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Article

Marine Heterobranchia (Gastropoda, Mollusca) in Bunaken National Park, North Sulawesi, Indonesia—A Follow-Up Diversity Study

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Abstract: Bunaken National Park has been surveyed for a fourth time in 14 years, in an attempt to establish the species composition of heterobranch sea slugs in a baseline study for monitoring programs and protection of this special park. These molluscs are potentially good indicators of the health of an ecosystem, as many are species-specific predators on a huge variety of marine benthic and sessile invertebrates from almost every taxonomic group. Additionally, they are known to contain bio-compounds of significance in the pharmaceutical industry. It is therefore of paramount importance not only to document the species composition from a zoogeographic point of view, but to assist in their protection for the future, both in terms of economics and aesthetics. These four surveys have documented more than 200 species, with an approximate 50% of each collection found only on that survey and not re-collected. Many species new to science have also been documented, highlighting the lack of knowledge in this field.

Keywords: biodiversity; Bunaken National Park; Heterobranchia; Indonesia; monitoring; Opisthobranchia; sea slugs; tourism

1. Introduction

Marine biodiversity studies in Indonesia are rare, and mainly documented in the Indonesian language [1]. However, documentation on specific localities, which are threatened by manifold factors, from global climate change down to increased local impact by humans, is rare, despite a strong

need by policy makers. The largest study on Indonesian marine life is the Rumphius Biohistorical Expedition to Ambon in 1990, which has been published as a series of reports on numerous marine taxa in the now-defunct *Zoologische Mededelingen*, e.g., Naturalis Biodiversity Center [2]. Recently, Kaligis et al. [1] published the results of a survey on marine Heterobranchia in Bunaken National Park (BNP) Indonesia performed in 2015. The main aim was to increase knowledge on the biodiversity of a taxon on the second trophic consumer level, thus reflecting the diversity of primary consumers such as sponges, cnidarians, ascidians, and bryozoans, and which of course is highly affected by changes in this community. The second aim was to identify putative changes in species composition after 12 years, comparing their results with a previous study [3].

Marine heterobranchs are of high economic value: They attract many diving tourists [4], but they also provide new marine drug leads, which was well documented recently from BNP by Fish et al. [5] and Böhringer et al. [6]. These authors specify more than 50 species that have never been investigated with regard to bioactivity, including 35 bacterial strains identified from nine nudibranchs collected in BNP which showed antibiotic activities [6]. However, knowledge on diversity is a basic requisite to identify targets and to monitor species shifts over time caused by natural or anthropogenic influences. Kaligis et al. [1] specifically discussed the increased local pressure on the habitats around BNP within the last decade, and compared their study with the only other existing study from this region from 2003 [3]. Only 21 species of the approximately 80 species recorded in 2003 were collected again in the follow-up study in 2015 [1]. This low overlap of species did not allow any statement to be made about habitat changes or shifts in species composition during the 15-year interval. Habitat selection of these two studies from that region was mainly the coral reefs; adjacent habitats such as sea grass beds, algal communities, and mangroves were not sampled. This is in line with many other studies, because coral reefs are more in focus for protection, being of high commercial value for local communities with regards to fish and corals [7,8]. However, tropical mangroves and sea grass beds are interconnected with coral reefs, and disturbances in these habitats inflict stress conditions on coral reefs. Additionally, mangroves act as filters against terrestrial influences, absorbing and storing carbon, thus mitigating climate change [9]. Kenchington and Hutchings [8] concluded that the ability to understand and predict changes in coral reefs is compromised by the lack of knowledge about these adjacent benthic systems, including the water column communities.

This study is a subsequent survey in which marine Heterobranchia were collected in coral reef structures in 2016 and 2017, similar to the studies in 2003 [3] and 2015 [1], in order to increase overall knowledge of diversity of this group. However, in this study, we also collected in sea grass beds and inter-reefal areas for the first time to create a broader baseline for future monitoring projects in this touristic area. These additional studies over two years during a different season (at the start of the rainy season compared to the dry season in 2003 [3] and 2015 [1]), as well as including new habitats, provide evidence that more than 200 species of marine Heterobranchia exist in BNP. These results are compared with other studies from Indonesia and lead to the conclusion that biodiversity assessment of the marine Heterobranchia is far from being complete for this specific region.

2. Materials and Methods

Expeditions occurred from 15 October to 3 November 2016 and 4 to 12 September 2017, with 30 snorkelling and diving events (two during the night) in 2016 and ten (one during the night) in 2017. Underwater searching time in 2016 with two or three divers was approximately 60 min up to 120 min per dive; thus, person hours approximate 110 h for diving and 12 h for snorkelling. The diving took place between 2 and 30 m. During these dives, the substrate was searched by close observation and, especially in shallow waters, coral rubble was turned over. Only one or two divers collected in 2017, amounting to approximately 25 person hours; however, approximately 20 person hours were spent searching for animals in the intertidal flats. Additionally, rhizomes, roots of seagrasses and sediment were brought back into the lab with subsequent close observation for approximately 10 h in larger bowls. Nineteen sites were visited for collections in these two years,

focusing around Bunaken Island with 14 sites, and Mantehage (two sites that were not visited in 2003 and 2015; Figure 1). Manado Tua, Siladen, and the mainland were revisited, with an overlap of collecting sites on Manado Tua and Siladen; however, another site was visited on the mainland (for details see Figure 1 and Table 1). Table 1 lists all collection sites and their characteristics. Sea slugs were photo-documented under water on their natural substrate with an Olympus TG 4 camera when possible, and preliminarily identified using various literature sources [10,11]. Additionally, photographic records were taken of each specimen, including its unique identifier number, in the lab with the same camera. The identifier contains information about the genus and species (first four letters), the year, and the area. Final identification followed by subsequent investigation of morphological details and consulting further literature (e.g., Yonow [12–14], Stoffels et. al. [15], Martynov and Korshunova [16], and Yonow and Jensen [17]). Validity of names was checked with the help of the World Register of Marine Species [18], and the systematics as well as genus affiliations suggested by this website were followed. Based on recent publications [19], several names have changed after the publication of Kaligis et al. [1]. This is taken into consideration in Table 2. All animals were recorded with metadata that will be available in the internet portal of Diversity Workbench within the module Diversity Collection [20]. Small animals less than 10–15 mm were usually preserved in 96% EtOH. Larger animals were preserved in formaldehyde/seawater and only a small piece of foot and/or body tissue was cut off and preserved in 96% alcohol for future molecular studies. Species numbers are analysed and visualised with Excel (Microsoft Office 14).

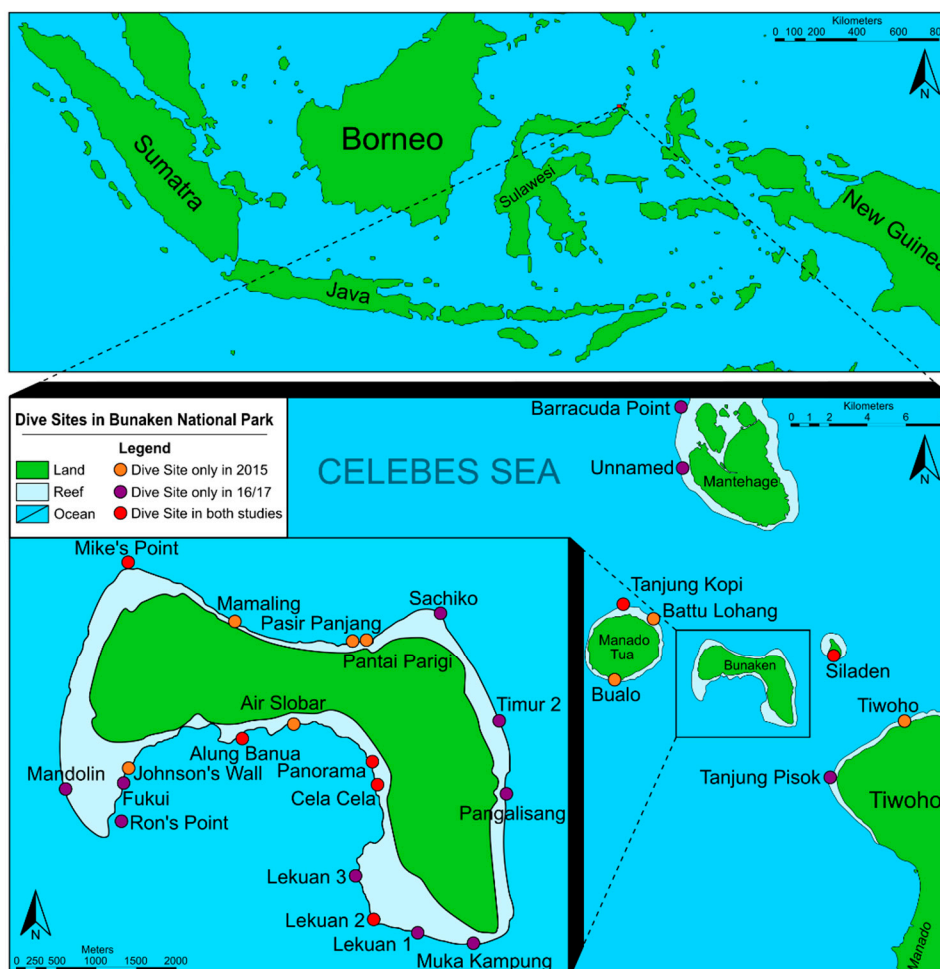


Figure 1. Location of study area: (A) Indonesia and Sulawesi with dashed lines indicating the close-up area in (B); (B) Diving sites (orange dots only in 2015, purple only in 2016 and 2017, and red in both studies) in Bunaken National Park and the islands sampled.

Table 1. Information about collection sites and dates of collections in 2016 and 2017.

Area and Name of Collection Site	Abbreviation	Geographic Location	Characterisation of the Habitat	Date of Collection
Bunaken South				
Alung Banua	AB	1°36'60.0" N 124°45'11.5" E	Wall-like coral reef structure with canyons and caves covered by a high diversity of sponges as well as soft and hard corals.	18 + 19 Oct 2016 02 + 03 Nov 2016
Cela Cela	CC	1°36'42.4" N 124°46'04.7" E	Wall-like coral reef structure with deep canyons, covered by a high diversity of soft and hard corals, hydrozoans, and tunicates.	20 + 25 Oct 2016 05 Sept 2017
Fukui	Fu	1°36'42.9" N 124°44'21.0" E	Large reef flat with large coral rubble fields, as well as large fields covered by <i>Acropora</i> and <i>Tubastraea</i> at 5 m depths; continuing into a slope down to 60 m with large sponges, <i>Acropora</i> , and several <i>Tridacna</i> . Larger sandy areas down to 12 m.	19 + 30 Oct 2016 02 Nov 2016
Lekuan 1	Le1	1°35'46.4" N 124°46'03.4" E	Steep winding coral wall with deep canyons down to 57 m; covered by large sponges, soft corals, gorgonians, hydrozoans, and ascidians. Overhanging areas with dense colonies of <i>Parazoanthus</i> .	20 + 27 Oct 2016 30 + 31 Oct 2016 06 Sept 2017
Lekuan 2	Le2	1°36'04.4" N 124°45'54.4" E	Coral and sand slopes with wall-like coral reef structures in-between.	18 Oct 2016 02 Nov 2016
Lekuan 3	Le3	1°36'19.2" N 124°46'01.5" E	Slope with white coral sand and large coral rocks continuing into a slope with corals covered by <i>Acropora</i> , soft corals, hydrozoans, and ascidians.	15 + 27 Oct 2016
Mandolin	Ma	1°36'39.5" N 124°43'57.2" E	Large winding coral wall with drop-offs down to 45 and then 60 m; with a high diversity including large black corals, soft corals, gorgonians, hydrozoans, ascidians, sponges. Overhanging areas with dense colonies of <i>Parazoanthus</i> .	17 Oct 2016
Muka Kampung	MK	1°35'35.9" N 124°46'44.1" E	Partially with coral wall areas with overhangs covered by black corals, hydrozoans, soft corals, ascidians; large colonies of <i>Parazoanthus</i> and one area with <i>Tubastraea</i> . Some areas with sandy slopes.	15 + 28 Oct 2016 03 Nov 2016
Panorama	Pa	1°36'50.0" N 124°46'03.4" E	Wall-like coral reef structure with deep canyons covered in sponges, soft and hard corals. Upper area dominated by larger ascidians. Upper reef structure partly with coral rubble and coral blocks.	16 Oct 2016 02 Nov 2016 03 Sept 2017 05–09 Sept 2017 11 Sept 2017
Ron's Point	RP	1°36'25.6" N 124°44'21.0" E	Highly diverse area with large coral blocks covered by algae, sponges, gorgonians; others with more soft corals and hydrozoans. Coral rubble in-between, as well as a few sandy areas. Reef flat with healthy living coral coverage.	17 + 29 Oct 2016 10 Sept 2017
Bunaken North				
Mike's Point	MP	1°38'12.6" N 124°44'23.0" E	Slope with terraces and many tiny caves. Less sponge-dominated than many other areas.	23 Oct 2016
Pangalisang	Pg	1°36'38.4" N 124°46'57.5" E	Wall-like coral reef structure with terraces and many tiny caves; with hard and soft corals, gorgonians, black corals, colonies of <i>Parazoanthus</i> , hydrozoans, and ascidians.	05 Sept 2017 12 Sept 2017

Table 1. Cont.

Area and Name of Collection Site	Abbreviation	Geographic Location	Characterisation of the Habitat	Date of Collection
Sachiko	Sa	1°37'41.7" N 124°45'60.0" E	Sloping coral wall structure with sediment slope in the deeper part as well as some vertical walls. Very diverse fauna, including large sponges, hard and soft corals; gorgonians and hydrozoans also in deeper areas.	22 + 28 Oct 2016 01 Nov 2016
Timur 2	Ti2	1°37'07.9" N 124°46'52.5" E	Steep coral wall with small caves and terraces with coral rubble or white sandy patches. Reef flat with living corals.	20 + 26 Oct 2016 03 Nov 2016
Manado Tua				
Tanjung Kopi	TK	1°39'07.1" N 124°41'49.6" E	Slope until 30 m and then a steep drop-off (wall-like).	23 Oct 2016
Mantehage				
Barracuda Point	BP	1°44'55.0" N 124°43'33.5" E	Destroyed reef structures on top with overgrowing turf algae; continuing into a large winding coral wall.	24 Oct 2016
Unnamed	Un	1°43'11.7" N 124°43'33.7" E	Destroyed reef structures on top, continuing to a coral wall (no further information collected).	24 Oct 2016
Siladen				
Siladen	Si	1°37'35.7" N 124°48'03.6" E	Wall with many tiny caves, dominated by soft corals, as well as whip gorgonians.	22 Oct 2016 01 Nov 2016 12 Sept 2017
Mainland				
Tanjung Pisok	TP	1°34'04.0" N 124°47'55.0" E	Highly diverse structured area, partly with walls, partly with slope-like coral structures, with some sandy slopes in-between. Some areas dominated by <i>Halimeda</i> algae and others with many hydrozoans; soft and hard corals, gorgonians, one area with many large <i>Tubastraea</i> colonies.	31 Oct 2016

Table 2. List of species and specimen identifiers for the three recent collection events, and including Kaligis et al. [1]. Species that were newly collected and recollected during the recent events are also indicated in the last column. Details of localities with abbreviations are provided in the last column. * indicates species that are not documented in literature or identification books, thus representing at-the-moment-unique specimens.

