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

Sadar ASLAM
Centre of Excellence in Marine Biology, University of Karachi, Karachi-75270 (Pakistan)

Trond R. OSKARS
Section of Taxonomy and Evolution, Department of Natural History, University Museum of Bergen, University of Bergen, PB7800, N-5020 Bergen (Norway) trond.oskars@uib.no (corresponding author)

Ghazala SIDDIQUI
Centre of Excellence in Marine Biology, University of Karachi, Karachi N75270 (Pakistan)

Manuel António E. MALAQUIAS
Section of Taxonomy and Evolution, Department of Natural History, University Museum of Bergen, University of Bergen, PB7800, N-5020 Bergen (Norway)

Submitted on 15 August 2018 | accepted on 19 December 2018 | published on 1 August 2019

KEY WORDS
Heterobranchia, Mollusca, Indian Ocean, Pakistan, mangroves, oyster reefs, DNA barcoding, morphology, new synonym.

ABSTRACT
The diversity of *Haminoea* Turton & Kingston, 1830 snails is poorly understood in the Indo-West Pacific. These gastropods occur in shallow subtidal and intertidal areas usually associated with algae, seagrass, or coral reefs, and one species, often identified as *Haminoea fusca* (A. Adams, 1850) is regarded to be restricted to mangrove habitats. In this paper we provide the first detailed description of this species by means of anatomical dissections, scanning electron microscopy, and DNA barcodes. A Bayesian COI gene tree including specimens from Pakistan and the Philippines together with other Indo-Pacific and Atlantic lineages was inferred and the possible existence of more than one species under the name *H. fusca* is highlighted and discussed. In Pakistan *Haminoea cf. fusca* was found to inhabit tidal estuarine mud-flats with oyster reefs.
INTRODUCTION

Haminoea Turton & Kingston, 1830 snails belong to the herbivorous family Haminoeidae Pilsbry, 1895, occurring worldwide in shallow marine waters along tropical and temperate latitudes (Gosliner 1991; Mikkelsen 1996; Malaquias & Cervera 2006; Gosliner et al. 2008, 2015). Species of the genus are well documented in the eastern Atlantic, Caribbean and eastern Pacific (Behrens & Hermosillo 2005; Malaquias & Cervera 2006; Hermosillo et al. 2006; Valdés et al. 2006; Malaquias 2014). However, most Indo-West Pacific (IWP) species are only known by their small, bulbous shells, which in many cases depict considerable interspecific similarity (Willan & Tagaro 2010; Malaquias 2011; Hori 2017).

The majority of species of the genus Haminoea have animals with dull colour patterns (e.g. H. natalensis (Krauss, 1848), H. japonica Pilsbry, 1895) but there are also several colourful species that have been recorded from tropical latitudes (e.g. H. cyanomarginata Heller & Thompson, 1983, H. cyanocaudata Heller & Thompson, 1983, H. cymbalum (Quoy & Gaimard, 1832), H. fusca (A. Adams, 1850), H. linda Er. Marcus & Burch, 1965, H. ovalis Pease, 1868) (Er. Marcus & Burch 1965; Rudman 1971; Gosliner et al. 2015; Tibiriçá & Malaquias 2017). The similarities in external features and shell between many species make the identification of Haminoea in the field difficult and often only a combination of DNA and morpho-anatomical characters enable accurate delimitation of species. Features of the male reproductive system, radula, and the chitinous gizzard plates are known to be useful to separate species in Haminoea (Er. Marcus & Burch 1965; Er. Marcus & Er. Marcus 1967; Rudman 1971; Talavera et al. 1987; Gibson & Chia 1989; Schaefer 1992; Malaquias & Cervera 2006).

References of the genus Haminoea in Pakistan are scarce and only available from non taxonomic works. The first recognisable record of Haminoea in Pakistan was made by Kazmi et al. (1996) who reported the species H. natalensis near Buleji, Karachi. The authors described the animals as green with darker markings and possessing a deeply bilobed cephalic shield. This seems to conform to descriptions of the most common morphs of the species (e.g. Gosliner 1987; Gosliner et al. 2015; Tibiriçá & Malaquias 2017; Pittman & Fiene 2018). Kazmi et al. (1996) also listed (not figured) the species H. tenera (A. Adams, 1850) which they described as pale greenish-white. According to the authors this species was previously recorded by Khan et al. (1973), however after careful revision of the works by Khan & Dastagir (1971, 1972) and Khan et al. (1973 supplement) we could only find references to the bubble shell heterobranch genera Bulla Linnaeus, 1758 and Hydatina Schumacher, 1817.

Haminoea japonica has been reported from the Karachi Mangroves, Sandspit (Barkati & Tirmizi 1987) and the Sindh Mangroves (Barkati & Rahman 2005), although this species is of temperate affinities (Gibson & Chia 1989; Álvarez et al. 1993; Gosliner & Behrens 2006; Hanson et al. 2013) and its presence in Pakistan is most likely a misidentification.

Iffat (2005: 90, fig. 61) identified a shell found in Manora, Cape Monze as H. elegans (Gray, 1825), which is again most certainly a misidentification as this species is to our best knowledge restricted to the Atlantic Ocean (Valdés et al. 2006). Kazmi & Khan (2014: 81, fig. 5) reported an unidentified species of Haminoea from the subtidal of Port Bin Qasim with an oval and narrow shell, which the authors considered similar to Atys Montfort, 1810 or Alculastrum Pilsbry, 1896, but nevertheless consistent, in our opinion, with species of IWP Haminoea (e.g. Pilsbry 1895a, b; Kobelt 1896; MacNae 1962; Higo et al. 1999, 2001; Hori 2017). Hameed et al. (2015) reported Cylichna crenilabris Melvill & Standen, 1901 (as Haeminoea [sic] crenilabris) possessing a brown periostracum occurring between the pneumatophore roots of mangroves. The illustrations included by the authors are difficult to use and therefore it is impossible to confirm which species were the authors dealing with. In fact, MolluscaBase (2018) regards the reference to Cylichna crenilabris by Melvill & Standen (1901) as taxon inquirendum.

More recently, Ullah et al. (2018) reported Haminoea exarata (Philippi, 1949) (as Haminoe [sic] exarata) from Korangi
and Sandspit near Karachi in their study of mangrove-associated molluscs. The specimens were found to favour elevated substrates of sand and clay, and occurred throughout the tidal zone, even crawling up the mangrove pneumatophores. However, this name is a junior synonym of the well-known and economically important species *Bullacta caurina* (Benson, 1842) (synonym of *Bullacta exarata* (Philippi, 1849)), which is endemic to South Korea and China (Tchang 1934; Habe 1952; Burn & Thompson 1998; Higo *et al.* 1999; Malaquias 2010).

