

New *Bakawan* (Mollusca: Gastropoda: Haminoeidae) species and records in mangrove-recolonised ponds in Oriental Mindoro, Philippines

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Abstract. Three species of mangrove-associated bubble snails (Heterobranchia: Haminoeidae) have so far been documented in the Philippines. Here, we describe a new species of *Bakawan* (*B. nasuso*, new species) and a new record of *B. puti* in Oriental Mindoro, Philippines. Specimens were found in abandoned fishponds that were recolonised by mangroves. Our comparative analyses included examination and measurements of shells, buccal apparatuses, genital anatomy, and DNA barcoding using cytochrome c oxidase 1 (cox1) gene. Anatomically, *B. nasuso*, new species, is most similar to *B. fusca* in that the ridges and pattern of the gizzard plates are diagonal and tapering, but they can be externally distinguished by the colour of the shells, which although similar in shape and overlapping in size ranges, it varies from citrine to maroon in *B. nasuso*, new species, whereas *B. fusca* has rufous-coloured shells. The genital anatomy differs from all other described *Bakawan* species in that the seminal duct of this new species is smooth and not warty. In terms of cox1 sequence divergence, *B. nasuso*, new species, differs from *B. fusca* by 10.5–11.1%, from *B. puti* by 8.2–9.7%, from *B. rotundata* by 8.7–9.4%, and from Australia's *B. hedleyi* by 10.8–11.1%. The discovery of *B. nasuso*, new species, and *B. puti* in abandoned, underdeveloped, and unproductive fishponds that were recolonised by mangroves underscores the hidden diversity that such environments can harbour and highlights the need for additional work in mangrove ecosystems across the Philippines.

Key words. bubble snail, mangrove-associate, new species, new record, Philippines

INTRODUCTION

Order Cephalaspidia, known colloquially as bubble snails or bubble-shells, is a diverse taxonomic group of gastropod molluscs with over 1,000 accepted species (MolluscaBase, 2025). Many researchers over the past decades have attempted to elucidate the phylogeny of this order (Mikkelsen, 1996), but were hindered by limited taxon sampling and inconsistencies in the group's complicated morphological characteristics. Recent studies utilised molecular techniques to provide a more complete and updated understanding of these gastropods' phylogeny at the family level (Malaquias et al., 2008; Oskars et al., 2015).

Haminoeidae Pilsbry, 1895 is largely considered one of the most diverse families among the cephalaspidians (Burn & Thompson, 1998; Oskars et al., 2019), with 169 nominal species (MolluscaBase, 2026) distributed across a range of marine habitats in both tropical and temperate waters (Oskars et al., 2019). The family, like the rest of its order, was

previously poorly defined due to insufficient morphology and shell-based classification. To address this, a comprehensive phylogenetic framework was recently established by Oskars et al. (2019), who integrated conchological, morpho-anatomical, and molecular data to redefine the taxonomy of the family, as well as validate its known genera. They found that *Haminoea* Turton & Kingston, 1830, the type genus of the family, is polyphyletic, encompassing three distinct, monophyletic lineages, each supported by diagnostic morphological features. These three main clades are the following: *Haloa* Pilsbry, 1921 (Indo-West Pacific (IWP) clade), *Haminoea* sensu stricto (Atlantic and Eastern Pacific clade), and *Smaragdinella* A. Adams, 1848 (tropical to subtropical IWP lineage). Another interesting finding from their study was the possibility of three informal ecological-morphological subclades within *Haloa*: dull-coloured species, only colourful species, and mangrove-associated species (Oskars et al., 2019).

Building upon these findings, Oskars & Malaquias (2019) further delved into the systematics of IWP *Haloa* based on a wider range of taxa with specimens from different subclades and biogeographic regions, using molecular phylogenetics (based on mitochondrial and nuclear genes) combined with morpho-anatomical data. The Indo-West Pacific and Australasian radiation was found to be composed of five genera, namely, *Haloa*, *Lamprohaminoea* T. Habe, 1952, and *Smaragdinella*, with two newly described genera, *Bakawan* Oskars & Malaquias, 2019, and *Papawera* Oskars & Malaquias, 2019 (Oskars & Malaquias, 2019; Oskars et

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al., 2019; Oskars & Malaquias, 2020a, b). Tethyan vicariance and ecological specialization were found to be the main drivers of these lineages' diversification (Oskars & Malaquias, 2019). Other studies have emphasised the critical importance of similar broad taxon sampling and integrative approaches for resolving cephalaspidean systematics (Malaquias et al., 2008; Oskars et al., 2015, 2019; Bharate et al., 2018; Oskars & Malaquias, 2019, 2020a, b; Turani et al., 2024).

Expanding on their previous work, Oskars & Malaquias (2020a) conducted further research on the genus *Bakawan*, integrating molecular techniques such as phylogeny reconstruction and species delimitation with careful analysis of shells and morpho-anatomy. They found that *Bakawan* represents a distinct mangrove-associated radiation within the Haminoeidae, comprising four recognised species: *B. rotundata* (A. Adams, 1850), *B. fusca* (A. Adams, 1850), and two newly described species, *B. puti* Oskars & Malaquias, 2020 and *B. hedleyi* Oskars & Malaquias, 2020 (Oskars & Malaquias, 2020a). *B. rotundata* was shown to be widespread across the eastern Indian Ocean to the western Pacific, *B. fusca* and *B. puti* are known only from the Philippines, and *B. hedleyi* is restricted to tropical eastern Australia. Ecologically, *Bakawan* is unique among related genera in being exclusively confined to mangrove environments and adjacent mudflats, where individuals are often observed on exposed mud during low tide (Oskars & Malaquias, 2020a). Additionally, the *Bakawan* species can be differentiated by subtle external and anatomical features. Colouration has been found to be a weak diagnostic trait due to potential dietary influence, whereas distinctions in the male reproductive system (particularly in the internal structure of the fundus) provide reliable species-level characters. For example, *B. fusca* has been shown to exhibit a uniquely modified pseudopenis (Oskars & Malaquias, 2020a).

Recently, one more genus and species under Haminoeidae was described by Oskars (2024) after conducting the same level of analysis. While initially thought to have been under the genus *Lamprohaminoea*, it was later found that *Confettiella malaquiasii* Oskars, 2024 is entirely new. This species was also collected in a mangrove habitat, and so far, is only known from the Philippines.

Aside from *Bakawan* and *Confettiella*, many other genera of bubble snails can be found in the Philippines that range across locations and habitats (Malaquias et al., 2008; Oskars et al., 2015). However, these mangrove-associated genera have so far only been confined to certain areas in the country. Of the three species of *Bakawan* occurring in the Philippines, two (*B. rotundata* and *B. puti*) have been observed in Panglao, Bohol and one (*B. fusca*) from Cagayan de Oro, Mindanao (Oskars & Malaquias, 2020a). Additionally, *C. malaquiasii* has only been collected from Panglao, Bohol (Oskars, 2024). These findings are likely an underestimation of the mangrove-associated bubble snail diversity in the country due to its large extent of mangroves.

Unfortunately, these crucial marine ecosystems are under threat. Since the 1970s, the Philippines has lost over 70%

of its original mangrove cover primarily due to large-scale conversion for aquaculture, which is a common trend across all of Southeast Asia (Baloloy et al., 2023; Contessa et al., 2023). Many aquaculture ponds were poorly managed and failed within a decade, leaving behind abandoned, underdeveloped, and unproductive (AUU) ponds with degraded conditions (Sidik et al., 2021; Tengku Hashim et al., 2021). The total extent of abandoned fishponds in the Philippines now exceeds 230,000 hectares (Salmo & Gianan, 2019; Dumalag et al., 2024).