Higher Taxon Affiliation	Identifier	Species Name	Localities of Expedition 2016/2017						Expedition 2016			Expedition 2017	
			Bunaken South	Bunaken North	Manado Tua	Mantehage	Siladen	Tiwoho	Number of Specimens	Size in mm	Depths in m	Number of Specimens	Size in mm
Cephalaspidea													
Haminoeidae Pilsbry, 1895	Hasp15Bu-1 Hasp16Bu-1	<i>Haminoea</i> spec. (<i>Haminoea</i> sp. 2 in Gosliner et al. [11]: 30)	AB	-	-	-	-	-	1	7	11.3	-	-
	Hasp3_16Bu-1	<i>Haminoea</i> spec. (<i>Haminoeid</i> sp. 2 in Gosliner et al. [11]: 34)	CC	-	-	-	-	-	1	2	2	-	-
	Hasp2_15Bu-1	<i>Haminoea</i> spec.*	-	-	-	-	-	-	-	-	-	-	-
	Hasp2_16Bu-1	<i>Haminoea</i> spec.*	AB	-	-	-	-	-	1	7	10	-	-
	Phsp3_16Bu-1	<i>Phanerophthalmus</i> cf. <i>albocollaris</i> Heller and Thompson, 1983	-	Ti2	-	-	-	-	1	35	2	-	-
	Phsp3_16Bu-1	<i>Phanerophthalmus</i> spec. (<i>Phanerophthalmus</i> sp. 3 in Gosliner et al. [11]: 33)	-	-	-	-	-	TP	1	10	10	-	-
Philinidae Gray, 1850 (1815)	Ilsp17Bu-1	<i>Philine</i> spec.*	Pa	-	-	-	-	-	-	-	-	1	4
Colpodaspididae Oskars, Bouchet and Malaquias, 2015		<i>Colpodaspis thompsoni</i> Brown, 1979	AB, CC, Fu, Le1, Le2, Ma	MP, Sa, Ti2	TK	BP, Un	Si	-	20	2–5	2–21.4	1	2
Aglajidae Pilsbry, 1895 (1847)	Agsp15Bu-1	Aglajidae spec.*	-	-	-	-	-	-	-	-	-	-	-
		<i>Chelidonura amoena</i> Bergh, 1905	Le2, Pa	-	-	-	Si	-	2	8	6–12	4	25–30
		<i>Chelidonura hirundinina</i> (Quoy and Gaimard, 1833)	-	-	-	-	-	-	-	-	-	-	-
		<i>Odontoglaja guamensis</i> Rudman, 1978	-	MP, Ti2	-	Un	Si	-	4	4–10	2–7	-	-
	Phisp16Bu-1	<i>Tubulophilinopsis</i> spec.*	AB	-	-	-	-	-	1	3	16.8	-	-
Gastropteridae Swainson, 1840	Gasp5_16Bu-1	<i>Gastropteron</i> spec. (<i>Gastropteron</i> sp. 5 in Gosliner et al. [11]: 56)	-	-	-	Un	-	-	1	3	7	-	-
		<i>Sagaminopteron psychedelicum</i> Carlson and Hoff, 1974	AB, Ma	MP	TK	BP	Si	-	6	3–10	2–11.7	2	5–6
	Sasp17Bu-1	<i>Sagaminopteron</i> spec.*	-	-	-	-	Si	-	-	-	-	1	4

Table 2. Cont.

Higher Taxon Affiliation	Identifier	Species Name	Localities of Expedition 2016/2017						Expedition 2016			Expedition 2017		
			Bunaken South	Bunaken North	Manado Tua	Mantehage	Siladen	Tiwoho	Number of Specimens	Size in mm	Depths in m	Number of Specimens	Size in mm	
Costasiellidae Clarke, 1984	Cosp17Bu-1	<i>Costasiella kuroshimae</i> Ichikawa, 1993	Pa	-	-	-	-	-	-	-	-	1	1	
	Cosp1_17Bu-1-2	<i>Costasiella</i> spec. (<i>Costasiella</i> sp. 1 in Gosliner et al. [11]: 79)	CC	-	-	-	-	-	-	-	-	2	2.8–3.5	
	Cosp8_17Bu-1	<i>Costasiella</i> spec. (<i>Costasiella</i> sp. 8 in Gosliner et al. [11]: 81)	-	Pg	-	-	-	-	-	-	-	1	4	
	Cosp3_16Bu-1-5	<i>Costasiella</i> spec. *	-	-	-	BP	-	-	-	5	3–4	13.8	-	-
Plakobranichidae Gray, 1840		<i>Elysia asbecki</i> Wägele, Stemmer, Burghardt and Händeler, 2010	Ma	Ti2	-	-	-	-	-	2	5–10	6–13	-	-
		<i>Elysia marginata</i> (Pease, 1871)	CC	-	-	-	-	-	-	1	10	2	-	-
		<i>Elysia mercieri</i> (Pruvot-Fol, 1930)	Fu	Ti2	-	BP	-	-	-	5	4–10	2–13	-	-
		<i>Elysia pusilla</i> (Bergh, 1871)	Ma, Pa	-	-	-	-	-	-	1	6	5	1	3
		<i>Elysia</i> spec. (<i>Elysia</i> sp. 25 in Gosliner et al. [11]: 89)	Le1	MP	-	-	-	-	TP	2	4–12	7–18.3	-	-
		<i>Elysia</i> spec. *	AB	-	-	-	-	-	-	1	3	3	-	-
		<i>Elysia</i> spec. *	AB	-	-	-	-	-	-	1	8	23	-	-
		<i>Elysia</i> spec. *	-	-	-	BP	-	-	-	1	6	4	-	-
		<i>Plakobranichus ocellatus</i> van Hasselt, 1824	Pa	-	-	-	-	-	-	-	-	-	1	23
		<i>Thuridilla albopustulosa</i> Gosliner, 1995	-	-	-	-	Si	-	-	1	12	4	-	-
		<i>Thuridilla flavomaculata</i> Gosliner, 1995	-	MP	-	Un	-	-	-	3	6–10	5.8–7.5	-	-
		<i>Thuridilla gracilis</i> (Risbec, 1928)	AB, CC, Le1, Pa	Ti2	-	BP, Un	Si	-	-	12	5–25	1.5–12.5	3	6–20
		<i>Thuridilla lineolata</i> (Bergh, 1905)	CC, Pa	MP	-	BP, Un	-	-	-	34	1.5–7.7	6–30	4	15–20
		<i>Thuridilla livida</i> (Baba, 1955)	Pa	MP	-	-	-	-	-	1	10	6	3	5–7
		<i>Thuridilla undula</i> Gosliner, 1995	CC	-	-	-	-	-	-	1	2	10	-	-
	<i>Thuridilla vataae</i> (Risbec, 1928)	-	MP	-	-	-	-	-	1	7	11	-	-	

Table 2. Cont.

Higher Taxon Affiliation	Identifier	Species Name	Localities of Expedition 2016/2017						Expedition 2016			Expedition 2017	
			Bunaken South	Bunaken North	Manado Tua	Mantehage	Siladen	Tiwoho	Number of Specimens	Size in mm	Depths in m	Number of Specimens	Size in mm
Chromodorididae Bergh, 1891	Cesp2_15Bu-3 Cesp1_17Bu-1	<i>Ceratosoma</i> spec. (<i>Ceratosoma</i> sp. 1 in Gosliner et al. [11]: 266)	Le1	-	-	-	-	-	-	-	-	1	12
		<i>Chromodoris annae</i> Bergh, 1877	AB, CC, Ma, Pa	MP	-	-	Si	-	17	23–42	2–28	4	4–20
		<i>Chromodoris</i> cf. <i>boucheti</i> Rudman, 1982	-	-	-	-	-	-	-	-	-	-	-
		<i>Chromodoris diana</i> Gosliner and Behrens, 1998	AB, CC, Pa	MP	-	-	Si	-	7	18–45	5–20	2	17–19
	Chsp30-15Bu-5	<i>Chromodoris lochi</i> Rudman, 1982	CC	-	-	-	Si	-	6	25–40	5.3–21.8	-	-
		<i>Chromodoris</i> cf. <i>michaeli</i> Gosliner and Behrens, 1998	-	-	-	BP	-	-	1	34	12	-	-
		<i>Chromodoris strigata</i> Rudman, 1982	-	-	-	-	-	-	-	-	-	-	-
		<i>Chromodoris willami</i> Rudman, 1982	CC	-	-	-	Si	-	4	18–50	10.5–17	-	-
		<i>Doriprismatica stellata</i> (Rudman, 1986)	CC, Pa	-	-	-	-	-	8	2.3–65	6.5–10	3	13–65
		<i>Glossodoris cincta</i> (Bergh, 1888)	Le1, RP	Sa, Pg	TK	Un	-	-	5	17–50	3–13	2	20–52
		<i>Glossodoris hikuensis</i> (Pruvot-Fol, 1954)	-	-	-	-	-	-	-	-	-	1	65
		<i>Goniobranchus fidelis</i> (Kelaart, 1858)	Le1	-	-	-	-	-	1	15	16	-	-
		<i>Goniobranchus geometricus</i> (Risbec, 1928)	Fu, Ma	MP	-	-	-	-	3	6–25	2–15	-	-
		<i>Goniobranchus reticulatus</i> (Quoy and Gaimard, 1832)	-	-	-	-	-	-	-	-	-	-	-
		<i>Goniobranchus</i> spec. (<i>Goniobranchus</i> sp. 40 in Gosliner et al. [11]: 230)	Le1	-	-	-	-	-	1	20	8.5	-	-
		<i>Hypselodoris apolegma</i> (Yonow, 2001)	-	Ti2	-	-	-	-	1	70	16	-	-
		<i>Hypselodoris maculosa</i> (Pease, 1871)	-	-	-	Un	-	-	1	11	4.8	-	-
	<i>Hypselodoris tryoni</i> (Garrett, 1873)	Ma	-	-	-	-	-	2	55–60	10	-	-	

Table 2. Cont.

Higher Taxon Affiliation	Identifier	Species Name	Localities of Expedition 2016/2017						Expedition 2016			Expedition 2017	
			Bunaken South	Bunaken North	Manado Tua	Mantehage	Siladen	Tiwoho	Number of Specimens	Size in mm	Depths in m	Number of Specimens	Size in mm
	Hysp16Bu-1	<i>Hypselodoris</i> spec. *	Ma	-	-	-	-	-	1	5	4	-	-
	Hysp2_16Bu-1	<i>Hypselodoris</i> spec. *	-	-	-	BP	-	-	1	6	16	-	-
		<i>Miamira sinuata</i> (van Hasselt, 1824)	-	-	-	-	Si	-	1	12	13	-	-
		<i>Thorunna australis</i> (Risbec, 1928)	-	-	-	-	-	-	-	-	-	-	-
		<i>Thorunna furtiva</i> Bergh, 1878	-	-	-	Un	-	-	1	10	7	-	-
	Dosp17Bu-4	<i>Verconia</i> spec. *	-	-	-	-	Si	-	-	-	-	1	4
Dendrodorididae O'Donoghue, 1924 (1864)		<i>Dendrodoris albobrunnea</i> Allan, 1933	-	-	-	-	-	-	-	-	-	-	-
		<i>Dendrodoris nigra</i> (Stimpson, 1855)	Pa	-	-	-	Si	-	1	20	3	2	4–5
	Rosp17Bu-1	<i>Dendrodoris</i> spec. *	Pa	-	-	-	-	-	-	-	-	1	5
		<i>Phyllidia coelestis</i> Bergh, 1905	Le3, Pa	Sa, Pg	-	-	Si	-	3	13–38	1–17.2	2	26–35
		<i>Phyllidia elegans</i> Bergh, 1869	Pa	MP	-	-	Si	-	1	30	2	1	23
		<i>Phyllidia ocellata</i> Cuvier, 1804	-	-	-	-	-	-	-	-	-	-	-
		<i>Phyllidia varicosa</i> Lamarck, 1801	AB, Pa	Sa	-	Un	Si	-	5	30–70	2–15.6	2	55–56
Phyllidiidae Rafinesque, 1814	Phsp17Bu-1	<i>Phyllidia</i> spec. *	Pa	-	-	-	-	-	-	-	-	1	16
		<i>Phyllidiella cf. annulata</i> (Gray, 1853)	AB	-	-	-	-	-	1	40	4	-	-
		<i>Phyllidiella pustulosa</i> (Cuvier, 1804)	AB, Pa	MP, Sa	TK	BP	Si	-	11	20–63	1.5–14.8	4	29–44
		<i>Phyllidiopsis pipeki</i> Brunckhorst, 1993	-	-	-	-	-	-	-	-	-	-	-
		<i>Phyllidiopsis sphingis</i> Brunckhorst, 1993	-	-	-	-	-	-	-	-	-	-	-
		<i>Phyllidiopsis xishaensis</i> (Lin, 1983)	Le2	-	TK	-	-	-	2	12	6.8–21.9	-	-

Table 2. Cont.

Higher Taxon Affiliation	Identifier	Species Name	Localities of Expedition 2016/2017						Expedition 2016			Expedition 2017	
			Bunaken South	Bunaken North	Manado Tua	Mantehage	Siladen	Tiwoho	Number of Specimens	Size in mm	Depths in m	Number of Specimens	Size in mm
Nudibranchia, Cladobranchia													
Arminidae Iredale and O'Donoghue, 1923		<i>Dermatobranchus diagonalis</i> Gosliner and Fahey, 2011	-	-	-	-	-	TP	1	20	8.8	-	-
		<i>Dermatobranchus fasciatus</i> Gosliner and Fahey, 2011	-	-	-	-	-	-	-	-	-	-	-
		<i>Dermatobranchus</i> cf. <i>kokonas</i> Gosliner and Fahey, 2011	-	-	TK	-	Si	-	2	7–8	3–14	-	-
		<i>Dermatobranchus</i> cf. <i>piperoides</i> Gosliner and Fahey, 2011	Le1	-	-	-	-	-	1	7	8	-	-
		Desp8_17Bu-1 <i>Dermatobranchus</i> spec. (<i>Dermatobranchus</i> sp. 8 in Gosliner et al. [11]: 302)	-	-	-	-	Si	-	-	-	-	1	8
		Dest15Bu-1 <i>Dermatobranchus</i> spec. *	-	-	-	-	-	-	-	-	-	-	-
		Desp1_16Bu-1 <i>Dermatobranchus</i> spec. *	-	MP	-	-	-	-	4	1	7	-	-
Proctonotidae Gray, 1853		<i>Janolus</i> cf. <i>mirabilis</i> Baba and Abe, 1970	Le1	-	-	-	-	-	1	7	5	-	-
	Cysp15Bu-1	<i>Janolus</i> spec. (<i>Janolus</i> sp. 11 in Gosliner et al. [11]: 308)	-	-	-	-	-	-	-	-	-	-	-
Scyllaeidae Alder and Hancock, 1855	Cross16Bu-1-8	<i>Crosslandia daedali</i> Poorman and Mulliner, 1981	Pa	-	-	-	Si	-	8	8–20	~0	-	-
Dotidae Gray, 1853		<i>Doto ussi</i> Ortea, 1982	Le1	Sa	-	BP	Si	TP	21	5–20	3–10	-	-
		<i>Kabeiro rubroreticulata</i> Shipman and Gosliner, 2015	Le1	-	-	-	-	TP	3	8	10–16	-	-
		Dotosp15Bu-1 <i>Kabeiro</i> spec. *	-	-	-	-	-	-	-	-	-	-	-
		Kasp16Bu-1-15+17 Kasp17Bu-1 <i>Kabeiro</i> spec. *	Fu, Le2, Ma, RP	-	-	-	Si	-	16	2–15	10–20	1	4
	Kasp16Bu-16 <i>Kabeiro</i> spec. *	-	-	-	-	Si	-	1	8	10	-	-	
Tritoniidae Lamarck, 1809		<i>Marianina rosea</i> (Pruvot-Fol, 1930)	-	-	-	BP	-	-	1	10	2	-	-
	Trsp8_16Bu-1	<i>Tritonia</i> spec. (<i>Tritonia</i> sp. 9 in Gosliner et al. [11]: 321)	-	MP	-	-	-	-	1	8	7.1	-	-

Table 2. Cont.

