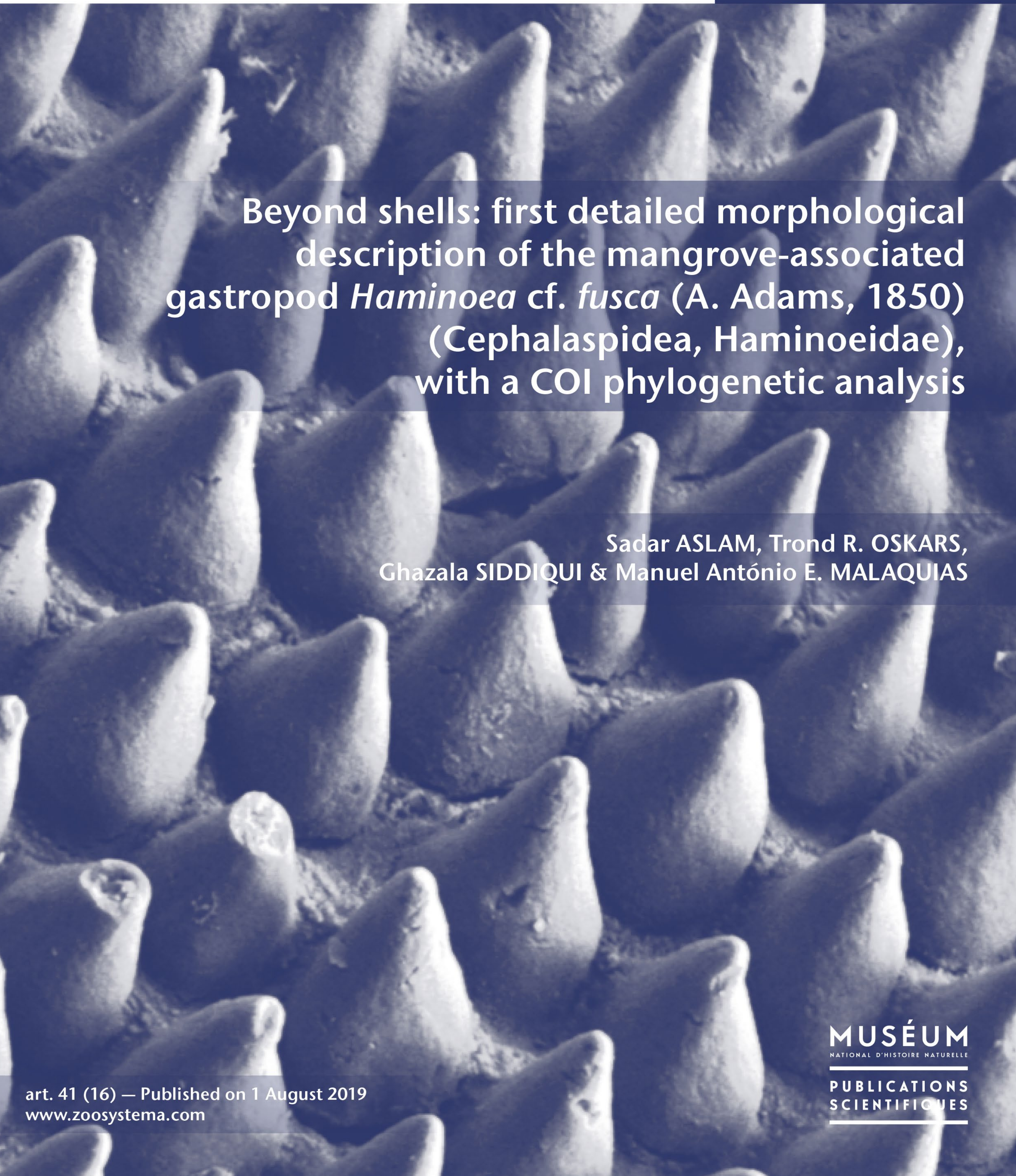
zoosystema
2019 • 41 • 16



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, Trond R. OSKARS,
Ghazala SIDDIQUI & Manuel António E. MALAQUIAS

art. 41 (16) — Published on 1 August 2019
www.zoosystema.com

MUSÉUM
NATIONAL D'HISTOIRE NATURELLE
PUBLICATIONS
SCIENTIFIQUES

DIRECTEUR DE LA PUBLICATION : Bruno David
Président du Muséum national d'Histoire naturelle