In this study, we confirm the occurrence of *Haminoea cf. fusca* (A. Adams, 1850) in Pakistan associated with intertidal mud flats with oyster reefs and we provide for the first time a detailed morphological characterization of the species by means of fine anatomical dissections and scanning electron microscopy. A COI molecular phylogeny is inferred to aid in species delimitation and to preliminary address species relationships.

**MATERIAL AND METHODS**

**Taxa Sampling**

Specimens of *H. cf. fusca* were collected during biodiversity assessments from intertidal oyster reefs in estuarine muddy areas on the Balochistan Coast in Pakistan. The sampling site is on the Sindh Province side of the mouth of the Hab River Delta (24°53'12.01''N, 66°42'14.00''E; also spelled Hub River Delta). Live animals were photographed, relaxed by freezing in sea water and preserved in 95% ethanol. Specimens were sent for study and are housed at the Invertebrate Collections, Department of Natural History, University Museum of Bergen, University of Bergen (voucher number: ZMBN 125424). Additional specimens and egg masses are stored at the Centre of Excellence in Marine Biology (Study collection of Sadar Aslam, Pakistan).

---

**Table 1. — List of specimens used in the phylogenetic analysis including voucher and GenBank accession numbers. New sequences marked with an asterisk.”**

| Taxon                        | Authorship                  | Locality                                      | Voucher no. | COI GenBank Acc. No. |
|-----------------------------|-----------------------------|-----------------------------------------------|-------------|----------------------|
| *Haminoea cf. fusca* (TH81) | (A. Adams, 1850)            | Pakistan                                      | ZMBN 125424 | MH385858*            |
| *Haminoea cf. fusca* (TH82) | Pakistan                    | ZMBN125424                                    | MH385857*   |
| *Haminoea fusca* (C37)      | (Bartsch, 1915)             | The Philippines                               | MNHN 42261  | KF615810             |
| *Haminoea japonica* (C52)   | Pilsbry, 1895               | France, Mediterranean Sea                     | NHMUK 20070029 | KF615824             |
| *Haminoea japonica* (149)   |                            | France, Mediterranean Sea                     | NHMUK 20070065 | KF615823             |
| *Haminoea japonica* (164)   |                            | France, Mediterranean Sea                     | NHMUK 20070028 | KF615822             |
| *Haminoea japonica* (GH10)  |                            | Japan, Tokyo Bay                              | Isolate D139| JN830673             |
| *Haminoea japonica* (GH8)   |                            | United States, Washington                     | Isolate D59  | JN830725             |
| *Haminoea natalensis* (68)  | Krauss, 1848                | United Arab Emirates                          | NHMUK 20080104 | KF615826             |
| *Haminoea natalensis* (153) |                            | South Africa, Indian Ocean                    | NHMUK 20070186 | KF615825             |
| *Haminoea sp. 1* (C3)       |                            | Indonesia                                     | NHMUK 20050660 | DH974673             |
| *Haminoea sp. 1* (83)       |                            | East Timor                                    | NHMUK 20060109 | KF615835             |
| *Haminoea sp. 2* (C26)      |                            | The Philippines                               | MNHN 42261  | KF615810             |
| *Haminoea cymbalum* (C28)   | (Quoy & Gaimard, 1832)     | The Philippines                               | NHMUK 20030302 | KF615842             |
| *Haminoea cymbalum* (18)    |                            | Indonesia                                     | MNHN 42249  | DH974675             |
| *Haminoea cf. ovalis* (C34) | Pease, 1868                 | United States, Hawaii                          | MNHN 42252  | KF615842             |
| *Haminoea hydatis* (166)    | (Linnaeus, 1758)           | France, Mediterranean Sea                     | NHMUK 20060326 | DH974674             |
| *Haminoea hydatis* (C53)    |                            | France, Mediterranean Sea                     | NHMUK 20060326 | KF615841             |
| *Haminoea fusari* (167)     | (Alvarez, Garcia & Villani, 1993) | Italy                                    | NHMUK 20070177 | KF615840             |
| *Haminoea navicula* (131)   | (da Costa, 1778)           | Portugal                                      | NHMUK 20070020 | KF615839             |
| *Haminoea navicula* (147)   |                            | United Kingdom                                | NHMUK 20070021 | KF615836             |
| *Haminoea alfredensis* (182) | (Bartsch, 1915)            | South Africa, Indian Ocean                    | NHMUK 20070315 | KF615815             |
| *Haminoea alfredensis* (183) |                           | South Africa, Indian Ocean                    | NHMUK 20070315 | KF615814             |
| *Haminoea alfredensis* (174) |                          | South Africa, Indian Ocean                    | NHMUK 20070314 | KF615816             |
| *Haminoea orbignyana* (148) | (Férussac, 1822)           | Portugal                                      | NHMUK 20030296 | KF615812             |
| *Haminoea orbignyana* (1)   |                            | Portugal                                      | NHMUK 20030296 | KF615813             |
| *Haminoea antillarum* (157) | (d’Orbigny, 1841)          | Mexico, Atlantic Ocean                        | NHMUK 20070091 | KF615819             |
| *Haminoea antillarum* (176) |                            | United States, Florida                        | NHMUK 20070316 | KF615817             |
| *Haminoea orteai* (48)      | Talavera, Murillo & Templado, 1987 | Canary Is, Spain                             | NHMUK 20030836 | KF615846             |
| *Haminoea orteai* (198)     |                            | Azores, Portugal                              | NHMUK 20070458 | KF615845             |
| *Haminoea vesicula* (202)   | (Gould, 1855)              | United States, California                     | CASIZ 97502  | KF615843             |
| *Haminoea sp. 3* (175)      |                            | United States, Florida                        | NHMUK 20070318 | KF615827             |
| *Haminoea sp. 3* (152)      |                            | United States, Florida                        | NHMUK 20070180 | KF615829             |
| *Haminoea sp. 4* (154)      |                            | United States, Florida                        | NHMUK 20070175 | KF615834             |
| *Haminoea sp. 4* (161)      |                            | United States, Florida                        | NHMUK 20070090 | KF615833             |
| *Atys jeffreysi* (168)      | Weinkauff, 1856            | Gnejna Bay, Malta                             | ZMBN 81800  | KX23206             |
Fig. 1. — Bayesian phylogenetic tree based on partial sequences of the COI gene. Figures on nodes are posterior probabilities, scale bar refer to branch lengths. Coloured squares refer to species that are Indo West Pacific in origin, whereas grey squares to Atlantic and eastern Pacific species. PP, 1. The specimen here used from the Philippines is depicted in Gosliner et al. 2015: 30, lower right.
For the molecular phylogenetic analysis 34 COI sequences of *Haminoea* from the Atlantic, East Pacific and Indo-West Pacific were obtained from GenBank (Table 1). The tree was rooted with the haminoeid *Atys jeffreysi* (Table 1; Fig. 1).