Higher Taxon Affiliation	Identifier	Species Name	Localities of Expedition 2016/2017						Expedition 2016			Expedition 2017	
			Bunaken South	Bunaken North	Manado Tua	Mantehage	Siladen	Tiwoho	Number of Specimens	Size in mm	Depths in m	Number of Specimens	Size in mm
	Trisp10_16Bu-1	<i>Tritonia</i> spec. (<i>Tritonia</i> sp. 10 in Gosliner et al. [11]; 321)	AB	-	-	-	-	-	1	20	14	-	-
	Trsp16Bu-1	<i>Tritonia</i> spec. *		Ti2	-	-	-	-	1	4	6	-	-
Flabellinidae Bergh, 1889		<i>Coryphellina delicata</i> (Gosliner and Willan, 1991)	Fu	-	-	-	-	-	1	15	-	-	-
		<i>Coryphellina exoptata</i> (Gosliner and Willan, 1991)	Le2, Ma	Sa, Pg	-	BP, Un	-	-	6	22–30	2–8.1	1	20
		<i>Coryphellina rubrolineata</i> O'Donoghue, 1929	RP	-	TK	-	-	-	2	15–25	7.3–8	-	-
Samliidae Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl and Picton, 2017		<i>Samla bicolor</i> (Kelaart, 1858)	AB, Le1, Ma	MP, Ti2	TK	BP, Un	-	-	11	6–23	1.5–17.5	1	12
		<i>Samla riwo</i> (Gosliner and Willan, 1991)	CC	Ti2	TK	-	-	-	3	8–17	2–17.5	-	-
Eubranchidae Odhner, 1934	Eusp22_16Bu-1	<i>Eubranchius</i> spec. (<i>Eubranchius</i> sp. 22 in Gosliner et al. [11]; 341)	RP	-	-	-	-	-	1	3	10	-	-
Tergipedidae Bergh, 1889	Cusp4_16Bu-1	<i>Cuthona</i> spec. (<i>Cuthona</i> sp. 4 in Gosliner et al. [11]; 343)	-	Ti2	-	-	-	-	1	3	2	-	-
	Cusp54_16Bu-1	<i>Cuthona</i> spec. (<i>Cuthona</i> sp. 54 in Gosliner et al. [11]; 353)	Ma	-	-	-	-	-	1	8	6	-	-
	Cusp65_16Bu-1	<i>Cuthona</i> spec. (<i>Cuthona</i> cf. sp. 65 in Gosliner et al. [11]; 343)	-	-	-	Un	-	-	1	2	2	-	-
Facelinidae Bergh, 1889		<i>Caloria indica</i> (Bergh, 1896)	Le1, Le2	Sa, Ti2	-	Un	Si	-	8	6–25	2–7.3	-	-
	Casp15Bu-1	<i>Caloria</i> spec. (<i>Caloria</i> sp. 1 in Gosliner et al. [11]; 362)	-	-	-	-	-	-	-	-	-	-	-
	Crsp5_16Bu-1	<i>Cratena</i> spec. (<i>Cratena</i> sp. 5 in Gosliner et al. [11]; 383)	-	-	-	Un	-	-	1	5	7.3	-	-
	Fasp3_16Bu-1+3-5	<i>Facelina rhodopos</i> Yonow, 2000 <i>Facelina</i> spec. (<i>Facelina</i> sp. 3 in Gosliner et al. [11]; 359)	-	Sa	TK	BP	-	-	4	3–4	5–15.8	-	-

Table 2. Cont.

Higher Taxon Affiliation	Identifier	Species Name	Localities of Expedition 2016/2017						Expedition 2016			Expedition 2017	
			Bunaken South	Bunaken North	Manado Tua	Mantehage	Siladen	Tiwoho	Number of Specimens	Size in mm	Depths in m	Number of Specimens	Size in mm
	Fasp3_16Bu-2	<i>Facelina</i> spec. (<i>Facelina</i> sp. 4 in Gosliner et al. [11]: 359)	-	-	-	-	Si	-	1	5	17	-	-
	Fasp8_16Bu-1	<i>Facelina</i> spec. (<i>Facelina</i> sp. 8 in Gosliner et al. [11]: 360)	-	MP	-	-	-	-	1	8	6	-	-
		<i>Favorinus japonicus</i> Baba, 1949	-	-	-	-	-	-	-	-	-	-	-
		<i>Favorinus mirabilis</i> Baba, 1955	AB	-	-	-	-	-	1	9	11.5	1	9
		<i>Favorinus tsuruganus</i> Baba and Abe, 1964	Fu	-	-	-	-	-	1	6	8.3	-	-
	Nosp13_16Bu-1-6 Nosp3_17Bu-1	<i>Noumeaella</i> spec. (<i>Noumeaella</i> sp. 3 in Gosliner et al. [11]: 367)	AB, MK, Pa	MP	-	-	Si	-	9	3–13	2–13	1	6
	Nosp6_17Bu-1-2	<i>Noumeaella</i> spec. (<i>Noumeaella</i> cf. sp. 6 in Gosliner et al. [11]: 368)	Pa	-	-	-	-	-	-	-	-	2	7–9
	Nosp12_16Bu-1	<i>Noumeaella</i> spec. (<i>Noumeaella</i> sp. 12 in Gosliner et al. [11]: 367)	-	MP	-	-	Si	-	1	4	2	-	-
	Nosp2_15Bu 1 Nosp2_16Bu-1-6	<i>Noumeaella</i> spec. *	CC, Le2	-	-	-	-	-	6	12–40	8–11.2	-	-
		<i>Phylloidesmium briareum</i> (Bergh, 1896)	-	Pg	TK	-	-	-	7	12–15	18.4	1	25
		<i>Phylloidesmium poindimiei</i> (Risbec, 1928)	-	Pg	-	-	-	-	-	-	-	1	4
		<i>Pteraeolidia semperi</i> (Bergh, 1870)	Ma	MP, Ti2	TK	Un	Si	-	11	4–70	2–17.5	1	30
	Fasp17Bu-1	Facelinidae spec. *	Le1	-	-	-	-	-	-	-	-	1	7
Aeolidiidae Gray, 1827		<i>Bulbaeolidia alba</i> (Risbec, 1928)	Le2	-	-	-	-	-	1	5	4.3	-	-

3. Results

In total, 385 specimens comprising 112 marine heterobranch species were collected in 2016 and 108 specimens comprising 57 species in 2017 (see Figure 21A). Both collecting events were in October, the month when the rainy season usually starts. The overall species number recorded and collected from BNP during the dry season in 2015 attains 79 species. Collecting efforts in 2016 with 112 species was the highest, but training efforts as well as increased collecting time in the recent surveys affects the results: The number of species that were only found in 2016 (63, Figure 21A) is high, and represents nearly 30% of the overall species (215 species, see below) recorded from this area. This clearly shows that some species are very rare, and the area is still under-sampled. This can also be seen when looking at the results of 2017 (Figure 21A) with a shorter collecting period, but focusing on inter-reefal habitats (31 species, representing 15% of the overall species record). It is possible that the collection months had some bearing on the numbers collected; however, the El Niño situation in 2016 with an increased water temperature and the lack of a distinct dry season in 2017 with continuous rainfalls throughout the year (pers. obs. SR), does not allow statements about seasonal differences yet.

Table 2 lists all species collected in 2016 and 2017, as well as the previously published data from 2015 [1]. The species recorded in 2003 [3] and recollected during these recent surveys are highlighted in a separate column. Any overlap with our recent survey is also highlighted in Figure 21A. Species that were ambiguous, and where re-identification was not possible (11 species in in Burghardt et al. [3], marked as +11 in Figure 21A), were not included in the species accumulation curve in Figure 21B. Identifiers are provided for unidentified and/or new species in Table 2 and in the Figure legends. Species authorities are provided in Table 2 and authorities will only be mentioned in the text for those species not listed in Table 2.

Figures 2–16 depict all species collected in 2016, and Figures 17–20 those collected additionally in 2017. Species and genera are compared to previous results [1], and discussed in detail either when not mentioned in Kaligis et al. [1], when considered problematic in identification, or when new to science. The work has a focus on specific groups which were united in the past as Opisthobranchia, and which is still used in many identification books (see the review in Wägele et al. [21]).

3.1. Animals Collected in 2016 (Figures 2–16)

3.1.1. Cephalaspidea and Runcinacea (16 species in eight genera belonging to five families, Figures 2A–4A)

Haminoeidae usually have a short posterior foot, as can be seen in the probably undescribed *Haminoea* species (Figure 2A), shown in *Haminoea* sp. 2 in Gosliner et al. [11] (p. 30), or *Haminoea* spec (Figure 2C). Some members exhibit a typically long “tail.” It is still unclear whether this group with long tails should have its own genus. One animal was retrieved (Figure 2B), which is similar to the Haminoeid depicted by Gosliner et al. [11] (p. 34) as Haminoeid sp. 2. This species is characterised by the white head appendages and a brownish flower-shaped pattern on a white body background.

Only during this study, two species of *Phanerophthalmus* were found with one animal each. *Phanerophthalmus albocollaris* (Figure 2D) is distinctive with white markings in the head region. However, the second species (Figure 2E) could not be assigned to any other described *Phanerophthalmus* species, although it resembles *Phanerophthalmus* sp. 3 in Gosliner et al. [11] (p. 33), a reddish to violet specimen with a white mark in the posterior part of the cephalic shield. The Bunaken specimen (Figure 2D) also bears some similarities to *Phanerophthalmus luteus* (Quoy and Gaimard, 1933) [17]. It was also illustrated in Burghardt et al. [3] as *Phanerophthalmus* cf. *smaragdinus*.

The Aglajidae is a widespread taxon with its highest diversity probably in the Philippines [22]. They are usually carnivorous, and many live in habitats with sand or sediment. Due to the focus on coral habitats, the species number present in our collection is limited to species characteristically known from coral habitats (*Chelidonura amoena* in Figure 2G, *Chelidonura hirundinina* [1], *Odontoglaja guamensis* in Figure 2H). One specimen (Figure 3A) looked similar to *Tubulophilinopsis pilsbryi* (Eliot, 1900), but with inverted coloration of that typical for *T. pilsbryi*. This specimen is tentatively assigned to this genus.

Gastropteridae are tiny-shelled slugs, some of them with striking colors. A small whitish *Gastropteron* was found with distinct white tubercles and patches (Figure 3B), similar to the one depicted by Gosliner et al. [11] (p. 56) as *Gastropteron* sp. 5. Kaligis et al. [1] illustrate five different *Siphopteron* species, including one new species. The new species (represented by two specimens) collected only at Siladen Island in 2015 was not found again at any other locality, and so a limited distribution is assumed. In contrast, *S. brunneomarginatum* (Figure 3D), *Siphopteron ladrones* (Figure 3E) and *Siphopteron nigromarginatum* (Figure 3F) were found again in various locations.

Runcinidae is a group of marine heterobranchs with small members of various colorations. They have not received much taxonomic attention in the past, and so identification is nearly impossible. Here a very small specimen (Figure 3G,H) is tentatively assigned to the genus *Runcina*. It has tiny pustules in the head area and a small pointed foot posteriorly that is a little bit longer than the notum. This animal is light brownish in color, and shows dots and spots even lighter in color. Another animal coming from the mainland was dark brown with no further color pattern (Figure 4A), and is clearly a different species.



Figure 2. Cephalaspidea: (A) *Haminoea* spec. (*Haminoea* sp. 2 in Gosliner et al. [11]: 30), Hasp16Bu-1; (B) *Haminoea* spec. (*Haminoeid* sp. 2 in Gosliner et al. [11]: 34), Hasp3_16Bu-1; (C) *Haminoea* spec., Hasp2_16Bu-1; (D) *Phanerophthalmus albocollaris*; (E) *Phanerophthalmus* spec. (*Phanerophthalmus* sp. 3 in Gosliner et al. [11]: 33), Phsp3_16Bu-1; (F) *Colpodaspis thompsoni*; (G) *Chelidonura amoena*; (H) *Odontoglaja guamensis*.

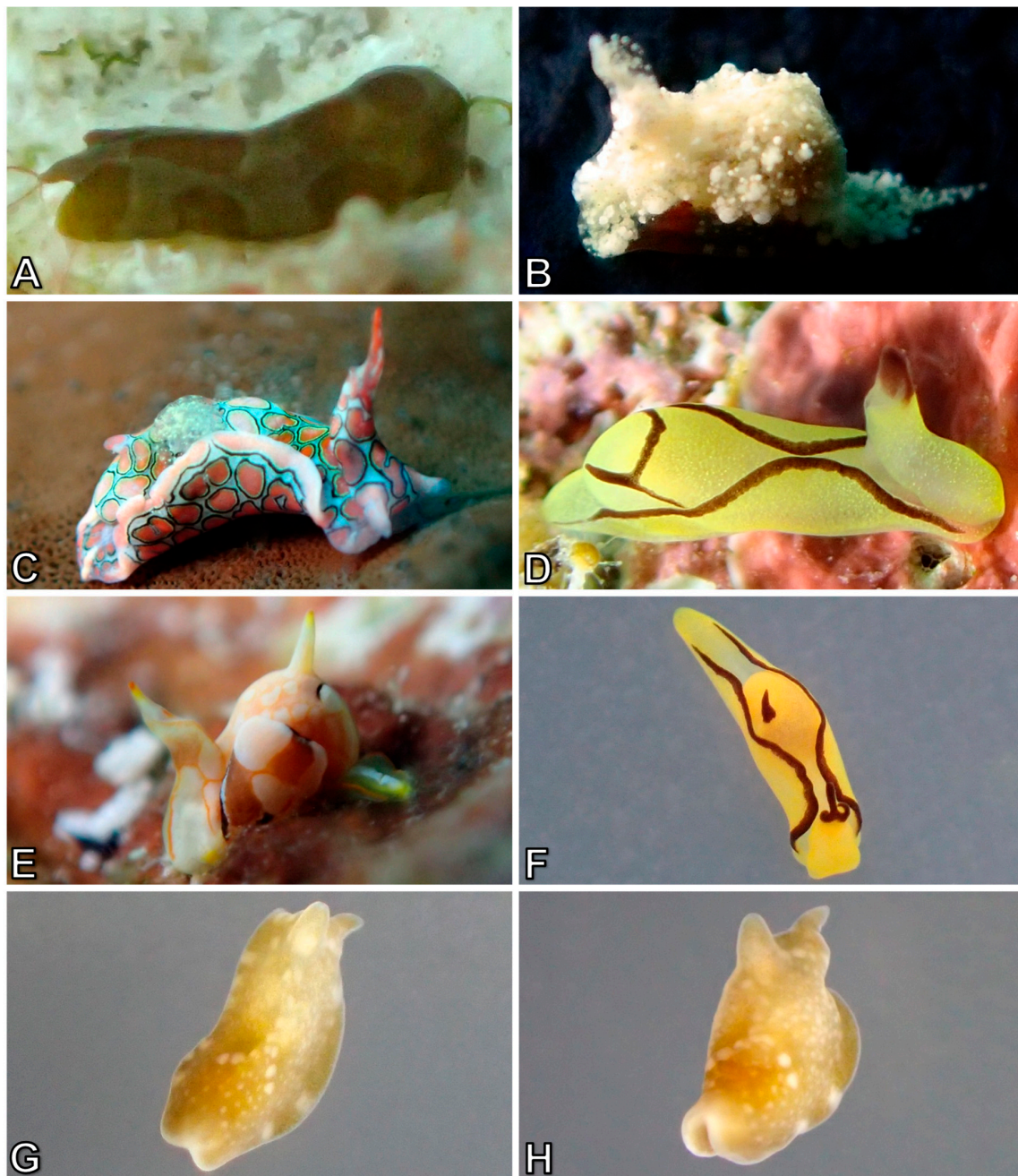


Figure 3. Cephalaspidea and Runcinacea: (A) *Tubulophilinopsis* spec., Phisp16Bu-1; (B) *Gastropteron* spec. (*Gastropteron* sp. 5 in Gosliner et al. [11]: 56), Gasp5_16Bu-1; (C) *Sagaminopteron psychedelicum*; (D) *Siphopteron brunneomarginatum*; (E) *Siphopteron ladrones*; (F) *Siphopteron nigromarginatum*; (G, H) *Runcina* spec., Rusp16Bu-1.