Philippine mangroves, protected under national law, are broadly classified as natural, recolonised, or restored stands (Gerona-Daga et al., 2024a; Gevaña et al., 2024), and all of these types can be found across the archipelago. For instance, Oriental Mindoro is a province that is considered as one of the biodiversity hotspots of the country (Gonzalez et al., 1999). It is near the Verde Island Passage, which is recognised as the centre of shorefish biodiversity (Carpenter & Springer, 2005). The province has almost 2,400 hectares of mangroves found to have all three varying types: natural, undisturbed sites, human-restored stands, and naturally recolonised fishponds (Alcanices, 2017).

When mangrove ecosystems are ecologically healthy, they support a diverse assemblage of terrestrial, brackish, and marine species across multiple trophic levels (Muro-Torres et al., 2019). However, disturbances degrade vegetation and sediment conditions, leading to reduced or displaced faunal communities, including molluscs (Bagarinao, 2020). As mangroves regrow naturally or are restored, improvements in vegetation structure, productivity, and sediment quality facilitate the gradual return and colonisation of mangrove-associated fauna (Salmo et al., 2013, 2017; Nam et al., 2016; Gerona-Daga et al., 2024b). As part of a study to understand the recovery of mollusc diversity in naturally recolonised fishponds, mollusc assemblages were assessed and compared across natural, recolonised, and restored mangrove stands (J.B. Fermo et al., unpublished data). It is in this research that we first came across bubble snails in the recolonised stands of Oriental Mindoro.

In this study, we describe a new species of *Bakawan* and report a new record of *Bakawan puti* from Oriental Mindoro, Philippines. Specimens were collected from AUU ponds that have been naturally recolonised by mangroves. Morphological, anatomical, and molecular comparisons with previously described congeners confirm the distinctiveness of the new species. These findings highlight the role of recolonised mangrove systems as reservoirs of overlooked biodiversity.

MATERIAL AND METHODS

Taxon sampling. A total of 17 specimens (15 live snails, 2 empty shells) were incidentally collected from leaf litter and sediment samples in two municipalities in Oriental Mindoro during expeditions in January and August 2023. The collection sites in Bongabong and Mansalay are recolonised

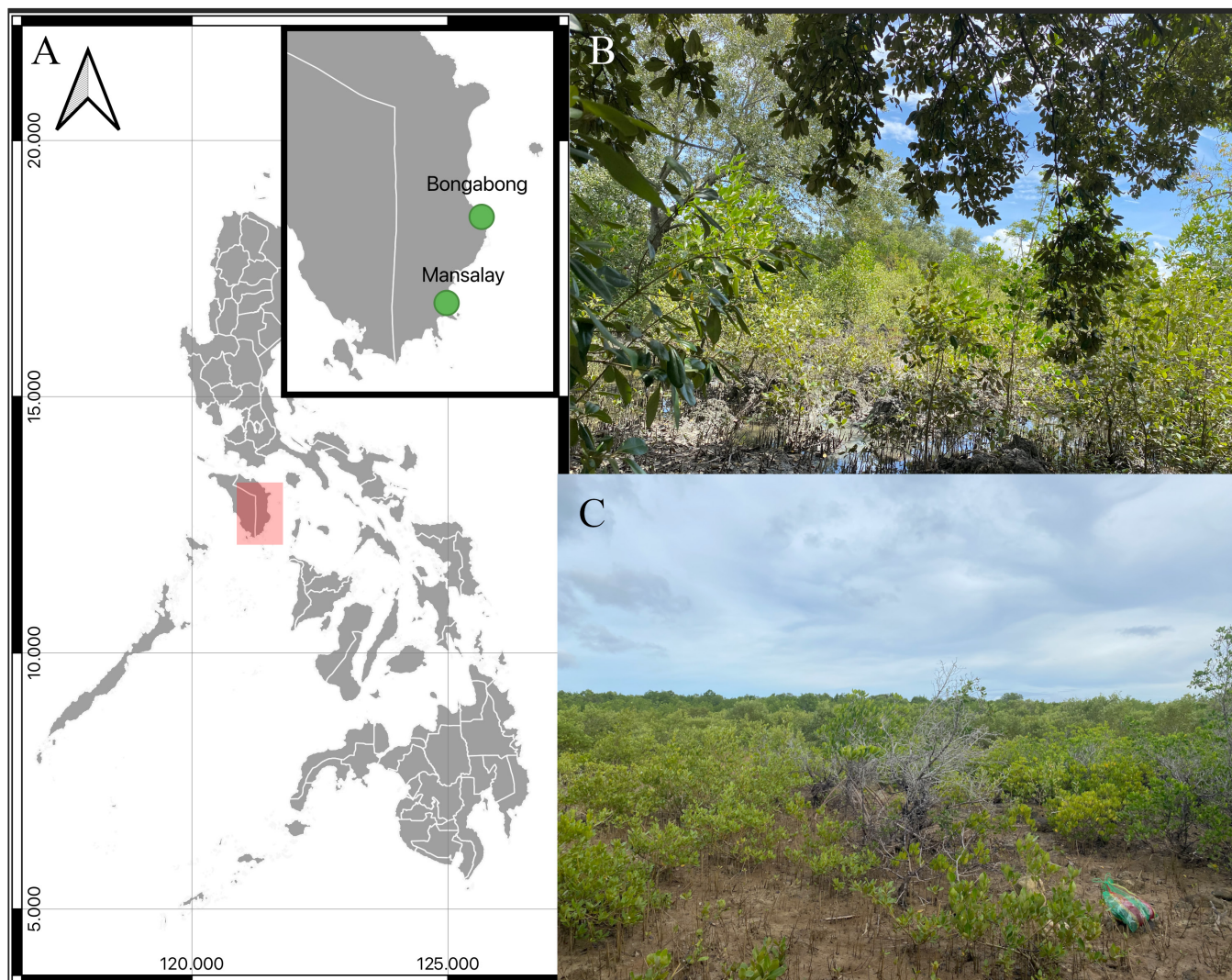


Fig. 1. A, map of the municipalities of Bongabong and Mansalay in Oriental Mindoro, Mindoro Island, Philippines. B, photo of the recolonised abandoned, underdeveloped and unproductive (AUU) pond in Bongabong, Oriental Mindoro. C, photo of the recolonised AUU pond in Mansalay, Oriental Mindoro.

AUU ponds (Fig. 1). Samples were relaxed in seawater with magnesium chloride, photographed, then preserved in absolute ethanol.

Morpho-anatomical work. Whole bodies were carefully twisted out of the shell using forceps. Due to the fragile nature of the shell, some apertures were chipped while taking out the soft tissues. Shell height (SH) and shell width (SW) were measured using a Wiha metric dial calliper. Standard views of the shells were imaged using a digital SLR camera. Dissection of genitalia, and extraction of gizzard plates were done under a Nikon SMZ1270 Stereomicroscope with DS-10 digital camera system. Line drawings of the male genital anatomy were produced using GNU Image Manipulation Program (GIMP) v.3.0.4.

Four of the 17 specimens were sent to the Senckenberg Ocean Species Alliance (SOSA) in Frankfurt, Germany for scanning electron microscope imaging of shell microsculpture, radula, gizzard plates, and jaw rods. A piece of shell broken off during shipping was sputter-coated with gold-palladium and imaged using a Hitachi TM4000Plus Tabletop SEM. Gizzard

plates, jaw, radula, and prostate gland were dissected using fine forceps and scissors, and dehydrated in absolute ethanol. The gizzard plate and prostate gland were critical-point dried, sputter-coated, and imaged using SEM. The radula and jaw, on the other hand, were transferred to hexamethyldisilazane (HMDS) through an ascending series of ethanol-HMDS mixtures, and then air-dried at room temperature in a fume hood overnight before mounting and SEM imaging.

Specimens referred to in this manuscript were deposited in the following institutions with their corresponding catalogue number abbreviations: Philippine National Museum of Natural History (PNM), and Senckenberg Natural History Museum in Frankfurt (SMF), and the University of the Philippines Marine Science Institute (UPMSI).