**Morpho-anatomical work**

Shells, male reproductive systems and anterior digestive system were dissected out of the animals. Shells were imaged with a DSLR camera equipped with macro lenses. The male reproductive system was drawn using a stereo microscope fitted with a drawing tube. The anterior digestive system was dissected and the gizzard and buccal bulb were dissolved in a solution containing 180 μl buffer ATL with 20 μl of protease K-solution incubated at 56°C for approximately 4-6 hours (protocol modified from Holznagel [1998] and Vogler [2013]) [buffer and enzymes were obtained from the Qiagen DNeasy® Blood and Tissue Kit, catalogue no. 69504. The gizzard plates were critical-point dried after cleaning to maintain natural shape. The radulae and gizzard plates were mounted 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.

**DNA extraction, amplification and sequencing**

DNA was extracted from foot tissue of two specimens (Catalogue No 69504) following the protocol recommended by the manufacturer. Barcodes consist of partial sequences (c. 640 bp) of the mitochondrial gene cytochrome c oxidase subunit I (COI) and were amplified using the universal primers designed by Folmer et al. (1994). Polymerase chain reactions (PCR) were performed following the protocol described by Malaquias et al. (2009) using Qiagen Taq DNA polymerase. Successful PCR products were purified according to the EXO-SAP protocol described by Eilertsen & Malaquias (2013). The purified products were sequenced using an ABI 3730XL DNA Analyser (Applied Biosystems). The generated sequences were deposited in GeneBank (Table 1).

**Sequence alignment and phylogenetic analyses**

Geneious v. 8.1.8 (Biomatters Ltd, Auckland, New Zealand; Kearse et al. 2012) was used to inspect, edit, and assemble the sequences, which were aligned with Muscle (Edgar 2004a, b) implemented in Geneious with default settings. The sequences were tested for saturation in MEGA 7 (Kumar et al. 2016) by plotting general time-reversible (GTR) pairwise distances against total substitutions (transitions + transversions) for the first, second, and third codon positions of COI. A slight level of saturation was observed in the 3rd codon, and therefore, two datasets one with all codon positions and one with only first and second positions, were prepared to test the effect of saturation on the topology of the COI phylogenetic tree. The jmodeltest software (Darriba et al. 2012) was used to find the best-fit model of evolution for both datasets under the Akaike information criterion (Akaiake 1974) (all codons: GTR + G; 1st + 2nd codon only: GTR+I). Phylogenetic analyses were performed in MrBayes (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) using three parallel runs of eight million generations with sampling every 100 generations. Convergence of runs was inspected in Tracer v1.5 (Rambaut & Drummond 2007) with a burn-in set to 25%. The COI gene tree was visualized with FigTree 1.4.2 (Rambaut & Drummond 2009). Graphics and figures were edited and finalized with Inkscape 0.91 (Inkscape Team 2015) and Gimp 2.8.10 (Matitis et al. 1995; Natterer & Neumann 2013). The in-group was formed by 36 sequences of *Haminoea* spp. and the tree was rooted with the haminoeid species *Atys jeffreysi* (Weinkauff, 1866). Uncorrected p-distances were calculated in MEGA 7.

**Results**

**Phylogenetic analyses**

Both analyses resulted in similar tree topologies, but the tree inferred from the dataset including the 3rd codon positions was better resolved with higher node supports (Fig. 1, Appendix). This latter analysis suggests a possible 18th putative species (Fig. 1). The specimens of *Haminoea cf. fusca* from Pakistan clustered together with a specimen of *H. fusca* from the Philippines with maximum support. The COI uncorrected p-distance between the Pakistani and the Philippine specimens varied between 7.3-7.5% and between the two Pakistani specimens was 0.2%. The clade with all specimens of *H. fusca* was the sister group of a clade (Fig. 1, PP = 0.97) including the tropical Indian Ocean species *H. natalensis* (Fig. 1, PP = 1; represented by specimens from South Africa and the United Arab Emirates) and the West Pacific *H. japonica* (Fig. 1, PP = 1), known to be invasive in the East Pacific coast of the United States and in the Mediterranean Sea (Gibson & Chia 1989; Álvarez et al. 1993; Gosliner & Behrens 2006; Hanson et al. 2013). The COI uncorrected p-distance between the *H. fusca* clade and the (*H. natalensis- *H. japonica*) clade ranged between 13-14%.

**Taxonomic section**

Class GASTROPODA Cuvier, 1795
Sub-class HETEROBANCHIA Burmeister, 1837
Order CEPHALASPIDEA P. Fischer, 1883
Family HAMINOEIDAE Pilshy, 1895
Genus *Haminoea* Turton & Kingston, 1830

_Haminoea cf. fusca_ (A. Adams, 1850) (Figs 2, 3, 4)

_Bulla fusca_ A. Adams, 1850: 581, pl. CXXIV, fig. 94.

_Haminoea (sic) fusca_ – Pilshy 1895a: 360, pl. 40, figs 89, 90.—Kobelt 1896: 196, pl. 15, figs 14, 15.

_Haminoea (sic) fusca_ – Bergh 1901: 266, pl. XIX, figs 4, 5, pl. XVIII, figs 44, 47.

_Halos fusca_ – Habe & Kira 1968: 137.
Haminoea sp. – Strack 1998: 26, 28, pl. 1, fig. 6. — Ng & Sivasothy 2001. — Lozouet & Plaziat 2008: 65, pl. 34, figs 5, 6. — Riek 2013; 2014.

Haminoea cf. fusca – Gosliner et al. 2008: 27, fig. 3; 2015: 30, lower left figure.

Halos vitrea – Hung 2013.

Haminoea tenenda – Mujiono 2016: 47, fig. 4a, b.

Haminoea edmundsi Yonow & Jensen, 2018: 3, fig. 2B, n. syn.

Haminoea (sic) exarata – Ullah et al. 2018: 129-132.

Haminoea fusca – Cobb 2018.

**MATeRIAL EXAMINEd.** — Pakistan. Balochistan Coast, Sindh Provin-
ces, Hab River Delta (24°53’12.01’’N, 66°42’14.00’’E), 20 speci-
mens (3 specimens dissected, 2 specimens sequenced), H, 3-7 mm,
ZMBN 125424.