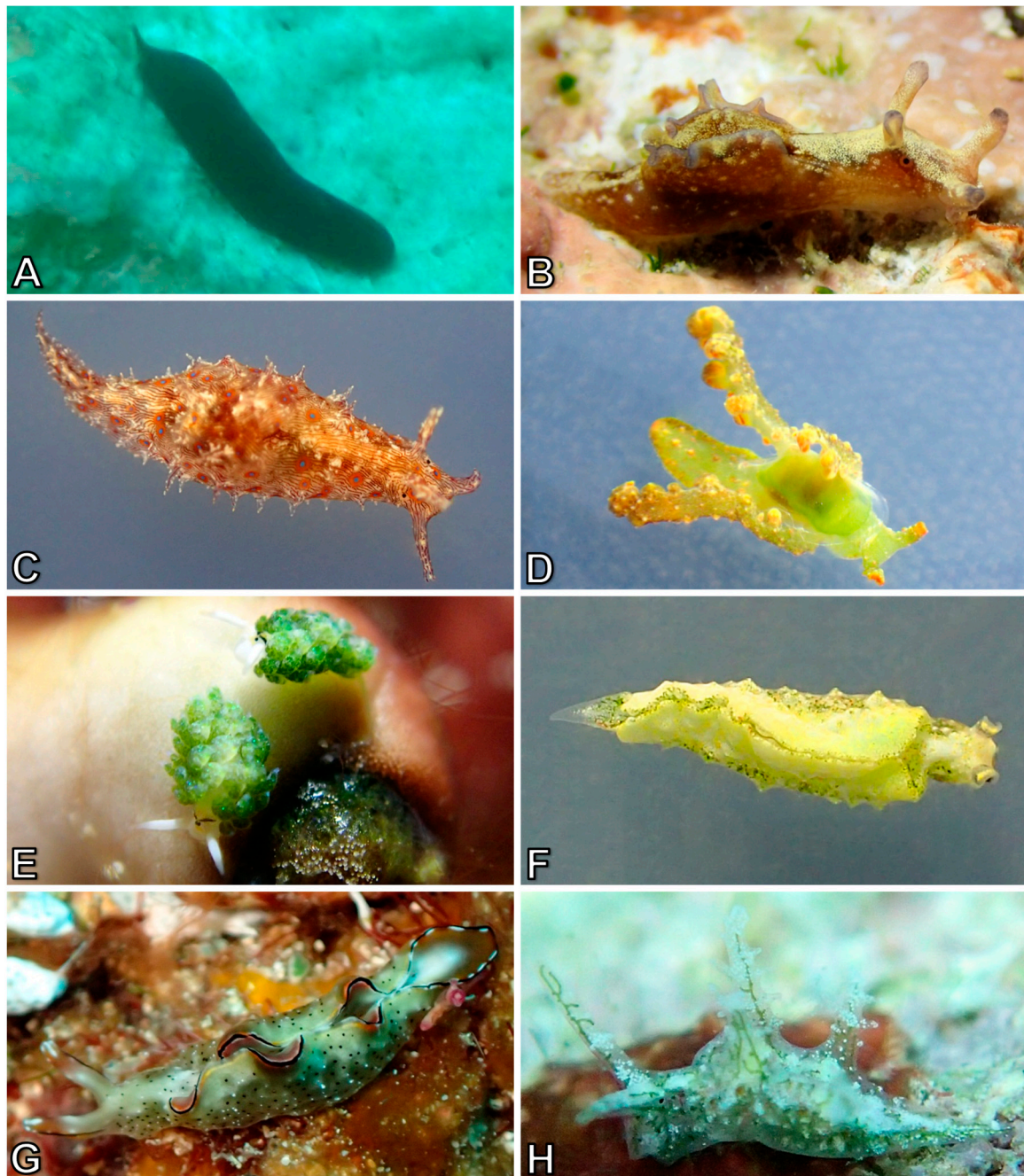


Figure 4. Runcinacea, Anaspidea and Sacoglossa: (A) *Runcina* spec., Rusp2_16Bu-1; (B) *Aplysia parvula*; (C) *Stylocheilus striatus*; (D) *Lobiger* spec. (*Lobiger* sp. 1 in Gosliner et al. [11]: 70), Losp1_16Bu-1; (E) *Costasiella* spec., Cosp3_16Bu-1; (F) *Elysia asbecki*; (G) *Elysia marginata*; (H) *Elysia mercieri*.

3.1.2. Anaspidea (two species in two genera belonging to one family, Figure 4B,C)

Aplysia parvula is a circumtropical species which might represent a species complex [11,23]. Our specimens (Figure 4B) showed the typical pinkish color with cream-colored dots, and darker parapodial and rhinophoral rims of the form associated with algae on coral reef flats and the intertidal [24]. They were collected in coral rubble in less than 7 m depth.

3.1.3. Sacoglossa (16 species in four genera belonging to three families, Figures 4D–6D)

Sixteen *Costasiella* species are described worldwide, and a further eight undescribed species are documented in Gosliner et al. [11]. Jensen et al. [25] described and illustrated a specimen from Guam (preliminarily identified as *Costasiella* “*kuroshimae*”) resembling our five specimens very closely, which were all collected together in Mantehage at Barracuda Point sitting close to a *Flabellia* alga in 14 m depth. The white head is typical for this species, which shows only a tinge of yellow in front and behind the eyes. The black markings behind the eyes render the impression of an “angry face” (Figure 4E). The green diamond-shaped patch, typical for *C. kuroshimae*, is absent. The rhinophores are rather transparent and do not show any black. Based on the phylogeny of *Costasiella* species from around the world, Jensen et al. [25] considered identification of *C. kuroshimae* as very difficult, because of the similarity of non-related specimens and a lack of a proper description of the original material of this species.

Eight species of *Elysia* were collected, but only few were observed on macro-algae. This is unfortunate as algal species are helpful in identification of sacoglossans since many are limited in their diet species. Most of them were collected from coral rubble or highly structured mini-habitats in the coral reef. Of the four undescribed *Elysia* species documented here, only one was found the previous year, identified as *Elysia* sp. 25 in Gosliner et al. [11] (p. 89) (see Figure 3g in Kaligis et al. [1]). This species has a characteristic black line in front of the parapodia and a peculiar crawling habit (Figure 5B). Two of the other new species of *Elysia* were collected in Alung Banua, on the southern coastline of Bunaken Island, which has a higher algal flora with tiny algal species, probably due to higher eutrophication. Elsp1_16Bu-1 (Figure 5C) is transparent (perhaps due to its small size of only 3 mm) with moderately branched green digestive gland shining through, whereas Elsp16Bu-1 was uniformly dark green with transparent rhinophores speckled with white dots and a few elevated white spots on the head, body, and parapodia (Figure 5D). Three specimens of another, probably undescribed, *Elysia* species were collected at a site in Mantehage. The rather white animals had a knobby appearance, and the outer sides of the parapodia were greenish (Figure 5E).

No new *Thuridilla* species were collected; however, one specimen of *Thuridilla undula* showed an aberrant habitus (Figure 6C): The parapodial rims were fused in the middle of the body.

3.1.4. Pleurobranchomorpha (one species in one genus belonging to one family, Figure 6E)

During night dives, many specimens of *Pleurobranchus forskalii* were found, some of them feeding on tunicates of the family Didemniidae. We collected a smaller specimen of brownish color (Figure 6E), which was found under coral rubble during the day. It can be distinguished from *Pleurobranchus peronii* Cuvier, 1804 by its compound tubercles.



Figure 5. Sacoglossa: (A) *Elysia pusilla*; (B) *Elysia* spec. (*Elysia* sp. 25 in Gosliner et al. [11]: 89), Elsp30_16Bu-3; (C) *Elysia* spec., Elsp1_16Bu-1; (D) *Elysia* spec., Elsp16Bu-1; (E) *Elysia* spec., Elsp16Bu-1; (F) *Thuridilla albopustulosa*; (G) *Thuridilla flavomaculata*; (H) *Thuridilla gracilis*.



Figure 6. Sacoglossa, Pleurobranchomorpha and Nudibranchia - Doridina: (A) *Thuridilla lineolata*; (B) *Thuridilla livida*; (C) *Thuridilla undula*; (D) *Thuridilla vataae*; (E) *Pleurobranchus forskalii*; (F) *Kaloplocamus* spec. (*Kaloplocamus* sp. 8 in Gosliner et al. [11]: 116), Kalsp8_16Bu-1; (G) *Kaloplocamus* spec. (*Kaloplocamus* sp. 9 in Gosliner et al. [11]: 116), Kalsp9_16Bu-1; (H) *Nembrotha kubaryana*.

3.1.5. Nudibranchia, Anthobranchia (40 species in 21 genera belonging to seven families, Figures 6F–11H)

The genus *Kaloplocamus* was represented with two different species, both new to science, possibly recorded by Gosliner et al. [11] (p. 116) as sp. 8 (Figure 6F) and sp. 9 (Figure 6G); if confirmed, this extends the range of these two species further west. *Kaloplocamus ramosus* (Cantraine, 1835) exhibits bioluminescence [26], but the two species collected in this survey were not investigated to see if they also exhibited this peculiar phenomenon.

Kaligis et al. [1] listed *Polycera japonica* and *Polycera risbeci*, both from the northern shorelines of Bunaken. The former was found again in Mantehage (Figure 7A), but *P. risbeci* was not collected again.

We record here a third species of *Polycera*, which is very cryptic in coloration (Figure 7B). It is probably a new species, most similar to *Polycera* sp. 5 in Gosliner et al. [11] (p. 113).

Aegiridae were investigated by Fahey and Gosliner [27], who described a new species, *Aegires malinus*, typified by a reddish color, and apple-green rhinophores and gills. This species was collected only once in this study (Figure 7E), in addition to the bright lemon yellow *Aegires citrinus* (Figure 7D).

Several *Gymnodoris* species are present in the collection, including *Gymnodoris tuberculosa* (Figure 7F), furthermore an undescribed species very similar to *Gymnodoris okinawae* Baba, 1936, but with less distinct orange dots (Figure 7G; see also *Gymnodoris* sp. 2 in Gosliner et al. [11] (p. 152)), and one species which could not be assigned to any described or depicted species (Figure 7H). The genus is characterised by its rather uniform tapering shape. Distinguishing features are the arrangement of the gills; some have peculiar color characteristics [11]. Nearly 60 undescribed species are depicted in Gosliner et al. [11], and so identification in surveys such as this must be preliminary until the genus is revised.

Some dorids mimic sponges and are therefore difficult to detect. A large cryptic species is *Asteronotus mimeticus* (Figure 8A,B) which shows various colorations, and sits on the underside of foliate sponges, such as *Phyllospongia*. One specimen tentatively assigned to *Sclerodoris* (Figure 8F) is depicted in Gosliner et al. [11] (p. 195) as *Sclerodoris* sp. 2.

Kaligis et al. [1] depicted a species under the name *Chromodoris* sp. with yellow rhinophores and gills, which is here identified as *Chromodoris lochi*; this yellow color morph is illustrated in Figure 9A. Several chromodorids show similarities in colors and patterns, and are therefore difficult to distinguish. The recent publication on color variation of some *Chromodoris* species mimicking other *Chromodoris* species adds to problems of correct identification [28]. Kaligis et al. [1] recorded *Chromodoris strigata*, which is very similar to *Chromodoris michaeli*, but unfortunately, Gosliner and Behrens [29] (original description) did not compare their new species with *C. strigata* which was described earlier by Rudman [30]. One main difference may be the more bluish color of *C. michaeli* compared to the more whitish *C. strigata*. Our specimen was not white but showed a tinge of blue (Figure 9B). The pattern of the black stripes is also very similar to the ones depicted in the original description of *C. michaeli*, and we therefore tentatively assign our animal to *C. michaeli*. *Goniobranchus* sp. (Figure 9H) appears similar to *Gymnodoris* species in its simple elongated body shape, and rather transparent coloration with tiny whitish dots on the dorsum. The notum has a narrow but distinct orange rim.

The taxon *Hypselodoris* has undergone changes in species affiliation in the last decade by new morphological and molecular analyses [31,32]. Nearly nothing is known about color variation during ontogeny, rendering identification of small specimens more difficult. Two specimens were found in Bunaken Island which may be new to science (Figure 10D,E). Both animals were very small (5 mm and 6 mm respectively). They somewhat resemble *Hypselodoris maculosa*, which was also found several times, and the recently resurrected *Hypselodoris decorata* (Risbec, 1828); however, both specimens barely show the violet tinge on the foot and velum, and do not have the characteristic color banding of the rhinophores. The larger one also lacks the orange colored gills which are white in this specimen. We cannot exclude that both of them represent juveniles of described species.

Six phyllidiid species were collected. Only one specimen of *Phyllidia elegans* was found at Mikes Point (Figure 11B), whereas Kaligis et al. [1] recorded 13 specimens, mostly from Siladen. The animal is similar to *Phyllidia alyta* Yonow, 1996, with yellow rhinophores and longitudinal black stripes, including a black line on the foot sole. However, our animal shows black lines connecting the longitudinal stripes at the back, more typical for *Phyllidia elegans*. Another animal was tentatively assigned to *Phyllidiella* cf. *annulata* (Figure 11D) based on the distinctive black crossed pattern on the dorsum, the thin black line at the mantle margin and the many small tubercles covering the notum.

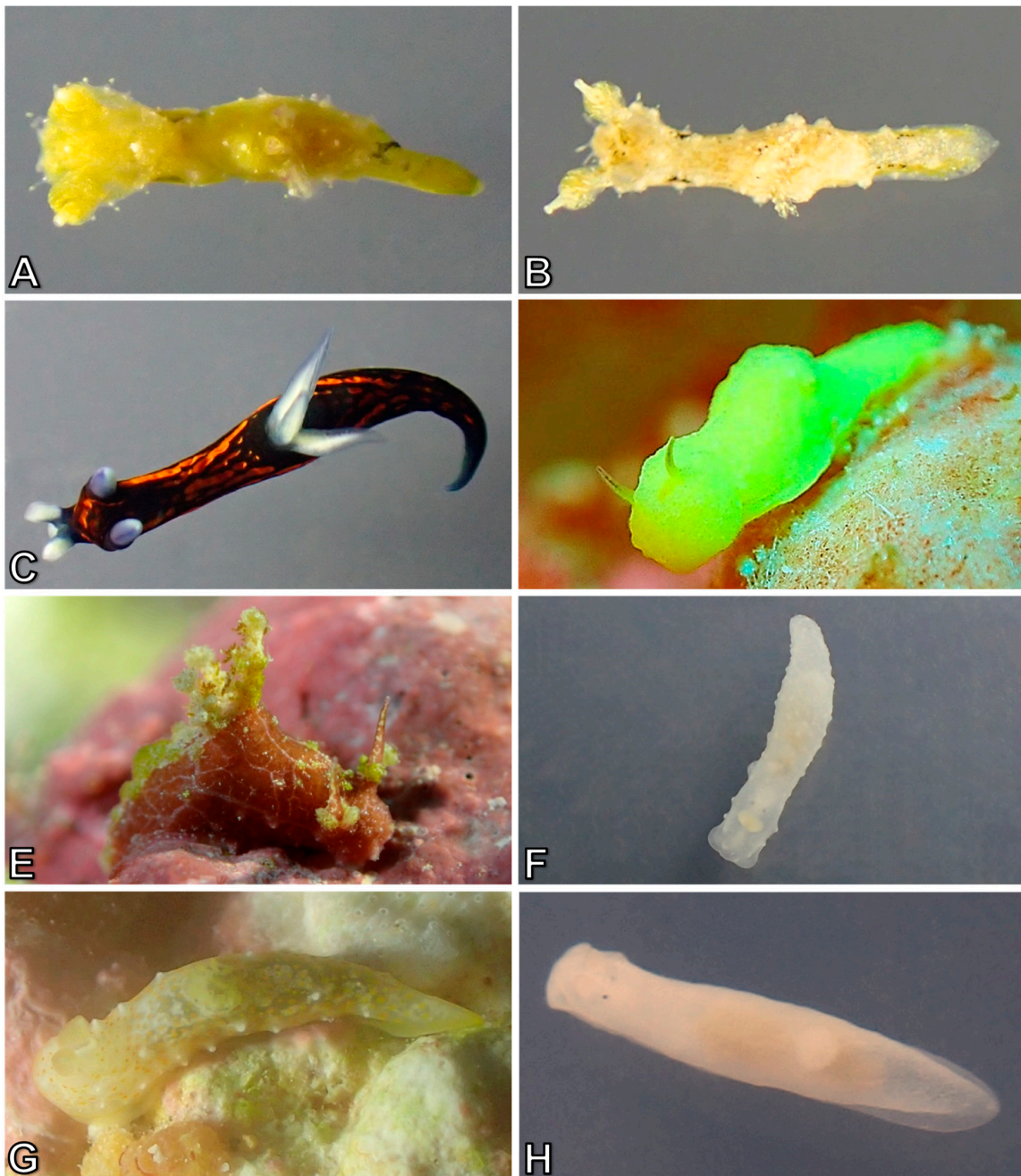


Figure 7. Nudibranchia - Doridina: (A) *Polycera japonica*; (B) *Polycera* spec. (*Polycera* sp. 5 in Gosliner et al. [11]: 113), Posp516Bu-1; (C) *Roboastra gracilis*; (D) *Aegires citrinus*; (E) *Aegires malinus*; (F) *Gymnodoris tuberculosa*; (G) *Gymnodoris* spec. (*Gymnodoris* sp. 2 in Gosliner et al. [11]: 152), Gysp2_16Bu-1; (H) *Gymnodoris* spec. (*Gymnodoris* cf. sp. 35 in Gosliner et al. [11]: 159), Gysp16Bu-1.