DNA barcoding. DNA was extracted from the foot muscle of seven specimens using the CTAB Method (Fontanilla et al., 2017). The DNA extracts were amplified using MyTaq HS Red Mix (Cat. No. BIO-25048, Biorline) and universal mitochondrial cytochrome c oxidase subunit I (cox1) gene primers (Folmer et al., 1994). A 25 μ L PCR Mix consisted

of 12.5 μL 2X MyTaq HS Red Mix (Cat. No. BIO-25048, Bioline), 1 μL (0.4 μM) each of the primers, 0.4–2 μL template DNA (20–50 $\text{ng}/\mu\text{L}$) and nuclease-free water up to 25 μL . Amplification conditions followed an initial denaturation for 3 min at 95 $^{\circ}\text{C}$, followed by 35 cycles of 45 s at 94 $^{\circ}\text{C}$, 45 s at 45 $^{\circ}\text{C}$, 2 min at 72 $^{\circ}\text{C}$, with a final extension of 10 min at 72 $^{\circ}\text{C}$ (Malaquias et al., 2008). PCR products were then visualized on 1% m/v agarose gels mixed with 1% v/v GelRed® Nucleic Acid Gel Stain (Cat. No. 41003). Successfully amplified PCR products were sent for sequencing to Macrogen Inc. (South Korea) for purification and bidirectional DNA sequencing. Sequences were then assembled using the STADEN package v.1.5.3 (Staden et al., 2000).

Bakawan sequences and additional haminoeid species were also downloaded from the GenBank database and utilised in the subsequent analysis (Table 1). Alignment was done in BioEdit v.7.2.5 (Hall et al., 1999) using the ClustalW algorithm (Thompson et al., 1994), applying its default penalties then trimmed to nucleotide positions common to all taxa (425 bp). The Xia Test for substitution saturation was performed in DAMBE v. 7.7.32 (Xia, 2018). Base frequencies were calculated using PAUP* v4.0b10 (Swofford, 2003) to characterize the sequences of each species. Through the ModelTest-NG v.0.1.7 (Darriba et al., 2012), the appropriate model of nucleotide substitution was selected based on the scores of the Akaike Information Criterion (Akaike, 1973) which was GTR+ Γ +I. PAUP* v4.0b10 (Swofford, 2003) and IQtree2 v2.3.6 (Minh et al., 2020) were used to construct the Neighbor joining (NJ) and Maximum Likelihood (ML) tree with branch supports for both tree-construction methods assessed through 1000 replicates of Bootstrap resampling (Felsenstein, 1985). Species delimitation analysis was carried out using the Automatic Barcode Gap Discovery (ABGD; Puillandre et al., 2012) method and Assemble Species by Automatic Partitioning (ASAP; Puillandre et al., 2021) utilising the K2P and simple distance using the ABGDpy 0.1 and ASAPy 1.0 from the iTaxoTools v 0.1 (Vences et al., 2021).

RESULTS

Of the 17 specimens examined, one specimen (PNM-041833) was identified as *Bakawan puti* Oskars & Malaquias, 2020 based on external morphology, gizzard plate morphology, and DNA barcode. This singleton co-occurred with the new species of *Bakawan* in Mansalay, Oriental Mindoro. As originally described by Oskars and Malaquias (2020), the colour of *B. puti* is pale orange, but we observed yellow specks in addition to the fine black dots all over the body. Instead of a whitish translucent shell, the specimen from Mindoro has a cinnamon brown shell. The gizzard plate is as described by Oskars & Malaquias (2020) wherein pseudoridges are only present anteriorly and the surface can be likened to coarse sandpaper. The specimen of *B. puti* from Mindoro is 0.9% different from *B. puti* from Bohol based on *cox1* sequences.

In total, 16 out of the 17 specimens were examined as a basis for describing the new species of *Bakawan*. Morphological and DNA barcoding results are described below.

SYSTEMATICS

Order Cephalaspeida P. Fischer, 1883

Family Haminoeidae Pilsbry, 1895

Genus *Bakawan* Oskars & Malaquias, 2019

Bakawan nasuso, new species

(Figs. 2–5)

Material examined. HOLOTYPE 1 specimen (PNM-041831; Fig. 2A) coll. G.A. Batomalaque and J.B. Fermo, January 2023, landward mangrove recolonised AUU pond in Bongabong, Oriental Mindoro.

PARATYPES: 5 lots (PNM-041832; SMF 383055; SMF 383058; UPMSI-MOLL-00651; UPMSI-MOLL-00652, Fig. 2C), same collector, collection date and site as holotype.

OTHERS: 8 lots (PNM-041834; SMF 383056; SMF 383057; UPMSI-MOLL-00653; UPMSI-MOLL-00654, Fig. 2D; UPMSI-MOLL-00655; UPMSI-MOLL-00656; UPMSI-MOLL-00657, Fig. 2E) coll. G.A. Batomalaque, August 2023, landward mangrove recolonised AUU pond in Mansalay, Oriental Mindoro. 2 lots (UPMSI-MOLL-00659, UPMSI-MOLL-00660) coll. J.J.A. Sarker, same collection site and date as previous material.

Etymology. The species name is a combination of two Tagalog words “na suso”, which translates to “is a snail”. This is meant to dispel the confusion among Filipinos brought by the genus name, because “bakawan” in Tagalog translates to “mangrove forest” or “mangrove tree”, and not an animal.

Diagnosis. Animal yellow to yellow-green in colour; cephalic shield distinctly dark green; yellow specks and black fine dots all over the body. Shell oval, white to light brown in colour. Spiral striae very fine and wavy. Periostracum cinnamon yellow to greyish maroon. Jaw rods rectangular to squarish, edge denticulate. Radular formula $32 \times 10.1.1.1.10$. Rachidian tooth tricuspid, cusps triangular and pointed, central cusp longer. Gizzard plates with 34–54 ridges covered in pointed rods; rods longer at peak, shorter along slope; space between ridges smooth. Prostate gland and seminal ducts smooth. Internal wall of seminal duct nodulose. Pseudopenis club-shaped with a central groove that runs towards fundus.

External morphology. Yellow to yellow-green body, darker green on cephalic shield and dorsal edge of parapodial lobes; dark green fine lines on cephalic shield of some individuals; yellow specks throughout body including foot sole; fine black dots along with yellow specks in some individuals. Colouration lost upon preservation in absolute ethanol. Cephalic shield squarish, broad, extending over the posterior part of the shell. Eyes visible black dots, widely spaced,

Table 1. List of specimens of *Bakawan* and outgroups used for cox 1 gene tree construction, with sampling localities, GenBank accession numbers, and the associated study where the sequences were generated.

