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Photographic Checklist, DNA Barcoding, and New Species of Sea Slugs and Snails from the Faafu Atoll, Maldives (Gastropoda: Heterobranchia and Vetigastropoda) †

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Abstract: Baseline biodiversity data are key for ecological and evolutionary studies and are especially relevant for areas such as the Maldivian Archipelago in the Indian Ocean, which can act as a stepping-stone for the transport of widely distributed marine species. We surveyed the islands and reefs of the Faafu and Malé Atolls with snorkeling and scuba diving, collecting the two gastropod subclasses, Heterobranchia and Vetigastropoda. Our inventory comprises 104 species photographed alive to create an identification guide. We also provide COI barcodes for most species, adding novel sequence data for the Maldivian malacofauna. Half of our species represent new records for the Maldives, emphasizing how much diversity remains to be discovered. Species distributions reflect ecological rarity, with almost 60% of taxa only found in one site. We also compiled a comprehensive checklist of heterobranchs and vetigastropods of the Maldives based on literature records, resulting in 320 species, which, together with barcoding data, indicate several potential cryptic species in the Indo-Pacific. Six new species are described, the nudibranchs *Limenandra evanescenti* n. sp., *Eubranchus putnami* n. sp., *Sakuraeolis marhe* n. sp., *Moridilla maldivensis* n. sp., *Tergiposacca perspicua* n. sp., and the sacoglossan *Costasiella fridae* n. sp.

Keywords: Maldives; biodiversity; COI barcoding; photographic guide; Heterobranchia; Vetigastropoda; sea slugs; sea snails; Gastropoda; cryptic species

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1. Introduction

The diversity of marine species shared between the southwest Pacific and the islands and coasts of the Indian Ocean has been the basis for the recognition of a common biogeographical realm [1], often referred to as the Indo-West Pacific. Nonetheless, the existence of cryptic species and species complexes has been increasingly recognized from taxa with such widespread distributions (e.g., [2,3]). To address both species delimitation and broad biogeographical patterns, it is crucial to have baseline data of species occurrences across areas, which is still lacking for many localities and invertebrate clades.

The Maldivian Archipelago comprises 26 atolls distributed in a chain stretching for over 820 km in the central Indian Ocean [4] (Figure 1). It is the seventh largest coral reef in the world [5], with 1190 islands sprinkled over approximately 90,000 km^2 of ocean [4]. Two seasons characterized by strong winds in opposing directions (wet SW monsoon between May and September, dry NE monsoon between November and March [6]) have been suggested as a mechanism for larval transport from the western Indian Ocean and from Indonesia [7], which could contribute to the widespread species distributions of the Indo-Pacific.

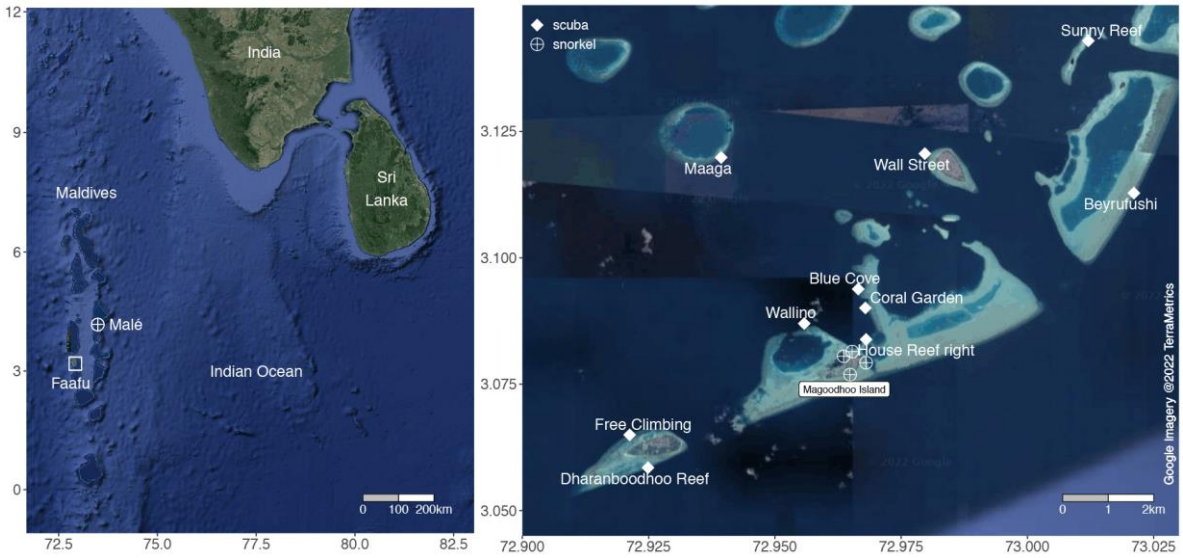

Figure 1. Maldivian Archipelago (**left**), highlighting the capital Malé (circle) and the Faafu Atoll (square), where most collecting sites are located (**right**). Scuba diving sites are labeled according to names used by staff at the MaRHE Center, based at Magoodhoo Island.

Faunistic surveys in the Maldives date back to an expedition by J. Stanley Gardiner throughout the archipelago [8], which resulted in the first inventory of mollusks in the area [9], as well as a specific list of nudibranchs [10]. Three other broad expeditions have covered marine mollusks since then (reviewed in [11]), resulting in inventories of multiple atolls [12,13]. Additional work has produced mollusk or invertebrate lists from specific atolls [11,14,15] or particular clades (e.g., Costellariidae [7]; Rissoinidae [16]; Polyplacophora [17]). In this study, we focus on two of the six subclasses of gastropods: Heterobranchia, with a worldwide marine diversity of about 9000 species, and Vetigastropoda, with over 4000 extant species [18]. Heterobranch-specific studies from the Maldives include Eliot [10], Marcus and Marcus [19], Rudman [20], and Yonow [21,22], while no publication so far has specifically targeted groups of vetigastropods.

In addition to inventories still being sparse, comprehensive documentation of identified fauna is often lacking, including vouchers in museum collections. In this paper, we provide a checklist of the heterobranch and vetigastropod fauna from the Faafu Atoll with specimen vouchers, photographic evidence of live specimens, and genetic barcode data for most of the collected species, which collectively will allow future cross-verification of species identities and further work on the ecology and evolution of marine biodiversity. We also compiled literature from other parts of the archipelago to provide a comprehensive checklist of both gastropod clades for the Maldives.

2. Material and Methods

2.1. Sampling and Checklist

Gastropods were collected in April 2019 during 23 visits to 14 unique sites in the Faafu Atoll (also known as North Nilandhe Atoll) and one site in the capital Malé (North Malé Atoll), Maldives (Figure 1). The main targets of the campaign were heterobranchs, and most vetigastropods found during fieldwork were also sampled. Specimens were collected by hand in benthic environments on and under rocks, rubble, corals, algae, and seagrass meadows while scuba diving or snorkeling. Twelve day-dives of about an hour each were performed by two divers down to 35 m depth, and the material was processed at the Marine Research and High Education Center (MaRHE Center) at Magoodhoo Island. Heterobranchs and vetigastropods were preliminarily identified following Gosliner et al. [23] and Okutani [24], respectively. Live animals were photographed in the lab with a Canon 80D using the Canon MP-E 65 mm and Canon 100 mm macro lenses. Specimens were anesthetized

with 7.5% $MgCl_2$ and preserved in 95% ethanol, with selected individuals also preserved in RNA*later* for future studies. All material was deposited in the Malacology Collection in the Museum of Comparative Zoology (MCZ), Harvard University (see Table S1 for voucher information, also listed in MCZBase). Identifications were refined with specialized literature [25–32]. COI sequence barcodes were also used for identification. Occurrence data for the entire Maldives were gathered from the Ocean Biodiversity Information System database (OBIS) [33] and literature records [9–15,19,21–23,26,27,34–40]. Maps and plots were built with the packages *ggmap* [41] and *ggplot2* [42] in the R environment [43].

2.2. DNA Barcoding

DNA was extracted from either foot or mantle tissue of individual specimens using the Qiagen DNeasy Blood and Tissue Kit following the manufacturer's protocol. For particularly small species, the entire organism was used for DNA extraction. The mitochondrial protein-coding gene cytochrome *c* oxidase subunit I (COI) was amplified using primer pairs LCO1490/HCO2198 [44] or jgLCO1490/jgHCO2198 [45]. Amplification reactions were carried out in a 25 µL-reaction volume using PuReTaq Ready-To-Go PCR Beads (GE Healthcare) with 1 µL of each primer, 2 µL of genomic DNA, and molecular-grade deionized water up to 25 µL. Amplification conditions included an initial denaturation step at 94 °C for 5 min, followed by 40 cycles of 94 °C for 15 s, 48 °C for 5 s, and 68 °C for 15 s, and a final extension at 72 °C for 7 min. Amplified products were purified using ExoSAP-IT (Affymetrix) and sequenced using Big-Dye Terminator in an ABI Prism 3730 XL Analyzer (Applied Biosystems). Forward and reverse sequences for each sample were assembled and edited in Geneious (v. 9.1.8) (https://geneious.com, accessed on 15 November 2022). Sequences were screened for contamination with BLAST [46] and a gene tree inferred with RAxML (v. 7.2.8) [47] based on an alignment from MAFFT (v. 7.309) [48] (Figure S1). Sequences were deposited in GenBank (accession numbers OQ206908–OQ207015; Table S1).

2.3. Genetic Delimitation of New Species

Phylogenetic trees were inferred for the new species being described here, together with publicly available sequences from related taxa retrieved from GenBank (https://www.ncbi.nlm.nih.gov/genbank, accessed on 15 November 2022) and BOLD Systems (https://boldsystems.org, accessed on 15 November 2022). Alignments were built in MAFFT using the G-INS-I algorithm implemented in Geneious. Phylogenetic analyses were performed on the CIPRES Science Gateway 3.3 (http://www.phylo.org, accessed on 15 November 2022), using maximum likelihood in IQ-TREE (v 2.1.2) [49] with the best substitution model selected in ModelFinder [50] accounting for codon positions. Branch support was estimated via ultrafast bootstrap with 1500 replicates [51]. Trees were visualized in FigTree (v. 1.4.4) (http://tree.bio.ed.ac.uk/software/figtree.

To further investigate the identity of the studied specimens, species delimitation tests were conducted. An Assemble Species by Automatic Partitioning (ASAP) [52] analysis was run using the web interface (https://bioinfo.mnhn.fr/abi/public/asap, accessed on 15 November 2022) with the Kimura (K80) distance model and default parameters (TS/TV = 2.0). Poisson Tree Processes (PTP) [53] was also run using the web interface (https://mptp.h-its.org, accessed on 15 November 2022).

3. Results

Marine heterobranchs and vetigastropods were collected in 14 sampling sites alongside the Faafu Atoll (mainly around Magoodhoo island) and one site in the capital Malé (Figure 1). In total, over 250 live specimens and 20 empty shells belonging to 104 species were collected, including 85 species of heterobranchs in 30 families and 19 species of vetigastropods in five families (Table 1). Over half of the species were collected in a single site (59%, Figure 2A), being mostly represented by a single specimen (58%, Figure 2B). Combined with previous occurrences from the literature, we compiled a checklist of 320 species for the

Maldivian Archipelago (Table 1). About 64% of all species are only listed by one reference source (Figure 2C).

Table 1. Checklist of heterobranch and vetigastropod species found in the Maldives, including new species and undetermined species (*sensu* Gosliner et al. [23] for heterobranchs). Species collected in this study are highlighted in bold, figure citations are included. Species names recorded from the literature were updated according to WoRMS [18] unless explicitly discussed in the source reference. From the OBIS database [33], only records with 'preserved specimens' were considered.