COUVERTURE / *COVER* :
SEM, detail of rodlets in dorsal part of gizzard plate of *Haminoea* cf. *fusca* (A. Adams, 1850).

Zoosystema est indexé dans / Zoosystema *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus®

Zoosystema est distribué en version électronique par / Zoosystema *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Zoosystema* sont référencés par / *Articles and nomenclatural novelties published in* Zoosystema *are referenced by:*
- ZooBank® (http://zoobank.org)

Zoosystema est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris / **Zoosystema** *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia, ***Geodiversitas***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, **Cryptogamie sous-sections *Algologie*, *Bryologie*, *Mycologie*.**

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9551/ ISSN (électronique / *electronic*) : 1638-9387

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

urn:lsid:zoobank.org:pub:0A1D7618-DE30-422E-BBC6-99933E34A9A7

Aslam S., Oskars T. R., Siddiqui G. & Malaquias M. A. E. 2019. — Beyond shells: first detailed morphological description of the mangrove-associated gastropod *Haminoea* cf. *fusca* (A. Adams, 1850) (Cephalaspidea, Haminoeidae), with a COI phylogenetic analysis. *Zoosystema* 41 (16): 313-326. https://doi.org/10.5252/zoosystema2019v41a16. http://zoosystema.com/41/16

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.

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

RÉSUMÉ

Au-delà de la coquille : première description morphologique détaillée du gastéropode associé aux mangroves Haminoea *cf.* fusca *(A. Adams, 1850) (Cephalaspidea, Haminoeidae), avec une analyse phylogénétique du gène COI.*
La diversité du genre *Haminoea* Turton & Kingston, 1830 est encore peu connue dans le bassin Indo-Pacifique. Ces gastéropodes se rencontrent en zones subtidales et intertidales peu profondes, généralement associées avec les algues, les herbiers marins ou les récifs coralliens. Une espèce, souvent identifiée comme *Haminoea fusca* (A. Adams, 1850) est considérée comme étant restreinte aux mangroves. Dans cet article, nous présentons la première description détaillée de cette espèce, au moyen de dissections anatomiques, de microscopie électronique à balayage et de barcodes ADN. Un arbre bayésien comprenant des spécimens d'*H. fusca* du Pakistan et des Philippines, ainsi que d'autres lignées indopacifiques et atlantiques a été produit pour le gène COI, et l'existence possible de plus d'une espèce rassemblées sous le nom *H. fusca* est mise en évidence et discutée. Au Pakistan, *Haminoeai* cf. *fusca* a été observée dans des vasières estuariennes à bancs d'huîtres.

MOTS CLÉS
Heterobranchia,
Mollusca,
océan Indien,
Pakistan,
mangroves,
bancs d'huîtres,
barcode,
morphologie,
synonyme nouveau.

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; Ev. 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 shelled 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 *Aliculastrum* 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 *Haeminoae* [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