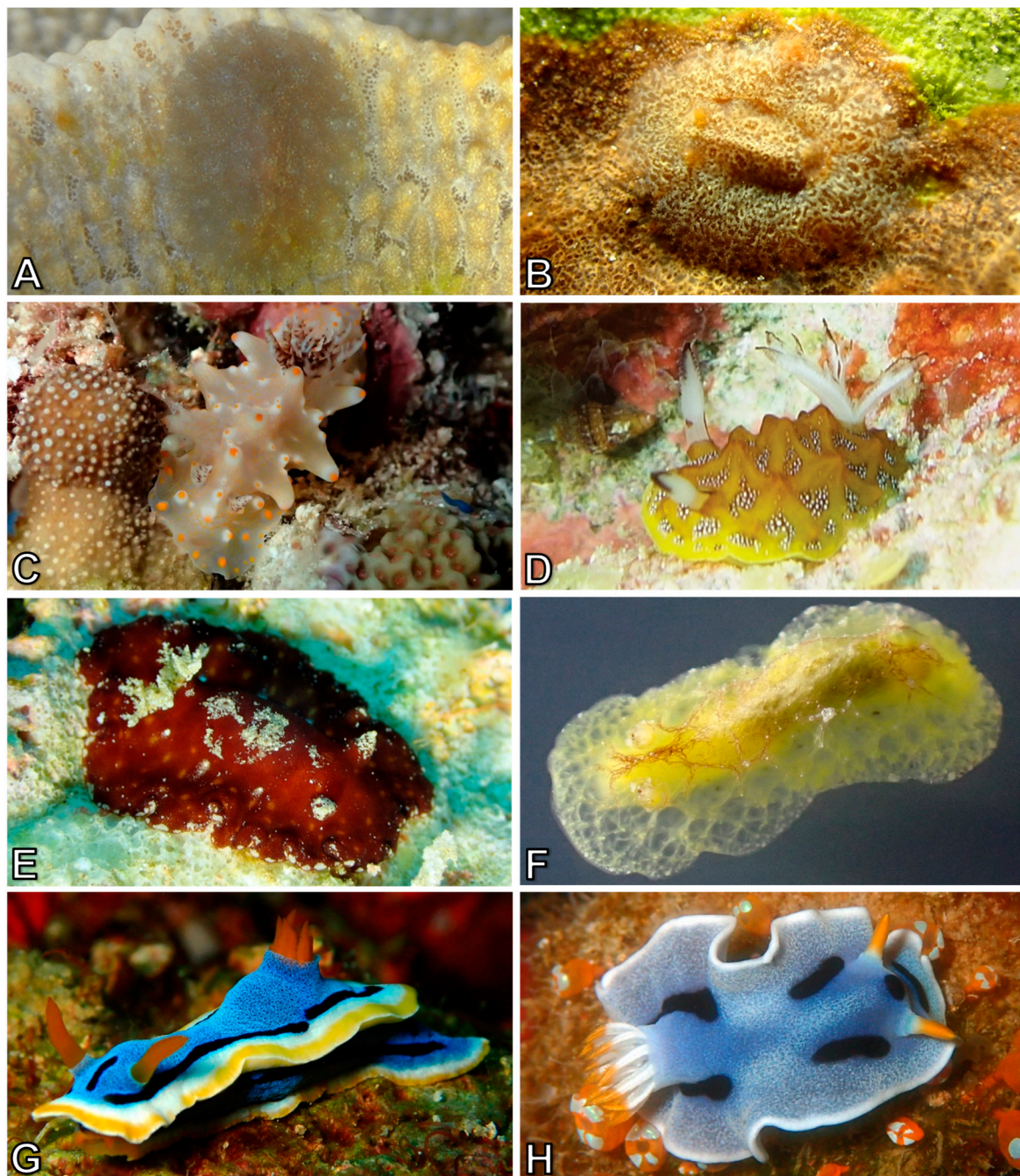


Figure 8. Nudibranchia - Doridina: (A) and (B) *Asteronotus mimeticus*; (C) *Halgerda batangas*; (D) *Halgerda tessellata*; (E) *Platydoris sanguinea*; (F) *Sclerodoris* spec. (*Sclerodoris* sp. 2 in Gosliner et al. [11]: 195), Scsp2_16Bu-1; (G) *Chromodoris annae*; (H) *Chromodoris diana*.

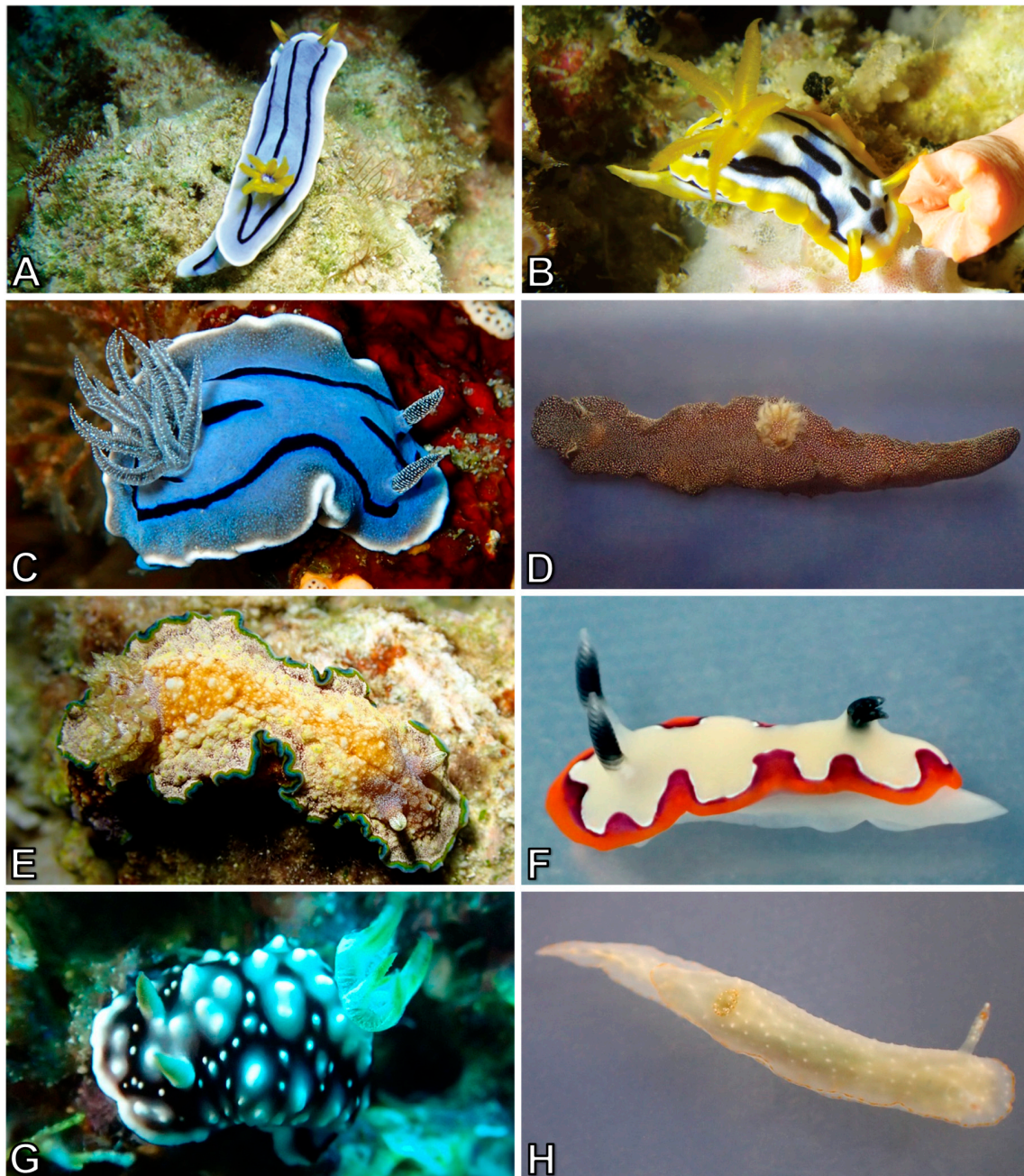


Figure 9. Nudibranchia - Doridina: (A) *Chromodoris lochi*; (B) *Chromodoris* cf. *michaeli*; (C) *Chromodoris willani*; (D) *Doriprismatica stellata*; (E) *Glossodoris cincta*; (F) *Goniobranchus fidelis*; (G) *Goniobranchus geometricus*; (H) *Goniobranchus* spec. (*Goniobranchus* sp. 40 in Gosliner et al. [11]: 230), Gosp40_16Bu-1.



Figure 10. Nudibranchia - Doridina: (A) *Hypselodoris apolegma*; (B) *Hypselodoris maculosa*; (C) *Hypselodoris tryoni*; (D) *Hypselodoris* spec., Hyps16Bu-1; (E) *Hypselodoris* spec., Hyps2_16Bu-1; (F) *Miamira sinuata*; (G) *Thorunna furtiva*; (H) *Dendrodoris nigra*.



Figure 11. Nudibranchia - Doridina and Nudibranchia - Cladobranchia: (A) *Phyllidia coelestis*; (B) *Phyllidia elegans*; (C) *Phyllidia varicosa*; (D) *Phyllidiella* cf. *annulata*; (E) *Phyllidiella pustulosa*; (F) *Phyllidiopsis xishaensis*; (G) *Dermatobranchus diagonalis*; (H) *Dermatobranchus* cf. *kokonas*.

3.1.6. Nudibranchia, Cladobranchia (36 species in 20 genera belonging to 11 families, Figures 12A–16B)

Four different species of *Dermatobranchus* were collected from various localities. Species of this genus often exhibit a rather whitish appearance with very unspecific dots or patches of darker color. Three of our specimens showed this coloration but probably belong to different species. Two of our specimens (Figure 11H) are very similar to *Dermatobranchus kokonas* Gosliner & Fahey, 2011, but have more brownish rhinophores with transparent tips. We tentatively assign our material to this species. *Dermatobranchus piperoides* Gosliner & Fahey, 2011 is distinguished by orange rhinophores with darker tips, but the single specimen we collected lacked the black tips, and assignment to *D. piperoides* is preliminary (Figure 12A). Another specimen (Figure 12B) also looks very similar to *D.*

piperoides in its notum coloration; however, this animal lacks the typical orange color on the rhinophores. This specimen depicted in Figure 12B cannot be assigned to any described *Dermatobranchus* species yet.

Some *Janolus* species differ from the typical habitus of the genus in having densely papillate cerata. We assign our specimen tentatively to the species *Janolus mirabilis* based on the color, the moderately papillate cerata, and a large gap between the anterior and posterior groups of cerata (Figure 12C).

One species of *Crosslandia* was collected from floating *Sargassum* close to Siladen and close to Bunaken (Figure 12D). The few known species are recorded from algae or sea grass beds. *Crosslandia daedali* was recorded previously as living on *Sargassum*, and is described with a similar coloration as that of our eight specimens [33]. These and subsequent records are all from the Pacific coast of America and south Atlantic coast of Brazil; however, there are recent records from areas around Singapore [34] that additionally confirms the presence of this species in the Indo-Pacific.

The genus *Kabeiro* (Dotidae) is usually found on leptothecate hydrozoans. It can be distinguished clearly from similarly looking aeolids (see below) by the presence of rhinophoral sheaths. Several specimens probably belonging to three different species were collected: Two undescribed species and three specimens of *Kabeiro rubroreticulata* (Figure 12F). The species depicted in Figure 12G was collected in several localities in the southern part of Bunaken Island, as well as Siladen Island. The species has characteristic tubercles arranged irregularly on the cerata. Another animal had more inflated cerata with a distinct terminal tubercle and just one row of smaller tubercles subapically around the cerata. This specimen was found in Siladen Island and certainly represents another species of *Kabeiro* (Figure 12H).

Three undescribed species of *Tritonia* were collected in different localities. One specimen similar to *Tritonia* sp. 10 in Gosliner et al. [11] (p. 321) was found on a partly overgrown hydroid colony (Figure 13B); however, *Tritonia* sp. 10 was described from a habitat with many *Xeniid* species. Specimens of a different species (Figure 13C) were observed swimming with a dorso-ventral movement, as mentioned by Gosliner et al. [11] for a very similarly colored animal (*Tritonia* sp. 9, p. 321). This species resembles *Tritonia khaleesi* Silva, Azevedo & Matthews-Cascon, 2014 from the tropical southern Atlantic in having very distinct whitish stripes on the dorsum [35], but our specimens showed a reticulate pattern in-between and underlying the broad white stripes. The third species (Figure 13D), only tentatively assigned to the genus *Tritonia*, was found on sponges.

The *Eubbranchus* species illustrated in Figure 14B was found on similar leptothecate hydrozoans, as were the species of *Kabeiro*. This particular species is possibly the same as *Eubbranchus* sp. 22 of Gosliner et al. [11] (p. 341).

Several undescribed aeolid species match photographs provided in Gosliner et al. [11]: Three species may belong to the genus *Cuthona* (Figure 14C–E), one to *Cratena* (Figure 14G) and three to *Facelina* (Figure 14H, Figure 15A,B). Three undescribed *Noumeaella* species were collected mainly from underneath lamellate sponges. One of them, with orange tips to the rhinophores and propodial tentacles and mottled brownish and orange cerata (Figure 15G) has already been recorded in Kaligis et al. [1]. Two species (Figure 15E,F) are depicted in Gosliner et al. [11] as *Noumeaella* sp. 3 (p. 367) and the much darker *Noumeaella* sp. 12 (p. 367).

Bulbaeolidia alba (Figure 16B) is the only member of the Aeolidiidae in our collections. It can be easily distinguished by the overall white color and the red markings behind the rhinophores.

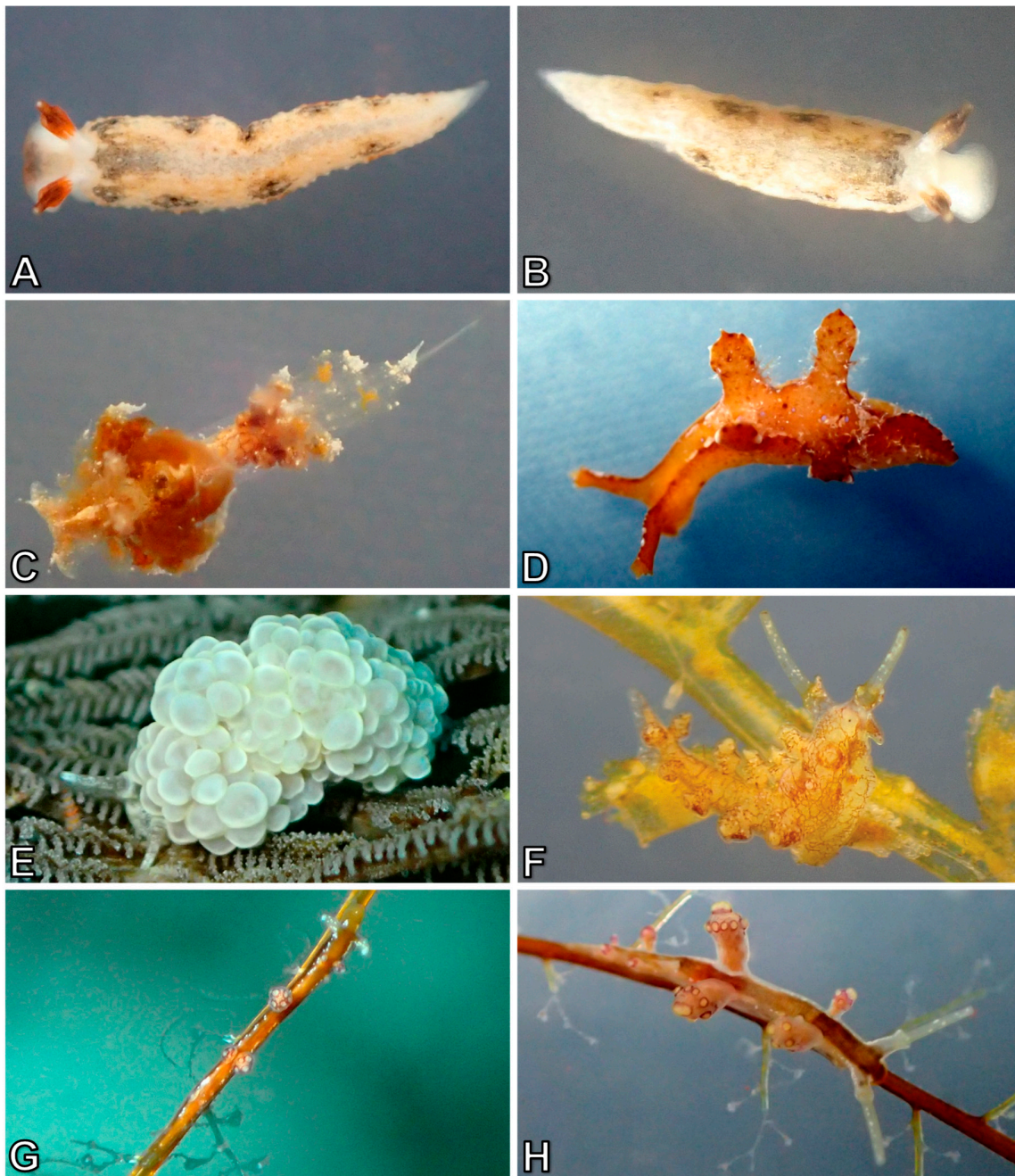


Figure 12. Nudibranchia - Cladobranchia: (A) *Dermatobranchus* cf. *piperoides*; (B) *Dermatobranchus* spec., Desp1_16Bu-1; (C) *Janolus* cf. *mirabilis*; (D) *Crosslandia daedali*; (E) *Doto ussi*; (F) *Kabeiro rubroreticulata*; (G) *Kabeiro* spec.; (H) *Kabeiro* spec., Kasp16Bu-16.