Species	Locality	cox1	Reference
<i>Aliculastrum cylindricum</i>	Panglao, the Philippines	DQ974671	Malaquias et al., 2008
<i>A. cylindricum</i>	Palau	MH933140	Oskars et al., 2019
<i>A. debilis</i>	Sulawesi, Indonesia	DQ974669	Malaquias et al., 2008
<i>A. debilis</i>	Bile Bay, Guam, Mariana Islands	KF992177	Oskars et al., 2015
<i>Bakawan fusca</i>	The Philippines	MK473530	Oskars & Malaquias, 2019
<i>B. hedleyi</i>	Junction of Susan and Mary rivers, Kangaroo Island, Queensland, Australia	MK473524	Oskars & Malaquias, 2019
<i>B. hedleyi</i>	Junction of Susan and Mary rivers, Kangaroo Island, Queensland, Australia	MK473525	Oskars & Malaquias, 2019
<i>B. puti</i>	Panglao, the Philippines	KF615821	Hanson et al., 2013
<i>B. rotundata</i>	Hub River Delta, Pakistan	MH638587	Aslam et al., 2019
<i>B. rotundata</i>	Hub River Delta, Pakistan	MH638588	Aslam et al., 2019
<i>B. rotundata</i>	Khor Kalba, Gulf of Oman, United Arab Emirates	MH933109	Oskars et al., 2019
<i>B. rotundata</i>	Surat Thani, Thailand	MH933110	Oskars et al., 2019
<i>B. rotundata</i>	Lim Chu Kang, Johor Strait, Singapore	MK473520	Oskars & Malaquias, 2019
<i>B. rotundata</i>	Sungei Buloh Wetland Reserve, Lim Chu Kang, Johor Strait, Singapore	MK473521	Oskars & Malaquias, 2019
<i>B. rotundata</i>	Sarawak, Borneo, Malaysia	MK473522	Oskars & Malaquias, 2019
<i>B. rotundata</i>	Sarawak, Borneo, Malaysia	MK473523	Oskars & Malaquias, 2019
<i>B. nasuso</i> , new species	Mindoro, Philippines	PX508252	This study
<i>B. nasuso</i> , new species	Mindoro, Philippines	PX508253	This study
<i>B. nasuso</i> , new species	Mindoro, Philippines	PX508254	This study
<i>B. nasuso</i> , new species	Mindoro, Philippines	PX508255	This study
<i>B. puti</i>	Mindoro, Philippines	PX508256	This study
<i>Haloa aptei</i>	Minicoy Is. Lakshadweep	MH638590	Bharate et al., 2018
<i>H. aptei</i>	Minicoy Is. Lakshadweep	MH638591	Bharate et al., 2018
<i>H. aptei</i>	Burmanallah, Andaman	MH638604	Bharate et al., 2018
<i>H. cf. nigropunctatus</i>	Makemo, Takaveke, Thaiti, French Polynesia	MK473473	Oskars & Malaquias, 2019
<i>H. cf. pemphis</i>	Mirya, India	MH638593	Bharate et al., 2018
<i>H. cf. pemphis</i>	Undi, Maharashtra, India	MH638605	Bharate et al., 2018
<i>H. cf. pemphis</i>	Red Sea, Djibouti	MH638609	Bharate et al., 2018
<i>Haloa cf. pemphis</i>	Budou-gai, Suna-machi, Maisaka-cho, Hamamatsu, Japan	MH933106	Oskars et al., 2019
<i>H. cf. pemphis</i>	Juańs surprise, Zavora, Mozambique	MK473476	Oskars & Malaquias, 2019
<i>H. cf. pemphis</i>	Nuarro Mangrove, Memba, Nampula, Mozambique	MK473477	Oskars & Malaquias, 2019
<i>H. cf. pemphis</i>	Doxa Rock Pool, Zavora, Mozambique	MK473478	Oskars & Malaquias, 2019
<i>H. cf. pemphis</i>	Doxa Rock Pool, Zavora, Mozambique	MK473479	Oskars & Malaquias, 2019
<i>H. cf. pemphis</i>	Doxa Rock Pool, Zavora, Mozambique	MK473480	Oskars & Malaquias, 2019
<i>H. crocata</i>	Hekili point, Maui, Hawaii	MK473469	Oskars & Malaquias, 2019

Species	Locality	cox1	Reference
<i>H. crocata</i>	Beach House, Kauai, Hawaii	MK473470	Oskars & Malaquias, 2019
<i>H. crocata</i>	Hekili point, Maui, Hawaii	MK473471	Oskars & Malaquias, 2019
<i>H. crocata</i>	Spreckelsville, Maui, Hawaii	MK473472	Oskars & Malaquias, 2019
<i>H. japonica</i>	Hakodate, Japan	JN830656	Hanson et al., 2013
<i>H. japonica</i>	Wando, South Korea	JN830668	Hanson et al., 2013
<i>H. japonica</i>	Sagami Bay, Japan	JN830670	Hanson et al., 2013
<i>H. japonica</i>	San Juan Islands, Washington, USA	JN830725	Hanson et al., 2013
<i>H. japonica</i>	Barcarès, Salses-Leucaté Lake, Mediterranean France,	KF615822	Hanson et al., 2013
<i>H. japonica</i>	Barcarès, Salses-Leucaté Lake, Mediterranean France	KF615823	Hanson et al., 2013
<i>H. japonica</i>	Barcarès, Salsès-Leucaté Lake, France, Mediterranean	KF615824	Hanson et al., 2013
<i>H. japonica</i>	Heshikiya, Okinawa	MK473509	Oskars & Malaquias, 2019
<i>H. japonica</i>	Bahia de Ogrove, Galicia, Spain	MK473510	Oskars & Malaquias, 2019
<i>H. japonica</i>	Bahia de Ogrove, Galicia, Spain	MK473511	Oskars & Malaquias, 2019
<i>H. musetta</i>	North Urélapa Island, Vanuatu	MK473460	Oskars & Malaquias, 2019
<i>H. musetta</i>	Baie De Maputo: Inhaca, Xixuane, Mozambique	MK473461	Oskars & Malaquias, 2019
<i>H. musetta</i>	Mauritius	MK473462	Oskars & Malaquias, 2019
<i>H. musetta</i>	North Urélapa Island, Vanuatu	MK473463	Oskars & Malaquias, 2019
<i>H. musetta</i>	Heshikiya, Okinawa	MK473464	Oskars & Malaquias, 2019
<i>H. musetta</i>	Baie De Maputo: Inhaca, Xixuane, Mozambique	MK473465	Oskars & Malaquias, 2019
<i>H. musetta</i>	Cocos, Guam	MK473466	Oskars & Malaquias, 2019
<i>H. musetta</i>	Heshikiya, Okinawa	MK473467	Oskars & Malaquias, 2019
<i>H. natalensis</i>	United Arab Emirates	KF615826	Hanson et al., 2013
<i>H. natalensis</i>	Mandavi, Gujarat India	MH638596	Bharate et al., 2018
<i>Haloa natalensis</i>	Baie de Maputo, Inhaca, Saco da Inhaca, Mozambique	MK473512	Oskars & Malaquias, 2019
<i>Haloa</i> sp.	South East, Sulawesi, Indonesia	DQ974673	Malaquias et al., 2008
<i>Haloa</i> sp.	Panglao, the Philippines	KF615810	Hanson et al., 2013
<i>Haloa</i> sp.	East side of Dili Bay, East Timor	KF615835	Hanson et al., 2013
<i>Haloa</i> sp.	Fiti, Solomon Islands	MH933105	Oskars et al., 2019
<i>Haloa</i> sp.	Queensland, Australia	MH933107	Oskars et al., 2019
<i>Haloa</i> sp.	Queensland, Australia	MH933108	Oskars et al., 2019
<i>Haloa</i> sp.	Doxa Rock Pool, Zavora, Mozambique	MK473468	Oskars & Malaquias, 2019
<i>Haloa</i> sp.	King's Beach, Queensland, Australia	MK473474	Oskars & Malaquias, 2019
<i>Haminoea alfredensis</i>	Kenton on Sea, Kariega river estuary, South Africa	KF615814	Hanson et al., 2013
<i>H. alfredensis</i>	Kenton on Sea, Kariega river estuary, South Africa	KF615815	Hanson et al., 2013
<i>H. alfredensis</i>	Kariega river estuary, Kenton, South Africa	KF615816	Hanson et al., 2013
<i>H. alfredensis</i>	Knysna lagoon, South Africa	MK473513	Oskars & Malaquias, 2019
<i>H. alfredensis</i>	Knysna lagoon, South Africa	MK473514	Oskars & Malaquias, 2019
<i>H. antillarum</i>	Bocana, Sisal, Yucatan, Mexico	KF615811	Hanson et al., 2013
<i>H. antillarum</i>	Jupiter inlet, Palm Beach, Florida	KF615817	Hanson et al., 2013