**type locality.** — Mindanao Island, the Philippines (A. Adams 1850).

**Diagnosis.** — Animal pale yellow-green to bright green; mantle
transparent; cephalic shield, squarish, broad; shallowly bilobed. Widely
spaced visible eyes. Hancock’s organ, simple, small horizontal ridge.
Shell, whitish translucent; slowly spiral striae; periostracum
light orange, darker in spiral striae; Aperture wide, slightly taper-
ing apically. Columella deeply concave anteriorly. Columellar lip
narrow. Chlamellae lips separated from last whorl by narrow umbil-
cal furrow. Outer lip rounded; shoulder rounded. Radular formula
30-35 × 10.1.1.1.1.10. Rachidian tooth tricuspid, cusps triangular,
with rounded tips; central cusp larger, broader, lateral cusps reduced.
Lateral teeth hook-shaped, smooth; inner lateral with broader cusp;
outer laterals tapering outwardly. Gizzard plates with flat surface;
ridges absent; central rachis present. Surface covered in small tightly
arranged pointed rods; rods tapering in size outwardly, larger rods
present on top of rachis. Male reproductive system compact, sparsely
covered in soft warts; consisting of atrium, thick-walled fundus,
thick seminal duct, and bulbous, nodulous prostate.

**COI barcodes.** — MH638588 (TH181), MH638587 (TH82).

**DiStRiBuTion.** — In the Indian Ocean Haminoea cf. fusca is known in Pakistan (present study) and in the West Pacific from Singapore (Ng & Sivasothy 2001), Mindanao, Bohol and Panglao Islands in the Philippines (Adams 1850; Lozouet & Plaziat 2008; Gosliner et al. 2008; 2015), Lombok and Ambon Islands, Indonesia (Strack 1998; Mujiono 2016; Yonow & Jensen 2018), Macau and Liyu Island, China (Bergh 1901; Hung 2013), New South Wales, Aus-
tralia (Gosliner et al. 2008, 2015; Cobb 2018; Riek 2013, 2014).

**DescriPtion**

**ExternaL morP hallOgy (Figs 1B, C; 3A)**

Animal pale yellow-green to bright green; mantle transpa-
rent, visceral mass reddish-brown. Cephalic shield, squarish,
broad; shallowly bilobed, posterior cephalic shield extending
over anterior part of shell. Eyes visible, widely spaced. Hancock’s
organ simple, small, horizontal ridge. Parapodial lobes, thick,
separated dorsally. Rounded pallial lobe, extending beyond apex.

**Shell (Fig. 3B)**

Shell whitish-brown translucent, dense, wavy spiral striae
throughout; periostracum light orange, darker in spiral striae;
shape bulbous, rounded. Aperture broad anteriorly, tapering
slightly posteriorly. Columella deeply concave anteriorly.

Columellar lip narrow. Narrow umbilical furrow separates
lip from last whorl. Outer lip rounded; shoulder rounded.

**RaduLa (Fig. 3C)**

Radular formula 30 × 10.1.1.1.10 (spc. TH81, H = 6.5 mm),
35 × 10.1.1.1.10 (spc. TH82, H = 7 mm). Rachidian tooth
tricuspid, cusps triangular, with rounded tips; central cusp
larger, lateral cusps reduced. Lateral teeth hook-shaped,
smooth; inner lateral with broader cusp, outer laterals taper-
ing outwardly.

**Gizzard plates (Fig. 3D-F)**

Flat surface, ridges absent. Rachis present. Surface covered
in small tightly arranged pointed rods; rods tapering in size
outwardly; larger worn rods on top of rachis.

**Male reproductive system (Fig. 4A, B)**

Compact and sparsely covered in soft warts; formed by
atrium, fundus (upper atrium), thick seminal duct, and a
bulbous nodulous prostate. Atrium with thin walls. Fundus
thick walled, externally looking as a rounded bulge (Fig. 4A,
arrow) internally with a distinct left lateral wall and right
lateral wall. Walls separated by a narrow central groove, and
both walls split by deep grooves. External seminal groove
entering genital aperture and running along atrium upwards

to the fundus, where it merges with the left lateral wall of the
fundus. Seminal duct discharging into fundus apically. Two
retractor muscles; one connected seminal duct to mantle, the
other to lower region of atrium.

**Egg-mass (Figs 2D, E, 3F)**

Yellowish in colour, gelatinous, cylindrical-elongated, with
short stalk attaching it to substrate. Egg-masses observed in
February of 2016, 2017 and 2018 (SA, pers. obs.). First oc-
currences in late January and greatest abundance observed in
mid-February before declining. Egg-masses mostly found in
shallow submerged areas (Fig. 2E).

**Ecology (Fig. 2)**

Specimens were found between December 2017 and March
2018 on intertidal estuarine muddy-sandy flats (between the
high- and mid-tidal zones) with oyster reefs formed by giant
oysters *Magallana gryphoides* (Schlotheim, 1820), backwa-
ter oysters *Magallana bilineata* (Röding, 1798), green algae
(*Ulva spp.*, *Oedogonium sp.*), and red algae (*Acanthophora sp.*,
*Gelidium sp.*) (Aslam pers. obs.) (Fig. 2C).

**RemarkS**

Bergh (1901) did not differentiate between the prostate and
the seminal duct in his study of *H. fusca*, yet, despite their
resemblance these are discrete organs as demonstrated in the
current study (Fig. 4A). Bergh (1901) described *H. fusca* as
possessing a glans (penis) in the “penissack”, but like in all other
known *Haminoea* of IWP origin (e.g. Er. Marcus & Burch
1965; Rudman 1971; Gosliner & Behrens 2006), *H. fusca*
has no penis or penial papilla enveloped by a penial sheet, but
instead a hollow atrium with a modified upper part here named
“fundus” (*sensu* Er. Marcus & Burch 1965). The fundus has thick walls forming folds resembling a penial papilla (Fig. 4B).