Family	Species	Authority	Figure	Reference
HETEROBRANCHIA				
ACOCHLIDIIMORPHA				
Parhedylidae	*Microhedyle gerlachi*	Er. Marcus & Ev. Marcus, 1960		[19]
ACTEONIMORPHA				
Acteonidae	*Japonacteon suturalis*	(A. Adams, 1855)		[13]
Acteonidae	*Pupa affinis*	(A. Adams, 1855)		[13]
Acteonidae	*Pupa alveola*	(Souverbie, 1863)		[38]
Acteonidae	*Pupa nitidula*	(Lamarck, 1816)		[12,40]
Acteonidae	*Pupa solidula*	(Linnaeus, 1758)		[12,40]
Acteonidae	*Pupa sulcata*	(Gmelin, 1791)		[38]
Acteonidae	***Pupa tessellata***	**(Reeve, 1842)**	**3a**	**[40], This study**
Aplustridae	*Aplustrum amplustre*	(Linnaeus, 1758)		[13,38]
APLYSIIDA				
Aplysiidae	*Aplysia* cf. *nigrocincta*	Martens, 1880		[21,22,34]
Aplysiidae	*Aplysia parvula*	Guilding in Mörch, 1863		[21]
Aplysiidae	***Dolabella auricularia***	**(Lightfoot, 1786)**	**3d**	**[13,19,21,22,34], This study**
Aplysiidae	***Dolabrifera dolabrifera***	**(Rang, 1828)**	**3e**	**[21,34], This study**
Aplysiidae	*Stylocheilus longicauda*	(Quoy & Gaimard, 1825)		[21]
Aplysiidae	***Stylocheilus striatus***	**(Quoy & Gaimard, 1832)**	**3f**	**This study**
ARCHITECTONICOIDEA				
Architectonicidae	*Architectonica modesta*	(Philippi, 1849)		[40]
Architectonicidae	*Heliacus infundibuliformis*	(Gmelin, 1791)		[33]
Architectonicidae	*Heliacus trochoides*	(Deshayes, 1830)		[33]
Architectonicidae	*Psilaxis radiatus*	(Röding, 1798)		[9,12,38,40]
CEPHALASPIDEA				
Aglajidae	*Biuve fulvipunctata*	(Baba, 1938)		[34]
Aglajidae	*Chelidonura castanea*	Yonow, 1994		[22]
Aglajidae	*Chelidonura electra*	Rudman, 1970		[21,34]
Aglajidae	*Chelidonura hirundinina*	(Quoy & Gaimard, 1833)		[21,34]
Aglajidae	*Chelidonura punctata*	Eliot, 1903		[21,33]
Aglajidae	*Chelidonura* sp.			[34]
Aglajidae	***Chelidonura varians***	**Eliot, 1903**	**4n**	**[21,22,33], This study**
Aglajidae	*Mariaglaja sandrana*	(Rudman, 1973)		[21,22,34]
Aglajidae	*Mariaglaja tsurugensis*	(Baba & Abe, 1959)		[33]
Aglajidae	*Nakamigawaia spiralis*	Kuroda & Habe, 1961		[34]
Aglajidae	*Odontoglaja guamensis*	Rudman, 1978		[34]
Aglajidae	*Philinopsis speciosa*	Pease, 1860		[22,33,34]
Aglajidae	*Tubulophilinopsis gardineri*	(Eliot, 1903)		[34]
Aglajidae	*Tubulophilinopsis pilsbryi*			[19]
Bullidae	*Bulla ampulla*	Linnaeus, 1758		[9,12,13,15,38]
Bullidae	***Bulla vernicosa***	**Gould, 1859**	**4b**	**This study**
Colpodaspiddidae	***Colpodaspis thompsoni***	**G. H. Brown, 1979**	**4c**	**[34], This study**
Gastropteridae	*Sagaminopteron psychedelicum*	Carlson & Hoff, 1974		[34]
Haminoeidae	"*Atys*" *xarifae* (cf. *Weinkauffia*)	Er. Marcus & Ev. Marcus, 1960		[19]

Table 1. *Cont.*

Family	Species	Authority	Figure	Reference
Haminoeidae	*Aliculastrum cylindricum*	(Helbling, 1779)		[40]
Haminoeidae	***Aliculatrum debile***	**(Pease, 1860)**	**4l**	**This study**
Haminoeidae	*Atys naucum*	(Linnaeus, 1758)		[40]
Haminoeidae	*Atys* sp. 1			[11]
Haminoeidae	*Atys* sp. 2			[11]
Haminoeidae	***Haloa aptei***	**(Bharate, Oskars, Narayana, Ravinesh, Biju Kumar & Malaquias, 2018)**	**4d**	**This study**
Haminoeidae	***Lamprohaminoea cymbalum***	**(Quoy & Gaimard, 1833)**	**4e**	**[21], This study**
Haminoeidae	**Long tail haminoid**		**4f**	**This study**
Haminoeidae	**Mini haminoid**		**4g**	**This study**
Haminoeidae	***Phanerophthalmus batangas***	**Austin, Gosliner & Malaquias, 2018**	**4h**	**This study**
Haminoeidae	***Phanerophthalmus* cf. *cylindricus***	**(Pease, 1861)**	**4i**	**This study**
Haminoeidae	*Phanerophthalmus* cf. *olivaceus*			[19]
Haminoeidae	***Phanerophthalmus minikoiensis***	**(E. A. Smith, 1903)**	**4j**	**This study**
Haminoeidae	***Vellicolla* cf. *muscaria***	**(Gould, 1859)**	**4k**	**This study**
Philinidae	***Philine orca***	**Gosliner, 1988**	**4m**	**[19], This study**
Tornatinidae	***Acteocina* sp.**		**4a**	**This study**
NUDIBRANCHIA				
Actinocyclidae	***Hallaxa fuscescens***	**(Pease, 1871)**	**6b**	**This study**
Actinocyclidae	***Hallaxa indecora***	**(Bergh, 1905)**	**6a**	**This study**
Aegiridae	*Aegires* sp.			[34]
Aegiridae	*Notodoris citrina*	Bergh, 1875		[34]
Aegiridae	*Notodoris gardineri*	Eliot, 1903		[10,21,22,33,34]
Aeolidiidae	*Baeolidia dela*	(Er. Marcus & Ev. Marcus, 1960)		[19]
Aeolidiidae	***Limenandra evanescenti* n. sp.**	**Fernández-Simón & Moles, 2023**	**5a**	**This study**
Arminidae	*Dermatobranchus striatus*	van Hasselt, 1824		[10,33]
Arminidae	*Pleurophyllidia gracilis*	Bergh, 1874		[10]
Bornellidae	*Bornella anguilla*	S. Johnson, 1984		[34]
Aeolidiidae	*Baeolidia variabilis*	Carmona, Pola, Gosliner & Cervera, 2014		[34]
Chromodorididae	*Ceratosoma gracillimum*	Semper in Bergh, 1876		[10,34]
Chromodorididae	*Ceratosoma trilobatum*	(J. E. Gray, 1827)		[10,33,34]
Chromodorididae	*Chromodoris elisabethina*	Bergh, 1877		[10,19,34]
Chromodorididae	*Chromodoris lochi*	Rudman, 1982		[21,22,34]
Chromodorididae	*Chromodoris pustulans*	Bergh, 1877		[10]
Chromodorididae	*Doriprismatica atromarginata*	(Cuvier, 1804)		[19]
Chromodorididae	***Glossodoris acosti***	**Matsuda & Gosliner, 2018**	**6c**	**[21,22,33,34], This study**
Chromodorididae	*Glossodoris hikuerensis*	(Pruvot-Fol, 1954)		[22,34]
Chromodorididae	*Glossodoris pallida*	(Rüppell & Leuckart, 1830)		[21,34]
Chromodorididae	***Goniobranchus albonares***	**(Rudman, 1990)**	**6h**	**This study**
Chromodorididae	*Goniobranchus cavae*	(Eliot, 1904)		[34]
Chromodorididae	*Goniobranchus coi*	(Risbec, 1956)		[33]
Chromodorididae	***Goniobranchus conchyliatus***	**(Yonow, 1984)**	**6f**	**[34], This study**
Chromodorididae	*Goniobranchus decorus*	(Pease, 1860)		[21]
Chromodorididae	***Goniobranchus fidelis***	**(Kelaart, 1858)**	**6g**	**[22,33,34], This study**
Chromodorididae	*Goniobranchus geminus*	Rudman, 1987		[33,34]
Chromodorididae	*Goniobranchus geometricus*	(Risbec, 1928)		[21,22,33,34]
Chromodorididae	***Goniobranchus gleniei***	**(Kelaart, 1858)**	**6d**	**[21,22,33,34], This study**

Table 1. *Cont.*

Family	Species	Authority	Figure	Reference
Chromodorididae	***Goniobranchus setoensis***	**(Baba, 1938)**	**6e**	**[34], This study**
Chromodorididae	*Goniobranchus tritos*	(Yonow, 1994)		[22,34]
Chromodorididae	*Hypselodoris bullockii*	(Collingwood, 1881)		[33]
Chromodorididae	*Hypselodoris emma*	Rudman, 1977		[22,33,34]
Chromodorididae	*Hypselodoris infucata*	(Rüppell & Leuckart, 1830)		[33]
Chromodorididae	*Hypselodoris krakatoa*	Gosliner & Johnson, 1999		[34]
Chromodorididae	***Hypselodoris maculosa***	**(Pease, 1871)**	**6m**	**[21,33,34], This study**
Chromodorididae	*Hypselodoris maridadilus*	Rudman, 1977		[34]
Chromodorididae	***Hypselodoris nigrostriata***	**(Eliot, 1904)**	**6n**	**This study**
Chromodorididae	*Hypselodoris rosans*	(Bergh, 1889)		[10]
Chromodorididae	*Hypselodoris rudmani*	Gosliner & Johnson, 1999		[34]
Chromodorididae	*Hypselodoris* sp. 16			[34]
Chromodorididae	*Hypselodoris whitei*	(Adams & Reeve, 1850)		[22,33,34]
Chromodorididae	*Mexichromis pusilla*	(Bergh, 1874)		[22]
Chromodorididae	***Mexichromis similaris***	**(Rudman, 1986)**	**6l**	**[34], This study**
Chromodorididae	*Miamira magnifica*	(Eliot, 1910)		[22,33,34]
Chromodorididae	*Miamira miamirana*	(Bergh, 1875)		[21]
Chromodorididae	*Miamira sinuata*	(van Hasselt, 1824)		[34]
Chromodorididae	*Thorunna* sp.			[19]
Chromodorididae	***Verconia simplex***	**(Pease, 1871)**	**6i**	**This study**
Chromodorididae	*Verconia varians*	(Pease, 1871)		[22,33]
Dendrodorididae	***Dendrodoris nigra***	**(Stimpson, 1855)**	**6j**	**[10,21,33,34], This study**
Discodorididae	*Asteronotus cespitosus*	(van Hasselt, 1824)		[34]
Discodorididae	*Atagema intecta*	(Kelaart, 1859)		[10]
Discodorididae	*Dictyodoris maculata*	Eliot, 1903		[10,33]
Discodorididae	*Discodoris boholiensis*	Bergh, 1877		[10,33,34]
Discodorididae	*Discodoris concinna*	(Alder & Hancock, 1864)		[10]
Discodorididae	*Discodoris pardalis*	(Alder & Hancock, 1864)		[10]
Discodorididae	*Halgerda iota*	Yonow, 1994		[22]
Discodorididae	*Halgerda tessellata*	(Bergh, 1880)		[21,34]
Discodorididae	*Jorunna funebris*	(Kelaart, 1858)		[34]
Discodorididae	*Jorunna rubescens*	(Bergh, 1876)		[34]
Discodorididae	*Peltodoris murrea*	(Abraham, 1877)		[34]
Discodorididae	*Platydoris cruenta*	(Quoy & Gaimard, 1832)		[33]
Discodorididae	*Platydoris scabra*	(Cuvier, 1804)		[10,33]
Discodorididae	*Platydoris* sp.			[22]
Discodorididae	***Rostanga* sp. 2**		**6k**	**This study**
Discodorididae	*Sebadoris nubilosa*	(Pease, 1871)		[19]
Discodorididae	***Thordisa* cf. *oliva***	**Chan & Gosliner, 2007**	**6o**	**This study**
Doridididae	*Doriopsis apicalis*	Bergh, 1890		[33]
Doridididae	*Doriopsis pecten*	(Collingwood, 1881)		[34]
Doridomorphidae	*Doridomorpha gardineri*	Eliot, 1903		[10,19,33]
Dotidae	***Doto* sp.**		**5b**	**This study**
Embletoniidae	***Embletonia gracilis***	**Risbec, 1928**	**5c**	**This study**
Eubranchidae	***Eubranchus putnami* n. sp.**	**Fernández-Simón & Moles, 2023**	**5d**	**This study**
Eubranchidae	***Eubranchus* sp.**		**5e**	**This study**
Facelinidae	***Caloria indica***	**(Bergh, 1896)**	**5g**	**[22,33,34], This study**
Facelinidae	*Cratena phylloda*	Er. Marcus & Ev. Marcus, 1960		[19]
Facelinidae	*Cratena simba*	Edmunds, 1970		[34]
Facelinidae	***Cratena* sp. 5**		**5i**	**[34], This study**