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	MH638588*
Haminoea cf. *fusca* (TH82)		Pakistan	ZMBN125424	MH638587*
Haminoea fusca (C37)		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 20060104	KF615826
Haminoea natalensis (153)		South Africa, Indian Ocean	NHMUK 20070186	KF615825
Haminoea sp. 1 (C3)		Indonesia	NHMUK 20050660	DQ974673
Haminoea sp. 1 (93)		East Timor	NHMUK 20060109	KF615835
Haminoea sp. 2 (C26)		The Philippines	MNHN 42261	KF615810
Haminoea cymbalum (C28)	(Quoy & Gaimard, 1832)	The Philippines	MNHN 42249	DQ974675
Haminoea cymbalum (16)		Indonesia	NHMUK 20030302	KF615842
Haminoea cf. *ovalis* (C34)	Pease, 1868	The Philippines	MNHN 42252	DQ974677
Haminoea cf. *ovalis* (333)		United States, Hawaii	ZMBN 81689	KF992184
Haminoea hydatis (166)	(Linnaeus, 1758)	France, Mediterranean Sea	NHMUK 20060326	DQ974674
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)		Mexico, Atlantic Ocean	NHMUK 20070175	KF615834
Haminoea sp. 4 (161)		Mexico, Atlantic Ocean	NHMUK 20070090	KF615833
Atys jeffreysi	(Weinkauff, 1856)	Gnejna Bay, Malta	ZMBN 81800	KX523206

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).