The limited research available on the genus *Haminoea* and ambiguous original descriptions of most IWP species often hampered authors to identify correctly the species. For example, Strack (1998: Indonesia), Ng & Sivasothi (2001: Singapore), Lozouet & Plaziat (2008: the Philippines), Rick (2013, 2014: Australia) referred to *H. fusca* as *Haminoea* sp., whereas Hung (2013) has named it *Haloa vitrea* (from China) and Mujiono (2016) *Haminoea tenera* (from Indonesia). Both latter species are of doubtful taxonomic validity and are known only from their original descriptions. Ullah *et al.* (2018) tentatively named specimens from mangroves in Korangi and Sandspit, Pakistan as *Haminoe exarata*, which could corresponded to *H. fusca*, since *Bullacta exarata* (correct spelling and combination) is endemic to the China Sea.
Yonow & Jensen (2018) have recently described the species *H. edmundsi* from Ambon, Indonesia based on features of the external morphology, colouration, and shells (no anatomical details were included). The authors claim that the animal did not resemble any extant species of *Haminoea*, but the image included in the work is a perfect match with live images of *H. fusca* (Gosliner et al. 2008; 2015; Hung 2013; Rick 2013, 2014, Mujiono 2016; Cobb 2018), and thus we here consider that *H. edmundsi* could be a junior synonym of *H. fusca*. However, the genetic distance found between the specimens from Pakistan and the one from the Philippines (COI uncorrected p-distance = 7.3-7.5%;

Fig. 3. — *Haminoea cf. fusca* (A. Adams, 1850): A, live specimen, ex situ. Length c. 10 mm; B, shell, apertural view (left image) and adepertural view (right image), height, 7 mm; C, SEM, detail of radula with rachidian and first lateral teeth; D, lateral view of whole gizzard plate; E, SEM, dorsal surface of whole gizzard plate; F, SEM, detail of rodlets in dorsal part of gizzard plate. Scale bars: C, 20 µm; D, E, 100 µm; F, 2 µm.
Fig. 1) suggests the possible occurrence of cryptic species under the name Haminoea fusca, but this requires additional specimens covering the geography of the species in order to be properly tested.

At present in WoRMS (consulted 24.XI.2018) “Pease, 1863” is mentioned as the authority of Haminoea fusca, but this is a mistake originated from Habe & Kira (1968) and later repeated by Gosliner et al. (2008) and Willan & Tagaro (2010) the latter being cited as the information source by WoRMS as their source information.
DISCUSSION

*Haminoea fusca* has been recorded between the eastern Indian Ocean and the West Pacific in central Indonesia extending northwards to south and central China and southwards until New South Wales in eastern Australia (see Taxonomic section for details). Yet, there are shell-based records in areas outside this geographical range such as the Kyushu and southward islands, Japan (Habe & Kira 1968: 137, pl. 42, fig. 30, as *Halota fusca*) and Somalia (Borri et al. 2002: 51, fig. 44). However, because of the difficulties in using shells to discriminate between IWP *Haminoea* species we regard these single occurrences as doubtful.

The original description of *H. fusca* (as *Bulla (Haminea) fusca*) by A. Adams (1850: 581, pl. 124, fig. 94) was based on shells, which the author described as ovo-globose, covered in fine spiral striae, with dark periostracum and internally brownish. A. Adams (1850)’s shells are similar to those from Pakistan; however, the latter ones are whitish-brown with a pale orange periostracum (Fig. 2B), and the specimen from the Philippines (here coded “C37”; Fig. 1; Table 1) and illustrated by Gosliner et al. (2008, 2015) has a completely white shell with an apparent translucent periostracum. Variability was also found in the COI gene with specimens from Pakistan and the Philippines (C37) varying between 7.3-7.5%, a range in Cephalaspidea gastropods, considered sufficient to indicate that lineages have speciated (Eilertsen & Malaquias 2013; Ohnheiser & Malaquias 2016).

This genetic variability together with the limited original description of *H. fusca* and the apparent variable features found in this species render its identity questionable and raise the possibility that more than one species of similar ecological requirements associated with mangroves and mud-flat habitats may in fact occur across IWP. Although, this can only be tested with a thorough study of the morphological and genetic diversity of the species including representatives from across its entire geographical distribution. Nevertheless, and since the type locality of the species is the Philippines, we cautiously refer to the Pakistani specimens as *Haminoea cf. fusca*.

The only known anatomical study of *H. fusca* was performed by Bergh (1901) based on preserved specimens from Macau. Bergh (1901) did not figure the animal or shell, but mentioned that the cephalic shield had a posterior shallow indentation. Additionally, he included detailed drawings of the radula, gizzard plate and male reproductive system (Fig. 2C). The drawings show a rachidian of similar shape to those of our specimens with rounded cusps, ridge-less gizzard plates covered in small rods and a compact male reproductive system with a lateral bulge and a bulbous prostate apparently continuous with the seminal duct. These similarities with our specimens suggest conspecificity between the samples from Pakistan and those studied by Bergh (1901) from the South China Sea (Macau).

The majority of *Haminoea* species live in shallow marine waters and *H. fusca* is the only intertidal mangrove-associated species of the genus (Strack 1998; Ng & Sivasothi 2001; Lozouet & Plaziat 2008; Hung 2013; Riek 2013, 2014; Mujino 2016; Cobb 2018; Yonow & Jensen 2018). It seems that this species has the capacity to crawl up the pneumatophore of the mangroves and tolerate periods of emersion (Ullah et al. 2018) and during our fieldwork campaigns specimens were observed outside water among intertidal oysters during low tide. In the Hab River Delta around Sonari (Sunhera) Beach (24°52′56.69″N, 66′41″12.77″E), nearby our sampling site, there used to be lush mangrove forests that disappeared after the construction of the Hab River’s dam has reduced the volume of freshwater with devastating consequences for the local mangrove habitats (Khan 1979). The average salinity in the area is now 34 parts per thousand which has been also causing decline of the oyster reefs and their associated ecosystems. Despite this fact, *H. cf. fusca* is, even in the absence of mangroves, still present and reproducing in the area.

Acknowledgements
We are thankful to Irene Heggstad (Laboratory for Electron Microscopy, Department of Earth Science, University of Bergen) for help with critical point dry and scanning electron microscopy and to Louise Lindblom (DNA Lab, Department of Natural History, University Museum of Bergen) for help with molecular sequencing. We are also thankful to J. Siegwold of the Department of Natural History, University Museum of Bergen for help with the French version of the Abstract. We are also deeply in debt to the two anonymous reviewers, who selflessly contributed to the quality of our paper.

REFERENCES

ADAMS A. 1850. — Monograph of the family Bullidae, in Sowerby G. B. (ed.). *Theaurus Conchyliorum, or Monographs of Genera of Shells*. Vol. II. Sowerby, London: 553-608, pls 119-125. https://doi.org/10.5962/bhl.title.10596

AKAIKE H. 1974. — A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716-723. https://doi.org/10.1109/TAC.1974.1100705

ÁLVAREZ L. A., MARTÍNEZ E., CIGARRÍA J., ROLÁN E. & VILLANI G. 1993. — *Haminoea callidegenita* Gibson & Chia, 1989 (Opisthobranchia: Cephalaspidea), a Pacific species introduced in European coasts. *Iberria* 11 (2): 59-65.

BARKATI S. & RAHMAN S. 2005. — Species composition and faunal diversity at three sites of Sindh mangroves. *Pakistan Journal of Zoology* 37 (4): 17-31.

