diagnostic features of *Papawera* gen. nov.).

4.2.5. The genus *Smaragdinella* A. Adams (1848)

The phylogeny rendered *Smaragdinella* nested within the IWP radiation of *Haloa* s. l. species, which conforms with the results by Oskars et al. (2019). *Smaragdinella* is the only Cephalaspidea genus that

inhabits intertidal rocky shores occurring inside crevices or dead barnacles (Risbec, 1951; Er. Marcus and Burch, 1965; Miller, 1969; Rudman, 1972, 2004; Chaban and Chernyshev, 2016). These snails have a broader, depressed body and a more flattish shell. They are also characterized by unique anatomical traits such as the presence of a fundus and a modified blind sac in the male reproductive system (Fig. 2G), which previously was believed to be a penis (Bergh, 1901; Chaban and Chernyshev, 2016), the elongated monocuspid rachidian (Risbec, 1951, Er. Marcus and Burch, 1965; Chaban and Chernyshev, 2016; Fig. 4E3), and the narrow, heavily denticulate jaw rods (Fig. 4E5) (see Table 2 for diagnostic features of *Smaragdinella*).

4.3. Conclusions and a revised classification for *Haminoea sensu lato*

The results obtained with this study once again have clearly showed the importance of broad taxon sampling representing not only the traditional lineages, but also, ideally the entire morphological disparity and geographical span of the target group. In Cephalaspidea, this was previously demonstrated first with the work by Malaquias et al. (2009) and recently even more emphatically with the works by Oskars et al. (2015, 2019) and Bharate et al. (2018). In the current work it was of chief importance for example to include representatives of what we previously have identified as *Haminoea natalensis*, *Haminoea cymbalum*, *Haminoea ovalis*, and *Haminoea fusca* from across the entire distribution of these species. Otherwise, we would not have recognized cryptic diversity and even in some cases generic lineages.

Molecular phylogenetics including a complete or nearly complete species level diversity of *Haminoea s. l.* and *Smaragdinella* yielded a surprising result with on one hand a radiation including *Haminoea s. s.* with all Atlantic and eastern Pacific species plus a temperate lineage occurring in South Africa, and on the other a Indo-West Pacific plus Australasian radiation containing five genera, namely *Haloa*, *Lamprohaminoea* (here reinstated as valid), *Smaragdinella*, *Bakawan* gen. nov., and *Papawera* gen. nov. Additionally, these molecular groups are all supported by several morphological unique characters, particularly in the male reproductive system (see theme 3.9. Taxonomic section and Table 2).

Moreover, the phylogenetic pattern recovered strongly suggests an important role of Tethyan vicariance and ecological specialization in the diversification of these haminoid snails.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ymp.2019.106557>.

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