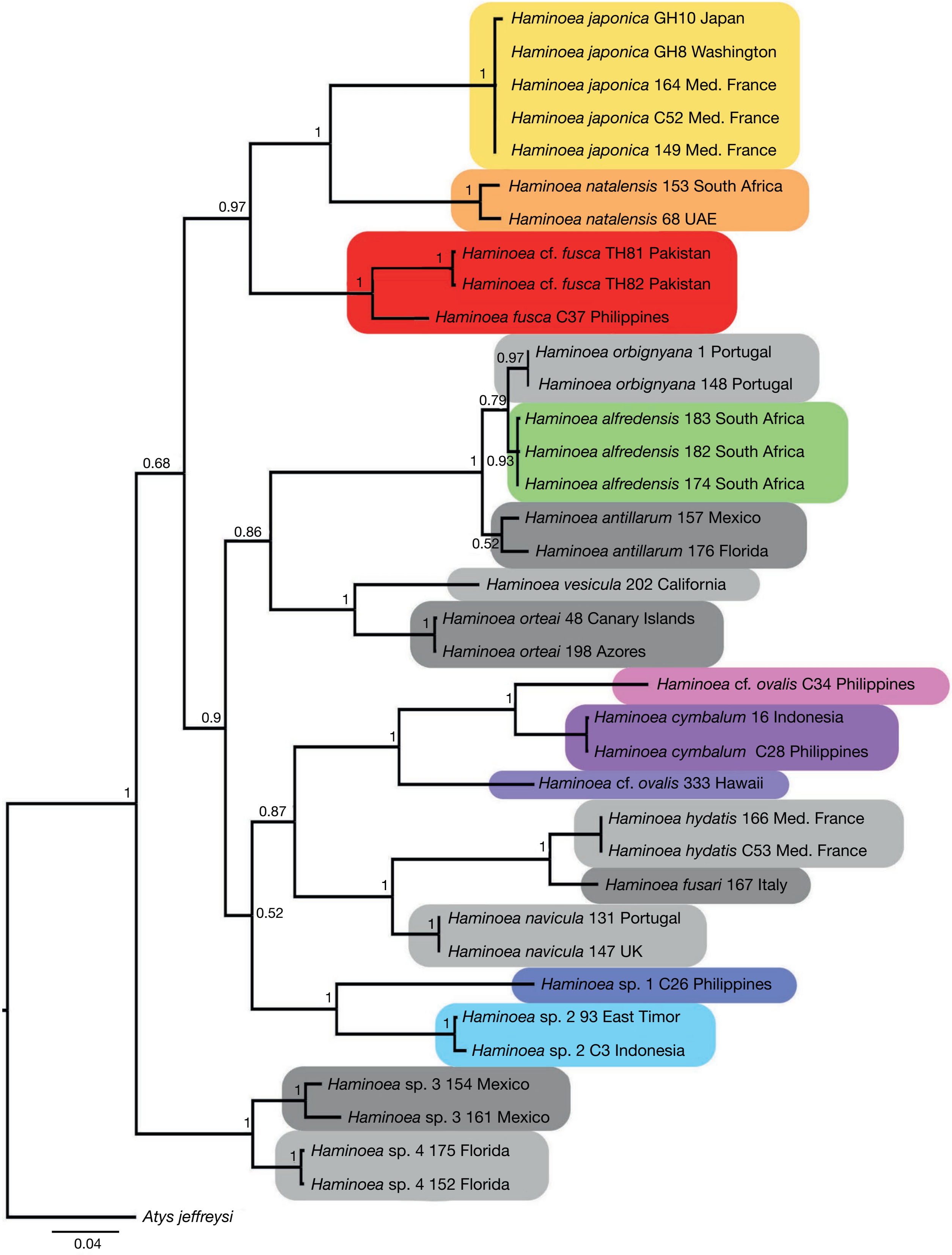


Fig. 1. — Bayesian phylogenetic tree based on partial sequences of the COI gene. Figures on nodes are posterior probabilities, scale bar refer to branch lengths. Coloured squares refer to species that are Indo West Pacific in origin, whereas grey squares to Atlantic and eastern Pacific species. PP, 1. 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 macrolens. 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 proteinase 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 using the Qiagen Dneasy® Blood and Tissue Kit (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 (Akaike 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 (Mattis *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 HETEROBRANCHIA Burmeister, 1837
Order CEPHALASPIDEA P. Fischer, 1883
Family HAMINOEIDAE Pilsbry, 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.

Haminea (sic) *fusca* – Pilsbry 1895a: 360, pl. 40, figs 89, 90. — Kobelt 1896: 196, pl. 15, figs 14, 15.

Haminaea (sic) *fusca* – Bergh 1901: 266, pl. XIX, figs 4, 5, pl. XVIII, figs 44, 47.

Haloa fusca – Habe & Kira 1968: 137.

Haminoea sp. – Strack 1998: 26, 28, pl. 1, fig. 6. — Ng & Sivasothi 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.

Haloa vitrea – Hung 2013.

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

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

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

Haminoea fusca – Cobb 2018.

MATERIAL EXAMINED. — **Pakistan**. Balochistan Coast, Sindh Province, Hab River Delta (24°53'12.01"N, 66°42'14.00"E), 20 specimens (3 specimens dissected, 2 specimens sequenced), H, 3-7 mm, ZMBN 125424.

TYPE LOCALITY. — Mindanao Island, the Philippines (A. Adams 1850).

DIAGNOSIS. — Animal pale yellowish-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; dense, wavy spiral striae; periostracum light orange, darker within spiral striae. Aperture wide, slightly tapering apically. Columella deeply concave anteriorly. Columellar lip narrow. Clumellar lips separated from last whorl by narrow umbilical furrow. Outer lip rounded; shoulder rounded. Radular formula 30-35 × 10.1.1.1.10. 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 (TH81), MH638587 (TH82).

DISTRIBUTION. — In the Indian Ocean *Haminoea* cf. *fusca* is known in Pakistan (present study) and in the West Pacific from Singapore (Ng & Sivasothi 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, Australia (Gosliner *et al.* 2008, 2015; Cobb 2018; Riek 2013, 2014).

DESCRIPTION

External morphology (Figs 1B, C; 3A)

Animal pale yellowish-green to bright green; mantle transparent, 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 form 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 tapering 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 occurrences 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), backwater 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

Fig. 2. — **A**, Hab River delta, Sindh Province, Balochistan Coast, Pakistan, showing estuary and associated oyster reefs; **B**, *Haminoea* cf. *fusca* (A. Adams, 1850) *in situ*; arrows show faecal matter tracks over muddy substrate; **C**, *H.* cf. *fusca in situ*, amongst green algae; **D**, egg-mass *in situ*, attached to muddy substrate; **E**, egg-mass *in situ*, submerged during low tide. Photograph: S. Aslam.