Figure 13. Nudibranchia - Cladobranchia: (A) *Marianina rosea*; (B) *Tritonia* spec. (*Tritonia* sp. 9 in Gosliner et al. [11]: 321), Trsp8_16Bu-1; (C) *Tritonia* spec. (*Tritonia* sp. 10 in Gosliner et al. [11]: 321), Trisp10_16Bu-1; (D) *Tritonia* spec., Trsp16Bu-1; (E) *Coryphellina delicata*; (F) *Coryphellina exoptata*; (G) *Coryphellina rubrolineata*; (H) *Samla bicolor*.

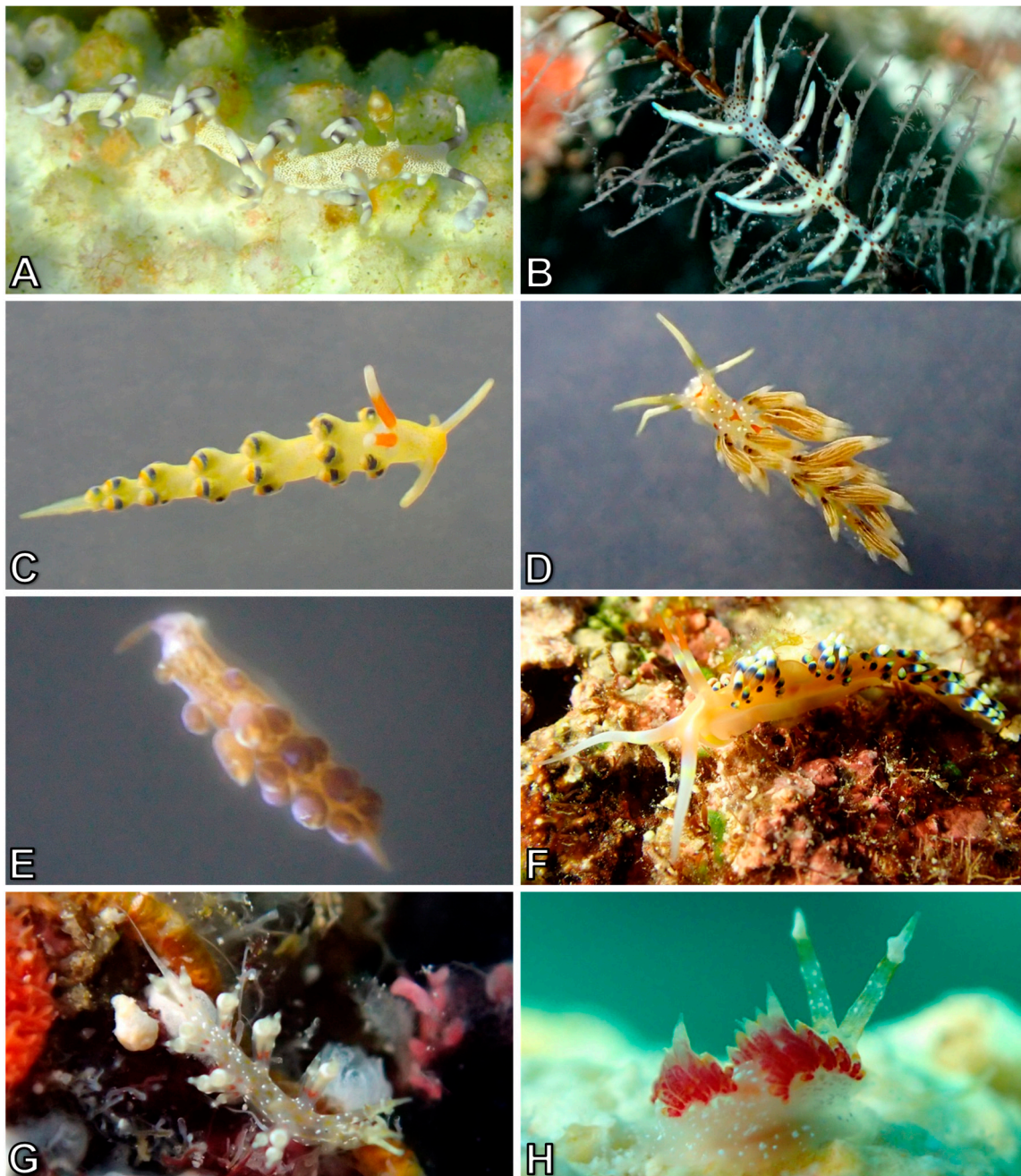


Figure 14. Nudibranchia - Cladobranchia: (A) *Samla riwo*; (B) *Eubranthus* spec. (*Eubranthus* sp. 22 in Gosliner et al. [11]: 341), Eusp22_16Bu-1; (C) *Cuthona* spec. (*Cuthona* sp. 4 in Gosliner et al. [11]: 343), Cusp4_16Bu-1; (D) *Cuthona* spec. (*Cuthona* sp. 54 in Gosliner et al. [11]: 353), Cusp54_16Bu-1; (E) *Cuthona* spec. (*Cuthona* cf. sp. 65 in Gosliner et al. [11]: 343), Cusp65_16Bu-1; (F) *Caloria indica*; (G) *Cratena* spec. (*Cratena* sp. 5 in Gosliner et al. [11]: 383), Crsp5_16Bu-1; (H) *Facelina* spec. (*Facelina* sp. 3 in Gosliner et al. [11]: 359), Fasp3_16Bu-3.



Figure 15. Nudibranchia - Cladobranchia: (A) *Facelina* spec. (*Facelina* sp. 4 in Gosliner et al. [11]: 359), Fasp3_16Bu-2; (B) *Facelina* spec. (*Facelina* sp. 8 in Gosliner et al. [11]: 360), Fasp8_16Bu-1; (C) *Favorinus mirabilis*; (D) *Favorinus tsuruganus*; (E) *Noumeaella* spec. (*Noumeaella* sp. 3 in Gosliner et al. [11]: 367), Nosp13_16Bu-1; (F) *Noumeaella* spec. (*Noumeaella* sp. 12 in Gosliner et al. [11]: 367), Nosp12_16Bu-1; (G) *Noumeaella* spec., Nosp2_16Bu-1; (H) *Phyllodesmium briareum*.

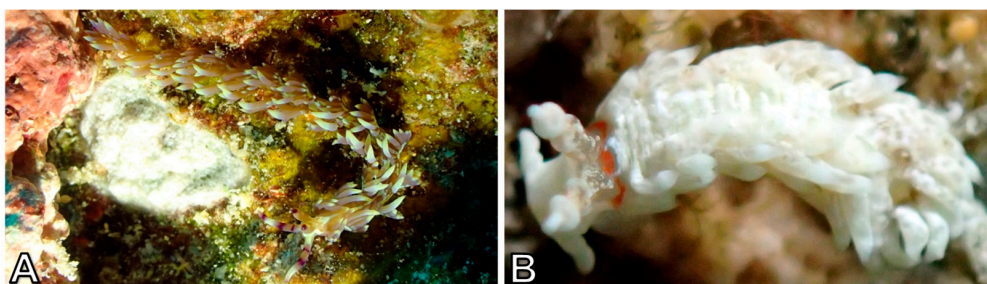


Figure 16. Nudibranchia - Cladobranchia: (A) *Pteraeolidia semperi*; (B) *Bulbaeolidia alba*.

3.2. Species Collected in 2017 (Figures 17–20)

In this section, we discuss the species that were not recorded previously, either in 2015 [1] or above.

3.2.1. Cephalaspidea (six species in five genera belonging to four families, Figure 17A,B)

One cephalaspidean specimen was collected whose assignment even to a genus is difficult. According to the form of the head shield and the posterior body parts, it seems likely that this animal is an undescribed *Philine* (Figure 17A).



Figure 17. Cephalaspidea, Anaspidea and Sacoglossa: (A) *Philine* spec., Ilsp17Bu-1; (B) *Sagaminopteron* spec.; (C) *Dolabella auricularia*; (D) *Dolabrifera dolabrifera*; (E) *Cylindrobulla* spec., Assp1_17Bu-2; (F) *Cyerce* cf. *bourbonica*; (G) *Sohgenia palauensis*; (H) *Costasiella kuroshimae*.

An undescribed *Sagaminopteron* species (Figure 17B) was collected from sponges on Siladen Island. Interestingly, the same species with same coloration was already photo-documented in 2016 from the same area, and it may be limited to a particular prey species found only at this locality. The species is similar to *Sagaminopteron bilealbum* Carlson & Hoff, 1973 with an overall white coloration and orange tips of the cephalic tentacles, but lacks the numerous orange dots, with only a few present along the rim of the parapodia. *Sagaminopteron nigropunctatum* is also similar to our specimen; however, this

species is usually characterised by a covering of tiny black dots. We cannot exclude that this small animal with a size of only 4 mm is a juvenile of a described species.

3.2.2. Anaspidea (four species in four genera belonging to one family, Figure 17C,D)

Collecting in the intertidal reef flats and upper sublittoral of the seagrass beds revealed two of the typical species for this area, *Dolabella auricularia* (Figure 17C) and *Dolabrifera dolabrifera* (Figure 17D). Although these species are large, they were not recorded in the previous years.

3.2.3. Sacoglossa (11 species in seven genera belonging to four families, Figures 17E–18C)

Sieving sand containing sea grass roots and rhizomes revealed a tiny *Cylindrobulla* species with a shell length of 10 mm (Figure 17E). The cephalic shield was as long as the shell but could be retracted almost completely into the shell.

Several *Cyerce* specimens were found during this expedition in front of Panorama (see Table 2), tentatively assigned to *Cyerce* cf. *bourbonica* (Figure 17F). This species was also recorded in Kaligis et al. [1] from further places around Bunaken Island.

Costasiella kuroshimae (Figure 17 H), as well as an undescribed *Costasiella* species (Figure 18A) (as *Costasiella* sp. 8 [11] (p. 81)), was collected from the chlorophyte alga *Avrainvillea*. *Costasiella* sp. 8 is characterised by the black spots at the base of the rhinophores, whereas *C. kuroshimae* has black rhinophoral tips. One undescribed species with a typical black band behind the eyes and with a medium white spot in this band (Figure 18B) was collected from *Flabellia* and is depicted in Gosliner et al. [11] as *Costasiella* sp. 1 (p. 79).

Plakobranthus ocellatus is a species complex, shown by Yonow and Jensen [17] and Meyers-Muñoz et al. [36]; the latter described a new *Plakobranthus* species from Indonesia that does not have ocellated spots but uniformly colored dots. Our specimen (Figure 18C) resembles best the variety they called *P. ocellata* variation F and *Plakobranthus* sp. 3 in Gosliner et al. [11] (p. 99) with large dark rings at the sides of the body and along the front of the head, filled with greenish to reddish color. It differs from the originally described specimen by van Hasselt (see Yonow and Jensen, Meyers-Muñoz et al. [17,36], which has smaller ringed dots next to the large rings, each with a dark center, on the parapodia. Our animal also had smaller rings on the parapodia, but these were darker in color with light-colored centers.

3.2.4. Pleurobranchomorpha (one species in one genus belonging to one family, Figure 18D)

One specimen was collected under coral rubble that most resembles *Berthellina citrina* (Figure 18D). Other species can have white markings or dots on the notum, which are missing in our specimen.

3.2.5. Nudibranchia, Anthobranchia (24 species in 16 genera belonging to seven families, Figures 18E–20B)

Two specimens of a *Gymnodoris* (Figure 18E) were collected in the coral rubble in front of Panorama. Both animals looked like *Gymnodoris* sp. 46 [11] (p. 161), except for the frontal margin of the velum, which was not orange in our animal.

Two small reddish dorids, mimicking sponge surfaces (Figure 18F,G), were found in coral rubble. No assignment to any genus is possible for these two specimens until further morphological and molecular analyses.

A small dark brown dorid with white tips of the rhinophores and white gills was found in the seagrass beds in front of Panorama resort (Figure 19A). It also showed white tips of the tubercles surrounding the rhinophores, and is very similar to *Discodorid* sp. of Yonow [14] (p. 154, Figure 15B); the same color pattern is illustrated for an undescribed *Diaulula* sp. 1 [11] (p. 197). This animal is probably associated with sponges living between the sea grass rhizomes.

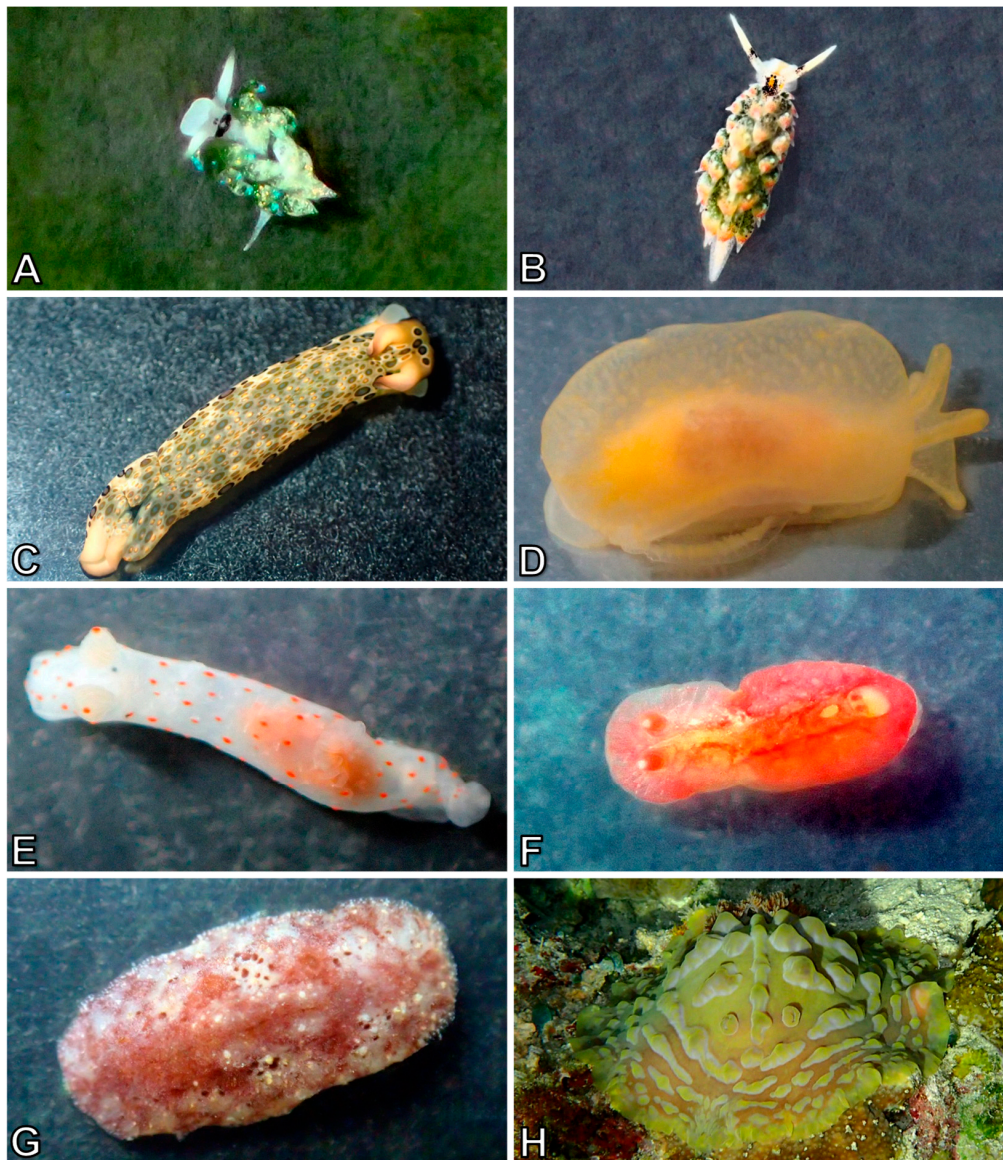


Figure 18. Sacoglossa, Pleurobranchomorpha and Nudibranchia - Doridina: (A) *Costasiella* spec. (*Costasiella* sp. 8 in Gosliner et al. [11]: 81), Cosp8_17Bu-1; (B) *Costasiella* spec. (*Costasiella* sp. 1 in Gosliner et al. [11]: 79), Cosp1_17Bu-1; (C) *Plakobranchus ocellatus*; (D) *Berthellina citrina*; (E) *Gymnodoris* spec. (*Gymnodoris* cf. sp. 46 in Gosliner et al. [11]: 161), Gysp22_17Bu-1; (F) Doridoidea spec., Dosp17Bu-3; (G) Doridoidea spec., Scsp1_17Bu-1; (H) *Asteronotus cespitosus*.