Table 1. *Cont.*

Family	Species	Authority	Figure	Reference
Facelinidae	***Cratena* sp. A**		**5h**	**This study**
Facelinidae	***Cratena* sp. B**		**5j**	**This study**
Facelinidae	***Sakuraeolis marhe* n. sp.**	**Fernández-Simón & Moles, 2023**	**5n**	**[34], This study**
Facelinidae	***Favorinus japonicus***	**Baba, 1949**	**5l**	**[34], This study**
Facelinidae	***Favorinus mirabilis***	**Baba, 1955**	**5k**	**This study**
Facelinidae	*Favorinus tsuruganus*	Baba & Abe, 1964		[34]
Facelinidae	***Herviella albida***	**Baba, 1966**	**5f**	**This study**
Facelinidae	*Herviella yatsui*	(Baba, 1930)		[33]
Facelinidae	*Moridilla brockii*	Bergh, 1888		[22,33,34]
Facelinidae	***Moridilla maldivensis* n. sp.**	**Fernández-Simón & Moles, 2023**	**5m**	**This study**
Facelinidae	*Moridilla* sp.			[34]
Facelinidae	***Noumeaella* sp.**		**5o**	**This study**
Facelinidae	*Noumeaella* sp. C			[34]
Facelinidae	*Phidiana unilineata*	(Alder & Hancock, 1864)		[33]
Facelinidae	***Pteraeolidia* aff. *semperi***	**(Bergh, 1870)**	**5p**	**[19,22,33,34], This study**
Fionidae	*Fiona* sp.			[33]
Fionidae	*Tergiposacca longicerata*	Cella, Carmona, Ekimova, Chichvarkhin, Schepetov & Gosliner, 2016		[34]
Fionidae	***Tergiposacca perspicua* n. sp.**	**Fernández-Simón & Moles, 2023**	**5q**	**This study**
Flabellinidae	*Coryphellina exoptata*	(Gosliner & Willan, 1991)		[34]
Flabellinidae	*Flabellina* sp.			[34]
Goniodorididae	***Goniodoridella* sp.**		**6p**	**This study**
Goniodorididae	*Trapania euryeia*	Gosliner & Fahey, 2008		[34]
Goniodorididae	*Trapania naeva*	Gosliner & Fahey, 2008		[37]
Hexabranchidae	***Hexabranchus sanguineus***	**(Rüppell & Leuckart, 1830)**	**-**	**[10,21,33,34], This study**
Lomanotidae	*Lomanotus vermiformis*	Eliot, 1908		[34]
Madrellidae	*Madrella ferruginosa*	Alder & Hancock, 1864		[10,33]
Myrrhinidae	***Godiva* sp.**		**5r**	**This study**
Phyllidiidae	***Phyllidia alyta***	**Yonow, 1996**	**6x**	**[10,21,33,34], This study**
Phyllidiidae	*Phyllidia coelestis*	Bergh, 1905		[34]
Phyllidiidae	*Phyllidia elegans*	Bergh, 1869		[33]
Phyllidiidae	*Phyllidia exquisita*	Brunckhorst, 1993		[21,34]
Phyllidiidae	***Phyllidia koehleri***	**Perrone, 2000**	**6v**	**[21,33,34], This study**
Phyllidiidae	*Phyllidia marindica*	(Yonow & Hayward, 1991)		[21,33,34]
Phyllidiidae	*Phyllidia multituberculata*	C. R. Boettger, 1918		[21]
Phyllidiidae	*Phyllidia ocellata*	Cuvier, 1804		[34]
Phyllidiidae	***Phyllidia picta***	**Pruvot-Fol, 1957**	**6y**	**This study**
Phyllidiidae	*Phyllidia rueppelii*	(Bergh, 1869)		[10]
Phyllidiidae	***Phyllidia* sp.**		**6t**	**This study**
Phyllidiidae	***Phyllidia varicosa***	**Lamarck, 1801**	**6z**	**[10,14,19,33,34], This study**
Phyllidiidae	*Phyllidiella meandrina*	(Pruvot-Fol, 1957)		[33]
Phyllidiidae	***Phyllidiella rosans***	**(Bergh, 1873)**	**6w**	**[14,21,33,34], This study**
Phyllidiidae	*Phyllidiella rudmani*	Brunckhorst, 1993		[14,21,33,34]
Phyllidiidae	***Phyllidiella* sp.**		**6u**	**This study**
Phyllidiidae	***Phyllidiella* sp. 1**		**6aa**	**This study**
Phyllidiidae	***Phyllidiella striata***	**(Bergh, 1889)**	**6ac**	**[10,21,33,34], This study**
Phyllidiidae	***Phyllidiella zeylanica***	**(Kelaart, 1859)**	**6ab**	**[21,33,34], This study**

Table 1. *Cont.*

Family	Species	Authority	Figure	Reference
Phyllidiidae	*Phyllidiopsis annae*	Brunckhorst, 1993		[33,34]
Phyllidiidae	*Phyllidiopsis cardinalis*	Bergh, 1876		[34]
Phyllidiidae	*Phyllidiopsis gemmata*	Pruvot-Fol, 1957		[21,34]
Phyllidiidae	*Phyllidiopsis krempfi*	Pruvot-Fol, 1957		[21]
Phyllidiidae	*Phyllidiopsis shireenae*	Brunckhorst, 1990		[21,34]
Phyllidiidae	***Phyllidiopsis* sp.**		**6ad**	**This study**
Phyllidiidae	*Phyllidiopsis* sp. 5			[34]
Phyllidiidae	*Phyllidiopsis sphingis*	Brunckhorst, 1993		[21,34]
Phyllidiidae	***Phyllidiopsis xishaensis***	**(Lin, 1983)**	**6ae**	**[21,33,34], This study**
Pinufiidae	*Pinufius rebus*	Er. Marcus & Ev. Marcus, 1960		[19]
Polyceridae	***Gymnodoris ceylonica***	**(Kelaart, 1858)**	**6r**	**[34], This study**
Polyceridae	*Gymnodoris crocea*	(Bergh, 1889)		[10,33]
Polyceridae	***Gymnodoris* sp.**		**6s**	**This study**
Polyceridae	*Martadoris amakusana*	(Baba, 1987)		[21,34]
Polyceridae	*Nembrotha cristata*	Bergh, 1877		[22,33,34]
Polyceridae	*Nembrotha guttata*	Yonow, 1994		[21,22,33,34]
Polyceridae	*Nembrotha kubaryana*	Bergh, 1877		[10,33]
Polyceridae	*Nembrotha lineolata*	Bergh, 1905		[34]
Polyceridae	*Nembrotha megalocera*	Yonow, 1990		[14]
Polyceridae	*Polycera* sp. 5			[34]
Polyceridae	***Roboastra gracilis***	**(Bergh, 1877)**	**6q**	**[21,22,33,34], This study**
Polyceridae	*Tambja affinis*	(Eliot, 1904)		[34]
Polyceridae	*Tambja morosa*	(Bergh, 1877)		[34]
Polyceridae	*Tambja olivaria*	Yonow, 1994		[22,34]
Polyceridae	*Thecacera vittata*	Yonow, 1994		[22,34]
Polyceridae	*Tyrannodoris nikolasi*	(Pola, Padula, Gosliner & Cervera, 2014)		[34]
Samlidae	***Samla bicolor***	**(Kelaart, 1858)**	**5t**	**[34], This study**
Samlidae	***Samla riwo***	**(Gosliner & Willan, 1991)**	**5s**	**[34], This study**
Samlidae	*Samla rubropurpurata*	(Gosliner & Willan, 1991)		[34]
Samlidae	*Samla* sp. 2			[34]
Trinchesiidae	*Cuthona netsica*	(Er. Marcus & Ev. Marcus, 1960)		[19]
Trinchesiidae	***Phestilla lugubris***	**(Bergh, 1870)**	**5u**	**This study**
Trinchesiidae	*Phestilla melanobrachia*	Bergh, 1874		[22,33,34]
Trinchesiidae	*Phestilla minor*	Rudman, 1981		[34]
Trinchesiidae	*Trinchesia sibogae*	(Bergh, 1905)		[34]
Tritoniidae	*Marionia arborescens*	Bergh, 1890		[10,34]
PLEUROBRANCHIDA				
Pleurobranchidae	***Berthella martensi***	**(Pilsbry, 1896)**	**3c**	**[22,33,34], This study**
Pleurobranchidae	***Berthellina delicata***	**(Rüppell & Leuckart, 1828)**	**3b**	**[22,33], This study**
Pleurobranchidae	*Pleurobranchus forskalii*	Rüppell & Leuckart, 1828		[34]
Pleurobranchidae	*Pleurobranchus grandis*	Pease, 1868		[34]
PTEROPODA				
Cavoliniidae	*Cavolinia globulosa*	Gray, 1850		[35]
Cavoliniidae	*Cavolinia* sp.			[35]
Cavoliniidae	*Cavolinia unicinata*	(d'Orbigny, 1835)		[13]
Cliidae	*Clio convexa*	(Boas, 1886)		[35]
Cliidae	*Clio cuspidata*	(Bosc, 1801)		[35]
Creseidae	*Boasia chierchiae*	(Boas, 1886)		[35]
Creseidae	*Creseis virgula*	(Rang, 1828)		[35]
Cymbuliidae	*Cymbulia* sp.			[35]
Peraclidae	*Peracle reticulata*	(d'Orbigny, 1835)		[35]

Table 1. *Cont.*

Family	Species	Authority	Figure	Reference
PYLOPULMONATA				
Pyramidellidae	*Longchaeus acus*	(Gmelin, 1791)		[12,15]
Pyramidellidae	*Longchaeus insularum*	(Pilsbry, 1922)		[13]
Pyramidellidae	*Longchaeus maculosus*	(Lamarck, 1822)		[12]
Pyramidellidae	*Obeliscus monilis*	A. Adams, 1854		[40]
Pyramidellidae	*Otopleura auriscati*	(Holten, 1802)		[12]
Pyramidellidae	*Otopleura mitralis*	(A. Adams, 1854)		[13]
Pyramidellidae	*Otopleura nodicincta*	(A. Adams, 1854)		[12,40]
Pyramidellidae	*Pyramidella dolabrata*	(Linnaeus, 1758)		[12,40]
Pyramidellidae	*Pyramidella* sp.			[11]
SACOGLOSSA				
Costasiellidae	***Costasiella fridae* n. sp.**	**Fernández-Simón & Moles, 2023**	**7f**	**This study**
Hermaeidae	***Cyerce elegans***	**Bergh, 1870**	**7a**	**This study**
Hermaeidae	*Cyerce nigra*	Bergh, 1871		[10]
Hermaeidae	*Hermaea minor*	Bergh, 1888		[10]
Hermaeidae	***Polybranchia jensenae***	**Medrano, Krug, Gosliner, Biju Kumar & Valdés, 2018**	**7k**	**This study**
Limapontiidae	***Stiliger* sp. 1**		**7g**	**This study**
Plakobranchidae	***Elysia* cf. *marginata***	**(Pease, 1871)**	**7c**	**[34], This study**
Plakobranchidae	***Elysia obtusa***	**Baba, 1938**	**-**	**This study**
Plakobranchidae	***Elysia pusilla***	**(Bergh, 1871)**	**7b**	**[36], This study**
Plakobranchidae	***Elysia* sp. 11**		**7d**	**This study**
Plakobranchidae	*Elysia* sp. 17			[34]
Plakobranchidae	***Elysia* sp. 44**		**7e**	**This study**
Plakobranchidae	*Plakobranchus ocellatus*	van Hasselt, 1824		[21,34]
Plakobranchidae	*Thuridilla coerulea*	(Kelaart, 1857)		[22]
Plakobranchidae	***Thuridilla gracilis***	**(Risbec, 1928)**	**7h**	**[21,22,33,34], This study**
Plakobranchidae	***Thuridilla livida***	**(Baba, 1955)**	**7j**	**[34], This study**
Plakobranchidae	*Thuridilla* sp. 1			[34]
Plakobranchidae	***Thuridilla vataae***	**(Risbec, 1928)**	**7i**	**[21,34], This study**
SIPHONARIIDA				
Siphonarioidea	*Siphonaria* cf. *normalis*	A. Gould, 1846		[11,13]
SYSTELLOMMATOPHORA				
Onchidiidae	*Peronia peronii*	(Cuvier, 1804)		[19]
Onchidiidae	*Peronia verruculatum*	(Cuvier, 1830)		[13]
UMBRACULIDA				
Umbraculidae	*Umbraculum umbraculum*	(Lightfoot, 1786)		[11]
VETIGASTROPODA				
FISSURELLIDA				
Fissurellidae	***Diodora singaporensis***	**(Reeve, 1850)**	**8b**	**[9,13], This study**
Fissurellidae	*Diodora* cf. *ticaonica*	(Reeve, 1850)		[13]
Fissurellidae	*Emarginella incisura*	(A. Adams, 1852)		[9,13]
Fissurellidae	***Emarginella nigromaculata***	**(Thiele, 1915)**	**8c**	**This study**
Fissurellidae	*Emarginella planulata*	(A. Adams, 1852)		[9]
Fissurellidae	***Emarginella* sp. 1**		**8d**	**This study**
Fissurellidae	*Emarginula dilecta*	A. Adams, 1852		[13]
Fissurellidae	*Emarginula souverbiana*	Pilsbry, 1891		[13]
Fissurellidae	***Emarginula* sp.**		**-**	**This study**
Fissurellidae	***Hemimarginula* cf. *biangulata***	**(G. B. Sowerby III, 1901)**	**8a**	**This study**
HALIOTIDA				
Haliotidae	*Haliotis clathrata*	Reeve, 1846		[12,26]
Haliotidae	***Haliotis ovina***	**Gmelin, 1791**	**8e**	**[9,11,13,15,26,33,38], This study**