"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), Riek (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.

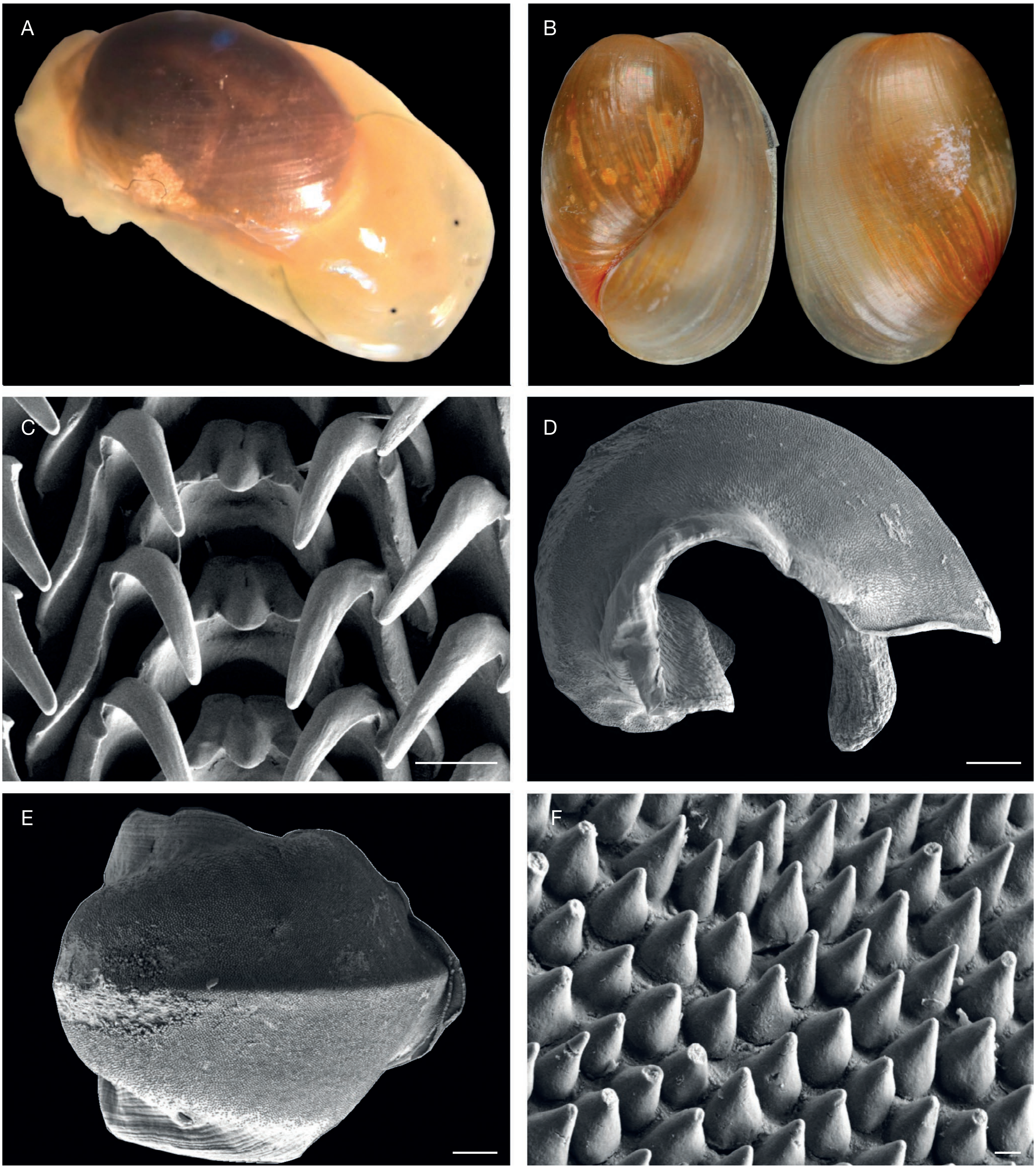


Fig. 3. — *Haminoea* cf. *fusca* (A. Adams, 1850): **A**, live specimen, *ex situ*. Length *c.* 10 mm; **B**, shell, apertural view (left image) and adepertural view (right image), height, 7 mm; **C**, SEM, detail of radula with rachidian and first lateral teeth; **D**, lateral view of whole gizzard 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.