Two specimens (Figure 19C,D) were collected which are simply assigned to the family Discodorididae pending further work. None of these species was illustrated in Tonožuka [37] covering Indonesian nudibranchs, or Yonow [14] describing dorids from Ambon or in Gosliner et al. [11].

A small white animal (Figure 19G) collected from a sponge on Siladen Island is similar to several *Verconia* species, especially *Verconia decussata* (Risbec, 1928) and *Verconia simplex* (Pease, 1871) (see Yonow [38] for generic placement discussion). However, our animal differed in the color pattern from all of these, by only exhibiting red rhinophores without any other red areas. This animal is small (4 mm) and might be a juvenile; therefore, assignment to any species is difficult.

Dendrodoris nigra and *Dendrodoris fumata* are known to exhibit a range of color patterns and to undergo ontogenetic color changes. Juvenile *D. nigra* usually have white dots irregularly distributed over the notum and are often pink to orange; however, the gills are numerous, 9–11, issuing from a small pocket. One of our specimens resembled the color of a juvenile *D. nigra*, but had only five gills.

Furthermore, the texture appeared more rigid, and not soft as in typical *Dendrodoris*. We therefore do not assign this rather small specimen to a species (Figure 19H).

At a depth of approximately 25 m within a cave, a specimen of a new species of Phyllidiidae (Figure 20A,B) was found that completely lacks tubercles, thus resembling a species of *Phyllidiopsis*; however, the oral tentacles are not fused, which indicate it belongs to the genera *Phyllidia* or *Phyllidiella*. The coloration is also very distinctive, but this animal was not recorded from any other site and was only found once. An interesting note is that the area where this animal was found was visited several times and searched during both night and day dives, but revealed no more specimens. We tentatively assign this specimen to the genus *Phyllidia*.

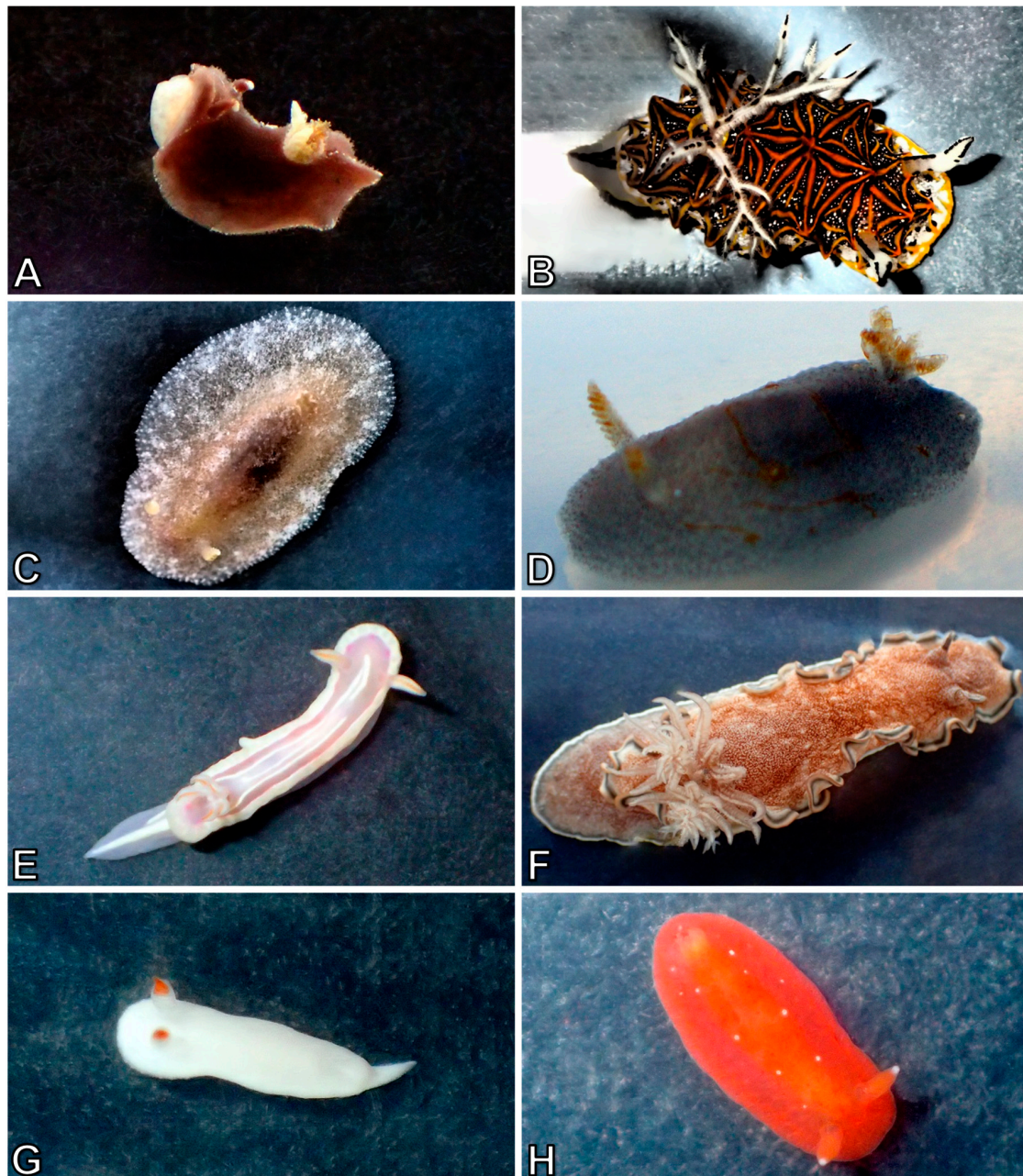


Figure 19. Nudibranchia - Doridina: (A) *Diaulula* spec. (*Diaulula* sp. 1 in Gosliner et al. [11]: 197), Disp1_Bu-1; (B) *Halgerda* cf. *tessellata*; (C) Discodorididae spec., Dosp17Bu-1; (D) Discodorididae spec., Dosp17Bu-2; (E) *Ceratosoma* spec. (*Ceratosoma* sp. 1 in Gosliner et al. [11]: 266), Cesp1_17Bu-1; (F) *Glossodoris hikuensis*; (G) *Verconia* spec., Dosp17Bu-4; (H) *Dendrodoris* spec., Rosp17Bu-1.

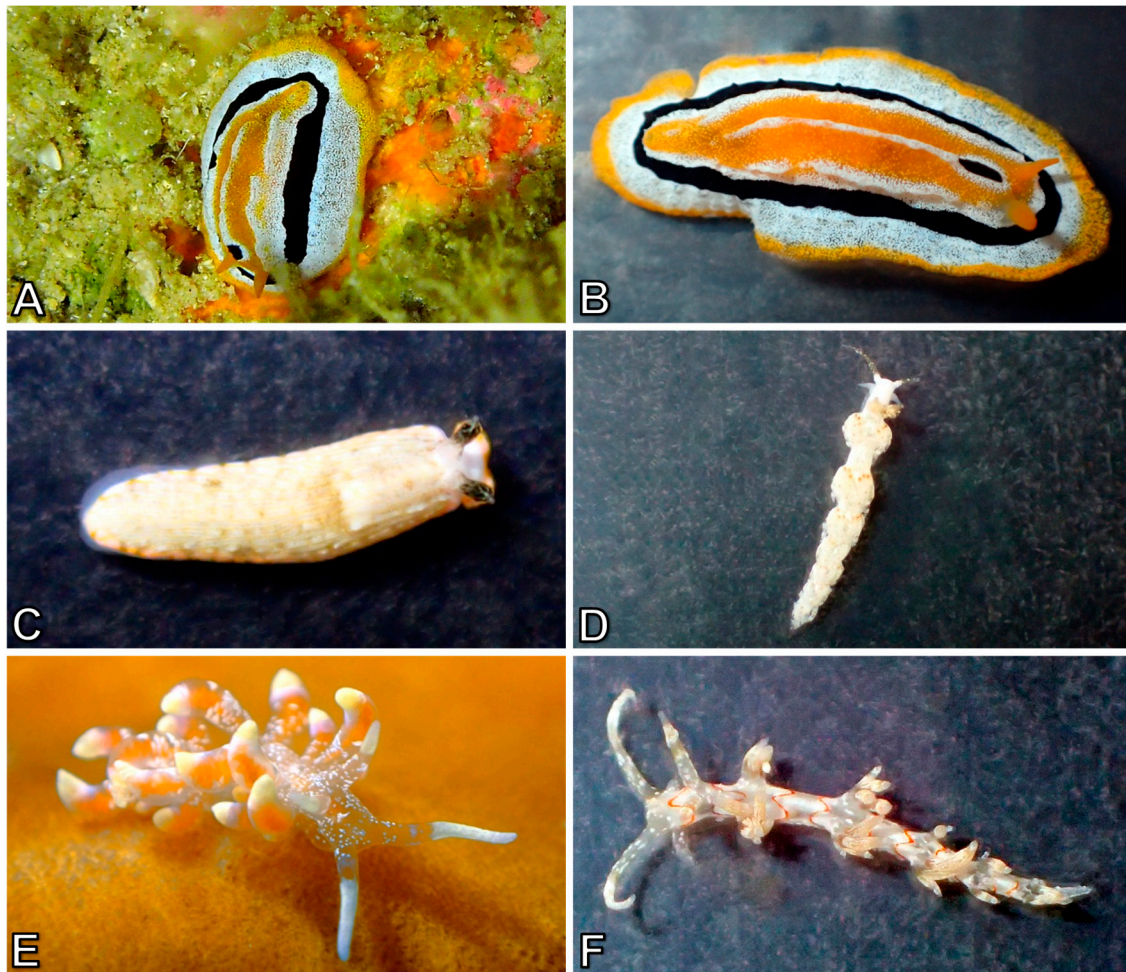


Figure 20. Nudibranchia - Doridina, Nudibranchia - Cladobranchia: (A, B) *Phyllidia* spec., Phsp17Bu-1; (C) *Dermatobranchus* spec. (*Dermatobranchus* sp. 8 in Gosliner et al. [11]: 302), Desp8_17Bu-1; (D) *Noumeaella* spec. (*Noumeaella* cf. sp. 6 in Gosliner et al. [11]: 368), Nosp6_17Bu-1; (E) *Phyllodesmium poindimiei*; (F) Facelinidae spec., Fasp17Bu-1.

3.2.6. Nudibranchia, Cladobranchia (11 species in nine genera belonging to five families, Figure 20C–F)

One *Dermatobranchus* species collected in Siladen was cream white with longitudinal lines, and the rim of the oral veil and foot in orange (Figure 20C). There are several creamy white *Dermatobranchus* species with longitudinal lines and darker dots in-between with similarly black rhinophores. *Dermatobranchus* sp. 8 depicted in Gosliner et al. [11] (p. 302) appears closest to our animal but lacks the orange foot rim. The rhinophores and orange margins are very similar to those in *D. albus*, which lacks the dark spots present in our species.

In 2015 several new *Noumeaella* species were collected, mainly from sponges, but also in-between *Caulerpa racemosa* [1]. One new *Noumeaella* species was observed for the first time in BNP living underneath foliaceous sponges (Figure 20D). The two collected specimens had the characteristic cream color with a distinct dark spot at the base of each ceras. Gosliner et al. [11] (p. 368) illustrate a similarly colored form from Indonesia.

A small facelinid species was collected by divers from a locality in the south of Bunaken, which has a very distinct color pattern with orange undulating lines running across the body (Figure 20F). The animal is whitish to transparent with many opaque white patches and dots of various sizes covering all parts of the body, including all tentacles.

3.3. A Comparison of the Bunaken NP Studies

In the following section, we compare the three years' collections from 2015 [1] to 2017 with the previous study of Burghardt et al. [3] based on a collection in 2003. We also try to re-identify the unidentified animals of this earlier study in light of further collections and recent documentation. In this study [3] 86 species are listed, 32 of which were not found again in the recent collections (Figure 21A). Many species are only listed as undescribed species, and therefore at least 11 species are difficult to compare with our recent material due to lack of photo-documentation. They are not included in the species accumulation curve in Figure 21B.

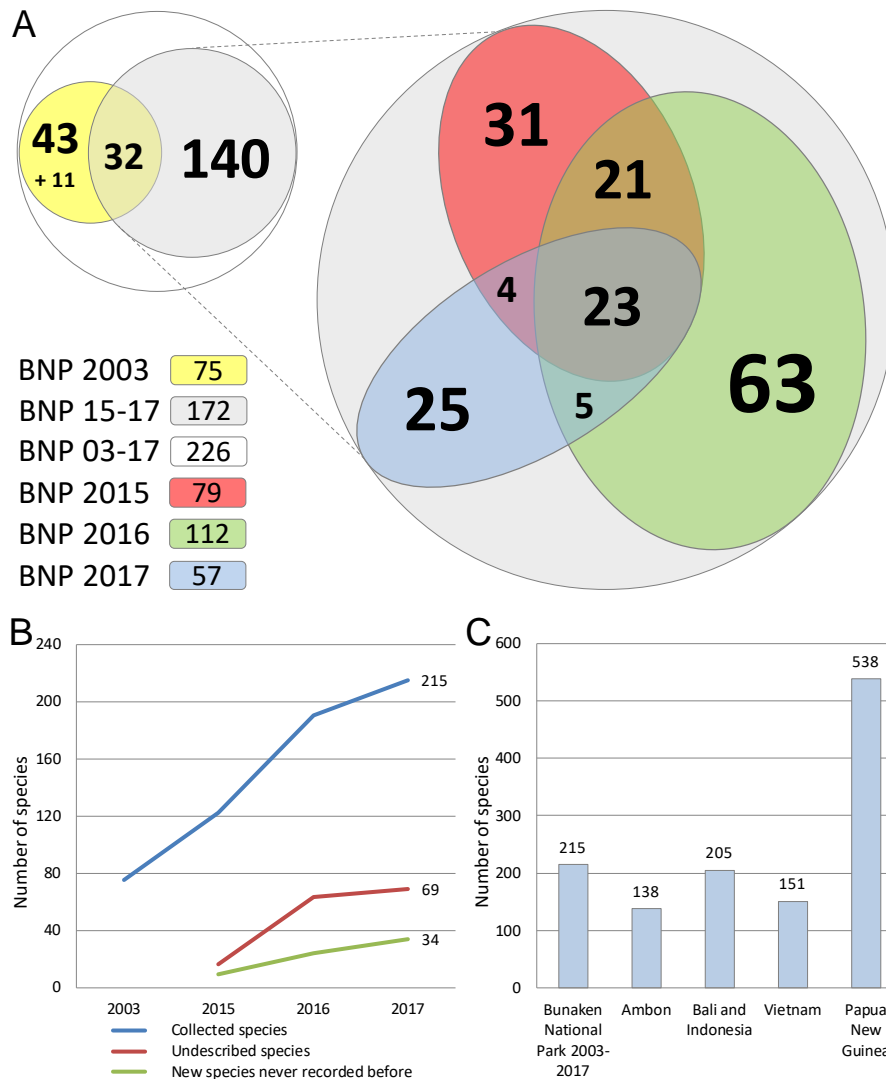


Figure 21. Summary of species numbers and overview in Bunaken National Park (BNP): (A) Comparison of collection efforts of the years 2003 with 2015, 2016, and 2017. (B) Species accumulation curves of overall species numbers (blue line), of undescribed species (red line), and of species that are not documented in literature or identification books, thus representing at-the-moment-unique species of BNP, North Sulawesi (green line). The species number for the collection event 2003 does not contain the 11 species that could not be reassessed. (C) Comparison of species numbers from geographic areas close by North Sulawesi. Data based on BNP: Kaligis et al. [1], Burghardt et al. [3], and this study; Ambon [12–14,17]; Indonesia with emphasis on Bali [37]; Vietnam [16]; and Papua New Guinea [39].