Table 1. *Cont.*

Family	Species	Authority	Figure	Reference
LEPETELLIDA				
Scissurellidae	*Scissurella quadrata*	Geiger & Jansen, 2004		[27]
Scissurellidae	***Scissurella rota***	**Yaron, 1983**	**-**	**[27], This study**
Scissurellidae	*Sukashitrochus estotiensis*	Lozouet, 1999		[27]
SEGUENZIIDA				
Chilodontaidae	*Perrinia angulifera*	(A. Adams, 1853)		[9]
TROCHIDA				
Angariidae	*Angaria delphinus*	(Linnaeus, 1758)		[13,38]
Angariidae	*Angaria* sp.			[11]
Colloniidae	*Collonista solida*	(Preston, 1908)		[13]
Liotiidae	*Liotia squamicostata*	E. A. Smith, 1903		[13]
Liotiidae	*Liotina* sp.			[13]
Phasianellidae	*Hiloa variabilis*	(Pease, 1861)		[13]
Trochidae	***Calliotrochus marmoreus***	**(Pease, 1861)**	**8g**	**[13,31], This study**
Trochidae	*Clanculus denticulatus*	(Gray, 1826)		[33]
Trochidae	*Clanculus pharaonius*	(Linnaeus, 1758)		[38]
Trochidae	*Clanculus puniceus*	(Philippi, 1846)		[12]
Trochidae	***Clanculus samoensis***	**(Hombron & Jacquinot, 1848)**	**8f**	**[9,11–13], This study**
Trochidae	*Ethalia striolata*	(A. Adams, 1855)		[13]
Trochidae	*Ethaliella rhodomphala*	(E. A. Smith, 1903)		[9,13]
Trochidae	*Jujubinus maldivensis*	(E. A. Smith, 1903)		[9,13]
Trochidae	*Monilea calyculus*	(W. Wood, 1828)		[9]
Trochidae	*Monilea simulans*	E. A. Smith, 1899		[9]
Trochidae	*Rossiteria nucleus*	(Philippi, 1850)		[13]
Trochidae	*Rubritrochus pulcherrimus*	(A. Adams, 1855)		[9,13]
Trochidae	*Stomatella auricula*	Lamarck, 1816		[9,11–13]
Trochidae	*Stomatella nigra*	Quoy & Gaimard, 1834		[12]
Trochidae	***Stomatella varia***	**(A. Adams, 1850)**	**8n**	**This study**
Trochidae	*Stomatia phymotis*	Helbling, 1779		[11–13]
Trochidae	*Stomatolina* cf. *irisata*	(Dufo, 1840)		[11]
Trochidae	***Stomatolina rubra***	**(Lamarck, 1822)**	**8l**	**This study**
Trochidae	***Stomatolina* sp. 1**		**8k**	**This study**
Trochidae	*Synaptocochlea* sp.			[13]
Trochidae	*Trochus* cf. *intextus*	Kiener, 1850		[11]
Trochidae	*Trochus flammulatus*	Lamarck, 1822		[39]
Trochidae	***Trochus maculatus***	**Linnaeus, 1758**	**8h**	**[9,11–15,38], This study**
Trochidae	*Trochus ochroleucus*	Gmelin, 1791		[13]
Trochidae	*Trochus radiatus*	Gmelin, 1791		[9,12,38]
Trochidae	*Trochus sacellum*	Philippi, 1855		[33]
Trochidae	***Trochus* cf. *stellatus***	**Gmelin, 1791**	**8i**	**[9], This study**
Trochidae	***Trochus* sp.**		**8j**	**This study**
Trochidae	*Trochus tubiferus*	Kiener, 1850		[9,13]
Turbinidae	*Astralium haematragum*	(Menke, 1829)		[33]
Turbinidae	*Astralium* cf. *helicinum*	(Gmelin, 1791)		[13]
Turbinidae	***Astralium rhodostomum***	**(Lamarck, 1822)**	**-**	**[11,12,33], This study**
Turbinidae	*Rochia conus*	(Gmelin, 1791)		[15]
Turbinidae	*Tectus fenestratus*	(Gmelin, 1791)		[12,33]
Turbinidae	***Tectus pyramis***	**(Born, 1778)**	**-**	**[12–14,33], This study**
Turbinidae	***Turbo argyrostomus***	**Linnaeus, 1758**	**-**	**[9,11–13,38,39], This study**
Turbinidae	*Turbo chrysostomus*	Linnaeus, 1758		[33]
Turbinidae	*Turbo intercostalis*	Menke, 1846		[15]
Turbinidae	***Turbo petholatus***	**Linnaeus, 1758**	**8m**	**[11,12,15,38], This study**
NERITIMORPHA				
CYCLONERITIDA				
Phenacolepadidae	***Zacalantica tenuisculpta***	**(Thiele, 1909)**	**8o**	**This study**

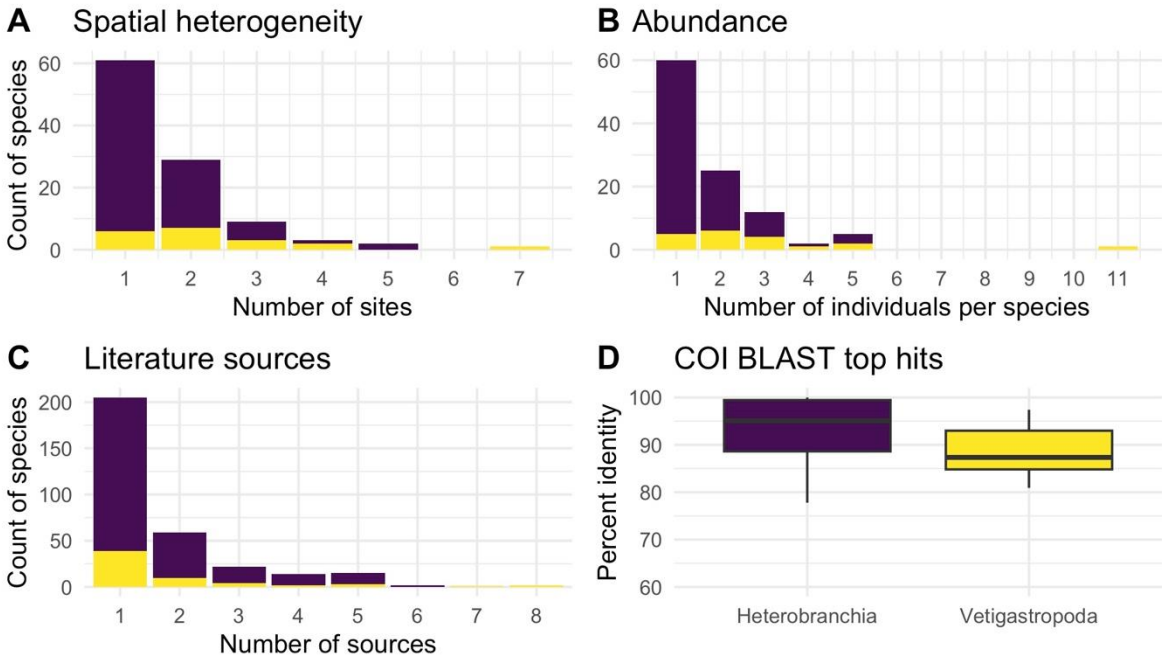

Figure 2. Distribution of species of Heterobranchia (purple) and Vetigastropoda (yellow) by (**A**) the number of sites where they were collected, (**B**) the number of specimens, and (**C**) the number of literature sources where the species is recorded. (**D**) Percent identity of the best BLAST hit for all barcoded specimens.

For heterobranchs, up to 46 species are reported for the first time in the Maldives (Table 1), thus increasing the country's known heterobranch diversity by 26% and expanding their distribution ranges. Species of Acteonoidea, Pleurobranchida and Aplysiida (Figure 3), Cephalaspidea (Figure 4), Nudibranchia (Cladobranchia, Figure 5; Doridina, Figure 6), and Sacoglossa (Figure 7) were collected. The most collected order was Nudibranchia, with 52 species, followed by Cephalaspidea, with 15 species, and Sacoglossa, with 12. Barcodes were useful to identify most of the species, but in other cases, no identical sequences (below 95% BLAST identity) were found in GenBank (Figure 2D, Tables S2 and S3). From the 58 species of heterobranchs that were successfully barcoded, no identical sequences were available for 21 species of nudibranchs, two pleurobranchs, two cephalaspideans, and three sacoglossans. From those, cases of (pseudo)cryptic speciation are evident for *Berthellina delicata* (Figure 3b), *Berthella martensi* (Figure 3c), *Colpodaspis thompsoni* (Figure 4c), *Philine orca* (Figure 4m), *Pteraeolidia* aff. *semperi* (Figure 5p), and *Elysia* spp. (Figure 7b–e), with insufficient molecular or taxon sampling to further contribute to their taxonomic status. Nevertheless, six new species are described here based on molecular data and external morphological characters (see Systematics section below). Phylogenetic, species delimitation tests, and discrete external morphological characters aided in their discrimination and diagnosis and, therefore, are here officially described to provide taxonomic assistance to the species of the genera *Limenandra*, *Eubranchus*, *Sakuraeolis*, *Moridilla*, *Tergiposacca*, and *Costasiella*.

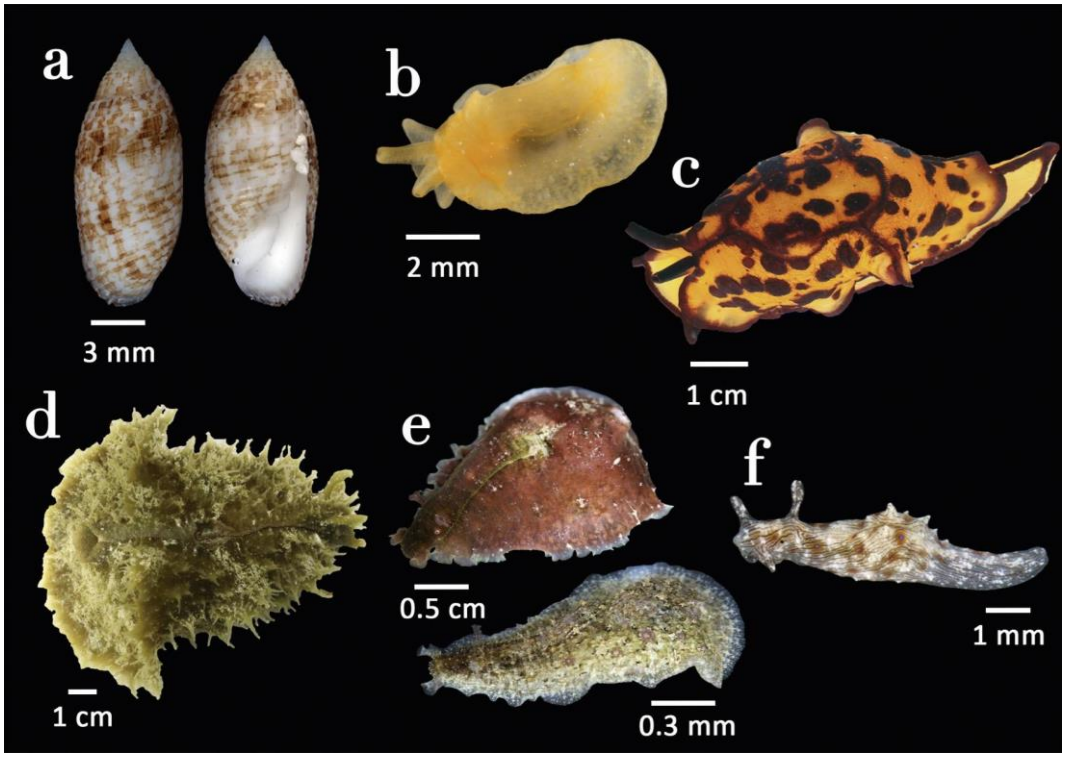

Figure 3. Acteonoidea: (**a**) *Pupa tessellata* (MCZ:Mala:393822), dorsal and ventral view; Pleurobranchida: (**b**) *Berthellina delicata* (MCZ:Mala:393775); (**c**) *Berthella martensi* (MCZ:Mala:393762); Aplysiida: (**d**) *Dolabella auricularia* (MCZ:Mala:393823); (**e**) *Dolabrifera dolabrifera* (MCZ:Mala:393776), two color morphotypes; (**f**) *Stylocheilus striatus* (MCZ:Mala:393764). Photos by T. J. Cunha.