BARKATI S. & TIRMIZI N. M. 1987. — Population structure and some aspects of the breeding behaviour of three gastropod species from Karachi mangroves. *Pakistan Journal of Scientific and Industrial Research* 30 (7): 539-544.

BEHRENS D. W. & HERMOSILLO A. 2005. — *Eastern Pacific Nudibranchs. A guide to the opisthobranchs from Alaska to Central America*. Sea Challengers: 137 p.

BERGH R. 1901. — *Reisen im Archipel der Philippinen von Sr. C. Semper... Wissenschaftliche Resultate. 7. Band. In Malacologische Untersuchungen. 4. Abteilung 3. Abdruck, Bullaece. 1. Lieferung*. C. W. Kreidel, Wiesbaden: 209-312, pls 17-24 (pls XVII-XXIV).

BORBÉ M., CIANFANELLI S., MARTIGNONI R., SONNI C., TALENTI E., VLPI C. & CALLEA A. 2002. — Marine Mollusca Gastropoda of the Soderi-Annovazzi collection from the coast of Somalia. *Atti della Società Italiana di Scienze Naturali e del Museo Civico Storia Naturale in Milano* 143: 13-66.
BURN R. & THOMPSON T. E. 1998. — Order Cephalaspidea, in BEELEY P. L., ROSS G. J. B. & WELLS A. A. (eds). Fauna of Australia, Mollusca: The Southern Synthesis. Part B, VIII, vol. 5. Cairo publishing, Melbourne: 943-959.

COBB G. 2018. — Haminoea fusca (A. Adams, 1850) at Sea Slugs of the Sunshine Coast (consulted 1 Jun 2018). http://www.nudibranch.com.au/pages/5016.htm

DARRIDA D., TABOADA G. L., DOALLO R. & POSADA D. 2012. — jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772.

EDGAR R. C. 2004a. — MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792-1797. https://doi.org/10.1093/nar/gkh340

EDGAR R. C. 2004b. — MUSCLE: a multiple sequence alignment method with reduced time and space complexity. BMC Bioinformatics 5: 113. https://doi.org/10.1186/1471-2105-5-113

EILERS M. H. & MALAQUIAS M. A. E. 2013. — Systematic revision of the genus Scaphander (Gastropoda, Cephalaspidea) in the Atlantic Ocean, with a molecular phylogenetic hypothesis. Zoological Journal of the Linnaean Society 167: 389-429. https://doi.org/10.1111/zol.12013

FISCHER P. 1880-1887. — Manuel de conchyliologie et de paléontologie conchyliologique. Paris, Savy: 1369 p. https://doi.org/10.5962/bhl.title.13213

FOLMER O., BLACK M., HOFER W., LUTZ R. & VRIENDHOFER R. 1994. — DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 5: 294-299.

GIBSON G. D. & CHA F. S. 1989. — Description of a new species of Haminoea, Haminoea callideginta (Mollusca: Opisthobranchia), with a comparison with the two other Haminoea species found in the northeast Pacific. Canadian Journal of Zoology 67 (4): 914-922. https://doi.org/10.1139/z89-133

GOSLINER T. M. 1987. — Nudibranchs of Southern Africa. A guide to the opisthobranch molluscs of Southern Africa. Sea Challengers, Jeff Hamann, Tokyo, 136 p.

GOSLINER T. M. 1991. — Morphological parallelism in opisthobranch gastropods. Malacologia 32 (2): 313-327.

GOSLINER T. M. & BEHRENS D. W. 2006. — Anatomy of an invasion: systematics and distribution of the introduced opisthobranch snail, Haminoea japonica Pilsbry, 1895 (Gastropoda: Opisthobranchia: Haminoeidae). Proceedings of the California Academy of Science 57 (37): 1003-1010.

GOSLINER T. M., BEHRENS D. W. & VALDES A. 2008. — Indo-Pacific nudibranchs and sea slugs. Sea Challengers Natural History Books and California Academy of Sciences, Gig Harbour: 426 p.

GOSLINER T. M., VALDES A. & BEHRENS D. W. 2015. — Nudibranchs & sea slugs. Identification. Indo-Pacific. New World Publications, Inc., Jacksonville: 408 p.

HABE T. 1952. — Arydai in Japan, in KURODA T. (ed.). Illustrated Catalogue of Japanese shells. Vol. 20. Malacological Society of Japan, Tokyo: 137-152, 20-21.

HABE T. & KIRA T. 1968. — Shells of the Western Pacific in Color, Vol. II. English edition, revised version 1968. Hoikusha Publishing, Osaka: 233 p.

HAMEED S., AHMED M., ZARRIEN A. & SIDDQUI G. 2015. — A handbook of marine gastropods of Pakistan, 1st edition. New College Publication, Lahore: 1-16.

HANSON D., COOKE S., HIRANO Y., MALAQUIAS M. A. E., CROCETTA F & VALDES A. 2013. — Slipping through the cracks: The taxonomic impediment conceals the origin and dispersal of Haminoea japonica, an invasive species with impacts to human health. PLoS ONE 8(10), e77452. https://doi.org/10.1371/journal.pone.0077457

HERMOSILLO A., BEHRENS D. W. & RIOS E. J. 2006. — Opisthobranchios de México. Guía de bajas marinas del Pacifico, Golfo de California y las islas oceánicas. Conabio, Guadalajara: 143 p.

HIGO S., CALLOMON P. & GOTO Y. 1999. — Catalogue and bibliography of the marine shell-bearing Mollusca of Japan. Gastropoda, Bivalvia, Polycladophora, Scaphopoda. Elle Scientific Publications, Osaka: 749 p.

HIGO S., CALLOMON P. & GOTO Y. 2001. — Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan: Type Figures. Elle Scientific Publications, Osaka.

HOLZMNLER W. E. 1998. — Research note: A nondestructive method for cleaning gastropod radulae from frozen, alcohol-fixed, or dried material. American Malacological Bulletin 14: 181-183.

HORI S. 2017. — Family Haminoeidae, in OKUTANI T. (ed.). Marine Mollusks in Japan, 2nd Edition. Tokai University Press, Hiratsuka: 437, 1093, pl. 393.

HUELENSBECK J. P. & RONQUETT F. 2001. — MRBAYES: bayesian inference of phylogenetic trees. Bioinformatics 17: 754-755. https://doi.org/10.1093/bioinformatics/17.8.754

HUNG C.-C. 2013. — Haloa vitrea (A. Adams, 1850) in Intertidal Zone of Liu Island. (consulted 01.VI.2018) http://taconet.pixnet.net/blog/post/43322143-%E7%8E%BB%E7%92%B3%E6%9C%88%E8%AF%A8%E8%96%BA

IFAY F. 2005. — Marine Gastropods of Karachi in the Collection of Zoological Survey Department. Records of the Zoological Survey of Pakistan XVI: 86-99.