Liloa mongii (listed as *Haminoea curta* in Burghardt et al. [3]) and *Limulatys* species are tiny cephalaspideans living in silty habitats. Our recent studies did not cover any silty areas, which might be the reason this species was not collected again. No figures were provided of the other haminoeid species, and therefore no comparison with our recently sampled undescribed *Haminoea* species is possible.

Phanerophthalmus cf. *smaragdinus* (Rüppell and Leuckart, 1830), now accepted as *Phanerophthalmus olivaceus* (Ehrenberg, 1828) and depicted in Figure 23 of Burghardt et al. [3], is similar to an animal we collected in 2016. We tentatively identify our specimen as *P.* cf. *albocollaris* as well as the animal depicted in Burghardt et al. [3] (Figure 23).

Burghardt et al. [3] (Figure 25) illustrated a specimen as *Phyllaplysia* sp. 1. Despite searching through seagrasses, where this genus is often found, we were not able to find another specimen of this or any other species of the genus again.

One *Cyerce* specimen documented in Burghardt et al. [3] (Figure 28) as *Cyerce* sp. 1 is very similar to the specimens we found during our current expeditions in various sites around BNP (see Table 2). They are all tentatively assigned to *Cyerce* cf. *bourbonica* (Figure 17F). *Cyerce elegans* Bergh, 1870 (see in Burghardt et al. [3] (Figure 29), Gosliner et al. [11], and Yonow and Jensen [17]) is characterised by its transparency and pale body color; it was not collected again.

Thuridilla bayeri and *Thuridilla gracilis* were mentioned by Burghardt et al. [3] as separate species, but photographs were not provided. The subsequent synonymy of *T. bayeri* Er. Marcus, 1965 with *T. gracilis* and *Thuridilla ratna* Er. Marcus, 1965 has been teased out by Yonow and Jensen [17] who advocate individual descriptions until the precise identities of this complex are firmly established. Burghardt et al. [3] also collected an undescribed *Thuridilla* species, but did not provide any photo-documentation of this animal. We did not find any unusual or undescribed *Thuridilla* species in our recent collections.

Burghardt et al. [3] listed *Pleurobranchus peronii* Cuvier, 1804 as well as an unidentified *Pleurobranchus* species. *P. peronii* may be mistaken for *Pleurobranchus forskalii*, which is the only *Pleurobranchus* species we recollected several times. The compound tubercles and a more heterogeneous coloration are typical for *P. forskalii*, in addition to the distinctive white markings, whereas *P. peronii* only has single tubercles and is more uniformly colored, be it in many shades of brown, orange, or red. Both species can show a wide variety of colors and patterns, especially the juveniles.

Burghardt et al. [3] listed two *Gymnodoris* species, *Gymnodoris citrina* Bergh, 1877, and an unidentified animal; neither is illustrated. *Gymnodoris* species are notoriously difficult to identify because of extensive color variations which are similar between species; there has been no review of this group. We were unable to assign any of the recently collected specimens to *G. citrina*.

Burghardt et al. [3] mentioned the dorid *Tambja morosa* Bergh, 1877, which usually inhabits steep slopes and drop-offs, as present on the southern coastline of Bunaken Island. It feeds on arborescent bryozoans, which have also been observed in BNP, but this species was not collected again in our recent survey. Interestingly, all recently recorded Polyceridae species ([1], this study) were low in specimen numbers, even supposedly common ones such as *Nembrotha kubaryana* and *Nembrotha cristata* (e.g., [13]).

Goniobranchnus decorus (Pease, 1860) (as *Chromodoris decora* in Burghardt et al. [3]) shows similar color patterns to some species of *Thorunna* and *Hypselodoris*. Usually they can be found under and among coral rubble as in this study, e.g., *Hypselodoris maculosa* and *Thorunna furtiva*. Rudman [40] discussed the *Chromodoris decora* color group, including at least 14 similarly colored species belonging to the above-named genera. While *G. decorus* is nominally a common species and appears to have somewhat variable color patterns, it is recognisable, but was not found again in studies subsequent to the collecting period in 2003 [3].

The same problem is observed for *Goniobranchus tinctorius* (Rüppell and Leuckart, 1830) (listed as *Chromodoris tinctoria* in Burghardt et al. [3], but not depicted), which is very similar in color pattern to *Goniobranchus reticulatus* (recorded in Kaligis et al. [1]) and *Chromodoris inopinata* Bergh, 1905. Yonow [13] has shown that the two species are distinct, although Rudman [41] had previously considered *C. reticulata* and *C. inopinata* as synonymous. Collections from the nearby island of Ambon included red-reticulated specimens that were clearly identified as *Chromodoris inopinata* [13]. Several *Goniobranchus* species with reticulate red pattern on a white background are depicted in Gosliner et al. [11].

Burghardt et al. [3] listed *Verconia varians* (Pease, 1871) (as *Noumea varians*) without including a picture. We also found a species of *Verconia*, but our animal is not *Verconia varians*, which is very distinct in body form and coloration; therefore *V. varians* is recorded only from the collection in 2003 [3].

Dendrodoris is a genus with members living in shallow water with a high variety in color morphs and similar color patterns. Burghardt et al. [3] recorded (but not illustrated) *Dendrodoris elongata*; we recently found only *Dendrodoris albobrunnea* [1], which is very similar to *D. elongata*. The differences were discussed in Yonow and Jensen [17].

Burghardt et al. [3] listed *Phyllidiella nigra* (van Hasselt, 1824), which is very similar to *P. pustulosa*, but can be differentiated upon close examination (e.g., Yonow [13] pp. 937–938). In our recent collections, *P. pustulosa* dominated in specimen numbers, and none of the recent specimens could be assigned to *P. nigra*. Identification of these species is difficult [15], and molecular analyses are warranted for future studies.

Burghardt et al. [2] (Figure 38) erroneously identified *Phyllidiopsis xishaensis* as *Phyllidiopsis striata* (Bergh, 1889); *P. xishaensis* was found again in 2016 (Figure 11F); it has been recorded in Indonesia previously [15]. *Bornella stellifera* (A. Adams & Reeve [in A. Adams], 1848) and *Embletonia gracilis* Risbec, 1928 [3] (Figure 42) were collected in 2003, but not again between 2015 [1] and 2017. Both taxa are rather large species, with lengths up to 30 mm, that live in shallow water under coral rubble and feed on hydrozoans.

Two *Janolus* species are figured in Burghardt et al. [3] (Figures 40 and 41). *Janolus mirabilis*, which is characterised by the white pattern and the distinct gap between anterior and posterior cerata, was recollected (this study, Figure 12C). The other *Janolus* species (as *Janolus* sp. 1 in Burghardt et al. [3], Figure 41) resembles *Janolus mirabilis* (both were of similar size of 6 mm). We found a third form that differs from both *J. mirabilis* and *J. sp. 1* of the 2003 collection [3], exhibiting much denser cerata with more acute papillae.

Phyllodesmium jakobsenae Burghardt and Wägele, 2004 (see Burghardt et al. [3]: Figure 44) is a typical xeniid feeder that was first described from the southern shorelines of Bunaken Island in shallow water, resulting from the 2003 collecting period [3,42]. Although Xeniididae are still present in this area, this species was not found again in the recent sampling periods despite extended snorkelling in this area.

Burghardt et al. [3] (Figure 45) illustrated an undescribed *Phyllodesmium* species that was subsequently described as *Phyllodesmium rudmani* by Burghardt and Gosliner (2006) [43]. We were not able to find this species either in the recent expeditions to BNP.

Phestilla species are closely associated with hard corals, such as *Porites* and *Goniopora*, and are easily overlooked despite large sizes of up to 60 mm. However, a thorough search of these corals, especially in the southern shorelines of Bunaken Island, did not reveal either of the two recorded species in Burghardt et al. [3], *P. lugubris* (Bergh, 1870), and *P. minor* Rudman, 1981.

Pseudovermis and *Acochliidiomorpha* are interstitial forms rarely recorded, unless specifically sampled for. Their absence in the recent sediment collections from the sea grass area might be attributed to the rough sieving, which destroys delicate animals more quickly than the shelled ones, or to not sampling the appropriate sediment habitats.

4. Discussion

Setiawan et al. [7] described declining conditions of reef fish and coral cover within BNP compared to 2006 and 2007, and related this to an increased number of local and foreign visitors, in addition to an increased number of permanent residents. Towoliu [44] identified diving and snorkelling activities as a major source of the decline in living coral coverage by comparing different sites around Bunaken Island. Whereas undisturbed areas had a live coral coverage of nearly 55% in 3 m depths, areas with snorkelers and divers showed coverage of only 17% coral cover at this depth. Although BNP is protected under regulations within the Regional Spatial Development Plan formed in 1990s, the existing tourist area was already twice the size in 2015 of the originally proposed area [45]. Despite the lack of wastewater management, investigation into water pollution did not yet show a decreased water quality around Bunaken Island [46]. Local people benefit from tourism and increase their income [47]; nevertheless, without regulations, these benefits will only be short-term, and allowing development beyond prescribed regulations is short-sighted. With an increase in diving tourism in the whole of the BNP [48] and an increase in general anthropogenic influences by locals [49] and tourists, demands on management strategies for dive sites are paramount within BNP. Only monitoring programs on characteristic and economically important but diverse taxa can provide the necessary data to recognise damages and threats to specific habitats, and will allow taking counteractions, preventative measures, or providing alternatives to a future sustainable use and maintenance of this unique region. A number of studies exist in which marine heterobranchs have been used as indicators for anthropogenic influences, such as the study on cadmium levels in the Mediterranean Sea [50] or the molluscan algal epifauna as a measure of habitat quality along the coast of Spain [51]. Another study shows that *Retusa obtusa* dominated in the most enclosed stations inside a harbor where sediments contained very high values of organic matter, lipids, and heavy metals, and thus could serve as a harbor sediment indicator in conjunction with three bivalves [52]. Shifts in nudibranch species composition has been used as an indicator for climate change in Australian waters [53]. Thus, surveying such a diverse group, which relies heavily on a healthy diverse habitat, including the water column for their larval distribution, and the adults with a high affiliation to specific prey items, will certainly provide information about environmental changes when properly monitored. With this study, including already published information from the same region, we create the baseline for monitoring habitats around the BNP in the future.

The total species number of marine heterobranchs in Bunaken National Park, North Sulawesi, attains 226 species, when including the 11 uncertainties in species re-identification of Burghardt et al. [3] (Figure 21A). The groups that were absent in our most recent collections, the Acochlidiiomorpha, Hedylopsidae, and Thecosomata increase the overall number of species. However, photo-documentation of non-collected species is not included in this number. The Venn diagram presented in Figure 21A shows the overlap of species in the three recent studies compared to the previous study in 2006 [3]; only 32 species of 215 species were collected twice. Of the 172 species recorded in the most recent three studies, only 23 species were common to all three. Pairwise comparison revealed an overlap of 44 species between 2015 [1] and 2016, 27 species between 2015 [1] and 2017, and 28 species between 2016 and 2017.

The present study revealed that out of the 69 undescribed species, representing 30% of the recorded species from BNP, 34 species have not been listed in diversity or taxonomic studies before, and they are presented here for the very first time (Figure 21B). The richness of this particular study area, also when comparing overall species diversity to other studies in Indonesia or other areas nearby [1,2] may be an indication that protection of a small area with a very diverse habitat structure is successful and worthwhile (Figure 21C).

The high species number found only once in all four surveys (162 species: Figure 21A) also suggests that the small area is worth protecting. While many marine heterobranchs, and especially nudibranchs, are ephemeral, the occurrence of even one specimen in a habitat presumes a richness of other marine invertebrate species, since many are species-specific with regards to food items. It also

indicates that species diversity is not fully documented and still needs more sampling. The number of confirmed heterobranch species from BNP is higher than in the geographically close area of Ambon (summarised from [12–14,17]), but similar to the general study from Indonesia and Bali [37] (Figure 21C). While interesting, and providing a good base for future studies, the reader must bear in mind that collecting time, effort, and sampled habitats varied in all the studies compared here; thus, direct comparisons are clearly not possible.

Looking at species abundance, one of the most commonly recorded species is *Phyllidiella pustulosa* (nearly 60), three *Chromodoris* species, *C. annae* (>80), *C. diana* (>70), and *C. willani* (40), as well as *Phyllodesmium briareum* (about 60), where most of the species were collected from a large *Briareum* colony (see also Table 2). Pungus et al. [54] began a survey on nudibranchs in Lembeh Strait, North Sulawesi, counting the most common species in a certain area. They also documented *P. pustulosa* and *C. annae* as the most frequently recorded species in that area. However, other species mentioned in their study, such as *Tambja gabriellae*, were not found in BNP. Aunurohim et al. [55] and Sari and Aunurohim [56] recorded a similar species composition with *C. annae* and *P. pustulosa* as the most dominant nudibranchs in Situbondo, East Java, and Phyllidiidae the dominant nudibranch family. The recently completed studies on the marine heterobranchs from Ambon [12–14,17] revealed *Dendrodoris fumata* as the most commonly recorded species, followed by *Phyllidiella pustulosa*, *Chromodoris magnifica*, and *Phyllidia varicosa*. Species composition and diversity of these enigmatic marine heterobranchs certainly differ in these regions of Indonesia; however, more studies are needed to understand influence of habitat structures caused by geological origins, currents, availability of food (and many others), as well as the influence of a changing environment (seasonal or long term). Another factor that hinders an accurate comparison at the moment is certainly the differences in collection efforts, experience of collectors, and habitat selection of the researchers. We therefore can merely describe the differences between the four study periods, without providing reasons.

Eight species were collected in 2003 [3], but not again in 2015 [1] to 2017. These comprise taxa from various habitats: *Cyerce elegans* from algal communities, *Phyllodesmium jakobsenae* from reef flats feeding on *Xenia* species, *Verconia varians* feeding on sponges, *Tambja morosa* from coral structures feeding on bryozoans, *Embletonia gracilis* and *Bornella stellifera* from coral structures feeding on hydrozoans, and finally the two *Phestilla* species, *P. lugubris* and *P. minor*, closely associated with certain hexacoral species and feeding on them. However, there is one example that might indicate a shift or deterioration of the habitat: *Phyllodesmium jakobsenae* was collected by snorkelling from xeniid colonies in the inter-reefal area in southern Bunaken Island, close to an area with several resorts, a small market, and a jetty. The type locality of this species faces a high increase in tourist numbers and boat traffic, including the building of a new resort as well as renovating an older one in the last five years. This high disturbance of the habitat may have contributed to the absence of *P. jakobsenae* from the recent collections, despite a particular search for this species. To address the increase of direct anthropogenic activities as one factor of species extinction, future collecting and monitoring of this area is desperately needed, clearly shown by studies on other metazoan taxa or organisms [7,44].

Based on the overall results from this special area, we consider the number of 215 species (plus another 11 uncertainties) a good baseline for future monitoring projects, and this baseline will help in understanding shifts of species composition, irrespective of causation factors. Our results also indicate that the diversity of marine heterobranchs is high in BNP, compared to the other results published on Indonesia [12–14,17,37]. Studies from Papua New Guinea [39] and the Philippine Islands [11], which were based on many more collection events and collecting times, indicate with much higher species numbers, what can be expected in the long run. Ongoing studies in nearby areas (Bangka Archipelago, Lembeh Strait, and Sangihe Island) will also help to better understand the richness in this hotspot of species diversity, as well as will help to understand differences in habitat structures resulting in a different species composition of these areas.

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