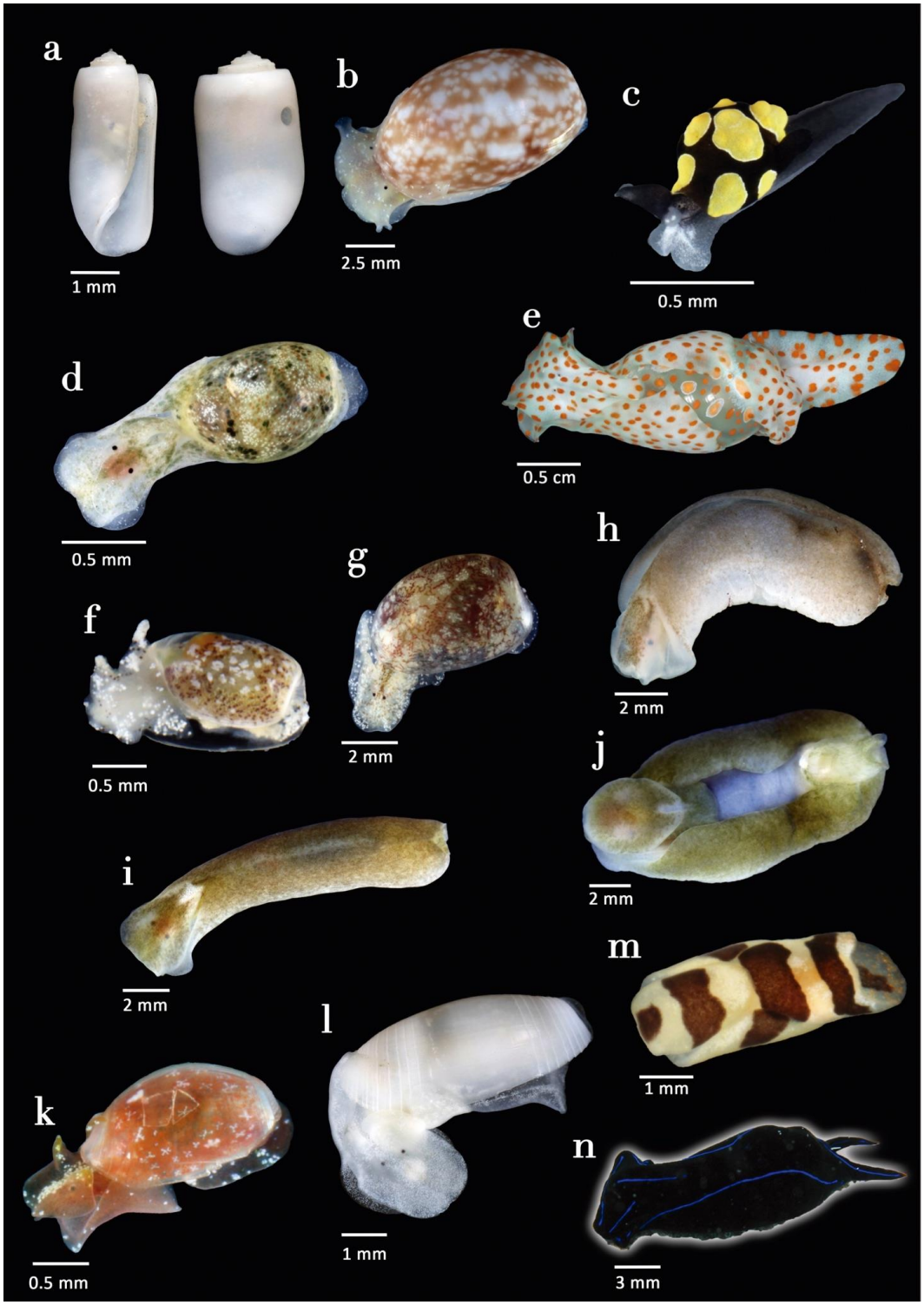

Figure 4. Cephalaspidea: (**a**) *Acteocina* sp. (MCZ:Mala:393847), dorsal and ventral view; (**b**) *Bulla vernicosa* (MCZ:Mala:393799); (**c**) *Colpodaspis thompsoni* (MCZ:Mala:393765); (**d**) *Haloa aptei* (MCZ:Mala:393843); (**e**) *Lamprohaminoea cymbalum* (MCZ:Mala:393734); (**f**) 'Long tail haminoid' (MCZ:Mala:393732); (**g**) 'Mini haminoid' (MCZ:Mala:393728); (**h**) *Phanerophthalmus batangas* (MCZ:Mala:393707); (**i**) *Phanerophthalmus* cf. *cylindricus* (MCZ:Mala:393777); (**j**) *Phanerophthalmus minikoiensis* (MCZ:Mala:393706); (**k**) *Vellicolla muscaria* (MCZ:Mala:393871); (**l**) *Aliculastrum debile* (MCZ:Mala:393820); (**m**) *Philine orca* (MCZ:Mala:393750); (**n**) *Chelidonura varians*. Photos by T. J. Cunha; image of (**n**) courtesy of Davide Seveso.

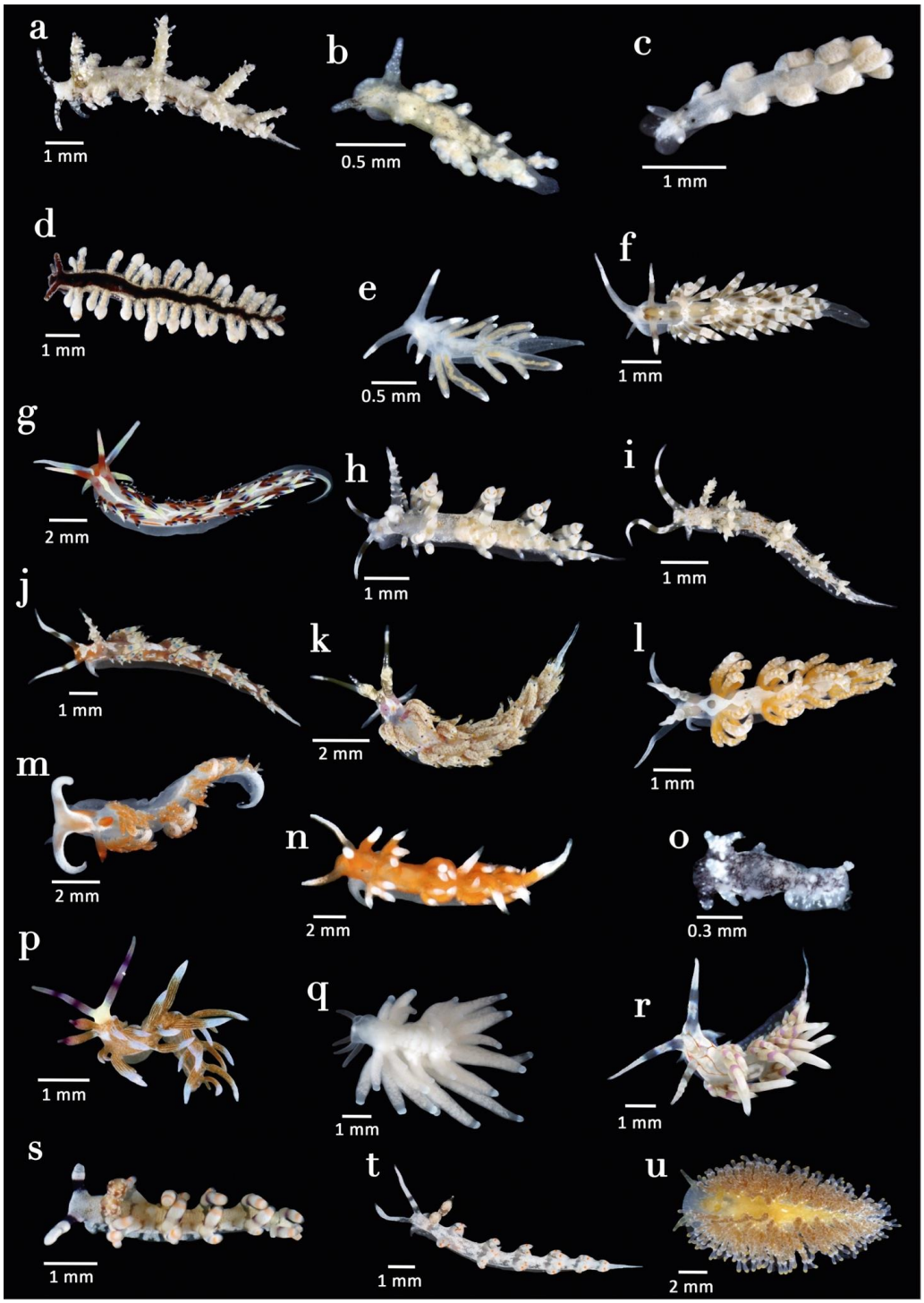

Figure 5. Nudibranchia, Cladobranchia: (**a**) *Limenandra evanescenti* n. sp. (MCZ:Mala:393766); (**b**) *Doto* sp. (MCZ:Mala:393816); (**c**) *Embletonia gracilis* (MCZ:Mala:393844); (**d**) *Eubranchus putnami* n. sp. (MCZ:Mala:393748); (**e**) *Eubranchus* sp. (MCZ:Mala:393798); (**f**) *Herviella albida* (MCZ:Mala:393849); (**g**) *Caloria indica* (MCZ:Mala:393881); (**h**) *Cratena* sp. A (MCZ:Mala:393850); (**i**) *Cratena* sp. 5 (MCZ:Mala:393846); (**j**) *Cratena* sp. B (MCZ:Mala:393872); (**k**) *Favorinus mirabilis* (MCZ:Mala:393795); (**l**) *Favorinus japonicus* (MCZ:Mala:393840); (**m**) *Moridilla maldivensis* n. sp. (MCZ:Mala:393739); (**n**) *Sakuraeolis marhe* n. sp. (MCZ:Mala:393879); (**o**) *Noumeaella* sp. (MCZ:Mala:393817); (**p**) *Pteraeolidia* aff. *semperi* (MCZ:Mala:393738); (**q**) *Tergiposacca perspicua* n. sp. (MCZ:Mala:393841), ventral view; (**r**) *Godiva* sp. (MCZ:Mala:393845); (**s**) *Samla riwo* (MCZ:Mala:393744); (**t**) *Samla bicolor* (MCZ:Mala:393873); (**u**) *Phestilla lugubris* (MCZ:Mala:393735). Photos by T. J. Cunha.

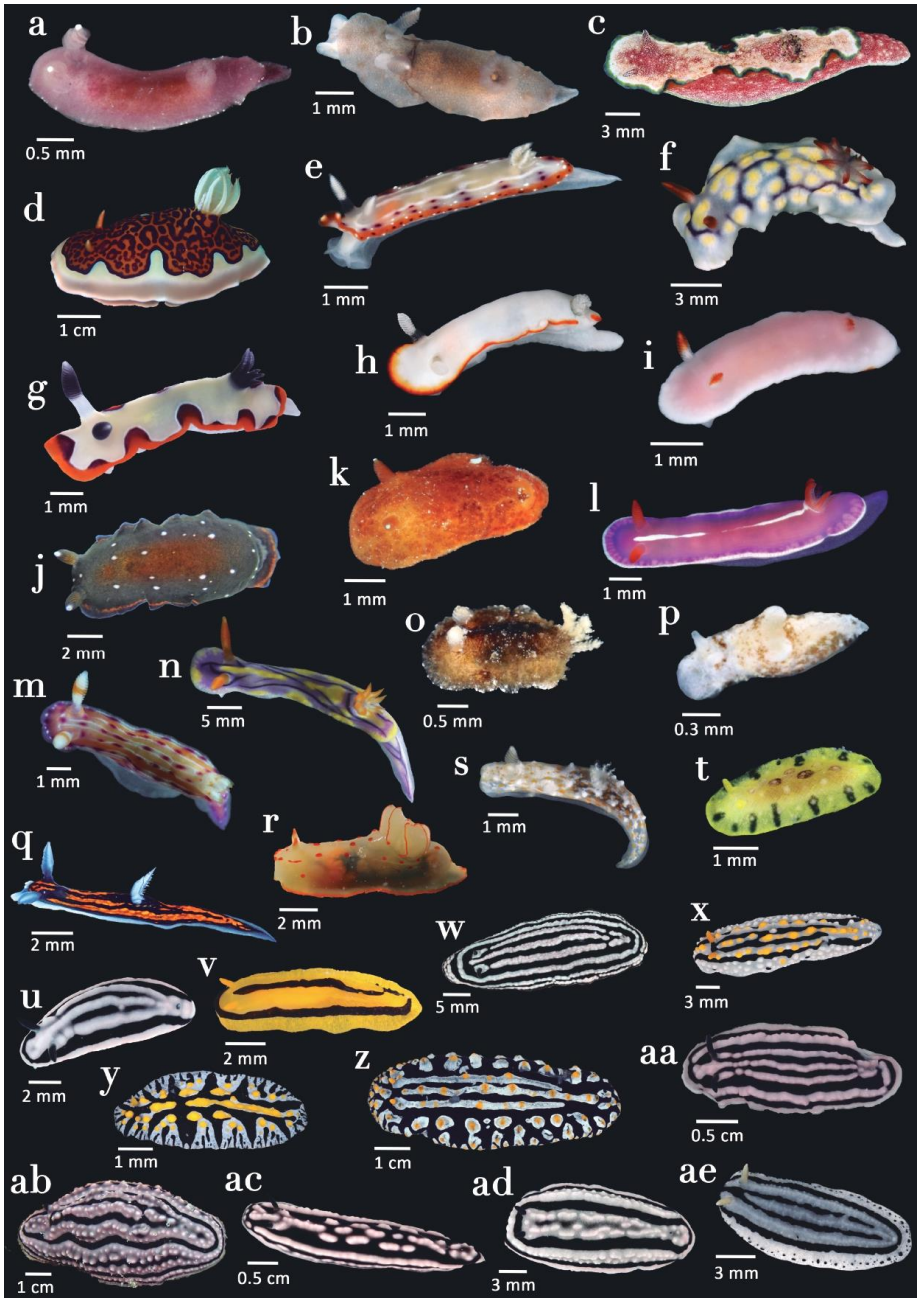

Figure 6. Nudibranchia, Doridina: (**a**) *Hallaxa indecora* (MCZ:Mala:393835); (**b**) *Hallaxa fuscescens* (MCZ:Mala:393778); (**c**) *Glossodoris acosti* (MCZ:Mala:393870); (**d**) *Goniobranchus glenei*; (**e**) *Goniobranchus setoensis* (MCZ:Mala:393833); (**f**) *Goniobranchus conchyliatus* (MCZ:Mala:393705); (**g**) *Goniobranchus fidelis* (MCZ:Mala:393721); (**h**) *Goniobranchus albonares* (MCZ:Mala:393832); (**i**) *Verconia simplex* (MCZ:Mala:393831); (**j**) *Dendrodoris nigra* (MCZ:Mala:393710); (**k**) *Rostanga* sp. 2 (MCZ:Mala:393742); (**l**) *Mexichromis similaris* (MCZ:Mala:393877); (**m**) *Hypselodoris maculosa* (MCZ:Mala:393783); (**n**) *Hypselodoris nigrostriata*; (**o**) *Thordisa* cf. *oliva* (MCZ:Mala:393780); (**p**) *Goniodoridella* sp. (MCZ:Mala:393815); (**q**) *Roboastra gracilis* (MCZ:Mala:393829); (**r**) *Gymnodoris ceylonica*; (**s**) *Gymnodoris* sp. (MCZ:Mala:393743); (**t**) *Phyllidia* sp. (MCZ:Mala:393878); (**u**) *Phyllidiella* sp. (MCZ:Mala:393785); (**v**) *Phyllidia koehleri* (MCZ:Mala:393746); (**w**) *Phyllidia rosans* (MCZ:Mala:393796); (**x**) *Phyllidia alyta* (MCZ:Mala:393788); (**y**) *Phyllidia picta* (MCZ:Mala:393774); (**z**) *Phyllidia varicosa* (MCZ:Mala:393757); (**aa**) *Phyllidiella* sp. 1 (MCZ:Mala:393736); (**ab**) *Phyllidiella zeylanica*; (**ac**) *Phyllidiella striata* (MCZ:Mala:393808); (**ad**) *Phyllidiopsis* sp. (MCZ:Mala:393747); (**ae**) *Phyllidiopsis xishaensis* (MCZ:Mala:393740). Photos by T. J. Cunha; images of (**d**,**r**,**ab**) courtesy of Davide Seveso; images of (**j**,**m**,**n**) courtesy of Davide Maggioni.