INKSCAPE TEAM 2015. — Inkscape 0.91. (consulted 01.VI.2018)

KAZMI Q. B. & KHAN M. 2014. — Some new records of marine molluscs from the Pakistan Coast. International Journal of Biological Research 2 (2): 79-84.

KAZMI Q. B., TIRMAZI M. T. & ZEHRA I. 1996. — A check list of opisthobranch snails of the Karachi Coast. Pakistan Journal of Marine Sciences, 5 (1): 69-104.

KHAN A. R. 1979. — River piracy and diversion in Karachi Basin. In Studies in Geomorphology and Prehistory of Sind. Grassroots 3 (2): 47-60.

KHAN M. D. & DASTAGIR S. G. 1971. — On the Mollusca: Gastropoda-fauna of Pakistan. Records of the Zoological survey of Pakistan 2 (1): 17-129.

KHAN M. D. & DASTAGIR S. G. 1972. — Pelecypoda fauna of Pakistan. Zoological survey of Pakistan/Printing Corporation of Pakistan press, Karachi ARC-2/375: 1-41.

KHAN M. D., DASTAGIR S. G. & ASHRAF S. A. 1973. — Gastropoda and Pelecypoda (Marine Fauna Supplement). Records Zoological Survey of Pakistan 4: 5-17.

KEARSE M., MOIR R., WILSON A., STONES-HAVAS S., CHEUNG M., STURROCK S., BUXTON S., COOPER A., MARKOWITZ S. & DURAN C. 2012. — Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647-1649.

KOBELT W. 1896. — Die Familie Bullidae, in MARTINI F. H. W. & CHEMNITZ J. H. (eds). Systematisches Conchylien-Cabinet 1 (9) Bauer Raspe, Nürnberg: 190 p.

KUMAR S., STECHER G. & TAMURA K. 2016. — MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33 (7): 1870-1874. https://doi.org/10.1093/molbev/msw054

LOZUOPE T. & PLAZIJAT J. C. 2008. — Mangrove environments and molluscs. Abaton River, Bohol and Panglao Islands, Central Philippines. ConchBooks, Hackenheim: 166 p.

MACNAN W. 1962. — Tectibranch molluscs from southern Africa. Annals of the Natal Museum 15 (16): 183-199.

MALAQUIAS M. A. E. 2010. — Systematics, phylogeny, and natural history of Bulla cava (Philippi, 1849): an endemic cephalaspidean gastropod from the China Sea. Journal of Natural History 44 (33-34): 2015-2029.

MALAQUIAS M. A. E. 2011. — Family Haminoeidae Pilbray, 1895, in SEVERNS M (ed.) Shells of the Hawaiian Islands, the Sea Shells. ConchBooks, Hackenheim, 225: 414-418.