Species	Locality	cox1	Reference
<i>H. antillarum</i>	Bocana, Sisal, Yucatan, Mexico	KF615820	Hanson et al., 2013
<i>H. fusari</i>	Lago di Miseno, Naples, Italy	KF615840	Hanson et al., 2013
<i>H. hydatis</i>	Mediterranean France	DQ974674	Malaquias et al., 2008
<i>H. hydatis</i>	Port Barcarès, Salses-Leucaté Lake, Mediterranean France	KF615841	Hanson et al., 2013
<i>H. navicula</i>	Eight Acre Pond, Hampshire, UK	KF615836	Hanson et al., 2013
<i>H. navicula</i>	Canal de Mira, Aveiro, Portugal	KF615838	Hanson et al., 2013
<i>H. navicula</i>	Triângulo da Barra, Aveiro, Portugal	KF615839	Hanson et al., 2013
<i>H. orbignyana</i>	Faro, Portugal	KF615812	Hanson et al., 2013
<i>H. orbignyana</i>	Rabat, Morocco	MH933103	Oskars et al., 2019
<i>H. ortei</i>	Boca das Caldeirinhas, Faial, Azores	KF615844	Hanson et al., 2013
<i>H. ortei</i>	Boca das Caldeirinhas, Faial, Azores	KF615845	Hanson et al., 2013
<i>H. ortei</i>	Barranco Hondo, Tenerife, Canary Islands	KF615846	Hanson et al., 2013
<i>H. ortei</i>	Lago Lucrino, Naples, Italy	KX383914	Garabedian et al., 2017
<i>Haminoea</i> sp.	Banana River, Florida	KF615828	Hanson et al., 2013
<i>Haminoea</i> sp.	Pine Channel, Florida	KF615832	Hanson et al., 2013
<i>Haminoea</i> sp.	Bocana, Sisal, Yucatan, Mexico	KF615833	Hanson et al., 2013
<i>H. vesicula</i>	Bodega Harbor, Sonoma Co., California	KF615843	Hanson et al., 2013
<i>H. virescens</i>	Venice, California	AF156142	Medina & Walsh, 2000
<i>Lamprohaminoea</i> cf. <i>ovalis</i>	Panglao the Philippines	DQ974677	Malaquias et al., 2008
<i>L.</i> cf. <i>ovalis</i>	Maui, Hawaii	KF992184	Oskars et al., 2015
<i>L.</i> cf. <i>ovalis</i>	Andaman Islands	MH638599	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Andaman Islands	MH638600	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Red Sea, Saudi Arabia	MK473486	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Manza Beach, Okinawa	MK473488	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Airport Beach, Maui, Hawaii	MK473489	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	South Moorena, Tahiti, French Polynesia	MK473490	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Manza Beach, Okinawa	MK473491	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Panglao, the Philippines	MK473492	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Malo, Vanuatu	MK473493	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Line Islands, Palmyra Atoll, West Lagoon	MK473494	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Plage de Lavanono, Madagascar	MK473506	Oskars & Malaquias, 2019
<i>L.</i> cf. <i>ovalis</i>	Ranavalona, Madagascar	MK473507	Oskars & Malaquias, 2019
<i>L. cyanomarginata</i>	Ihl Rabat, Malta	MH933112	Oskars et al., 2019
<i>L. cyanomarginata</i>	Lazaro, Regio, Calabria, Italy	MK473485	Oskars & Malaquias, 2019
<i>L. cyanomarginata</i>	Split, Croatia	MK473487	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Panglao, the Philippines	DQ974675	Malaquias et al., 2008
<i>L. cymbalum</i>	Pasar Wajo, Buton Is., South East Sulawesi, Indonesia	KF615842	Hanson et al., 2013
<i>L. cymbalum</i>	Magilao, Guam, Mariana Islands	KF992182	Oskars et al., 2015
<i>L. cymbalum</i>	Magilao, Guam, Mariana Islands	MK473495	Oskars & Malaquias, 2019

Species	Locality	cox1	Reference
<i>L. cymbalum</i>	Paindane, Mozambique	MK473496	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Segond Channel, vicinity of Marime College, Vanuatu	MK473497	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Lakshadweep, India	MK473499	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Lakshadweep, India	MK473500	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Magilao, Guam, Mariana Islands	MK473501	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Palikulo Peninsula, Vanuatu	MK473502	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Tidal reef, Paindane, Mozambique	MK473503	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Lakshadweep, India	MK473504	Oskars & Malaquias, 2019
<i>L. cymbalum</i>	Paindane, Mozambique	MK473505	Oskars & Malaquias, 2019
<i>Papawera maugeansis</i>	Curlewis Reef, near Clifton Springs, Victoria, Australia	MK473517	Oskars & Malaquias, 2019
<i>P. maugeansis</i>	Inverloch, Town Area, Victoria Australia	MK473518	Oskars & Malaquias, 2019
<i>P. maugeansis</i>	Shoreham Beach, Victoria, Australia	MK473519	Oskars & Malaquias, 2019
<i>P. zelandiae</i>	Waitemata harbour, north end of Eastern Beach, New Zealand	MK473515	Oskars & Malaquias, 2019
<i>Papawera zelandiae</i>	Waitemata harbour, north end of Eastern Beach, New Zealand	MK473516	Oskars & Malaquias, 2019
<i>Smaragdinella calyculata</i>	Maui, Hawaii	KF992185	Oskars et al., 2015
<i>S. cf. sieboldi</i>	Mozambique	MK473459	Oskars & Malaquias, 2019
<i>Smaragdinella</i> sp.	Panglao, the Philippines	DQ974682	Malaquias et al., 2008
<i>Smaragdinella</i> sp.	New Caledonia	DQ991938	Malaquias et al., 2008
<i>Smaragdinella</i> sp.	Pulau Jung, Singapore Strait, Singapore	KF992166	Oskars et al., 2015
<i>Smaragdinella</i> sp.	Pulau Jung, Singapore Strait, Singapore	MH933104	Oskars et al., 2019

inserted in small unpigmented periocular areas. Parapodial lobes almost meet at the anterior dorsal end of the shell. Pallial lobe extends beyond the shell apex. (Fig. 2B)

Shell. Oval; white to light brown; translucent; wavy spiral striae throughout (Fig. 3A). Periostracum colour ranges from cinnamon yellow to rufous; some greyish maroon. Columella concave; columellar callus thick. Aperture broad anteriorly, tapering posteriorly. Umbilical furrow narrow, separating lip from last whorl. Dimensions (13 specimens) SH = 10.5–19.3 mm, SW = 7.8–14.9 mm.

Jaws. Jaw plate semicircular. Rods rectangular to squarish; edges denticulate (Fig. 3B).

Radula. 32 × 10.1.1.1.10. Rachidian tooth tricuspid; cusps triangular and pointed; central cusp longer; lateral cusps pointing outwards (Fig. 3C, D).

Gizzard plates. 34–64 densely arranged separate ridges. Ridge surface covered in dense rods pointing posteriorly; rods longer at peak of each ridge; shorter rods along slope of each ridge. Space between ridges is smooth. Gizzard plate length (10 specimens) = 1.69–2.77 mm (Fig. 3E, F).

Male reproductive system. Compact and smooth; warts absent. Prostate gland smooth. Atrium with thin walls; fundus thick walled; externally bulbous or club shaped. Internally, lateral walls fuse to form thick foldable pseudopenis. Pseudopenis club-shaped with a central groove that runs towards fundus. Thickened wall or ring between fundus and seminal duct. Inner wall of seminal duct with nodules. Two retractor muscles; one connects seminal duct to body wall, another connects seminal duct to lower region of atrium (Fig. 4).

Genetic distances. *Bakawan nasuso*, new species, was found to be sister to all other *Bakawan* species based on cox1 (Fig. 5). Based on uncorrected p-distances, this new species is 8.2–9.7% distinct from *B. puti*, 10.5–11.1% distinct from *B. fusca*, 8.7–9.4% distinct from *B. rotundata*, and 10.8–11.1% distinct from *B. hedleyi*.