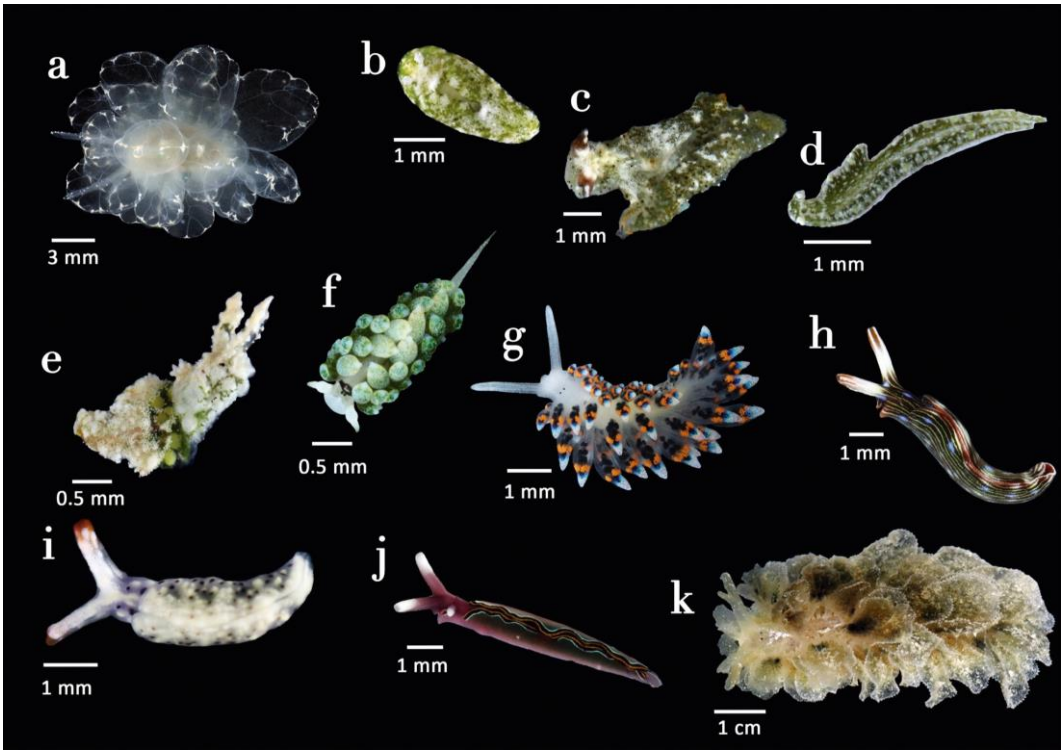

Figure 7. Sacoglossa: (**a**) *Cyerce elegans* (MCZ:Mala:393754); (**b**) *Elysia pusilla* (MCZ:Mala:393737); (**c**) *Elysia* cf. *marginata* (MCZ:Mala:393708); (**d**) *Elysia* sp. 11 (MCZ:Mala:393722); (**e**) *Elysia* sp. 44 (MCZ:Mala:393711); (**f**) *Costasiella fridae* n. sp. (MCZ:Mala:393874); (**g**) *Stiliger* sp. 1 (MCZ:Mala:393830); (**h**) *Thuridilla* sp. 6 (*T. gracilis* species-complex) (MCZ:Mala:393741); (**i**) *Thuridilla vataae* (MCZ:Mala:393868); (**j**) *Thuridilla livida* (MCZ:Mala:393767); (**k**) *Polybranchia jensenae* (MCZ:Mala:393800). Photos by T. J. Cunha.

For vetigastropods, seven of the 19 collected species (37%) are new records for the Maldives, resulting in a list of 60 vetigastropod species now known from the archipelago (Table 1, Figure 8). One additional species of *Trochus* could not be confidently identified to species (Figure 8j), and possibly represents one of the species already recorded in the literature. New records represent 17% of the previously known diversity for the group, and at least two of these species are likely new to science (*Emarginella* sp. 1 [Figure 8d] and *Stomatolina* sp. 1 [Figure 8k]). All but two vetigastropod species were successfully barcoded, with most having relatively distant matches in GenBank (Figure 2D; 88.6% average identity to the best match, range 80.9–97.4%).

The gastropod subclass Neritimorpha was not targeted in this study, but one uncommon limpet-like species (*Zacalantica tenuisculpta*) was collected. It is included here to make this new occurrence for the Maldives available in the scientific literature, together with photos of the live specimen and barcoding data (Table 1, Figure 8o).

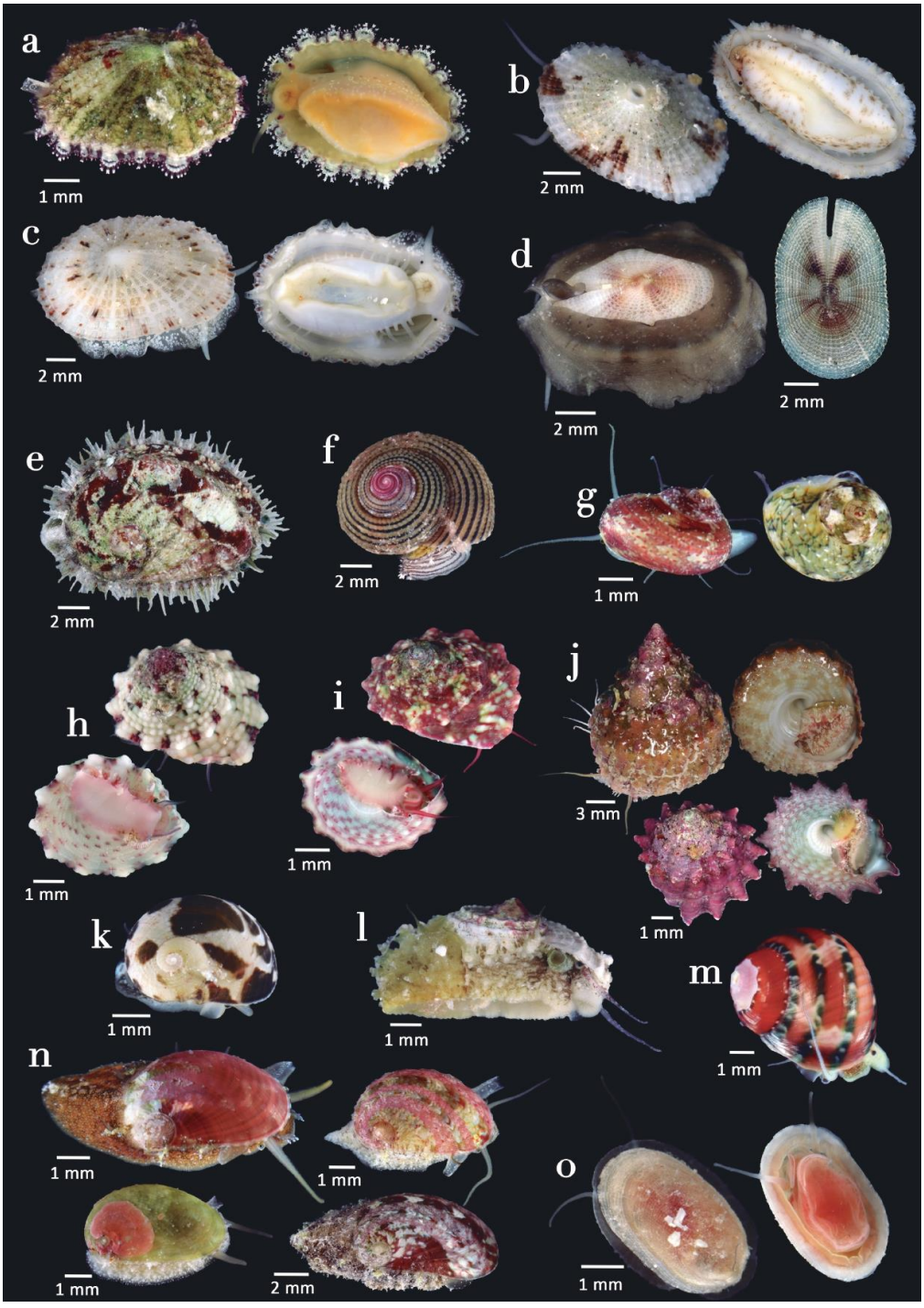

Figure 8. Vetigastropoda: (**a**) *Hemimarginula* cf. *biangulata* (dorsal: MCZ:Mala:393769, ventral: MCZ:Mala:393856); (**b**) *Diodora singaporensis* (MCZ:Mala:393718); (**c**) *Emarginella nigromaculata* (MCZ:Mala:393851); (**d**) *Emarginella* sp. 1 (live: MCZ:Mala:393792, shell: MCZ:Mala:393791); (**e**) *Haliotis ovina* (MCZ:Mala:393717); (**f**) *Clanculus samoensis* (MCZ:Mala:393713); (**g**) *Calliotrochus marmoreus*, with color variation (left: MCZ:Mala:393753, right: MCZ:Mala:393857); (**h**) juvenile of *Trochus maculatus* (MCZ:Mala:393804); (**i**) juvenile of *Trochus* cf. *stellatus* (MCZ:Mala:393864); (**j**) *Trochus* sp. 1 (adult: MCZ:Mala:393790, juvenile: MCZ:Mala:393863); (**k**) *Stomatolina* sp. 1 (MCZ:Mala:393763); (**l**) *Stomatolina rubra* (MCZ:Mala:393860); (**m**) juvenile of *Turbo petholatus* (MCZ:Mala:393786); (**n**) *Stomatella varia*, with color variation (top-left: MCZ:Mala:393752, top-right: MCZ:Mala:393811, bottom-left: MCZ:Mala:393797, bottom-right: MCZ:Mala:393859). Neritimorpha: (**o**) *Zacalantica tenuisculpta* (MCZ:Mala:393858). Photos by T. J. Cunha.

Systematics

Class Gastropoda Cuvier, 1795

Subclass Heterobranchia Burmeister, 1837

Order Nudibranchia Cuvier, 1817

Family Aeolidiidae Gray, 1827

Genus *Limenandra* Haefelfinger & Stamm, 1958

***Limenandra evanescenti* n. sp. Fernández-Simón & Moles, 2023** (Figure 5a)

ZooBank registration. urn:lsid:zoobank.org:act:48AAD3AC-062C-41AF-98CE-0C238-789E0D0

Holotype. MCZ:Mala:393766 (1 spm: 95% ethanol). Magoodhoo, Faafu, Maldives (3°04′45.3″ N 72°58′05.0″ E), 1 m depth. Collected by snorkeling at night on 5 April 2019 by J. Moles. GenBank (COI: OQ207002). Singleton, 6.5 mm in length.

MCZ link. mczbase.mcz.harvard.edu/guid/MCZ:Mala:393766

Etymology. The species name refers to the vanishing appearance of the dorsal pigmented rings, typical of the species of the genus.

Diagnosis. Body elongate, slender, dirty white; vanished pink circles on head, after first and third ceratal clusters, surrounded by yellow dots; yellow dots also seen in between other ceratal clusters; laterals transparent with white blotches and brown zooxanthellae punctuation, as for oral and propodial tentacles. Rhinophores papillate; tip white; periocular area under rhinophores depigmented. Cerata papillate, cylindrical, white-tipped, directed posteriorly, arranged in 7 rows; innermost longer, up to 1.3 mm in length; outermost slightly curved.

Distribution. Only known from the type locality in the Maldives.

Ecology. Found under coral rubble.

Remarks. The overall morphology and coloration of *L. evanescenti* n. sp. are similar to the type species *L. nodosa* Haefelfinger & Stamm, 1958, found in the Mediterranean and Atlantic Ocean, and to *L. confusa* Carmona, Pola, Gosliner & Cervera, 2014 from the Pacific Ocean [54]. However, the new species presents an opaque white coloration, and the typical pink and yellow dorsal rings appear diffuse and fragmented. Molecular data of all accepted species of *Limenandra* are available and included in our phylogenetic analysis (Figure S2), where *L. evanescenti* n. sp. was found to be an independent lineage and its own taxonomic unit according to the species delimitation tests.

Family Eubranchidae Odhner, 1934

Genus *Eubranchus* Forbes, 1838

***Eubranchus putnami* n. sp. Fernández-Simón & Moles, 2023** (Figure 5d)

Eubranchus sp. 1, Debelius & Kuiter 2007 [55]: 346.

Eubranchus sp. 26, Gosliner et al. 2018 [23]: 281.

Eubranchus sp. (brown *Eubranchus*), Ryanskiy & Ivanov 2019 [56]: 87.

ZooBank registration. urn:lsid:zoobank.org:act:3FC8F783-2632-450A-A78B-983261B-4F7E7

Material examined. *Holotype* MCZ:Mala:393748 (1 spm: 95% ethanol). Free-Climbing, Dharanboodhoo, Faafu, Maldives (3°03′53.9″ N 72°55′16.5″ E), 7 m depth. Collected using scuba on 4 April 2019 by J. Moles. GenBank (COI: OQ206999). Singleton, 7 mm in length.