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; Riek 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%;

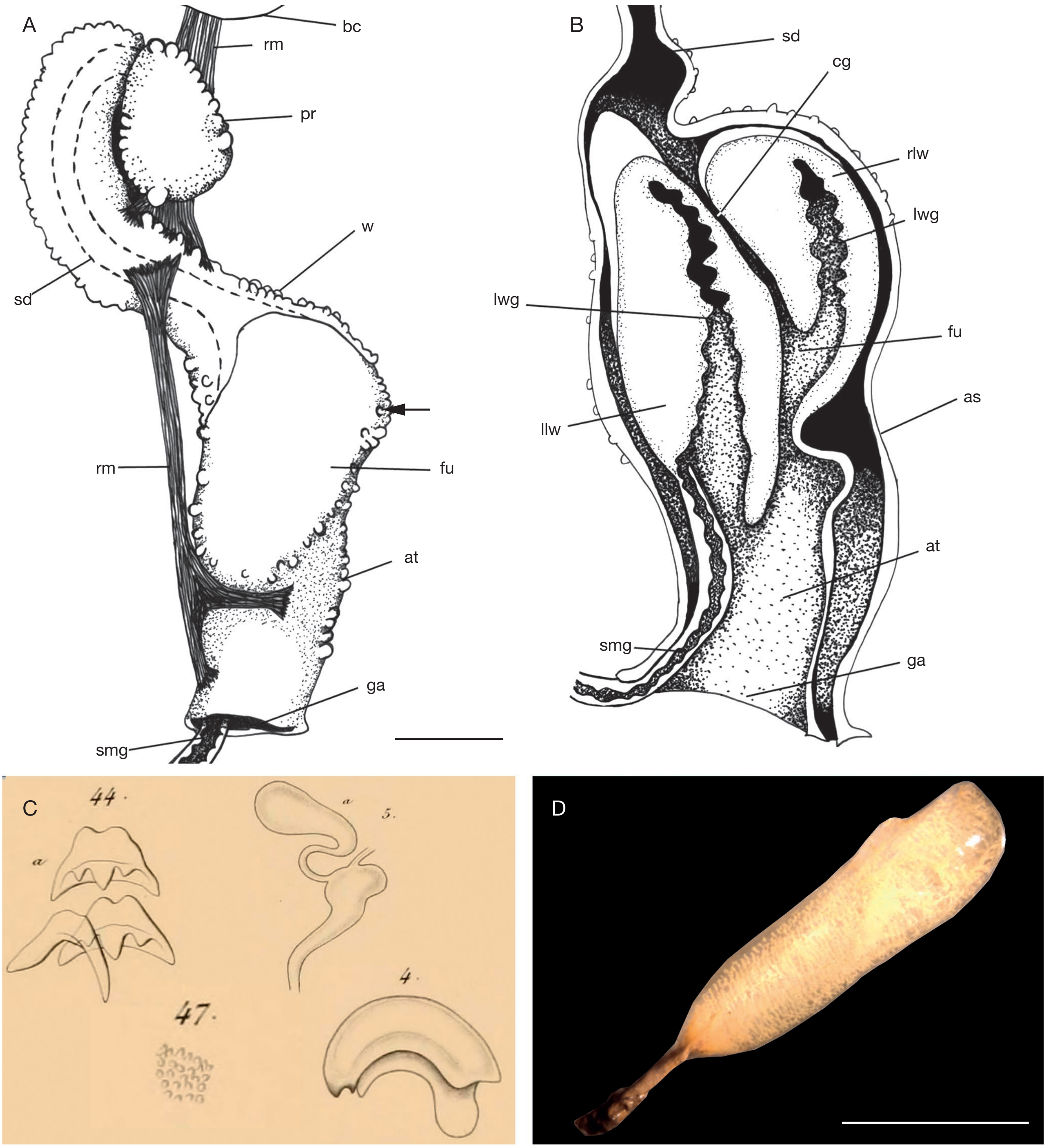


FIG. 4. — *Haminoea* cf. *fusca* (A. Adams, 1850): **A**, external view of male reproductive system, arrow denotes lateral bulge; **B**, detail of interior of atrium and fundus; **C**, figures modified from Bergh (1901: pl. 18, figs 44, 47, pl. 19, figs 4, 5), detail of radula with "a": central rachidian (pl. 18, fig. 44); detail of surface of gizzard plate (pl. 18, fig. 47); male reproductive system, "a": prostate (pl. 19, fig. 5); lateral view of gizzard plate (pl. 19, fig. 4); **D**, egg-mass. Abbreviations: **as**, atrium sheet; **at**, atrium; **bc**, body cavity; **cg**, central groove; **fu**, fundus; **ga**, genital aperture; **llw**, left lateral wall; **lwg**, grooves of lateral walls; **pr**, prostate; **rlw**, right lateral wall; **rm**, retractor muscles; **sd**, seminal duct; **smg**, seminal groove; **w**, soft warts. Scale bars: A, B, 0.5 mm; D, 1 cm.

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 *Haloa 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)' 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 2013; Malaquias *et al.* 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; Mujiono 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. Siegwald 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.). *Thesaurus 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. — *Haminaea callidegenita* Gibson & Chia, 1989 (Opisthobranchia: Cephalaspidea), a Pacific species introduced in European coasts. *Iberus* 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. Abtheilung. 3. Abschnitt, Bullacea. 1. Leiferung*'). C. W. Kreidel, Wiesbaden: 209-312, pls 17-24 (pls XVII-XXIV).

BORRI 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* Beesley P. L., Ross G. J. B. & Wells A. A. (eds). *Fauna of Australia, Mollusca: The Southern Synthesis. Part B, VIII, vol. 5.* Csiro 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/5016b.htm