MALAQUIAS M. A. E. 2014. — New data on the heterobranch gastropods (‘opisthobranchs’) for the Bahamas (tropical western
Atlantic Ocean). Marine Biodiversity Records 7, e27. https://doi.org/10.1017/S175526721400030X
MALAQUIAS M. A. E. & CERVERA J. L. 2006. — The genus Haminoea (Gastropoda: Cephalaspidea) in Portugal, with a review of the European species. Journal of Molluscan Studies 72 (1): 89-103.
MALAQUIAS M. A. E., MACKENZIE-DODDS J., BOUCHET P., GOSLINER T. & REID D. G. 2009. — A molecular phylogeny of the Cephalaspidea sensu lato (Gastropoda: Euthyneura): Architectibranchia redefined and Runcinacea reinstated. Zoologica Scripta 38: 23-41.
MALAQUIAS M. A. E., OHNHEISER L. T., OSKARS T. R. & WILLASEN E. 2016. — Diversity and systematics of philinid snails (Gastropoda: Cephalaspidea) in West Africa with remarks on the biogeography of the region. Zoological Journal of the Linnean Society 180 (1): 1-35. https://doi.org/10.1111/zoj.12478
MARCUS ER. & BURCH J. B. 1965. — Marine euthyneuran Gastropoda from Eniwetok Atoll, Western Pacific. Malacologia 3 (2): 235-262. https://biodiversitylibrary.org/page/13032285
MARCUS EV. & MARCUS ER. 1967. — American opisthobranch mollusks. Studies in Tropical Oceanography 6: 1-249.
MATTIS P., KIMBALL S. & SINGH M. 1995. — GIMP: GNU image manipulation program. (consulted 01.III.2018) Software: www.gimp.org
MIKELSEN P. M. 1996. — The evolutionary relationships of Cephalaspidea s. l. (Gastropoda: Opisthobranchia): a phylogenetic analysis. Malacologica 37: 375-442.
MELVIL J. C. & STANDEN R. 1901. — The Mollusca of the Persian Gulf, Gulf of Oman and Arabian Seas as evidenced mainly through the collections of Mr. F. W. Townsend, 1893-1900, with descriptions of new species. Part 1. Cephalopoda, Gastropoda, Scaphopoda. Proceedings of the Zoological Society of London 1901 (2): 327-460.
MOLLUSCABASE 2018. — Cylcica crenilabris Melvill & Standen, 1901. Accessed through World Register of Marine Species at: http://www.molluscabase.org/aplia.php?p=text&tid=761116 on 06.VI.2018.
MUJONO N. 2016. — Mangrove Gastropods from Lombok Island, West Nusa Tenggara. Osnalogoi dan Limnologi di Indonesia 1 (3): 39-50.
NATTERER M. & NEUMANN S. 2013. — GIMP 2.8.10. (consulted 01.III.2018). www.gimp.org/team.html
NG P. K. L. & SIVASOTHI N. 2001. — Guide to the Mangroves of Singapore, Molluscs. (consulted 02.VI.2018) in PETER K. L., NG & N. SIVASOTHI (eds) LIM K. K. P., MURPHY D. H., MORGANY T., SIVASOTHI N., NG P. K. L., SOONG B. C., HUGH T. W., TAN K., TAN S. & TAN T. K. Excerpt from A Guide to Mangroves of Singapore Volume 2: Animal Diversity. Raffles Museum of Biodiversity Research, the National University of Singapore & The Singapore Science Centre, Singapore: 168 p. http://mangrove.nus.edu.sg/guidebooks/text/20888.htm
OHNHEISER L. T. & MALAQUIAS M. 2013. — Systematic revision of the gastropod family Philinidae (Mollusca: Cephalaspidea) in the north-east Atlantic Ocean with emphasis on the Scandinavian Peninsula. Zoological Journal of the Linnean Society 167 (2): 273-326. https://doi.org/10.1111/zoj.12000
PILSBRY H. A. 1895a. — Polypelacophora. Acanthochitinidae, Cryptopilacea and appendix. Tectibranchia. Manual of Conchology, ser. 1, 15 (60): 181-436.
PILSBRY H. A. 1895b. — Catalogue of the marine shells of Japan with descriptions of new species and notes on others collected by Frederick Stearns. F. Stearns, Detroit: viii + 196 p. https://doi.org/10.5962/bhl.title.35863
PILSBRY H. A. 1896. — Philinidae, Gastropiteridae, Aglajidae, Aplysiidae, Oxynoeids, Runcinidae, Umbraculidae, Pleurobranchidae. Manual of conchology, structural and systematic, with illustrations of the species ser. 1, 16 (1): 1-262. https://doi.org/10.5962/bhl.title.6534
PITTMAN C. & FRIE P. 2018. — Haminoea cf. natalensis (Krauss, 1848) at Sea Slugs of Hawaii (consulted 03.VIII.2018) http://seaslugsofhawaii.com/species/Haminoea-natalensis-a.html
RAMBAUT A. & DRUMMOND A. J. 2007. — Tracer v1. 5. Computer program and documentation distributed by the Authors. (consulted 01.III.2018). http://tree.bio.ed.ac.uk/software.
RAMBAUT A. & DRUMMOND A. J. 2009. — FigTree v1. 4.2. Computer program and documentation distributed by the Authors. (consulted 01.III.2018). http://tree.bio.ed.ac.uk/software.
RIEK D. 2013. — Haminoea sp. at Sea Slugs and Other Marine Invertebrates of The Tweed-Byron Coast, Australia. (consulted 01.VI.2018) http://www.roboastra.com/Opisthobranch1/brop1861.htm
RIEK D. 2014. — Haminoea sp. at Sea Slugs and Other Marine Invertebrates Of The Tweed-Byron Coast, Australia. (consulted 01.VI.2018) http://www.roboastra.com/Opisthobranch1/brop2000.htm
RONQUIST F. & HUELENBECK J. P. 2003. — MRBAYES 3: bayesian phylogenetic inference under mixed models. Bioinformatics. 19:1572-1574. (consulted 01.III.2018). http://mrbayes.sourceforge.net.
RUDMAN W. B. 1971. — On the opisthobranch Genus Haminoea Turton & Kingston. Pacific Science 25: 545-559.
RODING P. F. 1798. — Museum Boltenianum sive Catalogus cimelorum e tribus regnis naturae quae olim collegarit Joa. Fried. Bolten M. D. p. d. Pars secunda continens Conchyliya sive Testacea univalvia, bivalvia et multivalvia. Johan Christi Trappii, Hamburg, 199 p. https://biodiversitylibrary.org/page/11067364
SCHAFFER K. 1992. — Haminoea exigua (Gastropoda, Opisthobranchia), a new cephalaspidian species from the Mediterranean Sea. Journal of Molluscan Studies 58 (3): 329-336. https://doi.org/10.1093/mollus/58.3.329
VON SCHLOTHIER T. & REID D. G. 2016. — Diversity and systematics of philinid snails (Gastropoda: Euthyneura): Archibranchia sensu lato. Zoosystema • 2019 • 41 (16)
STRACK H. L. 1998. — The Rumphius Biohistorical Expedition A story of present and past marine biology. De Rumphius Biohistorische Expedite Een verhaal over mariae biologie vroeger en nu. Vita Marina 45 (1-2): 17-40.
TALAVEIRA P., MURILLO L. & TEMPLADO J. 1987. — The genus Haminoea Turton & Kingston, 1830 (Opisthobranchia, Bullo- morpha) in the South East of Spain with the description of a new species. Bolletino Malacologico 23 (1-4): 53-68.
TCHANG S. 1934. — Contribution à l’étude des opisthobranches de la côte de Tsingtao. Contributions from the Institute of Zoology, National Academy of Peiping 2 (2), 1-148.
TIBIČAŘ Y. & MALAQUIAS M. A. E. 2017. — The bubble snails (Gastropoda, Heterobranchia) of Mozambique: an overlooked biodiversity hotspot. Marine Biodiversity 47 (3): 791-811. https://doi.org/10.1007/s12226-016-0500-7
TURTON W. & KINGSTON J. F. 1830. — Part II: The natural history of the District or, lists of the different species of animals, vegetables and minerals... in CARRINGTON N. T. The Teignmouth, Guide, 2., Conchology, nº 63. London, E. Croydon at the Public Library; C. and J. Rivington, Baldwin and Co.; Whittaker and Co.; Gore: Dawlish; Torquay: Cole and Lascombe; Exter: Exter Booksellers, unpagged.
ULLAH Z., ZEHR A. & GONDAI M. A. 2018. — Studies on the vertical distribution pattern in mangrove associated mollusks along the Karachi coast, Pakistan. Indian Journal of Geo-Marine Sciences 47 (1): 127-134.
VALDES Å., HAMANN J., BEHRENS D. & DUPONT A. 2006. — Caribbean Sea Slugs, A field Guide to the Opisthobranch Mollusks from the Tropical Northwestern Atlantic. Sea Challengers Natural
History Books, Gig Harbour: 289 p.
VOGLER R. E. 2013. — The radula of the extinct freshwater snail Aylacostoma stigmaticum (Caenogastropoda: Thiaridae) from Argentina and Paraguay. Malacologia 56: 329-332. https://doi.org/10.4002/040.056.0221
WEINKUFF H. C. 1866. — Nouveau supplément au catalogue des coquilles marines recueillies sur les Côtes de l’Algérie. Journal de Conchyliologie 14: 227-248.

WILLAN R. & TAGARO S. P. 2010. — Haminoeidae, in POPPE G. T. (ed.). Philippine marine mollusks, Volume III. ConchBooks. Hackenheim: 665 p.
YONOW N. & JENSEN K. R. 2018. — Results of the Rumphius Biohistorical Expedition to Ambon (1990). Part 17. The Cephalaspidea, Anaspidea, Pleurobranchia, and Sacoglossa (Mollusca: Gastropoda: Heterobranchia). Archiv für Molluskenkunde 147 (1): 1-48. https://doi.org/10.1127/arch.moll/147/001-048

Submitted on 15 August 2018; accepted on 19 December 2018; published on 1 August 2019.
Bayesian phylogenetic tree based on partial sequences of the COI gene with 1st and 2nd codons included only. Figures on nodes are posterior probabilities, scale bar refer to branch lengths.