MCZ link. mczbase.mcz.harvard.edu/guid/MCZ:Mala:393748

Etymology. This species is dedicated to George Putnam Jr. (1926–2019), a longtime supporter of the MCZ and founding donor of the Putnam Expeditionary Grant program that allowed this research.

Diagnosis. Body elongated, dark-brown. Head, rhinophores, dorsum, and laterals dark-brown; with two translucent bands on the upper laterals running from head (just below rhinophores) toward tail; digestive gland beige-whitish in color, seen by transparency. Rhinophores dark-brown, with white punctuation interspersed on the tips. Oral tentacles transparent. Cerata up to 1 mm in length, club-like, lateralized, up to 17 per side; transparent, digestive gland seen through, two crowns of white punctuation at base, tip swollen, milky white with subterminal orange ring.

Distribution. Indian (this study) and the Western Pacific Ocean [23].

Ecology. Found crawling on a plumularid hydroid, where it feeds upon.

Remarks. The morphology of *E. putnami* n. sp. is extremely characteristic with an elongated dark body and lateralized cerata, thus, resembling the hydroid colony it feeds on. To the best of our knowledge, no other species of *Eubranchus* has ever been described with this morphology. Somehow similar-looking morphotypes have been reported [23,55,56], and a molecular study of those throughout the distribution is required to further ascertain their status. A recent revision of *Eubranchus* found the genus divided into two clades [57], one formed by species recently emerged as *Amphorina* species, a genus containing species from the North Hemisphere. In our phylogenetic analysis, *E. putnami* n. sp. is almost the only tropical species and does not cluster with any sequenced species (Figure S3).

Family Facelinidae Bergh, 1889

Genus *Sakuraeolis* Baba, 1965

***Sakuraeolis marhe* n. sp. Fernández-Simón & Moles, 2023** (Figure 5n)

Facelina sp. 8, Gosliner et al. 2018 [23]: 303; Anderson 2018 [34]: 93.

ZooBank registration. urn:lsid:zoobank.org:act:4F708053-3E0E-4E4C-B8A0-4FA93FC-B0B69

Material examined. *Holotype* MCZ:Mala:393879 (1 spm: 95% ethanol). Sunny Reef, Faafu, Maldives (3°08′34.6″ N 73°00′43.4″ E), 20 m depth. Collected using scuba on 12 April 2019 by J. Moles. GenBank (COI: OQ207003). *Paratypes* as holotype. Specimens up to 4 mm in length.

MCZ link. mczbase.mcz.harvard.edu/guid/MCZ:Mala:393879

Etymology. This species is named in apposition after the MaRHE Center and staff, for the logistics and their help assisting in the field.

Diagnosis. Body bright orange, or slightly paler; tail milky white. Upper half of oral tentacles and upper third of rhinophores and cerata milky white, opaque, or slightly translucent. Rhinophores and oral tentacles conical, smooth. Cerata in four horseshoe-shaped clusters, first one in front of pericardium, slightly separated from the rest; four per cluster side, innermost longer, with upper third white; sometimes elongated cnidosacs seen by transparency. Propodial tentacles conical, tentaculiform, directed posteriorly.

Distribution. Only known from the Maldives (this study) and the Philippines [23].

Ecology. The three specimens were found on top of an encrusting bryozoan in symbiosis with hydroids where it feeds.

Remarks. *Sakuraeolis marhe* n. sp. looks like *Facelina* sp. 8 [23], but our external morphological examination and molecular data suggest a relationship to *Sakuraeolis* (Figure S4). Diagnostic characters of the genus are present in our specimens, such as smooth rhinophores and horseshoe-shaped ceratal clusters [58]. Genetically, *S. marhe* n. sp. clustered with unidentified facelinids and *S. arcana* Ellis-Diamond, Picton, Tibiriçá & Sigwart, 2021, *S. enosimensis* (Baba, 1930), and *S. japonica* (Baba, 1937). These unidentified specimens encompass a '*Facelina* sp. 8', two *Favorinus* sp. specimens likely belonging to another genus [59], and two *Caloria* sp. specimens with the typical orange coloration to its sister species, *S. arcana* [60]. Therefore, we believe these to be unidentified species belonging to *Sakuraeolis*, none of them being molecularly identical to *S. marhe* n. sp. according to the species delimitation tests (Figure S4). Chromatically, the most similar species of the genus is *S. arcana*, with a bright orange body and opaque white cerata, rhinophores, and oral tentacles. However, *S. marhe* n. sp. differs from *S. arcana* by having smooth rhinophores, shorter white coloration on the tip of the body appendages, and lacking a white stripe on the head.

Genus *Moridilla* Bergh, 1888

***Moridilla maldivensis* n. sp. Fernández-Simón & Moles, 2023** (Figure 5m)

Moridilla sp., Anderson 2018 [34]: 98.

ZooBank registration. urn:lsid:zoobank.org:act:C1B3DA53-526B-42C6-8E11-59EBCB-262542

Holotype. MCZ:Mala:393739 (1 spm: 95% ethanol). Dharanboodhoo, Faafu, Maldives (3°03′30.5″ N 72°55′29.6″ E), 20 m depth. Collected using scuba on 4 April 2019 by T. J. Cunha. GenBank (COI: OQ207008). Singleton, 12 mm in length.

MCZ link. mczbase.mcz.harvard.edu/guid/MCZ:Mala:393739

Etymology. The species name derives from the type locality, so far, the only known distribution of the new species.

Diagnosis. Body elongated, slender; translucent gray, with lateral white bands on each ceratal cluster and dorsally on tail; tail pointy. Head coloration with a triangular pale orange marking frontally; oral tentacle coloration distally milky white, running laterally, converging behind rhinophores; bright orange band at each side. Rhinophores smooth anteriorly, papillate posteriorly; apically bright orange, stalk transparent. Foot slender, translucent; propodial tentacles triangular, pointy. Cerata arranged in seven clusters, progressively decreasing posteriorly; coloration pale orange with white punctuation, white subterminal tips; innermost longer, curled, upper half milky white.

Distribution. Only known from the type locality in the Maldives.

Ecology. Found under coral rubble, with nocturnal habits [34].

Remarks. Overall, *Moridilla* species are very similar looking, yet a distinctive head coloration in *M. maldivensis* n. sp. helps distinguish it from all described species so far [61,62]. Similar coloration is found on *M. jobeli* Schillo & Wägele, 2019, though this one presents the tip of the oral tentacles in orange (COI similarity up to 83.7%). *Moridilla maldivensis* n. sp. has also white lateral bands under each ceratal botch as a diagnostic feature. Molecular data of all accepted species of *Moridilla* plus an undescribed one is available and included in our phylogenetic analysis (Figure S5), where *M. maldivensis* n. sp. was found to be an independent lineage according to both the phylogeny and the species delimitation tests.

Family Fionidae Gray, 1857

Genus *Tergiposacca* Cella, Carmona, Ekimova, Chichvarkhin, Schepetov & Gosliner, 2016

***Tergiposacca perspicua* n. sp. Fernández-Simón & Moles, 2023** (Figure 5q)

Tergiposacca longicerata Cella, Carmona, Ekimova, Chichvarkhin, Schepetov & Gosliner, 2016 [63]: 22, Figure 5C.

ZooBank registration. urn:lsid:zoobank.org:act:59BFDE70-D9E6-4722-BE96-CB1D4C-EBC9AA

Holotype. MCZ:Mala:393841 (1 spm: 95% ethanol). Pier, Magoodhoo, Faafu, Maldives (3°04′53.2″ N 72°57′55.1″ E), 1 m depth. Collected by snorkeling on 11 April 2019 by J. Moles. GenBank (COI: OQ207000). Singleton, 7 mm in length.

MCZ link. mczbase.mcz.harvard.edu/guid/MCZ:Mala:393841

Etymology. The specific epithet, *perspicua*, the feminine of *perspicuus*, is the Latin word for translucent because of the overall absence of body coloration.

Diagnosis. Body translucent, white viscera seen by transparency. Rhinophores and oral tentacles conical, smooth, transparent. Jaws white, seen by transparency. Cerata elongated, cylindrical, isodiametric; digestive gland granulose, beige, seen by transparency; subterminal ring transparent, terminal tips white. Propodium rounded.

Distribution. The Maldives (this study), the Philippines [63], Marshall Islands, and New Caledonia [64].

Ecology. Found under a rock.

Remarks. The only known species from the genus, *T. longicerata* Cella, Carmona, Ekimova, Chichvarkhin, Schepetov & Gosliner, 2016, was described based on several specimens from the Philippines with three different color morphotypes (see Figure 5 in Cella et al. [63]). However, only the specimen CASIZ177605, with orange pigmentation, was sequenced therein. This one showed a genetic divergence with *T. perspicua* n. sp. of 80%, rendering ours a new species. A burgundy color morphotype of *T. longicerata* was also found in the Maldives [34]. A broader molecular and systematic reevaluation of the latter and the brownish morphotypes found all over the Western Pacific [23,56] is needed to further ascertain the taxonomic status of all different color morphotypes. Nevertheless,

T. perspicua n. sp. differs from the type species in the translucid whitish coloration that inspired its name.

Superorder Sacoglossa von Ihering, 1876
Family Costasiellidae K. B. Clark, 1984
Genus *Costasiella* Pruvot-Fol, 1951
***Costasiella fridae* n. sp. Fernández-Simón & Moles, 2023** (Figure 7f)
Costasiella sp. 1, Gosliner et al. 2018 [23]: 412.
Costasiella sp., Ryanskiy & Ivanov 2019 [56]: 130.

ZooBank registration. urn:lsid:zoobank.org:act:22BACF60-8C18-449F-A7AE-DE37C-6352414

Examined material. *Holotype* MCZ:Mala:393874 (1 spm: 95% ethanol). Beyrufushi, Faafu, Maldives (3°06′46.1″ N 73°01′15.9″ E), 6 m depth. Collected using scuba on 11 April 2019 by J. Moles. GenBank (COI: OQ206988). *Paratype* as holotype. Specimens, 3 mm in length.

MCZ link. mczbase.mcz.harvard.edu/guid/MCZ:Mala:393874

Etymology. This species is named in honor of the Mexican artist Frida Kahlo for the resemblance of her iconic eyebrows to the distinct black, oval band behind the eyes of *C. fridae* n. sp.

Diagnosis. Body 3 mm in length; translucent white dorsum; snout milky white, converging into the middle of eyes; distinctive oval, black band behind eyes and rhinophores. Rhinophores cylindrical, bulbous when disturbed; upper two-thirds opaque white. Cerata moss green, innermost whiter; containing white, blue, and yellow iridescent dots, particularly on larger cerata; ceratal tips whitish.

Distribution. Tropical Indo-Pacific, cited in South Africa, the Maldives, Indonesia, Japan, Guam, and Hawaii [65].

Ecology. Two specimens found laying eggs on the green alga *Avrainvillea* sp.

Remarks. Specimens with similar coloration have been found all over the Indo-Pacific. The distinctive black, oval band behind the eyes is a diagnostic character of *C. fridae* n. sp., as is the white blotch in the snout area. Similar-looking specimens from Japanese waters have been identified as *C. iridophora* Ichikawa, 1993. Nevertheless, the overall head coloration of *C. fridae* n. sp. differs from Ichikawa's [66] description as it lacks a pigmented area around the eyes and possesses a diagnostic black band. In our phylogeny, *C. fridae* n. sp. does not cluster with any sequenced species (Figure S6). Eight of the 17 currently accepted species and nine additional undescribed ones were recently sequenced and included in our phylogeny [67,68]. From those, *C. fridae* n. sp. is externally more similar to *Costasiella* sp. 2, cf. *kuroshimae* (Figure 8 in Jensen et al. [67]) and *Costasiella* sp. 1 (Figure 1E in Christa et al. [68]), although genetically they present great divergence (COI similarity up to 79%).

4. Discussion

Half of our collected heterobranch and vetigastropod species comprise new records for the Maldives (53 out of 104), highlighting how much diversity remains to be discovered in future surveys. This is further evidenced by the fact that the sampling campaign was limited to under two weeks of hand-picking live specimens by two people in a relatively small geographic area (mostly islands on the south of the Faafu Atoll). In an enormous effort to estimate the magnitude of mollusk richness in tropical marine environments, Bouchet et al. [69] encountered high spatial and habitat heterogeneity in New Caledonia, with about a third of species being collected in a single site. Despite the much lower sampling effort in the Maldives, we found that over half of our species were collected in only one site (Figure 2A), similar to a macroinvertebrate survey of the Baa Atoll [14], indicating that further work on the more than one thousand islands of the archipelago is expected to uncover increasing diversity levels. The final checklist (Table 1), which also includes all records we encountered in the literature for the Maldives, sums up to 320 species of the two gastropod subclasses, Heterobranchia (259) and Vetigastropoda (61),

with our new records representing an increase of about 25% on the number of species known for the archipelago.