Distribution. Only known from Oriental Mindoro, Philippines.

Ecology. *Bakawan nasuso*, new species, was found in AUU ponds naturally recolonised by mangroves, in the landward zone of the mangrove forest where the water levels change

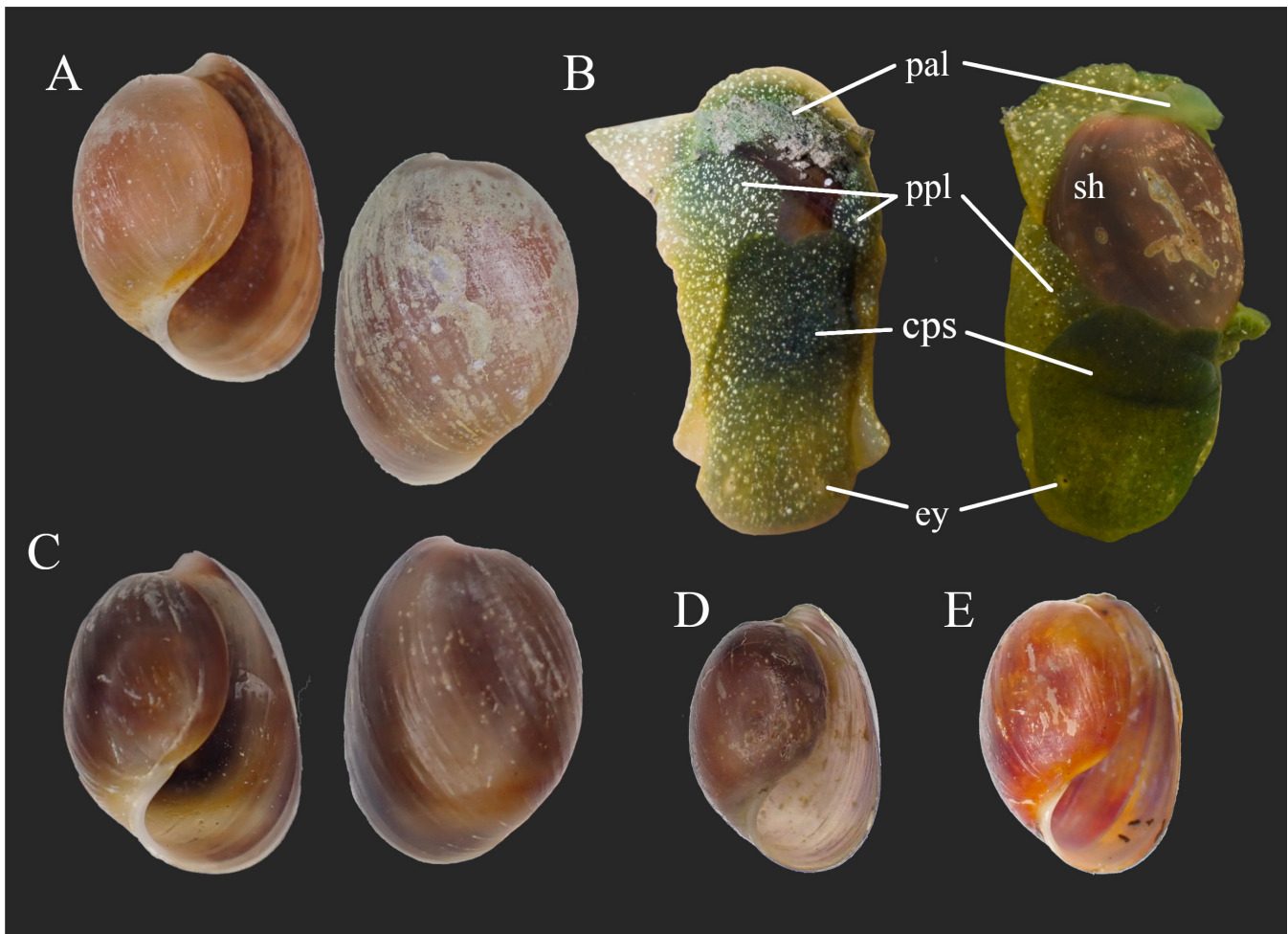


Fig. 2. *Bakawan nasuso*, new species. A, apertural and adapertural views of shell, holotype, PNM-041831 (SH = 19.3 mm). B, gross morphology of live individuals. Abbreviations: pal, pallial lobe; sh, shell; ppl, parapodial lobes; cps, cephalic shield; es, eyes. C, apertural and adapertural views of shell, paratype, UPMSI-MOLL-00652 (SH = 16.4 mm). D, apertural view of shell, UPMSI-MOLL-00654 (SH = 11 mm). E, apertural view of shell, UPMSI-MOLL-00657 (SH = 14.8 mm).

with the tides. *Avicennia marina* and *Sonneratia alba* were the dominant mangrove species in Bongabong, and the specimens were found gliding in isolated puddles during the lowest low tide, almost unnoticeable as they were covered in sandy mud. On the other hand, *A. marina*, *Ceriops tagal*, and *C. zippeliana* were the dominant mangrove species in Mansalay. Unlike in Bongabong, there were no puddles during the lowest low tide in Mansalay; instead, specimens of *B. nasuso*, new species, were gliding under a thin film of water and clayey mud.

Remarks. This species resembles *B. fusca* by having ridged gizzard plates but can be distinguished by squarish to rectangular jaw rods, smooth external surface of seminal duct, and club-shaped pseudopenis. Of note are the nodules inside the seminal duct of *B. nasuso*, new species, which were observed in all dissected specimens. There is no description of the live external morphology of *B. fusca*, but Oskars & Malaquias (2020) note that the preserved specimen has black blotches. The preserved specimens of *B. nasuso*, new species, on the other hand, does not have black blotches. Upon preservation in ethanol, the foot and mantle colour are white to apple green, and the yellow and black specks are no longer visible.

DISCUSSION

We describe here a new species of the haminoeid snail *Bakawan* from mangrove-recolonised AUU ponds in Oriental Mindoro, Philippines. Since the revision of the genus *Bakawan* by Oskars & Malaquias (2020), no further work has been done to explore the diversity of this genus in the Philippines. Although morphological differences are few and may suggest the possibility that *B. fusca* and *B. nasuso*, new species, may be conspecifics, *cox1* sequence data provides strong evidence that this species is distinct from the known species of *Bakawan*. We note that the phylogenetic placement of *B. nasuso*, new species, warrants further examination using other genetic markers. In this study, we also document a new locality record for *B. puti* (Fig. 6) and note the difference in shell colour of this specimen compared to individuals described from Bohol. Mangrove-associated molluscs have been surveyed in various sites across the Philippines (Lozouet & Plaziat, 2008; Masagca et al., 2010; Salmo & Duke, 2010; Cañada, 2020) but the sparse observation of *Bakawan* might be due to their cryptic appearance as they may look like algae to the untrained eye and are often covered in mud. As four species (*B. fusca*, *B. nasuso*, new species, *B. puti*, and *B. rotundata*) are now known to occur