Darriba 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

Eilertsen 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/zoj.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., Hoeh W., Lutz R. & Vrijenhoek R. 1994. — DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294-299.

Gibson G. D. & Chia F. S. 1989. — Description of a new species of *Haminoea, Haminoea callidegenita* (Mollusca: Opisthobranchia), with a comparison with two other *Haminoea* species found in the northeast Pacific. *Canadian Journal of Zoology* 67 (4): 914-922. 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. & 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. & Valdés 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., Valdés Á. & Behrens D. W. 2015. — *Nudibranchs & sea slugs. Identification. Indo-Pacific.* New World Publications, Inc., Jacksonville: 408 p.

Habe T. 1952. — Atydae 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. & Siddiqui 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 & Valdés Á. 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* 810, e77457. https://doi.org/10.1371/journal.pone.0077457

Hermosillo A., Behrens D. W. & Ríos E. J. 2006. — *Opistobranquios de México. Guia de babosas marinas del Pacífico, 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, Polyplacophora, 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.

Holznagel 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.

Huelsenbeck J. P. & Ronquist 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 Liyu Island. (consulted 01.VI.2018) http://taconet.pixnet.net/blog/post/43322143-%E7%8E%BB%E7%92%83%E6%9C%88%E8%8F%AF%E8%9E%BA

Iffat 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) Software: www.inkscape.org

Kazmi Q. B. & Khan M. 2014. — Some new records of marine molluscans from the Pakistan Coast. *International Journal of Biological Research* 2 (2): 79-84.