Notably, a high proportion of species (64%) in the checklist has only ever been found by a single source in the literature (Figure 2C, Table 1), which also reveals that several species recorded by previous authors were not found during our fieldwork. There are likely multiple reasons for that. Independent surveys in the Maldives show that a high proportion of taxa are collected in a single site and in low abundance, indicating ecological rarity (Figure 2A,B) [11,12,14]. This relates to the seasonality and habitat preferences of many species, resulting in the spatial heterogeneity found throughout marine environments [69]. Another related factor is the sampling methodology: besides time spent in the field and geographical breadth, most reported species in past mollusk surveys in the Maldives were only found as empty shells (e.g., [11,15]). Here we hand-picked live specimens during snorkeling and scuba diving to photograph live animals and obtain sequence data. More comprehensive sampling strategies, such as dredging, would likely produce a list with more overlap with previous studies (as discussed in Robertson [13]). Finally, habitat loss and climate change could also have had an important role in the turnover of species since past expeditions, such as the major event of coral mortality that heavily affected the Maldives in 1998 [5,70].

Yonow [21] stressed the significance of making new records of rare taxa available in the scientific literature, exemplifying with one sample of a sacoglossan from the Maldives [22], which turned out to be the only record for the entire Indian Ocean when the species was described a year later as having an Indo-West Pacific distribution [71]. Baseline biodiversity data, together with monitoring through time, are key resources for broader ecological and evolutionary studies, including evaluating the impact of environmental change. This is especially relevant in a place like the Maldives, where most islands are less than one meter above sea level and threatened by sea-level rise [4,72], which could hamper future studies in these habitats.

We note that a small part of the incongruence between literature records in our checklist could represent incorrect taxonomic identifications and, therefore, spurious occurrence data. We aimed to be as thorough as possible in the literature search so that our checklist reflects all heterobranchs and vetigastropods that, to our knowledge, have been recorded for the Maldives. However, many of these taxa lack systematic revisions and specialized resources for identification, which can potentially lead to the same species being identified with different names by different studies. Some examples are discussed in the sections below.

4.1. Heterobranchia in the Maldives: How Much Is to Be Learned?

Seven of the 14 known orders of heterobranchs inhabiting the Maldives waters were collected (Table 1). A single representative of the order Acteonimorpha was found and attributed to the species *Pupa tessellata* for its shell similarity. Regarding the order Pleurobranchida, *Berthella martensi* was already reported in the Maldives, yet DNA barcodes showed low similarity with other specimens of the same species, indicating that we may be dealing with a species complex (J. Moles unpubl. data). Our specimen of *B. martensi* likely fits with the original description (type locality: Mauritius [73]); thus, the other sequenced specimens should be reevaluated morphologically. Even though *Berthellina citrina* was previously recorded (e.g., [34]), our molecular evidence suggests this being *B. delicata*, which is, in turn, another complex of species to be further evaluated. Three species of the order Aplysiida were collected and barcoded, *Dolabella auricularia*, *Dolabrifera dolabrifera*, and *Stylocheilus striatus*. The latter two are the type species of genera recently found to contain species complexes with a wide distribution in the tropical Indo-Pacific [74,75].

Cephalaspidea is one of the major lineages of marine heterobranchs that reaches its highest diversity in tropical and subtropical waters of the Indo-Pacific [76]. To date, 26 species have been previously reported in the Maldives (Table 1), 10 being our new records. Within Haminoeidae, *Phanerophthalmus batangas* is reported here for the first time outside the Philippines [3] and in the Indian Ocean. Although *P. olivaceus* was previ-

ously recorded for the Maldives [19], we believe that specimen was likely a misidentified *P. minikoiensis*, a species also collected by us, given its color, jaws, and radular similarity. A likely third species, *P.* cf. *cylindricus* was identified here based on morphological data alone. *Aliculastrum debile*, *Haloa aptei*, and the two undescribed species of "mini and long-tail" haminoids in Oskars et al. [77] are also recorded in the region for the first time in this study. Additional new records for the Maldives include *Acteocina* sp. and *Bulla vernicosa*. Within the last genus, *B. ampulla* was already known to inhabit the Maldives [78] (Table 1), and here, *B. vernicosa* is reported for the region for the first time. Finally, in two cases, barcodes did not work to identify species, i.e., *Colpodaspis thompsoni* and *Philine orca*. Although sequences of both species were already available, barcodes were inconclusive in determining their identity (up to 91% of genetic divergence), which may indicate that we are dealing with species complexes that will require additional sampling.

Nudibranchs are one of the most diverse orders of heterobranchs, including Cladobranchia, with more than a thousand species [79]. A total of 35 species were previously reported for the Maldives, now supplemented with the 15 reported here for the first time, including the five new species described. Our barcodes demonstrated the existence of species complexes in some genera, hampering species identification. This is the case of *Cratena* [80], with 11 recognized species [18] but with many morphotypes to be described [23]. Here, three species of the genus were found, and only *Cratena* sp. 5 (*sensu* Gosliner et al. [23]) could be recognized and reported as widespread in the Indo-Pacific. Based on barcoding data, both our *Cratena* sp. 5 and *Cratena* sp. A were recovered in distant phylogenetic positions regarding the type species *C. peregrina* (Gmelin, 1791) and other represented species (Figure S4). Likewise, *Eubranchus* is a diverse genus with 46 species [18] and several more awaiting formal description [23]. However, the two undescribed species reported here become the first genus records for the Maldives. The only species successfully barcoded is described as *E. putnami* n. sp. (*Eubranchus* sp. 26 in Gosliner et al. [23]) based on its unique morphology and molecular identity. In addition, *Sakuraeolis marhe* n. sp. (*Facelina* sp. 8 in Gosliner et al. [23]) is described here based on its distinctive body coloration and reported for the first time outside the Philippines. Furthermore, the new species *Limenandra evanescenti* n. sp. is the first representative of the genus found in the Maldives, with a COI divergence of 83.7% from all other described species to date [54]. Moreover, *Tergiposacca perspicua* n. sp. is described here as the second recognized species of the genus. This species was thought to be a color morphotype of *T. longicerata* [63], meaning additional molecular data could still reveal new species within the different color variations. Finally, the new species *Moridilla maldivensis* n. sp. becomes the second species of the genus reported for the Maldives, after *M. brockii* Bergh, 1888 [34]. All the previous species of the genus have been sequenced [61,62], and ours was recovered as genetically distinct (it was also different morphologically). In addition, we provide a glimpse of other possible cryptic species, such as *Godiva* sp. 1, reported for the Maldives for the first time, and *Pteraeolidia* aff. *semperi*, genetically dissimilar to any other species known and sequenced [81]. In addition, *Phestilla lugubris*, a *Porites* coral-feeding species, became the second reported species of the genus for the Maldives after *P. melanobrachia*. Lastly, non-aeolid cladobranchs such as *Doto* and *Embletonia* were first reported for the region, but only *E. gracilis* could be identified at the species level.

The barcodes of Doridina were better matching with existing species. Eleven of them were identified at the species level through BLAST, while 10 had no matches on GenBank. The family Actinocyclidae is reported for the first time in the Maldives, with the species *Hallaxa fuscescens* and *H. indecora*. In addition, the first records for the region were found for the species *Verconia simplex* and for the genus *Goniodoridella* with a likely new species to be described (Paz-Sedano pers. comm.). Two species of the family Discodorididae were also reported and barcoded here for the first time, *Thordisa* cf. *oliva* and *Rostanga* sp. 2 (*sensu* Gosliner et al. [23]). Regarding Chromodorididae, we collected five species of *Goniobranchus*. *G. albonares* was first reported and, together with *G. setoensis*, was barcoded for the first time. In addition, representatives of two species of *Gymnodoris*

were found, a genus where still dozens of species await formal description [82], including our undescribed species. Despite being very abundant in Indo-Pacific reefs, Phyllidiidae taxonomy remains problematic because of its conservative morphology and color patterns, with several cases of cryptic speciation [83]. Here we found nine species belonging to *Phyllidia*, *Phyllidiella*, and *Phyllidiopsis*, with one unidentified species per genus. We provide molecular data for the endemic *Phyllidia koehleri* and evidence that *Phyllidiella rosans*, with different morphotypes across the Pacific [55], may also represent a species complex. Overall, despite their conspicuous abundance, several geographical and chromatic morphotypes of Phyllidiidae need to be sequenced to better comprehend their diversity [21].

Regarding Sacoglossa, the most species-rich genus *Elysia* (Plakobranchidae) currently contains more than 100 recognized species [18]. Thus, it is assumed that many of the species are poorly known or have complex taxonomic histories [84]. Here, five species were reported, and four of them were barcoded, although only two could be attributed to the non-described species *Elysia* sp. 6 (*sensu* Gosliner et al. [23]) and *E.* cf. *marginata* sp. 2 (*sensu* Krug et al. [84]), the latter recently unraveled from the species complex belonging to *E. ornata* [85]. *Elysia* sp. 44 (*sensu* Gosliner et al. [23]) and *E. pusilla* were identified by external morphology and both seem to have been sequenced here for the first time. The latter is almost 92% identical to *E. pusilla* Guam_19 from Vendetti et al. [86]; thus, we seem to have found here a new case of cryptic speciation of this sacoglossan species. Still, within Plakobranchidae, three species of *Thuridilla* were attributed to *T. livida, T. vataae,* and *Thuridilla* sp. 6, an undescribed species unraveled from the species complex of *T. gracilis* by Martín-Hervás et al. [87]. *Polybranchia jensenae* and *Cyerce elegans* were recorded for the first time in the Maldives, as well as the new species *Costasiella fridae* n. sp. and *Stiliger* sp. 1 (description in progress).

4.2. The Underestimated Diversity of Vetigastropoda

Trochidae, Fissurellidae, and Turbinidae, some of the most diverse families of vetigastropods in general, were accordingly the most diverse in our collections, as well as in the overall checklist compiled from the literature for the Maldives. At least two of the species collected here are likely new to science, the fissurellid *Emarginella* sp. 1 (Figure 8d) and the trochid *Stomatolina* sp. 1 (Figure 8k), both groups whose known diversity is still largely underestimated [88,89].

While COI barcoding data are often used to identify species of various animals through high-identity BLAST matches in GenBank, our results reveal how vetigastropods are underrepresented in such databases. For example, even the widely distributed and large-bodied *Turbo argyrostomus* was only represented by one specimen with COI data in GenBank so far. Interestingly, this was one of the species with the highest match, with our Maldivian specimens sharing 97% identity to the single public sequence from Japan. Another of the closest matches was for the turbinid *Astralium rhodostomum*, with 95% identity to public data from Thailand. For this species, sequence identity lowered to 88% relative to GenBank specimens identified as *A. rhodostomum* from the Philippines and Papua New Guinea. Matches with such low percent identity were relatively frequent for our vetigastropod species (Figure 2D). This could either indicate that mitochondrial divergence within species might be larger than expected for these groups, or that many of these lineages represent cryptic species that need further molecular investigation from a broader geographic range.

Another interesting case is that of the trochid *Calliotrochus marmoreus* (Figure 8g), for which our specimens shared a high identity of about 97% with specimens from the Red Sea (listed as Gastropoda sp. in GenBank but identified as *C. marmoreus* by us from a photo shared by the authors [90]). Sequence identity with specimens from the Philippines and Hawaii was 84–86%, suggesting that fauna from the Maldives might be more similar to the fauna of the Red Sea than to that of the Pacific. Morphologically recognized as the same species across oceans [31], genomic data could help clarify possible cryptic species and biogeographical patterns of divergence.

Our checklist of vetigastropods from the Maldives also alerts us to possible erroneous taxonomic identifications and, therefore, occurrences. For example, *Clanculus denticulatus* was only listed in the OBIS database, and it is morphologically very similar to *C. samoensis*, recorded by several sources. While we can assign our Maldivian specimens to *C. samoensis* (Figure 8f) based on systematic work for the genus [32], online resources seem to be wrongly attributing photos of *C. samoensis* to *C. denticulatus*, helping to perpetuate erroneous identifications. Similarly, *C. pharaonius* and *C. puniceus* are another pair of morphologically similar species recorded for the Maldives by a single author each [12,38] that could represent specimens of just one of these species.

Another example of possible misidentification is *Trochus flammulatus*, only recorded in the Maldives by one literature source [39], and otherwise only known from islands in the western Indian Ocean such as Aldabra, Mauritius, and Réunion [18]. Kohn [39] explicitly stated that his mollusk fauna was identified based on the collection of one natural history museum and that no further attempt had been made to verify the names used. Given that *Trochus* is a diverse genus often hard to identify at the species level, and that several other morphologically similar species have been recorded for the Maldives multiple times, *T. flammulatus* might represent a misidentification. For our specimens of *Trochus* spp., several of which are juveniles (Figure 8h–j), even COI barcoding helped little in confirming species identity: while sequences allowed to sort samples to different species (Figure S1), the best BLAST matches were in the range of 86–88% to various *Trochus* species represented in GenBank.

The cases discussed above exemplify and reflect the paucity of systematic revisions for diverse vetigastropod groups, the little photographic evidence of live animals, and the lack of synthetic literature for their identification. Some additional groups that we note as in need of revisionary work include the trochid subfamily Stomatellinae and several genera of Fissurellidae, including *Emarginella* spp. All our specimens were photographed alive, almost all were barcoded, and we hope these will be useful resources for future studies in the group.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d15020219/s1, Table S1. Voucher information and GenBank accession codes for collected specimens. Table S2. BLAST results from GenBank: the top 100 hits for each queried specimen. Table S3. BLAST results from GenBank: the best hit for each queried specimen. Figures S1–S6. COI gene tree for all barcoded specimens, and phylogenetic trees and species delimitation tests for the six newly described species [61,67,91–93].

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Data Availability Statement: Voucher information is fully available in MCZbase (https://mczbase.mcz.harvard.edu) and summarized in Table S1. COI sequences can be retrieved from GenBank (accession OQ206908–OQ207015).

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