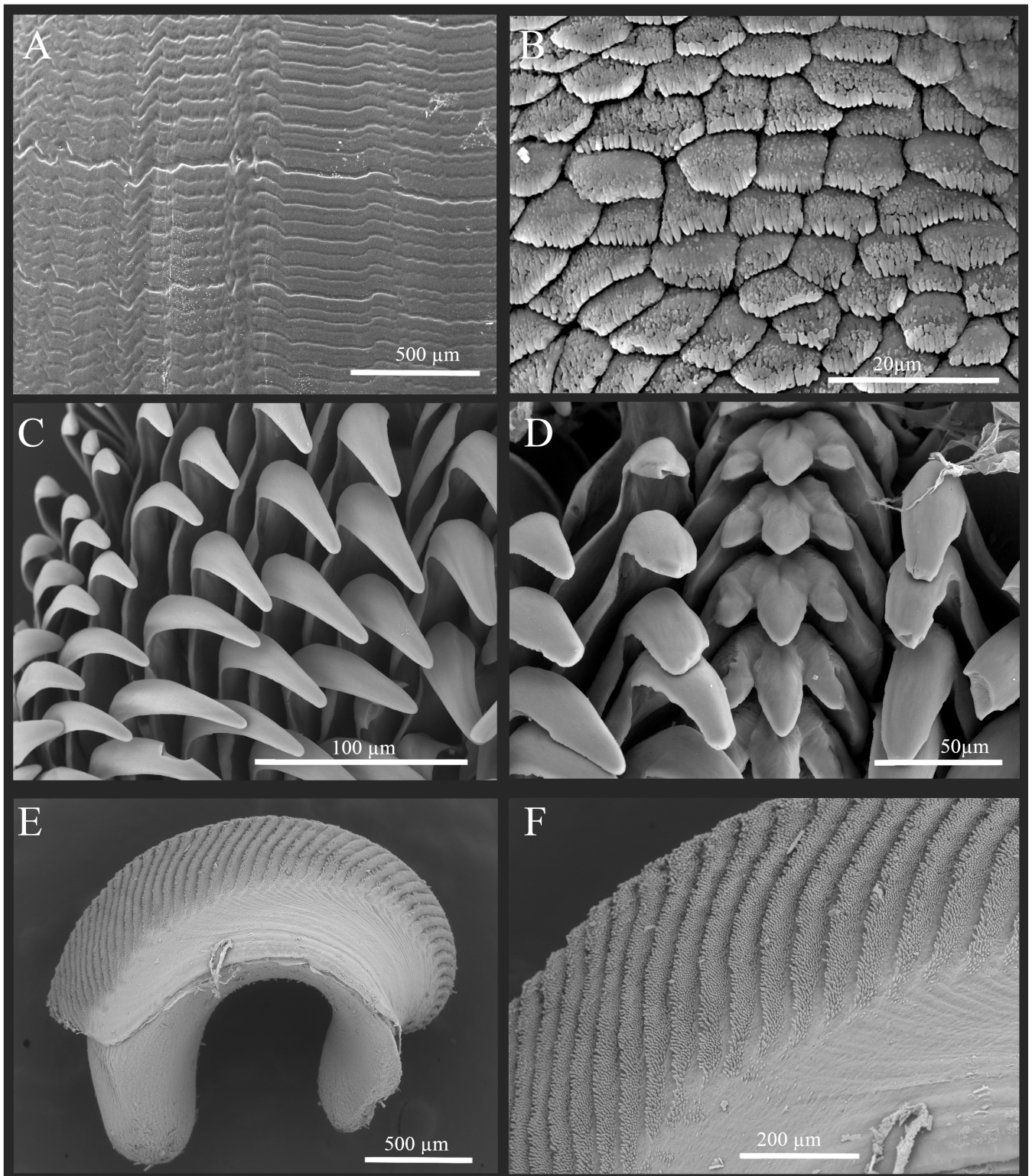


Fig. 3. Scanning electron microscopy (SEM) images of different structures in *Bakawan nasuso*, new species. A, wavy microsculpture of shell, paratype, SMF-383055. B, squarish to rectangular denticulate jaw rods, paratype, SMF-383059. C, D, lateral teeth and rachidian of radula, paratype, SMF-383059 paratype. E, F, gizzard plate and detail of ridges, paratype, SMF-383059.