Kazmi Q. B., Tirmizi 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: Gastropod-fauna of Pakistan. *Records of the Zoological survey of Pakistan* 2 (1): 17-129

Khan M. D. & Dastagir S. G. 1972. — *Pelecypod 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* 2812: 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 Biolology and Evolution* 33 (7): 1870-1874. https://doi.org/10.1093/molbev/msw054

Lozouet P. & Plaziat J. C. 2008. — *Mangrove environments and molluscs. Abatan River, Bohol and Panglao Islands, Central Philippines.* ConchBooks, Hackenheim: 166 p.

Macnae 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 *Bullacta exarata* (Philippi, 1849): an endemic cephalaspidean gastropod from the China Sea. *Journal of Natural History* 44 (33-34): 2015-2029.

Malaquias M. A. E. 2011. — Family Haminoeidae Pilsbry, 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 Reccords* 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. & Willassen E. 2016. — Diversity and systematics of philinid snails (Gastropoda: Cephalaspidea) in West Africa with remarks on the biogeography of the region. *Zoological Journal of the Linnean Society* 180 (1): 1-35. 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 Oceanograhy* 6: 1-249.

Mattis P., Kimball S. & Singh M. 1995. — GIMP: GNU image manipulation program. (consulted 01.III.2018) Software: www.gimp.org

Mikkelsen P. M. 1996. — The evolutionary relationships of Cephalaspidea s. l. (Gastropoda: Opisthobranchia): a phylogenetic analysis. *Malacologica* 37: 375-442.

Melvill 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. — *Cylichna crenilabris* Melvill & Standen, 1901. Accessed through World Register of Marine Species at: http://www.molluscabase.org/aphia.php?p=taxdetails&id=761116 on 06.VI.2018

Mujiono N. 2016. — Mangrove Gastropods from Lombok Island, West Nusa Tenggara. *Oseanologi 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/2088.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. — Polyplacophora. Acanthochitinidae, Cryptoplacidae and appendix. Tectibranchiata. *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.32672

Pilsbry H. A. 1896. — Philinidae, Gastropteridae, Aglajidae, Aplysiidae, Oxynoeidae, 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. & Fiene 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. & Huelsenbeck 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.

Röding P. F. 1798. — *Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturae quae olim collegerat Joa. Fried. Bolten M. D. p. d. Pars secunda continens Conchylia sive Testacea univalvia, bivalvia et multivalvia.* Johan Christi Trappii, Hamburg, 199 p. https://biodiversitylibrary.org/page/11067364

Schaefer K. 1992. — *Haminaea exigua* (Gastropoda, Opisthobranchia), a new cephalaspid species from the Mediterranean Sea. *Journal of Molluscan Studies* 58 (3): 329-336. https://doi.org/10.1093/mollus/58.3.329

Von Schlotheim E. F. 1820. — *Die Petrefactenkunde auf ihrem jetztigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt.* Becker, Gotha: 437 p.

Schumacher C. F. 1817. — *Essai d'un nouveau système des habitations des vers testacés.* Schultz, Copenghagen: iv + 288 p., 22 pls. https://doi.org/10.5962/bhl.title.35863

Strack H. L. 1998. — The Rumphius Biohistorical Expedition A story of present and past marine biology. De Rumphius Biohistorische Expeditie Een verhaal over mariene biologie vroeger en nu. *Vita Marina* 45 (1-2): 17-40.

Talavera P., Murillo L. & Templado J. 1987. — The genus *Haminoea* Turton & Kingston, 1830 (Opisthobranchia, Bullomorpha) 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.

Tibiriçá 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/s12526-016-0500-7

Turton W. & Kingston J. F. 1830. — *Part II: The natural history of the Distric 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, unpaged.

Ullah Z., Zehra I. & Gondal M. A. 2018 — Studies on the vertical distribution pattern in mangrove associated molluscs along the Karachi coast, Pakistan. *Indian Journal of Geo-Marine Sciences* 47 (1): 127-134.

Valdés Á., 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

WEINKAUFF 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.

APPENDIX

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.