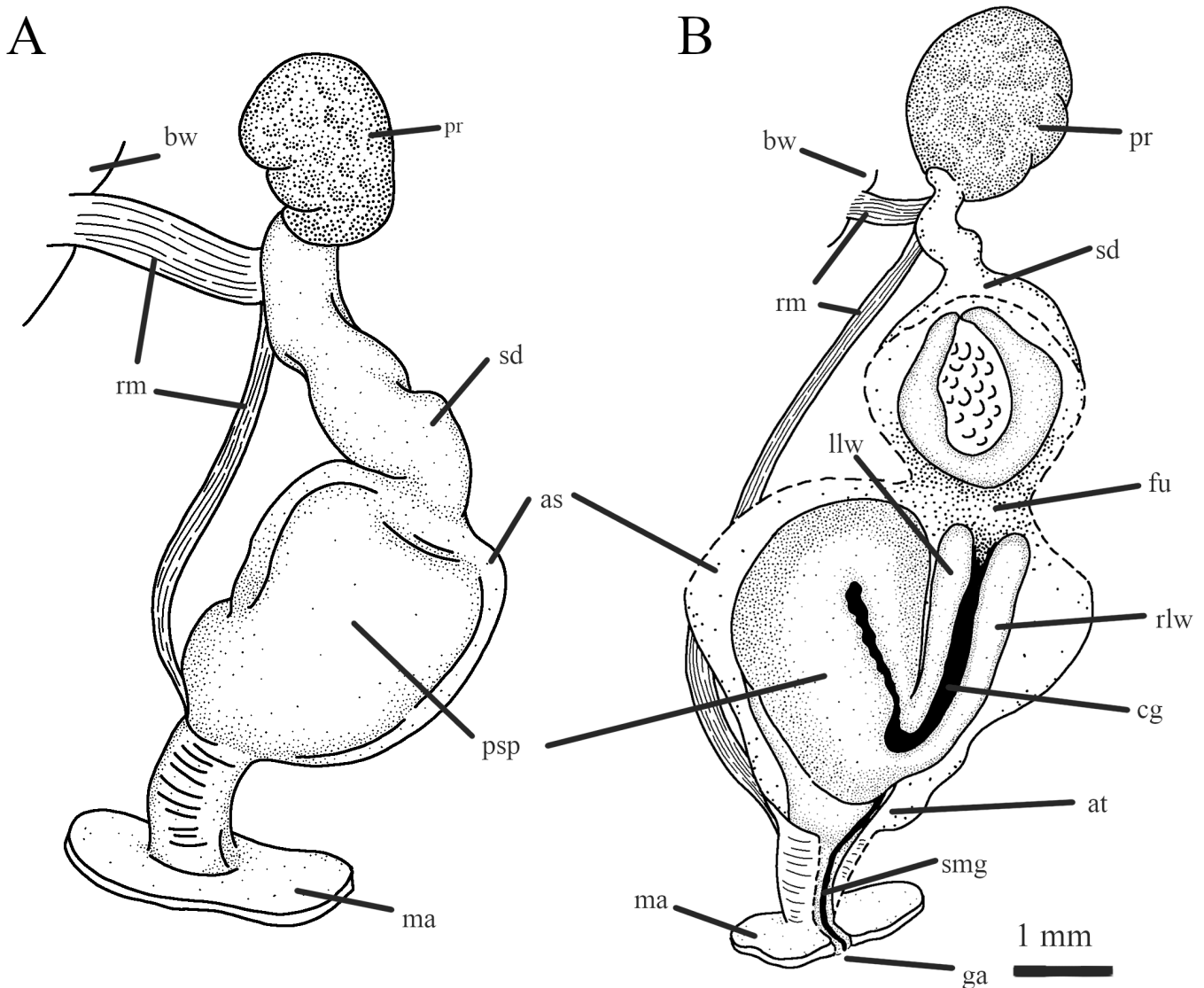


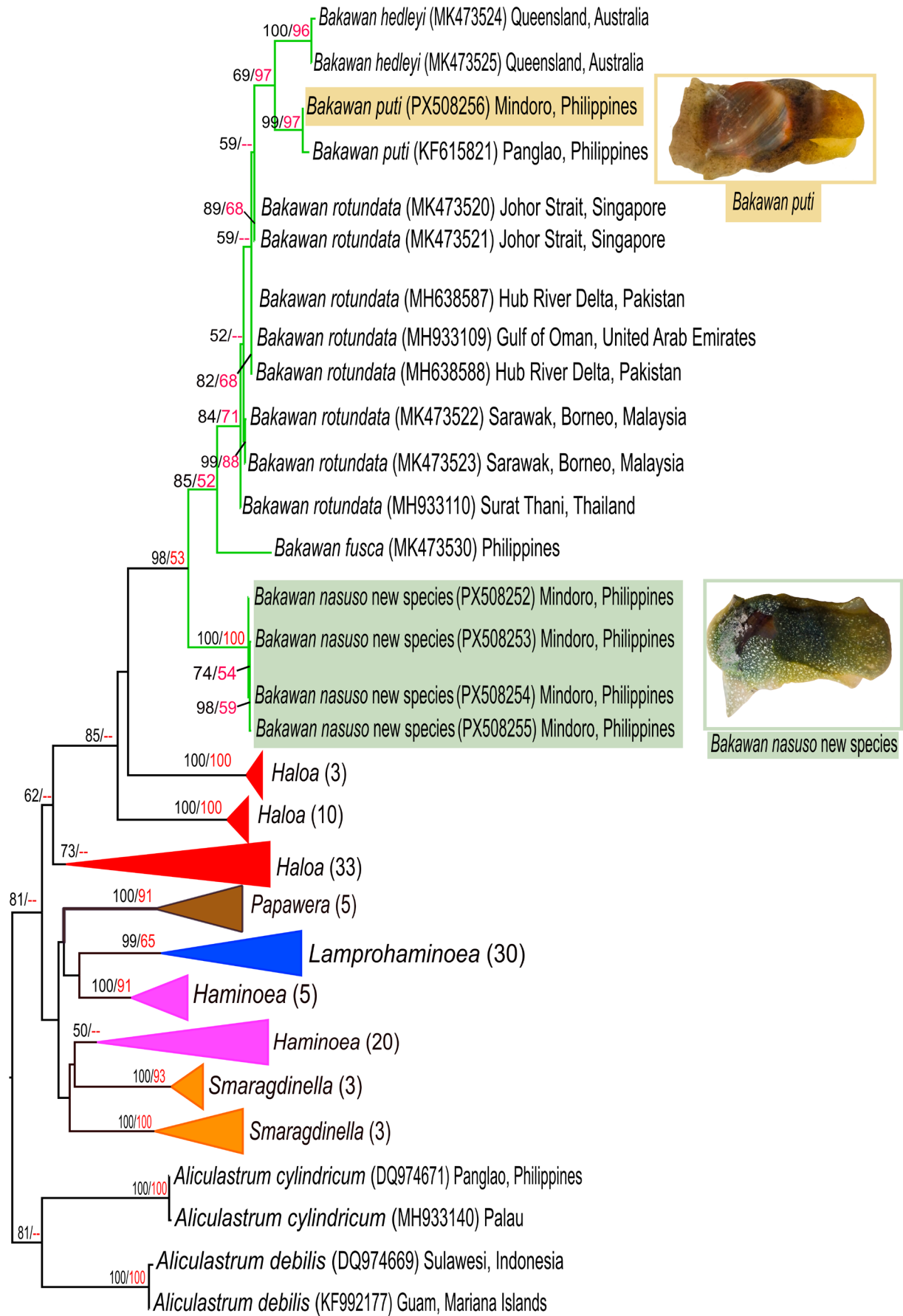
Fig. 4. *Bakawan nasuso*, new species, UPMSI-MOLL-00654. A, external view of male reproductive system. B, detail of interior of dorsally opened atrium and fundus. Abbreviations: as, atrium sheath; at, atrium; bw, body wall; cg, central groove; fu, fundus; ga, genital aperture; llw, left lateral wall; ma, mantle; n, nodules; pr, prostate gland; psp, pseudopenis; sd, seminal duct; smg, seminal groove; rlw, right lateral wall; sd, seminal duct; rm, retractor muscles.

in the Philippines, studying their distribution patterns across the archipelago and ecological requirements would be worth exploring. Revisiting and sampling populations from the type localities of *B. fusca* and *B. puti* would allow for a better understanding of the degree of interspecific and intraspecific variation in these snails.

There is a striking variation in shell colour and size among the individual specimens of *B. nasuso*, new species, from different collection sites. Specimens from Bongabong were larger (SH: 16.1–19.3 mm, n=4) compared to specimens from Mansalay (SH: 10.5–14.8mm, n=7). In terms of shell colour, Bongabong individuals had cinnamon to rufous shells, while the specimens from Mansalay also exhibited maroon shells. These morphological differences might be attributed to the habitat characteristics. In Bongabong, the mangroves

were taller and provided almost full shade, while mangroves in Mansalay had stunted growth leaving wider areas of the substrate exposed to the sun. The site in Bongabong had more muddy substrates, while the site in Mansalay had clayey soil due to poor drainage in this area (Jacob & Salmo, 2025). The effect of these environmental factors and available food on shell growth, body colour could be investigated further. The co-occurrence of *B. nasuso*, new species, and *B. puti* in Mansalay also warrants research on species interactions.

The discovery of this species in mangrove-recolonized AUU ponds highlights the potential of these habitats for harbouring malacofauna, and underscores the importance of prioritising the rehabilitation of such ponds in mangrove restoration efforts.



0.07

Fig. 5. Maximum likelihood (ML) tree based on *cox1* gene sequences (456 bp). Figures on branches representing the bootstrap support of maximum likelihood (in black) and neighbour joining (in red) analyses. Bootstrap values less than 50% are not shown. The tree is rooted with *Aliculastrum* spp.. Scale bar percentage of nucleotide substitutions per site.

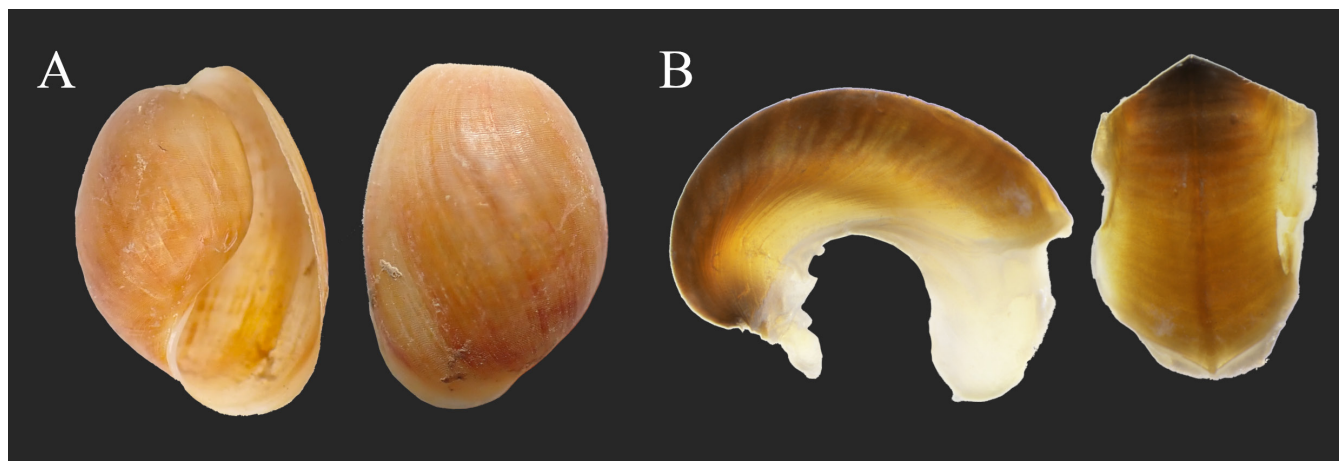


Fig. 6. *Bakawan puti*, PNM-041833. A, apertural and adapertural view of shell (SH = 11 mm). B, lateral and dorsal views of the gizzard plate imaged under a stereomicroscope (L = 1.69 mm).

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